ENTOMOGENOUS SPECIES OF HIRSU-TELLA, TILACHLIDIUM AND SYNNEMATIUM

E. B. MAINS

(WITH 20 FIGURES)

Patouillard (1892) described the genus *Hirsutella* in an article entitled "Une Clavariée entomogène." It was based on a species, *H. entomophila*, described from a specimen on a beetle collected by Lagerheim in Ecuador. Patouillard stated that the fungus has the appearance of an *Isaria*. He, however, placed the genus in the Basidiomycetes and included two other species not on insects, *Pterula setosa* Peck and *Typhula gracilis* Berk. & Desm. The basidia of *H. entomophila* are described as scattered on the clavula, ovoid with 1–2 subulata sterigmata. He states that the spores are hyaline, citriform, $8 \times 6 \mu$ and pointed at the ends.

Speare (1920) concluded that Hirsutella entomophila is not a Basidiomycete but one of the Fungi Imperfecti. He points out that the conidia are produced singly at the tips of the sterigmata and are surrounded by a gelatinous substance, that the conidia of H. entomophila are fusiform, $7.5 \times 1.5 \mu$ and that the description of Patouillard of citriform spores, $8 \times 6 \mu$, apparently included the gelatinous covering. Speare included four additional species in the genus, H. saussurei (Cooke) Speare on Polistes spp., H. floccosa Speare on Peregrinus maidis, H. citriformis Speare on Homoptera and H. fusiformis Speare on a cricket. He published excellent illustrations of the species. Unfortunately most of the specimens studied by Speare have apparently been lost. They are not in the United States Bureau of Entomology where his studies were made or in the Mycological Collections of the United States Bureau of Plant Industry. A specimen of Hirsutella citriformis is in the Farlow Herbarium and it is proposed that it should be recognized as the type of that species.

Petch (1923a) proposed a genus Trichosterigma for similar fungi, including three species, T. clavisporum on a caterpillar, T.

arachnophilum on a spider and T. attenuatum on a Pentatomid. He included the genus in the *Stilbaceae*. Later (1923b) he decided that Speare's conclusions concerning *Hirsutella* were correct and that *Trichosterigma* was synonymous with that genus.

The type specimen of *Hirsutella entomophila* from the Patouillard collection in the Farlow Herbarium has been studied. It consists of a beetle larva covered with a yellowish mycelium (FIG. 3). The synnemata, which arise from all parts of the insect, are simple, slender, terete, slightly narrowing upward, 1-3 mm. long and 0.1-0.2 mm. thick. They are light brown and are finely setose from the phialides. They consist of longitudinal, slightly interwoven hyphae forming a compact bundle. The phialides are scattered to moderately crowded over the synnemata and arise mostly as lateral cells from the outer hyphae or less frequently as terminal cells at the ends of the hyphae. The lower portions of the phialides are narrowly ovoid or ellipsoid, $8-12 \times 4-5 \mu$, abruptly narrowing at the apices into slender sterigmata, $12-20 \mu$ long. Immature phialides without sterigmata occur intermixed with the mature phialides. The conidia are oblong, $5-8 \times 1.5-3 \mu$. Most are covered with a persistent mucus forming a globose droplet $4-7 \mu$ in diameter. Apparently, as Speare has suggested, Patouillard described the droplets when he states that the spores are citriform, $8 \times 6 \mu$. Usually one conidium occurs in the droplet. Less often two are found. Some conidia without the mucus coverings were noted.

In the structure of synnemata and the origin and location of the philalides, *Hirsutella* resembles *Akanthomyces* and *Hymenostilbe* (see Mains **1950**) which have synnemata consisting of a compact bundle of longitudinal hyphae with the philalides occurring as lateral cells or on short lateral branches of the outer hyphae and forming a compact to loose hymenium over the surface of the synemma. This has been well illustrated by Speare for *Hirsutella* (**1920**, Pl. **3**, Figs. 1 and 6). *Akanthomyces* and *Hymenostilbe* have philalides with sterigmata short or lacking and conidia with little or no mucus. In contrast, the species of *Hirsutella* have philalides with inflated lower portions and long slender sterigmata and conidia usually covered with a copious mucus (FIGS. 1–19). In species of *Hirsut-*



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FIGS. 1-4. 1. Hirsutella citriformis, type, synnemata $\times 5$. 2. H. citriformis, type, portion of synnema showing phialides and conidia, $\times 200$. 3. H. entomophila, type, coleopterous larva and synnemata, $\times 8$. 4. H. barberi, Van Dine, Puerto Rico, synnemata, $\times 2$.

tella, only one conidium (FIG. 16) is usually found in the droplet of mucus at the apex of a sterigma. Occasionally two (FIG. 17) or rarely more occur, indicating that more than one conidium is produced by a phialide. Probably usually a conidium is detached before another is formed. When this does not happen the mucous coverings of the conidia coalesce, including them in an enlarged droplet of mucus. Speare has illustrated (**1920**, Pl. 3, Fig. 16) irregular clumps containing a number of conidia probably caused by the droplets of several phialides coalescing. In herbarium specimens the dried mucus is very persistent. Even after long standing in lacto-phenol preparations it remains undissolved and becomes practically an outer layer of the spore wall.

Entomogenous species having slender attenuated phialides and conidia covered with mucus have been reported in the genera *Tilachlidium* and *Synnematium*. The genus *Tilachlidium* differs from *Hirsutella* in several aspects. The type species is *T. pinnatum* Preuss (= *T. brachiatum* (Fr.) Petch) occurring on decaying fungi. This species has subulate phialides which mostly terminate the hyphae of the synnemata. Fewer are produced laterally. A number of conidia are produced from the apices of the phialides. These are irregularly arranged in spherical clumps similar to the condition found in *Cephalosporium*.

Synnematium was described by Speare (1920) based on S. jonesii Speare parasitizing Mezira emarginata and M. lobata in Louisiana. From the description and illustrations given by Speare and from a study of type specimens in the Farlow Herbarium Synnematium differs from Hirsutella and Tilachlidium in several important aspects. The conidia become brown in age. The phialides are not enlarged below as in Hirsutella but are subulate, gradually narrowing to the apex. They terminate the hyphae of the synnema and are not produced as lateral cells along the outer hyphae of the synnema as in Hirsutella. They bear globules containing a number of conidia similar to the condition found in Cephalosporium. A comparison of Speare's figures 1 and 4 of his Plate 4 with figures 1, 3, 4, 11, 12 and 14 of his Plate 3 shows these differences. Synnematium jonesii also produces sclerotia shown by Speare in figures 3, 5 and 6 of his Plate 4.



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FIGS. 5-8. 5. Hirsutella subulata, Berryville, Va., Dickson (W) showing section through bark with larva below and synnemata above, $\times 2$. 6. H. gigantea, FH 6199, synnemata, $\times 8$. 7. H. saussurei, on Polistes rubiginosus, Arkansas, Nest with infected wasps, $\times 0.75$. 8. H. saussurei, on Polistes annularis, Georgia, synnemata, $\times 3$.

This study is based mostly on North American collections in the Farlow Herbarium (FH),¹ the Herbarium of the New York Botanical Garden (NY), the Mycological Collections of the United States Bureau of Plant Industry (W), the Herbarium of the Florida Agricultural Experiment Station (F1), and the Herbarium of the University of Michigan (M).

1. HIRSUTELLA Pat. Rev. Mycol. 14: 69. 1892.

Synnemata cylindric to filiform, terete, usually somewhat attenuated upward, simple or branched, consisting of a compact bundle of more or less parallel, longitudinal, septate hyphae; phialides scattered to crowded over most of the synnema, mostly arising as lateral cells or buds or terminating short lateral branches along the outer hyphae of the synnema, a few developing as terminal cells of the hyphae of the synnema, occasionally developing on hyphae from the mycelial covering of the host, hyaline, inflated below, abruptly or gradually narrowing into long slender sterigmata; conidia oblong, subcylindric, fusoid to cymbiform, one-celled, hyaline, covered by a persistent mucus, single or 2–several occurring in droplets.

Type species: Hirsutella entomophila Pat.

A number of species of *Hirsutella* have been described which lack synnemata. The inclusion of these species in the genus is questionable. In the most generally accepted classification of the *Moniliales* such species belong in the *Moniliaceae* and those with synnemata, typified by *Hirsutella entomophila*, in the *Stilbaceae*. A classification which places little or no importance upon the union of conidiophores in synnemata necessitates an extensive revision of generic concepts and nomenclature in the *Moniliales*. This is not available. *Hirsutella*, therefore, is here treated as a stilbaceous condition of species whose final classifications and valid names will depend on their ascogenous conditions. It is probable that they will be species of *Cordyceps*. However, the ascogenous connections of most of the species of *Hirsutella* are not known.

¹ The writer is indebted to W. Lawrence White, Donald P. Rogers, John A. Stevenson and Erdman West, Curators in charge of the various herbaria, for the loan of specimens.

A. SPECIES ON ORTHOPTERA

HIRSUTELLA FUSIFORMIS Speare, Mycologia 12:70. 1920.

Synnemata simple, terete, slightly attenuated upward, 4–10 mm. long, 0.2 mm. thick, dark brown to nearly black; phialides arising as lateral cells or buds from the outer hyphae of the synnemata, the lower inflated portion fusoid, narrowing above into sterigmata 25– $35 \mu \log$; conidia fusoid, rounded at the ends, 9–10 × 2 μ , covered by a mucus.

On cricket, near Kingston, Jamaica, R. Thaxter (FH 6141).

The species was described by Speare on a cricket from Hawaii. The specimen in the Farlow Herbarium from Jamaica was determined by Petch. Since an examination of this specimen resulted in a failure to find phialides and conidia the description has been partly adapted from the description and illustrations given by Speare (see his Pl 3, Figs. 6–9). An ascogenous connection is not known.

B. SPECIES ON HOMOPTERA

HIRSUTELLA CITRIFORMIS Speare, Mycologia 12:70. 1920. FIGS. 1, 2, 13.

Trichosterigma attenuata Petch, Trans. British Mycol. Soc. 8: 215. 1923.

Mycelia brownish, more or less covering the hosts and attaching them to the substrata; synnemata aerial or procumbent, slender, up to 12 mm. long, terete, 0.2–0.3 mm. thick, sometimes simple, usually branched with short lateral branches, composed of a compact bundle of longitudinal hyphae, pubescent from the phialides; phialides forming a moderately compact layer over the surface of the synnema, mostly arising as lateral cells or less frequently as terminal cells of short lateral branches from the outer hyphae of the synnema, the inflated lower portions subgloboid, ellipsoid or subfusoid, 6–14 × 3–4 μ , narrowing at the apices into slender sterigmata, 30–40 μ long; conidia oblong, cymbiform to subfusoid, 5–8 × 2–2.5 μ , 1–2 in droplets of mucus 5–10 μ in diameter (Fig. 13).

Florida: on *Leptopharsa constricta*, Ft. Pierce, Sept. 10, 1945, N. Stahler (W); on *Corythuca ulmi*, Evinston, A. N. Tissot & J. O. Pepper (Fl 9345).



FIGS. 9-12. 9. Hirsutella radiata, FH 6160, synnemata. 10. Thilachlidium ramosum, type, portion of synnema showing phialides, $\times 400$. 11. Synnematium jonesii, type, FH 4150, synnemata, $\times 9$. 12. S. jonesii, FH 5369, dried agar culture showing synnemata, $\times 5$.

Puerto Rico: on *Bothriocera venosa*, El Yunque Mts., Sept. 29, 1940, L. E. Gregory & L. F. Martorell (W); on *B. venosa*, Dec. 12, 1941, G. N. Wolcott (W).

Hawaii: on *Syphanta acuta*, Oahu, A. T. Speare, type (FH 752); on *S. acuta*, Oahu, A. T. Speare (M).

In establishing this species Speare (1920) cites, as hosts, Fulgoridae from New Zealand and Puerto Rico, *Ricania discalis* from New Zealand, *Perkiniella saccharicida* from Hawaii and *Siphanta acuta* from Hawaii. The specimen in the Herbarium of the University of Michigan on *Siphanta acuta* from Hawaii collected by Speare was in the duplicate collections of the Farlow Herbarium. It is similar to specimen 752 in the Farlow Herbarium, Harvard University (FIGS. 1, 2). Both were collected by Speare. Since specimens do not occur in the collections of the United States Department of Agriculture at Washington, specimen 752 in the Farlow Herbarium should be recognized as the type of *Hirsutella citriformis*. The specimen on *Siphanta* in the Herbarium of the University of Michigan is a paratype.

There is considerable variation in the size of the symemata in this species. The collection on *Leptopharsa constricta* from Florida has symemata 0.3-3.5 mm. long, mostly simple or with a few short branches. In contrast the collection on *Syphanta acuta* from Hawaii has symemata up to 10 mm. long and much branched. These differences in development appear to be correlated with the size of the insect from which they arise.

The collection on *Bothriocera venosa* from the El Yunque Mts. of Puerto Rico differs from others in having many phialides produced at the ends of short lateral branches which arise from the outer hyphae of the symemata. Speare (1920) has illustrated such branches in his Pl. 3, Fig. 15. He considers them to be abnormal developments. There is a tendency to produce such phialide-bearing branches throughout the species although sessile phialides are mostly produced.

Petch (1923a) described a species on a Pentatomid from Hakgala (India) as *Trichosterigma attenuatum*. He (1923b) later decided that it was the same as *Hirsutella citriformis*. It would appear therefore that the species also occurs on Hemiptera. An



FIGS. 13-20. 13. Hirsutella citriformis, phialide and conidium. 14. H. entomophila, phialide and conidium. 15. H. stylophora, phialide and conidium. 16. H. barberi, terminal and lateral phialides and conidium. 17. H. subulata, phialide and conidia. 18. H. gigantea, phialide and conidium. 19. H. saussurei, phialide and conidia. 20. Tilachlidium ramosum, single and grouped phialides and conidia. All × 2000.

association of H. *citriformis* with an ascogenous stage has not been observed.

Hirsutella abietina (v. Höh.) Petch (1931) has been reported on leaf hoppers from Java and India. According to the description by Petch it has phialides with ovoid bases $8-10 \times 5 \mu$ and sterigmata 16μ long and ovoid or subcymbiform conidia, $5-6 \times 2-2.5 \mu$ which are aggregated into clusters of four spores. Petch (1933) has reported the conidial stage of Cordyceps clavulata (Schw.) Ellis & Ev. as Hirsutella lecaniicola (Jaap) Petch. For reasons published elsewhere the writer (1950) has placed this species in the genus Hymenostilbe.

C. SPECIES ON COLEOPTERA

HIRSUTELLA ENTOMOPHILA Pat. Rev. Mycol. 1892: 69. FIGS. 3, 14.

Mycelium yellowish to brown, slight to dense, covering hosts and attaching them to the substrata; synnemata arising from various parts of the host, composed of parallel, longitudinal, closely compacted hyphae, very variable in length, 1–20 mm. long, terete, 0.1–0.2 mm. thick, simple or branched, often procumbent and attached to the substratum and producing short erect secondary branches, brown to light cream color in the younger portions, minutely setose; phialides scattered over the synnema, most arising as lateral cells from the outer hyphae of the synnema, the inflated lower portions ellipsoid to obovoid, $5-10 \times 4-6 \mu$, abruptly narrowing above into slender sterigmata, $12-34 \mu$ long; conidia fusoid to subcylindric, $5-8 \times 1.5-2.5 \mu$, rounded at the ends, 1-2 included in droplets of mucus.

Trinidad: on beetles, Verdant Vale, R. Thaxter, 1912–13 (FH 2926, 2595, 2558); Maraval Valley, R. Thaxter, March 8, 1913 (FH 2596); Port-of-Spain, R. Thaxter, 1912–1913 (FH 622A).

Jamaica: on *Diabrotica* sp. in airplane baggage at Miami, Florida, Milnor, March 7, 1938 (Fl).

Ecuador: Pallatanga, Sept. 1891, de Lagerheim, type (FH).

The collections from Trinidad all developed on adult beetles. The synnemata of most of the specimens are considerably branched and appressed to the leaves on which the beetles were attached. The appressed condition was probably caused by the attachment of the beetles to the undersides of the leaves. In these respects they differ from the type specimen which is on a coleopterous larva and has free simple symmeta. The collection from Jamaica was apparently found in an inspection of baggage at Miami, Florida, on an airplane from Jamaica. *Hirsutella entomophila* has not been found in association with an ascogenous stage.

Hirsutella eleutheratorum (Nees ex Fr.) Petch is a similar species on beetles in Europe and the two species may eventually be found to be the same. Petch (1932b, 1939) has suggested that H. eleutheratorum is the conidial stage of Cordyceps entomorrhiza (Fr.) Link. The connection is questionable (Mains 1951).

Hirsutella stylophora sp. nov. FIG. 15.

Synnemata subulata, 1.5–4.5 cm. longa, 0.2–1.0 mm. crassa, obscure brunnea et pubescentia infra, griseo-brunnea et pulverulenta superne; phialides ellipsoideae, 6–10 × 3–4 μ , sterigmatibus 8–22 μ longis; conidia fusoidea vel obovoidea, 5–8 × 2.5–4 μ , muco tecta.

Ex larva scarabaei, Kent Lake, Mich. A. H. Smith, 7554. Herb. Univ. Mich.

Synnemata arising directly from larvae or as branches of the perithecial clavae, subulate, 1.5–4.5 cm. long, 0.2–1.0 mm. thick, dark brown and pubescent below, grayish brown and slightly pulverulent above; phialides produced on the synnemata and terminal portions and branches of the perithecial clavae, scattered, arising from the outer hyphae of the synnemata, the inflated lower portions ellipsoid, $6-10 \times 3-4 \mu$, narrowing above into slender sterigmata $8-22 \mu$ long; conidia fusoid to obovoid, $5-8 \times 2.5-4 \mu$, covered with a slight mucus.

Michigan: Kent Lake, Aug. 26, 1937, A. H. Smith, 7311 (M); Kent Lake, Oakland Co., Sept. 13, 1937, A. H. Smith, 7554, type (M).

New York: Catlin Lake, Adirondack Mts., Aug. 19, 1934, A. H. Smith, 395 (M); Warrensburg, Sept. 12, 1934, A. H. Smith, 843 (M).

Tennessee: Great Smoky Mts., Nat. Park, Aug. 22, 1938, A. H. Smith, 10400 (M); Indian Creek, Great Smoky Mts. Nat. Park, Aug. 1, 1943, Arthur Stupka (M).

This is the conidial stage of *Cordyceps stylophora* Berk. & Br. The conidial stage has not been previously described. It is desir-

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able to have a name for it since it sometimes occurs alone. Consequently it is described as a new form-species of *Hirsutella*.

The conidial development precedes that of the perithecia oftentimes upon the same fructification. The sporophores start their development in the summer and probably first produce conidia. In some instances perithecial stromata develop forming a cylindrical covering of the central third of the sporophore and the upper accumunate portion bears conidia. Sometimes conidia-bearing branches may be produced below the stromata. This species appears to be unique in that asci and ascospores mature after overwintering (Mains, 1941). This species of *Hirsutella* does not produce as conspicuous a covering of mucus over the conidia as in most of the species of the genus. The long sterigmata are characteristic of *Hirsutella*.

Petch (1937) has suggested that the conidial stage of *Cordyceps* variabilis on larvae of Coleoptera in North America is a *Hirsutella*.

D. SPECIES ON LEPIDOPTERA

HIRSUTELLA BARBERI (Giard) Petch, Trans. British Mycol. Soc. 21: 58. 1937. FIGS. 4, 16.

Isaria barberi Giard, Compt. Rend. Soc. Biol. 46: 824. 1894.

Larvae covered with a slight mycelium; synnemata arising from various parts of the host, slender, terete, slightly attenuated upward, up to 30 mm. long, 0.1–0.4 mm. thick, grayish brown, composed of closely compacted parallel longitudinal, 2–4 μ wide hyphae; phialides widely separated, arising as lateral cells or lateral buds or occasionally as terminal cells of the outer hyphae of the synnemata or from the mycelium, the lower portions short cylindric, obovoid or hemispheric, 4.5–10 × 3–4 μ , narrowed above into slender sterigmata 4–9 μ long; conidia ellipsoid to obovoid, 4–6 × 3–4.5 μ , contained in a small droplet of mucus or sometimes with slight or no evident covering of mucus.

Cuba: on larva of *Diatraea saccharalis*, April 22, 1929, H. K. Plank (W).

Puerto Rico: on larva of *Diatraea saccharalis*, March 26, 1913, J. A. Johnston, Lloyd Mycol. Herb. 37314 (W); on larvae of *Diatraea saccharalis*, Guanica, 1913, Van Dine (W); larva of *Diatraea saccharalis*, Guanica, Feb. 1940, L. F. Martorell (W).

Jamaica: on sugar cane borer, A. H. Ritchie, Lloyd Mycol. Herb. 42604 (W).

This species appears to be a fairly common parasite of the sugarcane borer, *Diatraea saccharalis* in the West Indies. Miss Charles (1941b) has reported it on *D. lineolata*. It has also been reported for the Barbados, Trinidad, Dominican Republic, and Louisiana (Petch, 1937; Charles, 1941a).

Hirsutella barberi was described by Giard (1894) from specimens on *Diatraea saccharalis* collected by C. A. Barber in St. Christopher and the Barbados of the West Indies. He also states that the fungus had been seen on Antigua. Massee (1895) described a fungus in the ascogenous stage which he states occurred on specimens at Kew sent by John R. Bovell labelled *Cordyceps bovellii*. On the assumption that *Isaria barberi* was the conidial stage he employed the name *Cordyceps barberi*. Lloyd (1916) and Petch (1937) state that they were unable to find collections in the Kew Herbarium to which Massee's description applies. The application of the name *Cordyceps barberi* is therefore doubtful.

HIRSUTELLA SUBULATA Petch, The Naturalist 1932: 48. FIGS. 5, 17.

Larvae covered with a slight mycelium; synnemata caespitose, slender, terete, slightly attenuated upward (5)-15-50 mm. long, 0.1–0.3 mm. thick, light brown to gray, simple or furcate, composed of closely bound, parallel, longitudinal hyphae 2.5–3.0 μ wide; phialides scattered, arising as lateral cells or buds of the cells of the outer hyphae of the synnemata or from the hyphae of the mycelium, the lower portions narrowly ellipsoid, broadly obovoid or conoid, 4–8(–10) × 3–5 μ , abruptly narrowing above into slender sterigmata 6–12 μ long; conidia narrowly ellipsoid, often slightly asymmetric, more convex on one side than the opposite, 4–8 × 1.5–2.5 μ , 1 or 2 in spherical droplets of mucus 6–7 μ in diameter.

Delaware: on larvae of *Carpocapsa pomonella*, F. S. Zimmerman, Nov. 1930 (W).

District of Columbia: on codling moth, Washington, Riley (FH 6241).

Indiana: on *Carpocapsa pomonella*, Vincennes, 1927, Alvah Peterson (W).

Maine: on larvae of Apatela dactylina, Kittery Pt., Aug. 1891, R. Thaxter (M).

New Jersey: on codling moth, no location or date given, R. Thaxter? (M).

New York: on larva of *Aegeria pyri* in apple bark, Flatbush, Long Island, Sept. 23, 1890, J. L. Zabriskie (FH 6230).

Ohio: on Pyrausta nubilalis, 1935, Armond (W).

Virginia: on codling moth larvae, Rosemont Orchard, Berryville, 8-6-40, Dickson (W); on *Carpocapsa pomonella*, 5 mi. N. W. Winchester, Sept. 9, 1940, W. S. Hough (W); on *Conopia (Synnanthedon) pyri* on *Pyrus malus*, Maychild Orchard, Mt. Jackson, May 18, 1941 (W); on *Carpocapsa pomonella*, Byrd Orchard, Berryville, 5-1-40, Hough (W); on *Carpocapsa pomonella*, Berryville, May 20, 1940, V. K. Charles (W).

Petch (1932b) described the species from a specimen in the Kew Herbarium on a caterpillar from England which had been reported by Berkeley and Broome (1881) as *Isaria floccosa* Fr. Petch has questioned the determination and has also pointed out that the combination *Hirsutella floccosa* has been employed by Speare for another fungus. Petch described the conidia as cymbiform, $2.5 \times 1 \mu$. In a later publication he (1937) discussed two collections from the Farlow Herbarium, nos. 6230 and 6241, and gave the measurements of the conidia as $4-6 \times 1.5-2 \mu$ and $4 \times 1.5 \mu$. Miss Wakefield has kindly had the type specimens in the Kew Herbarium examined and states that as far as can be determined from the few conidia seen they measure $5-6 \times 1.5-2 \mu$. The measurements given by Petch in his original description apparently are erroneous.

In the United States this species sometimes becomes an important parasite of codling moth, *Carpocapsa pomonella*. Miss Charles (1941b) has reported that as high as 40% of the larvae of codling moths were killed in an apple orchard at Berryville, Virginia, in 1940. She found that the fungus grew well on corn meal agar and Thaxter's potato-dextrose agar but did not produce synnemata. Synnemata were produced on infected larvae after being kept at a cool temperature for ten days.

The report of the species for the European corn borer, *Pyrausta* nubilalis, is based on a specimen determined as *Hirsutella* sp. in the Mycological Collections of the Bureau of Plant Industry. It has short symmeta bearing the characteristic phialides with long sterigma and conidia in droplets of mucus of *H. subulata*. With the specimen there is a note stating "Larva showing fungus in incubator room 1920 Parkwood Ave., Toledo, Ohio. Larva collected in the vicinity of Toledo, Ohio, fall of 1935. Communicated by Dr. Armond."

Hirsutella subulata has not been found associated with an ascogenous stage. It is very similar to H. barberi. It has a different distribution and the conidia tend to be asymmetric. The relationship of the species probably cannot be determined until the ascogenous stages are known.

HIRSUTELLA GIGANTEA Petch, Trans. British Mycol. Soc. 21: 48. 1937. FIGS. 6, 18.

Synnemata several, simple or branched from near the base, terete, slightly attenuated upward, 2–10 cm. long, 0.5–1.0 mm. thick, olivaceous below, brown above, pruinose to minutely setose, composed of closely compacted parallel longitudinal, 2.5–3 μ wide hyphae; phialides scattered to crowded, developing as lateral cells from the outer hyphae of the synnemata, the lower portions oblong to ellipsoid, 10–18 × 5–8 μ , abruptly narrowing into slender sterigmata 10–20 μ long; conidia oblong, slightly narrowing at each end, 5–8 × 2–2.5 μ , 1–2 or rarely more in droplets of mucus 6–16 μ in diameter.

Connecticut: New Hartford, 1888-1889, R. Thaxter (FH).

Maine: on cocoon of Apatela, York, R. Thaxter (FH 6199).

New Hampshire: on pupa of *Apatela americana*, above Diana's Bath, Intervale, July 1901, R. Thaxter, type (FH 6126).

A specimen of a *Hirsutella* on the spruce budworm, *Choristoneura fumiferana*, received from Donald M. MacLeod of the Forest Insect Laboratory, Sault Ste. Marie, Ontario may be this species. The synnemata are very short, not more than 5 mm. long. Their size may be due to immaturity and the small larvae on which they occur. The phialides and conidia agree with those of *H. gigantea*.

Petch (1937) has suggested that *H. gigantea* may be the conidial stage of *Cordyceps elongata* Petch. The stages have not been found associated. This species has larger, more cylindric phialides than

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H. barberi and H. subulata. The synnemata according to the description given by Petch are much longer. This may be correlated with the larger larvae from which they developed. Hirsutella exoleta (Fr.) Petch on lepidopterous pupae from England has brownish black synnemata. The phialides and conidia do not differ greatly from those of H. gigantea. Petch (1939) describes the phialides as having inflated flask-shaped bases $12-18 \times 5 \mu$ and sterigmata up to 20μ and cymbiform conidia $9 \times 2.5 \mu$.

Hirsutella clavispora Petch (1923b, 1924) was described on a caterpillar from Peradenija, Ceylon. The conidia are given as cylindric or clavate, $4-8 \times 1-1.5 \mu$, with a mucus, and the sterigmata as very short, $5-9 \mu$. Petch (1932a) has suggested that this is the conidial stage of Cordyceps tuberculata (Lebert) Maire. The conidia of that species do not have a mucus and are in chains (Mains, 1950). Hirsutella ramosa Mains (1949) has also been described on remains of a lepidopterous insect from Nova Scotia. A restudy of this collection has resulted in the conclusion that it is a Tilachlidium.

E. SPECIES ON DIPTERA

HIRSUTELLA RADIATA Petch, Trans. British Mycol. Soc. 19: 184. 1934. FIG. 9.

Synnemata simple or branched, erect or appressed to the substrata, very slender, terete, 4–20 mm. long, 70 μ thick, dark brown, cinereous toward the tips; phialides conoid or cylindric below, $5-18 \times 2-4 \mu$ narrowing into slender sterigmata 6–14 μ long; conidia cymbiform to ovoid, 6–9 × 2–4 μ , agglutinated into ovoid spore-clusters 9–11 × 6–7 μ .

North Carolina: on Diptera, Cranberry, Aug. 1887, R. Thaxter (FH 6156, 6160).

British Guiana: on flies, Essequibo, Sept. 10, 1916, C. B. Williams (FH 722).

There are three specimens in the Farlow Herbarium determined by Petch. Specimen No. 722 is fragmentary. Petch based his description of the species on specimens collected by C. B. Williams on Sept. 11, 1916. Phialides and conidia were not found on the two specimens from North Carolina. The description above is mostly adapted from that given by Petch. His figure shows a very slender synnema which has four long branches from its apex, one of which has secondary branches from its upper portion. Petch does not state that the conidia occur in a droplet of mucus but occurrence as a spore cluster indicates it. Specimen 6160 in the Farlow Herbarium has erect simple slender synnemata up to 20 mm. long. Specimen 6156 has slender appressed synnemata apparently due to the attachment of the host to the underside of a leaf. The ascogenous stage is unknown.

Hirsutella dipterigena Petch (1937) has been described on flies from England. According to the description, it has smaller phialides and longer sterigmata than H. radiata.

F. SPECIES ON HYMENOPTERA

HIRSUTELLA SAUSSUREI sensu Speare, Mycologia 12: 69. 1920. FIGS. 7, 8, 19.

Isaria crinita Lloyd, Mycol. Writings 6: 919. 1920.

Synnemata aerial or procumbent and appressed to the substratum, arising from various parts of the body and appendages of the host, slender, terete, somewhat attenuated upward, very variable in length, 1–17 mm. long, 0.1–0.3 mm. thick, light brown, composed of closely compacted, parallel, longitudinal, 2–4 μ wide hyphae; phialides scattered to moderately crowded, arising as lateral cells or buds from the outer hyphae of the synnema or as terminal cells of short lateral branches, the lower portions cylindric, obovoid or ellipsoid, 7–16 × 3–6 μ , attenuated above into slender sterigmata 10–40 μ long; conidia oblong to cymbiform, 5–8(–10) × 1.5–2.2 μ , 1 or more in droplets of mucus 5–10 μ in diameter.

Arkansas: on *Polistes rubiginosus*, 1950 from Sgt. James Gentry (M).

Florida: on *Vespula* sp. Ocala Nat'l Forest, Marion Co., 6– 11–1938, T. H. Hubbell (M); on wasp, T. Van Hyning, Lloyd Mycol. Col. 42608 (W); on *Polistes annularis*, Homestead, 1– 15–26, Mrs. C. H. Eigenman (loaned by J. Bequaert, Mus. Comp. Zoo. Harvard).

Georgia: on *Polistes annularis*, Savannah, June 6, 1949, Joe Carter (U. S. Bur. Ent. Pl. Quar. Lot 49-8624).

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North Carolina: on Ichneumonfly, Cranberry, 1887, R. Thaxter (FH 6261B).

Honduras: on wasp, Mt. Vyuca, Zamorave, alt. 5800 ft., July 12, 1948, T. H. Hubbell (M).

Panama: on wasps, Changuinola, June, 1921 (FH 6166 and NY).

Puerto Rico: on social wasp (Vespidae), San Sebastian farm, Nov. 14, 1935, M. R. Smith (W); on wasp, Mayaguez, Sept. 13, 1937, George A. Pfaffman, 7027 (W); on *Mischocyttarus cubensis*, Lares, Dec. 12, 1941, L. F. Martorell (W).

In addition to the above there are two specimens on wasps in the Mycological Collections of the U. S. Bureau of Plant Industry which were received from New Orleans, Louisiana. It is stated that the specimens were intercepted in shipments from Mexico and probably from Costa Rica. Speare (1920) also reports the species from California. The report of the species on *Bothriocera* sp. from Virginia by Miss Charles (1941a) is doubtful. The host (Homoptera) would indicate that the fungus probably is *Hirsutella citriformis*. From the records available *H. saussurei* appears to develop mostly on the social wasps. The report on an Ichneumonfly from North Carolina appears to be the only exception.

Most of the specimens of *Hirsutella saussurei* are single infected wasps. This probably indicates that generally infected individuals die away from the nest. One collection has been seen of a nest with number of infected wasps. This was brought to the writers attention by George W. Byers of the Museum of Zoology of the University of Michigan. Through him a loan of the collection was obtained from Sgt. James Gentry of the Fourth Army Area Laboratory of Ft. Sam Houston, Texas. The nest, which had been collected in Arkansas, had twelve parasitized wasps clinging to it (FIG. 7). This, however, may represent an unusual condition since the nest had been sprayed with DDT and death of the insects on the nest may have been caused by the insecticide rather than by the fungus.

Fungous parasites of wasps were noted and described as early as the first part of the 18th century. Since the descriptions in the early literature did not include microscope characters it is difficult to determine the species involved. It seems probable that Felton (1765) illustrated *H. saussurei* when he described a species of wasp, *Vespa crinita*, from a parasitized specimen of wasp from Jamaica. The symemata of the fungus are described as hairs arising from various parts of the insect. In 1817 Ditmar described *Isaria sphecophila* on a species of *Vespa* from Germany. His illustrations and description suggest a species of *Hirsutella*.

Saussure (1858) in connection with his discussion of diseases of social wasps illustrated and described a wasp (Pl. IX, Fig. 5) with a number of what appear to be linear synnemata arising from various parts of the thorax and abdomen. Saussure states that during the time which he spent in the tropics he found only one "quêpe vegetante" which was from Jamaica. For this he gives a description including perithecia and asci which was supplied by Lebert who placed it in a new genus and species Polistophtora antillarum. What connection the illustration cited by Saussure has with this species is difficult to determine. Saussure states, "l'espèce se trouva identique a celle qu'on voit figurée pl. XI, fig. 5 (Polistes americanus), mais j'eus le bonheur de rencontrer le cryptogame arrivé sou étât de parfaite maturité." Lebert's (1858) discussion and illustrations of the species do not include a condition such as illustrated by Saussure in his Plate IX, Fig. 5 but are of a fungus bearing perithecia, evidently the specimens to which Saussure refers as in "étât de parfaite maturité." It would appear that the figure 5 of Plate IX was not drawn from a collection by Saussure and the source of the specimen on which it is based is apparently unknown. However, Cooke (1892) proposed the name Isaria saussurei pro tem. based on this illustration. Speare (1920) made the combination Hirsutella saussurei (Cooke) Speare and gave a description and illustrations based on specimens on Polistes sp. from the British West Indies, North Carolina, California and Hawaii. Since Isaria saussurei was published by Cooke as a provisional name which was based on an illustration taken from a specimen of unknown origin the validity of the name is very questionable. The only other name which might be applicable is Isaria sphecophila Ditm. Speare suggested that Ditmar's fungus was a Hirsutella. As far as has been determined a Hirsutella is unknown on wasps in Europe. Petch (1937) states that "the available specimens in herbaria which would otherwise be referred to *Isaria sphecocephala* [error for *sphecophila*] are *Hymenostilbe*" and he published the combination *Hymenostilbe sphecophila* (Ditm.) Petch. The illustrations of Ditmar so strongly suggests a species of *Hirsutella* that the writer is reluctant to accept this conclusion. The setose condition strongly suggests the occurrence of the long sterigmata of the phialides of *Hirsutella* and the small globules between them the mucous droplets which commonly occur. However, it will be necessary to find specimens of *Hirsutella* on wasps in Europe to support this view. Under the circumstances, it does not seem desirable to propose a new name for the fungus. Therefore *Hirsutella saussurei* is employed in the sense used by Speare.

Petch (1934) has reported that three symemata of *Hirsutella* saussurei were found associated with perithecia bearing clavae of *Cordyceps humberti* on a Hymenopteron from Sarawak. *C. humberti* was illustrated by Saussure, Pl. V, Fig. 9, from a wasp from tropical Africa. It has not been reported from North America. *Cordyceps sphecocephala* has been reported a number of times on wasps for North America. According to Petch its conidial stage is *Hymenostilbe sphecophila*. Only one collection of this *Hymenostilbe* from North America (Puerto Rico) has been seen by the writer (1950) and it is not associated with an ascogenous stage. More information is needed before the relationship of *Hirsutella* saussurei can be considered as satisfactorily established.

Hirsutella formicarum was described by Petch (1934) on ants from British Guiana and Ceylon. The phialides are given as ovoid bases 8–11 × 4–6 μ and sterigmata 20 μ long and the conidia as narrowly cymbiform, 9–11 × 2 μ . It occurred associated with the perithecial stage of *Cordyceps unilateralis* (Tul.) Sacc. Kobayasi (1941) has reported *H. formicarum* from Japan. He describes the phialides with cylindric, ellipsoid or fusoid bases 8.5–17.5 × 2.8–4.2 μ and sterigmata 7–14 μ long. The conidia are given as ovoid, ellipsoid or fusoid, 3–4.2 × 1.2 μ . It is very doubtful that this is *H. formicarum* if Petch's measurements of conidia are correct. There is some doubt concerning this since, when he described *H. formicarum*, he referred to an earlier publication (1924) in which he described the conidia of the Ceylon specimens as $3-5 \times 1 \mu$. Petch (1937), in a discussion of *Cordyceps formicivora* (Schroet.) Sacc. in which he concluded it was synonymous with *C. unilateralis*, has stated that a specimen (6154) in the Farlow Herbarium bears *Hirsutella* conidiophores accompanying perithecial clavae. This specimen has been examined. The perithecial clavae are immature. They are accompanied by two short synnemata which bear subulate phialides and ellipsoid or ovoid conidia which are $2-2.5 \times 1-1.5 \mu$ with a slight mucus and which adhere in large numbers in groups 14-60 μ in diameter. It is certainly distinct from *Hirsutella* formicarum and does not appear to be a species of *Hirsutella*. From the meager material it is not possible to definitely place it. It hardly seems possible that these are all conidial stages of *Cordyceps unilateralis*.

Hirsutella liberiana Mains (1949), described on an ant from Liberia, has cylindric, narrow conidia, $3-4 \times 0.7-1.0 \mu$. It was associated with *Torrubiella liberiana* Mains.

SPECIES OF DOUBTFUL POSITION IN HIRSUTELLA

Hirsutella neo-volkiana Kobayasi (1941) on Coleoptera in Japan and H. volkiana Kobayasi (1941) on Coleoptera in Brazil have subulate phialides terminating hyphae and forming a dense palisade layer. They are not species of Hirsutella as the genus is here interpreted. Hirsutella arachnophila Petch on spiders from India has sterigmata only 2μ long and no mention is made of a mucus covering the conidia according to the description given by Petch (1923a, 1924).

The following species have been described in *Hirsutella* without synnemata and probably should be placed in the Moniliaceae: *Hirsutella versicolor* Petch (1932a) and *H. strigosa* Petch (1939) on leafhoppers from Ceylon; *H. acridiorum* Petch (1932c) on a grasshopper from Great Britain; *H. aphidis* Petch (1936) on aphis from England; *H. nodulosa* Petch (1926) on *Zeuzera coffeae* from India; *H. thompsonii* F. E. Fisher (1950) on *Phyllocoptruta olei*vora from Florida. Speare (1920) in describing *H. floccosa* on *Peregrinis maidis* from Jamaica stated that it is "somewhat unlike" the other species of *Hirsutella* in that "the synnemata are merely wart-like outgrowths arising from an external cotton-like subiculum." Petch (1937) has reported it on a leafhopper from North Carolina, describing phialides only on the mycelium. Fran. E. Fisher (1950) has described *H. besseyi* on *Lepidosaphes beckii* from Florida stating that synnemata, for which a description is not given, are infrequently produced. Specimens seen by the writer lacked synnemata. *Hirsutella verticillioides* Charles (1937) on *Leptopharsam heveae* from Brazil lacks synnemata and is considered by Petch (1939) to be the same as *Verticillium fuliginosum* Petch.

2. TILACHLIDIUM Preuss, Linnaea 24: 126. 1851.

Synnemata terete, simple to much branched, cylindric, narrowing toward the apices, consisting of bundles of parallel longitudinal usually closely compacted hyphae; phialides scattered, hyaline, subulate, gradually narrowing to acuminate apices, usually terminating hyphae of the synnema, or as lateral cells of the hyphae, single or sometimes in groups of two or three; conidia hyaline, covered with a mucus, agglutinating into large spherical or irregular clumps.

Type species Tilachlidium pinnatum Preuss.

Tilachlidium was described by Preuss (1851) based on T. pinnatum reported on dried fungi, chiefly Agaricus galericulatus. He described a stilbaceous fungus having simple or branched synnemata bearing phialides which produced obovoid-oblong spores in globose, white, shining, glutinous globules. The type of this species has not been available for study. Petch (1937) has concluded that Isaria brachiata Fr. is the same fungus. Three specimens of Isaria brachiata, Farlow Herbarium 759, Univ. Mich. Herb. Lowe Fl. 305, and Syd. Mycoth. Germ. 1048, have been available for study. It has been assumed that these are representative of the type species. The conclusions of Petch appear to be justified.

Most of the species which have been described in *Tilachlidium* are saprophytic on various substrata. Petch (1931) has described an entomogenous species T. *larvarum* on a lepidopterous insect. The subulate phialides and the type of clumping of the conidia of *Hirsutella ramosa* on a lepidopterous larva place that species in Tilachlidium.

Tilachlidium ramosum Mains, comb. nov. FIG. 20. Hirsutella ramosa Mains, Mycologia 41: 308. 1949.

Symmemata terete, composed of parallel longitudinal hyphae irregularly branched, the branches at right angles or slightly oblique often bearing secondary branches, up to 8 mm. long, 52–140 μ thick at the base slightly narrowing to the apices, the main stem light yellow below, the branches and upper part of the main stem white; phialides subulate, gradually narrowing to acuminate apices, 19.3–36.4 μ long, 2.1–3.2 μ wide at the bases, scattered on the upper portions of the main stem and branches, commonly terminating the hyphae of the symmemata, less frequently lateral along the outer hyphae; conidia oblong, 3.2–5.5 × 1–1.4 μ , covered with a slight mucus adhering to form spherical clumps of several spores.

On fragments of a lepidopterous larva on a mossy log, Salmon River, Nova Scotia, Sept. 7, 1931, L. E. Wehmeyer, 1474, type (M).

In describing this species as a *Hirsutella* it was noted that it differed from other species in the genus in having narrow subulate phialides. The clumps of conidia which contain a number of adhering spores do not have the thick covering of mucus as in *Hirsutella* and disintegrate fairly easily.

According to the description given by Petch, *Tilachlidium larvarum* on a microlepidopteron from Ceylon has symemata up to 1 mm. long. The phialides are simple, conical to slightly flaskedshaped, attenuated gradually upward and 14–22 × 2 μ . The conidia are narrow-oval with rounded ends, 4–6 × 2–2.5 μ , and form mucilaginous heads up to 14 μ in diameter.

3. SYNNEMATIUM Speare, Mycologia 12:74. 1920.

Synnemata simple or branched, terete, at first white, becoming brownish, consisting of parallel longitudinal hyphae; phialides subulate, terminating the hyphae, mostly fasciculate at the apices of the synnemata, some scattered laterally on the upper portions; conidia one-celled, hyaline to pale brown, light brown in mass, covered with a mucus, agglutinating into spherical droplets of several spores at the apices of the phialides; sclerotia spherical, at first white, becoming brown, composed of thick-walled cells.

Type species Synnematium jonesii Speare.

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SYNNEMATIUM JONESII Speare, Mycologia 12:74. 1920. FIGS. 11, 12.

Synnemata mostly dendroid-branched, occasionally simple, terete, 100-200 µ thick, 2-3 mm. long, in agar cultures up to 20 mm. long, at first white becoming brown, especially in the lower portions of the synnemata, consisting of parallel longitudinal hyphae which are hyaline at first, becoming light brown; phialides subulate, gradually narrowing to acuminate apices, $40-50 \mu \log_{10} 2.5-4 \mu$ thick below, terminating the hyphae of the synnemata, mostly fasiculate at the apices of the synnemata, some scattered on the upper portions of synnemata; conidia oblong, somewhat narrowed but rounded at the ends, 8–10 \times 2.5–4 μ , hyaline or very pale brown, produced successively from apices of phialides in a mucus, agglutinating to form spherical brownish droplets containing several spores on the scattered phialides, the droplets of terminal phialides cohering to form large spherical brownish masses $80-250 \mu$ in diameter, containing many spores; sclerotia spherical, 90–350 μ in diameter, at first white, becoming brown, consisting of thick-walled cells.

California: on *Harpalus* sp., Auburn, Aug. 8, 1890, Atkinson (FH 694).

District of Columbia: on *Pardomis* sp. from cedar wood, W. H. Weston, Jr. (FH 6262).

Louisiana: on *Mezira*, Baton Rouge, T. H. Jones, type (FH 4150); also agar cultures (FH 5263, 5369).

Maine: on *Philonthus* sp., Kittery Point, Sept. 1893, R. Thaxter (FH 6147).

Costa Rica: on large leafhopper, J. R. Johnston (FH 6143).

Under number 4150 in the Farlow Herbarium there are several dried agar cultures and one specimen on an insect. In addition there are several dried agar cultures under numbers 5263 and 5369 with the statement that they are from the type culture of Speare. Since as far as has been determined other collections of Speare do not exist these should be recognized as type collections and the specimen on *Mezira* as the type. It agrees with the illustration given by Speare, Pl. 5, Fig. 5, except that the synnemata are darker in color than indicated by the photograph. According to Speare's statement, his illustration represents a young condition and later in their development the synnemata are brown. The synnemata are short, 2–3 mm., and are dendroid-branched. The synnemata have

the structure shown by Speare in his Pl. 4, Fig. 1. As is well illustrated by Speare, the phialides are subulate and terminate the hyphae of the synnema, Pl. 4, Figs. 1 and 4. A few of the hyphae end before reaching the apex of the synnema and these produce scattered phialides mostly in the upper portions of the synnema. These bear small spherical heads of several conidia in a droplet of mucus (Speare, Pl. 4, Fig. 10). The number of conidia and the irregular arrangement in the droplet resemble that in Cephalo*sporium*. This differs from the condition found in *Hirsutella* where usually only one conidium is found in the mucus droplet. Less frequently two or more parallel conidia occur. Droplets containing a number of conidia similar to those usually produced in Synnematium occur in Hirsutella when droplets of adjacent phialides coalesce (Speare, Pl. 3, Fig. 16). Most of the hyphae of synnemata of S. jonesii on the insect do not terminate until they reach the ends of the synnemata and there they form fascicles of phialides. The droplets of spores produced by them coalesce to form large spherical aggregates which give a capitate appearance to the synnemata (Speare, Pl. 4, Fig. 1). Sclerotia were not observed on the insect.

Speare states that he was able to grow the fungus readily on potato agar. The dried cultures show certain differences from the fungus on the insect. The synnemata are longer, up to 20 mm. The hyphae of the synnemata are not as compactly bound together and more frequently terminate laterally on the synnema. As a result there are fewer terminal phialides and most synnemata do not produce the large heads of aggregated droplets. This condition is shown by Speare for synnemata arising from sclerotia, Pl. 4, Fig. 5. Many sclerotia occur in the dried cultures.

Other specimens in the Farlow Herbarium have been determined as Synnematium jonesii by Petch (1937) who has published a discussion concerning them. Numbers 6147 and 6262 have short synnemata and are without sclerotia, while numbers 694 and 6143 have sclerotia and no synnema. Petch also reports collections on Pororeus simulans from the Philippines, on Basilides bipinnis from Sierra Leone, on Promecotheca bicolor from Fiji and on Helopeltis sp. from the Belgian Congo, all having sclerotia and no synnema. Whether these collections are all of one species is somewhat uncertain. If so, the species has a wide host range infecting insects of several orders.

Kobayasi (1941) has described Synnematium graptopsaltriae, on Graptopsaltria nigrofuscata (Homoptera) in Japan. In the separation of the species from S. jonesii Kobayasi places emphasis on the length of the synnemata, "several centimeters," the lack of sclerotia and the non-fasciculated terminal phialides of S. graptopsaltriae. These are all variations which occur in S. jonesii. His illustration indicates that the branching is different. The branches develop at right angles to the main stem instead of occurring as irregular, somewhat dichotomous divisions of the synnema.

The Herbarium and the Department of Botany, University of Michigan, Ann Arbor, Michigan

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