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# *Apofrontonia lametschwandtneri* nov. gen., nov. spec., a new peniculine ciliate (Protozoa, Ciliophora) from Venezuela

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Apofrontonia lametschwandtneri was discovered in a highly saline mud and soil sample from a flooded area on the north coast of Venezuela (Maracay National Park). Its morphology was studied in vivo and in silver preparations, as well as in the scanning electron microscope. The new genus *Apofrontonia* belongs to the family Frontoniidae and is characterized by a combination of three features, viz., a pyriform vestibular opening occupying more than half of the body length; a bowl-shaped vestibulum that posteriorly gradually merges into the cell surface, completely exposing three similarly-structured peniculi; many (>6) vestibular kineties covering the sigmoidal right vestibular wall and not extending beyond the oral cavity. *Apofrontonia lametschwandtneri* nov. spec. differs from a European congener, *A. obtusa* (Song and Wilbert 1989) nov. comb. (basionym: *Frontonia obtusa* Song and Wilbert 1989), by body size (180 µm vs. 80 µm), number of somatic (155 vs. 90) and vestibular kineties (13 vs. 9), and the number (25 vs. 4–5) and location (scattered vs. lateral) of contractile vacuoles. Considering that *A. lametschwandtneri* has not been found in Europe, although it is a very large, conspicuous ciliate, it might be endemic to South America.

Key words: Apofrontonia obtusa nov. comb.; Biogeography; Frontoniidae; Peniculida; Saline soil; Soil ciliates.

# Introduction

Peniculine ciliates, the most prominent member of which is the "slipper-shaped animalcule" *Paramecium*, are comparatively well-known because all genera have been investigated with a variety of modern methods, especially silver impregnation (for reviews, see Corliss 1979; Didier and Puytorac 1994; Foissner et al. 1994, 1999; Strüder-Kypke et al. 2000). Interestingly, no new genus has been added to the group since 1985, when Small and Lynn established two new genera, which, unfortunately, were described rather superficially. Thus, we are proud to present a well-defined new

genus and species, *Apofrontonia lametschwandtneri*, discovered in a highly saline soil sample from a flooded area on the north coast of Venezuela. *Apofrontonia* differs from other peniculines mainly by its oral apparatus, a feature found also in a European congener described by Song and Wilbert (1989) as *Frontonia obtusa*.

# Materials and methods

Apofrontonia lametschwandtneri was discovered in a soil sample from the Maracay National Park on the north coast of Venezuela. The sample consisted of mud

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and soil from the surface of a flat, highly saline (>30 ‰), dry pool covered with halophytes and crusts of cyanobacteria. In the laboratory, the dry sample was rewetted, as described by Foissner (1987), to obtain a "non-flooded Petri dish" culture. The rewetted sample had pH 7.3 (in water).

Field material as obtained with the non-flooded Petri dish method was used for all investigations. Living cells were studied using a high-power oil immersion objective and differential interference contrast. Silver carbonate and silver nitrate impregnation and scanning electron microscopy were performed as described by Foissner (1991).

Counts and measurements on silvered specimens were performed at a magnification of  $\times 1000$ . In vivo measurements were conducted at a magnification of  $\times 40-1000$ . Drawings of live specimens were based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida. Scale bars are provided for all line drawings and those micrographs which are based on unsquashed specimens.

Terminology is mainly according to Corliss (1979).

### Results

Order Hymenostomatida Delage & Hérouard, 1896

Family Frontoniidae Kahl, 1926 Genus Apofrontonia nov. gen.

**Diagnosis:** Frontoniidae with large oral apparatus occupying at least half of ventral side. Vestibular cavity with pyriform opening, bowl-shaped and posteriorly gradually merging into cell surface, completely exposing three similarly-structured, comparatively large peniculi; right vestibular wall sigmoidal, covered by numerous (>6) vestibular kineties not extending beyond oral cavity.

Type species: Apofrontonia lametschwandtneri nov. spec.

**Etymology:** Composite of *apo* (derived from) and the generic name *Frontonia*. Feminine gender.

**Description of** *Apofrontonia lametschwandtneri* **nov. spec.** (Figs 1–42; Table 1)

**Diagnosis:** Large *Apofrontonia* with an average size of  $180 \times 120 \ \mu\text{m}$  *in vivo*. Obovate and dorsoventrally flattened up to 2:1. Macronucleus rod-like. About 30 scattered contractile vacuoles. Extrusomes fusiform and about 6  $\mu\text{m}$  long. Approximately 155 somatic ciliary rows. Vestibulum 2/3 of body length on average; right wall with an average of 13 vestibular kineties. Peniculus 1 com-

posed of about thirteen, peniculus 2 of about ten, and peniculus 3 of about 4 ciliary rows.

**Type location**: Saline soil from flooded grassland in the Maracay National Park, north coast of Venezuela, W 68° N 10°.

**Type specimens:** 1 holotype slide and 4 paratype slides of silver nitrate-impregnated specimens have been deposited in the Biology Center of the Museum of Upper Austria, Linz (LI), Austria. Relevant cells are marked by a black ink circle on the cover glass.

Dedication: We dedicate this species to Prof. Dr. Mag. Alois Lametschwandtner, an honest colleague and head of the Zoological Institute of Salzburg University.

**Description:** Cells conspicuous because of large size, look like hollowed eggs due to the large and deep vestibular cavity. Size rather stable, viz.,  $160-200 \times 105-140 \,\mu\text{m}$  in vivo, usually near  $180 \times 120$  µm; more variable in silver slides, viz.  $167-215 \times 115-180 \,\mu\text{m}$ , on average  $183 \times 145 \,\mu\text{m}$ ; length:width ratio 1.3-1.6, on average 1.5 in vivo and 1.3 in silver nitrate preparations (Table 1). Shape basically obovate and considerably asymmetrical since more or less flattened right laterally and ventrally and distinctly vaulted dorsally, where thickness gradually increases from anterior to posterior, an unusual pattern (Figs 8, 23). Anterior end almost invariably more broadly rounded than posterior, smoothly rounded or slightly tapering, especially in silver slides (Fig. 7); posterior end often slightly indented where postoral suture extends (Figs 1, 2, 20-28). Shape rather sensitive, becomes roundish in disturbed and preserved specimens (Figs 6, 7, 9-11). Macronucleus not in fixed position, rod-like and often rather tortuous, with a definite, deep constriction in about 5 % of specimens; one end often slightly inflated (Figs 1, 2, 6, 9, 10); contains many long fibres visible by interference contrast optics. Micronucleus not observed. About 30 contractile vacuoles scattered beneath body surface, each with one, rarely two excretory pores between ciliary rows; without collecting canals (Figs 1, 2, 8, 11, 32). Cortex composed of ordinary peniculine "units" easily recognizable with interference contrast optics; units less distinct dorsally, where the longitudinal ridges are more conspicuous than the transverse ones (Figs 14, 41, 42); after silver nitrate impregnation, three cortical patterns can be observed (Figs 15, 16, 29, 30): (i) quadrangular cortical meshes similar to those seen in vivo and, for instance, also in Fronto-



**Figs 1–8.** Apofrontonia lametschwandtneri from life (1–5, 8) and after Chatton-Lwoff silver nitrate impregnation (6, 7). **1, 2:** Ventral view of a representative specimen (1) and ventrolateral view of a large, broad cell (2), showing the vestibular kinety stripe (asterisks). Note the large, pyriform vestibular opening, the main feature of the genus. Cells are packed with lipid droplets and food vacuoles containing bacteria, coccal cyanobacteria, and ciliates. **3:** Resting extrusome, 6 µm long. **4:** Exploded extrusomes, up to 25 µm long. **5:** Cytoplasmic crystals, up to 3 µm. **6, 7:** Ventrolateral views of specimens with small (6) and large (7) vestibulum. **8:** Lateral view showing that cells thicken from anterior to posterior, while the vestibulum flattens posteriorly. AS – anterior (preoral) suture, C – cytostome, CV – contractile vacuoles, MA – macronucleus, P1, 2, 3 – peniculi, PS – postoral suture, V – vestibulum, VK – vestibular kineties. Scale bars 100 µm.

#### 226 W. Foissner and W. Song

Table 1. Morphometric data on Apofrontonia lametschwandtneri.

Characteristics <sup>1)</sup>	$\overline{X}$	М	SD	SE	CV	Min	Max	n
Body, length in vivo	181.4	180.0	10.8	2.3	6.0	160.0	200.0	22
Body, width in vivo	124.1	120.0	8.7	1.9	7.0	105.0	140.0	22
Body length:width, ratio in vivo	1.5	1.5	0.1	0.1	5.4	1.3	1.6	22
Body, length	182.6	183.0	11.8	2.6	6.5	167.0	215.0	21
Body, width	144.9	140.0	16.1	3.5	11.1	115.0	180.0	21
Body length:width, ratio	1.3	1.3	0.1	0.1	7.8	1.1	1.5	21
Body, thickness <sup>2</sup> )	100.8	101.5	20.5	6.5	20.4	70.0	130.0	10
Anterior body end to peniculus 1, distance	23.6	22.0	6.2	1.4	26.1	17.0	40.0	21
Anterior body end to posterior end of peniculus 1, distance	145.0	145.0	8.2	1.8	5.7	132.0	160.0	21
Posterior end of peniculus 1 to posterior body end, distance	35.9	35.0	8.7	1.9	24.3	20.0	55.0	21
Peniculus 1, length (~ length of vestibular opening)	122.8	124.0	5.4	1.2	4.4	115.0	130.0	21
Peniculus 3, length (chord)	98.2	100.0	6.1	1.3	6.2	85.0	105.0	21
Cytostome, length (chord of slit)	95.1	95.0	5.0	1.1	5.3	85.0	105.0	21
Vestibular opening, maximum width	38.8	40.0	3.4	0.7	8.7	33.0	45.0	21
Vestibular opening, width near posterior end <sup>3</sup> )	14.0	15.0	_	_	_	8.0	18.0	21
Macronucleus, length <sup>4</sup> )	124.8	120.0	15.3	3.3	12.3	105.0	155.0	21
Macronucleus, width (in or near centre)	19.4	20.0	2.1	0.5	11.0	15.0	24.0	21
Somatic ciliary rows, number <sup>5)</sup>	154.4	155.0	_	_	_	140.0	170.0	21
Vestibular kineties, number	12.9	13.0	0.9	0.2	6.6	12.0	14.0	21
Excretory pores ventral, number <sup>5)</sup>	12.7	12.0	_	_	_	9.0	18.0	7
Excretory pores dorsal, number <sup>5</sup> )	16.4	17.0	_	_	_	12.0	22.0	12
Excretory pores, diameter	2.2	2.0	-	-	-	2.0	3.0	21

<sup>1)</sup> Data based, if not stated otherwise, on Chatton-Lwoff silver nitrate-impregnated, randomly selected specimens from a non-flooded Petri dish culture. Measurements in  $\mu$ m. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean,  $\overline{x}$  – arithmetic mean.

<sup>2)</sup> Likely somewhat inflated due to preparation.

<sup>3)</sup> Approximate because right wall gradually merges into body proper.

<sup>4)</sup> From specimens, in which it is rod-shaped or nearly so.

<sup>5)</sup>Approximate values.

*nia* and *Paramecium* (Roque 1961; Dragesco and Dragesco-Kernéis 1986; Foissner et al. 1994, 1999; Petz et al. 1995); (ii) irregular, short transverse silverlines connecting neighbouring kineties, similar to those sometimes seen in *Paramecium* (Gelei 1937); and (iii) no pattern, likely due to insufficient impregnation. Extrusomes numerous, very regularly arranged possibly right of and within ciliary rows, that is, alternate with cilia, do not form distinct fringe because small compared to size of cell; fusiform, about  $6 \times 0.7 \ \mu m$  in size, become up to 25  $\mu m$  long, slightly curved rods when extruded (Figs 3, 4). Cytoplasm colourless, does not contain pigment granules or a granule spot (as some *Fron*-

tonia species do), cells however dark at low magnification ( $\leq \times 100$ ) because large and usually packed with food vacuoles, many lipid droplets up to 10 µm across, and some 1–3 µm-sized crystals (Figs 1, 2, 21, 22). Feeds on bacteria, coccal cyanobacteria and medium-sized ciliates, such as *Colpoda magna* and *Nassula* spp., digested in food vacuoles up to 30 µm across; the latter may make cells colourful due to the food vacuoles containing cyanobacteria in various stages of digestion. When undisturbed, cells remain almost motionless collecting food, and can thus be easily photographed (Figs 20–28); when disturbed, they glide and swim rather quickly by rotation about main body axis.



Figs 9–11. Apofrontonia lametschwandtneri after Chatton-Lwoff silver nitrate impregnation. 9, 10: Ventrolateral and ventral view of specimens with bipartite macronucleus. Note the pyriform or key-hole-shaped vestibular opening, the main generic feature. 11: Dorsal view showing pores of the contractile vacuoles. Scale bars 100 µm.

Somatic cilia about 15 µm long in vivo, arranged in approximately 155 closely spaced rows (Figs 1, 2, 12, 31–34; Table 1). Ciliary pattern basically as in *Frontonia* (Dragesco & Dragesco-Kernéis 1986; Foissner et al. 1994); that is, with a distinct preoral and postoral suture, both rather short and not extending onto dorsal side, anterior suture more conspicuous than posterior one because wider and first cortical unit of left side ciliary rows unciliated. Ciliary rows extend meridionally, those of ventral side abut to the sutures, except the vestibular kineties and about 10 postoral kineties gradually shortening from anterior to posterior along left mouth margin.

Details of kinetids as in other peniculines, especially *Frontonia* (Roque 1961; Gil and Perez-Silva 1964a-c; Didier 1971; Dragesco and Dragesco-Kernéis 1986). Briefly, cilia appear single in scanning electron micrographs and silver carbonate preparations, where each cortical unit contains a single, distinct granule, likely a basal body, associated with a kinetodesmal fibre extending anteriorly at the right side of the kinety (Fig. 34); sometimes, a faintly impregnated second granule is recognizable anterior of the strongly impregnated one; in vivo, the cortical units contain two granules (Figs 14, 41, 42), while usually even three granules forming conspicuous triangles are recognizable in silver nitrate preparations (Figs 15, 16, 18, 29, 30); the rightmost granule of the triangles often appears ring-like and slightly larger, suggesting that it is a parasomal sac or extrusome. Further, there is a minute ring (in vivo) or a granule (in silver nitrate preparation) between each two kinetids of a row; likely, this is an attachment site of a trichocyst.

Oral opening very large, occupying two thirds of body length and, at widest site, almost one third of body width on average, distance to anterior body end slightly shorter than to posterior; left margin convex and sharply defined, right gradually merging into body proper and sigmoidal, producing a highly characteristic pyriform or key-hole-shaped vestibular outline (Figs 1, 2, 6, 7, 12, 20–28; Table 1). Vestibular cavity deepest in anterior third, where it extends to mid of body, flattens in posterior half to gradually merge into cell surface at posterior mouth margin (Figs 8, 23, 27); fragile, that is, often flattens or even bursts in preparations. Left vestibular wall convex, covered by three conspicuous peniculi (Figs 1, 6, 7, 12, 18, 19, 26, 31, 33, 35-40; Table 1): peniculus 1 as long as vestibulum, slightly narrowed anteriorly and posteriorly, where kineties shorten along left margin, composed of about 13 rows of very regularly and densely spaced, approximately 20 µm long cilia; peniculus 2 close to peniculus 1, slightly cuneate, that is, widest anteriorly and slightly shorter than peniculus 1, composed of about 10 rows of very regularly and



**Figs 12–19.** Apofrontonia lametschwandtneri from life (14) and after silver carbonate (13) and Chatton-Lwoff silver nitrate (12, 15–19) impregnation. **12:** Ventral view of a representative specimen. **13:** Details of peniculi in anterior third. **14–16:** Cortex structure (14) and silverline pattern (15, 16). **17:** A vestibular kinety, likely accompanied by a row of extrusomes. **18, 19:** Anterior and posterior portion of oral apparatus at high magnification. AS – anterior (preoral) suture, C – cytostome, E – extrusome surrounded by a silverline, EP – excretory pore, F – fibres, PM – paroral membrane, PS – postoral suture, P1, 2, 3 – peniculi, VK – vestibular kineties. Scale bars 50 µm (12), 20 µm (18, 19) and 10 µm (14–16).



**Figs 20–30.** Apofrontonia lametschwandtneri from life (20–28; length 160–200 µm) and after Chatton-Lwoff silver nitrate impregnation (29, 30; scale bars 10 µm). **20**: Dorsal views. Asterisks mark anterior end. **21, 22**: Ventrolateral and ventral view of specimens packed with lipid droplets. **23**: Lateral view. **24–26**: Ventrolateral (24), slightly ventrolateral (25), and ventral (26) view of same specimen. Arrowheads mark vestibular opening, arrow denotes end of peniculus 3. **27, 28**: Ventral views of rare shape variants. Arrow denotes end of peniculus 3. **29, 30**: Cortical (CP) and silverline pattern, as shown in figures 14–16 and 41, 42. CV – contractile vacuoles, E – extrusome attachment sites, EP – excretory pore, K – kinetid, P – peniculi, V – vestibulum, VK – vestibular kinety stripe.



**Figs 31–34.** Apofrontonia lametschwandtneri after Chatton-Lwoff silver nitrate (31, 32) and silver carbonate (34) impregnation, and in the scanning electron microscope (33). **31, 32:** Infraciliature of ventral and dorsal side. Note the excretory pores (arrows) of the contractile vacuoles and the huge, pyriform vestibular opening, the main generic feature. **33:** Ventrolateral view. The vestibular cavity has flattened, exposing the fibrous plate (asterisk) between paroral membrane and cytostome. **34:** Distal portion of preoral suture. AS – anterior (preoral) suture, P – peniculi, PS – postoral suture, V – vestibulum, VK – vestibular kinety stripe. Scale bars 100 µm.



**Figs 35–39.** Apofrontonia lametschwandtneri from life (35, 36) and after silver carbonate impregnation (37–39). **35, 36:** Slightly squeezed specimen showing the huge, pyriform vestibular opening, the main generic feature. The right vestibular wall is flabby (arrow) and covered by about 13 kineties appearing as distinct lines, likely because underlaid by fibres (see figures 37, 40). **37–39:** Anterior half of oral apparatus. The vestibular kineties and the cytostomial area are underlaid by a complicated fibre system. Arrowhead marks a thick fibre formed by fine fibres originating from peniculi 1 and 2. Arrows mark successively shortened kineties at left margin of peniculus 1. The paroral membrane is at left margin of the vestibular stripe and composed of very closely spaced, zigzagging basal bodies. AS – anterior suture, C – cytostome, CV – contractile vacuoles, F – fibres, L – lipid droplets, PM – paroral membrane, P1, 2, 3, – peniculi, VK – vestibular kineties. Scale bars 50 µm.



**Figs 40–42.** *Apofrontonia lametschwandtneri* after silver carbonate impregnation (40) and from life (41, 42). 40: Oral apparatus showing the three large peniculi and the complicated fibre system under the vestibular kinety stripe. 41: Preoral suture. The first mesh (arrow) of each row lacks cilia. 42: Surface view of cortex in mid-body left of the vestibular opening. Arrowheads mark minute rings, likely trichocyst attachment sites (cp. figure 14). P1, 2, 3, – peniculi; VK – vestibular kineties. Scale bars 10 µm.

densely spaced, approximately 20 µm long cilia; peniculus 3 distinctly separate from peniculi 1 and 2, sigmoidal, posteriorly 20% shorter than peniculi 1 and 2, composed of only 4–5 rows of densely spaced, 5–10 µm long cilia forming many closely spaced, short, oblique rows. Right vestibular wall flabby, sigmoidal both in outline and surface view, covered by an average of 13 kineties, hardly recognizable if cells are viewed ventrally (Figs 1, 26, 28; Table 1), but forming a conspicuous stripe in specimens viewed slightly laterally (Figs 2, 6, 7, 21, 24); in preparations, the vestibular cavity and its right wall flatten, exposing the vestibular kinety stripe to the observer even if cells are viewed ventrally (Figs 12, 31, 33, 35, 36). Vestibular kineties as long as vestibular opening, do not extend postorally as in *Frontonia*, anteriorly gradually slightly shortened from left to right, while posteriorly distinctly shortened from right to left, composed of very closely spaced dikinetids zigzagging in posterior two thirds of rows.

Paroral membrane at left (proximal) margin of vestibular kinety stripe and thus distinctly shortened posteriorly, composed of very closely spaced, zigzagging dikinetids associated with fine fibres impregnating with silver nitrate and extending to the cytostomial slit (Figs 1, 12, 18, 19, 38). Cytostomial slit in mid vestibulum, sigmoidal, about as long as peniculus 3, and thus not extending to posterior end of vestibulum (Figs 1, 6, 8, 12, 18, 19, 38).

There is a complicated fibre system associated with the oral structures. It is shown and briefly described in the explanation to figures 37–40. Further, the vestibular wall contains a fine-meshed silverline pattern (Fig. 18).

# Discussion

#### **Familial classification**

We classify Apofrontonia into the family Frontoniidae because it has: (1) three similarly-structured peniculi (no quadrulus like Paramecium, Stokesia and Neobursaridium); (2) basically frontoniid vestibular kineties (lacking in Lembadion, Urocentrum, Paramecium, Neobursaridium); and (3) a pyriform vestibular opening more similar to the triangular one of Frontonia than to the bursiform or oval vestibular opening of Paramecium, Neobursaridium, Stokesia, Lembadion, and Urocentrum. See Corliss (1979), Didier & Puytorac (1994), Foissner et al. (1994, 1999), and Kahl (1931) for figures of the genera mentioned. Possibly, Frontonia or the planktonic Marituja are the closest relatives of Apofrontonia. The former is indicated by body shape, the location of the oral apparatus, and the general somatic ciliary pattern with the distinct preoral and postoral suture; the latter by the vestibular kineties, which cover the vestibular wall, while they are at the right margin of the vestibular opening in most other peniculines, especially Frontonia.

#### Comparison with related genera

Apofrontonia lametschwandtneri and A. obtusa (see below) both have an extraordinarily large oral apparatus, separating them from most peniculines, except Lembadion and Neobursaridium, both quite distinct and only distantly related (no vestibular kineties etc.). However, the main generic feature of Apofrontonia is the pyriform or key-hole-shaped vestibular opening not found in any other genus of the order. The generic feature "vestibular cavity bowl-shaped, completely exposing three similarlystructured peniculi" has been introduced specifically for separating Apofrontonia from Frontonia and *Disematostoma*. In both of the latter genera, the posterior portion of the peniculi cannot be seen because it is covered by a triangular postoral field (posterior vertex of the oral opening) bearing several short (postoral) kineties abutting to the postoral suture. Such a postoral field is definitely lacking in *Apofrontonia*, and thus the distal portion of the peniculi is exposed to the observer. The next feature "right vestibular margin sigmoidal and covered by many (>6) vestibular kineties not extending beyond oral cavity" also separates Apofrontonia clearly from Frontonia and Disematostoma. In Frontonia and Disematostoma, there are fewer than six vestibular kineties, and these extend postorally to abut on the postoral suture. Disematostoma, further, has a very long postoral suture extending to mid-body of dorsal side, where it abuts to the excretory pore of the contractile vacuole (Tuffrau and Savoie 1961; Serrano et al. 1990).

#### **Comparison with related species**

Apofrontonia lametschwandtneri has a very distinct identity due to the huge oral apparatus and the scattered contractile vacuoles. This combination of features separates it from all described peniculine species, except the Frontonia obtusa discovered by Song and Wilbert (1989) in a pond in Germany. Frontonia obtusa has the same generic features as A. lametschwandtneri and is thus transferred to that genus: Apofrontonia obtusa (Song and Wilbert, 1989) nov. comb. Apofrontonia obtusa differs from A. lametschwandtneri by the following features: body size (80 vs. 180 µm), number of somatic (90 vs. 170) and vestibular kineties (9 vs. 13), number of kineties in the peniculi (about 1/3higher in A. lametschwandtneri), and number (4–5 vs. about 30) and location (laterally vs. scattered) of the contractile vacuoles.

#### **Biogeographical considerations**

Both Apofrontonia lametschwandtneri and A. obtusa are conspicuous ciliates. In spite of this, they were discovered late, indicating that they are rare. The Venezuelan species occurred neither in about 100 other samples from South and Central America nor in many saline soil samples collected in Africa, Australia, Asia, and Europe (Foissner, unpublished). So it is difficult and perhaps premature to speculate about biogeography. However, there is an unpublished work by Niessen (1984, diploma thesis at Bonn University), who found a species highly similar to A. obtusa in soil from the margin of a sodium lake in Egypt (Wilbert, pers. comm. and Song and Wilbert 1989), suggesting that this species occurs also in Africa. The Venezuelan Apofrontonia is distinctly different from the German and Egyptian species, suggesting that it might be endemic to South America.

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