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Revision of the Genera *Gastronauta* Engelmann in Bütschli, 1889 and *Paragastronauta* nov. gen. (Ciliophora: Gastronautidae)

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ABSTRACT. The family Gastronautidae Deroux, 1994 is revised. The genus *Gastronauta* is divided into *Gastronauta* (with unciliated postoral stripe) and *Paragastronauta* (without unciliated postoral stripe). Main species characteristics are the location and structure of the dorsal brush, the number of postoral kineties with a curved anterior end, and the number of kineties in the right ciliary field. Five species are recognised, described, and illustrated in detail, including their ecologies. A user-friendly key is presented.

Supplementary key words. Biodiversity, Chilodonellida, Systematics, Saprobity.

1. INTRODUCTION

Gastronauta is a small cyrtophorid genus belonging to the order Chilodonellida. Until 1968, only the type species and a doubtful epizoic species, *G. fontzoui* Nie

Dashu and Ho Yün-Luan, 1943, from Chinese freshwater shrimps were known (Blatterer and Foissner 1992, Kahl 1931). Since then, four species were described and partially reviewed by Foissner et al. (1991) and Blatterer and Foissner (1992). However, several nomenclatural and taxonomic problems, which could be clarified only by a reinvestigation of the type material, remained unresolved.

The present review is based on a reinvestigation of the type material and detailed, critical literature research. All original illustrations are included, irrespective of quality, reclassified, and assigned to the respective species.

2. FAMILY GASTRONAUTIDAE DEROUX, 1994

Diagnosis. Middle-sized Chilodonellida with long, slit-like oral opening traversing cell in second quarter. Somatic ciliature complete (*Paragastronauta*) or with a barren, postoral stripe (*Gastronauta*), dividing it into a right and left ciliary field. Dorsal brush in several small fragments.

Type genus (by monotypy). *Gastronauta* Engelmann in Bütschli, 1889.

Remarks. Formerly, *Gastronauta* was assigned to the Lynchellidae (Corliss 1979). I agree with Deroux (1994) that it needs a family of its own because of the unique shape and orientation of the oral apparatus and the curious dorsal brush, which consists of several small kineties with a very distinct, species-specific location. Deroux (1994) emphasised the arcs the right ciliary rows form anteriorly and the ontogenesis of the circumoral kinety, which is, however, insufficiently known (Fig. 6, 38, 39). Family status was already suggested by Blochmann (1895), who also highlighted the structure and orientation of the oral apparatus.

I split *Gastronauta* into two genera, *Gastronauta* and *Paragastronauta*, depending on the presence/absence of a bare postoral stripe, like Jankowski (1967) did with *Chilodonella*/*Trithigmostoma*. Another feature for splitting the genus could be the dorsal brush pattern, which is highly characteristic (two to three rows on dorsal surface in *G. membranaceus* and *P. clatratus*; several minute groups at dorsal anterior body margin in *G. derouxi* and *G. aloisi*), but does not match the pattern of the ventral ciliature. This might indicate the need of further splitting, possibly at subgenus level, especially if further species are discovered.

As the family consists of only few species, each described and illustrated in detail, I do not provide a general overview, but refer to Figures 1 and 2, where the typical organisation is shown and the terminology and some minor problems are explained. Briefly, gastronautids are middle-sized (length 45 – 100 µm), dorsoventrally strongly flattened ciliates, whose most conspicuous feature is a slit-like oral opening traversing the body in the second anterior quarter. Only the ventral side is densely ciliated, as in other chilodonellids; the dorsal surface bears several small kinety fragments composing the so-called dorsal brush. The location and number of these fragments are the most important species characteristics. Ecologically, gastronautids are inhabitants of the Aufwuchs in freshwaters and brackish waters, only *G. derouxi* prefers terrestrial habitats.

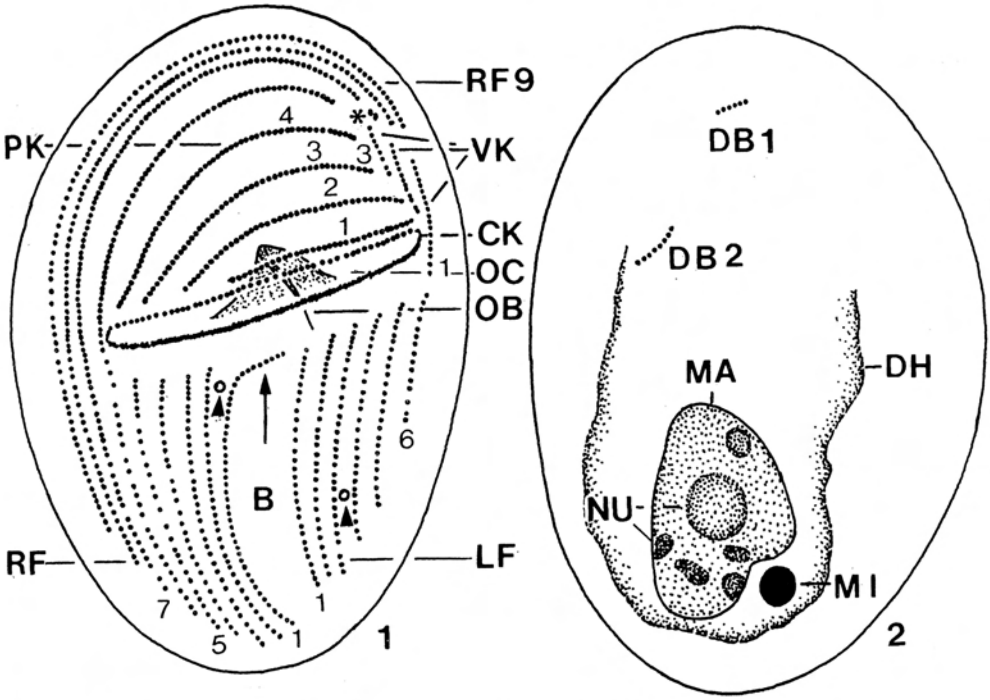

Fig. 1, 2. *Gastronauta membranaceus*, ventral and dorsal view after protargol impregnation, as an example for the general organisation of the gastronautids; length 47 µm. Arrow marks anteriorly curved inner kinety of right ciliary field; arrowheads mark excretory pore of contractile vacuoles. Asterisk denotes two mono- or dikinetids at anterior end of vertical kinety fragment 3; the origin and function of these kinetids are unknown. Numbers in Figure 1 mark ciliary rows; in the right field, there are five postoral, in the left six. Preoral kineties are those which abut to the anterior portion of the circumoral kinety. The long oral cleft, associated with an inconspicuous oral basket, is surrounded by a circumoral kinety, which is very likely composed of monokinetids in anterior half and of very narrowly spaced dikinetids in posterior; its cilia form a conspicuous, lamellar structure in vivo and protargol preparations (Fig. 66, 67, 85, 91). B – barren (unciliated) area between right and left ciliary field, CK – circumoral kinety surrounding oral cleft, DB1, 2 – dorsal brush rows, whose number and arrangement are very important species characteristics. DH – dorsal hump, LF – left ciliary field, MA – macronucleus, MI – micronucleus, NU – nucleoli, OB – oral basket, OC – oral cleft, PK – preoral kineties 1 – 4, RF – right ciliary field, RF9 – kinety 9 of right ciliary field, VK – vertical kinety fragments 1 – 3. Original drawings from Wilbert's *G. runcina* type slide. It is the same specimen as figured by Wilbert (Fig. 7, 8, 72).

3. DESCRIPTION OF GENERA AND SPECIES

3. 1. Genus *Gastronauta* Engelmann in Bütschli, 1889

1889 *Gastronauta* n. g. Engelmann in Bütschli, Protozoa, p. 1696.
1931 *Gastronauta* Engelmann, 1875 – Kahl, Tierwelt Dtl., 21: 233.
1979 *Gastronauta* Engelmann, 1875 – Corliss, Ciliated Protozoa, p. 228.
1982 *Gastronauta* Bütschli, 1889 – Curds, British Ciliated Protozoa, Part 1: 270.
1987 *Gastronauta* Bütschli, 1889 – Foissner, Arch. Protistenk., 133: 221.

Diagnosis. Gastronautidae Deroux, 1994 with unciliated postoral stripe dividing somatic ciliature in a right and left ciliary field. Dorsal brush in small fragments on dorsal surface or anterior body margin.

Type species (by monotypy). *Gastronauta membranaceus* Engelmann in Bütschli, 1889.

Etymology. Composite of two Latin nouns, gaster (stomach, abdomen) and nauta (sailor, skipper). Masculine gender.

Nomenclature. As the synonymy list shows, there is uncertainty who should be credited with the genus and species, Engelmann or Bütschli. Curiously enough, *Gastronauta* is neither mentioned in the Zoological Record nor the Nomenclator Zoologicus, and the reference given by Kahl (Engelmann 1875) and accepted by Corliss (1979) does not contain any indication of the genus name. Likewise, the reference given by Penard (1922), viz., Engelmann (1862), does not contain *Gastronauta*. However, if article 50.1 of the ICZN (1999) is applied, Engelmann is founder of the genus because Bütschli (1889) expressly stated (translated from German): " In Engelmann's notes an interesting hypotrichous ciliate is depicted, which he named "*Gastronauta membranacea* n. g. et sp. ".

Gastronauta membranaceus Engelmann in Bütschli, 1889
(Fig. 1 – 23, 66 – 74; Tables 1, 2)

1889 *Gastronauta membranacea* n. sp. Engelmann in Bütschli, Protozoa, p. 1696 (without figure !).

1895 *Gastronauta membranaceus* Bütschli – Blochmann, Mikroskopische Thierwelt, p. 97 (authoritative redescription with figure; " silent " emendation of species name).

1927 *Gastronauta membranaceus* Bütschli – Klein, Arch. Protistenk., 58: 110 (silver impregnation).

1929 *Clamidodon* (Ehrenberg) *stagnalis*, Nobis, Dumas, Microzoaires, 1er fascicule, p. 97 (new synonym).

1930 *Gastronauta membranaceus*, Engel. – Dumas, Microzoaires, 2^{e} fascicule, p. 114 (comparison of his *Clamidodon stagnalis* with Penard's redescription of *G. membranaceus*).

1931 *Gastronauta membranaceus* Engelmann, 1875 – Kahl, Tierwelt Dtl., 21: 233 (revision).

1968 *Gastronauta* sp. – Deroux & Dragesco, Protistologica, 4: 395 (silver impregnation; Fig. 16C, non Fig. 15, 16 A, B, which show *G. derouxi*).

1972 G*astronauta runcina* Wilbert, Protistologica, 7: 358 (synonym; silver impregnation and ecology).

1974 *Gastronauta runcina* Wilbert – Pätsch, Arb. Inst. landw. zool. Bienenkd., 1: 25 (silver impregnation).

1991 *Gastronauta membranaceus* Bütschli, 1889 – Foissner, Blatterer, Berger & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/91: 106 (" Ciliate-Atlas ", that is, taxonomic and ecological monograph).

Type material and material investigated. No type material is available from the old descriptions. Two slides with protargol-impregnated specimens (Wilbert's method) of *G. runcina*, a junior synonym (see above), are deposited in the Oberösterreichische Landesmuseum in Linz (LI), accession numbers: 1997/40,41.

For the present revision, I reinvestigated Wilbert's *G. runcina* slides, and thus can supplement his description with improved figures and morphometrical data (Fig. 1, 2, 70 – 74; Table 2). Furthermore, I briefly investigated specimens from the Breitenbach, a clean river in Germany (Fig. 66, 67; Packroff and Zwick 1996).

Synonymy. My synonymy is based on the data of Blochmann (1895), who provided not only the first detailed description, but also a figure showing the highly characteristic dorsal brush pattern (Fig. 3). Accordingly, the *G. membranaceus* populations of Penard (1922) and Deroux and Dragesco (1968) have been referred to other species. Deroux and Dragesco (1968) and Deroux (1976), who identified *G. derouxi* as *G. membranaceus*, overlooked that Blochmann (1895) unequivocally fixed the species by his detailed observations on the dorsal brush.

Many authors misplaced the contractile vacuoles (Fig. 3, 7, 9, 15, 21). This conclusion is likely, considering that all recent data invariably show them at the same sites in all species. Even Wilbert (1972), although having excellent protargol slides showing the excretory pores (Fig. 1), misplaced the postoral vacuole completely, as a reinvestigation of the type slide showed (cp. Figures 1 and 7) ! Thus, this feature cannot be used to distinguish species.

The identification by Kahl (1931) is doubtful because he mentioned: " There are some 4 – 5 µm long, fine dorsal bristles on the anterior dorsal body margin ". This indicates that he observed *G. derouxi* or *G. aloisi*, at least in 1931.

Synonymy of *Clamidodon stagnalis* is likely, although the data of Dumas (1929) are too superficial to be entirely sure. The postoral contractile vacuole is misplaced and a blanc postoral stripe is hardly recognisable (Fig. 21). Thus, Dumas (1929) probably observed *Paragastronauta clatratus*, and in 1930 he indeed compared his species with Penard's redescription of *G. membranaceus*, which shows *P. clatratus*. However, if Dumas' species is assigned to *P. clatratus,* this species, which is now well-established, would fall as a junior synonym. Thus, I prefer synonymising *C. stagnalis* Dumas (1929) with *G. membranaceus* Engelmann (1889).

Wilbert (1972) did not compare his *G. runcina* with the redescriptions of *G. membranaceus*, but only with the data of Deroux and Dragesco (1968), who studied, as we now know, mainly *G. derouxi*. All data provided by Wilbert (1972) and recognisable in the type slide, especially the characteristic dorsal brush pattern, suggest synonymy of *G. runcina* with *G. membranaceus* as redescribed by Blochmann (1895). Synonymy has been suggested also by Song Weibo and Wilbert (1989).

The organism redescribed as *G. membranaceus* by Alekperov (1993) is difficult to classify (Fig. 10, 11). If the observations are correct, then it is a new species because it is 180 – 250 µm long (up to 190 µm when prepared); has 14 ciliary rows (of which only 4 are postoral) in the right field and only a single group of basal bodies at the anterior margin of the dorsal side; and lacks the curved anterior end of the inner kinety of the right field. However, as the large size of the organism is far beyond any other size within the family, I assume a measurement error; and most

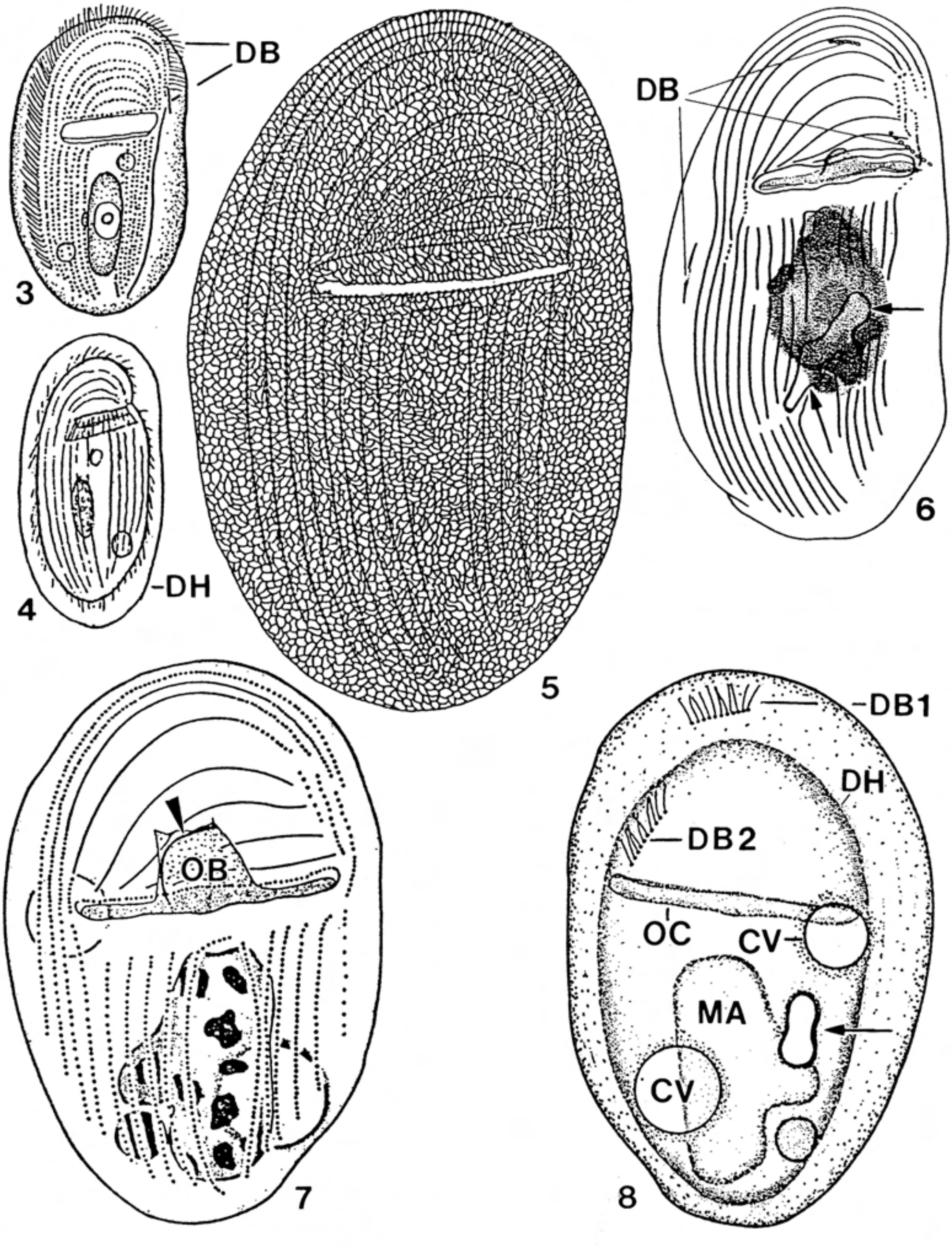

Fig. 3 – 8. *Gastronauta membranaceus* from life (3, 4), after silver nitrate (5) and protargol (6 – 8) impregnation. **3:** Ventral view, length 60 – 70 µm (redrawn from Blochmann 1895). **4:** Ventral view, 60 × 50 µm (from Kahl 1931). **5:** Silverline system of ventral side, length 62 µm (from Klein 1927). **6:** Middle divider, length 56 µm (from Deroux and Dragesco 1968). Arrows mark new circumoral kinety. **7, 8:** Ventral and dorsal view of *G. runcina*, a junior synonym of *G. membranaceus*, length 47 µm (from Wilbert 1972); improved in Figures 1 and 2. Arrow marks refractive structure; arrowhead denotes a kinety-like line produced, in my opinion, by the curved oral basket rods. CV – contractile vacuoles, DB1, 2 – dorsal brush rows, DH – dorsal hump, MA – macronucleus, OB – oral basket.

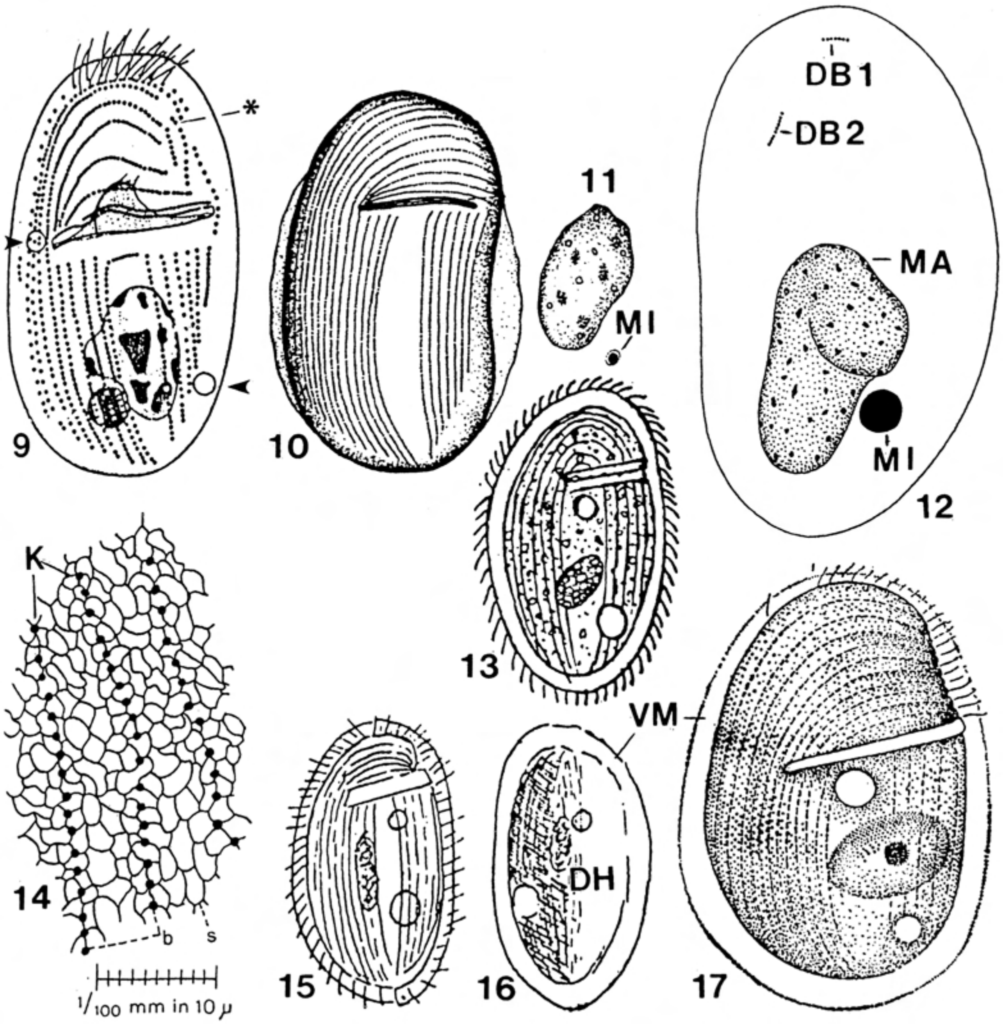

Fig. 9 – 17. *Gastronauta membranaceus* from life (13, 15 – 17) and after silver nitrate (10, 14) and protargol (9,12) impregnation. **9:** Ventral view of *G. runcina*, a junior synonym of *G. membranaceus*, length 50 μm (from Pätsch 1974). Arrowheads mark contractile vacuoles; asterisk denotes two kinetids at the anterior end of the vertical kinety fragments (cp. Fig. 1). **10, 11:** Ciliary pattern (very likely incomplete) and nuclear apparatus (Feulgen reaction) of a soil population, length 150 μm (very likely a mistake, see synonymy; from Alekperov 1993). **12:** Original figure of dorsal side of a specimen from Wilbert's *G. runcina* slides, length 62 μm. **13:** Ventral view, length 70 μm (from Vuxanovici 1962). **14:** Part of silverline system of ventral side (from Klein 1927). **15, 16:** Ventral and dorsal view, size not given (from Kahl 1926). **17:** Ventral view, 62 – 69 × 41 – 45 μm (from Gong Xunji and Shen Yunfen 1989). DB1, 2 – dorsal brush rows, DH – dorsal hump, K – somatic kineties, MA – macronucleus, MI – micronucleus, VM – bulged ventral margin.

of the other differences could be caused by insufficient impregnation because chilodonellids often do not impregnate well with the Chatton-Lwoff silver nitrate method used by Alekperov (1993). Possibly, slides for a reinvestigation are available, although not mentioned, from the Institute of Zoology, Academy of Sciences of Azerbaijan, Baku.

Nomenclature. Bütschli (1889) briefly described *G. membranaceus* according to the notes of Engelmann, who is thus also founder of the species. The species name was correctly emended from " *membranacea* " to " *membranaceus* " by Blochmann (1895).

Description. The description is based mainly on the data by Blochmann (1895), Klein (1927), Deroux and Dragesco (1968), Wilbert (1972), and some original observations (Fig. 66 – 69; Table 2). Most other descriptions are doubtful, as explained in the synonymy section.

Size in vivo 45 – 70 × 30 – 45 µm (Blochmann 1895, Gong Xunju and Shen Yunfen 1989,Vuxanovici 1962, Wilbert 1972; Table 2). Elliptical to broadly elliptical, left margin less curved than right. Strongly flattened, ventral side slightly concave causing broad, bulge-like fringe, which surrounds dorsal, wrinkled hump containing refractive structure right of midline[1] (Fig. 3, 4, 8, 15 – 17, 66 – 69). Macronucleus postoral in mid-body, that is, under barren postoral stripe, ellipsoidal with up to three distinct lobes, respectively, indentations containing single, large, globular micronucleus; with many peripheral nucleoli and large, central blister containing single nucleolus (Fig. 2 – 4, 8, 9, 12, 17, 69). Two contractile vacuoles and excretory pores, which are easily recognisable even in live specimens, in constant, characteristic position (Fig. 1, 4, 16, 17, 67, 69): anterior vacuole slightly right of midline underneath oral cleft with excretory pore between anterior portion of kineties 1 and 2 of right ciliary field, contracts every 10s at 22°C (Vuxanovici 1962); posterior vacuole in left posterior quadrant of cell with excretory pore between kineties 3 and 4 of left ciliary field, contracts rarely or not at all (Vuxanovici 1962). Extrusomes possibly lacking (Schneider 1930). Cytoplasm hyaline, cells thus colourless and transparent. Glides slowly on ventral surface.

Somatic and oral ciliary pattern shown in Figures 1 – 9, 12, 19, 70 – 74. 15 – 16 ciliary rows on postoral surface, postorally separated by a narrow, barren stripe. Left ciliary field composed of six kineties gradually shortened from right to left posteriorly, straight anteriorly, leftmost row almost continuous with vertical kinety fragment 1. Right ciliary field composed of nine to ten rows, of which four to six are postoral, while the others extend anteriorly forming wide arcs on anterior body margin; anterior portion of kinety 1 (innermost ciliary row) sharply curved to left almost touching anterior end of left ciliary field. Four to six slightly convex, widely spaced preoral ciliary rows between curved anterior portion of right ciliary field and circumoral kinety, shorten gradually from right to left at right end of oral cleft. Left above circumoral kinety three short, vertically extending kinety fragments: fragment 1 between leftmost kinety of left field and anterior end of penultimate kinety of right

[1] This structure, which has been observed also in some other species, is possibly the cytopyge. In protargol preparations, it appears as an about 4 µm wide and deep tube.

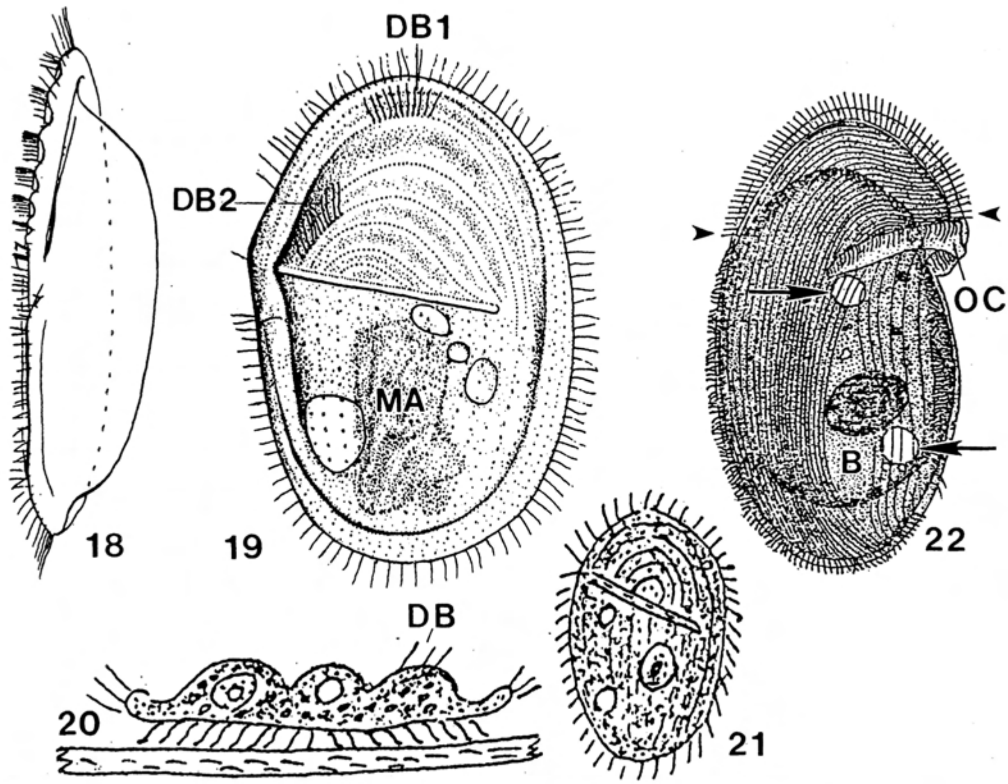

Fig. 18 – 21. Lateral (18, 20) and dorsal (19, 21) views, with ciliary rows shining through from ventral side, of *Gastronauta membranaceus* (18, 19; from Curds 1982) and its junior synonym, *Clamidodon stagnalis* (20, 21; from Dumas 1929). DB1, 2 – dorsal brush rows. MA – macronucleus.

Fig. 22. *Gastronauta fontzoui*, ventral view from life, length about 107 µm. Arrows mark contractile vacuoles. Arrowheads denote row of stiffer cilia (dorsal brush?) at anterior body margin. B – blank postoral stripe, OC – oral cleft. From Nie Dashu and Ho Yün-Lüan (1943).

field; at anterior end of fragment 3 two isolated mono- or dikinetids (Fig. 1, 9), overlooked by Wilbert (Fig. 7), as in *G. aloisi* and *P. clatratus*. Dorsal brush in two short fragments with 4 – 5 µm long cilia (Fig. 2, 3, 6, 8, 12, 73, 74): fragment 1 subapically in body midline and composed of 4 – 8 cilia (Deroux and Dragesco 1968; Table 1); fragment 2 at level of oral cleft left of midline, obliquely orientated and composed of 6 – 14 cilia. Silverline system narrowly meshed, meshes about 1 µm wide (Fig. 5, 14).

Oral opening in middle body third, traverses slightly obliquely almost entire ventral surface, cleft-like, bordered by circumoral kinety, whose cilia form a lamellar structure giving the oral apparatus the appearance of the slit of an ordinary letterbox (Kahl 1926; Fig. 66 – 68, 70 – 72). Posterior half of circumoral kinety strongly impregnated but seemingly without basal bodies, thus possibly unciliated. Oral basket very inconspicuous, recognisable only after protargol impregnation, conical, extends from mid of oral cleft dorsally producing a kinety-like, unciliated line of granules where it curves dorsally (Wilbert 1972; Fig. 7); granules very likely produced by the sharply curved, very fine oral basket rods (author).

Occurrence and ecology. Rare and usually not abundant in the Aufwuchs (periphyton; up to seven individuals cm^{-2} on exposed slides, Wilbert 1972) of running and stagnant waters, possibly preferring spring and autumn. One reliable record from brackish water, that is, the estuary of a river at the French Atlantic coast (Deroux and Dragesco 1968; Fig. 6). No marine records; that from Patterson et al. (1989) refers to Deroux and Dragesco's (1968) record cited above. Likewise, records from plankton are lacking (Foissner et al. 1999), although single, detached specimens may occur in river plankton (Bernerth 1982, Mauch 1999). Single, rather reliable record from soil (Alekperov 1993; Fig. 10, 11), other records (e.g. Stout 1958) not substantiated by morphological data; thus confusion with the later described *G. derouxi*, which occurs in soils worldwide (Foissner 1998), cannot be excluded. Kahl (1931) mentioned occurrence in *Sphaerium* mussels of the Hamburg harbour, but his description indicates that this was another species (see synonymy).

There are only about 40 records worldwide, most from Europe. The following compilation is a representative extract, emphasising records outside Europe and those substantiated by at least one figure: small rivers in Upper Austria (Blatterer 1994); Turiec river in Slovakia (Tirjaková and Degma 1996); unpolluted streams (Packroff and Zwick 1996, Pätsch 1974; Fig. 9, 66, 67) and large, mesosaprobic rivers (Main, Danube) in Germany (Bernerth 1982, Mauch 1999) and Hungary (Bereczky et al. 1983); slightly chloride-polluted rivers (< 200 mg l^{-1}) in Germany (Mihailowitsch 1989; Table 1). Ponds and lakes in Austria (Blatterer 1989, Foissner et al. 1991; Fig. 68, 69), Switzerland (Roux 1901), Germany (Kahl 1926, Packroff and Wilbert 1991, Song Weibo and Wilbert 1989, Wilbert 1969, 1972; Fig. 4, 15, 16; Table 1), Roumania (Vuxanovici 1962; Fig. 13), China (Song Weibo and Chen Zigui 1999), and bog lakes in Germany (Strüder-Kypke and Schönborn 1999). Waters in Austria (Klein 1927; Fig. 5), Germany (Blochmann 1895; Fig. 3), France (Dumas 1929; Fig. 20, 21), England (Curds 1982; Fig. 18, 19), China (Gong Xunji and Shen Yunfen 1989; Fig. 17), and Brazil (Hardoim and Heckmann 1996).

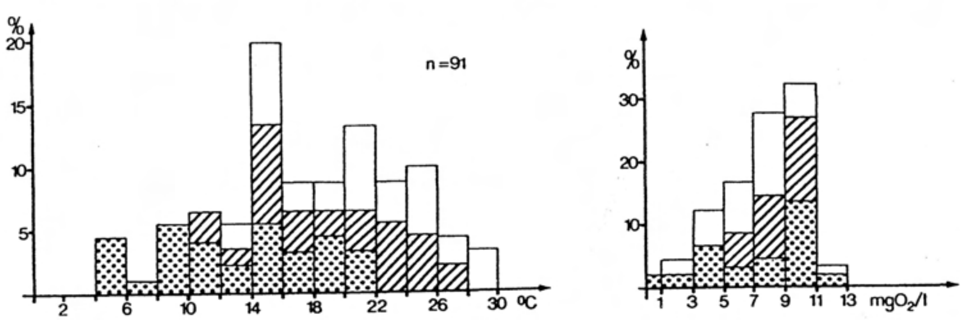

Fig. 23. Ecograms of *Gastronauta membranaceus* (from Bernerth 1982). Percentage occurrence in the temperature and oxygen spectrum of the river Main in Germany. Dotted: river entering power plant; diagonal: river leaving power plant; white: sites within power plant.

Gastronauta membranaceus feeds on bacteria (Bernerth 1982, Wilbert 1972), preferring iron-depositing species (Pätsch 1974). Biomass of 10^6 individuals about 15 mg. On artificial substrates, it is a primary coloniser, reaching highest abundances in the first week (Bereczky et al. 1983, Bernerth 1982, Pätsch 1974, Wilbert 1969, 1972). *Gastronauta membranaceus* has a rather wide ecological range, but avoids heavily and very heavily polluted waters (Fig. 23; Table 1). Accordingly, Foissner et al. (1991) classified it as beta-mesosaprobic indicator species in running waters: b; o = 2, b = 6, a = 2, I = 3, SI = 2.0. Very likely cosmopolitan, preferring limnetic habitats.

Table 1. Ecological data on *Gastronauta membranaceus.*

Parameters	Wilbert (1971)[a]	Bernerth (1982)[b]	Mihailowitsch (1989)[c]
Temperature (°C)	1.8 – 21.5	4.0 – 30.0	3.4 – 18.3
pH	7.5 – 8.3	7.2 – 8.4	6.7 – 8.0
µS cm^{-1}	nm[d]	420 – 790	4180 – 11030
O_2 (mg l^{-1})	4.2 – 22.4	0.5 – 13.0	6.9 – 11.3
CO_{2free} (mg l^{-1})	0.0 – 16.3	nm	11.1 – 89.0
NH_4^+ – N (mg l^{-1})	0.0 – 1.6	nm	0.08 – 0.8
NO_2^- – N (mg l^{-1})	0.0 – 0.12	nm	0.03 – 0.8
NO_3^- – N (mg l^{-1})	0.0 – 12.0	nm	2.3 – 5.8
H_sS (mg l^{-1})	0.0	nm	nm
DOC (mg l^{-1})	nm	4.8 – 17.0	nm
Cl^- (mg l^{-1})	nm	nm	35.4 – 171
Bacterial numbers ($\times 10^6 ml^{-1}$)	1.8 – 23.2[e]	0.02 – 0.35[f]	nm

[a] Data from the synonym *G. runcina*. Many analyses from oligotrophic to eutrophic ponds in Bonn, Germany.

[b] Many analyses from the cooling water system of an electric power station at the Main River in Germany. See also diagrams above.

[c] Data from the synonym *G. runcina*. 20 – 23 analyses from chloride-polluted rivers in Germany.

[d] nm – not measured.

[e] Direct counts.

[f] Standard cultures.

Gastronauta derouxi Blatterer and Foissner, 1992
(Fig. 24 – 39, 75 – 78, 82, 87; Table 2)

1968 *Gastronauta membranaceus* Engelmann – Deroux & Dragesco, Protistologica, 4: 392 (partim: Figures 15, 16A, B).

1992 *Gastronauta derouxi* Blatterer & Foissner, Arch. Protistenk., 142: 109.

Type material. 1 holotype slide and 3 paratype slides with protargol-impregnated specimens (Foissner's method) from the type location are deposited in the Oberösterreichische Landesmuseum in Linz (LI), accession numbers: 2000/10-13.

Description. Size in vivo about 60 – 70 × 40 µm, acontractile but very flexible; recently, I observed specimens with up to 100 µm in litter from a beech forest in Salzburg (Fig. 75, 76). Elliptical to almost circular, anteriorly more flattened (3:1) than posteriorly (2:1), cell margin projecting bulge-like above ciliated ventral surface, contains narrowly spaced, faintly impregnated fibres in protargol preparations; dorsal hump conspicuous and sometimes projecting above deeply grooved ventral surface, wrinkled and with prominent anterior slope, contains cylindroidal structure in mid-body right of midline (Fig. 24 – 26, 29, 31, 75, 76). Macronucleus in mid-body, ellipsoidal, with many globular chromatin bodies and a distinct nucleolus in conspicuously large, hyaline centre. Micronucleus sometimes rather distant from macronucleus, large and globular (Fig. 24, 25, 28, 32, 76, 87). Two contractile vacuoles in same position as in *G. membranaceus*, excretory pores recognisable both in vivo and after protargol impregnation, anterior pore between first and second inner kinety of right postoral ciliary field, posterior pore between third and fourth (second and third or third and fourth kinety in Deroux & Dragesco's population) kinety of left postoral ciliary field (Fig. 24, 27, 31, 75, 77). Cytoplasm colourless, contains food vacuoles with bacterial residues and fungal spores. Glides slowly on deeply grooved ventral surface, which is strongly thigmotactic but lacks a specific adhering organelle. When the water evaporates slowly on the slide, specimens become smaller and encyst (Fig. 34 – 37); after addition of biotope water, they excyst (Deroux & Dragesco 1968).

Ciliary pattern as shown in Figures 24, 25, 27, 28, 31 – 33, 75 – 78. 16 – 19 (mostly 16 in Madeiran specimens, 18 in Kenyan specimens, 19 in French and Salzburg specimens) ciliary rows on postoral surface, postorally separated by an about 9 µm wide, barren stripe; kineties accompanied by distinct fibre recognisable only after protargol impregnation at right side (Fig. 30). Left field usually composed of six kineties gradually shortened from right to left posteriorly, straight to perpendicularly curved anteriorly[2], leftmost row extends beyond oral cleft and abuts, separated by some loosely arranged basal bodies, to leftmost vertical kinety fragment. Right ciliary field composed of 11 rows (13 in French and Salzburg specimens), of which five (six in Salzburg specimens) are postoral and six to eight extend preorally forming wide arcs; anterior portion of innermost ciliary row sharply curved to left almost touching anterior end of left ciliary field. Four (five to six in Kenyan specimens) slightly convex preoral ciliary rows above circumoral kinety, shorten gradually from right to left at right end of oral cleft. Left above circumoral row three short, vertically extending kinety fragments, outer fragment between leftmost kinety of left field and anterior end of penultimate kinety of right field; at anterior end of fragment 3 two isolated mono- or dikinetids, overlooked by Blatterer and Foissner (1992), but discovered on reinvestigation of holotype specimen (Fig. 27). Dorsal

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[2] Mostly straight in Madeiran specimens, usually curved in Kenyan and French specimens (Fig. 31, 82), mixed in Salzburg population. Thus, the feature is highly variable and cannot be used to distinguish species or subspecies.

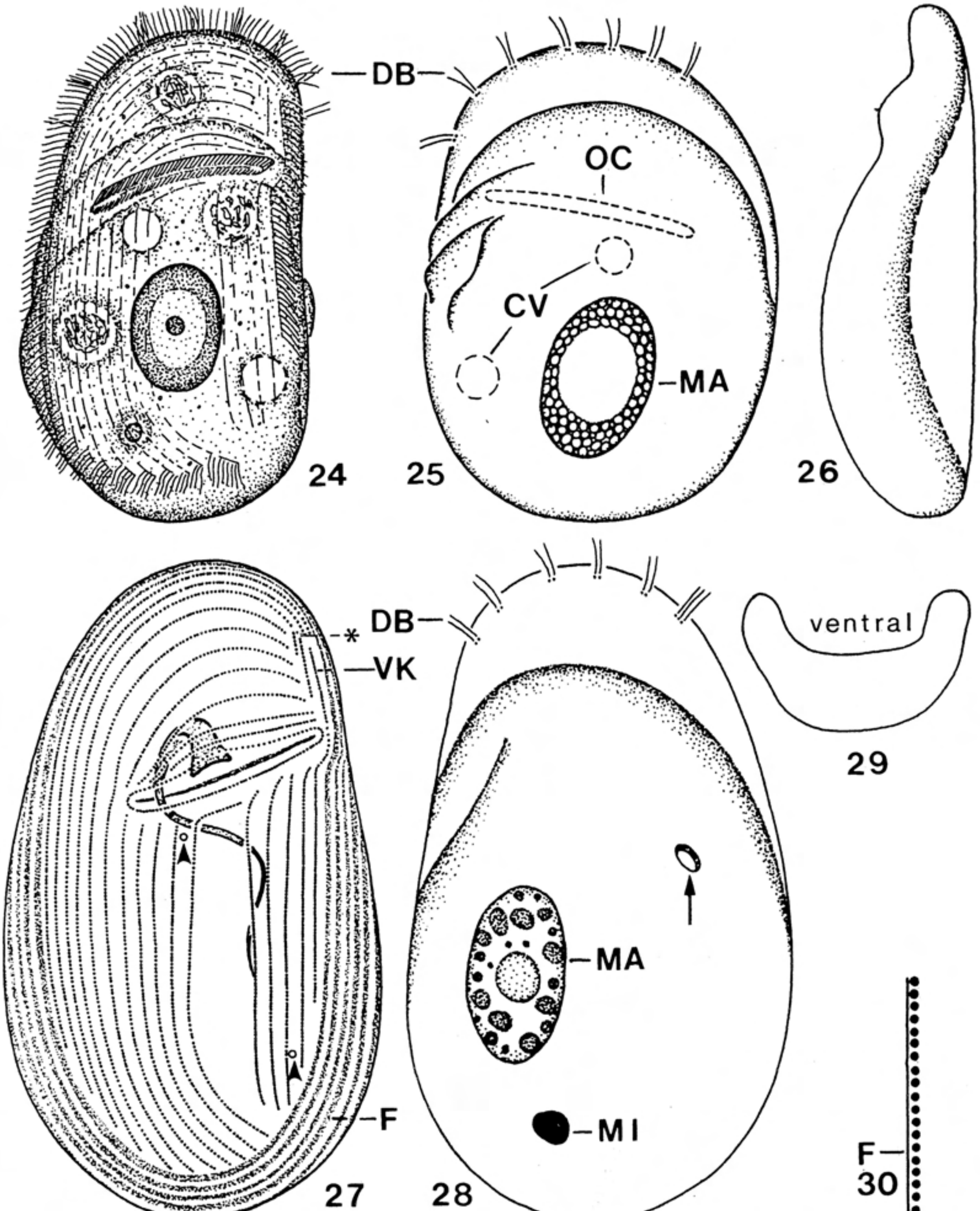

Fig. 24 – 30. *Gastronauta derouxi*, Madeiran type (27, 28, 30) and Kenyan (24 – 26, 29) population from life (24 – 26, 29) and after protargol impregnation (27, 28, 30). **24, 25:** Ventral and dorsal view, length 70 µm, 60 µm. **26, 29:** Lateral and transverse view showing excavated ventral surface. **27, 28:** Infraciliature of ventral and dorsal side, length 66 µm. Arrow marks cylindroidal structure; arrowheads denote pore of contractile vacuoles. Asterisk indicate couple of special kinetids. **30:** Ciliary rows are accompanied by a fibre. CV – contractile vacuoles, DB – dorsal brush, F – fibres, MA – macronucleus, MI – micronucleus, OC – oral cleft, VK – vertical kinety fragments. From Blatterer and Foissner (1992).

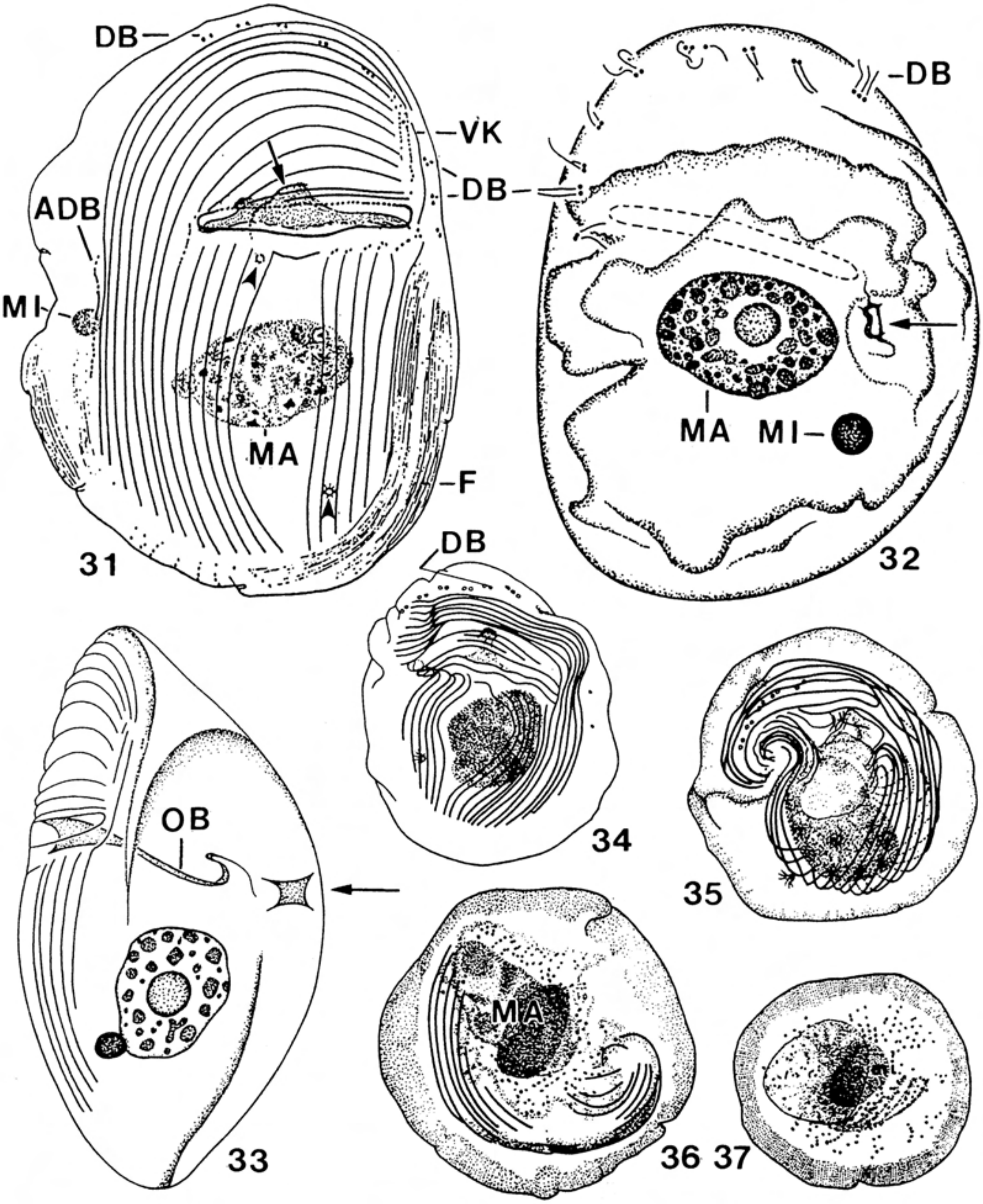

Fig. 31 – 37. *Gastronauta derouxi*, French (31, 34 – 37), Kenyan (32), and Madeiran (33) specimens after protargol impregnation. **31 – 33:** Infraciliature of ventral and dorsal side, and in lateral view, length 75 µm, 54 µm, 57 µm. Note highly similar dorsal brush in the French and Kenyan specimens. Arrow in Figure 31 marks granulated line in oral basket interpreted as kinety by Deroux and Dragesco (1968). Arrow in Figures 32 and 33 marks cylindroidal structure; arrowheads denote excretory pore of contractile vacuoles. **34 – 37:** Encystment. ADB – anlage of dorsal brush, DB – dorsal brush, F – fibres in ventral bulge, MA – macronucleus, MI – micronucleus, OB – oral basket, VK – vertical kinety fragments. 31, 34 – 37: from Deroux and Dragesco (1968); 32, 33: from Blatterer and Foissner (1992).

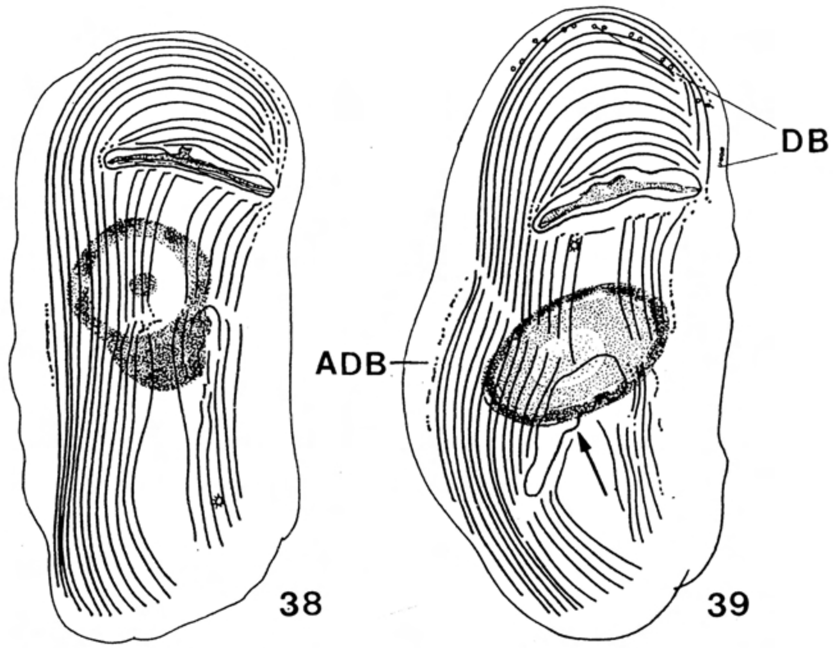

Fig. 38, 39. *Gastronauta derouxi*, early and middle divider after protargol impregnation. Arrow marks newly formed circumoral kinety. ADB – anlage of dorsal brush, DB – parental dorsal brush. From Deroux and Dragesco (1968).

brush along anterior and anterior left dorsal margin of cell, composed of five to seven (eight to ten in Kenyan specimens) evenly spaced clusters with two cilia each (rarely triplets or singles).

Oral opening tightly above end of anterior body third, slightly obliquely orientated to main body axis, extends from left body margin to right of midline, cleft-like, bordered by circumoral kinety whose cilia form a lamellar structure in vivo. Oral basket conical, narrow (1/4 – 1/5 of circumoral kinety length), recognisable only after protargol impregnation, extends anteriorly for a short distance and then curves dorsally and posteriorly, where it narrows strongly[3]; composed of fibres too fine to be counted (Fig. 24, 27, 31, 33, 75, 77, 78).

Occurrence and ecology. *Gastronauta derouxi* was discovered in a light reddish-brown soil grown with *Opuntia* sp. and tufts of grass in Madeira (Blatterer and Foissner 1992). It was also found in the upper, very saline soil layer from the shore of Lake Baringo, Kenya (Fig. 32, 82). Deroux and Dragesco (1968) collected it from wall and tree mosses near Roscoff, France. Lehle (1992) showed a protargol-impregnated specimen from a forest soil of the " Schwäbische Alb ", Germany.

[3] Deroux & Dragesco (1968) describe a kinety-like structure within the basket (Fig. 31). I suggest, as in *G. membranaceus,* that these granules are caused by the strongly curved basket rods.

Table 2. Morphometric data on *Gastronauta membranaceus* (upper line; original data from Wilbert's *G. runcina* slides; see synonymy), *G. aloisi* (middle line; from Oberschmidleitner and Aescht 1996), and *G. derouxi* (lower line; from Blatterer and Foissner 1992).

Characteristics[a]	$\overline{x}$	M	SD	SE	CV	Min	Max	n
Body, length	47.9	45.0	7.0	1.8	14.5	40.0	62.0	15
	45.3	46.2	5.1	1.2	11.2	36.0	53.0	18
	61.4	60.0	7.2	1.7	11.6	48.0	77.0	17
Body, maximum width	28.1	27.0	4.3	1.1	15.2	23.0	38.0	15
	34.7	33.6	3.8	0.9	10.9	29.0	47.0	18
	37.9	36.0	4.6	1.1	12.0	31.0	46.0	17
Distance between left and right postoral ciliary field	not investigated							
	11.1	10.8	2.4	0.6	21.4	8.0	15.0	18
	8.3	8.0	1.4	0.4	17.5	6.0	11.0	17
Distance from anterior cell end to circumoral kinety	17.3	17.0	2.4	0.6	13.9	14.0	23.0	15
	14.7	14.4	1.4	0.3	9.9	12.0	17.0	18
	16.9	17.0	1.8	0.4	10.7	13.0	20.0	15
Distance from anterior cell end to anterior brush row 1	3.6	4.0	0.6	0.2	17.6	3.0	5.0	15
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–
Distance from anterior cell end to posterior brush row 2	10.7	10.0	1.7	0.4	15.9	9.0	15.0	15
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–
Circumoral kinety, length of long axis	21.7	21.0	2.3	0.6	10.4	19.0	26.0	15
	22.7	22.5	2.1	0.5	9.3	19.0	27.0	18
	21.5	21.0	1.9	0.5	8.9	18.0	27.0	17
Circumoral kinety, length of short axis	2.5	3.0	0.5	0.1	20.4	2.0	3.0	15
	2.4	2.4	0.2	0.1	10.3	2.0	3.0	18
	3.1	3.0	0.3	0.1	9.8	2.0	4.0	17
Macronucleus, length	23.3	22.0	4.8	1.2	20.4	18.0	35.0	15
	14.6	14.7	2.4	0.6	16.1	12.0	20.0	18
	17.4	18.0	2.0	0.5	11.3	14.0	21.0	17
Macronucleus, width	13.1	13.0	2.9	0.7	21.9	6.0	17.0	15
	9.3	9.3	1.3	0.3	13.7	7.0	12.0	18
	10.5	10.0	1.1	0.3	10.1	8.0	13.0	17
Micronucleus, length	5.0	5.0	0.8	0.2	15.1	4.0	6.0	15
	2.7	2.4	0.5	0.1	18.9	2.0	4.0	18
	3.3	3.5	0.3	0.1	10.0	3.0	4.0	17
Micronucleus, width	4.5	4.0	0.6	0.2	14.1	4.0	6.0	15
	2.6	2.4	0.4	0.1	15.9	2.0	4.0	18
	3.2	3.0	0.3	0.1	9.3	3.0	4.0	17
Kineties in right ciliary field, number	9.2	9.0	–	–	–	9.0	10.0	15
	12.2	12.0	0.5	0.1	4.1	11.0	13.0	18
	11.0	11.0	0.0	0.0	0.0	11.0	11.0	17
Kineties in left ciliary field, number	6.0	6.0	0.0	0.0	0.0	6.0	6.0	15
	6.0	6.0	0.3	0.1	5.6	5.0	7.0	18
	5.1	5.0	–	–	–	5.0	6.0	17
Postoral kineties in right ciliary field, number	5.1	5.0	–	–	–	5.0	6.0	15
	5.2	5.0	0.5	0.1	9.7	4.0	6.0	18
	5.1	5.0	–	–	–	5.0	6.0	17
Preoral kineties, number	4.5	4.0	–	–	–	4.0	5.0	15
	3.1	3.0	0.5	0.1	14.7	2.0	4.0	18
	4.1	4.0	–	–	–	4.0	5.0	17

Table 2 (continued.

Characteristics[a]	$\overline{X}$	M	SD	SE	CV	Min	Max	n
Preoral, vertical kinety fragments, number[b]	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	2.0	2.0	0.6	0.1	28.9	1.0	3.0	18
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
Clusters formed by dorsal bristles, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
	3.6	3.0	0.7	0.2	19.3	3.0	5.0	18
	5.8	6.0	0.6	0.1	9.8	5.0	7.0	17
Cilia composing dorsal brush, number	17.0	17.0	1.0	0.3	5.6	16.0	19.0	12
	11.9	12.0	1.7	0.4	14.1	9.0	15.0	18
	13.5	13.0	1.2	0.3	8.8	12.0	16.0	17
Cilia composing (anterior) brush row 1, number	7.0	7.0	1.0	0.3	14.9	5.0	8.0	12
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–
Cilia composing (posterior) brush row 2, number	10.1	10.0	1.4	0.4	14.3	8.0	14.0	15
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–

[a] Data based on protargol-impregnated (various but basically very similar methods), mounted morphostatic specimens from field. 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; $\overline{X}$ – arithmetic mean.

[b] Possibly three in *G. aloisi*, too. See text footnote 4.

Bonkowski (1996) observed *G. derouxi* in beech-litter near Göttingen, Germany, and I found it in litter of a beech forest in Salzburg, Austria (Fig. 75, 76). Petz (1997) recorded *G. derouxi* from moss of continental Antarctica, and Blatterer (1994) observed a single specimen in moss hanging into a river in Upper Austria. These data indicate that *G. derouxi* is a cosmopolitan, euryhyaline soil and moss ciliate, possibly preferring the litter layer.

Remarks. The populations studied so far agree well, differing only slightly in kinety number (Table 2). The French population differs from the type by having slightly more dorsal brush clusters (7 – 9 vs. 5 – 7) and more kineties in the right (12 – 13 vs. 11) and left (6 vs. 5 – 6) ciliary field; it is very similar to the Kenyan (7 – 10 dorsal brush clusters; 13 and 5 – 6 kineties in the right and left ciliary field, respectively; 5 – 6 preoral kineties) and Salzburg (Fig. 75, 76) specimens. Thus, I consider all populations as conspecific.

Gastronauta derouxi is similar to *G. aloisi*, differing by the features mentioned in the description of that species.

Gastronauta aloisi Oberschmidleitner and Aescht, 1996 (Fig. 40 – 46, 79 – 81; Table 2)

1996 *Gastronauta aloisi* Oberschmidleitner & Aescht, Beitr. Naturk. Oberösterreichs, 4: 10 (Fig. 1 – 6 plus colour micrograph on journal cover).

Type material. 1 holotype slide with protargol-impregnated specimens (Foissner's method) from the type location is deposited in the Oberösterreichische Landesmuseum in Linz (LI), accession number: 1997/135.

Description. Size in vivo 50 – 70 × 40 µm, acontractile but very flexible. Broadly ellipsoidal, right side more convex than left; flattened dorsoventrally, anteriorly flatter than posteriorly, ventral side concave, dorsal distinctly vaulted and with furrows and crests, as well as a cylindroidal structure near mid-body right of midline (Fig. 40, 41, 46). Macronucleus in body centre according to original description, in posterior half of cell or left or in midline according to figures (Fig. 40, 46, 80, 81), ellipsoidal, with many peripheral chromatin bodies and a conspicuous nucleolus in hyaline, central region. Micronucleus often rather distant from macronucleus, large and globular. Two contractile vacuoles in ordinary position, contraction interval of anterior vacuole 17 – 22s ($\overline{x}$ 19, n 6), of posterior 27 – 41s ($\overline{x}$ 39, n 6), excretory pores recognisable both in vivo and after protargol impregnation, anterior pore between second and third inner kinety of right postoral field, posterior pore between third and fourth kinety of left ciliary field (Fig. 40, 41, 79). Cytoplasm colourless, contains food vacuoles with bacterial residues. Glides slowly and is thigmotactic. Encysts under slight cover glass pressure within a few minutes (Fig. 44).

Ciliary pattern as shown in Figures 40, 42, 45, 46, 79 – 81. 16 – 20 somatic ciliary rows on postoral ventral surface, postorally separated by an about 11 µm wide, barren stripe; at right side accompanied by distinct fibre recognisable only after protargol impregnation. Left field kineties gradually shortened from right to left posteriorly, leftmost ciliary row extends beyond oral cleft and abuts, separated by a minute gap, to anterior end of penultimate ciliary row of right field (Fig. 42)[4]. Right ciliary field composed of 11 – 13 rows, of which 4 – 6 are postoral and 6 – 7 extend preorally forming wide arcs; anterior portion of innermost two postoral ciliary rows sharply curved to left almost touching anterior end of left ciliary field. Three slightly convex, comparatively narrowly spaced preoral ciliary rows gradually shortened from right to left at right end of circumoral kinety. Left above circumoral ciliary row two short, vertically extending kinety fragments; outer fragment commences at left border of circumoral kinety and curves around inner fragment anteriorly, basal bodies of curved portion sometimes comparatively widely spaced and thus seemingly separated from posterior portion (Fig. 42, 45)[5]. Dorsal brush along left anterior margin of cell, consists of three to five clusters with two to six cilia each.

Oral cleft at end of anterior body third, slightly obliquely orientated to main body axis, extends from left body margin to right of midline, bordered by circumoral kinety whose cilia form lamellar structure. Oral basket conical, extends anteriorly for a short distance and then curves dorsally and posteriorly; composed of fibres too fine to be counted (Fig. 40, 42, 45, 79 – 81).

Occurrence and ecology. As yet found only at type location, that is, an activated sewage plant at Asten near Linz, Upper Austria. Here, it occurred in great

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[4] As described by Oberschmidleitner and Aescht (1996). I suggest another interpretation, viz., that the anterior portion is, as in the other species of the genus, a vertical kinety fragment.

[5] The anteriormost two kinetids of the curved portion are very likely homologous to the two isolated kinetids found in *G. membranaceus* and *P. clatratus* (see also explanation to Fig. 42).

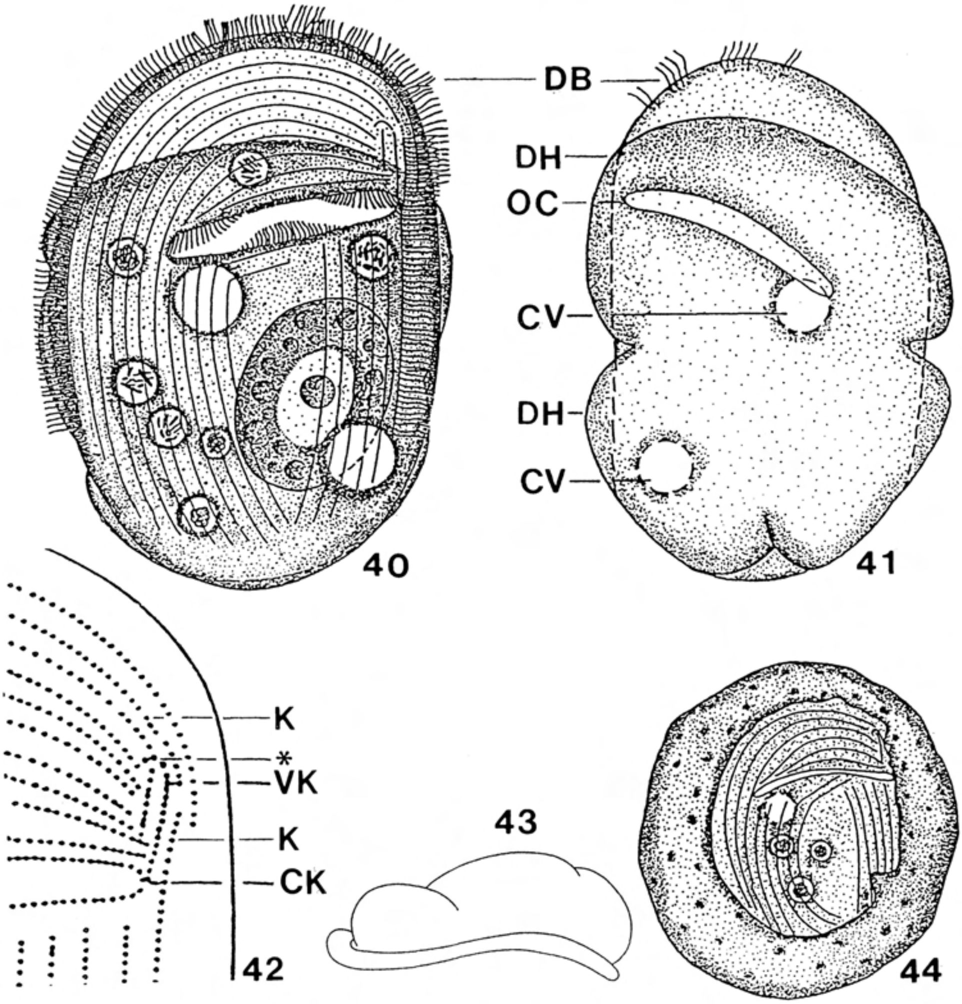


Fig. 40 – 44. *Gastronauta aloisi* from life (40, 41, 43, 44) and after protargol impregnation (42). **40, 41, 43:** Ventral, dorsal, and lateral view of a representative specimen, length about 60 µm. **42:** Ventral ciliary pattern in anterior left quadrant of cell (enlarged detail from Figure 45) showing that the outer vertical kinety fragment seemingly (VK) curves around the inner anteriorly. However, my interpretation is different, that is, the anteriormost kinetids are very likely homologous with the isolated kinetids (asterisk) found in most other species. The leftmost kinety (K) of the left postoral ciliary field extends above the circumoral kinety (CK) almost touching the anterior end of the penultimate kinety of the right ciliary field (but see footnote 4, below). **44:** Encysting specimen, diameter 32 µm. CK – circumoral kinety, DB – dorsal brush, DH – dorsal hump, K – somatic kineties, OC – oral cleft, VK – vertical kinety fragments. From Oberschmidleitner and Aescht (1996).

numbers on three sampling occasions and the following environmental conditions: pH 7.6 – 7.9; chloride (mg/l) 171 – 256; CSB (mg/l) 352 – 635; BSB_5 (mg/l) 140 – 215; PO_4-P (mg/l) 1.2 – 3.1; NO_3-N (mg/l) 0.7 – 1.0; NO_2-N (mg/l) 0.0; NH_4-N (mg/l) 30.9 – 43.7; Kjedahl-N (18.8 – 30.2). The high chloride concentrations indicate that

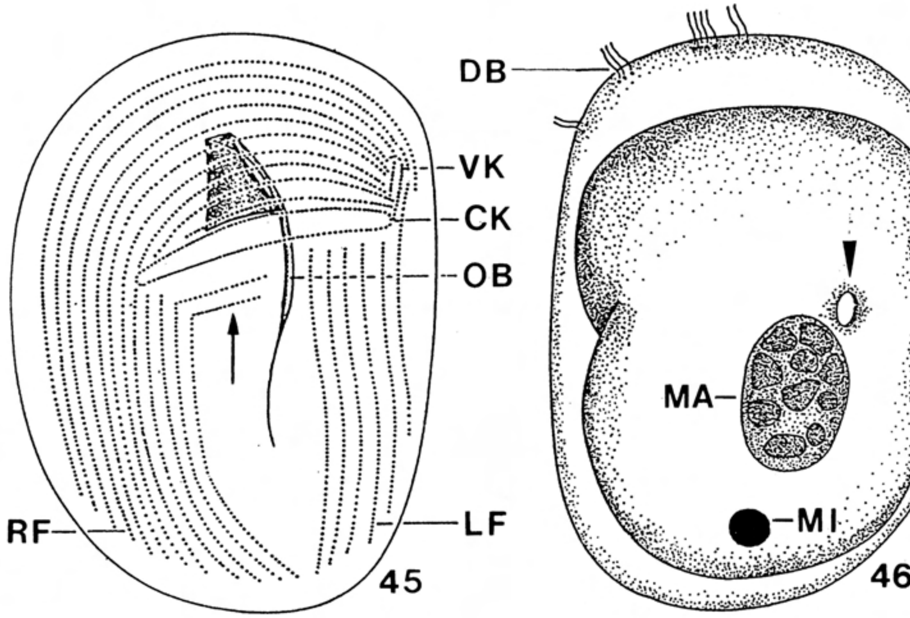


Fig. 45, 46. *Gastronauta aloisi*, ciliary pattern and nuclear apparatus after protargol impregnation, length 47 µm. Arrow marks curved anterior end of kineties 1 and 2 of the right ciliary field, the main species character. Arrowhead marks cylindroidal structure in dorsal hump. CK – circumoral kinety, DB – dorsal brush, LF – left ciliary field, MA – macronucleus, MI – micronucleus, OB – oral basket, RF – right ciliary field, VK – vertical kinety fragments. From Oberschmidleitner and Aescht (1996).

G. aloisi is euryhyaline, and the high NH_4 values suggest that it prefers polysaprobic conditions. *Gastronauta aloisi* could be maintained in sludge cultures for weeks and formed resting cysts because it could be reactivated from air-dried sludge samples.

Remarks. *Gastronauta aloisi* is a distinct species easily identified by the two curved postoral ciliary rows and the three to five tufts of dorsal brush cilia at the anterior left body margin. Within the genus, it is very likely most closely related to *G. derouxi*, which has only one curved postoral kinety and five to seven tufts of dorsal brush cilia.

Gastronauta fontzoui Nie Dashu and Ho Yün-Luan, 1943 (Fig. 22)

1943 *Gastronauta fontzoui* Nie Dashu & Ho Yün-Luan, Sinensia, 14: 143.

Type material. Unknown. Not mentioned in the paper, but the authors made haematoxylin stains, indicating that permanent slides may exist, probably at the National Medical College of Kiangsu, Pehpei, China.

Host. *Palaemon nipponensis*, a freshwater shrimp, collected from a sandy and pebbled stream near the National Medical College of Kiangsu, Pephei, China. Commonly found on the gill laminae of the neat and transparent hosts.

Description. Size 107.5 (92.5 – 117.5) × 54.5 (52.0 – 62.2) µm, length: width ratio about 2:1, number and condition (from life?) of specimens measured not indicated. Body more or less reniform, strongly dorsoventrally flattened, especially so peripherally, rounded at both extremities, with bill-like process jutting out from anterior fourth of left side, convex at mid-dorsal side, distinctly concave at ventral side. Macronucleus usually posterior to the middle, ellipsoidal. Two contractile vacuoles: one large and associated with small accessory vesicles, posteriorly located, close to the left side; one small, situated just below peristomal groove. Cytoplasm clear, densely granular. Swims very slowly among gill laminae with gliding movements; liable to be perished after removed from host.

Cilia of body confined to concave ventral surface, 6 or 7 rows on left side, 19 to 21 on right, dense and uniform in length except for a row of brush-like setae near anterior margin. A narrow spindle-shaped band at middle ventral surface not ciliated.

Peristome groove-like, extruding more or less horizontally from bill-like process at left anterior fourth to interior of body for a considerable distance ending close to right-side margin. Peristomal groove tends to vary in length (30 – 44 µm) and disposition, in some specimens very short and arched, in others long and horizontally framed, furnished only with cilia on its upper and lower edges.

Remarks. This species has not been recorded since the original description. The data are too incomplete to be sure about its generic home. However, the barren postoral stripe, the location of the contractile vacuoles, and the slit-like oral opening match *Gastronauta*. Furthermore, an epizoic occurrence is not unlikely because Kahl (1931) found a *Gastronauta* frequently in small *Sphaerium* mussels from the Hamburg harbor.

3. 2. Genus *Paragastronauta* nov. gen.

Diagnosis: Completely ciliated Gastronautidae Deroux, 1994. Dorsal brush in small fragments on dorsal surface.

Type species: *Gastronauta clatratus* Deroux, 1976.

Etymology : Composite of *para* (besides) and *Gastronauta*. Maculine gender.

Paragastronauta clatratus (Deroux, 1976) **nov. comb.**
(Fig. 47 – 65, 83 – 86, 88 – 94; Table 3)

1922 *Gastronauta membranaceus* Engelmann 1862 – Penard, Études Infusoires, p. 102 (misidentification).

1976 *Gastronauta clatratus* Deroux, Protistologica, 12 : 494.

1982 *Gastronauta clatratus* Deroux – Jutrczenki, Decheniana, 135: 107 (redescription after protargol impregnation).

1986 *Gastronauta clatratus* Deroux, 1976 – Wilbert, Acta Protozool., 25: 382 (redescription after protargol impregnation).

1989 *Gastronauta clatratus* Deroux, 1976 – Song Weibo & Wilbert, Lauterbornia, 3: 97 (redescription from life and after silver nitrate impregnation).

1991 *Gastronauta clatratus* Deroux, 1976 – Foissner, Blatterer, Berger & Kohmann, Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft, 1/91: 102 (" Ciliate-Atlas ", that is, taxonomic and ecological monograph).

1992 *Gastronauta clatratus* Deroux, 1976 – Blatterer & Foissner, Arch. Protistenk., 142: 116 (partial revision of genus).

1997 *Gastronauta clatratus* Deroux, 1976 – Foissner, Limnologica, 27: 212 (redescription after protargol impregnation).

Type material and material investigated. The type material consists of about 50 Nigrosin slides, which hardly show any details, and four protargol slides, of which those with the numbers B68/729, B68/821 and B68/822 each contain a few specimens usable for morphometry. My illustrations (Fig. 52, 53, 90 – 92) are from slide B68/821, which contains an excellent specimen at the right margin, very likely overlooked by Deroux because not marked. The slide is marked "Kernic B68 821 25 III 1968" and available from the Museum National d'Histoire Naturelle, Laboratoire de Biologie Parasitaire, 61 Rue Buffon, Paris.

From Dr. Norbert Wilbert (Bonn University), I obtained a slide of the Jutrczenki study. It contains many well-impregnated specimens, which I used for a detailed morphometry (Table 3) and photography (Fig. 84, 85, 93, 94). Unfortunately, Wilbert could not find the slide from the Canadian population he studied in 1968.

My material from the Illach river in Germany is deposited in the Oberösterreichische Landesmuseum in Linz (LI), accession numbers:1998/85,86.

Synonymy. Since the original description, this species has been plagued by the dorsal brush, which was erroneously and incompletely described by Deroux (1976), as previous authors supposed (Foissner 1997, Jutrczenki 1982, Song Weibo and Wilbert 1989, Wilbert 1986) and the reinvestigation of the type slides showed. Later, the dorsal brush was correctly illustrated by Jutrzcenki (1982), Song Weibo and Wilbert (1989) and Foissner (1997). Wilbert (1986) obviously placed row 2 at the wrong margin of the cell (Fig. 55). However, a slide for checking this was not available (see above). Deroux (1976) not only overlooked dorsal brush row 3 near the posterior end of the cell, but also illustrated a row at the anterior left margin of the cell (Fig. 48, 49). The reinvestigation of the type material not only showed the presence of a brush row near the posterior end of the cell, but also the lack of a kinety at the anterior left margin (Fig. 52, 53, 89, 90 – 92); there is usually a rather distinct furrow, whose margins impregnate more or less distinctly and were thus misinterpreted as a dorsal brush row by Deroux (1976) and Foissner et al. (1991).

Penard's *Gastronauta membranaceus* from Swiss mosses lacks a barren postoral stripe (Fig. 61, 62). Thus, it must be a *Paragastronauta*. However, a definite assignment is impossible because Penard (1922) observed only one dorsal brush row near the anterior margin of the cell (Fig. 63). I never found a *Paragastronauta* in mosses and soils, where *G. derouxi* mainly occurs (Foissner 1998). Thus, it can

Table 3. Morphometric data on *Paragastronauta clatratus*. 1st line: French type population from Deroux, reinvestigated; 2nd line: German population from Jutrczenki, reinvestigated; 3rd line: German population investigated by Foissner (1997).

Characteristics[a]	$\overline{X}$	M	SD	SE	CV	Min	Max	n
Body, length	55.1	54.0	3.5	1.3	6.4	51.0	60.0	7
	56.9	58.0	6.0	1.5	10.5	49.0	69.0	15
	59.2	64.0	7.6	2.0	12.8	47.0	64.0	14
Body, width	28.3	28.0	2.8	1.0	9.7	25.0	34.0	7
	29.9	29.0	2.9	0.8	9.7	27.0	36.0	15
	29.6	30.0	3.4	0.9	11.5	23.0	34.0	14
Anterior end to circumoral kinety, distance	17.7	18.0	2.0	0.8	11.2	14.0	20.0	7
	19.0	19.0	1.7	0.5	9.1	16.0	22.0	15
	19.1	20.0	1.3	0.3	7.0	17.0	21.0	14
Anterior end to macronucleus, distance	28.1	28.0	2.0	0.8	7.2	25.0	31.0	7
	28.8	29.0	2.9	0.8	10.1	24.0	34.0	15
	31.5	32.0	3.2	0.9	10.3	26.0	36.0	14
Anterior end to brush 1, distance	3.6	4.0	0.5	0.2	15.0	3.0	4.0	7
	4.1	4.0	0.8	0.2	20.2	3.0	5.0	15
	4.2	4.0	0.6	0.1	13.7	3.0	5.0	14
Anterior end to brush 2, distance	11.7	11.0	1.6	0.6	13.7	10.0	15.0	7
	12.5	12.0	1.6	0.4	12.4	10.0	15.0	15
	12.7	13.0	1.9	0.5	15.6	10.0	15.0	14
Anterior end to brush 3, distance	46.9	45.0	3.6	1.4	7.7	43.0	53.0	7
	48.9	50.0	5.6	1.5	11.6	41.0	60.0	15
	50.5	51.0	6.7	1.8	13.4	41.0	60.0	14
Macronucleus, length	15.1	14.0	2.2	0.8	14.5	14.0	20.0	7
	19.5	20.0	2.8	0.7	14.2	15.0	24.0	15
	16.6	17.0	2.5	0.7	15.2	13.0	21.0	14
Macronucleus, width	10.0	10.0	0.8	0.3	8.2	9.0	11.0	7
	13.4	13.0	2.4	0.6	18.2	9.0	17.0	15
	11.2	11.0	2.1	0.6	18.2	8.0	15.0	14
Micronucleus, length	2.8	3.0	–	–	–	2.5	3.0	6
	4.0	4.0	0.8	0.2	18.9	3.0	5.0	15
	3.6	4.0	0.6	0.2	16.5	3.0	5.0	14
Micronucleus, width	2.8	3.0	–	–	–	2.5	3.0	6
	3.5	3.0	0.6	0.2	18.1	3.0	5.0	15
	3.2	3.0	0.3	0.1	10.0	3.0	4.0	14
Contractile vacuole pores, number	2.0	–	–	–	–	–	–	1
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	6
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Somatic postoral kineties, number	20.5	21.0	–	–	–	20.0	21.0	6
	18.9	19.0	–	–	–	18.0	19.0	15
	19.9	20.0	1.0	0.3	5.0	19.0	23.0	14
Kineties anterior of oral slit, number	12.4	12.0	–	–	–	12.0	13.0	7
	11.0	11.0	0.0	0.0	0.0	11.0	11.0	15
	11.7	12.0	0.6	0.2	5.2	11.0	13.0	14
Preoral kineties, number	9.3	9.0	–	–	–	9.0	10.0	6
	8.0	8.0	0.0	0.0	0.0	8.0	8.0	15
	8.7	9.0	0.6	0.2	7.0	8.0	10.0	14

Table 3 (continued)

Characteristics[a]	$\overline{X}$	M	SD	SE	CV	Min	Max	n
Preoral vertical kinety fragments, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
	3.1	3.0	–	–	–	3.0	4.0	15
	3.1	3.0	–	–	–	3.0	4.0	14
Circumoral kinety, length of long axis	19.1	20.0	2.5	0.9	13.0	16.0	22.0	7
	20.7	21.0	1.6	0.4	7.7	18.0	23.0	15
	19.7	20.0	1.3	0.3	6.4	17.0	22.0	14
Circumoral kinety, length of short axis	1.7	2.0	–	–	–	1.5	2.0	7
	3.3	3.0	0.7	0.2	21.5	2.0	4.0	15
	2.8	3.0	0.5	0.1	19.2	2.0	4.0	14
Dorsal brush, number of groups	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
Dorsal brush 1, number of kinetids	10.0	10.0	1.2	0.6	12.3	9.0	12.0	5
	6.7	7.0	1.0	0.3	14.3	5.0	8.0	15
	8.5	8.0	1.1	0.3	12.5	7.0	11.0	14
Dorsal brush 2, number of kinetids	10.2	11.0	1.2	0.5	11.5	8.0	11.0	6
	9.2	9.0	1.0	0.3	11.0	7.0	11.0	15
	9.3	9.0	1.6	0.4	17.2	7.0	12.0	13
Dorsal brush 3, number of kinetids	8.6	8.0	0.9	0.4	10.4	8.0	10.0	6
	7.4	7.0	1.0	0.3	13.3	6.0	9.0	15
	8.2	8.0	0.9	0.3	11.3	7.0	10.0	13

[a] Data based on protargol-impregnated (various but basically very similar methods) and mounted morphostatic specimens from field. 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; $\overline{X}$ – arithmetic mean.

not even be excluded that Penard (1922) overlooked the barren postoral stripe and his specimens were *G. derouxi*.

Morphometry. As already mentioned, I reinvestigated Deroux' type slides and the population studied by Jutrzcenki (1982). These populations and that investigated by Foissner (1997) match extremely well not only in morphology but also in all main morphometrics (Table 3), leaving no doubt about conspecificity. Accordingly, the following description is based mainly on these three populations and Foissner et al. (1991).

Description. Size in vivo 45 – 75 × 25 – 40 µm, usually about 60 × 30 µm, as calculated from the few life measurements available and values shown in Table 3, assuming some shrinkage due to the preparation procedures. Acontractile but very flexible. Ellipsoidal to broadly ellipsoidal, length:width ratio 2:1 on average (Table 3), sometimes a small indentation at left anterior body margin. Up to 3:1 dorsoventrally flattened, ventral side concave and very thigmotactic (Penard 1922), dorsal convex and with irregular furrows; dorsal hump less extensible than in *G. derouxi* (Deroux 1976), gradually flattens producing bright fringe, contains cylindroidal structure (cytopyge?) subequatorially in midline (Fig. 47, 48, 52, 54, 59 – 61, 83, 90, 93, 94). Nuclear apparatus invariably underneath mid-body in midline of cell, difficult to recognise in vivo. Macronucleus with very irregular outline because of three or more distinct indentations, contains many small and middle-sized nucleoli. Micronucleus usually attached to posterior portion of macronucleus, globular (Fig. 48, 50, 53, 57, 60, 83, 86, 92, 94). Two contractile vacuoles in same position as in *Gastronauta* spp.[6]: anterior vacuole (excretory pore) underneath oral cleft in midline of cell between kineties 7/8 (Fig. 56) or 8/9 (Fig. 52, 59, 85, 88, 90, 93); posterior vacuole subterminally in left posterior quadrant of cell, invariably between posterior portion of kineties 3/4 (Fig. 52, 56, 59, 88, 93). Cytoplasm rather clear, cells thus transparent (Fig. 83). Obviously feeds mainly on diatoms (Deroux 1976; Fig. 60, 88). Glides slowly on slide surface showing great flexibility.

Conjugation observed by Penard (1922). Specimens attach mouth-to-mouth and remain almost motionless for half an hour showing an increased activity of the contractile vacuoles and inflated micronuclei (Fig. 64). Penard (1922) also observed encysting specimens (Fig. 65).

Ciliary pattern as shown in Figures 47 – 62, 84, 85, 88, 89 – 94. 18 – 23, usually 19 – 21 postoral somatic ciliary rows and 8 – 10, usually 8 – 9 preoral kineties form same pattern as in *Gastronauta*, except for the barren postoral stripe, which is lacking. Most ciliary rows gradually shortened posteriorly and interrupted by oral cleft, except for the three to four rightmost ones, which extend in wide arcs to left anterior end of cell. At anterior end of vertical kinety fragment 3, two to four monokinetids or dikinetids form a small, but distinct group overlooked by Deroux (1976), Wilbert (1986) and Song and Wilbert (1989). Invariably three dorsal brush rows in constant, highly characteristic position (misobservations, see synonymy!): brush row 1 subapically in midline of cell, consists of seven to ten cilia on average; brush row 2 at level of oral cleft between left body margin and midline of cell, consists of nine to eleven cilia on average; brush row 3 subterminally in midline of cell, consists of seven to eight cilia on average. Silverline system finely meshed (Fig. 56).

Oral cleft at margin of first and second third of body, traverses slightly obliquely almost entire ciliary field. Anterior half of circumoral kinety with distinct basal bodies, posterior half appears as heavily impregnated, thick line associated with a conspicuous ciliary lamella, which, according to Penard (1922), consists of two parallel ciliary rows (" double baguette "). Pharyngeal basket as inconspicuous as in *Gastronauta*, extends anterodorsally for a short distance and then posteriorly (Fig. 47 – 50, 52, 59, 61, 83 – 85, 88, 90, 91, 93).

Occurrence and ecology. Locus classicus is Roscoff at the French Atlantic coast, where Deroux (1976) discovered *P. clatratus* in the periphyton of slides exposed in a river and brackish estuaries. It was more frequent and abundant in the river than the estuaries, where numbers decreased after high tides. Later, *P. clatratus* was found in clean and mesosaprobic rivers of Germany (Albrecht 1984, 1986, Foissner 1997, Foissner et al. 1991, Jutrczenki 1982, Mauch 1999, Mihailowitsch

[6] Dr. Deroux informed U. Buitkamp and me that his specimens probably have four contractile vacuoles. However, this was disproved by the reinvestigation of the type material containing a single specimen with two clearly impregnated excretory pores in the position shown in Figure 52.

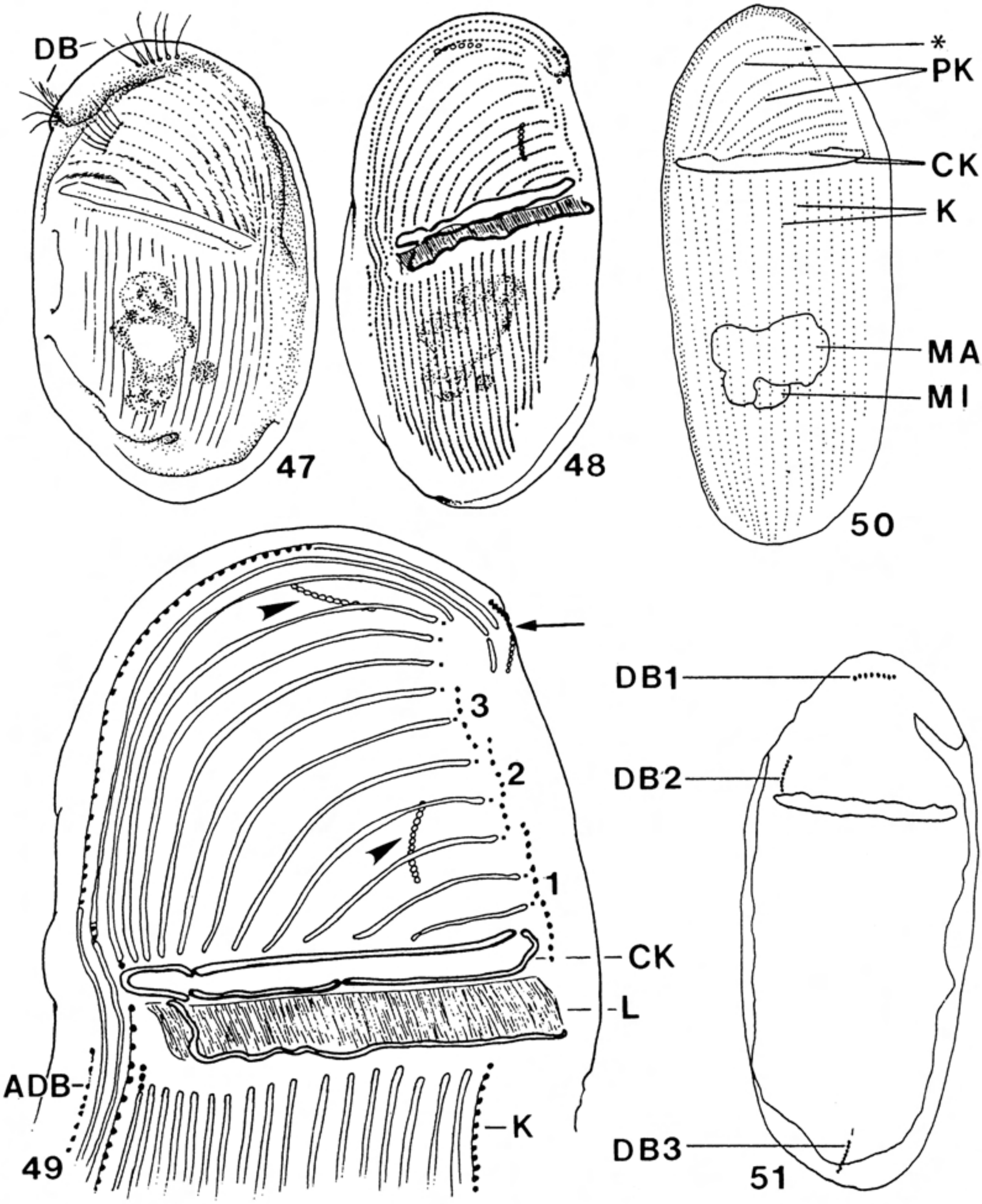
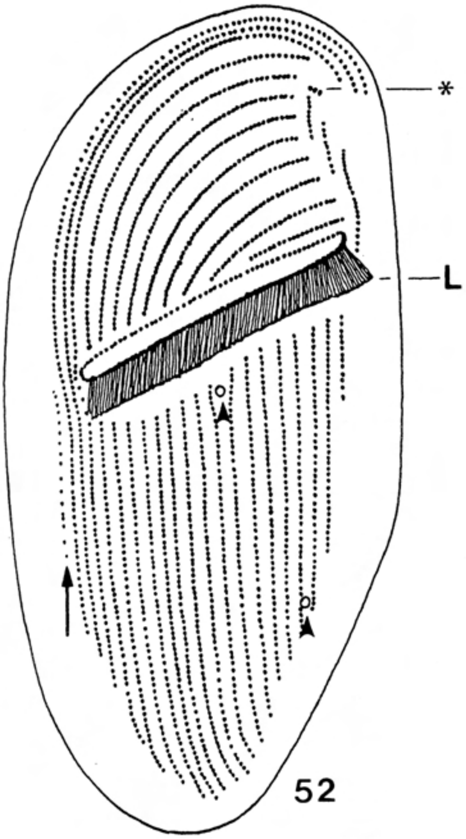
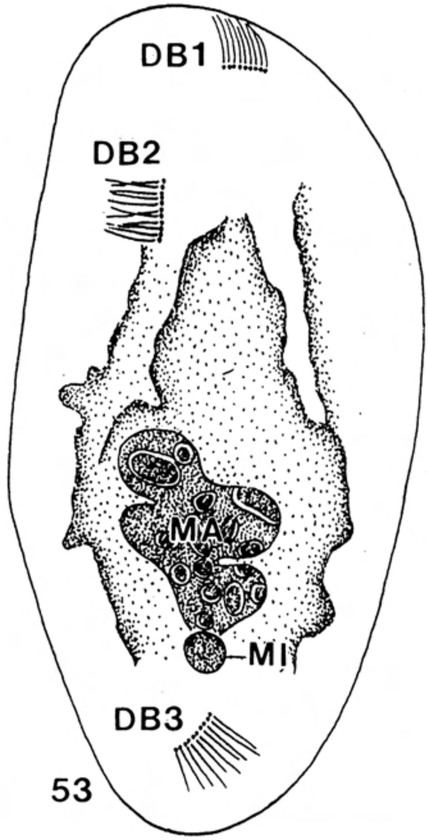


Fig. 47 – 51. *Paragastronauta clatratus*, infraciliature of ventral (48 – 50) and dorsal (47, 51) side after protargol impregnation. **47 – 49:** The French population has, according to Deroux (1976), dorsal brush row 3 at the left anterior margin (arrow), which was, however, disproved by a reinvestigation of the type material (Fig. 52, 53). Dots in Figure 49 mark the 10 preoral kineties. Arrowheads denote dorsal brush rows 1 and 2. **50, 51:** Jutrczenki's German population matches my observations (Fig. 59, 60). Asterisk denotes some special kinetids. ADB – anlage of dorsal brush. CK – circumoral kinety, DB1, 2, 3 – dorsal brush rows, K – somatic kineties, L = lamella formed by cilia of circumoral kinety, MA – macronucleus, MI – microncleus, PK – preoral kineties, 1 – 3 – vertical kinety fragments. Fig. 47 – 49 (from Deroux 1976), length 48 µm, 51 µm, 28 µm; Fig. 50, 51 (from Jutrczenki 1982), length 60 µm.





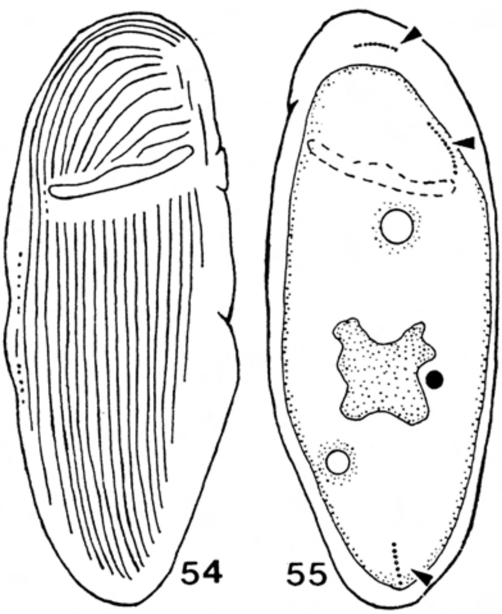


Fig. 52 – 55. *Paragastronauta clatratus*, nuclear apparatus and ciliary pattern of ventral (52, 54) and dorsal (53, 55) side after protargol impregnation. **52, 53:** Original figures from a specimen of the type slides of Deroux (1976), length 60 µm. It is very similar to the German populations (Fig. 50, 51, 59, 60). Arrow marks anlage of dorsal brush. Arrowheads denotes excretory pore of the contractile vacuoles. Asterisk marks three special kinetids at anterior end of vertical kinety fragment 3. **54, 55:** A specimen from the interstitial of Lake Ontario in Canada, length 67µm (from Wilbert 1986). Note that dorsal brush row 2 (middle arrowhead) is illustrated at the wrong margin of the cell (cp. Figure 53). DB1, 2, 3 – dorsal brush rows, L – lamella formed by cilia of circumoral kinety, MA – macronucleus, MI – micronucleus.

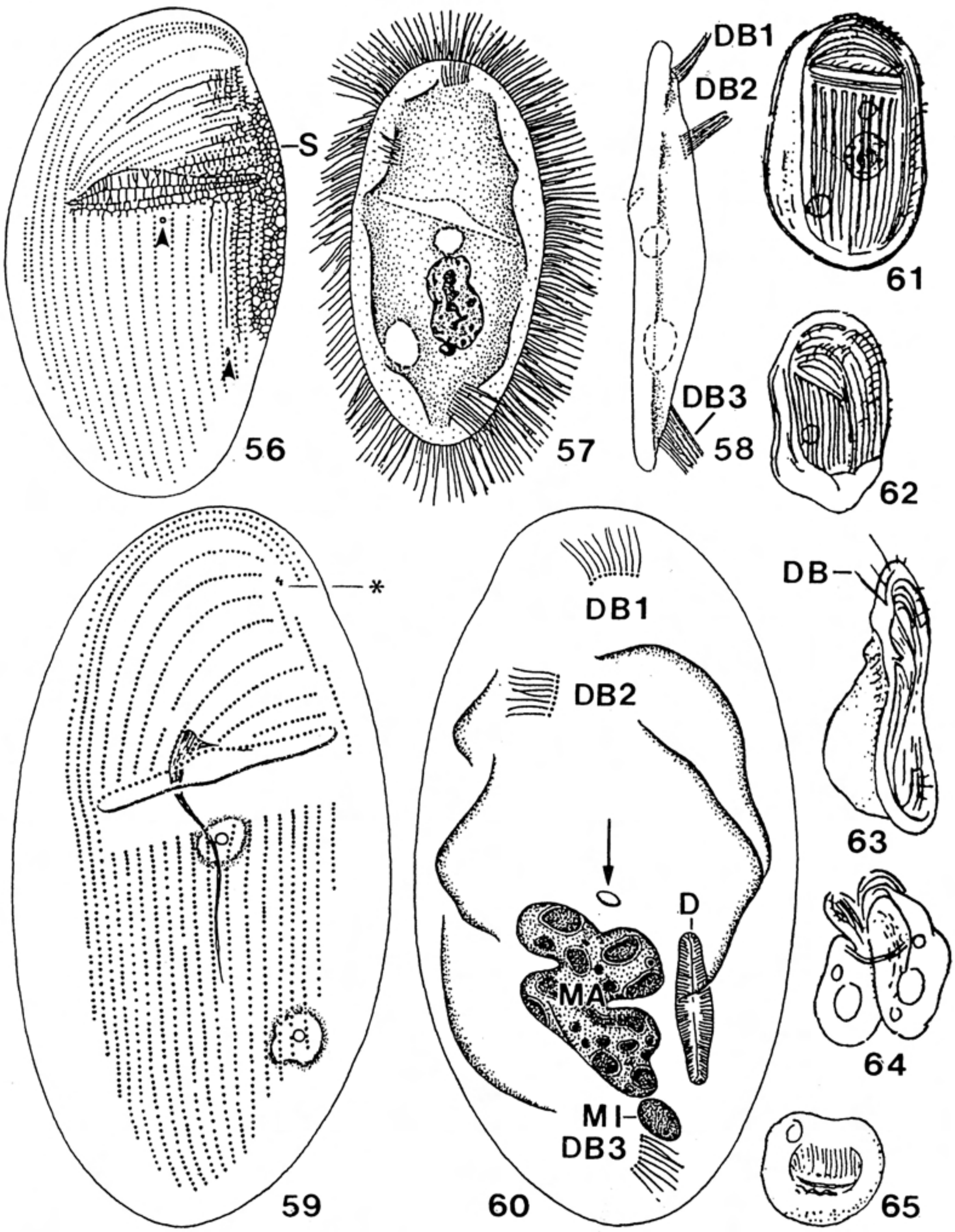


Fig. 56 – 65. *Paragastronauta clatratus* from life (57, 58, 61 – 65) and after silver nitrate (56) and protargol (59, 60) impregnation. **56 – 58:** Ventral, dorsal, and lateral view of a specimen from a pond in Germany, length 40 – 50 µm (from Song Weibo and Wilbert 1989). Arrowheads mark excretory pores. **59, 60:** Ciliary pattern of a specimen from a German river, length 55 µm (from Foissner 1997). Asterisk marks special kinetids. **61 – 65:** Swiss moss population, length 50 – 60 µm (from Penard 1922). D – diatom, DB1, 2, 3 – dorsal brush rows, MA – macronucleus, MI – micronucleus, S – silverline system.

1989, Packroff and Zwick 1996), Austria (Blatterer 1994), and Slovakia (Tirjaková and Degma 1996). It has also been recorded from the Aufwuchs and psammal of ponds and lakes in Germany (Song Weibo and Wilbert 1989), Canada (Wilbert 1986), and China (Song Weibo and Chen Zigui 1999). Penard (1922) found this or a similar species in Swiss moss (see synonymy).

Paragastronauta clatratus likely feeds mainly on diatoms (Deroux 1976; Fig. 60, 88) and occurs throughout the year (Albrecht 1984, 1986). Biomass of 10^6 individuals about 10 mg (Foissner et al. 1991). On slides exposed in clean rivers, it may grow to up to 40 individuals cm^{-2} during July (Jutrczenki 1982). Albrecht (1984, 1986) and Mihailowitsch (1989) observed *P. clatratus* in the periphyton of slides exposed in salt-polluted rives of Germany and emphasised that it is likely intolerant to higher salt concentrations, that is, prefers freshwater. On the other hand, Deroux (1976) found it in brackish estuaries, albeit less frequent and abundant than in a river. This shows that *P. clatratus* is holo-euryhaline but prefers ordinary freshwater. Albrecht (1984, 1986) found *P. clatratus* in 19% from 90 samples with a mean abundance of 9 individuals cm^{-2} under the following conditions: < 5°C – <20°C, 0 – 2000 mg l^{-1} Cl^-, 0.1 – 0.8 m s^{-1} streaming velocity, and a saprobity index of 2.5 – 3.0 (mostly 2.5 – 2.6). Mihailowitsch (1989) observed *P. clatratus* under the following conditions (9 – 10 analyses): 7.4 – 18.3°C, pH 7.5 – 7.9, CO_{2free} 11.1 – 31.9 mg l^{-1}, O_2 7.0 – 11.2 mg l^{-1}, NH_4^+–N 0.09 – 0.43 mg l^{-1}, NO_2–N 0.03 – 0.13 mg l^{-1}, NO_3–N 0.3 – 5.8 mg l^{-1}, Cl^- 35.5 – 174.4 mg l^{-1}, µS cm^{-1} 1102 – 10420.

These data show that *P. clatratus* is a holo-euryhaline, likely cosmopolitan ciliate, preferring mesosaprobic limnetic habitats. Foissner et al. (1991) suggested the following saprobic classification: b – a; o = 2, b = 4, a = 4, I = 2, SI = 2.2.

4. KEY TO GENERA AND SPECIES

1. With about 10 µm wide, barren postoral stripe............................*Gastronauta* (2)
– Without barren postoral stripe...........Single species, *Paragastronauta clatratus*
2. Length about 100 µm; 19 – 21 ciliary rows in right field; epizoic......... *G. fontzoui*
– Length usually < 80 µm; 9 – 12 ciliary rows in right field; free-living in limnetic, brackish, and terrestrial habitats..3
3. Two small dorsal brush rows: row 1 subapically in midline, row 2 at level of oral cleft between left margin and midline of cell; mainly freshwater.......................... .... *G. membranaceus*
– Three to seven minute clusters of dorsalbrush bristles on anterior dorsal margin..4
4. Anterior portion of innermost ciliary row of right field curved to left; mainly in moss and soil...*G. derouxi*
– Anterior portion of the **two** innermost ciliary rows of right field curved to left; activated sewage...*G. aloisi*

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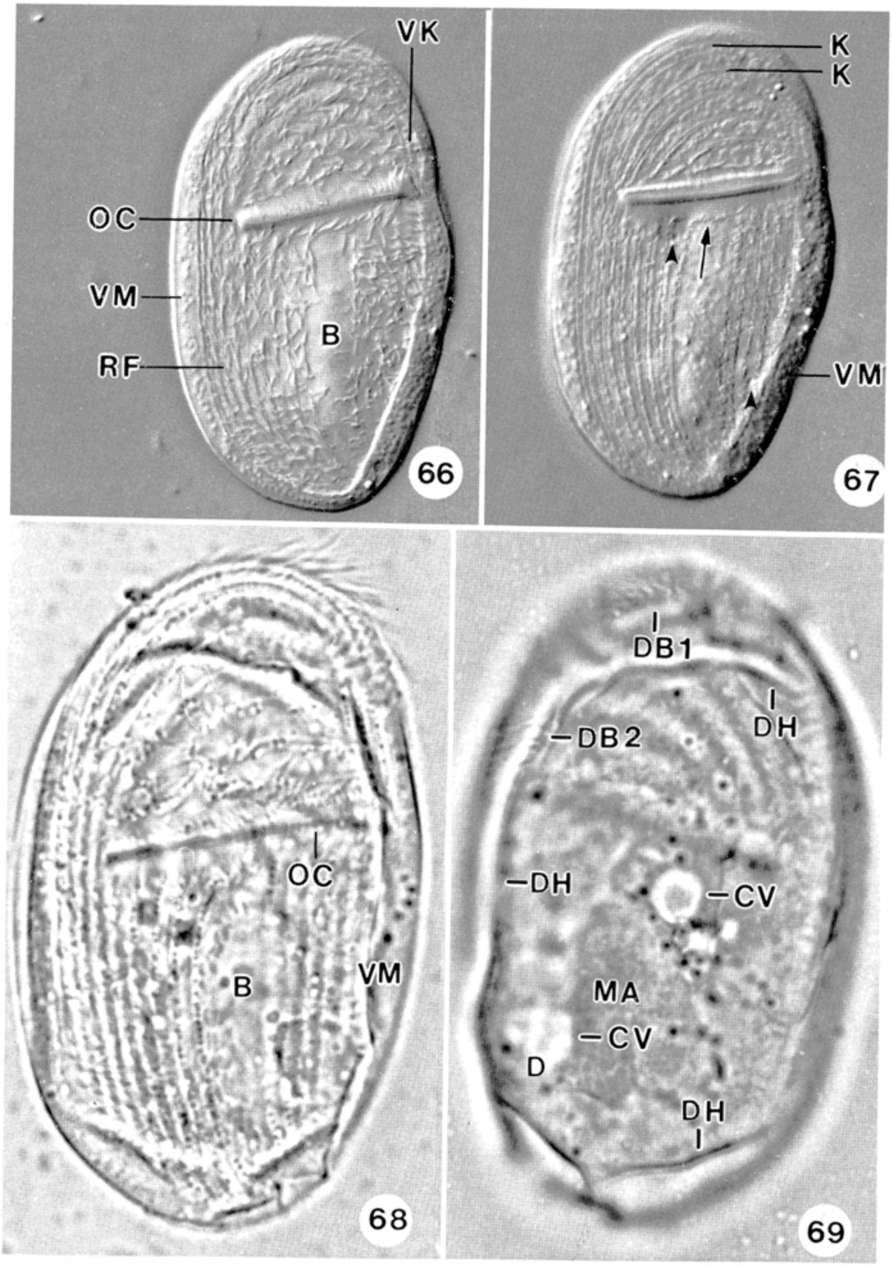

Fig. 66 – 69. *Gastronauta membranaceus*, ventral views (66 – 68) and dorsal view (69) from life at different focal plane. Arrow marks curved anterior end of innermost kinety of right ciliary field. Arrowheads mark pores of contractile vacuoles. B – blank postoral area, CV – contractile vacuoles, DB1, 2 – dorsal brush rows, DH – margin of dorsal hump, K – somatic kineties, MA – macronucleus, OC – oral cleft, RF – right ciliary field, VK – vertical kinety fragments, VM – bulged ventral margin.

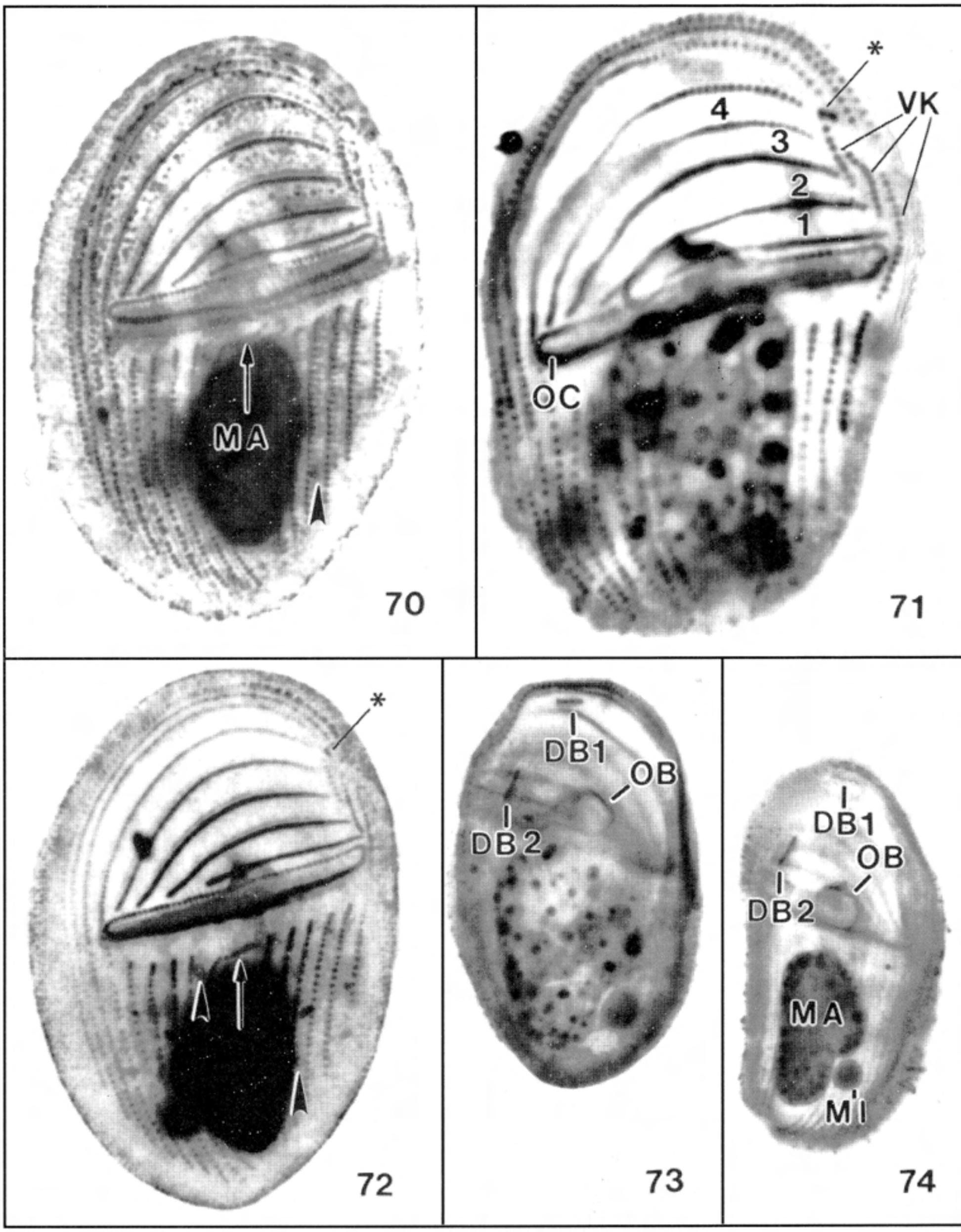

Fig. 70 – 74. *Gastronauta membranaceus*, ventral (70 – 72) and dorsal (73, 74) side after protargol impregnation (original micrographs from Wilbert's *G. runcina* slides). The specimen in Figure 72 is the same as shown in Figures 1 and 7. Arrow marks curved anterior end of inner kinety of right ciliary field. Arrowheads denote excretory pore of contractile vacuoles. Asterisk marks a special couple of kinetids at the anterior end of the vertical kinety fragments. DB1, 2 – dorsal brush rows, MA – macronucleus, MI – micronucleus, OB – oral basket, OC – oral cleft, VK – vertical kinety fragments, 1 – 4 – preoral kineties.

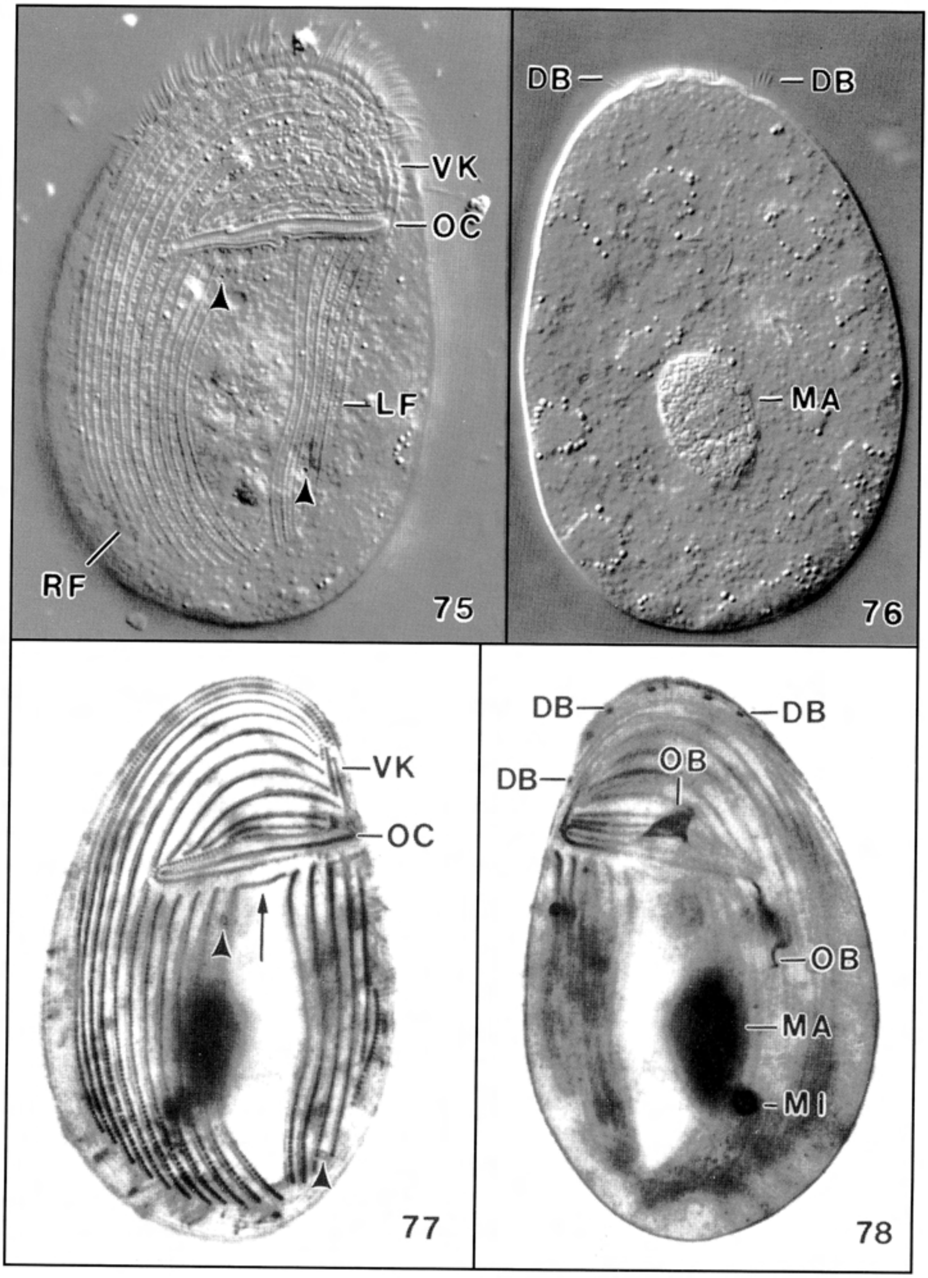

Fig. 75 – 78. *Gastronauta derouxi*, main organelles of Salzburg (75, 76) and Madeiran (77, 78) population from life (75, 76) and after protargol impregnation (77, 78). Arrowheads mark pore of contractile vacuoles; arrow marks curved portion of inner kinety of right field. DB – dorsal brush, LF – left ciliary field, MA – macronucleus, MI – micronucleus, OB – oral basket, OC – oral cleft, RF – right ciliary field, VK – vertical kinety fragments. 75, 76: originals; 77, 78: from Blatterer and Foissner (1992).

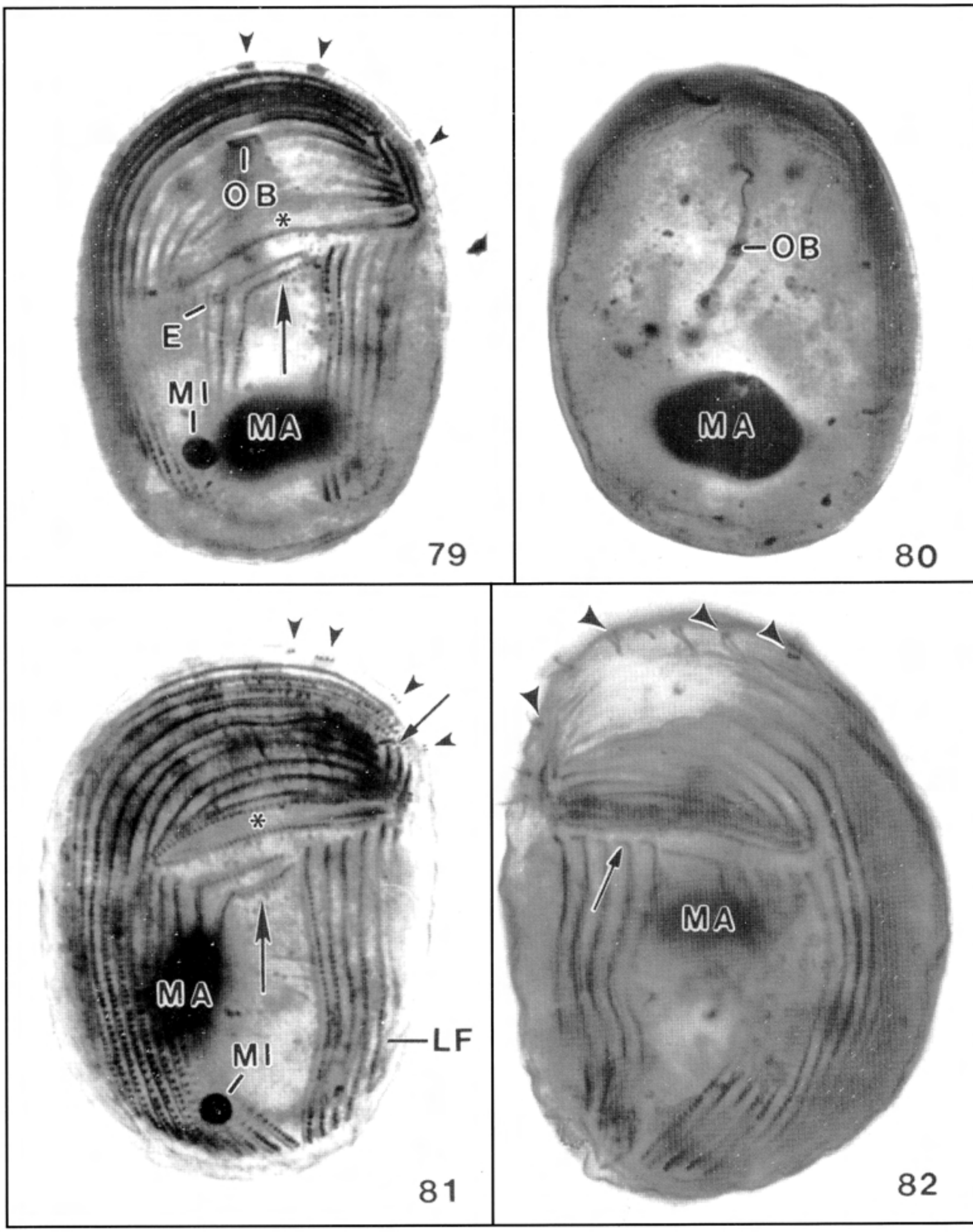

Fig. 79 – 81. *Gastronauta aloisi*, infraciliature of ventral (79, 81) and dorsal (80, 82) side after protargol impregnation. Arrowheads mark dorsal brush tufts. Small arrow denotes outer vertical kinety fragment; large arrow marks **two** curved ciliary rows, the main species character. Asterisk denotes oral cleft. E – pore of anterior contractile vacuole, LF – left ciliary field, MA – macronucleus, MI – micronucleus, OB – oral basket, RF – right ciliary field. From Oberschmidleitner and Aescht (1996) and unpublished.
Fig. 82. *Gastronauta derouxi*, Kenyan population after protargol impregnation. Infraciliature of dorsal and ventral side, showing nine dorsal brush clusters (some marked by arrowheads) and curved anterior ends (arrow) of ciliary rows of the left field. MA – macronucleus.

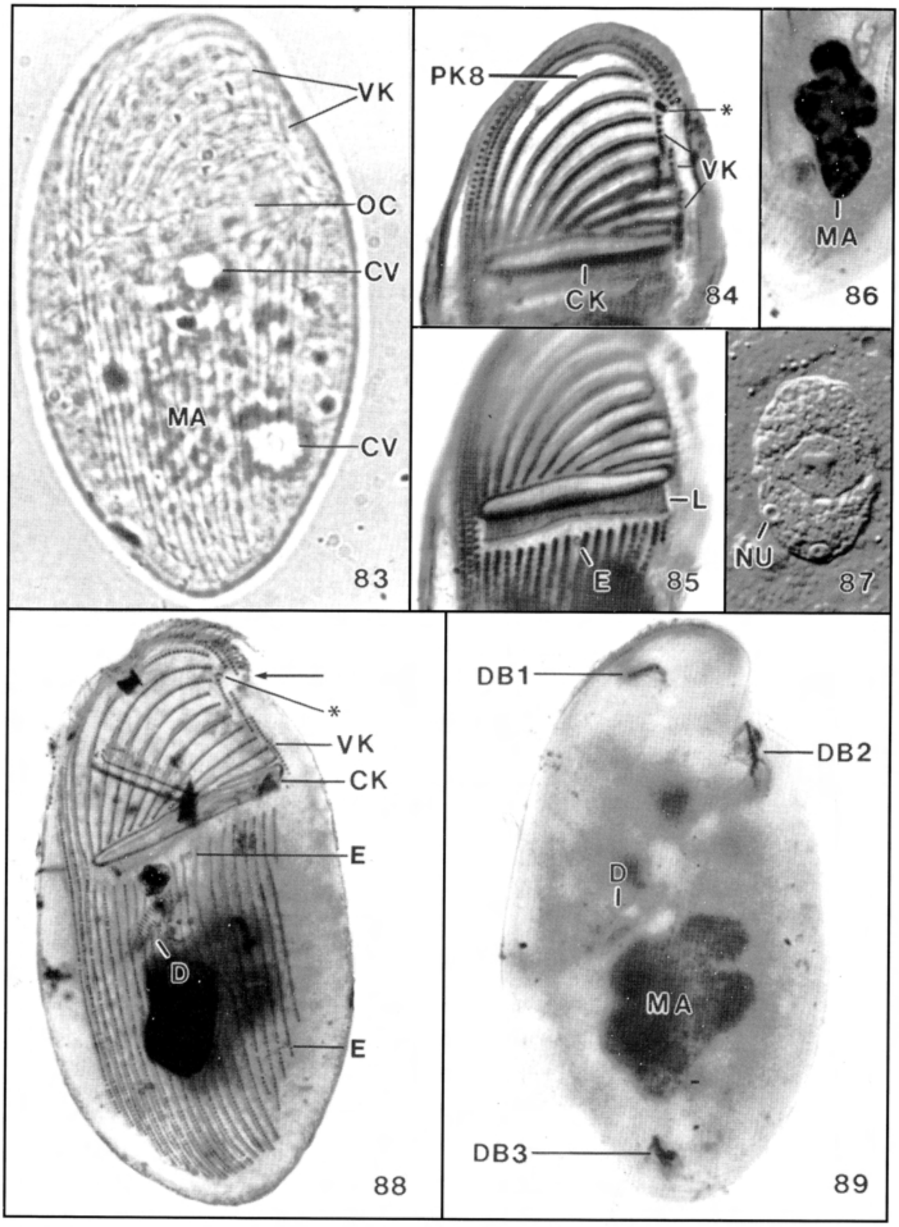

Fig. 83 – 89. *Paragastronauta clatratus* (83 – 86, 88, 89) and *Gastronauta derouxi* (87) from life (83, 87) and after protargol impregnation (84 – 86, 88, 89). Asterisk marks two isolated kinetids at anterior end of vertical kinety 3. **83, 86, 88, 89:** General organisation (from Foissner et al. 1991). Arrow marks a kinety-like line produced by a cortical furrow. **84, 85:** Anterior ventral half, original micrographs from Jutrczenki's slides. **87:** Macronucleus. CK – circumoral kinety, CV – contractile vacuoles, D – ingested diatoms, DB1, 2, 3 – dorsal brush rows, L – lamella formed by cilia of circumoral kinety, MA – macronucleus, NU – nucleoli, OC – oral cleft, PK – preoral kinety 8, VK – vertical kinety fragments.

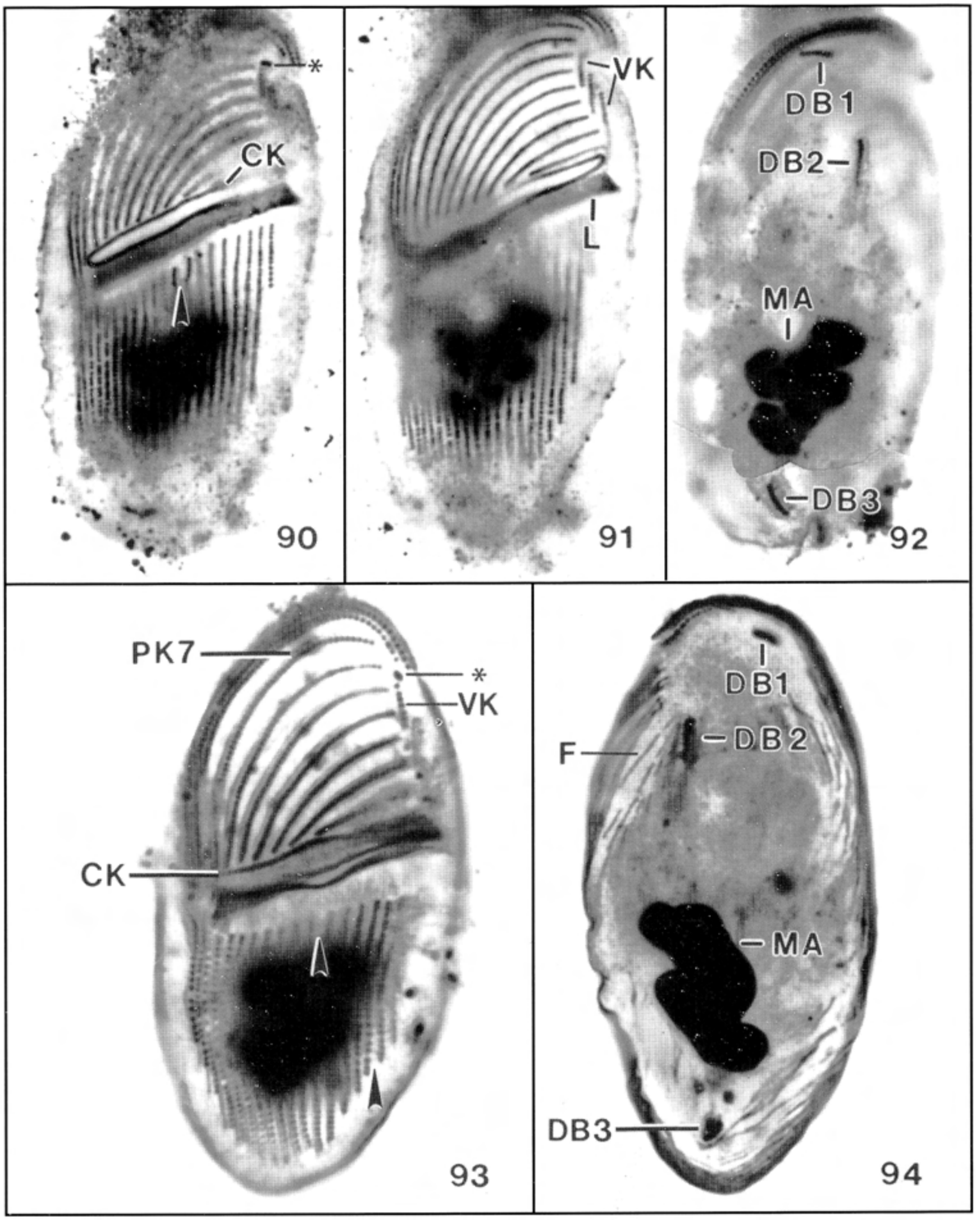

Fig. 90 – 94. *Paragastronauta clatratus*, main cell organelles after protargol impregnation. Arrowheads mark pore of contractile vacuoles. Asterisk marks two isolated kinetids at anterior end of vertical kinety 3. **90 – 92:** Original micrographs of a specimen, focused from ventral to dorsal side, from the type slides of Deroux (1976). **93, 94:** Original micrographs of specimens from the population investigated by Jutrczenki (1982). CK – circumoral kinety, DB1, 2, 3 – dorsal brush rows, F – fibres, L – lamella formed by cilia of circumoral kinety, MA – macronucleus, PK7 – preoral kinety 7, VK – vertical kinety fragment.