Census of Antarctic Marine Life
SCAR-Marine Biodiversity Information Network

BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

CHAPTER 6.1. TINTINNID CILIATES OF THE MARINE PLANKTON.

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SCIENTIFIC COMMITTEE ON ANTARCTIC RESEARCH

6.1. Tintinnid Ciliates of the Marine Plankton

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1. Tintinnids and their ecological role in the Southern Ocean

Tintinnids are a group of planktonic ciliates inhabiting the surface layer waters of nearly all marine and estuarine systems. The group, constituting the suborder Tintinnonea, is a very species-rich taxon; the standard monographs of Kofoid & Campbell (1929, 1939) catalogue over 700 species. In any given locale, usually many species co-exist. For example, a single sampling in the NW Mediterranean can yield 34 species (Dolan & Stoeck 2011). Large-scale biogeographic patterns are well-known. Tintinnids literally supply textbook examples of the latitudinal species gradient (e.g. Gaston & Spicer 2003). Most genera can be characterised as found in either coastal or open waters and furthermore as temperate, or tropical, or high latitude fauna (e.g. Pierce & Turner 1993). Using Pierce and Turner's terminology, some high latitude genera are "boreal", known only from Arctic and sub-Arctic zones and others are 'austral', found only in Antarctic or sub-Antarctic waters, here these later two zones are considered together as the Southern Ocean. Nonetheless, it should be pointed out that some tintinnid species appear to be cosmopolitan as they are found in all oceanographic biomes, *sensu* Longhurst (1998).

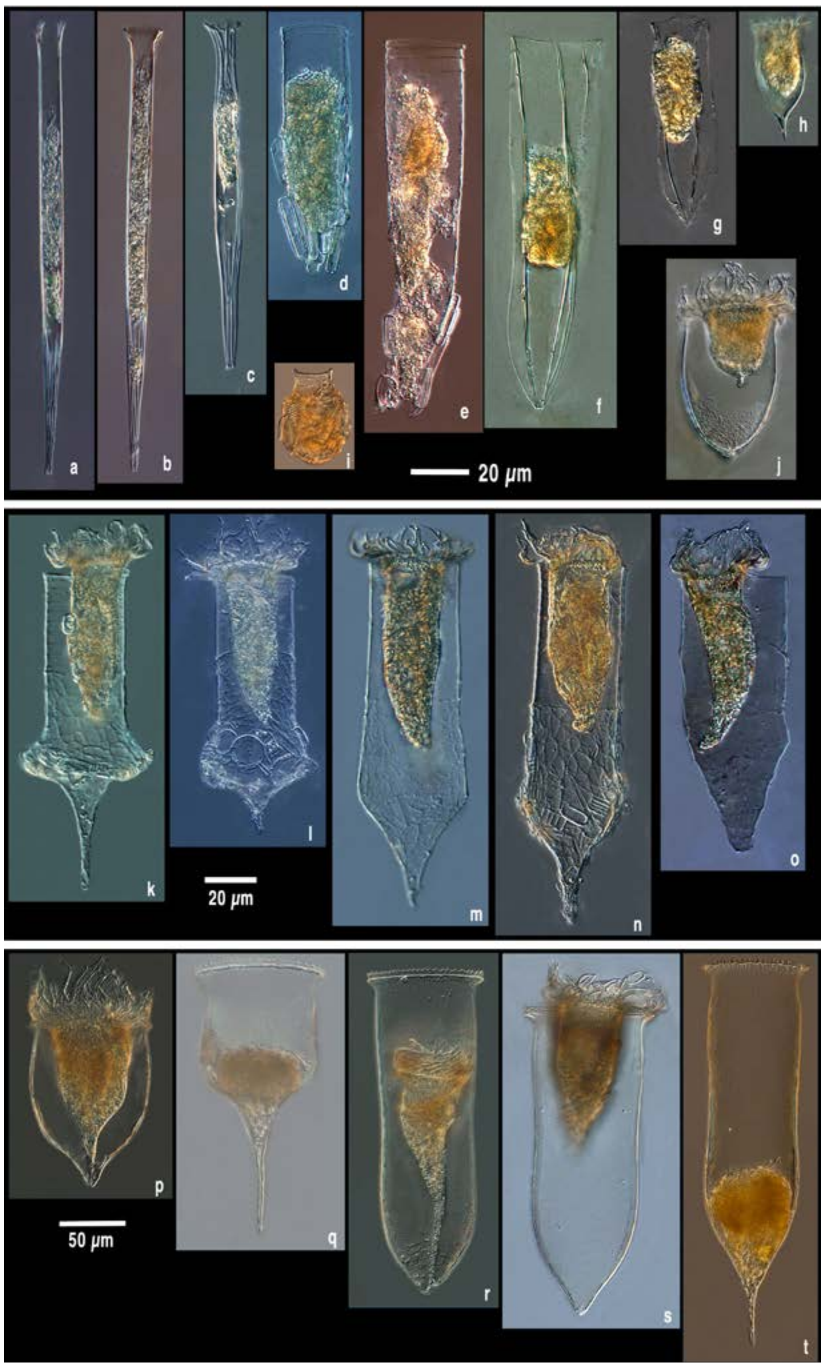


Photo 1 Examples of tintinnid species typical of the Southern Ocean: (a) *Salpingella laackmanni*, (b) *Salpingella decurtata*, (c) *Salpingella faurei*, (d) *Laackmanniella naviculaefera*, (e) *Laackmanniella* forma *prolongata*, (f) *Amphorellopsis quinquelata*, (g) *Amphorides laackmanni*, (h) *Acanthostomella obtusa*, (i) *Codonellopsis pusilla*, (j) *Epiplocylcoides reticulata*, (k) *Codonellopsis gaussi*, (l) *Codonellopsis gaussi*, (m) *Codonellopsis gaussi* forma *globosa*, (n) *Codonellopsis gaussi* forma *cylindricoconica*, (o) *Condonellopsis gaussi* forma *coxiella*, (p) *Cymatocylis affinis/convallaria*, (q) *Cymatocylis affinis/convallaria* forma *calcyformis*, (r) *Cymatocylis affinis/convallaria* forma *subrotundata*, (s) *Cymatocylis affinis/convallaria* forma *drygalski*, (t) *Cymatocylis affinis/convallaria* forma *cylindrica*. Species found only the Southern Ocean are *Laackmanniella naviculaefera* (d–e), *Amphorellopsis quinquelata* (f), *Codonellpsis gaussi* (k–o) and *Cymatocylis affinis/convallaria* (p–t). Note the different morphologies shown by the Southern Ocean endemics.

Species identifications of tintinnids are based on characteristics of the lorica or shell into which the ciliate cell can withdraw. The general shape of the lorica (or shell) of a tintinnid is a tube or vase shape but a very large range of lorica 'architecture' is shown by different forms, including those typical of the Southern Ocean (Photo 1). In terms of a functional group, tintinnid ciliates are part of the microzooplankton, that is they are among the group of organisms nominally between 20 and 200 microns in maximal dimension feeding primarily on small phytoplankton. As a functional group, microzooplankton are acknowledged to be the major consumers of primary production in the most planktonic systems (Calbet & Landry 2004). This is also true of different areas of the Southern Ocean but only when primary production is not dominated by large diatoms or *Phaeocystis* (e.g. Burkill *et al.* 1995, Caron *et al.* 2000, Froneman 2004, Tsuda & Kawaguchi 1997). Occasionally the feeding activity of tintinnids can dominate the consumption of phytoplankton but they are generally a minority component of the microzooplankton compared to other taxa of the microzooplankton such as oligotrich ciliates or heterotrophic dinoflagellates.

In tintinnids, gape size, in the form of the diameter of the mouth-end of the lorica, the lorica oral diameter (LOD), is related to the size of the food items ingested. The largest prey ingested is about half the LOD in longest dimension and they feed most efficiently, removing prey at maximum rates, on prey about 25% of LOD in size (Dolan 2010). The overwhelming majority of described species have an LOD between 20 and 60 μm indicating a typical prey size range of 5 to 15 μm for tintinnids. Specific growth rate (maximum rates for temperate zone species are in the range of 1–2 divisions per day) also scales but inversely with LOD; smaller mouth forms have higher growth rates than the forms with large mouth size (Montagnes 2013). In the Southern Ocean ecosystem, tintinnids are known to serve as prey for a surprisingly large variety of consumers ranging from copepods (Lonsdale *et al.* 2000, Kruse *et al.* 2009), krill (Hopkins 1987) and mysid shrimp (Mauchline 1980), to larger organisms such as salps, chaetognaths (Buck *et al.* 1992), and larval Antarctic Silverfish (Kellerman 1987) and even some benthic organisms such as octocorals (Orejas *et al.* 2003) and deep-sea isopods (Brökeland *et al.* 2010).

2. Studies of Southern Ocean tintinnids

The first record of tintinnids from the Southern Ocean is that of Cleve (1900) who reported on a variety of planktonic organisms. Interestingly, he also noted that some forms, (not only tintintinids but also diatoms and dinoflagellates of the phytoplankton) found in the Southern Ocean are also typical of northern temperate or Arctic waters while still others appeared to be "characteristic of the Antarctic Region". While his was not the first notation of the existence of apparently 'bipolar' species in the plankton, he was the first to describe a tintinnid, *Acanthostomella norvegica*, as such. Cleve believed his findings led support to Carl Chun's speculations on the existence of deep-sea currents linking Arctic and Antarctic waters. However, the existence of "bipolar" species is uncertain because in protists "cryptic species" are known. Arctic and Antarctic populations of protists, for example certain dinoflagellates, while morphologically similar do appear to be genetically distinct (e.g. Darling *et al.* 2007).

The first focused studies of tintinnids in the Southern Ocean date back to results from the German South Polar expedition of 1901–1903. Based on the samples gathered, Hans Laackmann first briefly described a few new species of tintintinids (Laackmann 1907) and subsequently produced a large monographic work, describing a considerable number of new species and varieties (Laackmann 1910). He was the first to note that the species "characteristic of the Antarctic", *Cymatocylis* and species now known as *Laackmanniella,* had close correspondence or similarity in general morphologies with the species typical of Arctic waters, *Ptychocylis*, *Parafavella* and *Leprotintinnus*.

Since Laackmann's time sampling in the Southern Ocean has been highly irregular in time. Figure 1 shows that relatively few locations were sampled in the Southern Ocean throughout the first half of the 20th century. The relatively large number of sites sampled in the 1960's is mostly the work of Enrique Balech on both dinoflagellates and tintinnids describing material gathered by Argentine expeditions. The most recent species records cataloged here for Southern Ocean tintinnids are the study of Fonda Umani *et al.* (2011) which focused on sites from the Straits of Magellan, and Wickham *et al.* (2011) reporting on material gathered from the Amundsen Sea.

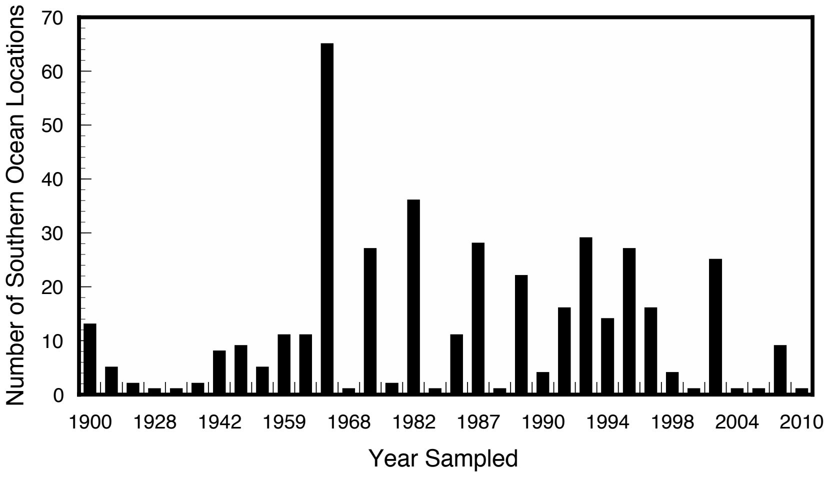


Figure 1 Temporal distribution of sampling effort in the Southern Ocean from reports of tintinnid occurrences. The large peak in the number of sites sampled in the 1960's is largely from E. Balech's reports of Argentine expeditions.

3. Data on Southern Ocean tintinnids

There have been no survey nor synoptic studies of tintinnids in the Southern Ocean or Antarctic waters. Species occurrence and distributions can only be assessed by synthesising the many individual reports mostly concerning a single or a few locations. Here then we describe patterns that emerge from a database of tintinnid species occurrence compiled from such reports in the literature. We consider the Southern Ocean to be the global zone between 40°S and 78°S. The original database was previously described and used to establish global patterns at the genus level (Pierce & Turner 1993). For Southern Ocean locations, the original database consisted of species names, latitude, longitude, and year of report from 23 publications containing 1150 Southern Ocean species records. It was updated to include post-1992 publications, the year of actual sampling for each species record, and revised to account for current taxonomy. The updated database consisted of 2047 species records (synonyms included) from 56 publications reporting on species found in 402 locations. The literature reports are given in the references.

It should be noted that we use the term 'species' in our descriptions of distributional patterns but the term could be replaced by the more accurate term 'morpho-species'. The overwhelming majority of tintintinid species were described based soley on the morpholigical characteristics of the lorica, considered to be species-specific. However, in ciliates, the relationship between morpho-species and the generally-accepted biological definition of 'species' is unclear because morphology, mating types, and genetics are often discordant (Hall & Katz 2011). For tintinnids the limited genetic data available suggests morpho-species of tintinnids, rather than grouping cryptic species (forms morphologically similar but genetically distinct), may more often be different phenotypes of the same genetic species (e.g., Bachy *et al.* 2012; Kim *et al.* 2013).

We collated records for 192 currently recognised species of tintinnids from the locations below 40°S, based on reports published from 1900 to 2011. Mapping the data shows that sites sampled to date are distributed very irregularly in the Southern Ocean (Map 1). As noted above, the temporal distribution of sampling effort has also been irregularly distributed over the past 112 years. Not surprisingly, nearly all of the sampling has been performed during the summer months of the Southern Hemisphere. The majority of species records are based on examination of plankton net material often with no data given on the volumes of water nominally sampled nor the mesh-size. Therefore, the data are qualitative only.

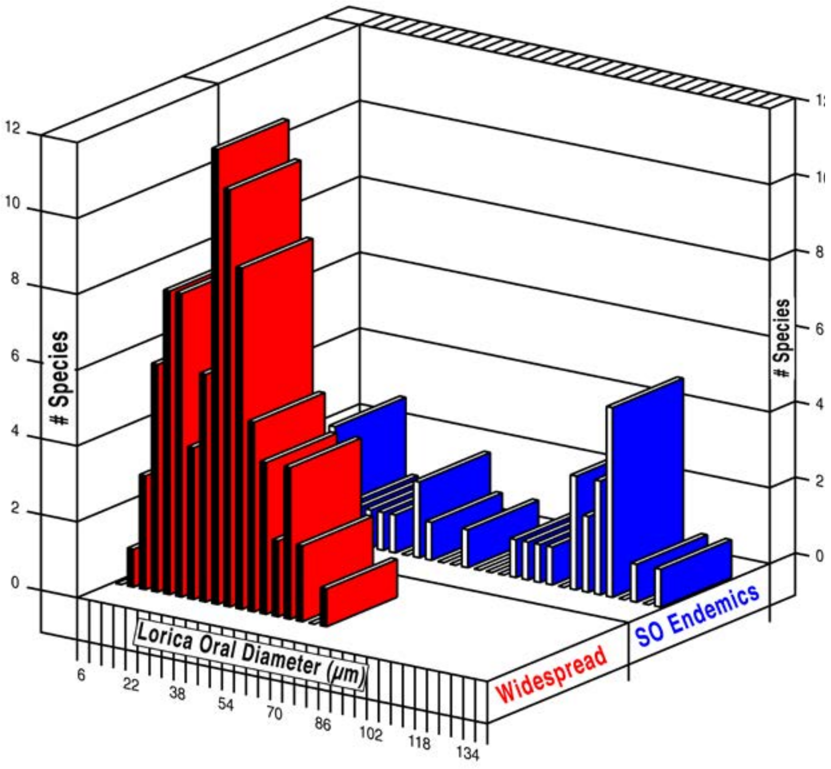


Figure 3 Among the Southern Ocean tintinnids, the assemblage of endemic species is distinct from that of the widespread species in terms of typical oral diameters, presumably reflecting exploitation of different sizes of prey items. The larger-mouthed endemic species are found mostly within the area bordered by the Polar Front.

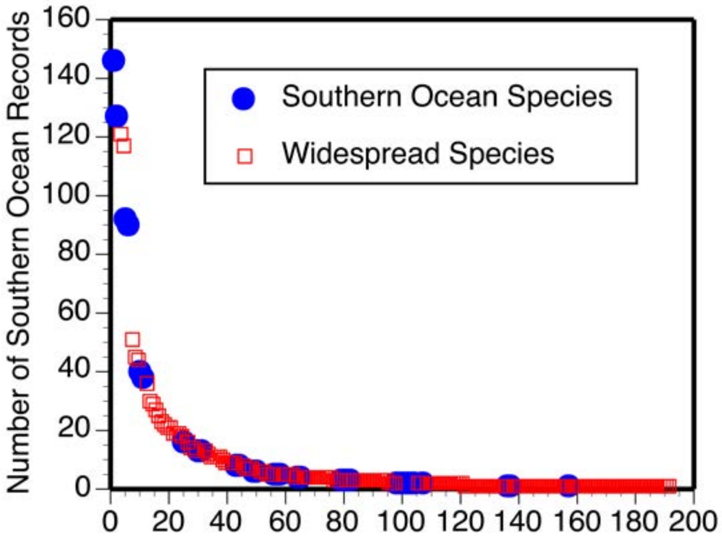


Figure 2 Species 'ubiquity rank' graph. The number of Southern Ocean records for each species ranges from about 150 for the most commonly reported species to only one record for most species. The number of sites from each species has been recorded defines its ubiquity. The species are then ordered by ubiquity, from most common to rare, and plotted in descending order of ubiquity (the number of records for the species). The graph shows the most commonly reported species are both Southern Ocean endemic species and widespread species.

4. Geographic distributions of Southern Ocean tintinnid species

The 192 species reported from locations between 40°S and 78°S can be parsed into 2 main groups: "Southern Ocean Species", those known only from 40°S and further south, and a second group — "Widespread Species", those

Table 1 Southern Ocean tintinnid species.

Southern Ocean Endemic Species	# records	Lat min	Lat max
Amphorellopsis quinquealata Laackmann, 1910	13	58	68
Codonellopsis antarctica Balech, 1958	6	48	62
Codonellopsis balechi Hada, 1970	38	49	78
Cymatocylis affinis Laackmann, 1910 s.l. (incl. *C. calcyformis, convallaria, drygalskii*)	146	50	78
Cymatocylis antarctica Cleve, 1901	90	45	65
Cymatocylis brevicaudata Laackmann, 1910	5	51	62
Cymatocylis crassa Kofoid & Campbell, 1929	2	59	60
Cymatocylis cristallina Laackmann, 1909	3	60	74
Cymatocylis culcullus Kofoid & Campbell, 1929	2	59	66
Cymatocylis cylindroides Kofoid & Campbell, 1929	2	59	60
Cymatocylis cylindrus Kofoid & Campbell, 1929	3	60	62
Cymatocylis ecaudata Kofoid & Campbell, 1929	4	60	75
Cymatocylis flava Laackmann, 1910	16	59	78
Cymatocylis folliculus Kofoid & Campbell, 1929	4	60	75
Cymatocylis glans Kofoid & Campbell, 1929	2	66	75
Cymatocylis kerguelensis Laackmann, 1910	2	49	55
Cymatocylis incondita Kofoid & Campbell, 1929	1	69	69
Cymatocylis nobilis Laackmann, 1910	8	58	75
Cymatocylis ovata Laackmann, 1910	5	60	65
Cymatocylis parva Laackmann, 1910	6	56	66
Cymatocylis scyphus Kofoid & Campbell, 1929	2	59	60
Cymatocylis subconica Kofoid & Campbell, 1929	3	66	75
Cymatocylis subrotundata Kofoid & Campbell, 1929	8	65	75
Cymatocylis typica Laackmann, 1910	5	59	62
*Cymatocylis vanhoeffen*i Laackmann, 1910	40	47	77
Cyttarocylis conica Brandt, 1906	3	60	62
Daturella frigida Hada, 1970	1	62	62
Eutintinnus subrugosa Balech, 1942	1	58	58
Laackmanniella naviculaefera Laackmann, 1907 + *L. prolonga* Laackmann, 1907	127	43	78
Helicostomella lemairei Balech, 1942	2	56	58
Steenstrupiella pozzi Balech, 1942	92	40	61
Tintinnopsis bacillaria Hada, 1970	13	41	64

Table 2 Widespread species with multiple Southern Ocean records.

Acanthostomella lata Kofoid & Campbell, 1929	*Eutintinnus fraknoi* Daday, 1887	*Salpingella subconica* Kofoid & Campbell, 1929
Acanthostomella norvegica Jorgensen, 1927	*Eutintinnus lusus undae* Entz Sr., 1884	*Steenstrupiella intumescens* Jorgensen, 1924
Amphorellopsis acantharus Kofoid & Campbell, 1929	*Eutintinnus medius* Kofoid & Campbell, 1929	*Steenstrupiella steenstrupii* Claparède & Lachmann, 1858
Amphorides amphora Claparède & Lachmann, 1858	*Eutintinnus rectus* Wailes, 1925	*Stenosemella avellana* Meunier, 1919
Amphorides brandti Brandt, 1906	*Eutintinnus tubulosus* Ostenfeld, 1889	*Stenosemella nivalis* Meunier, 1910
Amphorides laackmanni Jorgensen, 1924	*Helicostomella subulata* Ehrenberg, 1833	*Stenosemella ventricosa* Claparède & Lachmann, 1858
Amphorides quadrilineata Claparède & Lachmann, 1858	*Luminella* (*Stenosomella*) *pacifica* Kofoid & Campbell, 1929	*Stylicauda platensis* Cunha & Fonsca, 1917
Ascampbelliella acuta Kofoid & Campbell, 1929	*Ormosella haeckeli* Kofoid & Campbell, 1929	*Tintinnopsis baltica* Brandt, 1896
Ascampbelliella armilla Kofoid & Campbell, 1929	*Parundella aculeata* Jorgensen, 1924	*Tintinnopsis beroidea* Stein, 1867
Ascampbelliella protuberans Kofoid & Campbell, 1929	*Parundella caudata* Ostenfeld, 1899	*Tintinnopsis cylindrica* Daday, 1887
Ascampbelliella urceolata Ostenfeld, 1899	*Parundella crassicaudata* Balech & Souto, 1980	*Tintinnopsis gracilis* Kofoid & Campbell, 1929
Bursaopsis ollula Brandt, 1906	*Parundella pellucida* Jorgensen, 1899	*Tintinnopsis karajacensis* Brandt, 1896
Codonella amphorella Biedermann, 1893	*Poroecus curtus* Kofoid & Campbell, 1929	*Tintinnopsis lata* Meunier, 1910
Codonella aspera Kofoid & Campbell, 1929	*Proplectella claparedei* Entz Jr., 1908	*Tintinnopsis levigata* Kofoid & Campbell, 1929
Codonella elongata Kofoid & Campbell, 1929	*Proplectella fastigata* Jorgensen 1904	*Tintinnopsis lobiancoi* Daday, 1887
Codonellopsis morchella Cleve, 1900	*Proplectella globosa* Kofoid & Campbell, 1929	*Tintinnopsis major* Meunier, 1910
Codonellopsis pusilla Cleve, 1900	*Proplectella subacuta* Cleve, 1901	*Tintinnopsis meunieri* Kofoid & Campbell, 1929
Codonellopsis schabi Brandt, 1906	*Proplectella subcaudata* Jorgensen, 1924	*Tintinnopsis minuta* Wailes, 1925
Dadayiella ganymedes Entz Sr., 1884	*Protocymatocylis pseudiconica* Hada, 1961	*Tintinnopsis nucula* Fol, 1884
Dictyocysta californiensis Kofoid & Campbell, 1929	*Protorhabdonella curta* Cleve, 1901	*Tintinnopsis parva* Merkle, 1909
Dictyocysta duplex Brandt, 1906	*Protorhabdonella simplex* Cleve, 1899	*Tintinnopsis parvula* Jorgensen, 1912
Dictyocysta elegans Ehrenberg, 1854	*Rhabdonella amor* Cleve, 1900	*Tintinnopsis rapa* Meunier, 1910
Dictyocysta fenestrata Kofoid & Campbell, 1929	*Rhabdonella chilensis* Kofoid & Campbell, 1929	*Tintinnopsis sacculus* Brandt, 1896
Dictyocysta lepida Ehrenberg, 1854	*Rhabdonella indica* Laackmann, 1909	*Tintinnopsis turbo* Meunier, 1919
Dictyocysta mitra Haeckel, 1873	*Rhabdonella spiralis* Fol, 1881	*Tintinnopsis vasculum* Meunier, 1919
Dictyocysta reticulata Kofoid & Campbell, 1929	*Salpingella acuminata* Claparède & Lachmann, 1858	*Xystonella acus* Brandt, 1906
Dictyocysta speciosa Jorgensen, 1924	*Salpingella decurtata* Jorgensen, 1924	*Xystonella lanceolata* Brandt, 1906
Epiplocylis acuminata Daday, 1887	*Salpingella faurei* Kofoid & Campbell, 1929	*Xystonella longicauda* Brandt, 1906
Epiplocylis undella Ostenfeld & Schmidt, 1901	*Salpingella glockentögeri* Jorgensen, 1924	
Eutintinnus apertus Kofoid & Campbell, 1929	*Salpingella laackmanni* Kofoid & Campbell, 1929	

Table 3 Widespread species with a single Southern Ocean record.

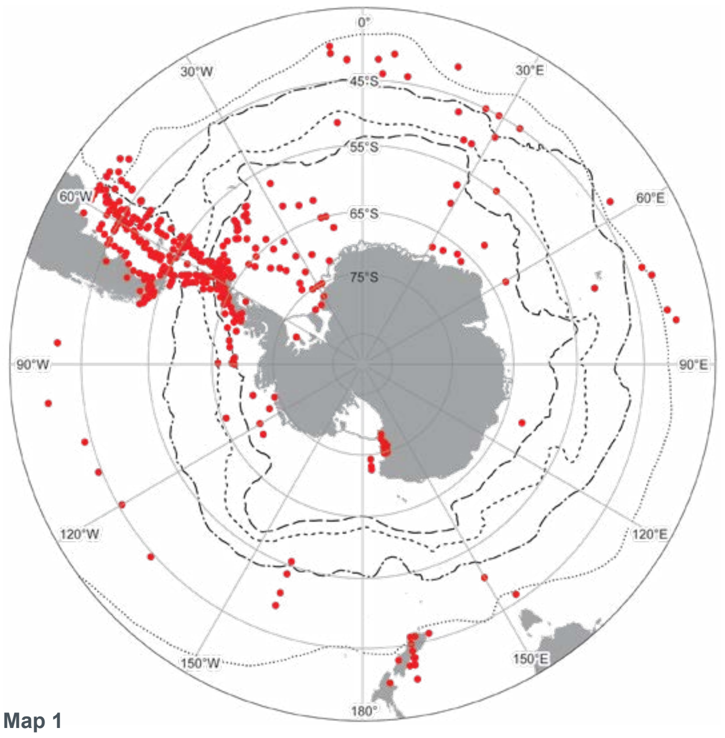
Acanthostomella conicoides Kofoid & Campbell, 1929	*Epiplocylis deflexa* Kofoid & Campbell, 1929	*Rhabdonella cornucopia* Kofoid & Campbell, 1929
Acanthostomella minutissima Kofoid & Campbell, 1929	*Epiplocylis exigua* Kofoid & Campbell, 1929	*Rhabdonella quantula* Kofoid & Campbell, 1929
Acanthostomella obtusa Kofoid & Campbell, 1929	*Epiplocylis healdi* Kofoid & Campbell, 1929	*Rhabdonellopsis apophysata* Cleve, 1900
Amphorellopsis acuta Schmidt, 1901	*Epiplocylis inflata* Kofoid & Campbekll, 1929	*Rhabdonellopsis intermedia* Kofoid & Campbell, 1929
Amphorellopsis laevis Kofoid & Campbell, 1929	*Epiplocylis lata* Kofoid & Campbell, 1929	*Salpingella acuminatoides* Laackmann, 1909
Amplectella monocollaria Laackmann, 1909	*Epiplocylis mira* Balech, 1958	*Salpingella secata* Brandt, 1896
Ascampbelliella aperta Marshall, 1934	*Eutintinnus attenuatus* Kofoid & Campbell, 1929	*Salpingella undata* (*acuminata*) Claparèrde & Lachmann, 1858
Climacocylis scalaria Brandt, 1906	*Eutintinnus australis* Balech, 1944	*Steenstrupiella gracilis* Jorgensen, 1924
Climacocylis scalaroides Kofoid & Campbell, 1929	*Eutintinnus elegans* Jorgensen, 1924	*Tintinnopsis brasiliensis* Kofoid & Campbell, 1929
Codonellopsis biedermanni Brandt, 1906	*Eutintinnus pacificus* Kofoid & Campbell, 1929	*Tintinnopsis bütschlii* Daday, 1887
Codonellopsis brevicaudata Brandt, 1906	*Eutintinnus pinguis* Kofoid & Campbell, 1929	*Tintinnopsis compressa* Daday, 1887
Codonellopsis contracta Kofoid & Campbell, 1929	*Eutintinnus stramentus* Kofoid & Campbell, 1929	*Tintinnopsis glans* Meunier, 1919
Codonellopsis indica Kofoid & Campbell, 1929	*Favella azorica* Cleve, 1900	*Tintinnopsis radix* Imhof, 1886
Codonellopsis ostenfeldi Schmidt, 1901	*Favella campanula* Schmidt, 1901	*Tintinnopsis rotundata* Jorgensen, 1889
Codonellopsis parvicollis Marshall, 1934	*Favella* (*Schmidingerella*) *taraikaensis* Hada, 1932	*Tintinnopsis tocantinensis* Kofoid & Campbell, 1929
Cymatocylis conica Laackmann, 1909	*Leprotintinnus nordqvisti* Brandt, 1906	*Tintinnopsis tubulosa* Levander, 1900
Cymatocylis subconica Kofoid & Campbell, 1929	*Metacylis annulifera* Ostenfeld & Schmidt, 1901	*Tintinnopsis urnula* Meunier, 1910
Daturella luanae Marshall, 1934	*Metacylis corbula* Kofoid & Campbell, 1929	*Undella declivis* Kofoid & Campbell, 1929
Dictyocysta obtusa Jorgensen, 1924	*Parafavella brandti* Hada, 1932	*Undella hemispherica* Laackmann, 1909
Dictyocysta polygonata Kofoid & Campbell, 1929	*Parundella messinensis* Brandt, 1906	*Undella parva* Kofoid & Campbell, 1929
Epiplocycloides acuta Kofoid & Campbell, 1929	*Petalotricha* (*Cyttarocylis*) *ampulla* Fol, 1881	*Undella turgida* Kofoid & Campbell, 1929
Epiplocycloides ralumensis Brandt, 1906	*Petalotricha pacifica* Kofoid & Campbell, 1929	*Xystonella treforti* Daday, 1887
Epiplocylis blanda Jorgensen, 19024	*Proplectella perpusilla* Kofoid & Campbell, 1929	
Epiplocylis constricta Kofoid & Campbell, 1909	*Rhabdonella brandti* Kofoid & Campbell, 1929	

whose extensive geographic ranges extend into the Southern Ocean. Tintinnid species restricted to the Southern Ocean comprise a group of 32 species which have not been reliably reported north of 40°S (Table 1). The figure of 32 accounts for recent findings (Kim *et al.* 2013) of likely synonymy with regard to several species: 4 species of *Cymatocylis* (*C. affinis* = *C. calcyformis*, *C. convallaria*, & *C. drygalskii*), 2 species of *Condonellopsis* (*C. gaussi* & *C. glacialis* = *Laackmanniella*) and 2 species of *Laackmanniella* (*L. prolongata* = *L. naviculaefera*). The spatial distributions of two genera with the largest number of recorded occurrences, *Cymatocylis* and *Laackmanniella* is shown in Maps 2 and 3. While both genera appear to be largely restricted to waters within the Polar Front, *Cymatocylis* has been found much more frequently outside the area delimited by the front compared to *Laackmanniella* which appears then to be more 'Antarctic' than *Cymatocylis*.

The second group of widespread species is comprised of 161 taxa found in not only in the Southern Ocean but elsewhere as well. This very large set of species can be divided into 2 sets: the 81 species which have been recorded multiple times in the Southern Ocean waters (Table 2) and the 70 species which have only been found once below 40°S (Table 3). The latter set of species with but a single Southern Ocean record can be considered as a list of 'strays' as not only are the species rare in the Southern Ocean, as evidenced by the single report, but none have been reported to occur in significant abundance. In contrast, many of the widespread species reported multiple times appear to be very common in tintinnid assemblages in the Southern Ocean. For example, *Codonellopsis pusilla* has been recorded nearly as often as the Southern Ocean species of *Cymatocylis* and *Laackmanniella*. The ubiquity, or conversely, the rarity of a species in the records from the Southern Ocean appears unrelated to whether or not the species is a Southern Ocean species. Figure 2 shows the number of records for each of 192 species ranked according to 'ubiquity' — their relative frequency of occurrence in the sites sampled. Widespread species, those found outside as well as inside the Southern Ocean, rank within the 10 most commonly reported species in records from the Southern Ocean. Nonetheless, examination of a map showing sites sampled in the Southern Ocean from which only endemic species were reported, thus apparently less inhabited by widespread species, shows a concentration of such sites inside the zone delimited by the average position of the Polar Front (Map 4). Conversely, sites from which only widespread species were recorded are concentrated at the northern edge of the Southern Ocean (Map 5). A very similar apparent dichotomy in distribution between endemic and widespread diatoms in the Southern Ocean has been reported (Armand *et al.* 2005, Crosta *et al.* 2005, Romero *et al.* 2005).

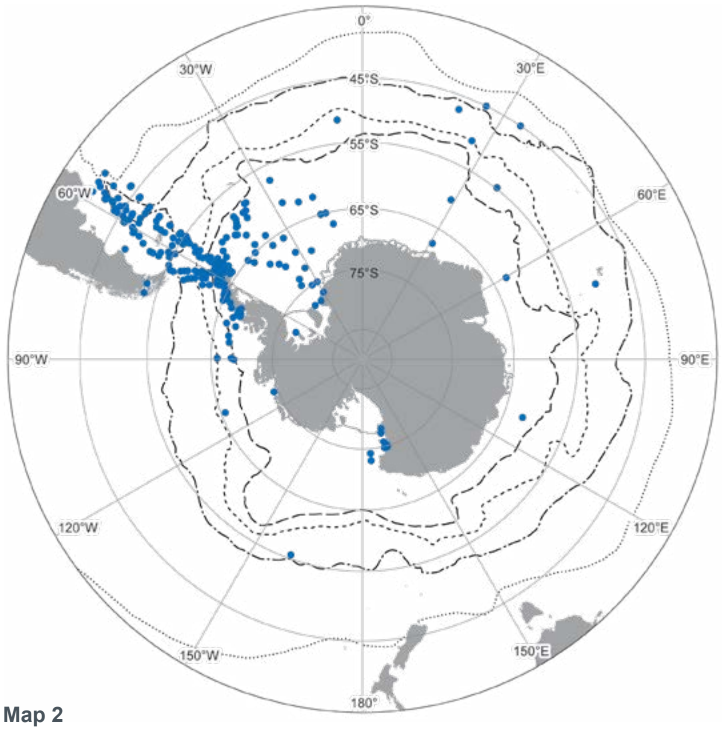
5. Characteristics of Southern Ocean tintinnids

The morphological characteristics of tintinnid assemblages, in terms of the spectrum of mouth sizes found in the species pool, the lorica oral diameters, can differ considerably between systems and is thought to reflect the size-spectrum of food items, mostly phytoplankton, exploited (Dolan *et al.* 2009). The species pool of Southern Ocean tintinnids, excluding species recorded but once (strays and questionable species), numbers 120. This large number of



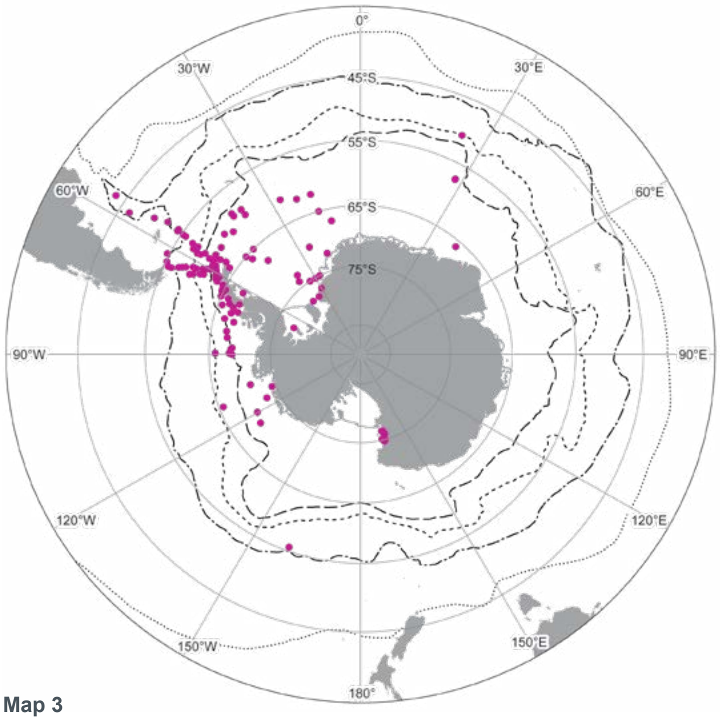
Map 1

● Records of Tintinnida south of 40°S



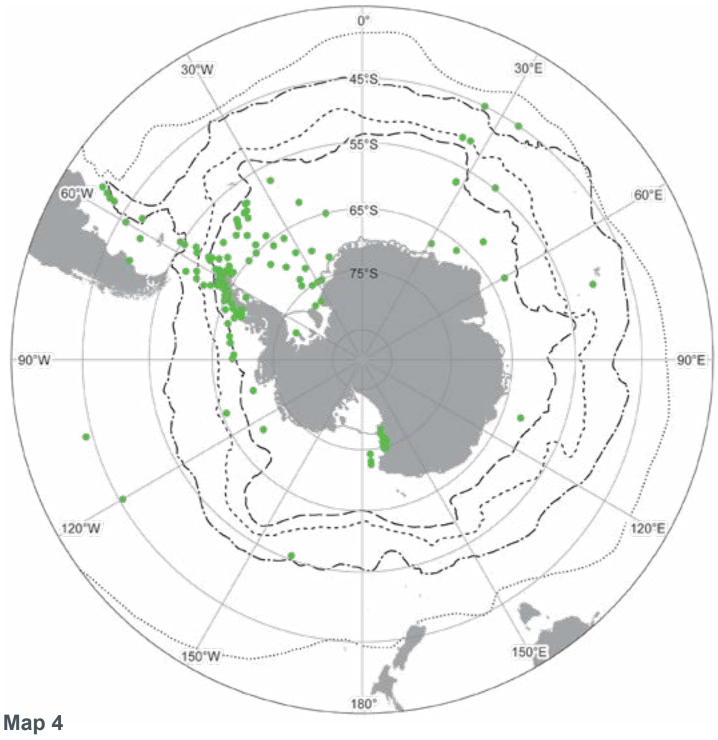
Map 2

● *Cymatocylis* spp.



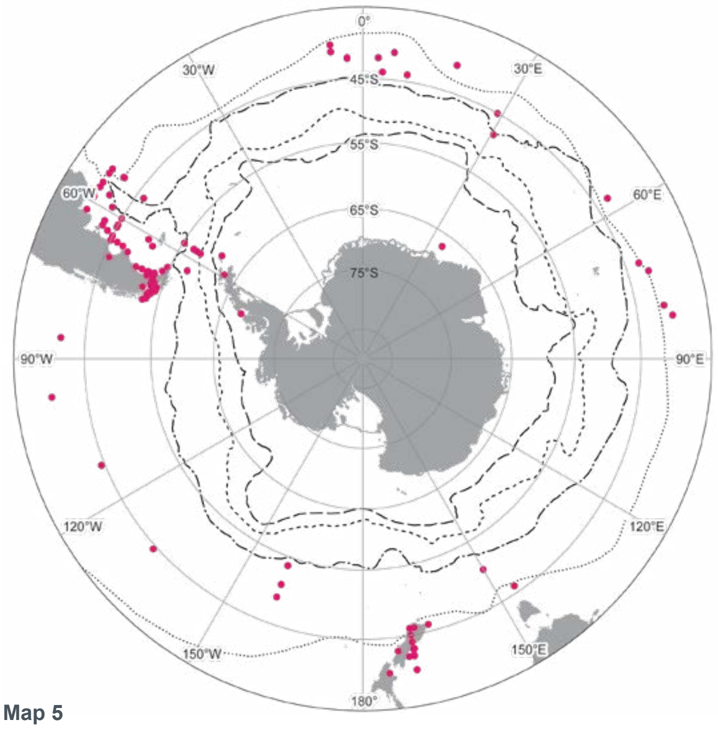
Map 3

● *Laackmanniella* spp.



Map 4

● Records of species endemic to the southern Ocean



Map 5

● Records of widespread species in the Southern Ocean

Tintinnida Maps 1–5 Map 1. Locations of all Southern Ocean sites from which tintinnids have been reported. Map 2. Location of sites from which *Cymatocylis* spp. have been reported. Map 3. Location of sites from which *Laackmanniella* spp. have been reported. Map 4. Locations from which only endemic tintinnid species have been reported; they are located mostly within the area confined by the average location of the Polar Front. Map 5. Locations from which only widespread tintinnid species were found; they are located largely in the northern portion of the Southern Ocean. Note that these sites do not represent the totality of reports (see map 2). Thus, mixed communities were found at some sites both within and outside the Polar Front.

species includes a very wide range of lorica oral diameters, approximately as wide as the global tintinnid species catalogue. The most common size classes of oral diameters are between 40 and 50 µm suggesting that most species likely exploit prey of 10–15 µm in size with the second peak of large-mouthed forms exploiting prey of about 30 µm in size. Among the tintinnids of the Southern Ocean, the endemic species appear to show a characteristic which distinguishes them from the widespread species found in the Southern Ocean. A considerable portion of the endemic species have very large oral diameters (>100 µm) while most of the widespread species have oral diameters between 40 and 60 µm in size (Photo 1).

The species typical of the Southern Ocean includes some which agglutinate particulate matter into the lorica, for example species of *Laackmaniella* and *Stenosomella*. Agglutination does not appear to be highly selective in these Southern Ocean species (Wasik *et al.* 1996). This is in contrast to other tintinnid species such as certain in the genera of *Codonella* and *Dictyocysta* which symetrically arrange coccoliths from a just few species of coccolithophoride phytoplankton (e.g. Lohmann 1912). *Laackmaniella* uses frustules from several different diatom species (Photo 1). At least with regard to *Stenosomella*, the type of particle used, coccoliths or diatom remains, seems to simply reflect their relative abundance in the water column (Henjes & Assmy 2008).

The abundances of tintinnids usually parallel those of other microzooplankton such as oligotrich ciliates and heterotrophic dinoflagellates. The highest concentrations of tintinnids, as well as other microzooplankters, have been reported to be associated with the ice edge during the Antarctic summer (Alder & Boltovskoy 1991). In a recent study of the Palmer Antarctica Long Term Ecological Research Area (Garzio & Steinberg 2013), tintinnids in January 2010 and 2011 were found in average abundances of about 30–40 per liter in the upper 100 m of the water column, representing 5–10% of total microzooplankton biomass. Certain species do appear to be associated with particular areas. Polynya sites, characterised by dense phytoplankton populations of *Phaeocystis,* contain mostly the Southern Ocean endemic species of *Cymatocylis* and *Laackmanniella* (Dolan *et al.* 2013).

6. Southern Ocean and Arctic tintinnids

There are some striking similarities comparing Arctic and Southern Ocean tintintinnid assemblages. Like the Southern Ocean assemblages, the tintinnid fauna of the Arctic Biome is a mixture of forms apparently restricted to the biome, species of the genera *Parafavella* and *Ptychocylis* as well as many widespread species (e.g. Burkovsky 1976). Some of the widespread species found in Arctic assemblages are also common in the Southern Ocean such as *Helicostomella subulata* and *Codonellopsis pusilla*. Both Arctic and Antarctic assemblages contain the "bipolar" species *Acanthostomella norvegica*.

One of the peculiarities of tintinnid genera largely restricted to the Arctic, the genera *Parafavella* and *Ptychocylis*, is shared by the Antarctic genera *Cymatocylis* and *Laackmanniella*. These genera all contain large numbers of different morphotypes, historically distinguished as species for the most part. These different morphologies can be shown to be a continuum, at least with regard to forms of *Cymatocylis* in which the 50 described species form but 5 statistically distinguishable morphotypes (Williams *et al.* 1994). Recently many of these distinct morphotypes have been shown to be genetically identical (Kim *et al.* 2013). Similarly, many of the 23 species of the Arctic *Parafavella* and 12 species *Ptychocylis* appear to be indistinguishable (Davis 1978, Davis 1980). Thus, the endemic forms of both Antarctica and the Arctic appear to be highly polymorphic with only the lorica oral diameter as a consistent, conservative, character. It may well be that through genetic studies the Arctic forms, species of *Parafavella* and *Ptychocylis* will also prove to be polymorphic. Unfortunately, the mechanisms underlying polymorphism are unknown. In both Arctic and Antarctic assemblages, "coxiella" forms are often abundant (e.g. Burkovsky 1976, Brandini 1993). The coxiella form appears to be an aberrant morphology of a not fully developed lorica, perhaps characteristic of a rapidly-growing population (Laval-Peuto 1977). Speculatively, we suggest that polymorphism in the Antarctic taxa may be associated with the occurrence of population growth in rapid, short-lived bursts with a consequence of cell division rates exceeding normal lorica-formation rates.

7. Conclusions

Tintinnids are at once a typical and unusual group of organisms for the Southern Ocean. As is the case for many taxa, there are genera and species of tintinnids found only in the Southern Ocean as well as bipolar species and many species found in the Southern Ocean are commonly considered cosmopolitan or widespread. The assemblage is unusual in terms of species richness, especially considering that tintinnids represent a very small portion, usually less than 5% of individuals, of the functional group of microzooplankton. The assemblage is also unusual as very large forms, species of *Cymatocylis*, are common and polymorphic species seem to be relatively common as well. Endemic forms, those restricted to the Southern Ocean can be distinguished from widespread species of tintinnids found in the Southern Ocean. In terms of geographic distribution, endemics are often the only forms found inside the Polar Front (Map 4) and many are characterised by unusually large oral diameters. While we can make such general statements concerning distributions and morphology, unfortunately, we lack even the most basic data on the ecology of individual species and the assemblage as a whole. For example, there are no data whatsoever concerning growth rates nor feeding rates of species from the Southern Ocean. Such ignorance considerably complicates the examination of fundamental questions which well merit examination. How can so many different forms successfully exploit waters of extreme seasonality? Is polymorphism an adaptation to or rather a consequence of a variable environment? We can only hope that future field work in Southern Ocean waters will include special attention to these intriguing organisms which are often neglected (e.g. Griffiths 2010).

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