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Revision of the genus *Stentor* Oken (Protozoa, Ciliophora) and description of *S.araucanus* nov. spec. from South American lakes

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Abstract. *Stentor* is a heterotrich ciliate which often forms lawn-like covers on the bottom and/or blooms in the pelagial of lakes worldwide. The species involved in these spectacular events were usually either not determined or misidentified because the keys are outdated and incomplete. Thus, we have revised the nominal species described since the first major revision by Ehrenberg (1838). Main species characteristics are the presence/absence of symbiotic algae, the shape of the macronucleus and the colour of the cortical pigment granules. The last character mentioned must be studied in live cells because the pigment bleaches in chemically fixed specimens. Nineteen valid species are recognized and dichotomously keyed according to these characteristics. Twenty-seven other species and varieties, described after Ehrenberg's revision, are synonyms or species indeterminata. A new species, *S.araucanus*, is described from South American lakes. It is a small, broadly trumpet-shaped *Stentor* with symbiotic algae, vermiform macronucleus and blue–green cortical granules. *Stentor araucanus* is probably euplanktic and restricted to the southern hemisphere. *Stentor auriculatus* Kahl, 1932 sensu Wang (1934) is recognized as a new species, *Condylostoma wangi*, and transferred to the genus *Condylostoma*. New nomenclatural corrections: *Stentor baicalius* nom. nov. (pro *S.pygmaeus*, preoccupied), *S.loricatus* nom. corr. (for *S.loricata*), *S.ruber* nom. corr. (for *S.rubra*).

Introduction

During several meetings on protozooplankton ecology, it turned out that members of the genus *Stentor* comprise a large proportion of the total ciliate biomass in many lakes worldwide. Usually, the species involved could not be identified because an updated key is lacking. The senior author was thus asked by several participants to prepare a new key. The discovery of a new species by the junior author, who was faced with many identification problems during his studies on the ciliate fauna of South American lakes, provides a good opportunity to comply with this request.

The literature on *Stentor* is enormous, we have 1300 records in our library. A comprehensive review would thus need several hundred pages, even if only the taxonomic, ecological and faunistic literature should be fully covered. We thus decided to prepare a very short version of such a monograph which should primarily aid plankton ecologists in identifying species properly.

Benchmark literature on the taxonomy and ecology of *Stentor*

The first comprehensive review of the genus *Stentor* was prepared by Ehrenberg (1838), whose detailed lists and discussions of the older synonyms and literature are still indispensable for taxonomic and nomenclature purposes. The next major revisions were performed by Stein (1867), Kent (1881), Johnson (1893) and Kahl (1932). Kahl's compilation was widely acknowledged, although, as our review shows, it is rather incomplete. More recently, Tartar (1961), Dragesco and Dragesco-Kernéis (1986) and Nilsson (1986) provided short, also rather incomplete, overviews.

Foissner *et al.* (1992) undertook a detailed review on the taxonomy and ecology of eight common freshwater species: *Stentor amethystinus*, *S.igneus*, *S.multiformis*, *S.niger*, *S.coeruleus*, *S.muelleri*, *S.polymorphus* and *S.roeselii*. This paper not only covers the major ecological and faunistic literature, but also contains many excellent micrographs showing the morphology of *Stentor* in life and after silver impregnation.

Revision of the genus *Stentor* Oken, 1815

Synonyms

Salpistes, Stentorella, Stentorina.

Diagnosis

Medium-sized (100 μm) to very large (up to 4 mm) heterotrich ciliates, sedentary or freely motile, in the former case attaching themselves by their posterior extremity (holdfast) to submerged aquatic objects, usually secreting a mucilaginous lorica. Body moderately to highly contractile: when swimming and contracted, clavate, pyriform or turbinate; when fixed and extended, slenderly to broadly trumpet shaped, i.e. broadly expanded anteriorly, tapering off and attenuate towards the attached posterior extremity. Somatic ciliature holotrichous, in even longitudinal rows, usually supplemented by sparingly scattered hair-like setae ('sensory bristles'). Adoral zone of membranelles at margin of elliptical to circular, rarely bilobate, peristomial bottom, its left-hand extremity or limb spirally involute, forming a small buccal cavity which leads to the cytostome, the right-hand limb free and usually raised considerably above the opposite or left-hand one. Macronucleus vermiform, nodulate, moniliform or composed of one to few spherical masses ('beads'). Contractile vacuole consisting of an anterior circular dilatation, which gives off a horizontal annular branch which underlies the circumference of the peristome, and a canal-like diverticulum which extends towards the posterior extremity of the body. Cortex with stripes of colourless or conspicuously pigmented (red, blue, green, brownish) granules. Some species with symbiotic green algae. Inhabiting mainly freshwater, rarely saltwater or terrestrial biotopes; mostly social, often forming lawn-like covers or water blooms.

Type species

Stentor muelleri Ehrenberg, 1831.

Nomenclature

Stentor is a nomen conservandum (Hemming, 1954; Kirby, 1954).

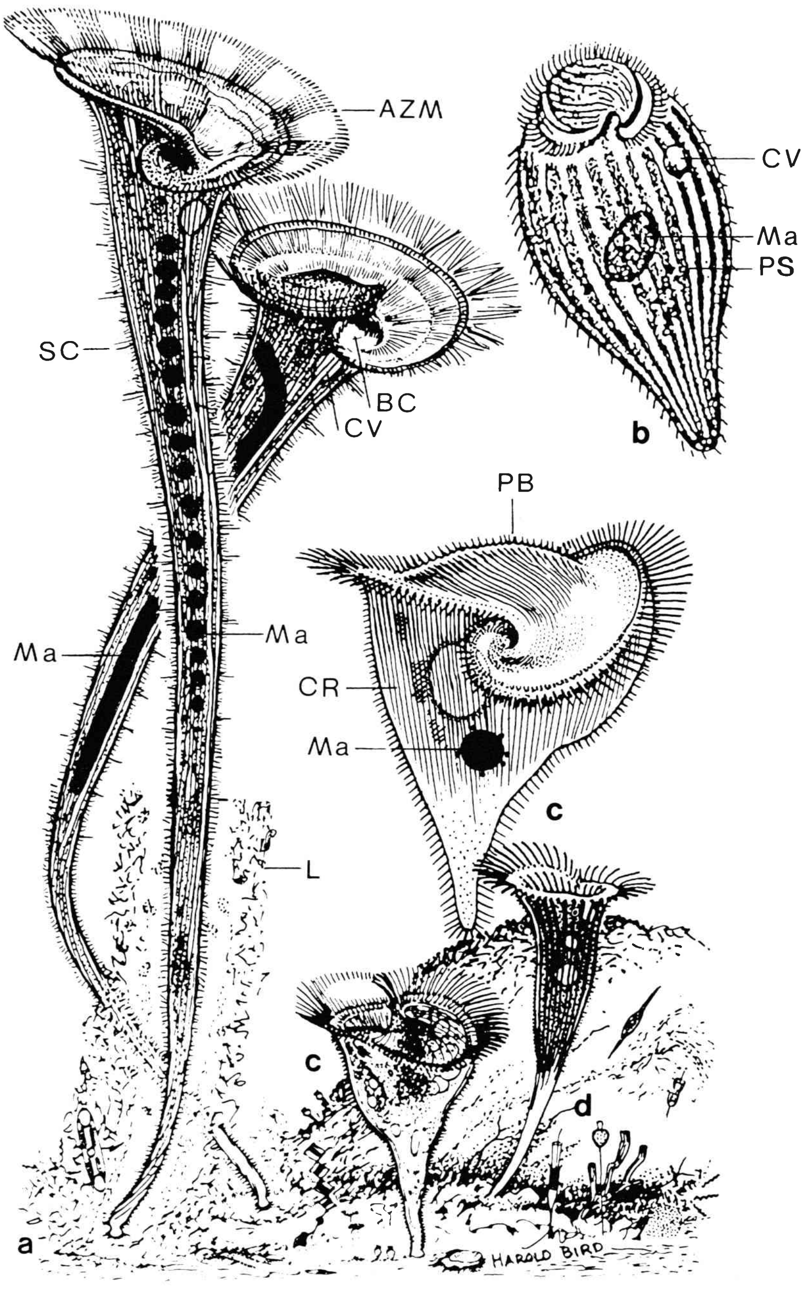

Fig. 1. A *Stentor* assemblage showing the main shape and macronucleus types [from Curds *et al.* (1983), modified]. (**a**) Large, slenderly trumpet-shaped species with a vermiform and a moniliform macronucleus, respectively. (**b**) Freely motile, turbinate specimen with coloured pigment stripes. (**c**) Small to medium-sized, broadly trumpet-shaped species with single, spherical macronucleus. (**d**) Campanulate species. AZM = adoral zone of membranelles; BC = buccal cavity; CR = ciliary rows; CV = contractile vacuole; L = lorica; Ma = macronucleus; PB = peristomial bottom; PS = pigment stripes; SC = sensory cilia.

Species characters in *Stentor*

This paper does not contain a detailed morphology of the genus, for which the reader is referred to Tartar (1961) and Figures 1–6, but merely discusses those characters which have been used, or which we recommend, in separating and identifying species. They are treated according to their reliability and usefulness. The main characters are endosymbionts, nuclear apparatus and cortical (pigment) granules. Weak characters are size, shape, contractility, number of somatic and peristomial ciliary rows and adoral membranelles, and geographic location. Useless characters are the presence/absence of a lorica and sensory cilia, the shape of the holdfast and the biotope.

Generally, most live drawings of Stentors are rather poor, i.e. too schematic. The best figures available are still those from Stein (1867) which, unfortunately, are too faint to be reproduced adequately. More recently, Curds *et al.* (1983) provided an excellent drawing, reproduced here as Figure 1.

Endosymbionts ('zoochlorellae')

Several *Stentor* species have apparently stable associations with symbiotic green algae, which belong to the *Chlorella vulgaris* group according to their physiological and ultrastructural characteristics (Reisser, 1984). The symbionts are usually 4–7 μm in size and have a single, cup-shaped chloroplast. They are located either mainly in the ecto–endoplasmic boundary (e.g. *S.amethystinus*) or scattered through the cytoplasm (e.g. *S.polymorphus*). Depending on species, size and physiological state, the number of symbionts varies, but usually there are at least some hundreds. Bacterial endosymbionts were recently described by Görtz and Wiemann (1987) in *S.multiformis*. Their taxonomic value is not known. Microsporidian parasites were found in *S.polymorphus* and *S.roeselii* (Görtz, 1987).

There is a long-lasting debate on whether symbiotic green algae can be used as a species character. I agree with many taxonomists that 'green populations' are usually distinct species because closer examination often reveals more or less pronounced morphological differences to the aposymbiotic congeners [see Foissner (1994) for examples]; furthermore, the integration of a symbiotic partner requires specific physiological mechanisms [see Reisser (1986) for a review] which can be considered, independently of morphological differences, as species characters. However, the stability of the association should be tested to exclude the possibility that a symbiosis is simulated by temporarily phagocytosed material (Reisser, 1986). If, however, the algae apparently belong to the *Chlorella* group and have a fixed location, viz. in the ecto–endoplasmic boundary, as in most green *Stentor* species, the symbiosis is very likely stable.

There is no reliable report in the literature that green Stentors lost their symbionts or that aposymbiotic species acquired symbionts under natural circumstances. However, under certain laboratory conditions, like prolonged cultivation in the dark or inhibition of the algal photosynthesis, aposymbiotic cells may be obtained (Schulze, 1951; Tartar, 1961; Reisser, 1986), but all authors emphasize that Stentors are not easily divested of their symbionts and often cannot survive for longer periods without the symbionts or, at least, some algal nutrition.

Nuclear apparatus

The shape of the macronucleus is the second main character for identifying *Stentor* species. Depending on species, it is vermiform (a cylindrical, irregularly curved body), nodular (a cylindrical, irregularly curved body with rather regularly spaced constrictions), moniliform (a chain of beads or nodules connected by thread-like elongations of the nuclear membrane), a single spherical mass or composed of few isolated, spherical nodules (Figure 34). Although there is some variability, the macronuclear shape is easily recognized if a few cells are carefully examined. Usually, several micronuclei surround the macronucleus. Their number is highly variable and has been used only once as a major species character (*S.multimicronucleatus*).

Cortical (pigment) granules

The cortex of *Stentor* has distinct striae due to broad stripes of granules which alternate with narrow, clear furrows containing the ciliary rows. The granules have a diameter of ~0.5–1 μm and are colourless or pigmented. In the latter case, the cortical striation becomes very conspicuous and mass development causes coloured benthic lawns or planktonic blooms. The colour of the granules is an important character, although it varies slightly, especially in intensity, and is subject to somewhat different interpretations. Small differences (e.g. yellow, yellowish, yellow–brown) should thus not be used to separate species. The pigment is called 'stentorin' and belongs to the meso-naphthodianthrone group of compounds, which also includes the photodynamic pigments hypericin and phagopyrin (Barbier *et al.*, 1956; Tartar, 1961; Moller, 1962). The function of the pigments is still under discussion. The most attractive hypothesis seems to be that the pigments mediate the orientation of the organisms in a light gradient (Moller, 1962). *Stentor coeruleus*, a blue-pigmented species without symbiotic green algae, exhibits negative phototaxis to visible light, in addition to a step-up photophobic response (Song *et al.*, 1980). Symbiont-bearing species show a positive phototaxis.

Shape

The shape is highly variable due to the contractility of the body and also depends on whether the cell is attached or freely motile. In the contracted and/or motile stage, all species look very similar. In the extended form, at least two types can be distinguished (Figure 1): slenderly (length:width >3:1) and broadly (length: width ≤2:1) trumpet shaped. A few other peculiarities occur, e.g. a bilobate peristomial bottom in *S.barretti* and a tail-like appendage in *S.caudatus*, which have some value. Generally, however, the character 'shape' is of little significance because one can hardly be sure whether a certain specimen is fully extended or not.

Size

The size depends, like the shape, on contractility and is thus also a weak character. Usually, the highly contractile species (e.g. *S.coeruleus*, *S.polymorphus*) are longer than the less contractile ones (e.g. *S.amethystinus*, *S.tartari*). Three size classes can be roughly distinguished: small (<200 μm), medium sized (200–1000 μm) and large (>1000 μm).

Contractility

Contractility is usually weaker in the smaller than in the larger species of the genus. However, it depends on various environmental factors, on the fitness of the specimen under investigation, and even on the patience of the investigator. The fully extended condition usually cannot be observed in a small drop of water under the microscope because the depth of the drop is less than the length of the cell. Generally, the optimum conditions for extension are difficult to meet. Thus, 'contractility', and the correlated characters 'shape' and 'size', are weak and useful only for separating groups of species.

Number of somatic and peristomial ciliary rows and adoral organelles

The few data available indicate a high variability within and between populations. As expected, the smaller species have fewer numbers of these organelles than the larger ones. At the present state of knowledge it is, however, impossible to estimate the taxonomic value of these characters. Very likely, they overlap to a great extent.

Geographic distribution and biotopes

See the section on ecology.

Lorica and sensory bristles

The presence/absence of a lorica was used by some authors as a species character. However, as with shape, size and contractility, this feature is highly ambiguous because the lack of a lorica is difficult to prove both under field conditions and in the laboratory. To mention only one example: *S.multiformis* was a caseless species for 150 years until Packroff and Wilbert (1991) showed that it inhabits an inconspicuous, mucilaginous lorica. The same applies for the presence/absence and arrangement of the stiff and slightly elongated sensory cilia which are difficult to recognize and have no correlate in the infraciliature

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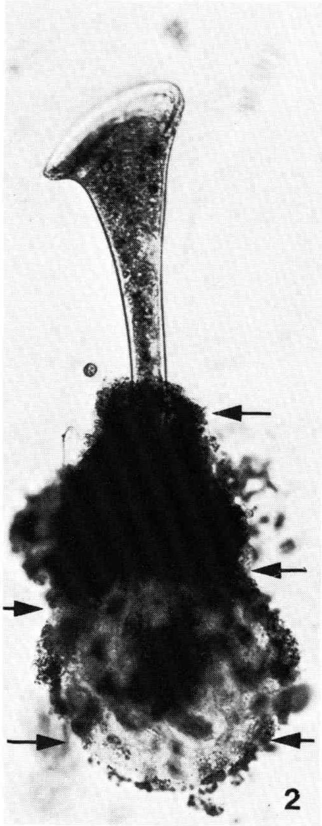
Figs 2–5. *Stentor roeselii* as example for the morphology of *Stentor* (from Foissner *et al.*, 1992). **Fig. 2.** Partially extended specimen with large, pyriform lorica (arrows). **Figs 3 and 5**. Silver (protargol)-impregnated cell showing vermiform macronucleus and organization of somatic and oral ciliary apparatus. Arrows mark the so-called contrast or ramifying zone at the ventral surface, where ciliary rows are more densely spaced and multiplicated. **Fig. 4.** Fully extended, slenderly trumpet-shaped specimen. AZM = adoral zone of membranelles; BC = buccal cavity; Ma = macronucleus; PBC = ciliary rows on surface of peristomial bottom; PM = paroral (undulating) membrane; SC = somatic ciliary rows.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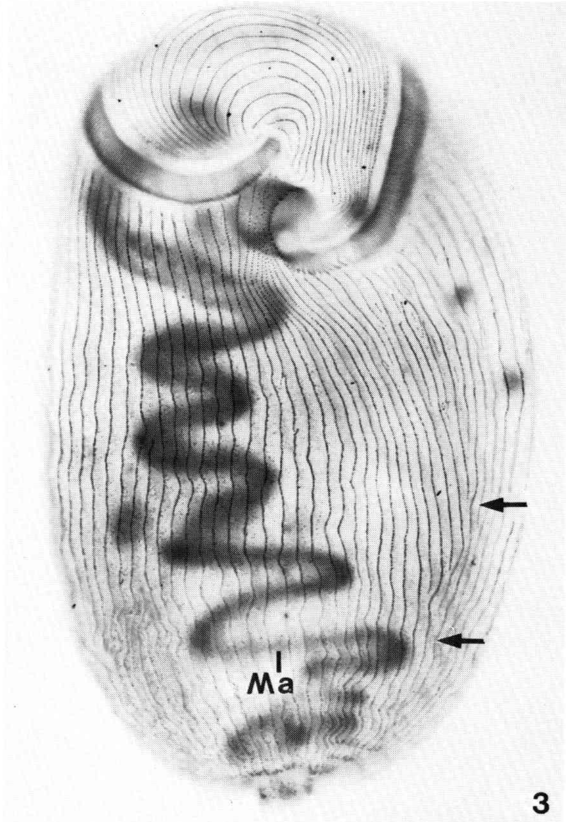
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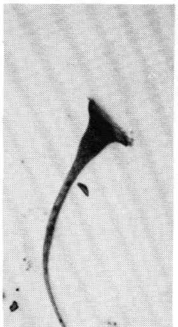
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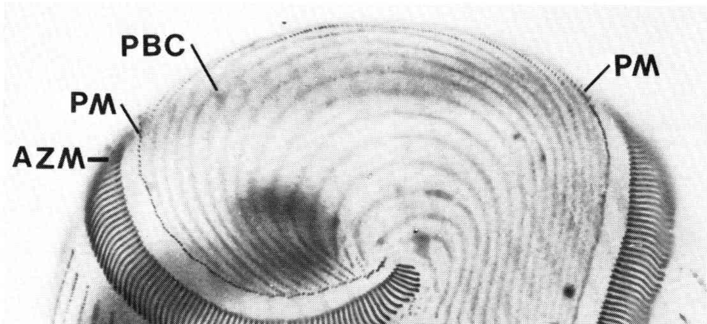
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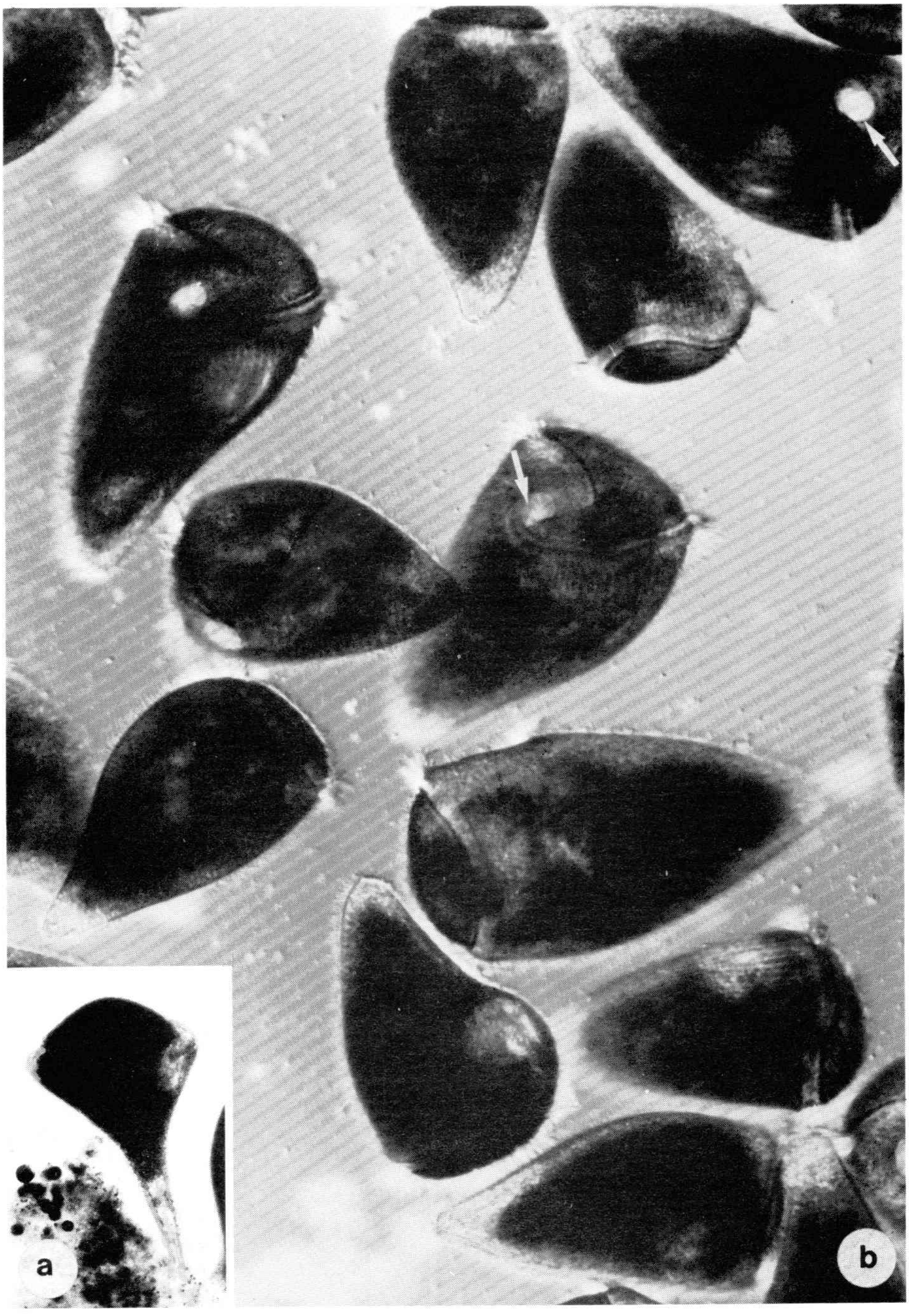


Fig. 6. Bloom of *S.amethystinus* (from Foissner *et al.*, 1992). The freely motile specimens are distinctly turbinate (**b**), while the sessile form is broadly trumpet shaped (**a**). Cells appear blackish due to purplish-red pigment granules and symbiotic green algae. Arrows mark the entrance to the buccal cavity.

(Dragesco and Dragesco-Kernéis, 1986; Foissner *et al.*, 1992). Very likely, all *Stentors* have sensory cilia and make a lorica under optimal conditions.

Holdfast

The shape of the posterior holdfast organelle was used by some authors as a species character. The data obtained by Andrews (1945) and reviewed by Tartar (1961) show that the observed differences result from incomplete observations.

Ecology of *Stentor*

A detailed review of the ecology and geographic distribution of the common *Stentor* species, namely *S.amethystinus*, *S.coeruleus*, *S.igneus*, *S.muelleri*, *S.multiformis*, *S.niger*, *S.polymorphus* and *S.roeselii*, has been published by Foissner *et al.* (1992). Here, we thus provide only a more general introduction focusing on data essential to plankton ecologists. Further details are mentioned in other chapters, especially as concerns the pigment granules, the endosymbionts and the geographic distribution.

Stentor is basically sessile via a specialized posterior holdfast organelle secreting a sticky substance (Tartar, 1961). Euplanktonic species occur only rarely, if at all. However, the small species of the 'dark' group, i.e. *S.amethystinus*, *S.fuliginosus* and *S.niger*, tend to be planktonic and often cause heavy blooms (Stein, 1867; Johnson, 1893; Kasturi Bai and Narayana Murthy, 1975; Bienert *et al.*, 1991; Foissner *et al.*, 1992; Figure 6). Planktonic blooms have been reported, at least once, in all common species (Foissner *et al.*, 1992) and may comprise >90% of the total ciliate biomass (Bienert *et al.*, 1991). The physicochemical and biotic factors which are responsible for blooming are not known. There is some evidence that *Stentor* blooms can cause fish mortality (Otterstrøm and Larsen, 1946), problems in drinking-water reservoirs and processing, as well as in small lakes used for swimming and recreation (Foissner *et al.*, 1992).

Most *Stentor* species occur in normal and dystrophic freshwaters, and in slightly brackish biotopes. Usually, in marine environments *Stentor* is replaced by folliculinids ('bottle animals') and condylostomatids. Only *S.multiformis* has been recorded from marine, freshwater and even terrestrial biotopes (Stein, 1867; Penard, 1922; Stout, 1961; Foissner *et al.*, 1992). However, it is uncertain whether all populations are conspecific. Resting cysts are known from a few species.

Data on geographical distributions are uncertain because identifications are often questionable. Some species are very likely cosmopolits (e.g. *S.igneus*, *S.multiformis*, *S.coeruleus*, *S.polymorphus*, *S.roeselii*), others are possibly restricted to Gondwanian areas (e.g. *S.araucanus*, *S.multimicronucleatus*); *S.baicalius* is possibly endemic to Lake Baikal.

Some *Stentor* species are fairly good indicators of organic pollution in running waters and can survive anaerobic conditions for up to 12 h. In activated sludge, Stentors usually indicate good operating conditions (Foissner *et al.*, 1992).

Stentor is polyphagous, i.e. it feeds on various heterotrophic (e.g. ciliates and flagellates) and autotrophic (e.g. diatoms) protists. Even small metazoans like rotifers and oligochetes are attacked, and cannibalism has been observed (Gelei, 1925; Grula and Bovee, 1977). Detailed autecological data are available mainly from *S.coeruleus* (Rapport *et al.*, 1972; Wenzel and Liebsch, 1975; Laybourn, 1976). These studies show that *Stentor* is a very efficient filter feeder and energy converter, which is reasonable considering its large oral apparatus.

Nominal species of the genus *Stentor*

This section alphabetically lists the nominal species described in and after the major revisions of the genus by Ehrenberg (1838) and Stein (1867), to which the reader is referred regarding the older synonyms and literature. Where appropriate, some comment on the taxonomic status and/or the distinctive characters is included. Usually, however, species characters are not detailed because these are contained in the key.

Stentor acrobaticus Silén, 1948 (Figure 23)

A peculiar marine species which certainly does not belong to the genus *Stentor*. It possibly secretes a rather compact rod on which it glides up and down rapidly. Found only once in small numbers on a *Fuscus* leaf on the west coast of Sweden.

Stentor albus Fromentel, 1876

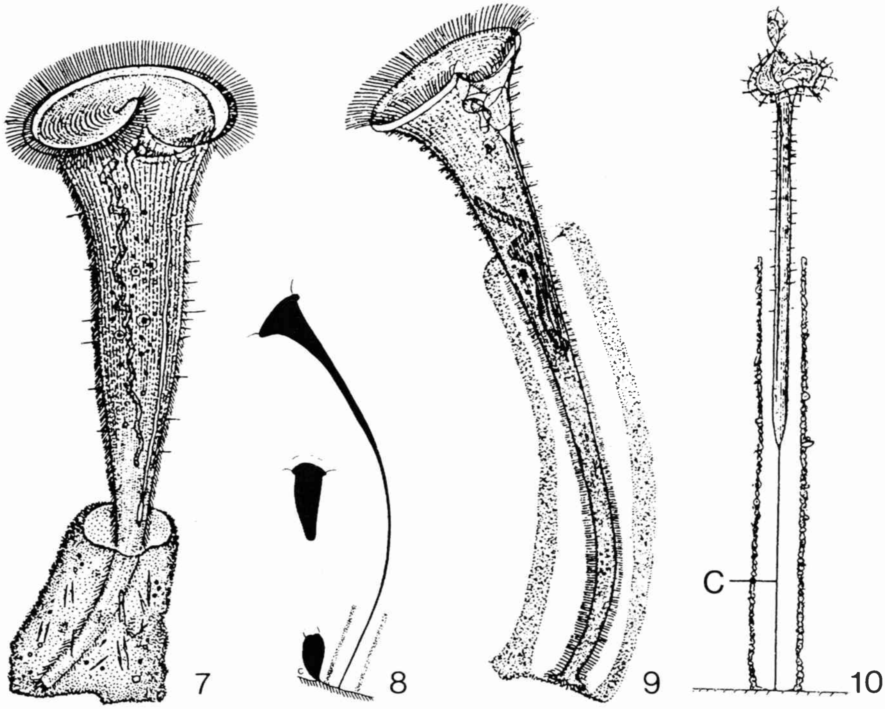
The figures clearly show freshwater tintinnids which left their lorica. Fromentel even mentions that the contractile vacuole moves up and down with the peristomial bottom, which is typical for tintinnids. A more accurate identification is, however, impossible. We thus suggest considering *S.albus* as a species indeterminata.

Stentor amethystinus Leidy, 1880 (Figures 6 and 27)

A detailed description and discussion of synonymy, morphology, and ecology can be found in Foissner *et al.* (1992). This violet to purple–red-pigmented, symbiotic algae-bearing freshwater species has been thoroughly redescribed by Dragesco (1970), Foissner (1980), Foissner *et al.* (1992) and Nilsson (1986). *Stentor amethystinus* has ~90–120 somatic kineties, 20–25 peristomial kineties and 200–300 adoral membranelles (Foissner *et al.*, 1992). It is probably often misidentified as *S.niger* which, however, lacks symbiotic algae and has brownish pigment granules. Easily confused with *S.fuliginosus* which differs from *S.amethystinus* by the colour of the cortical granules and the lack of pigment granules around the micronuclei.

Stentor anceps Fromentel, 1876

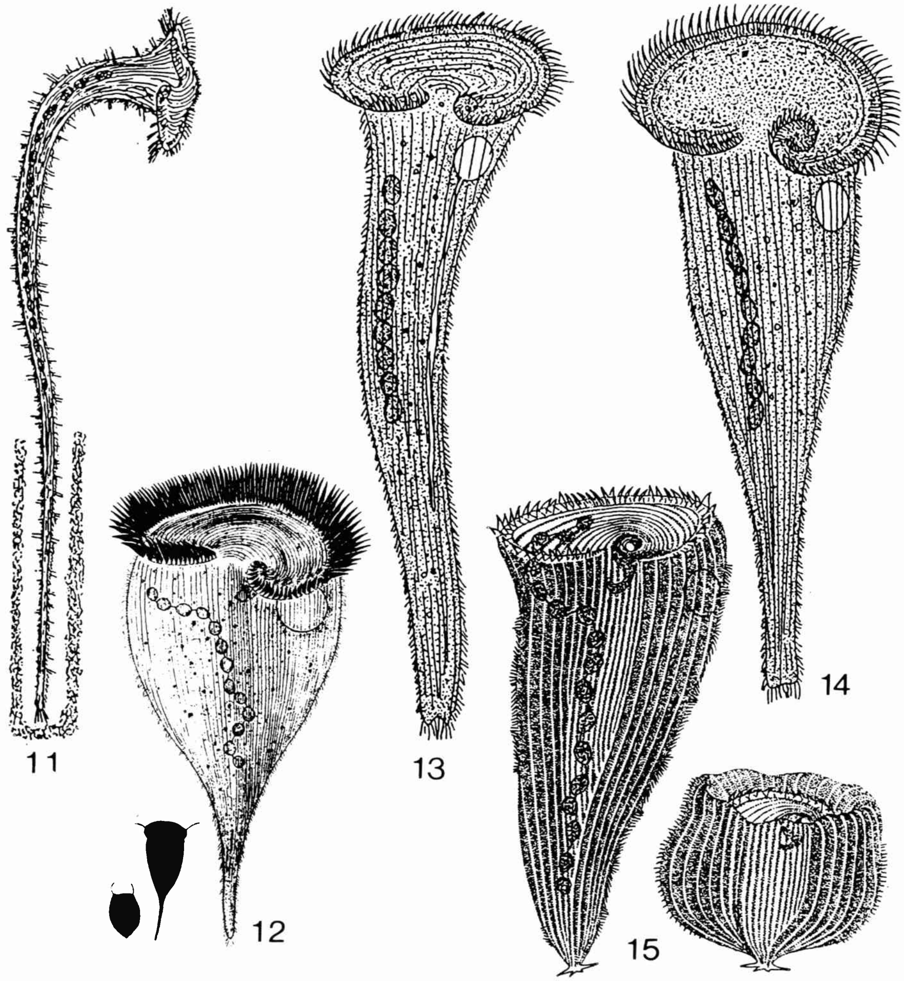
This ~90 μm long, cylindroid, colourless organism is very likely a telotroch stage of a peritrichous ciliate, as also discussed by Fromentel. The description is very incomplete and we thus suggest considering *S.anceps* as a species indeterminata.



Figs 7–10. *Stentor* species with vermiform or nodular macronucleus. **Fig. 7.** *Stentor roeselii* (after Stein, 1867), macronucleus vermiform, cortical granules colourless, no endosymbionts. **Fig. 8.** *Stentor roeselii* freely motile, attached and contracted, attached and extended (from Dragesco, 1970). **Fig. 9.** *Stentor loricatus* (from Bary, 1950), macronucleus vermiform, cortical granules dark green, no endosymbionts. **Fig. 10.** *Stentor barretti* (from Warren, 1985), macronucleus nodular, cortical granules colourless, no endosymbionts, peristomial bottom bilobate, posterior end cord like (C) elongated.

Stentor andreseni Nilsson, 1986

This binucleate, African freshwater species was thoroughly described and a possible synonymy with *S.tartari* was also considered. However, Nilsson (1986) decided against synonymy because she assumed that *S.tartari* 'should be a slender ciliate having about half the number of ciliary rows found in *S.andreseni*'. However, this is a weak character, especially considering the identical live size (~300 μm) in both species, which suggests that their ciliary row number is similar and was underestimated by Narayana Murthy and Kasturi Bai (1974) in *S.tartari*. We thus synonymize *S.andreseni* with *S.tartari*. The binucleate, purple–red *S.amethystinus* found by Vuxanovici (1961a) in Lake Herăstrău, near Bucharest, very likely also belongs to this species. *Stentor igneus* sensu Johnson (1893), found in two ponds in North America, is also *S.tartari*, as indicated by the characters given (reddish, two, rarely one, three, four, five or six macronuclear segments, symbiotic algae, rather broadly trumpet shaped).



Figs 11–15. *Stentor* species with moniliform macronucleus (see also Figures 16–18). **Fig. 11.** *Stentor muelleri* (from Kahl, 1932), cortical granules (CG) colourless, no endosymbionts (ES), slenderly trumpet shaped. **Fig. 12.** *Stentor caudatus* contracted and extended (from Dragesco, 1970), CG colourless, no ES, campanulate and posterior end tail like elongated. **Fig. 13.** *Stentor polymorphus* (from Dragesco and Dragesco-Kernéis, 1986), CG colourless, with ES. **Fig. 14.** *Stentor coeruleus* (from Dragesco and Dragesco-Kerenéis, 1986), CG cerulean blue, no ES, slenderly trumpet shaped and usually 1–2 mm long. **Fig. 15.** *Stentor introversus* extended and contracted (from Tartar, 1958), CG blue–green, no ES, broadly trumpet shaped and up to 500 μm long.

Stentor attenuatus Maskell, 1887

We agree with Kahl (1932) that this species is a junior synonym of *S.coeruleus* from which it supposedly differs by 'the remarkable slenderness and great length of the stem', a really insufficient character (cp. Figure 16).

Stentor auricula Kent, 1881

Very likely a *Condylostoma* or *Folliculina* (see the next species). We thus exclude it from *Stentor*. The species name is considered as a noun in apposition.

Stentor auriculatus Kahl, 1932

This marine species was described by Kahl after observations from Daday (1886) and Gruber (1884), who identified their populations as *S.auricula* Kent. Fauré-Fremiet (1936) reinvestigated *S.auriculatus* and showed that it belongs to *Condylostoma*. Later, Andrews (1948) suggested that Kent (1881) overlooked the beaded macronucleus, i.e. synonymy of *S.auricula* Kent and *S.auriculatus* Kahl. More recently, Jankowski (1978), without new evidence, constructed the new genus *Condylostentor* for *S.auriculatus* Kahl. Later, Jankowski (1980) even proposed a new family, Condylostentoridae, for this species—again without new data.

Stentor baicalius nom. nov. (pro *S.pygmaeus* Swarczewsky, 1929 preoccupied by *S.pygmaeus* Ehrenberg, 1831, now in the genus *Colacium*, Euglenophyta; Figure 24)

This species, which is attached to crustaceans of Lake Baikal, was originally described from formalin-fixed material only. It has been rediscovered by Gajewskaja (1933) who, however, synonymized it with *S.multiformis*. In our opinion, *S.baicalius* is well characterized by its sea green cortical granules, 4–6 macronuclear beads and the club-like body shape.

Stentor barretti Barrett, 1870 (Figure 10)

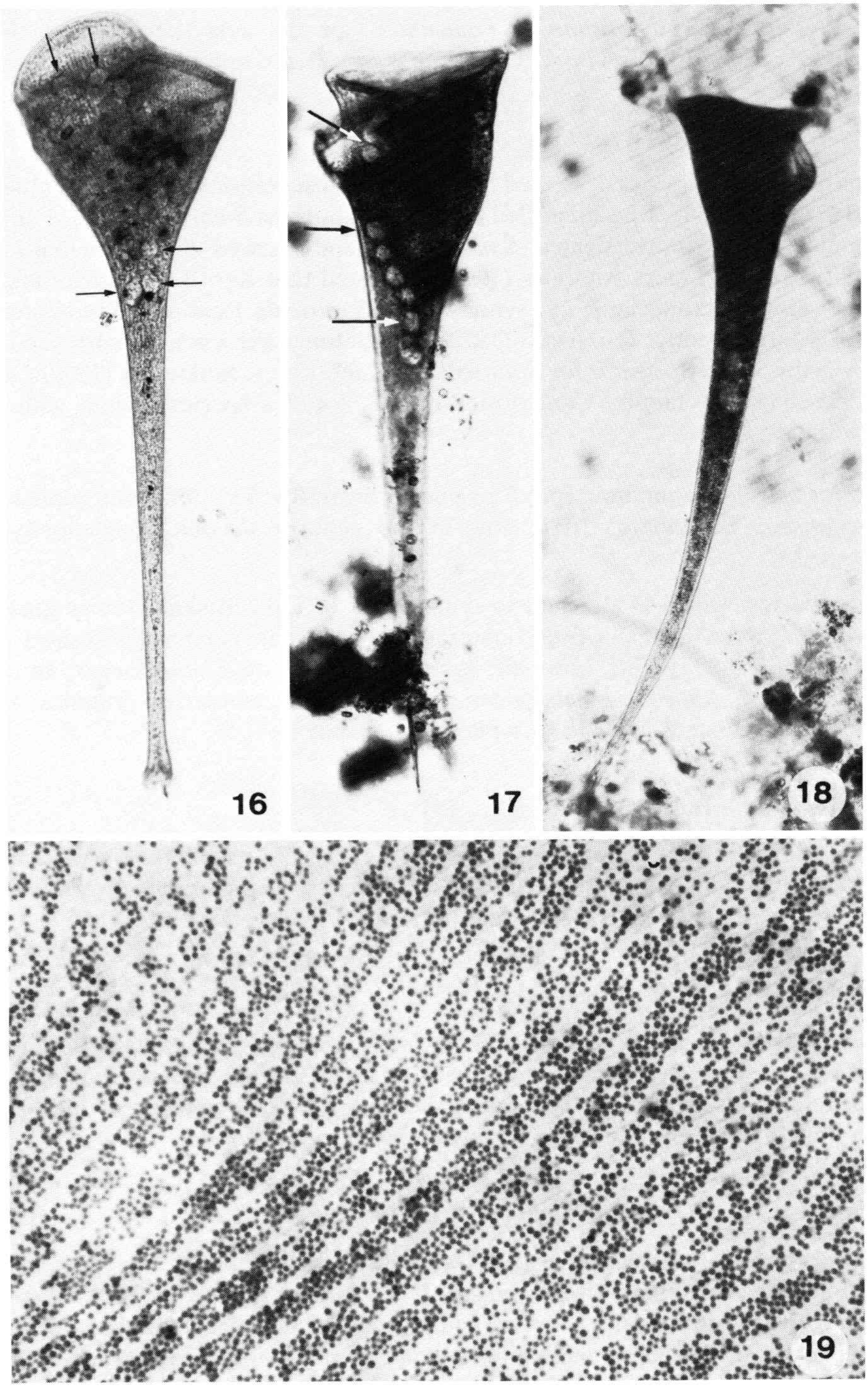
This colourless freshwater species is well defined by its bilobate peristomial bottom, its nodular macronucleus and a thread-like caudal elongation used to anchor the organism at the substrate (Warren, 1985).

Stentor castaneus Wright, 1859

This species, which was found in a freshwater pond of the Edinburgh Botanical Gardens, is very superficially described ('a small species of *Stentor* of a deep chestnut colour which is in the habit of secreting a lorica like that of *S.mülleri*'). We thus follow Stein (1867) in synonymizing it with *S.niger*.

Stentor caudatus Dragesco, 1970 (Figure 12)

This is an African freshwater species which was, however, observed only in an old culture of *Frontonia vesiculosa*. It is rather vaguely separated from *S.muelleri* (shape, absence of lorica and sensory bristles, vacuolated and fibrous cytoplasm), but has a distinctly higher number of macronuclear segments (30–42). We thus keep it separate. This species needs redescription.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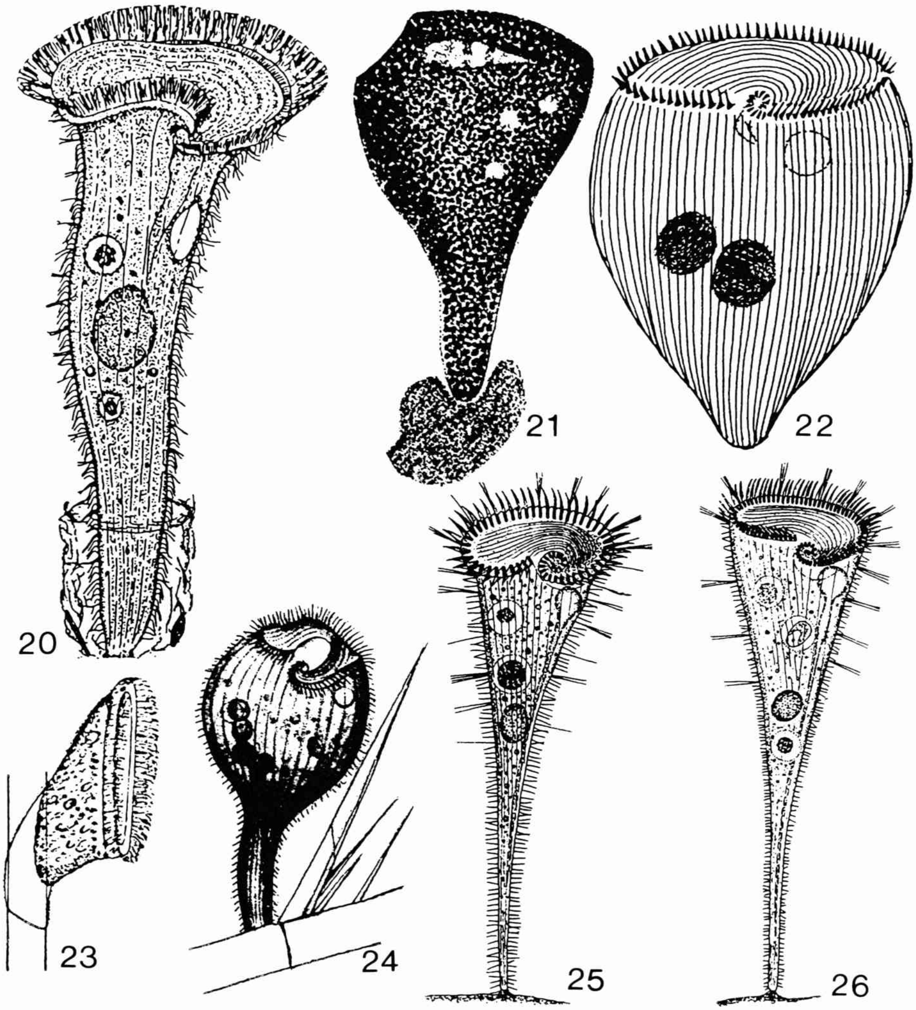
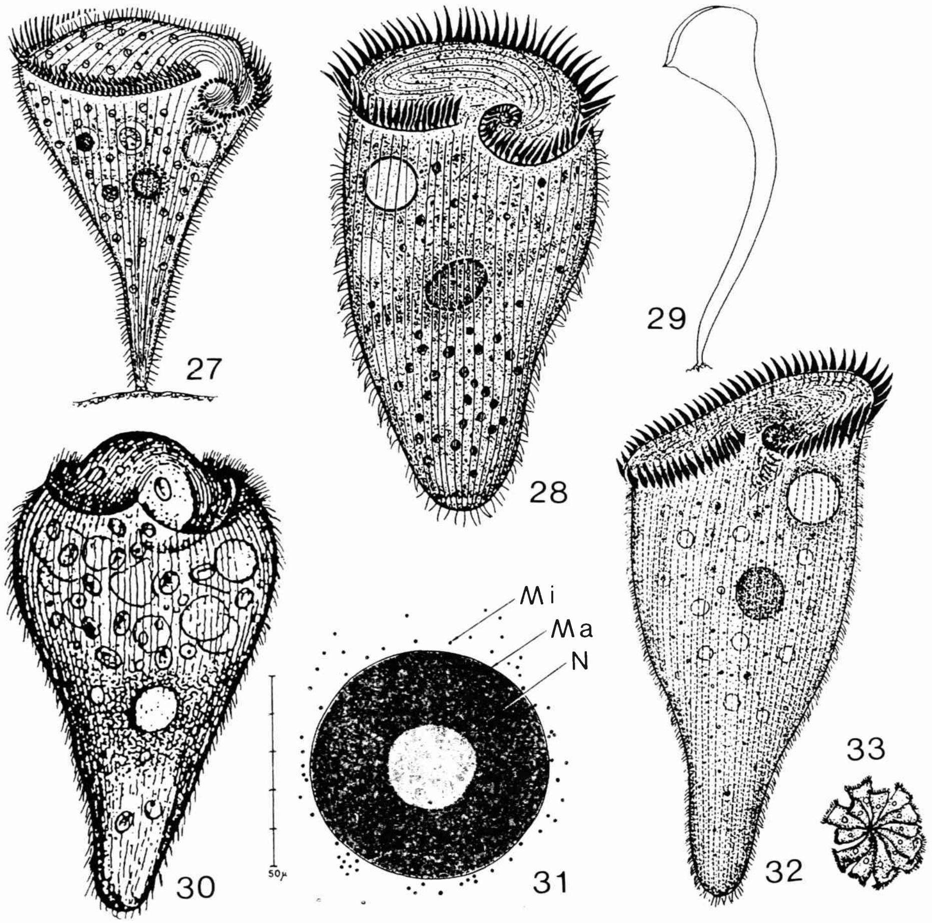


Figs 20–26. Small and medium-sized *Stentor* species with a single or few macronuclear beads (MB). **Fig. 20.** *Stentor multiformis* (from Packroff and Wilbert, 1991), single MB, cortical granules (CG) blueish, no endosymbionts (ES). **Fig. 21.** *Stentor pyriformis* (from Sokoloff, 1930b), 2–4 MB, CG colourless, with ES. **Fig. 22.** *Stentor tartari* (from Nilsson, 1986), two MB, CG purplish red, with ES. **Fig. 23.** *Stentor acrobaticus*, a ciliate of unknown affinity (from Silén, 1948). **Fig. 24.** *Stentor baicalius* (from Gajewskaja, 1933), usually four MB, CG blueish, no ES, distinctly club shaped, attached to crustaceans of Lake Baikal. **Fig. 25.** *Stentor igneus* (from Foissner, 1980), single MB, CG pink to red, no ES. **Fig. 26.** *Stentor elegans* (from Foissner, 1980), single MB, CG colourless, no ES, <100 somatic ciliary rows.

Figs 16–19. *Stentor* species with moniliform macronucleus (arrows). Bright field micrographs of fully or almost fully extended specimens (from Foissner *et al.*, 1992). **Fig. 16.** *Stentor coeruleus.* **Fig. 17.** *Stentor muelleri.* **Fig. 18.** *Stentor polymorphus.* **Fig. 19.** Blue cortical granules of *S.coeruleus.* Clear zones between pigment stripes contain a ciliary row each.



Figs 27–33. Small and medium-sized *Stentor* species with single, spherical macronucleus. **Fig. 27.** *Stentor amethystinus* (from Foissner, 1980), cortical granules (CG) purplish red, with endosymbionts (ES). **Figs 28 and 29.** *Stentor fuliginosus* freely motile and attached [from Dragesco (1966) and after Kawakami (1984), Figure 1], CG brownish, with ES. **Fig. 30.** *Stentor niger* (from Stein, 1867), CG brownish, without ES. **Figs 31–33.** *Stentor multimicronucleatus* freely motile and aggregated (from Dragesco, 1970), CG colourless, no ES, >200 somatic ciliary rows. Ma = macronucleus; Mi = micronucleus; N = central nucleolus.

Stentor coeruleus (Pallas, 1766) Ehrenberg, 1831 (basionym: *Brachionus stentoreus var. coerulei;* Figures 14, 16 and 19)

This large, blueish freshwater species has a moniliform macronucleus and is one of the favourites of the protozoologists. Many basic studies on the physiology and regeneration of ciliates were carried out with *S.coeruleus* and excellently reviewed by Tartar (1961). The morphological and ecological data were summarized by Foissner *et al.* (1992). The species has three synonyms: *S.attenuatus*, *S.sphaericus*, *S.striatus*. Fernández-Leborans and Zaldumbide (1983) reported symbiotic algae in this species. The algae are of the *Chlorella* type, but unusually large: 15 × 12 μm. Unfortunately, no details are provided for the ciliate, whose status thus cannot be evaluated.

Stentor conicum Vuxanovici, 1962

Described from a single, 1400 μm long specimen found in Lake Fundeni near Bucharest. We synonymize it with *S.elegans* (see there).

Stentor deformis Fromentel, 1867

This triangular, brown–yellow species is apparently acontractile, and has one contractile vacuole each in the anterior and posterior third. Size and nuclear apparatus are not indicated. The acontractility indicates that it belongs to another genus; very likely it is a morbid *Frontonia*, possibly *F.elliptica*, as indicated by the two contractile vacuoles. We suggest considering *S.deformis* as a species indeterminata.

Stentor elegans Fromentel, 1867 (Figure 26)

This colourless ('le tégument est blanc, transparent') freshwater species which is, like most of Fromentel's *Stentor* species, not mentioned in Kahl's revision, has an ellipsoid macronucleus. Although differing in some details, *S.conicum* and *S.pallidus* have the same main characteristics (cortical granules colourless, single macronuclear bead, no symbiotic algae) and must thus be synonymized with *S.elegans*. It is a rare species, all authors observed only one or a few specimens. We recently found a single specimen in a clean brook near Salzburg, Austria.

Stentor elongatus Minkéwitsch, 1898

This is apparently a long and slender freshwater species with a roundish macronucleus. Other details are not mentioned. We thus suggest considering *S.elongatus* as a species indeterminata.

Stentor felici Villeneuve-Brachon, 1940

The founder of this taxon did not compare it with species previously described. The most distinctive character mentioned is the yellow colour, all other details match small individuals of *S.muelleri*. However, Villeneuve-Brachon (1940) did not specify a reason for the colour. In our experience, all medium-sized and large, unpigmented Stentors look more or less yellowish or brownish simply because of their thickness. We thus synonymize *S.felici* with *S.muelleri*.

Stentor fimbriatus Fromentel, 1876

This 100 μm long freshwater species has, like dividing or regenerating Stentors, a lateral, lobed protuberance and, occasionally, a second contractile vacuole near the posterior end. Fromentel (1876) saw several such specimens, but does not mention whether in one or several populations. The nucleus is vermiform, the colour is not indicated. In our opinion, this species is a regenerating fragment of *S.roeselii*.

Stentor fuliginosus Forbes, 1891 (basionym: *S.igneus var. fuliginosus*; Figures 28 and 29)

We raise this freshwater variety to species level and rediagnose it as follows: slenderly trumpet shaped and 200–300 μm long when fully extended (see Figure 1 in Kawakami, 1984). Usually one macronuclear bead and several micronuclei. Appears black or black–brown at low magnification due to symbiotic green algae and brownish, yellow–brown or red–orange-coloured cortical and cytoplasmic granules. This diagnosis is based on the poor original description (without figure; size and macronucleus not indicated; pigment granules not described in detail) and on the description of *S.igneus* var. *nigricans* Johnson, 1893, as well as on the much more detailed data of Dragesco (1966) and Kawakami (1984), who identified their populations with *S.niger* which, however, lacks symbiotic algae. Dragesco (1966) studied 1068 specimens and found that 959 had one macronuclear bead, 82 two, 22 three, 3 four and 2 even five pieces. *Stentor fuliginosus* has, according to Dragesco (1966), 64–72 somatic kineties, 24 peristomial ciliary rows and ~140 adoral membranelles. However, a reinvestigation of the original slides, which were kindly supplied by Prof. Dragesco, showed that he greatly underestimated these characters (Table I). Thus, the morphometric characteristics of *S.fuliginosus* are very similar to those of *S.amethystinus*. Synonymy with that species cannot be excluded, although the cortical granules have a slightly different colour and the micronuclei of *S.fulginosus* are never surrounded by pigment granules (Dragesco, 1966, and personal communication), which is corroborated by a micrograph in Kawakami's paper.

Stentor fuscus Fromentel, 1867

All characters mentioned match *S.roeselii*.

Table I. Morphometric characteristics of *Stentor fuliginosus*[a]

Character	$\bar{x}$	M	SD	CV	Min	Max
Body, length	135.4	135.0	16.9	12.5	105	170
Body, width	129.5	129.0	17.8	13.8	105	170
Somatic kineties, number	114.4	115.0	6.3	5.5	105	125
Peristomial kineties, number	27.9	28.0	3.4	12.0	23	35
Adoral membranelles, number	279.5	265.0	33.3	11.9	240	340
Macronucleus, length	28.0	28.0	3.7	13.4	23	35
Macronucleus, width	25.2	25.0	2.2	8.7	22	28
Micronuclei, diameter	1.2	1.2	0.2	20.2	1	1.8

[a] All data are based on the investigation of 11 randomly selected, protargol silver-impregnated non-dividers from the field. Slides were kindly supplied by Prof. J.Dragesco. All measurements are in μm. Abbreviations: CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; SD = standard deviation; $\bar{x}$ = arithmetic mean.

Stentor gallinulus Penard, 1922

Name suggested by Penard (1922) for the freshwater form of *S.multiformis* if further research proves that it is different from the marine variety.

Stentor globator Stokes, 1885

A small (85 μm), spherical freshwater organism with two contractile vacuoles at the posterior end where a tail-like prolongation used to anchor the cell at the substrate temporarily appears. No data are available on the nuclear apparatus, the colour and the number of specimens observed. We agree with Kahl (1932) that this is a doubtful species, very likely a regenerating *Stentor* fragment. In the absence of newer records, we suggest considering *S.globator* as a species indeterminata.

Stentor igneus Ehrenberg, 1838 (Figure 25)

This small, reddish-pigmented freshwater species is well defined due to the redescriptions by Foissner (1980) and Song and Wilbert (1989). Foissner *et al.* (1992) reviewed the data available on its morphology and ecology. *Stentor igneus* lacks symbiotic algae and has two synonyms: *S.roseus* and *S.ruber*. For nomenclature, see Foissner (1987). Schulze (1951) mentions a *S.igneus* with symbiotic green algae. Unfortunately, the taxonomic status of this population remains obscure since no morphological data on the ciliate were provided.

Stentor igneus var. nigricans Johnson, 1893

We synonymize this variety with *S.fuliginosus* (see there).

Stentor introversus Tartar, 1958 (Figure 15)

This species matches most characters of *S.coeruleus*. It is, however, smaller [450 μm, up to 580 μm, according to Jones (1974); weak character] and the entire zone of adoral membranelles cannot only contract, but also retract. We recognize this form as a distinct species because heteroplastic graft combinations between *S.introversus* and *S.coeruleus* did not survive (Tartar, 1958), and because Tartar was an expert on *S.coeruleus*, making it unlikely that he was mistaken.

Stentor katashimai Kumazawa, 1973

This species has the main characteristics of *S.muelleri*, from which it is said to differ by the lack of a lorica, a more stocky shape and the possession of a buccal pouch (Kumazawa, 1974). These characters are clearly insufficient and *S.katashimai* is thus synonymized with *S.muelleri*.

Stentor loricatus nom. corr. Bary, 1950 (basionym: *S.loricata*; Figure 9)

This is a well-defined, medium-sized *Stentor* found attached to leaves and twigs in a small stream of New Zealand. Its dark green pigment granules are odd, but occur also in some hypotrich ciliates (Berger and Foissner, 1989).

Stentor magnus Kumazawa, 1973

This species has the main characteristics of *S.roeselii*, from which it is said to differ by the lack of a lorica and in body shape and proportions, as well as in the arrangement of the sensory bristles (Kumazawa, 1974). These characters are clearly insufficient and *S.magnus* is thus synonymized with *S.roeselii*.

Stentor muelleri Ehrenberg, 1831 (Figures 11 and 17)

A detailed description and discussion of synonymy, morphology and ecology can be found in Foissner *et al.* (1992). This freshwater species is well defined by its moniliform macronucleus and the absence of pigmented cortical granules. It has ~30–50 somatic kinetics and ~10 peristomial ciliary rows. *Stentor muelleri* has two junior synonyms: *S.felici* and *S.katashimai*.

Stentor multimicronucleatus Dragesco, 1970 (Figures 31–33)

This medium-sized, African freshwater species is well characterized by its 52–142 micronuclei which surround a conspicuously large macronuclear mass.

Stentor multiformis (Müller, 1786) Ehrenberg, 1838 (basionym: *Vorticella multiformis*; Figure 20)

A detailed description and discussion of synonymy, morphology and ecology can be found in Foissner *et al.* (1992). This is a small, blueish species occurring in marine, freshwater and terrestrial biotopes. It is, however, still uncertain whether the marine and freshwater populations are truly conspecific. In the absence of detailed evidence, we follow Stein (1867) and Kahl (1932), who assume conspecificity. This species is sparingly mentioned in faunal lists, although it is rather frequent (Schuberg, 1896; Foissner *et al.*, 1992); possibly it has often been mistaken for small individuals of *S.coeruleus*, *Stentor multiformis* has 34–45 somatic kineties, 6–9 peristomial ciliary rows and 100–150 adoral membranelles (Packroff and Wilbert, 1991). Two junior synonyms are known: *S.gallinulus* and *S.nanus*.

Stentor nanus Fromentel, 1876

The blueish colour, the ellipsoid macronucleus and the small size (50 μm) clearly indicate synonymy with *S.multiformis*, as also suggested by Penard (1922).

Stentor niger (Müller, 1773) Ehrenberg, 1831 (basionym: *Vorticella nigra;* Figure 30)

A detailed description and discussion of synonymy, morphology and ecology can be found in Foissner *et al.* (1992). This medium-sized, mononucleate freshwater

Stentor differs from *S.amethystinus* and *S.fuliginosus*, with which it has probably often been confused, mainly by the lack of symbiotic algae. This has been independently observed by Stein (1867) and Kahl (1932), and must thus be acknowledged as a main species character and difference from *S.amethystinus* and *S.fuliginosus*. *Stentor niger* has two junior synonyms: *S.castaneus* and *S.pediculatus*. *Stentor niger* sensu Dragesco (1966, 1970) and sensu Kawakami (1984) belong to *S.fuliginosus*.

Stentor oligonucleatus Sokoloff, 1930b

This species, which Sokoloff (1930a) first considered as a variety of *S.viridis*, very much resembles *S.tartari* in size, shape and nuclear apparatus, and is thus not a junior synonym of *S.polymorphus*, as suggested by Kahl (1932). It differs from *S.tartari*, *S.amethystinus*, *S.fuliginosus* and *S.nigra* by its colourless cortical granules. This, however, suggests synonymy with *S.pyriformis*, a species not mentioned in Kahl's revision. Nomenclature: described as species nova also by Samano and Sokoloff (1931).

Stentor pediculatus Fromentel, 1876

This small (250 μm), mononucleate, brown freshwater species is characterized by minute, V-shaped processes with which it attaches to the substrate. Such processes also occur in other species [e.g. *S.polymorphus*, Figure 16 in Foissner *et al.* (1992)] and are indeed a genus character (Andrews, 1945; Tartar, 1961). We thus agree with Kahl (1932), who synonymizes *S.pediculatus* with *S.niger*.

Stentor polymorphus (Müller, 1773) Ehrenberg, 1830 (basionym: *Vorticella polymorpha*; Figures 13 and 18)

A detailed description and discussion of morphology and ecology can be found in Foissner *et al.* (1992). *Stentor polymorphus* is well defined by its symbiotic algae and colourless cortical granules; it has no junior synonyms.

Stentor pygmaeus Swarczewsky, 1929

See *S.baicalius*.

Stentor pyriformis Johnson, 1893 (Figure 21)

This is a well-defined species overlooked by Kahl (1932). It even has a junior synonym: *S.oligonucleatus*.

Stentor roeselii Ehrenberg, 1835 (Figures 2–5, 7 and 8)

A detailed description and discussion of synonymy, morphology and ecology can be found in Foissner *et al.* (1992). This colourless and common freshwater species is highly variable (Dragesco, 1970) and thus has many synonyms: *S.fimbriatus*, *S.fuscus*, *S.gracilis*, *S.magnus*, *S.roeseli* f. *stagnalis*, *S.viridis*.

Stentor roeselii has ~40–80 somatic kineties, 14–42 peristomial ciliary rows and >150 adoral membranelles.

Stentor roeseli forma stagnalis Jirovec et al., 1953

This variety differs from the type by its paint brush-shaped holdfast, used to anchor it in the mud of polluted rivers. In our opinion, this character is insufficient to establish new species or varieties (cp. *S.pediculatus*).

Stentor roseus Fromentel, 1876

All characters mentioned match *S.igneus*.

Stentor ruber nom. corr. Bary, 1950 (basionym: *S.rubra*)

Bary distinguished this species from *S.igneus* by small shape differences, which we consider insufficient.

Stentor sphaericus Vuxanovici, 1961b

This poorly described species is very likely based on morbid specimens of *S.coeruleus* which occurred at the same site (Lake Fundeni, near Bucharest). This is also indicated by its small size (80–250 μm), the globular shape and moniliform macronucleus. The colour of the cortical granules is not mentioned; cytoplasm is said to be green–grey.

Stentor striatus Maskell, 1886

We agree with Kahl (1932) that this freshwater species is a junior synonym of *S.coeruleus*. Maskell (1886) did not compare his new species with those described earlier. Kahl (1932) cites this species as '*S.striatus* Barraud-Maskell, 1886'. However, Barraud only collected the species and is not the author of the paper.

Stentor tartari Narayana Murthy and Kasturi Bai, 1974 (Figure 22)

This freshwater species from Bangalore (India) is well defined by its two macronuclear beads, the reddish colour and the symbiotic green algae. It has two synonyms: *S.andreseni* and *S.igneus* sensu Johnson (1893).

Stentor viridis Ghosh, 1921

We agree with Kahl (1932) that this yellowish freshwater species from Calcutta is a junior synonym of *S.roeselii*. The characteristics mentioned by Ghosh (1921) are insufficient, namely size, lack of sensory bristles and lorica (cp. *S.magnus*), and yellow colour (cp. *S.felici*).

Key to *Stentor* species

The key uses simple characters easily recognizable with an ordinary light

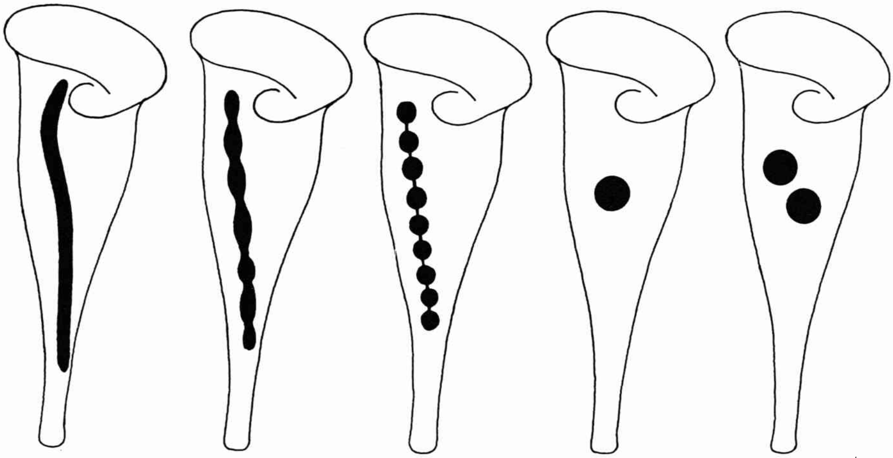


Fig. 34. Macronucleus types in *Stentor*.

microscope in unstained cells, i.e. silver impregnation is not necessary (but useful). For a correct identification it is, however, essential to study live cells because the colour of the cortical granules may change in specimens fixed with formalin or other chemicals. Shape and macronuclear characters used are explained in Figures 1 and 34.

1 (2) With symbiotic green algae 2
– Without symbiotic green algae 7
2 (1) Cortical granules colourless. Cells appear green, brownish or whitish at low magnification and to the naked eye 3
– Cortical granules pigmented. Cells appear black, blue, purplish red, brown or red–orange-coloured at low magnification and to the naked eye 4
3 (2) Macronucleus moniliform, usually consisting of >10 connected beads forming a pearl necklace-like figure. Slenderly trumpet shaped and up to 2 mm long when fully extended. Very likely cosmopolitic and mainly in freshwater .... *S.polymorphus* (Figures 13 and 18)
– Macronucleus consists of two (rarely one, three, four or five) isolated beads. Broadly trumpet shaped and up to 700 μm long when fully extended. Known from freshwaters of North America and Mexico .... *S.pyriformis* (Figure 21)
4 (2) Macronucleus vermiform to slightly nodular. Cortical granules blue–green. Broadly vase to trumpet shaped, 100–230 × 80–130 μm. Known from South America only; probably euplanktic.............................. .... *S.araucanus* (Figures 35–48)
– Macronucleus consists of one or several isolated beads 5

5 (4) Usually one (rarely up to five) spherical to ellipsoid macronuclear bead 6

– Usually two (rarely three) isolated macronuclear beads. Cortical granules purplish red. Broadly trumpet shaped, ~320 × 140 μm. Recorded from India (Bangalore) and Africa (Kenya) .... *S.tartari* (Figure 22)

6 (5) Cortical granules lilac or amethystine coloured or purplish red, surround also micronuclei. Broadly trumpet shaped, 250–500 μm (rarely up to 800 μm) long when fully extended. Known from freshwaters of Europe, North America and tropical Africa (Cameroons) .... *S.amethystinus* (Figures 6 and 27)

– Cortical granules yellowish brown, brownish or red–orange coloured, do not surround micronuclei. Broadly to slenderly trumpet shaped and 200–300 μm long when fully extended. About 10% of specimens have 2–5 macronuclear beads. Known from freshwaters of North America, Japan and tropical Africa (Gabon) ... *S.fuliginosus* (Figures 28 and 29)

7 (1) Without symbiotic green algae. Cortical granules colourless. Cells appear brownish, yellowish or whitish at low magnification and to the naked eye 8

– Without symbiotic green algae. Cortical granules pigmented. Cells appear dark, blueish, greenish, reddish or brownish at low magnification and to the naked eye 13

8 (7) Macronucleus moniliform or vermiform 9

– Macronucleus a single bead 12

9 (8) Macronucleus distinctly moniliform 10

– Macronucleus vermiform or nodular 11

10 (9) 10–20 macronuclear beads. Slenderly trumpet shaped and 500–1000 μm (rarely up to 3 mm) long when fully extended. Mainly in freshwater, but also in estuaries. Recorded from Europe, North America and China .... *S.muelleri* (Figures 11 and 17)

– 30–42 macronuclear beads. Broadly trumpet shaped and 450–1000 μm long when fully extended, posterior end elongated tail like. Known from tropical freshwaters only (Cameroons) .... *S.caudatus* (Figure 12)

11 (9) Peristomial bottom of usual structure. Macronucleus vermiform (in contracted cells more or less distinctly coiled and nodular). Slenderly trumpet shaped and 500–1200 μm (rarely up to 3 mm) long when fully extended. Very likely cosmopolitic and mainly in freshwater .... *S.roeselii* (Figures 2–5, 7 and 8)

– Peristomial bottom bilobate, i.e. with two small wings. Macronucleus nodular. Slenderly trumpet shaped, 1000 × 180 μm in size when fully extended. Anchored with long (up to 500 μm), cord-like tail at base of conspicuous, cylindrical lorica. Known from European rivers only .... *S.barretti* (Figure 10)

12 (8) Macronuclear bead conspicuously large, 45–62 μm, surrounded by 52–142 tiny (~1 μm) micronuclei. Broadly trumpet shaped and 500–900 μm long when fully extended. Known from tropical Africa

(Cameroons and Butare, Central Africa; J.Dragesco, personal communication) only .... *S.multimicronucleatus* (Figures 31–33)

– Macronuclear bead ≤40 μm in diameter, possibly only one (or few) micronucleus. Slenderly trumpet shaped and 200–1300 μm long when fully extended. Known from central and eastern Europe freshwaters only .... *S.elegans* (Figure 26)

13 (7) Without symbiotic algae. Cortical granules pigmented. Macronucleus moniliform or vermiform 14

– Macronucleus a single bead 17

14 (13) Macronucleus moniliform 15

– Macronucleus vermiform. Cortical granules dark green. Slenderly trumpet shaped, 625–1150 × 140–240 μm when fully extended. Known from type location only, namely a small freshwater stream in New Zealand .... *S.loricatus* (Figure 9)

15 (14) Usually 4–6 macronuclear beads. Attached to crustaceans of Lake Baikal. Cortical granules sea green. Distinctly club shaped, 175–350 μm long .... *S.baicalius* (Figure 24)

– 6–38 (usually >10) macronuclear beads. Distinctly blue–green and usually not attached to other animals 16

16 (15) Cortical granules blue–green. Slenderly trumpet shaped, usually 1000–2000 μm (up to 4 mm) long. Very likely cosmopolitic and mainly in freshwater .... *S.coeruleus* (Figures 14, 16 and 19)

– Cortical granules blue–green. Broadly trumpet shaped, ~450 μm when fully extended. Adoral zone of membranelles not only contractable (as usual), but also retractable, so that when resting or irritated the anterior end of the cell is conspicuously recessed and surrounded by a border of recurved ectoplasm somewhat scalloped. Known from type locality, an impounded freshwater goose pond on the eastern shore of Willapa Bay in the southwest corner of the state of Washington, and from an estuary in Alabama .... *S.introversus* (Figure 15)

17 (13) Macronucleus a single bead. Cortical granules not pink or red........ 18

– Macronucleus a single bead. Cortical granules pink or brick red. Slenderly trumpet shaped and 100–400 μm (usually ~250 μm) long when fully extended. Very likely cosmopolitic and mainly in freshwater .... *S.igneus* (Figure 25)

18 (17) Macronucleus a single bead. Cortical granules azure to sea green. Slenderly trumpet shaped and 200–500 μm (usually ~250 μm) long when fully extended. Freshwater, marine and even in terrestrial biotopes. Very likely cosmopolitic .... *S.multiformis* (Figure 20)

– Macronucleus a single bead. Cortical granules rusty brown to brownish. Cells appear yellowish, brownish or blackish to the naked eye and at low magnification. Broadly trumpet shaped and 200–350 μm long when fully extended. Reliably recorded from European freshwaters only .... *S.niger* (Figure 30)

Description of new species

Stentor araucanus nov. spec. (Figures 35–48, Tables II and III)

Methods used for studying live and prepared cells are described in Foissner (1991). Only formalin-fixed specimens were available for silver impregnation, which was performed with silver carbonate. The quality of the impregnation was not excellent, but sufficient to recognize some details, e.g. the number of somatic and peristomial kineties.

Diagnosis. Size *in vivo* 100–270 × 80–200 μm, broadly vase to trumpet shaped. Macronucleus vermiform to slightly nodular. Cytoplasm with symbiotic green algae. Cortical granules blue–green. Sixty-six somatic kineties, 10 peristomial ciliary rows and ~150 adoral membranelles on average.

Type location. Plankton of Lake Pirehueico, South Chile, 71°48′W, 39°56′S.

Type specimens. Not available because silver impregnation was too mediocre for preparing permanent slides.

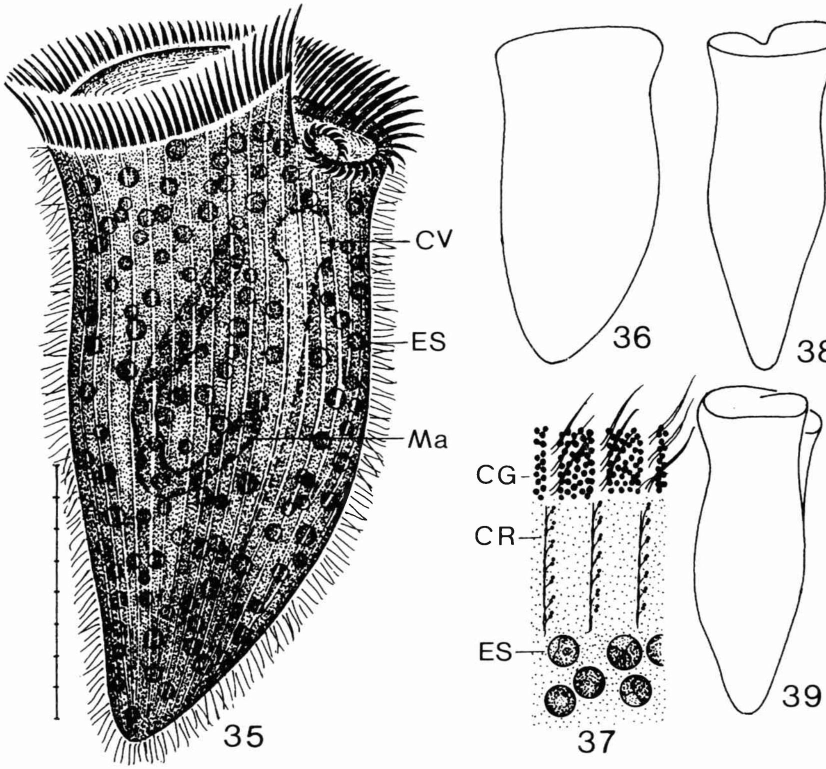
Etymology. 'Araucanus' refers to the native inhabitants of South Chile. Araucania is also a province in Chile and the name of a genus of lofty coniferous trees native to the southern hemisphere.

Description. Morphometric data shown in Table II are not repeated in this section. Freely motile specimens usually ~230 × 130 μm in size, starving cells became considerably smaller, ~100–150 × 80 μm. Only slightly contractile. Motile stage vase shaped to broadly turbinate, asymmetrical because flattened ventrally and bulging dorsally (Figures 35, 36, 38, 39, 41 and 42). Macronucleus vermiform to slightly nodular, usually in middle third of cell, 10–15 μm in diameter, shape highly variable, often horseshoe like, not covered by pigment granules. Up to 24 micronuclei with a diameter of 1.8–2.5 μm surround macronucleus (Figures 40 and 43). Contractile vacuole as in other members of genus. Cortical granules intensively blue–green, very similar to those of *S.coeruleus*, *in vivo* 0.8–1.2 μm in diameter, in formalin-fixed material 1–1.5 μm, arranged in distinct stripes between somatic kineties (Figures 35, 37, 45, 47 and 48). Cells appear as dark spots to the naked eye and blueish green in the dissecting microscope. Cytoplasm of all specimens and populations examined with symbiotic algae of the *Chlorella* type, i.e. having a green, cup-shaped chloroplast and producing four offspring during division. Symbionts spherical to slightly ellipsoid, 3–8 μm (usually 4–6 μm) in diameter, size and number (580–2300 per ciliate; Table III) depending on season (Figures 37, 44 and 46). In nature, probably feeding on various algae; in the laboratory, ingestion of long bacterial rods was observed. Swims rather slowly, ~2–3 times its length per second, by clockwise rotation (if viewed from anterior pole) about its longitudinal axis. Never attached to walls and natural sediment (vulcanic grains) in aquaria. Thus, *S.araucanus* is probably euplanktic; it has, however, a patch of

Table II. Morphometric characteristics of *Stentor araucanus*[a]

Character	Method	$\bar{x}$	M	SD	CV	Min	Max	n
Body, length	*in vivo*	208.6	216	20.8	10.0	176	235	9
Body, width	*in vivo*	147.0	157	28.3	19.2	90	176	9
Body, length	formalin 2%	177.4	180	22.3	12.6	126	220	50
Body, width	formalin 2%	139.6	140	16.3	11.7	108	180	50
Body, volume ($\times 10^6$ μm^3)	formalin 2%	1.8	1.7	0.6	32.0	1	3.4	50
Body, length	Lugol	176.3	180	19.3	11.0	90	250	85
Body, width	Lugol	119.7	118	12.1	10.2	90	160	85
Body, volume ($\times 10^6$ μm^3)	Lugol	1.3	1.3	0.4	28.2	0.4	2.3	85
Symbiotic algae, diameter	formalin	5.8	6	0.5	1.4	5	6.5	32
Cilia, length	silver impregnated	9.9	10	0.9	9.6	8	11	14
Somatic kineties, number	silver impregnated	65.9	66	3.7	5.6	60	71	19
Peristomial kineties, number	silver impregnated	10.5	10	1.9	17.7	8	15	16

[a]All data are based on the investigation of randomly selected non-dividers from the field. All measurements are in μm. Abbreviations: CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of cells investigated; SD = standard deviation; $\bar{x}$ = arithmetic mean.



Figs 35–39. *Stentor araucanus* from life. **Fig. 35.** Right lateral view of freely motile specimen. Scale bar division 10 μm. **Fig. 36.** Dorsal view of freely motile specimen. **Fig. 37.** Surface view of cortex and cytoplasm. **Figs 38 and 39.** Dorsal and lateral view of freely motile, vase-shaped specimen. CG = cortical granules; CR = ciliary rows; CV = contractile vacuole; ES = endosymbiotic algae; Ma = macronucleus.

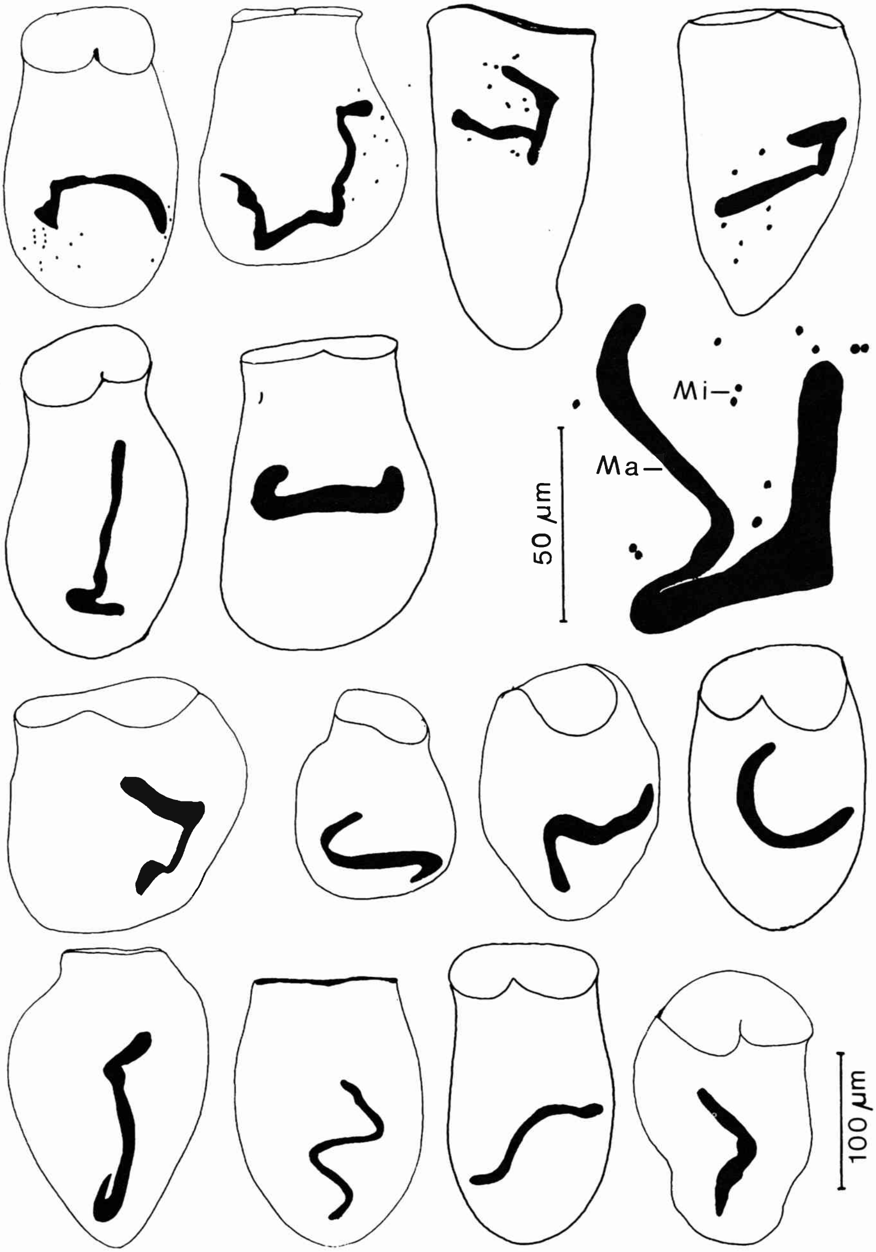


Fig. 40. DAPI-stained *S.araucanus* cells showing variability of nuclear apparatus.

Table III. Ecogram of *Stentor araucanus*[a]

Parameter	Minimum	Maximum	Number of observations
Abundance l^{-1}	1	772	205
Depth (m)	0	50	205
Number of symbiotic algae per cell	579	2260	187
pH	6.8	8.4	annual ranges
O_2 (mg l^{-1})	7.5	12.2	annual ranges
°C	6.5	20.0	annual ranges

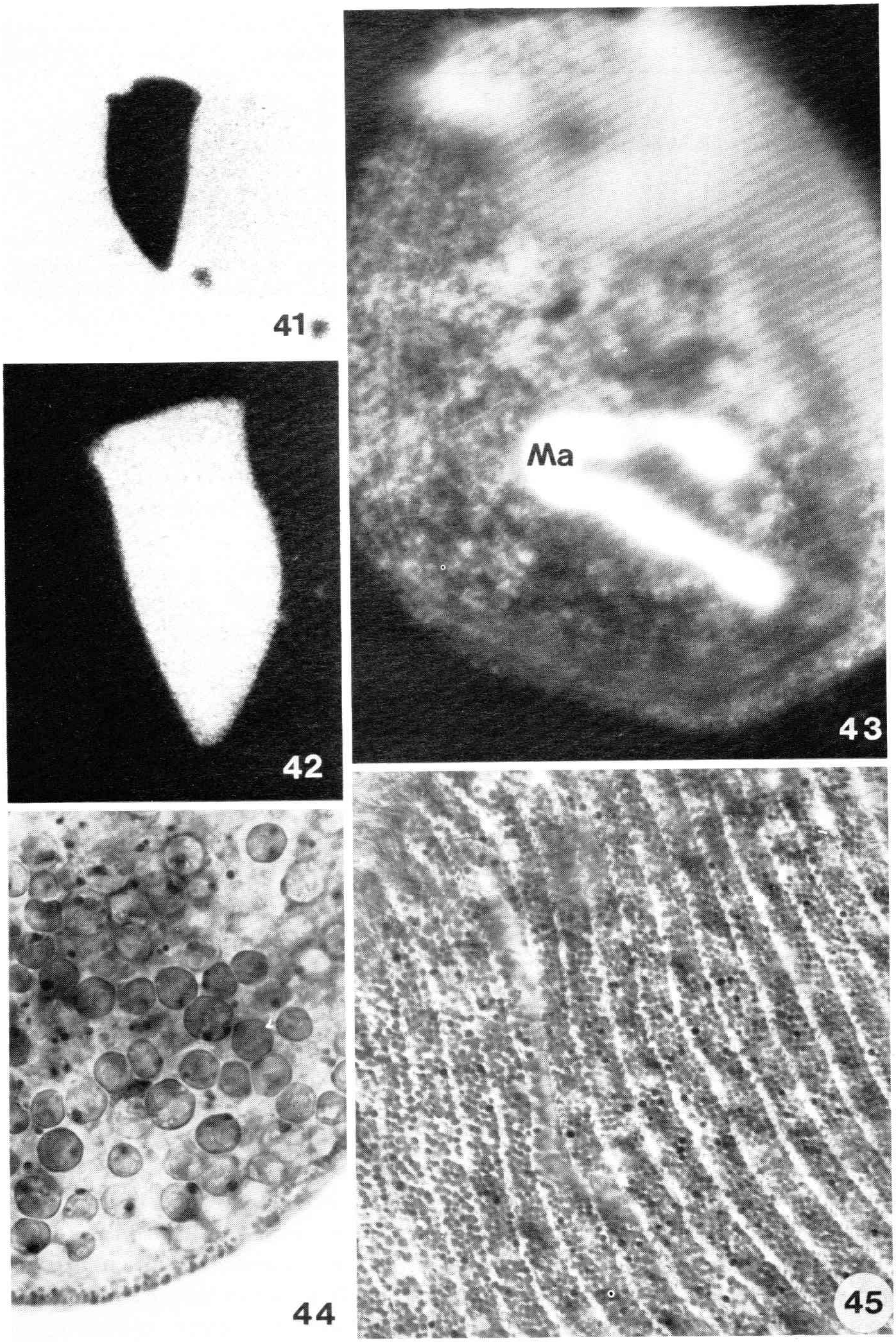
[a]Values include sewage-contaminated sites. Physicochemical data were kindly supplied by F.Pedrozo, Universidad Nacional del Comahue, Argentina, and H.Campos, Universidad Austral de Chile, Chile.

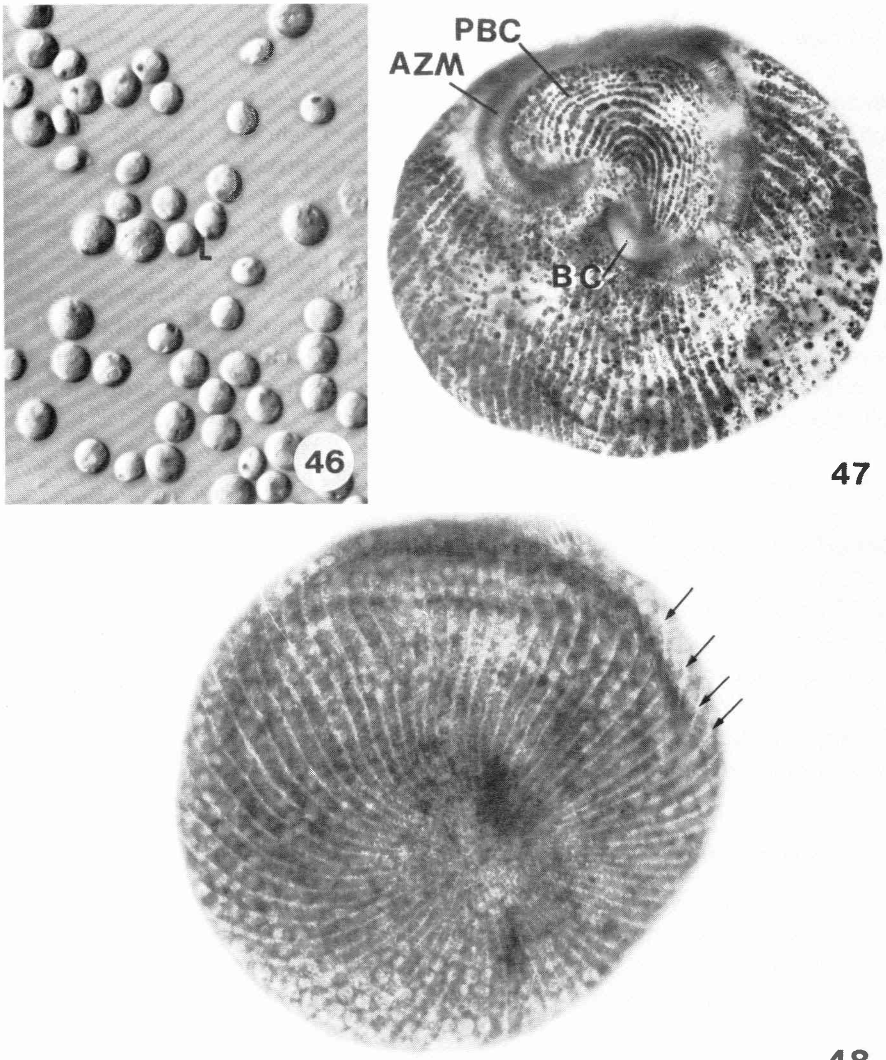
disordered basal bodies at its posterior end, indicating the presence of a holdfast organelle.

Somatic and oral infraciliature as in other small members of the genus, e.g. *S.amethystinus* (Foissner *et al.*, 1992) and *S.fuliginosus* (Dragesco, 1966).

Ecology and geographic distribution. The type location is a small (30.4 km^2, maximum depth 145 m), warm-temperate, oligotrophic andine lake 586 m above sea level (for details see Campos *et al.*, 1978). However, *S.araucanus* has also been found by the junior author in several other araucanian and patagonian lakes in southern Chile and Argentina (Lake Galletue, Villarica, Maihue, Rupanco, Llanquihue, Nahuel Huapi, Gutiérrez, Moreno, Vintter). Furthermore, Thomasson (1963) and Modenutti (1988) observed in many North Patagonian lakes 'an abundance of small black spots, i.e. *Stentor* specimens with a positive phototropism in the vials'. Daday (1902) and Löffler (1961) report mass occurrence of *Stentor coeruleus* in some of the lakes mentioned above. Our results suggest that it was *S.araucanus*. However, it cannot be excluded that at least some of these records relate to *S.amethystinus*, which we found several times coinhabiting the same lakes as *S.araucanus*. It seems possible that *S.araucanus* is restricted to South America, or at least to Gondwanian areas, because a similar species has never been recorded from the much better studied Laurasia.

The known autecological data for *S.araucanus* are summarized in Table III; a more detailed account will be published by the junior author. *Stentor araucanus* occurs preferentially in spring (October, November) and in the euphotic zone between a depth of 5 and 10 m. It shows positive phototropism and is eagerly eaten by *Mesocyclops longisetus*. Its abundance is usually higher in the coastal areas than in the lake centre. All lakes where we observed *S.araucanus* were (ultra)-oligotrophic; however, we found it also in sewage-contaminated coastal bays of Lake Nahuel Huapi. The numbers in these areas never exceeded the maximum number found in the non-contaminated lake centre, indicating that *S.araucanus* does not react positively to nutrient increase. It probably prefers, or at least tolerates, nutrient-poor conditions, possibly using its symbiotic algae or their metabolic products as an additional energy source.


41
42
Ma
43
44
45



Figs 46–48. *Stentor araucanus* (formalin fixed). **Fig. 46.** Endosymbiotic green algae. **Figs 47** and **48.** Anterior and posterior polar views showing striation caused by cortical pigment granules. Clear, white zones (arrows) contain ciliary rows. AZM = adoral zone of membranelles; BC = buccal cavity; PBC = ciliary rows and pigment stripes on peristomial bottom.

Figs 41–45. *Stentor araucanus.* **Figs 41 and 42.** Left lateral and dorsal view of freely motile specimens. **Fig. 43.** DAPI-stained macronucleus (Ma). **Fig. 44.** The cytoplasm contains many endosymbiotic green algae. **Fig. 45.** Formalin-fixed cell showing cortical stripes composed of narrowly spaced, blue granules (cp. Figure 37).

Condylostoma wangi nov. spec.

1934 *Stentor auriculatus* Kahl–Wang, C.C., *Rep. Mar. Biol. Assoc. China*, **3**, 59.

Diagnosis. Size *in vivo* 300 × 136 μm, slightly contractile. Body coloured dark green by symbiotic green algae (zoochlorellae), shortly trumpet shaped or turbinate when extended. Peristomial field greatly broadened, sometimes equal to or even exceeding height of body, which tapers very abruptly towards posterior extremity or point of attachment; interrupted on ventral side by deep groove or cleft which leads into a well-defined cytopharynx and gives the entire structure a bilobate or auriculate appearance. Pellicle finely ciliated and striated in longitudinal rows, striation on peristomial border more distinctly marked than those on body. Adoral zone of membranelles conspicuous. Macronucleus moniliform, consists of 18–20 nodules extending almost through entire length of cell. Contractile vacuole not observed.

Type location. Bay of Amoy, China. Attached on hydroids.

Remarks. The diagnosis is based on the data given by Wang (1934). This species is clearly different from *Stentor auricula* Kent, 1881 and *S. auriculatus* Kahl, 1932, which also belong to the genus *Condylostoma*, but lack symbiotic algae (cp. Gruber, 1884; Daday, 1886; Fauré-Fremiet, 1936). There is only one other *Condylostoma* species which has symbiotic algae: *C. tenuis* Fauré-Fremiet, 1958. It is easily distinguished from *C. wangi* by its very slender shape (200–400 × 26–30 μm) and the symbionts, which have short flagella and possibly belong to the genus *Chlamydomonas*.

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