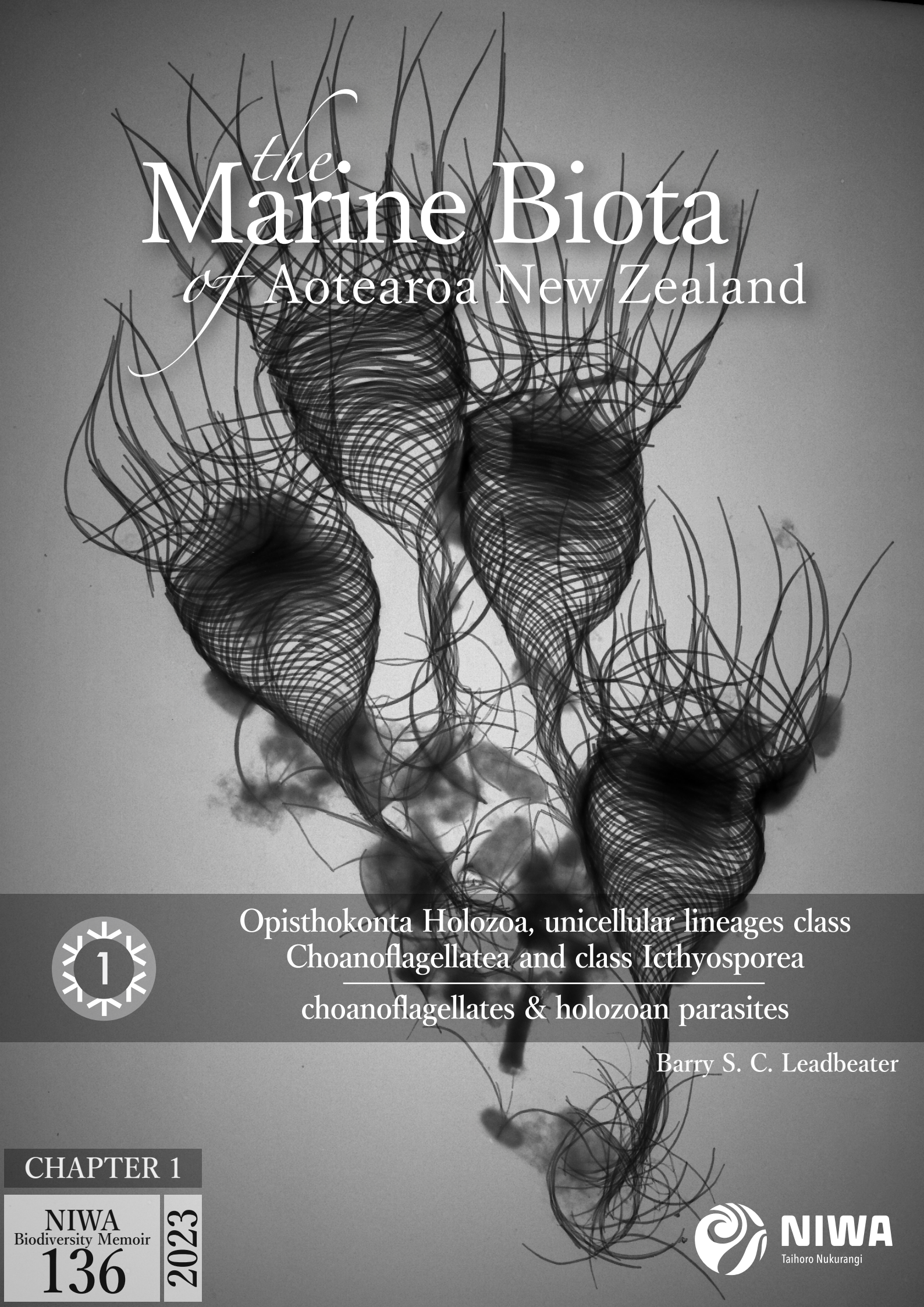

the Marine Biota of Aotearoa New Zealand

Opisthokonta Holozoa, unicellular lineages class Choanoflagellatea and class Icthyosporea

choanoflagellates & holozoan parasites

Barry S. C. Leadbeater

CHAPTER 1

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1 Opisthokonta-Holozoa, unicellular lineages classes Choanoflagellatea (choanoflagellates) & Ichthyosporea (holozoan parasites)

Barry S.C. Leadbeater

School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom;
b.s.c.leadbeater@bham.ac.uk; https://orcid.org/0000-0002-6353-7281

Summary

Gordon (2012) listed 42 marine, terrestrial and freshwater unicellular Choanozoa (now Holozoa), of which 22 species are marine; here we report on the marine species listed in Gordon (2012), and the considerable advances in the phylogenetic systematics of the (formerly) phylum Choanozoa (Table 1.1, Fig. 1.1). Moestrup (1979) made collections of nanoplankton, including choanoflagellates, from Leigh and Kaikoura, two coastal localities on the east coasts of the North and South Islands, respectively, of Aotearoa New Zealand. Bojo (2001) added more species from a study in Blueskin Bay, Otago. Some universally distributed loricate choanoflagellates recorded from mesotrophic waters of the South Pacific have also been added. A checklist of 35 extant New Zealand marine Holozoa is provided.

Introduction

Opisthokonta is a well-established major (unranked) group comprising the Fungi and Metazoa (animal lineage), as well as a number of groups of non-photosynthetic, unicellular, protistans (Adl *et al.* 2019). Two robust clades, Holomycota and Holozoa, are recognised within the Opisthokonta. Holomycota comprises the Fungi and the nucleariid amoebae (Cristidiscoidea) and is not considered further here. Holozoa contains the Metazoa and several unicellular groups including choanoflagellates, ichthyosporeans (Shalchian-Tabrizi *et al.* 2008) and filasterians. The absence of universal diagnostic morphological characters linking opisthokont taxa has meant that membership of the Opisthokonta has been largely dependent on molecular phylogenetic studies. A character that is widely shared is flattening of the mitochondrial cristae, although there is at least one record of tubular cristae in the ichthyosporean *Ichthyophonus hoferi* Plehn & Mulsow, 1911 (Ragan *et al.* 1996). Since Gordon (2012), advances in molecular phylogeny, with more species sampled, more genes analysed and more results available, has meant that there have been numerous changes and modifications to opisthokont taxonomy and nomenclature. In particular, Choanozoa, a name introduced by Cavalier-Smith (1981) for a diverse range of single-celled protists related to the origin of animals and fungi, has taken on a confusing variety of meanings. Since its first introduction, Choanozoa has been used for a combination of the choanoflagellates, Ichthyosporea and Filasterea (Shalchian-Tabrizi *et al.* 2008), or more recently, the choanoflagellates and animals (Brunet & King 2017). However, the name has now generally been replaced by Holozoa (Lang *et al.* 2002), which was introduced to group the choanoflagellates, Ichthyosporea and the Metazoa, a combination that has remained relatively stable during the last twenty years. Some species that were previously classified as fungi are now formally recognised as being members of the Holozoa, and some previously considered holozoans are now considered to be members of the Holomycota.

The best-known unicellular holozoans are the choanoflagellates, a distinctive group of free-swimming or attached, colourless, solitary or colonial protistans that are in most aquatic environments. All species share several characteristic features – a cell body with a single anterior flagellum, surrounded by a funnel-shaped collar, comprising a ring of microvilli. The shape and composition of the periplast (cell covering) varies between species and is taxonomically important.

Class Choanoflagellatea contains two orders (Nitsche *et al.* 2011): the Craspedida, comprising species that have an organic outer investment (see Fig. 1.1A), which in some species may be so thin that cells may appear naked (Leadbeater 2015); and, the Acanthoecida, which includes species with a siliceous basket-like lorica (see Fig. 1.1B) (Thomsen & Østergaard 2019 *et seq.*). Choanoflagellate loricae are composed of a framework of costae, which contain a linear series of rod-shaped units known as costal strips. These assemble in an astonishing process that follows certain 'rules' that govern the sequence of events whereby the siliceous strips are positioned within the developing lorica (Leadbeater 2015). Siliceous forms, with a few exceptions (Nitsche 2014), are found in marine and brackish environments. Choanoflagellates consume bacteria, cyanobacteria, and detritus, filtered by the collar microvilli from a current of water created by the motion of the flagellum (Leadbeater 2015), and reproduce by division of the cell.

Class Ichthyosporea comprises an ecologically and morphologically diverse group of predominantly parasitic unicellular holozoans that was covered

Table 1.1. Summary of marine Holozoa diversity in the Aotearoa New Zealand region expressed as total numbers and percentage change. Data for 2012 are derived from Gordon (2012: p. 113). OTU = Operational Taxonomic Unit.

	Choanoflagellatea		Ichthyosporea		Total		% change
	2012	2023	2012	2023	2012	2023	
Total species diversity	20	33	2	2	22	35	59
Described extant species	17	32	2	2	19	34	49
Undescribed extant species (OTU)	3	1	0	0	3	1	– 67
Described endemic extant genera	0	0	0	0	0	0	0
Described endemic extant species	0	0	0	0	0	0	0

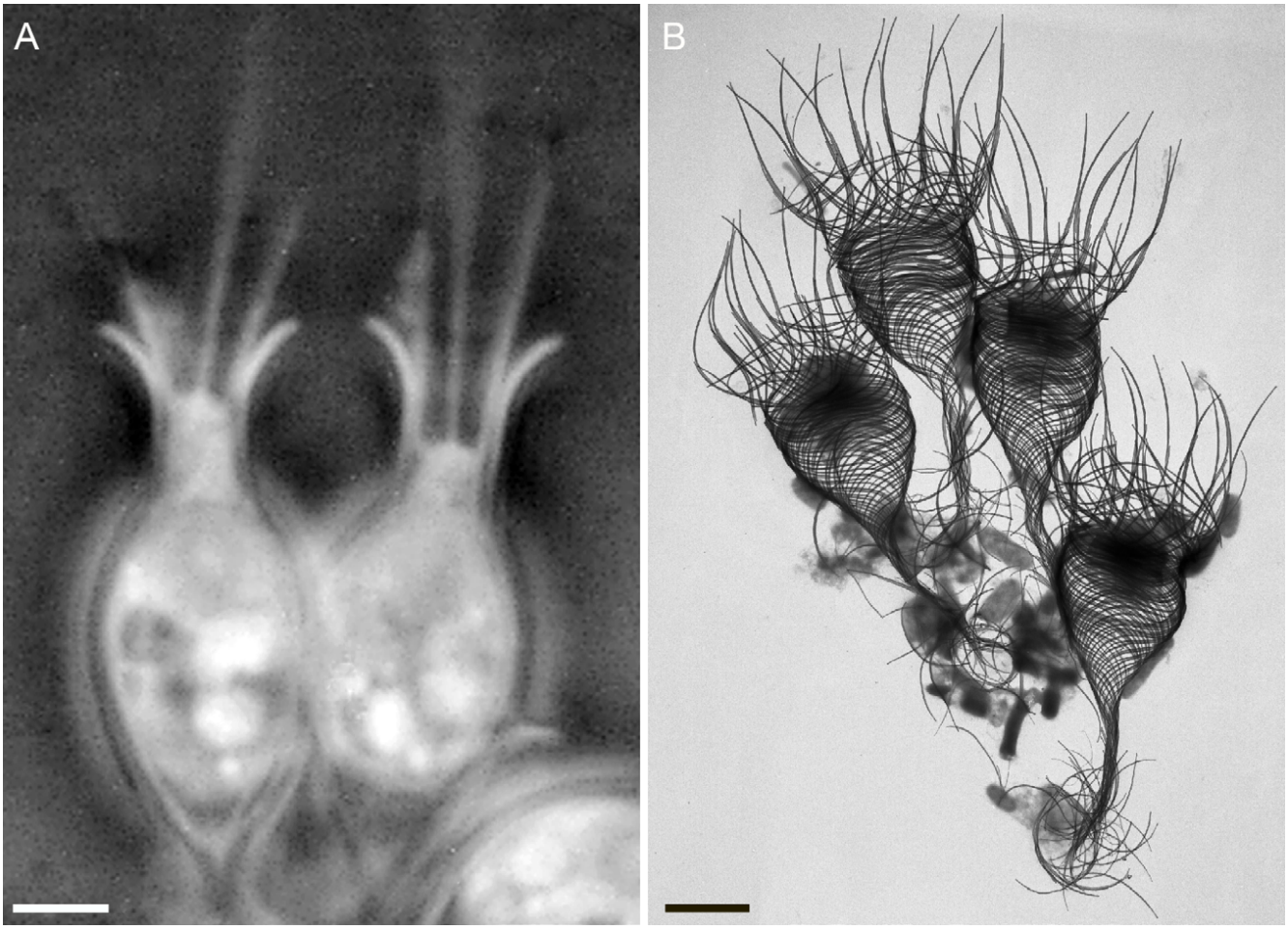

Figure 1.1. Examples of unicellular Holozoa: **A.** *Salpingoeca* sp. (Class Choanoflagellatea, order Craspedida), two living cells, each with a single anterior flagellum surrounded by a funnel shaped collar. The cell is enclosed within an organic theca; **B.** *Acanthoeca spectabilis* W.N.Ellis, 1930 (Class Choanoflagellatea, order Acanthoecida, family Acanthoecidae), showing a group of stalked loricae containing a large number of siliceous costae. Scale = 2 µm.

briefly in Gordon (2012). Ichthyosporea is represented in New Zealand by three genera that were included in the fungal class Trichomycetes (Zygomycota) in the orders Amoebidiales (*Paramoebidium*) and Eccrinales (*Enteromyces* and *Taeniella*). Fungoid forms are now termed protist trichomycetes (trichos). A comprehensive study of protist trichos, combining molecular phylogeny with a range of morphological and ecological characters by Reynolds *et al.* (2017), has provided a much-needed update on the taxonomy, evolution and ecology of these organisms. This study has shown that several morphological and ecological states, such as habitat, host type, host stage at time of infection, location within host, spore production, and growth form are significantly correlated with phylogeny. Reynolds *et al.* (2017) list five families of protist trichos comprising three re-named fungal orders, Amoebidiidae (*Amoebidium*), Eccrinidae (*Enterobryus, Enteromyces, Taeniella*) and Parataeniellidae (*Parataeniella*); in addition, there is a family named by Cavalier-Smith (2013), Ichthyophonidae (*Ichthyophonus*), and a new family Paramoebidiidae (*Paramoebidium*) (Reynolds *et al.* 2017). *Enteromyces callianassae* Lichtwardt, 1961 and *Taeniella carcini* Léger & Duboscq, 1911 (Eccrinidae) are marine and Pan-Pacific, possibly worldwide. In New Zealand, Williams and Lichtwardt (1990) found *E. callianassae* in the stomach of the ghost shrimp *Filhollianassa filholi* (A. Milne-Edwards, 1879), and *T. carcini* in both the ghost shrimp and the mud crab *Austrohelice crassa* (Dana, 1851), at New Brighton, Christchurch.

The resemblance of choanoflagellates to the collar cells (choanocytes) in the ciliated chambers of sponges has long been regarded as a possible evolutionary link between a unicellular protistan and a multicellular animal (see Leadbeater 2015 for discussion), although the alternate idea that choanoflagellates may be derived, by simplification, from sponges has also been advanced (James-Clark 1867; Kent 1878; Maldonado 2004). The demonstration of similarity at the ultrastructural level between the choanoflagellate cell and the sponge choanocyte has strengthened the connection between the two groups, although detailed ultrastructural analysis of the flagellar bases and associated root systems reveals fundamental dissimilarities between the two groups (Pozdnyakov *et al.* 2017). Molecular data are also ambivalent on this matter. A multigene phylogeny was published by Shalchian-Tabrizi *et al.* (2008), who sought to clarify the relationships among the various morphologies exhibited among the 'Choanozoa' (for a discussion of this see Gordon 2012).

Whilst the list of species provided below details holozoans positively identified from New Zealand territory and surrounding waters, since most choanoflagellate species are known to be universal in distribution it is most likely that the majority of currently named species recorded from neighbouring regions will also be present in New Zealand localities. For this reason, selected choanoflagellate species recorded in South Pacific mesotrophic waters (Kamennaya *et al.* 2022) and from Australian inshore waters have been included.

Acknowledgements

BSCL is grateful to Dr Martin Carr for helpful advice and making available unpublished information; to Professor Helge Thomsen for reviewing this manuscript and for drawing attention to recent publications by him and his co-authors that contained additional species identifications based on Professor Øjvind Moestrup's original 1978 New Zealand collections; and to Dr Michelle Kelly and NIWA for hosting my sabbatical stay in New Zealand in 2000.

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Checklist of extant unicellular Holozoa known from the New Zealand EEZ

This checklist is arranged according to the currently accepted systematics and classificatory scheme employed by the World Register of Marine Species (WoRMS) (https://www.marinespecies.org/), and follows Lang *et al.* (2002). There is only one current publication (Moestrup 1979) that contains original photographic images of loricate choanoflagellate species and these were collected in 1978 from New Zealand inland waters (Leigh and Kaikoura).

Moestrup (1979) recorded nine species and these are indicated by *M. The complete set of photographic negatives on which Moestrup's identifications were based have subsequently been made available to Prof. Helge Thomsen who has recognised an additional seven species indicated by *T. Reference to these seven species can be found respectively in the seven publications of Thomsen and co-authors (2019–2021). Also, based on Moestrup's 1978 collections, an additional new species, together with one of Moestrup's (1979) species, was re-named in Thomsen & Moestrup (1983) and is indicated by *TM. Added to the list of loricate choanoflagellates are ten species recorded from South Pacific mesotrophic waters (Stations SPMR 1–3 in Kamennaya *et al.* 2022). These species are indicated by *K. Where the same species has been found in New Zealand waters and in the South Pacific, the two relevant initials are indicated (e.g. *Bicosta antennigera* Moestrup, 1979 *MK). All other taxa are considered native by default, i.e. naturally occurring in New Zealand and elsewhere.

Class CHOANOFLAGELLATEA
Order ACANTHOECIDA
Family ACANTHOECIDAE
Acanthoeca spectabilis Ellis, 1930
Family STEPHANOECIDAE
Acanthocorbis apoda (Leadbeater) Hara & Takahashi, 1984*M
Acanthocorbis campanula (Espeland & Throndsen) Thomsen, 1991*T
Acanthocorbis haurakiana Thomsen, 1991
Apheloecion sp. Bojo, 2001
Bicosta antennigera Moestrup, 1979*MK
Bicosta minor (Reynolds) Leadbeater, 1978*M
Calliacantha aff. *natans* (Grøntved) Leadbeater, 1978*M
Calotheca alata Thomsen & Moestrup, 1983*TM
Campyloacantha spinifera (Leadbeater) Hara & Takahashi, 1987*K
Coronoeca conicella Thomsen, Hara & Østergaard, 2021*K
Coronoeca superpositus Thomsen, Hara & Østergaard, 2021*K
Cosmoeca ceratophora Thomsen, 1984*K
Cosmoeca norvegica Thomsen, 1984
Cosmoeca phuketensis Thomsen, 1984*T
Cosmoeca cf. *subulata* Thomsen, 1984
Cosmoeca ventricosa Thomsen, 1984*K
Crinolina isefiordensis Thomsen, 1976*M
Crucispina cruciformis (Leadbeater) Espeland, 1986*M
Diaphanoeca grandis Ellis, 1930
Didymoeca costata (Valkanov) Doweld, 2003
Parvicorbicula socialis (Meunier) Deflandre, 1960*K
Pleurasiga echinocostata Espeland, 1986*K
Pleurasiga minima Throndsen, 1970*K
Pleurasiga minutissima Thomsen, 2020 *T
Pleurasiga reynoldsii Throndsen, 1970*M
Polyfibula elatensis (Thomsen) Manton, 1981*T
Polyfibula sphyrelata (Thomsen) Manton, 1981*M
Saroeca paucicostata (Hara & Takahashi) Thomsen & Østergaard, 2019 *T
Stephanacantha oceanica Thomsen, 2021*K
Syndetophyllum pulchellum (Leadbeater) Thomsen & Moestrup, 1983*TM
Thomsenella infundibuliformis (Leadbeater) Özdikmen, 2009*T
Thomsenella acuta (Thomsen) Özdikmen, 2009*T

Class ICHTHYOSPOREA
Order ECCRINIDA
Family ECCRINIDAE
Enteromyces callianassae Lichtwardt, 1961
Taeniella carcini Léger & Duboscq, 1911

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