

# Global biogeography of marine tintinnids

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**ABSTRACT:** Literature records of tintinnid distributions (272 references, 1899 to 1992) were plotted with a computer. Distributions at the genus level revealed several distinct biogeographic patterns: cosmopolitan, neritic, warm-water, boreal, and austral. Some of the factors that may account for these patterns are examined. At the species level, certain disjunct distributions are examined, including the bipolar distribution of *Acanthostomella norvegica* and the interoceanic distributions of tropical tintinnids. Endemicism of species within certain genera, such as *Codonellopsis*, was also found.

## INTRODUCTION

Tintinnids (Protozoa, Ciliata) have been known to marine biologists since the beginnings of plankton study (Haeckel 1873, Daday 1887), and records for tintinnid occurrences appear from all the oceans of the world (Pierce & Turner 1992). Tintinnid biogeographic distributions in relation to hydrography are well-known for certain areas including the North Atlantic (Campbell 1942, Gaarder 1946, Zeitzschel 1966, 1967, Lindley 1975), South Atlantic (Balech 1971, Souto 1981), Pacific (Kofoid & Campbell 1939, Campbell 1942, Balech 1962), Mediterranean Sea (Jørgensen 1924, Balech 1959, Travers & Travers 1971, Travers 1973), western Arabian Sea (Zeitzschel 1969, 1982), the coast of India (Krishnamurthy et al. 1979, Naidu & Krishnamurthy 1985), the Adriatic Sea (Krsinic 1982, 1987a, b, 1988), the front between the Oyashio and Kuroshio Currents (Yamamoto et al. 1981, Taniguchi 1983) and the Southern Ocean (Laackmann 1907, 1909, Balech 1958a, b, 1971, 1973, Boltovskoy et al. 1989, Alder & Boltovskoy 1991a, b). Tintinnids as indicators of upwelling have also been investigated by Balech (1972). Nonetheless, a global synthesis of tintinnid biogeography has not emerged.

A major barrier to defining tintinnid biogeography is poor understanding of tintinnid taxonomy. This

taxonomy is based upon morphology of the lorica, or shell. Because tintinnid loricae are relatively sturdy, preserve well and are captured in fine-meshed plankton nets, there are many records of tintinnid occurrences scattered throughout the literature. In addition to studies on tintinnids or microzooplankton, many such records come from collection in phytoplankton samples. Tintinnid loricae have also left a fossil record dating back to the Ordovician (Tappan & Loeblich 1973). Unfortunately, from a taxonomic point of view, sizes and shapes of tintinnid loricae are highly variable within species. This variability has led to a proliferation of described species, many of which are probably not valid. Recent re-examinations of several tintinnid species and genera have resulted in suggestions to reduce many species to synonyms (Burkovskii 1973, Bakker & Phaff 1976, Davis 1978, 1981, Laval-Peuto 1981, 1983, Laval-Peuto & Brownlee 1986, van der Spoel 1986, Boltovskoy et al. 1990). The protargol silver-staining technique, which allows comparisons of infraciliary patterns, is used with increasing frequency for tintinnid taxonomy (Brownlee 1977, Sniezek et al. 1991, Snyder & Brownlee 1991, Choi et al. 1992).

Due to their hard loricae, tintinnids are the best known group of marine ciliates, but the durability of loricae can also cause problems. Collection with plankton nets has been found to cause tintinnids to abandon loricae (Paranjape & Gold 1982), and preservation may also destroy the fragile ciliate cell, leaving the lorica unaffected. Empty loricae sink at rates of up to  $1.5 \text{ m d}^{-1}$  (Smayda & Bienfang 1983), and

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loricae of estuarine tintinnids can be carried hundreds of kilometers offshore before settling to the sediments (Echols & Fowler 1973). Thus, it is difficult to tell if empty loricae in samples were occupied at the time of collection, or were abandoned and transported to different areas by currents. For biogeographic studies, it is important to know where an organism lives. Once this has been established, the presence of empty loricae of alien species can be used as indicators of unusual water mass movements.

## METHODS

Information on tintinnid distributions came from the 272 references listed in the Appendix. A data base was constructed using species name, and latitude and longitude of collection. When coordinates were not given, they were approximated based on either location names or maps included in the work. The resulting data base includes over 17 000 records, from more than 1400 locations (Fig. 1).

This data base was then used to produce maps showing the reports of each tintinnid genus. Six distribution patterns emerged from these maps: cosmopolitan, warm-water, neritic, boreal, austral, and tropical Pacific. The criteria used in selecting these distributions are discussed under each distribution. Genera were then fit by eye and assigned to these categories. A few minor genera did not have enough data for assignment to any distributional category.

In order to use as much of the data as possible, only the presence of a tintinnid at a particular location was used. While this approach ignores much useful infor-

mation in the form of water temperature, salinity, and depth of occurrence, it also allows for the inclusion of data that would otherwise be unusable. In addition to surveys and seasonal studies on tintinnids, information was also obtained from phytoplankton surveys and from larval fish and zooplankton feeding studies. Thus, although over 1400 locations have been included, many locations have only been sampled once, or did not identify all tintinnids which occur at that location.

Genus was used for plotting distributions for 3 reasons: it eliminates many taxonomic problems due to possible species misidentifications or synonymy; many of the approximately 900 described tintinnid species are represented by fewer than 15 recorded occurrences; and use of genus allows inclusion of data from phytoplankton surveys and larval fish feeding studies where only genus-level identification of tintinnids is common.

The use of genus also has limitations. Although taxonomic groups such as genus are ideally monophyletic, limitations in our knowledge often result in genera that are artificial (Balech 1975, Laval-Peuto 1981, 1983). Additionally, all members of a genus do not necessarily share the same biogeographic distribution. Thus, although a genus may have a cosmopolitan distribution due to many scattered species, no single species within the genus necessarily has a cosmopolitan distribution. Therefore, some species-level distributions have been included where appropriate.

## RESULTS AND DISCUSSION

Table 1 assigns most of the extant tintinnid genera to a biogeographic distribution category. Specific examples from each type of distribution are given in Figs. 2 to 18. We also discuss each type of distribution, and some of the physical and biological factors which may contribute to these distributions.

### Cosmopolitan distribution

Both Kofoid (1915) and Campbell (1954) considered most species of tintinnids to have cosmopolitan distributions, believing that most exceptions were due to incomplete sampling. Fig. 1 shows the locations of all data points used in our survey. Although large areas of the world ocean have not yet been sampled for tintinnids, enough data exist to determine that most genera are not cosmopolitan. Here we define cosmopolitan as occurring in all oceans from the Arctic, through the tropics, and into the Ant-

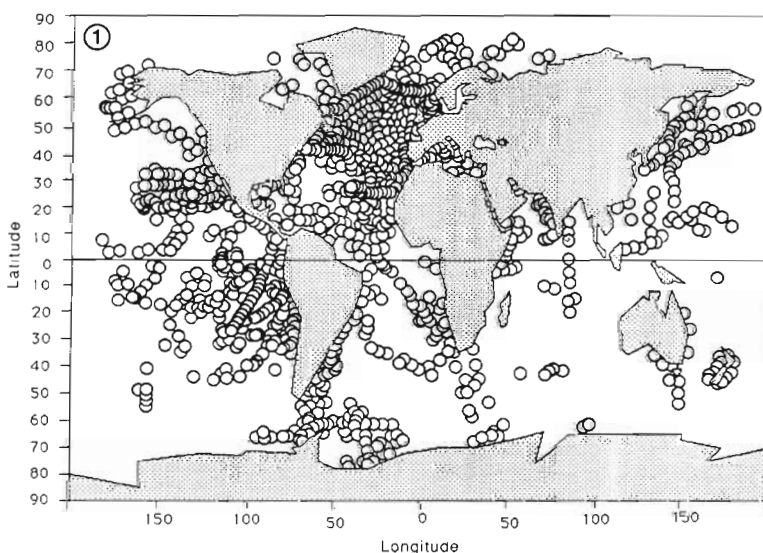


Fig. 1. Locations of all occurrences used in this survey ( $n > 1400$ )

Table 1. Biogeographic distribution of tintinnid genera

<b>Cosmopolitan</b>	<b>Warm water</b>
<i>Acanthostomella</i>	<i>Amplectella</i>
<i>Amphorellopsis</i>	<i>Ascampbelliella</i>
<i>Amphorides</i>	<i>Brandtiella</i>
<i>Codonella</i>	<i>Canthariella</i>
<i>Codonellopsis</i>	<i>Climacocylys</i>
<i>Coxliella</i>	<i>Codonaria</i>
<i>Dictyocysta</i>	<i>Cyrtarocylys</i>
<i>Epiplocylys</i>	<i>Dadayiella</i>
<i>Eutintinnus</i>	<i>Daturella</i>
<i>Ormosella</i>	<i>Epicancellula</i>
<i>Parundella</i>	<i>Epicranella</i>
<i>Protorhabdonella</i>	<i>Epiplocyloides</i>
<i>Salpingacantha</i>	<i>Epiorella</i>
<i>Salpingella</i>	<i>Epirhabdonella</i>
<i>Steenstrupiella</i>	<i>Petalotricha</i>
<i>Undella</i>	<i>Poroeucus</i>
<b>Neritic</b>	<i>Rhabdonella</i>
<i>Favella</i>	<i>Rhabdonellopsis</i>
<i>Helicostomella</i>	<i>Rhabdosella</i>
<i>Leprotintinnus</i>	<i>Stelidiella</i>
<i>Metacyclis</i>	<i>Undellopsis</i>
<i>Stenosemella</i>	<i>Xystonella</i>
<i>Stylicauda</i>	<i>Xystonellopsis</i>
<i>Tintinnopsis</i>	<b>Tropical Pacific</b>
<b>Boreal</b>	<i>Amplectellopsis</i>
<i>Parafavella</i>	<i>Codonopsis</i>
<i>Ptychocylys</i>	<i>Cricundella</i>
<b>Austral</b>	
<i>Cymatocylys</i>	
<i>Laackmanniella</i>	

### Endemicism

Although a genus may show a cosmopolitan distribution, this is not necessarily true for all the species within the genus. Fig. 4 shows the distributions of 3 species of *Codonellopsis*. *C. lagenula* is restricted to the North Atlantic and Mediterranean (Jørgensen 1924, Gaarder 1946, Lindley 1975), *C. gaussi* to the Southern Ocean (Laackmann 1907, 1909, Balech 1958a, b, 1971, 1973, Boltovskoy et al. 1989, Wasik & Mikolajczyk 1990, Alder & Boltovskoy 1991b), and *C. ecaudata* is found only in the tropical Pacific and Indian Oceans (Kofoid & Campbell 1939, Campbell 1942, Balech 1962, Zeitzschel 1982). Note that these distributions are tentative, as the cellular morphology of none of these species is known.

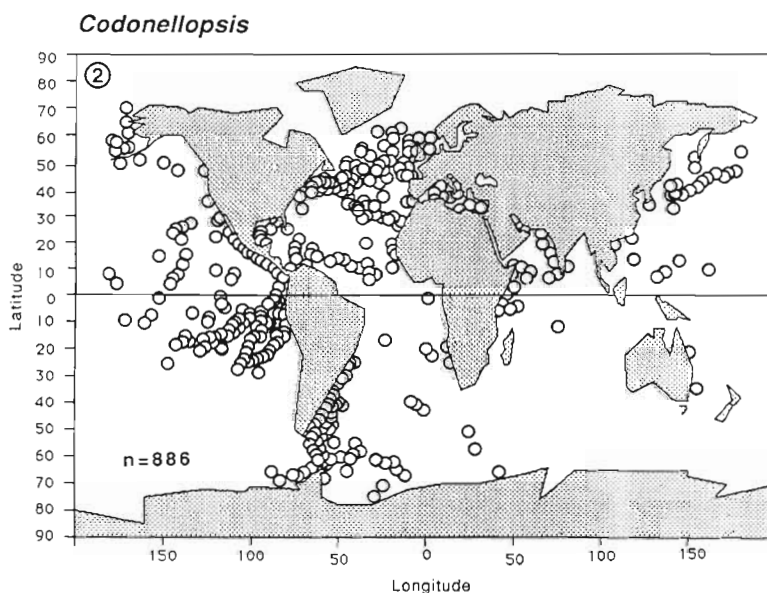
Because of taxonomic problems, it is uncertain how many tintinnids are endemic, but as an example, there are 103 species of genus *Tintinnopsis* listed in our data base. Of these, 27 have only been reported once, and another 11 can also be considered endemics. While many of these species are no doubt synonyms, and our data base does not contain every record ever reported, this endemicism of species within widely distributed genera appears to be a common pattern for tintinnids.

### Neritic distribution

Seven tintinnid genera have been found to be neritic, or restricted to relatively shallow waters. These include the genera *Tintinnopsis* (Fig. 5), *Stenosemella*

arctic, with no restrictions as to distance from shore. Cosmopolitan species do not necessarily occur in high arctic or antarctic waters, but they must occur in cold waters near these areas. It would not be unexpected to find species from cosmopolitan genera in any sample from marine waters. *Codonellopsis* (Fig. 2) and *Salpingella* (Fig. 3) are examples of genera showing cosmopolitan distributions. A total of 16 genera including *Coxliella* share this type of distribution (Table 1).

The inclusion of the genus *Coxliella* is somewhat problematic, however, since it has been shown that *C. annulata* and *C. decipiens* are phenotypic variations of *Favella eherenbergii* (Laval-Peuto 1981, 1983). It is unknown if the remaining members of the genus are valid species or alternate phenotypes of existing species, but Corliss (1979) suggested replacing the family name Coxliellidae with the name Metacyclididae as it is questionable if any valid *Coxliella* exist.

Fig. 2. Global distribution of the genus *Codonellopsis*



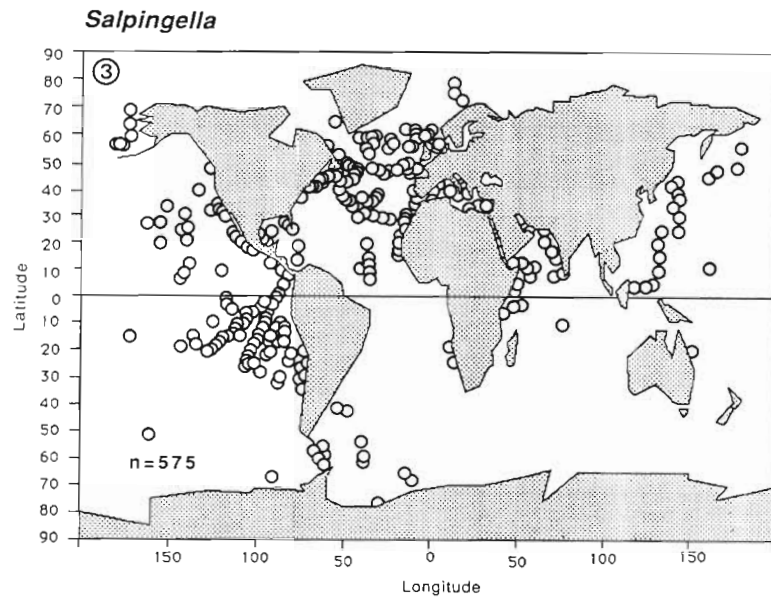


Fig. 3. Global distribution of the genus *Salpingella*

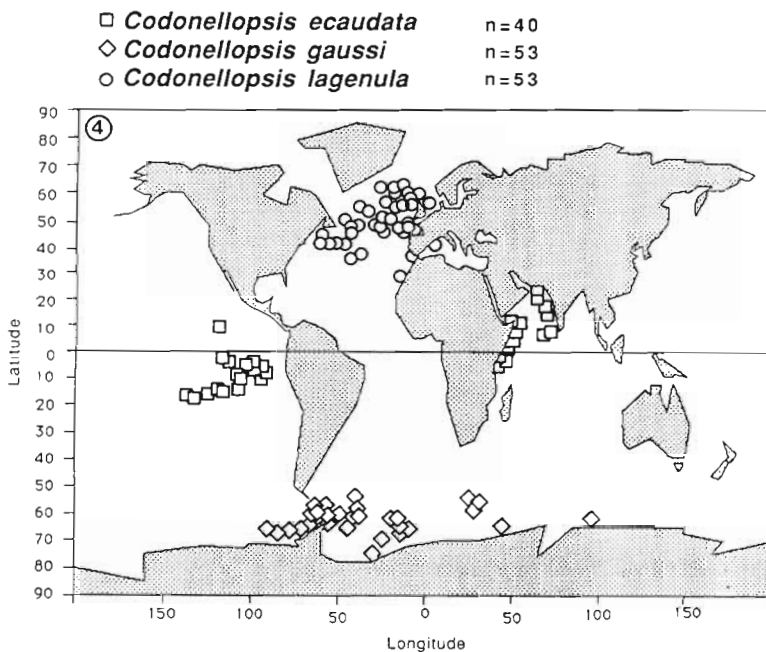


Fig. 4. Global distribution of *Codonellopsis ecaudata*, *Codonellopsis gaussi*, and *Codonellopsis lagenula*

(Fig. 6), *Helicostomella* (Fig. 7) and *Favella* (not shown). These are the most familiar genera upon which all but a few of the laboratory experiments on feeding or other aspects of tintinnid ecology have been done. Although neritic tintinnids may be collected offshore, this usually occurs in a major ocean current that has previously traveled along the coast, or near islands.

Neritic genera exhibit several characteristics that may limit their distributions. *Tintinnopsis*, *Stenosemella*, *Stylicauda*, and *Leprotintinnus* are noted for the incorporation of mineral flakes into loricae. Although other genera contain species that incorporate particles into their loricae, all species within these four genera do so. When offshore species of other genera such as *Codonella*, *Codonaria*, *Codonellopsis* and *Dictyocysta* incorporate particles into the lorica, coccoliths are typically used (Gold & Morales 1977, Takahashi & Ling 1984). In culture, when deprived of suitable particles, *Tintinnopsis* produces a clear, but much weaker lorica (Gold & Morales 1976). If mineral flakes are required to strengthen the loricae, tintinnids such as *Tintinnopsis* and *Stenosemella* may be restricted to shallow waters where these particles are readily available. Not all neritic tintinnids incorporate particles in loricae, however, as demonstrated by *Favella* and *Helicostomella*.

Another characteristic of neritic tintinnids is the production of resting cysts. Cysts have been found in *Tintinnopsis*, *Stenosemella*, *Leprotintinnus*, *Favella*, and *Helicostomella*. Other genera known to produce resting cysts include: *Acanthostomella*, *Amphorides*, *Cyttarocyllis*, *Eutintinnus*, *Parafavella*, *Parundella*, *Rhabdonella*, and *Salpingella* (Reid & John 1978). Smayda (1958) noted that many neritic diatoms also produce resting cysts, although not all such species do so.

In shallow waters tintinnid cysts typically sink and are found in the sediments (Krsinic 1987a, Kamiyana & Aizawa 1990). When appropriate conditions are provided, excystment and repopulation of the plankton occurs rapidly (Kamiyana & Aizawa 1990, 1992). Darkness inhibits excystment, suggesting that most cysts must be mixed back into the water column before excystment can occur (Kamiyama & Aizawa 1992). Cysts may be of little value for oceanic species, because once cysts

sink below the mixed layer, it is doubtful that they would ever be recruited back into the epipelagic population.

#### Warm-water distribution

The largest number of genera occur in tropical and temperate waters of the world's oceans (Table 1).

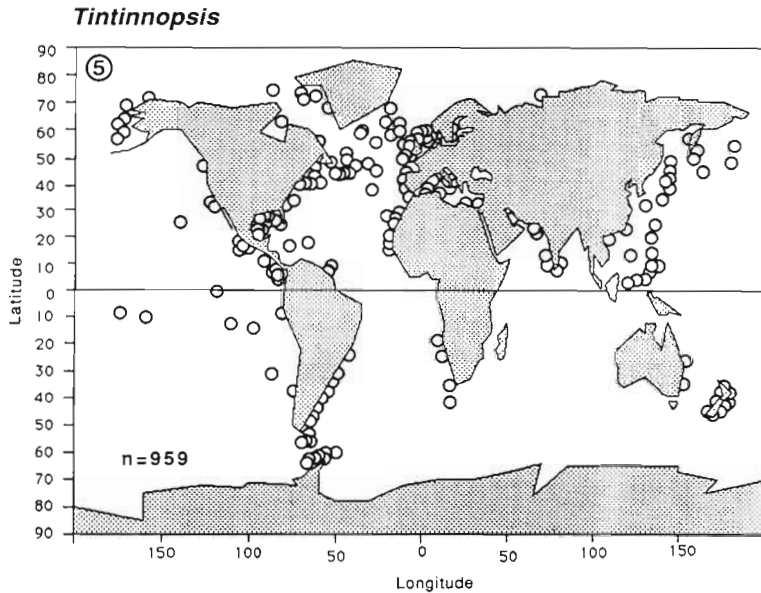


Fig. 5. Global distribution of the genus *Tintinnopsis*

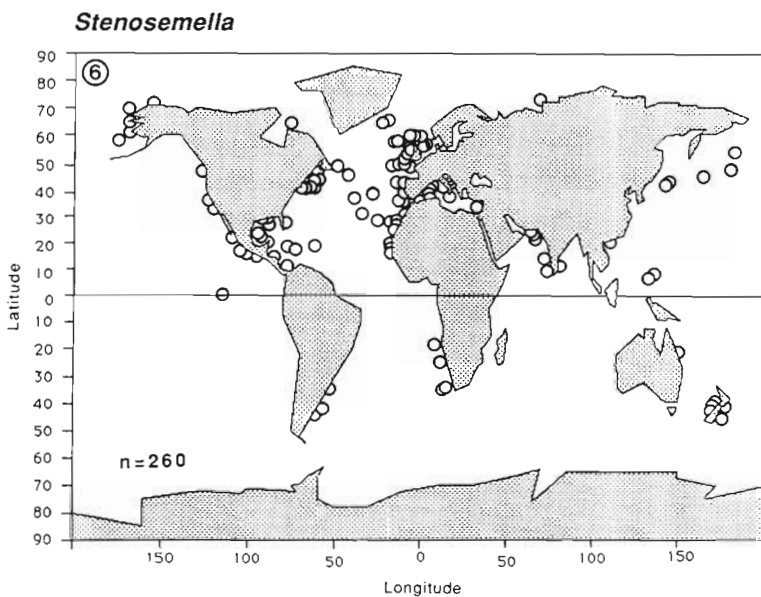


Fig. 6. Global distribution of the genus *Stenosemella*

Although records of occurrence rather than water temperatures were criteria for assigning this distribution, 2 examples, *Petalotricha* (Fig. 8) and *Rhabdonellopsis* (Fig. 9), suggest that distributions of these genera in the North Atlantic are limited by the Gulf Stream. The poleward distribution of warm-water species is probably limited by seasons, and fluctuations in mean axes or meanderings of warm currents.

Although the distributions of genera may easily be explained by past connections between the oceans,

there is an enigma with the circumglobal warm-water distribution at the species level. The distributions of *Petalotricha ampulla* (Fig. 10) and *Rhabdonellopsis apophysata* (Fig. 11) are 2 examples of species with circumglobal warm-water distributions. Although it is unknown if the Atlantic and Pacific populations of these tintinnids are isolated, their distributions suggest that genetic interchange between these populations would be rare. It may be that these species attained circumglobal distributions before the emergence of the Central American Isthmus, and that their present distribution is a relict of previous times. Alternatively, Atlantic and Pacific populations of these and similarly distributed planktonic organisms may be analagous species (Shih 1986).

Analagous species are species that were once considered to be widely distributed, but show subtle differences which justify splitting a single taxon into multiple distinct species. Analagous species typically occupy similar latitudinal ranges in different oceans. Shih (1979, 1986) discussed how this applies to several calanoid copepods, most notably *Calanus finmarchicus*. Prior to 1948, *C. finmarchicus* was considered to be widely distributed throughout the northern hemisphere and around the southern portions of South America, Africa, Australia and New Guinea. Presently the *C. finmarchicus* species group has been split into 8 species, each with more restricted but sometimes overlapping distributions. Although there is evidence that some copepod morphology is the result of phenotypic variation due to environmental factors, Frost (1989) and Sevigny et al. (1989) showed that subtle morphological differences in the copepod genus *Pseudocalanus* are supported by biochemical evidence for these differences.

The determination of analagous species in tintinnids is complicated by the large amount of morphological variation of the loricae within a species (Burkovskii 1973, Bakker & Phaff 1976, Davis 1978, 1981, Laval-Peuto 1981, 1983, Laval-Peuto & Brownlee 1986, van der Spoel 1986, Boltovskoy et al. 1990). This requires the application of techniques to



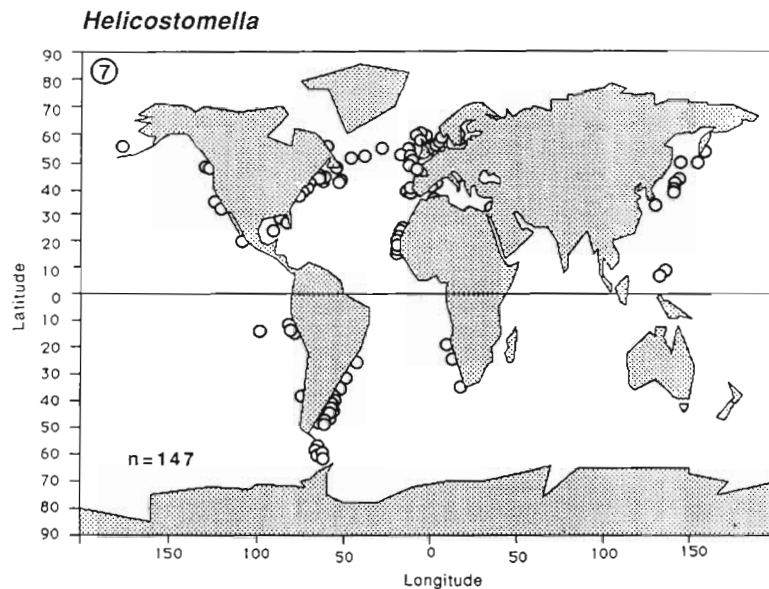


Fig. 7 Global distribution of the genus *Helicostomella*

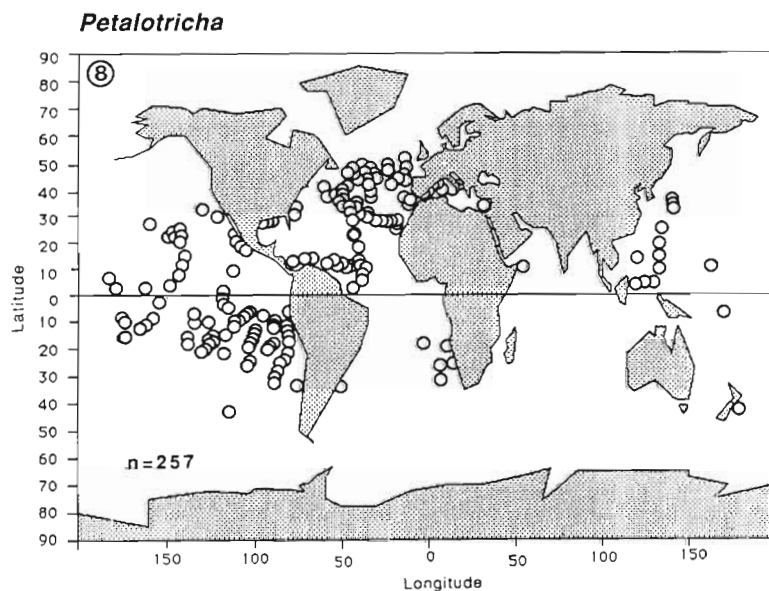


Fig. 8. Global distribution of the genus *Petalotricha*

examine the tintinnid cell. Unfortunately, neither genetic nor cell morphological differences between populations of any tintinnid species have been studied. Thus, the true nature of many tintinnid species distributions will likely remain enigmatic until such study is done.

A special subset of the warm-water distribution is found in three genera restricted to the tropical Pacific, namely *Amplectellopsis* (Fig. 12) and *Codonopsis* (not shown) and *Cricundella* (Fig. 13). These genera are somewhat

problematic in that they are represented by only a few species, often based on few individuals, and records for these genera are rarely reported in the literature. These genera are closely allied with larger, more widely distributed genera, such as *Amplectella* (for *Amplectellopsis*), *Codonella* (for *Codonopsis*), and *Undella* (for *Cricundella*). Thus, many of the species within these 3 genera may be aberrant individuals of these larger genera.

### Boreal distribution

Two genera, *Parafavella* (Fig. 14) and *Ptychocylis* (Fig. 15), have long been known to be restricted to cold waters in the Northern Hemisphere. These tintinnids are not truly arctic as they are often found in subarctic waters (Kofoid & Campbell 1929). Cape Hatteras is a well-known biogeographic boundary on the American east coast (Ekman 1953, Pielou 1979), and appears to be the southern limit of these tintinnids in the western Atlantic. Cape Hatteras is near the area where the Gulf Stream turns away from the coast and is deflected eastward. Similarly, in the North Pacific, the Kuroshio Current acts as the southern boundary for these species. As with warm-water genera, records of occurrence rather than water temperatures were used in assigning boreal distributions. There is an area of overlap between the warm and cold-water distributions, which probably represents changes in tintinnid fauna due to seasonal temperature changes, or meandering of western boundary currents such as the Gulf Stream or the Kuroshio.

Species identifications within *Parafavella* and *Ptychocylis* are complicated by the fact that both of these genera have been found to show a large amount of lorica variation within a species (Burkovskii 1973, Davis 1978, 1981). It is uncertain how many of the 23 *Parafavella* species described by Kofoid & Campbell (1929) are valid species. Burkovskii (1973) stated that there was so much variation and overlap of *Parafavella* specimens in the White Sea that only one species, *Parafavella denticulata*, was valid. Davis (1978) cautioned that this decision was premature, and that cell morphology must be studied before this determination can be made with confidence.

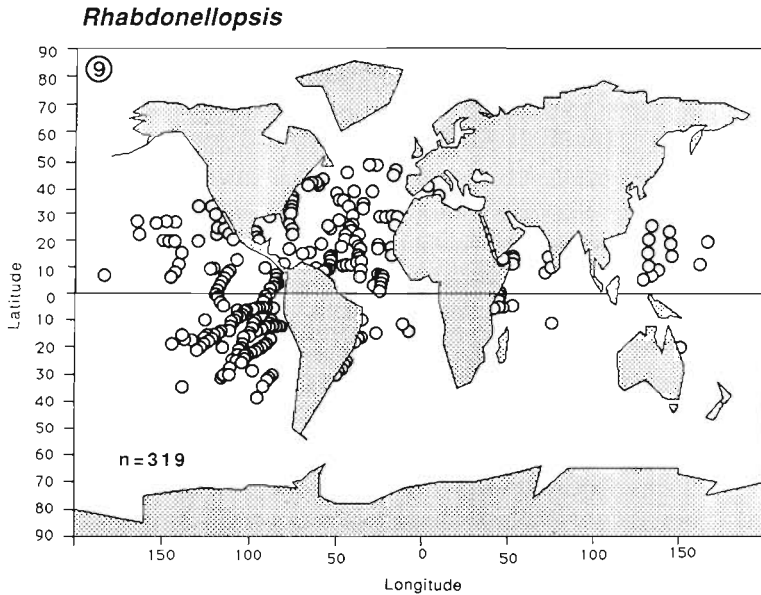


Fig. 9. Global distribution of the genus *Rhabdonellopsis*

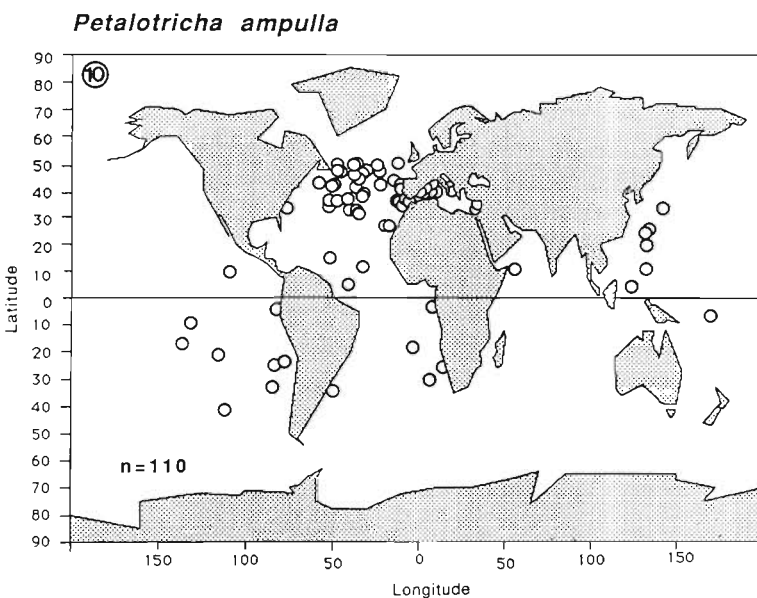


Fig. 10. Global distribution of *Petalotricha ampulla*

#### Austral distribution

Two genera, *Cymatocylix* (Fig. 16) and *Laackmanniella* (Fig. 17) are restricted to antarctic and subantarctic waters. Like its Northern Hemisphere counterparts *Parafavella* and *Ptychocylix*, *Cymatocylix* has been found to show considerable plasticity in lorica structure within a 'species' (van der Spoel 1986, Boltovskoy et al. 1990).

The distributional maps of *Cymatocylix*, *Parafavella*, and *Ptychocylix* all contain records for anomalous

species which should be viewed with skepticism, because they may represent misidentifications.

Northern Hemisphere records for *Cymatocylix* have only been reported by 2 authors, Silva (1953) and Lindley (1975). Silva (1953) reported a single specimen of *C. subconica* from the Lagoa de Obidos on the coast of Portugal. A brief discussion of the taxonomic history of *Cymatocylix* is relevant to understanding the confusion surrounding this genus.

When Kofoid & Campbell (1929) revised the genus *Cymatocylix*, they had to rely mostly on drawings from Laackmann (1909), based on specimens from the 'Deutschen Südpolar-Expedition 1901-1903'. Laackmann had adopted a trinomial system of nomenclature, however, and for each taxon described a forma *typica* followed by numerous 'Formenkreise'. It appears that Laackmann tried to show the typical form of a species, along with variations which occurred. Current thinking regarding the amount of variation of lorica morphology within a species (Burkovskii 1973, Bakker & Phaff 1976, Davis 1978, 1981, Laval-Peuto 1981, 1983, Laval-Peuto & Brownlee 1986, van der Spoel 1986, Boltovskoy et al. 1990), suggests that most of these 'Formenkreise' were aberrant examples with no taxonomic standing of their own. Kofoid & Campbell, however, in trying to adapt Laackmann's trinomial system to a binomial system, chose to raise each 'Formenkreis' to the level of species, cautioning that this was tentative pending re-examination of antarctic material. Unfortunately, Kofoid & Campbell never returned to this genus, and their classification has stood since 1929. Many other genera and species also established by Kofoid & Campbell require substantial revision. Of

the 45 *Cymatocylix* species Kofoid & Campbell (1929) described, only 19 have subsequently been reported in the literature examined for this study.

One of the species raised from the 'Formenkreis' level was *Cymatocylix subconica* (Kofoid & Campbell 1929). This was based on 2 specimens Laackmann named as *Cymatocylix cristalina* forma *conica* and *Cymatocylix flava* forma *conica*. Silva's (1953) single specimen is the only subsequent report of this species since 1929.



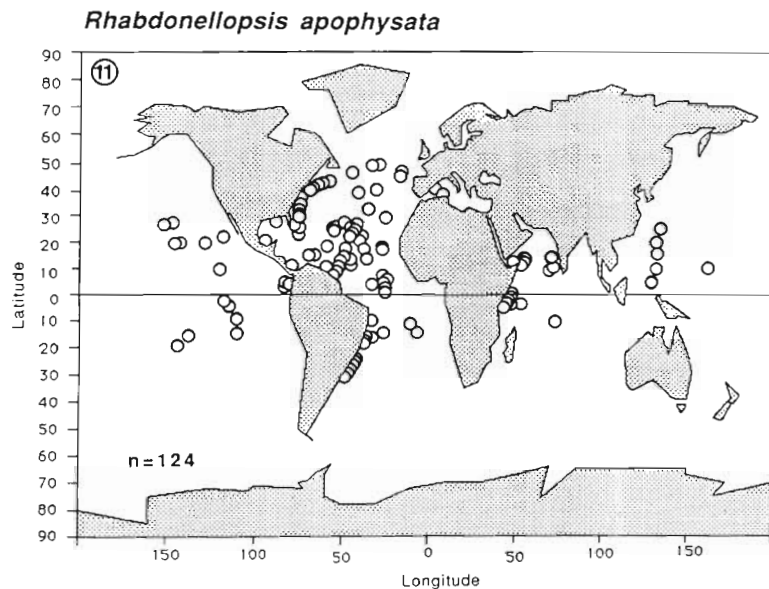


Fig. 11. Global distribution of *Rhabdonellopsis apophysata*

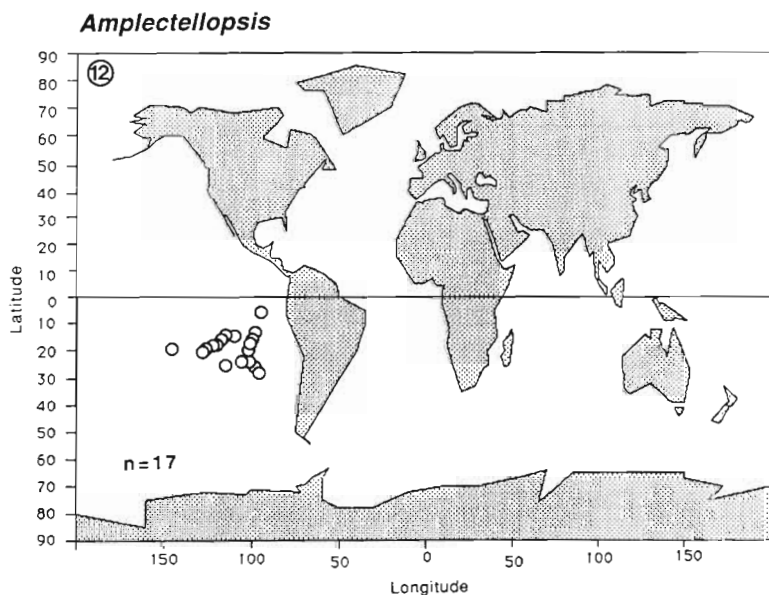


Fig. 12. Global distribution of the genus *Amplectellopsis*

Lindley (1975) also reported at least 13 specimens of an unidentified *Cymatocyclus* species collected with the continuous plankton recorder. This device is possibly not as gentle a method of collection as whole water samples, and although tintinnids are more sturdy than aloriccate ciliates, their loricae are much more fragile than thecate dinoflagellates and copepods which appear to be collected by the continuous plankton recorder with less distortion. Even the weight of a

coverslip will distort many tintinnid loricae such that measurements of the lorica oral diameter are useless for identification. With appropriate measures, such as the use of Sedgwick-Rafter chambers, this problem is avoided. Kofoid (1915) described how distortion of some *Dictyocysta* specimens may have been responsible for the description of a 'new species'. Thus, it is possible that distorted or aberrant specimens of the genus *Ptychocyclus* could easily be mistaken for *Cymatocyclus*. Lindley's records are also puzzling since the North Atlantic is one of the areas which has been well-surveyed for tintinnids, and no other *Cymatocyclus* specimens have been reported. However, Lindley has confirmed that *Cymatocyclus* has been found in subsequent continuous plankton recorder tows in the North Atlantic (pers. comm.).

Tumantseva (1989) reported 24 specimens of *Parafavella brandti* in the subantarctic Pacific, even though other species of this genus appear centered in boreal waters. *P. brandti* is a problematic species, first described by Hada (1932) for specimens which fit the description of *Parafavella gigantea*, but lacked the characteristic oral denticles. Davis (1978) noted that it was not unusual to find a certain number of loricae of *Parafavella* lacking the oral denticles in any given sample, and the presence, absence, or number of oral denticles was not a conservative taxonomic characteristic. However, none of Tumantseva's specimens had oral denticles, otherwise they would have been classified as *P. gigantea*. Species within the genera *Xystonella* and *Cyttarocyclus* possess reticulated loricae which could be confused with the typically hexagonal infrastructure of *Parafavella* loricae. Neither *Cyttarocyclus* or *Xystonella* have the well-defined oral denticles typically present in *Parafavella*.

Rampi (1948) reported *Ptychocyclus urnula* from the Ligurian Sea near San Remo, Italy, but gave no other details except to note that it was rare. *P. urnula* is widespread in both the North Atlantic and North Pacific, but Rampi's is the only record for this genus in the Mediterranean despite 2 extensive surveys of Mediterranean tintinnids (Jørgensen 1924, Balech 1959) and several extensive annual studies (Margalef & Morales 1960, Posta 1963, Travers & Travers 1971,



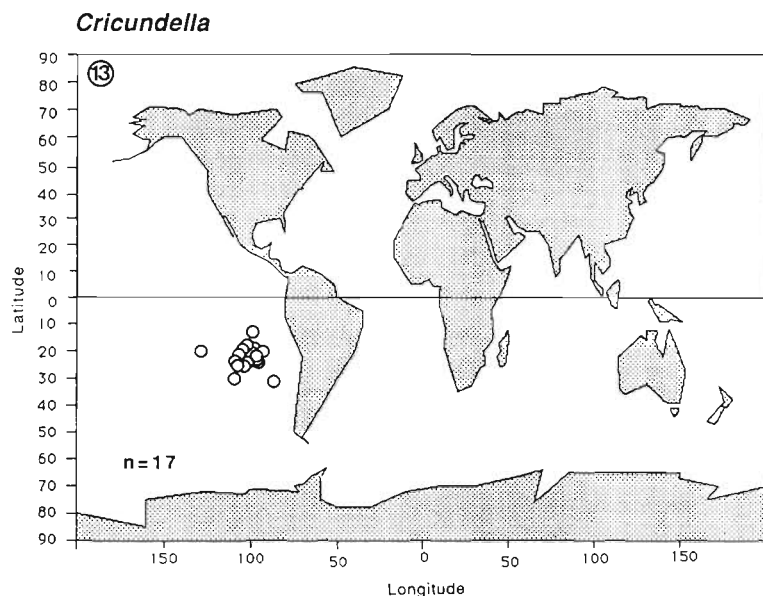


Fig. 13. Global distribution of the genus *Cricundella*

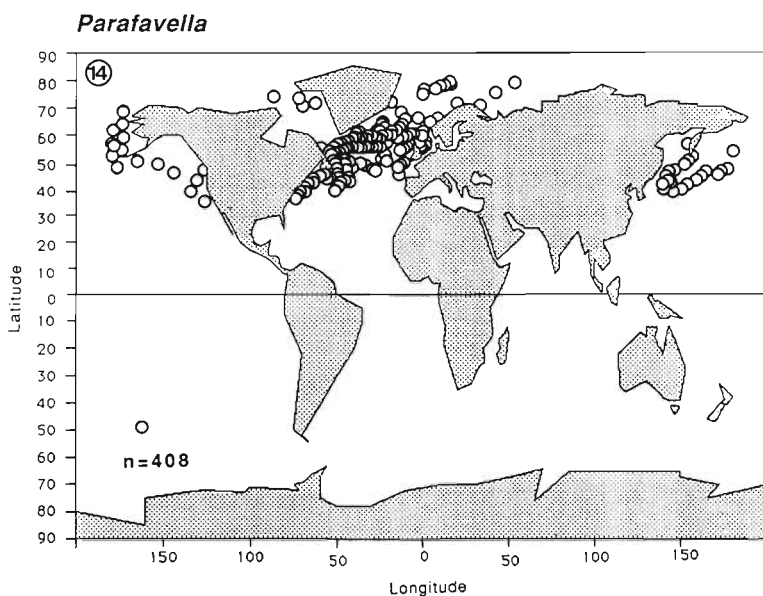


Fig. 14. Global distribution of the genus *Parafavella*

Travers 1973, Rassoulzadegan 1979). Although it is possible that Rampi's record could be an indication of an intrusion of North Atlantic water into the Mediterranean Sea, the distance to the next closest report of *Ptychocylis* (Fig. 15) makes this seem unlikely.

It is interesting that these anomalous records are for genera known to have highly variable lorica morphology, and that these records were based upon very

few specimens. Two of these species are also questionable members of the genus. Since no micrographs or drawings were given, it is impossible to confirm or deny that these reports are other than what the authors believed them to be. Assuming that it would be difficult for these cold water species to survive transport through the tropics, and these genera have been otherwise unreported in often thoroughly surveyed areas, it would not seem unreasonable to reassign these reports to the category of 'unidentified tintinnids', a category which usually accompanies any survey of these organisms.

Knowing the normal biogeographic ranges of certain tintinnid genera, workers who find what appear to be 'out of place' tintinnids would be alerted to the novelty of their find, and could take extra steps to document these range extensions. It would be important to note if loricae of such individuals were empty or damaged, thus suggesting long-distance transport. Conversely, if the loricae were occupied by the ciliate at the time of collection, it seems likely that it was either living where it was caught, or was not transported from a great distance.

### Bipolarity

*Acanthostomella norvegica* (Fig. 18) is the only tintinnid we found to have a bipolar distribution. If real, this distribution is puzzling, since Smayda (1958) argued that bipolarity cannot exist in either the phytoplankton or the zooplankton, suggesting that organisms which appear to show bipolarity are actually cosmopolitan, existing at depth within the tropics. We discuss 4 possible explanations to explain the bipolar distribution of *A. norvegica*. (1) The species may exist at depth in the tropics but has not yet been discovered.

This seems unlikely since, in terms of tintinnids, the North Atlantic has been one of the most thoroughly surveyed locations of the ocean, yet this species has been found only in the colder parts of this area. (2) Since the genus *Acanthostomella* is cosmopolitan (Kofoid & Campbell 1939, Campbell 1942, Gaarder 1946, Balech 1971, Lindley 1975, Taniguchi 1977, Souto 1981), the species *A. norvegica* may be polymorphic and cosmopolitan, existing in the tropics as a

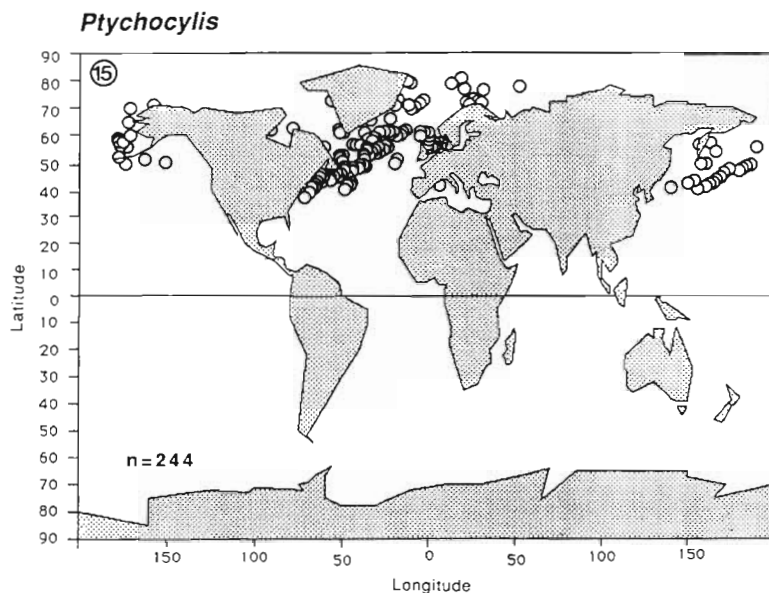


Fig. 15. Global distribution of the genus *Ptychocyliis*

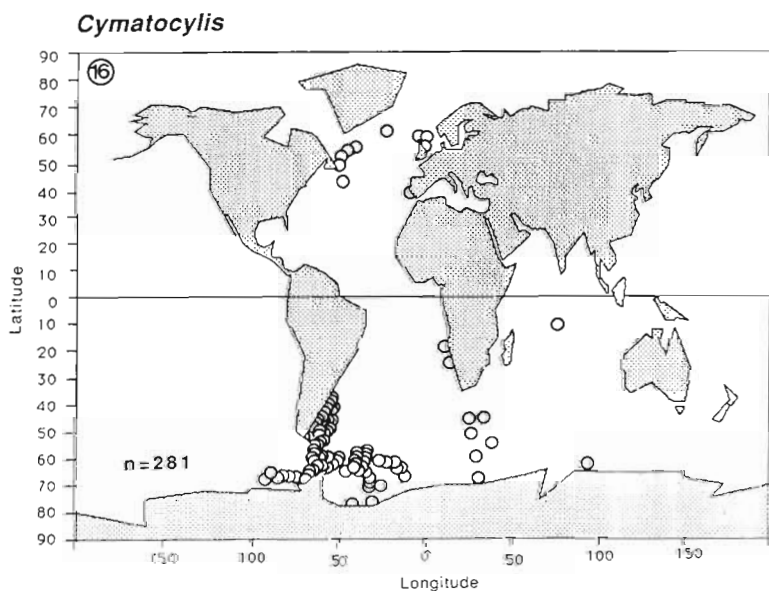


Fig. 16. Global distribution of the genus *Cymatocyliis*

form morphologically different enough from its polar conspecific to be currently considered a different species. Temperature has been shown to cause differences in lorica formation in other species (Gold & Morales 1974, 1975), but most of this variation is in lorica length. Lorica length is recognized as a highly variable character, and does not seem to be a major cause of taxonomic confusion in this case. Also, Taniguchi (1983) found that *A. norvegica* was a good indicator of the cold

Oyashio, but that this species was not collected in the warm Kuroshio. No other member of this genus was present in the Kuroshio even though *A. norvegica* was very abundant in Oyashio waters. (3) The northern and southern populations of *A. norvegica* are possibly an example of convergent evolution within the genus. Unfortunately, we have no information to either support or refute this hypothesis, although the application of genetic techniques and protargol silver staining may give us some insight in the future. (4) *A. norvegica* may have had a continuous distribution in the past, perhaps during the ice ages, but when the tropics warmed the species' distribution contracted toward the poles.

Hypothesis (4) is what Pielou (1979) classified as an evolutionary disjunction. The most notable example of an evolutionary disjunction is demonstrated by the euphausiid *Thysanoessa gregaria*, in which the northern and southern populations have not yet shown any apparent morphological or genetic divergences (Pielou 1979). Pielou also noted, however, that for this mechanism to work, the species involved must be restricted to the upper 200 m of the water column. Below this depth, water is relatively unaffected by atmospheric conditions, and organisms living there can travel more freely from pole to pole.

In one of the few studies on the vertical distribution of tintinnids, Kršinić (1982) found that over 90 % of the tintinnid population in the open waters of the Adriatic Sea lived in the top 100 m of the water column. Those species commonly found at depths of greater than 100 m were rarely found at shallower depths. *Acanthostomella norvegica* is typically found in the surface waters in both parts of its range, and so this distribution may be the result of an evolutionary disjunction.

Unfortunately, the fossil record for tintinnids is incomplete, so we may never be able to further examine this hypothesis. It is also doubtful that the tropics would be cool enough for this species even during periods of glaciation (CLIMAP Project Members 1976).

Smayda (1958) concluded that bipolar distributions are probably not due to the transport of diapausing cysts, and we agree in the case of *Acanthostomella norvegica*, even though this species is known to pro-

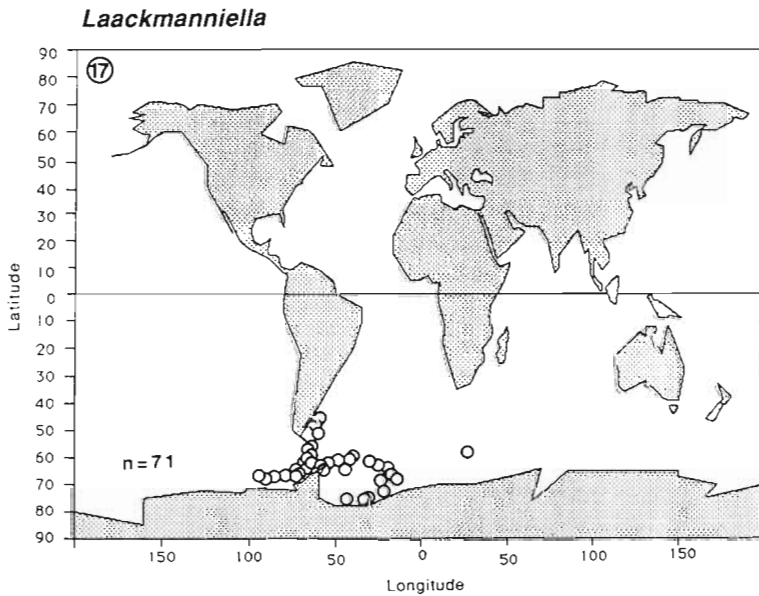


Fig. 17. Global distribution of the genus *Laackmanniella*

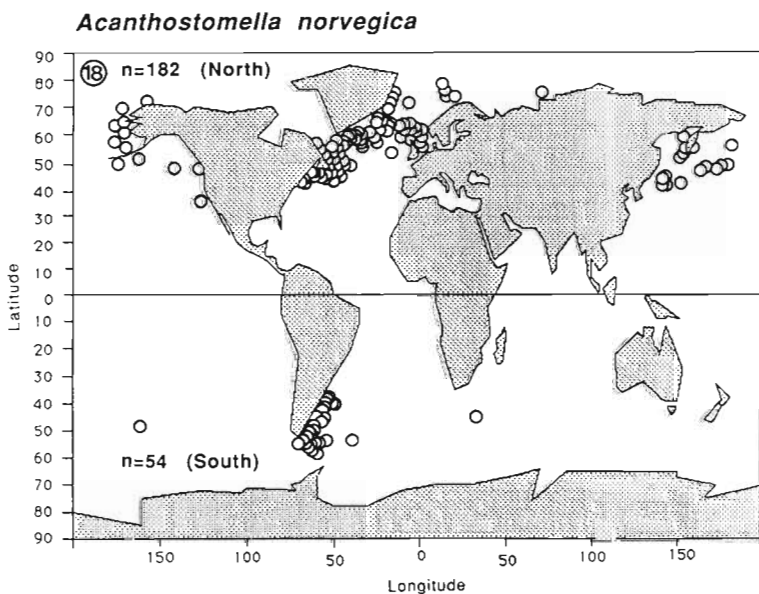


Fig. 18. Global distribution of the genus *Acanthostomella norvegica*

duce resting cysts. Tintinnid cysts probably have high enough sinking rates to be deposited in the benthos under the planktonic range of a species, rendering transoceanic deep transport through the tropics unlikely.

## CONCLUSION

Biogeography is the study of organisms and their distributions in space and time. These distributions are the end sum of all biotic and abiotic factors, and thus a knowledge of biogeography is highly relevant to ecological questions. This investigation shows that tintinnids are an appropriate topic for global biogeographic studies. Although identification at the species level is often problematic, genus may be useful. Laval-Peuto (1981, 1983), however, demonstrated that even genus-level identifications may be complicated in some instances by life-cycle events.

Many of the possible environmental factors limiting tintinnid distributions are discussed in this paper, but the relative importance of these factors to tintinnid distributions remains unclear. There are also many other questions which remain unanswered. For example, how does the presence of empty loricae in plankton samples affect our notions of tintinnid distributions? We do not know much about transport of empty loricae and how long empty loricae remain intact in the water column since sinking rates have only been calculated for a few species (Smayda & Bienfang 1983). Thus, before we can answer the problems regarding tintinnid biogeography, especially their use as indicator organisms, many more questions need to be answered.

## Appendix. Sources of biogeographic data

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|---|--|
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|   | Balech, E. (1958b). <i>Physis, B. Aires</i> , 21: 75-108   |

(Appendix continued on next page)



## Appendix (continued)

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