

The Infraciliature of *Cryptopharynx setigerus* KAHL, 1928 and *Apocryptopharynx hippocampoides* nov. gen., nov. spec. (Ciliophora, Karyorelictea), with an Account on Evolution in Loxodid Ciliates

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Summary: The morphology and infraciliature of *Cryptopharynx setigerus* KAHL, 1928, *Cryptopharynx* spp., and *Apocryptopharynx hippocampoides* nov. gen., nov. spec. were studied in live and protargol impregnated specimens. The entire somatic and oral infraciliature consists of dikinetids which have both or only the anterior basal bodies ciliated, depending on the region of the cell. The right side is densely ciliated. Its most remarkable specialization is a kinety which extends on the dorsolateral margin from mid-body along the broadly rounded posterior end to the postoral ventral surface. The left side bears a single ciliary row which extends along the cell margins, i.e. is almost circular. The oral infraciliatures of *Cryptopharynx* and *Apocryptopharynx* are, like the somatic infraciliatures, very similar to those of *Loxodes* and *Remanella*, i.e. consist of two specialized buccal kineties which extend along the right, anterior, and left margin of the buccal overture. These kineties form a paroral ciliature and very likely evolved from somatic ciliary rows, providing support for SMALL's hypothesis that the oral ciliature of the ciliates is of somatic origin. An intrabuccal kinety extends within the buccal cavity; possibly, it is part of the left lateral ciliature and would then be an adoral. The intrabuccal kinety is slightly curved in *Cryptopharynx* and clip-shaped elongated in *Apocryptopharynx hippocampoides* and *C. wardi* SMALL & LYNN, 1985, which is thus transferred to the new genus: *Apocryptopharynx wardi* (SMALL & LYNN, 1985) nov. comb. The family Cryptopharyngidae JANKOWSKI, 1980 is recognized and redefined. A phylogenetic (cladistic) system of loxodid ciliates is outlined, i.e. the Loxodida are defined with two synapomorphies (dorsolateral kinety, epipellicular mucus and/or scales) as monophyletic order containing three families, viz. Loxodidae (genera *Loxodes*, *Remanella*), Cryptopharyngidae (*Cryptopharynx*, *Apocryptopharynx* and, possibly, *Ciliofaurea*), and Kentrophoridae (*Kentrophoros*). Taxonomy and nomenclature of all supraspecific taxa are revised and refined definitions are provided.

Key Words: *Apocryptopharynx hippocampoides* nov. gen., nov. spec.; *Cryptopharynx setigerus*; Evolution; Infraciliature; Loxodida; Phylogeny.

Introduction

Scarce literature is available on *Cryptopharynx*, a small group of psammobiontic, karyorelictid ciliates. The most detailed studies date back to KAHL (1928), the founder of the genus, and KIRBY (1934), who reinvestigated the type species, *C. setigerus*. In the sixties, DRAGESCO (1960, 1965) described some new species

using, however, live observation only, like his predecessors. Very lately, SMALL & LYNN (1985) provided a single diagram of the ciliary pattern from protargol (silver) impregnated specimens of *C. wardi*, a new species overlooked in CAREY's (1992) compilation of marine interstitial ciliates. Although SMALL & LYNN's diagram

is highly schematized, the main conclusion that *Cryptopharynx* belongs to the loxodids is confirmed by the present results, which show for the first time detailed micrographs and diagrams of several cryptopharyngids, including a new genus and species, *Apocryptopharynx hippocampoides*.

With the present account, all genera, except for *Ciliofaurea* DRAGESCO, 1960, commonly assigned to the Loxodida have been reinvestigated with modern methods (DRAGESCO & DRAGESCO-KERNÉIS 1986; FOISSNER 1995, 1996a; FOISSNER & RIEDER 1983; PUYTORAC & NJINÉ 1970). The time is thus ripe for undertaking some speculations on their phylogeny and evolution.

Materials and Methods, Type Specimens, Terminology

The species described occurred sparsely in the mesopsammon of the French Atlantic coast at Roscoff. Samples were collected and treated exactly as described by FAURÉ-FREMIET (1951), i.e. the specimens were detached from the sand grains by adding about 5 ml of a 12% MgCl₂ solution to about 20 ml sand and sea water. The mixture was then gently rotated in a Petri dish so that the sand collected in the center and the ciliates could be picked up individually with a capillary pipette from the clear supernatant.

Cells were studied *in vivo* using a high-power oil immersion objective and differential interference contrast (FOISSNER 1991). The infraciliature was revealed by protargol impregnation [FOISSNER 1991; protocols 1 (FOISSNER's method) and 2 (WILBERT's method)], using a special fixative invented by Jean DRAGESCO (pers. comm.): 5 ml glutaraldehyde (25%), 5 ml saturated, aqueous mercuric chloride, 3 ml aqueous osmium tetroxide (2%), and 1 ml glacial acetic acid are mixed just before use. Specimens are fixed for 15–30 min. and washed three times in distilled water.

Counts and measurements on silvered specimens were conducted at a magnification of X 1000. *In vivo* measurements were performed at magnifications of X 100–1000. Although these provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations or contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens are based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida.

No type slides of *C. setigerus* are mentioned in the literature. Thus, I have deposited two neotype slides with specimens prepared as described in the Österreichisches Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass. Two type slides of *Apocryptopharynx hippocampoides* were deposited at the same locality.

Terminology is according to CORLISS (1979) and FOISSNER (1995) and strictly descriptive because ontogenetic data are incomplete and conflicting (KLINDWORTH & BARDELE 1993; NJINÉ 1970; TUFFRAU 1961).

Results

Morphometric data shown in Tables 1, 2 are repeated in this section only as needed for clarity. All observations are from field material. Thus, it cannot be excluded that different species were mixed, although I excluded specimens which deviated in at least one prominent character (see *Cryptopharynx* spp. described below).

Improved definitions are provided for all supraspecific taxa in the last chapter of the discussion.

• Redescription of *Cryptopharynx setigerus* KAHL (Figs. 1–13, Table 1)

My *in vivo* observations on this species are not very detailed and match the careful descriptions and diagrams (Figs. 1–5) given by KAHL (1928) and KIRBY (1934) to which the reader is referred. However, I did not observe the pronounced size variability (33–96×21–45 μm) mentioned by these authors (Table 1). Possibly, it is caused by the fact that KAHL and KIRBY combined observations from several populations, which usually increases variability, or used material contaminated with specimens from another, similar species (see *Cryptopharynx* sp. 1, described below). Very likely, they did not confuse *C. setigerus* with *Apocryptopharynx hippocampoides* because both described the buccal overture as "oval", whereas that of *A. hippocampoides* is distinctly elliptical.

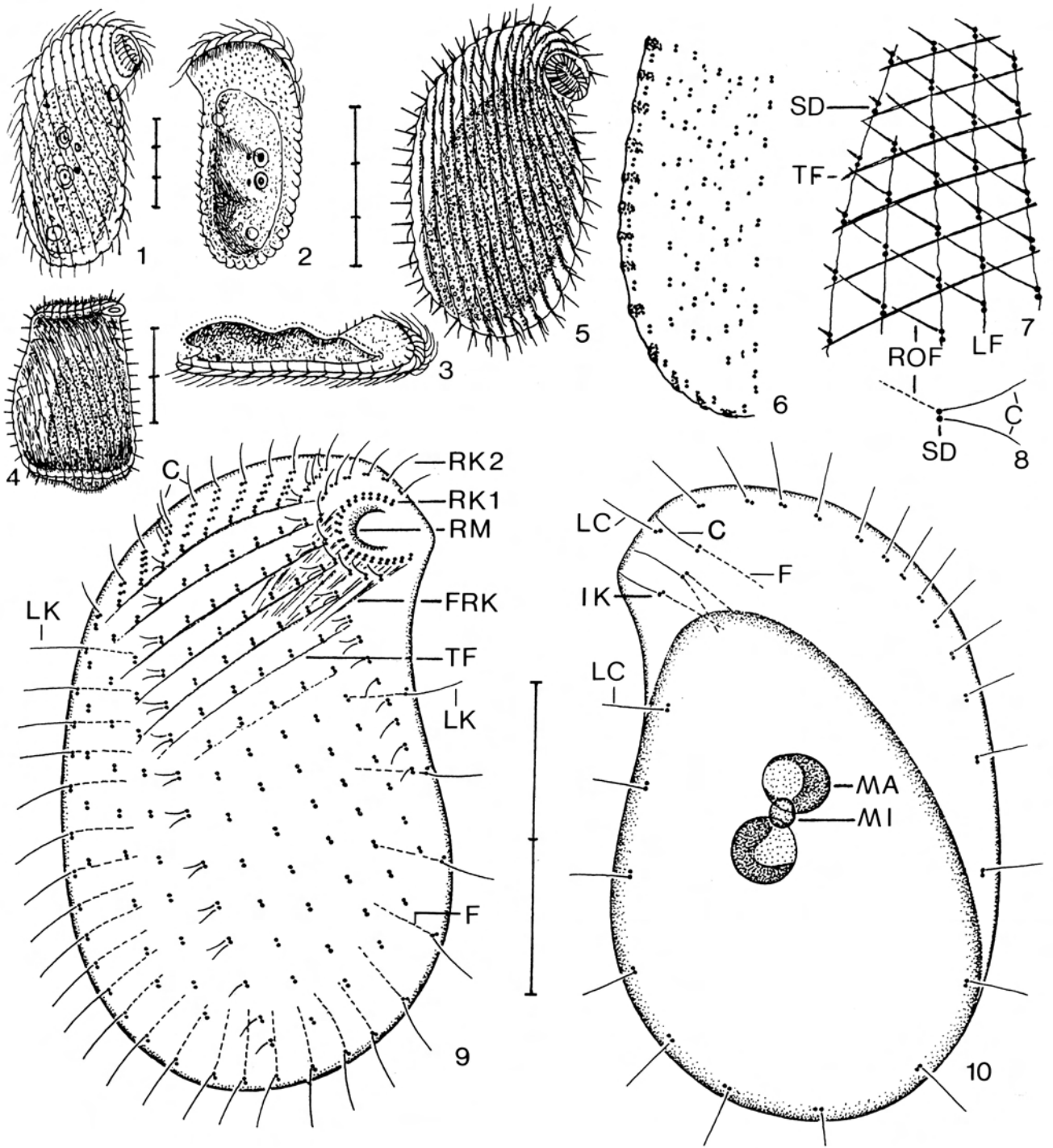
Right lateral somatic infraciliature: The right surface of *C. setigerus* is densely ciliated. The cilia are arranged in slightly oblique rows which extend between distinct cortical crests and are gradually shortened in the anterior right and posterior left portion of the cell (Figs. 9, 11–13). The crests contain few, strongly argyrophilic granules grouped to small clusters at the margins of the cell, especially between the dikinetids of the dorsolateral kinety (Fig. 6).

The entire infraciliature consists of dikinetids which, however, have a highly specialized ciliation and fibrillar system. The dikinetids are aligned approximately parallel to the kinety axes, except in the anterior portion of the kineties, where they become almost transversely orientated and more closely spaced, forming a densely ciliated ribbon (Figs. 9, 11, 12). Both basal bodies of the dikinetids are ciliated in the main part of the cell. The posterior cilium is lacking in 1–5 dikinetids at the posterior end of the ciliary rows and in all anterior, transversely orientated dikinetids. The dikinetids are associated with three very faintly stained fibrillar systems which form a conspicuous lattice (Figs. 7, 8). The thick fibres, which extend obliquely across and closely underneath the kineties, are recognizable only in the anterior body half (Fig. 9). The fibrillar lattice is lacking or, at least, not stained in the anterior region of the cell

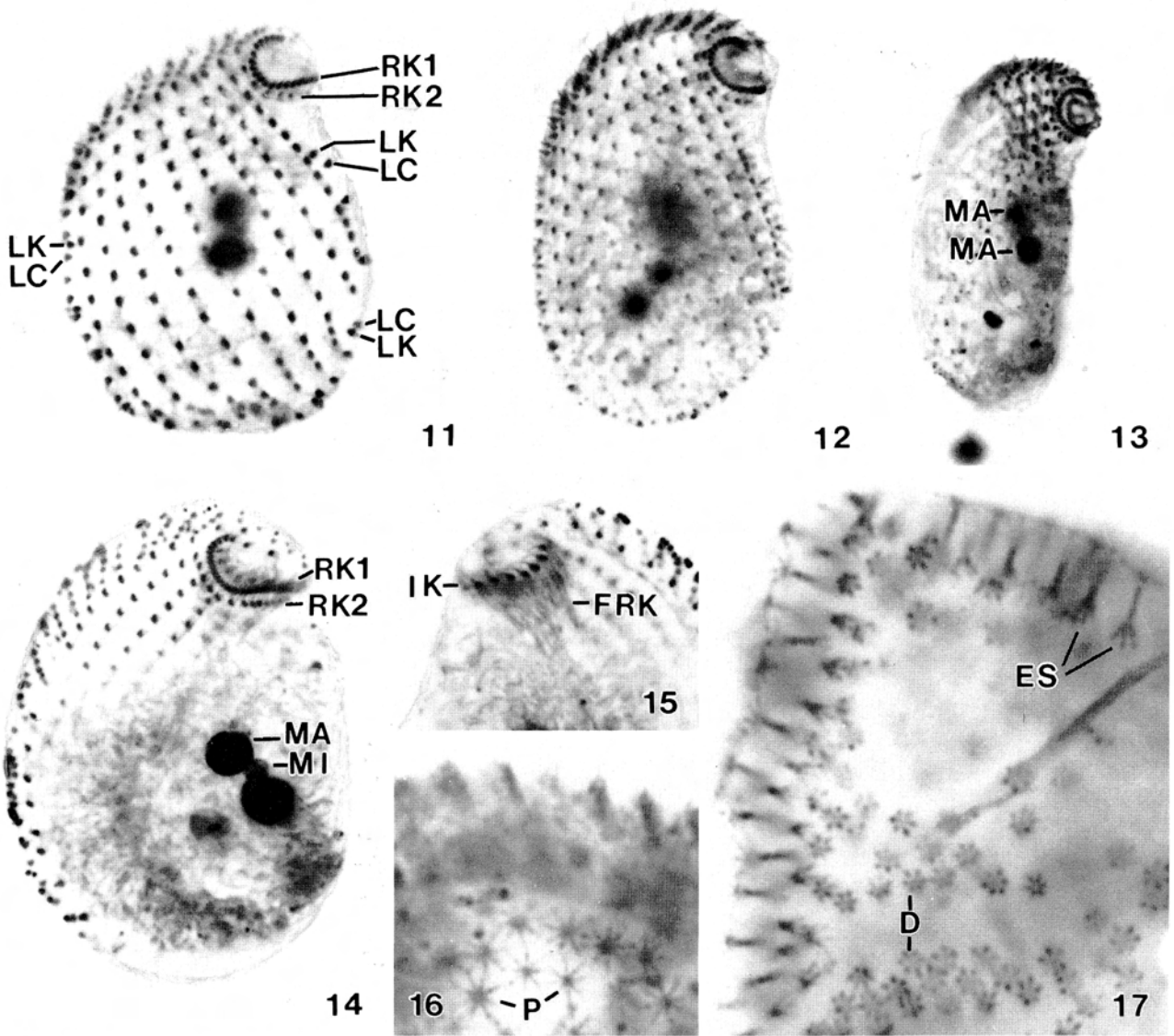
Table 1. Morphometric data from *Cryptopharynx setigerus*. First line: WILBERT's protargol method; second line: FOISSNER's protargol method; third line: all specimens combined¹⁾.

Character	\bar{x}	M	SD	SD $_{\bar{x}}$	CV	Min	Max	n
Body, length	34.2	33.0	5.8	1.6	16.8	26	47	13
	32.6	32.0	5.1	1.6	15.7	25	40	10
	33.5	33.0	5.4	1.1	16.2	25	47	23
Anterior end to proximal vertex of 2nd buccal kinety, distance	7.7	7.0	1.8	0.5	23.9	5	11	13
	7.4	7.0	1.2	0.4	15.9	6	10	10
	7.6	7.0	1.6	0.3	20.5	5	11	23
Anterior end to upper macronucleus, distance	13.7	14.0	2.9	0.8	21.4	9	20	13
	13.2	13.5	2.5	0.8	18.8	10	18	10
	13.5	14.0	2.7	0.6	20.0	9	20	23
Body, maximum postoral width	21.5	21.0	3.4	0.9	15.7	16	27	13
	16.0	16.0	2.3	0.7	14.1	13	19	10
	19.1	19.0	4.0	0.8	20.9	13	27	23
Left body margin to farthest point of intrabuccal kinety, distance	2.9	3.0	0.7	0.2	23.2	2	4	13
	2.7	2.5	0.3	0.1	9.6	2.5	3	10
	2.8	2.5	0.5	0.1	19.1	2	4	23
Chord of 2nd buccal kinety, length	6.2	6.0	0.7	0.2	11.7	5	8	13
	5.8	5.8	1.0	0.3	17.3	5	8	10
	6.1	6.0	0.9	0.2	14.0	5	8	23
Macronuclei, length	4.0	4.0	0.7	0.2	17.7	3	5	13
	3.3	3.5	0.3	0.1	7.8	3	4	10
	3.7	3.5	0.7	0.1	17.6	3	5	23
Macronuclei, width	3.5	3.5	0.5	0.1	14.8	2.5	4	13
	2.9	3.0	0.4	0.1	13.6	2.5	3.5	10
	3.2	3.0	0.5	0.1	16.9	2.5	4	23
Micronucleus, length	1.6	1.5	0.4	0.1	24.7	1	2.5	13
	1.5	1.5	0.2	0.1	15.7	1	2	10
	1.6	1.5	0.3	0.1	20.9	1	2.5	23
Micronucleus, width	1.5	1.5	0.4	0.1	25.9	0.8	2.5	13
	1.4	1.5	0.2	0.1	10.9	1	1.5	10
	1.5	1.5	0.3	0.1	20.5	0.8	2.5	23
Macronuclei, number	2.0	2.0	0.0	0.0	0.0	2	2	13
	2.0	2.0	–	–	–	2	3	10
	2.0	2.0	–	–	–	2	3	23
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1	1	13
	1.0	1.0	0.0	0.0	0.0	1	1	10
	1.0	1.0	0.0	0.0	0.0	1	1	23
Somatic kineties in mid-body, number	8.9	9.0	1.4	0.4	15.5	6	10	13
	9.4	10.0	1.3	0.4	14.4	6	11	10
	9.1	10.0	1.4	0.3	14.9	6	11	23
Dikinetids in median somatic kinety, total number	17.3	18.0	1.8	0.5	10.1	14	19	13
	16.8	17.0	2.1	0.7	12.5	14	20	10
	17.1	18.0	1.9	0.4	11.0	14	20	23
Oblique dikinetids in median somatic kinety, number	3.8	4.0	–	–	–	3	4	13
	3.7	4.0	–	–	–	3	4	10
	3.7	4.0	–	–	–	3	4	23
Dikinetids in 1st buccal kinety, number	19.9	20.0	3.0	0.8	14.9	14	26	13
	18.9	19.0	1.4	0.5	7.7	17	22	10
	19.5	19.0	2.4	0.5	12.5	14	26	23
Dikinetids in 2nd buccal kinety, number	10.8	11.0	2.2	0.6	20.7	5	14	13
	9.8	10.0	1.1	0.4	11.6	8	12	10
	10.4	11.0	1.9	0.4	18.0	5	14	23
Dikinetids in intrabuccal kinety, number	3.0	3.0	–	–	–	3	4	13
	3.0	3.0	–	–	–	3	4	10
	3.1	3.0	–	–	–	3	4	23

¹⁾ Data based on protargol-impregnated and mounted specimens from field. Measurements in μm . Abbreviations: CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SD $_{\bar{x}}$ – standard deviation of mean, \bar{x} – arithmetic mean.



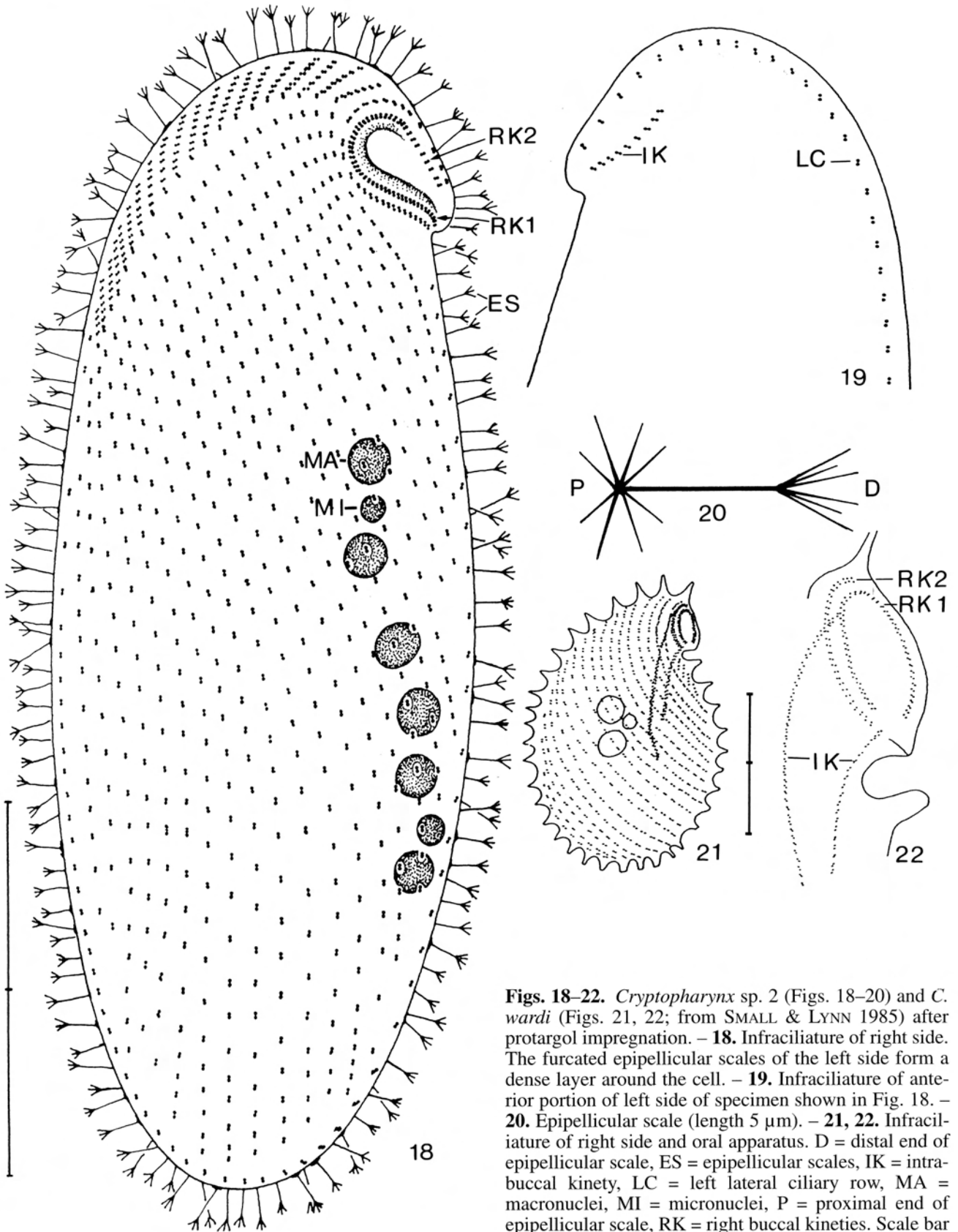
Figs. 1-10. *Cryptopharynx setigerus* from life (Figs. 1-5) and after protargol impregnation (Figs. 6-10). Figures 1-3 from KAHL (1931), Figs. 4, 5 from KIRBY (1934), Figs. 6-10 originals. - 1, 5. Right lateral views. - 2, 3. Left lateral and dorsal view. - 4. Specimen partially curled right laterally. - 6. Cortical granulation in right posterior region of right side. - 7, 8. Fibrillar system in centre of right side of anterior half (cp. Fig. 9). - 9, 10. Infraciliature of right and left side. C = cilia, F = fibres, FRK = fibres originating from buccal kineties, IK = intrabuccal kinety, LC = left lateral ciliary row, LF = longitudinal fibre in kinety axis, LK = dorsolateral kinety, MA = macronuclei, MI = micronucleus, RK = right buccal kineties, RM = right margin of buccal overture, ROF = right-oblique fibre, SD = somatic dikinetid, TF = thick fibre bridging kineties transversely in anterior region of right side. Scale bar division 10 μ m.



Figs. 11–17. *Cryptopharynx setigerus* (Figs. 11–13) and *Cryptopharynx* spp. (Figs. 14–17) after protargol impregnation. – 11, 12. Infraciliature of right side. Both the dorsolateral kinety (LK) and the left lateral ciliary row (LC) are recognizable because of the strong flattening of the cell. Note different (oblique) orientation and polymerization of dikinetids in anterior portion of right lateral somatic kineties. – 13. Specimen prepared with protargol protocol 1 showing typical shape of cell. – 14, 15. *Cryptopharynx* sp. 1 differs from *C. setigerus* by its slightly larger size and the longer intrabuccal kinety composed of about 8 dikinetids. – 16, 17. Anterior portion of left side of *Cryptopharynx* sp. 2, which differs from *C. setigerus* by its much larger size and the conspicuous epipellicular scales, forming a dense layer on the pellicle (cp. Figs. 18, 20). The scales are dumb-bell shaped (Fig. 17) and have 8 radiating processes at the proximal end (Fig. 16) and 6 at the distal (Fig. 17). D = distal end of epipellicular scales, ES = epipellicular scales, FRK = fibres originating from buccal kineties, IK = intrabuccal kinety, LC = left lateral ciliary row, LK = dorsolateral kinety, MA = macronuclei, MI = micronucleus, P = proximal end of epipellicular scales, RK = right buccal kineties.

where the dikinetids are transversely orientated (Fig. 9). The most interesting specializations are found in the rightmost kinety, which commences pre-equatorially and extends along the dorsolateral margin and the broadly rounded posterior end to the postoral ventral surface of the cell (Figs. 9, 11, 12). This U-shaped cil-

iary row, which is obviously homologous to the dorsolateral kinety found in *Loxodes* and *Remanella* (FOISSNER & RIEDER 1983; FOISSNER 1996a), only has the anterior basal bodies of the dikinetids ciliated (in the ventral portion, however, the posterior basal bodies appear ciliated, simple because the kinety curves



Figs. 18–22. *Cryptopharynx* sp. 2 (Figs. 18–20) and *C. wardi* (Figs. 21, 22; from SMALL & LYNN 1985) after protargol impregnation. – 18. Infraciliature of right side. The furcated epipellicular scales of the left side form a dense layer around the cell. – 19. Infraciliature of anterior portion of left side of specimen shown in Fig. 18. – 20. Epipellicular scale (length 5 μ m). – 21, 22. Infraciliature of right side and oral apparatus. D = distal end of epipellicular scale, ES = epipellicular scales, IK = intra-buccal kinety, LC = left lateral ciliary row, MA = macronuclei, MI = micronuclei, P = proximal end of epipellicular scale, RK = right buccal kineties. Scale bar division 20 μ m.

upward from the posterior end! Fig. 9). The cilia of the dorsolateral kinety are rather stiff, like those of the left lateral kinety (see below), and were thus misinterpreted as "pointed spines" by KAHL (1928) and KIRBY (1934). The ciliated basal body of the dikinetids of the dorsolateral kinety is associated with a fine, long fibre extending to the centre of the cell (Fig. 9). This fibre is very likely homologous to the "right oblique fibre" found in normal somatic dikinetids (Fig. 8).

Left lateral somatic infraciliature: The left side of *C. setigerus* is barren, except for the body margins, where widely spaced dikinetids with rather stiff cilia reside. A distinct gap, 1 - 2 dikinetids wide, occurs at the level of the oral apparatus. The anterior and dorsal dikinetids have the anterior basal bodies ciliated, whereas the postoral ventral dikinetids have the posterior basal body ciliated. Thus, the orientation of the left lateral dikinetids appears inverted by 180° both anterior and posterior of the gap (Figs. 10, 11). This peculiar pattern is most parsimoniously explained with the assumption of a single kinety extending along the body margins, quite similarly to the dorsolateral kinety (see above).

Oral infraciliature: The oral apparatus of *C. setigerus* is located on the broad, very flat prominence at the anterior left end of the cell. The buccal overture is roundish to broadly elliptical and usually only its right margin is distinct. A buccal cavity is not recognizable although distinct fibres originate from the buccal kineties (Figs. 9, 15).

The oral infraciliature is simple and composed of three differently organized kineties (Figs. 9, 10, 11-13). Two kineties (right buccal kineties 1, 2) extend semicircularly around the right, anterior and posterior margin of the buccal overture. Buccal kinety 1 is composed of closely spaced dikinetids very likely having only the outer (right) basal bodies ciliated. Buccal kinety 2 consists of comparatively widely spaced dikinetids which have the anterior basal body ciliated. Distinct fibres originate from the dikinetids of both right buccal kineties and extend obliquely dorsad, forming some sort of oral basket. Very likely, these fibres originate from both basal bodies of the dikinetids.

The third buccal kinety, which is very likely located within the buccal cavity, consists of 3-4 dikinetids only. The dikinetids of this intrabuccal kinety form a short, slightly curved row and have the posterior basal body ciliated. Each kinetid is associated with a delicate fibre originating from the barren basal body; in the central dikinetid(s) both basal bodies have such a fibre.

• *Cryptopharynx* sp. 1 (Figs. 14, 15)

This species, of which I found only few specimens in the protargol slides, is very similar to *C. setigerus*. However, it is slightly larger (about 50 µm), has more

somatic kineties (about 15), and the intrabuccal kinety is composed of about 8 dikinetids, forming a slightly curved row.

• *Cryptopharynx* sp. 2 (Figs. 16-20)

This species is obviously related to *C. kahli* DRAGESCO, 1954 (described, unfortunately, as a new taxon with a different name again by DRAGESCO 1960, viz. "*Cryptopharynx setigerum* KAHL var. *furcatum* n. var."), from which it differs by the less distinctly projecting oral area and the nuclear apparatus, which consists of about 6 macronuclei forming a distinct row near the ventral side.

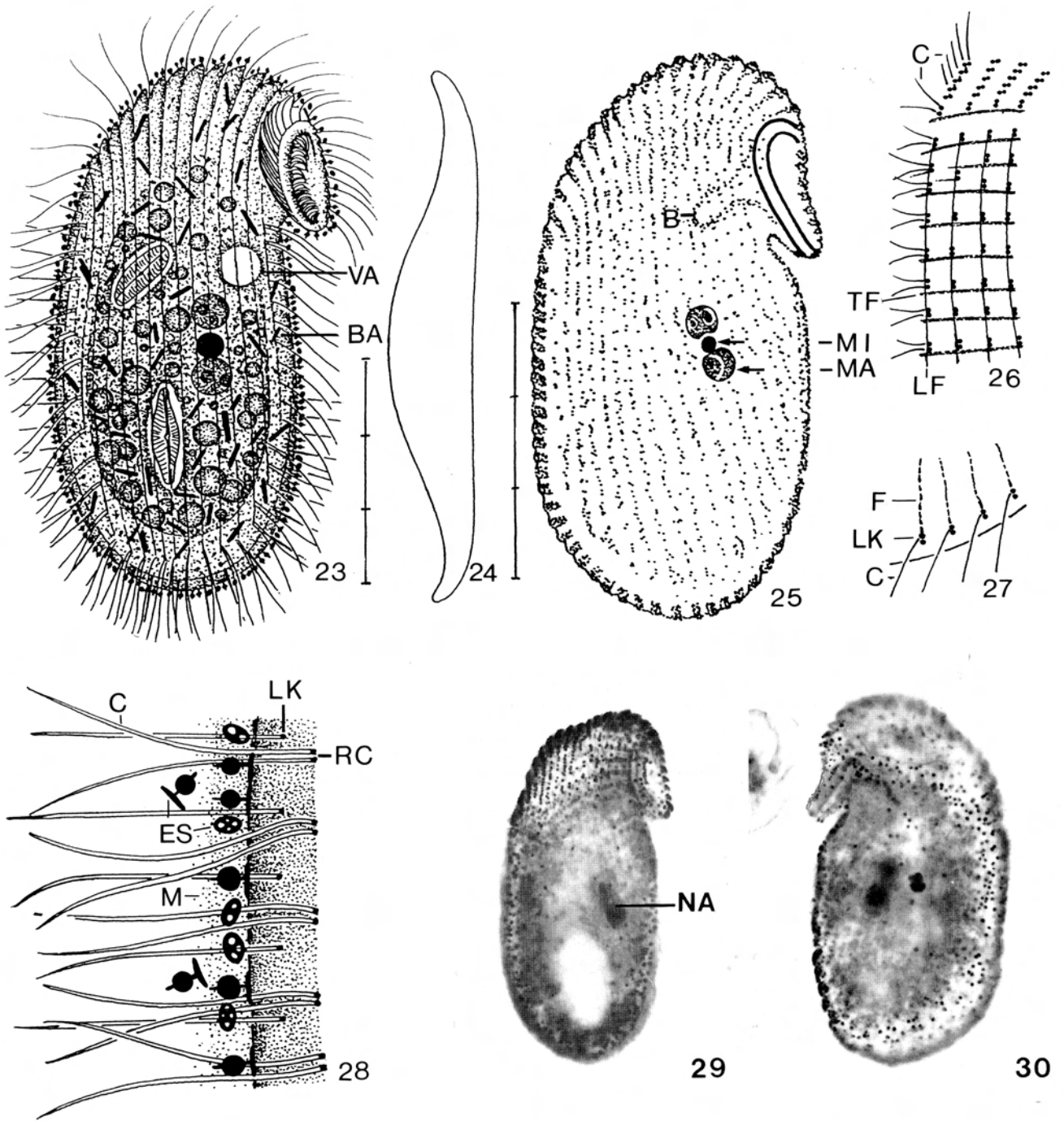
Unfortunately, I found only two specimens of this beautiful, large (length about 130 µm) organism in the slides and did not observe live cells. Thus, I do not describe it as new species, although it is very likely a new one, and the two specimens found were perfectly impregnated. The most conspicuous character is a left lateral lawn of tightly spaced, furcated scales. The scales are about 5 µm long and have 8 flatly radiating projections on the proximal end, and 6 distal processes forming a narrow cone (Figs. 16, 17, 20). The somatic infraciliature is identical to that described for *C. setigerus*, except for certain morphometric characters, of course. The oral infraciliature is also very similar to that of *C. setigerus*, but the buccal kineties extend not only along the right and anterior margins of the buccal overture but, like in *Apocryptopharynx hippocampoides*, also along the left margin, however, with dikinetids distinctly wider spaced than in the right portion. The intrabuccal kinety is a short, slightly curved row, as in *C. setigerus* and *Cryptopharynx* sp. 1.

• *Apocryptopharynx* nov. gen.

Diagnosis: Cryptopharyngidae JANKOWSKI with long, clip-shaped intrabuccal kinety extending deep into the organism.

Type species: *Apocryptopharynx hippocampoides* nov. spec.

Derivatio nominis and nomenclature: Composite of the Greek words "apo" (derived from) and "cryptopharynx" (hidden gullet). "Pharynx" is a noun of variable gender, masculine or feminine. According to article 30a (i) of the ICZN it has to be treated as masculine. KAHL (1928) did not fix the gender when establishing the genus, but used a masculine termination for the type species, viz. "setigerus". Thus, *Cryptopharynx* is without doubt of masculine gender and *Cryptopharynx multinucleatum* DRAGESCO, 1960 has, according to article 31b of the ICZN, to be corrected to *C. multinucleatus* DRAGESCO, 1960 nom. emend.



Figs. 23–30. *Apocryptopharynx hippocampoides* from life (Figs. 23, 24, 28) and after protargol impregnation (Figs. 25–27, 29, 30). – 23, 24. Right lateral and dorsal view. – 25, 29, 30. Cortical granulation of right and left side of typical, i.e. sea-horse shaped specimens; granules are found mainly between ciliary rows, in clusters between dorsolateral dikinetids, and around buccal cavity. – 26, 27. Somatic infraciliature of right side in anterior and posterior region of cell at high magnification. Note oblique orientation and polymerization of dikinetids in anterior portion of kineties. – 28. Optical section of right cell margin. The left side of the ciliate is covered with mucus and highly structured scales. Note dorsolateral kinety composed of single, stiff cilia. B = buccal cavity, BA = cytoplasmic bacteria, C = cilia, ES = epipellicular scales, F = fibre, LF = longitudinal fibre in kinety axis, LK = dorsolateral kinety, M = mucus, MA = macronuclei, MI = micronucleus, NA = nuclear apparatus, RC = right lateral ciliary row, TF = thick fibre bridging kineties transversely in anterior region of cell, VA = contractile (?) vacuole. Scale bar division 10 μ m.

Comparison with related genera: *Apocryptopharynx* differs from *Cryptopharynx* solely by the shape and length of the intrabuccal kinety. This might appear an insufficient character. However, the evolution of the intrabuccal kinety is obviously not correlated with that of the right buccal kineties and the body size, as evident from a comparison of *C. setigerus* and *Cryptopharynx* sp. 2 with *A. hippocampoides*: although being much larger than *A. hippocampoides*, *Cryptopharynx* sp. 2 has a short, inconspicuous intrabuccal kinety, very much like *C. setigerus*.

The epipellicular scales of *A. hippocampoides* are similar to the "ectoplasmatic inclusions" described by DRAGESCO (1960) in *Ciliofaurea mirabilis*, indicating some relationship between these genera.

• *Apocryptopharynx hippocampoides* nov. spec. (Figs. 23–41, Table 2)

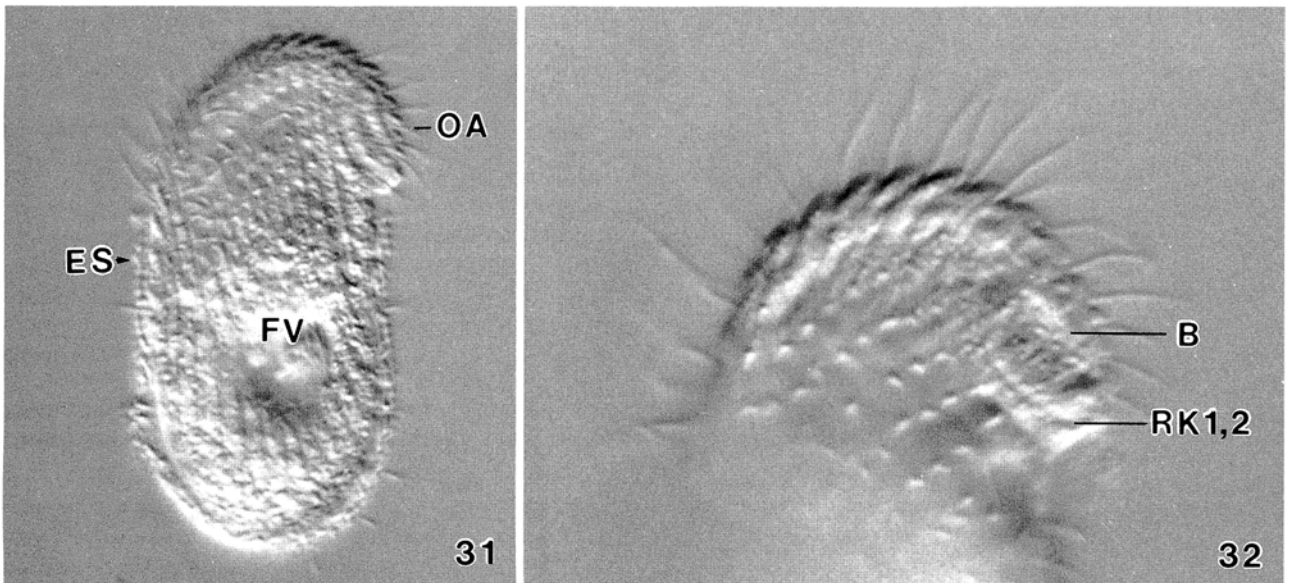
Diagnosis: In vivo about 50–90×30–40 μm, elliptical with protruding oral area. Colourless. 2 macronuclei with single interposed micronucleus near centre of cell. Left lateral surface covered with mucous material containing highly structured, globular epipellicular scales about 1 μm in size. 16 somatic kineties in mid-body on average. Right buccal kineties extend onto left margin

of buccal overture. Intrabuccal kinety consisting of about 22 dikinets.

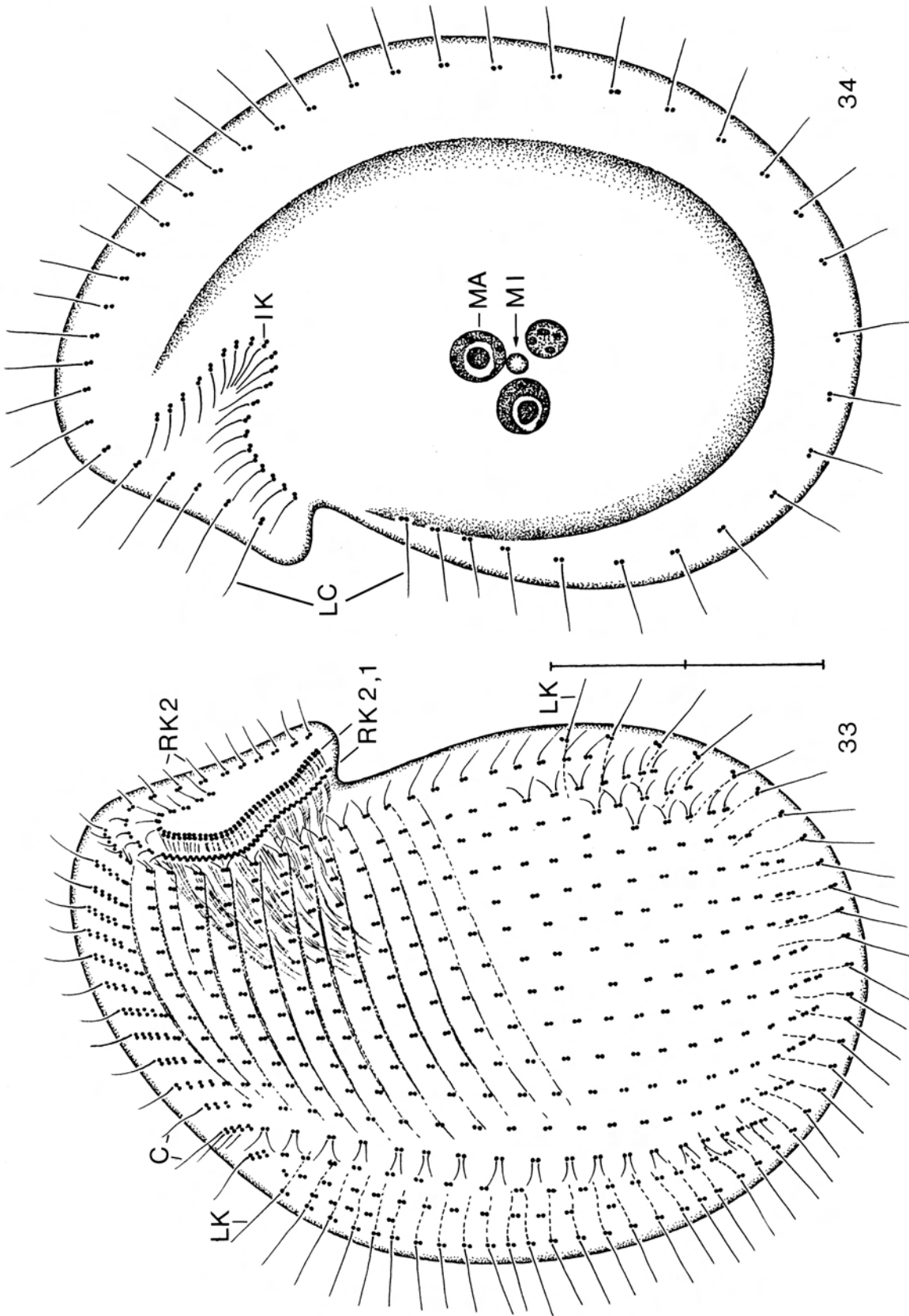
Type location: Mesopsammon of French Atlantic coast at Roscoff, W 4°, N 48° 50'.

Derivatio nominis: "hippocampoides" because the oral area resembles the head of a sea-horse (*Hippocampus*).

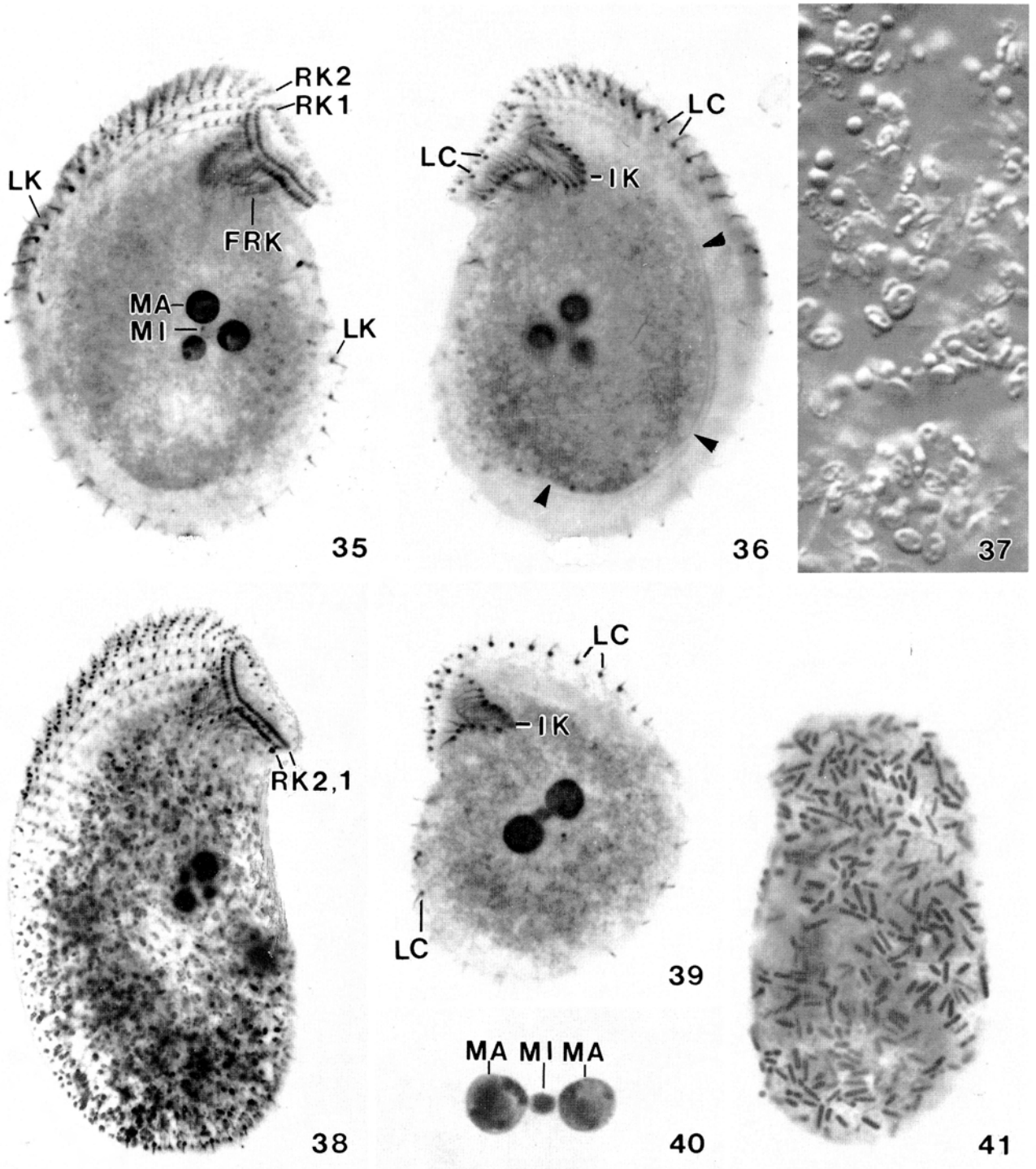
Description: Size of typical specimens in vivo about 70×30 μm. Shape ellipsoid, oral area usually distinctly protruding and deeply notched at posterior margin, producing sea-horse like appearance of anterior cell portion (Figs. 23, 25, 29, 30). Laterally distinctly, i.e. up to 3:1 flattened, oral area and cell margins especially so and thus very hyaline and flexible and often curled as described by KIRBY (1934) for *C. setigerus* (Fig. 4); anterior margin deeply notched by encroaching somatic kineties (Figs. 31, 32). Right side flat, left vaulted in central portion, producing more or less distinct sac filled with 1–4 μm sized, brightly shining fat globules and food vacuoles containing diatoms and unidentifiable debris (Figs. 23, 24, 31, 34, 36). Nuclear apparatus in mid-body left of cell median, macronuclei small (in vivo 5–6 μm) as compared to size of cell, with one large nucleolus or several small nucleoli; rarely cells with 3 or 4 macronuclei forming a cluster (Figs. 34, 35). Micronucleus in vivo about 4 μm in diameter, i.e. almost as large as macronuclei, compact and usually interposed between, rarely beside, macronuclei (Figs.



Figs. 31, 32. *Apocryptopharynx hippocampoides*, interference contrast light micrographs of living specimens. – 31. Right lateral view. Note fuzzy material (mucus and epipellicular scales) covering margin (left side) of cell, and slightly obliquely running, longitudinal cortical crests between ciliary rows. – 32. Anterior end at higher magnification. Note long, stiff cilia and flat buccal cavity. B = buccal cavity, ES = epipellicular scales, FV = food vacuole, OA = oral apparatus, RK = right buccal kineties.



Figs. 33, 34. *Apocryptopharynx hippocampoides*, infraciliature of right and left side after protargol impregnation (see Figs. 26, 27 for details of fibrillar system). C = cilia, IK = intrabuccal kinety, LC = left lateral ciliary row, LK = left lateral ciliary row, MA = macronucleus, MI = micronucleus, RK = right buccal kineties. Scale bar division 10 μ m.



Figs. 35–41. *Apocryptopharynx hippocampoides* from life (Fig. 37), after protargol impregnation (Figs. 35, 36, 38–40) and methyl green-pyronin staining (Fig. 41). – 35, 36, 38, 39. Infraciliature of right and left side. Note clip-shaped, invaginated intrabuccal kinety, the genus character. Arrowheads in Fig. 36 mark margins of left lateral hump. – 37. Surface view of left side showing many ellipsoid epipellicular scales embedded in mucuous material. – 40. Nuclear apparatus. – 41. The cytoplasm contains many rod-shaped bacteria. FRK = fibres originating from buccal kineties, IK = intrabuccal kinety, LC = left lateral ciliary row, LK = dorsolateral kinety, MA = macronuclei, MI = micronucleus, RK = right buccal kineties.

Table 2. Morphometric data from *Apocryptopharynx hippocampoides*¹⁾.

Character	Method ²⁾	\bar{x}	M	SD	SD _{\bar{x}}	CV	Min	Max	n
Body, length	W	57.3	52.5	14.1	3.3	24.5	43	90	18
	F	52.6	55.0	8.6	2.0	16.4	40	66	19
Anterior end to proximal vertex of 1st buccal kinety, distance	W	18.2	18.0	3.0	0.7	16.3	13	23	17
Anterior end to upper macronucleus, distance	W	26.1	22.5	9.6	2.3	36.6	17	57	18
Body, width	W	38.8	39.0	5.3	1.3	13.7	31	51	18
	F	30.6	30.0	4.6	1.1	15.0	26	40	19
Left body margin to farthest point of intrabuccal kinety, distance	W	13.8	14.0	2.7	0.7	19.4	10	21	16
Chord of 1st buccal kinety, length	W	14.5	14.0	2.5	0.6	17.4	12	20	17
Macronuclei, length	W	4.8	5.0	0.8	0.2	16.1	4	6.5	19
Macronuclei, width	W	4.6	5.0	0.6	0.1	13.5	4	6	19
Micronucleus, length	W	2.1	2.0	0.4	0.1	17.5	1.5	3	19
Micronucleus, width	W	2.0	2.0	0.4	0.1	17.6	1.5	2.5	19
Macronuclei, number	W	2.2	2.0	0.48	0.1	22.0	2	4	39
Micronuclei, number	W	1.0	1.0	–	–	–	1	2	39
Somatic kineties in mid-body, number	W	16.3	16.5	1.3	0.3	7.7	13	18	20
Dikinetids in median somatic kinety, total number	W	27.4	26.5	3.6	0.8	13.0	23	35	18
Oblique dikinetids in median somatic kinety, number	W	4.7	5.0	–	–	–	4	5	18
Dikinetids in 1st buccal kinety, number	W	46.2	46.5	6.1	1.8	13.2	37	55	12
Dikinetids in 2nd buccal kinety, number	W	34.7	35.0	6.6	1.7	19.1	21	44	15
Dikinetids in intrabuccal kinety, number	W	21.6	22.0	2.8	0.7	13.0	16	26	15

¹⁾ Data based on protargol-impregnated and mounted specimens from field. Measurements in μm . Abbreviations: CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SD _{\bar{x}} – standard deviation of mean, \bar{x} – arithmetic mean.

²⁾ WILBERT'S (W) and FOISSNER'S (F) method, respectively.

23, 25, 39, 40). A clear vacuole in postoral and sometimes also in subterminal ventral portion of cell; neither contractions nor excretory pores have been observed (Fig. 23).

Cortex bright, distinctly furrowed by ciliary rows and, respectively, cortical crests containing argyrophilic granules hardly recognizable in live cells and grouped to small clusters at cell margins, especially between dikinetids of dorsolateral kinety (Figs. 25, 29); granules irregularly distributed in left lateral cortex (Fig. 30), do not stain with methyl green-pyronin. Left surface densely covered with epipellicular scales embedded in thin, mucuous layer. Scales very small, i.e. about 1 μm , detach easily from pellicle (Fig. 28), do not stain with

methyl green-pyronin, composed of ellipsoid, 2 to 4-fold perforated basal plate attached to pellicle and compact, globular body anchored at some distance to centre of basal plate via small rod projecting at top of globule (Figs. 23, 28, 31, 37).

Cytoplasm bright, contains numerous rod-shaped bacteria, many of which were dividing; stain pink with methyl green-pyronin (Fig. 41) and occur also in epipellicular mucus. Movement moderately rapid, glides elegantly on and between sand grains and organic debris.

Oral cilia about 5 μm , somatic about 10 μm long, those of dorsolateral and left lateral kinety bristle-like, forming spiny processes. Somatic infraciliature, ciliation,

and fibrillar systems as described in *C. setigerus*, except for several morphometric characteristics (Table 2) and the right oblique fibres (Fig. 7), which are either lacking or were not stained (Figs. 26, 33–36, 38). No kinetids in postoral area, i.e. between and underneath buccal kineties and first somatic ciliary row. Oral infraciliature also very much like that of *C. setigerus*, with important differences, however. Buccal kineties extend not only along right and anterior margin of buccal overture but curve backwards along left overture margin, kinety 2 almost touching back end of kinety 1, which is shorter, i.e. ends in mid-region of left buccal margin. Curvature of buccal kineties causes remarkable alteration of ciliation, viz. dikinetids of right portion of buccal kinety 2 have ciliated anterior basal bodies, whereas posterior ones are ciliated in left branch (Figs. 33, 42). Intrabuccal kinety as described in genus diagnosis, extends obliquely posteriad and dorsad (Figs. 25, 34, 36, 39).

Comparison with related species: As concerns the distinctly protruding oral area, *A. hippocampoides* resembles *Cryptopharynx kahli* DRAGESCO, 1954 (with large, furcated epipellicular scales as described in *Cryptopharynx* sp. 2) and *C. multinucleatus* DRAGESCO, 1960 (many macronuclei scattered throughout cell). Whether these species belong to *Apocryptopharynx* can be not decided because nothing is known about their intrabuccal kinety.

• *Apocryptopharynx wardi* (SMALL & LYNN, 1985) nov. comb. (basonym: *Cryptopharynx wardi* SMALL & LYNN, 1985)

Cryptopharynx wardi (Figs. 21, 22), described very superficially and from protargol slides only, has, like *A. hippocampoides*, a long, clip-shaped intrabuccal kinety and is thus transferred to the genus *Apocryptopharynx*.

Discussion

Systematic relationships of *Cryptopharynx* and *Apocryptopharynx*

KAHL (1928) described *Cryptopharynx* together with some cyrtophorid ciliates, but suggested a relationship with *Loxodes* because of its nuclear apparatus. However, later KAHL (1931, 1933) again placed *Cryptopharynx* among the cyrtophorids, but suggested that it could be a "primitive" gymnostomatid: "Unfortunately, I recognized too late that it would be better placed near *Platyophrya*". Indeed, the size and gross morphology of the type species, *C. setigerus*, are highly reminiscent of

platyophryid ciliates, which are now far from the karyorelictids, viz. in the colpodid order Cyrtolophosidida [see FOISSNER (1993) for a detailed review]. Platyophryid colpodids have a dividing macronucleus and strongly developed transverse microtubules, i.e. characters which are apparently not shared by cryptopharyngids. Furthermore, the left lateral ciliatures of *Cryptopharynx* and *Platyophrya* are highly dissimilar. I thus interpret the similarities in the location and gross morphology of the oral apparatus and the right lateral ciliature as baffling examples of convergent evolution.

DRAGESCO (1960) and JANKOWSKI (1967) followed KAHL (1931) in placing *Cryptopharynx* among the cyrtophorids. JANKOWSKI (1967) even suggested a new family, Cryptopharyngidae, without, however, any new evidence. The family status was later appreciated by SMALL & LYNN (1985) and PUYTORAC (1994), who assigned *Cryptopharynx*, like JANKOWSKI (1980), to the loxodids, without, however, recognizing and discussing the deciding synapomorphies.

The present investigations show two previously unrecognized characters, also found in *Loxodes*, *Remanella* and *Kentrophoros*, viz. the dorsolateral kinety and the circular left lateral ciliary row. These traits are apomorphies of the loxodids (Fig. 43) and *Cryptopharynx* thus belongs to this assemblage. Furthermore, the complex oral structures of *Remanella* and *Loxodes* can be easily derived from those of *Cryptopharynx* and *Apocryptopharynx* (see below).

Systematic status of cryptopharyngid ciliates

JANKOWSKI (1967) erected a new family, Cryptopharyngidae, and later (JANKOWSKI 1980) even a new suborder, Cryptopharyngina. However, he neither provided new evidence nor any discussion for this rank raising of a single genus. My data suggest that *Cryptopharynx* and *Apocryptopharynx* should possibly be separated from *Loxodes* and *Remanella* at family level, although the somatic and oral infraciliatures of all four genera are very similar and would hardly justify such a splitting. Evolution obviously occurred mainly at cytoplasmic level, as in *Loxodes* and *Remanella* (FOISSNER 1996a).

The main difference between *Cryptopharynx*/*Apocryptopharynx* and *Remanella*/*Loxodes* concerns the absence, respectively, presence of Müller vesicles, which are organelles for gravity reception. On the other hand, *Loxodes* and *Remanella* lack the epipellicular scales so characteristic of *Cryptopharynx* and *Apocryptopharynx*. Further, less conspicuous differences concern the buccal kineties, which are uninterrupted in cryptopharyngids and interrupted in loxodids at the anterior buccal vertex (see next chapter), as well as the

dorsolateral kinety, which extends onto the ventral side in cryptopharyngids.

Origin and evolution of loxodid oral structures

Loxodes and *Remanella* have a comparatively simple oral infraciliature composed of four kineties which, albeit differing in length, location and ciliation, are composed of dikinetids throughout (FOISSNER 1996a). The evolution of this unusual pattern is still enigmatic due to the lack of reliable ontogenetic data (FOISSNER 1996b). However, the present results suggest a simple explanation, viz. that all oral kineties, with the possible exception of the intrabuccal kinety, derive from two right lateral somatic ciliary rows which curve around the anterior vertex of the oral apparatus, forming two distinct arcs at the margins of the buccal overture (Fig. 42). This hypothesis elegantly explains the peculiar ciliation of the loxodid oral kineties, i.e. that the dikinetids of the left outer buccal kinety (number 2 in Fig. 42) have ciliated posterior basal bodies, while the dikinetids composing the first somatic kinety have ciliated anterior basal bodies. Thus, the first kinety right of buccal kinety 1 consists of oralized somatic kinetids. Buccal kinety 1 lacks this inversion, very likely because its

dikinetids are almost transversely orientated; it is a paroral sensu stricto and simply curves around the anterior vertex of the buccal overture and thus has the anterior basal bodies ciliated throughout. The contact between the branches of the arcs is maintained in *Cryptopharynx* and *Apocryptopharynx*, while a small break evolved in *Remanella* and *Loxodes* at the upper buccal vertex, possibly due to the elongation of the anterior body end (Fig. 42). This interpretation suggests that the loxodid buccal overture is surrounded not by three or four kineties, as previous investigations indicated, but only by two. These kineties represent, according to their right lateral location and origin, the paroral ciliature. The intrabuccal kinety, possibly being a segment of the *left* lateral ciliature, would then be adoral.

According to this interpretation, the loxodid oral structures are very simple, i.e. composed entirely of oralized somatic kinetids, which would match the supposed primitiveness of karyorelictid ciliates (CORLISS 1979; PUYTORAC 1994). Furthermore, this interpretation is in accordance with the hypothesis by SMALL (1984) that the oral infraciliature of the ciliates is of somatic origin, while EISLER (1994), using ontogenetic data from nasulids, assumes that the somatic ciliature evolved from the paroral membrane.

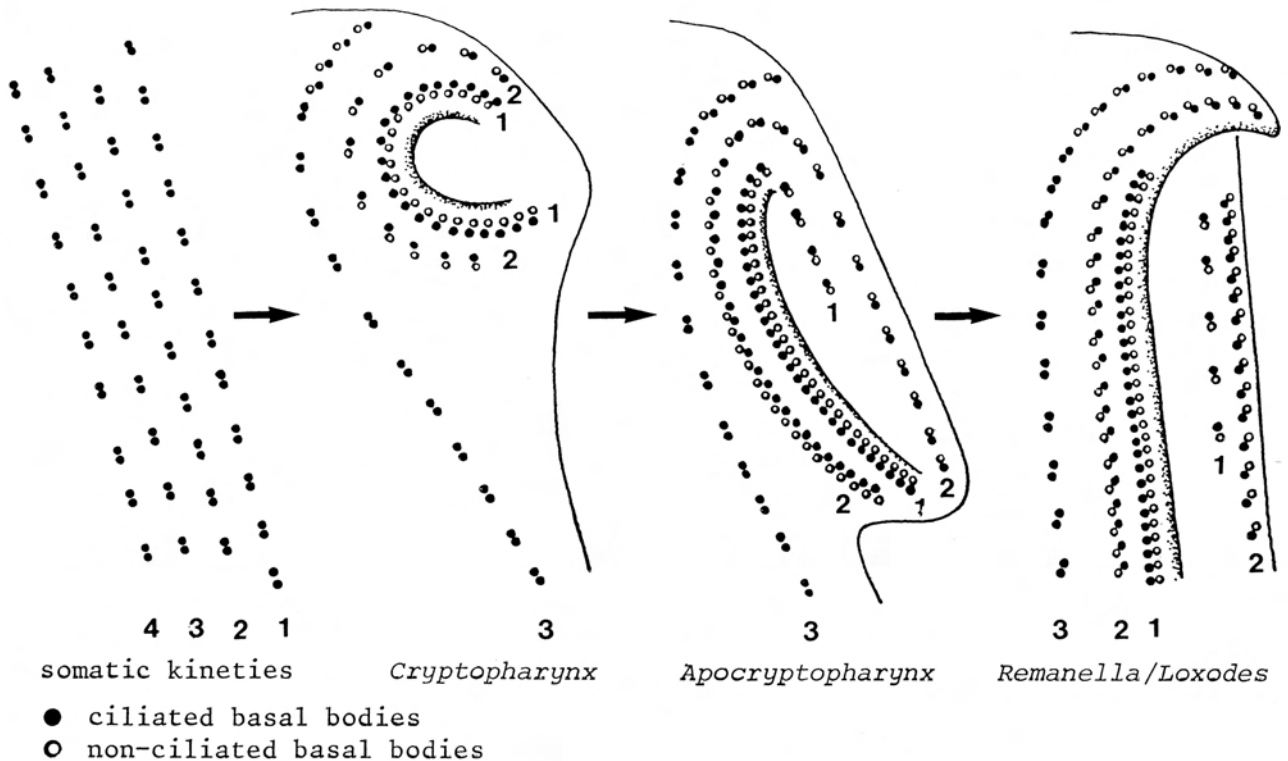


Fig. 42. Origin and evolution of the loxodid oral ciliature. See discussion for details.

Table 3. Characters and character states used in Fig. 43.

Apomorph	Plesiomorph
1 "circular" left lateral kinety	other
2 simple buccal (paroral) kinety (number 1 in Fig. 42)	compound buccal kinety, i.e. paroral associated with oralized somatic kinety (number 2 in Fig. 42)
3 apical oral apparatus	ventrolateral oral apparatus
4 freshwater	marine
5 epipellicular scales or mucilage	without
6 dorsolateral kinety	without
7 reduction of oral apparatus	complete oral apparatus
8 symbiotic kitchen garden	without
9 loss of epipellicular scales	epipellicular scales
10 Müller organelles	without
11 interruption of buccal kineties at anterior buccal vertex	buccal kineties uninterrupted
12 elongation of dorsolateral kinety to ventral side	dorsolateral kinety restricted to dorsal and posterior margin of cell
13 polymerization of buccal kinety 2	buccal kinety 2 not or inconspicuously polymerized
14 intrabuccal kinety clip-shaped and distinctly invaginated	intrabuccal kinety straight or slightly curved and not or inconspicuously invaginated
15 granules in Müller vesicles composed of barium	granules in Müller vesicles composed of strontium
16 cnidocysts	other
17 cytoplasmic skeleton rods	without

Evolution in loxodid ciliates

I tried to follow the evolution of loxodid ciliates with HENNIG's (1982) cladistic method, despite the lack of reliable ontogenetic and comparative ultrastructural data. The analysis, which is based on the present results and my previous light microscopical investigations on *Kentrophoros* (FOISSNER 1995) and *Remanella* (FOISSNER 1996a), is thus rather incomplete, i.e. some taxa remain paraphyletic because no or only weak synapomorphies were found (Fig. 43). However, I like this kind of presentation because it clearly summarizes the major characters and gaps in our knowledge of loxodid ciliates.

The character states [apomorph (= derived), plesiomorph (= ancestral)] were determined using trachelocercids as outgroup because they have, like loxodids, a specialized kinety on the left side and some even have a compound buccal ciliature (FOISSNER, manuscript in preparation). The apical location of the trachelocercid oral apparatus is assumed to be derived from a ventrolaterally mouthed ancestor.

The loxodid path is defined by two unique characters (apomorphies), viz. the dorsolateral kinety and the epipellicular scales, which are modified to a mucous layer in *Kentrophoros* and lost in *Remanella* and *Loxodes*. *Kentrophoros*, which feed on the symbiotic bacteria growing in the mucous layer, is in fact difficult to

place because its oral structures are either reduced to inconspicuous vestiges (FOISSNER 1995) or it is originally mouthless, as ORIAS (1976) assumes. I prefer the reduction hypothesis because both, *Kentrophoros* and *Cryptopharynx*/*Apocryptopharynx*, have the left body side covered with a peculiar organic layer. This conformity is more parsimoniously explained by a common ancestor rather than convergent evolution. Whether the epipellicular scales found in some freshwater gymnostomatids (FOISSNER 1994; NICHOLLS & LYNN 1984) evolved convergently to those of the cryptopharyngids or are an indication for some relationship remains enigmatic. Epipellicular scales are also found in the poorly known genus *Ciliofaurea* DRAGESCO, 1960, which is thus assigned to the Cryptopharyngidae.

The apomorphies and plesiomorphies of the Cryptopharyngidae have been discussed above, those of the Loxodidae by FOISSNER (1996a).

Taxonomic summary and characterization of higher taxa

Most higher loxodid taxa were founded by JANKOWSKI (1967, 1978, 1980). Unfortunately, he provided poor, almost useless definitions based solely on the very incomplete literature data. I shall thus redefine all taxa, using results from the present paper and from the more

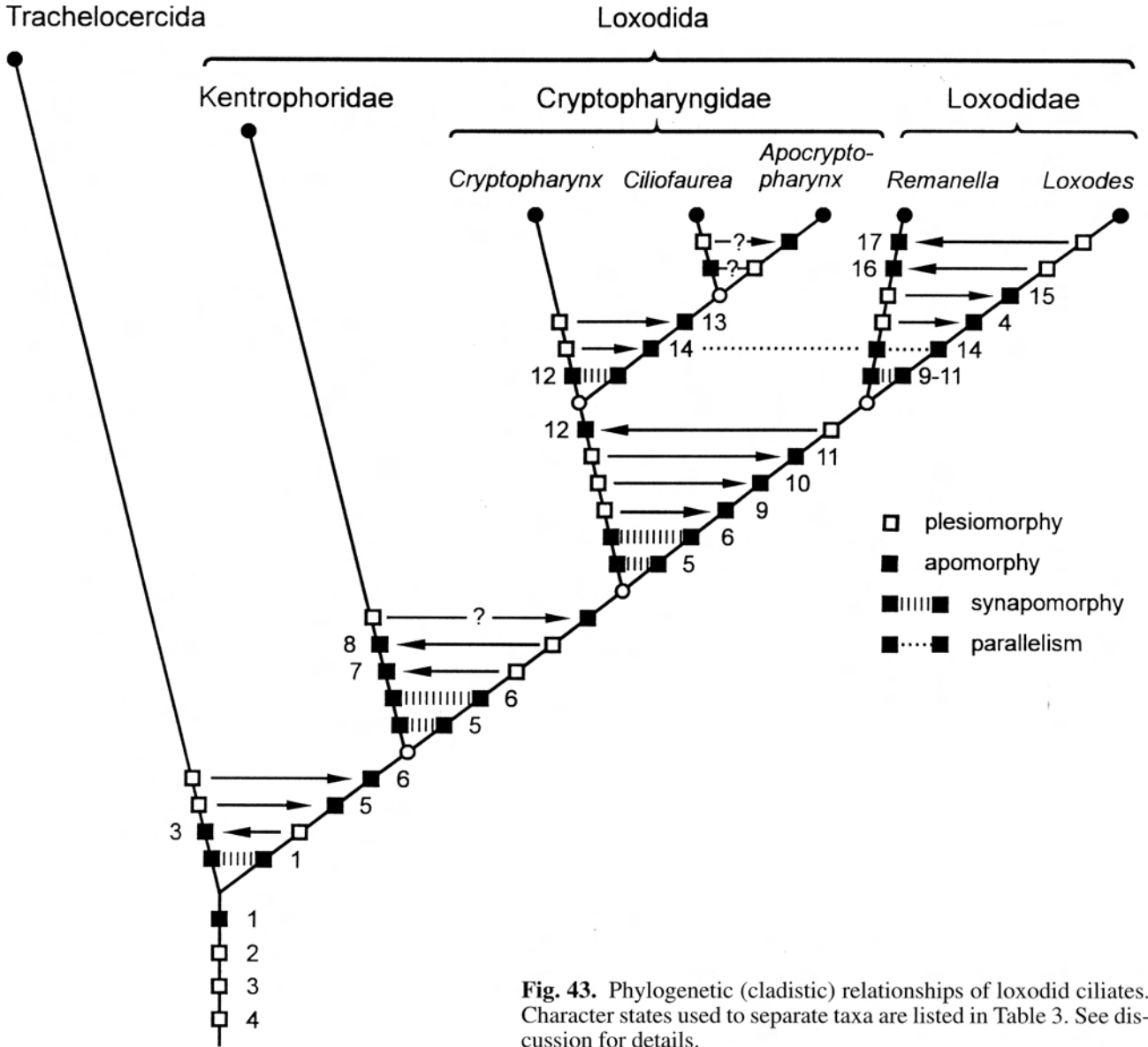


Fig. 43. Phylogenetic (cladistic) relationships of loxodid ciliates. Character states used to separate taxa are listed in Table 3. See discussion for details.

recent literature (CORLISS 1979; FOISSNER 1995, 1996a; PUYTORAC 1994). JANKOWSKI's overhasty taxa raising and poor definitions certainly discourage more serious workers and cause many nomenclatural problems, as indicated by the ambiguous authorships ascribed, e.g., by SMALL & LYNN (1985) to Jankowskian categories, viz. "order Loxodida JANKOWSKI, n. ord., respectively, Kentrophoridae JANKOWSKI, n. fam."

Order Loxodida JANKOWSKI, 1978: Small (~30 µm) to very large (~1 mm) Karyorelictea with specialized dorsolateral kinety and epipellicular mucus and/or scale layer, lacking in family Loxodidae, on left body sur-

face. Body laterally strongly compressed, right side completely ciliated, left barren except for single, circular (?) marginal kinety. Oral apparatus subapical on concave body surface, slit-like, secondarily (?) reduced in family Kentrophoridae; buccal overture ± completely surrounded by two specialized kineties, within oral cavity single, intrabuccal kinety (adoral?). Somatic and oral ciliature composed of dikinetids throughout, specialized and condensed in anterior region of cell. Stomatogenesis possibly buccokinetal. Primarily psammophilic forms, all marine except for *Loxodes*. Type family (by original designation): Loxodidae BÜTSCHLI, 1889.

Remarks: First defined in JANKOWSKI (1978) as "phagotrophic pleurostomatids with diploid macronucleus". Later, JANKOWSKI (1980) provided equally vague diagnoses for two new suborders, viz. "Order Loxodida JANKOWSKI, 1978 with diploid macronucleus. Free-living in marine benthos. Type: *Loxodes*. Two suborders can be distinguished according to the structure of the peristome: *Loxodina* s. str., subordo n. (type *Loxodes*; with very large and complex oral apparatus) and *Cryptopharyngina* subordo n. (type *Cryptopharynx*; with inconspicuous, simple oral apparatus)". The present results do not support JANKOWSKI's view because the somatic and oral infraciliatures of *Cryptopharynx* and *Loxodes* are almost identical.

Family Loxodidae BÜTSCHLI, 1889: Medium-sized (~100 µm) to very large (~1 mm) Loxodida with one to many gravity receptors (Müller vesicles) at dorsolateral margin and buccal kineties interrupted at anterior, projecting buccal vertex. Intrabuccal kinety long and rectilinear. Müller vesicles with single or compound barium or strontium granule, each vesicle associated with single dikinetid of left lateral ciliary row. Buccal overture and posterior, style-shaped portion of buccal cavity (pharynx) distinct because heavily pigmented. Marine and freshwater. Type genus (by monotypy): *Loxodes* EHRENBERG, 1830.

Genus *Remanella* FOISSNER, 1996: Marine Loxodidae with organic spicules forming conspicuous cytoplasmic skeleton, cnidocyst-like extrusomes (nematocysts), one or many Müller vesicles containing a single or compound strontium granule, and narrowed or tailed posterior end. Type species: *Remanella multinucleata* KAHL, 1933.

Remarks: Nomenclature see FOISSNER (1996a).

Genus *Loxodes* EHRENBERG, 1830: Freshwater Loxodidae with narrowed or broadly rounded posterior end and Müller vesicles with single, large barium granule. Type species (subsequent designation by FROMENTEL 1875): *Kolpoda rostrum* MÜLLER, 1773.

Remarks: Distinguished from *Remanella* mainly by the biotope (although some species can colonize brackish waters) and negative characters, viz. the absence of nematocysts and cytoplasmic skeletal rods.

Family Cryptopharyngidae JANKOWSKI, 1980: Small (~30 µm) to medium-sized (~150 µm) Loxodida with dorsolateral kinety extending onto ventral side. Left body surface covered with distinct, ornamented scales embedded in mucous layer. Buccal kineties continuous, intrabuccal kinety short and curved or long and clip-shaped; buccal overture roundish to ellipsoid, indistinct because not pigmented and narrow. Marine. Type genus (by original designation): *Cryptopharynx* KAHL, 1928.

Remarks: For further information see chapter "Systematic status of cryptopharyngid ciliates". The family is dated with 1980, i.e. the subordinal rank lowered and taken as date of family foundation because JANKOWSKI (1967) mentioned the family name only, which is insufficient according to the ICZN.

Genus *Cryptopharynx* KAHL, 1928: Intrabuccal kinety short and composed of few kinetids forming slightly curved row. Type species (by monotypy): *Cryptopharynx setigerus* KAHL, 1928.

Genus *Apocryptopharynx* nov. gen.: Intrabuccal kinety long and composed of many kinetids forming clip-shaped row extending deeply into the organism. Type species (original designation): *Apocryptopharynx hippocampoides* nov. spec.

Family Kentrophoridae JANKOWSKI, 1980: Loxodida with very likely functionless oral structures reduced to nematodesmata-bearing, condensed dikinetids in anterior body region. Left side covered with thick mucous layer inhabited by symbiotic sulphur bacteria phagocytised through cell surface and used as food source. Type genus (by monotypy): *Kentrophoros* SAUERBREY, 1928.

Remarks: For nomenclature see FOISSNER (1995). JANKOWSKI (1978) erected a new order, Thysanophorida (later named Kentrophorida, JANKOWSKI 1980), and then (JANKOWSKI 1980) even a new subclass, Symbiophagina, for this monotypic family. Both are unacceptable at the present state of knowledge. JANKOWSKI provided no evidence for the raise in rank.

Genus *Kentrophoros* SAUERBREY, 1928: With diagnosis of family. Type species (by monotypy): *Kentrophoros fasciolatus* SAUERBREY, 1928.

Incertae sedis: *Ciliofaurea* DRAGESCO, 1960. Original data very incomplete; no new investigations available. JANKOWSKI (1975) mentioned a new family Ciliofaureidae without, however, providing any characterization or type. Thus, the name is illegitimate, i.e. not in accordance with the rules of nomenclature.

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