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THE HELVELLACEAE: SYSTEMATIC REVISION AND OCCURRENCE IN NORTHERN AND NORTHWESTERN NORTH AMERICA

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Abstract

Epigeous genera of the Helvellaceae (Pezizales, Ascomycota) are separated into tribes Helvelleae and Gyromitreae on the basis of excipulum structure, while hypogeous genera are included as *incertae sedis* at the tribe level. Ornamentation of ascospores (SEM) is valuable in the delimitation of genera, subgenera, and species. New subgenera proposed are *Gyromitra* subgenus *Melaleucoides subgen. nov.*, with warted, nonapiculate, biguttulate ascospores; *Gyromitra* subgenus *Caroliniana subgen. nov.*, with coarsely reticulate ascospores with multiple spicules at the poles; *Helvella* subgenus *Cupuliformae subgen. nov.*, with regularly cupulate apothecia, solid terete stipes, and broadly ellipsoidal, finely rugose ascospores; and *Hydnotrya* subgenus *Cerebriformae subgen. nov.*, with globose, echinate ascospores. *Gyromitra* subgenus *Discina* is emended. New combinations include *Helvella* subgenus *Leucomelaenae comb. nov*, *Helvella* subgenus *Silvicolae comb. nov.*, *Helvella* subgenus *Macropodes comb. nov.*, and *Helvella* subgenus *Elasticae comb. nov.* Epigeous taxa and hypogeous taxa with chambered ascocarps were studied in detail. Collections of 44 species in six genera (*Gyromitra*, *Rhizina*, *Pseudorhizina*, *Helvella*, *Underwoodia*, and *Hydnotrya*) from northern and northwestern North America are described. One extralimital genus (*Gymnohydnotrya*) and 15 species outside the study area are included with systematic notes. The known geographic range for many species is extended and there are several new records for North America (*Helvella rivularis*, *H. verruculosa*, *H. unicolor*). Maps and keys for taxa in northern and northwestern North America are provided.

Keywords: Ascomycete systematics, Pezizales, Helvellaceae, *Gyromitra*, *Pseudorhizina*, *Rhizina*, *Helvella*, *Underwoodia*, *Hydnotrya*, *Gymnohydnotrya*

Introduction

The Helvellaceae comprise a diverse array of macroscopic discomycetes. The family has a global distribution but reaches its peak of diversity in northern temperate regions. Apothecia vary from simple cupulate to complex, lobed or convoluted and may be sessile or stipitate. Some attain considerable size, being among the largest fruiting bodies produced by ascomycetes of any kind (e.g., the "false morels" *Gyromitra gigas, G. esculenta*). Some species are mycorrhizal, while others are saprophytic or parasitic. Saprophytic species occur on a variety of substrata including soil, coniferous and deciduous litter, and rotted wood. *Rhizina undulata* is a serious pathogen of conifer seedlings in northwestern North America.

This monograph focuses on epigeous taxa and hypogeous taxa with chambered ascocarps (except *Barssia* linked to Helvellaceae by Kimbrough *et al.* 1996) of northern and northwestern North America and presents a comprehensive family outline (Table 1). Taxa with a solid or veined ascocarp interior were not considered in detail due to the limitations of the project.

Family characters were reviewed by Dissing (1972) and Harmaja (1969a, 1974a, 1976b), and have been discussed briefly in comprehensive works on Pezizales (Eckblad 1968; Korf 1972, 1973a; Trappe 1979). Monographs have focussed on genera (e.g., Dissing 1966b; Weber 1972; Zhang and Minter 1989b), have treated the genera in a more restricted sense than accepted here (McKnight 1969; Kempton and Wells 1973), or have considered only a selection of species within a genus (e.g., McKnight 1971, 1973; Harmaja 1969b, 1977a, b, 1979a, b).

While literature concerning the Helvellaceae in North America is abundant (e.g., Weber 1972, 1975; McKnight 1969, 1971, 1973; Kempton and Wells 1970, 1973; Ginns 1968, 1974a, b, c, d, e, 1975; Abbott and Currah 1988; Callan 1990; Anderson and Ickis 1921; Pfister 1980; Seaver 1921; Morse 1945; Kanouse 1946; Groves and Hoare 1953; Dissing and Lange 1967; Harmaja 1981; Gilkey 1916, 1939, 1947, 1954), only a few authors have concentrated on material from the arctic, coastal, boreal, montane, and alpine regions in our study area (Kempton and Wells 1970, 1973; Abbott and Currah 1988; Weber 1975). Additional reports occur in floristic accounts from the area (e.g., Larsen and Denison 1978; Abbott and Currah 1989; Currah *et al.* 1989; Schalkwyk 1977; Snyder 1936; Kanouse 1947; Hawker 1968b; Cummins 1930; Zeller 1927; Fogel and Trappe 1976; Fogel 1976; Groves and Hoare 1954; Huhtinen 1984; Hutchison *et al.* 1988) or in collections listed in broader taxonomic treatments dealing primarily with restricted groups of taxa and often extralimital material (e.g., Pfister 1980; Gilkey 1947; Harmaja 1979a; Ginns 1974a, b, c; McKnight 1969, 1971; Seaver 1921, 1928, 1942; Morse 1945; Kanouse 1949).

'*Elvela*' (=*Helvella*, orthographic variant) was erected by Linnaeus in 1753 to accommodate *Elvela mitra* (=*Helvella crispa* of Fries, 1823). Linnaeus cited P.A. Micheli, 1729, Nova Plantarum Genera 204, Tab. 86, Fig. 7 (=*H. crispa*) and Valliant, 1727, Botanicon Parisienne 57, Pl. 13, Fig. 1 (=*H. acetabulum*), the earliest records of species from this family. The Elvellaceae were established by Fries in 1823 and later published as Helvellaceae by Dumortier in 1829 and Corda in 1842. Fries restricted the family to stipitate taxa including *Morchella* and *Leotia*. Taxa treated by Fries (1821-1832, Systema Mycologicum) are sanctioned under the International Code of Botanical Nomenclature (ICBN Articles 13.1 and 15.1; Greuter *et al.* 1994) and established names for two genera (*Helvella* and *Rhizina*) as well as epithets for *Helvella crispa, H. lacunosa, H. acetabulum, H. macropus, H. atra, H. pezizoides, H. elastica, Gyromitra esculenta, G. infula, G. caroliniana, G. perlata,* and *Rhizina undulata*. Although Fries distributed these species among *Helvella*, *Morchella*, *Rhizina*, and *Peziza*, he clearly recognized the affinities among these various species. The first three genera were placed in his broadly conceived Elvellaceae, with the cupulate forms in the tribe Helvelloideæ of the Pezizaceae where affinity with *Helvella* and *Rhizina* was noted. Many taxa included by Fries originated in the earlier works of Linnaeus (1753), Schaeffer (1762-1774),

Scopoli (1772), Afzelius (1783), Bulliard (1780-1798), Persoon (1796, 1800), Holmskjøld (1790), and Bosc (1811).

Gyromitra and *Helvella* were considered separate genera by Fries in 1849 although this was not universally accepted (e.g., Seaver 1928; Kanouse 1946). Quélet (1873), Cooke (1878), and Gillet (1879) adopted the two genus concept for these taxa. Fries (1849) also separated the cupulate species of *Gyromitra* from *Peziza* placing them in the genus *Discina*. Quélet (1873) and Bresadola (1881-1900) still retained many cupulate taxa in the genus *Peziza*.

Another classification was proposed by Boudier (1885, 1907) and was based, in part, on earlier works of Fries (1849) and Fuckel (1869). Three of Boudier's ten genera (Boudier 1907), namely *Helvella*, *Gyromitra*, and *Rhizina*, are used here while the others at least reinforce the recognition of taxa we have defined as subgenera. In *Helvella*, we include Boudier's *Helvella*, *Leptopodia*, *Cyathipodia*, *Acetabula*, *Macropodia*, and *Wynnella*. The genus *Gyromitra* includes *Gyromitra*, *Physomitra*, and *Discina*. *Rhizina* was accepted as monotypic by Boudier in agreement with the concept of Fries (1823). Boudier's genus names which embody a narrow concept of genera defined on the basis of ascomatal morphology are used by both Dennis (1981) and Breitenbach and Kränzlin (1981).

A broader approach was initiated by Quélet in 1886 and later supported by Nannfeldt (1937, see below) who felt that variation in ascocarp morphology was too substantial to be considered a feature of taxonomic value at the generic level. Broad generic concepts have been adopted by many recent authors including Dissing (1966b), Weber (1972), Harmaja (1969a, 1974a), and Kimbrough *et al.* (1990).

The remaining epigeous genera of Helvellaceae include *Underwoodia*, established by Peck in 1890, and *Pseudorhizina*, erected by Jacevskij in 1913.

The affinity of indehiscent hypogeous taxa, many considered Tuberales *sensu* Korf (1973a), to the Helvellaceae was suggested by Trappe (1979). Genera which have been allied to the Helvellaceae include: *Choiromyces* and *Balsamia* described in 1831 by Vittadini; *Hydnotrya*, described in 1846 by Berkeley and Broome; *Barssia* described by Gilkey in 1925; *Fischerula* described in 1928 by Mattirolo; *Dingleya* described in 1979 by Trappe; *Cazia* described in 1989 by Trappe; *Gymnohydnotrya* described in 1989 by Zhang and Minter.

The concept of the Helvellaceae accepted by us, is founded on the concept outlined by Nannfeldt (1937) who considered the unique tetranucleate spores a unifying feature in the family. Ascospores also have oil reserves, visible as large guttules (lipid droplets *fide* Gibson and Kimbrough 1988a, b; Kimbrough *et al.* 1990). This concept has been adopted by Dissing (1966b), Harmaja (1976b), Korf (1972), Kimbrough (1970, 1991), and Eriksson and Hawksworth (1993). Kimbrough and others (Gibson and Kimbrough 1988a, b; Kimbrough and Gibson 1989; Kimbrough *et al.* 1990; Kimbrough 1991) have illustrated the uniformity of ascospore ontogeny and septal structures among epigeous taxa of the Helvellaceae.

Tetranucleate ascospores support the inclusion of the hypogeous taxa *Hydnotrya*, *Gymnohydnotrya*, *Choiromyces*, *Barssia*, and *Balsamia* (Berthet 1982; Zhang and Minter 1989a, b; Eriksson and Hawksworth 1989, Zhang 1991; Kimbrough *et al.* 1996, Donadini 1986b). *Cazia*, *Fischerula*, and *Dingleya* were considered possible members of the Helvellaceae based on morphological grounds (Trappe 1975b, 1979, 1989), but recent investigations have excluded them from the family (Trappe *et al.* 1992; Trappe pers. comm.).

Materials and methods

The study region includes arctic, coastal, boreal, parkland, prairie, montane, and alpine areas of northwestern North America. The boundaries encompass Yukon Territory (YT), Northwest Territories (NWT), British Columbia (BC), Alberta (AB), Saskatchewan (SK), Manitoba (MB), Alaska (AK), Washington (WA), Idaho (ID), Montana (MT), Oregon (OR), and Wyoming (WY). Collections were made at boreal, parkland, montane, and alpine sites in the interior northwest (Alberta, British Columbia, Yukon).

Over 2,500 specimens were examined and included collections from within the study area, type material and selected extralimital collections. New collections were made during 1987-1996. Most were photographed *in situ* using Kodacolor 400 ASA film but some were photographed in the laboratory using a copy stand with Ektachrome 100 ASA film. Macroscopic features of fresh specimens were described within six hours of collection. Specimens were air dried and packaged with dichlorobenzene crystals in plastic bags and then boxed. Macroscopic observations and measurements reported here were from dried material except where noted. Herbarium material was supplied by ALTA, BPI, C, CFB, CUP, DAOM, DAVFP, H, IMI, K, L, MICH, MU, NY, NYS, O, OULU, PC, PRC, S, TRTC, TUR, UAMH, UBC, UPS, UVIC, WIN, WSP, and WTU (acronyms follow Holmgren *et al.* 1981, Index Herbariorum). In addition, material was obtained from the private herbaria of Abbott (SA), Danielson (RMD), Wells and Kempton (WK), and Kristiansen (RK). The Danielson collections and the majority of Abbott collections are now deposited in ALTA; a few specimens from the Abbott collection are deposited in UAMH and K. Collections at OSC and MICH from within the study area were not examined due to constraints in time and resources.

Microscopic details of the hymenium and ascospores were observed from dried material rehydrated in distilled water. Squash mounts in distilled water were used primarily, but some additional mounts were made in 5% KOH, Melzer's reagent (Groves 1962), or lactophenol Cotton Blue (distilled water 20 ml, lactic acid 20 ml, phenol crystals 20 g, Cotton Blue 0.05 g, glycerol 40 ml). Measurements were taken with an ocular micrometer using distilled water mounts and an Olympus bright-field light microscope. Spore measurements are of mature spores including all ornamentation, and spores of unusually small or large size are in parentheses. Apothecial cross-sections were made with a freezing microtome and mounted in distilled water. De Barry bubbles were observed in KOH, Melzer's Reagent or lactophenol Cotton Blue mounts. Ascospore nuclei were stained via the Feulgen reaction with Schiff's reagent (Östergren and Heneen 1962).

SEM observations of ascospores were made using air-dried fragments of apothecia mounted with a double sided adhesive. A double coating of gold-paladium, applied with a Nanotech sputter coater, was the only pretreatment used before specimens were examined and photographed with a Cambridge S-250 SEM. Only ascospores which had been ejected and were adhering to the excipular surface were examined, except for *Hydnotrya* for which apothecial tissue was crushed to liberate or expose the ascospores. Observations of hymenium and excipulum used fresh apothecial tissue fixed in 4% glutaraldehyde in 0.07 M sodium phosphate buffer, rinsed in buffer, and postfixed in buffered osmium tetroxide. Tissue was dehydrated in a graded series of acetone from 70 to 100%, placed in a 1:1 ratio solution of acetone:Peldri II for one hour, and then immersed in 100% Peldri II for another hour before drying (Kennedy *et al.* 1989).

Culturing of some species was attempted by placing tissue explants and/or ascospores on agar media and incubating at room temperature (20-24°C). Media included Potato Dextrose Agar (PDA; Difco), Phytone Yeast Extract agar (PYE; Difco), Nobles' Malt Agar (NMA; 12.5 g malt extract, 20 g agar, 1000 ml water), and Cornmeal Agar (CMA; Difco), with and without antibiotics and/or chalk. Cultures are deposited in UAMH.

Characters and their use in systematics

Delimitation of the taxa of the Helvellaceae requires consideration of both macroscopic and microscopic characters. Some of these may vary in importance among taxa and suites of characters may differ from taxon to taxon depending on which characters show the most stability. The following is an assessment of the usefulness of traditional features such as fruitbody size, shape, colour, etc., microscopic characters, and an evaluation of the taxonomic potential of more recent data from scanning electron microscopy.

Macroscopic characters (Figs. 1-17)**.** Apothecial size varies from a few millimetres in some species of *Helvella* (e.g., *H. rivularis*)(Fig. 10) to 20 cm in species of *Gyromitra* (e.g., *G. esculenta*) and *Pseudorhizina* (e.g., *P. californica*)(Fig. 13).

The shape of the apothecium has often been used for taxonomic purposes, but delimitation of genera and species should allow for considerable variation. For example, cupulate species (Figs. 2b-c, 3a-e, 9-11) were placed in separate genera from those with auriculoid (erect, elongate, one-sided apothecia reminiscent of a rabbit's ear)(Fig. 4b-c) or irregularly lobed apothecia (Fig. 1a-b, 2a, 6-8, 13, 14). However, there is a morphological gradation from simple cupulate forms to species with more elaborately folded or convoluted and reflexed apothecia. Species in the genera *Helvella*, *Gyromitra*, and *Pseudorhizina* may have saddle-shaped or bilobate (Fig. 8) apothecia. These species also exhibit simple convex, trilobate, or irregularly lobed apothecia, often in the same collection with bilobate forms. Auriculoid apothecia are known in only one species (*Helvella silvicola*)(Fig. 4), but strongly one-sided cupulate forms are also known in other members of the genus (e.g., *H. leucomelaena*).

The apothecial margin is also useful for distinguishing among species. In *Helvella*, the margin can be strongly inrolled over the hymenium when immature and gradually expands with age (e.g., *H. maculata, H. compressa, H. crispa*)(Figs. 6, 7). In contrast, *H. lacunosa* and *H. elastica* are reflexed towards the stipe when young (Figs. 5b, 8) and often become fused to the stipe at maturity. Margin characters are not significant at the subgenus level in *Helvella* (see the sections of Dissing 1966b and Weber 1972). There is a gradation from inrolled to reflexed in several groups of related species (i.e., from strongly inrolled to incurved to reflexed in the *H. compressa, H. albella, H. elastica* group, and the *H. crispa, H. fusca, H. lacunosa* group). Species of *Gyromitra* are similar, with the cupulate species (e.g., *G. perlata*) typically having a strongly inrolled margin initially (Fig. 2c), while stipitate species (e.g., *G. infula*) always have a reflexed apothecial margin (Fig. 1) typically ingrown with stipe tissue. *Rhizina* is similar to sessile cupulate members of *Gyromitra*, but the apothecium is sessile and discoid or somewhat irregular at all stages. It is unique in its indeterminate marginal growth and rhizoid-like excipular projections. *Pseudorhizina* species always have a strongly reflexed apothecial margin which initially is rolled over the excipular surface on the underside of the apothecium (Figs. 13, 14). The margin typically remains free. Species of *Underwoodia* are unique in that the apothecium is fused over the entire surface to the apical region of the stipe (Fig. 12). Fusion may occur in *Helvella* and *Gyromitra* (e.g., *H. lacunosa, G. esculenta*), but only at intervals along the apothecial margin. In *Hydnotrya*, the sessile ascocarp is initially a subglobose or sparingly infolded structure with the hymenium lining the internal surface (Fig. 17). As development continues, the ascocarp becomes highly infolded creating numerous internal chambers (Fig. 16). The margin in species of *Hydnotrya* is often entirely fused to form an enclosed fruiting body at maturity, but may be only partially fused at the base of the ascocarp in immature stages.

The hymenium may be smooth, undulate-rugose, or strongly convoluted-rugose. Cupulate species of *Helvella* and *Gyromitra* are typically smooth (Figs. 2b, 3a, 4, 9, 10), especially when young (e.g., *H. chinensis, G. olympiana*), but most species slightly to strongly are undulate-rugose at maturity (Figs. 1, 2a, 5-8, 13, 14), and a few species in *Gyromitra* (e.g., *G. esculenta*) are strongly convoluted-rugose.

The excipular surface is typically smooth (Figs. 2b, 3a, 4a, 9), but may have distinct ribs continuous with those of the stipe (Figs. 3e, 11, 14b). The presence and degree of ribbing on the excipular surface is of taxonomic value at the species level.

Apothecia may be sessile, subsessile, or prominently stipitate. *Helvella* and *Gyromitra* contain both sessile and stipitate forms. This feature has been used to subdivide these taxa into several genera, but like apothecial shape, this feature also shows a progression from sessile through subsessile or indistinctly stipitate to distinctly stipitate and is not useful for generic delimitation (Harmaja 1969a; Donadini 1983). Stipe development is relatively constant within species, but some taxa (e.g., *H. leucomelaena*) may vary from subsessile to short stipitate, even within a single collection. Stipes of *Helvella* may be slender and terete (e.g., *H. macropus, H. elastica*)(Figs. 5b-c, 9), sulcate, fluted or ribbed (e.g., *H. solitaria, H. leucomelaena*)(Fig. 3a-b), or highly ribbed with anastomosis between ribs (e.g., *H. crispa, H. costifera*)(Figs. 3e, 8). Internal stipe construction may be solid (e.g., *H. corium, H. verruculosa*), hollow (e.g., *H. elastica*), or highly chambered (e.g., *H. crispa, H. lacunosa*). These features are generally constant within species, but may vary. For example, *H. solitaria* usually has a sparingly ribbed, solid stipe, but some are only slightly fluted while others are highly ribbed with occasional anastomosis between ribs and may have a few internal chambers. Stipitate species of *Gyromitra* have stipes which are infolded or less frequently terete (Fig. 1a), and are internally solid or chambered. *Pseudorhizina* species are prominently stipitate with strongly ribbed, solid or chambered stipes (Figs. 13, 14). *Underwoodia* stipes are prominently ribbed and chambered (Fig. 12). *Hydnotrya* species are sessile (Figs. 15-17).

Most members of the Helvellaceae are shades of grey and brown. In *Helvella*, hymenia are white (e.g., *H. lactea, H. crispa*)(Fig. 6) to black (e.g., *H. corium, H. atra*)(Fig. 5a, 8). Reddish browns occur in several species of *Gyromitra (G. esculenta), Helvella (H. silvicola),* and *Hydnotrya (H. tulasnei)*. Bright yellow brown or orange brown pigmentation is seen in some members of *Gyromitra* (e.g., *G. leucoxantha*) and *Hydnotrya* (e.g., *H. variiformis*). Excipular pigmentation is frequently paler than the hymenium (Fig. 2b, 7). White to cream excipular surfaces are common in *Helvella, Gyromitra, Pseudorhizina,* and *Rhizina*. The stipe is concolourous with the excipular surface, or paler, with the basal region usually white or pallid. Some species of *Gyromitra* (e.g., *G. ambigua, G. esculenta*) and species of *Pseudorhizina* have purplish red tints on the stipe. A mottled hymenium is evident in some specimens (e.g., *Helvella maculata, Gyromitra esculenta*), but is not diagnostic.

Vestiture (or lack thereof) on the excipular surface and stipe varies with development and between collections, but is constant enough to be important at the species level. For example, the species of *Helvella* vary from glabrous through pubescent to villose. *H. latispora* and *H. albella* are finely pubescent initially, but may be nearly glabrous by maturity. Some variation occurs between the excipulum and stipe. *Helvella atra*, for example, has a glabrous excipulum, but a finely pubescent stipe. Some species (e.g., *H. corium, H. verruculosa*) or individual specimens are often most densely pubescent at the margin, and have progressively finer vestiture towards the base and on the stipe. Variation is frequently seen in arctic and alpine species which have heavier vestiture in arctic regions than in temperate regions. Correlated with this is the presence of a white marginal region (Fig. 11a). The white margin is composed of fascicles of hyaline hyphal hairs and sometimes crystalline, probably calcium, deposits (Harmaja 1977b) (e.g., *H. corium, H. verruculosa,* and *H. aestivalis).* This feature has been used to subdivide species into several taxa (Nannfeldt 1937; Dissing 1964), but is not considered to have taxonomic value here since it likely reflects environmental rather than genetic differences. Vestiture in other genera is more uniform, and therefore of less use in defining species. *Gyromitra* species initially have a loose weft-like pubescence, but this often disappears at maturity.

Apothecium flesh is brittle in all species. *Gyromitra* species have thick flesh (2-5 mm), while *Helvella* and *Pseudorhizina* species have thin flesh (1-2 mm). Odour is usually indistinct in Helvellaceae, but is noticeable in dried ascocarps of *H. silvicola* and

strong in fresh specimens of at least some species of *Hydnotrya*. Strong odour in hypogeous species is associated with dispersal by mammals.

Microscopic characters. Measurements and observations from light microscopy (LM) were from distilled water mounts. McKnight (1968) reports alteration of spore size, shape, apiculation, and surface ornamentation in *Gyromitra* subgenus *Discina* when viewed in KOH, a commonly used rehydrant. KOH mounts are useful for observation of setoid paraphyses of *Helvella crassitunicata*. Some microscopic features of the hymenium and excipulum are presented in Figs.18-28.

The apothecium is divided into hymenium, subhymenium, medullary excipulum, and ectal excipulum (terminology following Korf 1973a)(Fig. 20), but a distinct ectal excipulum layer is not found in some taxa, and the subhymenium may be indistinct (Fig. 19). Excipulum anatomy has been used to delimit genera and species (Dissing 1966b; Harmaja 1977b, 1979a; Weber 1972; Eckblad 1968). We agree that this character is of great value in the recognition of tribes and genera within the family, but the thickness and pigmentation of tissue layers are highly variable and of limited use to delimit species (in agreement with Häffner 1987). The ectal excipulum is morphologically distinct from the medullary tissue in *Helvella* (Fig. 20), *Underwoodia*, and *Hydnotrya*. The medullary layer is *textura intricata* while the ectal excipulum is *textura angularis* or *textura prismatica* (terminology following Korf 1973a). The pubescence on the excipular surface of *Helvella* is composed of chains of cells and/or fascicled hyphal chains extending from the ectal excipulum (Fig. 18). In *Gyromitra*, *Pseudorhizina*, and *Rhizina*, the excipulum is *textura intricata* throughout, and is not divided into distinct medullary and ectal layers (Fig. 19) at maturity. The pubescence in some species of these genera is made up of undifferentiated protruding hyphae or an evanescent ectal excipulum present on immature apothecia.

Asci are hyaline, octosporous and cylindrical (Fig. 27), and tapered below the uniseriate ascospores (Figs. 23, 24). Some species of *Hydnotrya* (e.g., *H. tulasnei*) have clavate asci, especially when immature, with irregularly biseriate or clustered ascospores. Asci range from 10 µm diam. in *Pseudorhizina* to 30 µm diam. in *Hydnotrya*, and are usually 100-400 µm long. The indehiscent asci in *Hydnotrya* represent a derived feature associated with hypogeous fruiting. Hawker (1968b) and Zhang (1991) have also observed operculi (Fig. 28) in *Hydnotrya cerebriformis*.

Much attention has been given to the structure of the ascal base and mode of ascus development in *Helvella* (Weber 1972; Harmaja 1977a). Pleurorhynchous asci have a forked ascus base (Fig. 23) originating from a crozier during ascus development, while aporhynchous asci have a simple base (Fig. 24) from lack of a crozier during ascus development (Weber 1972). This feature is best observed in KOH squash mounts of immature asci and the feature is noted where taxonomically important. Differences have been used to define sections within the genus (Weber 1972; Harmaja 1977a); however, this feature may be variable. For example, *H. aestivalis* is described as having aporhynchous asci (Dissing 1983), but our observations clearly show croziers (Fig. 23). If the species with aporhynchous asci (*H. leucomelaena, H. crassitunicata*, and *H. oblongispora*) are more closely related to each other than to other species in our subgenus *Leucomelaenae*, this feature would support the recognition of the section *Leucomelaenae sensu stricto* within our subgenus.

Paraphyses are prominent in all taxa (Figs. 21, 27). Paraphyses are thin-walled, approximately the same length as asci, and range from 3-11 µm diam. at the apex. The broadest paraphyses are seen in species of *Gyromitra*, while *Hydnotrya* species tend to have slender paraphyses. Clavate paraphyses are typical (Fig. 27), and are gradually to abruptly enlarged at the apex. Paraphyses may be hyaline or strongly pigmented. In *Gyromitra*, the apical cells contain coarse pigmented granules, while in *Helvella* the contents are finely granular to nearly homogeneous. Some species (e.g., *Rhizina undulata*) have an extracellular pigmented matrix around the apex of the paraphyses. *Helvella crassitunicata* has thick-walled paraphyses similar to the setae of *Rhizina*

undulata (terminology following Fitzpatrick 1917). Setae are aseptate with brown wall pigmentation (Fig. 22), and arise in excipular tissue below the hymenium.

Ascospore size varies from approximately 10 to 50 µm in length and spore shape varies from globose, subglobose, broadly ellipsoidal, ellipsoidal, subfusoidal, to fusoidal. *Pseudorhizina sphaerospora* is the only epigeous species with globose ascospores, and these are the smallest (8.5-10 µm diam.) in the family. Most species of *Helvella* have broadly ellipsoidal spores, but one subgenus (*Macropodes*) has subfusoidal spores. *Gyromitra* species have ellipsoidal to fusoidal spores up to 40 µm long, and spore shape and size are diagnostic for subgenera of the genus. The large, fusoidal ascospores of *Rhizina* are similar to species in the subgenus *Discina* of *Gyromitra*. Ascospores of *Hydnotrya* species are the largest in the family at 25-55 µm diam., and are globose to broadly ellipsoidal.

Spore size is quite variable within species and individual ascocarps. Spore length may vary over a range of 2-10 µm within species or collections. Kempton and Wells (1973) reported that spore size varied in individual ascocarps of *Gyromitra esculenta* over a six week period, with early spores slightly smaller than later spores and that different regions of the hymenium on individual ascocarps matured at different times. Donadini (1986a) observed that submature but viable spores of some *Gyromitra* species are often ejected from the asci. Harmaja (1977b) reported that in *Helvella* submature spores within the asci were often slightly larger than fully mature ejected ascospores. Dissing and Nannfeldt (1966) and Harmaja (1977b) reported that abnormally large spores (macrospores) sometimes occur and this has been confirmed in this study. Spore volume may be somewhat more constant than spore dimensions (i.e., the longest spores are often the narrowest and vice versa). All ascospores are hyaline and thin-walled with the exception of *Hydnotrya* which has a thickened epispore. Spore ornamentation is an important character but is difficult to assess with the light microscope (see SEM notes below). By LM, spores of *Helvella* are smooth; the verruculose spores of subgenus *Macropodes* excepted. Species of *Gyromitra* vary from smooth to distinctly warted, roughened, or reticulate. The large nodulose warts visible on ascospores of *Underwoodia* are diagnostic at the generic level. *Hydnotrya* spores appear greatly thickened with a nearly smooth, nodulose, or echinate surface. The presence or absence of spore apiculi is diagnostic at the specific, subgeneric, and/or generic levels, but may be variable in some taxa. Spores of many species of *Gyromitra* and *Rhizina* appear apiculate in water mounts, while all species of *Helvella*, *Underwoodia*, and *Pseudorhizina* lack apiculi. One species of *Hydnotrya*, *H. cubispora*, has ascospores with a thickened apical region which may appear apiculate.

Ascospores of Helvellaceae contain large lipid reserves (Gibson and Kimbrough 1988a, b; Kimbrough *et al.* 1990), and variation in the number and distribution of guttules is useful. Species of *Helvella*, for example, have a large central subglobose guttule, while species of *Gyromitra* in subgenera *Gyromitra* and *Melaleucoides* have two smaller globose guttules. Most Helvellaceae lack de Bary bubbles (Dodge 1957), but they were observed in a small proportion of the spores mounted in KOH, Melzer's Reagent or Cotton Blue in *Gyromitra melaleucoides, G. infula, Pseudorhizina sphaerospora* (Fig. 26b), *P. californica, Rhizina undulata* (Fig. 26a), *Hydnotrya cerebriformis,* and *H. variiformis.* Harmaja (1973, 1974c) suggests that de Bary bubbles may be important at the generic level, but variability limits their use. For example Harmaja (1974c) reports rare de Bary bubbles in *Gyromitra ambigua*, but lacking in *Rhizina undulata.* Ascospores possess a cyanophilic (deeply stained in Cotton Blue) perispore at maturity with the exception of *Pseudorhizina*. This character is important at the generic level (Harmaja 1974b) and is useful in other genera of Pezizales (Harmaja 1974d; Egger pers. comm.). The ascospores of Helvellaceae contain four nuclei at maturity (Harmaja 1976b; Pfister 1980; Berthet 1982; Donadini 1986b; Kimbrough *et al.* 1990, 1996; Zhang and Minter 1989a,b). We have confirmed this in *Pseudorhizina sphaerospora*, *Helvella crispa*, and *Hydnotrya cerebriformis*.

SEM observations on spores of Helvellaceae, including the genera *Helvella, Underwoodia, Gyromitra, Pseudorhizina, Rhizina, Hydnotrya,* and *Gymnohydnotrya*

indicated spore wall features are useful (McKnight and Batra 1974; McKnight 1973; Dissing 1972; Harmaja 1976d; Donadini 1986a; Trappe 1976; Zhang and Minter 1989a, b). We have examined with the SEM spores of all species described here. The results have taxonomic value at the generic, subgeneric, and specific levels in various taxa of the family but must be interpreted cautiously. Variation among species is often no greater than that among individuals of the same species and often cannot be used as a primary means of species identification. Intraspecific variation in spore ornamentation between different collections and/or different spores from the same ascocarp is attributed primarily to ascospore maturity (see notes below). For this reason, it is necessary to standardize the parameters for selecting spores for measurement and description. In our work, we considered ascospores mature if they had been ejected (in epigeous forms) and were adhering to the excipulum. Hypogeous taxa were studied by crushing apothecial tissue on a stub; spores were considered mature if they had well developed ornamentation. Figs. 29-64 show the diversity of ascospore ornamentation and apiculation with the SEM.

Only *Gyromitra* has been studied intensively by SEM. McKnight and Batra (1974) divided species into three groups based on ascospore morphology. They recognized that closely related species had similar morphology, but their spore groups do not correspond to the subgenera proposed here. In a more comprehensive study, Donadini (1986a) discussed the variation in spore ornamentation of the genus. He showed that submature spores typically have a finer, less developed surface ornamentation and that these submature spores are often ejected from the asci before development is complete. This is significant in the interpretation of the observations by McKnight and Batra (1974) and Harmaja (1976d). Harmaja (1976d) describes *G. montana* as having less ornamentation than *G. gigas* and used this character to separate the taxa. Our observations show a similar degree of variation in ornamentation in collections referable to both taxa *sensu* Harmaja (Figs. 35-38). A similar situation occurred in the work of McKnight and Batra (1974) who separated weakly and strongly ornamented spores of *G. gigas* (as *G. gigas* and *G. fastigiata* respectively) and *G. leucoxantha* (as *Discina larryi* and *D. leucoxantha* respectively). Examination of the holotype of *G. larryi* indicates it is an immature specimen of *G. leucoxantha*. Recognition of the variation in spore morphology (and correlation with other features) permits the division of *Gyromitra sensu lato* into four subgenera. Subgenus *Gyromitra* has spores with finely rugose perispore ornamentation, only slightly inflated apiculi if present (Figs. 29, 30), and corresponds to McKnight and Batra's (1974) Group 1 (although they also include a species of *Pseudorhizina*). Subgenus *Discina* has finely to distinctly rugose submature spores (Figs. 31, 36, 37), often with a distinct, irregular reticulum in mature spores (Figs. 33, 34, 38). Inflated spore apiculi are present and may be well developed (Figs. 31, 33-35) or reduced in some species or individual spores (Figs. 32, 37, 38). This subgenus includes species in Group 2 and some species from Group 3 of McKnight and Batra (1974). Subgenus *Caroliniana* displays regular, widely spaced reticula and prominent spicules at the apices of ascospores (Fig. 39). Submature spores may be weakly ornamented as in subgenus *Discina*, but evidence of the reticulum and spicules is usually present. Species in this subgenus are referred to Group 3 of McKnight and Batra (1974). The fundamental difference between species with an irregular, closely spaced reticulum and solitary inflated apiculi and those with a regular, widely spaced reticulum and multiple apical spicules was not recognized when McKnight and Batra included all species with a reticulum in Group 3. The apiculi of species in the subgenus *Discina* are inflated regions of the perispore which often have some rugosity extending onto the apiculus surface, while the apical spicules of the subgenus *Caroliniana* are projections continuous with the reticulum. Subgenus *Melaleucoides* has a distinctive pattern of ornamentation separating it from all others in the genus; the rough ornamentation visible with the LM is of isolated warts (Fig. 40).

Pseudorhizina species have finely rugose spores (Fig. 41). This ornamentation is most similar to species in *Helvella* and *Gyromitra* subgenus *Gyromitra*, although even

less pronounced, and lead McKnight and Batra (1974) to include species of this genus in their Group 1.

The finely rugose ascospores of *Rhizina undulata* (Fig. 43) are similar to *Gyromitra ambigua* and other species of *Gyromitra* (compare Figs. 29, 30, 37, 43). The apicular striations (Fig. 44) are identical to *G. perlata* (Fig. 33) in subgenus *Discina*.

Ascospores of *Helvella* species appear smooth by LM and with the SEM at lower magnifications. At 1500X or greater, the finely rugose perispore is distinctive (Figs. 46, 49, and 50). The similarity in ornamentation of *H. silvicola* (Fig. 51) with others in the genus supports its inclusion in *Helvella* and rejection of the name *Wynnella*. The only *Helvella* species with a different ornamentation is *H. macropus*. The verruculose ornamentation by SEM consists of numerous short spines (Figs. 53-56). This feature, as well as ascospore shape and guttulation, supports Häffner's (1987) separation of the section *Macropodes* (*sensu stricto*), which is recognized as a distinct subgenus. Some spores may appear finely rugose (Fig. 57)(or smooth by LM), similar to other *Helvella* species, and probably represent submature spores.

Underwoodia has been synonymized with *Helvella* by some authors (Eckblad 1968; Harmaja 1974a), but unique ascospore ornamentation supports its retention in a separate genus. The spore is covered with irregular, broadly rounded, nodulose warts (Fig. 42). The small pits in the perispore, noted by McKnight and Batra (1974), and the irregular cracking of the spore surface (Fig. 42), are not of taxonomic value.

Species in *Hydnotrya* fall into two distinct spore groups which are given recognition at the subgenus level. Subgenus *Hydnotrya* has smooth spore walls which are extensively thickened with an adhering amorphous epispore, often with a broadly rounded or nodulose surface (Fig. 61). In subgenus *Cerebriformae*, the ascospores are echinate with distinct projections of the spore wall extending from the surface (Fig. 64). In *Hydnotrya cerebriformis*, the spore surface may be partially or completely covered with an adhering matrix similar to that observed by Hawker (1968a) for *Elaphomyces*. Spines are often aggregated by the adhering matrix, giving a warted or cracked appearance (Fig. 63). Species of *Gymnohydnotrya* also have echinate ascospores (Zhang and Minter 1989b).

Ecology and biogeography. The Helvellaceae demonstrate a wide variety of trophic abilities. *Gyromitra* and *Pseudorhizina* are common on wood and other plant debris and are assumed to be saprophytes (e.g., Benedix 1969), although *G. infula* might be a very weak pathogen (Egger and Paden 1986b). Some species of *Gyromitra* are easily cultured (Abbott unpublished data; Roponen and Kreula 1978; Raudaskoski *et al.* 1976; Egger and Paden 1986b; Groves and Hoare 1953) supporting the assumption that they are saprophytic. *Rhizina* is pathogenic on conifer seedlings (Ginns 1968, 1974a; Satô *et al.* 1974; Morgan and Driver 1973; Morgan *et al.* 1974; Thies *et al.* 1977; Egger and Paden 1986a; Callan 1990) and can be cultured also (Sato *et al.* 1974; Ginns 1974b; Egger and Paden 1986a, b).

The trophic strategies of *Helvella* are unknown, although *H. crispa* and *H. corium*, as well as *Gyromitra esculenta* and *G. infula*, are listed as mycorrhizal in Maia *et al.* (1996) and Trappe (1971) based on literature reports. Smits'ka (1981) also lists *Helvella* and *Gyromitra* as mycorrhizal. Mycorrhizal capabilities of *H. lacunosa* have been described by Martinez-Amores *et al.* (1991). It has not been possible to culture species of *Helvella* even though numerous attempts have been made (Abbott unpublished data; Weber pers. comm.), although one putative culture of *H. lacunosa* (UAMH 6474) was obtained from Europe. In general, the nutritional fastidiousness (*Helvella* and *Hydnotrya*) and the lack of conidia (*Gyromitra*) in the Helvellaceae may be evidence supporting mycorrhizal tendencies (Hutchison 1989). Hypogeous species are probably ectomycorrhizal with coniferous and deciduous trees (Maia *et al.* 1996), but experimental evidence is lacking (Trappe 1971). The recent collections of *Hydnotrya cubispora*, an endemic North American species, from non-native European plantations of *Picea*, also indicates a mycorrhizal relationship with conifers (Pegler *et al.* 1993).

Species exhibit some seasonality with respect to fruiting with some being vernal (e.g., *Gyromitra esculenta, G. perlata, Helvella leucomelaena*) others autumnal (e.g., *Gyromitra infula, Helvella lacunosa*) and some, such as *Helvella lacunosa, H. maculata, H. compressa,* and *Gyromitra infula,* may fruit throughout the winter in coastal regions. Some vernal species (e.g., *Gyromitra gigas, G. olympiana*) are often associated with melting snowbanks. Fruiting body development may occur slowly (especially in *Gyromitra*)(Kempton and Wells 1973; Jalkanen and Jalkanen 1981, 1984; Moravec 1966) and ascospores may mature at different times within different regions of individual ascocarps (Kempton and Wells 1973; Donadini 1986a). Both tactics maximize reproductive potential. Hypogeous species are dispersed primarily by rodents in addition to other mammals and invertebrates which feed on the fruiting bodies (Fogel 1976).

With respect to biogeography, some species are restricted to arctic and alpine tundra regions (e.g., *Helvella aestivalis, H. verruculosa*), while others are circumboreal, occurring in similar habitats in Europe, Asia, and North America (e.g., *Helvella crispa, Gyromitra esculenta*). Some are widely distributed in the northern hemisphere in a range of habitats including deciduous and coniferous woods or tundra, and on soil, humus, or rotted wood (e.g., *Helvella lacunosa, Gyromitra gigas*). Others prefer specific substrata such as wood (*Pseudorhizina sphaerospora*), leaf litter/humus (*Helvella macropus*), or mineral soil (*H. leucomelaena*). Many species of *Helvella* tend to fruit on calcareous soil (Dissing 1966b; Petersen 1985; Abbott pers. obs.).

Geographic distribution can help delimit species. Some species are endemic to Europe or North America (e.g., *Gyromitra parma* and *Gyromitra melaleucoides* respectively), while others are widely distributed in northern temperate regions (e.g., *Helvella crispa, Hydnotrya tulasnei*). A few have an even broader geographic range in the northern and southern hemispheres (e.g., *Helvella leucomelaena, H. chinensis*). Few have been described exclusively from montane tropical regions (e.g., *Helvella papuensis* Dissing 1979).

Species endemic to the study area include *Helvella robusta* and *H. crassitunicata*, but further collecting may expand this range. Several other species are restricted to western North America and occur south of the study area (*Gyromitra melaleucoides, Pseudorhizina californica, Helvella compressa,* and *H. variiformis*). The reported arcto-tertiary disjunct distribution of *Helvella maculata* in northwestern North America and China (Cao *et al.* 1990) is unique in the family.

Many closely related species are sympatric (e.g., *Helvella acetabulum* and *H. costifera*) throughout their range, while others are partially sympatric, especially if one is restricted in distribution (e.g., *Helvella crispa* and *H. maculata*).

Geographic distribution is useful in identification when two closely related species are allopatric. For example, *P. sphaerospora* occurs in Europe, Asia and eastern North America, while *P. californica* is only in western North America. The ranges of the two species approach each other on either side of the continental divide (Map 8). The species of *Underwoodia* are unusually disjunct with each of the three species restricted to North America, South America, and Australia respectively.

Morphologically distinct forms may occur in different environmental regions and in these cases it can be difficult to evaluate taxonomic identity (i.e., whether the morphological features are altered by different conditions, or if distinct species are restricted to different habitats)(e.g., *Helvella palustris* and *H. lacunosa,* Häffner 1991). Taxonomic problems also arise from morphological differences seen between geographic locations. For example, variations in *G. gigas* (*sensu lato*) in Europe, eastern North America, and western North America suggest possible taxonomic divergence, yet the degree of overlap in morphology and distribution is great.

Phylogenetic Relationships of the Helvellaceae

Relationships within the Pezizales. The Helvellaceae are placed in the Pezizales. Until recently this order was restricted to operculate taxa (e.g., Eckblad 1968; Korf 1972) but a broader concept now includes taxa with indehiscent asci that are clearly recent derivations from operculate forms (Trappe 1979; Eriksson and Hawksworth 1993). These include hypogeous members which were traditionally treated together (Harkness 1899; Massee 1909) and often classified in the Tuberales (Gilkey 1916, 1939; Hawker 1954, 1955, 1974; Korf 1973a). The Helvellaceae are among the few families in the order (also Pezizaceae and Otidiaceae) that include both operculate epigeous and indehiscent hypogeous taxa. Morphological similarities between epigeous and hypogeous taxa indicate that the family is monophyletic, despite obvious differences in ascus structure. The unified concept of the family is based on the presumed monophyletic origin of all taxa with tetranucleate ascospores.

The relationship of Helvellaceae to other Pezizales is unclear. The family is considered to be highly evolved because of the complex apothecia and tetranucleate spores (Nannfeldt 1937; Eckblad 1968; Dissing 1966b). Taxa considered primitive exhibit simple cupulate apothecia and uninucleate ascospores (Eckblad 1968). Korf (1972, 1973a) places the Helvellaceae in the suborder Pezizineae along with the families Morchellaceae, Pezizaceae, Pyronemataceae (*sensu lato*), and Ascobolaceae. This suborder is distinct from the Sarcoscyphineae (Sarcoscyphaceae and Sarcosomataceae) with suboperculate asci. Eckblad (1968) and Brummelen (1978) do not consider the two groups distinct subordinal taxa. The distinction is also not supported by Harmaja (1974c) who found that Sarcoscyphineae have perisporous ascospores, a characteristic also found in many Pezizaceae, Helvellaceae, and Pyronemataceae (*sensu lato*).

The 'helvelloid' taxa have been placed close to, and often in the same family with, the 'morchelloid' taxa (e.g., Fries 1823; Seaver 1928; Groves and Hoare 1953; Imai 1932, 1954). These groups are distinct because the Morchellaceae possesses multinucleate rather than tetranucleate ascospores, and ascospores with external rather than internal oil guttules (Eckblad 1968; Korf 1972; Eriksson and Hawksworth 1993). Smits'ka (1981) derives the Morchellaceae from the Helvellaceae. The similar excipulum structure in the Morchellaceae and in *Helvella* (Eckblad 1968) may indicate relationship. Samuelson (1978) reports that the ascal apices of *Helvella* and *Morchella* are also similar. Nannfeldt (1937) and Eckblad (1968) suggest that the Morchellaceae and Helvellaceae are monophyletic groups derived independently from less advanced members of the Pezizales, and that the complex ascocarps are the result of parallel or convergent evolution. However, given the diversity of species and genera in the Pezizales, it is likely that the Helvellaceae and Morchellaceae are more closely related to each other than to other families, such as Pezizaceae or Sarcosomataceae.

Several genera have been suggested as possible ancestors of the Helvellaceae. Nannfeldt (1937), Eckblad (1968), and Smits'ka (1981) suggest a close affinity between *Helvella* and *Pustularia* (=*Tarzetta*) based on similarities of excipulum, ascospores, and paraphyses. Maas Geesteranus (1967) even included *Pustularia* in the Helvellaceae. Eckblad (1968) further suggested that the Helvellaceae (*sensu* Eckblad) is derived from the Otideaceae (*sensu* Eckblad containing *Otidea*, *Pustulina* (=*Tarzetta*), *Sowerbyella*, *Geopyxis*, and *Ascosparassis*), and he separates the Otideaceae from the polyphyletic Pyronemataceae (supported by Kimbrough 1989). Benedix (1962) also suggests an affinity with *Geopyxis*. Dissing (1966b) considers these taxa distant from the Helvellaceae and was not able to suggest an ancestor. Recent transmission electron microscope (TEM) studies by Kimbrough and Gibson (1990) have shown that the structure of the ascus pore plugs and ascospore secondary wall in *Geopyxis* are most similar to the Helvellaceae. The uninucleate ascospores which contain only small oil reserves would exclude *Tarzetta* (=*Pustularia*, =*Pustulina*) and *Geopyxis* from the Helvellaceae.

Eckblad (1968) considered the Helvellaceae (*Helvella* and others) and Rhizinaceae (*Gyromitra* and others), as independent derivations from pezizoid ancestors. Smits'ka

and Slavnaya (1978) and Harmaja (1969a, 1974b) also accepted the Helvellaceae and Rhizinaceae although Harmaja (1976b) later included taxa of the Rhizinaceae in the Helvellaceae. Harmaja (1974b) also subdivided the Helvellaceae *sensu lato* by erecting the family Pseudorhizinaceae to accommodate *Pseudorhizina*, but this has received little support (Eriksson and Hawksworth 1993). Our observation of tetranucleate ascospores in *P. sphaerospora* supports the retention of *Pseudorhizina* in the Helvellaceae.

Smits'ka (1981) outlined different phylogenetic relationships among the genera: cupulate species were retained in the Pezizaceae (*sensu lato*) as the genera *Discina, Acetabula,* and *Macropodia*. The monotypic family Rhizinaceae (*Rhizina*) was derived from *Discina*. The Helvellaceae (*Helvella*) was derived from both *Macropodia* and *Acetabula* with *Helvella* giving rise to *Gyromitra* and *Helvellella* (=*Pseudorhizina*). Although this scheme recognizes the relationship between *Discina* (=*Gyromitra*) and *Rhizina,* it fails to note the even closer association of *Discina* and *Gyromitra* which are relegated to different families. The views of Eckblad (1968), Harmaja (1974b), and Smits'ka (1981) are untenable. Rather, the more unified concept of the family, as put forth by Dissing (1966b, 1972), Rifai (1968), Kimbrough (1970, 1991), Korf (1973a), Harmaja (1976b), Trappe (1979), and Eriksson and Hawksworth (1993), is supported here.

Relationships among genera. The subfamilies, genera and subgenera proposed or accepted in this study are listed in Table 1.

The five epigeous genera of Helvellaceae accepted here are divided into two tribes, Helvelleae and Gyromitreae, considered monophyletic and sharing a common ancestor. The Helvelleae includes *Helvella* and *Underwoodia*, while the Gyromitreae includes *Gyromitra*, *Pseudorhizina*, and *Rhizina*. These tribes are distinct based primarily on the structure of the excipulum and correspond to the families Helvellaceae and Rhizinaceae of Eckblad (1968). The Gyromitreae is emended to include members of the Discineae of Dissing (1966b) and Korf (1972, 1973a).

The hypogeous indehiscent genera assigned to the Helvellaceae are *Hydnotrya, Gymnohydnotrya*, *Choiromyces*, *Balsamia,* and *Barssia*. All have tetranucleate spores (Berthet 1982; Donadini 1986b; Zhang and Minter 1989a, b; Zhang 1991; Kimbrough *et al.* 1996). The subfamilial placement of these taxa is unclear. While it may seem justifiable to erect a tribe to accommodate the indehiscent, hypogeous taxa, it is possible that the hypogeous ascocarp has evolved in both tribes. Further study of these genera is needed to determine a phylogenetic placement; for now they should be considered as genera *incertae sedis* at the tribe level. Morphological similarity between *Helvella* and *Hydnotrya* has been noted by Korf (1973b) and Donadini (1983). Because species of Helvellaceae tend to become folded or convoluted, they may have easily adapted to a hypogeous existence, and the number of hypogeous genera included in Helvellaceae may continue to increase as relationships are recognized.

Within the Helvelleae, *Helvella* is considered closest to the basal taxon from which extant genera are derived. Both *Underwoodia* and *Hydnotrya* have been assigned to *Helvella* at one time or another (Eckblad 1968; Harmaja 1974a; Donadini 1983; Eriksson and Hawksworth 1993).

Eckblad (1968) and Harmaja (1974a) placed *Underwoodia* in *Helvella* but this is an untenable placement. *Underwoodia* is distinct because it has no free excipular surface; the excipulum is completely fused and continuous with the stipe tissue. The nodulose ascospores were also ignored as a character of value at the genus level, but the striking difference in morphology clearly supports taxonomic separation. The uniformity in spore morphology of all species of *Helvella* examined in this study (including those of subgenus *Macropodes*, see discussion in following section) is clearly diagnostic at the generic level and supports keeping *Underwoodia* separate from *Helvella*, although some relationship to *Helvella* is indicated by excipulum anatomy and stipe morphology.

Hydnotrya was united with *Helvella* by Donadini (1983) on the basis of similarities of excipulum structure and the uniguttulate ascospores with cyanophilic ornamentation. Excipular structure is similar in all taxa of the Helvellaceae, and species typically lacking

an ectal excipulum at maturity may have an evanescent ectal layer when immature (Harmaja 1976b; McKnight 1969, 1971; Abbott unpublished data). The structure of the excipulum in *Hydnotrya michaelis* as shown in Berthet (1982) and Kers (1989) is distinct from *Helvella* as depicted in Eckblad (1968), Dissing (1966b), and Dissing and Sivertsen (1980). Considering that a single guttule in a globose or broadly ellipsoidal spore (two equal sized guttules in a narrowly ellipsoidal spore and three, with largest central guttule, in a fusoidal spore) is a physically efficient way of storing lipids (Harmaja 1973), guttule number should not be relied upon as an indicator of phylogenetic relatedness. Some members of the Gyromitreae (e.g., *Pseudorhizina sphaerospora, Gyromitra gigas*) may also have uniguttulate spores. Cyanophilic perispore-periplasm structure of mature ascospores was demonstrated by Harmaja (1974c) for *Helvella, Gyromitra,* and *Rhizina,* and is reported here for *Hydnotrya*. This feature, although absent in *Pseudorhizina*, is common in the Helvellaceae and does not necessarily imply relatedness between *Hydnotrya* and *Helvella*. A more convincing link between these two taxa is found in the description of *Helvella astieri* by Korf (1973b). Although we have not examined the type or other specimens, the description and illustrations show similarities to both *Helvella* and *Hydnotrya*. The decision to place this species in *Helvella* was based on the functional operculum, although the gross morphology of the ascocarp is more similar to *Hydnotrya*. In our opinion, the presence versus absence of a functional operculum is taxonomically significant at the generic level, which corresponds to the current recognition of genera by Eriksson and Hawksworth (1993) and Egger (pers. comm.). The discovery of *H. astieri* is also of great importance in assessing the direction of evolution in Helvellaceae. Because an enclosed 'sparassoid' ascocarp has no need for a functional operculum, it can be concluded that the dehiscence mechanism is retained from its ancestry. It is thus apparent that the indehiscent asci of hypogeous 'sparassoid' species represents a loss and that those species are more derived than those with functional operculate asci. The presence of an operculum in *Hydnotrya cerebriformis* (Fig. 28), although it is apparently not functional, also supports the derivation of hypogeous taxa from epigeous ones.

Within the Gyromitreae, the relationship of *Rhizina* to members of *Gyromitra* (e.g., *G. ambigua* and *G. perlata*), is suggested by similarities in ascospore size, shape, apiculation, and ornamentation. *Rhizina* is retained as a distinct, taxonomically isolated genus on the basis of the indeterminate growth in the margin, the presence of rhizoids continuous with the excipular surface, the presence of setae in the hymenium, and its pathogenic habit. These are specialized evolutionary traits and *Rhizina* is therefore a highly derived genus.

The phylogenetic relationship between *Gyromitra* and *Pseudorhizina* is less clear. The two genera were often placed in the same genus (e.g., McKnight and Batra 1974; Korf 1973a), but the differences in perispore staining and spore guttulation discussed by Harmaja (1974b) support the retention of *Pseudorhizina*. In *Pseudorhizina*, the apothecium flesh is thinner than in *Gyromitra*, and the margin is typically free from the prominently ribbed stipe. The structure of the excipulum is distincitive but similar to other genera of the Gyromitreae.

Subgeneric taxa. The broad generic concepts in the Helvellaceae contain subsets of closely related species. These subsets have been given the rank of section in *Helvella* (e.g., Dissing 1966b; Weber 1972; Häffner 1987) and subgenus in *Gyromitra* (e.g., Harmaja 1973; Kimbrough *et al.* 1990). In this work, the primary subdivisions of genera are considered subgenera (see Table 1). Subgenera are treated as a higher rank than sections for nomenclatural purposes (ICBN Article 4.2, Greuter *et al.* 1994). Subgenus names previously erected are retained, although some are emended. Some previously published section names are raised to the rank of subgenus (ICBN Recommendation 22A.2, Greuter *et al.* 1994), but may include several sections described by other authors (e.g., Dissing 1966b; Weber 1972; Häffner 1987). These smaller groups could still be recognized as sections within the newly proposed subgenera, although no division of subgenera is considered here. Subgenera based on species not designated as types for

any previously described subgeneric division are newly described. To avoid confusion, new subgeneric names are proposed rather than using earlier generic names at the subgeneric level (unless previously established; e.g., subgen. *Discina*). These genera rarely corresponded exactly with the subgenera as outlined here, or the concept of the genus included members from more than one of the subgenera recognized in this work. The outline presented divides the genera into recognizable units of taxonomic affinity (Table 1).

The genus *Gyromitra* is divided into four subgenera on the basis of ascospore and ascocarp morphology. Subgenus *Melaleucoides* shares relatively small spore size and biguttulate ascospores with subgenus *Gyromitra*. Pfister (1980) confirmed the tetranucleate condition of *G. melaleucoides* ascospores and supports a broad concept of the genus *Gyromitra* to accommodate it. Pfister also comments that it could not be placed easily in either *Gyromitra* or *Discina sensu stricto*, recognizing the taxonomic isolation of this species. The subgenus *Discina* may also provide a link with subgenus *Melaleucoides* through *G. melaleuca*, but the placement of this species is uncertain. *G. melaleuca* is tentatively placed in the subgenus *Melaleucoides*, although it is somewhat aberrant. The spores are smaller than typical in members of the subgenus *Discina*, and the apiculi appear absent (although also inconspicuous in other species of the subgenus *Discina*, e.g., *G. olympiana*). Our SEM observations of the submature ascospores of *G. melaleuca,* along with those of Donadini (1986a), indicate that the spores appear intermediate between the rugose surface typical for subgenus *Discina* and the nodulose warted ornamentation typical for *G. melaleucoides*, the only other species in the subgenus *Melaleucoides*. The distribution of guttules within the ascospore is also intermediate. As illustrated in Benedix (1969), the spores are ellipsoidal, but some appear subfusoidal. The spores are most frequently biguttulate (with a small proportion of triguttulate spores), but the guttules are of unequal size. This pattern is also seen in a small proportion of spores in other species of the subgenus *Discina*, including *G. gigas*. Further investigation of *G. melaleuca* may reveal a closer affinity with the subgenus *Discina*. Species in subgenus *Caroliniana* have been closely allied with members of the subgenus *Discina* and were often grouped with them in the genus *Discina* (e.g., Eckblad 1968). The subgenus *Caroliniana* contains subsessile to distinctly stipitate species sharing common ascospore morphology (Fig. 39) and is more closely related to subgenus *Discina* than to other subgenera of the genus.

Rhizina is monotypic but is likely derived from a *Gyromitra*-like ancestor. The genus *Pseudorhizina* contains only a type subgenus with two closely related species (see also discussion under intergeneric relationships and notes under species).

Helvella is divided into six subgenera, which are emended to include species treated in various sections *sensu* Dissing (1966b) or Häffner (1987). Subgenus *Helvella* represents a high level of development due to the complex apothecium and stipe morphology (Figs. 6-8). The ancestral form of species in the subgenus *Helvella* may have been similar to *H. solitaria* placed in a basal taxonomic position of the subgenus *Leucomelaenae*. *H. solitaria* is a variable taxon; large representatives of this species have a pronounced stipe with anastomosed branches and internal chambers reminiscent of *H. maculata* in subgenus *Helvella*. Species in the subgenus *Leucomelaenae* with complex ribbing on stipe and excipular surface (e.g., *H. acetabulum, H. costifera*) (Fig. 3e) are derived from simpler forms similar to *H. leucomelaena* (Fig. 3a) or *H. solitaria* (Fig. 3b). The subgenus *Silvicolae* is likely derived from an ancestor similar to species in the subgenus *Leucomelaenae*. The indistinct, sparingly ribbed stipe of *H. silvicola* (Fig. 4a,c) is similar in construction to *H. leucomelaena* (Fig. 3a) and *H. aestivalis*. The strongly one-sided apothecium and ascocarp coloration typical of *H. silvicola* are also seen to a much lesser extent in the aforementioned taxa. The subgenus *Leucomelaenae* is also allied with the subgenus *Cupuliformae*. Small slender forms of *H. solitaria* are morphologically similar to *H. cupuliformis* and *H. corium* placed in the subgenus *Cupuliformae*. Subgenus *Macropodes* is most closely related to *Cupuliformae*. Subgenus *Elasticae* is clearly derived from species in the subgenus *Cupuliformae*. Similarities between members placed in a basal taxonomic position of the subgenus

Elasticae (e.g., *H. ephippium, H. pezizoides*) are only slightly more complex than some species of subgenus *Cupuliformae* (e.g., *H. chinensis*). The subgenus *Elasticae* represents an advanced lineage. Species such as *H. elastica* and *H. leucopus* are among the most highly derived species of subgenus *Elasticae* on the basis of elaborate apothecia reflexed to stipe, glabrous excipular surface, and hollow stipe.

The genus *Underwoodia* contains only a type subgenus of at least three closely related species. Although the species of *Underwoodia* have been said to differ little in ascocarp morphology from species such as *H. lactea* in *Helvella* subgenus *Helvella* (Harmaja 1974a), direct phylogenetic relationship between these taxa has not been demonstrated and evidence to indicate that *Underwoodia* is derived from subgenus *Helvella* is lacking (see also notes under intergeneric relationships).

Hydnotrya is divided into two subgenera on the basis of ascospore morphology. Members of the type subgenus have subglobose to broadly ellipsoidal ascospores with smooth walls that are irregularly thickened by an amorphous epispore (Figs. 59-62). *H. cerebriformis* is placed in a subgenus of its own on the basis of the unique globose, echinate ascospores (Figs. 63, 64). Trappe (1979) suggested that this may deserve generic separation, but is retained in *Hydnotrya* based on gross morphological similarity, an admittedly unreliable character in hypogeous fungi (Zhang 1991). The tetranucleate ascospores of *H. cerebriformis* confirms the placement of this species in the Helvellaceae. Ascospore morphology is also variable in the hypogeous genera *Choiromyces* (Helvellaceae; see Trappe 1979) and *Tuber* (Tuberaceae; see Lange 1956). The SEM studies of *Gymnohydnotrya* by Zhang and Minter (1989b) show similar ascospore ornamentation to *Hydnotrya cerebriformis*.

TABLE 1: Taxa of Helvellaceae[1]

FAMILY:	Helvellaceae (44)	
TRIBE:	Gyromitreae (11)	
GENUS:	*Gyromitra* (8)	
SUBGENUS:		*Caroliniana* (0)
		Discina (4)
		Gyromitra (3)
		Melaleucoides (1)
GENUS:	*Pseudorhizina* (2)	
GENUS:	*Rhizina* (1)	
TRIBE:	Helvelleae (33)	
GENUS:	*Helvella* (27)	
SUBGENUS:		*Cupuliformae* (4)
		Elasticae (7)
		Helvella (4)
		Leucomelaenae (10)
		Macropodes (1)
		Silvicolae (1)
GENUS:	*Underwoodia* (1)	
TRIBE:	genera *incertae sedis*	
GENUS:	*Hydnotrya* (5)	
SUBGENUS:		*Hydnotrya* (4)
		Cerebriformae (1)
GENUS:	*Gymnohydnotrya* (0)	
	Balsamia (not examined)	
	Barssia (not examined)	
	Choiromyces (not examined)	

[1] number of species examined from northern and northwestern North America in brackets after taxon.

Taxonomic part

Generic, subgeneric, and specific taxa are described and presented in alphabetical order within each higher taxon (i.e., species arranged alphabetically within subgenera, subgenera alphabetically within genera, genera alphabetically within tribes), with the exception of extralimital taxa which are listed alphabetically at the end of their respective subgeneric or generic section. Keys to all tribes, genera, and subgenera are included individually and should be followed sequentially. Only species found to occur within the study area are keyed. Extralimital species are included to elucidate differences between closely related or morphologically similar taxa, and notes are provided for all taxa reported from the area. Inclusion of other extralimital taxa was required to provide a more comprehensive view of the taxonomic diversity of the Helvellaceae.

Descriptions of genera and subgenera include authority and citation, synonyms, type species, and morphological features.

Species concepts are taxonomic (rather than biological or ecological) ones and are defined on the basis of multiple correlation of features. Our species are "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1988). Characters of importance at the species level include ascocarp size, shape, colour, excipulum vestiture, stipe construction, ascospore size, shape, and ornamentation, and features of the paraphyses and asci.

Species are presented with authority and citation, basionym and synonyms, type information, illustrations (included here), morphological description (in order of apothecium, stipe, asci, paraphyses, and ascospores) based on dried material except where noted, habitat (abundance, substratum, phenology, associated plant species in order of decreasing frequency, etc.), geographic distribution, taxonomic notes, and collections examined. Full descriptions are provided only for species from the study area, while nomenclatural information, geographic distribution, taxonomic notes, and collections examined are provided for extralimital species.

Synonyms provided are not exhaustive, and are provided to help users access names from recent North American and European references (or those in current use) and names for which type or authentic material has been examined. Type material likewise is provided to allow quick access to the status and location of type specimens, with notation if examined/selected in this study. Complete type specimen details are provided in the collections examined section.

The notes section includes a discussion of the species concept, subspecific taxa and relationships to similar taxa. Collections are listed by location, collector (including number) and date (month day year) together, and herbarium accession data. Further, they are arranged by province or state, west to east from the north to the south (i.e., read each province/state on a map from the upper left corner across, then down line by line) with those from the study region first (Canada first, then USA). National and provincial parks are indicated by N.P. and P.P., respectively; counties as Co. Other collections are listed by country in approximate order from west to east and north to south. *Exsiccatae* follow.

Helvellaceae Fries, 1823, Systema Mycologicum 2: 1. (s.n. Elvellaceae).

=Rhizinaceae Bonorden, 1851, Handbuch der allgemeinen mykologie als anleitung zum studieum derselben p. 200. (s.n. Rhizinacei).

=Balsamiaceae E. Fischer, 1897, Tuberaceen und Hemiasceen, in Rabenhorst Kryptogamen-Flora von Deutschland, Österreich und der Schweiz 5: 3-81.

=Hydnotryaceae M. Lange, 1956, Dansk Botanisk Arkiv 16: 27.

=Discinaceae Benedix, 1961, Zeitschrift für Pilzkunde 27: 100.

=Pseudorhizinaceae Harmaja, 1974, Karstenia 14: 110.

Key to tribes and genera of Helvellaceae

1. Ascocarps hypogeous; asci indehis cent; ascospores thick-walled and pigmented .....**Tribe *incertae sedis*.....*Hydnotrya***
1'. Ascocarps epigeous; asci operculate; ascospores thin-walled and hyaline.....2
   2. Apothecial excipular tissue (as seen in cross section) at maturity of *textura intricata* throughout, sometimes with an indistinct evanescent ectal layer of *textura angularis* (Fig. 19).....**Tribe *Gyromitreae*** 3
   2'. Apothecial excipular tissue (as seen in cross section) distinctly stratified at all stages of development, with medullary excipulum of *textura intricata* and prominent ectal excipulum of *textura angularis* and/or *textura prismatica* (Fig. 20).....**Tribe *Helvelleae*** 5
3. Ascocarps sessile, with rhizoids extending from excipular surface; thick-walled setae present in hymenium.....***Rhizina*** .....**(*R. undulata*)**
3'. Ascocarps stipitate or sessile, excipular surface lacking rhizoids; setae absent from hymenium.....4
   4. Ascospores at maturity with cyanophilic perispore (deeply stained in Cotton Blue); flesh of fresh apothecia relatively thick (2-5 mm).....***Gyromitra***
   4'. Ascospores at maturity lacking cyanophilic perispore; flesh of fresh apothecia relatively thin (1-2mm).....***Pseudorhizina***
5. Ascospores smooth to verruculose (with SEM spore surface uniformly finely rugose to finely verrucose); apothecium at least partially free of stipe with distinct excipular surface.....***Helvella***
5'. Ascospores nodulose (with SEM spore surface smooth with large isolated rounded warts); apothecium entirely fused to stipe and lacking a distinct excipular surface.....***Underwoodia*** .....**(*U. columnaris*)**

Tribe Gyromitreae Dissing, 1966, Dansk Botanisk Arkiv 25: 28. *emend. nov.*
=Tribe Discineae Dissing, 1966, Dansk Botanik Arkiv 25: 29.

Notes: This tribe is emended to include both tribe Gyromitreae and Discineae of Dissing 1966b. Three genera are recognized: *Gyromitra* (*sensu lato*), *Pseudorhizina,* and *Rhizina.*

Gyromitra Fries, 1849, Summa Vegetabilium Scandinaviae 2: 346. (*nomen conservandum* ICBN Appendix IIIA, Greuter *et al.* 1994).
=*Gyrocephalus* Persoon, 1824, in Mémoires de la Société Linnéene (Paris) 3: 77. (*nomen rejiciendum* ICBN appendix IIIA, Greuter *et al.* 1994).
=*Discina* (Fries) Fries, 1849, Summa Vegetabilium Scandinaviae 2: 348.
=*Physomitra* Boudier, 1885, Bulletin de la Societé Mycologique de France 1: 99.
=*Neogyromitra* S. Imai, 1932, The Botanical Magazine (Tokyo) 46: 174.
=*Paradiscina* Benedix, 1969, Die Kulturpflanze 17: 274.
=*Fastigiella* Benedix, 1969, Die Kulturpflanze 17: 276.
Type Species: *Gyromitra esculenta* (Persoon) Fries, 1849, Summa Vegetabilium Scandinaviae, 2: 346.

Macroscopic Features: ascocarp epigeous, sessile, subsessile, or distinctly stipitate; apothecium cupulate, discoid, convex, bilobate, or irregularly lobed, margin inrolled or reflexed; hymenium yellow brown to red brown or dark brown, nearly smooth to undulate-rugose or highly convoluted; excipular surface nearly glabrous to pubescent, smooth, leathery when dry; stipe equal, flaring and merging with apothecium, or tapered to base, white to red brown, or with purple tints, nearly glabrous

to pubescent, often fluted, internally solid or with hollow chambers; flesh thick, 2-5 mm when fresh, brittle. **Microscopic Features:** asci cylindrical, tapered to base, hyaline, operculate, containing eight uniseriate ascospores; paraphyses clavate, enlarged gradually or abruptly at apex, brown, contents finely to coarsely granular; ascospores ellipsoidal to fusoidal, hyaline, smooth to distinctly rough with light microscope, with SEM (or oil immersion) finely to coarsely rugose, reticulate, or distinctly warted, non-apiculate to distinctly apiculate, with one, two, or three guttules, tetranucleate, de Bary bubbles absent or rarely present, cyanophilic perispore present at maturity; tissues in cross section more or less uniform *textura intricata* with no distinct separation of medullary and ectal excipulum at maturity, an evanescent ectal layer of *textura angularis* present initially.

Key to subgenera of *Gyromitra*

1. Ascospores biguttulate..... 2
1'. Ascospores uniguttulate or triguttulate..... 3
   2. Ascospore ornamentation finely rugose (appearing smooth by LM).....**subgen. *Gyromitra***
   2'. Ascospore ornamentation of isolated rounded warts...**subgen. *Melaleucoides*** .....**(*G. melaleucoides*)**
3. Ascospore ornamentation rugose or an irregular, closely spaced reticulum; distinct or indistinct solitary apiculi present, apiculi formed from inflation of perispore at spore apices ..... **subgen. *Discina***
3'. Ascospore ornamentation a regular, widely spaced reticulum; distinct multiple apiculi present, apiculi formed from extension of reticulum into spine-like projections at spore apices ..... **subgen. *Caroliniana***

Gyromitra* Subgenus *Caroliniana S.P. Abbott, *subgen. nov.*

Apothecia subsessilia vel stipitata, convexa vel irregulariter cupulata, hymenium rugosum vel convolutum; ascosporae ellipsoideae vel subfusoideae, uniguttulatae vel triguttulatae, reticulatae, utroque apice spinuloso.

Type Species: *Gyromitra caroliniana* (Bosc : Fries) Fries, 1871, Öfvers. af Kongl. Vet.-Akad. Förhandl. 2: 173.

Ascocarp: subsessile to stipitate, cupulate, discoid, convex, or irregularly lobed; hymenium orange brown to red brown, rugose. **Ascospores:** ellipsoidal to subfusoidal, uniguttulate to triguttulate, appearing distinctly rough to reticulate with light microscope, with SEM ornamentation composed of coarse complete reticulum at maturity, apices with multiple spines arising from reticulum.

Notes: The subgenus is characterized by spores covered with a coarse, regular, widely spaced reticulum, and the apical regions are ornamented with multiple blunt spines continuous with the reticulum (Fig. 39). This is in contrast to the inflated solitary apiculi of subgenus *Discina*. The spore ornamentation develops slowly as in subgenus *Discina* and nearly smooth submature spores may be discharged from the asci (Abbott pers. obs.; see also Donadini 1986a). Ascospores are often uniguttulate, but the presence of one or two smaller apical guttules is not uncommon. Ascocarp morphology and coloration is also similar to species in the subgenus *Discina*, and these features suggest taxonomic affinity between subgenera *Discina* and *Caroliniana*.

Benedix (1969) recognized that the group of 'gyromitroid' fungi with regularly reticulate and apically spined spores deserved taxonomic recognition and erected the genus *Fastigiella* to accommodate *G. caroliniana*. The illustration of *F. caroliniana* represents *G. fastigiata* as recognized in this work in agreement with the concepts of Svrcek and Moravec (1972), Harmaja (1973), and Weber (1988). Harmaja (1976b) places *Fastigiella* in synonymy with *Gyromitra sensu lato*.

None of the three species recognized in this section is known from the study area.

Extralimital Species

Gyromitra caroliniana (Bosc : Fries) Fries, 1871, Öfvers. af Kongl. Vet.-Akad. Förhandl. 2 : 173.

≡*Morchella caroliniana* Bosc : Fries, 1823, Systema Mycologicum 2: 12.

≡*Morchella caroliniana* Bosc, 1811, Gesellschaft Naturforchender Freunde Berlin. Sitzungsberichte 5: 86.

≡*Elvela caroliniana* (Bosc) Nees, 1817, Das System der Pilze und Schwämme p. 176.

(additional synonyms see McKnight 1973; Weber 1988).

Type Material: Neotype (designated McKnight 1973) BPI, examined.

Distribution: Found in southeastern North America (McKnight 1973; Weber 1988). *G. caroliniana* is reported by Larsen and Denison (1978) from BC, WA, and OR, but all specimens from UBC and WTU examined in this study are assigned to *G. gigas* here. Reports from Europe are unsubstantiated and are due to confusion with *G. fastigiata* and *G. gigas*.

Notes: The species concept of *G. caroliniana* has been the source of much confusion, but the concept accepted here is based on the neotype selected by McKnight (1973), which we believe corresponds to that of Bosc (1811) and Fries (1823, 1871).

Collections Examined: **USA: Indiana:** Greencastle, Banker (1318) 04 28 1909, NY. **Virginia:** Lorton, Bland 04 24 1942, BPI (neotype). **North Carolina:** Curtis 2247, Herb. Berkeley 1879, K.

Gyromitra fastigiata (Krombholz) Rehm, 1896, Die Pilze, in Rabenhorst, Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 2nd ed. 1: 1194.

≡*Elvela fastigiata* Krombholz, 1834, Naturgetreue Abbildungen und Breschreibungen der essbaren, schädlichen und verdachtigen Schwämme 3: 28.

≠*Gyromitra fastigiata sensu* Mcknight, 1971 (=*G. gigas*).

=*Gyromitra brunnea* Underwood, 1894, Proceedings Indiana Academy of Science 1893: 33. (lectotype and authentic material NY, examined).

≡*Elvela underwoodii* Seaver,1928, The North American Cup-Fungi (Operculates) p. 254 (*nomen novum*); non *Elvela brunnea* Linnaeus. (*fide* McKnight 1973).

(additional synonyms see Weber 1988).

Type Material: none available (*fide* McKnight 1971).

Distribution: This species is known from eastern and southern North America (McKnight 1973, as *G. brunnea*; Weber 1988) and Europe (Svrcek and Moravec 1972; Ryman 1979; Krieglsteiner 1981; Kotlaba and Pouzar 1974). *G. fastigiata* reported from AB by Larsen and Denison (1978) follows nomenclature of McKnight (1971) and is a synonym of *G. gigas* (q.v.).

Notes: The species concept has been variously interpreted (McKnight 1971; Svrcek and Moravec 1972) due to the rather imprecise original description by Krombholz (1831-1846) and the lack of extant type material. After examination of the original publication, we accept the concept outlined by Svrcek and Moravec (1972) in agreement with Harmaja (1973) and Weber (1988). A neotype from the type locality is required.

Collections Examined: **CANADA: Ontario:** Terra Nova, Van Gerwin 05 31 1981, TRTC 49016; Halton Forest near Campbellville, Thompson (JFA 8363) 05 9 1978, WTU; Rondeau P.P., Hutchison 05 9 1987, TRTC. **USA: Iowa:** Iowa City, Kennedy 04 26 1955, ALTA 668, 669, 670. **Indiana:** Greencastle, Underwood 05 1892, 1893, 1894, NY (Lectotype of *Gyromitra brunnea*); Greencastle, Banker (3832) 04 21 1911, NY; near Fern, Banker (1344) 03 4, 8 1910, NY. **Ohio:** Red Bank near Cincinnati, Lloyd 04 21 1895, NY.

Gyromitra parma (J. Breitenbach & Maas Geesteranus) Kotlaba & Pouzar, 1974, Ceská Mykologie 28: 84-95.

≡*Discina parma* J. Breitenbach & Maas Geesteranus, 1973, Proceedings. Koninklijke Nedelandse Akademie van Wetenschappen. Series C. Biological and Medical Science 76: 101-108.

Type Material: Holotype L, examined; isotype K, examined.

Fig. 39.

Distribution: *G. parma* is found only in central Europe (Breitenbach and Maas Geesteranus 1973; Breitenbach and Kränzlin 1981; Bregazzi 1978; Hocevar 1978,1982).

Notes: This species is separated from the others in the subgenus by its subsessile, irregularly cupulate, apothecia. The apical spicules are more highly developed than in others of the subgenus (Fig. 39).

Collections Examined: **SWITZERLAND:** Kanton Obwalden, near Grafenort, von Büren 05 19 1972, L (holotype), K (isotype).

Gyromitra **Subgenus** ***Discina*** (Fries) Harmaja, 1973, Karstenia 13: 56, *emend. nov.*

Type species: *Gyromitra perlata* (Fries) Harmaja, 1969, Karstenia 9: 11.

Ascocarp: sessile to stipitate, cupulate, discoid, convex, or irregularly lobed; hymenium yellow brown, orange brown, red brown, to dark brown, undulate-rugose to convoluted-wrinkled. **Ascospores:** ellipsoidal to fusoidal, uniguttulate to triguttulate, appearing distinctly roughened with light microscope, with SEM spores coarsely rugose with anastomosing ridges forming an irregular reticulum, solitary polar apiculi virtually lacking to well developed.

Notes: Fries (1823) treated *Discina* as a subgeneric taxon of *Peziza*, but later (Fries 1849) gave *Discina* generic status. Harmaja reduces *Discina* to a subgenus of *Gyromitra* and notes that the lectotype was indirectly selected by Fries (1849) by restricting *Discina* to a monotypic taxon including only *D. perlata*. The subgenus *Discina* contains subsessile to distinctly stipitate species with highly ornamented spores and solitary apiculi. These may be slight inflations of the perispore (Figs. 32, 37, 38), or well developed and knob-like (Figs. 35, 36), pointed (Figs. 31, 33), or depressed (Fig. 34). The surface ornamentation develops slowly and may be incomplete on submature but viable spores ejected from the asci as described by Donadini (1986a). At maturity the spores are prominently and irregularly rugose with anastomoses between ridges which form an irregular close reticulum (Figs. 32-35, 38). The subgenus is emended to exclude taxa with coarsely reticulate ascospores and apical spicules (subgenus *Caroliniana* here).

Key to species of *Gyromitra* subgenus *Discina*

1. Ascospore apiculi depressed (concave); fresh hymenium bright yellow brown to orange brown..... ***G. leucoxantha***
1'. Ascospore apiculi broadly rounded, knob-like, or pointed; fresh hymenium yellow brown, orange brown, red brown, or brown 2
2. Ascospore apiculi pointed; fresh hymenium red brown to dark brown..... ***G. perlata***
2'. Ascospore apiculi broadly rounded or blunt knob-like projections; fresh hymenium yellow brown to orange brown.....3
3. Ascocarps stipitate; ascospore apiculi indistinct and broadly rounded to distinct and knob-like..... ***G. gigas***
3'. Ascocarps sessile; ascospore apiculi indistinct and broadly rounded..... ***G. olympiana***

Gyromitra gigas (Krombholz) Quélet, 1873, Les Champignons du Jura et des Vosges. 2: 382.

≡*Elvela gigas* Krombholz, 1834, Naturgetreue Abbildungen und Breschreibungen der essbaren, schädlichen und verdachtigen Schwämme 3: 28.

=*Gyromitra montana* Harmaja, 1973, Karstenia 13: 56. (holotype H, examined; isotypes BPI, K, examined)

=*Discina korfii* Raitviir, 1970, Tartu riikliku ülikooli toimetised 268. Botaanika-alased tõõd 9: 371. (paratype CUP, examined).

≡*Gyromitra korfii* (Raitviir) Harmaja, 1973, Karstenia 13: 56.

Type Material: none available (*fide* McKnight 1971).

Figs. 2a, 35-38.

Apothecium: 30-65 mm diam., 20-70 mm high (up to 140 x 90 mm fresh), irregularly lobed, convex, appressed and fused to stipe, although some apothecial lobes may be free, hymenium yellow brown to orange brown fresh, medium to dark brown when dried, undulate-rugose, excipular surface cream to yellow brown, smooth or with broadly rounded ribs continuous with those of the stipe, glabrous to finely pubescent. **Stipe:** 10-75 x 15-60 mm (up to 130 x 100 mm fresh), robust, enlarged at base, white or cream to greyish brown with pink tints, pubescent, nearly smooth or typically fluted, with broadly rounded ribs, internally chambered. **Asci:** 400-450 x 13.0-24.0 µm. **Paraphyses:** 4.5-11.0 µm diam. at apex, terminal cell 35-60 µm long, clavate, enlarged gradually to abruptly at apex, brown, contents coarsely granular. **Ascospores:** 26.0-39.8 x 11.6-14.8 µm, ellipsoidal, subfusoidal, to fusoidal, hyaline, slightly to distinctly roughened, with SEM spore surface finely to coarsely rugose, ornamentation of individual ridges or anastomosing to form incomplete or complete reticulum, apiculus nearly absent to prominent, 1.0-5.8 µm long, broadly rounded thickening to distinct blunt knobs, very rarely depressed; uniguttulate to triguttulate, with one large globose to broadly ellipsoidal central guttule and 0-2 smaller globose polar guttules.

Habitat: Solitary to gregarious on litter and woody debris in coniferous or mixed woods, often near melting snow. Associated trees: *Picea glauca, Pinus contorta, Abies lasiocarpa, Abies grandis, Abies balsamea, Pseudotsuga menziesii, Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera, Betula occidentalis, Alnus* sp., and *Acer* sp. Associated shrubs: *Betula pumila* and *Salix* sp. Fruiting from April 3 in WA to July 13 in AK. June collections are most common.

Distribution: Widely distributed in boreal, montane and coastal regions from AK, NWT, BC, AB, WA, ID, OR, and WY. Reported from MT (McKnight 1971). Also in eastern North America (Weber 1988 as *G. korfii* and *G. montana*; Ginns 1975 as *Discina korfii*), Europe (Dennis 1978; Breitenbach and Kränzlin 1981), and Asia (Imai 1954, as *Neogyromitra gigas*). Map 5.

Notes: The concept and limitations of this species are unclear because of an inadequate original description lacking in microscopic data. Our concept agrees with Svrcek and Moravec (1972). Two closely related species *G. montana* (Harmaja 1973) and *Discina korfii* (Raitviir 1970) are considered conspecific. *Gyromitra korfii* was erected for North American specimens with prominently apiculate, fusoidal ascospores which are slightly narrower and shorter (29.2-37.3 x 9.7-12.0 µm, Raitviir 1970) than European specimens. Spores of *G. korfii* are more delicately reticulate and paraphyses expanded more abruptly to 13 µm diam. (Harmaja 1973). In North American material examined, paraphyses do not exceed 11 µm diam., and are no more distinctly capitate than European material. Spores by SEM vary from finely to coarsely rugose or reticulate in both North American and European material, supporting observations (Donadini 1986a) that finely ornamented spores are often ejected from submature ascocarps. The same variation in ornamentation is also observed in *G. perlata* and *G. olympiana*. The spores differ only slightly in size, and cannot be used to distinguish *G. korfii* from *G. gigas* (*sensu stricto*). The species should be considered conspecific even if subtle differences exist between European and North American material. *Gyromitra montana*,

recognized by McKnight (1971) as *G. gigas*, was later renamed by Harmaja (1973) after a reevaluation of the original concepts of *G. gigas* and *G. fastigiata*. *Gyromitra montana* has "slightly more ellipsoid, less fusoidal spores with somewhat broader ends, inconstancy of the spore apiculi, variable and often irregular shape and smaller size of the latter when discernable, slightly more delicate ornamentation of the perispore, thicker tips of the paraphyses which may even be capitate and attain a breadth of 13 µm, earlier fruiting time often near melting snow, and different distribution in the mountains of western North America and Austria in Europe" (Harmaja 1973). Paraphyses do not differ in size from *G. korfii* (Harmaja 1973), in which spore size is more similar to *G. gigas* of Europe than to *G. montana*. The more delicate perispore ornamentation is rejected because coarsely ornamented spores from collections otherwise typical of *G. montana* have been observed (Fig. 38), and because of the variability of spore ornamentation in other related species as discussed above (compare Figs. 35-38) and by Donadini (1986a). Ascospore shape and apiculation are perhaps the most diagnostic characters but the features overlap. In most collections typical of *G. montana*, including the type, some spores are subfusoidal and distinctly apiculate. In addition, some collections examined from the study area have both spore morphologies in approximately equal proportions (e.g., WTU Stz 17345). No macroscopic features have been found which distinguish these taxa. These taxa should be accepted as conspecific with a rather broad range of ascospore morphology.

Collections Examined: **CANADA: Northwest Territories:** Hay River, Green 07 1 1986, UVIC. **British Columbia:** Illicilwaet River, Glacier N.P., Abbott 06 9 1988, ALTA 8443; near Bolean Lake, Falkland, Ziller 06 8 1966, DAOM 116828; Cook Creek north of Qualicum, Vancouver Island, Lisson 05 5 1972, UVIC; Honeymoon Bay south of Cowichan Lake, Vancouver Island, Melburn 04 22 1967, DAOM 124683; Manning P.P., Flegel 06 20 1968, UBC F1327, F1330, DAOM 176039. **Alberta:** Carson-Pegasus P.P., Abbott (SA 762) 05 15 1993, SA; Poplar Creek Natural Area near Breton, Osis (SA 667) 05 24 1993, SA; Burnt Timber Creek on Forestry Trunk road, Danielson (RMD 1423) 07 10 1974, ALTA; Sheep River, Danielson (RMD 1385) 06 9 1974, ALTA; Cypress Hills P.P., Currah 05 6 1987, ALTA 8324; Cypress Hill P.P., Danielson (RMD 1944) 06 1 1976, ALTA. **Ontario:** south lookout trail, Algonquin P.P., Ammirati (JFA 8368) 05 16 1979, WTU. **USA: Alaska:** Thunderbird Falls trail north of Anchorage, Kempton 05 22 & 06 8 & 15 1961, 06 8 & 15 1966, WK 1590, 1591, 1593, 1600, 1602, 1603; Anchorage, Kempton 05 29 1960, 06 5 1961, 06 22 & 28 & 07 6 1972, 05 29 1990, WK 1597, 1592, 5798, 5799, 6740; Indian, south of Anchorage, Kempton 05 16 1960, WK 1598; south of Bird Flats, Kempton 05 22 1967, WK 1607; north of Palmer, Kempton 07 13 1971, WK 5041; Finger Lake near Palmer, Kempton 06 2 1970, 06 12 1973, WK 4391, 5265; Resurrection Pass trail, Kenai Peninsula, Kempton 06 3, 9 1973, WK 5264, 5266; Lower Russian Lake trail, Kenai Peninsula, Kempton 06 16 1973, WK 5268. **Washington:** Everett, Clark 04 1950, WSP CS25643; Lake Wenatchee State Park, (Stz 13569) 05 22 1966, WTU; Skykomish, Wells (Stz 17345) 05 11 1972, WTU; Skykomish, Koch 04 3 1947, WSP 23882; below Keechelus Lake, Brough (21) 05 5 1956, WTU; Liberty, Retnam (Stz 1885) 05 4 1946, WTU; Tacoma, Griggs 05 22 1933, WTU; Tumwater Forestry camp, (Stz 14177) 05 21 1967, WTU; Teal Spring, Umatilla National Forest, Garfield Co., Shaw 06 5 1948, WSP CS25657; Teanaway, Dilly (Stz 18286) 05 5 1974, WTU; Stampede Pass, (Stz 13180) 07 1964, WTU; White Chuck River campground, Maguire, WTU; unknown, (Stz 1211, 1215), Quinby (22F), WTU. **Idaho:** Hayden Lake area, Chariton 05 10 1989, WTU; east of Viola, Damsteegt 05 27 1959, WSP 49134; east of Viola, Shaw 05 21 1948, WSP CS17387; west end of Thatuna Ridge, Latah Co., Cooke 05 16 1947, WSP 24508; Goose Lake, New Meadows, Jeanne & Smith 07 3 1962, DAOM 191998; French Creek Summit near McCall, Miller 07 12 1964, WSP 54594; Brundage Reservoir, Miller 06 20 1964, WSP 54304. **Oregon:** Mt. Ashland near Ashland, Isaacs (Is 1777) 06 10 1962, WTU; east of MacDougall Camp, Umatilla Co., Cooke 05 16 1947, 06 17 1948, WSP 24508, 19870; south of Spout Springs, Umatilla National Forest, Blue Mountains, Union Co., Cooke 06 17 1948, WSP 19872; Horseshoe Meadows, Blue Mountains, Wallowa Co., Cooke 06 10 1949, WSP AS31819. **Wyoming**: west side of Teton Pass, Teton Co., McKnight (KHM 10351) 06 24 1967, H (holotype of *G. montana*) BPI, K (isotypes); Medicine Bow Mountains, Carbon Co., Solheim & Cronin 07 3 1950, DAOM 114944. **North Carolina:** north of Greensboro, Whetzel 05 4 1940, CUP 28997 (paratype of *G. korfii*). **SWEDEN:** Upland, Bösslinge Skog, south of Börje near Uppsala, Lundell 05 15 1945, K. **FINLAND:** Varsinais-Suomi, Lohja rural commune, Harmaja 06 6 1972, H. UNKNOWN: Wynne 03 1874, Herb. Berkeley, K.

Gyromitra leucoxantha (Bresadola) Harmaja, 1969, Karstenia 9: 11.

≡*Discina leucoxantha* Bresadola, 1882, Revue de Mycologie 4: 212.

=*Discina leucoxantha* var. *fulvescens* Rea, 1928, Transactions of the British Mycological Society 13: 254. (isotype BPI, examined).

=*Discina larryi* McKnight, 1974 The Michigan Botanist 13: 52. (holotype BPI, examined).

≡*Gyromitra larryi* (McKnight) Harmaja, 1976, Karstenia 15: 30.

=*Discina convoluta* Seaver, 1921, Mycologia 13: 70. (*fide* McKnight 1969).

Type Material: Holotype S, examined; isotype K, examined.

Fig. 34.

Apothecium: 10-35 mm diam., 5-15 mm high (up to 65 x 20 mm fresh), irregularly cupulate to reflexed, hymenium orange brown to bright orange brown fresh, when dry bright red brown, undulate-rugose, excipular surface white to pallid brown, pubescent, smooth or with few ribs at base. **Stipe:** usually distinct, often buried in substratum, 5-15 x 5-10 mm (up to 25 x 15 mm fresh), equal, flaring and merging with apothecium, white to pallid brown, pubescent, fluted, ribs broadly rounded, solid. **Asci:** 19.1-22.3 µm diam. **Paraphyses:** 6.4-9.0 µm diam. at apex, clavate, gradually enlarged to abruptly swollen at apex, brown, contents coarsely granular. **Ascospores:** 25.9-31.1 x 11.1-13.9 µm, subfusoidal to fusoidal, hyaline, distinctly roughened to reticulate, with SEM spore surface of coarse rugose wrinkles or anastomosing to form reticulum, apiculi prominent, 1.5-2.8 µm long, with depressed (concave) apiculi at maturity, submature spores with slight apical thickenings, truncate knobs, or small depressed apiculi; uniguttulate to triguttulate, with one large central globose to ellipsoidal guttule, with 0-2 smaller globose polar guttules.

Habitat: Solitary to gregarious on soil, litter, or woody debris in coniferous woods. Associated trees: *Abies lasiocarpa, Picea glauca, Pinus contorta, Pseudotsuga menziesii, Thuja plicata*, and *Populus balsamifera.* Associated shrubs include *Alnus crispa, Acer glabrum* and *Berberis repens*. Fruiting from May 10 to June 8 in BC.

Distribution: Rare in montane forests from BC and AB. This species is newly reported for AB and BC. It is known from ID and OR (Larsen and Denison 1978), and is also in eastern North America (Ginns 1974d; Weber 1988; Seaver 1921) and Europe (Breitenbach and Kränzlin 1983; Ryman 1979, Rea 1928). Map 5.

Notes: This species is easily distinguished from others in the subgenus on the basis of the unique depressed apiculus, although spores of *G. gigas* (q.v.) are rarely depressed. Spore ornamentation places the species in this subgenus along with *G. perlata* (q.v.), *G. gigas*, and *G. olympiana* (q.v.). Due to similarities in ascocarp coloration, spore ornamentation and apiculation, and the short stipe, *G. leucoxantha* may be most closely related to *G. gigas*, although the species are easily recognized and considerably isolated taxonomically. Variety *fulvescens*, described by Rea (1928) for darker orange brown specimens (rather than the typical bright yellow to yellow brown hymenium coloration originally described), has no other correlative features. Fresh specimens from southern Alberta exhibited orange brown hymenia, but since ascocarp coloration is variable in other taxa, such as *G. gigas* and *G. olympiana*, there is little support for maintaining this taxon above a form level. *Gyromitra larryi* was differentiated from *G. leucoxantha* on the basis of less pronounced spore ornamentation and small depressed apiculi (McKnight and Batra 1974). After examination of the holotype, the specimens appear to represent submature individuals of *G. leucoxantha*, and we therefore consider *G. larryi* a synonym. Most asci were immature, and most spores lacked the typical apiculus and reticulate ornamentation, but several mature spores found were typical for *G. leucoxantha*. Submature spores may be ejected from the asci before ascocarp maturity (Donadini 1986a) and could have been collected for SEM examination using the methods employed by McKnight and Batra (1974). The bright red brown dried hymenium typical of *G. leucoxantha* is also present in the type of *G. larryi*.

Collections Examined: CANADA: British Columbia: Giant Cedars, Mount Revelstoke N.P., Egger (1026) 06 8 1985, DAOM 199539; Kootenay Lake near Procter, Linton 05 10

1978, UVIC. **Alberta:** Crandell Lake, Waterton Lakes N.P., Abbott (SA 320) 05 27 1990, SA; Upper Waterton Lake trail, Waterton Lakes N.P., Abbott (SA 336) 05 28 1990, SA. **USA: Utah:** west portal of Duchesne Tunnel, Summit Co., McKnight (KHM 11777) 05 29 1970, BPI (holotype of *G. larryi*). **UNITED KINGDOM:** near Perth, Scotland, Menzies 05 12 1924, BPI (holotype of *G. leucoxantha* var. *fulvescens*). **ITALY:** Bresadola, S (holotype), K (isotype).

Gyromitra olympiana (Kanouse) Harmaja, 1973, Karstenia 13: 56.

≡*Discina olympiana* Kanouse, 1947, Mycologia 39: 648.

=*Discina olympiana* var. *diluta* McKnight, 1969, Mycologia 61: 625. (holotype BPI, examined).

=*Discina apiculatula* McKnight, 1969, Mycologia 61: 616. (holotype BPI, examined).

≡*Gyromitra apiculatula* (McKnight) Harmaja, 1973, Karstenia 13: 56.

Type Material: Holotype MICH (unavailable for loan).

Figs. 2b, 32.

Apothecium: 9-50 mm diam., 10-15 mm high (up to 54 x 25 mm fresh), deeply to shallowly cupulate to discoid or reflexed, margin inrolled initially, margin rarely splitting in age, hymenium (fresh) pale to dark yellow brown to brown or red brown in age, sometimes with olivaceous tints, dark brown when dried, smooth to undulate-rugose, excipular surface cream to pallid brown, glabrous to pubescent, leathery. **Stipe:** lacking to rudimentary, up to 4 x 4 mm (to 20 x 20 mm fresh), flaring and merging with apothecium, cream to whitish brown, smooth or slightly fluted, finely pubescent, solid. **Asci:** 16.7-26.6 µm diam. **Paraphyses:** 5.6-13.1 µm diam. at apex, terminal cell 84-218 µm long, clavate to irregularly lobed, gradually enlarged or abruptly swollen at apex, sometimes bent or branched at apex, when present branches bifurcate at apex or paraphyses with knob-like branch bud below primary apex, yellow brown, brown in mass, contents coarsely granular. **Ascospores:** (24.4) 27.2-39.8 (40.7) x (10.7) 12.0-17.6 (19.5) µm, ellipsoidal to subfusoidal or fusoidal, hyaline, finely roughened, with SEM spore surface finely to coarsely rugose, wrinkles isolated or anastomosing into incomplete reticulum, apiculi virtually absent or broadly rounded thickenings, sometimes distinct broad truncate knobs, uniguttulate or less frequently triguttulate, large globose central guttule, with 0-3 smaller globose polar guttules.

Habitat: Solitary, gregarious, or scattered on soil or duff in coniferous forests or mixed woods, frequently near melting snow. Associated trees: *Abies lasiocarpa, Pinus contorta, Picea glauca, Pseudotsuga menziesii, Populus balsamifera, Populus tremuloides*. Associated shrub: *Alnus crispa*. Fruiting from May 17 in OR to June 24 in WY.

Distribution: Infrequent in montane regions from BC, AB, WA, OR, and WY. This species is newly reported for BC and AB. Also known from eastern North America (McKnight 1969). The identity of specimens reported as *G. apiculatula* from Europe (Donadini 1986a) is not confirmed. Map 3.

Notes: Spore ornamentation and apiculation, ascocarp colour, and habitat suggest affinity with *G. gigas* (q.v.), while ascocarp morphology is more similar to *G. perlata*. McKnight (1969) relies on the presence of the unique branching paraphyses to separate this species from *G. apiculatula*. However, this varies within and among collections. Irregular or branched paraphyses are often restricted to isolated regions on an ascocarp. Also, McKnight (1969) erected var. *diluta* which he described as having unbranched paraphyses. We rarely observe apically branched paraphyses in *G. ambigua* (q.v.). Furthermore, other features that were correlated with paraphysis morphology, including size and coloration of the ascocarp (McKnight 1969), do not correlate in our investigations. The variation in ascospore size within and among collections exceeds the subtle differences noted in *G. olympiana* and *G. apiculatula* by McKnight (1969).

Collections Examined: CANADA: British Columbia: Illicilwaet River, Glacier N.P., Abbott 06 9 1988, ALTA 8442; Lightning Lakes trail, Manning P.P., Egger (2022) 06 9 1985,

DAOM 199544. **Alberta:** Watridge Lake area, Kananaskis country, Danielson (RMD 3815) 06 9 1991, ALTA; Lineham Creek area, Waterton Lakes N.P., Abbott (SA 319) 05 26 1990, SA; Rowe Lake trail, Waterton Lakes N.P., Abbott (SA 325, 326, 329, 331) 05 27 1990, SA; Bauerman Creek trail, Waterton Lakes N.P., Abbott (SA 334) 05 28 1990, SA. **USA: Washington:** Cascade Christian Camp, Ammirati (JFA 9297), WTU; Stampede Pass, Dassow (Stz 16007) 06 1 1970, WTU. **Oregon:** Hood River Co., Sieger 05 17 1986, WTU. **Wyoming**: west of Teton Pass, Teton Co., McKnight (KHM 10340) 06 24 1967, BPI (type of *G. olympiana* var. *diluta*). **Utah**: north of Aspen Grove, Utah Co., McKnight (KHM F5477) 06 5 1962, BPI (holotype of *G. apiculatula*).

Gyromitra perlata (Fries) Harmaja, 1969, Karstenia 9: 11.

≡*Peziza perlata* Fries, 1823, Systema Mycologicum 2: 43.

≡*Discina perlata* (Fries) Fries, 1849, Summa Vegetabilium Scandinaviae 2: 348.

=*Gyromitra macrospora* (Bubák) Harmaja, 1973, Karstenia 13: 56. (lectotype BPI, examined; authentic material BPI, examined).

=*Gyromitra fluctuans* (Nylander) Harmaja, 1986, Karstenia 26: 42. (*fide* McKnight 1969; Harmaja 1986)(see notes).

=*Gyromitra warnei* (Peck) Harmaja, 1973, Karstenia 13: 56. (holotype NYS, examined; isotype K, examined).

?=*Gyromitra mcknightii* Harmaja, 1986, Karstenia 26: 42. (see notes).

(additional synonyms see Harmaja 1973, 1986; Weber 1988).

Type Material: unknown (*fide* McKnight 1969).

Figs. 2c, 31, 33.

Apothecium: 8-70 mm diam., 3-20 mm high (to 120 x 40 mm fresh), shallowly cupulate, discoid, or reflexed, margin inrolled initially, hymenium red brown to medium or dark brown fresh, dark brown to blackish brown when dried, nearly smooth or typically undulate-rugose, excipular surface white to cream or pale grey brown, nearly glabrous to pubescent, leathery when dried, smooth or somewhat ribbed near stipe, ribs rarely extending onto three quarters of excipular surface. **Stipe:** virtually lacking or with a thickened base to distinct, up to 45 x 25 mm (to 30 mm diam. fresh), flaring and merging with apothecium, white to cream or pale red brown, nearly glabrous to pubescent, typically fluted with broadly rounded ribs, solid or with few chambers. **Asci:** 350-375 x 17.0-25.0 µm. **Paraphyses:** 5.1-10.7 µm diam. at apex, terminal cell 64-103 µm long, clavate, gradually enlarged to abruptly swollen, brown individually, dark brown in mass, contents coarsely granular. **Ascospores:** 27.6-45.6 x 11.6-16.1 µm, subfusoidal to fusoidal, hyaline, nearly smooth to distinctly roughened at maturity, with SEM spore surface coarsely rugose to reticulate, apiculi well developed, pointed, 1.7-5.4 µm long, some spores rarely non-apiculate; uniguttulate to triguttulate, large central guttule globose to broadly ellipsoidal, with one or two small globose polar guttules.

Habitat: Solitary, gregarious or subcaespitose and numerous, scattered on soil, litter, or woody debris, less frequently on rotted wood or burnt debris, under conifers or rarely in deciduous or mixed woods. Associated trees: *Picea glauca, Picea engelmannii, Pinus contorta, Abies lasiocarpa, Abies balsamea, Pseudotsuga menziesii, Tsuga* sp., *Thuja plicata, Populus balsamifera, Populus tremuloides, Alnus* sp., and *Betula papyrifera*. Associated shrubs: *Acer glabrum, Acer circinatum, Salix* sp., *Vaccinium* sp., and *Rosa* sp. Fruiting from March 27 in coastal WA to July 10 in AB. May and June collections are typical. March and early April collections are known from southern coastal regions.

Distribution: Widely distributed in boreal, montane, and coastal forests from AK, BC, AB, SK, MB, WA, ID, OR, and WY. Also in eastern North America (Weber 1988; Seaver 1928, as *Discina ancilis*) and Europe (Breitenbach and Kränzlin 1981; Graddon 1976). Map 4.

Notes: This species constitutes *G. perlata sensu lato*. Forms deviating in apiculus size and shape, as well as slight differences in spore size, are not considered distinct at the specific level. Thus, *G. macrospora* and *G. warnei*, recognized as distinct by many

recent authors (McKnight 1969; Ginns 1974c) are considered synonyms. This agrees with the concept of Seaver (1928). Weber (1988) also raises doubts about these species because they are indistinguishable macroscopically. In addition, many collections examined in this study show considerable variation and intermediate microscopic features. *Gyromitra macrospora* is reported to differ from *G. perlata sensu stricto* in its large apiculi (3.5-5 µm long in McKnight 1971) and more fusoidal ascospores, while *G. perlata* has short apiculi (1-3 µm long in McKnight 1971) from subfusoidal spores. Many collections from the study area show apiculi 2-4 µm long and spore shape can vary (even within an individual ascocarp) from subfusoidal to fusoidal. Spore shape is also influenced by the degree of apiculation and these characters are not independent. Harmaja (1986) has recently synonymized *G. macrospora* with the older *G. fluctuans* and has described the new species *G. mcknightii* with apiculi intermediate between *G. perlata* and *G. macrospora*. We have not examined the types but they would likely be synonymous with *G. perlata sensu lato* as described here.

Collections Examined: **CANADA: British Columbia:** Revelstoke, Ziller 06 8 1950, DAOM 33248; Summit Trail, Mount Revelstoke N.P., Shoemaker 06 23 1986, DAOM 195910; south of Spillimacheen, Parmelee 05 20 1969, DAOM 128524; Kindensly Creek, Kootenay N.P., Rushton 06 16 1969, UVIC; Procter, Linton 05 7 1977, UVIC; Cowichan Lake, Vancouver Island, Ziller 05 15 1948, DAOM 26093; Ladysmith, Vancouver Island, Bandoni 04 18 1960, UBC F3220; Victoria, Vancouver Island, Hockley 04 16 1964; Bedford road woods, Vancouver Island, Melburn 04 20 1957, DAOM 56641; Saturna Island, VMS 04 7 1985, UBC F12435; Grouse Mountain, North Vancouver, UBC F3221; Lynne Valley, North Vancouver, Waugh 04 19 1952, DAOM 29520; Point Grey, Vancouver, Barr 05 11 1952, UBC F3219; Ford Lookout trail, Chilliwack, Rabas 05 16 1971, UBC F3222; Lightning Lake trail, Manning P.P., Egger (2034, 2039) 06 9 1985, DAOM 199555, 199560; Paxton Valley, Ginns 06 4 1968, DAOM 129267, K. **Alberta:** near Hondo, Kennedy 05 5 1983, ALTA 8150; Carson-Pegasus P.P., Abbott (SA 763) 05 15 1993, SA; Wagner Natural Area, Abbott (SA 747) 05 9 1993, SA; near Edmonton, Moss 05 27 1927, DAOM 2988; Devonian Botanic Garden near Devon, Abbott (SA 27) 05 1987, SA; Forest Reserve Boundary on Forestry Trunk road 40 km from Trans-Canada highway, Danielson (RMD 1420) 07 10 1974, ALTA; Marmot Creek, Kananaskis Valley, Danielson (RMD 2025) 07 5 1976, ALTA; Brown-Lowery Natural Area, Danielson (RMD 739, 758, 763, 764, 768, 2545) 06 14 & 19 1973, 06 5 1977, ALTA; Fish Creek P.P., Calgary, Danielson (RMD 27) 06 9 1972, ALTA; Glenmore Park, Calgary, Danielson (RMD 32) 06 7 1972, ALTA; Sheep River, Danielson (RMD 1380, 1382) 06 9 1974, ALTA; Blackiston Falls Trail, Waterton Lakes N.P., Abbott (SA 342, 344) 05 29 1990, SA; Upper Waterton Lake trail, Waterton Lakes N.P., Abbott (SA 337, 345) 05 28 1990, SA; Cypress Hills P.P., Danielson (RMD 1958, 1964) 06 2 & 3 1976, ALTA. **Saskatchewan:** Prince Albert N.P., Zelmer (PA 2, 469) 1994 & 1995, ALTA. **Manitoba:** Victoria Beach, Lake Winnipeg, Bisby 06 2 & 13 1928, DAOM 156564, 156990, 206827, 206828; Grand Marais, 05 29 1969, CFB WINFM 11342, 11381, 11382c; Lac du Bonnet, Bisby 06 6 1935, DAOM 206826. **USA: Alaska:** Anchorage, Kempton 06 5 1959, 06 20 1973, WK 1121, 5273; Beaver Lake near Palmer, Kempton 06 15 1967, WK 1135; butte area on old Palmer highway, Kempton 06 29 1961, 06 18 1962, 06 22 1967, WK 1126, 1127, 1136; Glacier campground, Matanuska valley, Kempton 06 15 1971, WK 4872. **Washington:** Glacier, Paden (JWP 696, 698) 05 5 1969, UVIC; Friday Harbor, San Juan Island, Brough (Is 62) 04 21 1967, WTU; San Juan Campground, Garland Spr. area, (Stz 14189) 05 27 1967, WTU; Twisp, Benedict (Stz 17341) 05 21 1972, WTU; Lake Wenatchee State Park, NC (Stz 6236) 05 27 1951, WTU; east of Skykomish, Cohen (Stz 6710), WTU; near Greenacres, Deuton (Stz 21647) 04 27 1982, WTU; Seattle, Ammirati (JFA 9897) 03 27 1989, WTU; Seattle, Stuntz 05 1980, WTU; Seattle, Zeller (245), WTU; Seattle, CRS 03 1916, WTU; Watermain Woods, Richmond, (Stz 18237) 04 28 1974, WTU; between Snoqualmie Pass and Keechelus Lake, Isaacs (Is 1678) 05 12 1962, WTU; near Keechelus Lake, Stuntz (Is 1733b), WTU; Kachess Lake, Isaacs (Is 1669) 05 6 1962, WTU; Cle Elum, Snyder (95) 05, WTU; Olympia, Snyder (95) 03, WTU; south of Olympia, McKenny (Stz 13488) 03 1966, WTU; Tumwater Forestry Camp, (Stz 6215) 04 30 1951, WTU; between Burnett and Wilkeson, Isaacs (Is 1659) 05 7 1962, WTU; Ewartsville, Duran 05 1 1983, WSP 67338; Lee Forest near Maltby, Cohen (Stz 6699) 05 3 1952, WTU; Lee Forest near Maltby, Stuntz (Is 1653) 04 29 1962, WTU; Lee Forest near Maltby, Brough (20) 04 25 1956, WTU; Indian Creek, upper Teanaway, Stuntz (Stz 6223) 05 13 1951, WTU; divide between West and Middle Fork, Teanaway River, van de Bogart 05 10 1980, WTU; lower Jack Creek, Teanaway, van de Bogart 05 10 1980, WTU; Teanaway, Dilly 04 30 1978, WTU; Teanaway, (Stz 16650) 06 20 1971, WTU; Fish Lake, 04 19 1981, WTU; West Mountain road, Ammirati (JFA 9270) 06 12 1986, WTU; Novelty Hill road, White (Stz 20313) 04 7 1978, WTU; unknown, Volz (Stz 14751) 06 1968, Puget Sound Mycological Society (Stz 15447) 05 11 1969, (Stz 17875) 05 1973, WTU. **Idaho:** Sagle, van de Bogart (FVB 3523) 06 1975,

WTU; Thatuna Ridge, Latah Co., Hisil 04 29 1964, WSP 56317; Thatuna Ridge, Latah Co., Paden 05 4 1964, WSP 56311. **Oregon:** Crater Lake N.P., Cooke 06 28 1972, MU F26575. **Wyoming:** Teton Co., Mcknight (10273) 06 12 1967, DAOM 146504. **New York:** Oneida, Warne 1874, NYS (holotype of *G. warnei*), K (isotype). **CZECHOSLOVAKIA:** Bohemia, Tábor, Búbak 04 29 1904, BPI (lectotype of *G. macrospora*); Bohemia, Tábor, Búbak 04 23 1905, BPI. **Exsiccata**: Solheim, Mycoflora Saximontanensis Exsiccata, 1539, Medicine Bow National Forest, WY, USA, Solheim 06 25 1970, s.n. *Discina ancilis*.

Gyromitra Subgenus *Gyromitra*

Type species: *Gyromitra esculenta* (Persoon) Fries, 1849, Summa Vegetabilium Scandinaviae 2: 346.

Ascocarp: distinctly stipitate; apothecium irregularly convex, irregularly lobed; hymenium orange brown to dark red brown, undulate-rugose to highly convoluted; excipular surface felty pubescent to nearly glabrous. **Ascospores:** narrowly ellipsoidal, ellipsoidal, or subfusoidal, biguttulate, appearing smooth with LM, but finely rugose with SEM, non-apiculate or with broadly rounded, inflated apiculi.

Notes: The subgenus has biguttulate, ellipsoidal to narrowly ellipsoidal or narrowly subfusoidal ascospores. Apiculi are absent or present as rounded swellings of the perispore. Spore ornamentation is indistinct with the LM, but finely rugose by SEM (Figs. 29, 30).

Key to species of *Gyromitra* subgenus *Gyromitra*

1. Fruiting period vernal.....***G. esculenta***
1'. Fruiting period autumnal.....2
   2. Ascospores non-apiculate, narrowly ellipsoidal, 17-23 µm long.....***G. infula***
   2'. Ascospores apiculate, subfusoidal, 21-30 µm long.....***G. ambigua***

Gyromitra ambigua (P. Karsten) Harmaja, 1969, Karstenia 9: 17.

≡*Helvella ambigua* P. Karsten, 1879, Meddelanden af Societas pro Fauna et Flora Fennica 5: 53.

=*Gyromitra infula* var. *apiculatispora* Raitviir, Eesti NSV Teaduste Akadeemia Toimetised 14 (Bioloogiline Seeria 3): 322. (*fide* Harmaja 1969b).

(additional synonyms see Harmaja 1969b).

Type material: Holotype H, examined.

Figs. 1a, 21, 29.

Apothecium: 3-46 mm diam., 2-25 mm high (up to 70 mm diam. fresh), irregularly lobed, often bilobate, margin flared when young, becoming appressed to stipe, usually fused to stipe and along apothecium, hymenium (fresh) red brown to dark red brown, often with violet tints, dark red brown to blackish red brown when dry, undulate-rugose or rarely smooth, excipular surface white to cream or light red brown, pubescent. **Stipe:** 3-58 x 1.5-21 mm, equal, enlarged gradually to base, or enlarged slightly at base and apex, pale pinkish cream or purple brown often with strong violaceous tints, pubescent, terete or fluted at base, solid, rarely hollow at base. **Asci:** 220-394 x 13.9-18.6 µm. **Paraphyses:** 5.4-8.8 (10) µm diam. at apex, clavate, gradually enlarged or abruptly swollen, yellow brown to red brown, dark red brown in mass, contents granular, apical cell 43-66 µm long. **Ascospores:** 21.4-30.0 x 7.7-11.2 µm, typically subfusoidal, sometimes ellipsoidal and fusoidal spores also present, smooth, finely rugose with SEM, biguttulate, very rarely with 1 or 3 guttules, distinctly or indistinctly apiculate, apiculi 1-2 µm long, broadly rounded.

Habitat: Solitary, gregarious, or scattered in soil or duff or on rotted wood under conifers. Associated trees: *Picea glauca, Pinus contorta, Pinus banksiana, Thuja plicata,*

and *Abies lasiocarpa*. Associated shrubs: *Alnus crispa, Arctostaphylos uva-ursi, Viburnum edule*, and *Vaccinium myrtilloides*. Fruiting from July 23 in AK to February 7 in BC. November through February collections are known only from southern coastal regions.

Distribution: Widely distributed in boreal, montane and coastal forests from AK, YT, BC, AB, SK, MB, and WA. Reported from MT (Raitviir 1965, as *G. infula* v. *apiculatispora*). This species is newly reported for SK and MB. Also distributed in eastern North America (Huhtinen 1982; Weber 1988), Europe (Harmaja 1969b, 1976c) and Asia (Raitviir 1965, as *G. infula* v. *apiculatispora*). Map 3.

Notes: *Gyromitra ambigua* is closely related to *G. infula* (q.v.), the only other autumnal species in North America. The two share similar habitat and geographic regions. Macroscopically they are difficult to separate, although *G. ambigua* tends to be darker red brown with stronger violaceous tints, and is typically smaller. Although some authors suggest that fresh specimens of the two species cannot be distinguished macroscopically (e.g., Kempton and Wells 1973), the senior author is able to identify most collections of *G. ambigua* in the field. Spore size and apiculation are the most important and reliable differentiating features. Although spore size and degree of apiculation vary somewhat in other taxa, such as *G. esculenta* (q.v.), they are consistent and distinct in *G. ambigua* and *G. infula*.

Collections Examined: CANADA: Yukon: Watson Lake, Ziller 07 30 1962, DAOM 92258; Watson Lake, Abbott (SA 191, 198, 199) 08 19 & 20 1989, SA; Murphy Creek, Ginns, DAOM) Vancouver, Waugh 08 30 1956, DAOM 57615; Vancouver, Melburn 02 7 1957, DAOM 54645. **Alberta:** 145 km north of Fort McMurray, Danielson (RMD 1726) 09 1 1975, ALTA; Riley Lake, Jasper N.P., Abbott (SA 1055) 09 7 1995, SA; Strachan, southwest of Rocky Mountain House, Nordin 08 21 1956, CFB 3168; Lake Minnewanka, Banff N.P., Funk 10 2 1961, DAOM 92260. **Saskatchewan:** Prince Albert N.P., Zelmer (PA 554, 616) 08 9 1995, ALTA. **Manitoba:** Clear Lake, Bisby 09 23 1933, DAOM 206808. **Québec**: Chibougamau, Ammirati (JFA 7652), WTU; Dufesne River, Ammirati (JFA 7742) 04 3 1978, WTU. **USA: Alaska:** near Fairbanks, Kempton 08 23 1966, WK 859; WK 4778; Talkeetna junction, Kempton 08 15 1970, WK 4724, 4725, 4726, 4727; near Copper Centre, Kempton, WK 4886; near Palmer, Kempton 07 23 1970, WK 4536; Anchorage, Kempton 08 30 1967, 09 28 1971, WK 869, 5673; Hope road, Kempton 07 27 1968, WK 875, 878; Turnagain Pass, Kempton 09 30 1971, WK 5693; Beaver Lakes, Matanuska valley, Kempton 08 20 1970, Homer, Kempton 09 2 1967, WK 870, 872; Katmai National Monument, Kempton 09 4 1971, WK 5457. **Washington:** Seattle area, van de Bogart 11 15 1975. **FINLAND:** Karsten (PAK 3289) 07 30 1866, H (holotype). **Exsiccata**: Solheim, Mycoflora Saximontanensis, 302, Colorado, USA, Shope 09 9 1937, s.n. *Helvella infula*, WSP.

Gyromitra esculenta (Persoon : Fries) Fries, 1849, Summa Vegetabilium Scandinaviae 2: 346.

≡*Helvella esculenta* Persoon : Fries, 1823, Systema Mycologicum 2: 16.

≡*Elvela esculenta* Persoon, 1800, Commentarius Fungorum Bavariae indigenorum, 64.

=*Gyromitra bubacii* Velenovsky, 1922, Ceské houby p. 893, Praha. (holotype PRC, examined).

(additional synonyms see Harmaja 1979b; Weber 1988).

Type material: unknown (*fide* Harmaja 1979b).

Figs. 19, 30.

Apothecium: 5-90 mm diam., 5-55 mm high (up to 140 x 110 mm fresh), irregularly lobed, highly convoluted, margin reflexed, fused to the stipe in several locations, rarely free when young, hymenium (fresh) medium to dark red brown, sometimes orange brown or with paler red to orange brown regions, dark red brown to blackish red brown when dry, undulate-rugose to convoluted-wrinkled, excipular surface white to pale yellow brown or pale red brown, finely pubescent. **Stipe:** 5-90 x 3-30 mm (100 x 70 mm fresh), equal, enlarged at base, or tapered to base, cream, yellow brown, or red brown, typically with strong purple tints, pubescent, slightly to

strongly fluted at base or along entire stipe, often terete when young, solid or with hollow chambers. **Asci:** 180-220 x 15-17 µm. **Paraphyses:** 2-9 (10) µm diam. apex, clavate, gradually enlarged or abruptly swollen, pale brown, brown in mass, contents granular, apical cell 39-77 µm long. **Ascospores:** (17) 19.1-28 x 10-13.1 (14) µm, ellipsoidal to subfusoidal, hyaline, spore deposit white to ochraceous, smooth, finely rugose with SEM, biguttulate, apiculus absent or apices slightly thickened to 1 µm.

Habitat: Solitary, gregarious, subcaespitose, or scattered on ground in soil, litter, or woody debris under conifers or in mixed woods. Occasionally on well rotted wood or burnt debris. Associated trees: *Picea glauca, Picea engelmannii, Picea mariana, Pinus contorta, Pinus banksiana, Pinus ponderosa, Pinus taxicola, Pinus monticola, Populus tremuloides, Populus balsamifera, Abies lasiocarpa, Abies grandis, Betula papyrifera, Pseudotsuga menziesii, Thuja plicata, Larix occidentalis, Tsuga sp., Arbutus menziesii* and *Arctostaphylos* sp. (manzanita). Associated shrubs: *Potentilla fruticosa, Shepherdia canadensis, Arctostaphylos uva-ursi, Juniperus horizontalis, Viburnum edule, Vaccinium myrtilloides*, and *Symphoricarpos* sp. Fruiting period from February 8 on Vancouver Island, BC to July 5 in ID, with the majority of collections in May and June. February through April collections are known only from southern coastal regions.

Distribution: Widely distributed throughout boreal, montane, and coastal forests from AK, YT, BC, AB, MB, WA, ID, OR, and WY. Also distributed in eastern North America (Groves and Hoare 1953; Weber 1988), Europe (Harmaja 1979b), and Asia (Imai 1954; Korf and Zhuang 1991). Map 1.

Notes: *Gyromitra esculenta* is separated from other species in the subgenus by the large convoluted apothecium and vernal fruiting pattern. The morphologically similar *G. infula* (q.v.) and *G. ambigua* (q.v.) are also separated by spore size and apiculation, ascocarp coloration, and degree of apothecial convolution.

Harmaja (1979b) recognized three distinct ascospore morphologies differing in size, shape, apiculation, and guttulation. Although these features vary considerably among collections, there seems no correlation between these features and other characteristics separating taxa. Furthermore, spore size and shape vary considerably within individual ascocarps. The holotype of *Gyromitra bubacii* represents an extreme with large ascospores, which vary in size from 21.7 to 35.3 µm long (Moravec 1986), but the guttules are smaller than described for Harmaja's (1979b) Type III which also has large ascospores. Moravec (1986) considers it a variety of *G. esculenta*. Due to the extreme variability seen in *G. esculenta* and lack of correlated characteristics, *G. bubacii* is placed in synonymy.

Collections Examined: **CANADA: Yukon:** Annie's Lake, Schalkwyk 07 4 1981, DAOM 183550, 183551, 183552. **British Columbia:** Burns Lake, Arnold 06 18 1965, DAOM 113992; Revelstoke, Macoun 05 9 1890, DAOM 44704; Mount Revelstoke N.P., Schumacker 05 23 1986, ALTA; Spuzzum Creek near Yale, Wood 05 31 1972, DAOM 143565; Procter, Linton 05 15 1978, UVIC; Lake Cowichan, Vancouver Island, Paden (JWP 1343, 1344, 1347) 05 22 1986, UVIC; Francis Park, Victoria, Vancouver Island, Egger 04 26 & 28 1985, DAOM 199519, 199526; Saltspring Island, Linton 04 20 1974, UVIC; Chilliwack River, Stirling 05 8 1982, UBC F907; Manning P.P., Egger 06 9 1985, DAOM 199550, 199552, 199559; Champion Lakes near Trail, Danielson (RMD 709) 06 3 1973, ALTA. **Alberta:** Richardson Fire Tower 150 km north of Fort McMurray, Danielson (RMD 1897) 04 27 1976, ALTA; east of Slave Lake, Hambleton & Richardson 05 22 1995, ALTA; Cross Lake, Ansley and Hichling 05 12 1977, ALTA 7488; Carson-Pegasus P.P., Abbott (SA 761) 05 15 1993, SA; Whitecourt, Stewart 06 5 1963, ALTA 685; Astotin Natural Area near Bruderheim, Abbott (SA 315) 05 13 1990, SA; Maligne Lake, Jasper N.P., 06 30 1996, SA 1160; south of Edson, Vitt 06 1 1974, ALTA 7182; near Robb, 05 23 1994, SA 938; Wabamun Lake, Seymour 05 26 1963, ALTA 684; Devonian Botanic Garden near Devon, Abbott (SA 358, 939, 1061, 1144) 06 9 1990, 05 30 1994, 05 28 1995, 05 26 1996, SA, K; Devonian Botanic Garden near Devon, Currah 05 18 1976, 06 30 1979, 05 15 1981, ALTA 7237, 7956, SA 13; near Devon, Osis and Gibson (SA 312) 05 12 1990, SA; north of Devon, Osis (SA 690) 06 13 1992, SA; North Saskatchewan River valley near Devon, Abbott (SA 645) 05 15 1992, UAMH 7350 (living culture); near Breton, Osis (SA 20, 356) 05 14 1989, 05 27 1990, SA; Poplar Creek Natural Area near Breton, Osis (SA 666) 05 24 1992, SA; Moose Hill, Poplar Creek Natural Area, van der Schoot 05 15 1994, SA 937; Strachan, southwest of Rocky Mountain House, Bourchier 05 27 1960, CFB 4040, 4041, 4044, 4045, 4046, 4047; Strachan, southwest of Rocky Mountain House, Bourchier 06 9 1961, CFB 4458; Cirque Lake, Banff N.P., Beil

06 24 1964, ALTA 671; Forestry Trunk Road, Danielson (RMD 2722) 06 18 1978, ALTA; Sheep River, Danielson (RMD 1383, 1520, 1925) 06 9 1974, 06 1 1975, 05 23 1976, ALTA; Blackiston Falls Trail, Waterton Lakes N.P., Abbott (SA 341) 05 29 1990, SA. **Manitoba:** Victoria Beach, Lake Winnipeg, Bisby 06 2 1928, 05 25 1931, DAOM 151579, 206571. **Ontario:** Lake Simcoe near Gilford, Ammirati (JFA 8367) 05 17 1979, WTU; Nancy Lake west of King, Bell 05 21 1940, TRTC 18475; Black Sturgeon Lake, Hale 06 8 1976, WTU (JFA 7360); near Carlsbad Springs, Horner 05 23 1954, K. **Québec:** Masham, Darker & Shoemaker 05 31 1963, CFB WINFM 10931, DAOM 93064. **USA: Alaska:** Willow, Burner 06 18 1971, WK 5034; Eklutna Lake north of Anchorage, Kempton 06 22 1966, WK 1059; Bird Creek, Chugach National Forest, Cooke 06 21 1970, WSP 61117; Anchorage, Kempton 06 10 1971, WK 4866; Beaver Lakes, Matanuska valley, Kempton 05 28 1988 & 1989, WK 6551, 6616; Trail River near Seward, Kempton 06 19 & 21 & 29 1971, WK 5021, 5022, 5023; Russian River, Kenai Peninsula, Kempton 07 4 1971, WK 5040. **Washington:** Birch Bay near Blaine, Isaacs (Is 1588) 05 2 1962, WTU; Glacier, Paden (JWP 699, 700) 05 5 1969, UVIC; Colville, Conner 06 1 1948, WSP CS17389; Ford, Smith 05 2 1928, WSP 32173; Pend Oreille Co., Slipp 06 17 1942, WSP 49791; Mutiny Bay, Island Co., van de Bogart (FVB 3354) 03 2 1975, WTU; Seattle, Fitzpatrick (Stz 6652) 04 9 1952, WTU; Seattle, Parker (YNS 49) 03 24 1892, WTU; Watermain Woods, Redmond, van de Bogart (FVB 3599, 3404) 04 25 & 26 1975, WTU; east of Skykomish, Cohen (Stz 6711) 05 19 1952, WTU; east of Stevens Pass, Brough (70) 05 25 1957, WTU; below Goose Creek along Chiwawa River, Ammirati (JFA 9394) 05 23 1987, WTU; Big Tree Park, Snoqualmie Pass, Snyder (100) 04 15 1934, WTU; Kachess Lake turnoff near Snoqualmie Pass, Isaacs (Is 1679) 05 12 1962, WTU; American River, Beeman (Stz 1219) 05 31 1942, WTU; Clearwater R.S., Garfield Co., Goheen 06 4 1948, WSP CS25651; Amboy, Smith 04 5 1954, WSP 41138; Bingen, Suksdorf 04 7 1901, WSP 27278; Lee Forest near Maltby, Cohen (Stz 6687, 6704) 05 3 & 11 1952, WTU; Birmingham, Zeller (265) 04 6 1914, WTU; unknown, Snyder (5), Vogel (Stz 15446) 05 10 1969, Isaacs (Is 555) 03 31 1957, (Stz 10669) 04 1958, #10 6666, 6213, WTU. **Idaho:** Priest River Experimental Forest, Slipp 06 2 1942, WSP 49881; natural area of Priest River Experimental Forest, Miller 07 5 1964, WSP 54436; east of Viola, Shaw 05 21 1948, WSP CS17376, CS17388; north of Moscow, SMD 05 30 1954, WSP 41127; Thatuna Ridge, Latah Co., Cooke 05 1948, WSP AS30089, DAOM 26787; Upper Jerome Creek, Latah Co., Tylutki 05 10 1965, WSP 56315; Payette Lake, Ammirati (JFA 9276) 06 13 1986, WTU; Payette River south of McCall, Miller 06 4 1964, WSP 54406. **Oregon:** Sauvies Island near Portland, Hinds 03 14 1987, WTU; near MacDougall Camp, Blue Mountains, Umatilla Co., Cooke 06 16 & 17 & 18 1948, WSP 19851, 19848; near Spout Springs in Umatilla National Forest, Blue Mountains, Union Co., Cooke 06 17 1948, WSP 19850; south of Gold Hill, Isaacs (Is 1387), WTU; Medford, (Is 1349) 03 22 1961, WTU; Mt. Ashland near Ashland, (Is 1776) 06 10 1962, WTU. **Wyoming**: Lower Falls on Uncle Tom's Trail, Yellowstone N.P., Brough (80) 06 29 1957, WTU. **NORWAY:** Hedmark, Ringsaker, Muremyra, Minter 06 1 1988, IMI 328178. **SWEDEN:** near Storvreta, Upland, Lundell 05 1935, K. **UNITED KINGDOM:** Colchester, Essex, Hartley 04 10 1989, IMI 332384. **BELGIUM:** Meerdaal, Heinemann 04 19 1964, K. **CZECHOSLOVAKIA:** Dobris 05 15 1921, PRC 216 (holotype of *G. bubacii*). **Exsiccata**: Vancouver Island Fungi, 254, Sidney, BC, Canada, Macoun 02 8 1915, s.n. *Helvella lacunosa*, UBC F3270; Vancouver Island Fungi, 344, Vancouver Island, BC, Canada, Macoun 02 25 1915, s.n. *Gyromitra esculenta*, UBC F3237; Cooke, Mycobiota of North America, 319, Blue Mountains, Umatilla Co., OR, USA, Cooke 06 16 1948, s.n. *Helvella infula*, WSP 23656.

Gyromitra infula (Schaeffer : Fries) Quélet, 1886, Enchiridion Fungorum p. 272.

≡*Helvella infula* Schaeffer: Fries, 1823, Systema Mycologicum 2: 17.

≡*Helvella infula* Schaeffer, 1774, Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icones 4: ind. 105.

=*Helvella friesiana* Cooke, 1875, Mycographia, seu icones fungorum 1: 195. (lectotype, selected Harmaja 1969b, K, examined).

?=*Gyromitra columbiana* Harmaja, 1986, Karstenia 26:41. (see notes)

(additional synonyms see Harmaja 1969b).

Type Material: Neotype K (designated Harmaja 1969b, =lectotype of *H. friesiana*), examined.

Fig. 1b.

Apothecium: 17-80 mm diam., 25-70 mm high (up to 130 x 95 mm fresh), saddle-shaped to irregularly lobed, often bilobate, margin typically fused to stipe and along

apothecial margin, hymenium (fresh) yellow brown to orange brown, sometimes dark red brown in age, dark brown to red brown or blackish brown when dry, typically undulate-rugose, but sometimes wrinkled-convoluted or nearly smooth, excipular surface white to pale brown, pubescent. **Stipe:** 9-90 x 5-30 mm (up to 110 x 60 mm fresh), pallid pinkish cream to greyish purple brown, equal or enlarged at base, terete or often fluted at base, pubescent. **Asci:** 250-300 x 12-17 µm. **Paraphyses:** 7-10 µm diam. apex, clavate, gradually enlarged or abruptly swollen at apex, brown, contents granular. **Ascospores:** 17-23 x (7) 8-10 (11) µm, narrowly ellipsoidal, hyaline, spore deposit white to pale cream, smooth, finely rugose with SEM, biguttulate, very rarely with 1 or 3 guttules, non-apiculate.

Habitat: Solitary, gregarious, subcaespitose, or scattered on ground or more often on rotted coniferous or deciduous wood in coniferous or mixed woods, rarely in deciduous woods. Associated trees: *Picea glauca, Picea mariana, Picea sitchensis, Picea engelmannii, Pinus contorta, Pinus banksiana, Pinus monticola, Abies balsamea, Abies grandis, Pseudotsuga menziesii, Tsuga heterophylla, Larix occidentalis, Thuja plicata, Populus balsamifera, Populus tremuloides, Acer macrophyllum, Alnus* sp., and *Betula papyrifera*. Associated shrubs: *Alnus crispa*, *Salix* sp., and *Rosa* sp. Fruiting from July 15 to February 17 in BC, with the majority of collections in August, September, and October.

Distribution: Widely distributed throughout boreal, montane and coastal forests from AK, NWT, BC, AB, SK, MB, WA, ID, MT, and WY. Also reported from OR (Larsen and Denison 1978), eastern North America (Groves and Hoare 1953; Weber 1988), South America (Dennis 1970), Europe (Harmaja 1969b), and Asia (Korf and Zhuang 1991). Map 2.

Notes: Relatively small spore size, narrowly ellipsoidal shape, and lack of distinct apiculation are characteristic for *G. infula*. This species is closest to *G. ambigua* (q.v.). Some early authors (e.g., Seaver 1928) united *G. infula* with *G. esculenta* (q.v.), but the species are easily distinguished by fruiting time, in addition to macroscopic and anatomical differences. Kanouse (1946) states that one of the features separating *G. infula* from *G. esculenta* is the consistent association of *G. infula* with deciduous trees. This is questioned, but accepted by Groves and Hoare (1953). Collections of *G. infula* in the northwest of North America are much more frequently associated with coniferous wood. *G. infula* and *G. esculenta* are both associated with coniferous and deciduous trees and are widely distributed, often at the same localities. The two species are best distinguished by fruiting time, ascocarp coloration and structure, and ascospore morphology.

Harmaja (1986) described *G. columbiana* from British Columbia, and separated it from *G. infula* based on the densely folded hymenium and large clavate paraphyses, and from *G. esculenta* based primarily on smaller ascospores. He also notes that it was not possible to determine vernal versus autumnal fruiting pattern. Although we have not examined the type, the description seems consistent with *G. infula*. Several collections were examined with highly convoluted apothecia which were otherwise typical of *G. infula*, and our observations of paraphyses are not substantially different from those described for *G. columbiana*. Rahm (1970) describes *G. infula* forma *gyrosa* Benedix, which is highly convoluted and similar in habit to *G. esculenta*. Also, given our familiarity with the Shuswap region of British Columbia, we suggest that the collection made on July 30 represents an autumnal fruiting pattern, even given the elevation of 1500 metres.

Collections Examined: **CANADA: Northwest Territories:** Pine Point, Dube 09 1983, DAOM 188769. **British Columbia:** Muncho Lake P.P., Abbott (SA 208) 08 21 1989, SA; Procter, Linton 09 19 1978, UVIC; Cathedral Grove near Port Alberni, Vancouver Island, Smyth 10 10 1977, UVIC; Sidney, Vancouver Island, 12 16 1913, DAOM 44705; Victoria, Vancouver Island, Newcombe, K; James Island near Central Saanich, Simmonds 02 17 1977, UVIC; University of BC campus, Vancouver, Kroeger 10 29 1986, UBC F12833; Vancouver, Waugh 07 15 1951, 10 16 1960, DAOM 26944, 71910; Similkameen River, Manning P.P., Bandoni 07 16 1959, UBC F3271; near Yahk, 10 7 1993, SA 991. **Alberta:** Richardson Fire Tower 150 km north of Fort McMurray, Danielson (RMD 1703) 09 1 1975, ALTA; Fawcett Lake, Abbott 09 3 1988, ALTA 8451; Carson

Lake, Currah 08 26 1977, ALTA 7538; Sandy Lake, Schalkwyk 08 16 1980, DAOM 180173; William A. Switzer P.P., Abbott (SA 272, 274, 276, 277) 08 27 1989, SA; William A. Switzer P.P., Osis (SA 395, 396) 09 2 1990, UAMH 7349 (living culture), SA; Valley of the Five Lakes, Jasper N.P., 08 18 95, SA 1089; Fryatt valley, Jasper N.P., Richardson (SA 299) 09 22 1989, SA; near Onoway, Osis (SA 879) 08 8 1993, SA; east of Spruce Grove, Abbott (SA 897) 08 22 1993, SA; Spruce Grove area, Kennedy 08 20 1980, ALTA 8060; Wagner Natural Area, Abbott (SA 1104) 08 19 1995, SA; University of Alberta Forest Reserve, Edmonton, Traquair 09 14 1970, ALTA 4140; Whitemud Creek, Edmonton, Abbott 09 13 1987, ALTA 8450; Devonian Botanic Garden near Devon, Abbott (SA 1136) 09 9 1995, K; near Breton, Abbott (SA 385) 08 9 1990, SA; Fish Lake near Nordegg, Abbott (SA 283) 08 31 1989, SA; Crimson Lake, Kennedy 08 31 1976, ALTA 7239; Forestry Trunk Road, Forest Reserve, west of Calgary, Danielson (RMD 2818) 09 3 1978, ALTA; Yamnuska near Seebe, Danielson (RMD 1774, 1777) 09 9 1975, ALTA; Brown Lowery Natural Area, Danielson (RMD 451, 499, 1086, 1088, 1089, 1187) 08 27 & 09 2 1972, 08 26 & 09 3 1973, ALTA; Fish Creek P.P., Calgary, Danielson (RMD 996, 1062) 08 9 & 21 1973, ALTA; Marmot Creek, Kananaskis, Danielson (RMD 2316) 09 2 1976, ALTA; Laggan, Hone 08 23 1903, TRTC. **Saskatchewan**: Prince Albert N.P., Zelmer (PA 352, 611, 914) 1994 & 1995, ALTA; Candle Lake, Zalasky 09 1 1955, CFB WINFM 1339. **Manitoba:** Steep Rock Lake, Lawrence 09 18 1969, CFB WINFM 12354; Victoria Beach, Lake Winnipeg, Bisby 09 12 1926, DAOM 206805, 206806; Minaki, Bisby 09 27 1925, DAOM 206807; Singush Lake, Parker 09 21 1975, DAOM 187879; Duck Mountain, Parker 08 7 1977, DAOM 165377. **Ontario:** Thunder Bay District, Lahie 08 11 1978, TRTC. **USA: Alaska:** Fairbanks, Kempton 08 7 & 8 1970, WK 4639, 4666; Talkeetna junction, Suisitna valley, Kempton 08 15 1966, 08 16 1970, 08 29 1971, WK 856, 4723, 4728, 5239; Liberty Falls Creek, Copper River valley, Kempton 09 5 1970, WK 4588; Eklutna Lake north of Anchorage, Kempton 08 24 & 09 21 1971, WK 5199, 5215, 5614; Anchorage, Kempton 08 10 & 09 9 & 26 & 28 1971, WK 7133, 5505, 5658, 5672; Girdwood, Kempton 09 23 1969, WK 4310; Kenai Lake, Kenai Peninsula, Kempton 09 6 1967, WK 866; Haines, Kempton 09 9 1967, 09 20 & 21 1970, WK 873, 4963, 4971. **Washington:** Whidbey island, Meeure (Stz 17552) 10 31 1972, WTU; Blewett Pass, Cascade Mountains, Grant 08 1929, MU F14163; near Gifford, van de Bogart (FVB 834) 10 23 1971, WTU; Hermit Mountain trail, Puget Sound, Fink 07 1906, MU F1559; Seattle, Stuntz 11 1 1934, WTU; Seattle, Zeller (54, 205) 1911 & 03 1914, WTU; Seattle, Murril 10 20 & 11 1 1911, NY; Watermain Woods, Redmond, Williams (JWL 1683) 10 13 1973, WTU; confluence of north fork of Rogue and National Creek, Douglas Co., Isaacs (Is 198) 08 27 1957, WTU; Burping Brook, Mount Spokane, Simms 10 5 1968, WSP 58171; east of McCleary, van de Bogart (FVB 669) 11 3 1970, WTU; Silver Springs area, Chinook Pass, Isaacs (Is 1272) 10 1 1960, WTU; Tahoma Creek, Mount Rainier N.P., van de Bogart (FVB 1489) 10 22 1971, WTU; Tahoma Creek, Mount Rainier N.P., Brough 11 2 1963, UBC F3239; White River near Mount Rainier N.P., Isaacs (Is 673) 10 5 1958, WTU; Iron Butte, Cispus area near Randle, van de Bogart (FVB 1420) 10 21 1972, WTU; Bingen Mountain, Klickitat Co., Dietz 11 23 1901, WSP 27475; Teanaway, Woo (Stz 16689) 07 4 1971, WTU; south of Brown's Lake, van de Bogart (FVB 988) 11 13 1971, WTU; Lake Hannah, Stuntz (Stz 19958) 09 27 1976, WTU; road 1102/1102c junction, van de Bogart (FVB 938) 10 24 1971, WTU; road 1102 rock pit site, van de Bogart (FVB 828) 10 24 1971, WTU; Min. Park road, van de Bogart (FVB 2311) 10 21 1973, WTU; Moclips road, Stuntz (Stz 16859) 10 17 1971, WTU; unknown, Stuntz (Stz 13774, 17512) 10 29 1966, 10 22 1972, Williams (JWL 67), WTU. **Idaho:** Hunt Creek Road, Bonner/Boundary Co., Slipp 10 3 1940, WSP 49762; near Benton Spring, Priest River Experimental Forest, Bonner Co., Hayes 07 3 1941, WSP 49797; Coeur d'Alene, Rust (1014) 10 1918, WTU; Bovill, Rhoads 09 29 1920, UBC F3238; Dry Creek between Troy and Deary, Cooke 05 1948, WSP 30088; west end of Thatuna Ridge, Latah Co., Cooke 11 28 1947, WSP 24509; Laird Park, Latah Co., LES 10 28 1976, WSP 63256; Fall Creek at French Creek Grade, Idaho Co., Miller 09 4, 7 1964, WSP 53882, 53834; Upper Payette Lake, Miller 08 29 1964, WSP 54573; Snowslide Lake, Valley Co., Miller 08 18 1964, WSP 54557; Sater Meadows, Valley Co., Miller 08 6 1964, WSP 54187; Teels Creek road, van de Bogart (FVB 3732) 09 9 1976, WTU; Idaho, Slipp 09 16 1944, WSP 50858. **Montana:** Red Meadow Road, Flathead Co., Young 07 24 1967, WSP 57826; Echo Lake, Flathead National Forest, Cummins 07 23 1928, MICH. **Wyoming:** Grassy Lake, Targhee National Forest, Ammirati (JFA 9420) 08 7 1987, WTU. **California:** Lassen Volcanic N.P., Cooke 10 8 1976, WSP 63394. **New York:** Lake Placid, Adirondacks, Murrill 10 3-14 1912, NY 565. **COSTA RICA**: Cuericí, Talamanaca Ridge, Gómez 09 13 1969, K. **SWEDEN:** Uppsala, Fries, Herbarium Berkeley (lectotype of *H. friesiana* and neotype of *G. infula*); Gottsunda skog near Uppsala, Lundell 10 3 1935, K. **CZECHOSLOVAKIA:** Delroi Virgin Forest, Slovakia, 09 24 1964, K. **Exsiccata**: Vancouver Island Fungi, 33, Sidney, BC, Canada, Macoun 1912, s.n. *Helvella infula*, UBC F3269; Vancouver Island Fungi, 23, Sidney, BC, Canada, Macoun 1912, s.n. *Helvella crispa*, UBC F3247.

Extralimital Species

Gyromitra sichuanensis Korf and W.Y. Zhuang, 1985, Mycotaxon 22: 490.

Type Material: Holotype and paratype HKAS; isotype and isoparatype CUP, examined.

Distribution: Known only from China (Korf and Zhuang 1985; Cao 1988).

Notes: This species is closely related to *G. infula* (q.v.), but differs in its more coarsely ornamented ascospores.

Collections Examined: **CHINA:** Wu Geng mountains, Sichuan Province, Xing-jiang 08 12 1981, CUP CH2522 (isotype); Xiangchen Co., Sichuan Province, Xing-jiang 08 12 1981, CUP CH2523 (isoparatype).

Gyromitra tasmanica (Berkeley) Berkeley & Cooke, 1878, in Cooke, Mycographia, seu icones fungorum 1: 193, t. 90, f. 331.

≡*Helvella tasmanica* Berkeley

Type Material: Holotype K, examined.

Distribution: Tasmania and New Zealand (Cooke 1878; Raitviir 1965) and reported from Europe (Torre 1976; Calonge and Torre 1977).

Notes: This species is closely related to *G. esculenta* (q.v.), but is tentatively accepted as a distinct southern hemisphere species. It differs in its smaller stature and typically free apothecial margin. European specimens were not seen. Several specimens with gross morphology similar to *G. tasmanica* were found among the collections from northwest North America, but are included in the variable species *G. esculenta.*

Collections Examined: **AUSTRALIA:** Tasmania, Archer, Herbarium Berkeley 1879, K (holotype). **NEW ZEALAND**: Ringaringa, Stewart Island, Traill 08 28 1959, K; Wellington, Travers, Herbarium Cooke 1885, K; New Zealand, Colenso, K.

Gyromitra* Subgenus *Melaleucoides S.P. Abbott, *subgen. nov.*

Apothecia sessilia vel substipitata, cupulata, hymenium griseo-brunneum; ascosporae elipsoideae, biguttulatae, nonapiculatae, verrucosae.

Type species: *Gyromitra melaleucoides* (Seaver) Pfister, 1980, Mycologia 72: 615.

Ascocarp: subsessile to stipitate, cupulate, discoid, or reflexed; hymenium dark grey brown to brown, undulate-rugose; excipular surface glabrous to finely pubescent. **Ascospores:** ellipsoidal to broadly ellipsoidal, biguttulate, appearing distinctly roughened (LM), with SEM surface ornamentation composed of distinct isolated broadly rounded warts.

Notes: This subgenus is described on the basis of ascospore ornamentation which is distinctively verrucose by LM, consisting of numerous isolated rounded warts (Fig. 40) by SEM. The warts are uniform in size and distribution. Ascospores are nonapiculate and biguttulate, and a few contain de Bary bubbles at maturity.

Gyromitra melaleucoides (Seaver) Pfister, 1980, Mycologia 72: 615.

≡*Peziza melaleucoides* Seaver, 1928, The North American Cup-Fungi (Operculates), p. 225.

=*Paxina recurvum* Snyder, 1936, Mycologia 28: 487. (paratype and authentic material NY, examined).

≡*Gyromitra recurva* (Snyder) Harmaja, 1978, Karstenia 18: 57.

Type material: Holotype NY, examined; authentic material NY, examined.

Fig. 40.

Apothecium: 9-68 mm diam., 9-50 mm high (up to 110 mm diam. fresh), irregularly discoid, cupulate, or lobed, margin typically reflexed, free from stipe, hymenium dark grey brown, brown or dark red brown when dried, smooth to undulate-rugose, excipulum cream to pale yellow brown, glabrous to finely pubescent. **Stipe:** 15-50 x 3-26 mm, distinctly flaring at apex, below equal or enlarged at base, cream to pale yellow brown, glabrous to finely pubescent, infolded/fluted, internally with hollow chambers. **Asci:** 205-235 x 11.0-14.6 µm. **Paraphyses:** 5.4-9.0 µm diam. at apex, terminal cell 53-105 µm long, clavate, enlarged gradually to apex, pale yellow brown to brown individually, brown in mass. **Ascospores:** 11.6-14.4 x 8.0-9.4 µm, ellipsoidal to broadly ellipsoidal, especially when immature, hyaline, rough, warted, ornamentation of isolated rounded warts with SEM, non-apiculate, biguttulate or infrequently uniguttulate, guttules spherical, de Bary bubbles present in a small proportion of mature spores.

Habitat: Solitary, gregarious, subcaespitose, or scattered on soil, litter, or rotted wood in coniferous or mixed forests. Associated trees: *Picea* sp., *Pinus ponderosa, Abies grandis, Tsuga* sp., and *Arbutus menziesii*. Fruiting from April 11 in BC to July 22 in ID. May and June collections are most common.

Distribution: Endemic to northwestern North America in montane sites in the coastal and Rocky Mountains from AK, BC, AB, WA, and ID. Also reported from OR and MT as *Peziza melaleucoides* and *Paxina recurvum* respectively by Larsen and Denison (1978). This species is newly reported for AK and AB. Distribution extends south of the study area to Colorado (Pfister 1980). Map 6.

Notes: This species is morphologically distinct from all others in the genus, and is placed in its own subgenus on the basis of ascospores which are the smallest in the genus and relatively broader than other species. In addition, the spores bear distinct, isolated knob-like warts. The predominantly grey ascocarp is also unique. The biguttulate, ellipsoidal spores are more similar to the subgenus *Gyromitra* than subgenera *Discina* and *Caroliniana,* but the stipe of *G. melaleucoides* is less distinct than typical for species in the subgenus *Gyromitra*. *Gyromitra melaleuca* (q.v.) is similar to this species, but appears intermediate between *G. melaleucoides* and members of subgenus *Discina* (e.g., *G. olympiana*). Pfister (1980) regarded *G. melaleucoides* as morphologically intermediate between stipitate *Gyromitra* (*sensu stricto*) species and typically cupulate species of *Discina*, and therefore accepted the genus *Gyromitra* in a broad sense to encompass both genera.

Discrepancies between the type specimens of *P. recurvum* at NY and the protologue (Snyder 1936) are discussed by Harmaja (1979b). No holotype specimen was located in WTU or other herbaria in this study.

Collections Examined: CANADA: British Columbia: Saltspring Island, Linton 04 11 & 20 & 21, 1974, UVIC; Manning P.P., Egger 06 9 1985, DAOM 199548. **Alberta:** Whirlpool River valley, Jasper N.P., Baranyay 07 5 1960, CFB 4297; Watridge Lake area of Kananaskis country, Danielson (RMD 3816) 06 9 1991, ALTA. **USA: Alaska:** Hope road, Kempton 06 25 1967, 07 5 1970, WK 1137, 4455; Turnagain Pass near Seward, Kempton 07 21 1970, WK 4512. **Washington:** Stampede Pass, Paden (JWP 535) 06 3 1967, UVIC; Watermain woods, Redmond, Bolen (SLB 492) 04 21 1978, WTU; east of Skykomish, Cohen (Stz 6715) 05 19 1952, WTU; Snoqualmie Pass area, Stuntz (Stz 13313) spring 1965, WTU; Lake Keechelus, Snyder 04 15 & 05 5 1934, NY (type of *Gyromitra recurva*); east end of Lake Keechelus, (Is 1732) 05 27 1962, WTU; west of Lake Easton, Stuntz (Stz 1230) 06 21 1942, WTU; Cle Elum, (Stz 12348) 05 21 1961, WTU; Cle Elum, (Stz 20342) 05 13 1978, WTU; Iron Butte Road, van de Bogart (FVB 2875) 07 13 1974, WTU; Road West Mt., Ammirati (JFA 9271) 06 12 1986, WTU. **Idaho:** Priest River Experimental Forest, Miller 07 4 1964, WSP 54399; Snick's Bog, Paden (JWP 72) 06 6 1964, WSP 56310; North-South Ski Bowl, Benewah Co., Miller 06 1 1964, WSP 56300; Brundage Mountain, Paden (JWP 214) & Tylutki 07 22 1964, WSP 56295. **Colorado:** Tolland, Overholts (1792) 06 19 1914, NY (holotype); Giants Ladder, Tolland, Overholts (1809) 06 21 1914, NY; Jennie Creek, Tolland, Overholts (1874) 07 7 1914, NY.

Extralimital Species

Gyromitra melaleuca (Bresadola) Donadini, 1975, Bulletin de la Société Linnéenne de Provence 28: 74.

≡*Discina melaleuca* Bresadola, 1898, Fungi Tridentini novi, vel nondum delineati 2: 74.

≡*Peziza melaleuca* (Bresadola) Seaver, 1928, The North American Cup-Fungi (Operculates), p. 225.

Type Material: Holotype S.

Distribution: Known only from Europe (Donadini 1975, 1986; Benedix 1969; Ryman 1979). The North American reports by Seaver (1928, 1942) from Colorado and Washington are unconfirmed and may represent *G. melaleucoides*.

Notes: This species is tentatively placed in the subgenus *Melaleucoides* on the basis of morphological similarity and non-apiculate ascospores. Spores are often biguttulate, although the guttules are often different sizes and asymmetrical in the spore. Spores are warted to coarsely rugose, although material examined was of poor quality. Ascospores of *G. melaleuca* are larger than *G. melaleucoides* (q.v.). *Gyromitra melaleuca* may represent a taxonomic link between subgenera *Melaleucoides* and *Discina*.

Collections Examined: **FRANCE:** Sus le Croix Haute, Haute Alps, Allemant 05 20 1967, K; Colmars Basses Alpes, Riousset 05 25 1969, K. **GERMANY:** Neustadt, Weinstr., Thate 02-03 1975, K.

Pseudorhizina Jacevskij, 1913, Opredelitel gribov 1: 1913.

=*Helvellella* S. Imai, 1932, The Botanical Magazine (Tokyo) 46: 174.

=*Ochromitra* Velenovsky, 1934, Monographia Discomycetum Bohemiae p. 391.

=*Gyromitrodes* Vassilkov, 1942, Sovetskaya Botanika 6: 50.

Type Species: *Pseudorhizina sphaerospora* (Peck) Pouzar, 1961, Ceská Mykologie 15: 42.

Macroscopic Features: ascocarps epigeous, distinctly stipitate; apothecia irregularly convex, saddle-shaped, or irregularly lobed, margin reflexed; hymenium medium brown or grey brown to blackish brown; stipe deeply ribbed with ribs extending onto excipular surface, cream, often with vinaceous tints at base; flesh thin (1-2 mm), pliant to brittle. **Microscopic Features:** asci cylindrical, tapered to base, hyaline; paraphyses clavate; ascospores globose to ellipsoidal, appearing smooth with light microscope, with SEM very finely rugose to nearly smooth, non-apiculate, with one or two oil guttules, de Bary bubbles present at maturity, tetranucleate, cyanophilic perispore-periplasm complex absent at maturity, excipulum of *textura intricata* throughout, hyphae of excipulum thick-walled (0.7-2.0 µm diam., Harmaja 1974b).

Key to species of *Pseudorhizina*

1. Ascospores globose.....***P. sphaerospora***
1'. Ascospores ellipsoidal.....***P. californica***

Pseudorhizina californica (W. Phillips) Harmaja, 1973, Karstenia 13: 56.

≡*Helvella californica* W. Phillips, 1880, Transactions of the Linnean Society II Botany 1: 423.

≡*Gyromitra californica* (W. Phillips) Raitviir, 1965, Eesti NSV Teaduste Akadeemia Toimetised 14 (Bioloogiline Seeria 3): 320.

=*Elvela umbracauliformis* Seaver, 1928, The North American Cup-Fungi (operculates) p. 251. (*fide* Seaver 1942).

Type Material: Holotype K, examined.

Fig. 13.

Apothecium: 23-135 mm diam., 13-80 mm high, irregularly convex to lobed, margin reflexed, free from stipe, hymenium medium to dark brown (fresh and dried), nearly smooth to undulate rugose, excipular surface cream to pale yellow brown, pubescent, strongly ribbed, ribs sharp-edged, often reaching marginal region, continuous with those of the stipe. **Stipe:** 25-80 x 8-60 mm, tapering to base, flaring and merging with apothecium at apex, pale yellow brown, often with wine red tints near base, pubescent, deeply ribbed, ribs sharp-edged, widely spaced, internally sulcate and solid or with few chambers. **Asci:** 160-200 x 10-12 µm. **Paraphyses:** 6-8 µm diam. at apex, clavate, brown in mass. **Ascospores:** (14) 16.1-20.3 x (7.5) 8.4-10.7 µm, ellipsoidal, hyaline, smooth, with SEM very finely rugose, non-apiculate, biguttulate.

Habitat: Solitary to gregarious on soil, duff, or woody debris, rarely on rotted logs, in coniferous woods. Associated trees: *Tsuga heterophylla, Thuja plicata, Pseudotsuga menziesii, Picea engelmannii,* and *Pinus* sp. Fruiting from April 24 in BC to August 6 in ID and interior BC, June and July collections are common.

Distribution: Common west of the continental divide in montane and coastal forests from BC, WA, ID, and OR. Known distribution is extended north to the Queen Charlotte Islands, BC. This species is endemic to western North America, reported from MT (Raitviir 1965) and extending south to northern California, Colorado, and Nevada (Larsen and Denison 1978). Map 8.

Notes: This species is closely related to *P. sphaerospora*. The ellipsoidal, biguttulate, non-apiculate ascospores are similar to *Gyromitra* species in the subgenera *Gyromitra* and *Melaleucoides*. The finely rugose spore surface by SEM is also similar to species in *Gyromitra* subgenus *Gyromitra,* but is even less pronounced in *Pseudorhizina californica*. The holotype (K) matches the above description in all details.

Collections Examined: CANADA: British Columbia: near Masset, Graham Island, Queen Charlotte Islands, Egger (167) 06 9 1979, DAOM 172567; Mosquito Lake, Moresby Island, Queen Charlotte Islands, Ziller 07 2 1952, DAOM 56711; Mount Robson P.P., Wilson 07 29 1971, ALTA 4553; trail to Great Glacier, Glacier N.P., Shoemaker 08 1 1963, DAOM 109931; Mount Abbott near Marian Lake, Glacier N.P., Shoemaker 08 6 1963, DAOM 109223; Cussom Creek, Arrow Park, Ziller 07 8 1958, DAOM 62736; Meager Creek Hotsprings, Kroeger 06 14 1987, UBC F12874; Mount Seymour, North Vancouver, Waugh 05 27 1961, UBC F3242; Confederation Park, Vancouver, Waugh 06 5 1952, DAOM 29531; west of Sooke, Vancouver Island, Ziller 06 15 1971, DAOM 134985; near Sooke, Vancouver Island, Egger 07 10 1982, DAOM 199830; Hastings, Macoun 04 24 1889, DAOM 44702; BC, Burda 07 9 1983, UBC F11957. **USA: Washington:** Big Fir area near Nooksack, Mount Baker National Forest, Isaacs (Is 1790) 07 13 1962, WTU; Upper Baker trail, North Cascades N.P., Williams (JWL 199) 06 29 1969, WTU; Boulder Creek near Baker Lake, Leuthy (Brough 82) 06 21 1957, WTU; North Fork Quinault River, Olympic N.P., Stuntz (Stz 6725), WTU; above Jackson Guard Station, Olympic N.P., A.H. Smith (13378) 05 13 1939, K; Hoh River, Olympic National Forest, A.H. Smith (13172) 05 7 1937, DAOM 24717, K; Hoh River, Olympic National Forest, Kveruvik (Stz 20928) 05 18 1980, WTU; Mount Rainier N.P., Imshaug (488) 07 21 1948, K; Carbon River, Mount Rainier N.P., Cohen (Stz 6824) 07 7 1952, WTU; Round Pass, Mount Rainier N.P., Knowles (Stz 3900) 08 9 1948, WTU; Mount Adams area, Rafauelli (Stz 18846) 07 12 1975, WTU; Tucannon River, Garfield Co., Shaw 07 10 1948, WSP CS25652; White Horse, Snyder (15) 05 15 1932, WTU; Meadowdale, Snyder 05 10 1934, WTU; Muck Creek area, van de Bogart (FVB 1920) 07 16 1973, WTU; Washington, van de Bogart (FVB 1926) 06 25 1973, WTU; unknown, PSMS (Stz 17982, 18407, 21387) 08 1973, 1974, 06 8 1981, Mackintosh (Stz 17874) 05 1973, Leuthy (Stz 20585) 06 1979, (Stz 14513, 14830, 20622) 07 1968, 07 1979, WTU. **Idaho:** Canyon Creek, Priest River Experimental Forest, Bonner Co., Slipp 07 6 1941, WSP 49805; Boulder Creek, Priest River Experimental Forest,

Harrison 08 10 1964, DAOM 107197; Gold Creek north of Nordman, Miller 07 4 1964, WSP 54388; Binarch Creek, Bonner Co., Miller 07 8 1964, WSP 54345; Granite Creek, Bonner Co., Slipp 07 4 1939, 07 1 1942, WSP 49763, 49872; Station 1, Bonner Co., Slipp 1942, WSP 49910; Kaniksu National Forest, Bonner Co., Shaw 06 17 1948, WSP CS25646; near Emida, 06 23 1955, WSP 45128; east of Elk River, Clearwater Co., Paden 06 24 1965, WSP 56263; east of Pierce, Shaw 07 9 1959, WSP 48896; north of Bear Basin, Valley Co., Miller 07 24 1964, WSP 54640; Brundage Reservoir, Valley Co., Miller 08 6 1964, WSP 54168; Sater Meadows, Valley Co., Miller 08 6 1964, WSP 54201; No Business Ridge, Valley Co., Hawker 08 1962, K; south of No Business Lookout, Valley Co., Miller 07 23 1964, WSP 54597. **Oregon:** Lake Creek, Grayback area, Siskiyou Mountains, Whittaker 07 14 1949, WSP 25463. **California:** California, Harkness, Herbarium Cooke, K (holotype); Squaw Valley Creek, Mount Shasta, Cooke 07 10 1947, WSP 20304; Lower Panther Creek Meadows, Mount Shasta, Cooke 08 24 1949, WSP 25295. **Exsiccata:** Ellis and Everhardt, North American Fungi, 2737, BC, Canada, Macoun 06 28 1892, s.n. *Helvella californica*, K; University of California, California Fungi, 315, Jonesville, California, USA, Copeland 07 1929, s.n. *Elvella californica*, WSP 35289, TRTC; University of California, California Fungi, 317, Jonesville, California, USA, Copeland 07 1929, s.n. *Elvella umbraculiformis*, WSP 35269, WTU, TRTC.

Pseudorhizina sphaerospora (Peck) Pouzar, 1961, Ceská Mykologie 15: 42.

≡*Helvella sphaerospora* Peck, 1875, Annual Report. New York State Museum 27: 106.

≡*Gyromitra sphaerospora* (Peck) Saccardo, 1889, Sylloge fungorum omnium hucusque cognitarum 8: 16.

≡*Helvellella sphaerospora* (Peck) S. Imai, 1932, The Botanical Magazine (Tokyo) 46: 174.

(additional synonyms see Eckblad 1968).

Type Material: unknown (?NYS).

Figs. 14a,b, 26b, 41.

Apothecium: 8-90 mm diam, 5-35 mm high, irregularly convex, saddle-shaped, or lobed, margin strongly reflexed at all stages, free from stipe, hymenium medium brown to dark or blackish brown fresh, dark brown to black dried, rarely slightly mottled with lighter and darker shades of brown, margin sometimes slightly paler brown, undulate-rugose, excipular surface white to cream or pale grey brown, pubescent, with narrow-edged ribs continuous from stipe extending half to almost all the way to the margin. **Stipe:** 5-60 x 4-40 mm, often enlarged at base, less frequently equal or tapered to base, flaring and merging with apothecium at apex, white to cream, often with strong wine red tints at base or less frequently extending over lower two thirds of stipe, pubescent, deeply ribbed, ribs widely spaced, sharp-edged, in cross section sulcate and solid or with few chambers. **Asci:** 100-150 x 10-16.3 µm. **Paraphyses:** 4-7.5 µm diam. at apex, narrowly clavate, expanded gradually to apex, brown in mass, contents finely granular. **Ascospores:** 8.5-10.3 µm diam., globose, hyaline, smooth, with SEM very finely rugose, uniguttulate, one de Bary bubble in most spores at maturity.

Habitat: Solitary to gregarious or scattered and numerous on very rotted deciduous (or rarely coniferous) logs or woody debris, in deciduous or mixed woods. Associated trees: *Populus balsamifera, Populus tremuloides, Acer negundo, Betula papyrifera, Picea glauca*, and *Abies balsamea*. Often associated with mosses, especially feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*). Fruiting from June 3 to July 6 in AB.

Distribution: Infrequent in boreal regions in the eastern portion of the study area from AB, SK and MB. Known distribution in North America is extended north to Wood Buffalo National Park, AB, and west to Carson Lake, AB. Reported from MT by Cummins (1930, as *Helvella sphaerospora*), but no specimen in MICH could be located. Also distributed in eastern North America (Pomerleau 1980; Weber 1988), Europe (Pouzar 1961; Huhtinen 1983; Torkelsen 1985), and Asia (Imai 1954, as *Helvellella sphaerospora*). Map 8.

Notes: Easily distinguished from other epigeous members of the family because of its small globose spores. *Pseudorhizina sphaerospora* is macroscopically similar to *P. californica* (q.v.), but can be separated by spore shape and its habit of growing on deciduous logs. *Pseudorhizina californica* is primarily terrestrial and associated with conifers. Furthermore, *P. californica* is restricted to areas west of the continental divide in the Rocky Mountains. *Pseudorhizina sphaerospora* is found east of the Rocky Mountains in North America, Europe, and Asia.

Collections Examined: CANADA: Alberta: east of Garden Creek, Wood Buffalo N.P., Currah (RC 94-18) 06 9 1994, ALTA 9279; Fawcett Lake, Abbott (SA 38) 06 17 1989, SA; Cross Lake P.P., Abbott (SA 1011) 06 23 1994, SA; Shaw Lake, Abbott (SA 349, 350, 351, 352, 367) 06 4 & 23 1990, SA; Lac La Biche forest, Crites (SA 931, 932, 933) 06 3 & 6 & 23 1992, ALTA; Sir Winston Churchill P.P., Abbott (SA 1155) 06 19 1996; Carson Lake, Wong & Beliveau 07 6 1972, ALTA 7158; Whitemud Creek, Edmonton, Abbott 06 1985, ALTA 8263; Elk Island N.P., Lumley (SA 1145) 06 7 1996, K. **Saskatchewan:** Prince Albert N.P., Zelmer (PA 90) 1994, ALTA. **Manitoba:** Gorge Creek trail, Riding Mountain N.P., Hammerslay 06 30 1979, DAOM 182247; Victoria Beach, Bisby 06 22 1935, DAOM 206813, IMI 26845; Elk Island, Lake Winnipeg, Bisby 06 30 1924, DAOM 206829, 154797. **POLAND**: Biatowieza, Skirgiello 05 1957, K.

Rhizina Fries : Fries, 1823, Systema Mycologicum 2: 32.

Type Species: *Rhizina undulata* Fries, 1823, Systema Mycologicum 2: 33. (monotypic).

Macroscopic Features: ascocarp epigeous, sessile, adjacent fruiting bodies often fused; apothecium discoid or reflexed to convex; hymenium undulate-rugose, brown to red brown, margin yellow to pallid; excipulum with white to yellow rhizoids projecting to substratum; flesh relatively thick, 2-4 mm. **Microscopic Features:** asci cylindrical, tapered to base, hyaline, operculate; paraphyses clavate, hyaline, with dark encrusted pigment; thick-walled brown setae in hymenium arising from excipular tissue; ascospores narrowly fusoidal, rough, with SEM rugose, apiculate, with solitary pointed apiculi, with SEM apiculi twisted-striate (Figs. 43, 44); tetranucleate, typically biguttulate, sometimes with two smaller polar guttules in addition to two central guttules, de Bary bubbles in a small proportion of mature spores (Fig. 26), cyanophilic perispore-periplasm complex present at maturity; excipulum of *textura intricata* throughout at maturity.

Rhizina undulata Fries: Fries, 1823, Systema Mycologicum 2: 33.

≡*Rhizina undulata* Fries, 1815, Observationes Mycologicae 1: 161.

=*Rhizina inflata* (Schaeffer) P. Karsten, 1885, Acta Societatis pro Fauna et Flora Fennica 2: 112. (*fide* Eckblad 1968).

=*Rhizina zonata* Berkeley (holotype K, examined).

(additional synonyms see Eckblad 1968; Seaver 1928).

Type Material: unknown.

Figs. 22, 26a, 43, 44.

Apothecium: 14-86 mm diam. (up to 100 mm diam. fresh), discoid to convex and reflexed, margin expanded to reflexed at maturity, sometimes fused with adjacent apothecia, hymenium medium to dark red brown fresh to blackish brown when dried, undulate-rugose, typically with a distinct white to yellow or yellow brown marginal zone, excipular surface white to pallid brown, finely pubescent, with several to many white, yellow or pallid grey brown rhizoid-like projections extending to substratum and ingrown with debris, up to 30 mm long. **Stipe:** absent. **Asci:** 375-450 x 12.4-19.9 µm. **Paraphyses:** 5.4-7.9 µm diam. at apex, clavate, enlarged gradually to apex, hyaline, with brown encrusted pigment, contents finely granular. **Setae:** 6.6-8.1 µm diam. below, expanded to 8.8-10.9 µm diam. at apex, clavate, enlarged gradually to

apex, sometimes somewhat irregularly lobed, brown, thick-walled except apex thin-walled, aseptate. **Ascospores:** 30-45 x 8-15 µm, narrowly fusoidal, hyaline, biguttulate to tetraguttulate, rough, with SEM spore surface rugose, distinctly apiculate, apiculi pointed, appearing twisted with SEM.

Habitat: Solitary to gregarious or numerous and scattered on soil, duff or woody debris, typically in recently burned areas under conifers. Pathogen of conifer seedlings. Associated trees: *Pseudotsuga menziesii, Tsuga heterophylla, Picea mariana, Picea* sp., *Pinus banksiana,* and *Pinus* sp. Fruiting from March in WA to November 21 in BC.

Distribution: Widely distributed, common west of the Rocky Mountains, known from AK, NWT, BC, AB, SK, MB, WA, and ID. A detailed map of the distribution in BC is provided in Ginns (1974a). Reported from MT (Seaver 1928) and OR (Larsen and Denison 1978). Also known from eastern North America (Ginns 1974b), Europe (Breitenbach and Kränzlin 1981), and Asia (Korf and Zhuang 1991). Map 7.

Notes: This species is distinctive because of its indeterminate growth form, excipular rhizoid-like projections, hymenial setae, and ascospore morphology. It is similar to species of *Gyromitra* subgenus *Discina*, and to *G. perlata* (q.v.) in particular because of the discoid to reflexed apothecium, hymenium coloration, and fusoidal, rugose ascospores with large pointed apiculi. The setae are unusual in the family, but similar to the setoid paraphyses of *Helvella crassitunicata*. Large fruitings of this species were seen in northern Alberta in 1996 following the extensive fires of 1995 in the Mariana Lake area south of Fort McMurray.

Collections Examined: CANADA: Northwest Territories: South Rutledge Lake, Mackenzie District, Scotter 06 30 1962, DAOM 91443. **British Columbia:** Hazelton, Unger 10 21 1987, DAVFP 23589; Skidegate Lake, Queen Charlotte Islands, Foster 07 29 1943, TRTC; Cariboo Lake, near Likely, Erickson 09 24 1989, DAVFP 24045; Lois Lake, Powell River, Ginns 11 21 1967, DAOM 129015; Lynne Valley Park, North Vancouver, Kroeger 11 18 1981, UBC F10245; Lynne Canyon Park, North Vancouver, Vancouver Natural History Society 09 30 1961, UBC F3490; Stanley Park, Vancouver, Cummings 07 3 1961, UBC F3494; Stanley Park, Vancouver, Kroeger 09 16 1985, UBC F12460; Stanley Park, Vancouver, Waugh 07 28 1952, DAOM 34808; UBC endowment Lands, Vancouver, Brough, Perrin, & Koske 07 5 1969, 07 15 1970, UBC F3491, F3492; UBC endowment Lands, Vancouver, Bandoni 09 12 1969, UBC F1326; Salisbury Lake, Mission, Ginns 11 6 1967, DAOM 119359; Ucluelet, Vancouver Island, Ginns & Allen 11 9 1967, DAOM 126248; Port Renfrew, Vancouver Island, Ginns 11 15 1967, DAOM 119357; Jordan River, Vancouver Island, Ginns 11 15 1967, DAOM 129011; near Sooke, Vancouver Island, Egger 10 13 1983, DAOM 195834, 199775, 199776, 199777; near Sooke, Vancouver Island, Egger 10 26 1983, DAOM 199656, 199657, 199658; Brothers Creek trail, Hollyburn, Bandoni 10 15 1966, UBC F3493, DAOM 129748, 175778. **Alberta:** north of Mariana Lake, Abbott (SA 1208, 1210) 07 29 1996, SA; Long Lake P.P., States 06 16 1967, ALTA 652. **Saskatchewan**: 15 miles south of Buffalo Narrows, Gautreau 07 10 & 11 1970, CFB 20085, 20089, 20139; 50 miles north of Meadow Lake, Gautreau 07 13 1971, CFB 20576. **Manitoba:** Victoria Beach, Bisby 09 12 1928, DAOM 206821. **Ontario:** Algoma district, Cain 09 13 1956, TUR 73431, TRTC 32453, 34260; Chalk River, Riley 09 11 1941, TRTC 18518. **New Brunswick:** Richibucto, Cain 07 31 1963, WSP 56995, TRTC 41416. **Newfoundland:** Labrador, east of Esker, Heikkilä, Mäkinen, & Kankainen 07 20 1967, TUR 16879, 69218. **USA: Alaska:** Anchorage, Kempton 09 28 1975, WK 6290; Bird Creek south of Anchorage, Kempton 08 2 1967, WK 1528; Haines, Kempton 09 20 1972, WK 5983. **Washington:** near Longmire, Mount Rainier N.P., Snyder 09 1 1934, WTU; Barlow Pass area, Woo (Stz 16329) 10 28 1978, WTU; near Gold Basin, Builder (Stz 20494) 10 28 1970, WTU; Heart-o-Hills campground, Largent (1932) 10 23 1960, WTU; unknown, Nelson (Stz 16601) 03 1971, WTU. **Idaho:** near junction Benton Creek and Priest River, Rhoads 08 11 1920, MU 4094. **UNITED KINGDOM:** Loch Gallin, Inverness, Scotland, Reid 08 29 1975, K; unknown, Herbarium Berkeley 1879, K (holotype of *Rhizina zonata*). **NETHERLANDS:** Willemsbo, Nunspeet, Gremmen 07 22 1959, CFB 4882. **Exsiccata**: Vancouver Island Fungi, 105, Sidney, BC, Canada, Macoun 1913, s.n. *Rhizina undulata*, UBC F3495.

Tribe Helvelleae Dissing, 1966, Dansk Botanisk Arkiv 25: 28.

Helvella Linnaeus : Fries, 1823, Systema Mycologicum 2: 13.

≡*Helvella* Linnaeus, 1753, Species plantarum 2: 1180. (s.n. *Elvela*)
=*Paxina* Kuntze, 1891, Revisio generum plantarum 2: 864.
=*Acetabula* (Fries) Fuckel, 1869, Symbolae mycologicae 331.
=*Macropodia* Fuckel, 1869, Symbolae mycologicae 331.
=*Cyathipodia* Boudier, 1907, Histoire et classification des Discomycètes d'Europe 39.
=*Leptopodia* Boudier, 1885, Bulletin de la Societé de France 1: 99.
=*Wynnella* Boudier, 1885, Bulletin de la Societé de France 1: 102.
(additional synonyms see Weber 1972; Dissing 1966b).

Type Species: *Helvella crispa* Scopoli : Fries, 1823, Systema Mycologicum 2: 14.

Macroscopic Features: ascocarp epigeous, distinctly stipitate to subsessile; apothecium cupulate, auriculoid, saddle-shaped, convex, or irregularly lobed and reflexed; hymenium smooth to undulate-rugose, white to black or typically shades of grey and brown; excipular surface smooth or ribbed, villose to glabrous; stipe terete to highly fluted or ribbed, villose to glabrous, internally solid, hollow, or chambered; flesh relatively thin, 1-2 mm. **Microscopic Features:** asci cylindrical, tapered to base, hyaline, operculate, ascus base aporhynchous or pleurorhynchous; paraphyses clavate, hyaline to dark brown, contents finely granular; ascospores broadly ellipsoidal or rarely subfusoidal, hyaline, smooth with light microscope, finely rugose or rarely finely verrucose with SEM, non-apiculate, tetranucleate, uniguttulate or rarely triguttulate, de Bary bubbles absent; apothecial tissues clearly separated into medullary and ectal excipulum, medullary excipulum of *textura intricata*, ectal excipulum of *textura angularis* or *prismatica*, often with long chains of cells forming fascicled hyphal tufts on the ectal excipular surface.

Key to subgenera of *Helvella*

1. Apothecia convex to irregularly lobed 2
1'. Apothecia cupulate to auriculoid (like a rabbit's ear) 3
2. Stipe strongly ribbed, internally chambered ..... **subgen. *Helvella***
2'. Stipe terete to sparingly fluted, internally solid or hollow .... **subgen. *Elasticae***
3. Apothecium auriculoid (erect, elongate, one-sided apothecium, reminiscent of a rabbit's ear) ..... **subgen. *Silvicolae*** ..... ***(H. silvicola)***
3'. Apothecium cupulate 4
4. Stipe distinctly ribbed; stipe prominent or apothecium appearing subsessile and gathered at base; stipe typically expanded (flared) at apex ..... **subgen. *Leucomelaenae***
4'. Stipe terete to shallowly fluted; stipe discrete (elongate or short); stipe typically not enlarged noticeably at apex 5
5. Ascospores broadly ellipsoidal, uniguttulate, smooth (finely rugose by SEM) ..... **subgen. *Cupuliformae***
5'. Ascospores subfusoidal to fusoidal, typically triguttulate (rarely uniguttulate), verruculose (verrucose by SEM) ..... **subgen. *Macropodes*** ..... ***(H. macropus)***

Helvella* Subgenus *Cupuliformae S.P. Abbott *subgen. nov.*

Apothecia cyathiforme, extra pubescens vel villosum; stipes tereti, pubescenti vel villoso; ascosporae late ellipsoideae, uniguttulatae.

Type Species: *Helvella cupuliformis* Dissing & Nannfeldt, 1966, Svensk Botanisk Tidskrift 60: 326.

Ascocarp: cupulate, stipitate; hymenium medium grey brown to black, smooth; excipular surface lacking ribs, pubescent to villose; stipe terete to shallowly fluted, internally solid. **Asci**: pleurorhynchous. **Ascospores**: broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate, with large, central, broadly ellipsoidal oil guttule.

Notes: Ascospores are broadly ellipsoidal, uniguttulate, and are finely rugose with SEM. This subgenus includes small species with regularly cupulate apothecia and terete or indistinctly fluted stipes and includes some species in section *Macropodes* (*sensu lato* of Dissing 1966b) and section *Ephippium* of Häffner (1987).

Key to species of *Helvella* subgenus *Cupuliformae*

1. Ascocarp black; stipe indistinctly ribbed.....***H. corium***
1'. Ascocarp grey brown; stipe terete or shallowly fluted..... 2
   2. Stipe relatively short (length less than apothecium diameter) and stout (up to 5 mm diam.).....***H. cupuliformis***
   2'. Stipe relatively long (length equal to or greater than apothecium diameter) and slender (up to 2 mm diam.)..... 3
3. Apothecium dark brown, small (3-9 mm diam.).....***H. rivularis***
3'. Apothecium medium to dark grey brown, larger (10-25 mm diam.)...***H. chinensis***

Helvella chinensis (Velenovsky) Nannfeldt & L. Holm, 1985, in Lundell, Nannfeldt and Holm, Publications of the Herbarium University of Uppsala 18:5.

≡*Macropodia chinensis* Velenovsky, 1939, Novitates Mycologicae p. 200.

≠*Helvella sinensis* B. Liu & J.Z. Cao, 1985, in Liu, Du and Cao, Acta Mycologica Sinica 4: 214. (later homonym, *fide* Zhuang 1995).

= *Helvella dissingii* Korf, 1988, Mycotaxon 31: 381.

≡*Octospora villosa* Hedwig, 1789, Species Muscorum Frondosorum 2: 54, Table19 Figure B.

≡*Helvella villosa* (Hedwig ex Kuntze) Dissing & Nannfeldt, 1966, Svensk Botanisk Tidskrift 60: 330 (illegitimate, later homonym); non *Helvella villosa* Schaeffer, 1774, Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icones 4: 114. (*nomen dubium, ?=Thelephora hirsuta*).

=*Helvella pallidula* N.S. Weber, 1972, The Michigan Botanist 11: 171. (holotype MICH, examined).

(additional synonyms see Dissing 1966b as *H. villosa*).

Type Material: Holotype PR.

Fig. 48.

Apothecium: 10-25 mm diam., 5-10 mm high (up to 30 mm diam. fresh), shallowly cupulate to plane, sometimes laterally compressed initially, rarely reflexed-convex in age, hymenium grey to grey brown when dried, smooth, excipular surface grey brown, villose to densely pubescent. **Stipe**: 11-30 x 1-5 mm (up to 40 mm long fresh), equal or apex tapered slightly, grey brown, densely pubescent, terete and solid. **Asci**: 240-260 x 17-19 µm. **Paraphyses**: 5-7.5 µm diam. at apex, clavate, enlarged

gradually to apex, hyaline to pale brown. **Ascospores**: 16.5-20 x 10-12 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious or scattered and numerous on litter in deciduous, mixed, or coniferous woods. Associated trees: *Pseudotsuga menziesii, Picea* sp., *Arbutus menziesii, Populus balsamifera, Betula* sp., *Alnus* sp., *Arctostaphylos* sp. and *Acer* sp. Fruiting from April 9 in ID to October 26 in WA.

Distribution: Widely distributed in boreal, montane, and coastal regions from AK, AB, WA, and ID. Also in eastern North America (Weber 1972, as *H. villosa* and *H. pallidula*), Europe (Dissing 1966b; Dissing and Nannfeldt 1966, as *H. villosa*), Asia (Dissing 1966b; Cao 1988, as *H. villosa*) and Australia (Rifai 1968, as *H. villosa*). Map 18.

Notes: The species is closely related to *H. cupuliformis* (q.v.) which is distinguished by the yellow colour of dried ascocarps and short robust stipe, and *H. rivularis* (q.v.) with smaller, dark brown ascocarps. Macroscopically, it is very similar to *H. macropus* (q.v.) in subgenus *Macropodes*, resulting in some confusion and misidentification of herbarium specimens, but ascospore morphology separates them easily. Colour and habit of *H. chinensis* are similar to *H. solitaria* (q.v.), but *H. chinensis* never has prominent ribbing of the stipe and is always small. This species provides a definite link with members of the subgenus *Elasticae*, and is closely related to *H. ephippium* (q.v.) which is similar in stature and colour but has a more complex, lobed apothecium, typical of the subgenus.

Although this taxon has been referred most commonly to *H. villosa*, Korf (1988) rejected the name *H. villosa* as a later homonym and renamed the species *H. dissingii* based on the lectotype (iconotype) of *Octospora villosa* Hedwig. *H. dissingii* is a later synonym of *H. chinensis*. *Helvella pallidula* was described by Weber (1972) based on the pale ascocarp colour. No correlative features were provided in the original description and none was found in this study during examination of the holotype. Pale specimens of *H. chinensis* (reported as *H.* cf. *pallidula* by Kristiansen 1983) were also examined from Norway (RK 83.136) in the same locality as typical specimens of *H. chinensis*. Colour variants also occur in *H. lacunosa* (q.v.), *H. maculata* (q.v.), and *H. latispora* (q.v.).

Collections Examined: CANADA: Alberta: Fish Creek P.P., Calgary, Danielson (RMD 1300) 09 16 1973, ALTA 8289. **USA: Alaska**: Eklutna Lake north of Anchorage, Kempton 09 21 1971, WK 5612; Birchwood, north of Anchorage, Kempton 08 11 1969, WK 4127; butte area south of Palmer, Kempton 08 8 1960, WK 1562. **Washington**: Friday Harbor, San Juan Island, Stuntz (Stz 11771, 12360) 06 18 1960, 06 11 1961, WTU; Mount Constance, Olympic N.P., Stuntz (Stz 3614) 07 8 1948, WTU; Tenino south of Olympia, Bennedict (Is 1753) 05 30 1962, WTU; P.P.P., Leatham (Stz 15087) 10 26 1968, WTU. **Idaho**: Upper Priest River, Bonner Co., Smith (NJS 2101) 10 1 1968, MICH; Fall Creek, French Creek Grade, Idaho Co., Smith (AHS 70096) 04 9 1964, MICH. **Michigan:** Montmorency Co., Smith (NJS 397) 07 24 1967, MICH (holotype of *H. pallidula*). **Iowa**: Iowa City, Martin 06 29 1941, UBC F3318; Decorah, Holway 09 1882, NY. **Pennsylvania**: Bethlehem, Ellis 07 1883, NY. **Missouri**: Meramec Heighlands, Saint Louis, Glatfelter 06 12 1909, NYS. **NORWAY**: Østfold, Hvaler, Kirkeøy, Ørdal, Kristiansen 09 9 1988, 09 24 1989, RK 88.33, 89.94; Østfold, Hvaler, Kirkeøy, Grønvoll-Ørdal, Kristiansen 09 13 1986, RK 86.110; Østfold, Hvaler, Kirkeøy, near Brekke, Kristiansen 07 3 1983, 07 7 1985, 09 9 1988, RK 83.136, 85.07, 88.34; Østfold, Hvaler, Asmaløy, Enerstad, Kristiansen 08 31 1988, RK 88.26; Østfold, Kråkerøy, near Allerød, Kristiansen 10 4 1988, RK 88.44. **SWEDEN**: Halland, Onsala parish, Presse, Björkhamra, Karlvall (6944) 07 8 1956, K. **Exsiccata**: Ellis and Everhardt Fungi Columbiani, 1219, London, Canada, Dearness 08 1897, s.n. *Peziza subclavipes*, NY, K; Ellis North American Fungi, 985, Newfield, New Jersey, USA, 06 and 09 1882, s.n. *Peziza subclavipes*, NY (packet C).

Helvella corium (Weberbauer) Massee, 1895, British Fungus Flora 4: 463.

≡*Peziza corium* Weberbauer, 1873, Die Pilze Norddeutschlands mit besonderer Berücksichtigung Schlesiens 1: 7, Table 3 Figure 7a-d.

=*Helvella arctica* Nannfeldt, 1937, Svensk Botanisk Tidskrift 31: 60. (isotype K, examined).

(additional synonyms see Dissing 1966b).

Type Material: Holotype WRSL, examined.

Fig. 47.

Apothecium: 3-25 mm diam., 2-10 mm high (up to 40 x 12 mm fresh), deeply to shallowly cupulate, margin inrolled initially, expanding at maturity, hymenium black (fresh and dried), smooth, excipular surface black or blackish brown, often with white to greyish white marginal pubescence, densely pubescent to villose near margin, smooth or rarely with ribs extending onto basal quarter of excipular surface. **Stipe**: 2-29 x 0.5-8 mm (up to 40 mm long fresh), equal or enlarged at base, black or very dark brown, often white or pale grey at base, pubescent, terete or often slightly fluted especially at base, rarely strongly ribbed, terete or slightly sulcate and solid. **Asci**: 225-250 x 12.2-17 µm. **Paraphyses**: 4.1-8 µm diam. at apex, clavate, enlarged gradually to abruptly at apex, brown, contents finely granular. **Ascospores**: 16.1-20.6 x 9.4-13 (15) µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary or typically gregarious to numerous and scattered, often on bare soil, typically with willows in deciduous or mixed woods or tundra. Associated trees: *Populus tremuloides* and *Thuja plicata*. Associated shrubs: *Salix herbacea, Salix glauca, Salix* spp., *Shepherdia canadensis,* and *Dryas* sp. Fruiting period from May 20 in WA to September 28 in AK. June to August collections are typical.

Distribution: Widely distributed but uncommon in boreal, montane, alpine, coastal, and arctic regions from AK, YT, NWT, BC, AB, SK, MB, WA, and ID. This species is newly reported for NWT and SK. Reported from OR by Larsen and Denison (1978). Also in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987; Schumacher and Mohn Jenssen 1992), and Asia (Liu *et al.* 1985). Map 17.

Notes: This species is characterized by its cupulate apothecium, black ascocarp, densely pubescent excipulum, and terete to shallowly fluted stipe. Other black species include *H. atra* (q.v.), *H. pezizoides* (q.v.), and *H. lacunosa* (q.v.), all of which have an irregular, lobed apothecium. *Helvella arctica* was distinguished by the white marginal pubescence by Nannfeldt (1937) and Dissing (1964), but the variability of this feature was later recognized (Dissing 1966b). White marginal pubescence is not seen in all individuals and tends to be more pronounced in arctic or alpine collections. White marginal pubescence occurs in other arctic and alpine taxa including *H. verruculosa* and *H. aestivalis*. Dark specimens of *H. verruculosa* may appear similar, but can be differentiated by the strongly ribbed stipe with ribs extending onto the excipular surface. The morphological similarities among *H. corium*, *H. verruculosa,* and *H. solitaria* suggests an affinity with the subgenus *Leucomelaenae*.

Collections Examined: CANADA: Yukon: Dempster Highway near Dawson, Ginns 07 2 1982, DAOM 195465; east of Dawson, Calder & Billard 06 24 1949, DAOM 25983; near Conglomerate Mountain, Ginns 06 29 1984, DAOM 195291. **Northwest Territories**: 50 km northwest of Dickson Canyon, District of Mackenzies, UNL 07 19 1977, UVIC; Thelon River, Baker Lake, Ohenoja 08 16 1974, DAOM 155327; Coral Harbor, Southampton Island, Savile 08 16 1959, DAOM 67074. **British Columbia**: UBC endowment lands, Vancouver, Redhead 06 3 1970, UBC F3390. **Alberta**: Clifford E. Lee Natural Area, Abbott (SA 1091) 08 19 1995, SA; Devonian Botanic Garden near Devon, Currah 08 20 1985, ALTA 8267; Athabasca Glacier, Columbia Ice Fields, Jasper N.P., Abbott (SA 373) 08 2 1990, SA; near Banff, Banff N.P., Danielson (RMD 1644) 08 10 1975. **Saskatchewan**: Prince Albert N.P., Zelmer (PA 485, 489, 961) 07 12 1995, ALTA; Saskatoon, Ledingham 07 7 1934, DAOM 206816. **Manitoba**: Victoria Beach, Bisby 06 23 1928, DAOM 206815. **Ontario**: Bow Lake, Madawaska Mines, Malloch & Lahaie 06 16 1979, TRTC 48416. **Québec**: Kuujjuarapik, Great whale River, Poste-de-la-Baleine, Huhtinen 08 24 1982, TUR 78759; north of airport, Schefferville, Kankainen 07 10 1967, TUR 53425, 78760; McGill Subarctic Research Station, Schefferville, Kallio 07 19, 31 1978, TUR 78714, 78727; north end of Knob Lake, Schefferville, Kallio 07 20 1978, TUR 69168. **Newfoundland**: Labrador, between Schefferville and the

Indian village, Mäkinen 07 8 1967. **USA**: **Alaska**: Livengood road near Fairbanks, Kempton 08 18 1971, WK 5336; Birch Lake near Fairbanks, Kempton 08 22 1966, WK 1530; Fielding Lake near Paxon Lake, Kempton 09 3 1973, WK 6055; near Nome on Seward Peninsula, Kempton 08 13 1981, WK 6407; Earthquake Park, Anchorage, Kempton 08 11 1976, WK 6315; Alaska Pacific University campus, Anchorage, Kempton 08 8 & 09 28 1971, 06 28 1972, WK 5235, 5670, 5815; Caswell Creek, Susitna River valley, Kempton 06 20 1970, WK 4388; near Sterling on Kenai Peninsula, Kempton 08 13 1981, WK 6407; Katmai National Monument on Alaska Peninsula, Kempton 09 6 1971, WK 5489; Anchorage Cove, Glacier Bay National Monument, Sprague 08 9 1952, WSP AS33709; Forest Creek, Glacier Bay National Monument, Sprague 08 15 1952, WSP AS33716, AS33719. **Washington**: Naches Pass area, Laycock 05 20 1987, WTU. **Idaho**: Payette Lake, Valley Co., Smith & Bigelow (AHS 44224, 44434, 44847, 45154) 06 26 & 30, 07 10 & 18 1954, MICH. **Wisconsin**: Madison, Harper 05 27 1904, WSP 52063; Columbia National Forest, Lewis Co., 07 9 1948, WSP 19572, 28587. **SVALBARD**: Loven Glacier, Currah 08 12 1988, ALTA. **SWEDEN**: Torne Lappmark, Jukkasjärvi parish, Abisko, Nannfeldt (1523) 07 8 1928, K (isotype of *H. arctica*). **POLAND**: Georgenberg Landeck, Weberbauer 05 1870, 1871, 1873, WRSL (holotype, authentic material). **Exsiccata:** Bartholomew, Fungi Columbiani, 2329, Denver, Colorado, USA, Bethel 05 1905, s.n. *Macropodia corium*, WSP 3425.

Helvella cupuliformis Dissing & Nannfeldt, 1966, Svensk Botanisk Tidskrift 60: 326.

Type Material: Holotype UPS, examined; paratype K, examined.

Fig. 58.

Apothecium: 9-35 mm diam., 4-16 mm high, deeply cupulate initially, expanding to shallowly cupulate at maturity, margin inrolled initially, sometimes splitting in age, hymenium dark brown to grey brown when dried, smooth, excipular surface grey brown, paler than hymenium, densely pubescent to villose. **Stipe**: indistinct to prominent, 2-10 x 2-8 mm, equal, white to cream or light grey brown near apex, densely pubescent to villose (especially at apex), terete or slightly fluted, internally solid. **Asci**: 250-300 x 15-17 µm. **Paraphyses**: 4.3-6.6 µm diam. at apex, clavate, enlarged gradually to apex, pale brown to brown in mass, contents finely granular. **Ascospores**: 18.4-21.0 x 11.4-12.2 µm, broadly ellipsoidal to ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Gregarious on clay soil under *Arbutus menziesii* and *Arctostaphylos* sp. Collected only on March 24 in OR.

Distribution: Rare in the cascade range of OR. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b; Dissing and Nannfeldt 1966), and Asia (Tewari *et al.* 1971). Map 17.

Notes: This species is closely related to *H. chinensis* (q.v.) and *H. rivularis* (q.v.), but is separated by ascocarp colour, the relatively short stout stipe, and slightly longer ascospores. The collection ascribed to *H. cupuliformis* by Kempton and Wells (1970) belongs to *H. albella* (q.v.). North American collections reported here differ from European ones in being vernal. Differences in paraphysis staining in Cotton Blue between *H. cupuliformis* and *H. villosa* (=*H. chinensis*) reported by Dissing and Nannfeldt (1966) were not confirmed in this study.

Collections Examined: USA: Oregon: reservoir hill, Gold Hill, Stuntz (Stz 10939) 03 24 1959, WTU. **Texas**: Tyler, Harris 05 1892, NY. **South Carolina**: Aiken, Ravenel (922b), NY. **SWEDEN**: near Kåbo, Uppsala, Uppland, Ridelius 07 30 1936, UPS (holotype); near Skogshall, Uppsala Stadsskogen, Uppland, Eriksson & Morander 07 7 1948, K (paratype). **SWITZERLAND**: Arosa, Rahm 10 21 1963, K. **Exsiccata**: Ravenel Fungi Americani Exsiccati, 760, Aiken, South Carolina, USA, Ravenel, s.n. *Peziza* (*Sarcoscypha*) *corium*, NY; Ellis North American Fungi, 984, Aiken, South Carolina, USA, Ravenel, s.n. *Peziza corium*, NY.

Helvella rivularis Dissing & Sivertsen, 1980, Botanisk Tidsskrift 75: 101.

Type Material: Holotype TRH; isotype C, examined.

Fig. 10.

Apothecium: 3-9 mm diam., 2-5 mm high (up to 18 x 9 mm fresh), deeply cupulate to cupulate, margin inrolled initially, hymenium dark grey brown to dark brown fresh, when dry blackish brown, smooth, excipular surface dark grey brown to dark brown, when dried dark brown to blackish brown, densely pubescent to villose, vestiture often tufted. **Stipe**: 2-5 x 1-2 mm (up to 10 x 2.5 mm fresh), equal, medium grey brown to brown, when dry dark brown, pubescent, terete and internally solid. **Asci**: 13.5-15.6 µm diam. **Paraphyses**: 2.4-6.2 µm diam. at apex, clavate to nearly equal, gradually enlarged to apex, pale brown, contents finely granular. **Ascospores**: 17.0-20.1 x 10.5-12.9 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on bare soil or mossy humus in mixed woods. Associated trees: *Populus tremuloides, Populus balsamifera, Betula papyrifera,* and *Picea glauca*. Associated shrubs: *Salix discolor*. Fruiting from July 6 in AB to September 19 in the NWT.

Distribution: Rare in boreal and arctic regions from AB and NWT. This species is newly reported for North America; previously known in Europe from Scandinavia and Greenland (Dissing and Sivertsen 1980) and Asia (Cao *et al.* 1990). Map 18.

Notes: *Helvella chinensis* (q.v.) is similar, but has larger, grey apothecia, with a more elongate stipe, and has a finer vestiture on the excipulum. Häffner (1987) suggests that *H. rivularis* may be conspecific with *H. villosa* (=*H. chinensis*), but specimens examined are morphologically distinct and are tentatively retained as separate species. *Helvella macropus* (q.v.) shares the villose excipulum with tufted and fascicled hairs, but is paler in colour and has larger, subfusoidal, verrucose ascospores. The description provided here based on North American specimens matches the features of the holotype in all respects, although the holotype specimens reach 12 mm diam., and a stipe size of 9 x 2 mm.

Collections Examined: CANADA: Northwest Territories: Gull Creek, Inuvik area, Huhtinen 09 19 1984, TUR 98400. **Alberta**: Notikewin P.P., Abbott (SA 134) 08 7 1989, SA; Iosegun Lake east of Fox Creek, Abbott (SA 128) 08 6 1989, SA; Wagner Natural Area, Hill-Rackette (SA 940) 07 6 1994, SA. **NORWAY**: Nordland, Rana, Krokstrand, Tørbekken, Dissing & Sivertsen (72.95) 09 7 1972, C (isotype); Østfold, Skjeberg, Hafslund parken, Kristiansen 08 11 & 16 1986, RK 86.45; Østfold, Kråkerøy, Tørkopp, Kristiansen 09 1 1986, RK 86.93; Østfold, Hvaler, Kirkeøy, Ordal, Kristiansen 08 29 1987, RK 87.45.

Helvella* Subgenus *Elasticae (Dissing) S.P. Abbott *comb. nov.*

≡*Helvella* section *Elasticae* Dissing, 1966, Dansk Botanisk Arkiv 25: 128.

=*Helvella* section *Ephippium* Dissing, 1966, Dansk Botanisk Arkiv 25: 114.

Type Species: *Helvella elastica* Bulliard : Fries, 1823, Systema Mycologicum 2: 21.

Ascocarp: stipitate; apothecium irregularly lobed to saddle-shaped or reflexed, margin inrolled initially or reflexed initially; hymenium pale, medium, or dark brown to grey or black, smooth to somewhat undulate-rugose; excipular surface white to black, villose to glabrous, lacking ribs; stipe white to black, equal or enlarged at base, apex typically tapered, terete to fluted but not ribbed, internally terete to slightly sulcate and solid to hollow. **Asci**: pleurorhynchous. **Ascospores**: broadly ellipsoidal, smooth, with SEM finely rugose, uniguttulate, with large central broadly ellipsoidal oil guttule.

Notes: The subgenus includes all species in the sections *Elasticae* and *Ephippium* of Dissing (1966b), but only some in section *Ephippium* of Häffner (1987)(see also comments under subgenus *Cupuliformae*). The genus *Leptopodia* (*sensu* Boudier 1907), based on *H. elastica*, included many of the species ascribed to this subgenus, but not *H. monachella* (= *H. leucopus*) which was retained in the genus *Helvella sensu stricto*.

Key to species of *Helvella* subgenus *Elasticae*

1. Apothecia and stipe black (or very dark grey brown)..... 2
1'. Apothecia light, medium, or dark grey to brown; stipes white to light grey brown..... 3
2. Excipular surface pubescent to villose; apothecial margin strongly inrolled initially, typically remaining somewhat incurved at maturity.....***H. pezizoides***
2'. Excipular surface finely pubescent to glabrous; apothecial margin only slightly incurved initially, soon becoming reflexed to strongly reflexed at maturity.....***H. atra***
3. Apothecial margin reflexed initially and at maturity; excipular surface glabrous at all stages; stipe hollow.....***H. elastica***
3'. Apothecial margin inrolled initially, remaining inrolled, incurved, or becoming reflexed at maturity; excipular surface finely pubescent to villose initially, remaining distinctly pubescent or becoming glabrous at maturity; stipe solid or rarely hollow..... 4
4. Excipular surface densely pubescent to villose..... 5
4'. Excipular surface finely pubescent or glabrous..... 6
5. Stipe grey brown, at least in dried condition; apothecium (up to 10 mm diam.) and stipe (up to 15 x 2 mm) relatively small.....***H. ephippium***
5'. Stipe white to cream in fresh and dried condition; apothecium (up to 20 mm diam.) and stipe (up to 50 x 6 mm) relatively large.....***H. compressa***
6. Hymenium pale brown to light yellow brown when dried; ascospores 16.5-21 µm long.....***H. latispora***
6'. Hymenium medium to dark grey brown to brown or blackish brown when dried; ascospores 18.5-23.5 µm long.....***H. albella***

Helvella albella Quélet, 1896, Compte Rendu Assoc. Franc. Avancem. Sci. Conf. (Bordeaux, 1895) 24: 621.

≡*Leptopodia albella* (Quélet) Boudier, 1904-1911, Icones mycologicae, ou iconographie des champignons de France 4: 123.

Type Material: none available (*fide* Dissing 1966b).

Apothecium: 6-24 mm diam., 5-24 mm high (up to 55 x 50 mm fresh), irregularly lobed to bilobate and saddle-shaped, rarely irregularly discoid initially, margin inrolled to incurved initially, becoming flared to reflexed at maturity, free from stipe, hymenium medium to dark brown or grey brown fresh, when dried dark brown to blackish brown, rarely slightly mottled with paler patches, smooth to slightly undulate-rugose, excipular surface white or pallid greyish white, when dried light grey to pale yellow brown, pubescent to finely pubescent or nearly glabrous in age. **Stipe**: 8-58 x 1-9 mm (up to 100 x 10 mm fresh), equal or enlarged slightly to base, apex typically tapered, white, pale yellow brown when dried, finely pubescent to pubescent, terete or shallowly fluted, internally solid to hollow. **Asci**: 280-330 x 14.4-20.8 µm. **Paraphyses**: 6.0-9.9 µm diam. at apex, terminal cell 35-65 µm long, clavate, enlarged gradually to quite abruptly or irregularly at apex, pale brown to brown in mass, contents finely granular. **Ascospores**: 18.6-23.3 x (10.3) 11.8-13.9 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on ground in coniferous or mixed woods. Associated trees: *Picea glauca, Pinus contorta, Pseudotsuga menziesii, Tsuga* sp., *Betula* sp., *Alnus* sp., *Populus balsamifera,* and *Populus tremuloides*. Associated shrubs: *Salix discolor* and *Betula pumila.* Fruiting from July 17 in Alaska to December 6 in WA.

Distribution: Widely distributed but infrequent in boreal, montane, and coastal regions from AK, BC, AB, WA, and ID. Also distributed in Colorado (Weber 1975),

eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987) and Asia (Liu and Cao 1988). Map 21.

Notes: This species is closly related to *H. elastica* (q.v.), but differs in its pubescent excipulum and initially inrolled apothecial margin. In addition, the apothecial margin of *H. albella* is always free from the stipe. Older specimens of *H. albella* with near glabrous excipular surface and reflexed apothecial margin may be difficult to separate from *H. elastica*, but can be identified if submature individuals are present. Ascospore size for the two species listed by Dissing (1966b) and Weber (1972) indicate that *H. albella* has slightly broader ascospores, but this is not confirmed by Häffner (1987) or here. *Helvella elastica* has ascospores of variable width, overlapping the range in *H. albella*. *Helvella latispora* (q.v.) is also close and shares the initially incurved apothecium which becomes reflexed at maturity and the finely pubescent excipulum. These species are easily distinguished by hymenium colour and fruiting time. The apothecial margin of *H. latispora* is also more highly inrolled over the hymenium in immature stages. Lack of extant type material hampers clear delimitation from similar species.

Collections Examined: CANADA: British Columbia: Stone Mountain P.P., Abbott (SA 164) 08 12 1989, SA; Kaslo, Bell 08 18 1959, UBC F3265. **Alberta**: Fawcett Lake, Abbott 09 3 1988, ALTA 8316, 8317; Edmonton, Redhead 09 3 1970, UBC F3268; Glenmore Park, Calgary, Danielson (RMD 274) 09 11 1972, ALTA 8288. **USA**: **Alaska**: Eklutna Lake, Kempton 07 27 1974, WK 6157; Juneau, Kempton 07 30 1966, WK 1587. **Washington**: Seattle, Stuntz 12 6 1934, WTU; Seward Park, Snyder 10 28 1933, WTU; Green Lake, Mount Rainier N.P., Stuntz (Stz 7605) 10 19 1952, WTU. **Idaho**: Priest River Experimental Forest, Bonner Co., Slipp, WSP 49798. **SWEDEN**: Uppsala, Carolinaparken, Melderis 09 30 1945, K. **UNITED KINGDOM**: Quantocks, Somerset, Marrage 09 20 1960, IMI 83231. **GERMANY**: Neuensorgen Forest, Engel (423) 07 25 1974, K.

Helvella atra Holmskjøld : Fries, 1823, Systema Mycologicum 2: 19.

≡*Helvella atra* Holmskjøld, 1790, Beata ruris otia Fungis Danicis impensa 2: 47, Table 25.

=*Helvella subglabra* N.S. Weber, 1972, The Michigan Botanist 11: 179. (holotype MICH, examined).

(additional synonyms see Dissing 1966b).

Type Material: Lectotype in Holmskjøld, 1790, Beata ruris otia Fungis Danicis impensa 2: 47, Table 25, (selected Dissing 1966b).

Figs. 5a, 46.

Apothecium: 3-16 mm diam., 3-18 mm high (up to 30 mm diam. fresh), bilobate to somewhat irregularly lobed, often laterally compressed initially, margin incurved very slightly initially, soon becoming reflexed, sometimes appressed but free from stipe, hymenium black to blackish grey brown (fresh and dried), smooth to undulate-rugose, excipular surface pale to medium grey brown, finely pubescent. **Stipe**: 3-26 x 1-4 mm (up to 50 x 8 mm fresh), equal or enlarged at base, medium grey brown to blackish grey brown, typically yellowish grey to white at base, pubescent, terete or shallowly fluted (especially at base), internally solid, rarely hollow at base. **Asci**: 192-225 x 12.9-17 µm. **Paraphyses**: 4.7-9 µm diam. at apex, terminal cell 11.6-19.3 µm long, clavate, enlarged gradually to abruptly at apex, brown to dark brown in mass, contents finely granular. **Ascospores**: 15-20.6 x 10-13.1 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Gregarious to scattered and numerous on ground or rotted wood in deciduous or mixed woods. Associated trees: *Populus tremuloides*, *Alnus tenuifolia*, *Betula papyrifera, Picea mariana,* and *Larix laricina*. Associated shrub: *Salix discolor*. Fruiting period from July 14 in MT to September 2 in AB.

Distribution: Uncommon in boreal and montane regions of AB and MT. Also in eastern and southern North America (Weber 1972, as *H. subglabra* and *H. atra*), Europe (Dissing 1966b; Häffner 1987), and Asia (Liu *et al.* 1985). Map 23.

Notes: This species is most closely related to *H. pezizoides* (q.v.). *Helvella atra* has a finely pubescent excipulum, slightly incurved apothecial margin at submature stage and

reflexed at maturity, and a grey to black ascocarp. Both *Helvella atra* and *H. pezizoides* are occasionally collected from rotted wood and Häffner (1987) suggests they may be synonymous. The species are certainly closer to each other than to other species in the genus, and intermediate collections are sometimes found, but the correlation of colour, vestiture, and marginal curvature warrant tentative specific recognition. Weber (1972) separated *H. subglabra* from *H. atra* on the basis of grey to dark grey ascocarp and very fine excipular vestiture, as opposed to the black glabrous apothecium of *H. atra*. Both of these features are variable in others (e.g., *H. lacunosa*, *H. albella*, and *H. latispora*) and are insufficient to warrant specific recognition, in agreement with Häffner (1987).

Collections Examined: CANADA: Alberta: Minnie Lake near Glendon, Abbott 08 10 1983, ALTA 8265; Wagner Natural Area, Abbott (SA 1038, 1050, 1107) 08 25 & 09 4 1994, 08 19 1995, SA; Devonian Botanic Garden near Devon, Abbott 07 25 & 28 1987, 09 2 1988, 07 27 1989, ALTA 8266, 8297, 8310, SA 110. **Ontario**: Aubinadong River, Algoma District, Cain 08 2 1956, TRTC 35344. **USA**: **Montana**: Echo Lake, Flathead National Forest, Cummins 07 14 1928, MICH. **Michigan**: Reese's Bog, A.H. Smith 07 10 & 27 1963, UBC F3241, F3267.

Helvella compressa (Snyder) N.S. Weber, 1975, Beihefte Nova Hedwigia 51: 35.

≡*Paxina compressa* Snyder, 1936, Mycologia 28: 486.

Type Material: Holotype WTU, examined; isotype NY, examined.

Fig. 49.

Apothecium: 4-19 mm diam., 3-20 mm high, irregularly lobed, margin strongly inrolled initially, often remaining somewhat inrolled at maturity, free from stipe, hymenium when dry dark brown, smooth, excipular surface when dry cream to pale grey brown, densely pubescent to villose. **Stipe**: 5-50 x 1-6 mm, enlarged at base to nearly equal, typically tapered at apex, when dry cream to pale yellow brown, pubescent to villose, especially at apex, terete or fluted at base, internally solid or rarely hollow in large specimens. **Asci**: 280-349 x 15.2-22.0 µm, cylindrical, tapered to base, hyaline, pleurorhynchous. **Paraphyses**: 4.3-8.6 µm diam. at apex, clavate, enlarged gradually to apex, pale brown to brown in mass, contents finely granular. **Ascospores**: 19.7-23.8 x 11.4-14.8 µm, broadly ellipsoidal, smooth, with SEM finely rugose, uniguttulate, with large central globose to broadly ellipsoidal oil guttule.

Habitat: Solitary, gregarious, subcaespitose, or scattered and numerous on soil or litter, rarely with burnt woody debris, in coniferous or infrequently in mixed or deciduous woods. Associated trees: *Pseudotsuga menziesii, Abies grandis, Pinus ponderosa, Thuja plicata, Quercus garryana, Alnus rubra*, and *Acer* sp. Associated shrubs: *Symphoricarpos* sp. Fruiting from March 9 to December 25 in coastal WA. April to June collections are common.

Distribution: In coastal and montane regions in the western portion of the study area from AK, BC, WA, ID, and OR. Endemic to western North America, and known only west of the Rocky Mountains. This species is newly reported from AK, BC, ID, and OR. Known distribution extends south of the study area to California (Weber 1975). Map 22.

Notes: This species is closely related to *H. latispora* (q.v.) but is distinguished by geographic distribution, ascocarp pigmentation, and excipulum vestiture (see also notes under *H. latispora*). Both species apparently have a prolonged fruiting period, although vernal collections are typical.

Collections Examined: CANADA: British Columbia: Goldstream P.P., Vancouver Island, Ramsay 04 5 1978, UVIC; Mount Douglas Park, Victoria, Vancouver Island, Paden (JWP 583, 584, 1383) 04 5 & 7 1968, 03 20 1987, UVIC; Mount Douglas Park, Victoria, Vancouver Island, Egger (877, 955) 04 10 1982, 03 29 1983, DAOM 199815, 199816, 199793; University of Victoria campus, Vancouver Island, Paden (JWP 710, 743) 05 10 1969, 04 3 1970, UVIC; Roche Cove Park, East Sooke, Paden (JWP 1326) 04 26 1986, UVIC; Sooke road, Vancouver Island, Paden (JWP 1171) 05 11 1981, UVIC; near Saturna Beach, Saturna Island, Kroeger 05 16 1986, UBC F12511. **USA: Alaska**: Eklutna Lake north of Anchorage, Kempton 08 29 1972, 09 11 1973, WK 5901, 6057. **Washington**: Friday

Harbor, San Juan Island, Snyder (Stz 12223) 11 12 1960, WTU; Friday Harbor, San Juan Island, McCabe (Stz 19893) 11 20 1976, WTU; Friday Harbor, San Juan Island, Brough (56, 67) 04 21 & 05 5 1957, WTU; Friday Harbor, San Juan Island, Stuntz (Stz 2378, 12143, 12173, 12270, 12371) 10 30 & 11 5 & 12 25 1960, 06 4 1961; Friday Harbor, San Juan Island, Isaacs (Is 1711a, b) 05 19 & 20 1962, WTU; Friday Harbor, San Juan Island, SDL-B (Stz 21688) fall 1981, WTU; Lower Priest Point Park, Olympia, Mason & Mead (Brough 96) 03 9 1958, WTU; south of Olympia, Isaacs (Is 1754) 05 30 1962, WTU; Easton, Snyder 05 5 1934, NY (isotype), WTU (holotype); California Creek near Valley Ford, Cooke 06 8 1947, WSP; Bingen Mountain, Klickitat Co., Suksdorf 05 1 1899, WSP 27476, 27477; unknown, FHL fire trail, SDL-B 03 25 & 04 9 1977, WTU. **Idaho**: northeast of Robinson Lake, Latah Co., Koenigs 07 19 1964, WSP 55003. **Oregon**: Wilsonville, Ardrey (CA 1166) 04 20 1987, WTU; Mary's Peak road, Paden 03 26 1970, UVIC. **Exsiccata**: Vancouver Island Fungi, 499, Vancouver Island, BC, Canada, Macoun 04 13 1915, s.n. *Helvella elastica*, UBC F3256.

Helvella elastica Bulliard : Fries, 1823, Systema Mycologicum 2: 21.

≡*Helvella elastica* Bulliard, 1785, Herbier de la France, Plate 242.

≡*Leptopodia elastica* (Bulliard : Fries) Boudier, 1885, Bulletin de la Societé Mycologique de France 1: 99.

(additional synonyms see Dissing 1966b).

Type Material: Lectotype in Bulliard, 1785, Herbier de la France, Plate 242 Figures A, B, D-G (selected Dissing 1966b).

Fig. 5b.

Apothecium: 5-40 mm diam., 4-20 mm high (up to 45 x 40 mm fresh), irregularly lobed to bilobate and saddle-shaped or irregularly convex, sometimes slightly laterally compressed initially, margin reflexed from initial stages, may be appressed to stipe but typically remaining free, rarely fused to stipe, hymenium medium to dark brown or greyish brown fresh, rarely slightly mottled with paler patches, when dried dark brown to blackish brown, slightly undulate-rugose to smooth, excipular surface white to pallid greyish white or pale yellow brown when dried, glabrous. **Stipe**: 5-50 x 2-5 mm (up to 105 x 11 mm fresh), equal or enlarged at base, white to cream or pale yellow brown when dry, glabrous to finely pubescent or pubescent, terete or fluted especially at base, terete or slightly sulcate and internally hollow. **Asci**: 280 x 19 µm. **Paraphyses**: 5-7 µm diam. at apex, clavate, enlarged gradually to apex, pale brown, contents finely granular. **Ascospores**: 17.9-22 x 10.8-15 µm, broadly ellipsoidal, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on soil, litter, moss, or rarely rotted wood, in coniferous or mixed woods. Associated trees: *Picea glauca, Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla, Pinus contorta, Pinus banksiana, Abies balsamea, Larix laricina, Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera,* and *Betula occidentalis*. Associated shrubs: *Salix serissima, Salix bebbiana, Salix discolor, Alnus* sp., *Prunus pensylvanica, Viburnum edule, Shepherdia canadensis, Vaccinium vitis-idaea, Cornus canadensis,* and *Linnaea borealis*. Fruiting from June 5 in ID to December 25 in coastal WA.

Distribution: Widely distributed and common throughout boreal, montane, and coastal regions from AK, YT, BC, AB, SK, MB, WA, ID, MT, and WY. Also reported from OR by Larsen and Denison (1978). Distributed in eastern North America (Weber 1972; Groves and Hoare 1953; Anderson and Ickis 1921), Europe (Dissing 1966b; Häffner 1987), and Asia (Liu *et al.* 1985; Imai 1954; Kar and Pal 1970). Map 20.

Notes: This species is characterized by the apothecium, which is never inrolled and is reflexed from initial stages, glabrous excipulum, and hollow stipe. *Helvella elastica* is closest to *H. albella* (q.v.). The two species are similar in colour and habit, but distinguished by excipular vestiture and margin characteristics (see also notes under *H. albella*). *Helvella latispora* (q.v.) is also similar, but differs in its paler hymenium, pubescent excipulum at least in initial stages, and initially strongly inrolled margin.

Collections Examined: CANADA: Yukon: Yukon River southeast of Boundary, Ginns 07 19 1984, DAOM 195457; Campbell Highway, Ginns 08 4 1980, DAOM 195456. **British**

Columbia: Tetsa River P.P., Abbott (SA 221, 223, 225) 08 22 1989, SA; Fort Nelson, Szczawinski 07 27 1962, DAOM 14424; Mount Robson P.P., Abbott (SA 926) 08 29 1993, SA; south of Wells Gray P.P., Goward 09 8 1980, DAOM 186396; near Clearwater, Goward 09 10 1982, DAOM 191772; Adams River south of Adams Lake, Goward, 10 21 1982, DAOM 191779; Francis Park, Victoria, Vancouver Island, Melburn 11 1 1962, DAOM 109932; Victoria, Vancouver Island, Newcombe, K. **Alberta**: Shaw Lake east of Lac La Biche, Abbott (SA 102) 07 15 1989, SA; Musreau Lake south of Grande Prairie, Abbott (SA 246, 247, 253, 261) 08 26 1989, SA; Iosegun Lake east of Fox Creek, Abbott (SA 125) 08 6 1989, SA; William A. Switzer P.P., Abbott (SA 265, 270) 08 27 1989, SA; William A. Switzer P.P., Osis (SA 389, 390) 09 2 1990, SA; Wagner Natural Area, Abbott (SA 1041, 1046) 08 25 & 09 4 1994, SA, K; North Saskatchewan River valley, Edmonton, Zelmer 08 22 1995, ALTA; Devonian Botanic Garden near Devon, Abbott (SA 920, 1084) 07 27 1987, 08 25 1993, 08 9 1995, ALTA 8269, SA, K; Devonian Botanic Garden near Devon, Currah 08 19 1980, ALTA 8270; near Ponoka, Stewart 08 16 1962, ALTA 667; Fish Lake near Nordegg, Abbott (SA 281, 287, 288, 382, 399) 08 31 1989, 08 4 & 09 8 1990, SA. **Saskatchewan**: Candle Lake, Zalasky 08 30 1955, CFB WINFM 1289. **Manitoba**: Clear Lake, Bisby 08 17 1935, DAOM 206804. **Ontario**: Lake Temagami, Jackson 08 21 1930, TRTC 1780; Blue Lake, Brant Co., Cain 10 14 1956, WSP 45561. **Québec**: Richmond Gulf area, Huhtinen 08 30 1982, TUR 78713; Astray Lake, Schefferville, Huhtinen & Kosonen 08 12 1979, TUR 63423. **USA: Alaska**: Harding Lake near Fairbanks, Kempton 08 26 1965; Fox Springs near Fairbanks, Kempton 08 7 1970, WK 4620; Eklutna Lake north of Anchorage, Kempton 08 29 1961, WK 1580; Lower Skilak Lake, Kenai Peninsula, Kempton 09 27 1965, WK 1581; Bartlett River trail, Glacier Bay National Monument, Cooke 09 1 & 4 & 9 1979, 09 1 1981, WSP 64398, 67208, MU F34794, F36152; Haines, Kempton 09 21 1970, WK 4974; Auke Bay near Juneau, Kempton 09 13 1967, WK 1586. **Washington**: north of Mount Bonaparte and Lost Lake, east of Tonasket, Brazle, WSP 64709; Friday Harbor, San Juan Island, Stuntz (Stz 3602, 8997, 12270, 15271) 06 8 1948, 11 13 1954, 12 25 1960, 11 29 1968, WTU; Friday Harbor, San Juan Island, Isaacs (Is 2013) 11 11 1962, WTU; Friday Harbor, San Juan Island, McCabe (Stz 19893) 11 20 1976, WTU; Friday Harbor, San Juan Island, Tyler (Stz 12221) 11 12 1960, WTU; San Juan campground, Stevens Pass road, SDLB 09 26 1976, WTU; Seattle, Zeller (180), WTU; Isput Creek, Mount Rainier N.P., Williams (JWL 1228) 10 20 1971, WTU; Trout Lake-Cispus junction, van de Bogart (FVB 1015) 10 23 1971, WTU; Iron Butte, van de Bogart (FVB 3805) 10 31 1976, WTU; Iron Creek, van de Bogart (FVB 2882) 07 13 1974, WTU; unknown, Stuntz (Stz 982, Stz 15084) 10 26 1968, WTU. **Idaho**: Clearwater Canyon east of Lenore, Nez Perce Co., Cooke 06 5 1947, WSP 24506; Fall Creek at French Creek Grade, Idaho Co., Miller 09 4, 7 1964, WSP 53685, 53845, 54086. **Montana**: Echo Lake, Flathead National Forest, Cummins 07 20 & 30 1928, MICH. **Wyoming:** Turpin Meadow road, Ammirati (JFA 9546) 08 13 1987, WTU. **Michigan**: Pellston, Isaacs (Is 26a) 07 20 1957, WTU. **SWEDEN**: Uppsala, Fries, K. UNKNOWN: Coch 09 1872 Herbarium Berkeley, K; Toscana Bicchi autumn 1859, K; Petrak 08 1936, IMI 38460. **Exsiccata**: Fungi Suecici, Hejdeby parish, Gotland, Pettersson 10 11 1946, WSP 31527; Flora Hungarici Exsiccata, 208, Iglófüred, 08 1913, s.n. *Leptopodia elastica*, TRTC.

Helvella ephippium Léveillé, 1841, Annales des Sciences Naturelles Botanique, Ser. 2, 16: 240.

=*Helvella murina* (Boudier) Saccardo & Traverso, 1910, in Saccardo, Sylloge fungorum omnium hucusque cognitarum 19: 849. (*fide* Dissing 1966b).
(additional synonyms see Dissing 1966b).

Type Material: not available (*fide* Dissing 1966b). Dissing (1966b) suggests that the illustration in Léveillé be chosen as lectotype. One authentic collection examined by Léveillé, discussed by Dissing (1966b) could perhaps be chosen as neotype.

Apothecium: 5-10 mm diam., 5-10 mm high, irregularly lobed to saddle-shaped, sometimes laterally compressed initially, margin strongly inrolled initially, remaining incurved at maturity, hymenium medium to dark brown fresh, when dried dark grey brown, smooth, excipular surface medium brown to grey brown, pubescent to villose. **Stipe**: 15 x 1.5-2 mm, equal, nearly white to pale grey brown, pubescent, terete, not fluted, internally solid. **Asci:** 150-280 x 17-19 µm, cylindrical, tapered to base, hyaline. **Paraphyses**: 3-7 µm diam. at apex, clavate, enlarged gradually to apex, brown, contents finely granular. **Ascospores**: 17-21 x 10.1-13 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary on soil or humus in deciduous, mixed, or coniferous woods. Associated trees: *Picea glauca, Abies balsamea, Populus balsamifera*, and *Populus tremuloides*. Associated shrubs: *Cornus stolonifera*. Fruiting from August 1 in MB to October 1 in AB.

Distribution: Rare in boreal regions of the study area. Known from AB and MB. Also in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987), and Asia (Imai 1954). Map 23.

Notes: This species is close to *H. pezizoides* (q.v.) and *H. atra* (q.v.) which are distinguished by their black ascocarps, and *H. latispora* (q.v.) which lacks the villose excipulum. Also, *H. ephippium* lacks fluting on the slender stipe. *H. ephippium* is also similar to *H. chinensis* (q.v.) in the subgenus *Cupuliformae* which has the same colour and stature, but *H. chinensis* is typically cupulate, while *H. ephippium* has a more complex folded and lobed apothecium.

Collections Examined: CANADA: Alberta: Notikewin P.P., Abbott (SA 138) 08 7 1989, SA; Emily Murphy Park, Edmonton, Tsuneda 09 15 1976, ALTA 7446; Emily Murphy Park, Edmonton, Zelmer (SA 930) 10 1 1993, SA; North Saskatchewan River valley, Edmonton, Zelmer 08 24 1995, ALTA; Pearce Estate, Calgary, Danielson (RMD 1278) 09 14 1973, ALTA 8287. **Manitoba**: Victoria Beach, Bisby 08 1 1927, DAOM 154814. **NORWAY**: Ørdal, Kirkoy, Hvaler, Østfold, Kristiansen 07 22 & 10 24 1982, RK.

Helvella latispora Boudier, 1898, Bulletin de la Societé Mycologique de France 14: 16.

=*Helvella stevensii* Peck, 1904, Bulletin of the Torrey Botanical Club 31: 182. (holotype NYS, examined).

≡*Leptopodia stevensii* (Peck) Le Gal, 1937, Revue de Mycologie 2: 156.

=*Helvella connivens* Dissing & M. Lange, 1967, Mycologia 59: 351. (*fide* Weber 1972; Häffner 1987).

=*Leptopodia corbieri* Malençon, 1927, Bulletin de la Societé Mycologique de France 43: 95, Pl. 3 Fig. 7. (*fide* Dissing 1966b).

Type Material: Holotype PC, examined.

Fig. 5c.

Apothecium: 3-16 mm diam., 5-15 mm high, irregularly lobed to bilobate and saddle-shaped, margin inrolled initially, becoming reflexed at maturity, hymenium pale grey brown to medium brown fresh, when dried pale yellow brown to brown, smooth to slightly undulate-rugose, excipular surface cream to pallid grey brown, finely pubescent to pubescent. **Stipe**: 6-20 x 1-5 mm, equal or slightly enlarged to base, apex typically tapered, white, when dried cream to pallid greyish yellow brown, finely pubescent to pubescent, terete or shallowly fluted at base, internally solid. **Asci**: 290-330 x 13.3-15.6 µm. **Paraphyses**: 5.1-8.6 µm diam. at apex, clavate, enlarged gradually to apex, hyaline, contents finely granular. **Ascospores**: (16.5) 18.6-19.9 (20.8) x (10.9) 11.4-12.4 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Gregarious on soil or litter in deciduous, mixed, or coniferous woods. Associated trees: *Alnus rugosa*, *Populus* sp., and *Picea glauca*. Fruiting from June 27 in ID to August 29 in MB.

Distribution: Rare in boreal and montane regions from AB, MB, and ID. Distributed in eastern North America (Weber 1972 as *H. stevensii*) and Europe (Dissing 1966b; Häffner 1987). This species is newly reported from AB and MB. Larsen and Denison (1978) report it (as *H. stevensii* and *H. connivens*) from OR and WA, but these reports may refer to *H. compressa*. Map 22.

Notes: This species is closely related to *H. compressa* (q.v.) and the two are primarily distributed in eastern and western North America respectively. They can be easily separated by the villose excipular surface and darker hymenium of *H. compressa*. *Helvella latispora* is also close to *H. albella* (q.v.), but separable by colour. The apothecial margin of *H. latispora* is also more strongly inrolled over the hymenium in initial stages. The specimens from ID (see also Weber 1975) and AB are extreme western

collections of *H. latispora*, and share the pale hymenium and finely pubescent excipulum typical of eastern collections. Häffner (1987) synonymizes *H. stevensii* with Boudier's (1898) older *H. latispora*, and type of material is similar. Dissing (1966a, b) retained *H. latispora* as distinct on the basis of the broad ascospores (13.5-18 µm in Dissing 1966b), but our measurements of spores in distilled water from the type specimen show a range from 11.8 to 14.0 µm in width.

Collections Examined: CANADA: Alberta: Fish Lake near Nordegg, Abbott (SA 374, 376) 08 3 1990, SA. **Manitoba**: Rolling River road, Riding Mountain N.P., Ginns & Hammersley 08 23 1979, DAOM 176223; near Bear Lakes, Riding Mountain N.P., Redhead 08 29 1979, DAOM 175852. **Ontario**: Lake Opinicon, Elliott & Groves 07 12 1961, TUR 38572, DAOM 87941; Nashville, Cain 10 2 1954, TRTC 30370; Nashville, Luck-Allen 09 30 1963, TRTC 43727. **USA: Idaho**: Twin Lakes, Kootenai Co., Weber (NSW 3653) 06 27 1972, MICH. **Michigan**: Detroit, Stevens 06 1903, NYS (holotype of *H. stevensii*); Pellston Hills west of Pellston, Shaffer 07 14 1964, UBC F951. **Iowa**: Amana, Martin & Brasfield 06 7 1938, ALTA 664, 665, 666. **NORWAY**: Østfold, Kråkerøy, Rød, Ekheim-parken, Kristiansen 07 28 1985, RK. **UNITED KINGDOM**: Kirk Lane, Priory, Yorkshire, Holland 09 13 1983, IMI 290669; Chevering Park, Kent, Reid 10 16 1982, K. **FRANCE**: France, Boudier Herbier Mycologique, PC (holotype).

Helvella pezizoides Afzelius : Fries, 1823, Systema Mycologicum 2: 20.

≡*Helvella pezizoides* Afzelius, 1783, Kongl. Vetensk. Akad. Nya Handl. 4: 308. (additional synonyms see Dissing 1966b).

Type Material: Lectotype in Afzelius, 1783, Kongl. Vetensk. Akad. Nya Handl. 4: 308, Plate 10 Figure 2 (selected Dissing 1966b).

Apothecium: 2.5-8 mm diam., 2-7 mm high, bilobate or irregularly lobed to irregularly cupulate or discoid, occasionally laterally compressed initially, margin strongly inrolled initially, remaining incurved at maturity, hymenium when dry black, smooth or rarely slightly undulate-rugose, excipular surface dark brown to dark grey brown, pubescent to villose. **Stipe**: 3-25 x 0.5-3 mm, enlarged slightly to base, apex tapered, when dry dark brown to dark grey brown or blackish brown, pubescent to villose, terete or fluted at base, internally solid. **Asci**: 100-315 x 14.1-18.6 µm. **Paraphyses**: 4-8.6 µm diam. at apex, terminal cell 40-60 µm long, clavate, enlarged gradually to abruptly at apex, brown to dark brown in mass, contents finely granular. **Ascospores**: 16.9-20.8 x 10.7-13.3 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on soil, humus, or rotted wood in woodland, bog or tundra habitats. Fruiting from July 27 in AK to August 16 in the NWT and AK.

Distribution: Rare in boreal, coastal, and arctic regions from AK, NWT, and AB. This species is newly reported for the NWT and AK. Also in eastern North America (Weber 1972), southern North America (Dissing 1966b), Europe (Dissing 1966b), and Asia (Liu *et al.* 1985; Tewari *et al.* 1971). The specimens from Jamaica (and likely the ones described as *H. atra* by Denison 1963 from Costa Rica) are somewhat intermediate between *H. pezizoides* and *H. atra*, but are assigned to *H. pezizoides* based on the densely pubescent excipular surface and incurved apothecial margin. Map 23.

Notes: This species is very close to *H. atra* (q.v.), but differs in its strongly involute apothecial margin, densely pubescent to villose excipular surface, and strong brown pigmentation of the excipulum and stipe (see also notes under *H. atra*). In addition, *H. pezizoides* is occasionally irregularly cupulate to discoid, while *H. atra* is regularly bilobate to irregularly lobed. Collections of *H. pezizoides* from Alaska were referred to *H. atra* by Kempton and Wells (1970). *Helvella ephippium* (q.v.) is also related, but is easily separated by the paler ascocarp.

Collections Examined: CANADA: Northwest Territories: mouth of Thelon River, Baker Lake, Ohenoja 08 16 1974, DAOM 155302; Williamson Lake, Rankin Inlet, Ohenoja 08 10 1971, DAOM 155313. **Alberta**: Kinsmen ravine, Edmonton, Elisens 08 1977, ALTA 7606. **Québec**: Richmond Gulf area, Huhtinen 08 31 1982, TUR 78796. **USA: Alaska**: near Nome, Seward Peninsula, Kempton 08 12 1967, WK 1533; butte area near Palmer, Kempton 07 27 & 08 16 1961, WK 1534, 1535. **Michigan**: Tahquamenon Falls State Park, Brough (513) 08 9 1963, UBC F3266.

JAMAICA: Blue Mountain, Dennis 12 20 1949, K. **NORWAY**: Østfold, Borge, Torp, Kristiansen 07 6 1984, 08 1 1987, RK 87.21. **FRANCE**: Paris, Reid 08 10 1989, K. **Exsiccata**: Karsten Fungi Fenniae, 446, På ängsbackar vid Mustiala, Karsten 08 1866, s.n. *H. atra*, K.

Extralimital Species

Helvella leucopus Persoon, 1823, Mycologica Europaea 1: 213.
=*Helvella monachella* auct.; non *H. monachella* Scopoli : Fries (=*Gyromitra* sp.)(*fide* Dissing 1966b).
(additional synonyms see Dissing 1966b).

Type Material: Lectotype (selected Dissing 1966b) L, examined.

Distribution: Known from Europe (Dissing 1966b; Moravec 1980), north Africa (Dissing 1966b) and Asia (Liu *et al.* 1985). No specimens referable to this taxon were found during this investigation. Dissing (1966b) reported it from ID. Weber (1975) could not confirm its presence in ID, but describes a specimen with some similarities. These are the only reports, and its occurrence in North America is questionable.

Notes: This species is close to *H. elastica* (q.v.) and *H. albella* (q.v.), but has a darker hymenium, larger ascocarp, robust stipe, and more complex lobed apothecium. Häffner (1987) and Dissing (1966b) synonymize the older *H. spadicea* Schaeffer, but no type material is known for this taxon, without which we could not support adoption of a forgotten name for this well known species. This taxon is referred to *Helvella monachella* by many authors, but the original concept of *H. monachella* (Fries 1823) is based on a *Gyromitra* species (Dissing 1966b).

Collections Examined: NETHERLANDS: Herbarium Persoon, L 8945-2 (lectotype); Ijselmeerpolders, Flevoland, De Abbert, Bas 05 14 1977, TRTC. **Exsiccata**: Herbarium Mycologicum Romanicum, 667, Mutenia, district Ilfov, Rumania, Savulescu & Alexandri 05 8 1933, s.n. *Helvella monachella*, IMI 29629, TRTC.

Helvella Subgenus *Helvella*

≡*Helvella* section *Helvella*

≡*Helvella* section *Crispae* Dissing, 1966, Dansk Botanisk Arkiv 25: 85.
=*Helvella* section *Lacunosae* Dissing, 1966, Dansk Botanisk Arkiv 25: 98.

Type Species: *Helvella crispa* Scopoli : Fries, 1823, Systema Mycologicum 2: 13.

Ascocarp: apothecium irregularly lobed to irregularly convex, margin inrolled initially or reflexed, free or fused to stipe; hymenium white, brown, grey, or black, undulate-rugose; excipular surface pubescent to glabrous; stipe distinct, strongly ribbed, usually lacunose, internally chambered. **Asci:** pleurorhynchous. **Ascospores:** broadly ellipsoidal, hyaline, smooth with light microscope, with SEM finely rugose, uniguttulate.

Notes: The type subgenus *Helvella* includes species treated in sections *Crispae* and *Lacunosae* of Dissing (1966b). The broad concept employed here includes species with a prominent, strongly ribbed stipe posessing lacunae and a chambered internal structure. The apothecium is highly lobed and irregularly folded. The differences in excipular pubescence, apothecial marginal curvature, and fusion with the stipe, used to separate the sections of Dissing (1966b) are not considered taxonomically significant at the subgenus level (although they may show relationships among individual species within the subgenera). These characters show greater or lesser prominence in different species, and form a progression of morphological intermediates between the extremes (see also discussion under taxonomic significance of macroscopic characters). The subgenus *Helvella* corresponds closely to the genus *Helvella* in its most restricted sense (e.g., Boudier 1885, 1907; Breitenbach and Kränzlin 1981).

Key to species of *Helvella* subgenus *Helvella*

1. Apothecial margin inrolled initially, remaining free from stipe at maturity..... 2
1'. Apothecial margin reflexed initially, becoming fused with stipe at maturity..... 3
2. Hymenium white to cream; excipular surface pubescent.....***H. crispa***
2'. Hymenium medium to dark brown; excipular surface densely pubescent to villose.....***H. maculata***
3. Ascocarp dark grey brown to black.....***H. lacunosa***
3'. Ascocarp white.....***H. lactea***

Helvella crispa Scopoli : Fries, 1823, Systema Mycologicum 2: 14.

≡*Phallus crispus* Scopoli, 1772, Flora carniolica 2: 475.

=*Helvella leucophaea* Persoon, 1799, Observationes mycologicae 2: 19. (holotype K, examined).

=*Helvella mitra* Linnaeus, 1753, Species Plantarum 2: 1180. (*fide* Dissing 1966b). (additional synonyms see Dissing 1966b).

Type Material: Lectotype (selected Dissing 1966b) in Micheli, 1729, Nova Plantarum Genera 204, Tab. 86 Fig. 7.

Figs. 6a,b, 45.

Apothecium: 5-50 mm diam., 5-50 mm high (up to 70 x 55 mm fresh), irregularly lobed, occasionally bilobate, margin inrolled over hymenium initially, becoming reflexed at maturity, free from stipe, hymenium white to cream fresh, often drying tan to yellowish brown, rugose, excipular surface cream to beige, typically slightly darker than hymenium, finely pubescent to pubescent, sometimes with few small ribs extending onto basal third of excipular surface from stipe. **Stipe:** 6-130 x 2-35 mm, equal or enlarged at base, white to cream or pallid grey brown, highly ribbed, often lacunose, finely pubescent to pubescent, internally chambered. **Asci:** 225 x 14.4-17 µm. **Paraphyses:** 5.8-8 µm diam. at apex, apical cell 14-37 µm long, clavate, enlarged gradually or abruptly at apex, hyaline, contents finely granular. **Ascospores:** 16.5-20.6 x 10-13 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary, gregarious, or scattered on soil and litter in deciduous or mixed woods. Associated trees: *Populus tremuloides, Populus balsamifera, Betula papyrifera, Betula occidentalis, Alnus tenuifolia, Arbutus menziesii, Picea glauca, Picea sitchensis, Pinus banksiana, Pinus contorta, Abies grandis*, and *Pseudotsuga menziesii*. Associated shrubs: *Salix bebbiana, Salix discolor, Corylus cornuta, Alnus crispa, Prunus pensylvanica, Amelanchier alnifolia, Shepherdia canadensis, Viburnum edule, Lonicera involucrata*, and *Rosa* sp. Fruiting from July 11 in AB to November 15 in WA.

Distribution: Widely distributed in boreal, coastal, and montane regions from AK, YT, NWT, BC, AB, SK, MB, WA, ID, and OR. This is a very common species in boreal and aspen parkland regions in the study area. Also found in eastern North America (Weber 1972), Europe (Dissing 1966b, Häffner 1987), and Asia (Liu *et al.* 1985; Imai 1954). Map 9.

Notes: This distinctive species is most closely related to *H. maculata* (q.v.) and *H. fusca* (q.v.) which share the initially inrolled, free margin and pubescent excipular surface and stipe. Distinction is made on the basis of ascocarp coloration, degree of vestiture, and habitat. *Helvella crispa* superficially resembles *H. lactea* (q.v.) which is also white to cream, but can be separated by its reflexed margin fused to stipe and glabrous excipular surface.

Collections Examined: **CANADA: Yukon:** Dempster Highway near Dawson, Ginns 08 8 1980, DAOM 195471; 3 km northeast of Mayo, Calder 08 1 1949, DAOM 25986. **Northwest Territories:** Hay River, Green 08 30 1984, UVIC. **British Columbia:** Tetsa River P.P., Abbott (SA 218, 219, 222, 226) 08 22 1989, SA; Moberly Lake P.P., Schalkwyk 08 15 1977, DAOM 175734; Prince George, Brough (651) 09 20 1968, UBC F3244; 50 km south of Quesnel, Calder, Savile & Ferguson 09 4 1954, DAOM 45603; Wells Gray P.P., Abbott (SA 923) 08 28 1993, SA; Spahats Creek P.P., Abbott (SA 924) 08 28 1993, SA; San Josef Bay, Vancouver Island, (SDLB 617) 08 28

1975, WTU. **Alberta:** north of Meander River, Abbott (SA 144) 08 8 1989, SA; Notikewin P.P., Abbott (SA 129, 136) 08 7 1989, SA; McKay River south of Fort McMurray, Dumais 07 27 1968, ALTA 663; Fawcett Lake, Abbott 09 3 1988, ALTA 8318, 8319, 8320; Musreau Lake, Abbott (SA 245, 249, 255, 256, 257) 08 26 1989, SA; Sheep Creek north of Grande Cache, Abbott (SA 263, 264) 08 26 1989, SA; Long Lake, States 08 13 1967, ALTA 662; Sandy Lake, Schalkwyk 07 11 1975, ALTA 7907, DAOM 175714; east of Redwater, Schalkwyk 09 5 1978, ALTA 7901; William A. Switzer P.P., Abbott (SA 269) 08 27 1989, SA; William A. Switzer P.P., Osis (SA 386) 09 2 1990, SA; near Onoway, Osis (SA 880) 08 8 1993, SA; Muir Lake area, Bozniak & Wheelock 09 14 1965, ALTA 661; Wagner Natural Area, Abbott (SA 1039, 1052, 1111) 08 25 & 09 4 1994, 08 19 1995, SA, K; Forest Reserve, Edmonton, Kennedy 09 15 1976, ALTA 7292; Emily Murphy Park, Edmonton, Tsuneda 08 1976, ALTA 7359; Devonian Botanic Garden near Devon, Currah 09 4 1977, 07 1979, 08 31 1980, 07 21 1982, ALTA 7534, 7957, 8268, 8275; Devonian Botanic Garden near Devon, Abbott (SA 108, 716, 764, 895, 919, 928, 1083, 1086) 09 3 1987, 07 25 1989, 08 15 & 09 3 1992, 08 16 & 25 & 09 11 1993, 08 9 & 08 11 1995, ALTA 8276, SA, K; Devonian Botanic Garden near Devon, Richardson 09 1 1988, ALTA 8311; 10 km south of Leduc, Abbott 08 8 1981, ALTA 8283; near Cynthia, Osis & Gibson 08 14 1988, ALTA 8309; near Breton, Osis & Gibson 08 1 & 20 1988, ALTA 8300, 8303; Fish Lake near Nordegg, Abbott (SA 282, 375, 400) 08 31 1989, 08 3 & 09 8 1990, SA. **Saskatchewan:** Turtle Lake near Turtleford, Zelmer 08 1994 (not accessioned). **Manitoba:** Gilbert Plains, Provincial Horticulturalist 09 1954, DAOM 45142; Victoria Beach, Bisby 09 11 & 12 & 19 1926, 08 8 1928, 09 7 1931, DAOM 206802, 206801, 206800, TRTC; Victoria Beach, Reid 09 8 1968, WIN; Pinawa, Bisby 09 2 1935, DAOM 206803; Manitoba Agricultural College, Winnipeg, Bisby & Gordon 08 5 1928, DAOM 154794; Winnipeg, Frankton 08 28 1956, DAOM 54284; Melbourne, Oliver 09 7 1969; Darwin, Sutton 09 10 1968, CFB WINFM 10304. **Ontario:** Apsley, Cain 09 26 1956, TRTC 32970; Angus, Cain 10 10 1954, WSP 43051. **Québec:** Lac La Pêche, Gatineau, Cain 09 22 1973, TRTC 48034. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton 08 24 1963, 1971, WK 1575, 5200; butte area north of Anchorage, Kempton 08 8 1960, 09 25 1982, WK 1574, 6429. **Washington:** Seward Park, Seattle, Stuntz (Brough 48) 11 15 1956, WTU; Olympic Hot Springs, Olympic N.P., Smith (17192) 09 22 1941, MICH; Money Creek, Litke 09 1 1981, WTU 21467. **Idaho:** near Coolin, Priest Lake, Bonner Co., Harrison (6355) 10 6 1966, MICH; Capoose Creek, Seven Devils Mountain, Idaho Co., Smith (46550) 08 23 1954, MICH; Seven Devils Range, Hawker 08 10 1962, K. **Oregon:** Bellview-Tolman Creek area near Ashland, Isaacs (Is 1456) 11 11 1961, WTU. **Minnesota:** Lake Co., Paim 08 20 1956, TRTC. **Ohio:** Antioch Forest, Yellow Springs, Cooke 10 20 1962, WSP 55743. **New Mexico**: east of Santa Fe, Simms 09 19 1965, WSP 57198. **SWEDEN:** Uppsala Botanical Garden, Melderis 09 28 1946, K. **UNITED KINGDOM:** The Staits, North Hampshire, 10 23 1960, IMI 83683. **NETHERLANDS:** between Bergen and Schoorl, Maas Geesteranus 10 2 1965, TRTC 14777; unknown, Persoon, K (holotype of *Helvella leucophaea*). **Exsiccata:** Fungi Suecici, Västmanland, Sala, Sweden, Morander (1348) 07 24 1948, s.n. *Helvella crispa*, WSP 31528; Flora Hungarica Exsiccata, Sectio Botanica Musei Nationalis Hungarici, Cent III, Fungi 29, 209, Iglófüred, Filarszky 08 1913, s.n. *Helvella crispa*, TRTC; M.C. Cooke, Fungi Britannici Exsiccati, Editio Secunda, 541, Durncore, United Kingdom, Cooke, s.n. *Helvella crispa*, IMI 29260; E. Bartholomew, Fungi Columbiani, 3329, London, Ontario, Canada, Dearness 10 1908, 1909, 1910, s.n. *Helvella crispa*, WSP 3107.

Helvella lactea Boudier, 1907, Histoire et Classification des Discomycètes d'Europe p. 36.

Type Material: Holotype PC, examined.

Apothecium: 4-40 mm diam., 6-35 mm high, irregularly lobed, often bilobate, margin reflexed and fused to stipe, rarely free from stipe in immature specimens, hymenium white fresh, when dried bright yellow brown to medium brown, lacking grey pigmentation, undulate-rugose to nearly smooth, excipular surface white, when dry cream to pallid yellow, glabrous or rarely very finely pubescent, ribs virtually absent or extending onto basal half of excipular surface. **Stipe:** 9-95 x 2-20 mm, equal, tapering, or enlarged to base, white, when dry cream to bright yellow, very finely pubescent, strongly ribbed, lacunose, internally chambered, occasionally sulcate and solid in small specimens. **Asci:** 287-325 x 13.2-20.1 µm. **Paraphyses:** 3.9-7.0 µm diam. at apex, clavate, enlarged gradually to apex, hyaline, contents finely granular. **Ascospores:** 15.6-22.1 x 10.7-13.9 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on soil or litter in coniferous or mixed woods. Associated trees: *Abies* sp. Fruiting from July (exact date unknown) in MB to December 25 in WA.

Distribution: Infrequent in boreal and coastal regions from MB and WA. This species is newly reported from western North America. Collections from coastal WA significantly extend its range to the west in North America, while collections from MB represent the most northerly collections described from North America. The disjunct population is locally common in WA. Also known from eastern North America (Dissing 1966a; Dissing and Lange 1967), Europe (Dissing 1966b; Calonge and Arroyo 1990), and Asia (Liu and Cao 1988). Map 9.

Notes: Although similar in colour, *H. crispa* (q.v.) is distinct in its cream to pale brown pubescent excipular surface and inrolled free apothecial margin. *Helvella lactea* is distinguished from the closely related *H. lacunosa* (q.v.) by the lack of grey pigmentation. Even pale forms of *H. lacunosa* (e.g., SA 211, Smith 75904 MICH) are grey in fresh and dry specimens, while *H. lactea* is entirely white when fresh and yellow, especially on the stipe, when dried. *Helvella lactea* has a much more restricted distribution than *H. lacunosa*. Häffner (1987, 1991) considers this species a pigmentless form of *H. lacunosa*. One collection (WTU Stz 12122) was mixed with *H. lacunosa*. Close association between these two species may support recognizing *H. lactea* as a variety or form.

Collections Examined: **CANADA: Manitoba:** Indian Bay, Shoal Lake, Tan 07 1966, WIN. **Ontario:** Bear Island, Lake Timagami, Jackson 08 21 1937, TRTC 11140; Algonquin P.P., Jackson 09 15 1939, TRTC 18492. **USA: Washington:** Friday Harbor, San Juan Island, Stuntz (Stz 12122) 10 30 1960, WTU; Robinswood Park, Bellevue, Martin (FVB 1702) 11 16 1972, WTU; Tacoma Prairies, Snyder (50) 11 10 1934, WTU; Yelm, Stuntz (Stz 4870) 10 17 1948, WTU; Rainier, (Stz 6116) 11 5 1950, WTU; Rainier woods, Stuntz (Stz 4921), 11 13 1948, WTU; Humbug Mountain trail, Ardrey (901) 12 25 1985, WTU. **SWEDEN:** Botanic Garden, Uppsala, Hylander 07 25 & 08 2 1939, K. **FRANCE:** Meaux, Dumeé 06 1902, PC (holotype). **SPAIN:** Cadalonia, Reid 11 2 1985, K.

Helvella lacunosa Afzelius : Fries, 1823, Systema Mycologicum 2: 15.

≡*Helvella lacunosa* Afzelius, 1783, Kongl. Vetensk. Akad. Nya Handl. 4:303.

=*Helvella mitra* Persoon, 1797, Commentario de Fungis Clavaeformibus sistens specierum hus usque notarum descriptiones cum differentiis specificis, nec no autorum synonomis p. 61. (type K, examined)(later homonym); non *Helvella mitra* Linnaeus (=*H. crispa*).

=*Helvella subcostata* Cooke, 1879, Mycographia, seu icones fungorum Fig. 169. (holotype K, examined).

=*Helvella sulcata* Afzelius: Fries, 1823, Systema Mycologicum 2: 15. (*fide* Dissing 1966b).

(additional synonyms see Dissing 1966b).

Type Material: not available (*fide* Dissing 1966b).

Fig. 8.

Apothecium: 5-47 mm diam., 4-60 mm high (up to 70 mm diam. fresh), irregularly lobed and reflexed, rarely trilobate to bilobate or irregularly saddle-shaped, margin reflexed even when immature, margin fused to stipe or rarely free, hymenium black to dark grey or dark brown (fresh and dried), rarely pale grey brown or somewhat mottled with darkly and lightly pigmented regions, undulate-rugose, excipular surface pallid grey to dark grey brown, glabrous, ribs absent or extending to near marginal regions of excipular surface. **Stipe:** 20-140 x 3-35 mm, equal or enlarged at base, rarely tapered slightly to base, dark grey brown or pallid in part especially if submerged in substratum, glabrous, highly ribbed, lacunose, internally chambered, rarely sulcate and solid especially at apex. **Asci:** 238-268 x 13.1-17 µm. **Paraphyses:** 3.9-(10) µm diam. at apex, terminal cell 124-165 µm long, clavate, enlarged gradually to abruptly at apex, brown, contents finely granular. **Ascospores:** 14.5-(20) x 10-13 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious, subcaespitose, or scattered on soil or litter, rarely on rotted or burnt wood, in coniferous or mixed woods. Associated trees: *Picea glauca, Picea mariana, Picea sitchensis, Pinus contorta, Pinus banksiana, Pinus ponderosa, Pseudotsuga menziesii, Abies balsamea, Abies grandis, Larix occidentalis, Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera, Betula occidentalis, Alnus* sp., and *Acer macrophyllum*. Associated shrubs: *Salix discolor, Salix bebbiana, Salix planifolia, Salix myrtillifolia, Salix alaxensis, Salix reticulata, Alnus crispa, Betula pumila, Ledum groenlandicum, Shepherdia canadensis, Juniperus communis, Arctostaphylos viscida, Cornus stolonifera, Symphoricarpos* sp., and *Rosa* sp. Fruiting from June in MB to April 15 in coastal southern BC. November through April fruitings are known only from southern portions of the study area in BC, WA, ID, and OR. June to August collections are known only from AK, YT, NWT, BC, AB, SK, and MB.

Distribution: Widely distributed in boreal, montane, coastal, and arctic regions from AK, YT, NWT, BC, AB, SK, MB, WA, ID, and OR. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b), and Asia (Liu *et al.* 1985; Imai 1954; Korf and Zhuang 1991). Map 11.

Notes: The species is characterized by the darkly pigmented ascocarp, reflexed apothecial margin, and glabrous excipular surface and comprises *H. lacunosa sensu lato* (*sensu* Dissing 1966b, Abbott and Currah 1988, Calonge and Arroyo 1990). We could not support recognition of taxa, such as *H. sulcata sensu* Weber 1972 or Benedix 1972, as either a species or variety. Closely related species include *H. lactea* (q.v.) which differs in colour, *H. palustris* (q.v.), and *H. phlebophora* Patouillard & Doass. which has smaller ascocarps, convex apothecia with the margin free and reflexed, and a solid stipe. Häffner (1987, 1991) suggests that *H. phlebophora*, *H. palustris*, and *H. lactea* are best treated as varieties of *H. lacunosa*. Occasionally, ascocarps approaching the overall morphology of *H. phlebophora*, (as described in Dissing 1966b; Breitenbach and Kränzlin 1984 edition only) appear with typical specimens of *H. lacunosa* (e.g., ALTA 8314). *Helvella palustris* was synonymized with *H. lacunosa* by Dissing (1966b), but was accepted by Weber (1972) and Harmaja (1977b). After examination of the holotype and collections from Michigan, *H. palustris* is tentatively accepted as distinct from *H. lacunosa* by the small apothecium, often with free margin, slender stipe with few or no lacunae and little anastomosis between ribs. Some collections (e.g., TUR 78771) are intermediate between *H. lacunosa* and *H. palustris*. Many collections of *H. palustris* are from bogs or stream banks and associated with bryophytes.

Collections Examined: CANADA: Yukon: Watson Lake, Abbott (SA 179, 180, 185, 192, 193, 194) 08 14 & 20 1989, SA. **Northwest Territories**: Striae Hill, Axel Heiberg Island, Beschel 08 10 1962, DAOM 91441; Baker Lake, Ohenoja 08 1962, DAOM 155310; Hay River, Green 09 5 1982, UVIC. **British Columbia:** Muncho Lake P.P., Abbott (SA 211, 212, 213) 08 21 1989, SA; Tetsa River P.P., Abbott (SA 220, 227, 230) 08 22 1989, SA; Mount Robson P.P., Abbott (SA 925) 08 29 1993, SA; near Valemount, Wohlebbe 09 20 1987, ALTA 8366; Mahood Lake, Person 10 10 1977, UBC F3282; 10 km north of Clearwater, Goward 09 12 1982, DAOM 191776; Shuswap Lake near Scotch Creek, Goward 10 2 1982, DAOM 191777; Revelstoke, Funk 10 10 1962, DAOM 14578; Brandywine Falls near Whistler, Bandoni 10 21 1977, UBC F3281; Brandywine Falls P.P., Mackinnon 10 4 1980, UBC F587; Cheekye, Bandoni 09 26, UBC F3274; Procter, Linton 10 18 1977, UVIC; Cottonwood Lake near Nelson, Harrison (6030A) 07 6 1966, MICH; Lions Bay, Perrin 10 8 1968, UBC F3278; Lynne Valley Park, North Vancouver, Kroeger 11 18 1981; UBC F10244; Lynne Valley Park, North Vancouver, Bandoni 10 4 1959, UBC F3276; Lynne Canyon, Vancouver, Pantidou 10 3 1962, DAOM 92265; UBC endowment lands, Vancouver, Waugh 10 29 1958, UBC F3272; UBC endowment lands, Vancouver, Brough (661) 11 24 1972, UBC F1345, F3279; UBC endowment lands, Bandoni 12 8 1962, UBC F3277; UBC campus, Brough (626) 11 3 1967, UBC F3273; UBC campus, Redhead 11 18 1969, UBC F1344; UBC campus, Bandoni 10 27 1962, 04 15 1988, DAOM 91102, 199922; Little Qualicum Falls P.P., Vancouver Island, Lee 10 30 1979, UBC M047; Long Beach, Pacific Rim N.P., Brigham 11 8 1980, Wood 11 25 1974, UVIC; Spectacle Lake, Vancouver Island, Pantidou 10 19 1962, DAOM 92263; Robert's Bay, Vancouver Island, Macoun 10 21 1913, UBC F3292; Langford, Vancouver Island, Hinders 11 11 1943, DAVFP 21936; Francis Park near Victoria, Vancouver Island, Egger (857) 12 27 1981, DAOM 199857; Mount Douglas Park, Victoria, Vancouver Island, Egger 09 29 1983, DAOM 199768; Crescent Beach, Krajina 10 10 1970, UBC F3280; Saltspring Island, Paden 10 13 1969, UVIC; Saturna Island, Pillsbury 11 13 1960, UBC F3275; Cortez Island, Ring 11 11 1986,

UVIC. **Alberta:** Fawcett Lake, Abbott 09 3 1988, ALTA 8314, 8315; Iosegun Lake, Abbott (SA 111, 112, 118) 08 4 & 5 1989, SA; Musreau Lake, Abbott (SA 248) 08 26 1989, SA; William A. Switzer P.P., Abbott (SA 267, 271) 08 27 1989, SA; William A. Switzer P.P., Osis (SA 388) 09 2 1990, SA; Wagner Natural Area, Abbott (SA 1037, 1051, 1108) 08 25 & 09 4 1994, 08 19 1995, SA; Forest Reserve, Edmonton, Kennedy 09 15 1976, ALTA 7291; Devonian Botanic Garden near Devon, Abbott (SA 1082, 1130, 1140) 08 24 1987, 08 9 & 24 & 09 12 1995, ALTA 8271, SA, K; Alder Flats, Zelmer (SA 929) 09 25 1993, SA; Riley Lake, Jasper N.P., Abbott (SA 1054) 09 7 1994, SA; Wabasso, Jasper N.P., Zelmer (SA 927) 07 17 1993, SA; Athabasca River valley 3 km west of Sunwapta Falls, Jasper N.P., Abbott (SA 372) 08 2 1990, SA. **Saskatchewan:** Turtle Lake near Turtleford, Zelmer 08 1994 (not accessioned). **Manitoba:** Churchill, Huhtinen 08 19 1981, TUR 78771; Victoria Beach, Bisby 07 29 1928, DAOM 206811; Indian Bay, Shoal Lake, Tan 06 1966, WIN. **Ontario:** Angus, Cain 10 10 1954, WSP 43248. **USA: Alaska:** Eagle summit 175 km north of Fairbanks, Kempton 08 19 1971, WK 5348; Fairbanks, Kempton 08 7 1970, WK 4619; Nome on Seward Peninsula, Kempton 08 25 1970, WK 4793; Nancy Lake, Susitna valley, Kempton 08 15 1968, 09 7 1985, WK 1570, 6470; Eklutna Lake north of Anchorage, Kempton 08 24 1971, WK 5189; Anchorage, Kempton 08 30 1966, 08 31 1971, 09 5 1986, WK 1565, 5395, 6508; Glacier Bay National Monument, Cooke 09 7 & 8 & 10 1979, 08 31 & 09 5 & 9 1981, WSP 65708, 64400, 64439, 64797, 64854, 67209, 66865, 66866, DAOM 176194, 176213, MU F34857, F36149; near Haines, Kempton 09 20 1970, 09 16 1971, WK 4953, 5596; near Juneau, Kempton 09 13 1967. **Washington:** Nooksack Falls, Mount Baker area, Whatcom Co., Symons 11 11 1965, UBC F3283; San Juan Island, Waugh 11 19 1966, UBC F3284; Friday Harbor, San Juan Island, (Stz 12122, 12222) 10 30 & 11 12 1960, WTU; Whidbey Island, Stuntz (Stz 13874, 14513, 14552) 09 8 1966, 11 5 1967, 11 14 1967, WTU; Sandy Hook, Whidbey Island, (Stz 13854) 09 8 1966, WTU; Langley, Whidbey Island, (Stz 14538) 09 14 1962, WTU; east of Springdale, Cooke 09 27 1947, WSP 24512; Barnes Creek trail, Olympic N.P., Clallam Co., Cooke 10 26 1950, WSP 25049; near Staircase, Olympic N.P., McKenny, 10 24 1962, UBC F3287; Bremerton, Flett 11 26 1930, WSP AS29265; Marysville, Grant 11 1931, MU F14172; Mercer Island near Seattle, Parker (Herbarium Young Naturalists Society 200) 12 1893, WTU; Seward Park, Seattle, (Stz 11583) 10 19 1959, WTU; Seattle, Zeller (57) 1911, WTU; Seattle, Snyder (29) fall, WTU; Watermain Woods, Redmond, SDLB 11 2 1980, WTU; California Creek near Valley Ford, Cooke 11 8 1947, WSP 24513; north of Copalis, Clallam Co., Williams (JWL 999) 10 11 1970, WTU; Burnis Lake near Olympia, Williams (JWL 1719) 11 3 1973, WTU; Olympia, Snyder 12 4 1933, WTU; south of Spanaway, Simms 11 12 1966, WSP 57197; Tahoma Vista, Mount Rainier N.P., van de Bogart (FVB 2245) 10 28 1973, WTU; south of Cispus turnoff, van de Bogart (FVB 1036) 10 23 1971, WTU; Bear Creek, Grouse Flats, Garfield Co., Shaw 11 1 1954, WSP 41533; Medicine Creek drainage, Asotin Co., Shaw 11 2 1959, WSP 47623; Bingen, Suksdorf 01 24 1900, WSP 27480; Falcon Valley, Klickitat Co., Suksdorf 11 1 1901, WSP 27479; Lee Forest near Maltby, Brough (12) 10 16 1956, WTU; Lee Forest near Maltby, Cohen (Stz 6982) 11 16 1952, WTU; Millersylvania State Park, Spur (Stz 16987) 11 13 1971, WTU; Fort Lewis, Stuntz 11 1 1934, WTU; Troublesome Creek, (Stz 14954) 09 26 1968, WTU; Browns Lake, van de Bogart (FVB 2451, 2570) 11 3 1973, WTU; unknown, Browns 11 13 1971, WTU 906, 11 16 1974, WTU 3295, Isaacs (Is 1362) 03 21 1961, Ardery (1290), Williams (JWL 33), WTU. **Idaho:** Nordman, Shaw 10 16 1954, WSP 41576; Priest Lake, Rogers 10 27 1963, WSP 56475; Priest River Experimental Forest, Slipp 10 28 1940, WSP 49792; Hayden Lake, Kootenai Co., White 10 1959, WSP 47630; Moscow Mountain, Ward 09 28 1947, WSP 30113; Moscow Mountains, Miller 09 14 1964, WSP 54048, 54484; Laird Park, Latah Co., Miller 10 17 1962, WSP 52704; Clearwater Canyon east of Lenore, Cooke 11 30 1946, WSP 24511; Rackliff Ridge trail along Selway River, Nez Perce National Forest, Cooke 10 26 1946, 11 1 1947, WSP 24510, DAOM 26783; Rackliff Creek, Idaho Co., Cooke 10 22 1949, WSP 30112; Ticks Creek road, van de Bogart (FVB 3729) 09 9 1976, WTU. **Oregon:** Coos Co. Forest, Ardrey (538), WTU; west of Ruch, Isaacs (Is 558, 560) 01 26 1958, WTU; Bellview-Tolman Creek area, Isaacs (Is 1455) 11 11 1961, WTU; McReady Springs, Paden 04 20 1972, UVIC. **California:** Lake Siskiyou, Bangsberg 04 25 1980, WSP 66107; Bear Springs, Mount Shasta, Cooke 10 10 1958, WSP 55868; Mineral, Cooke 09 2 & 3 1977, 09 1978, 10 6 1981, WSP 63395, 63396, 60991, 67210; Jonesville, Copeland 09 30 1938, WSP 31526; San Francisco Bay region, Morse spring 1934, UBC F3296; Walnut Creek, Contra Costa Co., Baltzo 01 8 1984, UBC F13113. **Michigan**: Tahquamenon, Bas 08 12 1963, UBC F3285; Pine Barrens, Topinabee, Smith (75904) 08 10 1968, MICH. **SVALBARD:** Endahlen, Currah 08 17 1988, ALTA 8305; Sverdrupbyen, Currah 08 16 1988, ALTA 8313. **UNITED KINGDOM:** Twyford Forest, Lines, Roberts 09 9 1988, IMI 310080; Andover, Hampshire, Herbarium Berkeley 1879, K (holotype of *Helvella subcostata*). **BELGIUM:** Demoulin (CBS 404.74), UAMH 6474 (living culture) **SPAIN**: Cuenca, Calonge & Arroyo 05 28 1985, K. **NETHERLANDS:** Persoon, K (type of *Helvella mitra*). **Exsiccata**: Mycobiota of North America, 246, Rackliff Creek, Nez Perce National Forest, Idaho, USA, Cooke 11 16 1946, s.n. *Helvella lacunosa*, WSP 21369; Ellis and Everhardt's

Fungi Columbiani, 1931, Stockton, Kansas, USA, Bartholomew 06 3 1903, s.n. *Helvella lacunosa*, WSP 3108; Pacific Slope Fungi, 256, Stanford University, Santa Clara Co., California, USA, Banker 02 18 1902, s.n. *Helvella lacunosa*, WSP 23883; California Fungi, 316, Trinidad, Humbolt Co., California, USA, Parks 11 1931, s.n. *Elvella mitra*, WSP 35290, WTU, TRTC.

Helvella maculata N.S. Weber, 1975, Beihefte Nova Hedwigia 51: 27.

Type Material: Holotype MICH, examined.

Fig. 7.

Apothecium: 10-45 mm diam., 5-26 mm high (up to 40 x 30 mm fresh), irregularly lobed, margin strongly inrolled over hymenium initially, free from stipe, hymenium light to dark brown to grey brown (fresh and dried), sometimes mottled with patches of paler pigmentation, undulate-rugose, excipular surface white or cream to pallid grey, densely pubescent to villose, ribs absent or extending onto basal third of excipular surface. **Stipe:** 10-120 x 3-30 mm, enlarged at base, white, often with localized regions of brown to grey brown pigmentation, finely pubescent, highly ribbed, lacunose, internally chambered. **Asci:** 268-300 x 15.2-19 µm. **Paraphyses:** 5.6-9 µm diam. at apex, clavate, enlarged gradually to abruptly at apex, brown, finely granular. **Ascospores:** 18-23.4 x 11-14 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate, with large, central, broadly ellipsoidal to subglobose oil guttule.

Habitat: Solitary, gregarious, or scattered on soil or duff in coniferous or mixed woods. Associated trees: *Picea glauca, Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla, Populus tremuloides, Populus balsamifera*. Associated shrubs: *Salix* sp., *Rosa* sp., *Viburnum edule, Cornus stolonifera,* and *Alnus* sp. Fruiting from August 1 in AB to November 30 in coastal WA. Collections from January to March in coastal BC, WA and OR and May in BC are considered unusual for this typically autumnal species. August and September collections are usual for AK, AB and MB, while October and November collections are typical of WA, ID, and BC.

Distribution: Widely distributed in montane, coastal, and boreal regions, but abundant only in the west from AK, BC, AB, MB, WA, ID, and OR. The range is significantly expanded eastward to MB and north to AK. Distributed only in western North America (Weber 1975) and China (Cao 1988; Liu and Cao 1988). Map 10.

Notes: This species is closely related to *H. crispa* (q.v.) and *H. fusca* (q.v.)(see notes under *H. crispa*). The darkly pigmented apothecium has lead to confusion with *H. lacunosa* (q.v.), which has a reflexed apothecium margin even in immature fruiting bodies, and the margin fused to the stipe. *Helvella maculata* was originally described as having consistently mottled apothecia (Weber 1975). This feature is found in Chinese material (Cao pers. comm.; Cao and Liu 1990), but in fresh and dried material examined in this study, many were uniform in colour. Cao (pers. comm.) has suggested that specimens with uniform pigmentation may be referable to another taxon, but there are no correlating features supporting this. Mottled hymenia are sometimes found in *H. lacunosa* (q.v.), *H. albella* (q.v.), and *H. elastica* (q.v.), and may be due in part to the degree of exposure of the hymenium at the surface of the substratum. Darkly pigmented regions on the white stipe are sometimes observed in *H. maculata*.

Collections Examined: CANADA: British Columbia: Brandywine Falls near Whistler, Bandoni 10 27 1977, UBC F3281; Yale, Macoun 05 17 1889, DAOM 44703; Sidney, Vancouver Island, Macoun 1912, UBC F3297; Mount Douglas Park, Victoria, Vancouver Island, Paden 11 11 1988, UVIC; University of Victoria campus, Vancouver Island, Paden (JWP 1378) 01 5 1987, UVIC; University of Victoria campus, Vancouver Island, Fogarty 11 18 1988, UVIC; ravine near Houlihan Way, Gordon Head, Goodacre 11 8 1976, UVIC. **Alberta:** William A. Switzer P.P., Osis (SA 387) 09 2 1990, SA; west-end ravine, Edmonton, Osis & Gibson 08 1 1988, ALTA 8301; near Breton, Osis & Gibson 08 20 1988, ALTA 8304; Fish Lake near Nordegg, Abbott (SA 380) 08 3 1990, SA; Bragg Creek P.P., Danielson (RMD 2343) 09 18 1976, ALTA 8292; Fish Creek P.P., Calgary, Danielson (RMD 359) 08 20 1972, DAOM 143866; Kananaskis, Vellinga (SA 295) 08 1989, SA, L. **Manitoba:** Clear Lake, Bisby 09 23 1933, 08 17 1935, DAOM 206812, 206808. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton 08 11 & 24 1963, WK 1576, 1577; butte area north of

Anchorage, Kempton 09 22 1965, WK 1578; mile 40 Haines cutoff road, Kempton 09 20 1970, WK 4962. **Washington:** Friday Harbor, San Juan Island, Isaacs (Is 2019) 11 11 1962, WTU; Friday Harbor, San Juan Island, Stuntz (Stz 8996, 11594, 12087, 15306, 15869, 17044) 11 13 1954, 11 1 1959, 10 16 1960, 11 30 1968, 11 29 1969, 11 26 1971, WTU; Friday Harbor, San Juan Island, Williams (JWL 564, 1307) 11 9 1969, 11 7 1971, WTU; Friday Harbor , San Juan Island, van de Bogart (FVB 3864) 11 1976, WTU; San Juan Island, Bandoni 11 20 1966, UBC F3286; Mutiny Bay, Island Co., van de Bogart (FVB 3362) 03 2 1975, WTU; east of Duvall, van de Bogart (Stz 14460) 11 5 1967, WTU; Olympia, Snyder 10 8 1933, WTU; unknown, van de Bogart (FVB 3687) 11 15 1975, (Stz 12121, 13810, 15221) 10 28 1966, 11 10 1968, WTU. **Idaho:** Hoodoo Mountain, Bonner Co., Smith (NJS 2124) 10 5 1968, MICH (holotype); Jerome Creek, Latah Co., Paden & Tylutki 10 11 1964, WSP 56274; Moscow Mountain, Latah Co., Milne 10 18 1965, TRTC. **Oregon:** near Gold Hill, (Stz 10929) 03 27 1959, WTU.

Extralimital Species

Helvella fusca Gillet, 1879, Champignons de France. Les Discomycètes, p. 9.

Type Material: Neotype selected here: S, Italy, Al Deserto, Bresadola 05 21 1898, examined.

Distribution: Restricted to Europe (Dissing 1966b).

Notes: This species is similar to *H. maculata* (q.v.) in colour, but differs in excipular pubescence and habitat. Vernal and autumnal collections are known for both species. This species is reported from Alaska and Oregon (Kempton and Wells 1970; Larsen and Denison 1978), but no specimens were encountered during this investigation and reports are likely based on *H. maculata*. Although there is no authentic material of Gillet (Dissing 1966b), the modern concept of *H. fusca* is primarily based on the description and excellent specimens of Bresadola preserved in S. The 'Al Deserto 05 21 1898' (illustrated in Dissing 1966b) is chosen as neotype.

Collections Examined: **ITALY:** Al Deserto, Bresadola 05 21 1898, S (neotype); bei Trient, Bresadola 06 1898, S; prope Trento, Bresadola 05 18 1903, S; Gocciadora, Bresadola 10 1901, S.

Helvella palustris Peck, 1880, Annual Report New York State Museum 33: 31.

=*Helvella philonotis* Dissing, 1964, Botanisk Tidsskrift 60: 117. (*fide* Weber 1972).

Type Material: Holotype NYS, examined.

Distribution: Known from eastern North America (Weber 1972; Huhtinen 1982) and Europe (Harmaja 1977b, Dissing 1966b, as *H. philonotis*; Hallgrimsson 1968, as *H. philonotis*).

Notes: This species is closely related to *H. lacunosa* (q.v.), but is separated by its small size, slender solid stipe with parallel ribs which show little anastomosis and no lacunae, and the discoid to convex apothecium which remains free from the stipe. Häffner (1987) considers it a variety of *H. lacunosa*, but the correlation of many morphological features warrants tentative retention of specific status. No specimens from the study region have been assigned to this taxon, but several collections of *H. lacunosa* (e.g., DAOM 91441, TUR 78771) are intermediate. Reports from northern Manitoba (Huhtinen 1984; Hutchison *et al.* 1988) are based on TUR 78771, which contains some specimens with chambered and lacunose stipes typical of *H. lacunosa*. Other collections of *H. lacunosa* contain immature fruiting bodies resembling *H. palustris*. The collection from Norway shows more similarities to the description of *H. philonotis* (Dissing 1966b) than to other collections of *H. palustris* examined here.

Collections Examined: **CANADA: Québec:** Astray Lake, Schefferville, Huhtinen & Kosonen 08 12 1979, TUR 63425. **USA: Michigan:** Tahquamenon Falls State Park, Brough UBC F3295; UMBS, Emmet Co., Rogerson 08 6 1964, UBC F3293; south of Rose City, Ogemaw Co., A.H. Smith 07 16 1963, UBC F3294. **New York:** Manlius Center, Peck 08, NYS (holotype); Southbay near Whitehall, Burnham 08 20 1908, NYS. **NORWAY:** south of Kongsvoll, Oppland, Kristiansen 08 8 1991, RK.

Helvella Subgenus *Leucomelaenae* (Dissing) S.P. Abbott *comb. nov.*

≡*Helvella* section *Leucomelaenae* Dissing, 1966, Dansk Botanisk Arkiv 25: 36.
=*Helvella* section *Acetabulum* Dissing, 1966, Dansk Botanisk Arkiv 25: 49.
=*Helvella* section *Solitariae* Häffner, 1987, Beihefte zur Zeitschrift für Mykologie 7: 46.

Type Species: *Helvella leucomelaena* (Persoon) Nannfeldt, 1941, in Lundell and Nannfeldt, Fungi Exsiccati Suecici Praesidium Upsaliensis Fasciculata 19-21: 21, no. 952.

Ascocarp: cupulate to irregularly cupulate, subsessile to short stipitate; apothecium margin incurved or reflexed; hymenium smooth or sparingly rugose, shades of brown and grey; excipular surface pubescent to villose, ribs absent or extending to marginal region; stipe present as fluted base or distinct and prominently ribbed, solid or chambered, pubescent. **Asci:** bases aporhynchous to pleurorhynchous. **Ascospores:** broadly ellipsoidal to ellipsoidal, hyaline, smooth, surface with SEM finely rugose to nearly smooth, uniguttulate, with large, central, globose to broadly ellipsoidal oil guttule.

Notes: Subgenus *Leucomelaenae* contains indistinctly to distinctly stipitate species with prominently ribbed stipe and cupulate to reflexed apothecia. The subgenus comprises the sections *Leucomelaenae* and *Acetabulum* of Dissing (1966b) and section *Solitariae* of Häffner (1987), and closely corresponds to the genus *Acetabula* (*sensu* Boudier 1907).

Key to species of *Helvella* subgenus *Leucomelaenae*

1. Ascus base simple (aporhynchous)..... 2
1'. Ascus base forked (pleurorhynchous)..... 3
   2. Ascospores 18-24 µm long; setoid paraphyses absent..... ***H. leucomelaena***
   2'. Ascospores 23-28 µm long; setoid paraphyses present..... ***H. crassitunicata***
3. Distribution in arctic and alpine tundra regions..... 4
3'. Distribution in boreal and montane forest regions..... 5
   4. Hymenium red brown; stipe indistinct; excipular surface lacking ribs or indistinctly ribbed over basal portion..... ***H. aestivalis***
   4'. Hymenium brown; stipe distinct; excipular surface prominently ribbed over basal half..... ***H. verruculosa***
5. Ascospores very broadly ellipsoidal to subglobose (12.5-16 µm diam.)..... 6
5'. Ascospores ellipsoidal to broadly ellipsoidal (10-13.5 µm long)..... 7
   6. Ascocarps small to medium (4-22 mm diam. dried); hymenium medium to dark grey brown; excipular surface densely pubescent to villose..... ***H. unicolor***
   6'. Ascocarps large (50-90 mm diam. dried); hymenium light to medium brown; excipular surface pubescent..... ***H. robusta***
7. Ribs on excipular surface extending to marginal area, branched and anastomosed..... 8
7'. Ribs on excipular surface, if present, extending only slightly onto basal portion, simple and unbranched..... 9
   8. Ribs sharp-edged; excipular surface medium brown to yellow brown; ascospores 16-20 x 11-13.5 µm..... ***H. acetabulum***
   8'. Ribs blunt-edged; excipular surface medium to light grey brown, lacking yellow coloration; ascospores 14.5-20 x 9.5-12.5 µm..... ***H. costifera***
9. Stipe medium to pale brown, with conspicuous, dark pubescence; ribs extending onto basal half of excipular surface..... ***H. hyperborea***
9'. Stipe white to grey brown, with hyaline pubescence; ribs absent from excipular surface or extend only onto basal region..... ***H. solitaria***

Helvella acetabulum (Linnaeus : Fries) Quélet, 1886, Enchiridion Fungorum, p. 275.

≡*Peziza acetabulum* Linnaeus, 1753, Species Plantarum 2: 1181.

≡*Peziza acetabulum* Linnaeus : Fries, 1823, Systema mycologicum 2: 44.

≡*Paxina acetabulum* (Linnaeus : Fries) Kuntze, 1891, Revisio generum plantarum 2: 864.

(additional synonyms see Dissing 1966b).

Type Material: Lectotype in Valliant, 1727, Botanicon Parisienne 57, Plate 13, Figure 1 (*fide* Dissing 1966b).

Apothecium: 10-80 mm diam., 5-20 mm high, deeply cupulate, margin expanding to slightly reflexed in age, hymenium medium to dark brown (fresh and dried), smooth, excipular surface brown near margin, yellow brown to white at base, pubescent to densely pubescent, prominently ribbed, with sharp, branching and anastomosing ribs extending to marginal region. **Stipe**: 3-45 x 2-30 mm, equal or tapered to base, white to light yellow brown, pubescent, highly ribbed, rarely lacunose, ribs sharp or rarely blunt, branched and anastomosed, internally chambered. **Asci**: 260-330 x 16-18 µm, pleurorhynchous. **Paraphyses:** 4-6 µm diam. at apex, clavate to nearly equal, enlarged gradually to apex, pale brown, contents finely granular. **Ascospores**: 16-20 x 11-13.7 µm, broadly ellipsoidal, hyaline, smooth, with SEM surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious on soil or litter in coniferous, mixed or deciduous woods. Associated trees: *Populus tremuloides, Populus balsamifera, Arbutus menziesii, Quercus garryana, Alnus* sp., *Thuja plicata, Picea glauca* and *Pseudotsuga menziesii*. Associated shrubs: *Cornus stolonifera* and *Amelanchier alnifolia*. Fruiting from March 21 in OR to July 15 in BC.

Distribution: Widely distributed, although infrequent in boreal, montane and coastal regions from BC, AB, MB, WA, ID, OR, and WY. Also in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987), and Asia (Liu *et al.* 1985). Map 13.

Notes: This species is most closely related to *H. costifera* (q.v.), and perhaps represents a single variable species. They are distinguished by ascocarp colour, ribbing of stipe and excipular surface, and fruiting period. *Helvella unicolor* (q.v.) is distinguished on ascospore morphology and less prominent ribbing of stipe and excipular surface. *Helvella verruculosa* (q.v.) differs in its smaller ascocarp size, stronger pubescence, less prominent stipe and ribbing of excipular surface, and habitat (see also notes under species mentioned above). The lack of extant holotype material seriously impedes characterization of this species, and distinction from similar taxa (especially *H. costifera*) is uncertain based on the lectotype illustration.

Collections Examined: CANADA: British Columbia: Vancouver, Waugh 07 15 1951, DAOM 27436; Bamberton P.P., Vancouver Island, Paden 06 7 1974, 05 6 1987, UVIC; Victoria, Vancouver Island, Robertson 04 14 1973, UVIC; Winter Cove, Saturna Island, Kroeger 04 2 1984, UBC F979. **Alberta:** William A. Switzer P.P., Osis (SA 418) 07 5 1990, SA; Devonian Botanic Garden near Devon, Currah 06 25 1979, ALTA 7958; North Saskatchewan River valley, Devon, Yurkiw & Abbott (SA 1159) 07 3 1996, SA; west of Millet, Kennedy 06 30 1964, ALTA 626; Bow Valley P.P., Danielson (RMD 2046) 07 1 1976. **Manitoba**: Manitoba Agricultural College, Winnipeg, Bisby 07 2 & 10 1932, DAOM 206814; Manitoba Agricultural College, Winnipeg, Bisby & Conners 07 14 1927, DAOM 183375. **Ontario:** Queen's Biological Station, Lake Opinicon, Kendrick 06 9 1963, TUR 38458, DAOM 91836; Lake Simcoe District, Taylor 06 16 1961, WIN. **USA: Washington**: Seattle, Greene (Snyder 123) 04 1929, WTU; Mercer Island east of Seattle, Ziegler (Stz 9369) 04 24 1941, WTU; Tacoma prairies, Snyder 05 15 1935, WTU; Bingen Mountain, Suksdorf 05 1 1899, WSP 27646, 27647; unknown, (Stz 7771) 07 8 1953, (Stz 1009, 18408), WTU. **Idaho**: Priest River Experimental Forest, Slipp 07 4 1941, WSP 50463. **Oregon**: near Goldhill, (Stz 10898) 03 27 1959, WTU; near Central Point, Isaacs (Is 1352) 03 21 1961, WTU; Antelope Creek road near Camp White, Isaacs (Is 518) 03 31 1957, WTU. **Wyoming**: Wyoming, van de Bogart, WTU. **UNITED KINGDOM**: Earlswood, Warwickshire, England, Ellis 05 6 1979, IMI 253044; Esher Common, Surrey, England, Spooner 05 25 1980, K. **NETHERLANDS**: Herbarium Persoon, L 8945-3. **FRANCE**: Corsica, Reid 06 3 1965, K. **SCANDINAVIA**: Öland, Böda parish, road to Bränslegardarna, Schöldström 05 31

1967, K. **Exsiccata**: North American Discomycetes, 1181, Ithaca, New York, USA, Durand 06 3 1901, s.n. *Acetabula vulgaris*, WSP 23744; Ellis and Everhardt's Fungi Columbiani, 1801, Stockton, Kansas, USA, Bartholomew 06 3 1903, s.n. *Acetabula vulgaris*, TRTC; Petrak, Mycotheca generalis, 204, Comit. Győr, Bönyretalap, Hungary, Nagy 05 1928, s.n. *Acetabula vulgaris*, WSP AS18071.

Helvella aestivalis (R. Heim & Remy) Dissing & Raitviir, 1974, Eesti NSV Teaduste Akadeemia Toimetised, Bioloogia 23(2): 105.

≡*Acetabula aestivalis* R. Heim & Remy, 1925, in Heim, Bulletin de la Societé Mycologique de France 41: 460, plate XXIX Figures 10-12.

Type Material: not available (*fide* Dissing and Raitviir 1974).

Fig. 23.

Apothecium: 3-26 mm diam., 1-17 mm high, deeply cupulate, margin inrolled initially, margin often splitting at maturity, rarely split to form a one sided lobe, rarely laterally compressed when immature, hymenium dark red brown to blackish red brown fresh, when dried blackish red brown, smooth, excipular surface dark brown at margin, pale orange/yellow brown at base, densely pubescent, occasionally with dense white marginal pubescence, ribs absent or extending onto basal two thirds of excipular surface. **Stipe**: virtually lacking to indistinct, 1-8 x 1-6 mm, tapered to base, white to pallid yellow/orange brown, pubescent, shallowly ribbed or fluted, sulcate and internally solid or with few chambers. **Asci**: 250-300 x 17-19 µm, pleurorhynchous. **Paraphyses**: 6.0-8.0 µm diam. at apex, clavate, enlarged abruptly at apex, brown to dark brown in mass, contents finely granular. **Ascospores**: (18.0) 20.1-22.7 (25.0) x (12.1) 12.8-15.4 (16.6) µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious or scattered and numerous on soil or humus. Associated shrubs: *Salix* sp., *Cassiope* sp., *Andromeda* sp., and *Dryas* sp. Fruiting from July 17 in YT to August 15 in NWT.

Distribution: Widely distributed in arctic and alpine tundra regions in northern portions of the study area from YT and NWT. This species is newly reported from YT and extends the known range considerably to the west in North America. Circumpolar in North America, Europe (Dissing 1983, 1985; Schumacher and Mohn Jenssen 1992), and Asia (Dissing and Raitviir 1974). A global distribution map is provided in Dissing (1985). Map 14.

Notes: This species resembles *H. verruculosa* (q.v.). Both have northern distributions, are subsessile to short stipitate, and share a densely pubescent excipular surface with ribs often extending from stipe onto the basal portion. The two can be separated by ascocarp colour and spore size. *Helvella verruculosa* also tends to have more pronounced stipe and ribbing. Dissing (1983) reported the ascal bases as aporhynchous, but pleurorhynchous bases with croziers were observed in this study (Fig. 23) in both North American and European material. This feature is perhaps variable and lends support to the merging of sections *Leucomelaenae* and *Acetabulum sensu* Dissing (1966b). *Helvella leucomelaena* can be distinguished by the lack of reddish pigmentation, finely pubescent excipular surface, and spore size and shape. The only other species in the genus with a red brown ascocarp is *H. silvicola* (q.v.) in the subgenus *Silvicolae*.

Collections Examined: CANADA: Yukon: mountain west of Blackstone River, Ginns (18384) 07 17 1984, DAOM 195288. **Northwest Territories**: Hazen camp, Lake Hazen, Ellesmere Island N.P., Richards (77) 07 25 94, ALTA; west side Blister Hill, Ellesmere Island N.P. Richards (78) 07 4 94, ALTA; Alexandra Fjord, Ellesmere Island, Dissing & Raitviir (EI84.48, EI84.15, 84.16, EI84.25, EI84.35, EI84.40, EI84.47, EI84.59, EI84.76, EI84.84) 1984, C; Sverdrup Pass, Ellesmere Island, Cohen (LK84.41) 1984, C; Axel Heiberg Island, Beschel 07 29 1960, DAOM 75774; Axel Heiberg Island, Kuc 08 8 1967, DAOM 124703, 124707; east of Repulse Bay, Ohenoja 08 4 1974, OULU; Coal Harbor, Southampton Island, Savile 08 15 1959, DAOM 67075; Longstaff Bluff, Baffin Island, Parmelee & Seaborn 08 9 1967, DAOM 117582, 117583. **SVALBARD**: near Loven Glacier, Currah 08 12 1988, ALTA 8306; Loven Glacier, Currah 08 12 1988, ALTA 8307.

Helvella costifera Nannfeldt, 1953, in Lundell & Nannfeldt, Fungi Exsiccati Suecici Praesidium Upsaliensis Fasciculata 41-42: 37, No. 2061. (*nomen novum*).

≡*Peziza costata* Fries, 1851, Acta Regiae Societatis Scientiarum Uppsala Ser. 3 Vol. 1: 120. (illegitimate, later homonym)(holotype UPS, examined; isotype K, examined); non *Phallus costatus* Batsch, 1789, Elenchus Fungorum 129. (=*H. lacunosa*); non *Helvella costata* Schweinitz : Fries, 1823, Systema mycologicum 2: 19. (=*H. acetabulum*).

=*Helvella griseoalba* N.S. Weber, 1972, The Michigan Botanist 11: 162. (holotype MICH, examined).

(additional synonyms see Dissing 1966b).

Type Material: Holotype UPS, examined; isotype K, examined. (s.n. *Peziza costata*).

Fig. 3e.

Apothecium: 16-42 mm diam., 10-20 mm high, deeply cupulate, margin slightly inrolled initially, expanding at maturity, sometimes laterally compressed initially, hymenium medium to dark grey brown (fresh and dried), smooth to slightly undulate-rugose, excipular surface medium to pale grey brown, often white near base, finely to densely pubescent, ribbed, ribs white to cream, branching and anastomosing, blunt and rounded, extending to marginal region. **Stipe**: 8-20 x 8-10 mm, tapering to base or nearly equal, white to cream, finely pubescent, strongly ribbed, sometimes sparingly lacunose, ribs blunt, branched and anastomosed, internally chambered. **Asci**: 313-381 x 13.3-17.1 µm, pleurorhynchous. **Paraphyses**: 3.6-6.2 µm diam. at apex, terminal cell 13.3 µm long, clavate, enlarged gradually to apex, pale brown, brown in mass, contents finely granular. **Ascospores**: 14.4-19.7 x 9.6-12.4 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious on soil in coniferous or mixed woods. Associated trees: *Populus tremuloides, Populus balsamifera, Betula papyrifera, Alnus* sp., *Picea glauca,* and *Pseudotsuga menziesii*. Fruiting from June 4 in coastal WA to August 24 in AK.

Distribution: Infrequent in boreal, montane, and coastal regions from AK, YT, AB, WA, and ID. This species is newly reported for AB. Also distributed in eastern North America (Weber 1972; Pomerleau 1980; as *H. griseoalba*), Europe (Dissing 1966b; Häffner 1987; Harmaja 1979a; Benedix 1965 as *Acetabula costifera*), and Asia (Dissing and Raitviir 1974; Cao *et al.* 1990). Map 14.

Notes: This species is often difficult to distinguish from *H. acetabulum* (q.v.). The two species have been separated on the basis of colour, ribbing, and fruiting time (Dissing 1966b; Harmaja 1977b, 1979a). *Helvella costifera* is greyer and the excipulum is not yellow brown. Specimens of *H. costifera* from Norway (RK) are typical except for a strong brown pigmentation (see also Dissing 1966b). The ribs of *H. costifera* are blunt and often more widely spaced than in *H. acetabulum*, but rare specimens otherwise typical of *H. acetabulum* with blunt ribs have been examined. *Helvella costifera* also fruits later (Dissing 1966b), but the collections referred to this taxon from North America overlap with later collections of *H. acetabulum*. The two taxa are tentatively retained, but more correlating features are required. *Helvella unicolor* (q.v.), *H. hyperborea* (q.v.), and *H. robusta* (q.v.) are also close and are distinguishable by characters discussed in the notes under those taxa.

Helvella griseoalba was described by Weber (1972) as distinct from *H. costifera* (which was not recognized from North America) on the basis of pale grey hymenium and lack of pigmentation in the ectal excipulum. Although Häffner (1987) verified the differences in excipulum pigmentation pattern in the type specimens, he questioned the usefulness of this character in specific delimitation. Our observations support Häffners concept of *H. costifera*.

Collections Examined: CANADA: Yukon Territory: Kluane Lake, Ahti (23071) 1967, H. **Alberta**: Shaw Lake near Lac La Biche, Abbott (SA 100) 07 15 1989, SA; 10 km south of

Leduc, Abbott 07 8 1979, ALTA 8264. **USA: Alaska**: Eklutna Lake north of Anchorage, Kempton 08 11 & 24 1963, 07 13 1966, 08 24 1971, WK 1536, 1537, 4013, 5202. **Washington**: Friday Harbor, San Juan Island, Stuntz (Stz 12380) 06 4 1961, WTU. **Idaho**: Rackliff Creek, Idaho Co., Cooke 07 6 1947, WSP 30103. **Michigan**: Grapevine Point, Douglas Lake, Cheboygan Co., Smith (NJS 982) 06 10 1968, MICH (holotype of *H. griseoalba*). **NORWAY**: near Bodo, Nordland, Johnson 07 1 1983, RK. **SWEDEN**: Uppsala Botanic Garden, Fries, UPS (holotype of *Peziza costata*), K (isotype). **Exsiccata**: Fungi Exsiccati Suecici Praesertim Upsalienses, 2061, Uppsala, Sweden, Nannfeldt (9956) 07 9 1948, s.n. *Helvella costifera*, S, K.

Helvella crassitunicata N.S. Weber, 1975, Beihefte Nova Hedwigia 51: 27.

Type Material: Holotype MICH, examined.

Fig. 52.

Apothecium: 4-50 mm diam., 3-33 mm high (up to 100 x 60 mm fresh), deeply cupulate, margin inrolled initially, expanding to shallowly cupulate or somewhat reflexed at maturity, hymenium medium to dark brown fresh, when dried dark brown to blackish brown, smooth to slightly undulate-rugose, excipular surface medium to dark brown, sometimes paler at basal region, pubescent to densely pubescent, ribs extending onto basal half of excipular surface (rarely extending only slightly onto excipulum). **Stipe**: 2-20 x 2-13 mm (up to 50 x 40 mm fresh), flaring and merging with apothecium, medium brown to pallid (especially at base), finely pubescent to pubescent, ribs indistinct to prominent, rounded, widely separated, may be bifurcate branched, but with no anastomosis between ribs, sulcate and internally solid. **Asci**: 350-400 x 17-20 µm, aporhynchous. **Paraphyses**: 5.4-8.8 µm diam. at apex, dimorphic, most thin-walled, terminal cell in some becoming elongated and thick-walled, clavate, expanding gradually to apex, often slightly irregular, terminal cell of thin-walled paraphyses 67-94 µm long, terminal cell of thick-walled paraphyses 235-300 µm long, pale brown to brown, contents finely granular, walls of thick-walled paraphyses pigmented. **Ascospores**: 22.7-27.6 x 12.6-14.6 µm, broadly ellipsoidal or ellipsoidal to subcylindrical, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Single, gregarious, or subcaespitose on soil under conifers. Associated trees: *Picea* sp., *Tsuga mertensiana, Pseudotsuga menziesii*, and *Thuja plicata.* Fruiting from May 20 in WA to October 13 in WA.

Distribution: Endemic to the interior and coastal mountains of northwestern North America, but rare, from AK, BC, and WA. Not known outside the study area. This species is newly reported from BC, and its occurrence in AK (Weber 1975) is confirmed. Map 16.

Notes: This species is unique in the family in its thick-walled paraphyses, and has the largest ascospores in the genus. Harmaja (1977b) discusses the usefulness of the length of the terminal cell of the paraphyses. Although this character is of limited value for some taxa, the thick-walled apical cell of the paraphyses of *H. crassitunicata* are the longest in the genus. The apical cell of the more numerous thin-walled paraphyses is much shorter and within the usual range for the genus. The thick-walled paraphyses of *H. crassitunicata* are similar to the setae of *Rhizina undulata* (q.v.). Both are thin-walled at the apex, pigmented, and aseptate. Setae of *Rhizina* are longer and arise below the hymenium. The aporhynchous ascal base and gross morphology suggest an affinity to *H. leucomelaena* (q.v.). *Helvella crassitunicata* can be distinguished by ascocarp colour, stronger pubescence of the excipular surface and stipe, and more pronounced ribbing of stipe and excipular surface. *Helvella pocillum* Harmaja (not examined) is reported to have very large ascospores similar to *H. crassitunicata*, but lacks thick-walled paraphyses (Harmaja 1976a). Specimens reported by Kempton and Wells (1970) as *H. leucomelaena* are referable to this taxon as suspected by Weber (1975).

Collections Examined: **CANADA: British Columbia**: Mount Abbott near Marian Lake, Glacier N.P., Shoemaker 08 6 1963, DAOM 109231; Trail to Glacier crest, Glacier N.P., Shoemaker 08 4 1963, DAOM 109227, 109230; trail to Great Glacier, Glacier N.P., Shoemaker 08 1 1963, DAOM 109228, 109229; Diamond Head, Garibaldi P.P., Abbott (SA 1029) 08 18 1994, SA; Cypress Bowl near Squamish, Abbott (SA 1028) 08 18 1994, SA. **USA: Alaska**: Turnagain Pass,

Seward Highway, Kempton 07 21 1970, 08 27 1970, WK 4517, 4518, 4809. **Washington**: Bogachiel Peak, Olympic N.P., Smith (2745) 09 27 1935, MICH; Pierce Co., A.H. Smith, MICH (holotype); base of Carbon Glacier, Mount Rainier N.P., Tschudy (Snyder 103) 05 20 1934, WTU; Mount Rainier N.P., Smith (29746, 30598, 40077, 40875, 40916) 08 2 & 25 1948, 09 20 & 10 12 & 13 1952, MICH; Green Lake, Rainier, (Stz 7604), WTU; Iron Butte, van de Bogart (FVB 3794), WTU; Buck Creek area, van de Bogart (FVB 1915) 07 16 1973, WTU; unknown, 08 2 1948, WTU 3803.

Helvella hyperborea Harmaja, 1978, Karstenia 18: 57.

Type Material: Holotype H, examined.

Apothecium: 10-18 mm diam., 5-10 mm high, cupulate, laterally compressed initially, margin inrolled initially, hymenium dark brown when dried, smooth to slightly undulate-rugose, excipular surface dark brown near margin, medium brown below to yellowish brown at base, pubescent to densely pubescent, strongly ribbed, ribs blunt, single or bifurcate branched, no anastomosis between ribs, extending onto basal quarter to two thirds of excipular surface. **Stipe**: 15-19 x 3-6 mm, flared at apex, equal below, medium brown at apex to medium or light yellowish brown below when dried, pubescent, vestiture darker than background tissue, strongly ribbed, ribs blunt, branched and anastomosed, rarely lacunose, internally chambered. **Asci**: 300 x 19 (immature), pleurorhynchous. **Paraphyses**: 4.1-6.9 µm diam. at apex, terminal cell 30-40 µm long, clavate, enlarged gradually to apex, pale brown to brown in mass, contents finely granular. **Ascospores**: 16.1-17.8 x 10.1-10.9 µm (immature), broadly ellipsoidal, hyaline, smooth, uniguttulate.

Habitat: Gregarious on duff in coniferous woods. Associated trees: *Picea* sp. and *Tsuga* sp. Collected only on July 28 in AK.

Distribution: Rare in northern coastal regions from AK. This species is newly reported from Alaska and significantly extends the range westward in North America. Previously known only from northeastern North America (Harmaja 1981) and northern Europe (Harmaja 1978, 1979a). Map 13.

Notes: Harmaja (1979a) suggests this species is closest to *H. costifera* (q.v.), but *H. acetabulum* (q.v.) and *H. verruculosa* (q.v.) are equally close. Although immature, the specimens from Alaska are otherwise identical to the type collection from Finland. The two ascocarps were part of a larger collection of *H. leucomelaena* (q.v.), but are easily separated by their pleurorhynchous ascus base, in addition to the prominent, slender, distinctly ribbed stipe with dark pubescence and medium brown ascocarp.

Collections Examined: CANADA: Newfoundland: Labrador, north end of Astray Lake, southeast of Schefferville, Mäkinen (67-1371) 08 4 1967, TUR 66271. **USA: Alaska**: near Hope, Kempton 07 28 1968, WK 1542b. **FINLAND**: Juuma, Kuusamo, Harmaja 08 27 1970, H (holotype).

Helvella leucomelaena (Persoon) Nannfeldt, 1941, in Lundell and Nannfeldt Fungi Exsiccati Suecici Praesidium Upsaliensis Fasciculata 19-20: 21, no. 952.

≡*Peziza leucomelas* Persoon, 1822, Mycologica Europaea 1: 219.

=*Helvella confusa* Harmaja, 1977, Karstenia 17: 43. (holotype H, examined; isotype C, examined).

≡*Helvella solitaria sensu* Dissing 1966b; non *H. solitaria* P. Karsten.

=*Helvella pedunculata* Harmaja, 1978, Karstenia 18: 57. (holotype OULU, examined).

=*Acetabula calyx* Saccardo, 1873, Mycologieae Venetae Specimen p. 168. (holotype K, examined).

=*Peziza debeauxii* Roumeguère, 1882, Revue de Mycologie 4: 156. (syntype K, examined).

=*Helvella melaleuca* Rifai, (specimen labeled type at K, examined, but no reference found to this species in Rifai 1968 or in Index of Fungi).

(additional synonyms see Dissing 1966b).

Type Material: Lectotype selected here: L 8945-6, Herbarium Persoon, examined. **Figs. 3a, 20, 50.**

Apothecium: 4-60 mm diam., 3-34 mm high (up to 70 mm diam. fresh), deeply cupulate, initially subglobose and nearly closed, margin expanding at maturity to shallowly cupulate, often becoming split and somewhat reflexed, occasionally laterally compressed when immature, cups rarely irregular and repand when growing in clusters, hymenium dark brown to grey brown fresh, rarely with paler regions, when dry dark brown to blackish brown, smooth to slightly undulate-rugose, excipular surface brown to dark brown at margin, pallid brown below, white near base, pubescent, ribs absent or extending onto basal quarter only. **Stipe**: 1-20 x 1-15 mm, expanding and merging with apothecium, below equal or base rarely slightly enlarged, white, finely pubescent, sparingly ribbed, ribs broad and rounded, internally sulcate and solid or chambered. **Asci**: 225-330 x 14.6-20 µm, aporhynchous. **Paraphyses**: 4.9-9 µm diam. at apex, terminal cell 144-145 µm long, clavate, enlarged gradually to abruptly at apex, pale brown to brown, contents finely granular. **Ascospores**: 18-24.2 x 10.9-15 µm, broadly ellipsoidal to ellipsoidal, hyaline, smooth, with SEM finely rugose to smooth, uniguttulate.

Habitat: Solitary, gregarious, subcaespitose, or scattered and numerous on bare soil, moss, or litter in coniferous woods. Associated trees: *Pinus contorta, Pinus ponderosa, Abies lasiocarpa, Picea glauca, Picea engelmannii, Pseudotsuga menziesii, Larix occidentalis, Tsuga heterophylla, Thuja plicata, Populus tremuloides,* and *Alnus tenuifolia*. Associated shrubs: *Alnus crispa, Acer glabrum, Menziesia ferruginea,* and *Juniperus* sp. Fruiting from April 23 in WA and BC to September 3 in AB.

Distribution: Widely distributed in montane regions from AK, BC, AB, WA, ID, OR, and WY. Newly reported from WY. Also distributed in eastern North America (Weber 1972), South America (Dissing 1966b), Europe (Dissing 1966b, Häffner 1987; Calonge and Arroyo 1990), north Africa and the Middle East (Dissing 1966b; Nemlich and Avizohar-Hershenzon 1972, as *Paxina leucomelas*), Asia (Korf and Zhuang 1991; Waraitch 1976, as *H. solitaria*) and Australia (reported here based on the specimen labeled *H. melaleuca*). This species has the broadest global distribution of any in the genus, and is the only one found in South America. Map 12.

Notes: *Helvella confusa*, although recognized previously by Abbott and Currah (1988) and others (Harmaja 1977a), is considered a synomym. The species, originally treated as *H. solitaria* by Dissing (1966b) and described as the new species *H. confusa* by Harmaja (1977a), was separated from *H. leucomelaena* on the basis of ascocarp size, prominence of stipe, spore size, and fruiting time. Ascocarp size is a dubious character, as recognized by Dissing (1966b), and may reflect degree of maturity or differences in environmental conditions. Stipe development may vary with individual and habitat. Large collections of *H. leucomelaena* show wide variation in ascocarp size and stipe prominence and cover a range of features typical for *H. leucomelaena sensu stricto* and *H. confusa*. Stipe morphology varies in collections of other species including *H. solitaria* (q.v.) and *H. elastica* (q.v.). Our examination of type material showed that spores of *H. confusa* are slightly shorter than *H. leucomelaena*, but width showed the same range of variation, contrary to that reported by Dissing (1966b) and Harmaja (1977a). A number of collections with rather small spores were found, but other features did not correlate with those expected for *H. confusa*. Since the spore size difference is very slight and not correlated with other features of importance, it seems reasonable to accept a slightly greater range of variation for one widely distributed and variable species. Harmaja (1977a) suggests that *H. confusa* may have a slightly later fruiting time than *H. leucomelaena*, although the type collection is from May. A number of collections from northwest North America were examined from July and August. One from August (ALTA 8290) is typical for *H. leucomelaena* (*sensu stricto*) in all other respects including large ascocarp size, spores up to 23 µm long, and short indistinct stipe. Fruiting time, especially in montane environments, varies with environmental conditions, even for typically vernal species. Unusual fruiting times are also known for *H. maculata* (q.v.) and *H. acetabulum* (q.v.). Specimens referred to *H. leucomelaena* by Kempton and

Wells (1970) represent *H. crassitunicata* (q.v.), while specimens described as *H. solitaria* are *H. leucomelaena*.

Helvella pedunculata is a synonym for similar reasons. Harmaja (1978, 1979a) distinguished the species as having shorter ascospores, a well differentiated stipe, and slightly denser pubescence on the excipular surface. In fact, the table in Harmaja (1979a) showing key distinguishing features provides a good indication of the similarity between the three taxa (*H. leucomelaena, H. confusa, H. pedunculata*). The differences noted there, including details of the excipulum, are not diagnostic in these taxa.

The lectotype of *H. leucomelaena*, chosen from several excellent collections in the Persoon Herbarium, Leiden, is consistent with the description above in all details. *Helvella leucomelaena* (*sensu lato*) is characterized by the short, white stipe with well separated blunt ribs which do not extend noticeably onto the finely pubescent excipular surface, darkly pigmented hymenium, relatively large ascospores, and aporhynchous ascus base.

Collections Examined: CANADA: British Columbia: Canal Flats, Funk 06 26 1960, DAOM 82875; Lumby, Bandoni 05 28 1960, UBC F3398; Procter, Linton 05 15 1978, UVIC; Jocelyn Hill, highlands near Victoria, Ceska 04 23 1977, UVIC. **Alberta**: near Nojack, Abbott (SA 56, 57, 84) 06 24 & 29 1989, SA; Winfield, Strand 07 8 1975, ALTA 7342; Penstock Creek, Jasper N.P., Currah 08 29 1987, ALTA 8274; Moraine Lake, Banff N.P., Suttill 09 3 1980, UVIC; Marmot Creek basin near Seebe, Danielson (RMD 309) 08 13 1972, ALTA 8290; Summit Lake trail, Waterton Lakes N.P., Egger (731) 08 11 1980, DAOM 177741, SA; Bertha Lake trail, Waterton Lakes N.P., Egger (602) 07 7 1980, DAOM 177719; Crandell Lake trail, Waterton Lakes N.P., Abbott (SA 322) 05 27 1990, SA; Bauerman Creek trail, Waterton Lakes N.P., Abbott (SA 335) 05 28 1990, SA; Upper Waterton Lake trail, Waterton Lakes N.P., Abbott (SA 340) 05 28 1990, SA. **Ontario**: Halton Forest, Halton Co., Ammirati (JFA 8022) 05 18 1978, WTU. **Québec**: southeast ends of John Lake and Dolly Lake, Schefferville, Kallio & Mäkinen 07 28 1978, TUR 63428. **Newfoundland**: Labrador, northeast end Astray Lake, southeast of Schefferville, Kallio & Heikkilä 08 4 1967, TUR 53429, 66269, 66270, 66272. **USA: Alaska**: Eklutna Lake north of Anchorage, Kempton 07 13 1966, WK 1538, 1539; Hope road, Kempton 07 28 1968, 07 14 1970, WK 1542a, 4480; Turnagain Pass on Seward Highway, Kempton 08 27 1968, WK 1553. **Washington**: Friday Harbor, San Juan Island, Isaacs (Is 1704) 05 19 1962, WTU; Entiat Mountains, Chelan Co., Ammirati (JFA 9400) 06 7 1987, WTU; Cle Elum pine flats, Isaacs (Is 1738) 05 27 1962, WTU; Cle Elum pine flats, Stuntz (Stz 12310, 11709) 05 21 & 22 1960, WTU; Cle Elum pine flats, McCarkle (Stz 11691) 05 15 1960, WTU; near Yelm, Walters (JFA 8499) 05 4 1981, WTU; Ewartsville, Whitman Co., Duran 05 1 1983, WSP 67339; Kamiak Butte, Whitman Co., Cooke 05 17 1948, WSP 29343; WSU campus, Pullman, Sulzbach 04 23 1963, WSP 53392; WSU campus, Pullman, Waldron 05 9 1963, WSP 51810; Boulder Lake trail, (Stz 8835) 08 2 1954, WTU; unknown, Snyder 05 5 1934, (Stz 10977) 05 24 1959, WTU. **Idaho**: Priest Lake, Slipp 05 27 1941, WSP 50807; Priest River Experimental Forest, Bonner Co., A.H. Smith 07 5 1964, WSP 54318; Ida Creek, Priest River Experimental Forest, Slipp 06 11 1942, WSP 55594; Coeur d'Alene National Forest, Shoshone Co., Scates (1962) 06 30 1972, MICH; Dry Creek between Troy and Deary, Cooke 05 1948, WSP 30102; Laird Park, Latah Co., Paden (JWP 515) 05 20 1967, UVIC; Payette Lake, Valley Co., Smith (44737) 07 2 1954, MICH; Karney Lakes, Boise Co., Trueblood (1029) 05 8 1960, MICH; Idaho, English, WSP 23948. **Oregon**: Bear Springs, Wasco Co., Carson 06 3 1951, MICH. **Wyoming**: north Fork French Creek, Medicine Bow Mountains, Albany Co., Smith (35784) 08 15 1950, MICH. **ARGENTINA**: La Plata, Ceppi 08 1936, ex Herbario Spegazzini (2235) Museo De La Plata, TRTC. **SWEDEN**: Älvkarleby parish northeast of Gardskär, Eriksson & Lundquist 06 30 1965, K. **FINLAND**: Kiiminki, Keskikylä, Esteri & Ohenoja 07 2 1975, OULU (holotype of *H. pedunculata*). **DENMARK**: Klitmoller, northern Jutland, Toft & Dissing 05 15 1965, H, (holotype of *H. confusa*), C (isotype of *H. confusa*). **NETHERLANDS**: Herbarium Persoon, L 8943-7, L 8945-4, L 8945-5, L 8945-6 (lectotype), L 8945-8. **ITALY**: Padova, Saccardo, Herbarium Cooke 1885, K (type of *Acetabula calyx*). **AUSTRALIA**: K (holotype of *H. melaleuca*). **Exsiccata**: Roumeguère Fungi Gallici Exsiccati, 2174, Algeria, Debeaux 04 1882, s.n. *Peziza debeauxii*, K (syntype of *P. debeauxii*); Kryptogamae exsiccatae, 1824, near Baden, Austria, De Höhnel, IMI 11963.

Helvella robusta S.P. Abbott, 1988, in Abbott and Currah, Mycotaxon 33: 242.

Type Material: Holotype DAOM, examined; paratype ALTA, examined.

Fig. 25.

Apothecium: 50-90 mm diam., irregularly cupulate or centrally depressed with margins reflexed, hymenium when dry medium brown, undulate-rugose, excipular surface when dry white to pale brown, pubescent, prominently ribbed, ribs branching and anastomosing, extending to marginal region. **Stipe**: 30-50 x 30-50 mm, expanding and merging with apothecium, white to pale brown, pubescent, prominently ribbed and lacunose, ribs branching and anastomosing, internally chambered. **Asci**: 220-345 x 15-19.3 µm, pleurorhynchous. **Paraphyses**: 4.5-7.5 µm diam. at apex, terminal cell 65-75 µm long, clavate, enlarged gradually to apex, pale brown in mass, contents finely granular. **Ascospores**: 15-19 x 10.5-14 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary on soil under deciduous trees. Associated trees and shrubs: *Populus balsamifera* and *Salix* sp. The type locality is a dry hilly grassland with poplars and shrubs in ravines and gullies. This habitat is unlike that of any other species of *Helvella* examined in this study. Fruiting from August 30 to September 11 in AB.

Distribution: Rare in parkland regions. This species is known only from AB (Abbott and Currah 1988, 1989). Map 14.

Notes: The large size, robust prominently ribbed stipe, strongly reflexed apothecial margins, and autumnal fruiting are characteristic. Closely related species include *H. costifera* (q.v.), *H. unicolor* (q.v.), and *H. acetabulum* (q.v.). Autumnal fruiting indicates a close relationship with *H. costifera*, which differs in its grey coloration, smaller stature, and narrower paraphyses. *Helvella unicolor* is similar in ascospore size and shape, but differs in size, colour, and excipular vestiture. *Helvella acetabulum* is more darkly pigmented with slightly longer ascospores, and fruits earlier.

Collections Examined: CANADA: Alberta: Nose Hill area, Calgary, Danielson (RMD 459) 08 30 1972, DAOM 143869 (holotype); Glenmore Park, Calgary, Danielson (RMD 537) 09 11 1972, ALTA 8291 (paratype).

Helvella solitaria P. Karsten, 1871, Bidrag Kännedom af Finlands Natur och Folk 19: 37. (unintentional *nomen novum*).

≡*Peziza solitaria* P. Karsten, 1869, Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandingar 10: 115. (illegitimate, later homonym); non *Peziza solitaria* Schweinitz.

≠*Helvella solitaria, sensu* Dissing 1966b (=*H. leucomelaena*).

=*Helvella queletii* Bresadola, 1882, Revue de Mycologie 4: 211. (*fide* Harmaja 1977a).

(additional synonyms see Dissing 1966b as *H. queletii*)

Type Material: Holotype H, examined.

Fig. 3b.

Apothecium: 13-60 mm diam., 4-44 mm high (up to 120 x 50 mm fresh), cupulate, often laterally compressed initially, often becoming bilobate, shallowly cupulate, or somewhat reflexed in age, margin slightly inrolled initially, hymenium grey brown to dark brown fresh, when dry dark grey brown to blackish brown, smooth to slightly undulate-rugose, excipular surface medium to dark grey brown at margin, base typically paler grey brown to white, pubescent to densely pubescent, ribs absent or extending very slightly onto base of excipular surface. **Stipe**: 7-105 x 2-50 mm (up to 120 x 50 mm fresh), equal or enlarged at base, apex flaring slightly, white to pale or grey brown, occasionally dark grey brown at apex, finely pubescent to pubescent, highly ribbed or rarely with sparse ribbing, ribs simple or branching and anastomosed, sulcate and internally solid or with few chambers. **Asci**: 240-300 x 14-18 µm, pleurorhynchous. **Paraphyses**: 7-8 µm diam. at apex, terminal cell 89-144 µm long,

clavate, brown, contents finely granular. **Ascospores**: 17-21 x 11-13.5 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary or often gregarious to numerous and scattered on ground in soil or litter in coniferous, mixed, or occasionally deciduous woods. Associated trees: *Picea glauca, Picea engelmannii, Pinus contorta, Pseudotsuga menziesii, Abies grandis, Abies* sp., *Tsuga heterophylla, Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera,* and *Alnus* sp. Associated shrubs: *Salix bebbiana, Rosa* sp., *Lonicera involucrata,* and *Cornus stolonifera.* Fruiting from April 19 in coastal WA to October 4 in eastern WA. April and May collections are known only from WA and OR, June to August collections are typical for AK, NWT, AB, MB, ID, and WY.

Distribution: Widely distributed in boreal, montane, coastal, and arctic regions from AK, NWT, BC, AB, SK, MB, WA, ID, OR, and WY. Also distributed in eastern North America (Weber 1972, as *H. queletii*) and Europe (Dissing 1966b, as *H. queletii*; Harmaja 1977; Häffner 1987). Map 15.

Notes: Closely related species in the subgenus *Leucomelaenae* include *H. costifera* (q.v.) which is similar in colour, but distinguished by more prominent ribbing on stipe and excipular surface and relatively broader stipe. *Helvella hyperborea* (q.v.) is similar in ascocarp shape, but can be distinguished by the prominent ribbing of the excipular surface and ascocarp colour. *Helvella unicolor* (q.v.) is easily distinguished by ascospore shape. *Helvella solitaria* is also similar to *H. leucomelaena* (q.v.), which is aporhynchous and has larger ascospores.

This variable species may provide an indication of relationships between the subgenus *Leucomelaenae* and other subgenera. Small, cupulate specimens are similar in many respects to species in the subgenus *Cupuliformae* (*H. cupuliformis* (q.v.), which never attains a large size, has an unpigmented stipe, and lacks prominent ribbing on the stipe with the ribs always absent from the base of the excipulum and *H. chinensis* (q.v.) which is a similar colour, but can be separated by ascospore size as well as the characters mentioned above for *H. cupuliformis*). Large specimens of *H. solitaria* are similar to members of the subgenus *Helvella*. The strongly ribbed, elongate stipe which is sometimes chambered, and the brown somewhat reflexed apothecium are reminiscent of *H. maculata* (q.v.) in particular.

Collections Examined: CANADA: Northwest Territories: east of Repulse Bay, Ohenoja 08 4 1974, DAOM 155395; Baker Lake, Ohenoja 08 9 1974, DAOM 155395; Fort Smith, Loan 08 8 1950, DAOM 26124. **British Columbia**: Tetsa River P.P., Abbott (SA 229) 08 22 1989, SA; Kokanee Glacier P.P. near Nelson, Harrison (6061) 07 11 1960, MICH; Gold Creek near Golden Ears P.P., Rabas 06 27 1971, UBC F3392; Golden Ears P.P., Redhead & Liu 06 7 1970, UBC F3393; Manning P.P., Morrison 08 3 1963, UBC F3397. **Alberta**: Shaw Lake near Lac La Biche, Abbott (SA 99, 101, 103) 07 14 & 15 1989, (SA 362, 366) 06 22 1990, SA; Cross Lake P.P., Abbott (SA 1012) 06 23 1994, SA; near Redwater, Currah (SA 481) 07 6 1991, SA; Wagner Natural Area, Abbott (SA 941, 1045) 07 6 & 09 4 1994, SA; Devonian Botanic Garden near Devon, Abbott (SA 443) 06 15 1991, SA; Poplar Creek Natural Area near Breton, Osis (SA 811) 07 11 1993, SA; Forestry Trunk road near Sundre, Abbott 07 19 1988, UAMH M565; Fish Creek P.P., Calgary, Danielson (RMD 911) 07 25 1973, ALTA 8295; Brown-Lowery Natural Area, Danielson (RMD 214) 07 29 1972, DAOM 143867. **Saskatchewan:** Prince Albert N.P., Zelmer (PA 133) 1994, ALTA. **Manitoba**: Russell, Bisby 06 20 & 30 1921, DAOM 206810; Manitoba Agricultural College, Winnipeg, Bisby 06 16 1925, DAOM 206820; Birds Hill, Bisby 07 1 1927, 07 6 1935, DAOM 206809, 206819. **USA: Alaska**: Matanuska Glacier, north of Palmer, Kempton 07 13 1964, 07 18 1971, WK 1546, 5058; Eklutna Lake north of Anchorage, Kempton 07 2 1973, WK 5290; Thunderbird Falls, Kempton 06 27 & 07 5& 11 1960, 07 10 1973, WK 1540, 1541, 1545, 5291; Thompson subdivision, Anchorage, Kempton 07 22 & 08 10 1971, WK 5079, 5131; Erickson Gold Mine, Girdwood, south of Anchorage, Kempton 08 17 & 09 3 1968, WK 1543, 1544; Potter, Kempton 09 11 1971, WK 5526. **Washington**: Friday Harbor, San Juan Island, Brough (Is 58) 04 21 1957, WTU; Friday Harbor, San Juan Island, Stuntz & Isaacs (Is 1703), WTU; Seattle, Greene (Snyder 122) 05 1929, WTU; Watermain woods, Redmond, Stuntz (Stz 21769) 04 19 1981, WTU; Watermain woods, Redmond, Jones (SLB 289) 01 1 1974, WTU; eastern Washington, Chiltan (Stz 19075) 10 5 1975, WTU; Lower Tahoma at Fish Creek, Stuntz (Stz 3902) 08 9 1948, WTU; Gold Creek campground, van de Bogart (Stz 13496) 04 30 1966, WTU; southwest of Fort Lewis, Hellya (Stz 7364) 05 14 1961, WTU; Aspus Centre, Masford (Stz 16672) 06 25 1971, WTU. **Idaho**: southwest of McCall, Miller 07 14 1964, WSP 54644; Coyote Creek, Owyhee Co.,

Trueblood (2174) 07 6 1963, MICH. **Oregon**: Hood River, Kienholz 05 16 1933, WSP 15136. **Wyoming**: Moose, Teton National Forest, Teton Co., Cain 07 1 1955, TRTC 31911; Medicine Bow National Forest, Albany Co., Kanouse 09 5 1923, MICH. **New York**: east of Lewis, Essex Co., Cain 06 15 1968, TRTC 45919. **NORWAY**: Østfold, Kråkerøy, Fuglevik, Kirkebakken, Kristiansen 06 7 & 20 1987, RK 87.10. **FINLAND**: Mustiala, Karsten (PAK 3288) 09 21 1866, H (holotype). **RUMANIA**: Mutenia, district Dâmbovita-Badulesti, Racovitza & Savulescu 07 5 1944, IMI 28970. **Exsiccata**: Ellis and Everhardt's Fungi Columbiani, 1801, Stockton, Kansas, USA, Bartholomew 06 3 1903, s.n. *Acetabula vulgaris*, K, WSP 2; Fungi Dakotenses, 502, Nyland's Grove, Kulm, North Dakota, Brenckle 07 4 1922, s.n. *Acetabula vulgaris*, WSP 23419.

Helvella unicolor (Boudier) Dissing, 1966, Revue de Mycologie 31: 219.

≡*Acetabula unicolor* Boudier, 1917, Bulletin de la Societé Mycologique de France 33: 14, plate 22 Figure 3.

Type Material: Neotype PC (selected Dissing 1966a), examined.

Figs. 3c,d.

Apothecium: 4-22 mm diam., 2-18 mm high (up to 52 x 30 mm fresh), deeply cupulate, becoming shallowly cupulate or somewhat repand, margin inrolled initially, expanding to slightly reflexed at maturity, hymenium medium to dark grey brown fresh, when dried blackish brown, smooth initially, typically becoming somewhat undulate-rugose at maturity, excipular surface medium to dark grey brown, typically slightly paler than hymenium, when dried medium to dark brown, densely pubescent to villose, ribs absent or extending onto basal two thirds of excipular surface. **Stipe**: 2-16 x 1-9 mm (up to 27 x 17 mm when fresh), equal, tapered to base, or base enlarged, white to cream, when dry cream to brown, finely pubescent to pubescent, sparingly ribbed or fluted when immature, becoming prominently ribbed at maturity, ribs blunt, sulcate and solid or with few chambers. **Asci**: 16.7-18.8 µm diam., pleurorhynchous. **Paraphyses**: 4.5-6.6 µm diam. at apex, terminal cell 81-170 µm long, clavate, enlarged gradually to apex, pale brown, contents finely granular. **Ascospores**: 17.4-20.8 x 13.1-15.2 µm, very broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Gregarious to scattered on soil in mixed woods. Associated trees: *Betula papyrifera, Alnus tenuifolia, Populus tremuloides, Populus balsamifera,* and *Picea glauca*. Associated shrubs: *Salix discolor* and *Viburnum edule*. Found in the study area only on August 7 in AB.

Distribution: Rare in boreal forest region east of the Rocky Mountains from AB. This species is newly reported for North America. Also distributed in Europe (Dissing 1966a, b). Map 12.

Notes: The species, as described here based on North American collections, differs from the type collection and other European collections in several respects. European collections have a finely pubescent excipulum, although Dissing (1966a) described loose tufts of fascicled hyphae projecting from the outer excipulum, which were also observed here. European collections also have an earlier fruiting period from March to May (Dissing 1966b). European and North American specimens possibly represent distinct varieties or species, but the similarity in ascocarp morphology and the distinctive broad ascospores suggest they are conspecific. More collections from North America and fresh collections from Europe should be examined to provide a clear concept of this taxon. *Helvella unicolor* is similar to *H. solitaria* (q.v.) and shares the overall ascocarp morphology, and in both species the stipe varies from slender and sparingly ribbed to robust and distinctly ribbed. They differ in ascospore size and shape, and the ribs which extend onto the excipulum in *Helvella unicolor*. *H. unicolor* is similar to *H. costifera* (q.v.), *H. acetabulum* (q.v.), and *H. verruculosa* (q.v.). *Helvella costifera* shares the greyish coloration of fresh specimens and blunt ribs of stipe and excipulum. *Helvella acetabulum* shares the brown coloration seen in dry specimens, but *H. unicolor* lacks the yellow pigments often seen on excipular surface and stipe. Both species have less pubescence on the excipulum than the specimens described here. *H. verruculosa* shares ascocarp coloration, smaller size, less pronounced stipe, variable degree of ribbing on

excipular surface, blunt ribs, and densely pubescent excipular surface. *Helvella unicolor* is found in boreal regions with a more southerly distribution than the arctic and alpine *H. verruculosa*. Very broad ascospores are also seen in *H. robusta* (q.v.) and *H. aestivalis* (q.v.).

Collections Examined: **CANADA:** **Alberta**: Notikewin P.P., Abbott (SA 131, 132, 135, 139) 08 7 1989, SA. **FRANCE**: commune de Savigné, Vienne, Grelet 04 22 1927, PC (neotype); France, Riousset 03 1974, K.

Helvella verruculosa (Saccardo) Harmaja, 1978, Karstenia 18: 57.

≡*Geopyxis verruculosa* Saccardo, 1889, Sylloge fungorum 8: 68. (unintentional *nomen novum*).

≡*Peziza verruculosa* Berkley and Curtis, 1860, Proceedings of the American Academy of Arts and Sciences 4: 127 (illegitimate, later homonym); non *Peziza verruculosa* Weinmann, 1827, Sylloge plant. nov. 2: 111.; nec *Peziza verruculosa* Berkley and Broome, 1875, Journal of the Linnean Society London 14: 105.

=*Helvella arctoalpina* Harmaja, 1978, Karstenia 17: 58. (Holotype O, examined).

=*Helvella dryadophila* Harmaja, 1978, Karstenia 17: 58. (Holotype O, examined).

Type Material: Holotype K, examined; isotype FH.

Fig. 11a,b.

Apothecium: 8-30 mm diam., 3-14 mm high, cupulate, margin inrolled initially, expanding at maturity, hymenium when dried blackish brown to black, smooth to slightly rugose, excipular surface dark brown at margin, pale brown to yellow brown at base, densely pubescent, margin villose and sometimes with distinct white hairs, base pubescent, with ribs extending onto basal half of excipular surface. **Stipe**: 5 x 6-9 mm, nearly equal to tapered to base, when dry white to cream or rarely pale brown at apex, pubescent to finely pubescent, distinctly ribbed, ribs sharp or blunt with little branching and anastomosis, sulcate and solid or with few chambers. **Asci**: 250-300 x 14-16.7 µm, pleurorhynchous. **Paraphyses**: 5.1-7.7 µm diam. at apex, apical cell 32-124 µm long, clavate, gradually enlarged to apex, pale brown to brown, dark brown in mass, contents finely granular. **Ascospores**: 17.8-22.1 x 11.8-13.5 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious or scattered and numerous on soil or humus with low shrubs in tundra. Associated shrubs: *Salix reticulata*, *Salix arctica*, *Vaccinium vitis-idaea*, *Cassiope* sp., and *Dryas integrifolia*. Fruiting from July 30 to August 15 in NWT.

Distribution: Widely distributed in arctic and alpine tundra regions in northern areas from NWT and AB. This species is newly reported for North America. Circumpolar distribution in North America, Europe (Harmaja 1977b; Schumacher and Mohn Jenssen 1992; as *H. arctoalpina*), and Asia (Harmaja 1979a). Map 13.

Notes: This species is most similar to *H. aestivalis* (q.v.)(see notes under that species), *H. costifera* (q.v.) and *H. acetabulum* (q.v.). Dissing (1966b) and Pfister (1977) considered it an arctic form of *H. acetabulum*, but Harmaja recognized distinct species. Harmaja (1978, 1979a) verified the status of *Geopyxis verruculosa* Saccardo as a valid species closely related to *H. arctoalpina* and *H. dryadophila*. Unfortunately, the problem was complicated by Harmaja's (1977b) description of the two new species from arctic collections. On examination of holotypes, *H. verruculosa* is the oldest valid name for this arctic and alpine taxon, with *H. arctoalpina* and *H. dryadophila* considered conspecific. In fact, the table in Harmaja (1977b) listing pertinent distinguishing characters is more useful if the three species are combined. The features used by Harmaja to separate *H. verruculosa*, *H. arctoalpina*, and *H. dryadophila* include spore size and shape, details of the excipulum in cross section, and length of the terminal cell of the paraphyses. All of these are variable in other species of this genus and no correlation was found that would make separation possible. *Helvella acetabulum* and *H. costifera* are larger and have more prominent stipes, more pronounced ribbing and anastomosis of

ribs on the excipular surface and stipe, finely pubescent excipular surface, and temperate distribution.

Collections Examined: **CANADA: Northwest Territories**: Blister Hill Creek delta near Hazen Lake, Ellesmere Island, Powell, 07 30 1958, DAOM 67088; Skeleton Creek north of Hazen camp, Ellesmere Island, Forest 08 10 1962, DAOM 91575; southwest of Hazen camp, Ellesmere Island, Savile 07 30 1962, DAOM 91574; Fox valley southwest of Hazen camp, Ellesmere Island, Savile 07 30 1962, DAOM 91576; Tanquary Fjord, Ellesmere Island N.P., Richards (79) 07 26 1994, ALTA; Bathurst Island, Bissett 08 6 & 15 1977, DAOM 165336, 165335; Stanwell-Fletcher Lake, Somerset Island, Savile 08 11 1958, DAOM 60267; northeast of Repulse Bay, Ohenoja 08 5 1974, DAOM 159682; southeast of Repulse Bay, Ohenoja 08 4 1974, DAOM 155308; Coral Harbor, Southampton Island, Cody 08 6 1948, DAOM 20767; Coral Harbor, Southampton Island, Savile 08 15 1959, DAOM 67075; Longstaff Bluff, Baffin Island, Parmelee & Seaborn 08 7 1967, DAOM 117583; near Melvin Bay, Rankin Inlet, Ohenoja 08 12 1971, DAOM 159712. **Alberta**: Cardinal River Divide near Cadomin, Annett (SA 624) 08 1982, SA. **SVALBARD**: Gipsvika, Currah 08 15 1988, ALTA 8308. **NORWAY**: Lom, Oppland, Eckblad 08 29 1957, O (holotype of *H. dryadophila*); Eidfjord, Hordaland, Eckblad 08 1 1959, O (holotype of *H. arctoalpina*). **USSR**: Russian S.F.S.R., Magadan obl., Chukotski Peninsula, Arakamachene Island, Bering Strait, Stony Hills, Wright 08 11 1855, K (holotype of *Geopyxis verruculosa*).

Extralimital Species

Helvella oblongispora Harmaja, 1978, Karstenia 18: 57.

Type Material: Holotype C, examined.

Fig. 24.

Distribution: *H. oblongispora* is known from Europe (Harmaja 1978, 1979a, 1982; Häffner 1987) and Asia (Cao *et al.* 1990).

Notes: This species differs from *H. leucomelaena* (q.v.) in having a paler brown to ochre brown apothecium and more prominent ribbing on stipe and basal third of excipular surface. *Helvella oblongispora* resembles *H. unicolor* (q.v.) in gross morphology, but can easily be separated by colour, excipulum vestiture, ascal base, and ascospore shape.

Collections Examined: **GERMANY**: near River Isar, Munich, Einhellinger 07 23 1969, C (holotype).

Helvella ulvinenii Harmaja, 1979, Karstenia 19: 42.

Type Material: Holotype H, examined; isotype OULU.

Distribution: Known only from Europe (Harmaja 1979a).

Notes: This species is tentatively accepted. Comparative studies are needed to clearly delimit this taxon from *Helvella solitaria* (q.v.), *H. alpestris* Boudier (see Häffner 1987), and *H. dovrensis* T. Schumacher (Schumacher 1992; Schumacher and Mohn Jenssen 1992).

Collections examined: **FINLAND:** prov. Enontekiön Lappi, par. Enontekiö, Kilpisjärvi, Harmaja 08 25 1979, H (holotype).

Helvella* Subgenus *Macropodes (Dissing) S.P. Abbott *comb. nov.*

≡*Helvella* section *Macropodes* Dissing, 1966, Dansk Botanisk Arkiv 25: 62, emend. Häffner, 1987, Beihefte zur Zeitschrift für Mykologie 7: 92.

Type Species: *Helvella macropus* (Persoon : Fries) Karsten, 1870, Notiser ur Sällskapets pro Flora et Fauna Fennica Förhandlingar 11: 224. (Monotypic).

Ascocarp: stipitate, cupulate to discoid; hymenium brown, smooth; excipular surface brown to grey brown, densely pubescent to villose, lacking ribs; stipe equal or tapered at apex, brown to grey brown, densely pubescent to villose, terete to shallowly

fluted, internally solid. **Asci**: pleurorhynchous. **Ascospores**: subfusoidal to ellipsoidal, smooth to verruculose, with SEM distinctly verrucose at maturity, with numerous small isolated pointed warts, triguttulate or rarely uniguttulate, with large central subglobose oil guttule and typically two smaller globose polar guttules.

Notes: Häffner (1987) restricted the section *Macropodes* to one species, *H. macropus*, (based on subfusoidal and triguttulate spores which are verrucose at maturity). The spores are often subfusoidal, but some spores in each mount are more or less ellipsoidal. These ellipsoidal spores, and some of the subfusoidal ones, typically possess only one large central guttule typical of *Helvella*. In fact, in some collections the uniguttulate spores outnumber the triguttulate ones. Ascospore ornamentation as observed with SEM shows mature spores of *H. macropus* with numerous small, pointed spines (Figs. 53-56). However, submature spores in the same apothecia can be finely rugose (Fig. 57) and virtually indistinguishable from the pattern of ornamentation seen in all other members of the genus (Figs. 45-52). Other species of section *Macropodes* (*sensu* Dissing 1966b) are referred to subgenus *Cupuliformae* here. The genera *Macropodia* and *Macroscyphus* were established with *H. macropus* as type, recognizing the taxonomic isolation of this species.

Helvella macropus (Persoon : Fries) P. Karsten, 1870, Notiser ur Sällskapets pro Flora et Fauna Fennica Förhandlingar 11: 224.

≡*Peziza macropus* Persoon : Fries, 1823, Systema Mycologicum 2: 57.

≡*Peziza macropus* Persoon, 1796, Observationes Mycologicae 2: 26.

≡*Cyathipodia macropus* (Persoon : Fries) Dennis, 1960, British Cup Fungi, p. 7.

=*Peziza subclavipes* W. Phillips & Ellis, 1887, in Ellis and Everhart, North American Fungi, Number 985. (Lectotype selected here: NY, Newfield, New Jersey, USA, Phillips (3651) 06 6 1882, examined).

≡*Paxina subclavipes* (W. Phillips & Ellis) Seaver, 1928, The North American Cup-Fungi (Operculates), p. 206.

≡*Macropodia subclavipes* (W. Phillips & Ellis) Rehm, 1904, Annales Mycologici (Berlin) 2: 35.

=*Helvella macropus* var. *brevis* Peck, 1902, Bulletin of the Torrey Botanical Club 29: 74. (holotype NYS, examined).

≡*Helvella brevis* (Peck) Harmaja, 1974, Karstenia 14: 104.

(additional synonyms see Dissing 1966b).

Type Material: unknown (*fide* Dissing 1966b).

Figs. 9, 18, 53-57.

Apothecium: 5-35 mm diam., 4-12 mm high, deeply cupulate, expanding to shallowly cupulate or discoid in age, often laterally compressed initially, margin inrolled initially, hymenium dark brown (fresh and dried), smooth, excipular surface light to medium brown or grey brown, sometimes with olivaceous tints, densely pubescent to villose. **Stipe**: 4-60 x 1-9 mm when fresh, equal or enlarged at base, apex typically tapered, light to medium grey brown, densely pubescent to villose, terete or fluted over basal half, terete to slightly sulcate and internally solid. **Asci**: 175-250 x 14-18 µm. **Paraphyses**: 5-9.6 µm diam. at apex, clavate, enlarged gradually to abruptly at apex, pale brown to brown in mass, contents finely granular. **Ascospores**: 18-25.1 x 10.3-12.2 µm, subfusoidal, hyaline, smooth to verruculose, with SEM distinctly verrucose with numerous small, isolated, pointed warts, triguttulate or infrequently uniguttulate.

Habitat: Solitary to gregarious on litter or soil, infrequently on rotted wood, in deciduous, mixed, or coniferous woods. Associated trees: *Betula papyrifera, Alnus* sp.,

Picea glauca, *Abies balsamea*, and *Thuja plicata*. Associated shrubs: *Alnus crispa* and *Lonicera involucrata*. Fruiting from July 18 in BC to October 19 in WA.

Distribution: Widely distributed throughout boreal, montane, and coastal regions from AK, BC, AB, MB, WA, and ID. Also in eastern North America (Weber 1972; Rehm 1904, as *Macropodia subclavipes*), southern North America (Seaver 1928, as *Paxina subclavipes*), Europe (Dissing 1966b; Häffner 1987), Asia (Dissing & Nannfeldt 1966; Liu *et al.* 1985), and Central America and the Caribbean (Dissing 1966b). Map 19.

Notes: Variation in the distinctive verrucose ascospore ornamentation is illustrated in Figs. 53-56. *Helvella macropus* is similar in habit to species in the subgenus *Cupuliformae*. *Helvella cupuliformis* (q.v.) and *H. chinensis* (q.v.) show the greatest similarity, but differ in colour and ascospore morphology. Collections referred to as *Helvella macropus* var. *brevis* or *Helvella brevis* in recent literature on the genus (Weber 1972; Harmaja 1974a; Abbott and Currah 1988) are considered conspecific here. Seaver (1928) recognized *Paxina subclavipes* and listed *Helvella macropus brevis* as a synonym, and Dissing (1966b) listed *P. subclavipes* as a synonym of *H. macropus*. There are several specimens of *P. subclavipes* from the Ellis collections, as well as several packets of Ellis North American Fungi Number 985, (NY). Of these, one collection (Phillips, June, 1882) annotated by Ellis is the oldest collection from which the species was originally described. It is selected as lectotype of *Peziza subclavipes*. Some specimens of *H. chinensis* (q.v.) were distributed as *Peziza subclavipes* in Ellis & Everhart Fungi Columbiani 1219.

Collections Examined: CANADA: British Columbia: Clearwater Lake area, Wells Gray P.P., Goward 08 28 1980, DAOM 186405; Clearwater River, Goward 08 20 1980, DAOM 194786; Mount Revelstoke N.P., Shoemaker 07 18 1963, DAOM 107075; near Mike Lake, Garibaldi P.P., McClaren 07 1964, UBC F3217; Golden Ears P.P., Kroeger 08 1 1982, UBC F1018. **Alberta**: near Fort McMurray, Danielson (RMD 1460) 07 31 1974, ALTA 8294; Iosegun Lake east of Fox Creek, Abbott (SA 120, 124) 08 6 1989, SA; Devonian Botanic Garden near Devon, Abbott (SA 1221) 08 24 1996, SA. **Manitoba**: Victoria Beach, Bisby 08 8 1928, DAOM 206817. **Ontario**: Black Sturgeon Lake, Redhead (1084) 08 8 1974, TRTC 47330; Ottawa, Malloch & Ginns 08 10 1972, TRTC 47743. Stethan Lake, Sudbury District, Malloch 09 12 1972, TRTC 47742; U of T forest, Muskoka District, Cain 09 17 & 18 1965, TRTC 43145, 43158. **Québec**: Resérve Chibougamau, Stanis 08 20 1976, TRTC. **USA**: **Alaska**: near Talkeetna, Kempton 08 26 1972, WK 5252; Thunderbird falls trail, north of Anchorage, Kempton 08 8 1960, WK 1554; Alaska Pacific University campus, Anchorage, Kempton 08 31 & 09 28 1971, WK 5400, 5676; Anchorage, Kempton 07 21 1979, WK 6368; Finger Lake, Matanuska valley, Kempton 08 5 1968, 09 25 1973; Nancy Lake, Susitna valley, Kempton 08 15 1968, WK 1559. **Washington**: Issaquah, van de Bogart (FVB 3565) 10 11 1975, WTU; Fall City, Thompson 08 3 1963, WTU; Lower Tahoma River, Mount Rainier N.P., Imshaug 07 30 1948, DAOM 24706; Hood Canal are, State Park, Waugh 08 1968, DAOM 126108; unknown, PSMS (Stz 15660) 10 19 1969. **Idaho**: Upper Priest River, Boundary Co., Smith (NJS 2002) 09 21 1968, MICH; Tule Bay, Beaver Creek, Priest Lake, Bonner Co., Smith (NJS 2120) 10 3 1968, MICH. **Wisconsin**: Algona, Dodge 08 11 1904, WSP 52070. **Michigan**: Tahquamenon Falls State Park, A.H. Smith 08 7 & 12 1963, UBC F3210, F3215; Cross Village, Emmet Co., Shaffer 08 5 1964, UBC F952; Mud Lake near Cheboygan, Brough 07 19 1963, UBC F3214; north of Lewiston, A.H. Smith 07 31 1963, UBC F3209; Ogemaw Co., Brough 07 23, 08 5 1963, UBC F3211, 3213; Reese's Bog, A.H. Smith 07 19 1963, UBC F3208; Grass Bay, Brough 07 9 1963, UBC F3212. **New York**: Ithaca, Long 07 22 1902, WSP 3109. **Massachusetts**: Massachusetts, Morris, NYS (holotype of *H. macropus* var. *brevis*); Massachusetts, Davis 1906, NYS. **New Jersey**: Newfield, Phillips (3651) 06 6 1882, NY (lectotype of *Peziza subclavipes*); Newfield, Ellis (3709), K; Newfield, Ellis collection 09 27 1882, NY; campground, Newfield, Ellis collection 11 1882, NY; Newfield, Ellis Collection 09 1899, NY; Newfield, Herbarium Massee, NY; Plainfield, Meschutt 07 2 1882, NY. **JAPAN**: between Yuno-ko and Karikomi-ko, Honshu Island, Cannon 08 23 1983, IMI 312582. **Exsiccata**: Rabenhorst Fungi europaei, 1413, Oberösterreich, Schiedermayr 09 1870, s.n. *Helvella macropus*, K. Ellis North American Fungi, 985, Newfield, New Jersey, USA, 06 & 09 1882, s.n. *Peziza subclavipes*, NY (packets A & B), K.

Helvella Subgenus *Silvicolae* (S.P. Abbott) S.P. Abbott *comb. nov.*

≡*Helvella* section *Silvicolae* S.P. Abbott, 1988, in Abbott and Currah, Mycotaxon 33: 245.

=*Wynnella* Boudier, 1885, Bulletin de la Société Mycologique de France 1: 102.

Type Species: *Helvella silvicola* (Beck) Harmaja, 1974, Karstenia 14: 103. (Monotypic).

Ascocarp: subsessile to indistinctly stipitate; apothecium auriculoid (erect, elongate, one-sided, reminiscent of a rabbit's ear); hymenium dark purplish red brown, smooth to slightly rugose; excipular surface red brown, glabrous; stipe indistinct, glabrous, shallowly fluted, sulcate and solid or becoming sparingly chambered; odour strong in dried specimens. **Asci**: pleurorhynchous. **Ascospores**: 19-24 x 14-17 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate, with large, central, broadly ellipsoidal guttule.

Notes: *Helvella silvicola* is frequently maintained in the monotypic genus *Wynnella* on the basis of apothecial structure, coloration, excipular vestiture and flesh consistency (e.g., Dissing 1972). Ascospore morphology (Fig. 51) and excipulum anatomy suggest placement of this taxon in *Helvella*, but other characters warrant recognition of the monotypic subgeneric section proposed by Abbott and Currah (1988)(see notes under *H. silvicola*).

Helvella silvicola (Beck) Harmaja, 1974, Karstenia 14: 103.

≡*Otidea silvicola* Beck, 1889, in Saccardo Sylloge Fungorum omnium hucusque cognitarum 8: 97.

≡*Wynnella silvicola* (Beck) Nannfeldt, 1966, Annales Botanici Fennici 3: 309.

=*Otidea auricula* auct. (see Kanouse 1949); non Schaeffer (*fide* Harmaja 1974).

(additional synonyms see Eckblad 1968; Abbott and Currah 1988)

Type Material: unknown.

Figs. 4a-c, 27, 51.

Apothecium: 5-23 mm diam., 10-60 mm high (up to 50 x 80 mm fresh), auriculoid or rarely irregularly cupulate with one enlarged lobe, margin inrolled initially, expanding and rarely somewhat reflexed in age, hymenium dark purplish red brown to dark brown fresh, when dry blackish brown, smooth or rarely slightly undulate-rugose in extreme age, excipular surface medium red brown or pale red brown to white near base, glabrous. **Stipe**: 2-10 x 2-9 mm (up to 8 x 20 mm fresh), tapered to base or nearly equal, yellow brown to pale yellow or white at base, shallowly fluted or ribbed, sulcate and solid or with central chamber. **Asci**: 200 x 15-19 µm, pleurorhynchous. **Paraphyses**: 5-6 µm diam. at apex, clavate, brown, contents finely granular. **Ascospores**: 17-24 x 11.5-17 µm, broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate.

Habitat: Solitary to gregarious or scattered and numerous on duff, rarely in burned areas, under conifers. Associated trees: *Picea glauca, Picea engelmannii, Picea mariana, Pinus contorta, Pinus ponderosa, Abies lasiocarpa,* and *Larix laricina*. Associated shrubs: *Salix discolor, Shepherdia canadensis, Symphoricarpos* sp., *Amelanchier alnifolia*, and *Rosa* sp. Fruiting from June 5 to September 22 in AB. July and August collections are common.

Distribution: Widely distributed throughout boreal and montane regions from AK, YT, BC, AB, MB and MT. Reported from ID and WA (Larsen and Denison 1978, as *Wynnella silvicola*). Also in eastern North America (Huhtinen 1985; Kanouse 1949, as *Otidea auricula*), Europe (Harmaja 1974a; Cannon *et al.* 1985) and Asia (Dissing and Raitviir 1974, as *Wynnella silvicola*). Map 16.

Notes: This species has been placed in the monotypic genus *Wynnella* Boudier (Dissing 1966b, 1972; Eckblad 1968; Larsen and Denison 1978). Ascospore

morphology (size, shape, ornamentation and guttulation) and excipulum anatomy, which are primary defining characters in the genus *Helvella*, are comparable to other *Helvella* species. The slightly to distinctly fluted or ribbed stalk, which may be elaborately infolded or somewhat chambered in some specimens (Fig. 4a,c), is an additional character linking this species with *Helvella*. Stipe morphology is similar in *H. silvicola* and *H. leucomelaena* (q.v.) (compare Figs. 3a and 4a,c). The species is distinctive in having a reddish brown, auriculoid ascocarp with a glabrous excipulum. Dried ascocarps are horny in consistency and are difficult to rehydrate in water or KOH. Dried specimens also have a unique strong odour (although none was detected in fresh collections).

The most similar species are in subgenus *Leucomelaenae*. *Helvella leucomelaena* and *H. aestivalis* (q.v.) rarely have the one sided lobe. *Helvella aestivalis* is also the only other species in the genus which has reddish pigmentation. They can be easily distinguished on the basis of excipular surface vestiture, ascospore size and shape, and habitat. Other species with a glabrous excipular surface include *H. lacunosa* (q.v.) and *H. lactea* (q.v.) in the subgenus *Helvella*, and *H. elastica* (q.v.) and *H. atra* (q.v.) in the subgenus *Elasticae*.

Collections Examined: **CANADA:** **Yukon**: Carmacks, Ziller 08 4 1962, DAVFP 14359, DAOM 93065. **British Columbia**: Kindersly Creek, Kootenay N.P., Rushton 06 16 1969, UVIC; Bull River winter range, east Kootenays, Paden spring 1976, UVIC. **Alberta**: Winfield, Strand 07 8 1975, ALTA 7341; Astoria River valley, Jasper N.P., Currah 07 25 1988, ALTA 8312; Highwood Pass, Jasper N.P., Currah 07 15 & 23 1983, ALTA 8277, 8278; Fryatt valley, Jasper N.P., Richardson (SA 300) 09 22 1989, SA; Athabasca River valley, 14 km from Sunwapta falls, Jasper N.P., Abbott (SA 371) 08 2 1990, SA; Fish Lake near Nordegg, Abbott (SA 379) 08 3 1990, SA; Fish Lake near Nordegg, Abbott 07 16 1987, ALTA 8272; 30 km east of Nordegg, Abbott (SA 1150) 06 13 1996, SA; 50 km west of Rocky Mountain House, Abbott 07 27 1987, ALTA 8273; Raven Fish Hatchery near Caroline, Abbott 07 6 1980, ALTA 8284; Red Deer River valley on Forestry Trunk road, Abbott 07 18 1988, UAMH M552; above Lake Louise, Banff N.P., Ostafichuk 08 3 1965, ALTA 605; Sawback range Mount Ishbell, Banff N.P., Rushton 09 5 1968, UVIC; Bow Valley P.P., Abbott (SA 750) 06 5 1993, SA. **Manitoba**: east end of Whitemud Lake, Parker 07 6 1971, DAOM 134578. **Québec**: Manitounuk Islands, Poste-de-la-Baleine area, Huhtinen, 07 1982, TUR 78781. **USA**: **Alaska**: Forest Nature trail, Glacier Bay National Monument, Cooke 07 9 & 11 & 20 & 27 1980, WSP 67850, MU F35984, F36302, 36347; Bartlett Cove, Glacier Bay National Monument, Cooke 07 6 1978, 08 28 1979, 06 20 1980, DAOM 179108, 179112, MU F36557. **Montana**: Echo Lake, Flathead National Forest, Cummins 07 31 1928, MICH. **RUMANIA**: Lacul Rosu, dist. Harghita, Toma 06 16 1961, K.

Underwoodia Peck, 1890, Annual Report. New York State Museum 43: 32.
=*Geomorium* Spegazzini, 1922, Anales de la Sociedad Científica Argentina 94: 79.

Type Species: *Underwoodia columnaris* Peck, 1890, Annual Report. New York State Museum 43: 32.

Macroscopic Features: ascocarp epigeous, stipitate; apothecium appressed to upper portion of stipe, apothecial margin entirely fused to stipe; hymenium pallid to brown, longitudinally wrinkled to undulate-rugose; excipular surface indistinct and merging with stipe; stipe cylindrical, white, pubescent, highly ribbed and lacunose, internally highly chambered. **Microscopic Features**: ascospores broadly ellipsoidal, hyaline, nodulose-warted, with large, isolated, broadly rounded warts of unequal size, nonapiculate, uniguttulate, tetranucleate; asci operculate, pleurorhynchous; paraphyses clavate, enlarged gradually to apex, hyaline, contents finely granular; apothecial tissue in cross section divided distinctly into ectal and medullary layers, ectal excipulum of *textura angularis*, medullary excipulum of *textura intricata*.

Underwoodia columnaris Peck, 1890, Annual Report. New York State Museum 43: 32.

≡*Helvella columnaris* (Peck) Eckblad, 1968, Nytt Magasin Botanikk 15: 91.

Type Material: Type material at NY listed by Eckblad (1968).

Figs. 12, 42.

Apothecium: 5-20 mm diam., 55-160 mm high, appressed to upper portion of stipe, rarely covering entire stipe surface, excipular surface and margin entirely fused to stipe surface, hymenium when dried orange brown to red brown or medium brown (pallid to cream when fresh), longitudinally folded-wrinkled, undulate-rugose, surface often cracking. **Stipe**: 60-130 x 5-30 mm, equal, when dried white to cream, pubescent, highly ribbed and lacunose, base often folded-fluted, internally highly chambered. **Asci**: 300-400 x 14.0-20 µm, pleurorhynchous. **Paraphyses**: 4.0-6.0 µm diam. at apex, clavate, enlarged gradually to apex, hyaline. **Ascospores**: 18.8-22.1 x 11.8-13.7 µm, broadly ellipsoidal, hyaline, verrucose to nodose or smooth when immature, with SEM warts large, isolated, broadly rounded; typically uniguttulate, rarely aguttulate or biguttulate.

Habitat: Solitary or gregarious on soil or leaf litter in deciduous woods. Fruiting from July 10 to August 1 in MB.

Distribution: Rare in boreal regions in the eastern portion of the study area from MB. Also in eastern North America (Seaver 1928, 1942; Jensen 1977). This species is endemic to eastern North America extending into the study area only in the extreme south east. Map 23.

Notes: This species is close to *U. beatonii* (q.v.) and *U. fuegiana* (q.v.) from Australia and Argentina respectively. *U.nderwoodia columnaris* is distinguished by its smaller ascospores. Excipulum structure is similar between *U. columnaris* and *U. fuegiana*, but is distinct from that in *U. beatonii* (Rifai 1968)(see also notes under *U. beatonii*).

Collections Examined: **CANADA: Manitoba**: east Manitoba Agricultural College, Winnipeg, Bisby 07 13 1927, 07 28 1928, DAOM 206822, 206823; Manitoba Agricultural College, Winnipeg, Bisby 08 1 1927, DAOM 154831; Red River, south Manitoba Agricultural College, Winnipeg, Bisby 08 1 1928, DAOM 1080, 206824; Winnipeg, Bisby 07 10 1932, K. **USA: Michigan**: Middle Maple River, A.H. Smith & Stuntz (Stz 2800) 07 15 1947, WTU.

Extralimital Species

Underwoodia beatonii Rifai, 1968, Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde II, 57(3): 69.

≡*Helvella beatonii* (Rifai) Harmaja, 1974, Karstenia 14: 103.

Type Material: Holotype K, examined.

Distribution: Known only from Australia (Rifai 1968).

Notes: It is distinguished from *U. columnaris* (q.v.) by its larger ascospores (22.7-25.4 µm excluding ornament in *U. beatonii*). *Underwoodia beatonii* differs from both *U. columnaris* and *U. fuegiana* (q.v.) in its thin ectal excipulum layer, broader hyphae of the medullary excipulum, and presence of large nematode-like cells in the medullary excipulum (Rifai 1968).

Collections Examined: **AUSTRALIA**: Anglesea campground, Victoria, Beaton (215) 07 18 1964, K (holotype).

Underwoodia fuegiana (Spegazzini) Gamundí, 1957, Darwiniana 11: 419.

≡*Geomorium fuegianum* Spegazzini, 1922, Anales de la Sociedad Científica Argentina 94: 79.

≡*Helvella fuegiana* (Spegazzini) Eckblad, 1968, Nytt Magasin Botanikk 15: 92.

Type Material: unknown.

Distribution: Known from South America (Gamundí and Horak 1979).

Notes: Close to the other two species examined, but differs in geographic distribution and morphology (see notes under *U. columnaris* and *U. beatonii*). Specimens of *U. singeri*, also described from South America (Gamundí and Horak 1979) were not examined.

Collections Examined: ARGENTINA: Nahuel Huapi, Gilbert 1949, K spirit collection 191.

Tribe: genera *incertae sedis*

Hydnotrya Berkeley & Broome, 1846, Annals and Magazine of Natural History 18: 78.

=*Geoporella* Soehner, 1951, Zeitschrift für Pilzkunde 8: 8. (*fide* Trappe 1975a).

=*Gyrocratera* Hennings, 1899, Verhandlungen Botanischer Verein der Provinz Brandenburg 41: 9. (*fide* Trappe 1975a).

Type Species: *Hydnotrya tulasnei* (Berkeley) Berkeley & Broome, 1846, Annals and Magazine of Natural History 18: 78.

Macroscopic Features: ascocarp hypogeous, sessile, irregularly globose to ellipsoidal, often somewhat dorsoventrally flattened, irregularly lobed and convoluted; hymenium enclosed within infolded chambers, may be exposed through base or external opening, internally hollow or sparsely to highly infolded and chambered; excipular surface shades of brown, glabrous to pubescent; stipe absent. **Microscopic Features**: ascospores broadly ellipsoidal to globose, brown, hyaline when immature, nodulose-verrucose, punctate, to echinulate, nonapiculate to apiculate, aguttulate to uniguttulate, de Bary bubbles absent or present in small proportion of mature spores, tetranucleate; asci clavate to cylindrical, tapered to base, hyaline, indehiscent, containing eight uniseriate to irregularly clustered ascospores; paraphyses filiform to clavate, enlarged gradually to apex, hyaline, contents finely granular; tissues in cross section separated into medullary excipulum of *textura intricata* and ectal excipulum of *textura angularis* or *textura prismatica*.

Key to subgenera of *Hydnotrya*

1. Ascospore wall smooth with amorphous, irregularly thickened to nodulose epispore.....**subgen. *Hydnotrya***

1'. Ascospore wall echinate.....**subgen. *Cerebriformae*** (***H. cerebriformis***)

Hydnotrya Subgenus *Hydnotrya*

Type Species: *Hydnotrya tulasnei* (Berkeley) Berkeley & Broome, 1846, Annals and Magazine of Natural History 18: 78.

Ascocarp: hypogeous to erumpent, sessile, irregularly globose to ellipsoidal or irregularly lobed; hymenium enclosed or exposed at base or through localized openings, internally hollow to sparingly or highly chambered. **Ascospores**: globose to broadly ellipsoidal, brown at maturity, wall smooth, becoming irregularly thickened over entire spore surface from adhering amorphous epispore, surface irregular, punctate or often nodulose, with large, isolated, broadly rounded warts, thick polar regions (appearing as apiculi) present or absent, uniguttulate to aguttulate, de Bary bubbles absent or present in small proportion of mature spores.

Notes: The type subgenus includes species with irregularly thickened to nodulose, globose to broadly ellipsoidal ascospores (Figs. 59-62).

Key to species of *Hydnotrya* subgenus *Hydnotrya*

1. Ascospores (epispore) distinctly nodulose at maturity..... 2
1'. Ascospores (epispore) irregularly thickened to punctate at maturity.....3
   2. Ascospores globose to subglobose.....***H. tulasnei***
   2'. Ascospores ellipsoidal to broadly ellipsoidal.....***H. michaelis***
3. Ascospores (epispore) at maturity cylindrical, surface irregularly rugose, with large apical thickenings often appearing as depressed apiculi.....***H. cubispora***
3'. Ascospores at maturity broadly ellipsoidal, surface roughened to punctate, nonapiculate.....***H. variiformis***

Hydnotrya cubispora (Bessey & B.E. Thompson) Gilkey, 1939, Oregon State Monographs, Studies in Botany 1: 23.

≡*Genea cubispora* Bessey & B.E. Thompson, 1920, Mycologia 12: 284.

Type Material: Isotype MICH, examined, isotype OSC, ?holotype MSC.

Figs. 16, 59, 60.

Ascocarp: 6-33 mm diam., 5-22 mm high, irregularly lobed, subglobose to ellipsoidal, excipular surface (exterior) pallid grey brown to light brown or orange brown to red brown dried, pubescent to glabrous, undulate-rugose, margin entirely fused (enclosed) or open at base, internally highly convoluted, chambered, with some closely appressed folds and large open chambers (rarely a single large chamber), chambers white, felty-pubescent. Stipe absent. **Asci**: 25-35 µm diam., cylindrical. **Paraphyses**: 6.9-11.6 µm diam. at apex, clavate, hyaline, contents finely granular. **Ascospores**: 42.8-53.6 x 29.1-36.0 µm, broadly ellipsoidal to subglobose, brown at maturity from wall pigmentation, hyaline when immature, epispore thickening by maturity resulting in cylindrical spores which may appear subrectangular or 'cuboidal', often with an irregularly thickened wall with the surface irregularly undulate rugose or slightly nodose with SEM, epispore extensively thickened at poles when mature giving the appearance of large cupulate apiculi, apiculi often striate on inner surface.

Habitat: Hypogeous or in rotted wood, solitary to gregarious in soil or rotted woody debris in coniferous woods. Associated trees: *Picea sitchensis*, *Pinus monticola*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Tsuga* sp. Fruiting from September 12 in WA to November 8 in BC.

Distribution: Uncommon in montane and coastal regions from AK, BC, and WA. This species is newly reported from BC. Also distributed in eastern and southern North America (Gilkey 1939; Miller and Miller 1982). British collections at Kew (examined with B. Spooner) are the first reports from Europe (in Pegler *et al.* 1993). Map 24.

Notes: This species is included in the type subgenus on the basis of the irregularly thickened epispore which may become inconspicuously nodulose. This feature suggests a closer relationship with *H. tulasnei* (q.v.) and *H. michaelis* (q.v.) than to *H. cerebriformis* (q.v.) of the subgenus *Cerebriformae*. Also, ascocarp morphology and colour are similar. *Hydnotrya cubispora* is easily distinguished by its cylindrical, apically thickened spores that have large cupulate apiculi when mature. The concept of this taxon has been somewhat confused since its original description in which the ascospores were said to be cuboidal or polygonal. Examination of the isotype (MICH) revealed that the description is based on immature and submature specimens which lack apiculi on most spores. Spore measurements reported above were taken only from mature ascospores and are considerably larger than in the original description (27-42 x 24-28 µm in Bessey and Thompson 1920) due to degree of epispore thickening. Gilkey (1954) recognized that early descriptions had been based on immature specimens, and stated that the spore ornamentation is not papillate, but irregularly thickened with the thickenings sometimes resulting in unusually elongated spores in the apical region of the ascus. Apical thickening of the spore wall precedes apiculus development. The collections from the United Kingdom were likely introduced with nursery stock of *Picea sitchensis* and Trappe (1971) lists this species as mycorrhizal with conifers. One specimen (IMI 311325) was somewhat atypical but was presumed to be an immature *H. cubispora*. It should be reexamined in light of the recently described *H. confusa* (Spooner 1992; Pegler *et al.* 1993).

Collections Examined: CANADA: British Columbia: Forest Nursery at Haney, Bandoni (Stz 13359) 11 8 1965, WTU. **Québec**: south of Chigoubiche River, Lac St. Jean Ouest Co., Redhead 09 4 1976, DAOM 160752; St. Donat, Montcalm Co., Rousseau 1965, DAOM 197990; Parc de la Gatineau, Chemin du Lac Lapêche, Dalpé 07 30 1985, DAOM 197989. New Brunswick: Moore's Falls, Kings Co., Harrison 08 1 1953, DAOM 143006; Glenmont, Harrison 10 10 1952, DAOM 111849; Casey's Corner, Harrison 10 12 1952, DAOM 111848. **USA: Alaska**: Girdwood, Kempton 09 18 1969, WK 4288; Turnagain Pass on Seward highway, Kempton 10 21 1963, WK 3033. **Washington**: the Pines, Copalis, Roger (Stz 20390) 09 24 1978, WTU; the Pines, Copalis, Stuntz (Stz 20629) 09 12 1979, WTU, K; near Copalis, SDL-B (SLB 1523) 09 24 1978, WTU, K; Troublesome Creek, Stuntz (Stz 20389) 09 25 1978, WTU, K. **Michigan**: between Bass and Little Bass Lakes, Cisco Lake Chain, Gogebic Co., Bessey & Darlington (123) 08 14 1919, MICH (isotype). **West Virginia**: Canaan valley, Tucker Co., Cooke 08 3 1985, WSP 68005. **UNITED KINGDOM:** Scotland, Dumfries and Galloway, Forest of Ae, Redfern 10 1 1975, K ex E; Scotland, Grampian, Durris, Mintbrae, Alexander 10 12 1982, K ex E; Soudley Ponds, Gloucestershire, Clark 08 16 1986, IMI 311325.

Hydnotrya michaelis (E. Fischer) Trappe, 1975, Mycotaxon 2: 113.

≡*Geopora michaelis* E. Fischer, 1898, Hedwigia 37: 59.

=*Hydnotrya ploettneriana* (Hennings) Hawker, 1974. Transactions of the British Mycological Society 63: 68. (authentic material K, examined).

=*Hydnotrya yukonensis* Gilkey, 1947, Mycologia 39: 445. (holotype DAOM, examined).

(additional synonyms see Trappe 1975a)

Type Material: Holotype TO.

Fig. 15.

Ascocarp: 13-18 mm diam., 8-10 mm high, irregularly globose, flattened, lobed, exterior surface pale brown to reddish brown dried, pubescent to glabrous, undulate-rugose, margin entirely fused (enclosed), internally highly convoluted and chambered, chambers white to cream, felty pubescent, odour strong when fresh. Stipe absent. **Asci**: 235-330 x 28.7-29.2 (38.6) µm, cylindrical. **Paraphyses**: 6.9-9.4 µm diam. at apex, clavate, enlarged gradually to apex, hyaline, contents finely granular. **Ascospores**: 27.5-33.0 x 20.5-25.5 µm, broadly ellipsoidal, brown, hyaline when immature, aguttulate or uniguttulate especially when immature, epispore surface nodulose, with SEM surface with large, isolated, broadly rounded warts, immature spores smooth.

Habitat: Solitary to gregarious in soil in mixed woods. Associated trees: *Picea glauca*, *Tsuga* sp., and *Alnus* sp. Fruiting from early July in YT to July 27 in AK.

Distribution: Rare in montane and coastal regions from YT and AK. Also distributed in Colorado (Fogel and Trappe 1976), Europe (Kers 1989; Vries 1981; Patouillard 1925; Teudorowiczc 1928, as *Geopora michaelis*) and Asia (Cao 1988). A map of global distribution is provided in Kers (1989). Map 25.

Notes: Close to *H. tulasnei* (q.v.), which has similar ascospore ornamentation. *Hydnotrya michaelis* has paler ascocarps, larger lobes and internal chambers, and broadly ellipsoidal ascospores. *Hydnotrya cubispora* (q.v.) is macroscopically similar, but easily differentiated by its irregularly thickened cylindrical epispore which often appears apiculate.

Collections Examined: **CANADA: Yukon**: near Potato Hills, Mayo Landing, Broadfoot early 07 1943, DAOM 14081 (holotype of *H. yukonensis*). **USA: Alaska**: near Hope, Kempton 07 27, WK 3028. **UNITED KINGDOM**: Soudley Ponds near Littledean, Gloucestershire, Francis 05 23 1981, IMI 259183, 259184. **GERMANY**: Engel (415) 07 14 1974, K; Plöttner (1325) 05 1900, K. **AUSTRIA:** Mähr-Weisskirchen, Petrak 08 1929, WSP 31544.

Hydnotrya tulasnei (Berkeley) Berkeley & Broome, 1846, Annals and Magazine of Natural History 18: 78.

≡*Hydnobolites tulasnei* Berkeley, 1844, Annals and Magazine of Natural History 13: 340-360.

=*Hydnotrya carnea* (Corda) Zobel, in Corda 1854. Icones fungorum hucusque cognitorum 6: 1-91. (authentic material K, examined).

=*Hydnotrya intermedia* (Bucholtz) Soehner. 1942. Notizblatt des Botanischen Gartens und Museums zu Berlin 15: 762-782. (*fide* Gilkey 1954).

(additional synonyms see Gilkey 1954).

Type Material: Holotype K; authentic material K, examined.

Fig. 61.

Ascocarp: 10-18 mm diam., 8-16 mm high, irregularly globose to subglobose, margin entirely fused (enclosed), excipular (exterior) surface red brown to dark red brown dried, glabrous, undulate-rugose, internally highly convoluted and chambered, chambers white to pallid, felty pubescent. Stipe absent. **Asci**: 300-340 x 26-36 µm, cylindrical to clavate (especially when immature). **Paraphyses**: 5-6 µm diam. at apex, clavate, enlarged gradually to apex, hyaline, contents finely granular. **Ascospores**: 26.8-34.3 x 25.5-33.2 µm globose to subglobose, brown at maturity, hyaline when immature, uniguttulate to aguttulate, epispore surface nodulose, with SEM surface with broadly rounded warts.

Habitat: Hypogeous, solitary or gregarious in duff or rotted wood under conifers. Associated trees: *Pinus contorta, Pseudotsuga menziesii*, and *Tsuga heterophylla*. Fruiting from June 20 to 27 in OR.

Distribution: Rare in montane regions from OR (see also Fogel 1974). Also distributed in eastern North America (Gilkey 1954), Europe (Lange 1956), and Asia (Trappe 1976; Cao 1988). Map 24.

Notes: This species is characterized by dark red brown excipulum, highly convoluted and infolded interior, and globose to subglobose, nodulose ascospores. It is most closely related to *H. michaelis* (q.v.), but is separated on colour, degree of infolding, and ascospore shape (see also notes under *H. michaelis*). Ascospore ornamentation is very similar between the two species. Gilkey (1954) discusses the variation in specimens with clavate to cylindrical asci, and synonymizes *H. carnea* and *H. intermedia* with *H. tulasnei*.

Collections Examined: **USA: Oregon**: southwest of Bend near Mount Bachelor, Egger (1135) 06 27 1984, DAOM 199694; near Bend, Miller (SM 745) 06 20 1984, WTU. **Michigan**: Tahquamenon Falls State Park, A.H. Smith 08 28 1951, DAOM 178576. **New York**: near Twin Ponds, Star Lake, Rosenthal 08 9 1974, DAOM 148902. **UNITED KINGDOM**: Woodbury Castle, Devon, Roberts 08 9 1986, IMI 311344; Westwood, Malborough, Wiltshire, Wright 08 15 1987, IMI

318223; Collingbourne Wood, Hampshire, Fletcher 08 16 1987, IMI 318214. **DENMARK**: Elsehoved, Fyn, Lange (3082) 08 11 1949, K. **NETHERLANDS**: De Steeg Prov. Felderland, Bas (1055) 08 7 1956, K. **CZECHOSLOVAKIA**: Prague, Corda, Herbarium Berkeley 1879, K; Bohemia, Bubák 08, IMI 11956. **Exsiccata**: Sydow, Mycotheca germanica, Schlesien, bei Krummhübel, Riesengebirge, Germany, Sydow 08 17 1922, s.n. *Hydnotrya carnea*, K; Sydow, Mycotheca germanica, Schlesien, Grenzdorf bei Schwarzbach, Isergebirge, Germany, Sydow 07 28 1922, s.n. *Hydnotrya carnea*, K; Petrak, Mycotheca generalis, 433, Steiermark, Mürzzuschlag, Mitterdorf, Keissler 07 06 1940, s.n. *Hydnotrya tulasnei*, WSP AS18300.

Hydnotrya variiformis Gilkey, 1947, Mycologia 39: 444.

Type Material: Holotype OSC.

Figs. 17, 62.

Ascocarp: 4-19 mm diam., 5-10 mm high (up to 40 mm diam. fresh), irregularly lobed, globose to subglobose, typically flattened, margin entirely fused or with basal opening, excipular surface pallid to pale yellow brown or orange brown to dark red brown dried, pubescent, internally hollow or highly convoluted and chambered, chambers white to cream, felty pubescent. Stipe absent. **Asci**: 258-264 x 26-29 µm, cylindrical. **Paraphyses**: 5.8-10.5 µm diam., nearly equal to clavate, enlarged gradually to apex, hyaline, contents finely granular. **Ascospores**: 28.5-36.6 x 18.0-28.7 µm, broadly ellipsoidal, yellow brown at maturity, hyaline when immature, aguttulate or uniguttulate especially when immature, with large central globose oil guttule, de Bary bubbles present in small proportion of mature spores, epispore surface verruculose to punctate, with SEM surface appearing punctate and with small irregular nodulose wall thickenings.

Habitat: Hypogeous in woody debris or embedded in rotted wood, solitary to gregarious in coniferous woods. Associated trees: *Abies lasiocarpa* and *Tsuga mertensiana*. Fruiting from July 28 to August 22 in ID.

Distribution: Infrequent in montane and coastal forest regions from AK, BC, ID, OR, and WY. Reported also from Washington (Trappe pers. comm.). This species is endemic to north west North America. It is newly reported for BC and AK, significantly extending its range to the north, and it is distributed south of the study area in California. Map 24.

Notes: Spore ornamentation is less developed than other species in the subgenus, but is irregularly thickened and slightly nodulose at maturity. The punctate spores are unique in the genus. Some specimens are distinctly yellow, especially when immature. All collections are from rotted wood (or no annotation of substratum was provided), while other species in the genus are frequently collected from soil. This species is similar to *H. michaelis* (q.v.) in spore shape and size but *H. variiformis* lacks the well developed nodulose epispore surface. *Hydnotrya cerebriformis* (q.v.) is similar in having de Bary bubbles in a small proportion of mature spores (see also notes under *H. cerebriformis*).

Collections Examined: CANADA: British Columbia: Port Renfrew, Vancouver Island, Dorworth 05 16 1988, DAVFP 23631. **USA: Alaska**: near Hope, Kempton 07 28 1968, WK 3016. **Idaho**: Brundage, Hawker 08 2 & 8 1962, K; Brundage road, Hawker 08 22 1962, K. **Oregon**: Three Creek Lake southwest of Sisters, Deschutes Co., Fogel (1174) 08 20 1976, DAOM 178574, K. **Wyoming**: Medicine Bow Mountains, Carbon Co., Binegar 08 10 1950, WSP 28610, MU F35625. **California**: Sisson Southern trail, Mount Shasta, Cooke 06 27 1947, WSP 39119; Panther Creek Meadows, Mount Shasta, Cooke 07 1 1951, WSP 30042; horse camp area, Mount Shasta, Cooke 08 17 1962, 07 18 1966, WSP 55752, 58743.

Hydnotrya* Subgenus *Cerebriformae S.P. Abbott *subgen. nov.*

Ascocarpae hypogaea, subglobosa, caverna fere simplice aut gleba compactis plicis composita; ascosporae globosa, echinatae.

Type Species: *Hydnotrya cerebriformis* Harkness, 1899, Proceedings of the California Academy of Sciences, Series 3, Botany 1: 266. (monotypic).

Ascocarp: hypogeous to erumpent, sessile, irregularly lobed, globose to ellipsoidal, typically flattened, margin fused (enclosed) or with basal opening; exterior surface pallid yellow or orange brown to dark red brown, pubescent to glabrous; internally highly convoluted and chambered, chambers white, felty-pubescent. **Ascospores**: globose to broadly ellipsoidal, brown at maturity, hyaline when immature, thin-walled and smooth when immature, becoming thick-walled at maturity, aguttulate or uniguttulate especially when immature, with large central subglobose oil guttule, de Bary bubbles in a small proportion of mature spores, appearing warted to echinulate, with SEM surface covered with numerous long pointed spines, but often appearing warted or cracked from adhering debris and clumping of spines.

Notes: This monotypic subgenus is established on the basis of the globose, echinate ascospores of *H. cerebriformis* (Figs. 63, 64). The isolated taxonomic position of this species was noted by Trappe (1979).

Hydnotrya cerebriformis Harkness, 1899, Proceedings of the California Academy of Sciences, Series 3 Botany 1: 266.

=*Hydnotryopsis suevica* Soehner, Notizblatt des Botanischen Gartens und Museums zu Berlin 15: 779. (*fide* Trappe 1975a).

≡*Geoporella suevica* (Soehner) Soehner, 1951, Zeitschrift für Pilzkunde 8: 8.

Type Material: Holotype BPI.

Figs. 28, 63, 64.

Ascocarp: 8-24 mm diam., 8-13 mm high (up to 50 mm diam. fresh), irregularly lobed, globose to broadly ellipsoidal, typically flattened, margin fused or with an opening at base, excipular surface pale orange brown to dark red brown dried, pubescent to glabrous, undulate-rugose, internally highly convoluted and chambered, chambers white to cream, felty pubescent. Stipe absent. **Asci**: 260-370 x 26.8-36.8 µm, cylindrical or rarely somewhat clavate. **Paraphyses**: 6.6-11.1 µm diam. at apex, terminal cell 45-50 µm long, clavate, enlarged gradually to abruptly at apex, hyaline, contents finely granular. **Ascospores**: 26.1-32.8 x 24.2-27.8 µm, globose, subglobose, or broadly ellipsoidal, brown at maturity, hyaline when immature, aguttulate or uniguttulate especially when immature, appearing echinate, warted or verrucose, with SEM surface covered with numerous, long, pointed spines, but often appearing warted or cracked due to adhering matrix.

Habitat: Hypogeous to erumpent, solitary to gregarious in soil and litter in coniferous woods. Associated trees: *Picea engelmannii*, *Picea sitchensis*, *Pinus* sp., and *Abies* sp. Fruiting from July 29 to September 20 in AK.

Distribution: Infrequent in montane and coastal regions from AK and ID. This species is newly reported from AK and greatly extends the northerly range. Also reported from OR (Trappe pers. comm.), south west North America (Gilkey 1916, 1939; Fogel and Trappe 1976), Europe (Soehner 1951, as *Geoporella suevica*) and Asia (Cao 1988). Map 25.

Notes: This species is distinct, and relationship to other *Hydnotrya* species is unclear. *Hydnotrya variiformis* (q.v.) has de Bary bubbles in mature ascospores, but *H. cerebriformis* differs in its globose to subglobose ascospores with prominent echinate ornamentation. In many cases, the spores have distinct spines or coalesced clumps of spines, but often the surface appears irregularly cracked. This is attributed to adhering perispore or mucoid material being stuck to the spines. Hawker (1968a; Hawker *et al.* 1967) shows that spore features of *Elaphomyces* are influenced by fruiting body age and rate of drying during preservation. This may also apply to this species since spore

morphology resembles *Elaphomyces* species (Hawker *et al.* 1967; Hawker 1968a; Trappe 1976; Samuelson *et al.* 1987). The echinate spores are fundamentally different from the irregularly thickened ones of the other species of the genus and warrant recognition at the subgeneric level.

Collections Examined: **USA: Alaska**: Girdwood, Kempton 08 28 1973, WK 6037; Ptarmigan Creek campground, Kenai Peninsula, Kempton 09 9 1965, WK 3023, DAOM 178553, K; Chilkoot Lake near Haines, Kempton 09 20 1970, 09 16 1971, WK 4950, 5590; Juneau, Kempton 07 29 1966, WK 3022. **Idaho**: Upper Payette Lake, Valley Co., A.H. Smith (60171) 08 17 1958, K; Vulcan Hot Springs, South Fork of Salmon River, Valley Co., A.H. Smith (66207) 08 26 1962, K; Squaw Meadows, Valley Co., A.H. Smith (60274) 08 18 1958, DAOM 178552; Brundage Reservoir, A.H. Smith 08 18 1962, K.

Gymnohydnotrya B.C. Zhang & Minter, 1989, Mycological Research 92: 192.

Type Species: *Gymnohydnotrya australiana* B.C. Zhang & Minter, 1989, Mycological Research 92: 193.

Macroscopic Features: ascocarps hypogeous, sessile, irregularly lobed to subglobose; hymenium exposed at outer surface and regions on the internal surface; internally hollow to infolded and chambered; basal mycelial tuft present. **Microscopic Features**: asci indehiscent, cylindrical, hyaline; ascospores ellipsoidal, hyaline, with large central globose oil droplet and two to many smaller polar guttules, tetranucleate, appearing rough to verrucose, with SEM surface echinate, spines often with adhering extramatrical tissue forming irregular reticulum of coalesced spines (Zhang and Minter 1989b).

Extralimital Species

Gymnohydnotrya australiana B.C. Zhang & Minter, 1989, Mycological Research 92: 193.

Type Material: holotype K, examined.

Distribution: Known only from Australia (Zhang and Minter 1989).

Notes: This species is distinguished from the other two members of the genus, *G. echinulata* (q.v.) and *G. ellipsospora* (Cribb) B.C. Zhang and Minter, by its larger more echinate ascospores. Ascocarps of *G. australiana* are more highly infolded and chambered with internal hymenial surface in addition to hymenium covering the exterior surface. Due to the variation of infolding and resultant chambers seen in some *Hydnotrya* species, such as *H. variiformis* (q.v.), *H. cubispora* (q.v.), and *H. michaelis* (q.v.), this character is of dubious importance at the specific level. Ascospore size and ornamentation are also somewhat variable in other taxa of the family (see notes under *Hydnotrya* species).

Collections Examined: **AUSTRALIA**: Rye, Victoria, Keane 01 1984, K spirit collection 1032 (holotype).

Gymnohydnotrya echinulata (G.W. Beaton) B.C. Zhang & Minter, 1989, Mycological Research 92: 194.

≡*Sphaerozone echinulatum* G.W. Beaton, 1978, in Beaton & Weste, Transactions of the British Mycological Society 71: 165.

Type Material: Holotype MELU; authentic material K, examined.

Distribution: Known only from Australia (Beaton and Weste 1978, 1982).

Notes: see notes under *G. australiana.*

Collections Examined: **AUSTRALIA:** Little River near Alexandra, Victoria, Crichton (Beaton 314) 08 20 1965, K spirit collection.

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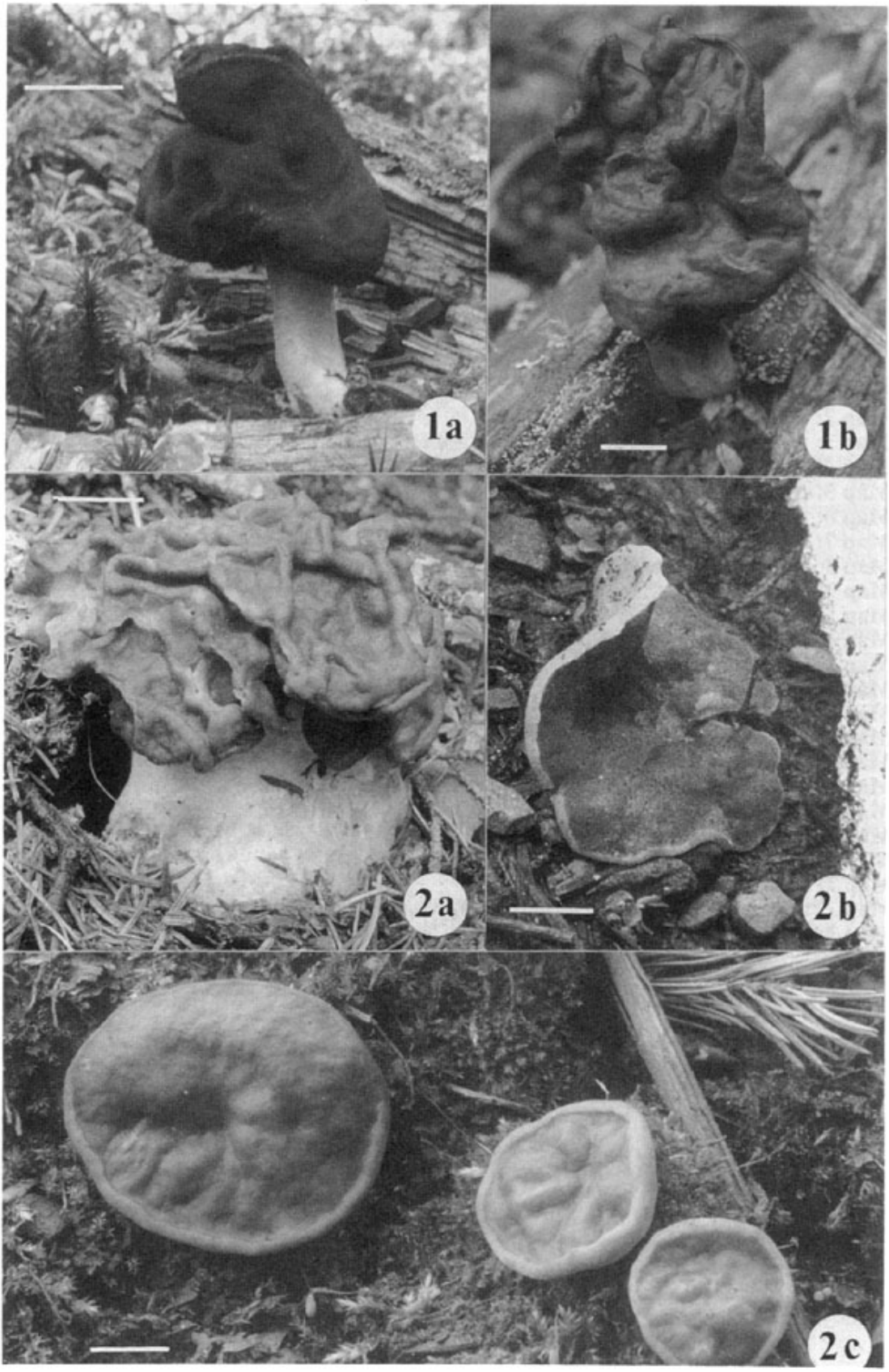
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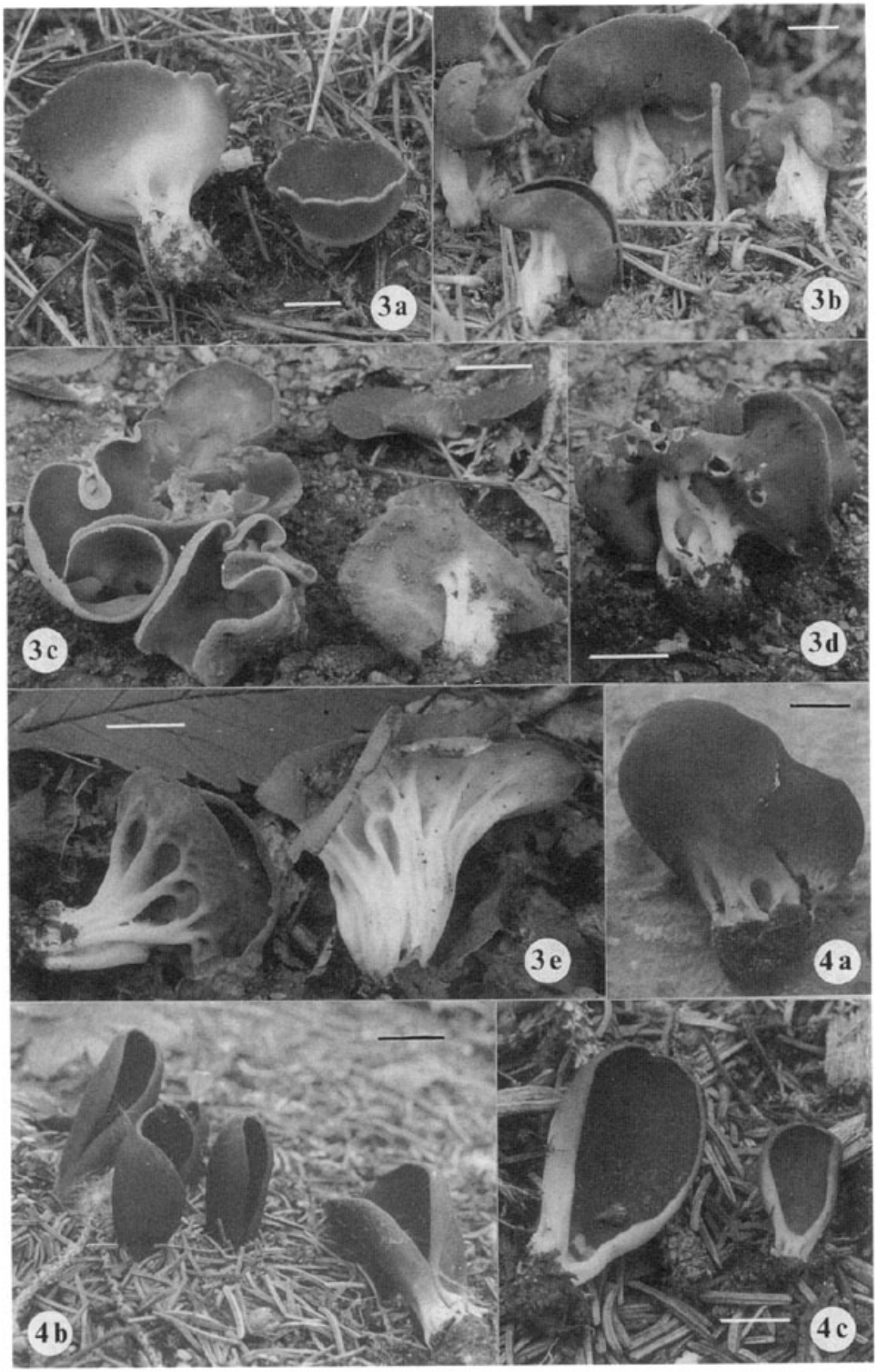
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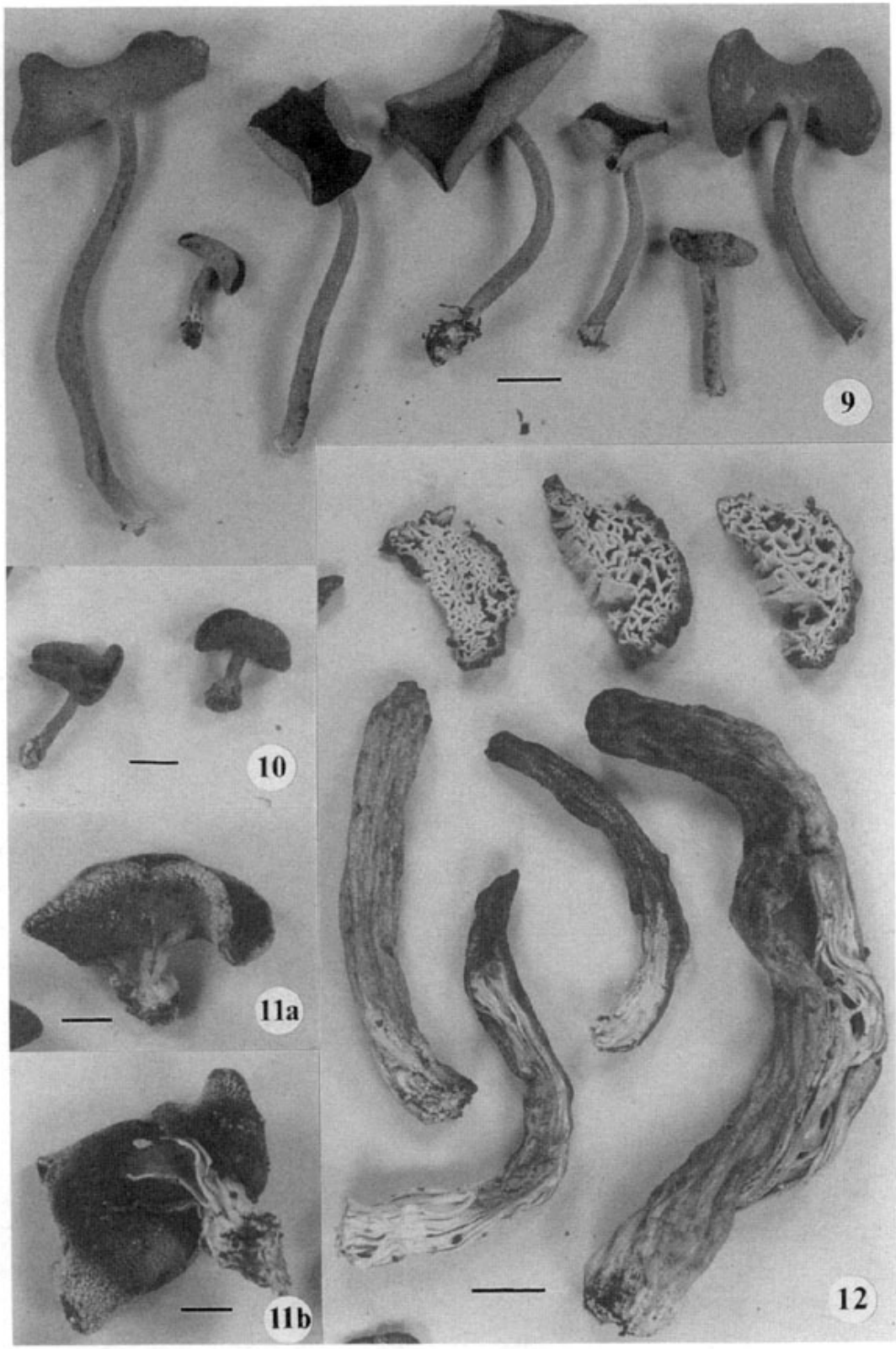
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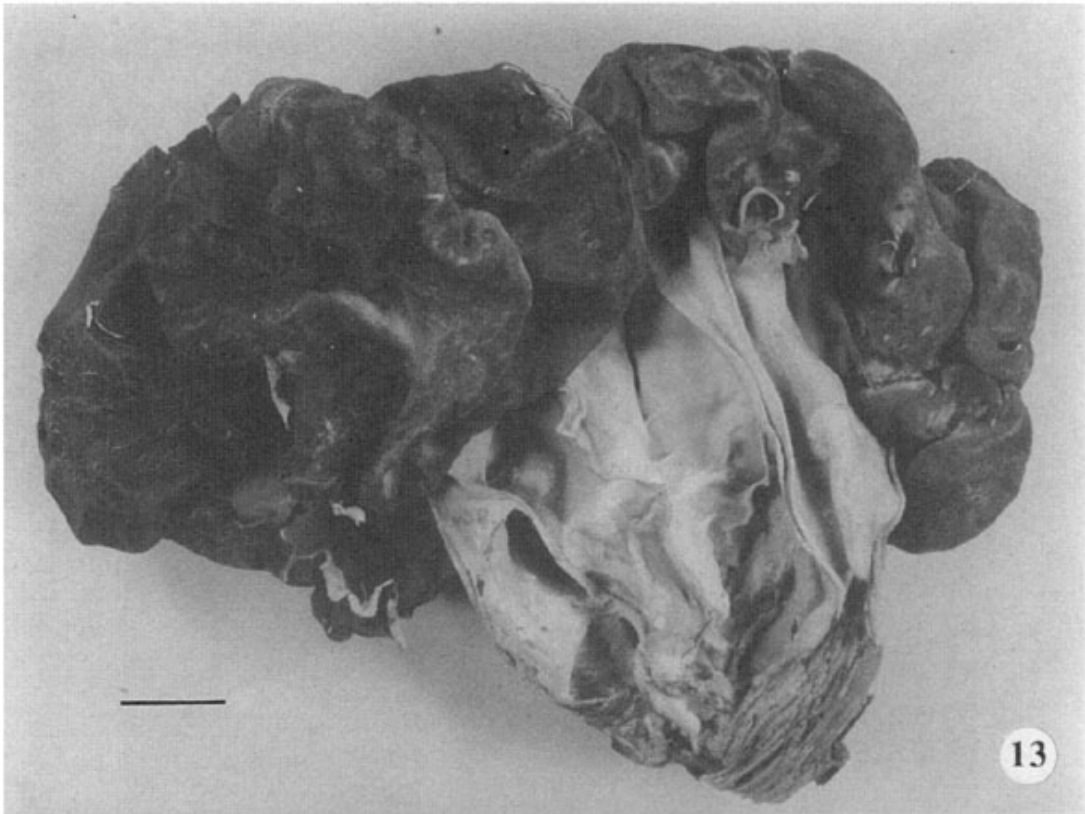
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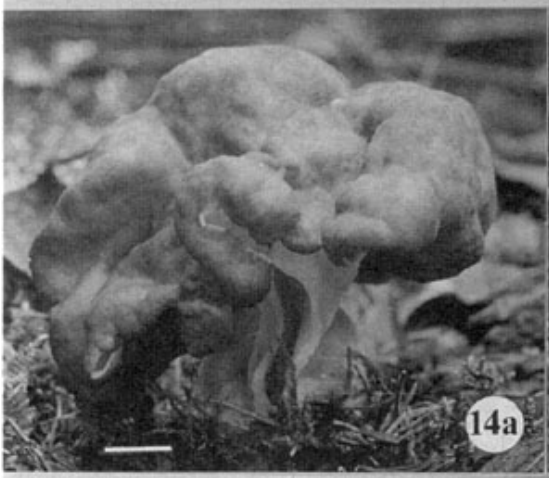
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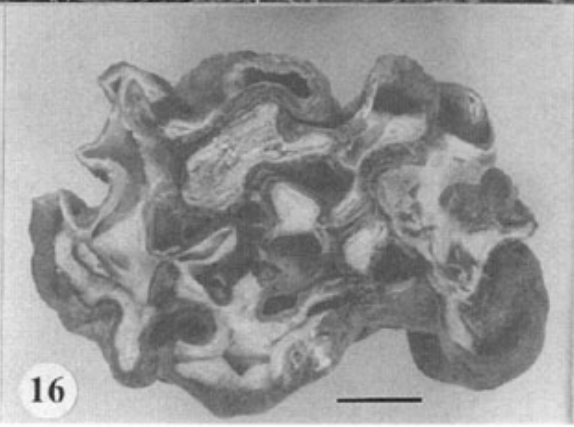
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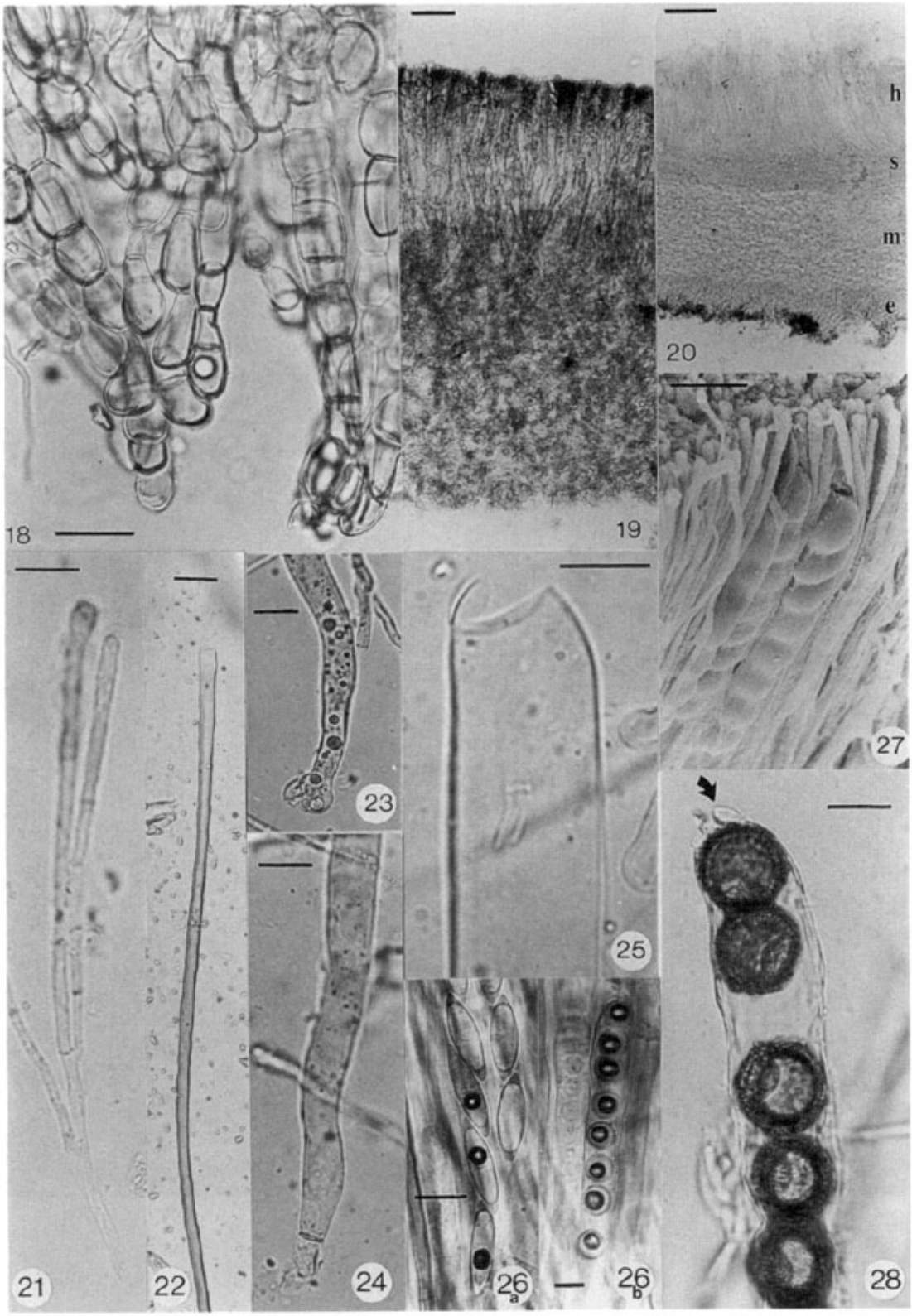
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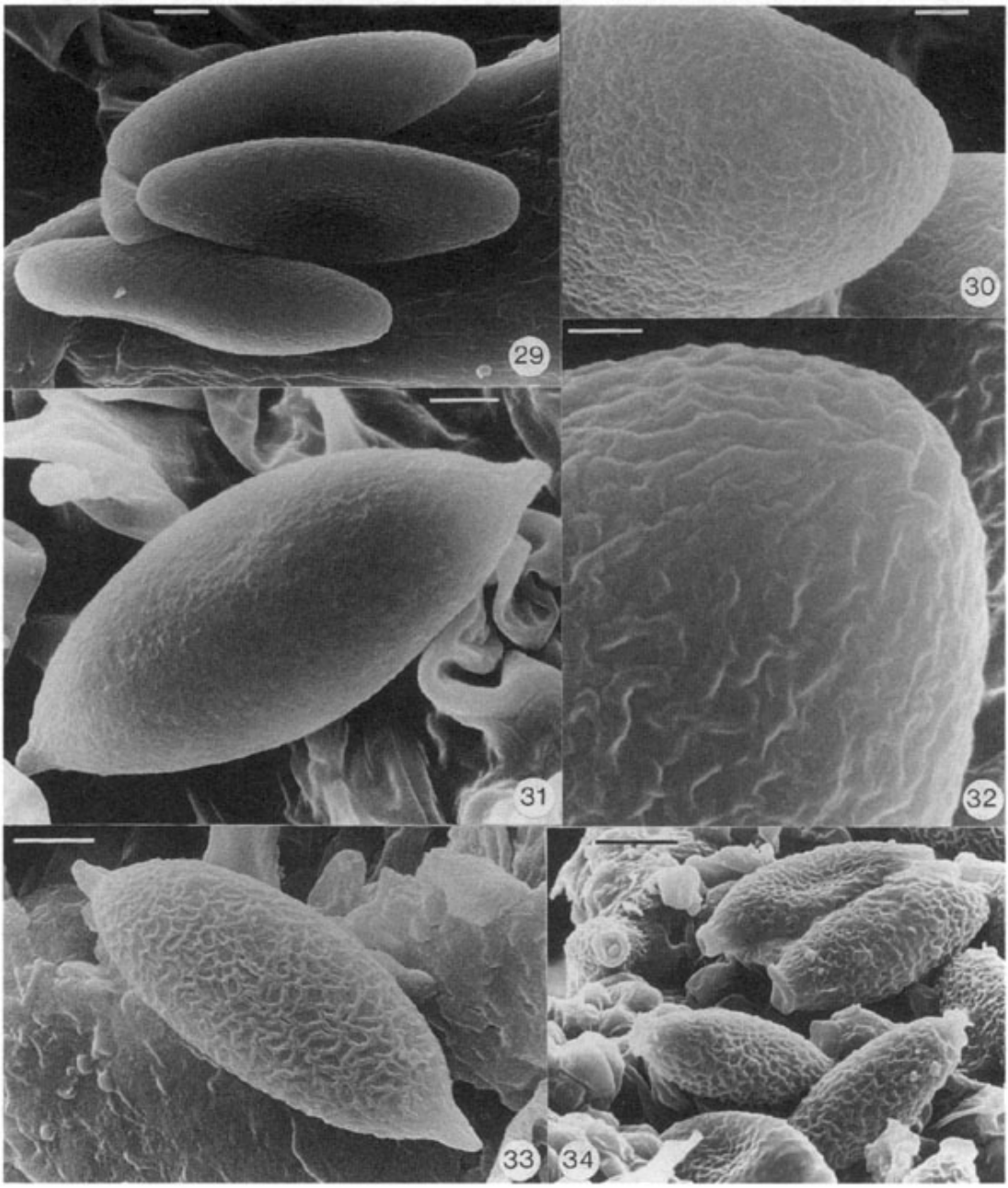
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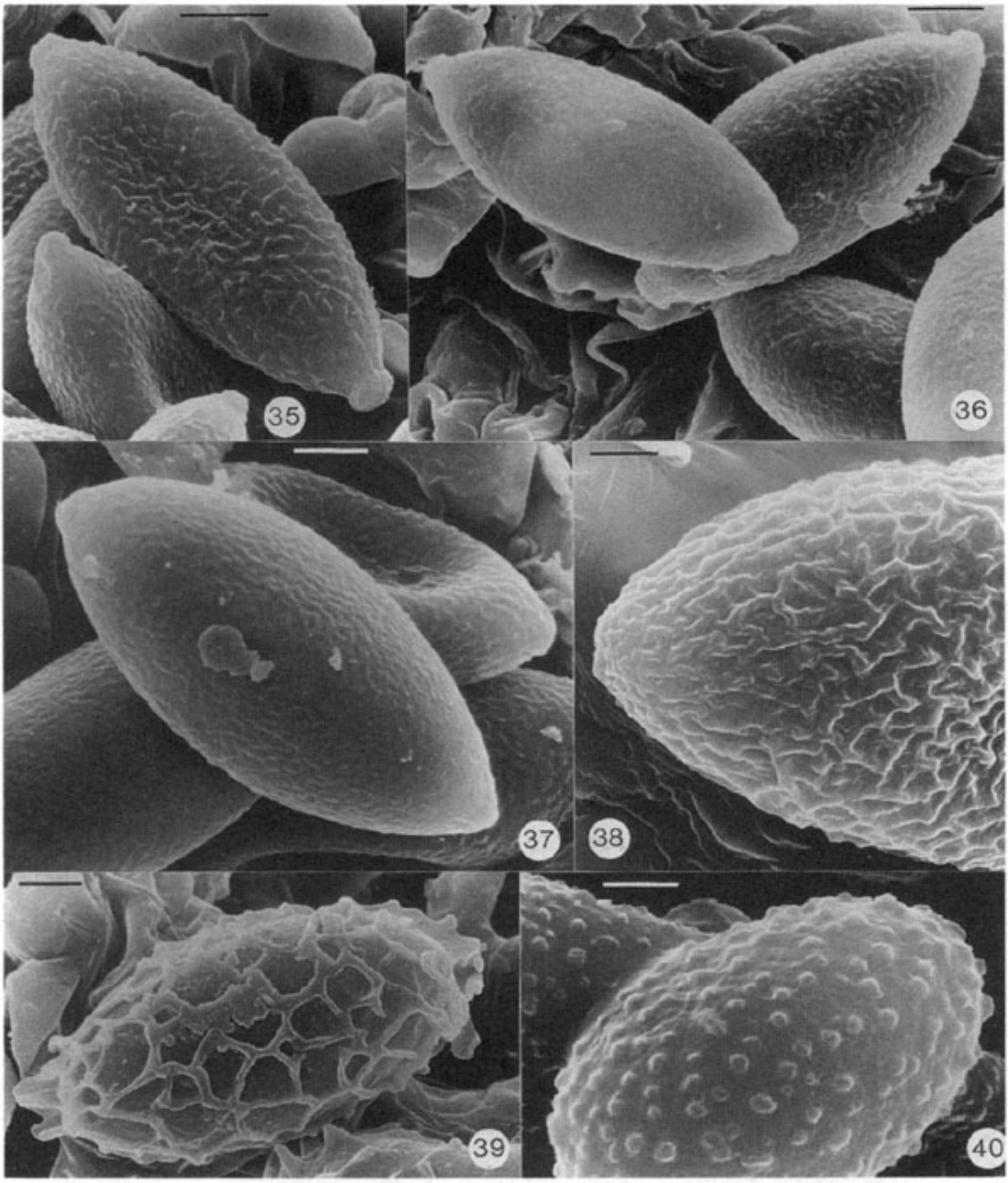
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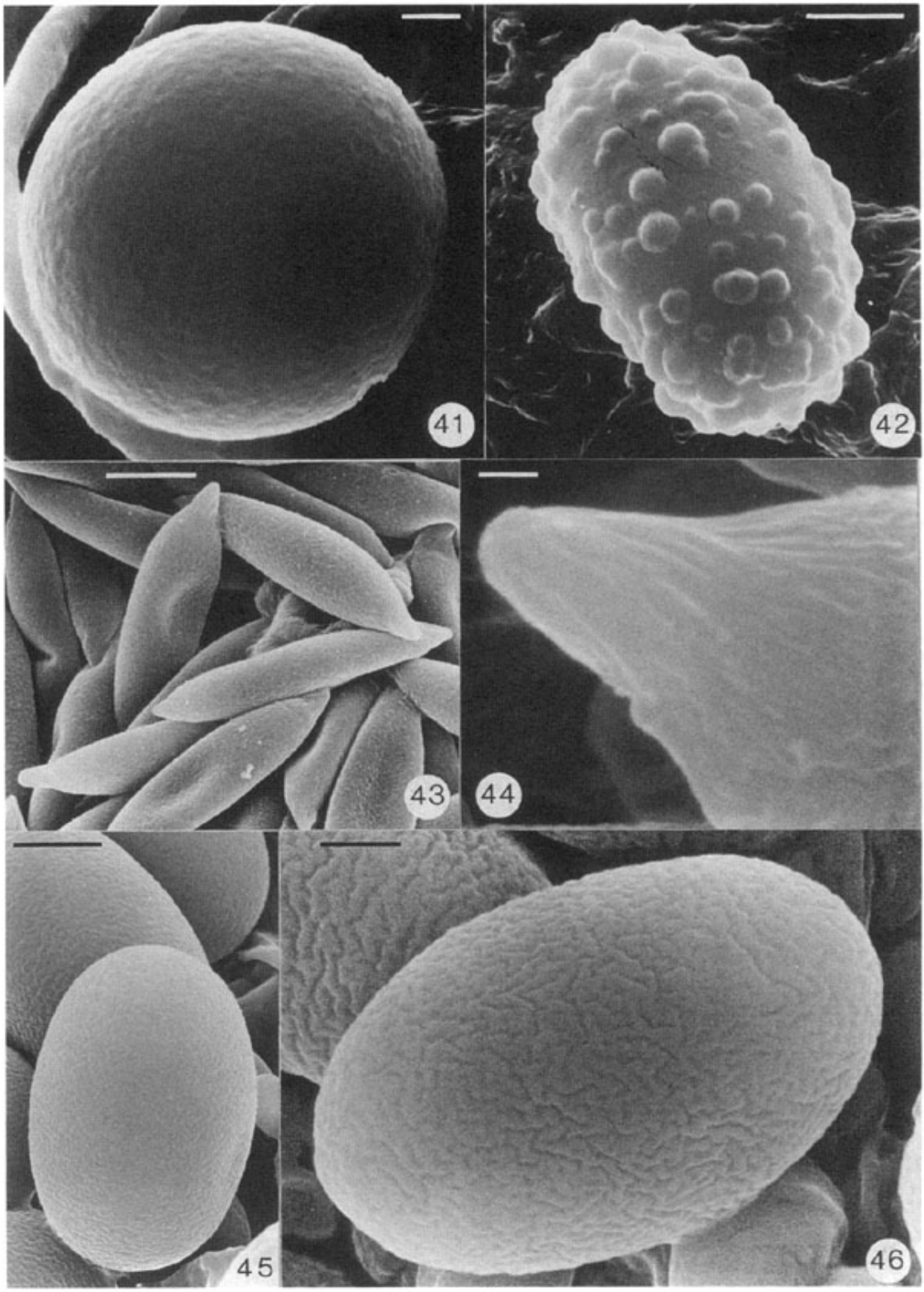
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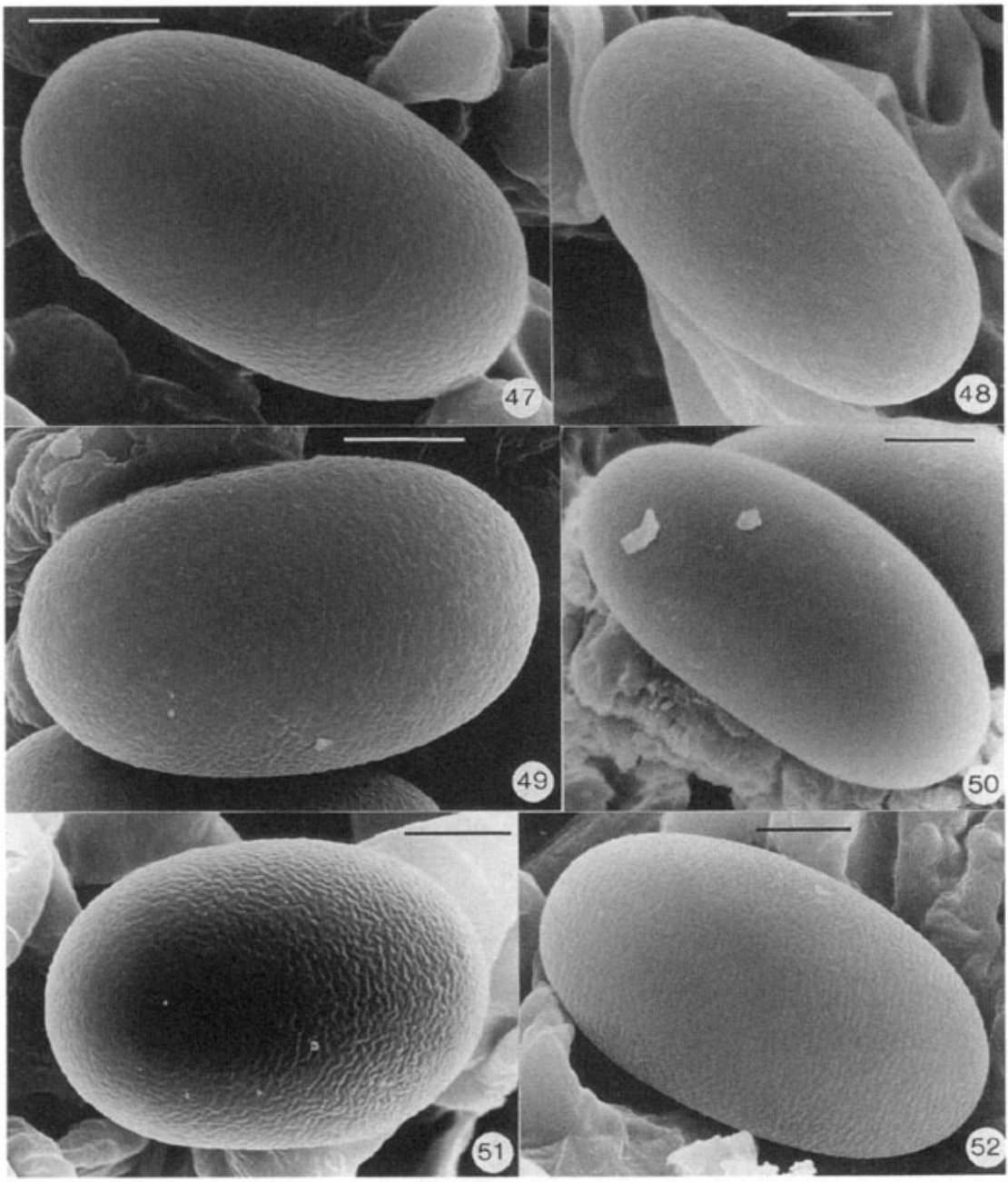
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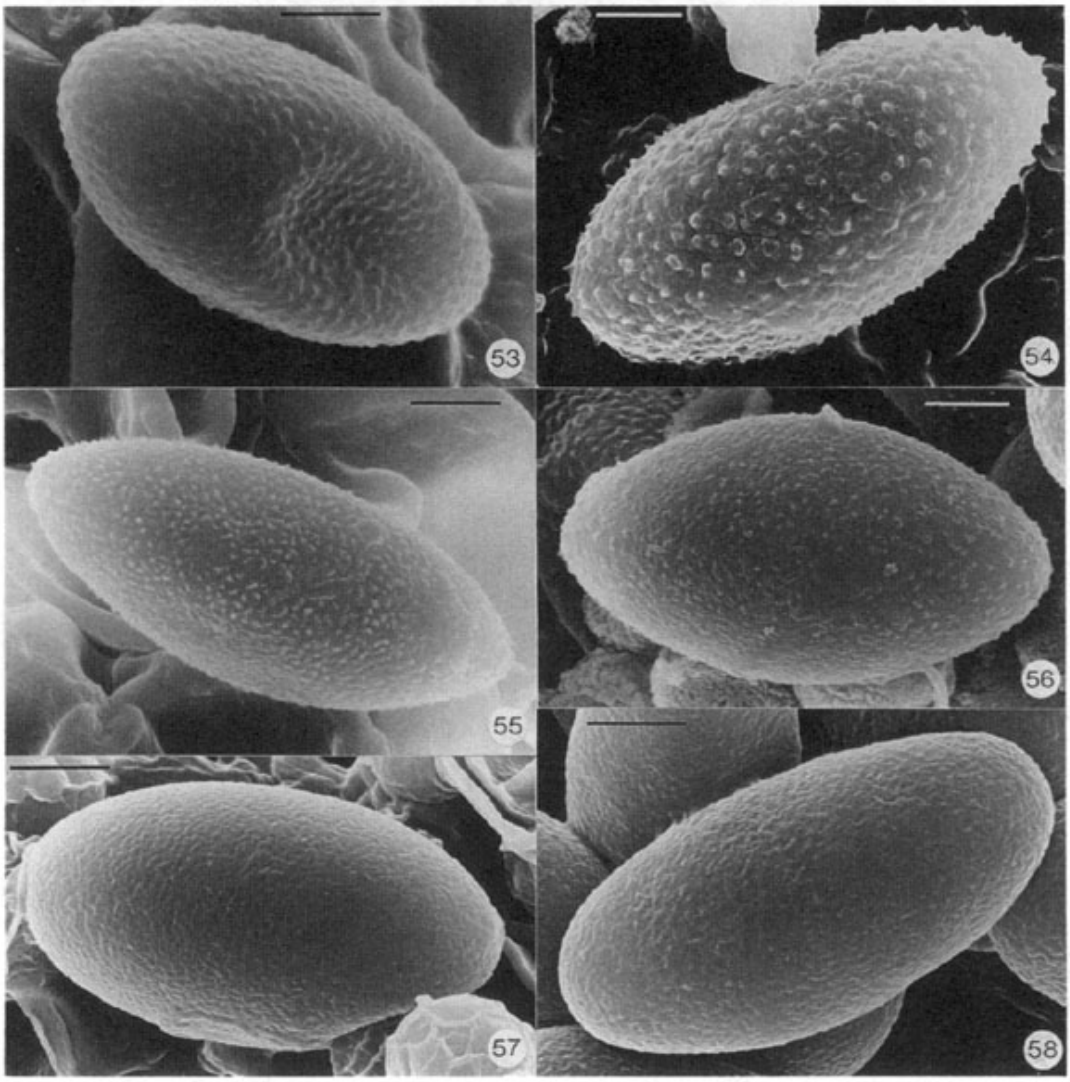
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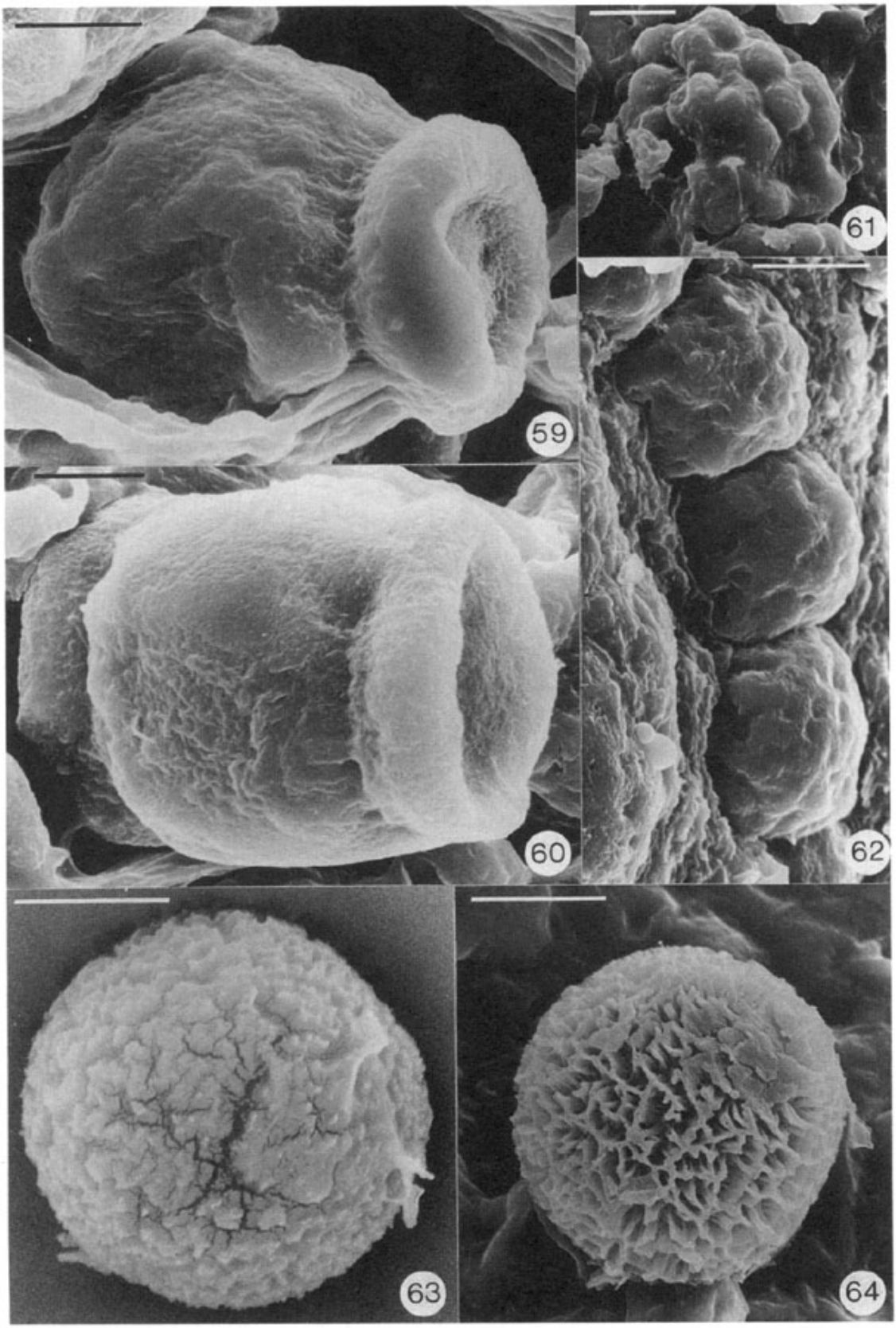
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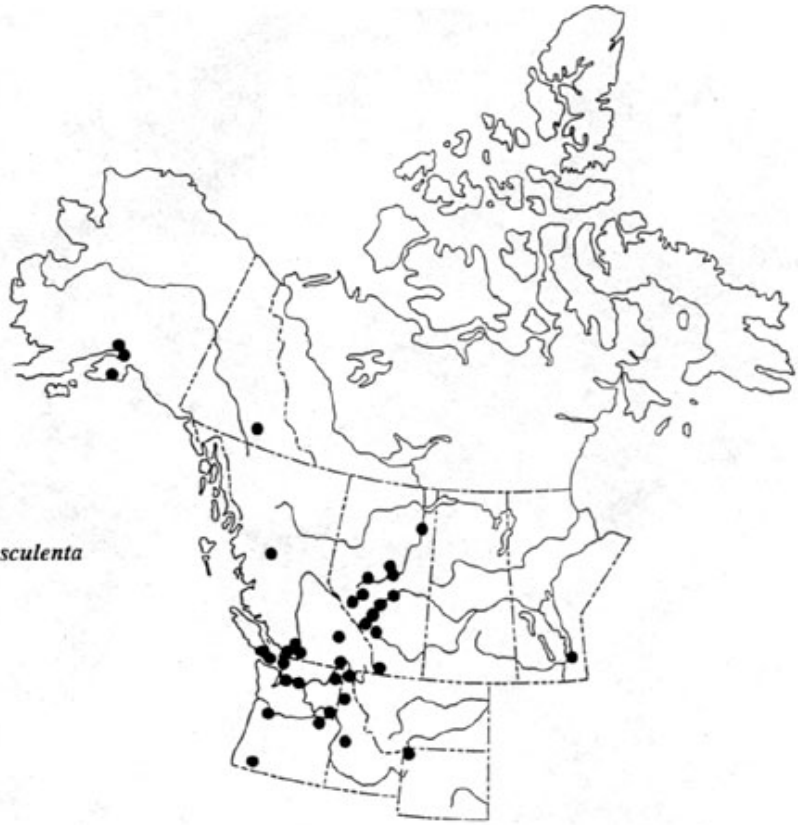

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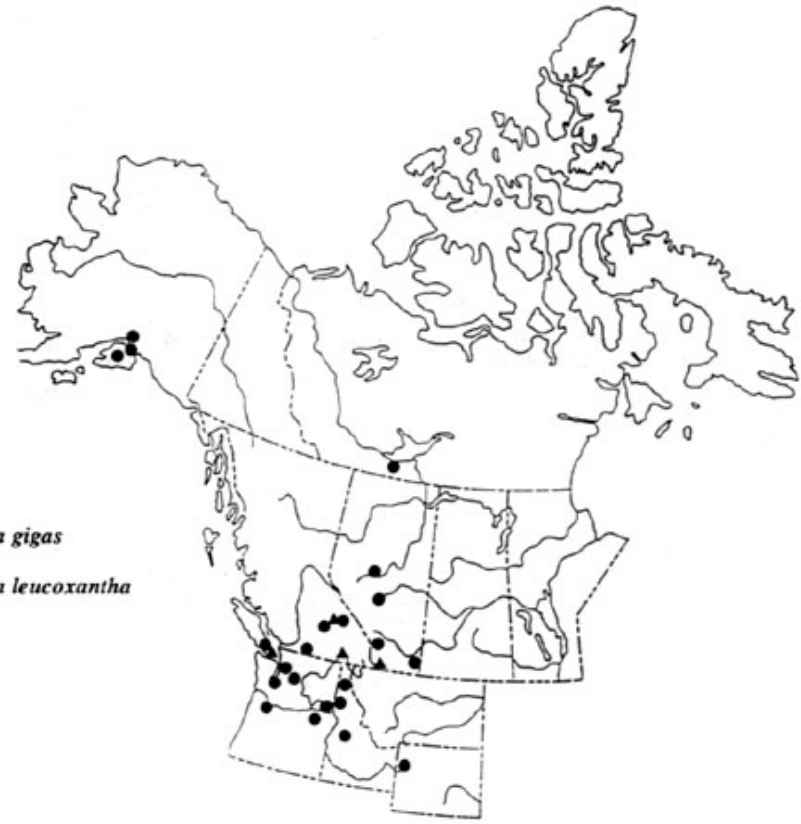

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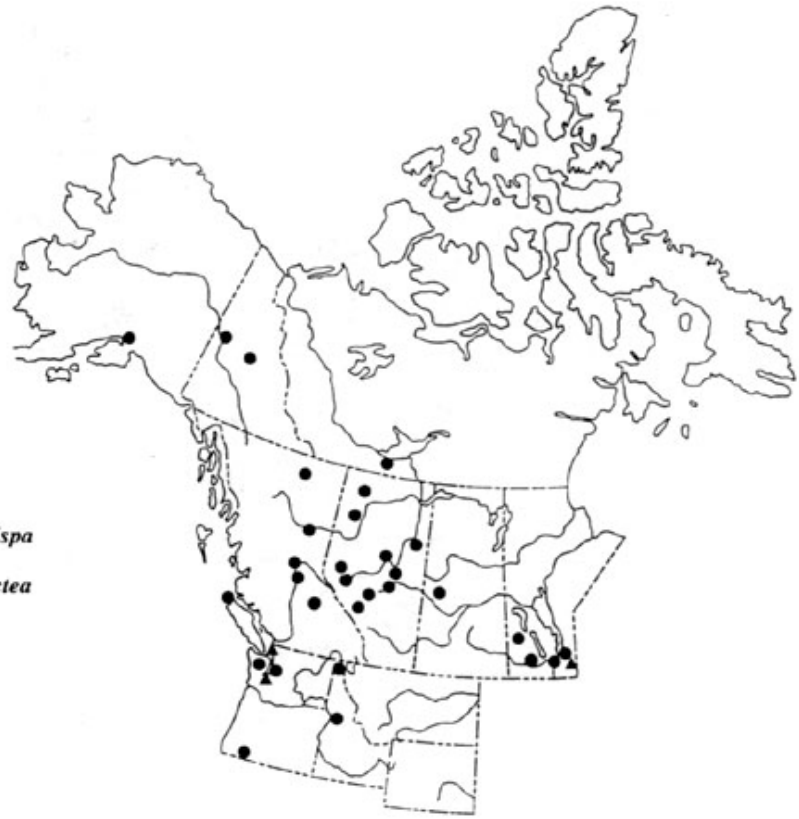

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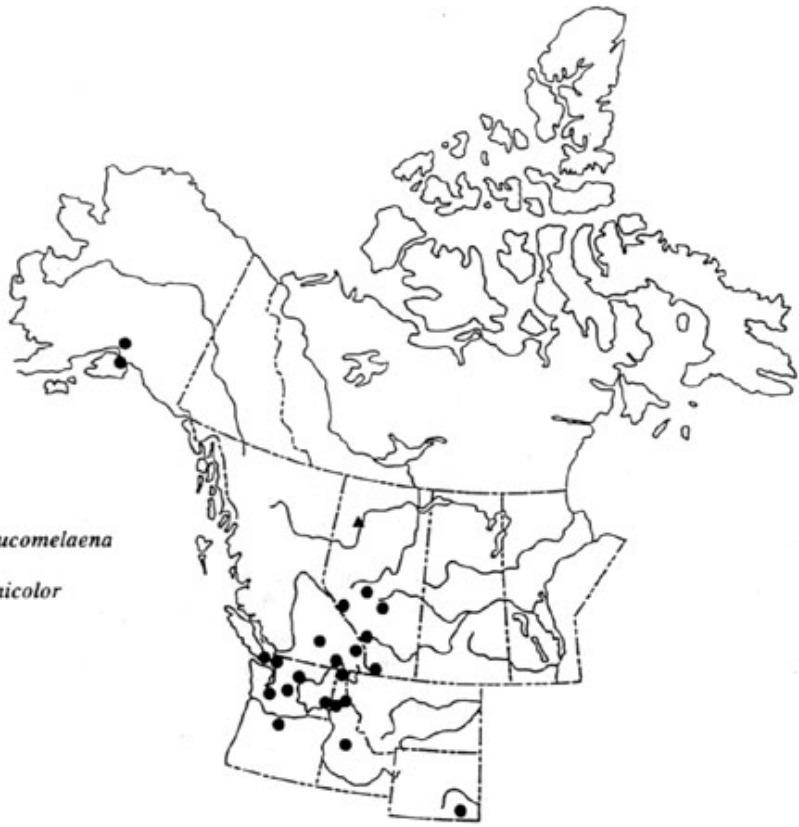

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