

NORTH AMERICAN SPECIES OF THE GEOGLOSSACEAE. TRIBE CUDONIEAE¹

E. B. MAINS

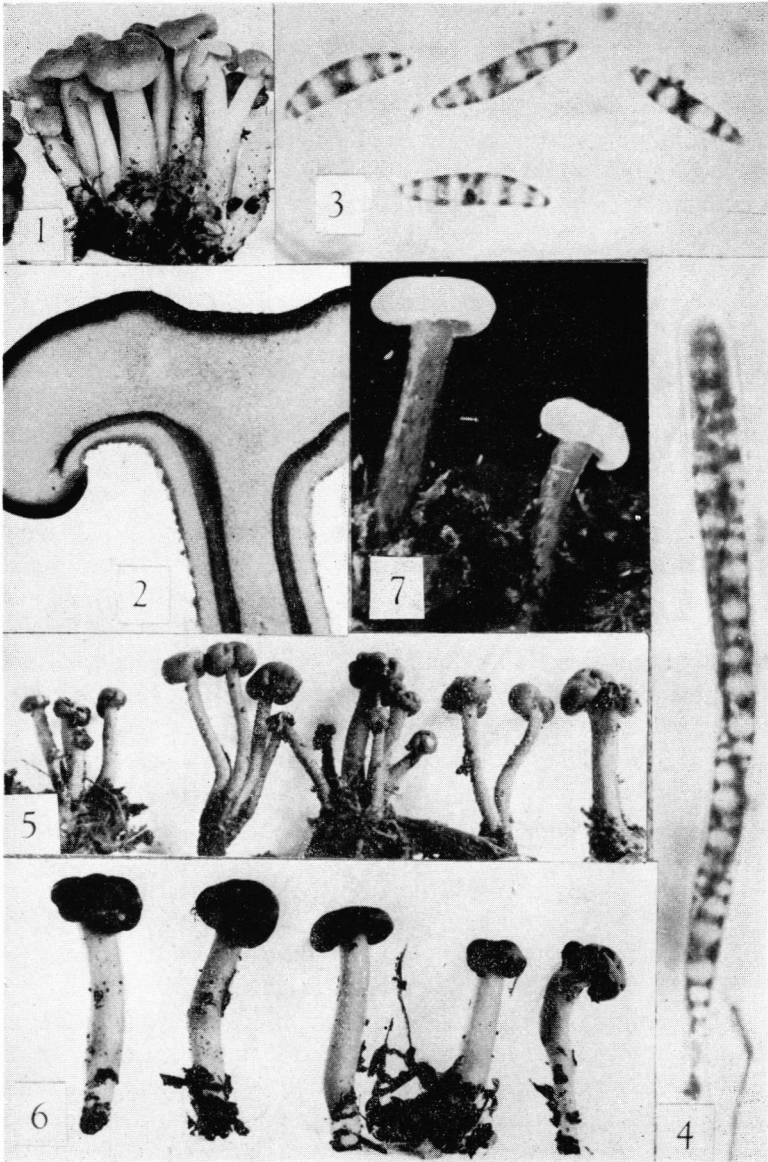
(WITH 23 FIGURES)

The family Geoglossaceae was formerly treated as a subfamily of the Helvellaceae. In recent classifications where Boudier's separation of the Discomycetes has been followed the Geoglossaceae has been recognized as a family in the Inoperculates and therefore far removed from the Helvellaceae in the Operculates. In Nannfeldt's (1932) treatment of the Discomycetes it is placed in the Helotiales and is recognized as closely related to the Helotiaceae. As distinguished from the Helotiaceae, the Geoglossaceae is usually separated by having clavate, capitate or pileate ascocarps with the hymenium covering the convex upper portion and the Helotiaceae having discoid, saucer-shaped or cupulate ascocarps (Durand 1908, Nannfeldt 1932, Martin 1940, Seaver 1951).

In this study, Durand has been followed, with some modifications in the division of the Geoglossaceae into two tribes, the Geoglosseae and the Cudonieae. The Geoglosseae, with ascocarps that are capitate or clavate, has been treated in previous papers (Mains 1954, 1955). The Cudonieae, as discussed here, has ascocarps that are pileate. Imai (1941) has treated these taxa as subfamilies, Geoglossoideae and Cudonioideae, and has recognized a third subfamily, the Hemiglossoideae, for one genus *Hemiglossum*, which has branched coralloid ascocarps with unilateral hymenia. This genus has not been reported for North America.

The genera of the Cudonieae appear to occupy positions intermediate between the Geoglosseae and the Helotiaceae. *Leotia* has multiguttulate ascospores (FIG. 3) similar to those found in *Microglossum* of the Geoglosseae but the structure of its ascocarps differs from that of all of the other genera of the Geoglossaceae. The ascocarps consist of a central tissue of gelatinous hyphae separated from an outer layer of gelatinous hyphae by a distinct layer of non-gelatinous hyphae (FIGS. 2, 8). This is a structure which is found in *Ombrophila* and *Ascotre-*

¹ Paper from the Herbarium and the Department of Botany of the University of Michigan.



FIGS. 1-4. *Leotia lubrica*. 1. Ascocarp, approx. $\times 0.5$. 2. Longitudinal section of an ascocarp showing nongelatinous middle layer stained dark, approx. $\times 10$. 3. Ascospores, $\times 900$. 4. Ascus, $\times 900$. FIG. 5. *Leotia atrovirens*, ascocarps, approx. $\times 1$. FIG. 6. *Leotia viscosa*, approx. $\times 0.8$. FIG. 7. *Leotia albiceps*, ascocarps, approx. $\times 2$. (Photograph by H. S. Jackson.)

mella of the Ombrophiloideae of the Helotiaceae sensu Nannfeldt. *Leotia* differs from the latter genera in having well developed stipes and pileate ascocarps.

Vibrissea is distinguished from other genera of the Geoglossaceae by the long filiform ascospores (FIG. 12). Nannfeldt (1932) placed this genus in the Ostropaceae of the Ostropales. It, however, does not have asci with walls hemispherically thickened at the apices and fragmentation of ascospores which are given as characteristic of that family. There is considerable variation in the shape of ascospores in the Geoglossaceae and the genus is retained. *Apostemidium* is included in the Geoglossaceae by Durand. It has filiform spores like *Vibrissea* but the ascocarps are sessile and pulvinate and therefore it is excluded.

Cudonia is closely related to *Spathularia* in the Geoglossaceae. It has similar ascospores, which in some species produce conidia on sterigmata (FIG. 18), as in some species of *Spathularia*. *Cudonia lutea*, like *Spathularia velutipes*, has the hymenium covered by a well developed membrane until late in the development of the ascocarp (FIG. 16). On the other hand, *Cudonia* is related to *Helotium*. As has been discussed elsewhere (Mains 1956) the type species of *Cudoniella* (*Cudoniella queletii* = *Helotium aciculare*), which has been included in the Geoglossaceae (Schroeter 1897, Rehm 1895, Clements and Shear 1931), is the same as that for *Helotium*. Except for size, the ascocarps of *Helotium aciculare* are very similar to those of *Cudonia* in form and structure. The principal distinction is in fusoid ascospores.

Corner (1930), in his study of the evolution of the ascocarp in the Discomycetes, has concluded that "*Cudoniella acicularis*" occupies an intermediate position in the series between the Helotiaceae and the Geoglossaceae. Only relatively few of the many species which have been included in *Helotium* are similar to *Helotium aciculare*. As discussed elsewhere (Mains 1956) the inclusion of *Helotium* (*Cudoniella*) as typified by *H. aciculare* in the Geoglossaceae would involve extensive studies concerning the limitations of the genus *Helotium*, the relation of genera in the Helotiaceae and probably a realignment of the genera of the Helotiaceae and Cudonieae. In this study it is not included and the Cudonieae as recognized by Durand has been followed with modifications as discussed. *Helotium* has, however, been included in the key for convenience.

KEY TO THE GEOGLOSSACEAE

- A. Ascocarps clavate, spathulate or capitate, the hymenium covering most or all of the head or the upper part of the club..... **Geoglossaceae**
(see Mains 1954, 1955)

- A. Ascocarps pileate, the pilei convex, the hymenium covering the upper surface, the lower surface sterile..... **Cudonieae**

CUDONIEAE

1. Ascocarps gelatinous..... *Leotia*
 1. Ascocarps fleshy..... 2
 2. Ascospores filiform..... *Vibrissea*
 2. Ascospores acicular or narrowly clavate..... *Cudonia*
 2. Ascospores fusoid..... *Helotium* (*Cudoniella*)
 (see Mains 1956)

LEOTIA Fr. Syst. Myc. 2: 25. 1822

Ascocarps pileate, stipitate, gelatinous, with an outer gelatinous layer separated from an inner gelatinous center by a layer of non-gelatinous hyphae; hymenia covering the upper surface of the convex pilei; asci clavate, —I, 8-spored; ascospores subfusoid or narrowly ellipsoid, usually asymmetric, mostly multiguttulate, hyaline; paraphyses filiform, branched.

Type: *Leotia lubrica* Fr.

As treated by Fries in the Systema, *Leotia* was divided into two sections, *Hygromitra* having gelatinous ascocarps and *Cucullaria*, with fleshy ascocarps, including *Leotia circinans*. He later (1849) limited the genus to the gelatinous section and the genus *Cudonia* was established to which *Leotia circinans* was transferred.

Durand treats three species for North America. They are closely related, differing mostly in color of the ascocarps, and show considerable intergradation. Imai (1941) has considered them as forms of *Leotia lubrica* and has recognized eight additional forms differing mostly in size and color. Since the color is often considerably changed by drying, accurate determination of dried specimens is frequently impossible.

Durand and Imai state that the ascospores of species of *Leotia* are at first continuous, finally 3–5-septate. In the specimens examined in this study, the discharged ascospores are usually multiguttulate (FIG. 3) as in *Microglossum*. Septate spores were not seen.

The structure of the ascocarps is distinctive (FIGS. 2, 8). The central core of the stipe is made up of interwoven hyphae having narrow lumina and very gelatinous walls. Although these hyphae grow in various directions, the longitudinal direction is the most pronounced. At the upper end of the stipe they diverge outward and make up the medulla of the pileus. Surrounding the central gelatinous core of the stipe is a cylinder of compact non-gelatinous longitudinal hyphae. Above they spread outward and form a middle layer between the

medulla and the ectal layer on the lower side of the pileus. The outer layer of the stipe consists of gelatinous hyphae similar to those of the central core. Although they are very interwoven, they appear to arise from the non-gelatinous layer and develop outwardly. A continuation of the outer layer forms the ectal layer of the lower side of the pileus.

The structure of the ascocarps of *Leotia* relates it to species of the Ombrophiloideae of the Helotiaceae sensu Nannfeldt. According to von Höhnel (1918) the ascocarps of *Ombrophila violacea*, the type of *Ombrophila*, have a structure similar to that which has been described here for *Leotia*. The ascocarps of *Ombrophila* are substipitate to short-stipitate and the hymenia plane, plano-convex or somewhat concave. It should be noted that the ascocarps of *Ombrophila clavus*, which Seaver recognizes as the type of *Ombrophila*, do not have this structure. Von Höhnel, however, excludes *O. clavus* from *Ombrophila* and suggests that it belongs in *Helotium*. *Ascotremella*, placed by Nannfeldt in the Ombrophiloideae, also has ascocarps having an outer and inner gelatinous tissue separated by a non-gelatinous layer. The ascocarps are sessile to substipitate and the hymenia plane to convex. *Leotia* differs therefore principally in having well-developed stipes and more convex hymenia. This is also true for *Ombrophila albiceps* Peck. The ascocarps of this species also have the structure of *Leotia* and the species is therefore transferred here to *Leotia*.

KEY TO THE SPECIES OF LEOTIA

1. Ascospores $5-7.5 \times 2-3 \mu$*L. albiceps*
1. Ascospores $16-25 \times 4-6 \mu$2
2. Ascocarps buff, ochraceous or cinnamon, sometimes olivaceous.....*L. lubrica*
2. Ascocarps dark green, sometimes with stipe light green.....*L. atrovirens*
2. Ascocarps with the hymenium dark green and the stipe and lower surface of the pileus white, yellow or orange.....*L. viscosa*

LEOTIA LUBRICA Fr. Syst. Myc. 2: 29. 1822. FIGS. 1-4

Leotia punctipes Peck, Bul. Torrey Bot. Club 34: 102. 1907.

Ascocarps cespitose, gregarious or sometimes scattered, 2-7 cm long, pileate, gelatinous or under dry conditions appearing somewhat fleshy, buff, ochraceous or cinnamon, sometimes with a greenish tinge or olivaceous; pilei convex, smooth or somewhat furrowed or wrinkled above, squamulose below, 8-40 mm broad consisting of three layers continuous with those of the stipe; stipes terete, equal or somewhat enlarged below, 5-10 mm thick, minutely squamulose or furfuraceous, consisting of three layers, a central core of interwoven gelatinous hyphae, a middle layer of non-gelatinous longitudinal hyphae and an outer layer

of gelatinous hyphae; asci clavate, $115-150 \times 7-10 \mu$; ascospores subfusoid, narrowly ellipsoid, straight or slightly curved, rounded at the ends, $16-23 \times 4-6 \mu$, multiguttulate; paraphyses filiform, somewhat enlarged at the apices, branched below, usually somewhat agglutinated with amorphous matter.

On soil or sometimes on rotting wood. Collected in Michigan from July 9 to October 25.

Specimens studied: 88 from California, Kentucky, Maine, Maryland, Massachusetts, Michigan, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Tennessee, Vermont, Virginia, Washington, Nova Scotia, Ontario, Quebec (all MICH).

Leotia lubrica is the most abundant species in North America as well as elsewhere. It is very variable in size and through the greenish variants intergrades into *L. viscosa* and *L. atrovirens*. Durand recognized two forms, *L. lubrica* f. *stevensoni* having greenish or olivaceous ascocarps with firm consistency and *L. lubrica* f. *lloydii* having olive-ochraceous ascocarps with firm consistency which on drying become darker green or olive with olive-green stipes.

LEOTIA ATROVIRENS Pers. ex Fr. Syst. Myc. 2: 30. 1822. FIG. 5

Leotia chlorocephala Schw. ex Fr. Syst. Myc. 2: 30. 1822.

Ascocarps scattered or cespitose, 0.5-4 cm long, pileate, gelatinous or subgelatinous, similar in structure to *L. lubrica*; pilei convex, 3-10 mm wide, 2-5 mm thick, dark green, squamulose below; stipes terete, 2-4 mm thick, concolorous with pilei or lighter green, usually prominently squamulose; asci clavate, $125-150 \times 8-10 \mu$; ascospores subfusoid, straight or somewhat curved, $16-22 \times 4-5 \mu$, multiguttulate; paraphyses filiform, somewhat enlarged at the apices, branched below, green above, somewhat agglutinated with green amorphous matter.

On soil. Collected in Michigan from Aug. 10 to Sept. 11.

Specimens studied: 19 from Florida, Massachusetts, Michigan, New Hampshire, New York, North Carolina, Ontario, Quebec (all MICH).

This species differs from *L. lubrica* in its definitely green color, smaller size, firmer consistency and more prominently squamulose condition. It is treated by Durand under the name *L. chlorocephala* Schw. Both Durand and Nannfeldt (1942) have noted the close similarity to *L. atrovirens* of Europe. They do not appear to differ sufficiently to justify the recognition of two species. There is some question concerning the name which should be employed. Both are published by Fries in 1822 on the same page of his Systema. Fries refers to the

publication of *L. chlorocephala* by Schweinitz in his Synopsis Fungorum Carolinae published in 1822 and to the publication of *L. atrovirens* by Persoon in his Mycologia Europaea pt. 1 also published in 1822. Rogers (1944) has concluded that Schweinitz's Synopsis Fungorum Carolinae was published later in 1822 than Persoon's Mycologia Europaea. Consequently *L. atrovirens* appears to have precedence over *L. chlorocephala*. *L. stevensoni* Berk. & Br. may also be this species. Massee (1897) and Durand, however, consider it to be a greenish form of *L. lubrica*.

LEOTIA VISCOSA Fr. Syst. Myc. 2: 30. 1822. FIG. 6

Leotia stipitata Schroeter. Engl. Prantl. Nat. Pfl. 1: 166. 1894.

Ascocarps cespitose or scattered, 3-9 cm long, pileate, gelatinous, similar in structure to *L. lubrica*; pilei convex, 2-3 cm wide, 5-10 mm thick, olive-green to dark green; stipes terete or somewhat flattened, 5-10 mm thick, white, yellow or orange, green-punctate or furfuraceous; asci clavate, $125-160 \times 8-11 \mu$; ascospores subfusoid to narrowly ellipsoid, straight or slightly curved, rounded at the ends, $17-26 \times 4-6 \mu$, multiguttulate; paraphyses filiform, branched below, somewhat enlarged at the apices, green above, usually somewhat agglutinated with green amorphous matter.

On soil or sometimes on rotten wood. Collected in Michigan from July 24 to November 13.

Specimens studied: 43 from Massachusetts, Michigan, New Hampshire, New York, North Carolina, Oregon, South Carolina, Tennessee, Virginia, Nova Scotia, Ontario, Quebec (all MICH).

This species was treated by Durand as *L. stipitata*. It is very similar to *L. lubrica* and is distinguished from it by the dark green pilei and white to orange stipes. It might be desirable to recognize varieties based on the color of the stipes.

Leotia albiceps (Peck) comb. nov. FIGS. 7-9

Ombrophila albiceps Peck Ann. Rep. N. Y. State Mus. 42: 34. 1889.

Ascocarps solitary, gregarious or cespitose, 5-30 mm long, pileate, stipitate, gelatinous with gluten often covering stipe and lower surface of the pileus, drying horny, structure similar to *L. lubrica*; pileus hemispherical, 3-12 mm broad, 2-3 mm thick, watery white or carneous at first, becoming ochraceous to army brown, with the hymenium convex on the upper surface, with the margin becoming recurved; stipe terete, 2-4 mm thick below, above widening into the pileus, smooth or rough through irregular drying of the gluten, brown with lilac tinge; asci

clavate, $40-60 \times 4-6.5 \mu$; ascospores subfusoid to narrowly ellipsoid, $5-7 \times 2-3 \mu$, guttulate; paraphyses linear, slightly exceeding the asci.

TYPE: On decaying wood, North Elba, N. Y., Sept., Charles H. Peck (NYS).

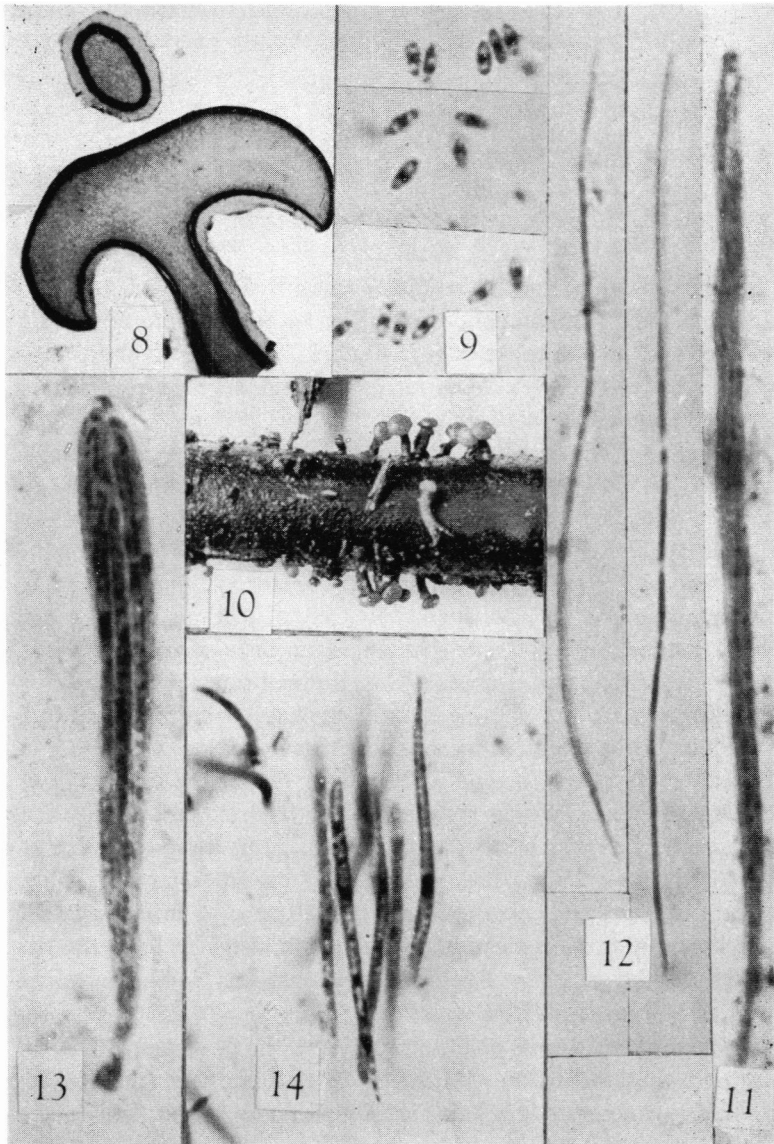
On rotting poplar wood.

Specimens studied: Michigan E. B. & E. E. Mains, 33-658 (MICH). New York, C. H. Peck, TYPE (NYS). Ontario, H. S. Jackson *et al*, TRT 3082, 5936, 5937, 5938, 5939, 5940, 5960, 7953, 7955, 7956, 9711.

In correspondence with the late Professor H. S. Jackson, he suggested that the Michigan collection might be *Ombrophila albiceps* Peck and stated that he had collected it in Ontario. He was doubtful whether it was a species of *Ombrophila* or *Leotia* and noted a resemblance in the young stages to *Ascotremella turbinata*.

Through the kindness of Roy C. Cain, the specimens in the Herbarium of the University of Toronto were loaned for study. They are 11 ample collections with notes by Professor Jackson. He described the color of pilei of the fresh ascocarps as "pearly or watery white at first often with flesh tints becoming ochraceous" and the stipes as brownish, often with a lilac tinge. A study of sections of the ascocarps showed a structure similar to that found in *L. lubrica* (Fig. 8). The central core of the stipe consists of longitudinal interwoven hyphae with very gelatinous walls. Upwards these hyphae spread outward to form the medulla of the pileus. Surrounding this is a layer of compact longitudinal non-gelatinous hyphae which continues on the underside of the pileus. Apparently arising from this layer and extending outward are gelatinous hyphae which form an outer gelatinous layer of the stipe and underside of the pileus. Jackson mentions an outer layer of gluten in his notes and suggests that it is in the nature of a universal veil. It probably is due to the excessive gelatinization of the walls of the hyphae of the outer layer. The Michigan specimen has a similar structure. It was army brown in color when collected.

Through the kindness of Stanley Jay Smith, the type of *Ombrophila albiceps* in the Herbarium of the New York State Museum was loaned for study. It consists of several ascocarps up to 15 mm long with pilei up to 8 mm broad, with well developed stipes. They are dark reddish brown. Peck described the pilei of the fresh ascocarps as "whitish or sometimes with a faint incarnate tinge" and the stipes as "pallid or reddish brown" appearing covered with gluten in wet weather. The asci are clavate, $50-55 \times 4 \mu$, and the ascospores $5-6 \times 2-2.5 \mu$. In section the ascocarps have two gelatinous layers separated by a layer of non-



FIGS. 8, 9. *Leotia albiceps*. 8. Longitudinal section of ascocarp (below) and cross section of stipe (above) showing nongelatinous middle layer stained dark, approx. $\times 10$. 9. Fourteen ascospores, $\times 900$. FIGS. 10-12. *Vibrissea foliorum*. 10. Ascocarps, approx. 0.5. 11. Ascus, $\times 900$. 12. Two filiform ascospores, $\times 900$. FIGS. 13, 14. *Cudonia circinans*. 13. Ascus, $\times 900$. 14. Ascospores, $\times 900$.

gelatinous hyphae as described for the Ontario specimens. The Michigan and Ontario specimens are therefore *Ombrophila albiceps*. However, its well developed stipe, convex hymenium and structure similar to *L. lubrica* place it in *Leotia*.

Imai (1941) has described a species *Neocudoniella jezoensis* from Japan with gelatinous ascocarps which from his discussion appears somewhat similar to *L. albiceps*. Information concerning the structure of the ascocarps is not given.

VIBRISSEA Fr. Syst. Myc. 2: 31. 1822

Ascocarps pileate, stipitate, fleshy or subgelatinous; pilei convex, with the margins often involute, with hymenia on the upper surfaces; stipes terete, well developed; asci subcylindric to narrowly clavate, narrowing to the base, —I; ascospores 8, filiform, multiseptate, hyaline; paraphyses filiform, enlarged at the apices, simple or branched.

Type: *Vibrissea truncorum* Fr.

This genus is distinguished by its long, filiform, multiseptate ascospores (FIG. 12). Nannfeldt (1932) places it in the Ostropaceae, apparently mostly on account of its filiform ascospores. Since there is great variation in the ascospores of the Geoglossaceae, this is not sufficient to exclude it from the family. The ascospores of *Vibrissea* do not break up into part spores and the asci do not have a pronounced hemispherical thickening of the apical wall as in the Ostropaceae.

The hyphae of the interior of the stipes are hyaline, compact and longitudinal. There is usually no well differentiated outer layer. The outer hyphae are somewhat wider and sometimes brownish. The outermost hyphae may become free to form hairs or clumped to form scales. The hyphae diverge into the pileus, becoming compactly interwoven in the medulla. The outer hyphae of the stipe continue to form a layer of parallel hyphae on the underside of the pileus, diverging somewhat at the margin.

VIBRISSEA TRUNCORUM Fr. Syst. Myc. 2: 31. 1822. FIGS. 10–12

Vibrissea foliorum Thaxter, in Durand, Ann. Myc. 6: 454. 1908.

Ascocarps gregarious, cespitose or scattered, pileate, stipitate, fleshy to subgelatinous, 3–20 mm high; ascogenous portion convex, thin, 2–5 mm wide, flesh-colored, pinkish buff or yellowish buff, with hymenium on the upper surface, sterile underneath, with margin frequently involute; stipes terete, 1–2 mm thick, white, minutely tomentose, frequently matted and appearing smooth; asci narrowly clavate, gradually narrow-

ing from near the apex, variable in length, $175-325 \times 5-6 \mu$; ascospores filiform, very variable in length $(80-125-250(-275) \times 1 \mu$, multiseptate; paraphyses straight, simple or branched, filiform below, enlarged at the apices.

On decaying wood, leaves etc. in cold wet places, often in streams. Collected in Michigan from June 13 to August 6.

Specimens studied: 27 from Connecticut, Michigan, New Hampshire, New York, Washington, Ontario, Quebec (all MICH).

This is a species which develops under cold wet conditions. It often fruits early in the year submerged in cold running water where the long ascospores projecting above the hymenium vibrate in the stream and give it a white silky appearance.

Durand distinguished *V. foliorum* from *V. truncorum* on differences in habitat and sizes of asci and ascospores. The asci of *V. truncorum* were described as $200-325 \times 5-6 \mu$ and the ascospores as $175-250 \times 1 \mu$ and it is stated that the species develops on wholly or partly submerged sticks in brooks mostly in high altitudes. *V. foliorum* was described from one specimen on dead oak leaves, acorn cups etc. in a wet place and the asci are given as $150-180 \times 5-6 \mu$ and the ascospores as $80-100 \times 1 \mu$. A study of part of the type collection (Rel. Farlowiana 175) has resulted in finding asci $150-200 \mu$ long and ascospores $80-135 \mu$.

In other collections examined in this study, considerable differences in ascospore length were found. Although collections from submerged wood tend to have longer spores than those on leaves and sticks in wet places, collections with asci up to 300 and ascospores up to 200 and 250μ have been seen from the latter. Also in submerged collections short ascospores (up to 135 and 150μ) occur. It therefore seems desirable to recognize only one species.

CUDONIA Fr. Summa Veg. Scand. 348. 1849

Ascocarps pileate, stipitate, fleshy or fleshy-leathery, pilei usually convex, with the hymenium on the upper surface, sterile beneath, with the margin often involute; asci clavate, —I, 8-spored; ascospores acicular or narrowly clavate, hyaline, 1-celled or multi-septate; paraphyses filiform, hyaline.

Type species: *Cudonia circinans* Fr.

Durand treats three species of *Cudonia* for North America, *C. circinans*, *C. lutea* and *C. ochroleuca*. The identity of the last species is very uncertain. It was described by Cooke and Harkness from a specimen collected at San Rafael, California. Durand states that the color

of the dried specimen is very different from that given in the description. Specimens which have been identified as *C. ochroleuca* have been *Cudonia monticola* and the lichen *Baeomyces roseus*. Since Durand's monograph, two other species have been described, *C. monticola* Mains and *C. grisea* Mains. Imai (1955) has recently proposed a genus *Pachycudonia* which he distinguishes from *Cudonia* by "long-tailed" asci, the spores being constricted at the middle portion and not perfectly acicular, and the circinate paraphyses. He includes *C. constrictospora*, *C. spathulata* and *C. monticola*. *C. monticola* has asci attenuated below (FIG. 19), but this occurs to some extent in other species, such as *C. lutea* (FIG. 17). The ascospores of *C. monticola* (FIG. 20) are not constricted or only rarely so. Throughout the genus *Cudonia* the paraphyses are strongly curved, uncinatate or circinate above. It seems doubtful that a generic separation is justified. In this study (Mains 1955) *C. spathulata* has been included in *Spathularia*.

The development of *Cudonia lutea* has been studied by Duff (1922). An outer layer of tissue develops early in the growth of the ascocarp. This later becomes the veil which completely covers the ascocarp. The hymenium develops beneath the veil on the upper surface of the young pileus. With the expansion of the young pileus the covering veil breaks and sloughs off except for a few adhering remnants (FIG. 16). Portions of the veil are usually found in most collections of *C. lutea*. Whether a veil is formed in other species of the genus is unknown. If formed, it probably is poorly developed and evanescent. The ascospores of *Cudonia* are usually one-celled. Septa are sometimes formed and the spores then may become 2- to several-celled. In *C. circinans* and *C. lutea* the ascospores commonly produce conidia on short sterigmata. When this occurs within the asci, the conidia may entirely replace the ascospores.

Cudonia appears to be very closely related to *Spathularia* of the Geoglosseae. The two genera have a parallel series of species differing in types of asci, formation of conidia and development of veil over the hymenium.

KEY TO THE SPECIES OF CUDONIA

- | | |
|--|---------------------|
| 1. Ascospores 18-25 μ long..... | 2 |
| 1. Ascospores mostly more than 30 μ long..... | 3 |
| 2. Pilei drab or dark gray, stipes fuscus..... | <i>C. grisea</i> |
| 2. Pilei pinkish cinnamon or pinkish buff, stipes avellaneous or wood brown..... | <i>C. monticola</i> |
| 3. Ascospores (28-)32-40(-46) μ long..... | <i>C. circinans</i> |
| 3. Ascospores (48-)50-65(-70) μ long..... | <i>C. lutea</i> |

CUDONIA CIRCINANS Fr. Summa Veg. Scand. 348. 1849. FIGS. 13, 14
Leotia circinans Fr. Syst. Myc. 2: 27. 1822.

Ascomcarps gregarious or cespitose, pileate, stipitate, fleshy, drying leathery, 1.5–7 cm long; pileus thin, up to 2 cm broad, convex, smooth, wrinkled or sometimes convoluted, cream to dark brown, with the hymenium on the upper surface, with the lower surface sterile, with the margin often involute; stipe terete, 2–12 mm thick, furfuraeous, striate to ridged, drab to dark brown; asci clavate, $90\text{--}150 \times 8\text{--}10 \mu$; ascospores acicular (28–)32–40(–46) $\times 2 \mu$, 1-celled or sometimes several-septate, the wall thin, gelatinous; conidia commonly produced on short sterigmata by the ascospores, subspherical to broadly ellipsoid, $3\text{--}4 \times 2 \mu$, hyaline, sometimes replacing the ascospores in the asci; paraphyses filiform, branched below, strongly curved or uncinata above, hyaline.

On soil, less commonly on rotting wood. Collected in Michigan from August 4 to October 3.

Specimens studied: 99 from Colorado, Idaho, Michigan, New York, Oregon, Tennessee, Washington, Nova Scotia (all MICH).

This is the most common species in North America. It varies considerably in color. In the fresh condition the pileus may be cream, pinkish buff, cinnamon-buff, vinaceous buff, avellaneous or wood brown and the stipe usually darker, drab, vinaceous brown, wood brown or bone brown. Fries commented on the variation in color of this species.

The central portion of stipe and pileus consists of very loosely interwoven hyphae and may become hollow in the larger ascocarps. The hyphae of the outer portion of the stipe and lower side of the pileus are compact more or less parallel to the surface. The furfuraeous condition is due to groups of short branches arising from the outer hyphae and consisting of short ellipsoid to oblong cells.

Nannfeldt (1942) has followed Bresadola in recognizing a species *C. confusa* in Europe which is distinguished from *C. circinans* mostly by color.

CUDONIA LUTEA (Peck) Sacc. Atti Real. Inst. Venet. 6: 725. 1885.
FIGS. 15–18

Vibrissea lutea Peck, Rep. N. Y. State Mus. 25: 97. 1873.

Leotia lutea Cooke, Bul. Buffalo Soc. Nat. Sci. 2: 287. 1875.

Ascomcarps gregarious or scattered, pileate, stipitate, fleshy, drying leathery, 1–6 cm long; pileus up to 1.5 cm broad, convex above, margin often involute, upper surface smooth, frequently with portions of the veil adhering to the margin or as patches on the surface, yellowish, orange-buff, ochraceous or ochraceous buff, the lower surface of pileus

furfuraceous, often with ridges continuing down the stipe; stipe terete, up to 6 mm thick, concolorous with the pileus or lighter, minutely furfuraceous; asci clavate, $110-160 \times 10-12 \mu$; ascospores acicular (48-) $50-65(-70) \times 2 \mu$, 1-celled or multiseptate, wall thin, with an outer gelatinous layer; conidia frequently produced on short sterigmata by the ascospores, subspherical to broadly ellipsoid, $3-4 \times 2 \mu$, hyaline, sometimes replacing the ascospores in the asci; paraphyses filiform, branched below, strongly curved to circinate above, hyaline.

TYPE: North Elba, Essex Co., N. Y., Charles Peck in the Herbarium of the N. Y. State Museum.

On decaying leaves usually of beech. Collected in Michigan from July 30 to October 7.

Specimens studied: 33 from Michigan, New Hampshire, New York, North Carolina, Ohio, West Virginia, Vermont, Nova Scotia, Quebec (all MICH); also the type from N. Y. S. Museum.

The ascospores of *C. lutea* are larger than those of *C. circinans*. Similarly the wall gelatinizes and they commonly produce conidia (FIG. 18).

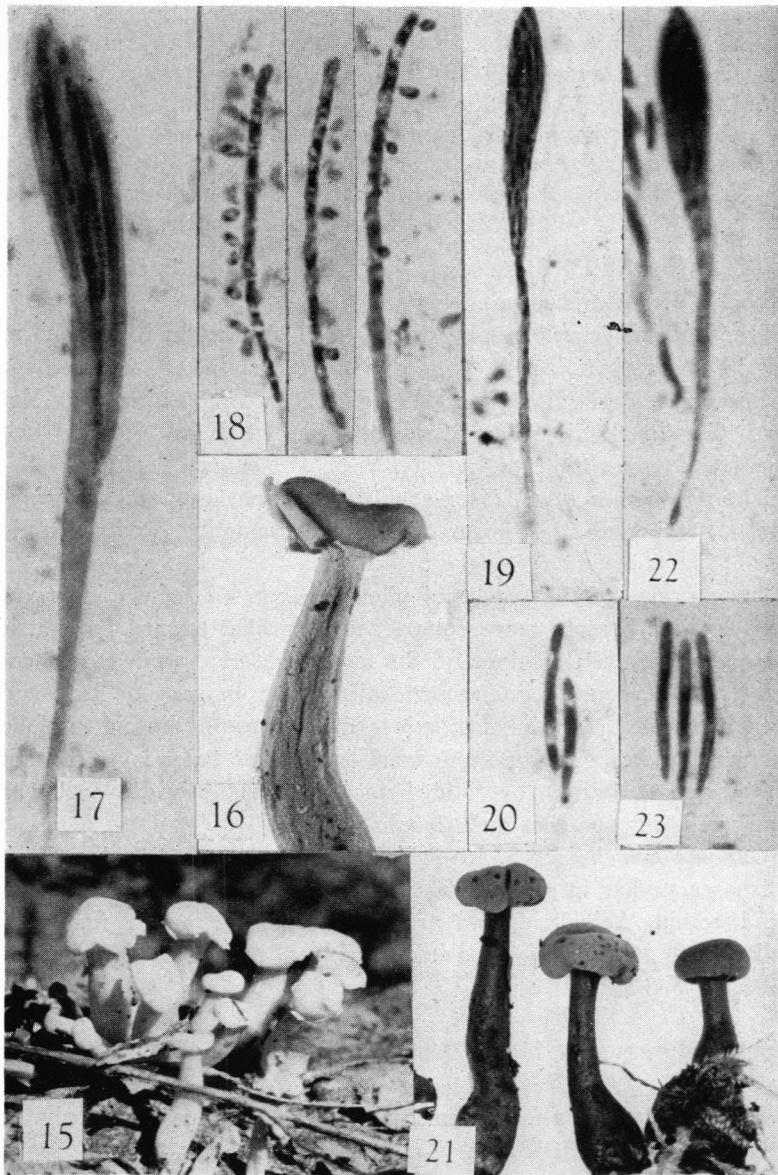
The interior of the stipe and pileus consists of loosely interwoven hyphae which become more compact and parallel toward the outside. The outer layer of the stipe and the lower side of the pileus is a compact tissue of densely interwoven cells which in sections is pseudoparenchymatous. On the outside it forms clumps of ellipsoid to globoid cells which give the furfuraceous condition. This outer layer continues in the young condition over the hymenium and forms the veil which later breaks into patches and sloughs off.

Cudonia helvelloides S. Ito & Imai in Japan is described as having ascospores similar in size, $48-60 \times 1.5-2 \mu$. The pilei are at first convex, becoming helvelloid, and are at first pale yellowish, finally pale avellaneous. *C. japonica* Yasuda of Japan has much larger spores $65-85 \times 2.5-3.5 \mu$.

CUDONIA MONTICOLA Mains, Am. Jour. Bot. 27: 322. 1940. FIGS. 19, 20

Pachycudonia monticola Imai, Sci. Rep. Yokohama Nat. Univ. Ser. 2, no. 4: 2. 1955.

Ascocarps closely gregarious to cespitose, pileate, stipitate, fleshy-leathery, 3-10 cm long; pilei 1-3 cm broad, convex, irregularly hemispherical, laterally compressed or helvelloid, rugose, pinkish cinnamon, pinkish buff or grayish brown; stipe somewhat compressed, 5-7 mm thick below, somewhat narrowed above, becoming hollow in age, pallid



FIGS. 15-18. *Cudonia lutea*. 15. Ascocarps, approx. $\times 1$. 16. Ascocarp showing fragments of veil at margin of hymenium, approx. $\times 2$. 17. Ascus, $\times 900$. 18. Three ascospores with conidia, $\times 900$. FIGS. 19, 20. *Cudonia monticola*. 19. Ascus, $\times 900$. 20. Two ascospores, $\times 900$. FIGS. 21-23. *Cudonia grisea*. 21. Ascocarps, approx. $\times 1$. 22. Ascus, $\times 900$. 23. Three ascospores, $\times 900$.

avellaneous or wood brown, glabrous; asci clavate, $90-125 \times 8-10 \mu$, narrowing rapidly below the upper third, becoming $2-4 \mu$ thick below; ascospores acicular or narrowly clavate $(15-18-24(-28) \times 2 \mu$, 1-celled or rarely 1-septate; paraphyses filiform, strongly curved to uncinately above, hyaline.

TYPE: Lake Crescent, Washington. A. H. Smith 14060, in the Herbarium of the University of Michigan.

On soil, coniferous debris or rotting wood.

Specimens studied: California, CU 521118; Idaho, A. H. Smith 45210, 45224 (MICH); Washington, A. H. Smith 13785, 14009, 14060, TYPE (MICH); Wm. B. Gruber, June 22, 1942 (MICH).

This is the largest species in North America. It has much smaller ascospores (FIG. 20) than either *C. circinans* or *C. lutea*. The structure of the ascocarp is similar to *C. circinans*.

Cudonia osterwaldii P. Henn. in Germany is described as having small, 0.5-1.5 cm, ascocarps with dark chestnut colored pilei and pallid stipes. The ascospores are narrowly clavate, $18-28 \times 2-4 \mu$, and multi-guttulate. *Cudonia constrictospora* S. Ito & Imai in Japan is described as having yellowish, pale isabelline or subochraceous ascocarps and ascospores which are narrowly clavate, $20-27.5 \times 2 \mu$ and constricted in the middle.

CUDONIA GRISEA Mains, Am. Jour. Bot. 27: 322. 1940. FIGS. 21-23

Ascocarps gregarious, pileate, stipitate, fleshy, 1.5-5 cm long; pilei 0.5-1.5 cm broad, convex, smooth, drab or dark grey; stipe terete, 3-8 mm thick below, narrowing upward, smooth, fuscus; asci clavate, $70-110 \times 6-10 \mu$, narrowing below the upper third, attenuated below; ascospores acicular $18-22(-24) \times 1.5-2 \mu$, 1-celled or rarely 1-septate; paraphyses filiform, strongly curved above, hyaline.

TYPE: Hoh River, Washington, A. H. Smith 13521 in the Herbarium of the University of Michigan.

On rotting coniferous wood.

Specimens studied: Washington, A. H. Smith 13521, TYPE, 14100, 14482 (all MICH).

Cudonia grisea has similar ascospores to those of *C. monticola*. The ascocarps are smaller and differ in color.

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