

ORIGINAL PAPER

Sphenoderiidae (fam. nov.), a New Clade of Euglyphid Testate Amoebae Characterized by Small, Round Scales Surrounding the Aperture



Auriel P. Chatelain^a, Ralf Meisterfeld^b, Ludovic Roussel-Delif^{a,c}, and Enrique Lara^{a,1}

^aLaboratory of Soil Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2000 Neuchâtel, Switzerland

^bInstitut für Biologie II (Zoologie), Abt. Zellulare Neurobionik, Mies Van Der Rohe Strasse 15, 52074, Aachen, Germany

^cPresent address: Laboratory of Microbiology, University of Neuchâtel, Rue Emile-Argand 11, CH-2000 Neuchâtel, Switzerland

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Euglyphid testate amoebae are a highly conspicuous group of Cercozoa whose systematics is based mainly on the shape and ultrastructure of the shell. However, only a couple of species have been studied with molecular methods. As a consequence, there are still some genera whose classification remains uncertain. Amongst those are *Sphenoderia* and *Trachelocorythion*, two genera with diverging ecological requirements that share a collar composed of small scales around the aperture. We demonstrate here with a molecular and morphological approach that they are closely related, and propose a new family, Sphenoderiidae fam. nov. to group these species. Some species share almost similar morphology in spite of being genetically distantly related (*Sphenoderia minuta* and *S. pseudominuta* sp. nov.), underlining the importance of combining ultrastructural and morphological data when describing new species of protists. In addition, we describe here *Sphenoderia valdiviana* sp. nov., a new species isolated from Southern Chile temperate rainforests.

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Introduction

Euglyphid filose testate amoebae are a group that is most common in soil litter and mosses, but that can also be encountered in various freshwater and marine habitats (Meisterfeld 2002). They have also conquered relatively extreme environments, such as the thin water layer covering the ice on certain

Chilean glaciers (Santibanez et al. 2011). Although their fossil record is relatively poor in comparison to other protists with mineral shells, there is unambiguous evidence that the main extant genera were already present since the beginning of the Neogene (Boeuf and Gilbert 1997; Foissner and Schiller 2001; Frenquelli 1933); earlier fossils have been dated back to the Permian (Kumar et al. 2011), although the exact affiliation of these early forms remains dubious. Some Precambrian microfossils also show resemblances to extant forms

¹Corresponding author; fax +41 32 7183001
e-mail enrique.lara@unine.ch (E. Lara).

(Porter and Knoll 2000; Porter et al. 2003). Meiotic processes and nuclear fusion have been documented in many forms, and it is assumed that some are obligate sexual organisms (Lahr et al. 2011). Most species typically harbour an ornamented shell composed of self-secreted siliceous plates that are held together by organic cement. Together with the Arcellinida (i.e. lobose testate amoebae), Euglyphida are often used for bioindication of environmental conditions such as pH and water-table depth in peat bogs (Charman and Warner 1992; Tolonen 1986; Warner 1987), and also to measure human impact on the environment (Nguyen-Viet et al. 2007). As the shells of some species (such as *Assulina muscorum* and *A. seminulum*) are preserved in peat, they have been used successfully as bioindicators in palaeoecology, and contributed to the reconstruction of ancient climates (Mitchell et al. 2008). Their ability for fast colonisation of new habitats and their large distribution areas (Lara et al. 2011) further validate their use in bioindication. Recently, they have been shown to play a major environmental role, as it has been demonstrated that they are responsible for the biomineralisation of half of total silica present in soils, roughly as much as all vascular plants together (Aoki et al. 2007; Wilkinson 2008).

The systematics of euglyphid testate amoebae was traditionally based on overall shell morphology (Meisterfeld 2002). The introduction of molecular approaches and more precisely sequencing of the gene coding for the rRNA present in the small subunit of the ribosome (SSU rRNA) placed these organisms within the Cercozoa, together with many amoeboflagellates, as well as the photosynthetic chlorarachniophytes (Bhattacharya et al. 1995) and the equally silicified thaumatomonads (Cavalier-Smith and Chao 1997) and phaeodareans (Polet et al. 2004); their morphological similarity with lobose testate amoebae appeared to be the result of convergent evolution. Their monophyly has been demonstrated also with SSU rRNA gene sequences (Wylezich et al. 2002). Later, the relationships within euglyphid taxa were also determined using this molecular marker and led to the definition of five families, namely Cyphoderiidae, Paulinellidae, Assulinidae, Trinematidae and Euglyphidae. It appeared that the scaling pattern of the shells was the morphological criterion that allowed a classification that suited best the phylogenetic tree of the euglyphids as obtained with molecular methods; it was suggested that scaling patterns tended to gain complexity as the organisms adapted to life in relatively dryer conditions (Lara et al. 2007b). Assulinidae, with only

one type of scales, were suggested to be the basal-most euglyphid family that conquered terrestrial environments, Euglyphidae and Trinematidae being more derived (Lara et al. 2007b). Scale size, shape and disposition patterns revealed to be equally important for species-level discrimination, as shown within family Cyphoderiidae (Heger et al. 2010; Todorov et al. 2009).

However, several genera still remain unclassified within euglyphids. *Trachelocorythion pulchellum*, initially described as *Corythion pulchellum* (Trinematidae; Penard 1890) was subsequently removed from that family and placed in a new, monospecific genus due to its small scales around the shell aperture, which is slightly subterminal (Bonnet 1979). Molecular data did not confirm its placement within Trinematidae, nor did it contradict it, because the support for the group formed with the other Trinematidae was weak (Lara et al. 2007b). However, as Bonnet created a new genus to accommodate *C. pulchellum*, he noticed the resemblance between this species and genus *Sphenoderia*, which differed only by its round section and its asymmetrical pseudostome. Following this intuition, we gathered specimens from genus *Sphenoderia*, sequenced their SSU rRNA gene and documented them with light and electron microscopy. In the light of these results, we propose a new hierarchical classification of the Euglyphida based on these results.

Results

We obtained sequences of the SSU rRNA gene between 1600 and 1800 base pairs long; we did not detect large sized (i.e. over 10 base pairs) transcribed insertions or introns. All sequences obtained from the five picked clones per PCR product were exactly identical after careful examination of the pherograms. We therefore did not detect any hidden diversity within a sample.

In the first analysis, each Euglyphida family (Trinematidae, Assulinidae, Cyphoderiidae and Paulinellidae) as defined in (Lara et al. 2007a) was robustly supported, with the exception of family Euglyphidae whose monophyly was not supported. Our six sequences from genus *Sphenoderia* branched together with *Trachelocorythion pulchellum* (AJ418789) with a 98% bootstrap value and 1.00 posterior probability; we called this new clade family Sphenoderiidae. The new family branched together with Trinematidae, Euglyphidae and Assulinidae in a robust clade, 88% bootstrap value and 0.95 posterior probability (Fig. 3). A basal position of Assulinidae was supported with

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