CONIOCHAETA EXTRAMUNDANA, WITH A SYNOPSIS OF OTHER CONIOCHAETA SPECIES

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SUMMARY

The new species of *Coniochaeta*, described here, was isolated from soil of a chaparral community in southern California during post-fire and heat-simulation studies. It is distinguished from other *Coniochaeta* species by its uniquely flattened, flying-saucer-shaped ascospores. Characteristics of the new species are compared with those of 31 other species of *Coniochaeta*.

During recent studies of chaparral soil microfungi in southern California, we encountered four strains (1-2 isolates/strain) of an unusual previously undescribed *Coniochaeta*. Each strain represents a different surface soil collection site. Two of the strains, SA557 and SA711, were isolated by soil dilution from soil collected by the junior author (34) in May, 1976, and June, 1977, respectively. A wild fire had swept that area of the chaparral in August, 1975. The other strains, H526 and H555, were isolated by the senior author from soil collected in November, 1978, in an adjacent area of the same chaparral, unburned for many years. The latter two resulted from heat simulation studies employing oil bath heat treatments of the soil, 110 C (H526) and 90 C (H555) each for 30 min with subsequent soil dilution. Glucose ammonium nitrate agar (18) was the isolation medium in all cases.

Unless otherwise noted, the descriptions that follow are based on cultures from Leonian's agar (35); measurements were recorded from water mounts. The type description is based on single ascospore cultures of strain SA557.

Coniochaeta extramundana Mahoney et LaFavre, sp. nov. FIGS. 1-17

Perithecia nigra, late pyriformia, in collum brevem truncatum producta, a capillis numero vario hyalinis in brunneum obscurum abeuntibus flexuosis septatis, colli superioris in clavos dilute tinctos reductis, induta (setis nullis), 140-400(-450) × 90-300 μm; peridium membranaceum vel infirme coriaceum, lamella exteriori exigue prosen-

chymatica, e cellulis inflatis fuscis, lamellis interioribus prosenchymaticis, e cellulis minoribus complanatis dilute tinctis compositis; canalis ostiolaris a periphysibus multis brevibus hyalinis obductus; asci cylindrici, octospori, figuris apicalibus distinctis nullis, breviter stipitati, (80–)90–105(–112) × (11–)12.5–15(–17) μm; paraphyses multae, simplices, filiformes, hyalinae, septatae, ascis aequae vel paulum longiores; ascosporae oblique uniseriatim ordinatae, fusco-brunneae vel nigrae, leves, strato mucoso nullo, forma disci inaequaliter complanati late ellipsoidales, partibus peripheralibus quam pars centralis applanatioribus, instar patellae volucris fictae, (14–)16–18(–21) × (8–)9–12(–14) × (6–)7–9(–10) μm, fissura germinali laterali notata; sporae emissae in massam globosam juxta ostolum collectae. Fungus homothallicus; status conidialis *Phialophora*. Conidiogenesis blastica, vel prope e cellulis hyphalibus vel ex phialidibus brevibus simplicibus hyalinis, forma variantibus inter papillas inconspicuas et corpora distincta recta vel flecta, anguste conica, nonnumquam lageniformia, collarulis apicalibus expansis vulgo inconspicuis ornata vel non; conidia in glomerulis parvis solutis juxta phialidis apicem collecta, vulgo gemmantia in conidia secondaria, omnia hyalina, levia, continua vel raro bicellularia, ad vertices guttulata, forma varia, plerumque elongato-ellipsoidea, reniformia, vel allantoidea, basim versus attenuata vel non, (4–)7–10(–14) × (1.5–)2–4(–6) μm.

Colonies center-inoculated onto Leonian's agar in 9 cm plastic Petri dishes spreading slowly, covering the agar surface in 3–4 wk at room temperature, diurnal lighting. Mycelial mat close-knit and mostly submerged with aerial growth low. Colonies at first white to off-white, with initial dark pigmentation accompanying the appearance of immature perithecia during the second week. Pigment usually restricted to the central portion of the colony (where perithecial production is the heaviest), to occasional radial splotches or growth sectors and to peripheral areas or other areas where foreign substances or foreign colonies are encountered. These areas dirty buff soon becoming dark buff-brown to blackish. Despite local pigmentation, the overall colony appearance is characterized by abundant dark perithecia against an off-white translucent background. Radial furrowing slight near the colony center. Reverse and media uncolored. No growth at 37 C, good growth and sporulation at 15 C.

Perithecia (FIG. 1) maturing 4–5 wk after inoculation, numerous, separate to clustered, superficial to submerged (most uniform development occurring on the agar surface; descriptions are based on these perithecia), black, broadly pyriform, variable in size 140–400(–450) × 90–300 μm with a swollen, often nearly globose venter and a broad short neck 50–75(–100) μm long, rarely longer, which tends to be truncate or slightly flared apically. Ostiolar canal lined with numerous short hyaline periphyses which are conspicuous around the opening in older perithecia. Perithecia, though sometimes appearing superficially glabrous, are covered with a variable number of hyaline to dark brownish, flexuous, simple to branched, septate hairs that on the upper neck near the ostiole are reduced to short, more lightly pigmented, clavate pegs or tubercles. Peridium membranaceous to weakly coriaceous, blackish, opaque, pseudoparenchymatous, consisting of several cell layers. The outermost cell layers of large swollen darkly pigmented cells (least pseudoparenchymatous of the cell layers), the innermost of small flattened nearly hyaline cells (forming a
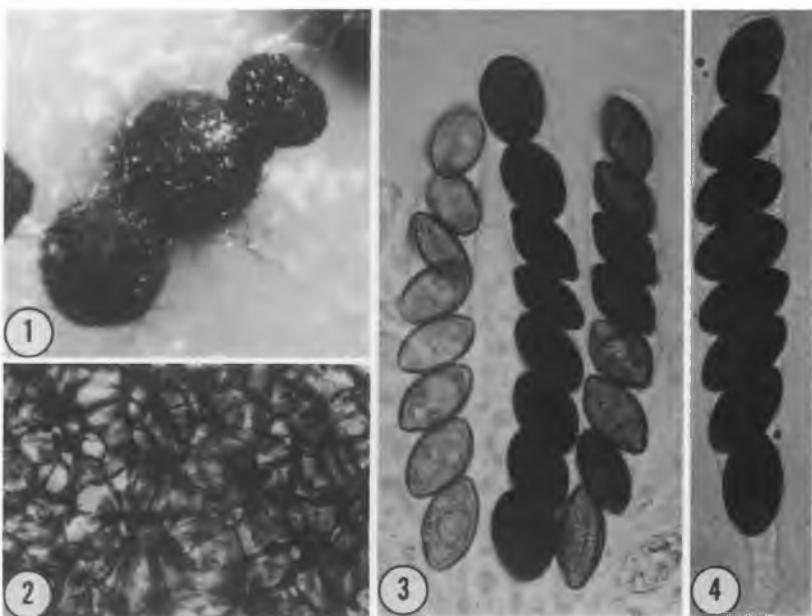
FIGS. 1-4. *Coniochaeta extramundana*. 1. Perithecia with exuded ascospores. Overhead and side views directly from the surface of Leonian's agar, ×100. 2. Peridium from a mature perithecium grown on corn meal agar, showing outermost layers of pseudoparenchyma. Unstained water mount, ×1000. 3-4. Asci and ascospores from Leonian's agar. Unstained water mounts, ×1000. 3. Ascospores in side and face views and in various stages of maturity. 4. Ascus with typical stipe, ascospores in face view.

more typical pseudoparenchyma). Pigment development in the outer cell layer is initiated along the radial walls. Through this "pigment reticulum" can be seen the underlying smaller, less pigmented, more compressed cells of the inner layers. Peridia developing on fructifications produced on Leonian's agar and on Difco potato dextrose agar (PDA) soon become too dark to easily distinguish cell detail although the more weakly pigmented peridia on cornmeal agar reveal such detail at maturity (FIG. 2). In age the peridium is often covered with a loosely appressed layer of flexuous hairs.

Asci (FIGS. 3, 4) cylindrical, 8-spored (infrequently 4-7-spored), broadly rounded apically, without any distinct apical ring or other structures, non-amyloid in Meltzer's reagent, with a short stout stipe, $(80-)90-105(-112) \times (11-)12.5-15(-17)$ μm. Asci persistent after spore discharge; the apex often torn away. Paraphyses numerous, filiform, septate, simple, hyaline, narrowly rounded above, as long as or slightly longer than the asci.

Ascospores (FIGS. 3-9) arranged obliquely uniseriately, at first hyaline but soon passing through amber brown shades to dark choco-

late brown or black, without sheaths, smooth, uniquely bilaterally flattened, ellipsoidal (best observed in intermediate stages of pigment development), with peripheral portions of the spore more flattened than its central region, presenting the appearance of an ellipsoidal flying saucer (FIGS. 8, 9). Face views (FIGS. 5, 8, 9) broadly elliptical, infrequently somewhat ovate, with a fusoid-ellipsoid raised area running lengthwise down the center. This mound rising rather abruptly from the flattened spore periphery to a narrowly rounded ridge. Side views (FIGS. 6, 8, 9) weakly to strongly limoniform with the face-view mounds seen along most of the long axis edges and the flattened periphery of the spore running as a narrowly-rounded crest down the center to the ends. End views (FIGS. 7-9) cruciform with the face-view mounds in one axis and the flattened edge of the spore perpendicular to that in the other. Length (14-)16-18(-21) × width (face view) (8-)9-12(-14) × thickness (side view width) (6-)7-9(-10). Germ slit straight, extending from one end to the other along one side of the flattened spore (in side view seen as a straight clear line running lengthwise down the center). Following spore discharge, spores collecting in a large globose mass at the mouth of the ostiole (FIG. 1), with none observed on the Petri-dish lid or on the agar surface. Transfer of fresh ascospores to new media resulting in fair to good germination 12-24 h after inoculation. One to three germ tubes emerging from the germ slit and these immediately branching and producing conidia. Homothallic.

Conidial stage (anamorph) a *Phialophora*. Conidiogenesis enteroblastic from a point directly on the hyphal cell or from the narrow apices of small simple phialides of varied size and shape (FIGS. 12-14). Phialides hyaline or lightly pigmented, smooth, thin-walled, one per hyphal cell, usually lacking a basal septum, varying from inconspicuous papillae to distinctive, straight or bent, narrow cone-shaped, or less frequently bottle-shaped structures which are generally much shorter than the conidia produced, with bases slightly to decidedly broader than apices. Terminally flared collarettes present or not, usually inconspicuous, observed infrequently and with difficulty due to the small diameter and hyaline nature of most phialide apices. Conidia produced consecutively from the phialides, collecting in small loose clusters. These conidia frequently budding to produce smaller, similarly-shaped secondary conidia (FIGS. 15-17). Buds appearing singly from any surface of the primary conidium. Primary and secondary conidia hyaline, smooth, one-celled (rarely 2-celled in older areas), usually with a single guttule at each pole, varied in shape and size, mostly oblong-ellipsoid to reniform or allantoid (less often ovoid), narrowing somewhat basally or not, (1.5-)2-4(-6) × (4-)7-10(-14) μm.

Comments on other strains and other media.—Colonies of strains SA711 and H526 on Leonian's agar were also fertile and culturally
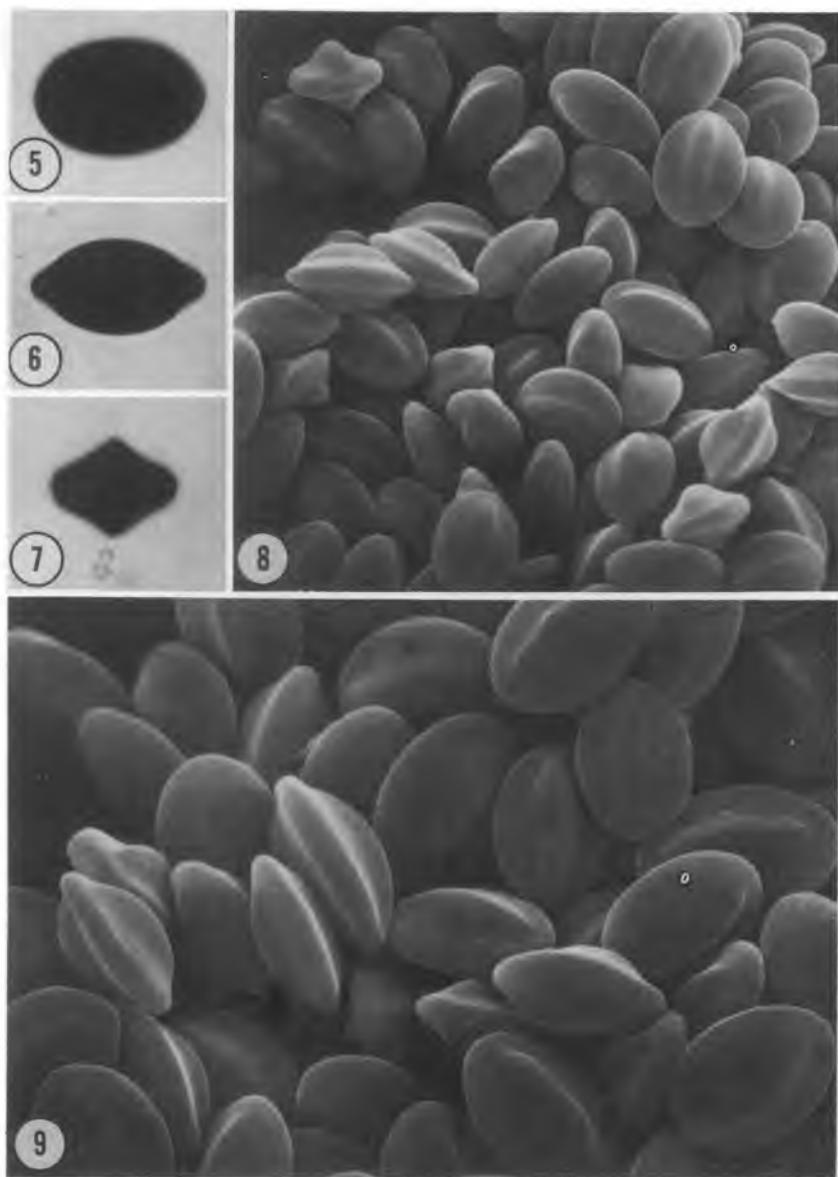
FIGS. 5–9. *Coniochaeta extramundana.* Ascospores from colonies on Leonian's agar. 5–7. Standard brightfield microscopy, unstained water mounts. Face, side and end views, respectively, ×1200. 8, 9. Scanning electron microscopy, showing various views. ×1000 and ×1500, respectively.
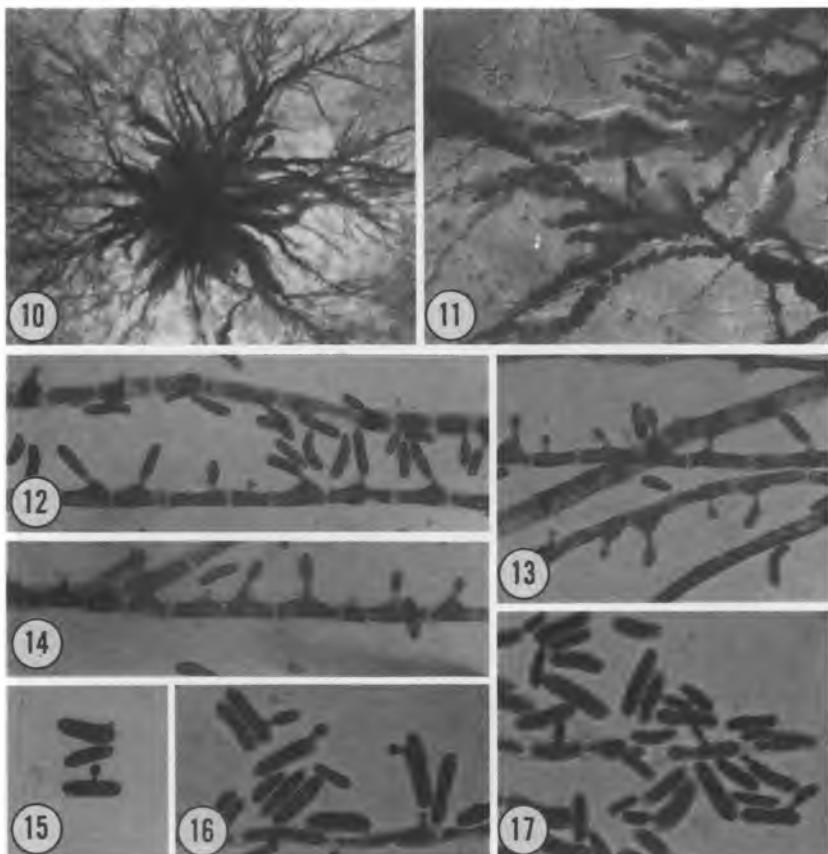
FIGS. 10-17. *Phialophora* conidial stage of *Coniochaeta extramundana*. 10, 11. Views directly onto the surface of a 6-da-old colony on corn meal agar (unstained), showing the yeast-like appearance near the colony center and along radiating hyphae which results from the budding of conidia, ×12 and ×60, respectively. 12-17. From 3-da-old colonies on Leonian's agar. Stained with cotton blue in lactophenol, ×1000. 12-14. Phialides and conidia, showing phialide diversity and conidia in various stages of development. 15. Two of three conidia showing a single guttule at each pole. 15-17. Budding of conidia.

and morphologically similar to those of SA557 described above. Difco PDA yielded colonies with good perithecial production for SA557 and SA711 but not for H526. With age, the predominantly submerged colonies of SA557 and SA711 on PDA gradually became more darkly pigmented throughout than those on Leonian's while also developing more conspicuous radial furrowing and irregular mounding in the center $\frac{1}{2}$ to $\frac{2}{3}$'s of the colony. Strain H526 on PDA remained a light

dirty buff color except in sectors which produced perithecia. In these
sectors, H526 resembled the colonies overall of SA557 and SA711.
Other media on which these three strains were grown—Difco corn
meal, malt extract (55) and Czapek's (55) agar—yielded poorer and
more anomalous ascocarp production or no ascocarps at all. Conidia
were abundant on all media.

Observations of strain H555, shortly after its isolation, revealed
only a few fertile perithecia. Since that time it has become sterile. Cul-
turally, it differs from the other three strains by its more restricted
growth (colonies 5.5–6.5 cm in diam after more than two mo growth
on PDA and Leonian's), its more aerial hyphae, its lighter buff to
amber appearance and its lack of dark pigmentation. Colonies of
these four strains occasionally appeared moist, membranaceous and
partially yeast-like, particularly near the colony centers. Conditions
seeming to favor such an appearance include (1) plate inoculation
with conidia or ascospores rather than hyphae, (2) growth in tubes
with plastic caps rather than cotton plugs, and (3) the type of media
employed: plates of glucose ammonium nitrate agar and Difco corn
meal agar yielded colonies initially somewhat yeast-like whereas Leo-
nian's agar did not. FIGURES 10 and 11 illustrate 6-da-old colonies on
Difco corn meal agar where plentiful yeast-like conidial budding
along some of the main hyphae radiating from the colony center has
contributed to this appearance.

Etymology.—From the Latin "extramundanus", meaning other
worldly; descriptive of the unique flying-saucer-shaped ascospores.

Type locality.—Twenty-five miles east of Los Angeles, California,
U.S.A.

Habitat.—From arid chaparral soil, 3,000 feet elevation, north of Up-
land and Claremont, California, near the San Antonio Dam on the
lower southern slopes of the San Gabriel Mountains. Dominant
shrubs *Adenostoma fasciculatum* H. & A. (chamise) and *Salvia melli-
fera* Greene (black sage). Dominant microfungi include *Penicillium
canescens* Sopp, *P. restrictum* Gilman & Abbott, *P. frequentans* West-
ling, *P. victoriae* Szilvinyi, *Aspergillus fumigatus* Fresenius, *Aureoba-
sidium pullulans* (deBary) Arnaud, *Trichoderma koningii* Oud. apud
Oud. & Koning, *Mortierella thaxteri* Bjorling, *Geomyces pannorus*
(Link) Sigler & Carmichael, sphaeropsidaceous and dematiaceous
non-sporing fungi and particularly on recently burned areas *Conio-
chaeta tetraspora* Cain, *Neosartorya fischeri* (Wehmer) Malloch and

Cain and *Humicola* sp. Soil a neutral to slightly acid sandy loam. For detailed soil analyses and climatological data see LaFavre (34).

Type cultures.—Dried agar cultures of strain SA557 have been deposited at The New York Botanical Garden (holotype on Leonian's agar), at the Commonwealth Mycological Institute (isotype, IMI 213149 on Leonian's agar) and at Uppsala University, Sweden (isotype on Difco PDA). Living specimens are preserved at the American Type Culture Collection (ATCC 42291), at the Centraalbureau voor Schimmelcultures (CBS 247.77) and at Uppsala University. Strains SA711, H526 and H555 are preserved as living specimens in the laboratory of the senior author.

DISCUSSION

In 1887, Cooke (12) elevated Saccardo's subgenus *Coniochaeta* of *Rosellinia* (59) to generic rank[1] although few workers noted the change until the 1930's when Cain (5) described several coprophilous species. In the late 1940's and during the fifties, Munk (45-47), Arx and Müller (1), Moreau (43) and Moreau and Moreau (44) briefly discussed the genus and further augmented its number of coprophilous and lignicolous forms. Soil isolations during the fifties yielded the first records from that substrate (7, 9, 14). With Cain's 1934 paper as the starting point, geographically scattered reports bring the present species total to approximately thirty-two. Among these are many transfers of lignicolous species from *Rosellinia* and coprophilous species from *Sordaria* and other sordariaceous genera. *Coniochaeta* species are distinguished from xylariaceous forms like *Rosellinia* by their nonstromatic ascocarps and relatively simple, nonamyloid ascus apices and from sordariaceous genera by their ascospores with longitudinal germ slits. The seemingly intermediate position that they occupy has been recognized by Malloch and Cain who erected the family Coniochaetaceae (39) for *Coniochaeta* and its non-ostiolate counterpart *Coniochaetidium*. Presently, the Coniochaetaceae also includes the genera *Poroconiochaeta* (64), *Germslitospora* (36, 3) and *Ephemeroascus* (69, 3, 38). The former is perithecial while the latter two are cleistothecial. Ascospores of *Poroconiochaeta* and *Germslitospora* are pitted, in two of three species so finely so that a scanning electron microscope is necessary to clearly discern the pitting. The monotypic

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[1] Other publications have cited Massee (40) as the authority instead of Cooke. That error, corrected herein, was brought to our attention by Nils Lundqvist (pers. com.).

Ephemeroascus is characterized by smooth ascospores with very inconspicuous germ slits and a *Verticillium* anamorph.

According to Hawksworth (**23**), collections of *Coniochaeta* are infrequently received for identification at the Commonwealth Mycological Institute. However, their gradual accumulation there and elsewhere—most notably collections of *C. ligniaria* (Grev.) Cooke (Hawksworth, pers. com.), the inter- and intraspecific variation noted—particularly among *C. ligniaria* collections (**20, 31, 45,** Hawksworth pers. com.) and the increasing number of newly described species, especially among soil isolates, all underline the need for a comprehensive treatment. That effort will be complicated by (1) the need to reexamine old, widely scattered, often poorly described and poorly preserved type material, (2) the lack of any monograph for *Rosellinia,* where a number of *Coniochaeta* species still reside (Cain, pers. com.), and (3) the fact that although most *Coniochaeta* species are described as strictly wood, dung or soil inhabitants, many may be more opportunistic than was formerly envisioned (**53, 63**). The following literature summary of *Coniochaeta* species and their characteristics is provided to clarify the position of the new species described herein among existing species and to establish a framework for further studies. No attempt is made to deal with nomenclatural problems of any species.

Coniochaeta *species, listed by natural substrate.*—Italicized references contain a description of the species and often a list of synonyms. Earlier descriptions under different binomials are not listed, unless noted.

Species isolated from soil only. (1) *Coniochaeta extramundana* Mahoney & LaFavre. (2) *Coniochaeta ellipsoidea* Udagawa (**67**). (3) *Coniochaeta tetraspora* Cain (**7, 19, 25, 34, 37, 41, 66, 70, 71**). (4) *Coniochaeta nodulisporioides* Hawksworth (**23**). (5) *Coniochaeta nepalica* Minoura, Morinaga & Muroi (**42**). (6) *Coniochaeta ovata* Matsushima (**41**).

Species reported from dung (D) and/or higher plant surfaces, usually decaying wood (W), in addition to soil (S). (1) *Coniochaeta ligniaria* (Grev.) Cooke (S—*14*; D—*45, 46, 47,* 65; W—*1,* 13, *45, 46, 47,* 57). *Coniochaeta discospora* (Auersw.) Cain (S—*70, 71, 72*; D—*5,* 6, *17, 43*) is occasionally reported as a distinct species but is treated as a synonym of *C. ligniaria* here and by most workers, following Munk (**45**). (2) *Coniochaeta velutina* (Fuckel) Cooke (S—*63*; D—*63*; W—*13,* 47, *63; 68* on *Stereum* sp.). Taylor (**63**) discusses the synonym, or possible synonym, *C. kellermanni* (Ellis & Everh.) Munk (S—*4*; W—*47*). (3) *Coniochaeta subcorticalis* (Fuckel) Cooke (S—*41*; W—*47*). (4) *Conio-*

chaeta scatigena (Berk. & Br.) Cain (S—19; D—*5, 13, 43, 47,* 48). (5) *Coniochaeta leucoplaca* (Berk. & Rav.) Cain (S—*62*; D—*5,* 6, *13, 17, 33, 47*; W—24, *44*). (6) *Coniochaeta saccardoi* (March.) Cain (S—*62*; D—*5, 33*).

Species reported from wood only. (1) *Coniochaeta malacotricha* (Auersw.) Cooke (*1, 13,* 29, *32, 47, 58*). A species apparently restricted to coniferous wood. (2) *Coniochaeta pulveracea* (Ehrh.) Munk (*1, 13, 45, 47*). (3) *Coniochaeta niesslii* (Auersw.) Cooke (*1*). (4) *Coniochaeta* sp., described without a specific epithet by Munk (*47*) who noted "cfr. *Rosellinia xylarispora* (Cooke & Ellis) Sacc." (5) *Coniochaeta myricariae* (Fuckel) Arx & Müller (*1*). (7) *Coniochaeta sarothanni* (Schroet.) Arx & Müller (*1*). (7) *Coniochaeta elaeicola* (Henn.) Moreau & Moreau (*44*). (8) *Coniochaeta sordaria* (Fr.) Petrak (*51*). Synonym listed by Petrak is *Rosellinia sordaria* (Fr.) Rehm (*59*) which Munk (47) and Taylor (*63*) report as a questionable synonym of *R. velutina*. (9) *Coniochaeta albido-mucosa* Petrak (*50*). (10) *Coniochaeta phalacrocarpa* Carroll & Munk (*8*). (11) *Coniochaeta gymnosporae* Kale & Kale (*28*). (12) *Coniochaeta williamsi* Hansford (*22*). (13) *Coniochaeta caryotae* Rao (*54*). (14) *Coniochaeta tilakii* Kale (*27*). (15) *Coniochaeta microspora* Reddy & Bilgrami (*56*). (16) *Coniochaeta ambigua* (Sacc.) Cooke (*52*). Synonym listed by Popuschoi is *Rosellinia ambigua* Sacc. (*59*) which Arx and Müller (1) list as a synonym of *C. niesslii*. (17) *Coniochaeta calva* (Tode) Cooke (*52*). Synonym listed by Popuschoi is *Rosellinia calva* (Tode) Sacc. (*59*).

Species reported from dung only. (1) *Coniochaeta hansenii* (Oudem.) Cain (*5, 13, 43, 47*, 48, *65*). (2) *Coniochaeta multispora* Cain (*5*). (3) *Coniochaeta philocoproides* (Griffiths) Cain (*5*). Originally described as *Sordaria philocoproides* Griffiths (*20*). (4) *Coniochaeta polysperma* Furuya & Udagawa (*16*).

Certain trends among species are apparent from closer examination of the above listing by substrate. The only species with 4-spored asci, *C. tetraspora* and *C. nodulisporioides*, are among the forms found thus far only in soil, while those restricted to dung are the only species with multispored asci, *C. philocoproides* (32 spores), *C. hansenii* (64–128 spores), *C. polysperma* (512 spores) and *C. multispora* (appx. 1000 spores). All other species have 8-spored asci. Few species have been recorded frequently enough to assess their ecology. Others like *C. ligniaria* and *C. leucoplaca* are more common and cosmopolitan but the extent of their morphological variation still raises enough questions to make any ecological analysis premature. Among the soil forms several are common in post-fire soils. These are referred to as carbonicolous forms by Wicklow (**71, 72**) and include *C. extramundana, C. tetraspora* (**25**, 34, **70, 71**), *C. ligniaria*—recorded as *C. dis-*

cospora (**70, 71, 72**)—and perhaps others. The same forms and others, as yet unidentified (senior author, unpubl.), may be isolated in the laboratory by heat and alcohol treatments of the soil (**37**). Wicklow (**71**) suggests that an ascospore heat shock, similar to that demonstrated for many sordariaceous forms, is also required for ascospore germination in these species. This remains to be proven, however, since the only reports of actual ascospore germination in *Coniochaeta* reveal germination without special treatment—*C. extramundana, C. ligniaria* (**14, 57**), *C. malacotricha* (**58**) and *C. velutina* (**11**). *Coniochaeta velutina* has been the subject of a joint ecological-pathological-genetic study by Taylor and others (**2, 10, 11, 26, 49, 63**). As a result, its ecology on sugar maple trees, dung and soil in Ontario, Canada, is better understood. Similar joint efforts on other Coniochaetas, particularly those now infrequently reported only from wood, may reveal their capacity to grow on other substrates and, in turn, their possible synonymy with other species. None of the plant or woody decay species has been reported as strongly pathogenic. They appear on dead tissue or as opportunistic invaders of previously infected, wounded or senescent tissues.

Axenic culture on agar media, sexual (teleomorph) and asexual (anamorph) stages.—One or more strains of sixteen species have been cultured to sporulation (conidia and/or fertile perithecia). These include all the species restricted to soil, all the mixed-substrate species, three wood or plant decay species, *C. malacotricha, C. elaeicola* and *C. microspora,* and *C. polysperma* among the species restricted to dung. Cultures for five of the species yielded only perithecia: *C. ellipsoidea* (**67**), *C. ovata* (**41**), *C. subcorticalis* (**41**), *C. microspora* (**56**) and *C. polysperma* (**16**). Nine of the species produced both perithecial and conidial states in culture: *C. extramundana, C. tetraspora* (**7, 34, 37, 66, 71**), *C. nodulisporioides* (**23**), *C. nepalica* (**42**), *C. ligniaria* (**57**), *C. velutina* (**63, 68**), *C. leucoplaca* (**44**), *C. saccardoi* (**33**) and *C. elaeicola* (**44**). Another, *C. malacotricha* (**58**), yielded only conidia in cultures inoculated from field-collected ascospores. The conidial status of *C. scatigena* (**19**) was not reported.

The relative abundance of the anamorph and teleomorph varies depending on the strain, the medium, and the environmental conditions, with sporulation increasing or decreasing following each transfer to fresh media. With the exception of *C. tetraspora* and perhaps *C. velutina,* only one or at most a few strains of each species has been cultured. Already, however, strain variations and subculturing effects are obvious. *Coniochaeta ligniaria* yielded only conidia in one strain (**57**) and only perithecia (**14**) in another. A reduction in

numbers of conidia or their complete absence has been reported among strains of *C. tetraspora* (34, 41) and for laboratory-induced mutants of *C. velutina* (49). In our own experience we have likewise witnessed a reduction in perithecial numbers or complete loss of the teleomorph with successive transfers. Although all of the *Coniochaeta* species cultured on agar are homothallic, except for one heterothallic strain of *C. velutina* (11) and possibly *C. malacotricha,* it is quite possible that heterothallic species do exist. We have isolated many soil strains whose conidial states resemble those of *Coniochaeta* species. To date, however, none of the attempted matings has been successful.

The anamorph for nine of the ten species with conidia is a *Phialophora,* assignable to the *P. hoffmannii* species group (30, 60, 61). The related *Poroconiochaeta discoidea* Udagawa and Furuya (64) also has a similar anamorph. *Coniochaeta nodulisporioides* has a *Nodulisporium*-like anamorph. As presently understood, the *Phialophora* states of different Coniochaetas are too similar to be readily distinguishable. Good descriptions of the *Phialophora* state are provided by Rogers for *C. ligniaria* (57) and *C. malacotricha* (58). Secondary conidia, the result of conidial budding, have been reported for *Phialophora* states of *C. tetraspora* (7, 34, 66), *C. velutina* (63), the aforementioned species studied by Rogers and the new species described herein. Conidial states of *Coniochaeta* species have only been reported following their appearance on agar media. None has been described in association with the perithecia on dung or plant remains although they must be present there also.

Perithecia.—Certain generalizations are warranted for *Coniochaeta* perithecia despite the diverse environments under which different species developed and the age and maturity differences at the time of their descriptions. The only thorough developmental study of perithecia is that of Doguet (14) for *C. ligniaria.*

Stromata. Coniochaeta species are considered nonstromatic although at least two references cite thin basal stromata or subicula associated with the woody decay species described therein. Arx and Müller (1) describe thin (1-few cell layers), dark, pseudoparenchymatous stromata on or within which the perithecia sit, and Petrak (50) emphasizes a thin, white basal subiculum.

Perithecial shape, color and size. Perithecial shape is not a feature which distinguishes species. In general, perithecia are characterized as having a globose or subglobose body with a short neck. The merger of neck and body is usually gradual with the apex typically broad and papilliform. The ostiole is centrally located and lined with numerous

hyaline periphyses. Perithecia are normally dark brown to black and opaque although perithecia of two dung species, *C. multispora* and *C. polysperma*, and a soil inhabitant, *C. nodulisporioides*, are noted as sometimes semitransparent. *Coniochaeta microspora* is unique with its transparent, yellowish cream-colored perithecia which have a black region near the ostiole. Size is variable but all species except one have perithecia less than 500 μm high (*C. elaeicola* to 600 μm), with perithecia of most species measuring 200-400 × 150-350 μm. Features such as multispored asci and large, uniseriately arranged ascospores usually correlate with species whose perithecia range to 400-500 μm high just as 4-spored asci or 8-spored asci with smaller or biseriately arranged ascospores usually correlate with species whose perithecia are less than 200 μm high.

Setae. As the generic suffix indicates, the presence of chaetae (setae, spines, stiff hairs or bristles) on the perithecium was an important early character for distinguishing members of the genus. Although ascus and ascospore characteristics are now given greater emphasis, setae are still a prominent feature of most *Coniochaeta* species. Setae of the various species may be generally described as dark brown to black, straight to sometimes bent or curved, smooth, unbranched, rigid hairs that taper to a point. Scanning electron microscopy of *C. leucoplaca* (24) reveals them to be smooth, terete and rounded api-. cally. They are typically <50 μm long and 3-5 μm in diam at the base but setae ranging upwards to 60-100 μm long are recorded for *C. nepalica*, *C. hansenii*, *C. polysperma*, *C. multispora* and some strains of *C. malacotricha* (32, 47). Setae of some species are septate, of others aseptate, but for most species no information is provided. Strains of *C. leucoplaca* are described as having both septate (21) and aseptate (33) setae. Setae may be scattered over the perithecial surface or concentrated on its upper portion. The latter condition is described for most species, particularly those on dung where sunken portions lack· setae. Presently, there is not enough information available on setae to clearly distinguish one setose *Coniochaeta* from another on that basis alone. Only seven species are described as lacking setae: *C. extramundana*, *C. ellipsoidea*, *C. nodulisporioides*, *C. microspora*, *C. myricariae*, *C. phalacrocarpa*, and usually *C. pulveracea*. Perithecia of these species are variously described as smooth or with few to many, short to long, rather nondescript hairs. In addition to these seven, some nonsetose strains are occasionally reported for normally setose species. Munk (47) reported that his collections of *C. leucoplaca* were glabrous except for "a few among hundreds." Doguet's strain of *C. ligniaria* (14) was completely smooth. On the other hand, Arx and Müller (1)

described short brown bristles detaching prematurely from some perithecia of the normally nonsetose *C. pulveracea*. Care should be taken when examining older perithecia. Taylor (**63**) reported that setae of *C. velutina* sometimes break off in age, a characteristic also reported by Ellis and Everhart (**15**). Clearly, then, the presence of setae no longer characterizes the genus as a whole. In fact, further observations are necessary to demonstrate the stability and reliability of setae at the species level.

Peridium. Descriptions of *Coniochaeta* species differ considerably in the emphasis given this character. Generally, the peridia are described as pseudoparenchymatous, the outer peridium composed of slightly flattened, dark, distinct to indistinct, sometimes moderately thick-walled, angular, polygonal or subglobose cells and the inner peridium of more strongly flattened, hyaline, distinct to indistinct, thinner-walled, angular to elongate cells. Peridia are usually reported as membranaceous or membranaceous to somewhat coriaceous, rarely as coriaceous, and vary from very thin (*C. microspora*) to usually <35 μm thick. *Coniochaeta phalacrocarpa* is distinctive with its thick, three-layered peridium, the outer layer consisting of an amorphous hyphal weft. Much of the peridium in *C. nodulisporioides* is composed of irregularly-shaped cells, some almost pseudoparenchymatous but many hypha-like (textura intricata). The earlier description of unevenly pigmented cells in the outer peridium of *C. extramundana* is reminiscent of a similar description for Doguet's *C. ligniaria* (**14**).

Asci and paraphyses.—Doguet (14) traces the development of asci and paraphyses during perithecial ontogeny in *C. ligniaria*. Paraphyses emerge early from the base and lower sides of the enlarging cavity followed by asci which grow up among them. Our own observations of *C. extramundana* are in agreement with this sequence. Little is known of the development in other species although the descriptions of paraphyses are remarkably uniform. In general, they are numerous, hyaline, filiform (more ventricose below in species with multispored asci), tapering somewhat apically, simple, septate and as long as or usually slightly longer than the asci. In our own experience the paraphyses are less obvious and more difficult to find as asci mature and the ascospores are discharged. Whether they are evanescent, as Udagawa reports for *C. tetraspora* (**66**), or only very compressed is not clear. In some species they are reported as gelatinizing—*C. myricariae* and *C. pulveracea* (1), or agglutinating—*C. malacotricha* and *Coniochaeta* sp. (**47**).

Asci are typically described as thin-walled with a short stipe and a

truncate to rounded apex which is slightly thickened to form a simple, indistinct or obscure (less frequently distinct) periapical ring. Descriptions of the apex appear, at times, to vary as much on the basis of the observer's emphasis and experience as on the basis of real differences. *Coniochaeta leucoplaca, C. elaeicola, C. scatigena, C. ligniaria* and *C. hansenii* are all described by Moreau (43) and Moreau and Moreau (44) as having a distinct well-developed periapical ring structure. Others describing two of the same species, *C. ligniaria* (46) and *C. leucoplaca* (33, 47), report the ring as faintly developed. The four multispored, dung-restricted species, however, are all uniformly described as having a distinct apical apparatus. Apical structures of the soil forms, with which we are most familiar, are very difficult to discern. The possible relationship of ascal tip development to manner of ascospore discharge and substrate preference is suggested, though the information is far from complete. The soil-inhabiting forms *C. extramundana, C. nodulisporioides, C. tetraspora* (7) and soil-inhabiting strains of *C. ligniaria* (14) do not forcibly discharge their spores which collect in a mass at the mouth of the ostiole. Forcible discharge has been reported in some soil strains of *C. tetraspora* (34, 71) and *C. ligniaria* [as *C. discospora* (71, 72)], from moistened perithecia in wood collections of *C. ligniaria* (57) and in agar cultures of wood-inhabiting *C. velutina* (11). The nonamyloid nature of the ascus apex, as noted earlier, is considered to be an important generic character. Relatively few authors (23, 32, 43), however, cite any iodine test results as part of their descriptions of taxa.

Ascus shape for most species is cylindrical with ascospores arranged uniseriately. Exceptions include the clavate or broadly cylindrical to clavate shapes of multispored asci in the dung-restricted species and the more narrowly clavate shapes of asci with a biseriate spore arrangement, *C. nepalica* and *C. ellipsoidea*. Spore arrangement and ascus shape are not noted for Munk's *Coniochaeta* sp. (47) but the similarity of its ascospores to those of *C. nepalica* (TABLE I) make a biseriate arrangement seem likely. Ascus size of most species lies in the range 65–130 × 7–15 μm with 4-spored, biseriately-arranged and small-spored asci somewhat smaller and multispored and larger-spored asci somewhat larger. Occasionally strains are reported among normally 8-spored species which have asci with fewer than eight spores. One strain of *C. malacotricha* (58) was described with up to 25% of its asci bearing 1–7 but usually 4–5 spores. Other reports note some minor variation in *C. ligniaria* (45), *C. albido-mucosa* (50) and *C. extramundana*. In our opinion, such minor variation is to be expected. Carroll and Munk (8) emphasized faint, delicate, branched, longitudi-

TABLE I

Coniochaeta ASCOSPORES: A LITERATURE SUMMARY

Species with broadly elliptical to nearly circular spores in face view (length × width usually < 2:1).[a]
Arranged roughly in order of decreasing size

Species	Literature reference(s)	Size (μm)[b]	Shape[c]
C. scatigena	5,13,43	16-23 × 10-19 × 8-15	Disc.: f.v. circ. to br. ellipt., s.v. very nar. ellipt. to sl. ovate
C. extramundana		14-21 × 8-14 × 6-10	See earlier desc.
C. ligniaria	1,5,13,14,20 21,31,43,45,46	9-20 × 8-15 × 4-8	Disc.: f.v. br. ellipt. to subcirc. or sl. ovate, s.v. nar. ellipt.
C. nodulisporioides	23	15-20 × 12-15 × 9-11	Sl. flat., ellips., sl. apic. at ends
C. albido-mucosa	50	11-16 (rarely 19 × 10-15)	Glob., rarely br. ellips. or ovoid
C. pulveracea	47	9-15 × 9-14 × 7-8	Sl. flat., br. ellips. to subglob.
	1,13[d]	10-14 × 6-8	Br. ellips.
C. malacotricha	32,47,58	10-14 × 9-13 × 6-8	Mill-stone shaped, flat. with obtuse edge; disc.: f.v. br. ellipt., s.v. inequil. to nar. ellipt.
	1[d]	9-12 × 6-7	Sl. flat., br. ellips.
C. tetraspora	7,34,41,66	10-16 × 6-10 × 5-7	Disc.: f.v. br. ellipt., s.v. nar. ellipt.
C. sarothamni	1	10-15 × 6-8	Ellips., flat. on 1 side
C. subcorticalis	41,47	8-13 × 6-9 × 5-6	± Br. ovoid-ellips., sl. irreg.
C. tilakii	27	11-13 × 6-8	No shape desc.
C. ambigua	52,59	10-12 × 6-8	Flat., ellips. to subglob.
C. myricariae	1	9-12 × 5-8	Strongly flat., br. ellips.
C. phalacrocarpa	8	11-12 × 5-7 × 3-4	Lent.[e]
C. leucoplaca	5,13,17,20,21 33,44,47,62	7-10 × 5-9 × 4-8	Disc. (lent.[e]): f.v. br. ellipt. to circ., s.v. nar. ellipt.
C. velutina	13,47,63,68	6-10 × 4-7 × 3-5	Sl. disc.: sl. irreg.-ovoid, ellips. to br. ellips.
C. kellermanni	47	4-6 × 3-4	Ellips., very br. rounded at ends
C. williamsi	22	7-9 × 4-6	Ovoid with obtuse ends
C. hansenii	5,13,43,47,65	6-9 × 5-9 × 4-7	Disc. (lent.[e]): f.v. br. ellipt. to circ. or ovate, s.v. nar. ellipt.
C. philocoproides	5,20,21	8 × 6-8	Sl. flat.: f.v. br. ellipt. to subcirc., s.v. nar. ellipt.
C. polysperma	16	7-8 × 6-8 × 4-5	Disc.: f.v. circ. to br. ovate, s.v. ellipt.

C. multispora	5	5–7(f.v.) × 3–6(s.v.)[f]	Disc.: f.v. circ., s.v. ellipt.
C. sordaria	51,59	4–8 × 4–7	Sl. flat., br. ovoid or ellips., often subglob.

Species with narrowly elliptical to fusiform spores in face view (length × width usually >2:1).[a]
Arranged roughly in order of decreasing size

Species	Literature reference(s)	Size (μm)[b]	Shape[c]
C. caryotae	54	20–26 × 7–10	Ellips. or fusoid
C. ellipsoidea	67	18–23 × 9–13 × 5–8	Ellips., often 1 side flat., both ends subapic., sometimes 1 end apic.
C. ovata	41	17–23 × 8–10 × 6–8	Ovoid, 1 end round, other apic.
C. calva	52,59	16–20 × 8–11	Ellips.
C. niesslii	1,5	16–20 × 8–9	Disc. (5); br. ellips. (1)
C. gymnosporae	28	17–19 × 5–7	No shape desc.
C. saccardoi	5,33,62	14–20 × 6–9 × 5–6	Sl. flat., ellips. or nar. ellips.
C. elaeicola	44	12–17 × 6–8	Sl. flat., ellips.-fusoid, apic. at ends
Coniochaeta sp.[g]	47	11–14 × 4–6	Nar. ellips. or fusoid
C. nepalica	42	9–11 × 3–5 × 3–4	Flat., nar. ellips.
C. microspora	56	7–10 × 3–5	Flat., br. ellips., 1 end sl. apic.

[a] Species separation on length × width ratios of > 2:1 vs. < 2:1 employed in TABLE I necessitates rather arbitrary placement of the border-line species *C. sarothamni*, *C. tilakii*, *C. myricariae*, *C. phalacrocarpa*, *C. calva*, *C. niesslii*, and *C. microspora*.
[b] Size ranges are expanded to include all references cited. Measurements are presented as face views (length × width) × side views (thickness).
[c] Terminology is, as close as possible, that of reference descriptions. Abbreviations: apiculate (apic.), broadly (br.), circular (circ.), discoid (disc.), ellipsoid (ellips.), elliptical (ellipt.), face view (f.v.), flattened (flat.), globose (glob.), inequilateral (inequil.), irregular (irreg.), lenticular (lent.), narrowly (nar.), side view (s.v.), slightly (sl.).
[d] Potentially confusing. Only 2-dimensional measurements are noted. The width measurement, or what we assume to be the width, is similar to the thickness measurement of strains reported by other authors. Arx and Müller (1) and most pre-Cain (5) reports for this and other species seem to omit the measurement of the third dimension (the thickness).
[e] Munk (8,47) distinguishes lenticular (bi-convex) from discoidal (flattened). Others employ discoidal more generally to include lenticular.
[f] We have assumed this from the author's description.
[g] *Coniochaeta* sp. is unidentified by Munk (47) but noted "cfr. *Rosellinia xylarispora*."

nal internal cytoplasmic ribs in empty asci of *C. phalacrocarpa* which had been stained with dilute aqueous cotton blue. Similarly stained empty asci of *C. extramundana* failed to reveal any ribbing.

Ascospores.—TABLE I records ascospore sizes and shapes of *Coniochaeta* species. The narrowly ellipsoid to fusoid-spored and broadly ellipsoid to nearly globose-spored groupings of the species were originally suggested to the senior author by R. F. Cain (pers. com.). Future more careful observations of the ascospore shapes, which record any tendency toward slight or marked flattening, and more careful three dimensional measurement are, we believe, important keys to a better grasp of *Coniochaeta* species. This is especially true among the 8-spored forms with overlapping ascospore size ranges. The scanning electron microscope will be a great aid in this endeavor. The extent to which spores are flattened varies from species to species, with species in the broadly ellipsoid group seeming to have developed that feature more strongly than those in the ellipsoid-fusoid group. Flattening in some cases is described as occurring only on one side, in other cases as occurring on both sides and in the case of *C. extramundana* as occurring more strongly only along the edges on both sides. Both groups have some species whose spores tend to be ellipsoid-ovoid to strongly ovoid. In time, these may be considered in a category of their own.

Mature ascospores are one-celled, smooth and typically very dark near dark brown to black or occasionally in dark olivaceous or greyish shades. From our survey of the literature, spore color no longer appears to be the important character that Munk (47) considered it when he suggested that a coprophilous group tended toward dark-colored spores and a lignicolous group toward olive-greenish spores. Future comparative work will be necessary, however, before spore color differences can be discounted. A straight longitudinal germ slit extends from one end to the other along one side of the spore. Its position on the narrow edge (side view) and the spore's dark color often make it indistinct and difficult to locate in mature spores. Its presence, as noted earlier, is of paramount importance to membership in the genus. Though perhaps this feature was present on the spore, we were unable to find it noted in descriptions of *C. albido-mucosa, C. ambigua, C. williamsi, C. philocoproides, C. sordaria* and *C. gymnosporae.* According to N. Lundqvist (pers. com.), *C. philocoproides* (Scandinavian) and *C. sordaria* (Sclerom. Suec. Exs. 270, coll. orig.) have germ slits that go all the way around the spore, a feature he notes as being common among coprophilous species of the genus. This type of germ slit has not been reported previously for species of *Conio-*

chaeta although the related *Coniochaetidium ostreum* Malloch and Cain (39) has such a structure. Hyaline, gelatinous sheaths, ranging from narrow, irregular and indistinct to prominent, are present in some species of *Coniochaeta*, absent in others and not noted in most. As Cain commented in 1934 (5), this character appears most frequently among coprophilous species but even among these fresh ascospores must be examined and results are often variable.

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