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Cyttarocylis ampulla, a Polymorphic Tintinnid Ciliate of the Marine Plankton

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Tintinnid species are traditionally distinguished via lorica features. Recently, sequencing has revealed polymorphism, i.e., genetically identical individuals with distinct lorica morphologies. One such polymorphic species is *Cyttarocylis ampulla*; individuals can display lorica morphologies of formally different species of *Cyttarocylis* and *Petalotricha*, well-represented in the literature. We compiled and analysed a global database of species records to determine if there is a main form and if different morphotypes have distinct temporal or spatial distributions. The two genera show very similar widespread distributions but with some statistical evidence of spatial segregation. Examining co-occurrence among the common 'species' we found most were rarely found alone, only 6-14% of the records for all species except for 2 forms: *C. eucecryphalus* and *P. ampulla* reported alone in 34% and 43%, respectively, of their records. We identify them as the main forms and analysed data of global distributions, spatial distribution across the Mediterranean in summer and winter and temporal distributions from a site in the Adriatic. The two main forms show frequent co-occurrence, similar lack of strong seasonality and widespread geographic distributions. We tentatively conclude that the different lorica morphologies may only reflect conditions of high temporally variability such as quantities and composition of prey. Directions for further research are suggested.

Key words: Choreotrichida; ITS; microzooplankton; polymorphism; SSU rDNA; Tintinnina.

Contents

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Introduction

Sequencing of protistan cells has revealed the existence of a variety of interesting phenomena. These range from evidence of gene flow between Arctic and Antarctic populations in the benthic ciliate *Euplotes nobilii* (Di Giuseppe et al. 2013) to the existence of truly cryptic species in the diatom genus *Pseudo-nitzschia* (Amato et al. 2007) and pseudo-cryptic species in the foraminifer *Globoconella inflata* (Morard et al. 2011). Recently a case was uncovered of genetic homogeneity among morphologically diverse and geographically separated populations of the foraminiferan *Globigerinoides sacculifer* providing clear evidence of 'inconsistent scaling of morphological and genetic diversity' in protists (Andre et al. 2013).

For tintinnid ciliates, features of the lorica (or shell) have been traditionally used to distinguish species and group higher level taxa. Experimental work has shown that different lorica types can be constructed by the same species, specifically those of *Favella* (Laval-Peuto 1977, 1981, 1983). Lorica characteristics alone have long and often been described as seemingly inadequate for delineating species (e.g. Boltovskoy et al. 1990; Davis 1981; Schulz and Wulff 1929; Williams et al. 1994). However, the case of *Favella*, shown to construct loricas attributed previously to the genus *Coxiella*, while calling into question the reality of the entire genus *Coxiella* (e.g. Agatha and Strüder-Kypke 2013), was the singular unequivocal case of polymorphism until recently. Now sequencing of single cells of tintinnid ciliates has unveiled the existence of both cryptic species and polymorphic species in variety of tintinnid genera.

For example, in the cosmopolitan genus *Helicostomella*, most of the described species are difficult if not impossible to distinguish unambiguously as the morphological characteristics of the lorica, supposedly distinguishing species, actually form a continuum between species (Santoferrara and Alder 2009). In Korean waters, sampling daily over an annual cycle showed two temporally disjunct populations, those of summer and winter, and both are morphologically variable (Xu et al. 2012). Sequencing of single cells revealed that the summer and winter populations are genetically distinct, likely different species, both apparently capable of forming loricas characteristic of a variety of *Helicostomella* species and therefore indistinguishable using lorica morphology. Likewise, recently three species of the genus *Cymatocylis* with very different lorica morphologies were shown to be variants of a single species (Kim et al. 2013). These examples concern species within a genus but perhaps the more intriguing case is that which forms the subject of this study: several species, previously of two genera from different families, found to be genetically identical.

Bachy et al. (2012) found identical SSU-rDNA and ITS sequences for several tintinnids with loricas corresponding to those of various species of the genus *Cyttarocylis*, family Cyttarocylididae, and the genus *Petalotricha*, family Petalotrichidae (Fig. 1). Consequently, they proposed a new combination *Cyttarocylis ampulla* for the forms sequenced. The species concerned can be considered as 'flagship species' (Foissner et al. 2009) as all are relatively large and conspicuous; furthermore some have been known for well over a century as original descriptions date back to Haeckel (1873) and Fol (1881).

In a recent classification (Agatha and Strüder-Kypke 2013), the two genera concerned are the singular genera of different families. In traditional morphological terms, the families are distinguished primarily by the structure of the lorica wall and secondarily by overall shape. Thus, according to Kofoid and Campbell (1939), the family Petalotrichidae for the genus *Petalotricha*, has as its distinguishing characteristic 'hyaline or minutely aveolar wall' and 'stout bowl-shaped lorica' while the family Cyttarocylidae, for the genus *Cyttarocylis*, the "distinguishing characters are in its regularly reticulated pattern of wall structure and its more conical bowl". For well over a century (Saville Kent 1881) *Petalotricha* with relatively smooth-surfaced, bowl-shaped lorica were thought completely different from *Cyttarocylis* showing a reticulated or sculpted lorica structure of a conical shape. Comparing the drawings which illustrated the original descriptions