

Morphology, morphogenesis, and phylogeny of an *Anteholosticha intermedia* (Ciliophora, Urostylida) population from the United States

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Abstract

A distinct population of *Anteholosticha intermedia* was isolated from soil in the Great Smoky Mountains of North Carolina, USA, and its morphology, morphogenesis and molecular phylogeny investigated by microscopic observations of live and protargol-prepared specimens and analyses of the sequence of small subunit (SSU) rDNA. Our population closely resembles the populations from Austria and Korea. Members of the genus *Anteholosticha* have been regarded as ontogenetically diverse, which is confirmed by the present work. The most noteworthy ontogenetic feature of the American population of *A. intermedia* is that the oral primordium in the proter appears apokinetally at the posterior end of the undulating membranes anlage at the beginning of division and then dedifferentiates midway through morphogenesis. Molecular phylogenetic analyses demonstrate, with high support, that the American population of *A. intermedia* is clearly distinct from congeners and branches as part of a sister lineage to the *Bakuella*–*Urostylo* clade that belongs to the major clade comprising the order Urostylida.

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Introduction

The subclass Hypotrichia Stein, 1859 is a large group of ciliated protists that are exceptionally diverse in terms of biology and morphology, making them abundant and widespread in various ecosystems worldwide (e.g. Berger 1999, 2001, 2006, 2008, 2011; Bharti et al. 2016; Dong et al. 2016;

Foissner 2016; Kahl 1928, 1932; Kumar et al. 2016; Li et al. 2016; Pan et al. 2016; Shao et al. 2013, 2015; Song et al. 2009; Wang et al. 2016). Recently, phylogenetic analyses have led to a better understanding of systematic and evolutionary relationships among hypotrichs (e.g., Gao et al. 2010, 2016; Huang et al. 2010, 2016; Wang et al. 2015; Yi et al. 2010a,b; Yi and Song 2011). In particular, the diverse, polyphyletic members of the *Holosticha* complex were classified into four genera, *Holosticha* s. str., *Anteholosticha*, *Caudiholosticha* and *Biholosticha* by Berger (2003). Only recently, Huang et al. (2014) transferred three species of *Anteholosticha*, i.e. *A. warreni* (Song and Wilbert, 1997) Berger, 2003; *A. scutellum* (Cohn, 1866) Berger, 2003, and *A. petzi*

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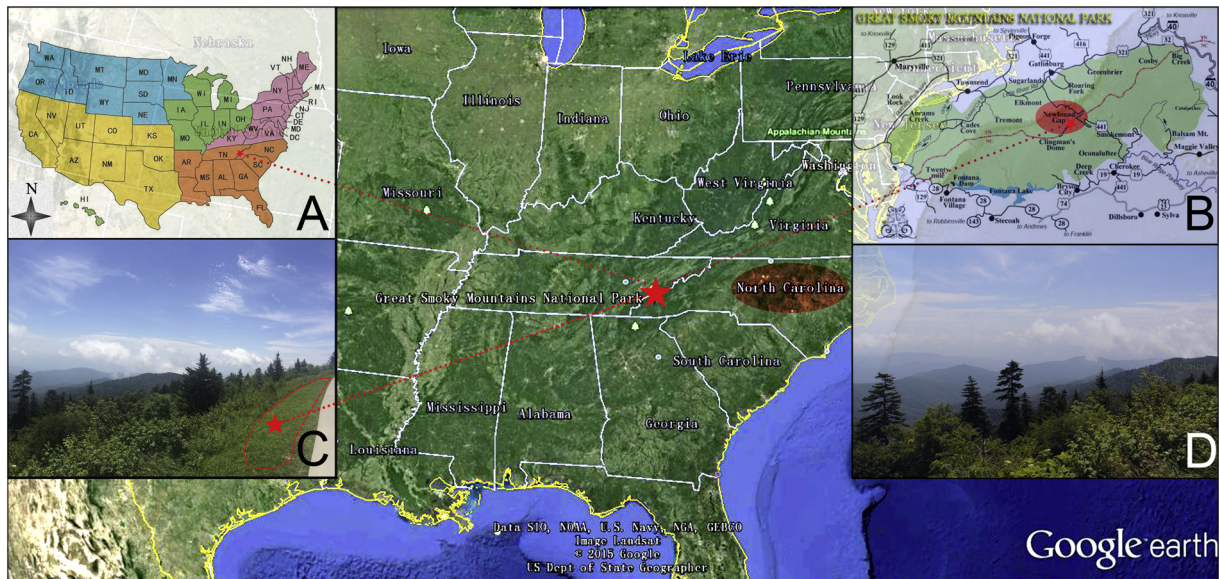


Fig. 1. (A–D) Map of the United States (background from Google earth) showing the sampling sites. (A, B) Map showing the location of the Great Smoky Mountains National Park, North Carolina, USA. (C, D) Photographs of habitats from which soil samples were collected.

Shao et al., 2011, to the genus *Arcuseries* Huang et al., 2014, each with a roughly U-shaped pattern of transverse cirri supporting the distinct separation from other groups in the molecular tree. Likewise quite recently, Li et al. (2017) transferred *Holosticha stueberi* Foissner, 1987 (type species of the genus *Caudiholosticha*) to the subgenus *Uroleptus* (*Caudiholosticha*) Berger, 2003 and classified other 16 species of *Caudiholosticha* in six newly erected genera, namely, *Extraholosticha*, *Adumbratosticha*, *Acuholosticha*, *Limnoholosticha*, *Multiholosticha*, and *Caudikeronopsis*, based on available morphological and molecular data.

More than 40 species of *Anteholosticha* have been revised or investigated by Berger (2003, 2006, 2008) and other workers (e.g., Fan et al. 2014; Kumar et al. 2010; Li et al. 2007, 2011; Park et al. 2012, 2013; Xu et al. 2011). Berger (2003, 2006) concluded that *Anteholosticha* is non-monophyletic due to the lack of an apomorphy, a statement later confirmed by Fan et al. (2014) and other workers (e.g., Lv et al. 2015; Zhao et al. 2015).

In the summer of 2014, we isolated a population of *Anteholosticha intermedia* from soil samples collected in the Great Smoky Mountains National Park, North Carolina, United States. The present paper describes its morphology, morphogenesis, and molecular phylogeny based on analyses of data from sequences of the gene coding for small-subunit rRNA (SSU rRNA).

Material and methods

Sampling and cultivation

Living individuals of *Anteholosticha intermedia* were isolated from a soil sample (0–10 cm) that was collected nearby

Newfound Gap, the Great Smoky Mountains National Park (35°21'49"N, 83°15'12"W), North Carolina, United States (Fig. 1). Three samples (about 500 g each) were collected in July 2014, air-dried for one month, sealed in a large paper envelope for ventilation, and investigated during October 2014 to March 2015. The Smoky Mountains are an ancient geological formation, comprising some of the oldest mountains on Earth. They began forming more than 400 mya, and were uplifted by the collision of Africa and North America during the formation of the supercontinent of Pangaea, beginning approximately 380 mya (Cook et al. 1979).

The non-flooded Petri dish method was used to stimulate ciliates to excyst (Foissner et al. 2002). Ciliates were isolated and cultures were established at room temperature (24 °C) in Petri dishes containing distilled water with squeezed rice grains to enrich the availability of bacterial food.

Unfortunately, we could not establish a clone and therefore we cannot be 100% sure that the specimens used for the morphological studies and molecular analyses belong to the same species. However, as no other *Anteholosticha* morphotypes have been present in the protargol preparations, the probability is extremely high that our morphological and molecular studies deal with the same species.

Morphologic observations

Living cells were observed using bright field and differential interference contrast microscopy at 100–1000×. The protargol method was used to reveal the ciliature and nuclear apparatus (Wilbert 1975). Counts and measurements of cellular structures on stained specimens were performed with an ocular micrometer. Drawings were made with the aid of a camera lucida. Changes occurring during morphogenetic

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