

**Clarifying the Taxonomic Identity of a Phylogenetically Important Group of Eukaryotes:
Planomonas Is a Junior Synonym of *Ancyromonas***

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Supplementary Material

Pages 2–3: Pages 247–248 from Saville Kent, W. (1882): *A Manual of the Infusoria*, Volume I.

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Pages 4–6: Plate XIII and accompanying explanations from Saville Kent, W. (1882): *A Manual of the Infusoria*, Volume III.

Source and licencing information are as for the material on pages 2–3.

Pages 7–8: Transcription (p. 7) and translation (p. 8) from p. 97 of Hänel, K. (1979): Systematik und Ökologie der farblosen Flagellaten des Abwassers. *Arch Protistenk* **121**: 73-137.

Hänel's work is a catalogue of protists that he found in a sewage treatment plant. His accounts were broken into categoric points, each delineated by a letter: thus the subsections of the second section, and the rather cryptic notes for category e. We have provided his labels from the Introduction of his work for the categories in each case.

In general, we have attempted a literal translation, to preserve the original wording and meaning as closely as possible, rather than to render the text into fluid English.

Page 9: Plate 4 from Hänel, K. (1979): Systematik und Ökologie der farblosen Flagellaten des Abwassers. *Arch Protistenk* **121**: 73-137.

Page 10: Section transcribed from p. 547 of Cavalier-Smith, T.; Chao, E. E.; Stechmann, A.; Oates, B.; Nikolaev, S. (2008): Planomonadida ord. nov. (Apusozoa): Ultrastructural Affinity with *Micronuclearia podoventralis* and Deep Divergences within *Planomonas* gen. nov. *Protist* **159** (4): 535-562.

affected with these minute parasites occupied a restricted portion only of the premises on which they were first discovered. One point especially worthy of remark, as recorded by Mr. Lewis, has reference to the position of the flagellum. If, as he is inclined to maintain, this organ is produced from the posterior extremity, and propels instead of draws the animalcule through the inhabited serum, we have presented a structural and functional feature without parallel among the other representatives of these *Protozoa flagellata*, the recognition of which would demand the creation of a distinct generic and family group for the reception of these singular organisms. The correspondence of these animalcules, this last-named interpretation of the flagellum being correct, with the spermatozoa or male genetic elements of ordinary Metazoic animals, is most remarkable, and not unnaturally affords a foundation for the suggestion that further investigation may possibly demonstrate their identity with the discharged spermatocytic elements of the minute Nematodes, Micro-filariæ, or other Metazoic endoparasitic forms known to flourish amid the same surroundings.

GENUS VII. ANCYROMONAS, S. K.

(Greek, *ancyra*, anchor; *monas*.)

Animalcules ovate or elongate, free-swimming or adherent at will; flagellum single, trailing, adhesive or anchorate at its distal extremity, vibratile throughout the remainder of its length; endoplast and contractile vesicle conspicuous.

The single type referred to this genus is of much interest, it combining in its single trailing filament the functions of both the trailing and vibratile flagella of such genera as *Heteromita* or *Anisonema*. It is further remarkable as corresponding in its mature form with the earlier or larval condition of the representatives of these two last-named generic types, in the former of which more especially (see *Heteromita rostrata* and *H. uncinata*) it has been demonstrated by Messrs. Dallinger and Drysdale that the trailing or anchorate flagellum is the first to make its appearance, and continues for a while the sole organ of locomotion.

Ancyromonas sigmoides, S. K. PL. XIII. FIGS. 49-53.

Body persistent in form, gibbously ovate or sigmoidal, about three times as long as broad, the anterior extremity pointed and recurved ventrally, the posterior one sometimes rounded, but more often shortly pointed and slightly recurved in an opposite direction; flagellum continuous with the recurved anterior extremity, reflected backwards or ventrally, about twice the length of the body, the distal extremity adhesive or anchorate, the remaining portion vibratile or undulating; endoplast spherical, subcentral; contractile vesicle situated close to the anterior extremity. Length 1-5000'' to 1-4000''.

HAB.—Salt water, among decaying *Fucus*. Increasing by oblique fission and by encystment and breaking up of the body into spores.

This species was obtained at St. Heliers, Jersey, in September 1878, in vast quantities, among a mucilaginous exudation from fronds of the seaweed *Fucus siliquosa* that had been macerated in sea-water for the space of one week. As first seen with a magnification of 800 diameters only, the author was inclined to anticipate that the long, reflected and adherent flagellum was only one of two flagellate appendages, and that another finer vibratile one was stationed at the anterior extremity which would thus identify the animalcule with the typical representatives of the genus

Heteromita. A more careful investigation, however, aided by the employment of a $\frac{1}{80}$ -inch objective with a magnification of from 2500 to 5000 diameters, conclusively demonstrated that no other flagellate appendage existed, and that the single one present fulfilled in a remarkable manner the functions performed in *Heteromita* by two such organs. In the free-swimming animalcules, which were less numerous than the adherent ones, progression was effected in a straight line, accompanied by an oscillating motion, the single flagellum trailing in the rear like the posterior one of *Heteromita*, but slowly undulating throughout its length, and accomplishing by its vibrations the advancement made. In the temporarily adherent forms, fixed to the glass object-carrier or fragments of vegetable debris by the adhesive extremity of the same flagellum, a similar undulating action of the remaining length of this organ was apparent, this undulating action causing the entire organism to oscillate slowly up and down (see Pl. XIII. Fig. 50), and inducing at the same time a current to set in towards the animalcule's body. Viewed in profile, the motile flagellum seen just beneath the ventral surface of the body, presented at times an appearance closely corresponding with that of a minute undulating membrane; the body, however, in the next minute tilting away from the flagellum, exhibited its true nature. The phenomena attending the process of fission in this species were further observed to be somewhat abnormal. This takes place obliquely, the first indication of the impending process being a lengthening out of the body, accompanied by the greater prolongation of the more or less pointed posterior extremity until it attains a curvature, though in a reversed direction, corresponding with that of the anterior end, and develops at its apex a flagellum similar in all ways to the anterior one originally possessed. No trace of segmentation, however, has as yet made its appearance, and the animalcule remains riding at anchor or floats through the water, presenting (as shown at Pl. XIII. Fig. 51) a symmetrically sigmoidal contour closely identical with that of *Trepomonas agilis*, as seen from a lateral point of view (see Pl. XIX. Fig. 11), the two similar flagella divergent from each recurved point assisting to complete this likeness. Presently a faint oblique line makes its appearance, extending from above the median point of the dorsal surface of the original animalcule, downwards and backwards to behind the median point of the ventral region. This faint line gradually increases in the clearness of its delineation, and soon assumes the aspect of a distinct groove, which gradually deepens until the anterior and posterior halves become separated from one another as two precisely similar and undistinguishable units. Both bear the characteristic reflected flagellum, and likewise the central endoplast and antero-terminal contractile vesicle, these respective structures having also made their appearance previous to the commencement of the fission process, the former by the segmentation of the original endoplast, and the latter by independent development. The encystment of zooids which previously exhibited an irregular amoeboid phase, and the subdivision of these into eight or sixteen macrospores, giving rise to animalcules similar in shape to, but of much smaller size than the adults, have been observed, but not as yet the coalescence or genetic union of two or more units, and the breaking up of their united masses into more minute and abundant microspores.

Fam. II. PLEUROMONADIDÆ, S. K.

Animalcules naked or illoricate, entirely free-swimming, flagellum single, lateral or ventral; no distinct oral aperture.

GENUS I. PLEUROMONAS, Perty.

Animalcules free-swimming, kidney-shaped, bearing a single vibratile flagellum which projects from the centre of the concave ventral side; no distinct oral aperture.

PLATE XIII.

EXPLANATION.

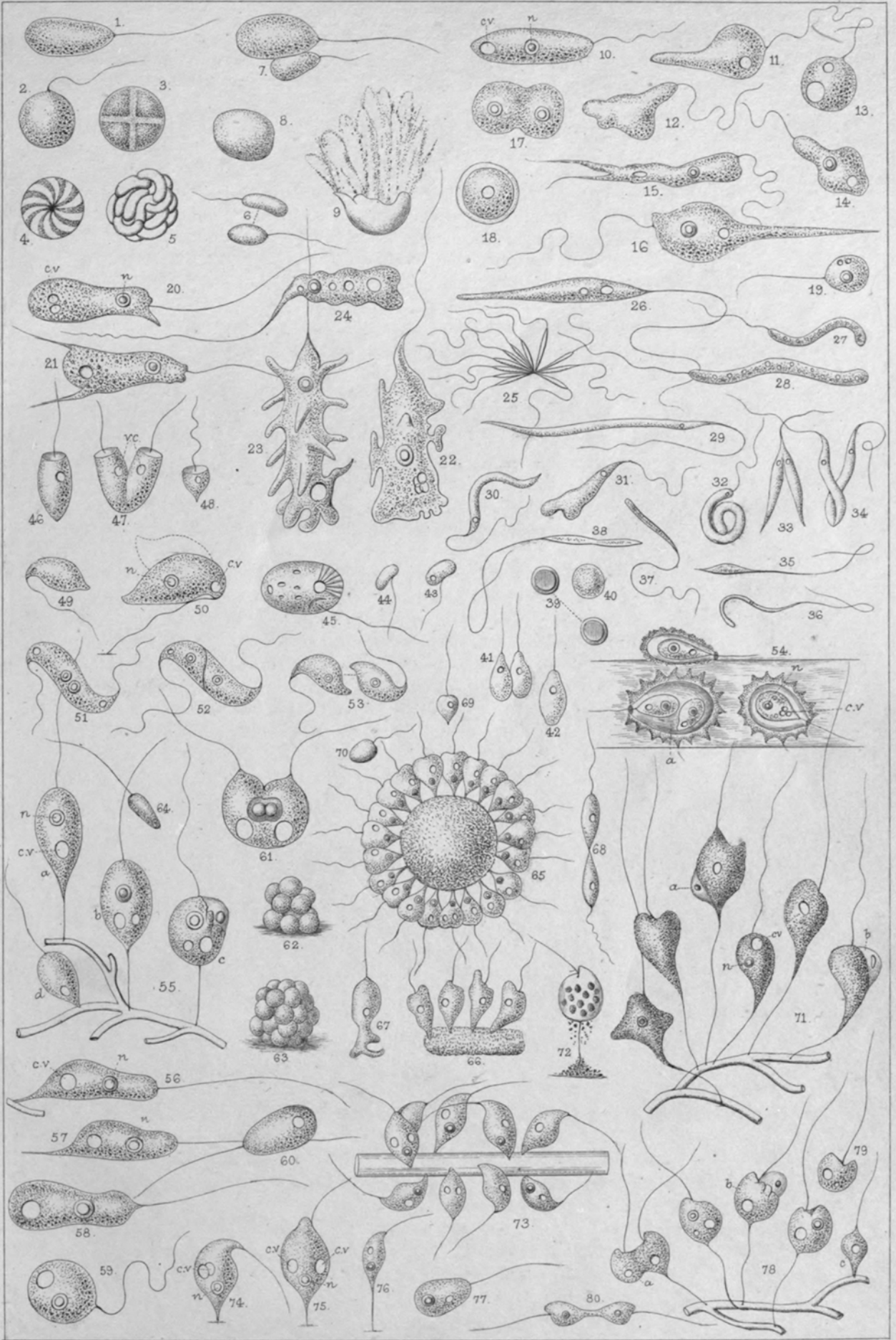
FIG.

- 1-9. *MONAS DALLINGERI*, S. K. (after Dallinger and Drysdale).—1, Normal adult form, $\times 2000$; 2, monad preparing to assume an encysted state; 3, 4, 5, progressive phases following upon encystment, and resulting in the production of a spherular aggregation of elongate vermicular macrospores; 6, the same macrospores liberated as simple monads resembling the parent, but of smaller size; 7, conjugation of larger and smaller monads; 8, encystment resulting from such conjugation; 9, the compound cyst bursting and liberating infinitesimally minute microspores.
- 10-18. *MONAS FLUIDA*, Duj.—10, Typical adult monad, $\times 1000$; 11-16, metamorphic forms of similar adult monads; 17, congregation of two zooids; 18, their encystment.
19. *MONAS IRREGULARIS*, Pty. (Cienkowski), $\times 350$.
- 20, 21. *MONAS OBESA*, Stein sp., $\times 650$ (Stein).
- 22-24. *MONAS RAMULOSA*, Stein sp. $\times 600$ (Stein).
- 25, 26. *LEPTOMONAS BUTSCHLII*, S. K. (Bütsch.).—25, A group attached by their posterior extremities, $\times 600$; 26, a free-swimming monad, $\times 1500$.
- 27, 28. *OPHIDOMONAS JENENSIS*, Ehr., $\times 600$ (Ehr.).
- 29-34. *HERPETOMONAS MUSCÆ-DOMESTICÆ*, Burnet sp. (Stein).—29-32, Polymorphic phases of the adult monads, $\times 650$; 33 and 34, monads dividing by longitudinal fission.
- 35-40. *HERPETOMONAS LEWISII*, S. K. (Lewis).—35-38, Various contours of the adult organism, $\times 800$; 39, two red and forty-one colourless corpuscles of the rat's blood which they inhabited, equally magnified to show proportionate size.
- 41, 42. *SCYTOMONAS PUSILLA*, St., $\times 650$ (Stein).
- 43, 44. *PLEUROMONAS JACULANS*, Pty., $\times 500$ (Perty).
45. *MEROTRICHA BACILLATA*, Meresch. (Dimensions unrecorded) (Mereschkowski).
- 46, 47. *CYATHOMONAS ELONGATA*, From.—47, Dividing by longitudinal fission, 600 (De Fromentel).
48. *CYATHOMONAS TURBINATA*, From., $\times 400$ (De Fromentel).
- 49-53. *ANCYROMONAS SIGMOIDES*, S. K.—49, Free-swimming animalcule, $\times 1500$; 50, animalcule fixed by distal termination of the single flagellum, the dotted outline indicating the position alternately assumed by the body with relation to the flagellum in the course of its rapid oscillations, $\times 2500$; 51-53, showing the several progressive phases of oblique fission.

EXPLANATION OF PLATE XIII. (*continued*).

FIG.

54. *PLATYTHECA MICROPORA*, St.—Three loricae with their contained animalcules attached to a joint of conferva; at *a* two zooids, the result of fission, occupy the same lorica, $\times 650$ (Stein).
- 55-64. *OIKOMONAS MUTABILIS*, S. K.—55, A group of four monads attached to vegetable fibre, showing at *a* and *b* normal sedentary forms, at *c* an example ingesting food-matter at its lateral periphery, and at *d* a young and recently adherent example, not having yet developed a filiform pedicle, $\times 800$; 56, an adult monad about to exchange its sedentary for a free-swimming condition; 57, the same monad detached and free-swimming, still retaining an attenuation of its posterior and previously fixed extremity; 58, typical free-swimming zooid; 59 and 60, more aberrant forms; 61, a motile zooid dividing by longitudinal fission; 62 and 63, spore-masses produced by segmentation of encysted animalcules; 64, a young monad developed from a spore.
- 65-70. *OIKOMONAS STEINII* (S. K.)—65, A group of monads attached to a spheroidal bacterial mass, $\times 650$; 66, four monads similarly attached, exhibiting a considerable irregularity of contour; 67, a free-swimming animalcule with branched posterior extremity; 68, a free-swimming animalcule dividing by transverse fission; 69 and 70, young free-swimming monads (Stein).
71. *OIKOMONAS QUADRATUM*, S. K.—A group of five monads; at *a* and *b*, zooids ingesting food at opposite regions of the periphery, $\times 800$.
72. *OIKOMONAS OBLIQUUS*, S. K., filled with artificially administered carmine-particles, a portion of which it is discharging from its posterior extremity, $\times 2500$.
- 73-77. *OIKOMONAS ROSTRATUM*, S. K.—73, A group of monads attached to a vegetable-fibre, $\times 800$; 74 and 75, two attached monads, the one with and the other without a posteriorly developed pedicle, $\times 1000$; 76, an example with an abnormally long pedicle; 77, a free-swimming monad with pedicle retracted.
- 78-80. *OIKOMONAS TERMO*, J.-Clark sp.—78, A group attached to vegetable fibre, showing at *a* a zooid dividing by longitudinal fission, at *b* an example ingesting food-matter, and at *c* a young, recently attached and almost stalkless zooid, $\times 1000$; 79, a free-swimming monad; 80, a free-swimming zooid dividing by fission.



Transcription from p. 97 of Hänel, K. (1979): Systematik und Ökologie der farblosen Flagellaten des Abwassers. *Arch Protistenk* **121**: 73-137.

Gattung: *Ancyromonas* Kent 1880

Die Vertreter dieser Gattung sind durch den Besitz nur einer Geißel gekennzeichnet. Die Gattung wurde deshalb von Lemmermann (1914) zu den Oicomonadaceae gestellt. Die beiden bislang beschriebenen Arten, *Ancyromonas sigmoides* Kent und *A. contorta* (Klebs) Lemm. (= *Phyllomonas contorta* Klebs) unterscheiden sich jedoch in ihrem Habitus so stark voneinander, daß sie weder in die gleiche Gattung noch in die gleiche Familie gehören. Während *Phyllomonas contorta* (der ursprüngliche Name muß wegen der systematischen Unterschiede zwischen beiden Flagellaten wieder angewendet werden) systematisch schwer einzuordnen ist, stellt *Ancyromonas sigmoides* einen typischen Vertreter der Bodonidae dar. Das auffallendste Merkmal dieses Bodonen ist die Reduktion der Schwimmgeißel.

Phyllomonas contorta tritt in den Abwässern so selten auf, daß sie hier nicht gesondert behandelt wird. Sie wurde nur wenige Male im Bewuchs der Abläufe von Nachklärbecken sehr gut arbeitender Tropfkörperanlagen gefunden.

Ancyromonas sigmoides Kent 1880 (Abb. 4, Fig. 10 und 11)

b [Literatur]. Bütschli (1883-1887), Kent (1880-1882)

c [Artmerkmale]. Die Zellen sind 2,5 ... 6 μm lang, 2 ... 3 μm breit und im Umriß oval bis bohnenförmig. Am Vorderende befindet sich ventral ein nasenförmiger, etwas veränderlicher Vorsprung, unterhalb dessen der Ursprungsort der 2...2,5mal körperlangen Schleppgeißel, das Cytostom und der Beginn der sigmoid verlaufenden Ventralfurche liegen. Die pulsierende Vakuole befindet sich dorsal im Vorderende. Das Vorderende ist abgestutzt und zum Teil leicht eingebuchtet. Die Fortbewegung erfolgt durch Kriechen, wobei das Auftreten starker Zuckungen charakteristisch ist.

d [Vorkommen]. Verbreitet, aber nur in geringer Individuenzahl auftretend. In den unteren Schichten gut arbeitender Tropfkörper, im aerob stabilisierten Belebtschlamm und im Bewuchs der Ablaufgerinne der Nachklärbecken.

e [Saprobienstufe — Indikatorwert]. α [alpha-mesosaprobe] — 4 (Tabelle 2)

Translation from p. 97 of Hänel, K. (1979): Systematik und Ökologie der farblosen Flagellaten des Abwassers. *Arch Protistenk* **121**: 73-137.

Genus: *Ancyromonas* Kent 1880

The representatives of this genus are identified by their possession of only one flagellum. The genus was thus placed in Oicomonadaceae by Lemmermann (1914). The two species described so far, *Ancyromonas sigmoides* Kent and *A. contorta* (Klebs) Lemm. (= *Phyllomonas contorta* Klebs), are distinguished so strongly from one another in their typical morphology that they belong neither in the same genus nor in the same family. While *Phyllomonas contorta* (the original name must again be adopted on account of the systematic difference between both flagellates) is difficult to classify systematically, *Ancyromonas sigmoides* depicts a typical representative of Bodonidae. The most conspicuous character of these bodonids is the reduction of their locomotory flagellum.

Phyllomonas contorta occurs so seldomly in wastewater that it will not be discussed separately here. It was found only a few times in the fouling matter of the effluent from reclamation streams of properly-functioning sewage-treatment trickle filters.

Ancyromonas sigmoides Kent 1880 (Plate 4, Fig. 10 and 11)

b [reference]. Bütschli (1883-1887), Kent (1880-1882)

c [species notes]. The cells are 2.5 – 6 μm long, 2 – 3 μm wide, and oval to bean-shaped in profile. At the end of the anterior is found ventrally a nose-shaped, somewhat plastic protrusion; underneath that lie the place of origin of the 2 – 2.5 -body-length manipulative flagellum, the cytostome, and the beginning of the continuous, sigmoid ventral furrow. The contractile vacuole is found dorsally at the anterior end. The anterior end is truncated and in part slightly emarginate. Locomotion is achieved through crawling, in which strong twitching is a characteristic occurrence.

d [occurrence]. Common, but only occurring in slight numbers of individuals. In the lower stages of properly-functioning trickle filters, in aerobically stabilised activated sludge, and in the fouling matter of effluent sluices of reclamation streams.

e [saprobic level — usefulness as indicator]. α [alpha-mesosaprobe] — 4

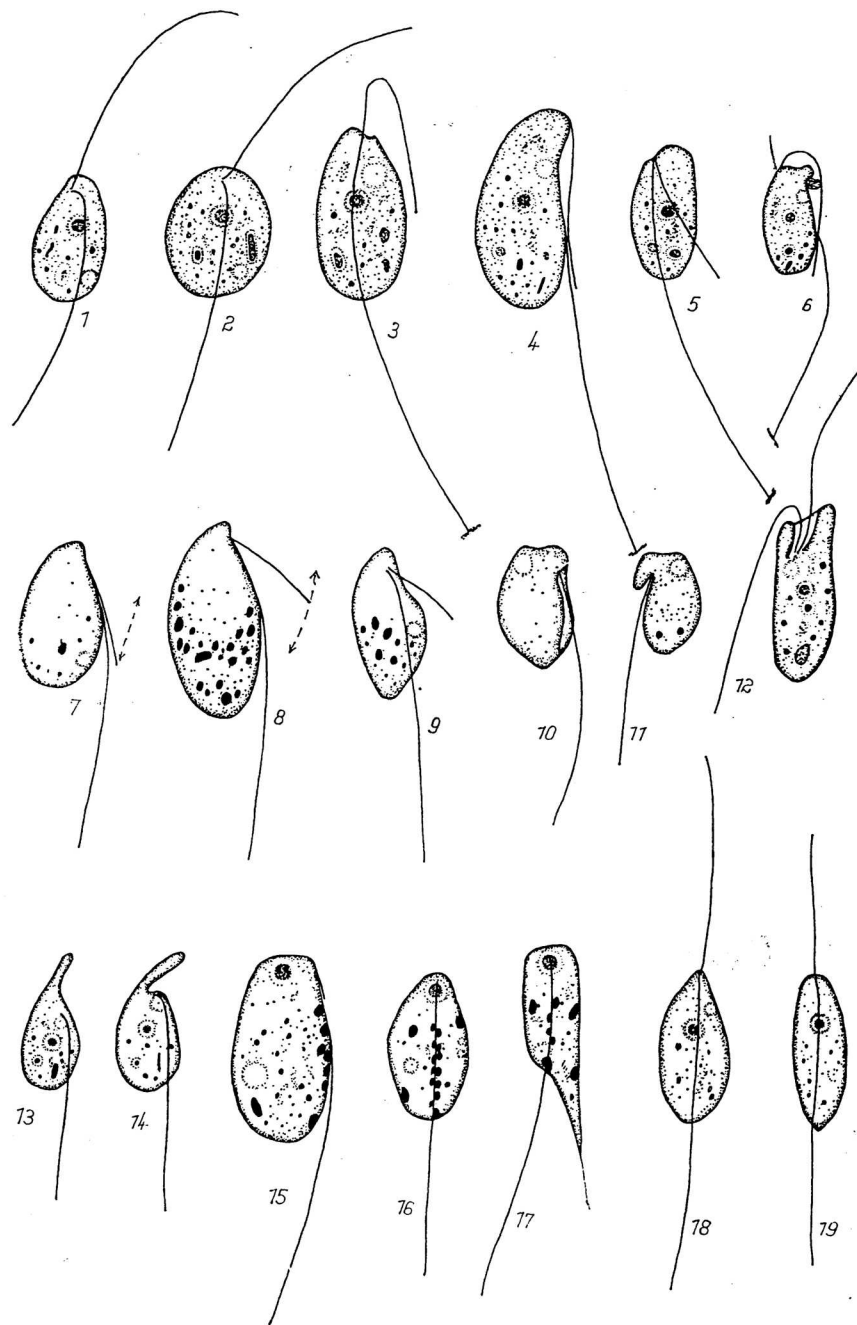


Abb. 4.

Fig. 1 und 2 : *Bodo lens* (MÜLLER) KLEBS

Fig. 3 ... 6 : *Bodo saltans* EHRB. (Fig. 6: Nahrungsaufnahme)

Fig. 7 ... 9 : *Pseudobodo minimus* HOLLANDE

Fig. 10 und 11 : *Ancyromonas sigmoides* KENT

Fig. 12 : *Phyllomitus amylophagus* KLEBS

Fig. 13 und 14 : *Rhynchomonas nasuta* (STOKES) KLEBS

Fig. 15 ... 17 : *Helkesimastix faecicola* WOODCOCK und LAPAGE

Fig. 18 : *Cercobodo bodo* (MEYER) LEMM.

Transcribed from page 547 of Cavalier-Smith, T.; Chao, E. E.; Stechmann, A.; Oates, B.; Nikolaev, S. (2008): Planomonadida ord. nov. (Apusozoa): Ultrastructural Affinity with *Micronuclearia podovernalis* and Deep Divergences within *Planomonas* gen. nov. *Protist* **159** (4): 535-562.

Had Kent studied Mylnikov's strain or *P. limna* (or even *P. howeae* where the anterior cilium is more obvious) without the benefit of DIC he would probably have overlooked the anterior cilium, even though he first assumed one must be there and searched rigorously for one with a 1/50 in objective. With such a careful search he should not have missed those of *P. cephalopora* or *P. micra*, both readily detectable by oil immersion bright field light microscopy using lenses no better than available to Kent. More importantly, however, *A. sigmoides* Kent was not a gliding flagellate at all, had a completely different shape from *P. mylnikovi*, *micra*, *howeae*, *cephalopora* and (to a lesser extent) *limna* and divided entirely differently! It cannot possibly be the same genus and might not even belong to the same phylum. The name *Ancyromonas* was chosen because it anchored itself by the tip of its sole cilium, while undulating it (Kent 1880—1882). No organism identified as *Ancyromonas* from 1979 onwards does this. The single cilium of *A. sigmoides* Kent was continuous with its anterior extremity, not in a deep ventral pocket posterior to it as in *Planomonas*; by contrast with the recurved anterior of *Ancyromonas* the rostrum of *Planomonas* lies between its two cilia. Nowhere does Kent mention that *Ancyromonas* is strongly flattened, whereas *Planomonas* always is. He describes it as dividing obliquely (Fig. 3h, 51—53), entirely different from *Planomonas*, which does so longitudinally in the plane of flattening (Fig. 3S—U, e—g, j). He also mentions the formation of cysts and their subsequent division into eight or sixteen flagellates; neither process has ever been observed in any *Planomonas*. An odd feature for a marine strain was the presence in *Ancyromonas* of a contractile vacuole (Kent 1880—1882), never reported in marine *Planomonas* (but found in soil and freshwater strains: Ekelund and Patterson 1997; Lee et al. 2005, and our Lake Baikal strains). Finally *Ancyromonas* usually had a pointed posterior recurved in the opposite direction to the anterior (hence the name *sigmoides*, entirely inappropriate for any planomonads); *Planomonas* never does, its posterior being smoothly rounded. *Ancyromonas* was also more elongated and longer than *Planomonas mylnikovi* (5—6.5 μm not 4—5 μm).