Contribution to the Themed Section: Scaling from individual plankton to marine ecosystems

HORIZONS

Planktonic protists: little bugs pose big problems for biodiversity assessments

JOHN R. DOLAN[1,2]*

[1]SORBONNE UNIVERSITÉS, UPMC UNIV. PARIS 06, UMR 7093, LABORATOIRE D'OCÉANOGRAPHIE DE VILLEFRANCHE, 06230 VILLEFRANCHE-SUR-MER, FRANCE AND [2]CNRS, UMR 7093, B.P. 28, STATION ZOOLOGIQUE, LABORATOIRE D'OCÉANOGRAPHIE DE VILLEFRANCHE, 06230 VILLEFRANCHE-SUR-MER, FRANCE

*CORRESPONDING AUTHOR: dolan@obs-vlfr.fr

The view that current species inventories (lists of binomial species) of planktonic protists significantly underestimate true diversity is widespread. However, the existence of synonyms in species lists, due to repeated descriptions of the same form, and polymorphism in which different "forms" or life-history stages are but one species, are generally underappreciated. Recent studies have shown that synonyms are probably common, significantly inflating species lists, and taxa previously thought to be distinct species based on morphology have been revealed to be simple variants of single species. Given here are examples from among tintinnid ciliates, dinoflagellates and foraminifera. The commonality of synonyms and the phenomena of both polymorphism and crypticism underscore a need for taxonomic reviews as well as species-focused studies involving molecular biologists, taxonomists and ecologists.

KEYWORDS: cryptic species; dinoflagellate; polymorphism; synonymy; tintinnid

INTRODUCTION

Preceding the widespread adoption of sequencing technologies, cryptic species and polymorphic species received about equal attention. Now there is a very large and growing literature on cryptic species including perhaps most planktonic taxa, both metazoan and protistan. For example, recent studies have described cryptic species in rotifers (Gabaldón and Carmona, 2015), daphniids (Ma *et al.*, 2015), copepods (Halbert *et al.*, 2013; Andrews *et al.*, 2014; Cabrol *et al.*, 2015), as well as tintinnid ciliates (Santoferrara *et al.*, 2015), diatoms (Degerlund *et al.*, 2012; Kaczmarsk *et al.*, 2014), coccolithophores (Bendif *et al.*,

2014), dinoflagellates (John *et al.*, 2014) and even prokaryotes-cyanobacteria (Premanandh *et al.*, 2009). Consequently, cryptic species are now commonly assumed to be the norm in planktonic taxa (e.g. de Vargas *et al.*, 2015). Added to cryptic species, findings of large numbers of sequences from environmental survey's OUT's operational taxonomic units, unattributable to known species or higher taxa (e.g. Massana *et al.*, 2014), it appears that diversity in the plankton is likely far greater than that based on existing lists of binomial species (e.g. WoRMS or ALGAEBASE lists). However, existing species inventories may actually be over-estimates of diversity among some groups of planktonic protists. The inflator of species lists is the existence of synonyms. These "taxonomic errors" can be due to not only to a lack of communication among taxonomists, leading to repeated description of the same species under different names, but also a lack of appreciation of phenotypic variability or polymorphism in planktonic protists. Here I provide some examples among taxa of planktonic protists. At present, the relative importance of crypticism masking diversity or synonymy inflating diversity is simply unknown. Basically, synonymy can result from different sources. Best known perhaps is the error of attributing a new name to a previously described species either due to ignorance of a previous description or raising to species status a minor morphological variety. The second is the phenomenon of polymorphism in which a species exhibits distinct morphologies such that describing the morphs as distinct species could be termed a "justifiable" error. The third is a special case of the preceding in which life-history stages of a single organism are described as distinct species. It should be noted that here we are referring to classically defined binomial species or morpho-species. Here I will discuss examples and hopefully show that in addition to the genetic studies clearly of current interest and effort, there is a pressing need to support careful, critical taxonomic reviews as well as investigations, both laboratory and field, focused on single species if we are to construct realistic species inventories for planktonic protists.

An inconvenient truth: synonyms are common

Among taxonomists, synonymy, the existence of multiple names for the same species is headache regularly dealt with. However, for non-taxonomists, the problem is largely under-appreciated. For example, synonyms in the literature are known to be a problem frequently overlooked in most biodiversity studies, both terrestrial and aquatic (Costello, 2015) concerning almost all taxa. Anecdotally, it has been remarked that while the number of known mammal species is ∼4000, the British Natural History Museum houses type specimens for 9000 species (Gaston and Mound, 1993). The problem is significant. It appears that for marine taxa on average "... for every 5 species described as new to science, at least 2 had already been described" and interestingly, the level of synonymy may scale with intensity of study, e.g. for cetaceans that are certainly well-studied, there are over 1200 names for just 87 species repeatedly discovered (Appeltans *et al.*, 2012). Among the planktonic protists, the tintinnid ciliate re-described as *Rhizodomas tagatazi* by Sacca *et al.* (Saccà *et al.*, 2012) and whose biogeography was recently reviewed (Sacca and Giuffré, 2013) is an example of a planktonic protist that has been repeatedly discovered over the past 90 years.

Rhizodomus tagatzi is a relatively large tintinnid ciliate with a very distinctive morphology (Fig. 1), seemingly difficult to overlook; it is likely that language barriers and descriptions in relatively obscure journals contributed to its repeated discovery. It was probably first described by Busch in 1925 as a form of another species, *Tintinnopsis karajensis* he found in coastal waters of Indonesia, reported and illustrated in a paper in German. In 1950, Strelkow
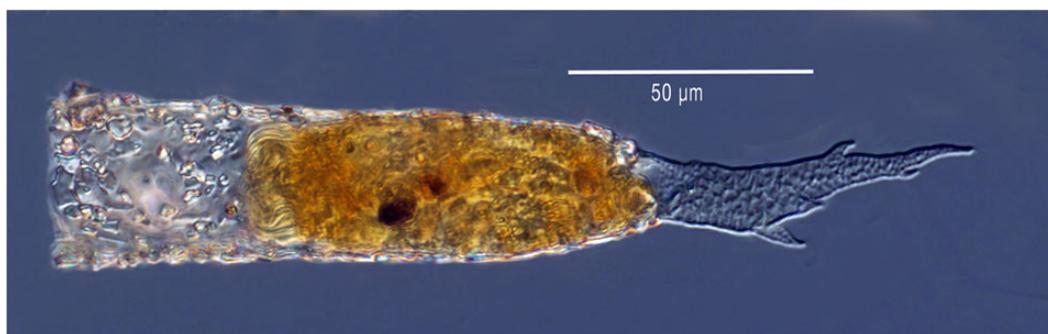

Fig. 1. The species now known as *R. tagatzi* described by Strelkow and Wirketis (Strelkow and wirketis, 1950), formerly described as a variety of *T. karajensis* (Busch, 1925), as well as *T. corniger* (Hada, 1964) and *T. nudicauda* (Paulmier, 1997). Specimen from Sète, France, on the Northwest coast of the Mediterranean Sea, original micrograph.

and Wirketis, in an article on tintinnids from the Pacific coast of Russia, described it as a new genus and species *R. tagatzi*, in a Russian journal. In 1964, Hada described it as *Tintinnopsis corniger* from Japanese coastal waters in English in the *Bulletin of the Suzugamine Women's College*. Some time later, Paulmier (Paulmier, 1997) found it in lagoons in the Western Mediterranean Sea, gave it another name, *Tintinnopsis nudicauda* and published his discovery in a French language research institute report. This later name, although clearly declared a junior synonym in 2012 (Sacca *et al.*, 2012), and by far the least common in the literature, can be found as a recent entry in a database of invasive species as a species introduced into the Black Sea (http://www.corpi.ku.lt/databases/index.php/aquanis/introductions/view/id/4304).

How common are synonyms? For the well-studied dinoflagellate genus *Gymnodinium*, an autotroph common in coastal waters, of the 268 described species 103 have never been observed since their description, so-called oncers, and a large portion are likely synonyms (Thessen *et al.*, 2012). A very similar level of synonymy or dubious species was found for another genus of dinoflagellates, the relatively rare *Histioneis*, heterotrophic dinoflagellates found in open waters. Gomez (Gomez, 2007) reviewed the genus and found that of the 90 species described with some illustrations (thus not including *nom nudum*), 37 were "oncers", never seen subsequent to "discovery", and most appear to be synonyms of previously described species. It is difficult to argue that planktonic protists are not subject to the same level of synonymy, commonly ∼40%, as that attributed to the average for marine taxa (Appeltans *et al.*, 2012). The figure of 40% would translate into species richness of roughly 1500 rather than 2500 dinoflagellates and 1600 rather than 2600 ciliates (species numbers from World Register of Marine Species). However, taxonomic reviews are very few and far between (especially compared with studies presenting phylogenetic trees) so we do not really know what level of synonymy exists for most taxa.

Polymorphism is another inconvenient truth

While a species can be repeatedly described because of ignorance of previous work, the peculiar phenomenon of polymorphisms, shape-shifters as it were, may be the source of understandable taxonomic error. Both culture work and single cell sequencing have revealed the existence of species with quite variable morphologies, corresponding to those previously described as distinct species. Among tintinnid ciliates, the phenomenon was first described by Laval-Peuto in 1977 based on culture work with the tintinnid *Favella ehrenbergii*. She found the species capable of displaying a wide variety of loricas (shells) including those characteristic of different species of another

genus, *Coxiella*, of another family (Kofoid and Campbell, 1939). The variability in lorica structure and shapes found in her cultures of *F ehrenbergii* and examples of variability in a natural population are shown in Fig. 2. Her findings called into question the reality of all 19 *Coxiella* species as not distinct species but likely simply aberrant forms of other tintinnid species. Culture work with the dinoflagellate *Ceratium ranipes* revealed another case of mistaken identities.

Ceratium ranipes was described by Cleve (Cleve, 1900) as a species with spectacular long "fingers" extending from its horns. The fingers are filled with chloroplasts and have been assumed to be an adaptation to low light conditions (Taylor and Pollingher, 1987). Forms or varieties without "fingers" were considered by some as different species, and varieties of a single species by others (e.g. Böhm, 1931). Different forms have as well been hypothesized to be either damaged, having lost the fingers or adapted to distinct conditions of temperature, light or water column structure. Brought into culture, it was discovered that with, or without fingers, were not different forms, or due to different conditions, but were rather distinct day and night morphologies (Pizay *et al.*, 2009). The species known for its long appendages absorbs them after sunset, a process that takes a couple of hours, and at night is "fingerless" (Fig. 3). Finger formation begins at dawn and takes ∼3 h.

Single cell sequencing has also revealed polymorphism in planktonic protists. Among foraminifera, sequencing of individual cells of specimens corresponding to four species of *Globigerinoides* (*G. sacculifer*, *G. trilobus*, *G. immaturus* and *G. quadrilobatus*) showed very low genetic variation in RNA regions (SSU and ITS-1) "suggesting taxonomical overinterpretation" (André *et al.*, 2012). The authors concluded that the four forms represent a single species and that the different morphologies are probably different and variable growth stages (André *et al.*, 2012). The conclusions concerning ontogenetic variability can be termed speculative. Although there is a very, very large literature concerning the occurrence of *Globigerinoides*, like other planktonic foraminifera, no species has been cultured through an entire life cycle; laboratory studies to date on planktonic foraminifera have been conducted on wild-caught individuals held for short periods of time (days to weeks) before the cells die or go into gametogenesis (reviewed in Lombard *et al.*, 2009).

Another case of single cell sequencing revealing polymorphism concerns not congeners but forms previously considered different species in different genera of different families. Bachy *et al.* (Bachy *et al.*, 2012) found that several morphotypes corresponding with different species of tintinnid genera *Cyttarocylis* and *Petalotrichia* were identical in RNA regions (SSU and ITS-1) and proposed a single name grouping what were previously five species.
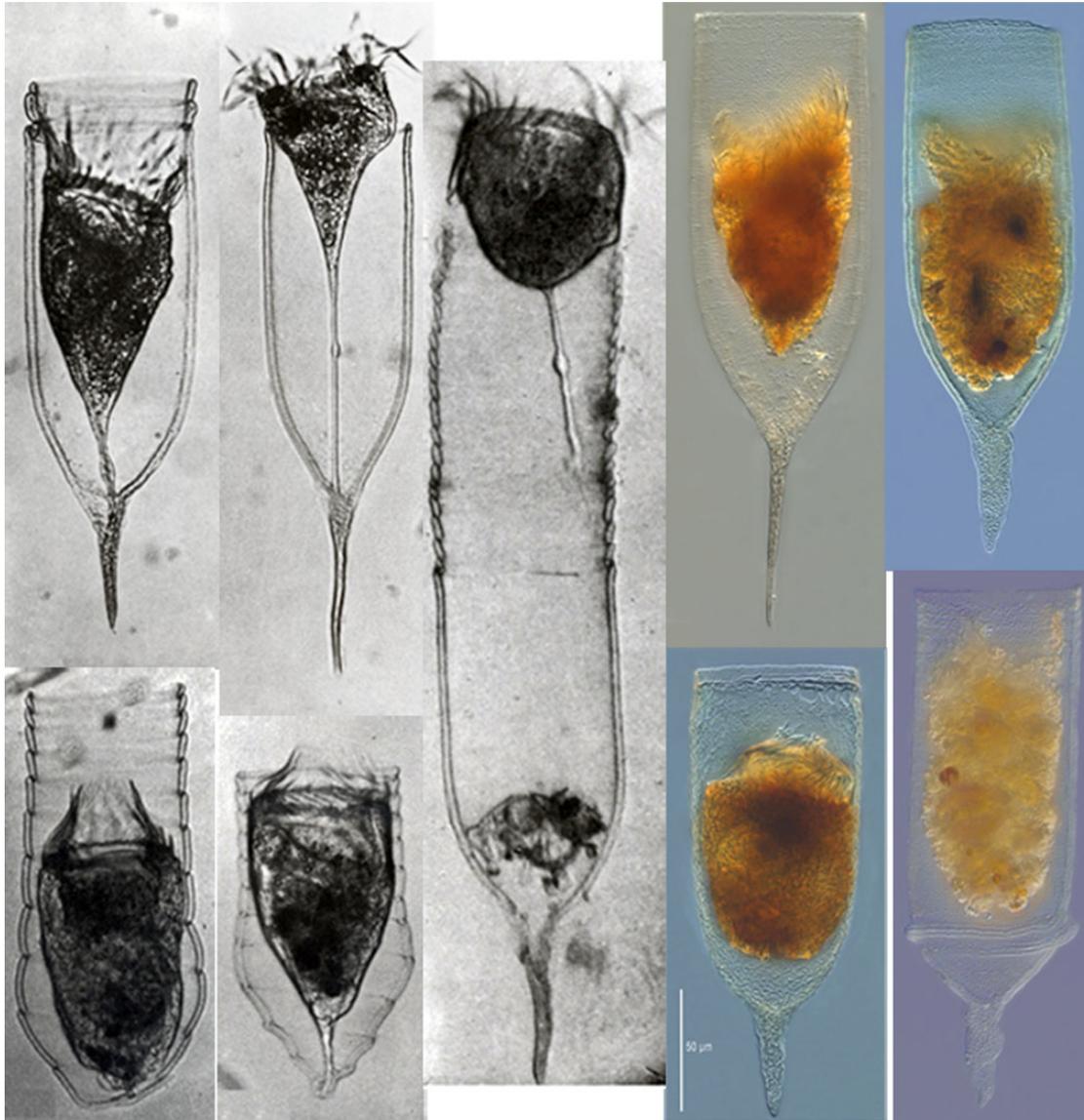
Fig. 2. Variability of *F. ehrenbergii* in culture and a natural population. Left and center image are bright field photomicrographs of the different loricas formed in culture [adapted from Laval-Peuto (Laval-Peuto, 1983), with permission of author/copyright holder]. Right side images are differential interference contrast photomicrographs of cells from a natural population in a mesocosm experiment, original micrographs.

The species concerned are large conspicuous forms with numerous of records of occurrence dating back to historic descriptions by Haeckel (Haeckel, 1873) and Fol (Fol, 1870). Dolan *et al.* (Dolan *et al.*, 2014) reviewed available species records in an attempt to determine if distinct morphotypes were associated with different environments, geographic areas or seasons. They found no evidence of disjunct distributions either temporal or spatial, but did find that different forms tended to be reported together much more often than chance would predict.

The main or most common forms now united under the name *Cyttarocylis ampulla* by Bachy *et al.* (Bachy *et al.*, 2012) were previously known as *Cyttarocylis cassis* (Haeckel, 1873), *Petalotricha ampulla* (Fol, 1881) and *Cyttarocylis eurycephalus* (as a radiolarian in Haeckel, 1887). *Petalotricha ampulla* was described from the Bay of Villefranche where all the three forms have been reported to occur (Balech, 1959), hence, a fitting site for a field study of the occurrence of different morphs. Data reported here are from work in progress on samples from the Bay of Villefranche. Figure 4 shows the three common morphotypes and temporal changes in their abundances in 2013–2014 and 2014–2015 based on a weekly plankton net tow (0–75 m, 50 μm mesh) at a standard sampling station, "Point B".
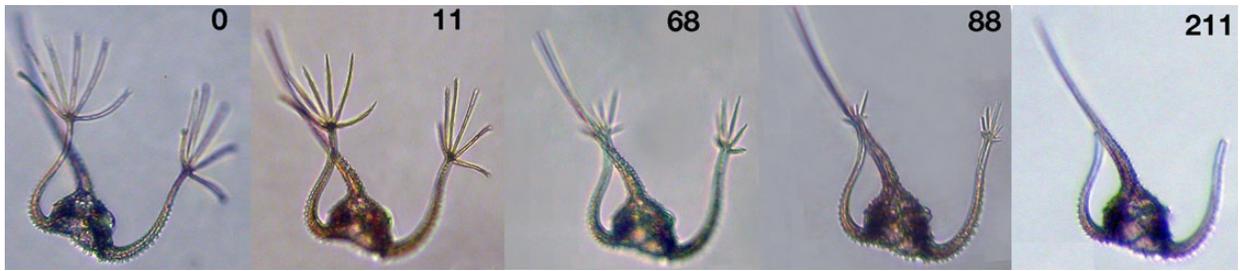
Fig. 3. The dinoflagellate *C. ranipes* absorbs its "fingers" at night. Images are of the same individual photographed at intervals from the beginning of the dark period, 0, to after 211 min of darkness. Absorption of the fingers takes about 2 h, fingers are re-formed at the beginning of the light period. Adapted from Pizay *et al.* (Pizay *et al.*, 2009), with permission of Elsevier.
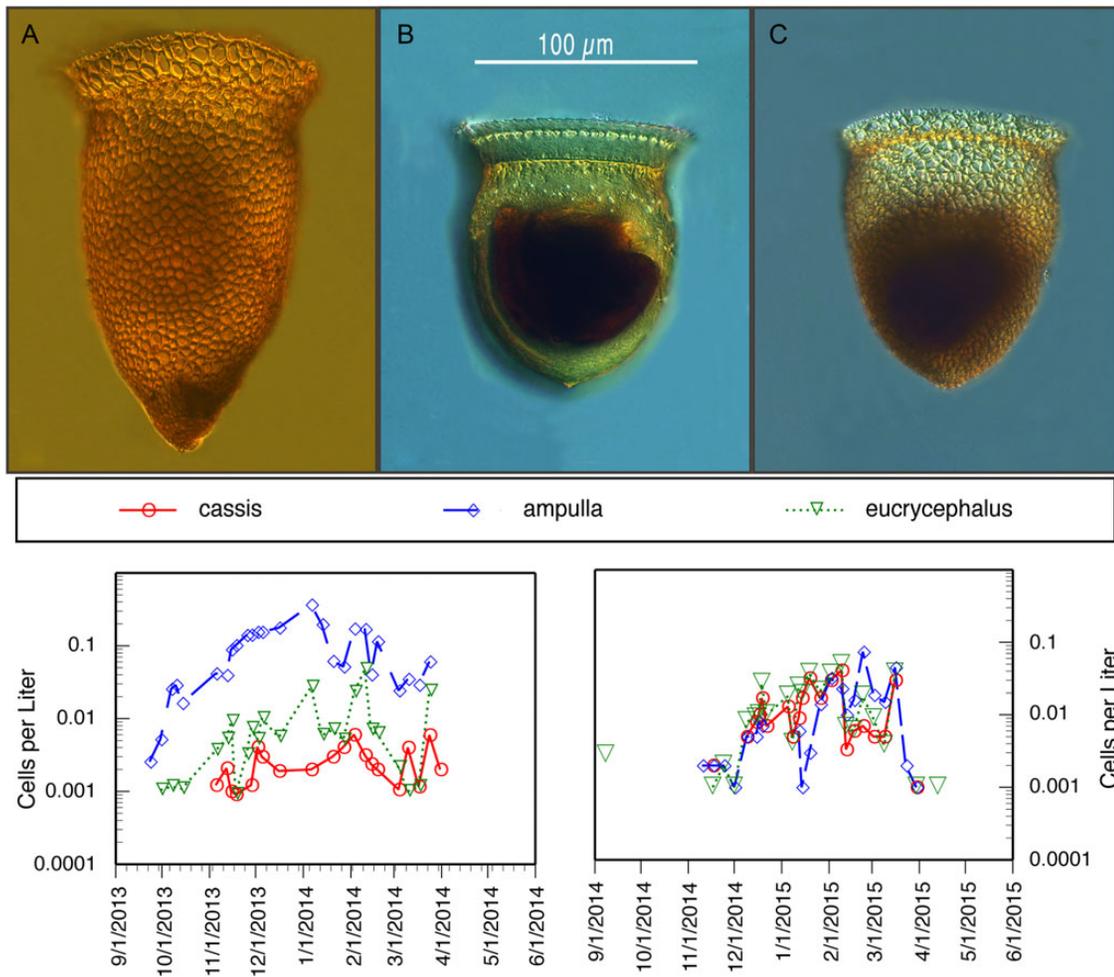

Fig. 4. The three most common morphs of *C. ampulla*: cassis (**A**), ampulla (**B**), eucrycephalus (**C**) and their abundance in the Bay of Villefranche in autumn−winter of 2013−2014 and autumn−winter of 2014−2015. From the beginning of September to the end of May, for each date material from the equivalent of 500 L (plankton net tow 0−75 m) was examined yielding a detection limit of 0.002 cells per liter averaged over 0−75 m. Original micrographs.

In both the years 2013−2014 and 2014−2015, the three morphotypes appeared abruptly in the autumn, then irregularly oscillated together and all disappeared simultaneously in early spring. The relative abundance of each morph appeared fairly consistent within a period of occurrence but differed comparing 2013−2014 with 2014−2015. The consistency of co-occurrence can be taken as evidence that in the Bay of Villefranche whatever is controlling the abundance of one morph is acting upon the other two morphs as well. This argues against

significant ecological or functional differences among the morphs. Here, no explanation not purely speculative can be provided concerning polymorphism in *Cyttarocylis*. It is worth noting that polymorphism, its generation and maintenance, have proved very difficult topics over decades of work in species very well-studied with regard to ecology and genetics such as the land snail *Cepea nemoralis* and remain today unresolved (Cook, 2013).

Some species might not be at all what we think they are

A special case of polymorphism is when different life-history stages are morphologically distinct. Many protists have very complex life cycles and life histories with a potential for distinct stages being thought to be distinct organisms. An excellent example is parasitic dinoflagellates that produce a variety of spores, flagellated and non-flagellated (e.g. Coats and Bachvaroff, 2013). Some currently recognized free-living dinoflagellate species are suspected of being stages of a parasitic taxon (Cachon and Cachon, 1987). Foraminifera have complex life cycles, with an alternation of generations. Culture work with benthic foraminifera in recent years (Dettmering *et al.*, 1998) has confirmed the existence of an old hypothesis, that rather than two forms, as in most alternation of generations, at least some foraminifera show "Trimorphism", a species has three forms. The phenomenon was described nearly 50 years ago as a significant challenge to traditional classification as different forms have been given different names (Cushman, 1968). These cases illustrate the need for studies which marry not only molecular and morphological methods (i.e. McManus and Katz, 2009) but also culture work. A recent study provides a fine example. It concerns one of the 18 very enigmatic but apparently common marine stramenopile MAST lineages of presumed nano-flagellates, enigmatic because many are without any clear taxonomic affinity. Yubuki *et al.* (Yubuki *et al.*, 2015) isolated two heterotrophic flagellate species, one planktonic, one benthic, cultured them and characterized the cells morphologically as well using molecular methods. They found them to be affiliated with MAST clade 13 and to be 2 previously described heterotrophic, bacterivorous nano-flagellates (Yubuki *et al.*, 2015). The heretofore mysterious MAST clade 13 is now known to be a lineage containing the well-known heterotrophic flagellates of the genera Bicosoeca *and* Cafeteria.

CONCLUSION

How bothersome is it that we do not know about levels of synonymy in taxa of planktonic protists? One way to assess the possible importance is to gauge how much effort overall a taxa receives; after all, if no one is studying it, using it, mentioning it, synonymy is likely unimportant. Consider then that in 2014 alone, there were 460 articles mentioning the foraminferid genus *Globigerinoides* (according to Google Scholar). Commonly used in paleo-climate studies, *Globigerinoides* has not been cultured but only maintained for short periods of study. To uncover natural variability, there is a need for studies of plankton protists focused on the biology and ecology of a single species be it field studies or laboratory work. The numerous and ubiquitous species of *Ceratium*, mentioned in 665 articles in 2014 (Google Scholar), have not been critically reviewed since Sournia's 1967 publication in French (Sournia, 1967). To be sure we know what we are talking about there is a need for critical and thorough taxonomic reviews. Ideally, studies should incorporate independent lines of evidence: morphological characterization, culture or intensive field studies to establish magnitudes of variability, and molecular approaches to allow phylogenetic classification.

Molecular surveys have provided a wealth of data but the data that can only be truly understood by knowing what sequences go with what organism and what the organisms are doing. It is time for targeted, integrative studies involving collaboration between molecular biologists with taxonomists and ecologists. Without the knowledge of the biology of individual species and especially without agreement as to which form is which species, addressing past, present or future biodiversity will prove difficult.

ACKNOWLEDGEMENTS

REFERENCES

André, A., Weiner, A., Quillévéré, F., Aurahs, R., Morard, R., Douady, C. J., de Garidel-Thoron, T., Escarguel, G. *et al.* (2012) The cryptic and the apparent reversed: lack of genetic differentiation within the morphologically diverse plexus of the planktonic foraminifer *Globigerinoides sacculifer*. *Paleobiology*, **39**, 21–39.

Andrews, K. R., Norton, E. L., Fernandez-Silva, I., Portner, E. and Goetze, E. (2014) Multilocus evidence for globally distributed cryptic species and distinct populations across ocean gyres in a mesopelagic copepod. *Mol. Ecol.*, **23**, 5462–5479.

Appeltans, W., Ahyong, S. T., Anderson, G., Angel, M., Artois, T., Bailey, N., Bamber, R., Barber, A. *et al.* (2012) The magnitude of global marine species diversity. *Curr. Biol.*, **22**, 2189–2202.

Bachy, C., Gómez, F., López-García, P., Dolan, J. R. and Moreira, D. (2012) Molecular phylogeny of tintinnid ciliates (Tintinnida, Ciliophora). *Protist*, **163**, 873–887.

Balech, E. (1959) *Tintinnoinea del Mediterraneo*. Instituto Espanol de Oceanographia, Madrid, Trabajo numero 28, pp. 84.

Bendif, E. M., Probert, I., Carmichael, M., Romac, S., Hagino, K. and de Vargas, C. (2014) Genetic delineation between and within the widespread coccolithophore morpho-species *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Haptophyta). *J. Phycol.*, **50**, 140–148.

Böhm, A. (1931) *Distribution and Variability of Ceratium in the Northern and Western Pacific*. Bernice P. Bishop Museum Bulletin Number 87, Honolulu, 46 pp.

Busch, W. (1925) Beitrag zur Kenntnis de Gehäuseebildung bei den Tintinnidae und zur Kenntnis mariner Ciliaten. *Arch. Protistenk.*, **53**, 183–190.

Cabrol, J., Winkler, G. and Tremblay, R. (2015) Physiological condition and differential feeding behaviour in the cryptic species complex *Eurytemora affinis* in the St Lawrence estuary. *J. Plankton Res.*, **37**, 372–387.

Cachon, J. and Cachon, M. (1987) Parasitic dinoflagellates. In Taylor, F. J. R. (ed.), *The Biology of Dinoflagellates*. Wiley-Blackwell, West Sussex, pp. 571–610.

Cleve, P. T. (1900) Plankton from the southern Atlantic and the southern Indian Ocean. *Öfversigt Kongl. Vetenskaps-Akad. Förhand.*, **57**, 919–938.

Coats, D. W. and Bachvaroff, T. R. (2013) Parasites of tintinnids. In Dolan, J. R., Montagnes, D. J. S., Agatha, S., Coats, D. W. and Stoecker, D. K. (eds), *The Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton*. Wiley-Blackwell, West Sussex, pp. 145–170.

Cook, L. M. (2013) Selection and disequilibrium in *Cepaea nemoralis*. *Biol. J. Linn. Soc.*, **108**, 484–493.

Costello, M. J. (2015) Biodiversity: the known, unknown and rates of extinction. *Curr Biol.*, **25**, R362–R383.

Cushman, J. A. (1968) *Foraminifera, Their Classification and Economic Use*. 4th edn. Harvard University Pres, Harvard.

Degerlund, M., Huseby, S., Zingone, A., Sarno, D. and Landfald, B. (2012) Functional diversity in cryptic species of *Chaetoceros socialis* Lauder (Bacillariophyceae). *J. Plankton Res.*, **34**, 416–431.

De Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C. *et al*. (2015) Eukaryotic plankton diversity in the sunlit ocean. *Science*, **348**, 1261605. doi:10.1126/science.1261605.

Dettmering, C., Röttger, R., Hohenegger, J. and Schaljohann, R. (1998) The trimorphic life cycle in foraminifera: observations from cultures allow new evaluation. *Eur. J. Protistol.*, **34**, 363–368.

Dolan, J. R., Pierce, R. W. and Bachy, C. (2014) *Cyttarocylis ampulla*, a polymorphic ciliate of the marine plankton. *Protist*, **165**, 66–80.

Fol, H. (1881) Contribution a la connaissance de la famille des Tintinnodea. *Archiv Sci. Phys. Natur.*, **5**, 5–24.

Gabaldón, C. and Carmona, M. J. (2015) Allocation patterns in modes of reproduction in two facultatively sexual cryptic rotifer species. *J. Plankton Res.*, **37**, 429–440.

Gaston, K. J. and Mound, L. A. (1993) Taxonomy, hypothesis testing and the biodiversity crisis. *Proc. R. Soc. Lond. B*, **251**, 139–142.

Gomez, F. (2007) Synonymy and biogeography of the dinoflagellate genus *Histioneis* (Dinophysiales: Dinophyceae). *Rev. Biol. Trop.*, **55**, 459–477.

Hada, Y. (1964) New species of the Tintinnida found from the Inland Sea. *Bull. Suzugamine Women Coll., Natur. Sci.*, **11**, 1–4.

Haeckel, E. (1873) Ueber einige neue pelagische Infusorien. *Jen. Zeitschr. Naturwiss.*, **7**, 561–568.

Haeckel, E. (1887) Report on the Radiolaria. *Report of the Scientific Results of the Challenger Expedition during the years 1873-1876*, Vol. XVIII.

Halbert, K. M. K., Goetze, E. and Carlon, D. B. (2013) High Cryptic Diversity across the global range of the migratory planktonic copepods *Pleuromamma piseki* and *P. gracilis*. *PLoS ONE*, **8**, e77011.

John, U., Litaker, R. W., Montresor, M., Murray, S., Brosnahan, M. L. and Anderson, D. M. (2014) Formal revision of the *Alexandrium tamarense* species complex (Dinophyceae) taxonomy: the introduction of five species with emphasis on molecular-based (rDNA) classification. *Protist*, **165**, 779–804.

Kaczmarska, I., Mather, L., Luddington, I. A., Muise, F. and Ehrman, J. M. (2014) Cryptic diversity in a cosmopolitan diatom known as *Asterionellopsis glacialis* (Fragilariaceae): implications for ecology, biogeography, and taxonomoy. *Am. J. Bot.*, **101**, 267–286.

Kofoid, C. A. and Campbell, A. S. (1939) Reports on the scientific results of the expedition to the Eastern Tropical Pacific, in charge to Alexander Agassiz, by U.S. Fish Commission Steamer "Albatross" from October 1904 to March 1905, Lieut. Commander L.M. Garrett, U.S.N. commanding. 37. The Ciliata: The Tintinnoinea. *Bull. Mus. Compar. Zool. Harvard*, **84**, 1–473.

Laval-Peuto, M. (1983) Sexual reproduction in *Favella ehrenbergii* (Ciliophora, Tintinnina). Taxonomical implications. *Protistologica*, **19**, 503–512.

Lombard, F., Labeyrie, L., Michel, E., Spero, H. J. and Lea, D. W. (2009) Modelling the temperature dependent growth rates of planktic foraminifera. *Mar. Micropaleontol.*, **70**, 1–7.

Ma, X., Petrusek, A., Wolinska, J., Gießler, S., Zhong, Y., Hu, W. and Yin, M. (2015) Diversity of the *Daphnia longispina* species complex in Chinese lakes: a DNA taxonomy approach. *J. Plankton Res.*, **37**, 56–65.

Massana, R., del Campo, J., Sieracki, M. E., Audic, S. and Logares, R. (2014) Exploring the uncultured microeukaryotic majority in the oceans: reevaluation of ribogroups within stramenopiles. *ISME J.*, **8**, 854–866.

McManus, G. B. and Katz, L. A. (2009) Molecular and morphological methods for identifying plankton: what makes a successful marriage? *J. Plankton Res.*, **31**, 1119–1129.

Paulmier, G. (1997) Tintinnides (Ciliophora, Oligotrichida, Tintinnina) de l'atlantique boréal, de l'Océan indien et de quelques mers adjacentes: Méditerranée, Mer Caraïbe, Mer Rouge. Inventaire et distribution. Observations basées sur les loricas. IFREMER; DRV/RH/RST/ 97–17.

Pizay, M.-D., Lemeé, R., Simon, N., Cras, A.-L., Laugier, J.-P. and Dolan, J. R. (2009) Night and day morphologies in a planktonic dinoflagellate. *Protist*, **160**, 565–575.

Premanandh, J., Priya, B., Prabaharan, D. and Uma, L. (2009) Genetic heterogeneity of the marine cyanobacterium *Leptolyngbya valderiana* (Pseudanabaenaceae) evidenced by RAPD molecular markers and 16S rDNA sequence data. *J. Plankton Res.*, **31**, 1141–1150.

Sacca, A. and Giuffrè, G. (2013) Biogeography and ecology of *Rhizodomus tagatzi*, a presumptive invasive tintinnid ciliate. *J. Plankton Res.*, **35**, 894–906.

Saccà, A., Strüder-Kypke, M. and Lynn, D. H. (2012) Redescription of *Rhizodomus tagatzi* (Ciliophora: Spirotrichea: Tintinnida), based on morphology and small subunit ribosomal RNA gene sequence. *J. Euk. Microbiol.*, **59**, 218–231.

Santoferrara, L. F., Tian, M., Alders, V. A. and McManus, G. B. (2015) Discrimination of closely related species in Tintinnid Ciliates: new insights on crypticity and polymorphism in the genus *Helicostomella*. *Protist*, **166**, 78–92.

Sournia, A. (1967) Le genre *Ceratium* (Péridinien planctonique) dans le canal de Mozambique. Contribution à une révision mondiale. *Vie Milieu A*, **18**, 375–499.

Strelkow, A. A. and Wirketis, M. A. (1950) New planktonic infusorian (suborder Tintinnoinea) from Peter the Great Bay. *Rep. USSR Acad. Sci.*, **74**, 389–391 (in Russian).

Taylor, F. J. R. and Polllingher, U. (1987) Ecology of dinoflagellates. In Taylor, F. J. R. (ed.), *The Biology of Dinoflagellates*. Blackwell, Oxford, pp. 399–530.

Thessen, A. E., Patterson, D. J. and Murray, S. A. (2012) The taxonomic significance of species that have only been observed once: the genus *Gymnodinium* (Dinoflagellata) as an example. *PLoS ONE*, **7**, e44015.

Yubuki, N., Pánek, T., Yabuki, A., Čepička, I., Takishita, K., Inagaki, Y. and Leander, B. S. (2015) Morphological identities of two different marine stramenopile environmental sequence clades: *Bicosoeca kenaiensis* (Hilliard, 1971) and *Cantina marsupialis* (Larsen and Patterson, 1990) gen. nov., comb. nov. *J. Euk. Microbiol.*, **62**, 532–542.