

**STUDIES ON SECOTIACEOUS FUNGI—IV  
GASTROBOLETUS, TRUNCOCOLUMELLA AND CHAMONIXIA**

ALEXANDER H. SMITH AND ROLF SINGER<sup>1</sup>

University of Michigan, Ann Arbor, and  
Universidad Nacional de Tucumán, Tucumán, Argentina

Malençon (1931) showed that a series of related genera connected *Lactarius* and *Russula* of the Agaricales to certain genera of the Gastromycetes, including some hypogeous genera. He used the name "La Série des Asterosporés" for this group. The present paper deals with a second, analogous series which we here designate the "*Gastroboletus* Series." At the level of the Hymenomycetes this series includes the Boletales in the sense of Singer (1951). At the secotioid level in the Gastromycetes it includes *Gastroboletus*, *Truncocolumella* and *Rhizopogon* represent progressively more gastromycetous genera. We regard *Chamonixia* as belonging to this series at the level of *Truncocolumella*. *Rhizo-*

---

<sup>1</sup> Papers from the University Herbarium and the Department of Botany No. 1081, University of Michigan.

*pogon* is not treated here because it is such a large genus that it represents a major study in itself. However, we should like to emphasize here that a revision of that genus in the light of our series of papers on secotioid fungi is now urgently needed to clarify the trends of evolution among hypogeous Basidiomycetes. One other genus, *Gautieria*, eventually may be found to belong to this series, but we are not including it in this paper. By its spore characters it resembles *Chamonixia*, but it differs in the gelatinous-cartilaginous texture of the tissues of the gastrocarp.

The field work on which this paper is partly based was made possible through grants to the senior author from the Faculty Research Fund of the University of Michigan, from the University of Michigan Herbarium, and from the National Science Foundation. It is a pleasure to acknowledge our indebtedness to Professor Dr. G. Cufodontis of the Botanical Institute of the University of Vienna, Austria for the loan of the type collection of *Gastroboletus boedijnii* Lohwag, and to Professor Walter H. Snell of Brown University, Providence, R. I. for the loan of the type of *Boletus turbinatus*.

#### Key to genera of the *Gastroboletus* series

- Spores forcibly discharged from basidia; context of pileus soft and fleshy; hymenophore typically tubular *Boletus*
- Spores not forcibly discharged.
  - Hymenophore (gleba) tubular, usually exposed at least in places around the stipe-columella; columella terete and merely a continuation of the stipe *Gastroboletus*
  - Columella decidedly reduced or modified from a simple continuation of the stipe; gleba still showing a fundamentally tubular structure if a columella is present.
    - Spores longitudinally ribbed and rusty brown; columella and tramal plates not cartilaginous or gelatinous. *Chamonixia*
    - Spores smooth
      - Columella present, truncate, or as a series of branches from a sterile base. *Truncocolumella*
      - Columella absent; gastrocarps lacking a definite point of attachment. *Rhizopogon*

#### I. *Gastroboletus* Lohwag, Beih. Bot. Centralbl. 42<sup>2</sup>: 273. 1926.

Fruiting body resembling that of a *Boletus* in that it is differentiated into a "stipe," "pileus" and tubular hymenophore. Spores not forcibly discharged from the basidia and tubes not positively oriented geotropically.

Type species: *Gastroboletus boedijnii* Lohwag.

Our attention was drawn to this genus through a series of collections from the Western United States which appeared to belong in the Boletales even though repeated attempts to obtain spore deposits failed. Since repeated collections were made from given localities and since the fruiting bodies represented all stages of development, it was finally recognized that the species in question simply did not discharge spores, and that it was a secotioid Gastromycete. On the basis of dried material, similarities with the type of *Boletus turbinatus* Snell were recognized. This species was described from dried material, and there was no record of a spore print. Because of certain spore characters, Singer had transferred Snell's species to *Boletellus*. One feature of this species is curious but significant and indicates that it is a Gastromycete. Although the hymenophore is strikingly boletoid in character, the tubes themselves are not positively geotropic and are often oriented differently on any two sides of the stipe-

columella.<sup>2</sup> Since *Gastroboletus* was the only genus of secotioid fungi known to us with this glebal structure, a study was made of the types of *G. boedijnii* and *B. turbinatus*, and of our western collections previously mentioned. The study revealed that we were dealing with a single genus of the Gastromycetes. Among Smith's collections we found one specimen which matched precisely a Chinese collection illustrated and described by H. Lohwag (1937) for *G. boedijnii*. In this specimen the peridium reached the stipe on one side but not on the other, thus producing a one-sided "ring-hole" causing the fruiting body to appear "angiocarpous" on one side and "gymnocarpous" on the other. We mention this to show that morphologically the American specimens match perfectly those from China.

#### Key to the Species

Spores 11-14  $\times$  4-5.5  $\mu$ .

*G. boedijnii*

Spores 13.5-18(-20)  $\times$  6.5-9.5  $\mu$ .

*G. turbinatus*

#### 1. *Gastroboletus boedijnii* Lohwag, Beih. Bot. Centralbl. 42<sup>2</sup>: 273. 1926.

Fruiting body boletoid in aspect, consisting of a pileus (peridium), tubular hymenophore (gleba) and stipe (stipe-columella); peridium unpolished, yellowish brown; gleba tubular, less than 3 mm deep as dried, yellow to olive-yellow, at least partly free from stipe-columella; stipe-columella distinct and percurrent, the surface brownish and unpolished as dried. Figs. 2-4.

Spores 11-14  $\times$  4-5.5  $\mu$ , smooth or doubtfully ornamented (seen under oil-immersion lens), suboblong or often narrowed in midportion as seen in either the face or the profile view, rarely obscurely inequilateral, pale yellow in KOH and in Melzer's reagent, lacking both an apical pore and a callus; spore wall thickened slightly.

Hymenium: Basidia 1- or 2-spored, 30-44  $\times$  8-11  $\mu$ , clavate, the content yellowish in KOH but becoming hyaline, the yellow pigment diffusing through the mounting medium; sterigmata conic and straight, 5-7  $\mu$  long, about 2  $\mu$  wide at base, the spores eccentrically to acropetally attached; cystidia present as fusoid cells about the size of the basidia and some with the ventricose portion in the upper half causing the cell to resemble a one-spored basidium in shape, the color and the lack of distinctive markings the same as in the basidia.

Trama: Hymenophoral trama as revived in KOH golden yellow, the pigment dissolving in the medium; mediostratum very thin and entirely filamentous, diverging in the area next to it, all the hyphal cells filamentose to the base of the basidium; epicutis of peridium a tangled mass of crooked hyphae (probably a trichodermium which has collapsed) with yellow content in KOH but this soon fading; hyphal cells frequently irregular in shape and at the cross walls often constricted slightly, the hyphae 4-7  $\mu$  in diameter, their walls thin and smooth; clamp connections absent.

The above description is based on our restudy of the type collection. For a comparison see the discussion under *Gastroboletus turbinatus*.

<sup>2</sup> In this group of fungi and in the truly stipitate Gastromycetes there is no correct term for the combined columella and stipe. We propose the term *stipe-columella*. In species in which the peridium dehisces from the stipe-columella or in which the gleba is exposed in the manner of a mature agaric or bolete, the word columella loses its meaning. The dividing line between them becomes obliterated inasmuch as the point of attachment of the peridium to this structure is the only line of demarcation.

2. *Gastroboletus turbinatus* (Snell) Smith & Singer, comb. nov., var. *turbinatus*. Fig. 1, Plate 1.

*Boletus turbinatus* Snell, Mycologia 28: 20. 1936.

*Boletellus turbinatus* (Snell) Singer, Farlowia 2: 134, without citation of basionym. 1945; Lilloa 22: 696. 1951.

Gastrocarp 20–50 (–80) mm broad, convex, becoming plane or slightly depressed; peridium thick for a “*Secotium*,” thin for a “bolete” as far as the upper portion or disc is concerned, thin in the vertical (marginal) zone; surface dry and velvety, in age subtomentose, bister to mummy-brown, golden-yellow or bay-red, or with a reddish to orange-salmon tinge at least along the marginal region, not showing a distinct tendency to become areolate in age.

Gleba tubulose, readily separable from the peridium; tube-chambers reaching 10–30 mm or more in length but from the broadest point of the hymenophore readily diminishing in depth (length of tubes) in both directions (ventricose), strongly projecting beyond the peridium or remaining covered by its extended thin portion, either strongly depressed or nearly free from the apex of the columella, more rarely broadly attached to the columella; pores round at first and about 0.5 mm in diameter, on old specimens with large angular depressions reaching 1 mm in diameter; interior of gleba yellow and quickly changing to blue upon exposure, the pores in some specimens becoming reddish at the mouths at maturity or in age.

Stipe-columella short, 10–20 (–70) mm long, 8–20 mm thick, equal or tapered downward, often not projecting much beyond the lower level of the gleba, solid, unpolished above, yellow or more orange-yellow to reddish toward the base, turning blue when bruised, sometimes finally becoming reddish, frequently finely rivulose because of the cracking of a brownish to reddish layer, the layer finally breaking up into minute points, at times brown-furfuraceous in a narrow zone; stipe finally glabrescent; veil none.

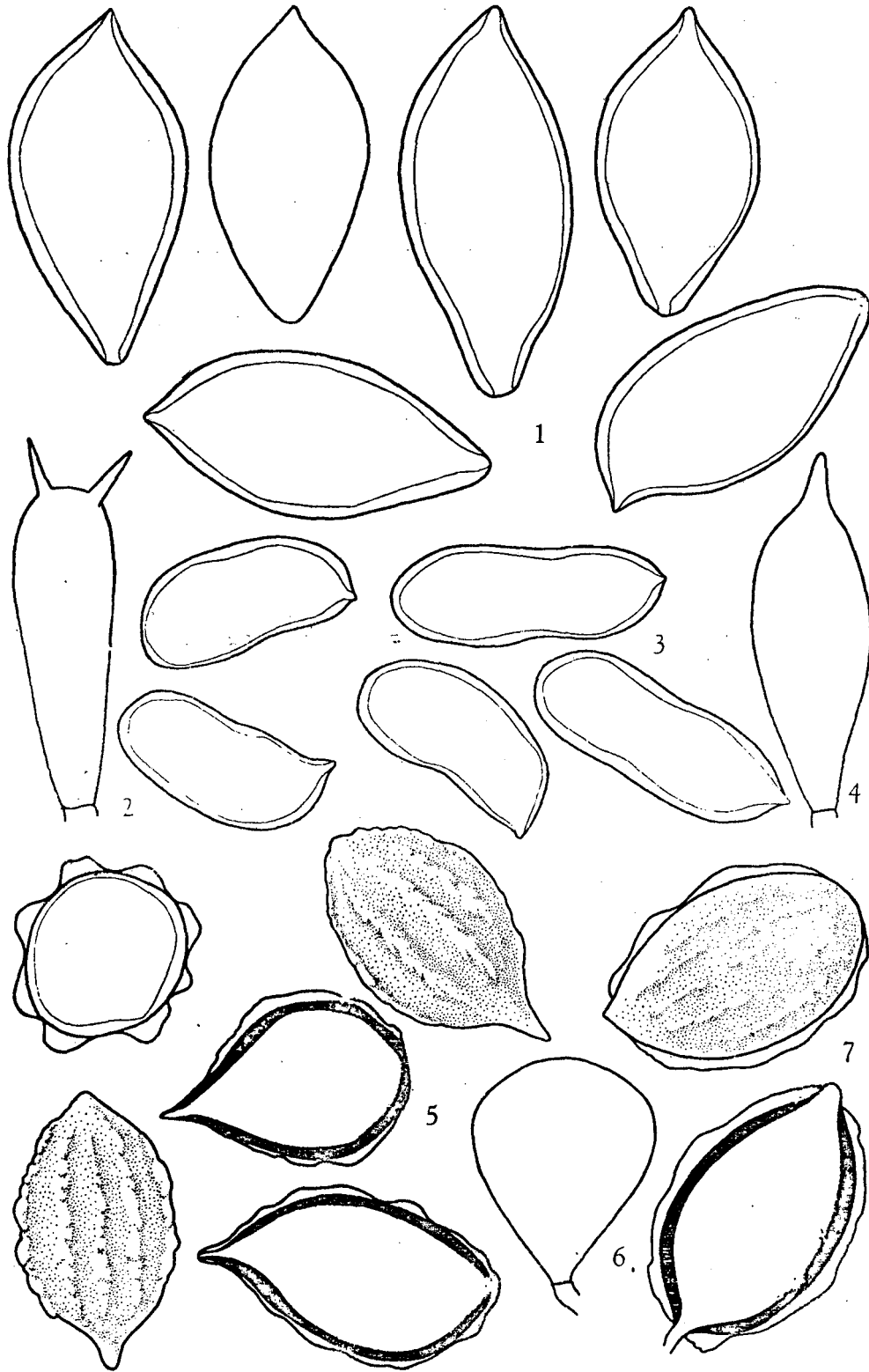
Context yellow in the peridium, often partly pinkish in the stipe-columella, tending to stain blue when injured and later becoming red to brownish in these areas, especially on drying; taste and odor slight and insignificant.

Spores (9.5–) 13.5–18 (–20) × (5.5–) 6.5–9.5  $\mu$ , ellipsoid to oblong or slightly ovate as viewed in face view, somewhat inequilateral as seen in profile; sterigmatal appendage<sup>3</sup> when present slightly oblique; color golden melleous to deep melleous, often with a fulvous tinge; wall simple at first, later thickening and becoming 3-layered; apex obtuse to acute and the wall there either continuous or showing a slight pore.

Hymenium: Basidia mostly 4-spored, but sometimes with 1, 2 or 3 spores. 35–38 × 9–14  $\mu$ , rather voluminous, vesiculose-pedicellate to clavate, hyaline or

<sup>3</sup> The projection on the spore, marking the original attachment of the spore to the sterigma, has been called an apiculus, a hilar appendage, and a pedicel. We propose the term *sterigmatal appendage* because this can be applied with equal accuracy to all basidiospores. We suggest the shortened form *sterigmatal*, in preference to *sterigmatal* or *sterigmatic*, because it is short and easy to pronounce.

FIG. 1. *Gastroboletus turbinatus*, spores (type). FIGS. 2–4 (all from type). *G. boedijnii*: FIG. 2. Basidium; FIG. 3. Spores; FIG. 4. Cystidium. FIG. 5. *Chamonixia ambigua*, spores (type). FIGS. 6–7 (all from type). *Chamonixia brevicolumna*: FIG. 6. Pseudoparaphysis; FIG. 7. Spores.



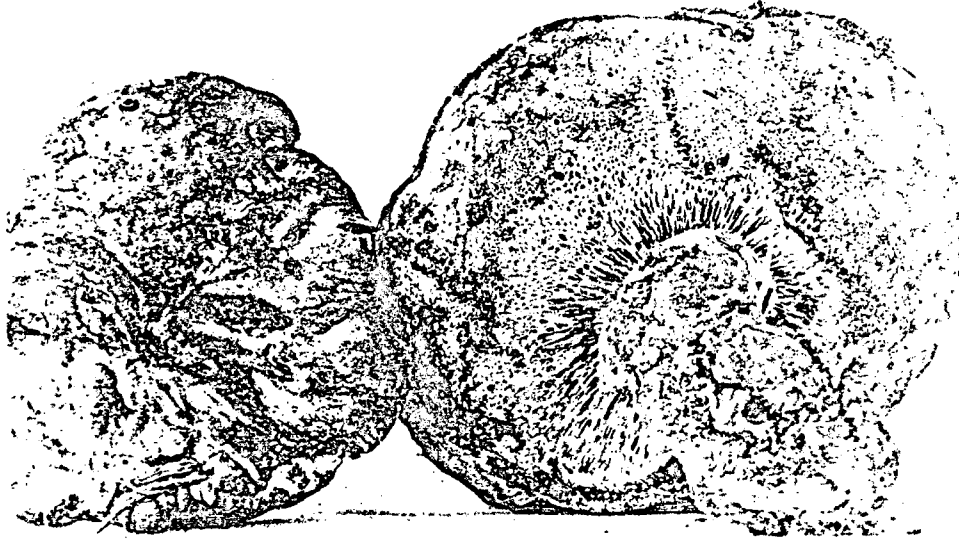
yellow in KOH; sterigmata straight to slightly curved and thorn-like, 5–5.5  $\mu$  long; basidioles variable in size and shape, about  $33 \times 9 \mu$ , mostly somewhat clavate, hyaline, scattered; pseudoparaphyses similar in size and shape to the basidioles but without protoplasmic content and hence not likely to produce spores; cystidia 35–60  $\times$  9.5–17  $\mu$  (young or apparently retarded cystidia of the most recently formed chambers 34–36  $\times$  5–7  $\mu$ ), rare but present in the interior as well as at the pores, ventricose-mucronate to (more often) ventricose in the middle and ampullaceous-pedicellate, often with a long thin neck, hyaline, later either hyaline or golden yellow to brownish, the apex usually obtuse.

Tissues: Hyphae of the hymenophoral trama bilaterally arranged (*Boletus* type, Singer 1945); mediostratum light melleous, slightly interwoven (axially oriented), the lateral stratum hyaline, strongly divergent, its hyphae sufficiently gelatinized to cause them to appear separated; context of peridium directly underneath the epicutis strongly golden yellow from a pigment soluble in KOH; cuticular layer of interwoven hyphae and some strands of parallel hyphae, the elements filamentous, hyaline or golden yellow, the yellow often predominant at the extreme surface, the hyphae there 3–5.5 (–9)  $\mu$  in diameter, cylindric or nearly so, being the remnants of an epicuticular palisade of earlier stages; palisade of ascendant-erect cystidium-like hyphal ends which are rather thin-walled (0.5  $\mu$ ), the terminal cells 30–55  $\times$  3–5.5 (–9)  $\mu$ , more or less cylindric and tapered at the very apex to a subacute or obtuse tip; surface of the stipe-columella exhibiting a basal subhymenium-like layer from which fragments of a palisade emerge, these containing fertile basidia 27  $\times$  9  $\mu$ , pseudoparaphyses 15–26  $\times$  9–14  $\mu$ , and caulocystidia which are 40  $\times$  10  $\mu$ , ventricose, mucronate, and melleous; hyphae of all tissues inamyloid, but in the epicutis the yellow elements turning pale bister in Melzer's reagent; clamp connections absent; chemical reactions not studied.

On humus under conifers (often *Abies* sp.), along mountain paths and roadsides, Idaho, Oregon and Washington, apparently widely distributed in the Western United States and also found in Missouri. It fruits from July through September. Obviously it is often overlooked because it is mistaken for an abortion; consequently its area is likely to be broader than the collections to date indicate.

The variability in this species is great. At Mt. Rainier one population showed a decided tendency to become red over the tubes, especially the mouths, and to have red pruina on the stipe. In Idaho the collections from the south fork of Lake Fork Creek showed a tendency to produce a pigment causing the pileus and stipe to be nearly sulphur yellow. Brick red specimens were found in this same spot during the season of 1958. In all collections a KOH-soluble yellow pigment is present. The spores are the most reliable character for distinguishing between this species and the type species of the genus.

MISSOURI: Valley Park, D. H. Linder (*Snell Herb. 345*), Type of *Boletus turbinatus*. IDAHO: South Fork, Lake Fork Creek, Payette Lakes, 3 Aug 1954, *Smith 45872* (MICH). Numerous collections from the same general region: *Smith 45282, 45601, 45872, 46336, 46902, 59231, 59581, 59600, 59791, 59924, 60154, 60287, 60318, 60540* (all MICH). WASHINGTON: Mt. Rainier National Park, 5 Aug 1948. *Smith 29606* (MICH). Also many collections from the same general area, *Smith 29607, 29888, 30266, 30727, 31042, 31387, 31403, 31459*, and *Imshaug 788, 1114, 1311* (all MICH). OREGON: Timberline Lodge, Mt. Hood, 21 Aug 1946, *Smith 23612* (MICH).



GASTROBOLETUS TURBINATUS  
(SNELL) SMITH & SINGER  
ABOUT 5/6 NATURAL SIZE  
UPPER FIGURE: SMITH 59231    LOWER FIGURE: SMITH 45972



UPPER FIGURE: GASTROBOLETUS TURBINATUS VAR. FLAMMEUS SMITH. X 1.  
(TYPE, SMITH 59581).  
LOWER FIGURE: TRUNCOCOLUMELLA CITRINA ZELLER. X 1.  
(SMITH 30456)

2a. *Gastroboletus turbinatus* var. *flammeus* Smith, var. nov. Plate 2.

Carpophoris turbinatis, irregularibus, stipitatis; gastrocarpio 3-7 cm lata, aurato, tactu caerulescente; glebae tubulis adnatis, luteis, poris minutis, aurantio-rubris; sporis 11-14  $\times$  7-9  $\mu$ . Specimen typicum, *Smith 59581* (MICH).

Gastrocarp 30-70 mm broad, convex to very irregular, often 2-3 fused together; peridium dry and pruinose to subtomentose, pale golden yellow splashed with red but soon staining blue where touched, and the bruised places finally dark brown; surface uneven.

Gleba 20-25 mm deep, golden yellow but quickly blue when cut, attached to the columella for two-thirds to three-fourths its depth but free at the lower edge and flaring away from the stipe, made up of tubes, the mouths of the tubes minute (0.3-0.5 mm diam.) and evenly scarlet red when young, the mouths mostly remaining unopened and the lower part of the tube often curved away from a vertical alignment for the last 5 mm of its length, preventing release of the spores by discharge in the normal manner of a bolete.

Stipe-columella crooked, 40-80 mm long, 8-16 mm thick, solid, rich yellow and minutely scurfy, when injured changing to blue and finally blackish but in age developing reddish tones variously over the lower portion.

Context of peridium rich yellow but almost instantly turning blue when cut; odor none; taste mild; context of stipe yellow and quickly changing to blue when cut.

Spores 11-14  $\times$  7-9  $\mu$ .

Cespitose to gregarious under *Abies*, Brundage Mt., McCall, Valley County, Idaho, 5 Aug 1958, *Smith 59581* (type, MICH).

In spite of the fact that *G. turbinatus* var. *turbinatus* is exceedingly variable in the size and color of the gastrocarp, the spore size, the degree to which the tube mouths are colored, and the stage at which this color develops, variety *flammeus* has been found to be constant and appears worthy of recognition. It points out a connection with certain species of *Bolbitellus*, such as *B. pictiformis* (Murrill) Singer (section *Chrysocentroides*) in which the tube mouths are also red. In most collections of variety *turbinatus* the tube mouths merely become somewhat reddish as the specimen ages, as in certain species of *Bolbitus* (*sensu lato*) outside of the section *Luridi*. The difference in spore size, taken along with the colored tube mouths, might appear to be sufficient grounds for the recognition of this fungus as an autonomous species; as indicated above, we do not believe this to be desirable. In general we find a wider range of variation in spore size among the secotioid forms than in related agaric or bolete forms.

II. *Truncocolumella* Zeller, *Mycologia* 31: 6. 1936.

Fructifications depressed-spheroid to reniform, from a rhizomorphic base and with a central point of attachment; columella stump-like to dendroid, prominent; peridium persistent, indehiscent, not separating from the gleba but sometimes soon evanescent; gleba olive to brown; spores smooth, ellipsoid, as seen individually almost hyaline.

Type species: *Truncocolumella citrina* Zeller

Spores 11-14  $\times$  4-5.5  $\mu$ .

*T. rubra*.

Spores 6-9  $\times$  3.5-5  $\mu$ .

Many spores pseudoamyloid; peridium at times separating from the columella to slightly expose the gleba.

*T. citrina* var. *separabilis*.

Few if any spores pseudoamyloid; peridium not separating from the columella.

*T. citrina* var. *citrina*.

1. *Truncocolumella citrina* Zeller, *Mycologia* 31: 6. 1939, var. *citrina*. Plate 2.

Fructifications 20–30 mm broad, 15–40 mm high, obovate, subelliptic, globular, depressed-globose to reniform or cordate, the surface typically unpolished and dry in appearance, pale greenish yellow darkening to olive fuscous in age; immature stages sometimes whitish before they become exposed to light, drying pale yellow to dull greenish yellow, or, where bruised, *old gold*; columella stump-like to dendroid, the base and branches of pallid yellowish tissue composed of loosely arranged hyphae 4–7  $\mu$  in diameter; sterile base merely the broad base of the columella, citrine yellow, usually arising from yellow rhizomorphs.

Spores 6.5–9.7  $\times$  3.6–4.2 (–5)  $\mu$  (6–10  $\times$  3.5–5  $\mu$  according to Zeller); smooth, yellowish in KOH, darker yellow in Melzer's reagent (in mass ochraceous tawny), ellipsoid to subovoid, in profile view lacking a suprahilar depression, thin-walled or the wall scarcely thickened and showing no differentiation of a pore at spore apex.

Hymenium: Basidia 23–26  $\times$  6–7  $\mu$ , narrowly clavate, 4-spored, the sterigmata 5–6  $\times$  2  $\mu$ , conic; pseudoparaphyses abundant, 18–30  $\times$  10–17  $\mu$ , broadly clavate to subglobose, subcylindric or subfusoid (almost cystidioid in some); cystidia not seen (except for large pseudoparaphyses).

Trama: Tramal plates of subgelatinous hyphae 3–6 (–8)  $\mu$  in diameter and divergent from a thin central strand; subhymenium cellular; peridium 70–100  $\mu$  thick (but rather variable in a single specimen); epicutis possibly a collapsed trichodermium, in revived sections apparently consisting of loosely arranged more or less appressed hyphae 3–15  $\mu$  in diameter, with thin, non-incrusted walls yellowish in KOH; interior to this a body of interwoven-subradial hyphae 5–9  $\mu$  in diameter, slightly gelatinous to floccose in KOH, and almost colorless; clamp connections readily observed at the cross walls.

Solitary to gregarious, rarely caespitose in the duff or only slightly projecting, usually in association with Douglas fir, throughout the Pacific Northwest, late summer and fall, often rather common.

The above redescription is based on Zeller's original account, Smith's field observations on numerous collections, and a study of the detailed anatomy and spore characters from specimens, including the type.

OREGON: Comstock, Douglas County, 20 Oct 1937, *Zeller 8320*, type (NY); Mt. Hood National Forest: East Fork of Salmon River, 30 Sep 1944, *Smith 19300*, below Timberline Lodge, 4200 ft., 21 Sep 1946, *Smith 23618*, Frog Lake, 23 Sep 1947, *Smith 26773*, Twin Bridges, 27 Sep 1947, *Smith 26988*, East Fork of Salmon River, 30 Sep 1947, *Smith 27117*, Bear Springs, 23 Oct 1954, *Smith 49494*. WASHINGTON: Olympic National Park, Hurricane Ridge, 20 Sep 1941, *Smith 17044*; Mt. Angeles, 21 Sep 1941, *Smith 17105*, *17117*; Olympic Hot Springs, 22 Sep 1941, *Smith 17173*; Mt. Rainier National Park, Lower Tahoma Creek, 22 Aug 1948, *Smith 30456*; Mt. Rainier National Park, Eagle Peak, 20 Sep 1952, *Smith 40053*; St. Andrews Creek, 21 Sep 1954, *Smith 40135*; Longmire, 11 Sep. 1954, *Smith 47372*; 13 Sep 1954, *Smith 47427*; 11 Oct 1954, *Smith 48771*; 17 Oct 1954, *Smith 49162*. IDAHO: McCall, Valley Co., near Boulder Lake, 30 Jul 1941, *Smith 15823*; Stanley Lake, Sawtooth Mountains, 19 Aug 1954, *Smith 46365*, *46374*. CALIFORNIA: Zeller listed collections, not seen by us, from California.

1a. *Truncocolumella citrina* var. *separabilis* Smith, var. nov.

Gastrocarpio 30–40 mm alto, 50–70 mm lato, 30–40 mm crasso, irregolari, olivaceo-citrino; sporis 7–9  $\times$  3.5–4  $\mu$ , pseudoamyloidiis. Specimen typicum, *Smith 59553* (MICH).

Gastrocarp 30–40 mm high and 40–70 mm wide, 30–40 mm thick, irregular in outline, uneven and lobed at base; peridium unpolished and pale greenish

yellow (near "olive ochre"), finally dark olive-fuscous in old age, becoming watery olive where handled.

Gleba occasionally separating from around the base of the columella (and then the tube-mouths visible as in *Gastroboletus* but plugged), or separating also to some extent from the branches of the columella, olive gray when young, olive fuscous in age, with lines of olive-yellow sterile tissue penetrating through it; chambers small and tubular in structure.

Columella 8-10 mm broad, dendroid and the branches in the form of thin plates of variable length; context yellowish, becoming bister in the base when old, *i.e.* darkening as in the stipes of many agarics.

Spores 7-9  $\times$  3.5-4  $\mu$ , smooth, nearly oblong, pale greenish yellow in KOH, many of them reddish brown in Melzer's reagent in mounts of fresh material.

Hymenium: Basidia 20-23  $\times$  6-7  $\mu$ , narrowly clavate, yellow in Melzer's reagent as seen in isolated individuals, 4-spored; sterigmata straight, 4-6  $\mu$  long, thin (about 1  $\mu$  at base); pseudoparaphyses clavate, 18-24  $\times$  10-15  $\mu$ , present mostly in the hymenium near the peridium; cystidia none.

Tissues: Hyphae of tramal plates "glassy" (slightly gelatinous) in KOH, interwoven (observed on mature fresh specimens); peridium a single layer with loose floccose, clamped hyphae exteriorly to the main hyphal body; clamps not the medallion type, all the hyphae of the peridium thin-walled, 8-15  $\mu$  in diameter and not incrustated.

Scattered near a road in Douglas fir zone, Brundage Mt., McCall, Valley County, Idaho, 3 Aug 1958, *Smith 59553* (type, MICH).

The tendency of the gleba to separate from the stipe-columella and from the plate-like branches of the columella, the distinct tubular nature of the gleba, and the rather strong pseudoamyloid reaction of the spores in Melzer's reagent are the characters which distinguish this variety. The interwoven arrangement of the hyphae of the tramal plates is unexpected, but further observations on younger specimens are desired. If all these characters should turn out to be constant, this variety should be considered an autonomous species.

## 2. *Truncocolumella rubra* Zeller, *Mycologia* 31: 7. 1939. Figs. 8-10.

Gastrocarp 20-50 mm broad, 20-40 mm high, broadly pyriform to subglobose; peridium yellowish at first, becoming reddish where exposed, aniline yellow where covered by soil, thin and almost entirely evanescent at maturity.

Gleba dingy pale yellow, changing to bluish on bruising or exposure, drying raw umber to rusty brown, the cavities relatively large, labyrinthiform.

Columella stout, 7-15 mm thick, almost percurrent at times and also with narrow plate-like branches radiating laterally and terminally, extended below as a sterile base, yellowish, changing to blue when bruised or exposed, drying yellowish.

Spores (10-)11-14(-15)  $\times$  4-5.5(-6)  $\mu$ , (10-12.5  $\times$  4.5-5.5  $\mu$  according to Zeller), narrowly ovate in face view to nearly oblong, in profile obscurely inequilateral with a slight suprahilar depression; wall thickened up to 0.5  $\mu$ , yellowish in KOH, weakly pseudoamyloid, smooth; sterigmatal appendage very small.

Hymenium: Basidia 4-spored, 26-33  $\times$  9-11  $\mu$ , clavate; the sterigmata 4-5  $\mu$  long and 1  $\mu$  thick at the base; pseudoparaphyses none; cystidia scattered, fusoid-ventricose, 38-50  $\times$  9-14  $\mu$ , thin-walled, hyaline to yellow in KOH, tapered gradually to an acute apex, a few with yellow inclusions in KOH, lacking any incrustations.

Tissues: Hyphae of tramal plates arranged in a yellow central strand as revived in KOH or this strand lacking, if present flanked by subparallel, hyaline subgelatinous hyphae; if not, the entire trama of subgelatinous subparallel to interwoven hyaline hyphae; subhymenium cellular; context of peridium of hyphae 5–10  $\mu$  in diameter, interwoven, thin-walled, yellowish in KOH, and not incrustated; epicutis present as a palisade of thin-walled dermatocystidia over the youngest peridia; clamp connections absent.

Emergent from heavy duff under conifers, especially hemlock, during late summer in the Cascade Mountains of Washington.

WASHINGTON: Snoqualmie Pass, King County, 19 Aug 1937, *Zeller Herb 8272* (type, NY). Hannegan Pass, Mt. Baker N. F., 17 Aug 1941, *Smith 16218* (MICH).

Our revised description is taken from the original account, from Smith 16218 which was identified by Zeller, and from the type collection. Certain discrepancies are to be noted between the microscopic characters of Zeller's account and Smith 16218. In the latter the basidia are much larger and characteristic fusoid bolete cystidia occur in the hymenium. The spores are larger and the gastrocarps were larger and possibly older than those available to Zeller when he first described the species.

A study of Zeller's type gave the following data: Spores 9–13 (–14)  $\times$  5–6.5  $\mu$ , rarely 3.5–4  $\mu$  wide, narrowly ovate in face view, obscurely inequilateral in profile; wall thickened, smooth over exterior, lacking any differentiation at spore apex, ochraceous in KOH, pale ochraceous-tawny in Melzer's reagent; basidia 20–24  $\times$  7–9  $\mu$ , clavate, 4-spored, sterigmata 4–5  $\mu$  long, thin, conic, wall hyaline to yellow in KOH; pseudoparaphyses if present resembling immature basidia; cystidia scattered, fusoid-ventricose, with subacute apices, 46–60  $\times$  6–10  $\mu$ , hyaline to yellowish in KOH, thin-walled, the content homogeneous; hyphae of tramal plates hyaline, subgelatinous in KOH, yellow, if poorly revived, 4–7  $\mu$  in diameter, interwoven to subparallel; subhymenium of filaments like those of the tramal plates; epicutis of peridium in the form of a turf of elongate dermatocystidia which are smooth, yellow in KOH, and become decumbent in age; clamp connections none.

*T. rubra* in a number of respects is close to the following genus *Chamonixia*, but we retain it in *Truncocolumella* because of the smooth and slightly paler spores. It appears now that whereas *T. citrina* is close to the Boletaceae, *T. rubra* is close to *Boletellus* of the *Strobilomycetaceae*. It should be remembered that there are species of *Boletellus* with practically smooth spores, and on this basis there should be no objection to including smooth spored species in *Chamonixia*. It should also be remembered that in *Gastroboletus* one species has smooth spores and in the second, although we have described them as smooth, we must admit to having seen traces of ornamentation in a few spores.

*T. rubra* differs very sharply from *T. citrina* by the lack of clamp connections, in the length and width of the spores, by the bluing of the context and by the presence of cystidia. It may even be that the non-bilateral type of hymenophoral trama is an additional character which separates the two. At the time of writing this paper we do not have data on the tramal structure in young specimens of *T. citrina* var. *separabilis*.

For the present we refrain from transferring *T. rubra* to *Chamonixia*, to which it is obviously closer than it is to *T. citrina*, and thus we leave intact the

single spore character which at present serves to distinguish the two genera in their original circumscription. However, we do wish to emphasize that a serious discussion of the character, scope and affinities of *Truncocolumella* can be attempted only with the fact in mind that *T. rubra* is not a true representative of that genus.

With this in mind let us now consider briefly the position of *Truncocolumella* in the *Gastroboletus* series. First, it is generally accepted that *Truncocolumella* is identical with *Dodgea* Malençon, which was based on the single species *D. occidentalis*, and published about one month after the publication of Zeller's genus. Both authors commented on the similarity of their fungi to the boletes. Whereas Malençon considered his *Dodgea* as a transition between *Rhizopogon* and *Boletus*, and derived from the latter, both Zeller (in litt.) and C. W. Dodge (1931) considered it as intermediate between *Boletus* (or one of its segregates) and *Rhizopogon*, deriving it from the latter. Zeller (1939) stressed the similarity to early stages of *Boletus*, the change of the tissue to blue when cut or bruised, and the shape of the spores in *T. rubra*.

We have not examined specimens of *Dodgea occidentalis* and hence must rely on the original description in making a comparison with *T. citrina*. It is evident from comparing descriptions that *T. rubra* and *D. occidentalis* are distinct, but we cannot be absolutely certain at this point whether *D. occidentalis* and *T. citrina* are synonymous, or represent separate species. The specimens on which *Dodgea occidentalis* was based were preserved in alcohol and color notes were lacking. The peridium was described by Malençon as whitish but the actual color of the fresh specimens is unknown. Our spore measurements coincide with Zeller's for *T. citrina* whereas Malençon's description of *D. occidentalis* indicates somewhat larger spores. We consistently found basidia larger than those indicated by Zeller. Malençon states that the basidia are very fugacious and scattered. He described them as inconspicuous, and claims to have observed a 5-spored one. We found numerous basidia and certainly would not characterize them as inconspicuous in relation to the other structures of the hymenium. It should also be pointed out that basidia with more than four spores are not unknown even in the Agaricales. We agree with Malençon and Zeller that there are no cystidia, and we agree with Malençon that there are always "basidioles" which seem devoid of protoplasm. This is a character often seen in Secotiaceous fungi and does not present any extraordinary feature. As we observed these structures they may be almost cystidioid in shape at times. Zeller did not comment on these structures if he observed them.

A particularly interesting character is exhibited by the tramal plates. The hymenophoral trama is strictly bilateral as in the boletes, more precisely of an intermediate type between the *Phylloporus*-type and the *Boletus*-type of bilaterality as defined by Singer (1945). The lateral stratum is more divergent and gelatinized, less dense, and somewhat broader than usual for the *Phylloporus* type, but the hyphae of the mediostratum and the lateral stratum scarcely differ in color, diameter, or septation and most hyphae in both are hyaline though exceptional yellowish hyphae in the mediostratum can be observed.

The structure of the hymenophoral trama of *Truncocolumella* is quite similar to that of certain boletes, namely *Xerocomus badius*. It might be interpreted as the prototype of both the subtypes as observed in the Boletaceae. Zeller did

not comment on this. He stated (1939) that the septa<sup>4</sup> are formed by loose large almost parallel hyphae. This observation is erroneous and does not coincide with that of Malençon who states in his description of "septa" about the same facts as those we have indicated. He has also seen an "obscure" cellular subhymenial zone which for us is quite distinct and consists of relatively large irregular subsodiametric cells and other more elongate cells. This is a type of structure not uncommon in the Secotiaceae.

Zeller did not publish a critical account of the anatomical features, so we cannot actually compare all of our observations with his. On the other hand, Malençon's description compares well with ours and even mentions the structure of the sterile base of the carpophores and indicates the presence of clamp connections. These clamp connections are unusually large and often exactly of the type called medallions.

In a paper by Lange and Hansen (1954), it has been shown that some agarics such as the Paxillaceae, especially wood-inhabiting species, form clamp connections reminiscent of the medallion clamps found in certain Aphyllophorales. Such clamps, however, also occur in the Hygrophoraceae and other groups not suspected of having aphyllophoraceous affinities.

Summing up our findings on *Truncocolumella*, it appears that this genus is indeed a link between the true boletes and the family Rhizopogonaceae with which it has in common tubiform glebal chambers, the lack of a true stipe, gastroid spore production, and spore structure. It must be kept in mind, however, that there are other links, namely *Gastroboletus* and *Chauniolella*, between *Truncocolumella* and the true boletes. It depends on the importance of such a relatively rudimentary form as *Truncocolumella*, whether or not the latter genus is to be considered part of the Rhizopogonaceae. There is no doubt in our minds, however, as to its position in the *Gastroboletus* series. Judging from recent data in the literature the genus *Leratia* Pat. also may belong in this series. In 1933 Fischer placed this genus among those incompletely known. Heim (1951) restudied *Leratia similis* and stated that it reminds one of the more extreme types of degradation which, among the boletes, represent the more distinctly angiocarpous forms characterized by the generic names *Truncocolumella* and *Rhizopogon*. He also stated that the spores, pigment, cystidia, and covering layers suggest *Xerocomus*, e.g. the *versicolor*<sup>5</sup> group. It does not seem to us that Heim's comparisons of *Leratia* with the boletes—even less with a species such as *Boletus rubellus*—are based on sufficient evidence. He did not describe the hyphal arrangement of the tramal plates, so that we do not know whether it is bilateral in the manner of *Truncocolumella citrina* and *Gastroboletus turbinatus*. If Heim had reported on the presence or absence of clamp connections it would have been helpful. The presence of a germ pore in the spores of *Leratia* sug-

---

<sup>4</sup> We prefer to use the terms hymenophoral trama or tramal plates, the former expression taken from the terminology of the Agaricales, the other introduced long ago in the terminology of the Gastromycetes. The term septa is misleading since it is also used in the sense of hyphal cross walls.

<sup>5</sup> Singer (1945) has shown that *Boletus versicolor* Rostk. is not a valid name. The valid name for this species is *Boletus rubellus* Kromb. and it is not a *Xerocomus* because of the typically boletoid, not phylloporoid hymenophoral trama, and because of further strong similarities with other species of *Boletus*, *sensu stricto*.

gests, if it suggests anything, as far as a relationship in the boletes is concerned, that the affinities of the genus are with *Boletellus* and related groups, and certainly not in the neighborhood of *B. rubellus*.

Another possibility to be considered is that *Leratia* is related to the Agaricales in the neighborhood of *Nivatogastrium* and *Weraroa*. It is interesting to note that Patouillard (1907) stated that *Leratia similis* resembled certain forms of *Secotium erythrocephalum* (*Weraroa erythrocephala*). *Leratia* cannot be identical with *Weraroa* because the spores are "very little colored" and its columella is not percurrent. The question of the presence or absence of clamp connections is important at this point. Any speculation as to the relative position of *Leratia* in relation to *Truncocolumella* and *Gastroboletus*, let alone *Boletus*, must be postponed until more evidence is available.

### III. *Chamonixia* Rolland, Bull. Soc. Mycol. Fr. 15: 76. 1899.

Gastrocarp globose or nearly so, 10–50 mm in diameter, often somewhat folded in appearance when several gastrocarps develop in a cluster and their shape is modified from mutual pressures; peridium present, often staining blue when bruised; gleba fleshy, of chambers which at the most are only partly filled with spores; columella reduced or absent, with a central point of attachment; spores rusty brown, striate to ribbed.

Type species: *Chamonixia caespitosa* Rolland.

We have studied what we consider to be American material of this species, and, in addition, material of three other species which appear to belong in the same genus.

Context not changing to blue when bruised.

1. *C. caudata*.

Context changing to blue when cut or bruised.

Columella a rounded-truncate unbranched basal plug of sterile tissue.

2. *C. brevicolumna*.

Columella percurrent or nearly so, or its branches extending through the gleba to the

upper part of the peridium in young specimens.

3. *C. ambigua*.

Spores 8–11  $\mu$  broad.

Spores either broader or narrower.

Spores 12–15  $\mu$  broad; gleba exposed around the stipe-columella when young;

columella percurrent; peridium white at first.

4. *C. caespitosa*

Spores not over 6  $\mu$  broad; gleba not exposed; columella not quite percurrent;

peridium yellowish or yellow at first.

See *Truncocolumella rubra*

#### 1. *Chamonixia caudata* (Zeller & Dodge) Smith & Singer, comb. nov. Figs 14–17.

*Arcangiella caudata* Zeller & Dodge, Ann. Mo. Bot. Gard. 6: 49. 1919.

*Arcangiella behrii* var. *caudata* (Zeller & Dodge) Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 366. 1935.

Gastrocarp 8–20 mm in diameter, globose or pyriform, the base attenuate, the apex flattened or rounded; peridium varying from light brown to dark yellowish brown or maroon except for a small area around the short stalk.

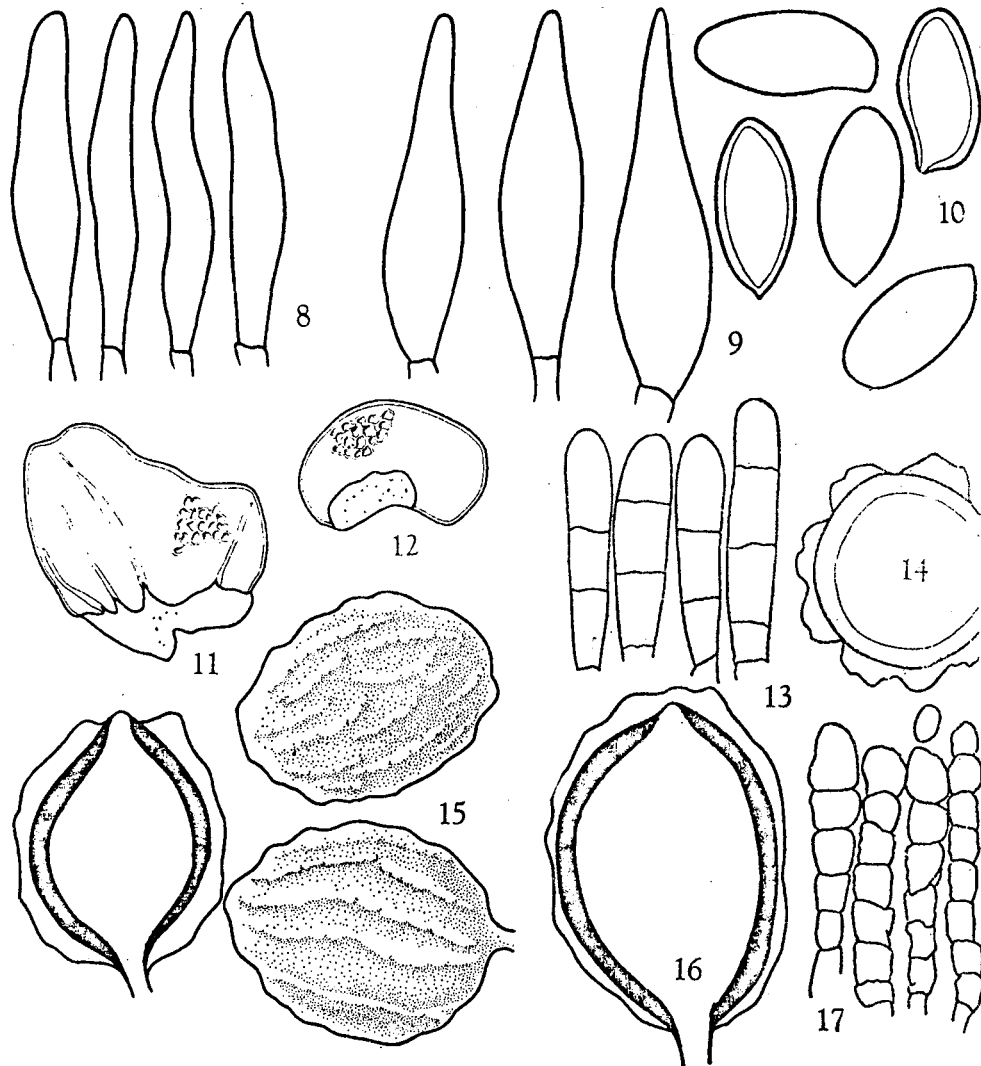
Gleba fleshy, white to yellowish, cinnamon-brown in age or as dried; chambers small, irregular and radiating somewhat from the base of the columella.

Stipe-columella with the stipe portion almost white, near mummy-brown to olive-brown as dried (in the type), the surface velvety; columella portion present as a sterile base varying to percurrent or with lateral branches.

Spores 9–15  $\times$  9–11  $\mu$ , ellipsoid to ovate, with a distinct apical pore, dull brown in KOH, dark red brown in Melzer's reagent, ornamented, the primary ornamentation in the form of longitudinal ridges irregular in shape and extending from over one half to the full length of the spore, the secondary ornamenta-

tion as cross ridges and tubercles, causing the spores to appear reticulate at times; inner wall thick ( $1.5-2 \mu$ ).

Hymenium. Basidia 2- and 4-spored, the sterigmata prominent; cystidia and paraphyses not seen (the hymenium revived poorly) ("cystidia hyaline, large,



FIGS. 8-10. (all from Smith 16218). *Truncocolumella rubra*: FIG. 8. Dermatocystidia; FIG. 9. Hymenial cystidia; FIG. 10. Spores. FIG. 11. *Chamonixia ambigua*, longitudinal section of gastrocarp (type). FIG. 12. *Chamonixia brevicolumna*, longitudinal section of gastrocarp (type). FIG. 13. *Hymenogaster caerulescens* Söhner, elements of trichodermium (Parks 4622). FIGS 14-17 (all from type). *Chamonixia caudata*: FIG. 14. Transverse view of spore; FIGS. 15-16. Longitudinal section and face view of spores; FIG. 17. Elements of peridial trichodermium.

In all figures the spores are reproduced at approximately  $\times 1000$ , all other microscopic structures  $\times 450$ .

clavate; paraphyses cylindrical, obtuse hyaline, septate,  $19-20 \times 4-5 \mu$ ," according to Zeller & Dodge).

Tissues. Hyphae of tramal plates poorly revived ("hyaline . . . of loosely interwoven hyaline hyphae," according to Zeller & Dodge); epicutis of peridium a trichodermium of septate hyphae in which the cells are narrowed to the cross walls and some of the apical cells actually become separated; clamp connections not seen.

In leaf mould of *Quercus*, Oregon and California, November, Gardner 219 (Dodge & Zeller 1623) (type, NY).

This species does not stain blue and has spores with less conspicuous longitudinal ridges and grooves than in the other species of *Chamonixia*. Some oleiferous hyphae were seen in the peridium and it was on the basis of these that the original authors placed the species in *Arcangeliella*. The trichodermium is the type found in many species of *Boletellus*, and this along with the spores, and lack of clamp connections clearly point to a relationship with that genus. The pseudoamyloid character of the spores is quite pronounced. The fact that the species is also frequently parasitized by *Sepedonium chrysospermum*, a common parasite of boletes, may have some phylogenetic significance.

## 2. *Chamonixia brevicolumna* Smith & Singer, sp. nov. Figs. 6, 7 and 12.

Gastrocarpio 18-25 mm lato, ochraceo-olivaceo, tactu caerulescente; sporis  $15-18 \times 10-13 \mu$ , subtruncatis; columella truncata, brevissima. Specimen typicum, Smith 60519 (MICH).

Gastrocarp 18-25 mm broad, 15-20 mm deep, subglobose, the surface unpolished, at times with scattered thin rhizomorphs over it; peridium at first near olive-ochre or bluish-olive but soon stained blue when bruised, with a distinct basal point of attachment.

Gleba chambered, the cavities minute, having a basically tubular structure, reddish cinnamon when fresh but the tramal plates staining blue when cut.

Columella a truncate to rounded basal plug extending into the gleba from one fifth to one third of the gleba's thickness much as in *Truncocolumella citrina* but unbranched in the specimens at hand, buff-yellow fresh but soon stained blue when cut.

Spores  $15-18 \times 10-13 \mu$ , ellipsoid, many with a small sterigmatal appendage at base; outer layer of the wall forming ridges, the inner layer deeper colored (rusty cinnamon or fulvous) in KOH and dark reddish rusty brown in Melzer's reagent, the external portion of the inner layer (episporium?) darker in color in KOH than the innermost zone; ridges (in KOH) varying from subhyaline to yellowish or pale cinnamon, wavy or more rarely straight, often anastomosing, irregular, not all extending from the base to the apex of the spore but roughly longitudinal, entire or lacerate; apical pore or callus usually distinct but generally with a blister of outer wall material over it; hyaline perisporium present but seldom very distinct.

Hymenium: Basidia 2- or 4-spored,  $27-41 \times 12-17 \mu$ , hyaline in KOH, often with a large and opaque vacuole; sterigmata small or somewhat elongated (up to  $10 \times 12 \mu$ ), conic to straight or curved either inwards or outwards; pseudo-paraphyses  $12-20 \mu$  broad; cystidia none.

Tissues: Subhymenium narrow and rather poorly developed, consisting of versiform (subvesiculose, elongated, small and irregular) hyaline elements which often seem to curve away from the trama (which however, is not of the bilateral

type); hymenophoral trama uniform, hyaline, not gelatinized, its hyphae 3–8.5  $\mu$  in diameter, thin-walled, elongated and interwoven; peridium duplex, its hyphae elongated, the outer layer a trichodermial palisade, consisting of elongated thin-walled elements which are frequently septate with some cells inflated (about 16–19.5  $\times$  15–18  $\mu$ ), the outermost portion consisting of mostly filamentous elements which are often decumbent over the surface to give a falsely fibrillose effect (but not forming a mature cutis); inner layer of peridium (context) bright lemon to chrome yellow in KOH from a pigment dissolving in the mount, consisting of hyphae 2.5–5  $\mu$  in diameter, arranged tangentially or occasionally ascending, interwoven; hyphae of the columella hyaline, filamentous, irregularly interlaced but loosely arranged, 2–7  $\mu$  in diameter; all hyphae without clamp connections.

Gregarious under spruce-fir, Middle Fork of Lake Fork Creek, Payette National Forest, Idaho, 26 Aug 1958, *Smith 60519* (type, MICH).

Although the spores are ornamented and colored as in *Gautieria* the peridium is that of a bolete of the *Xerocomus* type, the columella is that of *Truncocolumella* (fleshy, not cartilaginous), the gleba is basically tubular in structure and the color change to blue is in line with the other bolete characters. The ornamentation of the spores is in line with that found on a number of species of *Boletellus*. Specimens of *Gautieria* are commonly encountered in central Idaho. Those Smith has observed there invariably have a firm cartilaginous consistency not at all like that of *Chamonixia*. The sterigmata in *C. brevicolumna* are curious because of their variable size and in being more like agaric than gastromycete sterigmata. Since species of boletes (*B. chrysenteron* group) are known to have spores with an apical pore similar to that found in *C. brevicolumna*, this character can be regarded as consistent with the other bolete characters the species possesses.

### 3. *Chamonixia ambigua* (Zeller & Dodge) Smith & Singer, comb. nov. Figs. 5, 11.

*Arcangiella ambigua* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 365. 1935.

Gastrocarp pyriform to irregularly and variously lobed, up to 50 mm broad and 30 mm high, dingy pallid but turning blue when touched, finally wine-colored to black but drying honey-yellow to light brownish olive, on standing becoming dingy brown; surface smooth, to rimose and flaky after splitting of the thick peridium; columella thick, basal, truncate (as in *Truncocolumella*) with thinner extensions extending to the peridium; gleba chocolate color to wine color fresh, the cavities small, sinuous, rich russet throughout as dried.

Spores 11–15 (–18)  $\times$  9–11 (–12)  $\mu$ , rusty brown in KOH and Melzer's reagent, broadly ellipsoid to ovate in face view, in profile obscurely inequilateral to subelliptic, with a prominent sterigmatal appendage, the surface ornamented with irregular longitudinal ridges and some isolated warts, the ridges obtuse and 1–1.5  $\mu$  high, the apex with an inconspicuous thin spot in the wall but never truncate.

Hymenium: Basidia 2- and 4-spored, 20–25  $\times$  7–11  $\mu$ , clavate, hyaline, thin-walled; sterigmata 6–8  $\times$  1.5–2  $\mu$ , often subapical, the spores borne acropetally; pseudoparaphyses present, 10–13  $\mu$  broad, broadly clavate; cystidia none; hyphal arrangement in tramal plates indistinct on sections revived in KOH; peridium of interwoven hyaline filaments 5–10  $\mu$  in diameter and with thin smooth walls; oleiferous hyphae scattered through the tissue; clamp connections none.

Cespitose and partly buried in hard soil under oak, May and June in California.

Our description is based on the original account and on our own data obtained from an examination of the part of the type now in the Zeller herbarium (NY). It might be inferred from the fact that this species was described in *Arcangeliella* that gastrocarps exuded a latex when cut, but it appears to us that no latex could have exuded from cut surfaces of the fresh material.

The structures referred to as lactiferous hyphae in the original account are those which students of the Agaricales now term oleiferous hyphae. These structures are widely distributed throughout the genera of the Basidiomycetes. The ribbed ornamentation of the spore of *C. ambigua* is quite prominent in the specimens examined rather than inconspicuous as originally described.

This species is closely related to *C. brevicolumna* but the latter differs in the following characters: a distinct pore can be observed on immature spores; there is a basic difference in the structure of the outer layer of the peridium (it is a trichodermium in *C. brevicolumna*); and the color of the surface of the peridium in *C. ambigua* is whitish at first instead of olive-ocher. Zeller and Dodge (1935) apparently placed this species in *Arcangeliella* on the basis of what they interpreted as laticiferous ducts in association with the color change noted by Parks when he collected the specimens. The species, of course, is in no way related to the members of the astrogastraceous series except that both are members of the Gastromycetes close to the level of the Secotiaceae.

**4. *Chamonixia caespitosa*** Rollaud, Bull. Soc. Myc. Fr. 15: 76. 1899.

Fruiting bodies 20–30 mm broad, 13–20 mm high, subglobose to flattened on top, slightly lobed, depressed around a short stipe; peridium separable, silky fibrillose, about 0.4 mm thick when fresh, thinner in places, white at first, slightly tinged buffish brown when the spores mature, rapidly turning deep indigo blue when bruised, this color eventually fading to greenish blue, but then remaining almost unchanged in drying; peridium absent or very little developed around the stipe, the gleba thus visible in a meridional furrow, on mature fruiting bodies the peridium often peeling away in places; odor and taste not distinctive.

Stipe about 4 mm high, 3 mm wide, solid, white, turning blue like the peridium, narrowed toward the base which continues into white rhizomorphs; gleba white at first, then dark army brown to vinaceous buff; chambers small, oblong, not filled with spores at maturity; columella percurrent through the gleba as a narrow but distinct unbranched structure about 0.5 mm broad.

Spores 18–20.5 × 12.7–15.2  $\mu$ , oblate, rich brown when mature; epispore long remaining hyaline, finally brown, irregularly wrinkled to form 8–10 longitudinal ribs; sterigmal appendage short, narrow and hyaline; spore apex slightly papillate but this often obscured by the wrinkles of the epispore.

Basidia 4-spored, mostly about 36 × 18  $\mu$ , in a true hymenium.

Tissues: Hyphae of tramal plates 4–5  $\mu$  broad, hyaline, only slightly gelatinous; subhymenium somewhat indefinite in thickness, of isodiametric cells; epicutis of peridium of appressed yellowish hyphae 7–9  $\mu$  broad; hypodermial zone of almost isodiametric cells somewhat radially arranged; context of filamentose hyphae similar to those of the tramal plates; clamp connections absent.

The above description refers to plants in late stages of development. Very young plants which have not yet reached a diameter of more than about 2 mm have a somewhat different appearance, similar to that of young specimens of

agarics. The stipe is almost as large as in fully developed specimens, and the rest of the fruit-body is convex, deeply depressed around the stipe. In section the columella is more prominent, the gleba made up of a few large chambers. The morphology of still younger stages is illustrated by Fischer (1922, 1933).

The above account is adopted from that of Lange and Hawker (1951). The structure of the peridium readily separates this species from *C. ambigua*, but other less striking differences such as the slightly larger spores of *C. caespitosa* are evident if the descriptions are compared.

*Hymenogaster caerulescens* Söhnner (Fig. 13) may be a fifth species of *Chamonixia*, as the spores clearly indicate that it belongs to that genus, but we have not seen the type. It has been placed in the synonymy of *C. caespitosa*, but this may or may not be correct. Zeller & Dodge (1934) described it as lacking a columella and reported it from California. The large spores separate it from the species of *Chamonixia* recognized in this work with one exception, *C. caespitosa*. Rolland in his original description of the latter wrote "Les glibes charnues, couleur de chair, se composent de petites cellules rondes ou ovales et ne présentent pas de parties stériles." If this means that there is no columella then the account of Lange and Hawker, which we have used here for Rolland's species, is incorrect with respect to this detail.

We believe that redistributing the species placed in *Arcangeliella* by Zeller and Dodge will do much to clarify genera and species among the hypogeous Basidiomycetes. The removal of *A. caudata* and *A. ambigua* to *Chamonixia* certainly clarifies *Arcangeliella* and the addition to *Chamonixia* of a fourth, previously undescribed species only goes to show that once a genus in the higher Basidiomycetes is well founded and its relationships are made evident, new discoveries readily fall into a logical place.

Many bolete characters are evident in the genus *Chamonixia*; these include the blue stain that three of the species develop when injured, the basically tubular structure of the gleba in *C. brevicolumna*, the trichodermial structure of the outer layer of the peridium in both *C. brevicolumna* and *C. caudata*, and the *Boletellus*-like spores which are the most striking character.

The arrangement of the hyphae of the tramal plates is a possible point of difference between the Boletales and *Chamonixia* and deserves some discussion. In *Gastroboletus* and in *Truncocolumella citrina* the arrangement of hyphae in the tramal plates is bilateral as it is in the boletes. In *T. citrina* var. *separabilis* and in *T. rubra* the hyphae are interwoven or, as revived in KOH, subparallel in *T. rubra*. In *Chamonixia* the actual arrangement of the hyphae in the tramal plates of *C. caudata* has not been demonstrated. In *C. brevicolumna* they are interwoven and in *C. ambigua* their arrangement was not clear to us from revived sections. Lange and Hawker did not mention it in their account of *C. caespitosa*. Obviously a study of this character in additional young fresh specimens is required to establish the hyphal arrangement for most species.

As was pointed out by Singer (Farlowia 2: 286. 1945), the bilaterality of the hymenophoral trama has diagnostic value mainly if studied in young specimens which have only begun to sporulate. In some cases the arrangement of the hymenophoral elements remains essentially the same even in old specimens, but in many others it is known to change from bilateral to regular or interwoven to irregular. Such a situation has been observed repeatedly in *Boletus*, and Singer (1940) found the trama of *Catathelasma ventricosum* (Pk.) Singer to

be regular in sections from dried material but later observed (1951) that young fresh material had decidedly bilateral structure. On material collected in Idaho and studied while fresh Smith observed that in *C. ventricosum* no trace of a bilateral arrangement was present in mature carpophores though clearly evident in the young ones. Here in *Chamonixia* and in *T. citrina* var. *separabilis* we may be dealing with a comparable change in hyphal arrangement.

If one searches for additional genera which might possibly be included, eventually, in the *Gastroboletus* series, *Gautieria* must be considered first because its spores are like those of *Chamonixia*, as previously mentioned. *Ropalogaster transversarius* (Bosc) Johnston is a remote possibility. This is a secotiaceous fungus without clear affinities to the Agaricales. It has spores of a boletoid type which are melleous and symmetric, 4-spored basidia, a hyphous filamentous peridium, and a gelatinized layer; there is no bilaterality of the hymenophoral trama. It lacks both clamp connections and cystidia. Macroscopically this genus has the aspect of a *Podaxis*.

#### Literature Cited

- Dodge, C. W. 1931. *Alpova*, a new genus of the Rhizopogonaceae with further notes on *Leucogaster* and *Arcangeliella*. Ann. Mo. Bot. Gard. 18: 457-464.
- Fischer, E. 1933. In Engler & Prantl, Natürl. Pflanzenfam. ed. 2, 7a: 1-22.
- Heim, E. 1951. Notes sur la flore mycologique des Terres du Pacifique Sud IV. Le genre néocalédonienne *Le-Ratia* Pat. Rev. Mycol. 16: 154-158.
- Lange, M. & Hawker, L. E. 1951. Some hypogean Gasteromycetes from Jamtland, Sweden, and adjacent districts in Norway. Svensk Bot. Tidskr. 45: 591-596.
- Lange, M. & Hansen, L. 1954. The phylogenetic position of Agaricales. Bot. Tidskr. 51: 185-194.
- Lohwag, H. 1937. In Handel-Mazzetti, H. Symbolae Sinicae 2: 54-55.
- Malençon, G. 1931. La série des Asterosporés. Recueil d. trav. dédié à Louis Maugin, Paris. pp. 377-396.
- . 1939. *Dodgea occidentalis* Malençon Nouveau genre et nouvelle espèce de Rhizopogonaceae. Bull. Soc. Mycol. Fr. 54 (for 1938): 193-203.
- Patouillard, N. 1907. *Le-Ratia* nouveau genre de la série des *Cauloglossum*. Bull. Soc. Mycol. Fr. 23: 50-52.
- Rolland, L. 1899. Excursion à Chamonix—été et automne 1898. Bull. Soc. Mycol. Fr. 15: 73-78.
- Singer, E. 1943. Das System der Agaricales II. Ann. Mycol. 40: (for 1942): 1-132.
- . 1945-47. The Boletineae of Florida with notes on extralimital species. I. *Farlowia* 2: 97-141. 1945; II. *Farlowia* 2: 233-303. 1945; III. Amer. Midl. Nat. 37: 1-135. 1947; IV. *Farlowia* 2: 527-567. 1946.
- . 1951. The Agaricales (mushrooms) in modern taxonomy. Lilloa 22 (for 1949): 5-832.
- Snell, W. H. 1936. Notes on boletes. IV. Mycologia 28: 13-23.
- Zeller, S. M. 1939. New and noteworthy Gastromycetes. Mycologia 31: 1-32.
- Zeller, S. M. & Dodge, C. W. 1919. *Arcangeliella*, *Gymnomyces* and *Macowanites* in North America. Ann. Mo. Bot. Gard. 6: 49-59.
- . 1935. New species of Hydnangiaceae. Ann. Mo. Bot. Gard. 22: 365-373.

Authors' note: Throughout this paper the term *series* is used in a non-technical sense denoting a group of genera forming a progressive (or retrogressive) evolutionary sequence. The term is not used in the formal nomenclatural sense.