The species of *Cordyceps* which are parasitic on *Elaphomyces*, a genus of subterranean ascomycetous fungi, are very closely related. By their parasitism they are markedly separated from other species which infect insects and spiders. However, in their general morphology they are similar to the other species of the genus. Two species, *C. ophioglossoides* and *C. capitata*, have been recognized on *Elaphomyces* in Europe. In addition, *C. canadensis* and *C. nigriceps* have been described from North America. Both however are usually treated as synonyms of *C. capitata*. *C. intermedia*, *C. japonica* and *C. jezoensis* have been described from Japan.

The stromata of these species are elongated, either clavate or capitate. They are attached to the ascocarps of the subterranean hosts either directly as in *C. capitata* or by rhizomorphs as in *C. ophioglossoides*. The stipe consists of compact somewhat interwoven longitudinal hyphae which continue upward spreading outward to form a central core of more or less densely interwoven hyphae in the upper ascogenous portion of the stroma. Covering this upper core is the perithecial layer. This consists of an inner tissue of loosely interwoven outwardly developing hyphae and an outer dense cortex. In some species the cortex is simple, consisting of densely irregularly interwoven hyphae, pseudoparenchymatous in section. In other species it is duplex, made up of an inner layer of densely interwoven hyphae and an outer layer having short parallel hyphae at right angles to the surface, palisade-like in section. These differences are used in this study as diagnostic distinctions in the separation of species. The perithecia are completely embedded. They have well differentiated walls of a compact pseudoparenchymatous structure and short ostioles lined with periphyses. The asci are long, cylindrical narrowing below. The walls are very thin, with hemispherical thickenings at the apices which are provided with narrow pores. The ascospores are hyaline, filiform, acuminate at the ends and multisepitate. They break into one-celled fragments. It is difficult to distinguish and study the ascospores and measurements are given of the part-spores. Since the terminal segments obscure differences they are excluded from the measurements which are given.

This treatment of the species for North America includes *C. ophioglossoides* and *C. capitata*. *C. nigriceps* is considered the same as *C. capitata*. *C. canadensis* is recognized as a valid species. Although *C. japonica* has not been seen from North America it probably occurs and consequently has been included. Three species are described as new.

In addition to the specimens in the Herbarium of the University of
Michigan (MICH), collections from the Farlow Herbarium (FH), the Herbarium of the New York Botanical Garden (NY), the Herbarium of the New York State Museum (NYS), the Herbarium of the University of California (UC) and the National Fungus Collections of the U.S. Bureau of Plant Industry (BPI) have been studied.1

KEY TO SPECIES

A. Stromata clavate, the ascogenous portion not abruptly enlarged from the stipe ........................................... B
B. Cortex of the ascogenous portion having an ectal layer of short parallel hyphae palisade-like in section; segments of ascospores 6-8 x 1-1.5 μ ............................................... 3. C. tenuispora
B. Cortex of ascogenous portion without a differentiated ectal layer .................................................................. C
C. Ascospore-segments 2-4 x 2 μ ............................................... 1. C. ophioglossoides
C. Ascospore-segments 10-18 x 3-4 μ ............................................... 2. C. japonica
D. Cortex of the ascogenous portion having an ectal layer of short parallel hyphae palisade-like in section .................................................................................................................. E
D. Cortex of the ascogenous portion without a differentiated ectal layer .................................................................. F
E. Ascospore-segments (18)34-48(54) x 4-6 μ .................................................................................. 5. C. canadensis
E. Ascospore-segments 3-6 x 2 μ .................................................................................. 6. C. californica
F. Ascospore-segments 8-25(32) x 2.5-3 μ .................................................................................. 4. C. capitata
F. Ascospore-segments 2-5 x 1.5-2 μ .................................................................................. 7. C. fracta

1. Cordyceps ophioglossoides (Fr.) Link Handb. 3: 347. 1833. (figs. 1 & 2). Sphaeria ophioglossoides Fr. Syst. Myc. 2: 324. 1832. Torrubia ophioglossoides Tul. Sel. Fung. Carp. 3: 20. 1865. Torrubia parasitica Schroeter, in Cohn Krypt. Flora Schles. 3 pt. 2: 277. 1908. Cordyceps parasitica P. Henn. Nerthus 6: 4. 1904 according to Seaver N. Am. Flora 5 pt. 1: 53. 1910. Stromata clavate, simple or rarely branched above, 2-8 cm long, usually attached to the host by rhizomorphs; ascogenous portion one-fourth to one-half the length, not sharply enlarged from the stipe, 3-8 mm thick, reddish brown to olivaceous brown, punctate with the ostioles of the perithecia, with a cortex consisting of one layer of closely interwoven hyphae pseudoparenchymatus in section; stipes 2-8 mm thick, olivaceous to dark brown; perithecia ovoid, 600-800 x 250-500 μ, entirely embedded in the stroma; ascii cylindrical, narrowing below, 400-450 x 5-8 μ, with a 

1 The writer is indebted to the Curators I. Mackenzie Lamb, Donald P. Rogers, Stanley Jay Smith, Lee Bonar and John A. Stevenson for the loan of specimens for this study.
hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled segments 2–4(5) × 1.5–2 μ.

On Elaphomyces cernulans, E. granulatus, E. muricatus, E. ravigatus and Elaphomyces sp.

Specimens studied: 165 from Connecticut (BPI, FH), District of Columbia (BPI), Iowa (BPI), Maine (FH, MICH, NY), Maryland (BPI, MICH), Massachusetts (FH, NY, BPI), Michigan (MICH), New Hampshire (FH, MICH, NY, BPI, UC), New York (FH, MICH, NY, BPI, NYS), New Jersey (NY), North Carolina (BPI, MICH), Ohio (MICH), Oregon (MICH), Pennsylvania (NY, MICH), Rhode Island (FH, NY), Tennessee (FH, MICH, BPI), Vermont (FH, NY, BPI), Virginia (MICH, NY, BPI), Washington (MICH), West Virginia (MICH, NY), Ontario (MICH, NY, BPI), Quebec (MICH, NY, BPI).

In addition 40 specimens from Austria, Belgium, Czechoslovakia, England, Finland, France, Germany, Hungary, Italy, Russia, Switzerland, and Japan were studied. Of the exsiccati cited by Fries in the Systema, Mengel-Nestler no. 565 has been studied and is proposed as the lectotype.

This is the most common species. It is distinguished by the small segments of the ascospores (fig. 2) which are 2–4 × 1.5–2 μ, and the clavate stromata in which the asogenous portion is not sharply enlarged from the stipes (fig. 1). The stromata are usually attached to the hosts by rhizomorphs (fig. 1). The cortex of the asogenous portion of the stromata is made up of very closely interwoven brown hyphae and does not have a differentiated ectal layer.

2. Cordyceps japonica Lloyd. Myc. Writings 6: 913. 1920. (fig. 3). Cordyceps nummurai Imai Trans. Sapporo Nat. Hist. Soc. 11: 32. 1929. Stromata clavate, 2.5–7 cm long, developing directly from the host; asogenous portion one-third to one-half of the length, 4–10 mm thick, rough from projecting ostioles, black when dry, with a cortex consisting of one layer of closely interwoven brown hyphae pseudoparenchymatous in section; stipes 2–7 mm thick, dark olivaceous brown or black; perithecia ovoid; 500–700 × 250–350 μ, entirely embedded; asci cylindrical, 250–400 × 7–10 μ with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindrical segments 10–18(20) × 2.5–4 μ.

On Elaphomyces japonica, Mikawa, Japan, J. Nummura, June 1916, type (BPI); Elaphomyces sp. Feldkirch, Austria, T. Murr. Oct. 1915 (FH).

Although this species has not been found in North America it probably occurs. It was originally reported by Lloyd (1916) as Cordyceps capitata var. canadensis. He later (1920) recognized it as a distinct species and named it C. japonica. The type from the Lloyd Herbarium of the National Fungus Collection, U.S. Department of Agriculture, has been studied. As illustrated by Lloyd (1916 fig. 860, 1920 fig. 1621) the stromata are clavate with less differentiation between the stipe and asogenous portion than in C. ophioglossoides. A specimen from Austria identified as C. ophioglossoides in the Farlow Herbarium is very similar in stromata, cortex and part-
yaline, filiform, 6-8 x 1-1.5 μ.

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spores. C. japonica is similar to C. ophioglossoides in clavate stromata and cortex. However, it differs in having the stromata directly attached to the host without rhizomorphs, and in having larger part-spores (fig. 3). Imai (1929) has described a clavate species, C. jezoensis, from Japan which has part-spores much larger 16-50 x 3.5-4.5 μ.

3. Cordyceps tenuispora sp. nov. (fig. 4). Stromatibus clavatis, 7 cm longis, supra 10-15 mm crassis, castaneis; cortice duplici interne pseudoparenchymato externae valliformi; perithecis anguste ovoidaeis, 750-1000 x 250-300 μ, immersis; asci cylindricis, 430-600 x 4-6 μ; ascosporis hyalinis, filiformibus, multisepatis, in unicellularia fragmenta scendentibus 6-8 x 1-1.5 μ.


Stromata up to 7 cm long, clavate; ascogenous portion obovoid, 10-15 x 8-10 mm, not abruptly enlarged from the stipe, dark chestnut-brown when dried, with a cortex having an inner layer of closely interwoven brown hyphae pseudoparenchymatous in section and an ectal layer of parallel hyaline hyphae palisade-like in section; stipes 3-5 mm thick, yellowish brown; perithecia narrowly ovoid, 750-1000 x 250-300 μ, narrowing to an acute base below, narrowing to a slender neck above, completely embedded; asci cylindric 430-600 x 4-6 μ, with a hemispherical thickening of the wall at the apex; ascosporae hyaline, filiform, breaking into 1-celled cylindric segments 6-8 x 1-1.5 μ.

Host not found, probably on Elaphomyces sp. Thornton, Delaware Co., Pennsylvania, May 27, 1919, C. F. Murphy type (NY); Cumberland, Maryland, W. T. Lakin, Lloyd Coll. 37226 (BPI).

This species has clavate stromata. It differs from both C. ophioglossoides and C. japonica in having a cortex with a palisade-like ectal layer. The ascospores are very slender (fig. 4) and the segments are somewhat longer than those of C. ophioglossoides and much shorter than those of C. japonica. Although the hosts were not collected there is not much doubt that they are species of Elaphomyces.

4. Cordyceps capitata (Fr.) Link. Handbuch 3: 347. 1833 (figs. 5-7). Sphaeria capitata Fr. Syst. Myc. 2: 324. 1832. Cordyceps nigriceps Peck Bul. Torrey Bot. Club 27: 21. 1900. Stromata capitata, 2-11 cm long; ascogenous portion abruptly enlarged into ovoid, spherical or subcyllindric heads, 5-20 x 5-15 mm, natal-brown, olivaceous-brown to olive-black, punctate to rough from the ostioles of the perithecia, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section; stipes 2-8 mm thick, ochre-yellow, olive-buff, olive-grey to olive-black, furfuraceous; perithecia ovoid, 650-950 x 250-420 μ, entirely embedded; asci cylindric, 350-540 x 10-12 μ, gradually narrowing below, with a hemispherical thickening of the wall at the apex; ascosporae hyaline, filiform, multisepate, breaking into I-celled, cylindric or somewhat fusoid segments 8-25(32) x 2.5-3 μ.

On Elaphomyces cervinus, E. granulatus and Eaphomyces sp.

Specimens studied: 46 from Alabama (MICH, BPI), Florida (FH, MICH, BPI, NY), Maine (NYS), Massachusetts (FH, BPI, NY, NYS),
North Carolina (BPI), Oregon (MICH), South Carolina (BPI, NY),
Virginia (MICH), Washington (MICH), Manitoba (BPI), Quebec (BPI);

Specimens from Belgium, France and Hungary have been studied, in-
cluding exsiccati, Flora Hungarica Exsiccatata Cent. 1 Fungi 8; Moug.-
and Nestler Stirpes Crypt. Vog.-Rhen. 763; Rehm Ascomycetes 1186b;
Ronnequiere Fungi Gall. Exs. 781; Westendorp et Wallays Herb. Crypt.
Belg. 21.

One of the results of this study has been the discovery that two species
have generally been included in Cordyceps capitata. Both have capitate
stromata (fig. 5). One has the segments of the ascospores cylindric or
slightly fusoid (fig. 7), 8-25 × 2.5-3 μ and the cortex of the ascogenous
portion of the stroma consisting of closely interwoven brown hyphae with-
out a differentiated ectal layer (fig. 6). The other has the segments of the
ascospore more or less fusoid (fig. 8), mostly 24-48 × 4-5 μ, often with the
end walls thickened and has a cortex of two layers (fig. 9). The inner layer
consists of closely interwoven brown hyphae (fig. 9). The outer layer is
made up of short parallel hyaline or slightly brown hyphae which are at
right angles to the surface of the stroma forming a palisade layer (fig. 10).

C. capitata, has been mostly described as having the larger spore segments
but specimens of both are in herbaria under that name and both occur in
Europe. It is not possible to determine to which the name Sphaeria capitata
Fr. applies from the description given by Fries in the Systema. However
he gives the following citation 'Moug.-Crypt. exs. C. VIII. ined.' This
evidently refers to Mougot et Nestler, Stirpes Cryptogamiae Voges- 
Rhenannae 763 which was issued in 1823 a year after the publication by
Fries. Three specimens of this number at the New York Botanical Garden
and the Farlow Herbarium have been available for study. They have
cylindric part-spores (12)14-22(32) × 2.5-3 μ and a cortex of densely
interven brwon hyphae without a differentiated ectal layer (figs. 6 & 7). The
Mougeot-Nestler no. 763 is accepted in this study as the lectotype of the
species C. capitata.

Peck (i.e.) described a species Cordyceps nigriceps which he distin-
guished from C. capitata by 'free margin of the club' and narrow spore
segments. He describes the segments of the ascospores as cylindric 20-40 ×
4 μ. The specimen of Cordyceps nigriceps collected by C. L. Fox in Maine
labeled type in the Herbarium of the New York State Museum has been
studied. It consists of one broken stroma. The segments of the ascospores
are cylindric, 14-22 × 3 μ and the cortex does not have a differentiated ectal
layer. The ascogenous portion projects slightly downward over the stipe.
It appears to be C. capitata as recognized here.

1910. Stromata capitate, 5–8 cm long; ascogenous portion abruptly enlarged into spherical, ovoid or subcylindric heads, 6–17 × 5–17 mm brown, olive-brown to black, punctate or roughened from the ostioles, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section having a well differentiated ectal layer of short hyaline or brownish parallel hyphae palisade-like in section; stipes 3–8 mm thick, yellow, olive-yellow, olive-brown or black, furfuraceous; perithecia ovoid, 550–1000 × 270–450 μ, entirely embedded; asci cylindric 300–550 × 12–16 μ, gradually narrowing below, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled, subfusoid segments, (18)24–48 × 4–5 μ, often with the end walls thickened.

On Elaphomyces granulatus, E. muricatus, E. variegatus and Elaphomyces sp.

Specimens studied: 58 from Alabama (MICH), Connecticut (FH), Delaware (NY), District of Columbia (BPI), Florida (NY, FH, BPI), Kentucky (NY, BPI), Maine (NY, FH), Maryland (BPI), Massachusetts (NY, FH, NYS, BPI), Michigan (MICH), New Jersey (NY), New York (MICH, CU, NY), Pennsylvania (BPI, NYS), Tennessee (FH, MICH), Virginia (BPI), Ontario (NY, FH, BPI, MICH), Mexico, Hidalgo (MICH).

Four specimens from Germany have been studied including Rehm Ascomycetes 1186; Sydow Myc. March. 279; Rabenh.-Winter-Paszchke Fungi Europ. 3957.

This species has been generally included in Cordyceps capitata. The species was described by Ells and Everhart (l.c.) from a collection made by Dearness no. 2641 at London, Canada. They state that the ascospores separate “into cylindrical segments, 10–20 (mostly 15) × 2–2.5 μ”. It is emphasized that “the slender cylindrical segments of the sporidia are only about half as long and wide as in C. capitata (Holmsk.) and very different from the globose-ellipsoidal joints of the sporidia of C. ophioglossoides (Ehr.).”

Among the specimens in the Ellis Herbarium which is now in the Herbarium of the New York Botanical Garden is a packet bearing the label “Cordyceps canadensis Ell. & Dearness”. This is pasted over writing on the flap of the packet which viewed by transmitted light reads as follows “Scarcely more than a form of C. ophioglossoides. 2641. Cordyceps canadensis Ell. & Dearness”. Below on the packet is written “When fresh quite different from C. ophioglossoides. Stipe shorter and stouter, head capitate, joints of sporidia oblong or fusoid 15 μ, asci 300–325 × 7–8 μ. Seems to agree with capitata except that joints are 15 instead of 25–40 μ. Joints 12–15 × 2–2½, 12–20.” These measurements have been crossed out and written on the packet in another handwriting is “joints 30–45 μ long”. This appears to be the specimen from which Cordyceps canadensis was described. It consists of a stipe and a portion of a spherical head. The cortex consists of two definite layers (fig. 9), an inner of closely interwoven hyphae and an ectal layer of short palisade hyphae (fig. 10). The segments
of the ascospore are fusoid (26)36–48 × 4 μ with the end walls thickened. With the emphasis which Ellis placed upon the small size of the spore segments in distinguishing the species *C. canadensis* this is puzzling. While Ellis’ description agrees with that of *C. capitata* as treated here the specimen is not that species but is the other species which has been commonly described as *C. capitata*. It seems necessary therefore to use the name *C. canadensis* for it. This species has the largest part-spores of the species which have been found in North America (fig. 8). Imai (1929) has described a species *C. jazoenis* from Japan with part-spores 16–50 × 3.5–4.5 μ. This has clave stromata similar to *C. ophioglossoides*.

6. **Cordyceps valliformis** sp. nov. **Stromatibus capitatis, 5–7 cm longis; capitulis sphaeroideis vel ovoideis, 3–15 × 3–12 mm, atrobrunneis; cortice duplice interne pseudoparenchymato externe valliformi; stipitibus 1–5 mm crassis, atrobrunneis; peritheciis ovoideis, 500–700 × 200–350 μ, immersis; ascis cylindricis, 230–460 × 6–8 μ; ascosporis hyalinis, filiformibus, multisepatis, in unicellularia fragmenta secendentibus 3–8 × 2 μ.


Stromata capitata, 5–7 cm long; heads spherical or ovoid, 3–15 × 3–12 mm, abruptly enlarged from the stipe, dark brown with a cortex having an inner layer of closely interwoven brown hyphae pseudoparenchymatous in section and an ectal layer of short hyaline parallel hyphae palisade-like in section; stipes 1–5 mm thick, dark brown, smooth or furfuraceous; perithecia ovoid, 500–700 × 200–350 μ, entirely embedded; ascis cylindric, 230–460 × 6–8 μ, with a hemispherical thickening of the wall at the apex; ascospores hyaline, filiform, multisepate, breaking into 1-celled cylindric segments 3–8 × 2 μ.


This species differs from *C. canadensis* in having much smaller segments of the ascospores. From *C. capitata* it differs in having a differentiated ectal layer of the cortex and smaller segments of the ascospores. *C. intermedia* Imai (1934) in Japan is similar in size of segments of the ascospores. It is described as attached to the host by short rhizomorphs. Information is not available concerning the cortex. Collections which Kobayasi (1941) has reported from Japan as *C. capitata* may belong here. He describes and figures a differentiated palisade-like ectal layer for the cortex. He however gives the segments of the ascospores as more fusoid and 13–23 × 2–4 μ.

7. **Cordyceps fracta** sp. nov. **Stromatibus capitatis, 1.5–2.5 cm longis; capitulis sphaeroideis, 2.5 mm erasis, purpureoatris; cortice pseudoparenchymato; stipitibus 0.5–1.0 mm erasis, flavoviridis vel olivaceis; peritheciis ovoideis, 500–600 × 250–350 μ, immersis; ascis cylindricis, 300–480 ×
walls thickened. The sporopores of the species V. K. Chari (1929) has described as 16-50 × 3.5-4.5 μ.

Stromata capitate, 1.5-2.5 cm long, arising directly from the host; heads 2.5 mm in diameter, purplish black, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section without a differentiated ectal layer; stipes slender, 0.5-1.0 mm thick, yellowish green to olivaceous; perithecia ovoid, 500-600 × 250-350 μ, entirely embedded; asci cylindrical, 300-480 × 5-6 μ, with wall hemispherically thickened at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindrical segments 2-5 × 1.5-2 μ.

On Elaphomyces appalachensis. Known only from the type specimen.

The specimen upon which this species is based was previously reported as C. intermedia Imai (Mains 1939). According to the description given by Imai, C. intermedia has larger stromata attached to the host by rhizomorphs and somewhat larger, specially wider, segments of the ascospores. C. fracta has part-spores (fig. 11) similar to C. valliformis which differs in having a differentiated ectal layer to the cortex.


d walls thickened. The sporopores of the species V. K. Charles described as 16-50 × 3.5-4.5 μ.

Stromata capitate, 1.5-2.5 cm long, arising directly from the host; heads 2.5 mm in diameter, purplish black, with a cortex of closely interwoven brown hyphae pseudoparenchymatous in section without a differentiated ectal layer; stipes slender, 0.5-1.0 mm thick, yellowish green to olivaceous; perithecia ovoid, 500-600 × 250-350 μ, entirely embedded; asci cylindrical, 300-480 × 5-6 μ, with wall hemispherically thickened at the apex; ascospores hyaline, filiform, multiseptate, breaking into 1-celled cylindrical segments 2-5 × 1.5-2 μ.

On Elaphomyces appalachensis. Known only from the type specimen.

The specimen upon which this species is based was previously reported as C. intermedia Imai (Mains 1939). According to the description given by Imai, C. intermedia has larger stromata attached to the host by rhizomorphs and somewhat larger, specially wider, segments of the ascospores. C. fracta has part-spores (fig. 11) similar to C. valliformis which differs in having a differentiated ectal layer to the cortex.

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