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Phylogenetics of the Pezizaceae, with an emphasis on *Peziza*

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Abstract: Phylogenetic relationships among members of the Pezizaceae were studied using 90 partial LSU rDNA sequences from 51 species of *Peziza* and 20 species from 8 additional epigeous genera of the Pezizaceae, viz. *Boudiera, Iodophanus, Iodowynnea, Kimbropezia, Pachyella, Plicaria, Sarcosphaera* and *Scabropezia,* and 5 hypogeous genera, viz. *Amylascus, Cazia, Hydnotryopsis, Ruhlandiella* and *Tirmania.* To test the monophyly of the Pezizaceae and the relationships to the genera *Marcelleina* and *Pfistera* (Pyronemataceae), 6 species from the families Ascobolaceae, Morchellaceae and Pyronemataceae were included. Maximum parsimony and maximum likelihood analyses of these sequences suggest that the Pezizaceae is paraphyletic, because the non-amyloid *Marcelleina* is nested within it. If *Marcelleina* were transferred to the Pezizaceae, then the family would be monophyletic. Although the Pezizaceae is traditionally characterized by amyloid asci, our results indicate that the amyloid reaction is a symplesiomorphy, which has been lost in some lineages, e.g., in those including *Marcelleina* and *Cazia.* Nodes deep in the tree could not be resolved, but 7 groups of species (I–VII) are generally well supported or present in all trees. *Peziza* species, which constitute the core of the family, are present in all groups except group III, confirming the non-monophyly of the genus. The analyses suggest that the other included genera of the Pezizaceae are all nested within *Peziza,* the placement of *Iodophanus* being unresolved. The morphologically distinct *Peziza gerardii,* which forms a clade with *Marcelleina,* appears to be the sister group to the rest of the Pezizaceae. Morphological features were studied and evaluated in the context of the phylogeny. Distinct types of ascus amyloid reactions were found to support different rDNA lineages, e.g., a distinct amyloid ring zone at the apex is a synapomorphy for group IV, an intense and unrestricted amyloid reaction of the apex is mostly found in group VI, and asci that are weakly or diffusely amyloid in the entire length are present in group II. Other morphological features, such as spore surface relief, guttulation, excipulum structure and pigments, while not free from homoplasy, do support the groupings. Anamorphs likewise provide clues to higher-order relationships within the Pezizaceae. Several macro- and micromorphological features, however, appear to have evolved several times independently, including ascomatal form and habit (epigeous, semihypogeous or hypogeous), spore discharge mechanisms, and spore shape. Parsimony-based optimization of character states on our phylogenetic trees suggested that transitions to truffle and truffle-like forms evolved at least three times within the Pezizaceae (in group III, V and VI). The 9 hypogeous species included are nested in lineages with epigeous pezizaceous taxa. Species with apothecia of various shapes and with forcible spore discharge are spread among all groups and the apothecium is suggested to be symplesiomorphic in the Pezizaceae. The results indicate that the apothecia forming Pezizaceae have given rise to at least 3 different forms of hypogeous ascomata without forcible spore discharge: ptychothecia, stereothecia and exothecia.

Key Words: ascus amyloid reactions, epigeous-hypogeous evolution, molecular phylogeny, nLSU rDNA, Pezizales, systematics

INTRODUCTION

The Pezizaceae (Pezizales) displays great variation in ascomatal forms. It includes taxa that produce epigeous, sessile or stipitate, cupulate, discoid, turbinate, pulvinate or sparassoid ascomata, or semi-hypogeous to hypogeous, closed, folded to solid ascomata (FIGS. 1–21). The ascomata range in size from a few mm to more than 10 cm in diam, and are often fleshy, soft and brittle. Anatomical and biochemical diversity is found in characters such as spore discharge mechanism; amyloid reaction of the ascus; spore shape, color, ornamentation, and guttulation; pigmentation of the paraphyses; and excipulum structure (TABLE I).

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FIGS. 1–12. Ascoma forms and color variation in the Pezizaceae (group I–IV). 1. Pulvinate apothecia with protruding asci. *Iodophanus carneus* (JHP-00.027, C) ×15. 2–3. Group I. Discoid apothecia on broad obconical bases. 2. *Peziza gerardii* (KH-98–86, C) ×3. 3. *Marcelleina persoonii* (TL-5346, C) ×3. 4. Group II. *Peziza subisabellina* (RK83.115, herb. Roy Kristiansen) ×1.3. 5–8. Group III. 5. *Pachyella punctispora* (KH-98–77, C) ×1.5. 6. Turbinate apothecia with a convex hymenium. *Boudiera dennisii* (JHP-93.095, C) ×6. 7. Highly pustulate outer surface. *Scabropezia flavovirens* (Fuckel) Dissing & Pfister (KH-97–68, C) ×2. 8. Stereothecium. *Amylascus.* (5728, OSC) ×1.5. 9–10. Group IVa. 9. Cup-shaped, shortly stipitate apothecia. *Peziza arvernensis* (KH-98–08, C) ×0.4. 10. *Peziza ammophila* (KH-98–88, C) ×0.8. 11–12. Group IVb. 11. *Peziza exogelatinosa* (KH-97–75, C) ×0.8. 12. *Peziza subcitrina* (KH-97–133, C) ×1.3.

Photos: 1, 2, 6, 7, 11 J.H. Petersen. 5, 9, 12 K. Hansen. 8 M. Castellano. 10 S.A. Elborne. 3 T. Læssøe. 4 R. Kristiansen.

Ecologically, the family covers a broad range of niches, fruiting on all types of soil, sand, clay, limestone, burnt ground, dung and wood. Many species are known to prefer soil with a high pH and in some cases a low content of organic matter (Petersen 1967, 1985). The family is primarily restricted to temperate zones and arctic-alpine areas, although a few strictly tropical taxa are known. The majority of species are considered to be saprotrophs, although most hypogeous and a few epigeous species are claimed to be ectomycorrhizal (Maia et al 1996 and references therein), but in general their trophic statuses are not

TABLE I. Characters used in the delimitation of genera in the Pezizaceae (based on published and original observations)

Genus	Ascoma: position[b]; +/− forcible spore discharge	Ascoma: type; shape when epigeous	Ascus: +/− amyloid; type of amyloid reaction	Spore: shape; guttulation	Spore: color; +/− ornamentation
Amylascus	hy, se; −	Ptychothecium to stereothecium	+; weakly over the entire length	Globose; 1 or several	Hyaline to pale brown; + spines, rods or cones
Boudiera	ep; +	Apothecium, subglobose, turbinate to pulvinate	+; weakly over the entire length	Globose; 1 or several	Pale brown; + echinulate to reticulate
Cazia[a]	hy; −	Stereothecium	−	Ellipsoid; 1	Hyaline; + minutely warty-reticulate
Hapsidomyces[a]	ep; +	Apothecium, turbinate	+; weakly over the entire length	Globose; 0	Hyaline to pale yellow; + reticulate and spiny
Hydnobolites	hy; −	Stereothecium	+/−; weakly (2% KOH pretreatment)	Globose; 0	Hyaline to pale brown; + reticulate
Hydnotryopsis	hy; −	Stereothecium	+; diffusely over the entire length	Ellipsoid; ?	Hyaline to brownish yellow; + warty to pitted to ridged
Iodophanus	ep; +	Apothecium, pulvinate	+; weakly over the entire length	Ellipsoid to broadly ellipsoid; 0	Hyaline; + warty or episporium wrinkled
Iodowynnea[a]	ep; +	Apothecium, convoluted to highly folded, arising from a hypogeous stipe	+; intensely over the entire length	Ellipsoid; 1 or 2, rarely several	Hyaline; + longitudinally ridged and warty
Kimbropezia[a]	ep; +	Apothecium, discoid	+; intensely over the apex	Ellipsoid; 0	Hyaline; −
Mycoclelandia	hy, se; −	Ptychothecium	+; diffusely, more intense near the apex	Broadly ellipsoid to subglobose; 1 or 2	Hyaline; −
Pachyella	ep; +	Apothecium, discoid, flat to pulvinate, broadly attached to the substrate	+; diffusely over the entire length	Ellipsoid; 2	Hyaline; −/+ warty, ridged
Pachyphloeus	hy; −	Stereothecium	±; weakly over the entire length	Globose; 0 ?	Hyaline to pale brown; + spinose to verrucose, +/− embedded in mucilage
Peziza	ep, rarely se, hy; + rarely −	Apothecium, discoid to cupulate, rarely sparassoid, or rarely ptychothecium	+; ring zone at the apex, intensely unrestricted over the apex or evenly over the entire length (diffusely, weakly or intensely)	Ellipsoid or fusiform; 0, 2-or multi-guttulate, rarely 1	Hyaline or pale brown; −/+ warty, ridged to reticulate, spiny, apiculate

TABLE I. Extended

Paraphyses: pigments; gelatinous matrix; epithecium	Excipulum: outer	Excipulum: medullary	Trophic status; substrate[c]	Anamorphs
Absent	Outermost textura globulosa to angularis, giving rise to surface tomentum. Inner layer of broad hyphae, mixed with inflated cells	Textura intricata, +/− large cells	ec ?; te	Unknown
Hyaline or brownish walls	Textura globulosa to angularis	Dense textura intricata	sa ?, ec ?; te	Unknown
Paraphyses present: pigments ?	Textura intricata, at septa, the cells often inflated	Textura intricata	ec ?; te	Unknown
Yellowish contents	Textura globulosa to angularis	Textura intricata	sa; co	Unknown
Absent	Textura globulosa (± isodiametric cells) with brownish, amorphous material in the intercellular spaces	Textura globulosa (± isodiametric cells), or textura intricata	ec ?; te	Unknown
Paraphyses present: pigments ?	Textura globulosa (± isodiametric cells), sometimes with interwove hyphae	Textura intricata	ec ?; te	Unknown
Usually containing carotenoid pigments	Textura globulosa to angularis, sometimes with interwoven hyphae	Textura intricata	sa ?; te, co, py	*Oedocephalum*
Hyaline	Textura globulosa intermixed with hyphae, outermost cells arranged in short chains	Textura globulosa intermixed with hyphae	ec ?; te	Unknown
Hyaline	Textura intricata, with very short hyphae, extending towards outside	A layer of textura intricata, between two layers of textura angularis to globulosa	sa ?; te	Unknown
Hyaline	Textura intricata or textura globulosa	Textura globulosa, of large, thin-walled cells	ec ?; te	Unknown
Dark granules in the apical cells	Textura globulosa to angularis, outer cells terminating in flexuous hairs embedded in a gelatinous matrix	Textura intricata +/− gelatinous matrix	sa ?; li	Oedocephalum-like
Absent	Subangular to globose isodiametric cells, on outside scabrous to verrucose	Isodiametric cells	ec ?; te	*Glischroderma* ?
+/− pigmented granules; +/− embedded in granular matrix	Textura globulosa or textura angularis, of large, thin-walled cells +/− interwoven hyphae, or smaller globose cells elongating to a hyphoid layer towards the outside	One, two or more layers, of textura globulosa or textura angularis, of large, thin walled cells +/− interwoven hyphae, or of parallel hyphae	sa, ec; te, co, py, li	*Oedocephalum, Chromelosporium,* Chromelosporium-like, or hyaline to colored, 0–3 septate resting spores

TABLE I. Continued

Genus	Ascoma: position[b]; +/− forcible spore discharge	Ascoma: type; shape when epigeous	Ascus: +/− amyloid; type of amyloid reaction	Spore: shape; guttulation	Spore: color; +/− ornamentation
Plicaria	ep; +	Apothecium, discoid to cupulate	+; weakly over the entire length	Globose; few to multi-guttulate	Pale brown; −/+ warty, spiny, reticulate
Rhodopeziza[a]	ep; +	Apothecium, cupulate	+; over the entire length	Broadly ellipsoid; 1 small evanescent guttule	Pale yellowish; + tuberculate
Ruhlandiella	se; −	Exothecium	+; weakly over the entire length	Globose; 1	Pale brown; + reticulate-areolate
Sarcosphaera[a]	ep, se; +	Apothecium, hollow, initially hypogeous, becoming exposed and split into acute rays	+; weakly over the entire length (a little stronger at the apex)	Ellipsoid; 2	Hyaline; + low warty
Scabropezia	ep; +	Apothecium, cupulate	+; over the entire length	Globose; 1	Pale brown; + truncate or delicate warts
Sphaerozone[a]	hy, se; −	Exothecium	+; weakly, over the entire length	Globose; 0	Reddish brown; + irregular warty
Terfezia	hy; −	Stereothecium	−	Globose; 0	Hyaline to pale brown; + spiny, papillate, reticulate, −/+ mucilage-embedded
Tirmania	hy; −	Stereothecium	+; diffusely, +/− weakly	Globose to broadly ellipsoid; 1	Hyaline; −/+ minutely roughened

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[a] Monotypic genus.

[b] Position of ascoma; ep = epigeous, hy = hypogeous, se = semihypogeous.

[c] Trophic status: sa = saprobic, ec = ectomycorrhizal. Substrate: te = terrestrial, co = coprophilous, li = lignicolous, py = pyrophilous.

well studied. A study by Warcup (1990), with single spore isolation and incubation experiments did, however, show several species, both epigeous and hypogeous, to be ectomycorrhizal.

Eriksson (2000) lists 19 genera in the Pezizaceae, with a circumscription based mainly on Rifai (1968), Kimbrough (1970) and Trappe (1979). Recent molecular phylogenetic studies have led to the inclusion of *Pachyphloeus* and *Terfezia* in the family (Norman and Egger 1999, Percudani et al 1999) (TABLE I). The Pezizaceae is chiefly characterized by amyloid asci, a feature shared only with the Ascobolaceae within the Pezizales. The spores are uninucleate, usually thin-walled, globose, ellipsoid or fusiform, hyaline or pale brown, smooth or with cyanophilic ornaments. The excipulum consists, at least partly, of large isodiametric cells. In addition, ultrastructural and refined cytochemical studies have led to further delimiting characters such as the presence of electron-opaque convex and biconvex bands in septal pores of the ascal bases (so far recorded in *Peziza, Plicaria, Iodophanus, Sarcosphaera, Pachyella* and *Hydnobolites*) (Curry and Kimbrough 1983, Kimbrough and Curry 1985, Kimbrough et al 1991, Kimbrough 1994).

Molecular phylogenetic studies of the Pezizales to date have included relatively few taxa from the groups with amyloid asci. With regard to the Pezizaceae, the work of Norman and Egger (1996, 1999) deserves special note, because it provides broader

TABLE I. Extended Continued

Paraphyses: pigments; gelatinous matrix; epithecium	Excipulum: outer	Excipulum: medullary	Trophic status; substrate[c]	Anamorphs
Embedded in dark granular matrix	Textura globulosa to angularis, and intermixed broad hyphae	Textura globulosa and intermixed broad hyphae	sa ?, ec; py	*Chromelosporium*
Orange granules (carotenoid granules)	Textura globulosa to angularis, of subglobose to polygonal cells	Small textura globulosa angularis, occasionally intermixed with hyphae	sa ?; te	Unknown
Gelatinous sheath; exceeding the asci	Textura globulosa to angularis, thick-walled cells	Textura globulosa to angularis	ec; te	Chromelosporium-like
Brownish contents	Textura epidermoidea, to textura prismatica towards the outside	Textura globulosa	ec ?; te	Unknown
Small brownish guttules; embedded in a coloured, granular matrix	Textura globulosa, outermost cells thick-walled, forming conical pustules	Textura intricata	sa ?, ec ?; te, li	*Glischroderma* ?
Exceeding the asci	Textura globulosa to angularis, cells thick-walled	Textura globulosa to angularis	ec ?; te	Unknown
Absent	Textura intricata, of broad hyphae with inflated cells	Textura intricata, of broad hyphae with inflated cells	ec ?; te	Unknown
Absent	Textura intricata, of broad, thin-walled hyphae and many inflated cells	Textura intricata, of broad, thin-walled hyphae and many inflated cells	ec ?; te	Unknown

sampling of the family than any previous study. Nevertheless, further sampling of *Peziza* species and inclusion of additional genera, as described here, are necessary to critically assess generic limits within the family and to work toward a phylogenetic classification. The main objectives of this research were: i) to resolve the major lineages within the Pezizaceae, especially within *Peziza,* using LSU rDNA sequences, and to compare these with previous morpho-taxonomic classifications, ii) to explore the circumscription of *Peziza* itself, and iii) to evaluate and refine morphological characters previously used in the delimitation of genera within the Pezizaceae. The results should give direction to further morphological and molecular studies.

BACKGROUND INFORMATION

The family: delimitation and important morphological characters.—For nomenclatural purposes the Pezizaceae can be traced to Dumortier (1829) (Hawksworth and David 1989), as a family of the order Fungarieae (fungi with a distinct external hymenium), to include genera with the spores born on the upper surface of a cup-shaped receptacle. Dumortier's circumscription was essentially the same as used by Fries (1822, as "Pezizeæ"), but Fries did not use a consistent method of ranking in his system, and therefore Fries is not accepted as author of the Pezizaceae contrary to the use by, e.g., Eckblad (1968), Kimbrough (1970) and Korf (1972). Dumortier (1829) listed *Peziza* and *Ascobolus,* along with other genera of the discomycetes, *Stictis, Bulgaria, Tympanis, Cenangium, Patellaria* and *Helotium,* and two genera of basidiomycetes, *Solenia* and *Ditiola.* This system was based solely on macroscopic features and has long been regarded as artificial.

Boudier (1885) was the first to delimit a group, "the Aleuriés," which more or less circumscribes the core of the Pezizaceae as we recognize it today. The group was placed in the "division Operculés," distinguished by asci that open with an operculum. Besides the presence or absence of an operculum, Boudier introduced and used further important microscopic characters, such as the amyloid reaction of asci, spore shape and number of oil guttules in the spores in his classification of the "fleshy discomycetes." The "Aleuriés" was distinguished by amyloid asci and in general having cup-shaped, sessile ascomata without hairs on the receptacle. The genera *Lepidotia* Boud., *Aleuria* (Fr.) Gill. and *Galactinia* (Cooke) Boud. (= *Peziza*), *Sarcosphaera*, *Sphaerosoma* Klotzsch, and *Plicaria* were included. Later Boudier (1907) treated the group at tribus level ("Aleuriées") and added his new genus *Pachyella*, but *Sphaerosoma* was excluded. *Pachyella* was segregated from *Peziza* and *Psilopezia* Berk. on the basis of the pulvinate to convex apothecia and lack of or only weakly amyloid asci. The absence of an amyloid reaction for taxa in the tribe was contrary to the definition of "Aleuriées," but Boudier also knowingly included species in *Plicaria* that had non-amyloid asci.

Boudier's (1907) circumscription of the Aleuriées was generally followed by Le Gal (1947, as tribus Aleurieae), Rifai (1968), Eckblad (1968) and Korf (1972, 1973b) (as Pezizaceae), and Dennis (1981, as tribus Pezizeae). Additional characters, such as spore ornamentation of cyanophilic material (Le Gal 1947), uninucleate spores (Berthet 1964a), absence of carotenoid pigments (Arpin 1969) and the anatomy of the ascomata, consisting of mostly large isodiametric cells, were discovered and used to refine the limits of the family. In culture, many species of the Pezizaceae were found to produce *Oedocephalum* or *Chromelosporium* conidial states (Rifai 1968).

Trappe (1979) emended the family to include hypogeous taxa with chambered or marbled glebae and cylindric to saccate asci which lacked functional opercula. He recognized the artificial nature of the Tuberales, abandoned the order and assigned most taxa to families within the Pezizales. Hypogeous species of *Peziza*, and the genera *Mycoclelandia*, *Hydnotryopsis*, *Amylascus* and *Tirmania* were accepted in the Pezizaceae. Trappe considered the hypogeous taxa to be derived from various epigeous taxa within the family. This hypothesis was based primarily on similarities in the anatomy of the excipulum and on the presence of amyloid asci. Currently 10 genera, almost half of the genera accepted in the Pezizaceae, have semi-hypogeous to hypogeous ascomata (Eriksson 2000, TABLE I), while six hypogeous species are placed in *Peziza* (e.g., FIGS. 17–18) (Trappe 1979).

The amyloid reaction. Amyloid asci were described by Nylander (1868), Karsten (1869) and Boudier (1879) in a number of species of *Peziza* and *Ascobolus* Pers. Korf (1972) attached some importance to ascus amyloid reactions. He recognized the Pezizaceae for taxa with ascus amyloid reactions: i) in an apical ring, ii) over the apex, or iii) rarely in their whole length. Taxa in the Ascobolaceae tribus Iodophaneae were described as having diffusely amyloid asci (tribus Ascoboleae showed non-amyloid or diffusely amyloid asci). Nevertheless, Korf included *Pachyella*, characterized by diffusely amyloid asci, in the Pezizaceae. Except for the genera *Pachyella*, *Iodophanus* and *Boudiera*, the location and extent of the amyloid reaction have not been used as characters to delimit taxa within the Pezizaceae. Within the Ascobolaceae, differences in ascus reactions were noticed for some sections in the genus *Ascobolus*: intensely amyloid in sect. *Dasyobolus* (Sacc.) Brumm. (in all but one species), faintly amyloid or none at all in several mainly terrestrial and lignicolous species of sect. *Ascobolus*, and non-amyloid in sect. *Pseudoascodesmis* Brumm. (van Brummelen 1967). All species in the remaining four sections of *Ascobolus* showed a "general" amyloid reaction of the ascus wall. Van Brummelen (1967) found the intensity of the reaction to be constant for each species although significant differences existed between related species. A diffuse amyloid reaction was described by Pfister (1973) in *Pachyella* as "not restricted to the apex of the ascus, nor is it in the form of a J+ ring at the apex of the ascus," and that it "is present either as an external layer on the ascus wall (which may separate from the ascus wall proper), or occurs in the gel which surrounds the asci and paraphyses and is not restricted to the wall."

Morphological and cytochemical studies of amyloid asci were performed on five species of the Pezizaceae and Ascobolaceae, using light microscopy and transmission electron microscopy (TEM) (Samuelson 1978). The amyloid site in *Peziza succosa*, *Saccobolus depauperatus* (Berk. and Broome) E.C. Hansen and *Thecotheus pelletieri* (Crouan) Boud. appeared to be an exogenous mucilaginous coat, whereas in *Iodophanus granulipolaris* Kimbrough it appeared to be the ascal wall proper. However, Samuelson stated that the amyloid reaction may be the result of more than one site of activity. *Peziza succosa* was strongly but unrestrictedly amyloid over the apex ("10–14 μm down the sides of the ascal wall"). *Peziza* species with a distinct amyloid ring zone at the apex were not studied. According to van Brummelen (1978) the site of the amyloid reaction is strictly confined to an extra-ascal layer, the periascus (a mucilagenous substance), which varies in thickness. In *Boudiera* and *Iodophanus* it is more or less uniform, but in *Peziza ammophila* and *P. succosella* it develops into a ring-shaped thickening at the apex. In *P. ammophila* a thick ring with an indented central portion forms, whereas in *P. succosella* the periascus is considerably thickened but uniformly so over the ascus apex (van Brummelen 1978: figs. 7, 8). Such ultrastructural studies help to explain the variation in the amyloid reaction of asci, which is observed in the Pezizaceae.

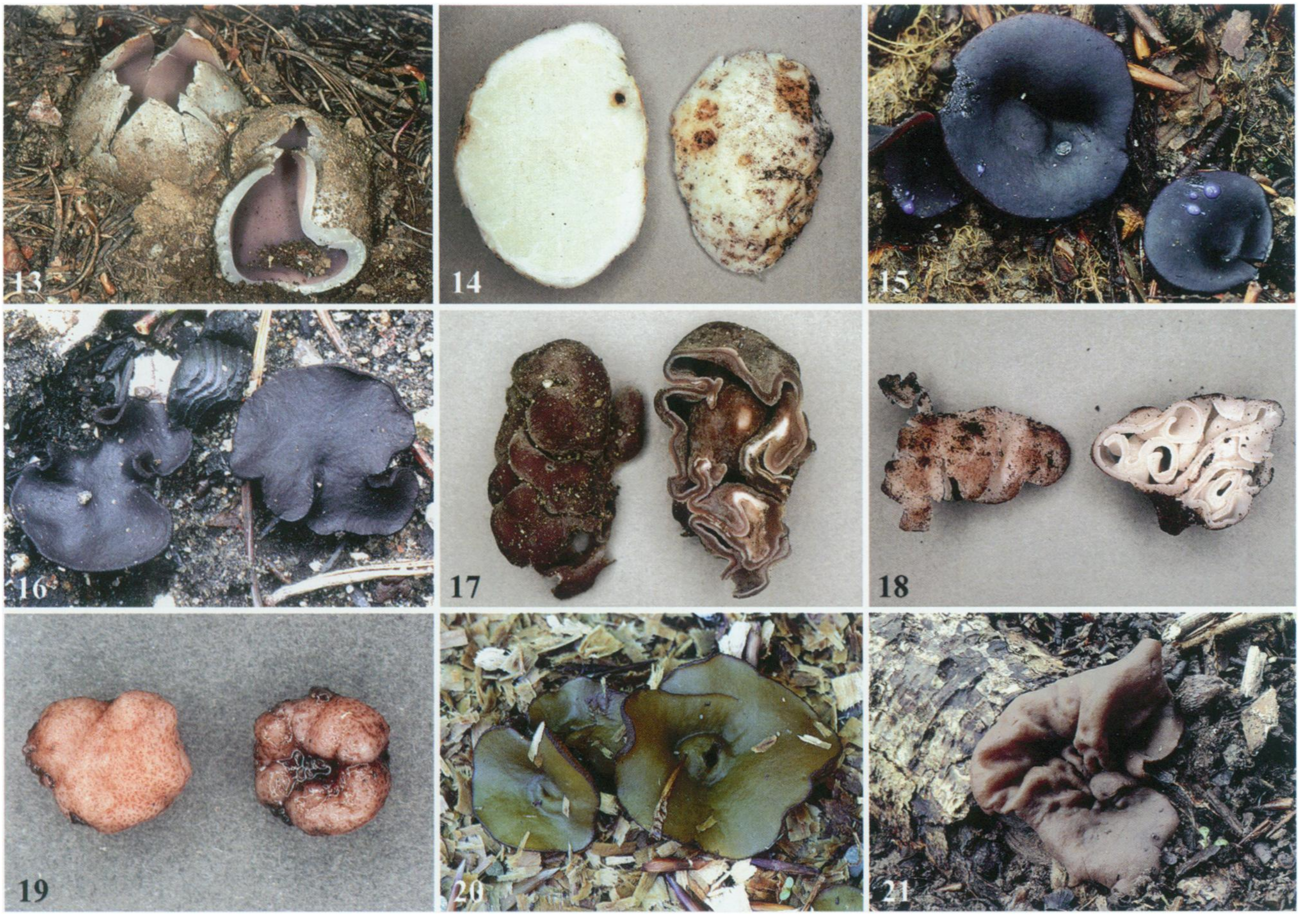
The genera: delimitation and relationships.—Epigeous genera. Peziza Fr. (1822) is the largest genus within the Pezizales, with approximately 100 currently accepted species (Hohmeyer 1986, Korf 1972). It is a complex and heterogeneous assemblage, that constitutes the core of the Pezizaceae. Although many keys (Dissing 2000, Hohmeyer 1986, Häffner 1995, Le Gal 1941, Maas Geesteranus 1967, Moser 1963, Romagnesi 1978) and descriptions (e.g., Donadini 1978, 1979a, b, 1980a, Moravec 1985) of European species exist, *Peziza* has never been monographed and the infrageneric relationships are poorly understood. A number of subgenera and sections have been proposed, but only few attempts to provide a coherent system have been made (Donadini 1977, 1978). Furthermore, controversy has surrounded the generic delimitation of *Peziza.* Recent molecular studies suggest that the genus is not monophyletic, but rather is composed of at least two distinct clades (Norman and Egger 1996, 1999).

The nomenclature of *Peziza* is complicated on several counts. It is a pre-starting point name originating from Dillenius (1719). It has been applied to a number of cup-shaped fungi including both basidiomycetes and ascomycetes. Linnaeus (1753) adopted the name *Peziza* in Species Plantarum, the starting point work, for a group of fungi now referred to *Cyathus* Willd. (Basidiomycota) (Dennis 1983). Post-linnaean authors, particularly Bulliard (1791) and Persoon (1801), included primarily discomycetes, both operculate and inoperculate, in *Peziza,* thus making important contributions to the modern concept of the genus. Since Fries (1822) adopted the concept of these authors (not Linnaeus's concept) and placed what became the lectotype of *Peziza* L. (= *Peziza lentifera* L. = *Cyathus olla* Pers.) in *Nidularia* Fr. (Dennis 1983), Fries can be considered as having described *Peziza* as a new genus with a sanctioned status (Yao et al 1995). *Peziza* in the sense of Fries has been lectotypified by *P. vesiculosa* Bull. : Fr. (Wakefield 1939).

Boudier (1885, 1907) used two genera for taxa now placed in *Peziza. Aleuria* emend. Boud. non Fuckel for ellipsoid-spored species without oil guttules and *Galactinia* for ellipsoid-spored species with two guttules. Le Gal (1941, 1947) followed Boudier, but later (1953a) united the genera *Aleuria* and *Galactinia* in *Galactinia* with two sections: "Eguttulisporæ" nom illeg. and "Guttulisporæ" nom illeg. (corresponding to *Aleuria* and *Galactinia* sensu Boud. respectively). Le Gal abandoned *Peziza* as a "nomen confusum." The most recent classifications (Dennis 1981, Dissing and Pfister 1981, Dissing 2000, Eckblad 1968, Rifai 1968) follow Le Gal's (1953a) circumscription of the genus, but under the name *Peziza.* As such, *Peziza* is defined as having epigeous, discoid to cupulate apothecia, a few mm to ca 15 cm in diam, sessile or with a short stipe (FIGS. 2, 4, 9–12, 15, 20–21), amyloid asci, ellipsoid or rarely fusiform spores and an excipulum most often stratified in two or more layers of globose thin-walled cells intermixed with hyphae or a hyphal layer; lactiferous hyphae may be present. We have adopted this circumscription as the starting point for taxonomic comparisons in this study. Nevertheless, a few species are placed in the genus which produce more unusual ascomatal forms, i.e., sparassoid (Boudier 1899, Korf 1973a) or hypogeous, closed, hollow, often folded ascomata (FIGS. 17–18) (Burdsall 1968, Trappe 1979). The hypogeous forms have persistent hymenia and amyloid asci, but lack forcible spore discharge (TABLE I).

Sarcosphaera Auersw. (1869) was segregated from *Peziza* on the basis of its macro-morphology and initial hypogeous development. It produces large, enclosed, hollow apothecia, initially underground, which as they mature, usually become exposed and split into irregular acute rays (FIG. 13). The asci mature before the apothecia open, but are in organized hymenia, and the spores are forcibly discharged. Whether to recognize *Sarcosphaera* as distinct from *Peziza* has been questionable. Eckblad (1968) did not recognize *Sarcosphaera* as a distinct genus, and treated the species in *Peziza.* However, most contemporary taxonomists accept *Sarcosphaera* (Pouzar 1972, Korf 1973b, Pfister 1979a, Dissing 2000).

Plicaria Fuckel (1870) was introduced to accommodate species mostly treated by modern authors as *Peziza* and *Plicaria,* with both ellipsoid and globose spores, united by a few characters, e.g., thick-walled, brownish, ornamented spores. *Peziza vesiculosa* and others were placed in *Pustularia* Fuckel, while *Peziza* in Fuckel's classification included small stipitate inoperculate discomycetes. Fuckel erected *Aleuria* Fuckel for the non-amyloid, *P. aurantia* Pers. (the modern accepted concept of *Aleuria*). Boudier (1885) restricted *Plicaria* to the globose-spored species and was followed by most contemporary and later workers. Rehm (1894) used *Plicaria,* for only ellipsoid-spored species with amyloid asci, and erected *Plicariella* (Sacc.) Rehm for the globose-spored species; he rejected the name *Peziza.* Some authors have maintained *Plicaria* emend. Boud. as a separate genus (Eckblad 1968, Rifai 1968, Dennis 1981, Dissing and Pfister 1981, Hirsch 1985, Norman and Egger



FIGS. 13–21. Ascoma forms and color variation in the Pezizaceae (group V–VII). 13–14. Group V. 13. *Sarcosphaera coronaria* ×0.4. 14. Stereothecium. *Hydnotryopsis setchellii* (Trappe 19134, OSC) ×1.2. 15–19. Group VI. 15. *Peziza saniosa* (JHP-93.193, C) ×1. 16. On burnt ground. *Plicaria trachycarpa* (KH-97–89, C) ×1.3. 17. Ptychothecium. *Peziza ellipsospora* (Trappe 12996, OSC) ×1.3. 18. Ptychothecium. *Peziza whitei* (M1445, OSC) ×1. 19. Exothecium. *Ruhlandiella berolinensis* (12355, OSC) ×1. 20. Group VIIa. *Peziza polaripapulata* (KS-95–10, C) ×0.8. 21. *Peziza retrocurvata* (KS-94–182, C holotype, K, FH isotypes) ×0.6.

Photos: 15, 16 J.H. Petersen. 21 K. Hansen. 14, 17, 18 M. Castellano. 20 T. Læssøe. 13 D.S. Hibbett. 19 D. Luoma.

1996, Dissing 2000), while others have regarded it as a part of *Peziza* in the sense adopted here (e.g., following Korf 1960, 1972, Le Gal 1953b, 1962). Whether the shape of the spores is a reliable character at the generic level has been a persistent controversy. Other characters have been proposed to support the recognition of *Plicaria*. These are pale brownish spores, paraphyses embedded in a granular matrix, dark-colored apothecial pigments (brown pigment on the walls of the asci), *Chromelosporium* anamorphs and a carbonicolous habitat (FIG. 16). Egger (1987) found that *Plicaria trachycarpa, P. endocarpoides* and some species of *Peziza* (*P. atrovinosa, P. ostracoderma, Peziza* sp. #2), exhibited a positive tyrosinase reaction, while other species of *Peziza* had a negative reaction. Egger noted that if correlating characters were found, the concept of *Plicaria* might have to be modified to include ellipsoid-spored species as in the original concept. Moravec and Spooner (1988) reached the same conclusion based on a morphological study of brown-spored species of *Peziza* (*P. atrovinosa, P. vacinii, P. retiderma* Cooke, *P. rifaii* J. Moravec & Spooner and *P. ostracoderma*) and stated that if *Plicaria* is to be recognized "the inclusion in it of species with non-globose spores appears unavoidable." Phylogenetic analyses by Norman and Egger (1996) including most of these taxa, indicated that the globose-spored *Plicaria* is monophyletic, but nested within *Peziza*. They accepted the genus ad interim even though it implied a paraphyletic *Peziza*. In this study we are using the name *Plicaria* as emended by Boudier.

Boudiera Cooke (1877) has been placed in the Ascobolaceae (Boudier 1907, Korf 1972, 1973b) due to the turbinate to pulvinate ascomata (FIG. 6), protruding asci and pale brownish spores, but its relationship has been much disputed. Eckblad (1968) stated that *Boudiera* did not seem to be closely related to any other genus with protruding asci, but he, nevertheless, referred it to the Ascobolaceae. *Boudiera* was revised (Dissing and Schumacher 1979) and placed in the Pezizaceae by Dissing and Korf (1980) and Hirsch (1980) along with other genera with globose spores and amyloid asci. Dissing and Korf emphasized characters of the anatomy and morphology of the ascomata and suggested that *Boudiera* is in a line with *Plicaria* on the one hand, and *Ruhlandiella* and *Sphaerozone* on the other. Hirsch (1980) considered *Boudiera* closely related to *Plicaria,* as did Rifai (1968). Hirsch also pointed out similarities in the excipulum structure, besides spore color, amyloid reactions of asci (which blue evenly over the entire length in both *Plicaria* and *Boudiera*) (TABLE I), agglutination of paraphyses and often a complex spore ornamentation. He did not find protruding asci, a consistent generic character in *Boudiera.* Molecular phylogenetic analyses (Landvik et al 1997, Norman and Egger 1999) support the placement of *Boudiera* in the Pezizaceae.

Pachyella Boud. (1907) (FIG. 5) was synonymised with *Peziza* (Donadini 1980b, Eckblad 1968, Seaver 1928), but was accepted by Le Gal (1947, 1953a), Korf (1972) and Pfister (1973) based on the presence of a well-developed cortical zone of globose cells which on the outside terminate in hyaline, hyphoid hairs, embedded in a gel and asci usually diffusely amyloid. Donadini (1980b) gave *Pachyella* subgeneric rank under *Peziza.* Most taxonomists have followed Pfister (1973). Hirsch (1984) even regarded *Pachyella* as so isolated within the Pezizaceae that he proposed a tribus Pachyelleae for this taxon alone, opposed to tribus Pezizeae including all other genera of the family.

Iodophanus Korf (Kimbrough and Korf 1967) was segregated from *Ascophanus* Boud. (tribus Pseudoascoboleae, Ascobolaceae) and was, along with *Thecotheus* Boud., assigned to the tribus "Pezizeae" (Pezizaceae) rather than the tribus Theleboleae (Pezizaceae), because they possess amyloid asci, spores with cyanophilic spore markings and an *Oedocephalum* conidial state (Gamundi and Ranalli 1964). Korf (1972, 1973b) later treated *Iodophanus* in the Ascobolaceae (tribe Iodophaneae), emphasizing the thick-walled spores in early stages of development, the carotenoid pigments, and asci that protrude prominently at maturity (FIG. 1). Furthermore, Korf stated that the tribe Iodophaneae (*Iodophanus, Boudiera, Thecotheus* and *Sphaerosoma*) seems surely to represent the link between Pezizaceae and Ascobolaceae. On the contrary, *Iodophanus* has been regarded as a "primitive type" within the Pyronemataceae by Eckblad (1968), based on the paraphyses' containing carotenoid pigments, the excipular structure, and the diffusely amyloid type of ascus. A close relationship between *Iodophanus, Peziza* and *Plicaria* has been indicated by septal ultrastructure of asci and ascogenous hyphae (Kimbrough and Curry 1985). Two ascal septum types were found; the pezizoid and the ascoboloid. The genus *Thecotheus* shared the ascoboloid type with *Ascobolus* and *Saccobolus* Boud. Molecular phylogenetic studies support the relationship of *Iodophanus* to the Pezizaceae and of *Thecotheus* to Ascobolaceae (Landvik et al 1997, 1998).

Scabropezia Dissing & Pfister (1981) was segregated from *Plicaria* and *Peziza,* based on the anatomy of the apothecia. In this genus the outer surface of the ascomata is pustulate (FIG. 7), the pustules being composed of aggregates of globose to angular cells clearly separated from the medullary excipulum of textura intricata. Only two species are known.

Hapsidomyces J.C. Krug & Jeng (1984) was erected for *H. venezuelensis* Krug & Jeng and assigned to the Pezizaceae based on the amyloid asci and the thin-walled, pale-colored spores. Krug and Jeng considered it to be closely related to *Boudiera* (see TABLE I), but sufficiently distinct by its early cleistohymenial development; a distinct apothecial margin; short, narrow asci with a short stipe; a rather narrow operculum; filiform paraphyses with yellowish content; small, eguttulate spores, and a coprophilous habitat. As in *Boudiera,* the asci protrude at maturity.

Kimbropezia Korf & Zhuang (1991) was described on the basis of a cyanophilic and Congo Red-staining lens-shaped thickening ("opercular lens") within the ascus operculum. The asci were further noted to be unusually brittle and with rather abruptly narrowed and often twisted bases. The genus was assigned to the Pezizaceae, differing from *Peziza* only by the very peculiar asci (see TABLE I). Van Brummelen (1998) studied the ascus apical structure by TEM and found it to be unique. He considered *Kimbropezia* best placed as a rather aberrant genus in the Pezizaceae. On the contrary, molecular analysis by Norman and Egger (1999) placed *Kimbropezia* within *Peziza.*

Rhodopeziza Hohmeyer & Moravec (Moravec 1994) was described for *R. tuberculata* (Gamundí) Moravec & Hohmeyer (= *Aleuria tuberculata* Gamundí). It differs from *Aleuria* in having amyloid asci and tuberculate spores which are not regularly biguttulate. According to Moravec (1994) it has a special position in the Pezizales, with its carotenoid granules in the paraphyses and asci being amyloid over the entire length. It shares characters with *Iodophanus* in particular, especially the presence of carotenoids, ornamented spores and diffusely amyloid asci. It was placed in the Pezizaceae by Eriksson and Hawksworth (1995).

Iodowynnea Medel, Guzmán & Chacón (Medel et al 1996) was segregated from *Peziza* based on its large, convoluted to highly folded apothecia, arising from a buried stipe, and longitudinally verrucose-striate spores. One of the authors, Korf, reserved judgement on whether the new taxon should be considered a subgenus of *Peziza* or merit generic rank. Le Gal (1953a) and Pfister (1974) treated the species in *Galactinia* and *Peziza* respectively.

Marcelleina Brumm., Korf & Rifai (van Brummelen 1967) is included in this study to test the hypothesis of a close relationship to *Peziza gerardii.*

Hypogeous genera. The truffle or truffle-like genera presented below, except for *Mycoclelandia* and *Cazia,* were originally described in the order Tuberales (Tuberaceae or Terfeziaceae) due to their hypogeous habit and lack of forcible spore discharge.

Hydnobolites Tul. & C. Tul. (1843) was described for *H. cerebriformis* Tul. & C. Tul. It was referred to Tuberaceae by Gilkey (1954b) and Korf (1973b), but placed in the Terfeziaceae by Hawker (1954) and Trappe (1971, 1979) because the spores are globose and there is no organized hymenium with paraphyses at any stage of development. This position has been accepted by most subsequent authors. The genus was distinguished from others in the Terfeziaceae by having an interior layer of solid undifferentiated tissue in which the asci are randomly distributed. Meandering veins deeply penetrate the interior of the ascomata from the outer surface. These are lined with outer excipulum tissue. The asci are non-amyloid without pretreatment in KOH, therefore *Hydnobolites* was not placed in the Pezizaceae. Trappe (1979) regarded *Hydnobolites* to be close to both *Pachyphloeus* and *Terfezia.* The recent discovery of several cytological and ultrastructural features by Kimbrough et al (1991) made them suggest that *Hydnobolites* belongs in Pezizaceae. These features are the electron-dense, biconvex bands in septal pores of the asci, dextrinoid and weakly amyloid asci (only after pretreatment with 2% KOH) and a type of spore wall deposition similar to members of Pezizaceae.

Pachyphloeus Tul & C. Tul. (1844) was erected for *P. melanoxanthus* (Tul.) Tul & C. Tul. It was, like *Hydnobolites,* referred to Tuberaceae by Gilkey (1954b) and Korf (1973b), and placed in the Terfeziaceae by Trappe (1979). Hawker (1954) placed the genus in Eutuberaceae E. Fisch. It lacks a hymenium and asci irregularly line veins or are randomly produced in the medullary excipulum. An apical depression or pore leading into a few open veins is characteristic of the ascomata. The verrucose outer excipulum of isodiametric cells separates *Pachyphloeus* and *Hydnobolites* from other genera of the Terfeziaceae (Trappe 1979). However, amyloid asci occur in some species of *Pachyphloeus* (e.g., in the type species), and based on this and anatomical features, the genus has been placed in the Pezizaceae by Dissing and Korf (1980) and Dissing (2000). Molecular phylogenetic analyses has recently confirmed this placement (Norman and Egger 1999, Percudani et al 1999).

Terfezia (Tul. & C. Tul.) Tul. & C. Tul. (1851) was elevated from *Choiromyces* section *Terfezia* Tul. & C. Tul. to generic rank. It was distinguished by having pockets of fertile tissue separated by sterile, but otherwise undifferentiated veins, highly ornamented spores and non-amyloid asci (Trappe 1971, 1979). It is the type genus of Terfeziaceae, and the most heterogeneous genus of the family. Recent molecular phylogenetic analyses suggest that *Terfezia* is not monophyletic, and that it is nested within Pezizaceae (Norman and Egger 1999, Percudani et al 1999).

Sphaerozone Zobel (Corda 1854) was described for *S. tulasnei* Zobel (= *Sphaerosoma ostiolatum* Tul. & C. Tul.), which has reddish brown spores. Dissing and Korf (1980) studied the type species and discovered that the asci are amyloid, contrary to previous reports by Korf (1972, 1973b). Under the impression that asci were non-amyloid Korf treated the genus in Pyronemataceae, rather than a genus in Pezizaceae as was subsequently done by Dissing and Korf (1980). It differs from *Ruhlandiella* by having paraphyses without gelatinous sheaths and persistent asci.

Tirmania Chatin (1891) was described for *T. africana* Chatin (= *Tuber niveum* Desf.). It was placed in the Terfeziaceae by Trappe (1971) and Korf (1973b). It resembles *Terfezia,* but differs by having smooth or at most minutely roughened spores and amyloid asci. Based on the amyloid reaction and its anatomy, Trappe (1979) transferred the genus to the Pezizaceae.

Ruhlandiella Henn. (1903) was redescribed and emended by Dissing and Korf (1980), who selected a neotype for the type species *R. berolinensis.* They found the asci to be amyloid and the paraphyses to have characteristic gelatinous sheaths (features not mentioned in Hennings' original description). The ascomata are relatively small, hypogeous or semi-hypogeous, solid, pulvinate to globose ascomata and with the hymenium covering the outer surface and permanently exposed (FIG. 19) (Dissing and Korf 1980, Galán and Moreno 1998, Warcup and Talbot 1989 as *Muciturbo* Talbot). Asci are evanescent at maturity. Dissing and Korf (1980) referred *Ruhlandiella* to the Pezizaceae, with other globose-spored, amyloid genera. A close relationship to *Sphaerozone,* in a lineage with *Boudiera* and *Plicaria,* was suggested.

Hydnotryopsis Gilkey (1916) was erected for *H. setchellii,* but later synonymized with the globose-spored *Choiromyces* Vittad. (Tuberaceae) (Gilkey 1954b). Trappe (1975a), however, showed that it has amyloid asci and, based on this and its ellipsoid spores, the genus was reinstated. Fischer (1938) and Trappe (1979) placed the genus in the Pezizaceae. The ascomata are solid, but the asci and paraphyses are arranged in hymenia.

Amylascus Trappe (1971) (FIG. 8) was segregated from *Hydnobolites* on the basis of its thick-walled, amyloid asci, echinulate spores and the verrucose outer excipulum of large inflated cells which gives rise to a tomentose outer surface (Trappe 1971, 1975b, Beaton and Weste 1982). It was described in the Terfeziaceae for a single species, *H. herbertianus* Cribb. Later, Trappe (1975b) considered the genus to be closely related to the Geneaceae in both form and anatomy, and the similarities between *Hydnobolites* and *Amylascus* to be the result of parallel evolution. When restricting Terfeziaceae to include only genera with non-amyloid asci, however, Trappe (1979) transferred *Amylascus* to Pezizaceae.

Mycoclelandia Trappe & Beaton (1984) was proposed to replaced *Clelandia* Trappe (1979), a homonym of *Clelandia* J.M. Black (Violaceae). It was placed in the Pezizaceae, and noted to resemble *Peziza* s.l. in several anatomical features, but differing in its "cleistothecial" ascomata and indehiscent asci (Trappe 1979). The asci are diffusely amyloid with the reaction strongest near the apex.

Cazia Trappe (1989) was assigned initially to the Helvellaceae due to the non-amyloid asci and large isodiametric cells in the excipulum. It differed from other similar hypogeous genera by its hyaline, minutely ornamented spores, crooked asci and a yellow KOH reaction of the fresh medullary excipulum. The genus was identified as a member of the Pezizaceae, using sequences from the nLSU and nSSU rDNA (O'Donnell et al 1997).

MATERIALS AND METHODS

Material studied.—Forty eight collections of *Peziza* representing 39 species were selected to cover the range of macro- and micromorphological characters, and habitats and substrates recognized within the genus. To critically assess the monophyly of *Peziza* and define its sistergroup relationships, representatives of the genera *Amylascus, Boudiera, Hydnotryopsis, Iodowynnea, Pachyella, Ruhlandiella* and *Tirmania* were included (Tables I, II). For a few selected species more than one collection was sequenced to verify the LSU rDNA sequences and estimate the intraspecific variation. LSU rDNA sequences from 12 additional species of *Peziza* and representatives of the genera *Cazia, Iodophanus, Kimbropezia, Plicaria, Sarcosphaera* and *Scabropezia* were obtained from GenBank (TABLE II). To assess the monophyly of the Pezizaceae and the relationship to the genera *Marcelleina* and *Pfistera* Korf & W.Y. Zhuang (currently placed in the Pyronemataceae), species belonging to the Ascobolaceae (*Ascobolus*), Morchellaceae (*Verpa* Fr.) and Pyronemataceae (*Aleurina* Massee, *Otidea* (Pers.) Bonord., *Smardaea* Svrček) were included. Generic type species were used as far as possible (TABLE II). *Neolecta vitellina* was used to root the tree because phylogenetic analyses at more inclusive levels places *Neolecta* Speg. basal to the rest of the fruitbody producing ascomycetes and the budding yeasts (Landvik et al 1993, Landvik 1996). To test the influence of the outgroup on the analyses, *Neolecta* was replaced with *Orbilia* Fr., which has been suggested as the sister group to the Pezizales (Harrington et al 1999, Platt and Spatafora 2000).

Several collections of most included *Peziza* species have been studied morphologically, and existing types or other original material have been examined. The amyloid reactions of asci have been examined in additional specimens of other included genera. A list of the specimens is available from KH. The published voucher specimen for *Pachyella clypeata* (ALTA 9029, GenBank SSU: AF133144, LSU: U40619) (Norman and Egger 1999) was examined by KH and DHP and was redetermined as *Peziza subisabellina.* The voucher specimens for the other sequences obtained from GenBank have not been studied morphologically by us.

Morphological methods.—The voucher material was studied using light microscopy, and was identified or identifications were verified by KH. All species of *Pachyella* were further confirmed by DHP. Special notice was paid to the intensity and location of the amyloid reaction in asci by using Melzer's reagent (1.5 g iodine, 5.0 g potassium iodide, 100 g chloral hydrate, 100 mL distilled water), applied with or without KOH pretreatment (2% or 10% KOH). Other chemicals used were Cotton Blue in lactic acid (1% in 875 mL lactic acid, 63 mL glycerol, 62 mL water) and Congo Red in ammonia (0.3% in commercial ammonia cleaner). For critical species the spore surface was viewed by an AMRay 1000 scanning electron microscope (SEM). The anatomical structures of the excipulum were studied using hand sections (for fresh material) or sections made on a freezing microtome. Microanatomical terminology follows Korf (1973b). Photographs of the ascus amyloid reactions were made with an Olympus BH 2 microscope and an Olympus C35AD–4 camera, and processed in Photoshop (Adobe Photoshop 4.0).

Molecular methods.—DNA was isolated from dried or fresh ascomata and was extracted as outlined in Hansen et al (1999). Serial dilutions of DNA (1:10, 1:100, 1:1000) were used as template for the polymerase chain reaction (PCR). The 5′ end of the nuclear large subunit rDNA (nLSU-rDNA), spanning domains D1 and D2, was amplified using the primers LROR and LR5 (for a few taxa LR5 was replaced with LR3 or LR7) (Moncalvo et al 2000). PCR products were purified either directly or following agarose gel electrophoresis and band excision using QIAquick spin columns (Qiagen 1997). In addition to the primers used for PCR, internal primers PNL2 (O'Donnell et al 1997) and LSU0354–5′ (5′- GCA AGA GAC CGA TAG CGC ACA AGT AG−3′) designed for *Peziza,* were used for BigDye terminator cycle sequencing (Applied Biosystems, Foster City, California) following the manufacturer's protocol, except that reaction volumes were 10 μL. Sequencing reactions were purified using ethanol/sodium precipitation (ABI protocol). Sequencing reactions were electrophoresed and data collected on an Applied Biosystems 377 automated DNA sequencer (Perkin-Elmer/ABI).

Analytical methods.—Sequences were edited and contigs assembled using Sequencher 3.0 (GeneCodes, Ann Arbor, Michigan). Sequences are deposited in GenBank (TABLE II). Nucleotide sequences were aligned manually in the data editor of PAUP*4.0b3a (Swofford 1998) with alignment gaps inserted to optimize aligned sites. The data matrix is available from TreeBASE (http://phylogeny.harvard.edu/treebase) as accessions S612 and M947. Nucleotide diversity (e.g., Nei 1987, equation 10.6), as the average number of nucleotide differences per site between two LSU rDNA sequences, were calculacted within and between selected species.

Phylogenetic analyses were performed in PAUP*4.0b3a (Swofford 1998) on an iMac 350 MHz (unless otherwise stated). Maximum parsimony (MP) analyses with heuristic searches were performed, with 1000 random stepwise addition replicates and TBR branch swapping. All characters were equally weighted and unordered. Gapped positions were included, treated as missing data (gap = missing), or excluded in separate analyses. A two-step search was performed based on strategies designed by Maddison et al (1992) and Olmstead et al (1993): first, only up to two trees per replicate were kept, then exhaustive swapping was performed on all of the most parsimonious trees discovered, with MAXTREES set to 15 000. Relative robustness of individual branches was estimated by bootstrap, using 500 replicates, with heuristic searches, 10 random addition sequences, TBR branch swapping and MAXTREES set at 100.

Maximum likelihood (ML) analyses were performed using two different starting trees for TBR branch swapping: one of the most parsimonious trees and a tree generated with one random taxon addition sequence. Empirical nucleotide frequencies were used, with the Felsenstein (1984) two-parameter model for unequal base frequencies. The proportion of invariable sites was set to zero and an equal rate of substitution was assumed for all sites. The starting parameter values were obtained using the Rogers-Swofford method (Swofford 1998). To find the optimal tree, searches were repeated by varying the transition:transversion ratio until the best ML score was reached. Due to the large number of taxa, ML bootstrap values were generated using a "fast" stepwise sequence addition, with 100 replicates and a transition:transversion ratio of 1.9:1 (the optimal value from the previous analyses). This method does not optimize trees by swapping branches (Swofford 1998) and is therefore fast but not thorough. Equal bootstrap values (± 5%) were obtained with ML analysis using fastDNAml V. 1.0.8 (Olsen et al 1994), with 100 replicates. The latter analysis however, required a 14-d search on a Pentium 600 MHz computer, whereas the "fast" bootstrapping was conducted on an iMac 350 MHz in 6 d.

MacClade 3.04 (Maddison and Maddison 1992) was used to infer historical patterns of transformation between an epigeous and a hypogeous habit, with equally-weighted transformations. Topologically constrained parsimony analyses were used to evaluate the hypothesis that all hypogeous Pezizaceae have been derived (repeatedly) from epigeous taxa, with loss of forcible spore discharge. MacClade was used to construct constraint trees. Parsimony analyses were performed under the constraints, using the same settings as specified above, but with MAXTREES set to only 400 in the second step of the search. The Kishino-Hasegawa test (Kishino and Hasegawa 1989) was used to compare 400 trees under the constrained and unconstrained topologies in PAUP 4.0b3a. Maximum likelihood analyses were also performed under the constraints (with a transition:transversion ratio of 1.9:1) and compared to the optimal ML tree.

RESULTS

Alignment.—The dataset consisted of partial LSU rDNA sequences from 90 specimens. Sixty-eight new sequences were determined in this study. For most specimens, a 900 bp region at the 5′ end of the LSU rDNA was sequenced on both strands. For eight species of *Peziza* (*P. cerea, P. depressa, P. granulosa, P. proteana, P. saniosa, P. subviolacea, P. succosella* and *Peziza* sp. 1) only a c 620–680 bp. region at the 5′ end was determined. Sequences obtained from GenBank (27 specimens) were likewise c 620 bp. Missing data were spaced out with gaps in the alignment, and these positions were therefore either treated as missing data or excluded from analyses. The aligned length of all sequences including inserted gaps was 966 bp. The missing data could have introduced error in the phylogenetic estimates (Maddison 1993, Wiens 1998), however analyses of only the 620 bp region for the full dataset resulted in the same basic topologies and bootstrap values, with only slightly fewer resolved nodes.

No size variability due to introns was observed. LSU rDNA sequences from the same morphological species showed either no (e.g., *P. depressa, P. echinispora*) or several substitutions or deletions (e.g., *P. gerardii, P. subisabellina, Pachyella babingtonii*). Intraspecific genetic variation was in some cases larger than interspecific variation, e.g., the nucleotide diversity within *P. gerardii* was 3.1% and within *Pachyella babingtonii* 1.7%, whereas the average nucleotide diversity between the *Peziza* species within group IVa was only 1.3%. Identical sequences of the same morphological species were left out of the analyses.

Phylogenetic analyses.—Under gap = missing coding there were 319 parsimony informative characters. With gapped positions omitted this number decreased to 249. Maximum parsimony analysis produced over 15 000 equally most parsimonious trees

TABLE II. List of species used in the molecular phylogenetic study, with voucher specimen information and GenBank accession numbers. Information on new sequences are listed first, followed by information on sequences obtained from GenBank. Numbers in parentheses are used to indicate multiple collections of a single taxon.

Species	Voucher and geographic origin	Year and collector	GenBank
Nov. gen. ?	T. Laessøe 6236 (C). Malaysia	1999, T. Laessøe	AF335111
Aleurina imaii (Korf) W.Y. Zhuang & Korf	CUP-CH 2333 (CUP). China	1981, R-y. Zheng, R.P. Korf	AF335112
Amylascus tasmanicus (Rodway) Trappe	Trappe 18084 (C, dubl. OSC). Australia	1996, J. Trappe	AF335113
Boudiera dennisii Dissing & Sivertsen	HK 90.074 (C). Russia	1990, H. Knudsen	AF335114
Hydnotryopsis setchellii Gilkey[a]	Trappe 19134 (C, dubl. OSC). USA	1996, J. Trappe	AF335115
Hydnotryopsis sp.	Trappe 17231 (C, dubl. OSC). USA	1995, J. Trappe	AF335116
Iodowynnea auriformus (Le Gal) Medel, Guzmán & Chacón[a] (1)	CUP-ME566 (CUP). Mexico	1986, Ramón-Farias	AF335117
Iodowynnea auriformis (2)	18510 PAN (FH). India	1981, R. Kaushal	AF335118
Marcelleina persoonii (P. Crouan & H. Crouan) Brumm.[a]	HD S85-96 (C). Svalbard	1985, H. Dissing	AF335119
Marcelleina tuberculispora K. Hansen & Sandal	All-94-8 (C, type). Denmark	1994, K. Hansen, S.K. Sandal	AF335120
Otidea onotica (Pers.: Fr.) Fuckel[a]	KH-98-107 (C). Denmark	1998, K. Hansen	AF335121
Pachyella babingtonii (Berk. & Broome) Boud. (1)	KS-94-45 (C). Denmark	1994, K. Hansen, S.K. Sandal	AF335122
Pachyella babingtonii (2)	KH-99-09 (C). USA	1999, K. Hansen, D.H. Pfister	AF335123
Pachyella punctispora Pfister	KH-98-77 (C). Austria	1998, K. Hansen	AF335124
Pachyella violaceonigra (Rehm) Pfister[a]	s.n. (FH). Switzerland	1979, A. Nyffenegger	AF335125
Peziza ammophila Durieu & Mont.	SAE-1245 (C). Denmark	1984, S.A. Elborne	AF335126
Peziza ampelina Quél.	KH 00.011 (C). Denmark	1994, C. Lange	AF335127
Peziza ampliata Pers.: Fr.	JHC 92-386 (C). Denmark	1992, J. Heilmann-Clausen	AF335128
Peziza apiculata Cooke	Winterhoff 86239 (herb. Winterhoff). Germany	1986, W. Winterhoff	AF335129
Peziza arvernensis Roze & Boud. (1)	KH-98-08 (C). Denmark	1998, A. Storgaard	AF335130
Peziza arvernensis (2)	KH-98-12 (C). Denmark	1998, B. Klug-Andersen	AF335131
Peziza badiofusca (Boud.) Dennis	KH-98-113 (C). Sweden	1992, S.-Å. Hanson	AF335132
Peziza bananicola (Rehm) Sacc.	V. Demoulin 5529 (FH). New Guinea	1979, V. Demoulin, L. Smeets	AF335133
Peziza cerea Bull.: Fr.	KH-97-54 (C). Denmark	1997, J.H. Petersen	AF335134
Peziza depressa Pers. (1)	KH-98-28 (C). Denmark	1998, H. Knudsen	AF335135
Peziza depressa (2)	KH-98-18 (C). Denmark	1998, K. Hansen, T. Læssøc	AF335136
Peziza domiciliana Cooke	C no. 52152 (C). Denmark	1989, P.M. Petersen	AF335137
Peziza echinispora P. Karst (1)	Jukka Vauras 9110F (TURA). Finland	1994, J. Vauras	AF335138
Peziza ellipsospora (Gilkey) Trappe	Trappe 13017 (C, dubl. OSC). USA	1993, J. Trappe	AF335139
Peziza emileia Cooke	Brummelen 1921 (L) The Netherlands	1994, G. Piepenbroek-Groters	AF335140
Peziza exogelatinosa K. Hansen & Sandal	KS-94-149 (C, dubl. FH) Denmark	1994, K. Hansen, S. K. Sandal	AF335141
Peziza gerardii Cooke (1)	KH-98-86 (C). Denmark	1998, K. Hansen	AF335142
Peziza gerardii (2)	KH-97-90 (C). Denmark	1997, M. Christensen, K. Hansen	AF335143
Peziza gerardii (3)	KH-98-42 (C). Denmark	1998, T. Læssøe, K. Hansen	AF335144
Peziza granulosa Schumach.	KH 00.012 (C). Denmark	1994, K. Hansen, S.K. Sandal	AF335145
Peziza howsei Boud.	KH-97-98 (C). Denmark	1997, J.H. Petersen, C. Lange	AF335146

TABLE II. Continued

Species	Voucher and geographic origin	Year and collector	GenBank
Peziza limnaea Maas Geest.	HFG 94.2 (C). Denmark	1994, H.F. Gøtzsche	AF335147
Peziza luteoloflavida Svček	T. Schumacher & K. Østmoe D 170/83 (O). Norway	1983, T. Schumacher, K. Østmoe	AF335148
Peziza michelii (Boud.) Dennis	KH-98-13 (C). Denmark	1998, T. Laessøe	AF335149
Peziza micropus Pers.: Fr. (1)	KH-97-107 (C). Denmark	1997, K. Hansen	AF335150
Peziza micropus (2)	KH-99-04 (C). USA	1999, Z. Yang	AF335151
Peziza natrophila A.Z.M. Khan (1)	Kew 59522 (K, Isotype). Bangladesh	1970, G.B. Hants et al.	AF335152
Peziza natrophila (2)	JHP 93.021 (C). Denmark	1993, J. Vesterholt et al.	AF335153
Peziza nivalis (Hein & Remy) M.M. Moser	KH-97-44 (C). USA	1997, K. Hansen	AF335154
Peziza phyllogena Cooke (1)	KH-99-03 (C). USA	1999, K. Hansen, D.H. Pfister	AF335155
Peziza phyllogena (2)	s.n. (TUR, type of *Peziza kallioi*). Finland	1965, K. Mäkinen	AF335156
Peziza polaripapulata (J. Moravec) K. Hansen	KS-95-10A (C). Denmark	1995, H. Knudsen, M. Sasa	AF335157
Peziza proteana (Broud). Seaver f. *proteana*	Ginns 4156 (FH). Canada	1997, J. Ginns	AF335158
Peziza retrocurvata K. Hansen & Sandal	KS-94-182 (C). Denmark	1994, K. Hansen, S.K. Sandal	AF335159
Peziza saniosa Schrad.: Fr.	KH-97-137 (C). Denmark	1997, C. Lange	AF335160
Peziza subcutrina (Bres.) Koif (1)	KS-94-133 (C). Denmark	1994, K. Hansen, S.K. Sandal	AF335161
Peziza subcitrina (2)	KH-97-133 (C). Denmark	1997, C. Lange, K. Hansen	AF335162
Peziza subisabellina (Le Gal) Blank, Haffner & Hohmeyer (1)	RK 96.54 (herb. Roy Kristiansen). Norway	1996, R. Kristiansen	AF335163
Peziza subisabellina (2)	Winterhoff 8844 (herb. Winterhoff.). Germany	1988, W. Winterhoff	AF335164
Peziza subviolacea Svrček (1)	KH-98-29 (C). Denmark	1998, B. Klug-Andersen	AF335165
Peziza succosa Berk.	KH-98-07 (C). Denmark	1998, A. Storgaard	AF335166
Peziza succosella (Le Gal & Romagn.) Aviz.-Hersh. & Nemlich	KH-97-139 (C). Denmark	1997, C. Lange	AF335167
Peziza whitei (Gilkey) Trappe	Trappe 17049 (C, dubl. OSC). Australia	1995, J. Trappe	AF335168
Peziza sp. 1	KH-98-30 (C). Denmark	1998, K. Hansen	AF335169
Peziza sp. 2	C. no. 52153 (C). Denmark	1982, S.A. Elborne, H. Knudsen	AF335170
Peziza sp. 3	PM-120-97 (Herb. Roy Kristiansen). Norway	1997, P. Marstad	AF335171
Peziza sp. 4	KH-97-85 (C). Denmark	1985, J.H. Petersen, K. Hansen	AF335172
Peziza sp. 5	HD S.85.41 (C). Svalbard	1985, H. Dissing	AF335173
Pfistera pyrophila Korf & W.Y. Zhuang[a]	CUP-MM 854 (CUP, type). Canary Islands	1976, R.P. Korf et al.	AF335174
Ruhlandiella berolinensis Henn.[a]	Mycoflora of Macaronesia 1230 (C, isoneotype). Canary Islands	1976, R.P. Korf et al.	AF335175
Smardaea amethystina (W. Phillips) Svrček[a]	KH-97-132 (C). Denmark	1997, C. Lange, K. Hansen	AF335176
Tirmania nivea (Desf.: Fr) Trappe[a]	Trappe 23190 (C, dubl. OSC). Israel	1983, C.H. de Vries	AF335177
Tirmania pinoyi (Maire) Malençon	Trappe 13587 (C, dubl. OSC). Saudi Arabia	1982, H. Bakhary	AF335178
Published sequences:			
Ascobolus lineolatus Brumm.	NRRL A23604	Unknown	AF133159
Cazia flexiascus Trappe[a]	JMT 12993	USA	U42694
Glischroderma sp.	CUP62651	USA	AF133160
Iodophanus carneus (Pers.) Korf[a]	ARON 2102	Norway	AF133161

TABLE II. Continued

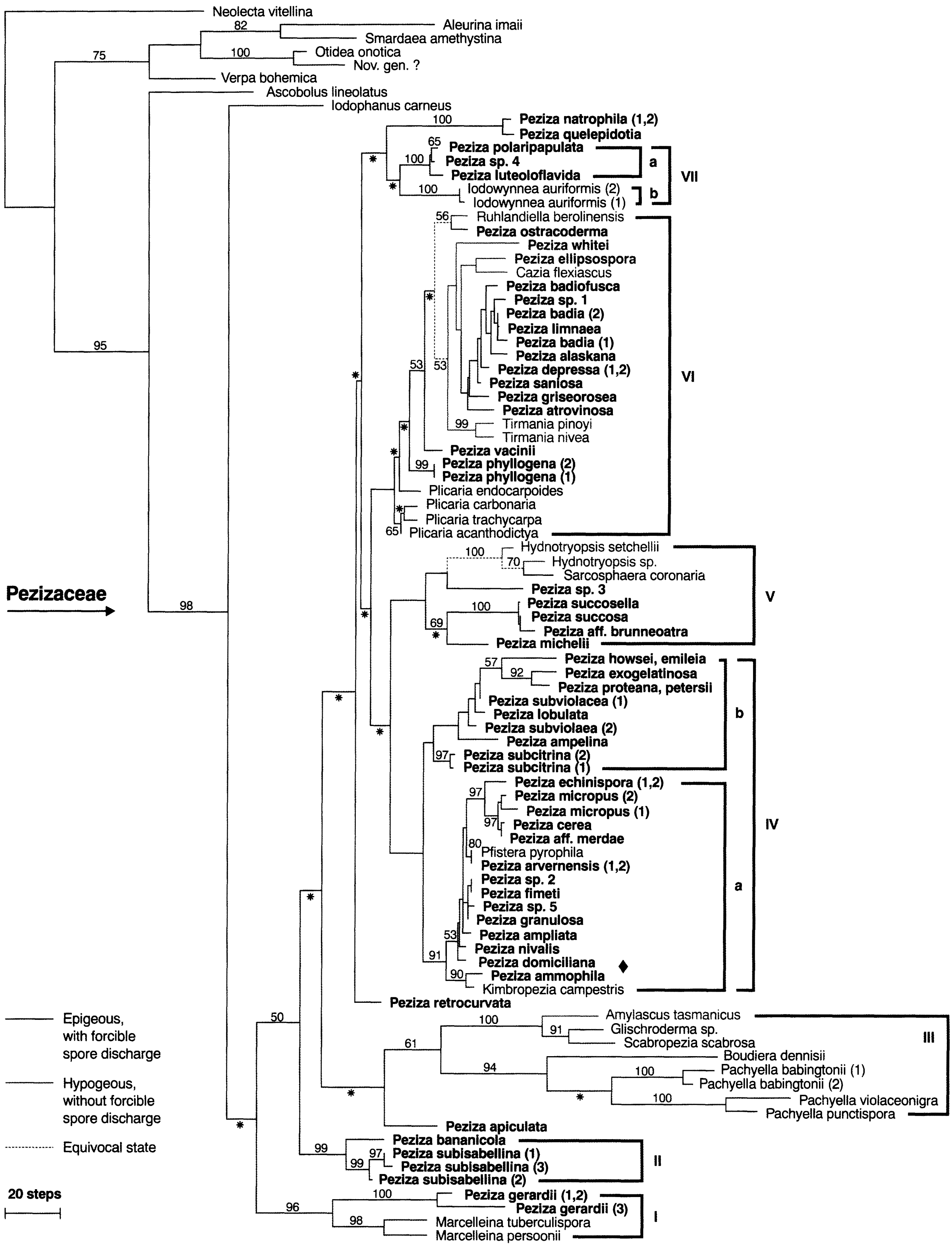
Species	Voucher and geographic origin	Year and collector	GenBank
Kimbropezia campestris Korf & W.Y. Zhuang[a]	CUP MM 2761	Canary Islands	AF133163
Neolecta vitellina (Bres.) Korf & J.K. Rogers	NSW 6359	USA	U42695
Peziza alaskana Cash	ALTA 8477	Canada	U40615
Peziza atrovinosa Cooke	DAOM 199606	USA	U40613
Peziza badia Pers. (1)	KNE 2205	Canada	U40614
Peziza badia (2)	UC 1475104	Sweden	U42692
Peziza aff. *brunneoatra* Desm.	KNE 2143	Canada	U40617
Peziza echinispora (2)	DAOM 199749	Canada	AF133165
Peziza fimeti (Fuckel) E.C. Hansen[c]	ALTA 9066	Canada	AF133170
Peziza griseorosea Gerard	CUP 62472	USA	U40616
Peziza lobulata (Velen.) Svček (as *P. violacea* Pers. ss. Dennis 1978)	DAOM 199673	Canada	AF133171
Peziza aff. *merdae* Donadini	CUP RPK-206	USA	AF133166
Peziza ostracoderma Korf	DAOM 199608	Canada	U40612
Peziza petersii Berk.	DAOM 195796	Canada	AF133167
Peziza quelepidotia Korf & O'Donnell	NRRL 22205	USA	U42693
Peziza subisabellina (3)[b]	ALTA9029	Canada	U40619
Peziza subviolacea (2) (as *P. pratervisa* Bres. ss Dennis 1978)	DAOM 195816	Canada	U40618
Peziza vacinii (Velen.) Svrček	NSW 6752	USA	U40611
Plicaria acanthodictya Dissing & Hauerbach	C 530 (C)	Denmark	U40607
Plicaria carbonaria (Fuckel) Fuckel	20.X.1986 (C)	Denmark	U40608
Plicaria endocarpoides (Berk.) Rifai	DAOM 199089	Canada	U40610
Plicaria trachycarpa (Curr.) Boud.[a]	DAOM 195830	Canada	U40609
Sarcosphaera coronaria (Jacq.) Boud.[a]	ALTA 9605	Canada	AF133172
Scabropezia scabrosa (Cooke) Dissing & Pfister[a]	Pfister 13.8.83 (FH)	USA	AF133173
Verpa bohemica (Krombh.) Schröt.	NRRL 20858 = CBS 551.72	Germany	U42672

[a] Generic type species.

[b] Published as *Pachyella clypeata* (Schw.) Le Gal (Norman & Egger 1996, 1999).

[c] Published as *Peziza vesiculosa* Bull. (Norman & Egger 1999).

(MPT) of 1832 steps under gap = missing coding (consistency index [CI] = 0.362, retention index [RI] = 0.650), and 1366 steps with gapped positions omitted ([CI] = 0.354, [RI] = 0.658). Although the degree of resolution varied in parts of the trees, no conflict between the strict consensus trees of the two sets of analyses was observed (FIG. 23, trees with gapped positions excluded are not shown). Trees obtained in analyses with *Orbilia* as the outgroup (data not shown) were identical to trees obtained with *Neolecta* as the outgroup. The large number of equally parsimonious trees reflects the inability of the data to resolve the higher order relationships, and relationships between closely related species (FIG. 23). However, 7 clades were identified (groups I–VII) that were generally well supported (as measured by bootstrapping) or present in all trees (FIGS. 22–23). The Pezizaceae was suggested to be paraphyletic (bootstrap MPT 98%, ML 94%), because *Marcelleina* was nested within it (FIGS. 22–24). Ascobolaceae (represented by *Ascobolus* under this sampling) was confirmed to be its sister group. The included, currently accepted genera in the Pezizaceae (TABLE I) were all nested within *Peziza*, with *Iodophanus* (FIG. 1) in a basal position, either as the sister group to the rest of the Pezizaceae or nested within the Pezizaceae. *Peziza gerardii*, which forms a clade with *Marcelleina* (FIGS. 2–3) (bootstrap 96%), is the sister group to


Neolecta vitellina
82
Aleurina imaii
Smardaea amethystina
75
100
Otidea onotica
Nov. gen. ?
Verpa bohemica
Ascobolus lineolatus
Iodophanus carneus
100
Peziza natrophila (1,2)
Peziza quelepidotia
65
Peziza polaripapulata
100
Peziza sp. 4
Peziza luteoloflavida
a
VII
100
Iodowynnea auriformis (2)
Iodowynnea auriformis (1)
b
56
Ruhlandiella berolinensis
Peziza ostracoderma
Peziza whitei
Peziza ellipsospora
Cazia flexiascus
Peziza badiofusca
Peziza sp. 1
Peziza badia (2)
Peziza limnaea
Peziza badia (1)
Peziza alaskana
95
53
53
Peziza depressa (1,2)
VI
Peziza saniosa
Peziza griseorosea
Peziza atrovinosa
99
Tirmania pinoyi
Tirmania nivea
Peziza vacinii
99
Peziza phyllogena (2)
Peziza phyllogena (1)
Plicaria endocarpoides
Plicaria carbonaria
Plicaria trachycarpa
65
Plicaria acanthodictya
100
Hydnotryopsis setchellii
70
Hydnotryopsis sp.
Sarcosphaera coronaria
Pezizaceae
Peziza sp. 3
98
100
Peziza succosella
V
Peziza succosa
69
Peziza aff. brunneoatra
Peziza michelii
57
Peziza howsei, emileia
92
Peziza exogelatinosa
Peziza proteana, petersii
Peziza subviolacea (1)
Peziza lobulata
b
Peziza subviolaea (2)
Peziza ampelina
97
Peziza subcitrina (2)
Peziza subcitrina (1)
Peziza echinispora (1,2)
97
Peziza micropus (2)
Peziza micropus (1)
IV
97
Peziza cerea
Peziza aff. merdae
80
Pfistera pyrophila
Peziza arvernensis (1,2)
Peziza sp. 2
a
Peziza fimeti
Peziza sp. 5
Peziza granulosa
53
Peziza ampliata
Peziza nivalis
91
Peziza domiciliana ♦
90
Peziza ammophila
Kimbropezia campestris
Peziza retrocurvata
50
100
Amylascus tasmanicus
Epigeous, with forcible spore discharge
91
Glischroderma sp.
61
Scabropezia scabrosa
III
Boudiera dennisii
94
100
Pachyella babingtonii (1)
Hypogeous, without forcible spore discharge
Pachyella babingtonii (2)
100
Pachyella violaceonigra
Pachyella punctispora
Peziza apiculata
Equivocal state
99
Peziza bananicola
97
Peziza subisabellina (1)
99
Peziza subisabellina (3)
II
Peziza subisabellina (2)
20 steps
100
Peziza gerardii (1,2)
96
Peziza gerardii (3)
I
98
Marcelleina tuberculispora
Marcelleina persoonii

the rest of the Pezizaceae in the MLT (FIG. 24). In the strict consensus of the MPTs, the basal node of the Pezizaceae is unresolved, with *Iodophanus,* the clade of *P. gerardii* and *Marcelleina,* and the rest forming a trichotomy (FIG. 23). Species of *Peziza* occurred in all groups except group III, often along with other genera of the Pezizaceae. Several taxa constitute separate lineages of uncertain placement: *P. apiculata, P. retrocurvata* (FIG. 21), and the clade of *P. natrophila* and *P. quelepidotia* (FIGS. 22, 23).

The optimal MLT's found under the two sets of analyses using different starting trees do not have significantly different likelihood scores (Kishino-Hasegawa test, $P < 0.05$). The optimal MLT was found with a log likelihood score of -11308.898, under a transition:transversion ratio of 1.9:1 (FIG. 24), with the starting tree generated with one random taxon addition sequence. In analyses with one of the most parsimonious trees as starting tree for branch swapping, the optimal MLT was found with a log likelihood score of -11312.599, under a transition:transversion ratio of 2.0:1. The ML analyses recovered the groupings found by the MP analyses, with some minor changes. Deeper nodes in the MLT were resolved, but not strongly supported by bootstrapping (FIG. 24), and correspond to those branches that collapse in the strict consensus tree of the MPT's (FIG. 23).

Amyloid reaction types.—Distinct types of ascus amyloid reactions were found to correspond to different rDNA lineages (FIG. 24). The location and intensity of the amyloid reaction are constant in a given species, but varies between species. Four types of reactions were identified: (i) faintly amyloid over the entire length (sometimes more strongly in upper half), but intensely and unrestrictedly amyloid over the apex (most taxa in group VI, *P. succosa* and *P. michelii*); (ii) faintly amyloid over the entire length, except intensely amyloid in a distinct ring zone at the apex, restricted to the area of dehiscence of the operculum (a synapomorphy for group IV); (iii) evenly amyloid over the entire length, either: (iiia) weakly, perhaps slightly stronger at the apex, or diffusely amyloid [periascus and hymenial gel amyloid (Pfister 1973)], or rarely non-amyloid (*Iodophanus, P. gerardii,* group II, *Pachyella, Boudiera, Amylascus, Hydnotryopsis, Plicaria, Tirmania, Ruhlandiella, P. natrophila, P. polaripapulata* and *Peziza* sp. 4); (iiib) strongly amyloid (*Iodowynnea, P. ellipsospora, P. luteoloflavida, P. retrocurvata, P. whitei* and *Sarcosphaera*); (iv) Non-amyloid (*Marcelleina* and *Cazia*). The amyloid reaction is a fairly stable character, but rarely may be absent due to change of humidity (e.g., long periods of rain) or an overripe state of the hymenium, e.g., presumedly in *Pfistera* (van Brummelen 1998) and other *Peziza* species. The periascus (an extra-ascal mucilagenous coat, as defined by van Brummelen 1978) can also disappear after heating (Donadini 1985) or be removed in microscopic preparation by applying pressure on the cover slip and sliding it back and forth (Samuelsen 1978).

DISCUSSION

Overview.—The Pezizaceae appear to be paraphyletic as currently circumscribed (Eriksson 2000) because *Marcelleina* is nested within it. If *Marcelleina* is transferred to the Pezizaceae, then the family would be a strongly supported monophyletic group (FIGS. 22–24). Our data fail to resolve the higher level relationships within the Pezizaceae (FIG. 23) or result in resolutions of relationships that are not well-supported by bootstrap analyses (FIG. 24). The weakness in our estimate of the phylogeny may be due to having too few informative characters, or to missing key taxa in our sampling (especially species of *Peziza* with apiculate spores). Addition of more characters from other molecules (such as the protein-coding nuclear genes Beta-tubulin or RPB2), and expansion of the set of taxa to include more aberrant species of *Peziza,* may improve resolution deep in the tree and "break up" long branches (Graybeal 1998). Nevertheless, seven groups of species are identified that may eventually be formally recognized. Confirming recent molecular studies, *Peziza* is not supported as monophyletic (Norman and Egger 1996, 1999). *Peziza* species are spread among all groups, except group III, and it is evident from this that *Peziza* will have to be subdivided into several genera, or a very wide concept

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FIG. 22. Phylogeny of the Pezizaceae inferred from nLSU-rDNA sequences. One of more than 15 000 equally parsimonious trees (1832 steps), generated under gaps = missing coding. Terminal taxa represent individual specimens (TABLE II). Branches with asterisks collapse in the strict consensus of all most parsimonious trees. Numbers by branches are bootstrap frequencies (values greater than 50%). Branch lengths are proportional to the number of steps (character changes) along the branch. Branch colors and dotted branches represent character state optimizations (using MacClade). Species of *Peziza* are in boldface. Taxa in grey are hypogeous, without forcible spore discharge. Bracketed groups I–VII are discussed in the text. Diamond indicates suggested position of *P. vesiculosa* from subsequent analysis (see note added after acceptance of the manuscript).

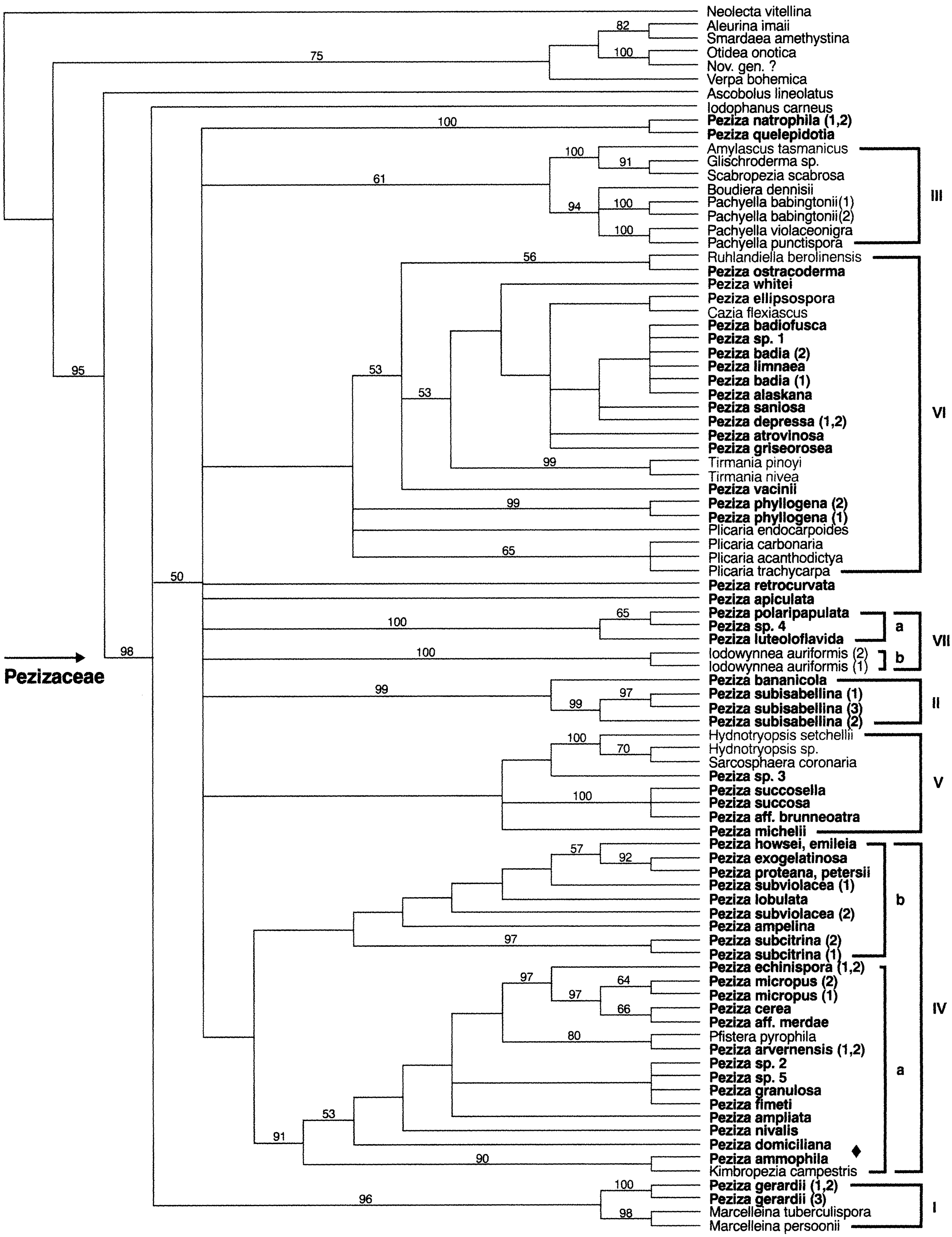

FIG. 23. Strict consensus of 15 000 equally parsimonious trees generated under gaps = missing coding. Numbers by branches are bootstrap frequencies (values greater than 50%). Species of *Peziza* are in boldface. Taxa in grey are hypogeous, without forcible spore discharge. Bracketed groups I–VII correspond to groups I–VII in FIG. 22. Diamond indicates suggested position of *P. vesiculosa* from subsequent analysis (see note added after acceptance of the manuscript).

would have to be accepted, to better reflect phylogeny.

Ascomata forms and habit.—Four different forms of ascomata exist within the Pezizaceae. Epigeous apothecia of various shapes (TABLE I) with forcible spore discharge, are the most common and occur in groups I–VII. This form is likely to be symplesiomorphic, implying that the apothecia-forming members of the Pezizaceae have given rise to at least three different forms of hypogeous ascomata without forcible spore discharge (sensu Weber et al 1997): (i) ptychothecia: enclosed, hollow, subglobose to globose, often convolute ascomata, which may have one or a few open chambers, and a persistent, recognizable hymenium of asci and paraphyses typically lining the hollow chambers (FIGS. 17, 18) (in group VI); (ii) stereothecia: more or less solid, fleshy ascomata, with the asci either solitary, scattered relatively evenly throughout the medullary excipulum or grouped in dispersed pockets or meandering veins (FIGS. 8, 14) (in group III, V, VI); (iii) exothecia: solid, pulvinate to globose ascomata, in which the hymenium covers the outer surface (leaving no discernible margin) and permanently exposed, with the asci distinctly shorter than the paraphyses (FIG. 19) (in group VI).

At least three independent origins of hypogeous forms within the Pezizaceae were supported by the LSU rDNA gene trees (in group III, V and VI) (FIGS. 22, 24). The most parsimonious interpretations of the molecular phylogenies suggest that forcible spore discharge has been lost once in group III; lost twice, or lost once and gained once in group V; and either lost twice and gained once, or lost once and gained twice in group VI (FIGS. 22, 24). However, separate constraint analyses forcing the hypogeous taxa within either group V or VI into monophyletic groups, could not be rejected using the Kishino-Hasegawa test (TABLE III). Forced monophyly of the hypogeous taxa within group VI, did not yield trees that were significantly worse ($P < 0.05$) than the unconstrained trees (TABLE III). Likewise, forced monophyly of the two species of *Hydnotryopsis* in group V could not be rejected ($P < 0.05$). Trees with constrained monophyly of the hypogeous taxa within groups V and VI, respectively, but analyzed together, were not significantly longer than the unconstrained MPTs ($P < 0.05$). However, under this constraint the MLT was significantly worse than the unconstrained optimal MLT ($P < 0.05$) (TABLE III). The most conservative conclusion is thus, that forcible spore discharge has been lost only once within each of the groups V and VI.

Phylogeny within the Pezizaceae.—Group I. This is a highly supported clade (bootstrap 96%) of the morphologically distinct *Peziza gerardii* and two species of *Marcelleina, M. persoonii* and *M. tuberculispora.* It is a likely sister group to the rest of the Pezizaceae (FIG. 24). Contrary to the current classification, which accepts *Marcelleina* in the Pyronemataceae (Eriksson 2000) or Otideaceae (Hawksworth et al 1995), our analyses place the non-amyloid *Marcelleina* in the Pezizaceae. The genus is restricted to species with small purplish apothecia, 2–10 mm in diam (FIG. 3), with light brown pigments in the walls of the hyphae in the outer excipulum and hyaline spores (Moravec 1987). The purplish (-brownish) pigments are found in the paraphyses and subhymenium. *Smardaea* and *Aleurina,* presumed to be closely related to *Marcelleina* (Zhuang and Korf 1986, Moravec 1987, Hansen et al 1998), are supported in the Pyronemataceae (grouping with *Otidea* and an undescribed genus (TL 6236)) (FIGS. 22, 23). *Smardaea* and *Greletia* Donadini (the latter not included in this study) are distinguished by purplish pigments in all parts of the apothecia, including the spore ornamentation, and by a clearly differentiated medullary excipulum (Svrček 1969, Donadini 1979c, Moravec 1987). Korf (1972) placed *Marcelleina* (as *Pulparia* P. Karst.) in the subfamily Ascodesmidoideae (Pyronemataceae). To him, the genus seemed to provide a link between *Sphaerozone* and *Aleurina* (as *Jafneadelphus* Rifai). Moravec (1987) revised and placed *Marcelleina* in a new subfamily, Aleurinoideae (Pyronemataceae), along with *Aleurina, Eoaleurina* Korf & W.Y. Zhuang, *Greletia, Smardaea* and *Sphaerosoma.*

Although the Pezizaceae has generally been characterized by amyloid asci, these results indicate that the amyloid reaction might be lost (type iv) in some lineages, such as in the branch leading to *Marcelleina* (FIGS. 22, 24). Boudier (1907) placed species of *Marcelleina* (as *Plicaria*), including the type species *M. persoonii,* in the "Aleuriées" (= Pezizaceae), presumably based on the globose spores and the excipulum structure. He fully realized that the asci were non-amyloid (Boudier 1905–1910, plate 308). Eckblad (1968) also regarded *Marcelleina* to be very close to *Plicaria,* the non-amyloid asci being one of only a few differentiating characters. He placed it in the Pezizaceae, despite the non-amyloid asci, and concluded that it would be "... attaching too much importance to a single, widely distributed character to keep *Marcelleina* out of its otherwise close affinity to *Plicaria* and *Peziza.*" Other contemporary taxonomists have considered *Marcelleina* as logically placed among the non-amyloid genera. However, morphological similarities between *P. gerardii* and *Marcelleina* (FIGS. 2, 3), *Smardaea* and *Greletia* were noted by Schumacher and Jenssen (1992).

Macroscopically, and in habitat requirements (en-

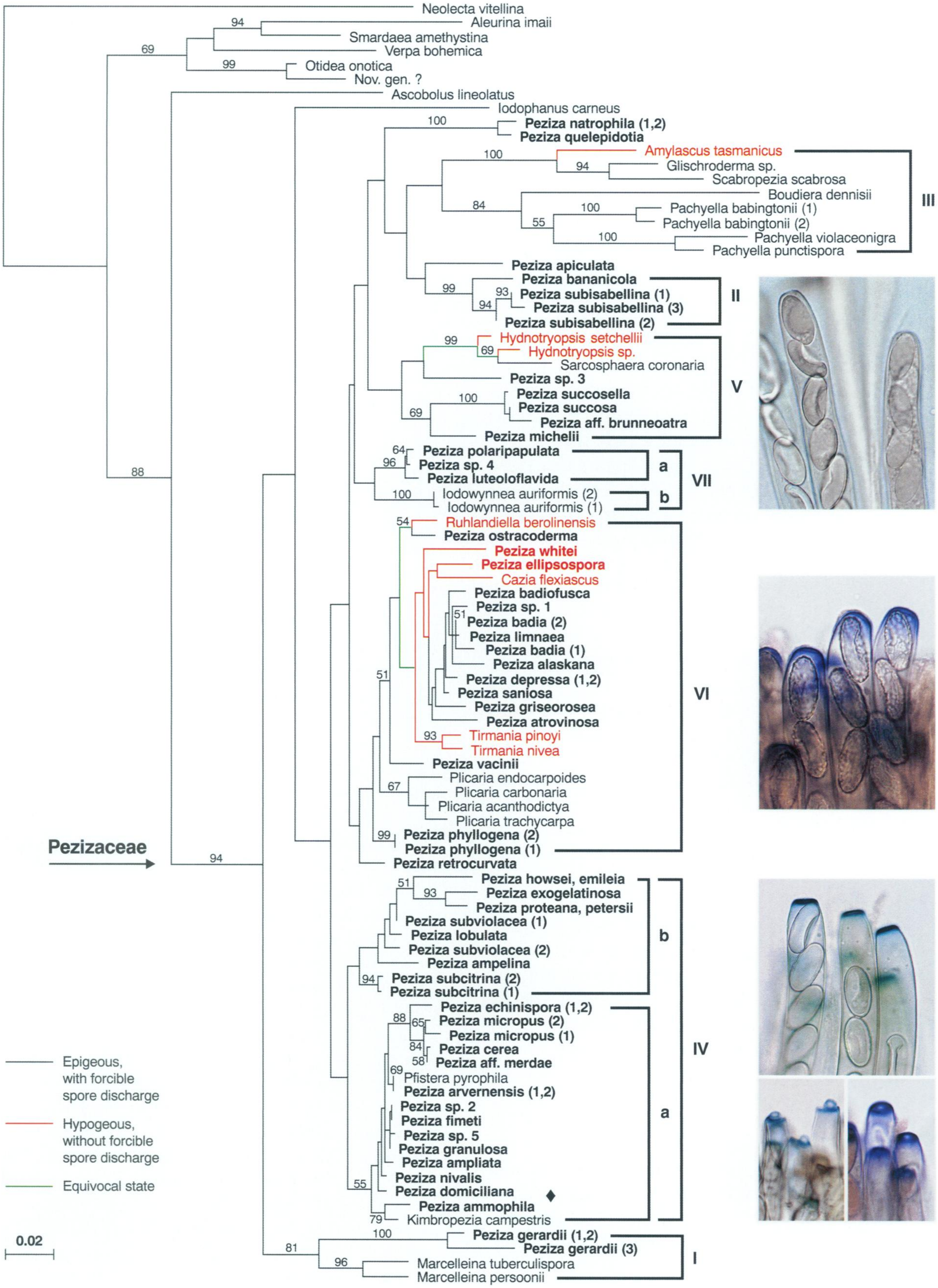
Neolecta vitellina
94
Aleurina imaii
Smardaea amethystina
69
Verpa bohemica
99
Otidea onotica
Nov. gen. ?
Ascobolus lineolatus
Iodophanus carneus
100
Peziza natrophila (1,2)
Peziza quelepidotia
100
Amylascus tasmanicus
94
Glischroderma sp.
Scabropezia scabrosa
Boudiera dennisii
84
100
Pachyella babingtonii (1)
55
Pachyella babingtonii (2)
100
Pachyella violaceonigra
Pachyella punctispora
III
Peziza apiculata
Peziza bananicola
99
93
Peziza subisabellina (1)
94
Peziza subisabellina (3)
Peziza subisabellina (2)
II
99
Hydnotryopsis setchellii
69
Hydnotryopsis sp.
Sarcosphaera coronaria
Peziza sp. 3
100
Peziza succosella
Peziza succosa
69
Peziza aff. brunneoatra
Peziza michelii
V
64
Peziza polaripapulata
96
Peziza sp. 4
Peziza luteoloflavida
a
VII
88
100
Iodowynnea auriformis (2)
Iodowynnea auriformis (1)
b
54
Ruhlandiella berolinensis
Peziza ostracoderma
Peziza whitei
Peziza ellipsospora
Cazia flexiascus
Peziza badiofusca
Peziza sp. 1
51
Peziza badia (2)
Peziza limnaea
Peziza badia (1)
Peziza alaskana
51
Peziza depressa (1,2)
Peziza saniosa
Peziza griseorosea
Peziza atrovinosa
VI
93
Tirmania pinoyi
Tirmania nivea
Peziza vacinii
67
Plicaria endocarpoides
Plicaria carbonaria
Plicaria acanthodictya
Plicaria trachycarpa
99
Peziza phyllogena (2)
Peziza phyllogena (1)
Pezizaceae
94
Peziza retrocurvata
51
Peziza howsei, emileia
93
Peziza exogelatinosa
Peziza proteana, petersii
Peziza subviolacea (1)
Peziza lobulata
Peziza subviolacea (2)
Peziza ampelina
b
94
Peziza subcitrina (2)
Peziza subcitrina (1)
88
Peziza echinispora (1,2)
65
Peziza micropus (2)
Peziza micropus (1)
84
Peziza cerea
58
Peziza aff. merdae
69
Pfistera pyrophila
Peziza arvernensis (1,2)
Peziza sp. 2
Peziza fimeti
Peziza sp. 5
Peziza granulosa
Peziza ampliata
IV
a
Peziza nivalis
55
Peziza domiciliana ◆
79
Peziza ammophila
Kimbropezia campestris
Epigeous, with forcible spore discharge
Hypogeous, without forcible spore discharge
Equivocal state
0.02
81
100
Peziza gerardii (1,2)
Peziza gerardii (3)
96
Marcelleina tuberculispora
Marcelleina persoonii
I

TABLE III. Evaluation of different constrained tree topologies in MP and ML analyses, compared to the MPTs and the optimal MLT, respectively, using the Kishino-Hasegawa test ($p < 0.05$)

	MP		ML			
Tree	Tree length[a]	Significantly worse?	Ln likelihood	Difference in LnL	Standard deviation	Significantly worse?
Unconstrained optimal MLT			−11308.898			
Unconstrained MPT	1832					
Hypogeous taxa within group VI monophyletic	1839 (+7)	no	−11348.976	−40.078	27.051	no
Hypogeous taxa within group V monophyletic	1835 (+3)	no	−11326.140	−17.243	25.651	no
Hypogeous taxa within group VI and V both monophyletic	1842 (+10)	no	−11352.500	−43.602	16.248	yes

[a] Difference in length between MPTs and constrained trees in parentheses.

riched, often calcareous soil), species of *Marcelleina* (FIG. 3) are very similar to *P. gerardii* (FIG. 2). *Peziza gerardii* shares anatomical characters with *Marcelleina,* although the fusiform spores are very different. Within the Pezizaceae, *P. gerardii* has a unique spore shape and ornamentation (observed by SEM): large, slightly inequilateral, narrowly fusiform spores, with an ornamentation of low, longitudinal, cyanophobic ribs (Berthet 1970), and 1 to 3 large and several small guttules. Spores in *Marcelleina* are globose, smooth or ornamented, with one large guttule. The purplish (-brownish) pigments in *P. gerardii* are located in the paraphyses, subhymenium and excipulum. *Peziza gerardii* and species of *Marcelleina* have an excipulum composed entirely of globose to angular cells, which, toward the outer surface, become smaller (outer excipulum hardly discernible), and from which scattered short rows of cells project (appressed, hyphoid, septate hairs). The weakly amyloid, general staining of the asci (type iiia) in *P. gerardii* is also a distinct and rare feature within the genus *Peziza.*

Group II. This strongly supported (bootstrap 99%) group includes two unusual species of *Peziza, P. subisabellina* (FIG. 4) and *P. bananicola.* Both species have asci that are diffusely amyloid (type iiia) (FIG. 24). Presumably based on this feature, *P. subisabellina* has recently been combined in *Pachyella* (FIG. 5) (Trimbach 1999), a placement in contradiction with our molecular results (FIGS. 22, 24) as well as the morphological characters. Diffusely amyloid asci are typical for the genus *Pachyella,* but *P. subisabellina* does not possess other pachyelloid characters (see Background Information). Spore shape and guttulation in *Pachyella* is uniform, broadly ellipsoid containing two large guttules, and differs from *P. subisabellina* which has almost fusiform spores with many small guttules. Our analyses support *Pachyella* in group III.

Peziza sect. *Purpureodiscus* G. Hirsch (Hirsch 1992) was proposed for *P. subisabellina* and *P. kreiselii* G. Hirsch, based on the diffusely amyloid asci, reddish pigments in the apothecia (FIG. 4), smooth spores without guttules and clavate paraphyses. A segregation of *P. subisabellina* from the "core group of *Peziza* species" is also supported by our analyses. Sequences from three different collections of *P. subisabellina* are included in this study, one occurring on wood (Winterhoff 8844) and two on soil (RK96.54, ALTA9029). Several differences in the LSU have accumulated between these individuals, with the two specimens on soil grouping together, although all three form a well-supported monophyletic group (bootstrap 99%) (FIG. 22).

Peziza bananicola is one of the few strictly tropical *Peziza* species. It has two unique features: an extensive subiculum that covers and binds debris from ba-

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←

FIG. 24. The tree with the highest likelihood (lnL−11308), obtained from maximum-likelihood analyses. Branch lengths correspond to genetic distance (expected nucleotide substitutions per site). Numbers by branches are "fast" bootstrap frequencies (values greater than 50%). Branch colors represent character state optimizations (using MacClade). Taxa in red are hypogeous, without forcible spore discharge. Species of *Peziza* are in boldface. Diamond indicates suggested position of *P. vesiculosa* from subsequent analysis (see note added after acceptance of the manuscript). Bracketed groups I–VII correspond to groups I–VII in FIG. 22. Types of ascus amyloid reactions supporting group II, IV and VI are shown. Microscopic photos: diffusely amyloid (type iii, *P. subisabellina,* RK96.54, at the top) ca ×400; intensely and unrestrictedly amyloid over the apex (type i, *P. badia,* KH-97-84, in the middle) ca ×600; intensely amyloid in a distinct ring zone at the apex (type ii, *P. cerea,* KH-97-01, at the bottom) ca ×550. Photos: K. Hansen.

nana plants, and a peculiar spore ornamentation of sparse, irregularly spaced, very thin, acutely pointed spines (Pfister 1991). The spores are narrowly ellipsoid and eguttulate. *Peziza subisabellina* and *P. bananicola* share certain excipular features, being very thick and dense. However, the medullary excipulum is stratified in three layers in *P. bananicola,* but is composed of a single uniform layer in *P. subisabellina.* Other less known tropical species, e.g., *P. luteorosella* (Le Gal) Pfister and *Galactinia tapesioides* Le Gal (Le Gal 1960), are morphologically similar to *P. bananicola* (Pfister 1991) and may belong to group II. *Peziza luteorosella* has spore ornamentation much like *P. bananicola,* but has an unstratified excipulum like *P. subisabellina.* Hymenial colors in the three tropical species and *P. subisabellina* range from whitish, yellowish, rose, reddish to purplish brown.

Group III. Four genera and one form-genus are represented in this clade (bootstrap MPT 56%, supported by all MPT, FIG. 23). *Boudiera dennisii* (FIG. 6) forms a monophyletic group with three species of *Pachyella, P. violaceonigra, P. punctispora* (FIG. 5) and *P. babingtonii* (bootstrap MPT 91%, MLT 84%). This is in contradiction with the ML analysis by Norman and Egger (1999) based on nSSU rDNA sequences. In their analysis *Boudiera* (*B. acanthospora* Dissing & Schumacher) clusters with *Iodophanus* (FIG. 1), basally in the Pezizaceae (<50% bootstrap), which supports the placement of these genera in a tribe, Iodophaneae (Korf 1972, 1973b). However, *Pachyella* is not represented in the study by Norman and Egger (1999), since the included *Pachyella* is *Peziza subisabellina* (see Materials and Methods). A close relationship between *Boudiera* and *Plicaria,* as has been suggested (see Background Information), is also not supported by our analyses. Species of *Boudiera* lack gelatinous excipular tissues and hyphoid hairs embedded in a gel, typical in the genus *Pachyella.* Nevertheless, the lineage is united by asci evenly amyloid over the entire length (type iiia) and the overall anatomical structure of a medullary excipulum of textura intricata, an outer excipulum of textura angularis to globulosa and an indistinct subhymenium (TABLE I). Species of *Boudiera* and *Pachyella* occur on water-soaked, regularly inundated substrates, although *Pachyella* species most commonly occur on wood, and *Boudiera* species on sand. The relationship between the two genera is unresolved in the strict consensus tree, but monophyly of *Pachyella* is weakly supported in the MLT (55% bootstrap). The two subclades of *Pachyella* species are both highly supported (100% bootstrap). Some of the longest branches in the MPT (FIG. 22) occur in group III. The branch leading to *Boudiera* is 63 steps. The branches uniting the lineages of *P. violaceonigra* and *P. punctispora,* and the lineages of *P. babingtonii* are each 42 and 26 steps. The branch uniting the lineages of *Boudiera* and *Pachyella* is 39 steps. Long internode lengths could most probably be obviated in this clade by including more species of *Boudiera* and *Pachyella.*

Scabropezia and the mitosporic *Glischroderma* Fuckel form a highly supported clade with the truffle *Amylascus tasmanicus* (bootstrap 100%). Another truffle, *Pachyphloeus melanoxanthus* (type of *Pachyphloeus*), is suggested as closely related to *Scabropezia,* based on nSSU rDNA sequences (Norman and Egger 1999) and morphology (Dissing and Pfister 1981). Both truffles produce ascomata with a tough-fleshy medullary excipulum and asci randomly distributed throughout the tissue (= stereothecia) (FIG. 8). The asci are weakly amyloid over the entire length (type iiia), but some other species of *Pachyphloeus* are described with non-amyloid asci (Dissing and Korf 1980, Dissing 2000). Dissing and Pfister (1981) noted the similarities in the structure of the outer excipular layers in *Pachyphloeus* and *Scabropezia,* which is highly pustulate or verrucose (FIG. 7), of thick-walled, large, globose cells, a feature also shared with *Amylascus* (Trappe 1971, 1975b, Beaton and Weste 1982). *Scabropezia scabrosa, A. tasmanicus* and *P. melanoxanthus* have globose spores, with an ornamentation of prominent conical or truncate warts, which in *P. melanoxanthus* and *A. tasmanicus* are embedded in mucilage. The spores in *Scabropezia* and *P. melanoxanthus* are brownish at maturity. *Scabropezia* often occurs on calcareous soil, or rarely on decaying wood, and attempts to germinate spores of *Scabropezia* failed (Dissing and Pfister 1981). Based on these observations, and the fact that most hypogeous fungi are thought to be ectomycorrhizal (Trappe and Maser 1977), we believe this lineage could be mycorrhizal.

Group IV. This group is weakly supported by bootstrap analyses (<50%), but is present in all MPTs (FIG. 23) and in the MLT (FIG. 24). The presence of a distinct amyloid ring zone at the apex of the asci (type ii, FIG. 24) is a synapomorphy for group IV. Such a reaction is present in all species, except in *Kimbropezia,* in which asci are strongly amyloid apically (Korf and Zhuang 1991), and in *P. emileia, P. howsei* and *P. ampelina,* which show a less restricted amyloid reaction, although *P. howsei* (KH-97–98) showed a distinctly amyloid ring zone in fresh material. Asci with a strongly amyloid ring were noted previously by Svrček (1970) in several of the species in clade IVa. Group IV is also united by the type of anamorph produced. All species with known anamorphs produce an *Oedocephalum* state. An exception is *Peziza* aff. *merdae* which produces a *Chromelosporium* state (Norman and Egger 1999). *Oedocephalum* anamorphs are reported for species in both clade

IVa (for *P. ammophila, P. ampliata, P. cerea, P. echinispora, P. micropus, P. repanda, P. sylvestris, P. varia* and *P. vesiculosa*) and in IVb [for *P. subviolacea* (as *P. praetervisa*), *P. petersii* and *P. lobulata* (as *Galactinia violacea* (Pers.) Le Gal)] (e.g., Berthet 1964a, b, Paden 1972, 1973, Webster et al 1964). Additionally, spores with a unilateral gelatinous coating have only been found in group IV. The gelatinous spore coating was observed in *P. ampliata, P. granulosa, P. subcitrina* and *P. vesiculosa*. This character has rarely been reported, probably because it is difficult to observe in dried material.

Group IV includes one strongly supported clade, IVa, with bootstrap MPT 91%, MLT 55% (equivalent to Boudier's genus *Aleuria* pro parte 1907). This clade contains common *Peziza* taxa, characterized by mostly large, yellowish brown disc- to cup-shaped apothecia (FIG. 9), finely warted or smooth, eguttulate spores (*P. domiciliana* has two small guttules in the spores), and simple, hyaline or pale yellowish paraphyses. They occur on rich soil mixed with litter or woody debris or mortar, on strongly decayed trunks, manured substrate or dung. A subset of these taxa was also highly supported as monophyletic in ML analysis by Norman and Egger (1999). Since the type species of *Peziza, P. vesiculosa*, is included, this clade will have to serve as a core group for a future circumscription of the genus.

Morphological, ecological, and molecular divergence (nLSU rDNA) based on the branch lengths (FIGS. 22, 24) and nucleotide diversity are low within group IVa, which may suggest a recent radiation. Additionally, species limits are controversial and the number of species recognized varies. The group is taxonomically problematic due to lack of diagnostic morphological characters. *Peziza* species with ellipsoid, smooth, small (ca 15 μm) and eguttulate spores were referred to as the "*Peziza repanda-varia-micropus-cerea* complex" by Rifai (1968). He stated that this complex needs a prolonged field and laboratory study to establish species limits. The most detailed study of this complex is by Svrček (1970), who also included species with finely warted spores. A detailed study of group IVa using morphology and more rapidly evolving sequences is in progress.

Peziza ammophila differs in its habitat and development. It fruits partly buried in sand (FIG. 10), among *Ammophila* (Poaceae). The (pseudo-)stipitate ascomata are deeply cup-shaped and the margins split into irregular rays, becoming flattened on the sand surface. Based on this characteristic development, *P. ammophila* has been placed in *Sarcosphaera* (FIG. 13) (e.g., Kotlaba and Pouzar 1963, Seaver 1928). Pouzar (1972) considered *P. ammophila* and another species, *P. austrogaster* (Rodway) Rifai, to be a "unique" entity within *Peziza*. He proposed a new subgenus of *Peziza, Asterosphaera* Pouz., with *P. ammophila* as the type species. Most authors have considered the similarities in macromorphological development between *Sarcosphaera* and *P. ammophila* to be a result of convergent or parallel evolution. These hypotheses is congruent with the molecular results. Furthermore, *P. ammophila* shares all other morphological characters of clade IVa. *Peziza echinispora* differs from other members of this clade in its spore ornamentation of isolated, regular spines and its occurrence on burnt ground. Other characters such as eguttulate spores, an *Oedocephalum* anamorph, and the distinctly amyloid ascus ring zone, justify its placement in this group. Apart from the guttulate spores, *P. domiciliana* is also aberrant in this clade by having a pinkish (violet) tinge in the hymenium otherwise characteristic of clade IVb.

The monotypic genera *Kimbropezia* and *Pfistera*, described on the basis of peculiar ascus apices (Korf and Zhuang 1991) are nested within clade IVa. *Kimbropezia campestris* was assigned to the Pezizaceae, while *Pfistera* was excluded due to the supposedly non-amyloid asci. Asci in *Pfistera pyrophila* were described as having a very thin, arched apical dome at maturity, which may split vertically, horizontally or irregularly. Van Brummelen (1998) studied the ascus apical structures in these species, and in species he supposed might be related [*P. michelii, P. emileia* and *Geopyxis majalis* (Fr.) Sacc.] using TEM. Our results support van Brummelen's conclusion, that *Pfistera campestris* belongs in *Peziza*. It was found to display two different types of ascus dehiscence, the second type perhaps developing from the first type, resulting from less than optimum conditions during development. The apical structure of the "typical" ascus was of the *Peziza* type. In addition, *Pfistera pyrophila* shows several characters that are typical for clade IVa and microscopic examination (by DHP and KH) revealed a few small patches of faintly amyloid material in the hymenium, around some ascal tips (pretreated with 2% KOH). Van Brummelen observed "remains of a moderately reactive periascus, too thin to be observed by light microscopy." Contrary to the phylogenetic analysis by Norman and Egger (1999) and to our results, van Brummelen considered *Kimbropezia* to be distinct from *Peziza*. He found that asci of *Kimbropezia*, in addition to having the unique "opercular lens," was more strongly amyloid than those of *Peziza*, and the annular indentation or weakened zone characteristic of *Peziza* was completely absent. Dehiscence was found to be by a circumscissile, rather irregularly delimited rupture in the thin part of the ascus wall, around the opercular lens. We suggest that this apical structure and the mechanism of dehiscence are derived within clade IVa from a typical *Peziza*-type and that the "opercular lens" is an autapomorphy. The excipulum structure in *Kimbropezia* is, as also pointed out by Korf and Zhuang (1991), typical for species in clade IVa; the spores are ellipsoid, smooth and eguttulate (TABLE I). Therefore, *Kimbropezia* should be included in *Peziza*. The operculate dehiscence has been lost completely several times within *Peziza* (e.g., see Group VI) and the Pezizales (e.g., Trappe 1979, O'Donnell et al 1997, Percudani et al 1999). It should be noted that in ML analysis by Norman and Egger (1999) the truffle *Terfezia terfezioides* (Matt.) Trappe is supported within, or as a sister lineage to, group IV based on nSSU rDNA.

An assemblage of nine *Peziza* species, clade IVb, is a sister group to clade IVa. Clade IVb, like IVa has mostly smooth or warted spores, but mostly have two, small guttules. Common to this group are apothecia with violaceous to vinaceous pigments in the hymenium (FIG. 11), either dark and intense or at least with a pink, bluish or lilaceus tinge. *Peziza subcitrina* deviates in its golden yellow ascomata (FIG. 12) and eguttulate spores. *Peziza lobulata* has eguttulate spores, while *P. proteana* and *P. petersii* have spores with low, short branched ridges and warts. Four of the species are pyrophilous, *P. petersii, P. proteana, P. subviolacea* and *P. lobulata*. *Peziza exogelatinosa* occurs on naked calcareous soil, with a high pH and a low content of organic matter similar to the conditions on burnt ground. *Peziza ampelina, P. subcitrina, P. emileia* and *P. howsei* are found on naked, clayey soil in rich deciduous forests.

The two clades in group IV recall to some degree Boudiers (1907) classification, based mainly on presence or absence of guttules. *Peziza* species in clade IVa were placed in the genus *Aleuria* (*P. domiciliana* and *P. ammophila* were not treated by Boudier), whereas species in clade IVb were treated in both *Aleuria* and *Galactinia*. Although these phylogenetic results suggest that guttulation is a homoplasious character that has been lost and gained several times, a second interpretation is possible. The oil guttules in clade IV are smaller and less prominent than those in, e.g., *Peziza* species in group VI, and these two types may not be homologous. Guttules may, however, always be present to a greater or lesser degree, but the character may not be expressed in some species. If such is the case, lack of guttules is not phylogenetically informative. The "outlines" of two guttules have been observed (by KH in fresh material) in the spores of several specimens of group IVa. These "outlines" appear as aggregations of many smaller oil drops, after pretreatment in 10% KOH, staining with Sudan black in alcohol (a lipid stain) and clearing with 50% alcohol.

Group V. In these analyses, *Sarcosphaera* and two species of the hypogeous *Hydnotryopsis, H. setchellii* and *H.* sp. form a highly supported clade within group V (bootstrap 100%) (FIGS. 22–24). The ascomata of *Hydnotryopsis* have hymenia located in labyrinthiform chambers or meandering veins, but these are folded and compressed, making them solid (= stereothecia) (FIG. 14) (Trappe 1979). Hypogeous fruiting of *Sarcosphaera* may occur (Trappe 1975a, 1979). In such cases the apothecia occasionally become folded and form chambers, thus resembling ptychothecia, but the asci retain functional opercula. *Sarcosphaera coronaria* fruits in spring to early summer and its development is likely associated with selection for reduction in water loss, as it is thought to be in truffles (e.g., Thiers 1984). The excipulum is thick and tough, probably also correlated with microclimatic aridity and initial development underground. It is composed of a distinct outer layer (ca 750 μm) of textura epidermoidea to textura prismatica on the outermost region, a medullary layer (ca 450 μm) of large globose cells and a subhymenium of smaller globose cells. A close relationship between *Sarcosphaera* and *Hydnotryopsis* has not previously been suggested. Trappe (1979) suggested that, "in its evolution to a solid gleba, *Hydnotryopsis* is related to *Peziza* a step farther away than *Mycoclelandia*." *Sarcosphaera* differs anatomically from *Peziza* in the outer excipular layer. *Hydnotryopsis* and *Sarcosphaera* both have asci evenly amyloid over the entire length (type iii), and ellipsoid, amorphous ornamented spores (in SEM spores of *Sarcosphaera* have an ornamentation of low, rounded warts, covered by a thin amorphous layer). *Sarcosphaera* is only found associated with mycorrhiza-forming trees, and is often locally abundant where it occurs, year after year in the same spot, suggesting that it is ectomycorrhizal. Basal to these taxa is an as yet unidentified species of *Peziza* sp. 3, collected on experimental plots treated with urea (supported by all MPT's and the MLT, but bootstrap <50%). It shares features with species of *Peziza* in group IV (a whitish, cup-shaped apothecium, smooth, biguttulate spores, and hyaline or pale yellowish paraphyses, slightly enlarged and curved towards the apices), but has asci strongly amyloid over the apex.

The *Hydnotryopsis/Sarcosphaera* clade appears as a sister group to common epigeous species of *Peziza* sharing features with those in group VI. However, *Peziza succosa, P. succosella* and *P. michelii* possess lactiferous hyphae in the excipulum, which yield a yellow juice when cut or bruised. *Peziza* species with apothecia that yield a colored juice are also present in group VI (for example *P. saniosa* (FIG. 15) and *P. badiofusca*), but in these hyphae yield a bluish or watery juice. This character however, needs further study, since lactiferous hyphae are likely to be present in many species of *Peziza*. Thus, Le Gal (1937, 1953a) described and illustrated lactiferous hyphae also in species without or seemingly without staining flesh or juice. *Peziza succosa, P. succosella* and *P. michelii* have spores with irregular, elongated warts and two large guttules, asci strongly amyloid over the apex (type i), and brownish colors in the hymenium (yellowish brown, olivaceous yellow to greyish brown, or first violet, then brownish). They occur on rich disturbed soil in deciduous forests, always in association with ectomycorrhizal fungi. *Peziza* aff. *brunneoatra* deviates by having dark brown apothecia, lacking a yellow juice and in having finely warted spores packed with numerous small guttules (sensu Dennis (1978) in Norman and Egger (1999)).

Group VI. Although group VI has low bootstrap support (< 50%), it is present in all equally parsimonious trees (FIG. 23) and in the MLT (FIG. 24). It includes one weakly supported clade (bootstrap MPT 53%, MLT 51%) of 11 epigeous species of *Peziza* (equivalent to Boudier's genus *Galactinia* pro parte 1907) and several truffles and truffle-like taxa. The epigeous *Peziza* species are united morphologically by mostly dark brownish, disc- to cupshaped apothecia, often with an olivaceous or purple tinge; highly warted, ridged to reticulate spores, with two, rarely one, large guttules; dark pigmented paraphyses; and asci intensely and unrestrictedly amyloid over the apex (type i). The hypogeous taxa have asci that are evenly amyloid over the entire length, either weakly or strongly (type iii), or are non-amyloid (type iv).

The relationship of several of the epigeous ellipsoid-spored species has been studied, and discussed in relation to the globose-spored *Plicaria* (Pfister 1979b, Egger 1987, Moravec and Spooner 1988, Norman and Egger 1996, 1999) (see Background Information for previous hypotheses). Our analyses confirm a close relationship of *Plicaria* (FIG. 16) to the more inclusive *Peziza* clade within group VI (FIG. 15). *Plicaria* is supported as monophyletic in the MLT (bootstrap 67%) (FIG. 24), but the placement of the smooth-spored *P. endocarpoides* (the only smooth-spored species in group VI) is unresolved in the MPTs (FIGS. 22, 23). The three *Plicaria* species with ornamented spores are supported as monophyletic with a 65% bootstrap value. Globose, ellipsoid to fusiform-spored taxa group together in several lineages within the Pezizaceae (in group I, III, VI) (TABLE I), indicating that spore shape is not phylogenetically informative at these higher taxonomic levels. As shown by Norman and Egger (1996, 1999) to maintain *Plicaria* as a monophyletic group will leave *Peziza* (or the *Peziza* species in group VI) as a paraphyletic group. Some important characters of *Plicaria* are shared with some of the *Peziza* species, e.g., pale brownish spores at maturity and paraphyses encrusted with amorphous matter. Such characters seem to be synapomorphic to the *Peziza* species in group VI. Pale brownish spores are found in *P. atrovinosa, P. vacinii* and *P. alaskana.* Paraphyses encrusted with amorphous matter are present in *P. alaskana, P. badiofusca, Peziza* sp. 1, *P. vacinii, P. depressa* and *P. phyllogena.* Other *Peziza* species reported with pale brownish spores, e.g., *P. retiderma* and *P. rifaii* (Moravec and Spooner 1988), and paraphyses encrusted with amorphous matter, e.g., *P. badiofuscoides* Donadini (Donadini 1979b), are likely members of group VI, but have not been sequenced by us. In contrast to the rest of the epigeous taxa in group VI, the asci in *Plicaria* are weakly amyloid over their entire length (type iiia).

The 11 epigeous *Peziza* species in the more inclusive clade of group VI constitute a homogeneous group, both in macro- and microscopical features, and levels of divergence in the nLSU rDNA sequences are low based on the branch lengths (FIGS. 22, 24). The clade of *P. badiofusca, Peziza* sp. 1, *P. badia, P. limnaea* and *P. alaskana* (FIGS. 22–24) represents a complex of species centering around *P. badia* (see Le Gal 1937, Donadini 1979b, Pfister 1979b), that possesses spores with ornamentations of warts elongated into short ridges, which may anastomose to form an incomplete to almost complete, irregular reticulum. Less known unsampled species that may belong to this clade are *P. phlebospora* (Le Gal) Donadini, *P. badiofuscoides* and *P. badioides* Donadini. A closer study of these species, mainly distinguished by small differences in spore size and ornamentation and in habitat, is needed. *Peziza depressa* differs from members of this group by having spores ornamented with distinct, regular, high warts, and a warm reddish brown hymenium. *Peziza saniosa, P. badiofuscoides* and *P. badiofusca* are distinct by possessing apothecia that yield a bluish, blue opalescent or watery juice when cut or bruised (FIG. 15).

Peziza phyllogena (syn. *P. kallioi* Harmaja, *P. badioconfusa* Korf ss. auct.) is included in group VI, but outside the core group of *Peziza* species (next to *Plicaria*) in the MLT (FIG. 24); its relationship to the rest of the clade is not resolved in the strict consensus tree (FIG. 23). It shares many features with the group VI *Peziza* species, and it has been confused with *P. badia* (Korf 1954, Elliott and Kaufert 1974). It is recognized by the bluish violet, pubescent to villose base of the apothecium (seen easily on fresh material); spores ornamented with delicate, irregular warts, which become fused towards the poles, often forming apical caps; and its fruiting habit, on decaying wood or woody debris in wet habitats (Wells and Kempton 1967, Elliott and Kaufert 1974, Ginns 1980, Harmaja 1986). Its spores do not possess two large guttules as is typical for the group VI *Peziza* species, but rather have many small guttules that aggregate towards the poles.

The truffles and truffle-like taxa nested within group VI show diverse ascomatal forms. Two hypogeous species of *Peziza, P. whitei* (FIG. 18) and *P. ellipsospora* (FIG. 17), produce ptychothecia (TABLE I) (Gilkey 1916, Trappe 1975a, 1979, Beaton and Weste 1982). Both species have hyaline, broadly ellipsoid spores, which are minutely papillose in *P. ellipsospora* and reticulate in *P. whitei.* Gilkey (1916) described *P. ellipsospora* in *Hydnotrya* Berk. & Broome, based on the macro-morphology, but erected a new genus, *Hydnoplicata* Gilkey for *P. whitei* (Gilkey 1954a). *Peziza whitei* has been placed in *Hydnocystis* Tul. and *Hydnotrya* (see Trappe 1975a). Burdsall and Korf (Burdsall 1968) and Trappe (1975a, 1979) transferred the two species to *Peziza,* based on the amyloid reaction of the asci, spore ornamentation, ascocarp structure, and supposedly operculate asci. Later Trappe (pers comm) found that these species lack an operculum and the spores are not forcibly discharged. Our molecular results support the placement of the two species among the core group of epigeous *Peziza* species in group VI (FIGS. 22–24). *Peziza ellipsospora* is a sister species to *Cazia.* Other phylogenetic analyses (Norman and Egger 1999, Percudani et al 1999) have further shown *Cazia* to be closely related to the truffle *Terfezia arenaria* (Moris) Trappe. *Cazia* and *Terfezia* produce stereothecia and both have non-amyloid asci (type iv) (TABLE I). As in the branches leading to *Marcelleina* (in group I) and *Terfezia terfezioides* (possibly in group IV based on Norman and Egger 1999), the amyloid reaction might be lost along a branch leading to *Cazia flexiascus* and *Terfezia arenaria.* This suggests that the amyloid reaction has been lost at least three times within the Pezizaceae. *Cazia flexiascus* has ellipsoid, hyaline, incompletely warty-reticulate spores, with one guttule (Trappe 1989), much like the spores of *P. whitei* and *P. ellipsospora.* Two species of *Tirmania, T. nivea* and *T. pinoyi,* also producing stereothecia (Trappe 1971, Moreno et al 2000), are nested within group VI. They group strongly together (bootstrap MPT 99%, MLT 93%) as a sister group to most of the epigeous and the hypogeous *Peziza* species and *Cazia* (FIGS. 23–24). The similarity in excipulum structure between *Cazia, Terfezia* and *Tirmania* adds support to the close relationship between these taxa (TABLE I).

Ruhlandiella berolinensis produces exothecia (FIG. 19) (Dissing and Korf 1980, Warcup and Talbot 1989 as *Muciturbo,* Galán and Moreno 1998). The excipulum is composed entirely of globose to angular cells. Asci are evanescent at maturity. The paraphyses in both *R. berolinensis* and *P. whitei* exceed the asci and are embedded in a gelatinous sheath. Spores in *R. berolinensis* are probably dispersed when the hymenium and upper part of the ascoma break down to form a mucilaginous mass. *Ruhlandiella berolinensis* groups with *P. ostracoderma* in all trees (FIGS. 22–24), but with low bootstrap support.

Few anamorphs have been reported for the group VI taxa, but where reported they are referable to *Chromelosporium* (*Peziza ostracoderma, Plicaria endocarpoides, P. trachycarpa*), *Chromelosporium*-like states (*Ruhlandiella*), or are unnamed states, producing hyaline to colored, 0–3 septate resting spores [*P. saniosa, P. phyllogena* as *Galactinia badioconfusa* (Korf) Svrček](Berthet 1964a, b, Paden 1972, Hennebert 1973, Hennebert and Korf 1975, Warcup and Talbot 1989). Most of the epigeous *Peziza* species occur on bare, often disturbed soil, under ectomycorrhiza-forming trees. *Plicaria* species and *Peziza vacinii* are pyrophilous, while *P. ostracoderma* also occurs on other types of sterilized soil and *P. griseorosea* on very degraded wood or soil mixed with wood.

Group VII. Two highly supported clades, VIIa and VIIb (bootstrap 96% to 100%) are united in group VII, but with only weak support in the MLT and the MPT (bootstrap <50%)(FIG. 22, 24). Clade VIIa includes three species of *Peziza, P. polaripapulata, P.* sp. 4 and *P. luteoloflavida.* The apothecial colors of these species are in the range of pale yellow, ochre-yellow, warm yellow, brownish yellow to golden brown, dark brown with an olivaceous tinge, or olive yellow to olive (FIG. 20) (Kristiansen and Schumacher 1993, Hansen et al 1998). They are united by asci being evenly amyloid over the entire length (type iii). The spores contain two small guttules or are eguttulate. *Peziza* sp. 4 has smooth spores (in SEM), whereas *P. luteoloflavida* has spores with a fine, irregular, undulating reticulum, and *P. polaripapulata* has spores with isolated, rounded to elongated warts, becoming more or less fused at the poles to a cap-like thickening. Based on the spore ornamentation *P. polaripapulata* has been placed with the "pseudoapiculate *Peziza* species" in subgenus *Phaeopezia* (Sacc.) J. Moravec (Häffner 1995), along with *P. phyllogena* and the apiculate-spored *P. apiculata.* A close relationship of these taxa is not supported in our analyses, which places *P. phyllogena* in group VI and *P. apiculata* either as a sister lineage to group II or III. However, to test the monophyly of taxa with pseudoapiculate and apiculate spores, more sampling is necessary. *Peziza* *polaripapulata* (FIG. 20) occurs on very degraded hardwood, sawdust or soil in calcareous forests and *P. luteoloflavida* on sand on river banks. *Peziza* sp. 4 was collected among mossess, on a forest road surfaced with cinders.

Clade VIIb consists of two collections of the strictly subtropical or tropical genus, *Iodowynnea*. Our results support the segregation of *Iodowynnea* from the main groups of *Peziza*, but a close relationship to the *Peziza* species in clade VIIa is possible. The asci in *Iodowynnea auriformis* are evenly and strongly amyloid over the entire length (type iiib), and the apothecial colors have red tones. It fruits on soil or vegetable debris in forests with ectomyccorhizal trees (Medel et al 1996).

Taxa not supported in group I–VII. Peziza natrophila and *P. quelepidotia* form a highly supported lineage (bootstrap 100%, FIGS. 22–24), the placement of which is unresolved. But, in our analyses this group never falls within the main groups of *Peziza*. This observation is supported by the ascus amyloid reaction in *P. natrophila*, which is weak over the entire length (type iiia). *Peziza quelepidotia* was placed in its own genus *Lepidotia*, recognized by ellipsoid, eguttulate spores and distinctly stipitate or obconical apothecia with triangular, submembranaceous scales (Boudier 1885). On morphological grounds Korf and O'Donnell (Korf 1973c) did not consider *Lepidotia* generically different from *Peziza* s.l. In contrast Norman and Egger (1999), on molecular phylogenetic grounds, stated that *P. quelepidotia* is not a member of *Peziza*, and should be maintained in *Lepidotia*. Although, in their analysis *P. quelepidotia* forms a clade with *P. subisabellina* (in Norman and Egger misnamed as *Pachyella clypeata*). In our MLT (FIG. 24) the lineage of *P. natrophila* and *P. quelepidotia* is the sister group to the clade of group II (including *P. subisabellina*) and group III. *Peziza natrophila* is mostly known from experimental plots treated with sodium- and potassium carbonate (Petersen 1970, Khan 1976), but one of our specimens, *P. natrophila* (2) (JHP 93.021), occurred on soil in an old peat bog. This is similar to the substrate reported for *P. quelepidotia*, Sphagnum-pots and peat-moss agar ("Jiffy-7 Pellet infusion agar") (Korf 1973c, O'Donnell and Beneke 1973). The apothecia of *P. natrophila* are olivaceous brown, subsessile or stalked (2–10 mm high), with an outer surface covered by short branching hyphae, much as described for *P. quelepidotia* by Korf (1973c). *Peziza natrophila* has distinctly ornamented spores, while *P. quelepidotia* is illustrated with less dense markings. Until further comparative studies have been carried out we cannot exclude the possibility that these species are con-specific.

Taxonomic conclusions.—The 14 genera sampled by us, and currently accepted in the Pezizaceae (Eriksson 2000), are confirmed to be members of the family. The analyses, however, suggest that the Pezizaceae should be emended to include the non-amyloid genus *Marcelleina*. The Ascobolaceae is confirmed to be the sister group to the Pezizaceae, which supports the general view that the amyloid reaction of the ascus is phylogenetically informative in the Pezizales. *Peziza* and most other genera of the Pezizaceae, as they are currently delimited, cannot be maintained in a monophyletic classification system. *Peziza* is composed of at least 6 major lineages, most of which include other genera of the Pezizaceae, and 4 species of *Peziza* occur in separate lineages of yet uncertain placement. *Peziza* should be disassembled into groups that more closely reflect the phylogeny, and several genera now recognized in the family require emendation or change in status. Group IV includes the type species of *Peziza, P. vesiculosa,* and should serve as a core group for a future circumscription of *Peziza*. The genera *Kimbropezia* and *Pfistera* should be included in *Peziza*. A close relationship between *Sarcosphaera* and the truffle *Hydnotryopsis* is suggested for the first time. Likewise, a close relationship between *Scabropezia* and the truffle *Amylascus* is strongly indicated.

Overall, these LSU analyses imply that there has been extensive homoplasy in some of the morphological characters that previously have been used to delimit taxa. Hypogeous ascomata with concomitant loss of active spore discharge have evolved independently several times, suggesting that their derivation from apothecial Pezizaceae may involve relatively simple genetic changes. For example, stereothecia have been derived within group III, V and VI. In addition, ptychothecia and exothecia have evolved within group VI. Derivation of ptychothecia and stereothecia from apothecia involves the evolution of enclosed hymenia or asci, while the derivation of exothecia involves the evolution of extremely convex hymenia. Spore shape has been emphasized in the delimitation of genera, but our results indicate that species with divergent spore form may be closely related. Globose-spored species occur in group I, III and VI, along with ellipsoid- or fusiform-spored species. The amyloid reaction of the ascus appears to be a variable character that has been lost in some lineages. On the other hand, different types of ascus amyloid reactions correspond to different lineages and seem to provide clues to relationships within the Pezizaceae. Other characters, such as apothecial colors, spore surface relief, guttulation, excipulum structure and anamorph morphologies, seem to be phylogenetically informative, although considerable variation within and between groups occur. For example, apothecial colors are purplish in group I, in the range of yellowish, rose, reddish to purplish (brown) in group III, paler yellowish-brown in group IVa, violaceous to vinaceous in group IVb, and dark brownish in group VI. Smooth or finely verrucose spores, without or with two small guttules, are mostly present in group IV species, while highly ornamented spores with two large guttules occur mostly in group VI species. Excipulum structure, although not clear-cut, seem to be fairly uniform within most groups. *Oedocephalum* anamorphs are produced by taxa in group III and IV, and by species of *Iodophanus,* while *Chromelosporium* anamorphs are produced mainly by group VI taxa.

It is still premature to propose a phylogenetic classification of the Pezizaceae. For example, the monophyly of some of the genera, e.g., *Boudiera* and *Scabropezia,* has not been tested and six genera (TABLE I) are not represented in this study. Most importantly, an additional dataset is needed to provide a more robust estimate of the phylogeny. Further studies of morphological characters, especially of pigment composition and excipulum structure, and of anamorph type and trophic status in the context of a robust molecular phylogeny, that will facilitate refining hypotheses of homology, may be useful in understanding relationships within the Pezizaceae.

Note on *P. vesiculosa* added after acceptance of the manuscript.

In a detailed and large scale study now underway of the group IVa *Peziza* species using ITS rDNA sequences it was discovered that the published voucher specimen for *P. vesiculosa* (ALTA 9066, GenBank LSU: AF133170, SSU: AF133155, ITS: AF133182) (Norman and Egger 1999) was misidentified. The specimen (ALTA 9066) has been examined morphologically by K. Hansen and has been determined to be *Peziza fimeti.* A comparison of the ITS1 sequence of ALTA 9066 with the larger ITS data set confirms this finding. In this paper ALTA 9066 has been renamed *P. fimeti* in FIGS. 22, 23 AND 24, and in TABLE II. Unfortunately, this misidentification has resulted in *P. vesiculosa,* the type species of *Peziza,* being omitted from the study. However, we have now sequenced the LSU rDNA (D1 and D2) from a collection of *P. vesiculosa* (TL-6398, C) (GenBank AF378367), and analyses of our LSU dataset including this sequence suggest that group IVa does in fact include *P. vesiculosa* (bootstrap 86%). The presence of a distinct amyloid ascus ring zone in *P. vesiculosa* also supports this placement. The placement of *P. vesiculosa* within group IVa is unresolved in the strict consensus tree of the MPT's based on LSU, but ITS sequences suggest a possible relationship with *P. ammophila.*

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