

Revision of the Genus *Coriplites* Foissner, 1988 (Ciliophora: Haptorida), with Description of *Apocoriplites* nov. gen. and Three New Species

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Summary. The genera *Coriplites* Foissner, 1988 and *Apocoriplites* nov. gen., which differ by the number of dorsal brush rows (3 vs. 2), belong to the haptorid Litostomatea and have a distinct feature in common: they lack oral extrusomes. Based on three new species, the diagnosis of the genus *Coriplites* is amended to include the wide spacing of the brush dikinetids and the heavily refractive cortical granules. Using standard methods, we redescribe *C. terricola* Foissner, 1988 and describe three new species: *C. grandis* (from swamp soil of Australia), *C. proctori* (from tanks of bromeliads in Jamaica), and *Apocoriplites lajacola* (from granitic rook-pools in Venezuela). Species are distinguished by the nuclear apparatus (a single nodule vs. two nodules with a micronucleus in between), the body size (<100 µm vs. >100 µm), the number of ciliary rows, and details of the dorsal brush (isostichad vs. heterostichad). In over 1,000 soil samples, only *C. terricola* has been found in all main biogeographic regions, while the other species have been found only at their type locality, i.e., in the southern hemisphere, where the genus possibly originated.

Key words: Australia, biodiversity, Bromeliaceae, geographic distribution, Jamaica, Laja, Venezuela.

INTRODUCTION

Coriplites belongs to a group of haptorids, which has, at first glance, a quite simple organization: the body is a completely ciliated sac, of which the narrower anterior end bears the mouth opening. Complex oral structures are absent, except of a dikinetid circumoral kinety at the base of an inconspicuous oral bulge. Thus, such ciliates are difficult to identify *in vivo* (Kahl 1930). It was only during the past 20 years that silver impregnation and transmission electron microscopy provided new features for a more reliable identification and clas-

sification, especially details of the oral basket and the dorsal brush, a field of paired cilia with unknown function (Foissner and Foissner 1988, Foissner and Xu 2007, Foissner *et al.* 2002, Puytorac 1994).

Coriplites belongs to the Acropisthiina Foissner and Foissner (1988), a fairly large group of haptorids, in which the oral basket is not only composed of rods originating from the circumoral kinety but also from oralized somatic monokinetics in the anterior region of the somatic ciliary rows. Originally, the Acropisthiina contained a single family (Acropisthiidae) with four genera: *Acropisthium*, *Fuscheria*, *Papillorhabdos* and *Actinorhabdos*. Several new genera were added by Foissner (1988, 1996, 1998a, 1999) and Foissner *et al.* (1999, 2002), viz., *Pleuroplites*, *Pleuroplitoides*, *Balantidion*, *Coriplites*, *Chaenea*, *Diplites*, *Dioplitophrya*, *Sikorops*, and *Clavoplitites*. Here,

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a fourteenth fuscheriid genus is added: *Apocoriplites*. These genera were classified in three families (Foissner and Foissner 1988, Foissner 1996, Foissner *et al.* 2002): the Pleuroplitidae (with subapical, extracystostomal extrusome bundle and enchelydonid general organization with meridional kineties), the Fuscheriidae (general organization enchelydonid with meridional kineties), and the Acropisthiidae (general organization spathidiid with kineties more or less curved anteriorly).

The genus *Coriplites* was established with a single species by Foissner (1988). It is unique in having lost the oral extrusomes, a main feature of the haptorids (Corliss 1979). During the past 20 years, we have investigated over 1,000 soil samples collected globally. In these samples, we discovered not only most of the genera cited above, but also three new coriplitids which will be described in this paper. This great increase in genera and species shows a huge portion of undescribed ciliate diversity (for a review, see Foissner *et al.* 2008).

MATERIAL AND METHODS

The origin of the material is provided in the individual species descriptions. Basically, all samples are from terrestrial or semiterrestrial habitats. With the exception of the sample containing *Coriplites proctori*, all materials were air-dried for at least one month and then stored in plastic bags. Later, samples were investigated with the non-flooded Petri dish method, as described by Foissner *et al.* (2002). Briefly, this simple method involves placing 50–500 g soil in a Petri dish (13–18 cm wide, 2–3 cm high) and saturating, but not flooding it, with distilled water. These cultures were analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28. Except of *C. proctori*, the descriptions of the new species were based on material obtained from such cultures, *i.e.*, no pure cultures were established. *Coriplites proctori* was discovered in the tanks of a Jamaican bromeliad. The species became rather abundant in a mixed culture of tank water with the original organism community and some squashed wheat grains.

Morphological and presentation methods followed Foissner (1991) and Foissner *et al.* (2002). However, *C. proctori* was fixed in 50% ethanol (final concentration) – the specimens shrank considerably and did not impregnate well with protargol. Terminology follows Corliss (1979) and the refinements introduced by Foissner and Xu (2007).

RESULTS AND DISCUSSION

General part

Systematic classification: The coriplitids (= *Coriplites* and the new genus *Apocoriplites* described be-

low) belong to the haptorids, according to their general organization (Foissner 1988; Foissner *et al.* 2002). However, they fall into a distinct subgroup lacking oral extrusomes (toxicysts), a main feature of the haptorids (Corliss 1979). Further, they have oralized somatic monokinetids, that is, oral basket rods originate not only from the dikinetidal circumoral kinety but also from the anterior kinetids of the somatic ciliary rows (Foissner 1988). This type of haptorids has been classified in a distinct suborder, the Acropisthiina, by Foissner and Foissner (1988). The body organization of the coriplitids is enchelydonid, and thus they belong to the family Fuscheriidae, as defined by Foissner *et al.* (2002).

Genera within the Fuscheriidae are distinguished by the number of dorsal brush rows (two in *Fuscheria* Berger *et al.* 1983, *Actinorhabdos* Foissner 1984, *Diplites* Foissner 1998a, and *Apocoriplites* nov. gen.; three in *Coriplites* Foissner 1988, *Balantidion*, as re-described by Foissner *et al.* 1999, and *Diopliophrya* Foissner *et al.* 2002) and the shape and types of extrusomes (lacking in *Coriplites* and *Apocoriplites*; oblong in *Balantidion*; pin-shaped in *Fuscheria*, graver-shaped in *Actinorhabdos*; pin-shaped and clavate in *Diopliophrya*; rod-shaped somatic and narrowly ovate or ellipsoidal oral toxicysts in *Diplites*).

Morphological characterization: *Coriplites* was established with a single species: *C. terricola* Foissner, 1988. Thus, the diagnosis focused on the most conspicuous feature, *i.e.*, the absence of oral toxicysts. Here, we describe two further species and a new, closely related genus, *Apocoriplites*, all having two further specific features in common: widely spaced brush dikinetids (Figs 1e, 2e, 3e, 4h, 5b, 6a) and conspicuous cortical granules (Figs 3a, b), likely mucocysts, which can be extruded, forming a thick, yellowish-impregnated cover in protargol preparations (Figs 1h, 5e). Both features are rare in haptorids and thus useful for the definition of the genus.

Coriplitids lack oral extrusomes, that is, a main diagnostic feature of the haptorids (Corliss 1979, Foissner and Foissner 1988). We consider it unlikely that they are too small to be recognizable in the light microscope, especially because they are also absent from the large *C. grandis* (~180 × 35 µm). Usually, haptorids of this size have toxicysts longer than 5 µm. In all likelihood, the coriplitids lost their extrusomes, which is observed in a variety of haptorid genera, for instance, in *Arcuospathidium cooperi* and *Edaphospathula inermis*, both described in Foissner and Xu (2007).

The occurrence of extrusome-less species in various haptorid genera provokes the question whether *Coriplites* and *Apocoriplites* are “good” genera at all. Could they belong to another acropisthiid genus? We cannot exclude this possibility at the present state of knowledge, but it is unlikely that they belong to one of the described acropisthiid genera (Foissner *et al.* 2002). There are three features that support our assumption, *viz.*, the specific nuclear pattern present in most coriplitids (two globular macronucleus nodules with a micronucleus in between), the widely spaced dorsal brush dikinetids, and the highly refractive cortical granules. Although individual features are found in other haptorids (Blatterer and Foissner 1988, Foissner *et al.* 2002, Foissner and Xu 2007), they never occur together, as in the coriplitids.

Occurrence and ecology: Coriplitid ciliates prefer semiterrestrial habitats, such as mossy puddles, swamp soil, and bromelian cisterns. Records from lakes or running waters are not known, while *C. terricola* occurs in true terrestrial habitats, *i.e.*, in soil from deciduous and coniferous forests (Foissner 1988, Blatterer and Foissner 1988).

All coriplitids are rare, at least under the isolation method used (non-flooded Petri dish culture). Thus, their geographic distribution is difficult to estimate. In over 1,000 soil samples (Foissner 1998b; Foissner *et al.* 2002, 2005), only *C. terricola* occurred in all main biogeographic regions, while the three other species have been found only at their type locality. Except for the cosmopolitan *C. terricola*, all species have been found only in Gondwanan areas, suggesting an origin of the genus in the southern hemisphere.

Detailed autecological data from coriplitids are not known. They occur in a wide variety of habitats (see below) with a pH range from about 3.5 to 7. In the non-flooded Petri dish cultures, their abundance is low to moderate.

Key to species of *Coriplites* and *Apocoriplites*: All species can be identified on careful live observation, though identification of *C. terricola* and *Apocoriplites lajacola* should be confirmed in protargol preparations.

- 1 Two globular macronucleus nodules with a micronucleus in between..... 2
One macronucleus..... *Coriplites proctori*
- 2 Body length $\leq 110 \mu\text{m}$ *in vivo* 3
Body length $\geq 130 \mu\text{m}$, usually about $180 \mu\text{m}$ *in vivo*..... *Coriplites grandis*
- 3 Three dorsal brush rows..... *Coriplites terricola*
Two dorsal brush rows..... *Apocoriplites lajacola*

Diagnoses and descriptions of genera and species

Genus *Coriplites* Foissner, 1988

Improved diagnosis: Fuscheriidae Foissner and Foissner (1988) without oral extrusomes and with widely spaced brush dikinetids. Cortex gelatinous, 1–2 μm thick due to highly refractive granules, likely mucocysts. Nuclear apparatus usually consisting of two globular macronucleus nodules and a micronucleus in between.

Type species (by original designation): *Coriplites terricola* Foissner, 1988.

Etymology: The generic name is a composite of the Greek words “coris” (without) and “hoplites” (soldier), meaning a ciliate without extrusomes. Masculine gender.

Coriplites terricola Foissner, 1988 (Figs 1a–h, Table 1)

1988 *Coriplites terricola* Foissner, Stapfia 17:93 (1 holotype and 1 paratype slide with protargol-impregnated specimens from type locality have been deposited in the Museum of Natural History, London. The holotype is contained in that slide which contains the type of *Birojimia terricola* Berger and Foissner, 1989).

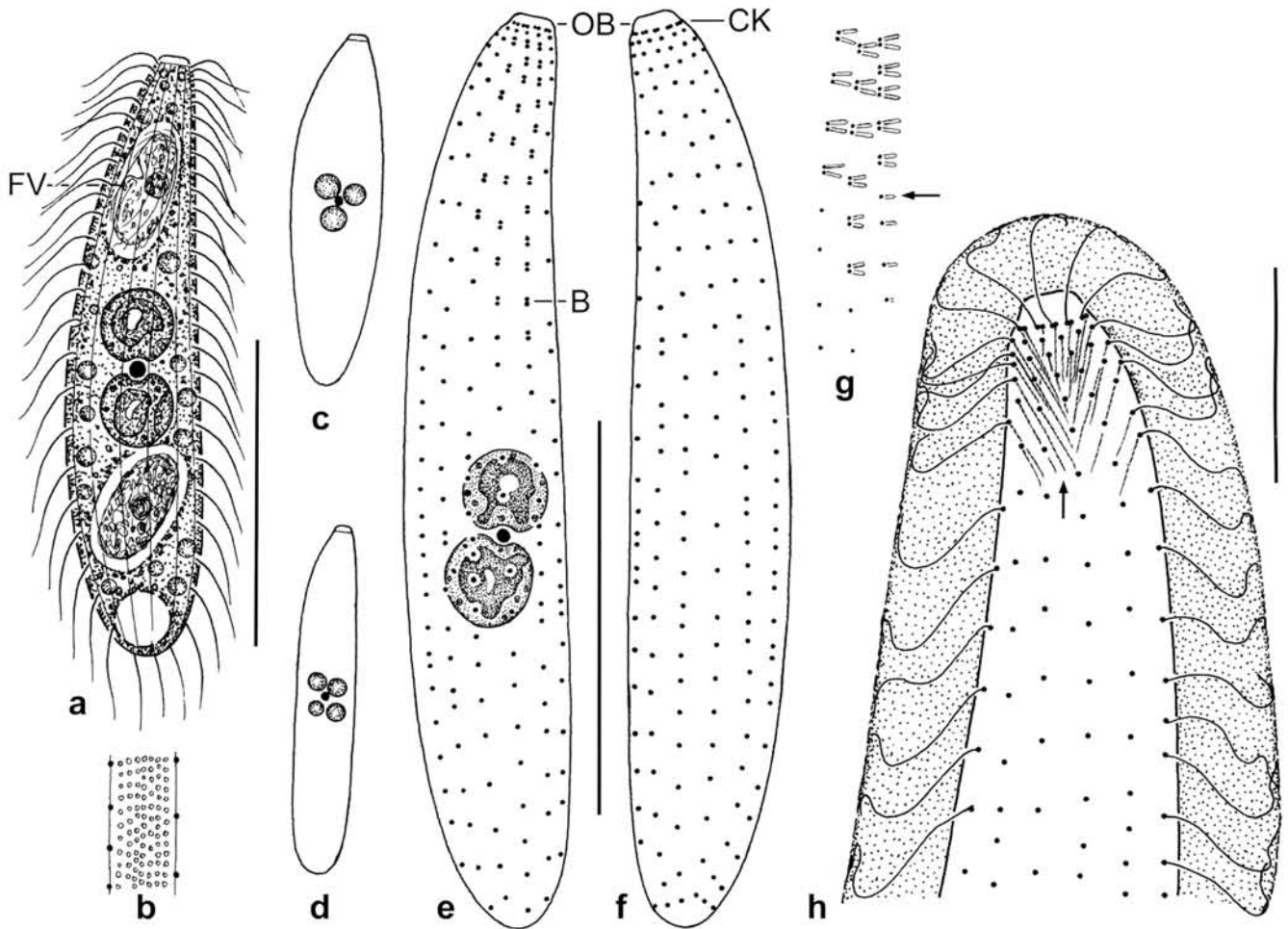
Improved diagnosis (based on 5 populations): Size about $60 \times 13 \mu\text{m}$ *in vivo*; elongate bursiform to narrowly ellipsoidal. Two globular macronucleus nodules with a globular micronucleus in between. On average 12 ciliary rows, three anteriorly differentiated to a heterostichad dorsal brush occupying about 34% of body length.

Type locality: Upper soil layer of a deciduous forest in the surroundings of Birojima, Amakusa, Kumamoto Prefecture, Japan, E129° N32°30'.

Etymology: Not given in original description. Obviously, the Latin *terricola* (living in soil) refers to the habitat the species was discovered.

Description: Five populations from Japan, Australia, and South America have been studied *in vivo* and protargol preparations. However, detailed data from silvered specimens are available only from the Japanese and one of the two Australian populations (Table 1). All populations match well, suggesting conspecificity. Thus, the data are combined in the diagnosis and description.

Size little variable within and between populations, *i.e.*, $50\text{--}80 \times 10\text{--}15 \mu\text{m}$ *in vivo* ($n = 9$), usually near $60 \times 13 \mu\text{m}$; length:width ratio on average 4–5:1 both *in vivo* and protargol preparations. Shape elongate bursiform, rarely ellipsoidal or almost cylindrical; unflat-



Figs 1a–h. *Coriplites terricola*, specimens from Japan (a, b, e, f, h), Australia (c), the Easter Islands (d), and Venezuela (g) from life (a, b, g) and after protargol impregnation (c–f, h). **a** – right side view of a representative specimen, length 60 μm ; **b** – surface view showing cortical granulation; **c**, **d** – body shape and nuclear apparatus of post-conjugants from Australia and the Easter Islands; **e**, **f** – ciliary pattern of dorsal and ventral side and nuclear apparatus of holotype specimen. Note the widely spaced dikinetids of the dorsal brush (B) and the special configuration of the nuclear apparatus, *viz.*, two macronucleus nodules and a micronucleus in between; **g** – dorsal brush of a Venezuelan specimen, bristles up to 2.5 μm long. Arrow marks begin of monokinetid tail of brush row 3; **h** – anterior body portion showing the yellowishly impregnated cover of the cell and the oral basket rods (arrow), which originate from the circummoral kinety and oralized somatic monokinetids in the anterior portion of the ciliary rows. B – dorsal brush, CK – circummoral kinety, FV – food vacuole, OB – oral bulge. Scale bars 10 μm (h) and 30 μm (a, e, f).

tened; brush side moderately convex, ventral side flat, slightly concave or slightly convex, specimens thus somewhat asymmetrical (Figs 1a, c–f); slightly contractile under mild coverslip pressure, specimens from the Easter Islands shorten by up to 20% when removed from sample or slide with a fine pipette. Nuclear apparatus on average slightly posterior of mid-body, highly characteristic, *i.e.*, composed of two globular macronucleus nodules and a single micronucleus in between (Figs 1a, e). Macronucleus nodules spherical to broadly ellipsoidal, contain a circular or reticular nucleolus,

7–8 μm across *in vivo*. Micronucleus globular, about 1.5 μm across *in vivo*. Postconjugants with 1–4 small, globular macronucleus nodules (Figs 1c, d). Cortex colourless, very flexible, smooth to rather distinctly furrowed by ciliary rows, conspicuous due to the highly refractive granules contained in an about 1 μm thick, gelatinous layer; individual granules about $0.8 \times 0.4 \mu\text{m}$ in size, arranged in circa eight narrowly spaced rows between two kineties each (Fig. 1b), become extruded during fixation, forming a thick, yellowish-impregnated envelope (Fig. 1h). Cytoplasm colourless, rather

Table 1. Morphometric data on a Japanese (upper line) and Australian (lower line) population of *Coriplites terricola*. Data based on mounted, protargol-impregnated (Foissner 1991, protocol A), and 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 individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, \bar{X} – arithmetic mean.

Characteristics	\bar{X}	M	SD	SE	CV	Min	Max	n
Body, length	61.5	63.0	8.7	2.3	14.2	43	74	15
	54.9	56.0	6.6	2.0	12.0	46	65	11
Body, width	12.5	13.0	2.0	0.5	16.2	10	17	15
	10.9	11.0	1.4	0.4	12.6	9	13	11
Oral bulge, width	3.6	4.0	–	–	–	3	4	15
	4.0	4.0	–	–	–	3	5	11
Anterior body end to macronucleus, distance	31.1	31.0	7.4	1.9	23.9	20	44	15
	23.6	24.0	5.1	1.6	21.8	15	33	11
Brush kinety 1, length	15.5	14.0	2.6	0.7	16.7	13	21	15
	12.4	12.0	1.4	0.4	11.0	10	14	11
Brush kinety 2, length	20.9	21.0	3.5	0.9	16.6	15	27	15
	18.6	18.0	1.5	0.5	8.1	16	21	11
Brush kinety 3, length	21.6	21.0	3.8	1.0	17.5	15	28	15
	17.5	18.0	1.9	0.6	10.6	14	20	11
Macronucleus nodules, length	6.8	7.0	1.1	0.3	16.4	6	10	15
	6.0	6.0	1.4	0.4	23.6	3	9	11
Macronucleus nodules, width	6.1	6.0	0.7	0.2	11.5	5	7	15
	5.3	5.3	0.9	0.3	17.6	3	7	11
Micronucleus, diameter	1.3	1.3	–	–	–	1.2	1.5	15
	1.4	1.3	–	–	–	1.2	1.6	11
Ciliary rows, number	11.8	12.0	0.7	0.2	5.7	11	13	15
	12.0	12.0	0.6	0.2	5.3	11	13	11
Basal bodies in a ventral ciliary row, number	25.9	25.0	4.8	1.2	18.7	20	37	15
	24.3	24.0	4.5	1.4	18.6	18	31	11
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3	3	15
	3.0	3.0	0.0	0.0	0.0	3	3	11
Dikinetids in brush row 1, number	6.3	6.0	1.4	0.4	22.9	5	10	15
	6.7	6.0	1.1	0.3	16.4	5	8	11
Dikinetids in brush row 2, number	9.4	9.0	1.2	0.3	13.2	8	12	15
	10.3	10.0	1.8	0.5	17.5	8	13	11
Dikinetids in brush row 3, number	10.9	11.0	1.6	0.4	14.5	9	14	15
	11.0	11.0	1.0	0.3	9.1	10	13	11
Macronucleus nodules, number ^a	2.0	2.0	0.0	0.0	0.0	2	2	15
	2.5	2.0	1.5	0.5	59.2	2	7	11
Micronuclei, number ^a	1.0	1.0	0.0	0.0	0.0	1	1	15
	1.0	1.0	0.0	0.0	0.0	1	1	8

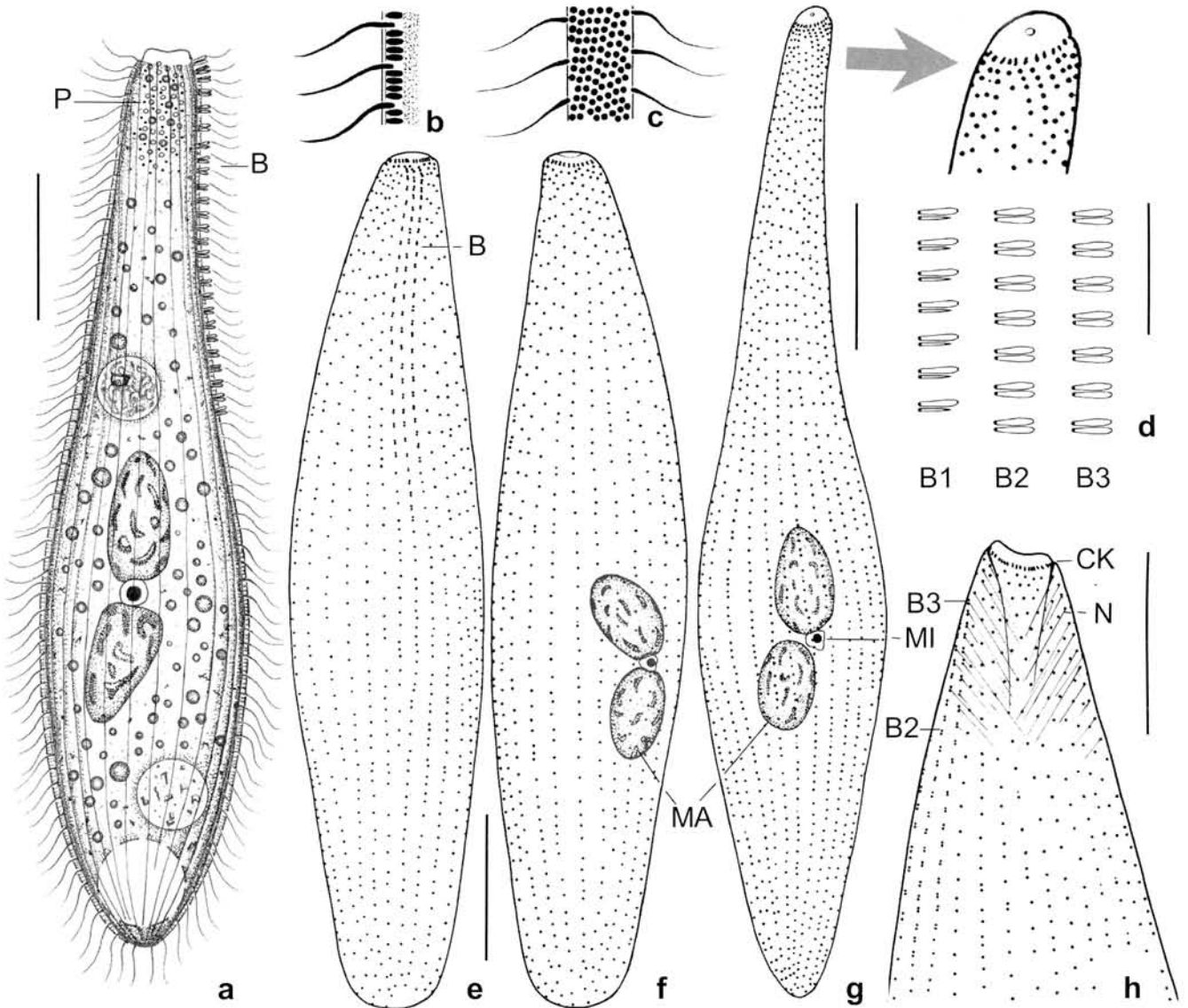
^a Australian specimens include postconjugates.

hyaline, especially in anterior quarter containing some faint, 1–3 μm long structures, likely mitochondria; main body portion more or less opaque due to lipid droplets 1–4 μm across and up to 10 μm -sized food vacuoles with heterotrophic flagellates and small ciliates, such as *Drepanomonas pauciciliata*, *Protoctylidium muscicola*, and *Cyrtolophosis mucicola* (Fig. 1a). Swims rather rapidly to rapidly rotating about main body axis.

Cilia about 8 μm long *in vivo*, ordinarily spaced except subapically where some more narrowly and regularly spaced kinetids form a circular pattern; arranged in an average of 12 longitudinal, equidistant, ordinarily spaced rows (Figs 1e, f, h). Dorsal brush occupies an average of 34% of body length, heterostichad because row 1 shorter

than row 2 by about 40%; rows 2 and 3 of similar length, row 3 with a monokinetidal tail extending to mid-body with 1 μm long bristles; anterior tails composed of 1–2 monokinetids; row 1 composed of an average of 6 dikinetids, row 2 of 10, and row 3 of 11. Brush bristles inconspicuous because only 2–3 μm long, V-like spread, rod-shaped to flame-like; anterior basal body of dikinetids of rows 1 and 2 possibly with an ordinary cilium in Japanese population (Foissner 1988), while both bristles are about 2.5 μm long in a Venezuelan specimen (Fig. 1g).

Oral bulge transverse truncate and more or less depressed in centre, inconspicuous because *in vivo* only about 5 μm across, 2–3 μm high, and indistinctly set off from body proper, except of Venezuelan specimens



where it is slightly narrowed and thus more distinct. Circumoral kinety circular, composed of about 12 slightly oblique dikinetids (Figs 1e, f). Nematodesmata short and fine, do not form bundles, originate from circumoral dikinetids and 3–8 oralized somatic monokinetids at anterior end of ciliary rows (Fig. 1h).

Occurrence and ecology: *Coriplites terricola* has been found in all main biogeographic areas, except of Antarctica, suggesting cosmopolitan distribution (Foissner 1998b, Foissner et al. 2002): Austria (Foissner et al. 2005), Japan and Australia (Foissner 1988, Blatterer and Foissner 1988), Namibia (Foissner et al. 2002), and South America (Venezuela, Easter Islands; Foissner 1998b). Obviously, *C. terricola* occurs in a variety of soils suggesting a wide ecological range, but it never became abundant in the non-flooded Petri dish cultures. The prey is ingested whole because still recognizable in the food vacuoles.

Comparison with related species: Ciliates of this type are rather frequent and thus difficult to identify. Fortunately, *C. terricola*, the most common coriplitid, has two highly characteristic features easy to recognize: the lack of oral extrusomes and the special nuclear pattern, which is rare in other haptorids. *Coriplites grandis*, which has the same features, is much larger ($180 \times 35 \mu\text{m}$ vs. $60 \times 13 \mu\text{m}$).

***Coriplites grandis* nov. spec. (Figs 2a–h, 3a–g; Table 2)**

Diagnosis: Size about $180 \times 35 \mu\text{m}$ *in vivo*; obclavate. Two ellipsoidal macronucleus nodules with a globular micronucleus in between. On average 26 ciliary rows, three anteriorly differentiated to an isostichad dorsal brush occupying about 40% of body length.

Type locality: Upper soil layer (0–5 cm) of a swamp near Eubenangee, south of Cairns, Australia, 17°S 145°E .

Type material: One holotype slide and 5 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: The Latin adjective *grandis* (large) refers to the comparatively large size.

Description: Three populations from Australia were studied *in vivo*, namely, from the east coast (Eubenangee) and from two localities near Alice Springs in the red centre of the continent. The populations match very well, therefore diagnosis and description summarize all observations except of some differing details. Protargol preparations are available only from the type locality.

Size $150\text{--}220 \times 30\text{--}40 \mu\text{m}$ *in vivo*, usually about $180 \times 35 \mu\text{m}$; length:width ratio 3–6:1, on average 4:1 in protargol preparations, where specimens are slightly shrunken in length, but inflated in width ($162 \times 38 \mu\text{m}$; Table 2). Shape more or less obclavate, rarely almost fusiform, distinctly narrowed and more or less curved in anterior third; body symmetric and flexible, unflattened to slightly flattened (Figs 2a, e–g, 3c, d). Specimens from Alice Springs pyriform under coverslip because narrowed anterior half contracted up to 40%. Nuclear apparatus up to $75 \mu\text{m}$ long *in vivo*, on average $40 \mu\text{m}$ in protargol preparations, in or underneath mid-body, conspicuous because composed of two ellipsoidal macronucleus nodules and a globular micronucleus in between; individual nodules up to $30 \times 15 \mu\text{m}$ *in vivo*, while only about $20 \times 11 \mu\text{m}$ in protargol preparations, likely due to some preparation shrinkage; nucleoli scattered, numerous, globular, oblong or forming irregular masses. Micronucleus surrounded by a distinct, membrane-like structure, about $5 \mu\text{m}$ across *in vivo* (Figs 2a, f, g; Table 2). Contractile vacuole in rear end. No oral extrusomes detectable by light microscopy in any of the populations. Cortex flexible, gelatinous, colourless, rather distinctly furrowed by ciliary rows, conspicuous because about $1.5 \mu\text{m}$ thick due to highly refractive granules (Figs 2b, c, 3a, b); individual granules about $1.3 \times 0.8 \mu\text{m}$ in size, arranged in 7–10 narrowly spaced rows between each two kineties, can be extruded but do not swell, slightly less conspicuous in one of the two Alice Springs populations. Cytoplasm colourless, packed with many lipid droplets $0.5\text{--}5 \mu\text{m}$ across and $12\text{--}30 \mu\text{m}$ -sized food and fecal vacuoles containing organic debris and crystals $3\text{--}5 \mu\text{m}$ in size. In oral area a pharyngeal mass composed of rather refractive globules about $1 \mu\text{m}$ across (Fig. 2a). Feeds on medium-sized ciliates, such as *Gonostomum affine*, ingested wholly because still iden-



Figs 2a–h. *Coriplites grandis* from life (a–d) and after protargol impregnation (e–h). **a** – left side view of a representative specimen. Note lack of oral extrusomes; **b, c** – optical section (b) and surface view (c) showing the conspicuous cortical granulation; **d** – part of dorsal brush; **e, f** – ciliary pattern of dorsal and ventral side and nuclear apparatus of holotype specimen. Note similar length of dorsal brush rows and wide spacing of their dikinetids; **g** – ventral ciliary pattern of a slender paratype specimen with condensed ciliature around oral opening (arrow); **h** – right anterior portion showing the somatic and oral infraciliature. Nematodesmata originate from the circumoral dikinetids and the anterior basal bodies of the ciliary rows. B(1–3) – dorsal brush (rows), CK – circumoral kinety, MA – macronucleus, MI – micronucleus, N – nematodesmata, P – pharyngeal mass. Scale bars $30 \mu\text{m}$ (a, e–g), $20 \mu\text{m}$ (h) and $10 \mu\text{m}$ (d).

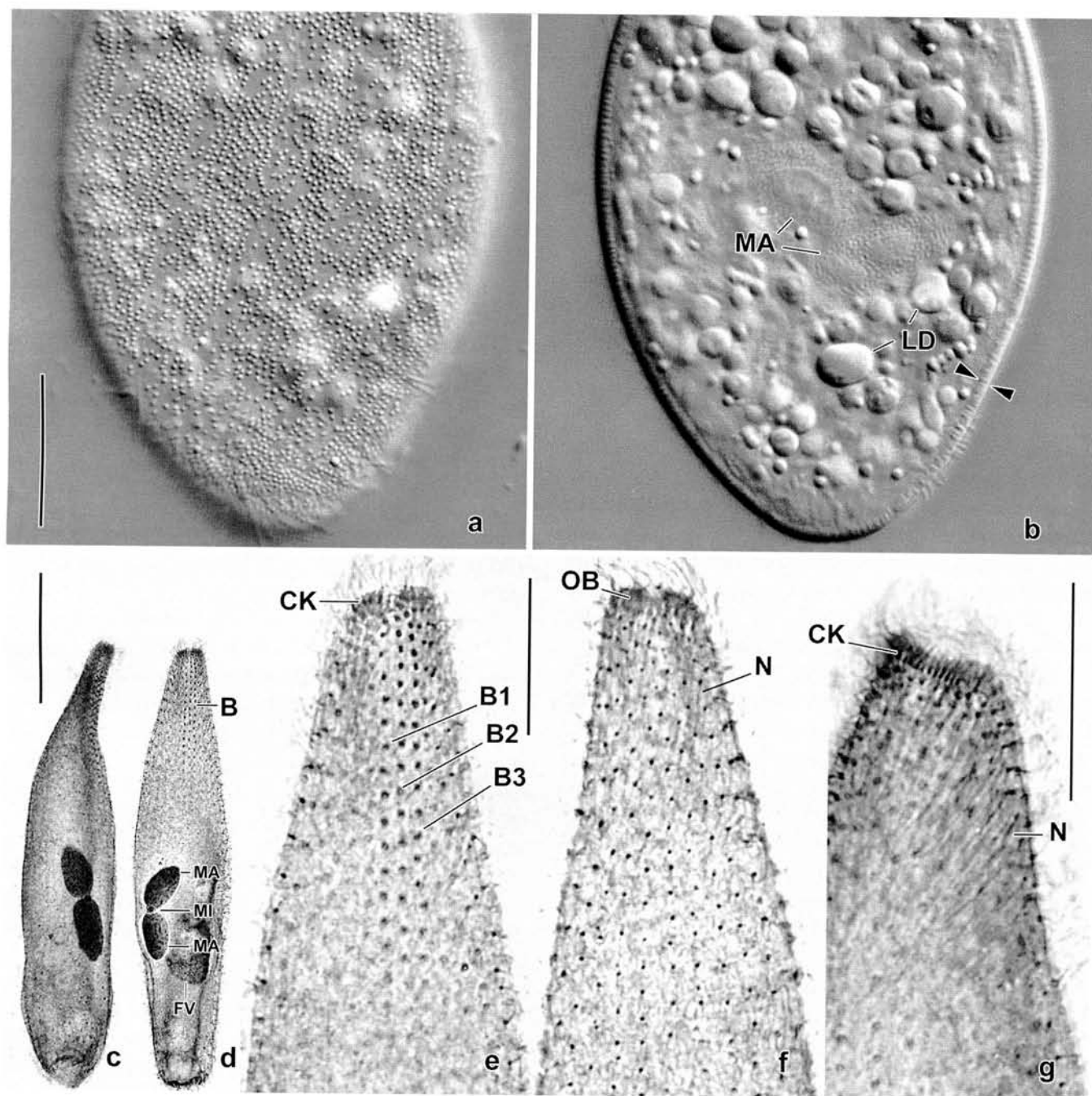
Table 2. Morphometric data from *Coriplites grandis* (upper line) and *Coriplites proctori* (lower line). Data from *Coriplites grandis* based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Data from *Coriplites proctori* based on ethanol-fixed, mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a raw 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 error of arithmetic mean, \bar{X} – arithmetic mean.

Characteristics	\bar{X}	M	SD	SE	CV	Min	Max	n
Body, length	162.0	160.0	17.5	3.8	10.8	138.0	206.0	21
	41.9	40.5	5.1	1.1	12.2	34.0	54.0	22
Body, width	38.0	40.0	6.4	1.4	16.9	25.0	50.0	21
	15.3	14.0	2.2	0.5	14.5	13.0	20.0	22
Body length:width, ratio	4.4	4.2	0.8	0.2	17.7	3.5	6.0	22
	2.8	2.7	0.5	0.1	16.9	2.1	3.7	22
Oral bulge, width	7.6	7.5	1.4	0.3	18.4	6.0	10.0	18
	3.3	3.0	–	–	–	3.0	4.0	21
Oral bulge, height	1.3	1.3	–	–	–	1.0	1.5	16
	1.5	1.5	–	–	–	1.0	1.5	21
Anterior body end to macronucleus, distance	81.5	75.5	16.1	3.4	19.7	50.0	120.0	22
	14.7	15.0	2.8	0.6	19.1	10.0	19.0	21
Macronucleus figure, length	41.7	41.0	4.7	1.1	11.2	34.0	53.0	19
	–	–	–	–	–	–	–	–
Macronucleus nodules, length	20.1	20.5	3.0	0.6	15.0	15.0	25.0	22
	14.6	14.0	1.9	0.4	13.0	11.0	19.0	21
Macronucleus nodules, width	11.4	11.0	1.9	0.4	16.4	9.0	15.0	22
	5.4	5.0	0.5	0.1	10.0	4.0	6.0	21
Micronucleus, diameter without membrane ^a	2.3	2.5	–	–	–	2.0	2.5	20
	2.6	2.5	–	–	–	2.0	4.0	16
Micronucleus, diameter with membrane	3.9	4.0	0.6	0.1	15.3	3.0	5.0	20
	–	–	–	–	–	–	–	–
Somatic ciliary rows, number	26.2	26.0	0.9	0.3	3.5	25.0	28.0	10
	12.4	12.0	1.1	0.3	9.0	10.0	14.0	19
Kinetids in a ventral kinety, number ^b	63.7	60.0	8.8	2.0	13.8	50.0	80.0	19
	29.7	28.5	3.8	0.9	12.8	26.0	39.0	18
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	13
Dikinetids in brush row 1, number	22.0	22.0	1.7	0.5	7.6	20.0	25.0	11
	6.7	7.0	0.8	0.2	11.2	5.0	8.0	13
Dikinetids in brush row 2, number	26.5	27.0	3.0	0.8	11.4	23.0	32.0	13
	8.1	8.0	1.0	0.3	12.2	6.0	10.0	15
Dikinetids in brush row 3, number	27.1	26.5	2.2	0.6	8.3	24.0	32.0	14
	4.6	4.5	0.7	0.2	15.2	4.0	6.0	10
Brush row 1, length ^c	52.1	53.0	6.4	1.8	12.3	41.0	63.0	13
	7.4	7.0	1.3	0.4	18.0	6.0	10.0	13
Brush row 2, length ^c	59.6	57.5	9.0	2.4	15.1	46.0	75.0	14
	8.7	9.0	0.8	0.2	9.4	8.0	11.0	15
Brush row 3, length ^c	59.7	58.5	8.7	2.3	14.5	48.0	75.0	14
	4.8	4.5	1.0	0.3	21.5	4.0	7.0	10

^a Micronucleus of *Coriplites proctori* disk-shaped, thus diameter corresponds to length in side view.

^b Including ciliated and unciliated basal bodies.

^c Distance between circumoral kinety and last dikinetid of row.



Figs 3a–g. *Coriplites grandis* from life (a, b) and after protargol impregnation (c–g); **a, b** – surface view (a) and optical section (b) showing the conspicuous cortical granulation and the thick cortex (opposed arrowheads); specimen broadened by coverslip pressure; **c, d** – body shape and nuclear pattern of paratype (c) and holotype (d) specimen; **e, f** – dorsal and ventral view of anterior portion of holotype specimen showing somatic and oral ciliature. Note the widely spaced dikinetids of the dorsal brush; **g** – infraciliature of right anterior body portion. Nematodesmata originate from the circumoral dikinetids and the anterior basal bodies of the ciliary rows. B(1–3) – dorsal brush (rows), CK – circumoral kinety, FV – food vacuole, MA – macronucleus, MI – micronucleus, LD – lipid droplets, N – nematodesmata originating from somatic, oralized monokinetids, OB – oral bulge. Scale bars 50 μm (c, d) and 20 μm (a, b, e–g).

tifiable in the food vacuoles. Moves serpentine and rather slowly by rotation about main body axis.

Cilia about 10 μm long *in vivo*, ordinarily spaced, arranged in an average of 26 longitudinal, equidistant, ordinarily spaced rows more densely ciliated around oral entrance in some specimens (Figs 2e–g, 3d–f; Table 2). Dorsal brush isostichad, occupies an average of 40% of body length, bristles up to 3 μm long; brush row 1 slightly shorter than rows 2 and 3, composed of about 22 dikinetids, rows 2 and 3 each composed of an average of 27 dikinetids. Row 1 dikinetids associated with a longer anterior and a shorter posterior bristle, rows 2 and 3 composed of slightly inflated bristles of same length (Figs 2a, d, e, h, 3d, e); at least row 3 followed by a monokinetidal bristle tail.

Oral bulge broadly elliptical, inconspicuous because low and indistinctly set off from body proper, about 8 μm wide and 1–2 μm high *in vivo*, slightly depressed in centre. Nematodesmata about 20 μm long, originate from 12–16 oralized somatic monokinetids at anterior end of ciliary rows and from circumoral dikinetids at base of oral bulge (Figs 2h, 3f, g). Circumoral kinety composed of vertically orientated dikinetids.

Occurrence and ecology: To date found only at type locality and in two soil samples from Erldunda, a village in the surroundings of Alice Springs, Central Australia. Thus, *Coriplites grandis* is possibly restricted to this continent. The soil from type locality was grey and had pH 3.8, while it was red and circumneutral (pH 6.3) in one of the samples from Central Australia. Both samples contained much litter and many fine roots. *Coriplites grandis* from type locality reached significant abundance in the non-flooded Petri dish culture one month after rewetting, whereas the two populations from Alice Springs appeared already two weeks, respectively, three days after rewetting of the sample, suggesting different ecotypes.

Comparison with related species: *Coriplites grandis* can hardly be confused with other haptorids because few show such conspicuous body shape and nuclear pattern. Nearly all of them, including *C. terricola*, are much smaller (< 100 μm) and have less than half the number of ciliary rows. Species with the same nuclear pattern are, *inter alia*, *Apocoriplites lajacola*, *Cultellothrix* spp. (Foissner & Xu 2007), *Epitholiolus chilensis* and *Apoenchelys bamforthi* (Foissner *et al.* 2002); the latter is the only one reaching a similar length as *Coriplites grandis*.

***Coriplites proctori* nov. spec. (Figs 4a–i, 6f, g; Table 2)**

Diagnosis: Size about 65 \times 25 μm *in vivo*; bursiform and slightly curved. Macronucleus oblong with single discoidal micronucleus attached laterally. On average 12 ciliary rows, three anteriorly differentiated to a heterostichad dorsal brush occupying about 20% of body length.

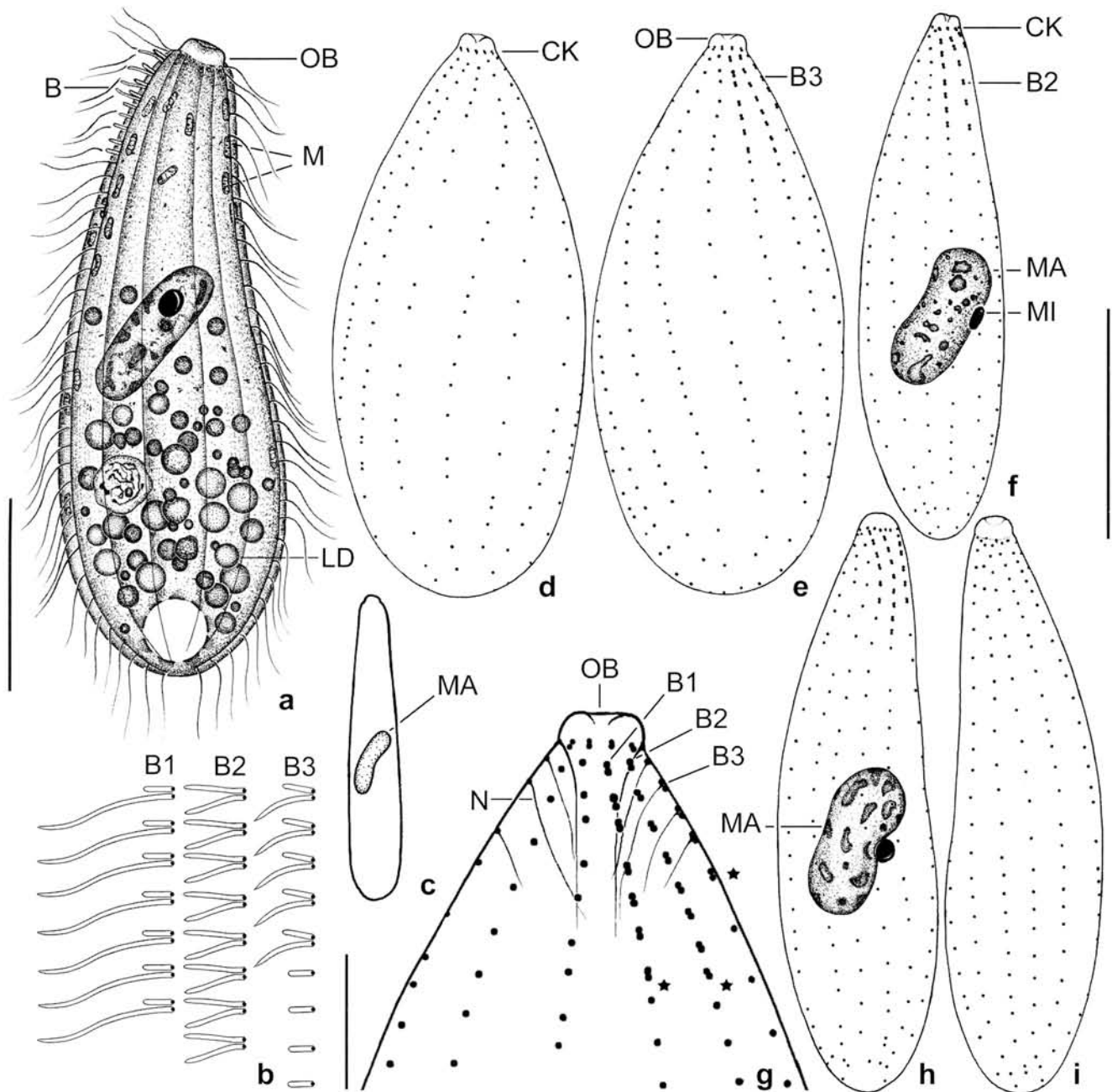
Type locality: Tanks of *Achmea paniculigera* (Bromeliaceae) in western Jamaica, *i.e.*, near the road between the villages of Aberdeen and Quick Step (parish St. Elizabeth), E77°42' N18°13'. *Achmea paniculigera* is endemic to Jamaica (Adams 1972).

Type material: One holotype slide and 2 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Dedication: This species is named in honour of the famous botanist Dr. Georg R. Proctor (Jamaica Museum of Natural History, Kingston), who joined our field trips in February 2008 and identified the bromeliads to species level.

Description: As the specimens shrank considerably, *i.e.*, about 35% due to alcohol fixation and protargol preparation, we base data on average *in vivo* bodysize.

Size 50–80 \times 20–30 μm *in vivo*, usually near 65 \times 25 μm ; length:width ratio on average 2–4:1, both *in vivo* and in protargol preparations (Table 2). Shape of ordinary specimens bursiform to almost ellipsoidal; unflattened; anterior half narrowed and brush side moderately convex, ventral side flat, slightly concave or slightly convex, specimens thus somewhat asymmetrical (Figs 4a, c, d–f, h, i, 6f, g). Theronts more slender (~6:1) and almost cylindrical (Fig. 4c, 6f), trophonts distinctly bursiform (2–3:1; Figs 4d, e, 6g). Macronucleus in, slightly anterior, rarely posterior of mid-body, frequently reniform or oblong and about 15 μm long in protargol preparations; nucleoli of various shapes, scattered. Micronucleus discoidal, 2–4 \times 0.5 μm , attached to macronucleus laterally (Figs 4a, f, h, 6f, g; Table 2). Contractile vacuole in rear end. No oral extrusomes detectable in the light microscope. Cortex flexible, colourless, rather distinctly furrowed by ciliary rows, granulation as distinct as in congeners (Fig. 4a). Cytoplasm colourless, rather hyaline, especially in anterior third containing some faint structures, 2.5 \times 1 μm , likely mitochondria; main body portion more or less opaque due to lipid droplets 1–3 μm across and some food vacuoles with remnants of small ciliates (Fig. 4a). Moves rather rapidly.



Figs 4a–i. *Coriplites proctori* from life (a–c) and after protargol impregnation (d–i). **a** – right side view of a representative specimen, length 65 μm . Note lack of oral extrusomes; **b** – dorsal brush; **c** – slender theront with reniform macronucleus; **d, e, g** – ventrolateral (d) and dorsolateral (e) view of ciliary pattern of the well-nourished, trophontic holotype specimen. End of dorsal brush rows marked by asterisks (g). Row 3 is shorter by more than 40% than row 2, and thus the brush is heterostichad. Nematodesmata supplemented from another specimen; **f, h, i** – dorsolateral (f, h) and ventrolateral (i) views of ciliary and nuclear pattern of slender paratype specimens (theronts). Note the discoidal micronucleus attached to the reniform macronucleus. B(1–3) – dorsal brush (rows), CK – circumoral kinety, LD – lipid droplets, M – mitochondria, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 20 μm (a, d–f, h, i) and 5 μm (g).

Cilia about 8 μm long *in vivo*, ordinarily spaced, arranged in an average of 12 longitudinal or slightly spiral, equidistant, ordinarily spaced rows more densely

ciliated anteriorly than posteriorly (Figs 4a, d–f, h, i; Table 2). Dorsal brush heterostichad, occupies an average of 20% of body length, dikinetids widely spaced

in vivo while ordinarily in protargol preparations due to the heavy shrinkage mentioned above. Rows 1 and 2 of nearly same length, row 1 composed of an average of seven dikinetids with a bristle anteriorly and a normal cilium posteriorly; row 2 composed of about eight dikinetids having two bristles with 2.5 µm each; row 3 about half as long as rows 1 and 2, composed of four to six dikinetids each having a 1.5 µm long bristle anteriorly and a 3 µm long bristle posteriorly; dikinetids of row 3 followed by four to five monokinetids with 1.5 µm long bristles (Figs 4a, b, e–h, g).

Oral bulge rather distinctly set off from body proper, about 4–5 µm across and 1–2 µm high *in vivo*, slightly depressed in centre (Figs 4a, d–i). Nematodesmata originate from oralized somatic monokinetids at anterior end of each ciliary row and from the circumoral dikinetids at base of oral bulge (Figs 4g, 6g). Details of oral structures recognizable in only few specimens.

Occurrence and ecology: To date found at type locality, as described above, and in tanks of *Guzmania monostachia* from the grounds of Marshall's Pen, a Jamaican Great House close to Mandeville (parish Manchester), western Jamaica. *Guzmania monostachia* occurs in Jamaica and the Dominican Republic (Adams 1972).

Comparison with related species: *Coriplites proctori* differs from the congeners by the single, reniform macronucleus. It is easily confused with *Pleuroplites australis* Foissner, 1988 which, however, has a subapical extrusome bundle and a complex brush consisting of about eight rows. Likewise, it may be confused with *Enchelys gasterosteus*, as redescribed by Foissner *et al.* (1995), which, however, has 6–7 µm long extrusomes in the oral bulge.

Apocoriplites nov. gen.

Diagnosis: Fuscheriidae with two dorsal brush rows. Oral extrusomes not recognizable by light microscopic means.

Type species: *Apocoriplites lajacola* nov. spec.

Etymology: Composite of the Greek prefix *apo* (derived from), the Greek adjective *coris* (without) and the Greek noun *hoplites* (soldier), referring to the genus *Coriplites* and the lack of extrusomes, respectively. Masculine gender.

Comparison with related genera: The oral basket of *Apocoriplites lajacola* consists of nematodesmata originating from monokinetids in the anterior region of the somatic kineties and from oral dikinetids, which are clearly separated from the somatic ciliary rows and thus form

a distinct circumoral kinety. Accordingly, *Apocoriplites* belongs to the family Fuscheriidae as defined by Foissner *et al.* (2002), specifically, it is related to *Coriplites* which also lacks detectable extrusomes, differing mainly by the number of dorsal brush rows, *viz.*, two *vs.* three. Admittedly, this is a rather inconspicuous generic feature which, however, likely represents a distinct evolutionary branch because the fairly large size of *Apocoriplites lajacola* excludes simple spatial constraints. The genus *Apoenchelys* is based on the same difference (Foissner *et al.* 2002). In *Coriplites* brush rows 2 and 3 are of similar composition and length as rows 1 and 2 in *Apocoriplites*, indicating loss of brush row 1 in the latter.

Apocoriplites lajacola nov. spec. (Figs 5a–i, 6a–e; Table 3)

Diagnosis: Size about 80 × 20 µm *in vivo*; cylindrical to elongate bursiform. Two globular macronucleus nodules with a micronucleus in between. On average 12 ciliary rows, two anteriorly differentiated to an isostichad dorsal brush occupying about 23% of body length and composed of widely spaced dikinetids.

Type locality: Mosses from a roadside Laja (granitic rock-pool) and from trees of a tropical dry forest (Selva Veranera) about 150 km NE of Puerto Ayacucho, Venezuela, E66°05' N7°.

Type material: One holotype slide and 5 paratype slides with protargol-impregnated specimens have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Named after the habitat found, *i.e.*, granitic rock-pools called "Laja" in Venezuela.

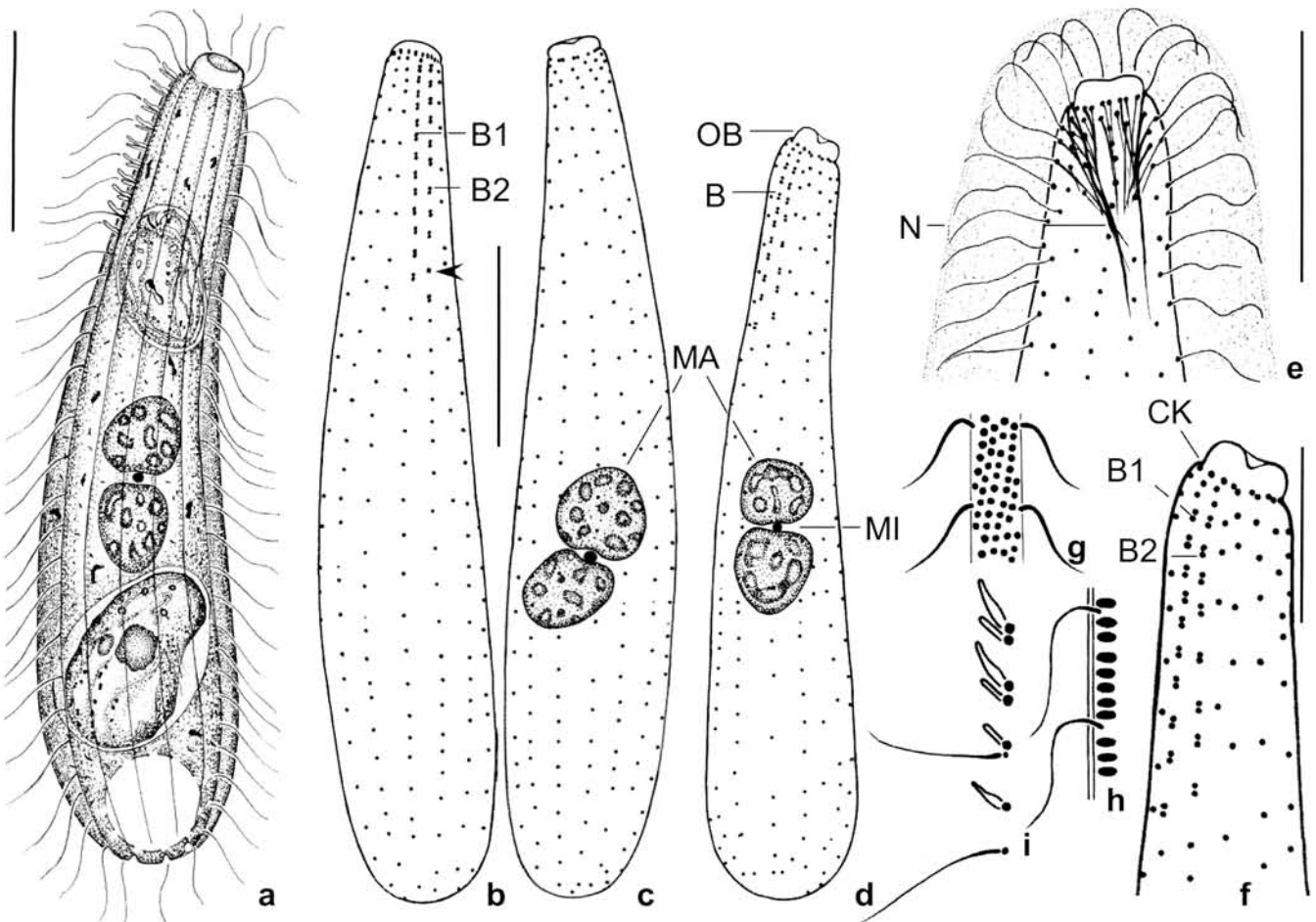
Description: Size 60–100 × 15–30 µm *in vivo*, usually about 80 × 20 µm, length:width ratio 3–6:1, on average 4:1 in protargol preparations (Table 3). Shape inconspicuous, cylindrical, elongate bursiform or indistinctly obclavate; unflattened and acontractile (Figs 5a–d, 6a, b). Nuclear apparatus at or slightly posterior to mid-body, conspicuous because composed of two globular, almost abutting macronucleus nodules and a minute, globular micronucleus in between; nucleoli scattered, numerous, globular, rarely forming oblong or irregular masses (Figs 5a, c, d, 6b; Table 3). Contractile vacuole in rear end, several excretory pores in pole area. No extrusomes detectable by light microscopy. Cortex very flexible, contains about four narrowly spaced rows of granules between adjacent kineties, probably mucocysts because cells are enveloped in a thick, slightly agyrophilic layer in protargol preparations; individual granules rather re-

fractive and about 1 (0.5 μm in size, thus forming distinct arrays (Figs 5e, g, h). Cytoplasm colourless, with some lipid droplets and food vacuoles 10–30 μm across, often containing almost intact small ciliates, mainly *Drepanomonas revoluta* and *Leptopharynx costatus* (Fig. 5a). Swims rather rapidly by rotation about main body axis.

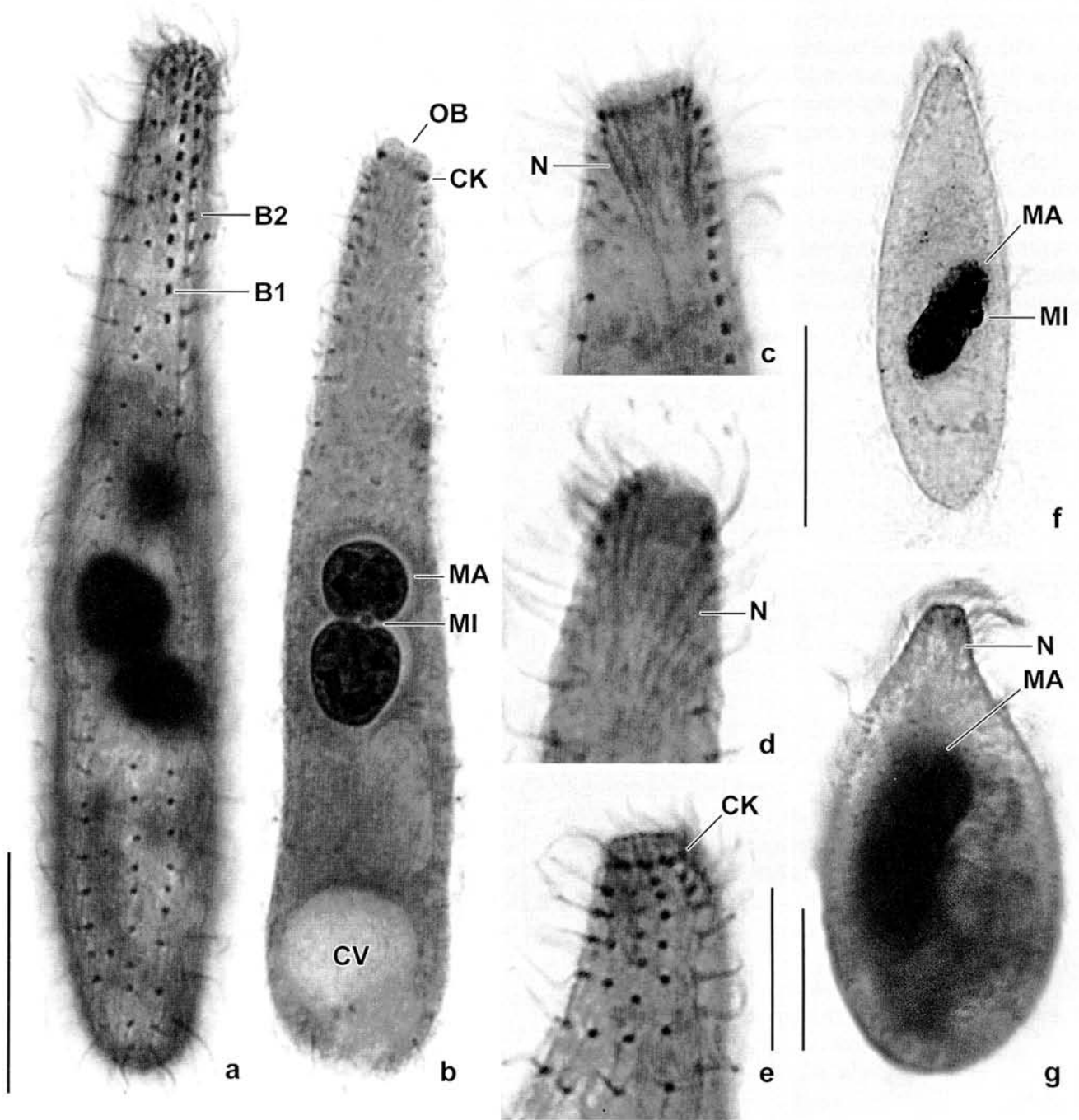
Cilia about 8 μm long *in vivo*, ordinarily spaced, arranged in an average of 12 longitudinal, equidistant rows slightly more densely ciliated and indistinctly curved in anterior region (Figs 5a–f, 6a, e; Table 3). Dorsal brush occupies an average of 23% of body length, inconspicuous because bristles only up to 3 μm long; both rows of about same length and composed of an average

of 10 widely spaced dikinetids in row 1 and of about 9 dikinetids in row 2; anterior tails composed of 1–2 monokinetids (Figs 5a, b, i, 6a); posterior region of row 2 heteromorphic in some specimens, that is, composed of dikinetids bearing a bristle and an ordinary cilium and monokinetids bearing ordinary cilia.

Oral bulge about 6 μm across and 2–3 μm high *in vivo*, small as compared to size of cell but fairly distinct because slightly set off from body proper and slightly depressed in centre (Figs 5a–f, 6b–e). Nematodesmata originate from about four oralized somatic monokinetids at anterior end of each ciliary row and from circumoral dikinetids at base of oral bulge, forming bundles some-



Figs 5a–i. *Apocoriplites lajacola* from life (a, g–i) and after protargol impregnation (b–f); **a** – right side view of a representative specimen having engulfed two *Drepanomonas* specimens, length 80 μm . Note lack of oral extrusomes; **b**, **c** – ciliary pattern of dorsal and ventral side and nuclear apparatus of holotype specimen. The brush rows have almost same length, and row 2 has a heteromorphic end, that is, a monokinetid (arrowhead) between the dikinetids; **d**, **f** – ciliary pattern of right side of a slender paratype specimen; **e** – ventral anterior portion showing the somatic and oral infraciliature and the slightly argyrophilic layer enveloping the cell; very likely the layer is composed of extruded mucocysts shown in Figures (g, h). Nematodesmata originate from the circumoral dikinetids and the anterior basal bodies of the ciliary rows; **g**, **h** – surface view and optical section showing cortical granulation; **i** – heteromorphic posterior portion of brush row 2. B(1, 2) – dorsal brush (rows), CK – circumoral kinety, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 20 μm (a–d, e) and 10 μm (f).



Figs 6a–g. *Apocoriplites lajacula* (a–e) and *Coriplites proctori* (f, g) after protargol impregnation. **a** – ciliary pattern of dorsal side of holotype specimen. The two brush rows have almost same length and are composed of widely spaced dikinetids; **b** – optical section of a slender paratype specimen showing body shape and the curious nuclear pattern made of two macronucleus nodules and a minute, globular micronucleus in between; **c**, **d** – optical sections showing the somatic and oral infraciliature. Nematodesmata originate from the circumoral dikinetids and the anterior basal bodies of the ciliary rows; **e** – left side view of anterior body portion. Ciliary rows slightly curved and more densely ciliated anteriorly. Circumoral kinety composed of slightly obliquely orientated dikinetids; **f** – slender specimen showing the main feature of this species, that is, the oblong macronucleus with a discoidal micronucleus attached laterally; **g** – broad trophont with reniform macronucleus. B(1–2) – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuole, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bars 20 μm (a, b, f) and 10 μm (c–e, g).

Table 3. Morphometric data on *Apocoriplites lajacola*. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected 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 error of arithmetic mean, \bar{X} – arithmetic mean.

Characteristics	\bar{X}	M	SD	SE	CV	Min	Max	n
Body, length	70.8	70.0	7.5	1.5	10.6	55.0	85.0	24
Body, width	17.6	16.8	3.0	0.6	16.9	14.0	25.0	24
Body length:width, ratio	4.1	4.0	0.8	0.2	18.8	2.9	5.6	24
Oral bulge, width	5.0	5.0	0.5	0.1	10.2	4.0	6.0	24
Oral bulge, height	2.0	2.0	–	–	–	1.5	2.0	24
Anterior body end to macronucleus, distance	30.7	33.0	6.9	1.4	22.6	17.0	41.0	23
Macronucleus, length	9.7	10.0	1.7	0.3	17.3	7.0	13.0	23
Macronucleus, width	6.8	6.0	1.1	0.2	16.6	5.0	9.0	23
Micronucleus, diameter	1.3	1.3	–	–	–	1.3	2.0	22
Somatic ciliary rows, number	12.4	12.0	1.0	0.2	7.8	11.0	15.0	24
Ciliated kinetids in a ventral kinety, number	25.6	26.0	4.0	0.8	15.4	19.0	37.0	24
Dorsal brush rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	23
Dikinetids in brush row 1, number	10.0	10.0	1.5	0.3	15.4	7.0	13.0	22
Dikinetids in brush row 2, number	9.0	9.0	1.4	0.3	15.7	7.0	12.0	22
Brush row 1, length ^a	15.9	15.0	2.5	0.5	15.9	10.0	21.0	22
Brush row 2, length ^a	15.6	15.0	2.9	0.6	18.8	10.0	24.0	22

^aDistance between circumoral kinety and last dikinetid of row.

times crossing each other and extending to second third of body (Figs 5e, 6c, d). Circumoral kinety composed of slightly obliquely orientated dikinetids (Figs 5f, 6e), frequently with some irregularities, such as monokinetids and small, staggering fragments; irregularities possibly caused by a previous conjugation, as indicated by exconjugants with four globular macronucleus nodules in the protargol preparations.

Occurrence and ecology: As yet found only at type locality. Likely, it is a moss or soil species. *Apocoriplites lajacola* reached moderate abundance in the non-flooded Petri dish culture one month after rewetting the sample, indicating, that it is a k-selected species.

Comparison with related species: *Apocoriplites lajacola* is highly similar to *Coriplites terricola*, differing mainly by the number of dorsal brush rows (two vs. three); further, it is slightly larger ($80 \times 20 \mu\text{m}$ vs. $60 \times 13 \mu\text{m}$). *Apocoriplites lajacola* is not identical with

any of the species compared by Foissner (1988) on occasion of the description of *Coriplites terricola*. As other coriplitids, *Apocoriplites lajacola* is rather easily identified *in vivo* by the lack of oral extrusomes and the distinct cortical granulation.

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