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Title: THE GENUS LEUCOGASTER (BASIDIOMYCETES,
LEUCOGASTRACEAE)

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Three provisional species are described as new: Leucogaster couchii, L. gelatinosus, and L. microsporus. Leucophlebs candida is transferred to Leucogaster, completing the transfer of all Leucophlebs species to Leucogaster. L. columellatus is transferred to Sclerogaster. L. longisterigmatus is synonymized with L. rubescens, L. foveolatus with L. odoratus, and L. fulvimaculatus with L. anomalus. Two new subgenera are proposed: subgenus Leucogaster with four species (L. levisporus, L. liosporus, L. magnatus, and L. rotundisporus); subgenus Rubidi, with 15 species: L. anomalus, L. araneosus, L. badius, L. candidus, L. carolinianus, L. citrinus, L. couchii, L. floccosus, L. gelatinosus, L. luteo-maculatus, L. microsporus, L. nudus, L. odoratus, L. rubescens, and L. tozziana.

The Genus Leucogaster (Basidiomycetes, Leucogastraceae)

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THE GENUS LEUCOGASTER (BASIDIOMYCETES, LEUCOGASTRACEAE)

I. INTRODUCTION

Leucogaster is a hypogeous fruiting Basidiomycete or false truffle traditionally placed in the Melanogastraceae on the basis of its latex filled locules that lack an organized hymenium. It is a small genus, infrequently collected in large numbers in western North American forests and even more rarely in eastern North America and western Europe. Its species are often macroscopically confused with other hypogeous basidiomycetes e. g., in the genera Martellia, Alpova, or Mycolevis and occasionally with the Ascomycete genus Tuber.

The history of Leucogaster dates from the description of Leucogaster liosporus from Germany by Hesse in 1882. He described a second European species in 1889 and then redescribed both species in 1891. Mattiolo (1900, 1903) later described two additional European species, Treves (1930) one, and Velenovsky (1922, 1939) three. The most recent treatments of European species are the regional summaries of Svrček (1958), Soehner (1924), and Szemere (1965). Unfortunately no adequate monographic treatment of European species has ever been attempted.

Zeller and Dodge's (1924) monograph of Leucogaster and Leucophlebs in North America contained nine North American and

five extralimital Leucogaster species. Included in the nine North American species were four new species and three previously placed by Harkness (1899) in Leucophleps (spelling corrected by Ferry (1900) to Leucophlebs). The two species remaining in Leucophlebs were relegated to the Fungi Imperfecti. Zeller (1941) later transferred one of the two remaining Leucophlebs species to Leucogaster leaving only Leucophlebs candida Harkn. in the Fungi Imperfecti. Except for three new Leucogaster species described by Zeller (1941, 1947), one by Coker and Couch (1928), and one new combination each by Dodge and Zeller (1936) and Zeller (1941), no subsequent revision of Zeller and Dodge's (1924) North American monograph has been made.

Leucogaster braunii was described by Rick (1934) from eucalyptus plantations in Brazil but Trappe (1975) has stated that this species might be an Alpova on the basis of the description. The type is apparently lost.

Good representations of Leucogaster species are difficult to assemble. Material dried after pickling revives very poorly; its value is thereby reduced, because critical examination of hymenial elements and other tissues is extremely difficult if not impossible. The limited geographic area in which I collected fresh material, mainly western Oregon, Washington, Idaho, Colorado, and northern California, plus the infrequent occurrence of Leucogaster are

additional limiting factors. Consequently, this treatment is preliminary and subject to major revision as more adequate collections with good accompanying notes become available.

II. METHODS AND MATERIALS

The present approach to Leucogaster employs the methods amply outlined by Smith and Zeller (1966) in their work on Rhizopogon. In this approach macroscopic features are correlated with microscopic characters and the results of simple macrochemical tests (reactions of tissues to contact with 3% iron sulphate, iron sulphate followed by 95% ethanol, 2.5% potassium hydroxide, and Melzer's solution containing iodine, designated hereafter as FeSO_4 , $\text{FeSO}_4 + \text{EtOH}$, KOH , and I respectively).

The specimens most valuable for future study ought to have standardized herbarium labels similar to the type proposed by Beschel and Soper (1970). Presently many herbarium labels are illegible and lack data on location, stand type, and notes on fresh characteristics. As a result many herbarium specimens are unusable to the monographer; they do not contribute to our understanding of geographic distribution or community composition. Development of adequate species descriptions is thereby hindered. Collections of hypogeous fungi, especially Leucogaster, should include notes on color of sporocarp and gleba, surface features, latex, rhizomorphs or columella, locules, odor, macrochemical reactions of the peridium, stains or bruising reactions, and the phanerogams, particularly possible mycorrhizal associates, at or near the collection sites.

Colors were determined using Ridgway (1912) and then converted to ISCC-NBS near synonyms (Kelly and Judd, 1965).

Specimen Collection

Searching for hypogeous fungi entails random digging or use of clues like small pits left in the forest floor by rodents such as squirrels and chipmunks that harvest sporocarps. Many partially consumed or overlooked sporocarps are found in this manner. Small mounds in the forest floor litter layer are another useful clue. Once a promising site has been selected, a small hand cultivator or rake is used to remove the overburden of litter and then to dig 5-10 cm into the mineral soil, exposing any sporocarps present. The collector often goes unrewarded, since the probability of finding a hypogeous sporocarp in any 1 m² quadrat during the peak periods of sporocarp production in western Oregon is only 34 to 66% (Fogel, unpubl.). Outside peak production periods, the probability lessens considerably.

Second growth forests, campgrounds, or stands of certain tree species such as Douglas-fir offer the easiest collecting because they have fewer of the thick impenetrable mats of tree roots that often characterize other forest habitats. The probability of finding hypogeous fungi is thereby improved. In old growth forests, old abandoned road beds are usually searched for similar reasons. Stands of

endomycorrhizal hosts, such as Thuja or Sequoia, are avoided.

Leucogaster is most frequently found in subalpine and old growth stands which have large numbers of entangled roots near the soil surface, rather to the dismay of those who would collect them.

Herbarium Deposits

Sporocarps were dried in repeated changes of activated 6-16 mesh silica gel (Hoseney, 1963) or in a forced air oven at 25-30°C for 48-72 hours and then packeted. Pieces of some sporocarps were placed in screw-cap vials of FAA for later staining and sectioning.

All collections were assigned Fogel collection numbers and deposited in the Oregon State University Herbarium (OSC). Collections were also examined by loan from these herbaria: Waite Agricultural Research Institute (ADW); National Fungus Collections (BPI); Cornell University (CUP); Central Washington State College (CWSC); Farlow, Harvard (FH); University of Tasmania (HO); Botanische Staatssammlung, München (M); University of Michigan (MICH); University of North Carolina (NCU); New York Botanical Garden (NY); Botany Department of National Herbarium, Prague (PR); Botanical Department, Naturhistoriska Riksmuseum, Stockholm (S); San Francisco State University (SFSC); Istituto Botanico della Università, Torino (TO); University of California, Berkeley (UC); Washington State University (WSP).

Microscopy

Light photomicrographs were made with a Polaroid J66 camera back mounted on a trinocular Zeiss GFL research microscope. A Vickers Instruments J35 automatic exposure unit was used to obtain proper exposure for Polaroid 200, type 42, 8.5 x 10.5 cm film.

Crush mounts and free hand sections mounted in KOH or I as well as saffranin-fast green stained paraffin embedded sections, prepared by the tertiary butyl alcohol dehydration series, were prepared for examining spore masses, individual hyphae, and tissues.

Dried herbarium material was prepared for scanning electron microscopy by the trichlorotrifluoroethane-freon 13 critical point drying method. Hymenial segments, about 5 mm square, were placed in small Whatman filter paper packets and rehydrated in distilled water for 30 minutes, then transferred at 10 minute intervals through a graded water: acetone series (30, 50, 70, 85, 100%) followed by dehydration in a graded acetone: trichlorotrifluoroethane series (30, 50, 70, 85, 100%). Dried spores were dusted directly on tacky silver paint or on small pieces of broken coverslips, previously coated with cellulose acetate and affixed to 15 mm diam aluminum stubs with silver paint. The prepared stubs were then coated with approximately 100 Å of gold: palladium (60:40) alloy as they were rotated in a Varian-10 vacuum evaporator. The stubs were examined and photographed

with an International Scientific Instruments MSM-2 Mini-SEM on
P/N 55 Polaroid film.

III. TAXONOMIC FEATURES

Development

Development in the Gasteromycetes has been described as lacunar, coralloid, pileate or multipileate depending on the manner in which the gleba is formed (Lohwag, 1926; Fischer, 1933; Cunningham, 1942). Leucogaster exhibits lacunar development, the simplest and most common type of those Gasteromycete genera which have been examined.

In lacunar development, chambers of the gleba are formed schizogenously within the undifferentiated primordial tissues enclosed by the rudimentary peridium and are scattered randomly into zones or groups. They are largest in the center and grade to smaller towards the periphery (Cunningham, 1942). Fischer (1922, 1933) has described development of what he called L. floccosus Hesse, although it might have been L. tozziana (Cav. & Sacc.) Mattiolo. The locules were not lined with a hymenium in the youngest stage studied (3.5 x 2.5 mm) but rather with thin-walled pseudoparenchyma. Fischer (1922) considered the pseudoparenchymous cells to be sterile whereas Dodge (1931) felt them to be vestigial conidia that had lost their original function. Zeller and Dodge (1924) confirmed the presence of the pseudoparenchymous cells in the juvenile stage (2 x 3 mm) of L. floccosus. In later stages (11 x 4-5 mm, 4 x 5 mm) the

pseudoparenchymous cells autolyzed forming the gel or latex into which the apobasidia developed (Zeller, 1939; Dodge, 1931; Zeller and Dodge, 1924).

The trama in the youngest stage (3.5 x 2.5 mm) of L. floccosus consists of subparallel, thin-walled hyphae (Zeller and Dodge, 1924). The apobasidia, which may be clavate or long-pedicellate, develop directly from the trama, growing into the gel formed by the autolyzing pseudoparenchyma. A catahymenium is formed since there is no organized palisade of hymenial elements and the apobasidia gelatinize or autolyze by maturity. Further modification of the apobasidia include long sterigmata in some species, perhaps induced by development in gel rather than air (Donk, 1964). Dodge (1931) states that Leucogaster includes stichobasidial and chiasobasidial species, that is cylindrical, with longitudinal nuclear spindles or clavate, with transverse nuclear spindles.

Macroscopic Characters

Since the basidiocarp of Leucogaster is a relatively simple structure, a tubercle with a lacunose interior, there are few gross morphological characters to consider. The more useful features include the structure of the peridium, its color and color changes following application of certain chemicals. Unfortunately, these features were neglected in many of the early descriptions. Zeller

and Dodge (1924), for instance, based their key and descriptions on dried or pickled herbarium specimens.

Shape and size: The basidiocarp is basically globose; any deviation from the norm is more likely to result from external pressures or the fusing of two separate sporocarps than the result of genetic differences. The smaller sporocarps in a collection tend to be more nearly globose than older ones, which reflect the effects of obstructions or mutual pressure as sporocarps enlarge. Size does not consistently indicate maturity. Generally one expects smaller sporocarps to be immature, but this is not always the case.

Consistency of the basidiocarp: Consistency is relatively unimportant in Leucogaster. All sporocarps, except those that are very mature or partly decomposed, are firm and rubbery when fresh. After drying, however, species in subgenus Leucogaster are friable and tend to crumble when sectioned. Species in subgenus Rubidi become very hard but section easily, especially the older sporocarps. Material that has first been preserved in fluid and then dried usually becomes extremely hard and difficult to section in either case. Some species stored in FAA for a year or more gradually disintegrate so that preparation of paraffin sections is difficult.

Peridium: Color of Leucogaster species changes distinctively on drying or when certain reagents are applied. Sporocarps of species in subgenus Leucogaster are usually white to ivory yellow fresh,

drying ochraceous-orange to cream-buff. Species in subgenus *Rubidi* may be white to chrome-yellow to brick red fresh; on drying some species develop a very dark red to black, glassy pigment. It is especially important to record fresh peridium color for those species with red, glassy pigment. During wet weather sporocarps may be guttate or form clear droplets of liquid on the peridium.

Color changes following the application of chemicals are best recorded from fresh material but some show on dried specimens. All Leucogaster sporocarps tested with KOH have given a positive test ranging from pink through vinaceous red or lilac. When FeSO_4 is applied to the peridium, some sporocarps do not react, some turn a light grey, and many turn green. When the application of FeSO_4 is followed by ethanol some sporocarps turn bright blue (ethanol is presumed to act as a wetting agent for the FeSO_4). Melzer's reagent will produce a green reaction when applied to the peridium of some species in subgenus *Leucogaster*. A few species in subgenus *Leucogaster* also have peridial hyphae that will react green, blue-grey, or grey in Melzer's reagent after drying. Not all sporocarps that react positively when fresh will do so after drying.

Rhizomorphs: Sporocarps of Leucogaster spp. often have remnants of rhizomorphs attached to the sporocarp. These may arise at more than one point on the surface of the basidiocarp or may be attached in a basal cluster.

Gleba: Glebal color is of little taxonomic value. All species are white, occasionally with some greenish discolorations, and dry to cream color or ivory yellow. The locules vary in size within a sporocarp and do not offer many features of taxonomic significance. Those of species in subgenus *Leucogaster* (pl. I, fig. 2) are small, 2 to 3 per mm, labyrinthiform, and may or may not be filled with spores. The locules of species in subgenus *Rubidi* (pl. I, fig. 1) are spherical, larger, 0.5 to 3 mm diam, and may or may not be filled with spores. The locules on the periphery of a sporocarp are usually smaller and often filled with spores while the locules in the center are larger and usually empty, reflecting the lacunar mode of development. No significant color change on application of macrochemicals has been noted.

Microscopic Characters

Basidiospores: *Leucogaster* spores are basically globose to subglobose except for *Leucogaster rotundisporus* Fogel and Trappe in Trappe (pl. IV, fig. 4, pl. V, fig. 4), the only species with broadly ellipsoidal spores. However occasional elongate or angular spores are often scattered among globose spores in other species. Spores are typically hyaline to subhyaline and may be light yellow in mass if the sporocarp has been preserved in fluid and then dried. Many species have spores with short pedicels or sterigmal scars. Spores

in subgenus *Leucogaster* often have a thin spot or pore (pl. V, fig. 1, 2) where they are attached to the basidium. No amyloid spores occur in the genus, but immature spores may react with lactic acid-acid fuchsin or cotton blue, or appear subhyaline to dark orange in Melzer's reagent.

Spore size and ornamentation are important characters. Several species can be differentiated by spore size. Many species, however, have spores that vary greatly in size in a given sporocarp, perhaps due in part to basidia maturing and releasing spores at different rates. Another factor influencing spore size is the number of spores per basidium. Spores twice as large as the average in a mount are occasionally found still attached to a one or two-spored, very thick walled basidium. Spore ornamentation is spinose-verrucose in subgenus *Leucogaster* and alveolate in subgenus *Rubidi*.

The spinose-verrucose ornamentation of some *Leucogaster* species is so minute (pl. IV, fig. 2; pl. V, fig. 2) that earlier workers described the spores as smooth. The spines of some species are only $\leq 0.25 \mu\text{m}$ high. Many earlier workers may also have considered spores of subgenus *Leucogaster* to be smooth because of gelatinous matrix embedding the ornamentation. If pressure is applied to the coverslip the ornamentation plus the gelatinous matrix separates from the spore and the spore itself is usually broken.

Species in subgenus *Rubidi* have alveolate spores (pl. IV, fig. 3;

pl. V, fig. 3) which are enclosed in a hyaline envelope or perisporeal sac (Pegler and Young, 1971). The spore reticulation is distinctive unless spores have been preserved in fluid and then dried or preserved as glycerin mounts. Spores preserved in glycerin seem to change in refractive index so that they appear transparent and devoid of ornamentation. The hyaline sac enclosing the spores expands free of the tips of the spines found at the junction of alveolar walls in KOH and Melzer's reagent and may rupture to release the spore if sufficient pressure is applied to the coverslip. The sac is thus very different than the gelatinous spore covering in subgenus *Leucogaster*.

Apobasidia: The basidium in *Leucogaster* (pl. II, fig. 1, 2, 4) is quite different than the basidium of the hymenomycetes or other Hymenogastrales. The apobasidia extend into the gel-filled locules forming a catahymenium since there is no organized palisade of hymenial elements. They vary in shape from subglobose to clavate-pedunculate and usually autolyze by maturity. The spores may be sessile or borne on long, straight or flexuous sterigmata. The lateral walls and sterigmata of an occasional spore-bearing basidium may become thick-walled and gelatinized with the apex occasionally thin. It is very difficult to locate basidia in mature sporocarps and those that have been dried. The walls and content are never colored (KOH) and no significant color reaction has been noted with the reagents normally used.

Sterile elements projecting into the locules are termed basidi-oles due to their resemblance to apobasidia. They are typically slightly narrower than basidia and thin-walled. No cystidia have been noted in any of the collections examined.

Tramal plates: Width of tramal plates is used here only occasionally as a taxonomic character since the width often varies with developmental stage or even within a given sporocarp. For this presentation, tramal width refers to the minimum distance between spore masses in two adjacent locules (pl. III, fig. 2, 4). The mediostratum and hymenophoral hyphae are usually included in this measurement but the hymenophoral hyphae may not be present in a mature sporocarp. The extensive use of tramal plate width by Zeller and Dodge (1924) accounts for much of the difficulty in using their keys. The hyphae of the tramal plate or mediostratum may be subparallel, narrow, or interwoven; the cells may be variably inflated, apparently depending on maturity of the sporocarp. Sphaerocysts occur in the axes of the tramal plates in mature specimens of L. carolinianus Coker and Couch. As sporocarps mature the mediostratum hyphae of many species gelatinize, increasing the rubbery texture of the gleba.

In Hymenogastreales with euhymenia, the hyphal layer next to the mediostratum and giving rise to the hymenial elements is referred to as subhymenium. The catahymenial elements in Leucogaster are loosely interwoven and project into the gel-filled locules. These

apparently unorganized analogs of the subhymenial hyphae have been termed hymenophoral hyphae in this presentation. The hymenophoral hyphae are often the first to gelatinize and may be present or not at maturity. Often the hymenophoral hyphae differ in diameter from the mediostratum hyphae.

Peridium: The peridium in most species is composed of appressed hyphae showing little or no differentiation except for intercellular and intracellular pigment deposits (pl. III, fig. 1, 3). The dark red glassy pigment produced in large quantities by many of the species in subgenus *Rubidi* on drying obscures hyphal details and dissolves in Melzer's reagent to produce "pigment balls" or droplets. Melzer's reagent reacts with the peridial hyphae of Leucogaster magnatus (Harkn.) Zeller and L. levisporus Zeller to produce a diffuse green intercellular pigment or a blue or grey-blue change in the walls of a few peripheral hyphae.

No epicutis or specialized cells such as seta has been found in the genus. The cells may be of equal diameter, narrow (2-4 μm) or broad (5-15 μm), or inflated to produce a "pseudoparenchymous" appearance in mature specimens of some species. The walls are typically smooth and thin, but thick-walled oleiferous hyphae occasionally occur. Walls may be colored as revived in KOH or remain hyaline, apparently depending in part on the method of preservation. The thickness of the peridium varies enormously even on a single

specimen and has been deemphasized as a taxonomic character.

Nonetheless, it can be a useful character in differentiating some widely contrasting species.

Clamp connection: None have been noted.

IV. HABIT, HABITAT, SEASONAL OCCURRENCE, AND SPORE DISPERSAL

Hypogeous fungi are usually found fruiting gregariously at the interface between the forest floor litter layer and the mineral soil or in the top 5-10 cm of the mineral soil. Occasionally in stands with thick litter layers, e. g., subalpine forests, sporocarps may occur in the H or F layers. Hypogeous sporocarps may also be found in old decayed logs which have been partially incorporated into the forest floor and invaded by tree roots, a particularly good place to examine if the forest floor seems very dry.

Temperature and moisture are the two most obvious factors governing the seasonal occurrence of Leucogaster and other fungal sporocarps (Smith, 1949). Another factor is vegetation type, reflecting the availability of a particular substrate or mycorrhizal symbiont. Leucogaster is most frequently found in subalpine stands of Picea-Abies in the early fall and in old growth (ca 450 years old) Pseudotsuga menziesii stands in both spring and early fall on the Pacific slope of Oregon and Washington. Eastern North American and German collections from Quercus-Fagus stands have been made in the late summer and early fall (Zeller and Dodge, 1924; Hesse, 1891). Mendocino County, California collections from Sequoia-Lithocarpus or Pinus muricatas stands have been made in December and a collection under Abies in June from Hildalgo, Mexico (Trappe and Guzmán,

1971).

The mycorrhizal forming ability of Leucogaster has not been experimentally confirmed, but circumstantial evidence suggests that ability. The tree associates of Leucogaster are in the Pinaceae and Fagaceae, both ectomycorrhizal families (Trappe, 1962). Mycorrhizae with mantles concolorous with the peridium of associated Leucogaster sporocarps have also been observed. Unfortunately, my attempts to establish tissue explant cultures for pure culture synthesis of mycorrhizae have failed.

The hypogeous habit and morphology of Leucogaster preclude aerial spore dispersal. Many hypogeous fungi with a similar habit and morphology effect spore dispersal through mycophagy by arthropods, mollusks, deer, squirrels, chipmunks, and wild pigs (Fogel, 1973, 1974, 1975a; Fogel and Trappe, 1975; Buller, 1922; Ingold, 1973; Gillis, 1959; Gross, 1969; Tevis, 1953). Adaptions of Leucogaster for mycophagous dispersal include a gelatinous spore sheath, sticky spore-containing latex, and rather strong odor at maturity.

In addition some species have bright colored peridia which might aid location once the sporocarp has been unearthed.

Although many Leucogaster sporocarps have apparently been damaged by insects before their collection, no insects have been reported associated with Leucogaster sporocarps or noted during routine isolation and subsequent identification of insects from

hypogeous sporocarps (Fogel and Peck, 1975). One possible explanation is that the sticky latex exuded by a damaged Leucogaster might impede insect invasion.

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V. PHYLOGENY

Much confusion currently exists about the relationships of families and genera generally placed in the Hymenogastrales. Traditionally the Hymenogastrales has been a catchall for Basidiomycetes with mostly hypogeous sporocarps, indehiscent peridia and glebae of one or more chambers (Zeller, 1949). Dring (1973) has recently attempted a more rigorous definition that entails absence of capillitium, hypogeous habitat, aulacate development, and subfusoid, acrosporus basidia with well developed sterigmata. He also recognizes the Melanogastrales as delimited in part by hypogeous sporocarps, lacunar development, and infertile primary basidia gelatinizing to give way to sporogenous secondary basidia. Leucogaster fits the traditional definition of the Hymenogastrales but is placed in the Melanogastrales by Dring (1973) and Svrček (1958).

Similar confusion exists on the familial placement of Leucogaster. Irrespective of Order, Leucogaster has been proposed as a member of the Hymenogastraceae (Dring, 1973; Fischer, 1933; Mattiolo, 1934; Svrček, 1958; Cunningham, 1942; Shaffer, 1968; Szemere, 1965; Zeller, 1949), Rhizopogonaceae (Gäumann and Dodge, 1928; Lange, 1956); Leucogastraceae (Moreau, 1954); and of uncertain position (Smith, 1973). Leucogaster does not fit the currently accepted delimitation of the Hymenogastraceae because its basidia

are not arranged in a palisade and the locules are filled with gel or latex. Trappe (1975) has recently restricted the Melanogastraceae to Melanogaster and Alpova, excluding Leucogaster because it has ornamented spores enclosed in a gelatinous exospore or perisporeal sac and no apparent affinities to Rhizopogon. Similarly Leucogaster is excluded from Zeller's (1949) concept of the Rhizopogonaceae because of its unorganized hymenium and ornamented spores.

Examination of proposed phylogenetic schemes reinforces the unlikelihood of the relationship between Leucogaster and other members of the Melanogastrales. Zeller and Dodge (1924), followed by Guzmán (1971), proposed a relationship between Leucogaster and Scleroderma. Favorable arguments are the subhyaline immature spores of Scleroderma and the smooth to echinulate or reticulate spore ornamentation commonly enclosed within a gelatinous sheath (pl. VI, fig. 3). I feel this proposal is untenable because Scleroderma has pigmented spores, knots of fertile hyphae instead of hymenium, powdery gleba, apical dehiscence, and nurse hyphae surrounding developing spores.

Dodge and Zeller (1936) also proposed a phylogenetic line from Leucogaster through Sclerogaster to Hydnangium or Arcangeliella without comment on their previously proposed link between Leucogaster and Scleroderma. The spores of Sclerogaster are globose, small (4-9 μm diam), minutely echinulate to verrucose, without a gelatinous

sheath (pl. VI, fig. 4). Macroscopically Sclerogaster resembles subgenus Leucogaster of Leucogaster except for the presence of a columella and lack of latex in the former. Other discrepancies are the presence of clamp connections on hyphae of the columella, short clavate basidia, and pedicellate spores of Sclerogaster. Hydnangium differs from Leucogaster in having clamp connections, pedicellate spores (pl. VI, fig. 2), clavate basidia arranged in a hymenium, and lack of gelatinous spore sheath. Singer and Smith (1960) included Hydnangium and Arcangeliella in the astrogastraceous series but Smith (1973) later placed Hydnangium in genera of uncertain affinity. The relationship of Leucogaster to Sclerogaster seems more tenable than to Scleroderma but unanswered questions on anatomy and developmental morphology of Sclerogaster precludes definite conclusions.

It is clear that Leucogaster is not related to the other members of the Melanogastrales and should be placed in a family of its own, if not a new order. Leucogastraceae has been proposed by Moreau (1954), but he did not validly publish the family (Cooke and Hawksworth, 1970).

LEUCOGASTRACEAE Fogel nom. prov.

= Leucogastraceae Moreau nom. nud., Les Champignons 2:1952.

1954.

TYPE GENUS: Leucogaster Hesse.

Basidiocarps hypogeous to emergent, globose to irregular, development lacunate. Peridium well developed, white to yellow or red, variable in thickness. Gleba loculate, usually filled with spores embedded in a sub-gelatinous mass and often exuding as a white, sticky latex when opened. Columella lacking. Apobasidia in a catahymenium, subglobose to clavate-pedunculate, autolyzing by maturity. Basidiospores hyaline to subhyaline, globose to broadly ellipsoid, minutely spinose-verrucose or alveolate, enclosed in a gelatinous matrix or separate hyaline sac. Clamp connections absent.

LEUCOGASTER Hesse, Jahrb. Wiss. Bot., Berlin 13:189-194. 1882.

= Leucophleps Harkness, Calif. Acad. Sci. Proc., Bot. III.

1:257-259. 1899. (Orthographically corrected to Leucophleps, Ferry 1900).

Type species: Leucogaster liosporus Hesse.

Etymology: Greek, leuco (white), gaster (stomach).

Basidiocarps hypogeous to emergent, globose to irregular.

Peridium well developed, white to yellow or red, variable in thickness, fragile, sometimes rupturing at maturity, reacting pink to vinaceous with KOH, occasionally reacting green to blue-grey with FeSO_4 and I reagent. Gleba loculate. locules spherical to polyhedral or sinuate, usually filled with spores embedded in a gelatinous mass separated by white veins and often exuding the white, sticky latex when opened.

Columella lacking. Apobasidia in a catahymenium, subglobose to clavate-pedunculate, four-spored, occasionally three or five-spored, autolyzing by maturity. Basidiospores hyaline to subhyaline, globose to broadly ellipsoid, minutely spinose-verrucose or alveolate, enclosed in a gelatinous matrix or separate hyaline sac. Clamp connections absent.

The peridium of Leucogaster characteristically varies substantially in thickness, even in individual specimens. This variation is due to the intrusion of glebal chambers or groups of chambers into the subcutis in some places, with gaps in outer chamber placement in others.

Harkness (1899) described Leucophleps (Leucophlebs) with five species to accommodate asexual states of Leucogaster. Zeller and Dodge (1924) transferred L. citrina Harkn., L. odorata Harkn., and L. foveolata Harkn. to Leucogaster due to the presence of basidia, relegating Leucophlebs candida and L. magnata to the Fungi Imperfecti. Zeller (1941) later discovered basidia in L. magnata and transferred it to Leucogaster. My examination of the holotype of Leucophlebs candida Harkn. also revealed basidia. Thus all Leucophlebs species are transferred to Leucogaster.

VI. KEYS

Introduction to Keys

Spore measurements include ornamentation, but not perisporal sac. Infrequent large spores e. g., twice as large as average, are ignored in couplets requiring spore size range. Mediostratum refers to the central portion of the tramal plate, excluding hymenophoral hyphae, apobasidia, and basidioles.

Key to Subgenera of *Leucogaster*

1. Spores spinose-verrucose or foveate, not alveolate, ornamentation embedded in a gelatinous matrix, not enclosed by a separate, hyaline envelope, ornamentation plus matrix separating from spore wall when sufficient pressure applied to coverslip; glebal latex scanty, locules labyrinthiform, 2-3 per mm.

SUBGENUS LEUCOGASTER p. 29

1. Spores alveolate, enclosed in a hyaline envelope separate from ornamentation (KOH, Melzer's reagent) and separating from spore when pressure applied to coverslip; glebal latex copious in fresh, moist specimen, locules spherical, 1-2 per mm.

SUBGENUS RUBIDI p. 42

Subgenus Leucogaster nom. prov.

Sporocarps subglobose to irregularly lobed, white to yellow.

Gleba white; scant, sticky latex produced when damaged; locules labyrinthiform, 0.25-0.5 mm broad, filled with spores at maturity.

Basidiospores subglobose to broadly ellipsoidal, spinose-verrucose or foveate, embedded in a gelatinous matrix.

Type species: Leucogaster liosporus Hesse.

Subgenus Leucogaster, Key to Species

- | | |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------|
| 1(0). Spore ornamentation $\leq 0.5 \mu\text{m}$ high. | 2 |
| 1(0). Spore ornamentation $\geq 1.0 \mu\text{m}$ high. | 3 |
| 2(1). Tramal plates $\pm 150 \mu\text{m}$ thick; spores broadly ellipsoidal, mean length-width ratio 1.3:1 with sterigmal peg. | 4. <u>rotundisporus</u> |
| 2(1). Tramal plates 50-90 μm thick, spores mostly subglobose to globose, mean length-width ratio 1.1:1 including sterigmal peg; an occasional angular spore present. | 1. <u>levisporus</u> |
| 3(1). Spores (10-) 15-17 (-22) μm diam, ornamentation of spines 1-2 μm high; tramal plates 40-80 μm thick; | |

locules 0.5 mm broad; western

North America.

3. magnatus

3(1). Spores (11-) 12-15 (-17) μm diam,

ornamentation of spines 1 μm high;

tramal plates 100-150 μm thick;

peridium 160-200 μm thick; locules

0.25 mm broad; western Europe.

2. liosporus

1. LEUCOGASTER LEVISPORUS Zeller, Mycologia 33:206. 1941.
pl. I, fig. 2; pl. III, fig. 2; pl. IV, fig. 2; pl. V, fig. 2; pl. VII.

Basidiocarps up to 25 mm diam, globose to irregularly lobed, rugose, chalk or milk-white becoming grayish, drying light ochraceous-buff (moderate orange yellow) with darker brown areas. Gleba white, drying ochraceous-orange (strong orange yellow), tramal plates concolorous, locules labyrinthiform, 0.5 mm broad, filled with spores at maturity. Consistency as dried pith-like but sectioning easily without crumbling. Smaller sporocarps with single basal rhizomorph, small rhizomorphs abundant on older specimens.

Chemical reactions of peridium: KOH pink to red, FeSO_4 negative, $\text{FeSO}_4 + \text{EtOH}$ negative, I green. Odor slight to acrid (celery seed?) on drying.

Basidiospores 10-13 x 10-11 μm , including ornamentation, mostly subglobose to globose, an occasional angular spore present, mean length-width ratio 1.1:1, subhyaline in mass (KOH), hyaline singly, mature spores staining slowly in lactic acid-acid fuchsin, verrucose; ornamentation of crowded spines $\leq 0.25 \mu\text{m}$ high, embedded in a gelatinous matrix; spore wall plus ornamentation and gelatinous matrix 1-1.5 μm thick, short sterigmal peg present occasionally. Apobasidia 45-50 x 9-10 μm , clavate, four-spored, thin-walled, content granular in KOH, sterigmata 6-8 x 1.5-2.0 μm broad (Zeller: up to 22.5 x 2.5 μm , but I found none of this size).

Basidioles $\pm 50 \times 10 \mu\text{m}$, clavate, hyaline (KOH), thin-walled. Tramal plates (30-)50-90 μm wide, mediostratum of subparallel, hyaline, thin-walled, septate hyphae 4-5 μm broad at septa, the cells becoming inflated to 10 μm , to appear nearly pseudoparenchymous. Peridium 100-120 μm thick, drying to 25-50 μm , of interwoven, hyaline hyphae 2-4 μm diam near the surface, becoming 10 μm diam toward locules, layer obscured by pale yellow, diffuse intercellular pigment (KOH), some surface hyphae thick-walled and blue-grey in Melzer's reagent.

ETYMOLOGY: Latin, *levo* (to make smooth), spore.

DISTRIBUTION, HABITAT, AND SEASON: Western North America (pl. VII), in coniferous forest duff, June to December.

COLLECTIONS EXAMINED: HOLOTYPE: OREGON, Wallowa County, Hat Point, 23 miles above Imnaha, 26 July 1939, leg. A. M. Rogers (NY). ALASKA, Kenai Peninsula, V. L. Wells and P. E. Kempton w-k-7/25/65#1 (MICH). ARIZONA, Apache National Forest, Hanagan Meadows Campground, H. D. Thiers 28981, 29064, 29069, 29073, 29103, 29132, 29220 (all SFSC). Coronado National Forest, Riggs Flat Lake, H. D. Thiers 29365 (SFSC). Coconino Co.: R. Fogel F636 (OSC). CALIFORNIA, Sierra Co.: H. D. Thiers 23656 (SFSC), Siskiyou Co.: W. B. and V. B. Cooke 34307. Stanislaus Co.: H. D. Thiers 16985, 16992, 17182 (all SFSC). COLORADO, San Juan Mountains, A. H. Smith 52922 (MICH). Boulder Co.: R. Fogel F383, F684 (all OSC). Chaffee Co.: R. Fogel F281a,

F287, F290, F293. Clear Creek Co.: R. Fogel F481, F688, F689,
 F694 (all OSC), leg. C. T. Rogerson (NY). Grand Co.: leg. C. T.
 Rogerson and E. G. Simmons (NY). Jackson Co.: R. Fogel F645,
 F661, F662, F664, F673 (all OSC). Larimer Co.: R. Fogel F657,
 F682, F701 (all OSC). IDAHO, Adams Co.: A. H. Smith 65588 (leg.
 N. J. Smith), 68891, 70426 (all MICH). Bonner Co.: A. H. Smith
 67928 (leg. N. J. Smith) pro part, 68033, 68575, 68655, 68657,
 67928 (leg. N. J. Smith), 68663, 7-14-64 (leg. N. J. Smith) (all
 MICH). Valley Co.: A. H. Smith 65214 (leg. N. J. Smith), 65390,
 65453, 65769 (leg. N. J. Smith), 65770 (leg. N. J. Smith), 65821
 (leg. N. J. Smith), 66082 (leg. R. Jeonne), 68809 (leg. P. Miller),
 68920 (leg. P. Miller and A. H. Smith), 68925 (leg. P. Miller),
 69019 (leg. N. J. Smith), 69585 (leg. H. Burdsall), 69613 (leg.
 K. Harrison), 69763 (leg. K. Harrison and P. Miller), 69764 (leg.
 P. Miller and K. Harrison) (all MICH). OREGON, Benton Co.:
 M. Doty 226a (BPI), Long 10045 (BPI), Zeller 2323 (NY). Coos
 Co.: J. M. Trappe 2688. Jefferson Co.: J. M. Trappe 1947.
 Linn Co.: leg. F. H. Smith (NY). Wasco Co.: R. Oswald 10
 (MICH), J. M. Trappe 3964 (leg. R. Oswald). WASHINGTON,
 Kittatas Co., J. M. Trappe 3644. Pend Orielle Co.: A. H.
 Smith 68072 (leg. P. Miller), 68075, 68087, 68205 (leg.
 N. J. Smith), 68207 (leg. N. J. Smith), 68208 (leg. N. J.
 Smith) (all MICH).

L. levisporus is one of the more frequently collected species of Leucogaster. Commonly reported tree associates are species of Picea, Larix, Abies and Psuedotsuga menziesii. This species has not been collected east of the Rocky Mountains despite much wider distribution of the probable mycorrhizal host genera.

L. levisporus is easily separated from L. magnatus and L. liosporus by its slightly smaller spores and taller spore ornamentation height. L. levisporus differs from L. rotundisporus in having subglobose rather than ellipsoidal spores and light colored peridium as dried if the holotype of L. rotundisporus is representative.

After examining dried and preserved type material, I concluded that the peridium is composed of prosenchymatic hyphae 2.5-4 μm diam which become inflated to 10-15 μm diam next to locules, instead of polygonal parenchyma as stated by Zeller (1941). No conidiophores were observed. Spores of old and young holotype specimens consistently possessed short ($\leq 0.25 \mu\text{m}$) ornamentation.

2. LEUCOGASTER LIOSPORUS Hesse, Jahrb. Wiss. Bot., Berlin

13:189-194. 1882.

_____ = Octaviana silesiaca Becker, Die Natur 35:356. 1886.

_____ = Octaviana? Gautiera? pityophila Becker nom. illeg.,

Die Natur 35:356. 1886.

OTHER REFERENCES: Fischer (1899) p. 311; Hesse (1891) p. 70-71; Saccardo (1891) p. 281; Szemere (1965) p. 206; Svrček (1958) p. 547-548, 800; Zeller and Dodge (1924) p. 389, 402.

ILLUSTRATIONS: Hesse (1882) fig. 1-6; (1891) pl. 3, fig. 14-15; Svrček (1958) fig. 197:1.

Basidiocarps 15 x 18 mm as preserved in fluid, subglobose or reniform to irregularly lobed, citron yellow (light yellow). Gleba white fresh, pallid yellow preserved, locules labyrinthiform, 0.25 mm broad, filled with spores. Rhizomorphs thick, 0.5-1 mm diam, basal, concolorous with peridium. No data available on odor or macrochemical tests.

Basidiospores (11-)12-15 (-17) μ m diam, including ornamentation, occasional spores larger than 15 μ m, subglobose, spinose-verrucose; ornamentation of spines 1 μ m high embedded in a gelatinous matrix, spore wall 2 μ m thick, excluding ornamentation, most with narrow basal pore. Spores pale yellow in mass, hyaline singly (KOH). Apobasidia 55-60 x 14-17 μ m, clavate, pedicellate, two to four-spored, hyaline, thin-walled, sterigmata 5-8 x 1.5-2 μ m,

straight. Basidioles not noted. Tramal plate 100-150 μm wide, mediostratum of interwoven, hyaline, thin-walled, septate hyphae 3-6 μm diam. Peridium 160-200 μm thick, of very loosely woven, hyaline, thin-walled hyphae 3-7 (-13) μm diam, a few inflated to 13 μm at the septum, acuminate hyphae occasionally projecting from the surface. No pigment droplets or clamp connections observed.

ETYMOLOGY: Greek, lio (smooth), spore.

DISTRIBUTION, HABITAT, and SEASON: Western Europe, hypogeous under birch and conifers, May.

COLLECTIONS EXAMINED: AUSTRIA: von Hoehnel 2705^a (FH).
CZECHOSLOVAKIA: leg. Melzer (PR 485777).

-----Apparently the type of L. liosporus is deposited in Marburg (MB) but loan of specimens or slide preparations was denied. Consequently my description is based on the literature and the few collections I was able to obtain.

-----L. liosporus is separated from L. magnatus, the other species with pronounced spore ornamentation, by having wider tramal plates, smaller locules, larger apobasidia, smaller spores (12-15 vs. 15-17 μm), and slightly thicker peridium (160-200 vs. 120-180 μm).

3. LEUCOGASTER MAGNATUS (Harkness) Zeller, Mycologia 33:

207. 1941. pl. II, fig. 2; pl. IV, fig. 1; pl. V, fig. 1,
pl. VII

= Leucophleps magnata Harkness, Calif. Acad. Sci. Proc.
Bot. III. 1:257-258. 1899.

OTHER REFERENCES: Svrček (1958) p. 555, 802.

ILLUSTRATIONS: Knapp (1954) tab. 7, fig. 10. Svrček (1958)
fig. 197:5.

Basidiocarps up to 30 mm diam, subglobose, reniform or
elongate, rugulose, white, light yellow in depressions, becoming
pallid yellow, drying medium brown. Gleba white, freshly cut
surface showing a blue tint which soon vanishes, drying ochraceous-
orange (strong orange yellow) or pale yellow, scant sticky latex
produced on cutting fresh specimens, locules labyrinthiform ± 0.5 mm
broad near center, smaller toward surface, empty in center or filled
with spores at maturity. Rhizomorphs innate-appressed, concolorous
with peridium. Odor on drying astringent (celery seed?). Chemical
tests on peridium: KOH pink, FeSO_4 negative, $\text{FeSO}_4 + \text{EtOH}$ nega-
tive, I green.

Basidiospores (10-)15-17 (-22) μm diam, including ornamenta-
tion, globose, light yellow singly (KOH, I), verrucose; ornamentation
of very slender, closely spaced spines 1-2 μm high, embedded in
a gelatinous matrix, spore wall 1-2 μm thick, with basal pore.

Apobasidia 30-50 x 6-12 μ m, clavate, hyaline, thin-walled, four-spored, sterigmata 5-8 x 2 μ m. Basidioles 30-50 x 6-12 μ m, clavate to claviform, hyaline, thin-walled, simple septate at base. Tramal plates (40-) 60-80 μ m wide, mediostratum of subparallel, hyaline, thin-walled, septate hyphae 3-5 μ m diam, the cells becoming inflated to 7 μ m. Peridium (80-) 120-180 μ m thick, of periclinal, hyaline, thin to thick-walled (0.5 μ m) hyphae 3-6 μ m diam, obscured by yellow, intercellular pigment (I), and hyaline crystals; some areas staining green in I, fading in intensity after 10-15 minutes and occasional hyphal ends staining grey to grey-blue.

ETYMOLOGY: Latin, magnus (large).

DISTRIBUTION, HABITAT, AND SEASON: Western North America (pl. VII), hypogeous in subalpine stands of Abies and Tsuga from June to October, and low-elevation second growth stands of Pseudotsuga menziesii from April to May in western Oregon and December in northern California.

COLLECTIONS EXAMINED: HOLOTYPE: CALIFORNIA,

Napa County, Calistoga, April, H. W. Harkness 154 (BPI). Mendocino Co., R. Fogel F405 (OSC). Sierra Co., H. D. Thiers 23603 (SFSC). IDAHO, Valley Co., A. H. Smith 66019. 69947 (leg. P. Miller)(all MICH). OREGON, Benton Co., R. Fogel F394 (OSC). S. M. Zeller 8511 (NY, OSC). S. M. Zeller 8513 (NY). Josephine Co., E. Stewart 404, 405. Lane Co., R. Fogel F576 (OSC). Linn

Co., leg. H. M. Gilkey and D. P. Rogers (NY). Polk Co., leg. D. R. Hosford (OSC). leg. J. M. Trappe (OSC). WASHINGTON, Mt. Rainier National Park, D. R. Hosford H-126 (part), H-136, H-154, H-170, H-282, H-313, H-315, H-137, H-345, H-370, H-409, H-422, H-466, H-468, H-478, H-523, H-1006, H-1007 (all CWSC).

L. magnatus is separated from L. rotundisporus and L. levisporus by its relatively high spore ornamentation (1-2 μm vs. $\leq 0.25 \mu\text{m}$ high). It is differentiated from L. liosporus, the other species with relatively high ornamentation in subgenus Leucogaster, by its larger spores, large locules, and narrower tramal plate.

Macroscopically this species resembles L. levisporus. Both species possess the strong acrid smell (celery seed?) after drying, are found in similar habitats, and have peridia that react green after application of Melzer's reagent. The difference in spore size and spore ornamentation height is striking and consistent except for a few collections that have spore ornamentation 0.5-0.75 μm high.

These collections are rare and may indicate hybridization of the two species or evolutionary divergence from a common ancestor.

4. LEUCOGASTER ROTUNDISPORUS Fogel and Trappe in Trappe,

Nova Hedw. Beih. (in press). 1975. pl. IV, fig. 4;

pl. V, fig. 4.

= Cremeogaster levisporus Mattiolo in Lloyd, Mycol. Writ. 7:

1278. 1924. non Leucogaster levisporus Zeller,

Mycologia 33:206. 1941.

OTHER REFERENCES: Fischer (1936) p. 232; Mattiolo

(1934) p. 248; Zeller (1947) p. 283-284; Zeller and Dodge (1924)

p. 398.

ILLUSTRATIONS: Lloyd (1924) fig. 2845, 2846, 2847.

Basidiocarps drying up to 20 x 35 mm, subglobose to irregularly lobed, rugulose, granulate, very dark red, appearing black dried. Gleba cream color, drying pallid orange with white tramal plates, locules labyrinthiform, 0.3-0.5 mm broad, filled with spores at maturity. Consistency friable as dried. Fibrils not present on holotype. No data available on odor or macrochemical tests.

Basidiospores 8-13 (-19) x 7-10 (-14) μ m, including ornamentation, broadly ellipsoidal, (mean length-width ratio = 1.3:1), hyaline, finely verrucose; ornamentation of spines $\leq 0.1 \mu$ m high embedded in a gelatinous matrix, spore wall 1-2 μ m thick, sterigmal peg present, central to rarely oblique. Apobasidia 45-50 x 9 μ m,

clavate-pedicillate, four-spored, thin-walled, hyaline, sterigmata $6 \times 1.5 \mu\text{m}$. Basidioles $45-50 \times 8 \mu\text{m}$, clavate-pedicellate, thin-walled, hyaline. Tramal plates $\pm 150 \mu\text{m}$ wide; mediostratum of sub-parallel, hyaline, thin-walled hyphae $2-4 \mu\text{m}$ diam, cells inflated up to $20 \mu\text{m}$ and \pm isodiametric, obscured by diffuse, intercellular, orange pigment.

ETYMOLOGY: Latin, rotundus (almost circular), spore.

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous under Pinus ponderosa during December. Known only from the type collection.

COLLECTIONS EXAMINED: HOLOTYPE: CALIFORNIA, San Antonio Mountains, San Antonio Canyon, 15 December 1918, Coll. L. M. Johnston 263. ISOTYPES: Lloyd 15584 (BPI), NY, Soehner 482 (M).

The fine spore ornamentation and broadly ellipsoidal spores separate L. rotundisporus from other species in subgenus Leucogaster.

Zeller and Dodge (1924) stated that L. rotundisporus agreed with L. citrinus "in all respects except that it is slightly younger material and the spore is scarcely pitted yet." Zeller (1947) later stated that "a critical study of this genus (Cremeogaster) and species has led the writer to agree with Fischer that it is a good genus independent from Leucogaster . . . it differs from Leucogaster in

ellipsoidal, smooth spores which do not possess a gelatinous sheath. " My examination of L. rotundisporus showed that it does possess ornamentation of very fine ($\leq 0.1 \mu\text{m}$ tall) spines embedded in a thin gelatinous matrix, most noticeable microscopically when slightly out-of-focus. Zeller (1947) stated that the spores of L. levisporus were smooth, when, in fact the ornamentation is of spines $\leq 0.25 \mu\text{m}$ tall.

Subgenus Rubidi nom. prov.

Sporocarps subglobose, reniform, or irregularly lobed, white becoming yellow, drying scarlet to dark brown due to exuded pigment which forms pigment droplets in I reagent. Gleba white, exuding copious, milky latex when damaged; locules spherical to polyhedral, 0.5-3.5 mm broad, empty or filled with spores at maturity. Basidiospores subglobose, alveolate, enclosed in a hyaline perisporal sac.

Type species: Leucogaster rubescens Zeller and Dodge.

Subgenus Rubidi, Key to Species

- | | |
|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| <p>1(0). Spores (6-)7-8 x 5-7 μm, including ornamentation.</p> | <p>15. <u>microsporus</u></p> |
| <p>1(0). Most spores larger than 8 x 7 μm.</p> | <p>2</p> |
| <p>2(1). All but a few spores 8-10 μm long, including ornamentation.</p> | <p>3</p> |
| <p>2(1). All spores larger than 10 μm.</p> | <p>9</p> |
| <p>3(2). Peridium 240-600 μm thick.</p> | <p>5. <u>anomalous</u></p> |
| <p>3(2). Peridium less than 210 μm thick.</p> | <p>4</p> |
| <p>4(3). Peridial hyphae 1-2 μm diam.</p> | <p>6. <u>araneosus</u></p> |
| <p>4(3). Peridial hyphae 2-3.5 μm diam. or broader.</p> | <p>5</p> |
| <p>5(4). Cells of mediostratum inflated up to 25 μm diam.</p> | <p>13. <u>gelatinosus</u></p> |
| <p>5(4). Cells of mediostratum not inflated or inflated to no more than 8 μm.</p> | <p>6</p> |
| <p>6(5). Junctions of alveolar ridges formed as low cones 0.5 μm tall and 1 μm broad at base; mediostratum hyphal cells inflated up to 7 μm.</p> | <p>17. <u>odoratus</u></p> |
| <p>6(5). Junctions of alveolar ridges formed as spines taller than broad; mediostratum cells 3-5 μm diam, not inflated.</p> | <p>7</p> |

- 7(6). Trama 45-70 μm wide; peridial
hyphae 2-3.5 μm diam. 14. luteomaculatus
- 7(6). Trama 90-170 μm wide; peridial
hyphae 3-5 μm diam. 8
- 8(7). Spore ornamentation 0.5 μm tall;
fresh sporocarps white; apobasidia
 $\pm 45 \times 8-9 \mu\text{m}$. 11. couchii
- 8(7). Spore ornamentation 1 μm tall; fresh
sporocarps citron (light greenish
yellow); apobasidia 100-125 \times 5-7 μm . 10. citrinus
- 9(2). Spores 13-16(-17) \times (12-)13-14(-15) μm ;
peridial hyphae 4-5 μm broad, not
inflated. 16. nudus
- 9(2). Spores smaller or peridial hyphae
inflated to 8-10 μm . 10
- 10(9). Spore ornamentation 0.25-0.5 μm tall;
mediostratum hyphae 2-3 μm diam. 8. candidus
- 10(9). Spore ornamentation 0.5 μm or more
tall; some mediostratum hyphae broader
than 3 μm . 11
- 11(10). Spore ornamentation 0.5-1.0 μm tall;
peridial hyphae 1.5-3 μm diam. 9. carolinianus

- 11(10). Spore ornamentation 1 μm tall or taller;
 peridial hyphae 3-7 μm diam or cells
 inflated even broader. 12
- 12(11). Peridium 200-300 μm thick; mediostratum
 hyphae 4-10 μm diam. 12. floccosus
- 12(11). Peridium less than 180 μm thick;
 mediostratum hyphae 3-5 μm diam. 13
- 13(12). Peridial hyphae 4-7 μm diam, not
 inflated; glebal locules 0.3-0.5 μm
 diam. 19. tozziana
- 13(12). Peridial hyphae 3-5 μm diam at septa,
 the cells inflated up to 8-12 μm diam;
 glebal locules 0.5-1.5 mm diam;
 peridium with red to dark red pigment
 balls in Melzer's reagent. 14
- 14(13). Peridium 60-100 μm thick; apobasidia
 50-125 x 8-14 μm ; North America. 18. rubescens
- 14(13). Peridium 120-190 μm thick; apobasidia
 20-40 x 7-9 μm ; Southern Europe. 7. badius

5. LEUCOGASTER ANOMALUS (Peck) Zeller and Dodge, Ann.

Mo. Bot. Gard. 11:399-400. 1924.

= Hymenogaster anomalus Peck, N. Y. State Mus. Bull. 116:

31-32. 1907.

= Leucogaster fulvimaculosus Zeller and Dodge, Ann. Mo.

Bot. Gard. 11:401. 1924.

OTHER REFERENCES: Coker and Couch (1928) p. 44-45.

Saccardo and Trotter (1912) p. 496.

ILLUSTRATIONS: Zeller and Dodge (1924) pl. 11, fig. 4a, 4b, 4c, 8.

Basidiocarps as dried 10-25 mm diam, globose to irregularly lobed, glabrous, slightly lacunose, drying cinnamon-buff (light yellowish brown), clay color (moderate yellowish brown), and tawny olive (moderate yellowish brown) to Mikado brown (light brown) above, Hay's russet to liver-brown (moderate reddish brown) below.

Gleba drying amber-brown (strong brown) to Sudan brown (light brown), sometimes lighter; locules subglobose to spherical, 0.5-3.5 mm broad, the larger empty and in the center of the sporocarp, the smaller filled with spores and next to peridium; hard as dried, but sectioning easily. Rhizomorphs "root-like," basal. Odor slight, agreeable. No data available on fresh color, latex or macrochemical tests.

Basidiospores 8-10(-15) x 8-9(-13) μ m, including alveolate

ornamentation, globose to occasionally broadly ellipsoidal, hyaline, enclosed in a hyaline perisporeal sac; ornamentation of spines 0.5-1 μm high, 1.5-2.5 μm apart, reticulations minute and difficult to discern; spore wall 1 μm thick excluding ornamentation; almost sessile, sterigmal appendage stout, basal central. Apobasidia 50-90 x 6-10 μm , clavate, pedicellate, three to four-spored, hyaline (KOH), sterigmata conical, 1.5-2 μm long. Basidioles 50-55 x 5-11 μm , clavate, pedicellate, granular-guttulate, hyaline, thin-walled. Tramal plates 120-200 μm wide; mediostratum of interwoven, hyaline, thin-walled hyphae 3-5 μm diam; hymenophoral hyphae gelatinized, hyaline, loosely woven, 5 μm diam. Peridium 240-600 μm thick, of interwoven, hyaline, thin-walled hyphae 3-5 μm diam, with rare pockets of thin-walled sphaerocysts 15-25 μm diam; tissue near surface obscured by red pigment that forms red "pigment balls" in I reagent.

ETYMOLOGY: Latin, anomalus (abnormal, probably referring to its relation to other Hymenogaster sp.).

DISTRIBUTION, HABITAT, AND SEASON: Eastern North America, hypogeous in mixed woods, August to September.

COLLECTIONS EXAMINED: HOLOTYPE: DISTRICT OF COLUMBIA, Washington, Rock Creek Park, September 1906, leg. T. E. Wilcox. Zeller 1459 (NY). NEW YORK, leg. A. F. Blakeslee (FH, holotype of L. fulvimaculosus).

The thick peridium (thickest for the genus) and the short, conical sterigmata separate L. anomalus from L. citrinus and L. couchii. The tramal plate width, used by Zeller and Dodge (1924) to separate L. fulvimaculosus from L. anomalus, was within the range of variation of L. anomalus and the two agreed in all other characters.

The holotype of L. anomalus appeared to have been preserved in fluid then dried; hymenial elements and spore ornamentation revived poorly. No rhizomorphs or fibrils were present on the holotype and a "sterile base" as reported by Zeller and Dodge (1924) was not observed. Fresh colors noted by Zeller and Dodge (1924) were the same as the pickled material.

6. LEUCOGASTER ARANEOSUS Zeller and Dodge, Ann. Mo. Bot. Gard. 11:399. 1924.

OTHER REFERENCES: Coker and Couch (1928) p. 43.

Basidiocarp as preserved in fluid, 6 mm diam, globose, brown. Gleba brown; locules spherical, 0.25-0.5 mm broad, filled with spores at maturity. Rhizomorphs large, few, adnate, somewhat branched. No data available on fresh color, odor, or macrochemical reactions.

Basidiospores 8-10 (-16) x 8-9 (-14) μ m including alveolate ornamentation, subglobose, hyaline, enclosed in a hyaline perisporeal sac; ornamentation of spines 1 μ m high, 2.5-3 μ m apart, joined by ridges to form 5-6 sided alveoli. Apobasidia 60-300 x 7-10 μ m, pedicellate, one to four-spored, thin-walled, hyaline, sterigmata lacking. Basidioles 55-300 x 4-9 μ m, pedicellate, thin-walled, hyaline, with granular content (KOH). Tramal plates 40-50 μ m wide; mediostratum of subparallel, loosely woven, subhyaline to light brown, thin-walled hyphae 2-3 μ m diam; hymenophoral hyphae loosely interwoven, hyaline, gelatinized, 4-5 μ m diam. Peridium 130-180 μ m thick, of loosely woven, light brown, thin-walled hyphae 1-2 μ m diam; interrupted by nests of sphaerocysts 12-15 μ m broad. No pigment droplets present in acid-fuchsin preparations.

ETYMOLOGY: Latin, araneosus (full of cobwebs).

DISTRIBUTION, HABITAT, AND SEASON: North Carolina,

August.

COLLECTIONS EXAMINED: HOLOTYPE: NORTH CAROLINA,
Cranberry, August 1896, R. Thaxter 96 (FH, Zeller 2624 (NY).

The very narrow peridial hyphae distinguish this species from all others in the genus. It is close to L. luteomaculatus, also from North Carolina, but differs in having a thicker peridium, thinner peridial hyphae, and smaller locules. Further collections are needed to verify these differences and expand the species description.

7. LEUCOGASTER BADIUS Mattiolo, Mem. Accad. Sci. Torino
Ser. 2. 53:356. 1903. Fig. 1, 2, 3.

OTHER REFERENCES: Coker and Couch (1928) p. 44; Saccardo and Saccardo (1905) p. 240; Szemere (1965) p. 205; Zeller and Dodge (1924) p. 400-401.

ILLUSTRATIONS: Zeller and Dodge (1924) pl. 11, fig. 9.

Basidiocarps as dried up to 20 x 24 mm diam, subglobose; surface smooth, glassy and chestnut brown (moderate reddish brown) from exuded dark red pigment. Gleba dark orange, locules spherical, 0.5-1 mm broad, empty. Dried consistency very hard, difficult to section (probably preserved in fluid, then dried). No data available on fresh color, latex, odor or macrochemical tests.

Basidiospores 12-14 (-15) x (10-)11-13 μ m diam, including alveolate ornamentation, globose to angular, enclosed in a hyaline perispore sac; ornamentation of spines 1-2 μ m high, 3 μ m apart joined by ridges to form 5-6 sided alveoli; spore wall 2 μ m thick excluding ornamentation, yellow. Apobasidia 20-40 x 7-9 μ m, clavate, four-spored, hyaline, thin-walled, sterigmata 1-2 μ m long.

Basidioles 40 x 7-12 μ m, clavate, hyaline, thin-walled. Tramal plate 40-50 μ m wide; mediostratum of subparallel, yellow, thin-walled hyphae 3 μ m diam; hymenophoral hyphae gelatinized, loosely interwoven, 1-2 μ m diam. Peridium 120-190 μ m thick, of periclinal to disorganized, hyaline, thin-walled hyphae 3-5 μ m diam, cells

rarely becoming inflated to 8-10 μm ; tissues obscured by red inter-cellular pigment that forms red "pigment balls" in I reagent.

ETYMOLOGY: Latin, *badius* (reddish-brown, dull brown).

DISTRIBUTION, HABITAT, AND SEASON: Western Europe under Abies and Quercus, July.

COLLECTIONS EXAMINED: ITALY: Apennino Pistoiese, leg. O. Mattiolo (TO). leg. O. Mattiolo (Lloyd 15581 (BPI). GERMANY: Egelhafer, E. Soehner 202 (M). Breitenbrunn, E. Soehner 238 (M).

L. badius is characterized by its large spores, 12-14 (-15) x (10-)11-13 μm , rarely inflated peridial and uninflated mediostratum hyphae. It differs from the other large-spored European species, L. nudus, in having a thicker peridium, somewhat smaller spores, and thinner mediostratum hyphae. L. badius has larger spores and locules than L. tozziana.

The Lloyd collection (BPI) is labeled "type" and corresponds in all details with the Torino collection. Zeller and Dodge's (1924) description is apparently based on a New York collection made by E. A. Burt. Their description differs strikingly from the type of L. badius in tramal plate width, peridial thickness, and lack of sterile base and stipe. I have placed the Burt collection in L. rubescens, which differs from L. badius in having sessile spores, larger apobasidia, and thinner peridium.

8. LEUCOGASTER CANDIDUS (Harkness) R. Fogel comb. nov.

prov. pl. 11, fig. 1.

= Leucophleps candida Harkness, Calif. Acad. Sci. Proc.

Bot. III. 1:258. 1899.

OTHER REFERENCES: Ferry (1900) p. 83; Saccardo and Sydow (1902) p. 252; Zeller and Dodge (1924) p. 407; Zeller (1948) p. 668.

Basidiocarps up to 20 mm diam when fresh, irregular, surface uniformly pocked with depressions of varying size, white when fresh, brown as pickled. Gleba white when fresh, brown as pickled, locules spherical, (0.5-)1 mm broad, filled with spores at maturity. Rhizomorphs and fibrils adnate, concolorous. No data available on odor or macrochemical tests.

Basidiospores 10-11(-12) x 9-10 μ m, averaging 10.9 x 9.4 μ m, including alveolate ornamentation, subglobose, enclosed in a hyaline envelope, spore content yellow; ornamentation of spines 0.25-0.5 μ m high, 2 μ m apart, joined by ridges to form 5-6 sided alveoli, spore wall 1 μ m thick including ornamentation, hyaline, sterigmal peg stout, central on the long spore axis, 1 x 1 μ m. Apobasidia 65 x 10 μ m, pedicellate, four-spored, thin-walled, with yellow, granular contents (KOH), sterigmata 1.5 x 1.5 μ m. Basidioles \pm 75 x 10 μ m, pedicellate, thin-walled, with yellow, granular contents (KOH).

Tramal plate 90-100 μ m wide; mediostratum of subparallel, yellow,

thin-walled, septate hyphae 2-3 μm diam; hymenophoral hyphae interwoven, hyaline, gelatinized, 4-7 μm diam. Peridium 80-120 μm thick, of periclinal, reddish-brown, thin-walled, septate hyphae 2-3 μm diam; tissues obscured by reddish brown intercellular pigment, no "pigment balls" formed in I reagent.

ETYMOLOGY: Latin, candidus (pure glossy white).

DISTRIBUTION, HABITAT, AND SEASON: Oregon and California, hypogeous under coniferous duff, June to August.

COLLECTION EXAMINED: HOLOTYPE: CALIFORNIA, Marin Co., Mill Valley, coll. H. W. Harkness 207 (BPI). Santa Clara Co., H. E. Parks 1160 (NY). OREGON, Jefferson Co., S. M. Zeller 8160 (NY).

Examination of the holotype revealed basidia (pl. II, fig. 1) so that the last Leucophlebs species can be transferred to Leucogaster.

Leucogaster candidus is separated from L. citrinus and L. couchii by its narrow (2-3 μm vs. 3-5) peridial and mediostratum hyphae, larger spores, and lack of red peridial pigment. It differs from L. araneosus and L. luteomaculatus in having larger spores, wider tramal plate, and shorter ornamentation (0.25-0.5 μm high vs. 0.75-1 μm).

9. LEUCOGASTER CAROLINIANUS Coker and Couch, The Gasteromycetes of the Eastern United States and Canada. p. 43-44. 1928.

---ILLUSTRATIONS: Coker and Couch (1928) pl. 27, 28, 198.

Fresh basidiocarps 5-17 mm diam, subglobose to reniform, white becoming antimony yellow (moderate orange yellow), clay color (strong yellowish brown), ochraceous buff (light yellowish pink), or tawny (brownish orange) in spots upon maturing, drying glassy smooth and dark red due to exuded droplets of dark red pigment. Rhizomorphs concolorous with peridium, fine, arising from top, sides, or bottom of sporocarp. Gleba white, drying dark orange; tramal plates white; locules spherical, 0.5-3 mm diam and filled with latex when fresh, as dried the walls lined with orange spore mass with empty central vacuole. Taste faintly sweet, pleasant; odor slight, in youth faintly nutty, but resembling machine oil at maturity. No data available on macrochemical tests.

Basidiospores 10-13(-16) x 9-11(-15) μ m, including alveolate ornamentation (one spore measured 20 x 17 μ m), subglobose to broadly ellipsoidal, length-width ratio 1.2:1; yellow singly, enclosed in a hyaline envelope; ornamentation of spines 0.5-1 μ m high, 2-3 μ m apart, joined by heavy ridges to form 5-6 sided alveoli; spore wall 2-3 μ m thick excluding ornamentation; sterigmal appendage central, basal, 1 x 1.5 μ m. Apobasidia 25-60(-150) x 6-10 μ m, pedicellate,

apex clavate, one to four-spored, thin-walled, content granular, spores sessile or on conical sterigmata $1-2 \times 1 \mu\text{m}$ (one basidium was one-spored, thick walled ($2 \mu\text{m}$), with sterigmata $5 \times 3 \mu\text{m}$). Basidioles $40-60 \times 6-10 \mu\text{m}$, pedicellate, mostly thin-walled but a few with walls $1 \mu\text{m}$ thick, hyaline. Tramal plate $50-110(-150) \mu\text{m}$ wide, becoming scissile; mediostratum $30-70 \mu\text{m}$ wide, of subparallel, yellow, thin-walled, septate hyphae $2-5 \mu\text{m}$ diam, the cells becoming inflated to $10 \mu\text{m}$, forming sphaerocysts $10-15 \mu\text{m}$ diam in axials of tramal plates. Hymenophoral hyphae interwoven, hyaline, gelatinized, $2.5-4 \mu\text{m}$ diam. Peridium $50-100(-220) \mu\text{m}$ thick, of periclinal, yellow, thin-walled, septate, compressed hyphae $1.5-3 \mu\text{m}$ diam; occasional, oleiferous, yellow, thin-walled hyphae $5 \mu\text{m}$ diam.

ETYMOLOGY: refers to type locality, North Carolina.

DISTRIBUTION, HABITAT, AND SEASON: North Carolina, hypogeous under Quercus and Fagus, August to October.

COLLECTIONS EXAMINED: HOLOTYPE: NORTH CAROLINA, Chapel Hill, upper Laurel Hill, 19 October 1927, coll. J. N. Couch and McCormick 8262 (NCU). leg. M. Stewart (NCU 14535). leg. C. Lander (NCU 9223).

L. carolinianus is separated from L. rubescens and L. nudus by its smaller spores and from L. gelatinosus by its narrow peridial hyphae ($1.5-3 \mu\text{m}$ vs. $3-5$) and sphaerocysts in the axials of the tramal plates. It is differentiated from the other eastern North

American species by the sphaerocysts in the tramal plate axials,
large spores, and inflated mediostratum hyphae.

10. LEUCOGASTER CITRINUS (Harkness) Zeller and Dodge,

Ann. Mo. Bot. Gard. 11:398. 1924

≡ Leucophleps citrina Harkness, Calif. Acad. Sci. Proc. Bot.

III 1:259. 1899.

OTHER REFERENCES: Cunningham (1942) p. 59; Dodge (1931) p. 462; Ferry (1900) p. 83; Saccardo and Sydow (1902) p. 252; Szemere (1965) p. 205.

ILLUSTRATIONS: Ferry (1900) pl. CCIV, fig. 10-11; Harkness (1899) pl. XLIII, fig. 8a, 8b; Zeller and Dodge (1924) pl. 11, fig. 7a, 7b.

Basidiocarps drying up to 20 x 15 mm after preservation in alcohol, reniform, citron color (light greenish yellow), imparting a reddish color to alcohol when immersed, drying dirty vinaceous buff. Gleba drying ivory-yellow (pale yellow), tramal plates darker, locules spherical, 1.5-3 mm broad, empty, smaller toward peridium. Consistency cartilaginous after drying. No data available on latex, odor, or macrochemical tests.

Basidiospores 9-10(-11) x (7-)8-9 μ m, averaging 10 x 8.2 μ m including alveolate ornamentation, subglobose, hyaline, enclosed in a hyaline perispore sac; ornamentation of spines 1 μ m high, 2-2.5 μ m apart, spine base 0.2 μ m wide, spore wall 1 μ m thick, excluding ornamentation. Apobasidia 100 x 5-7 μ m, clavate, four-spored, thin-walled, sterigmata lacking. Basidioles 100-125 x 5 μ m, claviform,

hyaline, content granular, thin-walled. Tramal plate 130-150 μm wide, mediostratum 30-50 μm wide, of subparallel, orange (I), thin-walled, gelatinous, 3-4 μm diam hyphae; hymenophoral hyphae gelatinous, hyaline, septate, 3 μm diam, loosely interwoven.

Peridium 60-200 μm thick, of periclinal, compact, pallid yellow hyphae 3-5 μm diam.

ETYMOLOGY: Latin, citrinus (lemon yellow).

DISTRIBUTION, HABITAT, AND SEASON: Oregon and California, under Douglas-fir, manzanita, and laurel, April to November.

COLLECTIONS EXAMINED: HOLOTYPE: CALIFORNIA, Marin Co., Mt. Tamalpais, April, coll. H. W. Harkness 168 (BPI, FH). H. E. Parks 2861 (UC 259864). Santa Clara Co., leg. H. E. Parks (UC 139175). Call of the Wild, H. E. Parks 376 (NY) (UC 653267). Sonoma Co., H. E. Parks 2963 (UC 126302). OREGON, Benton Co., M. Doty 3078 (NY). Lane Co., M. Doty 223 (NY).

L. citrinus differs from L. couchii in its fresh color (citron vs. white), western distribution, spore ornamentation height (1 vs. 0.5 μm), and narrow claviform basidia. It is separated from the other western species in subgenus Rubidi by having larger spores than L. microsporus, smaller spores than L. rubescens, and from L. gelatinosus in lack of inflated mediostratum hyphae.

Zeller and Dodge (1924) synonymized Creameogaster levisporus

with L. citrinus but later examination has shown it to be in subgenus Leucogaster as Leucogaster rotundisporus. I found the spores of the holotype of L. citrinus to be sessile, not borne on sterigmata 5-7 μ m long as reported by Zeller and Dodge (1924). Moreover, the holotype probably had red pigment in the peridium originally since Harkness (1899) noted that it gave a red tint to alcohol when immersed.

11. LEUCOGASTER COUCHII R. Fogel nom. prov.

Basidiocarps up to 23 x 13 mm, subglobose to lobed, surface smooth, white fresh, drying glassy, very dark red from exuded pigment. Gleba white fresh, drying orange, tramal plates lighter, locules spherical to oblong, 0.3-2 mm broad, larger in center of sporocarp, smaller toward peridium, empty. Rhizomorphs basal, absent on dried sporocarps. Odor lacking. No data available on latex or macrochemical reactions.

Basidiospores 9-10(-12) x 7-8(-10) μm , including alveolate ornamentation, some larger spores present, developing 1-2 spores per basidium (i. e., 13 x 12, 16 x 14, 25 x 17 μm), subglobose to broadly ellipsoidal, yellow singly, sessile, enclosed in a hyaline perispore sac; ornamentation of spines 0.5 μm high, 2 μm apart, reticulations fine forming 5-6 sided alveoli, spore wall 1.5-2 μm thick, excluding ornamentation, sterigmal appendage 1 x 1.5 μm broad, central, basal. Apobasidia 45 x 8-9 μm , clavate, pedicellate, four-spored, hyaline (KOH), thin-walled, sterigmata lacking.

Basidioles 45-55 x 9 μm , clavate, pedicellate, hyaline (KOH), content granular thin-walled. Tramal plate 90-170 μm wide, becoming scissile, mediostratum of subparallel, yellow, septate, thin-walled hyphae 3-5 μm diam, hymenophoral hyphae gelatinized, loosely interwoven, 2 μm diam. Peridium 100-210 μm thick, of periclinal, septate, yellow, thin-walled hyphae 3-5 μm diam, tissues obscured

by red pigment that forms droplets in I reagent.

ETYMOLOGY: named for J. N. Couch.

DISTRIBUTION, HABITAT, AND SEASON: Eastern North America, hypogeous to emergent in mixed woods from August to October.

COLLECTIONS EXAMINED: HOLOTYPE: NORTH CAROLINA, Highlands, 6 August 1931, J. N. Couch 9063 (NCU). Macon Co., leg. R. H. Peterson and C. T. Rogerson (NY). MAINE, Bar Harbor, leg. G. Llano (NY). Mt. Desert Island, leg. G. Llano (NY).

L. couchii differs from L. citrinus in fresh color (white vs. citron), eastern distribution, short spore ornamentation (0.5 vs. 1 μ m high), and by having shorter, broader basidia. It differs from other eastern species by lacking sterigmata, having a thinner peridium and hymenophoral hyphae (2 vs. 5 μ m diam), than L. anomalus, and in having wider peridial and mediostratum hyphae (3-5 vs. 2-3 μ m diam) plus wider tramal plates than L. araneosus or L. luteo-maculatus.

12. LEUCOGASTER FLOCCOSUS Hesse, Bot. Centralb. 40(2):

1-4, 33-36. 1889.

OTHER REFERENCES: Fischer (1899) p. 311; (1922) p. 301-307; Hesse (1891) p. 68-70; Knapp (1954) p. 151; Palmer (1968) p. 120; Rea (1927) p. 207; Reid and Austwick (1963) p. 333; Saccardo (1891) p. 281; Velenovsky (1922) p. 804; Zeller and Dodge (1924) p. 390, 402-403.

ILLUSTRATIONS: Hesse (1889) pl. 1, 2, fig. 1-9; (1891) pl. 3, fig. 8b, pl. 5, fig. 8, pl. 7, fig. 1-3, pl. 8, fig. 1-20, pl. 9, fig. 1-13; Knapp (1954) pl. 7, fig. 9; Svrček (1958) fig. 197: 2, 198; Velenovsky (1922) pl. 149, fig. 16; Zeller and Dodge (1924) pl. 11, fig. 10, 10a.

Basidiocarps up to 15-30 mm as dried, irregularly lobed, surface tomentose to villose, cracked between lobes, white flecked with sulfur yellow (light greenish yellow), becoming lemon yellow (strong greenish yellow) at maturity, drying reddish brown. Gleba white becoming yellowish, locules spherical, 0.7-1.5 mm broad, smaller toward peridium, empty, but lined with light brown spore mass. Rhizomorphs basal, clustered, concolorous with surface. Odor of mature sporocarps garlicky. Consistency waxy as dried. No data available on macrochemical tests.

Basidiospores 11-13(-19) x (10-)11-13(-17) μ m, including alveolate ornamentation, globose to subglobose, sessile, enclosed

in a hyaline perisporeal sac; ornamentation of blunt spines, 1 μ m high, 3 μ m apart, joined by heavy walls forming 5-6 sided alveoli, spore wall 2 μ m thick, excluding ornamentation, some with basal pore. Apobasidia $\pm 60 \times 7 \mu$ m, clavate, two to four spored, sterigmata lacking. Basidioles $60 \times 3-5 \mu$ m, claviform, content yellow, granulate, thin-walled. Tramal plate (60-)100-150 μ m wide, mediostratum 12-15 μ m wide, of subparallel, orange, thin-walled, septate hyphae 4-10 μ m diam, hymenophoral hyphae gelatinized, hyaline, 2-2.5 μ m broad, loosely woven. Peridium 200-300 μ m thick, of subhyaline, thick-walled hyphae 3-5 μ m diam, cells becoming inflated to 10 μ m, walls of outermost hyphae grey-blue (I), tissues obscured by orange or red intercellular pigment that forms red "pigment balls" in I reagent.

ETYMOLOGY: Latin, floccosus (floccose).

DISTRIBUTION, HABITAT, AND SEASON: Europe, hypogeous under Fagus and Quercus, solitary or gregarious, August to September.

COLLECTIONS EXAMINED: CZECHOSLOVAKIA, leg. J.

Urban (PR 692874); ENGLAND, leg. C. E. Broome, Rabenhorst Fungi Europaei 34 (FH); GERMANY, leg. R. Hesse (FH, NY).

L. floccosus differs from all other described Leucogaster species in having a tomentose to villose surface. It differs from the other european species by having smaller spores than L. nudus

and a much narrower mediostratum than either L. badius or L. tozziana. Additionally, the mediostratum hyphae in L. floccosus are larger in diam than L. badius or L. tozziana.

An Italian collection labeled L. floccosus and attributed to O. Mattiolo (Lloyd 15575 (BPI)) did not contain enough material to confirm its identity. Zeller and Dodge (1924) erroneously reported the Rabenhorst exsiccati number as 38 instead of 34. Microscopic details in the above description are based on the Hesse collection. The Rabenhorst exsiccatum had narrow (2-3 μ m diam) peridial and tramal hyphae but agreed in all other details.

13. LEUCOGASTER GELATINOSUS R. Fogel nom. prov.

Basidiocarps up to 12 x 18 mm, subglobose to flattened, ochraceous-orange (deep orange yellow), stained red, drying smooth and glassy due to exuded vinaceous-rufous pigment; fibrils innate-appressed, concolorous with peridium, scattered over surface; gleba white, drying cream color, locules spherical to elongate, 0.5 mm broad, exuding copious white latex, filled with spores as dried. Chemical reactions of peridium: KOH pink, FeSO_4 negative, EtOH + FeSO_4 negative, I negative. No odor noted.

Basidiospores 9-10(-11) x 7-8(-9) μm , including alveolate ornamentation, enclosed in a hyaline perispore sac, mostly subglobose to globose; ornamentation of spines 1 μm high, reticulations between spines very fine, spore wall 1 μm thick, excluding ornamentation, sterigmal appendage stout, basal. Apobasidia 45-75 x 8-12 μm , clavate, pedicellate, four-spored, thin-walled, a few gelatinized, thick-walled (1-2 μm), apex remaining thin-walled, hyaline, sterigmata \leq 1 μm long. Basidioles 45-75 x 8-12 μm , clavate, pedicellate, hyaline, thin-walled or a few with gelatinized walls 1-2 μm thick. Tramal plates 55-100 μm wide, mediostratum 35-50 μm wide, of interwoven, hyaline, gelatinized, septate hyphae 3-5 μm diam, cells becoming inflated to 25 μm diam. Peridium 150-200 μm thick, of periclinal, hyaline, thin-walled hyphae 3-5 μm diam, the cells becoming inflated up to 15 μm diam, outer 30-50 μm obscured by

reddish-orange pigment which dissolves in I reagent to form "pigment balls."

ETYMOLOGY: Latin, gelatinous (gelatinosus).

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous under Pseudotsuga menziesii, Lithocarpus densiflorus, or Pinus muricatus, December.

COLLECTIONS EXAMINED: HOLOTYPE: CALIFORNIA, Mendocino Co., vicinity of Woodland camp, near Mendocino, 4 December 1971, (leg. J. M. Trappe), R. Fogel F426 (OSC).

PARATYPES: R. Fogel F407, F411, F427, F428 (all OSC).

L. gelatinosus is separated from L. rubescens by thicker peridium (150-200 vs. 60-70 μ m), wider tramal plate (55-100 vs. 35-60 μ m), and smaller spores.

Dried sporocarps are extremely hard and difficult to section due to the gelatinization of the mediostratum. The fresh peridium of the paratypes produced a green color reaction on application of FeSO_4 followed by ethanol.

14. LEUCOGASTER LUTEOMACULATUS Zeller and Dodge,

Ann. Mo. Bot. Gard. 11:394-395. 1924.

OTHER REFERENCES: Coker and Couch (1928) p. 42-43.

Basidiocarps up to 25 x 10 mm, drying up to 15 x 8 mm, peanut shaped, surface uneven, chalk white with yellowish flecks, drying glassy and scarlet from exuded pigment. Gleba white, drying pallid orange, latex milky fresh, locules spherical, 0.5-1 mm broad, smaller toward surface, empty. No data available on odor or macrochemical tests.

Basidiospores 9-10(-11) x (7-)8-9 μm (one measured 15 x 11 μm), averaging 9.25 x 7.3 μm , including alveolate ornamentation, globose to subglobose, sessile, enclosed in a hyaline perispore sac; ornamentation of stout spines, 0.75-1 μm high, 2.5-3 μm apart, ridges joining spines forming 5-6 sided alveoli, spore wall 1.5 μm thick excluding ornamentation. Apobasidia 45 x 7-10 μm , narrowly oblong, hyaline (KOH), two-spored. Basidioles not observed.

Tramal plate 45-70 μm wide, mediostratum of subparallel, hyaline, gelatinized hyphae 3 μm diam; hymenophoral hyphae hyaline, gelatinized, 3 μm diam, loosely interwoven. Peridium 80-100 μm thick, of periclinal, hyaline hyphae 2-3.5 μm diam, obscured by red amorphous pigment which forms red "pigment balls" in I reagent.

ETYMOLOGY: Latin, luteolus (pale yellow), maculatus (spotted).

DISTRIBUTION, HABITAT, AND SEASON: North Carolina, hypogeous under Fagus grandifolia, August to November.

COLLECTIONS EXAMINED: HOLOTYPE: NORTH CAROLINA, Cranberry, 6 August 1896, R. Thaxter 3 (FH). Chapel Hill, "collected by Fungus Class" (NCU 11142).

L. luteomaculatus is separated from L. araneosus, another North Carolina species, by having a thinner peridium (80-100 vs. 130-180 μm) and larger peridial hyphae (2.3-5 μm vs. 1-2 μm diam). It differs from L. candidus, a western species, in having smaller, sessile spores.

Surface of the holotype is covered with grey soil and fine black roots, not rhizomorphs as Zeller and Dodge (1924) reported. Dodge (1931) synonymized L. luteomaculatus with L. nudus without discussion. However, the two species are distinct: L. luteomaculosus differs from L. nudus by having much smaller spores and thinner uninflated peridial and mediostratum hyphae.

15. LEUCOGASTER MICROSPORUS R. Fogel nom. prov.

Basidiocarps up to 31 x 20 mm, reniform, base indented with peridial tissue extending to the center of the sporocarp, glabrous, white with yellow stains, drying light coral red (strong reddish orange), peridium thin, showing outline of locules below. Gleba white, drying orange-buff (light yellowish pink), exuding white, sticky latex when cut, locules spherical, 0.5-1 mm broad, empty in center of sporocarp, filled with spores next to peridium. No rhizomorphs or fibrils noted or present on dried sporocarp. Chemical reactions on peridium: KOH pale yellow, FeSO_4 negative, $\text{FeSO}_4 + \text{EtOH}$ dull blue-violet. No odor noted.

Basidiospores (6-)7-8(-9) x 5-7 μm , averaging 7.3 x 5.9 μm , including alveolate ornamentation, subglobose, sessile, enclosed in a hyaline perispore sac; ornamentation of spines 0.25-0.5 μm high, 2 μm apart, ridges joining spines very fine, forming 5-6 sided alveoli. Apobasidia 30-60 x 6-7 μm , claviform, four-spored, thin-walled, hyaline, sterigmata lacking. Basidioles 30-35 x 3-4 μm , claviform, thin-walled, hyaline, some encrusted with a hyaline crystalline deposit (KOH). Trametes plates 60-125 μm wide, scissile, mediostratum of subparallel, yellow, septate, thin-walled hyphae 2-3 μm diam, cells becoming inflated to 10 μm . Peridium 100-300 μm thick, of periclinal, pallid yellow, thin-walled hyphae 3-5 μm diam, cells becoming inflated to 15 μm , some oleiferous, thin-walled

hyphae with yellow content present. Outer 60 μ m obscured in KOH by yellow, amorphous, intercellular pigment which forms yellow "pigment balls" in I reagent.

ETYMOLOGY: Greek, micro (small), spore.

DISTRIBUTION, HABITAT, AND SEASON: Western Oregon, hypogeous in Pseudotsuga menziesii-Tsuga heterophylla stands, August to November.

COLLECTIONS EXAMINED: HOLOTYPE: OREGON, Linn Co., Sheep Creek on South Santiam River above Mountain House, 7 August 1971, R. Fogel F390 (OSC). PARATYPE: Lane Co., R. Fogel F437 (OSC).

This species is characterized by having the smallest spores of subgenus Rubidi. inflated peridial and mediostratum hyphae, and thick peridium. Macroscopically L. microsporus resembles L. rubescens and has been found in some similar habitats.

16. LEUCOGASTER NUDUS (Hazslinsky) Hollós, Ann. Mus. Nat.

Hung. 6:319. 1908.

= Hydnangium nudum Hazslinsky, Verh. Zool. Bot. Ges. Wien

- 25:64-65. (1875) 1876.

= Hydnangium virescens Quelét, Mem. Soc. Emul. Montbeliard

Ser. II 5:538. 1875.

OTHER REFERENCES: Bataille (1923) p. 193-194; Dodge (1931) p. 462; Hazslinsky (1875) p. (9); (1877) p. 44; Hollós (1911) p. 98, 208; Pilát (1937) p. 262-263; Saccardo (1888) p. 177; (1895) p. 172; Svrček (1958) p. 552-554, 801; Zeller and Dodge (1924) p. 404-405.

ILLUSTRATIONS: Hollós (1911) pl. 3, fig. 34-35, pl. 5, fig. 33; Hazslinsky (1875) pl. 3; Pilát (1937) pl. 7; Svrček (1958) fig. 197: 4, 199, 200.

Basidiocarps up to 10-50 mm diam, subglobose to irregularly lobed, smooth, white then yellow, becoming dark blackish brown fresh, drying dark blackish brown to red-fuscus. Gleba pale ochre (light olive brown), locules spherical, 0.75-2 mm broad, smaller toward peridium, filled with spores, larger central, empty at maturity. Consistency cartilaginous fresh. No data available on rhizomorphs, latex, odor or macrochemical reactions.

Basidiospores 13-16(-17) x (12-)13-14(-15) μ m, including alveolate ornamentation, globose, enclosed in a hyaline perisporal

sac; ornamentation of spines 1 μm high, 3 μm apart, alveoli 5-6 sided, reticulations prominent, spore wall 1.5-2 μm thick, excluding ornamentation. Apobasidia and basidioles not observed. Tramal plate 50-75 μm wide; mediostratum of subparallel, light yellow, thin-walled hyphae 4-5 μm diam, the cells becoming inflated to 8 μm . Hymenophoral hyphae not observed. Peridium 85-100 μm thick, of periclinal, yellow, thin-walled hyphae 4-5 μm diam, the cells becoming inflated to 8 μm , obscured by dark red pigment which forms red "pigment balls" in I reagent.

ETYMOLOGY: Latin, nudus (bare).

DISTRIBUTION, HABITAT AND SEASON: Western Europe, hypogeous under conifers, August.

COLLECTIONS EXAMINED: HUNGARY: leg. F. Hazlinsky (FH). I. Bresadola (FH). CZECHOSLOVAKIA: leg. A. Pilát 214 (PR 37908). Packet labeled Hydnangium virescens with no other data (S). GERMANY: Wiener-Neustadt, leg. H. Huber (Soehner 1147 (M)). Weismain, comm. Ade (Soehner 1193 (M)).

L. nudus is separated from the other large spored member of subgenus Rubidi, L. rubescens, by its wider tramal plates, thinner peridium, and larger spores. It differs from L. badius and L. tozziana in its large spores, the largest in subgenus Rubidi, and inflated mediostratum hyphae. L. nudus has narrow tramal plates and lacks the tomentum of L. floccosus.

Hazslinsky collection (FH) labeled type with question
mark.

17. LEUCOGASTER ODORATUS (Harkness) Zeller and Dodge,

Ann. Mo. Bot. Gard. 11:396-397. 1924.

= Leucophleps odorata Harkness, Calif. Acad. Sci. Proc.

Bot. III. 1:258. 1899.

= Leucophleps foveolata Harkness, Calif. Acad. Sci. Proc.

Bot. III. 1:258. 1899.

= Leucogaster foveolatus (Harkness) Zeller and Dodge, Ann.

Mo. Bot. Gard. 11:397-398. 1924.

= Leucophleps gibbosum Harkness in Zeller and Dodge, Ann.

Mo. Bot. Gard. 11:397. 1924. nom. nud.

OTHER REFERENCES: Ferry (1900) p. 83, Saccardo and Sydow (1902) p. 252; Szemere (1965) p. 206; Zeller (1934) p. 461.

ILLUSTRATIONS: Ferry (1900) pl. CCIV, fig. 12; Harkness (1899) pl. XLIII, fig. 9a, 9b.

Basidiocarps up to 30-40 mm diam, oblong or irregularly lobed, surface pitted from locules below, the largest specimen finely cracked, light orange fresh, brown as pickled. Gleba white, brown as pickled, locules spherical, 0.5-1 mm broad, empty. Consistency rubbery as preserved. Rhizomorphs adnate, concolorous with peridium. Odor nauseous, no data available on macrochemical reactions.

Basidiospores (8-)9-10 x 8-10 μ m, including alveolate ornamentation, globose to slightly ellipsoidal, hyaline, enclosed in a

hyaline perisporeal sac; ornamentation of cones $0.5\text{ }\mu\text{m}$ high, $1\text{ }\mu\text{m}$ broad at base, $2\text{--}2.5\text{ }\mu\text{m}$ apart, alveoli 5-6 sided, reticulations very evident; spore wall $1.5\text{ }\mu\text{m}$ thick, excluding ornamentation, sterigmal appendage stout, basal, central. Apobasidia $30\text{--}70 \times 6\text{--}9\text{ }\mu\text{m}$, pedicellate, apex clavate, four-spored, thin-walled, hyaline, content granular (KOH), sterigmata $2\text{--}5 \times 1.5\text{--}2\text{ }\mu\text{m}$, straight; occasional one to two spored, thick-walled ($1\text{ }\mu\text{m}$) basidia present. Basidioles not observed. Tramal plates $(75\text{--})80\text{--}100\text{ }\mu\text{m}$ wide, mediostratum of subparallel, reddish brown, thin-walled, septate, content granular (KOH), hyphae $3\text{--}4\text{ }\mu\text{m}$ diam, cells becoming inflated to $7\text{ }\mu\text{m}$; hymenophoral hyphae loosely interwoven, light yellow, gelatinized, thin-walled, $2\text{ }\mu\text{m}$ diam. Peridium $60\text{--}100\text{ }\mu\text{m}$ thick, of periclinal, dark yellow, thin-walled hyphae $2\text{ }\mu\text{m}$ diam, the cells becoming inflated to $4\text{--}7\text{ }\mu\text{m}$, obscured by reddish, intercellular, diffuse pigment not forming "pigment balls" in I reagent.

ETYMOLOGY: Latin, odoratus (having a smell, usually sweet).

DISTRIBUTION, HABITAT, AND SEASON: California, under oaks, July.

COLLECTIONS EXAMINED: HOLOTYPE: CALIFORNIA, Shasta Co., Castle Crag, coll. H. W. Harkness 251 (BPI). Santa Clara Co., leg. D. Parks, H. E. Parks 816 (UC 653268).

L. odoratus is distinctive in subgenus Rubidi by its long sterigmata and inflated mediostratum hyphae. It is separated from the

European L. floccosus by its long sterigmata, glabrous surface, and shorter spore ornamentation.

L. foveolatus is a young stage of L. odoratus. Its fresh color was lighter, peridium thinner, and more locules next to peridium were devoid of spores. It agreed in all other details with L. odoratus. Zeller and Dodge (1924) attempted to separate these as two species on the basis of locule contents and compactness of hymenophoral hyphal layer. In my experience these characters are of little taxonomic value.

Parks 816 (UC 653268) was determined as L. citrinus by Zeller and Dodge (1924) but it has long sterigmata and agrees in all other details with L. odoratus.

18. LEUCOGASTER RUBESCENS Zeller and Dodge, Ann. Mo. Bot.
 11:395-396. 1924. pl. IV, fig. 3 ; pl. V, fig. 3; pl. VIII.
 = Leucogaster longisterigmatus Zeller, Mycologia 39:289-290.
 1947.

OTHER REFERENCES: Smith and Smith (1973) p. 310.

Basidiocarps 5-10 mm diam or up to 30 mm long, subglobose to irregularly lobed, surface smooth, uneven, viscid when moist, whitish to flesh pink (light yellowish pink), becoming brick red (moderate reddish brown) to Hessian brown (grayish reddish brown), drying smooth and glassy due to exuded orange-rufous (deep orange) pigment. Gleba white, drying cream color or ivory yellow (pale yellow), locules spherical, 0.5-1.5 mm broad, empty, lined with a clear gelatinous spore containing matrix, or filled with spores at maturity. Rhizomorphs innate-appressed and basal, concolorous or darker than surface. Odor none to fruity. Chemical reactions on peridium: KOH pink, FeSO_4 negative, $\text{FeSO}_4 + \text{EtOH}$ negative to grey-blue or green.

Basidiospores (10-)11-14(-15) x 10-12(-13) μm , including alveolate ornamentation, globose to mostly subglobose, hyaline, enclosed in a hyaline perispore sac; ornamentation of spines 1-2 μm high, 2.5-3 μm apart, reticulations very fine, forming 5-6 sided alveoli, staining pink in lactic-acid-acid-fuchsin, spore wall 2 μm thick, excluding ornamentation, sterigmatal appendage stout, basal,

central, 2-4 μm long. Apobasidia 50-125 x 8-14 μm , pyriform, pedicellate, four-spored, thin-walled, content pink in lactic-acid-acid-fuchsin, hyaline (KOH), sterigmata \leq 1-2 μm long. Basidioles 50-90 x 7-12 μm , clavate, pedicellate, hyaline (KOH), pink in lactic-acid-acid-fuchsin, thin-walled. Tramal plate 35-55 μm wide, becoming scissile, mediostratum of subparallel, hyaline, thin-walled, septate hyphae 3-5 μm diam; hymenophoral hyphae gelatinized, 2 μm diam. Peridium 60-100 μm thick, of gelatinized, thin-walled, hyaline hyphae 3-5 μm diam, cells becoming inflated to 10-12 μm diam, obscured on drying by dark red pigment which dissolves in I reagent to form "pigment balls."

ETYMOLOGY: Latin, rubescens (becoming red).

DISTRIBUTION, HABITAT, AND SEASON: Western North America, hypogeous in Thuja-Abies and Pseudotsuga menziesii stands, Michigan, New York, and Quebec, May to November (pl. VIII).

COLLECTIONS EXAMINED: HOLOTYPE: OREGON, Benton Co., Corvallis, 6 May 1922, L. M. Boozer (S. M. Zeller 2322 (NY)). CANADA, QUEBEC, L. Hawker (DAOM 63671). L. Hawker and M. Lange (MICH). U. S. A., ARIZONA, Coconino Co.: R. Fogel F634, F637 (OSC). Apache National Forest, Hanagan Meadow Campground, H. D. Thiers 29114 (SFSC). CALIFORNIA, Stanislaus Co.: H. D. Thiers 17180 (SFSC). COLORADO, Larimer Co.:

R. Fogel F648, F653 (OSC). Gunnison Pass Road, H. D. Thiers 26367 (SFSC). IDAHO, Adams Co.: A. H. Smith 68901, 69067 (leg. H. Burdsall) (all MICH). Bonner Co.: A. H. Smith 67893 (leg. N. J. Smith), 68259, 68446, 68465, 68500, 68501 (leg. N. J. Smith), 68587 (leg. H. Burdsall), 68684, 73395 (all MICH). Idaho Co.: A. H. Smith, 68980, 69309 (all MICH). Valley Co.: P. Miller 16b, 16f, A. H. Smith 45918 (leg. D. Stuntz), 65258 (leg. D. Largent), 65373, 65768 (leg. L. Hawker), 66231, 68918, 69405 pro part (leg. P. Miller), 69690 (all MICH), H. D. Thiers 11672 (SFSC), NEW MEXICO, Rio Grande National Forest, Tucker Ponds Campground, H. D. Thiers 26624 (SFSC). Bandeleir National Monument, H. D. Thiers 25862 (SFSC). NEW YORK, Slatterville, Cornell-Lloyd Preserve, P. E. Powell (CUP 50063, 50064, 52737). OREGON, Benton Co.: leg. C. A. Brown and C. H. Kauffman (NY), R. Fogel F395 (OSC), leg. M. Hoiseth (OSC). Jackson Co.: Trappe 2895. Lane Co.: R. Fogel F984 (OSC). Linn Co: leg. H. M. Gilkey, D. P. Rogers, and A. M. Rogers (NY--Holotype of Leucogaster longisterigmatus). Polk Co.: leg. D. R. Hosford (OSC), J. M. Trappe 1610, 1619, R. Fogel F466 (OSC). UTAH, Iron Co.: leg. D. R. Hosford (OSC). WASHINGTON, Mt. Rainier National Park, D. R. Hosford H-166, H-171, H-310, H-330, H-373, H-467, H-521, H-605, H-610, H-894, H-984, H-986 (all CWSC), J. M. Trappe 95 (MICH). Snoqualmie Pass, leg. Joann Russell (NY).

L. rubescens is separated from L. gelatinosus by its thinner peridium (60-100 vs. 150-200 μm), narrower tramal plates, and larger spores. It differs from the european L. tozziana by having larger spores, thinner peridium, larger diam peridial hyphae, and narrower tramal plates. L. rubescens has a thinner peridium, larger mediostratum hyphae, and longer, broader apobasidia than the european L. badius.

L. longisterigmatus is synonymized with L. rubescens because none of the basidia present in the holotype of the former had long sterigmata as reported by Zeller (1947) and the two species agreed in all other characters. Unfortunately the holotype of L. rubescens is immature, with only a few apobasidia bearing spores. The isotype cited by Zeller and Dodge (1924) as deposited in OSC (Zeller 3706) is now at NY.

19. LEUCOGASTER TOZZIANA (Cavara and Saccardo) Mattiolo

in Zeller and Dodge, Ann. Mo. Bot. Gard. 11:463. 1924.

= Endogone tozziana Cavara and Saccardo, Nuovo Bot. Ital. Ser.

II. 7:296. 1900 (July).

= Leucogaster fragrans Mattiolo, Malpighia 14:267. 1900

(December).

OTHER REFERENCES: Baccarini (1903) p. 80; Mattiolo (1900) p. 260-261; Saccardo and Sydow (1902) p. 249, 816-817; Svrček (1958) p. 550-551, 801-802; Szemere (1965) p. 206; Thaxter (1922) p. 326; Zeller and Dodge (1924) p. 403-404.

ILLUSTRATIONS: Svrček (1958) fig. 197:3; Zeller and Dodge (1924) pl. 11, fig. 11.

Basidiocarps up to 10-25 mm diam, irregular or gibbous, sulcate, sulphur-colored (light greenish yellow) fresh, vinaceous buff (light yellowish pink) or darker in alcohol, drying rusty brown. Rhizomorphs adnate to almost free, concolorous with peridium, mostly basal or surrounding the sporocarp. Gleba white fresh, sayal brown (moderate yellowish brown) in alcohol, locules spherical, 0.3-0.5 mm broad. Odor fragrant. No data available on latex or macrochemical reactions.

Basidiospores 10-12(-15) x 10-11 μ m, including alveolate ornamentation, globose, enclosed in a hyaline perispore sac; ornamentation of spines 1-2 μ m high, 2 μ m apart, walls joining

spines forming 5-6 sided alveoli, spore wall 1.5 μm thick, excluding ornamentation, hyaline to yellow. Apobasidia 20 x 7 μm , clavate, probably pedicellate, hyaline, thin-walled, sterigmata 2 μm long. Basidioles 50 x 7 μm , clavate, pedicellate, hyaline, thin-walled. Tramal plate 40-80 μm wide, mediostratum 20-25 μm wide, of interwoven, hyaline, gelatinized hyphae 3-5 μm diam, hymenophoral hyphae gelatinized, interwoven, 2-3 μm diam. Peridium 100-170 μm thick, drying 35-70 μm thick, of compressed, periclinal, gelatinized, thin-walled hyphae 4-7 μm diam, reviving poorly in I reagent, obscured by orangish, intercellular pigment and red "pigment balls" in I reagent.

ETYMOLOGY: ?

DISTRIBUTION, HABITAT AND SEASON: Italy, Czechoslovakia, hypogeous in pine and fir forests, June to November.

COLLECTIONS EXAMINED: ITALY: Vallombrosa, 1900, leg. O. Mattiolo (TO); 23 November 1899, leg. O. Mattiolo (NY, labeled type); Torino, 1910, leg. O. Mattiolo (Lloyd 15586 (BPI)); June 1898, leg. O. Mattiolo (UC 126289); October 1902, leg. O. Mattiolo (Trappe 1490 (OSC)); leg. A. Fiori, Mycotheca italica 1424 (NY, PR, Lloyd 15578, 15580 (BPI)); CZECHOSLOVAKIA: leg. L. Vacek (PR 692875).

L. tozziana differs from L. badius by its smaller spores and locules. The narrow tramal plates and presence of sterigmata differentiate L. tozziana from the North American species L. citrinus and L. couchii.

The synonymy of L. fragrans with L. tozziana is based on Zeller and Dodge (1924). They state that Mattiolo, author of L. fragrans, had made the transfer in litt. but I was unable to locate such a reference. Both species were collected in the same locality and descriptions published the same year, six months apart. Unfortunately the type of L. tozziana was not located and no portion of the Cavara collection exists at TO as reported by Zeller and Dodge (1924).

Mycotheca italica 1424 is misidentified as L. luteomaculatus by Zeller and Dodge (1924) and L. nudus by Svrček (1958). My examination confirms the original exsiccatum determination of L. fragrans (= L. tozziana) since the spores are too small for L. nudus and the hyphae are too large for L. luteomaculosus.

DOUBTFUL OR EXCLUDED SPECIES

LEUCOPHLEBS CLELANDI (Rodway) Zeller and Dodge, Ann Mo.

Bot. Gard. 23:596. 1936.

≡ Hydnangium clelandi Rodway, Pap. Proc. Roy. Soc. Tasmania 1924:
108. 1925.

≡ Octaviana clelandii (Rodway) G. H. Cunningham, Trans. Roy. Soc.
N. Z. 67:408. 1938.

Holotype was mature without any indication of how spores are borne. Cunningham (1942) indicated that the basidia are apparently one-spored, short, arranged in a scanty palisade. The spores are large, 23-37 μm diam, globose to irregularly flattened, pale green in mass (KOH), smooth; spore wall 4 μm thick.

The presence of basidia excludes this species from Leucophlebs and the smooth spores would exclude it from Octavianina and Hydnangium. I am unwilling to place it in Leucogaster because of the smooth spores, and uncertainty about basidia.

COLLECTION EXAMINED: HOLOTYPE: TASMANIA: Hobart,
Cascade Valley, May 1925, leg. L. Rodway (HO 319).

LEUCOGASTER BRAUNII Rick, Egatea 19:110. 1934.

Trappe (1975) has suggested on the basis of the type description that this species might be an Alpova. Its affinity to Leucogaster is

doubtful because of its "subfusiform, . . . often winged" spores.

Repeated attempts to locate the type collection have failed.

LEUCOGASTER BUCHOLTZII Mattiolo, Malpighia 14:267-268.

1900.

OTHER REFERENCES: Saccardo and Sydow (1902) p. 249;

Svrček (1958) p. 554, 800; Szemere (1965) p. 205; Zeller and Dodge (1924) p. 404.

No material of this species was located for examination.

Zeller and Dodge (1924) indicated that this species differs from L. tozziana in having aculeate instead of reticulate spores. Svrček (1958) placed this species in the doubtful category with the comment that it did not differ in any respect from L. tozziana.

LEUCOGASTER GLOBOSUS Velenovsky, Novit. Mycol. 1:172. 1939.

OTHER REFERENCES: Svrček (1958) p. 554, 802; Szemere (1965) p. 206.

Holotype is a dark brown sphere, probably pitch (?).

COLLECTION EXAMINED: HOLOTYPE: leg. J. Velenovsky (PR 154193).

LEUCOGASTER MINUTUS Velenovsky, Novit. Mycol. 1:172. 1939.

OTHER REFERENCES: Svrček (1958) p. 554, 802; Szemere (1965) p. 206.

Holotype very badly preserved, impossible to determine its position.

COLLECTION EXAMINED: HOLOTYPE: J. Velenovsky 29/1947 (PR 153899).

LEUCOGASTER RUDENSTEINERI Velenovsky, Ceske Houby IV-V:

804-805. 1922.

OTHER REFERENCES: Svrček (1958) p. 554, 802; Szemere (1965) p. 206.

According to Svrček (1958) this is not a fungus. Deposition of the type is also unknown. It is not in PRC as Svrček indicated (p. 802) or PR (Dr. Z. Urban, pers. comm.).

LEUCOGASTER MATTIROLII Treves, Roy. Acad. Sci. Torino Cl.

Fis. Mat. Nat. 65:123. 1930.

Type location unknown. On the basis of the description this species is close to L. tozziana.

OCTAVIANIA LIOSPERMA (Tulasne) Lloyd, Mycol. Writ. 7:1141.

1923.

≡ Hydnangium liospermum Tulasne, Fungi Hypog. p. 76. 1851.

≡ Leucogaster liospermus (Tulasne) Zeller and Dodge in Szemere,

Die Unterirdischen Pilze des Karpatenbeckens. p. 206. 1965.

OTHER REFERENCES: Hesse (1891) p. 84; Saccardo (1888)

p. 176; Soehner (1949) p. 19; Zeller and Dodge (1924) p. 407-408.

Deposition of type unknown. Tulasne (1851) in his illustration of the sporocarp shows a well developed columella and small spores with pedicels, suggestive of Sclerogaster. Szemere (1965) incorrectly credited Zeller and Dodge with transferring this species to Leucogaster.

SCLEROGASTER COLUMELLATUS (Zeller) R. Fogel comb. nov.

prov.

= Leucogaster columellatus Zeller, Mycologia 39:289. 1947.

Basidiocarp drying 10-20 mm diam, subglobose to reniform; surface felty, somewhat viscid fresh with particles of humus adhering, drying light brown. Gleba pure white, drying light buff, locules extremely small, 0.8-1.0 mm broad, almost filled with spores. Consistency chalky, crumbling when sectioned, except peridium which dries flinty hard and amber in section. Columella extending to the center of the sporocarp, drying 8 x 1 mm diam, simple, brittle, reddish amber. Chemical reactions of peridium and odor not known.

Basidiospores 5-7.5 μ m diam, including ornamentation, globose to subglobose, warted, the ornamentation 0.5 μ m high, hyaline, non-amyloid; spore wall 0.5 μ m thick, hyaline, sterigmal appendage 2-7 μ m long. Basidia 20-25 x 5-7 μ m, subcylindrical

to narrow clavate, 2-6 spored, hyaline, thin-walled, walls or content not staining in lactic acid-acid-fuchsin, sterigmata 3-4 x 1-1.5 μm (Zeller cites the longest as 25 μm long); basidioles not observed. Tramal plate 60 μm wide, mediostratum of subparallel, hyaline, thin-walled, septate hyphae 4-5 μm diam. Peridium \pm 225 μm thick, outer 40 μm of appressed, periclinal, subhyaline, gelatinized hyphae 4-10 μm diam; subcutis of hyaline hyphae, 4 μm diam at septa but cells often inflated up to 15 μm . Columella of hyaline, gelatinous, subparallel hyphae 2-4 μm diam at septa, cells becoming inflated to 15 μm ; inflated cells thin-walled; numerous medallion clamps present on uninflated hyphae.

ETYMOLOGY: Latin, columella (a small pillar).

DISTRIBUTION, HABITAT, AND SEASON: Hypogeous under Pinus ponderosa, May. Known only from the type locality.

COLLECTION EXAMINED: HOLOTYPE: CALIFORNIA, Rim of the World, northeast of San Bernardino, May 1923, N. L. Gardner 581 (NY), ISOTYPE: UC 233, 330.

This species is placed in Sclerogaster because of its small, globose, non-amyloid, minutely warted, thick-walled spores, small cylindric basidia, euhymenium, small locules, and thick, flocculent mycelium embedding the sporocarp. S. columellatus differs from other Sclerogaster species in having a columella, presence of clamp connections on hyphae of the columella, thick peridium, and long

sterigmata. No two-spored basidia or extremely long (25 μ m) sterigmata as reported by Zeller (1947) were observed.

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PLATE I

- Fig. 1 Glebal cross-section of dried Leucogaster gelatinosus showing spherical, 0.5-1 mm broad locules. Locules near surface are filled with dried spore-containing latex. Scale = 1 mm units.
- Fig. 2 Glebal cross-section of dried Leucogaster levisporus showing labyrinthiform, 0.25 mm broad locules.

PLATE II

- Fig. 1 Leucogaster candidus apobasidium. Scale line is 10 μ m in length.
- Fig. 2 Apobasidium of Leucogaster magnatus with long sterigmata and spore.
- Fig. 3 Six-spored basidium of Sclerogaster columellatus and pedicellate spore.
- Fig. 4 Leucogaster rubescens apobasidium, up to 125 μ m in length, and an aberrant, thick-walled, spore occasionally occurring in preparations of mature sporocarps.

PLATE III

- Fig. 1 Peridial cross-section of Leucogaster rubescens showing inflated and uninflated cells. 1, 285X.
- Fig. 2 Peridial cross-section of Leucogaster levisporus. 1, 285X.
- Fig. 3 Leucogaster rubescens tramal plate bound by locules on top and bottom. The hymenophoral hyphae have collapsed, leaving the mediostratum. 1, 285X.
- Fig. 4 Leucogaster levisporus tramal plate bound by locules, right and left. 1, 285X.

PLATE IV

- Fig. 1 Light photomicrograph of Leucogaster magnatus basidiospores. Compare the spore ornamentation height with L. levisporus. 1,508X.
- Fig. 2 Light photomicrograph of Leucogaster levisporus basidiospores showing the fine ornamentation. 1,508X.
- Fig. 3 Light photomicrograph of Leucogaster rubescens showing the alveolate ornamentation and hyaline perispore sac. 1,508X.
- Fig. 4 Light photomicrograph of Leucogaster rotundisporus. Compare the broadly ellipsoidal spores with the subglobose spore of L. levisporus. 1,508X.

PLATE V

- Fig. 1 SEM micrograph of Leucogaster magnatus basidiospore. There is only a slight indication of the gel-embedded spinose-verrucose ornamentation. Sterigmal scar on the right. 5,000X.
- Fig. 2 SEM micrograph of Leucogaster levisporus basidiospore showing the sterigmal scar and pore through the spore wall. Ornamentation obscured by gel. 6,750X.
- Fig. 3 SEM micrograph of Leucogaster rubescens basidiospore showing the alveolate ornamentation. The hyaline perisporeal sac is obscuring the spines at the junctions of the alveolar ridges. 6,750X.
-
- Fig. 4 SEM micrograph of Leucogaster rotundisporus basidiospore. 8,380X.

PLATE VI

- Fig. 1 SEM micrograph of Zelleromyces gilkeyae basidiospore. 3,955X.
- Fig. 2 SEM micrograph of Hydnangium sp. basidiospore. 7,145X.
- Fig. 3 SEM micrograph of Scleroderma cepa basidiospore. 3,880X.
- Fig. 4 SEM micrograph of Sclerogaster columellatus basidiospore. 11,455X.

PLATE VII

* Western North American distribution of Leucogaster magnatus collections.

* Western distribution of Leucogaster levisporus collections. Note Alaska collection.

PLATE VIII

Distribution of North American Leucogaster
rubescens collections.

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