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Heterotrophic flagellates (Protista) from marine sediments of Botany Bay, Australia

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Heterotrophic flagellates (protozoa) occurring in the marine sediments at Botany Bay, Australia are reported. Among the 87 species from 43 genera encountered in this survey are 13 new taxa: *Cercomonas granulatus* n. sp., *Clautriavia cavus* n. sp., *Heteronema larseni* n. sp., *Notosolenus adamas* n. sp., *Notosolenus brothernis* n. sp., *Notosolenus hemicircularis* n. sp., *Notosolenus lashue* n. sp., *Notosolenus pyriforme* n. sp., *Petalomonas intortus* n. sp., *Petalomonas iugosus* n. sp., *Petalomonas labrum* n. sp., *Petalomonas planus* n. sp. and *Petalomonas virgatus* n. sp.; and seven new combinations, *Carpediemonas bialata* n. comb., *Dinema platysomum* n. comb., *Petalomonas calycimonoides* nom. nov., *Petalomonas christeni* nom. nov., *Petalomonas physaloides* n. comb., *Petalomonas quinquecarinata* n. comb. and *Petalomonas spinifera* n. comb. Most flagellates described here appear to be cosmopolitan. We are unable to assess if the new species are endemic because of the lack of intensive studies elsewhere.

KEYWORDS: Biogeography, endemic biota, heterotrophic flagellates, taxonomy, protists.

Introduction

Marine heterotrophic protists are predators on bacteria and small phytoplankton, are prey for larger zooplankton, and facilitate remineralization and recycling of elements essential for phytoplankton and microbial growth (Azam *et al*., 1983; Porter *et al*., 1985; Sherr and Sherr, 1988; Jürgens and Güde, 1990; Kirchman, 1994; Pace and Vaqué, 1994). Consequently, the role of heterotrophic protists in planktonic microbial food webs of marine environments has received increasing attention. The benthic ecosystem is less well understood. Larger protozoa have been well studied (Fenchel 1967, 1968a, 1968b, 1969; Patterson *et al*., 1989), but quantitative studies of smaller protozoa such as flagellates are hampered because of difficulties in extracting and enumerating them (Bak and Nieuwland, 1989). Nonetheless, there has been a recent increase in interest in the ecology of flagellates and ciliates in freshwater and marine sediments (Bak and Nieuwland, 1989; Patterson *et al*., 1989; Alongi, 1991; Hondeveld *et al*., 1992, 1994, 1995; Gasol, 1993; Starink *et al*., 1996a, 1996b; Epstein, 1997a, 1997b).

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We have sought to develop an understanding of the diversity of benthic flagellates (Larsen and Patterson, 1990; Ekebom *et al*., 1996; Patterson and Simpson, 1996). Our current insights into large-scale patchiness of previous studies may be questioned on the basis of under-reporting (Lee and Patterson, 1998). The aim of this study was to conduct a long-term, intensive study of the diversity of heterotrophic flagellates at a single site and to use that information to address issues of endemism in this group (Lee and Patterson, 1998).

Previous taxonomic studies of marine benthic flagellates in Australia are Ruinen (1938), Larsen and Patterson (1990), Ekebom *et al*. (1996) and Patterson and Simpson (1996).

Materials and methods

This study was carried out at Port Botany, Botany Bay, New South Wales, Australia from February 1997 to March 1998. During the period, water temperature and salinity were in the range 15.8~27.0°C and 26~38‰, respectively. Samples were collected from intertidal sediments to a depth of about 1 cm from a 1 m^2 quadrat. To remove macrofauna, the samples was sieved and the samples were then placed in plastic trays in 1 cm deep layers. The sediments were covered with lens tissue and No. 1 22 × 22 mm coverslips were placed on the lens tissue. After 24 h the coverslips were removed and flagellates were observed using an Axiophot microscope (Zeiss) equipped with photographic facilities as described by Patterson (1982). The flagellates were also recorded on U-MATIC video tapes and records were also made with video prints. Specimens were also drawn. The samples were maintained at room temperature (~20°C) for 5 days.

Observations

Nomenclature follows the International Code of Zoological Nomenclature (ICZN) (International Commission of Zoological Nomenclature, 1985).

A list of species encountered during this study is presented in table 1.

Pelobiontida Page, 1976
Mastigamoeba* cfr. *simplex Kent, 1880
(figures 1a, 2a)

Description. Cell about 8 μm long, with very flexible amoeboid cell body. Pseudopodia are produced from the sides and posterior parts of the cell. With one emergent flagellum, which is about 20 μm long and thickened. The flagellum is directed forwardly and beats stiffly. The nucleus is located in the anterior part of the cell. One cell observed.

Remarks. Kent (1880) reported this species as *Mastigamoeba simplex* from freshwater sites. This species has been found at marine sites in subtropical and tropical Australia (Larsen and Patterson, 1990; Bernard *et al*., 1999) with cell lengths from 5 to 21 μm. This species was transferred to *Mastigella* by Lemmermann (1914) and by Larsen and Patterson (1990) because the nucleus is located away from the flagellar apparatus. Generic and specific boundaries in the pelobionts are often unclear because of polymorphism within species. *Mastigamoeba schizophrenia* Simpson *et al*., 1997, which was described through the use of cultures, varies in cell shape and size, numbers of nuclei and whether or not the flagellum is present (Simpson *et al*., 1997a). Species of *Mastigamoeba* Schulze, 1874 have to date been

Table 1. Species observed during this study.

Table 1. (*Continued*).

distinguished from species of *Mastigella* Frenzel, 1897 by the close association between the nucleus and flagellar apparatus in species of the former genus and the separation of the nucleus from the flagellar apparatus in the latter genus (Goldschmidt, 1907; Simpson *et al*., 1997a). In a recent study (Bernard *et al*., 1999), it was noted that, although in *M. simplex* the bulk of the nucleus may be removed

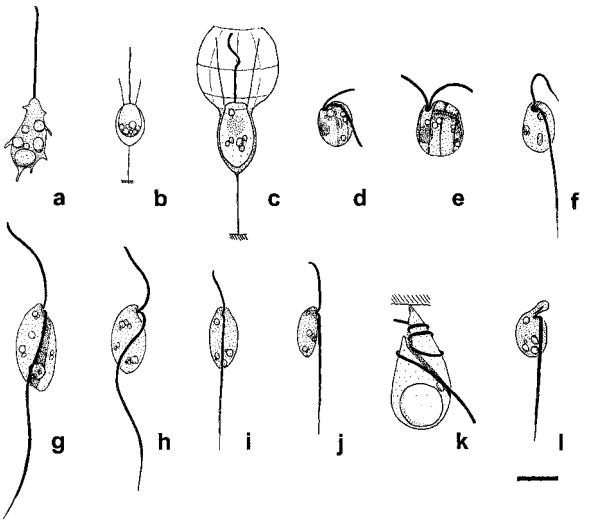


FIG. 1. Pelobiontida, Choanoflagellida, Cryptomonadida and Kinetoplastida, (a) *Mastigamoeba* cfr. *simplex*, (b) *Salpingoeca infusionum*, (c) *Stephanoeca diplocostata*, (d) *Goniomonas amphinema*, (e) *G. pacifica*, (f) *Bodo curvifilus*, (g) *B. cygnus*, (h) *B. designis*, (i) *B. platyrhynchus*, (j) *B. saliens*, (k) *Hemistasia phaeocysticola*, (l) *Rhynchomonas nasuta*. Scale bar = 5 μm for all figures.

from the base of the flagellum, there may still be a thin connection between them. Bernard *et al.* (1999) determined that mastigamoebid pelobionts should be assigned to *Mastigamoeba* if there was any connection between the nucleus and the base of the flagellum and to *Mastigella* if there is no such connection. We have complied with this interpretation.

Choanoflagellida Kent, 1880
Salpingoeca infusionum Kent, 1880
(figures 1b, 2b)

Description. Loricate choanoflagellate, lorica ovoid, with a pointed posterior end. With a pedicel which is shorter than the lorica. The cell body, which fills out the posterior part of the lorica, is about 5 μm long and 3 μm wide. Cells attach to the substratum by the pedicel. Two cells observed.

Remarks. This species has been described from subtropical Australia, Denmark, England, France, Gulf of Finland and USA (Kent, 1880; Griessmann, 1913; Boucaud-Camou, 1967; Norris, 1965; Tong *et al.*, 1997; Tong, 1997c). We identify this species with some uncertainty, but do so because of the close resemblance with individuals given the same name and reported by Tong (1997c) and Tong *et al.* (1997). Our observations are in accord with the original description of Kent (1880). *Salpingoeca infusionum* is a senior synonym of *S. longipes* Kent, 1880 (Boucaud-Camou, 1967; Tong, 1997c). *Salpingoeca infusionum* resembles *S. marina* James-Clark, 1867 in general appearance, and some authors regard these taxa as the same (Boucaud-Camou, 1967; Griessmann, 1913). According to Tong (1997c), the two species can be distinguished by the stiffness of the lorica and because the lorica of *S. infusionum* is slightly wider anteriorly than that of *S. marina*. *Salpingoeca infusionum* is similar to *S. inquillata* Kent, 1880 in cell length and cell shape, but is

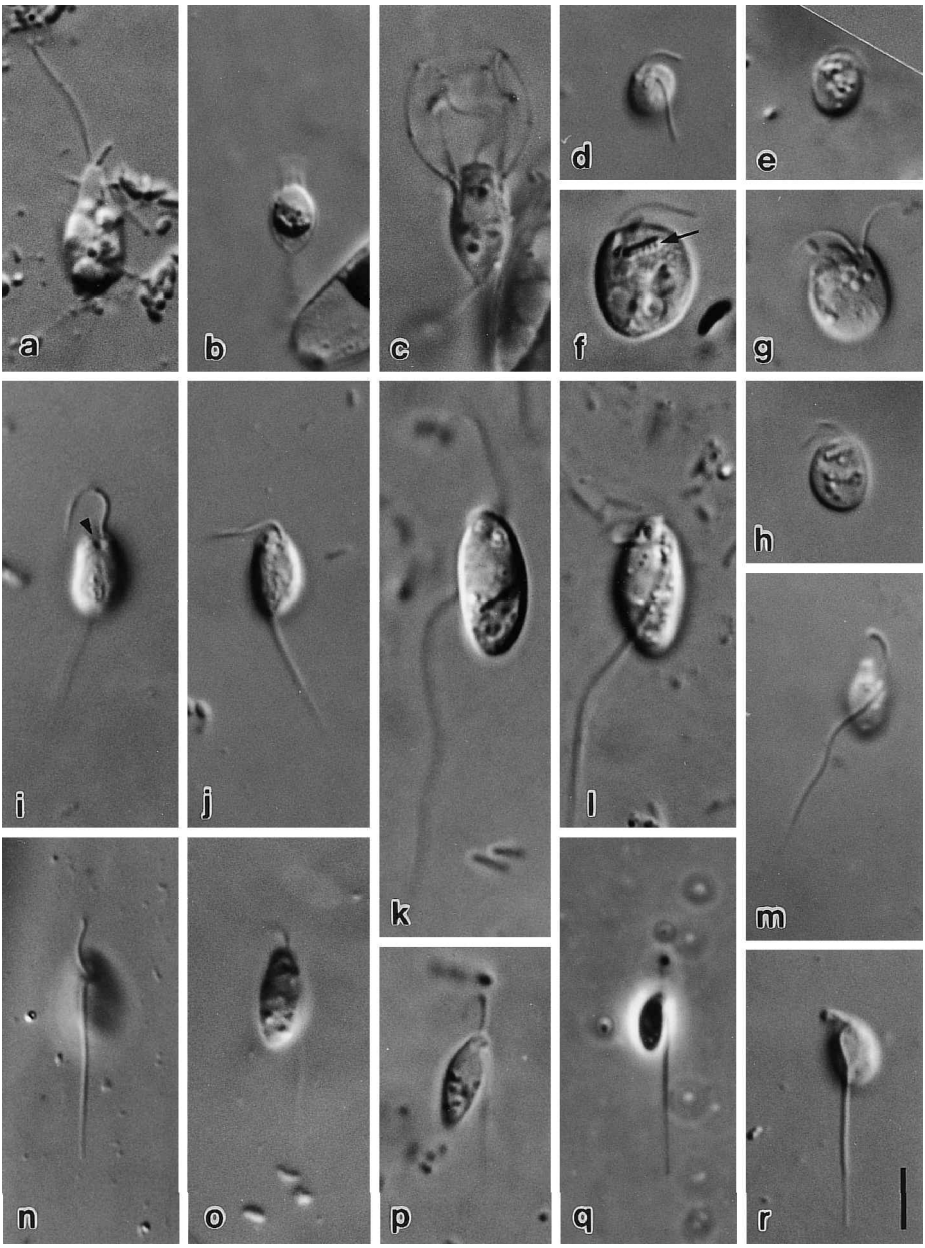


FIG. 2. (a) *Mastigamoeba* cfr. *simplex* showing pseudopodia, (b) *Salpingoeca infusionum*, (c) *Stephanoeca diplocostata*, (d, e) *Goniomonas amphinema*, (d) flagellar insertion, (e) general appearance of cell, (f–h) *Goniomonas pacifica* showing range of size, (f) extrusomes (arrow), (g) general appearance of cell, (i, j) *Bodo curvifilus*, (i) general appearance of cell and mouth (arrow head), (k, l) *Bodo cygnus*, general appearance of cell, (m) *Bodo designis*, general appearance of cell, (n, o) *Bodo platyrhynchus*, (n) ventral view showing flagellar insertion, (o) general appearance of cell, (p, q) *Bodo saliens*, general appearance of cell, (r) *Rhynchomonas nasuta*, general appearance of cell. All micrographs are DIC images with the exception of (q) which is a phase contrast image. Scale bar = 5 μm for all figures.

distinguished by a slight eversion of the anterior margin of the lorica of *S. inquillata*. *Salpingoeca inquillata* is said to be a synonym of *S. curvipes* Kent, 1880 and *S. ringens* Kent, 1880 (Boucaud-Camou, 1967). Many previously reported species assigned to this genus appear very similar and the species taxonomy is unclear (Vørs, 1992a).

Stephanoeca diplocostata Ellis, 1930
(figures 1c, 2c)

Description. Collar flagellate with lorica divided into two chambers by a waist at about two-fifths of the distance from the base of lorica. Loricae with transverse and horizontal costae. Cell has a single apical flagellum. The flagellum is as long as the cell body. The cell body is about 10 μm long with a pedicel and fills the posterior chamber of the lorica. The cells attach to the substratum with the pedicel or with the posterior end of the lorica. Two cells observed.

Remarks. This species resembles *Stephanoeca diplocostata* Ellis, 1930 in general appearance, size and shape. We identified this species as *S. diplocostata* with uncertainty because the identity of most acanthoecid choanoflagellates can only be confirmed through electron microscopical observation. This species has been found in Antarctica, subtropical Australia, Denmark, England, USA (Ellis, 1930; Thomsen, 1973; Thomsen *et al*., 1991, 1997; Leadbeater, 1994; Tong, 1997a, 1997b). One of two cells observed here had a pedicel, but another one did not. The pedicel in *Stephanoeca diplocostata* may be present or absent according to the stage of the life cycle (Leadbeater, 1979).

Cryptomonadida Senn, 1900
Goniomonas amphinema Larsen and Patterson, 1990
(figures 1d, 2d–e)

Description. Cell about 4–5 μm long, anteriorly truncate and posteriorly rounded, dorso-ventrally flattened, with several delicate stripes on both sides. Two flagella are unequal in length and insert obliquely in an anterior depression near one margin of the cell. The short flagellum is directed forwards, and the long flagellum usually trails over the body and is slightly longer than the cell. Food is ingested near the flagellar insertion. Commonly observed.

Remarks. This species has previously been found in marine sites in subtropical and tropical Australia, North Atlantic, Denmark, England, Fiji, Gulf of Finland and Panama, and size range was reported to be 4–8 μm (Larsen and Pattersen, 1990; Vørs, 1992a, 1992b; Patterson *et al*., 1993; Tong *et al*., 1998). *Goniomonas amphinema* is distinguished from *G. pacifica* Larsen and Patterson, 1990 and *G. truncata* Stein, 1878 by having two flagella which are unequal in length.

Goniomonas pacifica Larsen and Patterson, 1990
(figures 1e, 2f–h)

Description. Cell measuring 4–10 μm long, 3–7 μm wide, with several distinct longitudinal ridges on both sides of the cell. With a row of about seven to nine extrusomes near the anterior end of the cell which is truncated with the posterior end rounded. Two flagella of similar length emerge from a small anterior depression

and are directed anteriorly. When the cell is swimming, two flagella diverge in different directions. Less common than *G. amphinema*.

Remarks. Previous reported length ranges are 3–15 μm. *G. pacifica* has been found in marine sites in subtropical and tropical Australia, North Atlantic, Brazil, Denmark, England, Gulf of Finland, Hawaii and Panama (Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Patterson *et al.*, 1993; Ekebom *et al.*, 1996; Patterson and Simpson, 1996; Tong, 1997a; Tong *et al.*, 1998). *Goniomonas pacifica* is distinguished from *G. amphinema* because *G. amphinema* has two flagella of unequal length. *Goniomonas pacifica* is usually distinguished from *Goniomonas truncata* Stein, 1878 by having distinct longitudinal ridges and by its smaller size (Larsen and Patterson, 1990; Vørs 1992a, 1992b). Ridges in *G. amphinema* may be hard to see (Ekebom *et al.*, 1996; Patterson and Simpson, 1996) and comparable ridges have now been observed in organisms assigned (with uncertainty) to *G. truncata* (Ekelund and Patterson, 1997). Additionally, the length ranges overlap between the two species (*G. pacifica*, 4–15 μm; *G. truncata*, 3–25 μm). *Goniomonas truncata* was reported by Fresenius (1858), Bütschli (1878), Stein (1878), Ulehla (1911), Skuja (1939), Czosnowski (1948), Mignot (1965), Schuster (1968), Vørs (1992a, 1992b), Novarino *et al.* (1994) and Bernard *et al.* (1999) from marine and freshwater sites in Australia, Denmark, England, Gulf of Finland, Germany, Poland and USA. *Goniomonas truncata* lacks a clear identity (see discussion by Bernard *et al.*, 1999) possibly because more than one species has been described under this name. Usually, it is considered to be found only in freshwater. Further study is required to give *G. truncata* and *G. pacifica* well-defined identities.

Kinetoplastida Honigberg, 1963
Bodo curvifilus Griessmann, 1913
(figures 1f, 2i, j)

Description. Cell outline oval or bean-shaped, 5–8 μm long and 3–4.5 μm wide, flattened, pliable. The two flagella are unequal in length and insert subapically and to one side in a small pocket. The anterior flagellum is as long as the cell, is curved and beats with a paddling motion. The trailing posterior flagellum is acronematic and is about 2.5–3 times the length of the cell. Cells normally glide but may have a squirming movement. Often observed.

Remarks. Previous studies reported the length range to be 4–12 μm and this species has been described from marine sites in Antarctica, North Atlantic, Northeast Atlantic, Denmark, West Greenland, Arctic and Norway (Griessmann, 1913; Throndsen, 1969; Turley and Carstens, 1991; Vørs, 1992a, 1992b, 1993a; Patterson *et al.*, 1993; Tong *et al.*, 1997). Our description is in accord with Vørs (1992a). *Bodo curvifilus* is distinguished from other species of *Bodo* by the curved shape and the paddling beat of the anterior flagellum. This species has features similar to *Bordnamonas tropicana* Larsen and Patterson, 1990, but it can be distinguished by its very curved anterior flagellum, the acronematic posterior flagellum, and because *Bordnamonas tropicana* has a visible mouth.

Bodo cygnus Patterson and Simpson, 1996
(figures 1g, 2k, l)

Description. Cell 8–13 μm long, elliptical, with subapical indentation from which two unequal flagella emerge. The anterior flagellum is as long as the cell and may

wrap around the anterior end of the cell during feeding. The acronematic posterior flagellum is about 2.5 times the length of the cell. Cells have a spiral groove that is easy to overlook and that extends from the subapical indentation to the posterior end of the cell. Cells move by rotating swimming movements. Sometimes commonly observed.

Remarks. This species was first described from hypersaline marine sites by Patterson and Simpson (1996) and with lengths from 8 to 12 μm. Our observations are in accord with those of Patterson and Simpson (1996). *Bodo cygnus* may be confused with *B. designis* Skuja, 1948 in general appearance, rotational swimming movements and cell length, but it can be distinguished by its spiral groove. The groove is hard to see in swimming cells. Previously reported large *B. designis* may be referable to *B. cygnus* because the spiral groove may have been overlooked. Careful observation is needed to distinguish these two species.

Bodo designis Skuja, 1948
(figures 1h, 2m)

Description. Cell outline usually elliptical, 4–7 μm long, 2–4 μm wide. With two unequal flagella emerging from a subapical pocket. Cells are flexible. The anterior flagellum is about the length of the cell or slightly shorter and curves back over the rostrum. The anterior flagellum wraps around the anterior part of the cell and the mouth is pressed against food particles when the cell is feeding. The acronematic posterior flagellum is about 2–4 times the length of the cell and has a sinuous profile in swimming cells. Cells rotate around their longitudinal axes when swimming. The nucleus is located near the middle of the cell. Common.

Remarks. Cell length was previously reported to be from 7 to 15 μm. This species has been reported from marine sites in Antarctica, North Atlantic, subtropical and tropical Australia, Brazil, Denmark, Fiji, Gulf of Finland, Greenland, Hawaii, and Panama (Larsen and Patterson, 1990; Vørs, 1992a, 1992b, 1993a; Patterson *et al.*, 1993; Ekebom *et al.*, 1996; Patterson and Simpson, 1996; Tong, 1997a; Tong *et al.*, 1997, 1998). Generally, our observations are consistent with those of previous authors. *Bodo designis* has also been found in several freshwater sites. It appears to be cosmopolitan. Sometimes, this species occurs in large numbers. It has been characterized by the rotating behaviour of swimming cells, but *B. cygnus* reported by Patterson and Simpson (1996) and *B. platyrhynchus* also have a rotating swimming movement. *Bodo designis* sometimes co-occurs with *B. cygnus*, but *B. cygnus* can be distinguished because it has a spiral groove.

Bodo platyrhynchus Larsen and Patterson, 1990
(figures 1i, 2n, o)

Description. Cell 5–7 μm long and 2–3 μm wide, dorso-ventrally flattened, slightly flexible. The anterior margin of the cell is flattened. Cell outline is ovoid and two flagella insert subapically. The anterior flagellum is shorter than the cell and beats stiffly from side to side. The trailing posterior flagellum is about twice the length of the cell and is acronematic. Cells glide slowly with a waggling movement, but may more rarely swim with a slow rotating movement. Rarely observed.

Remarks. This species was described from marine sites in Brazil and Hawaii by Larsen and Patterson (1990) with a length of 3.5–7.5 μm. Generally, our observations are in good agreement with the original description of Larsen and Patterson (1990),

but they did not mention the rotating swimming movements. Two other species of the genus *Bodo* (*B. cygnus* and *B. designis)* have been reported as having a rotating swimming movement. We here add a third species with this movement, but note that this is not the normal mode of motion. *Bodo platyrhynchus* is distinguished from *B. cygnus* and *B. designis* by its flattened body and the waggling behaviour. Kinetoplastid status is unproven. This species resembles a few species of the genus *Cercomonas* because of the almost apical flagellar insertion and the gliding motion in close contact with the substratum. We have distinguished it because species of *Cercomonas* are more flexible and strands of cytoplasm may be drawn out from the posterior end of the cell.

Bodo saliens Larsen and Patterson, 1990
(figures 1j, 2p, q)

Description. Cell usually elongate elliptical and somewhat inflexible, 4–10 μm long (mostly 6–9 μm), 2–5 μm wide. Two flagella unequal in length emerge subapically from a shallow pocket. The anterior flagellum appears inactive, is as long as or slightly shorter than the cell and is held forwards with a single anterior curve held perpendicular to the substratum. The acronematic posterior flagellum is typically directed straight behind the cell and is about 2.2–3.5 times the cell length. Cells swim in rapid darts in straight lines. Frequently observed. Description based on observations of 21 cells.

Remarks. This species has been found in North Atlantic, subtropical and tropical Australia, Brazil, Arctic Canada, Denmark, West Greenland, Hawaii, Gulf of Finland and Panama, and previously reported size ranges are 5–15 μm (Larsen and Patterson, 1990; Vørs, 1992a, 1992b, 1993a; Patterson *et al*., 1993; Ekebom *et al*., 1996; Patterson and Simpson, 1996; Tong *et al*., 1998). Generally, our observations are in accordance with those of previous observers. *Bodo saliens* is distinguished from other species of the genus *Bodo* by its rapid darting movement and the posterior flagellum which is directed in a straight line. This species is similar in shape to *B. curvifilus* Griessmann, 1913, but it is distinguished because *B. curvifilus* has a paddling anterior flagellum which is curved along its entire length.

Hemistasia phaeocysticola (Scherffel, 1900) Elbrächter *et al*., 1996
(figures 1k, 4a–e)

Description. Cell outline pyriform, about 13–15 μm long, metabolic, with a flexible apical papillum and with an indistinct spiral groove. Two flagella insert subapically in a pocket, are unequal in length and wrap around the body during feeding. The posterior flagellum is slightly longer than the anterior flagellum and the cell. During swimming cells rotate. The cells often contain one large food vacuole up to 6 μm in the posterior part of the cell. Observed eating the cytoplasm of diatoms. The nucleus was not seen. Rarely observed.

Remarks. According to Elbrächter *et al.* (1996), this species is identical with *Hemistasia klebsii* Griessmann, 1913 and *Pronoctiluca phaeocysticola* (Scherffel, 1900) Pavillard, 1922. They observed this species inside the shells of diatoms, dinoflagellates and copepods, and in cultures the species attacked diatoms, dinoflagellates and prymnesiophytes. This species was found in marine sites by Scherffel (1900), Griessmann (1913), Elbrächter *et al.* (1996) and Tong *et al*. (1998). Previous reported cell lengths range from 10 to 25 μm. The genus *Hemistasia* resembles

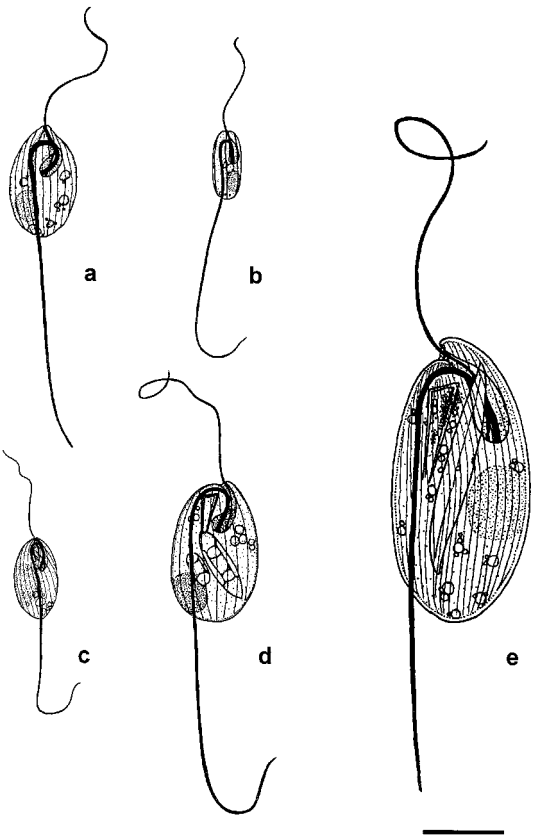


FIG. 3. Euglenida, *Anisonema* and *Dinema*; (a) *Anisonema acinus*, (b) *A. trepidum*, (c) *Dinema platysomum*, (d) *D. validum*, (e) *D. litorale*. Scale bar = 20 μm for all figures.

Entomosigma, *Rhynchobodo* and *Cryptaulax*. The latter two genera have recently been synonymized (Bernard *et al.*, 1999). *Hemistasia* can be distinguished from *Rhynchobodo* by its anterior papillum. *Hemistasia* may be the same as the genus *Entomosigma* Schiller, 1925 (Patterson, 1994). Figure 3 of Elbrächter *et al.* (1996) is similar to figure 21 (I–II) of *H. klebsii by* Griessmann (1913) and the figures of *Entomosigma peridinioides* Schiller, 1925, and figures 5, 6 of Elbrächter *et al.* (1996) are also similar to the figure 3 of *C. marina* of Throndsen (1969). *Cryptaulax marina sensu* Throndsen, 1969 is believed to be *H. phaeocysticola* (Bernard *et al.*, 1999).

Rhynchomonas nasuta Klebs, 1893
(figures 1l, 2r)

Description. Gliding cells with a bulbous motile snout. Cell 3.5–6 μm long, 2.5–4 μm wide, flattened, flexible. The snout, which contains a mouth, beats slowly. The anterior flagellum lies alongside the snout and is hard to see, and the trailing flagellum is about 2–2.7 times the cell length, and is acronematic. Cells consume attached bacteria. Commonly observed.

Remarks. The length of *R. nasuta* has previously been reported to be from 3 to 11 μm. This species has been found in marine sites in Antarctica, North Atlantic,

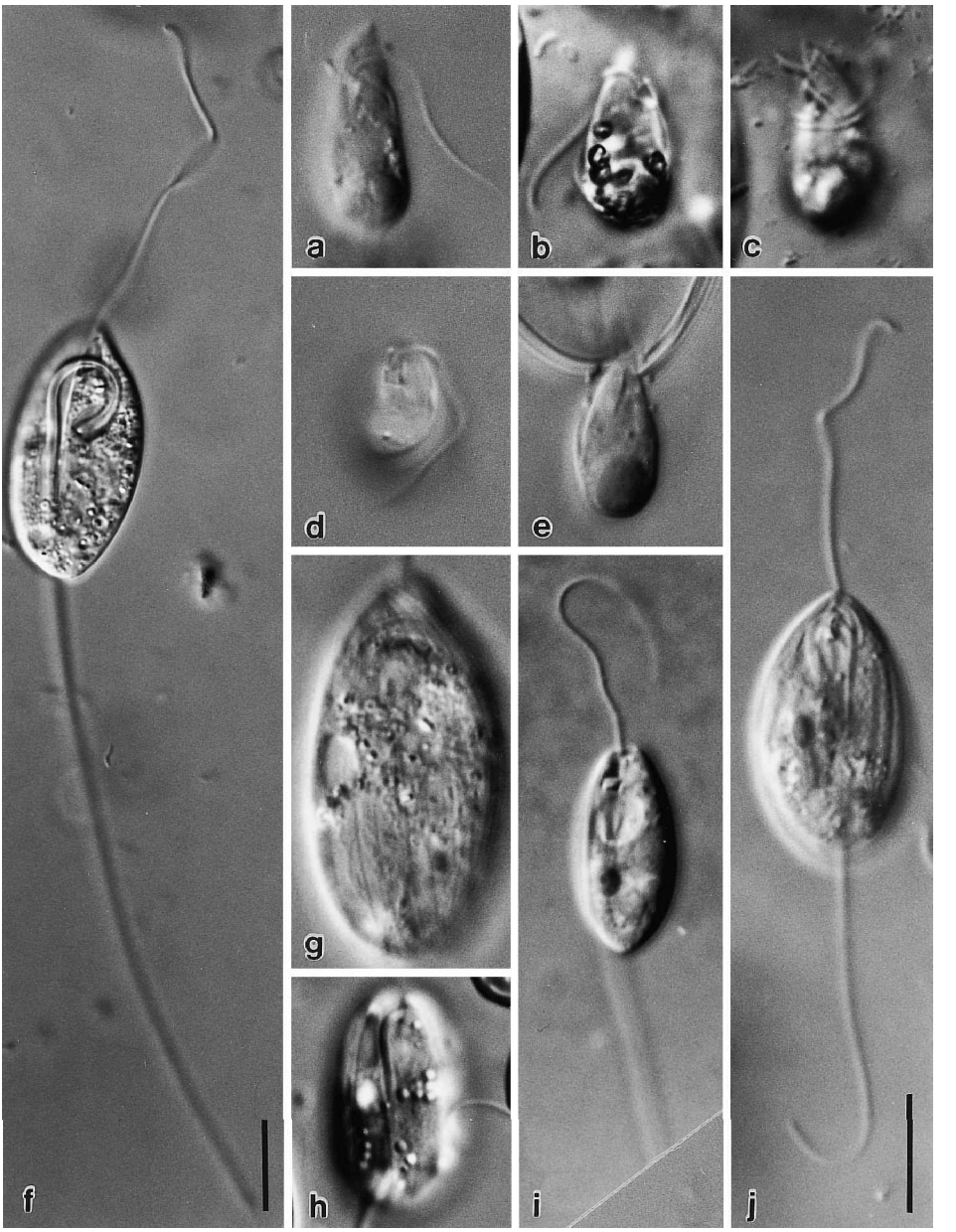


FIG. 4. (a–e) *Hemistasia phaeocysticola*, (f, g) *Anisonema acinus*, (f) general appearance of cell, (g) dorsal view showing surface striations, (h, i) *Anisonema trepidum*, (h) ventral view showing surface groovings, (i) general appearance of cell, (j) *Dinema platysomum*, general appearance of cell. All micrographs are DIC images. Scale bar in (f) = 10 μm, scale bar in (j) = 10 μm for (a–e) and (g–j).

subtropical and tropical Australia, Brazil, Canada, Denmark, Fiji, Gulf of Finland, Greenland, Hawaii, Norway and Equatorial Pacific (Griessmann, 1913; Throndsen, 1969, 1970; Burzell, 1973; Larsen and Patterson, 1990; Vørs, 1992a, 1992b, 1993a; Patterson *et al*., 1993; Vørs *et al*., 1995; Ekebom *et al*., 1996; Patterson and Simpson,

1996; Tong *et al*., 1997, 1998; Bernard *et al*., 1999). *Rhynchomonas nasuta* is common and widespread, but usually does not occur in large numbers. Our observations are in good agreement with those of Larsen and Patterson (1990). This species can be distinguished from small species of *Amastigomonas* by the bulbous snout.

Euglenida Bütschli, 1884
Anisonema acinus Dujardin, 1841
(figures 3a, 4f, g)

Description. Cell outline like a grain of barley, 21–37 μm long, 13–17 μm wide, flattened, with a ventral groove which diminishes posteriorly. With about nine longitudinal pellicular grooves on each of the ventral and dorsal faces of the cell. In some cells, the grooves are fine and difficult to see but in a few cells they are deeper. The anterior flagellum is about 1.5 times the cell length and beats freely from side to side. The trailing posterior flagellum is about 1.7–3.2 times the length of the cell, is thicker than the anterior flagellum, lies in the ventral groove, and tapers posteriorly. This species contained diatoms up to 25 μm long and one cell had four diatoms as long as 17 μm. The flagellar pocket is located in the left side of the cell and the nucleus is in the right side. This species glides smoothly, but jerks backwards when changing direction. Commonly observed. Description based on observations of 29 cells.

Remarks. Anisonema acinus was found in marine sites in the Danish Wadden Sea and in tropical Australia and Fiji by Larsen (1987) and Larsen and Patterson (1990), respectively. The length was previously reported to be from 22 to 40 μm (Klebs, 1893; Lemmermann, 1913; Huber-Pestalozzi, 1955; Larsen, 1987; Larsen and Patterson, 1990). Generally, our cells are in accordance with the cells described by previous authors. This species is very similar in general appearance and cell length to *Anisonema glaciale* Larsen and Patterson, 1990 but can be distinguished by the location of the nucleus and the pattern of movement. This species resembles *Dinema validum* Larsen and Patterson, 1990 in cell length and shape, but it is distinguished because *D. validum* has an ingestion apparatus, a squirming movement and somewhat thickened pellicle.

Anisonema acinus may have a smooth pellicle or have fine pellicular striations (Klebs, 1893; Lemmermann, 1913; Huber-Pestalozzi, 1955). Skuja (1939) created *A. prosgeobium*, which resembles *A. acinus*, but was distinguished by the lack of pellicular striations and because the nucleus lies in the right of the cell. However, all cells described in this study had a nucleus at the same position as in *A. prosgeobium.* The position of the nucleus may not be a good diagnostic character because it can be changed by food vacuoles (Larsen, 1987). We observed some cells with smooth pellicle but were otherwise indistinguishable from the individuals identifiable as *A. acinus*. We are of the view that *A. prosgeobium* is a junior synonym of *A. acinus*. This species is similar to *Dinema platysomum* (Skuja, 1939) Lee and Patterson, n. comb. in general appearance, but is not flexible.

Anisonema trepidum Larsen, 1987
(figures 3b, 4h, i)

Description. Cell profile oblong, 13–19 μm long, 6.5–10 μm wide, flattened. With three distinct grooves on the dorsal and ventral faces. Two emergent flagella are of unequal length. The anterior flagellum is approximately 1.5 times the cell length,

and the trailing posterior flagellum is stronger than the anterior flagellum, is approximately 3.5–5 times the cell length and tapers distally. The flagellar pocket and nucleus are in the left side of the cell. Cells contained small granules. The cells glide quickly and jerk when changing direction. Rarely observed.

Remarks. Cell length was previously reported to be 9–20 μm and this species was found in marine sites in tropical Australia, Brazil, Danish Wadden Sea, Fiji and Hawaii (Larsen, 1987; Larsen and Patterson, 1990; Ekebom *et al.*, 1996). Generally, our observations of the appearance of this species agree with those of Larsen and Patterson (1990), but we did not observe the arrests which Larsen and Patterson felt helped to distinguish this species. *Anisonema trepidum* is distinguished from *A. acinus* Dujardin, 1841 by its smaller size, cell shape and its behaviour. *Anisonema glaciale* Larsen and Patterson, 1990 has the same movement as *A. trepidium*, but can be distinguished by its larger size.

Dinema litorale Skuja, 1939
(figures 3e, 5d–g)

Description. Cell length varies from 45 to 95 μm. Cell spindle-shaped to ovate, with about 30 striations running longitudinally along extended cells or helically in contracted cells. Cortical grooves may be underlain by long thin inclusions. The ingestion apparatus is located slightly to the right of the midline of the cell, with two rods clearly visible and extending at least halfway down the cell. Refractile granules cluster around the ingestion apparatus. The flagellar pocket is difficult to see. Nucleus spherical and slightly posterior. The anterior flagellum may be as long as the cell. The posterior flagellum is about 0.5–1.5 times the cell length and is thick at its base and tapers towards the tip—as in *Anisonema*. Cells move by smooth gliding interrupted with sudden stops, they may jerk back while becoming more spherical and then continue gliding. Often with many refractile granules. Consume diatoms up to 56 μm long. Sometimes (late cultures) common. Observations based on 15 cells.

Remarks. Dinema litorale is distinguished from other species of *Dinema* except *D. griseolum* Perty, 1852 by its large size and its distinct pellicular striations. According to Skuja (1939), *D. litorale* is distinguished from *D. griseolum* by a more spindle-shaped body, the lack of granules (muciferous bodies) under cell surface, fewer fine and thick spiral striations and the somewhat larger size of *D. griseolum*. We found cells without muciferous bodies lining the pellicular strips of cells that could not otherwise be distingushed from those with inclusions (as in *D. griseolum*). We note that *Dinema griseolum* may be a senior synonym of *Dinema litorale* Skuja, 1939. The range of lengths was previously reported to be 40–95 μm (Skuja, 1939; Larsen, 1987; Larsen and Patterson, 1990; Ekebom *et al.*, 1996). Our observations are broadly in agreement with previous authors, but the two-fold size range suggests that more than one species may be included. We note some minor differences between earlier reports and our observations in respect of the number of grooves and of the relative lengths of the flagella. Cells without one flagellum or with truncated flagella were often observed, so we do not regard flagellar length as a good diagnostic character. In cells observed by us, the nucleus was not located at the extreme posterior as indicated by Larsen and Patterson (1990), but was similar to the position indicated by Ekebom *et al.* (1996) and Skuja (1939). Previously reported from marine sites in subtropical and tropical Australia, Brazil, Danish Wadden Sea (Larsen, 1987; Larsen and Patterson, 1990; Ekebom *et al.*, 1996).

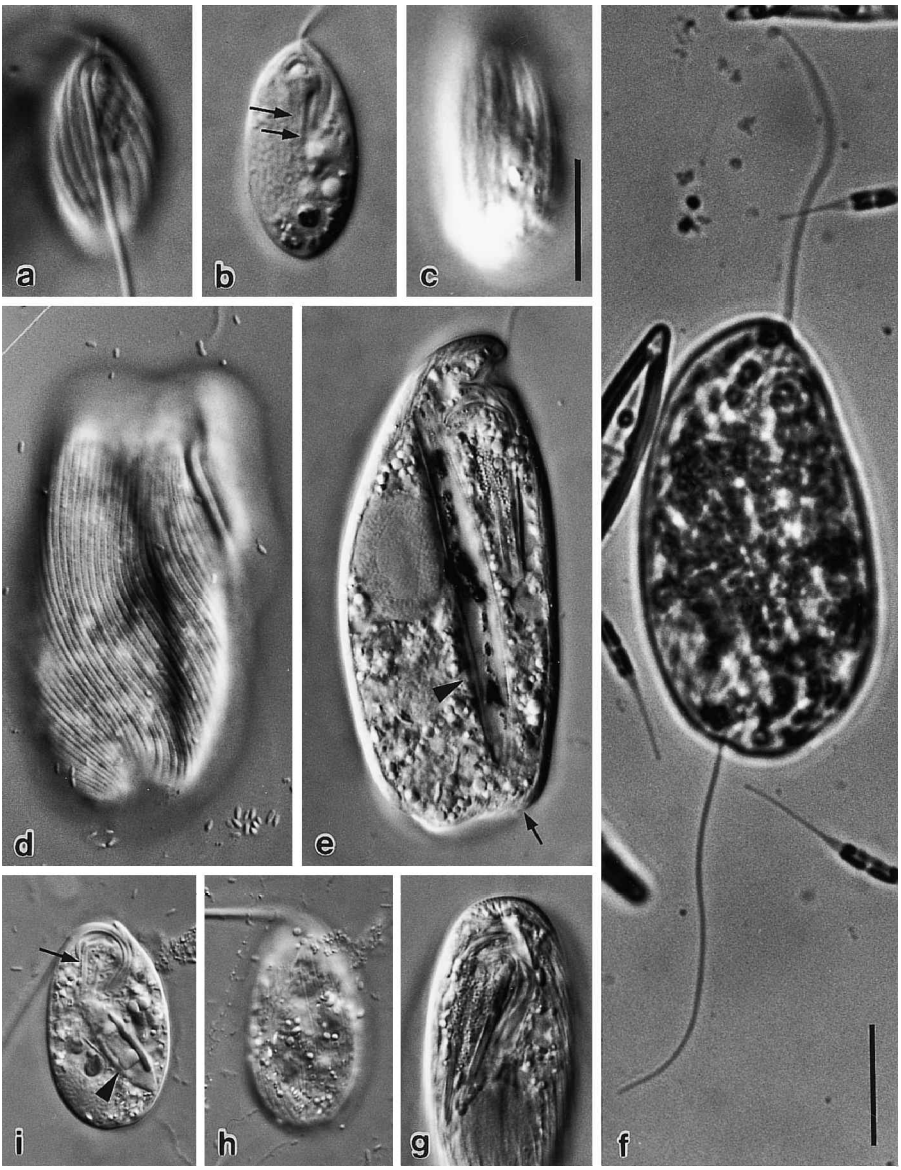


FIG. 5. (a–c) *Dinema platysomum*, (a) ventral view showing surface striations, (b) ingestion organelle (arrows), (c) dorsal view showing surface striations, (d–g) *Dinema litorale*, (d) surface striations, (e) thick cell wall (arrow) and diatom (arrow head), (f) general appearance of cell, (g) ingestion organelle, (h, i) *Dinema validum*, (h) dorsal view showing surface groovings, (i) ingestion organelle (arrow) and diatom (arrow head). All micrographs are DIC images with the exception of (f). Scale bar in (c) = 10 μm for (a–c), scale bar in (f) = 20 μm for (d–i).

Dinema platysomum (Skuja, 1939) Lee and Patterson, n. comb.
(figures 3c, 4j, 5a–c)

Description. Cell outline elliptical, 20–28 μm long, 9–14 μm wide, flattened, flexible when being compressed. With about 20 pellicular striations on ventral and

dorsal faces of the cell. The ventral striations are more distinct than the dorsal ones. The two flagella are unequal in length. The anterior flagellum is slightly thickened, is about 1.2 times the length of the cell and sweeps from side to side. The trailing posterior flagellum is thicker and is most strongly developed proximally. It lies in a ventral groove and is about 2–2.5 times the length of the cell. The flagellar pocket is located in the left side of the cell and the large elliptical nucleus is located on the right half in the middle of the cell. The ingestion apparatus may be easily seen. Cells occasionally stop and jerk when changing direction and then move again. The cells contained diatoms. Rarely observed. Description based on observations of five cells.

Remarks. This species was described as *Anisonema platysomum* from freshwater sites by Skuja in 1939. We assign this species to *Dinema* because it has an ingestion apparatus. This species is indistinguishable from *Dinema inaequale* Larsen and Patterson, 1990 in size, shape, and in having an ingestion apparatus and a ventral groove, and we regard the species as synonymous. This species has been found in marine sites in tropical Australia and Fiji and the cell length was previously reported to be 26–30 μm (Larsen and Patterson, 1990; Ekebom *et al*., 1996). Our observations are in agreement with observations of Skuja (1939) and Larsen and Patterson (1990). Cells observed by us were in the lower part of the range. Most cells had a nucleus at the right middle of the cell, but one cell had a nucleus in the right posterior part of the cell. We note therefore that the position of the nucleus may not be a reliable diagnostic character. *Dinema platysomum* is similar in general appearance to *Dinema validum* Larsen and Patterson, 1990, which can be distinguished by strong ventral pellicular striations and thin pellicle. This species resembles a few of species of the genus *Anisonema*, such as *A. acinus* and *A. glaciale* but can be distinguished by the ingestion apparatus and flexible body.

Dinema validum Larsen and Patterson, 1990
(figures 3d, 5h, i)

Description. Cell outline oblong to ovate, 32–53 μm long, 22–27 μm wide, with slightly thickened pellicle. About 16 wide longitudinal striations occur on both faces of the cell and slightly follow a S-helix. Dorsal striations are more distinct than ventral ones. The anterior flagellum is as long as the cell and beats with a sweeping motion. The posterior flagellum is approximately 3 times the cell length, is thicker than the anterior flagellum and emerges as a hook from the flagellar pocket which is in the left-hand side of the cell. The ingestion apparatus has two rods but may be difficult to see. It extends halfway down the cell. This species consumed diatoms as long as 16 μm. The nucleus is usually in the right posterior end of the cell but may be in the left-hand side. Moves by gliding and may undergo squirming movements. When changing direction, cells jerk backwards and then continue to move forward. Three cells observed.

Remarks. This species was previously reported from marine sites in subtropical and tropical Australia, Brazil and Fiji, with reported cell lengths from 26 to 38 μm (Larsen and Patterson, 1990; Ekebom *et al*., 1996; Patterson and Simpson, 1996). Although one of our cells was slightly pointed at both ends and the ingestion apparatus was hard to see, and was very much larger than the previously reported sizes, we assigned the cell to *D. validum* because of slightly thickened pellicle, hooked posterior flagellum and squirming movements. One cell observed had its nucleus in the left-hand side of the cell, thus we suspect that the position of a nucleus is not a

good diagnostic character. This species is distinguished from other species of the genus *Dinema* by its wide pellicular striations and the thickness of the recurrent flagellum; it is distinguished from *D. litorale* Skuja, 1939 by the smaller number of pellicular striations.

Heteronema exaratum Larsen and Patterson, 1990
(figures 6a, 7a–e)

Description. Cell ovate, 8–18 μm long, 6–13 μm wide, dorso-ventrally flattened, metabolic, but not vigorously so, with a small ingestion organelle. With pellicular striations following a S-helix on both faces of the cell. The dorsal striations are more strongly developed than the ventral ones. This species usually moves by skidding in a counter-clockwise direction. Two flagella are similar in length, are slightly longer than the cell and point in different directions when moving; the anterior flagellum points to the right, the posterior flagellum to the left. The posterior flagellum has a knob at its base within the flagellar pocket and is stronger than the anterior flagellum. In immotile cells, the flagella coil up. The reservoir and nucleus are in the left side of the cell. Common.

Remarks. This species has been found in marine sites in subtropical and tropical Australia, and Fiji with previously reported lengths from 15 to 20 μm (Larsen and

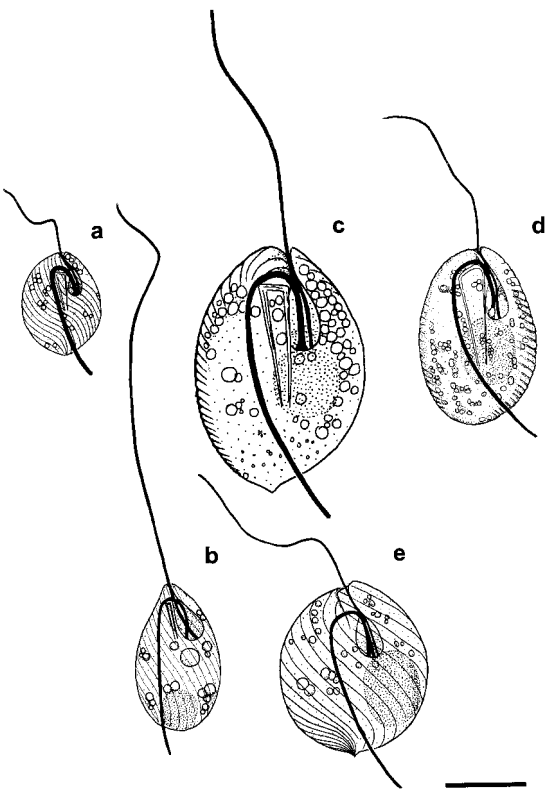


FIG. 6. Euglenida, *Heteronema* and *Metanema*, (a) *Heteronema exaratum*, (b) *H. globuliferum*, (c) *H. larseni*, (d) *H. ovale*, (e) *Metanema strenuum*. Scale bar = 10 μm for all figures.

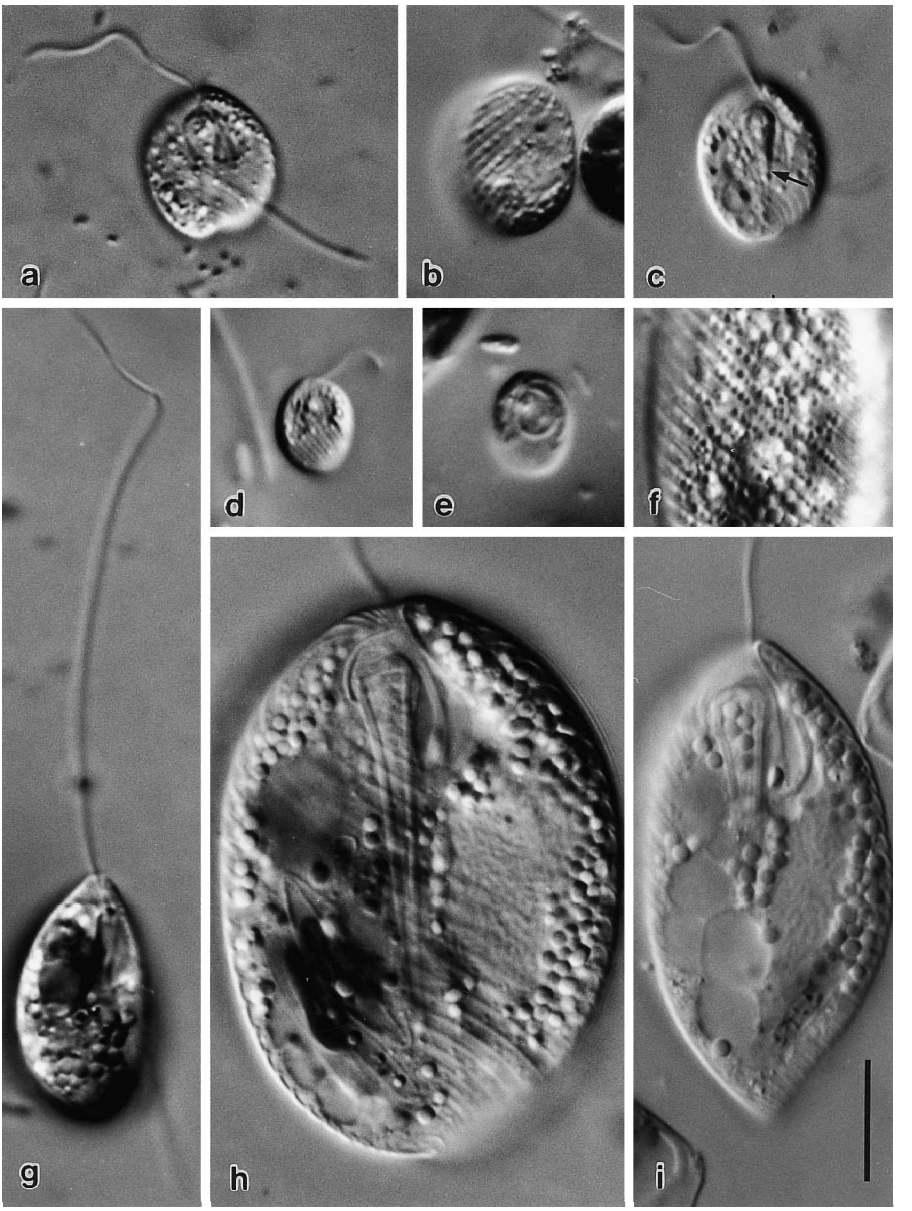


FIG. 7. (a–e) *Heteronema exaratum*, (a) general appearance of cell, (b) dorsal face showing striations, (c) ventral face showing ingestion organelle (arrow) and striations, (d–e) small cells, (g) *Heteronema globuliferum*, general appearance of cell, (f), (h, i) *Heteronema larseni*, (f) granular bodies on striations, (h) ingestion organelle and prey, (i) tail. All micrographs are DIC images. Scale bar = 10 μm for all figures.

Patterson, 1990; Patterson and Simpson, 1996). We have observed cells 8 μm long, and although we have not seen an ingestion organelle the cells are otherwise in agreement with previous accounts of *H. exaratum*. This species can be confused with *H. ovale* (see remarks to *H. ovale*), but is distinguished by less vigorous

squirming, the more weakly developed pellicular striations, and the differences between dorsal and ventral striations. It can be distinguished from *H. larseni* (below) because *H. exaratum* has weaker pellicular striations, is smaller, does not have a pointed posterior end, and has a less visible ingestion apparatus.

Heteronema globuliferum (Ehrenberg, 1838) Stein, 1878
(figures 6b, 7g)

Description. Cell outline elongate ovate, 20 μm long and about 8–11 μm wide, flattened, with squirming movement and with pellicular striations following a S-helix. Two emergent flagella are similar in width. The anterior flagellum is approximately 2–2.5 times the length of the cell and is longer than the posterior flagellum which is slightly longer than the cell. The ingestion organelle may be difficult to see. The reservoir is in the left ventral side of the cell and the nucleus is in the posterior part of the cell. Refractile bodies lie under the cell surface. Cells move by gliding. Rarely observed.

Remarks. Previous reported cell lengths range from 17 to 39 μm (Lemmermann, 1913; Stein, 1878; Huber-Pestalozzi, 1955; Larsen and Patterson, 1990). This species was found in marine sites in Brazil and Fiji (Larsen and Patterson, 1990). Generally, our observations are in agreement with Larsen and Patterson (1990). This species is distinguished by its elongate ovate shape. This species is similar to *H. nebulosum* Dujardin, 1841 in general appearance, but *H. nebulosum* is bigger and has a short recurrent flagellum. *Peranema globulosa* Dujardin, 1841 and *H. sacculus* Skuja, 1948 are synonyms of *H. globuliferum* (Stein, 1878; Larsen and Patterson, 1990). *Heteronema abruptum* Skuja, 1939 also appears to be a junior synonym of *H. globuliferum.* Skuja described *H. abruptum* without reference to *H. globuliferum*. *Heteronema abruptum* measures 17–30 μm which is within the range of *H. globuliferum*. The anterior flagellum of *H. abruptum* is about twice the cell length and the posterior flagellum is about 1–1.5 times the cell length. There are minor differences which we do not regard as significant; they have slightly different shapes and *H. abruptum* is slightly broader.

Heteronema larseni Lee and Patterson, n. sp.
(figures 6c, 7f, h, i. Type micrograph: figure 7h)

Diagnosis. *Heteronema*, ovate, 35–45 μm long, with a posterior point and about 36 well-developed pellicular striations. With or without globular pellicular granules.

Description. Cell ovate, 35–45 μm long, flattened, with a posterior point to the cell. Approximately 36 pellicular striations follow a S-helix. The striations of the ventral face are more distinct than the dorsal ones. The striations appear to overlap each other, with raised ridges being separated by flat regions. Some but not all cells have globular granules located along the grooves. This species is capable of squirming movements, but not vigorously so. The anterior flagellum is about the length of the cell and bends to the right while the cell is swimming. The posterior flagellum bends to the left while swimming, is slightly longer than the cell and is stronger than the anterior flagellum. The posterior flagellum is swollen near its base. The ingestion organelle has two conspicuous thick rods and extends to two-thirds of the length of the cell. Consumes diatoms, one cell containing diatoms up to 17 μm long. The reservoir is pear-shaped and in the left half of the cell. The nucleus is about 15 μm long and located in the left side of the cell near the midline. About 2 μm size refractile

bodies lie around the reservoir, ingestion organelle and nucleus. Cells move by skidding in close contact with the substratum. Four cells observed.

Remarks. This species was first described under the name *H. ovale* by Larsen (1987) and was redescribed by Larsen and Patterson (1990) and Ekebom *et al.* (1996). Larsen (1987) noted that the cells observed by him differed in cell length from *H. ovale* as described originally by Kahl (1928) (*H. ovale sensu* Kahl measured 25 μm, those of Larsen measured 35–42 μm). The cells described by Ekebom *et al.* (1996) differ from the cells reported here and those described by Larsen because they are smaller (16–24 μm), have no posterior point to the cell and may have vigorous squirming movements. We have found cells which are consistent with *H. ovale sensu* Kahl—see below. We conclude that the organisms described by Larsen (1987), Larsen and Patterson (1990) and here are not *H. ovale*. *Heteronema larseni* Lee and Patterson, n. sp. is erected for them. This species has been found in tropical Australia, Danish Wadden Sea and Fiji. Previously reported lengths are 20–42 μm (Larsen 1987; Larsen and Patterson, 1990) although it is possible that the small cells observed by Larsen and Patterson (1990) may be *H. ovale*. This species has strong pellicular striations and may have small bodies alongside the striations. *Heteronema ovale* also has pellicular bodies (see *H. ovale* below). We do not regard the refractile inclusions (small bodies) as a good diagnostic character of *H. larseni*. *Heteronema larseni* can be distinguished from *H. exaratum* and *H. ovale* by its larger size, pointed posterior end, and well-developed ingestion organelle.

Heteronema ovale Kahl, 1928
(figures 6d, 8a–e)

Description. Cell outline ovate, cell length 15–30 μm, flattened. The pellicular striations follow a S-helix on the ventral and dorsal faces of the cell and may or may not have associated refractile bodies. This species is capable of vigorous squirming movements. Two flagella are of almost equal length and are slightly longer than the cell. The posterior flagellum has a knob at its base and is stronger than the anterior flagellum. The ingestion organelle has two rods, eats diatoms. The reservoir and nucleus are located in the left side of the cell. Cells move by skidding or by vigorous squirming in contact with substratum. Sometimes common. Description based on the observation of 20 cells.

Remarks. Generally, our observations are in good agreement with the original description of Kahl (1928). As noted above under comments to *H. larseni*, the organism described by Larsen (1987) and by Larsen and Patterson (1990) as *H. ovale* is not, in our view, the same species as described by Kahl. *Heteronema ovale* described by Ekebom *et al.* (1996) may be the same species. *Heteronema ovale* can be confused with *H. exaratum* Larsen and Patterson, 1990 and *H. larseni* Lee and Patterson, n. sp. because they have a similar general appearance. However, *H. ovale* can be distinguished from *H. exaratum* because *H. exaratum* has differing dorsal and ventral pellicular striations and more vigorous squirming movements, but is not distinguished by size because there is considerable overlap. *Heteronema ovale* is distinguished from *H. larseni* by the vigorous squirming movements of *H. ovale*, and the pointed posterior end of *H. larseni*. *Heteronema ovale* is likely to be smaller.

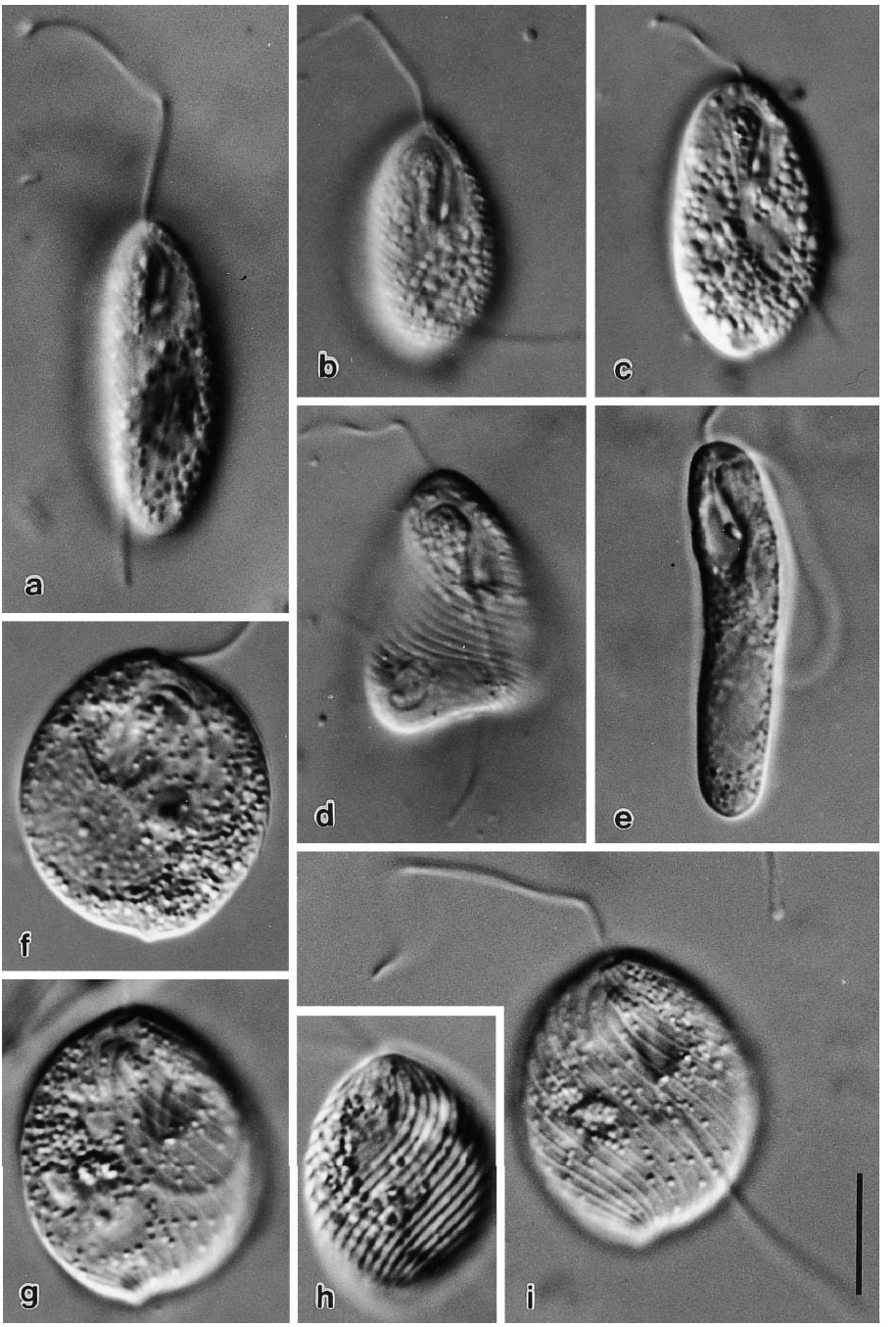


FIG. 8. (a–e) *Heteronema ovale*, all different cells, (b, c) general appearance of cell, (d) squirming cell, (e) elongated cell, (f–i) *Metanema strenuum*, (f) showing warty surface, (g) dorsal view showing striations, (h) different cell showing different striations, (i) general appearance of cell. All micrographs are DIC images. Scale bar = 10 μm for all figures.

Jenningsia fusiforme (Larsen, 1987) Lee *et al*., 1999
(figures 12c, 13g, h)

Description. Cell usually elongate, 30–35 μm long, with a narrowed anterior end and a rounded posterior end. With delicate pellicular striations following an S-helix. One flagellum emerges from a slit opening of the flagellar canal, is 40–50 μm long and beats mostly at anterior end. A refractile arc-like structure is located close to

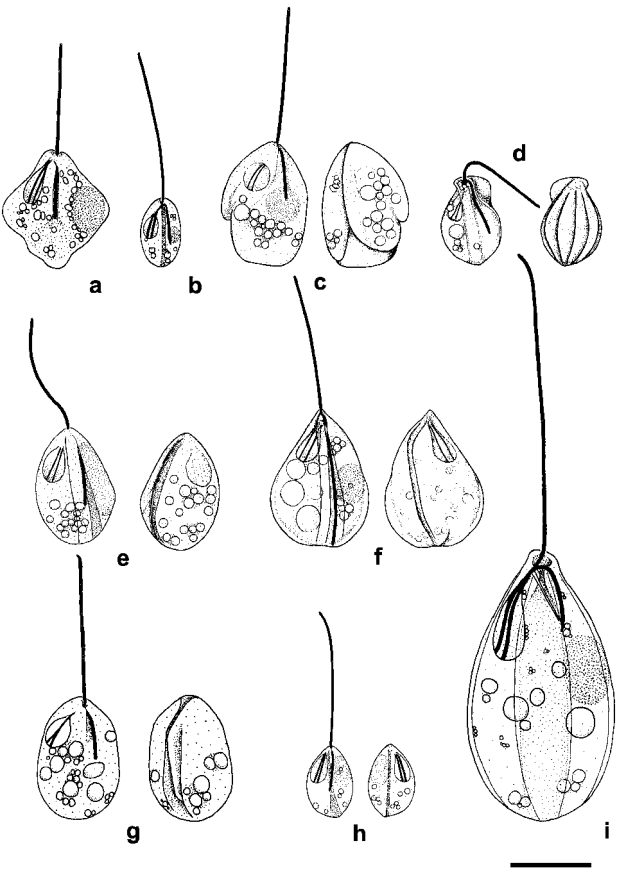
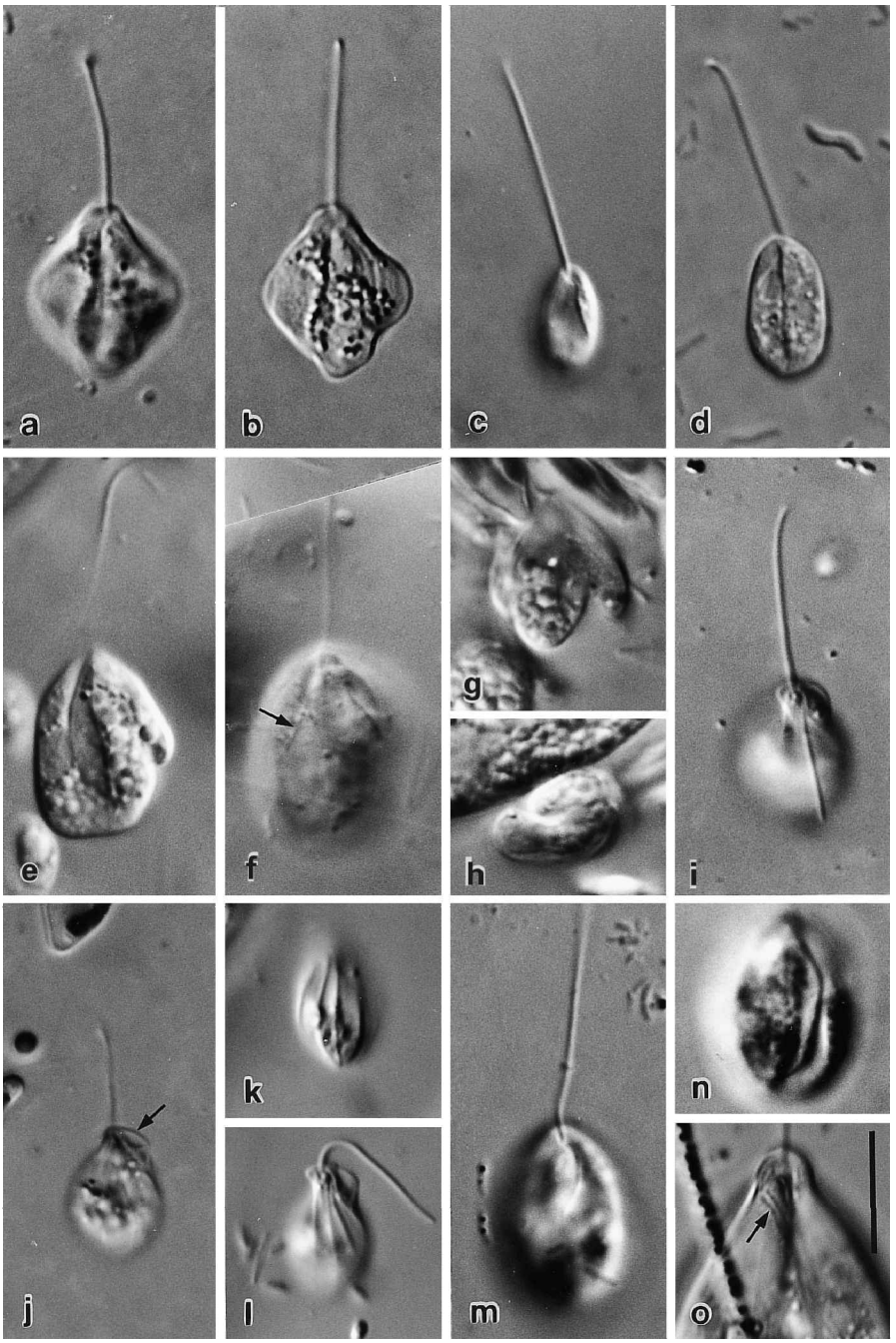


FIG. 9. Euglenida, *Notosolenus*, (a) *N. adamas*, (b) *N. apocamptus*, (c) *N. brothernis*, (d) *N. hemicircularis*, (e) *N. lashue*, (f) *N. pyriforme*, (g) *N. similis*, (h) *N. scutulum*, (i) *N. ostium*. Scale bar = 10 μm for all figures.

FIG. 10. (a, b) *Notosolenus adamas*, (a) ventral view showing narrow ventral groove and short posterior flagellum, (b) general appearance of cell, (c, d) *Notosolenus apocamptus*, (c) ventral view, (d) dorsal view showing groove, (e–h) *Notosolenus brothernis*, (e) general appearance of cell, (f) ventral view showing posterior flagellum, (g) dorsal view, (h) transverse section, (i–l) *Notosolenus hemicircularis*, (i) general appearance of cell, (j) hyaline semicircular collar, (k) dorsal view showing ridges, (l) ventral view showing fine ridges and a posterior flagellum, (m, n) *Notosolenus similis*, (m) ventral view, (n) dorsal view showing a groove with a well-marked ridge, (o) *Notosolenus ostium* showing ingestion organelle. All micrographs are DIC images. Scale bar = 10 μm for all figures.



the slit-like opening of the flagellar canal. The flagellar pocket is located in the first third of the cell on the left-hand side. The ingestion organelle with two fine rods is obvious. The nucleus is situated in the posterior of the cell. Moves by gliding or squirming movement. Relatively common. Description based on observations of nine cells.

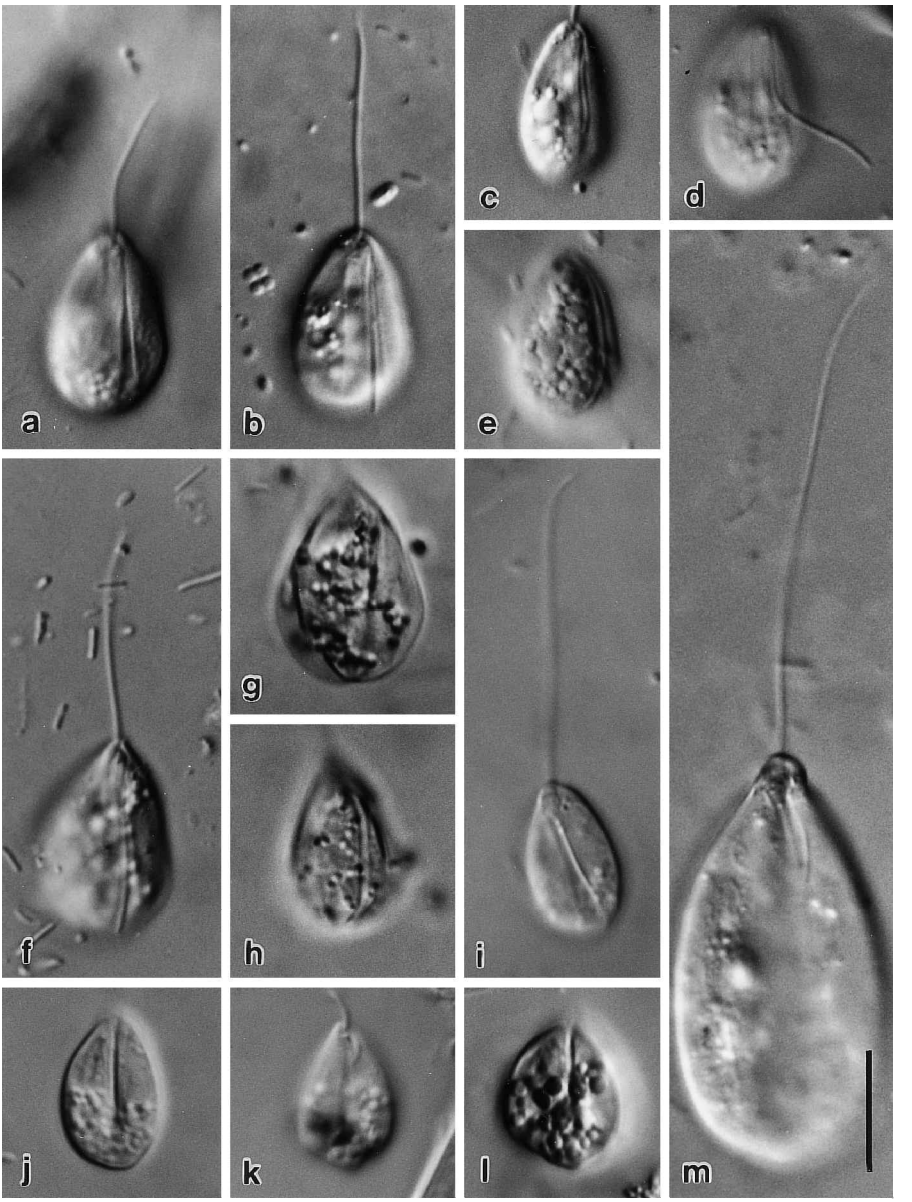


FIG. 11. (a–e) *Notosolenus lashue*, (a) ventral view, (b) general appearance showing ventral view, (c) and (d) showing different lengths of a posterior flagellum, (e) dorsal view showing a dorsal groove with a ridge, (f–h) *Notosolenus pyriforme*, (f) general appearance of cell showing ventral view, (g) dorsal view of same cell, (h) dorsal view of different cell showing a groove, (i–l) *Notosolenus scutulum*, (i) general appearance showing a ventral view, (j) dorsal view of same cell, (k) ventral view and (l) dorsal view of different cells, (m) *Notosolenus ostium* showing general appearance and ventral view. All micrographs are DIC images. Scale bar = 10 μm for all figures.

Remarks. Previously reported cell length ranges from 25 to 45 μm. This species was reported from marine sites in subtropical and tropical Australia, Brazil, Danish Wadden Sea, and Fiji as *Peranema fusiforme* (Larsen, 1987; Larsen and Patterson,

1990; Ekebom *et al*., 1996; Patterson and Simpson, 1996). Evidence has now been presented that the 'short recurrent flagellum' is now part of the internal architecture of the mouth region and this species has since been assigned to the genus *Jenningsia* (Lee *et al*., 1999). Our observations on this species are broadly in agreement with those of previous observers. This species is similar to *Jenningsia macrostoma* (see below), but it can be recognized by its smaller size and less developed ingestion organelle.

Jenningsia macrostoma (Ekebom *et al*., 1996) Lee *et al*., 1999
(figures 12e, 13j, k)

Description. Cell length about 80 μm, anteriorly narrowed or pointed and posteriorly rounded, very metabolic. With about 50 fine pellicular striations following a S-helix. Ventral striations are more distinct than the dorsal ones. The flagellar pocket is situated on the left ventral face of the cell and is up to 24 μm long. The flagellum is as long as the cell and beats freely. The ingestion organelle with two well-marked rods is strongly developed and up to 20 μm long. The rods appear hollow. There is a refractile arc-like structure associated with the slit-like opening of the flagellar canal. The nucleus is situated in the posterior end of the cell. Refractile granules are randomly distributed inside the cell. This species ingested eukaryotic cells as long as 16 μm. Glides with a squirming movement. Two cells observed.

In addition we observed three cells measuring 100–114 μm and with a narrow aspect. The ingestion organelle seems less developed than the cells described above and the nucleus is situated in the mid-position of the cell.

Remarks. This species was first described from a marine site in tropical Australia by Ekebom *et al*. (1996) with lengths of 64–87 μm as *Peranema macrostoma*. As with *Jenningsia fusiforme* (above) we note that the arc structure associated with the flagellar canal is not a flagellum but part of the architecture of the mouth, and for this reason this species was transferred to the genus *Jenningsia* (Lee *et al*., 1999). We note that the *Peranema* measuring 70 μm long found in Brazil by Larsen and Patterson (1990) may belong to this species. The smaller cells observed by us comply well with the description of Ekebom *et al*. (1996). Ekebom *et al*. (1996) observed one cell measuring 114 μm from One Tree Island (Patterson, unpubl. notes) and which probably corresponds with the larger cells observed here. These can be tentatively assigned to *J. macrostoma*. This species resembles *J. fusiforme* in general appearance but *J. macrostoma* is bigger and has larger rods in the ingestion organelle.

Metanema strenuum (Skuja, 1948) Larsen, 1987
(figures 6e, 8f, i)

Description. Biflagellate euglenid, ovate, about 22–27 μm long, flexible, flattened, with a knob at flagellar base. With a small posterior protruberance. There are about 24 very distinct striations on each face of the cell. Moves with a skidding action with the anterior flagellum directed towards the right and the posterior one to the left. Both flagella are slightly longer than the cell. The nucleus and reservoir are in the left-hand side of the cell. Ingestion organelle not visible. Rarely observed.

Remarks. This species was first described as *Anisonema strenuum* by Skuja (1948) and transferred to *Metanema* by Larsen (1987). *Metanema strenuum* from the Danish Wadden Sea measures 19–30 μm (Larsen, 1987). Our observations are generally in accordance with those of Larsen. This genus resembles some species of the genus

Heteronema, the only difference being the presence of an ingestion organelle in *Heteronema*. This species resembles *Heteronema larseni* Lee and Patterson, n. sp. in general appearance and in having a posterior point, but it lacks an ingestion organelle and most cells are smaller. This species is similar to *Metanema dexiotaxum* (Skuja, 1939) Larsen, 1987 in having a posterior point which was mentioned in the text and was shown in drawings of Skuja (1939), but *M. dexiotaxum* is slightly smaller (15–19 μm) and has a shallow ventral groove. If further work shows that the sizes overlap, then these species should be regarded as conspecific.

Notosolenus adamas Lee and Patterson, n. sp.
(figures 9a, 10a, b. Type micrograph: figure 10b)

Diagnosis. *Notosolenus*, cell diamond-shaped about 14 μm long and 9–12 μm wide, with a narrow ventral groove.

Description. Colourless euglenid with diamond-shaped or rhomboid hyaline body. About 14 μm long and 9–12 μm wide, dorso-ventrally flattened. The anterior flagellum is slightly longer than the cell. The posterior flagellum is about 0.5 times the cell length and emerges subapically at the end of a narrow median ventral groove. The reservoir is situated in the right side of the cell and the nucleus is in the left side. Small granules are often seen under the cell surface. Cells move slowly by gliding with the anterior flagellum directed anteriorly and with most motion at the tip of the anterior flagellum which moves actively. Rarely observed.

Remarks. This species has the characteristics of *Notosolenus* in being a rigid heterotrophic euglenid, being flattened, and in having two flagella emerging from a canal which opens subapically, moving by gliding, and with no visible mouth. It is distinguished from most other species of *Notosolenus* and *Petalomonas* by the cell shape. It is most similar to *N. rhombicus* Larsen, 1987. Larsen (1987) did not agree that the organisms referred to as *N. obliquus* (Klebs, 1893) Skuja, 1939 by Skuja (1939) were the same species as the organisms described for its basionym, *Petalomonas inflexa* var. *obliqua* Klebs, 1893. Larsen therefore provided a new name for the taxon observed by Skuja and himself. *Notosolenus adamas* is distinguished from *N. rhombicus* because the nucleus is not located posteriorly but near the equator and to the left, because it is flat, and because there is no anterior collar. This species resembles *N. papilio* (see Skuja, 1939) from freshwater in general shape and in having no dorsal ridges. *Notosolenus papilio* also has a short anterior neck. *Notosolenus pentagonus* (see Playfair, 1921) is similar to *N. adamas* in having a hyaline body, but is distinguished by its bigger size (about 21 μm), long posterior flagellum, and pentagonal cell shape. *Notosolenus adamas* resembles *N. scutulum* Larsen and Patterson, 1990 in size and in having a ventral groove, but can be distinguished because *N. scutulum* also has one deep dorsal groove. *Notosolenus adamas* is broadest in the middle of the cell, while *N. scutulum* is broader more posteriorly.

Notosolenus apocamptus Stokes, 1884
(figures 9b, 10c, d)

Description. Cell outline oval or ovate, 7–12 μm long (mostly 8–11 μm), 4–7 μm wide, about 2 μm thick, flattened. The anterior end is slightly narrowed, the posterior end is roundish. A deep longitudinal dorsal groove runs along the entire cell. Both sides of the groove are slightly rounded. Two flagella of unequal length emerge from an ovate reservoir in the right-hand side of the cell. The anterior flagellum is

approximately 1.5–1.8 times the cell length and the posterior flagellum is approximately 0.4–0.6 times the cell length. The nucleus is located on the left of the cell. Cells move by smooth gliding with anterior flagellum extended. Common.

Remarks. This species was first described by Stokes (1884) from freshwater sites. Previously reported with lengths from 6.5 to 18 μm (Stokes, 1884; Skuja, 1939; Larsen and Patterson, 1990; Ekebom *et al.*, 1996; Patterson and Simpson, 1996). This species was described from marine sites in subtropical and tropical Australia, Brazil and Fiji (Larsen and Patterson, 1990; Ekebom *et al.*, 1996; Patterson and Simpson, 1996). Generally, cells described here are consistent with those described by Larsen and Patterson (1990). This species is distinguished from others of the genus *Notosolenus* by its small size and deep dorsal groove. This species resembles *Petalomonas minuta* Hollande, 1942 in general appearance, but it is distinguished by the presence of a recurrent posterior flagellum and a dorsal groove. *Notosolenus apocamptus* is similar to *N. stenoschismus* Skuja, 1939 in general cell shape and in having a groove, but *N. stenoschismus* is slightly larger, has indistinct pellicular striations and has a ventral groove. This species can be confused with *N. similis* because of similar general appearance and length range (see *N. similis*, below).

Notosolenus brothernis Lee and Patterson, n. sp.
(figures 9c, 10e–h. Type micrograph: figure 10e)

Diagnosis. *Notosolenus* with irregular bulbous outline, 16 μm long and 9 μm wide; dorsal face formed by one wedge-shaped and one oblong plate.

Description. Colourless, cell outline irregular, about 16 μm long and 9 μm wide. The cell is anteriorly pointed and posteriorly rounded. The ventral face is flattened. The right half of the cell is slightly thicker than the left. The dorsal face is irregularly raised and seems to consist of two plates. The right plate of the dorsal face is wedge-shaped and shorter, and the left one is rather oblong and extends the full length of the left side of the cell. The wedge-shaped right plate slightly overlaps with the left one and the wide dorsal groove is formed between the two plates. The two flagella are unequal in length; the anterior flagellum is slightly longer and the front part of the flagellum is most active when the cell is moving forwards. The posterior flagellum is about 6 μm long. The ovate reservoir is situated subapically in the right-hand side of the cell and the nucleus is in the mid-position of the left-hand side. Cells move slowly and smoothly. Rarely observed.

Remarks. This species has the characteristics of the genus *Notosolenus* in being rigid, flattened and having two emergent flagella and no visible mouth. It is similar in length to *N. scutulum* Larsen and Patterson, 1990, *N. similis* Skuja, 1939, *N. triangularis* Larsen and Patterson, 1990 and *N. urceolatus* Larsen and Patterson, 1990 (see Huber-Pestalozzi, 1955; Larsen and Patterson, 1990), but it can be distinguished from these by its unusual shape. This species is similar to *Petalomonas sexlobata* Klebs, 1893 in that the dorsal face appears to be separated from the ventral face, but it is distinguished by its recurrent posterior flagellum and smaller size; *P. sexlobata* being 27–30 μm long (see Klebs, 1893).

Notosolenus hemicircularis Lee and Patterson, n. sp.
(figures 9d, 10i–l. Type micrograph: figure 10i)

Diagnosis. *Notosolenus*, 9–10 μm long, 6–7 μm wide, ventrally flattened, with a semicircular hyaline collar around a short neck and with five dorsal keels and three fine ventral ridges.

Description. Colourless, 9–10 μm long and 6–7 μm wide, ventrally flattened and dorsally convex. Both ends of the cell are pointed but there is a hyaline semicircular collar around the short anterior neck. This species has five dorsal keels running along the cell. Ventrally there are three fine ridges. The right and left ventral ridges arise at the neck. The left ventral ridge curves slightly from the anterior to the posterior forming an arc. The mid-ventral ridge arises from a small protrusion near the anterior end of the cell. Two are unequal in length and are slightly thickened. The anterior flagellum is about 1.2–1.4 times the length of the cell and the recurrent posterior flagellum is about 0.5–1.0 times the cell length. The reservoir lies anteriorly in the right-hand side of the cell and the nucleus in the left-hand side. Moves by gliding. Rarely observed.

Remarks. This species has the characteristics of the genus *Notosolenus* in that it is a heterotrophic euglenid with a rigid, flattened body, two emergent flagella and no visible mouth, and moves by gliding. This species can be distinguished from other small species of *Notosolenus* such as *N. apocamptus* Stokes, 1884 and *N. rhombicus* Larsen, 1987 by the semicircular hyaline collar and the five dorsal keels (see Huber-Pestalozzi, 1955; Larsen, 1987). *Notosolenus hemicircularis* is similar in general shape to *N. papilio* Skuja, 1939 and *N. urceolatus* Larsen and Patterson, 1990 (see Skuja, 1939; Larsen and Patterson, 1990), but it can be distinguished from both species by its smaller size and its strongly developed semicircular hyaline collar. *Notosolenus papilio* also has a ventral groove and lateral wings.

Notosolenus lashue Lee and Patterson, n. sp.
(figures 9e, 11a–e. Type micrograph: figure 11b)

Diagnosis. *Notosolenus*, mostly 14–15 μm long, with a longitudinal dorsal ridged groove to the left side, ventrally with a groove and one median ridge.

Description. Colourless flattened euglenid, about 13–16 μm long (mostly 14–15 μm) and 8–10 μm wide, the ratio of length to width is 1.4 to 2.1. Cell ovate or pear-shaped, anteriorly acute, posteriorly blunt or rounded. A distinct ventral groove running along the cell becomes broader towards the posterior. There is one fine median longitudinal ventral ridge which could easily be overlooked and which extends from the apex. A well-developed longitudinal dorsal groove runs along the left side of the cell. Two flagella of unequal length emerge from the flagellar canal. The anterior flagellum is about 1.0–1.3 times the cell length, it beats slowly when the cell is stopped but during normal gliding motion, the flagellum is extended and the front part is most active. The recurrent posterior flagellum inserts into the cell at the anterior end of the ventral groove. It is about 0.5–1.0 times the length of the cell and usually lies in the ventral groove when the cell is gliding. The ovate reservoir is situated anteriorly near the right ventral face of the cell. A large long nucleus lies in the left side of the cell. This species contains numerous refractile granules. Glides with the anterior flagellum directed anteriorly. Commonly observed.

Remarks. We assign this species to *Notosolenus* because it is a rigid colourless euglenid with a flattened body, no visible mouth and two emergent flagella. This species is the same length as *N. esulcis* Larsen, 1987, but it can be distinguished because *N. esulcis* has four shallow ridges on the dorsal face of the cell (Larsen, 1987). *Notosolenus lashue* resembles *N. canellatus* (see Skuja, 1948) and *N. pyriforme* Lee and Patterson n. sp. in having a dorsal groove, but this species can be distinguished because *N. canellatus* and *N. pyriforme* have lateral flanges and *N. lashue* has

a well-marked ridge in the dorsal groove. The dorsal face of *N. lashue* is similar to that of *N. similis* (see below) in having one longitudinal groove with a ridge, but *N. lashue* can be distinguished from *N. similis* because there is a ventral groove and ridge running along the entire cell. The ventral groove of *N. lashue* resembles that of *N. scutulum* (see Larsen and Patterson, 1990) in that the groove becomes gradually broader towards the posterior end of the cell, but the species can be distinguished by its round posterior end, the distinct ventral ridge and the central location of the dorsal groove.

Notosolenus ostium Larsen and Patterson, 1990
(figures 9i, 10o, 11m)

Description. Cell outline elongate ovate, 27–56 μm long, 15–24 μm wide, the ratio of length to width is 1.5 to 3.2. Dorso-ventrally flattened, dorsally with a median longitudinal groove, and ventrally a wide groove and four fine stripes. With a small obliquely oriented ingestion organelle with two fine rods near the anterior. The majority of the cells have a rounded posterior end but some cells have a slightly pointed posterior end. The reservoir is anteriorly situated in the right side of the cell and the nucleus in the left side. Two flagella of unequal length; the anterior flagellum is as long as the cell, held forward in gliding cells. The posterior flagellum is about 0.2–0.6 times the length of the cell. The organism contained eukaryotic algal material up to 8 μm long. Moves by smooth gliding with the anterior flagellum. Common in late culture. Description based on observations of 30 cells.

Remarks. Previously reported lengths of cells from marine sites (subtropical and tropical Australia, Brazil, Fiji, Hawaii and Panama) range from 24 to 40 μm (Larsen and Patterson, 1990; Ekebom *et al.*, 1996; Patterson and Simpson, 1996). Our observations extend the size range. We observed two cells measuring 43 and 56 μm which may be assignable to *N. ostium*. *Notosolenus ostium* is easily distinguished from other species of *Notosolenus* by its deep dorsal groove and visible ingestion organelle, which has not been seen in other species of the genus except *N. triangularis* Larsen and Patterson, 1990. *Notosolenus ostium* is similar to *N. lagenos* Skuja, 1948 in length and general appearance and in having a very short recurrent flagellum, but *N. ostium* can be distinguished by its wide grooves on both faces of the cell.

Notosolenus pyriforme Lee and Patterson, n. sp.
(figures 9f, 11f–h. Type micrograph: figure 11f)

Diagnosis. *Notosolenus*, cell pear-shaped, 15–18 μm long, 9–13 μm wide, with a longitudinal dorsal groove in left side, a ventral groove and a ventral ridge.

Description. Cell 15–18 μm long and 9–13 μm wide. Ventrally flattened and dorsally convex, cell outline pear-shaped. This species is anteriorly pointed or with a small collar at the anterior end of the cell and posteriorly rounded, but the raised central dorsal region may have a posterior point. The posterior lateral edges of the cell are thin and hyaline. This species has a median longitudinal groove, a ventral groove widening out towards the posterior end of the cell, and a fine median longitudinal ventral ridge parallel to the right margin of the ventral groove. The fine ventral ridge is hard to see but runs along the entire cell. The anterior flagellum is slightly longer than the cell and longer than the posterior flagellum. The recurrent posterior flagellum inserts into the anterior end of the ventral groove and varies from 0.5 to 1.2 times the cell length. It may lie in the ventral groove when the cell

is gliding. The reservoir and the nucleus are in the right and left sides, respectively. Small globular granules occur beneath the cell surface. Rarely observed.

Remarks. This species is assigned to genus *Notosolenus* because it is a rigid, flattened euglenid with two flagella emerging from a subapical canal opening and no visible mouth. *Notosolenus pyriforme* is similar to *N. canellatus* (see Skuja, 1948) in general appearance, but can be distinguished because *N. canellatus* has three dorsal grooves, not one, and also has an anterior protrusion. It is similar to *N. lashue* Lee and Patterson, n. sp. in having one dorsal groove and in size, but is distinguished because *N. pyriforme* has hyaline lateral flanges and pear-shaped body and because *N. lashue* has a dorsal groove with a well-marked central ridge, and is ovate. *Notosolenus pyriforme* may be the same as *N. canellatus sensu* Patterson and Simpson, 1996 described from Western Australia.

Notosolenus similis Skuja, 1939
(figures 9g, 10m, n)

Description. Cell outline oblong, 10–22 μm long (mostly 12–17 μm) and 6–12 μm wide, flattened. Usually with a narrowed anterior end and a rounded posterior end. The right half of the cell is thicker than the left half. The organism has a dorsal groove in the left-hand side of the cell with a well-developed undulating ridge and may or may not have a shallow median ventral groove. The two flagella are unequal in length; the anterior flagellum is about 1.0–1.7 times the cell length and the recurrent posterior flagellum is about 0.3–0.5 times the cell length. The reservoir lies in the right side of the cell, is usually roundish and the nucleus is in the left side. Cells glide with the anterior flagellum in contact with the substratum. Common, especially after coverslips have been in place for several days. Description based on observations of 43 cells.

Remarks. This species was first described by Skuja (1939) from freshwater sites and reported by Larsen and Patterson (1990) from tropical Australia and Brazil. Previously reported cell length ranges from 12 to 18 μm (Skuja, 1939; Larsen and Patterson, 1990). According to the original description of Skuja (1939), *N. similis* has a shallow ventral groove. Larsen and Patterson (1990) referred to a ventral groove, but their illustration (figure 21c) suggests a dorsal groove and this has been confirmed by reference to original notes. Although we have observed a shallow ventral groove in some cells, the major groove is located dorsally.

This species resembles *N. lashue* in size and in having a dorsal groove with a ridge, but it differs because *N. lashue* has a ventral groove in addition to the dorsal groove and a fine ventral ridge and because *N. lashue* is ovate or pear-shaped rather than oblong. *Notosolenus similis* can be easily confused with *N. apocamptus* Stokes, 1884 (6.5–16 μm) which is usually smaller than *N. similis* (12–22 μm) and has a deep dorsal groove—but this is without an undulating ridge and is located centrally not to the left of the cell. *Notosolenus similis* also resembles *N. stenoschismus* Skuja, 1939 in size and in dorsal groove, but *N. stenoschismus* can be distinguished by having indistinct longitudinal striations. The striations were noted by Skuja (1939) but not figured, and their presence has subsequently been confirmed (Schroeckh and Patterson, unpubl.). *Notosolenus stenoschismus* was not reported as having a thickened right margin to the groove. The distinctions between these species deserve further attention. *Notosolenus similis* is very similar to *Petalomonas involuta* Skuja,

1939 in cell length and general appearance, but is distinguished by the presence of a recurrent flagellum.

Notosolenus scutulum Larsen and Patterson, 1990
(figures 9h, 11i–l)

Description. Cell measuring about 9–15 μm long and 6.5–12 μm wide, flattened. Cells are anteriorly acute and posteriorly wide with a posterior prominence. The anterior flagellum is about 1.5–2.0 times the cell length and the trailing posterior flagellum is about 0.3–0.5 times the cell length. There is a deep narrow longitudinal dorsal groove which widens posteriorly and a ventral groove which also widens posteriorly. The reservoir is in the right-hand side of the cell and the nucleus is in the left side. Cells contained lots of food materials. Moves slowly by gliding. Rarely observed.

Remarks. Notosolenus scutulum was recorded from marine sites in Brazil by Larsen and Patterson (1990). Cells observed by us have a deep longitudinal dorsal groove, a ventral groove which widens out posteriorly and a posterior prominence, and one of three subtly different profiles (figures 11j–l)—which we regard here as conspecific.

Notosolenus scutulum is characterized by a deep longitudinal dorsal groove, a ventral groove which widens out posteriorly, and a posterior point. It is similar in size, shape, dorsal groove and posterior point to *N. skujai* described by Suxena (1955). There are minor differences: *N. skujai* has a broad dorsal groove and its nucleus is posterior to the middle of the cell, while *N. scutulum* has a narrow dorsal groove which is more visible than suggested by Suxena's drawings, and a ventral groove, and the nucleus is more central. We have seen no marginal gutters as are suggested by Suxena's drawings but not mentioned in the text. *Notosolenus scutulum* is similar to *N. orbicularis* in having a dorsal groove, but *N. orbicularis* Stokes, 1884 has no posterior prominence and has a very wide dorsal groove. This species looks like *N. triangularis* Larsen and Patterson, 1990, but *N. triangularis* is double the size (28 μm), has a small visible mouth and a triangular reservoir. *Notosolenus scutulum* is similar in size to *N. rhombicus* (Skuja, 1939) Larsen, 1987, but *N. rhombicus* has a smooth pellicle, a tiny collar surrounding the canal opening and no posterior point (see Larsen, 1987). This species is also similar to *N. ostium* Larsen and Patterson, 1990 in having a deep longitudinal groove and a ventral groove, but is distinguished because *N. ostium* has ventrally four fine pellicular stripes, has a visible mouth, is larger (20–56 μm), and has a short posterior flagellum relative to the cell length.

Notosolenus* cfr. *tamanduensis Larsen and Patterson, 1990
(figures 12a, 13a, b)

Description. Cell outline ovate, about 15 μm long and 11 μm wide, dorso-ventrally flattened, with a short neck around the flagellar canal. With a thin lateral flange in the left margin of the cell. This species has in total four ridges: two broad shallow ridges on both the ventral and dorsal faces of the cell and two fine ridges on the broad ventral ridge. The posterior end has a wedge-shaped protrusion, which is extended from the broad ridges. The anterior flagellum is as long as the cell and the posterior flagellum is about 0.8 times the cell length. The reservoir is rounded and situated in the right side of the cell, and the nucleus is in the left side of the cell and adjacent to the centre of the cell. Moves slowly by gliding. Rare.

Remarks. One cell observed. This species is similar to *N. tamanduensis* described by Larsen and Patterson (1990) from a marine site in Brazil. There are minor differences between our cell and *N. tamanduensis*: our cell was about half the size (29 μm) reported by Larsen and Patterson (1990) and we also have not seen an ingestion organelle, but that may be because of lack of material.

Notosolenus urceolatus Larsen and Patterson, 1990
(figures 12b, 13c–f)

Description. Cell outline broad posteriorly, narrow anteriorly, with a small neck around the flagellar canal, 11–17 μm (mostly 13–15 μm), 7–11 μm wide. This species has three dorsal keels, two lateral ridges and three fine ventral ridges. The right and left ventral ridges extend from the flagellar canal. The left one curves slightly from the anterior to the posterior and in some cells it forms an arc. The median ridge extends from the small protrusion near the anterior end of the cell. This species has an asymmetric posterior end with a small protrusion. With two flagella of unequal length; the anterior flagellum is slightly longer than the cell, and the posterior flagellum about 0.6–0.8 times the cell length, is recurrent and inserts to the left of the ventral protrusion in the neck. The reservoir lies in the right-hand side of the

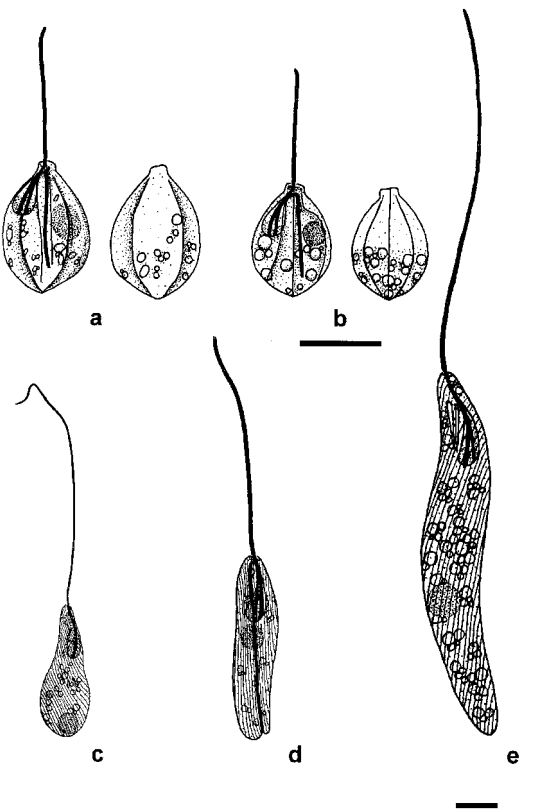


FIG. 12. Euglenida, *Notosolenus*, *Peranema* and *Jenningsia*, (a) *N.* cfr. *tamanduensis*, (b) *N. urceolatus*, (c) *Jenningsia fusiforme*, (d) *P. trichophorum*, (e) *Jenningsia macrostoma*. Scale bar in (b) = 10 μm for (a, b). Scale bar in (e) = 10 μm for (c–e).

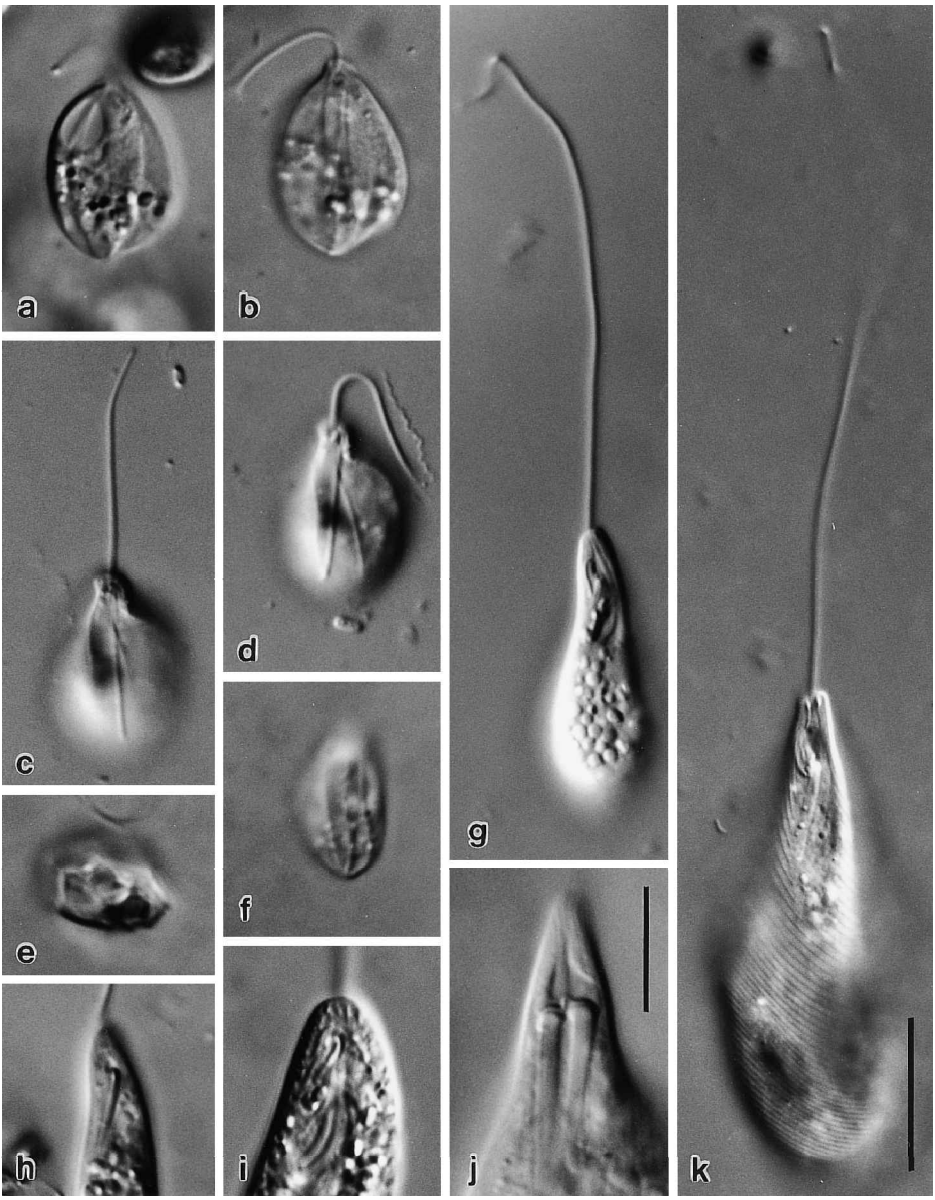


FIG. 13. (a, b) *Notosolenus* cfr. *tamanduensis*, (a) dorsal view, (b) ventral view, (c–f) *Notosolenus urceolatus*, (c) general appearance of cell, (d) ventral view, (e) transverse section showing three dorsal ridges, two lateral ridges and three fine ventral ridges, (f) dorsal view, (g, h) *Jenningsia fusiforme*, (g) general appearance of cell, (h) ingestion organelle, (i) *Peranema trichophorum* showing an ingestion organelle, (j–k) *Jenningsia macrostoma*, (j) ingestion organelle, (k) general appearance of different cell. All micrographs are DIC images. Scale bar in (j) = 10 μm for (a–j). Scale bar in (k) = 20 μm.

cell and the nucleus in the left. Glides slowly with the anterior flagellum directed anteriorly. Common. Description based on observations of 43 cells.

Remarks. Previously reported cell lengths are from 15 to 22 μm; this species was reported from tropical Australia and Brazil by Larsen and Patterson (1990). Our

cells are very similar in general appearance, in cell length, in having three dorsal keels and fine ventral ridges. Larsen and Patterson (1990) described a shallow median ventral groove. We have not seen a groove, but this may reflect feeding history. This species is characterized by its shape, longitudinal dorsal keels and fine ventral ridges. *Notosolenus urceolatus* is similar, in having dorsal ridges or keels, to *N. chelonides* Skuja, 1939 and *N. esulcis* Larsen, 1987. *Notosolenus chelonides* differs because it is twice the size and has several dorsal keels; *N. esulcis* has four shallow dorsal ridges. This species resembles *N. papilio* Skuja, 1939 in having dorsal keels and ventral ridges, and in cell length, but *N. urceolatus* is pitcher-shaped while *N. papilio* is slightly rhombic. There is some similarity with *N. canellatus* Skuja, 1948, but *N. canellatus* has one dorsal and one ventral groove. *Notosolenus urceolatus* is distinguished from *N. hemicircularis* Lee and Patterson, n. sp. by its larger size, the absence of a collar and in having three not five dorsal keels.

We note that our cells described here had two different shapes. 'Urceolate' cells which are broader and have more developed neck than the other 'ovate' cells. The urceolate cells are 11–17 μm long, 7–14 μm wide and the ovate cells are 13–16 μm long, 7–9 μm wide. Lengths of the forms overlap and in both the left ventral ridges curve to form an arc towards the posterior end of the cell.

Peranema trichophorum (Ehrenberg, 1830) Stein, 1878
(figures 12d, 13i, 15a, b)

Description. Cell metabolic, 35–48 μm long. With longitudinal pellicular striations around the cell. The anterior end of the cell is slightly pointed and the posterior end is truncated, rounded, indented or pointed. This species is slightly bent and the flagellar pocket is also bent to the right. The flagellar pocket including the flagellar canal is up to 40% the length of the cell. The anterior flagellum is as long as the cell, is thick and is directed forward when the cell is moving. The posterior flagellum may be hard to observe, is thin, and tightly adpressed to cell surface, lying in a fine longitudinal groove. The ingestion organelle with two rods is weakly developed and the nucleus is below the centre of the cell. Cell glides in contact with the substratum. Relatively common. Description based on observations of five cells.

Remarks. This species has been widely reported from around the world in freshwater sites with lengths from 22 to 81 μm (Stein, 1878; Playfair, 1921; Skuja, 1939, 1948, 1956; Chen, 1950; Huber-Pestalozzi, 1955; Schroeckh and Patterson, unpubl.), and in marine sites in tropical Australia and Danish Wadden Sea with lengths from 35 to 60 μm (Larsen, 1987; Larsen and Patterson, 1990; Ekebom *et al.*, 1996). Although cell length varies from 42 to 65 μm with environmental conditions (Chen, 1950), the range suggests that more than one species has been described under this name.

Our observations agree with the descriptions given by previous authors from marine sites. This species is similar to *P. dolichonema* Larsen and Patterson, 1990, in shape, size and in having a long recurrent flagellum which lies in the ventral groove, but *P. dolichonema* can be distinguished because the distal part of the recurrent flagellum trails behind the cell (Larsen and Patterson, 1990). Other species of *Peranema* which have a long posterior flagellum which lies in a groove are *P. dolichonema*, *P. inflexum*, *P. pleururum* and *P. trichophorum*. This species is very similar to *P. inflexum* Skuja, 1939 and *P. pleururum* Skuja, 1948 (see Huber-Pestalozzi, 1955) which were reported from freshwater sites. Previously reported cell

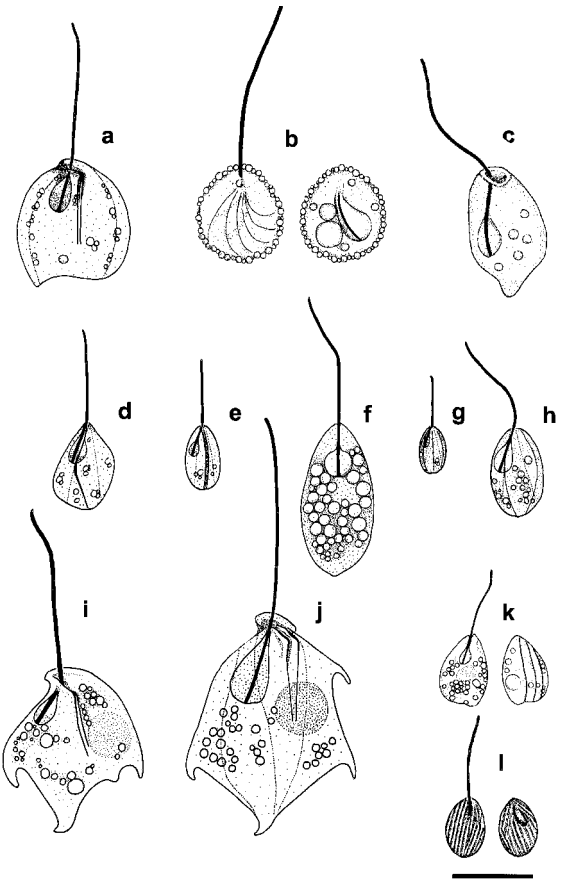


FIG. 14. Euglenida, *Petalomonas*, (a) *P. abscissa*, (b) *P. intortus*, (c) *P. labrum*, (d) *P. minor*, (e) *P. minuta*, (f) *P. planus*, (g–h) *P. poosilla*, (i) *P. raiula*, (j) *P. spinifera*, (k) *P. iugosus*, (l) *P. virgatus*. Scale bar = 10 μm for all figures.

lengths of *P. trichophorum* embrace the length of *P. inflexum* (30–41 μm) but *P. pleururum* (62–75 μm) is larger than *P. trichophorum*. Further study is required to establish the identities of these species. *Peranema trichophorum* differs from *Jenningsia fusiforme* (Larsen, 1987) Lee *et al.*, 1999 and *J. macrostoma* (Ekebom *et al.*) Lee *et al.*, 1999 because the species of *Jenningsia* lack a recurrent flagellum.

Petalomonas abscissa (Dujardin 1841) Stein 1859
(figures 14a, 15c–e)

Description. Cell 12–22 μm long, 8–19 μm wide, narrow anteriorly, widest slightly posterior to midline. With lateral hyaline flanges. This species has two dorsal keels which run along the entire cell; the right one is well developed. One narrow ventral groove with marginal ridges forming a double keel extends from the collar around the canal. One flagellum emerges from the canal and is about 1.0–1.2 times the cell length. The reservoir is situated in the right anterior side of the cell and the nucleus lies near the midline and adjacent to the left margin of the cell. Moves by gliding. Commonly observed, but not abundant.

Remarks. This species has been recently reported with lengths from 10 to 25 μm from marine sites in subtropical and tropical Australia, Brazil and in the temperate Danish Wadden Sea (Larsen, 1987; Larsen and Patterson, 1990; Ekebom *et al*., 1996; Patterson and Simpson, 1996). Generally, our observations are in accord with those of Larsen and Patterson (1990) although in contrast to most authors (Klebs, 1893; Lemmermann, 1914; Shawhan and Jahn, 1947; Huber-Pestalozzi, 1955; Larsen, 1987; Ekebom *et al*., 1996; Patterson and Simpson, 1996), Larsen and Patterson (1990) described *P. abscissa as* having one dorsal keel. We found one cell with one dorsal keel and included the cell here, and surmise that the number of dorsal keels may not be a good diagnostic characteristic. This organism resembles a few species of the genus *Petalomonas*, such as *P. spinifera* Lee and Patterson, n. comb. (see below), *P. mira* var. *bicarinata* Skuja, 1939 and *P. raiula* Larsen and Patterson, 1990 in having a ventral ridged groove. *Petalomonas abscissa* can be distinguished by its elliptical, regular cell shape and the indented posterior end (*P. spinifera*, *P. mira* var. *bicarinata* and *P. raiula* have posterior protrusions). It resembles *P. applanata* Skuja, 1939 in general appearance, but it has a posterior indentation and is smaller than *P. applanata* (30–36 μm).

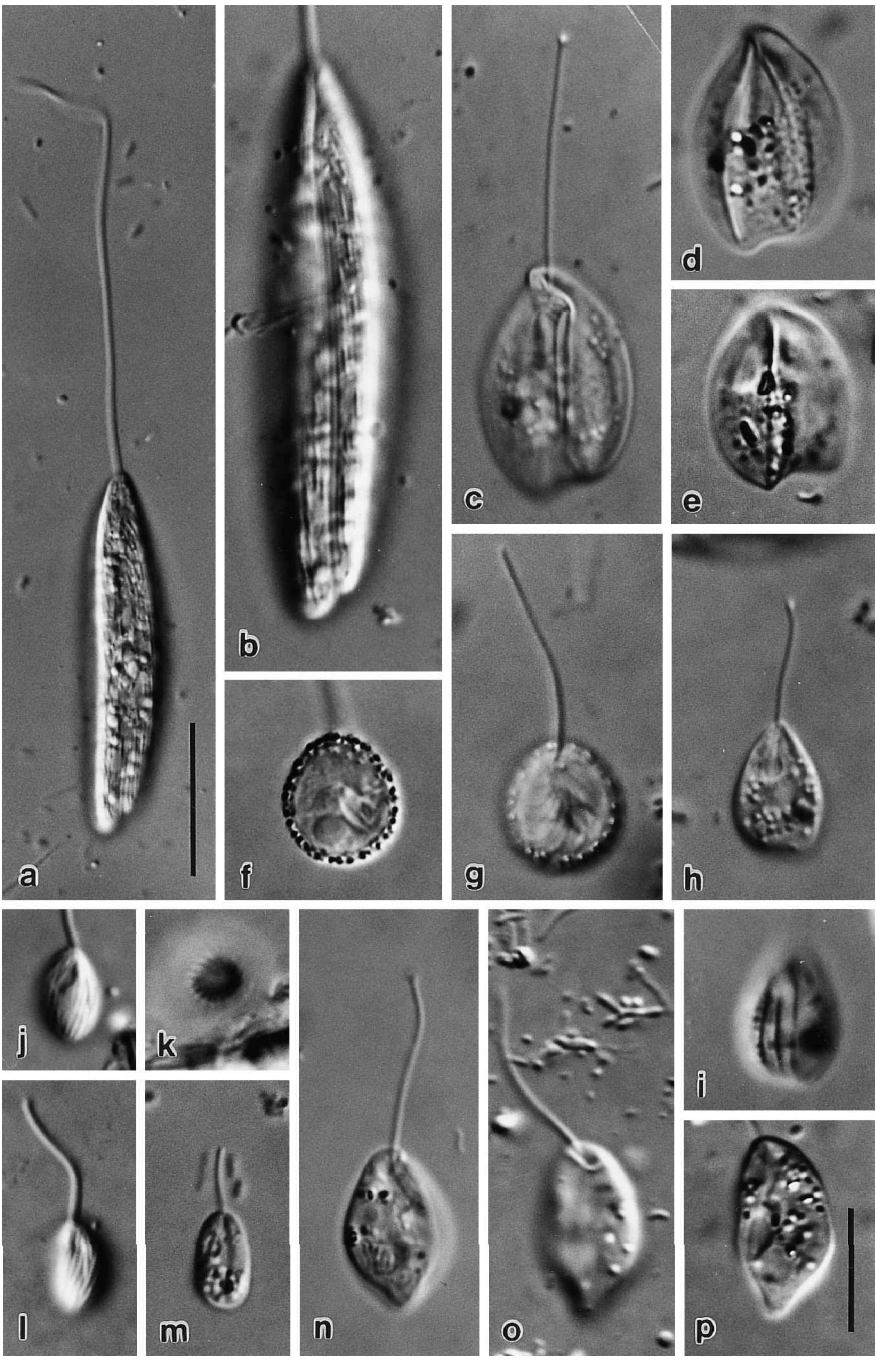
Petalomonas intortus Lee and Patterson, n. sp.
(figures 14b, 15f, g. Type micrograph: figure 15g)

Diagnosis. *Petalomonas*, 5–11 μm long, rounded body, flattened, with small particles adhering externally and with about 10 curving striations on the ventral face.

Description. Cell outline rounded, 5–11 μm long, very flattened. With tiny bodies adhering to the cell surface and with about 10 striations following a counter-clockwise path on the ventral face of the cell. No structures visible on the dorsal face. One flagellum emerges from the flagellar canal, is slightly thickened and is about 1.5–1.7 times the cell length. Cells move slowly with the emergent flagellum directed forwards and with most movement in the distal part of the flagellum in contact with the substratum. The ovate reservoir is situated in the left-hand side but adjacent to the antero-posterior axis of the cell. The nucleus is in the right anterior side of the cell. Not metabolic. Rare, description based on observations of seven cells.

Remarks. We assign this species to *Petalomonas* because it is rigid, flattened, and has one emergent flagellum and no visible mouth. *Petalomonas intortus* is characterized by its striations on the ventral face of the cell and the particles adhering to the cell surface. This species is distinguished from most other species in *Petalomonas* because of the adhering particles. Of those species with reported adhering elements, *P. intortus* is distinguished from *P. prototheca* Skuja, 1948 by its smaller size, its

FIG. 15. (a, b) *Peranema trichophorum*, (a) general appearance of cell, (b) ventral view of same cell, (c–e) *Petalomonas abscissa*, (c) general appearance showing a ridged ventral groove, (d) dorsal view of same cell showing two dorsal ridges, (e) dorsal view showing one dorsal ridge, (f, g) *Petalomonas intortus*, (f) dorsal view, (g) general appearance of cell showing spiral striations, (h, i) *Petalomonas iugosus*, (h) general appearance of cell, (i) dorsal view of same cell, (j–l) *Petalomonas virgatus*, (j) dorsal view, (k) transverse section, (l) general appearance of cell, (m) *Petalomonas minuta* showing a dorsal groove, (n–p) *Petalomonas labrum*, (n) general appearance of cell, (o) ventral, (p) dorsal view of same cell. All micrographs are DIC images. Scale bar in (a) = 20 μm. Scale bar in (p) = 10 μm for (b–p).



round shape and the lack of a short neck, from *P. punctatostriata* Skuja, 1939 by its finer spiral striations, and from *P. boadicea* which has rhomboid excrescences and a shorter flagellum. *Petalomonas intortus* is similar in general appearance to *Jenningsia granuliferum* (Penard, 1890) Lee *et al.*, 1999 (basionym, *Peranema*

granulifera), but it is round whereas *J. granuliferum* is oval; and *J. granuliferum* has spiral striations. *Jenningsia granuliferum* may have to be transferred to *Petalomonas* because it lacks a mouth and no reference has been made to metaboly. *Petalomonas ornata* Skvortzov, 1957 has a reservoir and nucleus at the same position as *P. intortus* but lacks the adhering particles; it is about 11–15 μm long and has no striations (see Skvortzov, 1957; Larsen and Patterson, 1990).

Petalomonas iugosus Lee and Patterson, n. sp.
(figures 14k, 15h, i. Type micrograph: figure 15i)

Diagnosis. *Petalomonas*, cell heart-shaped, 11–12 μm long, 8 μm wide, with an indentation of the posterior end and three longitudinal ridges on the dorsal right half of the cell.

Description. Colourless, rigid and gliding cell. Cell heart-shaped, 11–12 μm long and 8 μm wide, flattened, with an indentation in the posterior end of the cell. The left half of the cell is slightly longer than the right half. This species has three distinct longitudinal dorsal ridges running along the cell on the right half of the cell. There are two indistinct ventral ridges, the right one runs beneath the reservoir along the cell. One flagellum emerges from the canal and is as long as the cell. The distal part of the flagellum moves a little when the cell glides. The reservoir is situated anteriorly to the right of the antero-posterior axis of the cell. The nucleus is situated in a median position or just below the reservoir. Three cells observed.

Remarks. The species described here has the characteristics of the genus *Petalomonas* in being a rigid and flattened heterotrophic euglenid, and in having one emergent flagellum. *Petalomonas iugosus* can be distinguished by size from all species in the genus, excepting *P. minor* Larsen and Patterson, 1990, *P. minuta* Hollande, 1942 and *P. poosilla* Larsen and Patterson, 1990 (see Huber-Pestalozzi, 1955; Larsen and Patterson, 1990). It can be distinguished from these species by the presence of three longitudinal ridges. *Petalomonas iugosus* is similar in general cell shape to *P. steini* var. *cordiformis* Christen, 1962 and *P. triquetra* Skvortzov, 1929, but it is much smaller (*P. steini* var. *cordiformis* 40–45 μm, *P. triquetra* 30–33 μm), and has three dorsal ridges rather than one dorsal keel (*P. steini* var. *cordiformis*) or one ventral keel (*P. triquetra*) (see Huber-Pestalozzi, 1955; Christen, 1962b).

Petalomonas labrum Lee and Patterson, n. sp.
(figures 14c, 15n–p. Type micrograph: figure 15p)

Diagnosis. Petalomonas, 11–17 μm long, with a raised rim around a wide opening of the flagellar canal.

Description. Cell ovate and elliptical, 11–17 μm long, 6–10 μm wide, dorso-ventrally flattened, with a rim surrounding a wide apical opening of the flagellar canal. Cells have very indistinct or smooth pellicle and the ventral face of the cell is slightly concave. The cell tapers slightly towards the wedge-shaped posterior end. One flagellum emerges from the long narrow canal and is about as long as the cell or slightly longer. The flagellum only moves a little when the cell glides forwards. The reservoir is situated equatorially in the right-hand side of the cell. The nucleus is located in the left-hand side of the cell. Rare. Description based on observations of five cells.

Remarks. This species is assigned to *Petalomonas* because it is rigid, flattened, has an apical canal opening, one emergent flagellum and no visible mouth. This

species can be clearly distinguished from all other species of the genus *Petalomonas* by the wide opening of the flagellar canal and by the raised rim around the opening. It is most similar in size and outline to *P. gibbera* (see Christen, 1962b), but can be distinguished by the raised margin of the opening, by the smooth pellicle and by the smaller size (*P. gibbera* is 20–22 μm long). *Petalomonas ventritracta* (see Skuja, 1939) is similar to *P. labrum* in having a canal with a wide opening, but is distinguished by its shape, its ventral groove and its larger size (24–27 μm). Some species, such as *P. mediocanellata* var. *pleurosigma* Stokes, 1888, have a wide anterior end, which may indicate a canal with a wide opening.

Petalomonas minor Larsen and Patterson, 1990
(figures 14d, 16a–d)

Description. Cell outline ovate-rhomboid, 6–11 μm long, 4–8 μm wide. A distinct, longitudinal dorsal keel lies to the right of the midline. Two fine ventral ridges may be seen towards the posterior end. The dorsal face is slightly concave between the longitudinal dorsal keel and the lateral margin of the cell. With one flagellum about the same length as the cell inserting in a reservoir located in the right side of the cell. The nucleus is in the left side. Glides with the flagellum directed forwards. Commonly observed. Descriptions based on observations of 28 cells.

Remarks. Larsen and Patterson (1990) first described this species from marine sites in tropical Australia and Fiji. They reported lengths ranging from 7 to 9 μm. Generally, our observations are in accordance with observations of Larsen and Patterson (1990), but the species described here has two fine ventral ridges not reported by Larsen and Patterson (1990). They could easily have been overlooked. The species resembles *P. poosilla* (see below) in having two fine ventral ridges and in length, but it can be distinguished by its dorsal keel and cell shape. In having one distinct dorsal keel, the species is similar to a few other species in the genus *Petalomonas* such as *P. lata* Christen, 1962, *P. steinii* Klebs, 1893 and *P. variablilis* Christen, 1962 (see Huber-Pestalozzi, 1955; Christen, 1962b). It can be recognized from all of these by its small size.

Petalomonas minuta Hollande, 1942
(figures 14e, 15m)

Description. Cell outline ovate, 6–10 μm long (mostly 6–7 μm), 4–6 μm wide, flattened, with a deep longitudinal groove on the dorsal face. One cell had two indistinct ventral ridges which were hard to see, and two cells had a narrow ventral groove-like slit. With one flagellum inserting into a reservoir in the right-hand side of the cell, flagellum about same length as the cell. The nucleus is in the left-hand side of the cell. Glides. Often common. Description based on observations of 16 cells.

Remarks. This species was first described as *P. mediocanellata* var. *pusilla* by Klebs in 1893. This is not the same as *P. pusilla* Skuja, 1948 which differs in the absence of a surface groove. Because of the principle of co-ordination of the ICZN (Article 46) *P. pusilla* Skuja 1948 is a junior homonym. The same organism as observed by Klebs was described by Hollande (1942) as *P. minuta*. Although the correct name for this species under the provisions of the the ICZN is *P. pusilla* Klebs 1893, we believe that such usage would be confusing and given that *P. pusilla* Skuja 1948 is the legitimate use of this homonym under the regulations of the International Code of Botanical Nomenclature (Greuter *et al.*, 1994), we adopt

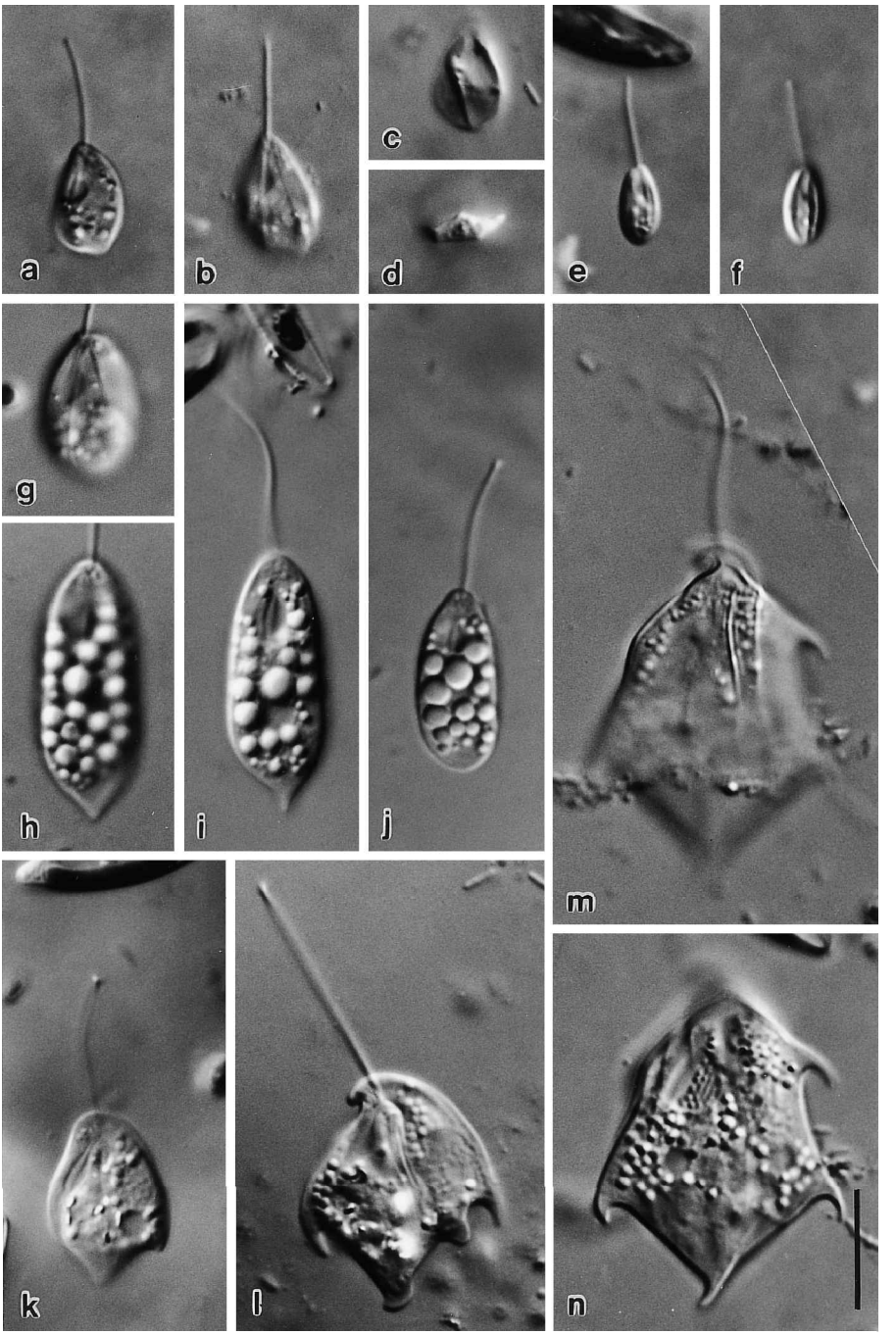


FIG. 16. (a–d) *Petalomonas minor*, (a) general appearance of cell, (b) ventral view showing fine ridges, (c) dorsal view, (d) transverse section, (e–g) *Petalomonas poosilla*, (e) general appearance of cell and (f) dorsal view showing dorsal ridges in small population, (g) large population showing fine ventral ridges, (h–j) *Petalomonas planus* showing different posterior ends, (i) and (j) general appearance of cell, (k, l) *Petalomonas raiula* showing general appearance of cells, (m, n) *Petalomonas spinifera*, (m) general appearance of cell showing ventral view and protrusions, (n) dorsal view of same cell. All micrographs are DIC images. Scale bar = 10 μm for all figures.

the approach of Larsen and Patterson (1990) and refer to this species as *P. minuta* Hollande, 1942. Like Larsen and Patterson (1990), we regard *P. minutula* Christen, 1962 as a junior synonym. *Petalomonas mediocanellata* var. *pusilla* Klebs, 1893 and *P. minutula* Christen, 1962 were described from freshwater sites. The drawing in Klebs shows the surface discontinuity by which this species is distinguished. Previously reported cell length for this species is 6–12 μm. This species has been found in marine sites in subtropical and tropical Australia, Brazil, Danish Wadden Sea, Denmark, Fiji, Gulf of Finland and North Atlantic (Larsen, 1987; Larsen and Patterson 1990; Vørs, 1992a, 1992b; Patterson *et al*., 1993; Patterson and Simpson, 1996). Since the description of Hollande (1942), *P. minuta* has been described as having a deep ventral groove, but Patterson and Simpson (1996) showed that the groove was dorsal. We confirm our cells have a deep dorsal groove. Our observations included one cell with two indistinct ventral ridges which could easily be overlooked and two cells having a narrow ventral groove-like slit. This species is otherwise in agreement with observations of Patterson and Simpson (1996).

This species resembles *P. poosilla* Larsen and Patterson, 1990 in general cell shape, cell length and flagellum length, but it can be distinguished by its deep dorsal groove. It resembles *P. minor* in length, but it does not have a dorsal keel. This species resembles *P. ventritracta* Skuja, 1939 in general appearance, but *P. ventritracta* has a ventral groove and is bigger. It is similar to *Notosolenus apocamptus* Stokes, 1884 in general appearance, cell length and in having a deep longitudinal dorsal groove, but it can be distinguished by the lack of a posterior flagellum and by its short anterior flagellum.

Petalomonas planus Lee and Patterson, n. sp.
(figures 14f, 16h–j. Type micrograph: figure 16i)

Diagnosis. Petalomonas, rigid, 15–24 μm long, dorso-ventrally flattened, hyaline body with one emergent flagellum, without grooves or ridges.

Description. Cell outline ovate, 15–24 μm long, 5–10 μm wide, rigid, dorso-ventrally flattened. Cells are rather hyaline. There are no grooves and no ridges on either side of the cell. Most cells have a pointed posterior end but some cells have a rounded posterior end. Small and large granules occupy the entire cell except at the poles. One flagellum emerges from the canal and is slightly shorter than the cell. The reservoir is situated subapically in the midline of the cell. Cells move by gliding with the flagellum in close contact with the substratum. Often common.

Remarks. We assign this species to *Petalomonas* because it is a rigid gliding heterotrophic euglenid with one emergent flagellum. This species is easily distinguished from most species of *Petalomonas* by its hyaline body and smooth cell surface. It is most similar to *P. simplex* Christen, 1962 in general appearance and hyaline body, but *P. simplex* is slightly larger (27.5–31 μm) (see Christen, 1962b).

Petalomonas poosilla Larsen and Patterson, 1990
(figures 14g, h, 16e–g)

Description. We describe two populations of cells.

Population 1: small cells; ovate, 5–9 μm long, 3–5 μm wide, dorso-ventrally flattened. This species may or may not have up to three dorsal ridges and the ridges may or may not be well developed. The organism may also have two fine ventral ridges which are difficult to observe. The right ventral ridge runs beneath the reservoir

along the cell. With one flagellum as long as the cell. The reservoir is in the right side of the cell and the nucleus is in the left side. Moves by gliding. Common.

Population 2: Larger cells; cell outline oblong-oval, 10–12 μm long and 5–6 μm wide, dorso-ventrally flattened. It has four ridges extending along the cell: two indistinct dorsal ridges located at the lateral margins of the cell; two fine ventral ridges, the right one of which runs beneath the reservoir. One flagellum is about as long as the cell or slightly longer. The ovate reservoir is anteriorly situated in the right-hand side of the cell and the nucleus in the left-hand side of the cell. Often co-occurs with the smaller cell.

Remarks. Larsen and Patterson (1990) provided a new name for *P. pusilla* Skuja, 1948 (*P. poosilla*) because under the principle of co-ordination of the ICZN, *P. pusilla* Skuja, 1948 is a homonym of *P. mediocanellata* var. *pusilla* Klebs, 1893 (Lemmermann, 1913)—which we refer to as *P. minuta* (see *P. minuta* above). *Petalomonas poosilla* and *P. minuta* resemble each other in shape and appearance, but can be distinguised by the presence of what we regard as a longitudinal groove in *P. minuta*.

Petalomonas poosilla was originally described under the name *P. pusilla* (5–12 μm long) from freshwater sites (Skuja, 1948) and has since been found in marine sites in Australia, Brazil, Danish Wadden Sea, Fiji, Gulf of Finland; Hawaii and NE Canada (Lackey and Lackey, 1970; Larsen, 1987; Larsen and Patterson, 1990; Vørs, 1992a; Patterson and Simpson, 1996; Tong *et al.*, 1998). We observed cells (in the small population) which are similar in size and outline to *P. poosilla* as described by Larsen and Patterson (1990). This species has been described without ridges or grooves (Skuja, 1948; Larsen and Patterson, 1990). Cells assigned to this species have been described more recently as having ridges (Patterson and Simpson, 1996; Schroeckh and Patterson, unpubl.). We suspect that this species has previously been under-described and regard the latter descriptions as more accurate than the former. The ventral face of this species is very similar to that of *P. minor*, described here, in having two fine ventral ridges and in the position of the ridges, but the two species can be distinguished by cell shape and the dorsal flange in *P. minor*. *Petalomonas poosilla* and *P. minuta* resemble each other in shape and appearance, but can be distinguised by the presence of what we regard as a longitudinal groove in *P. minuta*. This species resembles *P. cantuscygni* (see Cann and Pennick, 1986) from which it can be distinguished by never having fewer than six dorsal ridges.

We have observed larger cells about 10–12 μm long, but they consistently had four discrete ridges on both sides of the cell. The two populations often co-occur. Although these may represent a separate species, we have been unable to establish morphological discontinuities by which single cells could be easily identified when comparisons are made. Further studies are required to establish the status of the two populations.

Petalomonas raiula Larsen and Patterson, 1990
(figures 14i, 16k, l)

Description. Cell outline irregular, 15–20 μm long, 10–15 μm, with a ventral groove with raised margins which extend from the collar around the flagella canal. The organism has thin lateral hyaline flanges; the left one extends anteriorly to form an arc around the flagellum and the right one ends behind this arc. It has a wedge-shaped posterior end with, in most cells, a hyaline protrusion and lateral margins.

There is one emergent flagellum, which is about as long as the cell and is anteriorly directed. The reservoir is situated anteriorly in the right side of the cell and the nucleus is near the midline of the left-hand side. Sometimes commonly oberserved.

Remarks. Larsen and Patterson (1990) first described this species from marine sites in Brazil and Fiji, and the organism was found in subtropical Australia by Patterson and Simpson (1996). Previously reported cell length ranges 9–19 μm (Larsen and Patterson, 1990; Patterson and Simpson, 1996). Generally, the organisms described here are in accordance with observations of previous observers although we increase the known maximal size to 20 μm. *Petalomonas raiula* is usually distinguished from other small species of the genus *Petalomonas* by its posterior protrusions and ridged ventral groove. *Petalomonas dentata* Christen, 1962, *P. irregularis* Skuja, 1948, *P. lata* Christen, 1962, *P. praegnans* Skuja, 1948, *P. phacoides* Skuja, 1931, *P. platyrhyncha* Skuja, 1948, *P. mira* Awerinzew, 1907, *P. mira* var. *appendiculata* Skuja, 1939, *P. mira* var. *bicarinata* Skuja, 1939, *P. sinuata* Stein, 1878, *P. spinifera* (Lackey, 1962) Lee and Patterson, n. comb., *P. steinii* Klebs, 1893 and *P. tricarinata* Skuja, 1939 also have posterior protrusions but with different patterns (Huber-Pestalozzi, 1955; Christen, 1962b; Lackey, 1962). This species is a member of a group of *Petalomonas* species having one ridged ventral groove; the group also includes *P. abscissa*, *P. mira* and *P. triquetrus*.

Petalomonas spinifera (Lackey, 1962) Lee and Patterson, n. comb.
(figures 14j, 16m, n)

Description. Cell outline irregular, about 29 μm long and 21 μm wide, flattened, with three fine dorsal ridges and one distinct ridged ventral groove which extends from the collar around the flagella canal. The cell has four hyaline protrusions: one is located on a wedge-shaped posterior end of the cell, two are in the lateral posterior part, and the last one is in the anterior left-hand side or near the nucleus. One emergent flagellum, which is slightly shorter than the cell, is anteriorly directed. The large reservoir is situated anteriorly in the right-hand side of the cell and the nucleus is near the midline of the left-hand side. One cell observed.

Remarks. Lackey (1962) described *Pentamonas spinifera* Lackey, 1962 which is about 35 μm long. His description is not detailed, but is of organisms which resemble those described here in having one emergent flagellum, a rigid body and four protrusions, and in being flattened. We transfer *Pentamonas spinifera* to *Petalomonas*. It is similar to *P. raiula* Larsen and Patterson, 1990 in having protrusions and one ridged ventral groove, but is distinguished by its larger size, and in having four hyaline protrusions and three fine dorsal ridges. *Petalomonas spinifera* is distinguished from other species of *Petalomonas* by its four protrusions.

Petalomonas virgatus Lee and Patterson, n. sp.
(figures 14l, 15j–l. Type micrograph: figure 15j)

Diagnosis. Petalomonas, cell oval, about 7 μm long and 4 μm wide, not flattened. With one emergent thickened flagellum and numerous longitudinal ridges on both faces of the cell.

Description. Colourless, cell outline oval, about 7 μm long, 4 μm wide, not flattened. Cell outline is circular in cross section. The cell has prominent longitudinal ridges on both sides of the cell and has one thickened flagellum, which is about 1.5 times the cell length and emerges from a reservoir situated in the right-hand side of

the cell. Moves slowly by gliding. One cell observed from Botany Bay; the description also includes information on cells observed by Ekebom and co-workers on the Great Barrier Reef but excluded from Ekebom *et al.* (1996) because too few cells had been observed.

Remarks. This species is assignable to *Petalomonas* because it is a heterotrophic euglenid with a rigid body, one emergent flagellum, and subapical canal opening. It is not flattened, unlike most *Petalomonas* species. The ridges in *P. virgatus* resemble rod-shaped epibiotic bacteria such as those in *Postgaardi mariagerensis* Fenchel *et al.*, 1995 (Simpson *et al.*, 1997b). *Petalomonas virgatus* is easily distinguished from all other small gliding species by its ridges. It was found at One Tree Island in tropical Australia by Ekebom and co-workers but not reported. This species is very similar to *Calycimonas* Christen, 1959 which also has one emergent flagellum, and differs from *Petalomonas* by not being flattened (Christen, 1959). We do not regard this criterion as an effective taxonomic distinction and consider *Calycimonas* to be a junior synonym of *Petalomonas. Calycimonas* was created by Christen (1959) to segregate some species from the genus *Petalomonas* because he was of the view that it was becoming too big. *Calycimonas* contains four species; *C. physaloides* Christen, 1959, *C. pusilla* Christen, 1962, *C. quinquecarinata* Christen, 1962, *C. robusta* Christen, 1962 (see Christen, 1959, 1962a). They may be transferred to *Petalomonas* to create the new combinations; *P. physaloides* n. comb., *P. christeni* nom. nov., *P. quinquecarinata* n. comb. and *P. calycimonoides* nom. nov. As *Petalomonas pusilla* and *P. robusta* were introduced by Klebs (Klebs, 1893) (see *P. poosilla* above) and Christen (Christen, 1962b) respectively, the transfer of *C. pusilla* and *C. robusta* to *Petalomonas* creates homonyms. We therefore introduce *P. christeni* as a nom. nov. for *Calycimonas pusilla* and *Petalomonas calycimonoides* as a nom. nov. for *C. robusta*.

Ploeotia corrugata Larsen and Patterson, 1990
(figures 17a, 18a–d)

Description. Cell measuring 8–20 μm long (mostly 13–15 μm) and 6–12 μm wide. Cell outline elliptical to rhomboid, dorsally convex and ventrally flattened. Seven ridges on the dorsal side; two of which appear as a marginal rim. The right half of the cell is slightly thicker than the left, with a slight ridge down the middle of the ventral side against which the recurrent flagellum lies. The posterior end of the cell is indented. With two flagella of unequal length; the anterior flagellum is about the same length as the cell, beats rapidly from side to side with an irregular wave motion when the cell glides. The posterior flagellum is about 1.5–2.2 times the length of the cell and tapers slightly towards the posterior end of the cell. The reservoir is on the left ventral side of the cell and the ingestion organelle with two rods extends from right anterior of cell to left posterior. Moves by smooth gliding. Common, description based on observations of 15 cells.

Remarks. This species was first described by Larsen and Patterson (1990) from subtropical and tropical Australia, North Atlantic, Brazil, Danish Wadden Sea, Denmark, England, Fiji, Hawaii, Panama and has also been reported from the USA, and previous reported cell length ranges from 7 to 15 μm (Larsen and Patterson, 1990; Patterson *et al.*, 1993; Farmer and Triemer, 1994; Ekebom *et al.*, 1996; Patterson and Simpson, 1996; Tong *et al.*, 1998). It is widespread and often common, but not in the winter season. The cells described here are generally in agreement

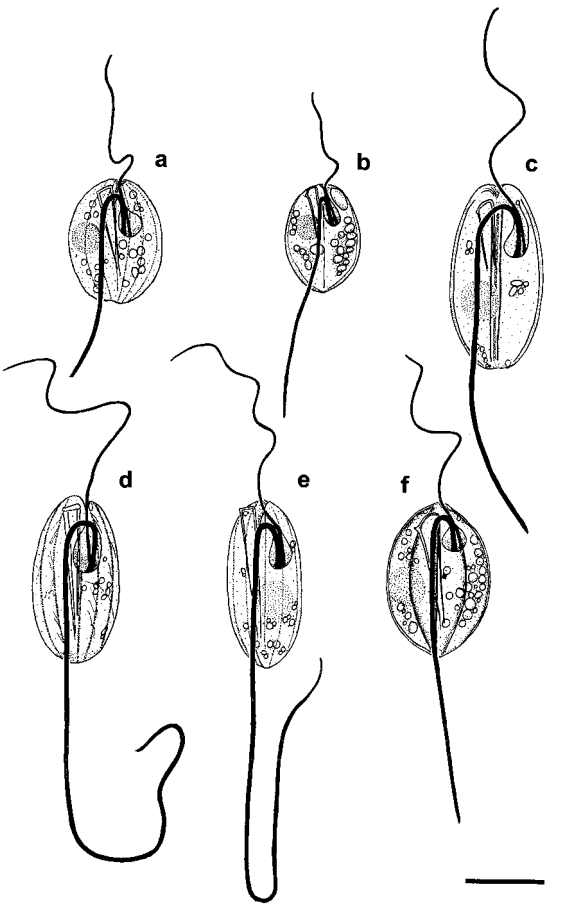


FIG. 17. Euglenida, *Ploeotia*, (a) *P. corrugata*, (b) *P. discoides*, (c) *P. oblonga*, (d) *P. plumosa*, (e) *P. pseudanisonema*, (f) *P. vitrea*. Scale bar = 10 μm for all figures.

with the observations of Ekebom *et al.* (1996) and of Farmer and Triemer (1994) under the name *Lentomonas applanatum* (basionym *Entosiphon applanatum* Preisig, 1979). We suspect that *L. applanatum* is synonymous with *P. corrugata* (Ekebom *et al.*, 1996) because the size ranges of the two species overlap; *L. applanatum*, about 10 μm, *P. corrugata*, 7–15 μm, and both species have seven ridges on the dorsal side of the cell. However, the species cannot be synonymized until the uncertainty with respect to protrusion of the ingestion apparatus of *L. applanatum sensu* Farmer and Triemer is clarified. *Ploeotia corrugata* resembles *P. decipiens* Larsen and Patterson, 1990 in general appearance, but it is distinguished by the number and prominence of the dorsal ridges, slightly smaller size and indented posterior end.

Ploeotia discoides Larsen and Patterson, 1990
(figures 17b, 18e–g)

Description. Cell outline oval or elliptical, 11–13 μm long, 7–8 μm wide, dorsoventrally flattened. Dorsally with two lateral grooves and one median groove, and

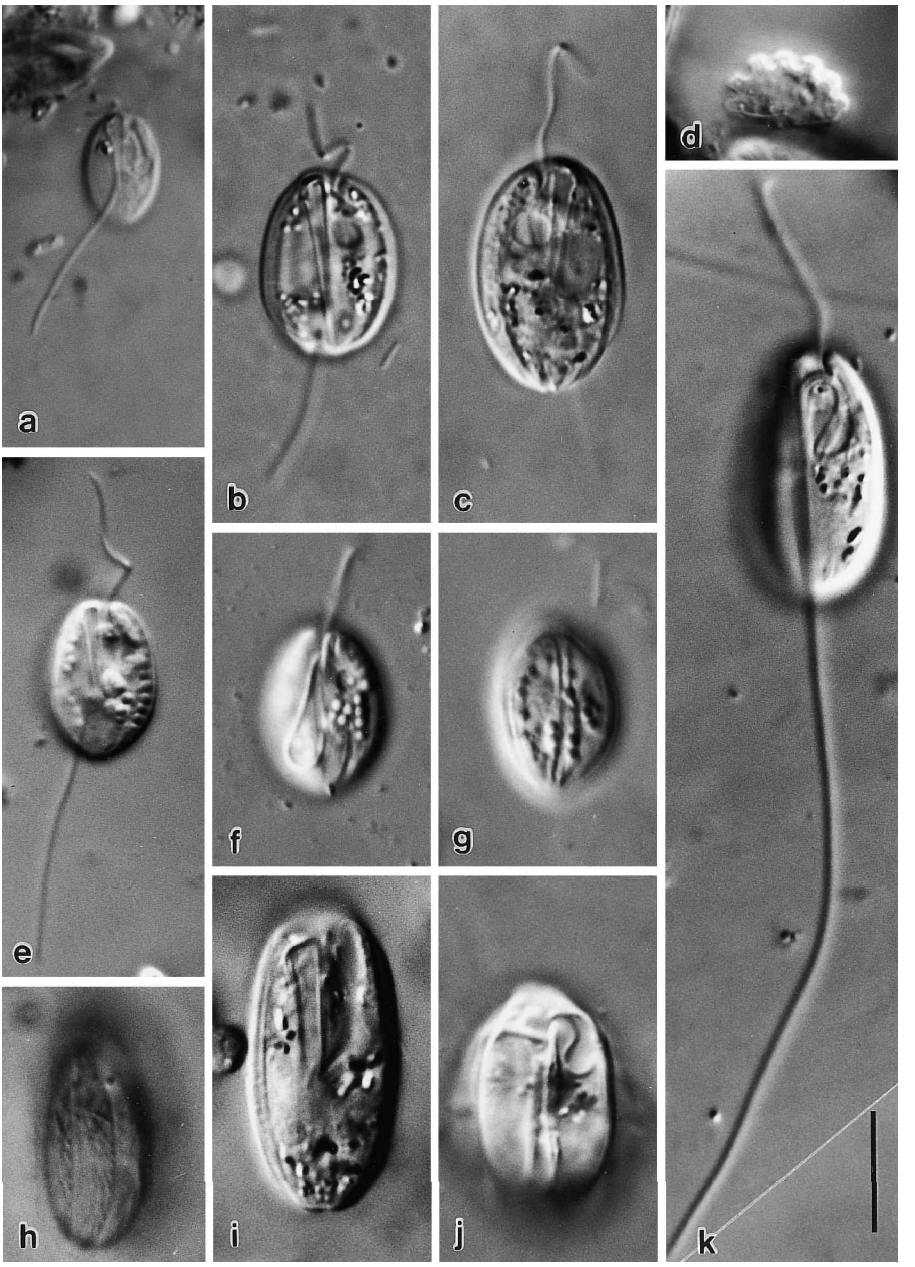


FIG. 18. (a–d) *Ploeotia corrugata* showing ranges of size and general appearance, (d) transverse section, (e–g) *Ploeotia discoides*, (e) general appearance of cell, (f) ventral face showing grooving, (g) dorsal face showing grooves, (i, j) *Ploeotia oblonga*, general appearance of different cells, (h, k) *Ploeotia plumosa*, (h) dorsal face showing surface grooves and inclusions, (k) general appearance of cell. All micrographs are DIC images. Scale bar = 10 μm for all figures.

ventrally with two lateral grooves which can be difficult to see. The reservoir is located anteriorly in the left side of the cell and is roundish. The anterior flagellum is about the length of the cell and the posterior flagellum is about 1.5–2 times the length of the cell. The ingestion organelle reaches almost to the posterior end of the cell. Rarely observed. Observations based on six cells.

Remarks. This species was first described by Larsen and Patterson (1990) from Brazil and cell length was previously reported to be 10–12 μm. *Ploeotia discoides* resembles *P. tenuis* in having three longitudinal dorsal grooves, but it is distinguished by its lack of ventral grooves, flatness, roundish reservoir, and by its smaller size (Larsen and Patterson, 1990). The ventral grooves are very hard to see and may be absent in some cells. The differences between *P. discoides* and *P. tenuis* are not great and future work may demonstrate that there is no unambiguous discontinuity between the two taxa.

Ploeotia oblonga Larsen and Patterson, 1990
(figures 17c, 18i, j)

Description. Cell about 27 μm long and 12 μm wide, slightly flattened; oblong, with two major grooves dorsally and three major grooves ventrally. The ridged median ventral groove is more prominent than the two lateral ones. Two flagella of unequal length emerge from the flagellar reservoir situated in the left-hand side of the cell. The anterior flagellum is about the length of the cell and sweeps sideways with irregular waves. The posterior flagellum is about twice the cell length and is thicker than the anterior flagellum. The ingestion organelle has two rods, is well developed and extends almost to the posterior end. Moves by gliding. The nucleus is in the right-hand side of the cell and near the centre. One cell observed.

Remarks. Previous reported cell length is from 16 to 36 μm; this species was found in marine sites in tropical Australia and Fiji (Larsen and Patterson, 1990; Ekebom *et al.*, 1996; Patterson and Simpson, 1996). Generally, our observations are in agreement with the original description of Larsen and Patterson (1990). We include records of one cell (figure 18j) which, although similar to *P. oblonga*, differs because the cell does not have lateral grooves and has lateral ridges. Further study is required to establish the identities of these taxa. *Ploeotia oblonga* is distinguished from other species of the genus by its size and by the strong rigid median ventral groove.

Ploeotia plumosa Ekebom *et al.*, 1996
(figures 17d, 18h, k)

Description. One cell observed, measuring about 20 μm long and 10 μm wide, slightly flattened. Cell outline oblong-ovate, with widely spaced grooves dorsally and ventrally. The dorsal grooves are more widely spaced than those of the ventral face. Often with a large hyaline inclusion reaching from the middle of the cell to the posterior end. Many slightly curved inclusions abut on the pellicular grooves. The two flagella are unequal in length; the anterior flagellum moves with sweeping motions and is about 1.5 times the cell length. The trailing posterior flagellum is about 3.5 times the cell length, is thicker than the anterior flagellum and emerges as a hook. The ingestion organelle has two prominent rods and extends almost to the posterior end of the cell. The reservoir is situated in the left-hand side of the cell. Glides smoothly in straight lines.

Remarks. This species was described from marine sites in subtropical and tropical Australia by Ekebom *et al.* (1996) and Patterson and Simpson (1996). Cell length was previously reported to be from 17 to 36 μm by previous authors. The individual described here was in the lower part of the size range reported by previous observers but otherwise our observations are in accord with the observations by previous authors. *Ploeotia plumosa* is easily distinguished from other species in the genus *Ploeotia* by the distinctive surface inclusions.

Ploeotia pseudanisonema Larsen and Patterson, 1990
(figures 17e, 19a, b)

Description. Cell outline oblong or elliptical, about 20 μm long and 10 μm wide, flattened. With several longitudinal narrow grooves extending along the cell. The left half of the cell is thicker than the right half. The anterior flagellum is about 1.5 times the cell length, and the posterior flagellum is about 4 times the cell length, emerges as a hook from the flagellar canal and is stronger than the anterior flagellum. The posterior flagellum lies in a ventral groove and tapers towards the tip of the flagellum. The nucleus is located near the middle of the cell and the reservoir is in the left ventral side. The ingestion organelle is well developed. Cell glides quickly and may jerk backwards—like *Anisonema*. One cell observed.

Remarks. Larsen and Patterson (1990) first described this species from marine sites in Australia, Brazil, Fiji and Hawaii, and this species has also been reported from other locations in Australia by Ekebom *et al.* (1996), Patterson and Simpson (1996) and Tong *et al.* (1998). Previously reported lengths range from 10 to 19 μm. Generally, our observations agree with the description by Larsen and Patterson (1990). This species is similar to *P. longifilum* Larsen and Patterson, 1990 in having a long trailing flagellum and in size, but is distinguished by general appearance and one ventral groove in *P. longifilum*. Also, *P. pseudanisonema* resembles *P. punctata* Larsen and Patterson, 1990 in general appearance and in having a long posterior flagellum, but it is distinguished because small internal bodies in *P. punctata* line the dorsal ridges. *Ploeotia pseudanisonema* is similar to *Anisonema obliquum* Roskin, 1931 and *A. trepidum* Larsen, 1987 in general appearance and length (Roskin, 1931; see Larsen, 1987), but is distinguished by the presence of an ingestion organelle.

Ploeotia vitrea Dujardin, 1841
(figures 17f, 19c–e)

Description. Cell oval, about 16–22 μm long and 10–14 μm wide, not flattened. This species has 10 longitudinal double raised ridges; four dorsally, two laterally, four ventrally. The anterior part of the cell is slightly obtuse and the posterior part of the cell is pointed. The anterior flagellum is as long as the cell, and the posterior flagellum is thick and twice as long as the cell. The ingestion organelle is well developed with a tiny protrusion at the top of the right-hand rod and tapers posteriorly. The nucleus is located in the right-hand side of the cell and the reservoir is in the left side. Rarely observed.

Remarks. This species has been found in marine sites in subtropical and tropical Australia, Brazil, Fiji, Hawaii and USA, and the reported length range is from 16 to 25 μm (Farmer and Triemer, 1988; Larsen and Patterson, 1990; Patterson and

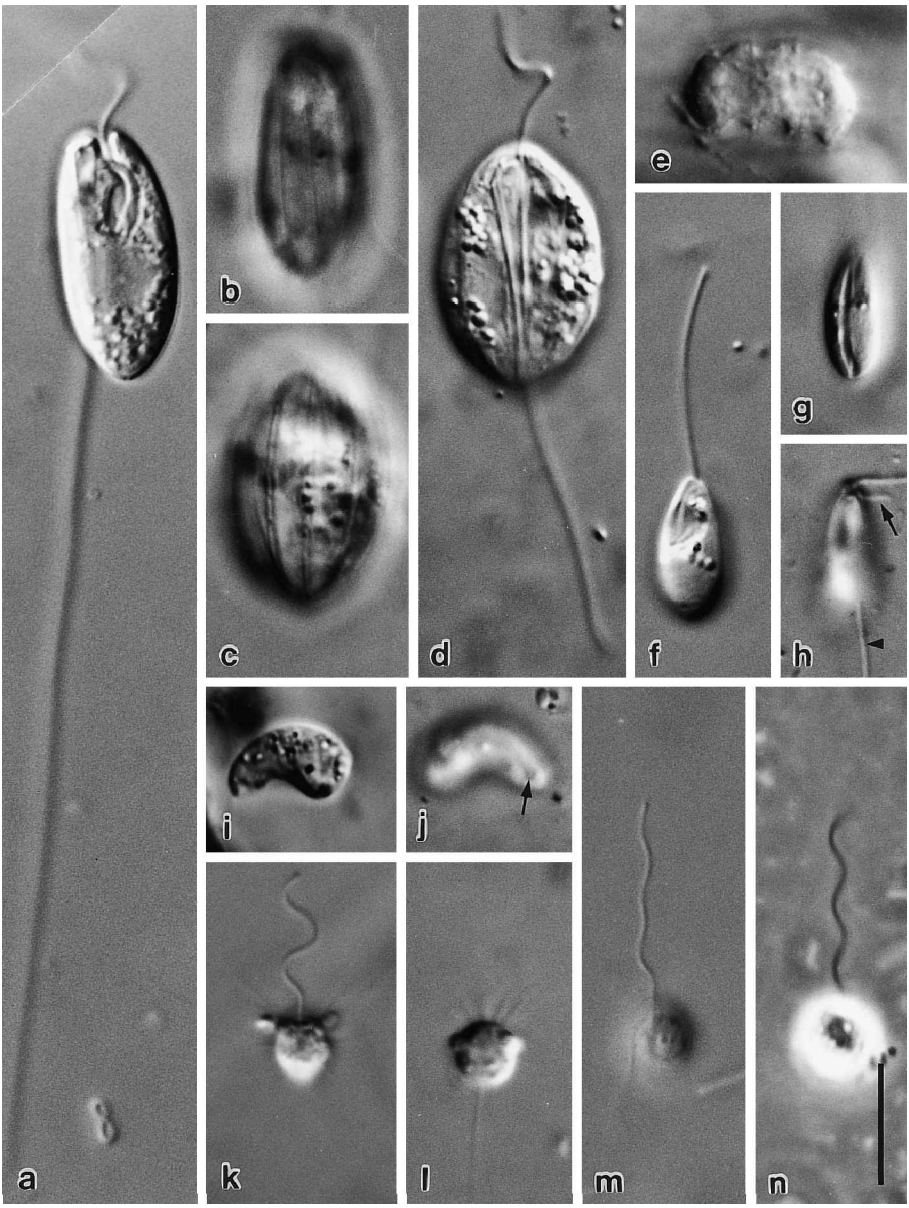


FIG. 19. (a, b) *Ploeotia pseudanisonema*, (a) general appearance of cell, (b) dorsal view showing surface grooving of same cell, (c–e) *Ploeotia vitrea*, (c) dorsal view showing double raised ridges, (d) general appearance of cell, (e) transverse section, (f–h) *Sphenomonas angusta*, (f) general appearance of cell, (g) dorsal groove, (h) showing two flagella, recurrent flagellum (arrow) and bacteria (arrow head), (i, j) *Anehmia exotica*, (i) dorsal view, (j) ventral view showing a mouth (arrow), (k, l) *Actinomonas mirabilis*/*Pteridomonas danica* showing arms around flagellum, (m, n) *Pseudobodo tremulans* showing general appearance of cell. All micrographs are DIC images with the exception of (n) (phase contrast image). Scale bar = 10 μm for all figures.

Simpson, 1996). Ultrastructural studies of *Ploeotia vitrea* were conducted by Farmer and Triemer (1988), and Larsen and Patterson (1990). Our observations are in agreement with Larsen and Patterson (1990). *Ploeotia vitrea* can be easily distinguished from other species in the genus by its 10 prominent ridges.

Sphenomonas angusta Skuja, 1956
(figures 19f–h, 20a)

Description. Cell measuring 10–14 μm long, 4–5 μm wide, not flattened, with a dorsal groove. Cells are anteriorly obliquely truncated, posteriorly rounded. The cell bodies are slightly curved: the right margin of the cell is straighter than the left one. With two flagella, unequal in length, emerging from a relatively large flagellar pocket located in the right anterior end of the cell. The anterior flagellum is about 1.5 times the cell length and its proximal part moves actively; the trailing posterior flagellum is less than 0.5 times the cell length. One large refractile inclusion often occupies the posterior part of the cell. Commonly observed.

Remarks. This species was first described from freshwater sites by Skuja (1956). Cells described here are below the length range 13–21 μm of Skuja (1956), but generally our observations are in accordance with his original description. Most species of the genus *Sphenomonas* have been found in freshwater sites, but we have commonly observed only one species, *S. angusta*, and seen it in all seasons. At times this species occurs in large numbers. *Sphenomonas elongata* Lackey, 1962 was found in marine sites and differs from *S. angusta* in its larger size (40–70 μm). *Sphenomonas angusta* is distinguished from other species of the genus by having one dorsal groove.

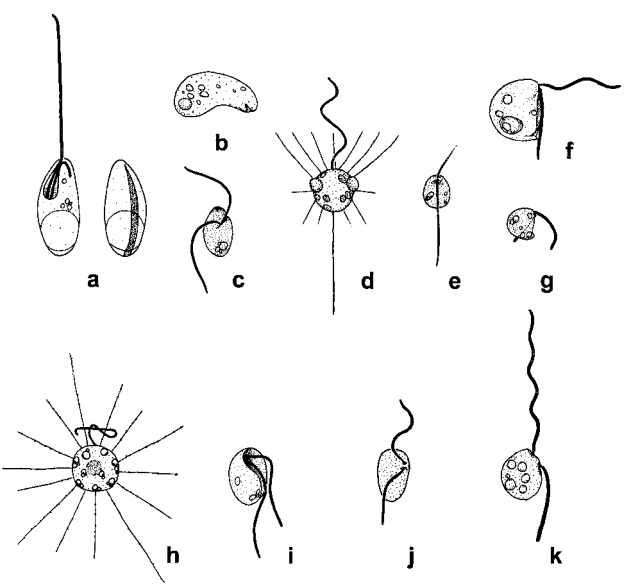


FIG. 20. Euglenida, Euglenozoa *incertae sedis*, stramenopiles and stramenopiles *incertae sedis*, (a) *Sphenomonas angusta*, (b) *Anehmia exotica*, (c) *Bordnamonas tropicana*, (d) *Actinomonas mirabilis*/*Pteridomonas danica*, (e) *Caecitellus parvulus*, (f) *Cafeteria marsupialis*, (g) *C. roenbergensis*, (h) *Ciliophrys infusionum*, (i) *Developayella elegans*, (j) *Pendulomonas adriperis*, (k) *Pseudobodo tremulans*. Scale bar = 5 μm for all figures.

Euglenozoa *incertae sedis*
Anehmia exotica Ekebom *et al.*, 1996
(figures 19i, j, 20b)

Description. Gliding protist, sausage shaped, about 10 μm long, without flagella, with a mouth opening at the anterior end of the cell. The posterior end is rounded and broader than the anterior end of the cell. Two cells observed.

Remarks. This species was found in marine sites in subtropical and tropical Australia by Ekebom *et al.* (1996) and Patterson and Simpson (1996). Previous authors reported the size range to be 12–15 μm. *Anehmia exotica* is easily distinguished from other gliding heterotrophic protists by its lack of flagella. Ekebom *et al.* (1996) assigned this species tentatively to Euglenozoa (Patterson and Simpson, 1996) because of its similarity to *Diplonema* (Simpson, 1997).

Bordnamonas tropicana Larsen and Patterson, 1990
(figures 20c, 21a)

Description. Cell measuring 4–7 μm long, 2.5–4 μm wide, flattened, anteriorly narrow, posteriorly broad. Cells are flexible, particularly when squashed. Two slightly thickened flagella, similar in length, insert subapically in the right ventral side of the cell and are approximately 1.5 times the length of the cell. The flagellae are not acronematic. The anterior flagellum beats stiffly and is held in a sigmoid arc, and the posterior flagellum curves near its flagellar insertion and is directed towards the rear of the cell. An apical mouth is visible by light microscopy. Moves by gliding or rapidly by skidding movements close to the substratum. Often observed. Description based on observations of 16 cells.

Remarks. Previous reported size range is 5–20 μm; this species has been reported from marine sites in subtropical and tropical Australia, North Atlantic, Brazil, Denmark, England, Fiji, Gulf of Finland, Ireland, Equatorial Pacific and Panama (Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Patterson *et al.*, 1993; Vørs *et al.*, 1995; Ekebom *et al.*, 1996; Patterson and Simpson, 1996). Cell appearance is entirely consistent with the description of Larsen and Patterson (1990). *Bordnamonas tropicana* can be confused with *Bodo curvifilus* Griessmann, 1913, because the anterior flagellum is held anteriorly in a curve, but can be distinguished by its swimming pattern, non-acronematic posterior flagellum, the thickness of the flagella and the anterior mouth. Simpson (1997) suggests that *Bordnamonas* may have an affinity with Euglenozoa rather than with stramenopiles (Larsen and Patterson, 1990). That view is adopted here.

Stramenopiles Patterson, 1989
Actinomonas mirabilis Kent, 1880/***Pteridomonas danica*** Patterson and Fenchel, 1985
(figures 19k, l, 20d)

Description. Cell measuring 4–6 μm long, with one flagellum emerging from a small depression in the anterior end of the cell. With a ring of arms around the flagellum and below the equator of the cell; the arms around the flagellum are evenly spaced. The anterior part of the cell is slightly broader than the posterior part. The single thickened flagellum is about three times the cell length and has an undulating beat. Cells usually swim rapidly, but are occasionally attached to the substratum

with a long posterior stalk trailing. Small particles are seen on the cell surface. Sometimes commonly observed.

Remarks. *Actinomonas mirabilis* Kent, 1880 has, as synonyms; *Actinomonas pusilla* Kent, 1880, *A. radiosa* Roskin, 1931, *A. marina* Kufferath, 1952, *Pteridomonas scherffelii* Lemmermann, 1914. Cell length was previously reported to be 4–8 μm. This species has been found from marine sites in Antarctica, North Atlantic, Brazil, Danish Wadden Sea, England, Fiji, France and Hawaii (Kent, 1880; Griessmann, 1913; Fenchel, 1982; Larsen, 1985a; Larsen and Patterson, 1990; Patterson *et al.*, 1993; Vørs, 1993a, 1993b; Tong, 1997b; Tong *et al.*, 1997).

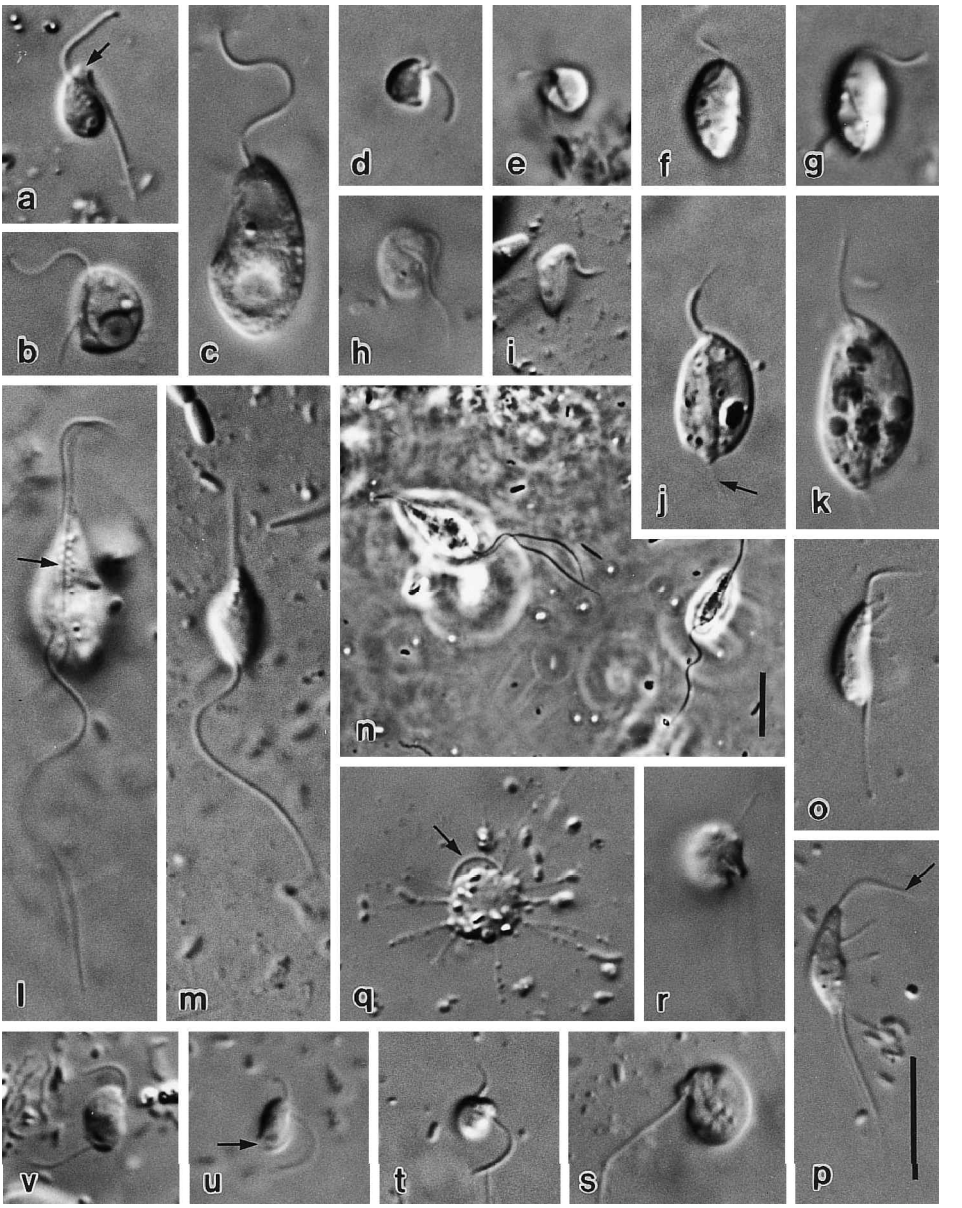
Pteridomonas danica Patterson and Fenchel, 1985 has been described from subtropical and tropical Australia, Brazil, Canada, Denmark, England, Fiji, Greenland, Hawaii and the equatorial Pacific and has lengths ranging from 3.5 to 6.5 μm (Patterson and Fenchel, 1985; Larsen and Patterson, 1990; Vørs, 1993a, 1993b; Vørs *et al.*, 1995). According to previous authors, swimming cells may withdraw tentacles (or arms) and the stalk may be of variable length. This species grazes on suspended bacteria and small organisms.

At the ultrastructural level, *Actinomonas mirablis* can be distinguished from *Pteridomonas danica* because *P. danica* has flagellar transitional bands (Larsen and Patterson, 1990; Larsen, 1985a; Patterson and Fenchel, 1985). At the light microscopical level, *A. mirabilis* and *P. danica* are very similar and hard to distinguish with confidence. *Actinomonas mirabilis* more frequently has posterior or lateral arms and more commonly has two anterior wreaths of arms; it typically has a more substantial flagellum.

Caecitellus parvulus (Griessmann, 1913) Patterson *et al.*, 1993
(figures 20e, 23k)

Description. Cell 2–4.5 μm long, somewhat triangular or rounded, with mouth protruding on the right ventral side of the cell. Two flagella; the acronematic anterior flagellum beats slowly and stiffly with a small excursion, and inserts apically. It is slightly longer than cell length. The non-acronematic posterior flagellum is about 2.3–3 times the cell length, emerges from the ventral face of the cell and trails under the body. Moves slowly by gliding with the anterior flagellum in close contact with the substratum. Rare.

FIG. 21. (a) *Bordnamonas tropicana* showing general appearance and mouth (arrow), (b, c) *Cafeteria marsupialis*, (b) general appearance of cell showing groove, (c) swimming cell, (d, e) *Cafeteria roenbergensis*, (d) general appearance of cell, (e) showing groove and recurrent flagellum, (f, g) *Pendulomonas adriperis* showing flagellar insertion, (h) *Developayella elegans* showing general appearance of cell and flagellar insertion, (i) *Amastigomonas debruynei*, general appearance of cell, (j, k) *Amastigomonas mutablis*, (j) note anterior flagellum project from sleeve, recurrent flagellum (arrow), (l–n) *Cercomonas granulatus*, (l) dividing cell, note rows of bodies on ventral side, (m) general appearance, (n) general appearance, (o, p) *Cercomonas* sp., note pseudopodia and acronematic tip (arrow) of anterior flagellum, (q) *Massisteria marina*, general appearance of cell showing pseudopodia and flagella (arrow), (r–t) *Ancyromonas sigmoides*, (r) short anterior flagellum (arrow), (s) general appearance of same cell, (t) note slightly thick anterior flagellum with acronematic tip, (u, v) *Barthelona vulgaris* showing general appearance of cell, note ventral groove (arrow). All micrographs are DIC images with the exception of (n) which is phase contrast image. Scale bar in (n) = 10 μm. Scale bar in (p) = 10 μm for (a–m) and (o–v).



Remarks. The size range 3–7 μm has been reported in previous studies. *Caecitellus parvulus* has been found in subtropical and tropical Australia, North Atlantic, Brazil, Danish Wadden Sea, England and equatorial Pacific (Larsen and Patterson, 1990; Patterson *et al*., 1993; Ekebom *et al*., 1996; Patterson and Simpson, 1996; Tong, 1997a; Tong *et al*., 1998). Our observations are in agreement with the observations of Griessmann (1913) and Larsen and Patterson (1990) of organisms reported under the name *Bodo parvulus*. *Caecitellus parvulus* is characterized by the protrusion on the ventral side of the cell, the beat pattern and the insertion of the flagella. Recent ultrastructural work suggests that *Caecitellus* is a stramenopile and perhaps a

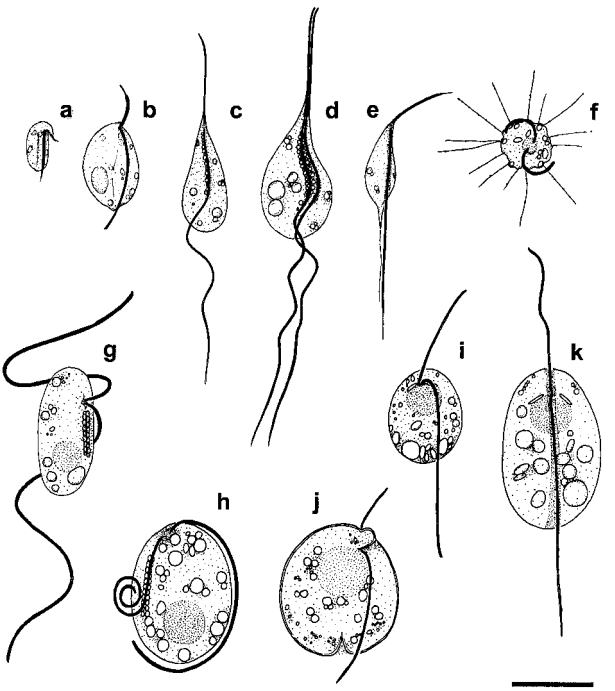


FIG. 22. Apusomonadidae, Cercomonadida, Kathablepharidae and Thaumatomonadidae, (a) *Amastigomonas debruynei*, (b) *A. mutabilis*, (c, d) *Cercomonas granulatus*, (d) showing dividing cell, (e) *Cercomonas* sp., (f) *Massisteria marina*, (g) *Kathablepharis remigera*, (h) *Platychilomonas psammobia*, (i) *Protaspis gemmifera*, (j) *P. obliqua*, (k) *P. tegere*. Scale bar = 10 μm for all figures.

bicosoecid although it has a gliding motility and a raptorial feeding behaviour, and lacks a hairy flagellum (O'Kelly *et al.*, 1998).

Cafeteria marsupialis Larsen and Patterson, 1990
(figures 20f, 21b, c)

Description. Biflagellated, D-shaped cells somewhat variable in shape, when attached 5–12 μm long, mostly about 7–8 μm long, and 5–10 μm wide; up to 7–10 μm long and 3–5 μm wide when swimming. Attach to the substratum by the tip of the posterior flagellum, which lies in a deep ventral groove. The anterior flagellum is directed normal to the groove. The organism may feed on suspended bacteria, which are drawn towards the body by the activity of the anterior flagellum, entering along a curved channel at the posterior end of the ventral groove. The anterior flagellum of the attached cell is about 1.5–2 times the cell length and the posterior flagellum is slightly longer than the cell. A single nucleus with a rounded nucleolus lies just below the insertion of the flagella. The cell body may include many—sometimes large—food vacuoles. Undigested residues of food are egested by the fusion of old food vacuoles with the plasma membrane. Swimming cells are more rounded, with anterior flagellum directed to the anterior, recurrent flagellum trailing. It often occurs with *Carpediemonas membranifera* and *C. bialata*. More frequent in slightly anaerobic preparations. Description based on observations of 95 cells.

Remarks. This organism has the characteristics of the genus *Cafeteria* in being

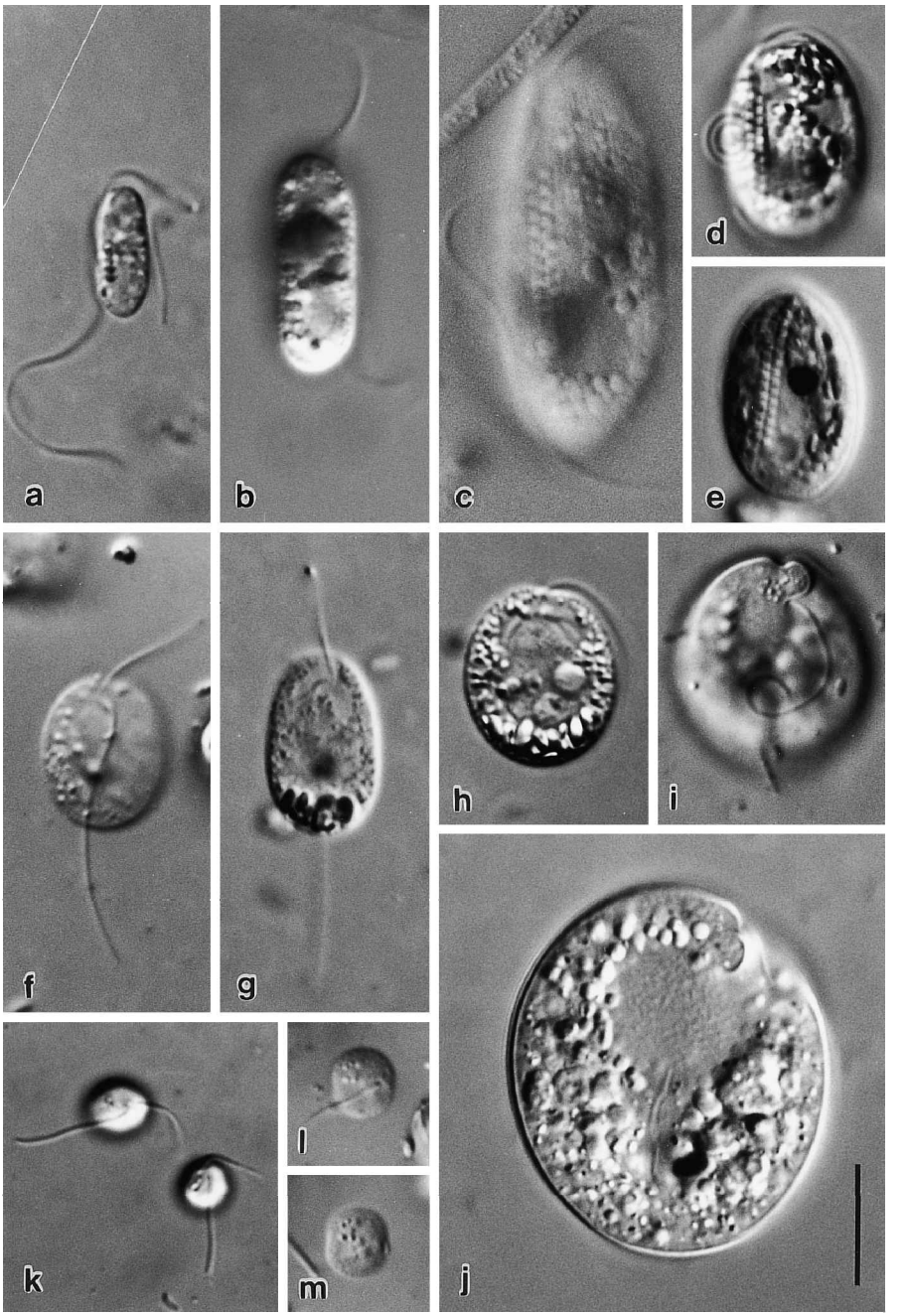


FIG. 23. (a–c) *Kathablepharis remigera* showing ranges of size, (a) general appearance of cell, (c) showing extrusomes and surface striations, (d, e) *Platychilomonas psammobia*, (d) coiled posterior flagellum, (e) extrusomes, (f–h) *Protaspis gemmifera*, (f) general appearance of cell showing ventral face, (g) ventral view showing reserve materials in posterior end, (h) nuclear caps, (i, j) *Protaspis obliqua* showing ranges of size, note anterior protrusion, (i) insertion of flagella, (j) thick wall, (k) *Caecitellus parvulus*, (l, m) *Discocelis punctata*, showing general appearance of cell. All micrographs are DIC images. Scale bar = 10 μm for all figures.

a stramenopile (anterior flagellum which draws water towards the body of the cell and is therefore hispid) which adheres to the substratum by the tip of the posterior flagellum and has no peri-flagellar collar. It differs from other species in the genus by the large ventral pocket and posterior curving food ingestion region. A size range 5–15 μm has previously been reported by Larsen and Patterson (1990) from tropical Australia and Brazil, and by Ekebom *et al.* (1996) from tropical Australia. The organism described here may graze on large bacteria as long as 0.7 times the cell length.

Cafeteria roenbergensis Fenchel and Patterson, 1988
(figures 20g, 21d, e)

Description. Cells are D-shaped, 3.5–5 μm long, and laterally compressed. There is a shallow groove on the left side of the cell. Two flagella of similar length emerge subapically and are slightly longer than the cell. The anterior flagellum is directed perpendicular to the ventral face of the cell of attached cells. The posterior flagellum is reflexed, passing over one face of the cell and then attaching to the substratum by the tip. In swimming cells, the anterior flagellum is directed forwards and beats with a sine-wave, and the posterior flagellum is directed backwards and trails. Usually moves fast following a spiral path, but sometimes moves slowly. Food particles (bacteria) may be ingested near the posterior part of the ventral groove. Not common.

Remarks. Generally, our observations are consistent with descriptions of Fenchel and Patterson (1988) and Larsen and Patterson (1990). Previous studies reported the size range to be 1.5–10 μm (Fenchel and Patterson, 1988; Larsen and Patterson, 1990; Vørs, 1992a, 1992b, 1993a, 1993b; Patterson *et al.*, 1993; Vørs *et al.*, 1995; Ekebom *et al.*, 1996; Patterson and Simpson, 1996; Tong, 1997a, 1997b; Tong *et al.*, 1997, 1998; Bernard *et al.*, 1999). This species has been widely found from marine sites in Antarctica, subtropical and tropical Australia, North Atlantic, Baltic, Denmark, England, Gulf of Finland, Greenland and equatorial Pacific. This species resembles *Cafeteria minuta* (Ruinen, 1938) Larsen and Patterson, 1990 in general appearance, but is distinguished because *C. minuta* has a longer anterior flagellum. *Cafeteria roenbergensis* resembles *C. marsupialis* Larsen and Patterson, 1990 in general appearance and in having a short anterior flagellum, but *C. marsupialis* is larger and has a ventral groove with a posterior channel leading into the cell. It may not be clearly distinguished from *Acronema sippewissettensis* (Teal *et al.*, 1998), the flagella of which are said to be acronematic. *Cafeteria roenbergensis* may occasionally occupy about 6–20% of the heterotrophic flagellate population (Fenchel, 1982; Tong, 1997b) and is cosmopolitan.

Ciliophrys infusionum Cienkowski, 1876
(figure 20h)

Description. Helioflagellate, in the heliozoan stage the cell measures about 5 μm across, with a central nucleus and one flagellum held in a figure of eight. The cell is spherical with delicate pseudopodia extending radially from the body and bearing extrusomes. The cell may change from the heliozoan stage with pseudopodia and a slow beating flagellum to a swimming flagellate without pseudopodia and with the flagellum beating rapidly. Observed to consume suspended bacteria. When feeding,

bacteria adhere to the pseudopodia and then are drawn to the body. One cell observed in enrichment culture.

Remarks. *Ciliophrys marina* Caullery, 1909 and *Dimorpha monomastix* Penard, 1921 are synonyms of this species. *Ciliophrys infusionum* has been found in marine sites in SE North America, subtropical and tropical Australia, Denmark, England, English Channel, Fiji, Gulf of Finland, Hawaii, Mediterranean, Norway and equatorial Pacific, and lengths of 3.5–20 μm have been reported (Caullery, 1909; Griessmann, 1913; Throndsen, 1969; Davidson, 1982; Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Vørs *et al.*, 1995; Patterson and Simpson, 1996; Tong, 1997a, 1997b; Tong *et al.*, 1998). Generally, the cell described here is in agreement with observations by Larsen and Patterson (1990). This species is similar to *Massisteria marina* Larsen and Patterson, 1990, but can be distinguished by its regular symmetry, its stiff pseudopodia, by not being adpressed to the substratum and in having one flagellum. It resembles small heliozoa in having pseudopodia extending radially from the body, but is distinguished by having a flagellum.

Pendulomonas adriperis Tong, 1997
(figures 20j, 21f, g)

Description. Cell ovoid or droplet-shaped, about 4–9 μm long, 2.5–5 μm wide, somewhat flexible and not flattened, with two flagella similar in length emerging subapically (about one-third of the way down). The flagella are slightly longer than the cell and not acronematic. The anterior flagellum projects in front of the body and beats with an asymmetric pattern, and the posterior flagellum trails behind the body and may be held in a curve or obliquely. Sometimes, the posterior flagellum beats stiffly and rapidly in non-swimming cells. Cells usually swim by slow rotating movements and the cell bodies wag. When cells swim rapidly, the anterior flagellum beats quickly and cells do not wag. Cells may attach to the substratum by the tip of the trailing flagellum. In attached cells, cells may wag or tremble rapidly. Commonly observed in enrichment cultures.

Remarks. This species has been found in marine sites in subtropical Australia and England, cell length range is reported to be 5–8.5 μm (Tong, 1997a, 1997b). Like naked bicosoecids (*Cafeteria* and *Pseudobodo*) this species attaches to the substratum by the tip of the posterior flagellum. This species can be distinguished from all species of the genus *Cafeteria* by the orientation and beat pattern of the flagella. It is similar to *Phyllomitus* in general shape, but is easily distinguished because the two flagella of *Phyllomitus* insert together to an anterior pocket, while those of *Pendulomonas* insert separately in a subapical groove.

Pseudobodo tremulans Griessmann, 1913
(figures 19m, n, 20k)

Description. Cell about 5 μm long. The insertion sites of the two flagella are separated by a protrusion at the anterior of the cell. The anterior flagellum has a sine-wave beating pattern and is about 3.5 times the length of the cell, and the posterior flagellum is about twice the length of the cell and may attach to the substratum by its tip. The cell moves by swimming with the anterior flagellum directed forwards. One cell observed.

Remarks. *Pseudobodo tremulans* was reported to be 2–8 μm long and has been found in marine sites in subtropical and tropical Australia, Antarctica, Brazil,

Denmark, Hawaii (Griessmann, 1913; Ruinen, 1938; Fenchel, 1982; Larsen and Patterson, 1990; Patterson *et al*., 1993; Vørs, 1993b; Fenchel *et al*., 1995; Patterson and Simpson, 1996; Tong, 1997a, 1997c; Tong *et al*., 1997). This species may be confused with *Cafeteria minuta* (Ruinen, 1938) Larsen and Patterson, 1990 but can be distinguished by a collar around the anterior part of the cell in unstressed feeding cells. In our cell we could not observe the anterior collar, but we assigned the cell to *Pseudobodo tremulans* because of the shape and size of the cell, swimming and feeding behaviour, and lengths of the flagella. This species is similar to *Pendulomonas adriperis* Tong, 1997 in cell length, but is distinguished by the insertion and orientation of the flagella, and the beat pattern of the anterior flagellum which is sinusoidal and slow in *Pendulomonas*.

Stramenopiles *incertae sedis*
Developayella elegans Tong, 1995
(figures 20i, 21h)

Description. Cell outline oval, 5–6 μm long, with two flagella emerging from a depression in the right anterior part of the ventral side of the cell. The anterior flagellum is about 1.3 times the length of the cell and the posterior flagellum is about 1.5–1.7 times the length of the cell. Cells attach to the substratum by means of the posterior flagellum. In attached cells the anterior flagellum is held in a curve and beats slowly up and down, and the posterior flagellum beats rapidly with a shallow excursion. Cells move by swimming. Rarely observed.

Remarks. Developayella elegans has been described from subtropical Australia and England and the cell length had been reported to range from 3.5 to 10 μm (Patterson and Simpson, 1996; Tong, 1995, 1997a, 1997b; Tong *et al*., 1998). Generally, our observations are in accord with the descriptions of Tong (1995). When *D. elegans* attaches to the substratum, it is recognized from other free-living flagellates, such as *Cafeteria*, *Colponema*, *Jakoba* and *Phyllomitus*, which have two flagella and a large ventral depression, by the beat pattern of the flagella—the anterior flagellum beats slowly up and down and the posterior flagellum beats rapidly with small excursion.

Apusomonadidae Karpov and Mylnikov, 1989
Amastigomonas debruynei De Saedeleer, 1931
(figures 21i, 22a)

Description. Cell 5–6 μm long, dorso-ventrally flattened, flexible but not amoeboid. The anterior flagellum emerges from the tip of a laterally directed sleeve, the posterior flagellum trails under the cell and occasionally protrudes behind the cell; strands of cytoplasm may be drawn out behind the cell. The nucleus is situated in the anterior left of the cell. Rarely observed.

Remarks. Amastigomonas is a senior synonym of *Thecamonas*. *Amastigomonas debruynei* is the same as organisms described as *T. trahens*, *A. borokensis* and *A. caudata* (Ekebom *et al*., 1996). Previously reported lengths are 3–7.5 μm. *Amastigomonas debruynei* was previously recorded from marine sites in subtropical and tropical Australia, North Atlantic, Brazil, Arctic Canada, Denmark, England, Gulf of Finland, Greenland, Hawaii and Panama (Larsen and Patterson, 1990; Vørs 1992a, 1992b, 1993a, 1993b; Patterson *et al*., 1993; Ekebom *et al*., 1996; Tong, 1997a, 1997b; Tong *et al*., 1998). Other species in the genus include *A. bermudensis*,

A. filosa and *A. mutabilis*. This species can be distinguished from *A. bermudensis* Molina and Nerad, 1991 by its smaller size (*A. bermudensis*, 8–11.5 μm), and from *A. mutabilis* by its smaller size (*A. mutabilis* measures up to 15 μm) and the lack of granules located ventrally adjacent to the posterior flagellum. It is distinguished from *A. filosa* because it lacks the thin cytoplasmic extensions which are distinctive for *A. filosa*.

Amastigomonas mutabilis (Griessmann, 1913) Molina and Nerad, 1991
(figures 21j, k, 22b)

Description. Cell elliptical, 11–16 μm long, dorso-ventrally flattened, flexible. With a flexible sleeve around the base of the anterior flagellum. The anterior flagellum is about 0.5 times the length of the cell and is the same thickness as the posterior flagellum. The recurrent posterior flagellum is slightly longer than the cell and trails under the body, to which it attaches loosely in a slight groove. The nucleus is situated subapically near the right margin of the cell. Some cells have granules alongside the recurrent flagellum. Relatively rare.

Remarks. This species was first described as *Rhynchomonas mutabilis* by Griessmann (1913), transferred to *Thecamonas* by Larsen and Patterson (1990) and to *Amastigomonas* by Molina and Nerad (1991). Previously reported length ranges are 7–15 μm. It has been described from marine sites in subtropical Australia, Brazil, Denmark, England, France, Greenland and North Atlantic (Griessmann, 1913; Ruinen, 1938; Larsen and Patterson, 1990; Vørs, 1992b, 1993a; Patterson *et al.*, 1993; Patterson and Simpson, 1996; Tong, 1997b; Tong *et al.*, 1998;). Some cells lack the rows of granules which follow the line of the posterior flagellum and were suggested to be distinctive by Larsen and Patterson (1990). *Amastigomonas mutabilis* is distinguished from *A. debruynei* by its larger size and the presence of granules alongside the posterior flagellum, and by its longer anterior flagellum. This species resembles *A. bermudensis* Molina and Nerad, 1991 at 8.0–11.5 μm in general appearance and their size ranges overlap. *Amastigomonas bermudensis* may be a synonym of *A. mutabilis*. Further work is required to clarify the identities of species in this genus.

Cercomonadida Vickerman, 1983
Cercomonas granulatus Lee and Patterson, n. sp.
(figures 21l–n, 22c–d. Type micrographs: figure 21l–m)

Diagnosis. Cercomonas, cell pyriform, 7–15 μm long, with row of refractile bodies on the ventral side.

Description. Cell outline pyriform, 7–15 μm long, flexible, with two rows of refractile bodies on the ventral side of the cell. The anterior flagellum is slightly longer than the cell, beats from side to side with entire length, and the basal part of the flagellum adheres to a rostrum. The posterior flagellum is about 2.5–3.5 times the cell length, tapers posteriorly and appears to lie next to the row of the bodies on the ventral side of the cell or to lie in a ventral groove. The flagellum adheres to the body surface for part of its length and beats slowly from side to side as cells glide. Flagella are of similar thickness and are not acronematic. During gliding the anterior part of the cell is elongated. Strands of cytoplasm were drawn from the posterior end of the cell. Glides with the flagella in contact with the substratum and

may swim like a snake. Rarely observed, but sometimes often observed in late cultures.

Remarks. This species has general characteristics of the genus *Cercomonas* in that two unequal flagella emerge near the anterior end of a pliable body which can emit cytoplasmic threads; one is recurrent and adheres to the substratum, the other beats stiffly. This species can be distinguished from all other species of *Cercomonas* by its row of refractile bodies on the ventral side. The composition of the genus is uncertain and we make comparisons only with the most similar nominal taxa. *Cercomonas granulatus* is distinguished from *C. agilis* (Moroff, 1904) Lemmermann, 1914 because *C. agilis* does not have the bodies on the ventral side and has an elongated cell shape (see Lemmermann, 1914). It is similar to *C. rhynchophorus* (see Skuja, 1939) in having a long posterior flagellum and in cell length, but is distinguished by its refractile bodies. This species is also distinguished from *Cercomonas ovata* (Dujardin, 1841) Tong *et al*., 1997 by its cell shape, size and the ventral bodies; *C. ovata* at 12.5–30 μm is rather larger than *C. granulatus.* Some species of the genera *Amastigomonas*, *Cercomonas*, *Dimastigella* and *Procryptobia* have a posterior flagellum adhering to the ventral surface. This species is similar to *Cryptobia coryphaenoideana* (see Noble, 1968) found from the stomach of a bathypelagic marine fish (*Coryphaenoides acrolepis*) in general appearance and cell length, but is distinguished in having the ventral bodies. *Cercomonas* resembles *Dimastigella*, but is usually distinguished by having a ventral groove and strands of cytoplasm drawn from the posterior end of the cell; *Dimastigella* seems to be rather flattened compared to *Cercomonas*. This species is similar in general shape and size to *Dimastigella trypaniformis* Sandon, 1928 but the basal part of the anterior flagellum in that species is attached to a discrete rostrum and lacks the refractile bodies on the ventral side. *Dimastigella trypaniformis* is more spindle-shaped and has no strands of cytoplasm drawn from the posterior end of the cell, and the posterior flagellum adheres to the cell surface along the entire length of the cell. *Dimastigella mimosa* (Frolov *et al*., 1996) is distinguished from *C. granulatus* by the lack of ventral bodies.

Cercomonas sp.
(figures 21o, p, 22e)

Description. Gliding cell, 7–10 μm long, flexible, flattened, anteriorly narrow, posteriorly broad. Two thickened flagella insert apically. The anterior flagellum beats slowly from side to side and is as long as the cell. The acronematic tip is hard to see. The acronematic posterior flagellum is about 2–2.5 times the cell length, lies in a mid-ventral groove, is hard to see, and trails alongside the margin of the body. Pseudopodia are produced from the ventral groove; during gliding the pseudopodia move from the anterior end of the cell toward the posterior and then are drawn out behind the posterior end. Ingested bacteria with ventral pseudopodia are transported into the posterior part of the cell through pseudopodia.

Remarks. This species was often observed in this study. It is similar to *Amastigomonas* in having an acronematic posterior flagellum and pliable body, but is distinguished because it is not covered with a theca and is less pliable. This species appears to be the same as the cell described by Tong (1994) as C*ercomonas* sp., but there are some differences in the location of ingestion and where pseudopodia are produced. Ingestion of bacteria took place on the ventral side of the cell as reported

by Mignot and Brugerolle (1975) for other species, but Tong (1994) observed ingestion to take place on the dorsal side.

There are probably many synonyms in the genus *Cercomonas* (Patterson and Zölffel, 1991; Tong *et al*., 1997). Additionally, Skvortzov (1977) reported 83 species (73 of them new species) under the name *Cercobodo*—a synonym of *Cercomonas* (Lee, 1985). This genus is in urgent need of attention. We are unable to establish the species identity of this taxon, but record its presence to establish its occurrence in marine sediments.

Massisteria marina Larsen and Patterson, 1990
(figures 21q, 22f)

Description. Cells measuring 3–6.5 μm, dorso-ventrally flattened irregular body. Cells produce delicate pseudopodia with extrusomes, which extend radially from the cell and normally adhere to the substratum. Two short curved flagella arise from the dorsal side of the cell and are relatively inactive. Rarely observed.

Remarks. Generally, our observations are in good agreement with those of Larsen and Patterson (1990). Previously reported size ranges are 2.5–5 μm (Patterson and Fenchel, 1990), 3–9 μm (Larsen and Patterson, 1990; Vørs, 1992a, 1992b), 4.2–7 μm (Ekebom *et al*., 1996), 2.5–4 μm (Tong, 1997a) and 2–9.5 μm (Tong *et al*., 1998). This species was found in marine sites in subtropical and tropical Australia, Brazil, Denmark, Gulf of Finland, equatorial Pacific and Panama (Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Vørs *et al*., 1995; Ekebom *et al*., 1996; Tong, 1997a; Tong *et al*., 1998).

Kathablepharidae Vørs, 1992
Kathablepharis remigera (Vørs, 1992) Clay and Kugrens, 1999
(figures 22g, 23a–c)

Description. Cell measuring 12–18 μm long, not flattened, with two rows of extrusomes located ventrally. Cells are oblong or cylindrical with two flagella inserting subapically. The flagella are thick, longer than the cell, unequal in length and may coil around the body during swimming. The anterior flagellum is about twice the length of the cell and may coil up during resting, and the posterior flagellum is about three times the cell length. The nucleus lies in the middle of the cell. Cells rotate while swimming. Rarely observed.

Remarks. This species was recently transferred from *Leucocryptos* to the genus *Kathablepharis* by Clay and Kugrens (1999). It has been found from marine sites in Canada, Denmark, England, Gulf of Finland and Greenland, and the length was reported to be 7–25 μm under the name *Leucocryptos remigera* (Vørs, 1992a, 1992b, 1993a; Vørs *et al*., 1995; Tong, 1997b). We observed one very large cell (40 μm) which bore the general characteristics of *Kathablepharis* (figure 23c), but the posterior flagellum coiled up in the resting cell like *Platychilomonas psammobia*. The cell has pellicular striations. This species resembles *Leucocryptos marina* (Braarud, 1953) Butcher, 1967, but *L. marina* may be distinguished by the droplet-shaped body, two flagella of similar length, flagellar beat patterns, and different swimming pattern (see Vørs, 1992c).

Platychilomonas psammobia Larsen and Patterson, 1990
(figures 22h, 23d, e)

Description. Cell outline oval, 18–20 μm long, 11–13 μm wide, laterally compressed, with two rows of extrusomes lying at the margin of the cell. Two flagella

insert laterally and subapically in a depression in the right ventral side of the cell and are longer than the cell. In resting cells, the anterior flagellum is held to the left margin of the cell and the posterior flagellum is coiled up. The nucleus is located in the posterior part of the cell. Cells move rapidly by swimming and contained other algae as food. Rarely observed. Description based on observations of six cells.

Remarks. Larsen and Patterson (1990) described this species from marine sites in Danish Wadden Sea, England and Fiji, and cell length was reported to be 15–20 μm. *Platychilomonas psammobia* can be easily distinguished from other colourless flagellates by being flattened, by its two rows of extrusomes and its coiled posterior flagellum. This species is like *Kathablepharis remigera* in having two rows of extrusomes and in swimming patterns, but when the cell rests it can be distinguished by the coiled posterior flagellum and its flatness.

Thaumatomonadidae Patterson and Zölffel, 1991
Protaspis gemmifera Larsen and Patterson, 1990
(figures 22i, 23f–h)

Description. Cell outline oval or roundish, 9–16 μm long and 9–11 μm wide, dorso-ventrally flattened. Cell surface is rather warty. Two flagella insert subapically in an indistinct ventral furrow. The anterior flagellum is as long as the cell and the posterior flagellum is about 1.3–3 times the cell length. The posterior flagellum inserts in an antero-posterior line of the anterior flagellum and trails behind the cell. The nucleus is situated anteriorly below the flagellar insertion, has caps and is roundish. Reserve material may be present as oval or rod shaped bodies. Glides very fast with the anterior flagellum. Produces pseudopodia from the ventral furrow. Sometimes commonly observed. Description based on observations of 33 cells.

Remarks. Generally, our observations agree with the original description of Larsen and Patterson (1990) although they did not refer to the warty surface. *Protaspis gemmifera* was recorded from Brazil and North Atlantic by Larsen and Patterson (1990) and Patterson *et al.* (1993), respectively. Cell lengths were previously reported as 10–17 μm (Larsen and Patterson, 1990; Patterson *et al.*, 1993). Nuclear caps were not seen in any of the cells described by Patterson *et al.* (1993) but this character may have been overlooked because the nuclear caps may be difficult to see in fast moving cells. Some cells did not have reserve materials in the posterior end of the cell, and reserve materials may not be useful as a diagnostic character although we have not seen the distinctive rod-shaped reserve materials in any species other than this one. *Protaspis gemmifera* resembles *P. verrucosa* Larsen and Patterson, 1990 in general appearance and length, but it has been distinguished by the longitudinal ventral furrow in *P. verrucosa* and the presence of nuclear caps in *P. gemmifera*. Figure 60b in Larsen and Patterson (1990), which is the type micrograph for *P. verrucosa*, shows some similarity to our cells in figure 23h. We are not sure whether these two species are clearly distinguishable. *Protaspis gemmifera* is probably detritivorous (Patterson *et al.*, 1993). The organism referred to as *P. simplex* by Tong *et al.* (1998) has probably been illustrated by pictures of *P. gemmifera*, but having consulted original records, we can confirm that both species were present.

The genus contains nine species: *P. gemmifera* Larsen and Patterson, 1990, *P. glans* Skuja, 1939, *P. major* Skuja, 1939, *P. metarhiza* Skuja, 1939, *P. obovata* Skuja, 1948, *P. obliqua* Larsen and Patterson, 1990, *P. simplex* Vørs, 1992, *P. tegere*

Larsen and Patterson, 1990 and *P. verrucosa* Larsen and Patterson, 1990. The boundaries among many species are not clear (table 2), and this genus needs more attention.

Protaspis obliqua Larsen and Patterson, 1990
(figures 22j, 23i, j)

Description. Cell slightly oval or roundish, 12–32 μm long, 10–27 μm wide, dorsoventrally flattened, with thickened cortex. With a ventral median groove; cell indented anteriorly and posteriorly where groove meets margin. Subapically, the right margin of the groove forms a protrusion. With two flagella inserting under the protrusion; the anterior flagellum is about 0.5 times the length of the cell and the posterior flagellum is about 0.5–1.5 times the length of the cell. The nucleus is without nuclear caps, is located subapically in a median position, is rounded and is 5–13 μm in diameter. Contained many food particles up to 5 μm long. Commonly observed. Descriptions based on observations of 16 cells.

Remarks. This species was described from marine sites in tropical Australia, Fiji

Table 2. Characteristics to distinguish *Protaspis* spp. 1: Skuja (1939), 2: Skuja (1948), 3: Larsen (1985b), 4: Larsen and Patterson (1990), 5: Vørs (1992a), 6: Vørs (1992b), 7: Patterson *et al.* (1993), 8: Ekebom *et al.* (1996), 9: Tong (1997b), 10: Tong *et al.* (1998) with corrections as indicated under *P. gemmifera* and *P. tegere* (above), 11: present study. + = present, − = absent, nc = no comment or no data.

Species	Ref.	Cell size (μm)	Nuclear caps	Ventral groove
P. gemmifera Larsen and Patterson, 1990	4	10–14	−	+
	6	10–17	−	+
	11	9–16	+	+
P. glans Skuja, 1939	1	14–19	nc	+
	3	14–19	nc	+
	4	12–16	nc	+
	5	20–30	nc	+
	6	12–20	nc	+
	9	11.5–17.5	nc	+
P. major Skuja, 1939	1	24–40	nc	+
	3	30	nc	+
P. metarhiza Skuja, 1939	1	30–36	nc	+ (dorsal)
	9	27.5–28.5	nc	+
P. obovata Skuja, 1948	2	26–40	nc	+
P. obliqua Patterson and Larsen, 1990	4	14–20	−	+
	9	8.5–12.5	nc	nc
	11	12–32	−	+
P. simplex Vørs, 1992	5	10–25	nc	+
	6	10–25	nc	+
	9	7–10	nc	+
P. tegere Larsen and Patterson, 1990	4	14–20	+	+
	8	18	+	+
	10	15–18	+	+
	11	14–25	+	+
P. verrucosa Larsen and Patterson, 1990	4	10–18	–	+
	5	5–10	nc	nc
	6	10–15	nc	nc
	10	9–10.5	nc	+

and England by Larsen and Patterson (1990) and Tong (1997b). Cell length was reported to be 8.5–20 μm by previous authors. Generally, our observations are in accordance with those of Larsen and Patterson (1990) although our length range extends the previous range. Although the identities of most species within the genus are difficult to establish, the protrusion near the flagellar insertions makes this species easy to identify.

Protaspis tegere Larsen and Patterson, 1990
(figures 22k, 25a–d)

Description. Cell oblong, ovate or obovate, slightly flattened, 14–25 μm long and 8–14 μm wide. The ratio of length to width is 1 to 0.7. In some cells the cell surface is warty. A longitudinal median ventral groove extends from the site of flagellar insertion to the posterior end of the cell. Two flagella, unequal in length; the anterior flagellum inserts subapically in the slight depression and is as long as the cell. The posterior flagellum inserts posterior to the anterior flagellum and is about 1.5–2.5 times the cell length. The large nucleus is disc-shaped with anterior caps and is located anteriorly on the right-hand side or near the midline of the cell. Pseudopodia may be produced from the groove. Moves by gliding. Sometimes common. Description based on observations of 32 cells.

Remarks. Cells described here are in agreement with the original description by Larsen and Patterson (1990) although we have extended the size range from the

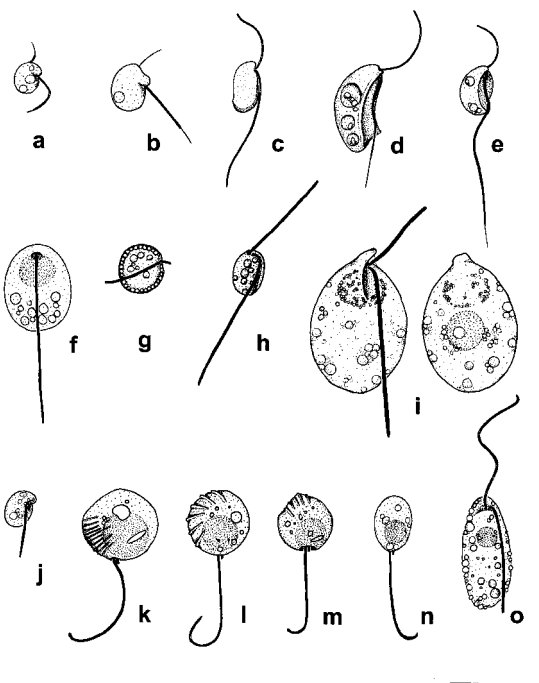


FIG. 24. Protista incertae sedis, (a, b) *Ancyromonas sigmoides*, (c) *Barthelona vulgaris*, (d) *Carpediemonas bialata*, (e) *C. membranifera*, (f) *Clautriavia cavus*, (g) *Discocelis punctata*, (h) *Glissandra innuerende*, (i) *Heterochromonas opaca*, (j) *Metopion fluens*, (k–m) *Metromonas grandis*, (n) *M. simplex*, (o) *Phyllomitus granulatus*. Scale bar = 10 μm for all figures.

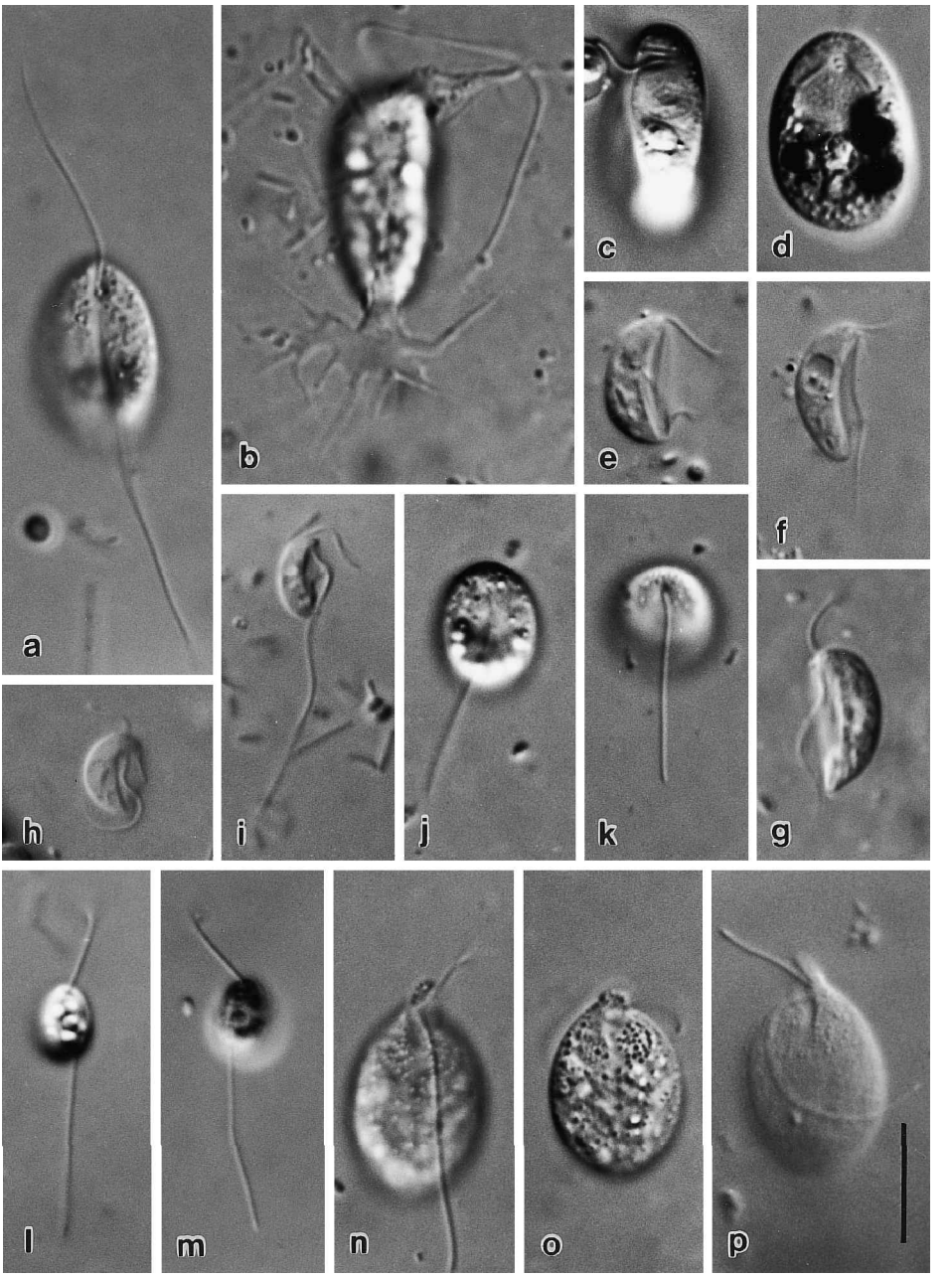


FIG. 25. (a–d) *Protaspis tegere*, (e–g) *Carpediemonas bialata*, (h, i) *Carpediemonas membranifera*, (j, k) *Clautriavia cavus*, (l, m) *Glissandra innuerende*, (n–p) *Heterochromonas opaca*. All micrographs are DIC images. Scale bar = 10 μm for all figures.

previously reported 14–20 μm. This species has been reported from marine sites in subtropical and tropical Australia, Fiji and Hawaii (Larsen and Patterson, 1990; Ekebom *et al*., 1996; Tong *et al*., 1998). *Protaspis tegere* resembles *P. glans* in general appearance but is distinguished by the nuclear caps in *P. tegere* (Larsen and

Patterson, 1990) and by the position of nucleus. The position of the nucleus in *Protaspis metarhiza* Skuja, 1939 may change with the age of cells (Skuja, 1939) and this may also be in the case of *P. glans* (Larsen, 1985b). Assuming that nuclear caps in *P. glans* have been overlooked in previous studies, *P. tegere* may prove to be a junior synonym of *P. glans* because they are distinguished only by the nuclear caps. Tong *et al.* (1998) described *P. tegere* without nuclear caps, but in their figure 9r the nuclear caps are shown. We note that in respect of nuclear caps the illustration is correct and the text is in error. *Protaspis major* Skuja, 1939 is distinguished from *P. tegere* due to it being larger (24–40 μm) with an oblique ventral groove.

Protista *incertae sedis*

Ancyromonas sigmoides Kent, 1880

(figures 21r–t, 24a, b)

Description. Gliding flagellate, cell outline oval, 3–7 μm long (mostly 3–5 μm) and 2–3.5 μm wide, dorso-ventrally flattened. This species has a shallow groove ventrally near an antero-lateral margin of the cell. Cells may or may not have a thin stiff anterior flagellum emerging from an anterior depression. The anterior flagellum can be easily overlooked. The posterior flagellum is about 1.5 times the length of the cell and may not be acronematic. Moves by gliding with the posterior flagellum trailing. Common. Description based on observations of 31 cells.

Remarks. Previously reported lengths range from 2 to 7.6 μm. This species has been reported from marine sites in Antarctica, Australia, Arctic Canada, Denmark, Fiji, Gulf of Finland, Greenland, Hawaii and Panama (Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Ekebom *et al.*, 1996; Tong, 1997a; Tong *et al.*, 1997, 1998; Bernard *et al.*, 1999). Our observations are in agreement with the observations of previous authors. *Ancyromonas sigmoides* can be confused with *Metopion fluens*, but is distinguished by the anteriorly directed flagellum; the second flagellum in *M. fluens* is thicker and is directed to the rear. It is similar to *A. melba* Patterson and Simpson, 1996, found in hypersaline habitats of Shark Bay, subtropical Australia, but *A. melba* has an anterior flagellum which is as thick as the posterior flagellum, and the cell is slightly larger. We observed one cell having an anterior flagellum which was basally thickened (figure 21t).

Barthelona vulgari Bernard *et al.*, 1999

(figures 21u, v, 24c)

Description. Cell outline ovate, about 5 μm long. With two flagella inserting into a pocket. Cells have a groove from near the flagellar pocket to the posterior edge of the cell following the cell margin. The anterior flagellum is slightly longer than the cell, and the posterior flagellum is about 2.5 times the cell length and sometimes lies partly in the groove. The cells usually attach to the substratum with the anterior flagellum and then draw food materials into the groove by using the posterior flagellum. Sometimes common in late cultures.

Remark. This species was found from anoxic marine sites in subtropical Australia by Bernard *et al.* (1999). It is similar to some members of the genus *Bodo*, but can be easily distinguished by the groove and the feeding behaviour. *Barthelona vulgaris* is similar to *Bordnamonas tropicana* Larsen and Patterson, 1990 and *Pendulomonas*

adriperis Tong, 1997 in length, but is distinguished by the groove, the feeding behaviour and the swimming pattern.

Carpediemonas bialata (Ruinen, 1938) Lee and Patterson, n. comb.
(figures 24d, 25e–g)

Description. Cell outline kidney-shaped, 6–14 μm long (mostly, 9–12 μm), not rigid, with a longitudinal ventral groove. A membrane moves down along the groove every 4–6 s. Two flagella emerge from the anterior part of the cell; the anterior flagellum bends backwards, is about the length of the cell and beats over the cell with a slow sweeping motion. The acronematic posterior flagellum beats asymmetrically and is about 1.5 times the cell length. The posterior flagellum may vibrate actively in the groove when not beating. Cells consume bacteria up to 5 μm and food materials are transferred by the moving membrane to the back of the cell. The cells may have many food vacuoles and attach to the substratum with the tip of the posterior flagellum. Cells move slowly by skidding or gliding with the anterior flagellum beating with a flicking motion. Commonly observed in late cultures.

Remarks. Ruinen (1938) described *Cryptobia bialata* from Australia as a biflagellated protist with a ventral groove, and with an undulating membrane and symmetrical walls. In respect of general appearance, size and flagellar lengths, the organisms from the present site agree well with Ruinen's description. Body form, flagellar beating and distribution of this species agree well with *C. membranifera*, and we here transfer *Cryptobia bialata* to *Carpediemonas*.

We believe that *Carpediemonas bialata* has already been described with cells of *C. membranifera* under the name *Percolomonas membranifera* in Larsen and Patterson (1990) (see Remarks to *C. membranifera)*. This species often co-occurs with *C. membranifera*. *C. bialata* can be distinguished from *C. membranifera* by its larger size and the cell shape. *Carpediemonas bialata* resembles *Jakoba libera* (Ruinen, 1938) Patterson, 1990 in general cell shape and the orientation of two flagella, but is distinguished by its acronematic anterior flagellum, the direction of curvature of the anterior flagellum, by the length of the posterior flagellum and by the moving membrane. The moving membrane has been seen in other taxa such *Chilomastix cuspidata* (Simpson, unpubl. note). We note that those species may be related to each other.

Carpediemonas membranifera Ekebom *et al.*, 1996
(figures 24e, 25h–i)

Description. Cell elliptical or obovate, 3–6 μm long, with a longitudinal ventral groove which extends most of the cell length. When squashed, the cell is pliable. Two flagella unequal in length emerge from the anterior distal part of the cell; the anterior flagellum bent over backwards is as long as the cell and beats stiffly. The acronematic posterior flagellum is about 2.5–4 times the cell length, beats actively in the ventral depression and usually lies in the depression. Usually moves by skidding with the anterior flagellum beating with a stiff paddling motion. Cells consume bacteria. Commonly observed in anoxic conditions. Description based on observation of 80 cells.

Remarks. It would appear that in their description of *Carpediemonas membranifera* as *Percolomonas membranifera*, Larsen and Patterson (1990) included two species; one usually measuring 6 μm or less and the other measuring 6 μm or

more. The type micrograph depicts the smaller species, which now bears the name *C. membranifera.* It has a relatively long posterior flagellum, moves by skidding with the anterior flagellum beating in a paddling motion. It was transferred to the new genus *Carpediemonas* by Ekebom *et al.* (1996) because unlike confirmed species in *Percolomonas*, it had only two flagella. Ultrastructural studies (Simpson, unpubl. data) have confirmed that this is an amitochondriate protist unrelated to *Percolomonas*. The larger species resembles *Cryptobia bialata* of Ruinen (1938) and is here referred to as *Carpediemonas bialata*.

This species has been described from marine sites in Australia and Brazil (Larsen and Patterson, 1990; Ekebom *et al.*, 1996; Bernard *et al.*, 1999). *Carpediemonas membranifera* is distinguished from *C. bialata* by its smaller size, the absence of the moving membrane and the relatively long posterior flagellum. It consumes bacteria (Larsen and Patterson, 1990; Ekebom *et al.*, 1996) and usually occurs in large numbers with *Cafeteria marsupialis* and *Carpediemonas bialata*.

Clautriavia cavus Lee and Patterson, n. sp.
(figures 24f, 25j, k. Type micrograph: figure 25j)

Diagnosis. *Clautriavia,* cell oval about 8 μm long, flattened, with subapically a shallow ventral groove and one trailing flagellum emerging from a ventral depression.

Description. Cell outline oval, 8–10 μm long, flattened and rigid. One flagellum directed posteriorly, emerges from a ventral subapical depression, is about 1.5–2 times the length of the cell and makes close contact with the substratum when the cell is gliding. Cells have a shallow, wide ventral groove which is easy to overlook. The ventral face of the cell appears to be slightly concave. The cell surface may be rather warty and food particles are seen in the posterior part of the cell. Cells glide slowly and smoothly with the posterior part slightly raised above the substratum. Often observed, but not in large numbers. Description based on the observations of eight cells.

Remarks. We assign this organism to the genus *Clautriavia* because it has general features of the genus: it is a gliding flagellate with one trailing flagellum and a mid-ventral groove. *Clautriavia* is reminiscent of *Protaspis* and *Allantion*, but can be recognized from *Protaspis* by having only one flagellum. This species is less easy to distinguish from *Allantion* because *Clautriavia* lacks a rostral prominence at the anterior end of the cell and has a concave ventral face. The genus *Clautriavia* to date contains two nominal species, *C. mobilis* (see Massart, 1900) and *C. parva* (see Schouteden, 1907). *Clautriavia cavus* differs from *C. mobilis* because *C. mobilis* is twice as large, has a relatively short flagellum and has a nucleus at the right posterior of the cell. According to Patterson and Zölffel (1991), *Clautriavia parva* may be the gliding stage of *Metromonas*. This species may be the same as 'Glissander' by Tong (1994).

Discocelis punctata Larsen and Patterson, 1990
(figures 23l–m, 24g)

Description. Cell about 6 μm long, disc-shaped, dorso-ventrally flattened, anteriorly concave and posteriorly convex. Two flagella emerge from a depression on the anterior end of the cell. The recurrent flagellum trails behind the gliding cell and is slightly longer than the cell. The shorter flagellum is less than 1 μm long, is hard to see and is inactive. The nucleus is located anteriorly in the right half of the

cell. There is a line of bodies around the margin of the cell. Glides smoothly in closely contact with the substratum. Rare. One cell observed.

Remarks. Discocelis punctata has been described by Larsen and Patterson (1990) and Tong *et al.* (1998) from marine sites in Brazil and Fiji, and our observations are in accord with their description except our cell is smaller than the previously reported cell dimensions of 6.5–9 μm. The size of the cell observed here is between that of *D. saleuta* and *D. punctata*. *Discocelis saleuta* may have peripheral bodies (Vørs, 1988; Larsen and Patterson, 1990) but these are not visible by light microscopy. We assign this individual to *D. punctata* because the peripheral granules were easy to see. Future work may indicate that we need to combine these two species. This species can be confused with the genus *Metromonas* in having one long recurrent flagellum and one short, inactive flagellum, but it is distinguished by the flatness of the cell, the pattern of movement, and the peripheral bodies.

Glissandra innuerende Patterson and Simpson, 1996
(figures 24h, 25l, m)

Description. Cell outline elliptical, 5–6 μm long, 3–5 μm wide, about 3 μm thick, slightly flattened, with a small depression at the anterior part of the cell and with a ventral groove extending from the depression to the posterior end of the cell. Two thickened flagella are unequal in length and insert subapically into the depression. The anterior flagellum is about 3.5 times the cell length and the tip of the flagellum moves back and forth. The trailing posterior flagellum is about 3–4 times the cell length and may lie in the ventral groove. Cells may attach to the substratum by the tip of the posterior flagellum. During gliding, the cells usually appear to move obliquely. The cells are filled with small granules up to 1.5 μm in diameter. Sometimes often observed.

Remarks. We regard this species as the same as *Glissandra innuerende* Patterson and Simpson, 1996 although our cells had an elliptical cell body. *Glissandra innuerende* resembles *Protaspis simplex* Vørs, 1992 but lacks the nuclear caps and flagellar orientation of *Protaspis* differs (see Vørs, 1992a, figure 45: 1–12).

Heterochromonas opaca Skuja, 1948
(figures 24i, 25n–p)

Description. Cell outline oval, about 18 μm long and 11 μm wide, somewhat dorso-ventrally flattened, rigid, with an anterior protrusion and a central nucleus. Cells have a deep ventral depression and are somewhat warty. Two flagella insert subapically into the depression; the anterior flagellum is about 0.5 times the cell length, and the posterior flagellum is slightly longer than the cell and inserts below the anterior flagellum. Moves by gliding with the anterior flagellum directed forwards and the posterior flagellum trailing. Three cells observed.

Remarks. The organisms observed are very similar to *Heterochromonas opaca* Skuja, 1948 in cell length and the position of nucleus, in having two flagella which differ in length, and having a ventral depression and the anterior protrusion. In the original description of Skuja (1948) the anterior flagellum is longer than the posterior flagellum. *Heteronema opaca* is similar to *Diplonema papillatum* (Porter, 1973) Triemer and Ott, 1990 in general appearance and cell length, but it can be distinguished because *D. papillatum* is flexible. Also, *H. opaca* resembles *Abollifer prolabens*

Vørs, 1992; *A. prolabens* has one flagellum, but sometimes the second shorter flagellum may appear before cell division (Vørs, 1992a). *Heterochromonas opaca* resembles *Cruzella marina* (see de Faria *et al*., 1922), but can be distinguished because *C. marina* is flexible and has a long anterior flagellum. It is distinguished from other species of *Heterochromonas* by the anterior protrusion. This genus includes about 13 species; *Heterochromonas bodoides* Skuja, 1948, *H. chlorophaga* Skuja, 1956, *H. cryptostigma* Skuja, 1939, *H. globosa* Skuja, 1948, *H. gotlandica* Skuja, 1956, *H. hovassei* Fiatte and Joyon, 1965, *H. nobilis* Skuja, 1956, *H. ovaca* Skuja, 1948, *H. polysticta* Skuja, 1948, *H. rotundata* Skuja, 1956, *H. spaerophora* Skuja, 1956, *H. vivipara* (Ehrenberg, 1838) Pascher, 1912 and *H. vulgaris* (Cienkowsky, 1870) Pascher, 1912 (see Pascher, 1912; Skuja 1939, 1948, 1956).

Metopion fluens Larsen and Patterson, 1990
(figures 24j, 26a, b)

Description. Cell outline ovate, 5–9 μm long and 3.5–7 μm wide, laterally compressed, with a small rostrum anterior to the flagellar insertion. Small bodies are seen in the protrusion or at the proximal anterior part of the cell. Two flagella of unequal size emerge from a ventral groove located in the left side of the cell. The long flagellum is about 1.5 times the cell length, is thickened and is not tapered at the tip, and the short flagellum may be difficult to see. With small granules in the

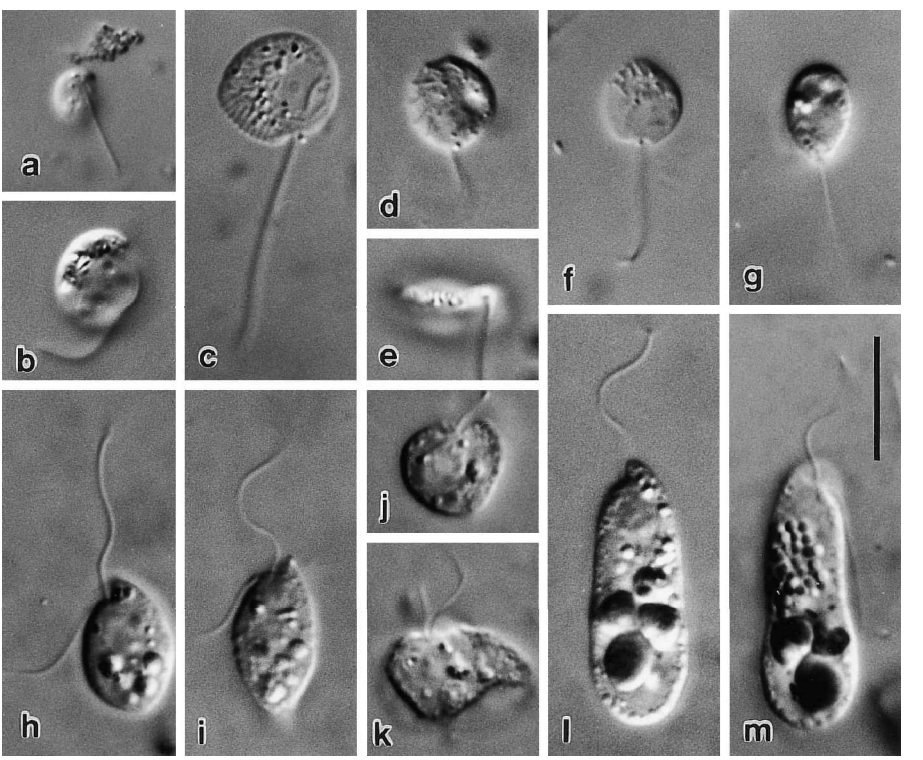


FIG. 26. (a, b) *Metopion fluens*, (c–f) *Metromonas grandis*, (g) *Metromonas simplex*, (h–l) *Phyllomitus granulatus*. All micrographs are DIC images. Scale bar = 10 μm for all figures.

posterior part of the cell. The nucleus is situated near the groove. Moves by gliding. Rarely observed.

Remarks. Previous reported with cell lengths from 3 to 9 μm. This species has been found in marine sites in tropical Australia, Denmark, Brazil, England, Fiji, Gulf of Finland (Larsen and Patterson, 1990; Vørs, 1992a, 1992b; Patterson and Simpson, 1996; Tong, 1997b; Tong *et al.*, 1998). Our observations are in accord with the observations of previous authors. This species may be confused with *Ancyromonas sigmoides*, but can be distinguished by its broad anterior end and by the position of the second flagellum—that of *M. fluens* is directed posteriorly, while that of *Ancyromonas sigmoides* is directed anteriorly. According to Tong (1997b), *M. fluens* may feed on other flagellates as well as bacteria.

Metromonas grandis Larsen and Patterson, 1990
(figures 24k–m, 26c–f)

Description. Cell outline leaf-shaped or slightly roundish, 5–10 μm long (mostly 7–10 μm), 4–10 μm wide and about 2 μm deep, dorso-ventrally flattened. One side of the cell appears folded. With two flagella; a long flagellum is 1.2–2.2 times the length of the cell and trails behind the cell when gliding. There is a short inactive flagellum, less than 2 μm long, which inserts to the right of the major flagellum and is always present. Cells attach to the substratum with the longer flagellum and move with a nodding action—like a pendulum. The nucleus is near the flagellar insertion. Relatively common.

Remarks. This species was described from marine sites in tropical Australia, Brazil, Fiji, Hawaii and cell length reported was 9–12 μm (Larsen and Patterson, 1990; Tong *et al.*, 1998). Generally, our observations are in agreement with the observations of Larsen and Patterson (1990), but we observed three different shapes in the cells (figures 26c, d, f). *Metromonas grandis* is relatively common when diatoms are abundant, but is usually less common than *M. simplex* (Griessmann, 1913) Larsen and Patterson, 1990. It is distinguished from *M. simplex* by its slightly larger size and folded margin. The folded margin may be a good diagnostic character for this species, but in some cells which contain many granules or prey, the folded margin may be difficult to see. This species usually co-occurs with *M. simplex*. We believe that Tong *et al.* (1997) included *M. grandis* within their account of *M. simplex* (see figure 7a in Tong *et al.*, 1997) and that the figure 9m referred to as *M. simplex* in Tong *et al.* (1998) was of *M. grandis*, but having consulted original records we confirmed that both species were present.

Metromonas simplex (Griessmann, 1913) Larsen and Patterson, 1990
(figures 24n, 26g)

Description. Cell obovate, 3–8 μm long (mostly 4–7 μm), 2–6 μm wide, dorso-ventrally flattened, pellicle smooth. The abflagellar margin of the cell is thicker than the (posterior) margin. Two flagella of very unequal length arise from the posterior part of the cell. The major flagellum is always present, is about 1.5–3.0 times the length of the cell and may be attached to the substratum. The short inactive flagellum is about 1 μm long and inserts to the right of the major flagellum. It may be difficult to see. Cells normally attach to the substratum and swing from side to side like a pendulum and the cells may also glide with the cell body in front of the flagellum. Common. Description based on observations of 85 cells.

Remarks. This species was first described under the name *Phyllomitus simplex* by Griessmann (1913). It was found in marine sites in Antarctica, Australia, Brazil, Arctic Canada, Denmark, England, Fiji, Gulf of Finland, France, Germany, Arctic Greenland, Hawaii and cell lengths from 4 to 9 μm were reported (Griessmann, 1913; Larsen and Patterson, 1990; Vørs, 1992a, 1992b, 1993a; Ekebom *et al.*, 1996; Patterson and Simpson, 1996; Tong, 1997b; Tong *et al.*, 1997, 1998). This species sometimes appears in large numbers. *Metromonas simplex* feeds on bacteria and flagellates through the lateral margin of the cell (Patterson unpubl. obs.) or the anterior part of the cell (Griessmann, 1913).

Phyllomitus granulatus Larsen and Patterson, 1990
(figures 24o, 26h–m)

Description. Cell outline sac-shaped, very flexible (almost amoeboid), 7–21 μm long (mostly 10–12 μm) and 4–10 μm wide, slightly flattened. Refractile granules underlie the cell surface. Two flagella emerge from an anterior pocket. The anterior flagellum beats with a sine-wave, is about 1.0–1.5 times the length of the cell and is slightly curved to the right during swimming. The posterior flagellum inserts to the left of the anterior flagellum, varies in length from 0.5 to 2.5 times the length of the cell. Cytoplasm is drawn out at the posterior end. The nucleus is located below the anterior pocket, near the centre of the cell and is roundish. Cells seem to migrate to air-droplets and some contained ingested eukaryotic algae. Sometimes very common (late culture).

Remarks. Larsen and Patterson (1990) first described this species from tropical Australia, Brazil and Hawaii, and it was reported by Vørs (1992b) from Denmark. Previously recorded cell length ranges from 8 to 18 μm (Larsen and Patterson, 1990; Vørs, 1992b). Generally, our observations are in accord with those of Larsen and Patterson (1990). *Phyllomitus granulatus* can be distinguished from all species of the genus *Phyllomitus* by its granules. The organism is phagotrophic and may consume relatively large particles such as detritus and diatoms much larger than the flagellate (see Larsen and Patterson, 1990). It is similar to *Protaspis* in the position of the nucleus, but can be distinguished by its flexible body, movement and flagellar beat pattern.

Unidentified flagellates

We have observed further species of *Kiitoksia*, *Notosolenus*, *Paraphysomonas*, *Petalomonas*, *Platychilomonas*, *Ploeotia*, *Protaspis*, *Rhynchobodo*, *Thaumatomastix* and *Urceolus*, but most were insufficiently documented to allow their identities to be established unambiguously.

Discussion

In addition to documenting the diversity of marine benthic flagellates, this study sought to contribute to the understanding of the geographical distribution of heterotrophic flagellates. The emerging understanding is that most morpho-species of free-living protozoa have a cosmopolitan distribution (Ekebom *et al.*, 1996; Finlay, 1998; Finlay *et al.*, 1998; Lee and Patterson, 1998).

Lee and Patterson (1998) used the cluster analysis in the PRIMER programs (Clarke, 1993) to compare communities from differing geographical locations and showed that communities from similar geographic locations do not cluster together.

Communities from extreme (hypersaline and anoxic) sites have distinctive compositions, thereafter communities of heterotrophic flagellates group on habitat type (those from the water column group together and remote from those from benthic sites—whether freshwater or marine) (Lee and Patterson, 1998). We confirm that the community observed here has considerable overlap with communities reported previously from intertidal marine benthic sites—world-wide.

Of the 87 species encountered in this survey, 67 have previously been found in one or more other continents. Thirteen species are reported here for the first time, but it is not possible to assess the biogeographic distribution of taxa reported from single studies. In order to assess cosmopolitanism, surveys of equal or greater intensity are required at similar and remote locations. Endemism is indicated either by the exclusive co-occurrence of sister taxa in the same region or by the recurrent presence of a species in one geographical location and its recurrent absence from all other geographic locations. Seven species have been reported from Australia only. A survey of the literature (Patterson and Lee, 1999) confirms that more taxa have been reported from Australia than any other location world-wide excepting Europe. At this early stage in documenting diversity, it is likely that Australia will have the second highest level of records of taxa not reported elsewhere. However, this reflects the intensity of the surveys in Australia and is not likely to be an observation of the geographic distribution of the organisms. Until further studies elsewhere are carried out, we are inclined to retain our model (Lee and Patterson, 1998) that free-living heterotrophic flagellates have a cosmopolitan distribution.

Most new species occurred in the genera *Notosolenus* and *Petalomonas* which are well represented in samples of sediments which contain large numbers of diatoms. Although mouths are not usually reported in these genera [but see descriptions of *Notosolenus ostium* and *N. tamanduensis* by Larsen and Patterson (1990)], the presence of algal material in food vacuoles suggests that they do have mouths. This suggests that the definition of these genera will need to be adjusted or the genera will have to be divided. We favour the first option. Many of the taxa assigned to these genera, for example—*Notosolenus apocamptus*, *N. similis*, *N. scutulum*, *Petalomonas poosilla*, are only subtly different from each other. *Notosolenus scutulum* described here has three subtly different shapes and *Petalomonas poosilla* described here includes two populations (small and larger cells). Additionally, we have found three different shapes in *Metromonas grandis* with only minor differences among them. These observations do suggest that our present application of the morpho-species concept may need to be refined. Our options are to loosen the concept so that species become more expansive, or to tighten it to create more restrictive definitions. We suspect that the latter approach is the proper one, but feel no action should be taken until we can establish which concept has greater relevance to the distribution of taxa in nature, and until we have accumulated considerably more information to establish if there are frequently encountered discontinuities within morpho-species.

This survey is based on about 35 sampling occasions. We have summarized the number of occasions on which each species has been observed in figure 27 which is based on observations of 79 species made on samples taken on 22 occasions. Figure 27 is different from the hollow curves of Lee and Patterson (1998) which show the frequency with which taxa have been reported in over 30 surveys from around the world, or from an analysis of the literature (Patterson and Lee, 1999). In previous surveys, most species are reported occasionally and very few are reported

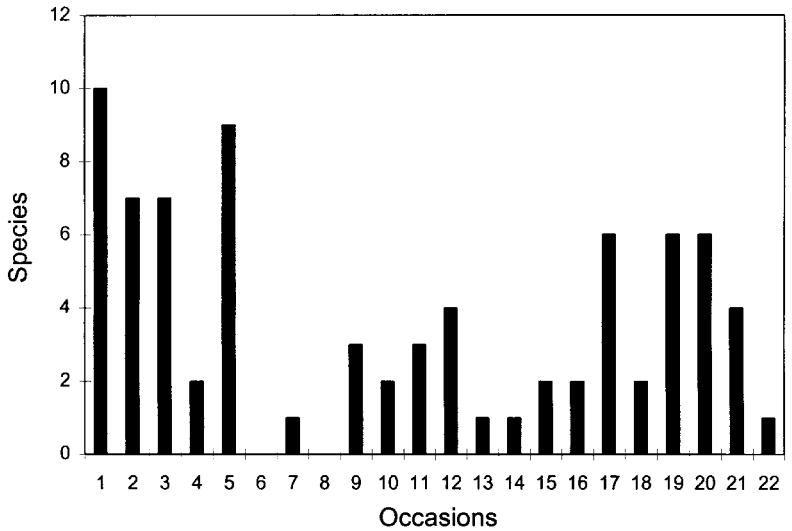


FIG. 27. Frequency with which species have been reported in 22 occasions of this study (after Patterson and Lee, 1999).

frequently. This suggests that most species are sparsely distributed. The study reported here is an intensive survey, and in it 32% of the species were encountered on 17 or more of the sampling occasions and may be regarded as common. We believe that the hollow curves referred to above are distortions of the true situation and are caused by extrinsic factors. Despite the protracted nature of this survey, 44% of the species were observed on five occasions and less. Many species were represented by fewer than five cells during the sampling period. These included *Anehmia exotica*, *Ciliophrys infusionum*, *Discocelis punctata*, *Dinema platysomum*, *D. validum*, *Heterochromonas opaca*, *Heteronema globuliferum*, *H. larseni*, *Mastigamoeba* cfr. *simplex*, *Notosolenus* cfr. *tamanduensis*, *Petalomonas iugosus*, *P. labrum*, *P. virgatus*, *P. oblonga*, *P. plumosa*, *P. pseudanisonema*, *P. vitrea*, *Pseudobodo tremulans*, *Salpingoeca infusionum* and *Stephanoeca diplocostata*.

We note that the reduction in unique records strengthens the case for cosmpolitanism. Therefore, we are of the view that most marine free-living heterotrophic flagellates have a wide distribution, but acknowledge that our insights about biogeography and community structure remain overly influenced by species concepts, sampling and reporting procedures, and other extrinsic factors.

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