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Description of two new *Drepanomonas* taxa and an account on features defining species in *Drepanomonas* Fresenius, 1858 (Ciliophora, Microthoracida)

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Abstract

Using standard methods, we describe two new *Drepanomonas* taxa: *Drepanomonas hymenofera* (Horváth 1956) nov. comb., which is composed of two (biogeographical?) subspecies, viz., *D. hymenofera venezuelensis* nov. subspec. and *D. hymenofera hymenofera* (Horváth 1956), was discovered in soil from Venezuela and Iceland, respectively. Both are comparatively large-sized (50 × 20 μm and 40 × 18 μm in vivo), differing in the cortex pattern and the structure of kineties 3 and 4. We agree with Corliss (1979) and Chardez (1990) that the genus *Pseudocristigera*, which was established by Horváth (1956) for *Drepanomonas hymenofera*, is a junior synonym of *Drepanomonas*. *Drepanomonas vasta* nov. spec., which was discovered in the mud of a tree hole in Austria, is a middle-sized species (35 × 18 μm) with thick body, wide left side ridges, a single anterior dikinetid in kinety 4, and an average of 99 basal bodies; it is unique in having the dorsal side much more flattened than the ventral side, thus being cuneate in transverse view. Ontogenetic data show that the ciliary pattern of *Drepanomonas* is homologous to that of *Leptopharynx*, specifically, the structure and origin of the postoral complex. Main features for distinguishing *Drepanomonas* species are discussed.

Keywords: Austria; Biogeography; Iceland; *Pseudocristigera*; Soil ciliates; Venezuela

Introduction

The present study continues our effort to clarify species features and phylogeny of the Microthoracidae by investigating the morphology and ontogeny of the generic type species (Omar and Foissner 2012b) and of new species discovered in various habitats globally (Foissner et al. 2011; Omar and Foissner 2011, 2012a,b). *Drepanomonas* Fresenius, 1858 is commonly found in terrestrial and semi-terrestrial habitats, such as mosses and soil from floodplains. Most *Drepanomonas* species are small and have a complex cortex. Thus, they are difficult to investigate in the light microscope. Scanning electron microscopy is very helpful for this kind of ciliates because it shows clearly the cortical ridge and furrow pattern (Foissner 1999; Foissner et al. 1994, 2011; present study).

As yet, ten nominal species have been described, four of which have been investigated or reinvestigated with modern methods: *D. exigua* Penard, 1922, *D. pauciciliata* Foissner, 1987, *D. revoluta* Penard, 1922, and *D. sphagni* Kahl, 1931 (Foissner 1979, 1987, 1999). Most data are available from *D. revoluta*, a frequent species occurring also in freshwater (reviewed by Foissner et al. 1994). The present study adds

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three taxa and can thus meaningfully discuss the features used for species discrimination, for instance, body size which has low variability coefficients and is thus a useful character.

Many microthoracids have the somatic ciliature strongly reduced; thus, the homologization of the ciliary patterns is difficult, needing special structures and/or ontogenetic data. We shall show that the ciliary pattern of *Drepanomonas* is homologous to that of *Leptopharynx* because we could homologize the postoral complex, a structure with a special ontogenesis (Omar and Foissner 2012b).

Material and Methods

For details on samples and locations, see the individual species descriptions. All were reactivated from the resting cysts of air-dried soil samples by the non-flooded Petri dish method (NFPM). Briefly, the NFPM involves placing 50–500 g litter and soil in a Petri dish (13–18 cm wide, 2–3 cm high) and saturating, but not flooding it, with distilled water. Such a culture is analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28; for a detailed description of the NFPM, see Foissner et al. (2002).

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast optics. The infraciliature and various cytological structures were revealed by protargol impregnation and the Klein–Foissner silver nitrate technic (Foissner 1991); *Drepanomonas hymenofera venezuelensis* was investigated also with the scanning electron microscope (SEM). Counts and measurements on silvered specimens were conducted at a magnification of 1000×. The "total number of basal bodies" excludes those of the adoral membranelles, which are difficult to count. In vivo measurements were performed at magnifications of 40–1000×. For kinety designation and numbering, see Fig. 5. The data available suggest classifying the microthoracid body length as (in vivo average): very small (10–19 μm), small (20–29 μm), middle-sized (30–39 μm), large (40–49 μm), and very large (≥50 μm). Terminology is according to Omar and Foissner (2012b). Drawings of live specimens were based on free-hand sketches and micrographs, while those of impregnated cells were made with a drawing device.

Results

Drepanomonas hymenofera (Horváth 1956) nov. comb.

Improved diagnosis. Size in vivo about 50 × 20 μm or 40 × 18 μm. Body semi-ellipsoidal with convex dorsal margin and flat but highly structured ventral side. Right side basically smooth, left with a shallow, narrow furrow in middle third or with a distinct, narrow furrow whole body length. Somatic kinety 3 with basal bodies throughout or with a break in middle third. Kinety 4 with narrow vs. very wide break in middle third. Kinety 6 only partially ciliated. On average a total of about 100 basal bodies. Oral apparatus slightly above mid-body.

Drepanomonas hymenofera venezuelensis nov. subspec. (Figs 1–29; Tables 1 and 2)

Diagnosis. Size in vivo about 50 × 20 μm. Left side with shallow, narrow furrow in middle third of body. Somatic kinety 3 with basal bodies throughout. Kinety 4 with narrow break in middle third.

Type locality. Soil and litter under a large tree with leguminose understorey in the floodplain of the Lower Orinoco River near to the village of Cabruta, Venezuela, N7°38′ W66°14′.

Type material. One holotype slide with protargol-impregnated specimens and eight paratype slides with protargol-impregnated and Klein–Foissner silver nitrate-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI), reg. no. 2012/116–125. The holotype (Figs 8 and 9) and important paratype specimens have been marked by black ink circles on the coverslip.

Etymology. Named after the country in which it was discovered.

Description. Size in vivo 40–60 × 15–25 μm, usually about 50 × 20 μm, as calculated from some in vivo measurements and the morphometric data (Table 1), assuming 15 and 25% preparation shrinkage in protargol and SEM preparations, respectively. Body semi-ellipsoidal to slenderly semi-ellipsoidal, length:width ratio 2.3:1 in live micrographs and protargol preparations, 2.1:1 in silver nitrate-impregnated cells, and 2.4:1 in SEM preparations; usually slightly wider in posterior than anterior half. Laterally flattened up to 3:1, right side flat, left slightly convex (Figs 1, 2, 6, 7, 12–16, 25–27; Table 1). Nuclear apparatus in or near mid-body, slightly right of body midline, i.e., in curve formed by oral basket. Macronucleus about 8 μm across in vivo and in protargol preparations, globular to very broadly ellipsoidal, with many peripheral nucleoli; micronucleus near or attached to ventral side of macronucleus, globular (Figs 1, 9, 12, 15, 16, 19; Table 1). Contractile vacuole posterior to and slightly dorsal of buccal cavity, with tube recognizable in protargol preparations and extending into buccal cavity posterior to adoral membranelles (Figs 1, 8, 14, 19; Table 1). Cytopyge posterior and slightly left of contractile vacuole in lateral view, usually forming a blister containing some food remnants (e.g., bacterial spores); in silver nitrate preparations represented by a thick, short silverline posterior to buccal cavity; in SEM micrographs appearing as a slightly oblique concavity posterior to oral cavity (Figs 10, 11, 16, 23, 25, 27–29). Extrusomes left of somatic kineties and posterior to preoral kineties, lenticular, not as compact as in other microthoracids (e.g., *Leptopharynx costatus*), i.e., with fluffy centre, about

Table 1. Morphometric data on *Drepanomonas hymenofera venezuelensis* (DHV), *D. hymenofera hymenofera* (DHH), and *D. vasta* (DVA).

Characteristics[a]	Species	$\bar{x}$	*M*	SD	SE	CV	Min	Max	*n*
Body, length in protargol preparations	DHV	40.8	42.0	2.3	0.5	5.5	36.0	44.0	21
	DHH	35.3	35.0	1.5	0.3	4.2	32.0	37.0	21
	DVA	27.6	28.0	1.5	0.3	5.3	24.0	31.0	21
Body, width in protargol preparations	DHV	18.0	18.0	1.0	0.2	5.4	16.0	20.0	21
	DHH	15.6	16.0	0.9	0.2	5.9	14.0	17.0	21
	DVA	14.3	14.0	1.0	0.2	6.7	12.0	16.0	21
Body length:width, ratio in protargol preparations	DHV	2.3	2.3	0.1	0.1	4.2	2.1	2.4	21
	DHH	2.3	2.3	0.1	0.1	5.5	2.1	2.6	21
	DVA	1.9	1.9	0.1	0.1	4.5	1.8	2.1	21
Body, length in dry silver nitrate preparations	DHV	49.2	49.0	2.2	0.5	4.5	45.0	55.0	21
	DHH	40.1	41.0	2.4	0.5	5.9	36.0	44.0	21
	DVA	32.8	33.0	2.7	0.6	8.3	28.0	41.0	21
Body, width in dry silver nitrate preparations	DHV	23.1	23.0	2.1	0.5	9.1	20.0	27.0	21
	DHH	18.7	19.0	1.5	0.3	8.0	16.0	21.0	21
	DVA	18.1	18.0	1.8	0.4	10.1	15.0	24.0	21
Body length:width, ratio in dry silver nitrate preparations	DHV	2.1	2.1	0.2	0.2	8.7	1.9	2.5	21
	DHH	2.2	2.1	0.1	0.1	5.1	2.0	2.4	21
	DVA	1.8	1.8	0.1	0.1	5.1	1.7	2.1	21
Body, length in scanning micrographs	DHV	35.3	35.0	2.2	0.5	6.2	32.0	40.0	16
Body, width in scanning micrographs	DHV	14.9	15.0	0.9	0.2	5.8	14.0	17.0	13
Body length:width, ratio in scanning micrographs	DHV	2.4	2.4	0.2	0.1	6.5	2.1	2.6	13
Body length:width, ratio in vivo (from micrographs)	DHV	2.3	2.3	0.1	0.1	4.7	2.1	2.5	15
Anterior body end to adoral membranelles, distance	DHV	16.0	16.0	1.1	0.2	7.0	14.0	18.0	21
	DHH	13.8	14.0	1.2	0.3	8.5	12.0	16.0	21
	DVA	12.9	13.0	0.7	0.2	5.7	11.0	14.0	21
Body length: anterior body end to adoral membranelles, ratio (protargol)	DHV	2.6	2.6	0.2	0.1	6.8	2.2	2.9	21
	DHH	2.6	2.5	0.2	0.1	6.1	2.3	2.9	21
	DVA	2.2	2.2	0.1	0.1	3.2	2.0	2.3	21
Anterior body end to macronucleus, distance	DHV	15.2	15.0	1.5	0.3	9.7	13.0	19.0	21
	DHH	11.3	11.0	1.3	0.3	11.3	9.0	14.0	21
	DVA	10.2	10.0	0.7	0.2	6.8	9.0	11.0	21
Macronucleus, length	DHV	7.9	8.0	0.6	0.1	7.3	7.0	9.0	21
	DHH	7.5	8.0	0.5	0.1	6.8	7.0	8.0	21
	DVA	5.5	5.0	0.6	0.1	11.0	5.0	7.0	21
Macronucleus, width	DHV	7.3	7.0	0.6	0.1	8.8	6.0	9.0	21
	DHH	5.8	6.0	0.7	0.2	11.7	5.0	7.0	21
	DVA	4.6	5.0	–	–	–	4.0	5.0	21
Micronucleus, diameter	DHV	2.1	2.0	–	–	–	2.0	3.0	21
	DHH	1.9	2.0	–	–	–	1.5	3.0	21
	DVA	2.0	2.0	–	–	–	1.5	2.5	21
Anterior body end to excretory pore of contractile vacuole, distance	DHV	19.4	20.0	1.0	0.2	5.0	17.0	21.0	21
	DHH	16.4	17.0	1.1	0.2	6.6	14.0	18.0	21
	DVA	15.4	15.0	0.9	0.2	5.6	13.0	17.0	21
Oral basket, width	DHV	2.7	3.0	–	–	–	2.0	3.0	21
	DHH	3.0	3.0	0.0	0.0	0.0	3.0	3.0	3

Table 1 (*Continued*)

Characteristics[a]	Species	$\bar{x}$	*M*	SD	SE	CV	Min	Max	*n*
	DVA	Not recognizable							
Somatic kineties, number	DHV	9.0	9.0	0.0	0.0	0.0	9.0	9.0	21
	DHH	9.0	9.0	0.0	0.0	0.0	9.0	9.0	21
	DVA	9.0	9.0	0.0	0.0	0.0	9.0	9.0	21
Somatic kinety 1, number of dikinetids	DHV	5.2	5.0	0.5	0.1	9.9	4.0	6.0	21
	DHH	6.1	6.0	–	–	–	6.0	7.0	21
	DVA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Somatic kinety 1, number of monokinetids	DHV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21
	DHH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21
	DVA	7.8	8.0	0.6	0.1	7.7	7.0	9.0	21
Somatic kinety 2, number of dikinetids	DHV	2.7	3.0	–	–	–	2.0	4.0	21
	DHH	2.6	3.0	–	–	–	2.0	3.0	21
	DVA	3.1	3.0	0.4	0.1	14.1	2.0	4.0	21
Somatic kinety 2, number of monokinetids	DHV	4.6	5.0	1.5	0.3	32.1	2.0	7.0	21
	DHH	3.4	3.0	0.8	0.2	23.6	2.0	5.0	21
	DVA	3.9	4.0	0.4	0.1	11.2	3.0	5.0	21
Somatic kinety 3, number of dikinetids	DHV	8.0	8.0	0.7	0.2	8.8	7.0	10.0	21
	DHH	6.1	6.0	0.6	0.1	9.8	5.0	7.0	21
	DVA	5.5	5.0	0.6	0.1	11.0	5.0	7.0	21
Somatic kinety 3, number of monokinetids	DHV	5.6	6.0	1.2	0.3	20.7	3.0	7.0	21
	DHH	5.1	5.0	1.3	0.3	24.8	3.0	8.0	21
	DVA	5.4	5.0	0.9	0.2	16.0	4.0	7.0	21
Somatic kinety 4, number of dikinetids	DHV	3.1	3.0	–	–	–	3.0	4.0	21
	DHH	3.0	3.0	–	–	–	2.0	3.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic kinety 4, number of monokinetids	DHV	7.2	7.0	0.5	0.1	7.1	6.0	8.0	21
	DHH	4.0	4.0	0.3	0.1	7.9	3.0	5.0	21
	DVA	10.0	10.0	0.0	0.0	0.0	10.0	10.0	21
Somatic kinety 5, number of dikinetids	DHV	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DHH	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Somatic kinety 5, number of monokinetids	DHV	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
	DHH	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
	DVA	5.0	5.0	0.0	0.0	0.0	5.0	5.0	21
Somatic kinety 6, number of monokinetids (does not have dikinetids)	DHV	7.5	7.0	0.8	0.2	10.0	6.0	9.0	21
	DHH	8.0	8.0	0.0	0.0	0.0	8.0	8.0	21
	DVA	8.0	8.0	0.0	0.0	0.0	8.0	8.0	21
Somatic kinety 7, number of monokinetids (does not have dikinetids)	DHV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DHH	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DVA	3.1	3.0	–	–	–	3.0	4.0	21
Somatic kinety 8, number of dikinetids in anterior portion	DHV	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DHH	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DVA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Somatic kinety 8, number of monokinetids in anterior portion	DHV	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DHH	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21

Table 1 (*Continued*)

Characteristics[a]	Species	$\bar{x}$	*M*	SD	SE	CV	Min	Max	*n*
Somatic kinety 9, number of monokinetids in posterior portion	DHV	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DHH	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DVA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Preoral kineties, number	DHV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DHH	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DVA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Preoral kinety 1, number of dikinetids (does not have monokinetids)	DHV	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DHH	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	DVA	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Preoral kinety 2, number of dikinetids	DHV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DHH	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DVA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Preoral kinety 2, number of monokinetids	DHV	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DHH	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Preoral kinety 3, number of dikinetids	DHV	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DHH	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	DVA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Preoral kinety 3, number of monokinetids	DHV	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DHH	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Left row of postoral complex, number of monokinetids[b]	DHV	4.1	4.0	–	–	–	4.0	5.0	21
	DHH	4.1	4.0	0.0	0.0	0.0	4.0	4.0	21
	DVA	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Right row of postoral complex, number of monokinetids[c]	DHV	1.1	1.0	–	–	–	1.0	2.0	21
	DHH	1.1	1.0	0.0	0.0	0.0	1.0	1.0	21
	DVA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Basal bodies, total number[d]	DHV	102.9	103.0	2.1	0.5	2.1	98.0	107.0	21
	DHH	95.8	96.0	1.0	0.2	1.0	94.0	97.0	21
	DVA	99.4	99.0	1.0	0.2	1.0	98.0	102.0	21

[a] Data based, if not mentioned otherwise, on protargol-impregnated, randomly selected specimens from non-flooded Petri dish cultures. Measurements in μm. CV, coefficient of variation in %; *M*, median; Max, maximum; Min, minimum; *n*, number of specimens investigated; SD, standard deviation; SE, standard error of mean; $\bar{x}$, arithmetic mean.

[b] This is the posterior portion of somatic kinety 8.

[c] This is the middle portion of somatic kinety 9.

[d] Except of basal bodies of adoral membranelles and anterior portion of kinety 9, which is recognizable only in dividers.

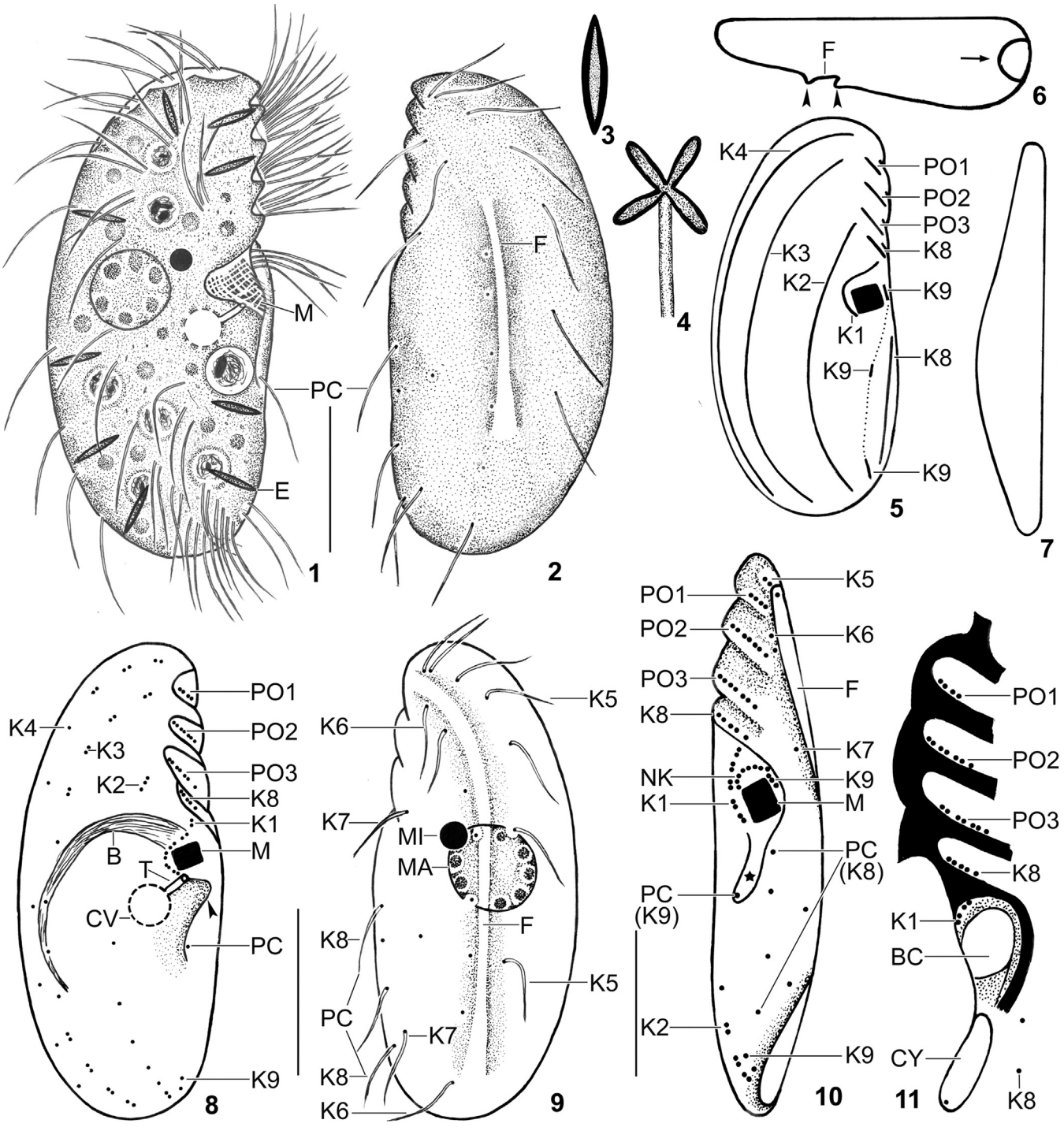
5 × 1.5 μm in size when resting and with four elongate ellipsoidal arms when exploded (Figs 1, 3, 4, 15, 18). Cytoplasm colourless, contains some lipid droplets 1–2 μm across and 3–8 μm-sized food vacuoles with fluffy contents and/or bacterial spores (Figs 1, 12–16). Fed mainly on spore-forming bacteria. Swims rather rapidly by rotation about main body axis and creeps vividly on microscope slides (Table 2).

Cortex rigid and glossy, contains or is underlain by countless, minute ellipsoidal structures sometimes recognizable in vivo (Fig. 13) and in SEM micrographs (*D. revoluta*, Foissner et al. 1994). Right side cortex smooth, except of distinct crenellation in dikinetidal anterior portion of kinety 4 and of ciliary pits in general (Figs 1, 12, 14, 25). Middle third of left side cortex with shallow, narrow furrow limited by inconspicuous ridges; furrow distinctly flattens to body ends, not recognizable in one third of specimens (Figs 2, 6, 13, 17, 26) and sometimes more distinct in protargol preparations than in vivo and in the SEM (Fig. 9). Ventral side dominated by furrows and ridges associated, inter alia, with preoral kineties and oral apparatus (Figs 10–12, 25–29). Preoral kineties and anterior segment of kinety 8 in distinct furrows, producing five conspicuous teeth; ridge posterior to anterior segment of kinety 8 curves around left margin of oral opening; right mouth margin produced by right side cortex, sigmoidal with convex part covering oral apparatus laterally (Figs 1, 10–12, 25, 28). Mouth opening obovate,

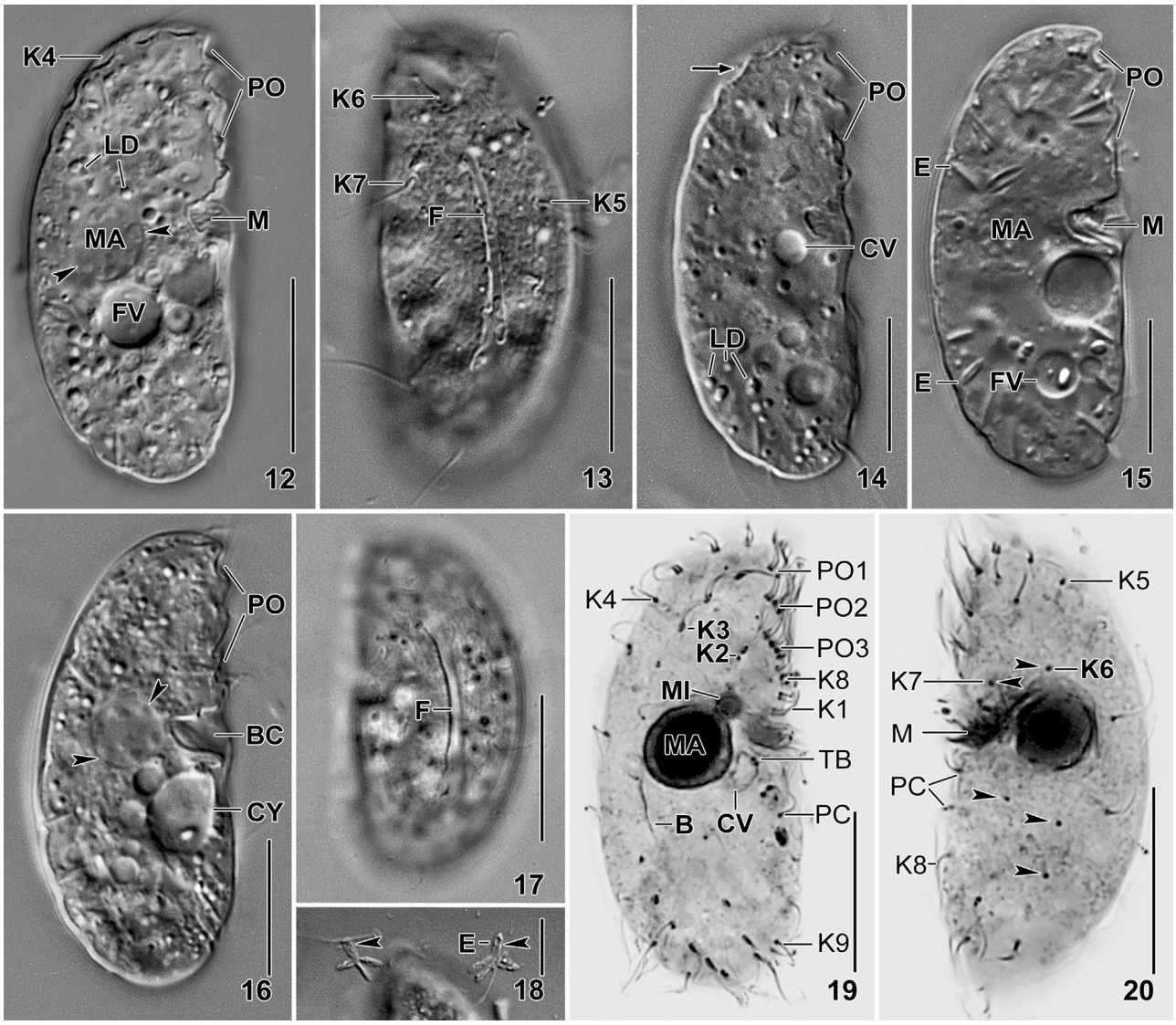
Table 2. Comparison of main features in various species of *Drepanomonas*.

Characteristics (data sources)	*D. hymenofera venezuelensis*[a]	*D. hymenofera hymenofera*[a]	*D. vasta*[a]	*D. revoluta* (Foissner 1987; Foissner et al. 1994)	*D. sphagni* (Foissner 1987)	*D. pauciciliata* (Foissner 1987)	*D. exigua* (Foissner 1999)	*D. muscicola* (Foissner 1979)
Body, length (μm)[b]	36–44 (41)	32–37 (35)	24–31 (28)	18–21 (20)	18–28 (22)	20–28 (22)	17–23 (20)	27–35 μm[e]
Body, width (μm)[b]	16–20	14–17	12–16	8–10	8–12	10–13	9–11	?
Left side ridges	Indistinct, narrow	Distinct, narrow	Distinct, wide	Distinct, wide	Indistinct, narrow	Distinct, narrow	Distinct, wide	Absent
Right side ridges	Absent	Absent	Present	Present	Absent	Absent	Present	Absent
Spines	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent
Oral apparatus, position	Slightly anterior to mid-body	Slightly anterior to mid-body	Mid-body	Mid-body	Slightly anterior to mid-body	Mid-body	Mid-body	Posterior to mid-body
Basal body spacing in left row of postoral complex	Wide	Wide	Wide	Rather narrow	Wide	Very narrow	Very narrow	Very narrow
Kinety 4, dikinetids in anterior half	3	3	1	3–4	4	2	3	4
Kinety 6, ciliation	Partially	Partially	Partially	Partially	Fully	Fully	Partially	Partially
Kinety 7, number of monokinetids	3	3	3	3	2? 4?	1	3	?
Basal bodies, total number	98–107 (103)	94–97 (96)	98–102 (99)	77–83 (80)	82–86 (84)	60–70 (65)	69–75 (72)	85
Arrangement of kineties 2 and 3[c]	Slightly converging (1.5:1)	Slightly converging (1.5:1)	Strongly converging (2.5:1)	Slightly converging (1.3:1)	Slightly converging (1.6:1)	Slightly converging (1.1:1)	Slightly converging (1.6:1)	Slightly converging (1.5:1)
Movement[d]	Ordinary	Ordinary	Only swimming	Ordinary	Ordinary	Ordinary	Ordinary	Ordinary
Specimens investigated, number[b]	21	21	21	12	15	12	13	Some

[a] For details, see text and Table 1. Arithmetic means in parentheses.
[b] After protargol impregnation.
[c] The ratio between the width of the anterior and posterior end of the area between kineties 2 and 3 in parentheses.
[d] Swimming and creeping on solid surfaces.
[e] From live observation.



Figs 1–11. *Drepanomonas hymenofera venezuelensis* from life (1–4, 6, 7), after protargol impregnation (5, 8–10), and redrawn from scanning electron micrographs (11). **1, 2.** Right and left side view of representative specimens, showing the smooth right side, the inconspicuous left side furrow between kineties 5 and 6, and the five distinct teeth in the preoral region; length 50 μm. **3, 4.** A resting (~5 × 1.5 μm) and an exploded extrusome. **5.** Kinety designation and numbering according to the ontogenetic data; for left side, see Fig. 9. **6.** Transverse section in mid-body, showing the ridge and furrow pattern (arrowheads) of the convex left side. The arrow marks the concave buccal cavity. **7.** Dorsal view showing the convex left side. **8, 9.** Right and left side view of holotype specimen, length 43 μm. Arrowhead marks the right mouth margin partially covering the cytopyge. Dots in (9) indicate the non-ciliated basal bodies in kineties 6–8. Note the indistinct furrow between left side kineties 5 and 6. **10.** Ventral view of a paratype specimen, showing the obliquely arranged preoral kineties, the oral basal bodies, and the postoral complex. The asterisk marks the cytopyge concavity. **11.** Ridge pattern (black) of ventral side. The stippled area is less deepened than buccal cavity. B, oral basket; BC, buccal cavity; CV, contractile vacuole; CY, cytopyge concavity; E, extrusomes; F, furrow; K1–9, somatic kineties; M, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; PC, postoral complex; PO1–3, preoral kineties; T, excretory tube. Scale bars 15 μm (1, 2, 8, 9) and 10 μm (10).

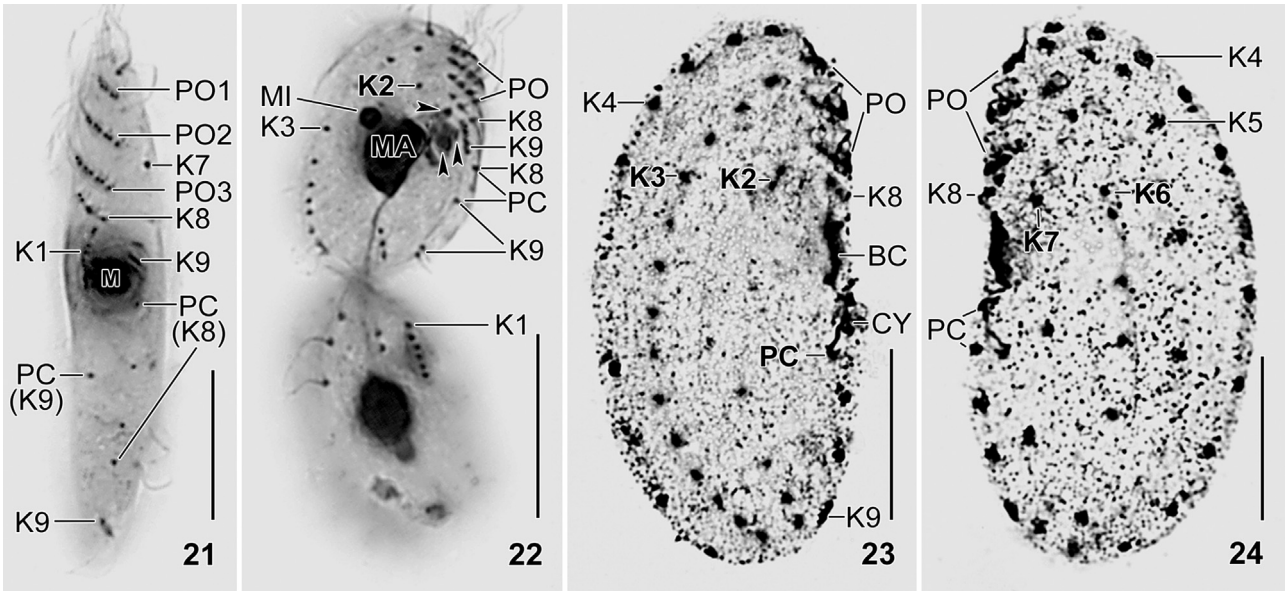


Figs 12–20. *Drepanomonas hymenofera venezuelensis* from life (12–18) and after protargol impregnation (19, 20). **12, 14–16.** Right side views of freely motile specimens, showing the variability of body shape; the deep buccal cavity; the extrusomes (15); the crenellation in the anterior portion of kinety 4 (12; 14, arrow); and the five teeth made by the furrows in the preoral region (12). Arrowheads mark the peripheral nucleoli of the macronucleus. **13, 17.** Left side views, showing the narrow left side furrow. The cortex is underlain by countless, minute structures (13). **18.** Exploded extrusomes, showing the ellipsoidal arms (arrowheads). **19, 20.** Right and left side view, showing the ciliary and nuclear pattern. The arrowheads in (20) mark the barren monokinetids in kineties 6 and 7. B, oral basket; BC, buccal cavity; CV, contractile vacuole; CY, cytopyge; E, extrusomes; F, furrow; FV, food vacuoles; K1–9, somatic kineties; LD, lipid droplets; M, adoral membranelles; MA, macronucleus; MI, micronucleus; PC, postoral complex; PO(1–3), preoral kineties; TB, base of tube of contractile vacuole. Scale bars 20 μm (12, 13, 17), 15 μm (14–16, 19, 20), and 10 μm (18).

forms key-hole-shaped pattern with elliptical concavity containing cytopyge and single cilium of right part of postoral complex; both separated by anterior margin of cytopyge (Figs 10, 11, 25, 28, 29). Silverline pattern as described by Foissner et al. (2011) in *Leptopharynx bromelicola*, that is, cortex studded with minute, argyrophilic granules and some silverline meshes between preoral kineties (Figs 23, 24).

Somatic cilia 8–10 μm long in protargol preparations and SEM micrographs. Invariably nine somatic and three preoral kineties with a total of 103 basal bodies on average. Kineties 3, 4 and 6 bipolar, while 1, 2, 5 and 7–9 shortened anteriorly and/or posteriorly; kineties 1–4 on right side of cell, 5–7 on left, and kineties 7–9 on ventral side (Figs 1, 2, 5, 8–11, 13, 19–21, 23–29; Table 1).

Kinety 1 very short, extends at right margin of oral cavity, composed of 4–6 narrowly spaced, usually ciliated dikinetids (Figs 5, 8, 19, 28). Kinety 2 begins in second quarter of cell with a single dikinetid and a single monokinetid, both ciliated and spaced so narrowly that a highly characteristic trikinetid is formed, resembling that found in *D. sphagni* (Figs 8, 19, 25); followed by a wide break and an average of five widely spaced, ciliated monokinetids and 1–3



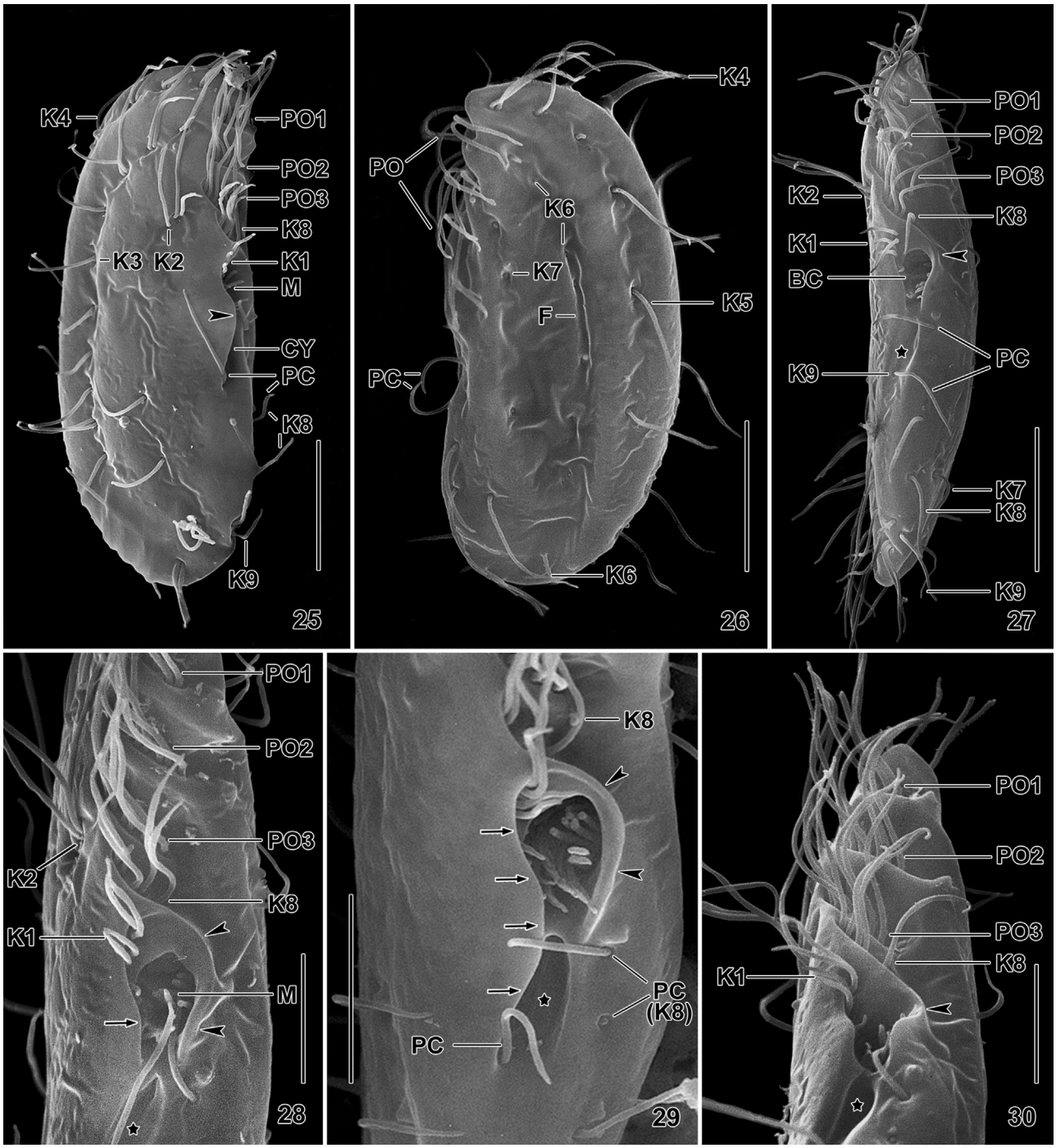
Figs 21–24. *Drepanomonas hymenofera venezuelensis* after protargol (21, 22) and Klein–Foissner silver nitrate impregnation (23, 24). **21.** Ventral view of a paratype specimen, showing the slightly convex left side, the oblique preoral kineties, and the postoral complex. Kinety 8 consists of two portions and kinety 9 consists of three portions. **22.** A late divider, showing the three adoral membranelles in the proter (arrowheads), the two portions of somatic kinety 8, and the three portions of kinety 9. Somatic kinety 1 is likely composed of dikinetids, and the postoral complex consists of the posterior portion of kinety 8 and the middle portion of kinety 9. **23, 24.** Right and left side view, showing the ciliary pattern and the dense, argyrophilic granulation. BC, buccal cavity; CY, cytopyge; K1–9, somatic kineties; M, adoral membranelles; MA, macronucleus; MI, micronucleus; PC, postoral complex; PO(1–3), preoral kineties. Scale bars 10 μm (21) and 15 μm (22–24).

ciliated dikinetids at posterior end. Kinety 3 composed of widely spaced, ciliated dikinetids in anterior and posterior third and of widely spaced, ciliated monokinetids in middle third (Figs 8, 19, 23, 25). Kineties 4 and 5 limit dorsal margin of right and left body side, respectively; kinety 4 composed of three widely spaced, ciliated dikinetids in anterior portion, followed by two widely spaced, ciliated monokinetids separated by a one-kinetid-wide break from 4–6 posterior monokinetids (Figs 8, 12, 19); kinety 5 composed of a single, ciliated dikinetid followed by five widely spaced, ciliated monokinetids, ends near posterior third of body (Figs 9, 20, 26). Kinety 6 composed of six to nine widely spaced monokinetids, usually only two and one kinetid ciliated in anterior and posterior end of row, respectively (Figs 9, 20, 26). Kinety 7 begins in second third of body, consists of three (rarely of four) widely spaced monokinetids, middle kinetid usually barren. Kinety 8 consists of two portions (Figs 5, 10, 11, 28, 29): anterior portion posterior and very similar to preoral kineties, consists of two ciliated dikinetids and one ciliated monokinetid at left (posterior) end; posterior portion composed of four widely spaced monokinetids, the second of which usually barren (see postoral complex). Kinety 9 consists of three portions (Figs 5, 10, 19, 21, 22, 25, 27, 29): anterior portion left of adoral membranelles and composed of few, likely barren monokinetids recognizable only in dividers (Fig. 22) and protargol-impregnated, appropriately oriented specimens (Figs 10, 21); middle portion a single, ciliated monokinetid in posterior end of cytopyge concavity (see postoral complex and Figs 10, 19); posterior portion composed of two ciliated monokinetids at rear cell margin (Figs 10, 19, 25).

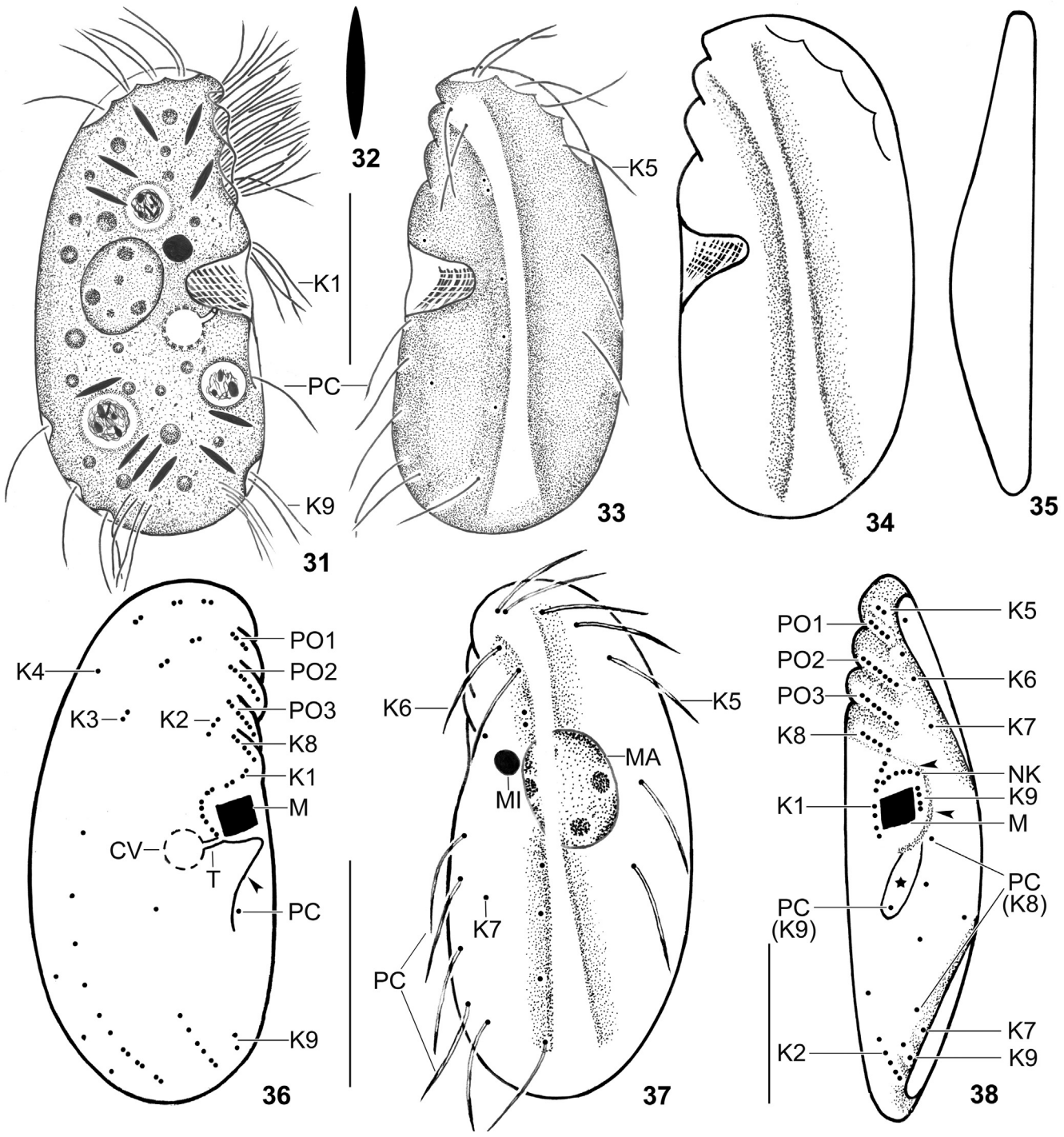
Three oblique preoral kineties on ventral side, composed of ciliated dikinetids and a ciliated monokinetid at left end of kineties 2 and 3. Postoral complex composed of monokinetidal posterior portion of kinety 8 and the single, ciliated monokinetid in mid of kinety 9 (Figs 1, 5, 8–12, 14, 19–21, 23–27, 29; Table 1).

Oral apparatus slightly anterior to mid-body. Buccal cavity distinctly concave when seen laterally (Figs 1, 8, 10, 15, 16, 20, 21, 25, 27–29; Table 1). Two or three adoral membranelles. Membranelle 1 distinctly smaller than membranelles 2 and 3, recognizable only in dividers (Fig. 22); membranelles 2 and 3 close together, obliquely arranged to main body axis, compact, details thus remain obscure. Oral basket recognizable only in deeply impregnated specimens, about 3 μm wide at distal end occupied by nasse kinetosomes, extends to body midline where it curves posteriorly and narrows gradually, forming a sickle-shaped tube (Figs 8, 19).

Occurrence and ecology. As yet found only at type locality, that is, in alluvial soil from the floodplain of the Orinoco River in Venezuela. Soil slightly acidic (pH 5.2), loamy, with a thin litter layer overgrown by fungal hyphae. The species appeared one month after rewetting the sample and could be cultivated in Eau de Volvic (French mineral water) enriched with squashed wheat grains.



Figs 25–30. *Drepanomonas hymenofera venezuelensis* (25–29) and *Drepanomonas* sp. (30) in the scanning electron microscope. **25, 26.** Ventrolateral and left side view, showing the ciliary pattern, the convex right mouth margin (arrowhead), and the inconspicuous left side furrow close to kinety 6. The furrows in the preoral region are closed at the right end by the right side cortex (25). **27–29.** Ventral views, showing the slightly convex left side, the furrows accompanying the preoral kineties closed at right by the right side cortex, and the obovate oral opening. Arrowheads denote the ridge which extends posterior to kinety 8 and along left margin of the oral opening. The arrows mark the convex right mouth margin. The oral opening and the cytopyge concavity (asterisks) form a key-hole-shaped pattern and are separated from each other by the anterior margin of the cytopyge. **30.** Ventral view of *Drepanomonas* sp. (possibly *revoluta*) found in the same sample as *D. hymenofera venezuelensis*. The arrowhead marks the left mouth margin which is thinner and less curved along kinety 8 than in *D. hymenofera venezuelensis*. BC, buccal cavity; CY, cytopyge concavity; F, furrow; K1–9, somatic kineties; M, adoral membranelles; PC, postoral complex; PO(1–3), preoral kineties. Scale bars 10 μm (25–27) and 5 μm (28–30).



Figs 31–38. *Drepanomonas hymenofera hymenofera* from life (31–35) and after protargol impregnation (36–38). **31, 33, 34.** Right and left side views of representative specimens, showing the variability in body shape, the flat right side, the narrow but distinct left side furrow and ciliation, and the crenellation in the anterior portion of kineties 4 and 5; length about 40 μm. **32.** A resting extrusome, about 4 μm long. **35.** Dorsal view showing the strong cell flattening and the slightly convex left side. **36, 37.** Right and left side view of the main voucher specimen, length 34 μm, showing the semi-ellipsoidal body shape, the ciliation of the left side, and the distinct furrow extending between kineties 5 and 6. The arrowhead marks the right mouth margin partially covering the cytopyge. Dots in (37) indicate the non-ciliated basal bodies in kineties 6 and 7. The oral basket did not impregnate. **38.** Ventral view showing the convex left side, the obliquely arranged preoral kineties, the anterior portion of kineties 8 and 9, the oral basal bodies, and the postoral complex composed of the posterior portion of kinety 8 and the middle portion of kinety 9. The asterisk marks the cytopyge concavity. The arrowheads indicate the ridge left of the oral opening. CV, contractile vacuole; K1–9, somatic kineties; M, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes at distal end of oral basket; PC, postoral complex; PO1–3, preoral kineties; T, excretory tube of contractile vacuole. Scale bars 10 μm (38) and 15 μm (31, 33, 36, 37).

Drepanomonas hymenofera hymenofera (Horváth 1956) (Figs 31–46, 61–64; Tables 1 and 2)

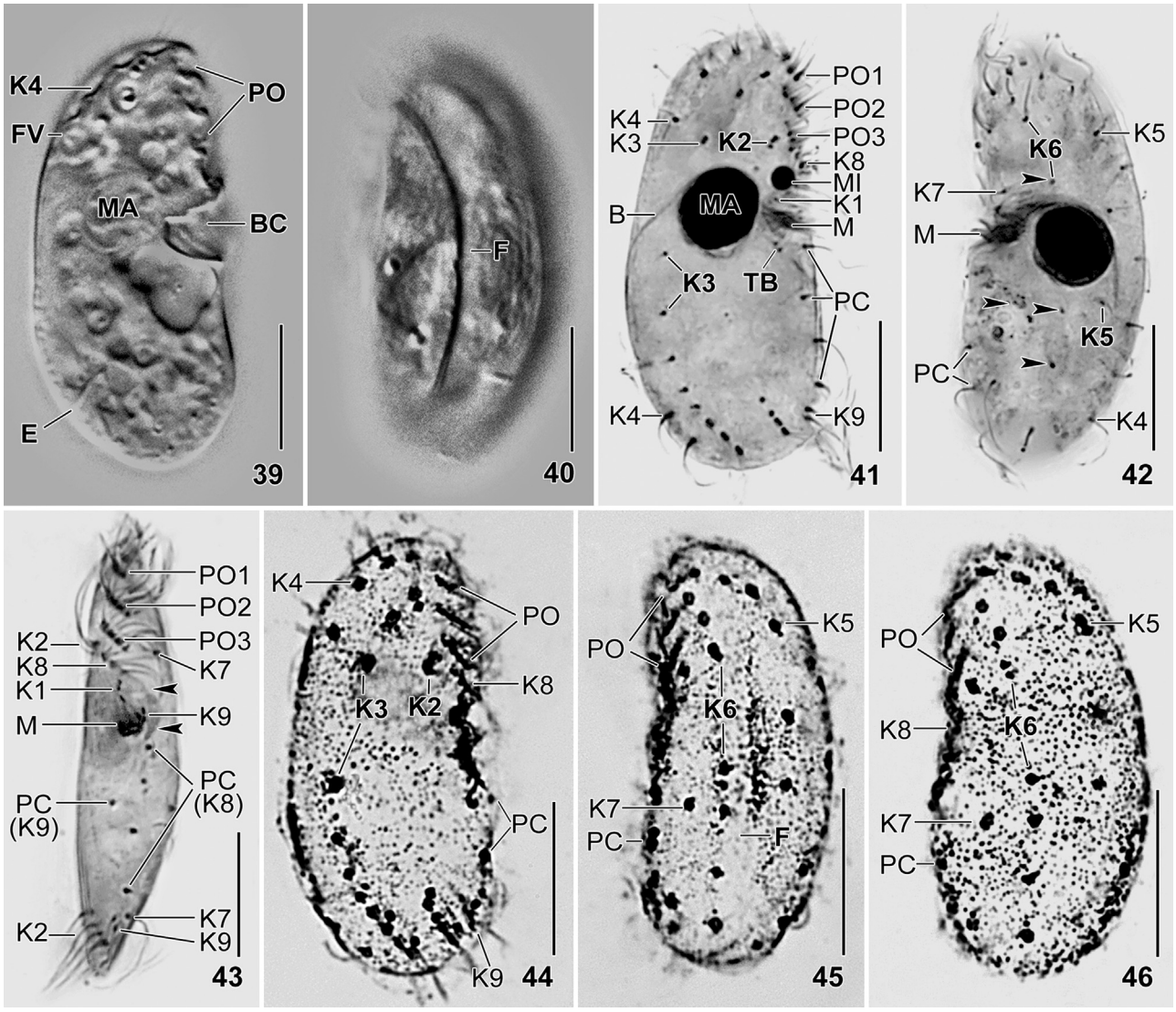
Improved diagnosis. Size in vivo about 40 × 18 μm. Left side with distinct, narrow furrow whole body length. Somatic kineties 3 and 4 with a one-kinetid-wide break and with a very wide break in middle third, respectively.

Material investigated. Large sedge peat (*Carex rostrata*) with *Eriophorum angustifolium* and *Comarum palustre* in the Thingvellir National Park, Southwest Iceland, N64°15′W21°4′.

Voucher material. Six slides with protargol-impregnated specimens and three slides with Klein–Foissner silver nitrate-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI), reg. no. 2012/126–134. The main voucher (Figs 36, 37) and important other specimens have been marked by black ink circles on the coverslip.

Remarks. The type locality is the sandy soil of a reservoir of the Tisza River in Hungary. We did not neotypify this species with the Iceland population because it should be possible to find *D. hymenofera* in the type locality region.

Description. We do not describe the nominotypical subspecies in detail because it matches *D. hymenofera*



Figs 39–46. *Drepanomonas hymenofera hymenofera* from life (39, 40), after protargol impregnation (41–43), and in Klein–Foissner silver preparations (44–46). **39, 40.** Right and left side view, showing the rather large buccal cavity and the distinct left side furrow. The cortex is underlain by minute structures (40). **41, 42.** Right and left side view, showing the ciliary and nuclear pattern. **43.** Ventral view, showing the preoral kineties and the postoral complex. Arrowheads mark ridge left of oral opening. Kinety 8 consists of two portions, kinety 9 of three. **44–46.** Right and left side views, showing the ciliary pattern and the argyrophilic granulation. B, oral basket; BC, buccal cavity; E, extrusome; F, furrow; FV, food vacuole; K1–9, somatic kineties; M, adoral membranelles; MA, macronucleus; MI, micronucleus; PC, postoral complex; PO(1–3), preoral kineties; TB, base of tube of contractile vacuole. Scale bars 10 μm (39–43) and 15 μm (44–46).

venezuelensis, except of the features mentioned in the diagnosis. Further, it is documented by a multitude of figures. Two further but minor differences should be mentioned: (i) extrusomes about 4 μm long and as compact as, e.g., in *Leptopharynx costatus*, (ii) swims slowly, frequently staying motionless on microscope slide.

Occurrence and ecology. To date found at type locality and in the Thingvellir National park, Southwest Iceland as described above.

Drepanomonas vasta Foissner and Omar nov. spec. (Figs 47–60; Tables 1 and 2)

Diagnosis. Size in vivo about 35 × 18 μm. Body semi-ellipsoidal with distinctly convex dorsal side and straight ventral side; transverse shape cuneate because hardly flattened ventrally and moderately dorsally. Right side with two conspicuous ridges right of the distinctly converging kineties 2 and 3 commencing on right half of ventral side; left side with two more or less distinct ridges lining the wide area between kineties 5 and 6. Swims continuously and appears slightly helical at low magnification, very likely caused by the special arrangement of kinety ridges 2 and 3 and the cuneate transverse body shape. Kinety 4 with one dikinetid anteriorly, kinety 6 only partially ciliated. A total of 99 basal bodies on average.

Type locality. Mud from a tree hole in Styria, Austria, N47°15′ E14°53′.

Type material. One holotype and eight paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI), reg. no. 2012/135–144. The holotype (Figs 51, 52) and important paratype specimens have been marked by black ink circles on the coverslip. Unfortunately, the silver nitrate slides (Figs 59, 60) bleached due to insufficient fixation.

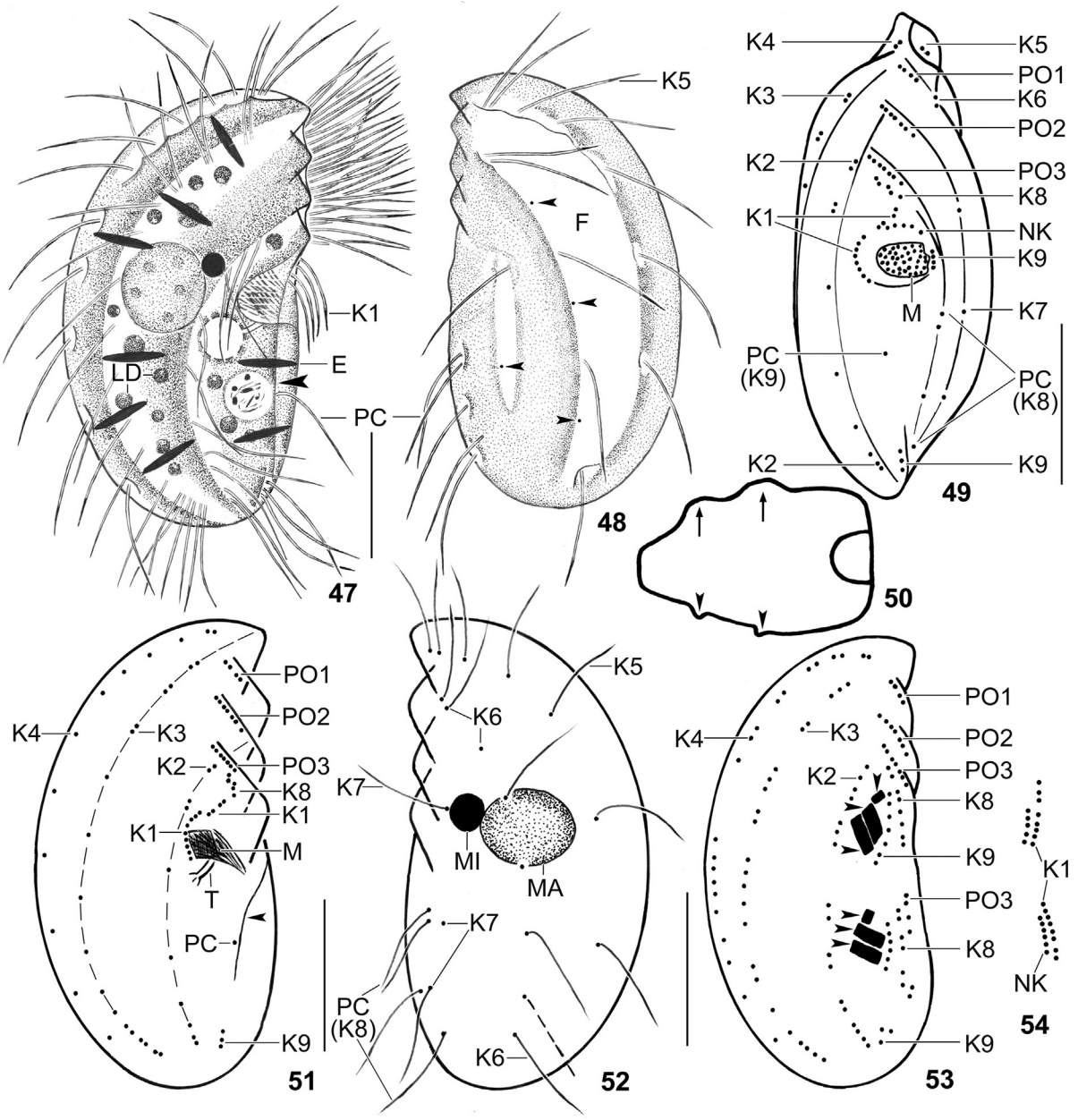
Etymology. The Latin adjective *vasta* refers to the thick body.

Description. Size in vivo 28–40 × 15–20 μm, usually about 35 × 18 μm, as calculated from some measurements of live specimens and values shown in Table 1, assuming 15–20% preparation shrinkage. Body semi-ellipsoidal with a length:width ratio of 1.8–2.1:1, on average 1.9:1; hardly flattened ventrally and moderately dorsally, producing a cuneate transverse shape (Fig. 50) contributing to the somehow helical appearance caused by the distinctly converging and ventrally commencing kinety ridges 2 and 3. Dorsal margin distinctly convex, ventral margin flat, anterior end tapered, posterior widely rounded, body thus wider in posterior than anterior half (Figs 47–49, 51, 55–57, 59, 60; Table 1). Nuclear apparatus in or slightly anterior to mid-body (Figs 47, 52, 55; Table 1). Macronucleus about 6 μm across in protargol preparations, globular to broadly ellipsoidal; nucleoli very pale in vivo. Micronucleus near or attached to ventral side of macronucleus, globular. Contractile vacuole posterior to mid-body, excretory tube recognizable in protargol preparations and extending into buccal cavity posterior to adoral membranelles. Cytopyge posterior and slightly left of contractile vacuole, contains granular material (Figs 47, 51, 55; Table 1). Extrusomes left of somatic kineties and posterior to preoral kineties, lenticular and 5–6 μm long (Fig. 47). Cytoplasm colourless with few to many lipid droplets 1–2 μm in size (Figs 47, 55). Swims continuously by rotation about main body axis; never creeps (Table 2).

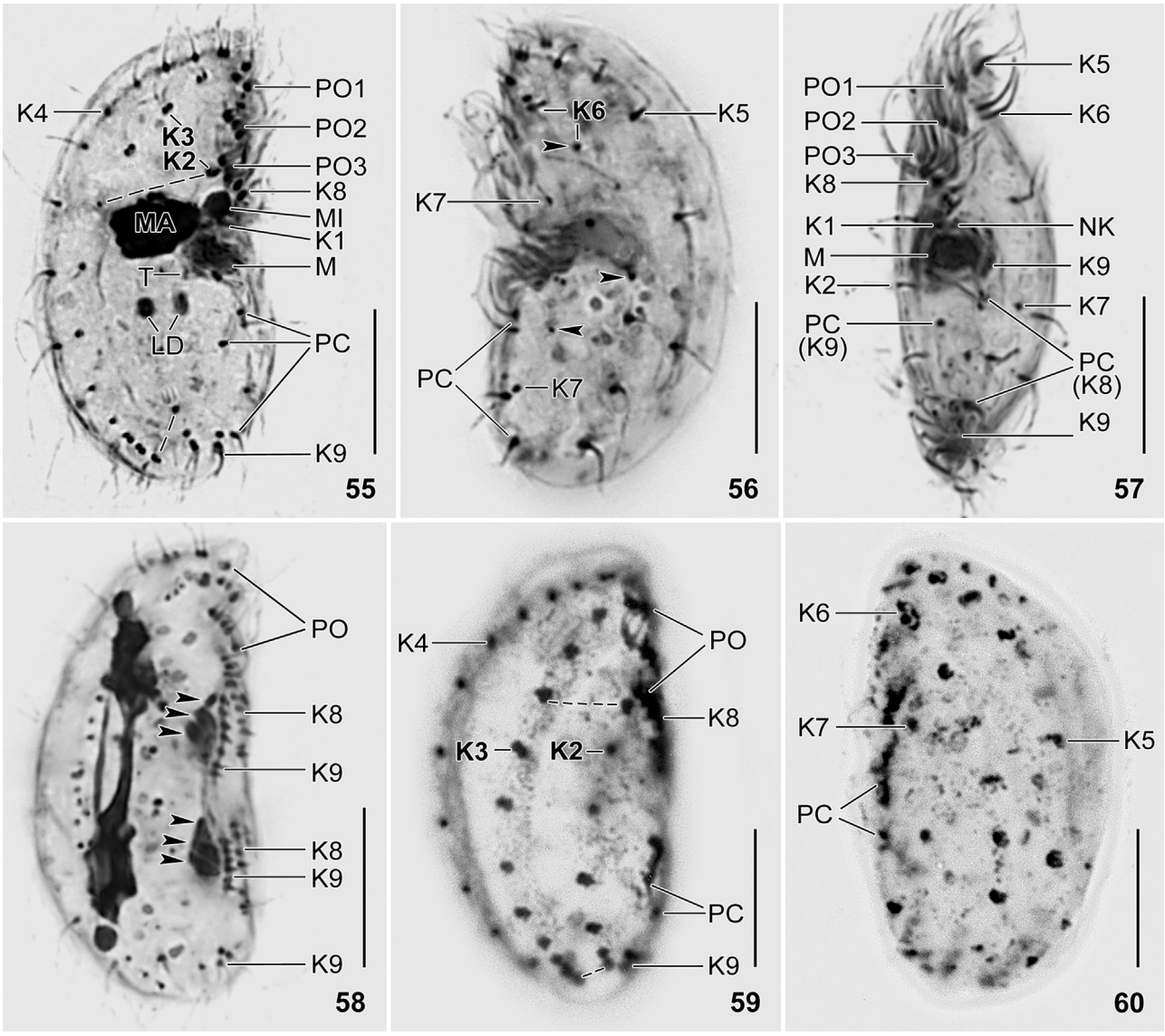
Cortex rigid and glossy, crenellated only along kineties 4 and 5. Right side with two distinct ridges right of somatic kineties 2 and 3; ridges commence on ventral side, extend upon right side, and continue posteriorly gradually reducing the interkinetal distance by up to 50%, possibly contributing to the helical appearance of swimming cells (Figs 47, 51, 55, 59). Left side with two more or less distinct ridges lining wide area between kineties 5 and 6 (Figs 48, 50). Details of ventral side difficult to observe, possibly organized as follows: preoral kineties and anterior portion of kinety 8 in distinct furrows closed at right by right side cortex; buccal cavity in mid-body, deep, in lateral view roofed over by right side cortex continuing posteriorly, producing a sharp line left of postoral body margin (Figs 47, 49, 51, 57). Silverline pattern as described in *D. hymenofera venezuelensis* (Figs 59, 60).

Somatic cilia about 10 μm long in vivo. Invariably nine somatic and three preoral kineties with a total of 99 basal bodies on average. Kineties 2 and 3 and cortical ridges strongly converging posteriorly; kineties 3, 4 and 6 bipolar; kineties 1, 2, 5 and 7–9 shortened anteriorly and/or posteriorly; kineties 1–4 on ventral and right side of body; kineties 5–7 on left and ventral side, and kineties 1, 2, 7, 8 and 9 on ventral side (Figs 47–49, 51–60; Table 1).

Kinety 1 very short, extends at right margin of oral cavity, consists of two portions: anterior portion composed of narrowly spaced dikinetids with about 6 μm long cilia, forming a motionless bundle spread posteriorly; posterior portion slightly shifted dorsally and composed of very narrowly spaced, ciliated monokinetids (Figs 47, 51). Kinety 2 begins in second quarter of cell, composed of some widely spaced, ciliated dikinetids at anterior and posterior end and of some widely spaced, ciliated monokinetids in middle portion (Figs 49, 55). Kinety 3 composed of widely and narrowly spaced, ciliated dikinetids in anterior and posterior third, respectively, and of widely spaced, ciliated monokinetids in middle third. Kineties 4 and 5 limit dorsal margin of right and left body side, respectively (Figs 52, 56); kinety 4 composed of a single, ciliated dikinetid followed by 10 widely spaced, ciliated monokinetids; kinety 5 composed of a single, ciliated dikinetid followed by five widely spaced, ciliated monokinetids, ends in or near posterior third of body. Kinety 6 composed of widely spaced, partially ciliated monokinetids, first two monokinetids close together (Figs 52, 56). Kinety 7 begins in second quarter of body, consists of three widely spaced monokinetids, middle kinetid usually barren. Kinety 8 consists of two portions (Figs 49, 57): anterior portion



Figs 47–54. *Drepanomonas vasta* from life (47, 48) and after protargol impregnation (49–54). **47, 48.** Right and left side view of representative specimens, length about 35 μm, showing the conspicuous ridges on the right side; the distinct, wide furrow between kineties 5 and 6; the ciliation of the right and left side, and the crenellation along kineties 4 and 5. Arrowhead in (47) denotes the sharp line formed by the right side cortex covering the buccal cavity laterally. Arrowheads in (48) mark the non-ciliated basal bodies in kineties 6 and 7. **49.** Ventral view of a paratype specimen, showing the thick body, an important species feature; the obliquely arranged preoral kineties; the oral basal bodies; the postoral complex; and the ridges accompanying preoral and somatic kineties. **50.** Transverse section in mid-body, showing the right (arrows) and the left (arrowheads) side ridges. **51, 52.** Right and left side view of holotype specimen, length 30 μm, showing ciliary and nuclear pattern. Kinety 1 consists of two portions. Arrowhead marks the right ventral margin. Kineties 2 and 3 strongly diverging anteriorly (hatched lines). Kineties 6 and 7 partially ciliated. The hatched line in (52) indicates a frequently ciliated basal body in kinety 6. **53, 54.** A dividing specimen, showing three adoral membranelles (arrowheads) in both the proter and opisthe; possibly, membranelle 1 occurs only in dividers. Kinety 1 and nasse kinetosomes (54) cover the adoral membranelles in specimens oriented laterally. E, extrusome; F, furrow; K1–9, somatic kineties; LD, lipid droplets; M, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; PC, postoral complex; PO1–3, preoral kineties; T, excretory tube of contractile vacuole. Scale bars 10 μm.



Figs 55–60. *Drepanomonas vasta* after protargol (55–58) and Klein–Foissner silver impregnation (59, 60). **55, 56.** Right and left side view of the holotype and a paratype specimen, respectively, showing the ciliary and nuclear pattern, the barren monokinetids in kineties 6 and 7 (arrowheads), the preoral kineties, and the strongly converging kineties 2 and 3 (hatched lines). **57.** Ventral view, showing the thick body, the oblique preoral kineties, the oral ciliature, and the postoral complex. Kinety 8 consists of two portions, kinety 9 of three, and the postoral complex is composed of the posterior portion of kinety 8 and the middle portion of kinety 9. **58.** A mid-divider, showing the three adoral membranelles (arrowheads) in both the proter and opisthe. Kineties 8 and 9 each consists of a single row of kinetids left of the adoral membranelles. **59, 60.** Right and left side view, showing the ciliary pattern and the strongly diverging anteriorly kineties 2 and 3 (hatched lines). K1–9, somatic kineties; LD, lipid droplets; M, adoral membranelles; MA, macronucleus; MI, micronucleus; NK, nasse kinetosomes; PC, postoral complex; PO(1–3), preoral kineties; T, excretory tube. Scale bars 10 μm.

posterior and very similar to preoral kineties, composed of two obliquely arranged, ciliated dikinetids and one ciliated monokinetid at left (posterior) end; posterior portion composed of four widely spaced, ciliated monokinetids, first two kinetids close together (see postoral complex). Kinety 9 consists of three portions (Figs 49, 57, 58): anterior portion left of adoral membranelles and composed of few, likely barren kinetids recognizable only in dividers and appropriately oriented protargol-impregnated specimens; middle portion a single, ciliated monokinetid far posterior to buccal cavity (see postoral complex); posterior portion composed of three ciliated monokinetids near rear cell margin.

Three oblique preoral kineties mainly on left half of ventral side, composed of ciliated dikinetids and a ciliated monokinetid at left end of kineties 2 and 3. Postoral complex composed of the monokinetidal posterior portion of kinety 8 and the single, ciliated monokinetid in mid of kinety 9 (Figs 47–49, 51, 52, 55–57, 59, 60; Table 1).

Oral apparatus in mid-body. Buccal cavity deeply concave when seen laterally (Figs 47, 49, 51, 55, 57; Table 1). Two or

three adoral membranelles. Membranelle 1 distinctly smaller than membranelles 2 and 3, recognizable only in dividers (Figs 53, 58); membranelles 2 and 3 close together, obliquely arranged to main body axis, compact, details thus not recognizable. Nasse kinetosomes anterior to adoral membranelles (Figs 49, 54); oral basket not recognizable.

Occurrence and ecology. As yet found only at type locality as described above. Possibly a planktonic species because we never saw it creeping.

Discussion

Homologization of the ciliary pattern of *Drepanomonas* and *Leptopharynx*

Using the structure and the ontogenetic origin of the postoral complex, the ciliary patterns of *Drepanomonas* and *Leptopharynx* (Foissner et al. 2011; Omar and Foissner 2011, 2012a,b) can be homologized; of course, the different number of kineties (9 vs. 10 or 11) must be taken into account. Briefly, the posterior portion of kinety 8 of *Drepanomonas* is homologous to the posterior portion of kinety 9 in *Leptopharynx* and forms the left portion of the postoral complex. Similarly, the middle portion of kinety 9 of *Drepanomonas* is homologous to the middle portion of kinety 10 in *Leptopharynx* and forms the right portion of the postoral complex. Antes and Wilbert (1987), who studied the ontogenesis of *D. revoluta*, did not recognize the anterior portion of kinety 8, which they mixed with preoral kinety 3, and the middle portion of kinety 9, which they misinterpreted as the pore of the contractile vacuole. Thus, they could not recognize the postoral complex.

Species characteristics of *Drepanomonas*

The genus *Drepanomonas* was monotypic when it was established by Fresenius (1858). Thus, he could not give details for species discrimination. Based on previous studies (Foissner 1979, 1987, 1999; Foissner et al. 1994; Kahl 1931; Penard 1922) and the present investigations, we can discuss the taxonomic significance of various features in *Drepanomonas* (Table 2). The characteristics are separated into two types, viz., important ones and others which are not or less informative at the present state of knowledge, either because they are similar in all species described or because their value is not yet known, e.g., the oral apparatus because it is difficult to analyze; the nuclear apparatus which is very similar in all species; the location of the contractile vacuole and the cytopyge; the extrusome size and shape; and the silverline pattern. The important features include:

(i) detailed morphometrics which are indispensable for distinguishing species as shown by Foissner (1987, 1999) and the present study (Tables 1 and 2);

(ii) body size because of its low variability coefficients (4.2–10.9%; average of 10 taxa 7.1) in eight populations (Foissner 1987, 1999; present study and unpubl.) and the significant difference in various species, for example, *D. dentata* (about 70 μm) and *D. revoluta* (about 30 μm). Using the average coefficient of variation (7.1%), taxa with rather similar length can be differentiated, for instance, *D. hymenofera venezuelensis* and *D. hymenofera hymenofera*: 40.8 μm → 39.4–42.2 μm and 35.3 μm → 34.1–36.5 μm, respectively;

(iii) body shape which is markedly different in, e.g., *D. dentata*, *D. lunaris*, *D. obtusa*, and *D. revoluta* (Foissner 1979; Kahl 1931; Penard 1922; present study);

(iv) cortical ridges and furrows which are useful features, especially when their phenotypic variability is known (Foissner et al. 2011; Omar and Foissner 2012b). The present and previous investigations (Foissner 1979, 1987, 1999; Foissner et al. 1994; Kahl 1931; Penard 1922) show a low phenotypic variability, for example, in *D. revoluta* in which the distinct left side ridges occur in all populations studied so far. The same applies, e.g., to the unique oral spine of *D. exigua*;

(v) the somatic basal body and ciliary pattern which should be supplemented by detailed morphometrics. All species investigated have nine somatic kineties, three preoral kineties, and a postoral complex. Most important features are the arrangement of kineties 2 and 3 (see *D. vasta*), the spacing of the kinetids in kineties 3 and 4, the number of dikinetids in the anterior half of kinety 4, the ciliation of kinety 6, and the spacing of the kinetids in the posterior portion of kinety 8 (Table 2);

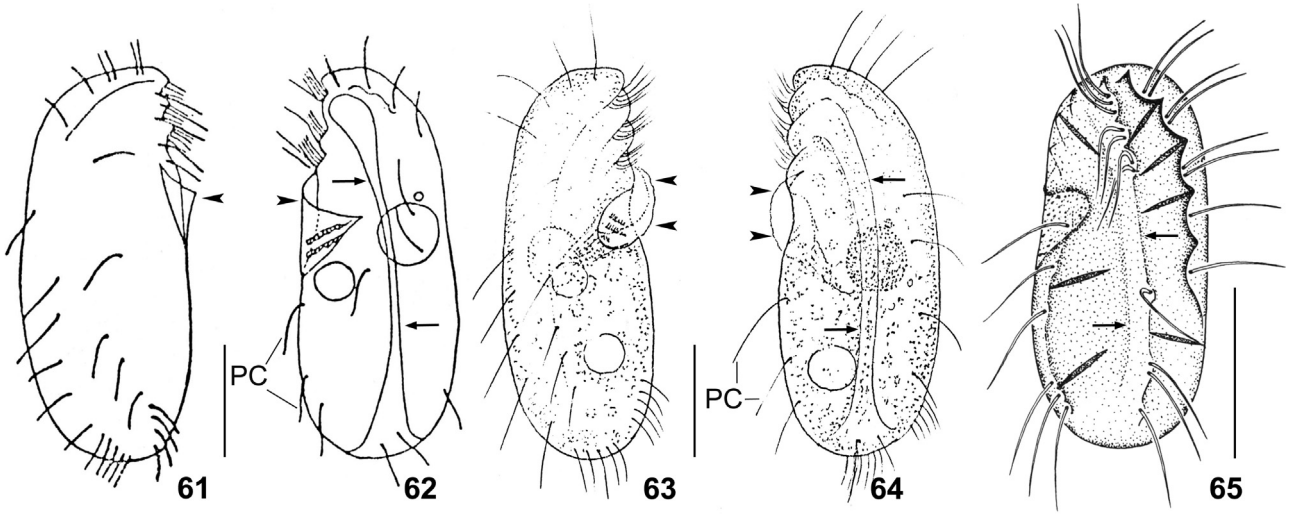
(vi) the total number of basal bodies which seems to be very valuable in *Drepanomonas* (Table 2) and in *Leptopharynx* (Omar and Foissner 2011). Further, the total number of basal bodies seems to be rather independent of body size, for example, the comparatively small *D. vasta* has a similar number (99) as the large *D. hymenofera venezuelensis* (103);

(vii) the location of the oral apparatus either in mid-body or slightly anterior or posterior of mid-body (Table 2);

(viii) the movement because *D. vasta* swims continuously while other species also creep on solid surfaces.

The genera *Drepanomonas* Fresenius, 1858 and *Pseudocristigera* Horváth, 1956

Both genera have been incompletely diagnosed. Later, the clear circumscription of *Drepanomonas* by Kahl (1931) has been widely acknowledged. Horváth (1956) mentioned only the projecting hymen as main feature of *Pseudocristigera* and did not compare his species with *Drepanomonas*. However, Corliss (1979), Chardez (1990), and Foissner (1998) recognized the similarity with *Drepanomonas*, and thus classified



Figs 61–65. *Drepanomonas hymenofera hymenofera* from Horváth (1956; 61, 62, from life) and Chardez (1990; 63, 64, from life), and *D. sphagni* from Foissner (1987; 65, combination of life and protargol-impregnated specimens). The arrows mark the narrow left side furrow, the arrowheads denote, in our opinion, the distinct ridge along the left margin of the oral opening (cp. Figs 27–30). PC, postoral complex. Scale bars 10 μm.

Pseudocristigera as a junior synonym of *Drepanomonas*. Although we basically agree and have some explanation for the hymen of *Pseudocristigera* (see below), we cannot exclude the existence of *Drepanomonas*-like species with a conspicuous convexity in the oral area (Figs 61–64). If so, a distinct genus would be likely correct.

However, we believe that the hymen of *Pseudocristigera hymenofera* is a more or less distinct ridge along the left margin of the oral opening in most or all *Drepanomonas* species (Foissner et al. 1994 and Figs 27–30 in this study). If this is anticipated and the ciliary pattern is put aside because Horváth (1956) did not have the advantage of protargol impregnation, then the Iceland *Drepanomonas* would match *D. hymenofera* rather well in body size (35–45 μm and 30–35 μm), body shape (cp. Figs 39, 41, 42 with Figs 61–64), and the rather inconspicuous left side furrow (cp. Figs 33, 34, 37, 40 with Figs 62, 64).

Chardez (1990) did not formally transfer *Pseudocristigera hymenofera* to *Drepanomonas* because he did not use "nov. comb." We make it up for the sake of nomenclatural demands: *Drepanomonas hymenofera* (Horváth 1956) nov. comb. (basionym: *Pseudocristigera hymenofera* Horváth 1956).

Comparison of *Drepanomonas hymenofera*

The overall appearance of *D. hymenofera* is similar to that of *D. revoluta* Penard, 1922, *D. sphagni* Kahl, 1931 (Fig. 65), and *D. muscicola* Foissner, 1987. *Drepanomonas hymenofera* differs from these species and most other congeners by the larger, non-overlapping body size and the higher, non-overlapping total number of basal bodies (Table 2). The following differences are minor but might be useful to distinguish these species more properly. *Drepanomonas hymenofera* differs from *D. revoluta*, as redescribed by Foissner (1987) and Foissner et al. (1994), also by the absence (vs. presence) of cortical ridges on the right body side, the narrow (vs. wide) furrow on the left side, and the oral cortex pattern (cp. Figs 28–30). *Drepanomonas sphagni*, as redescribed by Foissner (1987), is further distinguished from *D. hymenofera* by the presence (vs. absence) of a very wide break in mid of kinety 3, the ciliation of kinety 6 (fully vs. partially), and the location of the oral apparatus (at 32% vs. 39% of body length). *Drepanomonas muscicola*, for which a sound morphology is still lacking, differs from *D. hymenofera* also by kinety 3 (without vs. with basal bodies in middle third) and the location of the oral apparatus (posterior vs. anterior of mid-body).

The most important difference between the subspecies *D. hymenofera venezuelensis* and *D. hymenofera hymenofera* is possibly the total number of basal bodies because it does not overlap and is a very stable feature in the Microthoracidae (Omar and Foissner 2011). The distinct furrow in the left side of *D. hymenofera hymenofera* resembles that of *D. revoluta* but is much narrower (cp. Figs 33, 41 with Figs 12, 21 in Foissner et al. 1994).

We interpret the differences between *D. hymenofera venezuelensis* and *D. hymenofera hymenofera* biogeographically because they are in an order found in many other ciliate species and subspecies (Foissner 2006; Foissner et al. 2002, 2010; Katz et al. 2005; Xu and Foissner 2005).

Comparison of *Drepanomonas vasta*

Of the ten congeners, *D. vasta* is most similar to *D. revoluta* because of body shape and the wide distance of the left side ridges (Table 2). However, they differ by three distinct features (Table 2): somatic kinety 4 anteriorly with 1 vs. 3 or

4 ciliated dikinetids, the total number of basal bodies (99 vs. 80 with non-overlapping extremes) and the thick body (vs. distinctly flattened) producing a broad ventral side exposing five (vs. three) somatic kineties. The single dikinetid in the anterior half of kinety 4 of *D. vasta* is as yet unique because all other species have two to four dikinetids. The total number of basal bodies is discussed above. The following features are considered as minor but emphasize the distinctness of *D. vasta* from *D. revoluta* (Table 2): (i) continuously swimming vs. swimming and gliding on solid surfaces; (ii) body length on average 28 μm vs. 20 μm with non-overlapping extremes in protargol preparations; (iii) kineties 2 and 3 strongly vs. slightly converging posteriorly; and (iv) the slightly helical (vs. ordinary) body caused by the reasons given in the diagnosis.

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