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Taxonomy and ecology of some ciliates (Protozoa, Ciliophora) of the saprobic system. III. Revision of the genera *Colpidium* and *Dexiostoma*, and establishment of a new genus, *Paracolpidium* nov. gen.

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Abstract

The genera *Colpidium* Stein, 1860 and *Dexiostoma* Jankowski, 1967 are revised. Our monographic treatment is based on a morphologic and biometric reinvestigation of the main species of these genera and on an evaluation of data from the literature. *Colpidium* comprises four species, namely *C. colpoda* (Losana, 1829), *C. singulare* Vuxanovici, 1961, *C. acuminatum* Vuxanovici, 1962, and *C. kleini* Foissner, 1969. The monotypic genus *Dexiostoma* contains *D. campyla* (Stokes, 1886) and is distinguished from *Colpidium* by a different oral infraciliature and the position and shape of the preoral suture. A new genus, *Paracolpidium* nov. gen., is suggested for *Colpidium truncatum* Stokes, 1885 because its oral infraciliature deviates from both *Colpidium* and *Dexiostoma*. Contrary to *Colpidium* and *Dexiostoma*, the silverline system of *Paracolpidium truncatum* lacks secondary meridians but shows short projections to the left of the primary meridians indicating a phylogenetic relationship to *Tetrahymena*.

Introduction

Members of the genus *Colpidium* are widespread all over the world and can be found in samples of very different perennial biotops like running waters, lakes, and ponds. Although the number of described species is small, identification is loaded with problems especially for field ecologists who are not well trained in the taxonomy of this group of protozoa (Foissner, 1982a). McCoy (1974a) and Corliss (1979) stressed that we are badly in need of all kinds of review for this genus. Even recently published illustrations of species of the genus *Colpidium* are faulty and do not give a satisfactory impression of details of the somatic and oral infraciliature (e.g. Dragesco & Dragesco-Kernéis, 1986).

In the present paper, therefore, the review of the genus *Colpidium* Stein, 1860 is based on a detailed reinvestigation of four species (including the type species) by modern taxonomic methods and takes into account the complete bulk of existing literature. In the course of this study it turned out that *Colpidium* is heterogeneous. Thus, *Dexiostoma* Jankowski, 1967 is resurrected and a new genus, *Paracolpidium*, is suggested.

Material and methods

Colpidium colpoda, Colpidium kleini, and *Dexiostoma campyla* were found in a macrophyte-based waste water treatment system in Ardenberg (Upper Austria) in February 1985. Cultivation was done in petri-dishes at room temperature with Eau de Volvic (French table water) as culture medium and squeezed wheat grains added to support bacterial growth. Every two weeks about 25 cells were inoculated into fresh medium. *Paracolpidium truncatum* was collected in rather high numbers in March 1986 from the bank of the river Salzach in Salzburg. Some attempts to cultivate this species failed. In these samples of the river Salzach the other three species mentioned above occurred, too. To facilitate a comparison we used this uncultivated material for the drawings of specimens prepared by the Chatton-Lwoff silver method (Figs. 126–129). Photographs showing the living aspect of *P. truncatum* were shot from a population found in the river Ager near Marchtrenk (Upper Austria) in April 1987. This population was successfully cultivated by the same method described above but the petri-dishes were put in a refrigerator (4–8 °C). Photographs showing the living aspect of *C. colpoda* were shot from a population taken from a brook in the surroundings of Salzburg in May 1987.

Living observation was performed on cells which were not covered by a cover glass. Details, however, were studied on more or less squeezed individuals with an oil immersion objective in bright field and Normanski contrast. To reveal the infraciliature we used the protargol silver staining method (Foissner, 1982b; bleaching with Eau de Javelle in *P. truncatum* and partly in *C. kleini*) and the pyridinated silver carbonate method (Fernández-Galiano, 1976) as improved by Augustin *et al.* (1984). The silverline system was studied by the dry and wet silver nitrate methods of Foissner (1976) and Corliss (1953a), respectively. All measurements were carried out by an ocular micrometer. Statistical procedures were performed on a TI-66 minicomputer of Texas Instruments and follow methods described in Sachs (1984). All drawings, except for those showing living aspects, were made with the help of a camera lucida.

Type material

Slides of neotype specimens of *Colpidium colpoda, C. kleini, Dexiostoma campyla, and Paracolpidium truncatum* (impregnated by the methods of Foissner, 1976, 1982b; Augustin *et al.*, 1984; and Corliss, 1953a) are deposited in the collection of microscope slides of the Upper Austrian Museum in Linz. Slides prepared by the dry silver method of Foissner (1976) were deposited earlier at this locality. However, this material is from other sources. McCoy (1974a) designated strain UI-7196 as the neotype of *Colpidium campylum* (now *Dexiostoma campyla*) and was expecting to preserve the neotype strain in liquid nitrogen. We have no information whether this really has been done.

Historical survey

Stein (1860) established the genus *Colpidium* recognizing that *Paramecium colpoda* Ehrenberg, 1831 is different from typical members of the genus *Paramecium*. Stokes (1885a, 1886) described *Colpidium truncatum, Tillina campyla* (later changed into *Colpidium campylum* by Bresslau, 1922), *Colpidium striatum*, and *Colpidium putrinum*. Unfortunately, the brief descriptions of Stokes did not clearly separate the single species from each other and since that time they have been mixed up repeatedly by different authors. Bresslau (1922) brought some clarifying aspects into the field by separating unequivocally *C. campylum* from *C. colpoda* using the number of ciliary rows. The new method of silver staining provided further criteria to distinguish between those two species (Klein, 1926, 1927, 1928). Kahl (1931), who conceded *Colpidium* only the status of a subgenus of the genus *Glaucoma*, accepted just two species, *C. colpoda* and *C. campylum*, and regarded the others as unreliable. Russo (1914) described *Colpidium echini*, a parasitic form in the intes-

tinum of sea-urchins, which is now recognized to be a species of the genus *Entodiscus* (Foissner, 1985). Two additional species were described by Gelei (1932, 1935), namely *Colpidium glaucomaeforme* and *Colpidium pannonicum*. However, it was soon recognized by Furgason (1940) that *C. glaucomaeforme* belongs to his genus *Tetrahymena*. *C. pannonicum*, on the other hand, is obviously a *Dexiotricha sp.*, as already mentioned by McCoy (1974a; comp. Peck, 1974). The important papers of Furgason (1940) and Corliss (1952, 1953b) showed furthermore that in American laboratories frequently used names like *'C. campylum'* and *'C. striatum'* represent in reality members of the genus *Tetrahymena*. We follow the suggestion of Corliss (1953b) that *C. putrinum* is best treated belonging to the genus *Tetrahymena*. Very probably it represents a member of the *Tetrahymena pyriformis*-complex. In 1947, Šrámek-Hušek described *Colpidium campyloides*.

The first review of the genus was published, as an abstract only, by Corliss (1953c). Decisions proposed there were used without much reconsideration for a long period of time (e.g. Czapik, 1968; Pätsch, 1974). Corliss recognized five valid species by the characters of body size and shape, number of kineties, extent of preoral torsion, and position of contractile vacuole: *C. colpoda* (Losana, 1829), *C. striatum* Stokes, 1886, *C. campylum* (Stokes, 1886), *C. colpidium* (Schewiakoff, 1892), and *C. truncatum* Stokes, 1885. Corliss & Dougherty (1967) initiated the decision of the International Commission of Zoological Nomenclature that the *Paramaecia kolpoda* of Losana (1829) is regarded as the original description of *C. colpoda* and not the *Paramecium kolpoda* of Ehrenberg (1831).

In the early sixties, Vuxanovici (1961, 1962a, b) described *Colpidium singulare, Colpidium acuminatum,* and *Colpidium colpoda* var. *pusillus*. Jankowski (1967) divided the genus into *Colpidium* (including *C. colpoda* and presumably *C. kleini*), and *Dexiostoma* (including *C. campylum* only). This suggestion, however, has not been accepted by others (e.g. McCoy, 1974a; Foissner & Schiffmann, 1980). In 1969, Foissner described *Colpidium kleini*. Fernández-Galiano & Ruiz (1972) established a further new species, *Colpidium uncinatum*. However, they gave no differentiating features to *C. kleini*. McCoy (1974a) recognized three species only, *C. colpoda* (Losana, 1829), *C. campylum* (Stokes, 1886), and *C. kleini* Foissner, 1969. He suggested that *C. truncatum* is identical with *C. campylum* and that the former name is the valid one, but recommended the retention of *C. campylum* as nomen conservandum. Foissner & Schiffmann (1980), however, redescribed *C. truncatum* Stokes, 1885 and gave a critical summary of important characters for a differentiation between *C. colpoda, C. truncatum, C. campylum*, and *C. kleini*. Recently, Martín-González *et al.* (1981) and Iftode *et al.* (1984) studied the morphogenesis of *C. colpoda* and *C. kleini*.

For a better understanding of the history of the genus *Colpidium* we list nominal species in Table 1.

Characterization of the genera *Colpidium* Stein, 1860, *Dexiostoma* Jankowski, 1967, and *Paracolpidium* nov. gen.

The reinvestigation of the four *Colpidium*-species showed that they are very probably not congeneric. There are rather marked differences in the oral structures and the silverline systems which can be used to distinguish at least three distinct groups, designated here as genera. Their general morphology, however, is so similar that it seems wise to treat them together for this comprehensive characterization as *Colpidium-Dexiostoma-Paracolpidium* (*C-D-P*) group (Fig. 1).

Small to medium sized oval organisms, body length ranges from 30 to 150 μm. Monomorphic, free-living, freshwater forms, reproduction by binary fission in free-swimming condition. Stomatogenesis parakinetal. Conjugation frequently observed. Cysts do not occur. Maintenance in axenic cultures successful only in *Dexiostoma campyla* (McCoy, 1974a; Pitelka, 1961).

Anterior part of body somewhat rotated from right to left and slightly bent to the ventral side,

Table 1. Nominal species of the genera *Colpidium, Dexiostoma*, and *Paracolpidium.*

Original name	Present name
Colpidium acuminatum Vuxanovici, 1962	*Colpidium acuminatum*
Colpidium campyloides Šrámek-Hušek, 1947	?*Paracolpidium truncatum*
Colpidium colpoda var. *pusillus* Vuxanovici, 1962	?*Dexiostoma campyla* or ?*Paracolpidium truncatum*
Colpidium echini Russo, 1914	*Entodiscus echini*
Colpidium glaucomaeforme Gelei, 1935	Member of the *Tetrahymena pyriformis*-complex
Colpidium kleini Foissner, 1969	*Colpidium kleini*
Colpidium pannonicum Gelei, 1932	*Dexiotricha* sp.
Colpidium putrinum Stokes, 1886	Member of the *Tetrahymena pyriformis*-complex
Colpidium singulare Vuxanovici, 1961	*Colpidium singulare*
Colpidium striatum Stokes, 1886	*Dexiostoma campyla*
Colpidium truncatum Stokes, 1885	*Paracolpidium truncatum*
Colpidium uncinatum Fernández-Galiano & Ruiz, 1972	*Colpidium kleini*
Glaucoma colpidium Schewiakoff, 1892	*Dexiostoma campyla*
Paramaecia Kolpoda Losana, 1829	*Colpidium colpoda*
Tillina campyla Stokes, 1886	*Dexiostoma campyla*

producing a distinct ventral depression. A small hyaline elevation on the anterior top, except for *Paracolpidium truncatum*. Cross-sectional view approximately round, preoral slightly narrower than postoral. Oral aperture placed in the anterior third, oriented obliquely to the long body axis, its outline oval to triangular, posterior narrower than anterior, right margin convex, left one concave or straight. Oral cavity funnel-shaped, extends to the middle of the body, always pointing at the left and the dorsal direction. Pellicle colourless, elastic, slightly indented by ciliary rows. Underneath the pellicle a layer of rod-shaped mucocysts, *in vivo* about 2×0.3 μm sized which can easily be induced to produce voluminous slimy envelopes by numerous substances (Bresslau, 1921a, b). Endoplasm colourless, containing numerous refractile granules, 0.5–2.0 μm in diameter. Macronucleus single, centrally located, round, oval, or band-shaped, containing small (~1 μm), irregularly distributed chromatin bodies. A single spherical to slightly oval micronucleus is adjacent to the macronucleus. Contractile vacuole discharges through single (occasionally paired) pore on the right side of the body. Cytoproct slit-like, ventrally, near the posterior end. Food vacuoles 5–30 μm in diameter, bacteria serve as main food source although occasionally the uptake of flagellates or algae is reported (Vuxanovici, 1961; Bick, 1968a; Madoni, 1981).

Ciliation dense, with slightly elongated caudal cilia which are stiffer than the normal cilia. Somatic kineties bipolar except for 2–6 postoral kineties. The right-most postoral kinety is stomatogeneous and defined as kinety number 1.[1] Preoral suture positioned more or less left to the median, distinctly curved to the right in *Colpidium* and *Paracolpidium,* straight in *Dexiostoma*. Kinety fragments placed immediately to the left of the oral aperture. Anterior ends of bipolar kineties possess paired basal bodies, very probably with exception of *P. truncatum* which has apparently single basal bodies anteriorly. However, this has

[1] The postoral kineties are counted pragmatically as those kineties that end below the oral aperture and those that are separated from the kinety fragments by a distinct gap. In a strict sense, however, a differentiation can be made between primary postoral kineties originating from the development of the anarchic field in the beginning of stomatogenesis, and secondary postoral kineties which are produced by the rotation of the new oral structures at the end of the stomatogenetic process.

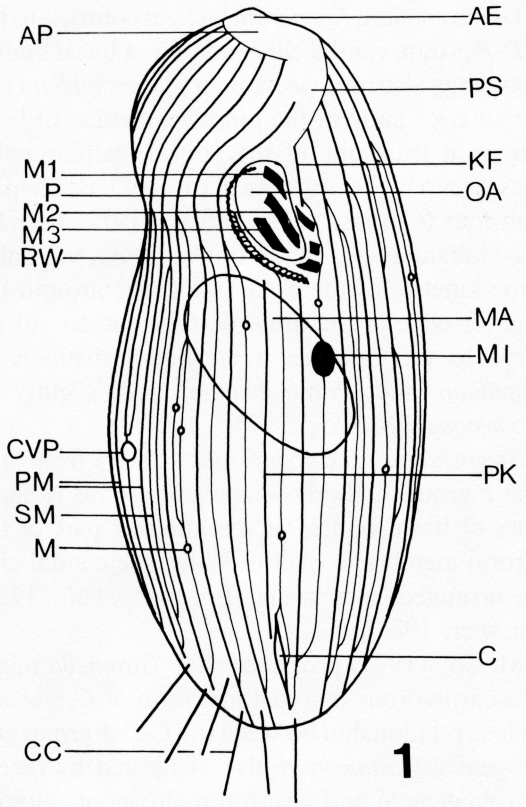


Fig. 1. Scheme of important morphological characters of species in the *C-D-P* group. AE = apical elevation, AP = apical pole field, C = cytoproct, CC = caudal cilia, CVP = contractile vacuole pore, KF = kinety fragment, M = mucocyst, M1–3 = membranelles 1–3, MA = macronucleus, MI = micronucleus, OA = oral aperture, P = paroral membrane, PK = postoral kinety (kinety number 1), PM = primary meridians, PS = preoral suture, RW = ribbed wall, SM = secondary meridian.

to be proved by electron microscopic investigations. A parasomal sac is present anterior to each basal body. On the right side, somatic kineties are slightly shortened posteriorly, in this area the caudal cilia emerge.

Oral infraciliature tetrahymenid, composed of three left adoral membranelles (M1–3) and a right paroral (undulating) membane (Figs. 130–133). Membranelles are attached to the left dorsolateral wall of the oral cavity and principally oriented obliquely to the long body axis. In *Colpidium*, M1 consists of two rows of basal bodies in the posterior two thirds, the anterior part is made of three rows of basal bodies. In *Dexiostoma* and *Paracolpidium*, on the other hand, M1 is made of a single row of basal bodies with a short brush of cilia on the anterior tip that consists of three basal body rows. Membranelle 2 consists of three basal body rows in all three genera and is usually slightly S-formed. In *P. truncatum* it possesses anteriorly a group of slightly posteriorwards shifted basal bodies, giving the impression of a sharp bend. Membranelle 3 shows the highest heterogeneity within the *C-D-P* group. In *Colpidium*, it is very long and consists of four rows of basal bodies which have different length. In *Dexiostoma*, M3 is rather short and is made of three basal body rows which become shorter from left to right. The three rows of basal bodies in the M3 of *Paracolpidium*, however, become slightly shorter from right to left. Note the general tendency that peculiar structures of the membranelles (e.g. gaps in the basal body rows) are restricted to their anterior parts (Figs. 130–133).

Paroral membrane consists of two files of basal bodies with dyads arranged in a characteristic zigzag pattern. According to Lynn & Didier (1978) and Iftode *et al.* (1984) only dyads of the anterior section of the paroral membrane possess anteriorly ciliated basal bodies, whereas the remaining major part of the paroral membrane consists of non-ciliated basal bodies. Correlated with these non-ciliated basal bodies are the so-called oral papillae (easily observable with Normanski contrast), small ectoplasmatic elevations which are the place of origin of microtubuli of the ribbed wall on the right side of the oral cavity. As a unique feature, the paroral membrane in *P. truncatum* is extremely short and takes a somewhat different course compared to the other two genera.

Silverlines longitudinally oriented, composed of primary and secondary meridians except for *P. truncatum* which lacks secondary meridians and has a *Tetrahymena*-like silverline system (Figs. 126–129, 144–151). Primary meridians connect basal bodies of each kinety, secondary meridians connect mucocysts. They originate from the primary meridians at the level of the oral aperture, run parallel to them, and find con-

nection with them again, posteriorly. The number of secondary meridians between two kineties and their behavior during the process of regeneration of mucocysts are valuable features for a separation of species in the genus *Colpidium* and between *Colpidium* and *Dexiostoma* (Foissner, 1969a; Foissner & Schiffmann, 1980). Silverlines lie in the epiplasm and can not be correlated with certain fibrillar structures (Foissner, 1977, 1981; Foissner & Simonsberger, 1975a, b).

Delimitations to closely related genera

On the basis of the present data and those of other authors the genera *Colpidium, Dexiostoma*, and *Paracolpidium* (*C-D-P* group) can be distinguished from *Tetrahymena* by the following characters: 1) Oral aperture oriented obliquely to the long body axis in the *C-D-P* group, parallel to it in *Tetrahymena*; 2) During stomatogenesis the new oral structures of the opisthe rotate somewhat to the left in the *C-D-P* group and break one or more kineties to the left of kinety number 1 in two parts. Thus, kinety fragments are produced which are not present in *Tetrahymena* (Iftode *et al.*, 1984); 3) Membranelle 3 is comparatively long, with clearly recognizable rows of basal bodies in the *C-D-P* group whereas it is reduced to a short, somewhat disordered membranelle with a low number of basal bodies in *Tetrahymena* (Nilsson & Williams, 1966; McCoy, 1974b; Williams & Bakowska, 1982); Exceptions are the macrostomes of *Tetrahymena* which have a well developed M3 (Njine, 1972); 4) Paroral membrane consists of mostly non-ciliated basal bodies in the *C-D-P* group, in *Tetrahymena*, basal bodies of the outer row of the paroral membrane are ciliated (Nilsson & Williams, 1966; Lynn & Didier, 1978; Nelsen, 1981); 5) According to Iftode *et al.* (1984) the isolated oral apparatus in the *C-D-P* group (and *Turaniella*) can be characterized as predominantly microfilamentous, whereas in *Tetrahymena* (and *Glaucoma*) it is mostly microtubular; 6) Numerous caudal cilia present in the *C-D-P* group, single or absent in *Tetrahymena* (Corliss, 1979).

Glaucoma and *Epenardia* lack, in contrast to the *C-D-P* group, caudal cilia and paired basal bodies (probably also not present in *Paracolpidium*) at the anterior ends of the bipolar kineties. In both genera at least one of the adoral membranelles possesses a higher number of rows of basal bodies than four (Corliss, 1971; McCoy, 1975; Fernández-Galiano *et al.*, 1985). In *Glaucoma*, preorally, some kineties of the right side curve around the anterior edge of the oral aperture but do not recurve to the right as it is shown distincly in *Colpidium* and *Paracolpidium*, and slightly in *Dexiostoma* (McCoy, 1975).

Stegochilum and *Spirozona* differ from the *C-D-P* group in body shape and some isolated pairs of basal bodies at the anterior part of the paroral membrane. Additionally, the caudal cilia are arranged in a circle (Foissner *et al.*, 1981; Foissner, 1986).

McCoy (1975) proposed that *Turaniella* might be a carnivorous macrostome form of *Colpidium*. A close relationship between the *C-D-P* group and the genus *Turaniella* is also suggested by recent morphogenetic and electron microscopic studies (Iftode & Versavel, 1968; Iftode *et al.*, 1969; Didier *et al.*, 1970; Lynn & Didier, 1978). Therefore, Iftode *et al.* (1984) transferred *Colpidium* to the Turaniellidae Didier, 1971. They stated that the presence of kinety fragments to the left of the oral aperture uniquely separates both *Colpidium* and *Turaniella* from the other tetrahymenine hymenostomes. Recent investigations, however, have shown kinety fragments also in other hymenostome families, e.g. the Glaucomidae (Fernández-Galiano *et al.*, 1985), the Spirozonidae (Foissner, 1986), and the Bursostomidae (Ganner *et al.*, 1987). Thus, this character is no longer valid. Other great similarities between the *C-D-P* group and *Turaniella* which are mentioned in the above cited papers and by Foissner & Schiffmann (1980) strongly support the suggestion of Iftode *et al.* (1984). The most closely related genera are probably *Paracolpidium* and *Turaniella* both of which have a tetrahymenid silverline system (Iftode *et al.*, 1969; Foissner, unpublished observations).

Biometrical comparison of some populations of the species in the *C-D-P* group (Tables 2, 3)

Mean body length and width in protargol impregnated specimens of *Colpidium colpoda* and *Dexiostoma campyla* are strikingly small compared to literature data, most of which are however from *in vivo* measurements (Bresslau, 1922; Kahl, 1931; Foissner & Schiffmann, 1980). In addition, data of body sizes in our cultivated populations are somewhat contradictory when results of protargol and Chatton-Lwoff slides are compared. In *C. colpoda* and *D. campyla* mean body size is distinctly higher in Chatton-Lwoff slides than in protargol impregnated specimens. On the contrary, *C. kleini* is largest in protargol preparations. In *Paracolpidium truncatum* (which had not been cultivated at the moment of preparation but was fixed from 2–5 day-old raw samples) mean body size is rather similar with both preparation techniques. Similar results have been obtained with *Bursostoma bursaria* (Ganner *et al.*, 1987).

It is reasonable to explain the small body sizes of our populations as a culture effect. This interpretation is supported when mean body sizes of natural populations of *C. colpoda* and *D. campyla* from the river Salzach (Table 3) are compared to the cultivated material. It can, however, not be ruled out that these differences are partly due to the natural variability of populations. Contradictory results of mean body size in protargol and Chatton-Lwoff slides between *C. colpoda* and *D. campyla* on the one side, and *C. kleini* on the other, are very probably an effect of the age and condition of cultures at the moment of fixation. Further studies using cultures of the same age are necessary. Our data, however, demonstrate that body size in these species is a rather variable character. In spite of this, it is helpful to distinguish between the larger sized species *C. colpoda* and *C. kleini* (and *C. singulare*) on the one side, and the smaller sized species *D. campyla* and *P. truncatum* (and *C. acuminatum*) on the other.

Length of adoral membranelles is very similar in *C. colpoda* and *C. kleini*. Membranelle 3 is the longest membranelle in these species, followed by M2 and M1. On the contrary, in *D. campyla* length of adoral membranelles decreases from M1 to M3. In *P. truncatum*, the three membranelles have approximately the same length. Length of paroral membrane nearly equal in *C. colpoda* and *C. kleini*, distinctly shorter in *D. campyla*, shortest in *P. truncatum*.

Size of macronucleus also very similar in *C. colpoda* and *C. kleini*. *D. campyla* has a distinctly smaller macronucleus than the other three species. This is obvious when ratios body length/macronucleus length are compared.

Position of contractile vacuole pore on the long axis of body separates *C. colpoda* and *C. kleini*, where it is positioned slightly below the middle of the body, from *D. campyla* and *P. truncatum*, which have the pore situated in the posterior third of body. Position of contractile vacuole pore on the transverse axis of the body separates clearly *C. colpoda* and *D. campyla* from each other and from the other two species.

Number of kineties is constant in our population of *D. campyla*, a phenomenon that has already been reported by Gelei & Horváth (1931). McCoy (1974a) and Foissner & Schiffmann (1980), on the other side, found a high variability in this character. A surprisingly high variability of kineties has also been stated for two populations of *P. truncatum* by Foissner & Schiffmann (1980), contrary to the low variability of our population. *C. colpoda* possesses a distinctly higher, *D. campyla* a distinctly lower mean number of kineties than the other two species, which are very similar in this character.

Foissner & Schiffmann (1980) mentioned a maximum of two postoral kineties in their populations of the *C-D-P* group, except for *P. truncatum*, where they observed a higher number. Biometrical analysis of our populations, however, revealed that in all species more than two postoral kineties can occur. Still, *P. truncatum* shows the highest median in this character in our comparison.

Gelei & Horváth (1931) reported for *D. campyla* a higher number of basal bodies in the single kineties than we did, namely 24–37 basal bodies in kinety number 1, and 36–48 in a dorsal kinety

Table 2. Biometric comparison of *Colpidium colpoda* (1. line), *C. kleini* (2. line), *Dexiostoma campyla* (3. line), and *Paracolpidium truncatum* (4. line).

Character[2]	M	$\bar{x}$	s	$s_{\bar{x}}$	V	Min	Max	n
Body, length (A)	65.0	66.0	6.7	1.30	10.2	54.6	78.0	25
	72.0	71.0	9.6	1.92	13.6	44.2	83.1	25
	39.0	37.2	5.7	1.14	15.4	26.0	45.5	25
	53.3	52.5	5.6	1.13	10.7	42.9	61.1	25
Body, length (B)	87.1	82.6	10.1	2.00	12.2	65.0	102.7	25
	62.4	60.9	6.0	1.20	9.9	49.4	71.5	25
	48.1	47.3	4.6	0.92	9.7	32.5	53.3	25
	47.5	49.8	6.8	1.36	13.6	38.6	63.7	25
Body, width (A)	39.0	38.4	4.4	0.89	11.6	29.9	48.1	25
	37.0	38.3	5.9	1.18	15.4	29.9	49.4	25
	15.6	15.7	2.3	0.46	14.5	10.4	19.5	25
	31.2	31.7	4.7	0.94	14.9	24.7	46.8	25
Body, width (B)	45.5	46.1	5.6	1.10	12.1	32.5	55.9	25
	28.6	27.9	3.6	0.70	13.0	20.8	32.5	25
	19.5	19.4	2.0	0.40	10.4	15.6	22.7	25
	29.9	31.6	5.1	1.03	16.3	23.4	40.3	25
Ratio, body length/ width (A)	1.8	1.7	0.1	0.03	7.8	1.4	1.9	25
	1.8	1.9	0.3	0.05	13.9	1.3	2.5	25
	2.4	2.4	0.2	0.05	9.8	1.9	3.0	25
	1.7	1.7	0.2	0.03	9.9	1.1	1.9	25
Macronucleus, longest axis (A)	26.0	26.5	3.2	0.63	12.0	22.1	32.5	25
	24.7	24.6	3.4	0.69	13.9	16.2	31.2	25
	10.4	10.5	1.3	0.25	12.2	8.5	13.0	25
	21.5	21.3	2.5	0.50	11.8	16.9	26.0	25
Macronucleus, shortest axis (A)	15.0	14.9	2.2	0.43	14.5	10.4	19.5	25
	10.4	11.5	2.2	0.45	19.5	7.8	16.9	25
	7.8	8.1	1.1	0.23	13.9	5.2	10.4	25
	16.7	16.7	1.9	0.39	11.6	13.0	22.1	25
Ratio, body length/ longest axis of macronucleus (A)	2.5	2.5	0.3	0.07	13.0	1.8	3.2	25
	2.9	3.0	0.7	0.14	23.4	1.6	5.1	25
	3.5	3.6	0.7	0.14	20.0	2.5	5.2	25
	2.5	2.5	0.2	0.04	8.8	2.2	2.9	25
Micronucleus, longest axis (A)	3.0	3.1	0.5	0.10	16.5	2.6	3.9	25
	2.6	2.8	0.5	0.10	17.1	2.6	4.5	25
	2.5	2.4	0.2	0.04	9.8	2.0	2.6	25
	3.9	3.9	0.7	0.13	17.1	2.6	5.2	25
Micronucleus, shortest axis (A)	2.6	2.8	0.4	0.07	12.6	2.4	3.9	25
	2.6	2.7	0.3	0.06	10.4	2.6	3.9	25
	2.4	2.4	0.2	0.03	6.5	2.0	2.7	25
	2.6	2.6	0.4	0.08	15.8	2.0	4.5	25
Adoral membranelle number 1, length (A)	8.9	8.5	0.7	0.14	8.5	7.0	9.4	25
	9.8	9.9	0.9	0.19	9.6	9.0	13.0	25
	6.5	6.3	0.6	0.11	8.9	5.2	7.2	25
	9.1	9.0	1.0	0.19	11.0	6.5	11.7	25

Table 2. (continued)

Character[2]	M	$\bar{x}$	s	$s_{\bar{x}}$	V	Min	Max	n
Adoral membranelle	11.0	10.9	0.9	0.18	8.4	9.1	13.0	25
number 2, length (A)	11.0	10.8	1.0	0.20	9.2	9.1	13.0	25
	5.2	5.2	0.6	0.12	11.3	3.9	6.5	25
	9.1	9.0	1.1	0.22	12.4	6.5	13.0	25
Adoral membranelle	13.0	13.2	0.6	0.12	4.6	11.7	14.3	25
number 3, length (A)	12.4	12.4	0.8	0.16	6.5	10.4	13.6	25
	4.2	4.4	0.6	0.12	13.9	3.2	5.8	25
	9.1	9.2	0.6	0.12	6.7	8.0	10.4	25
Paroral membrane,	11.7	11.7	0.8	0.16	6.8	10.4	13.0	25
length (A)	11.7	11.8	1.0	0.19	8.2	10.4	13.6	25
	7.8	7.7	0.9	0.18	11.5	5.2	9.1	25
	7.2	7.4	0.8	0.17	11.5	6.0	9.1	25
Distance, anterior	37.7	37.1	2.8	0.57	7.6	32.5	42.9	25
end of body to the	41.6	42.2	5.4	1.09	12.9	29.9	50.7	25
contractile vacuole	28.6	28.1	3.2	0.64	11.3	22.1	35.1	25
pore (A)	39.0	39.6	5.3	1.05	13.3	31.2	54.6	25
Ratio, body length/	1.8	1.8	0.2	0.04	11.5	1.4	2.2	25
distance anterior end of	1.7	1.7	0.3	0.06	16.2	1.1	2.2	25
body to contractile	1.4	1.3	0.3	0.06	20.6	0.9	1.9	25
vacuole pore (A)	1.4	1.4	0.2	0.05	16.9	1.0	1.9	25
Number, kineties (A, C)	60.0	59.6	1.7	0.34	2.9	56.0	63.0	25
	39.0	39.2	1.4	0.28	3.5	37.0	44.0	25
	24.0	24.0	0.0	0.00	0.0	24.0	24.0	25
	41.0	41.3	1.9	0.34	4.5	39.0	44.0	29
Number, postoral	3.0	3.0	0.7	0.14	22.8	2.0	5.0	25
kineties (A, C)	3.0	2.7	0.6	0.11	20.7	2.0	4.0	25
	2.0	2.1	0.3	0.07	15.6	2.0	3.0	25
	4.0	3.7	0.7	0.15	19.8	3.0	6.0	25
Number, kinety	2.0	1.9	0.7	0.14	36.6	1.0	4.0	25
fragments (A, C)	2.0	1.6	0.5	0.09	29.8	1.0	2.0	25
	1.0	1.1	0.3	0.06	25.6	1.0	2.0	25
	2.0	1.9	0.6	0.13	33.3	1.0	3.0	25
Number, kinety interrupted	14.0	14.6	0.7	0.14	4.8	14.0	16.0	25
by the contractile vacuole	10.0	9.9	0.5	0.11	5.3	9.0	11.0	25
pore (counted to the left	5.0	5.0	0.0	0.00	0.0	5.0	5.0	25
of kinety number 1) (A, C)	11.0	11.3	0.7	0.14	6.1	10.0	12.0	25
Number, basal bodies	32.0	31.7	3.9	0.79	12.4	24.0	40.0	25
of kinety number 1 (A, C)	31.0	31.2	6.0	1.21	19.4	20.0	43.0	25
	19.0	18.7	2.7	0.53	14.3	13.0	23.0	25
	27.0	27.1	6.9	1.42	25.6	14.0	40.0	24
Number, basal bodies	48.0	49.3	6.4	1.31	13.0	40.0	68.0	24
of a dorsal kinety (A, C)	50.0	48.5	8.2	1.64	16.9	35.0	66.0	25
	27.0	26.7	4.2	0.83	15.6	19.0	36.0	25
	37.0	37.9	6.2	1.26	16.2	25.0	50.0	24
Number, basal bodies	6.0	6.0	1.6	0.32	26.4	3.0	9.0	25
of the first kinety	9.0	9.0	1.0	0.19	10.8	7.0	10.0	25
fragment (A, C)	7.0	6.5	0.7	0.14	11.0	5.0	8.0	25
	2.0	2.2	1.1	0.22	51.2	1.0	5.0	25

Table 2. (continued)

Character[2]	M	$\bar{x}$	s	$s_{\bar{x}}$	V	Min	Max	n
Number, basal bodies	6.0	6.2	1.3	0.26	20.8	4.0	9.0	25
of the second kinety	8.0	8.1	0.9	0.18	10.9	6.0	10.0	25
fragment (A, C)	–	–	–	–	–	–	–	–
	3.0	3.8	1.6	0.33	42.6	2.0	8.0	25
Number, secondary	2.0	1.8	0.4	0.07	20.3	1.0	2.0	25
meridians (B)	1.0	1.0	0.0	0.00	0.0	1.0	1.0	25
	1.0	1.0	0.0	0.00	0.0	1.0	1.0	25
	none							

A = based on protargol preparation; B = based on Chatton-Lwoff preparation; C = based on pyridinated silver carbonate preparation.

[2] All measurements in μm. Legend: M, median; Max, maximum value; Min, minimum value; n, sample size; s, standard deviation; $s_{\bar{x}}$, standard error of the mean; V, coefficient of variation in %; $\bar{x}$, arithmetic mean.

Table 3. Body size of natural populations of *Colpidium colpoda* (upper line) and *Dexiostoma campyla* (lower line).

Character[3]	M	$\bar{x}$	s	$s_{\bar{x}}$	V	Min	Max	n
Body, length (A)	101.0	101.1	11.0	2.20	10.9	75.4	127.4	25
	62.4	63.1	7.4	1.48	11.8	48.1	80.6	25
Body, width (A)	57.2	58.1	8.1	1.62	13.9	39.0	74.1	25
	31.2	32.2	5.1	1.01	15.7	22.1	42.9	25

A = based on protargol preparation.

[3] Measurement in μm. Legend: M, median; Max, maximum value; Min, minimum value; n, sample size; s, standard deviation; $s_{\bar{x}}$, standard error of the mean; V, coefficient of variation in %; $\bar{x}$, arithmetic mean.

(Table 2). Very probably, this is an effect of the small body size in our cultivated population.

Low mean number of kinety fragments separates *D. campyla* from the other species, however, the data overlap. Number of basal bodies in kinety fragments is of little taxonomic value since nearly all data overlap. *P. truncatum* shows a distinctly lower mean number in this character, but the coefficient of variation is strikingly high.

Descriptions of species

Although it takes a certain amount of space, we decided (and the editor generously supported it) to give nearly all original drawings mentioned in the list of synonyms for several reasons: a) to demonstrate the variability of species; b) to facilitate the determination of species; c) to give subsequent authors a better chance to separate further species without having to examine the enormous amount of literature. In addition, there are indications that at least *C. colpoda* and *D. campyla* represent a complex of species. If this can be verified by biochemic and genetic investigations, then the appropriate drawings and species names for reactivation will be available.

Biometric data in our redescriptions represent a summary of all reliable values given by different authors cited in the lists of synonyms.

Genus *Colpidium* Stein, 1860

Diagnosis: Turaniellidae; Preoral suture distinctly curved to the right. Membranelle 1 consists of

2 rows of basal bodies in the posterior two thirds, M3 long and composed of 4 rows of basal bodies. Silverlines longitudinally oriented, 1 or 2 secondary meridians between 2 primary meridians.

Type species (designated by the International Commission of Zoological Nomenclature; see Corliss & Dougherty, 1967): *Colpidium colpoda* (Losana, 1829).

Key to species

1a Macronucleus long, band-shaped, anteriorly bipartite; body length ca. 80 μm; about 45 kineties ..... *C. singulare*

1b Macronucleus round or oval 2

2a More than 50 somatic kineties; body length ca. 100 μm, shape commonly a broad oval; contractile vacuole pore subequatorially, between kinety number 13–17; usually 2 (sometimes only 1!) secondary meridians between 2 primary meridians ..... *C. colpoda*

2b Between 30 and 50 somatic kineties 3

3a Body length ca. 100 μm, shape commonly a slender oval; contractile vacuole pore subequatorially, between kinety number 8–12; usually 1 (sometimes 2!) secondary meridian between 2 primary meridians ..... *C. kleini*

3b Body length ca. 40 μm, shape markedly sigmoid, posterior end tapered; contractile vacuole pore in the posterior third of body ..... *C. acuminatum*

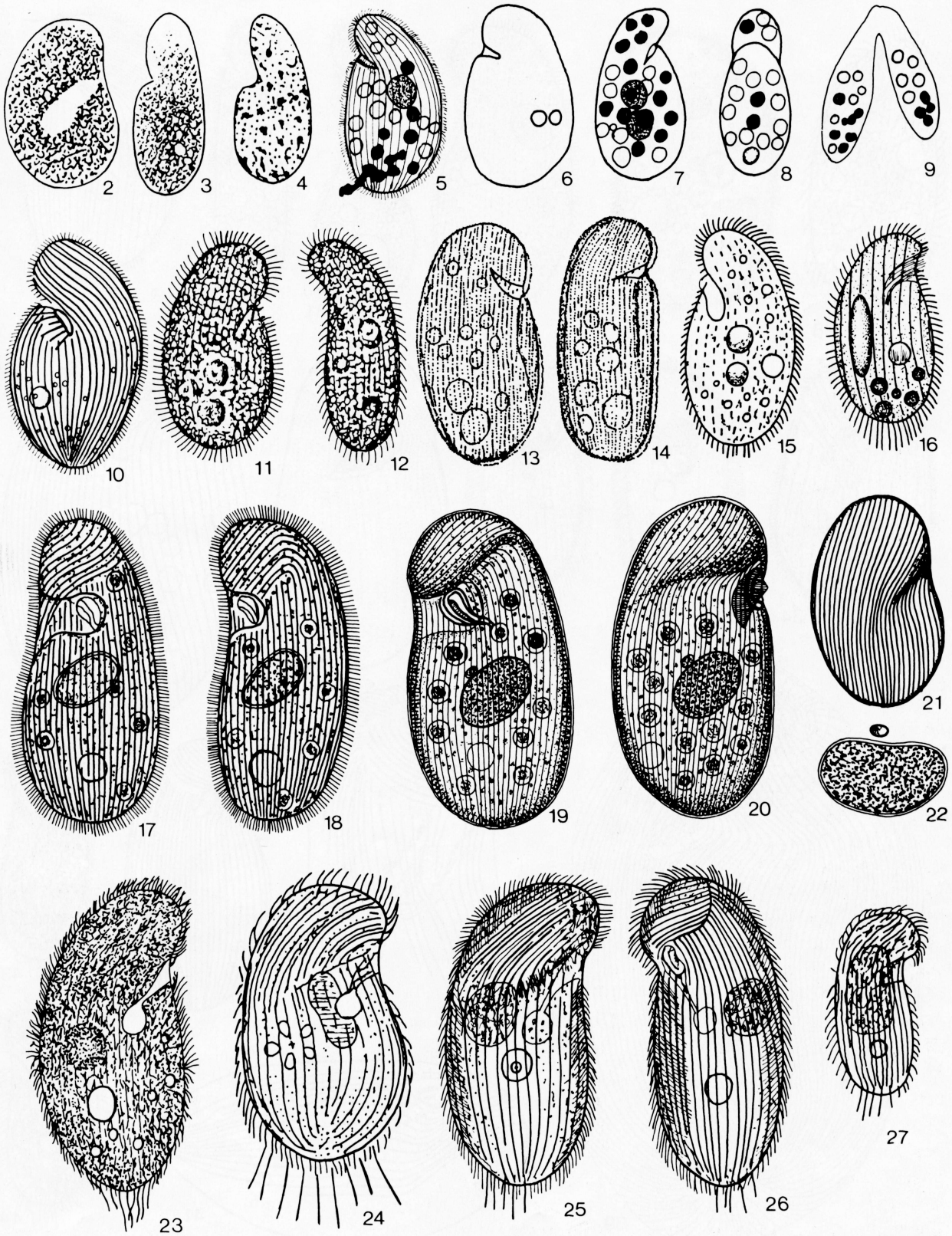
Colpidium colpoda (Losana, 1829) Stein, 1860

?1773 *Kolpoda Ren* – Müller, Vermium terrestrium et fluviatilium, p. 57;?1776 *Colpoda cucullus* – Schrank, Beyträge zur Naturgeschichte, p. 17, 23, Tafel I, Fig. 21;?1786 *Kolpoda Ren* – Müller, Animalcula infusoria, p. 107, Tab. XV, Figs. 20–22 (redrawn as Figs. 2, 3); 1829 *Paramaecia Kolpoda* – Losana, Memorie Accad. Sci. Torino, v. 29, p. 45, Tavel II, Fig. 20 (redrawn as Fig. 4); 1831 *Paramecium Kolpoda* – Ehrenberg, Abh. dt. Akad. Wiss. Berl., p. 114; 1833 *Paramecium Kolpoda* E.! – Ehrenberg, Abh. dt. Akad. Wiss. Berl., p. 174, 324, Tafel III, Figs. IIIa–m; 1838 *Paramecium Colpoda* – Ehrenberg, Die Infusionsthierchen, p. 352, Tafel XXXIX, Fig. IX (redrawn as Figs. 5–9); ?1838 *Colpoda? Ren* – Ehrenberg, Die Infusionsthierchen, p. 348, Tafel XXXIX, Fig. III; 1838 *Kolpoda cucullus* – Dujardin, Annls Sci. nat., v. 10, p. 273, 293, 294, 300, 314, Figs. G.2., G.3. (nec F.1.–F.5., G.1., G.4.); 1841 *Kolpoda cucullus*. – Dujardin, Histoire naturelle, p. 479, Pl. IV, Figs. 29b, d (nec a, c, which represent probably *Glaucoma*; nec Pl. XIV, Fig. 5, which represents a *Colpoda sp.*) (redrawn as Figs. 11, 12); 1852 *Colpoda Ren* M. – Perty, Zur Kenntniss kleinster Lebensformen, p. 145, Tab. V, Fig. 7 (partim) (redrawn as Figs. 13, 14); 1859 *Paramecium Colpoda*. Ehr. – Claparède & Lachmann, Mém. Inst. natn. génev., v. 6, p. 267; 1860 *Colpidium colpoda* – Stein, Sber. k. böhm. Ges. Wiss. Prag, p. 47; 1876 *Colpidium colpoda* – Bütschli, Abh. senckenb. naturforsch. Ges., v. 10, p. 312, Tafel IX, X, Figs. 7–11, 26–28; 1882 *Colpidium cucullus*, Schrank sp. – Kent, A manual of the infusoria, p. 537, Pl. XXVII, Fig. 49 (redrawn as Fig. 15);?1883 *Colpidium colpoda* (Stein) – Maupas, Archs Zool. exp. gén., v. 1, p. 459, Pl. XIX, Figs. 30, 31; 1885 *Tillina helia*, sp. nov. – Stokes, Am. J. Sci., v. 29, p. 317, Pl. III, Fig. 21 (redrawn as Fig. 16); 1886 *Colpidium colpoda* Ehrbg. – Blochmann, Die mikroskopische Thierwelt des Süsswassers, p. 62, 66, Pl. V, Fig. 151 (redrawn as Fig. 10); 1888 *Tillina helia*, Stokes – Stokes, J. Trenton Nat. Hist. Soc., v. 1, p. 158, Pl. IV, Fig. 15; 1889 *Colpidium Colpoda* Ehrbg. sp. – Bütschli, Protozoa, p. 1704, Pl. 62, Figs. 6a, b (redrawn as Figs. 17, 18); 1889 *Colpidium colpoda* – Maupas, Archs Zool. exp. gén., v. 7, p. 238, Pl. XIV, XV, Figs. 1–30; 1889 *Colpidium colpoda*. Ehrbg. sp. – Schewiakoff, Biblthca zool., v. 1, p. 42, Tafel V, Figs. 65–68 (redrawn as Figs. 19–22); 1895 *Colpidium colpoda* (Ehrbg.) – Blochmann, Die mikroskopische Thierwelt des Süsswassers, p. 99, Tafel VI, Fig. 189; 1901 *Colpidium colpoda* Ehrbg. – Roux, Faune infusorienne, p. 57, Pl. III, Fig. 10; 1906 *Colpoda helia* Stokes – Edmondson, Proc. Davenport Acad. Sci., v. 11, p. 80, Pl. XVII, Fig. 129; 1922 *Colpidium colpoda* – Bresslau, Zool. Anz., v. 55, p. 21, Figs. 2–4 (redrawn as Fig. 38); 1922 *Colpidium colpoda* (Ehrenb.) Stein – Penard, Études sur les infusoires d'eau douce, p. 128, Fig. 130 (redrawn as Fig. 24);?1925 *Colpidium colpoda* Stein – Gulati, J. Bombay nat. Hist. Soc., v. 30, p. 749, Pl. II, Fig. 15 (redrawn as Fig. 28); 1927 *Colpidium colpoda* Stein – Klein, Arch. Protistenk., v. 58, p. 113, Fig. 40 (redrawn as Fig. 39);?1927 *Colpidium colpoda*, Stein – Sandon, Protozoan fauna of the soil, p. 182, Pl. VI, Fig. 4; 1928 *Colpidium colpoda* Ehrbg. – Klein, Arch. Protistenk., v. 62, p. 191, Tafel 7–10, Figs. 1–23; 1931 *Colpidium (Paramecium) colpoda* (Ehrb. 1831) Stein, 1860 – Kahl, Tierwelt Dtl., v. 21, p. 334, Figs. 21, 22 on p. 331 (redrawn as Figs. 25–27); 1931 *Colpidium colpoda* Ehrbg. – Tai, Sci. Rep. natn. Univ. Peiping, v. 1, p. 41, Pl. XII, Fig. 1 (redrawn as Fig. 29); 1934 *Colpidium colpoda* – Kidder & Diller, Biol. Bull., v. 67, p. 211, Figs. 5A–G; 1936 *Colpidium colpoda* (Ehrenberg) Stein – Bhatia, Protozoa: Ciliophora, p. 174, Fig. 78; 1936 *Colpidium colpoda* – Liebmann, Z. Hyg. InfektKrankh., v. 118, p. 40, Figs. 6–15 (redrawn as Figs. 30–32); 1947 *Colpidium colpoda* (Ehrbg) Stein – Šrámek-Hušek, Čas. národ. Mus., v. 116, p. 41, Figs. 9, 10 (redrawn as Fig. 33); 1950 *Colpidium colpoda* – Bary, Trans. R. Soc. N.Z., v. 78, p. 315, Figs. 2a, b, 3 (redrawn as Figs. 35–37); 1951 *Colpidium colpoda* Stein –

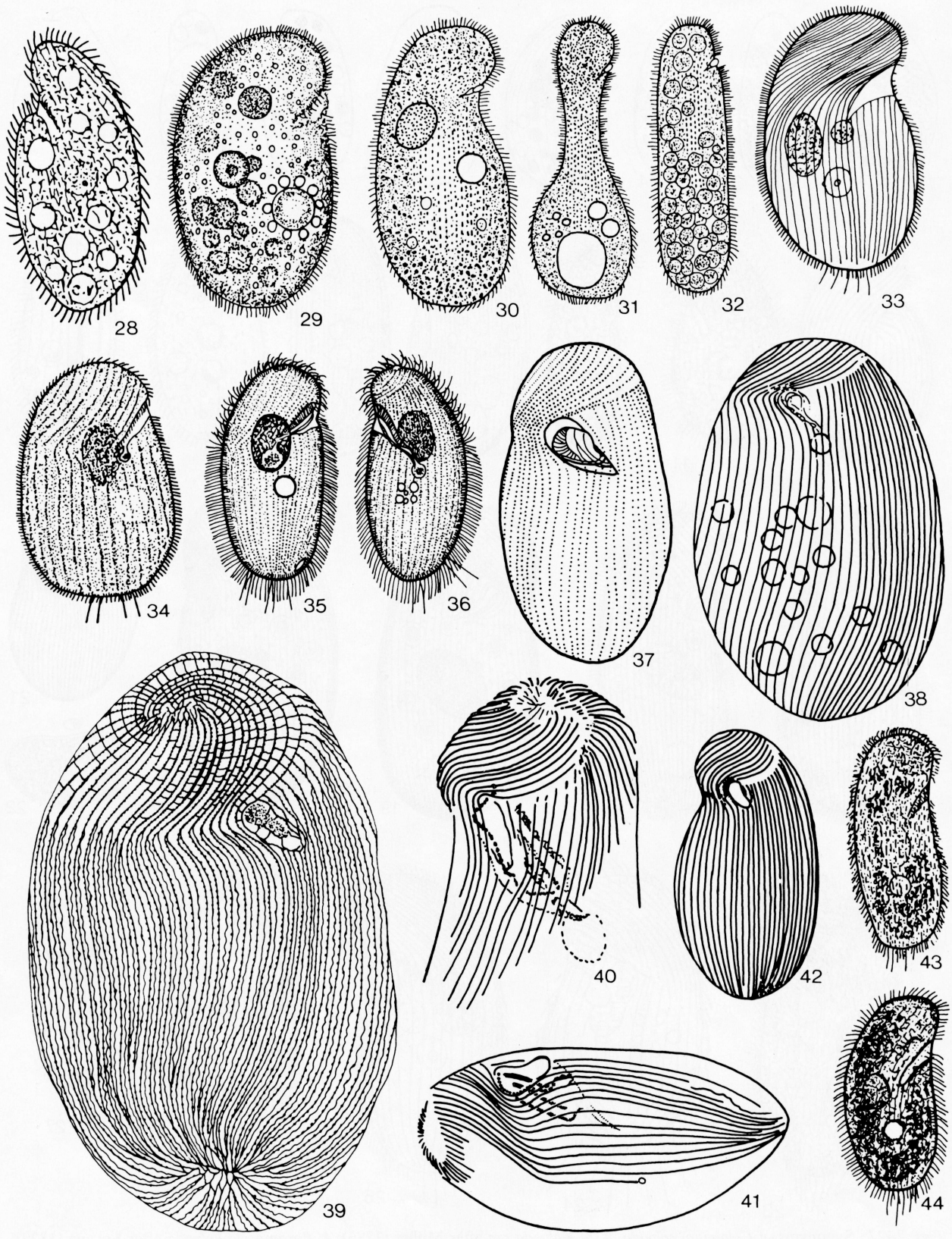
Liebmann, Handbuch der Frischwasser- und Abwasserbiologie, p. 263, Abb. 163, 164, Tafel III, IV, Figs. 4, 10 (redrawn as Fig. 23); 1955 *Colpidium colpoda* (Ehrenberg) – Barwick *et al.*, Tuatara, v. 5, p. 91, Pl. I, Fig. 3 (redrawn as Fig. 34); 1962 *Colpidium colpoda* – Cheissin & Mosewich, Arch. Protistenk., v. 106, p. 181, Figs. 1–11, Pl. 10–15, Figs. 1–23; 1967 *Colpidium colpoda* (Ehrbg., 1830) Stein, 1860 – Jankowski, Zool. Zh., v. 46, p. 17, Pl. 1, Fig. 3 (nec Figs. 1, 2, which represent *C. kleini*); 1968 *Colpidium colpoda* (Ehrenberg, 1831) – Czapik, Acta Protozool., v. 5, p. 342, Pl. IV, Fig. 24; 1969 *Colpidium colpoda* Ehrb. – Foissner, Acta Protozool., v. 7, p. 18, Tafel V, Figs. 17–20; 1969 *Colpidium colpoda* – Iftode *et al.*, Protistologica, v. 5, p. 531, Figs. VA, C, D (redrawn as Figs. 40, 41); 1972 *Colpidium colpoda* (Ehrenberg) – Bick, Ciliated protozoa, p. 80, Fig. 43; 1974 *Colpidium colpoda* Ehrenberg – Foissner, Die Wimpertiere und ihr Silberliniensystem, p. 19, Abb. 21, 22; 1975 *Colpidium colpoda* – Foissner & Simonsberger, Protoplasma, v. 86, p. 5, Abb. 1–19; 1975 *Colpidium colpoda* – Foissner & Simonsberger, Mikroskopie, v. 31, p. 193, Abb. 6–8, 10–14; 1978 *Colpidium colpoda* (Ehrenberg) – Matthes & Wenzel, Die Wimpertiere, p. 58, Bild 42a, b; 1979 *Colpidium colpoda* – Corliss, Ciliated protozoa, p. 257, Pl. IV, XXVI, Figs. 23, 43, 11–13 (redrawn as Fig. 42); 1980 *Colpidium colpoda* (Ehrenberg, 1831) Stein, 1860 – Foissner & Schiffmann, Naturk. Jb. Stadt Linz, v. 24, p. 21, Tafel II, VI, Figs. 12, 14, 31; 1981 *Colpidium colpoda* (Ehrenberg) Stein – Madoni, I protozoi ciliati, p. 88, Fig. 32; 1981 *Colpidium colpoda* – Martín-González *et al.*, Boln R. Soc. esp. Hist. nat. (Biol.), v. 79, p. 93, Pl. I-III, Figs. 1–21; 1982 *Colpidium colpoda* – Bernerth, Cour. Forsch.-Inst. Senckenberg, v. 57, p. 81, Abb. 47c; 1985 *Colpidium colpoda* – Streble & Krauter, Das Leben im Wassertropfen, p. 242, Fig. 4 (redrawn as Fig. 43); 1985 *Colpidium colpoda* – Wegl, Das Leben im Abwasser, p. 106, Abb. 6 (redrawn as Fig. 44).

Discussion of synonymy. Paramaecia kolpoda Losana, 1829 was established as the original description of *Colpidium colpoda* by the authority of the International Commission of Zoological Nomenclature (see Corliss & Dougherty, 1967) (Fig. 4). Some authors (Perty, 1852; Kent, 1882) identified their *C. colpoda* with *Kolpoda ren* Müller, 1773 and *Colpoda cucullus* Schrank, 1776. However, the figures of the latter do not allow a reliable decision as to whether identification is justified or not (Figs. 2, 3). Perty (1852) figured beside large forms (Figs. 13, 14) some tiny forms which he designated as young stages of *C. colpoda*. Very likely they represent a separate species. The figure of Kent (1882) shows two macronuclei which is very uncommon for tetrahymenid ciliates (Fig. 15). A questionable synonym is *C. colpoda* sensu Maupas (1883) whose figure does not show the characteristic course of ciliary rows on the ventral side. Likewise, the illustrations of Bütschli (1889) and Schewiakoff (1889) are partly not correct because in their drawings dorsal kineties overlap to the ventral side (Figs. 17–19). We omitted to give the figures of Blochmann (1895) and Roux (1901) because they are very similar to those of Schewiakoff (1889). The same is true for the figures of Bick (1972) and Matthes & Wenzel (1978) which are redrawn from Kahl (1931). *C. colpoda* sensu Gulati (1925) is very probably a *Colpoda fastigata* because of body shape, position of contractile vacuole and the ability to form cysts (Fig. 28; comp. Foissner, 1980). *Tillina helia* Stokes, 1885 has been synonymized with *C. colpoda* by Kahl (1931). Although the position and shape of macronucleus deviate somewhat from that of *C. colpoda,* we agree with this decision (Fig. 16). Various authors placed the contractile vacuole untypically near the posterior end of body (Bütschli, 1889; Schewiakoff, 1889; Edmondson, 1906).

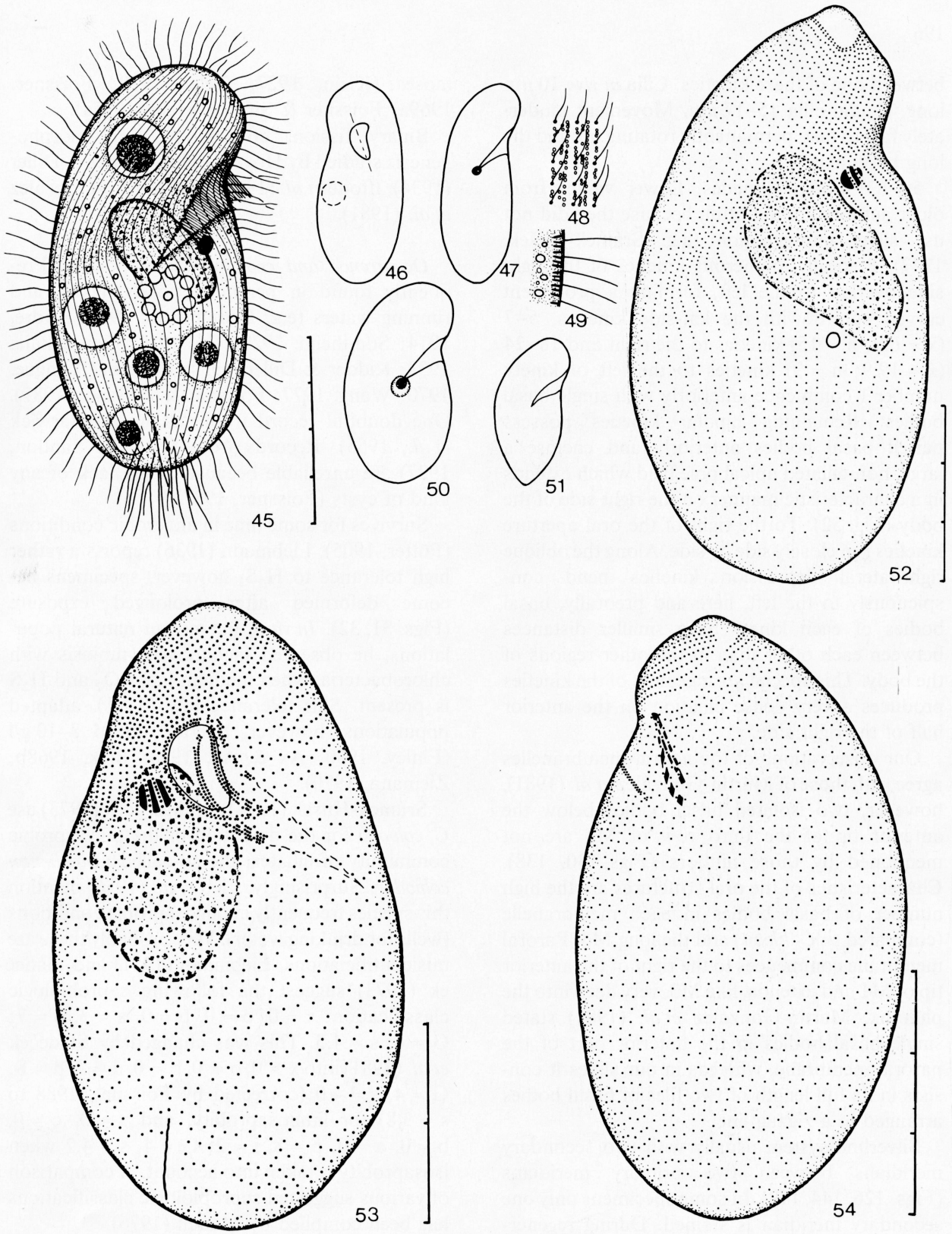
Redescription (Figs. 45–54, 126, 130, 134, 138, 142, 144, 149). *In vivo* 60–150 × 28–80 μm, a size of about 100 × 50 μm is common. Broadly bean-shaped or reniform, about twice as long as it is broad. Anterior and posterior pole distinctly rounded. In old cultures there occur extremely small individuals (~35 μm) with a tapered posterior end, which can easily be confused with *Paracolpidium truncatum* (comp. Bresslau, 1922; Kahl, 1931; Liebmann, 1936) (Fig. 51). Distinct oblique depression on the right side. Mucocysts arranged in two rows between two kineties and between the cilia of each kinety (Figs. 48, 49). Cheissin & Mosevich (1962) report also trichocyst-like structures which could not be observed by us. Macronucleus oval, *in vivo* 28–40 × 12–25 μm, very often oriented diagonally to the pharynx. Contractile vacuole subequatorially, *in vivo* 10 μm in diameter, during diastole with a conspicuous rosette of smaller vacuoles ('Nebenblasen'; Gelei, 1939). Contractile vacuole pore *in vivo* 2,5 μm in diameter, interrupts kinety number 13–17, mostly 14–16, sometimes it lies



Figs. 2–27. Synonyms of *Colpidium colpoda*. 2, 3: *Kolpoda ren* after Müller (1786); 4: *Paramaecia kolpoda* after Losana (1829); 5–9: *Paramecium colpoda* after Ehrenberg (1838), ca. 100 μm; 10: after Blochmann (1886); 11, 12: *Kolpoda cucullus* after Dujardin (1841), 20–90 μm; 13, 14: *Colpoda ren* after Perty (1852); 15: *Colpidium cucullus* after Kent (1882); 16: *Tillina helia* after Stokes (1885b), 85 μm; 17, 18: after Bütschli (1889), up to 120 μm; 19–22: after Schewiakoff (1889), 90–120 μm; 23: after Liebmann (1951), 90–150 μm; 24: after Penard (1922), 110 μm; 25–27: after Kahl (1931), 100–150 μm (25, 26) and 40 μm (27).



Figs. 28–44. Synonyms of *Colpidium colpoda* (continued). 28: after Gulati (1925), 70 μm; 29: after Tai (1931), 121 μm; 30–32: after Liebmann (1936), ca. 120 μm; 33: after Šrámek-Hušek (1947), 70–150 μm; 34: after Barwick *et al.* (1955), 90–150 μm; 35–37: after Bary (1950); 38: after Bresslau (1922), 100–130 μm; 39: after Klein (1927), dry silver preparation; 40, 41: after Iftode *et al.* (1969); 42: after Corliss (1979); 43: after Streble & Krauter (1985), 90–150 μm; 44: after Wegl (1985), 90–150 μm.



Figs. 45–54. Colpidium colpoda, originals from life (45–51) and after protargol impregnation (52–54). 45: Right-lateral view; 46: Ventral view; 47: Right-lateral view of a slender individual; 48, 49: Arrangement of mucocysts in top plan view (48) and lateral view (49); 50: Right-lateral view of a fat cell; 51: Body shape of a degenerated individual. Note the small body size (down to 35 μm) and the tapered posterior end; 52: Infraciliature of the right side; 53: Infraciliature of the ventral side; 54: Infraciliature of the left side. Scale bar divisions: 10 μm.

between one of these kineties. Cilia *in vivo* 10 μm long, caudal cilia 15–17 μm. Movement moderately fast to fast, permanently rotating around the long body axis.

50–63 somatic kineties. Lower values from older authors are doubtful, because they did not use silver impregnation (e.g. Šrámek-Hušek, 1947). Preorally, numerous kineties of the right side overlap to the left, forming a prominent curved suture with the left-side kineties. 5–7 ($\bar{x}$ = 6.2; n = 15) kineties to the right and 18–24 ($\bar{x}$ = 19.9; n = 9) kineties to the left of kinety number 1 commence anteriorly with single basal bodies. Remaining bipolar kineties possess paired basal bodies anteriorly and enclose a large, non-ciliated apical pole field which extends in a characteristic manner on the right side of the body (Fig. 52). To the right of the oral aperture kineties run closely side by side. Along the oblique right-lateral depression kineties bend conspicuously to the left, here and preorally, basal bodies of each kinety have smaller distances between each other than in the other regions of the body. This special arrangement of the kineties produces a very dense ciliation on the anterior half of the right side.

Our observations of the adoral membranelles agree with those of Martín-González *et al.* (1981), however, two isolated basal bodies below the anterior tip of the third row of M3 are not mentioned by those authors (Figs. 130, 138). Characteristics of the oral structures are the high number of basal bodies in each membranelle (compared to *C. kleini*) and the long M3. Paroral membrane commences to the right of the anterior tip of M1 and extends, like M3, very deep into the pharynx. Martín-González *et al.* (1981) stated single basal bodies in the anterior part of the paroral membrane, whereas in our slides it consists in its full length of two files of basal bodies arranged in a zigzag line.

Silverline system usually with two secondary meridians between two primary meridians (Figs. 126, 144, 149). In some specimens only one secondary meridian is stained. During regeneration of mucocysts the secondary meridians split into 4–5 parallel lines and form numerous anastomoses (Klein, 1927; Gelei, 1939; Foissner, 1969a; Foissner & Simonsberger, 1975a).

Binary fission, conjugation, and morphogenesis studied by Hoyer (1899), Kidder & Diller (1934), Iftode *et al.* (1969), and Martín-González *et al.* (1981).

Occurrence and ecology. Cosmopolitan. Frequently found in perennial ponds, lakes, and running waters (e.g. Edmondson, 1906; André, 1914; Sondheim, 1929; Tai, 1931; Gajewskaja, 1933; Kidder & Diller, 1934; Cairns & Yongue, 1970; Wang, 1977; Foissner & Foissner, 1987). One doubtful record from salt water (Barwick *et al.*, 1955). Records from soil (e.g. Sandon, 1927) are unreliable because of the lack of any kind of cysts (Foissner, 1987).

Survives for some time in anaerobic conditions (Pütter, 1905). Liebmann (1936) reports a rather high tolerance to H_2S, however, specimens become deformed after prolonged exposure (Figs. 31, 32). *In vitro*, but not in natural populations, he observed facultative symbiosis with chlorobacteria, when medium lacks O_2 and H_2S is present. Salt tolerance low (3 g/l), adapted populations, however, tolerate up to 8–10 g/l (Finley, 1930; Ax & Ax, 1960; Bick, 1968b; Ziemann, 1970).

Šrámek-Hušek (1958) and Sládeček (1973) use *C. colpoda* for the definition of the polysaprobic community of ciliates, the so-called *Colpidietum colpodae*. Surprisingly, Lieb *et al.* (1956) mention this species frequently in oligosaprobic conditions (wells for drinking water). Very probably these are misidentificiations. Liebmann (1951) and Sládeček (1973) suggest the following saprobiologic classification: x = 0, o = 0, b = 0, a = 3, p = 7; G = 4, s = 4.5. This was changed by Sládeček *et al.* (1981) into x = 0, o = 0, b = 0, a = 2, p = 8; G = 4, s = 4.0 (corrected by Foissner, 1988 to s = 3.8) for limnosaprobity, and x = 0, o = 0, b = 0, a = 0, p = 8, i = 2; G = 4, s = 4.2 when isosaprobity is taken into account. A comparison of various suggested saprobiologic classifications has been compiled by Mauch (1976).

Remarkable physiological studies done by Burbanck (1942) and Burbanck & Gilpin (1946).

Growth has been studied by Mučibabić (1953). Rogerson & Berger (1982, 1983) showed that the presence of *C. colpoda* enhanced the *in vitro* microbial decradation of crude oil. Toxic response to hydrocarbons investigated by Rogerson *et al.* (1983).

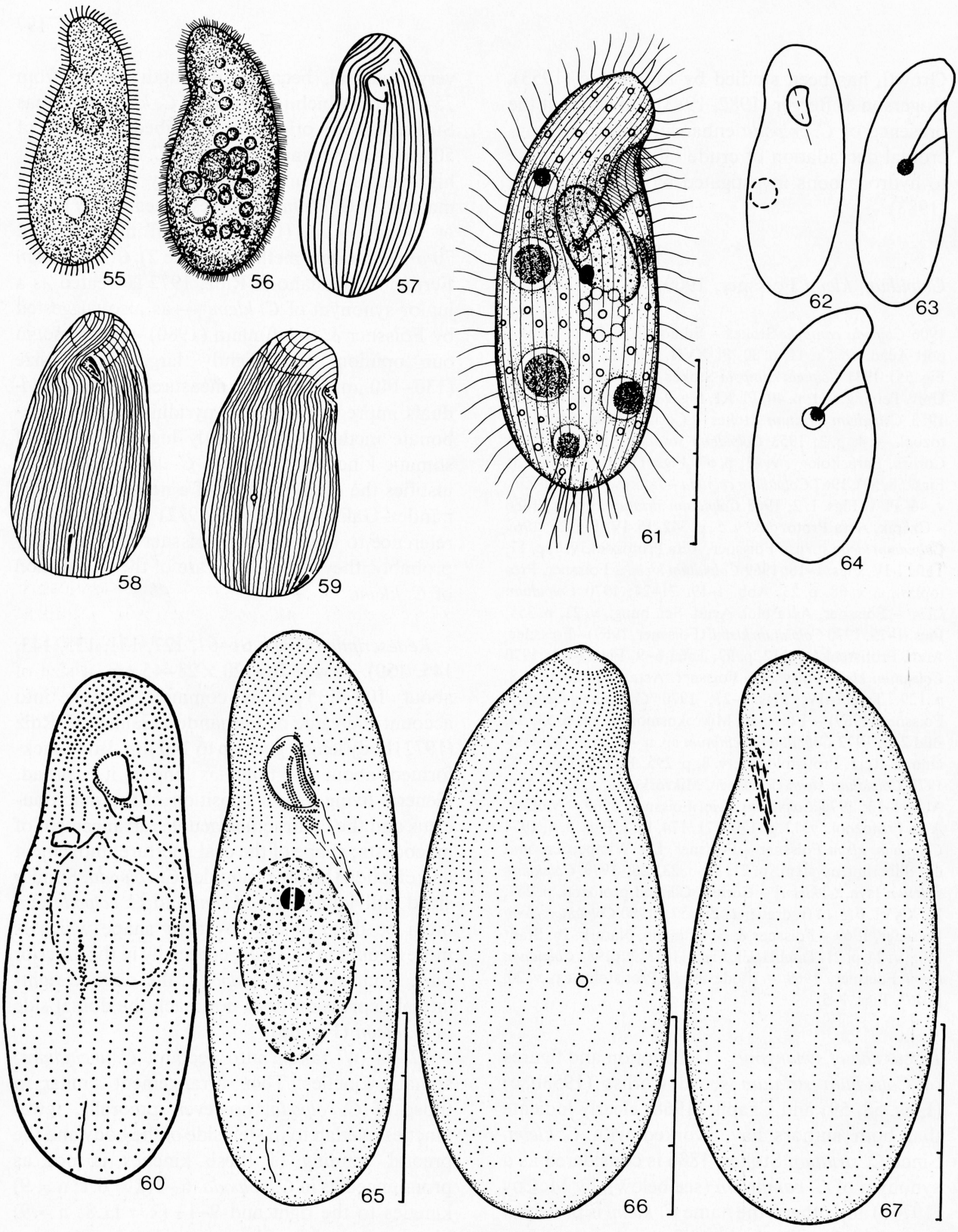
Colpidium kleini Foissner, 1969

1906 *Colpoda campyla* Stokes – Edmondson, Proc. Davenport Acad. Sci., v. 11, p. 80, Pl. XVII, Fig. 132 (redrawn as Fig. 55); 1931 *Colpoda campyla* Stokes – Tai, Sci. Rep. natn. Univ. Peiping, v. 1, p. 40, Pl. XI, Fig. 9 (redrawn as Fig. 56); 1953 *Colpidium striatum* Stokes – Corliss, Proc. Soc. Protozool., v. 4, p. 3; 1953 *Colpidium striatum* Stokes, 1886 – Corliss, Parasitology, v. 43, p. 67, Figs. 11a, b (redrawn as Figs. 58, 59); 1967 *Colpidium colpoda* – Jankowski, Zool. Zh., v. 46, Pl. 1, Figs. 1, 2; 1968 *Colpidium striatum* Stokes, 1886 – Czapik, Acta Protozool., v. 5, p. 342, Pl. IV, Fig. 25; 1969 *Colpidium kleini* sp. n. – Foissner, Acta Protozool., v. 7, p. 17, Tafel I-IV, Figs. 1–16; 1969 *Colpidium kleini* – Foissner, Protoplasma, v. 68, p. 23, Abb. 1–19, 21–24; 1970 *Colpidium kleini* – Foissner, Acta biol. Acad. Sci. hung., v. 21, p. 355, Figs. 1–15; 1970 *Colpidium kleinii* (Foissner, 1969) – Foissner, Arch. Protistenk., v. 112, p. 99, Tafel 6–9, Figs. 1–11; 1970 *Colpidium kleini* Foissner – Foissner, Acta Protozool., v. 8, p. 129, Tafel I–IV, Figs. 1–23; 1970 *Colpidium kleinii* – Foissner, 1969) – Foissner, Mikrokosmos, v. 59, p. 53, 54, Bild 2, 3; 1972 *Colpidium uncinatum* sp. n. – Fernández-Galiano & Ruiz, Protistologica, v. 8, p. 295, Pl. 1, 2, Figs. 1–8; 1973 *Colpidium kleini* (Foissner, Mikroskopie, v. 29, p. 179, Abb. 1–13; 1974 *Colpidium kleini* Foissner, 1969 – McCoy, Acta Protozool., v. 13, p. 170, 171, 174, Pl. I, Figs. 3, 4; 1974 *Colpidium kleini* Foissner – Foissner, Die Wimpertiere und ihr Silberliniensystem, p. 21, Abb. 23, 26; 1979 *Colpidium striatum* [syn. *C. kleini*] – Corliss, Ciliated protozoa, p. 257, Pl. XXVI, Fig. 14 (redrawn as Fig. 57); 1980 *Colpidium kleini* Foissner, 1969 – Foissner & Schiffmann, Naturk. Jb. Stadt Linz, v. 24, p. 21, Tafel II, VI, Figs. 11, 13, 29; 1984 *Colpidium kleini* Foissner, 1969 – Iftode *et al.*, Protistologica, v. 20, p. 463, Figs. 1–5;

Discussion of synonymy. Description and figures of *Colpidium striatum* sensu Corliss (1953b, c) (Figs. 58, 59) and Czapik (1968) clearly indicate that both authors have worked with *C. kleini*. Since *C. striatum* Stokes, 1886 is considered as a synonym of *C. campylum* (see below), by McCoy (1974a) and others, the name *C. kleini* is preferred here. Additionally, the identification of the population of Corliss (1953c) with *C. striatum* seems very doubtful, because its length ranges from 75–95 μm (which is typical of *C. kleini*) whereas Stokes (1886) originally described a length of 50 μm (which is more typical of *C. campylum*) for his species. Even our extremely small culture material of *C. kleini* possesses a mean body length of about 60 μm (Chatton-Lwoff method) and 70 μm (protargol method) (Table 2). *C. uncinatum* Fernández-Galiano & Ruiz, 1972 is treated as a junior synonym of *C. kleini* — as also suggested by Foissner & Schiffmann (1980) — because, in our opinion, the slightly larger body size (130–140 μm; possibly measured from individuals impregnated by the pyridinated silver carbonate method) and slightly higher number of somatic kineties (40–47) of *C. uncinatum* hardly justifies the establishment of a new species. Fernández-Galiano & Ruiz (1972) did not give a reference to the paper of Foissner (1969a). Very probably, they were not aware of the description of *C. kleini*.

Redescription (Figs. 61–67, 127, 131, 135, 143, 145, 150). *In vivo* 70–120 × 28–45 μm, a size of about 100 × 35 μm is common. Taking into account the value of Fernández-Galiano & Ruiz (1972) body length goes up to 140 μm. Body sack-formed, about 2–3 times as long as it is broad. General living aspect (position of the macronucleus and the contractile vacuole; arrangement of mucocysts; shape of the oral aperture; movement and ciliation) highly resembles *C. colpoda*. Similar sized individuals of *C. kleini* and *C. colpoda* can often be distinguished by their shape which is more slender in *C. kleini*, especially in the anterior part. Contrary to *C. colpoda*, the oblique right-lateral depression does not reach the dorsal side in *C. kleini* (Fig. 66).

32–44 (47 taking into account *C. uncinatum*) somatic kineties. Their arrangement similar to those of *C. colpoda*, however, preorally, fewer kineties overlap to the left side of the body and the preoral bending of these kineties is not as pronounced as in *C. colpoda*. 6–7 ($\bar{x}$ = 6.1; n = 9) kineties to the right and 9–13 ($\bar{x}$ = 11.8; n = 9) kineties to the left of kinety number 1 commence anteriorly with single basal bodies. Remaining bi-



Figs. 55–67. Colpidium kleini and synonyms. 55: *Colpoda campyla* after Edmondson (1906), 100 μm; 56: *Colpoda campyla* after Tai (1931), 117 μm; 57: *Colpidium striatum* after Corliss (1979); 58, 59: *Colpidium striatum* after Corliss (1953b); 60: after Iftode *et al.* (1984), 90 μm; 61–67: originals from life (61–64) and after protargol impregnation (65–67). 61: Right-lateral view; 62: Ventral view; 63, 64: Variation in body shape; 65: Infraciliature of the ventral side; 66, 67: Infraciliature of the right (66) and the left (67) side. Scale bar divisions: 10 μm.

polar kineties possess paired basal bodies, anteriorly. The characteristic extension of the apical pole field on the right side of *C. colpoda* is not present in *C. kleini*. Contractile vacuole pore interrupts subequatorially kinety number 8–12, mostly 9–11.

Construction of adoral membranelles in *C. kleini* is almost identical with that of *C. colpoda*. However, there are fewer basal bodies in the membranelles (Fig. 131). For example, the leftmost row of M3 consists of about 50 basal bodies in *C. colpoda* (Martín-González *et al.* 1981) and of about 25 basal bodies in *C. kleini* (Iftode & Fryd-Versavel, 1980; Iftode *et al.*, 1984). This is in rough accordance with our observations.

Silverline system extensively studied by Foissner (1969, 1970a, b, c, d, 1973) and according to this author is the most reliable feature for a differentiation between *C. colpoda* and *C. kleini* (Figs. 127, 145, 150). As shown in Table 2, in the cultivated population of *C. kleini* just one secondary meridian is constantly present between two primary meridians in Chatton-Lwoff preparations, whereas there are usually two in *C. colpoda*. In natural populations of *C. kleini*, however, and in culture material stained with the dry silver nitrate method occasionally individuals with two secondary meridians occur. The difference between the silverline structures in *C. colpoda* and *C. kleini* is difficult to explain, since *in vivo* the arrangement of mucocysts is the same in both species (Fig. 48). During regeneration of mucocysts the secondary meridians split into 2–3 parallel lines (4–5 in *C. colpoda*). Contrary to *C. colpoda*, anastomoses between the split lines occur rarely in *C. kleini*.

Morphogenesis studied by Foissner (1970a, b), Iftode & Fryd-Versavel (1980), and Iftode *et al.* (1984).

Beside other characters, the highly similar oral structures of *C. colpoda* and *C. kleini* strongly suggest a conspecifity of both species. However, numerous characters (body shape; number of kineties; details in the silverline system; number of basal bodies composing the adoral membranelles) justify in our opinion the maintenance of two separated species. On the other hand, the existance of populations with an intermediate number of kineties can make a differentiation difficult (McCoy, 1974a; Fernández-Galiano & Ruiz, 1972). Perhaps, it is a complex of sibling species.

Occurrence and ecology. Foissner (1969a) found *C. kleini* in three different localities in Upper Austria without giving any ecological background data. He cultivated it in plant infusions. Iftode *et al.* (1984) isolated it in June 1979 from water taken from a hole in a sandstone rock on the campus of the University of Orsay and cultivated it in lettuce medium inoculated with *Aerobacter aerogenes*. Corliss (1953b) isolated it from a commercial *Amoeba* culture. Tai (1931) and Edmondson (1906) observed it in a culture of pond water.

Foissner & Schiffmann (1980) and Foissner *et al.* (1982) designated *C. kleini* as predominantly a-mesosaprobic indicator organism. Recently, however, a more polysaprobic classification was suggested: x = 0, o = 0, b = 0, a = 3, p = 7; G = 4, s = 3.7 (Foissner, 1988). This is in rough accordance with the sample localities mentioned in 'material and methods'.

Colpidium singulare Vuxanovici, 1961

1961 *Colpidium singulare* n. sp. – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.), v. 13, p. 453, Pl. II, fig. 9 (redrawn as Fig. 106).

Description. Body size 76 μm, shape similar to *C. colpoda*. 22–24 ciliary rows on one side of the body. Macronucleus long, band shaped, anteriorly bipartite. Endoplasm hyaline, containing algae, darkly granulated.

Occurrence. Observed by Vuxanovici in high numbers in stale cultures with decaying plants from Lake Tei (Roumania) in October 1959.

Remarks. The characteristic form of the macronucleus requires a consideration of *C. singulare* as a distinct species (Fig. 106). The bipartition of the macronucleus, however, is very uncommon for tetrahymenids and suggests that this species belongs to another group of ciliates. Another possi-

bility is that the smaller segment represents the micronucleus which is not mentioned by Vuxanovici (1961).

Colpidium acuminatum Vuxanovici, 1962

1962 *Colpidium acuminatum* n. sp. – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.), v. 14, p. 341, Pl. IV, fig. 24 (redrawn as Fig. 107).

Description.: Body size 38–40 μm, shape sigmoid, posteriorly narrowing. Oral cavity and membranelles said to be very silmilar as in *C. colpoda*. 20–24 ciliary rows on one side of the body. Endoplasm hyaline, bright, with digestive vacuoles. Somatic cilia short.

Occurrence. In high numbers in 15-day-old cultures from Lake Fundeni, Bucharest (Roumania) in March 1960.

Remarks. The sigmoid body shape is not typical of the genus *Colpidium* (Fig. 107). However, the short description of Vuxanovici (1962a) is not sufficient for a decision about whether or not this species is a member of the genus.

Genus *Dexiostoma* Jankowski, 1967

Diagnosis: Turaniellidae; Preoral suture straight, nearly median, slightly inclined to the left. Membranelle 1 consists in its main parts of a single row of basal bodies, M3 short and composed of 3 rows of basal bodies. Silverlines longitudinally oriented, 1 secondary meridian between 2 primary meridians.

Type species: *Dexiostoma campyla* (Stokes, 1886)

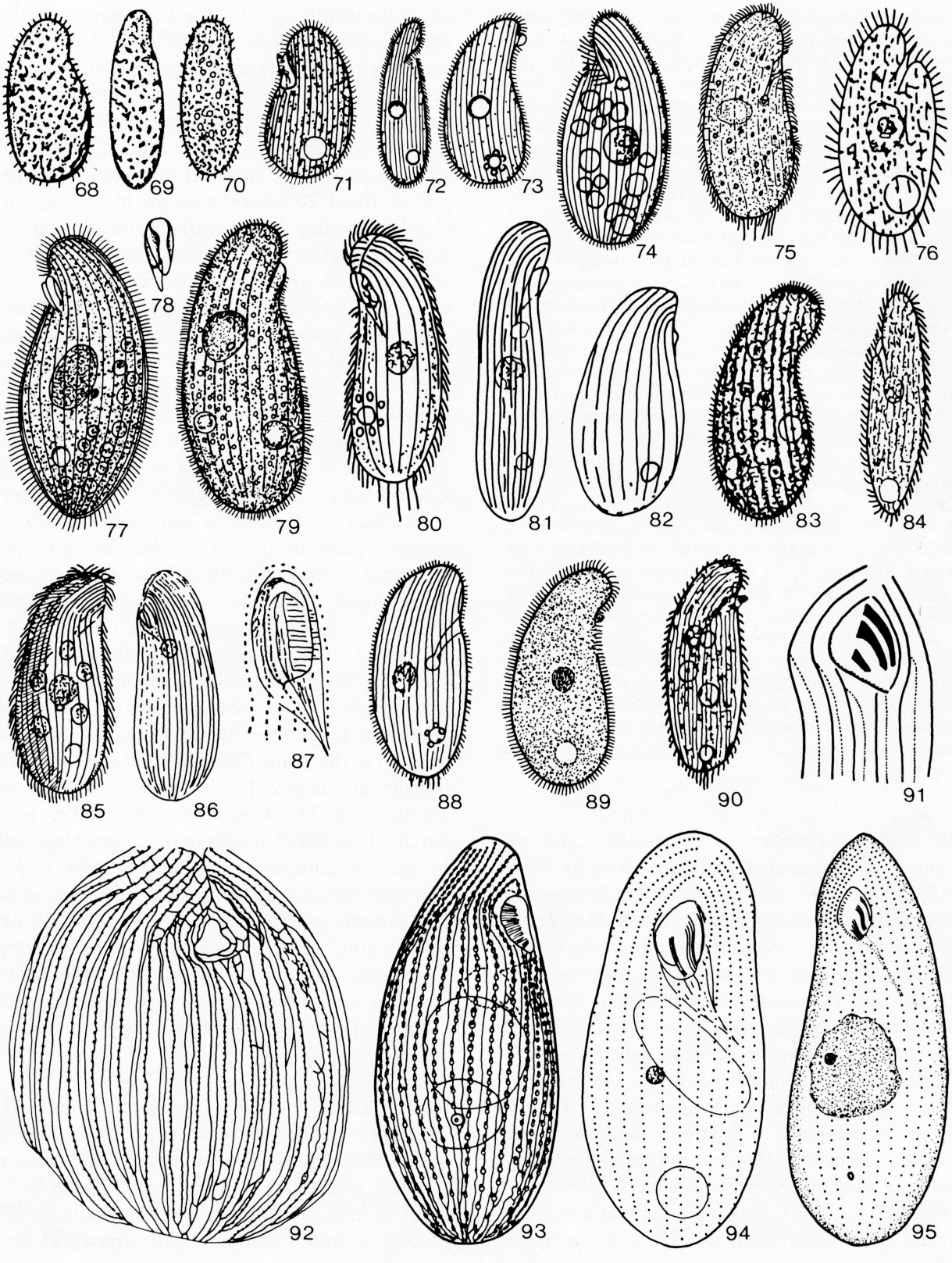
Dexiostoma campyla (Stokes, 1886) Jankowski, 1967

?1852 *Paramecium griseolum* – Perty, Zur Kenntniss kleinster Lebensformen, p. 144, Tab. IIII, Figs. 11A–C (redrawn as Figs. 68–70);?1859 *Colpoda parvifrons* – Claparède & Lachmann, Études sur les infusoires, p. 270, Pl. IX, Fig. 3 (redrawn as Fig. 71); 1886 *Tillina campyla*, sp. nov. – Stokes, Ann. Mag. nat. Hist., v. 17, p. 101, Pl. I, Fig. 8 (redrawn as Fig. 72); 1886 *Colpidium striatum*, sp. nov. – Stokes, Ann. Mag. nat. Hist., v. 17, p. 103, Pl. I, Fig. 12 (redrawn as Fig. 73); 1886 *Glaucoma pyriformis* (Ehrenberg, sp.) – Gourret & Roeser, Archs Zool. exp. gén., v. 4, p. 513, Pl. XXXIV, Fig. 6 (redrawn as Fig. 74); 1888 *Tillina campyla*, Stokes – Stokes, J. Trenton Nat. Hist. Soc., v. 1, p. 159, Pl. IV, Fig. 20; 1888 *Colpidium striatum*, Stokes – Stokes, J. Trenton Nat. Hist. Soc., v. 1, p. 177, Pl. IV, Fig. 28;? 1889(*Colpidium truncatum* Stokes – Maupas, Archs Zool. exp. gén., v. 7, p. 249, Pl. XV, Figs. 31–38; 1892 *Glaucoma colpidium* n. sp. – Schewiakoff, Verh. naturh.-med. Ver. Heidelb., v. 4, p. 555; 1893 *Glaucoma colpidium* nov. sp. – Schewiakoff, Zap. imp. Akad. Nauk SSSR, v. 41, p. 44, Tafel III, Figs. 42, 43 (redrawn as Fig. 77, 78); 1906 *Colpidium striatum* Stokes – Edmondson, Proc. Davenport Acad. Sci., v. 11, p. 79, Pl. XVII, Fig. 128 (redrawn as Fig. 89); 1916 *Colpidium colpoda* – Prowazek, Arch. Protistenk., v. 36, p. 72; 1920 *Colpidium colpoda* – Oehler, Arch. Protistenk., v. 41, p. 34;?1920 *Colpidium truncatum* – Dehorne, Archs Zool. exp. gén., v. 60, p. 119, Figs. LXXIX–CVIII; 1921 *Colpidium colpoda* – Bresslau, Naturwissenschaften, v. 9, p. 57, Fig. 4; 1921 *Colpidium colpoda* – Bresslau, Verh. dt. zool. Ges., v. 26, p. 35; 1922 *Colpidium campylum* – Bresslau, Zool. Anz., v. 55, p. 21, Fig. 1;?1925 *Colpidium striatum* Stokes – Gulati, J. Bombay nat. Hist. Soc., v. 30, p. 748, Pl. II, Fig. 13 (redrawn as Fig. 76);?1925 *Colpidium compyla* Stokes – Gulati, J. Bombay nat. Hist. Soc., v. 30, p. 748, Pl. II, Fig. 14 (redrawn as Fig. 84); 1926 *Glaucoma colpidium* Schew. – Kahl, Arch. Protistenk., v. 55, p. 345, Figs. K2c, d, f (redrawn as Figs. 85–87); 1928 *Colpidium campylum* Stockes – Klein, Arch. Protistenk., v. 62, p. 191, Figs. 9–18 (redrawn as Fig. 92); 1929 *Colpidium campylum* Stockes – Klein, Der Naturforscher, v. 10, p. 463, Tafel 81, Figs. 5–9; 1929 *Colpidium campylum* Stokes – Klein, Arch. Protistenk., v. 65, p. 201, Textfigs. 17–20, 22, Tafel 9, Figs. 10–14; 1931 *Colpidium campylum* Stokes – Gelei & Horváth, Arb. I. Abt. ung. biol. ForschInst., v. 4, p. 40, Figs. 9–11 (redrawn as Fig. 93); 1931 *Colpidium (Tillina) campylum* (Stokes, 1886) Bresslau, 1922 – Kahl, Tierwelt Dtl., v. 21, p. 334, Figs. 17–19 on p. 331 (redrawn as Figs. 80–82); 1931 *Colpidium striatum* Stokes, 1886 – Kahl, Tierwelt Dtl., v. 21, p. 334, Fig. 10 on p. 348; 1931 *Colpidium striatum* Stokes – Sokoloff & Sámano, Monografias Inst. Biol. Univ. nac. Méx., v. 1, p. 27, Fig. 49 (redrawn as Fig. 83); 1931 *Colpidium striatum* Stokes – Tai, Sci. Rep. natn. Univ. Peiping, v. 1, p. 41, Pl. XII, Fig. 2 (redrawn as Fig. 79); 1934 *Colpidium campylum* – Kidder & Diller, Biol. Bull., v. 67, p. 207, Figs. 3A–G; 1936 *Colpidium campylum* (Stokes) Bresslau – Bhatia, Protozoa: Ciliophora, p. 173, Fig. 77; 1936 *Colpidium striatum* Stokes – Bhatia, Protozoa: Ciliophora, p. 175, Fig. 79; 1947 *Colpidium campylum* (Stokes) Breslau 1922 – Šrámek-Hušek, Čas. národ. Mus., v. 116, p. 42, Fig. 11 (redrawn as Fig. 88); 1953 *Colpidium colpidium* (Schew., 1893) nov. comb. – Corliss, Proc. Soc. Protozool., v. 4, p. 3; 1953 *Colpidium truncatum* Stokes, 1885 – Corliss, Proc. Soc. Protozool., v. 4, p. 4; 1957 *Colpidium*

truncatum – Sonneborn, Breeding system, reproductive methods, and species problem in protozoa, p. 311; 1961 *Colpidium campylum* – Pitelka, J. Protozool., v. 8, p. 75, Figs. 1, 3, 4, 9–12, 15, 26, 27; ?1962 *Colpidium colpoda* var. *pusillus* n. var. – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.), v. 14, p. 559, Pl. IV, fig. 28 (redrawn as Fig. 90); 1967 *Dexiostoma campyla* (Stokes) gen. nov. and *Colpidium campylum* (Stokes, 1886) Bresslau, 1922 – Jankowski, Zool. Zh., v. 46, p. 20, Pl. 1, 2, Figs. 4, 5, 1, 2 (redrawn as Fig. 91); 1969 *Colpidium campylum* Stockes – Foissner, Protoplasma, v. 68, p. 433, Abb. 1–5; 1969 *Colpidium campylum* Stockes – Foissner, Acta Protozool., v. 7, p. 23, Tafel VI, Figs. 21–24; 1972 *Colpidium campylum* Stokes – Bick, Ciliated protozoa, p. 78, Fig. 42; 1974 *Colpidium campylum* Stokes – Foissner, Die Wimpertiere und ihr Silberliniensystem, p. 19, Abb. 19, 20; 1974 *Colpidium campylum* – McCoy, Acta Protozool., v. 13, p. 163, Pl. I, Figs. 1, 2; 1974 *Tetrahymena pyriformis* (Ehrenberg) – Pätsch, Arb. Inst. landw. Zool. Bienenkd., v. 1, p. 30, Abb. 16 (redrawn as Fig. 94); 1977 *Colpidium campylum* – Foissner, Acta biol. Acad. Sci. hung., v. 28, p. 59, Figs. 1–27; 1978 *Colpidium campylum* (Stokes) – Matthes & Wenzel, Die Wimpertiere, p, 57, Bild 42c; 1979 *Colpidium campylum* – Corliss, Ciliated protozoa, p. 257, Pl. VII, XXVI, Figs. 8, 15a, b; 1980 *Colpidium campylum* (Stokes, 1886) Bresslau, 1922 – Foissner & Schiffmann, Naturk. Jb. Stadt Linz, v. 24, Tafel I, V, Figs. 7, 9, 28; 1982 *Colpidium campylum* – Bernerth, Cour. Forsch.-Inst. Senckenberg, v. 57, p. 81, Abb. 47b; 1983 *Colpidium campilum* – Wegl, Wass. Abwass, v. 26, p. 115; 1985 *Colpidium campylum* – Wegl, Das Leben im Abwasser, p. 106, Abb. 5; 1985 *Colpidium campylum* – Streble & Krauter, Das Leben im Wassertropfen, p. 242, Fig. 3 (redrawn as Fig. 75); 1986 *Colpidium campylum* (Stokes, 1886) Bresslau, 1922 – Dragesco & Dragesco-Kernéis, Cilies libres, p. 289, Pl. 72, Figs. A, B (redrawn as Fig. 95).

Discussion of synonymy. Among the numerous figures of *Paramecium griseolum* given by Perty (1852), some are highly reminiscent of *Dexiostoma campyla* (Figs. 68–70), others look like *Tetrahymena pyriformis*. Acception of synonymy would require changing the name *D. campyla* into *D. griseola*. However, because of the common usage of this species we suggest preservation of the name *D. campyla* in accordance with the '50 year recommendation' of the International Code of Zoological Nomenclature (1985). *Colpoda parvifrons* Claparède & Lachmann (1859) is probably also a member of the *Tetrahymena pyriformis*-complex or a *Glaucoma sp.* (Fig. 71). Bütschli (1889) regarded it as a possible synonym of *Colpoda steinii*. There is no doubt about the identification of our *D. campyla* with the original description of Stokes (1886). Since body form of *Colpidium striatum* Stokes, 1886 falls into the variability of *D. campyla* and no other characters for a clear separation have been given by Stokes, we suggest synonymy (comp. discussion of synonymy of *C. kleini*). Prowazek (1916) reported about 25 ciliary rows for his *C. colpoda*, clearly indicating that he worked with *D. campyla*. Likewise, Oehler (1920) and Bresslau (1921a, b) confused *D. campyla* with *C. colpoda*. As mentioned by Bresslau (1922), body form of *Colpidium truncatum* sensu Dehorne (1920) strongly suggests that it is *D. campyla*. As discussed by McCoy (1974a) the material of Maupas (1889) represents very probably *D. campyla*. Habitat, cyst formation, and shape of *C. striatum* sensu Gulati (1925) indicate that it is very probably a *Cyrtolophosis mucicola* (Fig. 76). Position of micronucleus in *C. compyla* sensu Gulati (1925) makes relationship to *Spirozona* possible (Foissner, 1986) (Fig. 84). *Glaucoma colpidium* Schewiakoff, 1892 has been synonymized with *D. campyla* by numerous authors (Kahl, 1931; McCoy, 1974a; Foissner & Schiffmann, 1980) (Figs. 77, 78). In an earlier work of Kahl (1926), however, it is described as a 'good' species of *Glaucoma* (Figs. 85–87). Corliss (1953c) transferred it to the genus *Colpidium* and distinguished it from *D. campyla* by the number of somatic kineties (24–33). Considering the rather high variability of this character in *D. campyla* reported by several authors (e.g. McCoy, 1974a), this seems to be too weak to separate this species at the present state of knowledge. Foissner & Schiffmann (1980) suggested synonymizing *C. colpoda* var. *pusillus* Vuxanovici, 1962 with *C. truncatum*, however, body size, shape, and number of kineties also allow a synonymization with *D. campyla* (Fig. 90).

Redescription (Figs. 96–105, 128, 132, 136, 141, 146, 151). *In vivo* 35–90 × 15–35 μm, a size of about 60 × 20 μm is common. Body form a slender, sometimes a broad oval, about three times as long as it is broad. Anterior pole round, preoral section ventrally slightly truncated and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markedly indented by ciliary rows, resulting in a rather conspicuous ribbing of the anterior non-ciliated area of the left side (Fig. 100). Posterior pole round, occasionally weakly tapered. Laterally slightly compressed, gradually becoming broader from anterior to posterior. Mucocysts arranged in a single row between two kineties and between the cilia of each kinety (Figs. 101, 102). Macronucleus approximately round, *in vivo* 12–20 μm in diameter. Contractile vacuole *in vivo* 6–12 μm in diameter, located at the posterior third of body, its pore *in vivo* 1 μm in diameter. The pore interrupts kinety number 5–7. The pore is placed erroneously at the end of kinety number 1 by Dragesco & Dragesco-Kernéis (1986) (Fig. 95). McCoy (1974a) found that the contractile vacuole pore is positioned at a fixed distance from the posterior end, regardless of cell length. Cilia *in vivo* 8–10 μm long, caudal cilia 12–15 μm. Movement fast with permanent rotation around the long axis of the body.

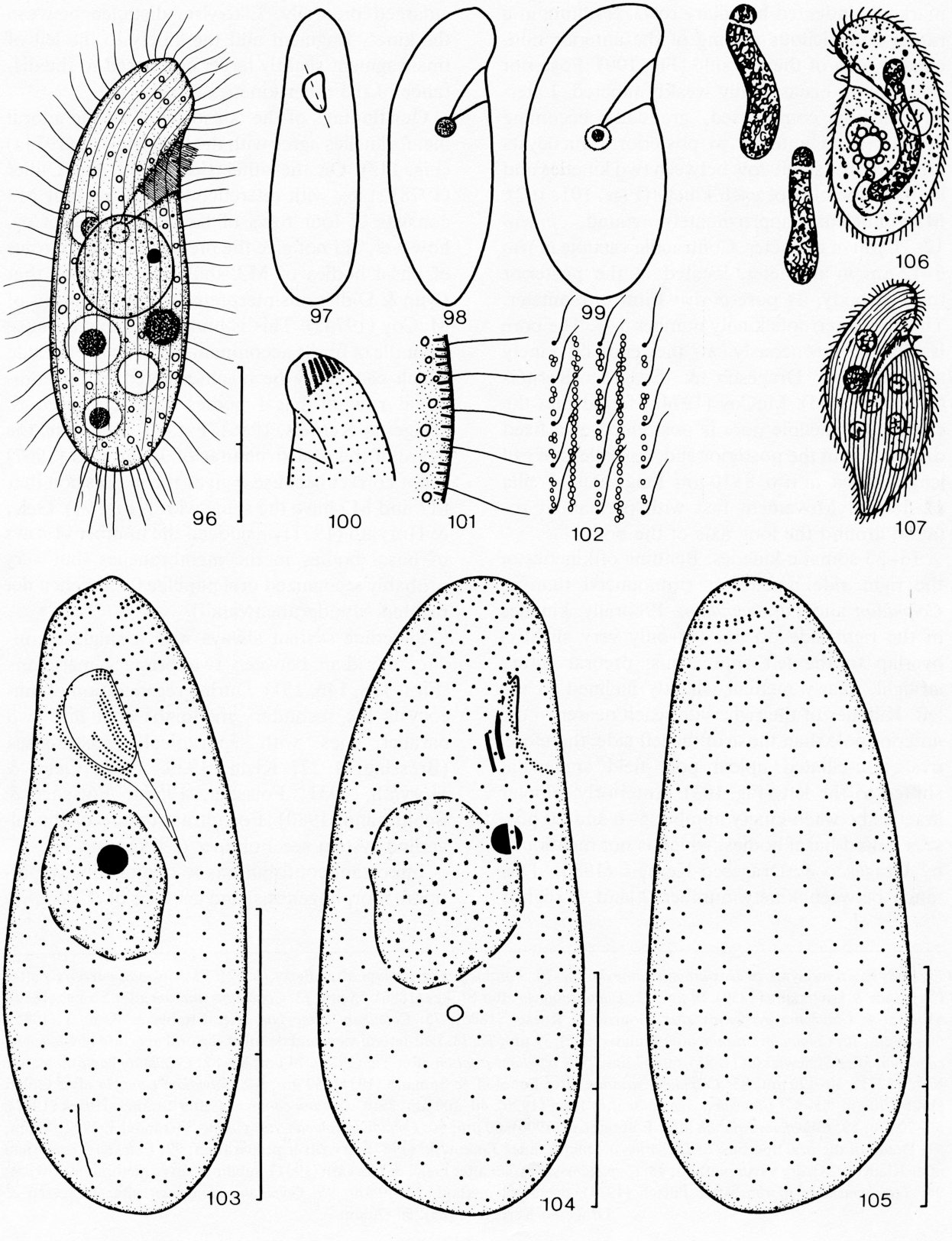
16–33 somatic kineties. Bending of kineties of the right side much less pronounced than in *Colpidium* and *Paracolpidium*. Preorally, kineties of the right side do not (or only very slightly) overlap to the left side. Thus, preoral suture straight, nearly median, slightly inclined to the left. Kineties of the right side reach nearer to the anterior pole than those of the left side, therefore, oval non-ciliated apical pole field somewhat shifted to the left (Fig. 103). Anteriorly, bipolar kineties between kinety number 5–6 and 20 possess paired basal bodies, which is not mentioned by Dragesco & Dragesco-Kernéis (1986). Distance between kinety number 2 and 3 slightly enlarged preorally. Likewise, distance between the kinety fragment and the kinety to the left of this fragment slightly larger compared to the distance of the other kineties of this side.

Our findings of the construction of the adoral membranelles agree with those of McCoy (1974a) (Fig. 132). On the other side, Lynn and Didier (1978) state, with reference to McCoy, that M3 consists of four rows of basal bodies. McCoy, however, did not give the precise number of rows of basal bodies of M3, thus, it is obvious that Lynn & Didier misinterpreted the photographs of McCoy (1974a). This is understandable because a bundle of fibrils accompanies M3 on the left side which can easily be misinterpreted as an additional row of basal bodies (e.g. Dragesco & Dragesco-Kernéis, 1986) (Fig. 95). Likewise, the figure of the oral structures of Jankowski (1967) is not correct because it gives the impression that M1 and M2 have the same width (Fig. 91). Gelei & Horváth (1931) misjudged the number of rows of basal bodies in the membranelles, but very probably recognized oral papillae ('Zähnchen der rechten Mundgrubenwand').

Silverline system always with a single secondary meridian between two primary meridians (Figs. 128, 146, 151). During regeneration of mucocysts the secondary meridians split into two parallel lines with sporadical anastomoses (Bresslau, 1922; Klein, 1928, 1939; Gelei & Horváth, 1931; Foissner, 1969a; Foissner & Schiffmann, 1980). For ultrastructure of the silverline system see Foissner (1977).

Important contributions to conjugation, bipartition, morphogenesis, and genetics of *D. campyla*

◀ *Figs. 68–95.* Synonyms of *Dexiostoma campyla*. 68–70: *Paramecium griseolum* after Perty (1852); 71: *Colpoda parvifrons* after Claparède & Lachmann (1859), 39 μm; 72: *Tillina campyla* after Stokes (1886), 55 μm; 73: *Colpidium striatum* after Stokes (1886), 51 μm; 74: *Glaucoma pyriformis* after Gourret & Roeser (1886); 75: *Colpidium campylum* after Streble & Krauter (1985), 50–70 μm; 76: *Colpidium striatum* after Gulati (1925), 35 μm; 77, 78: Left-lateral view and detail of the oral aperture of *Glaucoma colpidium* after Schewiakoff (1893), 60–67 μm; 79: *Colpidium striatum* after Tai (1931), 74 μm; 80–82: *Colpidium campylum* after Kahl (1931), 50–120 μm; 83: *Colpidium striatum* after Sokoloff & Sámano (1931), 50 μm; 84: *Colpidium compyla* after Gulati (1925), 70 μm; 85–87: *Glaucoma colpidium* after Kahl (1926), 40–100 μm; 88: *Colpidium campylum* after Šrámek-Hušek (1947), 50–70 μm; 89: *Colpidium striatum* after Edmondson (1906), 60 μm; 90: *Colpidium colpoda* var. *pusillus* Vuxanovici, 1962, 40 μm; 91: Detail of the oral aperture of *Dexiostoma campyla* after Jankowski (1967), dry silver preparation; 92: *Colpidium campylum* after Klein (1928), dry silver method; 93: *Colpidium campylum* after Gelei & Horváth (1931), sublimat silver method, 50–70 μm; 94: *Tetrahymena pyriformis* after Pätsch (1974), protargol method, 25–40 μm; 95: *Colpidium campylum* after Dragesco & Dragesco-Kernéis (1986), 50–70 μm.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include those of Maupas (1889), Dehorne (1920), Chatton & Chatton (1925), Klein (1929a, b), Sonneborn (1932, 1957), Kidder & Diller (1934), Devide (1951), and Morat (1970).

Occurrence and ecology. Cosmopolitan. Frequently recorded in perennial ponds, lakes and running waters (e.g. Schewiakoff, 1893; Tai, 1931; Bhatia, 1936; Gellert & Tamás, 1959; Patrick, 1961; McCoy, 1974a; Foissner & Foissner, 1987). Cairns & Ruthven (1972) recorded it from cultivated soil samples from Abaco Islands (Bahamas) which appears highly questionable because no cysts of any kind are known from this species. Salt tolerance low, about 3g/l (Kahl, 1931; Bick, 1968b; Albrecht, 1984). Endures even higher values of ammonium (up to 160 mg/l) than *C. colpoda* (Bick, 1968a).

Sládeček *et al.* (1981) give the following saprobiological classification: x = 0, o = 0, b = 0, a = 1, p = 9; G = 5, s = 4 (corrected by Foissner, 1988 to s = 3.9) for limnosaprobity, and x = 0, o = 0, b = 0, a = 0, p = 3, i = 7; G = 4, s = 4.3, when isosaprobity is taken into account. This polysaprobic classification is supported by recent results of Greiser (1974), Stössel (1979), Foissner & Schiffmann (1980), and Foissner *et al.* (1982). A comparison of various saprobiological classifications has been compiled by Mauch (1976).

Remarkable studies on growth, nutrition, and consumption of *D. campyla* made by Dive (1973, 1975), Dive *et al.* (1974), Laybourn & Stewart (1975), and Taylor & Berger (1976a). Effect of different bacterial species on growth of *D. campyla* investigated by Taylor & Berger (1976b). The presence of *D. campyla* in cultures can influence the growth rate of other ciliates (Stillwell, 1967). Energy consumption and its effect on mean cell volume and reproduction studied by Laybourn & Stewart (1974) and Laybourn (1975). For general feeding behavior and ecology see Legner (1973), Fenchel (1980), and Taylor (1981). The behavior of *D. campyla* in forming aggregations of high numbers of individuals which are equally dispersed in observation chambers at room temperature (Kersken & Laudien, 1979), could also be observed in the petri-dishes of our cultures. Reactions to pesticids and other toxicants investigated by Dive & Leclerc (1977) and Dive *et al.* (1980).

Genus *Paracolpidium* nov. gen.

Diagnosis: Turaniellidae; Preoral suture curved to the right. Membranelle 1 consists in its main parts of a single row of basal bodies, M3 moderately long and composed of 3 basal body rows. Silverline system *Tetrahymena*-like, lacks secondary meridians.

Type species: *Paracolpidium truncatum* (Stokes, 1885) nov. comb. (Basionym: *Colpidium truncatum* Stokes, 1885).

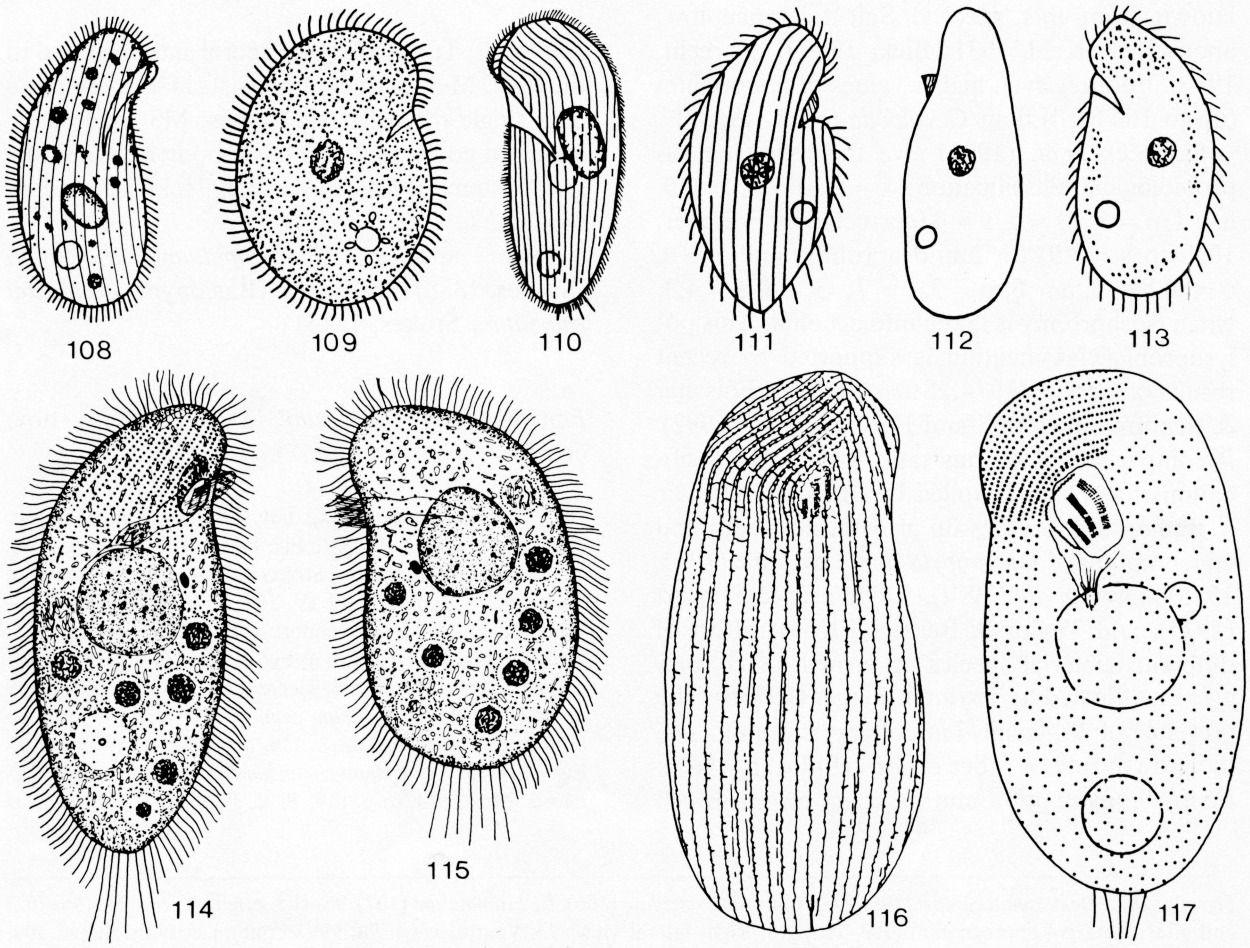
Paracolpidium truncatum (Stokes, 1885) nov. comb.

1885 *Colpidium truncatum*, sp. nov. – Stokes, Ann. Mag. nat. Hist., v. 15, p. 443, Pl. XV, Fig. 17 (redrawn as Fig. 108); 1888 *Colpidium truncatum*, Stokes – Stokes, J. Trenton Nat. Hist. Soc., v. 1, p. 176, Pl. IV, Fig. 27;?1906 *Colpoda sp.* – Edmondson, Proc. Davenport Acad. Sci., v. 11, p. 81, Pl. XVII, Fig. 133 (redrawn as Fig. 109); 1931 *Colpidium truncatum* Stokes, 1885 – Kahl, Tierwelt Dtl., v. 21, p. 334, Fig. 9 on p. 348; 1947 *Colpidium campyloides* sp. n. – Šrámek-Hušek, Čas. národ. Mus., v. 116, p. 42, Fig. 12 (redrawn as Fig. 110); 1957 *Colpidium campylum* Bresslau – Buchar, Čas národ. Mus., v. 126, p. 139, Pl. 2, Figs. A–C (redrawn as

Figs. 96–107. Dexiostoma campyla (96–105), *Colpidium singulare* (106), *C. acuminatum* (107). 96–105: originals from life (96–102) and after protargol impregnation (103–105). 96: Right lateral view; 97: Ventral view; 98, 99: Variation in body shape; 100: Prominent ribbing of the anterior area of the left side caused by indentions of the ciliary rows; 101, 102: Arrangement of mucocysts in lateral view (101) and top plan view (102); 103: Infraciliature of the ventral side; 104,105: Infraciliature of the right (104) and the left (105) side; 106: Left lateral view from life after Vuxanovici (1961), 76 μm. Note the drawings of the band-shaped macronucleus which is anteriorly bipartite; 107: Right lateral view from life after Vuxanovici (1962a), 45 μm. Note the sigmoid body shape. Scale bar divisions: 10 μm.

Figs. 111–113);?1962 *Colpidium colpoda* var. *pusillus* n. var. – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.), v. 14, p. 559, Pl. IV, fig. 28 (redrawn as Fig. 90);?1974 *Colpidium colpidium* (Schewiakoff) – Pätsch, Arb. Inst. landw. Zool. Bienenkd. v. 1, p. 28, Abb. 15 (redrawn as Fig. 117); 1980 *Colpidium truncatum* Stokes, 1885 – Foissner & Schiffmann, Naturk. Jb. Stadt Linz, v. 24, p. 28, Abb. 1–6, Tafel I, III–VI, Figs. 8, 10, 15–27, 30 (redrawn as Figs. 114–116).

Discussion of synonymy. We agree with the conclusions made by Foissner & Schiffmann (1980) concerning the identification of their populations of *Colpidium truncatum* with the original description of Stokes (1885a). *Colpidium colpidium* sensu Pätsch (1974) was synonymized with *C. truncatum* by Foissner & Schiffmann (1980), because of its numerous postoral kineties (Fig. 117). In the figures of Pätsch (1974), M1 consists of four rows of basal bodies which is not common in the *C-D-P* group. It is conceivable that this population represents a variety of *C. colpoda*. Šrámek-Hušek (1947) separates *Colpidium campyloides* from the other species of the *C-D-P* group by its body shape, which is broad at the site of the oral opening and narrowing anteriorly and posteriorly (Fig. 110). Considering the variability which we found in our material, body shape is not



Figs. 108–117. Synonyms of *Paracolpidium truncatum*. 108: *Colpidium truncatum* after Stokes (1885a), 40–50 μm; 109: *Colpoda sp.* after Edmondson (1906), 45 μm; 110: *Colpidium campyloides* Šrámek-Hušek, 1947, 40–50 μm; 111–113: *Colpidium campylum* after Buchar (1957); 114–116: *Colpidium truncatum* after Foissner & Schiffmann (1980), from life (114, 115) dry silver method (116), 54–95 μm; 117: *Colpidium colpidium* after Pätsch (1974), protargol method, 65–85 μm.

sufficient to distinguish between species. Perhaps the most important difference between *Paracolpidium truncatum* and *C. campyloides* is the straight suture of the latter. However, Šrámek-Hušek studied only living material. Until further data are available, this species is best treated as a synonym of *P. truncatum*.

Redescription (Figs. 118–125, 129, 133, 137, 140, 147, 148). *In vivo* 35–85 × 24–45 μm, a size of about 60 × 30 μm is common. Body approximately bean shaped, 1.5–2.5 times as long as it is broad. Anterior part dorsally and ventrally conspicuously flattened producing a pyramidal appearance of the preoral region and a prominent dorsal hump at the level of the oral apparatus. In impregnated specimens the characteristic form of the anterior area is often partly lost, especially the ventral flattening. Distinct oblique depression on the right side. This body shape is very characteristic of this species. Although Foissner & Schiffmann (1980) report mucocysts in their populations of *C. truncatum*, our material lack these organelles. Macronucleus large in relation to body size, slightly oval, *in vivo* 15–25 × 12–20 μm in size. Obviously, Buchar (1957) has drawn the macronucleus too small. Micronucleus not stained with protargol in about 50% of the individuals, the reason for this behavior is unkown. Contractile vacuole *in vivo* 8–10 μm in diameter, positioned in the posterior third of body. Its pore interrupts kinety number 10–12. Cilia *in vivo* 8–10 μm long, caudal cilia scarcely longer, 12–15 μm. A helpful feature for *in vivo* identification is a bundle of slightly elongated cilia, originating from the anterior tip of M1 and projecting out of the oral aperture (Fig. 118). Movement very characteristic and different from the other species of the *C-D-P* group. It frequently rotates around the lateral axis of the body in one place (turning somersaults), often hastily swimming forward describing a spiral. Thigmotactic, prefers to be in contact with any kind of particle or living material (bacterial masses, algal filaments, thus often nearly motionless). We sometimes observed that when swimming free, *P. truncatum* pulls with it different materials (e.g. small particles of mud, detritus, even diatoms) by a filamentous slimy strand.

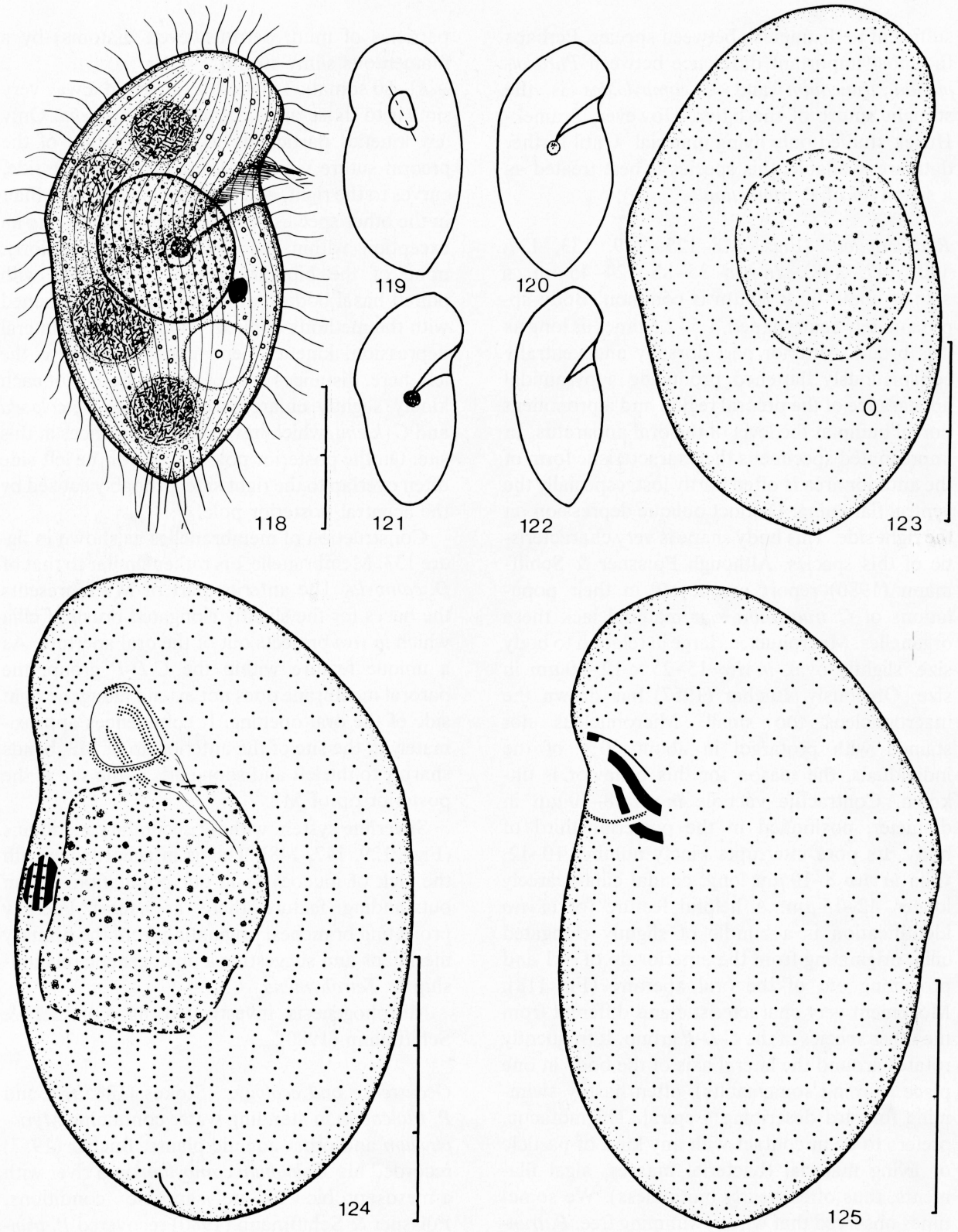
31–50 somatic kineties, arranged in a way very similar to those of *C. colpoda* and *C. kleini*. Only few kineties participate in the formation of the preoral suture which is located on the left side, curves to the right, and is somewhat broader than in the other species of the *C-D-P* group. Being an exception within the *C-D-P* group, anteriorly, none of the bipolar kineties commence with paired basal bodies, at least they are not stained with the methods applied. Along the right-lateral depression, kineties bend conspicuously to the left, here, distances between basal bodies of each kinety slightly enlarged, contrary to *C. colpoda* and *C. kleini*, which have smaller distances at this site. On the posterior pole kineties of the left side often overlap to the right side, probably caused by the acentral posterior pole.

Construction of membranelles as shown in figure 133. Membranelle 1 is rather similar to that of *D. campyla*. The anterior part of M1 represents the bases for the slightly elongated brush of cilia which *in vivo* projects out of the oral aperture. As a unique feature within the *C-D-P* group, the paroral membrane does not extend along the right side of the oral opening. It commences approximately at the site of the anterior tip of M3, bends sharply to the left and soon ends at the site of the posterior tip of M2.

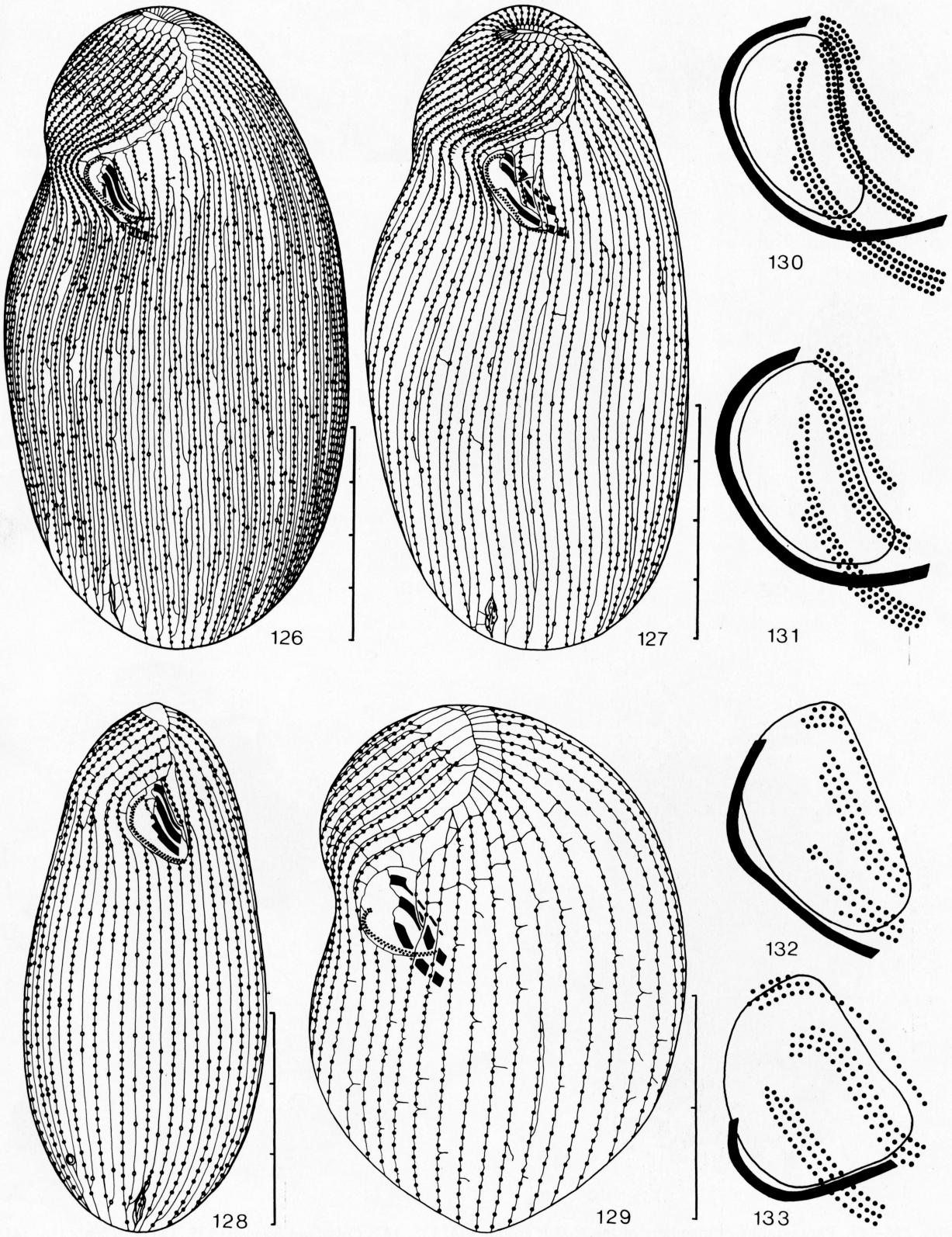
Silverline system without secondary meridians (Figs. 129, 147, 148). This is in accordance with the lack of mucocysts in our population. As an outstanding feature there are short laterally projecting branches, originating from the primary meridians and suggesting a phylogenetic relationship to *Tetrahymena*.

Morphogenesis investigated by Foissner & Schiffmann (1980).

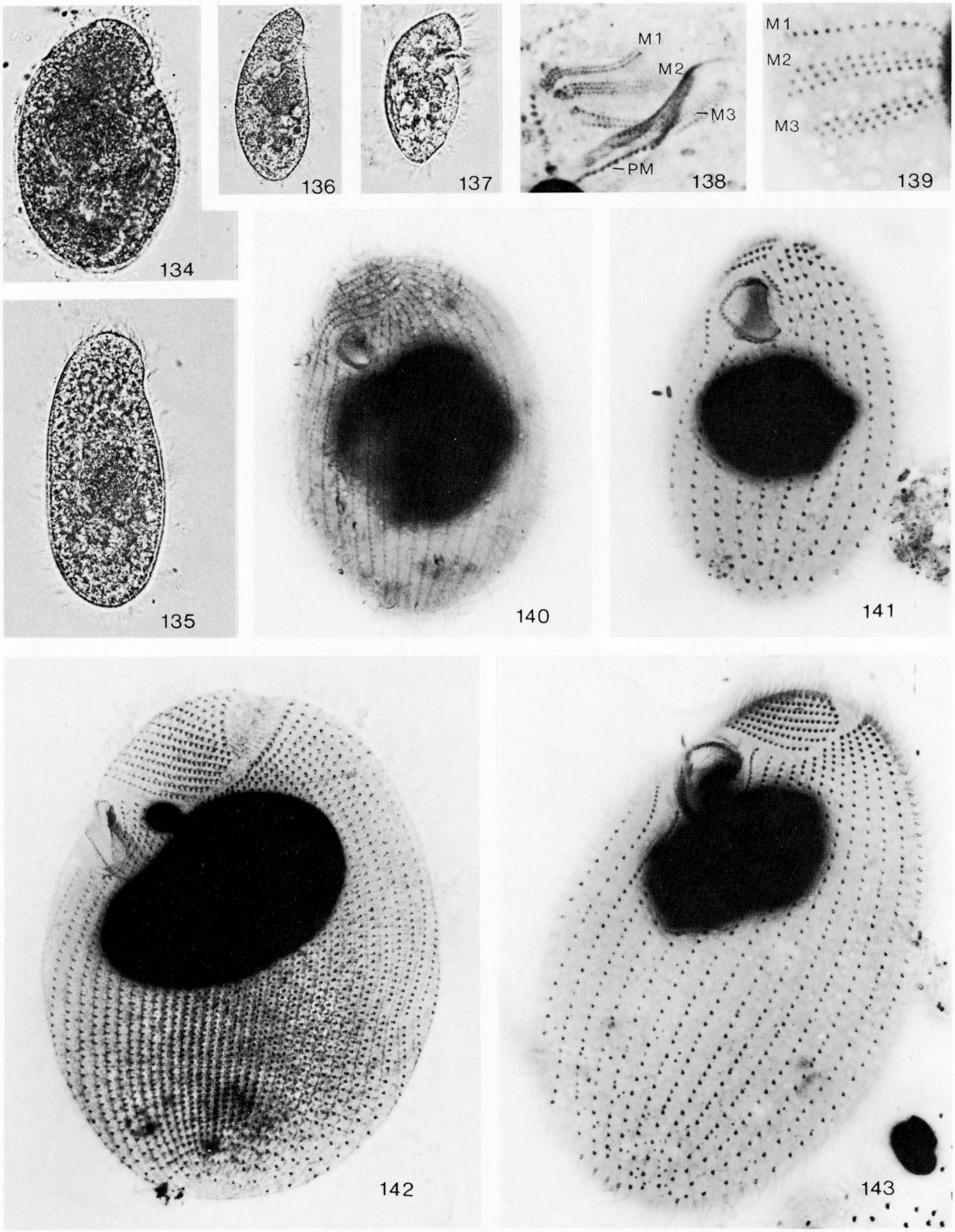
Occurrence and ecology. Stokes (1885a) found *P. truncatum* in standing water containing *Myriophyllum* and other aquatic plants. Buchar (1957) recorded his *'Colpidium campylum'* in a river with a-mesosaprobic to polysaprobic conditions. Foissner & Schiffmann (1980) recovered *P. truncatum* in winter 1974/75 in *Sphaerotilus*-tufts of



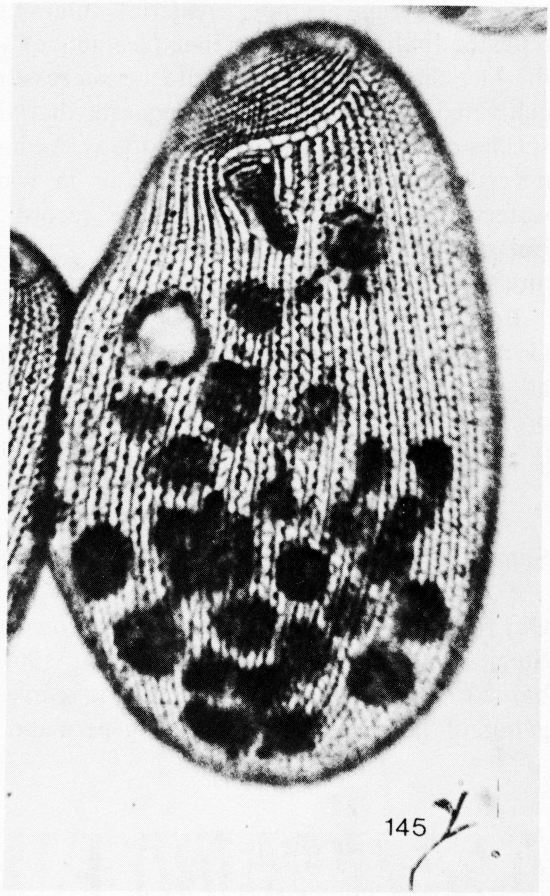
Figs. 118–125. Paracolpidium truncatum, originals from life (118–122) and after protargol impregnation (123–125). 118: Right lateral view; 119: Ventral view. Note the acentral posterior pole; 120–122: Variation in body shape; 123: Infraciliature of the right side; 124: Infraciliature of the ventral side; 125: Infraciliature of the left side. Scale bar divisions: 10 μm.

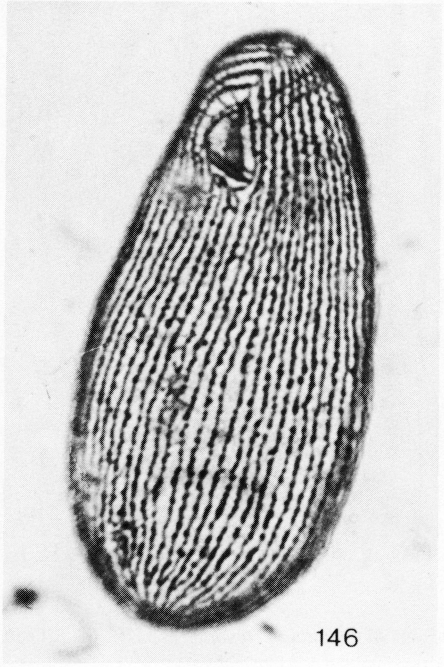


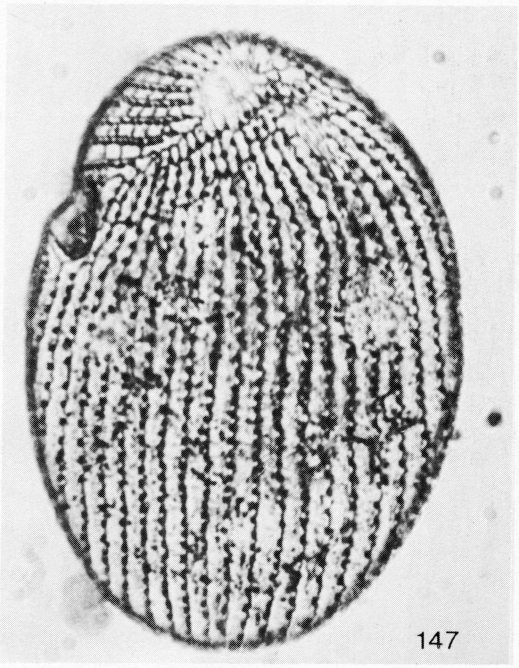
Figs. 126–133. Silverline system (Chatton-Lwoff method) and detail of the oral infraciliature (protargol and pyridinated silver carbonate method) of *Colpidium colpoda* (126, 130), *C. kleini* (127, 131), *Dexiostoma campyla* (128, 132) and *Paracolpidium truncatum* (129, 133). (Explanation in the text). Scale bar divisions: 10 μm.

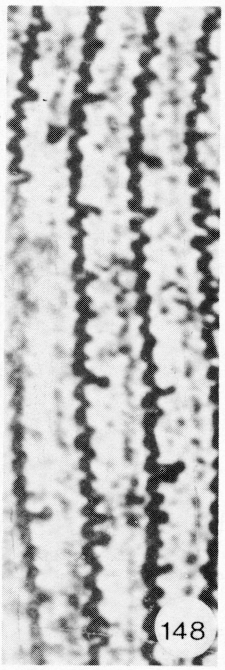


Figs. 134–143. Photographs of members of the *C-D-P* group; 134, 138, 142: *Colpidium colpoda;* 135, 143: *C. kleini;* 136, 141: *Dexiostoma campyla;* 137, 140: *Paracolpidium truncatum.* 134–137: In vivo aspect after sublimat fixation (Stieve) showing characteristic body shapes; 138–143: Oral infraciliature in detail (138, 139) and somatic infraciliature in ventral to left lateral view (140–143) after impregnation by the pyridinated silver carbonate method. M1-3 = membranelles 1–3, PM = paroral membrane.









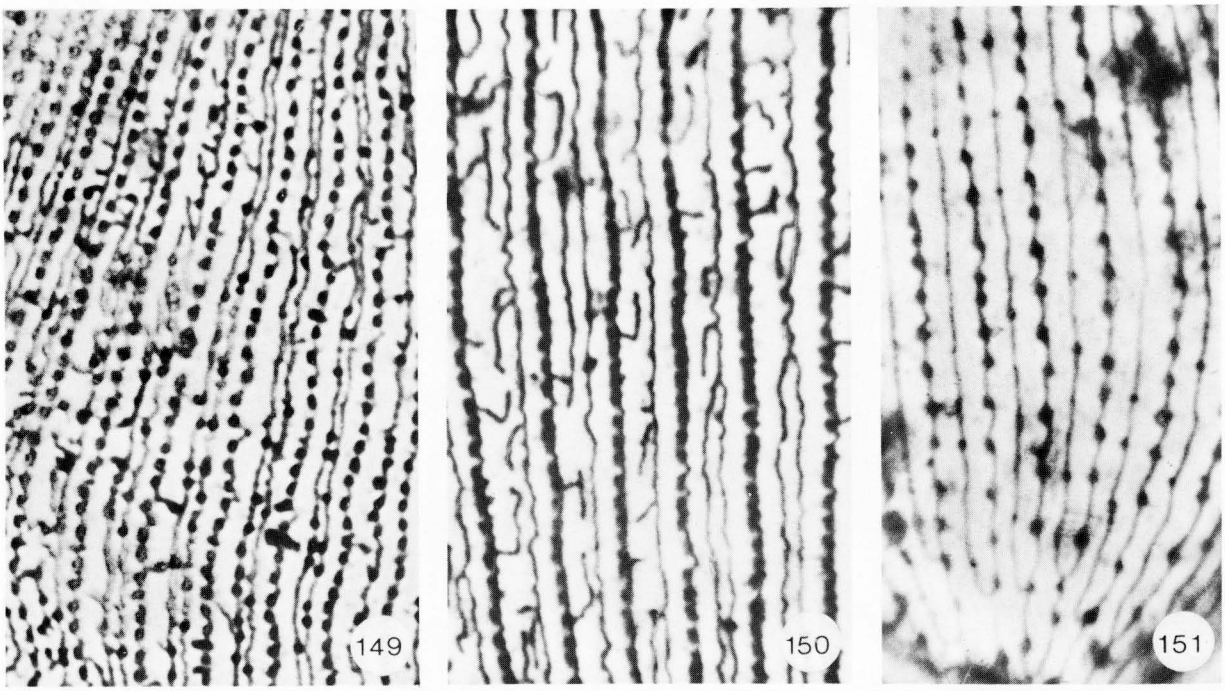
Figs. 144–148. Photographs of the silverline system of dry silvered individuals of *Colpidium colpoda* (144), *C. kleini (145), Dexiostoma campyla* (146), *Paracolpidium truncatum* (147, 148 in detail).

the river Traun (Upper Austria). Our own repeated findings in winter time (see above) and the fact that *P. truncatum* could be successfully cultivated in the refrigerator suggests that this species prefers cold waters. Until today, we have never observed it in summertime or in warm waters, the only exception is the record of Foissner *et al.* (1982), however, water temperature was below 10 °C.

Foissner & Schiffmann (1980), Foissner *et al.* (1982), and Foissner (1988) classify *P. truncatum* as a predominantly a-mesosaprobic indicator organism with the saprobic valencies: x = 0, o = 0, b = 2, a = 6, p = 2; G = 3, s = 3.0.

Summary

Our revision of the widespread genera *Colpidium* Stein, 1860 and *Dexiostoma* Jankowski, 1967 is based on a morphologic and biometric reinvestigation of the main species of these genera and on an extensive evaluation of data from literature. *Colpidium* consists of four species, namely *C. colpoda* (Losana, 1829), *C. singulare* Vuxanovici, 1961, *C. acuminatum* Vuxanovici, 1962, and *C. kleini* Foissner, 1969. Hitherto, only two of them, *C. colpoda* (type species) and *C. kleini* are well investigated. Their general morphology and the construction of their adoral membranelles are very similar, however, they can be separated by characters of body shape, number of kineties, details of the silverline system, and number of basal bodies in the adoral membranelles. A key to the species of the genus *Colpidium* is given. *Dexiostoma* is monotypic and contains *D. campyla* (Stokes, 1886). It is distinguished from *Colpidum* by a different oral infraciliature and the position and shape of the preoral suture. A new genus, *Paracolpidium* nov. gen., is suggested for *Colpidium truncatum* Stokes, 1885 because its oral infraciliature deviates from both *Colpidium* and *Dexiostoma*. In addition, the silverline system of *Paracolpidium truncatum* lacks, contrary to *Col-*



Figs. 149–151. Photographs of details of the silverline system of dry silvered individuals of *Colpidium colpoda* (149), *C. kleini* (150), and *Dexiostoma campyla* (151).

pidium and *Dexiostoma*, secondary meridians but shows short projections to the left of the primary meridians indicating a phylogenetic relationship to *Tetrahymena*. Delimitations of *Colpidium*, *Dexiostoma*, and *Paracolpidium* to closely related genera like *Tetrahymena*, *Glaucoma*, *Epenardia*, *Spirozona*, and *Stegochilum* are discussed.

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