

## ORIGINAL PAPER

# Marine Isolates of *Trimastix marina* Form a Plesiomorphic Deep-branching Lineage within Preaxostyla, Separate from Other Known Trimastigids (*Paratrimastix* n. gen.)



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Trimastigids are free-living, anaerobic protists that are closely related to the symbiotic oxymonads, forming together the taxon Preaxostyla (Excavata: Metamonada). We isolated fourteen new strains morphologically corresponding to two species assigned to *Trimastix* (until now the only genus of trimastigids), *Trimastix marina* and *Trimastix pyriformis*. Unexpectedly, marine strains of *Trimastix marina* branch separately from freshwater strains of this morphospecies in SSU rRNA gene trees, and instead form the sister group of all other Preaxostyla. This position is confirmed by three-gene phylogenies. Ultrastructural examination of a marine isolate of *Trimastix marina* demonstrates a combination of trimastigid-like features (e.g. preaxostyle-like I fibre) and ancestral characters (e.g. absence of thickened flagellar vane margins), consistent with inclusion of marine *T. marina* within Preaxostyla, but also supporting its distinctiveness from ‘freshwater *T. marina*’ and its deep-branching position within Preaxostyla. Since these results indicate paraphyly of *Trimastix* as currently understood, we transfer the other better-studied trimastigids to *Paratrimastix* n. gen. and Paratrimastigidae n. fam. The freshwater form previously identified as *T. marina* is described as *Paratrimastix eleionoma* n. sp., and *Trimastix pyriformis* becomes *Paratrimastix pyriformis* n. comb. Because of its phylogenetic position, ‘true’ *Trimastix* is potentially important for understanding the evolution of mitochondrion-related organelles in metamonads.

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## Introduction

Trimastigids are a group of free-living heterotrophic flagellates with four flagella and a broad ventral feeding groove (Brugerolle and Patterson 1997; Grassé 1952; Saville Kent 1880-1882). Although little studied for most of the last 100 years, trimastigids have recently become important for researchers interested in eukaryotic cell evolution. Firstly, ultrastructural examinations have shown that trimastigids lack classical mitochondria, having instead small, double-membrane-bounded organelles without cristae (Brugerolle and Patterson 1997; O'Kelly et al. 1999; Simpson et al. 2000). Analyses of nuclear transcripts from '*Trimastix pyriformis*' (see below) have detected mRNAs for >20 putative 'mitochondrial proteins' (Hampl et al. 2008; Zubáčová et al. 2013). These include a complete glycine cleavage system, elements of which have been localized to the organelle, and hydrogenase maturases (Zubáčová et al. 2013), the presence of which suggests indirectly that the organelles might function as hydrogenosomes. Secondly, molecular phylogenetic studies of trimastigids demonstrated a close relationship to oxymonads, a better-known and more diverse group of anaerobic symbionts that had previously been of uncertain affinities (Dacks et al. 2001). Trimastigids and oxymonads figured prominently in systematic or evolutionary schemes for eukaryotes proposed near the turn of the 21<sup>st</sup> century, having been suggested as members of many of the various putatively deep-branching higher taxa within eukaryotes and not clearly related to well-established eukaryotic lineages (Cavalier-Smith 1998, 2002; Dacks et al. 2001). More recent phylogenetic analyses have shown that trimastigids and oxymonads are specifically related to other anaerobic excavates, including the mostly parasitic/commensal diplomonads, retortamonads and parabasalids, and the free-living *Carpediomonas*-like organisms, or 'CLOs' (Hampl et al. 2005, 2008, 2009; Kolisko et al. 2010; Simpson et al. 2006; Takishita et al. 2012). Trimastigids may therefore be useful organisms for investigations into the evolution of anaerobic mitochondrion-related organelles (Dacks et al. 2001; Hampl et al. 2008).

Despite this important evolutionary position, detailed data on the diversity and basic biology of trimastigids are limited. The only genus of trimastigids, *Trimastix*, was erected by Saville Kent in the late 19<sup>th</sup> century (Saville Kent 1880-1882), when he described *Trimastix marina* from a marine habitat. Later, Bernard et al. (2000) encountered organisms similar to Saville Kent's *T. marina* in both

fresh water and marine-derived cultures. Adopting a broad species concept they regarded both types as belonging to the nomenclatural species *Trimastix marina*. Subsequent ultrastructural studies and molecular phylogenetic analyses of '*T. marina*' have used a freshwater isolate from Albury, Australia (Bernard et al. 2000; Dacks et al. 2001; Simpson et al. 2000, 2006). *Trimastix* currently includes at least two other described species, the marine *Trimastix inaequalis* and freshwater *Trimastix pyriformis* (Bernard et al. 2000), with a third entity, *Trimastix convexa* (Grassé 1952), presently regarded as a synonym of *T. pyriformis* (see Bernard et al. 2000). Further, Dumas (1930) described the freshwater *Trimastix elaverinus*, which is of uncertain relationship to other trimastigids (see discussion). There are substantial data from isolates of *T. pyriformis* sensu lato (Brugerolle and Patterson 1997; O'Kelly et al. 1999; Simpson et al. 2000), however no marine isolates of *Trimastix*, especially of *T. marina*, have been characterized using ultrastructural or molecular techniques. Molecular phylogenetic studies have shown that several groups of small heterotrophic flagellates that were formerly treated as a single euryhaline species or genus have turned out to be composed of distinct marine and freshwater clades - ancyromonads/planomonads and *Goniomonas* for example (Cavalier-Smith et al. 2008; Shalchian-Tabrizi et al. 2008; von der Heyden et al. 2004). It is possible that freshwater strains may only represent a portion of the major lineage diversity of trimastigids, therefore it is important to examine the similarities and phylogenetic relationships amongst trimastigids from marine and freshwater habitats.

Here we report SSU rRNA gene phylogenies that include numerous new trimastigid isolates, including marine isolates of *T. marina*. A three-gene phylogenetic analysis is also conducted. Surprisingly, marine and freshwater isolates identified as *T. marina* are not specifically related to each other, with marine *T. marina* forming the deepest known branch within Preaxostyla. An ultrastructural study of a marine *T. marina* isolate illustrates its morphological distinctiveness from the freshwater forms, including some potentially ancestral cytoskeletal features relative to other trimastigids. The classification of trimastigids is re-evaluated as a result of their division into at least two clades that are apparently not specifically related. Since *T. marina* is the type of *Trimastix*, the genus name *Trimastix* is retained for the clade containing 'true' (marine) *T. marina* isolates. However, *T. pyriformis* is moved to a new genus, *Paratrimastix* gen. nov., and a new species, *Paratrimastix eleionoma* sp. nov., is

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