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A Fossilized Microcenosis in Triassic Amber

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ABSTRACT. Detailed data on bacterial and protistan microfossils are presented from a 0.003 mm³ piece of Triassic amber (Schlierseerit, Upper Triassic period, 220–230 million years old). This microcenosis, which actually existed as such within a very small, probably semiaquatic habitat, included the remains of about two bacteria species, four fungi (*Palaeodikaryomyces baueri, Pithomyces*-like conidia, capillitium-like hyphae, yeast cells) two euglenoids, two chlamydomonas (*Chlamydomonas* sp., *Chloromonas* sp.), two coccal green microalgae (*Chlorella* sp., *Choricystis*-like cells), one zooflagellate, three testate amoebae (*Centropyxis aculeata* var. *oblonga*-like, *Cyclopyxis eurystoma*-like, *Hyalosphenia baueri* n. sp.), seven ciliates (*Pseudoplatyophrya nana*-like, *Mykophagophrys terricola*-like, *Cyrtolophosis mucicola*-like, *Paracondylostoma* sp., *Bryometopus triquetrus*-like, *Tetrahymena rostrata*-like, *Paramecium triassicum* n. sp.) The microfossils correspond to or diverge from extant species only slightly.

Key Words. Evolutionary comments, fossilized bacteria, ciliates, flagellates, fungi, green algae, testaceans, preservation, Schlierseerit.

THE "Schlierseerit", amber which comes from layers of Raibler Sandstone of the "Leitnernase" near the village of Schliersee (Bavaria, Germany), has been investigated intensively for 10 years by many scientists. This amber dates from the Upper Triassic period (Carnian stage of Keuper) and may be 220–230 million years old. Its finder, U. Ch. Bauer, discovered the amber as small pieces of < 1 mm to max. 20 mm. A summary of all findings concerning this amber has been compiled by Vavra (1996; see also Nickel 1995). Using carbon-13-nuclear magnetic resonance spectra, the resin source is probably a coniferous plant of the Araucariaceae (Lambert, Johnson, and Poinar 1996), already known from the Palaeozoic period. The preliminary investigation on this amber was carried out by Poinar, Waggoner, and Bauer (1994; see also Bauer 1993) who described bacteria, fungi, algae, testaceans, and ciliates. Since there are only scant findings of freshwater (or terrestrial) protists from early geological periods, the above-mentioned are the earliest known soft-bodied forms. The present paper describes in more detail a microcenosis of an amber fragment with a volume of only 0.003 mm³, and comments on evolutionary and ecological consequences of these discoveries.

METHODS

The size of the pieces of Schlierseerit exploited in the present paper ranges from nearly 100 μm to some mm. Since the microfossils are situated tridimensionally in the amber, simple microscopic observation and taking micrographs is difficult; usually the distance between object and lens is too large. Sections are impossible because many inclusions would be destroyed. Breaking it into smaller pieces is the best method because the inclusions remain undamaged and are eventually set free from the amber.

Tiny or broken amber pieces were at first investigated in water, photographed, and after air drying, treated with a neutral mixture of paraffin oil and alkylaromates (Chemisches Labor Carl Zeiss, Oberkochen, Germany); the density (1.525) of this mixture is similar to that of the Schlierseerit. The oil penetrates the amber and microfossils, especially fungal hyphae, and clears the structures, but only in the first 30–60 min, which is the most favorable time for microscopic investigations. After 60 min the oil dissolves the amber and destroys the pieces.

For preservation, small chambers ("sarcophages") were burned with the help of CO_2 laser in glass microscope slides. An amber piece containing microfossils was placed in the chamber, covered with a cover glass, and sealed by phytohistol (Carl Roth GmbH & Co., Karlsruhe, Germany).

A Zeiss-Microscop Axioplan equipped with differential interference contrast and a throughlight-stereoscopic picture microscope Axiolab (up to 1000× enlargement without restriction of resolution) were used to observe the inclusions tridimensionally.

RESULTS

Fungi (Fig. 1–7)

Many fungal remnants were included in the amber between remains of plants, bacteria, and protists. Five types of fungi were regularly observed:

1. *Palaeodikaryomyces baueri*-like Dörfelt, already described from the Schlierseerit (Dörfelt and Schäfer 1998), could be newly confirmed. It is a saprophytic fungus with non-septate hyphae and vesiculi, developing septae, branches at the vesiculi, great clamps or loops, and cysts at the loops (Fig. 1, 2, 3).
2. A saprophytic fungus with septate hyphae and oogonia-like cysts, possibly a stage from *Palaeodikaryomyces baueri*-like (Fig. 4) or an as yet undescribed saprophytic fungus.
3. Thick-walled, capillitium-like hyphae with papillary ornaments and occasionally with blastoconidia (Fig. 5), probably an as yet undescribed species.
4. Remnants from a saprophytic fungus, which may be a yeast cell of a dimorphic fungus or a separated visicle from *Palaeodicaryomyces baueri*, germinating with small hyphae (Fig. 6).
5. *Pithomyces*-like conidia, dark brown, muriform (Fig. 7), may be macroconidia belonging to the capillitium-like hyphae described above.

Bacteria (Fig. 8, 9)

We found many filamentous and single bacterial structures (Fig. 8, 9), but it is impossible to identify them without chemical analysis.

Algae (Fig. 10–17)

Euglenoids. Two specimens of euglenoid flagellates were found in the Triassic amber. One cell body was spirally twisted, indicating the typical metabolic character of *Euglena* cells (Fig. 10). The cell was approximately 25 μm long (unfortunately, the apical part was covered and hence not clearly visible), width varied between 2–6 μm. The cell had a short caudal spine. Inside the cell, different granulated and refractile structures

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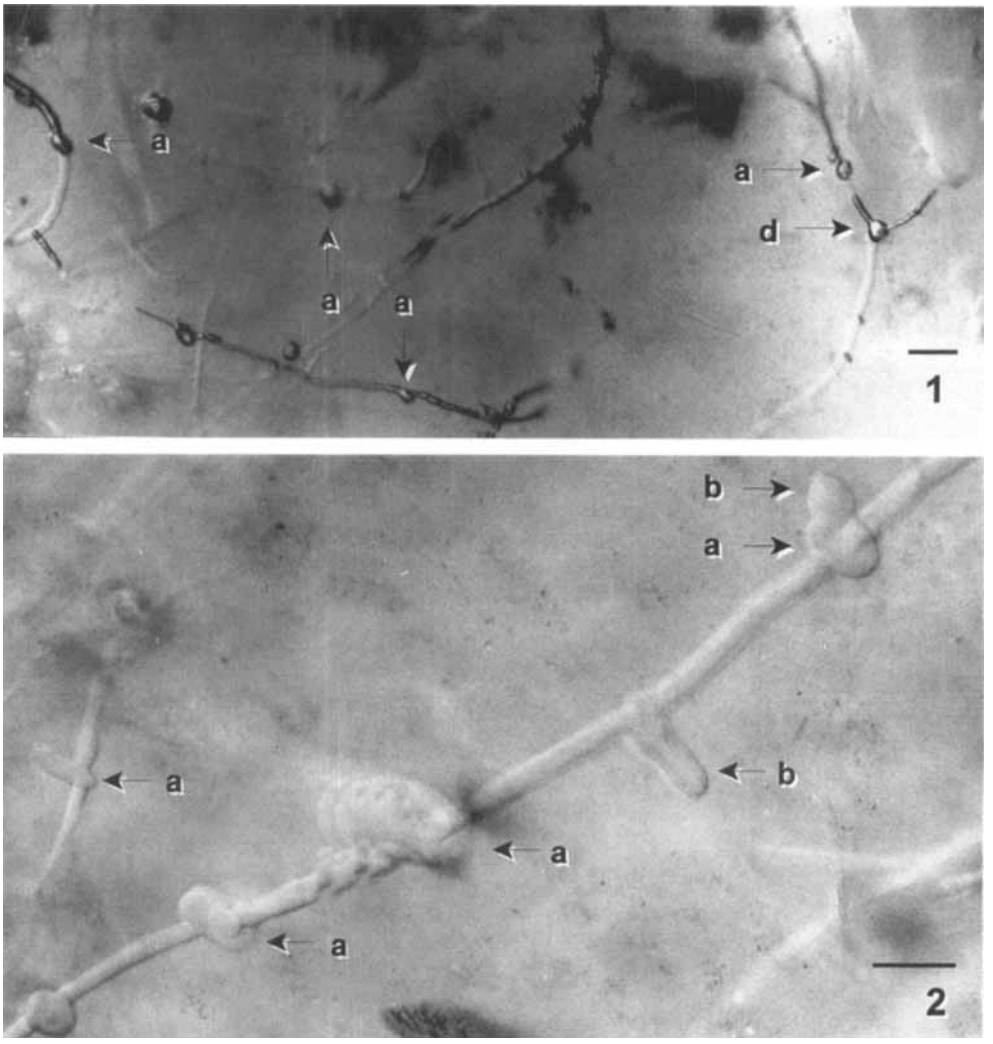


Fig. 1–2. *Palaeodikaryomyces baueri*. a, clamps or loops; b, cysts, growing from the clamps; d, vesicles. Fig. 1, bar 5 μm; 2, bar 20 μm.

were visible, possibly chromatophores, paramylon grains, vacuoles, and reddish carotene-containing oil droplets. The other cell, about 50 × 12 μm in size, exhibited a fusiform shape (Fig. 11).

Monadal chlorophytes. There were two types of ovoidal chlorophytes in the amber. The thick-walled cells clearly indicate the character of monodal algae, although flagella were missing. The cells were oval in longitudinal view, and spherical in the apical view. The first type of cells (Fig. 11) had a size of 4–6 × 8–10 μm. It contained a cup-shape chloroplast equipped with a pyrenoid in the basal part. These cells can be identified as the genus *Chlamydomonas*. The second type of cells had a size of about 15–18 × 28–32 μm. The inner side of the cell wall was covered by a chloroplast, which did not contain a pyrenoid. In the central part of the cells several vacuoles were visible. A reddish-colored, stigma-like structure was found near the apical region in some cells. These cells are comparable with extant species of the chlamydophycean genus *Chloromonas* (Fig. 11–15).

Chlorococcal picoplankton. Wide areas of amber were filled with minute spherical structures. In most cases, these might be artifacts. However, some specimens showed the character of algal cells, containing chloroplasts and vacuoles. We classified these small structures, with a size of 2–5 × 3–6 μm, in two different morphotypes: more or less spherical cells resembling extant *Chlorella* species (Fig. 12, 16), and slightly ellipsoidal cells resembling extant *Choricystis*-like cells because they contained trough-like parietal chloroplasts. The cells at the lower region of the size spectrum (< 3 μm) were identified as "picoplankton" (Fig. 15, 17).

Zooflagellates (Fig. 18–20)

About ten inclusions resembled longish cells with a thread-like elongation on one end, very likely a flagellum. The length ranged from 9.6–13.0 μm (including flagellum). Zoochlorellae were not visible, so these inclusions were very likely heterotrophic flagellates.

Testate Amoebae (Fig. 21–27)

Three testacean species could be identified.

1. *Hyalosphenia baueri* n. sp. (Fig. 21, 22)

Diagnosis. Shell about 60.0 × 95.5 μm, indistinctly vase-shaped, with two opposite lateral pores, membraneous, structureless, brown, compressed, with a small collar around the aperture, which is terminal and (probably) oval.

Type location. Triassic amber from Mount Leitnernase near the village of Schliersee (Bavaria, Germany).

Type material. Holotype (Fig. 22)

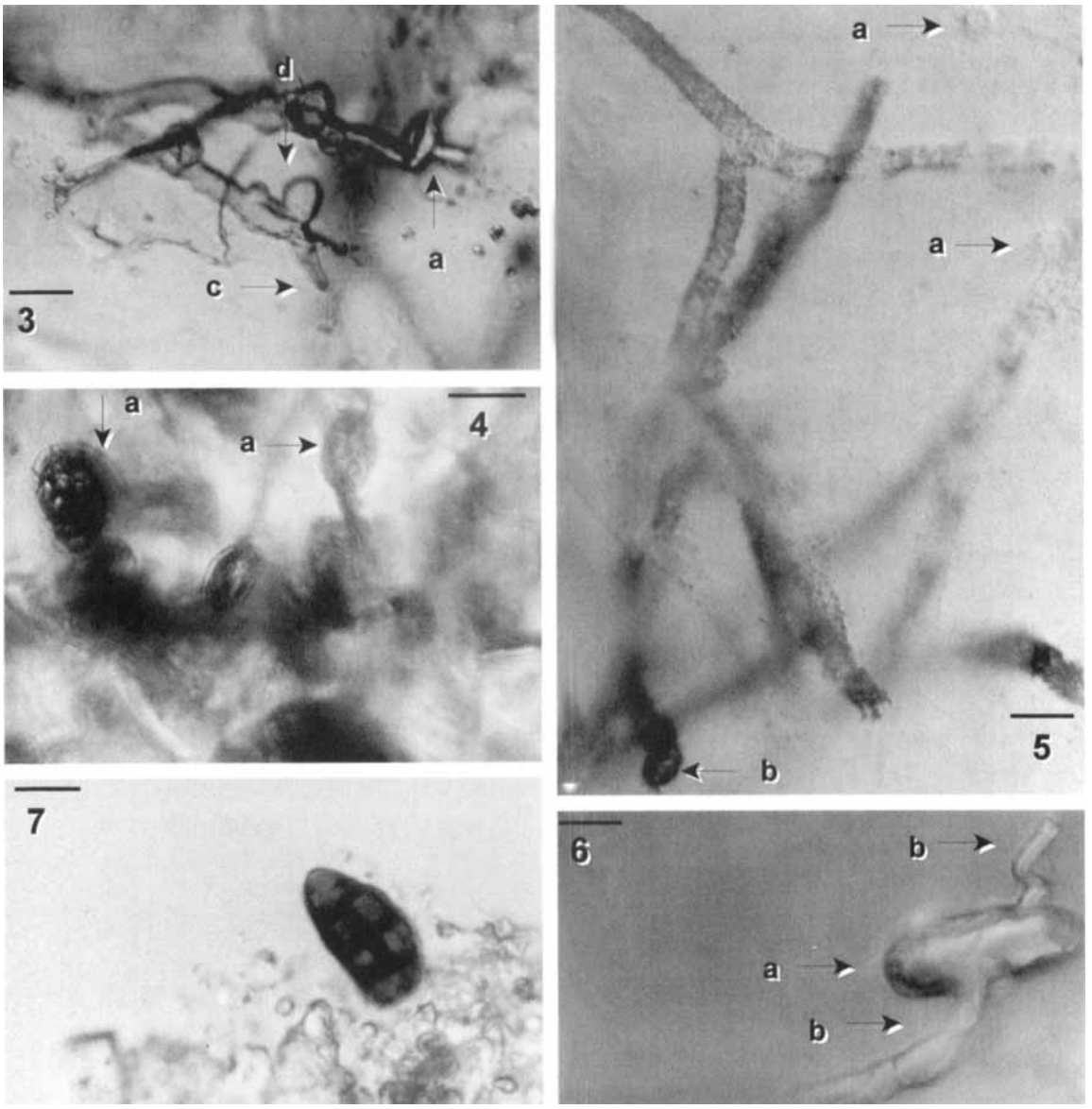


Fig. 3–7. *Palaeodikaryomyces baueri*, and other fungal remnants. **3**. *Palaeodikaryomyces baueri*, hyphae; a, clamps or loops; c, rounded apiculus of the hyphae; d, vesicles. **4**. Oogonia-like structure (a) of a saprophytic fungus. **5**. Thick-walled capillitium-like hyphae of a saprophytic fungus (a, diameter of hyphae; b, blastoconidium). **6**. Hypha-body or separated vesicle (a), germinating with smaller hyphae (b). **7**. Conidium, dark brown and muriform. Fig. **3**, **4**, **5**, **6**, bars 20 μm; **7**, bar 10 μm.

Etymology. Named in honour of U. Ch. Bauer, the finder of the Triassic amber.

Description and discussion. The photographed shell is somewhat obliquely arranged, showing the narrow side. The opposite pore is marked by a minute indentation. Fig. 21 is an interpretation of the micrograph in Fig. 22. The shell has an indefinable content. Only further shell remnant also showing a pore could be found.

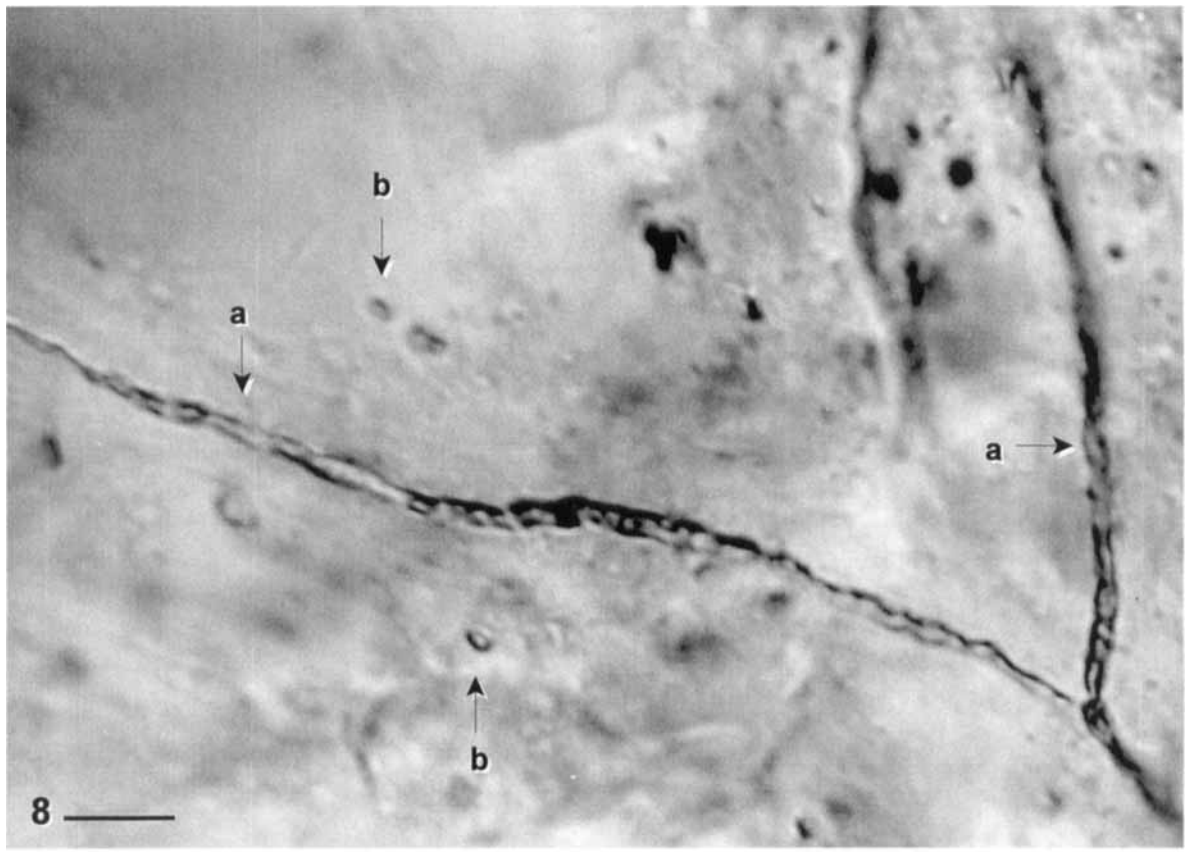
Empty shells of extant *Hyalosphenia* species are extremely lacking in features. But compressed and structureless shells with two opposite lateral pores belong without doubt to this genus. There are also some few extant species without pores. The new species shows a certain similarity with *Hyalosphenia humicola* Decloitre, 1973 (Decloitre 1973). But the shell of this extant species is broader, does not posses pores and is sparsely covered with xenosomes.

2. *Cyclopyxis eurystoma*-like Deflandre, 1929 (Fig. 23)

The shell of this species was hemispheric, 75.0 μm in diameter, had a wide pseudostome, and was covered with small grains. A single shell found standing out from an amber piece, was oriented dorsally and showed the wide, central pseudostome, the unmistakable feature of this species. The shell covering consisted of small sand grains, clearly different from amber-borne bubble concentrations.

3. *Centropyxis aculeata* var. *oblonga*-like Deflandre, 1929 (Fig. 24–27)

The shell was wedge-shaped, irregularly covered with small sand grains, showed two robust spines, and had a size of at least 80.0 μm (without spines); real length very likely nearly 100 μm considering the oblique placement. The shell lay at an



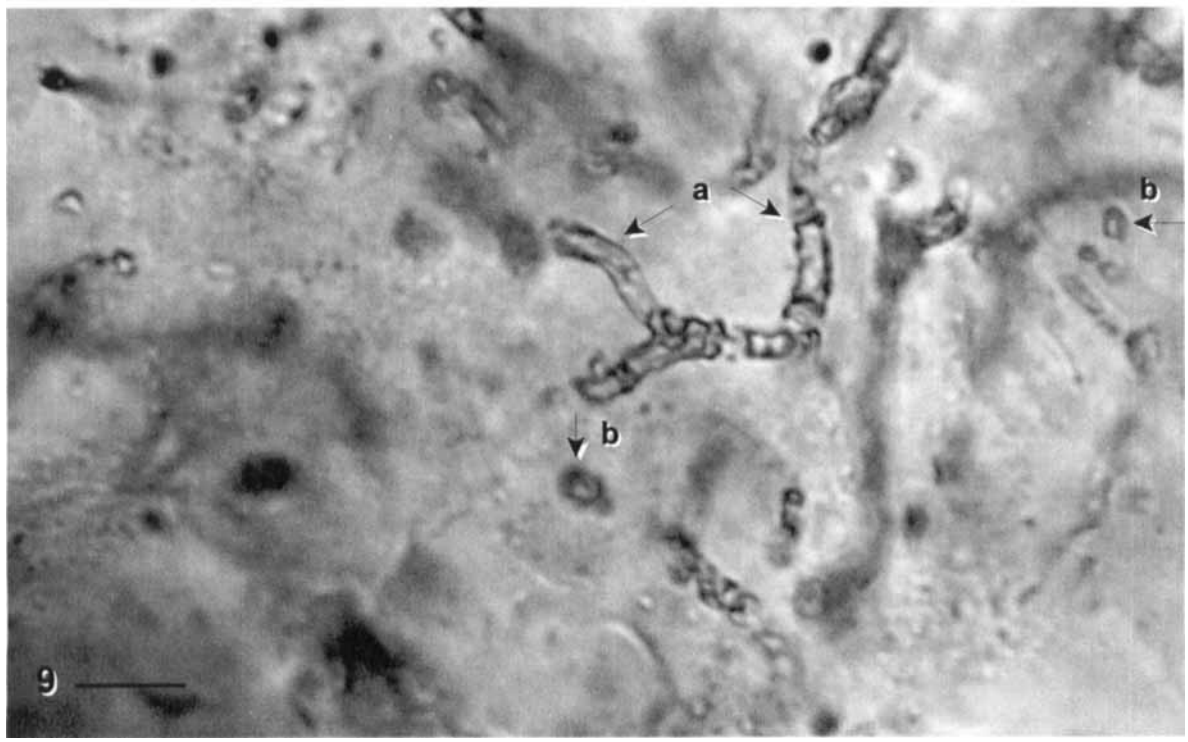


Fig. **8–9**. Fossilized bacteria. **8**. Long branched filaments of bacteria (a), nearly 1.0 μm in diameter, single bacterial cells (b), nearly 2–1.3 μm. **9**. Short branched filaments of bacteria (a), nearly 1.2 μm in diameter, single bacterial cells (b), nearly 2–1.2 μm. Fig. **8**, **9** bars 5 μm.

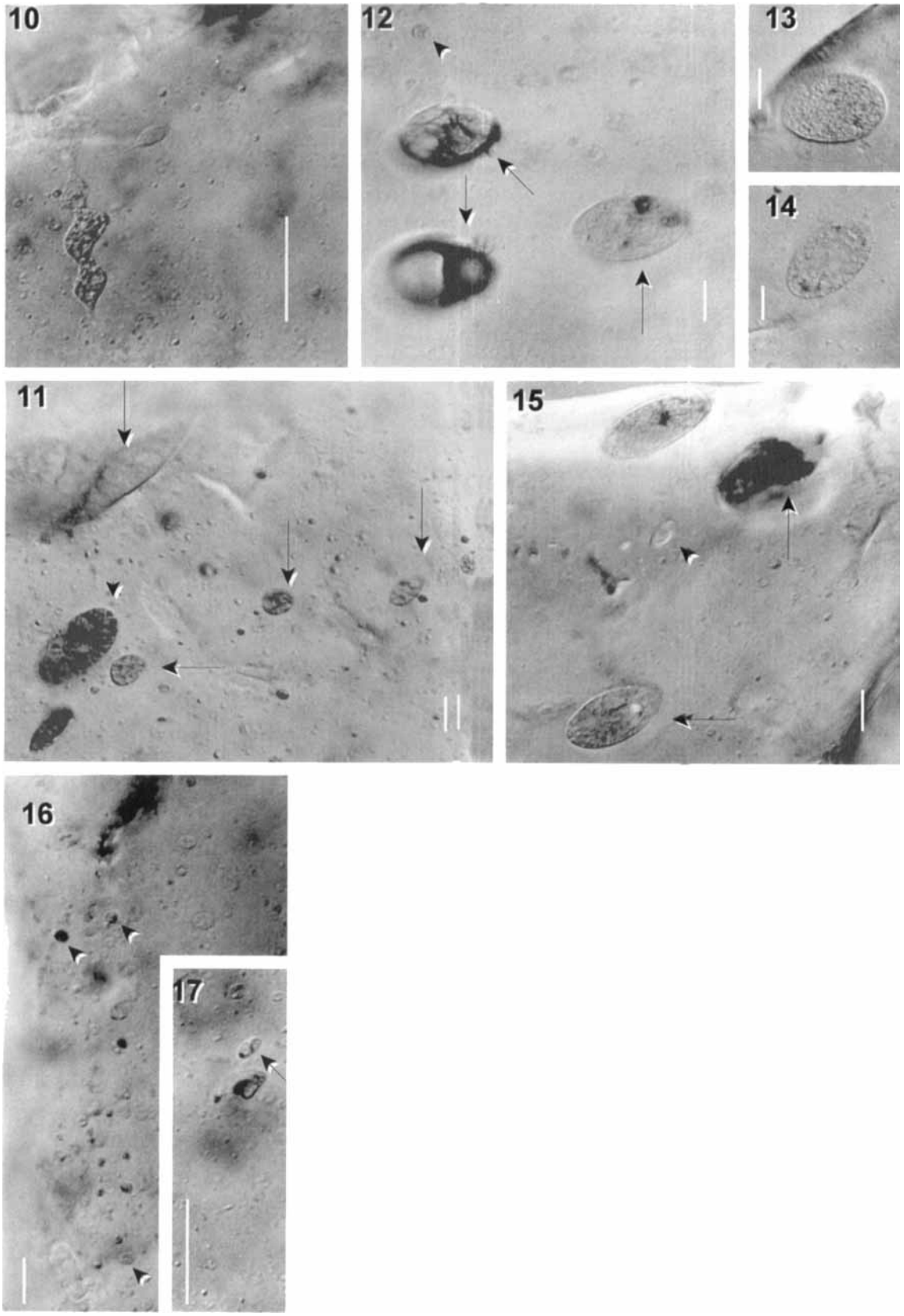
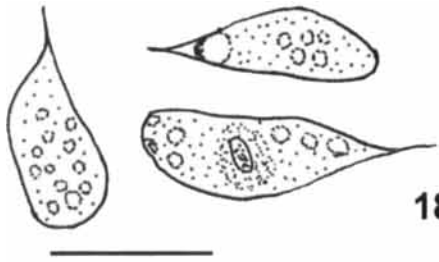


Fig. **10–17**. Fossilized microalgae. **10**. *Euglena*-like cell with a spirally twisted cell body. **11**. Spindle-shaped *Euglena* (uppermost arrow) and monadal chlorophytes: *Chloromonas*-like (arrowhead) and *Chlamydomonas*-like (arrows). **12**. *Chloromonas*-like (arrows) and a *Chlorella*-like cell (arrowhead). **13–14**. *Chloromonas* cells. **15**. *Chloromonas* (arrows) and a *Choricystis*-like cell (arrowhead). **16–17**. Small coccal cells resembling extant species of *Chlorella* (arrowheads) and *Choricystis* (arrow). Fig. **10–17**, bars 10 μm.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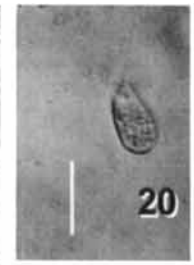
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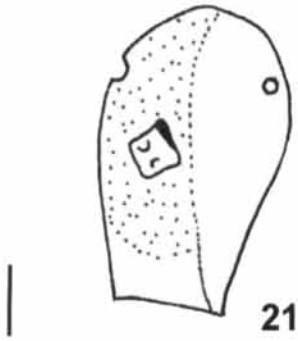
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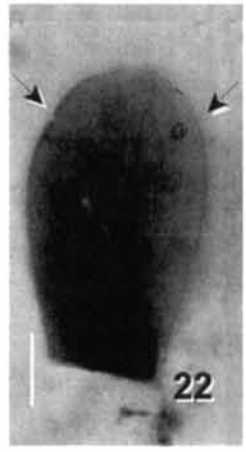
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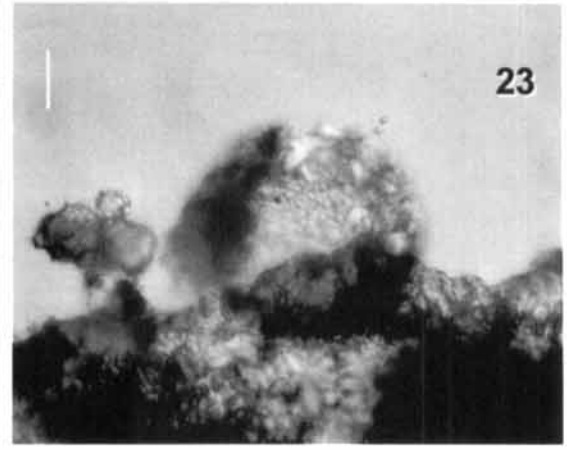
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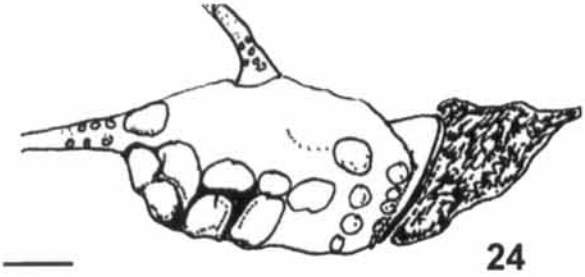
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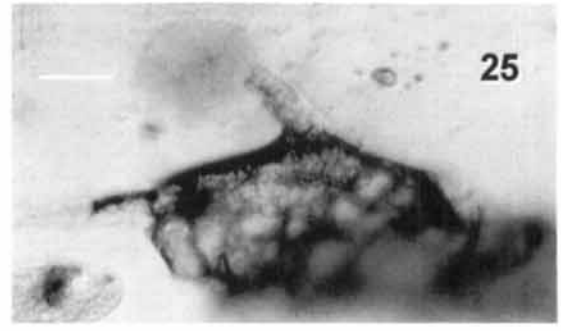
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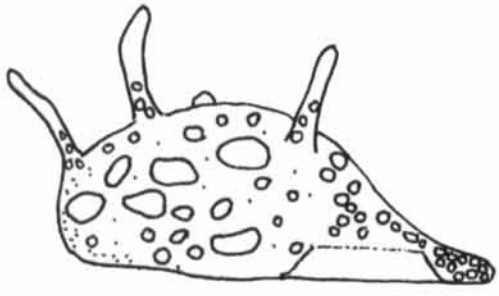
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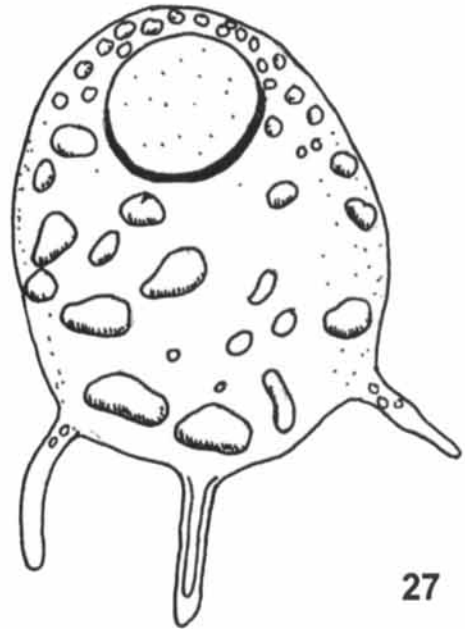
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angle to the broad surface of the amber piece with the posterior end upward. Therefore, the anterior side of shell could be documented only poorly (Fig. 24, 25). The pseudostome was closed by detritus, which frequently occurs also in extant shells. Figures 26 and 27 show an extant specimen in frontal and lateral view. A second specimen had only one spine.

Ciliophora (Fig. 28–61)

Six ciliate-like extant species and one undescribed species could be identified in the amber. Most are very well preserved and look like specimens embedded in artificial resin for transmission electron microscopy. Several other organisms were found, which are also possibly ciliates. However, they showed too few details to be definitely assigned. Thus, they will not be described here.

1. *Pseudoplatyophrya nana*-like (Kahl, 1926) Foissner, 1980 (Foissner 1980b; Kahl 1926) (Fig. 28–33) and
2. *Mykophagophrys terricola*-like (Foissner, 1985) Foissner, 1995 (Foissner 1985, 1995) (Fig.34–38)

These species referred to extant representatives belonging to a particular group of small (length 10–70 μm) colpodid ciliates, which live only in terrestrial habitats and feed exclusively on fungi and yeasts (for review, see Foissner 1993). Feeding occurs by a unique, minute (2–4 μm) organelle, the feeding tube, which perforates the cell wall and takes up the hyphal content (Fig. 28–32, 34). *Pseudoplatyophrya* and *Mykophagophrys* are distinguished by the released extrusomes, which are globular in the former and conspicuously nail-shaped in the latter (Fig. 35). The occurrence of obligate fungal feeders in the amber under investigation is not too surprising, considering the mass of fungal hyphae present (Fig. 33, 36, 38). Both species are very common in terrestrial habitats worldwide (Foissner 1993).

The amber specimens of *P. nana* and *M. terricola*-like cells matched the extant ones in size and shape (cp. Fig. 28–30 with Fig. 33 and Fig. 34 with Fig. 36, 38), and showed the highly characteristic feeding tube (Fig. 33, 36, 38). Two of the *M. terricola* specimens showed a distinct, striated fringe (Fig. 36, 37, arrows), which is very similar to the fringe formed by partially released extrusomes in extant specimens (Fig. 35). Extant specimens of *P. nana* and *M. terricola* differ in the food vacuoles, which are inconspicuous in the former (Fig. 28, 32) and rather large and compact in the latter (Fig. 34). The same was evident in the amber specimens: *P. nana*-like looked clear (Fig. 33), while distinct globules were recognizable in the cytoplasm of *M. terricola* (Fig. 36, 37). The *P. nana* specimen had a homogenous, globular inclusion in mid-body (Fig. 33), possibly, the nuclear apparatus, which is relatively large in this species (Fig. 28, 32).

3. *Cyrtolophosis mucicola*-like Stokes, 1885 (Stokes 1885) (Fig. 39–43)

Cyrtolophosis mucicola is a small (18–39 × 8–15 μm) colpodid ciliate, which is very common in limnetic and terrestrial habitats, although the latter are preferred (for review, see Foissner 1993). At least two specimens were found in the amber. One specimen (Fig. 41) matched the extant species (Fig. 39, 40) perfectly in body size and shape, as well as in the location of the oral apparatus and the contractile vacuole. The extant *C. mucicola* lives in a slimy tube, several of which form pseudocolonies (Fig. 42). A rather similar amber inclusion showed a bifurcated structure with an organism in the anterior end of the left fork (Fig. 43).

4. *Paracondylostoma*-like Foissner, 1980 (Foissner 1980a) (Fig. 44–46)

Paracondylostoma included colpodid bursiform ciliates with a deep buccal cavity extending from anterior end to mid-body. It is closely related to *Bursaridium* (Fig. 47) and *Bryometopus* (for reviews, see Foissner 1993; Foissner and Kreutz 1998). Only two species are known, viz. *P. setigerum* (Fig. 44, 45) and *P. cavicola,* which differ in size (65–90 × 28–43 μm vs. 30–60 × 18–25 μm), number of ciliary rows (about 47 vs. 20), and habitat (boggy ponds vs. ephemeral puddles). One of the amber organisms strongly resembled *Paracondylostoma* in having a deep buccal cavity, extending from the anterior end to mid-body, and was of similar size and shape (Fig. 46). According to the size (50 × 20 μm), it is more closely related to *P. cavicola* than to *P. setigera.*

5. *Bryometopus triquetrus*-like Foissner, 1993 (Foissner 1993) (Fig. 48–50)

Bryometopus is a colpodid ciliate, very common in terrestrial and semi-terrestrial habitats (for review, see Foissner 1993). *Bryometopus triquetrus* is the smallest species of the genus (45–55 × 25–35 μm) and has a unique, triangular shape (Fig. 48, 49) found in hardly any other soil ciliate. Thus, we interpret the triangular amber organism (Fig. 50) as *B. triquetrus*-like, although it shows few other details. However, the size (42 × 25 μm) also matches very well, and there are two faint lines in the anterior region, which can be interpreted as margins of the oral aperture. There is a small blister in the middle of the posterior third (Fig. 50). Possibly, it is the contractile vacuole because this is the usual place for this organelle in most species of the genus; however, in *B. triquetrus* it is in mid-body near the left margin of the cell (Fig. 48, 49).

6. *Tetrahymena rostrata*-like (Kahl, 1926) Corliss, 1952 (Corliss 1952; Kahl 1926)

Tetrahymena rostrata is a slightly fusiform, hymenostome ciliate with a great size range, that is, 25–80 × 20–30 μm (usually about 40 × 25 μm). It occurs in limnetic and terrestrial habitats, but is also often a facultative parasite in various invertebrates (for review, see Corliss 1973). Three organisms (two shown in Fig. 54, 55) were found, which strongly resemble extant *T. rostrata* (Fig. 51–53) in size, shape, and location of the macronucleus, which is conspicuous in one specimen (Fig. 55). The amber surrounding the ciliates is full of minute globules, very likely bacteria, the preferred food of *T. rostrata.*

7. *Paramecium triassicum* Foissner and Schönborn n. sp. (Fig. 57, 59 61)

Diagnosis. Size 42–61 × 12–17 μm; slipper-shaped with distinct oral groove; two contractile vacuoles, one in anterior quarter, the other in rear sixth; nuclear apparatus in anterior half.

←

Fig. **18–27**. Fossilized zooflagellates and testate amoebae. **18–20**. Reconstructed drawings (**18**) of the fossilized zooflagellates (**19, 20**). **21–22**. Reconstructed drawing (**21**) of the fossilized *Hyalosphenia baueri* (**22**). Arrows show the two opposite lateral pores. **23**. *Cyclopyxis eurystoma*-like. Ventral view. **24–25**. Reconstructed drawing (**24**) of the fossilized *Centropyxis aculeata* var. *oblonga*-like (**25**). **26–27**. Extant individuals of *Centropyxis aculeata* var. *oblonga.* Lateral (**26**) and ventral (**27**) view. Fig. **18, 19, 20** bars 8 μm, **21, 22**, bars 15 μm, **23, 24, 25, 26, 27**, bars 20 μm.

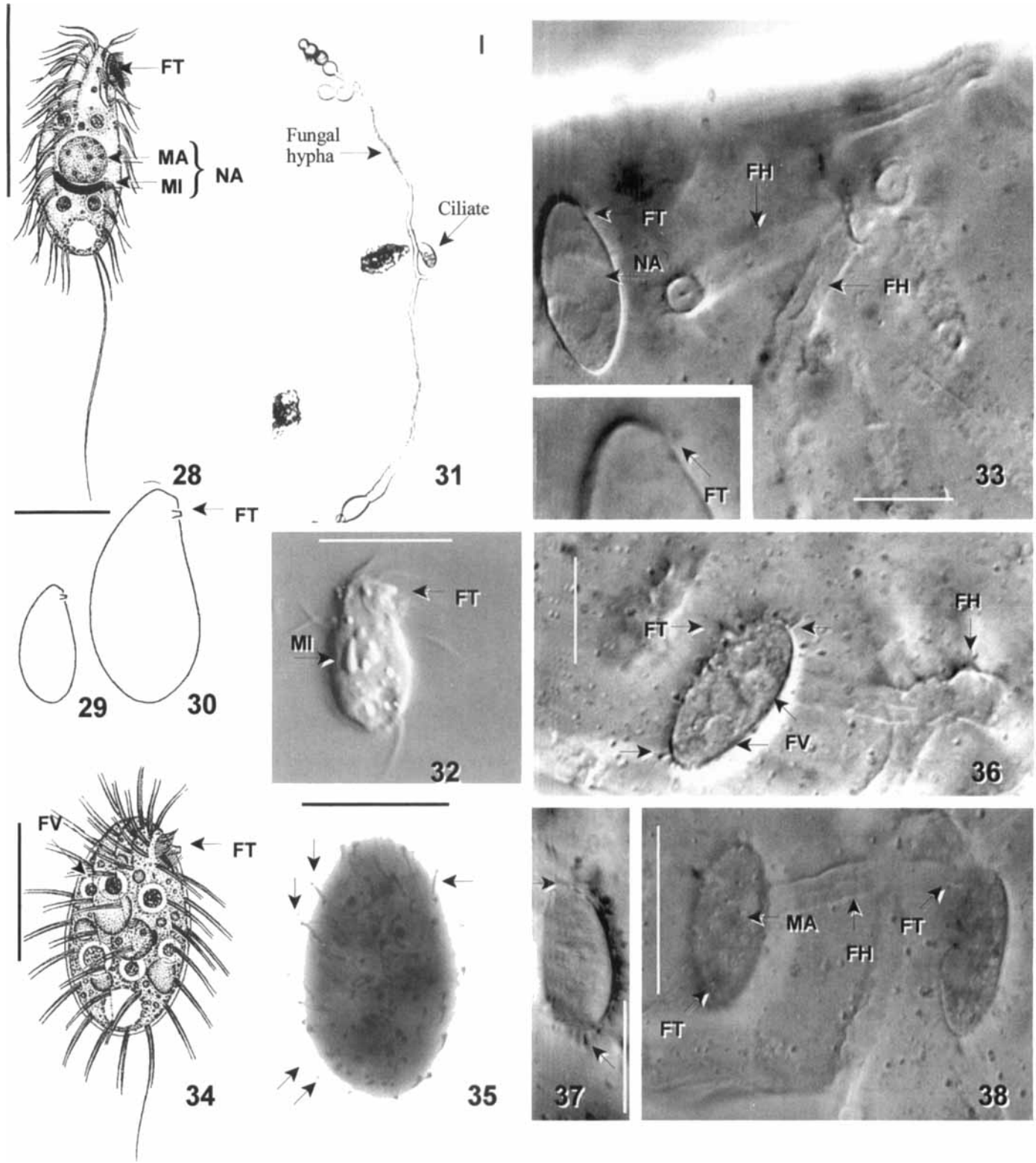

Fig. **28–38**. Extant (**28–32**, **34**, **35**; from [Foissner 1993, 1995]) and fossilized (**33**, **36–38**) *Pseudoplatyophrya nana*-like (**28–33**) and *Mykophagophrys terricola*-like (**34–38**). Both species are obligate fungal feeders. Feeding is achieved by a unique, minute (1–2 μm) organelle, the feeding tube (FT), which is clearly recognizable in the fossilized material. **28**, **32**, **34**. Right lateral views of representative specimens. **29**, **30**. Size and shape variability in a single extant population. **31**. A specimen sucking on a fungal hyphae. **33**. A fossilized specimen among fungal hyphae. The minute feeding tube is clearly recognizable at high magnification (inset). **35**. A methyl green-pyronin-stained extant specimen, which has partially extruded nail-shaped extrusomes (arrows). **36–38**. Fossilized specimens with a fringe of small rods (arrows), very likely partially released extrusomes (cp. Fig. **35**). FH—fungal hyphae, FT—feeding tube, FV—food vacuoles, MA—macronucleus, MI—micronucleus, NA—nuclear apparatus. Bars 20 μm.

Type location. Triassic amber (220–230 million years old) from Mount Leitnernase near the town of Schliersee, Bavaria, southern Germany, about 47°40′N/11°50′E.

Type material. Holotype as shown in Fig. 61, paratypes as shown in Fig. 57, 59.

Etymology. Named after the geological period found.

Description and discussion. The description and interpretation of structures are based on the assumption that the organisms belong to the genus *Paramecium* (see detailed discussion below). Three well-preserved specimens were found. The first organism (Fig. 57), which is fusiform and very likely dorsolaterally orientated, shows many clear blisters and a homogeneous, rather large (13 × 6 μm), ellipsoidal structure in the anterior body region, very likely the macronucleus. In midbody there is an indentation, possibly the buccal cavity. This specimen, whose cortex is sharply contoured, has a size of 61 × 17 μm. The second specimen (Fig. 59), which is laterally orientated and elongate reniform, has a size of 43 × 12 μm and clearly shows the genus-specific oral groove. The third organism (Fig. 61), which is ventrally orientated and distinctly slipper-shaped, shows many food vacuoles and two blisters, which we interpret as contractile vacuoles because they are clear (without content) and have exactly the same location as in extant *Paramecium* spp. (Fig. 56, 60); even the specific detail that the posterior vacuole is more terminally located than the anterior is recognizable. This specimen has a size of 42 × 13 μm.

DISCUSSION

Many of the structures found in the amber are doubtlessly protists. This is indicated not only by such general characteristics as size and shape, but also by many specific features (e.g. contractile vacuoles, nuclear apparatus, food vacuoles, eye spots, chloroplasts, paramylon grains, pyrenoids, tubes, and shells), which have exactly the same location as in the extant relatives. Indeed, many of the organisms look so similar to extant species that they have been classified with them. Probably, this is too conservative. On the other hand, it would be difficult to provide characters, which would definitely separate them from the extant forms.

Fungi. The specimens found are not identical with extant species, but appear to be nearly related to extant groups. The *Pithomyces*-like conidia resemble extant conidia of the "Phaeodictyae." However it was not possible to describe the fungi as a new Triassic species because the material was too scant for a serious interpretation. Actually we have abundant material only from *Palaeodikaryomyces baueri,* a Triassic genus (Dörfelt and Schäfer 1998).

Palaeomycologists often ignored the problems surrounding the identification of fossil fungi. Approximately 600 fossilized fungi have been described, but many of these are dubious: see e.g. the compiled works by Meschinelli (1892), Pia (1927), Pirozynski (1976), Tiffney and Baarghoorn (1974). Palaeomycological investigations had only a marginal influence on the knowledge of the evolutionary history of fungi (Kreisel 1983).

Most fossilized fungi were reported from the Tertiary and Carboniferous sources. The preservation of hyphae and reproductive structures in wood or other plant parts is far more likely than the preservation of fungal structures in soil. Thus, many authors are of the opinion that fungi are primarily parasitic or symbiotic organisms. However, the fungi in the Schlierseerit, especially *Palaeodikaryomyces baueri,* represent a saprophytic group from a terrestrial ecosystem. They show that not only symbiotic or parasitic fungi lived in the Palaeo- and Mesozoic.

Palaeodikaryomyces baueri is a fungus of the Eumycota (Zygo-, Asco- and Basidiomycetes s.l., without the "Mastigomycotina"). It shows similarities with the parasitic or symbiotic fungi of the genus *Palaeomyces* from Devon (Kidston and Lang 1921) and with *Archagaricon* from the Carboniferous (Pia 1927), which have non-septate hyphae with vesicles, like many recent Zygomycetes, e.g. *Basidiobolus* or div. Endogonales.

Bacteria. From the Schlierseerit sheated bacteria and cyanobacteria were described (Poinar, Waggoner, and Bauer 1994). A filamentous organism is identified as "resembling extant representatives of the genera *Crenothrix* and *Sphaerotilus.*" Another filamentous structure is described as "resembling extant representatives of the genus *Scytonema.*" Our filamentous and single bacterial structures (Fig. 8, 9) could not be identified exactly.

Algae. The unicellular microalgae found, belong to the oldest as well as to the best-preserved fossils of their systematic group in Triassic amber. Fossils of euglenoid flagellates are very sparse and date back to the Tertiary (Walne and Kivic 1989). Our present findings of vegetative cells of *Euglena* from the Triassic amber are the oldest known fossils of this genus. The oldest fossils of monadal and coccal chlorophytes were described from the Pre-Cambrian (Floyd and O'Kelly 1989). The most exciting fossils of the chlamydophycean algae are the calcite shells of the solitary flagellate *Phacotus* dating back to the Oligocene and probably to pre-Tertiary periods (Müller and Oti 1981; Rutte 1953). Indeed, the fragile cells inside the calcite-loricae have not been preserved. The cells of *Chlamydomonas* and *Chloromonas* from the Triassic amber presented here are the oldest fossils of cell bodies of these flagellates. It is especially remarkable that the fragile vegetative cell bodies of these organisms are properly preserved. Even details inside the chloroplast, e.g. the stigma and the pyrenoid, are recognizable. Discussions about the differentiation of the two extant genera by means of the pyrenoids (*Chlamydomonas* with, *Chloromonas* without pyrenoid) remain controversial (Ettl 1970). Nevertheless, it can be demonstrated that this diacritical criterion existed already in the Triassic period.

The Chlorococcales have fossil records from the late Pre-Cambrian to the Holocene (Loeblich 1974). The picoplanktonic Chlorococcales in the Triassic amber attracted our special interest. It can be deduced from the small spheroid Pre-Cambrian acritarchs that these organisms are older than Triassic, but either did not fossilize or have been overlooked due to their minute size. Investigations on the recent species of *Nanochlorum* and *Choricystis* (so called *Nanochloris*-like green algae) revealed a polyphyletic origin of green eukaryotic picoplankton (Huss and Sogin 1990; Krienitz, Huss, and Hümmer 1996).

A comparison of the algal community found in the Triassic amber with extant biocenoses showed great similarity with the inhabitants of small acid bog lakes, referred to the composition of chlamydophyceans and coccal green microalgae (picoplankton) (Krienitz, Hehmann, and Casper 1997).

Zooflagellates. In the literature there are no references to palaeontologic zooflagellates. The present paper gives the first descriptions of fossil zooflagellates.

Testate Amoebae. Structures resembling shells of the testacean family Centropyxidae (*Centropyxis, Cyclopyxis*) occurred frequently in the Triassic amber. The elements of these structures are very likely small bubbles (vacuoles?). Their concentrations simulate shells, and gaps in the arrangement of the bubbles resemble shell apertures. There are amber fragments containing a wide spectrum of size of these amber-borne artifacts, some of which might be testacean shells. Only three testacean species could be identified unambiguously. They occur, contrary to the other protists found, in low density.

Testacean fossils before the Triassic period are sparse and doubtful (Pokorny 1958; Wolf 1995). In spite of the doubtfulness of the Palaeozoic testacean records, the Triassic findings

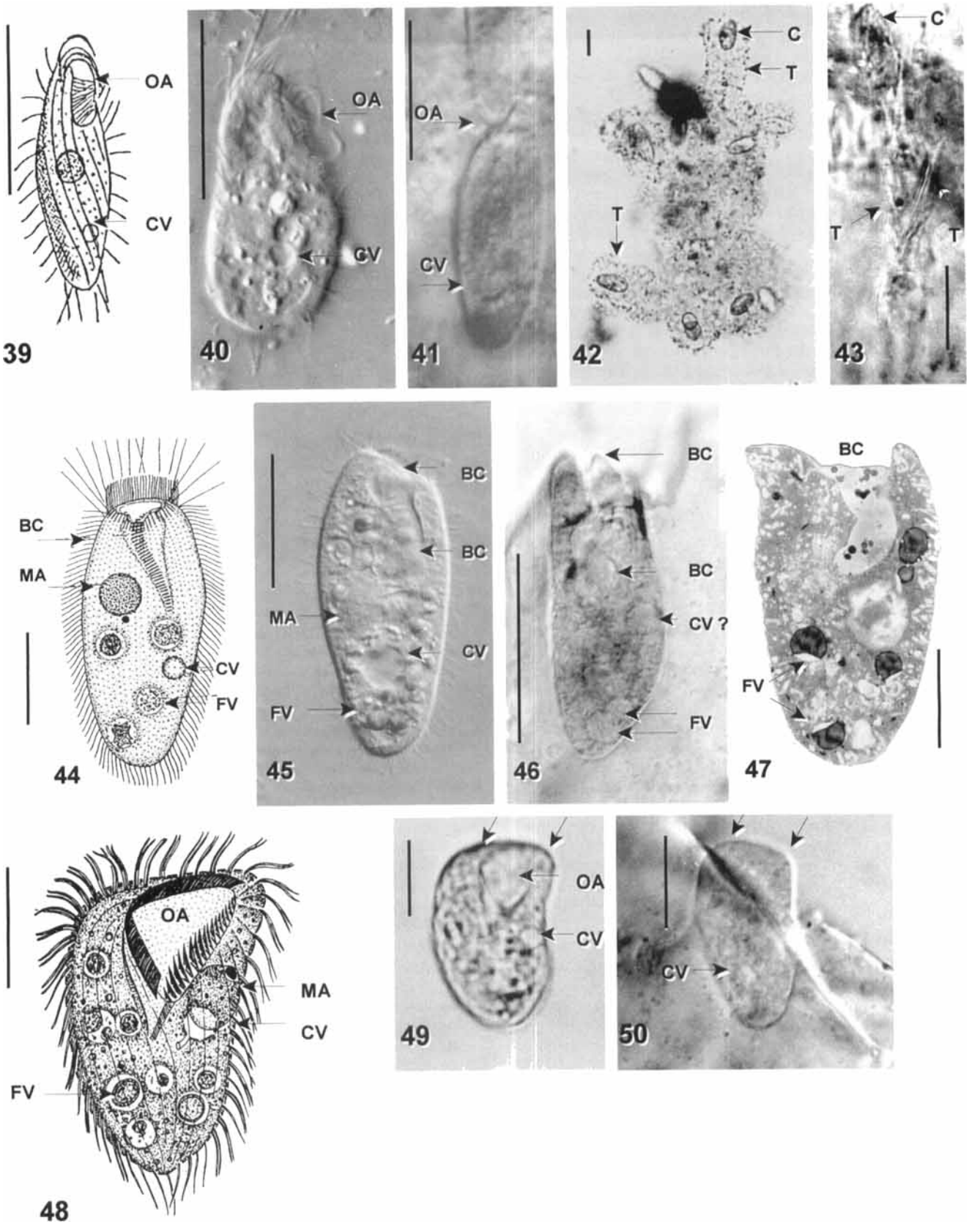

Fig. **39–43**. Extant (**39**, **40**, **42**; from [Foissner 1993]) and fossilized (**41**, **43**) *Cyrtolophosis mucicola*-like. **39**, **40**. Right lateral views of representative specimens; that shown in Fig. **40** is slightly broadened due to cover glass pressure. **41**. A fossilized specimen, which clearly matches the extant form (**39**, **40**) in body size and shape as well as in the location of the oral apparatus and the contractile vacuole. **42**. Extant *Cyrtolophosis mucicola* lives in a slimy tube, several of which form pseudo-colonies. **43**. A bifurcated amber inclusion with an organism sitting in the left tube.

show that forms similar extant species existed during that period.

Ciliophora. Ciliates date back to at least the Ordovician (about 500 million years), where loricas of tintinnids have been found (for review, see Tappan and Loeblich 1968). Aloricate ciliates do not usually fossilize, except in amber and lignite, where some doubtful reports are available. The first were probably some soft-bodied ciliates (*Aspidisca eocenica, Cinetoconia crassa, Ploesconia cycloides*) from Eocenic lignite (Renault and Roche 1868; Renault 1903). However, these findings have been questioned (Deflandre and Deunff 1957). Deflandre and Deunff (1957) mentioned, very briefly, a *Paramecium* in their paper on Cretaceous folliculinids from Gabon. "Une forme apparentée aux Paramécies aurait été trouvée dans une inclusion aqueuse de l'ambre. Nous n'avons pas eu confirmation de cette découverte." Similarly, (Wichterman 1986 p. 62) mentioned a *Paramecium* in amber from Canada. Unfortunately, neither the report by Deflandre and Deunff (1957) nor that of Wichterman (1986) is illustrated. However, the specimen Wichterman refers to (1986) is shown in Poinar (1992) and might indeed be a *Paramecium,* although it shows fewer details than our material.

Comparison with related species: when the Fig. 56–61 are compared, there can hardly be any doubt that they show congeneric organisms, viz. *Paramecium* species. The length: width ratio and the highly characteristic body shape and location of the contractile vacuoles of the fossilized specimens (Fig. 57, 59, 61) perfectly match extant members of the *Paramecium aurelia* complex (Fig. 56, 58, 60 for reviews, see Berger, Foissner, and Kohmann 1997; Wichterman 1986). However, all slipper-shaped *Paramecium* species (*P. aurelia, P. caudatum, P. multimicronucleatum, P. wichterman, P. africanum, P. ugandae*) are larger than 90 μm, usually between 150 and 300 μm (Wichterman 1986). Thus, the species from the Triassic amber, which is only 42–61 μm long, is very likely a new one. It is unlikely that the small size is caused by excessive shrinkage during fossilization because the other amber ciliates, which could be identified to species level, are very similar in size to the extant forms.

More recently, Poinar, Waggoner, and Bauer (1994) described three ciliate species from amber of the same locality we studied. However, some of the figures provided are not entirely convincing and need some reinterpretation. Their Fig. A shows, in our opinion, not the ciliate *Cyrtolophosis,* but a *Peranema*-like flagellate. This is indicated by the size (52 μm), the fusiform shape, and the large, globular inclusions highly resembling paramylon grains; the cilia, which are not recognizable in the figure, might be mucocysts, which are very distinct in some euglenids. Figure C shows "three ciliates resembling extant members of the genus *Paramecium.*" Indeed, size (about 160 μm) and shape resemble *Paramecium,* but we would interprete the "cilia" as discharging trichocysts. The *Paramecium* we found (Fig. 57, 59, 61) is much better preserved and smaller (42–61 μm), and thus doubtlessly a different species. Figure D probably shows, as suggested by Poinar, Waggoner, and Bauer (1994), a *Nassula*-like ciliate. Our results, especially those from the ciliates, agree with the interpretation by Poinar, Waggoner, and Bauer (1994) that "all of those fossils represent a biocenosis comprising a community of organisms that lived on the resin-bearing plant." Except for *Paramecium triassicum,* all species identified are common in soil and bark habitats (Foissner 1998). Five of the seven species identified belong to the Colpodea, a group of mainly terrestrial and r-selected ciliates (Foissner 1993). This indicates that the habitat was ephemeral, possible mud and soil in branch bases and bark crevices. On the other hand, all extant members of *Paramecium* are unable to form dormant stages (resting cysts) (Wichterman 1986). This might indicate that either the progenitors of the present day paramecia were able to form resting stages or that several different, ephemeral and more permanent, habitats were conserved in the amber. We favour the latter hypothesis because (1) the biocenosis found by Poinar, Waggoner, and Bauer (1994) and ourselves are rather different, although the amber is from the same locality, and (2) the organism communities surrounding the fossilized ciliates are distinctly different, viz., mainly fungal hyphae in the obligate fungal feeders *Pseudoplatyophrya nana* and *Mykophagophrys terricola* (Fig. 33, 36, 38) and bacteria and flagellates in *Tetrahymena rostrata,* a bacteria feeder (Fig. 54, 55).

Members of the family Colpodidae, which are the most common and typical soil ciliates (Foissner 1987), were lacking in the amber ciliate community observed by Poinar, Waggoner, and Bauer (1994) and ourselves. This is surprising and might shed doubt on the habitat interpretation. However, Wright and Lynn (1997), who calculated the maximum ages of ciliate lineages using a small subunit rRNA molecular clock, found that the Colpodidae evolved only about 180 million years ago, that is, after the deposition of the amber, which is 220–230 million years old. On the other hand, *Pseudoplatyophrya,* which evolved about 280 million years ago (Wright and Lynn 1997), was common in the amber. Whether this correspondence between our and Wright's and Lynn's data is a mere chance or a real, and fortunate result, needs further investigations.

General remarks. The bacteria and protists come from an amber piece of only 0.003 mm^3 volume. Therefore they represent a microcenosis which really existed and was not accumulated allochtonously (taphocenotically). It can be concluded that the habitat of the microfossils was semi-aquatic. There are both terriphilous and aquatic species in the cenosis. Terriphilous forms: fungi, extant *Cyclopyxis* (but occurs also in small waters), most ciliates (but some occur in shallow waters too). Aquatic forms: algae, extant *Centropyxis aculeata* var. *oblonga* (this species occurs in many subfossil samples of lakes and bogs, see Schönborn 1990), *Hyalosphenia* species (they occur in soils, mosses, and waters), extant *Paramecium* species (exclusive aquatic forms). The semi-aquatic habitat could have been an astatic pond, an extremely shallow water, moist soil or a phytotelma in the bark of the resin-producing plant. The latter is supposed by Poinar, Waggoner, and Bauer (1994).

The composition of the Triassic microcenosis also reminds of extant communities, especially documented by the ciliates

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This pattern strongly resembles extant pseudo-colonies of *C. mucicola* (Fig. **42**). C—ciliate, CV—contractile vacuole, OA—oral apparatus, T—tubes. Bars 20 μm.

Fig. **44–47**. Extant *Paracondylostoma setigerum* (**44**, **45**; from [Foissner 1993, Foissner & Kreutz 1998]) and *Bursaridium pseudobursaria* (**47**, from [Foissner 1993]) strongly resemble a fossilized amber organism (Fig. **46**). All have a similar size, shape and, especially, a deep buccal cavity. BC—buccal cavity, CV—contractile vacuole, FV—food vacuole, MA—macronucleus. Bars 30 μm.

Fig. **48–50**. Extant (**48**, **49**; from [Foissner 1993]) and fossilized (**50**) *Bryometopus triquetrus*-like. The extant and fossilized specimens match in shape, size, and location of the oral aperture, the anterior margins of which are marked by arrows. CV—contractile vacuole, FV—food vacuole, MA—macronucleus, OA—oral apparatus. Bars 20 μm.

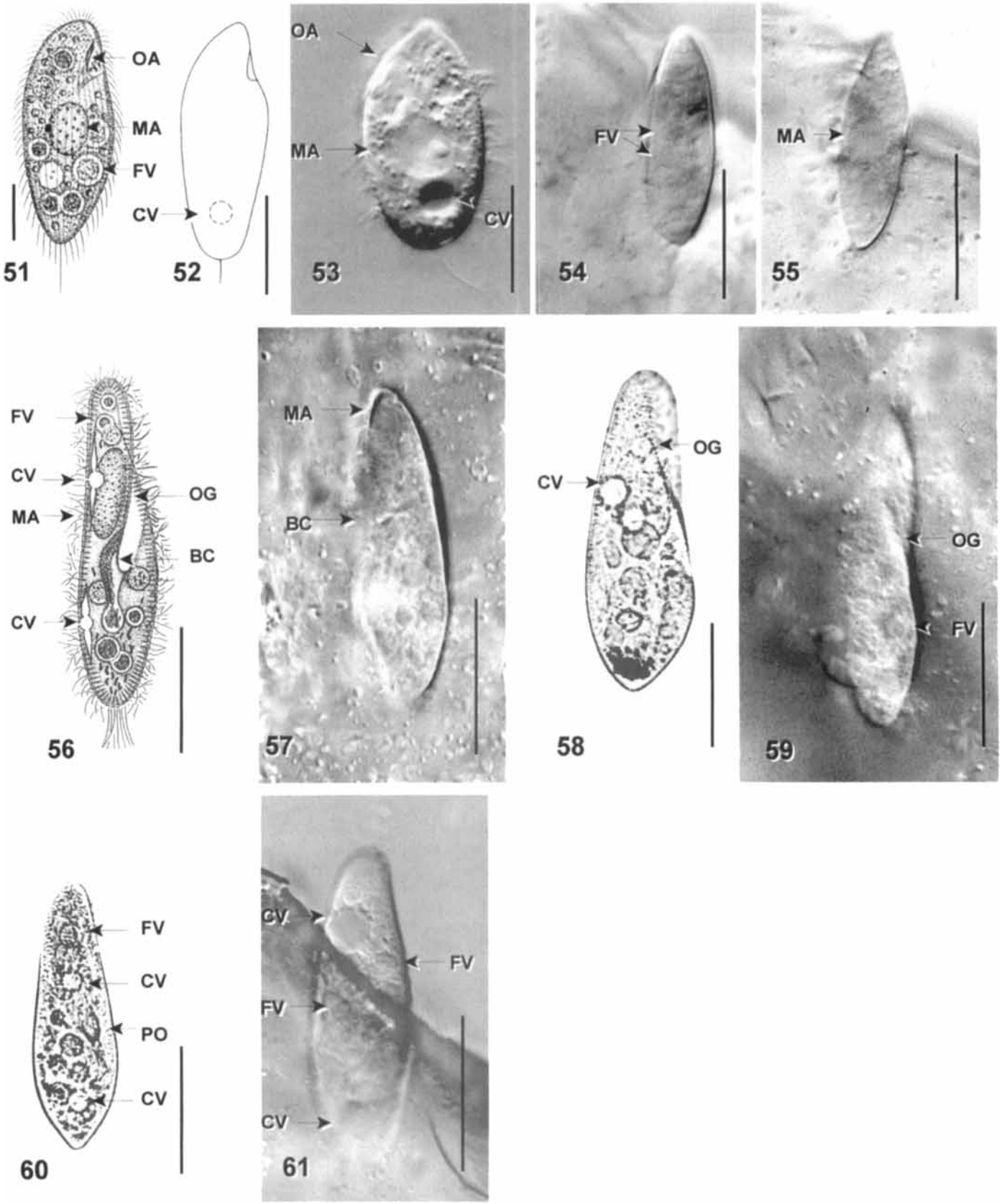

Fig. **51–55**. Extant (**51–53**; from [Foissner 1987]) and fossilized (**54, 55**) *Tetrahymena rostrata*. Note that the specimen shown in Fig. **53** was compressed, and was thus flattened, to show the macronucleus. The fossilized organisms match the extant *T. rostrata* in shape, size, and location of the macronucleus, which is extraordinarily well preserved in the specimen in Fig. **55**. Note many tiny globules, very likely bacteria in the amber around the ciliates. CV—contractile vacuole, FV—food vacuole, MA—macronucleus, OA—oral apparatus. Bars 20 μm.

and their prey organisms (fungi) as well as by the *Nannochloris*-like green algae community in small acid bog lakes.

It can be concluded that the morphological evolution of many protists was slow or stationary (Poinar, Waggoner, and Bauer 1994), which is also supported by molecular studies (Frankel 1983). Stationary evolution may be caused by long-time occupation of the habitat niches. In the case of extinction events (e.g. in the Upper Triassic period, and previously in Permian) new colonization may have led again to the same forms (in consequence of the same information).

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Fig. **56–61**. Extant *Paramecium aurelia* (**56**, **58**, **60**; from [Berger et al. 1997]) and fossil amber *P. triassicum* n. sp.(**57**, **59**, **61**). Obviously, both species are very similar, except for the size, which is about 150 × 50 μm in *P. aurelia* and 42–60 × 12–17 μm in *P. triassicum*. Note the excellent preservation of the oral groove and the contractile vacuoles in the fossilized specimens. BC—buccal cavity, CV—contractile vacuoles, FV—food vacuoles, MA—macronucleus, OG—oral groove, PO—pharyngeal opening. Bars 60 μm (Fig. **56**, **58**, **60**) and 20 μm (Fig. **57**, **59**, **61**).

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