

***Tetragoniomyces* gen.nov. and Tetragoniomycetaceae fam.nov. (Tremellales)<sup>1</sup>**

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The general structure of *Tremella uliginosa* Karst. is discussed. Basidia of the species are thick walled, deciduous, and germinate directly, i.e., without spore production. Dikaryotic hyphae grow directly from the basidium, or alternatively, a pair of germ tubes conjugate outside the basidium to initiate the dikaryon. Because of its distinctive basidial structure and function, the species is placed in a new genus, *Tetragoniomyces* gen.nov., and family, *Tetragoniomycetaceae* fam.nov.

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Les auteurs discutent la structure générale de *Tremella uliginosa* Karst. Les basides ont une paroi épaisse, elles sont décidues et germent directement, c'est-à-dire sans production de spores. Les hyphes dicaryotiques croissent directement à partir de la baside ou, alternativement, une paire de tubes germinatifs se conjuguent à l'extérieur de la baside pour initier le dikaryon. A cause de la structure et de la fonction particulières de sa baside, l'espèce est rangée dans un nouveau genre, *Tetragoniomyces* gen.nov., et une nouvelle famille, les *Tetragoniomycetaceae* fam.nov.

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*Tremella uliginosa* was described by Karsten (1833) from material collected in Finland. To our knowledge, the only report of the species subsequent to 1883 is that of Koske (1972) who collected the species in Canada. Koske obtained cultures of the species and noted that its basidia are deciduous and that germination of the basidia is by direct formation of hyphae. In August 1979, a collection of the species was made in Germany. Studies of all specimens available, as well as cultures of the Canadian and German collections, have led us to conclude that the species differs markedly from all other described Tremellaceae. Accordingly, the genus *Tetragoniomyces* and a new family, Tetragoniomycetaceae, are proposed here for the taxon.

***Tetragoniomyces* Oberwinkler & Bandoni, gen.nov.**

Fungi parasitici inter cellulas sclerotiorum hospitalium crescunt convivia cum haustoriis ex fibulis nascentibus apparant. Basidia in apicibus hypharum ramulorumque earum oriuntur et fibulis affixa sunt. Probasidia ellipsoidea vel globosa plus minusve hyalina inde in partes quattuor divisa sunt procedente tempore parietes

basidiorum sculpturis internis ornantur. Mature basidia hyphis abscidentur et per aquam distribuntur; temporis opportunitate hyphis plerumque fibulatis germinant et haustoria producunt.

TYPUS GENERIS: *Tetragoniomyces uliginosus* (Karst.) Oberw. & Band.

BASIONYM: *Tremella uliginosa* Karst.

ETYMOLOGY: τετρα, four; γωνη, birth, seed; μυκης, fungus.

***Tetragoniomyces* Oberwinkler and Bandoni, gen.nov.**

Mycoparasitic, mucedinoid, the basidiocarp developing on the surfaces of sclerotiumlike structures of the host. Hyphae with clamps, arising between the enlarged cells of the host, attached to the latter by haustoria. Basidiophores branched, the branch apices bearing successive basidia and elongating slightly before producing each new basidium, the clamp vestiges remaining on the basidiophores. Probasidia ellipsoid to globose, becoming four-celled, the cells becoming rounded and developing thick walls, held together by the thickened, sculptured outer wall; at maturity, the cells occupy a single plane, older basidia often appearing roughly rhomboidal in profile. Germination of detached basidia is by direct formation of dikaryotic hyphae, or by the formation of germ tubes by individual cells and

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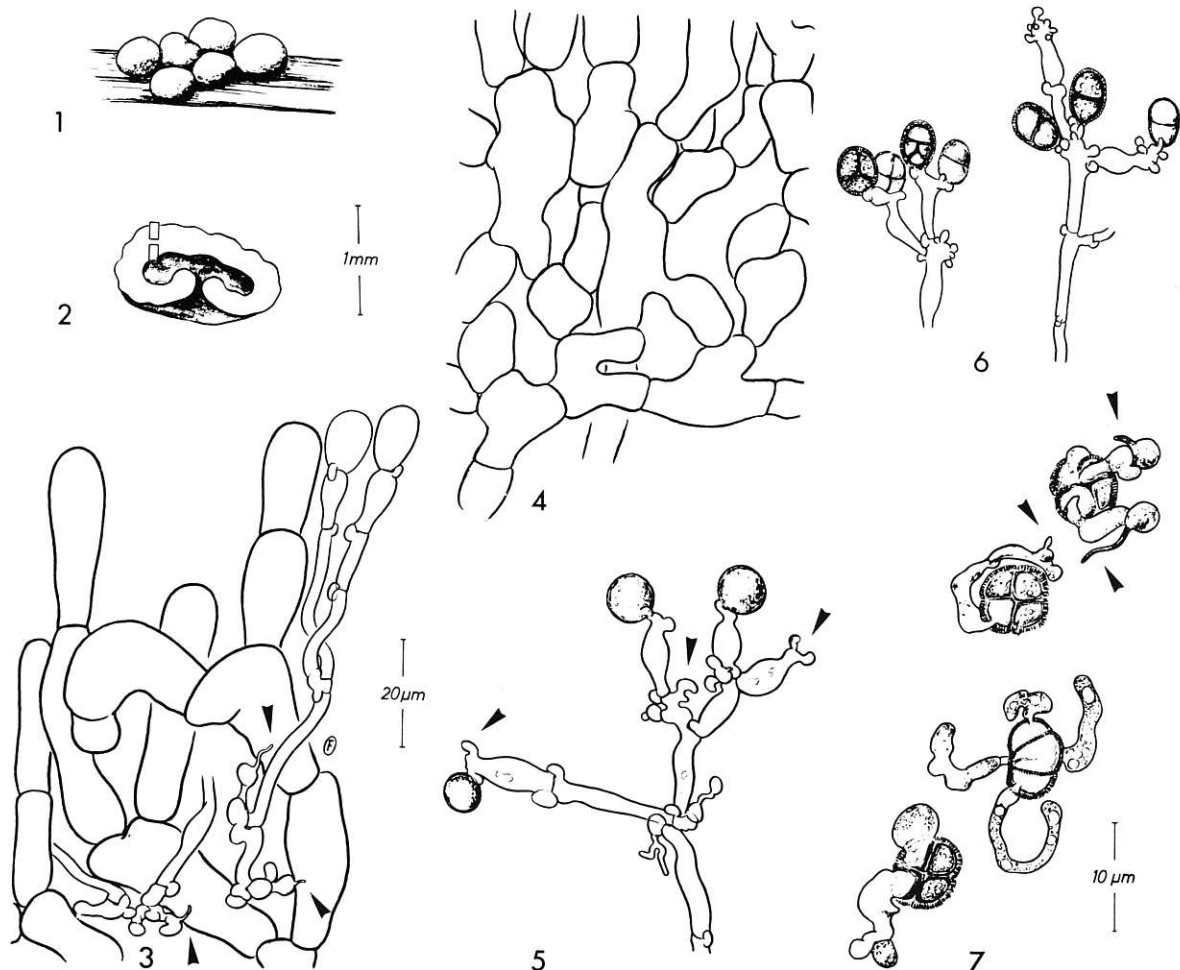


FIG. 1. Habit of host sclerotium infected by *Tetragoniomyces uliginosus*. FIG. 2. Section of mature host sclerotium with hollow central region. (Upper rectangle indicates source for Fig. 3; lower rectangle for Fig. 4.) FIG. 3. Peripheral portion of host sclerotium showing hyphae of *T. uliginosus* attached by haustoria (arrows) to sclerotial cells. FIG. 4. Uninfected internal portion of host sclerotium. FIG. 5. Young basidiophore showing branching and clamp vestiges (arrows) where basidia have been released. FIG. 6. Basidiophore with nearly mature and developing basidia; note also the numerous fingerlike clamp vestiges. FIG. 7. Germinating basidia in culture. The two lower basidia have germinated by direct production of germ tubes from basidial cells; the two upper basidia have formed dikaryotic hyphae (arrows indicate haustoria).

conjugation of these tubes outside the basidium to produce the dikaryotic hyphae.

TYPE SPECIES: *Tremella uliginosa* Karst.

*Tetragoniomyces uliginosus* (Karst.) Oberw. & Band.,  
comb. nov. Figs. 1-3, 5-24

= *Tremella uliginosa* Karsten, Symb. Mycol. Fenn.  
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1833.

Parasitic, the basidiocarp forming a surface layer on small sclerotiumlike structures of the basidiomycetous host, mucedinoid, yellowish to orange or brownish-

orange, smooth to cerebriform, the shape conforming to that of the host structure which usually does not exceed 1 mm in diameter. Hyphae narrow, with clamps, 2-5  $\mu$ m in diameter, attached to the inflated host cells by haustoria. Basidia borne terminally on branched basidiophores, the latter elongating slightly before producing each basidium, the clamp vestiges remaining on the basidiophore; probasidia at first ellipsoid to globose or pyriform, thin walled when first produced, becoming thick walled before division, four-celled at maturity; walls of the compartments also becoming secondarily thickened, the cells rounding off and becoming almost

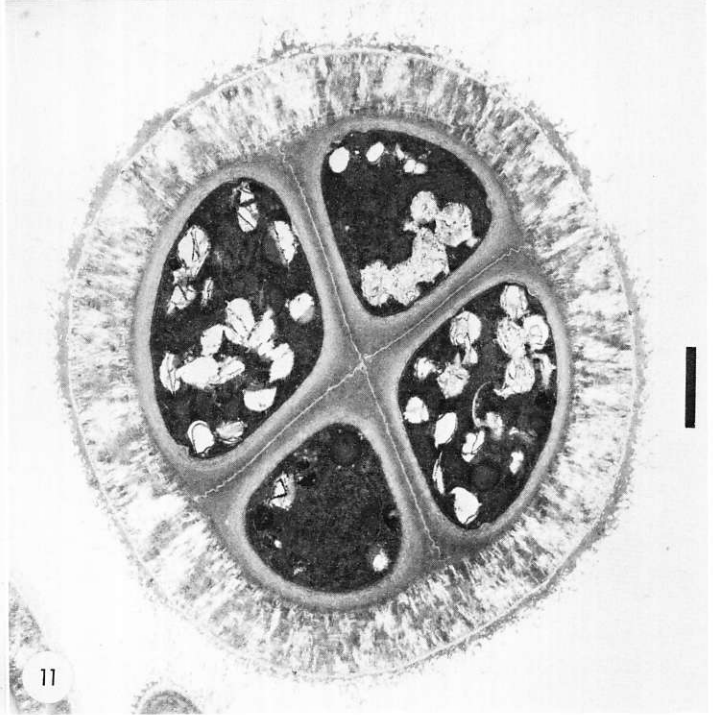
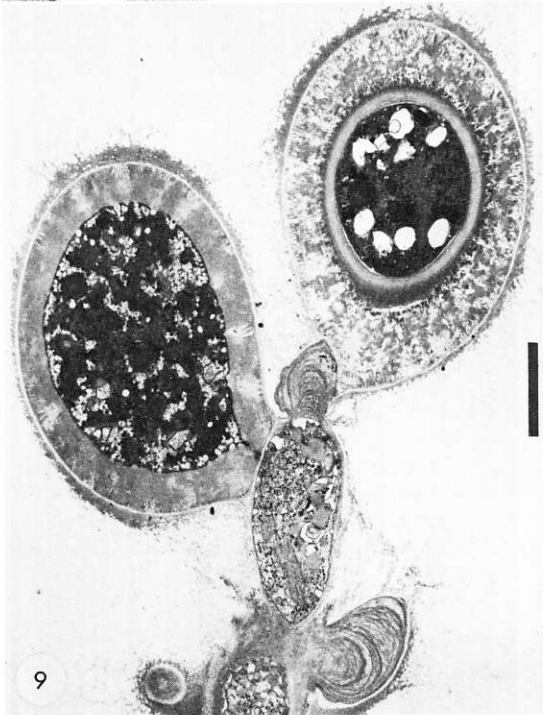
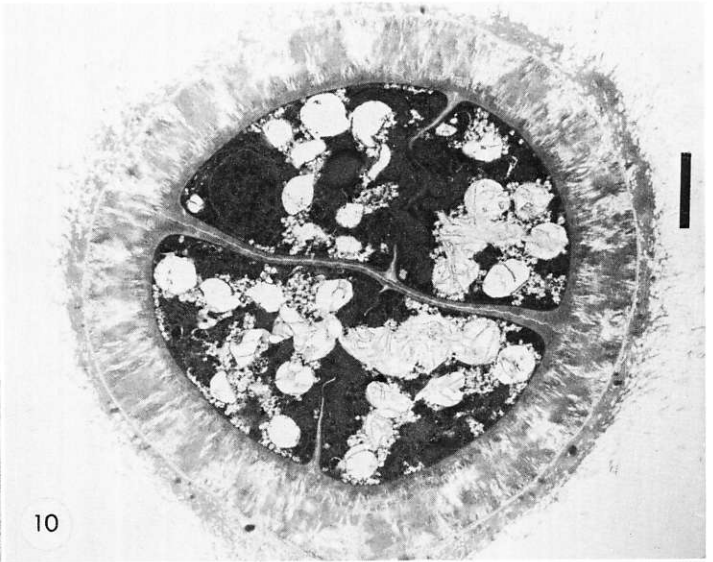
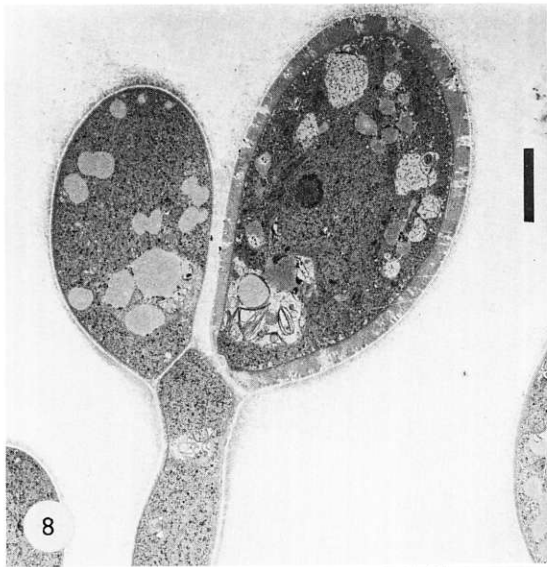


FIG. 8. Basidiophore and two probasidia, the younger on the left. Note that the probasidium on the left has only a thin, electron-opaque wall layer; the older probasidium has, within the electron-opaque layer, the developing secondary spongy wall layer. Bar = 2  $\mu$ m. FIG. 9. Basidiophore with thick-walled probasidium (left) and oblique section through mature basidial cell. A section through a clamp vestige is also visible (lower right). Bar = 2  $\mu$ m. FIG. 10. Four-celled basidium, the first cross wall is complete and secondary thickening has commenced; the two walls at right angles to the first are not yet complete. Bar = 2  $\mu$ m. FIG. 11. Median section of mature basidium showing cruciate septation and thick inner walls surrounding each inner compartment. Bar = 2  $\mu$ m.

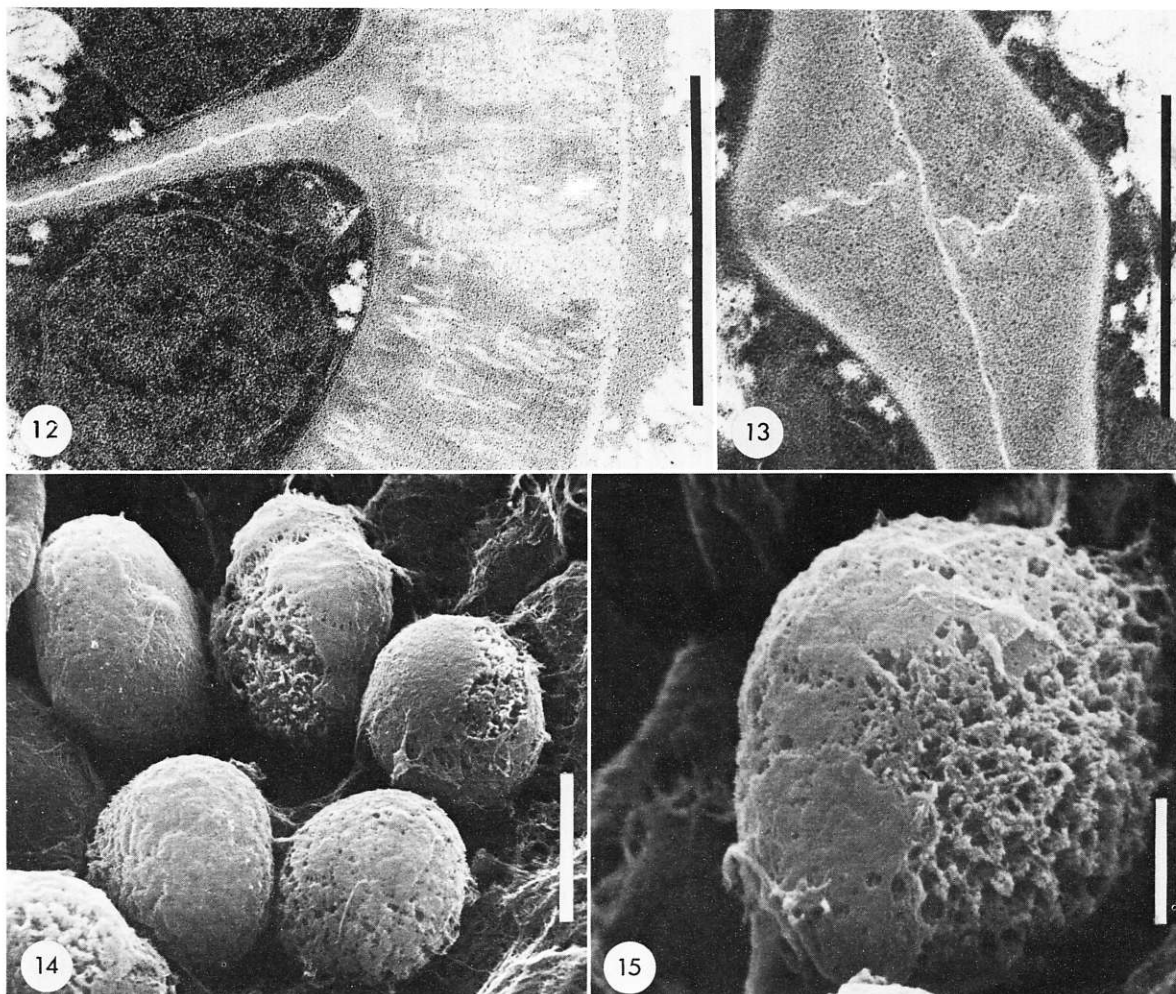


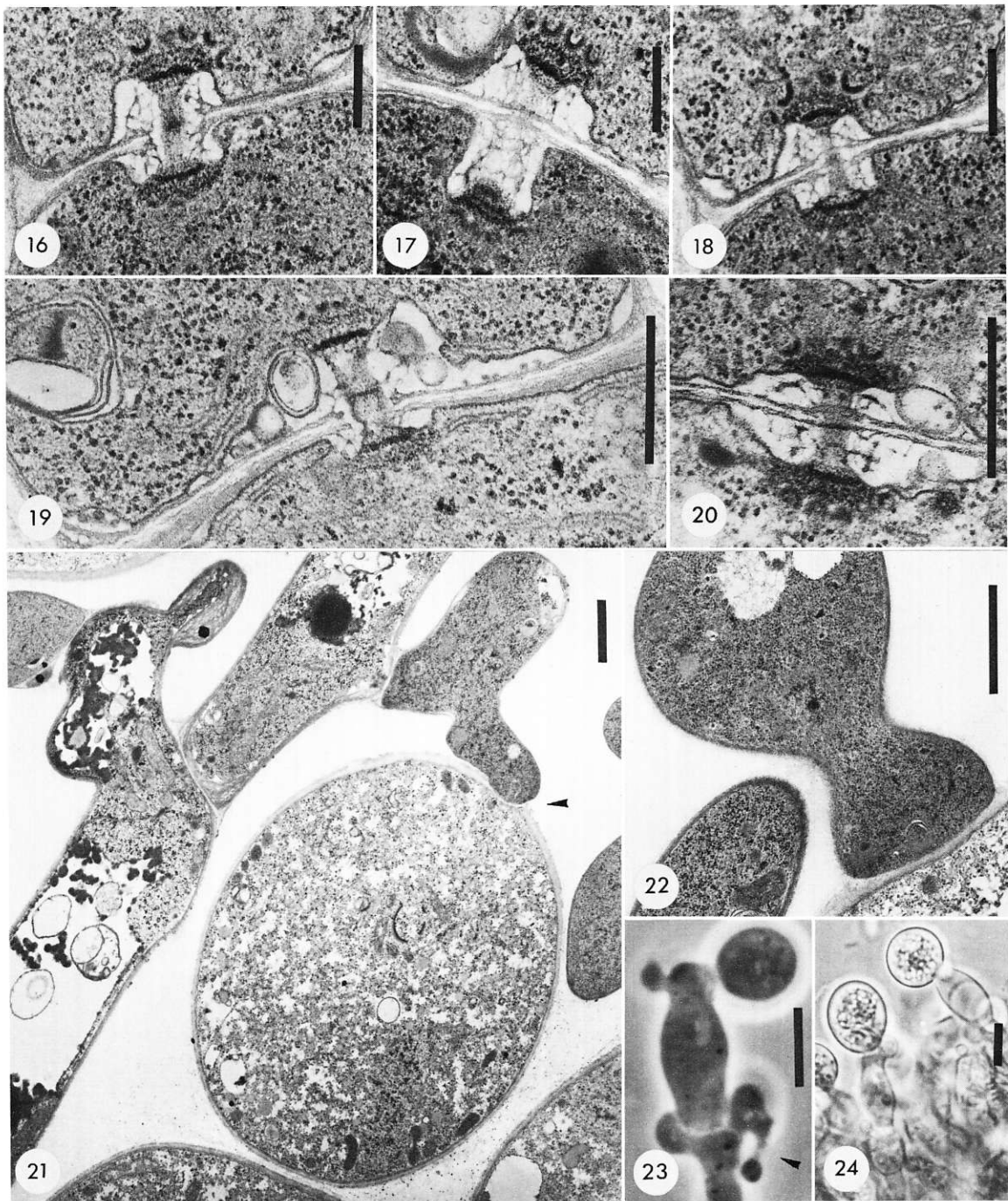
FIG. 12. Portion of periphery of young basidium showing radiately channeled secondary wall layer, cytoplasm, and nucleus. Bar = 2  $\mu$ m. FIG. 13. Enlarged central portion of a basidium, the first cross wall of which has formed. Centripetal development of secondary thickening of septa at right angles to the first is suggested in this figure. Bar = 2  $\mu$ m. FIG. 14. Scanning electron micrographs of several basidia. Bar = 5  $\mu$ m. FIG. 15. SEM of a single, mature basidium showing porous nature of basidial wall. Bar = 2  $\mu$ m.

globose, held together by the sculptured, closely appressed outer wall. Mature basidia deciduous, rhomboidal in outline, the cells occupying a single plane, 10–12(–15)  $\times$  7–10  $\mu$ m; germination by direct outgrowth of dikaryotic hyphae or by the formation of germ tubes which conjugate outside the basidium and initiate development of dikaryotic hyphae.

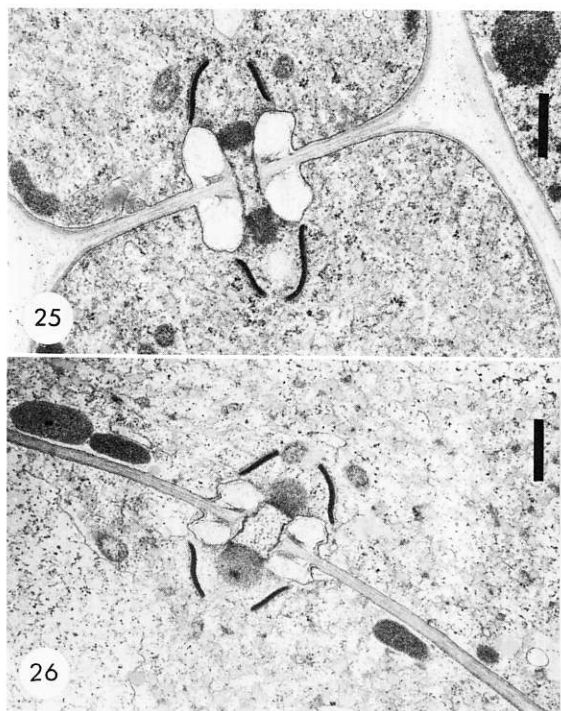
**HABITAT:** On decaying plant material in wet habitats.

**SPECIMENS EXAMINED:** P. Karsten, Finland, near Mustiala, July 1869 (H holotype); R. E. Koske, January and July 1971 (Nos. 109 and 513; UBC), Vancouver, Canada; B. and F. Oberwinkler and R. Bandoni, No. 29254, Germany, Baden-Wurtemberg, Laiz bei Sigmaringen, Donau-Altwasser, August 1979; TUB.

Although no mention was made of the habitat by Karsten, the type material is covered by remains of several freshwater algae. The specimens examined by Koske developed on wet petioles of *Acer macrophyllum* Pursh maintained at 4 and 10°C in laboratory incubators. The collection from Germany was on wet, decaying leaves of *Glyceria maxima* (Hartm.) Holmb. immediately adjacent to the water of a shallow oxbow lake, a former meander of the Danube River. The deciduous basidia may well be an adaptation for water dispersal. The four-lobed form of old, detached basidia, and the thickened, apparently porous outer wall may also be adaptations for water dispersal. Although the thick outer wall appears to be sculptured by light microscopy (and is so designated in the generic and species descriptions



FIGS. 16–20. Sections of dolipore septa of *Tetragoniomyces uliginosus*. Figures 16 and 18 are of median sections of young dolipores; note electron-transparent zones at either end of pores. In Fig. 17, a nonmedian section showing *Tremella*-like parenthesome. Figures 19 and 20 are of apparently older dolipore structures in which disintegration appears to be occurring. FIG. 21. Hypha and haustorium of *T. uliginosus* attached to host cell (arrow; not a median section). Bar = 1  $\mu$ m. FIG. 22. Hyphal structure of *T. uliginosus* appressed to host cell wall. Bar = 1  $\mu$ m. FIG. 23. Phase-contrast photograph of a basidiophore with a young basidium and clamp vestige above; a portion of a haustorium is present at the lower right. Bar = 5  $\mu$ m. FIG. 24. Light micrograph of basidiophores and probasidia at periphery of host sclerotium. Bar = 5  $\mu$ m.



FIGS. 25, 26. Median sections of dolipores in hyphae of host of *T. uliginosus*. Bar = 1  $\mu$ m. Note differences in parentheses structure of this fungus and that of *T. uliginosus*.

above), ultrathin sections (Figs. 8–11) suggest an irregular, radiately channeled structure. It is possible that this porous structure results from expansion of the basidium without concurrent deposition of new wall material.

*Tetragoniomyces uliginosus* differs from all other described taxa in the Tremellaceae in having deciduous, thick-walled basidia that germinate directly. With respect to basidiophore proliferation, there is a superficial similarity to *Basidioidendron*, a genus in which, however, the basidia are retained on the basidiophore.

Young probasidia (Figs. 8, 9, 23, 24) are ellipsoid to subglobose and each is subtended by a clamp. As can be seen in Figs. 8 and 9, a thick wall is deposited just inside the outer wall layer; this occurs before the probasidium has reached its maximum size. Walls in some species of *Tremella* may become thickened, probably owing to weather conditions, slow development, and age. In *T. uliginosus*, the thickening results from deposition of an apparently specialized wall layer. The layer becomes pierced by irregular radial channels (Figs. 10, 11, 12); the “spongy” nature of this wall layer is visible in the scanning electron microscope (SEM) figures of basidia (Figs. 14, 15).

The walls of the inner compartments of the basidia also are thickened and unlike those of other Tremella-

ceae. In Fig. 10, the primary septa are visible; the thick secondary walls visible in Figs. 11–13 appear to develop centripetally soon after compartments have formed.

After formation and abscission of a basidium, the clamp vestige remains on the basidiophore apex (Figs. 5, 6, 23); an ultrathin section through a clamp vestige is shown in Fig. 9. Conidiophores of several Heterobasidiomycetes, e.g., *Tremella obscura* (Olive) Christianesen, *T. polyporina* Reid, and *Platygløea abdita* Bandoni, proliferate and retain clamp vestiges in the same manner. The dikaryotic conidia of such species are probable homologues of basidia, but basidiophores of the same taxa do not proliferate in this same manner.

Koske (1972) reported that basidial germination occurs only by the direct formation of hyphae in *T. uliginosus*; our studies have confirmed this. Two adjacent basidial cells apparently conjugate within the basidial wall, a dikaryotic hypha growing from one of the two cells (Fig. 7). Alternatively, germ tubes develop from the basidial cells and conjugate outside the basidium. In either case, contents of the basidial cells empty into the developing hyphae. Haustoria are produced soon after dikaryotic hyphal growth commences; similar structures are attached to the host cells in the basidiocarps (Figs. 3, 21). The haustoria are like those observed in species of *Tremella* (Olive 1946; Bandoni 1961; Bezerra and Kimbrough 1978). The dolipore cap structure of *T. uliginosus* (Figs. 16–20) also is similar to that of *Tremella* species as reported by Khan (1976), Bezerra and Kimbrough (1978), and Moore (1978).

The absence of basidiospores, basidia functioning as disseminules, and unusual wall structure all indicate that *T. uliginosus* is not closely related to the known Tremellaceae. Yet features such as the septal structure, haustoria and mycoparasitism, and the four-celled basidia link *Tetragoniomyces* with *Tremella* and *Sirobasidium*. The differences suggest that *T. uliginosus* diverged from these taxa in the distant past and should not be placed in the Tremellaceae. We therefore propose a new family, Tetragoniomycetaceae, for the genus.

#### **Tetragoniomycetaceae** Oberwinkler & Bandoni, fam. nov.

Fungi mycoparasitici basidiis decidentibus sine sterigmatibus sporisque. Basidia ipsa diasporae sunt et hyphis fibulatis germinant.

TYPUS FAMILIAE: *Tetragoniomyces*.

We were unable to identify the basidiomycete parasitized by *T. uliginosus*. The general structure of the sclerotia is illustrated in Fig. 4; that of the dolipore apparatus is shown in Figs. 25 and 26. These features are suggestive of the *Rhizoctonia complex*, especially *Thanatephorus* Donk as characterized by Tu and Kim-

brough (1978). However, we were unable to obtain a basidial stage of the species.

### Acknowledgements

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