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A new discovery of *Novechiniscus armadilloides* (Schuster, 1975) (Tardigrada, Echiniscidae) from Utah, USA with considerations on non-marine Heterotardigrada phylogeny and biogeography

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Abstract

The discovery of a new population of the non-marine heterotardigrade *Novechiniscus armadilloides* from Utah, USA, allowed us to reanalyse the species by means of scanning electron microscopy and differential interference contrast microscopy. This analysis confirmed the presence of bar shaped, unpaired segmental plates and of a long filament E in addition to the filament A always present in the class Heterotardigrada. It also provided additional information on characters not explicitly cited in the previous descriptions of this monotypic genus, such as details of the head cirri and clavae, details of the buccal tube and pharyngeal bulb, sculpture of the dorso-lateral and leg plates, details of the claws. The population is bisexual, but no secondary sexual dimorphism was observed. The male and female gonopores were described. New characters such as red eyes and red body colour were used in analysing the phylogeny of the family Echiniscidae. The phylogeny and biogeography of non-marine heterotardigrades provide intriguing questions for further research.

Keywords: Heterotardigrada; Echiniscidae; Phylogeny; Zoogeography; SEM

Introduction

The marine Arthrotardigrada, one of the two orders of the class Heterotardigrada, are considered the most ancient order within the phylum Tardigrada (Kristensen 1976, Renaud-Mornant 1982). At the beginning of the 20th century (Thulin 1928, Marcus 1929) and in more recent taxonomic works (Ramazzotti and Maucci 1983), its family Halechiniscidae was considered the stem group of all other tardigrades. However, Renaud-Mornant (1982) stated that *Parastygarctus* (family Stygarctidae) should be considered the tardigrade genus with the greatest number of plesiomorphic characters. One of the latter features are the dorsal cuticular plates, which are present in some marine Arthrotardigrada, but above all, these plates characterize the terrestrial family Echiniscidae (belonging to Echiniscoidea, the other order of Heterotardigrada). Phylogenetic discussions of the so-called ancestral tardigrade have nearly neglected the terrestrial heterotardigrades, represented by the families Oreellidae and

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Echiniscidae (Kristensen 1987, Jørgensen 2000). Recently, Nichols et al. (2006) suggested the Oreellidae without plates as the basal heterotardigrade family. In the latter case, the dorsal plates should have developed several times by convergence in heterotardigrades (Jørgensen 2000), i.e. the dorsal plates of Echiniscidae and Renaudarctidae/Stygarctidae would be convergent structures. This again places the focus on the family Echiniscidae, in which the two genera with the most plesiomorphic characters are *Parechiniscus* and *Novechiniscus*. In this paper, we present new information on the genus *Novechiniscus*.

Parechiniscus armadilloides Schuster, 1975 was described and illustrated with two scanning electron microscope (SEM) photographs. Schuster (1975) examined a population collected in moss and lichen from Logan Canyon near Logan, Utah (USA), the only site known for that species so far. Kristensen (1987) reconsidered the taxonomic position of *P. armadilloides* in his revision of the Echiniscidae (Echiniscoidea), the most diverse family of semiterrestrial Heterotardigrada, and proposed the erection of the genus *Novechiniscus* for that species. He also redescribed *Novechiniscus armadilloides* (Schuster, 1975) from two paratypes. His description was accurate and detailed, but due to the demanding task of describing or redescribing all the genera of Echiniscidae in the same paper, he represented *N. armadilloides* with one habitus drawing and two cladograms (buccopharyngeal apparatus and claw). However, all observations were made on poorly preserved specimens on old microslides. The discovery of a new population of *N. armadilloides* allows us to report additional information on those characters not specifically cited in the previous descriptions or to modify the characters, and to discuss the phylogeny and biogeography of non-marine heterotardigrades in general. This paper indicates that *Parechiniscus* and *Novechiniscus* belong to two different evolutionary lines in the family Echiniscidae, and that the two genera are not closely related (sister groups).

Material and methods

A moss, *Grimmia laevigata* (Bridel) Bridel, growing on basaltic rock was collected (sample code C1934, 4 August 1995) from St. George, Snow Canyon, Utah (USA), about 550 km from the locus typicus in the opposite corner of the State. The moss sample contained large amounts of red soil. The tardigrades living in that moss belonged to two species: the heterotardigrade *Novechiniscus armadilloides* (Schuster, 1975) and the eutardigrade *Milnesium tardigradum* Doyère, 1840.

About 60 specimens of *N. armadilloides* were extracted from the moss and used for this study. Specifically, 34 specimens and three exuviae containing 1 or 2 eggs each were directly mounted in polyvinyl-lactophenol. Females and males were found; eight specimens were juveniles with only two claws per leg and without anus or gonopore ('two-clawed larvae' according to the terminology used by tardigradologists; see Ramazzotti and Maucci 1983, Bertolani et al. 1984). Slides were examined with a Leitz DM RB microscope equipped with phase contrast and differential interference contrast (DIC) up to the 100 × objective, and connected to a Polaroid DMC Ie Low Light Kit digital camera. Fifteen specimens of *N. armadilloides* were prepared for SEM analysis, following the protocols by Guidetti et al. (2000). In addition, two specimens were treated with NaClO and the buccophagyngeal apparatus

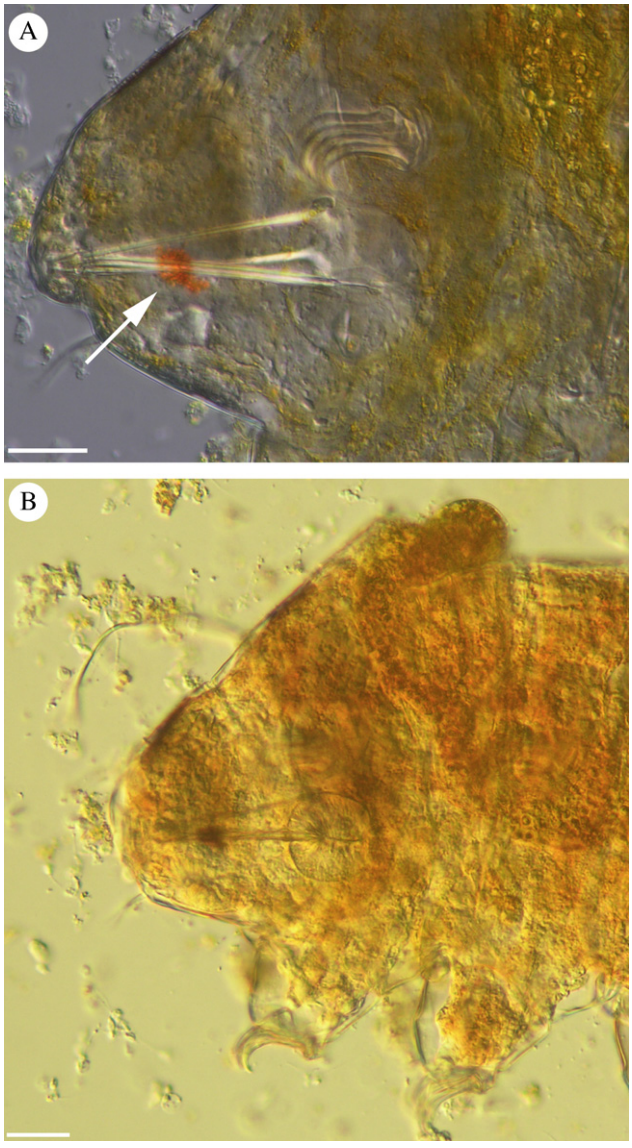

Fig. 1. *Novechiniscus armadilloides* (in vivo; DIC): (A) Head with a red eye (arrow). (B) Carrot-red colour of body. All scale bars = 20 μm.