and on cladistic analysis of morphological data. *J. Euk. Microbiol.*, 40:411-421.

Warton, A. & Honigberg, B. M. 1979. Structure of trichomonads as revealed by scanning electron microscopy. *J. Protozool.*, 26:56-62.

Watkins, R. A. , O'Dell, W. D. & Pinter A. J. 1989. Redescription of flagellar arrangement in the duck intestinal flagellate, *Cochlosoma anatis,* and description of a new species, *Cochlosoma soricis* n. sp. from shrews. *J. Protozool.*, 36: 527-531.

Wenrich, D. H. 1921. The structure and division of *Trichomonas muris* (Hartmann). *J. Morphol.*, 36:119-155.

Wenrich, D. H. 1943. Observations on the morphology of *Histomonas* (Protozoa, Mastigophora) from pheasants and chickens. *J. Morphol.*, 72:279-303.

Wenrich, D. H. 1944a. Studies on *Dientamoeba fragilis* (Protozoa). IV. Further observations, with an outline of present-day knowledge of this species. *J. Parasitol.*, 30:322-338.

Wenrich, D. H. 1944b. Comparative morphology of the trichomonad flagellates of man. *Am. J. Trop. Med. Hyg.*, 24:39-51.

Wenrich, D. H. 1944c. Morphology of the intestinal trichomonad flagellates in man and of similar forms on monkeys, cats, dogs and rats. *J. Morphol.*, 74:189-211.

Wenrich, D. H. & Emerson, M. A. 1933. Studies on the morphology of *Tritrichomonas foetus* (Riedmüller) (Protozoa, Flagellata) from American cows. *J. Morphol.*, 55:193-205.

Wenrich, D. H. & Nie, D. 1949. The morphology of *Trichomonas wenyoni* (Protozoa, Mastigophora). *J. Morphol.*, 85:519-531.

Yamin, M. 1979a. Flagellates of the orders Trichomonadida Kirby, Oxymonadida Grassé, and Hypermastigida Grassi & Foà reported from lower termites (Isoptera families Mastotermitidae, Kalotermitidae, Hodotermitidae, Termopsidae, Rhinotermitidae, and Serritermitidae) and from the wood-feeding *Cryptocercus* (Dictyoptera: Cryptocercidae). *Sociobiology,* 4:3-117.

Yamin, M. 1979b. Scanning electron microscopy of some symbiotic flagellates from the termite *Zootermopsis*. *Trans. Am. Microsc. Soc.*, 98:276-279.

ORDER RETORTAMONADIDA, GRASSÉ

by
GUY BRUGEROLLE and JOHN J. LEE

Retortamonads are small (5-20 µm) bacterivorous flagellates with two or four flagella; one of them is turned backward and associated with a conspicuous antero-ventral cytostomal aperture (Fig. 1a). Basal bodies of the flagella are closely associated with the anterior nucleus and with the two fibrils lining the cytostome. The right lip of the cytostome is bordered by a striated or paracrystalline fiber which terminates by a posterior hook (Fig. 1d,e). The cell surface is underlain by a corset of microtubules (Fig. 1c) except in the bottom of the cytostome where endocytosis takes place. The recurrent flagellum has typically two to three fin-like lamellae along the axoneme (Fig. 1d,e). There are no mitochondria, Golgi apparatus, hydrogenosomes, or axostyles. They reproduce by binary fission and the mitotic spindle is intranuclear. They are transmitted from host to host by resistant cysts. Most of them are parasitic in the digestive tract of animals; however, free-living species have been reported (Bernard et al., 1997). The group has been described in Brugerolle (1991); Brugerolle and Mignot (1990); Vickerman (1982). Only two genera have been described: *Retortamonas* and *Chilomastix.*

FAMILY RETORTAMONADIDAE

Genus ***Retortamonas*** Grassi

Retortamonas (syn=*Embadomonas, Plagiomonas, Waskia*) are small pyriform or fusiform flagellates with only 2 flagella. The recurrent flagellum is associated with the cytostomal pocket but extends posteriorly (Fig. 2). Electron microscopy has shown that 1 basal body in each pair has no flagellum (barren basal body) and a striated fiber connecting the nucleus to 1 pair of basal bodies. They form ovoid cysts. Among the 18 species described, several live in the lower gut of insect larvae of Trichoptera, Coleoptera, Diptera, such as *R. alexeieffi, R. agilis* (Mackinnon 1916) from the crane fly larvae *Tipula*, Orthoptera such as *R. gryllotalpae* from the mole cricket (Wenrich, 1932), also in water bugs, roaches, termites; list of invertebrate species in Grassé (1952). Other species live in intestine of vertebrates such as *R. intestinalis* from humans and monkeys (Wenyon,

1926), *R. caviae* from the guinea pig caecum (Nie, 1950), *R. mitrula* from *Marmotta* (Kirby and Honigberg, 1950). Still other species have been reported in the caecum of mammals (monkeys, sloth, sheep) and in the rectum of lizards, snakes, tortoises, anurans, and urodeles (Bishop, 1931). A complete list of vertebrate species is provided by Kulda and Nohynkovà (1978). Electron microscopic study by Brugerolle (1977).

Genus ***Chilomastix*** Alexeieff

Chilomastix (syn=*Macrostoma, Fanapetia*) have a pyriform and twisted cell with 3 anteriorly directed flagella and 1 recurrent flagellum beating in the ventral cytostomal pocket (Figs. 1,3). The right fibril bordering the cytostome is thicker and forms a hook at its posterior extremity where the

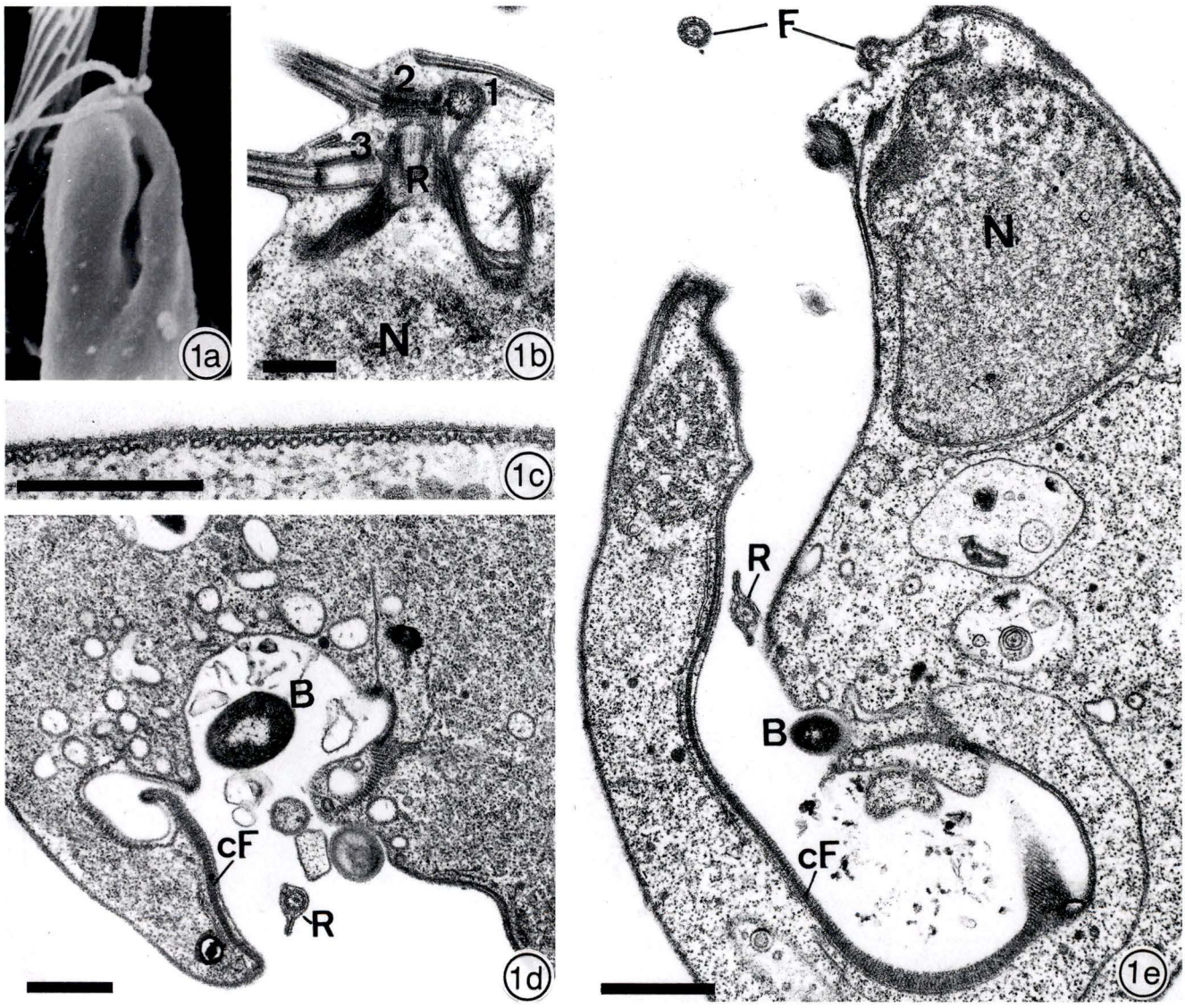
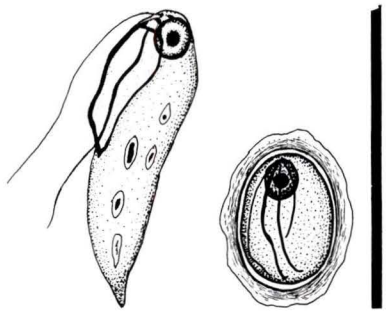


Fig. 1a,b,c,d,e. Scanning and transmission electron microscopic views of *Chilomastix*. Fig. 1a. Scanning view of *C. bettencourti* from the caecum of mouse, showing the three apical flagella inserted at the top of the elongated cytostomal opening. Fig. 1b. Basal bodies 1,2,3 of the anteriorly directed flagella, arranged around the basal body of the recurrent intracytostomal flagellum (R). Fig. 1c. Corset of interlinked microtubules under the plasma-membrane. Figs. 1d,e. Transverse and longitudinal sections of the cytostome/cytopharynx containing the recurrent flagellum (R) and bordered by a paracrystalline right fiber (cF). Bacteria in course of phagocytosis at the bottom of the cytopharynx; nucleus (N). Bar=10 µm. (Photographs from G. Brugerolle)

cytopharynx takes place. Pyriform cysts have a single nucleus and internal cytostomal fibers (Fig. 3). Among the 29 species described, several live in invertebrates hosts (see list in Grassé, 1952): termites, sea urchins, and leeches such as *C. aulastomi* (Bêlâr, 1921). Among the species living in vertebrates, several live in mammals (Geiman, 1935), *C. mesnili* from man (Fig. 3)(Kofoid and Swezy, 1920; Wenyon, 1926) is a common parasite which multiplies in diarrheic stools; *C. bettencourti* (Fig. 1a) is common in the caecum of rodents. Other species occur in primates, rodents, lagomorphs, horse, goat, ducks, galliform birds, lizards, amphibians, and marine fishes; *C. gallinarum* (Boeck and Tanabe, 1926) from the caecum of poultry is a potential pathogen. A complete list of *Chilomastix* species of vertebrates is provided by Kulda and Nohynkovà (1978). Electron microscopic study by Brugerolle (1973).



Figs. 2. *Retortamonas agilis* from *Tipula* larvae (after Mackinnon, 1916); flagellate and cyst. Bar=1 µm.

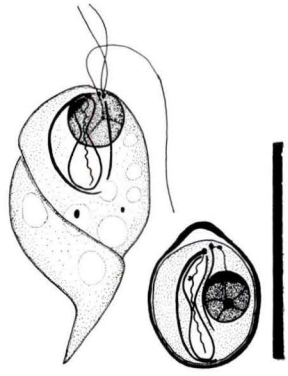


Fig. 3. *Chilomastix mesnili* from man (after Kofoid and Swezy, 1920); flagellate and cyst. Bar=10 µm.

LITERATURE CITED

Bêlar, K. 1921. Protozoenstudien III *Chilomastix aulastomi. Arch. Protistenkd.,* 43:439-446.

Bernard, C., Simpson, A. G. & Patterson, D. J. 1997. An ultrastructural study of a free-living retortamonad, *Chilomastix cuspidata* (Larsen et Patterson, 1990) n. comb. (Retortamonadida, Protista). *Europ. J. Protistol.*, 33:254-240.

Bishop, A. 1931. A description od *Embadomonas* n. sp. from *Blatta orientalis, Rana temporaria, Bufo vulgaris, Salamandra maculosa*, with a note upon the "cyst" of *Trichomonas. Parasitology,* 23:286-300

Boeck, W. C. & Tanabe, M. 1926. *Chilomastix gallinarum*, morphology, division and cultivation. *Am. J. Hyg.,* 6:319-336.

Brugerolle, G. 1973. Etude ultrastructurale du trophozoite et du kyste chez le genre *Chilomastix* Alexeieff, 1910 (Zoomastigophorea, Retortamonadida Grassé, 1952). *J. Protozool.,* 20:574-585.

Brugerolle, G. 1977. Ultrastructure du genre *Retortamonas* Grassi 1879 (Zoomastigophorea, Retortamonadida Wenrich 1931). *Protistologica,* 13:233-240.

Brugerolle, G. 1991. Flagellar and cytoskeletal systems in amitochondrial flagellates: Archamoebae, Metamonada and Parabasala. *Protoplasma,* 164:70-90.

Brugerolle, G. & Mignot, J. P. 1990. Phylum Zoomastigina, class Retortamonadida. *In*: Margulis, L., Corliss, J. O., Melkonian, M. & Chapmann, D. J. (eds.), *Handbook of Protoctista*. Jones & Bartlett Publishers Boston. pp 259-265

Geiman, Q. M. 1935. Cytological studies of the *Chilomastix* of man and other mammals. *J. Morphol.,* 57:430-453.

Grassé, P.- P. 1952. Ordre des Retortamonadines. *In:* Grassé, P.-P. (ed.), *Traité de Zoologie*. Vol. I. Masson et Cie, Paris. pp 824-831

Kirby, H. & Honigberg, B. M. 1950. Intestinal flagellates from a wallaroo, *Macropus robustus. Univ. Calif. Publ. Zool.,* 55:35-66.

Kofoid, C. A. & Swezy, O. 1920. On the morphology and mitosis of *Chilomastix mesnili* (Wenyon), a common flagellate of the human intestine. *Univ. Calif. Publ. Zool.*, 20:177-244.

Kulda, J. & Nohynkovà, E. 1978. Flagellates of the human intestine and of the intestines of other species. *In*: Kreier, J. P. (ed.), *Parasitic Protozoa.* Vol. 2. Academic Press, New York. pp 2-138

Mackinnon, D. L. 1916. Studies on parasitic protozoa. III. (a) Notes on the flagellate *Embadomonas*. (b) The

multiplication cysts of Trichomastigine. *Q. J. Microsc. Sci.*, 61:105-118.
Nie, D. 1950. Morphology and taxonomy of the intestinal protozoa of the guinea-pig, *Cavia porcella*. *J. Morphol.*, 86:381-493.
Vickerman, K. 1982. Mastigophora. *In*: Parker S. P. (ed.), *Synopsis and Classification of Living Organisms*. Vol. I. McGraw-Hill Book Company, New York. pp 496-508
Wenrich, D. H. 1932. The relation of the protozoan flagellates, *Retortamonas gryllotalpae* (Grassi, 1879) Stiles, 1902 to the species of the genus *Embadomonas* Mackinnon, 1911. *Trans. Am. Microsc. Soc.*, 51:225-238.
Wenyon, C. M. 1926. *Protozoology*. Ballière, Tindall & Cox, London.

CLASS PRASINOPHYCEAE

T. Christensen ex P.C. Silva, 1980

By Øjvind Moestrup

The Prasinophyceae (synonyms=Micromonadophyceae, Prasinomonadida) comprises a small number of unicellular algae (probably 100-200 species), mainly flagellates measuring 2-30 μm in length. Much larger stages occur in the life cycle of some species, e.g. up to nearly 1 mm in *Halosphaera,* and an increasing number of extremely small species are presently being found in the marine picoplankton. The latter appear to be reduced rather than primitive forms. Members of the Prasinophyceae are considered to represent some of the most primitive green flagellates, and numerous fossils resembling extant prasinophyceans have been found in precambrian deposits (e.g., *Tasmanites*; 60 genera are mentioned by Tappan (1980) but not included below). The extant genera are morphologically very diverse, probably reflecting the long evolutionary history of the group. More advanced green algae are thought to derive from prasinophyceans, and attempts have been made to classify some of the genera in other classes of green algae with which these genera share common ancestors. However, the genera of the Prasinophyceae share many features indicating genuine phylogenetic relationship and specialists classify prasinophyceans into a single class (Moestrup and Throndsen, 1988; Melkonian, 1990; Sym and Pienaar, 1993). Classification into orders and families is based mainly on ultrastructural features and gene studies have provided no clear answers (Daugbjerg et al., 1995). A stable classification at the order and family level must await studies of additional genes.

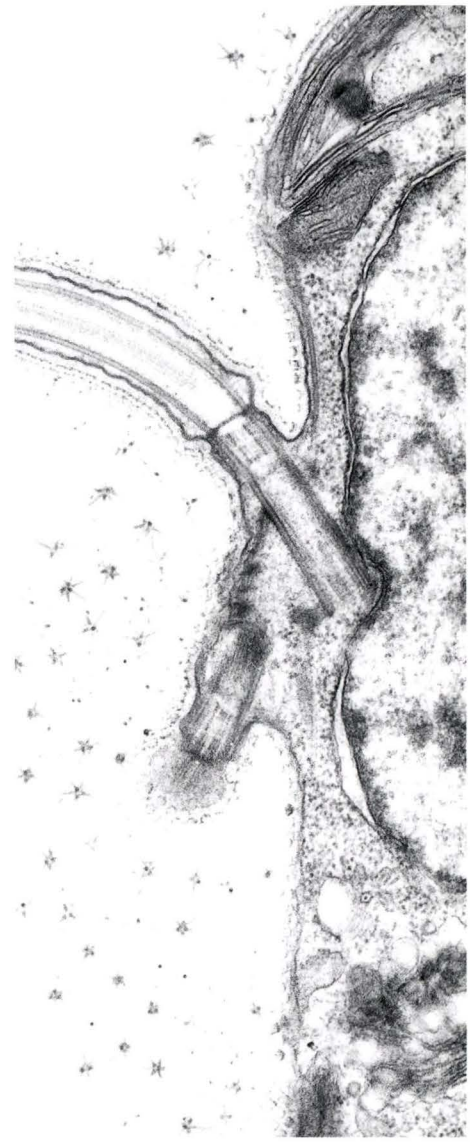


Fig. 1. *Nephroselmis rotunda,* showing periplast scales on cell body and flagella and the long basal bodies characteristic of prasinophyceans. x30,000. (From Moestrup and Ettl, 1979)