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Ultrastructural Features of *Cryptocaryon irritans*, a Ciliate Parasite of Marine Fish

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SUMMARY

The parasitic, reproductive, and free living phases of *Cryptocaryon irritans* Brown 1951, a ciliate parasite of marine fish, were studied by means of transmission and scanning electron microscopy. The ciliature of this protozoan is arranged in 78–80 monokinetid meridians which run lengthwise converging at the oral cavity and at the posterior pole of the cell. In the trophont, a crown of pointed ciliar triplets fused at the tip delimits a small cytostome whose radially ridged walls lead to a shallow cytopharynx. The trophont feeds on whole host cells and tissue debris. An electron-dense, foam-like, PAS-positive substance fills the pellicular alveoli of the growing trophont. The mechanism of its formation is yet to be determined and several possible functions for it are hypothesized. The macronucleus in the young trophont consists of four linked bead-like segments twisted in a crescent-shaped alignment; up to five micronuclei are adjacently located. At this stage, the macronucleus is homeomeric. Along with trophont growth, the macronucleus increases in volume and its coarse network of chromatin expands. As the trophont leaves the host, development proceeds onto the protomont and tomont stages, during which a substantial reorganization occurs in the cell. The dense chromatin clumps apparently coalesce while the electron-lucent matter expands and the four macronuclear segments fuse into one thick, elongated strand which coils throughout the protoplasm. The micronuclei are no longer detectable in the protomont. The tomont then begins to undergo palintomic division, yielding scores of tomites. In the tomite, the macronuclear chromatin bundles are thin and abundant within the electron-lucent matrix. The micronuclei reappear. Following excystment, the emerging infective theront actively seeks out its host. At this stage its oral apparatus appears as a narrow slit surrounded by cilia shorter than the somatic ones, and is presumably not yet functional. The macronucleus is homeomeric again, has assumed its characteristic quadripartite shape with adjacent micronuclei.

Introduction

The ciliate *Cryptocaryon irritans* Brown 1951 is a parasite of marine fish. This protozoan invades the integument of its host, severely impairing the physiological functions of skin and gills. The most conspicuous gross sign of cryptocaryoniasis is the formation of minute whitish blisters on the skin and eyes of the fish. On the gills, the parasite induces profuse mucus secretion and disruption of the lamellar structure which lead to respiratory distress.

Until fairly recently, reference to *C. irritans* in the scientific literature was limited to occasional case reports

in aquarium fish [15, 17, 23, 29]. In the last decade, however, with the advance of commercial marine fish farming technology, *C. irritans* has gradually become one of the most devastating parasites of both temperate [11, 19] and warm water mariculture [4, 6, 14, 18].

Research on *C. irritans* has hitherto dealt mainly with its development, life cycle and possible control strategies [6, 7, 18, 23]. Apart from a brief SEM study on the buccal apparatus of *C. irritans* [5] the ultrastructure of this protozoan is unknown, and important cytological details which have often been controversial among previous workers [2] have not been clarified to date.

Material and Methods

The terminology for the developmental stages of *C. irritans* was adopted from Canella and Rocchi-Canella [3] for the suborder Ophryoglenina, i.e. "phoront" for the invading stage settled into the host epithelium, prior to feeding (Fig. 1, A), "trophont" for the parasitic stage that feeds and grows on the host (Fig. 1, B), "protomont" for the stage encompassing the point when the mature trophont leaves the fish and the time when adhesion to the substrate and encystment start (Fig. 1, C), "tomont" for the encysted dividing stage off the host (Fig. 1, D), "tomite" for each daughter cell (Fig. 1, E) and "theront" for the excysted, free-swimming, non-feeding infective stage (Fig. 1, F).

Wild *Diplodus noct* (Valenciennes 1830) infected with *C. irritans* were caught in the northern Gulf of Eilat, Red Sea. The natural infection was transmitted to 1–2 gilt-head sea bream *Sparus aurata* L., which is cultured for research and commercial purposes at the facilities of the IOLR National Center for Mariculture in Eilat. The fish were kept at a salinity of 40 ± 1 ppt and a temperature of $22\text{--}27^\circ\text{C}$. Upon dropping off the host, *C. irritans* tomonts were transferred to serological plates and

incubated at 24°C in individual wells. Freshly excysted theronts were used for experimental infection of sea bream fingerlings.

The ultrastructure of *C. irritans* during its various phases of development in its host was studied using a Jeol 7 transmission electron microscope (TEM) and a Jeol 6400 scanning electron microscope (SEM).

For observations with TEM, excised tissue samples with embedded trophonts, as well as the off-the-host stages of the parasite, were fixed in cold 2.5 % glutaraldehyde in 0.1, 0.15 and 0.2 M sodium cacodylate buffer (pH 7.2), or 0.1 M Millonig's phosphate buffer with 1.08 % sucrose. Due to their small size, live theronts were concentrated by centrifugation, fixed as above and embedded in a 1.5 % solution of warm Noble agar. The samples were postfixed in 2 % osmium tetroxide in the corresponding buffer, dehydrated in an ascending ethanol series and embedded in Polaron-812 resin according to standard procedures [16]. Semithin sections were stained with methylene blue. Ultrathin sections were cut with a diamond knife and stained with uranyl acetate and lead citrate.

Precise localization of carbohydrates was carried out using the periodic acid-silver methenamine method as described by Ram-

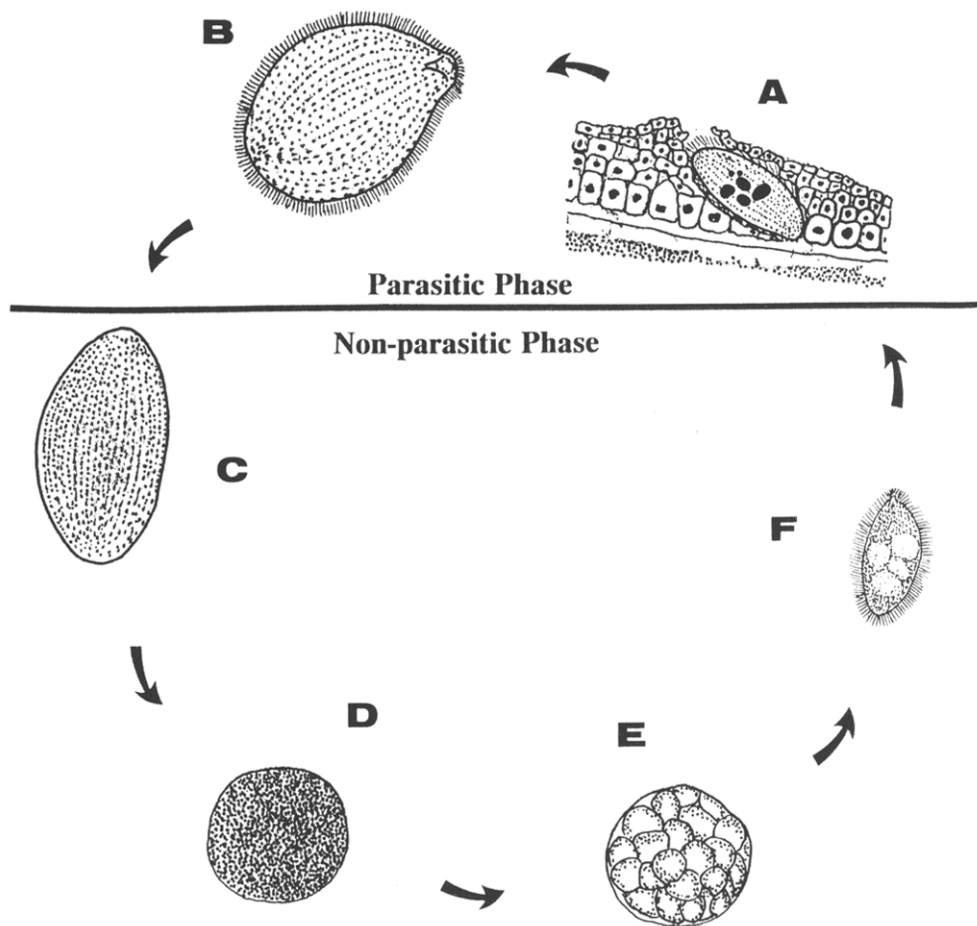
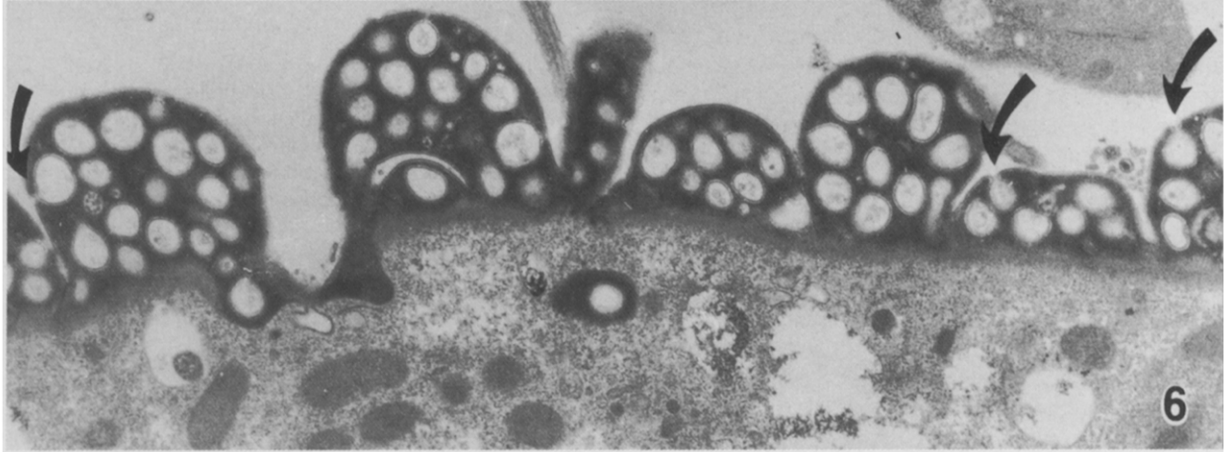
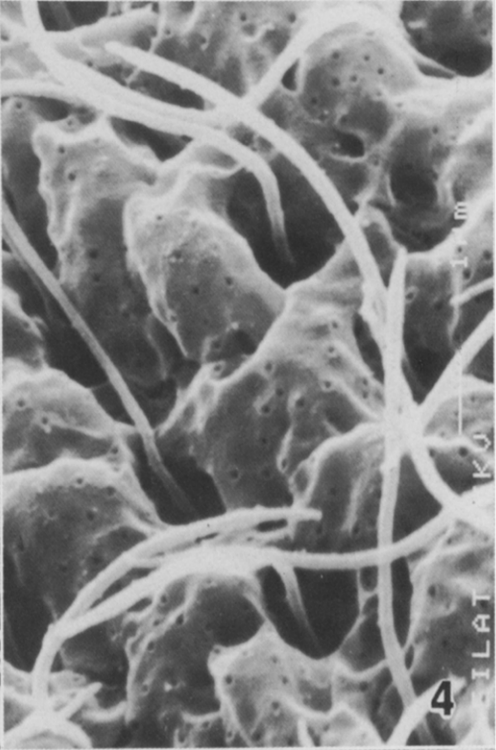
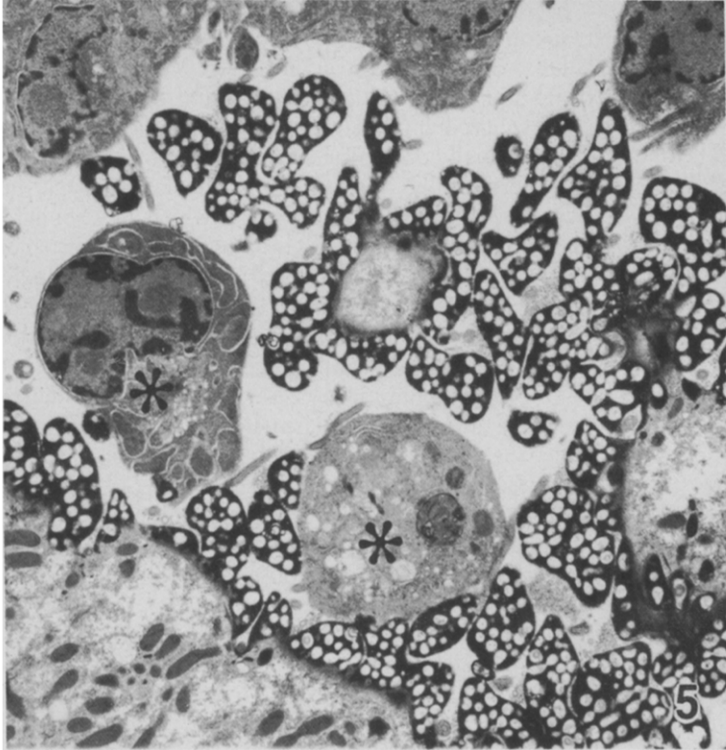
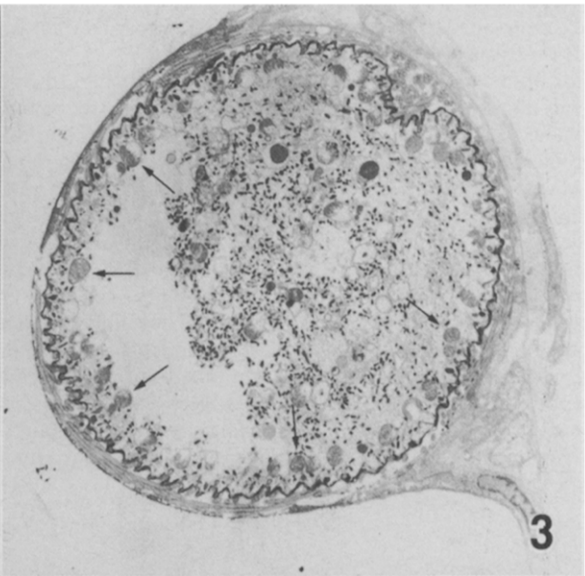
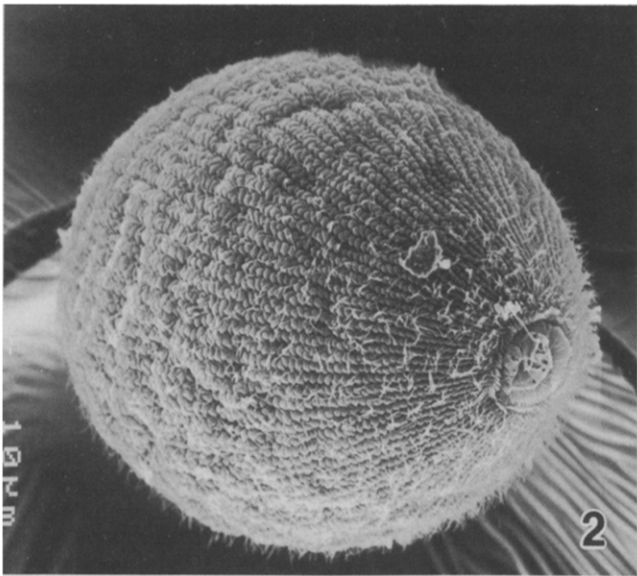


Fig. 1. Schematic presentation of *C. irritans* life cycle; A: phoront; B: trophont; C: protomont; D: tomont; E: tomites; F: theront.

Fig. 2. Protomont. SEM, $\times 400$. – Fig. 3. Cross section of a young trophont. Note the regular arrangement of the subcortical mitochondria (arrowed). TEM, $\times 2,440$. – Fig. 4. Organization of the monokinetid ciliary rows (young trophont). SEM, $\times 10,000$. – Fig. 5. A section through the cytopharyngeal region of a 3 day old trophont, showing abundance of foamy substance, and host leukocytes (asterisks) in the process of being ingested. TEM, $\times 3,300$. – Fig. 6. Cross section of the cortex of trophont displaying its coat of foam-like substance. Note the continuity of the membrane coating the vesicles with the foam outer membrane (arrowed). TEM, $\times 11,950$.



bourg [24] and Thiéry [28] for detecting PAS-positive structures in electron microscopy. No osmium tetroxide post-fixation was done on tissue prepared for this stain.

For observations with SEM, protomonts that emerged from heavily infected *S. aurata* were fixed in 10% buffered neutral formalin. Theronts were fixed in Bouin's fluid, according to a method modified by Prof. Eugene Small (Dept. of Zoology, Univ. of Maryland) for delicate marine protozoa. Briefly, a saturated solution of NaHCO_3 in concentrated formalin was decanted and saturated with picric acid. This solution was diluted 1:15 with filtered ($0.45\ \mu\text{m}$) seawater, and just prior to fixation, 1.3% glacial acetic acid was added. Three volumes of this fixative were used for every volume of seawater with live theronts. The protomonts were placed in porous synerglass capsules, the theronts in $15\ \mu\text{m}$ nylon mesh. After dehydrating them in an ascending ethanol series, the specimens were dried in a carbon dioxide critical point dryer. The specimens were then mounted onto aluminum stubs, gold-coated, and observed at an accelerating voltage of 15 kV.

Results

Morphology

Following initial contact with the host, theront penetration is very rapid, as the parasite is often found next to the epithelial basal membrane within 5 minutes. Phoronts are not dissimilar from the free-living theronts, being fusiform to pyriform in shape and measuring $20\text{--}30 \times 50\text{--}70\ \mu\text{m}$. Transition into the feeding stage (trophont) occurs within hours, and an increase in size can be perceived after 36–48 hours. Mature (4–5 d) trophonts average about $200 \times 250\ \mu\text{m}$. The body is slightly flattened at the mid region, and tapers towards the apical end, resulting in a spheroidal to pyriform shape with a somewhat pointed anterior tip.

Cortex and Infraciliature

The ciliature is short, fine and uniform, arranged in 78–80 monokinetid meridians (Fig. 3) which run lengthwise and converge at the oral cavity and the opposite pole (Figs. 2, 7). Each cilium emerges from a cortical invagination approximately $1\ \mu\text{m}$ wide (Fig. 4). An electron-dense, "foamy" layer of material is secreted to fill the pellicular alveoli of the growing, 2–3 d old trophont (Figs. 5–6). This substance is PAS-positive. The foamy layer builds up, reaching a maximum thickness of $2\text{--}3\ \mu\text{m}$ (Fig. 6). In the late trophont stage, it steadily diminishes and in the ensuing protomont, only sparse remnants of the foam persist giving way to the formation of the cyst wall of the tomont. The cyst wall thickens over the entire cell, embedding cilia as well as bacteria and cellular debris. The outer coat of the tomont appears devoid of any characteristic cortical structure. In the theront, somatic cilia appear denser and entirely hide the organism's cortex (Fig. 19).

Cytostome and Oral Ciliature

In the trophont, the cytostome-cytopharynx apparatus lacks accessory membranelles. A crown of pointed ciliar triplets fused at the tip delimits a small (about $20\ \mu\text{m}$) cytostome whose radially ridged walls lead to a shallow

cytopharynx (Figs. 11–12). In the theront, the oral apparatus appears as a narrow slit flanked by a crest of cilia (Figs. 20–21).

Cytoplasm and Cell Organelles

Food vacuoles increase in number as the trophont matures. The parasite ingests whole host cells and cell debris. At least 6 different types of cells were identified in such vacuoles: mucous cells (Fig. 14), melanocytes, erythrocytes, macrophages (Fig. 15), granulocytes and polymorphonuclear leucocytes. Host cells at different degrees of digestion could still be recognized in the cytoplasm of the protomont and early tomont.

Throughout the parasitic developmental stages mitochondria are uniformly spheroid and predominantly underlie the plasmalemma (Figs. 3, 13, and 21). Mitochondria have a diameter of about $0.9\ \mu\text{m}$, with the more elongated ones usually reduced in width ($0.7 \times 1.6\ \mu\text{m}$).

Secretory granules are present in the theront and early trophont. These inclusions appear as electron-dense, sacular to drop-shaped structures scattered in large numbers throughout the cytoplasm (Figs. 3 and 21). The secretory granules gradually disintegrate as the trophont develops and eventually disappear in 3–4 days old trophonts. They are substantially different from the larger, spear-head shaped ($200 \times 900\ \text{nm}$) mucocysts which are seen in both phoronts and trophonts. The mucocysts are distributed between the subcortical chondriome and the plasmalemma, their apical end pointing outwards (Figs. 9–10). They appear to become more conspicuous with the emergence of the cortical foam-like substance.

The Golgi apparatus consists of 3–4 stacked, flattened cisternae adjoining the plasmalemma (Fig. 8). This organelle was observed only in trophonts of at least 150–180 μm in size, corresponding to no less than 2–3 days of age. Ribosomes are generally inconspicuous in the trophont, but increase in density in the tomont. Sparse lipid globules (Fig. 13) were occasionally observed in all stages but were rare in the mature trophont.

Macronucleus

The macronucleus in the phoront and young trophont is moniliform, consisting of four linked bead-like segments twisted in a crescent-shaped alignment. The segments are ovoid, approximately $10\ \mu\text{m}$ long, $8\ \mu\text{m}$ wide, centrally located in the cell, and each contains at least 1–2 nucleoli. The macronuclear membrane has a trilaminar structure composed of an electron-lucent layer between two densely staining layers, the inner of which displays numerous nuclear pores. At this stage, the macronucleus is of the homeomeric type, with a network of chromatin clumps of irregular convoluted profiles largely interconnected and more or less evenly distributed within the electron-lucent matrix (Fig. 22). Along with trophont growth, however, the macronucleus rapidly increases in volume and its coarse network of electron-dense chromatin expands (Fig. 13). Later on, the dense chromatin clumps apparently coalesce to form winding, slender strands. In the proto-

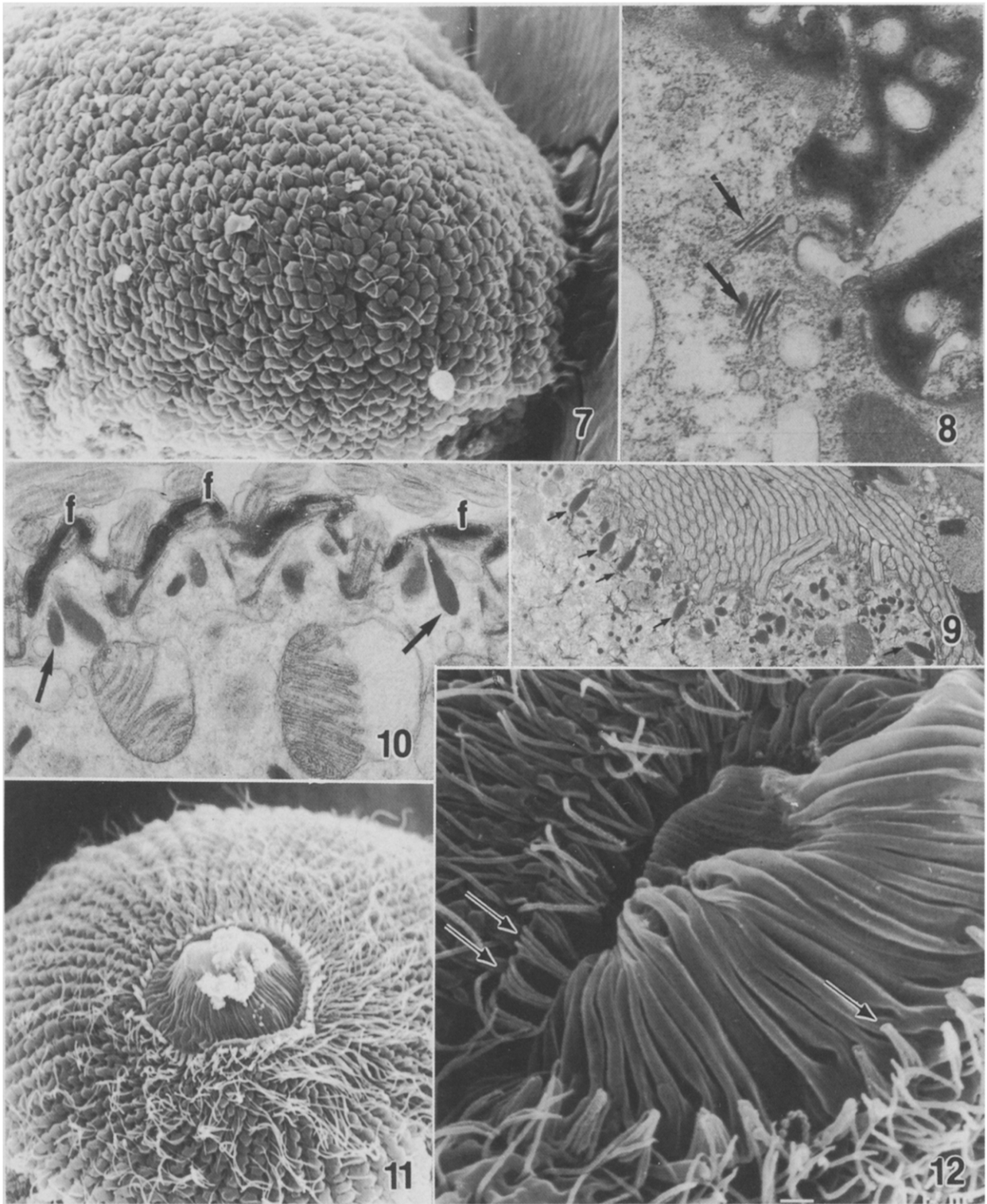


Fig. 7. Posterior end of protomont. SEM, $\times 975$. – Fig. 8. Golgi bodies (arrowed) in trophont. TEM, $\times 30,000$. – Figs. 9–10. Cross section of cortical area in phoront and trophont, respectively. Note the oval to spear-shaped organelles underlying the plasmalemma (arrowed) and, in the latter, the incipient secretion of foam-like (f) substance. TEM, 9: $\times 5,850$; 10: $\times 16,800$. – Figs. 11–12. Oral apparatus. Note the specialized ciliary triplets fused at the tip (Fig. 12, arrowed). SEM 11: $\times 1,280$; 12: $\times 5,600$.

mont, the macronucleus is elongated, its four segments indistinct. As development proceeds from the protomont to the undivided tomont stage, the four nuclear segments fuse into one thick, elongated, twisted strand which coils

throughout the protoplasm (Fig. 16). The electron-lucent material is now predominant and distinct nuclear pores are aligned along the nuclear membrane (Fig. 17). The chromatin is condensed in sparse patches from which twisted

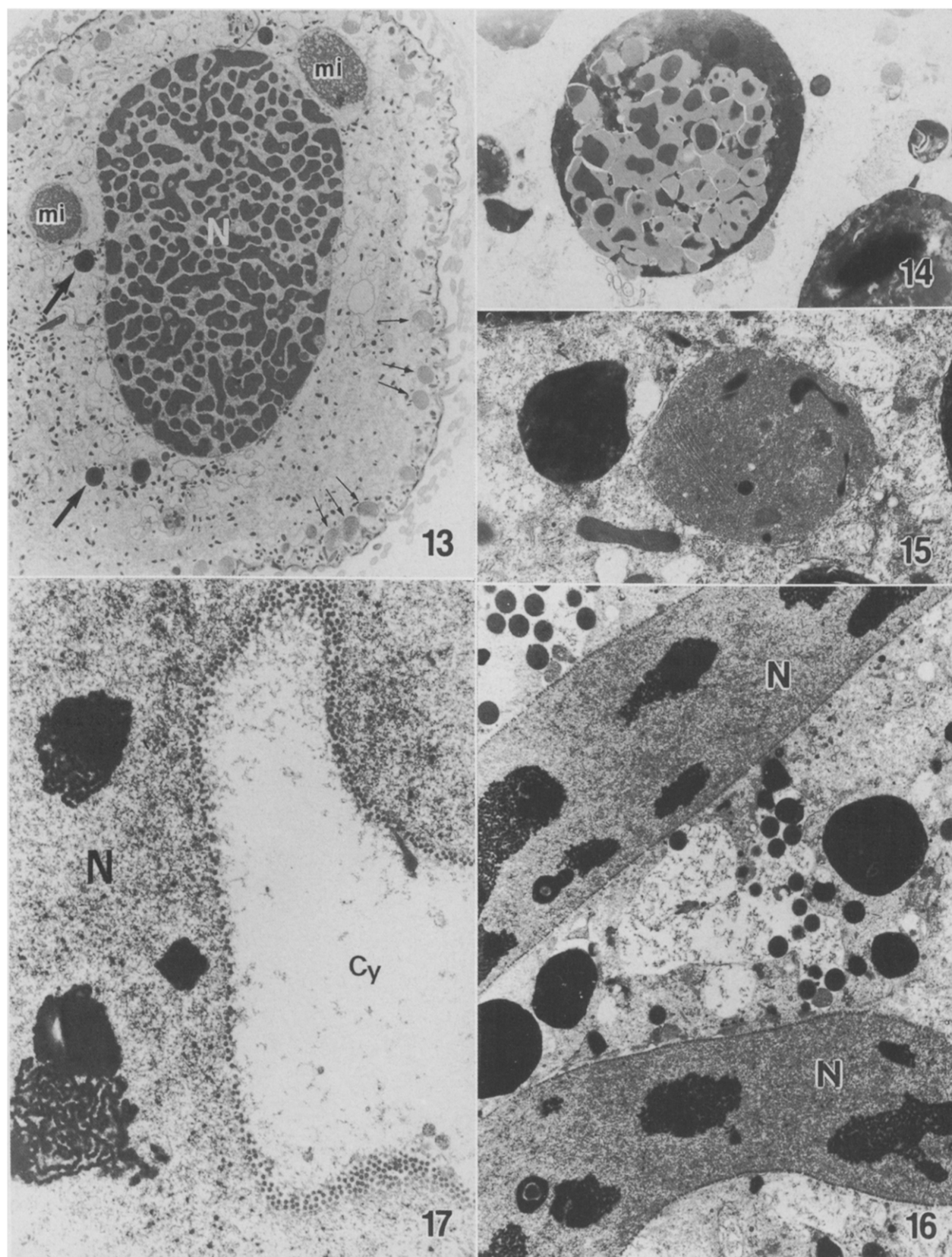


Fig. 13. Cross section of an approx. 2 day old trophont. Note the convoluted profiles of the macronuclear (N) chromatin, two micronuclei (mi), the mitochondria (small arrows) and presumably lipid inclusions (large arrows). TEM, $\times 3,320$. – Fig. 14. Ingested mucus cell in the cytoplasm of a protomont. TEM, $\times 4,100$. – Fig. 15. Ingested leukocyte in the cytoplasm of a protomont. TEM, $\times 5,000$. – Fig. 16. Two section of the elongated protomont macronucleus (N), with “patches” of chromatin. TEM, $\times 11,880$. – Fig. 17. Nuclear pores along the protomont nuclear membrane, N: macronucleus; Cy: cytoplasm. TEM, $\times 11,880$.

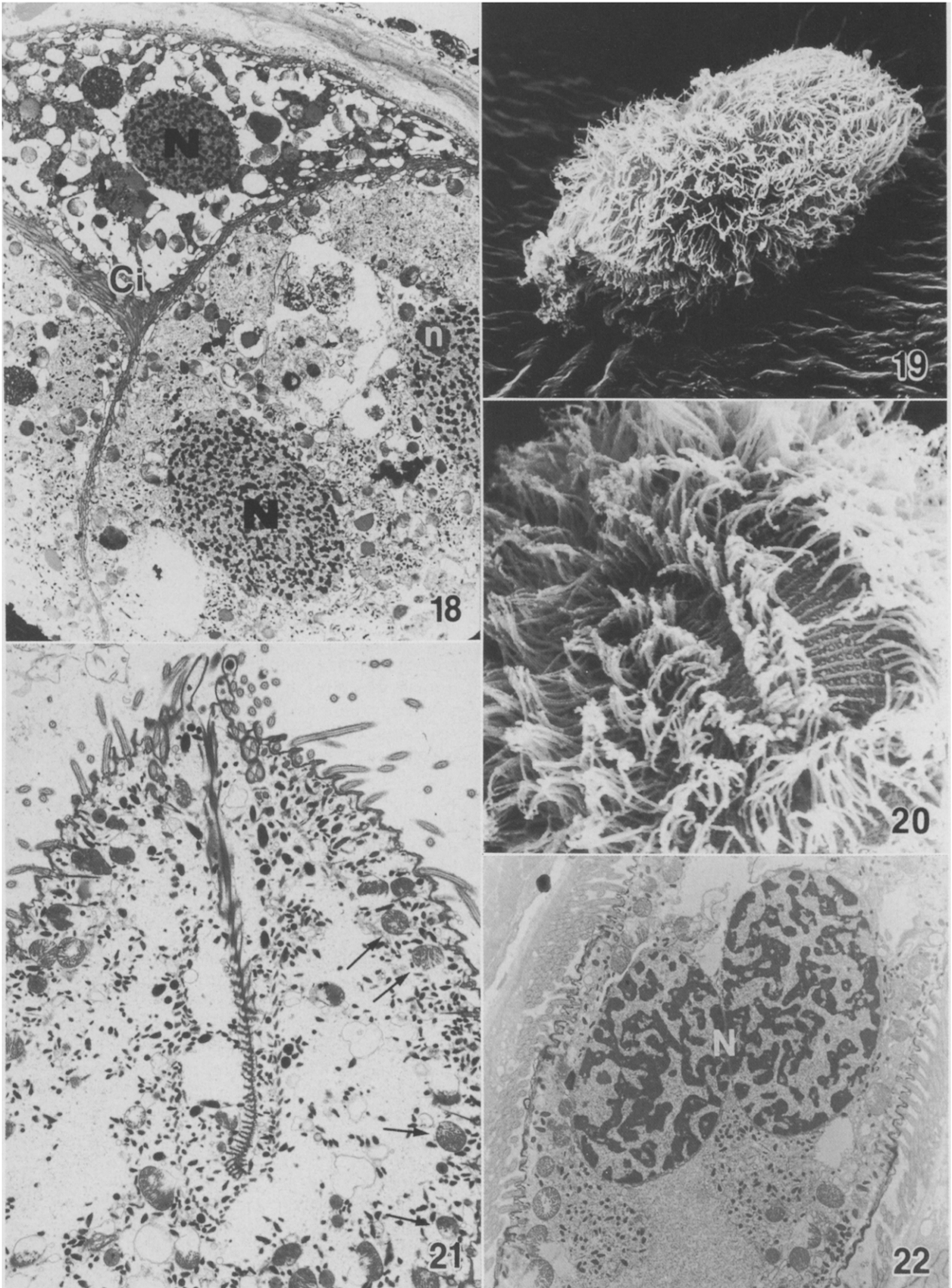


Fig. 18. Tomites in dividing tomont. Note the presence of cilia (Ci), macronuclei (N) with nucleolus (n) and micronuclei (mi) within the reorganizing cytoplasm. TEM, $\times 5,900$. – Fig. 19. Theront. SEM, $\times 2,300$. – Fig. 20. Theront oral apparatus. SEM, $\times 5,000$. – Fig. 21. Longitudinal section of theront, showing the presumably not yet functional oral area, the secretory granules and the regular distribution of the mitochondria (arrowed). TEM, $\times 5,000$. – Fig. 22. Trophont, about 1 day old. Note the homeomeric macronucleus (N). TEM, $\times 11,880$.

threads develop (Figs. 16–17). Within the tomont, the dense chromatin bundles are interspersed as discrete spherical or elongated accumulations in the electron-lucent material (Fig. 18). The nucleoli become less conspicuous or less numerous in the tomites. In the macronucleus of the theront they are absent. In the theront, the macronucleus becomes homeomeric again, with the dense chromatin bundles interdispersed in more equal proportions within the electron-lucent matrix.

Micronucleus

There are up to five micronuclei in the theront and phoront stages. The micronuclei are sub-spherical in shape, measure approximately $3\text{--}4 \times 4\text{--}5 \mu\text{m}$, and are located adjacent ($2 \mu\text{m}$ or less) to the macronuclear segments (Fig. 13). The micronuclear core consists of a thick, electron-dense mesh of chromatin embedded within and surrounded by a peripheral zone of lucent matrix. Compared with the macronuclear chromatin, the micronuclear web appears thicker but substantially less electron-dense. Micronuclei were not observed in the protomont stage.

Discussion

The “foamy”, electron-dense, alveolar inclusion of *C. irritans* trophonts is a feature unknown in other similar ciliates. A cloud of amorphous, sticky material discharged by mucocysts was described by Ewing et al. [13] as surrounding *Ichthyophthirius multifiliis* theronts during their approach and contact to a potential host. Mucocyst material is also secreted at later stage to form the cyst wall [12]. Precystic stages of another ciliate, *Tetrahymena rostrata*, also release mucocyst material that provides for the production of a cyst wall [22]. *C. irritans* mucocysts are identifiable with the spear-head shaped structures in Figs. 9–10, which are somewhat similar to the “mucous trichocysts” described by Roque et al. [26] in *I. multifiliis*. These structures, however, are rather inconspicuous in *C. irritans*. Even though they become more noticeable in the mature trophont, their involvement in the formation of the foam-like inclusion is dubious.

The foam appears to be delimited by a thin membrane which tightly coats its outward contours and is clearly in continuity with the walls of some of the electron-lucent vesicles (see arrowed areas in Fig. 6). As no other membrane is discernible at the cytoplasmic border of the foam, this membrane is most likely the parasite’s plasma-lemma.

The function of this foam-like substance is similarly unclear. Since the foam was not observed before the trophonts were approximately 2 days old, it may be hypothesized that the secretion of this substance is associated with an active preparatory phase the parasite undergoes before leaving the fish. However, as this substance thins out towards the end of the trophont stage, its function is unlikely to be osmoregulatory. Perhaps the numerous vesicles present within this substance contain

lytic enzymes essential for extracellular digestion. This would aid in the “tunnelling” action of the growing trophont in the fish integument. However, too little information on the physiological interaction between this parasite and its host is presently available to determine which of these interpretations, if any, is correct.

The protomont does not adhere immediately to the substrate, but remains active for up to several hours before gradually slowing down to immobility.

The parasite becomes sticky, while its cell wall thickens and condenses into a cyst that hardens in 8–12 hours (Colorni, unpubl.). This newly formed involucre is PAS-negative (Colorni, unpubl.), while the foam-like substance produced a strong positive reaction when the periodic acid-silver methenamine method for carbohydrates in TEM [24] was applied. This suggests that the foam-like substance consists of neutral mucopolysaccharides and further indicates that its secretion and the secretion of the cyst are two consecutive and independent phenomena.

The Golgi apparatus was detected at the trophont stage only.

The Lieberkühn’s (or “Watchglass”) organelle, a structure which lies between the kinetid ridges of the oral cavity of hymenostome ciliates [10, 21], was absent from all *C. irritans* stages.

As already observed by Brown [1], the macronucleus of *C. irritans*, unlike that of other ciliates, persists throughout all phases of the life cycle.

A substantial reorganization of the endoplasm proceeds inside the tomont. Although the breaking down of distinct structures at this stage is likely due to cellular autophagy, poor penetration of glutaraldehyde cannot be ruled out, as the hardened cyst is extremely efficient in isolating the parasite from a possible hostile environment at its delicate phase of reproduction. As previously noted [6, 23], tomita development is very asynchronous. Excystment can occur weeks apart even among tomonts spontaneously and nearly simultaneously dropped from the same host and incubated under identical conditions. Consequently, the precise stage at which cilia formation commences in the tomita could not be determined in the present study.

While the morphology of the theront’s oral apparatus suggests that the mouth is not functional at this stage, the trophont’s oral ciliature arranged in a circular “radula” seems particularly specialized for burrowing and scraping. Contrary to Sikama [27], who reported the presence of contractile vacuoles in young trophonts, neither in the present study nor in those of Nigrelli and Ruggieri [23] and Canella [2] were contractile vacuoles identified at any stage. A well defined area for evacuation of food residues (cytoproct or cytopye) was not detected.

The Red Sea strain appears nearly identical to that described by Nigrelli and Ruggieri [23]; some minor differences, however, exist: the protrusible apparatus reported by these authors, and identified as a round bulb protruding from the center of the cytopharynx by Cheung et al. [5], bears a vague resemblance to a “perforatorium” occasionally observed in Eilat theronts [8] but not in trophonts. Also, a higher number of kinetid rows (78–80

vs. 65–75) was present in the Red Sea strain. A caudal cilium, occasionally observed previously [Colorni, unpubl. data] in theronts, was not seen in the present study. The recent discovery of an apparently distinct, extremely virulent form of *Cryptocaryon* in the Mediterranean Sea [11] indicates that the genus *Cryptocaryon* may include more than one species.

The striking similarities between the marine *C. irritans* and the freshwater *I. multifiliis* (both are holotrich ciliates, both are histophagous fish parasites, both penetrate the epithelia as far as, but virtually never beyond the basal membrane, both have polymorphic life cycles with encystment and palintomic reproduction) have led several investigators [9, 20, 25] to consider them as respective “counterparts” which happen to live in different aquatic habitats. The present investigation has indicated that their development differs significantly and the similarities between the two ciliates are the result of an adaptive convergence of life histories rather than phylogenetic proximity. This further emphasizes the need for a reassessment of the taxonomical status of *C. irritans*, a ciliate still incertae sedis.

Acknowledgements

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