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Ovalopodium desertum n. sp. and the Phylogenetic Relationships of Cochliopodiidae (Amoebozoa)

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An amoeba isolated from a weakly saline semi-desert pond in Kazakhstan (Central Asia) resembles a small *Cochliopodium* in the light microscope, but has a dorsal fibrous cell coat without scales. Thus it can be identified morphologically as a new species of *Ovalopodium* Sawyer, 1980, and it is herein named *O. desertum*. Phylogenetic analysis of the SSU rRNA gene sequences of the new species and four *Cochliopodium* spp. sequenced additionally shows that *Ovalopodium desertum* is a sister clade to a robustly monophyletic *Cochliopodium*. The close relationship between *Ovalopodium* and *Cochliopodium* is also confirmed by the analysis of SSU rRNA secondary structure showing the specific helices in the region V5 in all species of both genera. Analysis of actin gene sequences fails to resolve the position of *Ovalopodium* but demonstrates that *Parvamoeba* Rogerson, 1993 is probably related to *Cochliopodium*. The position of Cochliopodiidae within Amoebozoa remains unresolved, despite our efforts to resolve it using broader taxonomic sampling of Amoebozoa, testing alternative tree topologies and removing the fast-evolving sites. Among sequenced genera, *Parvamoeba* and *Endostelium* Olive et al., 1984 are probable relatives to Cochliopodiidae. Molecular trees weakly support an inclusion of the family in Flabellinia (Discosea), but more phylogenomic data are necessary to test this hypothesis.

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Introduction

The family Cochliopodiidae De Saedeleer, 1934 as revised by Page (1987), comprises amoebae covered with a dorsal, flexible and transparent cell

coat. These include members of four genera - *Cochliopodium* Hertwig et Lesser, 1874, *Gocevia* Valkanov, 1932, *Paragocevia* Page, 1987 and *Ovalopodium* Sawyer, 1980. The latter genus, though not mentioned by Page (1987), was included in the Cochliopodiidae by Sawyer (1980) and later neither synonymized with any of the others nor invalidated. The unusual cell coat of cochliopodiids

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covers the plasma membrane dorsally and consists of scales in *Cochliopodium* (Bark 1973; Dyková et al. 1998; Kudryavtsev 1999, 2000, 2004, 2005, 2006; Kudryavtsev et al. 2004) or a fibrous cuticle in *Gocevia* and *Paragocevia* (Page and Willumsen 1980; Pussard et al. 1977), while in *Ovalopodium* its structure is still unclear (Sawyer 1980).

Current knowledge on the diversity of these genera is very incomplete. While the species composition of *Cochliopodium* with its about 13 species is becoming better characterised (e. g. Kudryavtsev, op. cit.), the other genera so far contain in total five species, among which only *Gocevia fonbrunei* Pussard, 1965 and *Paragocevia placopus* (Page et Willumsen 1980) have detailed electron microscopic descriptions (Page and Willumsen 1980; Pussard et al. 1977). Phylogenetic relationships within the Cochliopodiidae and between the Cochliopodiidae and other Amoebozoa are also unclear. The unique cell morphotype of the cochliopodids makes it difficult to infer these relationships from morphological features alone.

Different interpretations of cochliopoid morphology in a pre-molecular era (summarized in Kudryavtsev et al. 2005) finally led to establishment of the order Himatistenida by Page (1987). This order included only Cochliopodiidae and was placed within the subclass Testacealobosia. Later, Cavalier-Smith et al. (2004) abandoned Testacealobosia and included the Himatistenida in a newly established class Discosea based only on morphological evidence. Three rRNA gene sequences of *Cochliopodium* that appeared later (Kudryavtsev et al. 2005) form a very long deeply-branching monophyletic clade within Amoebozoa that does not show any close affinities to any other clades and changes its position in the tree depending on the set of species used for analysis (cf. Cole et al. 2010; Kudryavtsev et al. 2005; Pawlowski and Burki 2009; Smirnov et al. 2008; Tekle et al. 2008).

Though the cochliopodiid genera were considered to be related in the morphology-based systems of amoebae (Page 1987), this idea has recently been followed only by Cavalier-Smith et al. (2004). Smirnov et al. (2005) do not mention either the Himatistenida or Cochliopodiidae but list their genera separately as Amoebozoa *incertae sedis*. Meanwhile Adl et al. (2005) place the genus *Cochliopodium* alone in the Flabellinea and list the other genera as Flabellinea *incertae sedis* (*Paragocevia*, *Ovalopodium*) or even Amoebozoa *incertae sedis* (*Gocevia*).

Molecular data for cochliopodiid genera, other than *Cochliopodium*, are not available to test this, though recently the SSU rRNA gene of *Endostelium*

zonatum was sequenced (Shadwick et al. 2009). This species was considered to be related to *Gocevia fonbrunei* based on trophozoite morphology (Bennett 1986), but it was never formally included in the Himatistenida. Unfortunately, Shadwick et al. (op. cit.) did not assess the relationships between *Endostelium* and *Cochliopodium* in their recent phylogenetic analysis. In the absence of clarity on the monophyly of Cochliopodiidae, and even the genus *Cochliopodium* itself, the origin and evolution of the cell coat in these amoebae also remain unclear.

In this paper we present a new cochliopodiid amoeba that is very similar to *Cochliopodium* in its light-microscopic features, but lacks a tectum consisting of scales. This species formally corresponds to the diagnosis of the genus *Ovalopodium* Sawyer, 1980: therefore we describe it as *O. desertum* n. sp. and emend the diagnosis of the genus. Phylogenetic analysis of the SSU rRNA and actin gene sequences of the new amoeba, together with four additional species of *Cochliopodium* (Table 3) allows us to gain new insight into the phylogeny of Cochliopodiidae and assess the evolutionary significance of the cell coat in these amoebae.

Results

Morphology and Ultrastructure of *Ovalopodium desertum* n. sp.

During locomotion amoebae were dome-shaped, rounded or oval when viewed from above (Fig. 1A, B). Thick central granuloplasm was surrounded with a flattened hyaloplasmic sheet. The width of hyaloplasm in its anterior and lateral parts was approximately 1/4-1/3 the length of the cell, while the posterior part was narrower. Amoebae moved forward by the anterior expansion of hyaloplasm, and contracting posterior and lateral parts. The anterior edge of the cell usually produced numerous small waves and looked uneven (Fig. 1A, B), but subpseudopodia were never present. When the posterior part of the cell was contracting, it sometimes produced several short trailing filaments (Fig. 1A, D). The locomotive rate of amoebae on the glass surface at +18 °C was 9-22 µm/min (average 14 µm/min, n=15), or approximately 1-1.5 lengths of the cell per minute. During slower movement the anterior edge of the cell was less regular and produced more waves than during the fastest movement. Sometimes in slowly moving amoebae the anterior edge of the granuloplasm demonstrated eruptive hyaline waves (Fig. 1C) that were not directly involved in the locomotion of the cell. During

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