

Review of diversity and taxonomy of cercomonads

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Summary

Cercomonads are very common heterotrophic flagellates in water and soil. Phylogenetically they are a key group of a protistan phylum Cercozoa. Morphological and taxonomical analysis of cercomonads reveals that the order Cercomonadida (Vickerman) Myl'nikov, 1986 includes two families: Cercomonadidae Kent, 1880 (=Cercobodonidae Hollande, 1942) and Heteromitidae Kent, 1880 em. Myl'nikov, 2000 (=Bodomorphidae Hollande, 1952), which differ in several characters: body shape, temporary/habitual pseudopodia, presence/absence of plasmodia stage and microtubular cone, type of extrusomes. The family Cercomonadidae includes *Cercomonas* Dujardin, 1841 and *Helkesimastix* Woodcock et Lapage, 1914. All species of *Cercobodo* are transferred to the genus *Cercomonas*. The family Heteromitidae includes *Heteromita* Dujardin, 1841 emend. Myl'nikov et Karpov, *Protaspis* Skuja, 1939, *Allantion* Sandon, 1924, *Sainouron* Sandon, 1924, *Cholamonas* Flavin et al., 2000 and *Katabia* Karpov et al., 2003. The names *Bodomorpha* and *Sciviamonas* are regarded as junior synonyms of *Heteromita*. The genus *Proleptomonas* Woodcock, 1916 according to its morphology is not a cercomonad, and is not included in the order. The genus *Massisteria* Larsen and Patterson, 1988 is excluded from the order Cercomonadida on the basis of molecular evidence and different pseudopodia.

Key words: cercomonads, cercozoa, taxonomy, biodiversity, *Cercomonas*, *Massisteria*, *Helkesimastix*, *Cercobodo*, *Heteromita*, *Protaspis*, *Allantion*, *Sainouron*, *Cholamonas*, *Katabia*, *Bodomorpha*, *Proleptomonas*, *Sciviamonas*

INTRODUCTION

Cercomonads (the order Cercomonadida) are small heterotrophic flagellates, which are very common in water and soil habitats and have worldwide distribution. Since they are all similar, their diversity and taxonomy are not well known. They play an essential role in the

natural food chains, grazing bacteria. Cercomonads occupy a key position in the phylogenetic trees of eukaryotes (Cavalier-Smith, 2002; Simpson and Roger, 2002), but their cytoskeleton structure and molecular phylogeny are poorly studied (Karpov et al., 2003). Recent publications on the molecular phylogeny of cercomonads with new sequences of the SSU rRNA

gene of many cercomonads (Cavalier-Smith and Chao, 2003) have shown that this is an important group of a huge protistan branch, called Cercozoa, that includes thaumatomonads, some filose amoebae, chlorarachnids, plasmodiophorids, and several genera of heterotrophic flagellates.

Recently, more new genera have been described (Flavin et al., 2000; Vickerman et al., 2002; Karpov et al., 2003) or moved to Cercozoa (Vickerman et al., 2002), which may or may not be included in the order Cercomonadida. At the same time, the old names of some species and genera (e.g. *Heteromita/Bodomorpha*, *Cercomonas/Cercobodo*) are under discussion (Patterson and Zölffel, 1991).

As it is clear from this short introduction, we have to pay more attention to biology, biodiversity and taxonomy of cercomonads to resolve current questions. The goal of this paper is the revision of biodiversity and taxonomy of cercomonads.

GENERAL DESCRIPTION OF CERCOMONADS

Morphology. Cercomonads are normally free-living heterotrophic amoeboid flagellates with a naked body and two smooth heterodynamic flagella (Fig. 1). The anterior flagellum is directed forward and makes a flapping movement; the recurrent flagellum runs posteriorly under the ventral side of the cell. The flagellates commonly produce pseudopodia for feeding, not for movement.

Classification. Order Cercomonadida: as Cercomonadidea was established by Poche (1913) for replacement of Rhizomastigina Bütschli, 1883 and contained a tribe Cercomonadoidae Poche, which included a single family Cercomonadidae Kent with the genus *Cercomonas*. K. Vickerman (in: Honigberg, 1984; Lee, 1985) created a new definition of the order Cercomonadida with the genera *Cercomonas* and *Heteromita* based on the ultrastructure of two species of *Cercomonas*. Then the order was revised by Mylnikov (1986), who studied the ultrastructure of several cercomonad species. At present, the genera *Cercomonas*, *Heteromita*, *Bodomorpha*, *Helkesimastix* and *Massisteria* are generally accepted as cercomonads (Patterson and Zölffel, 1991; Mylnikov, 2000; Patterson et al., 2000). According to SSU rRNA gene analysis, *Massisteria* should be excluded from the order, whereas *Proleptomonas* should be included into it (Vickerman et al., 2002; Cavalier-Smith and Chao, 2003). The generic name *Bodomorpha* seems to be a younger synonym of *Heteromita* (see discussion below). Some other heterotrophic flagellates (*Allantion* and *Sainouron*) exhibit a certain similarity to cercomonads and have been included by A.P. Mylnikov in the order Cercomonadida *incertae sedis* (Mylnikov, 2000), though N. Vørs showed that they have only one anterior

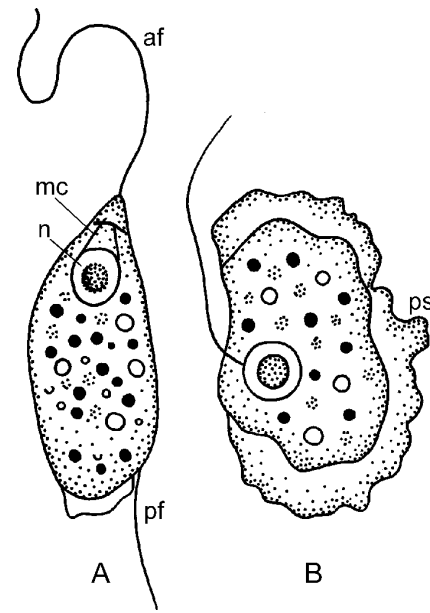


Fig. 1. General view of cercomonad flagellate (A) and amoeboid (trophic) stages (B) under the light microscope (after: Mylnikov, 1995). Abbreviations: af - anterior flagellum, mc - microtubular cone (nuclear projection), n - nucleus, pf - posterior flagellum, ps - pseudopodia.

flagellum and therefore excluded them from the otherwise biflagellate cercomonads (Vørs, 1992). Recent investigations added more new genera to cercomonads: *Cholamonas*, *Proleptomonas* and *Katabia* (Flavin et al., 2000; Vickerman et al., 2002; Karpov et al., 2003). Thus, at present we have about ten genera of cercomonads under discussion.

Habitat. Cercomonads live in marine, brackish and fresh waters, including anoxic habitats, and sewage treatment plants (Zhukov, 1971; Hänel, 1979; Starmach, 1985; Ekebom et al., 1995/96; Patterson and Lee, 2000; Bernard et al., 2000 *etc.*). They may occupy microbial mats around stromatolites (Al-Qassab et al., 2002). Heterotrophic flagellates of the genera *Cercomonas*, *Heteromita* and *Allantion* are very common in soil as well (Sandon, 1924, 1927; Ekelund and Patterson, 1997). Their biomass may compose half of the total biomass of soil protozoa (Arndt et al., 2000). Unfortunately, researchers normally overlook these flagellates, because they are rather small (about 10 μm) and difficult to identify.

Taxonomic and phylogenetic relationships. Some cercomonads investigated are similar to protostelids (primitive slime molds) in their life-cycle, tubular cristae of mitochondria, and some elements of cytoskeleton (Karpov, 1997). However, molecular phylogeny based on SSU rDNA suggests that *Cercomonas* and *Heteromita* are closely related to the heterotrophic flagellates *Thaumatomonas*, *Cryothecomonas*, and filose testate amoebae, e.g. *Euglypha rotunda* and *Paulinella*

chromatophora (Cavalier-Smith and Chao, 1996/97; 2003). All these organisms seem to be related to the desmothoracid heliozoans, chlorarachniophyte algae and the intracellular phytoparasitic plasmodiophorids (Cavalier-Smith and Chao, 2003; Nikolaev, 2003; Nikolaev et al., 2004).

DIVERSITY AND TAXONOMY OF THE GENUS *CERCOMONAS* DUJARDIN, 1841

The most complicated genus of cercomonads is *Cercomonas* Dujardin, 1841. There is common opinion that “Species identities within *Cercomonas* are currently unclear and this genus is in urgent need of attention.” (Al-Qassab et al., 2002, p. 136). This means that the cercomonad species are all similar to each other in samples, and even experts have great difficulties with their identification. A short historical issue of the genus taxonomy may partly explain this situation.

The genus *Cercomonas* was established for amoeboid flagellates with one flagellum, which usually produce posterior pseudopodia (Dujardin, 1841). Other authors used this name for gliding flagellates with two heterodynamic flagella (Wenyon, 1910, 1926; Hovasse, 1937), thereby changing the diagnosis of this genus. Some authors took into account that the posterior flagellum of these flagellates lies close to the ventral cell surface and might be concealed by posterior pseudopodia, and therefore considered that Dujardin had overlooked the posterior flagellum (Klebs, 1892; Wenyon, 1910). Indeed, some species of *Cercomonas* have a relatively short posterior flagellum, which is visible when the cell turns to change the direction of movement or after chemical fixation and staining (Zhukov, 1971; Mylnikov, 1986b). I. Krassiltschik described the second flagellum of such amoeboid flagellates, as well as the formation of pseudopodia, feeding and reproduction, and established a new name *Cercobodo* to distinguish them from uniflagellate *Cercomonas* Dujardin, 1841 (Krassiltschik, 1886). After this publication many authors used the name *Cercobodo* for such biflagellate protists (Lemmermann, 1910, 1914; Klug, 1936; Skuja, 1939, 1948, 1956). Thus, the diagnosis of genus *Cercomonas* formally differs from that of *Cercobodo* only in the absence of the second flagellum.

In the course of time several genera were established for the amoeboid biflagellate flagellates such as *Dimastigamoeba* Blochmann, 1894, *Prismatomonas* Massart, 1920, *Cercomastix* Lemmermann, 1914 and others (Patterson and Zölffel, 1991). The diagnoses of these genera are very similar and correspond to the diagnosis of the genus *Cercomonas* (Blochmann, 1886; Meyer, 1897; Massart, 1920). The majority of modern authors accept that Dujardin overlooked the second flagellum, and now use only the name *Cercomonas* for

such amoeboid flagellates (Mignot and Brugerolle, 1975; Schuster and Pollack, 1978; Zölffel, 1986). More or less the whole list of *Cercomonas* species was published under the name *Cercobodo* in some guides (Lemmermann, 1914; Zhukov, 1971; Starmach, 1985). It should be noted that most *Cercobodo* species were described by Skuja (1939, 1948, 1956).

At present, the name *Cercomonas* has to be considered as the senior synonym for the genera listed (Patterson and Zölffel, 1991), therefore new taxonomic combinations are required for such flagellates (see **Revised taxonomy of the order Cercomonadida** below).

DESCRIPTION OF THE GENUS *CERCOMONAS*

Light microscopy. *Cercomonas* unites flagellates with pseudopodia of different shape including flattened, thin, filose and branched. The cell size varies from 4 µm (*Cercomonas minimus*) to 65 µm (*Cercomonas gigantea*), but most species are about 10 µm (Mylnikov, 1986b, 2002). These flagellates can produce pseudopodia from any part of the cell, not only at the posterior end as noted in some references (Lemmermann, 1914; Zölffel, 1986). Although most species of *Cercomonas* form flattened wide or finger-like pseudopodia, reticulopodia (rhizopodia) were found in *Cercomonas cometa* and *C. metabolicus* (Hollande, 1942a; Mylnikov, 1986a; Zhukov and Mylnikov, 1987). All pseudopodia in *Cercomonas* are spread upon a solid substrate or the surface film of water and are almost always attached to the substrate in contrast to some amoebae (*Vexillifera* or *Nuclearia*), whose pseudopodia may be directed upwards (Page, 1988).

Cercomonas has two permanent heterodynamic flagella even in the amoeboid state. The anterior flagellum of motile oval or elongated cells is directed forward and beats slowly, with a flapping movement, often as if touching the substrate. The posterior flagellum trails back (and lies ventrally) close to the substrate. It lies either in a groove (*Cercomonas longicauda*, *C. granulatus*) (Mylnikov, 1986b, 1987; Lee and Patterson, 2000), or inside a cytoplasmic channel (*Cercomonas crassicauda*) (Mylnikov, 1989a), or is not associated with any discrete cell structure (*Cercomonas metabolicus*). Mobile cells usually have a small posterior pseudopodium. The motion of the anterior flagellum is not correlated with the gliding movement of the cell body. It has been observed that the posterior flagellum makes undulations, which seem to push the cell forward (Mylnikov, 1986b).

Actively gliding cells can relatively quickly transform to an amoeboid form, which loses anterior-posterior orientation. At the amoeboid (trophic) stage the cell is usually immobile and flattened. The amoeboid cells of *Cercomonas cometa* can aggregate

into cell clusters (Mylnikov, 1986a; 1990). The bright light of the microscope initiates rapid retraction of the pseudopodia and transformation of amoeboid cells to the motile state.

In motile cells the nucleus is situated in the front part of the cell near the insertion of the flagella. Sometimes, an anterior nuclear projection associated with microtubular cone is visible (Fig. 1 A). The contractile vacuoles do not usually occupy a fixed place in the cell (Mylnikov, 1986b). Only some species (*Cercomonas metabolicus*, *C. norrvicensis*, *C. ovatus*) have anteriorly located contractile vacuoles, and this is one of the essential taxonomic characters of these species (Zhukov, 1971; Zhukov and Mylnikov, 1987). Food vacuoles are located in the central and posterior parts of the cell.

Electron microscopy reveals a rather complex structure of the cell, rich in organelles (Mylnikov, 1986b, 1986c, 1986d, 1987, 1992, 1995; Karpov, 1997; Mylnikov et al., 2000). The general organelle distribution of *Cercomonas* is shown in Figure 2. The cell surface is constituted by the plasmalemma, with a rather thick glycocalyx in some species. One or two kinds of extrusomes are normally present in each species under the plasma membrane: trichocysts, osmiophilic granules or bodies, and microtoxicysts (Fig. 3). The nucleus is located near the anterior end of the cell in the vicinity of the basal bodies. Profiles of the microbody are normally found around the nucleus and in other parts of cytoplasm as well. Several mitochondria with tubular or vesicular cristae are scattered throughout the cytoplasm. Two basal bodies connected by fibrillar bridges occupy an apical position and have an approximately orthogonal orientation to each other (Fig. 2). The lumen of the basal bodies may be electron translucent or filled with amorphous material (Fig. 2). The flagellar transition zone contains a typical transverse plate at the level of the cell surface. There are two to four lateral microtubular rootlets associated with the basal bodies (Mylnikov, 1989b). Their exact position and orientation is not clear in all the species investigated. The main character of the flagellar apparatus of *Cercomonas* is a conspicuous fibrillar rootlet originating from the anterior basal body or both basal bodies (Fig. 2). It extends towards the nucleus and has a granule at the end, from which the microtubular arrays originate and extend alongside the nuclear surface, forming the so-called microtubular cone (Figs 1 A; 2).

Life cycle. In some species of *Cercomonas* (e.g. *C. crassicauda*) (Fig. 4) the life cycle consists of vegetative uninucleate cells (actively motile cells and slightly motile amoeboid cells), multinucleate plasmodia and uninucleate cysts (Mylnikov, 1995, 2000). Plasmodia usually appear in mature cultures. They are more or less flattened, with several nuclei, sets of flagella and

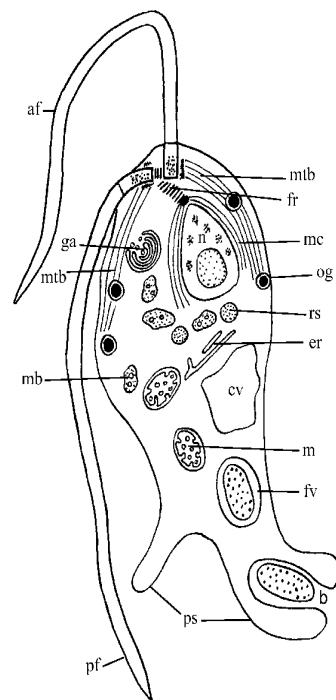


Fig. 2. Scheme of the internal organization of the cell in *Cercomonas* (after: Mylnikov, 1995, with corrections). *Abbreviations:* af – anterior flagellum, b - bacteria, cv - contractile vacuole, er - endoplasmic reticulum, fr - fibrillar rootlet, fv - food vacuole, ga - Golgi apparatus, m - mitochondria, mb - microbody, mc - microtubular cone, mtb - microtubular band, n - nucleus, og - osmiophilic granule, pf - posterior flagellum, ps - pseudopodia, rs - reserve substance.

contractile vacuoles. The plasmodium results from nuclear division without the consequent cell fission (Roberson, 1928; Zhukov and Mylnikov, 1987) or possibly also from the fusion of uninucleate cells (Shirkina, 1987). The number of nuclei in a plasmodium may reach 100 or more. The adult plasmodium produces extensions, this normally being followed by its fragmentation and disintegration into the uninucleate cells. Species producing plasmodia can also reproduce by normal binary fission. The cysts appear in mature cultures of some species as uninucleate spherical cells covered by a smooth (*Cercomonas gigantea*, *C. heidammene*) or plicate (*C. crassicauda*) envelope (Shirkina, 1987; Mylnikov, 2002).

Thus, the most complete life cycle of *Cercomonas* consists of several stages (Fig. 4). The transformation between the cyst, the flagellate and the amoeba may proceed in two ways, but the plasmodium may only produce flagellates, not amoebae or cysts. Other species of *Cercomonas* have more simple life cycles (Table 1). For instance, the life cycle of *Cercomonas metabolicus* consists of uninucleate motile and amoeboid cells

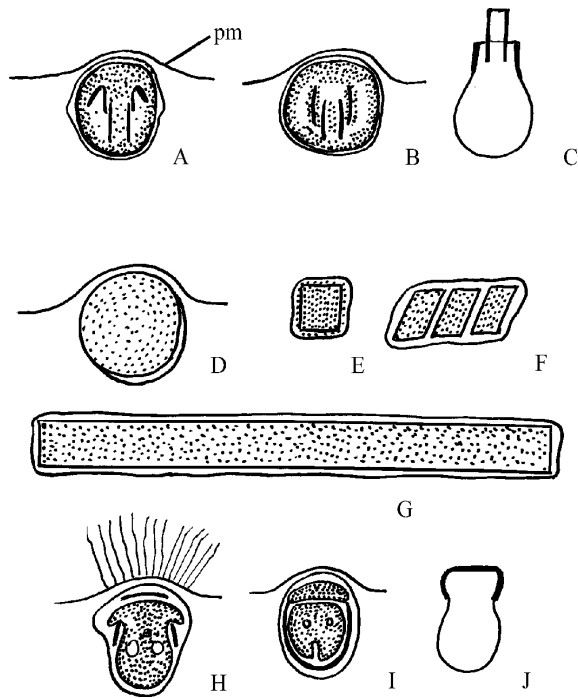


Fig. 3. Schematic drawing of the extrusomes of the cercomonads (after: Mylnikov, 1995, with corrections). A, B - mature microtoxycysts; C - discharged microtoxycyst; D - osmiophilic granule; E, F - cross sections of a single trichocyst (E) and battery of them (F); G - longitudinal section of trichocyst; H, I - mature kinetocysts; J - discharged kinetocyst. *Abbreviation:* pm - plasmalemma.

(Zhukov and Mylnikov, 1987). The presence and absence of plasmodia, swimming cells and cysts seem to be valuable taxonomic features (see below).

Habitat. *Cercomonas* is a widespread genus common in rivers and lakes (Lemmermann, 1914; Hamar, 1979; Auer and Arndt, 2002) and in freshwater reservoirs (Zhukov and Mylnikov, 1987). These flagellates are known from brackish waters (Tong et al., 1997; Arndt et al., 2000), and from soils of different types (Zhukov and Mylnikov, 1987; Ekelund and Patterson, 1997). Though *Cercomonas* spp. are aerobic protists, they occur at all stages of the sewage water treatment, including anoxic zones (Calaway and Lackey, 1962; Hänel, 1979; Mylnikov, 1986b; Zhukov and Mylnikov, 1983) as well as in natural anaerobic habitats (Bernard et al., 2000).

Species identification. Although *Cercomonas* flagellates have variable dimensions and a very flexible metabolic body of underdetermined shape, many species can be clearly identified, especially in cultures. Earlier it was shown that some conspicuous features such as the shape and sizes of motile cells, the length of flagella, the shape of pseudopodia, the location of the posterior

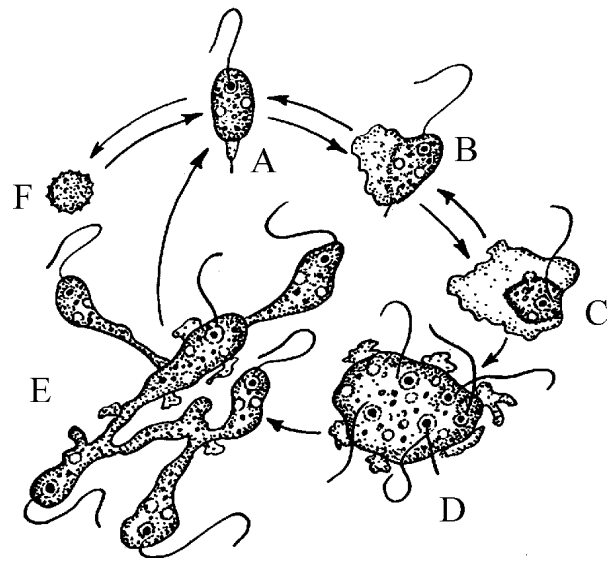


Fig. 4. The most complete life cycle of cercomonads (after: Mylnikov, 1995). A - flagellate; B-C - amoebae; D - plasmodium; E - plasmodium fragmentation; F - cyst. *Arrows* show the ways of cell transformation.

flagellum inside a cytoplasmic channel (or in a groove), the position of cell surface contact to the substrate, the number and position of contractile vacuoles, the cyst diameter and the character of its envelope and the presence of multinuclear plasmodia in the life-cycle could be successfully used for identification of *Cercomonas* species (Table 1). It was established that the so-called “culture” characters such as the presence of cysts and plasmodia in the life cycle can be maintained through several years of laboratory cultivation (Mylnikov, 1986b, 1992).

Molecular phylogenies based on SSU rRNA gene sequences show that *Cercomonas* splits in two clades (A and B), which are only sister groups on some trees (Cavalier-Smith and Chao, 2003). Clade A includes *C. plasmodialis*, *C. alexeieffi* and some other unidentified strains, and clade B contains *C. longicauda* plus 4 more unidentified strains. The authors explain this phenomenon by the presence of two long branches in clade B. Anyway, each clade has a high bootstrap support, and in one maximum likelihood tree they form a monophyletic group with low bootstrap support (Cavalier-Smith and Chao, 2003).

DIVERSITY AND TAXONOMY OF OTHER CERCOMONADS (FIG. 5)

Below descriptions are given of all other cercomonad genera with comments on their diversity and taxonomy. Morphological characters include the ultrastructural ones.

Heteromita Dujardin, 1841. This genus is represented by minute ovoid flagellates with a rigid body of definite

Table 1. Taxonomic features for the genus *Cercomonas*.

Species of <i>Cercomonas</i>	body length	body width	anterior flagellum	posterior flagellum	contr. vacuole number	cyst diameter	cyst surface	plasmodia	branched pseudopodia	extrusomes	symbiotic bacteria
<i>C. longicauda</i>	8-12	3-7	10-15	14-50	1-2	-	-	+	-	ob	-
<i>C. activus</i>	5-10	3-4	5-7	6-11	1	-	-	+	-	ob, tr	-
<i>C. cometa</i>	4-10	2-4	5-10	5-10	1	6-10	sm	+	+	mt	-
<i>C. crassicauda</i>	8-21	6-12	16-30	12-22	2-3	11-13	pl	+	-	ob	+
<i>C. metabolicus</i>	5-11	3-5	11-20	6-11	1-2	-	-	-	+	mt	+
<i>C. minimus</i>	3-6	2-3	2-3	5-6	1	2-3	sm	-	-	mt	-
<i>C. plasmodialis</i>	5-8	2-4	10-12	12-20	1	-	-	+	-	ob, tr	-
<i>C. varians</i>	6-13	6-7	15-20	12-18	1	-	-	+	-	ob	-
<i>C. ovatus</i>	8-10	6-8	12-18	12-17	1	-	-	-	-	-	-

Abbreviations: “-“ – absence of the feature, “+” – presence of the feature, mt – microtoxycysts, ob – osmiophilic bodies, sm – smooth, pl – plicate, tr – trichocysts. Dimensions are in μm .

shape and a small rostrum at the anterior end (Fig. 5). Flagella arise from a small pocket below the rostrum. A short anterior flagellum is directed laterally and makes frequent sweeps. The posterior end of the body is constantly shaking during movement. The flagellate produces small temporary pseudopodia for feeding at the anterior end of the cell. Cysts are found in some species. Plasmodia are not known. Bacterivorous.

The majority of *Heteromita* species including those described by Dujardin (1841) have been transferred to the genera *Colpodella* (= *Spiromonas*), *Dingensia* and *Bodo* (Lemmermann, 1910, 1914; Zhukov, 1971; Paterson and Zöllfel, 1991).

The modern concept of this genus is based on the study of *H. globosa* (Sandon, 1927; Robertson, 1928; Macdonald et al., 1977; Karpov, 1997). As neither Dujardin (1841) nor other authors have established the type species of this genus, we propose to consider the common and well-investigated species *H. globosa* sensu Macdonald et al. (1977) as a type species of this genus.

Heteromita globosa (Stein) Kent, 1880 emend. Macdonald et al., 1977. Neotype for the genus *Heteromita*: Stein, 1878: Taf. II; Macdonald et al., 1977.

Type figure 2, J (in: Macdonald et al., 1977, 258-260).

Diagnosis. Cells ovoid or pyriform, 5 – 8 μm in length and 3 – 6 μm in width. The anterior half of the body is slightly wider than the posterior region. Two heterodynamic acronematic flagella are inserted close together at the anterior extremity of the body. The anterior flagellum is slightly longer than the body and beats in antero-lateral direction in a helical manner from the proximal region to the tip. The posterior

flagellum is about twice as long as the other one and often trails passively behind the body. The flagellate moves forward in a vibratory manner. The longitudinal axis of the body is maintained at an angle of about 45° to the substratum and an acute angle to the posterior flagellum. The nucleus is close to the anterior cell end, the contractile vacuole is slightly posterior to the nucleus near the ventral surface. Bacteria are engulfed by short transient pseudopodia. The cysts are spherical, with a thin or a thick wall.

Differential diagnosis. *Heteromita globosa* differs from *H. reniformis*, *H. minima* and *H. terricola* in having a longer anterior flagellum.

Three species of *Heteromita* have already been investigated: *Heteromita globosa* (MacDonald et al., 1977), *Heteromita (Bodomorpha) reniformis* (Myl'nikov, 1984, 1995) and *Heteromita* sp. (Karpov, 1997). Their ultrastructural features may be summarised as follows (Fig. 6): the cell is covered only by the plasmalemma with single kinetocysts or batteries of them underneath, particularly in the flagellar pocket area; the basal bodies are inserted approximately at right angles to each other but in different planes; both basal bodies have dense cores in their lumen and are connected to each other by 3-4 fibrillar bridges; a spiral fibre, or cylinder connected to the A-tubules of the axoneme is present in the transition zone; the nucleus has a prominent nucleolus; a microbody or paranuclear body with amorphous contents is associated with the posterior part of the nucleus; the mitochondria have vermiform tubular or vesicular cristae. The structure of the rootlet system is not still clear. *Heteromita* has one striated

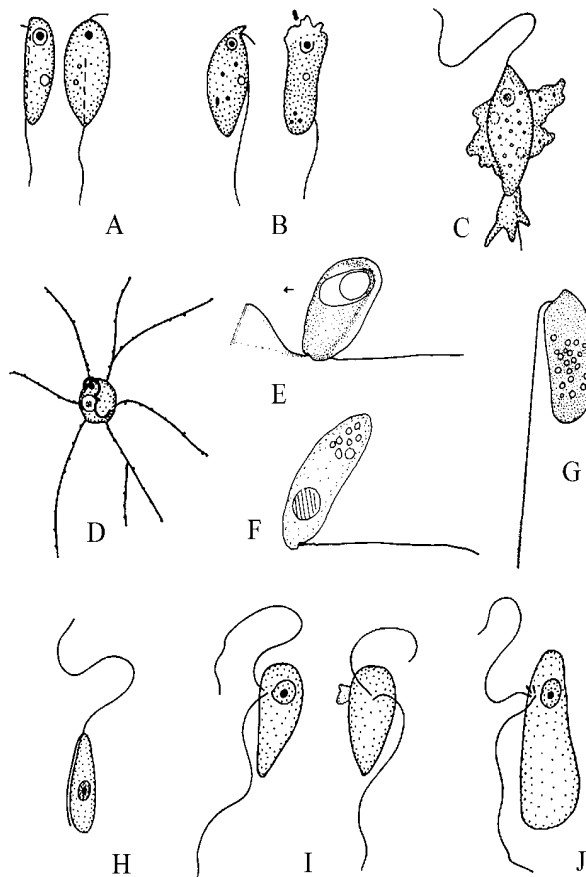


Fig. 5. Schematic drawings of cercomonads (after different authors). A - lateral (left) and dorsal (right) view of *Helkesimastix*; B - moving cell (left) and feeding cell (right) of *Heteromita*; C - *Cercomonas*; D - trophic cell of *Massisteria*; E - lateral view of *Protaspis* (arrow shows the direction of movement); F - lateral view of *Allantion*; G - *Sainouron*; H - *Proleptomonas*; I - lateral (left) and ventral (right) view of *Katabia*; J - *Cholamonas*. (The figures are not to scale).

fibrillar rootlet ending with a large dense granule near the surface of the nucleus. In *Heteromita*, unlike *Cercomonas*, this granule does not nucleate microtubules. The most prominent microtubular rootlet is associated with a fibrillar plate and has 4 to 8 microtubules. The nucleus has special extensions of the perinuclear space overlapping the posterior basal body with rootlets.

Species of *Heteromita* occur in fresh water and soil, including the Antarctic, and in brackish waters (Smith, 1978; Cowling and Smith, 1987; Tong et al., 1997). *H. globosa* was also reported from anoxic habitats (Bernard et al., 2000).

Molecular phylogeny based on SSU rRNA gene sequence shows that *H. globosa* groups with *Bodomorpha minima*, *Proleptomonas faecicola* and *Allantion* sp., forming a monophyletic group with both low and high

bootstrap values in different trees (Vickerman et al., 2002; Cavalier-Smith and Chao, 2003).

The genus *Bodomorpha* Hollande, 1952 was established by Hollande (1952) for small flagellates with a very short, laterally directed anterior flagellum and a long posterior flagellum, which had previously been assigned to *Pseudobodo* (Hollande, 1942b). Cells are kidney-shaped, and the flagella are inserted in a shallow subapical depression. The cell body is non-metabolic (Zhukov, 1971). The small flagellum and posterior end of the cell undergo a wobbling motion. Some clones of *Bodomorpha reniformis* can produce cysts.

Species of *Bodomorpha* occur in freshwater and soil and are widespread in Europe (Hollande, 1942; Zhukov and Mylnikov, 1987).

The descriptions of *Bodomorpha* and *Heteromita* are very similar. These flagellates have a rigid cell body without permanent pseudopodia and a relatively short anterior flagellum emerging from the small pocket. During gliding movement both flagellates characteristically shake their posterior end. Plasmodia and large pseudopodia are absent. The ultrastructure of *Bodomorpha reniformis* is very similar to that of *Heteromita globosa* (MacDonald et al., 1977; Mylnikov, 1984). The representatives of both species have a prominent microbody, kinetocysts, flagellar pocket, large mitochondria with tubular cristae, and a similar structure of flagellar apparatus. *Bodomorpha reniformis* differs from *Heteromita globosa* in the lateral position of the anterior flagellum and a lesser length. Similar cell structures were found in *Bodomorpha minima* (Mylnikov, 1995). These data demonstrate that the description of the genus *Bodomorpha* coincides with that of the genus *Heteromita* (because species of these two genera possess a similar set of main cell features). So, we agree with previous proposals (Patterson and Zölffel, 1991; Patterson et al., 2000) to consider *Bodomorpha* as a junior synonym of *Heteromita*.

Recently, a new small soil flagellate *Sciviamonas terricola* Ekelund et Patterson, 1997 was described (Ekelund and Patterson, 1997). The cells are 2.5- 4 µm long and have a roundish to ovate, D-shaped, laterally compressed body. Two heterodynamic flagella are inserted subapically at an angle of about 70°-90° to the anterior end of cell. The anterior flagellum is approximately of the cell length or slightly shorter, while the posterior flagellum is 1.5 to 2.0 times the cell length, and trails. Both flagella emerge from a broad subapical pocket. The area surrounding the flagellar pocket is rich in granules, possibly extrusomes. A contractile vacuole is located dorsally. Cells glide in a wobbling manner, much like *Heteromita globosa*. The posterior flagellum trails, while the anterior flagellum moves across the substrate in front of the cell. *Sciviamonas terricola* closely resembles *Heteromita* (= *Bodomorpha*) *minima* (Hollande, 1942b; Mylnikov, 1995), differing from it

only in the shorter posterior flagellum. This distinguishing character is of species level, therefore *Sciviamonas terricola* has to be transferred to the genus *Heteromita* where we retain it as *Heteromita terricola*.

Massisteria Larsen et Patterson, 1990. This genus was established for slightly motile and flattened flagellates. Their two short inactive flagella lie over the body surface in amoeboid cells. Cells form very thin branching pseudopodia, containing minute extrusomes and microtubules. Their rather complex life cycle includes, in addition to amoeboid cells, actively swimming biflagellated cells and plasmodia. Cysts are not known. Bacterivorous. To date only one marine species *M. marina* Larsen et Patterson, 1990 has been described. It resembles *Cercomonas cometa* in having thin branched pseudopodia, but *C. cometa* does not contain extrusomes in their pseudopodia (Mylnikov, 1990).

Ultrastructural investigations of amoeboid cells revealed the cercomonad-like organisation of the cell in *Massisteria marina* (Patterson and Fenchel, 1990). The flagellar basal bodies are inclined at an acute angle to each other and lie near the nucleus. A thin layer of amorphous electron dense material surrounds their proximal ends. A variable number of microtubules originate from the basal bodies and pass inside the cell and towards the cell surface. Both thin and branched pseudopodia are supported by several microtubules and contain small extrusomes with a concentric substructure. A single dictyosome is adjacent to the nucleus. The cell contains several mitochondria with tubular cristae. The nucleus has a central nucleolus. A homogeneous electron-dense microbody is close to the nucleus.

M. marina is widespread in marine waters (Larsen and Patterson, 1990; Vørs, 1992, 1993; Tong, 1997b; Tong et al., 1998; Ekeboom et al., 1995/96; Patterson and Lee, 2000).

Molecular phylogeny based on SSU rRNA gene sequence shows that *M. marina* does not belong to the *Cercomonas/Heteromita* branch, grouping with *Nuclearia*-like filose amoeba (Vickerman et al., 2002) or with N-Por filose amoebae and *Dimorpha*-like sp. with very low bootstrap support in all trees (Cavalier-Smith and Chao, 2003). Some of these organisms also have branching pseudopodia with granules, but their internal organisation is not known.

Massisteria has some characters similar to *Cercomonas*: complex life cycle including plasmodia, tubular cristae in mitochondria and microbody. But the latter characters are rather widespread among protists (Karpov, 2001), and cannot therefore specify a taxon. Pseudopodia of *Massisteria* are different from those of cercomonads, and acute angle between the basal bodies never occurs in cercomonads. Therefore we consider that the molecular phylogeny clarifies the position of *Massisteria* better than morphological analysis. As the

Massisteria branch is much further from cercomonads than thaumatomonads and even euglyphids, we do not include this genus in the order Cercomonadida.

Helkesimastix Woodcock et Lapage, 1914. This genus was erected for gliding, very metabolic elongated flagellates with a short anterior flagellum directed sideways, and a long posterior flagellum (Fig. 5). Both flagella emerge subapically from a small pocket. Cell body is cylindrical and elongated, with a small rostrum. A double row of refractile granules of unknown nature lies along the ventral side of the cell. A contractile vacuole is located posteriorly. A small unbranched pseudopodium forms at the posterior end of the cell.

This flagellate is similar to *Heteromita* in having a short anterior flagellum and rostrum, but differs in having a flexible body, a different type of gliding movement (the body does not shake) and in forming a posterior pseudopodium. The shape of the body and formation of pseudopodia make *Helkesimastix* similar to small species of *Cercomonas*, but the former differs from the latter in a much shorter anterior flagellum and the presence of a small rostrum. Cysts are unknown. The ultrastructure has not been studied.

These bacterivorous flagellates occur in fresh and brackish water, including sewage waters, and in soil (Woodcock and Lapage, 1914; Calaway and Lackey, 1962; Hänel, 1979; Zhukov and Mylnikov, 1983; Tong et al., 1997).

Allantion Sandon, 1924. Cells are oblong, cylindrical with rounded ends, and circular in cross section. The gliding flagellates have one visible trailing flagellum inserted subapically in a small ventral pocket (Fig. 5). The nucleus is located anteriorly. Refractile granules are located posteriorly. The cells glide rapidly and smoothly adhering to the substrate by the flagellum and the anterior end of the cell. The posterior end of the cell is raised at a sharp angle, and does not touch the substrate. Pseudopodia have not been observed. The cysts have a polyhedral shape. There are no published electron microscopic data on *Allantion*.

In general morphology *Allantion* is similar to *Heteromita*, differing from it in the absence of the anterior flagellum and in the raised position of the posterior end of the cell during movement (Vørs, 1992).

Species of this genus are rather common and widespread in soils from Arctic and Antarctic, Europe (Sandon, 1927; Tong et al., 1997); fresh and marine waters (Vørs, 1992, 1993; Tong, 1997a,b; Auer and Arndt, 2001). A.P. Mylnikov observed in samples that *Allantion* could capture small cercomonads and heterotrophic chrysomonads.

Molecular phylogeny based on SSU rRNA gene sequences shows that *Allantion* sp. is a sister branch to the *Proleptomonas/Heteromita* group (Cavalier-Smith and Chao, 2003).

Sainouron Sandon, 1924. These gliding flagellates have one visible trailing flagellum, which does not attach to the body (Fig. 5). A short anterior flagellum may be present. Cells have a rounded anterior end and generally narrower posterior end. The cell usually has a constant shape, but may occasionally become amoeboid. The cell length is usually 3–5 μm , rarely – 10–14 μm in cultures. A contractile vacuole is not visible. Cell conjugation was noted by Sandon (1927), who also observed (1924, 1927) that this flagellate might move like *Heteromita* with a rapid and wobbling motion, the flagellum trailing along the substrate, or less frequently might swim freely with a somewhat sinuous motion. The cysts are spherical, 6–8 μm in diameter. *Sainouron* can be distinguished from the similar *Allantion* by its capacity to produce amoeboid forms.

One species *S. mikroteron* was described from soil (Sandon, 1924). In morphology, behavior and habitat this species is similar to *Heteromita* and *Allantion*.

Protaspis Skuja, 1939. Heterotrophic gliding flagellates with two equal or subequal flagella inserting subapically on the ventral side. Usually they have a groove on the ventral surface, and a so-called nuclear cap, which looks like a microtubular cone of *Cercomonas*. A trailing flagellum is inserted to the left of the anterior flagellum, which beats stiffly. Ingestion takes place by means of pseudopodia emitted from the furrow (Skuja, 1939, 1948; Larsen and Patterson, 1990). Phagotrophic. One of the authors (A.P. Mylnikov) observed in samples that *Protaspis verrucosa* could capture small cells of bodonids and chryomonads.

These flagellates are found in brackish water, rarely in fresh waters and soil (Larsen and Patterson, 1990; Vørs, 1992, 1993; Tong, 1997a, 1997b; Tong et al., 1998; Ekelund and Patterson, 1997; Auer and Arndt, 2001).

There are no EM data published on *Protaspis*. The genus was previously included into the thaumatomonads because of the ventral furrow (Patterson and Zölffel, 1991). Thaumatomonads also have a flagellar pocket and scales on the cell surface. *Protaspis* does not have a flagellar pocket, has a microtubular cone and does not seem to have body scales. In these respects it is similar to cercomonads, and is therefore included in the order until further investigations.

Cholamonas Flavin et al., 2000. One species, *Cholamonas cyrtodiopsidis* Flavin et al., 2000, was described from the intestine of a diopsid fly, and was investigated in detail by light and electron microscopy (Flavin et al., 2000). These small flagellates measure 5–8 μm in length and 2–5 μm in width, have two long (1–1.5 times of body length) and two stubby flagella and a naked elongated body with one nucleus. The flagella emerge subapically. The stubby flagella contain very short axonemes consisting of nine singlet microtubules. The nucleus is closely associated with the flagellar

insertion. Golgi dictyosomes are located anteriorly to the nucleus, and a reticulate paranuclear body (microbody), posteriorly to it. There are two kinds of refractile granules in the cytoplasm, which correspond to the mushroom-like bodies of *Katabia* (see below). Mitochondria have tubular cristae. No contractile vacuoles have been detected. The kinetid consists of two symmetrical subunits, each with 2 basal bodies (one of which associates with a stubby flagellum). A compound microtubular rootlet of 6 to 10 microtubules runs posteriorly from each kinetid. There are additional fibers and bands associated with the basal bodies and developed cytoskeletal microtubules, which do not have connection with rootlets. Feeding on yeast is accomplished by rapid pseudopodial action at the posterior end of the cell.

The species is attributed to Cercomonadida because it possesses a microbody and has a kinetid architecture similar to some species of *Cercomonas*. But it has no microtubular cone characteristic of *Cercomonas*. It differs from all other cercomonads in its endocommensal habitat, swimming mode of movement, absence of microtubular cone, mycophagy, doubled kinetid, minimal production of pseudopodia. Because of the absence of a microtubular cone and production of temporary pseudopodia for feeding *Cholamonas* may be related to *Heteromita*.

Proleptomonas Woodcock, 1916. *Proleptomonas faecicola* (formerly considered a free-living kinetoplastid) is a soil cercomonad-like protist with a long anterior flagellum and a short posterior flagellum adhering to the cell body (Vickerman et al., 2002). It has an elongate cigar-shaped body 7–12 μm long and 1.5–3.0 μm wide. The long flagellum is 14–29 μm long and emerges apically. The posterior flagellum is as long as the body. Locomotion is very fast, with the body vibrating rapidly around a central midpoint. There is no phagotrophy, which means that the flagellate ingests by endocytosis, using coated pits. The nucleus is located in the middle of the cell, far from the kinetid, which produces microtubules superficially resembling the microtubular cone of *Cercomonas*. There are no extrusomes. The flagellate stage does not divide.

The rounded aflagellate stage is 6–9 μm in diameter. It has a central vesicular nucleus and vesicular inclusions. It undergoes binary fission to produce from 2 to 8 daughter cells inside the cyst wall.

This organism is similar to cercomonads in some respects: it has a naked surface, heterodynamic smooth flagella and tubular cristae in the mitochondria. However, it is different in many other respects: there is no nuclear-kinetosome connection, no extrusomes, no microbody, no pseudopodia. The microtubules of the cone emerge straight from the basal bodies (not from the fibrillar rootlet) and pass beneath the plasmalemma

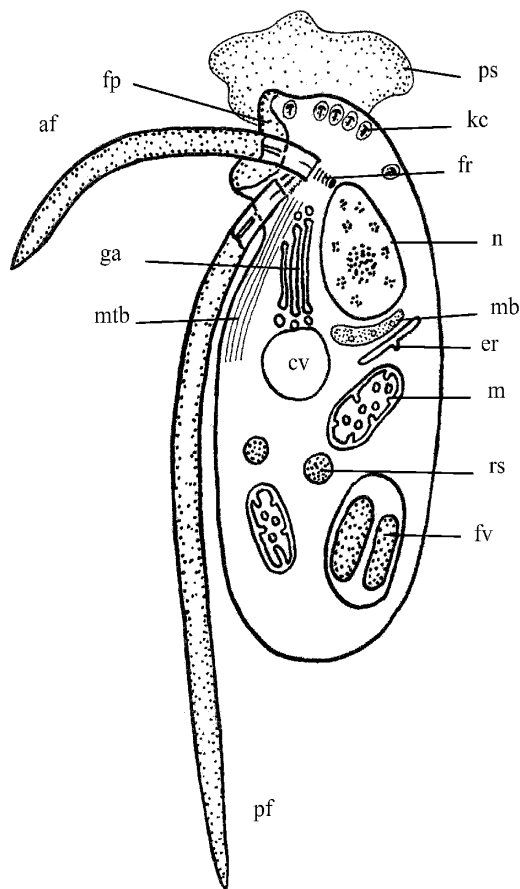


Fig. 6. Scheme of the internal organization of the cell in *Heteromita*. Abbreviations: fp - flagellar pocket, kc - kinetocysts. Other abbreviations are the same as in Figs 1 and 2.

(not around the nucleus), so it is not homologous to that of *Cercomonas*. Cercomonads do not have reproductive cysts in their life cycle. Thus, morphologically *Proleptomonas* does not look like a cercomonad. However, the molecular phylogeny based on SSU rRNA gene sequences shows that it is a cercomonad forming a sister group to *Heteromita* with a rather high bootstrap value (Vickerman et al., 2002; Cavalier-Smith and Chao, 2003). Following the authors (Vickerman et al., 2002) we place this genus among the Cercozoa Cavalier-Smith, 1998 incertae sedis. Thus, neither Vickerman with co-authors (2002), nor we include this genus in the order Cercomonadida.

Katabia Karpov, Ekelund and Moestrup, 2003. Only one species *Katabia gromovi* Karpov, Ekelund et Moestrup, 2003 is known and has been investigated in detail (Karpov et al., 2003). This soil swimming flagellate has a drop-like body with a flattened ventral side and prominent dorsal side (Fig. 5). The cell length is 8-12 μm and the cell width (in the broadest anterior part) is 5-7 μm . The flagella emerge subapically,

approximately 1/4 cell length from the anterior end. One flagellum, approximately 2.5 times the cell length, is oriented posteriorly to the left and has a long acronema. The anterior flagellum is 1.5 times longer than the cell length and has a shorter acronema. The cysts measure 7-8 μm in diameter, and are covered with a thick translucent mucilage-like wall.

Katabia has a typical cercomonad ultrastructure: the cell is covered only with a plasmalemma underlain by kinetocysts; the basal body of the posterior flagellum lies approximately at a right angle and in a different plane to the anterior one; there is a cylinder connected with the A-tubules of the axoneme in the flagellar transition zone; flagellar rootlet homology to those of *Heteromita* is clear; the nucleus is connected to the basal bodies by fibrillar rootlets; there is no microtubular cone; a microbody with amorphous contents is located near the nucleus; mitochondria have vermiform tubular or vesicular cristae. *Katabia* is morphologically very similar to *Heteromita*, but has a different mode of movement: it never glides, only swims. It also differs from *Heteromita* in the presence of unusual mushroom-like bodies, which are known in *Cercomonas* species, and in details of the cytoskeleton (Karpov, 1997; Karpov et al., 2003). The only complete investigation of a cercomonad cytoskeleton was performed on *Katabia* (Fig. 7).

Preliminary molecular data based on the partial sequence of SSU rDNA strongly suggest that *Katabia*'s closest relatives are *Heteromita*, *Cercomonas* and *Cryothecomonas* (Karpov et al., 2003).

IS IT POSSIBLE TO GROUP THE CERCOMONAD GENERA?

There are two different cercomonad genera - *Cercomonas* and *Heteromita*, which differences are rather clear.

Cercomonas representatives possess gliding amoeboid cells with two heterodynamic flagella. Pseudopodia are of various shape and may branch. The transformation from a monad to an amoeboid form takes only a few seconds. The cytoplasm contains microtoxycysts, osmiophilic bodies and trichocysts. The microtubular cone usually emerges from the basal bodies to the nucleus. Swimming cells are very rare in the life-cycle of cercomonads, which normally glide upon a surface. Many species of this genus are able to produce plasmodia in their life cycle.

Heteromita species have gliding cells with a rigid body and two heterodynamic flagella. During movement, the posterior end is constantly shaking, which is a very distinctive character of the genus. The anterior end of the cell has a small rostrum, and the flagella arise from a small pocket. The organisms produce temporary pseudopodia, only during the engulfment of food. The

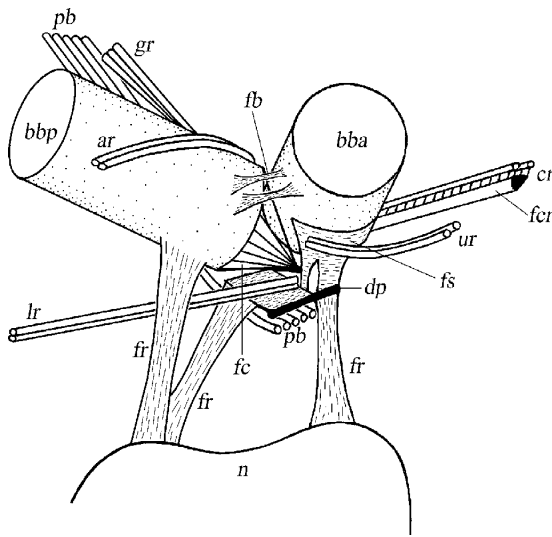


Fig. 7. Scheme of the microtubular cytoskeleton of *Katabia gromovi* (after: Karpov et al., 2003). The cell is seen from the anterior end, the dorsal side is towards the bottom of the page. Secondary microtubules of the rootlets are not shown. **Abbreviations:** ar - two-stranded microtubular anterior rootlet of BBP, bba - basal body of anterior flagellum, bbp - basal body of posterior flagellum, cr - composite rootlet, 2 microtubules are associated with fibrillar band in its proximal part, dp - dense plate, fb - fibrillar bridge between kinetosomes, fc - fibrillar cone of BBP, fcr - fibrillar band of CR, fr - fibrillar rootlet, fs - fibrillar sheath at the base of basal bodies, gr - girdle rootlet of 3 microtubules, lr - left rootlet originating from dense plate, pb - band of 4-5 microtubules, passing in a posterior direction, n - nucleus, ur - two-stranded microtubular (upper) rootlet of BBA.

- extrusomes: kinetocysts.
- no plasmodia in life-cycle

All cercomonad genera discussed above may be easily shared between two these families.

Cavalier-Smith and Chao (2003) also recognised two families in the order: Cercomonadidae (Kent) Cavalier-Smith and Chao, 2003 and Heteromitidae (Kent) Cavalier-Smith and Chao, 2003. Family Cercomonadidae (Kent) Cavalier-Smith and Chao, 2003 includes one genus (*Cercomonas*) and has the following diagnosis: cell surface very flexible, often prone to generate filopodia and typically drawn out posteriorly into a trailing point to which the posterior cilium normally adheres. Cell typically spindle shaped, sometimes with plasmodial stage. Family Heteromitidae (Kent) Cavalier-Smith and Chao, 2003 includes *Heteromita*, *Bodomorpha*, *Proleptomonas*, *Allantion*, and has the following diagnosis: cell surface semi-rigid, not generating filopodia or plasmodia, cell posterior normally rounded, not extended into a point adhering to the posterior cilium. Cell typically ovoid, but sometimes more elongate. Anterior cilium sometimes absent.

Thus, the distinguishing characters between the two families are: flexible/rigid cell surface, presence/absence of filopodia and plasmodia, shape of the cell is spindle/ovoid, and one enigmatic character (posterior point adheres to the posterior flagellum), which totally depends on the cell surface flexibility. Cercomonads produce both filopodia and lobopodia, they may present in Cercomonadidae over the cell cycle, and may be temporary in Heteromitidae. It means that the cell surface flexibility is the main character to distinguish these two families. In this respect and in the presence of plasmodia the family diagnoses given by Cavalier-Smith and Chao (2003) and the ones presented earlier (Myl'nikov, 2000) and in this paper overlap. The additional characters concerning the structure of extrusomes and presence/absence of microtubular cone are also essential. The microtubular cone is visible under the light microscope in some species. It was demonstrated by EM in all investigated species of *Cercomonas* (Myl'nikov, 1995; Karpov, 1997) and was never seen in *Heteromita*. There might be more characters in flagellar apparatus structure, different in the two main genera of the families, which is now under close investigation (Karpov et al., in preparation).

Below we give a complete revised list of cercomonad species.

cells contain only one kind of extrusomes, the kinetocysts. A microtubular cone is absent, and there are no plasmodia in the life cycle.

On the basis of these differences two families were established (Kent, 1880; Myl'nikov, 2000). We list below the main characters of each.

Family Cercomonadidae Kent, 1880 (=Cercobodidae Hollande, 1942).

- cercomonads with variable shape of the body
- habitual pseudopodia
- microtubular cone present
- extrusomes: microtoxicysts, trichocyst-like structures, osmiophilic bodies
- plasmodia in life cycle

Family Heteromitidae Kent, 1880 emend. Myl'nikov, 2000 (=Bodomorphidae Hollande, 1952)

- cercomonads with rigid body of definite shape
- temporary pseudopodia
- no microtubular cone

REVISED TAXONOMY OF THE ORDER CERCOMONADIDA

Order **Cercomonadida** Poche, 1913, em. Vicker-man, 1983, em. Myl'nikov, 1986

Amoeboflagellates with naked body, two smooth heterodynamic flagella, and pseudopodia used for feeding. Some species with complex life cycle including plasmodium stage and cysts. Flagellar basal bodies connected to nucleus. Mitochondria with tubular cristae, microbodies and extrusomes present.

Family **Cercomonadidae Kent, 1880** (=Cercobodinae Hollande, 1942) emend.

Amoeboflagellates with habitual pseudopodia of different types, 3 kinds of extrusomes (osmiophilic bodies, microtoxicysts, trichocysts), and often complex life cycle, including plasmodia and cysts. Microtubular cone emerging from basal bodies to nucleus.

Genus **Cercomonas Dujardin, 1841** (=Dimastigamoeba Blochmann, 1894 =Prismatomonas Massart, 1920 =Reptomonas Kent, 1880 =Cercomastix Lemmermann, 1913 =Cercobodo Krassiltschik, 1886 =Dimorpha Klebs, 1892).

Gliding flagellates, with flexible very metabolic body, usually able to produce pseudopodia of different shape, including branched ones, from any cell part. Cell body attached to the substrate during movement. Anterior flagellum making slow rowing motion, posterior flagellum trailing behind more passively. Some species with complex life cycle including multinuclear plasmodia and cysts. Microtubular cone usually present.

Type species: *Cercomonas longicauda* Dujardin, 1841 sensu Mylnikov, 1987.

Cercomonas activus Mylnikov, 1992 (= *Cercobodo activus* Mylnikov, 1987)

C. acutus comb. nov. (= *Cercobodo acutus* Skuja, 1948)

C. agilis comb. nov. (= *Dimastigamoeba agilis* Moroff, 1904)

C. alexeieffi comb. nov. (= *Cercobodo alexeieffi* Lemmermann, 1914)

C. alternans comb. nov. (= *Dimorpha alternans* Klebs, 1892)

C. angustus comb. nov. (= *Cercobodo angustus* Skuja, 1948)

C. bodo comb. nov. (= *Dimorpha bodo* Meyer, 1897)

C. breviantennatus comb. nov. (= *Cercobodo breviantennatus* Skuja, 1956)

C. chromatiophagus comb. nov. (= *Cercobodo chromatiophagus* Skuja, 1939)

C. cometa Mylnikov, 1992 (= *Cercobodo cometa* Hollande, 1942)

C. crassicauda Dujardin, 1841

C. cylindrica Dujardin, 1841

C. dactylopterus comb. nov. (= *Cercobodo dactylopterus* Skuja, 1939)

C. digitalis comb. nov. (= *Dimorpha digitalis* Meyer, 1897)

C. draco comb. nov. (= *Cercobodo draco* Skuja, 1956)

C. dubius comb. nov. (= *Cercobodo dubius* Skuja, 1939)

C. fusiformis Dujardin, 1841

C. gigantea Mylnikov, 2002

C. grandis Maskell, 1886

C. granulatus Lee et Patterson, 2000

C. granulifera comb. nov. (= *Cercobodo granulifera* Hollande, 1942)

C. heimi comb. nov. (= *Cercobodo heimi* Hollande, 1942)

C. incurvus comb. nov. (= *Cercobodo incurvus* Skuja, 1939)

C. kiaerdammane Mylnikov, 2002

C. laciniaegerens comb. nov. (= *Cercobodo laciniaegerens* Krassiltschik, 1886)

C. lagoenaris comb. nov. (= *Cercobodo lagoenaris* Hamar, 1979)

C. levis comb. nov. (= *Cercobodo levis* Skuja, 1939)

C. longicauda Dujardin, 1841 (= *Cercobodo amoebinus* Mylnikov, 1985)

C. metabolicus Mylnikov, 1992 (= *Cercobodo metabolicus* Mylnikov, 1987)

C. minimus Mylnikov, 1992 (= *Cercobodo minimus* Mylnikov, 1985)

C. norrvicensis comb. nov. (= *Cercobodo norrvicensis* Skuja, 1956)

C. onustus comb. nov. (= *Cercobodo onustus* Skuja, 1939)

C. ovata Tong, Vørs et Patterson, 1997 (= *Heteromita ovata* Dujardin, 1841)

C. pachypus comb. nov. (= *Cercobodo pachypus* Skuja, 1932)

C. plasmodialis Mylnikov, 1992 (= *Cercobodo plasmodialis* Mylnikov, 1985)

C. pronucleatus comb. nov. (= *Cercobodo pronucleatus* Skuja, 1948)

C. pseudodactylopterus comb. nov. (= *Cercobodo pseudodactylopterus* Skuja, 1948)

C. pyriformis comb. nov. (= *Cercobodo pyriformis* Skuja, 1956)

C. radiatus comb. nov. (= *Dimorpha radiatus* Klebs, 1892)

C. rhacodes comb. nov. (= *Cercobodo rhacodes* Skuja, 1939)

C. rhacodytes comb. nov. (= *Cercobodo rhacodytes* Klug, 1936)

C. rhynchophorus (= *Cercobodo rhynchophorus* Skuja, 1939)

C. robustus comb. nov. (= *Cercobodo robustus* Hamar, 1979)

C. simplex comb. nov. (= *Dimastigamoeba simplex* Moroff, 1904)

C. typicus Kent, 1880

C. varians Mylnikov, 1992 (= *Cercobodo varians* Skuja, 1948)

C. venticosus comb. nov. (= *Cercobodo venticosus* Hamar, 1979)

C. vibrans comb. nov. (= *Cercobodo vibrans* Sandon, 1927)

We do not accept here the new species of *Cercobodo* reported by Skvortzov (1977) because of unsatisfactory description.

Helkesimastix Woodcock et Lapage, 1914.

Gliding, very metabolic elongated flagellates with short anterior flagellum directed laterally, and with long posterior flagellum. Both flagella inserted subapically from small pocket. Anterior cell end with small rostrum. Double row of refractive granules lying below ventral cell surface. Cells with posterior contractile vacuole and small pseudopodium at posterior cell end. Cysts unknown.

Monospecific: *Helkesimastix faecicola* Woodcock et Lapage, 1914.

Family **Heteromitidae** Kent, 1880 emend. Mylnikov, 2000 (= *Bodomorphidae* Hollande, 1952)

Flagellates with rigid body, producing temporary pseudopodia. One kind of extrusomes (kinetocysts) present, no plasmodial stage, no microtubular cone.

Genus ***Heteromita*** Dujardin, 1841 emend. Mylnikov et Karpov (= *Bodomorpha* Hollande 1952, = *Sciviamonas* Ekelund et Patterson, 1997).

Oval biflagellated cells with small rostrum. Flagella inserted subapically. Anterior flagellum usually short, beating laterally and stiffly. Posterior flagellum trailing during gliding. Small pseudopodia, used to ingest bacteria, formed mostly from anterior cell end. Posterior cell end characteristically shaking during movement. Cysts known.

New type species: *Heteromita globosa* sensu Macdonald et al. (1977)

Heteromita globosa Stein, 1878

H. minima comb. nov. (= *Bodomorpha minima* Hollande, 1942)

H. reniformis comb. nov. (= *Bodomorpha reniformis* Zhukov, 1978)

H. terricola comb. nov. (= *Sciviamonas terricola* Ekelund et Patterson, 1997)

Protaspis Skuja, 1939

Rigid cell body with two heterodynamic subequal flagella inserted subapically on ventral cell side. Cells flattened dorso-ventrally, with ventral groove, producing pseudopodia for feeding from groove; nucleus often with nuclear cap.

Type species: *Protaspis glans* Skuja, 1939

P. gemmiferum Larsen et Patterson, 1990

P. glans Skuja, 1939

P. maior Skuja, 1939

P. metarhiza Skuja, 1939

P. obliqua Larsen et Patterson, 1990

P. obovata Skuja, 1948

P. simplex Vørs, 1992

P. tegere Larsen et Patterson, 1990

P. verrucosa Larsen et Patterson, 1990

Allantion Sandon, 1924

Gliding flagellates with rigid body and single visible trailing flagellum. Anterior flagellum not visible under light microscope. Cells cylindrical with rounded ends. Flagella inserted subapically in small ventral depression. Gliding relatively fast and smooth, flagellate attaching to the substrate by anterior end, with the posterior end elevated from the substrate. Anterior nucleus and several posterior refractile granules or food vacuoles usually visible. Polyhedric cysts present.

Monospecific: *Allantion tachyploon* Sandon, 1924

Sainouron Sandon, 1924

Soil flagellates with rigid oval or bean-like body, gliding upon substrate with characteristic vibration. Anterior flagellum invisible, posterior flagellum trailing, not attached to body. Occasionally amoeboid. Cysts present.

Monospecific: *Sainouron mikroteron* Sandon, 1924

Cholamonas Flavin et al. 2000

Cercomonads with four flagella¹, trophic cells with longitudinally arranged peripheral mitochondria; kinetid having one or more posteriorly directed compound microtubular rootlets and lacking perinuclear microtubular basket (cone); pseudopods not expressed except briefly around posterior ingestion area at the moment of prey ingestion; preying typically on eukaryotes. Endobiotic.

Monospecific: *Cholamonas cyrtodiopsisidis* Flavin et al. 2000.

Katabia Karpov et al. 2003

Soil flagellates with two heterodynamic flagella, drop-like body with broad anterior end and tapering posterior end. Amoeboid cells swimming, never gliding upon substrate. Cell cycle including amoeboid cells and cysts with thick translucent wall. Pseudopodia used for feeding. Cells containing microbody, refractive granules (mushroom-like bodies), kinetocysts and well-

¹ The authors did not include this statement in the diagnosis. Even in the species diagnosis they call *Ch. cyrtodiopsisidis* biflagellate (Flavin et al., 2000). We think that this very unusual character should be included in the diagnosis of the genus *Cholamonas*.

developed cytoskeleton similar to that of *Heteromita*.
 Monospecific: *Katabia gromovi* Karpov et al. 2003

Perspectives

Further investigations of cercoconads should proceed as follows. First of all, both ultrastructure and molecular phylogeny of poorly investigated genera (*Helkesimastix*, *Protaspis*, *Allantion*, *Sainouron*) have to be studied. This may clarify their relationship to other cercoconads. Revision of the most complicated genus *Cercomonas* calls for two research directions: isolation of clonal cultures and EM study (of both the general structure and the cytoskeleton), and investigation of molecular phylogeny. It has recently been shown by SSU rRNA analysis that all *Cercomonas* species split into two clades (Cavalier-Smith and Chao, 2003; Bass and Cavalier-Smith, 2004). This means that we need to check whether representatives of these clades are morphologically different and whether they should be separated into two genera.

Cytoskeletal investigations are urgently needed, as they may clarify not only the position and relationship of cercoconad species in the order, but may also help us to find homologous elements in other groups of protists to show the position of the order among other Cercozoa.

The complete cytoskeleton structure is known at present only for *Katabia* (Karpov et al., 2003). Broader study of the cercoconad flagellar apparatus will permit us to find the key cytoskeletal characters of the order Cercomonadida as a whole. One of the main goals of such work is realising the correspondence of cytoskeletal features with molecular phylogeny.

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Note added in proof:

In the very recent publication (Ekelund et al., 2004) the authors confirmed the presence of two clades (“type 1” and “type 2”) in the genus *Cercomonas*, and gave a new generic name to the clade “type 2” as *Neocercomonas* Ekelund, Fredslund & Daugbjerg, 2004. This genus with a new species *N. jutlandica* Ekelund, Fredslund & Daugbjerg, 2004 has to be included in the order

Cercomonadida, family Cercomonadidae. Another advantage of this paper is including the SSU rDNA signature sequences in the species description.

* Ekelund F., Daugbjerg N. and Fredslund L. 2004. Phylogeny of *Heteromita*, *Cercomonas* and *Thaumatomonas* based on SSU rDNA sequences, including the description of *Neocercomonas jutlandica* sp. nov., gen. nov. *Europ. J. Protistol.* 40, 119-135.