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BIATOROPSIS USNEARUM RÄSÄNEN, AND OTHER HETEROBASIDIOMYCETES ON *USNEA*

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Abstract: The pinkish galls on *Usnea*, often called *Biatoropsis usnearum* are shown to represent basidiomata of a previously unrecognized genus of heterobasidiomycetes with transversely septate basidia, to which the generic name *Biatoropsis* can be applied. The new genus is tentatively included in the Platygloeales. The hyphomycetous anamorph strongly resembles the genus *Hormomyces*. *Biatoropsis usnearum* is very frequent and widely distributed on *Usnea*, but has also been collected on *Protousnea*; the galls have been found parasitized by *Abrothallus usneae* and three species of *Lichenoconium*. Two other heterobasidiomycetes growing on *Usnea* are described: *Tremella santessonii* Diederich sp. nov. from Africa has transversally 1-septate basidia; *T. stevensiana* Diederich sp. nov. from Australia has longitudinally 1–3-septate basidia and a type of hyphomycetous anamorph poorly known in other species of Tremellales. Several other *Tremella*-like or gall-forming fungi on *Usnea* are briefly discussed.

Introduction

Gall-like deformations on thalli of *Usnea* are very frequent. The first author to study them was Dillenius (1742) who illustrated two species of the *Usnea barbata*-group (tab. 11, fig. 1, and tab. 12, fig. 6) in the *Historia Muscorum*. The first had normal disc-like apothecia, which he called *orbiculos*, and the second small fleshy nodules, closely appressed to the branches, which he described as *orbiculos raro profert, sunt vero ii exigui carnei, ramis absque limbo arcte adnati*. The small fleshy nodules of the second species clearly represent what later came to be described by Räsänen (1934) as *Biatoropsis usnearum*.

The 'Father of Lichenology' Erik Acharius commented several times on the two kinds of fruit-bodies to be found on species of *Usnea*. In a small paper in Swedish (Acharius 1795*a*), he wrote that the *fröredningsdelar* (i.e. seed-producing parts) of these lichens are flat and large, with a densely fringed rim in some species, whereas in others they appear nodule-like, are bulging, and have an inwardly curved rim without fibrils. Later in the same year, Acharius (1795*b*) described a new species of *Usnea* ('*Lichen comosus*') the *fröredningsdelar* with *scutellis convexiusculis, demum fuscis, torulosis*. These *scutellae*, which were well illustrated on the accompanying Plate 8, are evidently galls produced by *B. usnearum*. In his *Methodus lichenum*, Acharius (1803) distinguished between two kinds of apothecia in the genus *Usnea*, viz. *orbilla* and *cephalodia*; the former are the normal disc-shaped apothecia, and the latter we now know are basidiomata. In his *Lichenographia universalis*, Acharius (1810) does not mention *cephalodia* among the differential characters of the genus *Usnea*, but

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they are referred to in the description of the separate species, and on Plate 14 there are fine illustrations (in colour) of the *cephalodia* of *Usnea plicata* var. *comosa*.

Subsequent authors have described the gall-like deformations on thalli of *Usnea* species with the following terms: *cephalodia* (e.g. Gray 1821; Knowles 1929), *pseudo-cephalodia* (e.g. Smith 1918), or *patellulae* (Schaerer 1850). Räsänen (1934) described the galls as being the ascomata of a new ascomycete, *B. usnearum* Räsänen. The author recognized a well-developed hymenium, and hyaline, simple spores, 10–16 × 4–6·5 μm, which were rare and difficult to find. In a later publication (Räsänen 1939), the asci were said to be 8-spored. Santesson (1949) recognized that these convex pinkish bodies did not represent ascomata, and suggested that they were just galls caused by *Abrothallus parmeliarum* (Sommerf.) Arnold, the ascomata and conidiomata of which are frequently found growing on the galls. One year later, Galløe (1950) published careful anatomical studies on both the galls and the *Abrothallus* to specifically answer this question, and concluded that the galls, which he called *carpoids*, were not caused by the *Abrothallus* but were abortive apothecia. Von Keissler (1960) nevertheless repeats that the 'cephalodia' of *U. comosa* and other *Usnea* species are nothing but galls produced by the parasite *A. parmeliarum*.

In 1990, we studied Räsänen's type specimen and found that the galls are in reality basidiomata of a heterobasidiomycete with auricularioid basidia, and that no lichenicolous ascomycete is present in this material. The discovery that a large number of similar gall-like bodies growing on numerous other lichens (mainly macrolichens in the Lecanorales) also represent heterobasidiomycetes was reported to the Fourth International Mycological Congress in Regensburg in August 1990 (Diederich 1990). Two lichenicolous *Tremella* spp. have already been described: *T. lichenicola* Diederich on *Mycoblastus fucatus* (= *M. sterilis*), and *T. coppinsii* Diederich & Marson on *Platismatia* (Diederich 1986; Diederich & Marson 1988).

The ascospores described by Räsänen proved to represent young probasidia. As such ellipsoid or elongate non-septate hyaline probasidia recall asci, spores or conidia, and as the lichenologists who collected infected *Usnea* species generally had little experience with heterobasidiomycetes, the true nature of *B. usnearum*, as well as of other lichenicolous heterobasidiomycetes, has remained a mystery to lichenologists for two and a half centuries. The fact that lichens with strange galls that have no name, and the causal agent of which is unknown, are difficult to integrate into herbaria and to cite in publications has unfortunately induced most lichenologists to discard specimens with heterobasidiomycetes. The chance that *B. usnearum* had been given a name nearly 60 years ago has fortunately resulted in the existence of a large number of herbarium specimens from the whole world. In addition, there are a number of collections erroneously filed as *Abrothallus parmeliarum* or *A. usneae* Rabenh. that contain only *B. usnearum*.

Materials and Methods

We have studied material from B, E, ESS, GZU, H, HO, IMI, LG, LUX, M, STU, UBC and UPS, and from the private herbaria of A. Aptroot, P. v. d. Boom, M. Skytte Christiansen, C. Coste, P. Diederich, T. Feuerer, A. Gómez-Bolea, J. Hafellner, T. Lumbsch, C. Scheidegger, and C.

Smith. The complete *Usnea* collection of LG has been examined. In addition we have received a large number of infected *Usnea* specimens, mainly from Australia, from Dr G. N. Stevens, that are now kept in the herbarium of P. Diederich.

A certain number of specimens, including all those with abnormal morphological characters, have been studied microscopically (× 1000), using several stains, but mostly Phloxin (1 % in water) after pre-treatment with 5 % KOH.

In many specimens the determination of the host *Usnea* was difficult or impossible, and so the variability of *B. usnearum* objectively correlated at least partly with the host species could not be studied statistically. The microscopic description below is based on only a small number of representative specimens.

Results

Biatoropsis usnearum Räsänen

Ann. bot. Soc. Zool.-bot. fenn. '*Vanamo*' 5(9): 8 (1934). Type: Finland: Ostrobottnia borealis, Simo Kuusella, on '*Usnea comosa*', 1 July 1915, *Räsänen* (H-lectotype!; IMI-isotype, fide Hawksworth).

Icones: Acharius (1795*b*: tab. 8), Acharius (1810: tab. 14), Dillenius (1742: tab. 12, fig. 6, a–i), Galløe (1950: pl. 106 [fig. 697, 704], 112 [fig. 740–744], 113 [fig. 745–747, 749–751], 114 [fig. 752–754], 115 [fig. 763–764]), Schaerer (1850: tab. I, fig. 1c).

(Figs 1–4)

Basidiomata extremely variable in form, size and colour, generally subspherical and convex with a constricted base, often with lobate margins, sometimes flattened or with a concave central part, rarely effuse and covering larger areas around the branches of the host, surface smooth, rarely tuberculate, cartilaginous, pale pinkish, reddish brown, dark brown or black, 0·2–2·5 mm diam.; context hyphae 2–3 μm wide, mostly uniform, the walls not markedly thickened, clamps absent; haustorial branches frequent, mother cell subspherical or sometimes elongate, 2·5–4·5 μm diam., haustorial filament 0·5–1 μm thick, 3–7 μm long. *Hymenium* hyaline, sometimes reddish brown in the upper part and then yellow in 5 % KOH, thickness variable, containing numerous probasidia. *Basidia*, when mature, clavate to subcylindrical, with 1–3 transverse septa, 20–44 × 3–6·5 μm; epibasidia 2–3 μm thick, to 85 μm long. *Basidiospores* subglobose to ellipsoid, with a distinct apiculum, 4·5–8 × 4–7·5 μm. *Anamorph* hyphomycetous, often present, forming long branching chains of hyaline, ellipsoid, simple conidia, 3–5 × 2–3·5 μm.

Hosts: Usnea spp. and *Protousnea dusenii*. Numerous specimens of *Usnea* subgen. *Neuropogon* attacked by lichenicolous fungi were never found to support basidiomata of *B. usnearum*. Field studies have shown that in mixed populations of several *Usnea* species, not all species are attacked. As the taxonomy of the genus *Usnea* has been poorly known for a long time, many herbarium specimens are unreliably, or only provisionally determined, so that the full host-range of *B. usnearum* is difficult to assess at this time. We have seen specimens of the following species (names as indicated on herbarium labels; * = determined by Dr P. Clerc; ** = determined by Dr G. N. Stevens): *U. angulata*** (= *U. torquescens*), *U. articulata*, *U. barbata* coll., *U. bicolorata***,

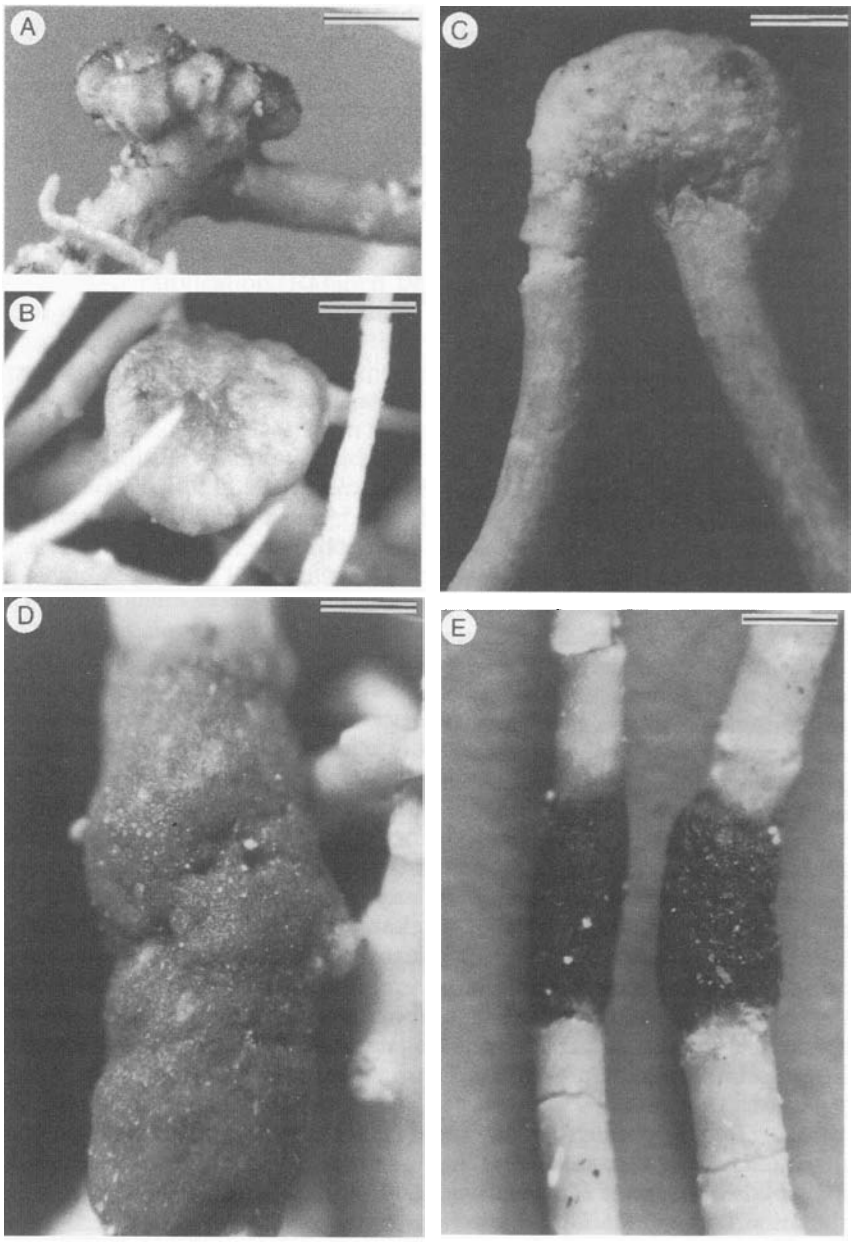

FIG. 1. Basidiomata of *Biatoropsis usnearum*. A, B, typical basidiomata. C, typical deformation of the host caused by *B. usnearum* (*Lambinon* 72/1083, LG). D, reddish brown poorly delimited basidioma spreading over the host thallus (*Diederich* 9513, hb. Diederich). E, dark brown to black basidiomata all round the host thallus (*Santesson* S353, UPS). Scale = 250 μm.

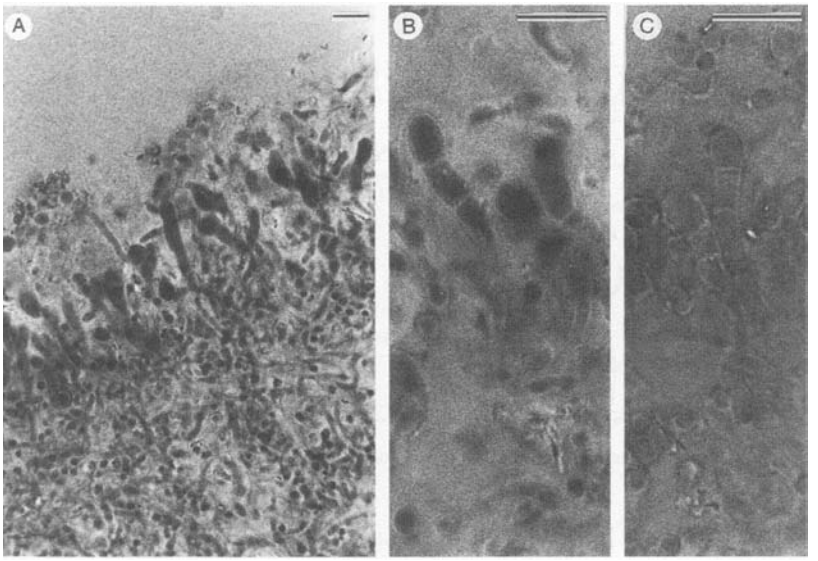

FIG. 2. Hymenium and basidia of *Biatoropsis usnearum* (H—holotype). Scale = 10 μm.

U. cf. *caucasica*, *U. ceratina**, *U. confusa***, *U. cornuta**, *U.* cf. *elongata*, *U. esperantiana**, *U. eulychniae* (LG—isotype), *U. exasperata*, *U. faginea*, *U. filipendula*, *U. flammea*, *U. flavescens*, *U. florida**, *U. fragilescens* var. *mollis**, *U. fulvoreagens*, *U. glabrata*, *U. glabrescens*, *U. hawaiiensis*, *U. himalayana* f. *major*, *U. hirta*, *U. inermis***, *U. intexta*, *U. lacerata*, *U. lapponica**, *U. laricina*, *U. lethariiformis*, *U. misamisensis*, *U. molliuscula***, *U. nidifica***, *U. nidulifera*, *U. oncodes***, *U. pectinata*, *U. rigida* s. lat.*, *U. rubescens***, *U. rubicunda***, *U. sanguinea***, *U. similis*, *U. simplicissima*, *U. sorediifera*, *U. subalpina***, *U. subeciliata***, *U. subfloridana**, *U.* aff. *tasmaniensis***, *U. torulosa***, *U. trachyna*, *U. undulata*** and *U. xanthopoga***. In some collections the host lichen does not seem to be damaged by the presence of *B. usnearum*, but in numerous specimens a characteristic curvature of the *Usnea* branches occurs (see Fig. 1C).

Distribution: We have seen 294 specimens of *B. usnearum* from most countries of Europe (Austria, Belgium, Denmark, Finland, France, Germany, Great Britain, Greece, Ireland, Italy, Luxembourg, Norway, Portugal, Russia, Spain, Sweden, Switzerland), from Africa (Kenya, Rwanda, Tanzania, Zaire, Zimbabwe), North America (Canada, U.S.A.), South America (Argentina, Chile, Colombia, Ecuador [Galapagos Islands], Peru, Venezuela), the Pacific Ocean (Hawaii), Asia (India, Japan, Malaysia, Mongolia, Nepal, Papua New Guinea) and Australia (incl. Tasmania). Its range may be considered as cosmopolitan, despite the lack of information from several regions (Fig. 3).

Discussion: For a long time we hesitated to treat specimens with pale and black basidiomata as conspecific. Although some specimens examined were

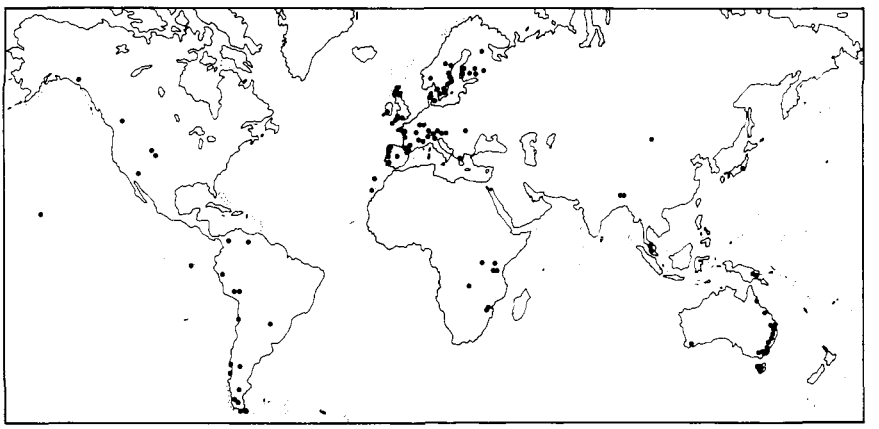

FIG. 3. World distribution of *Biatoropsis usnearum*.

attacked by parasitic fungicolous fungi with brown hyphae, or the basidiomata were covered with brown conidia of the fungiculous *Lichenoconium lecanorae*, in most cases the dark brown colour belongs to *B. usnearum* itself, the concentration of this pigment being responsible for the colour of the basidioma.

In a few specimens the reddish brown or black basidiomata are flattened and cover larger, poorly delimited areas of the host thallus (Fig. 1D–E). They appear distinct from typical basidiomata, but as the microscopic features correspond in all details with *B. usnearum*, and as intermediate morphological forms have been observed, we include these specimens in the concept of this species.

Well-developed, strongly convex basidiomata are sometimes made entirely of the tissue of the lichenicolous fungus, and the host hyphae can be recognized only at the base of the basidioma. In most collections, however, the pink or brown bodies consist of both the hyphae of the heterobasidiomycete and those of the host lichen, and sometimes even additional hyphae of a fungicolous *Abrothallus* or *Lichenoconium* species can be distinguished. These structures are most adequately referred to as galls, not as true basidiomata.

Even though *Biatoropsis* was initially described as a genus of ascomycetes, this generic name can nevertheless be used for *B. usnearum*, as the lectotype specimen clearly shows a hymenium with basidia (and no asci!), and Räsänen evidently saw basidia but interpreted them incorrectly. There is no nomenclatural obstacle to the use of his name for the basidiomycete teleomorph he clearly saw. Räsänen (1934) states in his original description that the hymenium turned blue with iodine. As neither the hyphae of the *Usnea* nor those of *B. usnearum* are coloured blue with iodine, it is possible that hyphae of *A. usneae* were present at least in some galls studied by Räsänen. As the lectotype specimen is very poor, we did not check the iodine reaction inside the galls. As the galls in the type specimen also include hyphae of the host, and perhaps even hyphae of *A. usneae* (but no ascomata!), we herewith lectotypify the name *B. usnearum* on the heterobasidiomycete present in the galls.

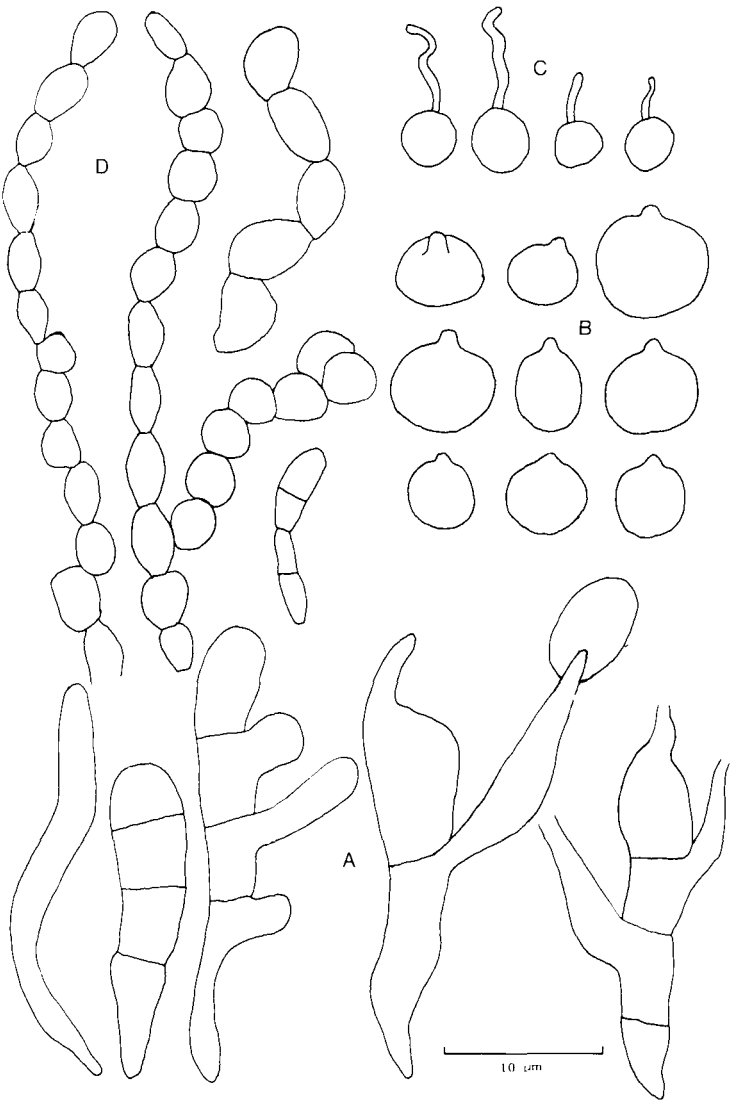

FIG. 4. *Biatoropsis usnearum*. A, basidia in different stages of development (*Christiansen* 4967, hb. Christiansen). B, basidiospores (*Doppelbauer* s.n., M). C, haustorial branches (*Lumbsch* 785, M). D, *Hormomyces*-like anamorph (*Lumbsch* 785, M; Räsänen, *Lichenoth. Fenn.* 599, M; *Wirth* 19891, M).

The systematic position of *B. usnearum* is unclear. Although several species of *Tremella* s.str. are known that have transverse or oblique basidial septa (e.g. *T. santessonii*, described below), and despite the typical tremelloid basidiospores and haustorial branches (Fig. 4), we tentatively exclude this species from the Tremellales and include it in the Platygloeales because of its

basidia, the absence of clamp connections, and its close resemblance to the genus *Mycogloea*. The definite inclusion of *Biatoropsis* in the Platygloeales must, however, await an ultrastructural analysis of the septal pores (Moore 1990). The genus *Biatoropsis* clearly differs from *Mycogloea* Olive in the non-deciduous basidia, and from related genera (e.g. *Platygloea* Schröter s.lat.) in the absence of distinct probasidia (i.e. swollen cells under the septate portion of the basidia).

The anamorph, present in numerous specimens (see Fig. 4D), strongly resembles the hyphomycete *Hormomyces aurantiacus* Bonorden (Tubaki 1976). This species has previously been suggested to be the anamorph of a *Tremella*, but no convincing evidence for this statement has been given until now.

Exsiccatae: Rabenhorst *Lich. Europ.* 551 (E).—**Finland**: Räsänen *Lich. Fenn.* 599 (B, H, M, hb. Diederich).—**France:** Follmann *Lich. Exs. Sel.* 257 (LG, hb. M. S. Christiansen 4967).—**U.S.A.:** Weber & McVean *Lich. Exs. Colorado* 205 (LG); Weber *Lich. Exs. Colorado* 432 (LG).—**Chile:** Follmann *Lich. Exs. Sel.* 40 (hb. M. S. Christiansen), 60 (LG).—**Ecuador:** Weber & Lanier *Lich. Exs. Colorado* 501 (LG).—**Tanzania:** Vězda *Lich. Sel. Exs.* 1174 (LG), 1472 (LG).—**India:** Kurokawa & Kashiwadani *Lich. Rar. Crit. Exs.* 339 (LG).—**Japan:** Kurokawa & Kashiwadani *Lich. Rar. Crit. Exs.* 350 (LG), 450 (LG).—**Malaysia:** Kurokawa *Lich. Rar. Crit. Exs.* 298 (LG).—**Nepal:** Kurokawa & Kashiwadani *Lich. Rar. Crit. Exs.* 340 (LG).—**Papua New Guinea:** Kurokawa & Kashiwadani *Lich. Rar. Crit. Exs.* 548 (LG).—**Australia:** Weber & McVean *Lich. Exs. Colorado* 328 (LG, hb. Diederich).

Additional specimens examined: (a) On *Usnea*. Numbers refer to the number of specimens; abbreviations of private herbaria: *Ap*–A. Aptroot, *Bo*–P. v. d. Boom, *Ch*–M. S. Christiansen, *Co*–C. Coste, *Di*–P. Diederich, *Fe*–T. Feuerer, *Go*–A. Gómez-Bolea, *Ha*–J. Hafellner, *Lu*-T. Lumbsch, *Sc*-C. Scheidegger, *Sm*-C. Smith.

Austria: *Kärnten* (4: GZU, Bo, Ch); *Salzburg* (4: Di); *Steiermark* (2: GZU, Bo); *Tirol* (4: GZU, Ha).—**Belgium** (2: LG, Di).—**Denmark:** *Jylland* (4: Ch); *Sjaelland* (1: Ch).—**Finland:** *Ostrobottnia australis* (2: H); *Regio kuusamoënsis* (1: H); *Satakunta* (1: H); *Savonia australis* (1: H); *Savonia borealis* (11: B, E, GZU, H, IMI, LG, M, UPS, Ch); *Tavastia australis* (2: H).—**France:** *Bretagne* (2: ESS, UPS); *Finistère* (2: UPS); *Hautes-Pyrénées* (3: LG, Bo, Di); *Lot* (1: B); *Pyrénées-Atlantiques* (4: Bo, Di); *Pyrénées-Orientales* (1: Di); *Savoie* (1: Di); *Seine-et-Marne* (1: Di); *Tarn* (1: Co); *Vendée* (1: Di).—**Germany:** *Baden-Württemberg* (3: M, Lu).—**Great Britain:** *Isles of Scilly* (2: UPS); *VC1* (2: Di); *VC2* (1: IMI); *VC3* (2: E, Di); *VC5* (2: Di); *VC11* (1: Di); *VC96* (1: Di); *VC104* (6: Di); *VC105* (3: Bo); *VC108* (1: Bo).—**Greece:** (1: Sc).—**Ireland:** *Kerry* (1: GZU).—**Italy:** *Trentino-Alto-Adige* (9: IMI, Bo, Fe, Lu).—**Luxembourg** (5: LG, LUX, Di).—**Norway:** *Oppland* (2: Bo, Ch).—**Portugal:** *Algarve* (1: Bo); *Estremadura* (1: Bo); *Madeira* (2: Di); *Minho* (3: Bo).—**Russia:** *Karelia* (8: H, UPS).—**Spain:** *Canary Islands* (4: LG, Di, Fe); *Castilla la Nueva* (2: Bo); *Catalunia* (1: Go); *Galicia* (1: LG).—**Sweden:** *Bohuslän* (1: UPS); *Gästrikland* (1: Bo); *Hälsingland* (1: UPS); *Jämtland* (1: UPS); *Medelpad* (1: UPS); *Småland* (1: UPS); *Södermanland* (1: E); *Uppland* (18: UPS); *Västergötland* (4: UPS); *Östergötland* (1: UPS).—**Switzerland:** *Valais* (4: Bo); *Appenzell* (1: Sc).

Kenya (1: Di).—**Rwanda** (16: LG).—**Tanzania** (1: LG).—**Zaire** (6: LG).—**Zimbabwe** (8: LG).

Canada: *British Columbia* (4: IMI, UBC); *Yukon* (1: Ch).—**U.S.A.:** *Arizona* (1: B).

Argentina: *Corrientes* (2: LG); *Rio Negro* (2: UPS); *Santa Cruz* (3: STU); *Tierra del Fuego* (2: UPS).—**Chile:** *Chiloé* (2: UPS); *Terr. Magallanes* (2: UPS); *Tierra del Fuego* (1: UPS); *Valdivia* (4: UPS).—**Colombia** (1: Ap).—**Peru:** *Amazonas* (1: GZU); *Apurimac* (1: GZU); *Cuzco* (2: UPS).—**Venezuela** (1: UPS).

Hawaii (1: Di, Sm).

Malaysia: *Pinang* (1: Ap).—**Mongolia** (1: H).—**Papua New Guinea** (11: LG, Di).

Australia: *New South Wales* (9: Di); **Queensland** (11: Di); Tasmania (15: HO, UPS, Di); *Victoria* (6: Di); *Western Australia* (2: Di).

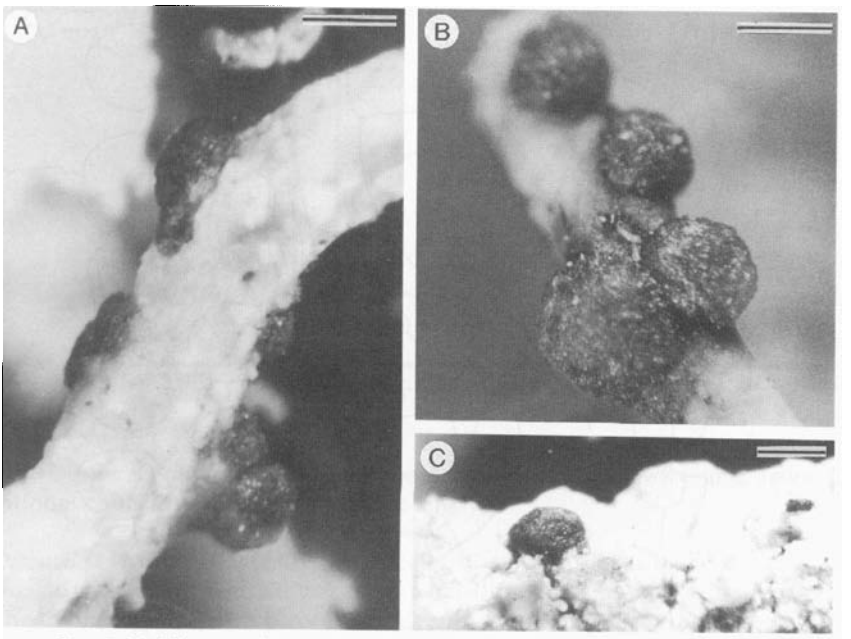

FIG. 5. Basidiomata of *Tremella santessonii* (LG—holotype). Scale = 250 μm.

(b) On *Protousnea dusenii*.

Chile: *Tierra del Fuego*, Sierra Sorondo, the northern slope, above Las Cotorras (about 20 km ENE of Ushuaia), 1940, *Santesson* 841b (UPS).

Tremella santessonii Diederich sp. nov.

Basidiomata lichenicola, in thallis *Usneis* crescentia, pulvinata, discoidea, firme gelatinosa, rufa, 0·2–0·3 mm diam. Hyphae 2·5–6 μm latae, fibulatae, vel 1–1·5 μm diam., non fibulatae. Haustoria desunt. Probasidia clavata vel ellipsoidea, transverse 1-septata, 16–21 × 8–9 μm. Epibasidia ad 60 μm longa, 2·5–3·5 μm lata. Basidiosporae subglobosae, 6·5–8 × 5·5–7 μm.

Typus: Zimbabwe ['Rhodésie'], entre Melsetter et Cashel, dans un fourré à *Philippia* et *Brachystegia*, on *Usnea*, alt. 1900 m, 10 January 1974, *C. Vanden Berghen* 748b (LG—holotypus; H, hb. Diederich—isotypi).

(Figs 5–7)

Basidiomata pulvinate, discoid, firm gelatinous, reddish brown, 0·2–0·3 mm diam.; context hyphae of two kinds, either 2·5–6 μm wide, thick-walled, with clamp connections, or 1–1·5 μm diam., thin-walled, with no clamp connections; haustorial branches not observed. *Hymenium* hyaline, containing numerous probasidia; probasidial initials clavate, proliferations occurring through the basal clamps. *Basidia*, when mature, ellipsoid, with 1 transverse septum, 16–21 × 8–9 μm, the upper cell 7–10 μm long and 8–9 μm broad, the lower cell more elongate, with an attenuated stalk-like base, 9–13 μm long and 6–10 μm broad; septum rarely diagonal or longitudinal; epibasidia 2·5–3·5 μm thick, up to 60 μm long. *Basidiospores* subglobose, with a large apiculum, 6·5–8 × 5·5–7 μm. *Anamorph* absent.

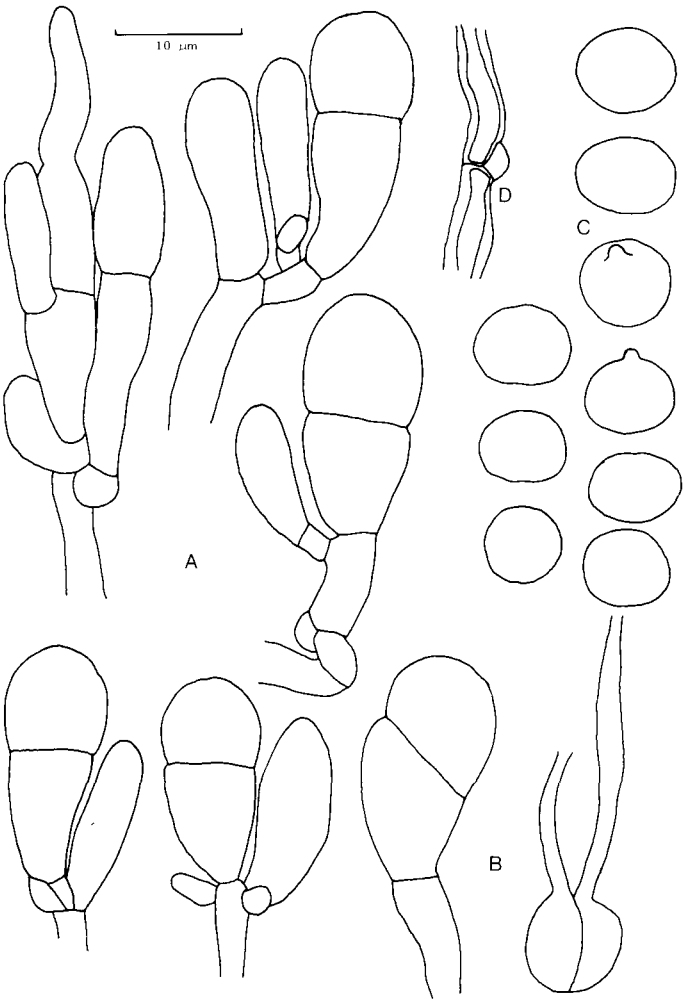

FIG. 6. *Tremella santessonii* (LG—holotype). A, Basidia with transverse septa. B, Basidia with oblique and longitudinal septa. C, Basidiospores. D, Hypha with clamp connection.

Etymology: The new species is named in honour of Prof. Rolf Santesson (Uppsala) who has made his important collections of lichenicolous heterobasidiomycetes, including more than 50 specimens of *B. usnearum*, available to us.

Hosts: Usnea spp. The basidiomata grow on the host thallus, which is not modified. The type collection consisted of an assemblage of several *Usnea* species, in which one single species was attacked by the new fungus, and another species by *B. usnearum*. In the Rwanda specimen the same thallus of *Usnea* is infected by both *T. santessonii* and *B. usnearum*.

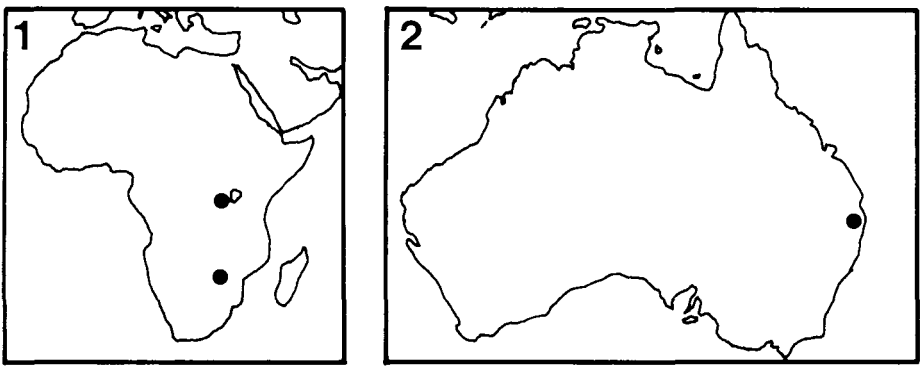

FIG. 7. World distribution of (1) *T. santessonii* and (2) *T. stevensiana*.

Distribution: Known from the type locality in Zimbabwe and from an additional collection from Rwanda (see Fig. 7).

Discussion: Morphologically this species is very similar to some forms of *B. usnearum* with small, regular dark brown basidiomata. It is easily distinguished by the hyphae having clamp connections, the constantly 1-septate basidia with an apical cell being as long as broad, and a narrower elongate basal cell. It is interesting to note that the majority of basidia have transverse septa, whereas some have diagonal or even typical tremelloid longitudinal septa, the basidia being subglobose, 8–12 μm diam. (see Fig. 6B).

Additional specimen examined: **Rwanda:** Bugesera, Karama, 1972, *Lambinon* 72/1083 (LG, TUB, hb. Diederich).

Tremella stevensiana Diederich sp. nov.

Basidiomata applanata ad pulvinata, discoidea, cartilaginea, ochracea ad atrorufa, 0·1–0·3 (–0·5) mm diam. Hyphae 1–3·5 μm latae, fibulatae. Haustoria desunt. Probasidia ellipsoidea, longitudinale 1–3-septata, 9–12 × 7·5–9 μm. Epibasidia 1·5–3 μm lata. Basidiosporae ellipsoideae ad subsphericae, 5·5–6·5 × 4·5–5·5 μm. Cellulae conidiogenae frequentes, inter basidia locatae, 9–21 × 1·5–4 μm, apice 5–30 conidiis juvenibus 2–3 × 1–2 μm; conidia matura ellipsoidea vel irregularia, 4–7 × 2·5–5 μm.

Typus: Australia, border of Queensland and New South Wales, Moss Garden Walk Lookout, 28°18′S, 152°27′E, alt. 900 m, on *Usnea confusa*, 2 February 1980, *G. N. Stevens* 4940 (MEL—holotypus; hb. Diederich 9824—isotypus!).

(Figs 7–9)

Basidiomata applanate to pulvinate, discoid, cartilaginous, pale yellowish brown to dark reddish brown, 0·1–0·3(–0·5) mm diam.; context hyphae 1–3·5 μm wide, thick-walled, often with clamp connections; haustorial branches not observed. *Hymenium* hyaline, containing numerous probasidia; probasidial initials ellipsoid, proliferations occurring through the basal clamps. *Basidia*, when mature, tremelloid, ellipsoid, with 1–3 longitudinal septa, 9–12 × 7·5–9 μm; epibasidia 1·5–3 μm thick. *Basidiospores* ellipsoid to subspherical, with a

large apiculum, 5·5–6·5 × 4·5–5·5 μm. *Anamorph* hyphomycetous; conidiophores very frequent, situated between the basidia, consisting of one 9–21 μm long and 1·5–4 μm thick conidiogenous cell, bearing in the upper part 5–30 young ellipsoid conidia 2–3 × 1–2 μm, developing successively to mature ellipsoid or irregular conidia 4–7 × 2·5–5 μm.

Etymology: The new species is named in honour of Dr G. Nell Stevens (Queensland, Australia) who has sent a large number of *Usnea* specimens from Australia with gall-like deformations to us, including this new species.

Hosts: Usnea confusa and *U. undulata* (det. G. N. Stevens). The basidiomata are growing on the host thallus, which is not modified.

Distribution: This species is known only from two neighbouring localities in Australia (see Fig. 7).

Discussion: The basidiomata are initially extremely small and concolorous with the host *Usnea* thallus and look like small papillae (see Fig. 8). For that reason they are difficult to recognize.

This new species is easily distinguished from the other Tremellales growing on *Usnea* by the typically tremelloid basidia, as well as the characteristic anamorph (see Fig. 9). Most conidiogenous cells only bear young conidia. From time to time one young conidium situated at the top develops into a much larger mature conidium, soon becoming detached. Young conidia are difficult to recognize, even in Phloxin, and a magnification of × 1000 is needed to study them. A similar case of conidiogenesis seems to occur in *Tremella isabellina* Lloyd (Bandoni 1958).

The basidiomata of *T. stevensiana* may easily be confused with the fructifications of *Species 1* and *Species 2* described below.

Additional specimens examined: **Australia:** Border of Queensland and New South Wales, Mt Clunie road, 2·7 km towards Guests road, 28°20′S, 152°31′E, alt. 640 m, on *Usnea undulata*, 4 August 1985, *G. N. Stevens* 5060 p.p. (hb. Diederich 9901); *ibid.*, on *U.* cf. *confusa*, *G. N. Stevens* 5060 p.p. (hb. Diederich 9972).

Fungicolous fungi

Contrary to the lichenicolous ascomycetes or deuteromycetes, the lichenicolous heterobasidiomycetes are frequently attacked by other fungi. In some cases these additional species may be considered as growing on the basidiomycete. In other cases, they appear to be primarily associated with the lichen, but prefer the regions around the parasitic basidiomata where the lichen is weakened or stressed. It is important to study these associated fungi, as the basidiomata have often been considered as galls produced by them (e.g. *A. usneae*).

Abrothallus usneae Rabenh.

This species has often been found associated with *B. usnearum*, but it also occurs on *Usnea* thalli that are not infected by that species. When it grows on *B. usnearum*, it is generally parasitic, the basidiomata being often reduced or destroyed. It has been studied and carefully illustrated by Galløe (1950).

FIG. 8. Basidiomata of *Tremella stevensiana* (BRIU—holotype). Scale = 250 µm.

We have seen specimens from Europe (France, Great Britain, Portugal [Madeira], Spain, Carpathian Mountains), Africa (Ethiopia, Rwanda), Asia (Nepal), and Australia. Galløe (1950) has illustrated material from Switzerland (pl. 113–115). In addition, the species has been mentioned in the literature from Romania (Bontea 1985, sub '*Abrothalus usnearum*, syn. *Biatoropsis usnearum*') and Madagascar (von Keissler 1933, sub '?*Abrothallus Parmeliarum*' growing on *Usnea* sp.); these records should be regarded as being doubtful, as a confusion with *B. usnearum* cannot be excluded.

Exsiccatae: Rabenhorst *Lich. Europ.* 551 (E).—**Nepal:** Kurokawa & Kashiwadani *Lich. Rar. Crit. Exs.* 340 (LG).—**Australia:** Weber *Lich. Exs. Colorado* 329 (LG).

Additional specimens examined: **France:** Cantal, Plomb du Cantal, Forêt du Lioran, on *U. rigida*, 1969, *M. S. Christiansen* 5930 (hb. Christiansen); Pyrénées-Atlantiques, 56 km S of Pau, 4 km NW of Col du Somport, 1987, *v. d. Boom* 6042 (hb. v. d. Boom); Tarn, Lacaune, 1990, *Coste* 305 (hb. Coste).—**Great Britain: VC98,** Argyll, Glasdrum, 1976, *Coppins & Tibell* (E); **VC104,** Isle of Skye, 1987, *Diederich* 8049, 8303, 8843 (hb. Diederich).—**Portugal:** Madeira, between Ponta do Sol and Porto Moniz, Rabaçal, 1992, *Diederich* 4917, 4918 (hb. Diederich).—**Spain:** Lerida, Vall d'Aran, Escunyau, on *U. florida*, 1988, *Riba* s.n. (hb. Gómez-Bolea).—**Ethiopia:** Borana, Arero (Meta-Gafersa), 1937, *Cufodontis* 378 (IMI).—**Rwanda:** Chaine des Birunga, Massif du Karisimbi, versant nord-est du Karisimbi, 1972, *Lambinon* 72/404 (LG).

Lichenoconium erodens M. S. Christ. & D. Hawksw.

This coelomycete is a common parasite of different lichens, including *Usnea* genera (Diederich 1989). We have seen one specimen in which *B. usnearum* is attacked by *L. erodens* and *L. lecanorae*.

Exsiccate (on *B. usnearum*): **Chile:** Follmann *Lich. Exs. Sel.* 40 (hb. S. Christiansen).

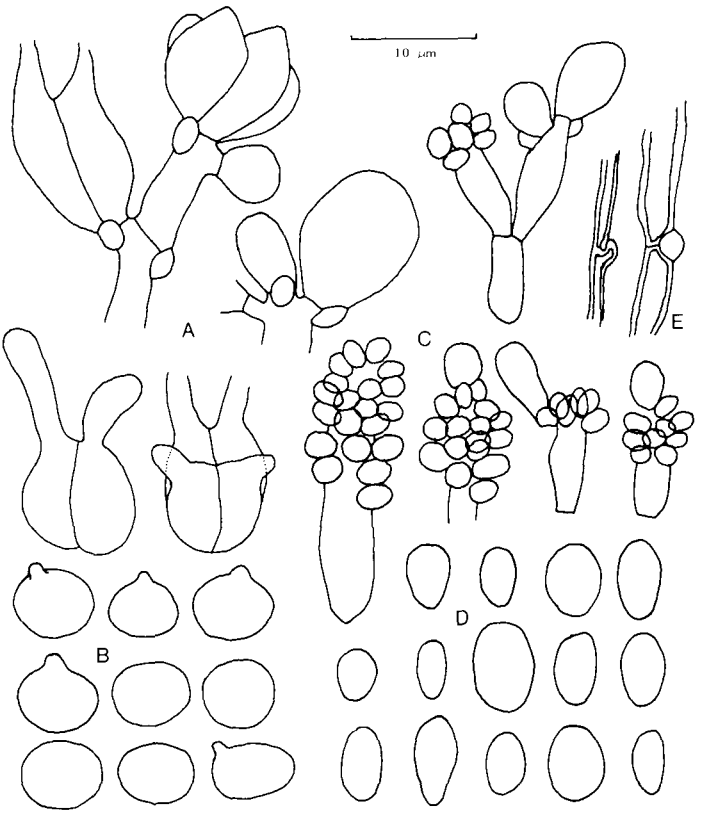

FIG. 9. *Tremella stevensiana* (BRIU—holotype). A, basidia. B, basidiospores. C, conidiophores with mainly young conidia. D, mature conidia. E, hyphae with clamp connections.

Lichenoconium lecanorae (Jaap) D. Hawksw.

We have seen one collection in which the galls of *B. usnearum* are attacked by two species of *Lichenoconium*: *L. erodens*, with small pycnidia, and *L. lecanorae*, with larger pycnidia, the conidia of which cover the gall almost completely. Although *L. lecanorae* has not been known until now as growing on *Usnea*, we attribute our fungus to this species because of the rather short conidiogenous cells.

Exsiccate (on *B. usnearum*): **Chile:** Follmann *Lich. Exs. Sel.* 40 (hb. S. Christiansen).

Lichenoconium usneae (Anzi) D. Hawksw.

This coelomycete is a common parasite of different lichens, including *Usnea* species (Hawksworth 1981). We have collected two specimens in which *B. usnearum* is attacked (*Diederich* 9120, 8316b, 9512). In a most interesting specimen (*Coste* 305), *L. usneae* has been found growing in the apothecia of *A. usneae* that were growing on *B. usnearum* on a thallus of *Usnea* (Bricaud *et al.* 1992).

Specimens examined (on *B. usnearum*): **France:** Tarn, Lacaune, 1990, *Coste* 305 (hb. Coste); Vendée, N Sables-d'Olonne, 1990, *Diederich* 9120 (hb. Diederich).—**Great Britain:** Isle of Skye (VC104), SSE Broadford, Ardnameacan, 1987, *Diederich* 8316b, 9512 (hb. Diederich).

Other *Tremella*-like or gall-forming fungi growing on *Usnea*

Morphologically, *B. usnearum* infections could be confused with some other lichenicolous fungi forming galls or gall-like apothecia on *Usnea*.

Endococcus alpestris D. Hawksw. produces perithecia on black gall-like terminal swellings on *Usnea* species (in Europe, mainly on *U. florida* and *U. subfloridana*; Hawksworth 1982), whereas basidiomata of *B. usnearum* are only exceptionally terminal. Some specimens of *Usnea* are attacked simultaneously by both species. We have seen material from Europe (France, Germany, Great Britain), Africa (Rwanda, Tanzania), South America (Brazil) and Australia (New South Wales and Tasmania).

Three different undescribed species of ascomycetes with black convex apothecia belonging to *Carbonea*, *Phacopsis*, and an unknown genus of Leotiales may be confused with the dark basidiomata of *B. usnearum*. They are currently being studied together with Dr D. Triebel.

The name *Stromatopogon baldwinii* Zahlbr. was based on a specimen of *Usnea* with gall-like formations containing perithecia, as well as pycnidia. Although the galls strongly resemble basidiomata of *B. usnearum*, and the 'stylospores' illustrated by Zahlbruckner (1897: fig. 9) are very similar to 3-septate probasidia, this species has been shown to represent a lichenicolous coelomycete (Diederich & Hawksworth, *in* Eriksson & Hawksworth 1991; Diederich 1992). It is known from the Sandwich Islands and from Tasmania.

A South American exsiccate named *B. usnearum* (**Brazil:** Kalb *Lich. Neotrop.* 204, GZU, H, M) has black galls, 0·3–1·5 mm diam. that are not caused by a basidiomycete. Microscopical sections show a dark brown to black stroma containing several subspherical hyaline regions that may represent young perithecia. As no asci are produced, we cannot proceed with this fungus until fertile material is available.

Whitish subspherical sorediate galls, 0·4–2·5 mm diam., have been found in several Australian collections on *U. mekista*, *U. subalpina*, *U.* aff. *torulosa* and *U. trichodeoides* (det. G. N. Stevens). Their causal agent is also unknown.

Specimens examined: **Australia:** New South Wales, Kosciusko National Park, 36°27'S, 148°20'E, on *Usnea subalpina*, *G. N. Stevens* 4693, 7204 (hb. Diederich 9943, 9966, 9970); *ibid.*, on *U.* aff. *torulosa*, *G. N. Stevens* 7052 (hb. Diederich 9944), Queensland, Atherton Tableland, Gadgarra State Forest, 17°18'S, 145°32'E, on *U. mekista*, *G. N. Stevens* 5408 (hb. Diederich 9942); *ibid.*, on *U. trichodeoides*, *G. N. Stevens* 5382 (hb. Diederich 9941).

Two species of fungi growing on *Usnea* macroscopically resemble *Tremella stevensiana*, but are easily separated by microscopic characters.

Species 1 (Fig. 10): Fructifications pulvinate to strongly convex, cartilaginous, pale yellowish brown, 0·08–0·25 mm diam.; context hyphae 1·5–2 μm diam., clamp connections absent; haustorial branches not observed. Hymenium hyaline, composed of irregularly branched hyphae, containing catenate conidia-like cells 3–5 μm diam., the chains often being characteristically curved (see Fig. 10D, arrow). Asci or basidia not observed.

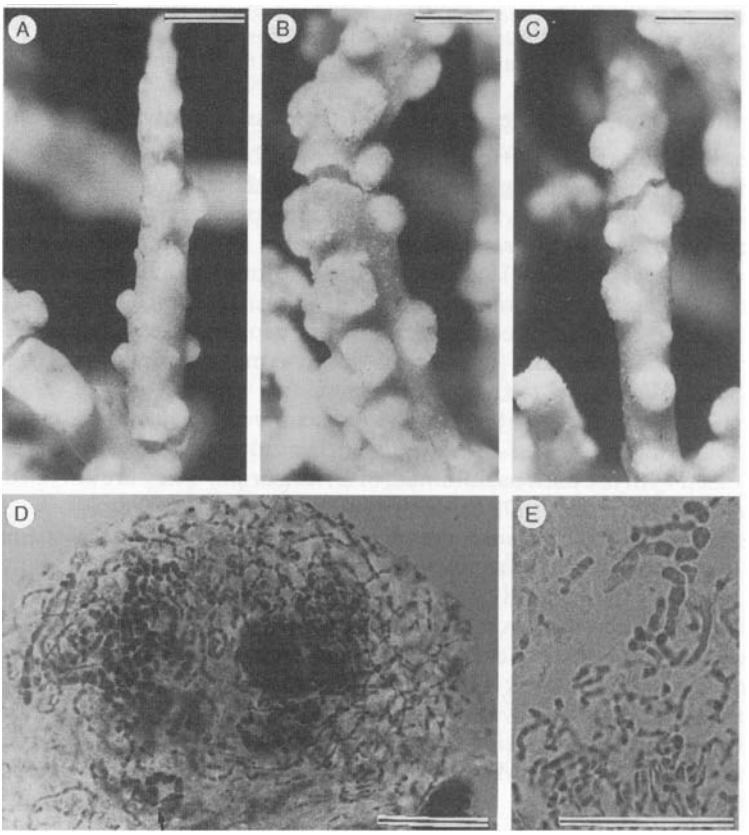

FIG. 10. *Species 1*. A, B, C, fructifications (hb. Diederich 9980). D, section through a fructification, showing catenate conidia-like cells (concentrated in the darker part of the photograph), with typically curved chains (arrow). E, context hyphae, with catenate conidia-like cells (hb. Diederich 9971). Scales: A–C = 250 μm; D & E = 50 μm.

Hosts: Usnea molliuscula, U. cf. *scabrida, U. scabrida* subsp. *elegans* and *U.* sp. (det. G. N. Stevens). The fructifications grow on the host thallus, which is not modified.

Distribution: Known from four Australian collections (New South Wales and Western Australia).

Discussion: Macroscopically this species looks very similar to *T. stevensiana*, but the fructifications are more strongly convex. It is easily distinguished from that species by the absence of basidia and conidiophores. It is mainly characterized by the presence of numerous chains of conidium-like cells that are typically curved, and that are concentrated in certain parts of the fructifications (see Fig. 10D–E). This species seems to be quite common in Australia, but it cannot be described until fertile specimens have been discovered and studied.

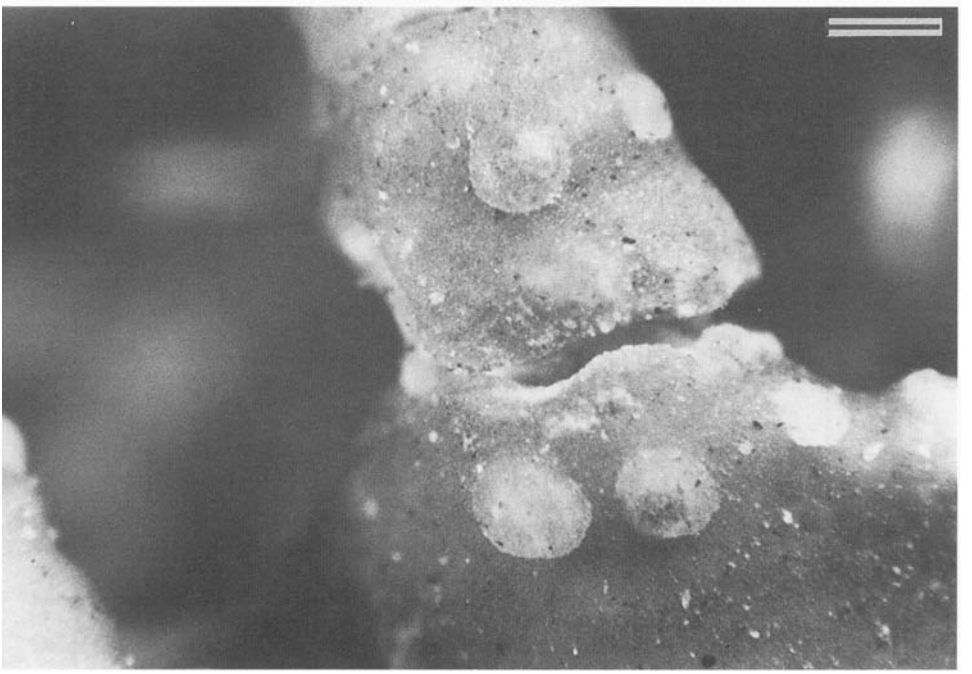

FIG. 11. Fructifications of *Species 2* on *Usnea himantodes* s.l. (Vězda *Lich. Sel. Exs.* 1772, LG). Scale = 250 μm.

Specimens examined: **Australia:** New South Wales, Liverpool Range past Pandora's Pass, 32°00'S, 150°00'E, on *Usnea scabrida* subsp. *elegans*, 1991, *G. N. Stevens* 7255 (hb. Diederich); New South Wales, several km N of Black Spring area, past Little River of Running Stream, 33°59'S, 149°47'E, on *U. molliuscula*, *G. N. Stevens* 7291 (hb. Diederich); Western Australia, Kubin, 32°44'S, 118°17'E, on *U.* cf. *scabrida* (hb. Diederich); Western Australia, Gairdner River, Southcoast Highway, on *Usnea* sp., 1980 (hb. Diederich).

Species 2 (Fig. 11): Fructifications applanate, discoid, cartilaginous, brittle, pale yellowish brown, 0·15–0·3 mm diam.; context hyphae 1·5–2·5 μm wide, thin-walled, clamp connections absent; haustorial branches not observed. Hymenium hyaline, composed of irregularly branched hyphae, cells often swollen, up to 4 μm thick, often with pointed ends. Asci or basidia not observed. Anamorph absent.

Hosts: Usnea gigas (det. P. Duvigneaud) and *U. himantodes* (det. Stevens). The fructifications are growing on the host thallus that is not modified. It is interesting to note that *U. gigas* and *U. himantodes* are closely related species (Stevens 1991), perhaps even conspecific (Stevens 1990). The lichenicolous fungus is probably restricted to this group of *Usnea*.

Distribution: Known from Africa (Zaire) and Australia (Queensland).

TABLE 1. *Diagnostic features for distinguishing the heterobasidiomycetes growing on* Usnea

Characters	*Biatoropsis usnearum*	*Tremella santessonii*	*T. stevensiana*
Basidiomata			
Shape	Convex or irregular	Pulvinate	Applanate-pulvinate
Colour	Pale brown to black	Dark reddish brown	Pale to dark reddish brown
Diameter	0·2–2·5 mm	0·2–0·3 mm	0·1–0·3(–0·5) mm
Hyphae			
Diameter (thin-walled)	2–3 μm	1–1·5 μm	
Diameter (thick-walled)		2·5–6 μm	1–3·5 μm
Clamps	Absent	Present	Present
Haustorial branches	Frequent	Absent	Absent
Basidia			
Basal clamps	Absent	Present	Present
Septation	Transverse	Transverse	Longitudinal
Number of cells	(2–)4	2	2–4
Dimensions	20–44 × 3–6·5 μm	16–21 × 8–9 μm	9–12 × 7·5–9 μm
Spore dimensions	4·5–8 × 4–7·5 μm	6·5–8 × 5·5–7 μm	5·5–6·5 × 4·5–5·5 μm
Anamorph		Unknown	
Conidiogenous cells	Monoblastic		Polyblastic
Conidia	Catenate		Solitary
Dimensions of mature conidia	3–5 × 2–3·5 μm		4–7 × 2·5–5 μm
Hosts	*Usnea, Protousnea dusenii*	*Usnea*	*Usnea*
Distribution	Cosmopolitan	Africa	Australia

Discussion: Macroscopically, this species is easily recognized by the strongly applanate fructifications, recalling the papillae of some *Usnea* species when young, but detaching or breaking away from the *Usnea* cortex by a regular circular fracture when old, leaving a deep hole in the lichen cortex (see Fig. 11). They are surely not a part of the lichen (Stevens, pers. comm.), but represent a lichenicolous fungus. When young they could be mistaken for basidiomata of *Tremella stevensiana*, but in that species older basidiomata become more convex and do not detach from the lichen. The systematic position of this species must await the discovery of fertile material.

Exsiccate: **Zaire:** Vězda *Lich. Sel. Exs.* 1772 (LG, hb. Diederich).

Additional specimens examined: **Australia:** Queensland, Binna Burra, in grounds of the lodge, 28°12′S, 153°11′E, on *Usnea himantodes*, 1988, *G. N. Stevens* 5206 (hb. Diederich); Queensland, Elginvala, 26°27′S, 152°10′E, on *U. himantodes, G. N. Stevens* 7298 (hb. Diederich).

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