The Cryptobasidiaceae of tropical Central and South America[1]

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A subfamilial concept of the Cryptobasidiaceae based on morphology and ultrastructure of numerous specimens from tropical Central and South America and one specimen from the Canary Islands is presented. These specimens are ascribed to 5 species in three genera. In *Clinoconidium* and *Drepanoconis* the basidiospores are dispersed singly, whereas in *Botryoconis* they are released in packets. *Clinoconidium* forms elliptic to round basidiospores. In *Botryoconis* the basidiospores are more or less elongate or pear-shaped, whereas in *Drepanoconis* they are more or less strongly curved, septate and thick-walled. *Botryoconis* is monotypic with the species *B. tumefaciens*. *Clinoconidium* comprises two species, *C. farinosum* with thick-walled and terminally swollen paraphyses and *C. bullatum* without hymenial paraphyses. Within the genus *Drepanoconis* two species, *D. larviformis* and *D. fructigena* are distinguished. The former has multiple-septate basidiospores and thin paraphyses without terminal swellings, the latter one-septate basidiospores and thick-walled, club-shaped paraphyses, very similar to those found in *Botryoconis*. A phylogenetic interpretation of the data is included.

Keywords: *Botryoconis*, *Clinoconidium*, Cryptobasidiaceae, *Drepanoconis*, Exobasidiales, Lauraceae, morphology, synonyms, ultrastructure, Ustilaginomycetes

The family Cryptobasidiaceae (as Cryptobasidieae) was introduced by Malençon (1953) in honour of Lendner (1920), who demonstrated, with the description of *Cryptobasidium* (= *Botryoconis*), the basidiomycetous nature of these fungi. Donk (1956), based on Malençon's description, classified *Botryoconis* H. & P. Syd., *Clinoconidium* Pat., *Coniodictyum* Har. & Pat. and *Drepanoconis* Schröt. & Henn. in the Cryptobasidiaceae. Begerow & al. (2002) added *Laurobasidium* Jülich to this group. *Coniodictyum chevalieri* Har. & Pat. lives on *Zizyphus mucronata* Wild. (Rhamnaceae) in Africa (Hariot & Pattouillard, 1909), whereas all other known species of

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this family parasitize Lauraceae, mainly in the tropics and subtropics of Central and South America and East Asia.

Except for *Laurobasidium lauri* (Geyler) Jülich, the Cryptobasidiaceae sporulate internally by producing holobasidia in peripheral lacunae of the host galls. During maturation, the galls rupture and liberate the basidiospore mass. The basidia are gastroid and lack sterigmata. *Laurobasidium lauri*, however, sporulates on the surface of the host organs, the basidia resemble those of Exobasidium, but they are gastroid-like in the other members of the Cryptobasidiaceae (Bauer & al., 2001; Begerow & al., 2002).

With the exception of *Coniodictyum chevalieri* (Malençon, 1953), the cryptobasidealean taxa have not been studied in detail. There are a number of New World specimens collected in the period from the late 18th century to the beginning of the 19th century. Therefore, in this paper the specimens were identified and examined by light, scanning electron and transmission electron microscopy. A phylogenetic interpretation of the data is presented.

Material and methods

The abbreviations of herbaria follow the Index Herbariorum (Holmgren & al., 1990). Fresh material was available only for the specimen of *Clinoconidium bullatum* from Canary Islands.

The specimens studied are listed after the description of the species with their original labels. Material used for the micrographs is indicated in the figure captions.

For light microscopy (LM) of hymenia, freehand sections through infected areas were mounted in lactophenol and examined with phase contrast optics. Basidiospore sizes are based on measurements of at least 150 spores.

For basidiospore germination, spores were spread thinly on malt-yeast-peptone agar (MYP) (Bandoni, 1972) in Petri dishes kept at room temperature. Nuclei were stained with Giemsa stain, as modified by Bauer (1987).

For transmission electron microscopy (TEM), specimens were fixed overnight in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) at room temperature. Following six transfers in 0.1 M sodium cacodylate buffer, samples were post-fixed in 1% osmium tetrocide in the same buffer for 2 h in the dark, washed in distilled water, and stained in 1% aqueous uranyl acetate for 1 h in the dark. After five washes in distilled water, samples were dehydrated in acetone, using 10-min changes at 25, 50, 70, 95, and three times in 100% acetone. Samples were embedded in Spurr's plastic (Spurr, 1969). Serial sections (65–75 nm) were cut with a Reichert-

Jung Ultracut E (Leica, Nußloch) equipped with a diamond knife. Sections were mounted on formvar-coated, single-slot copper grids, stained with lead citrate (Reynolds, 1963) at room temperature for 3–5 min, and washed again with distilled water. They were examined with a Zeiss EM 109 transmission electron microscope at 80 kV.

For scanning electron microscopy (SEM), small pieces of herbarium material were fixed on double-sided adhesive tape, mounted on specimen stubs, sputter-coated with gold-palladium and examined at 10 KV in a Cambridge REM s4-10 scanning electron microscope.

Results and discussion

Septal pores

The species studied here had an essentially identical septal pore apparatus: the simple pores are enclosed at both sides by membrane caps and the pore channels are narrowed by tubes (Fig. 1). The Cryptobasidiaceae share the presence of membrane caps enclosing the pores with the other members of the Exobasidiales, and also with the Entylomatales, Microstromatales and Doassansiales of the Exobasidiomycetidae. Among these taxa, the Cryptobasidiaceae share the presence of tubes within the pore channels only with the other members of the Exobasidiales, and with the Doassansiales (Bauer & al., 1997, 1998, 2001; Begerow & al., 2002).

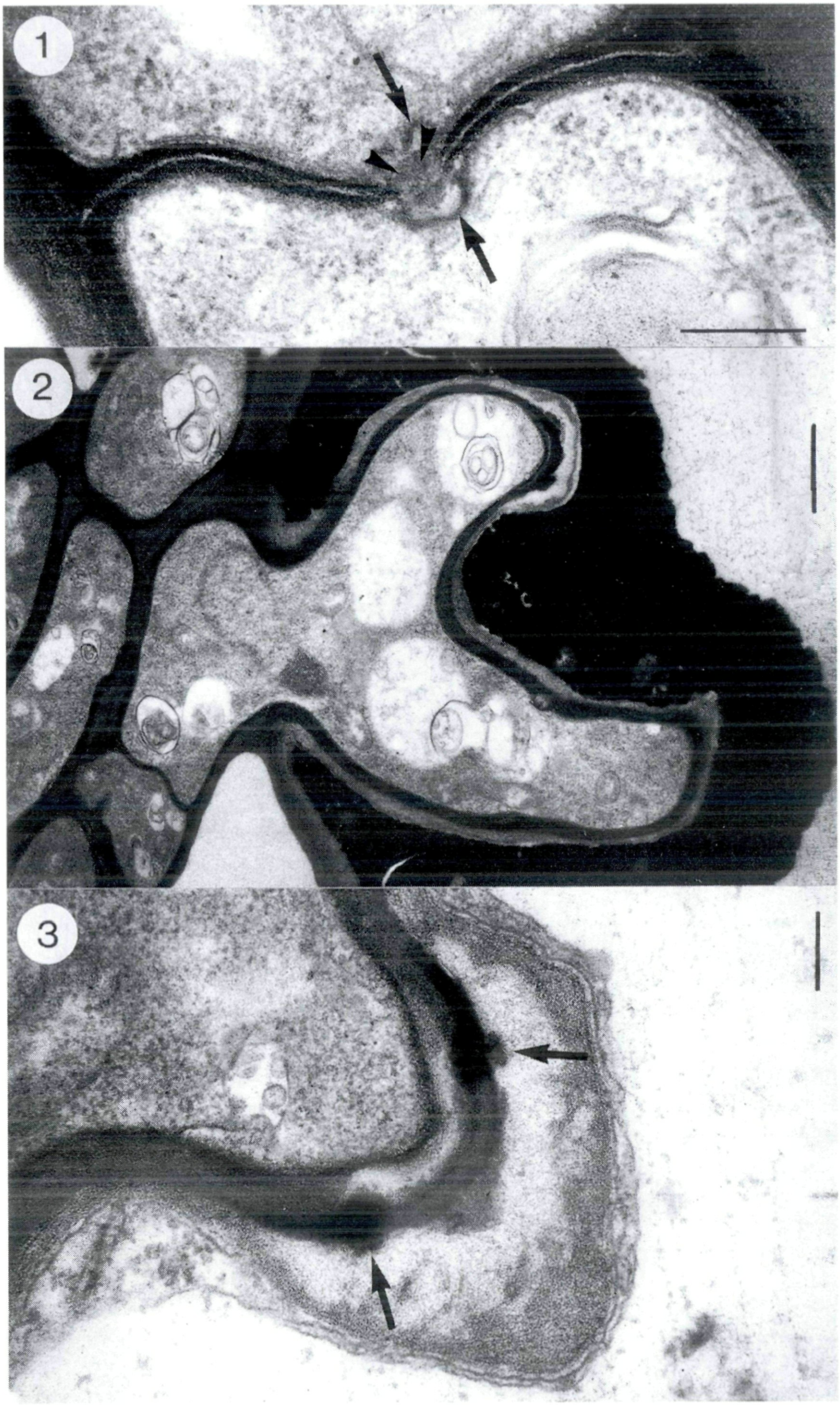
Haustoria

All specimens studied produced haustoria in the host cells. Haustoria were not constricted at the penetration point. Each haustorium extended a short distance into the host cell where it often formed several lobes (Fig. 2). At the top of these lobes interaction rings were visible (Fig. 3; for details of this structures see Bauer & al., 1997). Our data confirm the phylogenetic interpretations of Bauer & al. (1997, 1998, 2001) and Begerow & al. (2002). Thus, the Cryptobasidiaceae share the type of interaction apparatus with the formation of interaction rings only with the other members of the Exobasidiales.

Key to the Cryptobasidiaceae using mainly microscopic features

1. Basidiospores dispersed in bundles of 6–8 .... *Botryoconis tumefaciens*

1*. Basidiospores normally despersed singly, rarely in clusters of 4–5 2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2\. Basidiospores ± curved, septate, more than 16 µm in size ....3. ***Drepanoconis***
2*. Basidiospores globose to ellipsoid, not curved, unseptate, not more than 16 µm in length ....4. ***Clinoconidium***

3\. Basidiospores with 2 septa, up to 20 µm long, more than 2 spores per basidium .... *Drepanoconis fructigena*
3*. Basidiospores with more than two septa, up to 30 µm long, variable in form, mostly sickle-curved, two spores per basidium ....*Drepanoconis larviformis*

4\. Paraphyses 2–3 µm in diameter, with terminal swellings .... *Clinoconidium farinosum*
4*. Paraphyses absent .... *Clinoconidium bullatum*

Taxa

The genus *Drepanoconis* can be conclusively distinguished from the two other genera examined in this study by their curved, septate basidiospores with thick and gelatinous, smooth walls. In contrast, spore wall ornamentation is clearly visible on the mature basidiospores of *Clinoconidium* and *Botryoconis*. In addition, the basidiospores in these two genera are never septate. Furthermore, the genus *Botryoconis* is characterized by almost pear-shaped basidiospores, sticking together in bundles of 6–8 by their ornamental structures. The basidiospores of *Clinoconidium* are globose to elliptic and occur singly. In general, the basidia of *Clinoconidium* develop four basidiospores. The genus *Botryoconis* is monotypic. The two *Clinoconidium* species identified can be easily distinguished by the presence or absence of paraphyses: *C. farinosum* has paraphyses, whereas in *C. bullatum* paraphyses are lacking (Tab. 1). The two *Drepanoconis* species studied are easily distinguishable from each other by the number of basidiospores attached to the basidia, the number of septa within the basidiospores, the thickness of the basidiospore wall and the form of the paraphyses (Tab. 1).

***Botryoconis* H. & P. Syd.**, Ann. Mycol. 4: 344. 1906.
Synonym: *Cryptobasidium* Lendner, Bull. Soc. Bot. Genève, 2. Serie, 12: 122. 1920.

This genus is characterized by basidiospores which are released in packets from the basidia.

Figs. 1–3. – *Clinoconidium bullatum*. Sections of septal pore and haustoria. – 1. Simple septal pore with two membrane caps (arrows). Note the tube within the pore (arrowheads). – 2. Haustorium with two lobes. – 3. Apex of a haustorial lobe illustrating the interaction ring (arrows, three-dimensional configuration reconstructed from serial sections). – Hendrichs Nr. 1002. – Scale bars: 1, 3 = 0.2 µm, 2 = 1 µm.

Tab. 1. – Morphological characters of New World species of *Botryoconis*, *Clinoconidium* and *Drepanoconis*.

	Botryoconis	***Clinoconidium***		***Drepanoconis***	
	tumefaciens	***bullatum***	***farinosum***	***fructigena***	***larviformis***
Basidiospores:	in bundles	single	single	single	single
no. per basidium	(6–)8	4(–5)	2(–5)	4–6	2
shape	elongate, pear-shaped	round to elliptic	elliptic, seldom round	curved	sickle-shaped
septa	none	none	none	up to 2	(3)5(12)
size (μm)	10–16(–18) × 5–7	6–15 × 5–7	8–12(–17 × 6–9(–11)	16–19 × 5–6	12–30(–50) × 8–17
wall thickness (μm)	2	1(–2)	1–2	2–3	5–6
Paraphyses:	apically swollen	none	apically swollen	apically swollen	no apical swellings
diameter of stalk (μm)	2–3	–	2(–3)	2(–3)	1(–2)
length (μm)	up to 100 μm	–	up to 60 μm	up to 300 μm	up to 200 μm
sterile hyphae	present	present	present	present	present

***Botryoconis tumefaciens* (Winter) H. & P. Syd.**, Ann. Mycol. 4: 344. 1906. – Figs. 4–9.

Basionym: *Cephalosporium tumefaciens* Winter, Hedwigia 24: 256. 1885.

Synonyms: *Botryoconis saccardoi* H.& P. Syd., Ann. Mycol. 4: 344. 1906.
Botryoconis pallida H. & P. Syd., Ann. Mycol. 5: 339. 1907.
Cryptobasidium ocoteae Lendner, Bull. Soc. Bot. Genève, 2. Serie, 12: 122. 1920.
Drepanoconis tumefaciens (Winter) Viégas, Bragantia 6: 371. 1946.
Hyalopus tumefaciens (Winter) Maia, Publ. Inst. Micol. Univ. Recife 267: 18. 1960.
Botryoconis tumefaciens (Winter) W. Gams, Cephalosporiumartige Schimmelpilze: 220. 1971.

Type: *Cephalosporium tumefaciens* Winter, Hedwigia 24: 256. 1885; on an unspecified Lauraceae; leg. E. Ule.

The parasite, causing strongly deformed wood, leaves and fruits of *Ocotea*, is presently known only from Brazil and Costa Rica.

Under light microscopy one immediately recognizes the club-shaped paraphyses, extending beyond the hymenium by up to 100 µm (Figs. 4–5). Below, in the hymenium, the basidia are packed in a layer of thin, sterile hyphae. Normally eight, elongate, aseptate basidiospores [(10–)16(–18) µm × 5–7 µm] develop apically, directly from each basidium (Fig. 4). The basidiospores simultaneously break off the basidia in groups (Figs. 6–7) and often stick together at the lower half through parts of the ornaments (Figs. 8–9). These spore bundles can only be separated after applying high pressure. Basidiospores have a granular-verrucose surface (Fig. 7). Revealed by TEM, the warts are developed from a thick electron-opaque internal layer. A sheath covering the warts is often evident (Figs. 8–9).

Specimens examined. – *Cephalosporium tumefaciens* Wint. = *Botryoconis saccardiana* Syd. on Lauraceae; Brazil, Campinas; leg. F. Noack (S). – *Cephalosporium* (?) *tumefaciens* Winter; Brazil, near São Francisco; leg. E. Ule; Rabenhorst-Winter, Fungi europaei 3295 (M, type; S, isotype). – *Botryoconis saccardiana* Syd., on *Oreodaphne*; São Leopoldo 1906; Rick, Fungi Austro-Americani 140 (HBG, FH, PAD, HBG). – *Botryoconis saccardoana* Syd., (on *Nectandra*; São Leopoldo: leg. Rick 1907 !?, Rick 140. ?)[3] ex Herb. of F. Theissen (FH). – *Botryoconis saccardoi* Syd., on Canellinha; Brazil: São Leopoldo, leg. Rick 1905 (PAD).

Host range and distribution. – *Ocotea puberula* Nees; Brasil. *Ocotea pulchella* Mart.; Brasil. *Ocotea* spec. (*Ocotea* Aubl.); Costa Rica. *Oreodaphne* Nees & Mart. ex Nees (pro parte = *Ocotea* Aubl.); Brasil

[3] The fungus is stored together with material of *Drepanoconis*, which Rick found 1907 on *Nectandra*, but it is clearly Ricks No. 140. So *Oreodaphne* and not *Nectandra* is the host.

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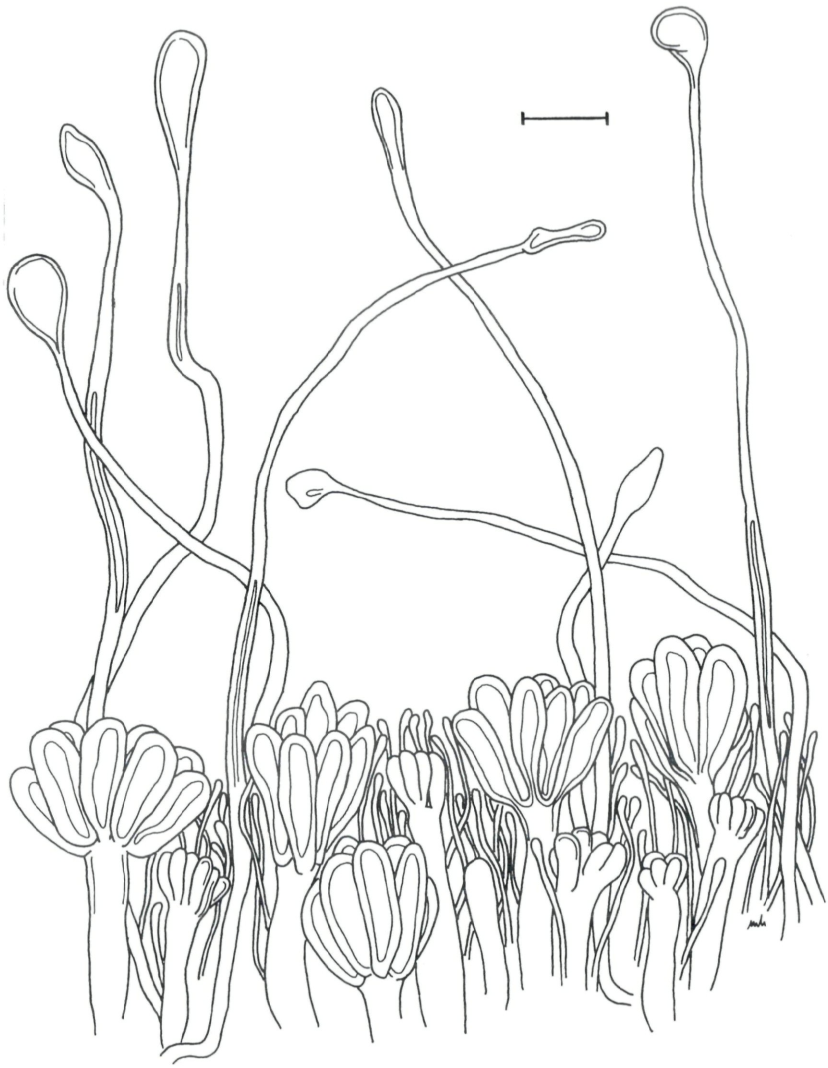

Fig. 4. – Line drawings of *Botryoconis tumefaciens*. Portion of the hymenium with basidia in different developmental stages, sterile hyphae and terminally swollen paraphyses protruding beyond the hymenium. – Rick Nr. 140 (HBG). – Scale bar = 10 µm.

Winter (1885) described a ‚Schimmel' on fruits and twigs of an unspecified host plant as *Cephalosporium tumefaciens*. H. & P. Sydow (1918) recognized this species as identical with *Botryoconis saccardoi*, resulting in the new combination *Botryoconis tumefaciens*

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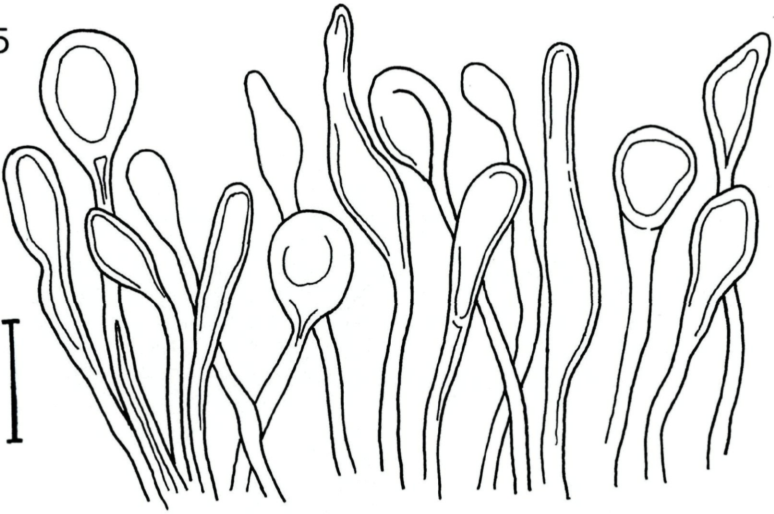

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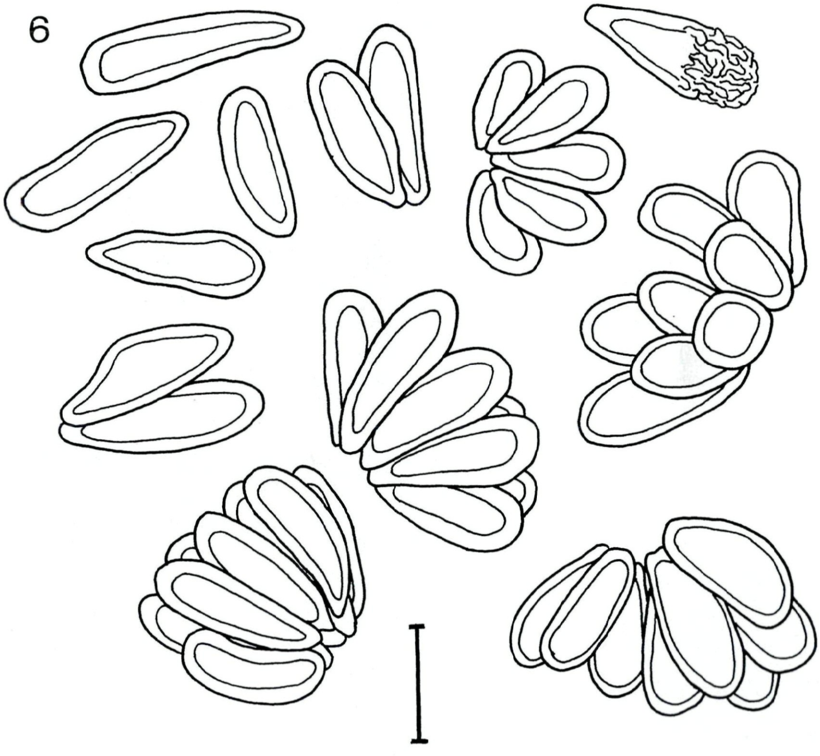
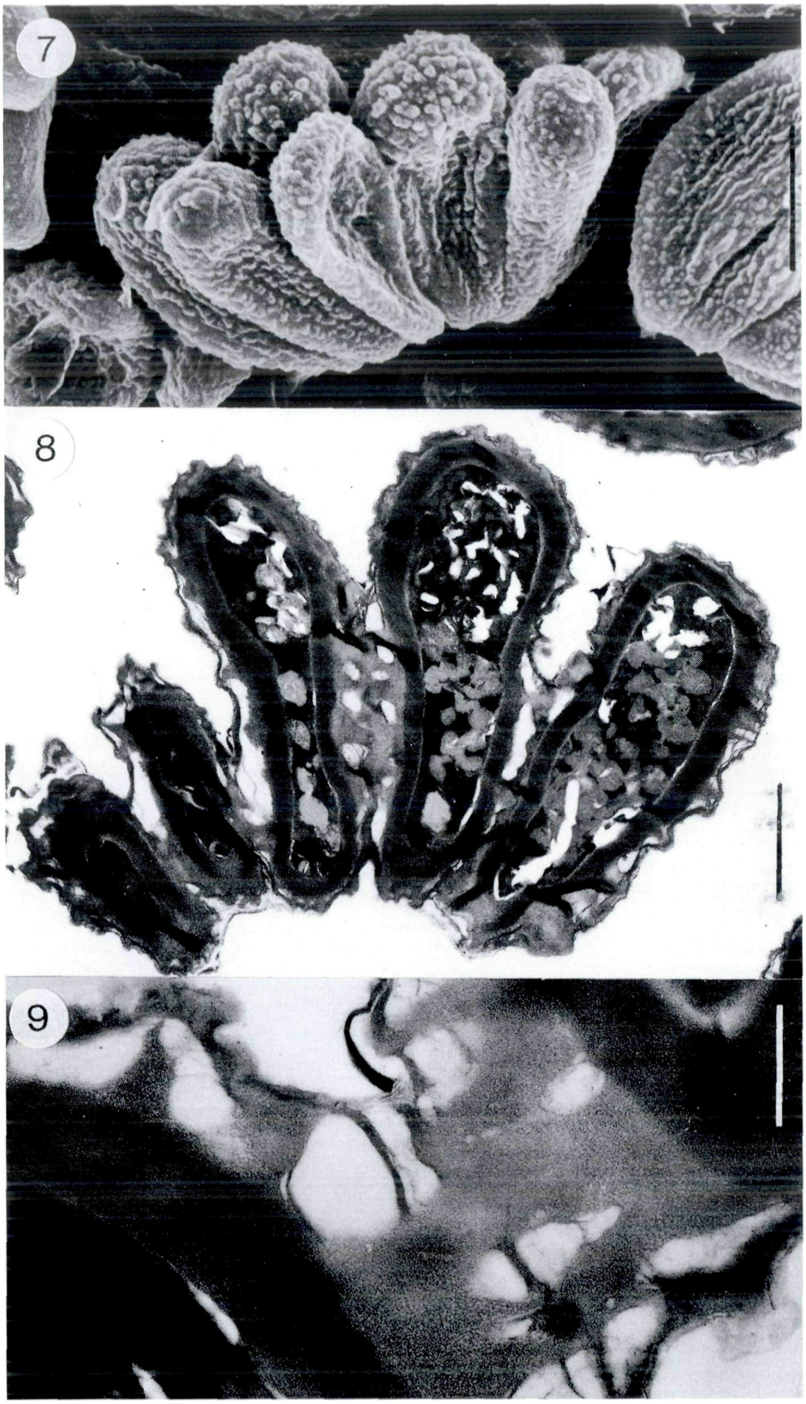


Figs. 5–6. – Line drawings of *Botryoconis tumefaciens*. Terminally swollen paraphyses (Fig. 5) and basidiospore bundles (Fig. 6) in detail. The single basidiospores illustrated in Fig. 6 originated from bundles by squashing. – Rick Nr. 140 (HBG). – Scale bar = 10 µm.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(Wint.) H. & P. Sydow, which Gams (1971) accepted. Lendner (1920) presented a drawing in his description of the basidiomycetous genus *Cryptobasidium* parasitic on *Ocotea* from Costa Rica, which Sydow (1926) identified as a species of *Botryoconis*. Besides the paraphyses, Lendner (1920) for the first time identified the characteristic spore-bundles as basidiospores.

Another species, *Botryoconis pallida*, was described by H. & P. Sydow (1907) for a fungus found on the fruits of *Ocotea puberula* Nees, in southern Brazil. The brighter basidiospores are the main difference to the former species. This feature, the spore size and the occurrence on fruits explain Maublanc's (1914) assumption that it could be a species of *Clinoconidium*. However, in 1926 Sydow considered a possible identity with *Botryoconis tumefaciens*. In addition, Viégas (1946) presented a detailed description and a table of figures for a fungus on *Ocotea pulchella* Mart. in Brazil, naming it *Drepanoconis tumefaciens* (Winter) Viégas. The data presented by Viégas are essentially identical to those of *Botryoconis tumefaciens*. Obviously, within the Cryptobasidaceae an infection of fruits alone appears to be an insufficient characteristic for species delimitation and the brighter appearance of the basidiospores, which Sydow (1926) used for the species differentiation, could result from different developmental stages. Furthermore, basidiospores are of variable size within the whole group.

Malençon (1953) presented a drawing of the characteristic spore bundles and integrated the genus *Botryoconis* in the family of the Cryptobasidiaceae (as Cryptobasidieae).

Tubaki (in Kominami & al., 1952) described a new species *Botryoconis sanguinea* Tubaki from Japan, which corresponds in its spore-size to *Botryoconis pallida*, but the added drawings and the isolation from the soil clearly show that it is not a species of *Botryoconis*.

***Clinoconidium* N. Pat.,** Bull. Soc. Mycol. France 14: 156. 1898.

This genus is characterized by unseptate, round to elliptic basidiospores which are dispersed singly (Figs. 10 and 14). The two known species sporulate on the leaves and fruits of Lauraceae found in Central and South America and on the Canary Islands.

Figs. 7–9. – *Botryoconis tumefaciens*. Basidiospore bundles. – 7. Bundle with ornamented basidiospores. Rick Nr. 140 (FH). – 8. Section through a spore bundle demonstrating that the basidiospores in the bundle are connected by their ornaments. – 9. Detail showing the substructure of the cell wall of two basidiospores, each with an electron-opaque internal layer and outer warts. The two spores are connected by their warts. Note also the diffuse material surrounding the warts. – Rick Nr. 140 (HBG). –Scale bars: 7 = 4 µm, 8 = 2 µm, 9 = 0.5 µm.

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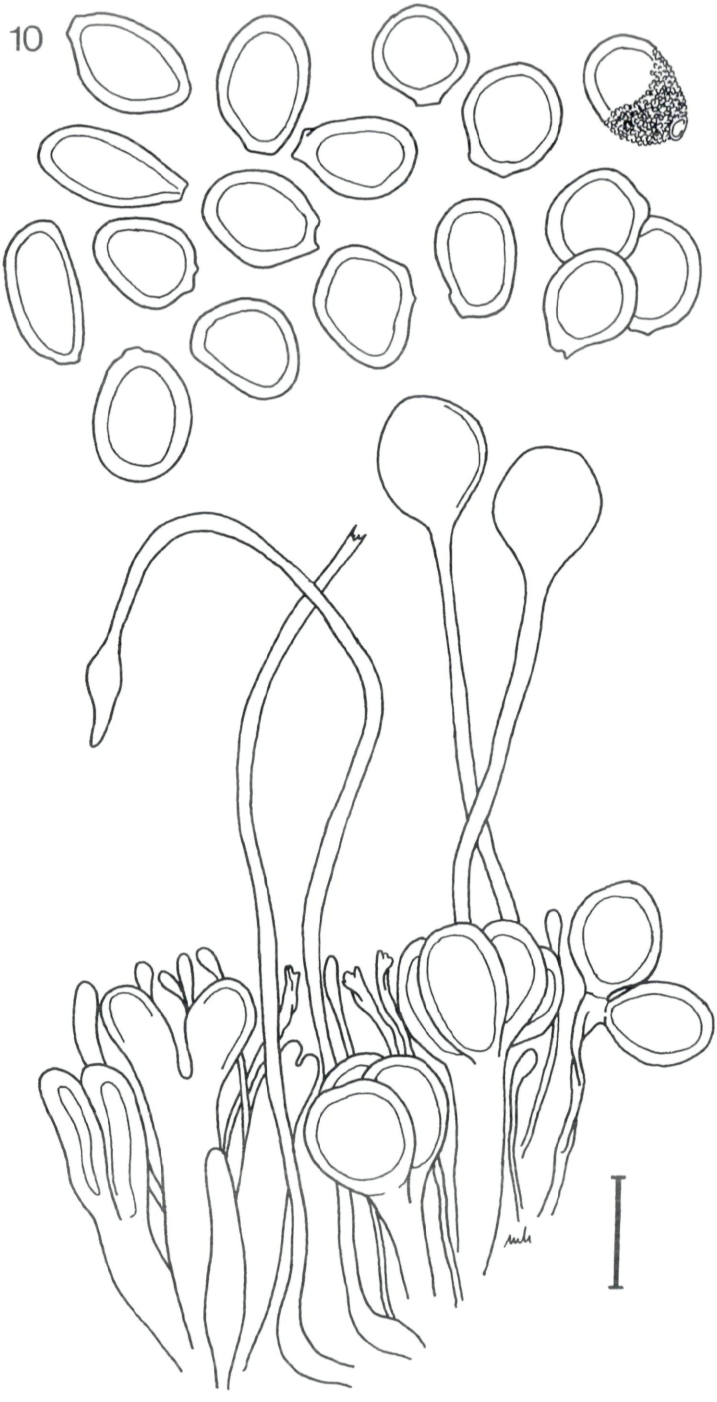


***Clinoconidium farinosum* (P. Henn.) N. Pat.**, Bull. Soc. Myc. Fr. 14: 156. 1898. – Figs. 10–13.

Basionym: *Uredo farinosa* P. Henn., Hedwigia 36: 216. 1897.
Synonym: *Uredo fructicola* P. Henn., Hedwigia 38, Beibl. 3: (129). 1899.
Type: *Uredo farinosa* P. Henn. on twigs tips and leaves of a Lauraceae; Brazil, Goyaz; leg. A. Glaziou 7. V. 1896 (Nr. 22689).

The fungus causes deformations of leaves, twigs and rarely of fruits of Lauraceae (*Nectandra* or *Oreodaphne*, possibly *Ocotea*). In addition one occasionally finds infections of the leaf tissues. The species is known from Argentina, Brazil and Puerto Rico.

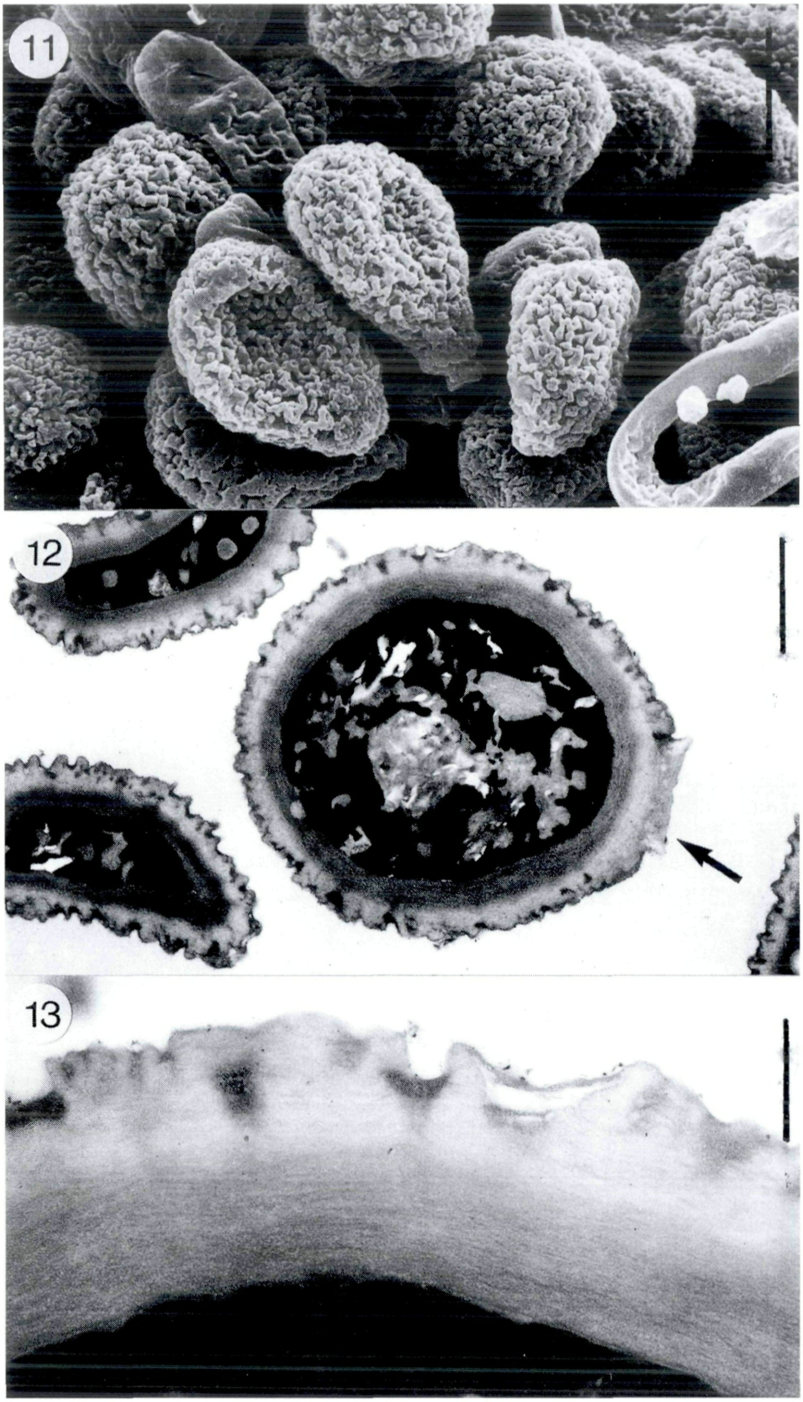
The gastroid basidia develop up to five, but normally only two spores. Club-shaped paraphyses often appear in pairs and protrude the hymenium up to 60 µm (Fig. 10). Basidiospores are granular-verrucose, round to elliptic in form, and 8–12(–17) × 6–9(–11) µm in size (Figs. 10–12). The spore wall is 1–2 µm thick, the electron-transparent ornaments sit on an inner fibrillar layer embedded in diffuse material (Fig. 13).

Specimens examined. – *Botryoconis saccardoana* Sydow, on *Nectandra/Oreodaphne*; Nova Petropolis; Rick 1923; (FH). – *Botryoconis saccardoana* Syd., on *Nectandra*; Sao Leopoldo, Rio Grande do Sul; Rick 1908; (FH). – *Clinoconidium farinosum* (P. Henn.) Pat.; Brazil, Manaos, Rio Negro; leg. E. Ule June 1910; Herb. Ule Nr. 3395 (S). – *Drepanoconis larvaeformis* Speg., on *Ocotea* sp.; La Plata; leg. et det. Lindquist April 1939; ex Herb. Spegazzini, Museo de La Plata (FH). – *Uredo farinosa* P. Henn., on leaves and twigs of a Lauraceae; Brazil, Goyaz; leg. A. Glaziou (Nr. 22689) 7. V. 1896; (B, type). – *Uredo farinosa* P. Henn., on leaves and twigs of a Lauraceae; Brazil, Goyaz; leg. A. Glaziou (Nr. 22689) 7. V. 1896; ex Herb. Ign. Urban (B, isotype).

Host range and distribution. – *Nectandra* Rol. ex Rottb. (many synonyms) or *Oreodaphne* Nees & Mart. ex Nees (pro parte = *Ocotea* Aubl.); Brasil. *Ocotea leucoxylon* (Sw.) Mez. (name uncertain, *Ocotea leucoxylon* Benth. & Hook. f., or, if *Ocotea leucoxylon* Mez, then = *Oreodaphne leucoxylon* Nees); Puerto Rico. *Ocotea* spec. (*Ocotea* Aubl.); Argentina.

Patoulliard (1898) transferred the fungus, described by Hennings (1897) as *Uredo farinosa*, into *Clinoconidium farinosum*. Maublanc (1914) discussed its affiliation to the genus *Botryoconis*. *Uredo fructicola* P. Henn., collected on fruits of *Nectandra* by Ule in Brazil, is synonymous to *Clinoconidium farinosum* (Sydow & Sydow, 1924). In 1926, Sydow described in detail the characteristics of *Clinoconidium farinosum*. Unfortunately, he overlooked the paraphyses

Fig. 10. – Line drawing of *Clinoconidium farinosum*. Hymenium with basidia in different developmental stages, sterile hyphae, long, terminally swollen paraphyses and mature basidiospores. – Glaziou Nr. 22689 (B). – Scale bar = 10 µm.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in the type material, so his clear delimination to *Botryoconis* is blurred.

The fungus found by Whetzel (Kern & Whetzel, 1926) in the inflorescence of *Ocotea leucoxylon* (Sw.) Mez in Puerto Rico, could not be examined in this study, so one has to accept its assignment to *Clinoconidium farinosum*.

***Clinoconidium bullatum* H. Syd.**, Ann. Mycol. 24: 283. 1926. – Figs. 1–3, 14–21.

Type: *Clinoconidium bullatum* Syd., on leaves of *Phoebe neurophylla* Mez & Pitt.; Costa Rica, Alajuela; leg. H. Sydow 10. I. 1925, Nr. 553 (= 165).

This species is known to parasitize species of *Cinnamomum*[4] in Costa Rica, *Ocotea* in Venezuela and *Apollonias* in the Canary Islands.

The basidia are packed in a dense layer with thin hyphae with slightly swollen apices (Figs. 14–15). Paraphyses are lacking. Normally four, rarely five basidiospores per basidium develop apically without sterigmata (Figs. 14, 16, 17). Basidiospores are often embedded in the hymenium. Spore shape is variable, often globose in the lower and pressured layers of the hymenium, and more elliptic in the upper hymenium (Fig. 14). Therefore, size of basidiospores varies between $6–15 \times 5–7$ µm. This led Sydow (1926) to differentiate between two forms (Nos. 553 and 554). In both, globose and elliptic spores can be determined, often the globose ones form groups of four (Fig. 18). Basidiospores are granular-verrucose (Figs. 14–18). Seen by TEM, electron-transparent spore ornaments rest on an internal layer of medium electron density and are embedded in electron-opaque diffuse material (Figs. 19–20).

Germination of basidiospore on MYP was observed with Giemsa staining. Freshly released spores were mononucleate. After six hours, the first nuclear division could be observed (Fig. 21a). Basidiospores germinated at one or both poles with thin rectangular branched pseudohyphae, having retraction septa. After 16 hours thin, filiform yeast cells were produced on the pseudohyphae (Fig. 21d).

[4] The neotropic species of the genus *Phoebe* are transferred to the genus *Cinnamomum* by Kostermans (1961).

Figs. 11–13. – *Clinoconidium farinosum*. Basidiospores. – 11. Ornamented basidiospores. Ule Nr. 3395 (S). – 12. Section through a dispersed basidiospore shows the hilar end (arrow). – 13. Cell wall of a mature basidiospore with an electron-opaque internal layer and electron-transparent ornaments which are embedded in diffuse material. – Glaziou Nr. 22689 (B). – Scale bars: 11 = 4 µm, 12 = 2 µm, 13 = 0.5 µm.

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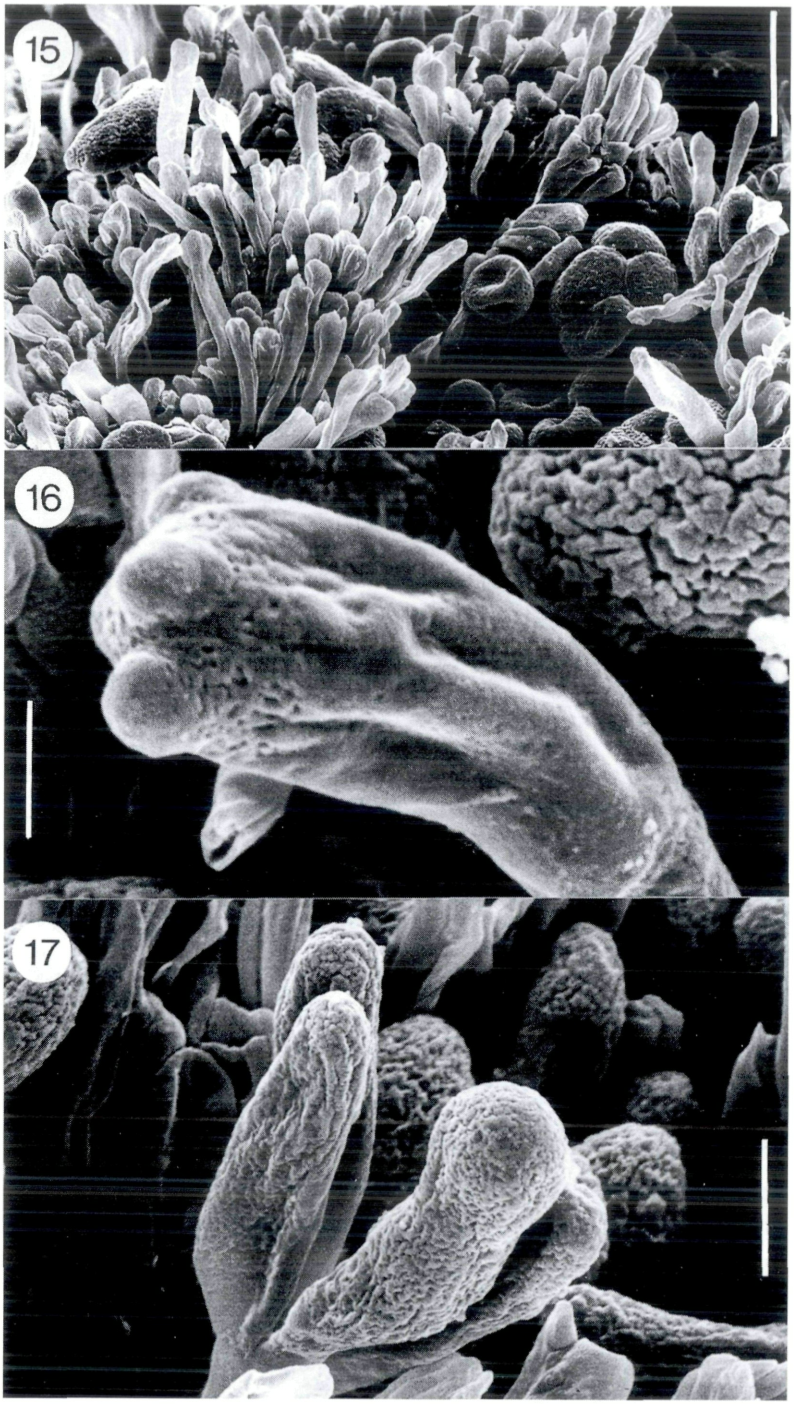
Fig. 14. – Line drawing of *Clinoconidium bullatum*. Hymenium with basidia in different developmental stages, sterile hyphae and mature basidiospores. Note the absence of paraphyses. The basidiospores vary in form. – Compiled from Sydow Nr. 553 + 554 (B), Hendrichs Nr. 1002. – Scale bar = 10 µm.

Specimens examined. – *Clinoconidium bullatum* Syd., on leaves of *Phoebe neurophylla*; Costa Rica, Alajuela; leg. H. Sydow 10. I. 1925; Sydow, Fungi exotici exsiccati Nr. 553 (B, type). – *Clinoconidium bullatum* Syd., on leaves of *Phoebe costaricana*; Costa Rica, San Pedro de San Ramon; leg. H. Sydow 23. I. 1925; Sydow, Fungi exotici exsiccati Nr. 554 (B, M, S, FH). – *Clinoconidium bullatum* Syd., on *Phoebe costaricana*; Costa Rica, San Pedro de San Ramon; leg. H. Sydow 23. I. 1925; ex F. Petrak Pilzherb. (B). – *Clinoconidium bullatum* Syd., on leaves of *Phoebe neurophylla*; Costa Rica, Alajuela; leg. H. Sydow 10. I. 1925; Sydow, Fungi exotici exsiccati Nr. 553 (M, S, PRM, FH isotype). – *Clinoconidium bullatum* Syd., on fruits of *Apollonias barbujana* (Cav.) Bornm.; Gran Canaria, Jardin Viera y Clavijo Tafira Alta; 100 m; leg. H. D. Frey 14. IV. 1998; Herb. M. Hendrichs Nr. 1002. – *Clinoconidium farinosum* (Henn.) Pat., on *Phoebe neurophylla* Mez & Pitt. or *Ocotea* spec.; Venezuela, Miranda, near Los Teques, 1200 m; leg. Chardon & Toro (Nr. 753) 29. VII. 1932 (FH).

Host range and distribution. – *Apollonias barbujana* (Cav.) Bornm.; Canary Islands. *Ocotea* spec. (*Ocotea* Aubl.); Venezuela. *Phoebe costaricana* Mez & Pitt. (= *Cinnamomum costaricanum* (Mez & Pitt.) Kosterm.); Costa Rica. *Phoebe neurophylla* Mez & Pitt.; (= *Cinnamomum neurophyllum* (Mez & Pitt.) Kosterm.); Costa Rica.

Sydow (1926) described the species *Clinoconidium bullatum*. He examined two samples from Costa Rica, one on the leaves of *Cinnamomum neurophyllum* (Mez & Pitt.) Kosterm., which Sydow (1926) determined as type material (here still as no. 165, later as no. 553). The fungus has globose, seldom elliptic basidiospores, which often remain in groups of four after breaking off the basidia. Paraphyses are lacking. The other sample, found on leaves of *Cinnamomum costaricanum* (Mez & Pitt.) Kosterm. as 'forma parum diversa' (no. 164 = no. 554) has also no paraphyses but rather elliptic basidiospores, which seldom are grouped in clusters of four. In both collections the fungus sporulate on the tissue as well as on the stalks of the leaves.

The material found on the fruits of *Apollonias barbujana* (Cav.) Bornm. on Gran Canaria can also be regarded as belonging to this species. The more elliptic and larger basidiospores, the different host species and dispersion are insufficient to characterize a new species within *Clinoconidium*. The variability of the spore sizes is within the range of the two collections examined by Sydow (1926). The form of the basidiospores may be adapted to the conditions in the hymenium. Initially, under the pressure of the covering host tissue the basidiospores probably remain almost round. If the host tissue is ruptured, however, they tend to an elliptic form. The ultrastructure of the spore wall and the ornaments are the same for all three collections. As in *Botryoconis* (see above) the location of infection seems not to be a sufficient character for species delimitation.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***Drepanoconis* J. Schröt. & P. Henn.**, Hedwigia 35: 211. 1896.

This genus is characterized by septate, curved basidiospores (Figs. 22, 27). In this analysis only the two neotropic species were examined.

***Drepanoconis larviformis* (Speg.) Speg.**, An. Mus. Nac. Buenos Aires, Ser. 3, 2: 9. 1903. – Figs. 22–26.

Basionym: *Helicomyces larvaeformis* Speg., An. de la Soc. Científ. Argent. ?: 158. 1884.

Synonyms: *Helicomyces anguisporus* Pat., Bull. Soc. Myc. Fr. 8: 137. 1892.
Drepanoconis brasiliensis J. Schröt. & Henn., Hedwigia 35: 211. 1896.
Marsonia brasiliensis (J. Schröt.) Rick, Brotéria 5: 53. 1906.
Drepanoconis anguisporus (Pat. & Lagerh.) Linder, Ann. Miss. Bot. Gard. 16: 344. 1929.

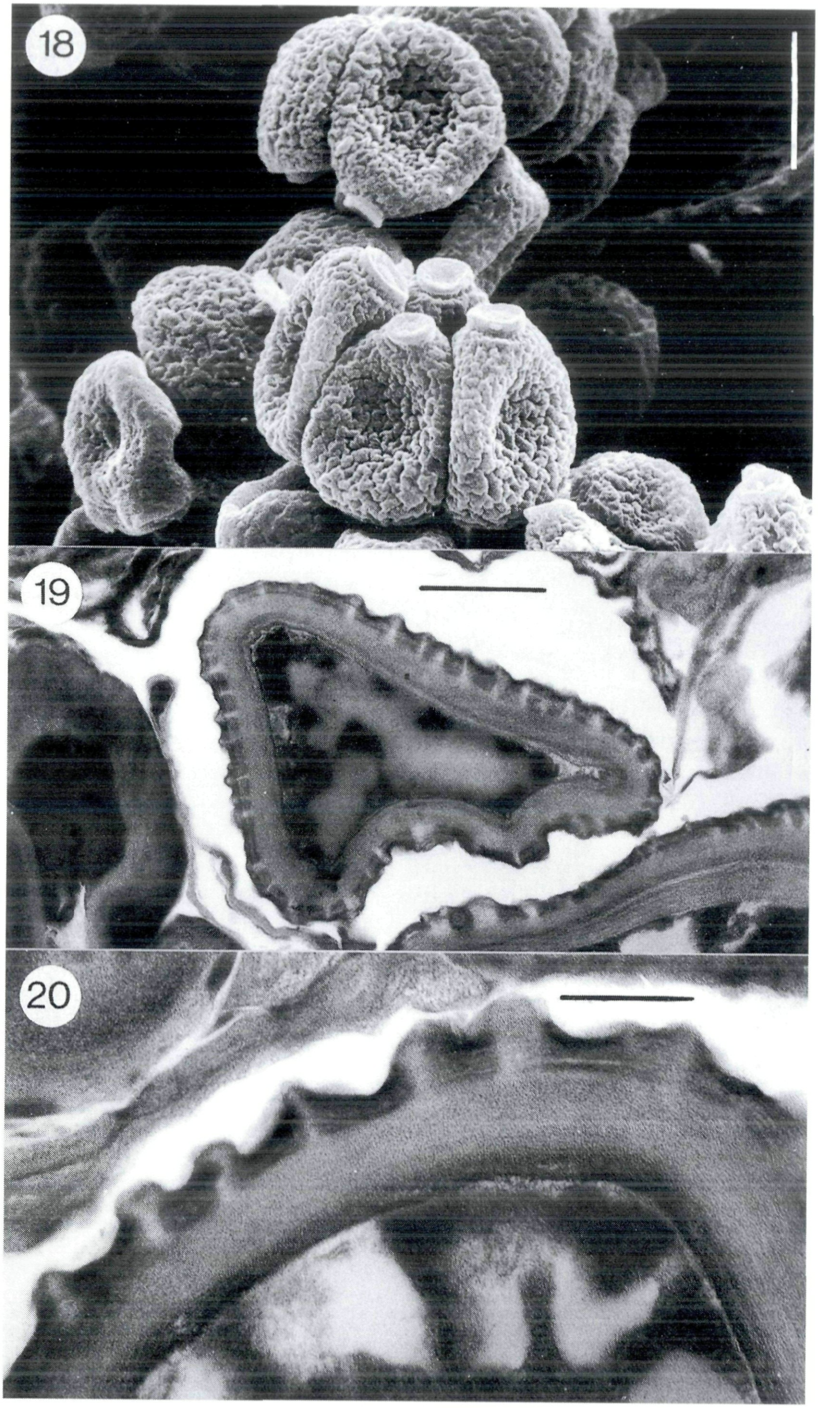
Type: *Helicomyces larvaeformis* Speg., on twigs and fruits of a Lauraceae (*Strychnodaphne suaveolens* Griseb.); Paraguay, Guarapi, 25. Nov. 1882; (Balansa, Pl. du Paraguay No. 3758).

This fungus parasitises species of *Nectandra* and *Ocotea*, and is known from Central and South America. The infection either remains very small or causes strongly deformed leaves and twigs. In addition, fruits can be infected. Slender paraphyses protrude beyond the hymenium up to 200 µm. Paraphyses are 2 µm in diameter, grow in groups and do not end in terminal swelings (Fig. 22). It is possible that the paraphyses contribute to the tearing of the host tissue.

The basidia develop two basidiospores (Fig. 22). Basidiospores vary in form and size but are normally sickle-shaped, 12–30(–50) × 8–17 µm. They are multiseptate, developing (3–)5–6(–13) septa (Figs. 23). The spore wall is up to six µm thick and appears smooth and gelatinous in the LM (Fig. 23). By SEM, however, the spore surface appears verrucose (Fig. 24). Seen by TEM, the spore wall of homogeneously layered material (Figs. 25–26).

Specimens examined. – *Drepanoconis brasiliensis* Schröt. et Hennings, on leaves and twigs of *Nectandra oppositifolia*; Brazil, St. Catharina; leg. Ule, Nr. 1482 (B, HBG). – *Drepanoconis brasiliensis* Schröt. et Henn., on leaves and fruits of *Ocotea* spec.; Brazil, Theresopolis pr. Rio; leg. E. Ule December 1896; ex Herb. Rabenhorst-Pazschke, Fungi europaei et extraeuropaei Nr. 4495 (M). – *Drepanoconis brasiliensis* P. Henn.; Brazil, São Leopoldo; Rick (?); ex Herb. P. Magnus (HBG). – *Drepanoconis brasiliensis* P. Henn.; Brazil, São Leopoldo; Rick Nr. 37; ex Herb. P. Magnus (HBG). – *Drepanoconis brasiliensis* Schroet. & Henn., on *Nectan-*

Figs. 15–17. – *Clinoconidium bullatum*. Hymenium and basidia. – 15. Hymenial surface showing clusters of young basidia (arrows) and some dispersed basidiospores. The dispersed basidiospores vary in form: globose as well as elongate basidiospores are visible. Petrak (B). – 16. Young basidium with four basidiospore initials. – 17. Apex of a basidium with four elongate basidiospores. – Hendrichs Nr. 1002. – Scale bars: 15 = 10 µm, 16 = 2 µm, 17 = 4 µm.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dra oppositifolia; Rick (?); ex Herb. P. Magnus (HBG). – *Drepanoconis brasiliensis* Henn., in leaves of *Nectandra*; São Leopoldo, March 1904; ex Rick, Fungi austro-americani Nr. 37 (HBG, PAD). – *Drepanoconis brasiliensis* Schröt. et Henn., on leaves and fruits of *Ocotea* spec.; Brazil, Theresopolis pr. Rio; leg. E. Ule December 1896; ex Herb. Rabenhorst-Pazschke, Fungi europaei et extraeuropaei Nr. 4495 (HBG, S, G). – *Drepanoconis brasiliensis* Schröt. et Henn., on *Ocotea* spec.; Theresopolis; 29.12.1896; Nr. 1074; ex Herb. Ule (HBG). – *Drepanoconis brasiliensis* Schrt. n. sp. g., auf *Nectandra rigida* Nees; Est. de Sta. Catharina, Tubarão; July 1889; E. Ule Herbarium Brazilse No. 1482 (HBG). – *Drepanoconis brasiliensis* Schröt. et P. Henn., on *Nectandra rigida* Nees; Pr. St. Catharina, Itajahy; Jan. 86; Ule Nr. 505 (HBG). – *Drepanoconis brasiliensis* P. Henn.; ex Herb. Mycol. P. A. Saccardo (PAD). – *Drepanoconis brasiliensis* P. Henn.; Brasilia; 1906; Rick n. 37; ex Herb. Mycol. P. A. Saccardo (PAD). – *Drepanoconis fructigena* Rick, on *Nectandra*; São Leopoldo, Rio Grande do Sul; 1931; Rick expeditions in Brazil (FH). – *Drepanoconis larvaeformis* Speg., on *Nectandra linhearia*; Brazil, Est. Experim. Pindorama; leg. H. P. Krug, 31. Aug. 1937; Krug Nr. 2118; ex United States Deptm. of Agric., Bureau of Pl. Ind., Mycol. Coll. 73810 (FH). – *Drepanoconis larvaeformis* Speg., on fruits of *Nectandra* sp.; St. Catharina, Porto Novo; leg. J. Rick 1928; Rick Nr. 97; Rick expeditions in Brazil (FH). – *Drepanoconis larvaeformis* Speg., on *Ocotea puberula*; La Plata, Fac. de Agron.; leg. J. C. Lindquist 8.III.1948; ex Universidad Nac. de la Plata Museo – Instituto Spegazzini, Colecciones micol. No. 15703 (FH). – *Drepanoconis larvaeformis* Speg., on *Nectandra antillana*; Jamaica, Portland, Montpellier; leg. R. I. Leather, 6.III.1962; (IMI Nr. 95499). – *Drepanoconis larvaeformis* Speg., on *Nectandra antillana*; Jamaica, At. Ann, Knapdale; leg. A. G. Naylor, 30.X.1958; (IMI Nr. 78223). – *Drepanoconis larviformis* Speg., on leaves of a Lauraceae; Brazil, Prov. São Paulo, Campinas; leg. F. Noack, Nov. 1907; ex Herb. Kabát et Bubák: Fungi imperf. exsiccati Nr. 549 (PRM, HBG). – *Drepanoconis larviformis* Speg., on leaves and twigs of a Lauraceae; Rio de Janeiro, pentes du Corcovado; leg. A. Maublanc 20.1.1914; ex A. Maublanc: Fungi brasiliensis Nr. 195 (FH). – *Helicomyces*? *larvaeformis* Spegazz., on fruits of a Lauraceae; Paraguay, Guarapi, 25. Nov. 1882; ex Herb. B. Balansa, Pl. du Paraguay No. 3758 (G, type). – *Marssonia brasiliensis*, on *Nectandra*; São Leopoldo; Rick 1907; (FH).

Host range and distribution. – *Nectandra antillana* Meissn.; Jamaica. *Nectandra oppositifolia* Nees & Mart. ex Nees (= *Nectandra rigida* Nees); Brasil. [*Nectandra linhearia*; Brasil (name unknown?)]. *Ocotea* spec. (*Ocotea* Aubl.); Brasil. *Ocotea puberula* Nees; Argentinia. *Strychnodaphne suaveolens* Griseb. (= *Ocotea puberula* Nees); Paraguay.

Spegazzini (1884) described the fungus, found by Balansa in 1882 on twigs and fruits of *Ocotea puberula* Nees from Paraguay, as *Helicomyces larvaeformis*, because of its strongly curved basidiospores. Hennings (1896) described the genus *Drepanoconis* and the

Figs. 18–20. – *Clinoconidium bullatum*. Basidiospores. – 18. Ornamented basidiospores. In some of them the hilar ends are visible. Sydow Nr. 553 (S). – 19. Section through a mature basidiospore. – 20. Cell wall of a mature basidiospore with an internal electron-opaque layer of medium electron density and electron-transparent warts. The warts are embedded in diffuse electron-opaque material. Sydow Nr. 554 (M). – Scale bars: 18 = 4 µm, 19 = 1 µm, 20 = 0.3 µm.

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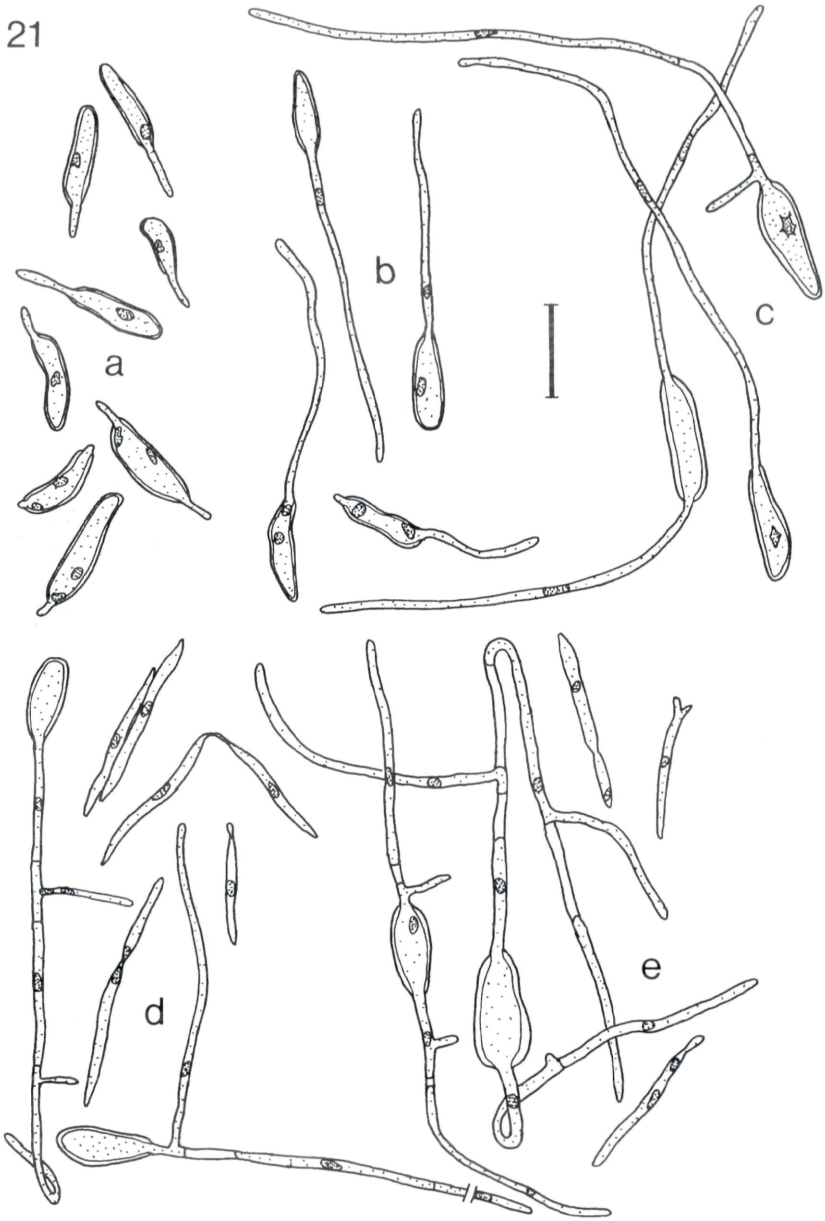

Fig. 21. – Line drawing of *Clinoconidium bullatum*. Giemsa-stained basidiospore germination on MYP. – a. 6 h after inoculation. – b. 9 h after inoculation. – c. 12 h after inoculation. – d. 16 h after inoculation. – e. 18 h after inoculation. – Hendrichs Nr. 1002. – Scale bar = 10 μm.

species *Drepanoconis brasiliensis* J. Schröt. & Henn. from two Ule collections, assembled 1886 in Itajaĕ, Brazil. Spegazzini realised, after a hint from Hennings (1902), the identity with the earlier described species (1884) and recombined in 1903 *Helicomyces larvaeformis* to *Drepanoconis larviformis* (Speg.) Speg.

The new combination of *Marsonia brasiliensis*, which Rick (1906) proposed was immediately rejected and within the same year corrected by the same author.

Maublanc (1914) examined fresh material and verified the multiple germination of the basidiospore of each spore chamber. In addition to the characteristically thin hyphae with the compartmentation of the cytoplasma by retraction septa, he also draw the filiform yeast cells.

For the fungus, described by Patouillard & Lagerheim (1892) from Ecuador as *Helicomyces anguisporus*, the description and the drawing allow one the ascription to *Drepanoconis larviformis*. Even in the new combination as *Drepanoconis anguisporus*, which Linder (1929) proposed, this species, however, still cannot be separated from *Drepanoconis larviformis* on the basis of its spore size.

***Drepanoconis fructigena* Rick,** Ann. Mycol. 3: 17. 1905. – Figs. 27–30.

Synonyms: *Marsonia fructigena* Bresadola, Ann. Mycol. 3: 17. 1905.
Marsonia fructigena Rick, Brotéria 5: 53. 1906.

Type: *Drepanoconis fructigena* Rick, on fruits of *Oreodaphne*; Brazil, São Leopoldo, leg. J. Rick June 1904 (Rick Nr. 42).

This species was found on fruits of *Oreodaphne*, *Ocotea* and *Persea* in Brazil and Uruguay. Paraphyses protrude beyond the hymenium up to 300 µm, are 2–3 µm in diameter, and are terminally swollen (Fig. 27). The basidium produces 4–5(–6) gastroid basidiospores without sterigmata. They are slightly curved, 16–19 × 5–6 µm in size and, are uniseptate, rarely biseptate (Fig. 27–28). The spore wall is 2–3 µm thick and appears gelatinous and smooth in LM (Fig. 27) and finely verrucose in SEM (Fig. 28). Seen by TEM, the spore wall consists of several layers, each composed of amorphous, spongy material (Figs. 29–30).

Specimens examined. – *Clinoconidium farinosum* Pat., on *Ocotea angustifolia* (Nees) Mez; Uruguay, Tacuarembo, Valle Eden; leg. Herter Sept. 1928; ex Herb. W. G. Herter, Plantae Uruguacenses Exsiccatæ no. 1255 (M, HBG). – *Drepanoconis brasiliensis* Rick, auf *Persea* sp.; Brazil, Rio Grande, Arroio do Meio; leg. J. Rick 1920; ex Herb. Mycolog. L. Romell (S). – *Drepanoconis fructigena* Rick n. sp., (without further data); (FH). – *Drepanoconis fructigena* Rick n. sp., on fruits *Oreodaphne*; São Leopoldo, June1904; ex Herb. F. Theissen, Rick, Fungi austro-americani Nr. 42 (HBG, type; FH, PAD, isotypes). – *Drepanoconis fructigena* Rick;

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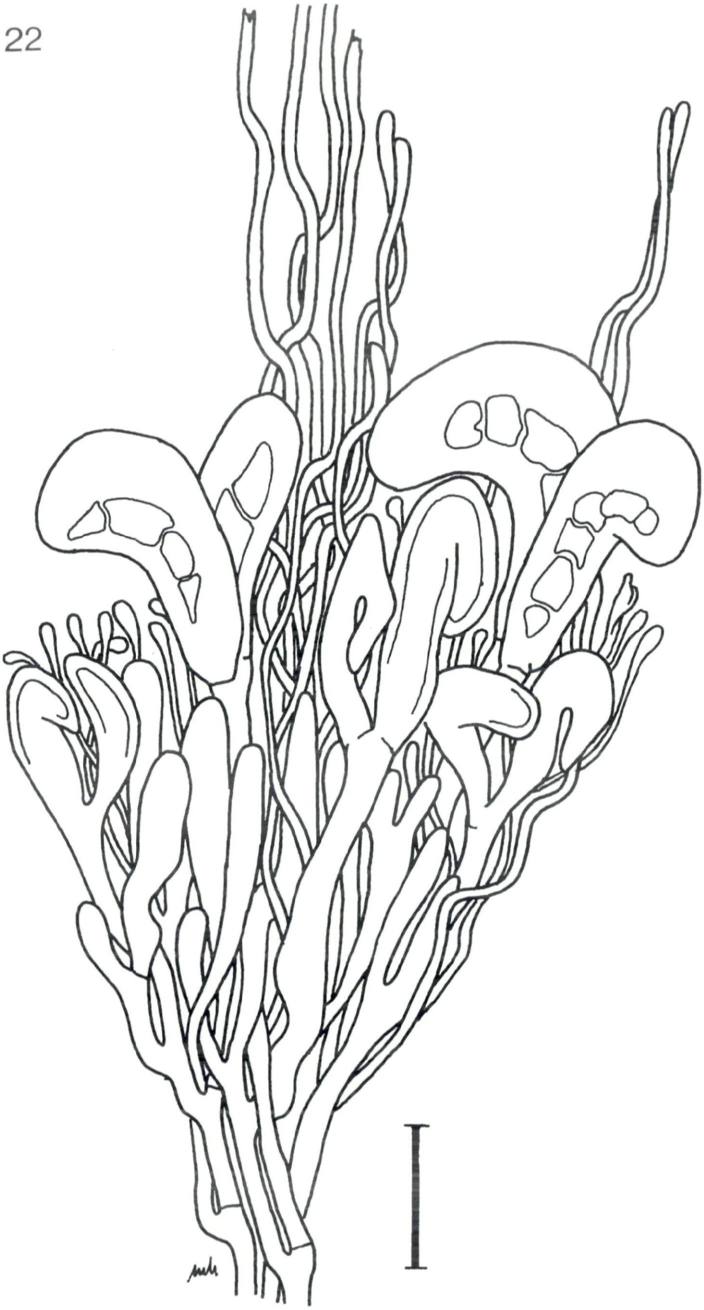

Fig. 22. – Line drawing of *Drepanoconis larviformis*. Hymenium with basidia in different developmental stages, sterile hyphae and long paraphyses. The paraphyses are without terminal swellings. – Ule Nr. 1482 (B, HBG). – Scale bar = 10 µm.

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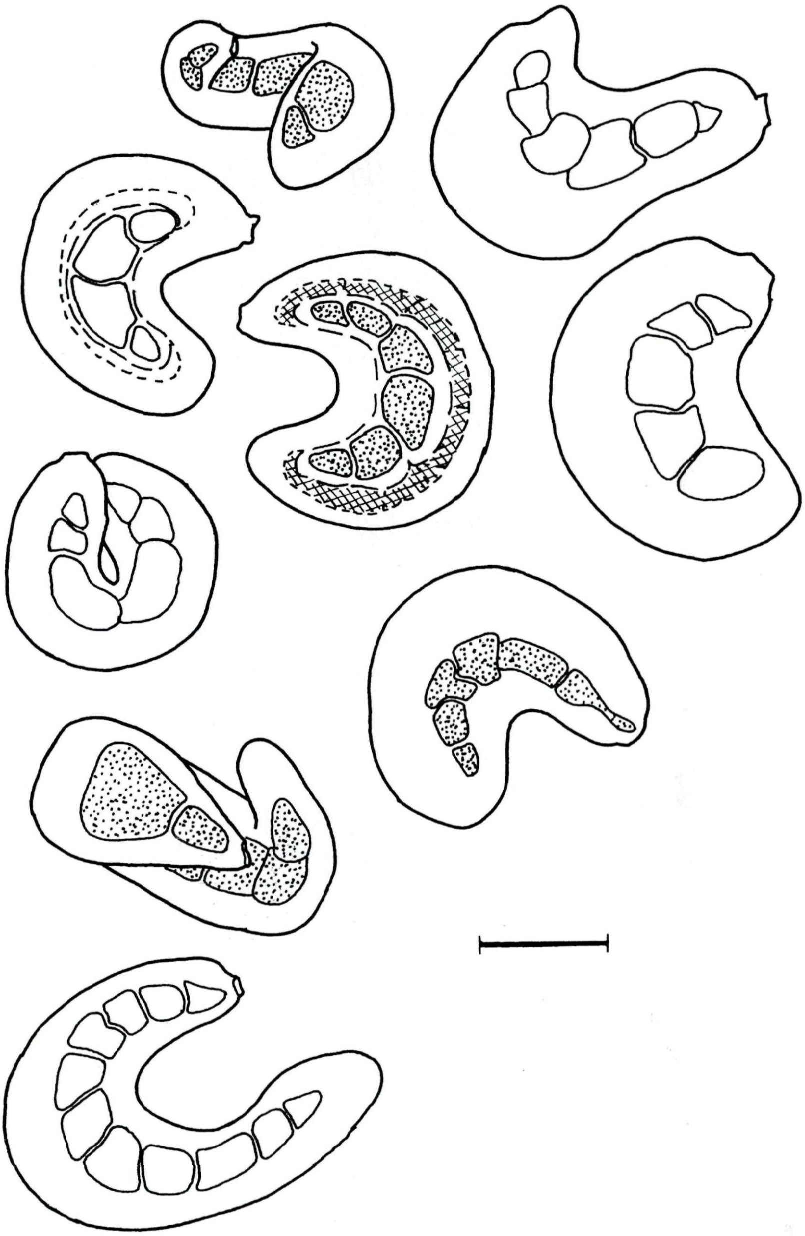
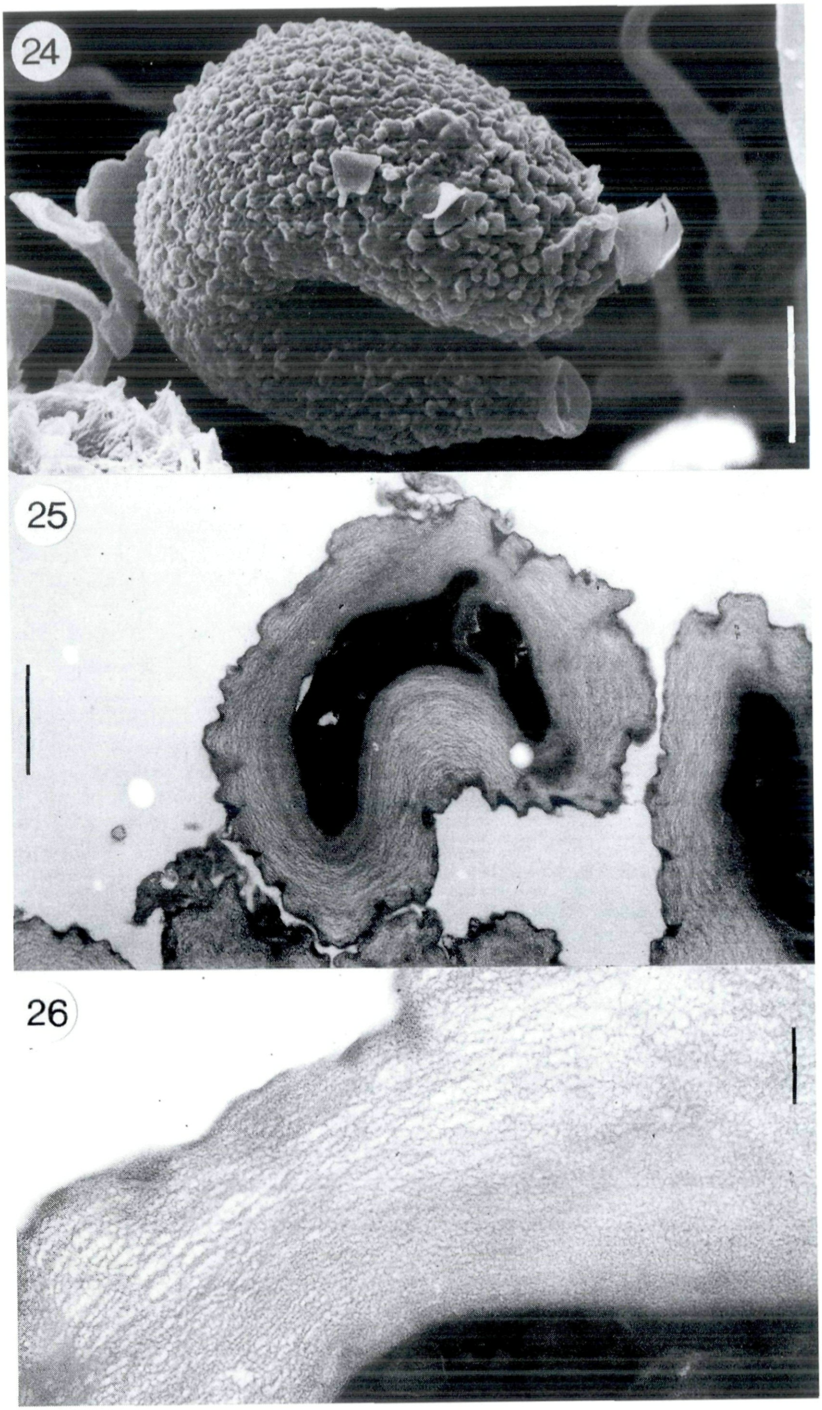


Fig. 23. – Line drawing of *Drepanoconis larviformis*. Mature, septate, curved basidiospores. The spore surface is smooth. – Ule Nr. 1482 (B). – Scale bar = 10 µm.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Brazil, São Leopoldo; July 1906; (HBG, topotype) *Drepanoconis (Marssonia) fructigena* Rick; Brazil; Rick no. 42; ex Herb. Mycol. P. A. Saccardo (PAD, isotype).

Host range and distribution. – *Ocotea angustifolia* (Nees) Mez (name uncertain, if *Ocotea angustifolia* Schrad., then = *Nectandra angustifolia* Nees & Mart. ex Nees; or = *Ocotea angustifolia* Pohl ex Meissn.); Uruguay. *Oreodaphne* Nees & Mart. ex Nees (pro parte = *Ocotea* Aubl.); Brasil. *Persea* spec. (*Persea* Plum. ex Linn.); Brasil.

This species, described by Rick (1905) as *Marsonia fructigena*[5] from Brazil, is collected exclusively on fruits. The basidiospores are rather uniform, not as strongly curved and clearly smaller than in *Drepanoconis larviformis*. They normally have only one septum and the paraphyses are wider in diameter and have terminal swellings. Although *Drepanoconis larviformis* occasionally sporulates on fruits, the two species can be easily differentiated.

A species very similar to *Drepanoconis fructigena* was named by Walker (1983) as *Drepanoconis nesodaphnes,* based on a fungus parasitizing on the fruits of *Beilschmiedia obtusifolia* (F. Muell. ex Meissn.) F. Muell. from Australia, first described as *Melampsora nesodaphnes* by Berkeley and Broome (1882). Another sample collected on the fruits of *Cinnamomum oliveri* F. M. Bail. was also assigned to this species by Walker (1983). The spore sizes and the number of septa within the basidiospores of *Drepanoconis nesodaphnes* are intermediately between the two species of *Drepanoconis* discussed in this paper.

In 1989, Ciccarone described a parasite on *Vitis vinifera* L. as *Drepanoconis divertigastra*. According to his description, the photograph and the host species, this fungus appears to be not a member of *Drepanoconis*.

[5] Rick's February 1905 paper, published first 1906 in Brotéria, introduces the new name *Marsonia fructigena* Rick. In a second 1905 paper published in Annales Mycologici, Rick terms the species *Drepanoconis fructigena* Rick. With reference to an oral suggestion from Bresadola, Rick gives here *Marsonia fructigena* Bres. as synonym.

Figs. 24–26. – *Drepanoconis larviformis*. Basidiospores. – 24. Curved basidiospore with the hilar end. Because the spores are smooth in lactophenol (see Fig. 23) and the gelatinous, spongy cell walls are without an ornamentation in TEM (see Figs. 25–26), the verrucose appearance of the spores in SEM may be the result of the drying process. Pazschke Nr. 4495 (M). – 25. Basidiospore showing one septum. Ornaments are lacking in the thick spore wall. – 26. Cell wall of a mature basidiospore illustrated to show the layered substructure. Note the absence of ornaments. Kabát Nr. 549 (HBG). – Scale bars: 24 = 4 μm, 25 = 2 μm, 26 = 0.2 μm.

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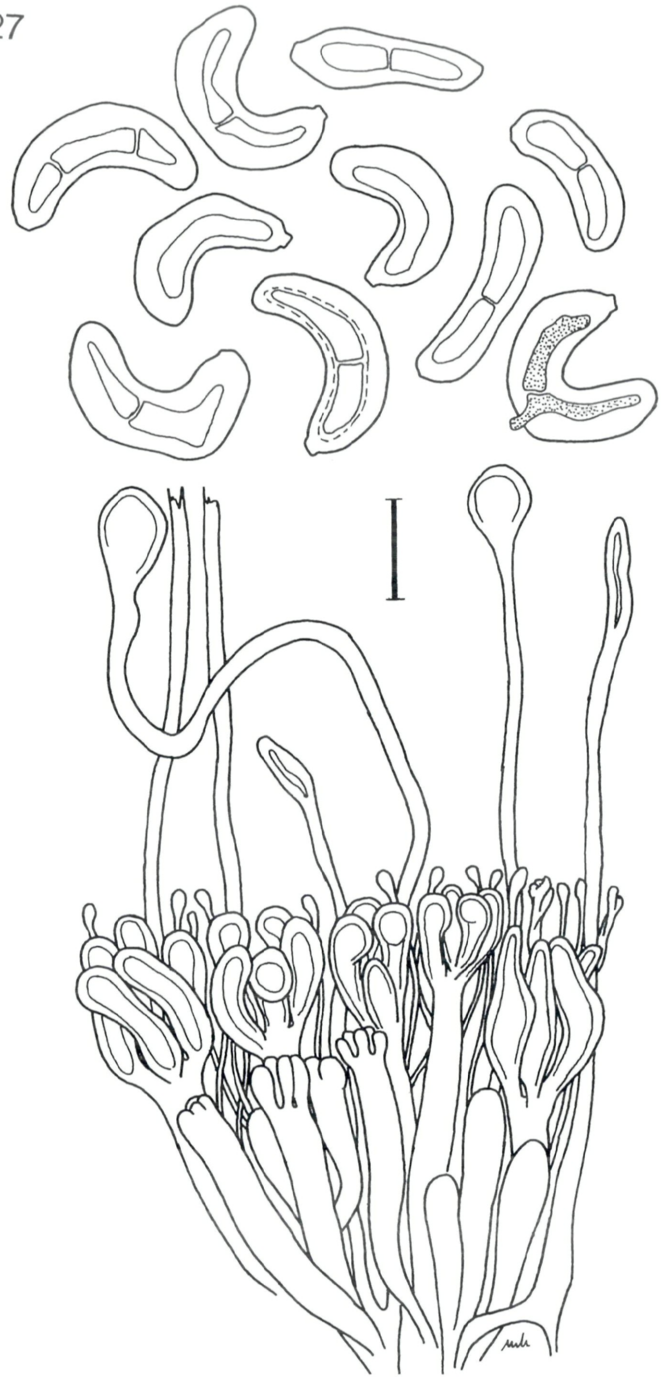
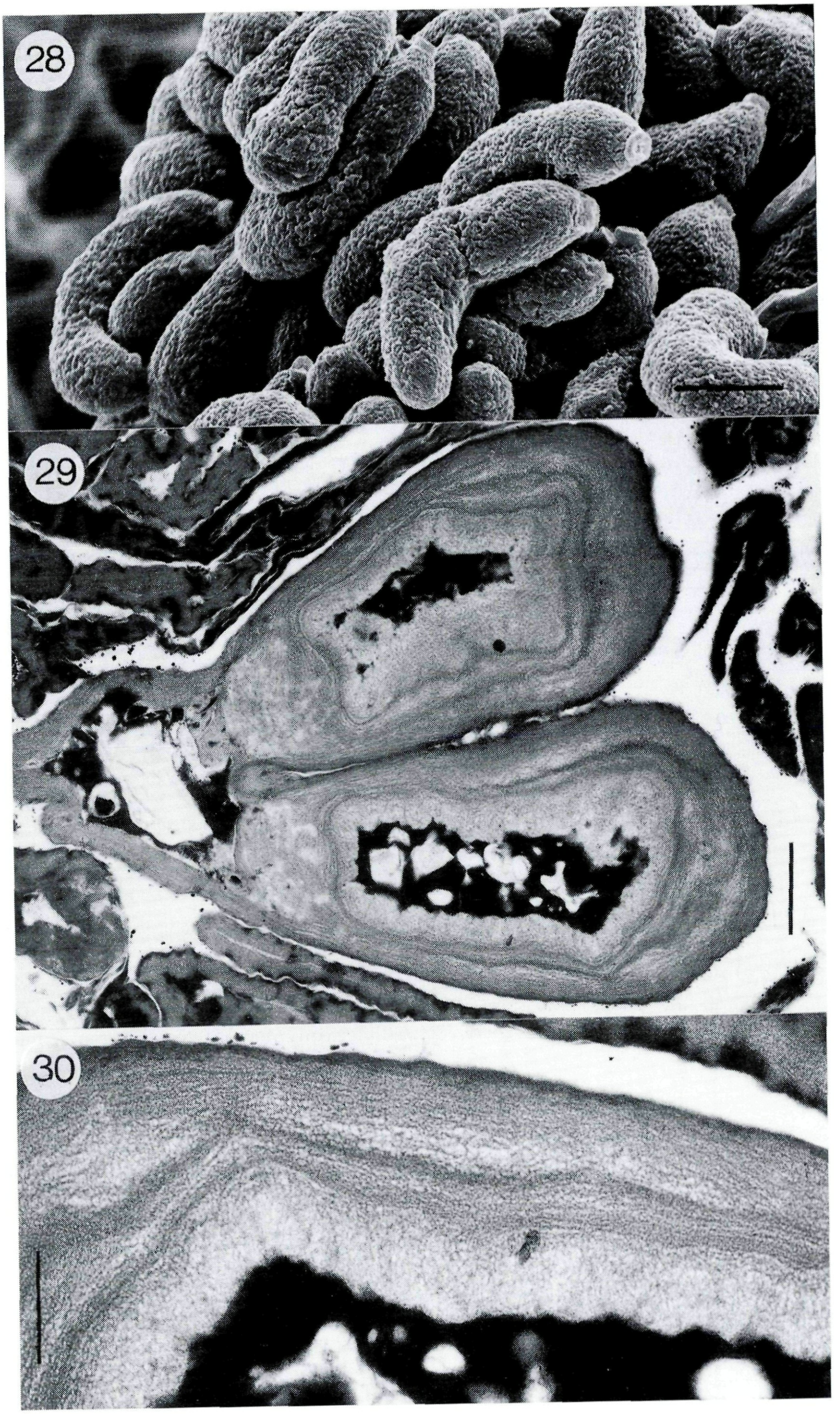


Fig. 27. – Line drawing of *Drepanoconis fructigena*. Hymenium with basidia in different develomental stages, sterile hyphae, long paraphyses with terminal swellings and mature basidiospores. The basidiospores are curved and predominantly one-septate. – Herter Nr. 1255 (M). – Scale bar = 10 µm.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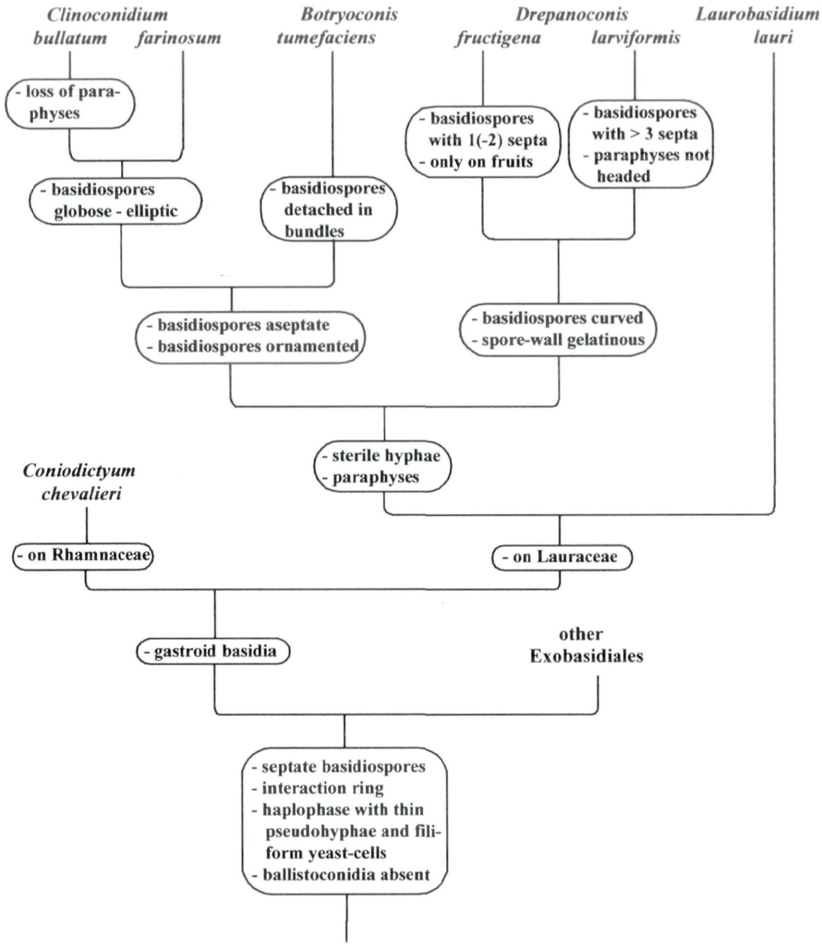

Fig. 31. – Phylogenetic analysis of the Cryptobasidiaceae based on apomorphies as discussed in the text. Their plesiomorphic states occur in the respective sister groups. The general features of the Exobasidiales are interpreted as plesiomorphic.

Figs. 28–30. – *Drepanoconis fructigena*. Basidiospores. – 28. Curved basidiospores. In some of them the hilar ends are visible. Because the spores are smooth in lactophenol (see Fig. 27) and the gelatinous, spongy cell walls are without an ornamentation in TEM (see Figs. 29–30), the finely verrucose appearance of the spores in SEM may be the result of the drying process . Herter Nr. 1255 (M). – 29. Apex of an old basidium with two basidiospores. The basidial wall is continuous with the outer layer of the cell wall of the basidiopores. – 30. Cell wall of a mature basidiospore illustrated to show the multilamellate, spongy substructure. Note the absence of ornaments. Herter Nr. 1255 (HBG). – Scale bars: 28 = 5 μm, 29 = 1 μm, 30 = 0.5 μm.

Phylogenetic interpretation

A phylogenetic interpretation of our data, based on the general characteristics of the Exobasidiales (see Bauer & al., 2001; Begerow & al., 2002) is illustrated in Fig. 31.

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