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Taxonomic Implications of Morphological Complexity Within the Testate Amoeba Genus *Corythion* from the Antarctic Peninsula



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Precise and sufficiently detailed morphological taxonomy is vital in biology, for example in the accurate interpretation of ecological and palaeoecological datasets, especially in polar regions, where biodiversity is poor. Testate amoebae on the Antarctic Peninsula (AP) are well-documented and variations in their population size have recently been interpreted as a proxy for microbial productivity changes in response to recent regional climate change. AP testate amoeba assemblages are dominated by a small number of globally ubiquitous taxa. We examine morphological variation in *Corythion* spp. across the AP, finding clear evidence supporting the presence of two morphospecies. *Corythion constricta* (Certes 1889) was identified on the AP for the first time and has potentially been previously misidentified. Furthermore, a southerly trend of decreasing average test size in *Corythion dubium* (Taránek 1881) along the AP suggests adaptive polymorphism, although the precise drivers of this remain unclear, with analysis hindered by limited environmental data. Further work into morphological variation in *Corythion* is needed elsewhere, alongside molecular analyses, to evaluate the potential for (pseudo)cryptic diversity within the genus. We advocate a parsimonious taxonomical approach that recognises genetic diversity but also examines and develops accurate morphological divisions and descriptions suitable for light microscopy-based ecological and palaeoecological studies.

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Introduction

‘The most impressive aspect of the living world is its diversity’. So wrote Ernst Mayr (1997, p. 124) 20 years ago, using this observation to introduce a discussion of the history and practice of taxonomy. He argued that, over the last 300 years, since European knowledge of biodiversity greatly expanded due to the great Enlightenment voyages of ‘discovery’, taxonomy has had to make sense of an ever-increasing range of diversity. First the new floras and faunas from around the world were described, then an increasing knowledge of aquatic organisms, and later the astonishing range of microbial diversity (e.g. Margulis and Chapman 2009); something we are only recently starting to fully comprehend via the application of modern molecular biological approaches. As part of this attempt to understand microbial diversity, within the last few decades there has been a long-running debate as to the extent to which microbial taxa exhibit cosmopolitan distributions; the so called ‘everything is everywhere’ or ‘global ubiquity’ hypothesis (Baas-Becking 1934; Finlay 2002; Fontaneto 2011). A key contribution to this debate will be clarifying the extent to which apparently cosmopolitan morphospecies may contain multiple different (pseudo)cryptic species – as Bass and Boenigk (2011, p. 101) emphasised, ‘for protists the species rank is usually much broader and less well defined, thereby contributing to the perception of broad distribution’.

Interest in testate amoebae has grown considerably in the last two decades and is reflected in an increasing number of scientific publications. However, studies concerning testate amoeba taxonomy, whether based on morphometrics or molecular phylogeny, have not increased at the same rate and the application of testate amoeba in both traditional (palaeoecology, environmental monitoring) and novel (forensics and ecotoxicology) contexts is hampered by poor taxonomy and inconsistent nomenclature, potentially leading to misinterpretations or inaccurate conclusions (Kosakyan et al. 2016a).

As with all biological groups, an accurate and sufficiently detailed morphological taxonomy is critical in studies of testate amoeba ecology and palaeoecology, as considerable differences in the environmental preferences of morphotypes within single polymorphic populations and species complexes have been observed (e.g. Bobrov et al. 1995; Singer et al. 2015), potentially limiting ecological interpretation. This is especially pertinent in areas such as the Antarctic Peninsula (AP), where over-

all species diversity is low (Royles et al. 2016), potentially limiting the extent to which assemblage changes over time can be used as biological indicators of climate and/or environmental change.

Morphospecific definition in testate amoebae relies principally on variations in test composition, morphology and size, with morphological taxonomies used in palaeoecological studies necessarily based on the examination of extant amoeba in modern surface samples. Subjective judgements (and, inevitably, disagreements!) as to what level of intraspecific variation or polymorphism is acceptable are subsequently common (Charman 1999). Comprehensive biometric datasets are rare in testate amoeba morphological taxonomy and new species and morphotypes are often described based on a small number of individuals (Charman 1999), especially in regions where overall populations are low (e.g. *Argygnia antarctica*, Grospletsch 1971). However, the use of minor variations in test morphometry and appearance for morphotypic delineation is complicated by the occurrence of adaptive polymorphism in certain species, such as *Trinema complanatum*, and between *Euglypha laevis* and *E. rotunda* (Schönborn 1992), or where morphological plasticity exists (e.g. Bobrov and Mazei 2004; Medioli et al. 1987; Mulot et al. 2017; Wanner 1995, 1999). Difficulties associated with species delineation based on morphological variation have also been documented in other protozoan groups (e.g. Finlay et al. 1996).

The phylogeny of testate amoebae remains highly complex, with several genera recently shown to be polyphyletic (Gomaa et al. 2012; Kosakyan et al. 2012, 2016a; Lara et al. 2008; Oliverio et al. 2014). Several recent studies also provide molecular evidence for cryptic (e.g. Kosakyan et al. 2012; Oliverio et al. 2014) and pseudo-cryptic diversity (e.g. Singer et al. 2015). Taxonomic studies based on DNA (or RNA) analysis are invaluable when examining the relationship between phenotypic and genotypic diversity in modern faunas, but possess limited applicability in (sub)fossil studies where pragmatic taxonomic schemes are still essential to undertake routine diversity and abundance assessments (Charman 1999). Morphological analysis remains the only practical method of identifying testate amoebae in palaeoecological studies (Mitchell et al. 2008). Therefore, a parsimonious approach that recognises diversity but applies realistic morphological divisions suitable for differentiation via light microscopy is often required both in (non-molecular) microbial ecology and palaeoecology.

Research into morphospecific and cryptic taxonomy within testate amoeba taxonomic complexes

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