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# Notes on ciliates (Protozoa, Ciliophora) from *Espeletia* trees and *Espeletia* soils of the Andean Páramo, with descriptions of *Sikorops espeletiae* nov. spec. and *Fragmocirrus espeletiae* nov. gen., nov. spec.

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**Abstract**

Ciliated protozoa from the giant rosettes of *Espeletia* trees (Compositae) and *Espeletia* soils were studied in four samples each from the Andean Páramo in Venezuela and Ecuador. Collections were analysed with the non-flooded Petri dish method, which reactivates the ciliates' resting cysts from air-dried samples. Species were identified by live observation and silver impregnation. Although most samples, especially those from soil, contained many testate amoebae, only 18 ciliate species could be found, indicating that the non-flooded Petri dish method was rather ineffective. Probably, ciliates from this region do not make "strong" (drought resistant) resting cysts because of the humidity of the habitats. Most of the ciliate species recorded are common in litter and soil world-wide. However, two of them are new: *Sikorops espeletiae* nov. spec. and *Fragmocirrus espeletiae* nov. gen., nov. spec. Both species are described in detail, including ontogenesis of *F. espeletiae*. Two other as yet insufficiently known species are redescribed: *Arcuospathidium muscorum* (Dragesco & Dragesco-Kernéis, 1979) and *Gonostomum affine* (Stein, 1859).

**Keywords:** *Fragmocirrus espeletiae* nov. gen., nov. spec., *Sikorops espeletiae* nov. spec., epiphytic ciliates, soil ciliates, testate amoebae, South America.

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## INTRODUCTION

Soil and epiphytic ciliates of the tropics have been poorly explored. Most of the sparse older literature, reviewed by Bamforth and Lousier (1995) and Foissner (1987), contains obvious misidentifications and is thus of limited value. Only recently, Blatterer and Foissner (1988), Foissner (1986, 1988, 1993a – c, 1995) and Hemberger (1985) provided some reliable data, indicating that tropical soils contain a highly diversified ciliate community. Foissner (1995), for instance, found 80 species in a single sample from a tropical forest in Costa Rica, including four new genera and seven new species.

During a stay at Merida, Venezuela, I collected some soil samples in the desert Páramo, one of the most extreme environments of the tropical high Andes, about 4200 m above sea-level. Furthermore, I obtained four similar samples from the Andean Páramo of Ecuador. Both regions are dominated by the giant rosettes of *Espeletia*, a Gondwanan Compositae. *Espeletia timotensis* Cuatr. and *Espeletia* sp. (possibly *grandiflora*; Ecuador), to which the present investigations refer, are monoaxial, unbranched rosette trees 2–3 m high with an average of 240 leaves per rosette (Fig. 1). In the Venezuelan Andes, the annual growth of the trunk of *E. timotensis* is about 15 mm, and the length of the life cycle has been estimated at 170 years. Leaves have a size of 50 × 3.5 cm and are spirally arranged. Leaf abscission does not occur; the leaves remain attached to the trunk and decompose very slowly (high C:N ratio) during the life cycle of each individual, thus forming a case of marcescent leaves down to its base. The trunk thus appears to be several times thicker than the real stem and acquires a columnar aspect. The marcescent leaf layer protects the vascular system of the plant from low night-time temperatures and balances the water regime; stripped specimens die within two months (Monasterio, 1986).

The leaf necromass forms a highly structured biotope colonised by many microarthropods (Diaz & Najt, 1990; Garay, 1981). Garay (1981), for instance, reported a density of 130,000 microarthropods in the standing dead mass of a single individual of *E. timotensis* with a trunk 110 cm high. Furthermore, the

leaf necromass is the most important nutrient sink in the region and contributes significantly to soil formation (Monasterio, 1986).

The present paper reports on the ciliates found on dead leaves of live and rotting *Espeletia*, in the (earthworm) soil around *Espeletia* trunks, and in the soil between *Espeletia* plants.

## MATERIALS AND METHODS

### Venezuela samples

A set of four samples was taken in the Páramo de Piedras Blancas (08° 52′ N, 70° 48′ W) at 4 200 m, Cordillera de Mérida, Venezuela, about 2 km east of the Pico del Aquila (Fig. 1). The following data are from Estrada et al. (1991). The vegetation of this area corresponds to the "Altiandino" desert Páramo with *Espeletia* giant rosettes leaving large areas of bare soil. The lower stratum is composed of different plant life forms such as mosses, lichens, dwarf cushions (e.g., *Mona*, *Azorella*, *Arenaria*, *Draba*, *Senecio*), and *Espeletia* juveniles. Climatic records for 24 continuous years show that the area has a mean annual temperature of 2.8°C and the difference between the coldest and warmest month is 2.7°C. The daily temperature fluctuations are approximately 10°C, and the mean annual precipitation (800 mm) falls between April and November. For the dry season, daily temperature fluctuations at 150 cm and 10 cm above soil, as well as on the soil surface are 13.5°C, 17.0°C and 50°C, respectively; likewise, the minimum temperatures are –2.5°C, –5.0°C and –10.0°C, respectively. During the wet season, daily ranges are 10°C at 150 cm, 11.1°C at 10 cm and 25.5°C at the soil surface; the minimum temperatures are 0°C, 0°C and 0.5°C, respectively.

The basestone is granitic. Soil type corresponds to a ranker, i.e., the soil has a simple A – C profile and moder type humus. Soil depth is usually less than 10 cm in areas between *Espeletia* plants and 10 – 20 cm around *Espeletia*. Solifluction is pronounced due to the steep slopes. In spite of the extreme climatic conditions, the soil is colonised by a rich and diverse


Fig. 1. *Espeletia timotensis* in the Páramo de Piedras Blancas, Venezuela. Numbered arrows mark sites were the author (bowed) and Prof. M. Paoletti collected samples.

community of microarthropods (Diaz & Najt, 1990), and even large earthworms must be frequent because many large casts have been seen, especially around the *Espeletia* plants.

Sample 1 (Fig. 1): Marcescent *Espeletia* leaves underneath the living rosette, about 5 – 15 years old. Leaves covered with greenish algal layer; between leaves some excrements of microarthropods. pH 5.6.

Sample 2: Decaying *Espeletia* leaves from dead, rotting trunks, very likely between 100 – 150 years old. Leaves, respectively, trunk partially covered with greenish algal layer and some small mosses; between leaves soil particles and excrements of microarthropods. pH 6.0.

Sample 3 (Fig. 1): Upper 0 – 10 cm soil layer under standing specimens of *Espeletia*. Soil dark brown, mainly consisting of earthworm casts and rotting *Espeletia* leaves; with many fine roots from neighbouring dwarf cushions. pH 6.0.

Sample 4 (Fig. 1): Upper 0 – 5 cm soil layer between *Espeletia* plants. Soil dark brown, very fine-grained, with many roots from dwarf cushions; without visible earthworm casts. pH 5.4.

**Ecuador samples**

Most of the following data were kindly provided by Maurizio Paoletti (Padua University, Italy), who collected the Ecuadorian samples about one week later than I did in Venezuela. As in Venezuela, a set of four samples was taken in the Reserva Ecologia "El Angel " (0° 38′ S, 77° 48′ W) about 4 000 m above sea-level. Mean annual temperature (about 6°C) and precipitation (about 1500 mm) are significantly higher than in the desert Páramo of the Cordillera de Mérida. Accordingly, vegetation is richer and denser and the ground is covered with Ericaceae, Equisetaceae, mosses, and ferns. Up to 5 m tall *Puya* trees are scattered between the *Espeletia* trees. The basestone is granitic. Soil is a peaty, almost black material mainly composed of insufficiently decayed leaf litter, mosses, and ferns. Only few and small earthworm casts were found. The *Espeletia* specimens from which the samples were taken were possibly *E. grandiflora* H. and B., a large species very similar to *E. timotensis* investigated in Venezuela.

Sample 5: Green *Espeletia* leaves from the living rosette. pH 6.0.

Sample 6: Decaying *Espeletia* leaves from trunk. Leaves darkbrown and mixed with some soil particles. pH 4.5.

Sample 7: Upper 0 – 10 cm soil layer under a standing specimen of *Espeletia*. Soil very fine-grained and compact, light black; with fine roots but without litter. pH 5.4.

Sample 8: Upper 0 – 5 cm peaty soil layer between *Espeletia* plants. Soil almost black, dusty when dry, with many fine roots. pH 5.4.

**Sampling, sample processing, and species identification**

The Venezuelan samples were taken during the dry season on 10 February 1996. Each sample was a composite from four *E. timotensis* specimens in an area of about 200 $m^2$; the soil sample from between *Espeletia* was a composite from 10 small cores in the same area (Fig. 1). The Ecuadorian samples were collected at the end of February 1996 during a very wet weather period. They were taken from a single *Espeletia* (possibly *grandiflora*) tree. The soil sample from between *Espeletia* was a composite from five small cores in an area of about 100 $m^2$. All samples were air-dried in the Salzburg laboratory for four weeks. In April 1996, the samples were processed with the non-flooded Petri dish method as described by Foissner (1987), which reactivates the ciliates' resting cysts from air-dried samples. Briefly, this simple method involves placing the dry soil and/or litter in an ordinary Petri dish (15 cm diameter) and saturating but not flooding it with distilled water. Such cultures were grown at room temperature (about 20°C) and analysed for ciliates on days 2, 7, 14, 21 and 28 by inspecting about 2 ml each of the run-off (= soil solution).

Identification, nomenclature, and terminology of species are according to Foissner (1987, 1991, 1998). Most of the species found were described or redescribed by my students and myself. Thus, determinations were done mainly on live specimens using a high-power (X100; N.A. 1.32) oil immersion objective and differential interference contrast. However, all "difficult", new, or supposedly new species were checked with the silver-staining techniques described in Foissner (1991).

**Cytological methods**

The species described were studied *in vivo* using a high-power oil immersion objective (X100; N.A. 1.32) and differential interference contrast. The ciliary pattern (infraciliature) was revealed by protargol impregnation and scanning electron microscopy as

described in Foissner (1991). The descriptions are based on material obtained with the non-flooded Petri dish method mentioned above, i.e. no clonal cultures were set up.

Counts and measurements on silvered specimens were performed at a magnification of X1,000. *In vivo* measurements were made at magnifications of X40 – 1,000. Illustrations of live specimens are based on freehand sketches and micrographs; those of impregnated cells were made with a camera lucida.

## RESULTS

### Remarks on the organism community of the individual samples (Table 1)

Sample 1: A great number of bacteria, fungal hyphae, and heterotrophic flagellates developed. *Colpoda steinii* became very abundant six days after rewetting. The darkbrown water (soil solution) was changed two weeks after rewetting, but no further ciliates developed.

Sample 2: This was the richest sample containing 17 ciliate species two of which were new and will be described below. Furthermore, a huge abundance of heterotrophic flagellates (mainly *Polytomella* sp.) and some naked and testate amoebae developed.

Sample 3: Only one ciliate species developed (*Pseudoplatyophrya nana*, an obligate fungal feeder), although there was a huge abundance of bacteria, fungal hyphae, and minute heterotrophic flagellates. Furthermore, there was a rich variety and number of testate amoebae, such as *Centropyxis aerophila*, *C. sphagnicola*, *C. plagiostoma*, *Phryganella acropodia*, *Plagiopyxis declivis*, *Trinema penardi*, *T. complanatum*, and *Tracheleuglypha* sp.

Sample 4: No ciliates occurred, although there was a rich community of bacteria and heterotrophic flagellates, as well as some small naked amoebae. Furthermore, there were many tests of *Centropyxis aerophila*, *C. sphagnicola*, *Phryganella acropodia*, *Plagiopyxis minuta*, *Schoenbornia humicola*, *Assulina muscorum*, and *Arcella* sp. Soil solution (water)

TABLE 1. Ciliate species found (+) and their distribution in four samples each from Venezuela (1 – 4) and Ecuador (5 – 8).

| Species[1] | Samples | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Arcuospathidium muscorum* (Dragesco & Dragesco-Kernéis, 1979) | – | + | – | – | – | – | – | – |
| *Colpoda cucullus* (Müller, 1773) | + | + | – | – | – | – | – | – |
| *Colpoda elliotti* Bradbury & Outka, 1967 | – | + | – | – | – | – | – | – |
| *Colpoda inflata* (Stokes, 1884) | + | + | – | – | + | – | – | – |
| *Colpoda steinii* Maupas, 1883 | + | + | – | – | – | – | – | – |
| *Cyrtohymena quadrinucleata* (Dragesco & Njiné, 1971)[2] | – | + | – | – | – | – | – | – |
| *Cyrtolophosis elongata* (Schewiakoff, 1892) | – | + | – | – | – | – | – | – |
| *Enchelydium terrenum* Foissner, 1984 | – | + | – | – | – | – | – | – |
| *Fragmocirrus espeletiae* nov. gen., nov. spec. | – | + | – | – | – | – | – | – |
| *Gonostomum affine* (Stein, 1859) | – | + | – | – | – | – | – | – |
| *Leptopharynx costatus* Mermod, 1914 | – | + | – | – | – | – | – | – |
| *Opercularia* ? sp. | – | + | – | – | – | – | – | – |
| *Platyophrya vorax* Kahl, 1926 | + | – | – | – | – | – | – | – |
| *Pseudocyrtolophosis alpestris* Foissner, 1980 | – | + | – | – | – | – | – | – |
| *Pseudoholophyra terricola* Berger, Foissner & Adam, 1984 | + | + | – | – | – | – | – | – |
| *Pseudoplatyophrya nana* (Kahl, 1926) | + | + | + | – | – | – | – | – |
| *Sikorops espeletiae* nov. spec. | – | + | – | – | – | – | – | – |
| *Urosomoida agiliformis* Foissner, 1982 | – | + | – | – | – | – | – | – |
| Number of species | 6 | 17 | 1 | 0 | 1 | 0 | 0 | 0 |

[1] See Foissner (1998) for combining authors.

[2] Cirral pattern and live aspect as described by Dragesco and Njiné (1971), Foissner (1984), and Shin and Kim (1996). Number of macronuclear nodules, however, rather variable: of 47 specimens investigated, 42 had four nodules (as is typical), 2 had five nodules, 2 had six nodules, and 1 specimen had seven nodules. Shin & Kim (1996) observed some specimens with only three nodules.

was changed two weeks after rewetting of the sample, but no ciliates developed.

Sample 5: *Colpoda inflata* and the heterotrophic flagellate *Polytomella* sp. became very abundant two weeks after rewetting the sample.

Sample 6: No ciliates developed, although there were many bacteria, diatoms, heterotrophic flagellates (*Polytomella* sp.), and some fungal hyphae. Furthermore, there was an abundance of testate amoebae, such as *Centropyxis sphagnicola*, *Phryganella acropodia*, *Assulina muscorum*, *Euglypha laevis*, *Arcella* sp., and *Nebela* sp. The lightbrown water (soil solution) was changed two weeks after rewetting, but no ciliates developed. The sample did not become putrid and had a musty smell.

Sample 7: No ciliates developed, although there were many bacteria, diatoms, flagellates (*Polytomella* sp.), and some small naked and testate amoebae. The soil solution was almost clear and colourless, and the sample did not become putrid.

Sample 8: No ciliates occurred, although bacterial, fungal hyphae, and heterotrophic flagellates (only one species, *Polytomella* sp.) were abundant; some small naked and testate amoebae (*Plagiopyxis declivis*, *Nebela* sp.) were also found. The soil solution was almost colourless, in spite of the dark colour of the soil, and was changed two weeks after rewetting the sample; but no ciliates developed. The sample did not become putrid and had a musty smell.

## Description of new and insufficiently known species

Morphometric data shown in Tables 2 – 4 are repeated in this section only as needed for clarity.

***Sikorops espeletiae*** nov. spec.
(Figs. 2 – 23, Tab. 2)

### Diagnosis

Size *in vivo* about 110 × 12 µm. Slenderly fusiform with anterior end obliquely truncated. Macronucleus filiform, tortuous. Extrusomes obclavate, about 0.8 × 0.6 µm. On average 11 somatic kineties and 3 dikinetids in brush row 1, 20 in row 2, and 13 in row 3.

### Type location

Venezuela, Cordillera de Mérida, Páramo de Piedras Blancas about 2 km east of the Pico del Aquila (08° 52′ N, 70° 48′ W), on *Espeletia* leaves from dead, rotting *Espeletia* trunks.

### Etymology

Genitive of genus *Espeletia*, the plant on which the species was found.

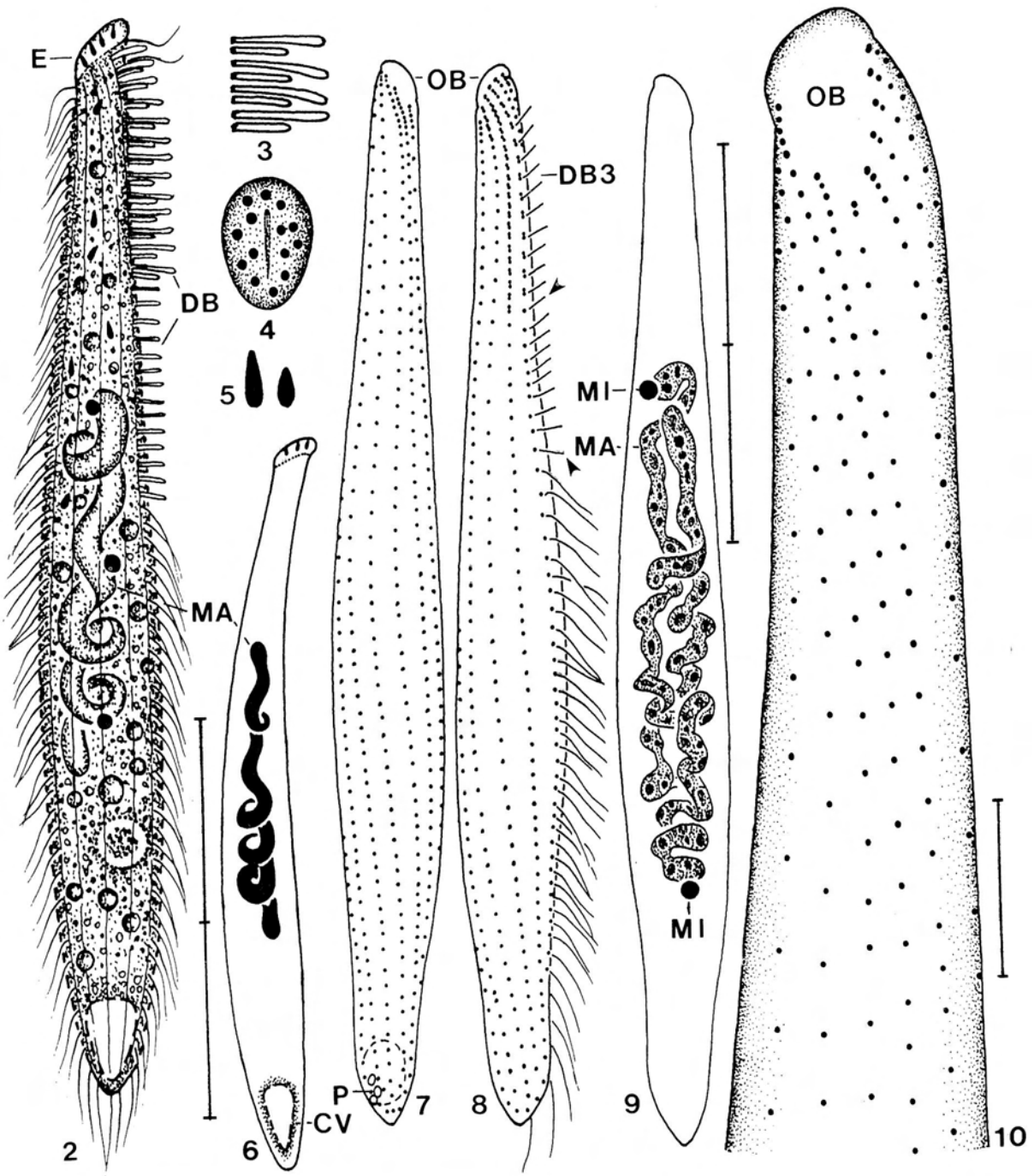
### Type material

Two slides (1 holotype and 1 paratype) with protargol-impregnated (protocol A in Foissner 1991) specimens have been deposited in the Oberösterreichische Landesmuseum, Linz (LI), Austria. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

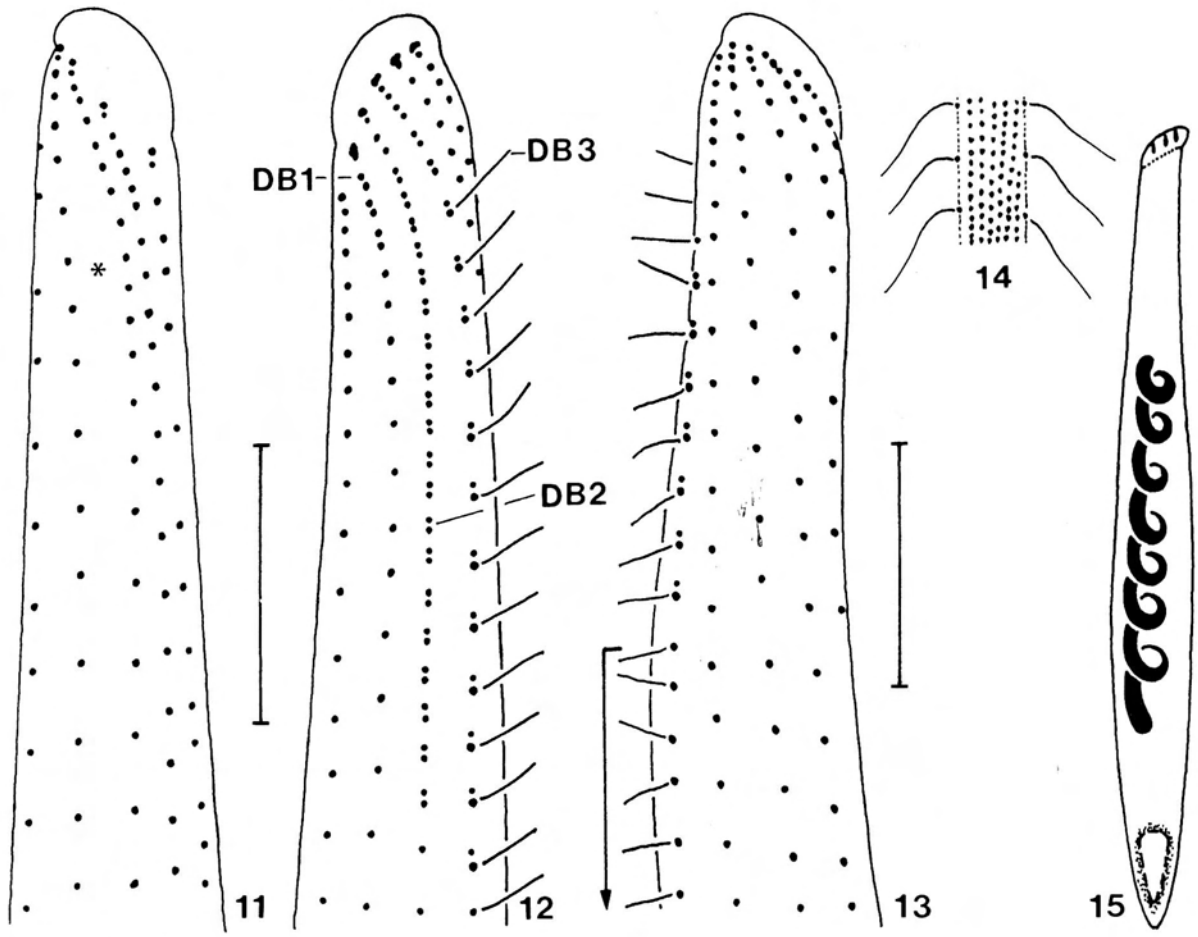
### Description

Size *in vivo* 70–140 × 8–16 µm, usually about 110 × 12 µm, length: width ratio also highly variable, 5:1 – 11:1, on average 8.5:1 (Fig. 2, Table 2). Cylindroidal to roughly fusiform, slightly narrowed towards both ends, posterior end tapered in about half of specimens (Figs. 2, 15). Macronucleus in central portion of cell, filiform, helically coiled in about one third of specimens, in others coiled only in posterior half or tortuous (Figs. 6, 9, 15, 16, 21). Usually three globular micronuclei attached to macronucleus in variable positions. Contractile vacuole in posterior end with about eight dorsolateral excretory pores (Fig. 7). Extrusomes in oral bulge and cytoplasm, obclavate, minute (0.7 – 1 × 0.5 – 0.7 µm) and thus difficult to recognise, do not stain with protargol (Figs. 1, 4–6). Cortex flexible, contains about six rows of minute (0.3 µm), colourless granules between each two ciliary rows (Fig. 14). Cells colourless and hyaline, never dark by food and/or other inclusions, contain some fat globules 1–3 µm across. Swims moderately fast by rotation about main body axis.

Cilia about 8 µm long, narrowly spaced in oral region of kineties. Ciliary rows extend meridionally and equidistantly, except in ventral anterior area, where three kineties are close together and separated from the neighbouring ciliary rows by a more or less distinct gap (Figs. 7, 11, 17). Anterior end of kineties slightly curved, bears single (possibly two in some dorsolateral kineties) dikinetid, whose anterior (ciliated?) basal body is slightly larger and more intensely impregnated than the (unciliated) posterior one; dikinetid lacking in ventralmost kinety in about half of specimens (Figs. 10–13, 17, 19, 22, 23). Dorsal brush in anterior region of three dorsolateral kineties, consists of narrowly spaced dikinetids having about 4 µm long, distally slightly inflated cilia associated with the anterior basal bodies and about 3 µm



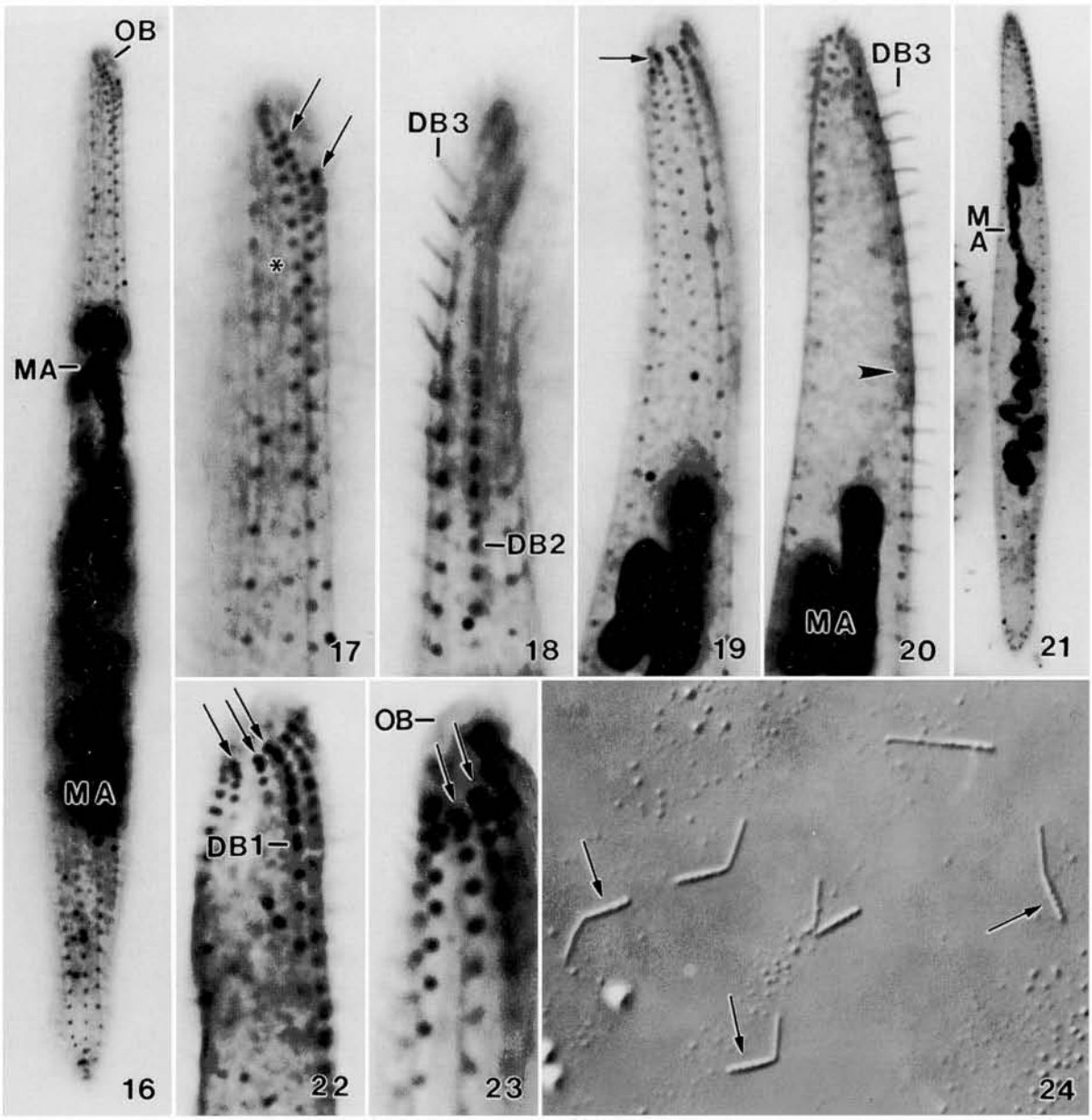

Figs. 2–10. *Sikorops espeletiae* nov. spec. from life (2–6) and after protargol impregnation (7–10). **2:** Left lateral view of a representative specimen. **3:** Part of dorsal brush with up to 4 µm long, distally slightly inflated cilia. **4:** Frontal view of oral bulge. The knobby extrusomes appear as black dots. **5:** Shape and size (0.7–1 × 0.5–0.7 µm) variability of extrusomes from oral bulge. **6:** Shape variant with macronucleus helically coiled in posterior portion. **7 – 9:** Infraciliature of right and left side and nuclear apparatus of a representative specimen. Note the highly specialised infraciliature of dorsal brush row 3 (arrowheads mark monokinetidal tail with shortened cilia; underneath the tail, the row has cilia of usual length, that is, extends posteriorly as an ordinary somatic kinety). **10:** Ventral anterior end at high magnification. Note the inconspicuous dikinetids (anterior basal body slightly enlarged and more darkly impregnated than posterior one) at the anterior end of the ciliary rows (cp. Figs. 11–13, 17, 19, 22, 23). CV – contractile vacuole, DB – dorsal brush, DB3 – dorsal brush row 3, E – extrusomes in oral bulge, MA – macronucleus, MI – micronuclei, OB – oral bulge, P – pores of contractile vacuole. Scale bar division 20 µm (Figs. 2, 7–9) and 5 µm (Fig. 10).




Figs. 11–15. *Sikorops espeletiae* nov. spec. from life (14, 15) and after protargol impregnation (11–13). **11, 12:** Infraciliature of right and left anterior portion of specimen shown in Figures 7 and 8. Note details of dorsal brush and indistinct circumoral dikinetid at anterior end of ciliary rows. Usually, the anterior basal body of the dikinetids is slightly larger and more darkly impregnated than the posterior one. Asterisk in Figure 11 marks slightly increased distance between ventral and lateral ciliary rows. **13:** Dorsolateral view of anterior portion of another specimen. A heavily impregnated cilium emerges from the posterior basal body of the dikinetids composing brush row 3 and from its monokinetidal tail (arrowed bracket). **14:** Surface view showing cortical granulation. **15:** Shape variant with helically coiled macronucleus. DB1-3 – dorsal brush rows. Scale bars 10 µm.

long, rod-shaped cilia with the posterior ones; usually some monokinetids or very narrowly spaced dikinetids at anterior end of each brush kinety (Figs. 1, 3, 8, 12, 18). Brush kinety 1 inconspicuous because composed of only three dikinetids on average (Figs. 12, 22, Table 2). Brush kinety 2 longest because composed of 20 dikinetids on average (Figs. 8, 12, 18). Brush kinety 3 shows several specialisations: (i) dikinetids more widely spaced than in rows 1 and 2, rows 2 and 3 thus of almost same length, although row 2 has seven dikinetids more than row 3 on average (Table 2), (ii) a monokinetidal tail with shortened cilia, (iii) anterior basal body of dikinetids smaller and more faintly impregnated than posterior one; (iv) posterior cilium of dikinetids and cilia of monokinetidal tail unusually heavily impregnated (Figs. 8, 12, 13, 18, 20).

Oral bulge inconspicuous and indistinctly set off from neck, obovate in frontal view, extrusomes contained appear as bright dots (Figs. 1, 4, 6–10, 16, 17, 23). No distinct circumoral kinety because only a single dikinetid at anterior end of somatic kineties, as described above. No nematodesmata recognisable, not even in over-impregnated specimens (Figs. 7, 8, 10–13, 17, 19, 22, 23).




Figs. 16–23. *Sikorops espeletiae* nov. spec., infraciliature and nuclear apparatus after protargol impregnation. **16:** Right side view of a representative specimen, length 110 µm (cp. Figs. 7–9, 17, 18). **17, 18:** Two focal planes of anterior portion of specimen shown in Figure 16. Note the heavily impregnated cilium emerging from the posterior basal body of the dikinetids composing brush row 3 (cp. Figs. 12, 13). Arrows mark circumoral dikinetid at anterior end of ciliary rows. Asterisk denotes slightly increased distance between ventral and lateral ciliary rows. **19, 20:** Two focal planes (ventrolateral and dorsolateral) of the anterior portion of an other specimen. The anterior end of the kineties is thickened due to a circumoral dikinetid (arrow). This pattern is quite typical for *Sikorops*. Note the heavily impregnated cilium emerging from the posterior basal body of the dikinetids composing brush row 3, which continues with a short monokinetidal tail (arrowhead) also having strongly impregnated, shortened cilia. **21:** Fusiform specimen with tortuous macronucleus. **22:** Left side view showing circumoral dikinetid (arrows) at anterior end of ciliary rows and brush kinety 1, which consists of only three dikinetids. **23:** Ventrolateral view showing circumoral dikinetid (arrows) at anterior end of ciliary rows. DB 1 – 3 – dorsal brush rows, MA – macronucleus, OB – oral bulge.

Fig. 24. *Arcuospathidium muscorum*, exploded toxicysts from life (differential interference contrast). The organelles, which are about 8 µm long and often knee-shaped, consist of a thin, opaque anterior and a thicker, granular posterior half (arrows).

**Occurrence**

As yet found only at type location.

**Generic classification and comparison with related species**

*Sikorops* Foissner, 1999 belongs to the Acropisthiidae and is characterised "by three dorsal brush rows and fusiform extrusomes in the oral bulge ". The Venezuelan population matches *Sikorops* not only in these characters (extrusome shape is slightly different but knobby as in the type species) but also in the inconspicuous oral kinetids, which do not form a distinct circumoral kinety (Figs. 7, 8, 10–13, 17, 19, 22, 23). There remains some uncertainty about family classification because no nematodesmata could be found, although the preparations were excellent (Figs. 16–23). However, they also did not impregnate in *Arcuospathidium muscorum* contained in the same slides, indicating a specific preparation failure.

*Sikorops espeletiae* differs from *S. woronowiczae*, type of the genus, by the macronucleus (filiform and tortuous vs. two ellipsoidal nodules with a single micronucleus in between), the shape of the extrusomes (obclavate vs. fusiform), and the higher number of dikinetids in brush row 2 (20 vs. 10).

***Arcuospathidium muscorum*** (Dragesco & Dragesco-Kernéis, 1979) Foissner, 1984
(Figs. 24–41, Table 2)

**Material**

A voucher slide with 6 protargol-impregnated (protocol A in Foissner 1991) specimens, each marked by a black ink circle on the cover glass, has been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria.

**Description**

Size *in vivo* 70–110 × 20–40 µm, usually about 90 × 30 µm, length: width ratio rather stable, viz. 3–4.5:1,

TABLE 2. Morphometric data on *Sikorops espeletiae* (S, upper line) and *Arcuospathidium muscorum* (AM, lower line).

| Character[1] | $\bar{x}$ | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 102.6 | 105 | 16.4 | 3.6 | 16.0 | 66 | 148 | 21 |
| | 86.5 | 83 | 11.1 | 3.0 | 12.8 | 71 | 105 | 14 |
| Body, width underneath oral bulge | 4.8 | 5 | 0.5 | 0.1 | 11.3 | 4 | 6 | 21 |
| | 15.1 | 15 | 3.9 | 1.0 | 25.8 | 9 | 23 | 14 |
| Body, maximum width | 11.7 | 12 | 1.4 | 0.3 | 12.4 | 9 | 15 | 21 |
| | 25.4 | 26 | 4.0 | 1.1 | 15.7 | 19 | 35 | 14 |
| Oral bulge, length (AM) | 30.9 | 32 | 4.1 | 1.1 | 13.3 | 23 | 38 | 14 |
| Macronuclear figure, length (S) | 45.6 | 45 | 10.2 | 2.2 | 22.4 | 30 | 75 | 21 |
| Macronucleus, width | 2.8 | 3 | 0.6 | 0.1 | 21.4 | 2 | 4 | 21 |
| | 4.4 | 5 | 0.9 | 0.3 | 21.2 | 3 | 6 | 14 |
| Macronuclei, number | 1.0 | 1 | 0.0 | 0.0 | 0.0 | 1 | 1 | 21 |
| | 1.0 | 1 | 0.0 | 0.0 | 0.0 | 1 | 1 | 14 |
| Micronuclei, diameter (S) | 1.9 | 2 | – | – | – | 1.5 | 2.5 | 21 |
| Micronuclei, number (S) | 3.1 | 3 | 1.0 | 0.2 | 30.7 | 1 | 5 | 21 |
| Somatic kineties, number in mid-body | 11.1 | 11 | 0.9 | 0.2 | 7.7 | 10 | 13 | 21 |
| | 13.3 | 14 | 1.5 | 0.4 | 10.8 | 11 | 15 | 14 |
| Basal bodies in a right lateral kinety, number | 60.1 | 60 | 11.4 | 2.5 | 19.0 | 35 | 88 | 21 |
| | 40.2 | 40 | 9.4 | 2.6 | 23.5 | 27 | 60 | 14 |
| Dorsal brush rows, number | 3.0 | 3 | 0.0 | 0.0 | 0.0 | 3 | 3 | 21 |
| | 3.1 | 3 | – | – | – | 3 | 4 | 14 |
| Circumoral kinety to end of brush row 1, distance | 3.8 | 3 | 1.3 | 0.3 | 33.2 | 3 | 8 | 21 |
| | 12.1 | 13 | 2.3 | 0.6 | 19.1 | 8 | 15 | 14 |
| Circumoral kinety to end of brush row 2, distance | 20.8 | 21 | 3.2 | 0.7 | 15.4 | 16 | 27 | 21 |
| | 11.4 | 12 | 1.7 | 0.5 | 15.2 | 8 | 14 | 14 |
| Circumoral kinety to end of dikinetidal portion of brush row 3, distance | 19.3 | 18 | 3.6 | 0.8 | 18.5 | 12 | 25 | 21 |
| | 7.7 | 8 | 1.8 | 0.5 | 23.0 | 5 | 11 | 14 |
| Dikinetids in brush kinety 1, number (S) | 3.2 | 3 | 1.1 | 0.3 | 35.2 | 1 | 5 | 21 |
| Dikinetids in brush kinety 2, number (S) | 19.8 | 20 | 2.3 | 0.5 | 11.7 | 15 | 26 | 21 |
| Dikinetids in brush kinety 3, number (S) | 13.4 | 13 | 2.0 | 0.4 | 15.0 | 10 | 18 | 21 |

[1]Data based on protargol-impregnated and mounted specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard deviation of mean, $\bar{x}$ – arithmetic mean.

usually 3.5:1 (Table 2). Spatular with anterior end (oral bulge) obliquely truncated and posterior broadly rounded (Figs. 25, 34); slightly flattened laterally, in oral area up to 3:1 (Fig. 35). Macronucleus in central portion of cell, filiform and tortuous (Figs. 25, 28, 38, 41); single micronucleus about 3 µm across in variable position near macronucleus. Contractile vacuole in posterior end, about 10 excretory pores in and near centre of pole (Figs. 27, 28, 33, 37, 38). Extrusomes (toxicysts) in single row each in right and left half of oral bulge and scattered throughout cytoplasm, rod-shaped to very slightly thickened proximally, about 4 × 0.4 µm in size (Figs. 25, 30, 36; 5–6 µm long and slightly curved in an other Venezuelan population, Fig. 31); exploded toxicysts about 8 µm long and frequently curved knee-like, club-shaped, anterior half thinner and brighter than posterior, which contains small globules, possibly toxin droplets (Figs. 24, 32). Cortex flexible, contains about five rows of minute (0.3 µm), colourless granules between each two ciliary rows (Fig. 29). Cells colourless but dark at low magnification (X100) when crammed with food inclusions and fat globules 1–3 µm across in posterior half. Glides moderately fast on slide surface and soil particles.

Cilia 8 µm long, rather irregularly spaced. Somatic kineties extend meridionally and equidistantly, distinctly separated from circumoral kinety, anterior ends curved dorsally on right side of cell and slightly ventrally on left (Figs. 27, 28, 37, 38). Dorsal brush in anterior region of three dorsolateral kineties, composed of narrowly spaced dikinetids; kinety 3 shorter than kineties 1 and 2 but with monokinetidal tail, composed of 2 µm long bristles, extending to midbody; brush cilia decreasing in length at both ends of brush, anterior cilium up to 4 µm long in rows 1 and 2 and up to 5 µm in row 3 (Figs. 25, 26, 28, 38, 39, 41).

Oral bulge obliquely truncated and slightly convex, wedge-shaped in frontal view, conspicuous because long and filled with extrusomes (Figs. 25, 34–36). Circumoral kinety at base of oral bulge, continuous, wedge-shaped like oral bulge, composed of narrowly spaced dikinetids (Figs. 27, 28, 33, 37–41); nematodesmata not impregnated.

**Occurrence**

This species, which was found in sample 2, occurs in terrestrial habitats (mosses, litter, mineral soils) world-wide (Foissner, 1998). It is, however, infrequent. Detailed ecological data are not available.

**Comparison with previous descriptions**

The type population, which was discovered by Dragesco & Dragesco-Kernéis (1979) in mosses from France, has a size of 37–86 × 10–54 µm ($\bar{x}$ 57 × 22 µm, n ?; protargol-impregnated specimens), a tortuous macronucleus, fine toxicysts 2 µm long (very likely measured from protargol-impregnated cells, where toxicysts frequently incompletely stain), and 16–18 (× ?, n ?) ciliary rows. An Austrian population, which was found by Berger et al. (1983) in a bottomland soil, has a size of 78–105 × 29–50 µm (× 93 × 40 µm, n 25; protargol-impregnated cells from pure culture), a tortuous macronucleus, fine toxicysts 5 – 6 µm long *in vivo* (also in populations from Greece and the Caucasus), and 16–27 (× 21.1, n 25) ciliary rows. The Venezuelan population has a size of 71–105 × 19–35 µm (86 × 25 µm, n 14; protargol-impregnated specimens from raw culture), a tortuous macronucleus, fine toxicysts 4 µm long *in vivo*, and 11–15 ($\bar{x}$ 13.3, n 14) ciliary rows. It is thus obviously rather similar to the French and Austrian populations, except for the number of ciliary rows, which is rather low, despite the considerable body size, which approaches that of the Austrian specimens. Accordingly, the Venezuelan population might be a stable modification representing a new subspecies. However, spathidiids are notorious for their high variability, and thus I prefer to consider the Venezuelan population as a geographical and/or habitat modification of *A. muscorum*.

***Fragmocirrus*** nov. gen.

**Diagnosis**

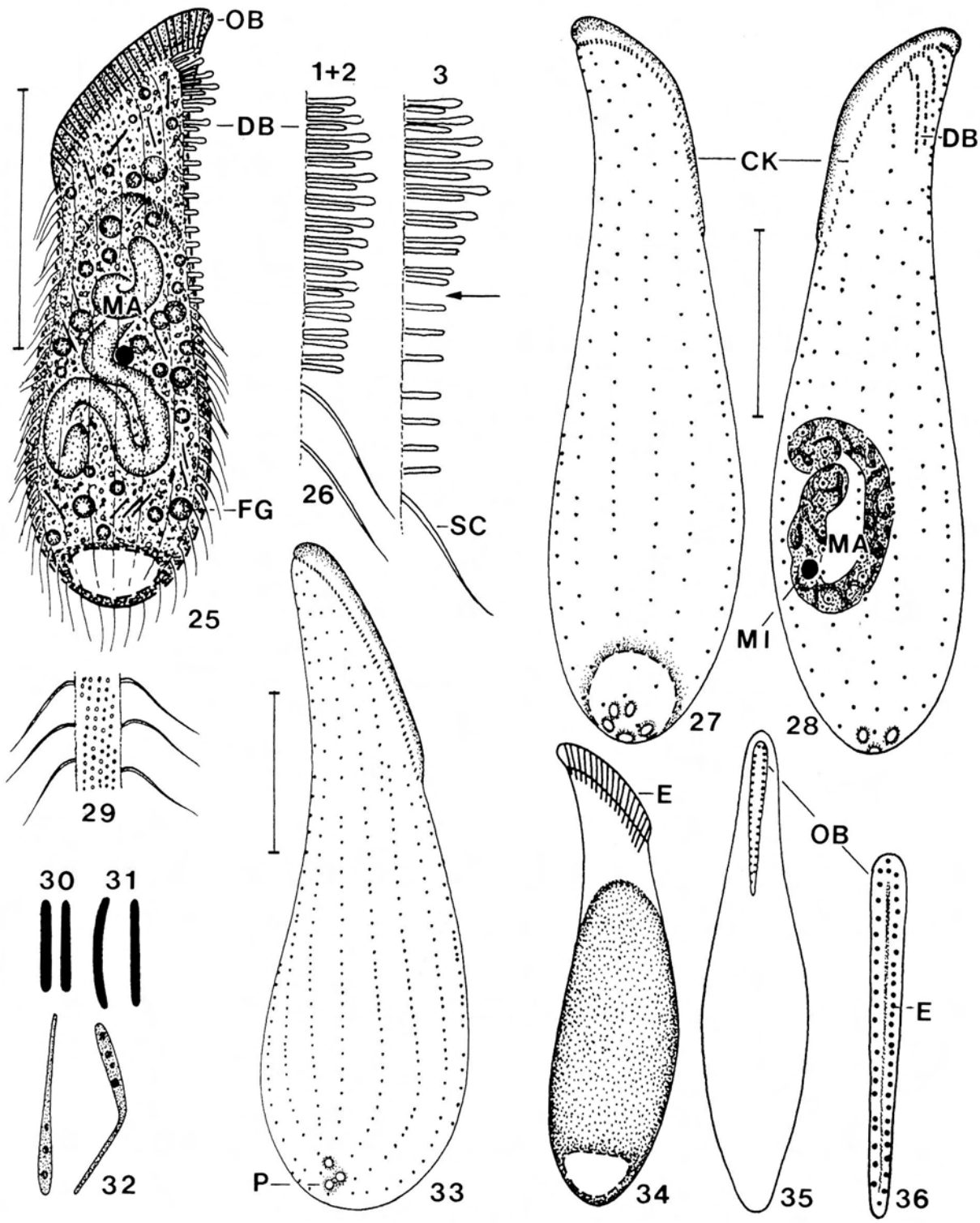
Parakahliellidae Eigner, 1997 with transverse and caudal cirri. Ventral cirral rows 4 and 5 each develop a V-shaped anlage producing proter's and opisthe's cirral rows 4 and 5. Two or more rows each of right and left marginal cirri, inner right and outer left row(s) more or less distinctly reduced. Dorsal kineties generated by within anlagen and dorsomarginally.

**Type species**

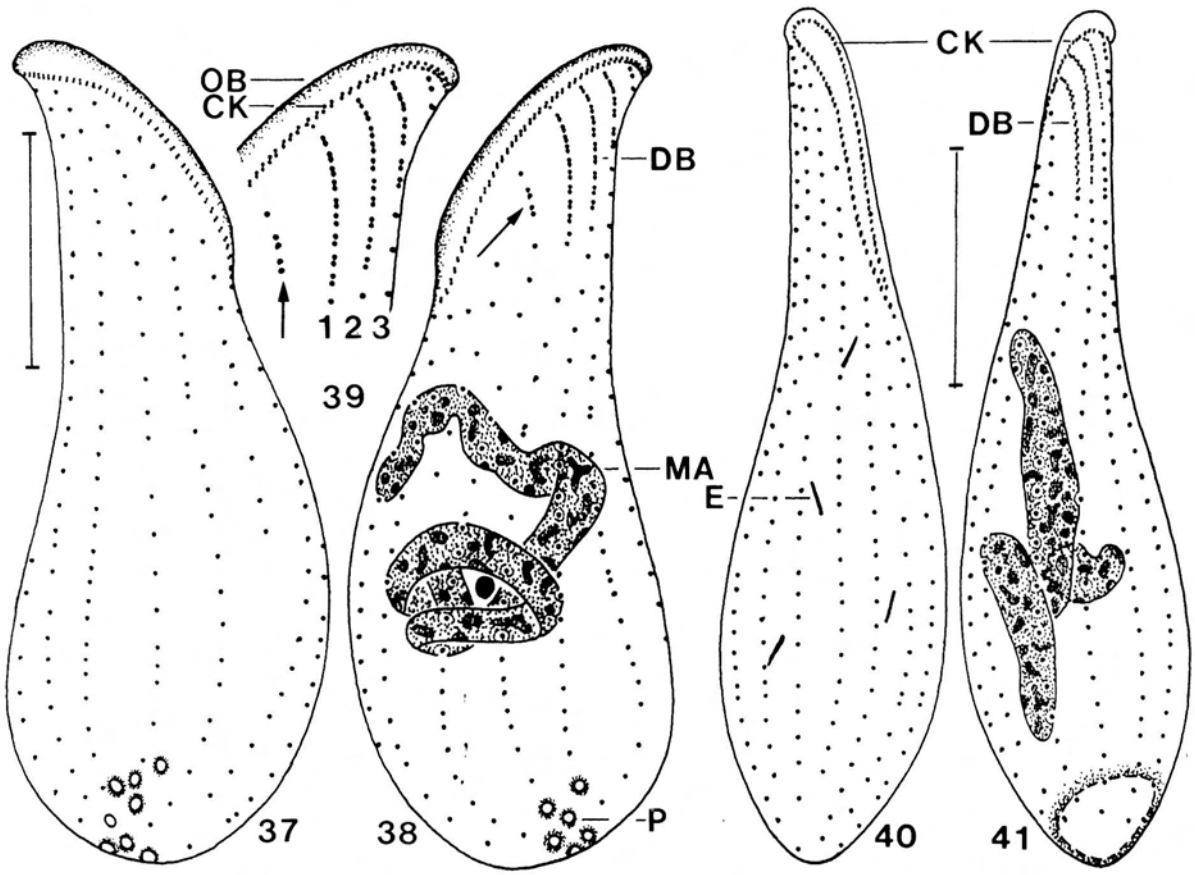
*Fragmocirrus espeletiae* nov. spec.

**Etymology**

Composite of the Latin nouns "fragmentum " (fragment) and "cirrus " (curl ~ compound cilia typical for hypotrichs), meaning a "hypotrichous ciliate with




Figs. 25–36. *Arcuospathidium muscorum* from life (Figs. 25, 26, 29–32, 34–36) and after protargol impregnation (27, 28, 33). **25:** Left side view of a representative specimen. **26:** Fine structure of dorsal brush. Arrow marks monokinetidal tail of row 3. **27, 28, 33:** Infraciliature of right and left side of slender to moderately broad specimens. **29:** Surface view showing cortical granulation. **30, 31:** Extrusomes of population from sample 2 are rod-shaped and 4 µm long, those of an other Venezuelan population are slightly curved and 5–6 µm long. **32:** Exploded toxicysts (cp. Figure 24) are about 8 µm long. **34, 35:** Right lateral and ventral view of same specimen. **36:** Frontal view of oral bulge. CK – circumoral kinety, CV – contractile vacuole, DB – dorsal brush, E – extrusomes (toxicysts), FG – fat globule, MA – macronucleus, MI – micronucleus, OB – oral bulge, P – pores of contractile vacuole, SC – ordinary somatic cilium, 8 µm long, 1, 2, 3 – dorsal brush rows. Scale bars 20 µm.




Figs. 37–41. *Arcuospathidium muscorum*, somatic and oral infraciliature after protargol impregnation. **37 – 39:** Right and left side view of a representative specimen. Figure 39 shows brush area at higher magnification. Arrows mark minute, additional brush row composed of two dikinetids. **40, 41:** Ventrolateral and dorsolateral view of same specimen. CK – circumoral kinety, DB – dorsal brush, E – extrusome, MA – macronucleus, OB – oral bulge, P – pores of contractile vacuole, 1,2,3 – dorsal brush rows. Scale bars 20 μm.

fragmented or incomplete ventral cirral rows ". Masculine gender.

**Comparison with related genera**

There are three genera that are obviously related to *Fragmocirrus*: *Paraurostyla* Borror, 1972; *Parakahliella* Berger et al., 1985; and *Parentocirrus* Voß, 1997. The characters separating these genera from each other and from *Fragmocirrus* are rather sophisticated, indicating that subgenus rank would probably be more appropriate. On the other hand, there are quite a lot of such species (see species comparison and several as yet undescribed species which I found in various soils), suggesting fast radiation and generic separation.

*Paraurostyla* differs from *Fragmocirrus* mainly by the genesis of the dorsal ciliary rows, that is, kinety 4 is generated from kinety 3 by posterior fragmentation, as in typical oxytrichids (Berger & Foissner, 1997; Wirnsberger et al., 1985). No fragmentation occurs in *Fragmocirrus* (Figs. 65, 67, 68, 83). Furthermore, *Paraurostyla* has only one right and left marginal cirral row. A specific character relating *Paraurostyla* and *Fragmocirrus* is the migration pattern of the rightmost, V-shaped ventral anlage (Wirnsberger et al., 1985): the streaks migrate parallel to each other anteriorly and posteriorly, seemingly forming a single ventral cirral row with a more or less distinct middle break (Figs. 63, 64, 66, 80, 82).

*Parakahliella* differs from *Fragmocirrus* mainly by the lack of transverse cirri (Berger & Foissner, 1989b; Berger et al., 1985). The remaining ciliary pattern and its ontogenesis are very similar in both genera. However, *Parakahliella* conserves some dor-

sal kinetids which form a new kinety each in the proter and opisthe (Berger & Foissner, 1989b).

*Parentocirrus* differs from *Fragmocirrus* mainly in the genesis of the dorsal ciliary pattern, which occurs as in *Paraurostyla* described above. Furthermore, the rightmost, V-shaped ventral anlagen of the proter and opisthe do not migrate and develop in the same row, while *Fragmocirrus* generates them in rows 4 and 5 (Figs. 56, 57, 59, 74–76). However, if rows 4 and 5 are considered as a single row, as explained in *Paraurostyla*, anlagen generation is very similar in *Parentocirrus* and *Fragmocirrus*. Likewise, the lack of migration is understandable because the ventral rows of *P. hortualis* are much longer than those of *F. espeletiae*.

***Fragmocirrus espeletiae*** nov. spec.
(Figs. 42–53, Table 3)

**Diagnosis**

Size *in vivo* about 160 × 60 µm; ellipsoidal. Four macronuclear nodules, 2 micronuclei, 36 adoral membranelles, 3 frontal cirri, 3 buccal cirri, 3 transverse cirri, and 3 caudal cirri on average. Five ventral cirral rows (anlagen) composed of 1 (1st frontal cirrus), 4 (2nd frontal cirrus plus buccal cirri), 4 (3rd frontal cirrus plus cirri underneath), 18 (row 4), and 14 (row 5) cirri on average. Four dorsal kineties, rows 1–3 originate intrakinetally, row 4 originates dorsomarginally and terminates near mid-body; rows 1 and 2 produce caudal cirri.

**Type location**

Venezuela, Cordillera de Mérida, Páramo de Piedras Blancas about 2 km east of the Pico del Aquila (08°52′N, 70°48′W), on *Espeletia* leaves from dead, rotting *Espeletia* trunks.

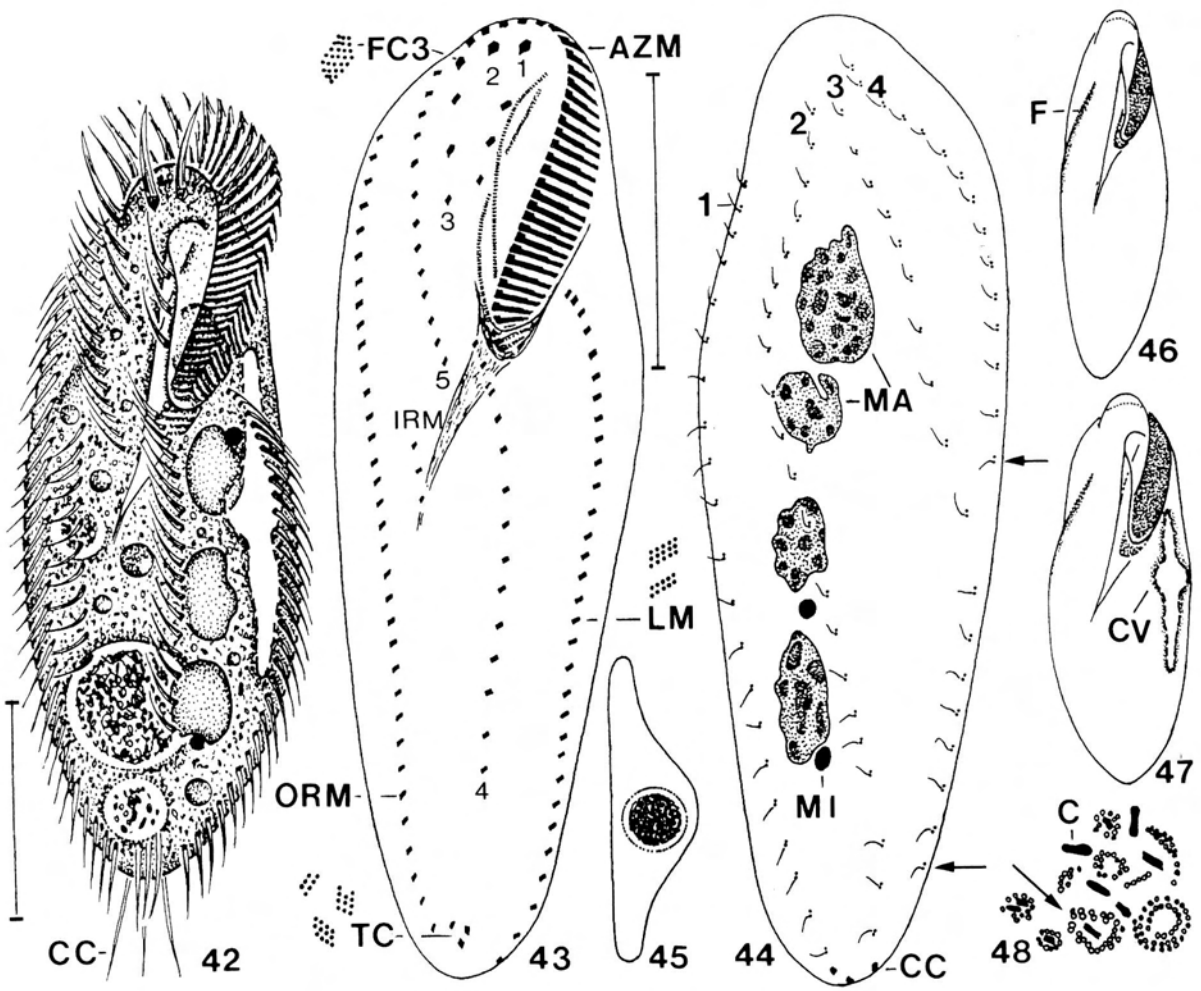
TABLE 3. Morphometric data on *Fragmocirrus espeletiae*.

| Character[1] | $\bar{x}$ | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 155.9 | 150 | 31.5 | 6.9 | 20.2 | 122 | 264 | 21 |
| Body, maximum width | 64.5 | 59 | 18.0 | 3.9 | 27.9 | 38 | 105 | 21 |
| Anterior somatic end to proximal end of adoral zone, distance | 53.9 | 50 | 13.4 | 2.9 | 24.9 | 40 | 100 | 21 |
| Macronuclear nodules, length | 17.4 | 18 | 3.3 | 0.7 | 19.2 | 12 | 23 | 21 |
| Macronuclear nodules, width | 11.1 | 11 | 3.5 | 0.8 | 31.4 | 6 | 20 | 21 |
| Micronuclei, length | 3.9 | 4 | 0.8 | 0.2 | 20.7 | 3 | 6 | 21 |
| Micronuclei, width | 3.2 | 3 | – | – | – | 3 | 4 | 21 |
| Adoral membranelles, number | 37.5 | 36 | 5.3 | 1.2 | 14.0 | 30 | 50 | 21 |
| Macronuclear nodules, number | 4.2 | 4 | 0.5 | 0.1 | 12.7 | 4 | 6 | 21 |
| Micronuclei, number | 2.5 | 2 | 1.0 | 0.2 | 39.6 | 1 | 6 | 21 |
| Dorsal kineties, number | 4.0 | 4 | 0.0 | 0.0 | 0.0 | 4 | 4 | 21 |
| Frontal cirri, number | 3.0 | 3 | 0.0 | 0.0 | 0.0 | 3 | 3 | 21 |
| Buccal cirri, number | 3.1 | 3 | 0.6 | 0.1 | 20.4 | 2 | 5 | 26 |
| Transverse cirri, number | 3.0 | 3 | – | – | – | 3 | 4 | 25 |
| Caudal cirri, number | 3.2 | 3 | 0.6 | 0.1 | 18.4 | 2 | 5 | 25 |
| Ventral cirral rows, number | 5.0 | 5 | 0.0 | 0.0 | 0.0 | 5 | 5 | 30 |
| Right marginal rows, number | 1.9 | 2 | – | – | – | 1 | 2 | 30 |
| Outer right marginal row, number of cirri | 31.8 | 31 | 3.1 | 0.7 | 9.7 | 27 | 39 | 21 |
| Inner right marginal row, number of cirri | 12.3 | 12 | 9.1 | 2.0 | 74.3 | 1 | 34 | 21 |
| Left marginal rows, number | 1.5 | 2 | – | – | – | 1 | 2 | 30 |
| Outer left marginal row, number of cirri | 6.6 | 5 | 5.0 | 0.9 | 75.1 | 1 | 25 | 30 |
| Inner left marginal row, number of cirri | 30.1 | 30 | 3.1 | 0.7 | 10.2 | 25 | 37 | 21 |
| 1st ventral row, number of cirri[2,3] | 1.0 | 1 | 0.0 | 0.0 | 0.0 | 1 | 1 | 21 |
| 2nd ventral row, number of cirri[2,3] | 3.9 | 4 | 0.6 | 0.1 | 14.8 | 3 | 5 | 30 |
| 3rd ventral row, number of cirri[2,3] | 3.7 | 4 | – | – | – | 3 | 4 | 30 |
| 4th ventral row, number of cirri[3] | 17.8 | 18 | 2.7 | 0.6 | 15.0 | 13 | 25 | 21 |
| 5th ventral row, number of cirri[3] | 14.4 | 14 | 2.3 | 0.5 | 15.8 | 11 | 20 | 21 |

[1]Data based on protargol-impregnated (protocol B in Foissner 1991) and mounted specimens from a non flooded-Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard deviation of mean, – $\bar{x}$ arithmetic mean.

[2]Note that the upper cirrus is differentiated as "frontal cirrus". 1st ventral row = 1st frontal cirrus; 2nd ventral row = 2nd frontal cirrus plus buccal cirri; 3rd ventral row = 3rd frontal cirrus plus ventral cirri underneath.

[3]For designation of ventral cirral rows, see Figure 43.




Figs. 42–48. *Fragmocirrus espeletiae* nov. spec. from life (Figs. 42, 45–48) and after protargol impregnation (Figs. 43, 44). **42:** Ventral view of a representative specimen. **43, 44:** Infraciliature of ventral and dorsal side. Numbers in Figure 43 denote ventral cirral rows (anlagen), those in Figure 44 denote dorsal ciliary rows. Arrows mark end of dorsal kineties 3 and 4. **45:** Lateral view of a specimen having just ingested large prey. **46, 47:** Shape variants. **48:** Crystals near cortex and in cytoplasm. Crystals are very likely formed within ring-shaped arrays of bright granules (arrow). AZM – adoral zone of membranelles, C – crystal, CC – caudal cirri, CV – contractile vacuole, F – furrow on dorsal side along kinety 4, FC3 – third frontal cirrus, IRM – inner right marginal row, LM – left marginal row, MA – macronuclear nodules, MI – micronucleus, ORM – outer right marginal row, TC – transverse cirri. Scale bars 50 µm.

**Etymology**

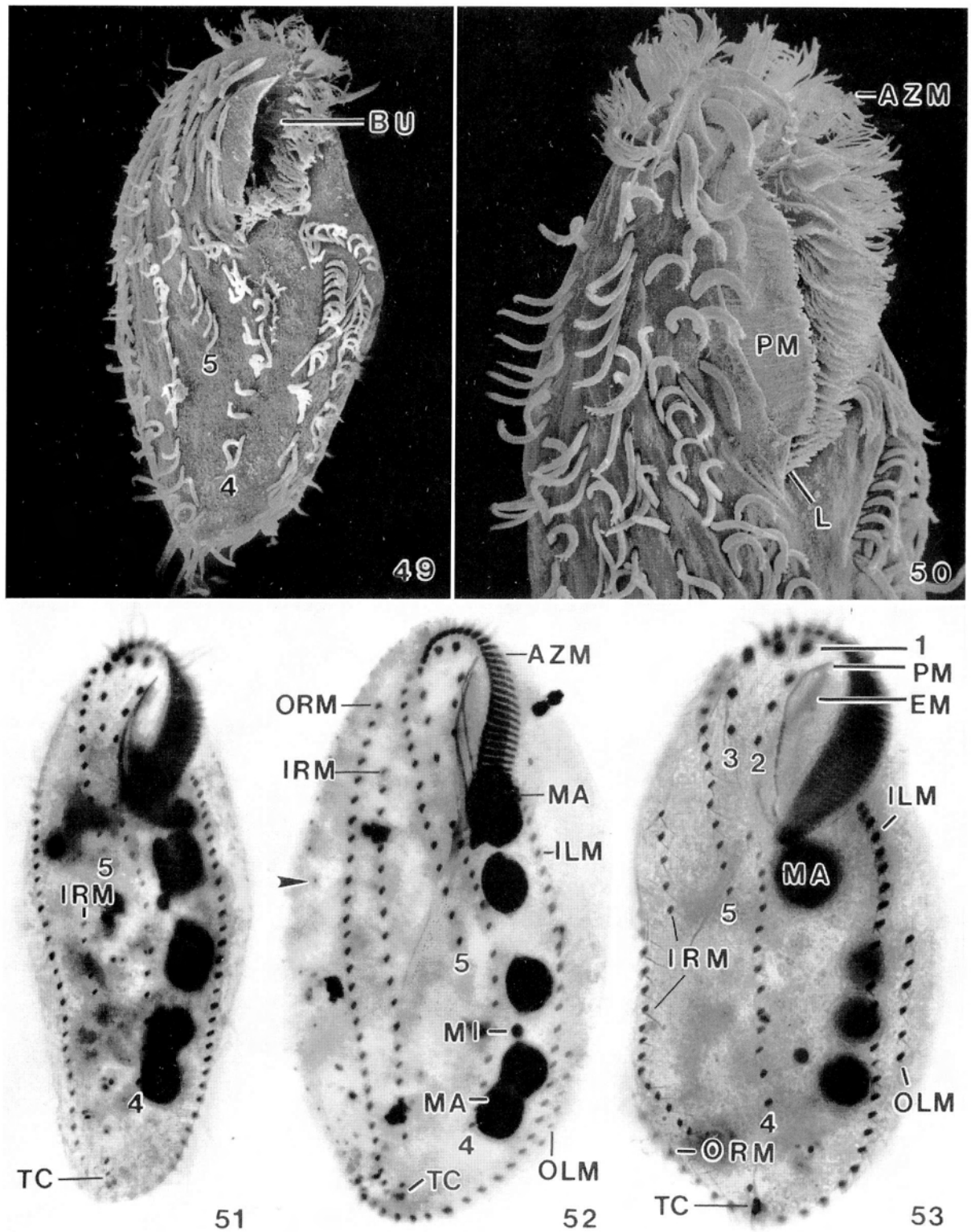
Genitive of genus *Espeletia*, the plant on which the species was found.

**Type material**

Six slides (1 holotype and 5 paratypes) with protargol-impregnated (Wilbert's method = protocol B in Foissner, 1991) morphostatic and dividing specimens have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria. The slides contain many specimens, with relevant cells marked by a black ink circle on the cover glass.

**Description**

This species is very variable as indicated by the high coefficients of variation, most being near or even above 20% (Table 3). Even characters which are known to be rather stable, such as the number of adoral membranelles and macronuclear nodules (Foissner, 1982), have variation coefficients higher than 10%. Interestingly, such pronounced variation is also found in species of the closely related genera (see above) *Paraurostyla* (Wirnsberger et al., 1985), *Parakahliella* (Berger & Foissner, 1989b; Berger et al., 1985), and *Parentocirrus* (Voß, 1997).




Figs. 49–53. *Fragmocirrus espeletiae* nov. spec., ventral cirral pattern and oral apparatus in the scanning electron microscope (Figs. 49, 50) and after protargol impregnation (Figs. 51–53). Note variability of cirral pattern, especially of marginal rows. Numbers 1 – 5 denote ventral cirral rows (anlagen). Arrowhead in Figure 52 marks end of dorsal kinety 4. AZM – adoral zone of membranelles, BU – buccal cavity, EM – endoral membrane, ILM – inner left marginal row, IRM – inner right marginal row, L – buccal lip, MA – macronuclear nodules, MI – micronucleus, OLM – outer left marginal row, ORM – outer right marginal row, PM – paroral membrane, TC – transverse cirri.

Size *in vivo* 130–280 × 40–100 µm, usually about 160 × 60 µm, length:width ratio fairly stable, that is, 2:1–3:1, with an average of 2.6:1 (Table 3); acontractile. Ellipsoidal to fusiform, occasionally slightly narrowed posteriorly (Fig. 43), anterior end rather broadly rounded, posterior narrowly rounded to bluntly pointed (Figs. 42, 46, 47); dorsoventrally flattened up to 2:1. Macronuclear nodules arranged one after the other left of cell's midline, broadly to slenderly ellipsoidal and often with irregular outline, contain many globular and oblong nucleoli. Micronuclei broadly ellipsoidal, near or attached to macronuclear nodules in variable positions. Contractile vacuole slightly above mid-body at left margin of cell, with two short, lacunar collecting canals. Cortex very flexible, without specific granules; there are, however, many 2–4 × 1–2 µm sized crystals, which very likely evolve from rings of bright granules near the cortex and in the cytoplasm (Fig. 48). Cytoplasm colourless, however, cells appear dark at low (≤ X100) magnification when packed with crystals, as described above, some fat globules up to 15 µm across, and up to 40 µm-sized food vacuoles containing heterotrophic flagellates and small (*Colpoda steinii*) and middle-sized (*C. lucida*, *Gonostomum affine*) ciliates. Glides moderately fast on slide surface and soil particles; never rests.

Cirri 13–17 µm long, except for caudal cirri and cilia of adoral membranelles, which are about 20 µm long. Cirral pattern highly variable, mainly due to the marginal cirral rows: both the inner right row(s) and the outer left row(s) are more or less distinctly reduced and may even be absent or complete (Figs. 42, 43, 49–53, 66). Usually 5, rarely 6 ventral cirral rows[1]: rows 1, 2, 3, 5 extend in frontal area, row 4 extends postorally. Ventral row 1 consists of 1st frontal cirrus; row 2 of 2nd frontal cirrus and buccal cirri; row 3 consists of 3rd frontal cirrus plus some cirri underneath; row 4 commences near buccal vertex left of row 5, from which it is separated by a small but distinct break, and extends posteriorly, terminating distinctly above the transverse cirri (Figs. 43, 51, 53); row 5 commences near rightmost frontal cirrus and extends to level of buccal vertex right of cell's midline; occasionally, rows 4 and 5 are longer as described above distinctly overlapping in buccal vertex area (Fig. 66). Transverse cirri near posterior body end and thus projecting beyond cell margin, inconspicuous because thin and few.

Dorsal bristles *in vivo* 3 µm long, form very stable pattern (Fig. 44): rows 1 and 2 extend left of cell's midline, both slightly shortened anteriorly; row 3 right of midline, slightly shortened anteriorly and posteriorly; row 4 in distinct furrow near right margin of cell, terminates near mid-body. Caudal cirri conspicuous because 20 µm long and rather motile; generated by dorsal ciliary rows 1 (produces 2–3, usually 2 cirri) and 2 (produces 1–2, usually 1 cirrus).

Oral apparatus of usual structure, adoral zone of membranelles occupies 35% of body length on average (Figs. 42, 43, 46, 47, 49–53; Table 3). Buccal cavity deep but rather narrow, anterior portion semicircularly curved *in vivo*; buccal lip long and rather broad, covers right half of buccal cavity (Figs. 42, 50). Paroral slightly curved, optically intersects endoral in mid-buccal area, both very likely composed of narrowly spaced dikinetids; pharyngeal fibres distinct.

**Occurrence**

As yet found only at type location (sample 2).

**Comparison with related species**

*Fragmocirrus espeletiae* is easily confused with species of the genera *Paraurostyla*, *Parakahliella*, and *Parentocirrus*. Reliable identification requires live observation and silver impregnation.

*Paraurostyla weissei* and most other freshwater *Paraurostyla* have only two macronuclear nodules and some have conspicuous, yellowgreen cortical granules (Kahl, 1932; Wirnsberger et al., 1985). *Paraurostyla granulifera* Berger and Foissner, 1989a, a soil species, has peculiar cortical granules, two macronuclear nodules, and conspicuous transverse cirri far away from the posterior end. *Paraurostyla pulchra* Buitkamp, 1977, also a soil species, has many (>20) scattered macronuclear nodules and five transverse cirri accompanied by two pretransverse cirri. *Paraurostyla buitkampi* Foissner, 1982, also a soil species, has four macronuclear nodules in two groups, three dorsal kineties, and lacks caudal cirri. *Paraurostyla polynucleata* Alekperov, 1993, a soil species from Russia, on average possesses nine macronuclear nodules and nine transverse cirri forming a distinct, oblique row. *Paraurostyla terricola*

[1] Ventral cirral rows are numbered according to the anlagen (usually 5) from which they develop during ontogenesis (see below).

Buitkamp 1977, which was combined with *Parakahliella* by Berger et al. (1985), very likely belongs to *Fragmocirrus*, although the presence of transverse cirri still has to be shown by ontogenetic data. However, the cirral pattern is very similar to that of *F. espeletiae* and the two subterminal cirri of *P. terricola* are very likely transverse cirri because they are distinctly set up and composed of 3 × 3 cilia, whereas ventral and marginal cirri consist of 4 × 3 cilia. Thus, I transfer this species to the new genus: *Fragmocirrus terricola* (Buitkamp, 1977) nov. comb. (basionym: *Paraurostyla terricola* Buitkamp, 1977). *Fragmocirrus espeletiae* and *F. terricola* differ in the number of macronuclear nodules (4 vs. 8), adoral membranelles (37 vs. 28), dorsal kineties (4 vs. 5), and left marginal cirral rows (1–2 vs. 3).

*Parakahliella* spp. lack transverse cirri and have a different dorsal ontogenesis (see genus comparison above). *Parakahliella macrostoma* (Foissner, 1982) Berger et al. (1985) has 11 macronuclear nodules and four left marginal rows. *Parakahliella haideri* Berger and Foissner (1989) whose ventral cirral pattern is very similar to that of *F. espeletiae*, has 47 adoral membranelles, six macronuclear nodules, and five dorsal kineties on average.

*Parentocirrus hortualis* (Voß, 1997) usually has eight macronuclear nodules, four distinct transverse cirri indistinctly separated from the ventral cirral rows, and six dorsal kineties.

### Ontogenesis of *Fragmocirrus espeletiae* (Fig. 54–83)

Most of the characters used to define *Fragmocirrus* are unequivocally recognisable only during cell division. Generally, ontogenesis of *F. espeletiae* is very similar to that of *Parakahliella macrostoma*, *P. haideri*, *Paraurostyla weissei*, and *Parentocirrus hortualis*, differing in details, such as production of transverse cirri and multiple marginal cirral rows (see genus characterisation).

#### Oral apparatus

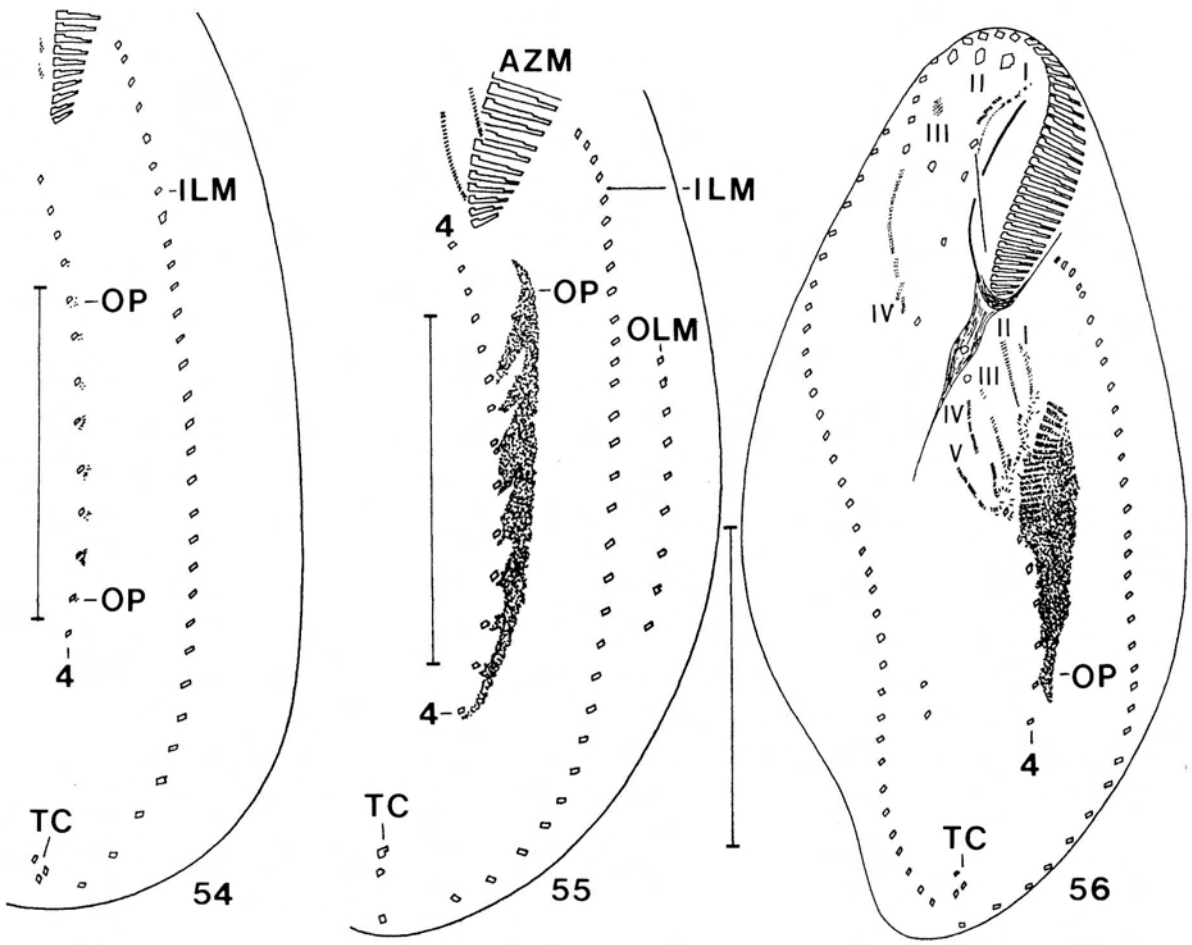
The oral primordium for the posterior daughter (opisthe) invariably develops postorally close to the cirri of ventral row 4 (Figs. 54–56, 71, 72). However, the ventral cirri appear unchanged and later generate cirral primordia IV and V. Furthermore, about four cirri at the anterior end of the row and one to three cirri at the posterior end are not involved in any anlagen formation and thus resorbed in middle and late dividers. The further development of the oral primordium is as in other parakahliellid and oxytrichid hypotrichs. For instance, the paroral and endoral membrane, which develop from a streak of scattered basal bodies at the end of the cirral anlagen, are patterned in late dividers; when the buccal cavity develops, the paroral optically moves over the endoral intersecting it in mid-buccal cavity (Figs. 61–64, 66, 79, 82).

The parental adoral zone of membranelles remains unchanged, while the buccal area, the paroral and the endoral, as well as the pharyngeal fibres are reorganised completely (Figs. 56–63, 74, 75, 79).

#### Ventral cirral pattern

*Fragmocirrus espeletiae* usually generates five cirral anlagen each in proter and opisthe. One or two additional anlagen of varying length may occur between anlagen III and V. Likewise, the number of cirri produced in anlagen IV and V is highly variable (Tab. 3). These irregularities produce part of the variability of the cirral pattern of *F. espeletiae*. Cirri not involved in anlagen formation are resorbed in late dividers and early postdividers. Very likely, no or few parental cirri are transmitted to the next generation.

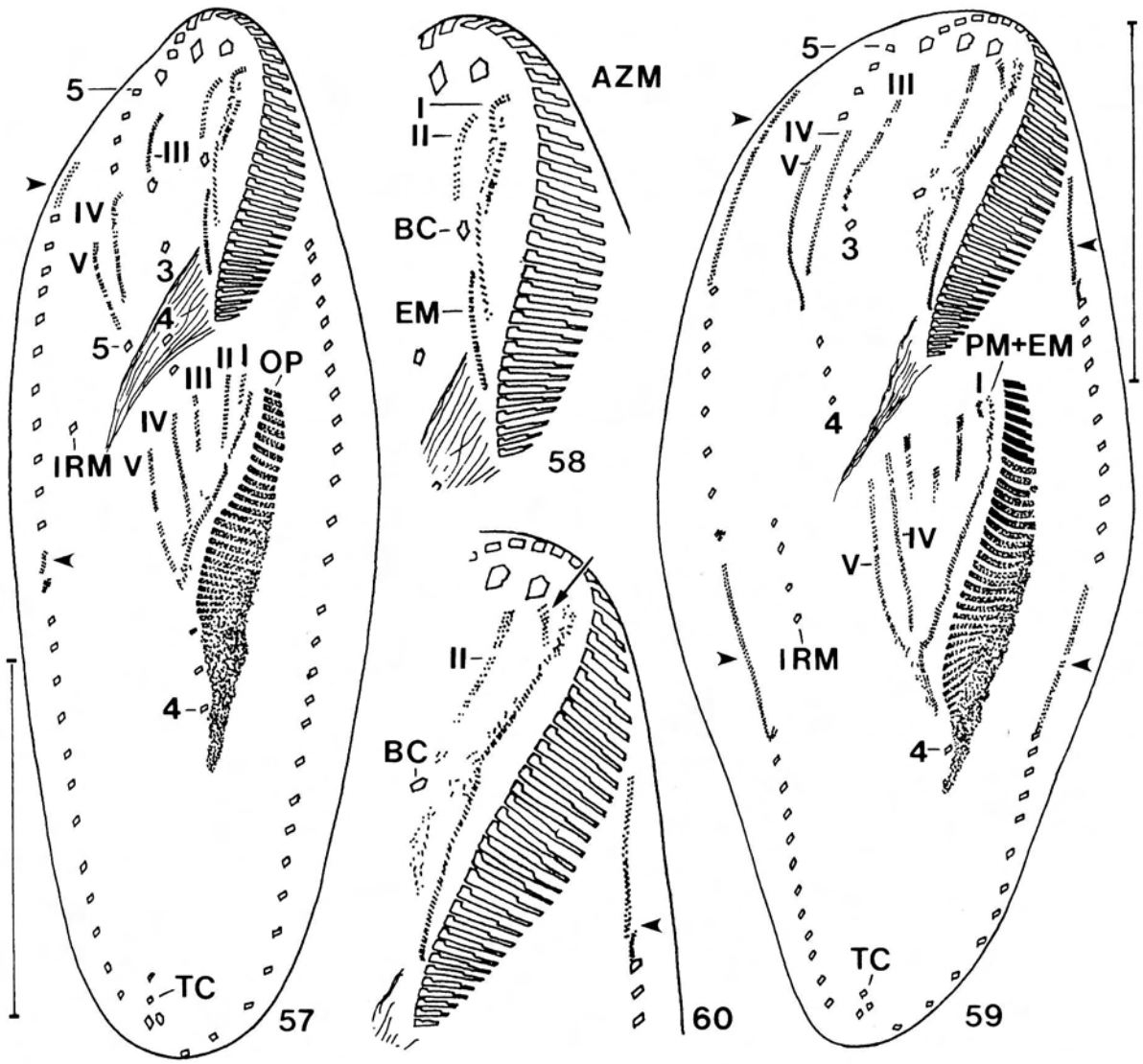
Proter anlage I is produced by the primordium for the undulating membranes and generates the 1st frontal cirrus. Proter anlage II, which is produced by the buccal cirri, generates the 2nd frontal cirrus and new buccal cirri. Proter anlage III, which is produced by cirral row 3, generates the 3rd frontal cirrus and a new ventral cirral row 3. The last cirrus of row 3 is probably not involved in anlagen formation. Proter anlagen IV and V, which produce new cirral rows 4 and 5, are generated in a special manner by cirral row 5. First, a single streak forms within cirral row 5 (Fig. 56). Then, the posterior third of the streak migrates right and produces basal bodies eventually forming a second streak. Finally, streaks IV and V form a conspicuous, V-shaped anlage (Figs. 57, 59, 61, 63, 74, 78, 79). When cytokinesis commences, the posterior portion of streak V separates and migrates posteriorly to form the inconspicuous transverse cirri (Figs. 63, 64, 78, 79). Next, streaks IV and V commence to migrate in opposite directions, the right one anteriorly, the left posteriorly, producing the specific cirral pattern of *F. espeletiae* (Figs. 64, 66, 70, 80 – 82). The uppermost 3 – 6 (usually 4) cirri and the posterior 1 – 4 (usually 1) cirri of row 5 are not involved in anlagen formation and resorbed (Figs. 63, 64, 66, 70, 75, 79, 82).




Fisg. 54–56. *Fragmocirrus espeletiae* nov. spec., ventral view of dividers after protargol impregnation. **54, 55:** Very early stages showing oral primordium (OP) developing very near to cirral row 4. **56:** Early stage. The oral primordium commences to form adoral membranelles in the right anterior portion. In the proter, the paroral membrane (anlage I) and the cirri modify to anlagen. In the opisthe, five fronto-ventral-transverse cirral anlagen are already recognisable; streaks I – III are generated by the oral primordium, while streaks IV and V are generated from cirral row 4. AZM – adoral zone of membranelles, ILM – inner left marginal row, OLM – outer left marginal row, OP – oral primordium, TC – transverse cirri, 4 – parental ventral cirral row 4, I – V – fronto-ventral-transverse cirral anlagen. Scale bars 50 μm.

Opisthe anlagen I – III originate from the oral primordium and produce the same cirri as described for the proter. Opisthe anlagen IV and V originate, similarly to the oral primordium described above, from the middle portion of cirral row 4. As in the proter, the streaks form a conspicuous, V-shaped anlage and migrate in opposite directions producing the species-specific cirral pattern during cytokinesis. Two to five cirri each at the anterior and posterior end of row 4 are not involved in any anlagen formation and are resorbed (Figs. 56, 57, 59, 61, 63, 66, 75, 76, 80 – 82).

Two primordia each are generated in the outer right and the inner left marginal row (Figs. 57, 59). In middle dividers, one or more short anlagen develop near the posterior end of each marginal primordium and proliferate dikinetids anteriorly (Figs. 61, 63, 77, 78, 79). These anlagen become the inner right and the outer left marginal rows (Figs. 80, 82). I could not clarify whether the anlagen are a split part of the regular marginal primordia or arise independently from parental marginal cirri. Furthermore, the outer left marginal cirral primordia (rows) are frequently lacking (Table 3). The different number and length of the inner right and outer left marginal primordia produce most of the interphase variability of the cirral pattern of *F. espeletiae* (Table 3).



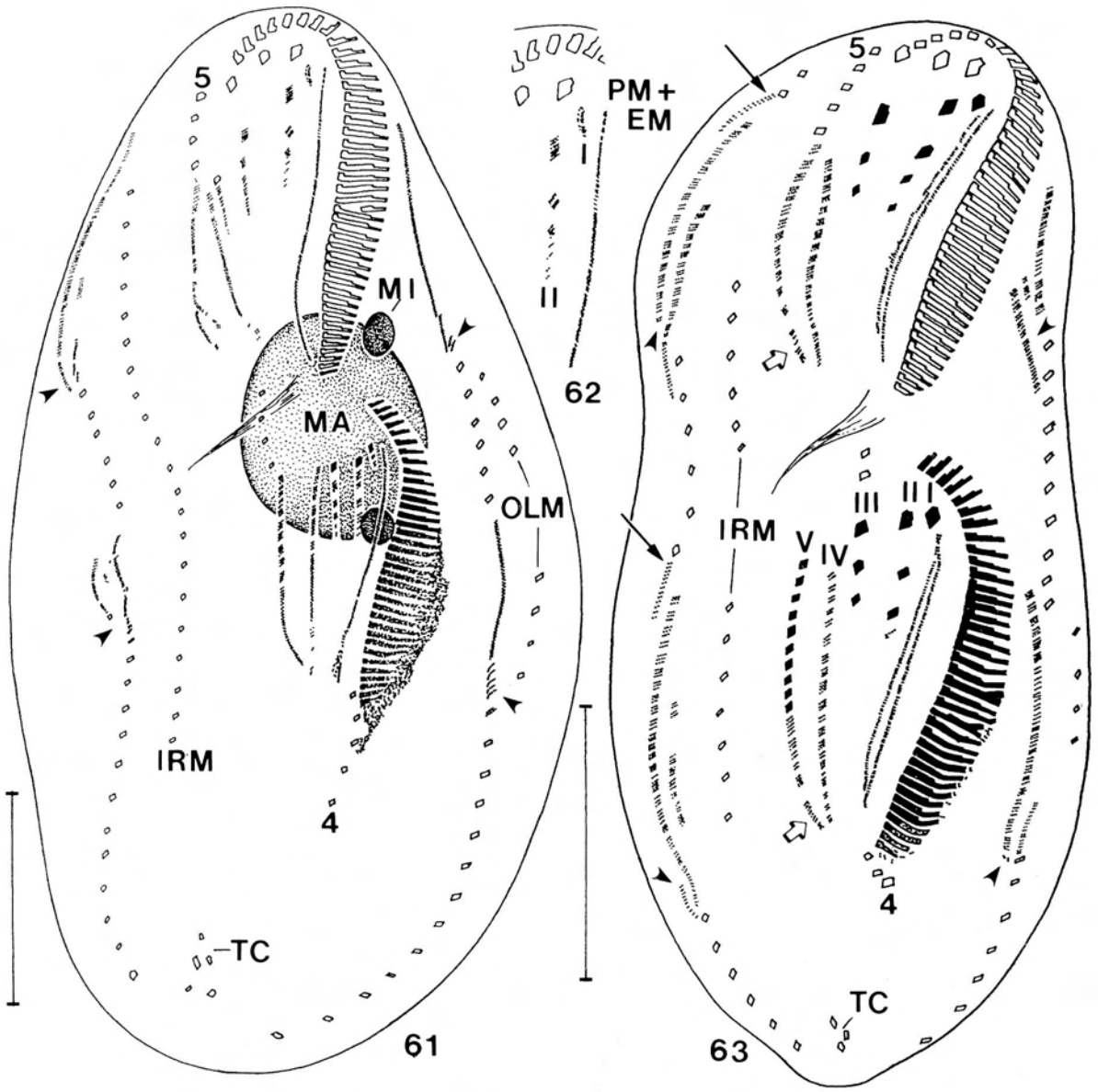

Figs. 57–60. *Fragmocirrus espeletiae* nov. spec., ventral views of early-middle dividers after protargol impregnation. Figures 58 and 60 are enlarged details from Figures 57 and 59. The oral primordium proceeds to form adoral membranelles from anterior to posterior. The parental paroral and endoral are completely reorganised. A streak of disordered basal bodies, which will become the opisthe's paroral and endoral, extends along the oral primordium. Most of the parental ventral cirri have modified to cirral anlagen, the rest is resorbed when division proceeds. Thus, five fronto-ventral-transverse cirral anlagen (I–V) are now recognisable each in proter and opisthe. Note that anlage I (first frontal cirrus) derives from the reorganising (proter; Fig. 60, arrow), respectively, newly forming (opisthe; Fig. 58) paroral membrane. Streaks IV and V form a V-like structure. Four anlagen (arrowheads) develop within the marginal rows. AZM – adoral zone of membranelles, BC – buccal cirrus, EM – endoral membrane, IRM – inner right marginal row, OP – oral primordium, PM – paroral membrane, TC – transverse cirri, 3,4,5 – parental ventral cirral rows, I – V – fronto-ventral-transverse cirral anlagen in proter and opisthe. Scale bars 50 µm.

**Dorsal infraciliature**

A primordium each develops within the proter and opisthe parental ciliary rows 1–3 (Figs. 67, 83). Row 4 originates dorsomarginally, that is, close to the first right marginal cirrus not involved in the formation of the marginal primordium (Figs. 63, 64, 78). This row, which is only about half as long as the cell, migrates dorsolaterally in late dividers (Figs. 66, 68, 82). Caudal cirri are produced only at the posterior end of rows 1 and 2, usually two cirri in row 1 and one cirrus in row 2 (Figs. 65, 68, 69, 83).

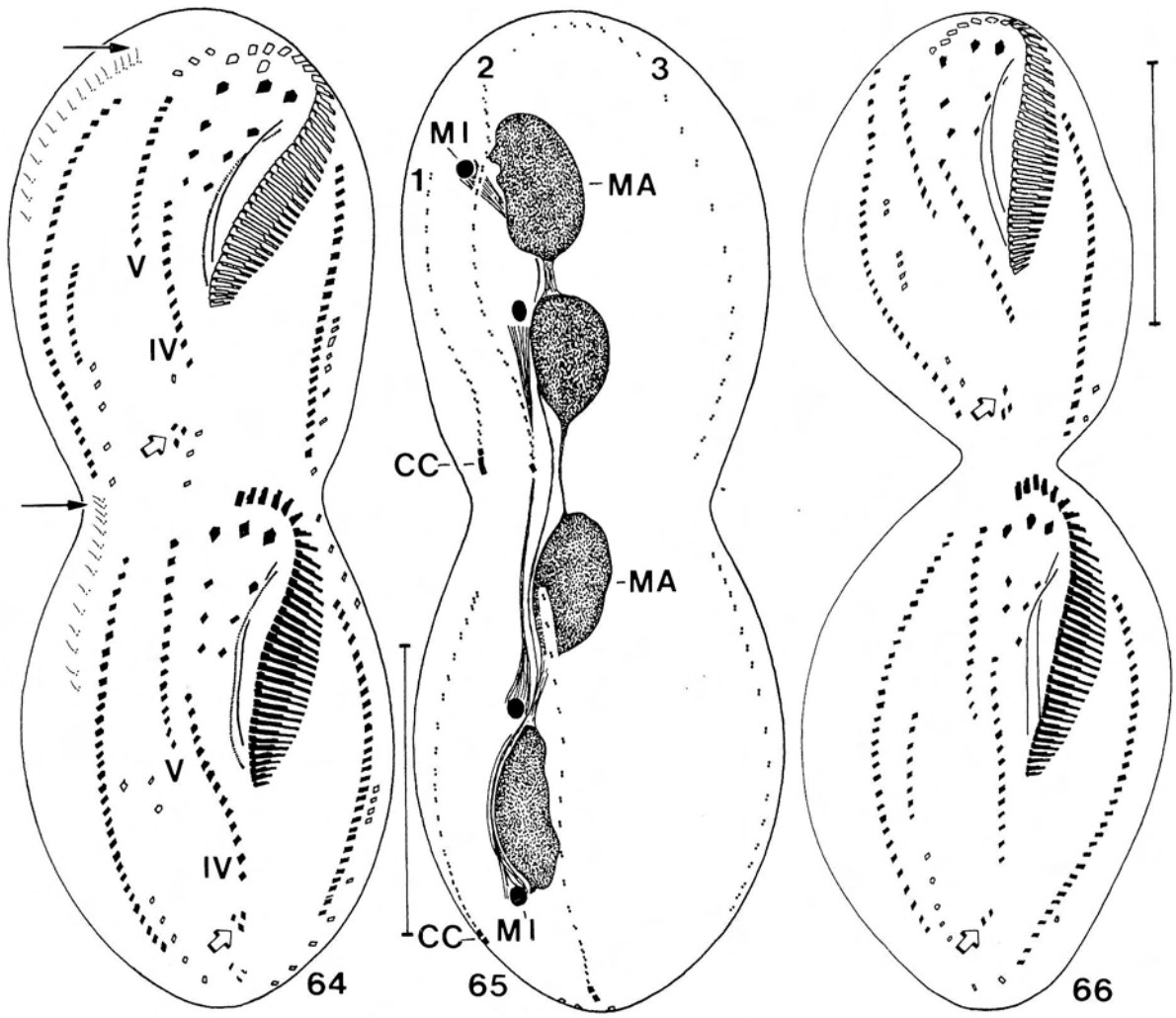
**Nuclear apparatus**

The nuclear apparatus reproduces as is usual. In mid-




Figs. 61–63. *Fragmocirrus espeletiae* nov. spec., ventral views of middle dividers after protargol impregnation. Figure 62 is an enlarged detail from Figure 61. Dorsal side and nuclear apparatus of specimen shown in Figure 63 are depicted in Figure 67. Parental structures shown by contour, newly formed shaded black. The opisthe's adoral zone of membranelles is almost complete, and the basal body streak along the adoral zone splits longitudinally to form the paroral and endoral membrane in both proter and opisthe. Cirri differentiate within the anlagen from anterior to posterior; transverse cirri are formed at posterior end of anlage V (open arrows). Small streaks of dikinetids develop near the posterior end of the marginal cirral primordia (arrowheads). These streaks are of highly varying length and become the inner right marginal row(s) and the outer left marginal rows(s). Arrows mark developing dorsal kinety 4. The macronuclear nodules fused to a globular mass (Fig. 61), which divides three times to form the species-specific number of macronuclear nodules (Figs. 65, 67, 68, 70). EM – endoral membrane, IRM – inner right marginal row, MA – macronucleus, MI – micronucleus, OLM – outer left marginal row, PM – paroral membrane, TC – transverse cirri, 4,5 – parental cirral rows, I – V – fronto-ventral-transverse cirral anlagen in proter and opisthe. Scale bars 50 μm.

dle dividers, the macronuclear nodules fuse to a globular mass (Figs. 61, 77, 79), which divides three (occasionally four) times, to produce the typical four nodules of *F. espeletiae* in late and very late dividers (Figs. 61, 65, 67, 70, 80, 82; Table 3). The micronuclei divide mitotically and do not fuse.




Figs. 64–66. *Fragmocirrus espeletiae* nov. spec., ventral (Figs. 64, 66) and dorsal (65) views of late (Figs. 64, 65) and very late (Fig. 66) dividers. Dorsal side and nuclear apparatus of specimen shown in Figure 66 are depicted in Figures 68, 69. Parental structures shown by contour, newly formed shaded black. The division furrow is now distinct and the oral apparatus is complete in proter and opisthe. Cirri have formed within the anlagen and most of the parental cirri have been resorbed or are in the process of resorption. Cirral anlagen IV and V migrate in opposite direction to produce the specific cirral pattern of *F. espeletiae*. Note lack of outer left marginal rows in both dividers and lack of inner right marginal row in the opisthe shown in Figure 64. Arrows mark dorsal kinety 4, which is migrating onto the dorsal side and thus not visible in Figure 66 (see Fig. 68). Open arrows mark newly formed transverse cirri, which split from anlage V and move posteriorly. Caudal cirri are generated at posterior end of dorsal kineties 1 and 2. Macronuclei and micronuclei are dividing. CC – caudal cirri, MA – macronuclear nodules, MI – micronuclei, 1, 2, 3 – dorsal kineties, IV , V – newly formed cirral rows 4 and 5. Scale bars 50 µm.

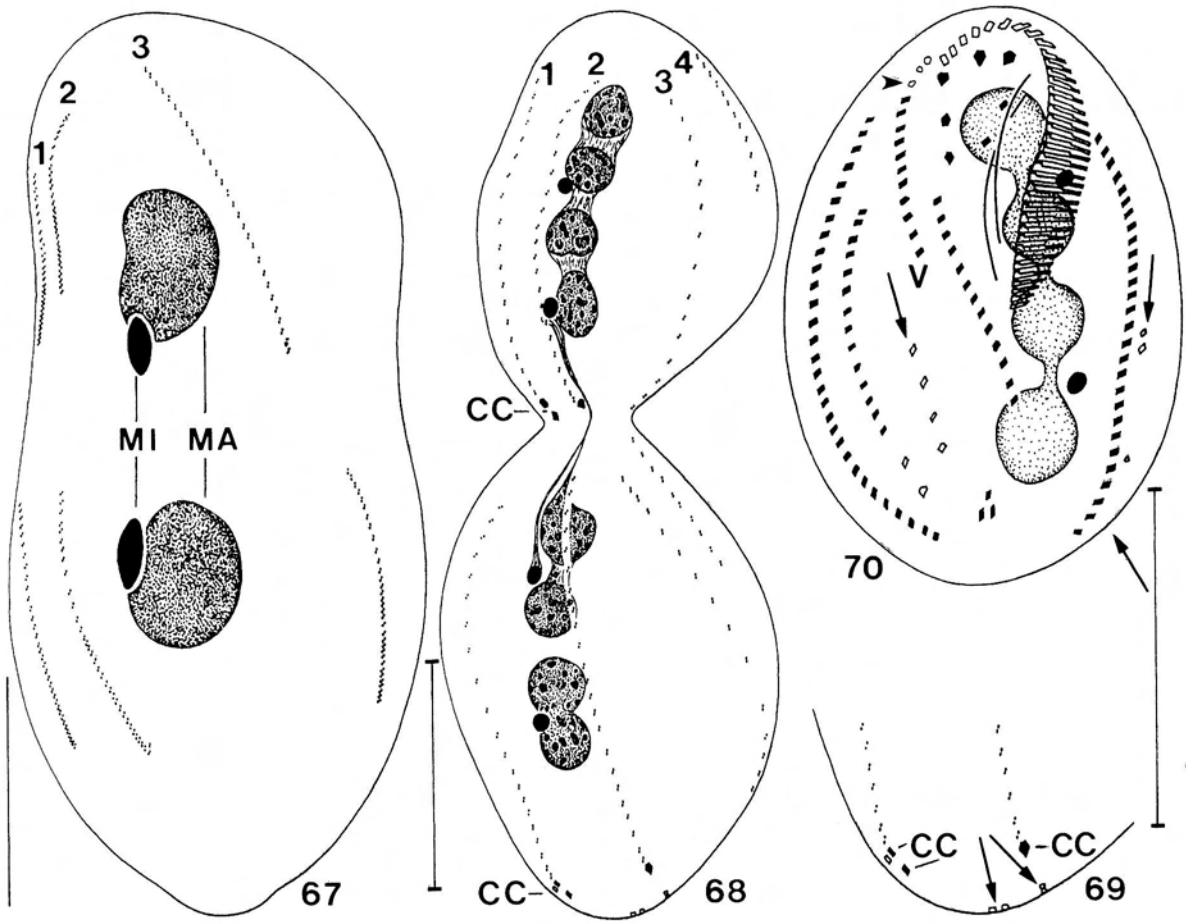
***Gonostomum affine*** (Stein, 1859) Sterki, 1878
(Figs. 84, 85, Table 4)

**Material**

A voucher slide with many protargol-impregnated (protocol A in Foissner 1991) specimens has been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria.

**Observations**

This common and highly variable species, which is possibly a sibling complex (Stoeck & Foissner, unpubl.), has 6–15, on average 11, frontoventral cirri (data from 18 soil populations investigated by Foissner, 1982; Shin & Kim, 1995; Stoeck & Foissner, unpubl.). The Venezuelan population is remarkable in having 14–18, on average 16, frontoventral cirri, a third of which form a distinct ventral row often ap-



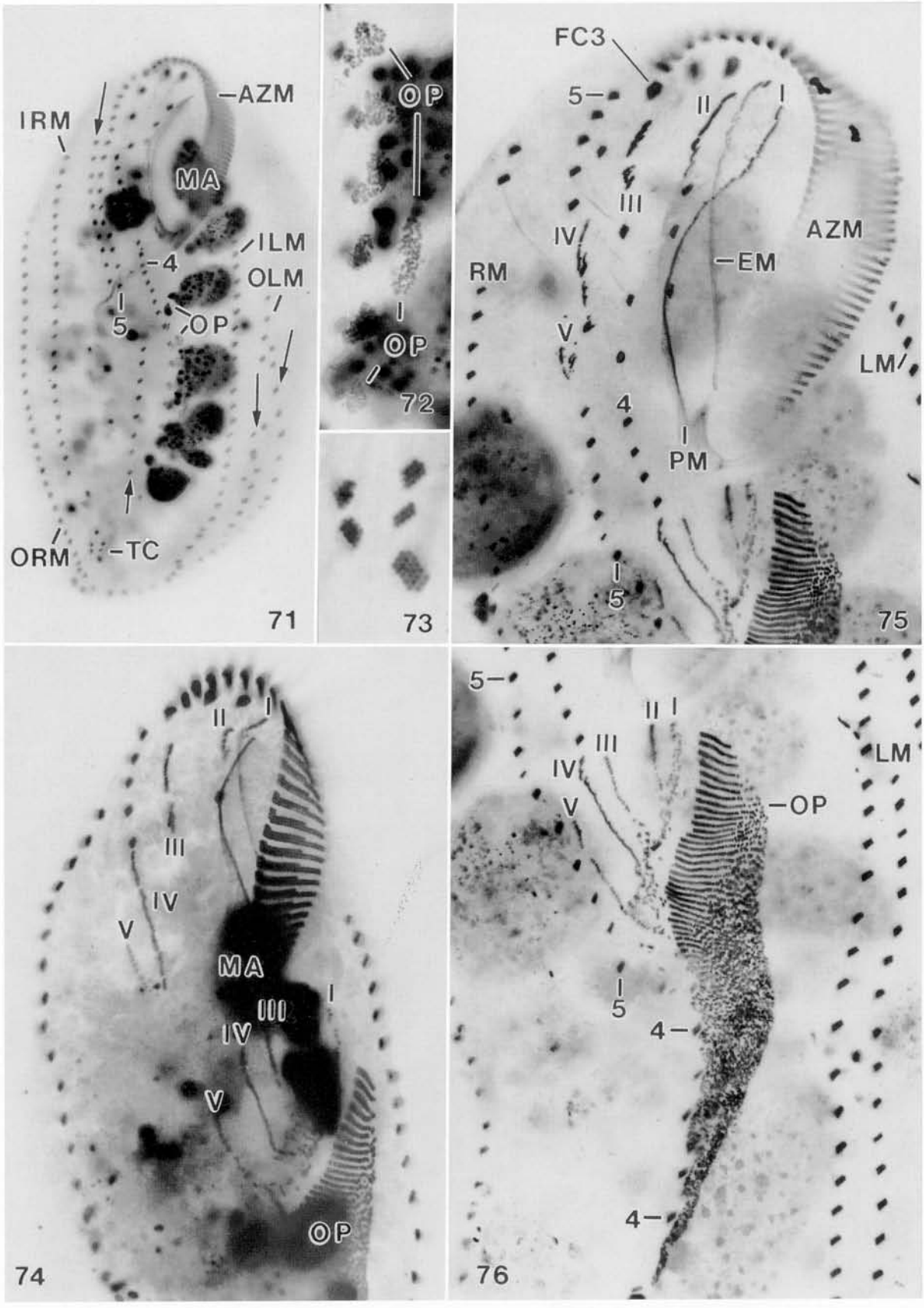

Figs. 67–70. *Fragmocirrus espeletiae* nov. spec., dorsal (Figs. 67–69) and ventral (Fig. 70) views of middle (Fig. 67; ventral side, see Fig. 63) and late (68; ventral side, see Fig. 66) dividers and of a postdivider (Fig. 70; a proter because there are still some parental cirri at the anterior end of anlage V, arrowhead) after protargol impregnation. Figure 69 is an enlarged detail from Figure 68; arrows marks parental caudal cirri. Parental structures shown by contour, newly formed shaded black. **67–69** (see Fig. 65 for an intermediate stage): Dorsal ciliary rows 1–3 originate by intrakinetal proliferation of kinetids in the parental kineties (not shown), while row 4 is generated dorsomarginally, that is, originates close to a parental right marginal cirrus (Figs. 63, 64, 78, 82) and then migrates dorsally (Figs. 63, 64, 66, 82). Caudal cirri are generated at posterior end of rows 1 and 2 only (Figs. 65, 67, 68). The fused macronuclear mass (Figs. 61, 77, 79) divides three times to obtain the species-specific 4 nodules (Figs. 65, 67, 68, 70); the micronuclei, which do not fuse, divide once (Figs. 65, 68). **70:** Postdividers are broadly ellipsoidal and already have the species-specific oral and cirral pattern. They continue to resorb parental cirri not involved in anlagen formation (arrows). CC – newly formed caudal cirri, MA – macronuclear nodules, MI – micronuclei, 1 – 4 – dorsal kineties, V – ventral cirral row anlage V. Scale bars 50 µm.

proaching or even surpassing the buccal vertex (Fig. 84, Table 4). Such a long ventral row is typical for *G. strenuum*, which, however, has 20–24, on average 20, frontoventral cirri (Song, 1990). Obviously, the Venezuelan population is in between *G. affine* and *G. strenuum*, casting doubt on the validity of the latter. Gene sequence data are necessary to explore the status of the Venezuelan population.

## DISCUSSION

### Interpretation of organism community

Of the 18 ciliate species found, most (17) occurred in sample 2 (Tab. 1). The low total number of species matches the general pauperisation of fauna and flora in high mountain regions (Franz, 1975) and observations on soil ciliates above the timber line in the Aus-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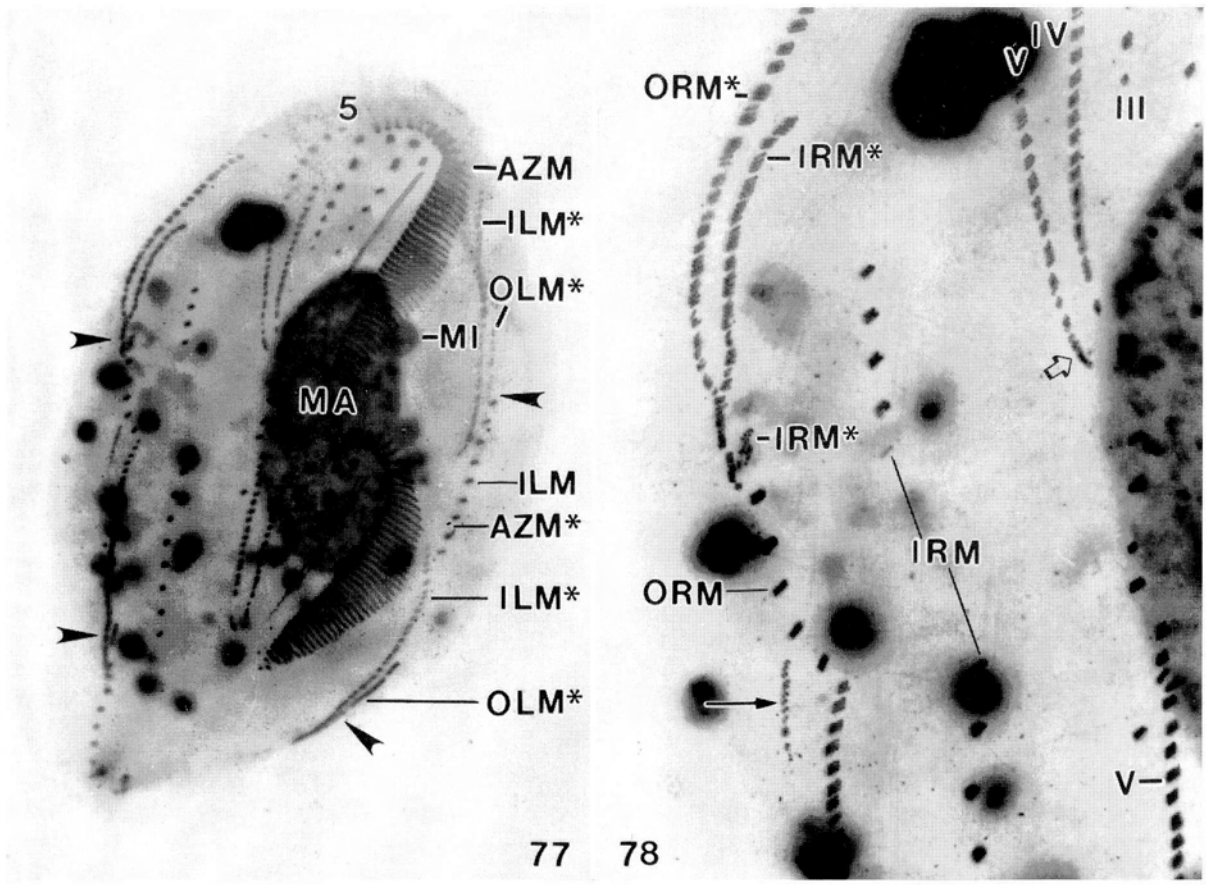
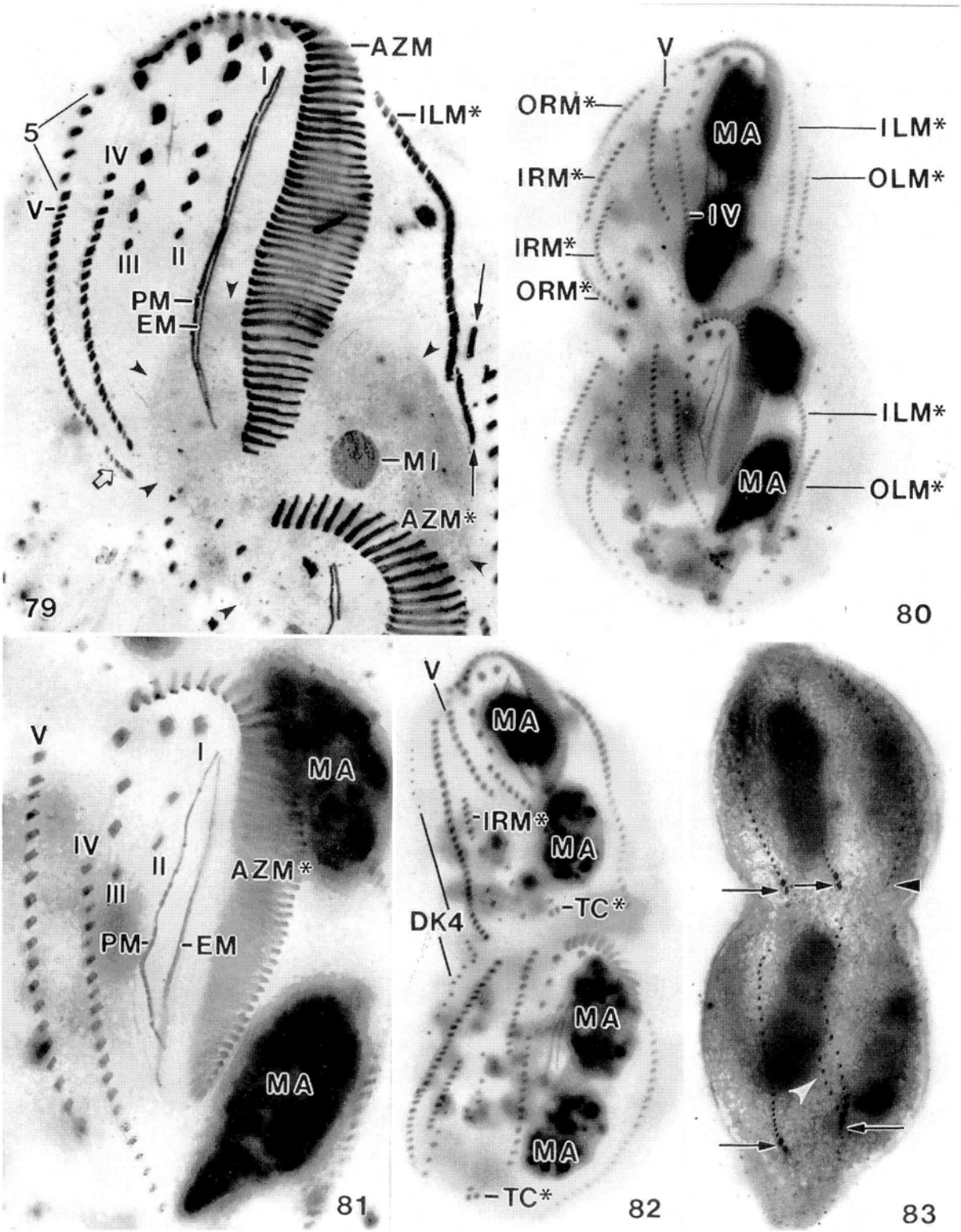



Figs. 77, 78. *Fragmocirrus espeletiae* nov. spec., ventral view of a middle divider after protargol impregnation (see also Fig. 79). Fig. 78 is an enlarged detail from Fig. 77. Symbols marked with an asterisk (*) denote newly formed structures. The opisthe's adoral zone of membranelles is complete. Cirri form within the anlagen streaks from anterior to posterior; transverse cirri separate at end of anlage 5 (open arrow). Small streaks develop near the posterior end of the marginal cirral primordia (arrowheads). These streaks are of highly varying length and will become the inner right marginal row(s) and the outer left marginal row(s). Arrow marks developing dorsal kinety 4. The macronuclear nodules fused to a globular mass. AZM – adoral zone of membranelles, ILM – inner left marginal row, IRM – inner right marginal row, MA – fused macronucleus, OLM – outer left marginal row, ORM – outer right marginal row, 5 – parental cirral row 5, III, IV, V – fronto-ventral-transverse cirral anlagen in proter and opisthe.

trian Central Alps (Foissner, 1981) and the Himalayas (Foissner, 1986). Furthermore, except for the two new species described below, all taxa are common soil inhabitants world-wide (Foissner, 1998) and of the Austrian Central Alps in particular (Foissner, 1981). However, it has to be emphasised that samples devoid of ciliates, as in the high Andes, are very rare in Austria. I thus suppose that the culture meth-

Figs. 71–76. *Fragmocirrus espeletiae* nov. spec., ventral views of dividers after protargol impregnation. **71 – 73:** Very early divider showing oral primordium developing close to the posterior portion of cirral row 4. Figure 73 shows 5 of the 6 transverse cirri at high magnification. Arrows mark supernumerary ventral and left marginal cirral rows. **74:** Early stage similar to that shown in Figures 75, 76 (see there for detailed explanation). **75, 76:** Upper and lower half of an early divider showing cirral anlagen (I–V) in proter and opisthe. Note that this specimen has 3 left marginal rows and cirral row 5 extends to mid-body. In the proter, the anterior portion of the paroral membrane forms anlage I, while anlagen II and III are generated by the anterior buccal cirrus and the cirri underneath frontal cirrus 3; anlagen IV and V are generated by cirral row 5 and grow to a V-shaped structure (Figs. 74, 79). The anterior portion of the endoral membrane is also reorganised. In the opisthe, anlagen I – III are generated by the oral primordium, which commences to form adoral membranelles in the right anterior portion; anlagen IV and V are generated by cirral row 4. AZM – adoral zone of membranelles, EM – endoral membrane, FC3 – third frontal cirrus, ILM – inner left marginal row, IRM – inner right marginal row, LM – left marginal rows, MA – macronuclear nodules, OLM – outer left marginal row, OP – oral primordium, ORM – outer right marginal row, PM – paroral membrane, RM – right marginal row, TC – transverse cirri, 4,5 – parental ventral cirral rows, I – V – fronto-ventral-transverse cirral anlagen in proter and opisthe.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83

TABLE 4. Morphometric data on *Gonostomum affine*.

| Character[1] | $\bar{x}$ | M | SD | SE | CV | Min | Max | N |
|---|---|---|---|---|---|---|---|---|
| Body, length | 81.0 | 80 | 9.8 | 2.1 | 12.1 | 67 | 100 | 21 |
| Body, maximum width | 30.1 | 30 | 3.6 | 0.8 | 12.1 | 22 | 35 | 21 |
| Anterior somatic end to proximal end of adoral zone, distance | 33.9 | 33 | 2.7 | 0.6 | 7.8 | 30 | 39 | 21 |
| Anterior somatic end to posteriormost frontoventral cirrus, distance | 34.5 | 35 | 4.3 | 1.0 | 12.6 | 29 | 43 | 21 |
| Macronuclear nodules, length | 15.9 | 15 | 2.5 | 0.5 | 15.5 | 13 | 23 | 21 |
| Macronuclear nodules, width | 6.2 | 6 | 0.6 | 0.1 | 9.7 | 5 | 7 | 21 |
| Micronuclei, length | 2.9 | 3 | – | – | – | 3 | 4 | 21 |
| Micronuclei, width | 2.0 | 2 | – | – | – | 2 | 3 | 21 |
| Adoral membranelles, number | 25.7 | 25 | 1.5 | 0.3 | 5.9 | 23 | 30 | 21 |
| Macronuclear nodules, number | 2.0 | 2 | 0.0 | 0.0 | 0.0 | 2 | 2 | 21 |
| Micronuclei, number[2] | 2.0 | 2 | 0.0 | 0.0 | 0.0 | 2 | 2 | 21 |
| Dorsal kineties, number | 3.0 | 3 | 0.0 | 0.0 | 0.0 | 3 | 3 | 21 |
| Anterior frontal cirri, number | 3.0 | 3 | 0.0 | 0.0 | 0.0 | 3 | 3 | 21 |
| Frontoterminal cirri, number | 3.9 | 4 | – | – | – | 3 | 4 | 21 |
| Buccal cirri, number | 1.1 | 1 | – | – | – | 1 | 2 | 21 |
| Other frontoventral cirri, number | 7.8 | 8 | 0.8 | 0.2 | 10.7 | 6 | 10 | 21 |
| Frontoventral cirri, total number[3] | 15.7 | 16 | 1.0 | 0.2 | 6.1 | 14 | 18 | 21 |
| "Ventral row", number of cirri[4] | 4.7 | 5 | 0.6 | 0.1 | 12.4 | 4 | 6 | 21 |
| Transverse cirri, number | 4.1 | 4 | 0.4 | 0.1 | 9.5 | 3 | 5 | 21 |
| Caudal cirri, number | 3.0 | 3 | 0.0 | 0.0 | 0.0 | 3 | 3 | 21 |
| Right marginal cirri, number | 22.7 | 23 | 1.7 | 0.4 | 7.4 | 20 | 27 | 21 |
| Left marginal cirri, number | 15.7 | 16 | 1.3 | 0.3 | 8.3 | 13 | 19 | 21 |
| Cilia composing paroral, number | 14.4 | 14 | 2.1 | 0.5 | 14.5 | 10 | 20 | 21 |

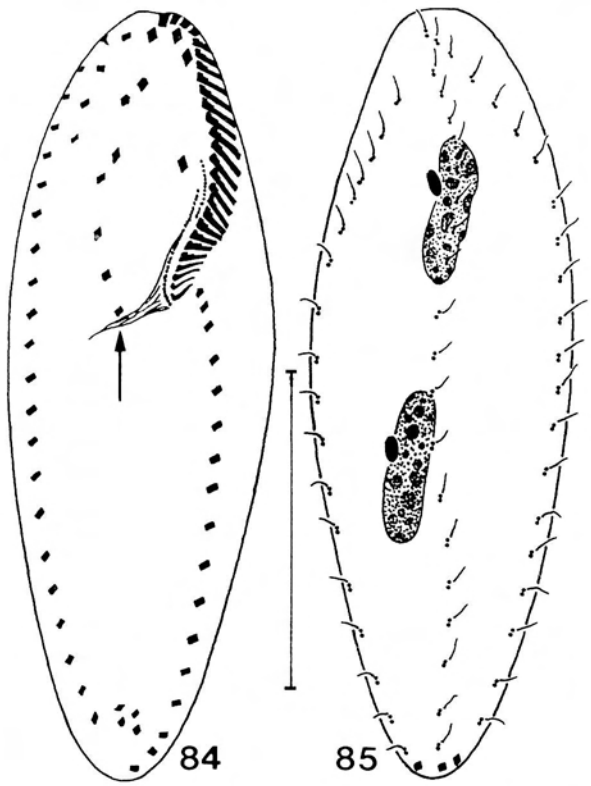
[1]Data based on protargol-impregnated (protocol A in Foissner, 1991) specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard deviation of mean, $\bar{x}$ – arithmetic mean.
[2]Of 30 specimens investigated, one had 3 micronuclei.
[3]Includes anterior frontal cirri, frontoterminal cirri, buccal cirri, and other frontoventral cirri.
[4]Included also in "other frontoventral cirri".

od applied is less effective for Andean than Austrian soils, possibly because the former are more permanently humid and the ciliates' resting cysts thus less drought resistant, as in rain forest soils (Foissner, 1997). This interpretation is supported by three observations: (i) the Ecuadorian samples, which are from a wet region (1500 mm annual precipitation), provided distinctly fewer ciliates than the Venezuelan samples (Table 1), which are from a dryer area (800 mm); (ii) all samples contain a variety of bacteria, fungal hyphae, flagellates, and testate amoebae (also frequent in moss samples; Grabandt, 1993), which indicates, in my experience, the presence of ciliates; (iii) *Espeletia* soils contain a rich and diverse community of microarthropods (Diaz & Najt, 1990) and earthworms. Thus, the samples investigated very likely contain more ciliates than shown in Table 1. Obviously, more and fresh material must be investigated to confirm or falsify this proposal.

ACKNOWLEDGEMENTS

Supported by the Austrian Science Foundation (Project P-12367-BIO). The technical assistance of Brigitte Moser,

Figs. 79–83. *Fragmocirrus espeletiae* nov. spec., dividers after protargol impregnation. Symbols with an asterisk (*) denote newly formed structures. **79:** Proter of a middle divider (cp. Figs. 77, 78) showing fused macronuclear nodules (arrowheads) and small kinetofragments (arrows), which will develop to outer left marginal rows (cp. Fig. 80). Transverse cirri separate from posterior end of anlage V (open arrow). **80–82** (Fig. 81 is an enlarged detail from Fig. 80): Ventral views of late dividers showing anlagen IV and V migrating in opposite directions, producing the species-specific cirral pattern. The fused macronuclear mass (Fig. 79) divided twice. Note shaping of paroral and endoral membrane (Fig. 81) and lack of outer left marginal rows in specimen shown in Figure 82. **83:** Dorsal view of a late divider showing production of caudal cirri (arrows) at end of dorsal anlagen 1 and 2; anlage 3 (black arrowhead) is barren. White arrowhead marks some parental kinetids. AZM – adoral zone of membranelles, DK4 – dorsal kinety 4, EM – endoral membrane, ILM – inner left marginal row, IRM – inner right marginal rows, MA – macronuclear nodules, MI – micronucleus, OLM – outer left marginal rows, ORM – outer right marginal row, PM – paroral membrane, TC – transverse cirri, 5 – parental cirral row 5, I – V – frontoventral-transverse cirral anlagen.




Figs. 84, 85. *Gonostomum affine*, infraciliature of ventral and dorsal side of a representative specimen from Venezuelan population. Arrow marks ventral row approaching level of buccal vertex. Note that the first frontal cirrus is not enlarged. Scale bar 40 µm.

Eva Herzog and Eric Strobl is acknowledged. Special thanks to Maurizio Paoletti (Padua University, Italy) for collecting samples in Ecuador.

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