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# Morphology and phylogeny of a new species, *Uroleptus* (*Caudiholosticha*) *antarctica* n. sp. (Ciliophora, Hypotricha) from Greenwich Island in Antarctica

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## Abstract

This paper describes the morphological features based on standard methods and estimates their phylogenetic position using small subunit ribosomal RNA (SSU rRNA) sequences of a *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.** population investigated from moss of the Greenwich Island, Antarctica. The morphology of *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.** is characterized as follows: 213.0–238.0×67.5–74.5 μm size *in vivo*; contractile vacuole located slightly above left of mid-body; cortical granules lacking; three frontal and two frontoterminal cirri; five to six transverse cirri; one pretransverse cirri; one right and one left marginal rows; six to seven dorsal kineties; three caudal cirri.

**Key words:** ciliate, moss, SSU rRNA, taxonomy, Uroleptidae

## Introduction

*Uroleptus* Ehrenberg, 1831 is a genus of hypotrich ciliates that are notoriously difficult to classify and identify the species. The species in *Uroleptus* were originally assigned or transferred to the genus by Berger (2001), based on the presence of a distinct tail. *Paruroleptus* Wenzel, 1953 was invalidly established by Kahl (1932) as subgenus of *Holosticha* for *Uroleptus*-like species with transverse cirri. Until recently, *Uroleptus* and *Paruroleptus* were assigned separately or as synonyms. Both to Berger (2006, p. 237) and Foissner and Stoeck (2006) suggested that *Caudiholosticha stueberi* should be placed in *Uroleptus* due to the presence of dorsomarginal kineties. These kineties are usually more or less distinctly shortened posteriorly, and lack caudal cirri (Martin 1982). Based on this, Li *et al*. (2016b) proposed dividing the genus *Uroleptus* into three subgenera, *Uroleptus* (*Uroleptus*), *U*. (*Paruroleptus*), and *U*. (*Caudiholosticha*), on the basis of the number of transverse cirri and the presence/absence of a tail.

The genus *Caudiholosticha* has 16 species, including the recently described species *C. marina* Li *et al*. 2016; *C. silvicola* Foissner 2016; *C. halophila* Foissner 2016; and *C. virginensis* Foissner 2016. However, Li *et al*. (2016b) rearranged this genus, and transferred all species other than the type species to other genera. The type species of this genus is *U*. (*Caudiholosticha*) *stueberi* which was discovered in both Austria and China. Consequently, *Uroleptus* (*Caudiholosticha*) has two species including our new species.

In this study, we described a new species *Uroleptus* (*Caudiholosticha*) *antarctica* collected from Greenwich Island, Antarctica. For precise identification and description, we investigated living organisms, protargol-impregnated specimens, and the SSU rRNA gene sequence.

## Materials and methods

**Sampling site and morphological identification.** A new species was discovered on Greenwich Island, Antarctica

(62°28′42.2″S, 59°39′36.2″W) in January 2014. The sample was collected from the top of layer of moss (*Sanionia* sp.). Ciliates were re-activated from air-dried samples using the non-flooded Petri dish method (Foissner *et al*. 2002).

Raw cultures were maintained both in Petri dishes and 50 mL tissue culture flasks at 8°C (SPL Life Sciences, Korea). Living specimens were observed under a light microscope (Axio Imager.A2, Carl Zeiss, Germany) at magnifications ranging from 50 to 1,000 times. Protargol impregnation following "Procedure A" of Foissner (2014) was performed to observe the infraciliature. Terminology and classification are mainly according to Berger (2006) and Li *et al.* (2016b).

**Genomic DNA extraction, amplification, and sequencing.** Each individual was washed repeatedly with distilled water. Extraction of genomic DNA from a single specimen was performed according to the manufacturer's protocol, using a RED-Extract-N-Amp Tissue PCR Kit (Sigma, St. Louis, USA). The New EukA primer modified from Medlin *et al*. (1988) and LSU rev3 primer (Sonnenberg *et al*. 2007) were used for PCR amplification of the nearly complete SSU rRNA sequence. The optimized PCR method was as follows: denaturation at 94°C for 3 minutes, followed by 40 cycles of denaturation at 95°C for 15 seconds, annealing at 56°C for 30 seconds, extension at 72°C for 4 minutes, and then a final extension step at 72°C for 7 minutes. The QIAquick® PCR Purification Kit (QIAGEN, Hilden, Germany) was used for purification of the PCR products. Two internal primers, 18S+810 and 18S-300 (Jung *et al*. 2014), were used for sequencing with an ABI 3700 sequencer (Applied Biosystems, Foster City, Ca, USA).

**Molecular analysis.** Sequenced fragments of the SSU RNA gene were assembled using the BioEdit program (Hall 1999) and were aligned using Clustal X 1.81 (Jeanmougin *et al*. 1998). MEGA 5.2.2 (Tamura *et al*. 2011) was used to calculate pairwise genetic distances, and 1,361 bp were used to reconstruct the phylogenetic trees. To confirm the systematic position of the new species, the sequences of all the known members of the genus *Uroleptus*, and each representative species of the genera in the family Uroleptidae and Urostyloidae, were retrieved from the GenBank databases.

We evaluated phylogenetic relationships using maximum likelihood (ML) and Bayesian inference (BI) analyses. To determine the appropriate DNA substitution model for ML and BI, we used the Akaike information criterion (AIC) to identify the best-fit model using the jModelTest 2.1.1 (Darriba *et al*. 2012). The model selected was GTR + I (0.5220) + G (0.4350). The ML analysis was conducted using PhyML version 3.1 (Guindon *et al*. 2010) with 1,000 bootstrap replicates. BI assessment was performed using MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003) by simulating a Markov chain Monte Carlo (MCMC) for 1,000,000 generations. Trees were sampled every 100 generations, from which the first 30% were discarded as burn-in.

## Results

### Order Sporadotrichida Fauré-Fremiet, 1961

### Family Uroleptidae Foissner and Stoeck, 2008

### *Uroleptus* Ehrenberg, 1831

*Uroleptus* (*Caudiholosticha*) Berger, 2003

### *Uroleptus* (*Caudiholosticha*) *antarctica*. n. sp.

(Fig. 1–3; Table 1)

**Diagnosis.** Size *in vivo* 213.0–238.0×67.5–74.5 μm; slender to elongated shape; flexible but not contractile; grayish under low magnification. Contractile vacuole located on slightly above left of mid-body. Two macronuclear nodules with one–three micronuclei. Exactly, 33–46 adoral membranelles, three enlarged frontal cirri, one buccal cirrus, two frontoterminal cirri, five–six transverse cirri. Midventral complex composed of 14–25 midventral cirral pairs; 27–37 left and 24–40 right marginal cirri. Six to seven kineties composed of three dorsal and three (rarely four) dorsomarginal kineties. Three caudal cirri.

**TABLE 1.** Morphometric data on protargol-impregnated specimens of *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.**

| Characteristics | N | Mean | SD | SE | CV | Min | M | Max |
|---|---|---|---|---|---|---|---|---|
| Body length, μm | 21 | 160.0 | 15.8 | 3.4 | 0.1 | 134.1 | 160.5 | 192.7 |
| Body width, μm | 21 | 67.3 | 16.2 | 3.5 | 0.2 | 45.3 | 63.8 | 102.9 |
| Adoral zone length, μm | 21 | 54.3 | 3.8 | 0.8 | 0.1 | 46.1 | 54.3 | 62.4 |
| Adoral membranelles, number | 21 | 40.2 | 3.6 | 0.8 | 0.1 | 33.0 | 41.0 | 46.0 |
| Ratio of body length: adoral zone length, μm | 21 | 2.5 | 0.5 | 0.1 | 0.2 | 1.6 | 2.5 | 3.2 |
| Anterior body end to last midventral pair, distance, μm | 16 | 40.6 | 6.2 | 1.6 | 0.2 | 24.5 | 39.9 | 50.4 |
| Macronucleus length, μm | 21 | 21.3 | 2.6 | 0.6 | 0.1 | 16.1 | 21.0 | 26.2 |
| Macronucleus width, μm | 21 | 13.2 | 2.3 | 0.5 | 0.2 | 9.6 | 13.1 | 18.1 |
| Macronuclear nodules, number | 21 | 2.0 | 0.0 | 0.0 | 0.0 | 2.0 | 2.0 | 2.0 |
| Micronuclei length, μm | 17 | 3.4 | 0.5 | 0.1 | 0.1 | 2.4 | 3.4 | 4.6 |
| Micronuclei width, μm | 17 | 3.2 | 0.5 | 0.1 | 0.2 | 2.3 | 3.2 | 4.5 |
| Micronucleus, number | 17 | 1.8 | 0.8 | 0.2 | 0.4 | 1.0 | 2.0 | 3.0 |
| Frontal cirri, number | 21 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 3.0 |
| Buccal cirrus, number | 21 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 1.0 |
| Frontoventral cirri, number | 21 | 2.0 | 0.0 | 0.0 | 0.0 | 2.0 | 2.0 | 2.0 |
| Midventral pairs, number | 17 | 19.4 | 3.0 | 0.7 | 0.2 | 14.0 | 19.0 | 25.0 |
| Pretransverse cirri, number | 17 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 1.0 |
| Transverse cirri, number | 16 | 5.6 | 0.5 | 0.1 | 0.1 | 5.0 | 6.0 | 6.0 |
| Dorsal and dorsomarginal kineties, number | 19 | 6.3 | 0.5 | 0.1 | 0.1 | 6.0 | 6.0 | 7.0 |
| Caudal cirri, number | 21 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 3.0 |
| Left marginal cirri, number | 18 | 30.9 | 2.6 | 0.6 | 0.1 | 27.0 | 30.0 | 37.0 |
| Right marginal cirri, number | 17 | 33.9 | 4.2 | 1.0 | 0.1 | 24.0 | 35.0 | 40.0 |

CV—coefficient of variation (%); Max—maximum; Min—minimum; N—number of specimens investigated; SD—standard deviation; SE—standard error of arithmetic mean.

**Type locality.** Moss from Greenwich Island, Antarctica (62°28′43.2″S, 59°39′36.2″W).

**Type slides.** One holotype slide (ACNS000108) and two paratype slides (ACNS000106, ACNS000107) of protargol-impregnated specimens have been deposited in the Korea Polar Research Institute (KOPRI), South Korea. Relevant specimens including the holotype have been marked with circles on the bottom of the slides.

**Etymology.** The name "*antarctica*" is derived from the region where the species was discovered: Antarctica.

**Gene sequence.** SSU rRNA sequence was deposited in the GenBank under the accession number MH718439.

**Morphological description.** Size 213.0–238.0×67.5–74.5 μm *in vivo* (Fig. 1A; 2A–E), on average 160.0 × 67.3 μm in protargol preparation, that is, length:width ratio 2.5:1 on average (Fig. 1C, D; 3A–D). Body slender to elongated in shape, anterior end widely rounded, tail absent, dorsoventrally flattened; flexible but not contractile; cell color grayish under low magnification (Fig. 1B; 2D, E; 3A–D). Invariably, on left of mid-body, two macronuclear nodules and one to three micronuclei (Fig. 1A, D; 2H; 3A, C, D). Macronuclear nodules ellipsoid, 16.1–26.2 × 9.6–18.1 μm (stained); spherical micronucleus closed to left side of each macronucleus, 2.4–4.6 × 2.3–4.5 μm (stained). One contractile vacuole slightly above left of mid-body, approximately 20 μm in diameter when fully extended, lacking conspicuous collecting canals (Fig. 1B; 2D). Feeds on green algae and diatoms.

Cirri 20–25 μm long *in vivo*, transverse cirri approximately 25 μm long *in vivo*; frontal, frontoterminal, marginal, ventral, pretransverse, and caudal cirri about 20 μm long, on ventral side, composed of three frontal cirri near proximal end of adoral zone of membranelles, one buccal, two frontoterminal, one pretransverse, and five to six transverse cirri (Fig. 1A; 3A, B, E). Two marginal cirral rows composed of one left and one right row, terminating at level of posterior-most transverse cirrus, marginal rows clearly separated at posterior body end. Invariably six dorsal kinety rows composed of three dorsal and three to four dorsomarginal kineties without any fragmentations. Dorsal bristles about 4 μm *in vivo*. One caudal cirrus at end of each dorsal kinety, invariably with three caudal cirri. Leftmost dorsal kinety anteriorly shortened.

Adoral zone composed of 33–46 membranelles in a continuous arrangement, occupying approximately 25% of body length in stained specimens. Undulating membranes curved, similar to that of *Cyrtohymena*; one buccal cirrus positioned on the right of paroral membrane and slightly above middle of paroral membrane (Fig. 1A, C; 2F; 3E).

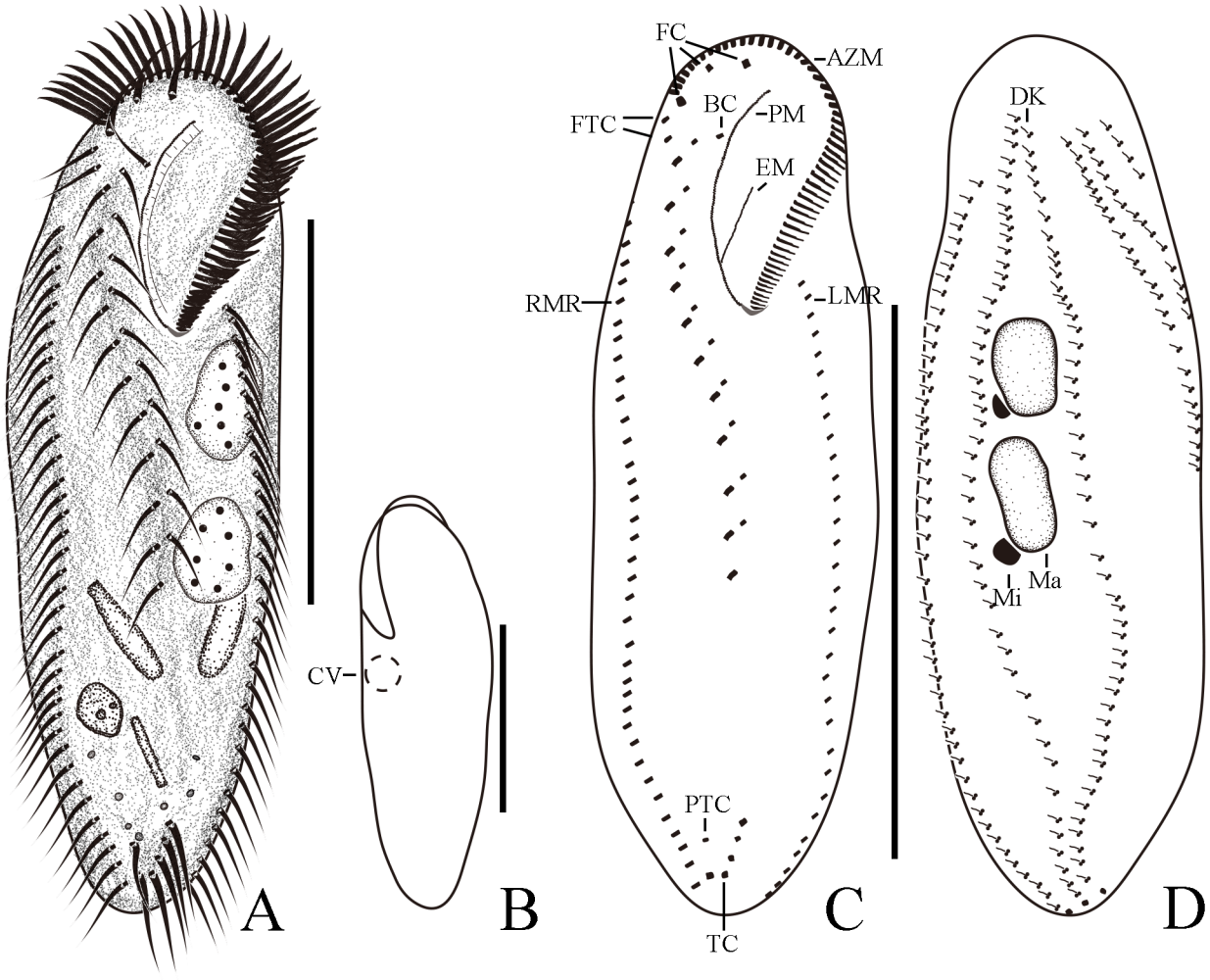


**FIGURE 1.** Morphology of *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.**, both *in vivo* (A, B) and after protargol impregnation (C, D). A. Ventral view of a representative specimen. B. Dorsal view showing contractile vacuole (CV). Ventral (C) and dorsal (D) view of holotype specimen. AZM—adoral zone of membranelles; BC—buccal cirrus; DK—dorsal kinety; EM—endoral membrane; FC—frontal cirri; FTC—frontoterminal cirri; LMR—left marginal cirral row; Ma—macronuclear nodules; Mi—micronucleus; PM—paroral membrane; RMR—right marginal cirral row; PTC—pretransverse cirri; TC—transverse cirri. Scale bars: 100 μm.

### Molecular analysis of *Urosleptus* (*Caudiholosticha*) *antarctica* n. sp.

The SSU rRNA sequence of *Uroleptus* (*Caudiholosticha) antarctica* (GenBank accession number MH718439) has a length of 1,309 bp and a G + C content of 47.0%. The topologies of the ML and BI trees are similar, and therefore only the BI tree is shown (Fig. 4). According to the phylogenetic analyses of the 51-taxon alignment, *U.* (*Caudiholosticha*) *antarctica* is closely related to the *U.* (*Caudiholosticha*) *stueberi* group (KT724201) and to an unidentified *Uroleptus* population (*Uroleptus* sp. WJC-2003; AY294646) in both trees with full support (BI/ML, 0.62/59). This sequence has 98.7% and 99.0% nucleotide similarity to *U.* (*Caudiholosticha*) *stueberi* (the type species of this genus) and to *U.* sp. WJC-2003, respectively. *Uroleptus gallina* (AF164130) is distinct within this cluster. These two groups (*U.* (*Caudiholosticha*) *antarctica* + *U.* (*Caudiholosticha*) *stueberi* + *U.* sp., and the remaining *Uroleptus* species, respectively) form a cluster with support in the BI tree (0.96/50).

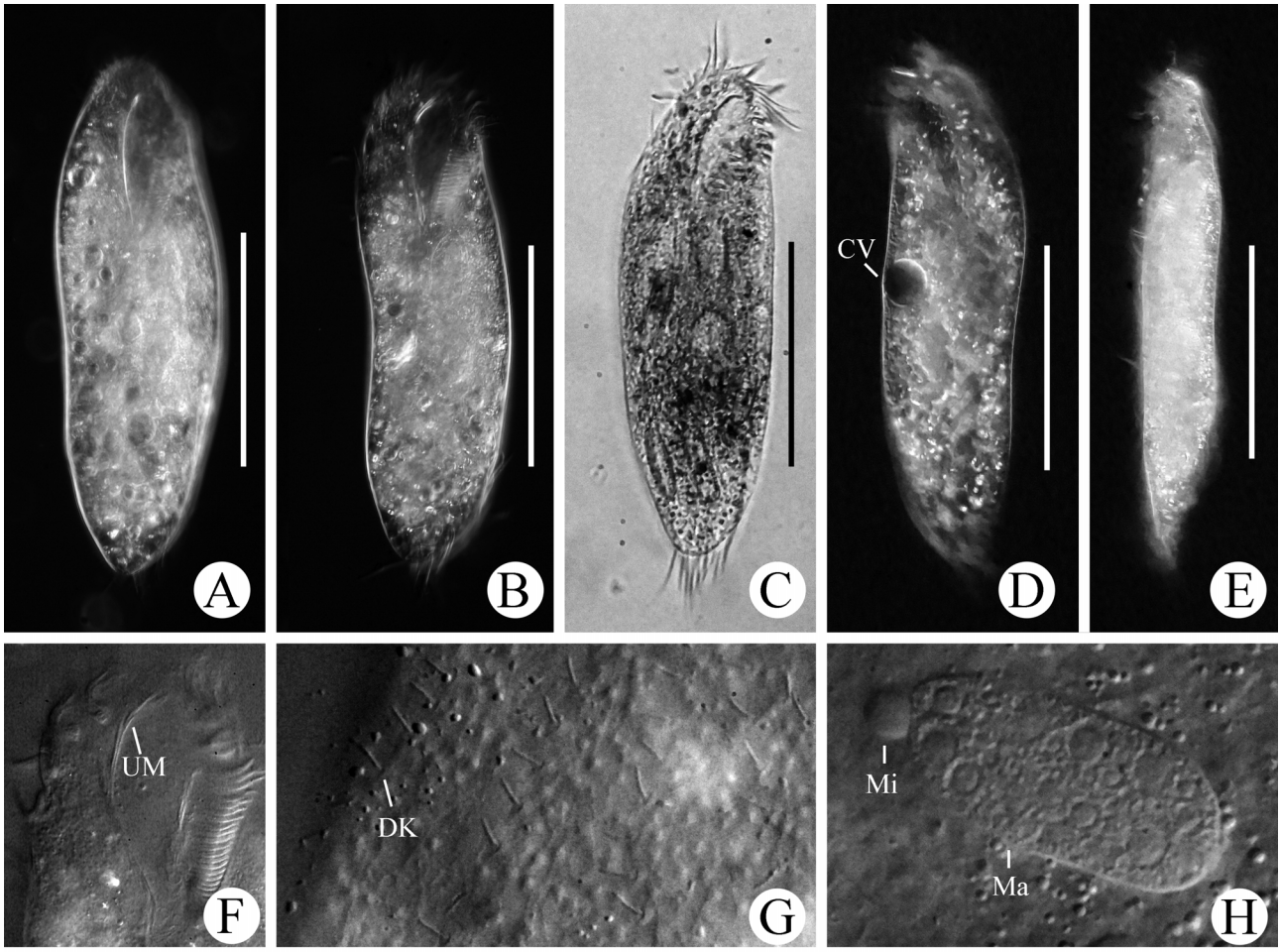


**FIGURE 2.** Photomicrograph of *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.** *in vivo*. A, B, C. Ventral views showing body shape of specimens. D. Dorsal view showing a contractile vacuole. E. Lateral view. F. Anterior ventral view showing the undulating membranes. G. Dorsal view showing a dorsal bristles (DB). CV—contractile vacuole; DK—dorsal kineties; Ma—macronuclear nodules; Mi—micronucleus; UM, undulating membranes. Scale bars: 100 μm.

## Discussion

**Morphological comparison of *U.* (*Caudiholosticha*) *antarctica* and related species.** Sixteen species of the genus *Caudiholosticha* have so far been described. However, Li *et al*. (2016b) recently rearranged the genus *Caudiholosticha*, and all species other than the type species were placed into several newly created genera: *Extraholosticha* Li *et al*. 2016; *Adumbratosticha* Li *et al*. 2016; *Acuholosticha* Li *et al*. 2016; *Limnoholosticha* Li *et al*. 2016; *Multiholosticha* Li *et al*. 2016; and *Caudikeronopsis* Li *et al*. 2016.

Li *et al*. (2016b) placed the genus *Caudiholosticha* within the genus *Uroleptus* as a new subgenus because *C. stueberi* have dorsomarginal kineties, a characteristic feature of *Uroleptus* (Berger 2006; Foissner and Stoeck 2006). *Uroleptus* (*Caudiholosticha*) *stueberi*, the sole species in this subgenus, was described by Foissner (1987) and Li *et al*. (2016b). Thus, *Uroleptus* (*Caudiholosticha*) *antarctica* was compared with both the Austrian and Chinese populations of *U.* (*Caudiholosticha*) *stueberi*. Their morphological features are summarized in Table 2 and are distinguished from *U.* (*Caudiholosticha*) *antarctica* by their cell size and number of ciliatures (e.g. transverse cirri, frontoterminal cirri, and dorsal bristles) (Table 2).

*Uroleptus* (*Caudiholosticha*) *stueberi* of the Austrian population can be distinguished from *U.* (*Caudiholosticha*) *antarctica* **n. sp.** based on numbers of frontoterminal cirri (2–3 vs. 2), transverse cirri (3 vs. 5–6), and macronuclear nodules (2–3 vs. 2). *Uroleptus* (*Caudiholosticha*) *stueberi* of the Chinese population can be separated from *U.* (*Caudiholosticha*) *antarctica* **n. sp.** by their body size (200–250 μm vs. 134–193 μm),

frontoterminal cirri (2–3 vs. 2), transverse cirri (3 vs. 5–6), and macronuclear nodules (2–4 vs. 2). Both species, *Uroleptus* (*Caudiholosticha*) *stueberi* and *U.* (*Caudiholosticha*) *antarctica*, differ mainly in the collecting canal (present vs. absent), and midventral cirral pairs (extends to near transverse cirri vs. separated).

**Molecular phylogeny of *U.* (*Caudiholosticha*) *antarctica*.** Based on the SSU rRNA gene phylogenetic tree, we identified that the genus *Uroleptus* clustered as a single group that is monophyletic in almost all studies (Fig. 4; e.g., Chen *et al*. 2016; Foissner *et al*. 2004; Li *et al*. 2016b; Sonntag *et al*. 2008).

Li *et al*. (2016b) divided the genus *Uroleptus* into three subgenera on the basis of the number of transverse cirri and the presence/absence of a tail. Among them, the subgenera *U*. (*Uroleptus*) and *U*. (*Paruroleptus*) are distinct from the group *U*. (*Caudiholosticha*) based on their morphology and phylogenetic tree.

The subgenus *U*. (*Caudiholosticha*) includes *U*. (*Caudiholosticha*) *stueberi* and *U*. (*Caudiholosticha*) *antarctica* **n. sp.**, which cluster together and have same apomorphy (absence of tail, dorsomarginal kineties present). Their similarity is 98.7% based on the SSU rRNA gene.

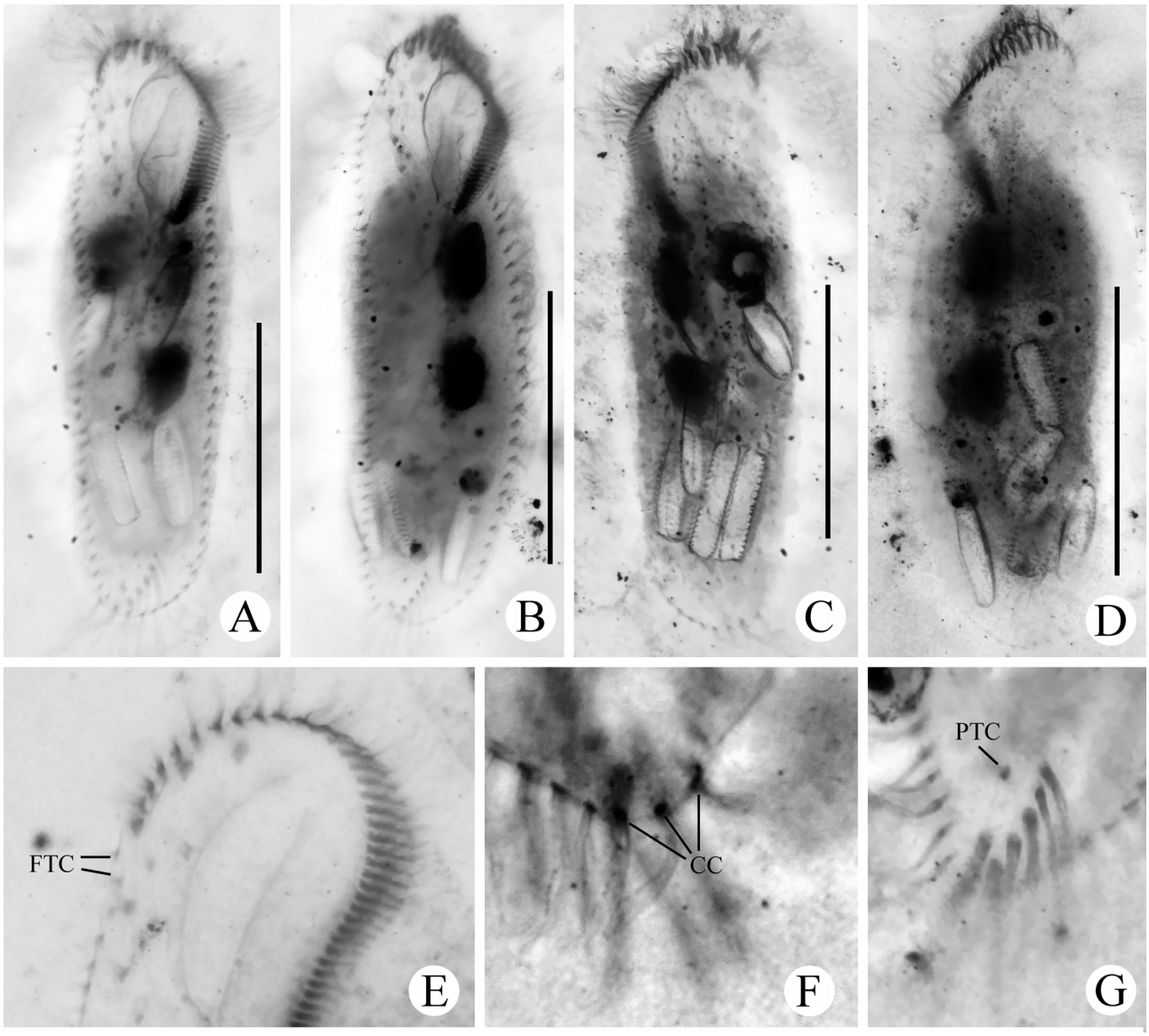


**FIGURE 3.** Photomicrographs of *Uroleptus* (*Caudiholosticha*) *antarctica* **n. sp.** after protargol impregnation. A, B. Ventral views of the specimens. C, D. Dorsal views of the specimens. E. Anterior ventral cell portion showing the undulating membranes, frontal, frontoterminal cirri, and buccal cirrus. F. Caudal cirri. G Pretransverse and transverse cirri. CC, caudal cirri; FTC, frontoterminal cirri; PTC, pretransverse cirri. Scale bar: 100 μm.

However, *Uroleptus* sp. WSJ-2003 clustered within the subgenus *U*. (*Caudiholosticha*). The morphological information for *Uroleptus* sp. WSJ-2003 was absent. Likewise, *U. piscis* having many transverse cirri related with species having few transverse cirri (Li *et al*. 2016b). This problem is because some species have not been the subject of a morphological study using protargol preparation (Foissner *et al*. 2004).

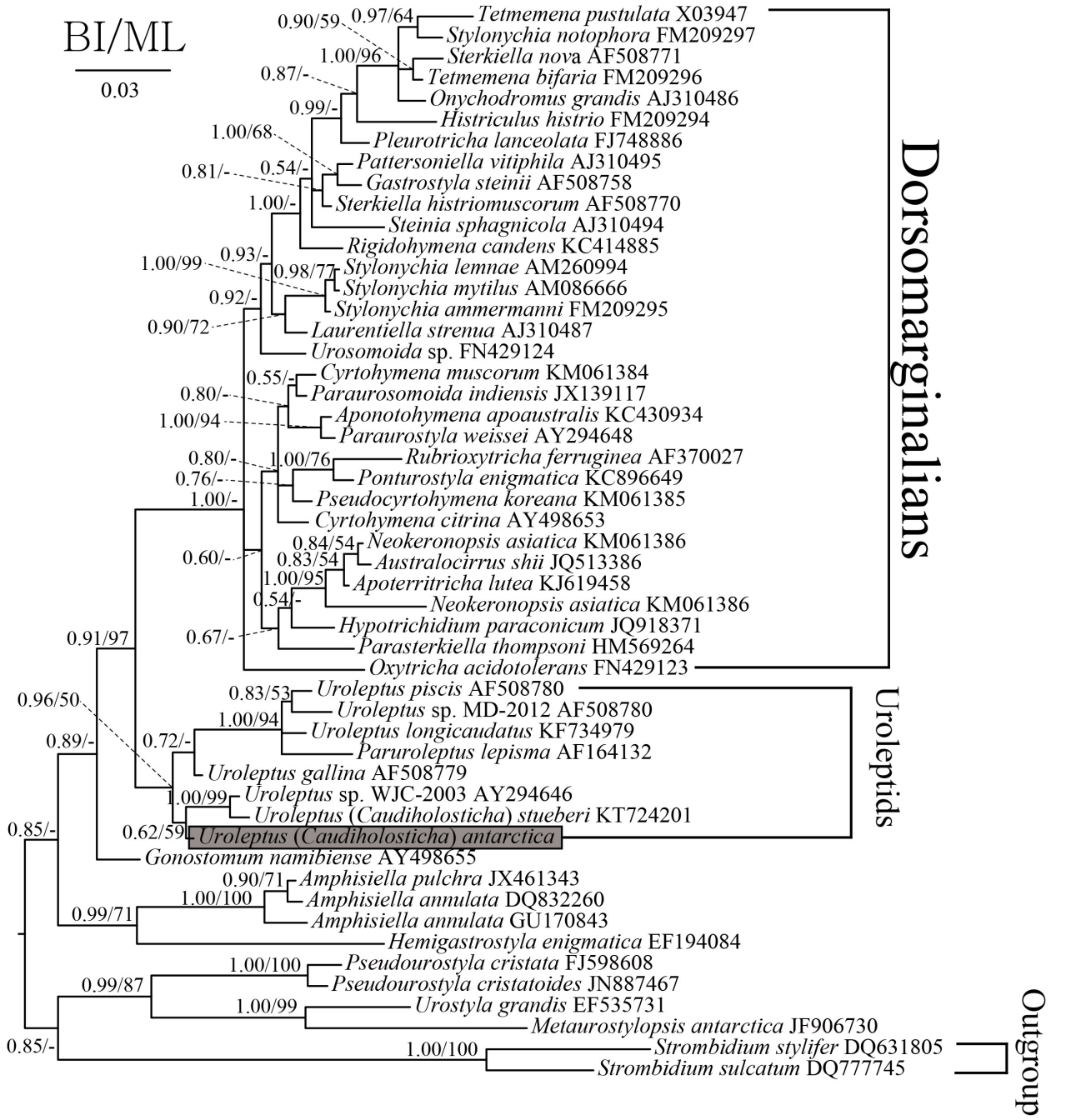


**FIGURE 4.** Majority consensus tree of Bayesian inference (BI) using SSU rRNA sequences. On interior branches, BI, and maximum likelihood (ML) bootstrap values are represented, respectively. Dashes denote values < 50% or different topologies in BI and ML phylogenies.

Therefore, data needs to be reinforced with regard to their molecular data and morphological information based on protargol preparation to resolve the relationship of three subgenera in this genus.

**TABLE 2.** Comparison of morphological features in *Uroleptus (Caudiholosticha*) *antarctica* n. sp. with closely related species.

| | *U.* (*Caudiholosticha*) *stueberi* from Austria | *U.* (*Caudiholosticha*) *stueberi* from China | *U.* (*Caudiholosticha*) *antarctica* **n. sp.** |
|---|---|---|---|
| Body length (stained), µm | 178–270 | 200–250 | 134–193 |
| Cortical granules | Absent | Absent | Absent |
| Adoral membranelles, number | 43–54 | 39–52 | 33–46 |
| Frontal cirri, number | 4[a] | 3 | 3 |
| Frontoterminal cirri, number | 2–3 | 2–3 | 2 |
| Right marginal cirri, number | 20–42 | 26–32 | 24–40 |
| Left marginal cirri, number | 23–38 | 24–36 | 27–37 |
| Pretransverse cirri, number | -[b] | 1 | 1 |
| Midventral cirral pair, number | 15–41[c] | 14–20[d] | 14–25 |
| Transverse cirri, number | 3 | 3 | 5–6 |
| Dorsal kineties including dorsomarginal rows | 5–7 | 7–8 | 6–7 |
| Macronuclear nodules, number | 2–3 | 2–4 | 2 |
| Position of midventral end | Near transvers cirri | Near transvers cirri | 2/3 of body length |
| Caudal cirri, number | 3 | 3 | 3 |
| Inconspicuous collecting canals | Absent | Absent | Present |
| Habitat | Terrestrial | Terrestrial | Terrestrial |
| Data source | Foissner (1987) | Li *et al*. (2016b) | Original |

Data of *U.* (*Caudiholosticha*) *stueberi* from Austria and China are based on 12 and 15 individuals, respectively.
[a]cirrus III/2 included.
[b]Likely at least one pretransverse cirrus is present in midventral pairs.
[c]Originally, left and right midventral cirri separately described. Minimum and maximum number of midventral cirri used.
[d]Rearmost pair not included.


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