

THE ANAMORPH GENUS *HELICOON*

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A monograph is provided of the anamorph genus *Helicoon*, with keys to and illustrations of all described species.

The genus *Helicoon* was established by Morgan (1892) to accommodate those helicosporous Hyphomycetes characterized by the production of non-proliferating, cylindrical, barrel-shaped conidia. The conidia are borne on distinct conidiophores, which may in some instances be very short and inconspicuous. Members of the genus most closely resemble those species of *Helicodendron* which also produce cylindrical, barrel-shaped conidia, but which differ from species of *Helicoon* in that proliferation from previously formed conidia always occurs, resulting in the formation of tangled masses of conidia (Goos *et al.*, 1985). The conidia are always produced singly in *Helicoon*, and proliferation does not occur. As emphasized by Linder (1929), this distinction may require careful examination, particularly in young material.

As presently constituted, the genus *Helicoon* contains eight accepted species. Seven of these were included by Linder (1929) in his monograph of the helicosporous fungi. Moore (1955) listed nine species in his key, and Abdullah (1980) discussed the seven species he found in Great Britain. Six species previously assigned to the genus are considered doubtful and are not included in the keys presented here. No teleomorph of *Helicoon* is known.

Most members of the genus belong to the ecological group known as aero-aquatic Hyphomycetes, which have been described as 'indwelling organisms characterized by the production of purely vegetative mycelium in substrata under water and by the formation of conidia with a special flotation device, formed only when the substrate on which the fungus is growing is exposed to a moist atmosphere' (Fisher, 1977). As in *Helicodendron*, the coiled conidium of *Helicoon* is an effective air trap, giving the conidium great buoyancy in water

(Michaelides & Kendrick, 1982). Those species that are not aero-aquatic are usually found on sodden substrates in moist places, and thus also show a requirement for very moist growing conditions.

Methods for the collection, isolation and culture of the aero-aquatic species have been described in several publications (Field & Webster, 1983; Fisher, 1977; Fisher & Webster, 1981; Webster & Descals, 1981) and need not be repeated here.

Culture characteristics included in the species descriptions are based on the following growth conditions: (a) cultures were grown in Petri dishes on Oxoid malt extract agar (usually 0.1% or 2%), (b) the plates were inoculated at the centre with a 3 mm diam plug of mycelium from an actively growing culture, (c) cultures were incubated at 10-12° under natural daylight supplemented with continuous near-uv illumination, (d) the plates were sealed with Sellotape to prevent excessive drying.

An alternative method for inducing sporulation in these fungi is to culture them in flasks on 3 cm disks of sterilized leaves of *Fagus sylvatica* submerged in water and incubated at 10-15°. After the fungus has colonized the leaf disks, they are removed from the flasks, gently washed to remove excess mycelium, placed in Petri dishes on moist filter paper, and incubated under light at 10-12°. Sporulation will usually occur within one to two weeks.

In preparing this paper, we have examined herbarium specimens of all readily available material, including all specimens kept at Herb. IMI, and numerous isolates obtained from nature. We have not examined material of *H. spirale* Boedijn.

HELICOON Morgan, *Cincinnati Soc. Nat. Hist. Jl* 15: 50 (1892).

Helicosporous Hyphomycetes. *Conidiophores* micronematous or macronematous, mononematous, erect, simple or branched, hyaline to brown, smooth or verrucose. *Conidiogenous cells* blastic, integrated, terminal or intercalary, sympodial or determinate, denticulate. *Conidia* solitary, dry, acrogenous or acropleurogenous, consisting of a septate filament coiled in three planes to form a cylindrical or ellipsoidal conidium; hyaline, yellow or fuscous.

TYPE SPECIES *Helicoon sessile* Morgan

The conidia of *Helicoon* and *Helicodendron*, unlike those of *Helicosporium* and *Helicomycetes*, do not uncoil in water.

DESCRIPTION OF SPECIES

HELICOON AURATUM (Ellis) Morgan. *Cincinnati Soc. Nat. Hist. Jl* 15: 50 (1982). (Figs 1, 9)
Helicosporium auratum Ellis, *Bull. Torrey bot. Cl.* 6: 106 (1876).

Colony on natural substrate golden yellow, effuse, pulverulent. *Conidiophores* erect, simple or, rarely, sparingly branched, fuscous below, sub-hyaline at terminal cells, $32-150 \times 3.5-5.5 \mu\text{m}$ diam. *Conidia* borne singly, or in clusters, never in chains, acropleurogenous on the upper, hyaline portion of the conidiophore, hyaline to light-yellow. *Conidial filament* $2.5-3.6 \mu\text{m}$ diam, coiled in three planes to form an ovoid to elongate-elliptical conidium of 8-16 coils, and $14-27 \times 36-45 \mu\text{m}$ in size.

On 2% MA colonies grow slowly (2.5 cm in 21 d) at 20°. The mycelium is mostly immersed,

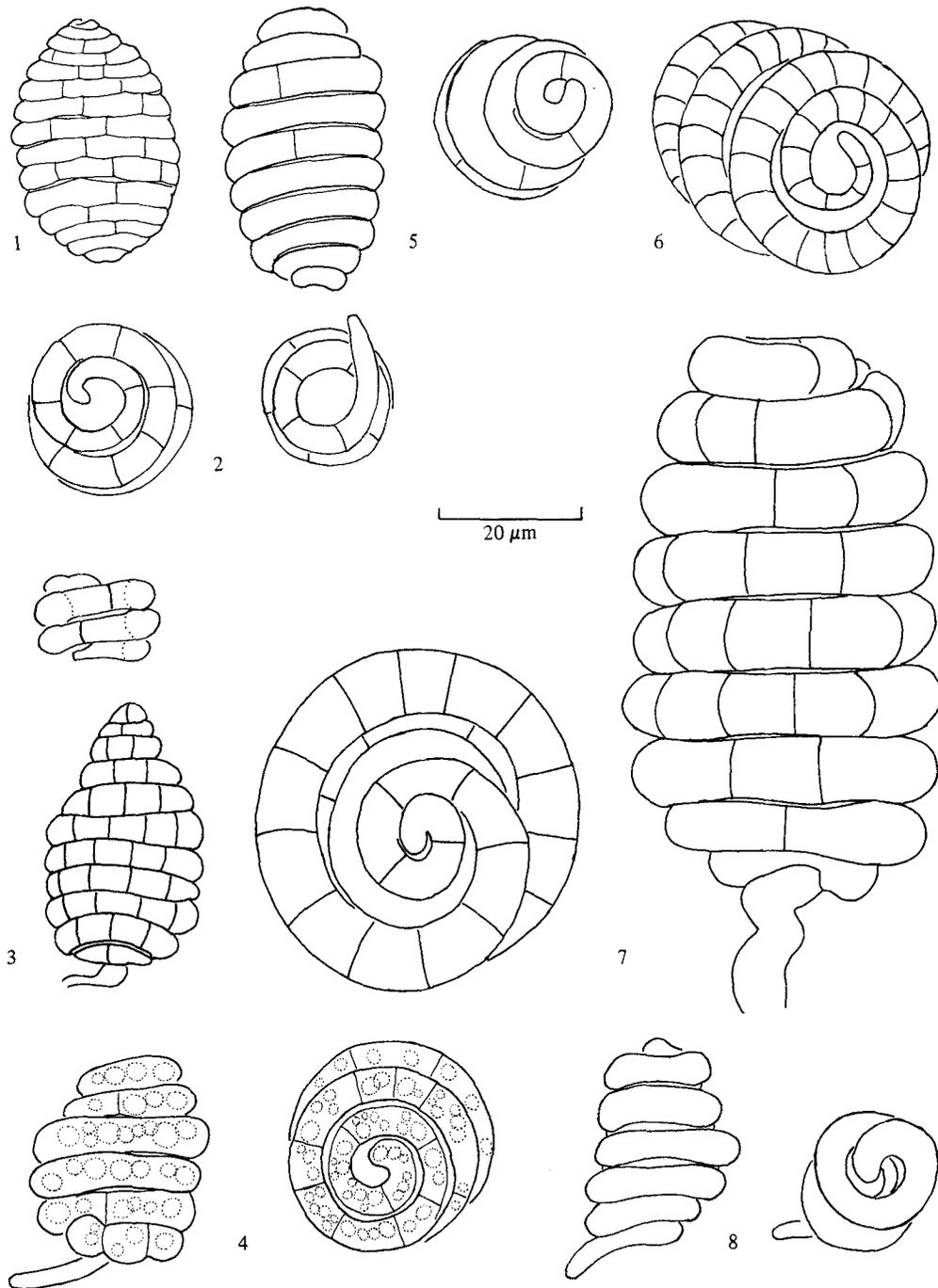
Table 1. Diagnostic characteristics of species of *Helicoon*

Species	Conidium colour	Conidium filament (μm)	Number of coils	Conidium size (μm)	Conidiophore size (μm)
<i>H. auratum</i>	y	2.5-3.6	8-16	14-27 × 36-45	32-150 × 3.5-5.5
<i>H. chlamydosporum</i>	f	3.0-4.0	4-5	14-17 × 15-18	15-90 × 3.5-4.5
<i>H. ellipticum</i>	lb	3.0-5.5	6-12	18-32 × 28-45	-800 × 4.5-5.5
<i>H. farinosum</i>	w	3.5-4.5	5-8	20-27 × 22-37	15-45 × 2.5-4.0
<i>H. fuscosporum</i>	f	2.7-4.5	6-12	17-25 × 20-50	-200 × 4.5-5.0
<i>H. pluriseptatum</i>	f	5.0-6.0	4-6	30-42 × 22-30	5-120 × 3.0-3.5
<i>H. richonis</i>	b	6.0-10	8-10	50-87 × 50-62	20-150 × 4.5
<i>H. sessile</i>	w	4.5-6.5	5-16	20-30 × 33-59	1-50 × 4.5

b, black; f, fuscous; lb, light brown; w, white; y, yellow.

KEY TO SPECIES OF *HELICOON*

1. Conidia in mass white 2
1. Conidia in mass distinctly coloured 3
 2. Conidia ellipsoidal, $20-30 \times 33-59 \mu\text{m}$; filaments $4.5-6.5 \mu\text{m}$, coiled 5-16 times, conidiophores inconspicuous *H. sessile*
 2. Conidia more or less ovoid in shape, $20-27 \times 22-37 \mu\text{m}$; filaments $3.5-4.5 \mu\text{m}$, coiled 5-8 times *H. farinosum*
3. Conidia in mass golden yellow, $14-27 \times 36-45 \mu\text{m}$; filaments $2.5-3.6 \mu\text{m}$, coiled 8-16 times *H. auratum*
3. Conidia brown to fuscous in mass 4
 4. Colonies floccose, conspicuous, conidiophores much branched, anastomosing; conidia light brown, $18-32 \times 28-45 \mu\text{m}$; filaments $3.0-5.5 \mu\text{m}$ *H. ellipticum*
 4. Colonies lacking floccose mycelium; conidiophores simple or little branched 5
5. Chlamydo-spores formed on agar media; conidia globose to subglobose, $14-17 \times 15-18 \mu\text{m}$; conidial filament $3.0-4.0 \mu\text{m}$ *H. chlamydosporum*
5. Chlamydo-spores lacking 6
 6. Conidia dark fuscous to black, large, $50-87 \times 50-62 \mu\text{m}$; conidial filament $6-10 \mu\text{m}$, coiled 8-10 times *H. richonis*
 6. Conidia smaller 7
 7. Conidial filament $2.7-4.5 \mu\text{m}$, coiled 6-12 times to form an oval conidium, $17-25 \times 20-50 \mu\text{m}$; conidiophores macronematous, up to $200 \mu\text{m}$ in length *H. fuscosporum*
 7. Conidial filament $5-6 \mu\text{m}$, loosely coiled 4-6 times, with 10-18 septa per coil, conidia oval, $30-42 \times 22-30 \mu\text{m}$ in size; conidiophores micronematous, $5-120 \mu\text{m}$ in length *H. pluriseptatum*



Figs 1–8. Conidia of *Helicoon* spp. Fig. 1: *H. auratum*. Fig. 2: *H. chlamydosporum*. Fig. 3: *H. ellipticum*. Fig. 4: *H. farinosum*. Fig. 5: *H. fuscosporum*. Fig. 6: *H. pluriseptatum*. Fig. 7: *H. richonis*. Fig. 8: *H. sessile*.

rarely superficial, cream, of septate hyphae, 1.5–2.5 μm diam, colony reverse cream. Conidia may be formed on tapwater agar supplemented with oat flakes.

Substrate. On partly buried and well-decayed wood in moist places.

Distribution. U.S.A. (Mass., R.I.). (Linder, 1929).

HELICOON CHLAMYDOSPORUM Abdullah & Webster, *Trans. Br. Mycol. Soc.* 75: 512 (1980).

(Figs 2, 10)

Colonies on 0.1% MEA reaching 2 cm diam after two weeks at 15°; *mycelium* loose, cottony, olivaceous brown, composed of branched, septate, light-brown hyphae, 2.5–3.5 μm diam, with abundant chlamydospores. *Chlamydospores* thick-walled, 7.5–14 μm diam, produced in groups, forming dark, fuscous to black sclerotium-like bodies, up to 400 μm diam. *Conidiophores* macro-nematous, 15–90 \times 3.5–4.5 μm , simple or branched, erect, septate, light fuscous, mostly arising from the aerial mycelium. *Conidiogenous cells* blastic, integrated, terminal and intercalary, sympodial or determinate, denticulate. *Conidia* solitary, dry, acropleurogenous. *Conidial filament* 3–4 μm diam, coiled 4–5 times in three planes to form a globose to subglobose conidium, 14–17 \times 15–18 μm .

Substrate. On submerged, decaying wood and leaves of *Quercus*; sheep dung; soil.

Distribution. Known only from Great Britain (Abdullah & Webster, 1980b).

HELICOON ELLIPTICUM (Peck) Morgan, *Cincinnati Soc. Nat. Hist. Jl* 15: 50 (1892). (Figs 3, 11)

Helicosporium ellipticum Peck, *Rept NY St Botanist* 27: 103 (1877).

Helicoryne ramosa Berkeley & Smith, *Gardn. Chron.* Apr. 1882.

Helicosporium ramosum (Berk. & Smith) Masee, *Br. Fungus Fl.* 3: 440–442 (1893).

Helicoon reticulatum Linder, *Ann. Mo. Bot. Gdn* 16: 327 (1929).

Colonies on natural substrate loose, cottony, separable from the substratum, brownish-olive; on 0.1% MEA, reaching 2 cm diam in 2 weeks at 15°; olivaceous-brown, cottony to velvety. *Mycelium* mostly superficial, composed of branched, septate hyphae, 4–4.5 μm diam. *Conidiophores* branched and anastomosing, micronematous to elongate, up to 800 μm in length and 4.5–5.5 μm diam. *Conidiogenous cells* blastic, integrated, intercalary, denticulate. *Conidia* borne singly on lateral, hyaline teeth; acropleurogenous. *Conidial filament* 3.0–5.5 μm diam, coiled tightly 6–12 times in three

planes to form an ellipsoidal conidium 18–32 \times 28–45 μm .

Substrate. On decaying coniferous wood and leaves in moist places.

Distribution. Great Britain, New Zealand, Sweden, U.S.A. (Ala., Conn., Maine, Mass., Miss.). (Abdullah, 1980; Hughes, 1978; Linder, 1929; Spec. No. 800, Herb. Upsaliensis, at Kew).

In describing *H. reticulatum*, Linder (1929) commented that this species closely resembles *H. ellipticum* in the appearance of the colonies and the conidiophores, but differs in having smaller conidia. Moore (1955) noted that in some collections of *H. ellipticum*, the range of conidium size extended over the range given for *H. reticulatum*, and suggested that the distinction noted by Linder may be due to environmental factors, rather than being a specific character. Abdullah (1980) found conidia of the type and of an authentic specimen deposited in the Farlow Herbarium to coincide in size with the measurements given by Linder for *H. ellipticum*. We have re-examined all the material of these two species kept at the Farlow Herbarium, and conclude that *H. reticulatum* should be considered a synonym of *H. ellipticum*.

HELICOON FARINOSUM Linder, *Ann. Mo Bot. Gdn* 16: 324–325 (1929). (Figs 4, 12)

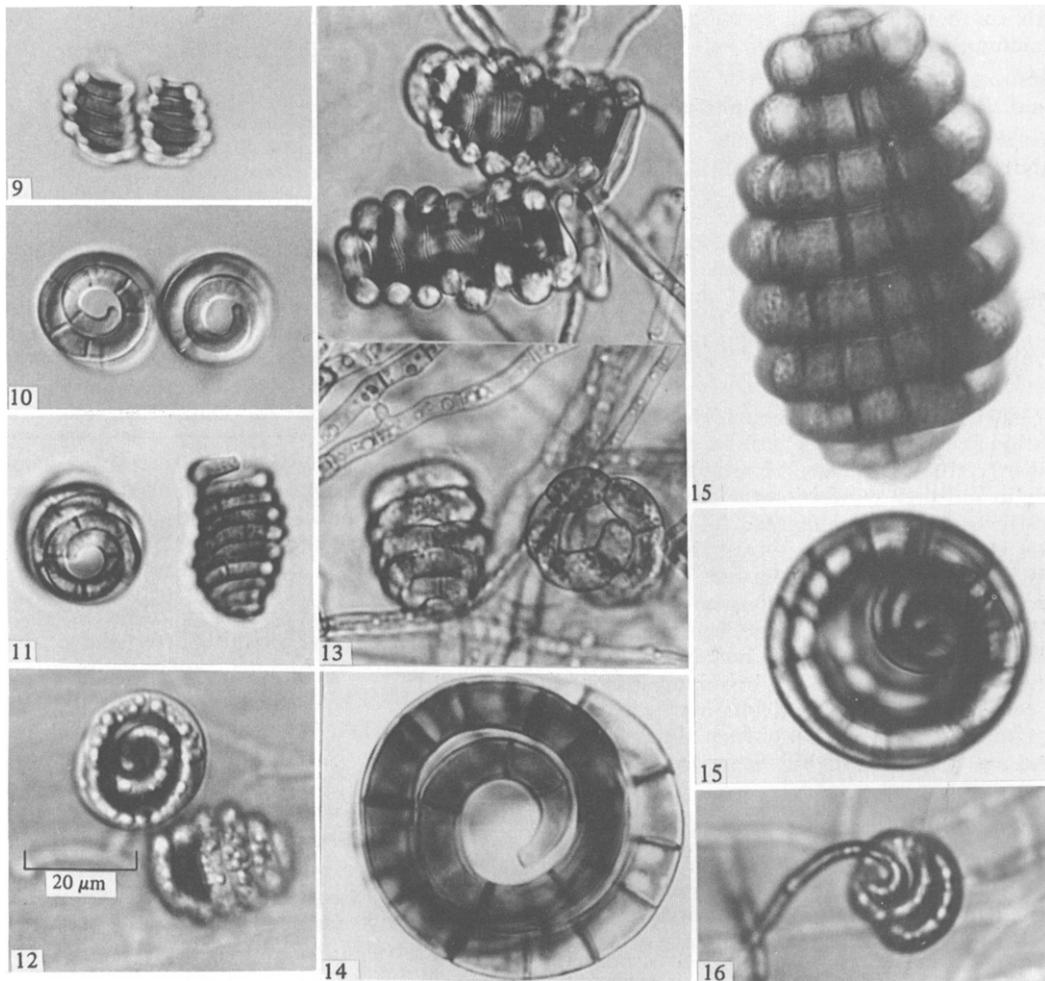
Colonies on natural substrate inconspicuous, white, powdery; on 0.1% MEA reaching 1.8 cm diam in 2 weeks at 15°; *mycelium* immersed, composed of branched, septate hyphae, 2.0–3.5 μm diam. *Conidiophores* micronematous, mononematous, inconspicuous, rarely branched, hyaline, straight or flexuous, smooth, 15–45 \times 2.5–4.0 μm . *Conidiogenous cells* monoblastic, integrated, terminal, determinate, denticulate. *Conidia* acro-genous, hyaline, solitary. *Conidial filament* 3.5–4.5 μm , coiled 5–8 times in three planes to form subglobose or ellipsoidal conidia, 20–27 \times 22–37 μm in size.

Substrate. Decaying wood.

Distribution. Great Britain, U.S.A. (Mass.). (Abdullah, 1980; Linder, 1929).

HELICOON FUSCOPORUM Linder, *Ann. Mo. Bot. Gdn* 16: 326 (1929). (Figs 5, 13)

Colony on natural substrate inconspicuous; on 0.1% MEA reaching 1.6 cm diam in 2 weeks at 15°; reverse fuscous black. *Mycelium* loose, cottony, dark brown, composed of branched, septate, light brown hyphae, 2.5–3.5 μm . *Conidiophores* macro-nematous, mononematous, erect, simple, or sparingly branched, fuscous below, subhyaline to dilute fuscous above, thick-walled, up to 200 μm in length



Figs 9–16. Conidia of *Helicoon* spp. Fig. 9: *H. auratum*. Fig. 10: *H. chlamydosporum*. Fig. 11: *H. ellipticum*. Fig. 12: *H. farinosum*. Fig. 13: *H. fuscosporum*. Fig. 14: *H. pluriseptatum*. Fig. 15: *H. richonis*. Fig. 16: *H. sessile*.

and 4.5–5.0 µm diam. *Conidiogenous cells* blastic, integrated, terminal or intercalary. *Conidia* acropleurogenous, fuscous, borne singly or more commonly in groups. *Conidial filament* 2.7–4.5 µm, coiled 6–12 times in three planes to form an ellipsoid to oval conidium 17–25 × 20–50 µm.

Substrate. On decaying leaves of various angiosperms from moist and submerged sites.

Distribution. Great Britain, Netherlands, Sweden, U.S.A. (Conn.) (Abdullah, 1980; Abdullah & Webster, 1980a; Beverwijk, 1954; Matsushima, 1975).

HELICOON PLURISEPTATUM van Beverwijk *Antonie van Leeuwenh. Ned. Tijds.* 20: 5 (1954).
(Figs 6, 14)

Colonies on 0.1% MEA reaching 3 cm diam in 2 weeks at 15°; reverse dark brown to black. *Mycelium* mostly superficial, composed of branched, septate, light brown, thick-walled hyphae, 3.0–3.5 µm diam. *Conidiophores* micronematous, mononematous, septate, simple or sparingly branched, light brown, 5–120 × 3.0–3.5 µm. *Conidia* simple, dry, acrogenous, light brown, becoming fuscous to fuscous-black. *Conidial filament*

5–6 μm , loosely coiled 4–6 times in three planes, with 10–18 septa per coil, forming a blunt, oval conidium, 30–42 \times 22–30 μm .

Substrate. On decaying leaves of *Betula*, *Quercus*, *Pinus*, *Rhododendron*, in moist places.

Distribution. Great Britain, Netherlands. (Abdullah, 1980; Beverwijk, 1954).

HELICOON RICHONIS (Boudier) Linder, *Ann. Mo Bot. Gdn* 16: 323–324 (1929). (Figs 7, 15)
Helicosporium richonis Boudier, *Icon. Mycol.* 3: tab. 599 (1910).

Helicoon ? *elegans* Arnaud, *Bull. Soc. mycol. Fr.* 69: 294 (1954).

Colonies darkening the substrate; on 0.1% MEA, reaching 1.8 cm diam in 2 weeks at 15°; olivaceous brown, cottony or velvety, becoming effused at the margin and slightly raised at the centre. *Mycelium* mostly superficial, composed of dark brown, branched septate hyphae, 2.5–4.0 μm diam; aerial hyphae verrucose or echinulate. *Conidiophores* macronematous, mononematous, 20–150 \times 4.5 μm , simple, erect, straight, or irregularly curved at the apex, septate, thick-walled. *Conidia* solitary, dry, acrogenous, at first hyaline, becoming fuscous to fuscous-black. *Conidial filament* 6–10 μm , multi-septate, tightly coiled 8–10 times in three planes to form an oval to slightly rounded conidium, 50–87 \times 50–62 μm .

Substrate. On decaying leaves and wood of *Quercus*, *Pinus*, *Salix*, *Populus* and unidentified species.

Distribution. Canada, Great Britain, France, Netherlands. (Michaelides & Kendrick, 1982 (as *H. elegans*); Abdullah, 1980; Linder, 1929; IMI 56107).

We have seen a specimen from an archaeological site near Beetley, Norfolk, England, presumed, from the abundance of pollen, to be a retting site for *Cannabis*, which appears to be assignable to *H. richonis*. The conidia of the subfossil are slightly larger than those of the extant species, but otherwise appear similar in shape and colour. The age of the specimen is about 650 years.

Arnaud (1954) illustrated and briefly described in French a fungus for which he proposed the name *Helicoon* ? *elegans*. His illustration is very good, and this, coupled with the conidial dimensions given for the fungus, leads us to conclude that this fungus can be properly assigned to *H. richonis*. The conidium size given by Arnaud is slightly larger than that reported for *H. richonis*, but is sufficiently near to suggest that this is the species he observed.

HELICOON SESSILE Morgan, *Cincinnati Soc. Nat. Hist. J.* 15: 50 (1892). (Figs 8, 16)

Helicoon fairmanii Sacc., *Annls mycol.* 4: 277 (1906).

Colonies on natural substrate pulverulent, inconspicuous, white to pinkish; on 0.1% MEA, reaching 1 cm diam in 4 weeks at 15°. *Mycelium* mostly immersed, composed of branched, septate hyphae. *Conidiophores* macronematous, mononematous, unbranched, hyaline, smooth, very short, seldom exceeding 50 μm in length in cultures. *Conidigenous cells* monoblastic, integrated, terminal, determinate. *Conidia* solitary, dry, acrogenous, hyaline to pinkish. *Conidial filament* smooth, septate, 4.5–6.5 μm , coiled 5–16 times in three planes to form an ellipsoidal conidium, 20–30 \times 30–59 μm .

On 2% MA colonies grow very slowly (1.2 cm in 28 d) at 20°. The mycelium is immersed, sometimes superficial, fluffy, white, made up of septate hyphae 2–3 μm diam, colony reverse beige.

Substrate. On decaying leaves, twigs and wood of *Acer*, *Quercus*, *Fagus*, and coniferous wood.

Distribution. Great Britain, U.S.A. (Mass., Maryland, N.J., Iowa) (Abdullah, 1980; Eaton & Jones, 1971; Linder, 1929; Shearer, 1972).

EXCLUDED AND DOUBTFUL SPECIES

Helicoon hyalosporum Arnaud, *Bull. Soc. Mycol. Fr.* 69: 294 (1954).

This species was named and illustrated by Arnaud (1954), but without a Latin diagnosis. The description is not adequate to place the species accurately.

Helicoon ovalisporum Krzemieniewska & Badura, *Acta Soc. Bot. Polon.* 23: 757–758 (1954).

Conidiophores erect, hyaline, ca 1 mm long, and 8.0 μm diam; the apex forming a spirally wound chainlet of conidia. *Conidia* ovate, colourless at first, becoming brown, 33.5–50.0 \times 13.0–20.0 μm .

In describing this fungus the authors compare it to *Helicoon tubulosum* (Reiss) Saccardo, considered a synonym of *Helicodendron tubulosum* by Linder (1929), and *H. politulum*, a fungus which was inadequately described and must be considered a questionable species (Linder, 1929; Moore, 1955). The illustration which accompanies Krzemieniewska & Badura's description shows a single conidiophore with a helical coil at the apex. It is difficult to determine whether the coil represents a single conidium, or a chain of conidia, as mentioned in the description. The height of the conidiophore, as

determined from the scale that accompanies the figure, is about 275 μm . The illustration suggests the genus *Helicocephalum*, and does not appear to be consistent with the genus *Helicoon*. Therefore, we have excluded it from consideration.

Helicoon spiralis Kamyschko, *Not. Syst. Sect. Crypt. Inst. Bot. Acad. Sci. USSR* 16: 95–99 (1963).

Colony on Czapek's agar reaching 0.5 cm diam in 10 d; slightly tomentose, grey to fuscous; reverse black at the centre, fuscous toward the margin. *Mycelium* composed of branched, septate hyphae, slightly constricted at the septa, 3.0–4.5 μm diam, breaking into cells 12–15 \times 3 μm . *Conidiophores* like the aerial mycelium, branched, septate, 60–80 μm in length, sometimes longer, and 2.5 μm diam, incurved at the apex and coiled helically up to 15 times, the spiral being 30 μm in length and 15–20 μm diam, and light grey. Cells of the conidiophores are swollen, clavate, being enlarged towards the apical end (racquet-shaped), and hyaline.

The *C. M. I. Index of Fungi* (3: 244) states that the name *H. spiralis* is a later homonym of *H. spirale* Boedijn. We have not examined the fungus, but the illustrations suggest a *Helicodendron* rather than a *Helicoon*.

Helicoon spirale Boedijn, *Rec. Trav. Bot. Néerl.* 26: 429 (1929).

Colony yellow, dusty, indistinct, with scant mycelium. *Mycelium* yellow-brown, composed of branched, septate hyphae, 2.5–6.5 μm diam, the tips becoming thin and hyaline, mostly 1.5 μm diam. *Conidia* formed on papillae that are 1–2 μm in length; coiled initially in a tight spiral, then uncoiling to form long, thin threads. They are hyaline to pale yellow, strongly septate, and 2.5–3.5 μm diam. The coiled conidium is 30–50 μm diam; the uncoiled conidium can be up to 400 μm in length.

We have not examined this fungus, but from the description and the illustration that accompanies it, it is clearly not a *Helicoon*. The fungus would appear to be better accommodated in the genus *Helicomycetes*.

Helicoon politulum (Schulzer) Lindau, in Rabenhorst's *Krypt. Fl. Deutschl., Oester. Schw.* 1(9): 277 (1908).

Helicosporium politulum Schulzer, *Flora* 60: 271 (1877).

Lindau's description of this fungus gives no measurement for the mycelium, conidiophores or the conidia. Linder (1929) regarded it as an

imperfectly known fungus, and we concur in this opinion.

Helicoon thaxteri Linder, *Mycologia* 25: 342–348 (1933).

This name was considered synonymous with *Helicorhoidion botryoideum* (Corda) Hughes by Hughes (1958). The genus *Helicorhoidion* differs from *Helicoon* in having dark, thick-walled, helicoid conidia resembling dictyosporos.

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