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Mycophagy, a New Feeding Strategy in Autochthonous Soil Ciliates

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Foissner [1] discovered in various soils of the world an enigmatic group of ciliates, the Grossglockneridae, with a peculiar feeding tube. Experiments proved conclusively that these ciliates feed exclusively on fungi and yeasts [2, 3]. In this paper we present for the first time electron microscope pictures of this feeding process and show perforations in sporangia, hyphae, and hyphal swellings of *Mucor mucedo* caused by the feeding tube.

Grossglockneria acuta [4] is a small, 40–60 × 15–35 μm, drop-shaped colpodid ciliate with a slightly arched ventral

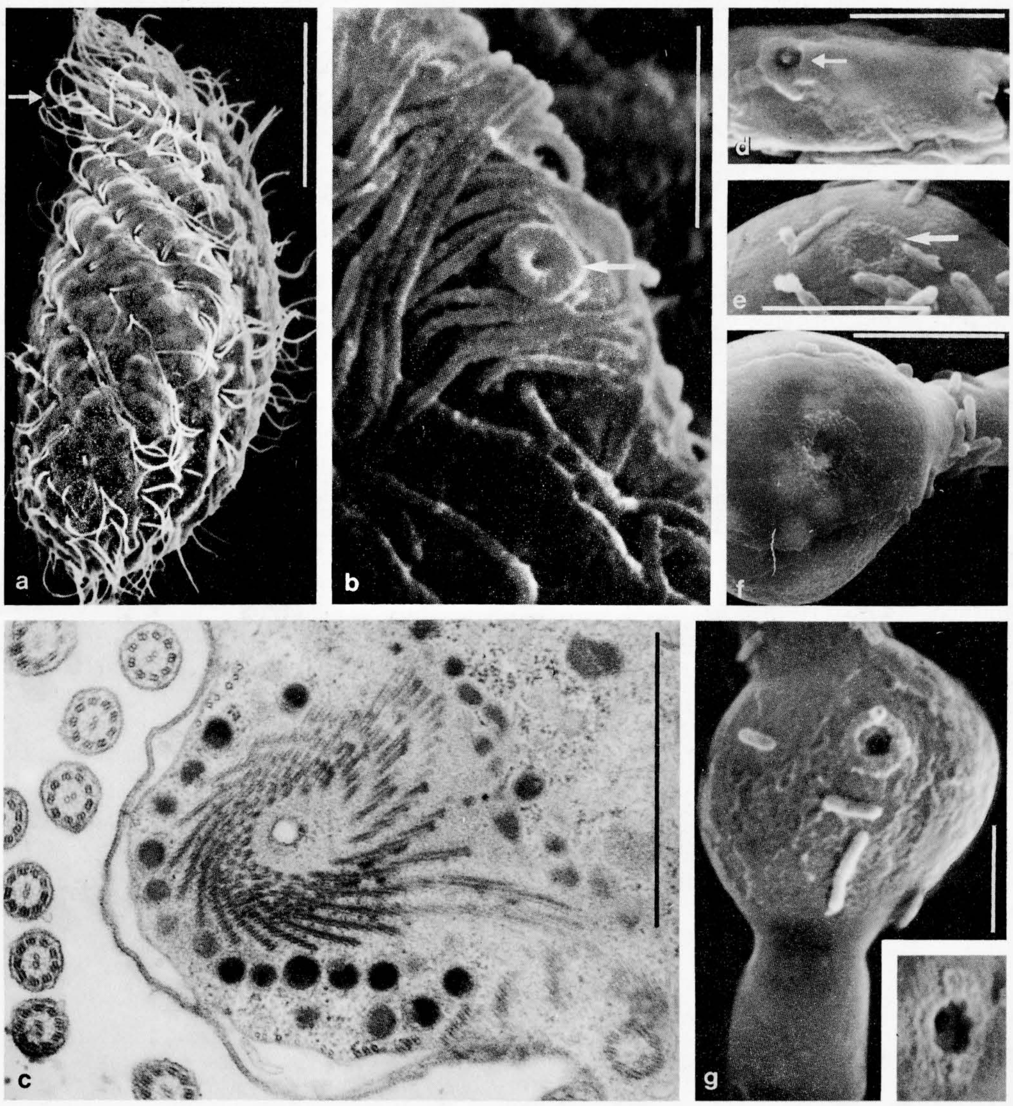

Fig. 1. a–c) Morphology of *Grossglockneria acuta*. a) Scanning electron micrograph (SEM) of left side. *Arrow* points to the position of the feeding tube. Bar 10 μm. b) Feeding tube, top view (SEM). Bar 2 μm. c) Feeding tube, transverse section (TEM). Note the rows of microtubules, the central endocytotic duct and dark globules surrounding the microtubular ribbons. Bar 1 μm. d–g) Different stages in the perforation process of the cell wall of *Mucor mucedo* caused by the feeding tube of *G. acuta* (SEM). d) A perforated hypha bordered by a ring of uncertain origin (*arrow*). Bar 4 μm. e–g) A sequence showing the perforation of the fungal cell wall. e) Early stage in a sporangium. A ring surrounds the still undisturbed site of later perforation (*arrow*). Bar 4 μm. f) Middle stage in a hyphal swelling. A deepening cylindrical depression within this ring results in a tiny hole in the fungal cell wall. Bar 4 μm. g) Final stages in hyphal swellings. The tiny hole at the base of the pit is enlarged and the perforation of the fungal cell wall is completed. Bar 2 μm

side (Fig. 1 a). The oral apparatus is situated in the anterior $^1/_5$–$^1/_6$ of the body (Fig. 1 b). Its most prominent characteristic is a tube-like structure, about 2 µm in length and 1–1.5 µm across at the base, slightly tapering distally. The disc-like tube entrance resembles a suction cup, about 1 µm in diameter, sometimes slightly projecting beyond the tube. A membrane-bounded endocytotic duct, ca. 0.1–0.2 µm in diameter, pervades the tube (Fig. 1 b, c).

Feeding begins with the establishment of a firm contact between the feeding tube and the cell wall of the fungus. Using the scanning electron microscope, various stages of the perforation process can be observed. At first, there is a ring, ca. 1.5–2 µm in diameter, surrounding a central area, measuring 0.7–1 µm across, which is still visually undisturbed (Fig. 1 e). This ring possibly consists of lyzed or digested cell-wall debris. Another possibility is that the ciliate releases a special substance to establish contact between the feeding tube and the cell wall of the prey. Later stages show a deepening cylindrical depression of this central area (Fig. 1 f, g). Frequently, the actual perforation at the base of the pit is smaller than the diameter of the depression, about 0.5 µm across (Fig. 1 g). In thinner cell walls, e.g., hyphae, the hole occupies the entire central area (Fig. 1 d). Perforations in sporangia (Fig. 1 e) and especially hyphal swellings (Fig. 1 f, g) are rather common, but perforated hyphae (Fig. 1 d) are rarely found. The feeding process lasts about 3–23 min ($\bar{x} = 10$ min), during which time the ciliate visibly enlarges, due to the ingestion of host cytoplasm. When finished, the ciliate detaches from the prey and moves away. In no case are hyphae or spores incorporated. The feeding activity seems to be light-dependent, as food uptake ceases when viewed with bright illumination.

The exact mechanism of breaking up the fungi is unknown, yet it is conceivable that the perforations are caused enzymatically. For instance, acid phosphatase has been reported in the algivorous ciliate *Pseudomicrothorax dubius* [5] and in suctorians [6, 7]. Chitinase and cellulase have been documented in naked amoebae with a feeding strategy similar to *G. acuta* [8, 9].

Little is known about the detailed process of incorporation of the host cytoplasm. Similarly to the food uptake by suctorian tentacles [10], the oral microtubules of *G. acuta* (Fig. 1 c) and a related species, *Pseudoplatyophrya nana* [11], may play a role in ingesting the cytoplasm. Active sucking seems unlikely. The electron-dense granules in the feeding tube (Fig. 1 c) are possibly membrane reservoirs for the formation of food vacuoles as in other ciliates [10, 12]. Algivorous freshwater rhizopods drive special feeding pseudopodia through the pierced cell wall of their prey and phagocytose the cell contents [13]. In contrast, the feeding of *G. acuta* looks like endocytosis.

Superficially, the perforations in hyphae and spores caused by mycophagous soil amoebae are quite similar. However, some differences exist: Naked amoebae engulf their prey, at least partially, prior to perforating them [14–16]; the ring surrounding the perforations is lacking; most of these amoebae cut out a circular disc from the host cell wall which is left undigested [14, 15].

We consider this morphologically very similar feeding strategy in soil and freshwater amoebae and soil ciliates as a most striking analogy which deserves closer examination. In addition, the rather narrow food requirements of the mycophagous soil ciliates and amoebae suggest some potential in biological control of soil-borne plant pathogenic fungi.

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