

Classicula: the teleomorph of *Naiadella fluitans*¹

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Abstract: A new genus, *Classicula*, and a new species, *Classicula fluitans*, are described in the Urediniomycetes for the teleomorph of *Naiadella fluitans*. *Classicula fluitans* forms transversely septate basidia with subapically swollen sterigmata and long fusiform basidiospores. An integrated analysis of morphological, ultrastructural and molecular data indicates that *Classicula fluitans* is a member of the Urediniomycetes. Among the Urediniomycetes, *Classicula fluitans* shares the formation of simple septal pores associated with microbodies and tremelloid haustorial cells only with the hyphomycete *Jaculispora submersa*. In addition, in our molecular phylogenetic analyses with at least two representatives of all known urediniomycetous groups, *Classicula fluitans* appears together with *Jaculispora submersa* in a statistically well-supported cluster. Accordingly, the family Classiculaceae and the order Classiculales are proposed to accommodate these fungi in the Urediniomycetes.

Key words: aquatic hyphomycetes, molecular phylogeny, mycoparasitism, *Naiadella*, systematics, ultrastructure, Urediniomycetes

INTRODUCTION

In 1987, Marvanová and Bandoni described the aquatic hyphomycete *Naiadella fluitans* Marvanová & Bandoni, isolated from leaf litter of *Scirpus microcarpus* Presl and from stream foam. The fungus forms hyphae with clamps, binucleate navicular conidia

with distal setose branches and tremelloid haustorial cells. Consequently, Marvanová and Bandoni (1987) concluded that this fungus is basidiomycetous. During our experiments with this fungus the basidial stage was observed.

Because *Naiadella fluitans* frequently is confused with the hyphomycete *Jaculispora submersa* H.J. Huds. & Ingold (Marvanová and Bandoni 1987), we added this fungus to our phylogenetic analyses. *Jaculispora submersa* was described from leaf litter in a stream in Jamaica (Hudson and Ingold 1960). A pure culture was not established from their material, and neither clamps nor other characters suggesting affinity to basidiomycetes were mentioned in the protologue. Matsushima (1987) reported isolate MFC 12864, which he identified as *Jaculispora submersa*, from a decomposing leaf in a terrestrial habitat. He illustrated conidia and hyphae with clamps but did not mention haustorial cells.

MATERIALS AND METHODS

Cultures of *Naiadella fluitans* [Robert J. Bandoni (RJB) 7484-A (ex-type culture) = American Type Culture Collection (ATCC) 64713] and *Jaculispora submersa* [Czech Collection of Microorganisms (CCM) 8127 = Matsushima Fungus Collection (MFC) 12864, deposited in CCM by R.J. Bandoni] were maintained on malt yeast-peptone agar (Bandoni 1972). Basidia of *Naiadella fluitans* were obtained by carefully placing pieces of culture (ca 10 mm in diam) in water in Petri dishes so that the aerial mycelium was not submerged. Petri dishes with the floating pieces of *Naiadella fluitans* were incubated at room temperature. Germination of conidia was observed on both malt yeast-peptone agar in Petri dishes and on microscope slides kept moist in Petri dishes and incubated at room temperature.

For transmission electron microscopy (TEM), pieces of cultures of *Naiadella fluitans* and *Jaculispora submersa* were fixed with 2% glutaraldehyde. After six transfers in 0.1 M Na-cacodylate buffer, the material was postfixed in 1% osmium tetroxide in the same buffer for 1 h in the dark, washed in distilled water, and stained in 1% aqueous uranyl acetate for 1 h in the dark. After five washes in distilled water, the material was dehydrated in an acetone series, embedded in Spurr's plastic and sectioned with a diamond knife. Serial sections were mounted on formvar-coated, single-slot copper grids, post-stained with lead citrate for 5 min and examined in a transmission electron microscope operating at 80 kV.

DNA sequences were obtained using the same methods

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as described earlier (Begerow et al 1997). We used the nuclear small-subunit rRNA gene to build an alignment of 1366 bp. The alignment was produced with Clustal X (Jeanmougin et al 1998) and optimized visually. Because of problems in the alignment the positions 187–197, 208–226, 269–285, 334–338, 624–633, 663–672, and 1075–1088 were excluded from the phylogenetic analyses. The alignment was analyzed with two methods. (1) Neighbor joining, in which Modeltest 3.0 (Posada and Crandall 1998) was used to determine a model of DNA substitution that fits the dataset, and TrNIG was selected from both likelihood ratio test and from Akaike information criterion [base frequencies: $\pi_A = 0.2494$, $\pi_C = 0.2053$, $\pi_G = 0.2840$, $\pi_T = 0.2614$; substitution rates: $A/C = A/T = C/G = G/T = 1.0000$, $A/G = 2.5185$, $C/T = 5.0665$; gamma shape parameter = 0.5548; percentage of invariant sites = 0.3769, see Swofford et al (1996) for an overview of these parameters]. Neighbor-joining analysis was done using genetic distances, according to the specified substitution model with PAUP 4.b10 (Swofford 2002). 10 000 replicates were used for bootstrap analysis. (2) The Bayesian approach, in which Monte Carlo Markov chains (MCMC) were used, as described by Huelsenbeck and Ronquist (2001). With this method it is possible to estimate the probabilities (“a posteriori probabilities”) of the monophyly of certain taxa under a given DNA alignment. Four incrementally heated simultaneous Monte Carlo Markov chains were run over 1 000 000 generations using the general time reversible model (six rate classes) of DNA substitution with gamma distributed substitution rates (see Swofford et al 1996), random starting trees and default starting parameters of the DNA substitution model (Huelsenbeck and Ronquist 2001). Trees were sampled every 100 generations, resulting in an overall sampling of 10 000 trees. From those trees that were sampled after the process had reached stationarity, a 50% majority-rule consensus tree was computed to obtain estimates for a posteriori probabilities. This Bayesian approach of phylogenetic analysis was repeated several times, always using random starting trees and default starting values for the model parameters to test the reproducibility of the results.

Species with sequences obtained from GenBank are: *Agaricostilbum hyphaenes* (Har & Pat.) Oberw. & Bandoni, U40809; *Auricularia auricula-judae* (Bull. ex St. Ann.) Wettst., L22254; *Boletus satanas* Lenz, M94337; *Chionosphaera apobasidialis* Cox, U77662; *Cronartium ribicola* Fischer, M94338; *Dacrymyces stillatus* Nees: Fr., L22258; *Erythrobasidium hasegawianum* (Yamada & Komagata) Hamamoto, Sugiyama & Komagata, D12803; *Filobasidiella neofomans* Kwon-Chung, D12804; *Graphiola cylindrica* Kobayasi, D63929; *Helicobasidium mompa* Tanaka, U77064; *Helicobasidium purpureum* Pat., D85648; *Heterogastridium pycnidioideum* Oberw. & Bauer, U41567; *Kondoa malvinella* (Fell & Hunter) Yamada, Nakagawa & Banno, D13776; *Kriegeria eriophori* Bres., U77063; *Leucosporidium scottii* Fell, Statzell, Hunter & Pfaff, X53499; *Microbotryum violaceum* (Pers.: Pers.) Deml & Oberw., U77062; *Mixia osmundae* (Nishida) Kramer, D14163; *Neurospora crassa* Shear & Dodge, X04971; *Nyssospora echinata* (Lév.) Arth., U77061; *Peridermium harknessii* J. P. Moore, M94339; *Pseudohydnum gelatinosum* (Scop.: Fr.) Karst., L22260; *Rhodosporidium torulo-*

ides Banno, X60180; *Saccharomyces cerevisiae* Meyen ex Hansen, J01353; *Sporidiobolus johnsonii* Nyland, L22261; *Sporobolomyces roseus* Kluyver & van Niel, X60181; *Taphrina deformans* (Berk.) Tul., U00971; *Tilletia caries* (DC.) Tul., U00972; *Tremella globispora* Reid, U00976; *Ustilago hordei* (Pers.) Lagerh., U00973; *Ustilago maydis* (DC.) Corda, X62396. Species with newly published sequences (cited with culture collection or herbarium number) are: *Helicogloea lagerheimii* Pat., Herbarium F. Oberwinkler 36341, AY124476; *Jaculispora submersa* H.J. Huds. & Ingold, CCM 8127, AY124477; *Naiadella fluitans* Marvanová & Bandoni, ATCC 64713, AY124478; *Occultifur externus* Sampaio, Bauer & Oberw., Portuguese Yeast Culture Collection (IGC) 4817, AY124475; *Cystobasidium fimetarium* (Schum.) Roberts, Herbarium R. Bauer 3086 (material obtained from K. H. Rexer), AY124479; *Platygløea vestita* Bourd. & Galz., Herbarium F. Oberwinkler 39734, AY124480; *Ustilentyloma fluitans* (Liro) Vánky, Herbarium R. Bauer 900, AY124481. The sequence alignment obtained is deposited in TreeBASE (<http://treebase.bio.buffalo.edu/treebase/>) with the accession numbers S 822 and M 1319.

RESULTS

Starting from the floating agar pieces, *Naiadella fluitans* aerial mycelium grew along the water surface where clusters of basidia with subapically swollen sterigmata (FIGS. 1, 2, 8–10) were produced after 10 wk. Because urediniomycetes having transversely septate basidia with subapically swollen sterigmata are unknown, a new genus and a new species are proposed:

Classicula Bauer, Begerow, Oberwinkler et Marvanová, gen. nov.

Fungi Urediniomycetum basidiis transverse septatis, sterigmatibus parte subapicali inflata, basidiosporis fusiformibus, cellulis haustorialibus tremelloideis.

Members of the Urediniomycetes having transversely septate basidia with subapically swollen sterigmata, fusiform basidiospores and tremelloid haustorial cells.

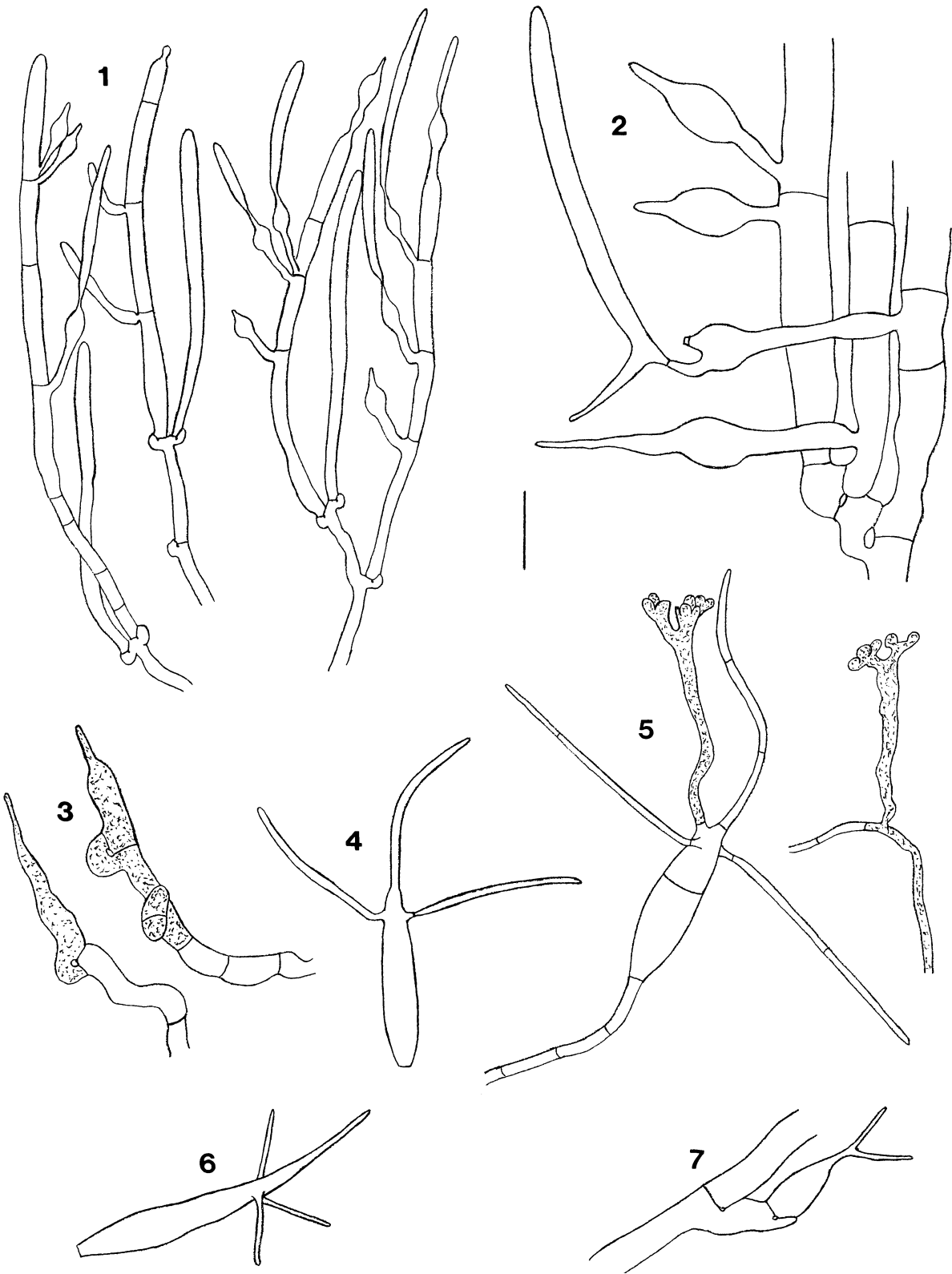
Typus generis. *Classicula fluitans* Bauer, Begerow, Oberwinkler et Marvanová.

Etymology. A cluster of aerial basidia produced on the water surface resembling a flotilla, Lat. = *classicula*.

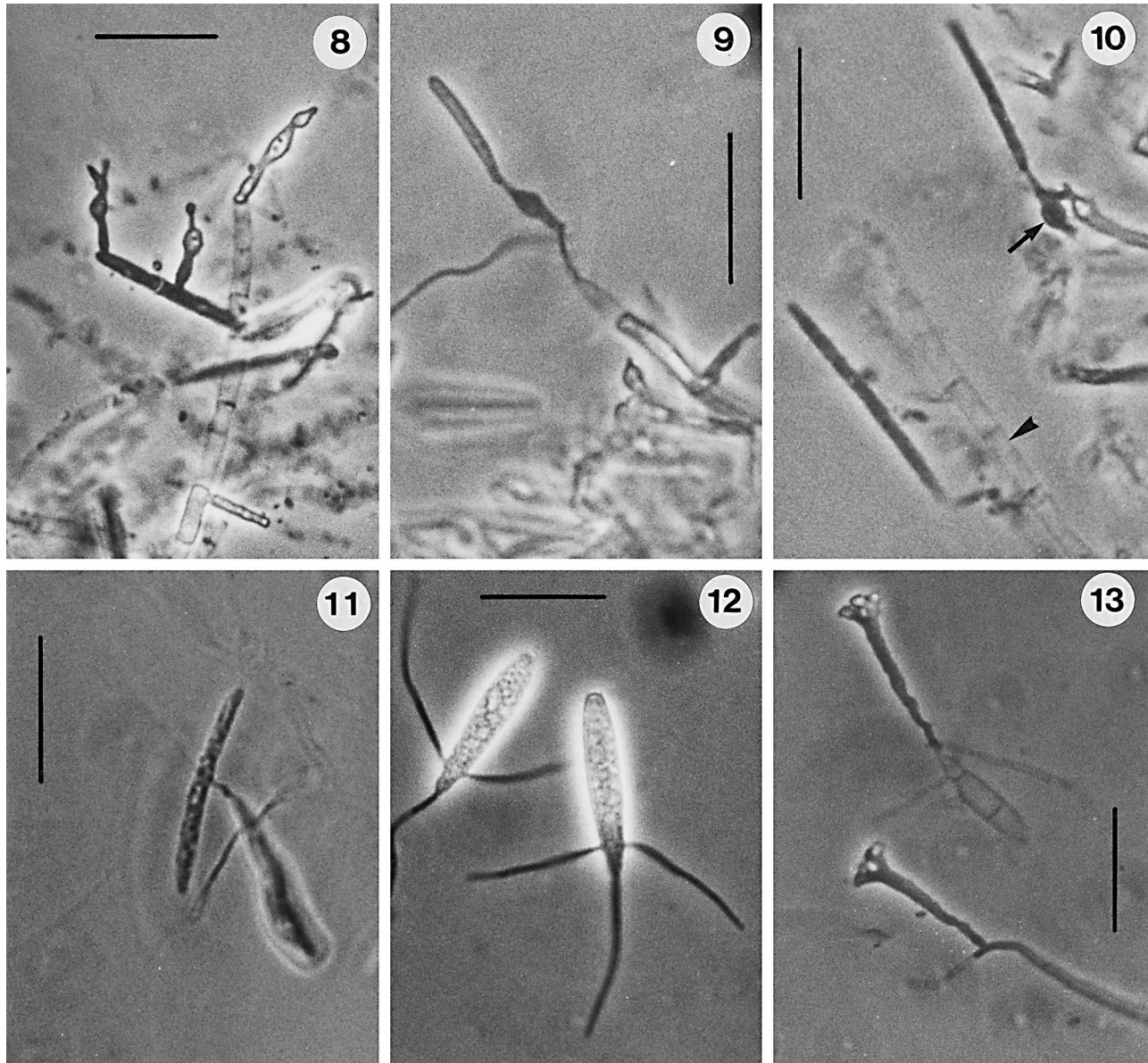
Classicula fluitans Bauer, Begerow, Oberwinkler et Marvanová, sp. nov.

Basidia supra aquae superficiem oriuntur, aggregata vel singularia, transverse 3-septata, cylindræ, 2.5–3 × 40–70 µm. Sterigmata parte subapicali inflata. Basidiosporae anguste fusiformes, leviter curvatae, 1.5–2 × 20–40 µm. Hyphae 1–3 µm diametro, hyalinae, septis regularibus, fibulatis, vel retractione cytoplasmatis orientibus, infibulatis. Cellulae haustoriales tremelloideae adsunt. Conidia navicularia, parte apicali uno, parte subapicali 2–3 ramis setaceis. Status anamorphus ad genus Naiadellae pertinet.

Basidia produced on the water surface, arranged



FIGS. 1-7. Line drawings of *Classicula fluitans* (1-5) and *Jaculispora submersa* (6, 7). Scale bar: 1, 4-6 = 10 μm ; 2, 3, 7 = 5 μm . 1. Cluster of basidia. Note the subapically swollen sterigmata and the fusiform basidiospores. 2. Sterigmata in detail. Note that one sterigma is furcate. 3. Tremelloid haustorial cells. Note the retraction septa lacking clamps. Cells filled with cytoplasm are dotted. 4. Conidium. 5. Germination of conidia with coralloid, appressorium-like structures on glass. Note the retraction septa lacking clamps. Cells filled with cytoplasm are dotted. 6. Conidium. 7. Tremelloid haustorial cell.

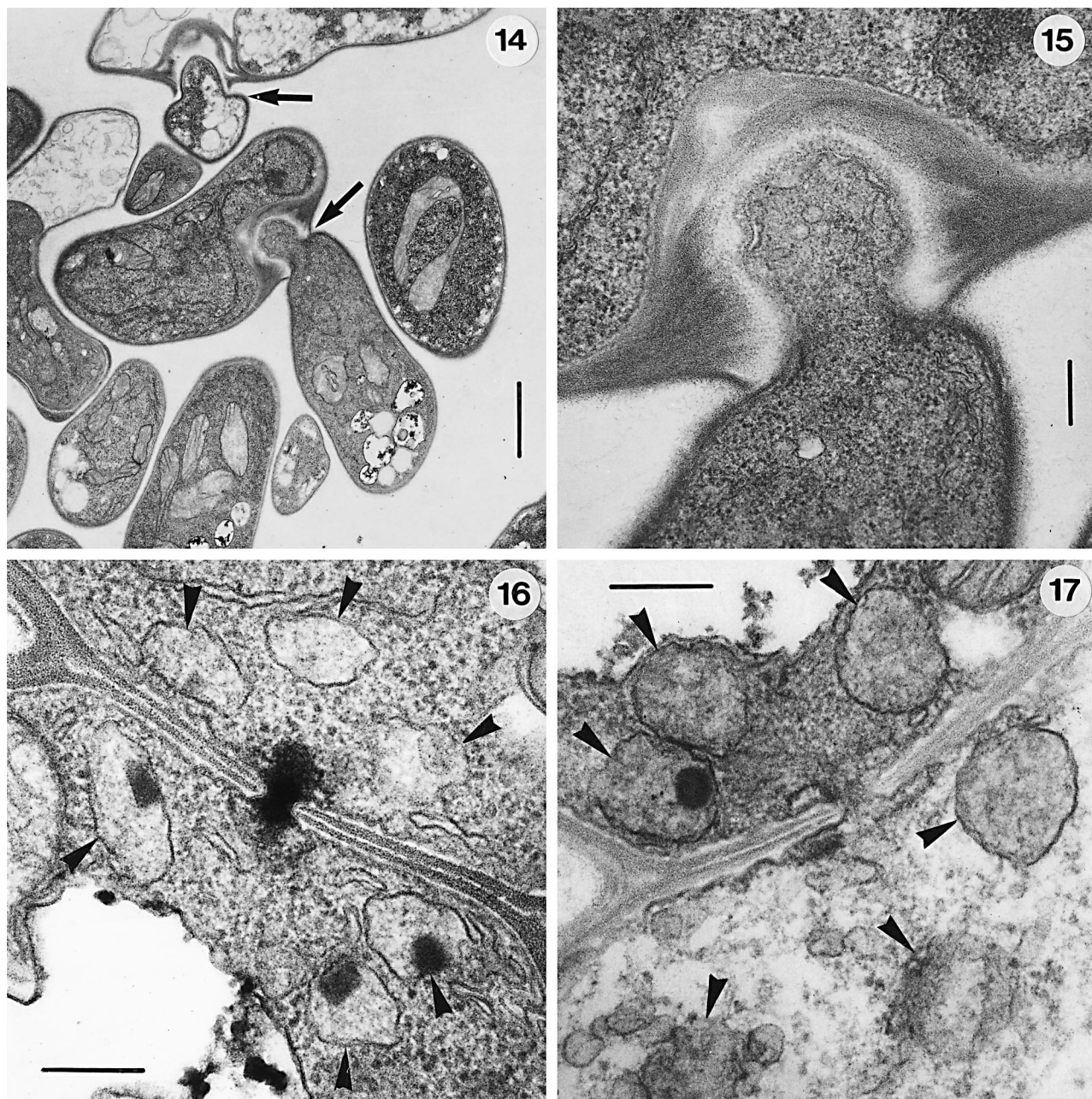


FIGS. 8–13. Phase contrast micrographs of *Classicula fluitans*. Scale bars = 20 μm . 8. Two-celled basidial fragment showing two subapically swollen sterigmata. Note that one of them is furcate. 9. Basidial apex with subapically swollen sterigma and attached basidiospore. 10. Two nearly mature fusiform basidiospores on already cytoplasm-free basidia. One basidium is visible at arrowhead, the other is outside the plane of focus. Note the subapically swollen sterigma (arrow). 11. Detached basidiospore. 12. Two conidia. 13. Germination of conidia with coralloid, appressorium-like structures on glass.

in clusters or isolated, transversely 3-septate and cylindrical, measuring $2.5\text{--}3 \times 40\text{--}70 \mu\text{m}$. Sterigmata subapically swollen. Basidiospores narrow-fusiform with obtuse ends, slightly curved, measuring $1.5\text{--}2 \times 20\text{--}40 \mu\text{m}$ (FIGS. 1, 2, 8–11). Hyphae $1\text{--}3 \mu\text{m}$ diam, hyaline, with both regular and retraction septa, the former with clamps, the latter without clamps (FIGS. 1, 3, 5). Tremelloid haustorial cells present (FIG. 3). Conidia navicular, with one apical and 2–3 bristle-like subapical branches (FIGS. 4, 12). Anamorphic state classified in the genus *Naiadella*.

Type and deposits. A living culture is deposited in the American Type Culture Collection as ATCC 64713 and in the TUB culture collection as RJB 7484-A. Dried specimen (HOLOTYPE) has been deposited in the TUB herbarium (RB 3085).

Sporadically, self-parasitism could be observed in pure culture of *Classicula fluitans*: tremelloid haustorial cells penetrated into hyphae of the same culture (FIGS. 14, 15). Basidiospore germination of *Classicula fluitans* was not observed. Conidia of this fungus became 1–2-septate by retraction septa during



FIGS. 14–17. Transmission electron micrographs of *Classicula fluitans* (14–16) and *Jaculispora submersa* (17). 14. Tre-melloid haustorial filaments (arrows) of *Classicula fluitans* penetrating into hyphae of mycelium. Scale bar = 1 μm . 15. Detail from 14 showing a penetration point. Note that the penetrating haustorial filament is separated from the “host hypha” by a secondary wall layer. Scale bar = 0.2 μm . 16, 17. Septal-pore apparatus of *Classicula fluitans* (FIG. 16) and *Jaculispora submersa* (FIG. 17), each with nonswollen pore margin and associated microbodies (arrowheads) in a more or less circular arrangement. Scale bars = 0.2 μm .

germination (FIGS. 5, 13). On malt yeast-peptone agar, conidia germinated with clamped hyphae (not illustrated). On glass, however, they formed coralloid structures (FIGS. 5, 13) that we interpret as appressoria.

Conidial morphology of *Classicula fluitans* is similar to that of *Jaculispora submersa* (compare FIG. 4 to

FIG. 6). In both species the conidia are navicular, having 3–4 distal setose branches. Conidia of the two species differ only slightly in thickness and form of the apical branch. In *Classicula*, it is discrete from the conidial body, whereas in *Jaculispora* it is integrated, i.e. it represents the gradually tapered, elongate apex of the conidial body. Like *Classicula flui-*

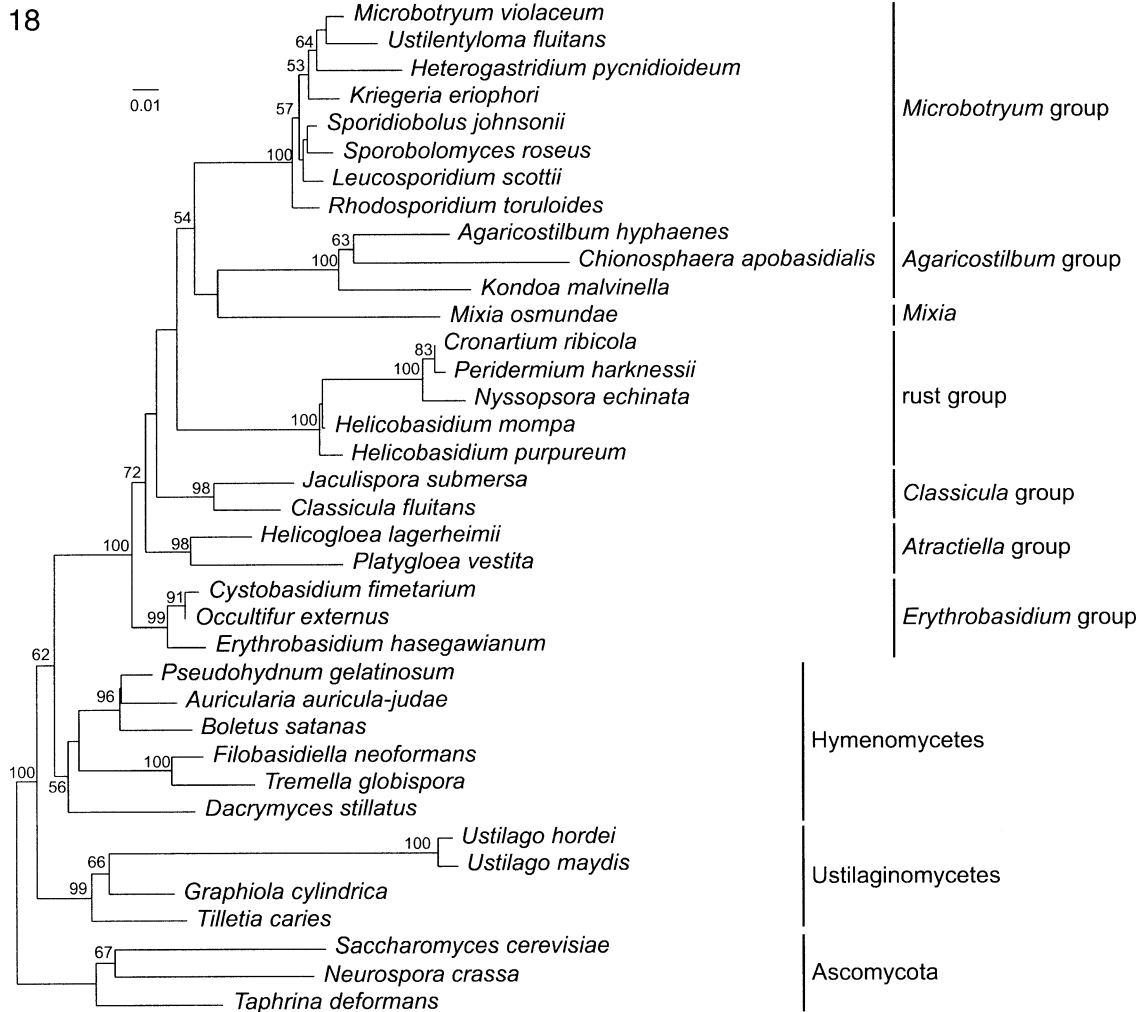


FIG. 18. Phylogeny of 36 basidiomycetes obtained by neighbor joining analysis of 1366 bp of the nuclear small subunit rRNA gene using TrNIG distance model, rooted with ascomycetes. Percentage of bootstrap values of 10 000 replicates are given at each furcation. Values smaller than 50% are not shown. Branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site.

tans, *Jaculispora submersa* formed clamped hyphae with tremelloid haustorial cells (compare FIG. 3 to FIG. 7). Furthermore, the septal-pore architecture in *Classicula fluitans* essentially is identical to that of *Jaculispora submersa*. In both species simple pores are surrounded by microbodies in a more or less circular arrangement (FIGS. 16, 17). In our molecular phylogenetic analyses using partial nuclear small subunit rRNA gene sequences, *Classicula fluitans* and *Jaculispora submersa* were tested together with at least two representatives of all known urediniomycetous major groups, some ustilagino- and hymenomycetes, and some ascomycetes. Using the ascomycetes as out-group, the statistically well-supported groups appearing in the trees (FIGS. 18, 19) were congruent to the groups discussed by Fell et al (2001) and Swann et al (1999, 2001). These are, in addition to *Mixia osmundae*, the *Microbotryum*, *Agaricostilbum*, rust, *Atractiella*

and *Erythrobasidium* groups. *Classicula* and *Jaculispora* were united in a statistically well-supported cluster (FIGS. 18, 19).

DISCUSSION

Phylogenetic aspects.—Among the Urediniomycetes, *Classicula* is unique in having subapically swollen sterigmata on the basidia. Conidia of *Classicula* are similar to those of *Jaculispora* in size and form. In addition, *Classicula* shares with *Jaculispora* two other significant characteristics, septal-pore architecture and formation of tremelloid haustorial cells. The septal-pore apparatus in both species is composed of a simple pore surrounded by microbodies in a circular arrangement. Among basidiomycetes, this type of septal-pore apparatus occurs only in the Urediniomycetes; while common among the rust group (see Bauer

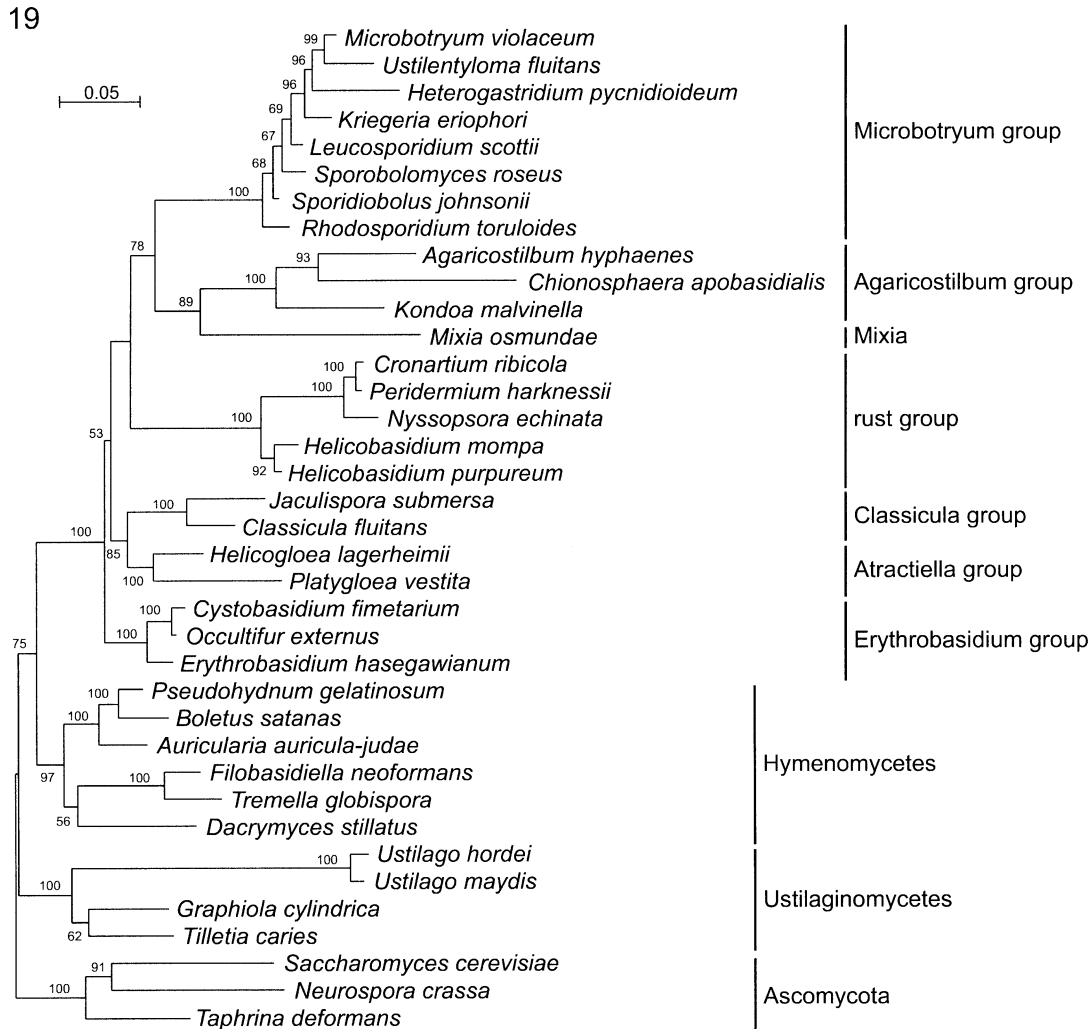


FIG. 19. Phylogeny of 36 basidiomycetes obtained by Bayesian inference, rooted with ascomycetes. Markov chain Monte Carlo analysis of an alignment of 1336 bp of the nuclear small subunit rRNA gene using the general time reversible model of DNA substitution with gamma distributed substitution rates, random starting trees and default starting parameters of the substitution model. Majority-rule consensus tree from 9000 trees that were sampled after the process had reached stationarity. The numbers on branches are estimates for a posteriori probabilities. Branch lengths are mean values over the sampled trees and are scaled in terms of expected numbers of nucleotide substitutions per site.

and Oberwinkler 1994, and the references therein) it occurs sporadically also in members of the *Microbotryum* and *Atractiella* groups. Thus, *Cryptomycocolax* and *Colacosiphon* in the *Microbotryum* group and *Saccolastia* in the *Atractiella* group possess this septal-pore type (Oberwinkler and Bauer 1990, Kirschner et al 2001). It appears that this septal-pore type, which occurs in these three different lineages and also in *Classicula* and *Jaculispora*, reflects a common ancestral type.

Both *Classicula* and *Jaculispora* form tremelloid haustorial cells. A clamp is subtended to each tremelloid haustorial cell, which consists of a more or less subglobose basal part with one or more thread-like filaments. These specific cells first were described

and designated as "haustoria" by Olive (1947). They are typical for the mycoparasitic Tremellales of the Hymenomycetes (Bandoni 1984, Oberwinkler et al 1984, Zugmaier et al 1994) but astonishingly occur also in mycoparasitic members of the Urediniomycetes. Thus, tremelloid haustorial cells are known from species of the urediniomycetous genera *Cystobasidium*, *Mycogloea*, *Occultifur*, *Spiculogloea* and *Zygo-gloea* (Oberwinkler 1990, Roberts 1994, 1996, 1997, Sampaio et al 1999, unpubl). It is unclear whether the tremelloid haustorial cells occurring in the Tremellales on the one hand and those of members of the Urediniomycetes on the other are homologous. However, at least in *Classicula* the tremelloid haustorial cells are binucleate (Marvanová and Bandoni

1987), whereas available data indicate that those occurring in the Tremellales are mononucleate (Bezerra and Kimbrough 1978, Oberwinkler et al 1984).

Except for *Classicula* and *Jaculispora*, all urediniomycetous mycoparasites having tremelloid haustorial cells possess septal-pore apparatus without associated microbodies (Oberwinkler 1990, Sampaio et al 1999, unpubl). In other words, among the Urediniomycetes, pore-associated microbodies and tremelloid haustorial cells occur only in *Classicula* and *Jaculispora*. This phylogenetic indication agrees with the molecular results. *Classicula* and *Jaculispora* form a statistically well-supported clade, separated from *Cystobasidium fimetarium* and *Occultifur externus*, the two urediniomycetous representatives in the trees with tremelloid haustorial cells. In contrast with neighbor joining, in the Bayesian tree *Classicula* and *Jaculispora* appear on a common branch together with two species representing the Atractiellales with an a posteriori probability of 85%. However, the presence of symplechosomes and the absence of tremelloid haustorial cells (Oberwinkler and Bauer 1989, Bauer and Oberwinkler 1991) clearly separate the Atractiellales from *Classicula* and *Jaculispora*. Accordingly, a new family and order are necessary to accommodate *Classicula* and *Jaculispora* in the Urediniomycetes.

Classiculaceae Bauer, Begerow, Oberwinkler et Marvanová, fam. nov.

Fungi Urediniomycetum poris septorum simplicibus, corpusculis minimis consociatis, cellulis tremelloideis haustorialibus.

Members of the Urediniomycetes having simple septal pores with associated microbodies and tremelloid haustorial cells.

Typus familiae. *Classicula* Bauer, Begerow, Oberwinkler et Marvanová.

Classiculales Bauer, Begerow, Oberwinkler et Marvanová, ord. nov.

Descriptio analoga familiae Classiculacearum.

Typus ordinis. *Classiculaceae* Bauer, Begerow, Oberwinkler et Marvanová.

Ecological aspects.—Ecologically, *Classicula* and *Jaculispora* share two significant characteristics: (i) both species form tremelloid haustorial cells. As discussed above, these specific cells are known from many basidiomycetous mycoparasites. As studied in detail by Bauer and Oberwinkler (1990a, b) and Zugmaier et al (1994), these cells are capable of interacting with host hyphae by fusing via a micropore. As in *Classicula* and *Jaculispora*, these mycoparasites tremelloid haustorial cells also are formed in the absence of the host. In addition, as in *Classicula*, self-parasitism is a common phenomenon of mycoparasites (Jeffries

and Cuthbert 1984, Kirscher et al 1999). These data suggest that *Classicula* and *Jaculispora*, though capable of axenic growth in pure culture (Marvanová and Bandoni 1987, Matsushima 1987, respectively), are mycoparasites or at least have the potential for mycoparasitism. In water it might be difficult to establish and maintain contact between two fungi. In this sense, the appressorium-like, coralloid structures formed at least in *Classicula* could serve as attaching organs. (ii) The conidia with broadly diverging branches in *Classicula* and *Jaculispora* resemble those of aquatic hyphomycetes (Ingold 1979). In addition, the long and small form of the basidiospores in *Classicula* also might have evolved in adaptation to water dispersal (Ingold 1979). Furthermore, at least *Classicula* appears to produce basidia only on the water surface. As noted by Marvanová and Bandoni (1987), *Classicula* and *Jaculispora* frequently were found in freshwater habitats. These data suggest that *Classicula* and *Jaculispora* prefer aquatic environments. As in *Classicula* and *Jaculispora*, conidia with radiating arms or setose branches also are formed by the heterobasidiomycete *Camptobasidium hydrophilum* Marvanová & Suberkropp and the basidiomycetous anamorph *Cyrenella elegans* Gochenaur, respectively. In these two fungi, tremelloid haustorial cells were not observed (Gochenaur 1981, Marvanová and Suberkropp 1990). However, *C. hydrophilum*, when grown in dual culture with other aquatic hyphomycetes, behaves like a contact biotrophic mycoparasite. Its hyphae coil around host hyphae or conidia, but penetration has not been seen (Marvanová and Suberkropp 1990).

In summary, our data suggest that *Classicula* and *Jaculispora* are two representatives of an urediniomycetous group of aquatic mycoparasites.

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