

Phagotrophy and development of *Paulsenella* cf. *chaetoceratis* (Dinophyta), an ectoparasite of the diatom *Streptotheca thamesis**

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ABSTRACT: Zoospores of the dinophyte *Paulsenella* cf. *chaetoceratis*, parasitizing the marine diatom *Streptotheca thamesis*, attach to the girdle region of the host and drive a peduncle into the cell interior. The peduncle consists of a non-cytoplasmic "crook", a cytoplasmic feeding tube, and a presumably cellulosic sheath around the proximal part of the feeding tube. The crook seems to be used for attachment and penetration of the host. The mobile feeding tube induces shrinkage of the host vacuoles and takes up the complete host cytoplasm within less than 1 h. Phagocytosis depends on an intact host plasmalemma, which is not penetrated by the feeding tube. The trophic phase ends with retraction of the feeding tube. While the food is digested within a large vacuole, the trophont transforms into a thick-walled primary cyst. After about 12 h the primary cyst divides to form 3 or 4 secondary cysts. Finally, about 24 h after attacking the host, each secondary cyst releases two zoospores which may be again ready for infection within 1 h, without passing through any intermediate stage. The developmental times (above referred to 20 °C) are highly dependent on the temperature and can vary considerably, even between sister cells.

INTRODUCTION

Among the biotic factors influencing the productivity and population dynamics of phytoplankton, parasites may play an important role. However, until now they have been paid little attention. A main reason is that routine phytoplankton studies are made on preserved material, i. e. on killed species which are more or less damaged. Thus, recognition and identification of parasitic stages are difficult and sometimes even impossible. Direct observations on living material freshly collected from the sea and combined with culture experiments are the only suitable means for successful studies. Due to own annual studies on plankton catches, eukaryotic plant parasites, being able to attack phytoplankton species, mostly belong to the lower fungi (phycomycetes), dinophytes, and flagellates of unknown taxonomic position.

The present communication deals with an ectoparasitic dinophyte, which preys on the marine planktonic diatom, *Streptotheca thamesis* Shrubsole. The parasite highly resembles *Paulsenella chaetoceratis* (Paulsen) Chatton, which was first described by Paulsen (1911) and with some doubt initially named *Apodinium* (?) *chaetoceratis*. The

* Dedicated to Dr. Dr. h. c. P. Kornmann on his 75th birthday.

epitheton indicates the hosts, *Chaetoceros borealis* and *C. decipiens*, and the type locality is coastal waters of eastern Greenland. Later, Chatton (1920) transferred this species into a new genus, *Paulsenella*.

P. chaetoceratis is regularly present in the North Sea (Drebes, 1974), and a further new record for the Gulf of Guinea is given by Aleem (1979). Since Drebes (1974) also observed this or similar species feeding on other diatoms like *Streptotheca thamesis*, *Eucampia zodiacus*, and *Cerataulina bergonii*, it remains to be investigated whether each diatom species has its host-specific parasite. Own experiments have shown that a *Paulsenella* strain, which grows on *Streptotheca thamesis*, was unable to attack *Eucampia zodiacus*. Preliminary observations on other host-parasite combinations likewise indicate a high host specificity of the *Paulsenella* parasite (Drebes, unpubl.).

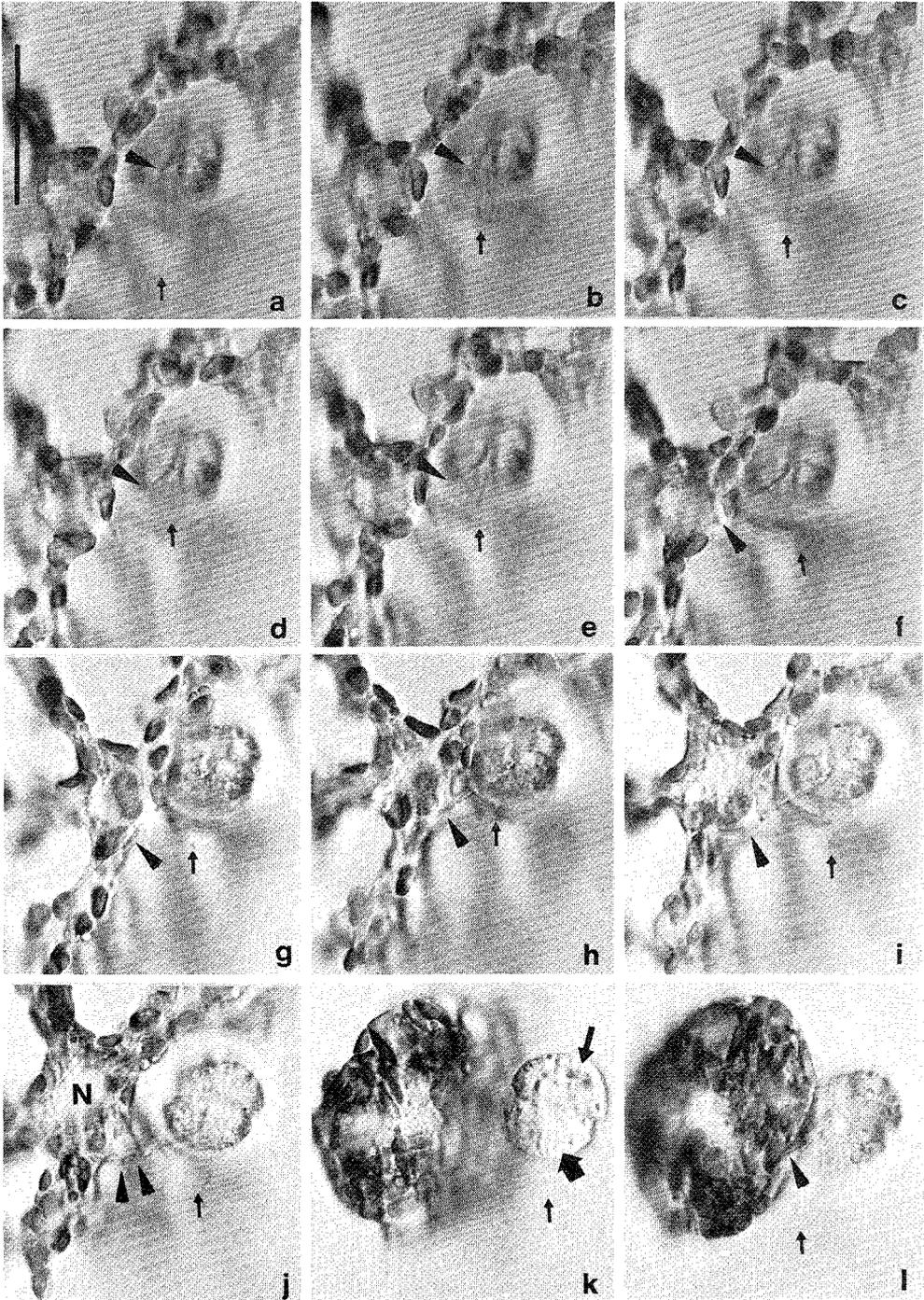
We investigated for the first time, in clonal cultures containing host and parasite, the phagotrophy of *Paulsenella* and its vegetative developmental cycle which was unknown as yet in most details.

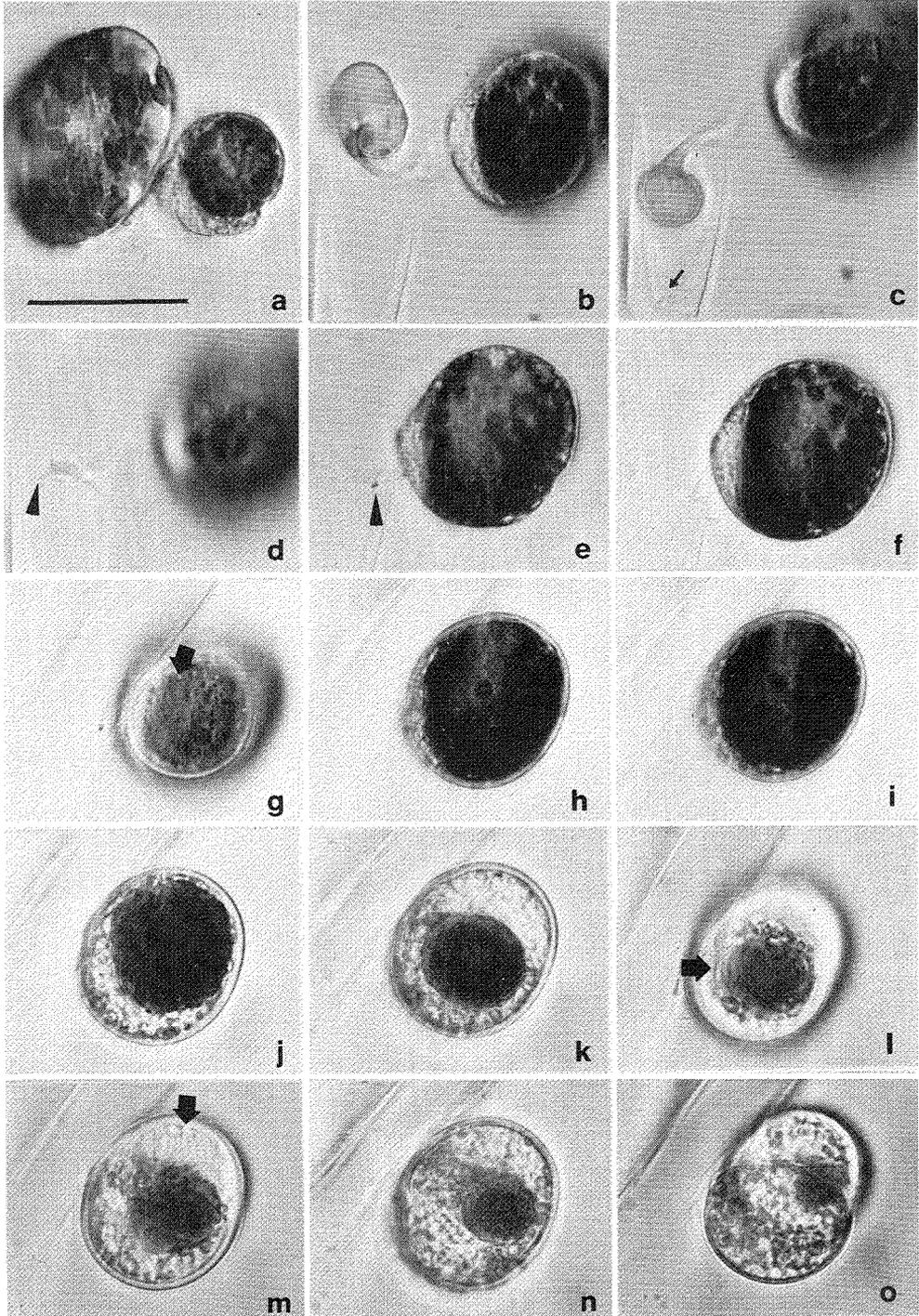
MATERIALS AND METHODS

The host, *Streptotheca thamesis* Shrubsole, was isolated from the Wadden Sea near the island Sylt (German Bight, North Sea) and cultivated in a nutrient enriched sea water medium (f/2-medium, McLachlan, 1973). The clonal cultures were maintained at 15 °C and under a 14 h light/10 h dark regime. The parasite, *Paulsenella* cf. *chaetoceratis* (Paulsen) Chatton was isolated at the same time (June 1981) and grown together with the *Streptotheca* clone. Inoculation of both was done once or twice a week. Since a complete exchange of the nutritional medium generally caused a shock with a subsequent delay in the development of *Paulsenella*, it proved useful to take as much as possible from the old culture solution containing *Paulsenella* and to add only small amounts of new solution together with host cells.

The observations on living material were mainly done at room temperatures with light microscopes equipped with sea water immersion objectives (Leitz) and flash light. Likewise, the various developmental times given in the text are all obtained at room temperatures (ca 20 °C). For epifluorescence we used a Zeiss ICM 405 microscope with the filter set G 365, FT 395 and LP 420, and formaldehyde fixed cells stained with Tinopal UP (Ciba/Geigy), which was used instead of Calcofluor White to identify cellulose and similar polysaccharides; both dyes are identical in their staining properties.

Fig. 1. *Paulsenella* cf. *chaetoceratis* on *Streptotheca thamesis*. Bar: 25 µm. Sequential series of the developmental cycle (continued in Figs 2 and 3). Formation of the peduncle and first stages of feeding. Small arrow: longitudinal flagellum; long arrow: the first chloroplast within the food vacuole; thick arrow: nucleus of *Paulsenella*; arrowhead: marks the tip of the elongating crook in a–e, the feeding tube in f, g, i, l, and the first chloroplast within the feeding tube in g; N: nucleus of the host. Time data (20 °C), a: zero time (10⁵⁰), beginning of crook formation; b: 30 sec; c: 1 min 30 sec; d: 2 min; e: 3 min, the crook is completed; f: 4 min; g: 7 min, beginning of food uptake; h: 11 min; i: 15 min; j: 18 min; k: 25 min, the first chloroplast has been taken up, collapse of the host cytoplasm, note the longitudinal and the transverse flagellum; l: 28 min, uptake of another chloroplast





RESULTS

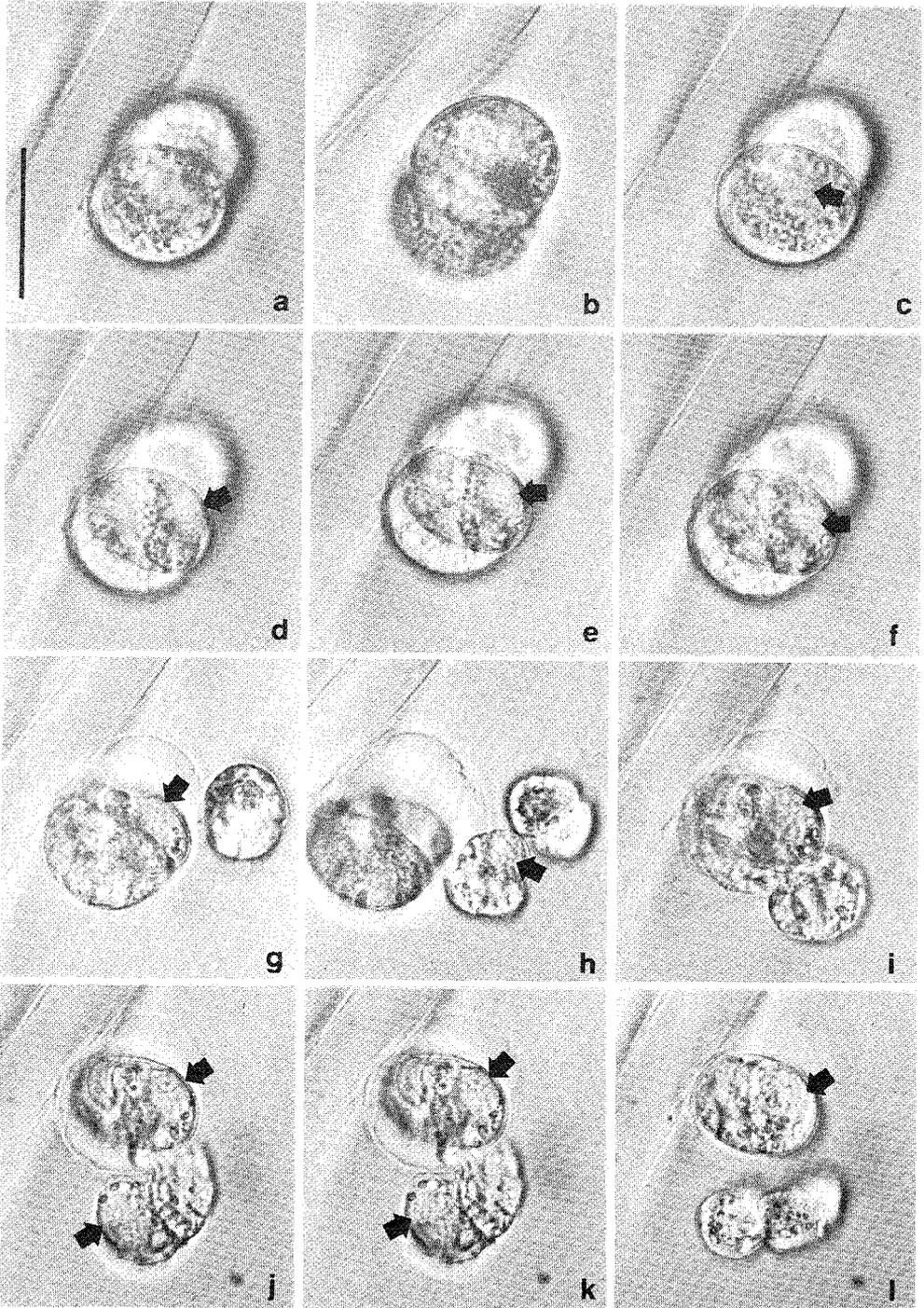
Though the neritic host species, *Streptotheca thamesis*, is widely distributed in all parts of the North Sea (Hendey, 1964), it seems to prefer shallow coastal waters such as the Wadden Sea area. There it is common during summer and autumn, but only seldom found in great quantities. Very often a certain percentage of *Streptotheca* cells is infected by *Paulsenella*. During the last two weeks of August 1982 the infection rate was determined to be varying between 3 and 9 %, and in September up to 20 % of the *Streptotheca* population was found infected. There is some evidence that under suitable environmental conditions the infection may even reach values of epidemic character.

The vegetative life cycle of *Paulsenella* is shown in Figs 1–3. It starts with biflagellate zoospores (= dinospores) showing a typically gymnodinoid structure (Fig. 6e). They are athecate, lacking chloroplasts, and measure 14–18 μm in length and 12–16 μm in width. The cingulum (girdle) is not displaced but equatorial, and the sulcus is restricted to the ventral side of the hypocone. The epicone is somewhat broader than the hypocone and contains many refractive granules. The nucleus, occupying the hypocone (Fig. 1k), is spherical, ca 6 μm in diameter, and exhibits a typically mesokaryotic structure.

Our observations indicate that freshly developed zoospores, after liberation from sporangial cysts, obviously need some time for maturation until they are ready to attack a new host cell. Just after being set free a zoospore swims around for some time; yet it is difficult to follow a single zoospore directly by microscope. However, in one case we could observe a cyst just releasing two zoospores which fortunately confined their migratory activities to the visual field of the microscope. Although these zoospores were of the same origin, they differed considerably regarding the time span until a new infection was accomplished. Whereas one zoospore needed only 47 min to start penetration of the host cell, nearly 4 h passed before the other zoospore succeeded. This incidental observation likewise demonstrates that zoospores are directly capable of infection without passing through any intermediate stage.

In Petri dishes, which contain only old zoospores, a newly inoculated host cell is within seconds densely crowded with several dozens of zoospores, indicating an apparently perfectly developed chemotactical attraction system (Fig. 6e). Excluding these unnatural multi-infections a zoospore in contact with a *Streptotheca* cell swims along its surface, often rotating, with the ventral side toward the diatom. After some time, usually more than 10 min, the zoospore attaches with the flagellar insertion region in the diatom girdle zone near the outer opening of the thecal junction, i. e. somewhat submedian on the hypotheca. The hypocone bearing the sulcus comes to lie toward the diatom

Fig. 2. *Paulsenella* cf. *chaetoceratis* on *Streptotheca thamesis*. Bar: 25 μm . Developmental cycle (continued). Final stages of food uptake, digestion, and cyst development. Thick arrow: nucleus with mesokaryotic structure; small arrow: labiate process in the theca of the host cell; arrowhead: end of the retracting feeding tube in d, and tip of the crook in e. Time data (20 °C): a: 34 min, note the longitudinal flagellum; b: 45 min, the uptake process is nearly completed; c: 49 min; d: 51 min, retraction of the retracting tube; e: 53 min, feeding tube retracted; f: 1 h 23 min; g: 2 h 30 min, a thick cyst wall has been formed; h: 3 h 15 min; i: 3 h 55 min; j: 6 h 50 min, the food vacuole begins to shrink; k: 10 h 25 min; l: ditto, other focus plane, mitosis; m: 11 h 30 min, beginning of the first cytokinesis; n: 13 h 15 min, cell division completed; o: 16 h, partial separation of the two daughter cells, the former primary cyst wall is no longer visible



epitheca. Generally, the zoospores tend to attach on the broad girdle side of the *Streptotheca* cell which has the form of a flat plate slightly twisted around the perivalvar axis (see v. Stosch, 1977). The flagella of the parasite continue to beat after settlement for a while (Fig. 1).

After some minutes some refractive granules appear near the sulcus. Gradually, they become distinct. About 5 min later new granules appear to form a rod-like structure which apically elongates in distal direction, parallel to the sulcus (Fig. 1a–e). They likewise soon increase in refraction. Finally, an often crook-shaped structure is formed with the initial group of granules as the handle (Fig. 6c). This crook is a non-cytoplasmic part of the peduncle. The crook reaches a length of about 6.5–14 μm ($\varnothing = 10.3\mu\text{m}$) and is placed between the overlapping epi- and hypocingulum of the diatom frustule, as seen in side view (Fig. 5a) (for the structure of *Streptotheca* which has a very weakly silicified frustule but a thick underlying organic layer see v. Stosch, 1977). Its formation takes about 10–15 min, the elongation phase proper about 4–5 min, with a maximum elongation rate of about 3 μm per min.

After some minutes another part of the peduncle becomes visible, the feeding tube (Fig. 1f–i). Initially, it is very thin and not refractive so that it cannot be said whether the elongation of the crook is accompanied by the elongation of the feeding tube. The feeding tube runs parallel with the crook within the intercingular slit (Fig. 4) and then bends into the lumen of the diatom cell. Generally, its free end is about 12–15 μm long. Its growth takes about 3–4 min; after that time it becomes more conspicuous, thicker (ca 1 μm) and forms distally a funnel-like opening (diameter ca 2–3 μm) which is closely appressed onto the host protoplast but does not penetrate the plasmalemma (Fig. 1c–j, 6a–b).

In heavily infected diatom cultures it happens that a zoospore settles upon an emptied or nearly emptied diatom cell. In this case, the feeding tube extends extraordinarily (Fig. 6c–d). It reaches a length of up to 40 μm . Its distal part moves about rather quickly and retracts (maximum rate 20 μm per sec) and re-elongates (maximum rate about 7 μm per sec). Only a proximal portion of about 10 μm (measured from the distal end of the crook) is rather immobile. The groping movements can last more than 30 min.

Under normal conditions, small portions of the host cytoplasm begin to move into the feeding tube when the funnel has been formed (Fig. 1h–l, Fig. 6a–b). Initially, only small granules are visible, and they usually stop at the distal end of the crook, i. e. at the site where the feeding tube enters the intercingular slit. At the beginning of the ingestion process there is, frequently, a flow in the backward direction when the attempts to overcome this bottle-neck fail. The streaming of the particles indicates that there is another narrow pass, in the region of the cingulum of the *Paulsenella* cell. Presumably,

Fig. 3. *Paulsenella cf. chaetoceratis* on *Streptotheca thamesis*. Bar: 25 μm . Development cycle (continued). Formation of secondary cysts, zoospore development and release. Thick arrow: nucleus with mesocaryotic structure. Time data (20 °C), a: 16 h, other focus plane than in Fig. 2 o; b: 18 h 10 min, only one of the daughter cells has received the undivided remnant of the food vacuole; c: 20 h 10 min, second mitosis; d: 21 h 15 min, the third mitosis is completed, development of zoospores; e: 22 h 17 min; f: 23 h 10 min; g: 23 h 43 min, release of zoospores from the first secondary cyst; h: 23 h 45 min, release of zoospores from the second secondary cyst; i: 23 h 52 min; j: 10 sec later; k: again 10 sec later; l: 23 h 52,5 min, the two zoospores of the secondary cyst have been released, the fourth secondary cyst still contains two zoospores

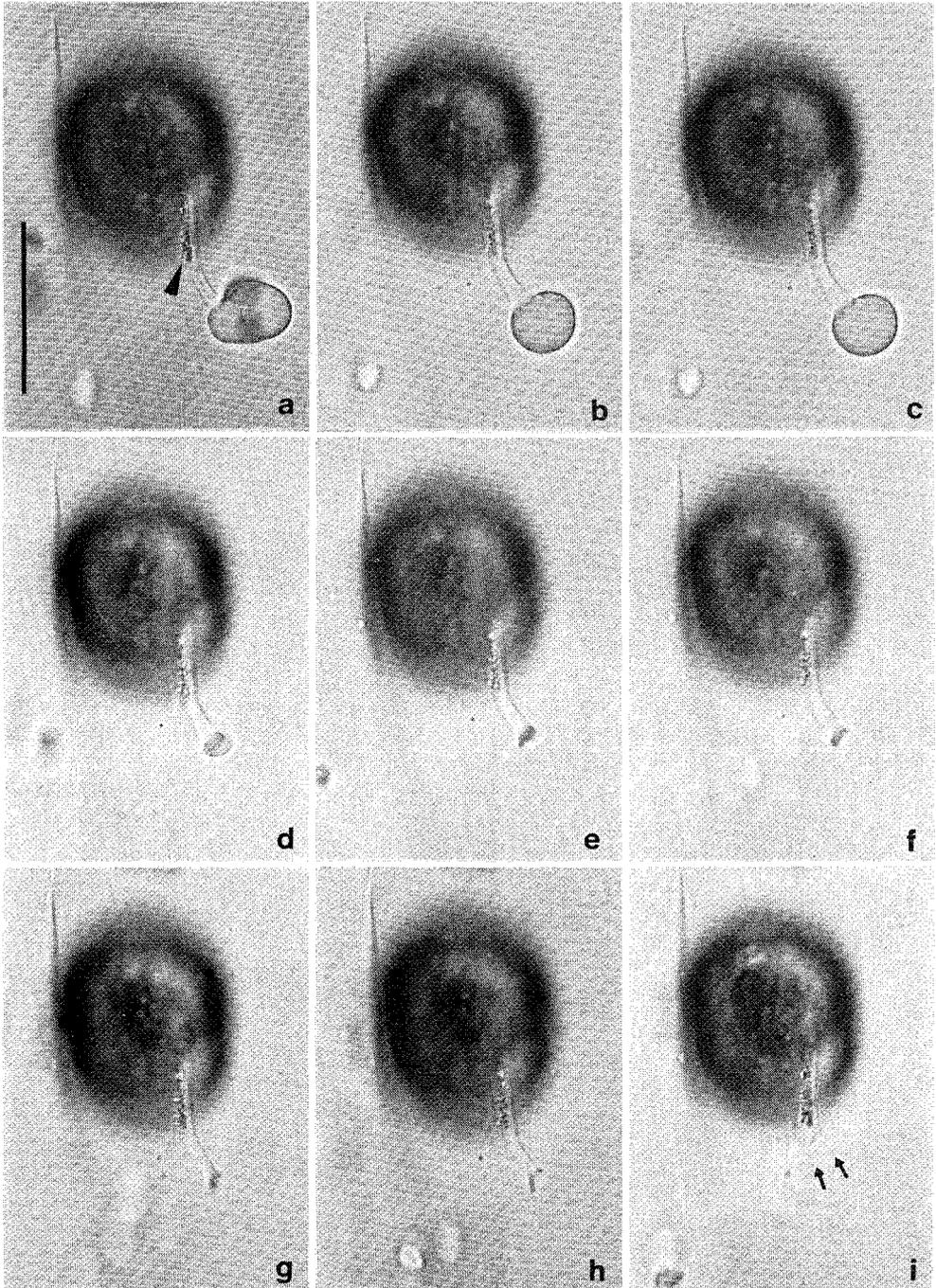


Fig. 4. *Paulsenella* cf. *chaetoceratis* on *Streptothecha thamesis*. Bar: 25 μ m. Arrowhead: distal end of the crook; small arrows: sheath opening of the feeding tube. a-d: final stages of food uptake; e-i: retraction of the feeding tube

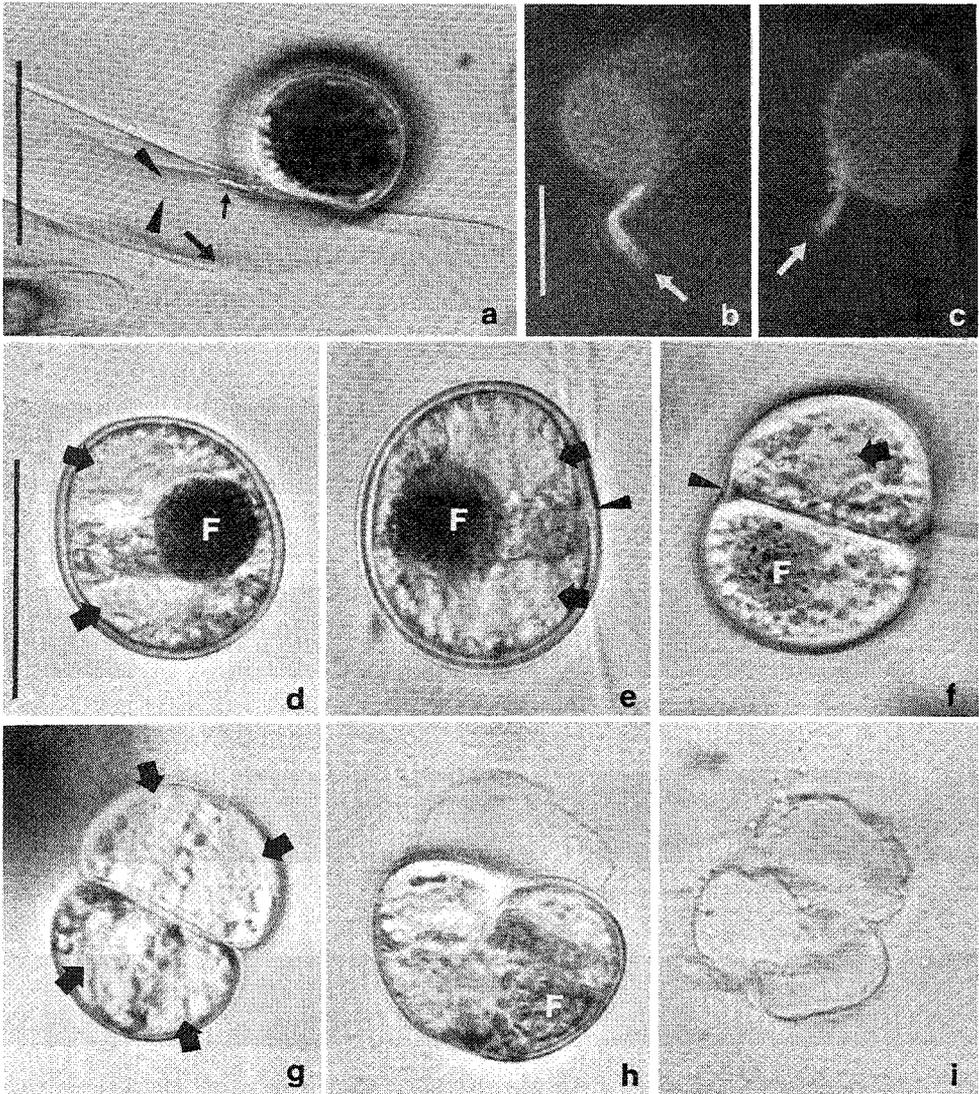


Fig. 5. *Paulsenella* cf. *chaetoceratis* on *Streptotheca thamesis*. Bar: 25 μ m. a: lateral view of the parasite upon a host well after food uptake, showing the crook (small arrow) within the slit between epi- and hypocingulum (the latter is more distinct on the opposite side, large arrow), and the sheath opening of the feeding tube (arrowheads); b, c: fluorescence of the sheath of the feeding tube in partially empty cysts after staining with Tinopal. b: combination of fluorescence and phase contrast microscopy; c: some irregular, fluorescent material is visible in the crook region; d-i: stages of cyst development. Thick arrow: nucleus with mesocaryotic structure, F: remnant of the food vacuole, arrowhead: indicating formation of the walls which surround the first daughter cells; d: primary cyst after first mitosis; e: beginning of first cell division; f: cell wall completed, reduction of the primary cyst wall, the remnants of it visible at the incision between the two daughter cells (e, f); g: second mitosis completed; h: one empty secondary cyst and two containing each two zoospores; i: three empty secondary cysts derived from one primary cyst

here the feeding tube enters the *Paulsenella* cell. The straight movement of the ingested granules is continued within the cell. They collect in the upper part of the epicone (Fig. 1k) and soon form a globular digestion vacuole (Fig. 2a)

The first portions of the host cytoplasm are ingested about 6–10 min after the crook has been completed. At the same time the host cytoplasm collapses gradually but rather rapidly beginning from that site where the funnel of the feeding tube is attached: the vacuoles shrink and the protoplast concentrates around the nucleus (Fig. 1j–l). Threads connecting the protoplast with the labiate processes remain for some time.

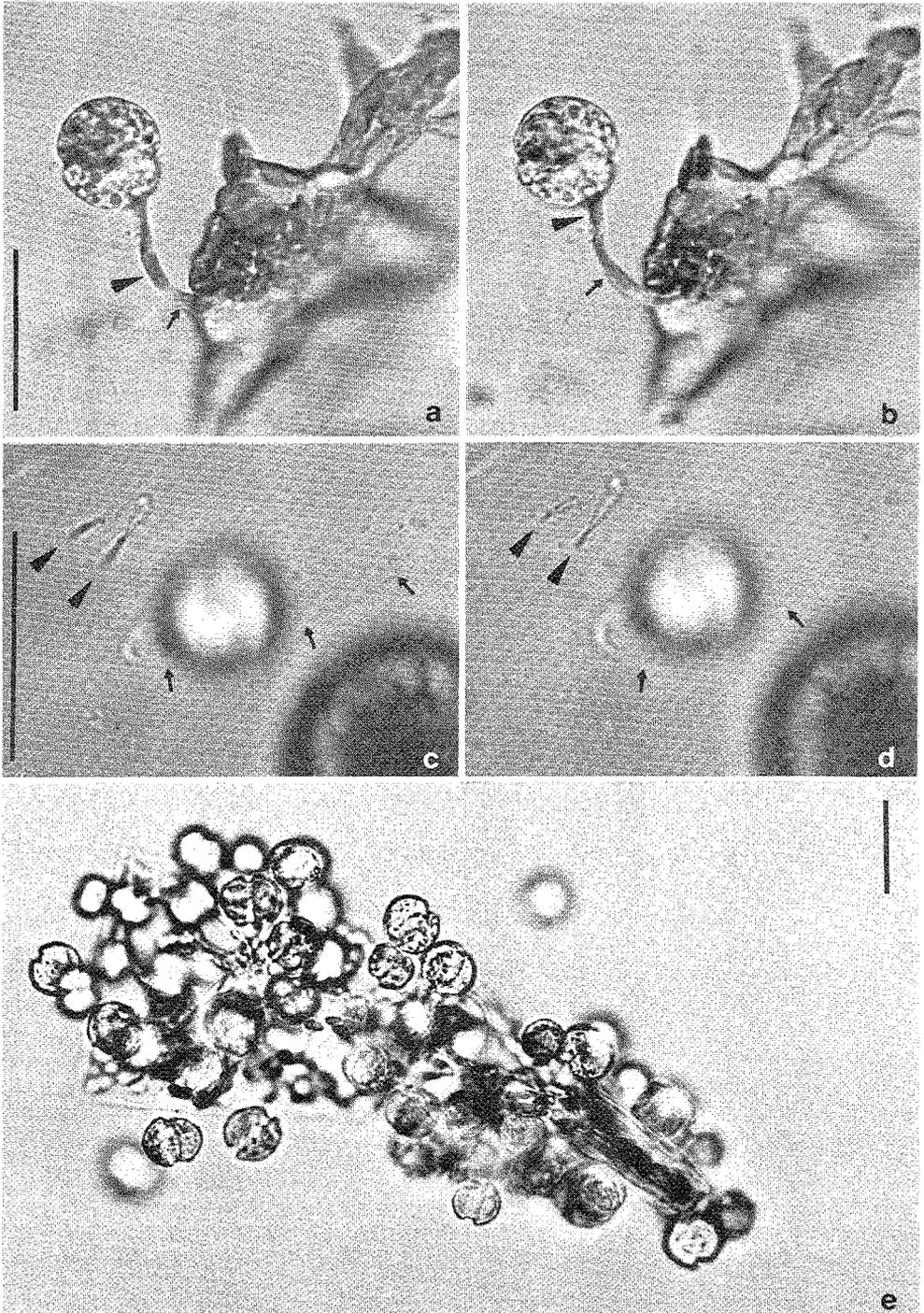
5–10 min after the start of feeding, the first chloroplast is taken up. Because of its size it is compressed and the feeding tube is widened transiently. When the first chloroplasts are ingested and the intercingular slit is enlarged by this way, the uptake rate is higher than in the beginning. A small particle passes through the feeding tube (total length about 20–28 μm) within 3–5 sec, a chloroplast takes 6–9 sec, if it is not jammed for some time. This situation can again induce a shuttle streaming. There are no indications of a peristaltic movement of the feeding tube which finally is so large that tiny particles are able to make some Brownian movement during the passage. When, by chance, the plasmalemma of the host cell bursts, the parasite is no longer able to take up the isolated food particles.

After about 40 min, nearly the complete host cytoplasm is ingested (Fig. 2b). Some small vacuoles usually are the last portions to be taken up (Fig. 2b–c, Fig. 4). At this time, the funnel at the end of the feeding tube and its attachment upon the surface of the protoplast can be seen especially well. When these remnants have also been taken up, usually accompanied by conspicuous movements and torsions of the distal part of the feeding tube, the funnel collapses within about 2 min (Fig. 2c–e, Fig. 4d–i). Then the feeding tube becomes thinner and is finally retracted within 5–10 sec.

The proximal end of the feeding tube is ensheathed by a very faint, flexible and transient tube-like wall. This sheath of the feeding tube stains with Calcofluor and can easily be visualized in the fluorescence microscope (Fig. 5b, c). Calcofluor positive granules are sometimes seen also in the proximal part of the crook (Fig. 5c). The crook does not change all the time; it persists very long.

During phagocytosis, the zoospore transforms into the trophont which finally lacks flagella (presumably they are retracted) (Fig. 2b–f). Cingulum and sulcus disappear, the cell becoming spherical or ovoid. By accumulating the host cytoplasm the trophont increases considerably in size, varying between 22–29 \times 25–31 μm (average: 25 \times 27 μm). The food vacuole measures initially about 17 μm in diameter and has a nearly central position. The nucleus, still lying in the former hypocone (identifiable by the crook) is strongly flattened (Fig. 2f–g). The size of the trophont depends on the amount of

Fig. 6. *Paulsenella* cf. *chaetoceratis* on *Streptotheca thamesis*. Bar: 25 μm . a, b: uptake of two chloroplasts (labeled with arrowhead and arrow, respectively), time distance between a and b: 5 sec; note the transverse flagellum; c, d: in an overinfected culture, a *Paulsenella* cell has attacked an empty or nearly empty *Streptotheca* cell and formed a very long, mobile feeding tube (arrows), searching inside the host cell for food. Arrowheads: crooks of former infection attempts; time span between c and d: 5 sec; e: hungry *Paulsenella* zoospores gather around a *Streptotheca* cell which was inoculated 30 sec before



ingested material, i. e., under normal circumstances, on the size of the attacked diatom cell, which was, during present investigations, 60 μm broad.

In cultures with prevailing parasites, multiple infections can occur. The trophonts then become smaller. Under these conditions it can also happen that a zoospore leaves the host cell with hardly any ingested material, after having formed the peduncle vainly. The crook is then left behind (Fig. 6c–d). As yet, we have not been able to observe whether such cells are capable of another infection.

At the end of its development, i. e. about 1 h after the firm settlement of the zoospore, the trophont remains attached to the diatom frustule and forms a relatively thick cyst wall (Fig. 2f–i).

The phase of digestion, during which the food vacuole diminishes considerably in size and the amount of cytoplasm increases, lasts about 10–12 h (Fig. 2h–k). Then the primary cyst begins to form secondary cysts (Fig. 2l–o, Fig. 3a–f). When it undergoes the first mitosis (Fig. 2l) and cytokinesis (Fig. 2m, Fig. 5d–f), the food vacuole is not divided but deposited in one of the daughter cells, in the former epicone region. Cell cleavage begins from the opposite pole (Fig. 5e). The wall of the primary cyst is retained up to the first cytokinesis. Then the two daughter cells, separating partially, become surrounded by an own cell wall whereas the wall of the primary cyst becomes rapidly thinner (Fig. 2m–o, Fig. 3a–b, Fig. 5d–g). Finally, it is impossible to recognize the primary cyst wall in the light microscope. After about 6 h a second division occurs (Fig. 3c, Fig. 5g). In most cases it is restricted to that secondary cell which includes the remnants of the food vacuole. Again, this residual body is not divided but taken up as a whole by one of the daughter cells.

These daughter cells again develop a cell wall. As a result, three secondary cysts are formed within the primary cyst (Fig. 5h, i). There are also primary cysts with four (after a further division of both secondary cells) (Fig. 3g–l), and very rarely with only two secondary cysts (without second division).

A short time after the last division, a further division occurs (Fig. 3d–f). It has the function of a morphogenetic division and gives rise to two naked cells within each secondary cyst (Fig. 3g–l, Fig. 5h). After 20–30 min they rupture the wall, squeeze through the small opening within 1–2 minutes, assume their typical shape outside the cyst within a few seconds, commence beating their flagella and swim away (Fig. 3g–l). The residual food body which was conspicuous because of its high refraction, and especially its red colour, has disappeared nearly completely when the zoospores are set free. The distribution of the residual body has no influence on the sequence of zoospore release which is successive rather than simultaneous. Thin, empty cyst walls are left (Fig. 5i). Taken together, the minimal length of the life cycle is slightly more than 24 h. The zoospores can survive several weeks without host.

Occasionally, especially in old, highly infected cultures, we observed a transient encystment of zoospores. The wall of these cysts is rather thin. This encystment which is not connected with cell division does not represent a regularly occurring step in development.

The times, given above, are measured during permanent observation under the microscope; the immersion objectives enable studies to be made in the normal Petri dishes used for cultivation. The developmental times vary considerably, even between secondary cysts which are derived from the same primary one and also between the two

sister cells of one secondary cyst. In both cases, the development of one can be retarded against the other for several hours. The length of the life cycle highly depends on the temperature, which was about 48 h at 15 °C.

The empty walls of the secondary cysts stain yellow and the crook yellow-brownish in zinc chloride-iodine; the latter is brown after treatment with OsO₄. The cysts show a strong fluorescence after staining with Calcofluor.

Colchicine (10⁻³M) does not inhibit the ingestion if it is running when the drug is applied. However, it interrupts normal development.

DISCUSSION

Within the life cycle of *Paulsenella* cf. *chaetoceratis*, four consecutive developmental stages can be distinguished, namely zoospore (= dinospore), trophont, primary cyst and secondary cyst. The free-swimming stage is only a short, transitional phase under good conditions. One feeding act results in more than two (usually 6–8) offsprings. We, therefore, regard *Paulsenella* as a parasitic dinophyte and not as a predatory one (see also Morey-Gaines & Elbrächter, in press).

The formation of zoospores within secondary cysts, derived from a primary one, corresponds with the development of *Dissodinium pseudolunula* (Elbrächter & Drebes, 1978). In the latter organism, one secondary cyst usually gives rise to 5–8 zoospores; in the *Paulsenella* species described here, one secondary cyst contains regularly two zoospores. In both cases, the wall of the primary cyst disintegrates largely or completely when the secondary cysts have been formed.

Sexual reproduction, and in which stage *Paulsenella* survives the winter season is still unknown. Investigations in that direction will be started, whereas those on ultrastructural details of the vegetative development are already in progress. Further studies are planned with *Paulsenella* species associated with different hosts (*Eucampia*, *Chaetoceros*). In so far, for the present, an intensive discussion about taxonomy and life cycle has to be deferred.

Most parasitic dinoflagellates are osmotrophic (Cachon & Cachon, 1971a). *Paulsenella* belongs to those species which are phagotrophic. A peduncle as an organelle of feeding and, at least in some cases, of attachment and penetration, is observed also in many other phagotrophic dinoflagellates (Spero, 1982). e. g. in *Apodinium* (Cachon & Cachon, 1973), *Protoodinium* (Cachon & Cachon, 1971a), *Dissodinium* (Drebes, 1978) *Myxodinium* (Cachon et al., 1969), *Gyrodinium* (Lee, 1977), and *Gymnodinium fungiforme* (Spero, 1982). However, it also occurs in osmotrophic dinoflagellates (Cachon et al., 1968: *Chytriodinium*, Cachon & Cachon, 1971b: *Oodinium*). The structure of the peduncle of the different dinoflagellates (not in every case was the structure in question named "peduncle") varies considerably.

The peduncle of *Paulsenella* consists of three different parts. The feeding tube is a transient cytoplasmic organelle which resembles the peduncle of *Gymnodinium fungiforme* (Spero, 1982), not only in its form and size but also in that it is easily and rapidly protruded and retracted. The main function of the feeding tube is surely the uptake of the cytoplasm from the host cell. As yet, the mechanism of the sucking process is not well understood. It depends on an intact host plasmalemma and is so powerful that plastids are deformed while passing through the tube. As deduced from the motion of small

particles, it is not driven by a peristaltic movement of the tube wall. Spero (1982) believes that the ingestion is done as in the tentacles of suctorian ciliates. The collapse of the *Streptothecha* cytoplasm in the very beginning of the feeding phase indicates another function of the feeding tube. It may be assumed that the tip of the feeding tube releases substances which change the permeability of the tonoplast and the plasmalemma drastically so that the vacuolar content leaks out while the integrity of the protoplast – necessary for its uptake – is retained. Therewith, the volume of the material to be ingested is reduced highly. Greuet & Ferru (1969) also assume a secretory function of the peduncle ("stomopod") of *Erythroopsis pavillardii*, believing that it injects lysing substances into the prey.

The crook as well as the sheath are non-cytoplasmic, persisting secretory products. Persisting parts of the peduncle are observed also e. g. in *Dissodinium* (Drebes, 1978) where a portion of the "sucker organelle" is left inside the invaded copepod egg after the feeding, and in *Myxodinium* (Cachon et al., 1969). The crook obviously has a twofold function. Initially, it appears to serve as an adhesive. Its primarily produced small proximal part fixes the parasite onto the hypotheca of the diatom. The elongated main part of the crook which is formed later seems to be used to open a path through the intercingular slit for the feeding tube, enzymatically as well as mechanically. The staining properties of the crook indicate that it is proteinaceous or lipoproteinaceous. It is probable, but unfortunately not directly visible in the living system, that the crook is secreted by the tip of the elongating feeding tube. The sheath around the basal part of the feeding tube seems to consist of cellulose or a similar polysaccharide as deduced from its longevity and its reaction with Tinopal (= Calcofluor).

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