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The Biology of Free-living Heterotrophic Flagellates

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7. Diversity and ecology of soil flagellates

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Abstract

About 260 species of heterotrophic and autotrophic flagellates have been recorded from soils world-wide. Published species lists are highly questionable and there is thus an urgent need for improvements in taxonomy in this area. Recent studies indicate that there are autochthonic soil flagellates. Detailed ecological literature on soil flagellates is sparse. Between 0 and 10^6 individuals per gram of soil have been reported. The biomass of flagellates (0.05 g dry mass m^{-2}) and their annual production (about 1 g dry mass m^{-2}) are low compared with naked and testate amoebae.

Introduction

Protozoa are an important link in the terrestrial food web and energy turnover (Foissner 1987; Beck 1989; Meisterfeld 1989). Plants and earthworms depend on protists as nutrient mineralizers and as food (Clarholm 1984; Rouelle *et al.* 1985).

Traditionally, soil protozoa are grouped into flagellates, naked amoebae, testate amoebae, and ciliates. There are several general reviews on soil protozoa (e.g. Stout and Heal 1967; Franz 1975; Foissner 1987; Bamforth 1988). Soil flagellates have not been previously reviewed in spite of their almost universal presence and their potential as causal agents of plant diseases (Kitajima *et al.* 1986). The most comprehensive works are those of Sandon (1927), Grandori and Grandori (1934), Cutler and Crump (1935), and Fehér (1948).

Diversity of soil flagellates

Sandon (1927) and Grandori and Grandori (1934) list about 80 and 130 species of soil flagellates in their reviews, respectively. Since that

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time the number of species recorded has increased to about 260, of which 208 are exclusively heterotrophic (Table 7.1). This is a respectable number, equalling those of soil ciliates and testate amoebae (Foissner 1987). Heterotrophic and autotrophic forms are traditionally included in 'soil flagellates' and this view has been adopted for the present review although heterotrophic forms are favoured. The number of species per locality varies from few (Antarctic soils; Smith 1978) to 47, which Varga (1956) recorded from reforested saline soils in Hungary.

Table 7.1 Flagellated organisms recorded from soils of the world

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
Actinomonas sp.	2	O	Rumania, USA
A. mirabilis Kent	3	O	Cosmopolitan
Allantion sp.	1	IS	USA
**A. tachyploon* Sandon	11	IS	Cosmopolitan
**Allas diplophysa* Sandon	10	IS	Cosmopolitan; even in Sahara
Amphimonas sp.	2	IS	Russia, Central Asia
A. fusiformis Mereschkovsky	1	IS	Russia
A. globosa Kent	1	IS	Russia
Ancyromonas contorta (Klebs) Lemmermann	2	IS	Europe
Anisonema sp.	4	E	Europe, USA
A. acinus Dujardin	2	E	Hungary, Italy
**A. minus* Sandon	6	E	Cosmopolitan
A. ovale Klebs	7	E	Europe, USA
A. striatum Klebs	2	E	Hungary, Italy
A. truncatum Stein	2	E	Hungary, USA
Anthophysa vegetans (Müller) Stein	1	CH	Italy
Apusomonas proboscidea Alexeieff	4	IS	Europe, Russia, Antarctica
Astasia sp.	7	E	Europe, USA, USSR, Greenland
A. curvata Klebs	1	E	USA
A. klebsii Lemmermann	8	E	Europe; also in saline soils
A. oblonga (Skvortzov)	1	E	Hungary
A. ocellata Khawkine	6	E	Europe; also in saline soils
A. variable (Skvortzov)	1	E	Hungary
Bicosoeca lacustris Clark	1	BI	Europe; rare
Bodo sp. (see also *Heteromita*)	13	K	Europe, Russia, USA
B. amoebinus Lemmermann	1	K	Europe; forest
B. angustus (Dujardin) Bütschli	10	K	Europe, USA, Africa
B. alexeieffi Lemmermann	1	K	Germany; forest
B. caudatus (Dujardin) Stein	23	K	Cosmopolitan
B. celer Klebs	28	K	Cosmopolitan; also saline soils
B. compressus Lemmermann	7	K	Europe, S. America, Antarctica

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
B. edax Klebs	34	K	Cosmopolitan; also saline soils
B. fusiformis (Stokes) Lemmermann	1	K	Rumania; forest
B. gracilis (Fantham?)	1	K	S. Africa; possibly nomen nudum
B. lens (Müller) Klebs	27	K	Cosmopolitan; also saline soils
B. minimus (Klebs)	11	K	Europe, Russia, Alaska, USA
B. mutabilis Klebs	10	K	Europe, Russia, USA
B. obovatus Lemmermann	22	K	Cosmopolitan; also saline soils
B. ovatus (Dujardin) Stein	20	K	Cosmopolitan; also saline soils
B. parvus (Nägler) Lemmermann	7	K	Europe, Russia, S. Africa
B. putrinus (Stokes) Lemmermann	4	K	Europe; also saline soils
B. repens Klebs	11	K	Europe, Russia, USA; also saline soils
B. rostratus (Kent) Klebs	8	K	Europe, Russia, Africa
B. saltans Ehrenberg	34	K	Cosmopolitan; also saline soils
**B. terricolus* (Martin) Sandon	10	K	Europe, Antarctica; saline soils
Bodo triangularis (Stokes) Lemmermann	2	K	Europe, USA
B. uncinatus (Kent) Klebs	2	K	Hungary, Russia
B. variabilis (Stokes) Lemmermann	3	K	Rumania, Russia
Bodopsis alternans (Klebs) Lemmermann	4	IS	Europe; Africa; also saline soils
B. godboldi Lackey	1	IS	USA; pine forest
Carteria dangeardii Troitzkaja	1	C	Hungary; fields
C. ovata Jacobson	1	C	Hungary; fields
C. scherffeli Szabados	1	C	Hungary; dung
Cephalothamnium cyclopum Stein	6	K	India, Java, S. America, Antarctica
Cercobodo sp.	9	IS	Eurasia, USA
C. agilis (Moroff) Lemmermann	29	IS	Cosmopolitan; also saline soils
C. alexeieffii Lemmermann	2	IS	Bulgaria, Algeria
C. bodo (Meyer) Lemmermann	19	IS	Eurasia, Africa, Java
C. digitalis (Meyer) Lemmermann	3	IS	Asia, Algeria, Java
C. grandis (Maskell) Lemmermann	3	IS	Germany, Algeria, Java
C. granulifera Hollande	1	IS	Mexico
C. ovatus (Klebs) Lemmermann	4	IS	Eurasia, Algeria
C. radiatus (Klebs) Lemmermann	7	IS	Europe, Russia, Algeria, Java, USA
C. simplex (Moroff) Lemmermann	2	IS	Germany, Algeria (Sahara)
**C. vibrans* Sandon	21	IS	Cosmopolitan; also saline soils
Cercomonas sp.	8	IS	Cosmopolitan
C. crassicauda Dujardin	44	IS	Cosmopolitan; also saline soils
C. longicauda Dujardin	40	IS	Cosmopolitan; also saline soils
Chilomonas sp.	2	CR	USA, S. Africa
C. paramecium Ehrenberg	11	CR	Cosmopolitan
Chlamydomonas sp.	8	C	Eurasia, Antarctica

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
C. alboviridis Stein	1	C	Russia; invalid species
**C. angustae ellipsoidea* Watanabe	1	C	Sumatra; paddyfield
**C. bacillaris* R. & L. Grandori	2	C	Italy, Hungary; saline soils
**C. chlorostellata* Flint & Ettl	1	C	Antarctica
C. cingulata Pascher	2	C	Europe; nomenclature unclear
C. cullens Ettl	1	C	Nepal; meadow soil
C. depauperata Pascher	3	C	Hungary, Italy
C. ehrenbergii Goroschankin	2	C	Europe, S. Africa
C. gloeogama Korschikoff	1	C	India; paddyfield
C. longeovalis Pascher	1	C	Hungary; forests
C. media Klebs	1	C	Hungary; forests
**C. megalis* Bischoff & Bold	1	C	USA; soil of Precambrian rock
C. moewussii moewusii Ettl	1	C	Sumatra; paddyfield
C. monadina Stein (same as *C. cingulata*; see above)			
**C. monticola* Watanabe	1	C	Japan; soil near pond
C. mutabilis Gerloff	1	C	Nepal; forests
C. peterfii Gerlach	1	C	Hungary; forests
C. pulvisculus Ehrenberg	1	C	Poland; invalid species
C. snowiae Printz	1	C	Czechoslovakia
C. umbonata umbonata Ettl	1	C	Sumatra; cassava field
Chlorangium stentorinum (Ehrenberg) Stein	1	C	Rumania; nomenclature unclear
Chlorogonium sp.	2	C	Hungary, India
C. euchlorum (Ehrenberg) Ehrenberg	4	C	Italy, Asia, S. Africa
C. elongatum (Dangeard)	1	C	Asia; nomenclature unclear
**Chloromonas palmelloides* Broady	1	C	Antarctica
Chromulina flavicans Bütschli	1	CH	Europe, Australia
C. ochracea (Ehrenberg) Bütschli	1	CH	Europe, Asia, Africa
C. ovalis Klebs	1	CH	Asia; rare
C. rosanoffii (Woronin) Bütschli	1	CH	Czechoslovakia; forest soil
C. verrucosa Klebs	1	CH	USA; rare
Chrysamoeba radians Klebs	5	CH	Europe, USA, S. Africa, Antarctica
Chrysocapsa planktonica pascher	1	CH	Europe
Chrysopyxis bipes Stein	1	CH	Europe
Ciliophrys infusionum Cienkowski	1	O	USA
Cladomonas sp.	1	IS	Spitsbergen
Clostenema socialis Stokes	1	E?	USA
Codonosiga botrytis (Ehrenberg) Kent	3	CO	Europe; also saline soils
Codonosigopsis robini Senn	1	CO	Bulgaria; fields
Coelomonas grandis (Ehrenberg) Stein	1	C?	Italy
**Colpodella gonderi* (Foissner & Foissner) Patterson & Zölffel	1	IS	Austria; ectoparasite of the ciliate *Colpoda*
Colponema loxodes Stein	4	IS	Germany, Hungary, Algeria

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
**C. symmetrica* Sandon	6	IS	Cosmopolitan; saline soils
Copromonas subtilis Dobell	1	E	England
Cryptoglena pigra Ehrenberg	2	E	Sweden, USA
Cryptomonas ovata Ehrenberg	3	CR	USA, Russia
C. obovoidea Pascher	1	CR	Spitsbergen
Cyathomonas truncata (Ehrenberg) Fromentel	4	CR	Europe, USA
Dallingeria drysdali Kent	1	IS	Algeria; even in Sahara desert
Dimastigamoeba radiata Klebs	1	IS	Poland
**Dimastigella trypaniformis* Sandon	2	K	Scotland, USA
Dimorpha mutans Gruber	4	O	Europe, Algeria
Dinomonas sp.	1	IS	Russia
D. tuberculata Kent	1	E	Hungary; dung
D. vorax Kent	10	IS	Europe, Russia, USA; saline soils
Distigma proteus Ehrenberg	8	E	Eurasia, USA, Mexico
Dunaliella lateralis Pascher & Jahoda	1	C	Nepal; meadow soil
Entosiphon sp.	1	E	Italy
E. ovatum Stokes	3	E	Hungary, Italy; also saline soils
E. sulcatum (Dujardin) Stein	10	E	Cosmopolitan, except Antarctica
Euglena sp.	4	E	Europe, India, New Zealand
E. acus Ehrenberg	3	E	Italy, Russia, USA
E. deses Ehrenberg	3	E	Europe, S. Africa
E. elongata Schewiakoff	1	E	Italy
E. gracilis Klebs	1	E	Europe
E. intermedia Klebs	2	E	Czechoslovakia
E. limnophila Lemmermann	1	E	Italy
E. minuta Prescott	1	E	India; fields
E. oxyuris Schmarda	2	E	Italy, S. Africa
E. pisciformis Klebs	1	IS	Hungary; dung
E. polymorpha Dangeard	2	E	India; fields
E. proxima Dangeard	1	E	Hungary; forest soils
E. spirogyra Ehrenberg	1	E	S. Africa
**E. terricola* Dangeard	2	E	Rumania; fields and forests
E. velata Klebs	1	E	Germany
E. viridis Ehrenberg	6	E	Eurasia, USA, S. Africa
Eutreptia viridis Perty	4	E	Europe, USA, Java
Glenodinium sp.	2	DF	USA; forests, grasslands
G. pulvisculus (Ehrenberg) Stein	3	DF	Hungary, Poland, S. Africa
Gloeodinium montanum Klebs	1	DF	Antarctica; in mosses
Helkesimastix faecicola Woodcock	14	IS	Cosmopolitan; even saline soils
**Hemimastix amphikineta* Foissner, Blatterer & Foissner	1	IS	Australia, S. America, Germany

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
**Herpetomonas terricolae* Fantham	1	K	S. Africa; nomen nudum?
Heteromita sp. (see also *Bodo*)	4	IS	England, India, Antarctica
H. globosa (Stein)	40	IS	Cosmopolitan; in saline soils
Heteronema sp.	1	E	Russia
H. acus (Ehrenberg) Stein	6	E	Europe, Russia, USA
Hexamita inflata Dujardin	6	DM	Europe, Greenland, USA
Hyalogonium klebsii Pascher	1	C	Italy
Lagenoeca globulosa Francé	2	CO	Germany, Algeria, even Sahara
Leptomonas jaculum (Léger) Lemmermann	1	K	Germany; forests
Mallomonas sp.	2	CH	Rumania, USA
Mastigamoeba sp.	13	RM	Eurasia, USA, Greenland, S. Africa
M. aspera Schulze	1	RM	Hungary; forests
M. invertens Klebs	7	RM	Eurasia, Algeria, even Sahara
M. limax Moroff	16	RM	Europe, USA, Mexico, Java, Algeria
M. longifilum Stokes	2	RM	USA, Alaska
**M. minuta* R. & L. Grandori	3	RM	Italy, Hungary
M. reptans Stokes	3	RM	Germany, USA, Algeria
Mastigella sp.	2	RM	Czechoslovakia, Russia
M. commutans (Meyer) Goldschmidt	6	RM	Europe, Russia, Algeria
**M. mutabilis* R. & L. Grandori	3	RM	Italy, Hungary
M. nitens Penard	1	RM	Algeria, even Sahara
M. penardii Lemmermann	3	RM	Germany, Hungary, Algeria
M. polyvacuolata (Moroff) Goldschmidt	1	RM	Algeria, even Sahara desert
M. radicula (Moroff) Goldschmidt	5	RM	Germany, Russia, Algeria
M. simplex Kent	1	RM	USA; litter
M. vitrea Goldschmidt	1	RM	Algeria, even Sahara desert
Menoidium incurvum (Fresenius) Klebs	2	E	USA, S. America
Monas sp.	12	CH	Eurasia, USA, Antarctica
M. amoebina Meyer	1	CH	Algeria, even Sahara desert
M. arhabdomonas (Fisch) Meyer	15	CH	Eurasia, Algeria, Java
M. elongata (Stokes) Lemmermann	4	CH	Eurasia, USA
M. dangeardii Lemmermann	2	CH	Italy, Hungary
M. guttula Ehrenberg	20	CH	Cosmopolitan, except Antarctica
M. minima Meyer	8	CH	Eurasia, USA
M. obliqua Schewiakoff	2	CH	Russia, Java
M. socialis (Kent) Lemmermann	11	CH	Europe, Russia, USA
M. sociabilis Meyer	2	CH	Russia, Bulgaria
M. vivipara Ehrenberg	17	CH	Europe, Russia, Algeria, USA, Java

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
M. vulgaris (Cienkowski) Senn	11	CH	Eurasia, Africa, even Sahara
Monosiga sp.	1	CO	Hungary
M. brevipes Kent	1	CO	Hungary; fields
M. gracilis Kent	1	CO	Hungary; fields
M. ovata Kent	6	CO	Cosmopolitan, except Antarctica
Multicilia lacustris Lauterborn	6	IS	Europe, Algeria, even Sahara
M. palustris Penard	2	IS	Germany, Algeria, even Sahara
Nephrochloris incerta Geitler & Gimesi	1	HM	Mexico
Notosolenus orbicularis Stokes	3	E	USA; forests and grasslands
Ochromonas crenata Klebs	1	CH	USA
O. mutabilis Klebs	3	CH	Sweden, Hungary, Mexico
O. variabilis Meyer	1	CH	Europe
Oikomonas sp.	11	CH	Eurasia, USA
O. dallingeri Kent	1	CH	USA
O. granulata Yakimoff *et al.*	2	CH	Asia
O. mutabilis Kent	26	CH	Cosmopolitan; in saline soils
O. obliqua Kent	1	CH	Hungary; dung
O. quadrata Kent	3	CH	Germany, Algeria, even Sahara
O. rostrata Kent	5	CH	Europe, Russia
O. socialis Moroff	9	CH	Europe, Russia
O. steinii Kent	6	CH	Eurasia, USA, S. Africa
O. termo (Ehrenberg) Kent	63	CH	Cosmopolitan; in saline soils
Ophidomonas sp.	1	O	England; now a sulphur bacterium
Pandorina morum (Müller) Bory	1	C	Poland; fields
Parapolytoma sp.	1	C	USA; fields
**P. satura* Jameson	1	C	USA; garden soil
Paratetramitus jugosus (Page)	1	HA	Scotland
Peranema sp.	2	E	Czechoslovakia, Russia
P. granulifera Penard	3	E	Czechoslovakia; forests
P. trichophorum (Ehrenberg) Stein	13	E	Cosmopolitan, except Antarctica
Petalomonas sp.	4	E	Europe, USA
P. abscissa (Dujardin) Stein	1	E	Sweden; garden soil
P. angusta (Klebs) Lemmermann	7	E	Europe, USA, Antarctica
P. angusta ovalis Skvortzov	1	E	Hungary; fields
P. angusta pusilla (Klebs) Lemmermann	2	E	Czechoslovakia, Antarctica
P. mediocanellata Stein	8	E	Europe, Greenland, USA, Antarctica
P. mediocanellata disomata Stokes	3	E	Europe, Antarctica
P. m. pleurosigma Stokes	1	E	S. Africa
Phacus sp.	1	E	India

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
P. longicauda (Ehrenberg) Dujardin	5	E	Europe, USA, S. Africa, Java
P. orbicularis Hübner	1	E	Italy
P. pyrum (Ehrenberg) Stein	2	E	Russia, USA
Phalansterium sp.	1	IS	India; common
P. digitatum Stein	2	IS	Mexico
**P. solitarium* Sandon	14	IS	Cosmopolitan
Phyllomitus sp.	2	K	Spitsbergen
P. amylophagus Klebs	5	K	Europe, USA, Africa, Indonesia
P. undulans Stein	13	K	Cosmopolitan; saline soils
Physomonas sp.	1	CH	Central Asia
P. elongata Stokes	2	CH	Sweden, USA
P. socialis Kent	1	CH	Sweden; garden soil
Pleuromonas jaculans Perty	34	K	Cosmopolitan (syn. *Bodo saltans*?)
Polypseudopodius bacterioideus Puschkarew	6	CH	Europe, Antarctica
Polytoma sp.	3	C	Eurasia, S. America
**P. caudatum astigmata* R. & L. Grandori	1	C	Italy
P. cylindraceum Pascher	1	C	Italy
**P. dorsiventrale papillatum* R. & L. Grandori	1	C	Italy
**P. longistigma* R. & L. Grandori	2	C	Italy
P. minus Pascher	1	C	Hungary; fields
P. papillatum Pascher	1	C	Hungary; fields
P. spicatum Krassilstschik	1	C	Hungary; fields
P. uvella Ehrenberg	19	C	Eurasia, USA, Java, Antarctica
Proleptomonas faecicola Woodcock	7	K	Cosmopolitan
Protomonas amyli (Cienkowski) Zopf	1	IS	Poland
Prowazekia sp.	1	K	Russia
P. ninae-kohlyakimov Yakimoff	2	K	Asia
P. turkestanica Yakimoff & Zeren	1	K	Asia
Rhizomastix gracilis Alexeieff	2	IS	Europe; fields, forests
Rhodomonas sp.	1	CR	S. Africa
Rhynchomonas nasuta (Stokes) Klebs	6	K	Eurasia, Algeria, even Sahara
**Sainouron mikroteron* Sandon	10	IS	Cosmopolitan
**S. oxu* Sandon	1	IS	Spitsbergen
Salpingoeca sp.	1	CO	Hungary; fields
S. ampulla Kent	1	CO	Poland
S. amphoridium Clark	1	CO	Sweden; garden soil
S. convallaria Stein	2	CO	Poland, Java; fields, forests
S. oblonga Stein	1	CO	Hungary; fields
S. polygonatum Penard	1	CO	Hungary; fields
S. pyxidium Kent	1	CO	Algeria, even Sahara
S. urceolata Kent	1	CO	Germany; forest soil

Table 7.1 (*cont.*)

Species[a]	No. records[b]	Taxon. group[c]	Geographic distribution; remarks[d]
S. vaginicola Stein	1	CO	Germany; forest soil
Scherffelliomonas granulata Szabados	1	IS	Hungary; dung
Scytomonas pusilla Stein	27	E	Cosmopolitan; even saline soils
Sphenomonas socialis Stokes	1	E	USA
S. teres (Stein) Kleibs	1	E	Italy
Spiromonas sp.	4	IS	USA
S. angusta (Dujardin) Kent	10	IS	Cosmopolitan
Spironema multiciliatum Klebs	5	IS	Europe, S. America, Antarctica
Spondylomorum quarternarium Ehrenberg	1	C	S. Africa
Spongomonas sp.	3	IS	Cosmopolitan
S. uvella Stein	4	IS	Antarctica
Sterromonas formicina Kent	2	CH	Russia, Algeria, even Sahara
Streptomonas cordata (Perty) Klebs	1	IS	Asia
Tetramitus sp.	5	HA	Eurasia, USA
T. descissus Perty	2	HA	Germany, Algeria, even Sahara
T. pyriformis Klebs	6	HA	Eurasia, S. America, Antarctica
T. robustus Szabados	1	HA	Hungary; dung
T. rostratus Perty	20	HA	Cosmopolitan; saline soils
**T. spiralis* Goodey	13	HA	Cosmopolitan
T. sulcatus Klebs	4	HA	Italy, Hungary, Rumania
T. variabilis Stokes	2	HA	Europe, USA
Trachelomonas sp.	1	E	India; fields
T. hispida (Perty) Stein	1	E	Italy
T. obovata Stokes	3	E	Italy, Hungary, Rumania
T. volvocina Ehrenberg	4	E	Europe, USA
Trepomonas agilis communis Klebs	2	DM	Europe
Urceolus cyclostomus (Stein) Mereschkowsky	1	E	S. Africa
U. entzii Szabados	1	E	Hungary; dung

[a] Table based on about 160 papers which contain information on the numbers and kinds of flagellates present in various soils. Species marked with an asterix (*) were first described from soil. Most species are listed as reported. Many identifications are probably incorrect and there are probably many synonymies. However, these matters cannot be effectively addressed in the absence of appropriate taxonomic revisions. Names are based mainly on *Die Süsswasser-Flora Deutschlands, Österreichs und der Schweiz* (Lemmermann, Pascher), on Stein (1878), and on original descriptions.

[b] Number of records refers to papers and not to sites.

[c] Taxonomic groupings mainly according to Margulis *et al.* (1989) and Patterson and Zölffel (Chap. 26, this volume). Abbreviations: BI = bicosoecids, C = chlorophytes, CH = chrysophytes, CO = choanoflagellates, CR = cryptomonads, DF = dinoflagellates, DM = diplomonads, E = euglenids, HA = heterolobosceids, HM = heteromonads, IS = *incertae sedis*, K = kinetoplastids, O = others.

[d] 'Cosmopolitan' does not include Australia for which almost nothing is known about soil flagellates.

Several conclusions are obvious from Table 7.1.

1. The most common (≥20 records) 'species' are *Bodo caudatus* (23), *B. celer* (28), *B. edax* (34), *B. lens* (27), *B. obovatus* (22), *B. ovatus* (20), *B. saltans* (34; plus a further 34 if records for *Pleuromonas jaculans* are added), *Cercobodo agilis* (29), *C. vibrans* (21), *Cercomonas crassicauda* (44), *C. longicauda* (40), *Heteromita globosa* (40), *Monas guttula* (20), *Oikomonas mutabilis* (26), *O. termo* (63), *Pleuromonas jaculans* (34), *Scytomonas pusilla* (27), and *Tetramitus rostratus* (20). All lack chloroplasts, are bacteria feeders, and many have been assigned to the kinetoplastids. Only few isolates of flagellates from soil have been studied with modern methods, such as electron microscopy. Patterson and Zölffel (Chap. 26, this volume) consider many to have an uncertain taxonomic position, supporting my view that the soil environment has been associated with the evolution of special types or at least has favoured colonization by aberrant forms from freshwater. Some of the more unusual species are depicted in Figs 7.1–7.8; others are described by Darbyshire *et al.* (1976; *Paratetramitus jugosus*), Karpov and Zhukov (1986; fresh water strain of *Apusomonas proboscidea*), MacDonald *et al.* (1977; *Heteromita globosa*), Vickerman (1978; *Dimastigella trypaniformis*), and Vickerman *et al.* (1974; soil strain of *Apusomonas proboscidea*).

2. Of the 260 species listed, there are 55 euglenids; 40 chlorophytes; 36 chrysophytes; 34 kinetoplastids; 14 choanoflagellates; 14 rhizomastigids; 6 heteroloboseid amoebae; 4 cryptomonads; 2 dinoflagellates; 2 diplomonads; 1 bicosoecid and 1 heteromonad; 44 species are of uncertain systematic position (see Patterson and Zölffel, Chap. 26, this volume). The high number of euglenids has been not recognized previously and is remarkable. I have found that euglenids are present

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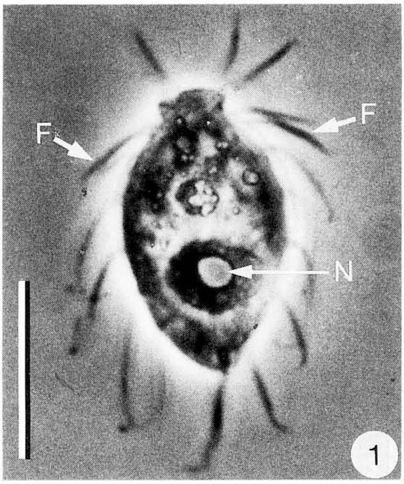
Figs 7.1–3 *Hemimastix amphikineta*, an enigmatic species and sole member of the phylum Hemimastigophora; pellicle structure suggests some relationship with the euglenids. (1) Silver carbonate impregnated specimen in phase-contrast. Bar = 10 μm. (2) Electron micrograph showing conspicuous membranous sac posterior to the basal body. Bar = 200 nm. (3) Electron micrograph showing a longitudinally sectioned kinetid. The small arrows point to the transitional plate which extends to the ciliary membrane. The short thick arrows mark the transitional fibres which are anchored slightly above the proximal end of the basal body. Note the absence of the epiplasm (EP) in the microtubule furrow. Bar = 500 nm. Abbreviations: DB = dense body, EP = epiplasm, F = flagellum, flagellar row, FV = food vacuole, G = granular substance, GO = Golgi apparatus, LM = longitudinal microtubules, LR = long microtubular ribbon connecting kinetids within the kinety, MF = microtubule furrow, M1, M2, M3 = subpellicular microtubule groups, MI = mitrochondrion, MN = micronemes, MP = micropores, MR = microtubule ring mediating contact between host and parasite, N = nucleus, NF = naked furrow, i.e. without microtubules, PE = pellicle of the ciliate, R = ridge between and around the flagella, S = membranous sac, SR = short microtubular ribbon.


F
F
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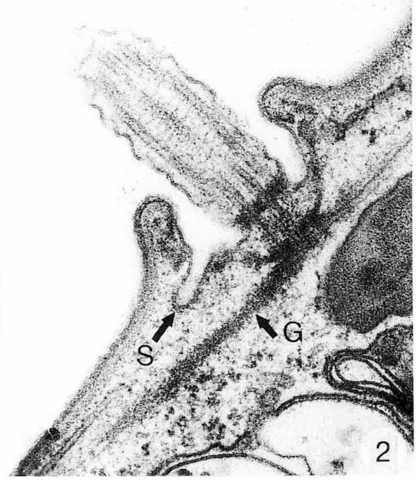
1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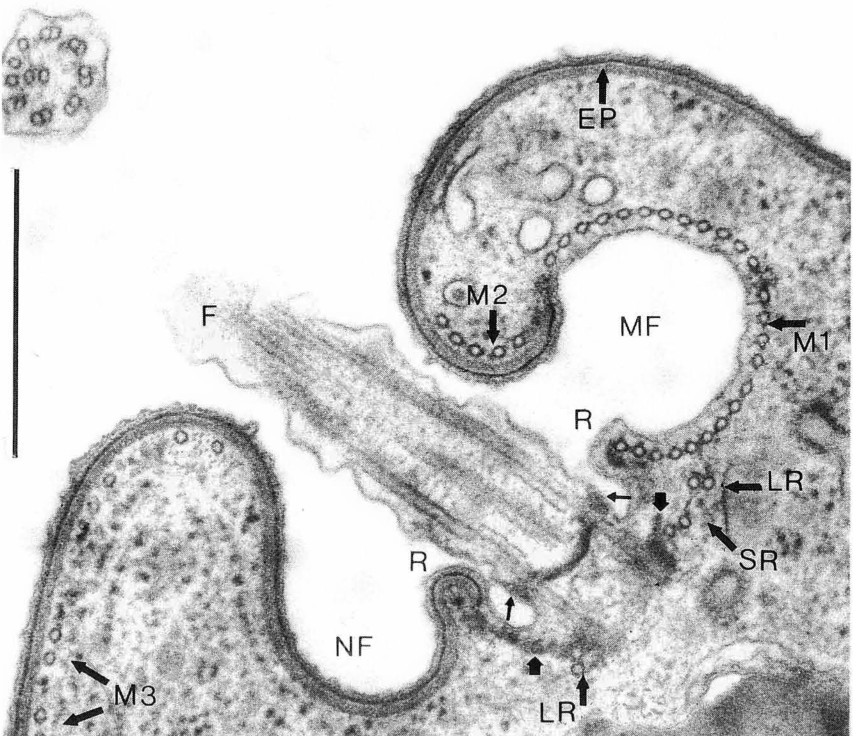
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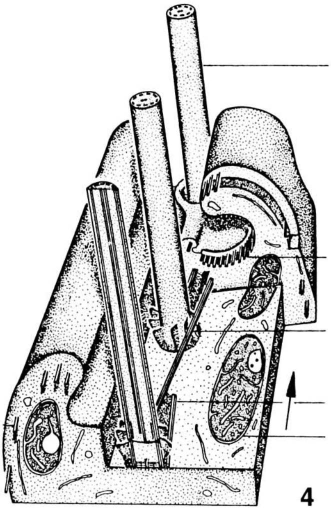

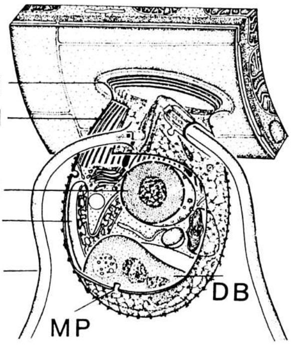

Figs 7.4–7.5 Reconstruction of pellicular and subpellicular organization of *Hemimastix amphikineta* (4) and *Colpodella gonderi* (5) (from Foissner and Foissner 1984 and Foissner *et al.* 1988). See Figs 7.1–3 for abbreviations.

in almost every soil sample, whereas dinoflagellates are extremely rare.

3. Most of the species recorded were originally described from freshwater habitats. Only 27 taxa have been recorded first from soil. This would suggest that most soil flagellates are invaders from freshwater. As with soil ciliates (Foissner 1987) it is reasonable to assume that some or even many of the soil flagellates are new species and only superficially resemble those found in freshwater. Most identifications were made by workers whose prime interest was ecology and not taxonomy.

4. Most of the 260 species have been recorded less than 10 times. This should not be interpreted as an indication of a restricted geographic distribution but probably reflects a lack of appropriate culti-

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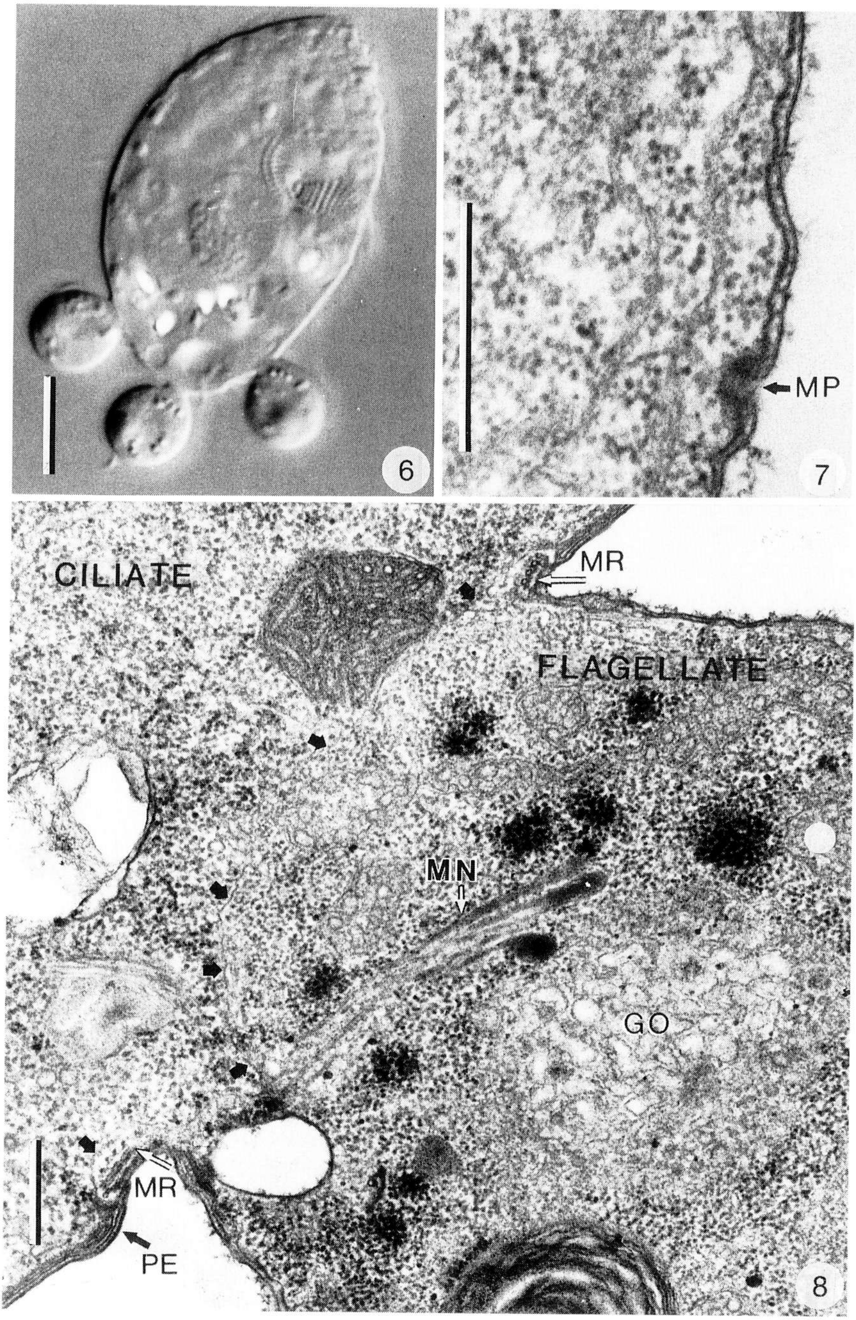
Figs 7.6–7.8 *Colpodella* (formerly *Spiromonas*) *gonderi*, a species related to the apicomplexan sporozoa because of the common presence of a three-layered pellicle with micropores and an apical complex with micronemes (from Foissner and Foissner 1984). (6) Interference contrast light micrograph of a *Colpoda steinii* parasitized by three *Colpodella gonderi*. Bar = 10 μm. (7) Electron micrograph of the pellicle with a micropore (MP). Bar = 400 nm. (8) Electron micrograph showing the parasite (flagellate) attached to the host's (ciliate) pellicle by a ring of microtubules (MR). The arrows mark the membrane which separates the parasite from the host. Bar = 400 nm. See Figs 7.1–3 for abbreviations.


6
MP
7
CILIATE
MR
FLAGELLATE
MN
GO
MR
PE
8

vation and identification methods. Some species, as with ciliates and testate amoebae (Foissner 1987), may have a restricted Laurasian or Gondwanian distribution (Foissner *et al.* 1988).

Ecology of soil flagellates

1. Individual number, biomass, and annual production

Flagellates are present in almost every soil, even in deserts and Antarctic environments (Varga 1936; Smith 1978). Hattori (1988) isolated flagellates from 80 per cent of 1–2 mm sized soil aggregates. In spite of this, their ecology has been poorly explored. There is a large bulk of available data about numbers in various soils of the world (e.g. Heal 1971). Most data, however, are based not on direct counts in fresh soil samples but on culture methods which are inappropriate for estimating the number of active cells (Bodenheimer and Reich 1933; Foissner 1987).

Direct counting methods, which were widely used before the culture techniques (e.g. Cutler and Crump 1935), indicate relatively few active soil flagellates, usually less than 10^4 g^{-1} of soil (e.g. Martin and Lewin 1915; Koch 1916). The direct counting technique of Lüftenegger *et al.* (1988) gives 2000–10 000 active flagellates g^{-1} dry mass (i.e. about $7–30 \times 10^6$ cells m^{-2} = 3–12 mg protozoan dry mass) in the litter layer of a spruce forest (Fig. 7.9). Culture techniques yield much higher abundances, usually more than 10^5 cells g^{-1} of soil (e.g. Cutler and Crump 1935; Bamforth and Peláez 1977; Persson *et al.* 1980) because trophic and cystic cells cannot be separated properly (Foissner 1987). There is strong evidence that flagellates are suppressed by soil microbiostasis in evolved soils (Foissner 1987) because the number of active cells markedly decreases with increasing fermentation of the litter (Rosa 1957; Szabó *et al.* 1964). Despite the high number of flagellates in many soils, the proportion that is active is unknown. The data from direct counts suggest that most are in an inactive encysted condition, as is true for ciliates and bacteria.

The problems inherent to the culture methods are possibly the reason for difficulties in correlating abundance with environmental factors (Cutler and Crump 1935) or why in watered litter fewer (or even no) active flagellates were recorded than in dry litter (Parker *et al.* 1984).

Meisterfeld (1989) found 1.6×10^9 cells m^{-2} (8.3×10^7–18.9×10^9) in the upper (0–3 cm) and 1.2×10^9 cells m^{-2} (6.1×10^7–7.3×10^9) in the lower (3–6 cm) litter and soil layer of a beech forest in Germany. Biomass and annual production were low when compared with those of the naked and testate amoebae, due to very small

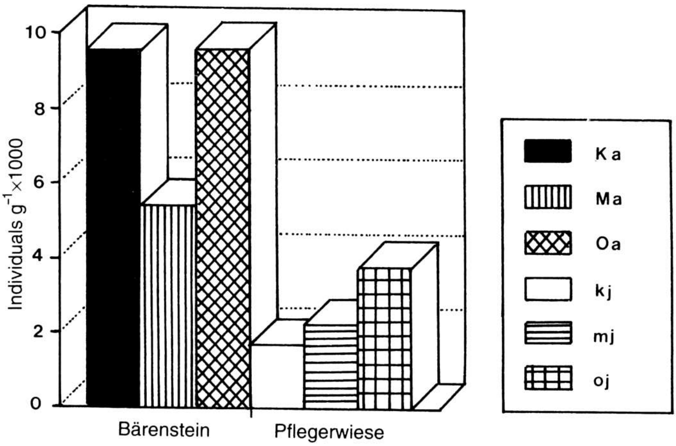


Fig. 7.9 Number (individuals g^{-1} dry mass of litter) of active flagellates in the litter layer (0–3 cm) of an old (80 years; Bärenstein) and a young (40 years; Pflegerwiese) spruce forest stand in Upper Austria (from Aescht and Foissner, unpublished observations). Counts by the direct method of Lüftenegger *et al.* (1988). Ka, kj = control plots; Ma, mj = fertilized plots (magnesite plus 10% dried fungal biomass); Oa, oj = fertilized plots (dried bacterial biomass from sewage plant). Differences between stands are significant, those between variants are not.

size of the flagellates (Fig. 7.10). The number (40×10^6 individuals m^{-2}) and biomass (16 mg dry mass m^{-2}) estimated by Persson *et al.* (1980) in a Swedish pine forest are similar to our data (see above) although they were obtained with a culture method. Davis (1981) calculated 1.5 mg (0.8–2.5) flagellate dry mass in Antarctic moss communities, which is much less than in the sites mentioned above, possibly due to the unfavourable environmental conditions.

The influence of natural and human activities on the number of soil protozoa, including flagellates, is reviewed elsewhere (Foissner 1987).

2. *Adaptations and autecological studies*

No special morphological or physiological adaptations have been reported for soil flagellates. Data on food selection in *Cercomonas crassicauda* and the generation times of *Oikomonas termo* and *Heteromita globosa* are to be found in Singh (1942), Cutler and Crump (1935), and Hughes and Smith (1989), respectively. Recently, Hughes and Smith (1989) found that an Antarctic isolate of *Heteromita globosa* is subject to *a*(adversity)-selection. This is an extreme form of *r*-selection, ensuring survival during diurnal freeze–thaw cycles and optimal utilization of resources during short periods of favourable conditions.

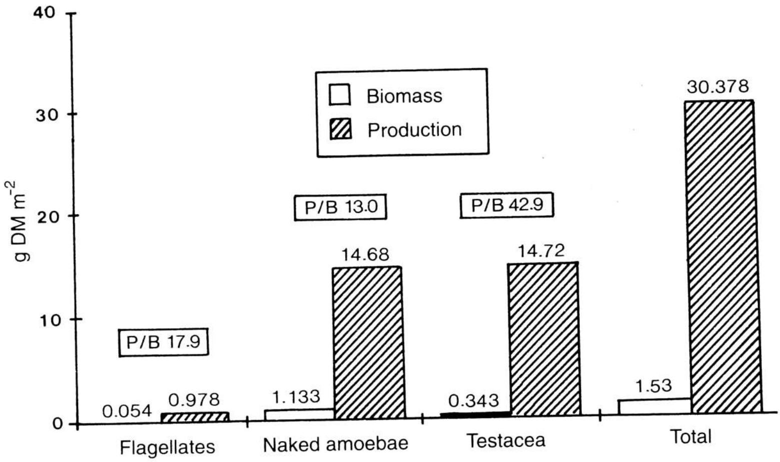


Fig. 7.10 Average biomass, annual production, and P/B quotient (biomass turnover) of the protozoa in a submontane beech forest in Germany (from Meisterfeld 1989). DM = dry mass of protozoa.

Generally, small size (most <20 μm) and amoeboid flexibility allow flagellates to inhabit even the small soil pores which cannot be exploited by most other protozoa nor of course by metazoa. I agree with Bamforth (1988) that there is a protozoan domain in the smaller pore spaces and a protozoa–nematode domain in the larger ones.

As with other soil protozoa, flagellates form resting cysts which withstand desiccation. Goodey (1914) reanimated *Monas termo, Cercomonas crassicauda, C. longicauda, Bodo saltans, Tetramitus spiralis,* and *Spironema multiciliatum* from dried soils which had been stored for 50 years. Varga (1961), however, could reanimate only a few species (*Monas vulgaris, Bodo celer, B. edax, Scytomonas pusilla*) from a litter sample stored for 8 years. Cysts in moist soil have a lower temperature (up to 50 °C) tolerance than those in soils which were air-dried for several months (up to 80 °C) (Bodenheimer 1935).

3. *Enrichment and isolation*

A simple but effective means for estimating species richness is the non-flooded petri dish method as described by Foissner (1987). It involves placing 10–50 g of a fresh or (better) air-dried litter or soil sample in a petri dish (10–15 cm diameter) and saturating but not flooding with distilled water (note: material must not be flooded; water should be added to the sample until 5–20 ml will drain off when the petri dish is tilted and the soil is gently pressed with a finger; this run-off contains the protozoa and can be used for further investigations). Usually, inspection of the cultures on days 2, 6, 10, 14, and 20 is sufficient.

Individual cells can be isolated from such cultures with micropipettes and cultivated in appropriate media, many of which are described in Varga (1934), Margulis *et al.* (1989), and Cowling (Chap. 27, this volume).

Summary and future needs

Soil flagellates have been largely ignored by taxonomists and ecologists. About 260 species have been recorded from soils world-wide. Twenty seven species were originally described from soil, the others were first found in limnetic or coprozooic biotopes. However, most of the records and taxonomic work on soil flagellates have been produced by workers not specially trained in these fields. Species lists are highly questionable. There is an urgent need for improved taxonomic skills in this area. The 'species' most commonly reported are the kinetoplastids *Bodo caudatus, B. celer, B. edax, B. saltans, B. lens*, and *Pleuromonas jaculans*; the cercomonads *Heteromita globosa, Cercobodo agilis, Cercomonas crassicauda*, and *C. longicauda*; the chrysomonads *Oikomonas mutabilis* and *O. termo*; and the euglenid *Scytomonas pusilla.* These taxa need especially urgent attention as their abundance suggests they are ideal candidates for autecological studies. Detailed ecological literature on soil flagellates is sparse. Although numbers between 0 and 10^6 per g of soil have been reported, most counts rely on culture techniques which do not give an accurate indication of the active cells present. Future work should include estimates of numbers with direct counting methods and estimates of annual production in representative ecosystems.

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