A FIELD KEY TO COMMON GENERA OF HYPOGEOUS AND GASTERIOD BASIDIOMYCETES OF NORTH AMERICA

Steven L. Miller

Botany Department University of Wyoming Laramie, Wyoming 82071

INTRODUCTION

To honor the tenth anniversary of the North American Truffling Society (NATS) in 1987, the author taught a course entitled "Truffles of the Pacific Northwest" at Linn-Benton Community College near Corvallis, Oregon. As part of that course he assembled and distributed a field key to hypogeous fungi, including both ascomycetes (true truffles) and basidiomycetes (false truffles), which would allow NATS members, most of whom did not have ready access to a microscope, to identify most of their collections to genus. The key was extensively used and revised. In honor of the twentieth anniversary of NATS, the present paper is a field key to hypogeous and gasteroid basidiomycetes (and one additional subdivision that may be confusing in the field).

The task of producing a field key to hypogeous fungi is a difficult one. Many of the characters that serve to distinguish genera and species require the use of a microscope. In order to use only macroscopic characters in this key, several not-so-common genera have been intentionally omitted. The key is admittedly artificial, but an attempt has been made to structure it so that omitted genera will key out to a related genus, and with the use of a microscope and appropriate literature, should be readily identifiable.

This key is not intended as a substitute for a well rounded regimen of ecological, morphological, and microscopical study. However, it is hoped that the key will allow interested persons that do not have access to a microscope to identify most common genera of hypogeous basidiomycetes.

METHODS AND MATERIALS

There are many sources describing the best ways to collect fleshy fungi (Miller 1978; Arora 1986) and there is no need to repeat this information here, except to point out that truffles are fleshy fungi too, and will become rotten and disgusting just like any mushroom if left in a plastic bag even for a few hours. Therefore collecting should be done with wax-paper bags or compartmentalized plastic fishing-tackle boxes. Although notes on the fresh condition should be taken as soon after collecting as possible, it is generally not advisable to cut into all of the sporocarps while in the field unless sufficient time can be spent to study the specimen and assess the best way to cut it to reveal the necessary structures. If you do follow that practice (admittedly, most of us can't always control our excitement), it is best to assess the fresh odor, taste, color etc. at the same time.

The following key is best used when a full range of developmental features are present in a single collection, i.e. young, mature and old specimens all collected from a relatively close proximity. Young, immature sporocarps will be difficult to identify, but may provide clues as to color, odor etc. Full utilization of the key also requires the use of a sharp knife or preferably a razor blade, hand lens and various macrochemical reagents. When the sporocarps are cut open to reveal detail in the gleba, a true vertical, median section should be used, i.e. cut vertically from the base through to the apex. This is important because the terminology of the columella, gleba, and peridium is based on a true, vertical, median view, and would otherwise be confusing. In addition, mushroom buttons (from both poisonous and nonpoisonous species) often resemble gasteroid and hypogeous fungi and the best way to tell the difference is to perform a true, vertical median section and look for the embryonic mushroom form that appears in mushroom buttons but not in hypogeous or gasteroid fungi. An incorrect, transverse section of a mushroom button will appear as concentric circles and not like any of the sporocarp or gleba types described below.

MORPHOLOGY

Many of the morphological features of the fungi treated in this key are continuous or intergrade, meaning that one sporocarp, columella or gleba type may overlap slightly or greatly with another. However, there are typically limits on the amount of intergradation for any given genus which can be recognized.

Sporocarp form

Agaricoid sporocarps generally have a stipe, a cap and either gills (lamellae) or tubes (pores) where the spores are produced. This is the typical mushroom morphology (Fig. 1). Gasteroid sporocarps can appear very similar, with stipe-like, cap-like and gill-like structures, or they can have some degree of enclosure of the spore producing tissue either from the cap surface or by wrinkling, contorting or chambering of the gill-like structures, or both (Figs 2, 4). Hypogeous sporocarps typically lack any true stipe-like structure, are more or less spherical or globose, and have little, if any exposure of the spore bearing tissue. A good analogy would be a golf-ball.

Stipe, stipe-columella, or columella

The columella (including stipe, stipe-columella, and columella) for the purposes of this key is considered a reduction series in the amount and location of stipe (stalk) tissue (Figs 4-11). A **stipe** is by definition found only in agaricoid sporocarps (Fig. 1), however, the **stipe-columella** found in some gasteroid fungi is indistinguishable from a stipe, and is likely to be homologous with it (Fig 4). The **stipe-columella** found in some gasteroid and hypogeous sporocarps is much reduced in extent, and no longer serves the function of elevating the sporocarp above the ground surface (Figs. 2, 8). The **columella** is yet a further reduction in the amount and location of sterile, stipe-like tissue, and is found almost exclusively in hypogeous fungi (Figs. 5-7, 9-10). Sporocarps of some hypogeous fungi lack columella tissue (Fig. 11).

To provide additional characteristics for the key, columella types have been further subdivided into several categories. A **percurrent** columella extends completely through the sporocarp as viewed in section (Figs. 4-5) and is a condition that can be either found in a stipe, stipe-columella or columella. A **dendritic** columella forms many branches from a more or less central mass of stipe-like tissue (Fig 5). A **diffuse** columella is similar to the dendritic form, but is much less evident in both branching pattern and extent (Figs 6-7). A **sterile base** can either resemble a short nonpercurrent stipe-columella (Fig 8) or a more reduced mass of stipe-like tissue at the base of a hypogeous sporocarp (Fig. 9). A **central** columella typically has a large spherical mass of sterile tissue near the center of the sporocarp from which rays of spore bearing tissue or peridioles radiate outward (Figs 10, 19). Other fungi exhibit **no columella** and possess no sterile stipe-like tissue when viewed in section (Figs 3, 11, 15, 17-19).

Gleba type

The gleba is a combination of sterile and spore-bearing tissue typically found enclosed by protective tissues in fungi such as puffballs, some gasteroid fungi, and hypogeous fungi. For simplicity, the term has been extended to gasteroid/agaricoid sporocarps, even though the sporebearing tissue is exposed (Figs. 2, 12-13). The lamellate gleba can range from gill-like, nearly indistinguishable from that of agaricoid sporocarps, to wrinkled, contorted or chambered, but retaining the radial pattern of lamellae (Fig. 12). The lamellate gleba is typically exposed, at least to some extent. The **labyrinthiform** gleba may also retain a partial radial pattern but is composed of large to small chambers, typically irregularly bent and crumpled, formed by wrinkles, contortions or cross-walls of the glebal plates (Figs. 2, 4, 5-6, 8, 13-14). There may also be some degree of exposure. The lacunate gleba appears in section to be formed of large to small shallow holes or chambers, which are more or less identical in shape, and are typically only rarely exposed (Figs. 3, 7, 9, 11, 15). The gleba may also appear solid (not necessarily implying tough) in section because the chambers are, or appear to be, filled or stuffed with material. The solid and rubbery gleba is typically composed of minute chambers difficult to discern even with a hand lens, and the sporocarp is usually difficult to cut into (Fig. 16). In the gel-filled gleba, the chambers are filled at maturity with a gelatinous, usually highly colored material (Fig. 17). In the liquid-filled gleba, the mature chambers are filled with a material that is more fluid, and appears to bleed or flow from the chambers (Fig. 18). This material is usually not highly colored. A concern for correct interpretation of the gel-filled and liquid-filled gleba types is the degree of maturity of the specimen. These gleba types should also not be confused with exudation of a latex from the sterile tissue between chambers. The **peridiate** gleba (Fig. 19) is formed from distinct, separable packets of spores called peridioles that look like seeds. This is a rare type of gleba restricted to only one or two genera and is usually associated with a central columella type.

Spore color

The color of spores in the gleba is an important characteristic in

identifying hypogeous and gasteroid fungi and should be interpreted carefully. Frequently, the color observed in the freshly cut section is not the color of spores, rather it is the color of the sterile tissue comprising the glebal elements. A good example is the genus *Hydnangium*, which often appears purplish or flesh colored in section. However, close examination of the glebal chambers with a hand lens reveals that the spores are whitish and the tissue is purplish.

KEY TO HYPOGEOUS AND GASTEROID BASIDIOMYCETES BASED ON MACROSCOPIC AND ECOLOGICAL CHARACTERISTICS

- Sporocarps globose to subglobose, rarely with a stipe; usually hypogeous; gleba either: solid, hard, lacking chambers or composed of a uniformly thickened layer lining a single, large, hollow chamber, usually with an orifice, grooves or openings to the inside or nearly hollow, stuffed with cottony mycelium young but powdery in age or composed of infolded partitions, the partitions either single or multiple and compact, in some nearly becoming solid; texture firm, solid to plastic-like, usually very brittle. Hypogeous members of Subdivision Ascomycotina.......................(see Trappe and Castellano 1991)

- 3. Sporocarps when cut with true vertical section possessing a small or large

	columella or small sterile base in the gleba or densely matted cluster of rhizomorphs resembling a sterile base4
3.	Sporocarps when cut with true vertical section not possessing a columella or sterile base in the gleba31
4.	Gleba of centripetally or radially arranged tramal plates or peridioles extending from central columella or sterile base or of chambers evident at youth but becoming powdery at maturity
4.	Gleba composed of numerous, small or large chambers, occasionally requiring a hand lens to be visible9
5.	Gleba of radially arranged, tapering black peridiolesPyrenogaster
5.	Gleba of radiating tramal plates or chambers in youth but rapidly becoming powdery at maturity
6.	Gleba with persistent central columella
6.	Gleba lacking a columella8
7.	Gleba brown, dark brown or black at full development; tramal plates radiating centripetally from spherical central columella or sterile base
7.	Gleba black at full development; tramal plates and chambers pendant from disk of sterile tissue supported by a percurrent columella composed of thick rhizomorphs; peridium thick, leathery, dehiscingSedecula
8.	Thick outer peridium tomentose, and usually splitting into well formed stellate pattern in age; gleba brown to dark brown usually contained in a leathery inner peridium
8.	Thick outer peridium mostly not splitting into stellate pattern in age, or if so, peridium not tomentose; gleba black, powdery at maturity and not contained in an inner peridium
9.	Gleba darkly or brightly colored, usually in the range of brown, pink, yellow, orange, green or blue-green10
9.	Gleba typically white or off-white
10.	Gleba gray-brown, brown, red-brown to dark brown 11
10.	Gleba variously colored, occasionally olive to olive brown but not brown
11.	Sporocarp lacking peridium; reaction to Melzer's reagent giving a dextrinoid reaction
11.	Sporocarp with well developed peridium entirely covering gleba; reaction to Melzer's reagent various, but usually not dextrinoid12
12.	Gleba of chambers filled with gel-like material
12.	Gleba of small or large chambers, containing spores but not filled at maturity with gel-like material13
	$Columella\ well\ developed,\ dendritic\ or\ percurrent\ \\ 14$
13.	Columella poorly developed or lacking; sterile base may be present16

14.	Sporocarps usually soft, fleshy, to firm but not cartilaginous or rubbery, columella or stipe-columella present
14.	Sporocarps usually cartilaginous, tough or rubbery; columella usually diffuse, never a percurrent stipe-columella or columella15
15.	Sporocarps medium to large; peridium usually thin, evanescent, white or pale brown; gleba gray brown, red brown, brown or dark brown
15.	Sporocarps usually small; peridium thick, persistent, white; gleba pink to red brown
16.	Gleba strongly amyloid in Melzer's reagent17
16.	Gleba not amyloid in Melzer's reagent, but may be slightly dextrinoid
17.	Brown color of gleba usually from discoloring reaction of tramal tissue and not from accumulation of spores; odor strong, oily, of maple syrup or slightly of rubber
17.	Brown color of gleba usually from accumulation of spores in the glebal chambers; odor absent or different
18.	Fresh sporocarps with strong, penetrating, farinaceous odor
18.	Fresh sporocarps with no or different odor
19.	Gleba usually some shade of green including yellow green, olive green, blue green
19.	Gleba some shade of pink, yellow, orange, or gray-blue22
20.	Columella derived from a stubby sterile base, percurrent or nearly percurrent, dentritic; fleshy but not cartilaginous or gelatinous except in age
20.	Columella absent or simple or branched; glebal tissues cartilaginous or gelatinous
21.	Sporocarps single or loosely clustered, habitat various; cartilaginous and rubbery, the peridium often cleanly separating from the gleba, associated with a variety of tree hosts
21.	Sporocarps, tightly clustered, encased in heavy mycelium, hyphal strands, soil and ectomycorrhizal rootlets, moderately gelatinous associated with <i>Eucalyptus</i>
22.	Fresh gleba when cut exuding a latex
22.	Fresh gleba when cut not exuding a latex
23.	Gleba amyloid in Melzer's reagentZelleromyces
	<u>=====================================</u>
23.	Gleba not amyloid in Melzer's reagent; with large orange spores that are visible with a hand-lens embedded in tissue Endogone (Zygomycete)
	Gleba not amyloid in Melzer's reagent; with large orange spores that are

	orange
25.	Gleba some shade of pink, associated with {\it Eucalyptus} {\it {\bf Hydnangium}}
25.	Gleba some shade of yellow or orange26
26.	Gleba amyloid in Melzer's reagent
26.	Gleba not amyloid in Melzer's reagentSclerogaster
27.	Columella or sterile base if present poorly developed $\underline{\mathbf{Martellia}}$
27.	Small stipe-columella, columella or sterile base present Gymnomyces
28.	Gleba amyloid in Melzer's reagent29
28.	Gleba not amyloid in Melzer's reagent
29.	Fresh sporocarps exuding latex when cutZelleromyces
29.	Fresh sporocarps not exuding latex when cut
30.	Columella or sterile base if present poorly developed
30.	Small stipe-columella, columella or sterile base present Gymnomyces
31.	Gleba composed of empty or gel-filled chambers, or powdery at maturity, with or without a latex32
31.	Gleba appearing solid or with orange spores embedded in tissue visible with a hand lens, no evidence of chambers surrounded by pale colored veins, with a latex
32.	Gleba with chambers filled with thick, colored gel-like material, these delineated by pale colored veins33
32.	Gleba composed of chambers that are not filled with a gel-like material at maturity, chambers may appear empty, filled with thin, white latex or with powdery content
33.	Gleba composed of black gel-filled chambers surrounded by pale colored veins; usually with a strong odor of latex paint
33.	Gleba yellow, brown, olive, brown or red colored, if black or nearly black then the peridium is colored bright yellow; usually with no or different odor
34.	Gleba white when fresh and mature, and with a scant or profuse white latex
34.	Gleba usually not white at maturity, with or without latex or if white then no latex is present
35.	Gleba with copious latex in fresh specimens; chambers 0.5-3.0 mm broad
35.	Gleba with scant latex in fresh specimens, this drying rapidly into a chalky, white surface, often obscuring the chambers; chambers 0.3-0.5 mm broad
36.	Gleba strongly amyloid in Melzer's reagent37
	Gleba not amyloid in Melzer's reagent
	Gleba white or off-white at maturity

37.	Gleba more darkly colored at maturity39
38.	Sporocarp very light in weight; with a fruity or nauseous odor; and fresh the gleba is dry
38.	Sporocarp more dense; with various odors but usually not nauseous, and fresh gleba moist
39.	Fresh sporocarps exuding a copious latex
39.	Fresh sporocarps moist but not exuding a copious latex40
	Fresh peridium quickly turning vinaceous in KOH
40.	Color of fresh peridium not affected by KOH41
41.	Columella or sterile base if present poorly developed; brown color of gleba usually from discoloring of tramal tissue, and not from accumulation of spores
41.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
42.	Gleba at first composed of chambers separated by pale colored veins, but at maturity gleba powdery
42.	Gleba not composed of chambers separated by pale colored veins, and is not powdery at maturity 43
43.	Gleba gray-brown, brown, red-brown to dark brown; usually with a strong, penetrating, farinaceous odor
43.	Gleba variously colored; with a variety of odors but not farinaceous44
44.	Gleba some shade of pink (like <i>Entoloma</i> spore print color) at maturity, found only in the southeastern and southwestern United States
44.	Gleba usually some shade of white, yellow, green or brown but if some shade of pink then not found in the southeast or southwest and gleba bruises black, blue or red
45.	Gleba white to cinnamon brown at maturity, discoloring on exposure; peridium white to pink at maturity, also discoloring upon bruising; scant latex may be present
45.	Gleba various colors, gleba infrequently discoloring on exposure; peridium various colors, frequently discoloring on bruising, latex usually lacking but if present then from the southeastern United States with sterile veins present in gleba
46.	Gleba chocolate brown, dark purple brown, smoky gray, or black at full development due to coloration of the spores in mass47
46.	Gleba white, yellow, orange, green, vinaceous (pale purple brown) or olive yellow, yellow brown, red brown to rusty brown at full development due to coloration of the spores in mass
47.	Stipe or stipe columella tough, woody in mature specimens; found in deserts and arid grasslands and steppe48

47.	Stipe or stipe columella fleshy, even in age; found in forests in the Rockies westward and infrequently in deserts and steppe
48.	Peridium dehiscing cleanly around the circumference of margin; gleba black, lamellate, hanging free from disk of pileus49
48.	Peridium not dehiscing cleanly, rather, breaking up and weathering randomly; gleba usually powdery at maturity50
49.	Stipe-columella with a persistent volva and annulus Gyrophragmium
49.	Stipe-columella with volva but lacking an annulus
50.	Resembling a large unopened <i>Coprinus</i> ("inky cap", or "shaggy-mane"); annulus absent or poorly developed 51
50.	Resembling a large, unopened <i>Agaricus</i> , often bruising red, or yellow when fresh; volva absent, annulus present
51.	Sporocarps large, many reaching 25 cm or so; external portion of stipe-columella prominent with a bulbous base; gleba often maturing from the base of the gleba upward
51.	Sporocarps typically smaller; all parts of gleba maturing simultaneously; external portion of stipe-columella poorly developed, tapering to the base
52.	Trama of gleba and stipe-columella colored pale orange to pale red, turning bright red in ETOH
52.	Trama of gleba and stipe-columella white or very pale, not turning bright red in ETOH53
53.	Sporocarp robust, fleshy54
53.	Sporocarp slender, fragile; not necessarily associated with conifers; pileus typically acutely conical; often found on dung or other decomposing organic matter; resembling an enclosed <i>Stropharia</i> or <i>Psilocybe</i>
54.	Hypogeous to subepigeous associated with Pinaceae; resembling an enclosed or partially enclosed <i>Gomphidius</i> ; gleba sublamellate and not powdery at maturity; usually yellowish near the base of the stipe-columella
54.	Hypogeous to subepigeous associated with Pinaceae in the Pacific Northwest; resembling a large unopened <i>Agaricus</i> button; gleba powdery at maturity; usually bruising vinaceous near the base of the stipe-columella
55.	Spores in mass in the chambers or tramal plates white, pale yellow or orange at full development
55.	Spores in mass in the chambers or tramal plates green, olive yellow, olive brown, vinaceous, yellow brown, red brown to rusty brown59
56.	Color of glebal trama pink to pale red; sterile base and/or small, non-percurrent columella present, easily lost or broken; gleba not amyloid in Melzer's reagent; found only in association with <i>Eucalyptus</i>

56.	Glebal and tramal characters not as above; may or may not be found with <i>Eucalyptus</i>
57.	Fresh gleba and/or peridium exuding latex when cut; resembling contorted or unopened <i>Lactarius</i>
57.	Neither fresh gleba or peridium exuding latex when cut58
58.	Percurrent stipe-columella or columella present; gleba loculate, labyrinthiform, or sublamellate, may or may not be exposed; resembling contorted or unopened <i>Russula</i>
58.	Sterile base or at most small, columella present; gleba usually loculate or at most labyrinthiform, not exposed $\underline{Gymnomyces}$
59.	Spores in mass in the chambers or tramal plates some shade of green to olive brown or vinaceous
	Spores in mass in the chambers or tramal plates some shade of yellow brown, red brown to rusty brown
60.	Gleba vinaceous at full development from coloration of spores in mass
60.	Gleba some shade of green, olive yellow to olive brown61
61.	Stipe-columella present, percurrent, simple unbranched62
61.	Columella present, usually branched, if percurrent then highly branched and obviously delimited from the gleba63
62.	Gleba tubular, pendant from substantial pileus disk $\underline{Gastroboletus}$
62.	Gleba loculate, adhering to the stipe-columella, no substantial pileus disk present
63.	Sporocarp obpyriforme, in median section with prolonged, tapering stalk-like columella, gleba found above, in the thick portion of the sporocarp, the columella dividing the gleba into sharply delimited sectors; found in eastern and southeastern North America. Phallogaster
63.	Sporocarp subglobose to turbinate or slightly elongated, but usually not obpyriforme; columella typically branching from sterile base
64.	Sporocarp slender; pileus conic, parabolic to cylindric, acute to narrowly obtuse
64.	Sporocarp more robust; pileus subglobose, convex or broadly conical
65.	Pileus surface filamentous under the hand-lens
65.	Pileus surface cellular under the hand lens , at least not distinctly filamentous or with velar patches; gleba lamellate; sporocarp soon deliquescent and slimy; found in pastures or grasslands

- 68. Not saprophytic on twigs or logs; found in grassland, steppe or forests.......69

General

Arora, D. 1986. Mushrooms Demystified. Ten Speed Press, Berkeley. 959 pp.

Miller, O. K., Jr. 1978. Mushrooms of North America. E. P. Dutton, New

- York. 368 pp.
- Trappe, J. M. and M. A. Castellano. 1991. Keys to the genera of truffles (Ascomycetes). McIlvainea 10: 47-65.

Alpova and Melanogaster

- Beaton, G., D. N. Pegler and T. W. K. Young. 1985. Gasteroid Basidiomycota of Victoria State, Australia: 5-7. Kew Bull. 40: 573-
- Clemençon, H. 1977. Über *Melanogaster microsporus* und *Alpova diplophloeus*. Schweiz. Ztschr. Pilzk. 55: 155-156.
- Dodge, C.W. 1931. *Alpova*, a new genus of Rhizopogonaceae, with further notes on *Leucogaster* and *Arcangeliella*. Ann. Bot. Gard. 18: 457-463.
- Fogel, R.D. 1977. A note on the nomenclatural problem associated with the name *Alpova luteus* (Basidiomycetes, Melanogastraceae). Mycologia 69: 840-843.
- Gross, G. 1980. Über einige *Alpova* -funde in den Bayerischen Alpen. Ztschr. Mykol. 46: 21-26.
- Svrcek, M. 1966. Distribution of *Melanogaster tuberiformis* Corda in the Central Bohemia. (Cz) Ceska Mykol. 20: 28.
- Trappe, J.M. 1975b. A revision of the genus *Alpova* with notes on *Rhizopogon* and the Melanogastraceae. Nova Hedwigia Beih. 51: 279-309.
- Zeller, S. M. 1939. New or noteworthy Gasteromycetes. Mycologia 31: 1-32.
- Zeller, S. M. and C. W. Dodge. 1935. New species of Hydnangiaceae. Ann. Mo. Bot. Gard. 22: 365-373.
- Zeller, S.M. 1939. Developmental morphology of *Alpova*. Oregon State College Mon. Bot. #2, 19 pp.
- Zeller, S.M., and Dodge, C.W. 1936. *Melanogaster*. Ann. Mo. Bot. Gard. 23: 639-655.

Arcangeliella, Gymnomyces, Macowanites, Martellia, and Zelleromyces

- Beaton, B., D. N. Pegler and T. W. K. Young. 1984. Gasteroid Basidiomycota of Victoria State, Australia 2. Russulales. Kew Bull. 39: 669-698.
- Dodge, C.W. 1931. *Alpova*, a new genus of Rhizopogonaceae, with further notes on *Leucogaster* and *Arcangeliella*. Ann. Bot. Gard. 18: 457-463.
- Miller, S.L., and Miller, O.K. Jr. 1986. *Zelleromyces stephensii-*an interesting member of the gasteroid Russulales from Europe. Mycol. Helv. 2:59-66.
- Miller, S. L. and T. Lebel . 1999. Hypogeous fungi from the southeastern United States II. The genus *Zelleromyces*. Mycotaxon (in press).
- Pegler, D. N. and T. W. K. Young. 1979. The gasteroid Rusulales. Trans. Brit. Mycol. Soc. 72: 353-388.
- Pfister, D. H. 1976. A new combination in the genus Gymnomyces.

- Occ. Paps. Farlow Herb. Crypt. Bot. 9: 43.
- Singer, R. and A.H. Smith. 1960. Studies on secotiaceous fungi. IX. The astrogastraceous series. Mem. Torrey Bot. Club 21: 1-112.
- Smith, A. H. 1962. Notes on astrogastraceous fungi. Mycologia 54: 626-639.
- Smith, A. H. 1963. New astrogastraceous fungi from the pacific northwest. Mycologia 55: 421-441.
- Stewart, E.L., and Trappe, J.M. 1975. *Gymnomyces monosporus* sp. nov. Mycotaxon 2: 209-213.
- Thiers, H. D. 1979. New and interesting hypogeous and secotioid fungi from California. Sydowia Beih. 8: 381-390.
- Thiers, H.D. 1984b. The genus *Arcangeliella* in the western United States. Sydowia 37: 296-308.
- Trappe, J.M., and Castellano, M.A. 1986. Newly described hypogeous fungi and the mycorrhizae they form <u>in vitro</u>. I. *Martellia medlockü* sp. nov. (Russulaceae). Mycologia 78: 918-921.
- Zeller, S. M. 1947. More notes on Gasteromycetes. Mycologia 39: 282-312.
- Zeller, S. M. and C. W. Dodge. 1935. New species of Hydnangiaceae. Ann. Mo. Bot. Gard. 22: 365-373.
- Zeller, S.M., and Dodge, C.W. 1919. *Arcangeliella*, *Gymnomyces*, and *Macowanties* in North America. Ann. Mo. Bot. Gard. 6: 49-59.
- Zeller, S.M., and Dodge, C.W. 1936. *Elasmomyces*, *Arcangeliella*, and *Macowanites*. Ann. Mo. Bot. Gard. 23: 599-638.

Astreus, Pyrenogaster, Radiigera

- DomÃnguez de Toledo, L. and M.A. Castellano. 1996. A revision of the genera *Radiigera* and *Pyrenogaster*. Mycologia 88(5): 863-884.
- Long, W. H. and D. J. Stouffer. 1948. Studies in the Gasteromycetes: XVI. The Geastraceae of the south-western United States. Mycologia 40: 547-585.
- Malençon, G. and L. Riousset. 1977. *Pyrenogaster pityophilus* G. Malençon et L. Riousset, noveau genre et nouvell espèce de gastéromycète (Geastraceae). Bull. Soc. Mycol. France 93: 310.
- Zeller, S. M. 1944. Representative of the Mesophelliaceae in North America. Mycologia 36: 627-637.
- Zeller, S. M. 1948. Notes on certain Gasteromycetes including two new orders. Mycologia 40: 639-668.
- Zeller, S. M. 1949. Keys to the orders, families and genera of the Gasteromycetes. Mycologia 41: 36-58.

Brauniellula and Gomphogaster

- Pacioni, G. and R. Fogel. 1990. *Brauniellula crassitunicata*, a new secotioid species of Gomphidiaceae (Boletales, Basidiomycotina). Mycologia 82: 617-621.
- Miller, O. K., Jr. 1973. A new gastroid genus related to Gomphidius.

- Mycologia 65: 226-229.
- Smith, A. H. 1965. New and unusual Basidiomycetes with comments on hyphal and spore reactions with Melzer's solution. Mycopath. Mycol. Appl. 26: 385-402.
- Smith, A. H. and R. Singer. 1958. Studies on secotiaceous fungi. VIII. A new genus in the Secotiaceae related to *Gomphidius*. Mycologia 50: 927-938.

Chamonixia, Truncocolumella and Gastroboletus

- Singer, R., and Both, E.E. 1977. A new species of *Gastroboletus* and its phylogenetic significance. Mycologia 69: 59-72.
- Singer, R., and Smith, A.H. 1964. Studies on secotiaceous fungi X. Additional data on *Gastroboletus*. Mycologia 56: 310-313.
- Smith, A.H., and Singer, R. 1959. Studies on secotiaceous fungi IV Gastroboletus, Truncocolumella, and Chamonixia. Brittonia 11: 205-223.
- Thiers, H. D. 1989. *Gastroboletus* Revisited. Mem. NY Bot. Gard. 49: 355-359.
- Thiers, H.D., and Trappe, J.M. 1969. Studies in the genus *Gastroboletus*. Brittonia 21: 244-254.

Chondrogaster

Maire, R. 1925. Etudes mycologiques II. Rev. Mycol. Soc. France 40: 293-317.

Destuntzia

Fogel, R. and J. M. Trappe. 1985. *Destuntzia*, a new genus in the Hymenogastraceae (Basidiomycotina). Mycologia 77: 732-742.

Endogone

- Trappe, J.M., and Gerdemann, J.W. 1972. *Endogone flammicorona* sp. nov. a distinctive segregate from *Endogone lactiflua*. Trans. Brit. Mycol. Soc. 59: 403-407.
- Nicolson, T.H., and Gerdemann, J.W. 1968. Mycorrhizal *Endogone* species. Mycologia 60: 313-325.
- Eckblad, F-.E. 1954. Studies in the hypogaean fungi of Norway I. *Endogone* and Tuberales. Nytt. Mag. J. Bot. 3: 35-41.
- Bonfante-Fasolo, P., and Scannerini, S. 1976. The ultrastructure of the zygospore in *Endogone flammicorona* Trappe and Gerdemann. Mycopathol. 59: 117-123.
- Bucholtz, F. 1911. Über die Befruchtung von *Endogone lactiflua* Berk. Ann. Mycol. 9: 329-330.
- Gerdemann, J.W., and Trappe, J.M. 1970. *Endogone incrassata*: a Zygosporic species with hollow sporocarps. Mycologia 62: 1204-

1208.

Gerdemann, J.W., and Trappe, J.M. The Endogonaceae in the Pacific Northwest. Mycologia Mem. 5: 1-76.

Endoptychum, Gyrophragmium, Phellorina, and Podaxis

- Long, W. H. 1946. The genus *Phellorina*. Lloydia 9: 132-138.
- Morse, Elizabeth, E. 1933. A study of the genus *Podaxis*. Mycologia 25: 1-33
- Quadracia, L. 1977. *Gyrophragmium delilei* (Montagne) Specie nuova per la flora italiana. Boll. Gruppo Micol. G. Bresadola 20(5-6): 133-139.
- Singer, R. and Smith, A.H. 1958b. Studies on secotiaceous fungi II. Endoptychum depressum. Brittonia 10: 216-221.
- Zeller, S.M. 1943. North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. Mycologia 35(4): 409-421.

Galeropsis, Gastrocybe, Nivatogastrium, Setchelliogaster and Weraroa

- Beaton, G., D. N. Pegler and T. W. K. Young. 1985. Gasteroid Basidiomycota of Victoria State, Australia: 5-7. Kew Bull. 40: 573-598
- Singer, R. 1960. Three new specie of secotiaceae from Patigonia. Persoonia 1: 385-391.
- Singer, R. 1963. Notes on secotiaceous fungi; *Galeropsis* and *Brauniella*. Nederland. Akad. van Wetensch. Proc. Ser. C. Biol. Med. Sci. 66(1): 106-117.
- Singer, R. and A. H. Smith. 1958. Studies on secotiaceous fungi III. The genus *Weraroa*. Bull. Torr. Bot. club 85: 324-334.
- Singer, R. P. Ponce De Leon. 1982. Galeropsidaceae west of the Rocky Mountains. Mycotaxon 14: 82-90.
- Singer, R., and Smith, A.H. 1959. Studies on secotiaceous fungi. V. *Nivatogastrium* gen. nov. Brittonia 11: 224-228.
- Singer, R., and Smith, A.H. 1959. Studies on secotiaceous, fungi. VI. Setchelliogaster Pouzar. Madroño 15: 73-79.
- Singer, R., and Wright, Jorge E. 1959. A new species of the genus *Weraroa* from South America. Darwinia. 11: 607-610.
- Thiers, H. D. and R. Watling. 1971. Secotiaceous fungi from western United States. Madroño 21: 1-48.
- Watling, R. 1968. Observations on the Bolbitiaceae. IV. A new genus of gastromycetoid fungi. Mich. Botanist 7: 19-24.
- Zeller, S.M. 1943. North American species of *Galeropsis*, *Gyrophragmium*, *Longia*, and *Montagnea*. Mycologia 35(4): 409-421.

Gautieria and Protogautieria

Fitzpatrick, H.M. 1913. A comparative study of the development of the fruit body in *Phallogaster*, *Hysterangium*, and *Gautieria*. Ann.

- Mycol. 11: 119-149.
- Rauschert, R. 1975. Die Gattung *Gautieria* (Gasteromycetes) in der DDR. Hercynia N.F., Leipzig 12(2): 217-227.
- Smith, A. H. 1965. New and unusual basidiomycetes with comments on hyphal and spore wall reactions with Melzer's solution. Mycopath Mycol. Appl. 26: 385-402.
- Smith, A.H., and Singer, R. 1959. Studies on secotiaceous fungi IV Gastroboletus, Truncocolumella, and Chamonixia. Brittonia 11: 205-223.
- Soehner, E. 1951. Bayerische Gautieria-Arten. Sydowia 5: 396-406.
- Stewart, E.L., and Trappe, J.M. 1975. *Gautieria albida* and *Hymenogaster monosporus* sp. nov. Trans. Brit. Mycol. Soc. 65: 330-332.
- Stewart, E.L., and Trappe, J.M. 1985. The new genus *Austrogautieria* (Basidiomycotina), segregate from *Gautieria*. Mycologia 77: 674-687.
- Zeller, S. M. 1939. New and noteworthy Gastromycetes. Mycologia 31: 6-1-32.
- Zeller, S.M., and Dodge, C.W. 1918. *Gautieria* in North America. Ann. Mo. Bot. Gard. 5: 133-142.

Gymnoglossum

- Cribb, J.W. 1957. The Gasteromycetes of Queensland--IV *Gautieria*, *Hysterangium* and *Gymnoglossum*. Pap. Dept. Bot. Univ.Queensland. 17: 153-159.
- Smith, A.H. 1966. Notes on *Dendrogaster*, *Gymnoglossum*, *Protoglossum*, and species of *Hymenogaster*. Mycologia 58: 100-124.
- Zeller, S. M. 1948. Notes on certain Gasteromycetes including two new orders. Mycologia 40: 639-668.

Hydnangium

- Cribb, J.W. The Gasteromycetes of Queensland--V. *Octaviania* and *Hydnangium*. Pap. Dept. Bot. Univ. Queensland. 25: 247-254.
- Dodge, C.W., and Zeller, S.M. 1936. *Hydnangium* and related genera. Ann. Mo. Bot. Gard. 23: 565-598.
- Hawker, L.E. 1952 Hypogeous fungi II. A new variety of *Hydnangium carneum* Wallr. from North Wales III. Three new British records. Trans. Brit. Mycol. Soc. 35: 279-284.
- Singer, R. and A.H. Smith. 1960. Studies on secotiaceous fungi. IX. The astrogastraceous series. Mem. Torrey Bot. Club 21(3): 1-112.
- Zeller, S. M. 1939. New or noteworthy Gasteromycetes. Mycologia 31:
- Zeller, S. M. 1941. Further notes on fungi. Mycologia 33: 196-214.
- Zeller, S. M. 1948. Notes on certain Gasteromycetes including two new orders. Mycologia 40: 639-668.
- Zeller, S. M. and C. W. Dodge. 1935. New species of Hydnangiaceae. Ann. Mo. Bot. Gard. 22: 365-373.
- Zeller, S.M., and Dodge, C.W. 1919. Arcangeliella, Gymnomyces, and

Hymenogaster

- Dodge, C.W., and Zeller, S.M. 1934. *Hymenogaster* and related genera. Ann. Mo. Bot. Gard. 21: 625-708.
- Fogel, R.D. 1985. Studies on *Hymenogaster* (Basidiomycotina): a reevaluation of the subgenus *Dendrogaster*. Mycologia 77: 72-82.
- Gross, G. 1969 Über Hymenogasterfunde mit Sporem von 35-35μ mittlerer Laenge (On *Hymenogaster* collections with spores having an average lenth of 25-35 u.). Z. Pilz. 35(3/4): 157-174.
- Malençon, G. 1959. La sporogenese des *Hymenogaster* et ses enseignement. Bull. Mycol. France 75: 99-131.
- Smith, A.H. 1966. Notes on *Dendrogaster*, *Gymnoglossum*, *Protoglossum*, and species of *Hymenogaster*. Mycologia 58: 100-124.
- Soehner, E. 1962 Die Gattung *Hymenogaster* Vitt. Nova Hedwigia Beih. 2: 1-113.

Hysterangium

- Beaton, G., Pegler, D.N., and Young, T.W.K. 1985c. Gasteroid Basidiomycota of Victoria State, Australia. 4. *Hysterangium*. Kew Bull. 40: 435-444.
- Castellano, M. A. 1990. The Taxonomy of the genus *Hysterangium* (Basidiomycotina, Hysterangiaceae) with notes on its ecology. Ph. D. Thesis, Oregon State University, 237 pp.
- Fischer, E. 1938. Hypogaeen studien. 1. Zur Kenntnis der Gattung *Hysterangium.* Schweiz. Bot. Gesell., 48: 29-44.
- Soehner, E. 1952. Bayerische Hysterangium-Arten. Sydowia 6: 246-264.
- Zeller, S. M. 1939. New or notworthy Gasteromycetes. Mycologia 31: 1-32.
- Zeller, S.M., and Dodge, C.W. 1929. *Hysterangium* in North America. Ann. Mo. bot. Gard. 16: 83-128.

Leucogaster and Leucophleps

- Zeller, S.M., and Dodge, C.W. 1924. *Leucogaster* and *Leucophlebs* in North America. Ann. Mo. Bot. Gard. 11: 389-410.
- Zeller, S. M. 1947. More notes on Gasteromycetes. Mycologia 39: 282-312.
- Zeller, S. M. 1941. Further notes on fungi. Mycologia 33: 194-214.
- Dodge, C.W. 1931. *Alpova*, a new genus of Rhizopogonaceae, with further notes on *Leucogaster* and *Arcangeliella*. Ann. Bot. Gard. 18: 457-463.
- Fogel, R.D. 1975. The genus *Leucogaster* (Basidiomycetes, Leucogastraceae) Ph.D. Thesis, Oregon State University, 114 pp.
- Fogel, R.D. 1979. The genus *Leucophleps* (Basidiomycotina Leucogastrales). Can. J. Bot. 57: 1718-1728.

Mycolevis

- Fogel, R.D. 1976. Notes on distribution and spore ornamentation of Mycolevis siccigleba (Basidiomycetes, Cribbeaceae). Mycologia. 68: 1097-1103.
- Smith, A. H. 1965. New and unusual Basidiomycetes with comments on hyphal and spore reactions with Melzer's solution. Mycopath. Mycol. Appl. 26: 385-402.

Octavianina

- Cribb, J.W. The Gasteromycetes of Queensland--V. *Octaviania* and *Hydnangium*. Pap. Dept. Bot. Univ. Queensland. 25: 247-254.
- Singer, R. and A.H. Smith. 1960. Studies on secotiaceous fungi. IX. The astrogastraceous series. Mem. Torrey Bot. Club 21(3): 1-112.
- Pegler, D. N. and T. W. K. Young. 1979. The gasteroid Russulales. Trans. Brit. Mycol. Soc. 72: 353-388.
- Smith, A. H. 1962. Notes on astrogastraceous fungi. Mycologia 54: 626-639.

Richoniella

- Pegler, D.N. 1977. A new species of *Richoniella* (Hymenogastrales) from Ghana. Kew Bull. 32: 12.
- Cribb, J. W. 1956. The Gasteromycetes of Queensland-III. *Rhizopogon*, *Hymenogaster* and *Richoniella*. Paps. Dept. Bot. Univ. Queensland 3: 127-129.
- Cunningham, G. H. 1940. *Richoniella pumila*, a rare Gasteromycete. New Zeal. J. Sci. Techn. 22: 62.
- Dodge, C. W. and S. M. Zeller. 1934. *Hymenogaster* and related genera. Ann. Mo. Bot. Gard. 21: 683.

Rhizopogon

- Gillis, William, T. 1959. Subterranean *Elaphomyces* and *Rhizopogon* in the Michigan jack-pine region. Mycologia 51: 364-367.
- Harrison, K.A., and Smith, A.H. 1968. Some new species and distribution records of *Rhizopogon* in North America. Can. J. Bot. 46: 881-899.
- Hosford, D.R. 1975. Taxonomic studies of the genus *Rhizopogon* I. two new species from the Pacific Northwest. Nova Hedwigia Beih 51: 163-169.
- Hosford, D.R., and Trappe, J.M. 1980. Taxonomic studies on the genus *Rhizopogon*, II. Notes and new records of species from Mexico and Caribbean Countries. Bol. Soc. Mex. Micol. 14: 3-15.
- Miller, S.L. 1986. Hypogeous fungi from the southeastern United States I. The genus *Rhizopogon*. Mycotaxon 27: 193-218.
- Smith, A.H. 1964. *Rhizopogon*; a curious genus of false truffles. Mich. Bot. 3: 13-19.

- Smith, A.H. 1968. Further studies on *Rhizopogon*. I. J. Elisha Mitchell Sci. Soc. 84: 274-280.
- Smith, A.H., and Zeller, S.M. 1966. A preliminary account of the North American species of *Rhizopogon*. Mem. N.Y. Bot. Gard. 14: 1-178.
- Trappe, J.M. 1975b. A revision of the genus *Alpova* with notes on *Rhizopogon* and the Melanogastraceae. Nova Hedwigia Beih. 51: 279-309.
- Zeller, S.M., and Dodge, C.W. 1918. *Rhizopogon* in North America. Ann. Mo. Bot. Gard. 5: 1-36.

Rhopalogaster and Phallogaster

- Fitzpatrick, H.M. 1913. A comparative study of the development of the fruit body in *Phallogaster*, *Hysterangium*, and *Gautieria*. Ann. Mycol. 11: 119-149.
- Johnston, J. R. 1902. On *Cauloglossum transverarium* Fries (Bosc.). Amer. Acad. Arts Sci. Proc. 38: 59-74.
- Morgan, A. P. 1892. Description of a new phalloid. J. Cinn. Soc. Nat. Hist. 15: 171.
- Peck, C. H. 1907. New extralimital species of fungi. Bull. NY State Museum 116: 31.
- Thaxter, R. 1893. Contributions from the Cryptogamic Laboratory of Harvard University. XIX. Note on *Phallogaster saccatus*. Botanical Gazette 18: 117-121.

Scleroderma

Guzmán, G. 1970. Monografía del género *Scleroderma* Pers. emend. Fr. Darwiniana 16: 233-407.

Sclerogaster

- Coker, W. C. and J. N. Couch. 1928. Gasteromycetes of the Eastern United States and Canada. Univ. of North Carolina Press, Chapel Hill. 201 p..
- Fogel, R.D. 1977. Additions to the hypogaeous mycoflora of Colorado II. *Sclerogaster xerophilum* (Basidiomycetes, Hymogastrales). Mycologia 66: 980-986.
- Hawker, L.E. 1951. Hypogeous fungi. I. A hypogeous Gasteromycete, *Sclerogaster macrosporus*. J. S. Afr. Bot. 38: 29-31.
- Zeller, S. M. and C. W. Dodge. 1935. New species of Hydnangiaceae. Ann. Mo. Bot. Gard. 22: 365-373.

Sedecula

Zeller, S. M. 1941. Further notes on fungi. Mycologia 33: 196-214.

Thaxterogaster and Cortinarius

- Bougher, N.L., and Malajczuk, N. 1986. An undescribed species of hypogeous *Cortinarius* associated with *Eucalyptus* in western Australia. Trans. Brit. Mycol. Soc. 86: 301-304.
- Halling, R.E. 1981. Thaxter's Thaxterogasters and other Chilean hypogeous fungi. Mycologia 73: 853-868.
- Horak, E. 1979 (1980). Fungi, Basidiomycetes Agaricales y Gasteromycetes Secotoides. Flora Criptogámica de Tierra del Fuego 11: 1-524.
- Singer, R. 1951. *Thaxterogaster* -- a new link between Gastromycetes and Agaricales. Mycologia 43: 215-228.
- Singer, R., and Smith, A.H. 1963. A revision of the genus *Thaxterogaster*. Madroño 17: 22-26.
- Thiers, H. D. and A. H. Smith. Hypogeous Cortinarii. Mycologia 61: 526-536.
- Watling, R. 1980. A hypogeous *Cortinarius* from Kashmir. Notes Roy. Bot. Gard. Edinburgh 38: 357-362.

- Figures 1-3. Sporocarp types. 1. Agaricoid sporocarps, *Russula* sp. 2. Gastroid sporocarps, *Arcangeliella* sp.. 3. Hypogeous sporocarps, *Martellia* sp.
- Figures 4-11. Stipe-columella or columella types. 4. Percurrent stipe-columella, *Thaxterogaster* sp. 5. Dendritic columella, *Truncocolumella* sp. 6-7. Diffuse columella. 6. *Gautieria* sp. 7. *Hymenogaster* sp. 8-9. Sterile base. 8. *Hydnangium*. 9. *Gymnomyces*. 10. Central columella, *Radiigera*. 11. No columella, *Rhizopogon*.
- Figures 12-19. Gleba types. 12. Lamellate gleba, *Macowanites*. 13. Labyrinthiform gleba, *Macowanites*. 14-16. Lacunate gleba. 14. Large lacunae, *Gautieria*. 15. Small lacunae, *Rhizopogon*. 16-18. Filled or stuffed lacunae. 16. Solid or rubbery gleba, *Hysterangium*. 17. Gel-filled gleba, *Melanogaster*. 18. Liquid-filled, *Leucogaster*. 19. Peridiate gleba, *Pyrenogaster*.





