

STUDIES IN FRUTESCENT LECIDEACEAE  
(LICHENIZED DISCOMYCETES)

I. MACKENZIE LAMB

[Continued from p. 129]

TONINIA Mass. emend. Th. Fr.

**Toninia conglomerata** (Ach.) Boist. Nouv. Flore Lich., Part 2 (1902) p. 105. Syn. *Lecidea conglomerata* Ach., Lichenogr. Univ. (1810) p. 201. *Thalloidima conglomeratum* Mass., Ricerch. Auton. Lich. Crost. (1852) p. 97. *Thalloedaema conglomeratum* Vain., Lichenogr. Fennic. II (1922) p. 145.

MATERIAL EXAMINED: Austria, Styria, Judenburg, "in saxis alpium," coll. *Welwitsch*, no date, 254, in Farlow Herb., s.n. *Thalloidima conglomeratum*.

The outward morphology of this not uncommon alpine species has been well and accurately described by Vainio, *loc. cit.* He mentions its caulescent habitus, its peculiar light-edged squamules, and its predominantly simple spores. Therefore only its anatomical characteristics will be considered in detail here, based on an examination of the Austrian specimen mentioned above.

The stipitate squamules are bicolorous, with gray edges and brownish centers. Squamules in section covered on upper side by a colorless, clear, amorphous or faintly horizontally striated, necrotic stratum 10–50  $\mu$  deep. Cortex at sides of squamule 30–70  $\mu$  thick, gradually  $\pm$  dark brown in outer 15–18  $\mu$  and also  $\pm$  heavily inspersed with sordid yellow-brownish depsidone-granules, which make the structure very indistinct; after treatment with KHO the cortex seems to be composed of intricate, conglutinated, gelatinous hyphae, forming on the outer surface distinct brown-pigmented cells like the heads of paraphyses. Cortex directly subtended by the algal stratum. In the center of the squamule the brown-pigmented outer layer is absent, and the cortex is greatly thickened to form a lentiform or bowl-shaped structure about 170  $\mu$  deep, which pushes the algal stratum downwards; in its upper half this structure is heavily inspersed with masses of brownish-yellow depsidone-substance, in its lower half it is colorless and hyaline, very gelatinized, with the thread-like, branched and reticulating hyphal lumina (about 1  $\mu$  wide) well visible in the clear gelatinous matrix. Medulla PD + orange-red or testaceous-red (also in other specimens examined, e.g. Rabenhorst, Lich. Europ. no. 738), the margins of the squamules also often staining. In KHO added to sections of the thallus under the microscope, the brownish-yellow depsidone-granules dissolve with effusion of yellow mist.

The radicate stipes are solid, devoid of algae, ecorticate or in places with a rudimentary and indistinct cortical layer up to 30  $\mu$  thick nubilated in its outer part with depsidone-granules. Internal medullary tissue  $\pm$  colorless



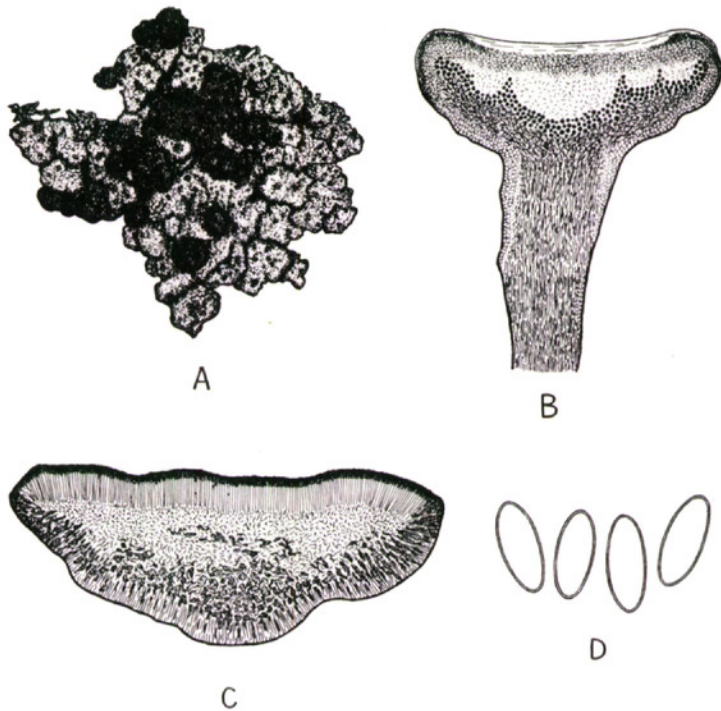


FIG. 8. *Toninia conglomerata* (Ach.) Boist. Specimen from Austria, Judenburg, coll. Welwitsch. A, part of thallus with apothecia ( $\times 2$ ). B, vertical section of a stipate squamule. C, vertical section of apothecium. D, spores.

and clear, composed of indistinct gelatinized hyphae  $2-3\ \mu$  thick closely compacted and running mainly longitudinally parallel.

The symbiotic algae of the thallus are cystococcoid, bright green, globose, separate, thin-walled,  $5.0-8.5\ \mu$  diam.

Excipulum entire at sides and below apothecium,  $85-135\ \mu$  thick, sordid pale yellowish or  $\pm$  colorless or isabelline in section, with irregular streaks of sordid yellow-brownish depsidone-substance between the hyphae; of flabellate-radiating structure, with parallel, conglutinated, gelatinized, thick-walled hyphae, only the fistulose lumina visible,  $1.0-1.3\ \mu$  wide. Central cone tissue (myelohyphic stratum) developed in lower part of apothecium, about  $200\ \mu$  deep, lax, interspersed with cloudy masses of yellowish-gray granular substance, the hyphae colorless,  $3-5\ \mu$  thick, loosely intricated in various directions. Hypothecium up to  $200\ \mu$  deep, colorless, hyaline or in places interspersed with irregular inclusions of sordid yellowish depsidone-substance, in the upper subhymenial part slightly sordid yellowish-cloudy; of compact gelatinized texture, with completely fused hyphae running in various directions, only the branching fistulose lumina visible,  $1.0-1.3\ \mu$  wide. Hymenium  $50-60\ \mu$  high, gradually or  $\pm$  abruptly olivaceous brown-blackish in uppermost  $8-12\ \mu$  ( $\text{HNO}_3$  + purple-crimson), otherwise colorless and hyaline. Paraphyses discrete under pressure in water,  $1.3-2.0\ \mu$  thick, not articulated, simple or sparingly branched, clavate-capitate up to  $3-4$  ( $-5$ )  $\mu$  at the pigmented tips. Asci clavate,  $40-48 \times 12-14\ \mu$ , with wall about  $1\ \mu$  thick at sides, at apex gelatinously thickened up to  $7\ \mu$ . Spores 8 in ascus irregularly biseriate; all simple and unseptated, ellipsoid to elongate-ellipsoid,  $9-13 \times (3.5-4-5)\ \mu$ . Hymenium persistently blue with Iodine. KHO added to sections of apothecium dissolves the depsidone-inclusions of excipulum and hypothecium with effusion of intense yellow mist.



This species stands on the borderline between *Toninia* and *Lecidea* sect. *Psora*, the spores being in many specimens, like the above, all eseptate. Zahlbruckner, Cat. Lich. Univ. IV (1926) p. 286, lists *Lecidea acervulata* Nyl. as a synonym, but according to Vainio's revision of the type, the latter is identical with *Toninia aromatica* (Turn.) Mass. (25, p. 133). The light-edged squamules of *T. conglomerata* resemble those of another European species, *T. nigrescens* Anzi, which is however quite distinct, having cylindric-fusiform, 3-septate spores  $22 - 26 \times 3.0 - 3.5 \mu$  (e. g. in Anzi, Lich. Rar. Langob. no. 116), and a negative reaction with Paraphenylenediamine.

***Toninia bumamma*** (Nyl.) Zahlbr. Cat. Lich. Univ. IV (1926) p. 263. Syn. *Lecidea bumamma* Nyl. in Journ. Linn. Soc. Lond., Botan. XV (1876) p. 177. *Lecidea styloumena* Stirt. in Trans. Glasgow Soc. Field Natural. V (1877) p. 217.

MATERIAL EXAMINED: the type-specimen of "*Lecidea styloumena*" Stirt. from South Africa, Somerset East, Klein Vischrivier, "in rimis rupium brecciarum ad ripas aridas," coll. P. McOwan, in herb. Stirton, Glasgow Museum.

On soil. Thallus of crowded, turgid squamules 1–3 mm. diam., produced downwards on the under side into stalk-like,  $\pm$  cylindrical, rooting structures  $\pm$  buried in the soil and up to 8 mm. long. Squamules up to 1 mm. thick, convex, glebose, round or  $\pm$  irregular in outline, not angulose, smooth, naked, now alutaceous or sordid brownish-yellow ("albidus vel pallidus vel pallide cervinus" in fresh condition, acc. to Stirton), matt. Under side concolorous or paler, ecorticate, usually not well visible on account of adherent soil particles. Radicate stipes arising from center or near edge of underside of squamules, whitish to brownish, ecorticate, somewhat fibrous, 0.3–0.8 mm. thick, conspurcated by adherent soil. Thallus externally KHO— or brownish (Nylander reports KHO + yellow in his material),  $\text{CaCl}_2\text{O}_2$  —, PD —. Medulla white, KHO — or faintly yellowish,  $\text{CaCl}_2\text{O}_2$  —, PD —. Apothecia superficial on squamules, one or several to a squamule, separate or 2–3 confluent, adpressed-sessile, not or hardly constricted at the base, convex and immarginate from the first, up to 0.8 (–1.0) mm. diam., black, matt or subnitid, not pruinose. Pycnidia rather abundant, indicated externally by minute, scattered, non-prominent, black spots on upper side of squamules.

Squamules corticate on upper side only. Cortex 60–70  $\mu$  thick, in outer half densely yellow-brownish-nubilated and opaque in section, in inner half clear and colorless, pseudoparenchymatous, of  $\pm$  isodiametric or oblong, obtusely angulose or rounded cells 3–6  $\mu$  diam., their walls about 1  $\mu$  thick, in KHO seen to be formed from vertical hyphae. Algal stratum  $\pm$  continuous, 45–65  $\mu$  deep. Algae cystococcoid, now pale yellowish green, round, thin-walled, 6–11  $\mu$  diam. Medulla loosely hyphose, clear and colorless or in places slightly yellowish-gray-cloudy, I —, of loosely intricate, thin-



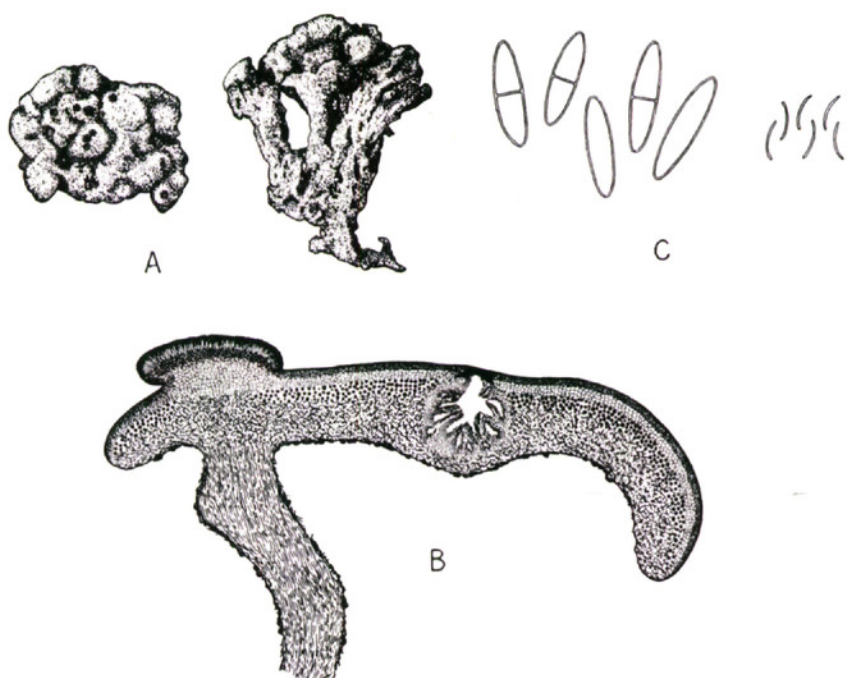


FIG. 9. *Toninia bumamma* (Nyl.) Zahlbr. The type-specimen of "*Lecidea styloumena*" Stirt. A, part of thallus seen from above and from the side ( $\times 2$ ). B, vertical section of a stipate squamule bearing an apothecium and a pycnidium. C, spores and pycnoconidia.

walled hyphae  $3.0\text{--}4.5\ \mu$  thick running in various directions. Lower side of squamules formed by the somewhat more compacted medullary hyphae, with adherent substratum-particles. Small colonies of Nostocoid blue-green algae occur occasionally on the underside of the squamules; in some cases they are superficial, but sometimes  $\pm$  enclosed by medullary hyphae. Stipes devoid of algae, ecorticate, sordid yellowish or pale brownish in section, formed of compacted, mainly longitudinally running medullary hyphae, more loosened and spreading on the outer side. The nubilation of the outer cortex of the squamules dissolves in KHO with yellow mist.

The apothecia rest with a broad base on compact thallus tissue (apparently lower part of cortex), and the algal layer is interrupted beneath them. In places where an apothecium is about to be formed, the cell walls of the cortex take on a blue-green tinge. Excipulum rudimentary, indistinct, dark blue-green or aeruginose-fuliginous, formed by the sterilized margin of the hymenium, into which it is gradually transformed. Hypothecium  $60\text{--}90\ \mu$  deep, unevenly pale sordid brownish or purple-brownish in section (KHO + violet-reddish),  $\pm$  pseudoparenchymatous, with  $\pm$  isodiametric cells about  $3\ \mu$  diam., their walls gelatinously fused and somewhat indistinct. Hymenium  $65\text{--}75\ \mu$  high, irregularly dark aeruginose or blue-green-blackish in uppermost  $9\text{--}18\ \mu$  (KHO -,  $\text{HNO}_3$  + sordid violet-red), otherwise  $\pm$  colorless or partly sordid isabelline; grading without sharp limit into the hypothecium. Paraphyses  $\pm$  concrete, rather stout,  $1.5\text{--}2.5\ \mu$  thick, at the dark aeruginose tips gradually  $\pm$  swollen (up to  $4\ \mu$ ) and there strongly conglutinated; simple or sparingly branched, not anastomosing, not articulated; in KHO becoming  $\pm$  discrete, but apparently much gelatinized. Whole hymenium persistently blue with Iodine. Asci clavate,  $45\text{--}65 \times 11\text{--}13\ \mu$ , with gelatinous wall about



1.5  $\mu$  thick at sides, 8–15  $\mu$  at apex. Spores 8 (or apparently often fewer) in ascus, irregularly biserial, ellipsoid-fusiform to cylindric-fusiform, colorless, simple or usually with 1 distinct median transverse septum,  $12-18 \times 4-5 \mu$ .

Pyrenidia immersed, with slightly indented ostiole, globose or subpyriform, 240–500  $\mu$  diam., with colorless, finely pseudoparenchymatic wall 5–10  $\mu$  thick, convoluted internally so as to form several intercommunicating chambers. Cortical tissue of thallus aeruginose-blackish around the ostiole. Pycnoconidia borne apically on crowded subulate conidiophores, shortly filiform, usually slightly bent,  $6-7 \times$  about 0.5  $\mu$ .

The original material of "*Lecidea bumamma*" Nyl. from the Cape of Good Hope has not been examined, but Nylander's short diagnosis describes the peculiar characters of the species so well that it can without hesitation be regarded as identical with Stirton's plant, following Stizenberger, *Lichenaea Africana* (1890–91) p. 162. Zahlbruckner, in Engler's *Bot. Jahrb.* LX (1926) p. 495, gives a detailed description of *T. bumamma*, based on a specimen from South Africa, Matjesfontein in the Great Karroo, which agrees closely with Stirton's material. He describes the squamules as 3–5 mm. diam. and the apothecia as finally reaching a size of nearly 2 mm.; the only notable discrepancies are in the color of the epithecium ("umbrino-nigricans") and the size of the conidia ("9–12  $\mu$  longa et 1,5–1,7  $\mu$  lata"). In *Ann. Cryptog. Exot.* V (1932) p. 240 he describes the species a second time, from a specimen collected by Slabbert at Jansenville, South Africa. This description also shows good agreement with the type of "*Lecidea styloumena*", except that the paraphyses are said to be up to 4  $\mu$  thick.

*T. bumamma* is a terricolous species occurring on soil in crevices of rocks, apparently in rather arid positions. The plant at first sight makes the impression of a parasymbiotic *Scutula* on an alien thallus, on account of the appearance of the closely adpressed, immarginate apothecia and their gelatinously concrete paraphyses. But a careful microscopic examination seems to indicate that the apothecia belong to the lichen, and especially the aeruginose coloration of the thallus cortex in places where apothecia are about to develop confirms this view. Also the finding of similar fertile material in several different localities of South Africa suggests that the apothecia are the natural fruiting bodies of the lichen.

**Toninia squalida** (Schleich. apud Ach.) Mass. Ricerch. Auton. Lich. Crost. (1852) p. 108. Syn. *Lecidea squalida*



Schleich. apud Ach., Lichenogr. Univ. (1810) p. 169. *Lecidea atrorufa* var. *squarrosa* Ach. in Kgl. Vetensk.-Akad. Nya Handl. XXIX (1808) p. 267. *Toninia squarrosa* Th. Fr., Lichenogr. Scand. I (1874) p. 331.

**T. squalida, f. caulescens** (Anzi) M. Lamb (n. comb.). Syn. *Toninia caulescens* Anzi, Cat. Lich. Prov. Sondr. (1860) p. 67. *Lecidea caulescens* Tuck., Gen. Lich. (1872) p. 182. *Lecidea squalida* var. *caulescens* Nyl. apud Stizenb. in Jahresber. St. Gallisch. Naturw. Ges. 1880-1881 (1882) p. 430. *Toninia squalida* subsp. *caulescens* Boist., Nouv. Flore Lich., Part 2 (1902) p. 105.

MATERIAL EXAMINED: the authentic, possibly isotype, material from Italy, alps of Bormio and Valle Tellina, in Anzi, Lich. Rar. Langob. no. 139 (Farlow Herb.); Switzerland, Wallis (Körber, Lich. Sel. German. no. 372, Farlow Herb.); Tirol, Windischmatri (Arnold, Lich. Exs. no. 672, herb. Arnold, München); U.S.A., California, no exact locality stated, coll. Bolander, 1871, no. 407, in herb. Tuckerman, Farlow Herb. The following description of this form of *T. squalida* is based on all four specimens cited, individual discrepancies being mentioned.

Squamules gray to reddish-brown, turgid and plicate,  $\pm$  imbricated, 0.5-1.5 mm. diam., conrescent into an effuse,  $\pm$  continuous crust. Radicate stipes well developed, buried in the earthy substratum, pale, ecorticate, up to 8 mm. long. Thallus externally and internally PD -. Apothecia usually numerous, scattered or crowded and confluent, entirely black, matt (or subnitid where rubbed), 0.5-0.9 mm. diam., at first plane with slightly prominent proper margin, then becoming  $\pm$  convex and immarginate, often subdividing into smaller secondary apothecia.

Squamules corticate above and on sides, in many places covered by a hyaline, necrotic, structureless layer up to 10  $\mu$  thick. Cortex of variable thickness, 15-100  $\mu$ , either entirely colorless and clear or in places dark brown in outer 7-15  $\mu$  (there composed of cells 3-5  $\mu$  diam. with distinct, thin, pigmented walls), the pale part composed of gelatinized and conglutinated, confluent, thick-walled hyphae in  $\pm$  vertical palisade-formation, the cell-lumina distinct, often slightly moniliform, 2-4  $\mu$  wide, embedded in a clear gelatinous matrix. Algal stratum interrupted or continuous, 35-110  $\mu$  deep; algae cystococcoid,  $\pm$  globose, 6.5-10.0  $\mu$  diam. Medulla  $\pm$  colorless, hyaline or grayish-cloudy, of thin-walled hyphae 2.0-4.5  $\mu$  thick somewhat loosely interwoven in various directions. Radicate stipes ecorticate, without algae, composed of indistinct, conglutinated and compacted,  $\pm$  thin-walled hyphae 2-3  $\mu$  thick running mainly  $\pm$  longitudinally in central part, at the periphery more intertexted in various directions; the tissue  $\pm$  colorless, not nubilated. In Arnold, Lich. Exs. no. 672, colonies of blue-green algae (chiefly *Stigonema*) are present on the outer surface of the stipes, and on the under side of the squamules some of them are included inside the fungal tissue, and seem to be forming primitive cephalodia.



Excipulum developed at sides, also continued vaguely for some distance below apothecium; 65–100  $\mu$  thick, dark purple-brown or brown-blackish from heavy pigment between the hyphae, which are flabellate-radiating (in Arn. Lich. Exs. 672 pigmented only in outermost 4–8  $\mu$ ). No myelohyphic stratum (central cone tissue) usually present; in Arn. Lich. Exs. 672 the lower hypothecium is looser in texture, with somewhat larger hyphae, and may be referable to central cone. Hypothecium colorless or faintly sordid isabelline, up to about 230  $\mu$  deep or produced indeterminately downwards into the

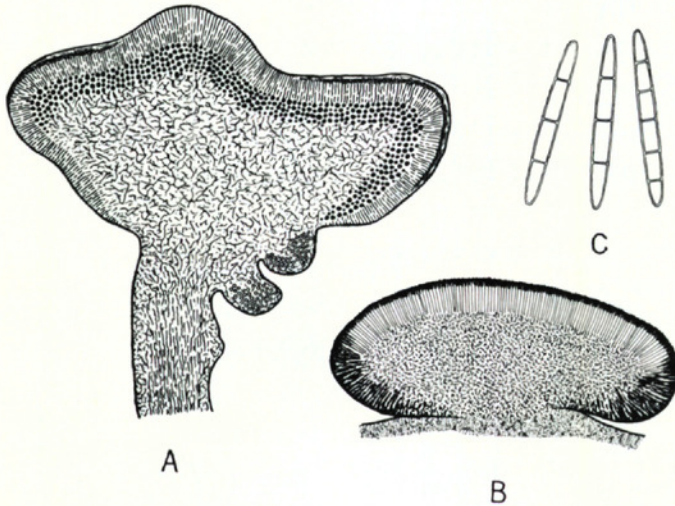


FIG. 10. *Toninia squalida* f. *caulescens* (Anzi) M. Lamb. A, vertical section of a stipate squamule, showing enclosed Cyanophyceous algae, in Arnold, Lich. Exs. no. 672 in Farlow Herb. B, vertical section of apothecium in Anzi, Lich. Rar. Langob. no. 139 in Farlow Herb. C, spores in Anzi, Lich. Rar. Langob. no. 139 in Farlow Herb.

stipe (in Bolander's California specimen with yellowish-gray, cloudy granules in upper part). Hymenium 55–70  $\mu$  high, gradually densely aeruginose-blackish in upper 10–17  $\mu$ , otherwise colorless and hyaline. Paraphyses  $\pm$  discrete in water, 1.5–2.5  $\mu$  thick, simple or sparingly branched, not articulated, clavate-capitate to 4 (–5)  $\mu$  at the  $\pm$  densely aeruginose and more conglutinated tips. Asci 45–60  $\times$  10–13  $\mu$ . Spores 6–8 in ascus, fusiform or cylindric-fusiform, straight, rounded or bluntly pointed at ends, 3–5-septate (up to 7-septate in Bolander's California specimen), 24–37  $\times$  3–4  $\mu$  (in Arn. Lich. Exs. 672 somewhat longer and narrower, 30–40  $\times$  3  $\mu$ ). Hymenium I + blue then wine-red. Excipulum and epithecium KHO – , HNO<sub>3</sub> + dark violet then violet-purple.

As Vainio (25, p. 131) and earlier authors have pointed out, *Toninia caulescens* is not specifically separable from *T. squalida*. They have exactly the same characters except for the well developed rooting stipes in the former. Stipes are developed to a lesser extent in typical *T. squalida*, as in *e.g.* Schaerer, Lich. Helv. Exs. no. 170, and *caulescens* can at best be distinguished only as a forma of that species.



Of three North American specimens determined by Tuckerman as "*Lecidea caulescens*" in his herbarium, only one belongs to *Toninia squalida* f. *caulescens*. The other two represent the related species *T. ruginosa* Tuck. Herre's Californian records of "*Toninia caulescens*" in Proc. Wash. Acad.

Sci. XII (1910) p. 102 also refer to *T. ruginosa*.

**Toninia ruginosa** (Tuck.) Herre in Proc. Wash. Acad. Sci. XII (1910) p. 103. Syn. *Lecidea ruginosa* Tuck., Lichens of California, Oregon and the Rocky Mountains (1866) p. 25; Synops. N. Amer. Lich. II (1888) p. 64.

MATERIAL EXAMINED: the type-specimen from California, Oakland Hills, coll. Bolander, no date, no. 102, in herb. Tuckerman (Farlow Herb.); California, San Mateo Co., near Point San Pedro, coll. A. W. Herre, 1904, in herb. Herre, Olympia, Wash., and Farlow Herb. The type-material, Bolander no. 102, is in two packets, one containing a specimen growing directly on a serpentine stone, the other containing two mounts of the same plant on stone-fragments covered with some detritus. Both are marked with the same collecting number, 102. The following description is made from one of the mounts in the latter packet, this specimen being chosen as the lectotype.

Thallus effuse, consisting of squamules attached either directly to the stone or to detritus over the latter; no dark hypothallus developed. Squamules reddish-brown, matt, (0.3-) 0.5-2.0 mm. diam., turgid and plicate, conerescent into a  $\pm$  continuous crust; no radicate stipes developed, but the arachnoid whitish medullary tissue from the under side of the squamules penetrates for some distance into the earthy detritus. Medulla PD -. Apothecia scattered, sessile on the squamules, 0.8-1.5 (-2.0) mm. diam., persistently plane and scutelliform, round or finally  $\pm$  flexuose, with thin to moderate, persistent,  $\pm$  prominent, black, matt or  $\pm$  nitid proper margin and reddish-black to black, naked, matt disc.

Squamules corticate on upper side; cortex well developed, 65-85  $\mu$  thick, faintly yellowish (isabelline) in section, clear and transparent, composed of completely conglutinated and gelatinized hyphae intricated in various directions or predominantly  $\pm$  vertical, only the lumina (1-2  $\mu$  wide) visible in the clear gelatinous matrix. Cortex in most places covered with an outer, colorless, hyaline, gelatinous, amorphous or horizontally striated necrotic layer up to 17  $\mu$  thick. Algal stratum directly below the cortex, continuous, 65-100  $\mu$  deep, becoming sparse downwards; algae cystococcoid, globose, thin-walled, 6-10  $\mu$  diam. Medulla loose, almost arachnoid, clear and colorless or in places  $\pm$  yellow-gray-cloudy, hyphose, of fine, thin-walled hyphae about 2 $\mu$  thick laxly entangled in various directions. This loose web of medullary hyphae runs down into the substratum for some distance.

Excipulum entire, continuous below apothecium, 100-135  $\mu$  thick at sides, 50-60  $\mu$  thick below, in outer third to half densely dark reddish-purple from



heavy pigment on and between the hyphae, in inner part gradually faint reddish-purple to  $\pm$  clear and colorless; of  $\pm$  distinct radiating structure, composed of  $\pm$  parallel, conglutinated, gelatinized, thick-walled hyphae, of which only the tubular lumina are visible,  $1-2\ \mu$  wide; at the sides with wider and shorter lumina (up to  $3\ \mu$  wide) and becoming indistinctly cellulose. The inner part of the excipulum grades without distinct limit into the hypothecium. Hypothecium  $170-200\ \mu$  deep, consisting of two parts: (a) a lower, colorless to faintly isabelline, clear and transparent  $135-155\ \mu$  (perhaps stratum myelohyphicum or central cone tissue), composed of completely fused and gelatinized hyphae, only their thread-like lumina (about  $1\ \mu$  wide) visible, intertexted in various directions in the clear gelatinous matrix; and (b) an upper, sordid yellow-brownish, cloudy but hardly pigmented  $50-60\ \mu$  of indistinctly cellulose structure, with cell-lumina about  $3\ \mu$  diam., reaching up to the base of the hymenium. Hymenium  $60-70\ \mu$  high, gradually dense purple-red-blackish in uppermost  $10-17\ \mu$ , otherwise colorless and hyaline. Paraphyses discrete, simple or sparingly branched, about  $1.5\ \mu$  thick, not articulated, at the tips capitate to  $3-5\ \mu$  and there  $\pm$  purplish-pigmented. Asci clavate,  $45-58 \times 10-12\ \mu$ , with wall  $1.0-1.3\ \mu$  thick at sides, at apex spuriously thickened to  $10\ \mu$ . Spores  $6-8$  in ascus, packed parallel in a bundle; acicular-fusiform, commonly rounded at one end and gradually tapered at the other, straight or rarely slightly curved, 3-septate,  $34-47 \times 2.0-2.5\ \mu$  (according to Tuckerman,  $25-40 \times 2-3\ \mu$ , sometimes with more than 3 septa). Hymenium I + blue then sordid olive-brownish. Epithecium and outer excipulum KHO + reddish-purple.

(No pycnoconidia seen; according to Tuckerman in Synops. N. Amer. Lich. II (1888) p. 65, they are filiform and curved.)

The Californian specimen collected by Herre and recorded as *T. caulescens* differs only slightly from the type-material described above. It is sparingly radicate-stipitate, the stipes being inconspicuous, developed only in places, and  $\pm$  ecorticate; most of the squamules, as in Tuckerman's material, are directly sessile on the substratum. The surface of the squamules is slightly nitid. The lower hypothecium is partially purplish or yellow-brownish, and the upper hypothecium is darker, reddish-brown. The hymenium is higher ( $75-90\ \mu$ ) and the spores slightly broader ( $3.0-3.5\ \mu$ ). These differences appear to come within the limits of normal specific variability.

The distributional area of this species, which differs from *T. squalida* chiefly in its purple-blackish (not aeruginose) epithecium, is interesting. The typical state and the f. *nigricans* described below constitute a Pacific North American element with an area extending from California to Washington; the var. *andicola*, here described for the first time, was found in the high mountains of the preandine Cordillera of prov. Catamarca in N. W. Argentina. This is an unusual type of bicentric



distribution, which seems to be without exact parallel in the flowering plants. There are a number of species common to N. W. Argentina and the highlands of Mexico, but the occurrence of a species of the N. American Pacific coast in the high "puna" region of S. America is surprising and not easily explained. The characters of var. *andicola* do not appear to justify specific separation from *T. ruginosa*.

**T. ruginosa, f. nigricans** M. Lamb (n. f.)

MATERIAL EXAMINED: the type-specimen from U.S.A., California, exact locality not stated, coll. 1866, *Bolander, 112*, in herb. Tuckerman (Farlow Herb.); Washington, Cascade Mountains, coll. 1883, *Brandeggee, 25*, in herb. Tuckerman (Farlow Herb.).

Thallo obscuriore (obscure fuscescens vel fusconigrescens) et apotheciis immarginato-convexis a specie typica differt.

*Description of the type-specimen (Bolander 112):*—On earthy detritus. Thallus effuse, of conrescent, turgid, plicate squamules similar to those of the typical species, but darker (dark brown to brown-blackish), matt or subnitid. Irregular radicate stipes are developed here and there from the underside of the squamules; they are pale, ecorticate, thin, root-like and branched, buried in the substratum. Medulla PD —. Apothecia numerous, sessile on the squamules, separate or crowded, entirely black, 1.0–1.5 (–2.0) mm. diam., matt (or nitid where rubbed), round, at first plane with thin, entire, non-prominent proper margin, then soon strongly convex and immarginate.

Excipulum developed at sides and below apothecium, 65–85  $\mu$  thick, pale to dark purple-brown in section or  $\pm$  colorless in inner part, of flabellate-radiate structure with the hyphae divided into distinct cells 5–7  $\mu$  long and 3–5  $\mu$  wide. Lower part of hypothecium (probably = central cone or myelohyphic stratum) yellowish-gray-cloudy, compact to  $\pm$  lax, formed of distinct, separate, thin-walled hyphae 3.0–3.5  $\mu$  thick interwoven in various directions (not gelatinously fused); upper part of hypothecium (= true hypothecium) 100–120  $\mu$  deep, varying in the same section from sordid isabelline to yellow-brownish or purplish-brown. Hymenium 55–65  $\mu$  high, gradually dark brownish-purple in upper 10–14  $\mu$ , otherwise colorless and hyaline. Paraphyses discrete, 1.0–1.8  $\mu$  thick, clavate-capitate to 3–4  $\mu$  at tips. Asci 45–50  $\mu$  long. Spores 6–8 in ascus, elongate-fusiform, straight or slightly curved, bluntly pointed at ends, sometimes gradually tapered towards one end, 5–7-septate, the septa distinct; 27–45 (–50)  $\times$  2.5–3.0  $\mu$ . Hymenium I + blue then sordid olive-brown. Outer excipulum, epithecium, and more colored parts of hypothecium KHO + reddish-purple.

The specimen from Washington agrees closely with the type. The hyphae of its lower hypothecium or central cone tissue are more gelatinously confluent, as in the type-specimen of *T. ruginosa*; its spores are 3–5-septate, 30–42  $\times$  3  $\mu$ .



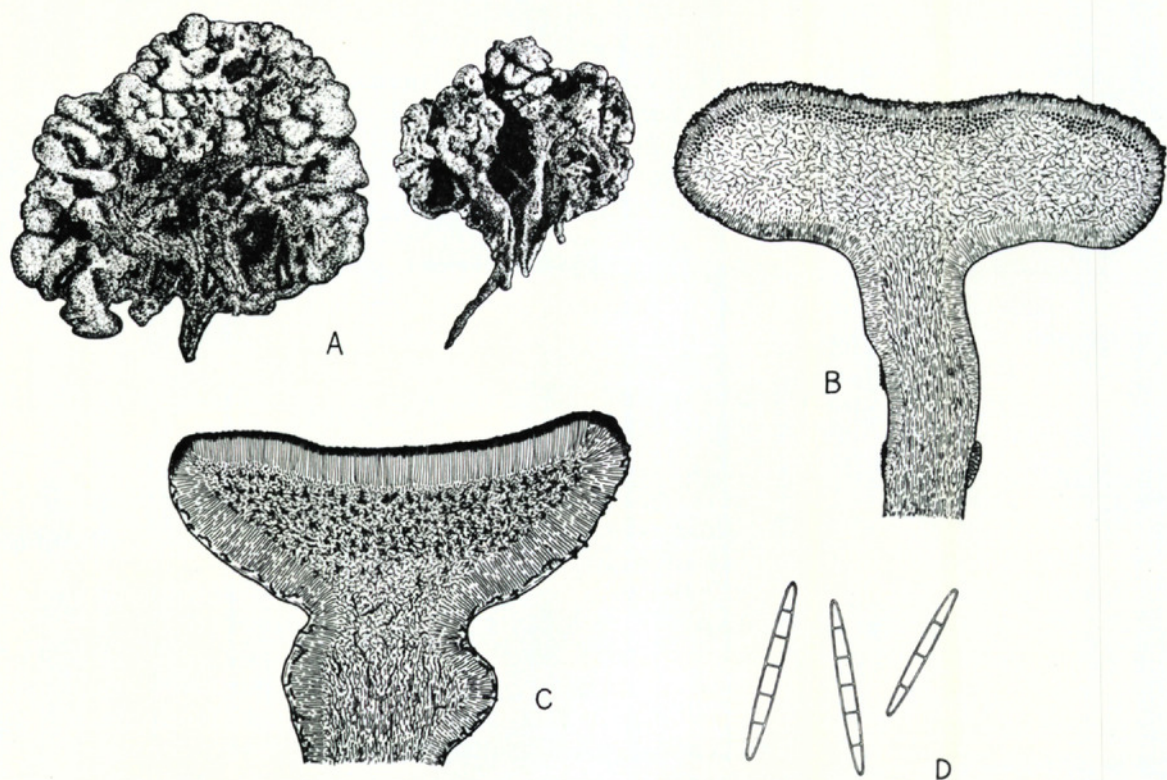


FIG. 11. *Toninia ruginosa* var. *andicola* M. Lamb. The type-specimen. A, parts of thallus showing radicate stipes ( $\times 2\frac{1}{2}$ ). B, vertical section of a stipate squamule. C, vertical section of apothecium (the dark masses in the hypothecium are included air). D, spores.

***T. ruginosa*, var. *andicola* M. Lamb (n. var.)**

**MATERIAL EXAMINED:** the type-specimen from N. W. Argentina, Prov. Catamarca, Nevados de Anconquiya, Quebrada de los Cazadores, altit. circ. 4500 m.s.m., in the puna-formation, on soil in crevices of a metamorphic rock face, not abundant, coll. 24. Nov. 1948, *I. M. Lamb*, 5599, in Herb. Nat. Mus. Canada, Ottawa, and isotype in Farlow Herb.

Squamulae clavato-bullatae, etiam latere inferiore corticatae, deorsum caulibus bene evolutis et partim corticatis munitae; ceteris notis ut in specie typica.

*Description of the type-specimen:*—Thallus effuse, in small patches; squamules crowded, turgid-inflated, 0.8–2.0 (–3.0) mm. diam., reddish-brown to dark brown (on lower side paler, yellowish-brown), matt, clavate-bullate, prolonged downwards into corticate, terete or irregularly rugose stipes 0.3–1.0 mm. thick which penetrate the substratum and continue downwards as brownish, root-like, ecorticate strands. Medulla PD —, I —. Apothecia scarce, sessile on the squamules, round or irregular, 1–2 mm. diam., entirely black, persistently plane or scutelliform, with slightly prominent, entire or  $\pm$  flexuose, moderate, matt or subnitid proper margin and matt, naked disc.



Cortex of squamules 35–50  $\mu$  thick, clear and colorless or faintly yellowish in section, in most places with brown torulose hyphae (parasite ?) on its outer surface; of  $\pm$  distinct palisade structure, composed of fused and gelatinized, thick-walled,  $\pm$  perpendicularly parallel hyphae, of which only the fistulose lumina are visible, 1.0–1.5 (–2.0)  $\mu$  wide. Algal stratum irregular, interrupted, up to 100  $\mu$  deep. Algae cystococcoid, bright green, globose, thin-walled, 7–14  $\mu$  diam. Medulla lax,  $\pm$  arachnoid, composed of colorless, thin-walled hyphae about 3  $\mu$  thick loosely interwoven in various directions. The cortex is continued for a long way down the sides of the stipes, which are devoid of algae, except for accidentally adherent external colonies of various Cyanophyceae, which are not enclosed in the fungal tissue. Central part of stipes composed of  $\pm$  compact, mainly longitudinally-running, colorless or faintly yellow-gray-cloudy, thin-walled hyphae 3–4  $\mu$  thick, obviously derived from the medulla.

The apothecial margin is an amphithecium continuous with the cortex of the thallus; 110–150  $\mu$  thick, entirely colorless and hyaline or yellow-brownish to purplish-brown in outermost 17–27  $\mu$ , composed of parallel-flabellate, fused and gelatinized hyphae of which only the tubular lumina are visible, 1–2  $\mu$  wide. Hypothecium 200–220  $\mu$  deep in center, colorless and hyaline, but with scattered dark masses of included air, mostly compact in texture, of conglutinated gelatinous hyphae 1.5–3.0  $\mu$  thick intricated in various directions. Hymenium 70–90  $\mu$  high,  $\pm$  gradually reddish-purple-blackish in upper 13–27  $\mu$ , otherwise colorless or faintly purple-brownish. Paraphyses  $\pm$  discrete in water, simple or sometimes branched, 2–3  $\mu$  thick, not articulated, towards the tips gradually purple-brown and there slightly to moderately thickened (up to 3.5–4.5  $\mu$ ). Asci clavate, 55–68  $\times$  10–14  $\mu$ , with wall 1.0–1.5  $\mu$  thick at sides, at apex thickened to 9–10  $\mu$ . Spores 4–6 (–8) in ascus, packed straight and parallel; elongate-fusiform, straight, bluntly tapered at ends, 3–5-septate, 30–40 (–50)  $\times$  3–4  $\mu$ . Hymenium I + blue to greenish then sordid wine-red. Epithecium KHO + reddish-purple, in HNO<sub>3</sub> unchanged or clearer reddish.

Apart from the morphological differences mentioned in the diagnosis, this specimen differs from the typical *T. ruginosa* in some microscopic characters, which are probably variable and non-taxonomic: the lesser pigmentation of the outer part of the apothecial margin, the quite colorless upper hypothecium, and the thicker paraphyses.

*T. ruginosa* may be related to the Australian *T. nitida* (Müll. Arg.) Zahlbr. and the Valdivian *T. badia* Räs.; the former differs in its impressed-punctulate squamules and larger spores, the latter in its much larger apothecia and aeruginose-brownish epithecium.

#### SPHAEROPHOROPSIS Vain.

**Sphaerophoropsis stereocauloides** Vain., Etud. Lich. Brésil, part 2 (1890) p. 7.

MATERIAL EXAMINED: the (lecto-) type-specimen from Brazil, Minas Geraes, Carassa, coll. 1885, Vainio, Lich. Brasil. Exs.



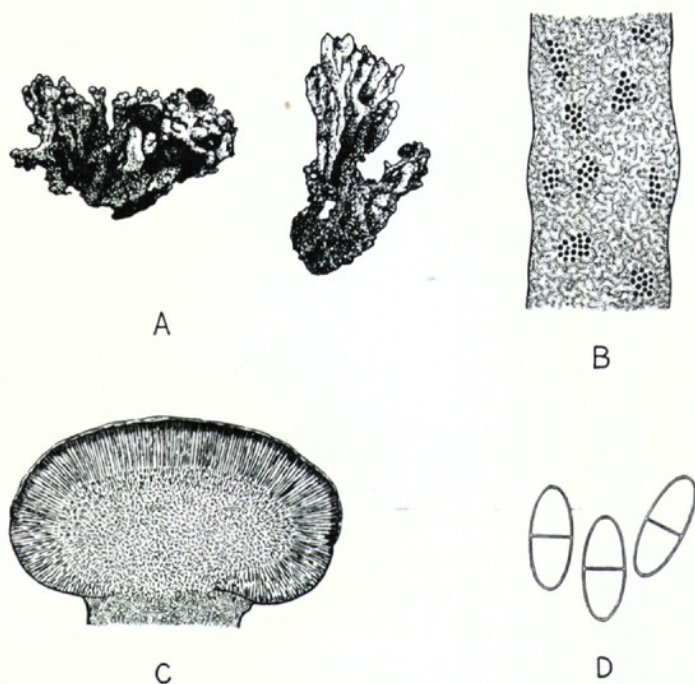


FIG. 12. *Sphaerophoropsis stereocauloides* Vain. Type-material in herb. Vainio. A, portions of plant showing habitus (on left part of the lectotype-specimen, Lich. Bra. il. Exs. no. 1475; on right part of Lich. Brasil. Exs. no. 1462) ( $\times 3$ ). B, longitudinal section of part of pseudopodetium in the lectotype-specimen. C, vertical section of apothecium in the lectotype-specimen. D, spores in the lectotype-specimen.

no. 1475, no. 12603 in herb. Vainio, Turku (Åbo); same locality, collector and date, Lich. Brasil. Exs. no. 1462, no. 12602 in herb. Vainio. Vainio mentioned six numbers in the original description, all from the same locality, without designating a holotype. The specimen of Lich. Brasil. Exs. no. 1475 in his herbarium has been chosen as the lectotype, and the following description is based upon it.

On sandy humus. No primary thallus developed; the pseudopodetia are directly attached to the substratum, not expanded at the base, and penetrate into it for a short distance only, appearing to die off at their immersed bases. They are upright, stipitate-caespitose, simple or sparingly branched  $\pm$  dichotomously, cylindric-dactylaeform, terete, rounded at the apex, the surface smooth and appearing as if corticate, cream-colored, cinereous-whitish, or pallid ochraceous, matt, not pruinose. The pseudopodetia are minute, 0.5–1.5 mm. long, 0.1–0.3 mm. thick. Where broken across, they are seen to be solid and light-colored internally. Apothecia developed somewhat sparingly on the surface of the tufts and terminal on the stipes; black to brown-blackish,  $\pm$  nitid, smooth, not pruinose, convex and immarginate from the first, finally pulvinate and sometimes dividing into two imperfectly separated convex discs. At maturity they are 0.3–0.6 mm. diam. Careful search under the binocular microscope failed to reveal any cephalodia. Pseu-



dopodetia externally PD —, internally PD — or in places + light persistent yellow.

The pseudopodetia are of simple, primitive, undifferentiated structure, homogeneous, without cortical layer and without any central strand of mechanical or conducting tissue. They are composed throughout of closely interwoven, very thick-walled, gelatinous but distinct, colorless hyphae  $6.5\text{--}9.5\ \mu$  thick running at random in various directions. A few small interstices are present here and there between the hyphae, but the structure is essentially compact. No nubilating granules or inclusions in section. On the outer side of the stipes the hyphae become somewhat compressed and gelatinously degenerated. Symbiotic algae very irregularly distributed in the pseudopodetia, not forming any continuous stratum, occurring in scattered groups buried in the tissue to a depth of  $200\ \mu$  from the surface, in places emerging almost to the surface itself. Algae cystococcoid, pale green, globose,  $6\text{--}10\ \mu$  diam., with colorless thin wall.

The excipulum is a sterilized lateral extension of the hymenium, and grades into the latter without sharp limit; it is reflexed to the under side,  $75\text{--}100\ \mu$  thick, in section faintly brownish, sordid isabelline, or almost colorless (depending on the thickness of the section), not nubilated, composed of flabellate-radiating, gelatinized and conglutinated, thick-walled hyphae, only their fistulose lumina visible, about  $1\ \mu$  wide,  $3\ \mu$  apart. No amphithecium present. No clear distinction between mycelohyphic stratum (central cone) and hypothecium; the whole interior of the apothecium, right up to the base of the hymenium (a depth of about  $500\ \mu$ ) is filled with a homogeneous, compact, pallid brownish to almost colorless, clear, gelatinized tissue, *i.e.* the hypothecium, consisting of completely fused hyphae with only the thread-like lumina visible, these about  $1\ \mu$  wide and intricated in various directions. Scattered spots and patches of a brownish pigment are present in the upper part of the hypothecium, but there are no granular inclusions. In the upper subhymenial  $70\text{--}100\ \mu$  the hyphae become more predominantly vertical, and between them are some cells with wider,  $\pm$  isodiametric or vertically oblong lumina up to  $5\ \mu$  diam. (remains of carpogonia?). Hymenium about  $70\ \mu$  high, rather ill-delimited from the hypothecium, unevenly pallid brownish in section, with vertical streaks of reddish-brown pigment extending through its whole depth; in uppermost  $6\text{--}9\ \mu$  more intensely reddish-brown, and covered on the surface by a structureless, colorless, gelatinous layer  $3\text{--}5\ \mu$  thick. Paraphyses not numerous, conglutinated and only with difficulty separable in water, about  $1.5\ \mu$  thick, vaguely and effusely  $\pm$  brownish-pigmented towards their tips, which are not noticeably thickened. Asci numerous, clavate,  $50\text{--}68 \times 10\text{--}14\ \mu$ , with wall about  $1\ \mu$  thick at sides, gelatinously thickened up to  $10\ \mu$  at the apex. Spores 8 and subbiseriate in ascus, colorless, ellipsoid to ellipsoid-fusiform, soon transversely 1-septate, the walls and septum thin and equal (about  $1\ \mu$ );  $12.0\text{--}13.5 \times 4.5\text{--}5.5\ \mu$ . Hymenium and upper part of hypothecium persistently blue with Iodine.

The other specimen examined, no. 1462, is very similar, but the apothecia are more numerous, and often laterally sessile near the ends of the stipes. The latter are finally sparingly branched, up to 6 mm. long, externally and internally KHO —, internally PD + persistent light yellow. Internal anatomy of apothecia similar to that of the lectotype; the hypothecial tissue however is more colored with unevenly dispersed reddish-brown pigment, more densely in the upper  $100\text{--}170\ \mu$ . Hymenium somewhat lower ( $50\text{--}60\ \mu$ ), unevenly dark brown in the upper  $5\text{--}8\ \mu$  below the gelatinous covering layer. Asci  $44\text{--}57\ \mu$  long. Spores 1-septate, seen only inside the ascus, about  $10 \times 4\ \mu$ .



Reinke (17, pp. 98–99) has described and figured this species, and his observations are quite accurate. However, the pseudopodetia are more closely crowded together than is shown in his fig. 35 (reproduced also in Zahlbruckner's treatment in Engler and Prantl, Nat. Pflanzenfam., VIII, 1926, p. 195), and the apothecia are usually terminal. As Reinke points out, the form of the thallus approaches that of *Toninia*, but it differs anatomically from the latter in its undifferentiated structure and lack of cortex. The holostelidious pseudopodetia, with the symbiotic algae buried in the tissue and not forming leprose or granulate excrescences on the surface, distinguish *Sphaerophoropsis* from *Catillaria* sect. *Hypocaulon* M. Lamb, in which the pseudopodetia are enteropodious in origin. The apothecial structure is similar to that of many species of *Catillaria* and *Eacidia*, so that the inclusion of *Sphaerophoropsis* in the *Lecideaceae*, near *Toninia* and *Catillaria*, seems quite correct. It probably represents a primitive isolated side-branch of the ancestral Catillario-Bacidoid stock.

*Sphaerophoropsis stereocauloides* has been recorded by Räsänen (16, p. 58) from Tierra del Fuego, on sterile material. The specimen has not been seen by the present author.

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#### SUMMARY

The development of upright orthotropic stipes below the apothecia in inoperculate Discomycetous fungi is found in non-lichenized as well as in lichenized groups. Of the former, the Geoglossaceae (Helotiales) are the best examples, and in these the stipe represents an extension of the apothecial tissues. In the latter, the development of stipes below the apothecia may be due to the elongation of either apothecial tissues (true podetia) or thalline tissues (pseudopodetia). True podetia may become secondarily clothed by thalline tissue containing algae and thereby converted into assimilative organs. Fruticose development in the lichenized Discomycetes is characteristic of the families Cladoniaceae



and Stereocaulaceae, both of which are obviously derived from prototypes corresponding to members of the family Lecideaceae. In the Lecideaceae there are at the present day some forms showing this tendency to a greater or less extent, in the form of either true podetia or pseudopodetia. Detailed descriptions of such forms are here given in order to elucidate the probable phylogenetic origins of some of the more highly evolved fruticulose genera belonging to the families Cladoniaceae and Stereocaulaceae.

Descriptions of the following species are given:—*Bacidia* (*Eubacidia*) *buchanani* (Stirt.) Hellb.; *Bacidia* (*Eubacidia*) *robinsonii* (Vain.) M. Lamb; *Bacidia* (*Weitenwebera*) *gomphillacea* (Nyl.) Zahlbr.; *Bacidia* (*Thamnopsis*) *fibrosa* M. Lamb; *Bacidia* (*Thamnopsis*) *stipata* M. Lamb; *Catillaria* (*Biatorina*) *columnatula* (Nyl.) Zahlbr.; *Catillaria* (*Hypocaulon*) *corymbosa* (Hue) M. Lamb; *Sphaerophoropsis* *stereocauloides* Vain.; *Toninia* *bumamma* (Nyl.) Zahlbr.; *Toninia* *conglomerata* (Ach.) Boist.; *Toninia* *ruginosa* (Tuck.) Herre (with f. *nigricans* M. Lamb and var. *andicola* M. Lamb); *Toninia* *squalida* (Schleich. apud Ach.) Mass. (f. *caulescens* (Anzi) M. Lamb). NEW SECTIONS:—*Bacidia* sect. *Thamnopsis* M. Lamb; *Catillaria* sect. *Hypocaulon* M. Lamb. NEW SPECIES: *Bacidia* (*Thamnopsis*) *stipata* M. Lamb. NEW VARIETY: *Toninia* *ruginosa* var. *andicola* M. Lamb. NEW FORM:—*Toninia* *ruginosa* f. *nigricans* M. Lamb. NEW NAME: *Bacidia* (*Thamnopsis*) *fibrosa* M. Lamb (Syn. *Stereocaulon* *laseroni* Dodge, non *Bacidia* *laseroni* Dodge). NEW COMBINATIONS:—*Bacidia* (*Eubacidia*) *robinsonii* (Vain.) M. Lamb (Syn. *Toninia* *Robinsonii* Vain.); *Catillaria* (*Hypocaulon*) *corymbosa* (Hue) M. Lamb (Syn. *Alectoria* *corymbosa* Hue); *Toninia* *squalida* f. *caulescens* (Anzi) M. Lamb (Syn. *Toninia* *caulescens* Anzi).

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