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Two species of Pyrenomycetes associated with resinous exudates of conifers are illustrated and described in the genus *Strigopodia* Bat.; the phragmoconidial and phialidic states are recognized as belonging to the form genera *Hormisciella* Bat. and *Capnophialophora* Hughes respectively.

The type species of Strigopodia, S. piceae Bat., is included as S. resinae (Sacc. & Bres.) n. comb., syn. Capnodium resinae Sacc. & Bres. In its mycelial state it was described as Racodium resinae Fr. β piceum Pers. Its phragmoconidial state is identified with Helminthosporium resinaceum M. C. Cooke, syn. H. resinae Bres., and Clasterosporium resinae Rilstone. This species occurs in Eastern United States of America (Maine, New Hampshire) and in Europe.

A new species S. batistae is recorded from Western United States of America (Calif., Wash., Idaho) and Western Canada (B.C.), and its phragmoconidial state is identified with Helminthosporium pseudotsugae W. B. Cooke.

The affinities of *Strigopodia* are with the capnodiaceous fungi rather than with the Parodiopsidaceae.

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Introduction

In North America and Europe a number of hyphomycetous fungi have been described on or associated with resinous exudates of coniferous trees. This is a peculiar ecological niche and so far as I am aware there has been little taxonomic work on the hyphomycetes that can thrive on such a substrate.

About a dozen species of hyphomycetes have been described on coniferous resin with the epithets resinae, resinacea, resinarium, or resinicola in Clasterosporium, Gyroceras, Hormodendron, Helminthosporium, Racodium, Stilbum, and Torula; no doubt other species have been described on resin with other epithets. Two of the earliest names applied to hyphomycetes on resin are Racodium resinae Fr., and Racodium resinae Fr. β piceum Persoon (1822). Racodium resinae Fr., which will be dealt with in another publication, is quite a different fungus from Persoon's β piceum.

R. resinae β *piceum* has the appearance of a thick, dense, sooty mold, being composed of a compact subiculum of wide, brown to dark olivaceous brown hyphae. According to Persoon's description, this infraspecific taxon was based on mycelium only but examination of the presumed type collection in Persoon's herbarium in Herb. L has shown the presence of phragmospores. I collected this fungus at Devil's Bridge,

Cardiganshire, Wales, in 1954 and 1955 with perithecia, phragmospores, and phialides which are being referred to the genera *Strigopodia* Bat., *Hormisciella* Bat., and *Capnophialophora* Hughes respectively. Since that time, 26 collections associated with coniferous resin in North America and Europe have been seen and two closely related species can be differentiated.

The first species occurs in Maine and New Hampshire (U.S.A.) in Eastern North America, and in Europe; it is illustrated (Figs. 1–3) and described as *Strigopodia resinae* (Sacc. & Bres.) n. comb. (\equiv *Capnodium resinae* Sacc. & Bres., =S. piceae Bat., the type species of *Strigopodia*). The second species is known from California, Washington, and Idaho (U.S.A.) and British Columbia (Canada) in Western North America; this is illustrated (Figs. 4–6) and described as *S. batistae* n. sp. The *Hormisciella* phragmoconidial state of *S. resinae* has been described twice in *Helminthosporium* and once in *Clasterosporium* and that of *S. batistae* once in *Helminthosporium*.

No cultural work has been carried out to prove the genetic connection between perithecia, phragmoconidia, and phialides in the two species of *Strigopodia*. However, their constant association and the fact that in each species the three states have been seen attached to the same kind of mycelium is strong evidence. Furthermore, in both species phialides on hyphae are indistinguishable from those produced on ascospores and phragmoconidia.

¹Contribution No. 671, Plant Research Institute.



FIG. 1. Strigopodia resinae from DAOM 48946. A, mature and young ascospores. B, young and mature Hormisciella phragmoconidia. C, ascospore with Capnophialophora phialides. D, hyphae bearing Capnophialophora phialides. \times 500.

Taxonomy

- Strigopodia resinae (Sacc. & Bres.) comb. nov.
 - ≡ Capnodium resinae Sacc. & Bres. in Bres. & Sacc., Malpighia, 11: 322. 1897 (as 'Capnodium (Limacinia) resinae').
 - ≡Limacinia resinae (Sacc. & Bres.) Sacc. & Bres. in Sacc., Sylloge Fungorum, 14: 475. 1899 (as 'Limacinia resinae Sacc. et Bres.').
 - ≡ Phragmocapnias resinae (Sacc. & Bres.) Bat.
 & Cif., Saccardoa, 2: 182. 1963 (as '(Sacc. & Bres.) Theiss. & Syd., Ann. Mycol., XV, p. 480. 1917').
- = Strigopodia piceae Bat. in Bat., Maia, & Vital, An. Soc. Biol. Pernambuco, 15: 440. 1957.

Mycelial state:

- = Racodium resinae Fr. β piceum Pers., Mycol. Europ. 1: 68. 1822.
- Phragmoconidial state:
- = Helminthosporium resinaceum M. C. Cooke, Grevillea, 17: 68. 1889.
- ≡ Hyphosoma resinacea (Cooke) Hughes, Can. J. Botany, 36: 781. 1958.
- = Helminthosporium resinae Bres. in Bres. & Sacc., Malpighia, 11: 322. 1897.
 - ≡ Sporhelminthium resinae (Bres.) Speg., Physis, 4: 292. 1918.
- *= Clasterosporium resinae* Rilstone, J. Bot. Lond. 79: 188. 1941.



FIG. 2. Strigopodia resinae. A, mature and young ascospores, and Capnophialophora phialides on ascospore and hypha, from the type of Capnodium resinae. B, mature and young ascospores from the type of Strigopodia piceae. \times 500.

Subicula are effuse, dense, up to 2 mm thick, dark olivaceous brown to black, woolly and associated with resinous exudates which often permeate the subicula.

Mycelium is composed of repent and erect, superficial hyphae which are cylindrical, branched (usually at right angles), pale brown to dark olivaceous brown, finely to coarsely roughened, thick-walled (up to 2μ), 5–11 μ wide, septate at 10–30 μ intervals, not or slightly constricted at the septa and showing frequent anastomoses. The hyphae occasionally grow out above the general level of the subiculum to form tapering fascicles up to 3 mm high.

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Hormisciella phragmoconidia at maturity are narrowly ellipsoidal to subcylindrical, straight or curved or more or less sigmoid, 7- to 14-septate, usually 9- to 11-septate, not constricted at the septa, 72–118 × 10.8–14.4 μ , thick-walled (up to 2 μ) except at the apex, pale brown to dark olive-brown, smooth-walled, rounded at the slightly paler apex and somewhat flattened at the basal scar, which is 3–3.5 μ wide. Conidia are sessile and develop singly along the hyphae as a blowing-out of the lateral wall of a hyphal cell.

Capnophialophora phialides are produced on hyphae, germinating ascospores, and occasionally on conidia, but in the collections available they are not common. On the hyphae they are usually crowded in groups, sessile or terminal and lateral on 1- or 2-celled stalks. They are more or less ovoid or subspherical $6.5-10.5 \mu$ long and $5.4-6.3 \mu$ wide, pale brown, slightly roughened, and bear a single, pale brown, broadly funnelshaped collarette, with a wide, open end at maturity; collarettes are $4-5 \mu$ wide and $3.0-3.5 \mu$ deep. Phialides commonly proliferate laterally just below a collarette to form another phialide which may also proliferate in this sympodial manner. Occasionally phialides produce a second collarette below the terminal one. Phialospores are apparently produced very sparsely; single ones observed within the collarette are hyaline, subspherical, and about $1.0-1.5 \mu$ in diameter.

Perithecia basally immersed or almost entirely immersed in the subiculum, black, scattered or in groups, subglobose, $130-200 \mu$ in diameter, and ostiolate at maturity; they bear numerous unbranched hypha-like appendages, up to 250μ long and up to 9μ wide, which anastomose and which may continue growth as ordinary hyphae which they so closely resemble.

Asci are fasciculate, broadly ellipsoidal, bitunicate, 8-spored, 65–80 \times 30–35 $\mu.$

Ascospores usually irregularly multiseriate, ellipsoidal, sometimes wider above the middle, brown to dark brown, thick-walled but thinwalled at base and apex which are bluntly rounded, transversely 5- to 7-septate, constricted at the septa, with one to four cells once or twice longitudinally septate, smooth, $34-45 \times 12.5-16.2 \mu$.

The ascospore initials are broadly ellipsoidal, continuous, and soon become subhyaline to pale brown; the first transverse septum formed is always median and a further septum is then laid down in each of the two equal cells. The initial enlarges, and typically, further single septa arise



FIG. 3. Strigopodia resinae. Hormisciella phragmoconidia. A, from the type of Capnodium resinae. B, from the type of Helminthosporium resinae. C, from the type of Strigopodia piceae. D, from the type of H. resinaceum. E, from the type of Racodium resinae β piceum. F, from collection No. 8 (listed). \times 500.

in the terminal cells to produce 5-septate ascospores. Additional single septa in each of the two central cells results in a 7-septate ascospore.

*Indicating states present: S. (perithecia), H. (phrag-

moconidia), C. (phialides).

Collections

(1) The type collection of *Capnodium resinae* Sacc. & Bres. in Herb. PAD, 'In resina in *Laricis*. Rabbi nel Trentino [Italy] Leg. G. Bresadola,' (S.H.C.),* Figs. 2A, 3A. (2) The type collection

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of Strigopodia piceae Bat., in Herb. BPI, on Picea rubra Link, Mt. Desert I., Maine, U.S.A., 30.VI.1929, coll. D. S. Johnson (S.H.C.), Figs. 2B, 3C. (3) The type collection of Helminthosporium resinaceum M. C. Cooke in Herb. K, 'H[elminthosporium]. resinaceum Cke with Sporotrichum resinae. Shere [England]. April 1870 [scr. Cooke]', (H.), Fig. 3D: (3 bis) A part of the preceding collection is preserved in Herb. NY, labelled 'From the Herbarium of George Massee. Purchased 1909. Helminthosporium resinaceum Cke. Shere, on fir-tree resin. Part of Type'. (4) The type collection of Helminthosporium resinae Bres. in Herb. S(a) and PAD(b); (a) '788 Helminthosporium resinae Bres. Riva-Valsesiae: 29 Magg. '91. Sulle cicatrices della corticcia des Larix ed Abies', (H.C.), Fig. 3B; (b) '788b. Helminthosporium resinae Bres. Status mycelialis Capnodis resinae Bres. In questo pezzetto troverà i conidii grandi multiseptati. Insieme ad esso trovasi Myxotrichum resinae. Riva-Valsesia. Carestia', (H.). (5) The type collection of Clasterosporium resinae Rilstone in Herb. BM, on resin on larch, W. Watson (H.). (6) The presumed type collection of Racodium resinae Fr. β piceum Pers. in Herb. L, H.L.B. 90.0.H. 910, 264-625, 'Hb. Pers. [scr. J. H. Schuurmans Stekhoven] Racodium piceum[†] An Racodium resinae Fries Observ. Mycol. 1. p. 216 ? [scr. Persoon]', (H.), Fig. 3E. (7) 'Common on resin on trunks of *Abies balsamea* (L.) Mill., Shelburne, White Mts. [New Hampshire, U.S.A.]' in Herb. K, (H.C.). (8) In Herb. NYS 'Helminthosporium. White Mts., on resin of Abies balsamea. W.G. Farlow', (H.C.), Fig. 3F; this is probably the same collection as No. 7. (9) In Herb. S, 'Flora Leutschoviensis. *Helmin*thosporium resinae Bres. In cortice Laricis supra muscos et lichenes. V.1891. Leg. V. Greschik. Habitat, Leutschoviae. Löcse, Hungaria Superior. 968.' (H.). (10) In Herb. PAD, 'Su resina di Abete rosso, V. Macra. leg. Prof. G. Gola,' (H.). (11) In Herb. K, 'Antennaria pinicola. Hormiscium. Keswick Foray [England, 1922] Det. A. L. Smith', (H.). (12) In Herb. K and IMI, 'on Larix, Kinloch, Isle of Rhum, Scotland, R. W. G. Dennis, 25.VII.1951, (H.). (13) In Herb. IMI, 'on Larix, Gairlock, Rossshire, Scotland, S. P. Wiltshire, 28.IX.1951', (H.). (14) DAOM 44587, on coniferous bark, Devil's Bridge, Cards., Wales, 8.VIII.1954, (H.C.). (15) DAOM 48946, on coniferous bark, Devil's

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Bridge, Cards, Wales, 23.X.1955, (S.H.C.), Fig. 1. Saccardo and Bresadola (in Bres. and Sacc., 1897) described Capnodium resinae (as 'Capnodium (Limacinia) resinae') on resin from Italy; the type is identical with that of Strigopodia piceae Bat. described from Maine (U.S.A.). However, Saccardo and Bresadola described the ascospores of their species as 3-septate and $30-32 \times 12 \mu$; considering the type (Fig. 2A) one can only assume that the authors saw only young ascospores. Strigopodia piceae was described as parasitic on *Picea rubra*; the type shows that the subiculum is associated with much resinous exudate. The asci of S. piceae were described as unitunicate, but in the type they are bitunicate; they are bitunicate in the type of C. resinae and in DAOM 48946.

Saccardo (1899) compiled Capnodium resinae as 'Limacinia resinae Sacc. et Bres.'. Theissen and Sydow (1917) considered that Capnodium resinae could possibly be included in their genus Phragmocapnias but they did not make the new combination. An examination of the type of P. betle (Syd. & Butl.) Theiss. & Syd. (\equiv Capnodium betle Syd. & Butl.), the type species, indicates that C. resinae is not congeneric with it. Batista and Ciferri (1963) included C. resinae in Phragmocapnias and ascribed the new combination to Theissen and Sydow.

Helminthosporium resinaceum M. C. Cooke (1889) was described from England, H. resinae Bres. (in Bres. and Sacc., 1897) from Italy as the conidial state of Capnodium resinae, and Clasterosporium resinae Rilstone (1941) was also described as new from England. The phragmoconidial state cannot adequately be classified in Helminthosporium or Clasterosporium. In 1918 Spegazzini included H. resinae Bres. in his genus Sporhelminthium but the type of this name is a Clasterosporium (Hughes, 1958). In 1958 Hughes included Helminthosporium resinaceum in the genus Hyphosoma Sydow (1924), type species H. hypoxyloides Syd., which was described from New Zealand. Considerable collecting of sooty molds in that country in 1963 enabled me to have a better understanding of the type collection of H. hypoxyloides and I now realize that the diagnosis is based on a mixture of species. The type collection is composed of five different species of sooty molds, and in most preparations I have made from it two species of phragmoconidium-bearing fungi (Hormisciella) are



FIG. 4. Strigopodia batistae, from Herb. WSP 26195. A, mature and young ascospores. B, Hormisciella phragmoconidia. C, Capnophialophora phialides on hyphae and on two Hormisciella phragmoconidia. \times 500.

present, and in some of them a third species. The name *Hyphosoma* and that of its type species are best regarded as nomina confusa. The generic name *Hormisciella* Bat. (1956), type species *H. atra* Bat., is now adopted to replace *Hyphosoma* for the phragmoconidial state of *Strigopodia*.

In the two collections from Maine and New Hampshire the *Hormisciella* conidia are slightly narrower than in those from Europe but the differences do not seem significant.

So far as I am aware the phialide state of S. resinae has not been described; it is considered suitably referred to Capnophialophora Hughes (1966).

Strigopodia batistae sp. nov.

Subiculum effusum, densum, ad 3 mm cr., atro-olivaceo-brunneum vel atrum.

Mycelium superficiale, ex hyphis repentis erectisque, cylindricis, ramosis, anastomosantibus, pallide brunneis vel atro-olivaceo-brunneis, asperatis, crasso-tunicatis (ad 2.1 μ), 7–10 μ lat., cellulis 15–47 μ long., ad septas non vel vix

constrictis, aliquando in fasciculis subulatis, erectis vel repentibus, ramosis, rectis vel irregulariter tortis, compositum.

Status phragmoconidialis ad genus Hormisciellam Bat. pertinet, sed sub Helminthosporio pseudotsugae W. B. Cooke descriptus fuit.

Status phialidicus ad genus Capnophialophoram Hughes pertinet.

Perithecia immersa vel basaliter tantum immersa, atra, subglobosa, 200–300 μ diam., ostiolata, hyphis mycelialibus numerosis, ad 300 μ long. ornata. Asci fasciculati, ellipsoidei, bitunicati, 8-spori, 80–95 × 27–38 μ . Ascosporae irregulariter multiseriatae, ellipsoideae, rectae vel leniter curvatae, brunneae vel atrobrunneae, crasso-tunicatae sed terminaliter tenuo-tunicatae, transverse 4- ad 6-, plerumque 4- ad 5-septatae, cellulis 1 vel 2 centralibus praeditis septo longitudinali unico, ad septas non vel vix constrictae, 30.5–46.5 × 12.5–16.2 μ .

Ascosporae in stato juvenile 2-septatae, cellulis polaribus parvioribus, cellula centrale majore. HUGHES: STRIGOPODIA



FIG. 5. Strigopodia batistae. A, mature and young ascospores, and 3 ascospores bearing Capnophialophora phialides from DAOM 51782. B, mature and young ascospores, with one group of eight ascospores from DAOM 56129. \times 500.

HABITAT: in resina et ad corticem Laricis occidentalis Nutt., Pseudotsugae taxifoliae (Poir.) Britt. var. taxifoliae, et P. taxifoliae var. glaucae (Mayr) Schneid. America borealis occidentalis.

TYPUS: in resina et ad corticem *Pseudotsugae taxifoliae* var. *taxifoliae*, Canada, British Columbia, Vancouver I., 21.VIII.1957, DAOM 56129.

The subiculum of S. batistae is similar to that of S. resinae described above.

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Hormisciella phragmoconidia are narrowly ellipsoidal to subcylindrical, straight or curved or rarely sigmoid, 8- to 12-septate, usually 9- to 11-septate, not constricted at the septa, 75–117 μ long, 12.6–17.1 μ wide, usually 14.4–16.2 μ wide, thick-walled except at the apex, pale brown to dark olive-brown, smooth-walled, rounded at the apex and somewhat flattened at the basal scar, which is 3–4 μ wide. They are sessile and occur singly along the hyphae; they arise as a blowing-out of the lateral wall of a hyphal cell.

Capnophialophora phialides are produced on hyphae, on germinating ascospores, and on phragmoconidia. They appear to be more frequently produced in S. batistae than in S. resinae. On the hyphae they may be locally aggregated on a hypha, are sessile or more usually terminal and lateral on short stalks, and may occur in botryose clusters. They are similar to those of S. resinae. The phialides commonly proliferate laterally just below a collarette to form another phialide which may also proliferate in this sympodial manner, and sympodial chains of six phialides have been seen. Phialides commonly bear a lateral collarette just below the terminal one. Phialospores have been observed only singly within the collarette and then presumably in a young stage of development: these are hyaline and minute.

Perithecia are similar to those of S. resinae.

Ascospores are usually irregularly multiseriate, ellipsoidal, straight or very slightly curved, brown to dark brown, thick-walled but thin-walled and paler at base and apex which are bluntly rounded, transversely 4- to 6-, mostly 4to 5-septate, not or scarcely constricted at the septa, with one or two central cells once longitudinally septate, $30.5-46.5 \times 12.5-16.2 \mu$.

Ascospore initials are broadly ellipsoidal, continuous, and soon become subhyaline to pale-brown. The first transverse septum is formed in the lower half of the initial and the second septum is then laid down toward the apex of the upper, larger cell. A three-celled initial results with the central cell usually longer than the end cells. With further growth of the initial a single septum develops in the central cell and also in the lower cell resulting in a 4-septate ascospore; a fifth septum, when formed, develops in the apical cell. One or two of the central cells may develop a single longitudinal septum.

Collections

On resin on *Pseudotsuga taxifolia* (Poir.) Britt. var. *taxifolia*, (1) Canada, B.C., Vancouver I., 21.VIII.1957, S.J.H., DAOM 56129 (S.H.C.), Type of *S. batistae*, Fig. 5B. (2) U.S.A., California, Trinity Co., 30.VIII.1956, D. F. Roy, DAOM 51782 (S.H.C.), Fig. 5A.

On resin on *Larix occidentalis* Nutt., (3) U.S.A., Idaho, Latah Co., 23.IX.1959, WSP 49320 (H.C.), Fig. 6D.

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FIG. 6. Strigopodia batistae. Hormisciella phragmoconidia. A, from the type of Helminthosporium pseudotsugae. B, from Herb. WSP 26195. C, from W. B. and V. G. Cooke 22905. D, from Herb. WSP 49320. \times 500.

On resin on *Pseudotsuga taxifolia* var. *glauca* (Mayr) Schneid., and all authenticated for *Helminthosporium pseudotsugae* W. B. Cooke. U.S.A. (4-10) Idaho; (4) Idaho Co., 13.XI.1946, W. B. & V. G. Cooke (18784), WSP 26197 (H.C.): (5) Idaho Co., 3.V.1947, W. B. Cooke (19660), DAOM 28985 (H.C.): (6) Idaho Co., 22.X.1949, W. B. & V. G. Cooke (26041), WSP 26192 (H.C.): (7) Latah Co., 16.V.1947, W. B. & V. G. Cooke (23429), WSP 26193 (H.): (8) Nez Perce Co., 19.V.1947, W. B. & V. G. Cooke (19510) (H.C.): (9) Nez Perce Co., 13.III.1948, W. B. & V. G. Cooke (22905), WSP 39101 (H.C.), Fig. 6C: (10) Nez Perce Co., 14.V.1949, W. B. & V. G. Cooke (25161) in Herb. WIS (H.C.),

this is the type of *H. pseudotsugae*, Fig. 6A: (11) Washington, Stevens Co., 26.IV.1954, W. B. & V. G. Cooke (19550), WSP 26195 (S.H.C.), Figs. 4, 6B.

In 1952 W. B. Cooke described *Helminthosporium pseudotsugae* as a new species on resin and bark of *Pseudotsuga taxifolia* var. *glauca*. In 1958 I erroneously regarded this species as identical with the *Hormisciella* phragmoconidial state included above as *Strigopodia resinae*. The phragmoconidia of the Western North American species are consistently wider than those of *S. resinae*.

The perithecial states of *Strigopodia resinae* and *S. batistae* as described above are readily

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distinguished by the order of development of septa in the ascospore initials and in the septation of the mature ascospores. In dimensions they are almost identical.

Cooke and Shaw (in W. B. Cooke, 1952) described a new species Coccodinium laricis from Idaho (U.S.A.) and claimed it to be the perfect state of H. pseudotsugae W. B. Cooke. The ascospores were described 'with 5 transverse septa and 1 longitudinal septum, 10- to 12-celled, averaging $21.6 \times 7.2 \,\mu$ '. I failed to find perithecia with such ascospores on the type collection but conclude from the description that the fungus is obviously different from Strigopodia batistae.

Discussion

Strigopodia was included by Batista in the Parodiopsidaceae. The hyphae were described with stomopodia but I believe that the structures which were so interpreted are, at least in part, the hyphal projections remaining after the separation of H-like anastomoses. The phragmoconidia were described as Septoidium conidia, but a conidial apparatus of this kind is, I believe, restricted to the genus Parodiopsis Maubl. (including Perisporina P. Henn.). Other differences between Strigopodia and Parodiopsis are evident on referring to Baker's (1955) treatment of Parodiopsis from Trinidad.

Strigopodia is far more closely related to such avowed sooty molds as Aithalomyces Woronichin (1926), described for A. arctica Woronich. and A. rhododendri Woronich., and Phaeocapnias Cif. & Bat. (in Batista and Ciferri, 1963), type species P. mucronata (Mont.) Cif. & Bat. $(\equiv Capnodium mucronatum Mont.)$. In the original species of these three genera the mycelium forms a superficial subiculum composed of cylindrical hyphae with the individual cells more or less barrel-shaped. Furthermore the asci are bitunicate and the perithecia bear hypha-like appendages. In Aithalomyces the ascospores are transversely 3-septate and rounded at the ends but in Phaeocapnias they are transversely 7-septate with mucronate ends. In Strigopodia the ascospores are transversely septate, rounded at the ends with one or more longitudinal septa. Phaeocapnias resembles Strigopodia in the production of Hormisciella conidia, and Aithalomyces in the production of a Hormisciomyces Bat. & Nasc. phialidic state: Strigopodia has a Capnophialophora phialidic state. So far as is known the two original species of Aithalomyces do not produce a Hormisciella phragmoconidial state; but in these pleomorphic fungi it is my experience that some particular conidial state or states may apparently be absent from the life history.

It is concluded that the species of Strigopodia are capnodiaceous sooty molds rather than parodiopsidaceous parasites. Although Strigo*podia* is very closely related to the earlier Aithalomyces I prefer, at the present time, to use the generic name available for the two resinicolous species.

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