Stentor

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Secondary article

Article Contents

Stentor, the trumpet animalcule, is a single-celled organism (protist) belonging to the ciliates (Ciliophora). It is interesting because of its trumpet shape, commonness, comparatively large size ($\sim$1 mm), attractive coloration and high regeneration capacity.

Introduction

Stentors were already described and figured by the pioneers of microscopy and protist research, viz., Antony van Leeuwenhoek (1632–1723), Otho Fridericus Müller (1730–1784), and Christian Gottfried Ehrenberg (1795–1876). However, it was only in 1815 that Oken formally recognized these organisms as a distinct group and named it '*Stentor*' (Oken, 1815). *Stentor* was the name of a Greek warrior in the Trojan war, whose voice was as powerful as fifty voices of other men. Oken indicated with the name the conical shape of the organism; later, stentors became familiar as 'Trompetentierchen' (trumpet animalcule) in the German and English speaking world. (*See* Leeuwenhoek, Antoni van)

Stentor is one of the largest protozoans known. This and its ability to contract and regenerate from minute pieces attracted not only many scientists but also ordinary people. Thus, a huge literature accumulated between 1830 and 1960. The knowledge culminated in 1961, when Tartar's *The Biology of Stentor* was published, an excellent, still highly valuable monograph summarizing and critically evaluating the data available. However, since then scientists have preferred other ciliates, mainly *Paramecium*, *Tetrahymena* and some hypotrichs, as model organisms, because they are more easily cultivated, maintained and prepared than *Stentor*; accordingly, the leading role of *Stentor* in protozoan biology has decreased. Now it is mainly limnologists that are interested in *Stentor* because it sometimes contributes significantly to the energy flux in lakes and ponds. (*See Paramecium*; *Tetrahymena*; Protozoa)

Brief Description and Taxonomic Assignment

Stentor belongs, according to its morphology and gene sequences, to the heterotrich ciliates, whose main features are a large, right-spiralled adoral zone of membranelles and a special arrangement of the fibres associated with the basal bodies of the cilies (Baroin-Tourancheau *et al.*, 1992; Foissner *et al.*, 1992).

Nineteen *Stentor* species are presently recognized (Foissner and Wölfl, 1994). They differ mainly in the presence/absence of symbiotic green algae (zoochlorellae), the shape of the macronucleus and the colour of the cortical pigment granules (**Figures 1**, **2** and **3**). The common species can be cultivated in defined media; axenic cultures have not yet been established. However, *Stentor* is often so abundant and constant in certain ponds and rivers that sufficient material is available at any time. (*See* Protozoan Taxonomy and Systematics)

Stentors are medium-sized (100 μm) to very large (up to 4 mm) ciliates, which basically are sessile via a posterior holdfast organelle secreting a sticky substance and, in some species, also a mucilaginous lorica. Although occasionally freely motile for part of the time, euplanktonic species occur rarely, if at all. The body is moderately to highly contractile due to nonactin microfilaments, which form small bundles, the so-called myonemes. When fixed and extended, the body is, depending on species, slenderly to broadly trumpet shaped, i.e. broadly expanded anteriorly, tapering off and attenuated towards the attached posterior

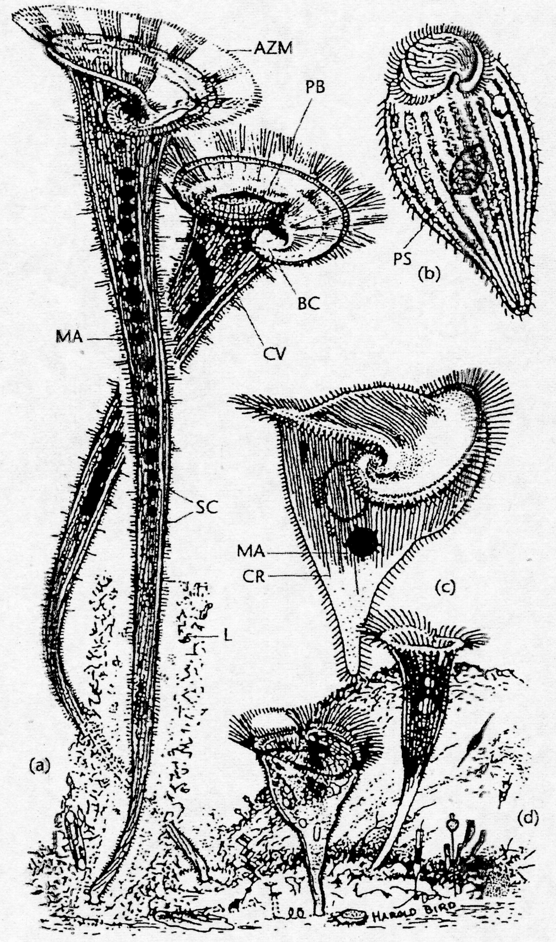

Figure 1 A *Stentor* assemblage showing the main shape and macronucleus types (from Curds *et al.* (1983), modified). (a) Large (1–4 mm), slenderly trumpet-shaped species with a vermiform and a moniliform macronucleus, respectively. (b) Freely motile, turbinate specimen with coloured pigment stripes. (c) Small to medium-sized (100–1000 μm), broadly trumpet-shaped species with single, spherical macronucleus. (d) Campanulate species.

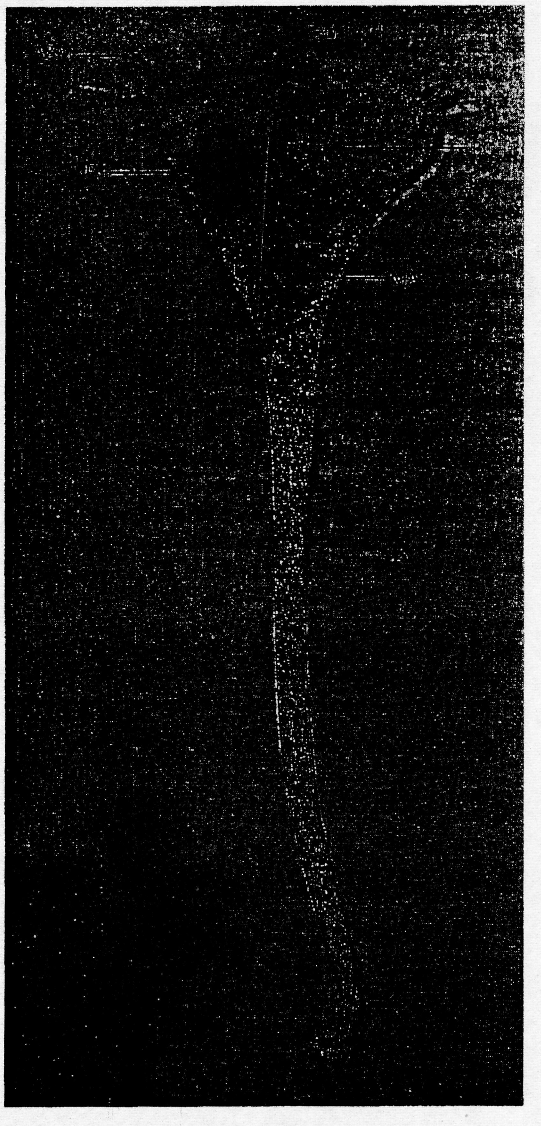

Figure 2 An almost fully extended *Stentor niger* adhering to the microscope slide (courtesy of M. Kreutz, Germany). This beautiful species is up to 1 mm long, has a single globular macronucleus (MA), and is yellow-brown due to brownish pigment granules. Note the mighty adoral zone of membranelles (AZM), which swirls food particles into the huge buccal cavity (BC). AZM, adoral zone of membranelles; BC, buccal cavity; CR, ciliary rows; CV, contractile vacuole; FV, food vacuole; L, lorica; MA, macronucleus; PB, peristomial bottom; PS, pigment stripes; SC, sensory cilia.

extremity. When swimming and contracted, the shape is clavate, pyriform or turbinate. The macronucleus is in the central portion of the cell and, depending on species, vermiform, nodular (a cylindrical body with rather regularly spaced constrictions), moniliform (a chain of beads connected by strands of the nuclear membrane), or composed of one or few spherical beads. Usually, there are many globular, tiny micronuclei around the macronucleus. The contractile vacuole consists of an anterior spherical dilatation, which gives off an annular branch underlying the circumference of the peristome and a canal-like diverticulum extending towards the posterior extremity of the body. (*See* Ciliophora)

The cortex (pellicle *sensu lato*) of *Stentor* has distinct striae due to broad stripes of granules, which alternate with narrow, clear furrows containing the ciliary rows

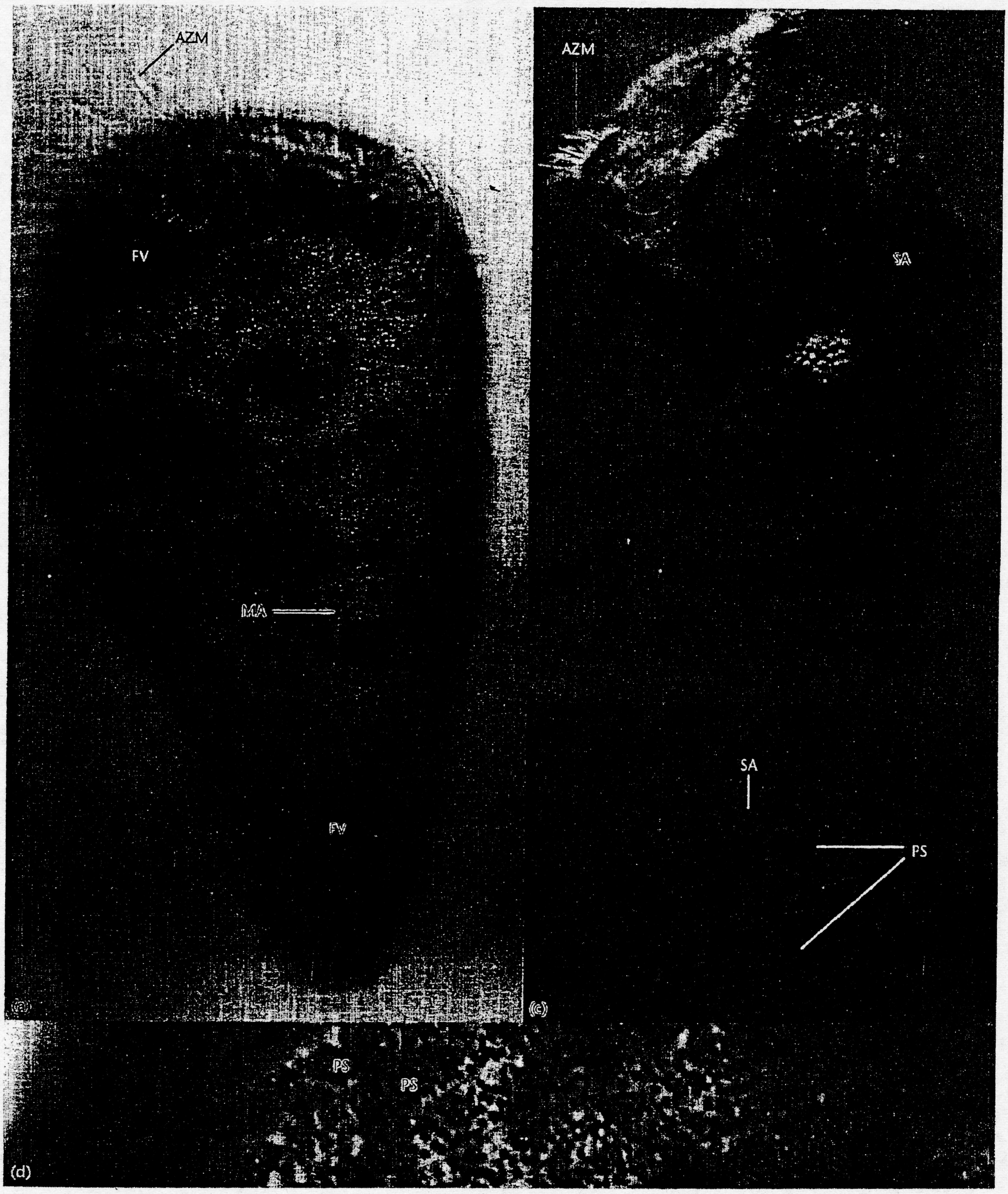

Figure 3 [*Figure is also reproduced in colour section.*] *Stentor multiformis* (a, d) and *S. amethystinus* (b, c), both slightly squashed to show details of the organization (courtesy of M. Kreutz and P. Mayer, Germany). *S. multiformis* is a small species (length about 250 μm when fully extended) with beautiful blue pigment stripes and a single globular macronucleus. The individual pigment granules are blue and about 1 μm across. The narrow white zones between the pigment stripes contain the ciliary rows. *S. amethystinus* is a medium-sized species (up to 500 μm long when fully extended), which appears dark at low magnification due to the lilac pigment stripes and the symbiotic green algae. This species often blooms in the pelagial of small lakes and ponds. AZM, adoral zone of membranelles; FV, food vacuoles; MA, macronucleus; PS, pigment stripes; SA, symbiotic green algae.

(**Figures 1, 3a,d**). The granules have a diameter of ~0.5–2 μm and are colourless or pigmented (red, blue, green, brownish). In the latter case, the cortical striation becomes very conspicuous and mass development causes coloured benthic lawns or planktonic blooms. The pigment granules have at least two functions, to mediate the orientation of the organism in a light gradient (Tao *et al.*, 1994) and to protect it from predation (Harumoto *et al.*, 1998). The pigment is called 'stentorin' and is an analogue of the photodynamic pigments hypericin and phagopyrin, which occur in higher plants. Stentorin is photodynamically active and thus kills cells exposed to intense visible light irradiation. Accordingly, *Stentor coeruleus*, a blue-pigmented species, exhibits negative phototaxis to visible light, that is, it swims to the shady areas of the habitat and of the sample jar. Symbiont-bearing species, such as *S. polymorphus* and *S. amethystinus*, show positive phototaxis (Tartar, 1961). Indeed, *S. coeruleus* is the only organism known that shows all three types of photoresponse: photophobic response ('avoiding reaction', backward swimming due to ciliary reversal), photokinesis (light-intensity dependent changes in swimming direction), and phototaxis (directed movement with respect to the direction of light).

Several *Stentor* species have stable associations with green algae, which belong to the *Chlorella vulgaris* group according to their physiological and ultrastructural characteristics (Reisser, 1986). The symbionts are 4–7 μm across 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*). The ciliate profits from the oxygen and sugars produced by the algae, while the symbionts get carbon dioxide and inorganic nutrients, especially nitrogen. Some species occasionally contain bacterial endosymbionts or are parasitized by microsporidians. (*See* Protozoan Symbioses; Green Algae; Endosymbionts)

Stentor has a mighty oral apparatus on the margin of the broad end. It is composed of hundreds of adoral membranelles (plates of closely spaced cilia acting together) which are, on the inner side, accompanied by a single row of cilia, the so-called undulating membrane. The ciliary plates, which are composed of 25 μm long cilia and beat 30 times per second, form a spiral band, the so-called adoral zone of membranelles, which plunges into a conical buccal cavity leading to the cytostome (mouth proper). The metachronal beat of the membranelles generates a strong current swirling food organisms with a velocity of 800 μm s^{-1} into the buccal cavity.

Stentor is holotrichously (completely) ciliated. The ciliary rows extend longitudinally and show four special features. First, there are elongated setae ('sensory bristles') interspersed between the ordinary cilia, which are about 12 μm long. Second, the ciliary rows are not uniformly spaced. The width of spacing of the ciliary rows grades imperceptibly around the circumference of the cell from the most widely spaced rows (separated by the broadest pigment stripes) situated to the left of the buccal cavity, to the most closely spaced ciliary rows (separated by the narrowest pigment stripes) located immediately posterior to the buccal cavity. Third, along the midventral meridian the most closely spaced rows abut on the most widely spaced rows at acute angles, forming a suture. This suture is called the contrast zone and is easily seen in living stentors as a 'locus of stripe contrast', where narrow pigment stripes meet broad ones. This site is of great significance in the experimental analysis of pattern formation in *Stentor*. Fourth, the peristomial (frontal) field, which is composed of curved ciliary rows of somatic origin, becomes oralized during ontogenesis, that is, the basal bodies of the cilia generate nematodesmata (oral basket rods). (*See* Cilia and Flagella)

Asexual reproduction (cell division) and sexual processes (conjugation) by temporary fusion of partner cells with cross-fertilization and complete renewal of the nuclear apparatus occur in *Stentor* as in other ciliates; however, many details of these processes have not yet been studied. (*See* Protozoan Sexuality; Protozoan Asexuality)

Significance in Biomedical Research

Stentor and ciliates in general play a minor role in biomedical research, although some fundamental processes, such as structural inheritance and RNA splicing were first discovered in ciliates. Part of this neglect of ciliates in biomedical research is certainly due to the lack of harmful human parasites. Another, more important reason might be that results from ciliates, which are a very distinct group of organisms, cannot be easily generalized; even their genetic code is different. Nonetheless, there are some areas where *Stentor* has played or could play a major role.

Regeneration and transplantation

Stentor is the ciliate *par excellence* for microsurgical experiments that have been performed in abundance and have yielded highly important results. Tartar (1961), de Terra (1974) and Frankel (1989) reviewed and interpreted the knowledge available. The experiments on *Stentor* and other ciliates, especially *Paramecium*, showed an important principle, now known as structural inheritance or cytotaxis, namely, that supramolecular organization can be inherited directly, that is, in the presence of a constant genotype. In other words, the time of cell division and organelle replication, e.g. the new basal bodies for the daughter oral apparatus, are not controlled by the nucleus but by the cortex (pellicle). Such structural inheritance is very likely a general principle because it has been observed in mammalian cells for the form of the cytoskeleton and the per litre may comprise >90% of the total ciliate biomass and, due to the symbiotic green algae, up to 70% of total plankton photosynthesis (Laybourn-Parry *et al.*, 1997). The physico-chemical and biotic factors responsible for blooming are not known. In lakes and reservoirs of New Zealand and Australia, where blooms of *S. amethystinus* are frequent, they are possibly caused by the absence of large crustacean predators (Laybourn-Parry *et al.*, 1997). (*See* Crustacea (Crustaceans); Protozoa)

Stentors are polyphagous, i.e. they feed on various heterotrophic (e.g. ciliates and flagellates) and autotrophic (e.g. diatoms, green algae) protists. Even small metazoans, such as rotifers and oligochaetes, are attacked, and cannibalism has been observed in several species. Nonetheless, feeding is a highly selective process, that is, Stentors can discriminate among various food items. Detailed ecological data are available mainly from *S. coeruleus*. These studies show that *Stentor* is a very efficient filter-feeder and energy converter (gross growth efficiencies 64–82%), which is reasonable considering the large oral apparatus and sessile mode of life. Furthermore, it can survive prolonged starvation due to the symbiotic green algae and/or the large quantitiy of nutrient reserves (fat, carbohydrates). On the other hand, generation time is comparatively long, about 3 days in nature and 2 days under laboratory conditions.

Formation of protective resting cysts occurs very rarely and has been observed in three species only (*S. coeruleus*, *S. polymorphos*, *S. niger*).

Impact on human welfare

Stentor is one of the few free-living ciliates that sometimes cause problems for human welfare. *Stentor* blooms, as described above, complicate water treatment when occurring in drinking-water reservoirs; filters become clogged and the water may become coloured by *Stentor* pigment. *Stentor* blooms colour the water, which is problematic in lakes used for swimming and recreation. Furthermore, the individual cells remain as tiny black spots on the skin, which may cause alarm. And there is also one report that extensive fish mortality was associated with a bloom of *S. polymorphus*.

Some *Stentor* species are fairly good indicators for the degree of organic pollution because they are common and easily identified. *Stentor amethystinus* and *S. igneus* indicate slight pollution, *S. muelleri* and *S. polymorphus* indicate moderate pollution, and *S. coeruleus* and *S. roeseli* prefer rather strongly polluted habitats. (*See* Protozoan Ecology)

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