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SYSTEMATIC STUDIES OF THE HELVELLACEAE IN NORTHERN AND NORTHWESTERN NORTH AMERICA

BY

SEAN P. ABBOTT ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

MYCOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Systematic studies of the Helvellaceae in northern and northwestern North America submitted by Sean P. Abbott in partial fulfillment of the requirements for the degree of Master of Science in Mycology.

Randolph Currah

R.S. Currah

R.J. Bayer

P. Blenis

DATE: December 19, 1991

Dedicated to the memory of John W. Paden for his contributions
to ascomycete taxonomy in northwestern North America.

ABSTRACT

Generic, subgeneric, and specific taxa in the Helvellaceae (Pezizales, Ascomycotina) are revaluated, and the taxonomic value of morphological features used in the identification of these taxa is reassessed. Taxa are separated into two subfamilial tribes (Helvelleae and Gyromitreae) on the basis of excipulum structure. The surface ornamentation of ascospores as observed with the scanning electron microscope proved highly valuable in taxonomic delimitation of genera, subgeneric sections, and species. 59 species, 45 of which occur in northern and northwestern North America are distributed among six genera (*Gyromitra*, *Rhizina*, *Pseudorhizina*, *Helvella*, *Underwoodia*, and *Hydnotrya*), and are described including details of morphology, habitat, distribution, and phylogenetic relationships. Four new subgenetic sections are proposed. These include *Gyromitra* section *Melaleucoides sect nov.*, characterized by nonapiculate, biguttulate ascospores with isolated warts, *Gyromitra* section *Caroliniana sect. nov.*, characterized by coarsely reticulate ascospores with multiple spicules at the poles, *Helvella* section *Cupuliformae sect. nov.*, containing species with regularly cupulate apothecia, solid terete stipes, and broadly ellipsoidal, finely rugose ascospores, and *Hydnotrya* section *Cerebriformae sect. nov.*, characterized by globose echinate ascospores. The subgeneric sections *Helvella*, *Leucomelaenae*, *Elasticae*, and *Discina* are emended. *Peziza subclavipes* Phillips & Ellis is an earlier synonym of *Helvella brevis* (Peck) Harmaja, and the new combination *Helvella subclavipes* (Phillips & Ellis) *comb. nov.* is proposed. Floristic work has extended the known distributional range for many species, including several new records for North America (*Helvella rivularis*, *H. arctoalpina*, *H. unicolor*). Distribution maps and keys to taxa in northern and northwestern North America are provided.

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I am pleased to acknowledge Dr. R.S. Currah for his supervision of this project, his input of helpful suggestions, and his devotion to my training program. I am sincerely grateful for the guidance and enthusiastic encouragement he has provided during the course of this study. Drs. R.J. Bayer, P. Blenis, D.H. Vitt, M. Dale, and G. Armstrong are gratefully acknowledged for their assistance during this project. The assistance of the curators and staff of the numerous herbaria which supplied materials for this study is deeply appreciated. Roy Kristiansen, Phyllis Kempton, and Bob Danielson provided additional specimens, complete with detailed descriptions and/or photographs. Their assistance and correspondence is deeply appreciated. The technical assistance provided by G. Braybrook (SEM) and L. McBain (ALTA) was invaluable to this study. A special thanks is due Leni Schalkwyk, Godo Stoyke, and Kathy Richarson for translation of pertinent Dutch, German, French, and Spanish literature. I would like to express my sincere gratitude to Drs. B. Spooner, T. Læssøe, and D. Pegler for their efforts to accommodate my research needs during my visit to the Royal Botanic Gardens Herbarium at Kew, and for their warm reception and continued correspondence. Drs. B.C. Sutton and P. Cannon and Janet Pryse are gratefully acknowledged for their assistance during my visit to the International Mycological Institute, Ferry Lane, Kew.

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INTRODUCTION

The Helvellaceae comprises a diverse array of macroscopic discomycetes. The family has a global distribution and reaches its peak of diversity in northern temperate regions. Some species are presumed to be mycorrhizal, while others are saprophytic or parasitic. Saprophytic species occur on a variety of substrates including soil, coniferous and deciduous litter, and rotted wood. *Rhizina undulata* is a serious pathogen of conifer seedlings in northwestern North America. Helvellaceae fruiting bodies vary from simple cupulate to complex lobed or convoluted apothecia and may be sessile or distinctly stipitate. Some members of the family attain considerable size, and have among the largest fruiting bodies produced by ascomycetes of any kind (*e.g. Gyromitra gigas, G. esculenta*). Thus, species of this conspicuous family are of paramount interest to mycological naturalists, and are commonly referred to as false morels. Few families of discomycetes (excepting perhaps only the Morchellaceae or morel family) rival the importance of the family to human populations. Most species of *Gyromitra* and *Pseudorhizina* contain toxic compounds, especially the 'gyromitrin-monomethylhydrazine' toxin group, although investigations into all taxa is far from complete (*e.g.* Ammirati *et al.* 1985; Harmaja 1976c). No toxins have been reported in other genera, but chemical composition is unknown for most species. Some species (e.g. *Gyromitra esculenta*) are known to have caused fatalities, especially when consumed raw. Despite the toxic nature of this family, several species (*e.g. G. esculenta, G. perlata,* and *G. gigas*) are prepared for human consumption by removal of the volatile toxin by boiling or drying. Recent investigations in Finland (Jalkanen & Jalkanen 1981, 1984) have explored the possibility of commercial production and semi-cultivation of *G. esculenta* in its natural habitat. *Helvella lacunosa* is commonly considered edible (*e.g.* Arora 1986) and is collected for human consumption in many areas. Identification of these fungi has been traditionally important to separate species from the true morels (family Morchellaceae).

As is common in ascomycete taxonomy, detailed monographic works on this family have been concentrated at the generic level (*e.g.* Dissing 1966; Weber 1972; Zhang & Minter 1989b; Trappe 1975b, 1989). In many taxonomic studies, the genera examined were treated in a more restricted sense than that accepted here (*e.g.* McKnight 1969; Kempton & Wells 1973) or only selected species of a genus were considered (*e.g.* McKnight 1971, 1973; Harmaja 1969b, 1977a, b, 1979a, b). Some discussion of family characters is provided by Dissing 1972 and Harmaja (1969a, 1974a, 1976b), and is often briefly discussed in comprehensive works on Pezizales (Eckblad 1968; Korf 1972, 1973a; Trappe 1979). Treatments of the family have been for the most part, restricted to floristic works, although many of these are of excellent quality and of great value in providing a comprehensive view of the family and subfamilial taxa. This study treats the family more comprehensively than has been done in the past, and it is intended that the delimitation of taxa will reflect a more homogeneous system of categorization reflecting the relationships within the Helvellaceae. Table 1 lists taxa examined in this study.

North American literature concerning this family is abundant (Weber 1972, 1975; Mcknight 1969, 1971, 1973; Kempton & Wells 1970, 1973; Ginns 1968, 1974a, b, c, d, e, 1975; Abbott & Currah 1988; Callan 1990; Anderson & Ickis 1921; Pfister 1980; Seaver 1921; Morse 1945; Kanouse 1946; Groves & Hoare 1953; Dissing & Lange 1967; Harmaja 1981; Trappe 1975b, 1989; Gilkey 1916, 1939, 1947, 1954), although perhaps somewhat less comprehensive than that of Europe (*e.g.* Dissing 1966b; Donadini

TABLE 1: Taxa of Helvellaceae

FAMILY	HELVELLACEAE		
TRIBE	GYROMITREAE		
GENERA	*GYROMITRA*	*RHIZINA*	*PSEUDORHIZINA*
SUBGENERIC SECTIONS AND NUMBER OF SPECIES	*GYROMITRA* (5 spp.) *MELALEUCOIDES* (2 spp.) *DISCINA* (4 spp.) *CAROLINIANA* (3 spp.)	1 Section (1 sp.)	1 Section (2 spp.)

TRIBE	HELVELLEAE		
GENERA	*HELVELLA*	*UNDERWOODIA*	*HYDNOTRYA*
SUBGENERIC SECTIONS AND NUMBER OF SPECIES	*HELVELLA* (6 spp.) *LEUCOMELAENAE* (11 spp.) *SILVICOLAE* (1 sp.) *CUPULIFORMAE* (4 spp.) *MACROPODES* (2 spp.) *ELASTICAE* (8 spp.)	1 Section (3 spp.)	*HYDNOTRYA* (4 spp.) *CEREBRIFORMAE* (1 sp.)

1986). The study area chosen comprises arctic areas of northern North America as well as coastal, boreal, montane, and alpine regions of northwestern North America. Studies from this area have been sparse and the region has not been comprehensively investigated. Published descriptions of species from the study area include those of Kempton & Wells (1970, 1973) from Alaska, Abbott & Currah (1988) from Alberta, and Weber (1975) from the pacific northwest United States. Additional reports may be found in floristic accounts from the area (*e.g.* Larsen & Denison 1978; Abbott & Currah 1989; Currah *et al.* 1989; Snyder 1936; Kanouse 1947; Hawker 1968; Cummins 1930; Zeller 1927; Fogel & Trappe 1976; Fogel 1976; Groves & Hoare 1954; Huhtinen 1984; Hutchison *et al.* 1988) or in collection lists of broader taxonomic treatments dealing primarily with restricted groups of taxa and often extralimital material (*e.g.* Pfister 1980; Trappe 1975, 1989; Gilkey 1947; Harmaja 1979a; Ginns 1974a, b, c; McKnight 1969, 1971; Seaver 1921, 1928, 1942; Morse 1945; Kanouse 1949). This work attempts to provide a more comprehensive examination of the floristics of this family in a relatively unexplored region and to compare taxonomic data with that from specimens in extralimital areas.

Historical taxonomic account of Helvellaceae

The first taxon of this family was the genus '*Elvela*' (=*Helvella*, orthographic variant) erected by Linnaeus in 1753 to accommodate the species *Elvela mitra* (=*Helvella crispa*). Linnaeus in Species Plantarum cited Micheli, 1729, Nov. Pl. Gen. 204, Tab. 86, Fig. 7 (=*H. crispa*) and Valliant, 1727, Botanicon Parisienne 57, Pl. 13, Fig. 1 (=*H. acetabulum*), which are the earliest records of species from this family. The family was established by Fries in 1822 (as 'Elvellaceae'), and later published as Helvellaceae by Dumortier in 1829 and Corda in 1842. The family as described by Fries was restricted to stipitate taxa, and included several taxa now removed from the group including *Morchella* and *Leotia*. The taxa treated by Fries (1821-1832, Systema Mycologicum) are considered sanctioned under the current International Code of Botanical Nomenclature (Berlin 1988) and establish the nomenclature for two genera (*Helvella* and *Rhizina*) and many important species (*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 in four different genera, *Helvella*, *Morchella*, *Rhizina*, and *Peziza*, he clearly recognized the affinities between these various species. The first three genera were grouped together in his broadly conceived Elvellaceae, while the cupulate members of this family were placed in the tribe Helvelloideæ of the Pezizaceae where affinity with *Helvella* and *Rhizina* was noted. Thus, it appears that the relatedness between members of this family was recognized at this early stage, although Fries only included species belonging to *Helvella*, *Gyromitra*, and *Rhizina* (*sensu meo*). Many taxa included by Fries have roots in the earlier works of Linnaeus (1753), Schaeffer (1762-1774), Scopoli (1772), Afzelius (1783), Buillard (1785), Persoon (1796, 1800), Holmskjøld (1799), and Bosc (1811).

The separation of *Gyromitra* from *Helvella* by Fries in 1849 was the next major event in the delimitation of the Helvellaceae. Although often ignored by later authors (*e.g.* Seaver 1928; Kanouse 1946), this separation clearly indicates the separation of 'helvelloid' and 'gyromitroid' taxa as is currently accepted. 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) still retained many cupulate taxa in the genus *Peziza*.

Another pattern of taxonomic division was elaborated by Boudier (1885, 1907) based, in part, on earlier works of Fries (1849) and Fuckel (1869). Boudier (1907) recognized helvellaceous species in the families Helvellaceae and Pezizaceae, and increased the number of recognized genera to ten. These genera are synonymous with three genera accepted in this work (*Helvella*, *Gyromitra*, and *Rhizina*), but the generic divisions reinforce the recognition of distinct groups of related species which are very similar to the subgeneric sections recognized here. The concept of the genus *Helvella* accepted here would include the genera *Helvella*, *Leptopodia*, *Cyathipodia*, *Acetabula*, *Macropodia*, and *Wynnella* of Boudier. Likewise, *Gyromitra* as recognized here includes *Gyromitra*, *Physomitra*, and *Discina* of Boudier. *Rhizina* was accepted as monotypic by Boudier in agreement with the concept of Fries (1822). The system of multiple generic names was accepted by many subsequent and recent authors including Dennis (1978) and Breitenbach & Kränzlin (1981).

A broader taxonomic approach to the genera of Helvellaceae was initiated by Quélet in 1886 and supported by Nannfeldt (1937). Nannfeldt shows the relations between stipitate and cupulate members of *Gyromitra sensu lato* and *Helvella sensu lato*. The concepts of these authors reflect the view that there are essential similarities in spore morphology among members of the respective genera (sensu lato) and that the tremendous variation in ascocarp morphology should be be considered as a morphological series or progression and is not 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 taxa of Helvellaceae considered valid at the generic level include *Underwoodia* established by Peck in 1890 and *Pseudorhizina* erected by Jachevsky in 1913.

The possible affinity of inoperculate hypogeous taxa to the Helvellaceae is a recent idea (Trappe 1979), although many genera have been clearly delimited taxa of the Tuberales (sensu Korf 1973a) for some time. Two genera were described in the 19th century: *Choiromyces* was established in 1831 by Vittadini and *Hydnotrya* was established in 1846 by Berkeley and Broome. Mattirolo described *Fischerula* in 1928, and the genus was recently reevaluated by Trappe (1975b). All other genera have been recently described and include *Dingleya* and *Cazia* of Trappe (1979 and 1989 respectively), and *Gymnohydnotrya* of Zhang & Minter (1989a). The known affinity of all hypogeous taxa ascribed to the Helvellaceae is dealt with more extensively in the following section.

Accepted concept of Helvellaceae

The concept of the Helvellaceae accepted in current classification schemes (*e.g.* Korf 1972; Eriksson & Hawksworth 1991) and in this work, is founded on the concepts outlined by Nannfeldt (1937) who ascribed taxonomic significance at the family level to the tetranucleate condition of the mature ascospores. In fact, it is the tetranucleate spores, found in no other group of discomycetes, that remains the unifying feature of the family. The Helvellaceae is also characterized by ascospores with large oil reserves, visible as large guttules within the spore. This concept has been adopted by Dissing (1966b), Harmaja (1976b), Korf (1972), and Kimbrough (1970, 1991). Kimbrough and others (Gibson & Kimbrough 1988a, b; Kimbrough & Gibson 1989; Kimbrough *et al.* 1990;

Kimbrough 1991) have demonstrated the uniformity of ascospore ontogeny and septal structures among epigeous taxa of the Helvellaceae.

The tetranucleate condition of mature ascospores, correlated with morphology, has also served to unite the inoperculate, hypogeous taxa of the genera *Hydnotrya*, *Gymnohydnotrya*, and *Choiromyces* within this family (Berthet 1982; Zhang & Minter 1989a, b; Eriksson & Hawksworth 1989). Other hypogeous taxa, including *Fischerula*, *Dingleya*, and *Cazia* have been linked to the Helvellaceae on morphological grounds (Trappe 1979, 1989), but further cytological investigations are necessary to confirm their familial placement.

Thus, the family circumscription as emended by Nannfeldt (1937), Dissing (1972), Korf (1973), and Trappe (1979) and as outlined by Eriksson & Hawksworth (1991) is accepted in this work. The delimitation of subfamilial taxa presented in this investigation is unique and represents a reanalysis and synthesis of current knowledge contributed by many authors (notably Dissing 1966b; Harmaja 1969a, 1973b, 1974a; McKnight & Batra 1974; Donadini 1986; Kimbrough 1991; Kimbrough *et al.* 1990; Trappe 1979; Zhang & Minter 1989b) in addition to the results obtained in this investigation.

MATERIALS AND METHODS

Delimitation of the study area

The study region chosen includes arctic, coastal, boreal, montane, and alpine areas of northwestern North America. The boundaries are political ones, and encompass two territories, four provinces, and six states (Yukon Territory, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Alaska, Washington, Idaho, Montana, Oregon, and Wyoming). The boundaries were chosen to encompass the primary ecological zones in northwestern North America and to provide an efficient means of locating regional specimens in the various herbaria utilized in this study. It should be noted that all areas are not equally represented, and some large areas remain unexplored (*e.g.* Saskatchewan, interior Northwest Territories). The known distribution of species from some areas (*e.g.* Oregon, Montana) may be incomplete due to problems of locating and obtaining loans of specimens from the various herbaria. Personal collection efforts have concentrated on boreal, montane, and alpine sites in the interior northwest, including Alberta, northern and eastern British Columbia, southern Yukon, and southwestern Northwest Territories, in order to obtain collection data from a previously understudied and ecologically unique region of northwestern North America.

Field examination and preparation of living specimens

Fresh specimens were examined and collected in their natural habitats during the 1987-1991 field seasons from Alberta, British columbia, and Yukon. Specimens were photographed *in situ* prior to collection using a Pentax MX camera with closeup lenses on Kodacolor 400 ASA film. Some collections were alternatively photographed in the laboratory using a photographic copy stand with Ektachrome 100 ASA film. Notes on habitat, including associated plant species, were prepared in the field at time of collection. Descriptions of macroscopic features were prepared within 6 hours of collection. Microscopic features were examined from fresh or dried ascocarps following the procedure outlined below for herbarium specimens. Fresh specimens were air dried and packaged with dichlorobenzene crystals in plastic bags within boxes for permanent herbarium records. All collections are deposited in ALTA, UAMH, or are retained in the private herbarium of the author.

Attempts were made to obtain isolates of selected species of Helvellaceae in axenic culture. Tissue explants and/or ascospore deposits were placed on agar medium and incubated at room temperature (20-24 C). Media used included Potato Dextrose Agar (PDA; Difco), Nobles Malt Agar (NMA; 12.5 g malt extract, 20 g agar, 1000 ml water), and Cornmeal Agar (CMA; Difco), with and without the inclusion of antibiotics and/or chalk to the medium.

Examination of herbarium specimens

Herbarium specimens of collections from within the study area were examined. In addition, type material and extralimital collections were examined where possible (in total approximately 2000 collections examined). Macroscopic features of each specimen were examined. Microscopic details of the hymenium and ascospores were observed in distilled water squash mount preparations for approximately 1500 collections. 100% of collections were examined microscopically if a limited number of collections were available or if microscopic examination was essential for identification of particular taxa. Mounts of some specimens were additionally made in 5% KOH, Melzer's reagent (Groves 1962), or Cotton Blue. Measurements of microscopic structures were taken with an ocular micrometer from distilled water mounts with an Olympus light microscope. Spore dimensions in this work include both fully mature and submature spores since both are found in the same mount and are not noticeably distinct from each other. Spores which were noticeably immature were omitted from descriptions, and macrospores or spores of unusually small or large size are reported in parentheses with the typical spore dimensions. Apothecial cross-sections were prepared with a freezing microtome and mounted in distilled water for morphological examination of excipulum anatomy. Ascospore nuclei were stained with Schiff's Reagent (Östergren & Heneen 1962). A procedure for analysis of crude protein using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) is provided in Appendix 2.

Herbarium material for this study was supplied by ALTA, BPI, C, CUP, DAOM, H, IMI, K, L, MICH, MU, NY, NYS, O, OULU, PC, PRC, S, UAMH, UBC, UPS, UVIC, WIN, WSP, and WTU (herbarium acronyms follow Index Herbariorum). In addition, material deposited in the private herbaria of Abbott (SA), Danielson (RMD), Wells and Kempton (WK), and Kristiansen (RK) were examined.

Scanning electron microscope (SEM) procedures

Observations of ascospore ornamentation were made from air dried material of apothecia from herbarium specimens mounted on stubs coated with a double sided adhesive. A double coating of gold-paladium was applied with a Nanotech sputter coater. Specimens were examined with a Cambridge S-250 SEM and photographed.

Observations of hymenium and excipulum structure were made from fresh specimens, fixed in 4% gluteraldehyde in 0.07 M sodium phosphate buffer, then rinsed in buffer before fixation in buffered osmium tetroxide. Tissue was dehydrated in a graded series of acetone from 70 to 100%. At this point, apothecial tissue was placed in a 1:1 ratio solution of acetone:Peldri II for one hour, after which tissue was immersed in 100% Peldri II for another hour before drying for examination with SEM (Kennedy *et al.* 1989).

Concepts of taxa

The species concept utilized in this study is that described for vascular plants by Cronquist (1988), in which species are defined as "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means."

The species I have recognized in Helvellaceae are all morphologically distinct from each other. Species are considered morphologically distinct only if several differential features are correlated. Differences in a single feature are not considered sufficient to warrant taxonomic separation at the species level. Characters of importance at the species level include ascocarp size, shape, and colouration, excipulum vestiture, stipe construction, ascospore size, shape, and ornamentation, and features of the paraphyses and asci.

Genera are recognized primarily by sudden discontinuities in excipulum anatomy, ascospore morphology, and/or ascus dehiscence mechanism. Microscopic features are of greater taxonomic value than macroscopic characteristics at the generic and subgeneric levels.

Format of taxonomic part

All generic, subgeneric, and specific taxa examined in this study are described, and are grouped to approximate phylogenetic relationships. The type section or species is described first under each genus or subgeneric section. Keys to all tribes, genera, and sections are included, but are provided only for species occurring within the study area.

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

Species descriptions are presented in the following standard order: taxon, authority and citation, basionym and synonyms, type information, illustrations included here, morphological description, habitat, geographic distribution, taxonomic notes, and collections examined. Full descriptions are provided only for species present within the study area, while other species examined include only taxon, citation, basionym, synonyms, type information, illustrations included here, geographic distribution, taxonomic notes, and collections examined.

Taxon, authority, date, and source of publication are provided consecutively on the first line. The basionym, synonyms, type information, and included illustrations are each provided on consecutive lines. Listed synonyms include those names which appear in recent North American and European references or references which are in current use, as well as names for which type or authentic material has been examined in this study. Type material includes status and herbarium location respectively, with an annotation if examined in this study.

Morphological descriptions are arranged in the following standard pattern to enable case of comparison between descriptions: apothecium, stipe, asci, paraphyses, and ascospores.

The habitat section includes information on abundance, substrate, associated plant species, seasonal occurrence, and other ecological factors of taxonomic relevance. Associated plants are listed in approximate descending order of frequency.

The geographic distribution section contains a summary of the distribution of species within the study area. In addition, notes on the global distribution of each taxon are provided. The taxonomic significance of biogeographic distribution is discussed and references to distribution maps are provided.

The taxonomic notes section includes a discussion of the species concept and defining features of each taxon. Subspecific taxa and relationships to similar taxa are also discussed.

The collections examined are presented in the following order: Canadian collections are listed first, followed by collections from the United States. Collections are arranged by province or state from west to east and north to south. Provinces and states within the study region are listed prior to extralimital collections. Within each province and state, collections are listed approximately from west to east and north to south. Other collections are listed by country in approximate geographic order from west to east and north to south at the end of the section. Exsiccati examined are listed in their own section at the end of the taxonomic part for each species. All collections are listed by location, collector and date, and herbarium accession data respectively, and are separated from other collections by a semicolon.

RESULTS AND DISCUSSION

Taxonomic significance of morphological characters in Helvellaceae

Macroscopic characters: Macroscopic features of the fruiting bodies of Helvellaceae have been used traditionally to separate species in the family. Although macroscopic characters are quite variable, they are consistent within a species and can be used as a primary means of identification. Often macroscopic morphology alone is insufficient to accurately assess species identity and must be used in concert with microscopic characters. Different characters are important in differentiating species in the different genera of the family. For example, characteristics of excipulum vestiture are important in *Helvella*, while this feature is of little importance in *Gyromitra* and *Hydnotrya*. Specific macroscopic characters will be discussed in detail below. Variation in macroscopic ascocarp morphology is illustrated by Figures 1-17.

The shape of the apothecium often has been used to distinguish genera and species of Helvellaceae. Cupulate species (Figures 3, 5, 9-11) were often placed in separate genera from those with auriculoid (Figure 4) or irregularly lobed apothecia (Figures 1, 2, 6-8, 13-15). While these differences are often very useful in distinguishing species, there is clearly a morphological progression linking simple cupulate forms to more elaborately folded or highly convoluted and reflexed apothecia, and no separation at the generic level is justified. Species vary over a limited range of morphological forms, but may exhibit some variation, especially in species which are intermediate between simple and complex apothecial morphologies (*e.g. Helvella ephippium, H. solitaria, Gyromitra perlata*). Many species in the genera *Helvella*, *Gyromitra*, and *Pseudorhizina* may have a saddle-shaped or bilobate apothecium. This feature is often observed repeatedly in collections of these species, but it is not consistently present. These species also typically exhibit forms with 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*)(Figure 4), but strongly one-sided cupulate forms are also known in other members of the genus.

Species in the genus *Underwoodia* are unique in apothecial morphology. In that genus, the apothecium is entirely fused over the entire surface to the apical region of the stipe (Figure 10). The apothecium is frequently fused to the stipe in some members of *Helvella* and *Gyromitra* (*e.g. H. lacunosa, G. esculenta*), but is typically fused only at several intervals along the apothecial margin, with the stipe apex free from fusion with the excipular surface.

Marginal characters of the apothecium are of great value in distinguishing species of Helvellaceae. In some species of *Helvella* (*e.g. H. maculata, H. compressa, H. crispa*), the apothecial margin is strongly inrolled over the hymenium surface when immature and gradually expands at maturity (Figure 6). In contrast, other species (*e.g. H. lacunosa, H. elastica*) are reflexed towards the stipe from initial stages (Figure 8) and often become fused to the stipe at maturity. Marginal characters are not considered here to be of taxonomic significance at the sectional level in *Helvella*, contrary to the views of Dissing (1966b) and Weber (1972). There is a progression from inrolled to reflexed in several groups of related species (for example the progression from strongly inrolled to incurved to reflexed in *H. compressa, H. albella, H. elastica*). Species of *Gyromitra* show similar tendencies with the cupulate species (*e.g. G. perlata*) typically exhibiting a strongly inrolled margin initially while stipitate species (*e.g. G. esculenta, G. gigas*) always have

Figure 1: *Gyromitra ambigua*, SA 198, fresh ascocarp *in situ*, scale = 10 mm.

Figure 2: *Pseudorhizina sphaerospora*, SA 350, fresh ascocarp *in situ*, scale = 10 mm.

Figure 3: *Helvella leucomelaena*, SA 56, fresh ascocarps *in situ*, scale = 10 mm.

Figure 4: *Helvella silvicola*, SA 379, fresh ascocarps with ribbed stipe (right) and internal stipe chamber (left), scale = 10 mm.

Figure 5: *Helvella costifera*, SA 100, fresh ascocarps *in situ*, scale = 10 mm.

Figure 6: *Helvella crispa*, ALTA 8319, fresh ascocarps *in situ*, scale = 20 mm.

Figure 7: *Helvella atra*, SA 110, fresh ascocarps *in situ*, scale = 10 mm.

Figure 8: *Helvella elastica*, SA 221, fresh ascocarp *in situ*, scale = 10 mm.


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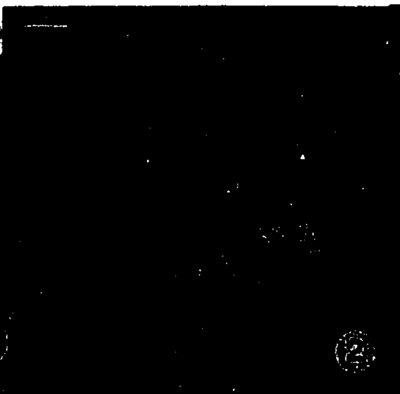
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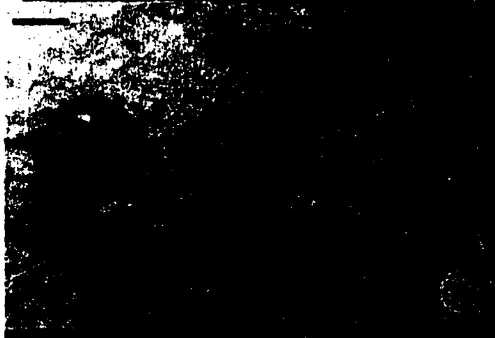
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Figure 9: *Helvella macropus*, UBC F3271, dried ascocarps, scale = 10 mm.

Figure 10: *Helvella rivularis*, C (part of holotype), dried ascocarps, scale = 10 mm.

Figure 11: *Helvella arctoalpina*, DAOM 20767, dried ascocarp, scale = 15 mm.

Figure 12: *Underwoodia columnaris*, DAOM 206823, dried ascocarps including longitudinal and cross sections (lower left), scale = 10 mm.

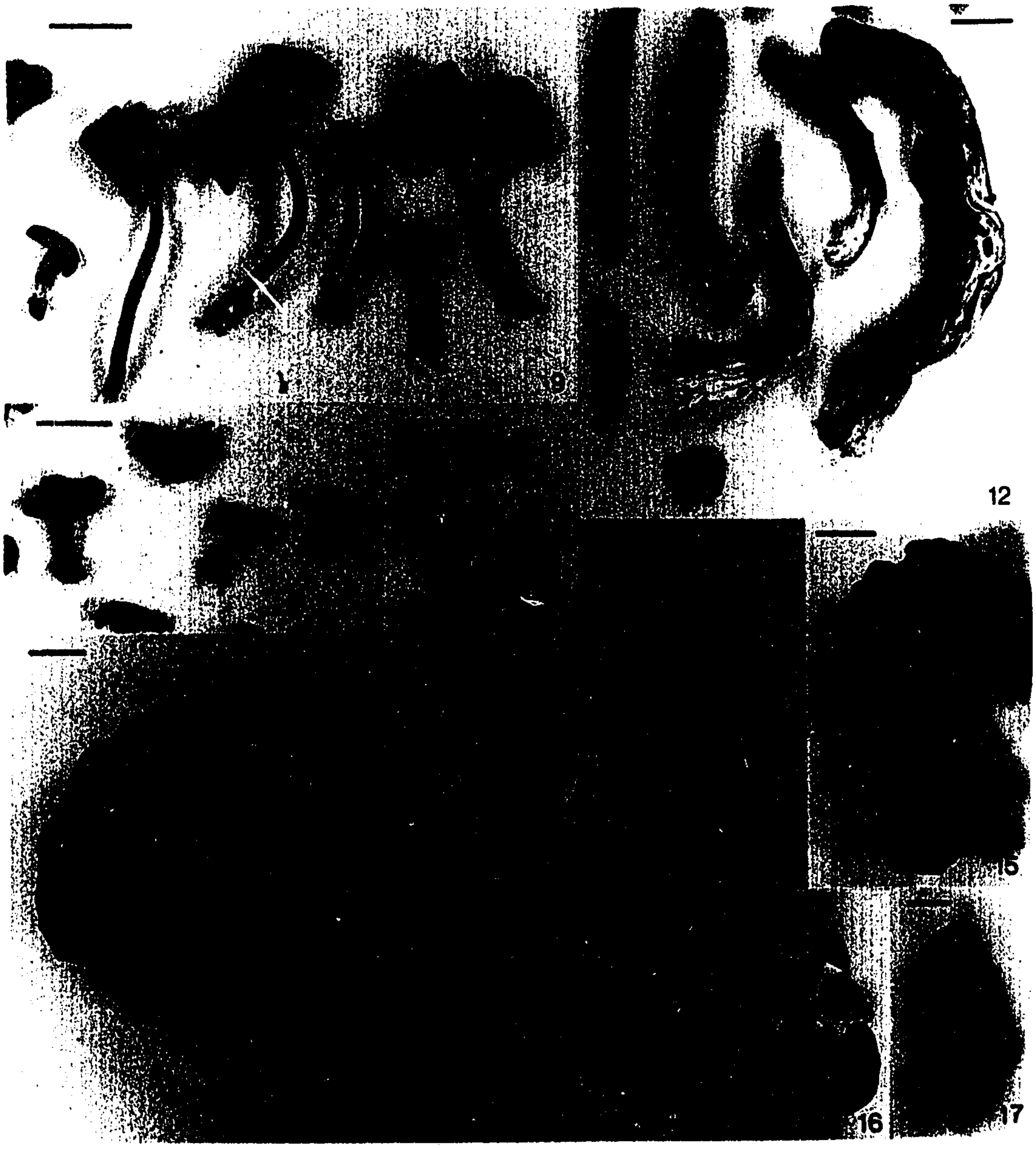
Figure 13: *Pseudorhizina californica*, DAOM 107197, dried ascocarp, scale = 15 mm.

Figure 14: *Helvella lactea*, PC (part of lectotype), dried ascocarp, scale = 15 mm.

Figure 15: *Gyromitra gigas*, BPI (part of isotype of *G. montana*), dried ascocarp, scale = 15 mm.

Figure 16: *Hydnotrya cubispora*, WTU (Stz 13359), dried ascocarp, longitudinal section, scale = 5 mm.

Figure 17: *Hydnotrya variiformis*, WSP 391 19, dried ascocarp, dorsal view, scale = 5 mm.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a reflexed apothecial margin which is typically ingrown with stipe tissue (Figure 15). The monotypic genus *Rhizina* is similar to sessile cupulate members of *Gyromitra*, but the apothecium is sessile and discoid or somewhat irregular at all stages. The genus is unique in its indeterminate marginal growth and rhizoid-like excipular projections. The two members of *Pseudorhizina* always possess an apothecial margin which is strongly reflexed towards the stipe and is typically rolled over the excipular surface on the underside of the apothecium (Figures 2, 13). The margin typically remains free from the stipe in this genus.

The margin in species of *Hydnotrya* is often entirely fused at maturity, but may be only partially fused at the base of the apothecium in immature stages. In *Hydnotrya*, the apothecium is initially a subglobose hollow or sparingly infolded structure with the hymenium lining the internal surface (Figure 17). As development continues, the apothecium becomes highly infolded creating numerous internal chambers (Figure 16).

Apothecial size varies from a few mm in some species of *Helvella* (*e.g. H. rivularis*)(Figure 11) to 15 cm in species of *Gyromitra* (*e.g. G. esculenta*) and *Pseudorhizina* (*e.g. P. californica*)(Figure 13).

The hymenial surface may be smooth, undulate-rugose, or strongly convoluted-rugose. Cupulate species of *Helvella* and *Gyromitra* are typically smooth (Figure 3, 4, 9, 10), especially at young stages (*e.g. H. dissingii, G. perlata*), but the majority of species are undulate-rugose (Figures 1-2, 6-8, 13-15) at maturity and a few species in *Gyromitra* (*e.g. G. esculenta*) are strongly convoluted-rugose. The excipular surface is typically smooth (Figure 9), but may have distinct ribs continuous with those of the stipe (Figures 5, 11). The presence and degree of ribbing on the excipular surface is of taxonomic value at the species level.

Ascocarps may be sessile, subsessile, or prominently stipitate. The genera *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 of taxonomic value in 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*)(Figures 8, 9), sulcate and fluted or ribbed (*e.g. H. solitaria, H. leucomelaena*)(Figure 3), or highly ribbed with anastomosis between ribs (*e.g. H. crispa, H. costifera*)(Figures 5, 6, 14). Internal stipe construction may be solid (*e.g. H. corium, H. arctoalpina*), hollow (*e.g. H. elastica*), or highly chambered (*e.g. H. crispa, H. lacunosa*). These features are typically constant within species, but some variation may occur. For example, *H. solitaria* typically has a sparingly ribbed, solid stipe, but some individuals 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 typically infolded and sulcate or less frequently terete (Figure 1) and are internally solid or chambered. *Pseudorhizina* species are prominently stipitate with strongly ribbed, solid or chambered stipes (Figures 2, 13). *Rhizina undulata* is astipitate, but possesses projections from the excipular surface which are attached to the substrate (termed rhizoids in Fitzpatrick 1917). *Underwoodia* species are prominently stipitate with strongly ribbed and internally chambered stipes (Figure 12). All species of *Hydnotrya* are astipitate (Figures 16, 17).

Ascocarp colouration is highly variable in the family, although most species are various shades of grey and brown. In *Helvella*, hymenial pigmentation varies from white (*e.g. H. lactea, H. crispa*)(Figure 6) to black (*e.g. H. corium, H. atra*)(Figure 7). Reddish brown colours are seen in several species of *Gyromitra, Helvella*, and *Hydnotrya* (*e.g. G. esculenta, H. silvicola, H. tulasnei*). Bright yellow or orange brown pigmentation is seen in some members of *Gyromitra* (*e.g. G. leucoxantha*) and *Hydnotrya* (*e.g. H. variiformis*) Excipular pigmentation is quite variable, but is frequently paler than that of the hymenium. White to cream excipular surfaces are common in *Helvella, Gyromitra, Pseudorhizina*, and *Rhizina*. Stipe colouration is frequently concolourous with the excipular surface or paler. The basal region of the stipe is usually white or pallid, even in species with dark stipe colouration. Some species of *Gyromitra* (*e.g. G. ambigua, G. esculenta*) and species of *Pseudorhizina* frequently exhibit purplish red tints on the stipe. Colouration is typically consistent within species, but degree of pigmentation may vary from quite pale to rather dark within species or collections. Mottled hymenial pigmentation is seen in some specimens of a variety of species (*e.g. Helvella maculata, Gyromitra esculenta*), but is not a diagnostic species characteristic. A pallid sterile zone is prominent only in *Rhizina*, but an inconspicuous zone may be found in *Pseudorhizina*.

Vestiture of excipular surface and stipe are important diagnostic features at the species level in the genus *Helvella*, in which the vestiture varies from entirely glabrous to villose. Many species are finely to densely pubescent. Some variation is seen between collections, but vestiture is relatively constant for most species. Some variation is also seen at different stages of development. For example, *H. latispora* and *H. albella* are finely pubescent initially, but may be nearly glabrous by maturity. There is often similar vestiture on the excipular surface and stipe, but some species show variation between these regions. *Helvella atra*, for example, exhibits a glabrous excipular surface, but a finely pubescent stipe. Vestiture may also vary between different regions of the excipular surface. Some species (*e.g. H. corium, H. arctoalpina*) or individual specimens are often most densely pubescent at the margin, and have progressively finer vestiture towards the base and on the stipe. This feature is most frequently seen in arctic and alpine species. Correlated with this is the presence of a white marginal region (Figure 11). The white margin is composed of fascicles of hyaline hyphal hairs and sometimes crystalline, probably calcium carbonate, deposits (Harmaja 1977b). A white marginal zone is known in some specimens of *H. corium, H. arctoalpina*, 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 species of the other genera in the family is more uniform, and therefore of lesser importance in specific delimitation. The vestiture of *Gyromitra* species is visible initially as a loose weft-like pubescence and often disappears at maturity.

Flesh consistency is brittle in all species, but *Gyromitra* species have thick flesh (2-5 mm), while other species have thin flesh (1-2 mm). The flesh of *Helvella silvicola* is less easily rehydrated in distilled water and KOH than other species of the family. Odour is typically indistinct in Helvellaceae, but is strong in dried ascocarps of *H. silvicola* and in fresh specimens of at least some species of *Hydnotrya*. Strong odour in hypogeous species is associated with mammalian vector dispersal.

Light microscopy: Microscopic features are often more reliable than macroscopic features for the delimitation of genera and species of ascomycetes (*e.g.* Harmaja 1969a, 1974a; Korf 1973b), and are of great taxonomic value in the Helvellaceae. All microscopic features should be correlated with macroscopic and habitat differences to delimit species in this family since microscopic features alone are rarely sufficient for confident assessment of species. All microscopic measurements and observations are made using distilled water mounts, rather than other solutions, since these reagents often alter the spore morphology. McKnight (1968) reports alteration of spore size, shape, apiculation, and surface ornamentation in *Gyromitra* section *Discina* when viewed in KOH, a commonly used rehydrant. KOH mounts were useful for observation of setoid paraphyses of *Helvella crassitunicata*. A representative sample of microscopic features of the hymenium and excipulum are presented in Figures 18-28.

The anatomical structure of the excipulum has been intensively examined by many authorities of the family, and has frequently used to delimit genera and species (Dissing 1966b; Harmaja 1977b, 1979a; Weber 1972; Eckblad 1968). My observations indicate that this character is of great value in the separation of subfamilial 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 ascocarp is divided into the hymenium, subhymenium, medullary excipulum, and ectal excipulum (terminology following Korf 1973a)(Figure 20), but the ectal excipulum may not be present in all taxa, and the subhymenium may be indistinct (Figure 19). The ectal excipulum is visible as a layer which is morphologically distinct from the medullary tissue in *Helvella* (Figure 20), *Underwoodia*, and *Hydnotrya*. The medullary layer is composed of *textura intricata* while the ectal excipulum is composed of *textura angularis* or *textura prismatica* (terminology following Korf 1973a). The pubescence seen on the excipular surface of *Helvella* is composed of chains of cells and/or fascicled hyphal chains extending from and continuous with the ectal excipulum (Figure 18). In *Gyromitra*, *Pseudorhizina*, and *Rhizina* the excipulum is composed of *textura intricata* throughout, and is not distinctly divided into a medullary and an ectal layer (Figure 19) at maturity. The felty pubescence seen in some species of these genera is the result of some undifferentiated protruding hyphae or an evanescent ectal excipulum present in immature individuals.

Asci are hyaline in all members of the family, and contain eight ascospores. Asci are typically cylindrical (Figures 25, 27, 28) and gradually tapered below the uniseriate ascospores (Figures 23, 24), but some species of *Hydnotrya* (*e.g. H. tulasnei*) have clavate asci, especially when immature, with irregularly biseriate or clustered ascospores. Ascus size ranges from 10 μm diam. in *Pseudorhizina* to 30 μm diam. in *Hydnotrya*, and are typically 100-400 μm long. Asci are operculate in all epigeous taxa (*i.e. Gyromitra, Pseudorhizina, Rhizina, Helvella, Underwoodia*). The indehiscent asci seen in *Hydnotrya* is considered a derived condition associated with a hypogeous existence. The presence of an operculum in *Hydnotrya cerebriformis* (Figure 28) is the first confirmed report for the genus, but Hawker (1968b) reported a "vestigial operculum or pore" in the same species. The illustrated operculum was the only one seen during the course of this investigation. Asci are typically indehiscent, and it is unlikely that functional opercula are present.

Much attention has been given to the structure of the ascal base and mode of ascus development in *Helvella* (Weber 1972; Harmaja 1977a). It was noted by these and other authors that some species exhibit an aporhynchous ascus development, while the majority of species display pleurorhynchous ascus development. Pleurorhynchous ascus

Figure 18: *Helvella subclavipes*, WK 6368, fascicled hyphae of ectal excipulum outer surface, scale = 25 μm.

Figure 19: *Gyromitra esculenta*, SA 20, apothecium cross section, hymenium and medullary excipulum, scale = 50 μm.

Figure 20: *Helvella leucomelaena*, SA 322, apothecium cross section, hymenium (h), subhymenium (s), medullary excipulum (m), and ectal excipulum (e), scale = 75 μm.

Figure 21: *Gyromitra ambigua*, SA 191, fascicled/branched, septate paraphyses, scale = 25 μm.

Figure 22: *Rhizina undulata*, WK 5983, thick-walled, aseptate seta, scale = 15 μm.

Figure 23: *Helvella aestivalis*, C EI84.48, pleurorhynchous ascus with crozier, scale = 15 μm.

Figure 24: *Helvella oblongispora*, C (holotype), aporhynchous ascus lacking crozier, scale = 10 μm.

Figure 25: *Helvella robusta*, ALTA 8291 (paratype), apex of operculate ascus, including operculum, after spore release, scale = 10 μm.

Figure 26: *Rhizina undulata*, WK 5983, ascospores with de Bary bubbles, scale = 20 μm.

Figure 27: *Helvella silvicola*, SA 379, SEM of hymenium cross section, asci with uniseriate ascospores and clavate paraphyses, scale = 20 μm.

Figure 28: *Hydnotrya cerebriformis*, WK 3023, apex of ascus including ascospores and operculum, scale = 20 μm.


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development is characterized by the presence of a crozier at the base of the ascus (Figure 23), while aporhynchous asci lack a crozier (Figure 24). This feature is most easily observed in KOH squash preparations of immature asci. These differences were used to separate subgeneric sections within the genus (Weber 1972; Harmaja 1977a), but the morphological similarities in all other features suggests to me that this feature should be used to separate taxa only at the specific level. One species, *H. aestivalis*, is described as having aporhynchous asci (Dissing 1983), but my observations clearly show that the asci are pleurorhynchous (Figure 23). It is unclear whether this feature is somewhat variable or if literature reports are erroneous. My observations of ascal bases in species of other genera show a high degree of variation and are inconclusive.

Paraphyses are prominent in all epigeous taxa (Figures 21, 27), but are somewhat reduced in *Hydnotrya*. Paraphyses are approximately the same length as asci, and range from 3-11 µm diam. at the apex. The largest paraphysis diameters are seen in species of *Gyromitra*, while *Hydnotrya* species tend to have very slender paraphyses. Clavate paraphyses are typical (Figure 27), and are gradually to abruptly enlarged apex, but rarely may be nearly equal in some taxa. Paraphyses may be hyaline or strongly pigmented. In *Gyromitra*, the apical cells contain large granular pigment material, while the intercellular contents of *Helvella* are finely granular to nearly homogeneous. Some species (*e.g. Rhizina undulata*) have an extracellular pigmented matrix around the apex of the paraphyses. Paraphyses are hyaline in *Hydnotrya*. Paraphyses are thin-walled in all species, but *Helvella crassitunicata* also has thick-walled paraphyses in the hymenium which are similar to the setae of *Rhizina undulata* (terminology following Fitzpatrick 1917)(Figure 22). Setae are aseptate with brown wall pigmentation and arise in excipular tissue below the hymenium.

Ascospores present several useful taxonomic features. Spore size varies from approximately 10 to 50 µm in length within the family, and spore shape varies from globose, subglobose, broadly ellipsoidal, ellipsoidal, subfusoidal, to fusoidal, but some common trends are seen within the various genera. Small globose to ellipsoidal spores (8.5-20 µm maximum diameter) are present in the genus *Pseudorhizina*. *P. sphaerospora* is the only epigeous species in the family with globose spores, and has the smallest spores in the family. Most members of the genus *Helvella* have broadly ellipsoidal spores, but one section (*Macropodes*) contains two species with subfusoidal spores. *Gyromitra* species have ellipsoidal to fusoidal spores up to 40 µm long. Spore shape and size is diagnostic for subgeneric sections of the genus. The large, fusoidal ascospores of *Rhizina* are most similar to those of species in the section *Discina* of *Gyromitra*. Ascospores of *Hydnotrya* species are the largest in the genus at 25-55 µm maximum diameter, and are globose to broadly ellipsoidal. Spore size is quite variable within species and individual ascocarps. Spore length may vary over a range of two to ten micrometers within species or collections. Kempton & Wells (1973) report spore size variation in individual ascocarps of *Gyromitra esculenta* over a six week period, with early spores slightly smaller than later spores. They also report that different regions of the hymenium on individual ascocarps mature at different times throughout the development of the fruiting body. The observations of Donadini (1986) show that submature spores of some *Gyromitra* species are often ejected from the asci, and are viable spores. Harmaja (1977b) discusses spore size variability and reports for *Helvella* that submature spores within the asci are often slightly larger than fully mature ejected ascospores. Dissing & Nannfeldt (1966) and Harmaja (1977b) report for *Helvella* the occurrence of spores which are considerably larger than is typical for the collection. These macrospores have also been observed in some species in this study. My observations suggest that spore volume is 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 species of *Hydnotrya*. In this genus, spores are distinctly thick-walled with brown wall pigmentation.

Spore ornamentation is also of primary taxonomic value, although often hard to assess with the light microscope (see also notes under following section). With the light microscope, the spore surface in *Helvella* is consistently smooth with the exception of species in the section *Macropodes* which are verruculose. 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 smooth, punctate, echinate, or nodulose. 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. Only one species of the genus *Hydnotrya*, *H. cubispora*, exhibits apiculate ascospores.

Ascospores of Helvellaceae contain large lipid reserves, and variation in the number and distribution of guttules within spores is a reliable taxonomic character. Species of *Helvella*, for example, are typically uniguttulate with a large central subglobose guttule, while species of *Gyromitra* in the sections *Gyromitra* and *Melaleucoides* are typically biguttulate with two relatively small globose guttules. Most taxa of Helvellaceae contain no de Bary bubbles in ascospores. Species found to have de Bary bubbles present in a small proportion of spores (mounted in Melzer's Reagent or Cotton Blue) include *Gyromitra melaleucoides*, *Pseudorhizina sphaerospora*, *P. californica*, *Rhizina undulata*, *Hydnotrya cerebriformis*, and *H. variiformis*. Harmaja (1973, 1974c) suggests that the presence or absence of de Bary bubbles is diagnostic at the generic level. My observations of *Rhizina undulata* (Figure 26) are contrary to those of Harmaja (1974c) who reported that de Bary bubbles were lacking in that species. Harmaja's (1974c) observation of rare de Bary bubbles in *Gyromitra ambigua* and my observations of *G. melaleucoides* and *Hydnotrya* species suggest that this feature is variable and of limited use in generic delimitation.

Ascospores of all taxa possess a cyanophilic perispore at maturity with the exception of species of *Pseudorhizina*, and this character is taxonomically important at the generic level (Harmaja 1974b). The presence or absence of a cyanophilic perispore was also found to be taxonomically useful in other genera of Pezizales (Harmaja 1974d; Egger pers. comm.).

The ascospores of members of the Helvellaceae are reported to contain four nuclei at maturity (Harmaja 1976b; Berthet 1982; Kimbrough *et al.* 1990). Ascospore nuclei of a variety of taxa were stained with Schiff's Reagent (Östergren & Heneen 1962) and mounted in acetic acid. The tetranucleate condition of ascospores of *Pseudorhizina sphaerospora*, *Helvella crispa*, and *Hydnotrya cerebriformis* was verified. Thick ascospore walls in mature spores of *H. cerebriformis* reduced the resolution of individual nuclei, but immature spores containing one or two nuclei were easily observed.

The value of SEM in taxonomy of Helvellaceae: SEM studies of spores in many groups of epigeous and hypogeous ascomycetes and basidiomycetes have recently added valuable characters for taxonomic evaluation (Dissing 1972; Hawker 1968; Malloch 1973; Fogel & Trappe 1985; Oolbekkink 1991). Published accounts of SEM observations on spores of Helvellaceae, including the genera *Helvella, Underwoodia, Gyromitra, Pseudorhizina, Rhizina, Hydnotrya,* and *Gymnohydnotrya* have emphasized the value of spore ornamentation in the taxonomy of the family (McKnight & Batra 1974; McKnight 1973; Dissing 1972; Harmaja 1976d; Donadini 1986; Trappe 1976; Zhang & Minter 1989a, b). Many of these treatments examine few representatives of the various genera and none of the above works treat the family in a comprehensive manner. In this work, spores of all species described were examined with the SEM. Previous studies, as well as my own observations, suggest taxonomic value of ascospore ornamentation at the generic, subgeneric, and specific levels in various taxa of the family. Intraspecific variation in spore ornamentation between different collections and/or different spores from the same ascocarp was observed over a relatively narrow range and is attributed primarily to ascospore maturity (see notes below). Variation within species is often no greater than that between individuals of the same species and can not be used as a primary means of species identification. Figures 29-64 illustrate the diversity of ascospore ornamentation and apiculation in the family as seen with the SEM.

Only the genus *Gyromitra* has received intensive examination with the SEM. McKnight & Batra (1974) divided species into three groups based on ascospore morphology, but did not assign taxonomic significance to them. Clearly they recognized that closely related species had similar morphology, but their spore groups do not correspond to the subgeneric sections proposed in this work. In a more comprehensive study, Donadini (1986) discussed the variation seen in spore ornamentation of the genus. Of most importance were his observations on perispore ornamentation at different stages of maturity. He showed that submature spores typically have a finer, less developed surface ornamentation. His observations also record that these submature spores are often ejected from the asci before development is complete. This is highly significant in the interpretation of results shown by McKnight & Batra (1974) and Harmaja (1976d). Harmaja (1976d) describes *G. montana* as having less well developed ascospore ornamentation than *G. gigas* and used this character to separate the taxa. My observations show a similar degree of variation in spore ornamentation in collections referable to both taxa *sensu* Harmaja (Figures 35-38). A similar situation occurred in the work of McKnight & Batra (1974) who placed weakly and strongly ornamented spores of *G. gigas* (as *G. gigas* and *G. fastigiata* respectively) and *G. leucoxantha* (as *G. larryi* and *G. leucoxantha* respectively) in different spore groups. My examination of the holotype of their new species, *G. larryi*, revealed that the specimen was merely an immature specimen of *G. leucoxantha*. Recognition of the variation in spore morphology (and correlation with other morphological and anatomical features) has enabled me to divide the genus *Gyromitra sensu lato* into four subgeneric sections which reflect phylogenetic relationships between species. Section *Gyromitra* is characterized by spores with finely rugose perispore ornamentation and only slightly inflated apiculi if present (Figures 29, 30). This section corresponds to McKnight & Batra's (1974) Group 1, although they also include species referred to the genus *Pseudorhizina* in this work. Section *Discina* includes species with finely to distinctly rugose submature spores (Figures 31, 36, 37), often forming a distinct irregular reticulum in well developed mature spores (Figures 33, 34, 38). Inflated spore apiculi are present and may be well developed (Figures 31, 33-35) or quite reduced in some species or individual spores

Figure 29: *Gyromitra ambigua*, DAOM 195475, ascospores, scale = 4 μm.

Figure 30: *Gyromitra esculenta*, SA 358, ascospore apex, scale = 1 μm.

Figure 31: *Gyromitra perlata*, WSP 56311, ascospore, scale = 4 μm.

Figure 32: *Gyromitra olympiana*, SA 325, ascospore apex, scale = 1 μm.

Figure 33: *Gyromitra perlata*, SA 337, ascospore, scale = 5 μm.

Figure 34: *Gyromitra leucoxantha*, K (herb. Bresadola), ascospores, scale = 10 μm.

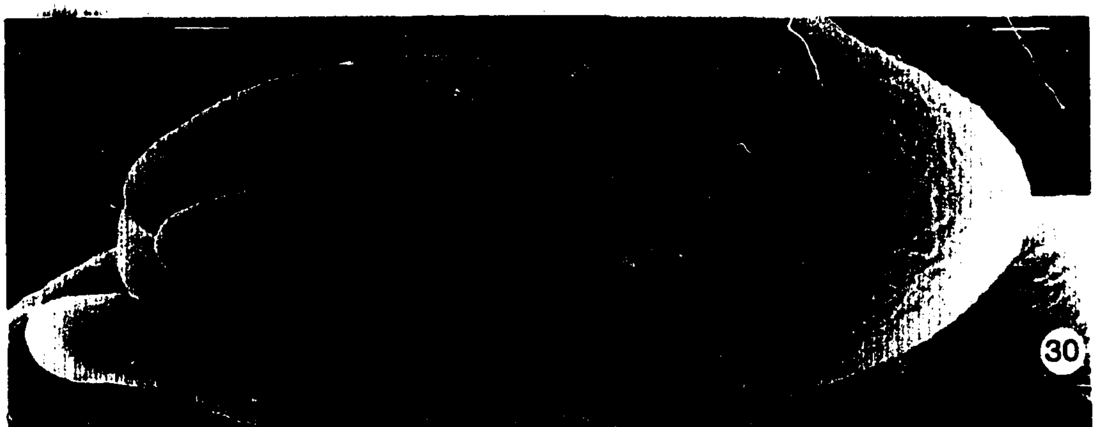
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Figure 35: *Gyromitra gigas*, K (Upland, Lundell May 15 1945), ascospore, scale = 5 μm.

Figure 36: *Gyromitra gigas*, WSP CS17387, ascospores, scale = 5 μm.

Figure 37: *Gyromitra gigas*, WTU (Stz 1885), ascospore, scale = 4 μm.

Figure 38: *Gyromitra gigas*, DAOM 191998, ascospore apex, scale = 2 μm.

Figure 39: *Gyromitra parma*, K (isotype), ascospore, scale = 4 μm.

Figure 40: *Gyromitra melaleucoides*, WTU (Stz 6715), ascospore, scale = 2 μm.

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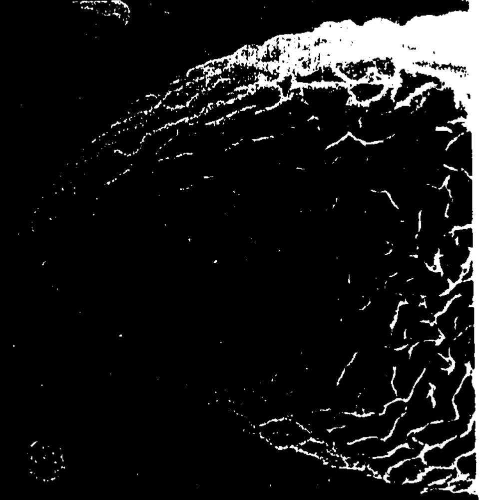

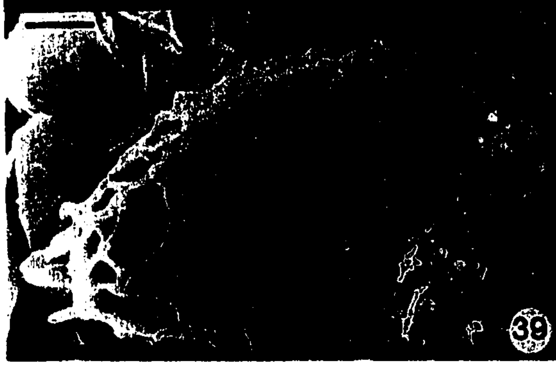

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Figure 41: *Pseudorhizina sphaerospora*, SA 38, ascospore, scale = 1 μm.

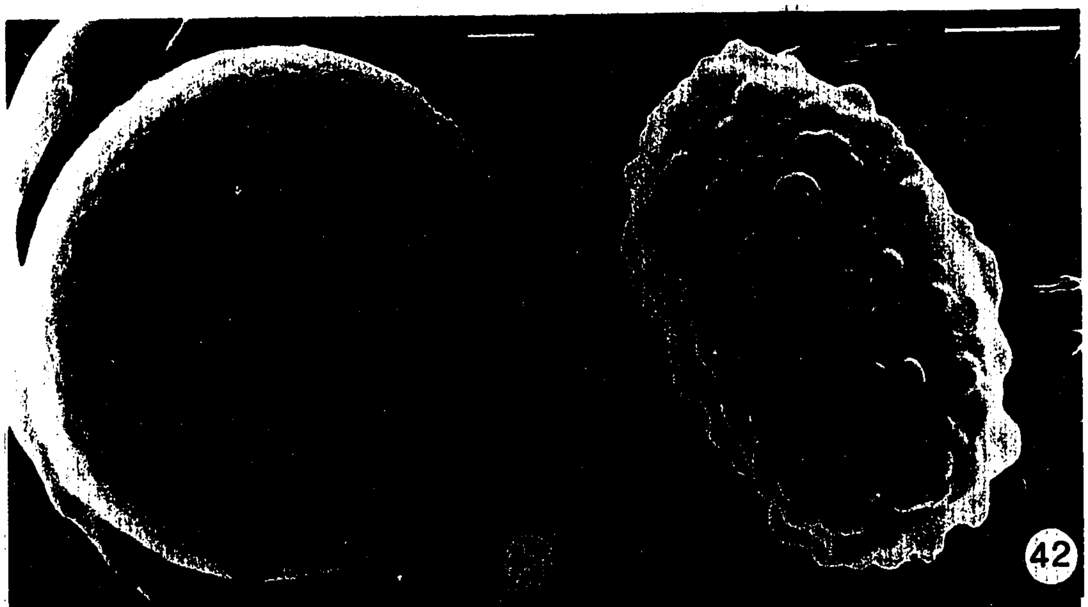
Figure 42: *Underwoodia columnaris*, DAOM 206824, ascospore, scale = 4 μm.

Figure 43: *Rhizina undulata*, WTU (Stz 16329), ascospores, scale = 10 μm.

Figure 44: *Rhizina undulata*, WTU (Stz 16329), ascospore apex, scale = 1 μm.

Figure 45: *Helvella crispa*, SA 257, ascospore, scale = 4 μm.

Figure 46: *Helvella atra*, SA 110, ascospore, scale = 2 μm.



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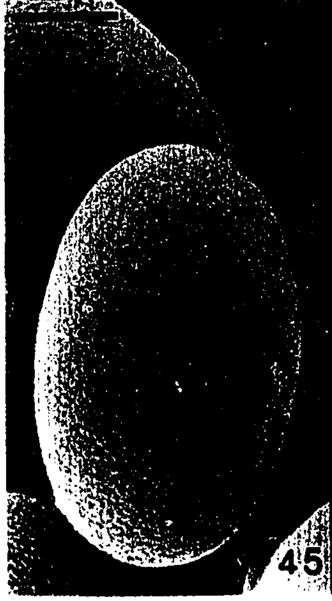

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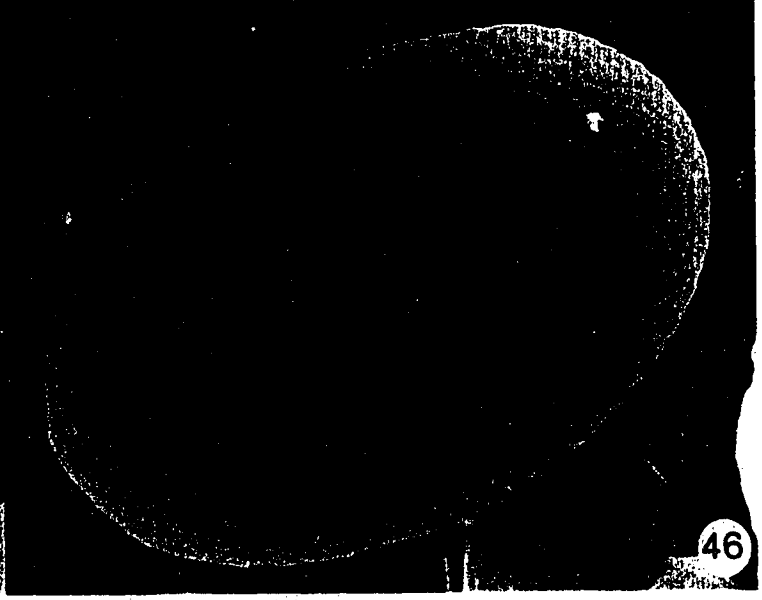

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Figure 47: *Helvella corium*, K (isotype of *H. arctica*), ascospore, scale = 4 μm.

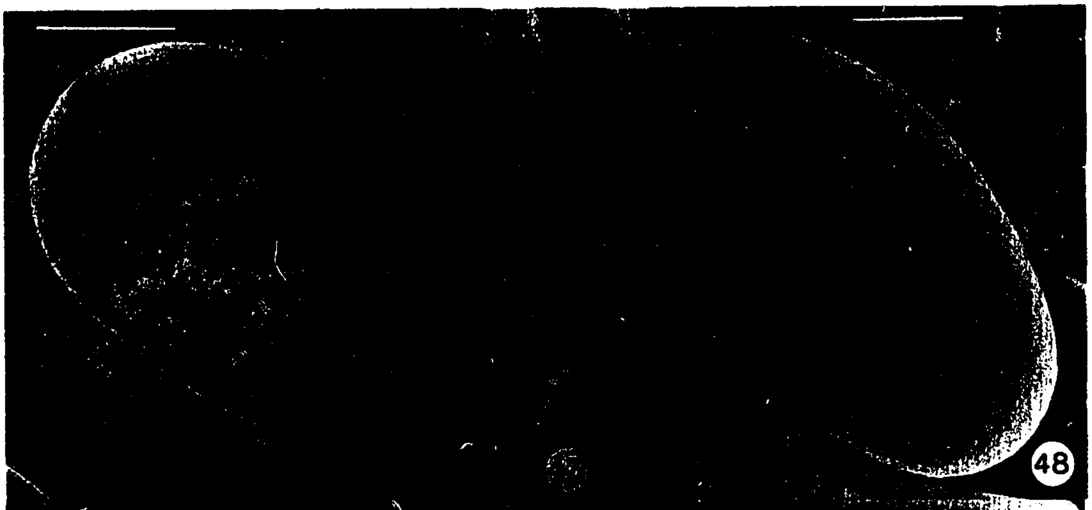
Figure 48: *Helvella dissingii*, WTU (Stz 11771), ascospore, scale = 4 μm.

Figure 49: *Helvella compressa*, WTU (SDLB March 25 1977), ascospore, scale = 4 μm.

Figure 50: *Helvella leucomelaena*, WSP 54318, ascospore, scale = 4 μm.

Figure 51: *Helvella silvicola*, ALTA 8273, ascospore, scale = 4 μm.

Figure 52: *Helvella crassitunicata*, MICH (holotype), ascospore, scale = 4 μm.



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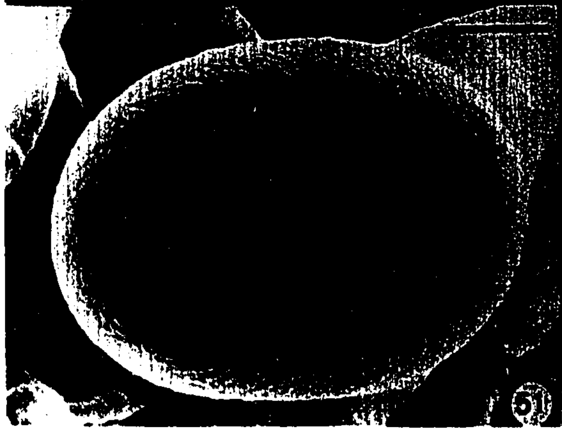

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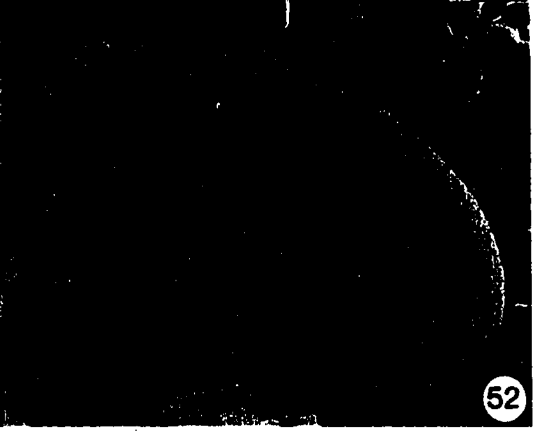

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Figure 53: *Helvella macropus*, SA 120, ascospore, scale = 4 μm.

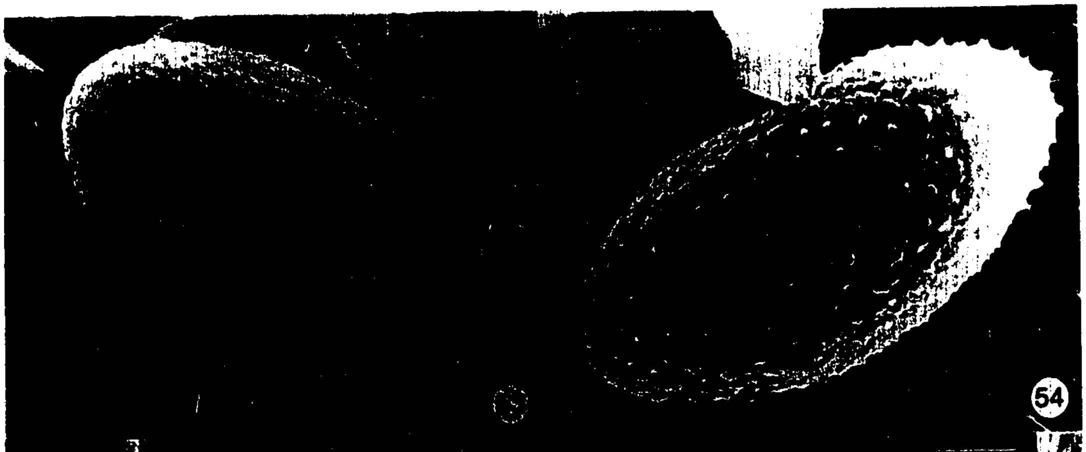
Figure 54: *Helvella subclavipes*, ALTA 8294, ascospore, scale = 4 μm.

Figure 55: *Helvella macropus*, SA 120, ascospore, scale = 4 μm.

Figure 56: *Helvella subclavipes*, K (Ellis North American Fungi 985), ascospore, scale = 4 μm.

Figure 57: *Helvella macropus*, DAOM 24706, ascospore, scale = 4 μm.

Figure 58: *Helvella cupuliformis*, K (paratype), ascospore, scale = 4 μm.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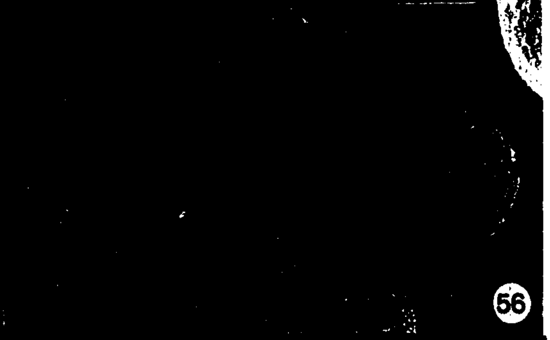
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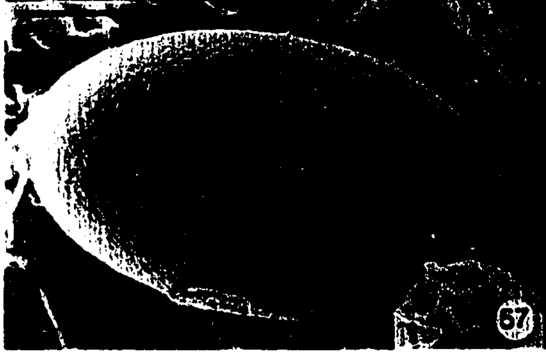
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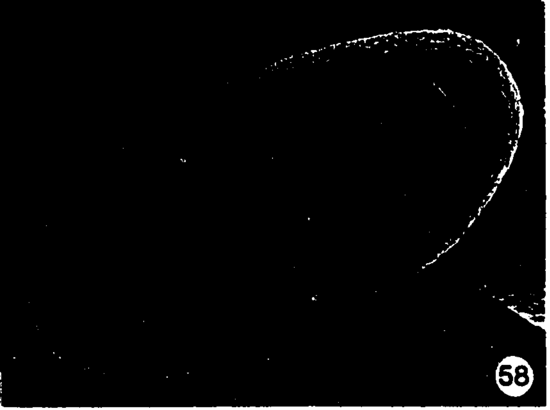
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Figure 59: *Hydnotrya cubispora*, WTU (SDLB 1523), ascospore, scale = 10 μm.

Figure 60: *Hydnotrya cubispora*, WTU (SDLB 1523), ascospore, scale = 8 μm.

Figure 61: *Hydnotrya tulasnei*, K (Lange 3082), ascospore, scale = 10 μm.

Figure 62: *Hydnotrya variiformis*, K (Fogel 1174), ascospores, scale = 10 μm.

Figure 63: *Hydnotrya cerebriformis*, K (Smith August 18 1962), ascospore, scale = 10 μm.

Figure 64: *Hydnotrya cerebriformis*, K (Smith August 18 1962), ascospore, scale = 10 μm.

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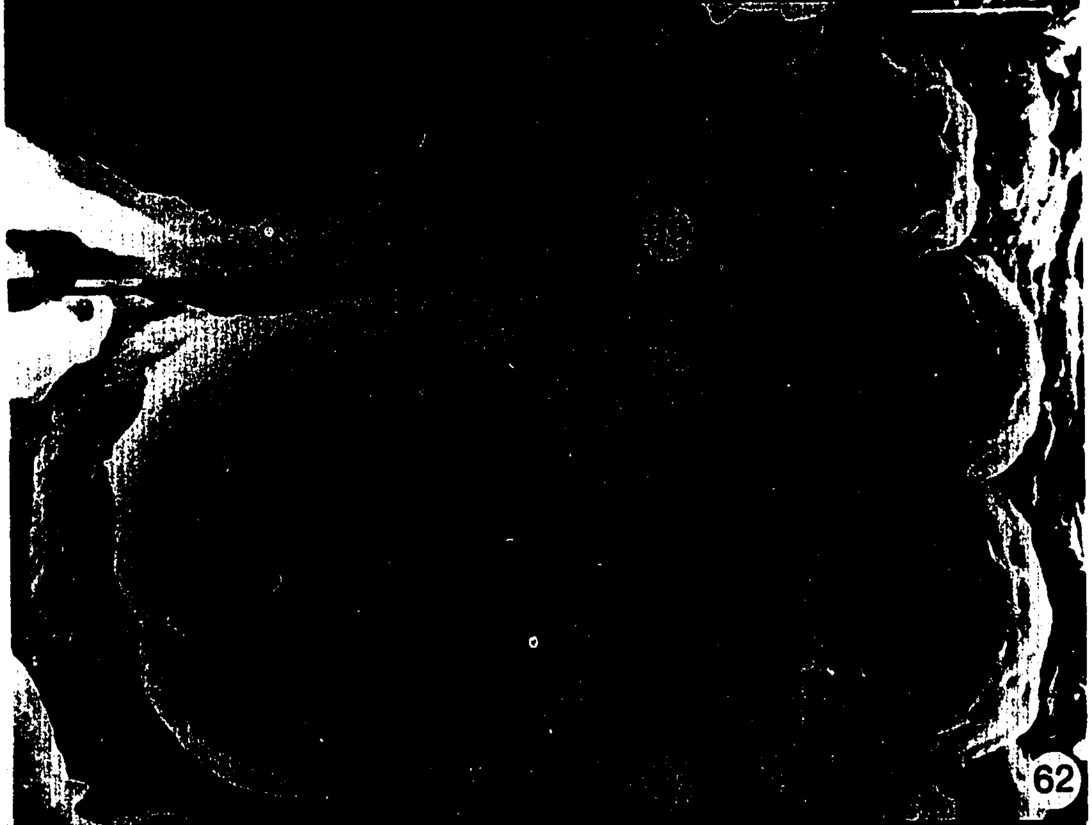

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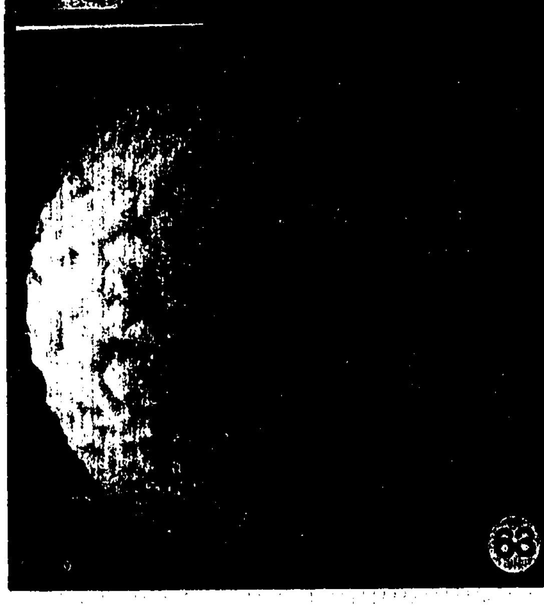

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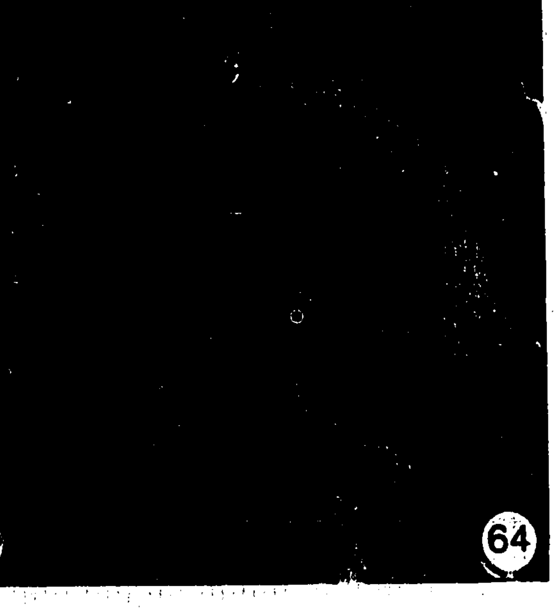

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(Figures 32, 37, 38). This section includes species in Group 2 and some species from Group 3 of McKnight & Batra (1974). Section *Caroliniana* shows a very distinctive spore pattern with a regular, widely spaced reticulum and prominent spicules at the apices of ascospores (Figure 39). Submature spores may be weakly ornamented as in Section *Discina*, but evidence of the reticulum and spicules is typically present. Species in this section are referred to Group 3 of McKnight & Batra (1974). The fundamental difference between species with an irregular closely spaced reticulum and solitary inflated polar apiculi and those with a regular widely spaced reticulum and multiple apical spicules was not recognized by McKnight & Batra (1974), who included all species with a reticulum in Group 3. The apiculi of species in the section *Discina* are inflated regions of the perispore which often show the rugose surface ornamentation extending onto the apiculus surface, while the apical spicules of species in the section *Caroliniana* are projections continuous with the reticulum on the spore surface. Section *Melaleucoides* shows a very distinctive pattern of spore ornamentation which separates it from all others in the genus. The rough ornamentation visible with the light microscope is composed of isolated rounded warts across the entire spore surface (Figure 40). This species has not been previously studied with the SEM.

The two species of the genus *Pseudorhizina* exhibit similar spore ornamentation which is very finely rugose (Figure 41). This ornamentation is most similar to species in *Helvella* and *Gyromitra* section *Gyromitra*, although even less pronounced, and lead McKnight & Batra (1974) to include species of this genus in their Group 1.

Finely rugose ascospore ornamentation of *Rhizina undulata* (Figure 43) is very similar to that of *Gyromitra ambigua*, and other species in the section *Gyromitra* (compare figures 29, 30, 43). My observations are in agreement with those of Dissing (1972), except that my observations indicate that the spore ornamentation extends slightly onto the apiculus surface. The twisted striate appearance of the apiculus (Figure 44) is identical to that seen in *G. perlata* (Figure 33).

Spore ornamentation has received little attention in the genus *Helvella*. To my knowledge, only one photograph of a single species, *H. acetabulum*, has been published (Dissing 1972). In that work, *Helvella* spores are referred to as smooth, with the exception of *H. macropus*. Preparation methods for SEM in Dissing (1972) are unknown, but judging from the similarity of features seen between my observations and Dissing's photos of other species of Helvellaceae, the methods utilized produced very similar results. My comprehensive SEM investigations have shown that surface ornamentation of ascospores of the genus are, for the most part, very consistent, but are typically finely rugose rather than entirely smooth. Slight variation in spore ornamentation can be compared in figures 46, 49, and 50. Ascospores of *Helvella* species appear smooth with the light microscope and with the SEM at lower magnifications. At magnifications of 1500X or greater, the finely rugose perispore ornamentation is distinctive. The similarity in ornamentation of *H. silvicola* (Figure 51) with the other members of the genus is used, in part, to support the inclusion of that species in the genus *Helvella* and the rejection of the genus *Wynnella*. The only *Helvella* species which exhibit different ascospore ornamentation are *H. macropus* and *H. subclavipes*. The verruculose ornamentation visible with the light microscope is seen with the SEM as numerous short isolated pointed warts or spines (Figures 53-56). This feature, as well as ascospore shape and guttulation, support Häffner's (1987) separation of the section *Macropodes* (*sensu stricto*) from other subgeneric sections of the genus. Some spores or collections of these species may appear finely rugose (Figure 57)(or smooth with light microscopy). These may represent submature spores, consistent with the morphology known for *Gyromitra* species (Donadini 1986; see notes above).

The genus *Underwoodia* has been synonymized with *Helvella* by some authors (Eckblad 1968; Harmaja 1974a), but the very different ascospore ornamentation lends support to the retention of a separate genus. My observations on the ascospores of *Underwoodia columnaris* are in agreement with those of McKnight & Batra (1974). The spore surface is covered with irregular broadly rounded nodulose warts (Figure 42). The presence of small pits in the perispore, noted by McKnight & Batra (1974), and the irregular cracking of the spore surface observed in this study (Figure 42) are of questionable taxonomic value.

In all of the epigeous operculate taxa of the family discussed above, the ascospores were observed by mounting the excipulum tissue and examining the ascospores adhering to the excipular surface. Only spores which had been ejected from the asci were studied to ensure some degree of uniformity of spore maturity, although both mature and submature spores may be ejected as discussed above. In the hypogeous indehiscent genus *Hydnotrya*, this was not possible, and apothecial tissue was crushed on the SEM stubs to liberate or expose the ascospores. Spores of these species were judged to be mature if spore ornamentation was well developed, and only these spores were examined for purposes of this study. Additional problems were encountered with the spores of *Hydnotrya*. In many cases, the spore surface was partially or completely covered with an adhering matrix. These results are similar to those discussed by Hawker (1968) for *Elaphomyces*, another inoperculate hypogeous ascomycete. Variation in spore surface features was attributed to degree of maturity and mode of preservation by Hawker (1968). The method of preparation for SEM is also reported to produce variability in perithecium surface features in *Sordaria* (Read, Porter & Beckett 1983).

Species of *Hydnotrya* appear to fall into two distinct spore groups, as confirmed with the SEM, and have been separated into subgeneric sections accordingly. Species in the section *Tulasnei* have spore walls which are extensively thickened and have slab-like to broadly rounded or nodulose spore wall protrusions. The spores of *H. tulasnei* described and illustrated in Trappe (1976) are consistent with the results obtained here. *H. tulasnei* and *H. michaelis* have large nodulose spore ornamentation (Figure 61). In one species, *H. cubispora*, the wall is thickened apically into cupulate apiculi at maturity (Figures 59-60). *H. variiformis* is punctate (Figure 62), a feature which is also visible with the light microscope. The spores of *H. variiformis* are not nodulose as in *H. tulasnei* and *H. michaelis*, but the irregularly rounded and thickened wall is quite similar to that seen in *H. cubispora* (Figure 59). In all species of this section the spore walls appear to be solid thickenings rather than discrete projections. In the section *Cerebriformae* the ascospores are echinate with distinct projections of the spore wall extending from the surface (Figure 64). The spore morphology is very similar that seen in species of *Elaphomyces* by Hawker (1968), Trappe (1976), and Abbott (unpublished), and observed variation is interpreted in the same way. The individual spines are often aggregated together by the adhering matrix, giving a warted or cracked appearance (Figure 63). Species of *Gymnohydnotrya* also have echinate ascospores (Zhang & Minter 1989b).

In order to examine details of the excipular vestiture, fresh material of selected species of *Helvella* was fixed and prepared for SEM study using methods employed in the preparation of living plant tissue (Kennedy *et al.* 1989). Unfortunately, all excipular pubescence was collapsed in these preparations and was not any more useful for taxonomic purposes than observations with stereo or light microscopy. Since details of the hymenium (asci and paraphyses) were well preserved by this method (Figure 27), it is assumed that the excipular vestiture is in a collapsed state when collected fresh.

Ecological and biogeographical aspects of Helvellaceae

Species of the Helvellaceae represent a diverse group of taxa, and therefore it is not surprising that they have evolved a wide variety of trophic abilities. Many members are saprophytes. Species of *Gyromitra* and *Pseudorhizina* are common on wood and other debris of plants, especially conifers, and are assumed to be saprophytic on these substrates (*e.g.* Benedix 1969). Some species of *Gyromitra* are easily established on artificial media (Abbott unpublished data; Roponen & Kreula 1978; Raudaskoski *et al.* 1976; Egger & Paden 1986b). This feature supports the assumption that they are saprophytic, but the known pathogen *Rhizina undulata* is also commonly cultured (Satô & Shôji 1974; Ginns 1974b; Egger & Paden 1986a, b). *Rhizina* is known to be pathogenic on conifer seedlings (Ginns 1968, 1974a; Satô & Shôji 1974; Morgan & Driver 1973; Morgan *et al.* 1974; Theis *et al.* 1977; Egger & Paden 1986a; Callan 1990). Egger & Paden (1986b) demonstrate that *Gyromitra infula* has only very weak, if any, pathogenic abilities. The nutritional abilities of *Helvella* are not known, although *H. crispa*, as well as *Gyromitra esculenta* and *G. infula*, are mentioned in Trappe's (1971) list of mycorrhizal ascomycetes based on literature reports. Smits'ka (1981) also lists *Helvella* and *Gyromitra* as mycorrhizal fungi. Hutchison (1989) reports the absence of conidial anamorphs *in vitro* of 96 species of basidiomycete ectomycorrhizal taxa. The absence of conidia was observed in three isolates of *Gyromitra infula* established in axenic culture, and may support Hutchison's (1989) view that conidial anamorphs may have been selected against in ectomycorrhizal fungi in favour of sexual spores for dissemination. Species of *Helvella* have not been established on artificial media, although numerous attempts have been made (Abbott unpublished data; Weber pers. comm.). This suggests complex nutritional requirements and indicates the possibility of mycorrhizal associations. Hypogeous species are assumed to be ectomycorrhizal with coniferous and deciduous trees, but experimental evidence is lacking since they have not been successfully isolated in culture (Trappe 1971). The recent European finds of *Hydnotrya cubispora*, an endemic North American species, are reported from non-native plantations of *Picea*. This indicates a very close, presumably mycorrhizal, relationship with conifers and supports the views of Trappe (1971).

Specific taxa may be adapted to vernal (*e.g. Gyromitra esculenta, G. perlata, Helvella leucomelaena*) or autumnal (*e.g. Gyromitra infula, Helvella lacunosa*) fruiting patterns. Some species (*e.g. Helvella lacunosa, H. maculata, H. compressa, Gyromitra infula*) are often collected throughout the winter in southern coastal regions of the study area. Fruiting body development over a long period is known for members of this family, especially the genus *Gyromitra* (Kempton & Wells 1972; Jalkanen & Jalkanen 1981, 1984). Maturity of ascospores is attained progressively within different regions of individual ascocarps over time (Kempton & Wells 1972; Donadini 1986). Spore dispersal over a prolonged period may increase reproductive success. Hypogeous species are dispersed primarily by rodents (notably the red squirrel, *Tamiasciurus hudsonicus*) in addition to other mammals and invertebrates which feed on the fruiting bodies (Fogel 1976).

Many species of Helvellaceae are constrained by biogeographic habitat preferences. Some species are restricted to arctic and alpine tundra regions (*e.g. Helvella aestivalis, H. arctoalpina*), while others are circumboreal in distribution and occur in similar habitats in Europe, Asia, and North America (*e.g. Helvella crispa, Gyromitra esculenta*). Some species are widely distributed in the northern hemisphere and can be found in a wide range of habitats including deciduous and coniferous woods or tundra on either soil, humus, or rotted wood substrates (*e.g. Helvella lacunosa*, *Gyromitra gigas*). Many species have a more specific substrate requirement, which may include wood (*Pseudorhizina sphaerospora*), leaf litter/humus (*Helvella macropus*), and mineral soil (*H. leucomelaena*). Many species of *Helvella* prefer calcareous soil (Dissing 1966b; Petersen 1985).

Biogeography can be of value in the delimitation of species in the Helvellaceae, as in most other groups of organisms. While many species are circumpolar or circumboreal, others have a more restricted geographic distribution. Some species are endemic to Europe or North America (*e.g. Gyromitra parma* and *Gyromitra melaleucoides* respectively), while others are widely distributed in temperate regions of Europe, Asia, and North America (*e.g. Helvella crispa*, *Hydnotrya tulasnei*). A few species are distributed over an even broader geographic range in the northern and southern hemispheres (*e.g. Helvella leucomelaena*, *H. dissingii*). Few species have been described exclusively from tropical regions (*e.g. Helvella papuensis* Dissing 1979).

Species endemic to the study area include *Helvella robusta* and *H. crassitunicata*, but these species may be found in a wider geographic area as collection continues in adjacent regions of North America. Several other species are restricted to western North America, but are known from areas to the south of the study area (*Gyromitra melaleucoides*, *Pseudorhizina californica*, *Helvella compressa*, *Hydnotrya cerebriformis* and *H. variiformis*). The disjunct distribution of *Helvella maculata* in northwestern North America and China (Arcto-Tertiary disjunct distribution) is unique in the family.

Many closely related species are sympatric in distribution (*e.g. Helvella acetabulum* and *H. costifera*) across the entire range of both species, while others are partially sympatric, especially if one species has a restricted geographic distribution (*e.g. Helvella crispa* and *H. maculata*).

Geographic distribution becomes a very useful aid in the identification and taxonomic separation of species when two closely related species are allopatric in distribution. Although this rarely occurs in species of Helvellaceae, the two species of *Pseudorhizina* are distributed in this manner. *P. sphaerospora* is known from Europe, Asia and eastern North America, while *P. californica* is known only from western North America. The distribution of the two species comes into close contact near the Rocky Mountains, but the ranges of the two species are restricted to opposite sides of the continental divide. The species of *Underwoodia* show a very unusual disjunct allopatric distribution with a different species restricted to North America, South America, and Australia respectively.

Some problems with taxonomic separation may be due to differences in habitat and geographic distribution. Taxa exhibiting distinct morphologies may occur in different environmental regions. In these cases it is often difficult to evaluate whether the morphological features are altered by different conditions, or if distinct species are restricted to different habitats. Problems of this nature arise in the separation of *Helvella palustris* and *H. lacunosa* (Häffner 1991). Taxonomic problems also arise from differences seen between geographic locations. For example, the slight differences seen 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. If taxonomic recognition is warranted, then the decision of which rank to use (*i.e.* specific, subspecific, or varietal) is unclear.

Phylogeny of Helvellaceae and delimitation of higher taxa

Placement of Helvellaceae in Ascomycotina: The Helvellaceae is placed in the polyphyletic group Discomycetes (typically given the rank of Class) due to the development of ascospores within asci arranged in a palisade hymenium in an apothecium. The family is placed in the Order Pezizales, the only order containing species with operculate asci. Although until recently this order has been restricted to operculate taxa (*e.g.* Eckblad 1968; Korf 1972), a broader concept has become accepted to include taxa with inoperculate or indehiscent asci that are clearly most closely related to operculate taxa (Trappe 1979; Eriksson & Hawksworth 1991). It is this broad concept of the Order Pezizales as emended by Trappe (1979) that is accepted here. These indehiscent taxa 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). These taxa are clearly derived from operculate epigeous groups, and are relatively distantly related to other inoperculate taxa (*e.g.* Leotiales). The Helvellaceae is among the few families in the order (also Pezizaceae and Pyronemataceae) to include both operculate epigeous and indehiscent hypogeous taxa, and the morphological similarities between the operculate genus *Helvella* and the indehiscent genus *Hydnotrya* provide a clear indication that the family is monophyletic, despite containing members with fundamentally different ascus morphology. The presence of an operculum in *Hydnotrya cerebriformis* reported here (Figure 28) provides conclusive evidence of the relationship between the operculate and indehiscent taxa.

The relationships of Helvellaceae to other families in the order are unclear. The family is considered to be at a high level of evolutionary development due to the complex apothecia and multinucleate spores (Nannfeldt 1937; Eckblad 1968; Dissing 1966b). Primitive taxa 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, and Ascobolaceae. This suborder is separated from the suborder Sarcoscyphineae (families Sarcoscyphaceae and Sarcosomataceae) by the suboperculate ascus of the latter group. Eckblad (1968) and Brummelen (1978) do not consider that the two groups should be treated as distinct subordinal taxa. Harmaja (1974c) described all members of the Sarcoscyphineae examined by him to possess persistently perisporous spores which are also typical of members of the Pezizaceae, Helvellaceae, and Pyronemataceae (although not exclusively), and these results do not support the isolated taxonomic position of the Sarcoscyphineae *sensu* Korf.

Eckblad considers taxa centred on *Helvella*, his family Helvellaceae, and taxa centred on *Gyromitra*, his family Rhizinaceae, to be derived independently from pezizoid ancestors. Smitskaya & Slavnaya (1978) and Harmaja (1969a, 1974b) followed the system of Eckblad (1968) and accepted the Helvellaceae and Rhizinaceae as separate families, 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 the genus *Pseudorhizina*, but this separation has received little support and most authors consider this family a synonym of the Helvellaceae (Eriksson & Hawksworth 1991). Smitskaya (1981) outlined a much different phylogenetic relationship between genera, assigning them to three families of Pezizales. The cupulate species were retained in the Pezizaceae (*sensu lato*) as the genera *Discina*, *Acetabula*, and *Macropodia*. From *Discina* the monotypic family Rhizinaceae was derived. The Helvellaceae (genus *Helvella*) was polyphyletically derived from both

Macropodia and *Acetabula*. *Helvella* then gives rise to *Gyromitra* and *Helvellella* (=*Pseudorhizina*). Although this scheme recognizes the relationships between *Discina* (=*Gyromitra*) and *Rhizina*, it fails to note the even closer association of *Discina* and *Gyromitra* which are relegated to different families. This view clearly is unacceptable given modern criteria for generic and familial delimitation. The views of Eckblad (1968), Harmaja (1974b), and Smitskaya (1981) are in opposition to the unified concept of the Helvellaceae adopted here in agreement with Dissing (1966b, 1972), Rifai (1968), Kimbrough (1970, 1991), Korf (1973), Harmaja (1976b) and Eriksson & Hawksworth (1991). The unified concept of the family is based on the presumed monophyletic origin of all taxa with tetranucleate ascospores.

The 'helvelloid' taxa were formerly placed close to and often in the same family with the 'morchelloid' taxa (e.g. Seaver 1928; Groves & Hoare 1953; Imai 1932, 1954). It is currently accepted that the Helvellaceae and Morchellaceae are well separated since the Morchellaceae possesses multinucleate rather than tetranucleate ascospores, and have external oil guttules in contrast to the internal ones of the Helvellaceae (Eckblad 1968; Korf 1972; Eriksson & Hawksworth 1991). Smitskaya (1981) derives the Morchellaceae from the Helvellaceae and *Helvella* in particular. The similarity in the excipulum structure between the Morchellaceae and *Helvella* (Eckblad 1968) may suggest a taxonomic affinity, but this is uncertain. Samuelson (1978) reports the similarity of the apical apparatus of asci in *Helvella* and *Morchella*. I am in agreement with Nannfeldt (1937) and Eckblad (1968) that the Morchellaceae and Helvellaceae are derived independently from less advanced members of the Pezizales, and that the complex ascocarps indicate parallel or convergent evolutionary development.

Several genera of operculate discomycetes have been suggested as possible ancestors of taxa in the Helvellaceae. Nannfeldt (1937), Eckblad (1968), and Smitskaya (1981) suggest a close affinity between *Helvella* and *Pustularia* (=*Tarzetta*) based on similarities of excipulum, spores, and paraphyses. Maas Geesteranus (1967) even included *Pustularia* in the Helvellaceae. Eckblad (1968) further suggested that the Helvellaceae (*sensu* Eckblad) are directly derived from the Otideaceae (*sensu* Eckblad containing *Otidea*, *Pustulina* (=*Tarzetta*), *Sowerbyella*, *Geopyxis*, and *Ascosparassis*), although he separates the Otideaceae from the Pyronemataceae in which these genera are currently placed (Eriksson & Hawksworth 1991). Benedix (1962) also suggests an affinity with *Geopyxis*. Dissing (1966b) regards these taxa as well separated from the Helvellaceae and could suggest no 'primitive' taxa which could be ancestral to the family. Recent transmission electron microscope (TEM) studies by Kimbrough & Gibson (1990) have shown that the structure of the ascus pore plugs and ascospore secondary wall in *Geopyxis* are most similar to those of species in the Helvellaceae. The uninucleate mature spores with little oil reserves excludes *Tarzetta* (=*Pustularia*, =*Pustulina*) and *Geopyxis* from the Helvellaceae as accepted here.

Intergeneric relationships: As discussed above, the various genera of the Helvellaceae have been placed, in various combinations, in a number of families (*e.g.* Eckblad 1968; Harmaja 1974b; Smitskaya 1981; Maas Geesteranus 1967). This contrasts with the family Helvellaceae *sensu lato* accepted here (see also comments above). Phylogenetic relationships between subfamilial, generic, and subgeneric taxa delimited in this study are presented in Figure 65. The six genera of Helvellaceae discussed in detail in this work can be divided into two subfamilial tribes, tribus Helvelleae and tribus Gyromitreae. Tribus Helvelleae includes the genera *Helvella*, *Underwoodia*, and *Hydnotrya*. Tribus Gyromitreae includes the genera *Gyromitra*, *Pseudorhizina*, and

Rhizina. These tribes are recognized as distinct based primarily on the structure of the excipulum. The tribus Gyromitreae is emended to include members of tribus Discineae (Benedix) Dissing of Dissing (1966) and Korf (1972, 1973). Kimbrough (1991) also recognizes two subfamilial tribes. The two tribes recognized here correspond to the families Helvellaceae and Rhizinaceae respectively of Eckblad (1968), although he did not consider *Hydnotrya* in his work. The morphological similarity between *Helvella* and *Hydnotrya* has been noted by Korf (1973b) and Donadini (1983) and placement in the Helvellaceae was confirmed by Berthet (1982) who demonstrated the tetranucleate condition of the spores of *Hydnotrya michaelis*. The tribus *Helvelleae* is here emended to include the hypogeous genus *Hydnotrya*. The two tribes are monophyletic and derived from a common ancestor.

Other hypogeous inoperculate genera assigned to the Helvellaceae include *Gymnohydnotrya*, *Fischerula*, *Dingleya*, *Cazia*, and *Choiromyces*. I have studied specimens only of the first of these. *Gymnohydnotrya* and *Choiromyces* are known to have tetranucleate spores (Zhang & Minter 1989a, b) and should be accepted within the Helvellaceae. To my knowledge, the number of nuclei in the spores of *Fischerula*, *Dingleya*, and *Cazia* has not been ascertained, but morphological and anatomical features link them with other hypogeous and epigeous members of the Helvellaceae (Trappe 1975b, 1979, 1989). The subfamilial placement of these taxa is unclear. While it may seem justifiable to erect a subfamilial tribe to accommodate the indehiscent, hypogeous taxa, it is possible that the development of the hypogeous ascocarp has occurred in both tribes of the family. Thus, the resultant similarity in morphology between hypogeous taxa would be the result of parallel evolutionary development and the tribe would not be a monophyletic unit. Further study of these hypogeous genera is needed to determine a phylogenetic placement and they should be considered as genera *incertae sedis* at the tribe level of the Helvellaceae.

Within the tribus *Helvelleae* the genus *Helvella* is considered closest to the basal taxon from which extant genera are derived. It is interesting that both *Underwoodia* and *Hydnotrya* have nodulose ascospores, but the phylogenetic relevance of this feature is uncertain. I consider it likely that this is a convergent feature, rather than one indicating a close relationship between *Underwoodia* and *Hydnotrya*. Both of these genera have been assigned to the genus *Helvella* at one time or another (Eckblad 1968; Harmaja 1974a; Donadini 1983; Eriksson & Hawksworth 1991).

Underwoodia is recognized as distinct at the generic level since it has no free excipular surface; the excipulum is completely fused and continuous with the stipe tissue. The nodulose ascospore ornamentation has hitherto been ignored as a character of value at the generic level, but the striking difference in morphology compared to all members of *Helvella* (*sensu meo*) clearly supports taxonomic separation. The uniformity in spore morphology of all species of *Helvella* examined in this study (including those of section *Macropodes*, see discussion in following section) is clearly diagnostic at the generic level and supports the retention of *Underwoodia* as a distinct genus. Harmaja (1974a) states "that at generic level most diagnostic value should be accorded to the sporal and anatomical characters, and not to ascocarp shape", yet disregards the distinctive spore ornamentation and unites *Underwoodia* with *Helvella*. In this case, correlation of ascocarp morphology and sporal features warrant generic status. Relationship to *Helvella* is indicated by the similarity in 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 which possess cyanophilic

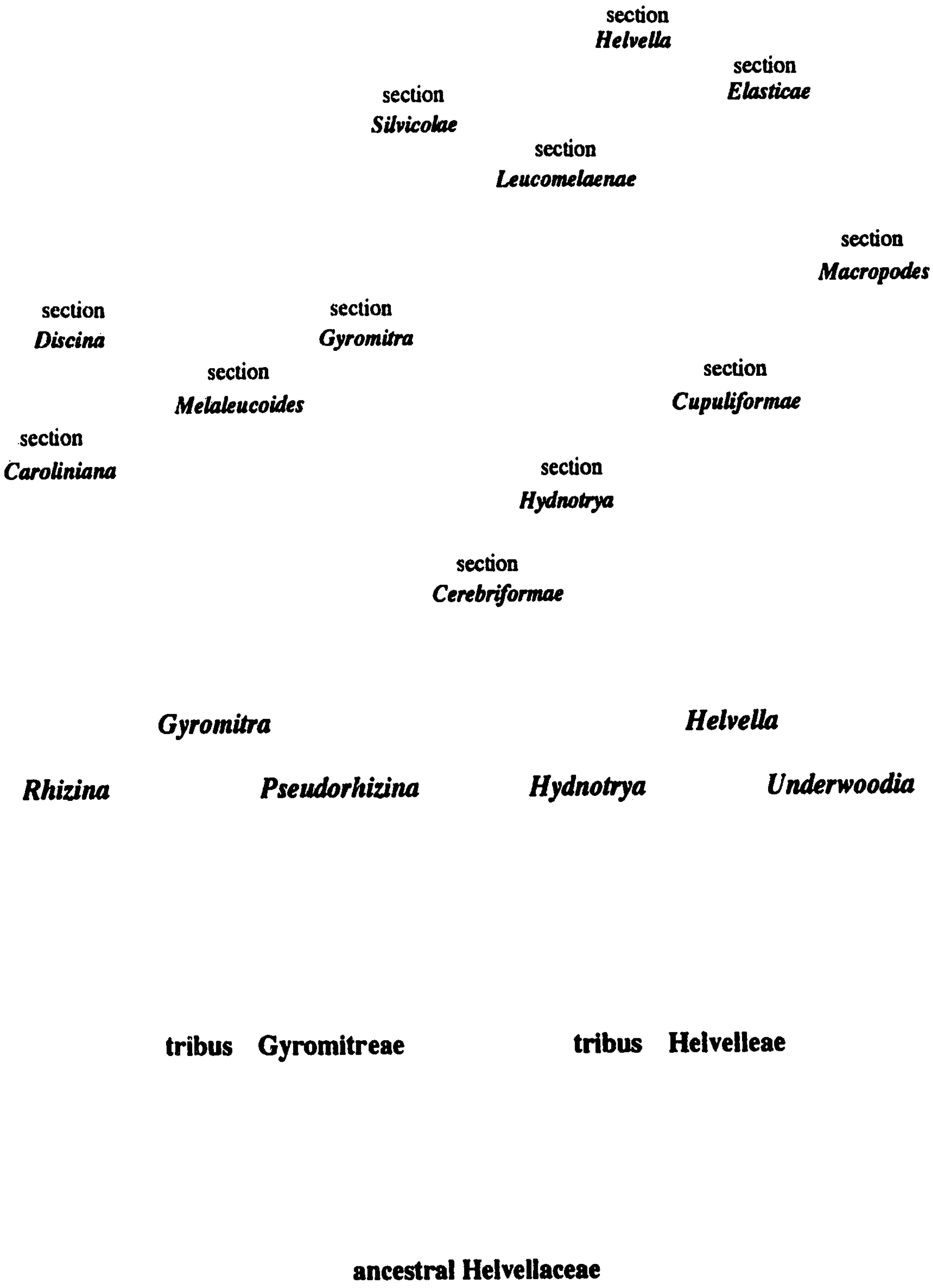

Figure 65: Phylogenetic relationships among subfamilial, generic, and subgeneric taxa of Helvellaceae.

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 1976; McKnight 1969, 1971; Abbott unpublished). The structure of the excipulum in *Hydnotrya michaelis* as shown in Berthet (1982) and Kers (1989) is quite distinct from that of *Helvella* as depicted in Eckblad (1968), Dissing (1966), and Dissing & Sivertsen (1980). The uniguttulate nature of globose and broadly ellipsoidal spores provides the most efficient distribution of oil guttules within the spores (Harmaja 1973), and may not reflect phylogenetic relatedness. The distribution of oil guttules in the ascospore may be controlled to a greater extent by selection pressures affecting spore shape than by relatedness of taxa. Some members of the tribus Gyromitreae (*Pseudorhizina sphaerospora*, *Gyromitra gigas*) have frequently 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*. The presence of this feature, although absent in *Pseudorhizina*, is clearly the common type in the Helvellaceae and does not necessarily imply relatedness between *Hydnotrya* and *Helvella*.

A convincing link between the aforementioned genera was the description of *Helvella astieri* by Korf (1973b). Although I have not examined the type or other specimens of this species, the description and illustrations provided by Korf (1983) show the similarities to both *Helvella* and *Hydnotrya*. The decision to place this species in *Helvella* was based on the observation of a functional operculum. In my 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 & Hawksworth (1991) and Egger (pers. comm.). The discovery of *H. astieri* is also of great importance in assessing the direction of evolution in tribus *Helvelleae*. Because an enclosed 'sparassoid' ascocarp has no need for a functional operculum, it can be concluded that the apical dehiscence mechanism is retained from its ancestry. It is thus apparent that the indehiscent asci of hypogeous 'sparassoid' species represents a secondary loss and that those species are evolutionarily more derived than those with functional operculate asci. The discovery here of an operculum in *Hydnotrya cerebriformis* (Figure 28), although it is probably not functional, also supports the derivation of hypogeous taxa from epigeous ones.

Within the tribus *Gyromitreae*, the relation of *Rhizina* to members of *Gyromitra*, especially *G. ambigua* and *G. perlata*, is demonstrated by similarities in ascospore size, shape, apiculation, and ornamentation. *Rhizina* is retained as a distinct genus on the basis of the indeterminate growth in the marginal region, the presence of rhizoids continuous with the excipular surface, the presence of setae in the hymenium, and the parasitic mode of existence. These features represent specialized evolutionary traits and *Rhizina* is a highly derived genus.

The phylogenetic relations between *Gyromitra* and *Pseudorhizina* are less clear. The two genera were often placed in the same genus (*e.g.* McKnight & Batra 1974; Korf 1973a), but the differences in perispore staining and spore guttulation discussed by Harmaja (1974b) support the retention of the genus *Pseudorhizina*. The biguttulate ascospores of *P. californica* suggest closer affinity to some members of *Gyromitra* (*e.g. G. esculenta, G. infula, G. melaleucoides*) than to taxa in the tribe *Helvelleae*. The structure of the excipulum, although distinctive, is very similar to the type commonly seen in other genera of the tribe *Gyromitreae*.

Subgeneric taxa and interspecific relationships: The broad generic concepts of taxa in the Helvellaceae contain other subset groups of very closely related species. These groups are given the rank of section in *Helvella* (*e.g.* Dissing 1966b; Weber 1972) and subgenus in *Gyromitra* (*e.g.* Harmaja 1973; Kimbrough *et al.* 1990). To standardize terminology, all subgeneric taxa are referred to as sections. Sections and subgenera are treated as being of the same rank for purposes of nomenclature (International Code of Botanical Nomenclature, Berlin 1988). Sectional and subgeneric names previously described are therefore conserved, although they may be emended in this work. Sections based on species not designated as types for any previously described subgeneric section are newly described. To avoid confusion, new sections are erected rather than using earlier generic names at the subgeneric level. These genera rarely corresponded exactly with the sections as outlined here, or the concept of the genus included members from more than one of the sections recognized in this work. The outline presented in this work divides the genera into recognizable units of taxonomic affinity (Figure 65).

The genus *Gyromitra* is divided into four subgeneric sections on the basis of ascospore morphology and is correlated with ascocarp morphology. Section *Melaleucoides* shares relatively small spore size and biguttulate ascospore contents with section *Gyromitra*. This similarity may indicate phylogenetic affinity, but relationships are unclear and the taxa are considered to be relatively distantly related. Pfister (1980) provides evidence that this species is a true member of the Helvellaceae and supports the broad concept of the genus *Gyromitra* to accommodate this species. Pfister also comments that it could not be easily placed in either *Gyromitra* or *Discina* in their restricted senses, clearly recognizing the taxonomic isolation of this species. The section *Discina* may also provide a link with section *Melaleucoides* through *G. melaleuca*, but the placement of this species is uncertain. *G. melaleuca* is tentatively placed in the section *Melaleucoides*, although it is somewhat aberrant. The spores are smaller than typical in members of the section *Discina*, and the apiculi appear absent (although also inconspicuous in other species of the section *Discina* (*e.g. G. olympiana*). My SEM observations of *G. melaleuca* are based on submature ascospores. The SEM photographs in Donadini (1986) and my SEM observations appear somewhat intermediate between the rugose surface typical for section *Discina* and the nodulose warted ornamentation typical for *G. melaleucoides*, the only other species in the section *Melaleucoides*. The distribution of oil guttules within the ascospore is also intermediate. As illustrated in Benedix (1969), the spores are typically ellipsoidal, but some appear subfusoidal. The spores are most frequently biguttulate (with a smaller proportion of triguttulate spores), but the guttules are of unequal size. This pattern is also seen in a smaller proportion of spores in other species of the section *Discina*, including *G. gigas*. Further investigation of *G. melaleuca* may reveal a closer affinity with the section *Discina* than the taxon it is ascribed to here.

Species ascribed to the section *Caroliniana* have been closely allied with members of the section *Discina* and were often grouped with them in the genus *Discina* (*e.g.* Eckblad 1968). The section *Caroliniana* as delimited in this work contains subsessile to distinctly stipitate species which share a common ascospore morphology (Figure 39) and is considered to be more closely related to section *Discina* than to other sections of the genus.

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

The genus *Helvella* is divided into six subgeneric sections in this work, which are emended to include species treated in various sections *sensu* Dissing (1966b) or Häffner (1987). The section *Helvella* is at a high level of development due to the complex apothecium and stipe morphology (Figures 6, 14) and is derived from less complex taxa of the genus. The ancestral form of species in the section *Helvella* may have been morphologically similar to *H. solitaria* placed in a basal taxonomic position of the section *Leucomelaenae*. *H. solitaria* is a variable taxon, and large forms of this species have a pronounced stipe with anastomosed branches and internal chambers very reminiscent of *H. maculata* in the section *Helvella*. Species in the section *Leucomelaenae* with complex ribbing on stipe and excipular surface (*e.g. H. acetabulum, H. costifera*)(Figure 5) are derived from simpler morphological forms similar to *H. leucomelaena* (Figure 3) or *H. solitaria*. The section *Silvicolae* is likely derived from an ancestor similar to species in the section *Leucomelaenae*. The indistinct sparingly ribbed stipe of *H. silvicola* (Figure 4) is similar in construction to that of *H. leucomelaena* (Figure 3) and *H. aestivalis*. The strongly one-sided apothecium and ascocarp colouration typical of *H. silvicola* are also seen to a much lesser extent in the aforementioned taxa. The section *Leucomelaenae* is also allied with the section *Cupuliformae*. Small slender forms of *H. solitaria* are morphologically similar to *H. cupuliformis* and *H. corium* placed in the section *Cupuliformae*.

The section *Elasticae* is clearly derived from species in the section *Cupuliformae*. Similarities between members placed in a basal taxonomic position of the section *Elasticae* (*i.e. H. ephippium, H. pezizoides*) are only slightly more complex than some species of section *Cupuliformae* (*i.e. H. dissingii*). The section *Elasticae* clearly represents an advanced lineage derived from a less complex taxon. Species such as *H. elastica* and *H. monachella* are among the most highly derived species of section *Elasticae* on the basis of elaborate apothecia reflexed to stipe, glabrous excipular surfaces, and hollow internal stipe construction.

The genus *Underwoodia* contains only a typical subgeneric section of at least three closely related species. Although the taxa included in *Underwoodia* have been said to differ little in ascocarp morphology from species such as *H. lactea* in the typical section of *Helvella* (Harmaja 1974a), direct phylogenetic relationship between these taxa has not been satisfactorily demonstrated to conclude that *Underwoodia* is derived from this taxonomic group (see also notes under intergeneric relationships).

I propose dividing the genus *Hydnotrya* into two sections on the basis of ascospore morphology. Members of the typical section have subglobose to broadly ellipsoidal ascospores with spore walls that are irregularly thickened in a nodulose or slab-like manner. Species in this section represent a monophyletic unit. *H. cerebriformis* is placed in a section of its own on the basis of the unique globose, echinate ascospores. The SEM studies of *Gymnohydnotrya* by Zhang & Minter (1989b) show similar ascospore ornamentation to that seen in *Hydnotrya cerebriformis*. The genus *Hydnotrya* was noticed to include species with a diversity of ascospore morphologies by Trappe (1979). Trappe suggested that the species with echinate, globose ascospores may deserve generic separation. The species is retained in *Hydnotrya* based on gross morphological similarity, an admittedly unreliable diagnostic character in hypogeous fungi. The presence of four nuclei in mature spores of *H. cerebriformis* is reported in this study, confirming the placement of this species in the Helvellaceae. Ascospore morphology is also variable in the hypogeous genus *Choiromyces* (Helvellaceae; see Trappe 1979) and *Tuber* (Tuberaceae; see Lange 1956).

Taxonomic revision of Helvellaceae including keys to taxa occurring in northern and northwestern North America

Key to subfamilial tribes and genera of Helvellaceae

1. Apothecium excipular tissue (as seen in cross section) at maturity of *textura intricata* throughout, sometimes with an indistinct evanescent ectal layer of *textura angularis*..Tribus Gyromitreae 2

1'. Apothecium 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*..Tribus Helvelleae 4

2. Ascocarps sessile, with rhizoids extending from excipular surface; thick-walled setae present in hymenium...*Rhizina* (*R. undulata*)

2'. Ascocarps stipitate or sessile, excipular surface lacking rhizoids; setae absent from hymenium 3

3. Ascospores at maturity with cyanophilic perispore (temporarily perisporous); flesh of fresh apothecia relatively thick (2-5 mm)...............................*Gyromitra*

3'. Ascospores at maturity lacking cyanophilic perispore (persistently perisporous); flesh of fresh apothecia relatively thin (1-2 mm)..........................*Pseudorhizina*

4. Asci indehiscent; ascospores thick-walled and pigmented; ascocarps hypogeous ....*Hydnotrya*

4'. Asci operculate; ascospores thin-walled and hyaline; ascocarps epigeous 5

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*)

Gyromitra Fries, 1849, Summa Vegetabilium Scandinaviae 2: 346.

Synonyms: *Discina* (Fries) Fries
Neogyromitra Imai
Paradiscina Benedix
Fastigiella Benedix

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 to 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, 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 subgeneric Sections of *Gyromitra*

1. Ascospores biguttulate 2
1'. Ascospores uniguttulate or triguttulate 3

2. Ascospore ornamentation finely rugose .... *Gyromitra*
2'. Ascospore ornamentation of isolated rounded warts .... *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 .... *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 .... *Caroliniana*

Section *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, to subfusoidal, appearing smooth with light microscope, with SEM spore surface finely rugose, non-apiculate or with broadly rounded, inflated apiculi, biguttulate.

Taxonomic Notes: The section *Gyromitra* is characterized by biguttulate, ellipsoidal to narrowly ellipsoidal or narrowly subfusoidal ascospores. The spore apiculi are virtually absent or appear as rounded swellings of the perispore at the apices. Spore ornamentation is typically indistinct with the light microscope, but is discernable with the SEM. The spore surface is evenly covered with a fine rugose ornamentation (Figures 29, 30).

Key to species of *Gyromitra* section *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 esculenta (Persoon) Fries, 1849, Summa Vegetabilium Scandinaviae 2: 346.

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

Synonyms: *Gyromitra bubacii* Velenovsky, holotype PRC, examined.

Type material: unknown.

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

Geographic distribution: Widely distributed throughout boreal, montane, and coastal forests from Alaska, Yukon, British Columbia, Alberta, Manitoba, Washington, Idaho, Oregon, and Wyoming. Also distributed in eastern North America (Groves & Hoare 1953), Europe (Harmaja 1979), and Asia (Imai 1954; Korf & Zhuang 1991). Map 1.

Taxonomic Notes: *Gyromitra esculenta* is separated from other species in the section 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 colouration, and degree of apothecial convolution. Harmaja (1979b) recognized three distinct ascospore morphologies differing in size, shape, apiculation, and guttulation. Although these features vary considerably between collections, there does not seem to be a correlation between these features and other characteristics which could justify the separation of distinct taxa. Furthermore, characters such as spore size and shape are considerably variable within individual ascocarps. The holotype of *Gyromitra bubacii* represents an extreme with large ascospores, but the variability in size is extreme (21.7-35.3 μm long) and the guttules are smaller than described for Harmaja's (1979b) Type III which also has large ascospores. Moravec (1986) considers this taxon as a variety of *G. esculenta*. Due to the extreme variability and lack of correlated characteristics, *G. bubacii* is synonymized with *G. esculenta*.

Collections Examined: CANADA: Yukon: Annie's Lake, Schalkwyk July 4 1981, DAOM 183550, 183551, 183552. **British Columbia:** Burns Lake, Arnold June 18 1965, DAOM 113992; Revelstoke, Macoun May 9 1890, DAOM 44704; Mount Revelstoke National Park, Schumacker May 23 1986, ALTA; Spuzzum Creek near Yale, Wood May 31 1972, DAOM 143565; Proctor, Linton May 15 1978, UVIC; Lake Cowichan, Vancouver Island, Paden (JWP 1343, 1344, 1347) May 22 1986, UVIC; Francis Park, Victoria, Vancouver Island, Egger April 26, 28 1985, DAOM 199519, 199526; Saltspring Island, Linton April 20 1974, UVIC; Chilliwack River, Stirling May 8 1982, UBC F907; Manning Provincial Park, Egger June 9 1985, DAOM 199550, 199552, 199559; Champain Lakes near Trail, Danielson (RMD 709) June 3 1973, ALTA. **Alberta:** Richardson Fire Tower 150 km north of Fort McMurray, Danielson (RMD 1897) April 27 1976, ALTA; Cross Lake, Ansley and Hichling May 12 1977, ALTA 7488; Whitecourt, Stewart June 5 1963, ALTA 685; Astotin Natural Area near Bruderheim, Abbott (SA 315) May 13 1990, SA; south of Edson, Vitt June 1 1974, ALTA 7[illegible]2; Wabamun Lake, Seymour May 26 1963, ALTA 684; Devonian Botanic Garden near Devon, Abbott (SA 358) June 9 1990, SA; Devonian Botanic Garden near Devon, Currah May 18 1976, June 30 1979, May 15 1981, ALTA 7237, 7956, SA [illegible] near Devon, Osis and Gibson (SA 312) May 12 1990, SA; near Breton, Osis (S[illegible]20, 356) May 14 1989, May 27 1990, SA; Cirque Lake, Banff National Park, Beil June 24 1964, ALTA 671; Forestry Trunk Road, Danielson (RMD 2722) June 18 1978, ALTA; Sheep

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

Exsiccata Examined: Vancouver Island Fungi, 254, Sidney, British Columbia, Macoun February 8 1915, s.n. *Helvella lacunosa*, UBC F3270; Vancouver Island Fungi, 344, Vancouver Island British Columbia, Macoun February 25 1915, s.n. *Gyromitra*, UBC F3237; Cooke, Mycobiota of North America, 319, Blue Mountains, Umatilla

County, Oregon, USA, Cooke June 16 1948, s.n. *Helvella infula* , WSP 23656.

Gyromitra tasmanica (Berkeley) Berkeley & Cooke, 1878, Mycographia 193, t. 90, f. 331.

Basionym: *Helvella tasmanica* Berkeley

Type Material: Holotype K, examined.

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

Taxonomic Notes: This species is closely related to *G. esculenta* (q.v.), but differs in its smaller stature and typically free apothecial margin.

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

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

Basionym: *Helvella infula* Schaeffer : Fries, 1822, Systema Mycologicum 2: 17. based on *Helvella infula* Schaeffer, Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icones 4: ind. 105. 1774.

Synonyms: *Helvella friesiana* lectotype K, examined.

Type Material: Neotype K (designated Harmaja 1969b), examined.

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 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, subcespitose, or scattered on ground or more often on rotted coniferous or deciduous wood in coniferous or mixed woods, rarely in deciduous woods. Associated tree species include *Picea glauca, Picea mariana, Picea sitchensis, 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 include *Alnus crispa, Salix* sp., and *Rosa* sp. Fruiting period from July 15 to February 17 in British Columbia, with the majority of collections in August, September, and October.

Geographic Distribution: Widely distributed throughout boreal, montane and coastal forests from Alaska, Northwest Territories, British Columbia, Alberta, Manitoba, Washington, Idaho, Montana, and Wyoming. This species is also reported from Oregon (Larsen & Denison 1978). Also distributed in eastern North America (Groves & Hoare 1953), South America (Dennis 1970), Europe (Harmaja 1969), and Asia (Korf & Zhuang

1991). Map 2.

Taxonomic Notes: Relatively small spore size, narrowly ellipsoidal shape, and lack of distinct apiculation are characteristic for *G. infula*. This species is most closely related to *G. ambigua* (q.v.), and is separated as discussed under the notes for that species. 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 (1948) 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 & Hoare (1953). Collections of *G. infula* in the northwest of North America are 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 colouration and structure, and ascospore morphology.

Collections Examined: CANADA: Northwest Territories: Pine Point, Dube September 1983, DAOM 188769. **British Columbia:** Muncho Lake Provincial Park, Abbott (SA 208) August 21 1989, SA; Proctor, Linton September 19 1978, UVIC; Cathedral Grove near Port Alberni, Vancouver Island, Smyth October 10 1977, UVIC; Sidney, Vancouver Island, December 16 1913, DAOM 44705; Victoria, Vancouver Island, Newcombe, K; James Island near Central Saanich, Simmonds February 17 1977; University of British Columbia campus, Vancouver, Kroeger October 29 1986, UBC F12833; Vancouver, Waugh July 15 1951, October 16 1960, DAOM 26944, 71910; Similkameen River, Manning Provincial Park, Bandoni July 16 1959, UBC F3271. **Alberta:** Richardson Fire Tower 150 km north of Fort McMurray, Danielson (RMD 1703) September 1 1975; Fawcett Lake, Abbott September 3 1988, ALTA 8451; Carson Lake, Currah August 26 1977, ALTA 7538; Sandy Lake, Schalkwyk August 16 1980, DAOM 180173; William A. Switzer Provincial Park, Abbott (SA 272, 274, 276, 277) August 27 1989, SA; William A. Switzer Provincial Park, Osis (SA 395, 396) September 2 1990, SA; Fryatt valley, Jasper National Park, Richardson (SA 299) September 22 1989, SA; Spruce Grove area, Kennedy August 20 1980, ALTA 8060; University of Alberta Forest Reserve, Edmonton, Traquair September 14 1970, ALTA 4140; Whitemud Creek, Edmonton, Abbott September 13 1987, ALTA 8450; near Breton, Abbott (SA 385) August 9 1990, SA; Fish Lake near Nordegg, Abbott (SA 283) August 31 1989, SA; Crimson Lake, Kennedy August 31 1976, ALTA 7239; Forestry Trunk Road, Forest Reserve, west of Calgary, Danielson (RMD 2818) September 3 1978, ALTA; Yamnuska near Seebe, Danielson (RMD 1774, 1777) September 9 1975, ALTA; Brown Lowery Natural Area, Danielson (RMD 451, 499, 1086, 1088, 1089, 1187) August 27, September 2 1972, August 26, September 3 1973, ALTA; Fish Creek Provincial Park, Calgary, Danielson (RMD 996, 1062) August 9, 21 1973, ALTA; Marmot Creek, Kananaskis, Danielson (RMD 2316) September 2 1976, ALTA. **Manitoba:** Victoria Beach, Lake Winnipeg, Bisby September 12 1926, DAOM 206805, 206806; Minaki, Bisby September 27 1925, DAOM 206807; Singush Lake, Parker September 21 1975, DAOM 187879; Duck Mountain, Parker August 7 1977, DAOM 165377. **USA: Alaska:** Fairbanks, Kempton August 7, 8 1970, WK 4639, 4666; Talkeetna junction, Suisitna valley, Kempton August 15 1966, August 16 1970, August 29 1971, WK 856, 4723, 4728, 5239; Liberty Falls Creek, Copper River valley, Kempton September 5 1970, WK 4588; Eklutna Lake north of Anchorage, Kempton August 24, September 21 1971, WK 5199, 5215, 5614; Anchorage, Kempton August 10, September 9, 26, 28 1971, WK 7133, 5505, 5658, 5672; Girdwood, Kempton September 23 1969, WK 4310; Kenai Lake, Kenai Peninsula, Kempton September 6 1967, WK 866; Haines, Kempton

September 9, 1967, September 20, 21 1970, WK 873, 4963, 4971. **Washington:** Whidbey island, Meeure (Stz 17552) October 31 1972, WTU; Blewett Pass, Cascade Mountains, Grant August 1929, MU F14163; near Gifford, van de Bogart (FVB 834) October 23 1971, WTU; Hermit Mountain trail, Puget Sound, Fink July 1906, MU F1559; Seattle, Stuntz November 1 1934, WTU; Seattle, Zeller (54, 205) 1911, March 1914, WTU; Seattle, Murril October 20, November 1 1911, NY; Watermain Woods, Redmond, Williams (JWL 1683) October 13 1973, WTU; confluence of north fork of Rogue and National Creek, Douglas County, Isaacs (Is 198) August 27 1957, WTU; Burping Brook, Mount Spokane, Simms October 5 1968, WSP 58171; east of McCleary, van de Bogart (FVB 669) November 3 1970, WTU; Silver Springs area, Chinook Pass, Isaacs (Is 1272) October 1 1960, WTU; Tahoma Creek, Mount Rainier National Park, van de Bogart (FVB 1489) October 22 1971, WTU; Tahoma Creek, Mount Rainier National Park, Brough November 2 1963, UBC F3239; White River near Mount Rainier National Park, Isaacs (Is 673) October 5 1958, WTU; Iron Butte, Cispus area near Randle, van de Bogart (FVB 1420) October 21 1972, WTU; Bingen Mountain, Klickitat County, Dietz November 23 1901, WSP 27475; Teanaway, Woo (Stz 16689) July 4 1971, WTU; south of Brown's Lake, van de Bogart (FVB 988) November 13 1971, WTU; Lake Hannah, Stuntz (Stz 19958) September 27 1976, WTU; road 1102/1102c junction, van de Bogart (FVB 938) October 24 1971, WTU; road 1102 rock pit site, van de Bogart (FVB 828) October 24 1971, WTU; Mtn. Park road, van de Bogart (FVB 2311) October 21 1973, WTU; Modips road, Stuntz (Stz 16859) October 17 1971, WTU; unknown, Stuntz (Stz 17512) October 22 1972, WTU; unknown, Williams (JWL 67), WTU; unknown, Stuntz (Stz 13774) October 29 1966, WTU. **Idaho:** Hunt Creek Road, Bonner/Boundary Counties, Slipp October 3 1940, WSP 49762; near Benton Spring, Priest River Experimental Forest, Bonner County, Hayes July 3 1941, WSP 49797; Coeur d'Alene, Rust (1014) October 1918, WTU; Bovill, Rhoads September 29 1920, UBC F3238; Dry Creek between Troy and Deary, Cooke May 1948, WSP 30088; west end of Thatuna Ridge, Latah County, Cooke November 28 1947, WSP 24509; Laird Park, Latah County, LES October 28 1976, WSP 63256; Fall Creek at French Creek Grade, Idaho County, Miller September 4, 7 1964, WSP 53882, 53834; Upper Payette Lake, Miller August 29 1964, WSP 54573; Snowslide Lake, Valley County, Miller August 18 1964, WSP 54557; Sater Meadows, Valley County, Miller August 6 1964, WSP 54187; Teels Creek road, van de Bogart (FVB 3732) September 9 1976, WTU; Idaho, Slipp September 16 1944, WSP 50858. **Montana:** Red Meadow Road, Flathead County, Young July 24 1967, WSP 57826; Echo Lake, Flathead National Forest, Cummins July 23 1928, MICH. **Wyoming:** Grassy Lake, Targhee National Forest, Ammirati (JFA 9420) August 7 1987, WTU. **California:** Lassen Volcanic National Park, Cooke October 8 1976, WSP 63394. **New York:** Lake Placid, Adirondacks, Murrill October 3-14 1912, NY 565. **COSTA RICA:** Cuericí, Talamanaca Ridge, Gómez September 13 1969, K. **SWEDEN:** Upland, Herbarium Berkeley (neotype); Gottsunda skog near Uppsala, Lundell October 3 1935, K. **CZECHOSLOVAKIA:** Delroi Virgin Forest, Slovakia, September 24 1964, K.

Exsiccata Examined: Vancouver Island Fungi, 33, Sidney, Macoun 1912, s.n. *Helvella infula*, UBC F3269; Vancouver Island Fungi, 23, Sidney, Macoun 1912, s.n. *Helvella crispa*, UBC F3247.

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

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

Synonyms: *Gyromitra infula* var. *apiculatispora* Raitviir, fide Harmaja 1969b.

Type material: Holotype H, examined.

Figures 1, 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 red brown to dark red brown, often with violet tints, 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, surface 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 on ground or on rotted wood under conifers. Associated tree species include *Picea glauca, Pinus contorta, Pinus banksiana, Thuja plicata,* and *Abies lasiocarpa*. Associated shrubs include *Alnus crispa, Arctostaphylos uva-ursi, Viburnum edule, and Vaccinium myrtilloides*. Fruiting period from July 23 in Alaska to February 7 in British Columbia. November through January collections are known only from southern coastal regions.

Geographic Distribution: Widely distributed in boreal, montane and coastal forests from Alaska, Yukon, British Columbia, Alberta, Manitoba, and Washington. Also distributed in eastern North America (Huhtinen 1982) and Europe (Harmaja 1969b). Map 3.

Taxonomic Notes: *Gyromitra ambigua* is closely related to *G. infula* (q.v.), the only other species in the genus with an autumnal fruiting pattern. Both species share a similar habitat and can be found in the same geographic regions. Macroscopically they are difficult to separate, although *G. ambigua* tends to be darker red brown with stronger violaceous tints. *G. ambigua* may be typically somewhat smaller in size and more common in northerly locations than *G. infula*. Spore size and apiculation are the most important differentiating features. Although spore size and degree of apiculation vary in other taxa, such as *G. esculenta* (q.v.), this character is considered to be consistently disjunct between *G. ambigua* and *G. infula* within and between collections, and is correlated with macroscopic morphological features.

Collections Examined: CANADA: Yukon: Watson Lake, Ziller July 30 1962, DAOM 92258; Watson Lake, Abbott (SA 191, 198, 199) August 19, 20 1989, SA; Murphy Creek, Ginns, DAOM 195475. **British Columbia:** Victoria, Vancouver Island, Melburn January 1 1957, DAOM 54649; Vancouver, Waugh August 30 1956, DAOM 57615; Vancouver, Melburn February 7 1957, DAOM 54645. **Alberta:** 145 km north of Fort McMurray, Danielson (RMD 1726) September 1 1975, ALTA; Lake Minnewanka, Banff National Park, Funk October 2 1961, DAOM 92260. **Manitoba:** Clear Lake, Bisby September 23 1933, DAOM 206808. **Quebec:** Chibougamau, Ammirati (JFA 7652), WTU; Dufesne River, Ammirati (JFA 7742) April 3 1978, WTU. **USA: Alaska:** near Fairbanks, Kempton August 23 1966, WK 859; WK 4778; Talkeetna junction, Kempton August 15 1970; WK 4724, 4725, 4726, 4727; near Copper Centre, Kempton, WK 4886; near Palmer, Kempton July 23 1970, WK 4536; Anchorage, Kempton August 30 1967, September 28 1971, WK 869, 5673; Hope road, Kempton July 27 1968, WK 875, 878; Turnagain Pass, Kempton September 30 1971, WK 5693; Beaver Lakes, Matanuska valley, Kempton August 20 1970, Homer, Kempton September 2 1967, WK 870, 872; Katmai National Monument, Kempton September 4 1971, WK 5457. **Washington:** Seattle area, van de Bogart November 15 1975. **FINLAND:** Karsten July 30 1866, H (holotype).

Exsiccata Examined: Solheim, Mycoflora Saximontanensis Exsiccata, 302, Colorado USA, Shope September 9 1937, s.n. *Helvella infula*, WSP.

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

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

Geographic Distribution: Known only from China (Korf and Zhuang 1985).

Taxonomic 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 August 12 1981, CUP CH2522 (paratype); Xiangchen County, Sichuan Province, Xing-jiang August 12 1981, CUP CH2523 (isoparatype).

Section *Melaleucoides* Abbott, *sect. 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, appearing distinctly roughened with light microscope, with SEM surface ornamentation composed of distinct isolated broadly rounded warts, biguttulate.

Taxonomic Notes: This new section is described on the basis of the ornamentation of the ascospores, which is distinctively verrucose with the light microscope. With the SEM, it is clear that the ornamentation is composed of numerous isolated rounded warts (Figure 40). The warts are evenly distributed over the spore surface and are all of comparable size. This section is also characterized by nonapiculate, biguttulate ascospores containing de Bary bubbles in a small proportion of spores at maturity.

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

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

Synonyms: *Gyromitra recurva* (Snyder) Harmaja, holotype NY, examined.

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

Figure 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, leathery. **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, 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 small proportion of mature spores.

Habitat: Solitary, gregarious, subcespitose, or scattered on ground in soil, litter, or on rotted wood in coniferous or mixed forests. Associated tree species include *Picea* sp., *Pinus ponderosa*, *Abies grandis*, *Tsuga* sp., *and Arbutus menziesii*. Fruiting period from April [illegible] in British Columbia to July 22 in Idaho. May and June collections are most common.

Geographic Distribution: Endemic to northwestern North America in montane sites in the coastal and Rocky Mountains from Alaska, British Columbia, Alberta, Washington, and Idaho. Also reported from Oregon and Montana as *Peziza melaleucoides* and *Paxina recurva* respectively by Larsen & Denison (1978). This species is newly reported for Alaska and Alberta. Known distribution extends south of the study area to Colorado (Pfister 1980). Map 6.

Taxonomic Notes: This species is morphologically distinct from all other members of the genus, and is placed in its own section on the basis of ascospore morphology. The ascospores are the smallest known in the genus, and are relatively broader than other known species. In addition, the spore ornamentation of distinct, isolated knob-like warts is unlike that of any other species in the genus. The predominantly grey ascocarp colouration is unique in the genus. The biguttulate, ellipsoidal spores are more similar to species in the section *Gyromitra* than to species in the sections *Discina* and *Caroliniana*, but the stipe of *G. melaleucoides* is less distinct than typical for species in the section *Gyromitra*. *G. melaleuca* (q.v.) is similar to this species, but appears intermediate between *G. melaleucoides* and members of section *Discina* (*e.g. G. olympiana*). Further investigations are required to clarify the relationship between *G. melaleuca* and *G. melaleucoides* (see notes under *G. melaleuca*). Pfister (1980) regarded the species 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.

Collections Examined: CANADA: British Columbia: Saltspring Island, Linton April 11, 20, 21, 1974, UVIC; Manning Provincial Park, Egger June 9 1985, DAOM 199548. **Alberta:** Watridge Lake area of Kananaskis country, Danielson (RMD 3816) June 9 1991, ALTA. **USA: Alaska:** Hope road, Kempton June 25 1967, July 5 1970, WK 1137, 4455; Turnagain Pass near Seward, Kempton July 21 1970, WK 4512. **Washington:** Stampede Pass, Paden (JWP 535) June 3 1967, UVIC; Watermain woods, Redmond, Bolen (SLB 492) April 21 1978, WTU; east of Skykomish, Cohen (Stz 6715) May 19 1952, WTU; Snoqualmie Pass area, Stuntz (Stz 13313) spring 1965, WTU; Lake Keechelus, Snyder April 15, May 5 1934, NY (type of *Gyromitra recurva*); east end of Lake Keechelus, (Is 1732) May 27 1962, WTU; west of Lake Easton, Stuntz (Stz 1230) June 21 1942, WTU; Cle Elum, (Stz 12348) May 21 1961, WTU; Cle Elum, (Stz 20342) May 13 1978, WTU; Iron Butte Road, van de Bogart (FVB 2875) July 13 1974, WTU; Road West Mt., Ammirati (JFA 9271) June 12 1986, WTU. **Idaho:** Priest River

Experimental Forest, Miller July 4 1964, WSP 54399; Snick's Bog, Paden (JWP 72) June 6 1964, WSP 56310; North-South Ski Bowl, Benewah County, Miller June 1 1964, WSP 56300; Brundage Mountain, Paden (JWP 214) & Tylutki July 22 1964, WSP 56295. **Colorado:** Tolland, Overholts (1792) June 19 1914, NY (holotype); Giants Ladder, Tolland, Overholts (1809) June 21 1914, NY; Jennie Creek, Tolland, Overholts (1874) July 7 1914, NY.

Gyromitra melaleuca (Bresadola) Donadini, 1975, Bulletin. Societé Mycologique de France 28:69-92.

Basionym: *Discina melaleuca* Bresadola, 1898, Fungi Tridenti 2: 74.

Synonyms: *Peziza melaleuca* (Bresadola) Seaver

Type Material: Holotype S.

Geographic Distribution: Known only from Europe (Donadini 1975, 1986; Benedix 1969; Ryman 1978). The North American reports by Seaver (1928, 1942) from Colorado and Washington are unconfirmed and may represent *G. melaleucoides*.

Taxonomic Notes: This species is tentatively placed in the section *Melaleucoides* on the basis of morphological similarity and non-apiculate ascospores. In addition, the spores are often biguttulate, although the guttules are often different sizes and asymmetrically placed in the spore. The surface ornamentation appears warted to coarsely rugose, although material examined was of poor quality. Ascospores of *G. melaleuca* are larger than those of *G. melaleucoides* (q.v.). *G. melaleuca* may represent a taxonomic link between sections *Melaleucoides* and *Discina*.

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

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

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

Ascocarp: sessile to distinctly 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, appearing distinctly roughened with light microscope, with SEM spore surface coarsely rugose, separate anastomosing ridges to partial or complete irregular reticulum, solitary polar apiculi nearly absent to well developed, uniguttulate to triguttulate.

Taxonomic Notes: Fries (1822) 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 section *Discina* is characterized by subsessile to distinctly stipitate species with highly ornamented spore surfaces and variously developed solitary terminal apiculi. The apiculi may be present as only slight inflations of the perispore at the apices (Figures 32, 37, 38), or may be well developed and knob-like (Figures 35, 36), pointed (Figures 31, 33), or depressed (Figure 34). The surface ornamentation develops slowly and may be incomplete on submature, although viable, spores ejected from the asci as described by Donadini (1986). At maturity the spores are prominently and irregularly rugose with anastomosis between ridges often forming an irregular close reticulum (Figures 32-35, 38). The section is emended to exclude taxa with coarsely reticulate ascospores and apical spicules (section *Caroliniana* here).

Key to species of *Gyromitra* section *Discina*

1. Ascospore apiculi depressed; 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 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 perlata (Fries) Harmaja, 1969, Karstenia 9: 11.

Basionym: *Peziza perlata* Fries, 1822, Systema Mycologicum 2: 43.

Synonyms: *Discina perlata* (Fries) Fries

Gyromitra macrospora (Bubák) Harmaja, lectotype BPI, examined; authentic material BPI, examined.

Gyromitra fluctuans (Nylander) Harmaja, fide Harmaja (1986).

Gyromitra warnei (Peck) Harmaja, holotype NYS, examined; isotype K, examined.

Type Material: unknown.

Figures 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, 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 subcespitose and numerously scattered on ground in soil, litter, or woody debris, less frequently on rotted wood or burnt areas, typically under conifers, but rarely in deciduous or mixed woods. Associated tree species include *Picea* *glauca, Picea engelmannii, Pinus contorta, Abies lasiocarpa, Pseudotsuga menziesii, Tsuga* sp., *Thuja plicata, Populus balsamifera, Populus tremuloides, Alnus* sp., and *Betula papyrifera.* Associated shrubs include *Acer glabrum, Acer circinatum, Salix* sp., *Vaccinium* sp., and *Rosa* sp. Fruiting period from March 27 in coastal Washington to July 10 in Alberta. May and June collections are typical. March and early April collections are known only from southern coastal regions.

Geographic Distribution: Widely distributed in boreal, montane, and coastal forests from Alaska, British Columbia, Alberta, Manitoba, Washington, Idaho, Oregon, and Wyoming. Also distributed in eastern North America (Seaver 1928, as *Discina ancilis*) and Europe (Breitenbach & Kränzlin 1981; Graddon 1976). Map 4.

Taxonomic Notes: This species as described here constitutes *G. perlata sensu lato.* Forms deviating in apiculus size and shape, as well as slight differences in spore size, are not considered to have taxonomic value at the specific level. Thus, species such as *G. macrospora* and *G. warnei* which are recognized by many recent authors (McKnight 1969; Ginns 1974c) are reduced to synonymy in this work. This agrees with the concept of Seaver (1928). Weber (1988) also questions the validity of taxonomic separation of these taxa since they are indistinguishable macroscopically. In addition, many collections examined in this study show considerable variation and intermediate conditions of microscopic features used to separate these taxa. *G. 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 ascospore shape, while *G. perlata* has short apiculi (1-3 μm long in McKnight 1971) from subfusoidal spores. Many collections from the study area show apiculi of 2-4 μm long and the spore shape often varies (even within an individual ascocarp) from subfusoidal to fusoidal. Apparent 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*. I have not examined types of these species but they would likely be synonymous with *G. perlata sensu lato* as described here.

Collections Examined: CANADA: British Columbia: Revelstoke, Ziller June 8 1950, DAOM 33248; Summit Trail, Mount Revelstoke National Park, Shoemaker June 23 1986, DAOM 195910; south of Spillimacheen, Parmelee May 20 1969, DAOM 128524; Kindensly Creek, Kootenay National Park, Rushton June 16 1969, UVIC; Proctor, Linton May 7 1977, UVIC; Cowichan Lake, Vancouver Island, Ziller May 15 1948, DAOM 26093; Ladysmith, Vancouver Island, Bandoni April 18 1960, UBC F3220; Victoria, Vancouver Island, Hockley April 16 1964; Bedford road woods, Vancouver Island, Melburn April 20 1957, DAOM 56641; Saturna Island, VMS April 7 1985, UBC F12435; Grouse Mountain, North Vancouver, UBC F3221; Lynne Valley, North Vancouver, Waugh April 19 1952, DAOM 29520; Point Grey, Vancouver, Barr May 11 1952, UBC F3219; Ford Lookout trail, Chilliwack, Rabas May 16 1971, UBC F3222; Lightning Lake trail, Manning Provincial Park, Egger (2034, 2039) June 9 1985, DAOM 199555, 199560; Paxton Valley, Ginns June 4 1968, DAOM 129267, K. **Alberta:** near Hondo, Kennedy May 5 1983, ALTA 8150; near Edmonton, Moss May 27 1927, DAOM 2988; Devonian Botanic Garden near Devon, Abbott (SA 27) May 1987, SA; Forest Reserve Boundary on Forestry Trunk road 40 km from Trans-Canada highway, Danielson (RMD 1420) July 10 1974, ALTA; Marmot Creek, Kananaskis Valley, Danielson (RMD 2025) July 5 1976, ALTA; Brown-Lowery Natural Area, Danielson (RMD 739, 758, 763, 764, 768, 2545) June 14, 19 1973, June 5 1977, ALTA; Fish Creek Provincial Park, Calgary, Danielson (RMD 27) June 9 1972, ALTA;

Glenmore Park, Calgary, Danielson (RMD 32) June 7 1972, ALTA; Sheep River, Danielson (RMD 1380, 1382) June 9 1974, ALTA; Blackiston Falls Trail, Waterton Lakes National Park, Abbott (SA 342, 344) May 29 1990, SA; Upper Waterton Lake trail, Waterton Lakes National Park, Abbott (SA 337, 345) May 28 1990, SA; Cypress Hills Provincial Park, Danielson (RMD 1958, 1964) June 2, 3 1976, ALTA. **Manitoba:** Victoria Beach, Lake Winnipeg, Bisby June 2, 13 1928, DAOM 156564, 156990, 206827, 206828; Lac du Bonnet, Bisby June 6 1935, DAOM 206826. **USA: Alaska:** Anchorage, Kempton June 5 1959, June 20 1973, WK 1121, 5273; Beaver Lake near Palmer, Kempton June 15 1967, WK 1135; butte area on old Palmer highway, Kempton June 29 1961, June 18 1962, June 22 1967, WK 1126, 1127, 1136; Glacier campground, Matanuska valley, Kempton June 15 1971, WK 4872. **Washington:** Glacier, Paden (JWP 696, 698) May 5 1969, UVIC; Friday Harbor, San Juan Island, Brough (Is 62) April 21 1967, WTU; San Juan Campground, Garland Spr. area, (Stz 14189) May 27 1967, WTU; Twisp, Benedict (Stz 17341) May 21 1972, WTU; Lake Wenatchee State Park, NC (Stz 6236) May 27 1951, WTU; east of Skykomish, Cohen (Stz 6710), WTU; near Greenacres, Deuton (Stz 21647) April 27 1982, WTU; Seattle, Ammirati (JFA 9897) March 27 1989, WTU; Seattle, Stuntz May 1980, WTU; Seattle, Zeller (245), WTU; Seattle, CRS March 1916, WTU; Watermain Woods, Richmond, (Stz 18237) April 28 1974, WTU; between Snoqualmie Pass and Keechelus Lake, Isaacs (Is 1678) May 12 1962, WTU; near Keechelus Lake, Stuntz (Is 1733b), WTU; Kachess Lake, Isaacs (Is 1669) May 6 1962, WTU; Cle Elum, Snyder (95) May, WTU; Olympia, Snyder (95) March, WTU; south of Olympia, McKenny (Stz 13488) March 1966, WTU; Tumwater Forestry Camp, (Stz 6215) April 30 1951, WTU; between Burnett and Wilkeson, Isaacs (Is 1659) May 7 1962, WTU; Ewartsville, Duran May 1 1983, WSP 67338; Lee Forest near Malthy, Cohen (Stz 6699) May 3 1952, WTU; Lee Forest near Malthy, Stuntz (Is 1653) April 29 1962, WTU; Lee Forest near Malthy, Brough (20) April 25 1956, WTU; Indian Creek, upper Teanaway, Stuntz (Stz 6223) May 13 1951, WTU; divide between West and Middle Fork, Teanaway River, van de Bogart May 10 1980, WTU; lower Jack Creek, Teanaway, van de Bogart May 10 1980, WTU; Teanaway, Dilly April 30 1978, WTU; Teanaway, (Stz 16650) June 20 1971, WTU; Fish Lake, April 19 1981, WTU; West Mountain road, Ammirati (JFA 9270) June 12 1986, WTU; Novelty Hill road, White (Stz 20313) April 7 1978, WTU; unknown, Volz (Stz 14751) June 1968, WTU; unknown, Puget Sound Mycological Society (Stz 15447) May 11 1969, WTU; unknown, (Stz 17875) May 1973, WTU. **Idaho:** Sagle, van de Bogart (FVB 3523) June 1975, WTU; Thatuna Ridge, Latah County, Hisil April 29 1964, WSP 56317; Thatuna Ridge, Latah County, Paden May 4 1964, WSP 56311. **Oregon:** Crater Lake National Park, Cooke June 28 1972, MU F26575. **Wyoming:** Teton County, Mcknight (10273) June 12 1967, DAOM 146504. **New York:** Oneida, Warne 1874, NYS (holotype of *G. warnei*), K (isotype). **CZECHOSLOVAKIA:** Bohemia, Tábor, Búbak April 29 1904, BPI (lectotype of *G. macrospora*); Bohemia, Tábor, Búbak April 23 1905, BPI.

Exsiccata Examined: Solheim, Mycoflora Saximontanensis Exsiccata, 1539, Medicine Bow National Forest, Wyoming, USA, Solheim June 25 1970, s.n. *Discina ancilis.*

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

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

Synonyms: *Discina leucoxantha* var. *fulvescens* Rea, holotype BPI, examined.
Gyromitra larryi (McKnight) Harmaja, holotype BPI, examined.
Discina convoluta Seaver, fide McKnight 1969.

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

Figure 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, 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 substrate, 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 reticulum, apiculi prominent, 1.5-2.8 µm long, typically with depressed 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 ground in soil, litter, or woody debris in coniferous woods. Associated tree species include *Abies lasiocarpa*, *Picea glauca*, *Pinus contorta*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Populus balsamifera*. Associated shrubs include *Alnus crispa*, *Acer glabrum* and *Berberis repens*. Fruiting period from May 10 to June 8 in British Columbia.

Geographic Distribution: Rarely encountered in montane forests from British Columbia and Alberta. This species is newly reported for Alberta and British Columbia. This species is reported from Idaho and Oregon (Larsen & Denison 1978), and is also distributed in eastern North America (Ginns 1974d; Seaver 1921) and Europe (Breitenbach & Kränzlin 1983; Ryman 1979). Map 5.

Taxonomic Notes: This species is easily distinguished from others in the section on the basis of the unique depressed ascospore apiculus, although spores of *G. gigas* (q.v.) are very rarely depressed. Spore ornamentation clearly places the species in this section along with *G. perlata* (q.v.), *G. gigas*, and *G. olympiana* (q.v.). Due to similarities in ascocarp colouration, spore ornamentation and apiculation, and the typical development of a short stipe, *G. leucoxantha* may be most closely related to *G. gigas*, although the species are easily recognized and considerably isolated taxonomically.

The variety *fulvescens* described by Rea (1928) for darker orange brown specimens (rather than the typical bright yellow to yellow brown hymenium colouration originally described) seems to have no other correlative features. Fresh specimens collected in southern Alberta exhibited orange brown hymenia, but since ascocarp colouration is variable in other taxa, such as *G. gigas* and *G. olympiana*, there is little support for maintaining this taxon above a form level.

G. larryi was differentiated from *G. leucoxantha* on the basis of less pronounced spore ornamentation and small depressed apiculi (McKnight & Batra 1974). After examination of the holotype, I would conclude that the specimens represent submature individuals of *G. leucoxantha*, and therefore consider *G. larryi* a synonym. Most asci in the specimens 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 1986) and could have been collected for SEM examination using the methods employed by McKnight & Batra (1974). The bright red brown colouration of the dried hymenium typical of *G. leucoxantha* is also present in the type of *G. larryi*.

Collections Examined: CANADA: British Columbia: Giant Cedars, Mount Revelstoke National Park, Egger (1026) June 8 1985, DAOM 199539; Kootenay Lake near Proctor, Linton May 10 1978, UVIC. **Alberta:** Crandell Lake, Waterton Lakes National Park, Abbott (SA 320) May 27 1990, SA; Upper Waterton Lake trail, Waterton Lakes National Park, Abbott (SA 336) May 28 1990, SA. **USA: Utah:** west portal of Duchesne Tunnel, Summit County, McKnight (KHM 11777) May 29 1970, BPI (holotype of *G. larryi*). **UNITED KINGDOM:** near Perth, Scotland, Menzies May 12 1924, BPI (holotype of *G. leucoxantha* var. *fulvescens*). **ITALY:** Bresadola, S (holotype), K (isotype).

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

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

Synonyms: *Discina olympiana* var. *diluta* McKnight, type BPI, examined.

Gyromitra apiculatula (McKnight) Harmaja, holotype BPI, examined.

Type Material: Holotype MICH (unavailable for examination).

Figure 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 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:** sessile to subsessile, 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 ground in soil or duff in coniferous forests or mixed woods, frequently near melting snow. Associated tree species include *Abies lasiocarpa, Pinus contorta, Picea glauca, Pseudotsuga menziesii, Populus balsamifera, Populus tremuloides*. Associated shrub *Alnus crispa*. Fruiting period from May 17 in Oregon to June 24 in Wyoming.

Geographic Distribution: Infrequently encountered in montane regions from British Columbia, Alberta, Washington, Oregon, and Wyoming. This species is newly reported for British Columbia and Alberta. Also known from eastern North America (McKnight 1969). The taxonomic identity of specimens reported as *G. apiculatula* from Europe (Donadini 1986) is not known. Map 3.

Taxonomic Notes: This species is characterized by the subsessile yellow brown to brown ascocarp, and non-apiculate to indistinctly apiculate ascospores. Spore ornamentation and apiculation, ascocarp colouration, and habitat suggest an affinity with *G. gigas* (q.v.), although the two species are taxonomically isolated from one another and are unlikely to be confused.

McKnight (1969) relies on the character of branching paraphyses, which are unique in the genus, to separate this species from *G. apiculatula*. However, this feature is highly variable, both within and between collections. Irregular or branched paraphyses are often restricted to isolated regions on individual ascocarps. It, therefore, seems likely that these unusual paraphyses may be lacking in some collections, or are unobserved since a fruiting body cannot be examined in entirety. Also, McKnight (1969) erected the variety *diluta* which he described as having unbranched paraphyses. Apically branched paraphyses were very rarely observed in *G. ambigua* (q.v.) during this investigation. Furthermore, other features that were correlated with paraphysis morphology, including size and colouration of the ascocarp (McKnight 1969), do not correlate in my investigations. The tremendous variation in size of ascospores seen within and between collections in this study greatly exceeds the subtle differences as listed between *G. olympiana* and *G. apiculatula* by McKnignt (1969).

Collections Examined: CANADA: British Columbia: Illicilwaet River, Glacier National Park, Abbott June 9 1988, ALTA 8442; Lightning Lakes trail, Manning Provincial Park, Egger (2022) June 9 1985, DAOM 199544. **Alberta:** Watridge Lake area, Kananaskis country, Danielson (RMD 3815) June 9 1991, ALTA; Lineham Creek area, Waterton Lakes National Park, Abbott (SA 319) May 26 1990, SA; Rowe Lake trail, Waterton Lakes National Park, Abbott (SA 325, 326, 329, 331) May 27 1990, SA; Bauerman Creek trail, Waterton Lakes National Park, Abbott (SA 334) May 28 1990, SA. **USA: Washington:** Cascade Christian Camp, Ammirati (JFA 9297), WTU; Stampede Pass, Dassow (Stz 16007) June 1 1970, WTU. **Oregon:** Hood River County, Sieger May 17 1986, WTU. **Wyoming:** west of Teton Pass, Teton County, McKnight (KHM 10340) June 24 1967, BPI (type of *G. olympiana* var. *diluta*). **Utah:** north of Aspen Grove, Utah County, McKnight (KHM F5477) June 5 1962, BPI (holotype of *G. apiculatula*).

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

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

Synonyms: *Gyromitra montana* Harmaja, holotype H, examined; isotypes BPI, K, examined.

Type Material: unknown.

Figures 15, 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, 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 ground in litter and woody debris in coniferous or mixed woods, often near melting snow. Associated tree species include *Picea glauca, Pinus contorta, Abies lasiocarpa, Abies grandis, Pseudotsuga menziesii, Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera, Alnus* sp., and *Acer* sp. Associated shrubs include *Betula pumila* and *Salix* sp. Fruiting period from April 3 in Washington to July 13 in Alaska. June collections are most common.

Geographic Distribution: Widely distributed in boreal, montane and coastal regions from Alaska, Northwest Territories, British Columbia, Alberta, Washington, Idaho, Oregon, and Wyoming. Also distributed in eastern North America (Weber 1988 as *G. korfii* and *G. montana*; Ginns 1975 as *Discina korfii*), Europe (Dennis 1978; Breitenbach & Kränzlin 1983), and Asia (Imai 1954, as *Neogyromitra gigas*). Map 5.

Taxonomic Notes: The concept and limitations of this species have been much confused in the literature since its inception in 1834 by Krombholz, in part due to the somewhat inadequate original description, particularly the microscopic observations. I choose here to accept the concept of the species as interpreted by Svrcek & Moravec (1972) and Harmaja (1973), although I would recognize a broader species concept than the latter author. Two closely related species have been described recently (*G. montana* Harmaja 1973, *Discina korfii* Raitviir 1970), but are considered conspecific in this work.

G. korfii was erected for North American species having prominently apiculate, fusoidal ascospores which are slightly more slender and shorter than known from European specimens (Harmaja 1973). Spores of *G. korfii* are described with a slightly more delicate reticulate ornamentation of the perispore and paraphyses expanded more abruptly to 13 µm diam. My investigations on North American material do not find paraphyses to exceed 11 µm diam., and are no more distinctly capitate than the European material examined. Scanning electron microscopy of the spores shows considerable variability from finely rugose to coarsely rugose or reticulate in both North American and European material. This supports the observations of Donadini (1986) that finely ornamented spores are often ejected from submature ascocarps. The same variation in the development of sporal ornamentation is also observed in *G. perlata* and *G. olympiana*. The differences in spore size are so slight that this feature cannot be used with any degree of certainty to distinguish the two taxa. It seems apparent that these two species should be considered conspecific, even if subtle differences can be correlated by a more comprehensive comparison between European and North American material.

G. montana poses somewhat more of a problem. The taxon was originally recognized by McKnight (1971, as *G. gigas*) and was later renamed by Harmaja (1973) after a reevaluation of the original concepts of the names *G. gigas* and *G. fastigiata*. It differs primarily from *G. gigas sensu stricto* in its "slightly more ellipsoid, less fusoidal spores with somewhat broader ends, the inconstancy of the spore apiculi, the variable and often irregular shape and smaller size of the latter when discernable, the slightly more delicate ornamentation of the perispore, the thicker tips of the paraphyses which may even be capitate and attain a breadth of 13 µm, the earlier fruiting time often near melting snow, and the different distribution in the mountains of western North America and Austria in

Europe" (Harmaja 1973). The size of the paraphyses does not differ from those found in *G. korfii* (Harmaja 1973), which is clearly has a spore morphology closer to *G. gigas* of Europe than to *G. montana*. The more delicate perispore ornamentation is rejected as a character of taxonomic value since coarsely ornamented spores from collections otherwise typical of *G. montana* have been observed (Figure 38), and the variability of the ornamentation of other related species as discussed by Donadini (1986) and by this author above (compare Figures 35-38). Ascospore shape and apiculation are perhaps the most easily recognized characters on which to separate the taxa, but the features exhibit a high degree of overlap. In most collections typical of *G. montana*, including the type, some spores seen are subfusoidal and distinctly apiculate. In addition, some collections examined from within 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. It, therefore, seems reasonable to accept these taxa as conspecific with a rather broad range of ascospore morphology. If further evidence lends support to a taxonomic separation of these forms, it is best accommodated at the varietal level.

Collections Examined: CANADA: Northwest Territories: Hay River, Green July 1 1986, UVIC. **British Columbia:** Illicilwaet River, Glacier National Park, Abbott June 9 1988, ALTA 8443; near Bolean Lake, Falkland, Ziller June 8 1966, DAOM 116828; Cook Creek north of Qualicum, Vancouver Island, Lisson May 5 1972, UVIC; Honeymoon Bay south of Cowichan Lake, Vancouver Island, Melburn April 22 1967, DAOM 124683; Manning Provincial Park, Flegel June 20 1968, UBC F1327, F1330, DAOM 176039. **Alberta:** Burnt Timber Creek on Forestry Trunk road, Danielson (RMD 1423) July 10 1974, ALTA; Sheep River, Danielson (RMD 1385) June 9 1974, ALTA; Cypress Hills Provincial Park, Currah May 6 1987, ALTA 8324; Cypress Hill Provincial Park, Danielson (RMD 1944) June 1 1976, ALTA. **Ontario:** south lookout trail, Algonquin Provincial Park, Ammirati (JFA 8368) May 16 1979, WTU. **USA; Alaska:** Thunderbird Falls trail north of Anchorage, Kempton May 22, June 8, 15 1961, June 8, 15 1966, WK 1590, 1591, 1593, 1600, 1602, 1603; Anchorage, Kempton May 29 1960, June 5 1961, June 22, 28, July 6 1972, May 29 1990, WK 1597, 1592, 5798, 5799, 6740; Indian, south of Anchorage, Kempton May 16 1960, WK 1598; south of Bird Flats, Kempton May 22 1967, WK 1607; north of Palmer, Kempton July 13 1971, WK 5041; Finger Lake near Palmer, Kempton June 2 1970, June 12 1973, WK 4391, 5265; Resurrection Pass trail, Kenai Peninsula, Kempton June 3, 9 1973, WK 5264, 5266; Lower Russian Lake trail, Kenai Peninsula, Kempton June 16 1973, WK 5268. **Washington:** Everett, Clark April 1950, WSP CS25643; Lake Wenatchee State Park, (Stz 13569) May 22 1966, WTU; Skykomish, Wells (Stz 17345) May 11 1972, WTU; Skykomish, Koch April 3 1947, WSP 23882; below Keechelus Lake, Brough (21) May 5 1956, WTU; Liberty, Retnam (Stz 1885) May 4 1946, WTU; Tacoma, Griggs May 22 1933, WTU; Tumwater Forestry camp, (Stz 14177) May 21 1967, WTU; Teal Spring, Umatilla National Forest, Garfield County, Shaw June 5 1948, WSP CS25657; Teanaway, Dilly (Stz 18286) May 5 1974, WTU; Stampede Pass, (Stz 13180) July 1964, WTU; White Chuck River campground, Maguire, WTU; unknown, (Stz 1211, 1215), WTU; unknown, Quinby (22F), WTU. **Idaho:** Hayden Lake area, Chariton May 10 1989, WTU; east of Viola, Damsteegt May 27 1959, WSP 49134; east of Viola, Shaw May 21 1948, WSP CS17387; west end of Thatuna Ridge, Latah County, Cooke May 16 1947, WSP 24508; Goose Lake, New Meadows, Jeanne & Smith July 3 1962, DAOM 191998; French Creek Summit near McCall, Miller July 12 1964, WSP 54594; Brundage Reservoir, Miller June 20 1964, WSP 54304. **Oregon:** Ashland Mountain near

Portland, Isaacs (Is 1777) June 10 1962, WTU; east of MacDougall Camp, Umatilla County, Cooke May 16 1947, June 17 1948, WSP 24508, 19870; south of Spout Springs, Umatilla National Forest, Blue Mountains, Union County, Cooke June 17 1948, WSP 19872; Horseshoe Meadows, Blue Mountains, Wallowa County, Cooke June 10 1949, WSP AS31819. **Wyoming:** west side of Teton Pass, Teton County, McKnight (KHM 10351) June 24 1967, BPI, K (isotypes of *G. montana*); Medicine Bow Mountains, Carbon County, Solheim & Cronin July 3 1950, DAOM 114944. **North Carolina:** north of Greensboro, Whetzel May 4 1940, CUP 28997 (paratype of *G. korfii*). **SWEDEN:** Upland, Bösslinge Skog, south of Börje near Uppsala, Lundell May 15 1945, K. **FINLAND:** Varsinais-Suomi, Lohja rural commune, Harmaja June 6 1972, H. **UNKNOWN:** Wynne March 1874, Herb. Berkeley, K.

Section *Caroliniana* Abbott, *sect. nov.*

Apothecia subsessilia vel stipitata, convexus vel irregulariter cupulatum, hymenium rugosum vel convolutum; ascosporae ellipsoideae vel subfusoideae, uniguttulatae vel triguttulatae, reticulatae, utroque apice spinulosae.

Type Species: *Gyromitra caroliniana* (Bosc : Fries) Fries, 1871, Öfvers. Kongl. Vet.-Akad. Förhandl. 2: 173-174.

Ascocarp: subsessile to distinctly stipitate, cupulate, discoid, convex, or irregularly lobed, hymenium orange brown to red brown, rugose. **Ascospores:** ellipsoidal to subfusoidal, 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, uniguttulate to triguttulate.

Taxonomic Notes: Species of this section are characterized by spores which, at maturity, are covered with a coarse, regular, widely spaced reticulum, and the apical regions are ornamented with multiple blunt spines which are formed as projections continuous with the reticulum (Figure 39). This is in contrast to the inflated solitary polar apiculi of species in the section *Discina*. The spore ornamentation develops slowly as in section *Discina* and nearly smooth submature spores may be discharged from the asci (pers. obs.; see also Donadini 1986). Ascospores are often uniguttulate, but the presence of one or two smaller apical guttules is not uncommon. Ascocarp morphology and colouration is also similar to species in the section *Discina*, and these features suggest taxonomic affinity between sections *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* clearly represents *G. fastigiata* as recognized in this work in agreement with the concepts of Svrcek & Moravec (1972), Harmaja (1973), and Weber (1988). Harmaja (1976b) places *Fastigiella* in synonymy with *Gyromitra sensu lato*.

Gyromitra caroliniana (Bosc : Fries) Fries, 1871, Öfvers. Kongl. Vet.-Akad. Förhandl. 2 : 173-174.

Basionym: *Morchella caroliniana* Bosc : Fries, 1822, Systema Mycologicum 2: 12. based on *Morchella caroliniana* Bosc, 181 1, Gesellschaft Naturforchender Freunde Berlin. Sitzungsberichte 5: 86.

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

Geographic Distribution: This species is distributed in southeastern North America (McKnight 1973; Smith & Weber 1980). *G. caroliniana* is reported by Larsen & Denison (1978) from British Columbia, Washington, and Oregon, but all specimens from UBC and WTU examined in this study are assigned to *G. gigas* here. Reports from Europe are unsubstantiated and have arisen due to confusion with *G. fastigiata* and *G. gigas*.

Taxonomic Notes: The species concept of *G. caroliniana* has been the source of much confusion, but the concept accepted by this author is based on the neotype selected by McKnight (1973), which I support as corresponding to the original concept described by Bosc (181 1) and Fries (1822).

Collections Examined: USA: Indiana: Greencastle, Banker (1318) April 28 1909, NY. **Virginia:** Lorton, Bland April 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, Oesterreich und der Schweiz, 2nd ed. 1: 1194.

Basionym: *Elvela fastigiata* Krombholz, 1834, Naturgetreue Abbildungen und Beschreibungen der essbaren, shädlichen und verdachttigen Schwämme 3: 28.

Synonyms: *Gyromitra brunnea* Underwood, lectotype NY, examined; authentic material, NY, examined.

Elvela underwoodii Seaver, fide McKnight (1973).

Geographic Distribution: This species is known from eastern and southern North America (McKnight 1973, as *G. brunnea*; Smith & Weber 1980; Weber 1988) and Europe (Svrcek & Moravec 1972; Ryman 1978; Krieglsteiner 1981; Kotlaba & Pouzar 1974). *G. fastigiata* reported from Alberta by Larsen & Denison (1978) follows nomenclature of Mcknight (1971) and is synonymized with *G. gigas* (q.v.) in this work.

Taxonomic Notes: The species concept for this taxon has been variously interpreted by recent authors (McKnight 1971; Svrcek & 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, I would agree with the concept as outlined by Svrcek & Moravec (1972) and followed by Harmaja (1973) and Weber (1988). An effort should be made to find authentic material or fresh collections from the type locality to serve as neotype and thus confirm the concept of the taxon.

Collections Examined: CANADA: Ontario: Halton Forest near Campbellville, Thompson (JFA 8363) May 9 1978, WTU. **USA: Iowa:** Iowa City, Kennedy April 26 1955, ALTA 668, 669, 670. **Indiana:** Greencastle, Underwood May 1892, 1893, 1894, NY (Lectotype of *Gyromitra brunnea*); Greencastle, Banker (3832) April 21 191 1, NY; near Fern, Banker (1344) March 4, 8 1910, NY. **Ohio:** Red Bank near Cincinnati, Lloyd April 21 1895, NY.

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

Basionym: *Discina parma* 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.

Figure 39.

Geographic Distribution: *G. parma* is distributed only in central Europe (Breitenbach & Maas Geesteranus 1973; Breitenbach & Kränzlin 1983; Bregazzi 1978; Hocevar 1982).

Taxonomic Notes: This species is separated from the other species of the section discussed here by its subsessile, irregularly cupulate, apothecia. The apical spicules are more highly developed in this species than any other in the section (Figure 39).

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

Rhizina Fries : Fries, 1822, Systema Mycologicum 2: 32.

Type Species: *Rhizina undulata* Fries, 1822, Systema Mycologicum 2: 33. Monotypic genus.

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 rhizoids projecting to substrate, 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 surface rugose, apiculate, with solitary pointed polar apiculi, with SEM apiculi twisted-striate (Figures 43, 44), typically biguttulate, sometimes with two smaller polar guttules in addition to two central guttules, de Bary bubbles present in a small proportion of mature spores (Figure 26), cyanophilic perispore-periplasm complex present at maturity, excipulum of *textura intricata* throughout at maturity.

Rhizina undulata Fries: Fries, 1822, Systema Mycologicum 2: 33.

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

Synonyms: *Rhizina inflata* (Schaeffer) Karsten, fide Eckblad (1968).
Rhizina zonata Berkeley, holotype K, examined.

Type Material: unknown.

Figures 22, 26, 43, 44.

Apothecium: 14-86 mm diam., discoid to reflexed, margin inrolled initially, expanded to reflexed at maturity, sometimes fused with adjacent apothecia, hymenium medium to dark red brown 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 to pallid brown rhizoid-like projections extending to substrate 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, rough, with SEM spore surface rugose, distinctly apiculate, apiculi pointed, appearing twisted with SEM, biguttulate to tetraguttulate.

Habitat: Solitary to gregarious or numerously scattered on ground in duff or woody debris, often in recently burned areas under conifers. Associated tree species include *Pseudotsuga menziesii, Tsuga heterophylla, Picea* sp., and *Pinus* sp. Fruiting period from March (exact date unknown) in Washington to November 21 in British Columbia.

Geographic distribution: Widely distributed, common west of the Rocky Mountains from Alaska, Northwest Territories, British Columbia, Alberta, Manitoba, Washington, and Idaho. A detailed map of the distribution in British Columbia is provided in Ginns (1974a). Reported from Montana (Seaver 1928) and Oregon (Larsen & Denison 1978). Also known from eastern North America (Ginns 1974b), Europe (Breitenbach & Kränzlin 1981), and Asia (Korf & Zhuang). Map 7.

Taxonomic Notes: This species is easily distinguished from species in all other genera by its indeterminate growth form, excipular rhizoid-like projections, hymenial setae, and ascospore morphology. It is similar to species of *Gyromitra* section *Discina*, and to *G. perlata* (q.v.) in particular on the basis of the discoid to reflexed apothecium, hymenium colouration, and fusoidal, rugose ascospores with large pointed polar apiculi. The setae are unusual in the family, but the setoid paraphyses of *Helvella crassitunicata* (q.v.) are morphologically similar.

Collections Examined: CANADA: Northwest Territories: South Rutledge Lake, Mackenzie District, Scotter June 30 1962, DAOM 91443. **British Columbia:** Lois Lake, Powell River, Ginns November 21 1967, DAOM 129015; Lynne Valley Park, North Vancouver, Kroeger November 18 1981, UBC F10245; Lynne Canyon Park, North Vancouver, Vancouver Natural History Society September 30 1961, UBC F3490; Stanley Park, Vancouver, Cummings July 3 1961, UBC F3494; Stanley Park, Vancouver, Kroeger September 16 1985, UBC F12460; Stanley Park, Vancouver, Waugh July 28 1952, DAOM 34808; UBC endowment Lands, Vancouver, Brough, Perrin, & Koske July 5 1969, July 15 1970, UBC F3491, F3492; UBC endowment Lands, Vancouver, Bandoni September 12 1969, UBC F1326; Salisbury Lake, Mission, Ginns November 6 1967, DAOM 119359; Ucluelet, Vancouver Island, Ginns & Allen November 9 1967, DAOM 126248; Port Renfrew, Vancouver Island, Ginns November 15 1967, DAOM 119357; Jordan River, Vancouver Island, Ginns November 15 1967, DAOM 129013; near Sooke, Vancouver Island, Egger October 13 1983, DAOM 195834, 199775, 199776, 199777; near Sooke, Vancouver Island, Egger October 26 1983, DAOM 199656, 199657, 199658; Brothers Creek trail, Hollyburn, Bandoni October 15 1966, UBC F3493, DAOM 129748, 175778. **Alberta:** Long Lake Provincial Park, States June 16 1967, ALTA 652. **Manitoba:** Victoria Beach, Bisby September 12 1928, DAOM 206821. **New Brunswick:** Richibucto, Cain July 31 1963, WSP 56995. **USA: Alaska:** Anchorage, Kempton September 28 1975, WK 6290; Bird Creek south of Anchorage, Kempton August 2 1967, WK 1528; Haines, Kempton September 20 1972, WK 5983. **Washington:** near Longmire, Mount Rainier National Park, Snyder September 1 1934, WTU; Barlow Pass area, Woo (Stz 16329) October 28 1978, WTU; near Gold Basin, Builder (Stz 20494) October 28 1970, WTU; Heart-o-Hills campground, Largent (1932) October 23 1960, WTU; unknown, Nelson (Stz 16601) March 1971, WTU. **Idaho:** near junction Benton Creek and Priest River, Rhoads August 11 1920, MU 4094. **UNITED**

KINGDOM: Loch Gallin, Inverness, Scotland, Reid August 29 1975, K; unknown, Herbarium Berkeley 1879, K (holotype of *Rhizina zonata*).

Exsiccata Examined: Vancouver Island Fungi, 105, Sidney, British Columbia, Canada, Macoun 1913, s.n. *Rhizina undulata* , UBC F3495.

Pseudorhizina Jachevsky, 1913, Opredelitel gribov 1: 1913.

Synonyms: *Helvellella* Imai
Ochromitra Velenovsky
Gyromitrodes Vasilkov

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 surface very finely rugose to nearly smooth, non-apiculate, with one or two oil guttules, de Bary bubbles present at maturity, tetranucleate at maturity, cyanophilic perispore-periplasm complex absent at maturity, excipulum anatomy 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 sphaerospora (Peck) Pouzar, 1961, Ceská Mykologie 15: 42.

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

Synonyms: *Gyromitra sphaerospora* (Peck) Saccardo

Type Material: unknown.

Figures 2, 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, 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 extending across half distance to margin to near marginal region, ribs continuous with those of the stipe. **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, internally 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 surface very finely rugose, uniguttulate, one de Bary bubble present in most spores at maturity.

Habitat: Solitary to gregarious or numerously scattered on very rotted deciduous (or rarely coniferous logs or woody debris on ground), in deciduous or mixed woods. Associated tree species include *Populus balsamifera, Populus tremuloides, Acer negundo, Betula papyrifera, Picea glauca,* and *Abies balsamea.* Often associated with mosses, especially feather mosses (*Ptilium crista-castrensis, Hylocomium splendens.,* and *Pleurozium schreberi*). Fruiting period from June 4 to July 6 in Alberta.

Geographic Distribution: Infrequently encountered in boreal regions in the eastern portion of the study area from Alberta and Manitoba. Known distribution in North America is extended north to Fawcett Lake, Alberta, and west to Carson Lake, Alberta. Reported from Montana by Cummins (1930, as *Helvella sphaerospora*), but no specimen in MICH could be located. Also distributed in eastern North America (Pomerleau 1980), Europe (Pouzar 1961; Huhtinen 1983), and Asia (Imai 1954, as *Helvellella sphaerospora*). Map 8.

Taxonomic Notes: This species is readily distinguished from all other members of the family on the basis of spore morphology. Globose spores are unique to this species among the epigeous taxa, and can be separated from the globose spores of the hypogeous *Hydnotrya cerebriformis* (q.v.) by the thick wall, brown pigmentation, coarse ornamentation, and larger size of the latter species. The ascospores, approximately 10 μm diam., are the smallest known in the family. *P. sphaerospora* shares many macroscopic morphological features with *P. californica* (q.v.), but can be separated with certainty by examination of spore shape. *P. sphaerospora* can additionally be separated by its habitat, occurring primarily on deciduous logs, while *P. californica* is primarily terrestrial and is associated with conifers. These two species also show a clear geographic separation with *P. californica* restricted to areas west of the continental divide in the Rocky Mountains and *P. sphaerospora* occurring east of the Rocky Mountains in North America, Europe, and Asia.

Collections Examined: CANADA: Alberta: Fawcett Lake, Abbott (SA 38) June 17 1989, SA; Shaw Lake, Abbott (SA 349, 350, 351, 352, 367) June 4, 23 1990, SA; Carson Lake, Wong & Beliveau July 6 1972, ALTA 7158; Whitemud Creek, Edmonton, Abbott June 1985, ALTA 8263. **Manitoba:** Gorge Creek trail, Riding Mountain National Park, Hammerslay June 30 1979, DAOM 182247; Victoria Beach, Bisby June 22 1935, DAOM 206813, IMI 26845; Elk Island, Lake Winnipeg, Bisby June 30 1924, DAOM 206829, 154797. **POLAND:** Biatowieza, Skirgiello May 1957, K.

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

Basionym: *Helvella californica* Phillips, 1880, Transactions Linnean Society II Botany 1: 423.

Synonyms: *Gyromitra californica* (Phillips) Raitviir

Type Material: Holotype K, examined.

Figure 13.

Apothecium: 23-135 mm diam., 13-80 mm high, irregularly convex to lobed, margin reflexed, free from stipe, hymenium medium to dark brown, 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 ground in soil, duff, or wood debris, rarely on rotted logs, in coniferous woods. Associated tree species include *Tsuga heterophylla, Thuja plicata, Pseudotsuga menziesii, Picea engelmannii,* and *Pinus* sp. Fruiting period from April 24 in British Columbia to August 6 in Idaho and interior British Columbia.

Geographic Distribution: Commonly encountered west of the continental divide in montane and coastal forests from British Columbia, Washington, Idaho, and Oregon. Known distribution is extended north to the Queen Charlotte Islands, British Columbia. This species is endemic to western North America, extending south to northern California, Colorado, and Nevada (Larsen & Denison 1979). Map 8.

Taxonomic Notes: This species is closely related to the only other member of the genus, *P. sphaerospora* (q.v.), and can be separated by the features discussed under that taxon. The ellipsoidal, biguttulate, non-apiculate ascospores are morphologically similar to those of *Gyromitra* species in the sections *Gyromitra* and *Melaleucoides*. The finely rugose spore surface as observed with SEM is also similar to that exhibited by species in *Gyromitra* section *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) June 9 1979, DAOM 172567; Mosquito Lake, Moresby Island, Queen Charlotte Islands, Ziller July 2 1952, DAOM 56711; Mount Robson Provincial Park, Wilson July 29 1971, ALTA 4553; trail to Great Glacier, Glacier National Park, Shoemaker August 1 1963, DAOM 109931; Mount Abbott near Marian Lake, Glacier National Park, Shoemaker August 6 1963, DAOM 109223; Cussom Creek, Arrow Park, Ziller July 8 1958, DAOM 62736; Meager Creek Hotsprings, Kroeger June 14 1987, UBC F12874; Mount Seymour, North Vancouver, Waugh May 27 1961, UBC F3242; Confederation Park, Vancouver, Waugh June 5 1952, DAOM 29531; west of Sooke, Vancouver Island, Ziller June 15 1971, DAOM 134985; near Sooke, Vancouver Island, Egger July 10 1982, DAOM 199830; Hastings, Macoun April 24 1889, DAOM 44702; British Columbia, Burda July 9 1983, UBC F11957. **USA: Washington:** Big Fir area near Nooksack, Mount Baker National Forest, Isaacs (Is 1790) July 13 1962, WTU; Upper Baker trail, North Cascades National Park, Williams (JWL 199) June 29 1969, WTU; Boulder Creek near Baker Lake, Leuthy (Brough 82) June 21 1957, WTU; North Fork Quinault River, Olympic National Park, Stuntz (Stz 6725), WTU; above Jackson Guard Station, Olympic National Park, A.H. Smith (13378) May 13 1939, K; Hoh River, Olympic National Forest, A.H. Smith (13172) May 7 1937, DAOM 24717, K; Hoh River, Olympic National Forest, Kveruvik (Stz 20928) May 18 1980, WTU; Mount Rainier National Park, Imshaug (488) July 21 1948, K; Carbon River, Mount Rainier National Park, Cohen (Stz 6824) July 7 1952, WTU; Round Pass, Mount Rainier National Park, Knowles (Stz 3900) August 9 1948, WTU; Mount Adams area, Rafauelli (Stz 18846) July 12 1975, WTU; Tucannon River, Garfield County, Shaw July 10 1948, WSP CS25652; White Horse, Snyder (15) May 15 1932, WTU; Meadowdale, Snyder May 10 1934, WTU; Muck Creek area, van de Bogart (FVB 1920) July 16 1973, WTU; Washington, van de Bogart (FVB 1926) June 25 1973, WTU; unknown, PSMS (Stz 21387) June 8 1981, WTU; unknown, PSMS (Stz 17982, 18407) August 1973, 1974, WTU; unknown, Mackintosh (Stz 17874) May 1973, WTU; unknown, Leuthy (Stz 20585) June 1979, WTU; unknown, (Stz 14830) July 1968, WTU; unknown, (Stz 20622) July 1979, WTU; unknown, (Stz 14513), WTU. **Idaho:** Canyon Creek, Priest River Experimental Forest, Bonner County, Slipp July 6 1941, WSP 49805; Boulder Creek, Priest River Experimental Forest, Harrison August 10 1964, DAOM 107197; Gold Creek north of Nordman, Miller July 4 1964, WSP 54388; Binarch Creek, Bonner County, Miller July 8 1964, WSP 54345; Granite Creek, Bonner County, Slipp July 4 1939, July 1 1942, WSP 49763, 49872; Station 1, Bonner County, Slipp 1942, WSP 49910; Kaniksu National Forest, Bonner County, Shaw June 17 1948, WSP CS25646; near Emida, June 23 1955, WSP 45128; east of Elk River, Clearwater County, Paden June 24 1965, WSP 56263; east of Pierce, Shaw July 9 1959, WSP 48896; north of Bear Basin, Valley County, Miller July 24 1964, WSP 54640; Brundage Reservoir, Valley County, Miller August 6 1964, WSP 54168; Sater Meadows, Valley County, Miller August 6 1964, WSP 54201; No Business Ridge, Valley County, Hawker August 1962, K; south of No Business Lookout, Valley County, Miller July 23 1964, WSP 54597. **Oregon:** Lake Creek, Grayback area, Siskiyou Mountains, Whittaker July 14 1949, WSP 25463. **California:** California, Harkness, Herbarium Cooke, K (holotype); Squaw Valley Creek, Mount Shasta, Cooke July 10 1947, WSP 20304; Lower Panther Creek Meadows, Mount Shasta, Cooke August 24 1949, WSP 25295.

Exsiccata Examined: Ellis and Everhardt, North American Fungi, 2737, British Columbia, Canada, Macoun June 28 1892, s.n. *Helvella californica*, K; University of California, California Fungi, 315, Jonesville, California, USA, Copeland July 1929, s.n. *Elvella californica*, WSP 35289; University of California, California Fungi, 317, Jonesville, California, USA, Copeland July 1929, s.n. *Elvella umbraculiformis*, WSP 35269, WTU.

Helvella Linnaeus : Fries, 1822, Systema Mycologicum 2: 13.

Type Species: *Helvella crispa* Scopoli : Fries, 1822, Systema Mycologicum 2: 14.

Synonyms: *Paxina* Kuntze
Acetabula Fuckel : Fries
Cyathipodia Boudier
Macropodia Fuckel
Leptopodia Boudier
Wynnella Boudier

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, 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 subgeneric sections of *Helvella*

1. Apothecia convex, bilobate, or irregularly lobed 2
1'. Apothecia cupulate to auriculoid 3

2. Stipe strongly ribbed, internally chambered .... *Helvella*
2'. Stipe terete to fluted, internally solid or hollow .... *Elasticae*

3. Apothecium auriculoid .... *Silvicolae*
(*H. silvicola*)
3'. Apothecium cupulate 4

4. Stipe distinctly ribbed .... *Leucomelaenae*
4'. Stipe terete to shallowly fluted 5

5. Ascospores broadly ellipsoidal, uniguttulate, smooth .... *Cupuliformae*
5'. Ascospores subfusoidal to fusoidal, uniguttulate to triguttulate,
verruculose .... *Macropodes*

Section *Helvella* *emend. nov.*

Type Species: *Helvella crispa* Scopoli : Fries, 1822, Systema Mycologicum 2: 13.

Synonyms: section *Crispae* Dissing
section *Lacunosae* Dissing

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.

Taxonomic Notes: The typical section *Helvella* is emended to include species treated in section *Lacunosae* of Dissing (1966b) and Häffner (1987). The broad concept employed here includes species with a distinct, strongly ribbed and anastomosed stipe, typically with lacunae and a chambered internal structure. The apothecium is typically 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 considered to represent a series that differ quantitatively rather than qualitatively and are not considered taxonomically significant at the sectional level (although they may show relationships between individual species within the sections)(see also discussion under taxonomic significance of macroscopic characters). The section *Helvella* as accepted here corresponds closely to that of the genus *Helvella* in its most restricted sense (*e.g.* Breitenbach & Kränzlin 1981).

Key to species of *Helvella* section *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, 1822, Systema Mycologicum 2: 14.

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

Synonyms: *Helvella leucophaea* Persoon, holotype K, examined.

Type Material: unknown.

Figures 6, 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, 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 ground in soil and litter in deciduous or mixed woods. Associated tree species include *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 include *Salix bebbiana, Salix discolor, Corylus cornuta, Alnus crispa, Prunus pensylvanica, Amelanchier alnifolia, Shepherdia canadensis, Viburnum edule, Lonicera involucrata,* and *Rosa* sp. Fruiting period from July 11 in Alberta to November 15 in Washington.

Geographic distribution: Widely distributed in boreal, coastal, and montane regions from Alaska, Yukon, Northwest Territories, British Columbia, Alberta, Manitoba, Washington, Idaho, and Oregon. This is a very common species of boreal and aspen parkland regions in the study area. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966, Häffner 1987), and Asia (Liu *et al.* 1985; Imai 1954). Map 9.

Taxonomic Notes: This 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. These species are separated on the basis of ascocarp colouration, degree of vestiture, and habitat. *H. crispa* is also superficially similar to *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. *H. crispa* is sufficiently distinct from all other species in the genus that little confusion has occurred with synonymy or annotation of herbarium specimens.

Collections Examined: CANADA: Northwest Territories: Hay River, Green August 30 1984, UVIC. **Yukon:** Dempster Highway near Dawson, Ginns August 8 1980, DAOM 195471; 3 km northeast of Mayo, Calder August 1 1949, DAOM 25986. **British Columbia:** Tetsa River Provincial Park, Abbott (SA 218, 219, 222, 226) August 22 1989, SA; Moberly Lake Provincial Park, Schalkwyk August 15 1977, DAOM 175734; Prince George, Brough (651) September 20 1968, UBC F3244; 50 km south of Quesnel, Calder, Savile & Ferguson September 4 1954, DAOM 45603; San Josef Bay, Vancouver Island, (SDLB 617) August 28 1975, WTU. **Alberta:** north of Meander River, Abbott (SA 144) August 8 1989, SA; Notikewin Provincial Park, Abbott (SA 129, 136) August 7 1989, SA; McKay River south of Fort McMurray, Dumais July 27 1968, ALTA 663; Fawcett Lake, Abbott September 3 1988, ALTA 8318, 8319, 8320; Musreau Lake, Abbott (SA 245, 249, 255, 256, 257) August 26 1989, SA; Sheep Creek north of Grande Cache, Abbott (SA 263, 264) August 26 1989, SA; Long Lake, States August 13 1967, ALTA 662; Sandy Lake, Schalkwyk July 11 1975, ALTA 7907, DAOM 175714; east of Redwater, Schalkwyk September 5 1978, ALTA 7901; William A. Switzer Provincial Park, Abbott (SA 269) August 27 1989, SA; William A. Switzer Provincial Park, Osis (SA 386) September 2 1990, SA; Forest Reserve, Edmonton, Kennedy September 15 1976, ALTA 7292; Emily Murphy Park, Edmonton, Tsuneda August 1976, ALTA 7359; Devonian Botanic Garden near Devon, Currah September 4 1977, early July 1979, August 31 1980, July 21 1982, ALTA 7534, 7957, 8268, 8275; Devonian Botanic Garden near Devon, Abbott September 3 1987, July 25 1989, ALTA 8276, SA 108; Devonian Botanic Garden near Devon, Richardson September 1 1988, ALTA 8311; 10 km south of Leduc, Abbott August 8 1981, ALTA 8283; near Cynthia, Osis & Gibson August 14 1988, ALTA 8309; near Breton, Osis & Gibson August 1, 20 1988, ALTA 8300, 8303;

Fish Lake near Nordegg, Abbott (SA 282, 375, 400) August 31, 1989, August 3, September 8 1990, SA; Muir Lake area, Bozniak & Wheelock September 14 1965, ALTA 661. **Manitoba:** Gilbert Plains, Provincial Horticulturalist September 1954, DAOM 45142; Victoria Beach, Bisby September 11, 12, 19 1926, August 8 1928, DAOM 206802, 206801, 206800; Victoria Beach, Reid September 8 1968, WIN; Pinawa, Bisby September 2 1935, DAOM 206803; Manitoba Agricultural College, Winnipeg, Bisby & Gordon August 5 1928, DAOM 154794; Winnipeg, Frankton August 28 1956, DAOM 54284. **Ontario:** Angus, Cain October 10 1954, WSP 43051. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton August 24, 1963, 1971, WK 1575, 5200; butte area north of Anchorage, Kempton August 8, 196[illegible], September 25 1982, WK 1574, 6429. **Washington:** Seward Park, Seattle, Stuntz (Brough 48) November 15 1956, WTU; Olympic Hot Springs, Olympic National Park, Smith (17192) September 22 1941, MICH; Money Creek, Litke September 1 1981, WTU 21467. **Idaho:** near Coolin, Priest Lake, Bonner County, Harrison (6355) October 6 1966, MICH; Capoose Creek, Seven Devils Mountain, Idaho County, Smith (46550) August 23 1954, MICH; Seven Devils Range, Hawker August 10 1962, K. **Oregon:** Bellview-Tolman Creek area near Ashland, Isaacs (Is 1456) November 11 1961, WTU. **Ohio:** Antioch Forest, Yellow Springs, Cooke October 20 1962, WSP 55743. **New Mexico:** east of Santa Fe, Simms September 19 1965, WSP 57198. **SWEDEN:** Uppsala Botanical Garden, Melderis September 28 1946, K. **UNITED KINGDOM:** The Staits, North Hampshire, October 23 1960, IMI 83683; unknown, Persoon, K (type of *Helvella leucophaea*).

Exsiccata Examined: Fungi Suecici, Västmanland, Sala, Sweden, Morander (1348) July 24 1948, s.n. *Helvella crispa*, WSP 31528; 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 October 1908, 1909, 1910, s.n. *Helvella crispa*, WSP 3107.

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

Type Material: Holotype MICH, examined.

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, 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 ground in soil or duff in coniferous or mixed woods. Associated tree species include *Picea glauca, Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla, Populus tremuloides, Populus balsamifera*, Associated shrubs include *Salix* sp., *Rosa* sp., *Viburnum edule, Cornus stolonifera*, and *Alnus* sp. Fruiting period from August 1 in Alberta to November 30 in coastal Washington. Collections from January to March in coastal British Columbia, Washington and Oregon and May in British Columbia are considered unusually late for this typically autumnal species. August and September collections are typical of Alaska, Alberta and

Manitoba, while October and November collections are typical of Washington, Idaho, and British Columbia.

Geographic Distribution: Widely distributed in montane, coastal, and boreal regions, but abundant only in the west from Alaska, British Columbia, Alberta, Manitoba, Washington, Idaho, and Oregon. The range of this species is significantly expanded to the east by the collections from Manitoba and to the north by collections from Alaska. Distributed only in western North America (Weber 1975) and China (Cao 1988; Liu & Cao 1988). Map 10.

Taxonomic Notes: This species is most 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 can easily be separated by the reflexed apothecium margin, even in immature fruiting bodies, and the margin fused to the stipe. *H. maculata* was originally described as having consistently mottled pigmentation of the apothecium (Weber 1975). This feature is also supported in Chinese material (Cao pers. comm.), but in fresh and dried material examined in this study, many apothecia were found to be uniform in colouration. Cao (pers. comm.) has suggested that specimens with uniform pigmentation may be referable to another taxon, but I have found no correlative features to support this view. Mottled hymenial surfaces are also infrequently encountered in other species such as *H. lacunosa*, *H. albella* (q.v.), and *H. elastica* (q.v.), and may be due in part to exposure of the hymenium at the surface. The presence of darkly pigmented regions on the white stipe is also frequently observed in *H. maculata*.

Collections Examined: CANADA: British Columbia: Brandywine Falls near Whistler, Bandoni October 27 1977, UBC F3281; Yale, Macoun May 17 1889, DAOM 44703; Sidney, Vancouver Island, Macoun 1912, UBC F3297; Mount Douglas Park, Victoria, Vancouver Island, Paden November 11 1988, UVIC; University of Victoria campus, Vancouver Island, Paden (JWP 1378) January 5 1987, UVIC; University of Victoria campus, Vancouver Island, Fogarty November 18 1988, UVIC; ravine near Houlihan Way, Gordon Head, Goodacre November 8 1976, UVIC. **Alberta:** William A. Switzer Provincial Park, Osis (SA 387) September 2 1990, SA; west end Ravine, Edmonton, Osis & Gibson August 1 1988, ALTA 8301; near Breton, Osis & Gibson August 20 1988, ALTA 8304; Fish Lake near Nordegg, Abbott (SA 380) August 3 1990, SA; Bragg Creek Provincial Park, Danielson (RMD 2343) September 18 1976, ALTA 8292; Fish Creek Provincial Park, Calgary, Danielson (RMD 359) August 20 1972, DAOM 143866; Kananaskis, Vellinga (SA 295) August 1989, SA, L. **Manitoba:** Clear Lake, Bisby September 23 1933, August 17 1935, DAOM 206812, 206808. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton August 11, 24 1963, WK 1576, 1577; butte area north of Anchorage, Kempton September 22 1965, WK 1578; mile 40 Haines cutoff road, Kempton September 20 1970, WK 4962. **Washington:** Friday Harbor, San Juan Island, Isaacs (Is 2019) November 11 1962, WTU; Friday Harbor, San Juan Island, Stuntz (Stz 8996, 11594, 12087, 15306, 15869, 17044) November 13 1954, November 1 1959, October 16 1960, November 30 1968, November 29 1969, November 26 1971, WTU; Friday Harbor, San Juan Island, Williams (JWL 564, 1307) November 9 1969, November 7 1971, WTU; Friday Harbor, San Juan Island, van de Bogart (FVB 3864) November 1976, WTU; San Juan Island, Bandoni November 20 1966, UBC F3286; Mutiny Bay, Island County, van de Bogart (FVB 3362) March 2 1975, WTU; east of Duvall, van de Bogart (Stz 14460) November 5 1967, WTU; Olympia, Snyder October 8 1933, WTU; unknown, van de Bogart (FVB 3687) November 15 1975; unknown, (Stz 12121, 13810, 15221) October 28 1966, November 10 1968, WTU. **Idaho:** Hoodoo Mountain, Bonner County, Smith (NJS 2124) October 5 1968, MICH (holotype); Jerome Creek, Latah County, Paden & Tylutki October 11 1964, WSP 56274. **Oregon:** near Gold Hill, (Stz 10929) March 27 1959, WTU.

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

Type Material: None known, fide Dissing (1966b).

Geographic Distribution: Known distribution restricted to Europe (Dissing 1966).

Taxonomic Notes: This species is closely related to *H. maculata* (q.v.), with which it shares ascocarp colouration, but differs in its finely pubescent excipular surface and habitat. Vernal and autumnal collections are known for both species. *H. fusca* is the most closely related species of the section *Helvella* (*sensu stricto*) to species such as *H. lacunosa* (q.v.) in the the section *Lacunosae* of Dissing (1966b). The pubescence is very fine and the apothecial margin is less strongly inrolled than other species of the section *Helvella* (*sensu stricto*). This species provides a link between the two sections proposed by Dissing (1966b). This species is reported from Alaska and Oregon (Kempton & Wells 1970; Larsen & Denison 1978), but no specimens referable to this taxon were encountered during this investigation and the reports are likely based on *H. maculata*.

Collections Examined: ITALY: Al Deserto, Bresadola May 21 1898, S; Bei Trient, Bresadola June 1898, S; Prope Trento, Bresadola May 18 1903, S; Gocciadora, Bresadola October 1901, S.

Helvella lacunosa Afzelius : Fries, 1822, Systema Mycologicum 2: 15.

Basionym: *Helvella lacunosa* Afzelius, 1783, Kungliga Vetenskaps-Akademiens. Nya Handlingar 4: 303.

Synonyms: *Helvella mitra* Persoon, type K, examined.
Helvella subcostata Cooke, holotype K, examined.
Helvella sulcata Afzelius: Fries, fide Dissing (1966b).

Type Material: unknown.

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 very rarely free, hymenium black to dark grey or dark brown, 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 substrate, 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious, subcespitose, or scattered on ground in soil or litter, rarely on rotted wood or burnt wood debris, in coniferous or mixed woods. Associated tree species include *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 include *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 period from June (date unknown) in Manitoba to April 15 in coastal southern British Columbia. November through April fruitings are known only from southern portions of the study area in British Columbia, Washington, Idaho, and Oregon. June to August collections are known only from Alaska, Yukon, Northwest Territories, British Columbia, Alberta, and Manitoba.

Geographic Distribution: Widely distributed in boreal, montane, coastal, and arctic regions from Alaska, Yukon, Northwest Territories, British Columbia, Alberta, Manitoba, Washington, Idaho, and Oregon. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b), and Asia (Liu *et al.* 1985; Imai 1954; Korf & Zhuang 1991). Map 11.

Taxonomic Notes: The species as circumscribed here is *H. lacunosa sensu lato* (*sensu* Dissing 1966b, Abbott & Currah 1988, Calonge & Arroyo 1990) and includes a wide variety of morphological forms. No correlation between features was found to warrant the separation of distinct taxa, such as *H. sulcata sensu* Weber 1972, at the specific or varietal level. The broad concept of this taxon eliminates confusion and sets the species distinctly apart from all others. The species is characterized by the darkly pigmented ascocarp, reflexed apothecial margin, and glabrous excipular surface.

Closely related species include *H. lactea* (q.v.) which is separated by ascocarp colouration, *H. palustris* (q.v.), and *H. phlebophora* Patouillard & Doass. which differs in smaller ascocarp size, convex apothecial shape with free reflexed margin, and solid stipe construction. Häffner (1987, 1991) suggests that *H. phlebophora, H. palustris,* and *H. lactea* may be best treated as varieties of *H. lacunosa*. I have examined no specimens referable to *H. phlebophora*, but occasional ascocarps approaching the overall morphology (as described in Dissing 1966b; Breitenbach & Kränzlin 1984 edition only) have been seen in collections with typical specimens of *H. lacunosa* (*e.g.* ALTA 8314). *H. palustris* was synonymized with *H. lacunosa* by Dissing (1966b), but has been considered a valid species by Weber (1972) and Harmaja (1977b). After examination of the holotype and collections from Michigan and Norway, *H. palustris* is accepted as distinct, and is separated from *H. lacunosa* by the small apothecium, often with free margin, slender stipe with few or no lacunae and little anastomosis between ribs. Many collections of *H. palustris* are from bogs or stream banks and associated with bryophyte

Collections Examined: CANADA: Yukon: Watson Lake, Abbott (SA 179, 180, 185, 192, 193, 194) August 14, 20 1989, SA. **NorthWest Territories:** Striae Hill, Axel Heiberg Island, Beschel August 10 1962, DAOM 91441; Baker Lake, Ohenoja August 1962, DAOM 155310; Hay River, Green September 5 1982, UVIC. **British Columbia:** Muncho Lake Provincial Park, Abbott (SA 211, 212, 213) August 21 1989, SA; Tetsa River Provincial Park, Abbott (SA 220, 227, 230) August 22 1989, SA; near Valemount, Wohlebbe September 20 1987, ALTA 8366; Mahood Lake, Person October 10 1977, UBC F3282; 10 km north of Clearwater, Goward September 12 1982, DAOM 191776; Shuswap Lake near Scotch Creek, Goward October 2 1982, DAOM 191777; Revelstoke, Funk October 10 1962, DAOM 14578; Brandywine Falls near Whistler, Bandoni October 21 1977, UBC F3281; Brandywine Falls Provincial Park, Mackinnon October 4 1980, UBC F587; Cheekye, Bandoni September 26, UBC F3274; Proctor Linton October 18 1977, UVIC; Cottonwood Lake near Nelson, Harrison (6030A) July 6 1966, MICH; Lions Bay, Perrin October 8 1968, UBC F3278; Lynne Valley Park, North Vancouver, Kroeger November 18 1981; UBC F10244; Lynne Valley Park, North Vancouver, Bandoni October 4 1959, UBC F3276; Lynne Canyon, Vancouver, Pantidou October 3 1962, DAOM 92265; UBC endowment lands, Vancouver, Waugh October 29 1958, UBC F3272; UBC endowment lands, Vancouver, Brough (661) November 24 1972, UBC F1345, F3279; UBC endowment lands, Bandoni December 8 1962, UBC F3277; UBC campus, Brough (626) November 3 1967, UBC F3273; UBC campus, Redhead November 18 1969, UBC F1344; UBC campus, Bandoni October 27 1962, April 15 1988, DAOM 91102, 199922; Little Qualicum Falls Provincial Park, Vancouver Island, Lee October 30 1979, UBC M047; Long Beach, Pacific Rim National Park, Brigham November 8 1980, Wood November 25 1974, UVIC; Spectacle Lake, Vancouver Island, Pantidou October 19 1962, DAOM 92263; Robert's Bay, Vancouver Island, Macoun October 21 1913, UBC F3292; Francis Park near Victoria, Vancouver Island, Egger (857) December 27 1981, DAOM 199857; Mount Douglas Park, Victoria, Vancouver Island, Egger September 29 1983, DAOM 199768; Crescent Beach, Krajina October 10 1970, UBC F3280; Saltspring Island, Paden October 13 1969, UVIC; Saturna Island, Pillsbury November 13 1960, UBC F3275; Cortez Island, Ring November 11 1986, UVIC. **Alberta:** Fawcett Lake, Abbott September 3 1988, ALTA 8314, 8315; Iosegun Lake, Abbott (SA 111, 112, 118) August 4, 5 1989, SA; Musreau Lake, Abbott (SA 248) August 26 1989, SA; William A. Switzer Provincial Park, Abbott (SA 267, 271) August 27 1989, SA; William A. Switzer Provincial Park, Osis (SA 388) September 2 1990, SA; Forest Reserve, Edmonton, Kennedy September 15 1976, ALTA 7291; Devonian Botanic Garden near Devon, Abbott August 24 1987, ALTA 8271; Athabasca River valley 3 km west of Sunwapta Falls, Jasper National Park, Abbott (SA 372) August 2 1990, SA. **Manitoba:** Victoria Beach, Bisby July 29 1928, DAOM 206811; Indian Bay, Shoal Lake, Tan June 1966, WIN. **Ontario:** Angus, Cain October 10 1954, WSP 43248. **USA: Alaska:** Eagle summit 175 km north of Fairbanks, Kempton August 19 1971, WK 5348; Fairbanks, Kempton August 7 1970, WK 4619; Nome on Seward Peninsula, Kempton August 25 1970, WK 4793; Nancy Lake, Susitna valley, Kempton August 15 1968, September 7 1985, WK 1570, 6470; Eklutna Lake north of Anchorage, Kempton August 24 1971, WK 5189; Anchorage, Kempton August 30 1966, August 31 1971, September 5 1986, WK 1565, 5395, 6508; Glacier Bay National Monument, Cooke September 7, 8, 10 1979, August 31, September 5, 9 1981, WSP 65708, 64400, 64439, 64797, 64854, 67209, 66865, 66866, DAOM 176194, 176213, MU F34857, F36149; near Haines, Kempton September 20 1970, September 16 1971, WK 4953, 5596; near Juneau, Kempton September 13 1967. **Washington:** Nooksack Falls, Mount Baker area, Whatcom County, Symons November 11 1965, UBC F3283; San Juan Island, Waugh November 19 1966, UBC F3284; Friday Harbor, San Juan Island, (Stz 12122, 12222) October 30, November 12 1960, WTU; Whidbey Island, Stuntz (Stz 13874, 14513, 14552) September 8 1966, November 5 1967, November 14 1967, WTU; Sandy Hook, Whidbey Island, (Stz 13854) September 8 1966, WTU; Langley, Whidbey Island, (Stz 14538) September 14 1962, WTU; east of Springdale, Cooke September 27 1947, WSP 24512; Barnes Creek trail, Olympic National Park, Clallam County, Cooke October 26 1950, WSP 25049; near Staircase, Olympic National Park, McKenny, October 24 1962, UBC F3287; Bremerton, Flett November 26 1930, WSP AS29265; Marysville, Grant November 1931, MU F14172; Mercer Island near Seattle, Parker (Herbarium Young Naturalists Society 200) December 1893, WTU; Seward Park, Seattle, (Stz 11583) October 19 1959, WTU; Seattle, Zeller (57) 1911, WTU; Seattle, Snyder (29) fall, WTU; Watermain Woods, Redmond, SDLB November 2 1980, WTU; California Creek near Valley Ford, Cooke November 8 1947, WSP 24513; north of Copalis, Clallam County, Williams (JWL 999) October 11 1970, WTU; Burnis Lake near Olympia, Williams (JWL

1719) November 3 1973, WTU; Olympia, Snyder December 4 1933, WTU; south of Spanaway, Simms November 12 1966, WSP 57197; Tahoma Vista, Mount Rainier National Park, van de Bogart (FVB 2245) October 28 1973, WTU; south of Cispus turnoff, van de Bogart (FVB 1036) October 23 1971, WTU; Bear Cree, Grouse Flats, Garfield County, Shaw November 1 1954, WSP 41533; Medicine Creek drainage, Astotin County, Shaw November 2 1959, WSP 47623; Bingen, Suksdorf January 24 1900, WSP 27480; Falcon Valley, Klickitat County, Suksdorf November 1 1901, WSP 27479; Lee Forest near Malthy, Brough (12) October 16 1956, WTU; Lee Forest near Malthy, Cohen (Stz 6982) November 16 1952, WTU; Millersyle State Park, Spur (Stz 16987) November 13 1971, WTU; Fort Lewis, Stuntz November 1 1934, WTU; Troublesome Creek, (Stz 14954) September 26 1968, WTU; Browns Lake, van de Bogart (FVB 2451, 2570) November 3 1973, WTU; unknown, Browns November 13 1971, WTU 906; unknown, November 16 1974, WTU 3295; unknown, Isaacs (Is 1362) March 21 1961, WTU; unknown, Ardery (1290), WTU; unknown, Williams (JWL 33), WTU. **Idaho:** Nordman, Shaw October 16 1954, WSP 41576; Priest Lake, Rogers October 27 1963, WSP 56475; Priest River Experimental Forest, Slipp October 28 1940, WSP 49792; Hayden Lake, Kootenai County, White October 1959, WSP 47630; Moscow Mountain, Ward September 28 1947, WSP 30113; Moscow Mountains, Miller September 14 1964, WSP 54048, 54484; Laird Park, Latah County, Miller October 17 1962, WSP 52704; Clearwater Canyon east of Lenore, Cooke November 30 1946, WSP 24511; Rackliff Ridge trail along Selway River, Nez Perce National Forest, Cooke October 26 1946, November 1 1947, WSP 24510, DAOM 26783; Rackliff Creek, Idaho County, Cooke October 22 1949, WSP 30112; Ticks Creek road, van de Bogart (FVB 3729) September 9 1976, WTU. **Oregon:** Coos County Forest, Ardrey (538), WTU; west of Ruch, Isaacs (Is 558, 560) January 26 1958, WTU; Bellview-Tolman Creek area, Isaacs (Is 1455) November 11 1961, WTU; McReady Springs, Paden April 20 1972, UVIC. **California:** Lake Siskiyou, Bangsberg April 25 1980, WSP 66107; Bear Springs, Mount Shasta, Cooke October 10 1958, WSP 55868; Mineral, Cooke September 2, 3 1977, September 1978, October 6 1981, WSP 63395, 63396, 60991, 67210; Jonesville, Copeland September 30 1938, WSP 31526; San Francisco Bay region, Morse spring 1934, UBC F3296; Walnut Creek, Contra Costa County, Baltzo January 8 1984, UBC F13113. **Michigan:** Tahquamenon, Bas August 12 1963, UBC F3285; Pine Barrens, Topinabee, Smith (75904) August 10 1968, MICH. **SVALBARD:** Endahlen, Currah August 17 1988, ALTA 8305; Sverdrupbyen, Currah August 16 1988, ALTA 8313. **UNITED KINGDOM:** Twyford Forest, Lines, Roberts September 9 1988, IMI 310080; Andover, Hampshire, Herbarium Berkeley 1879, K (type of *Helvella subcostata*). **SPAIN:** Cuenca, Calonge & Arroyo May 28 1985, K. **UNKNOWN:** Persoon, K (type of *Helvella mitra*).

Exsiccata Examined: Mycobiota of North America, 246, Rackliff Creek, Nez Perce National Forest, Idaho, USA, Cooke November 16 1946, s.n. *Helvella lacunosa*, WSP 21369; Ellis and Everhardt's Fungi Columbiani, 1931, Stockton, Kansas, USA, Bartholomew June 3 1903, s.n. *Helvella lacunosa*, WSP 3108; Pacific Slope Fungi, 256, Stanford University, Santa Clara County, California, USA, Banker February 18 1902, s.n. *Helvella lacunosa*, WSP 23883; California Fungi, 316, Trinidad, Humbolt County, California, USA, Parks November 1931, s.n. *Elvella mitra*, WSP 35290, WTU.

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

Synonyms: *Helvella philonotis* Dissing, fide Weber (1972).

Type Material: Holotype NYS, examined.

Geographic Distribution: Reported from northern Manitoba (Huhtinen 1984; Hutchison *et al.* 1988). Known from eastern North America (Weber 1972; Huhtinen 1982) and Europe (Harmaja 1977b, Dissing 1966b as *H. philonotis*; Hallgrimsson 1968, as *H. philonotis*).

Taxonomic 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 typically remains free from the stipe. Häffner (1987) considers that this species may be best treated as a variety of *H. lacunosa*, but the correlation of many morphological features warrants retention of specific status. Further investigations are required to more accurately assess the features separating these two taxa. No specimens from the study region have been assigned to this taxon, but several collections listed under *H. lacunosa* (*e.g.* DAOM 91441), are somewhat intermediate between the two taxa. Other collections of typical *H. lacunosa* contain immature fruiting bodies approaching the morphology typical for *H. palustris*.

Collections Examined: USA: Michigan: Tahquamenon Falls State Park, Brough UBC F3295; UMBS, Emmet County, Rogerson August 6 1964, UBC F3293; south of Rose City, Ogemaw County, A.H. Smith July 16 1963, UBC F3294. **New York:** Manlius Centre, Peck August, NYS (holotype); Southbay near Whitehall, Burnham August 20 1908, NYS. **NORWAY:** south of Kongsvall, Oppland, Kristiansen August 8 1991, RK.

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

Type Material: Holotype PC, examined.

Figure 14.

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, 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 ground in soil or litter in coniferous or mixed woods. Associated tree species include *Abies* sp. Fruiting period from July (exact date unknown) in Manitoba to December 25 in Washington.

Geographic Distribution: Infrequently encountered in boreal and coastal regions most northerly collections described from North America. The disjunct population is locally common in Washington. Also known from eastern North America (Dissing 1966a, 1967), Europe (Dissing 1966b, Calonge & Arroyo 1990), and Asia (Liu & Cao 1988). Map 9.

Taxonomic Notes: Although similar in ascocarp colouration, *H. crispa* (q.v.) is separated by its pale brown pubescent excipular surface and inrolled free apothecial margin. *H. 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) exhibit some grey colouration in fresh and dry specimens, while *H. lactea* is entirely white when fresh and typically yellow, especially on the stipe, when dried. *H. lactea* has a much more restricted geographic distribution than *H. lacunosa.* Häffner (1987, 1991) considers this species a pigmentless form of *H. lacunosa*, but I would retain it as a distinct species since the absence of pigment is a consistent and reliable feature, presumably with genetic basis. One collection from Washington (WTU Stz 12122) was mixed with *H. lacunosa*. Documentation of close association between these two species may support the reduction of *H. lactea* to the rank of variety or form.

Collections Examined: CANADA: Manitoba: Indian Bay, Shoal Lake, Tan July 1966, WIN. **USA: Washington:** Friday Harbor, San Juan Island, Stuntz (Stz 12122) October 30 1960, WTU; Robinswood Park, Bellevue, Martin (FVB 1702) November 16 1972, WTU; Tacoma Prairies, Snyder (50) November 10 1934, WTU; Yelm, Stuntz (Stz 4870) October 17 1948, WTU; Rainier, (Stz 6116) November 5 1950, WTU; Rainier woods, Stuntz (Stz 4921), November 13 1948, WTU; Humbug Mountain trail, Ardrey (901) December 25 1985, WTU. **SWEDEN:** Botanic Garden, Uppsala, Hylander July 25-August 2 1939, K. **FRANCE:** Meaux, Dumeé June 1902, PC (holotype). **SPAIN:** Cadalonia, Reid, November 2 1985, K.

Section *Leucomelaenae* Dissing, 1966, Dansk Botanisk Arkiv 25: 36, *emend. nov.*

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

Synonyms: section *Acetabulum* Dissing
section *Solitariae* Häffner

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.

Taxonomic Notes: The section *Leucomelaenae* is characterized by indistinctly to distinctly stipitate species with prominently ribbed stipe and cupulate to reflexed apothecia. The section as emended here comprises the sections *Leucomelaenae* and *Acetabulum* of Dissing (1966b) and section *Solitariae* of Häffner (1987). The broad concept adopted here more closely corresponds to the genus *Acetabula* (*sensu* Boudier

Key to species of *Helvella* section *Leucomelaenae*

1. Ascus base aporhynchous 2
1'. Ascus base 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 regions 4
3'. Distribution in boreal and montane 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. arctoalpina*

5. Ascospores very broadly ellipsoidal to subglobose (12.5-16 μm diam.) 6
5'. Ascospores ellipsoidal to broadly ellipsoidal (10-13.5) 7

6. Ascocarps large (50-90 mm diam.); hymenium medium to dark grey
brown; excipular surface densely pubescent to villose .... *H. unicolor*
6'. Ascocarps small to medium (4-22 mm diam.); 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 ....
.... *H. acetabulum*
8'. Ribs blunt-edged; excipular surface medium to light grey brown,
lacking yellow colouration .... *H. costifera*

9. Stipe medium to pale brown, with conspicuous darkly pigmented
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 leucomelaena (Persoon) Nannfeldt, 1941, In Lundell and Nannfeldt Fungi Exsiccati Suecici Praesidium Upsaliensis Fasciculata 19-20: 21, no. 952.

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

Synonyms: *Helvella confusa* Harmaja, holotype H, examined; isotype C, examined.
Helvella pedunculata Harmaja, holotype OULU, examined.
Helvella melaleuca Rifai, type K, examined.
Acetabula calyx Saccardo, holotype K, examined.
Peziza debeauxii Roumeguère, syntype K, examined.

Type Material: Lectotype selected here L 8945-6, Herbarium Persoon, examined.

Figures 3, 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, 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: Gregarious, subcespitose, or numerously scattered on ground in bare soil, moss, or litter in coniferous woods. Associated tree species include *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 include *Alnus crispa, Acer glabrum., Menziesia ferruginea,* and *Juniperus* sp. Fruiting period from April 23 in Washington and British Columbia to September 3 in Alberta.

Geographic Distribution: Widely distributed in montane regions from Alaska, British Columbia, Alberta, Washington, Idaho, Oregon, and Wyoming. Newly reported from Wyoming. Also distributed in eastern North America (Weber 1972), South America (Dissing 1966b), Europe (Dissing 1966b, Häffner 1987; Calonge & Arroyo 1990), north Africa and the Middle East (Dissing 1966b; Nemlich & Avizohar-Hershenzon 1972, as *Paxina leucomelas*), Asia (Korf & Zhuang 1991; Waraitch 1976, as *H. solitaria*) and Australia (reported here based on the holotype of *H. melaleuca*). This species has the broadest global distribution of any known species in the genus, and is the only one known at present from South America. Map 12.

Taxonomic Notes: This species is characterized by the short white stipe with well separated blunt ribs which do not extend noticeably onto the excipular surface, the darkly pigmented hymenium, the finely pubescent excipular surface which is darkly pigmented at margin with pale to white base, relatively large ascospores, and aporhynchous ascus base.

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 is also a character of questionable importance since development may be due in part to substrate variability or individual variation. Large collections of *H. leucomelaena* show tremendous variation in ascocarp size and stipe prominence and cover a range of features typical for *H. leucomelaena sensu stricto* and *H. confusa*. Variable stipe morphologies are seen between collections in other species including *H. solitaria* (q.v.) and *H. elastica* (q.v.). Spore sizes compared between the type and authentic collections of each species do suggest that the spores of *H. confusa* are slightly shorter, but spore width of both species showed the same range of variation, contrary to that reported by Dissing (1966b) and Harmaja (1977a). When further collections were examined, 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 reported is very slight and cannot be 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 collection 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, is affected by variable 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 & Wells (1970) represent *H. crassitunicata*, while specimens described under *H. solitaria* refer to *H. leucomelaena*.

H. pedunculata is also reduced to synonymy for similar reasons as those discussed above for *H. confusa.* Harmaja (1978, 1979a) distinguished the species as having shorter ascospores, a well differentiated stipe, slightly denser pubescence on the excipular surface, and details of the excipulum. 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 considered to be of importance in specific delimitation of these taxa.

The lectotype of *H. leucomelaena* selected here is chosen from several excellent collections deposited in the Persoon Herbarium, Leiden, and represents typical specimens of *H. leucomelaena sensu stricto*, and is consistent with the description above in all details.

Collections Examined: CANADA: British Columbia: Canal Flats, Funk June 26 1960, DAOM 82875; Lumby, Bandoni May 28 1960, UBC F3398; Proctor, Linton May 15 1978, UVIC; Jocelyn Hill, highlands near Victoria, Ceska April 23 1977, UVIC. **Alberta:** near Nojack, Abbott (SA 56, 57, 84) June 24, 29 1989; Winfield, Strand July 8 1975, ALTA 7342; Penstock Creek, Jasper National Park, Currah August 29 1987, ALTA 8274; Moraine Lake, Banff National Park, Suttill September 3 1980, UVIC; Marmot Creek basin near Seebe, Danielson (RMD 309) August 13 1972, ALTA 8290; Summit Lake trail, Waterton Lakes National Park, Egger (731) August 11 1980, DAOM 177741;

Upper Waterton Lake trail, Waterton Lakes National Park, Abbott (SA 340) May 28 1990. **Ontario:** Halton Forest, Halton County, Ammirati (JFA 8022) May 18 1978, WTU. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton July 13 1966, WK 1538, 1539; Hope road, Kempton July 28 1968, July 14 1970, WK 1542a, 4480; Turnagain Pass on Seward Highway, Kempton August 27 1968, WK 1553. **Washington:** Friday Harbor, San Juan Island, Isaacs (Is 1704) May 19 1962, WTU; Entiat Mountains, Chelan County, Ammirati (JFA 9400) June 7 1987, WTU; Cle Elum pine flats, Isaacs (Is 1738) May 27 1962, WTU; Cle Elum pine flats, Stuntz (Stz 12310, 11709) May 21, 22 1960, WTU; Cle Elum pine flats, McCarkle (Stz 11691) May 15 1960, WTU; near Yelm, Walters (JFA 8499) May 4 1981, WTU; Ewartsville, Whitman County, Duran May 1 1983, WSP 67339; Kamiak Butte, Whitman County, Cooke May 17 1948, WSP 29343; WSU campus, Pullman, Sulzbach April 23 1963, WSP 53392; WSU campus, Pullman, Waldron May 9 1963, WSP 51810; Boulder Lake trail, (Stz 8835) August 2 1954, WTU; unknown, Snyder May 5 1934, WTU; unknown, (Stz 10977) May 24 1959. **Idaho:** Priest Lake, Slipp May 27 1941, WSP 50807; Priest River Experimental Forest, Bonner County, A.H. Smith July 5 1964, WSP 54318; Ida Creek, Priest River Experimental Forest, Slipp June 11 1942, WSP 55594; Coeur d'Alene National Forest, Shoshone County, Scates (1962) June 30 1972, MICH; Dry Creek between Troy and Deary, Cooke May 1948, WSP 30102; Laird Park, Latah County, Paden (JWP 515) May 20 1967, UVIC; Payette Lake, Valley County, Smith (44737) July 2 1954, MICH; Karney Lakes, Boise County, Trueblood (1029) May 8 1960, MICH; Idaho, English, WSP 23948. **Oregon:** Bear Springs, Wasco County, Carson June 3 1951, MICH. **Wyoming:** north Fork French Creek, Medicine Bow Mountains, Albany County, Smith (35784) August 15 1950, MICH. **SWEDEN:** Älvkarleby parish northeast of Gardskär, Eriksson & Lundquist June 30 1965, K. **FINLAND:** Kiiminki, Keskikylä, Esteri & Ohenoja July 2 1975, OULU (holotype of *H. pedunculata*). **DENMARK:** Klitmoller, northern Jutland, Toft & Dissing May 15 1965, C (type of *H. confusa*). **UNITED KINGDOM:** Britain, Herbarium Berkeley 1879, K (type of *Peziza percevali*). **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*).

Exsiccata Examined: Roumeguère Fungi Gallici Exsiccati, 2174, Algeria, Debeaux April 1882, s.n. *Peziza debeauxii*, K (syntype of *P. debeauxii*); Kryptogamae exsiccatae, 1824, near Baden, Austria, De Höhnel, IMI 11963.

Helvella oblongispora Harmaja, 1978, Karstenia 18:57.

Type Material: Holotype C, examined.

Figure 24.

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

Taxonomic Notes: This species differs from the closely related *H. leucomelaena* (q.v.) in its paler brown to ochre brown apothecial colouration and more prominent ribbing on stipe and basal third of excipular surface. *H. oblongispora* resembles *Helvella unicolor* (q.v.) in gross morphology, but can easily be separated on apothecial colouration, vestiture of excipular surface, ascal base, and ascospore shape.

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

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

Type Material: Holotype MICH, examined.

Figure 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 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 virtually absent or extending onto basal half of excipular surface. **Stipe:** 2-20 x 2-13 mm (up to 50 x 40 mm fresh), flaring and merging with apothecium, cream to pale or medium brown, 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 distinctly 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: Singly, gregarious, or subcespitose on ground in soil under conifers. Associated tree species include *Picea* sp. and *Tsuga* sp. Fruiting period from May 20 in Washington to October 13 in Washington.

Geographic Distribution: Endemic to the interior and coastal mountains of northwestern North America, but rarely collected from Alaska, British Columbia, and Washington. No specimens of this species have been reported outside the study area. This species is newly reported from British Columbia, and its suggested occurrence in Alaska (Weber 1975) is confirmed. Map 16.

Taxonomic Notes: This species is unique in the family in its thick-walled paraphyses, and possesses the largest ascospores of any species in the genus. Harmaja (1977b) discusses the usefulness of the length of the terminal cell of the paraphyses. Although terminal cell length is of limited value for some taxa, the thick-walled apical cell of the paraphyses of *H. crassitunicata* are the longest known in the genus. Typical thin-walled paraphyses, which greatly outnumber thick-walled paraphyses, are much shorter and fall within the usual range of lengths seen in other taxa of the genus. The thick-walled paraphyses of *H. crassitunicata* are morphologically 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 suggests an affinity to *H. leucomelaena* (q.v.). *H. crassitunicata* can be distinguished by ascocarp colouration, stronger pubescence of the excipular surface and stipe, and more pronounced ribbing of stipe and excipular surface.

Specimens reported by Kempton & Wells (1970) as *H. leucomelaena* are referable to this taxon as suspected by Weber (1975). *H. pocillum* Harmaja, not examined in this study, is reported to have very large ascospores similar to *H. crassitunicata*, but lacks thick-walled paraphyses (Harmaja 1976a).

Collections Examined: CANADA: British Columbia: Mount Abbott near Marian Lake, Glacier National Park, Shoemaker August 6 1963, DAOM 109231; Trail to Glacier crest, Glacier National Park, Shoemaker August 4 1963, DAOM 109227, 109230; trail to

August 27 1970, WK 4517, 4518, 4809. **Washington:** Bogachiel Peak, Olympic National Park, Smith (2745) September 27 1935, MICH; Pierce County, A.H. Smith, MICH (holotype); base of Carbon Glacier, Mount Rainier National Park, Tschudy (Snyder 103) May 20 1934, WTU; Mount Rainier National Park, Smith (29746, 30598, 40077, 40875, 40916) August 2, 25 1948, September 20, October 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) July 16 1973, WTU; unknown, August 2 1948, WTU 3803.

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

Basionym: *Acetabula aestivalis* Heim & Remy, 1925, Bulletin. Société Mycologique de France 41: 460, plate XXIX Figures 10-12.

Type Material: unknown.

Figure 23.

Apothecium: 3-26 mm diam., 1-17 mm high, deeply cupulate, margin inrolled initially, margin often splitting at maturity, rarely split to form one sided lobe, rarely laterally compressed when immature, hymenium dark red brown to blackish brown, 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious or numerously scattered on ground in soil or humus. Associated shrubs include *Salix* sp., *Cassiope* sp., *Andromeda* sp., and *Dryas* sp. Fruiting period from July 17 in Yukon to August 15 in Northwest Territories.

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

Taxonomic Notes: This species shows strong affinities with *H. arctoalpina* (q.v.). Both species have northern distributions and are subsessile to short stipitate. They also share a densely pubescent excipular surface with ribs often extending from stipe onto basal portion. The two can be separated by ascocarp colouration and spore size. *H. arctoalpina* 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 (Figure 23). This feature is perhaps variable and lends support to the merging of sections *Leucomelaenae* and *Acetabulum sensu* Dissing (1966b). *H. 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 red suggest an affinity between the two species and sections.

Collections Examined: CANADA: Yukon: mountain west of Blackstone River, Ginns (18384) July 17 1984, DAOM 195288; **Northwest Territories:** 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 July 29 1960, DAOM 75774; Axel Heiberg Island, Kuc August 8 1967, DAOM 124703, 124707; east of Repulse Bay, Ohenoja August 4 1974, OULU; Coal Harbor, Southampton Island, Savile August 15 1959, DAOM 67075; Longstaff Bluff, Baffin Island, Parmelee & Seaborn August 9 1967, DAOM 117582, 117583; **SVALBARD:** near Loven Glacier, Currah August 12 1988, ALTA 8306; Loven Glacier, Currah August 12 1988, ALTA 8307.

Helvella arctoalpina Harmaja, 1978, Karstenia 18:57.

Synonyms: *Helvella dryadophila* Harmaja, Holotype O, examined.
?*Helvella verruculosa* (Saccardo) Harmaja (see notes).

Type Material: Holotype O, examined.

Figure 11.

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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious or numerously scattered on ground in soil or humus with low shrubs on tundra, or rarely coniferous woods. Associated tree species include *Abies lasiocarpa* and *Picea glauca*. Associated shrubs include *Salix reticulata*, *Salix arctica*, *Vaccinium vitis-idaea*, *Cassiope* sp., and *Dryas integrifolia*. Fruiting period from July 30 to August 15 in Northwest Territories.

Geographic Distribution: Widely distributed in arctic and alpine tundra regions in northern areas (one collection is known from a high elevation montane forest site) from Northwest Territories and Alberta. This species is newly reported for North America. Circumpolar distribution in North America, Europe (Harmaja 1977b), and Asia (Harmaja 1979a, as *H. verruculosa*). Map 13.

Taxonomic Notes: This species is most closely related to *H. aestivalis* (q.v.)(see notes under that species). It is also closely related to *H. costifera* (q.v.) and *H. acetabulum* (q.v.). Dissing (1966b) considered this species as an arctic form of *H. acetabulum*, but Harmaja recognized distinct species. Unfortunately, the problem was complicated by Harmaja's (1977b) erection of two new species from arctic collections. After examination of holotypes, I conclude that *H. arctoalpina* and *H. dryadophila* are conspecific. In fact, the table in Harmaja (1977b) listing pertinent distinguishing observations support the distinction.

Harmaja (1978, 1979a) verified the status of *Geopyxis verruculosa* Saccardo as a valid species closely related to *H. arctoalpina* and *H. dryadophila*. Although I have not examined the type of *H. verruculosa*, I suspect that this is the oldest valid name for this arctic and alpine taxon. 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 features are variable in other species of this genus and no correlation was found in this study to make taxonomic separation possible. *Helvella acetabulum* is distinguished by larger size, more prominent stipe, 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, July 30 1958, DAOM 67088; Skeleton Creek north of Hazen camp, Ellesmere Island, Forest August 10 1962, DAOM 91575; southwest of Hazen camp, Ellesmere Island, Savile July 30 1962, DAOM 915[illegible] Fox valley southwest of Hazen camp, Ellesmere Island, Savile July 30 1962, DAOM 91576; Bathurst Island, Bissett August 6, 15 1977, DAOM 165336, 165335; Stanwell-Fletcher Lake, Somerset Island, Savile August 11 1958, DAOM 60267; northeast of Repulse Bay, Ohenoja August 5 1974, DAOM 159682; southeast of Repulse Bay, Ohenoja August 4 1974, DAOM 155308; Coral Harbor, Southampton Island, Cody August 6 1948, DAOM 20767; Coral Harbor, Southampton Island, Savile August 15 1959, DAOM 67075; Longstaff Bluff, Baffin Island, Parmelee & Seaborn August 7 1967, DAOM 117583; near Melvin Bay, Rankin Inlet, Ohenoja August 12 1971, DAOM 159712. **Alberta:** Cardinal River Divide near Cadomin, Annett (SA 624) August 1982, SA; Bertha Lake trail, Waterton Lakes National Park, Egger (602) August 7 1980, DAOM 177719. **SVALBARD:** Gipsvika, Currah August 15 1988, ALTA 8308. **NORWAY:** Lom, Oppland, Eckblad August 29 1957, O (holotype of *H. dryadophila*); Eidfjord, Hordaland, Eckblad August 1 1959, O (holotype of *H. arctoalpina*).

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

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

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

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, 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 species include *Betula papyrifera*, *Alnus tenuifolia*, *Populus tremuloides*, *Populus balsamifera*, and *Picea glauca*. Associated shrubs include *Salix discolor* and *Viburnum edule*. Fruiting period in the study area only on August 7 in Alberta.

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

Taxonomic 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 examined have a finely pubescent excipular surface, although Dissing (1966a) describes loose tufts of fascicled hyphae projecting from the outer excipulum, which my observations support. European specimens also have an earlier fruiting period from March to May (Dissing 1966b). It is possible that European and North American specimens represent two distinct taxa at varietal or specific level, but the similarity in ascocarp morphology and the distinctive broad ascospores suggest that they are conspecific. More collections from North America and fresh collections from Europe should be examined to provide a clear concept of this taxon. *H. 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 can be easily separated by the ascospore size and shape, and the ribs extending onto the excipular surface in *H. unicolor*. *H. rivularis* resembles immature or small specimens in morphology, but never becomes as large with strongly ribbed stipe and excipular surface. The densely pubescent excipulum and ascocarp colouration are very similar in both species. *H. unicolor* is similar to *H. costifera* (q.v.), *H. acetabulum* (q.v.), and *H. arctoalpina* (q.v.) and appears most closely related to *H. costifera* which shares the greyish colouration and blunt ribs of stipe and excipulum. *H. acetabulum* shares the brown colouration seen in dry specimens, but *H. unicolor* lacks the yellow pigments often seen on excipular surface and stipe. North American specimens match the fruiting period of *H. costifera*, while European specimens match the fruiting period of *H. acetabulum*. Both species have less pubescence on the excipular surface than the specimens described here. *H. arctoalpina* shares ascocarp colouration, smaller size, less pronounced stipe, variable degree of ribbing on excipular surface, blunt ribs, and densely pubescent excipular surface and may be the most closely related species. Although fruiting times are similar, *H. unicolor* is found in boreal regions with a more southerly distribution than the arctic and alpine *H. arctoalpina*. Very broad ascospores are also seen in *H. robusta* (q.v.) and *H. aestivalis* (q.v.).

Collections Examined: CANADA: Alberta: Notikewin Provincial Park, Abbott (SA 131, 132, 135, 139) August 7 1989. **FRANCE:** commune de Savigné, Vienne, Grelet April 22 1927, PC (neotype); France, Riousset March 1974, K.

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

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

Synonyms: *Paxina acetabulum* (Linnaeus : Fries) O. Kuntze, fide Dissing 1966.

Type Material: Lectotype in Valliant, 1727, Botanicon Parisienne 57, Plate 13, Figure 1.

Apothecium: 10-80 mm diam., 5-20 mm high, deeply cupulate, margin expanding 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 ground in soil or litter in coniferous or mixed woods. Associated tree species include *Populus tremuloides, Populus balsamifera, Arbutus menziesii, Quercus garryana*, *Alnus* sp., *Thuja plicata, Picea glauca* and *Pseudotsuga menziesii.* Associated shrubs include *Cornus stolonifera.* Fruiting period from March 21 in Oregon to July 15 in British Columbia.

Geographic Distribution: Widely distributed, although infrequently encountered, in boreal, montane and coastal regions from British Columbia, Alberta, Manitoba, Washington, Idaho, Oregon, and Wyoming. Also distributed in eastern North America (Weber 1972), Europe (Häffner 1987), and Asia (Liu *et al.* 1985). Map 13.

Taxonomic Notes: This species is most closely related to *H. costifera* (q.v.), which can be separated on characters of ascocarp colouration, ribbing of stipe and excipular surface, and fruiting period (see also notes under *H. costifera*). *H. unicolor* (q.v.) is easily distinguished on ascospore morphology and less prominent ribbing of stipe and excipular surface. *H. arctoalpina* (q.v.) differs in its smaller ascocarp size, stronger pubescence, less prominent stipe and ribbing of excipular surface, and habitat (see also notes under *H. arctoalpina*).

Collections Examined: CANADA: British Columbia: Vancouver, Waugh July 15 1951, DAOM 27436; Bamberton Provincial Park, Vancouver Island, Paden June 7 1974, May 6 1987, UVIC; Victoria, Vancouver ISland, Robertson April 14 1973, UVIC; Winter Cove, Saturna Island, Kroeger April 2 1984, UBC F979. **Alberta:** William A. Switzer Provincial Park, Osis (SA 418) July 5 1990, SA; Devonian Botanic Garden near Devon, Currah June 25 1979, ALTA 7958; west of Millet, Kennedy June 30 1964, ALTA 626; Bow Valley Provincial Park, Danielson (RMD 2046) July 1 1976. **Manitoba:** Manitoba Agricultural College, Winnipeg, Bisby July 2, 10 1932, DAOM 206814; Manitoba Agricultural College, Winnipeg, Bisby & Conners July 14 1927, DAOM 183375. **Ontario:** Lake Simcoe District, Taylor June 16 1961, WIN. **USA: Washington:** Seattle, Greene (Snyder 123) April 1929, WTU; Mercer Island east of Seattle, Ziegler (Stz 9369) April 24 1941, WTU; Tacoma prairies, Snyder May 15 1935, WTU; Bingen Mountain, Suksdorf May 1 1899, WSP 27646, 27647; unknown, (Stz 7771) July 8 1953, WTU; unknown (Stz 1609, 18408), WTU. **Idaho:** Priest River Experimental Forest, Slipp July 4 1941, WSP 50463. **Oregon:** near Goldhill, (Stz 10898) March 27 1959, WTU; near Central Point, Isaacs (Is 1352) March 21 1961, WTU; Antelope creek road near camp White, Isaacs (Is 518) March 31 1957, WTU. **Wyoming:** Wyoming, van de Bogart, WTU. **UNITED KINGDOM:** Earlswood, Warwickshire, England, Ellis May 6 1979, IMI 253044; Esher Common, Surrey, England, Spooner May 25 1980, K. **NETHERLANDS:** Herbarium Persoon, L 8945-3. **FRANCE:** Corsica, Reid June 3 1965, K. **SCANDINAVIA:** Öland, Böda parish, road to Bränslegardarna, Schöldström May 31 1967, K.

Exsiccata Examined: North American Discomycetes, 1181, Ithaca, New York,

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

Synonyms: *Peziza costata* Fries, 1851, Acta Reg. Soc. Sci. Ups. Ser. 3 Vol. 1: 120. (illegitimate, later homonym), holotype UPS, examined; isotype K, examined. *Helvella griseoalba* Weber, Holotype MICH, examined.

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

Figure 5.

Apothecium: 16-42 mm diam., 10-20 mm high, deeply cupulate, margin inrolled slightly initially, expanding at maturity, sometimes laterally compressed initially, hymenium medium to dark grey brown, 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious on ground in soil in coniferous or mixed woods. Associated tree species include *Populus tremuloides, Populus balsamifera, Betula papyrifera, Alnus* sp., *Picea glauca,* and *Pseudotsuga menziesii.* Fruiting period from June 4 in coastal Washington to August 24 in Alaska.

Geographic Distribution: Infrequently encountered in boreal, montane, and coastal regions from Alaska, Yukon, Alberta, Washington, and Idaho. This species is newly reported for Alberta. Also distributed in eastern North America (Weber 1972; Pomerleau 1980; as *H. griseoalba*), Europe (Dissing 1966b; Häffner 1987; Harmaja 1979a), and Asia (Dissing & Raitviir 1974; Cao & Liu 1990). Map 14.

Taxonomic Notes: This species is closely related to, and often difficult to distinguish from *H. acetabulum* (q.v.). The two species have been distinguished on characters of colouration, ribbing, and fruiting time (Dissing 1966b; Harmaja 1977b, 1979a). *H. costifera* has more grey pigmentation and lacks yellow brown pigmentation of the excipular surface. Specimens of *H. costifera* from Norway (RK) appear typical for the taxon with the exception of strong brown pigmentation (see also Dissing 1966b). The ribs of *H. costifera* are blunt and often more widely spaced than in *H. acetabulum*, but specimens otherwise typical of *H. acetabulum* with blunt ribs have been examined. *H. costifera* also has a later fruiting time (Dissing 1966b), but the collections referred to this taxon from North America overlap with later collections of *H. acetabulum*. The two taxa appear to be distinct, but further clarification of correlating features is required. *H. unicolor* (q.v.), *H. hyperborea* (q.v.), and *H. robusta* (q.v.) are also quite closely related and can be distinguished by characters discussed in the notes under those taxa.

H. 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

(SA 100), July 15 1989, SA; July 15 1989 10 km south of Leduc, Abbott July 8, 1979, ALTA 8264. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton August 11, 24 1963, July 13 1966, August 24 1971, WK 1536, 1537, 4013, 5202. **Washington:** Friday Harbor, San Juan Island, Stuntz (Stz 12380) June 4 1961, WTU. **Idaho:** Rackliff Creek, Idaho County, Cooke July 6 1947, WSP 30103. **Michigan:** Grapevine Point, Douglas Lake, Cheboygan County, Smith (NJS 982) June 10 1968, MICH (holotype of *H. griseoalba*). **NORWAY:** near Bodo, Nordland, Johnson July 1 1983, RK. **SWEDEN:** Uppsala Botanic Garden, Fries, UPS (holotype of *Peziza costata*), K (isotype of *Peziza costata*).

Exsiccata Examined: Fungi Exsiccati Suecici Praesertim Upsalienses, 2061, Uppsala, Sweden, Nannfeldt (9956) July 9 1948, s.n. *Helvella costifera*, S, K.

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 ground in duff in coniferous woods. Associated tree species include *Picea* sp. and *Tsuga* sp. Fruiting period on July 28 in Alaska.

Geographic Distribution: Rarely encountered in northern coastal regions from Alaska. This species is newly reported from Alaska and significantly extends the range, previously known only from northern Quebec, westward in North America. Also distributed in northeastern North America (Harmaja 1981) and northern Europe (Harmaja 1978, 1979a). Map 13.

Taxonomic Notes: This species is characterized by the distinct, relatively slender, prominently ribbed stipe with dark pubescence, and the medium brown ascocarp colouration. Harmaja (1979a) suggests that this species is most closely related to *H. costifera* (q.v.), although I would consider *H. acetabulum* (q.v.) and *H. arctoalpina* (q.v.) equally close (see also notes under aforementioned species). Although immature, the specimens from Alaska are morphologically identical to the type collection from Finland. The two ascocarps were part of a larger collection of *H. leucomelaena* (q.v.), but are morphologically distinct and easily separated by the pleurorhynchous ascus base of *H. hyperborea*.

Collections Examined: USA: Alaska: near Hope, Kempton July 28 1968, WK

Helvella robusta Abbott, in Abbott & Currah, 1988, Mycotaxon 33: 242.

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

Figure 25.

Apothecium: 50-90 mm diam., mm high, 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, uniguttulate.

Habitat: Solitary on ground in soil under deciduous trees. Associated trees and shrubs include *Populus balsamifera* and *Salix* sp. Fruiting time from August 30 to September 11 in Alberta.

Geographic Distribution: Rarely encountered in boreal regions. This species is known only from Alberta (Abbott & Currah 1988). Map 14.

Taxonomic Notes: This species is characterized by large size, robust prominently ribbed stipe, strongly reflexed apothecial margins, and autumnal fruiting pattern. Closely related species include *H. costifera* (q.v.), *Helvella unicolor* (q.v.), and *H. acetabulum* (q.v.). Autumnal fruiting patterns indicate a very close relationship with *H. costifera*, which differs in its grey colouration, smaller stature, and narrower paraphyses. *H. unicolor* is similar in ascospore size and shape, but can be easily distinguished by ascocarp size and colouration, and excipular vestiture. *H. acetabulum* is more darkly pigmented with slightly longer ascospores, and has a vernal fruiting pattern.

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

Helvella solitaria Karsten, 1871, Bidrag Kännedom af Finlands Natur och Folk 19: 37.

Synonyms: *Peziza solitaria* Karsten, 1869, Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandingar 10: 115 (illegitimate, later homonym).
Helvella queletii Bresadola, fide Harmaja (1977a).

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 inrolled slightly initially, hymenium grey brown to dark brown, 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious or numerously scattered on ground in soil or litter in coniferous, mixed, or occasionally deciduous woods. Associated tree species include *Picea glauca, Picea engelmannii, Pinus contorta, Pseudotsuga menziesii, Abies grandis, Tsuga heterophylla, Abies* sp., *Thuja plicata, Populus tremuloides, Populus balsamifera, Betula papyrifera*, and *Alnus sp.* Associated shrubs include *Salix bebbiana, Rosa* sp., *Lonicera involucrata,* and *Cornus stolonifera.* Fruiting period from April 19 in coastal Washington to October 4 in eastern Washington. April and May collections are known only from Washington and Oregon, June to August collections are typical for Alaska, Northwest Territories, Alberta, Manitoba, and Idaho.

Geographic Distribution: Widely distributed in boreal, montane, coastal, and arctic regions from Alaska, Northwest Territories, British Columbia, Alberta, Manitoba, Washington, Idaho, Oregon, and Wyoming. Also distributed in eastern North America (Weber 1972, as *H. queletii*) and Europe (Dissing 1966b, as *H. queletii*; Harmaja 1977; Häffner 1987). Map 15.

Taxonomic Notes: Closely related species in the section *Leucomelaenae* include *H. costifera* (q.v.) which is similar in ascocarp colouration, but can be distinguished by the more prominent ribbing on stipe and excipular surface and relatively broader stipe. *H. hyperborea* (q.v.) is similar in ascocarp shape, but can be distinguished by the prominent ribbing of the excipular surface and ascocarp colouration. *H. unicolor* (q.v.) is easily distinguished by ascospore shape. *H. solitaria* is also closely related and morphologically similar to *H. leucomelaena* (q.v.), which is easily separated by the aporhynchous ascal bases and larger ascospore size. This species occupies a position in this section nearest members of the section *Cupuliformae.* Small specimens are similar in many respects to *H. cupuliformis* (q.v.), but the latter species 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 excipular surface. The slender cupulate forms of *H. solitaria* also resemble *H. dissingii* (q.v.) which exhibits similar ascocarp colouration, but the species can be separated by ascospore size as well as the characters mentioned above for *H. cupuliformis*. *H. solitaria* may also provide a link to members of the section *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 August 4 1974, DAOM 155395;Baker Lake, Ohenoja August 9 1974, DAOM 155395; Fort Smith, Loan August 8 1950, DAOM 26124. **British Columbia:** Tetsa River Provincial Park, Abbott (SA 229) August 22 1989, SA; Kokanee Glacier Provincial Park near Nelson, Harrison (6061) July 11 1960, MICH; Gold Creek near Golden Ears Provincial Park, Rabas June 27 1971, UBC F3392; Golden Ears Provincial Park, Redhead & Liu June 7 1970, UBC F3393; Manning Provincial Park, Morrison August 3 1963, UBC F3397. **Alberta:** Shaw Lake near Lac La Biche, Abbott (SA 99, 101, 103) July 14, 15 1989, SA; Shaw Lake near Lac La Biche, Abbott (SA 362, 366) June 22 1990, SA; near Redwater, Currah (SA 481) July 6 1991, SA; Devonian Botanic Garden near Devon, Abbott (SA 443) June 15 1991, SA; Forestry Trunk road near Sundre, Abbott July 19 1988, UAMH M565; Fish Creek Provincial Park, Calgary, Danielson (RMD 911) July 25 1973, ALTA 8295; Brown-Lowery Natural Area, Danielson (RMD 214) July 29 1972, DAOM 143867. **Manitoba:** Russell, Bisby June 20, 18 1971, WK 1546, 5058; Eklutna Lake north of Anchorage, Kempton July 2 1973, WK 5290; Thunderbird Falls, Kempton June 27, July 5, 11 1960, July 10 1973, WK 1540, 1541, 1545, 5291; Thompson subdivision, Anchorage, Kempton July 22, August 10 1971, WK 5079, 5131; Erickson Gold Mine, Girdwood, south of Anchorage, Kempton August 17, September 3 1968, WK 1543, 1544; Potter, Kempton September 11 1971, WK 5526. **Washington:** Friday Harbor, San Juan Island, Brough (Is 58) April 21 1957, WTU; Friday Harbor, San Juan Island, Stuntz & Isaacs (Is 1703), WTU; Seattle, Greene (Snyder 122) May 1929, WTU; Watermain woods, Redmond, Stuntz (Stz 21769) April 19 1981, WTU; Watermain woods, Redmond, Jones (SLB 289) January 1 1974, WTU; eastern Washington, Chiltan (Stz 19075) October 5 1975, WTU; Lower Tahoma at Fish Creek, Stuntz (Stz 3902) August 9 1948, WTU; Gold Creek campground, van de Bogart (Stz 13496) April 30 1966, WTU; southwest of Fort Lewis, Hellya (Stz 7364) May 14 1961, WTU; Aspus Centre, Masford (Stz 16672) June 25 1971, WTU. **Idaho:** southwest of McCall, Miller July 14 1964, WSP 54644; Coyote Creek, Owyhee County, Trueblood (2174) July 6 1963, MICH. **Oregon:** Hood River, Kienholz May 16 1933, WSP 15136. **Wyoming:** Medicine Bow National Forest, Albany County, Kanouse September 5 1923, MICH. **NORWAY:** Østfold, Krakenøy, Englevik, Kirkebakken, Kristiansen June 7, 20 1987, RK 87.10. **RUMANIA:** Mutenia, district Dâmbovita-Badulesti, Racovitza & Savulescu July 5 1944, IMI 28970.

Exsiccata Examined: Ellis and Everhardt's Fungi Columbiani, 1801, Stockton, Kansas, USA, Bartholomew June 3 1903, s.n. *Acetabula vulgaris*, K, WSP 2; Fungi Dakotenses, 502, Nyland's Grove, Kulm, North Dakota, Brenckle July 4 1922, WSP 23419.

Section *Silvicolae* Abbott, 1988, in Abbott & Currah, Mycotaxon 33: 245.

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

Synonyms: *Wynnella* Boudier

Ascocarp: subsessile to indistinctly stipitate, apothecium auriculoid, hymenium dark purplish red brown, smooth to slightly rugose, excipular surface red brown, glabrous, stipe indistinct, glabrous, shallowly fluted, sulcate becoming chambered, odour strong in dried specimens. **Asci:** pleurorhynchous. **Ascospores:** 19-24 x 14-17 μm, broadly ellipsoidal, hyaline, smooth, with SEM surface finely rugose, uniguttulate, with large central broadly ellipsoidal guttule.

Taxonomic Notes: *H. silvicola* is frequently maintained in the monotypic genus *Wynnella* on the basis of apothecial structure, colouration, excipular vestiture and flesh consistency (*e.g.* Dissing 1972). Ascospore morphology (Figure 51) and excipulum anatomy suggest placement of this taxon in the genus *Helvella*, but the differences are considered sufficient to warrant recognition of the monotypic section proposed by Abbott & Currah (1988)(see notes under *H. silvicola*).

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

Basionym: *Otidea silvicola* Beck in Saccardo, 1889, Sylloge Fungorum 8: 97.

Synonyms: *Wynnella silvicola* (Beck in Saccardo) Nannfeldt
Otidea auricula (Cooke) Massee, fide Harmaja (1974).
Wynnella auricula (Cooke) Boudier
Scodellina auricula (Cooke) Seaver, fide Harmaja (1974).

Type Material: unknown.

Figure 4, 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, 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 numerously scattered on ground in duff, rarely in burned areas, under conifers. Associated tree species include *Picea glauca, Picea engelmannii, Pinus contorta, Pinus ponderosa, Abies lasiocarpa,* and *Larix laricina.* Associated shrubs include *Salix discolor, Shepherdia canadensis, Symphoricarpos* sp., *Amelanchier alnifolia,* and *Rosa* sp. Fruiting period from June 16 in British Columbia to September 22 in Alberta. July and August collections are common.

Geographic Distribution: Widely distributed throughout boreal and montane regions from Alaska, British Columbia, Alberta, Manitoba and Montana. Reported from Idaho and Washington (Larsen & Denison 1978, as *Wynnella silvicola*). Also distributed in eastern North America (Huhtinen 1985; Kanouse 1949, as *Otidea auricula*), Europe (Harmaja 1974a) and Asia (Dissing & Raitviir 1974, as *Wynella silvicola*). Map 16.

Taxonomic Notes: This species has frequently been placed the monotypic genus *Wynnella* Boudier (Dissing 1966b, 1972; Eckblad 1968; Larsen & Denison 1978), but I support the inclusion of *H. silvicola* within the genus *Helvella*, in agreement with Harmaja (1974a) and Abbott & Currah (1988). The slightly to distinctly fluted or ribbed stalk which may become elaborately infolded or somewhat chambered in some specimens (Figure 4) is an additional character linking this species with those of the genus *Helvella.* Similarity in stipe morphology between *H. silvicola* and *H. leucomelaena* (q.v.) is clear (compare Figures 3 and 4). The species is distinctive in the auriculoid ascocarp morphology, colouration, and lack of vestiture on the excipular surface. The tissue of dried ascocarps is of rather horny consistency and is more difficult to revive in water or KOH than the tissue of other members of the genus, and dried specimens have a strong distinctive odour (although none was detected in fresh collections), unlike other known species. These observations support those of Weber (pers. comm.). The above features are sufficient to warrant recognition of a monotypic section to accommodate this species.

The most closely related species belong to the section *Leucomelaenae. H.*

ascospore size and shape, and habitat. Other species with glabrous excipular surfaces include *H. lacunosa* (q.v.) and *H. lactea* (q.v.) in the section *Helvella*, and *H. elastica* (q.v.) and *H. atra* (q.v.) in the section *Elasticae*.

Collections Examined: CANADA: British Columbia: Kindersly Creek, Kootenay National Park, Rushton June 16 1969, UVIC; Bull River winter range, east Kootenays, Paden spring 1976, UVIC. **Alberta:** Winfield, Strand July 8 1975, ALTA 7341; Astoria River valley, Jasper National Park, Currah July 25 1988, ALTA 8312; Highwood Pass, Jasper National Park, Currah July 15, 23 1983, ALTA 8277, 8278; Fryatt valley, Jasper National Park, Richardson (SA 300) September 22 1989, SA; Athabasca River valley, 14 km from Sunwapta falls, Jasper National Park, Abbott (SA 371) August 2 1990, SA; Fish Lake near Nordegg, Abbott (SA 379) August 3 1990, SA; Fish Lake near Nordegg, Abbott July 16 1987, ALTA 8272; 50 km west of Rocky Mountain House, Abbott July 27 1987, ALTA 8273; Raven Fish Hatchery near Caroline, Abbott July 6 1980, ALTA 8284; Red Deer River valley on Forestry Trunk road, Abbott July 18 1988, UAMH M552; above Lake Louise, Banff National Park, Ostafichuk August 3 1965, ALTA 605; Sawback range Mount Ishbell, Banff National Park, Rushton September 5 1968, UVIC. **Manitoba:** east end of Whitemud Lake, Parker July 6 1971, DAOM 134578. **USA: Alaska:** Forest Nature trail, Glacier Bay National Monument, Cooke July 9, 11, 20, 27 1980, WSP 67850, MU F35984, F36302, 36347; Bartlett Cove, Glacier Bay National Monument, Cooke July 6 1978, August 28 1979, June 20 1980, DAOM 179108, 179112, MU F36557. **Montana:** Echo Lake, Flathead National Forest, Cummins July 31 1928, MICH. **RUMANIA:** Lacul Rosu, dist. Harghita, Toma June 16 1961, K.

Section *Cupuliformae* Abbott, *sect. 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 fluted, internally solid. **Asci:** pleurorhynchous. **Ascospores:** broadly ellipsoidal, hyaline, smooth, with SEM finely rugose, uniguttulate, with large central broadly ellipsoidal oil guttule.

Taxonomic Notes: This section is described to include small species with typically regularly cupulate apothecia and terete or indistinctly fluted stipes. Ascospores are broadly ellipsoidal, uniguttulate, and appear finely rugose with SEM. This section represents species accommodated in section *Macropodes* (*sensu lato* of Dissing 1966b) and section *Ephippium* of Häffner (1987).

Key to species of *Helvella* section *Cupuliformae*

1. Ascocarp black; stipe indistinctly ribbed .... *H. corium*
1'. Ascocarp grey brown; stipe terete or shallowly fluted 2

2. Stipe relatively short and stout (length less than apothecium diameter,
up to 5 mm diam.) .... *H. cupuliformis*
2'. Stipe relatively long and slender (length equal to or greater than
apothecium diameter, 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. dissingii*

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

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

Figure 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 surface finely rugose, uniguttulate.

Habitat: Gregarious on ground in clay soil under *Arbutus menziesii* and *Arbutus* sp. Fruiting period only on March 24 in Oregon.

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

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

Collections Examined: USA: Oregon: reservoir hill, Gold Hill, Stuntz (Stz 10939) March 24 1959, WTU. **Texas:** Tyler, Harris May 1892, NY. **South Carolina:** Aiken, Ravenel (922b), NY. **SWEDEN:** near Kåbo, Uppsala, Uppland, Ridelius July 30 1936, UPS (holotype); near Skogshall, Uppsala Stadsskogen, Uppland, Eriksson & Morander July 7 1948, K (paratype). **SWITZERLAND:** Arosa, Rahm October 21 1963, K.

Exsiccata Examined: Ravenel Fungi Americani Exsiccati, 760, Aiken, South

Helvella dissingii Korf, 1988, Mycotaxon 31: 381.

Synonyms: *Octospora villosa* Hedwig, 1789, Species Muscorum Frond. 2: 54, Table 19 Figure B.

Helvella villosa (Hedwig ex O. Kuntze) Dissing & Nannfeldt, 1966, Svensk Botanisk Tidskrift 60: 330 (illegitimate, later homonym).

Helvella pallidula Weber, holotype MICH, examined.

Type Material: Lectotype in Hedwig, 1788, Species Muscorum Frond. 2: 54, Table 19 Figure B Number 3.

Figure 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious or numerously scattered on ground in litter in deciduous, mixed, or coniferous woods. Associated tree species include *Pseudotsuga menziesii*, *Picea* sp., *Arbutus menziesii*, *Arbutus* sp., *Populus balsamifera*, *Betula* sp., *Alnus* sp., and *Acer* sp. Fruiting period from April 9 in Idaho to October 26 in Washington.

Geographic Distribution: Widely distributed in boreal, montane, and coastal regions from Alaska, Alberta, Washington, and Idaho. Also distributed in eastern North America (Weber 1972, as *H. villosa* and *H. pallidula*), Europe (Dissing 1966b; Dissing & Nannfeldt 1966, as *H. villosa*), and Rifai (1968, as *H. villosa*). Map 18.

Taxonomic Notes: Korf (1988) rejects the name *H. villosa* as a later homonym and renamed the species based on the same lectotype (in accordance with the International Code of Botanical Nomenclature, Berlin, 1988).

This species is closely related to *H. cupuliformis* (q.v.) which is distinguished by more yellow pigmentation of ascocarps and short robust stipe and *H. rivularis* (q.v.) characterized by smaller, dark brown ascocarps. The macroscopic morphology is very similar to *H. macropus* (q.v.) in the section *Macropodes* resulting in some confusion and misidentification of herbarium specimens, but the two species are easily separated on ascospore morphology. Colouration and habit of *H. dissingii* is also similar to *H. solitaria* (q.v.), but *H. dissingii* never has prominent ribbing of the stipe and is always of small stature. This species provides a definite link with members of the section *Elasticae*, and is closely related to *H. ephippium* (q.v.) which is similar in stature and colouration, but exhibits a more complex, lobed apothecium, typical for that section. *Helvella pallidula* was described by Weber (1972) based on the pale ascocarp colouration. No correlative features were provided in the original description and none were found in this study during examination of the holotype. Pale specimens of *H. dissingii* (reported as *H.* cf. *pallidula* by Kristiansen & Soppforening 1983) were also examined from Norway (RK 83.136) in the same locality as typical specimens of *H. dissingii*. Variation in degree of pigmentation is also seen in *H. lacunosa* (q.v.), *H. maculata* (q.v.), and *H. latispora* (q.v.) and is not considered important for specific delimitation in these taxa. Clearly *H. pallidula* represents a pale extreme in the variable

Danielson (RMD 1300) September 16 1973, ALTA 8289. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton September 21 1971, WK 5612; Birchwood, north of Anchorage, Kempton August 11 1969, WK 4127; butte area south of Palmer, Kempton August 8 1960, WK 1562. **Washington:** Friday Harbor, San Juan Island, Stuntz (Stz 11771, 12360) June 18 1960, June 11 1961, WTU; Mount Constance, Olympic National Park, Stuntz (Stz 3614) July 8 1948, WTU; Tenino south of Olympia, Bennedict (Is 1753) May 30 1962, WTU; P.P.P., Leatham (Stz 15087) October 26 1968, WTU. **Idaho:** Upper Priest River, Bonner County, Smith (NJS 2101) October 1 1968, MICH; Fall Creek, French Creek Grade, Idaho County, Smith (AHS 70096) April 9 1964, MICH. **Michigan:** Montmorency County, Smith (NJS 397) July 24 1967, MICH (holotype of *H. pallidula*). **Iowa:** Iowa City, Martin June 29 1941, UBC F3318; Decorah, Holway September 1882, NY. **Pennsylvania:** Bethlehem, Ellis July 1883, NY. **Missouri:** Meramec Heighlands, Saint Louis, Glatfelter June 12 1909, NYS. **NORWAY:** Østfold, Hvaler, Kirkeøy, Ørdal, Kristiansen September 9 1988, September 24 1989, RK 88.33, 89.94; Østfold, Hvaler, Kirkeøy, Grønvoll-Ørdal, Kristiansen September 13 1986, 86.110; Østfold, Hvaler, Kirkeøy, near Brekke, Kristiansen July 3 1983, July 7 1985, September 9 1988, RK 83.136, 85.07.07, 88.34; Østfold, Hvaler, Asmaløy, Enerstad, Kristiansen August 31 1988, RK 88.26; Østfold, Kråkerøy, near Allerød, Kristiansen October 4 1988, RK 88.44. **SWEDEN:** Halland, Onsala parish, Presse, Björkhamra, Karlvall (6944) July 8 1956, K.

Exsiccata Examined: Ellis and Everhardt Fungi Columbiani, 1219, London, Canada, Dearness August 1897, s.n. *Peziza subclavipes*, NY, K; Ellis North American Fungi, 985, Newfield, New Jersey, USA, June and September 1882, s.n. *Peziza subclavipes*, NY (packet C).

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

Type Material: Holotype C, examined; isotype C, examined.

Figure 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, 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:** 3-5 x 1-2 mm (up to 10 x 2-3 mm fresh), equal, medium grey brown to brown, when dry dark brown, pubescent, terete and internally solid. **Asci:** x 13.5-15.6 μm. **Paraphyses:** 2.4-5.1 μm diam. at apex, clavate to nearly equal, gradually enlarged to apex, pale brown, contents finely granular. **Ascospores:** 17.4-20.1 x 10.5-12.9 μm, broadly ellipsoidal, hyaline, smooth, with SEM surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious on ground in soil or mossy humus in mixed woods. Associated tree species include *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera*, and *Picea glauca*. Associated shrubs include *Salix discolor*. Fruiting period from August 6 to August 7 in Alberta.

Geographic Distribution: Rarely encountered in boreal regions from Alberta. This species is newly reported for North America. Distribution previously known in Europe from Scandinavia and Greenland (Dissing & Sivertsen 1980) and Asia (Cao & Liu typically larger with a more elongate stipe, has a stronger grey colouration, and the excipular surface has slightly finer vestiture with less distinct tufts of fascicled hyphae. Häffner (1987) suggests that *H. rivularis* may be conspecific with *H. villosa* (=*H. dissingii*), but European and North American specimens of those taxa examined here are morphologically distinct and should be retained as distinct species. *H. macropus* (q.v.) and *H. subclavipes* (q.v.) share the villose excipular surface with tufted and fascicled hairs, but are paler in colouration and have 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 stipe size up to 9 x 2 mm.

Collections Examined: CANADA: Alberta: Iosegun Lake east of Fox Creek, Abbott (SA 128) August 6 1989, SA; Notikewin Provincial Park, Abbott (SA 134) August 7 1989, SA. **NORWAY:** Nordland, Rana, Krokstrand, Tørbekken, Dissing & Sivertsen (72.95) September 7 1972, C (holotype, isotype); Østfold, Skjeberg, Mafslund parken, Kristiansen August 11, 16 1986, RK 86.45; Østfold, Krakerty, Tørkopp, Kristiansen September 1 1986, RK 86.93; Østfold, Hvaler, Kirkeøy, Ordal, Kristiansen August 29 1982, RK 87.45.

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

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

Synonyms: *Helvella arctica* Nannfeldt, isotype K, examined.

Type Material: Holotype WRSL, examined.

Figure 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, 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 numerously scattered on ground in bare soil, typically with willows in deciduous or coniferous woods or tundra. Associated tree species include *Populus tremuloides* and *Thuja plicata*. Associated shrubs include *Salix herbacea*, *Salix glauca*, *Salix* spp., *Shepherdia canadensis*, and *Dryas* sp. Fruiting period from May 20 in Washington to September 28 in Alaska. June to August collections are typical.

Geographic Distribution: Widely distributed but rarely encountered in boreal, montane, alpine, coastal, and arctic regions from Alaska, Yukon, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Washington, and Idaho. This apothecium, black ascocarp pigmentation, densely pubescent excipular surface typically with white marginal pubescence, and terete to shallowly fluted stipe. Other species with black pigmentation include *H. atra* (q.v.), *H. pezizoides* (q.v.), and *H. lacunosa*(q.v.), all of which have an irregular, lobed apothecium. White marginal pubescence is typical for this taxon, but is not seen in all individuals and tends to be more pronounced in arctic or alpine collections. *H. arctica* was initially described based on this feature by Nannfeldt (1937) and supported by Dissing (1964), but the variability of this feature was later recognized and that species was reduced to synonymy (Dissing 1966b). My observations of the type of *H. arctica* support this conclusion. White marginal pubescence is also occasionally seen in other arctic and alpine taxa including *H. arctoalpina* and *H. aestivalis*. Dark specimens of *H. arctoalpina* may appear similar, but can be differentiated by the strongly ribbed stipe with ribs extending onto the excipular surface. The morphological similarities between *H. corium* and *H. arctoalpina* and *H. solitaria* suggests an affinity with the section *Leucomelaenae*.

Collections Examined: CANADA: Yukon: Dempster Highway near Dawson, Ginns July 2 1982, DAOM 195465; east of Dawson Calder & Billard June 24 1949, DAOM 25983; near Conglomerate Mountain, Ginns June 29 1984, DAOM 195291. **Northwest Territories:** 50 km northwest of Dickson Canyon, District of Mackenzies, UNL July 19 1977, UVIC; Thelon River, Baker Lake, Ohenoja August 16 1974, DAOM 155327; Coral Harbor, Southampton Island, Savile August 16 1959, DAOM 67074. **British Columbia:** UBC endowment lands, Vancouver, Redhead June 3 1970, UBC F3390. **Alberta:** Devonian Botanic Garden near Devon, Currah August 20 1985, ALTA 8267; Athabasca Glacier, Columbia Ice Fields, Jasper National Park, Abbott (SA 373) August 2 1990, SA; near Banff, Banff National Park, Danielson (RMD 1644) August 10 1975. **Saskatchewan:** Saskatoon, Ledingham July 7 1934, DAOM 206816. **Manitoba:** Victoria Beach, Bisby June 23 1928, DAOM 206815. **USA: Alaska:** Livengood road near Fairbanks, Kempton August 18 1971, WK 5336; Birch Lake near Fairbanks, Kempton August 22 1966, WK 1530; Fielding Lake near Paxon Lake, Kempton September 3 1973, WK 6055; near Nome on Seward Peninsula, Kempton August 13 1981, WK 6407; Earthquake Park, Anchorage, Kempton August 11 1976, WK 6315; Alaska Pacific University campus, Anchorage, Kempton August 8, September 28 1971, June 28 1972, WK 5235, 5670, 5815; Caswell Creek, Susitna River valley, Kempton June 20 1970, WK 4388; near Sterling on Kenai Peninsula, Kempton August 13 1981, WK 6407; Katmai National Monument on Alaska Peninsula, Kempton September 6 1971, WK 5489; Anchorage Cove, Glacier Bay National Monument, Sprague August 9 1952, WSP AS33709; Forest Creek, Glacier Bay National Monument, Sprague August 15 1952, WSP AS33716, AS33719. **Washington:** Nachess Pass area, Laycock May 20 1987, WTU. **Idaho:** Payette Lake, Valley County, Smith & Bigelow (AHS 44224, 44434, 44847, 45154) June 26, 30, July 10, 18 1954, MICH. **Wisconsin:** Madison, Harper May 27 1904, WSP 52063; Columbia National Forest, Lewis County, July 9 1948, WSP 19572, 28587. **SVALBARD:** Loven Glacier, Currah August 12 1988, ALTA. **SWEDEN:** Torne Lappmark, Jukkasjärvi parish, Nannfeldt July 8 1928, K (type of *H. arctica*). **POLAND:** Georgenberg Landeck, Weberbauer May 1870, 1871, 1873, WRSL (holotype, authentic material);

Exsiccata Examined: Bartholomew, Fungi Columbiani, 2329, Denver Colorado, USA, Bethel May 1905, s.n. *Macropodia corium*, WSP 3425.

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.

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 surface 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.

Taxonomic Notes: Section *Macropodes* is here restricted to two closely related species, *H. macropus* and *H. subclavipes*, due to their unique spore morphology. These are the only known species of the genus with frequently subfusoidal and triguttulate spores. In addition, these species have verrucose ascospore ornamentation at maturity. This difference was not considered of taxonomic significance above the species level by Dissing (1966b), but Häffner (1987) restricted the section *Macropodes* to one species, *H. macropus* (*H. subclavipes* was not considered as a distinct species) on this basis. The genera *Macropodia* and *Macroscyphus* were established with *H. macropus* as the type, clearly recognizing the isolated taxonomic position of this species and its ally. The distinguishing features are not fundamentally different from other species in the genus and do not warrant the recognition of a separate genus. The spores are often subfusoidal, but at least some spores in each mount were more or less ellipsoidal. These ellipsoidal spores, and some of the subfusoidal ones, typically possess only one large central guttule, the condition typical for members of *Helvella*. In fact, in some collections the uniguttulate spores outnumber the triguttulate ones. Also, mounts of some other species of *Helvella* (*e.g. H. cupuliformis*, *H. arctoalpina*) rarely contain a few subfusoidal spores, especially in immature spores. Thus, spore shape and guttulation are not considered substantially different between these taxa. Ascospore ornamentation as observed with SEM shows that at maturity, the spores of the *H. macropus* group are covered with numerous small, pointed spines (Figures 53-56). However, immature spores in the same apothecia appear finely rugose (Figure 57) and are virtually indistinguishable from the pattern of ornamentation seen in all other members of the genus (Figures 45-52).

Key to species of *Helvella* section *Macropodes*

1. Stipe equal to or typically longer than apothecium diameter; ascospores 20.5-25.5 μm long; terrestrial or lignicolous on soil, humus, litter, or rotted wood .... *H. macropus*

1'. Stipe equal to or typically shorter than apothecium diameter; ascospores 18-24 μm long; terrestrial on sandy soil .... *H. subclavipes*

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

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

Synonyms: *Cyathipodia macropus* (Persoon : Fries) Dennis, fide Dissing 1966.

Type Material: unknown.

Figure 9, 53, 55, 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, smooth, excipular surface light to medium brown or grey brown, sometimes with olivaceous tints, densely pubescent to villose. **Stipe:** 12-60 x 1.5-9 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:** 246-250 x 14-16 μm. **Paraphyses:** 5.1-9.6 μm diam. at apex, clavate, enlarged gradually to abruptly at apex, pale brown to brown in mass, contents finely granular. **Ascospores:** 19.3-25.1 x 10.7-12.2 μm, subfusoidal, hyaline, smooth to verruculose, with SEM surface distinctly verrucose with numerous small isolated pointed warts, triguttulate or infrequently uniguttulate.

Habitat: Solitary to gregarious on ground in litter or soil, infrequently on rotted wood, in deciduous, mixed, or coniferous woods. Associated tree species include *Betula papyrifera*, *Alnus* sp., *Picea* sp., *Abies balsamea*, and *Thuja plicata*. Associated shrubs include *Lonicera involucrata*. Fruiting period from July 18 in British Columbia to October 19 in Washington.

Geographic Distribution: Widely distributed throughout boreal, montane, and coastal regions from Alaska, British Columbia, Alberta, Manitoba, Washington, and Idaho. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987), Asia (Dissing & Nannfeldt 1966; Liu *et al.* 1985), and Central America and the Caribbean (Dissing 1966b). Map 19.

Taxonomic Notes: This species shares with *H. subclavipes* (q.v.) the subfusoidal, triguttulate, verrucose ascospores found in no other species of the genus. This feature, as well as ascocarp colouration and vestiture, show a very close relationship between these two species (see also notes under *H. subclavipes*). Variation in the distinctive verrucose ascospore ornamentation is illustrated in Figures 53 and 55. *H. macropus* is similar in habit to species in the section *Cupuliformae*. *H. cupuliformis* (q.v.) and *H. dissingii* (q.v.) show the greatest similarities, but differ in ascocarp colouration and ascospore morphology.

Collections Examined: CANADA: British Columbia: Clearwater Lake area of Wells Gray Provincial Park, Goward August 28 1980, DAOM 186405; Clearwater River, Goward August 20 1980, DAOM 194786; Mount Revelstoke National Park, Shoemaker July 18 1963, DAOM 107075; near Mike Lake, Garibaldi Provincial Park, McClaren July 1964, UBC F3217; Golden Ears Provincial Park, Kroeger August 1 1982, UBC F1018. **Alberta:** Iosegun Lake east of Fox Creek, Abbott (SA 120, 124) August 6 1989, SA. **Manitoba:** Victoria Beach, Bisby August 8 1928, DAOM 206817. **USA: Alaska:** near Talkeetna, Kempton August 26 1972, WK 5252; Thunderbird falls trail, north of Anchorage, Kempton August 8 1960, WK 1554; Alaska Pacific University campus, Anchorage, Kempton August 31, September 28 1971, WK 5400, 5676; Finger Lake, Hood Canal are, State Park, Waugh August 1968, DAOM 126108; unknown, PSMS (Stz 15660) October 19 1969. **Idaho:** Upper Priest River, Boundary County, Smith (NJS 2002) September 21 1968, MICH; Tule Bay, Beaver Creek, Priest Lake, Bonner County, Smith (NJS 2120) October 3 1968, MICH. **Wisconsin:** Algona, Dodge August 11 1904, WSP 52070. **Michigan:** Tahquamenon Falls State Park, A.H. Smith August 7, 12 1963, UBC F3210, F3215; Cross Village, Emmet County, Shaffer August 5 1964, UBC F952; Mud Lake near Cheboygan, Brough July 19 1963, UBC F3214; north of Lewiston, A.H. Smith July 31 1963, UBC F3209; Ogemaw County, Brough July 23, August 5 1963, UBC F3211, 3213; Reese Bog, A.H. Smith July 19 1963, UBC F3208; Grass Bay, Brough July 9 1963, UBC F3212. **New York:** Ithaca, Long July 22 1902, WSP 3109. **JAPAN:** between Yuno-ko and Karikomi-ko, Honshu Island, Cannon August 23 1983, IMI 312582.

Exsiccata Examined: Rabenhorst Fungi europaei, 1413, Oberösterreich, Schiedermayr September 1870, s.n. *Helvella macropus*, K.

Helvella subclavipes (Phillips & Ellis) Abbott, *comb. nov.*

Basionym: *Peziza subclavipes* Phillips & Ellis, 1887, North American Fungi, Number 985.

Synonyms: *Paxina subclavipes* (Phillips & Ellis) Seaver
Macropodia subclavipes (Phillips & Ellis) Rehm
Helvella macropus var. *brevis* Peck, holotype NYS, examined.
Helvella brevis (Peck) Harmaja

Type Material: Lectotype selected NY, Newfield, New Jersey, USA, Phillips (3651) June 6 1882.

Figures 18, 54, 56.

Apothecium: 2-11 mm diam., 1.5-6 mm high (up to 25 mm diam. fresh), cupulate to shallowly cupulate, laterally compressed initially, margin inrolled initially, hymenium when dried brown to dark brown, smooth, excipular surface when dry medium brown, densely pubescent to villose. **Stipe:** 1-4 x 0.5-2 mm (up to 7 x 2 mm fresh), when dry medium brown, concolourous with excipular surface, equal or enlarged at base, densely pubescent, terete and internally solid. **Asci:** 175-250 x 16-18 μm. **Paraphyses:** 5-7 μm diam. at apex, clavate, enlarged gradually to apex, pale brown to brown in mass, contents granular. **Ascospores:** 18-23.8 x 10.3-12.0 μm, subfusoidal, smooth to verruculose, with SEM surface distinctly verrucose with numerous small, isolated, pointed warts, uniguttulate to triguttulate.

Habitat: Solitary to gregarious on ground in sandy/clay soil in mixed woods. Associated tree species include *Betula papyrifera* and *Picea glauca*. An associated shrub is *Alnus crispa*. Fruiting period from July 21 in Alaska to July 31 in Alberta.

Geographic Distribution: Rarely encountered in boreal and coastal regions from Alaska and Alberta. This species is newly reported from Alaska. This species is more commonly encountered in eastern North America (Weber 1972 as *H. macropus* var. *brevis*), and has also been reported from the southern United States (Seaver 1928, as *Paxina subclavipes*). At present, this species is known only from the United States and Canada. Map 19.

Taxonomic Notes: This taxon has been referred to as *Helvella macropus* var. *brevis* or *Helvella brevis* in recent literature on the genus (Weber 1972, Harmaja 1974a, Abbott & Currah 1988). The epithet *subclavipes* has been ignored since Seaver (1928) described *Paxina subclavipes* and listed *Helvella macropus brevis* as a synonym. The species was originally described and distributed as an exsiccata. Based on examination of authentic material at NY and K, a lectotype can be selected. There are several specimens from the Ellis collections, as well as several packets of Ellis North American Fungi Number 985, deposited at NY. Of these, there is one collection made by Phillips in June of 1882 and annotated by Ellis, which clearly represents the oldest collection from which the species was originally described and later distributed as an exsiccata. All features of this collection are consistent with those ascribed to this species and it is here selected as lectotype of *Peziza subclavipes*. Since the species is represented in the study area by only two collections, and the lectotype is newly selected, the above description is based on all three of these collections.

This species is closely related to *H. macropus* (q.v.), the only other species in the section *Macropodes*. Many authors (Weber 1972; Dissing 1966b) consider this taxon to be conspecific with *H. macropus* or distinct from *H. macropus* at the varietal level only, but Harmaja (1974) raised the taxon to specific status on the basis of characters outlined by Weber (1972) for *H. macropus* var. *brevis*. These features include shorter and broader ascospores, short stipe, and preference for drier habitats. My observations confirm that the stipe is consistently shorter than that of *H. macropus*. In addition, the stipe of *H. subclavipes* is always terete and lacks the shallow fluting commonly observed in specimens of *H. macropus*. My investigations also verify the shorter and relatively broader ascospores of *H. subclavipes*. Although spore size is considerably variable in other taxa of the genus, the consistent correlation with macroscopic and ecological characters is considered significant. The collections from the study area and authentic material of *H. subclavipes* supports the observation that this taxon prefers dry sites and is always collected on bare, often sandy, soil. *H. macropus* is typically found in wet to moist sites with deep litter layers. It has been suggested (Weber 1972) that morphological differences exhibited are the result of growth under different environmental conditions. Although further investigations with the examination of more collections is required to confirm the recognition of this taxon as a distinct species, the correlation of macroscopic, microscopic, ecological, and geographic characters suggests that this taxon deserves recognition at the species level. Some specimens of *H. dissingii* (q.v.) were distributed as *Peziza subclavipes* in Ellis & Everhart Fungi Columbiani 1219.

Collections Examined: CANADA: Alberta: near Fort McMurray, Danielson (RMD 1460) July 31 1974, ALTA 8294. **USA: Alaska:** Anchorage, Kempton July 21 1979, WK 6368. **Massachusetts:** Massachusetts, Morris, NYS (holotype of H. macropus var. *brevis*); Massachusetts, Davis 1906, NYS. **New Jersey:** Newfield, Phillips (3651) June 6 1882, NY (lectotype); Newfield, Ellis (3709), K; Newfield, Ellis collection September 27 1882, NY; campground, Newfield, Ellis collection November 1882, NY; Newfield, Ellis Collection September 1899, NY; Newfield, Herbarium Massee, NY; Plainfield, Meschutt July 2 1882, NY.

Exsiccata Examined: Ellis North American Fungi, 985, Newfield, New Jersey, USA, June & September 1882, NY (packets A & B), K.

Section *Elasticae* Dissing, 1966, Dansk Botanisk Arkiv 25: 128, *emend. nov.*

Type Species: *Helvella elastica* Buillard : Fries, 1822, Systema Mycologicum 2: 21.

Synonyms: section *Elasticae* Dissing, *sensu stricto*
section *Ephippium* Dissing

Ascocarp: stipitate, 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 surface finely rugose, uniguttulate, with large central broadly ellipsoidal oil guttule.

Taxonomic Notes: The section as delimited here is emended to include all species in the sections *Elasticae* and *Ephippium* of Dissing (1966b), but only some of the species treated in the section *Ephippium* of Häffner (1987)(see also comments above). The genus *Leptopodia* (*sensu* Boudier 1907), based on *H. elastica*, included many of the species ascribed to this section, but failed to include *H. monachella* (= *H. leucopus*) which was retained in the genus *Helvella sensu stricto*.

Key to species of *Helvella* section *Elasticae*

1. Apothecia dark grey brown to black; stipes darkly pigmented 2
1'. Apothecia light , medium, or dark grey to brown; stipes white to medium grey brown 3

2. Excipular surface pubescent to villose, dark brown to grey brown; apothecial margin strongly inrolled initially, typically remaining somewhat incurved at maturity ....*H. pezizoides*
2'. Excipular surface finely pubescent to glabrous, dark grey brown to black; 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 pubescent, 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 elastica Buillard : Fries, 1822, Systema Mycologicum 2: 21.

Basionym: *Helvella elastica* Buillard, 1785, Herbier de France, Plate 242 Figures A, B, D-G.

Synonyms: *Leptopodia elastica* (Buillard : Fries) Boudier

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

Figure 8.

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, 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 surface finely rugose, uniguttulate.

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

Geographic Distribution: Widely distributed and commonly collected throughout boreal, montane, and coastal regions from Alaska, Yukon, British Columbia, Alberta, Manitoba, Washington, Idaho, and Montana. Also reported from Oregon and Wyoming by Larsen & Denison (1978). Distributed in eastern North America (Weber 1972; Groves & Hoare 1953; Anderson & Ickis 1921), Europe (Dissing 1966b; Häffner 1987), and Asia (Liu *et al.* 1985; Imai 1954; Kar & Pal 1970). Map 20.

Taxonomic Notes: This species is characterized by the apothecium which is never inrolled and is reflexed from initial stages, glabrous excipular surface, and hollow stipe. *H. elastica* is most closely related to *H. albella* (q.v.). The two species share ascocarp colouration and habit, but can be distinguished by excipular vestiture and margin characteristics (see also notes under *H. albella*). *H. latispora* (q.v.) is also similar, but differs in its paler hymenium pigmentation, pubescent excipular surface at least in initial stages, and initially strongly inrolled margin. This is the most commonly encountered species of the section *Elasticae* in the study area.

Collections Examined: CANADA: Yukon: Yukon River southeast of Boundary, Ginns July 19 1984, DAOM 195457; Campbell Highway, Ginns August 4 1980, DAOM 195456. **British Columbia:** Tetsa River Provincial Park, Abbott (SA 221, 223, 225) August 22 1989, SA; Fort Nelson, Szczawinski July 27 1962, DAOM 14424; south of Wells Gray Provincial Park, Goward September 8 1980, DAOM 186396; near Clearwater, Goward September 10 1982, DAOM 191772; Adams River south of Adams Lake, Goward, October 21 1982, DAOM 191779; Francis Park, Victoria, Vancouver Island, Melburn November 1 1962, DAOM 109932; Victoria, Vancouver Island, Newcombe, K. **Alberta:** Shaw Lake east of Lac La Biche, Abbott (SA 102) July 15 1989, SA; Musreau Lake south of Grande Prairie, Abbott (SA 246, 247, 253, 261) August 26 1989, SA; Iosegun Lake east of Fox Creek, Abbott (SA 125) August 6 1989, SA; William A. Switzer Provincial Park, Abbott (SA 265, 270) August 27 1989, SA; William A. Switzer Provincial Park, Osis (SA 389, 390) September 2 1990, SA; Devonian Botanic Garden near Devon, Abbott July 27 1987, ALTA 8269; Devonian Botanic Garden near Devon, Currah August 19 1980, ALTA 8270; near Ponoka, Stewart August 16 1962, ALTA 667; Fish Lake near Nordegg, Abbott (SA 281, 287, 288, 382, 399) August 31 1989, August 4, September 8 1990, SA. **Manitoba:** Clear Lake, Bisby August 17 1935, DAOM 206804. **Ontario:** Blue Lake, Brant County, Cain October 14 1956, WSP 45561. **USA: Alaska:** Harding Lake near Fairbanks, Kempton August 26 1965; Fox Springs near Fairbanks, Kempton August 7 1970, WK 4620; Eklutna Lake north of Anchorage, Kempton August 29 1961, WK 1580; Lower Skilak Lake, Kenai Peninsula, Kempton September 27 1965, WK 1581; Bartlett River trail, Glacier Bay National Monument, Cooke September 1, 4, 9 1979, September 1 1981, WSP 64398, 67208, MU F34794, F36152; Haines, Kempton September 21 1970, WK 4974; Auke Bay near Juneau, Kempton September 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) June 8 1948, November 13 1954, December 25 1960, November 29 1968, WTU; Friday Harbor, San Juan Island, Isaacs (Is 2013) November 11 1962, WTU; Friday Harbor, San Juan Island, McCabe (Stz 19893) November 20 1976, WTU; Friday Harbor, San Juan Island, Tyler (Stz 12221) November 12 1960, WTU; San Juan campground, Stevens Pass road, SDLB September 26 1976, WTU; Seattle, Zeller (180), WTU; Isput Creek, Mount Rainier National Park, Williams (JWL 1228) October 20 1971, WTU; Trout Lake-Cispus junction, van de Bogart (FVB 1015) October 23 1971, WTU; Iron Butte, van de Bogart (FVB 3805) October 31 1976, WTU; Iron Creek, van de Bogart (FVB 2882) July 13 1974, WTU; Turpin Meadow road, Ammirati (JFA 9546) August 13 1987; P.P.P., Stuntz (Stz 15084) October 26 1968, WTU; unknown, (Stz 982), WTU. **Idaho:** Clearwater Canyon east of Lenore, Nez Perce County, Cooke June 5 1947, WSP 24506; Fall Creek at French Creek Grade, Idaho County, Miller September 4, 7 1964, WSP 53685, 53845, 54086. **Montana:** Echo Lake, Flathead National Forest, Cummins July 20, 30 1928, MICH. **Michigan:** Ellston, Isaacs (Is 26a) July 20 1957, WTU. **SWEDEN:** Uppsala, Fries, K. **UNITED KINGDOM:** unknown, Coch September 1872 Herbarium Berkeley, K; Toscana Bicchi autumn 1859, K; Nadelwaldern, Petrak August 1936, IMI 38460.

Exsiccata Examined: Fungi Suecici, Hejdeby parish, Gotland, Pettersson October 11 1946, WSP 31527.

Helvella albella Quélet, 1896, Association Francaise pour l'Avancement des Sciences. Comptes-Rendus 24, 2: 621, Plate 6 Figure 16.

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, 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 surface finely rugose, uniguttulate.

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

Geographic Distribution: Widely distributed but infrequently encountered in boreal, montane, and coastal regions from Alaska, British Columbia, Alberta, Washington, and Idaho. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987) and Asia (Liu & Cao 1988). Map 21.

Taxonomic Notes: This species is very closely related to *H. elastica* (q.v.), but differs in its pubescent excipular surface 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 connected with the appropriate taxon 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 or in this study which observe a greater range of variation in the ascospore width of *H. elastica*. *H. latispora* (q.v.) is also closely related and shares the initially incurved apothecium which becomes reflexed at maturity and the finely pubescent excipular surface. These species are easily distinguished by hymenium colouration and fruiting time. The apothecial margin of *H. latispora* is also more highly inrolled over the hymenium in immature stages.

Collections Examined: CANADA: British Columbia: Stone Mountain Provincial Park, Abbott (SA 164) August 12 1989, SA; Kaslo, Bell August 18 1959, UBC F3265. **Alberta:** Notikewin Provincial Park, Abbott (SA 138) August 7 1989, SA; Fawcett Lake, Abbott September 3 1988, ALTA 8316, 8317; Edmonton, Redhead September 3 1970, UBC F3268; Fish Lake near Nordegg, Abbott (SA 374, 376) August 3 1990, SA; Glenmore Park, Calgary, Danielson (RMD 274) September 11 1972, ALTA 8288. **USA: Alaska:** Eklutna Lake, Kempton July 27 1974, WK 6157; Juneau, Kempton July 30 1966, WK 1587. **Washington:** Seattle, Stuntz December 6 1934, WTU; Seward Park, Snyder October 28 1933, WTU; Green Lake, Mount Rainier National Park, Stuntz (Stz 7605) October 19 1952, WTU. **Idaho:** Priest River Experimental Forest, Bonner County, Slipp, WSP 49798. **SWEDEN:** Uppsala, Carolinaparken, Melderis September 30 1945, K. **UNITED KINGDOM:** Quantocks, Somerset, Marrage September 20 1960, IMI 83231. **GERMANY:** Neuensorgen Forest, Lichten Fichtenwald, Engel (423) July 25 1974, K.

Helvella leucopus Persoon, 1822, Mycologica Europaea 1: 213.

Type Material: Lectotype L, examined.

Geographic Distribution: Known from Europe (Dissing 1966b), north Africa (Dissing 1966b) and Asia (Liu *et al* 1985).

Taxonomic Notes: This species is closely related to *H. elastica* (q.v.) and *H. albella* (q.v.), but differs in its darker hymenium colouration, larger ascocarp size, robust stipe, and more complex lobed apothecium. No specimens referable to this taxon were found during this investigation, but Dissing (1966b) reports this species from Idaho. Weber (1975) also reports this species from Idaho, but no specimen was located in MICH in this study. These are the only reports of this species from North America, and its occurrence on this continent is questionable. Häffner (1987) synonymizes the older *H. spadicea* Schaeffer, but I have not examined type material of this species.

Collections Examined: NETHERLANDS: Herbarium Persoon, L 8945-2 (lectotype).

Exsiccata Examined: Herbarium Mycologicum Romanicum, 667, Mutenia, district Ilfov-Comeful, Rumania, Savulescu & Alexandri May 8 1933, s.n. *Helvella monachella*, IMI 29629.

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

Synonyms: *Helvella stevensii* Peck, holotype NYS, examined.
Helvella connivens Dissing & Lange, fide Weber (1972).

Type Material: Holotype PC, examined.

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, 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 surface finely rugose, uniguttulate.

Habitat: Gregarious on ground in soil or litter in deciduous, mixed, or coniferous woods. Associated tree species include *Alnus rugosa, Populus* sp., and *Picea glauca.* Fruiting period from June 27 in Idaho to August 29 in Manitoba.

Geographic Distribution: Rarely encountered in boreal and montane regions from Manitoba and Idaho. Distributed in eastern North America (Weber 1972) and Europe (Dissing 1966b; Häffner 1987). This species is newly reported from Manitoba. Larsen & Denison (1978) report this species (as *H. stevensii* and *H. connivens*) from Oregon and Washington, but these reports may refer to *H. compressa.* Map 22.

Taxonomic Notes: This species is closely related to *H. compressa* (q.v.) and the two species are primarily distributed in the eastern and western north America. They can be easily separated by the villose excipular surface and darker hymenial pigmentation of *H. compressa*. *H. latispora* is also closely related to *H. albella* (q.v.), but can be separated by characters of ascocarp colouration. The apothecial margin of *H. latispora* is also typically more strongly inrolled over the hymenium in initial stages. The specimen from Idaho (see also Weber 1975) is the only western collection of *H. latispora* examined in this study, and shares the pale hymenium and finely pubescent excipular surface typical of eastern collections.

Häffner (1978) synonymizes *H. stevensii* with the Boudier's (1898) older *H. latispora*. The type of *H. latispora* is morphologically similar to the type of *H. stevensii*. Dissing (1966a, b) retained *H. latispora* as distinct on the basis of the broad ascospores (13.5-18 µm in Dissing 1966b), but my measurements of spores in distilled water from the type specimen show a range from 11.8- 14.0 µm in width. Ascospore size is not sufficient to warrant specific status unless other characters can be correlated.

Collections Examined: CANADA: Manitoba: Rolling River road, Riding Mountain National Park, Ginns & Hammersley August 23 1979, DAOM 176223; near Bear Lakes, Riding Mountain National Park, Redhead August 29 1979, DAOM 175852. **USA: Idaho:** Twin Lakes, Kootenai County, Weber (NSW 3653) June 27 1972, MICH. **Michigan:** Detroit, Stevens June 1903, NYS (holotype of *H. stevensii*); Pellston Hills west of Pellston, Shaffer July 14 1964, UBC F951. **Iowa:** Amana, Martin & Brasfield June 7 1938, ALTA 664, 665, 666. **NORWAY:** Østfold, Kråkerøy, Rød, Ekheim-parken, Kristiansen July 28 1985, RK. **UNITED KINGDOM:** Kirk Lane, Priory, Yorkshire, Holland September 13 1983, IMI 290669; Chevering Park, Kent, Reid October 16 1982, K. **FRANCE:** France, Boudier Herbier Mycologique, PC (holotype).

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

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

Type Material: Isotype NY, examined.

Figure 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 surface finely rugose, uniguttulate, with large central globose to broadly ellipsoidal oil guttule.

Habitat: Solitary, gregarious, subcespitose, or numerously scattered on ground in soil or litter, rarely with burnt wood debris, in coniferous or infrequently in mixed or deciduous woods. Associated tree species include *Pseudotsuga menziesii, Abies grandis, Pinus ponderosa, Thuja plicata, Quercus garryana, Alnus rubra,* and *Acer* sp. Associated shrubs include *Symphoricarpos* sp. Fruiting period from March 9 to December 25 in coastal Washington. April to June collections are common.

Geographic Distribution: Distributed in coastal and montane regions in the western portion of the study area from Alaska, British Columbia, Washington, Idaho, and Oregon. Endemic to western North America, and known only west of the Rocky Mountains. This species is newly reported from Alaska, British Columbia, Idaho, and Oregon. Known distribution extends south of the study area to California (Weber 1975). Map 22.

Taxonomic Notes: This species is closely related to *H. latispora* (q.v.) but is distinguished by geographic distribution, ascocarp pigmentation, and excipular surface 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 Provincial Park, Vancouver Island, Ramsay April 5 1978, UVIC; Mount Douglas Park, Victoria, Vancouver Island, Paden (JWP 583, 584, 1383) April 5, 7 1968, March 20 1987, UVIC; Mount Douglas Park, Victoria, Vancouver Island, Egger (877, 955) April 10 1982, March 29 1983, DAOM 199815, 199816, 199793; University of Victoria campus, Vancouver Island, Paden (JWP 710, 743) May 10 1969, April 3 1970, UVIC; Roche Cove Park, East Sooke , Paden (JWP 1326) April 26 1986, UVIC; Sooke road, Vancouver Island, Paden (JWP 1171) May 11 1981, UVIC; near Saturna Beach, Saturna Island, Kroeger May 16 1986, UBC F12511. **USA: Alaska:** Eklutna Lake north of Anchorage, Kempton August 29 1972, September 11 1973, WK 5901, 6057. **Washington:** Friday Harbor, San Juan Island, Snyder (Stz 12223) November 12 1960, WTU; Friday Harbor, San Juan Island, McCabe (Stz 19893) November 20 1976, WTU; Friday Harbor, San Juan Island, Brough (56, 67) April 21, May 5 1957, WTU; Friday Harbor, San Juan Island, Stuntz (Stz 2378, 12143, 12173, 12270, 12371) October 30, November 5, December 25 1960, June 4 1961; Friday Harbor, San Juan Island, Isaacs (Is 1711a, b) May 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) March 9 1958, WTU; south of Olympia, Isaacs (Is 1754) May 30 1962, WTU; Easton, Snyder May 5 1934, NY (isotype); California Creek near Valley Ford, Cooke June 8 1947, WSP; Bingen Mountain, Klickitat County, Suksdorf May 1 1899; FHL fire trail, SDL-B April 9 1977, WTU; unknown, SDL-B March 25 1977, WTU; unknown, Snyder May 5 1934, WTU. **Idaho:** northeast of Robinson Lake, Latah County, Koenigs July 19 1964, WSP 55003. **Oregon:** Wilsonville, Ardrey (CA 1166) April 20 1987, WTU; Mary's Peak road, Paden March 26 1970, UVIC.

Exsiccata Examined: Vancouver Island Fungi, 499, Vancouver Island, British Columbia, Canada, Macoun April 13 1915, s.n. *Helvella elastica*, UBC F3256.

Helvella atra Holmskjøld : Fries, 1822, Systema Mycologicum 2: 19.

Basionym: *Helvella atra* Holmskjold, 1799, Beata ruris otia Fungis Danicis impensa 2: 47, Table 25.

Synonyms: *Helvella subglabra* Weber, holotype MICH, examined.

Type Material: Lectotype in Holmskjøld, 1799, Beata ruris otia Fungis Danicis impensa 2: 47, Table 25, (selected Dissing 1966b).

Figures 7, 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, 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 fluted especially at base, terete or sulcate and 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 surface finely rugose, uniguttulate.

Habitat: Gregarious to numerously scattered on ground or rotted wood in deciduous or mixed woods. Associated tree species include *Populus tremuloides*, *Alnus tenuifolia*, and *Larix laricina*. An associated shrub is *Salix discolor*. Fruiting period from July 14 in Montana to September 2 in Alberta.

Geographic Distribution: Rarely encountered in boreal and montane regions east of the Rocky Mountains from Alberta and Montana. Also distributed 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.

Taxonomic Notes: This species is most closely related to *H. pezizoides* (q.v.). *H. atra* is characterized by the finely pubescent excipular surface, slightly incurved apothecial margin even in submature stages, and strong grey to black ascocarp colouration. Both *Helvella atra* and *H. pezizoides* are occasionally collected from rotted wood. Häffner (1987) suggests that the two species may be synonymous. The species are certainly more closely related to each other than to other species in the genus, and intermediate collections are sometimes found, but the correlation of ascocarp colouration, vestiture, and marginal curvature warrant specific recognition. Intensive studies of the two species should be undertaken to clarify differences between the two species.

Weber (1972) separated *H. subglabra* as distinct from *H. atra* on the basis of grey to dark grey ascocarp colouration and very fine excipular vestiture, as opposed to the black glabrous apothecium of *H. atra*. Both of these features are variable in other taxa of the genus (*e.g. H. lacunosa*, *H. albella*, and *H. latispora*) and are insufficient to warrant specific recognition. This supports the view of Häffner (1987).

Collections Examined: CANADA: Alberta: Minnie Lake near Glendon, Abbott August 10 1983, ALTA 8265; Devonian Botanic Garden near Devon, Abbott, July 25, 28 1987, September 2 1988, ALTA 8266, 8297, 8310; Devonian Botanic Garden near Devon, Abbott (SA 110) July 27 1989, SA. **USA: Montana:** Echo Lake, Flathead National Forest, Cummins July 14 1928, MICH. **Michigan:** Reese Bog, A.H. Smith July 10, 27 1963, UBC F3241, F3267.

Helvella pezizoides Afzelius : Fries, 1822, Systema Mycologicum 2: 20.

Basionym: *Helvella pezizoides* Afzelius, 1783, Kungliga Vetenskaps-Akademiens. Nya Handlingar 4: 308, Plate 10 Figure 2.

Type Material: Lectotype in Afzelius, 1783, Kungliga Vetenskaps-Akademiens. Nya Handlingar 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 surface finely rugose, uniguttulate.

Habitat: Solitary to gregarious on ground in soil, humus, rotted wood in woodland, bog or tundra habitats. Fruiting period from July 27 in Alaska to August 16 in the Northwest Territories and Alaska.

Geographic Distribution: Rarely encountered in boreal, coastal, and arctic regions from Alaska, Northwest Territories, and Alberta. This species is newly reported for the Northwest Territories and Alaska. Also distributed 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.

Taxonomic Notes: This species is closely related 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 excipular surface 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 & Wells (1970). *H. ephippium* (q.v.) is also related, but is easily separated by the paler ascocarp colouration.

Collections Examined: CANADA: Northwest Territories: mouth of Thelon River, Baker Lake, Ohenoja August 16 1974, DAOM 155302; Williamson Lake, Rankin Inlet, Ohenoja August 10 1971, DAOM 155313. **Alberta:** Kinsmen ravine, Edmonton, Elisens August 1977, ALTA 7606. **USA: Alaska:** near Nome, Seward Peninsula, Kempton August 12 1967, WK 1533; butte area near Palmer, Kempton July 27, August 16 1961, WK 1534, 1535. **Michigan:** Tahquamenon Falls State Park, Brough (513) August 9 1963, UBC F3266. **JAMAICA:** Blue Mountain, Dennis December 20 1949, K. **NORWAY:** Østfold, Borge, Torp, Kristiansen July 6 1984, August 1 1987, RK 87.21. **FRANCE:** Paris, Reid August 10 1989, K.

Exsiccata Examined: Karsten Fungi Fenniae, 446, På ängsbackar vid Mustiala, Karsten August 1866, s.n. *H. atra* , K.

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

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 when dried dark grey brown, smooth, excipular surface medium brown to grey brown, pubescent to villose. **Stipe:** 15 x 1.5-2 mm, equal, 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 surface finely rugose, uniguttulate.

Habitat: Solitary on ground in soil or humus in deciduous, mixed, or coniferous woods. Associated tree species include *Picea glauca, Abies balsamea,* and *Populus* sp. Associated shrubs include *Cornus stolonifera*. Fruiting period from August 1 in Manitoba to September 15 in Alberta.

Geographic Distribution: Rarely encountered in boreal regions of the study area. Known from Alberta and Manitoba. Also distributed in eastern North America (Weber 1972), Europe (Dissing 1966b; Häffner 1987), and Asia (Imai 1954). Map 23.

Taxonomic Notes: This species is related to *H. pezizoides* (q.v.) and *H. atra* (q.v.). Those species are distinguished by the black ascocarp colouration. Additionally, *H. ephippium* shows no fluting on the slender stipe. *H. ephippium* is also morphologically similar to *H. dissingii* (q.v.) in the section *Cupuliformae* which shares ascocarp colouration and stature, but *H. dissingii* is typically cupulate, while *H. ephippium* exhibits a more complex folded and lobed apothecium. These species provide a definite link between their respective subgeneric sections.

Collections Examined: CANADA: Alberta: Emily Murphy Park, Edmonton, Tsuneda September 15 1976, ALTA 7446; Pearce Estate, Calgary, Danielson (RMD 1278) September 14 1973, ALTA 8287. **Manitoba:** Victoria Beach, Bisby August 1 1927, DAOM 154814. **NORWAY:** Ørdal, Kirkoy, Hvaler, Østfold, Kristiansen July 22, October 24 1982, RK.

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

Synonyms: *Geomorium* Spegazzini

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 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.

Synonyms: *Helvella columnaris* (Peck) Eckblad

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

Figures 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, 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 or smooth when immature, with SEM warts large isolated broadly rounded, typically uniguttulate, rarely aguttulate or biguttulate.

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

Geographic Distribution: Rarely encountered in boreal regions in the eastern portion of the study area from Manitoba. Also distributed in eastern North America (Seaver 1928, 1942; Jensen 1977). This species is endemic to eastern North America and only extends into the study area in the extreme south east.

Taxonomic Notes: This species is closely related to the other two species in the genus, *U. beatonii* and *U. fuegiana*. These species are known from Australia and Argentina respectively. *U. columnaris* is distinguished from both species by its smaller ascospore size. 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 July 13 1927, July 28 1928, DAOM 206822, 206823; Manitoba Agricultural College, Winnipeg, Bisby August 1 1927, DAOM 154831; Red River, South Manitoba Agricultural College, Winnipeg, Bisby August 1 1928, DAOM 1080, 206824; Winnipeg, Bisby July 10 1932, K. **USA: Michigan:** Middle Maple River, A.H. Smith & Stuntz (Stz 2800) July 15 1947, WTU.

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

Basionym: *Geomorium fuegianum* Spegazzini, 1922, Anal. Soc. Scient. Arg. 94: 79.

Synonyms: *Helvella fuegiana* (Spegazzini) Eckblad

Type Material: unknown.

Geographic Distribution: Known from South America (Gamundi & Horak).

Taxonomic Notes: This species is closely related to the other two species of the genus, but differs in geographic distribution and morphology. I have seen no specimens of *U. singeri*, also described from South America (Gamundi & Horak 1979).

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

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

Synonyms: *Helvella beatonii* (Rifai) Harmaja

Type Material: Holotype K, examined.

Geographic Distribution: Known only from Australia (Rifai 1968).

Taxonomic Notes: This species is closely related to the two other species of the genus. It is distinguished from *U. columnaris* (q.v.) by its larger ascospore size. *U. 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

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

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

Synonyms: *Geoporella* Soehner
Gyrocratera Hennings

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

Macroscopic Features: ascocarp hypogeous, sessile, apothecium 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, inoperculate to operculate, 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 of textura intricata and ectal excipulum of textura angularis or textura prismatica..

Key to subgeneric sections of *Hydnotrya*

1. Ascospore ornamentation slab-like to nodulose .... *Hydnotrya*
1'. Ascospore ornamentation echinate .... *Cerebriformae*

Section *Hydnotrya*

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

Ascocarp: sessile, apothecium 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 ornamentation typically slab-like when submature, becoming greatly thickened over entire spore surface, often nodulose-verrucose, with large isolated broadly rounded warts, thick polar apiculi present or absent, uniguttulate to aguttulate, de Bary bubbles absent or present in small proportion of mature spores.

Taxonomic Notes: The typical section includes species with irregularly thickened to nodulose globose to broadly ellipsoidal ascospores (Figures 59-62).

Key to species of *Hydnotrya* section *Hydnotrya*

1. Ascospores distinctly nodulose at maturity.. 2
1'. Ascospores slab-like to punctate at maturity.. 3

2. Ascospores globose to subglobose..*H. tulasnei*
2'. Ascospores ellipsoidal to broadly ellipsoidal..*H. michaelis*

3. Ascospores at maturity with large depressed apiculi...............................*H. cubispora*
3'. Ascospores at maturity nonapiculate..*H. variiformis*

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

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

Synonyms: *Hydnotrya carnea* (Corda) Zobel, authentic material K, examined.
Hydnotrya intermedia (Bucholtz) Soehner, fide Gilkey (1954).

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

Figure 61.

Apothecium: 10-18 mm diam., 8-16 mm high, irregularly globose to subglobose, margin entirely fused, excipular (exterior) surface red brown to dark red brown, glabrous, undulate-rugose, internally highly convoluted and chambered, chambers white, 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, nodulose, with SEM surface with broadly rounded warts, uniguttulate to aguttulate.

Habitat: Hypogeous, solitary or gregarious in duff or rotted wood on the ground under conifers. Associated tree species include *Pinus contorta*, *Pseudotsuga menziesii*, and *Tsuga heterophylla.* Fruiting period from June 20-27 in Oregon.

Geographic Distribution: Rarely encountered in montane regions from Oregon (see also Fogel 1974). Also distributed in eastern North America (Gilkey 1954), Europe (Lange 1956), and Asia (Trappe 1976). Map 24.

Taxonomic Notes: This species is characterized by dark red brown colouration of excipular surface, highly convoluted and infolded with numerous tightly appressed internal chambers, and globose to subglobose nodulose-verrucose ascospores. This species is most closely related to *H. michaelis* (q.v.), but is separated on characters of ascocarp colouration, 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 Batchelor, Egger (1135) June 27 1984, DAOM 199694; near Bend, Miller (SM 745) June 20 1984, Elsehoved, Fyn, Lange (3082) August 11 1949, K. **NETHERLANDS:** De Steeg Prov. Felderland, Bas (1055) August 7 1956, K. **CZECHOSLOVAKIA:** Prague, Corda Herbarium Berkeley 1879, K; Bohemia, Bubák August, IMI 11956.

Exsiccata Examined: Sydow, Mycotheca germanica, Schlesien, bei Krummhübel, Riesengebirge, Germany, Sydow August 17 1922, s.n. *Hydnotrya carnea*, K; Sydow, Mycotheca germanica, Schlesien, Grenzdorf bei Schwarzbach, Isergebirge, Germany, Sydow July 28 1922, s.n. *Hydnotrya carnea*, K; Petrak, Mycotheca generalis, 433, Steirmark, Mürzzuschlag, Mitterdorf, Keissler June-July 1940, s.n. *Hydnotrya tulasnei*, WSP AS18300.

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

Basionym: *Geopora michaelis* Fischer, 1898, Hedwigia 37: 59.

Synonyms: *Hydnotrya ploettneriana* (Hennings) Hawker, authentic material K, examined.

Hydnotrya yukonensis Gilkey, holotype DAOM, examined.

Type Material: Holotype TO.

Apothecium: 13-18 mm diam., 8-10 mm high, irregularly globose, flattened, lobed, exterior surface pale brown to reddish brown, pubescent to glabrous, undulate-rugose, margin entirely fused at base, 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. **Ascospores:** 27.5-33.0 x 20.5-25.5 µm, broadly ellipsoidal, brown, hyaline when immature, nodulose-verrucose, with SEM surface with large isolated broadly rounded warts, immature spores smooth, aguttulate or uniguttulate especially when immature.

Habitat: Solitary to gregarious in soil in mixed woods. Associated tree species include *Picea glauca, Tsuga* sp., and *Alnus* sp. Fruiting period in early July in Yukon to July 27 in Alaska.

Geographic Distribution: Rarely encountered in montane and coastal regions from Yukon and Alaska. Also distributed in Colorado (Fogel & Trappe 1976) and Europe (Kers 1989; Patouillard 1925; Teudorowiczc 1928, as *Geopora michaelis*). A map of global distribution is provided in Kers (1989). Map 25.

Taxonomic Notes: This species is closely related to *H. tulasnei* (q.v.), which has very similar ascospore ornamentation. *H. michaelis* is distinguished by paler ascocarp colouration, larger lobes and internal chambers, and broadly ellipsoidal ascospores. *H. cubispora* (q.v.) is macroscopically similar, but can be easily differentiated by its apiculate ascospores.

Collections Examined: CANADA: Yukon: near Potato Hills, Mayo Landing, Broadfoot early July 1943, DAOM 14081 (holotype of *H. yukonensis*). **USA: Alaska:** near Hope, Kempton July 27, WK 3023. **UNITED KINGDOM:** Soudley Ponds near Littledean, Gloucestershire, Francis May 23 1981, IMI 259183, 259184. **GERMANY:** Fichtenwald, Engel (415) July 14 1974, K. **UNKNOWN:** Kiefernwald, Plöttner (1325) May 1900, K; Mähr-Weisskirchen, Petrak August 1929, WSP 31544.

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

Basionym: *Genea cubispora* Bessey & Thompson, 1920, Mycologia 12: 284.
Type Material: Isotype MICH, examined.
Figures 16, 59, 60.

Apothecium: 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, pubescent to glabrous, undulate-rugose, margin entirely fused or open at base, internally highly convoluted, chambered, with some closely appressed folds and large chambers, 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, with large cupulate apiculi at poles at maturity, apiculi often striate on inner surface, wall thickening often slab-like when submature resulting in angular or cuboidal appearance of submature spores, often with irregularly thickened wall and surface appearing undulate with SEM.

Habitat: hypogeous or embedded in rotted wood, solitary to gregarious in soil or rotted woody debris in coniferous woods. Associated tree species include *Picea sitchensis, Pinus monticola, Tsuga heterophylla*, and *Tsuga* sp. Fruiting period from September 12 in Washington to November 8 in British Columbia.

Geographic Distribution: Rarely encountered in montane and coastal regions from Alaska, British Columbia, and Washington. This species is newly reported from British Columbia. Also distributed in eastern and southern North America (Gilkey 1939; Miller & Miller 1982). Examination of British collections at K and IMI have uncovered three collections of this species. These are the first reports of the occurrence of this species in Europe (Spooner, pers. comm.). Map 24.

Taxonomic Notes: This species is well separated from all others in the genus, but is included in the typical section on the basis of the irregularly thickened spore wall which is often slab-like when immature and inconspicuously nodulose at maturity. This feature suggests a closer relationship with *H. tulasnei* (q.v.) and *H. michaelis* (q.v.) than to *H. cerebriformis* (q.v.) of the section *Cerebriformae*. In addition, ascocarp morphology and colouration are similar between these species. *H. cubispora* is easily distinguished by its large cupulate apical apiculi on mature ascospores. The concept of this taxon has been somewhat confused since its original description which characterized the species as having cuboidal or polygonal ascospores. Examination of the isotype (MICH) revealed that the species was originally described on the basis of immature and submature specimens. The spores of these specimens did not possess the typical well developed apiculi on most spores and this important distinguishing character was not reported. Spore measurements reported above were taken only from mature ascospores and therefore are considerably larger than reported in the original description (27-42 x 24-28 µm in Bessey & Thompson 1920). Gilkey (1954) recognized that early descriptions had been based on immature specimens, and revised the spore description. The spore description was amended to state that the cuboidal shape remains throughout maturity, and that the basic spore shape is ellipsoidal rather than globose. In addition, Gilkey which would have soon differentiated into distinct apiculi. My observations show that the angular spore shape is prominent only in submature spores and that apical thickening of the spore wall precedes apiculus development. My examinations support the observation that the spore proper is broadly ellipsoidal to subglobose, rather than globose. The collections from the United Kingdom represent the first reports of the species in Europe, but it is likely that it was introduced with planted conifers, and is essentially endemic to North America. Trappe (1971) lists this species as mycorrhizal with conifers and the new reports from Europe support this conclusion.

Collections Examined: CANADA: British Columbia: Forest Nursery at Haney, Bandoni (Stz 13359) November 8 1965, WTU. **Quebec:** south of Chigoubiche River, Lac St. Jean Ouest County, Redhead September 4 1976, DAOM 160752; St. Donat, Montcalm County, Rousseau 1965, DAOM 197990; Parc de la Gatineau, Chemin du Lac Lapêche, Dalpé July 30 1985, DAOM 197989. **New Brunswick:** Moore's Falls, Kings County, Harrison August 1 1953, DAOM 143006; Glenmont, Harrison October 10 1952, DAOM 111849; Casey's Corner, Harrison October 12 1952, DAOM 111848. **USA: Alaska:** Girdwood, Kempton September 18 1969, WK 4288; Turnagain Pass on Seward highway, Kempton October 21 1963, WK 3033. **Washington:** the Pines, Copalis, Roger (Stz 20390) September 24 1978, WTU; the Pines, Copalis, Stuntz (Stz 20629) September 12 1979, WTU; near Copalis, SDL-B (SLB 1523) September 24 1978, WTU; Troublesome Creek, Stuntz (Stz 20389) September 25 1978, WTU. **Michigan:** between Bass and Little Bass Lakes, Cisco Lake Chain, Gogebic County, Bessey & Darlington (123) August 14 1919, MICH (isotype). **West Virginia:** Canaan valley, Tucker County, Cooke August 3 1985, WSP 68005. **UNITED KINGDOM:** Scotland, October 1 1975, October 12 1982, K (M) 16811, 16812 ex E; Soudley Ponds, Gloucestershire, Clark August 16 1986, IMI 311325.

Hydnotrya variiformis Gilkey, 1947, Mycologia 39: 444.

Type Material: Holotype OSC.

Figures 17, 62.

Apothecium: 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 pale yellow brown or orange brown to dark red brown, 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, verruculose to punctate, with SEM surface appearing punctate and with small irregular nodulose wall thickenings, aguttulate or uniguttulate especially when immature, with large central globose oil guttule, de Bary bubbles present in small proportion of mature spores.

Habitat: Hypogeous or embedded in rotted wood, solitary to gregarious in woody debris in coniferous woods. Associated tree species include *Abies lasiocarpa* and *Tsuga* but is irregularly thickened and slightly nodulose at maturity. Punctate spore surface is unique in the genus. In addition, *H. variiformis* frequently exhibits strong yellow colouration when immature. All collections of *H. variiformis* examined were made from rotted wood (or no annotation of substrate was provided), while other species in the genus are frequently collected from soil substrates. This species is similar to *H. cerebriformis* (q.v.) in its yellow brown spore wall at maturity and the occurrence of de Bary bubbles in a small proportion of mature spores (see also notes under *H. cerebriformis*).

Collections Examined: USA: Alaska: near Hope, Kempton July 28 1968, WK 3016. **Idaho:** Brundage, Hawker August 2, 8 1962, K; Brundage road, Hawker August 22 1962. **Oregon:** Three Creek Lake southwest of Sisters, Deschutes County, Fogel (1 174) August 20 1976, DAOM 178574, K. **Wyoming:** Medicine Bow Mountains, Carbon County, Binegar August 10 1950, WSP 28610, MU F35625. **California:** Sisson Southern trail, Mount Shasta, Cooke June 27 1947, WSP 391 19; Panther Creek Meadows, Mount Shasta, Cooke July 1 1951, WSP 30042; horse camp area, Mount Shasta, Cooke August 17 1962, July 18 1966, WSP 55752, 58743.

Section *Cerebriformae* Abbott, *sect. nov.*

Ascocarpia 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.

Ascocarp: hypogeous to erumpent, sessile, irregularly lobed, globose to ellipsoidal, typically flattened, margin fused 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, 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, aguttulate or uniguttulate especially when immature, with large central subglobose oil guttule, de Bary bubbles in a small proportion of mature spores.

Taxonomic Notes: This monotypic section is established on the basis of the globose, echinate ascospores of *H. cerebriformis*.

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

Type Material: Holotype Harkness Collection, Stanford.

Figures 28, 63, 64.

Apothecium: 8-24 mm diam., 8-13 mm high (up to 50 mm diam. fresh), irregularly

Ascospores: 26.1-32.8 x 24.2-27.8 μm, globose, subglobose, or broadly ellipsoidal, brown at maturity, hyaline when immature, appearing pitted to verrucose, with SEM surface covered with numerous long pointed spines, but often appearing punctate due to adhering perispore, aguttulate or uniguttulate especially when immature.

Habitat: Hypogeous to erumpent, solitary to gregarious in soil and litter in coniferous woods. Associated tree species include *Picea engelmannii* and *Picea sitchensis*. Fruiting period from July 29 to September 20 in Alaska.

Geographic Distribution: Infrequently encountered in montane and coastal regions from Alaska and Idaho. This species is newly reported from Alaska and greatly extends the known northerly distributional range. Also distributed in south west North America (Gilkey 1916, 1939; Fogel & Trappe 1976). Map 25.

Taxonomic Notes: This species is taxonomically distinct, but may be most closely related to *H. variiformis* (q.v.) which is similar in macroscopic morphology and possesses de Bary bubbles in ascospores at maturity. *H. cerebriformis* differs in its globose to subglobose ascospores with prominent echinate ornamentation. The ornamentation of the ascospores as observed with SEM are quite variable. In many cases the spores appear echinate with distinct spines or coalesced clumps of spines, but often the spore surface appears irregularly cracked. This is attributed to adhering perispore or mucous tissue adhering to the spore wall ornamentation. This feature was observed by Hawker (1968a) in her SEM investigations of *Elaphomyces* species. Hawker (1968a; Hawker *et al.* 1967) shows that the spore features observed are influenced by the age of the fruiting body and rate of drying for preservation. This may also apply to this species since the spores are very similar in morphology to those of *Elaphomyces* species (Hawker *et al.* 1967; Hawker 1968a; Trappe 1976; Samuelson *et al.* 1987). The echinate spore ornamentation is fundamentally different than the irregularly thickened walls in the other species of the genus and warrants taxonomic separation at the subgeneric level.

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

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

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

Macroscopic Features: ascocarps hypogeous, sessile, apothecia 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 inoperculate, cylindrical, hyaline, ascospores ellipsoidal, hyaline, appearing rough to verrucose, with SEM surface echinate, spines often with adhering extramatrical tissue forming irregular reticulum or coalesced spines, with large central globose oil droplet and two to many smaller polar guttules, tetranucleate (Zhang & Minter 1989b).

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

Type Material: holotype K, examined.

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

Taxonomic Notes: This species is distinguished from the other two members of the genus, *G. echinulata* (q.v.) and *G. ellipsospora* (Cribb) Zhang & Minter, by its larger ascospores and more prominent echinate sporal ornamentation. Macroscopically the ascocarps of *G. australiana* are more highly infolded and chambered with internal hymenial surface in addition to hymenial layer over entire exterior surface. Due to the tremendous variation in complexity of infolding and resultant chambers seen within a single species (or collection) of some *Hydnotrya* species, such as *H. variiformis* (q.v.), *H. cubispora* (q.v.), and *H. michaelis* (q.v.), this character is considered 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 cerebriformis*). Further investigations with additional material of species in this genus are required to clarify distinguishing species characteristics.

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

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

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

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

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

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

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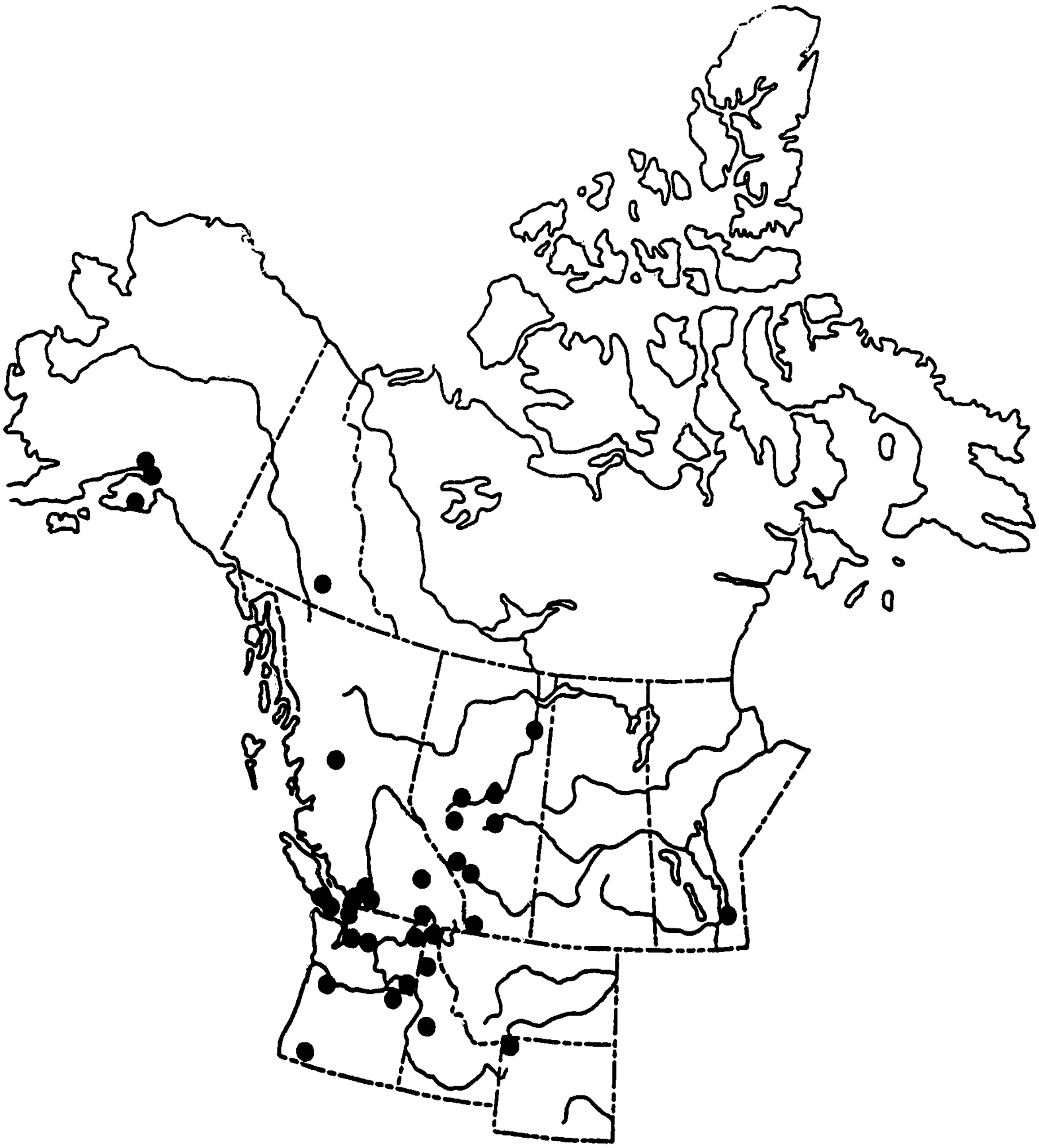
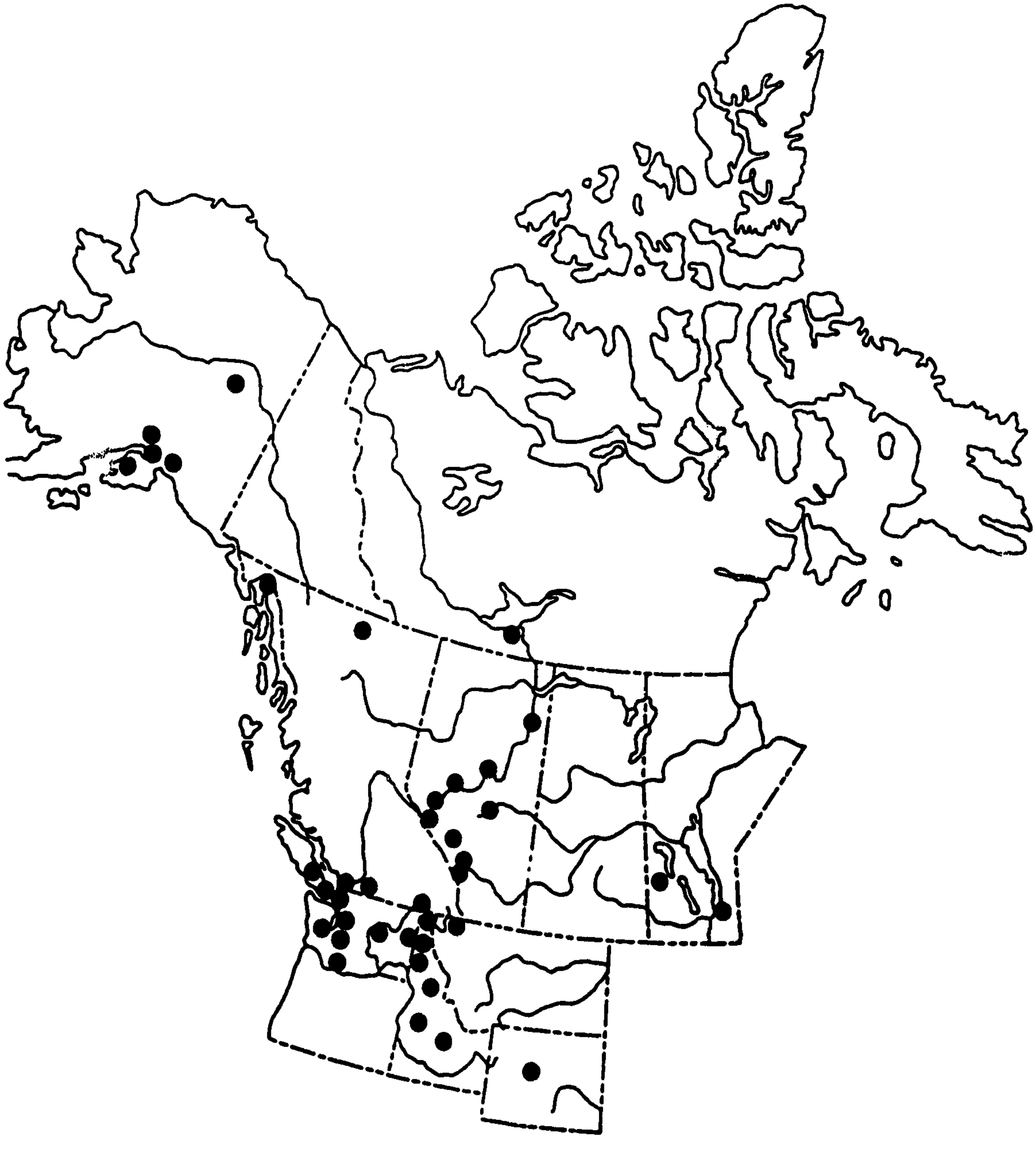
APPENDIX 1

Distribution maps of species of Helvellaceae occurring in northern and northwestern North America.



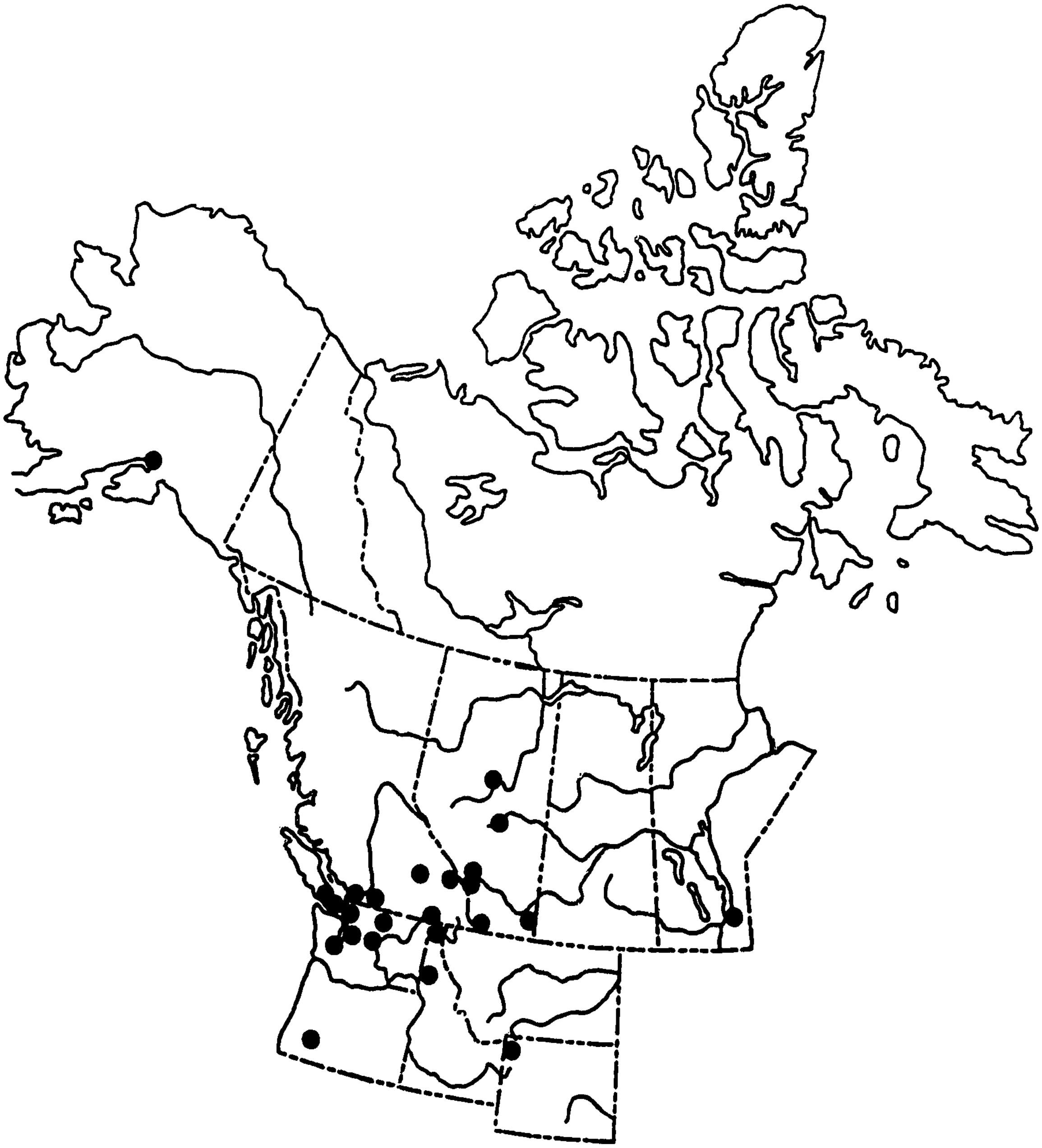
Map 1: ● *Gyromitra esculenta*



Map 2: ● *Gyromitra infula*

Map 3: ● *Gyromitra ambigua*

▲ *Gyromitra olympiana*



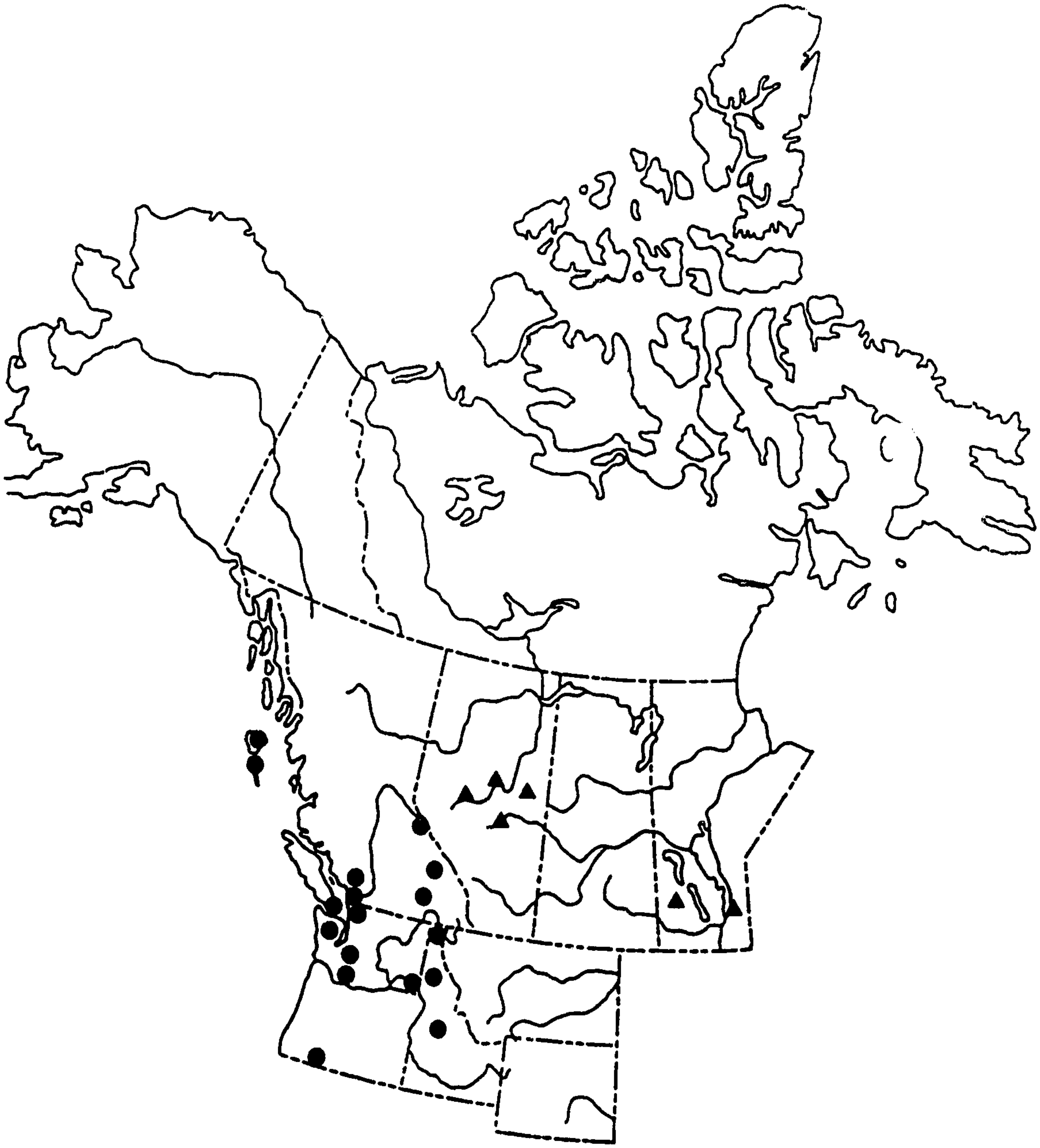
Map 4: ● *Gyromitra perlata*

Map 5: ● *Gyromitra gigas*

▲ *Gyromitra leucoxantha*

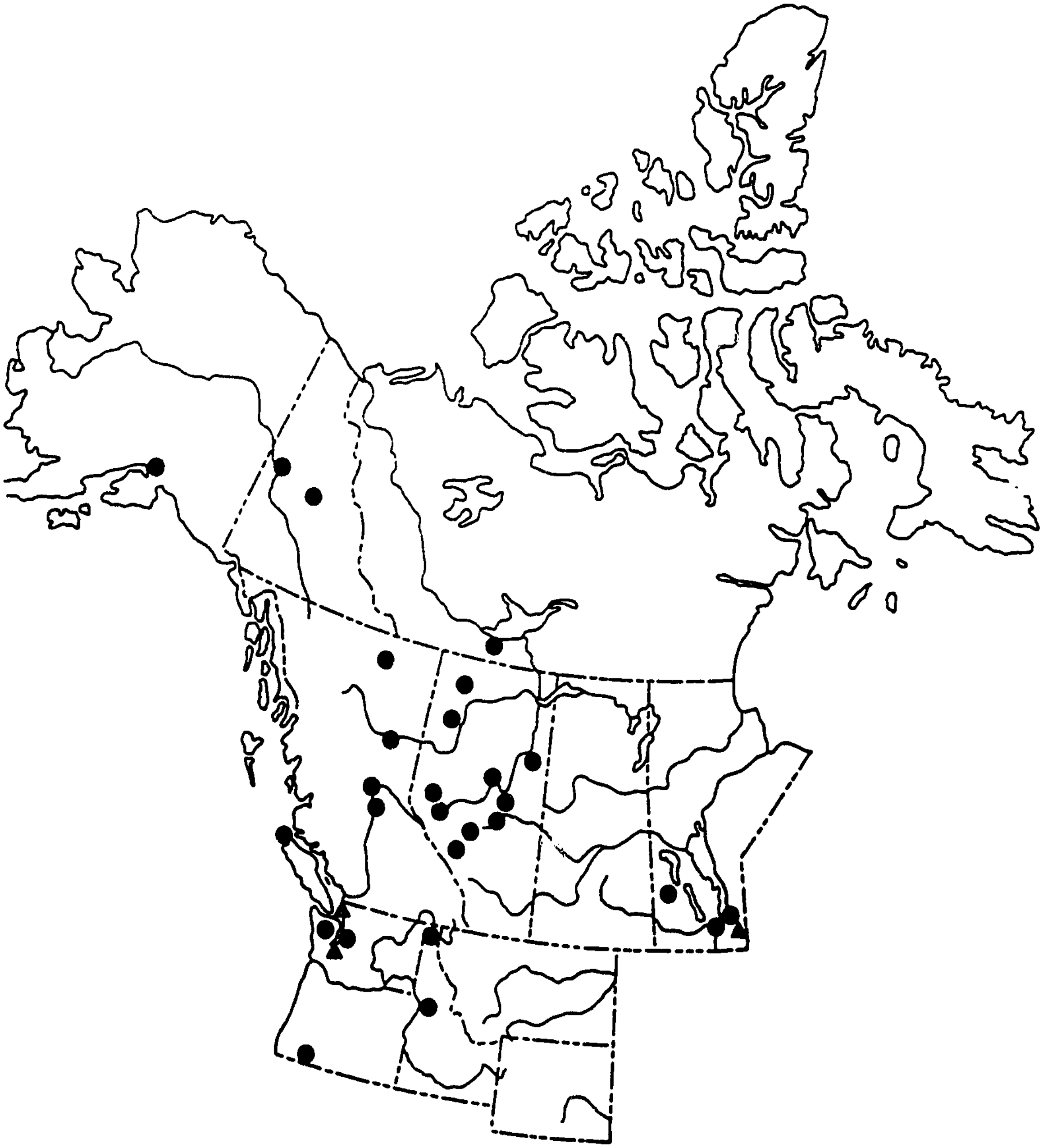
Map 6: ● *Gyromitra melaleucoides*

Map 7: ● *Rhizina undulata*



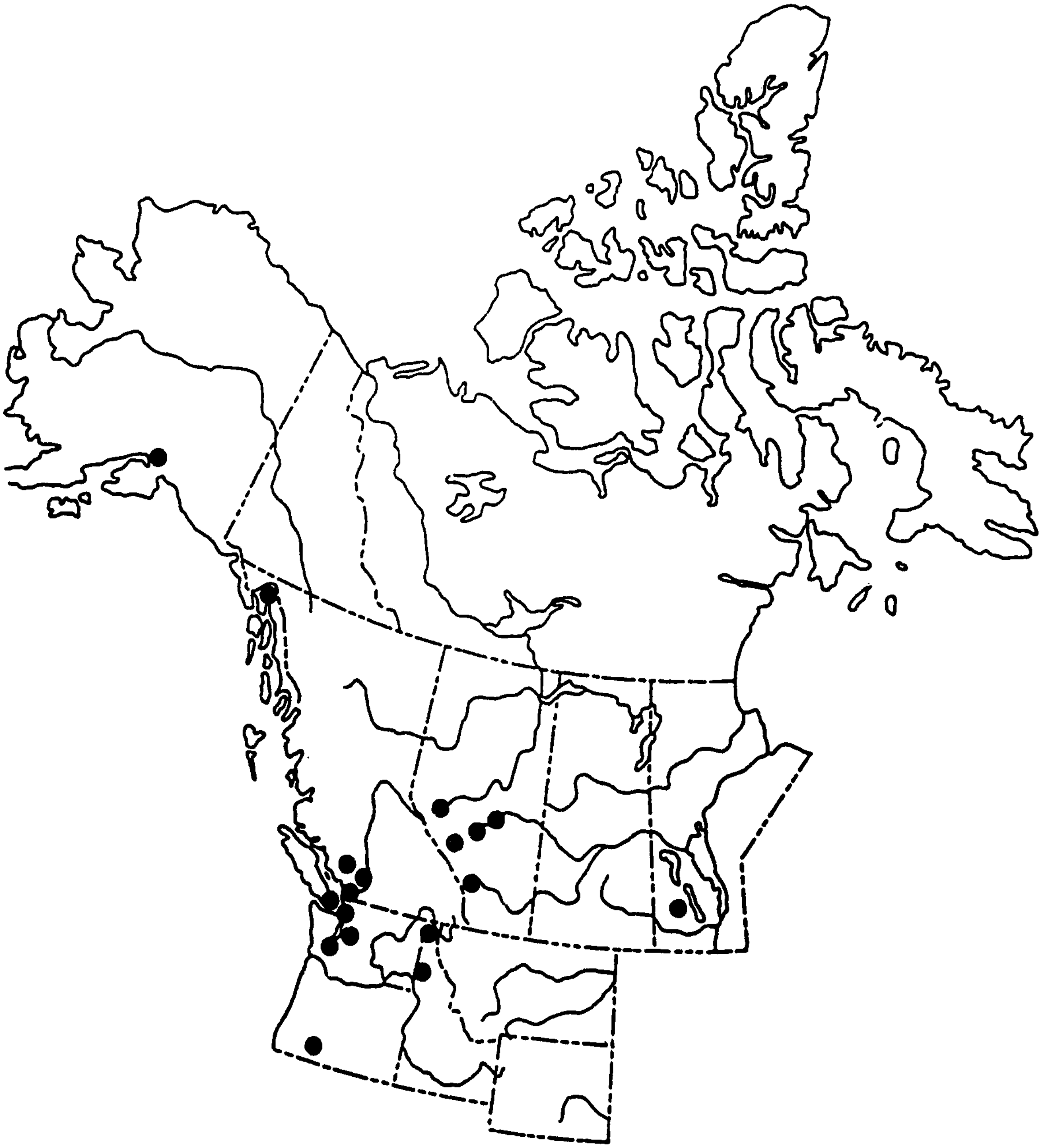
Map 8: ● *Pseudorhizina californica*

▲ *Pseudorhizina sphaerospora*

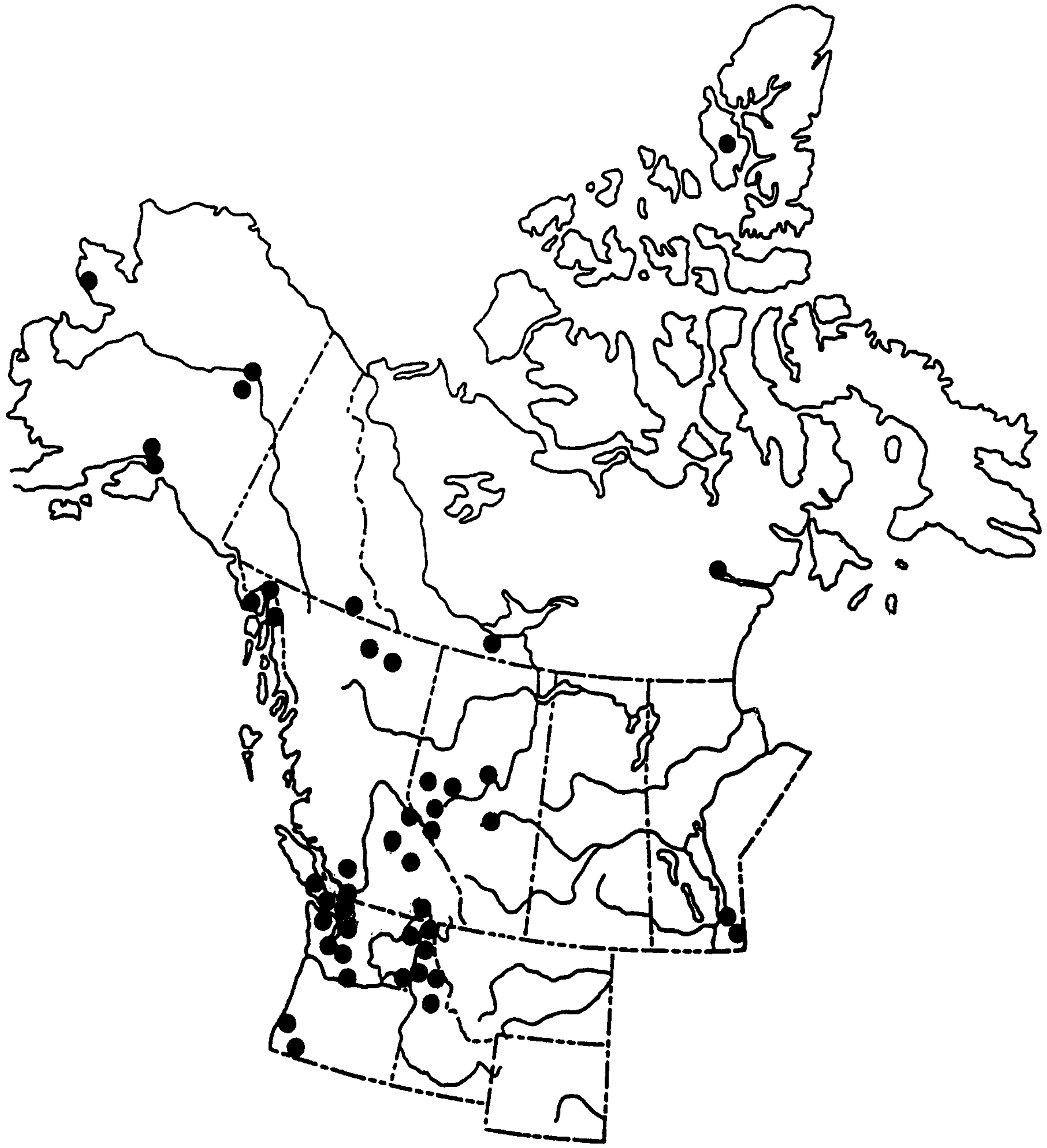


Map 9: ● *Helvella crispa*

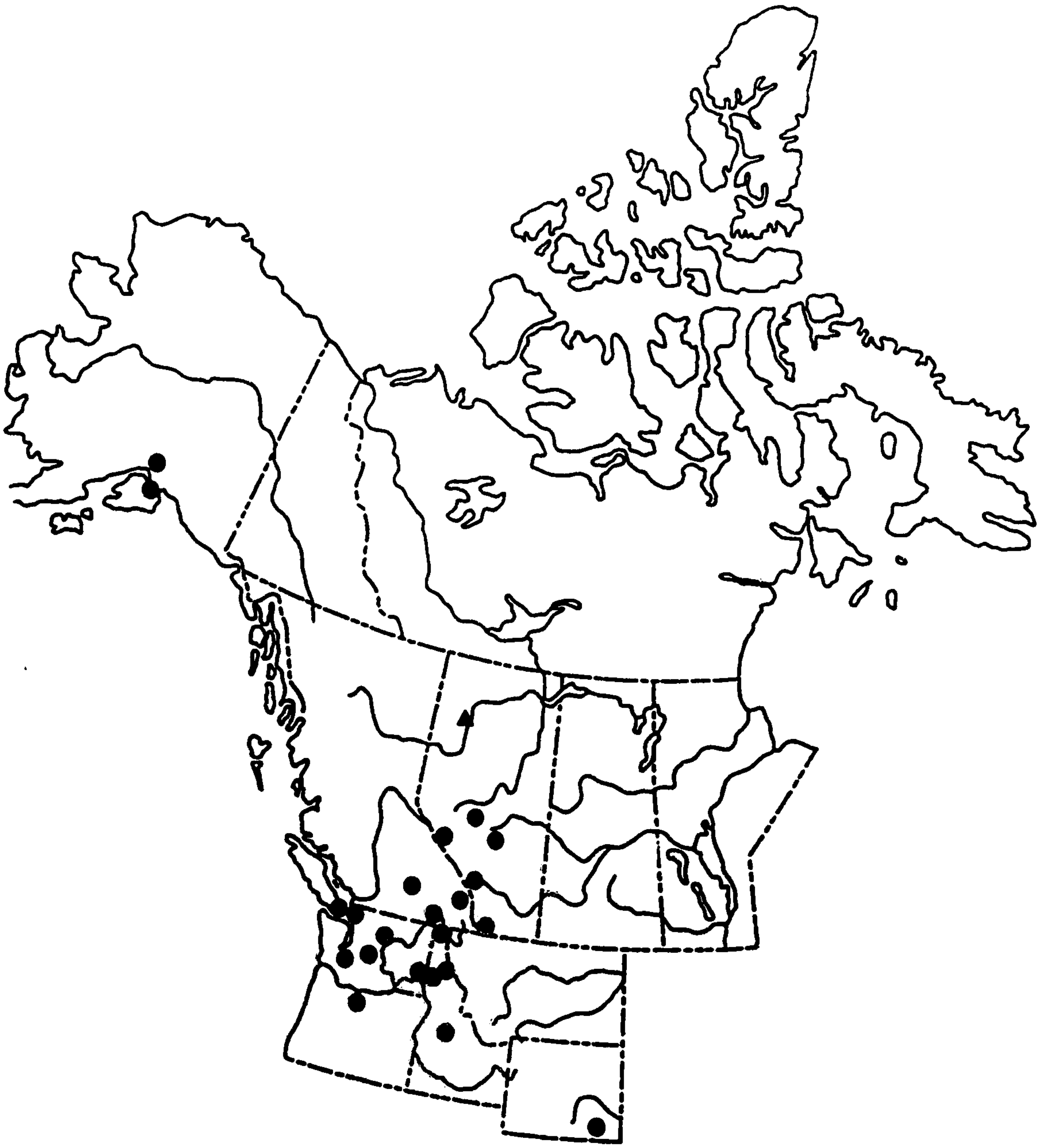
▲ *Helvella lactea*



Map 10: ● *Helvella maculata*

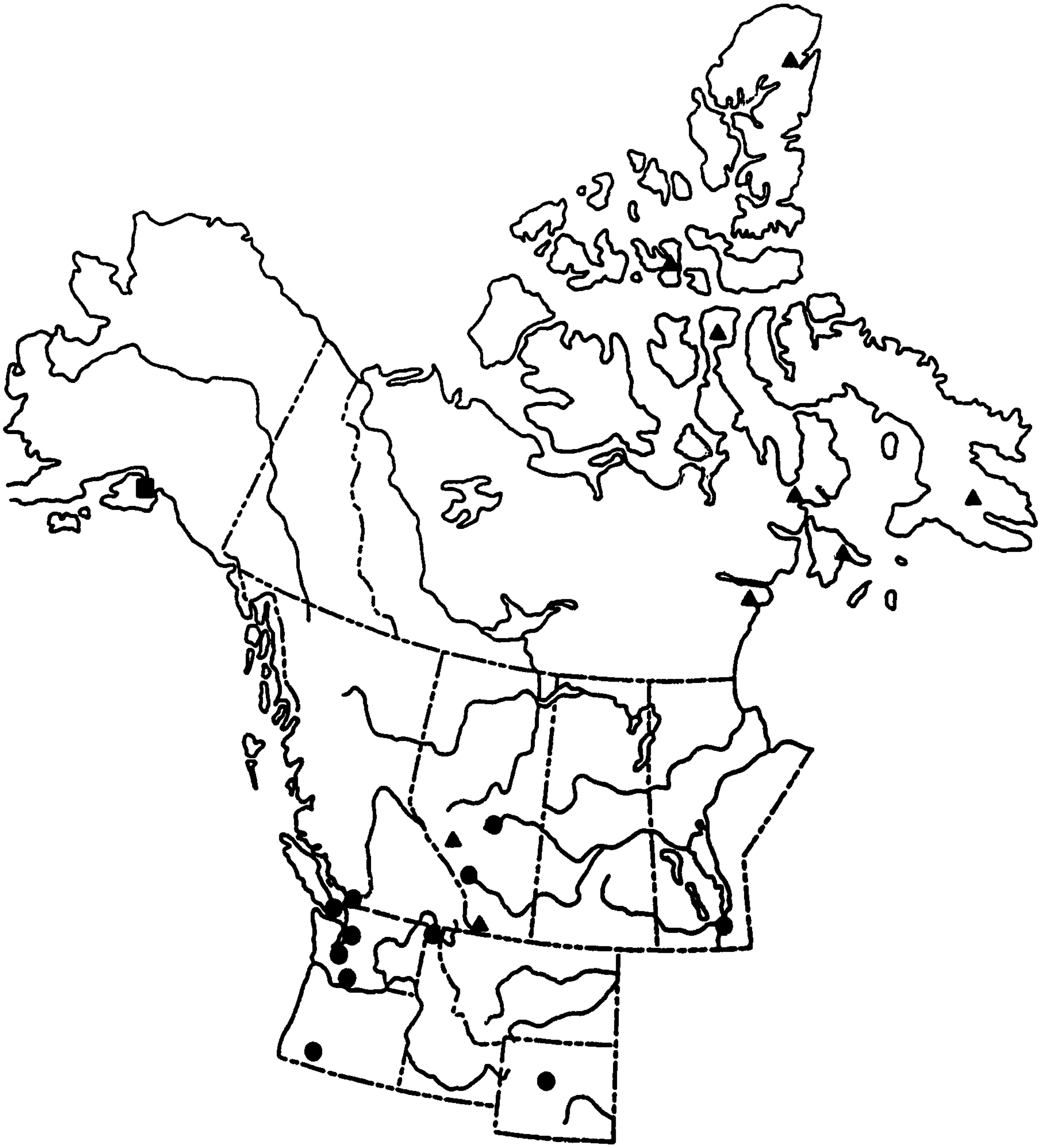


Map 11: ● *Helvella lacunosa*



Map 12: ● *Helvella leucomelaena*

▲ *Helvella unicolor*



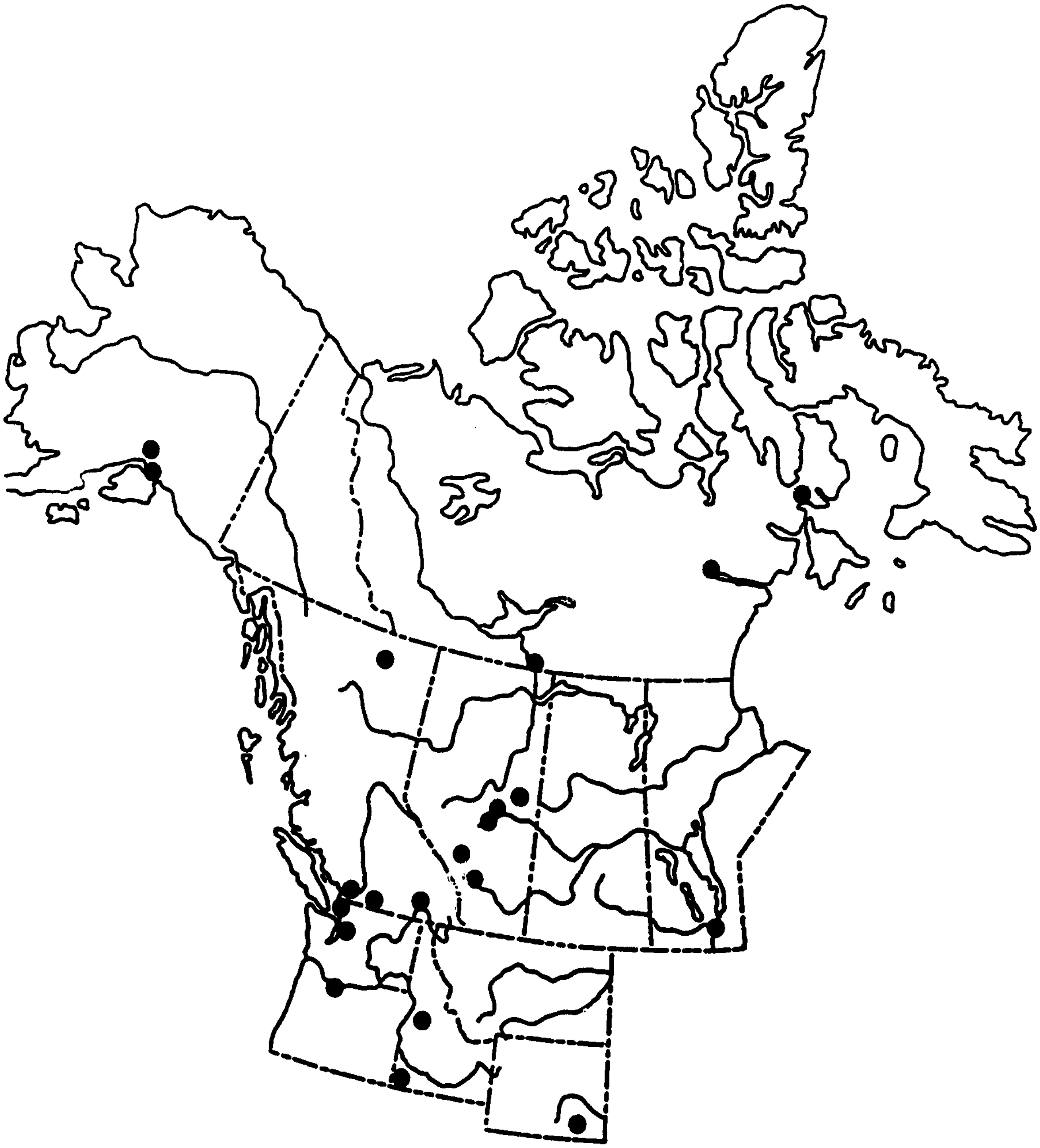
Map 13: ● *Helvella acetabulum*

▲ *Helvella arctoalpina*

Map 14: ● *Helvella costifera*

▲ *Helvella aestivalis*

■ *Helvella robusta*



Map 15: ● **Helvella solitaria**

Map 16: ● *Helvella silvicola*

▲ *Helvella crassitunicata*

Map 17: ● *Helvella corium*

▲ *Helvella cupuliformis*

Map 18: ● *Helvella dissingii*

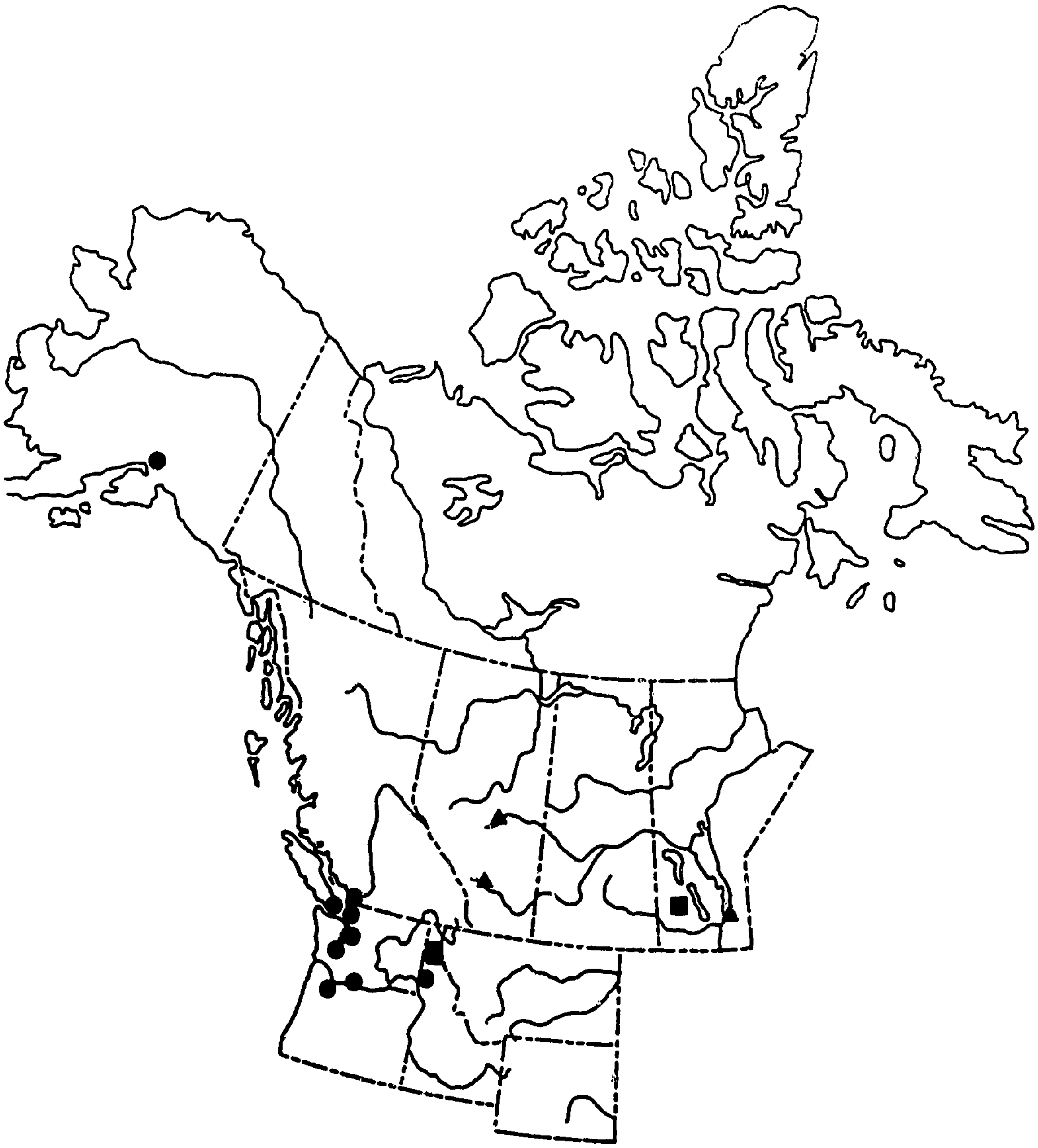
▲ *Helvella rivularis*

Map 19: ● *Helvella macropus*

▲ *Helvella subclavipes*

Map 20: ● *Helvella elastica*

Map 21: ● *Helvella albella*



Map 22: ● *Helvella compressa*

▲ *Helvella ephippium*

■ *Helvella latispora*

Map 23: ● *Helvella pezizoides*

▲ *Helvella atra*

■ *Underwoodia columnaris*

Map 24:
● *Hydnotrya cubispora*
▲ *Hydnotrya variiformis*
■ *Hydnotrya tulasnei*

Map 25: ● *Hydnotrya cerebriformis*

▲ *Hydnotrya michaelis*

APPENDIX 2

A procedure for analysis of crude protein from dried ascocarps of Helvellaceae using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE).

MATERIALS AND METHODS

Analysis of crude protein using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) was done using dried fungal specimens of selected taxa of Helvellaceae and other fungi. Collections examined include *Helvella crispa* (SA 256), *H. lacunosa* (SA 301), *Gyromitra infula* (SA 302), *Morchella esculenta* (SA 76), and *Hydnellum aurantiacum* (SA 303).

Dried tissue from the apothecium/hymenium and stipe was used. Tissue samples were left as unaltered fragments, finely chopped with a single-edged razorblade, or ground with a mortar and pestle. Samples were rehydrated in Milli-Q water for unaltered and chopped preparations, but were used dehydrated in ground preparations. Each sample contained approximately 0.01-0.1 g of fungal tissue. Five μl of Dithiothreitol (DTT) was added to each sample. All samples were suspended in 50 μl of sample buffer (SDS reducing buffer: distilled water 4.0 ml, 0.5 M Tris-HCL pH 6.8 1.0 ml, glycerol 0.8 ml, 10% SDS 1.6 ml, ß-mercaptoethanol 0.4 ml, 0.1% Bromophenol blue 0.2 ml). Sample tubes were centrifuged for one minute, then immersed in a boiling water bath for 30 to 60 minutes.

SDS-PAGE low Molecular Weight Standards (Bio-Rad) were used to calibrate the gels. Some fungal samples were treated with chitinase (1 μl, 100 units per ml) and buffer solution (citrate-phosphate buffer pH 6.4 10 μl). Chitinase treated samples were incubated for approximately 20 hours at 37°C.

The electrophoretic methods used in this study were developed after the system described by Laemmli (1970) using the mini-Protean II cell electrophoresis apparatus. Separating gels of 12.5% (Acrylamide:Bis 30:0.8 16.0 ml, 1.875 M Tris pH 8.8 6.0 ml, 0.2 M ethylenediaminetetraacetic acid (EDTA) 0.3 ml, Milli-Q water 10.9 ml, tetramethylenediamine (TEMED) 0.015 ml, 10% ammonium persulfate 0.3 ml) or 16% (Acrylamide:Bis 30.0:0.8 16.0 ml, Milli-Q water 7.4 ml) were used. The stacking gel (Acrylamide:Bis 30:0.8 2.5 ml, 1.0 M Tris pH 6.8 1.88 ml, 0.2 M EDTA 0.15 ml, Milli-Q water 10.3 ml, TEMED 0.008 ml, 10% ammonium persulfate 0.15 ml) was used at a concentration of 5%. Gels were poured between glass plates and 10 sample wells per gel were made using teflon 'combs'. Sample wells were drained before addition of 10 μl of prepared sample to each well. All wells and the gel system were filled with running buffer (Tris base (Sigma 7-9) 15.125 g, glycine 72.0 g, SDS 5.0 g, Milli-Q water 5 l). Electrophoresis was carried out at five Watts with constant current until the Bromophenol blue tracking dye reached the bottom of the gel (about 6 cm in 2 hours).

After electrophoresis was completed, the gels were stained with Coomassie Brilliant Blue, a triphenylmethane dye (Diezel *et al.* 1972) or lipopolysaccharide (LPS) Silver Stain (Tsai & Frasch 1982). Gels were immersed in Coomassie Brilliant Blue for 15 minutes, and then washed with destain solution (10% HoAC, 10% MeOH) for approximately one week for maximum band resolution. Gels stained with silver stain were immersed in fixer (40% ethanol, 5% acetic acid) immediately after electrophoresis and were allowed to stand for about 15 hours. Oxidizing reagent (periodic acid 1.4 g, 40% ethanol 5% acetic acid 200 ml) was used for one gel. After washing with Milli-Q water, gels were immersed in silver stain (1.0 N NaOH 2.8 ml, Milli-Q water 28 ml, 29% ammonium hydroxide 2 ml, 20% silver nitrate 5 ml, Milli-Q water 115 ml) for 10 minutes. Developer (37% formalin 0.5 ml, citric acid 50 mg, Milli-Q water 1 l) was used to produce visible bands, and development was stopped with 7% acetic acid. To further improve resolution, the gels were covered with dialysis membrane and dried on Whatman 3MM blotting paper using a vacuum heater at 80°C.

RESULTS AND DISCUSSION

Patterns of cell proteins as seen by electrophoresis directly reflect the cell's genetic composition and should be of value in taxonomy (Clare *et al.* 1968). Electrophoretic techniques have been widely used with good results for species identification and relationships in many groups of organisms. Plants (e.g. Bayer 1989) and bacteria (e.g. Owen *et al.* 1989), as well as most major groups of fungi, have been examined. Electrophoretic methods have been used successfully for determination of taxonomic relationships in basidiomycetes (Kerrigan & Ross 1988; Paranjpe *et al.* 1979; Shannon *et al.* 1973), ascomycetes (Gessner *et al.* 1987; Maghrabi & Kish 1985a, b, 1986, 1987), hyphomycetes (Cruikshank & Pitt 1987; Stasz *et al.* 1988), blastomycetes (Ponton & Jones 1986), oomycetes (Adaskaveg *et al.* 1988, Clare 1963), and myxomycetes (Franke *et al.* 1968).

The majority of electrophoretic experiments have examined enzymes using isozyme analysis (e.g. Micales *et al.* 1986). Unfortunately, the isozyme technique requires active enzymes which must be obtained from living specimens. Since many taxa of Helvellaceae cannot be grown in axenic culture, the technique is inappropriate for the study of this family.

Examination of crude protein by electrophoresis was shown to be of taxonomic value for the genus *Pythium* (oomycetes) by Clare (1963), and for *Rhizoctonia* (hyphomycetes) by Clare *et al.* (1968) and Reynolds *et al.* (1983). This method was also employed by Currah *et al.* (unpublished) for *Aphanoascus* and *Keratinophyton* (ascomycetes). These studies used living fungal material, but the technique could, theoretically, be applied to the examination of dried herbarium specimens.

A project was undertaken to develop a technique for analyzing crude protein from dried fungal fruiting bodies using SDS-PAGE to provide additional data for correlation with morphological evidence for species identification and/or phylogenetic relationships in the Helvellaceae. The hypothesis that crude protein could be extracted from dried fungal specimens and recorded by SDS-PAGE techniques was supported by this experiment. This is significant since biochemical data, in addition to traditional morphological data, can be obtained from the examination of preserved herbarium collections.

The most successful procedure for the detection of protein bands in polyacrylamide gels was by staining with Coomassie Brilliant Blue. Early electrophoretic studies (e.g. Clare 1963; Clare *et al.* 1968) frequently used Amido Black 10B for staining gels, while later workers (e.g. Adaskaveg *et al.* 1988; Reynolds *et al.* 1983) typically adopted Coomassie Brilliant Blue which has the advantage of increased sensitivity and is able to detect protein concentrations down to 0.5-2 μg per square cm (Diezel *et al.* 1972). LPS · Silver Stain was also used, but was found to be inferior to Coomassie Brilliant Blue on the basis of both number of bands detected and individual band resolution. Unfortunately, the high sensitivity of this stain noted by Tsai & Frasch (1982) for bacterial lipopolysaccharides was not evident in the fungal material examined. High sensitivity may, in fact, contribute to the poor resolution since a high degree of background staining was observed.

Polyacrylamide concentration in the separating gels was altered for maximum band resolution. 16% gels are more useful than 12.5% for assessment of total protein profiles of the fungi examined since the banding pattern is more evenly distributed over the entire gel. Since the majority of bands detected were of relatively low molecular weights (10000-50000 MW), banding patterns were crowded in the lower half of the 12.5% gels.

The amount of fungal tissue used in sample preparations varied approximately from 0.01 to 0.1 g. No definite correlation between sample size and banding pattern was detected, but large samples resulted in swollen, distorted lanes. Lanes containing very small samples were noticeably fainter than those of larger samples. Samples of 0.5 g are appropriate for this electrophoretic procedure.

Samples were immersed in the boiling water bath for 30 to 60 minutes. No differences were detected as a result of this variation. It is possible that more or different proteins would be extracted from the tissues for longer immersion times. It is, of course, equally possible that maximum leaching of crude proteins occurs in a time period shorter than 30 minutes. It would be necessary to run a series of samples immersed from 0 to 300 minutes in an otherwise constant system to assess whether immersion time affects protein profiles.

Fungal tissue was prepared for samples in three ways: unaltered tissue fragments, tissue finely chopped with a single edged razorblade, or tissue ground with a mortar and pestle. Banding patterns were detectable from all preparation techniques. In one run, distinct bands were detected from a rehydrated chopped preparation, but bands were lacking from a dehydrated ground sample. Ground preparations were observed to be undesirable since fungal tissue, especially stipe tissue, remained fibrous and could not be finely powdered. Also, the mortar and pestle created static electricity which hindered the recovery of the powdered portion of the fungal tissue. Although the unaltered preparations were not directly compared to chopped preparations, it was assumed that physical breakdown of fungal tissue would aid, or at least not hinder, the extraction of crude protein. For these reasons, the finely chopped rehydrated tissue preparation technique was selected as the most suitable for this study.

Since chitin is the primary 'skeletal' component of fungal cell walls (Webster 1980), it was hypothesized that treatment of fungal tissue with chitinase may release additional proteins into suspension, as was done by Torres-Bauza & Riggsby (1980) for *Candida albicans*. In the aforementioned experiment (Torres-Bauza & Riggsby 1980), chitinase was used on yeast stage and mycelium, while here it has been applied to tissue of the fungal fruiting bodies. Chitinase treatment produced no effects on the protein profiles, and chitinase did not produce a visible band in the control well. Unfortunately, the negative results of the chitinase treatment do not necessarily reject the hypothesis. Chitinase activity was not demonstrated in this study. Torres-Bauza & Riggsby (1980) determined chitinase activity on colloidal chitin by the release of N-acetylglucosamine. Also, even if the chitinase were active, sample preparation techniques may have been inadequate to produce detectable results. Such factors as incubation temperature, incubation time, chitinase concentration, or buffer solution used may be responsible for the negative results.

Examination of different fungal tissues or tissues of different ages may affect protein patterns. Evidence suggests that age of fungal tissue is an important factor for isozyme analysis, due to the expression of alleles at different stages of development (Micales *et al.* 1986). On the other hand, Clare (1963) reports that three different cultural ages produced identical patterns of crude protein bands. This result indicates that age of the fruiting body used in this study should not affect results, but age-related variability was reduced as much as possible by selecting only mature, spore-producing fruiting bodies. Age of herbarium collections may also be a factor, but visible banding patterns were observed in all specimens which varied from 2-14 months. Paranjpe *et al.* (1979) found protein differences between different tissues of the fruiting bodies in *Agaricus*. Fungal tissue was examined here from both the apothecium and the stipe. In some instances, there were considerable differences in the banding patterns between the two tissues, while other runs produced identical banding patterns. It is possible that differences reflect different proteins or concentrations of proteins in different tissues, but variation due to experimental procedure can not be eliminated as a source of error.

The taxonomic potential of the results can not be discussed with any certainty since a limited number of species were examined, repeat runs were done only to a limited extent, and comparison of multiple collections of the same species was not performed due to the time constraints and priorities of this study. The results of this investigation show that crude proteins can be extracted from dried fungal fruiting bodies by SDS-PAGE procedures, and that there is a greater similarity between banding patterns of the same specimen than between patterns of specimens of different species. Best results were obtained by finely chopping approximately 0.05 g of rehydrated fungal tissue for sampling, and running the samples in a 16% polyacrylamide gel stained for protein band detection with Coomassie Brilliant Blue. Further work is necessary to standardize all variables in order to produce consistent, reproducible results before this technique can be confidently applied to the taxonomic problems of species identification and recognition of phylogenetic relationships in the Helvellaceae.