Life-History Studies of Brazilian Ascomycetes 6 1)

Three species of *Tubeufia* with, respectively, dictyosporous/pyenidial and helicosporous anamorphs

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Abstract. Tubeufia amazonensis Samuels, Rossman & E. Müllersp. nov. (anamorph = Monodictys-like and Asteronella-like) is described. Tubeufia paludosa (Crouan & Crouan) Rossman (anamorph = Helicomyces-like) and T. palmarum (Torren) Samuels, Rossman & E. Müller comb. nov. (anamorph = Helicomyces-like) are redescribed from Brazilian collections. Taxonomy of the T. paludosa group is discussed. There are at least two species whose ascomata are morphologically identical to those of the type specimen of T. paludosa. The anamorph of one is helicosporous and is dictyosporous for the other. The name T. paludosa is referred to those collections having helicosporous anamorphs. The relationship of Tubeufia Penzia & Saccardo to Thaxteriella Petrak, Melioliphila Spegazzini and Byssocallis Sydow is discussed as are the helicosporous anamorphs found in Tubeufia and Thaxteriella.

Introduction

Rossman (1977) found that ascomata of the three original species of Tubeufia Penzig & Saccardo, T. anceps Penzig & Saccardo, T. coronata Penzig & Saccardo and T. javanica Penzig & Saccardo (the lectotype fide Clements & Shear 1931) cannot be distinguished from ascomata of T. paludosa (Crouan & Crouan) Rossman (= Nectria paludosa Crouan & Crouan, Rossman 1977). We have found, however, that the actual identity of the type species of Tubeufia is in doubt. Ascomata morphologically identical to those of T. paludosa are often associated with a helicosporous hyphomycete (fig. 1, B) and three recent Azorian collections (CUP) produced helicosporous conidia in cultures derived from solitary ascospores. Webster (1951) obtained helicosporous conidia from isolated ascospores of T. helicomyces Hohnel (= T. paludosa fide Rossman 1977) and helicoconidia are present on the type specimen of T. javanica (PAD!). These results

¹⁾ Part 1 in Sydowia 31. Supported in part by projecto Flora Amazonica— The New York Botanical Garden (NSF INT-77-17704) and by a grant from the American Philosophical Society to the senior author. Dr. O. Petrini, ETH Zürich, prepared the Latin diagnosis.

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suggest that *T. paludosa* is a common, well defined species that has a helicosporous anamorph. This picture was clouded by a New Zealand collection (GJS 77—24, PDD) which is morphologically identical to *T. paludosa*. Colonies derived from seven solitary ascospores produced a *Monodictys*-like state. *Monodictys*-like conidia were abundant on the substrate, rotting dicotyledonous wood, and were also found associated with a Panamanian collection (Dumont-PA 1838, NY!) of a *Tubeufia* which was seemingly identical to *T. paludosa*. Helicosporous conidia were not found on either of the specimens and they were not formed in cultures of the New Zealand collection. Furthermore, *Monodictys*-like conidia were not found in cultures of specimens of the Azorian collections.

There appear to be at least two species whose ascomata are morphologically identical to *Tubeufia paludosa* and, given our present knowledge, they can be distinguished only through their anamorphs. The species in the group have been described on the basis of ascosporal length and ascomatal ornamentation. The length of scolecosporous ascospores seems to be a function of age and the various ascomatal embellishments intergrade in their form. In the absence of information to the contrary, we accept the synonymy given by Rossman (1977) for *T. paludosa*. In an effort to save this old name, we refer those species having helicosporous conidia, the most common species, to *T. paludosa*. Whether one of the other names in the complex can be applied to the species having *Monodiycts*-like conidia is the subject of continuing study which is beyond the scope of the present paper.

A second problem concerning *Tubeufia* is its relationship to *Thaxteriella* Petrak. If we had only the type species, there would be no problem in distinguishing the two genera as *Tubeufia paludosa* and *Thaxteriella pezizula* (Berkeley & Curtis) Petrak (= *T. corticola* Petrak, Pirozynski 1972) are quite distinct from each other.

Tubeufia paludosa has waxy, pale yellow to white, egg-shaped, non-subiculose ascomata. The ascomatal wall is relatively thin and has a characteristic structure. Cells at the surface of the wall are distinctly horizontally elongated and the cells of the wall in longitudinal section are elliptic in outline, thin-walled and hyaline; asci arise from a more or less deep cushion of ascogenous hyphae. Ascospores are greater than 150 μm long. As was discussed above, two anamorphs are attributed to this ,,collective'' species, one helicosporous and one dictyosporous.

Thaxteriella pezizula has fleshy, black, globose ascomata produced composed of thick-walled cells. The cells at the surface of the wall have no apparent polarity. Asci arise from a hymenium of ascogenous hyphae that is evenly distributed over the lower ascomatal wall. Ascospores are less than $100 \mu m \log T$. The anamorph of T. pezi-

zula is Helicoma-like and pedicellate, dictyoseptate structures are associated with the helicosporous state (PIROZYNSKI 1972).

Thaxteriella is well defined. The four known species do not differ greatly from T. pezizula and the only known anamorphs, these for T. pezizula and T. roraimense Samuels & E. Müller, are helicosporous. The problem arises in deciding what is Not Tubeufia since the species included in that genus exhibit a continuous gradation from Thaxteriella pezizula to such hypocreoid, hyperparasitic genera as Melioliphila Spegazzini and Byssocallis Sydow (Table 1).

In Tubeufia-Thaxteriella three groups of species can be distinguished by ascomatal wall structure and, to a lesser extent, in ascomatal color. One group, including Tubeufia valudosa and T. amazonensis Samuels, Rossman & E. Müller has the characters outlined above for T. paludosa. A second group includes Thaxteriella pezizula and Tubeufia helicoma (Phillips & Plowright) Pirozynski. These species have the characteristics of Thaxteriella pezizula. Tubeufia amazonensis has features intermediate between the two groups and gives an indication of the close relationship between the two genera. The ascomatal wall has a structure similar to that of T. paludosa. It also resembles the T. paludosa-like collections from New Zealand and Panama because it forms a Monodictys-like anamorph. It is like Thaxteriella pezizula in having a dark ascomatal wall and the dictyoseptate structures associated with the helicosporous state may be analogous to the dictyoconidia of T. "paludosa" from New Zealand and of T. amazonensis.

A third group of species includes Tubeufia cerea (Berkeley & CURTIS) HÖHNEL and T. palmarum (Torrend) Samuels, Rossman & E. MÜLLER. Ascomata of these species are yellow but their structure is neither equivalent to that of T. paludosa nor to Thaxteriella pezizula. In features of ascomatal structure, asci, ascospores and fungicolous habitat, a relationship to Melioliphila and Byssocallis is suggested. Furthermore, the supposed, but unproven, anomorphs of Melioliphila, Byssocallis, Eriomycopsis Spegazzini and Chionomyces Deighton & Pirozynski (Deighton & Pirozynski 1972, Pirozynski 1976) have sympodial, holoblastic conidiogenous denticles and phragmosporous conidia. It is not difficult to see a similarity to these in the anamorphs of T. palmarum and T. cerea (figs. 5 C, D). Although T. cerea and T. palmarum are saprobic while Melioliphila and Byssocallis are hyperparasitic, all are fungicolous. This difference in habitat is no obstacle since many genera of fungi have species adapted to both specialized and non-specialized habitats.

A feature common to all of the above groups is the production of helicosporous anamorphs. Given our present poor state of knowledge concerning the helicosporous fungi, very little taxonomic use can be made of them. Most descriptions do not indicate the nature of the

conidiogenous loci. A comparison of conidiogenous loci of T. palmarum and T. cerea on one hand and the anamorph of T. paludosa on the other hand reveals major differences in conidiogenesis. In T. palmarum and T. cerea, conidia arise from thin-walled pegs that proliferate sympodially; no apparent scar remains on either the conidium or the conidiogenous peg after dehiscence. In T. paludosa the conidiogenous locus appears as a refractive, circular, cicatrized scar with a pore in the middle thus indicating that these are poroconidia. Such a development has not previously been reported for helicosporous hyphomycetes. A third type of conidiogenous scar is seen in Thaxteriella pezizula (Pirozynski 1972, fig. 13) and T. roraimensis (Samuels & MÜLLER 1979, fig. 2 D) wherein each locus has a flat, refractive scar but with no obvious pore. The wall of the conidiogenous peg is not appreciably thinner than that of the subtending hypha, as is the case in T. cerea and T. palmarum. These random observations suggest the possiblilty of recognizing three genera in this group of ascomycetes but many more helicosporous fungi must be examined before anything certain can be said. With the helicosporous hyphomycetes, as with many other groups, it is necessary to move beyond the spectacular aspect of the conidial morphology to the more significant feature of conidiogenesis. This need has already been expressed by Pirozynski (1972) who emphasized the need to carefully describe conidiogenous cells, attachment of conidia and associated conidial forms.

Descriptions of the Species

- Tubeufia paludosa (CROUAN & CROUAN) ROSSMAN, Mycologia 69: 383. 9 Mai 1977. — Figs. 1—2.
 - = Nectria paludosa Crouan & Crouan, Florule du Finistere p. 38. 1867.

ANAMORPH: Helicomyces-like.

TELEOMORPH: Mycelium not apparent except for black hyphae growing into the substrate from ascomatal base. Ascomata perithecioid, solitary, scattered; pale yellow becoming progressively brown from base to apex, darker when dry; elongate, ovoid to clavate, non-papillate, 380—480 $\mu m \, high \times 200-270 \, \mu m$ wide; wall smooth; collapsing by lateral pinching when dry, collapsed ascomata not swelling in 3% KOH; no soluble pigment or color change in 3% KOH or 100% lactic acid. Ascomatal wall ca. 35 μm wide, cells in surface view horizontally elongated, $10-16\times ca.$ 7 μm , walls 1.5-2 μm thick. Longitudinal section: cells elliptic to globose in outline, $10-16\times ca.$ 7 μm , walls 2-2.5 μm thick, becoming progressively more flattened toward the interior; cells lining the locule flat, thin-walled; cells at the surface of ascomatal base brown, joined to the substrate through brown, unbranched, septate, 4 μm wide hyphae. Ostiolar region lacking hairs or other ornaments; composed of elliptic, thin-walled or slightly

thick-walled, hyaline cells measuring ca. $9\times5~\mu m$; many cells in the region of the unopened ostiolar region papillate, ca. $10\times3-5~\mu m$.

Asci bitunicate, narrowly clavate, (135—) 165—225×9—11 µm, 8-spored; apices rounded, thickened, with a "nasse apicale"; bases pointed to pedicellate; ascospores multiseriate, the lower 10—50

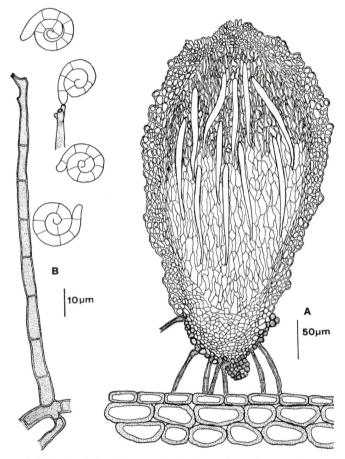


Fig. 1. Tubeufia paludosa (Dumont-BR 38): A. Longitudinal section of ascoma. B. Conidiophore and conidia from substrate (lactic acid, phase contrast)

(-90) µm of each ascus lacking ascospores; arising from different levels of a basal cushion of ascogenous hyphae that fills the lower $\frac{1}{4} - \frac{1}{2}$ of each ascoma.

As cospores fusiform with acute ends, 45-80×3-4 (-5) μm, (5-) 7 (-9)-septate, not constricted at the septa, hyaline, smooth. Interascal filaments 1-1.5 μm wide, septate, branching.

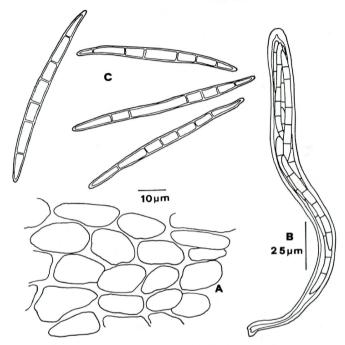


Fig. 2. Tubeufia paludosa (Dumont-BR 38): A. Surface view of ascomatal well. B. Ascus. C. Ascospores

 ${\bf Habitat} \colon {\bf On} \ {\bf lignified} \ {\bf and} \ {\bf non\text{-}lignified} \ {\bf plant} \ {\bf debris}.$

Specimen examined: Brazil: Amazonas, Embrapa experimental station at 30 km on the Manaus-Itacoatiara Rd.; on bark and decorticated wood; Freire, Hosford, Samuels & Buck; 3 Nov 1977 (Dumont-BR 38, INPA, NY).

Notes: For synonymy of T. paludosa see Rossman (1977). The above description of T. paludosa is taken from one Brazilian collection.

The species has a wide range characters; ascospores may be up to 150 µm long and a variety of hairs or cells may be found around the ostiolar opening. The helicosporous state associated with the Brazilian collection is illustrated in fig. 1, B. Conidiophores produced in cultures from an Azorian collection (CUP-MM 2484) did not have such obvious pores in the cicatrized, conidiogenous loci.

Asci in this Brazilian collection arise from different layers of a very deep cushion of ascogenous hyphae. This is probably an extreme case for the species. Asci in a collection of T. vylindrothecia Seaver (CUP 34643! = T. paludosa) also arise from a basal cushion, although it is not as extensive as in the specimen described here.

2. Tubeufia amazonensis Samuels, Rossman & E. Müllersp. nov. Fig. 3—4

Ascomata superficialia, nigra, gregaria, stromate absenti, fuscis hyphis ex basi ascomatis exorientibus atque in substratum penetrantibus, globosa vel obovata, papillis non instructa, 250–340 μm alta, 150–250 μm lata. Asci bitunicati, clavati, $60-80\times10-15$ μm , octospori. Ascosporae fusiformes, apicibus subacutis, rectae vel modice curvatae, 25–35 $\mu m\times3-4$ μm , tri- vel quinquseptatae, hyalinae. Paraphyses septatae, ramificantes. In ligno putrescenti. Status conidialis Monodictyae- et Asteromellae-similis.

Holotypus: Dumont-BR 149, NY. Isotypus: INPA.

ANAMORPH: Monodictys-like; pycnidial state Asteromella-like. TELEOMORPH: Mycelium not apparent. Ascomata perithecioid; gregarious, scattered on decorticated wood; superficial, nonstromatic, black, fleshy; dark hyphae growing from ascomatal base into substrate; globose to ovoidal, non-papillate, 250-340 um high x 150-250 µm wide; wall smooth; collapsing by lateral pinching or not collapsing when dry, no soluble pigment in 3% KOH or in 100% lactic acid but cells of ascomatal wall opaque in 3% KOH and translucent in 100% lactic acid. Ascomatal wall 20-40 µm wide; cells in surface view somewhat elongated horizontally, 16-25×10-13 μm, slightly thick-walled. Longitudinal section: 3-4 cell layers thick, cells elliptic in outline, $10-13\times4-5$ µm; cells at the surface with walls ca. 1.5 µm thick and pigmented, cells within thin-walled and hyaline. Ostiolar region composed of cells elliptic to circular in outline, 4-7 um diam. thin-walled, hyaline; ostiolar opening forming by cellular disintegration, non-periphysate.

Asci bitunicate, narrowly clavate to cylindric, $60-80\times10-15~\mu m$, 8-spored; apices broadly rounded, thickened, with a pronounced "nasse apicale", bases rounded to pedicellate; ascospores multiseriate, forming throughout the length of each ascus; arising from different levels of a cushion of ascogenous cells at the base of each ascoma. Ascospores fusiform with round ends, straight or slightly curved, $25-35\times3-4~\mu m$, 3-5-septate, not constricted at septa, hyaline, smooth; producing a single, unbranched, $15-30~\mu m$ long germ-tube

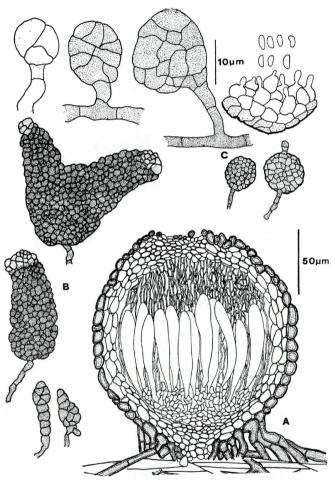


Fig. 3. Tubeufia amazonensis (holotype): A. Longitudinal section of ascoma. B. Monodictys-like conidia; young stages at bottom. C. Pycnidial development; mature pycnidia at lower right

from each end of each ascospore within 12 hrs. Interascal filaments ca. 2 μ m wide, septate, branched.

Characteristics in culture: Colonies on ME, OA and PDA, in 10 days, less than 1 cm diam, aerial mycelium lacking; surface of colony dark brown to olivaceous; immersed hyphae with globose, intercalary, solitary or catenate, brown, smooth or finely spinulose

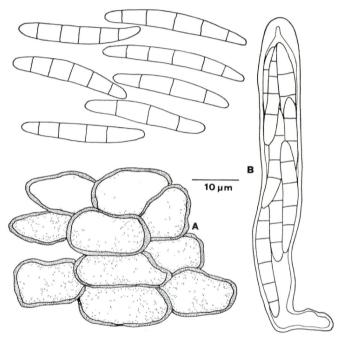


Fig. 4. Tubeufia amazonensis (holotype): A. Surface view of ascomatal wall. B. Ascus and ascospores

swellings. Conidiogenous cells arising as lateral outgrowths of hyphae; the initial cells dividing once and producing a 5–15 μm long stalk and a tip cell; tip cell dividing repeatedly to form an elongated, darkly pigmented, muriform conidium $100-140~\mu m$ $\log \times 50-70~\mu m$ wide; cells in surface view pseudoparenchymatous, 7–10 μm in greatest dimension with walls 1–2 μm thick; tips of conidia often lobed, remaining light brown.

Asteromella-like stage arising in the same fashion as the Monodictys-like stage but cellular mass remaining in the form of a 30—40 μm diam ball and at most only light brown; enclosed in a thin, amorphous membrane; all cells of the ball apparently conidiogenous, phialidic, nearly globose, 3—5 μm diam. Conidia allantoid to bacillar, $3-4\times1-1.5$ μm , hyaline; sometimes light brown, apical regions of Monodictys-like conidia producing conidiogenous locules.

Habitat: On decorticated wood.

Holotype: Brazil: Amazonas, Estacão Experimental de Silvicultura Tropical, on the Manaus-Caracaraí Rd at a point 45 km from the intersection of the Manaus-Itacoatiara Rd; on decorticated wood, Dumont, Freire, Hosford, Samuels, Steward, Buck; 6 Nov 1977 (Dumont-BR 149, NY; Isotype: INPA).

Note: The *Monodictys*-like state of \hat{T} . amazonensis is similar to M. lepraria (Berkeley) M. B. Ellis.

3. Tubeufia palmarum (Torrend) Samuels, Rossman & E. Müller comb. nov. Figs. 5 A—C.

= Ophionectria palmarum Torrend, Bull. Jard. Bot. Etat 4: 8. 1914

ANAMORPH: Helicomyces-like.

TELEOMORPH: Mycelium not apparent. Ascomata perithecioid, solitary to gregarious, scattered, superficial, non-stromatic, fleshy; bright orange to bright yellow when wet, darker and dull yellow when dry; ostiolar opening appearing as a dark, viscid dot in the top of each ascoma; 100-300 µm diam; wall furfuraceous to rugose; hairs arising from cells at surface of wall, 17-40 µm long, each comprised of a chain of 2-8 nearly circular cells measuring ca. 10 µm diam and with walls 1.5-2 µm thick; cells of adjacent hairs may be confluent thus forming warts; ascomata becoming slightly collabent or not collapsing when dry, a yellow pigment soluble in 3% KOH, 100% lactic acid and water. Ascomatal wall 20-40 µm wide. Longitudinal section: outer region 10-25 μm wide, cells circular in outline, up to 10 µm diam, walls ca. 0.5-1 µm thick, pigmented yellow in 100% lactic acid; may be aggregated at the surface to form warts. Inner region 10-30 µm wide; cells elliptic in outline, becoming more flattened toward the interior; 7-10×4-6 μm, walls 0.5-1 μm thick; locule lined by flattened, compressed cells. Ostiolar region composed of elliptic cells, ca. 7 µm diam, walls slightly thickened; non-periphysate.

As i bitunicate, broadly cylindrical, $75-110\times7-10$ µm, 8-spored; apices broadly rounded, thickened, with a "nasse apicale"; bases rounded to pedicellate, ascospores bi-to tri-seriate, forming throughout the length of each ascus; forming a hymenium over the

lower $\frac{1}{3} - \frac{1}{2}$ of each ascomatal wall.

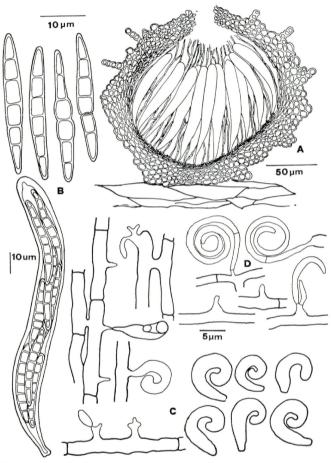


Fig. 5. A.—C. Tubeufia palmarum. A. Longitudinal section of ascoma (DUMONT-BR 144). B. Ascus (DUMONT-BR 529) and ascospores (DUMONT-BR 144). C. Conidiogenous cells and conidia from culture (DUMONT-BR 144; lactic acid, phase contrast). D. Tubeufia cerea (GJS 78—61): Conidiogenous cells and conidia (lactic acid, phase contrast)

As cospores fusiform with subacute to round ends, straight, $30-40~(-50)\times 3-4~\mu m$, 5-7~(-9)-septate; at first not constricted at septa, later may become constricted at median septum and spore cells separating; hyaline becoming pale yellow, smooth; producing from 2-5, terminal and lateral, unbranched or once branched, $35-60~\mu m$ long germ-tubes from each spore within 12 hrs.

Characteristics in culture: Colonies on Weak ME, in 2 weeks, 5 mm diam; aerial hyphae short, mycelium mostly immersed, light olivaceous-yellow. Conidiophores forming in extensive areas, morphologically indistinguishable from vegetative hyphae, indeterminate in length, conidia arising along the length. Conidiogenous cells polyblastic or monoblastic, intercalary; sympodial, proliferating 2—3 times, or determinate; denticulate, denticles acute, narrow, wall thinner than that of the remaining wall of the conidiogenous cell. Conidia solitary, dry, hook-shaped to coiled $\frac{1}{4}$ — $\frac{3}{4}$ times in one plane, O-septate; coils 4—6 μ m diam laterally and (5—) 7—8 μ m from the top of the coil to the point of dehiscence, conidial filament 1.5—2 μ m wide, basal abscission scar not seen. Sterile hairs not seen.

Habitat: On cortex, leaves of palms and ascomycetous stromata. Holotype: Congo: Kisantu, on leaves and fragments of palm, Vanderyst 237, 23 Dec 1906 (BR!).

Additional specimens examined: Brazil: Amazonas, Estação Experimental de Silvicultura Tropical, on the Manaus-Caracaraí Rd at a point 45 km from the intersection of the Manaus-Itacoatiara Rd; on cortex; Dumont, Freire, Hosford, Samuels, BUCK, STEWARD, 6 Nov 1977 (DUMONT-BR 144, INPA, NY); Territorio de Roraima, along the Manaus-Boa Vista Rd at a point ca. 382 km from the intersection of the Manaus-Itacoatiara Rd; in ascomata; DUMONT, HOSFORD, SAMUELS, BUCK, ARAUJO, SOUZA, BERNARDI, 18 Nov 1977 (DUMONT-BR 529, INPA, NY, ZT). - Colombia: Dept. Magdalena, Sierra de Santa Marta between Refugias de la Sierra (1850 m) and San Lorenzo (2200 m) above Santa Marta; on decorticated wood; Dumont, Oberwinkler, Ryvarden, Buritica; 18 Jun 1978 (DUMONT-CO 8866, CO, NY). — Ghana (GOLD COAST): Aburi; on dead bark covered with dematiaceous hyphae and stroma, filed as Calonectria invisibilis Massee ined. (NY). - Puerto Rico: along Rio Nueve Pasos, Dr. Luis Roure's property near Rosario, elev. 140 m; on fruit of ? Mammea americana; Korf, Benson, DIXON, HAINES, PFISTER, ROSSMAN, SANCHEZ, SKOG (ROSSMAN 206; CUP-PR 4178, NY).

Notes: Although the type specimen of T. palmarum is growing on a palm, there are several other fungi present as well and it is possible that one or more of those is the actual substrate of the

Tubeufia. The Brazilian collection Dumont-BR 529 was clearly growing on an old pyrenomycetous stroma.

While ascospores of the two Brazilian collections had a tendency to fall apart at the septa, this was not observed in any of the other specimens of this species that were examined. A Colombian collection (DUMONT-CO 8866), which we tentatively assign to this species, has apparently overmature ascospores that are, except for the hyaline endcells, brown.

The anamorph of T. palmarum is peculiar. Because the conidia are unicellular, hooked rather than coiled and because they arise from fine denticles, this conidial state cannot be easily accommodated in any of the known genera of helicosporous hyphomycetes.

 $Tubeufia\ palmarum$ is similar to $T.\ cerea$ (Berkeley & Curtis) Höhnel (Booth 1964). Ascomata of $T.\ cerea$ are dull yellow to brown and occasionally produce clavate, septate ascomatal hairs; ascospores measure $30-50\times3-5$ μm and have 7-10 transverse septa. The conidial state of $T.\ cerea$ (fig. 5 D) has been identified as $Heliocosporium\ vegetum\ Nees.$ Conidia are distinctly coiled and are larger than those of $T.\ palmarum$. $Tubeufia\ cerea$ is common in temperate North America and Europe where it is found on old, stromatic ascomycetes.

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Table 1. Comparison of the genera Tubeufia, Thaxteriella and Melioliphila/Byssocallis

	Thaxteriella pezizula	Tubeufia helicoma	Tubeufia amazonensis	Tubeufia 'paludosa'	Tubeufia palmarum	Tubeufia cerea	Melioliphila/ Byssocallis
Anamorph:	helicosporous	$^{\rm helicosporous}_{\rm +}_{\rm dictyosporous}$	dictyosporous + pycnidial	helicosporous/ or dictyosporous	helicosporous denticulate	helicosporous denticulate	phragmosporous denticulate
Teleomorph:							
Habitat	wood	wood, hard herbaceous tissue	wood	wood	wood, hard herbaceous tissue, fungi	ascomycetous stromata	black hyphae on Meliolaceae
Subiculum	present, black	present, black	lacking	lacking	lacking	lacking	present, white
Ascomatal color	black	black	black outside hyaline within	white to pale yellow	yellow to orange	orange to brown	yellow
Surface cells	circular	circular	elliptic, horizontally oriented	elliptic, horizontally oriented	angular	angular	angular
Ascomatal ornamentation	lacking	lacking	lacking	various: circular cells or hairs or lacking	chains of circular cells or warted	sometimes clavate hairs	acute, hyphal- like hairs
Ascogenous hyphae	diffused hymenium	? diffused hymenium	basal cushion	basal cushion	diffused hymenium	diffused hymenium	diffused hymenium
Ascosporal shape	phragmosporous $< 100~\mu \mathrm{m}$	$\begin{array}{l} phragmosporous \\ < 100~\mu m \end{array}$	phragmo- sporous < 100 μm	phragmo- scoleco- sporous < > 100 μm	$\begin{array}{l} phragmosporous \\ < 100~\mu\mathrm{m} \end{array}$	$\begin{array}{l} \rm phragmosporous \\ < 100~\mu m \end{array}$	$\begin{array}{l} phragmo-\\ sporous \\ < 100~\mu m \end{array}$

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Zeitschrift/Journal: Sydowia

Jahr/Year: 1978/1979

Band/Volume: 31

Autor(en)/Author(s): Samuels Gary J., Müller Emil

Artikel/Article: Life-History Studies of Brazilian Ascomycestes 6. 180-192