FIFTEEN

Phylum CERCOZOA

cercomonads, filose testate amoebae, Phaeodaria, plasmodiophoras, *Gromia*, haplosporidans, and kin

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ercozoa means 'tailed animals' and alludes to the locomotory cilium in many of the species. The phylum is extremely morphologically diverse, encompassing ancestrally biciliate 'zooflagellates', euglyphid and other filose testate amoebae, shelled phaeodarians (which used to be classified as radiolarians), phytomyxean plant parasites like *Plasmodiophora*, the invertebrateparasitic Acetosporea, and *Gromia*. In contrast with the parasitic forms, the freeliving cercozoan zooflagellates have been very little studied, even though some of them, like the cercomonads, are the most uniquitous flagellates in soil and important predators of bacteria in virtually all aquatic habitats (Cavalier-Smith & Chao 2003; Bass & Cavalier-Smith 2004; Karpov et al. 2006). The groups that currently make up the Cercozoa used to be distributed among several protozoan phyla, and even in the fungi in the case of the plasmodiophoras.

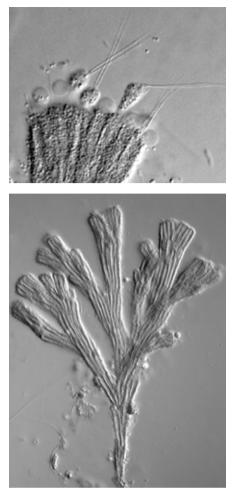
Partly synonymous with the former Rhizopoda, the phylum Cercozoa was the first major eukaryote group to be recognised primarily as a result of molecular-phylogenetic analyses. Until recently, the phylum suffered from a corresponding lack of shared ultrastructural characters (Cavalier-Smith & Chao 2003; Hoppenrath & Leander 2006a; Adl et al. 2005; Simpson & Patterson 2006), but Cavalier-Smith et al. (2008) discovered two unusual structures in the transitional region (the most proximal part) of the cilium, comprising shared derived features (synapomorphies) for the phylum. Leander (2008) has remarked on the remarkable degree of convergent evolution that exists among microbial eukaryotes. Whether they live in planktonic environments, interstitial environments, or the intestines of animal hosts, protozoans and microbial chromists from several different phyla can superficially resemble each other in quite striking ways. As indicated above, such is the case among the many cercozoan taxa that morphologically resemble species of Euglenozoa, Amoebozoa, Ochrophyta, Bigyra, Foraminifera, Radiozoa, and Heliozoa, among others. At its core, Cercozoa comprises a group of soft-bodied free-living phagotrophs with two pervasive but not universal properties - the propensity to glide on surfaces by a posterior cilium and/or to protrude slender pseudopodia (filopodia), often branching (rhizopodia) and sometimes anastomosing as a net (undulipodia).

The classification of the phylum used here is a combination of that proposed by Cavalier-Smith and Chao (2003), Bass et al. (2009), and Howe et al. (2011), comprising two subphyla and eleven classes, not all of which have been found in New Zealand. Subphylum Filosa, in part representing the old taxon Zooflagellata, includes naked and shelled, ciliated and filopodial, free-living forms; subphylum



Two individuals of *Cercomonas paravarians* (Cercomonadida). David Bass, University of Oxford

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A whole colony and close-up of a branch tip of the freshwater cercozoan *Rhidipodendron splendidum* (Spongomonadida). William Bourland, per Micro*scope (MBL)

Endomyxa includes mostly parasitic forms. Filosa was introduced by Cavalier-Smith and Chao (2003) with varied diagnostic characters depending largely on the form and locomotion of the cell. Endomyxa (from the Greek *endo-*, within, and *myx-*, slime), was coined by Cavalier-Smith (2002)"because they are typically plasmodial endoparasites of other eukaryotes."

The New Zealand cercozoan fauna comprises only 83 species and is patchily known, with some groups better studied than others.

Subphylum Filosa

Class Granofilosea is possibly represented by the semi-cosmopolitan marine epizoite *Wagnerella borealis*, although its precise affinities are still unknown. It has been traditionally classified in the Heliozoa. Bass et al. (2009) suggested that the genus"may, like desmothoracids, turn out to granofilosean."It is a tiny stalked protist with a spherical 'head' from which project radiating spicules. It was first recorded in New Zealand waters on the tubes of a spirorbine polychaete (Dons 1921; Dawson 1992).

Records of class Sarcomonadea in New Zealand are few, even though its species include the dominant flagellates of soils, including members of the orders Cercomonadida and the recently recognised Glissomonadida (Howe et al. 2009). Maskell (1887) described Cercomonas grandis from unnamed freshwater localities in the Wellington region. The species seems not to have been reported in New Zealand since, but Myl'nikov and Karpov (2004) included it in a global list of Cercomonas species. Subsequently, Cavalier-Smith and Karpov (in press) have changed it to Neocercomonas. Karpov et al. (2006) sequenced and provisionally illustrated two unnamed species of Cercomonadidae (New Zealand localities not noted), including one in the newly circumscribed genus Paracercomonas. These, and two additional species, were formally described by Bass et al. (2009b). Maskell (1887) also recorded the enigmatic flagellate then known as Heteromita *lens*, subsequently designated by Patterson and Zölffel (1992) as the type species of their new genus Kamera. The affinities of Kamera lens are entirely unknown but this widespread species is listed at the end of the Cercozoa checklist so that it is not overlooked.

Taxon	Described species + subspecies	Known undescribed/ undeter- mined species	unknown species	Adventive species	Endemic species	Endemic genera
Filosa	67+2	1+1	120	0	6?	0
Chlorarachnea	0	0	2	0	0	0
Granofilosea	1	0	20	0	0	0
Sarcomonadea	5	0	50	0	2?	0
Metromonadea	0	0	4	0	0	0
Thecofilosea	18	1	14	0	3	0
Imbricatea	38+2	0+1	22	0	0	0
Incertae sedis	5	0	8	0	1	0
Endomyxa	13	2	15	9?	4	0
Proteomyxidea	1	0	7	0	0	0
Phytomyxea	9	0	2	9?	0	0
Gromiidea	1	0	1	0	0	0
Ascetosporea	2	2	5	0	4	0
Incertae sedis	1	0	0	0	0	0
Totals	80+2	3+1	135	9?	10?	0

Summary of New Zealand living cercozoan diversity

PHYLUM CERCOZOA

Members of class Thecofilosea comprise cells that are surrounded by a flexible secreted covering (tectum) or a rigid test with one or two apertures through which hyaline filopodia emerge. These pseudopodia fold like a jackknife when retracted. The best-known examples, in the order Tectofilosida, are such genera as Amphitrema and Pseudodifflugia, and the family Chlamydophrvidae with a flexible membrane (not yet found in New Zealand). In contrast, members of the order Euglyphida (class Imbricatea) have a rigid test of overlapping silica scales (for classification, see Meisterfeld 2000). Members of these two testate orders resemble the testate lobose amoebae of the protozoan phylum Amoebozoa, and the general comments on the ecology and history of discovery of testate amoebae given in the Amoebozoa chapter (Chapter 7) apply here. Testate amoebae with filopodia have been studied using molecular methods (Bhattacharva et al. 1995; Burki et al. 2002; Wylezich et al. 2002). Available evidence suggests that the ability to build a test emerged at least three times during evolution among the Cercozoa (Pseudodifflugia, Euglyphida, and Gromia). The sequence data of Wylezich et al. (2002), based on several genera, show that Euglyphida is monophyletic and the euglyphid testate amoebae form a sister group to flagellates like Cercomonas. The siliceous body-plates are considered to be homologous in all Euglyphida.

Phaeodarians also feature silica in the test. The group is solely marine and used to be classified among the radiolarians (phylum Radiozoa) (Bass et al. 2005) but a recent molecular study of protein genes squarely places phaeodarians in the Cercozoa (Polet et al. 2004). Along with silica, the phaeodarian test also incorporates organic matter and there can be traces of other minerals. There is a central capsule housing the nucleus as in radiolarians, but this is thicker and has a single major opening (the astropylum, a complicated type of cytopharynx), usually with two smaller openings (parapylae) at the opposite pole. The astropylum tends to be cone-like and connects the central capsule with the outer, extracapsular, test. Prey organisms are captured by spine-supported axopodia and the filopodial extensions of the cytoplasm, ingested through the astropylum, and digested outside or inside the central capsule. Another characteristic feature of phaeodarians is the presence of a phaeodium, which consists of darkly pigmented waste products, usually in the region of the astropylum.

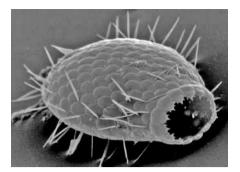
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Taxon	Marine	Freshwater [†]	Terrestrial ⁺	Fossil		
Filosa	14	49+2	30+3	3		
Chlorarachnea	0	0	0	0		
Granofilosea	1	0	0	0		
Sarcomonadea	0	1	4	0		
Metromonadea	0	0	0	0		
Thecofilosea	11	8	0	3		
Imbricatea	3	35+2	26+3	0		
Incertae sedis	0	5	0	0		
Endomyxia	6	3	7	0		
Proteomyxidea	0	1	1	0		
Phytomyxea	1	2	6	0		
Gromiidea	1	0	0	0		
Ascetosporea	4	0	0	0		
Incertae sedis	0	1	0	0		
Totals	20	53+2	37+3	3		

Summary of New Zealand cercozoan diversity by environment

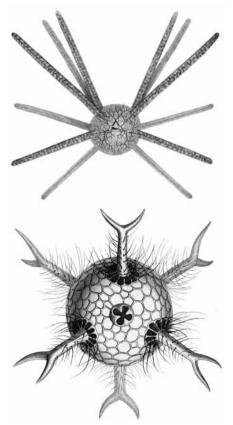
[†] Some species can occur in more than one environment, reflected in the tabulation. Hence total

numbers across all environments will exceed the overall species tally in the previous table.

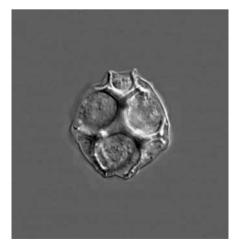
* This is taken to be the environment of the major host in the case of parasitic species.



A soil-testate cercozoan, *Euglypha strigosa* (Euglyphida). Ralf Meisterfeld



Two phaeodarians from marine plankton – *Coelothauma duodenum* (Phaeodendrida) (upper) and *Circospathis sexfurca* (Phaeocalpida). From Haeckel 1887



Ebria tripartita (Ebriida). David Patterson, per Micro*scope (MBL)

Despite the siliceous test in many species, there are only sparse records of phaeodarians in Recent sediments. A number have no skeleton at all, or have one represented by loose spines. When a complete skeleton is developed, its bars are hollow (rather than solid as in polycystine radiolarians), and its silica is supported by an organic matrix, for which reason phaeodarians are rarely found in sediments. Even so, the Southwest Pacific is one of very few regions where fossil phaeodarians have been recovered – initially in Neogene sediments in the north Tasman Sea (Dumitrica 1973) and, more recently, in Late Cretaceous sediments from DSDP site 275, with three species found (Dumitrica & Hollis 2004). This discovery was highly significant as these species comprise some of the earliest-known phaeodarians. Nine living species have been reported in the seas around New Zealand (Haeckel 1887; Tibbs & Tibbs 1986; Dawson 1992).

A single species of cryomonad is known in New Zealand waters – *Protaspa* (formerly *Protaspis*) *tanyopsis*, found only once, off Curtis Island on the Kermadec Ridge (Norris 1961).

Ebriids (ebridians) have an internal skeleton of silica and, not surprisingly, have a good fossil record, but there are only two monotypic genera. The group has long defied precise classification and suggested relationships have linked them to silicoflagellates, dinoflagellates, and radiolarians among others, or simply as incertae sedis. Thus ebriid affinities seemed to be with any of three major chromistan groups – rhizarians, heterokonts, or alveolates. Phylogenetic analysis of ribosomal DNA sequences have recently demonstrated unequivocally that ebriids belong to the Cercozoa, close to the cryomonads (Hoppenrath & Leander 2006b).

The better-known of the two living species is *Ebria tripartita*, in which the skeleton has three branches. Cells are phagotrophic and range from 25 to 40 micrometres in length. The cilia, which are inserted in the cell near the apex, are hard to see. The name *Ebria*, from the Latin *ebrius*, inebriated, alludes to the distinctive swimming mode. *Ebria tripartita* is widespread in coastal waters of the world and is of ecological interest because cell concentrations can occasionally reach high numbers, making it a significant grazer of phytoplankton, especially nannoplanktonic diatoms and also dinoflagellates. It was reported in New Zealand waters by Cassie (1961) in the Hauraki Gulf, but is also known from the Eocene Oamaru diatomite (Mandra et al. 1973; Dawson 1992).

More problematic but probably also belonging to the Thecofilosea is the Pompholyxophryidae. Traditionally classified among the Heliozoa, members of this family have spherical cells with not only finely radiating axopodal spines but a variety of siliceous elements that cover the cell surface. In *Pompholyxophrys* they are spherical. These structures are diagnostic of species but are so tiny they must be viewed using electron microscopy. Nichols and Dürrschmidt (1985) reported three species in New Zealand lakes and ponds where they feed on algae and detritus.

Class Imbricatea is represented in New Zealand not only by the Euglyphida (above) but also order Spongomonadida, comprising two genera of colonial freshwater flagellates whose cells are embedded in granular mucus (Maskell 1886, 1887). Colonies are fan-shaped in species of *Rhipidodendron* and globular or cylindrical in *Spongomonas*. These genera have defied precise classification in the past.

Subphylum Endomyxa

Endomyxa includes two classes of free-living, often predatory, amoeboid forms and two classes of obligate parasites. Class Proteomyxidea in New Zealand is exemplified by *Biomyxa vagans*, found in mosses or wet grassland soils (Stout 1962, 1984). Superficially, this species resembles a naked foraminiferan, and putative relatives resemble slime moulds. Highly mobile and changeable, its filopodia branch and anastomose.

Species of class Phytomyxea live as endobiotic parasites in a wide range of organisms including flowering plants, brown algae, diatoms and oomycetes. In New Zealand, there are nine species in seven genera, of which the best-known is *Plasmodiophora brassicae*, which causes club root of crucifers. The disease manifests itself when roots of cabbages and other brassicas become grossly swollen. The infectious stage of the organism is biciliate zoospores that penetrate host root hairs and develop into microscopic multinucleate plasmodia. Each plasmodium forms sporangia that produce either swimming zoospores or aggregations of thick-walled cysts. These can persist in the soil and, when conditions are right, germinate into a zoospore. Several races of this pathogen have been reported from New Zealand (Lammerink 1965). Similarly adventive *Plasmodiophora eleagni* infects exotic *Eleagnus*.

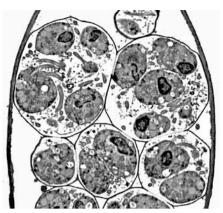
Other plasmodiophorids in New Zealand infect a range of hosts. *Ligniera pilorum* attacks perennial ryegrass *Lolium perenne*, a significant component of winter pasture that is also useful in erosion control. *Polymyxa graminis* infects wheat and *Sorosphaera veronicae* attacks introduced *Veronica*. *Spongospora sub-terranea* causes powdery scab of potatoes, but can also serve as a vector for viruses and much research has gone into investigating methods of chemical control (e.g. Falloon et al. 1996). Species of *Woronina*, unusually, infect chromistans. *Woronina polycytis* attacks mycelia of the water-mould *Saprolegnia* and *W. pythii* the potato-blight organism *Pythium*.

Tetramyxa parasitica is a widespread plasmodiophorid of marine and brackishwater angiosperms in different parts of the world. In New Zealand it has been found infecting *Ruppia megacarpa* in South Canterbury (Karling 1968). It is likely that other marine phytomyxids occur in New Zealand. For example, Maier et al. (2000) discovered that their new phytomyxid *Maullinia ectocarpii*, found to infect the filamentous brown alga *Ectocarpus siliculosus* in Chile, was capable of infecting a laboratory culture of the same species from New Zealand as well as New Zealand *Acinetospora crinita*. While *M. ectocarpii* has not yet been found in New Zealand, it has been found in southeastern Australia (Neuhauser et al. 2011). These authors suspect that a phytomyxid may be capable of transmitting viruses in brown algae, such as the virus that causes epidemic die-back in the kelp *Ecklonia radiata*.

Class Gromiidea comprises free-living, mostly marine forms. The bestknown example is cosmopolitan *Gromia oviformis*. It is relatively large, achieving five millimetres in diameter (two millimetres is common), and thus quite visible to the naked eye. It has an organic test, but, unlike other testate cercozoans, and the testate lobose amoebozoans, the cell body is multinucleate and hence plasmodial, as in other Endomyxa. It is common in New Zealand in the intertidal zone, under rocks, in *Corallina* turf, or associated with kelp holdfasts, but it can be found at shelf depths and also in muddy and sandy sediments (Hedley 1962; Hedley & Bertaud 1962; Hedley et al. 1967). Stout (1984) even found individuals in seasonally flooded grassland five metres above sea level at Castlepoint on the southeast coast of North Island. Salinity was nil and the overall protozoan fauna was a mixture of soil and freshwater forms. Hedley (1962) wondered if more than one species is represented in the marine environment, and the form encountered by Stout (1984), tolerating fresh water, highlights the extraordinary range of environments in which *Gromia* is found.

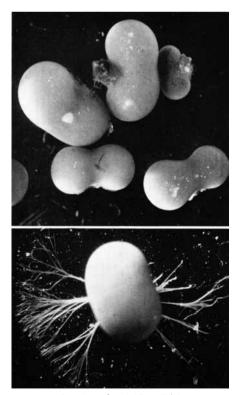
In marine habitats, small individuals tend to be spherical, whereas large individuals are kidney-shaped or bilobed, or even quite irregular. The test is muddy-brown and shiny. Branching filose pseudopodia radiate across the substratum either side of the aperture for a distance equivalent to test diameter. When *Gromia* is about to reproduce, numerous small nuclei, each with associated cytoplasm, differentiate in the upper part of the test into a creamy layer of uniciliate zoospores that are subsequently released.

Class Ascetoporea comprises mostly molluscan parasites. There are four orders, only one of which, Haplosporida (phylum Haplosporidia in some



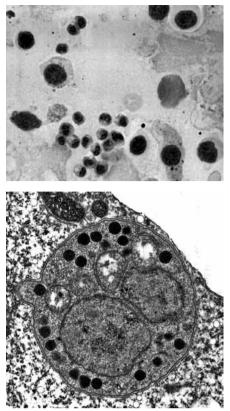
Transmission electron micrograph of secondary zoospores of *Plasmiodophora brassicae* (Plasmodiophorida) in a root hair of Chinese cabbage.

Plasmodiophorid Home Page [www.ohio.edu/people/braselto/ plasmos/], courtesy of James P. Braselton, University of Ohio



Gromia oviformis (Gromiida). From Hedley et al. 1967

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Bonamia exitiosa (Haplosporida) in the tissues of Bluff oyster Ostrea chilensis. Upper, a stained preparation showing a cluster of cells at bottom with uninfected blood cells elsewhere in the field. Lower, a binucleate cell of Bonamia with numerous haplosporosomes of unknown function.

Benjamin K. Diggles and P. Michael Hine

treatments), has so far been recorded in New Zealand. Haplosporidans are histozoic (inhabiting tissues) or coelozoic (inhabiting the digestive canal). Their cells contain organelles called haplosporosomes - spherical or vermiform, electron-dense structures with an outer bounding membrane and a separate interior membrane. The function of the haplosporosomes is unknown. The best-known haplosporidan in New Zealand is Bonamia exitiosa, the cause of bonamiosis in the Bluff oyster Ostrea chilensis (see Cranfield et al. 2005) Although first recognised in New Zealand in 1986, the causative organism was not formally named until 15 years later (Hine et al. 2001; Berthe & Hine 2004). It is a tiny (2-3 micrometres diameter) intracellular parasite of oyster haemocytes (blood cells) and is transmitted directly, from oyster to oyster. When Bonamia enters an uninfected ovster, the haemocytes recognise it as foreign and engulf it. Once inside the haemocyte, Bonamia feeds on the cytoplasm of the cell and grows, dividing many times until up to 24 parasites may be found in one haemocyte. When the cell bursts, the released parasites are engulfed by other haemocytes, carrying on the cycle. The oyster stops producing eggs or sperm and instead puts energy into producing more haemocytes, further favouring the parasite. Eventually the oyster dies of exhaustion. Bonamia exitiosa appears to have an annual pattern of infection. In Foveaux Strait it is usually hard to detect in late winter/early spring, and numbers usually increase with the spawning of predominantly male oysters in November-January (Hine 1991). However, B. exitiosa appears to rely heavily on the lipid reserves in oyster eggs, and it is during absorption of unspawned eggs, in the 25% of female oysters that do not spawn, that it uses host lipid and reaches its highest levels (Diggles et al. 2002a). A second Bonamia-like organism has since been found in Foveaux Strait oysters (P. M. Hine & B. K. Diggles pers. obs.). The phylogenetic relationships of Bonamia have exercised researchers for some time. The work of Carnegie et al. (2000) and Hine et al. (2009) supports inclusion in the Haplosporida.

Howell (1967) described a haplosporidan – *Urosporidium constantae* – that is associated with a trematode (fluke) parasite of *Ostrea chilensis* in Tasman Bay. The protozoan was noted as causing total mortality of those embryonic cercaria larvae of the fluke that it parasitised. Owing to the difficulty of obtaining the haplosporidan in the wild, it was not deemed to be a prospective biological-control agent for use against trematode infection of the oyster in Foveaux Strait.

The third, and most enigmatic, New Zealand haplosporidan remains undescribed, but represents a new genus and species that taxonomically falls at the very base of the Haplosporida (Reece et al. 2004; Hine et al. 2009). It affects juvenile and adult paua (*Haliotis iris*), causing haplosporidosis (Diggles et al. 2002b; Hine et al. 2002; Reece & Stokes 2003). The symptoms are lethargy, loss of the righting reflex, wasting of the foot, and chronic mortalities (80–90%) of juveniles during the summer months. This disease agent has been observed only once, in aquacultured individuals in 2000, and has not been recorded since. This suggests that paua may be an accidental host and that its usual hosts may be other mollucs, perhaps one of the many species of intertidal gastropods. There is no known effective method of treatment. Since wild-caught adult paua may be reservoirs of infection, broodstock paua ought to be kept separate from cultured juveniles (Diggles et al. 2002b).

In summary, the Cercozoa is an ecologically and economically important phylum of protists in New Zealand that is significantly understudied. This review touches on the known diversity, information about which is scattered in the literature. At least 135 more species can be expected in New Zealand's aquatic and terrestrial environments, but this figure should be taken as conservative.

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Checklist of New Zealand Cercozoa

Classification follows Cavalier-Smith and Chao (2003). Abbreviations: E, endemic; S, species with southern distribution in New Zealand; * unpublished records (R. Meisterfeld) from humus collected at Nelson (South Island) and Station Ridge near Orongorongo Valley Field Station (southern North Island) collected by Yeates (see Yeates & Foissner 1995). Habitats of taxa are indicated as follows: F, fresh waters and/or wet habitats like Sphagnum moss; M, marine and brackish; T, terrestrial (in soil water or in terrestrial hosts); P, parasitic or commensal in invertebrates (in) or plants (PI).

KINGDOM CHROMISTA SUBKINGDOM HAROSA INFRAKINGDOM RHIZARIA PHYLUM CERCOZOA SUBPHYLUM FILOSA INFRAPHYLUM MONADOFILOSA Class GRANOFILOSEA Order INCERTAE SEDIS GYMNOSPHAERIDAE? Wagnerella borealis Merechowsky, 1878 M

Class SARCOMONADEA Order CERCOMONADIDA CERCOMONADIDAE Cercomonas media Bass & Cavalier-Smith in Bass et al., 2009 T Cercomonas paravarians Bass & Cavalier-Smith in Bass et al., 2009 T Neocercomonas grandis (Maskell, 1887) F E Paracercomonas minima Mylnikov, 1985 T Paracercomonas vonderheydeni Bass & Cavalier-Smith in Bass et al., 2009 T Class THECOFILOSEA

Order TECTOFILOSIDA AMPHITREMIDAE Amphitrema paparoensis (van Oye, 1956) F E Amphitrema wrightianum Archer, 1869 F Archerella flavum (Archer, 1877) F Archerella jollyi (van Oye, 1956) F E CHLAMYDOPHRYIDAE Chlamydophrys stercorea Cienkowski, 1876 F Lecythium sp. F PSEUDODIFFLUGIIDAE Pseudodifflugia fulva Penard, 1902 F Pseudodifflugia gracilis Schlumberger, 1845 F

Subclass PHAEODARIA Order PHAEOCYSTIDA AULACANTHIDAE Aulodendron australe Haeckel, 1887 E

Order PHAEOSPHAERIDA SAGOSPHAERIDAE Sagoscena lampadophora Haecker, 1905 Sagoscena ornata Haeckel, 1887

Order PHAEOCALPIDA CASTANELLIDAE *Castanarium huxleyi* Haeckel, 1887 *Castanidium bromleyi* Haeckel, 1887 CIRCOPORIDAE *Circospathis sexfurca* (Haeckel, 1887)

Order PHAEODENDRIDA COELODENDRIDAE *Coelodrymus lappulatus* Haeckel, 1887 COELOGRAPHIDIDAE *Coelothauma duodenum* Haeckel, 1887

Order PHAEOGROMIDA MEDUSETTIDAE Gazelletta orthonema Haeckel, 1887

Subclass INCERTAE SEDIS Order CRYOMONADIDA PROTASPIDAE Protaspa tanyopsis (Norris, 1961) M E

Order EBRIIDA EBRIIDAE *Ebria tripartita* (Schumann, 1867) M

Class IMBRICATEA Order SPONGOMONADIDA SPONGOMONADIDAE Rhipidodendron huxleyi Saville-Kent, 1882 F Rhipidodendron splendidum Stein, 1956 F Spongomonas discus Stein, 1878 F Spongomonas sacculus Saville-Kent, 1880 F

Order THAUMATOMONADIDA THAUMATOMONADIDAE *Thaumatomastix bipartita* Beech & Moestrup, 1986 M

Thaumatomastix salina (Birch-Anderson, 1973) M

Thaumatomastix tripus (Takahashi et Hara) Beech & Moestrup M

Order EUGLYPHIDA CYPHODERIIDAE Cyphoderia ampulla (Ehrenberg, 1840) F EUGLYPHIDAE Assulina muscorum Greeff, 1888 FT Assulina seminulum (Ehrenberg, 1848) F Euglypha acanthophora (Ehrenberg, 1843) FT Euglypha bryophila Brown, 1911* FT Euglypha ciliata (Ehrenberg, 1848) FT Euglypha ciliata f. glabra Cash, Wailes & Hopkinson, 1915 FT Euglypha compressa Carter, 1864 FT Euglypha compressa f. glabra Cash, Wailes & Hopkinson, 1915 FT Euglypha cristata Leidy, 1874 F Euglypha denticulata Brown, 1912 FT Euglypha filifera Penard, 1890* FT Euglypha laevis Perty, 1849 FT Euglypha polylepis Bonnet, 1959* T Euglypha rotunda Wailes & Penard, 1911 FT Euglypha rotunda small form Wailes, 1915* FT Euglypha scutigera Wailes & Penard, 1911 FT Euglypha simplex Decloitre, 1965* T Euglypha strigosa (Ehrenberg, 1871) FT Euglypha strigosa f. glabra Wailes & Penard, 1911 FT Euglypha tuberculata Dujardin, 1841 F Placocista spinosa (Carter, 1865) Leidy, 1879 F Sphenoderia fissirostris Penard, 1890 F Sphenoderia minuta Deflandre, 1931* FT Sphenoderia rhombophora Bonnet, 1966* T Tracheleuglypha dentata (Vejdovsky, 1882) F Trachelocorythion pulchellum (Penard, 1890* FT TRINEMATIDAE Corythion delamarei Bonnet & Thomas, 1960* T Corythion dubium Taranek, 1882 FT Corythion d. gigas Thomas, 1954* FT Playfairina valkanovi Golemansky, 1966* FT Trinema complanatum Penard, 1890* FT Trinema c. platystoma Schönborn, 1964* T Trinema enchelys (Ehrenberg, 1838)? FT Trinema galeata (Penard, 1902) FT Trinema grandis Chardez, 1960* FT Trinema lineare Penard, 1890 FT

MONADOFILOSA INCERTAE SEDIS Feuerbornia lobophora Jung, 1942* FT S

INFRAPHYLUM INCERTAE SEDIS POMPHOLYXOPHRYIDAE Pompholyxophrys exigua Hertwig & Lesser, 1874 F Pompholyxophrys ossea Dürrschmidt in Nicholls & Dürrschmidt, 1985 F E Pompholyxophrys ovuligera Penard, 1904 F

SUBPHYLUM ENDOMYXA Class PROTEOMYXIDEA Order ACONCHULINIDA BIOMYXIDAE *Biomyxa vagans* Leidy, 1879 FT

Class PHYTOMYXEA Order PLASMODIOPHORIDA PLASMODIOPHORIDAE *Ligniera pilorum* Fron & Gaillat, 1925 T PPI *Plasmodiophora brassicae* Woronin, 1877 T PPI *Plasmodiophora elaeagni* Schröter, 1886 [1889]. T PPI *Polymyxa graminis* Ledingham, 1939 T PPI *Sorosphaera veronicae* (Schröter, 1886) [1889] T PPI *Songospora subterranea* (Wallroth, 1842) T PPI *Tetramyxa parasitica* Goebel, 1884 M PPI *Woronina polycystis* Cornu, 1872 T PPI *Woronina pythii* Goldie-Smith, 1956 T PPI

Class GROMIIDEA Order GROMIIDA GROMIIDAE Gromia oviformis Dujardin, 1835 M

Class ASCETOSPOREA Order HAPLOSPORIDA HAPLOSPORIDIIDAE Bonamia exitiosa Hine, Cochennec-Laureau & Berthe, 2001 M Pin E Urosporidium constantae Howell, 1967 M PIn E Gen. nov. et n. sp. Diggles et al. 2002 M PIn E Gen. et sp. indet. Hine & Diggles pers. obs. M PIn E

PHYLUM INCERTAE SEDIS Kamera lens (Müller, 1773) F

Checklist of New Zealand fossil Cercozoa

Abbreviations for Stage names are based on Cooper (2004).

PHYLUM CERCOZOA SUBPHYLUM FILOSA Superclass MONADOFILOSA Class THECOFILOSEA Subclass PHAEODARIA Order PHAEOGROMIDA CHALLENGERIDAE Challengeron takhashii Dumitrica & Hollis, 2004 Mh Challengeron sp. Dumitrica & Hollis 2004 Mh Protocystis pacifica Dumitrica & Hollis, 2004 Mh