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More amoebae from the deep-sea: Two new marine species of *Vexillifera* (Amoebozoa, Dactylopodida) with notes on taxonomy of the genus

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Abstract

Two marine members of the genus *Vexillifera* Schaeffer, 1926 (Amoebozoa, Dactylopodida) are described. *Vexillifera abyssalis* n. sp. originates from an abyssal sample of the Western Atlantic 4.5 km deep, which is the first unambiguous record of a deep-sea *Vexillifera*. The second species, *V. kereti* n. sp. was isolated from the soft bottom sediments of the White Sea (depth 106 m). An analysis of available data on the genus *Vexillifera* shows that it comprises many different species, yet they are very unevenly studied. The majority of species have only been described using light microscopy, and their phylogenetic relationships with other amoebae are unclear. However, available small-subunit (SSU) rRNA gene sequences of *Vexillifera* spp. form a robust, yet very heterogeneous clade in the phylogenetic tree. These species demonstrate a wide range of morphological and ultrastructural characters and originate from diverse habitats, suggesting that *Vexillifera* may need to be subdivided into several genera in the future. In addition to the described species, we sequenced the COI gene of original CCAP strains of *Vexillifera bacillipedes*, *V. minutissima* and *Pseudoparamoeba pagei*, thereby performing a phylogenetic reconstruction of the Dactylopodida based on a decent taxonomic sampling.

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Introduction

Knowledge of the diversity of lobose amoebae in the deep-sea bottom sediments is fragmentary, yet the situation has been changing slowly during the recent years (Kudryavtsev and Pawlowski 2013, 2015; Kudryavtsev et al. 2011; Moran et al. 2007). Members of several major amoebozoan clades have been isolated and described from these habitats, among them are different representatives of Dactylopodida, including members of *Neoparamoeba* and *Paramoeba* (Kudryavtsev et al. 2011; Moran et al. 2007; Volkova and Kudryavtsev 2017), as well as a recently described genus *Cunea* (Kudryavtsev and Pawlowski 2015). The dactylopodid genus *Vexillifera* Schaeffer, 1926 is one of the most diverse taxa of naked lobose amoebae comprising 24 species studied to a very different extent (Supplementary Table 1). They were isolated from the marine or estuarine (Anderson 1994;

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Bovee 1956, 1985; Page 1972, 1979a; Sawyer 1975; Wailes 1932) and freshwater (Bovee 1985; Mascaro et al. 1985; Page 1969; Penard 1890, 1902; Schaeffer 1926; Van Wichelen et al. 2016) biotopes, as well as tissues of different marine and freshwater fishes (Dyková et al. 2011; Dyková and Kostka 2013). Amoebae assigned to this genus have only once been reported from the deep-sea habitats (Hausmann et al. 2002). However, no morphological or molecular data on this isolate were published.

Amoebae of the genus *Vexillifera* are characterized by predominantly elongated, flattened locomotive forms with long and slender subpseudopodia produced from the margin of the cell as well as from its dorsal surface. These subpseudopodia have a central core of microfilaments (Dyková et al. 2011; Page 1987). They never furcate or have pointed tips, like those of Acanthamoebidae (Page 1969). According to Bovee (1951, 1953a,b, 1985), it is not only the shape, but also the movement pattern of the subpseudopodia that best defines this genus and allows to distinguish it from morphologically similar taxa.

The majority of species, including the type one, were described using only light microscopy (Bovee 1985; Page 1976; Sawyer 1975; Schaeffer 1926). Only a quarter of this diversity has been characterized using molecular data (Dyková et al. 2011; Fahrni et al. 2003; Van Wichelen et al. 2016) and just one-third – with the electron microscopy (Anderson 1994; Dyková et al. 2011; Mascaro et al. 1985; Page 1979a). In spite of the availability of ultrastructure and molecular data, attempts to use them in order to provide a modern definition of the genus *Vexillifera* were never made, and this genus remains defined solely at the light-microscopic level (Bovee 1985; Page 1979a,b).

The genera of amoebae related to *Vexillifera* have recently been changing their taxonomic position with accumulation of molecular data (Kudryavtsev et al. 2011; Kudryavtsev and Pawlowski 2015; Smirnov et al. 2011). Initially, Page (1987) established the family Vexilliferidae comprising the genera *Vexillifera*, *Pseudoparamoeba* and *Neoparamoeba*, and separated it from the family Paramoebidae Poche, 1913, in which the genera *Paramoeba*, *Mayorella* and '*Dactylamoeba*' (now *Korotnevella*) were left. The main difference between these families was the presence or absence of the central core of microfilaments in the subpseudopodia, respectively. Both families were included in the order Euamoebida, class Lobosea, phylum Rhizopoda (Page 1987). With accumulation of molecular phylogenetic data, the need for changes in the system became evident, therefore Cavalier-Smith et al. (2004) proposed the order Glycostylida comprising suborders Vannelloidea and Paramoeboidea, the latter comprising families Paramoebidae and Vexilliferidae in their original composition. Smirnov et al. (2005) proposed the order Dactylopodida with the same two families within the class Flabellinea. However, they excluded the genus *Mayorella* from Paramoebidae and placed it incertae sedis. In the same year it was suggested that the restoration of the family Mayorellidae Schaeffer, 1926 including the genus *Mayorella* was reasonable (Kudryavtsev et al. 2005). This point of view was later accepted by Smirnov et al. (2011). Kudryavtsev et al. (2011) emphasized that the topology of the Dactylopodida clade in the molecular phylogenetic tree did not correspond to the composition of Page's families, as both Paramoebidae and Vexilliferidae as originally outlined became paraphyletic. Therefore, the composition of the families was changed, and *Vexillifera* became a sole genus in the monotypic family Vexilliferidae.

The purpose of this paper is to describe two new marine species of *Vexillifera* that were isolated from the deep-sea bottom sediments of the western Atlantic Ocean (depth ca. 4.5 km) and sublittoral bottom sediments of the White Sea (northwestern Russia) at a depth of 106 m and discuss morphological diversity and molecular phylogeny of this genus based on these new findings.

Material and Methods

Sampling, cultivation and microscopy

Vexillifera abyssalis n. sp. strain DIVA3 564/2 was isolated from the surface of a stone picked by Agassiz trawl during the DIVA3 cruise of the German research vessel "Meteor" from the bottom of Brazilian abyssal plain (ca. 26.64S 35.2395W, depth 4527 m), western Atlantic Ocean on July 24th, 2009. *Vexillifera kereti* n. sp. strain WS12-01.1 was isolated from the soft bottom sediments (upper reddish-brown mud layer) of the sublittoral area at the outlet of Chupa Inlet, Kandalaksha Bay, the White Sea (northwestern Russia; 66.291716N 34.065166E, depth 106 m) picked by a grab sampler on September 13th, 2012. Once on board, material was picked from the samples using flame-sterilized forceps and spoon, and placed in sterile plastic containers. Sampled material was further inoculated in 90-mm Petri dishes filled with Millipore-filter-sterilized (0.2 μm pore size) seawater with salinity 35 and 30‰, respectively. Autoclaved wheat grains were added in inoculated samples (2–3 per dish). Procedures for cloning and maintenance of cultures were essentially as described in Kudryavtsev et al. (2011). Light microscopic observations and recording were performed at room temperature (+18 to 22 °C) on living amoebae from clonal cultures placed on the surface of glass coverslips using Carl Zeiss Axiovert 200 and Leica DM 2500 microscopes, both equipped with phase contrast and differential interference contrast (DIC) optics. For transmission electron microscopy amoebae were fixed at +4 °C using two protocols that gave approximately the same result: (1) Fixation with 2.5% solution of glutaraldehyde for 30–40 min followed by postfixation with 1% solution of osmium tetroxide for 30–60 min; (2) Brief prefixation (5 min) with 0.5% solution of osmium tetroxide, followed by 2.5% solution of glutaraldehyde for 30–40 min and postfixation with 1% solution of osmium tetroxide for 30–60 min. All fixatives were prepared with 0.05 M sodium cacodylate buffer (pH 7.4) on seawater,

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