

ORIGINAL PAPER

A Novel Lineage of ‘Naked Filose Amoebae’; *Kraken carinae* gen. nov. sp. nov. (Cercozoa) with a Remarkable Locomotion by Disassembly of its Cell Body



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The term ‘filose amoebae’ describes a highly polyphyletic assemblage of protists whose phylogenetic placement can be unpredictable based on gross morphology alone. We isolated six filose amoebae from soils of two European countries and describe a new genus and species of naked filose amoebae, *Kraken carinae* gen. nov. sp. nov. We provide a morphological description based on light microscopy and small subunit rRNA gene sequences (SSU rDNA). In culture, *Kraken carinae* strains were very slow-moving and preyed on bacteria using a network of filopodia. Phylogenetic analyses of SSU sequences reveal that *Kraken* are core (filosan) Cercozoa, branching weakly at the base of the cercozoan radiation, most closely related to *Paracercomonas*, *Metabolomonas*, and *Brevimastigomonas*. Some *Kraken* sequences are >99% similar to an environmental sequence obtained from a freshwater lake in Antarctica, indicating that *Kraken* is not exclusively soil dwelling, but also inhabits freshwater habitats.

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Introduction

Protists, especially small bacterivorous amoebae, are difficult to distinguish due to few morphological characters. Therefore many amoebae (or

amoebiflagellates) have been lumped into morphotypes or morphospecies which often comprise high cryptic diversity, and in some cases morphologically defined taxa have been shown to be polyphyletic or paraphyletic (Bass et al. 2009b; Smirnov and Brown 2004; Smirnov 2011; Wylezich et al. 2002). Despite convergent morphological traits; the ecology of protists can differ enormously

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(Pouličková et al. 2008). Therefore it is of high interest to phylogenetically resolve amoeboid morphotypes as accurately as possible.

The informal term 'naked filose amoebae' has been used by protistologists for more than 150 years enabling a quick categorization of amoebae (Cienkowski 1865). Naked filose amoebae were placed in various taxonomic groups, such as Proteomyxidea (Lankester 1890) or Reticulosa (Cash and Hopkinson 1905; Rhumbler 1904). Molecular phylogenies have shown some such groups to be polyphyletic: many filose amoebae are now known to branch in various places in cercozoan phylogenies, but others are distributed across the eukaryotic tree of life, in the stramenopiles, opisthokonts, excavates, and Amoebozoa (Adl et al. 2012; Amaral Zettler et al. 2001; Bass et al. 2009a; Berney et al. 2015; Cavalier-Smith 1998a, b).

The Cercozoa were established as a phylum within the last 20 years (Cavalier-Smith 1998a, b; Cavalier-Smith and Chao 2003). Environmental DNA surveys of terrestrial, limnic and marine systems have shown a high hidden diversity of Cercozoa that needs to be described by morphological and ecological means (Bass and Cavalier-Smith 2004). Since then, many studies obtained molecular data of already described or previously unknown Cercozoa, showing that cercozoans are highly diverse in morphology and ecology, comprising e.g. bacterivorous flagellates, algivorous and mycophagous amoebae as well as endophytic biotrophs (e.g. Bass et al. 2009a, b; Dumack et al. 2016; Howe et al. 2009, 2011; Neuhauser et al. 2014).

Further species descriptions and taxonomic approaches combined with morphological as well as molecular data showed that even within Cercozoa, 'naked filose amoebae' are of polyphyletic origin. Granofilosean amoebae such as *Limnofila* have previously been misidentified as other taxa (*Gymnophrys* Cienkowski, 1876, *Biomyxa* Leidy, 1875) that most likely belong to Endomyxa or Retaria, the endomyxan *Filoreta* Cavalier-Smith and Bass, 2009 has been confused with the amoebozoan *Corallomyxa* Grell, 1966 (Bass et al. 2009a), and some vampyrellids (Hess et al. 2012; Berney et al. 2013) strongly recall variosean Amoebozoa, at least in still photographs (Berney et al. 2015). This problem is compounded by the difficulty of representing such variable forms in illustrations, leading to redundancy in taxon descriptions. An overlooked example of this is *Penardia*, (Cash 1904) as a probable synonym of *Chlamydomyxa* (Archer 1875), Cash's illustration of *Penardia* being the typical trophozoite of *Chlamydomyxa* (Eckhard

Völcker pers. comm.). Recent studies conclusively show that intensive light microscopy combined with well-sampled molecular phylogenies are essential for accurate and robust species descriptions to enable an enduring protistan taxonomy, particularly for morphologically elusive lineages such as those under the umbrella of 'naked filose amoebae'.

In this study we describe *Kraken* gen. nov., a novel filosan cercozoan with possible phylogenetic affinities to the gliding biflagellate bacterivorous cercomonads (Cercomonadidae). We provide detailed description of six cultured strains, comprising four genotypes, and describe a new genus and species by differential interference contrast (DIC) high definition video microscopy and SSU rDNA phylogeny.

Results

Sampling and Abundance

Kraken cells were isolated from 6/129 screened soil samples (Table 1). In each of these six samples independent of sampling site, they were present at an abundance of 350–400 Individuals \times g⁻¹ dry weight soil as determined by the Liquid Aliquot Method (LAM).

Morphology

Trophozoite: The cell bodies of *Kraken carinae* (Fig. 1, Supplementary Material 2) were roundish with a length/width ratio of 1.0 ± 0.0 ($n=41$). The diameter of 5 of the 6 obtained isolates was $7.75 \pm 0.9 \mu\text{m}$ ($n=41$) whereas clonal cells of one isolate (KD0248) were slightly larger: $8.75 \pm 0.9 \mu\text{m}$ ($n=43$, $F=29.16$, $p<0.001$). The cell body usually contained one nucleus, rarely two nuclei, with a single round nucleolus in the middle, a contractile vacuole, one large food vacuole and several small granules (Fig. 1 B, D). The nucleus diameter was approximately $3.4 \pm 0.2 \mu\text{m}$. The diameter of the nucleolus was about $1.6 \pm 0.2 \mu\text{m}$. A cell covering was not observed. Each cell usually formed one long, thin and narrowing filopodium that branched and anastomosed (Fig. 1 A, C). The filopodium originated from a localised point usually located at the basal end of the cell body (Supplementary Material 2). The filopodium usually branched close to this point multiple times and expanded in all directions up to a length of 200–300 μm , so the whole diameter of an active cell may be more than 500 μm wide. Usually only individuals cultured for several weeks without disturbance showed anastomosing, highly branching filopodia. When mechanically disturbed, *Kraken* individuals tended

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