Tirisporella gen.nov., an ascomycete from the mangrove palm *Nypa fruticans*

E.B.G. Jones, K.D. Hyde, S.J. Read, S.T. Moss, and Siti Aisyah Alias

Abstract: ***Tirisporella beccariana*** comb.nov. is redescribed from decomposing leaf petiole (or rachis) bases of *Nypa fruticans* recently collected in Malaysia and the Philippines. The superficial ascomata bear bitunicate asci with (3−)5(−7)-septate ascospores that are brown and verrucose, except for the prominent hyaline basal cell, and furnished with a distinctive apical appendage that arises from the spore wall. The ultrastructure of the fungus is contrasted with that of species of *Corollospora* and *Corallicola*, with particular reference to the mode of ascospore appendage formation. The species was originally described from a Sarawak collection as *Sphaeria beccariana* and later transferred to *Melanomma* and given the new name *Melanomma cesatianum*. *Gibberidea nipae* is a synonym. The recent collections were compared with type specimens. The fungus is not properly placed in *Melanomma* or *Gibberidea* or other known genera and a new genus ***Tirisporella*** is described.

Key words: Ascomycotina, ascospore appendage, mangrove fungus, taxonomy, ultrastructure.

Résumé : Les auteurs redécrivent le ***Tirisporella beccariana*** comb.nov. venant sur la base (rachis) des pétioles foliaires en décomposition du *Nypa fruticans* récemment récoltés en Malaysie et aux Philippines. Les ascomata superficiels portent des asques bituniqués avec (3−)5(−7) ascospores septées qui sont brunes et verruqueuses, sauf pour la cellule basale proéminente hyaline et munie d'une appendice apicale typique qui provient de la paroi sporale. L'ultrastructure du champignon est comparée avec celle d'espèces de *Corollospora* et de *Corallicola* avec une attention particulière au mode de formation de l'appendice ascosporale. L'espèce provient originalement d'une récolte effectuée au Sarawak comme *Sphaeria beccariana* et transférée par après au genre *Melanomma* avec le nouveau nom de *Melanomma cesatianum*. Le *Gibberidea nipae* est un synonyme. Des récoltes récentes ont été comparées avec les spécimens types. Le *Melanomma* ou le *Gibberidea* ou d'autres genres connus ne conviennent pas pour ce champignon et les auteurs décrivent un nouveau genre, le ***Tirisporella***.

Mots clés : Ascomycotina, appendices ascosporales, champignon de mangrove, taxonomie, ultrastructure.
[Traduit par la rédaction]

Introduction

Bitunicate ascomycetes are frequent fungi of the intertidal zone of mangroves (Jones and Hyde 1988; Kohlmeyer and Volkmann-Kohlmeyer 1991). Many possess a gelatinous or mucilaginous sheath that swells in water and may serve an adhesive role (Read et al. 1992*b*; Hyde and Jones 1989).

During a study of the mangrove fungi of Malaysia (Jones and Kuthubutheen 1989; Jones and Agerer 1992; Whalley et al. 1994) and the Philippines (K.D. Hyde, unpublished data), a bitunicate ascomycete was collected on *Nypa fruticans* (Thunb.) Wurmb.

Sphaeria beccariana Ces. was described from *N. fruticans* collected in Sarawak by Cesati (1880) and later synonymized with *Melanomma cesatianum* (Ces.) Sacc. by Saccardo (1883). Cesati (1880) described ascospores as cylindric-lunate, brown, and 3-septate (although illustrated as 5-septate), while Saccardo (1883) described them as 5-septate.

Received December 6, 1995.

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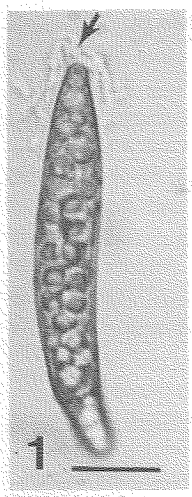
An identical taxon, *Gibberidea nipae*, was later described from dead rachides of *N. fruticans* by Hennings (1908). Ascomata were described as being superficial, ovoid, carbonaceous, and with a conical papilla. Holm (1968) discussed *G. nipae* in a review of the genus *Gibberidea* Fuckel. He found the species remarkable in several aspects, particularly its ascospore type, and suggested it probably cannot be accommodated in any genus so far described. Müller (in Holm 1968) also examined the taxon and stated "Es gibt immer wieder etwas Neues." As Holm was unfamiliar with tropical fungi, he was unwilling to describe a new genus.

Neither *Gibberidea* nor *Melanomma* are suitable genera to accommodate this taxon. In *Gibberidea*, ascomata and pycnidia cover a well-developed hypostroma, asci are bitunicate, and ascospores are yellowish brown, almost cylindrical, with 3-transsepta (Holm 1968). In *Melanomma*, as represented by *Melanomma pulvis-pyrius* (Pers.:Fr.) Fuckel, ascomata are superficial, often densely gregarious in large groups, and ascospores are 3-septate and concolourous (Barr 1990; Mathiassen 1993). In *M. cesatianum*, ascospores are curved cylindrical, almost clavate, with a hyaline basal cell. For this reason, a new genus, *Tirisporella*, is described to accommodate the species. *Tirisporella* differs from species of *Gibberidea* and *Melanomma*, in that the first septum delimits a basal, hyaline cell and the pseudoparaphyses are broad at the base and taper distally. It cannot be assigned to the Melanommataceae (sensu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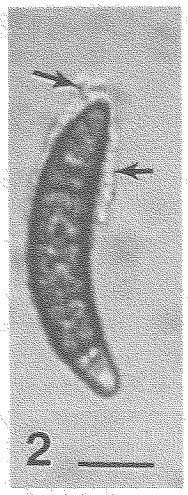
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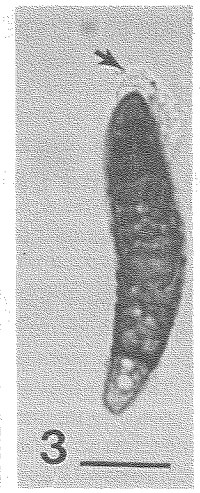
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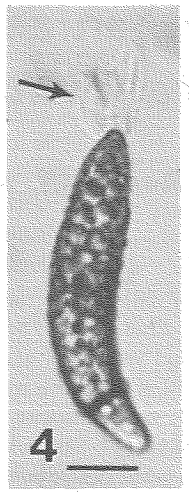
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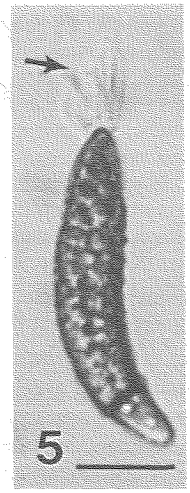
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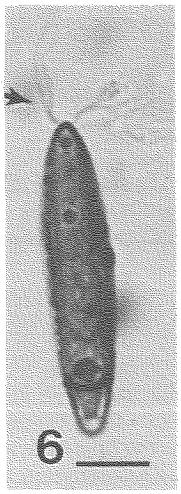
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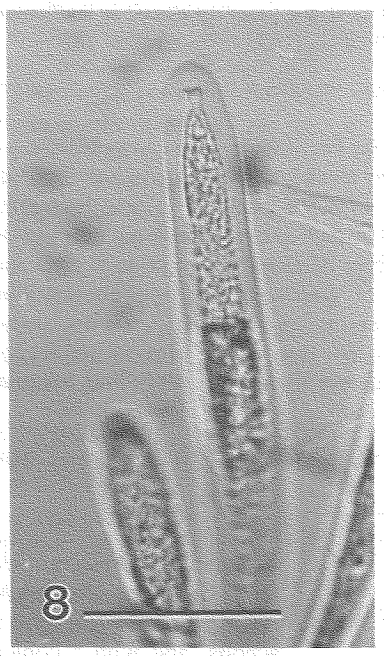
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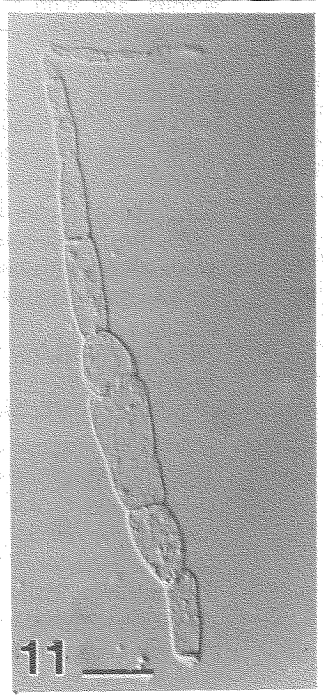
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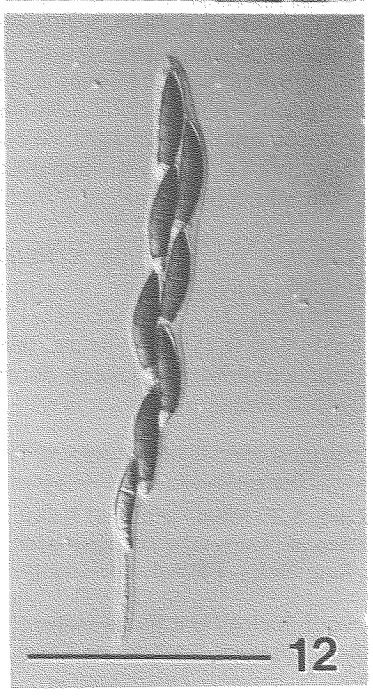
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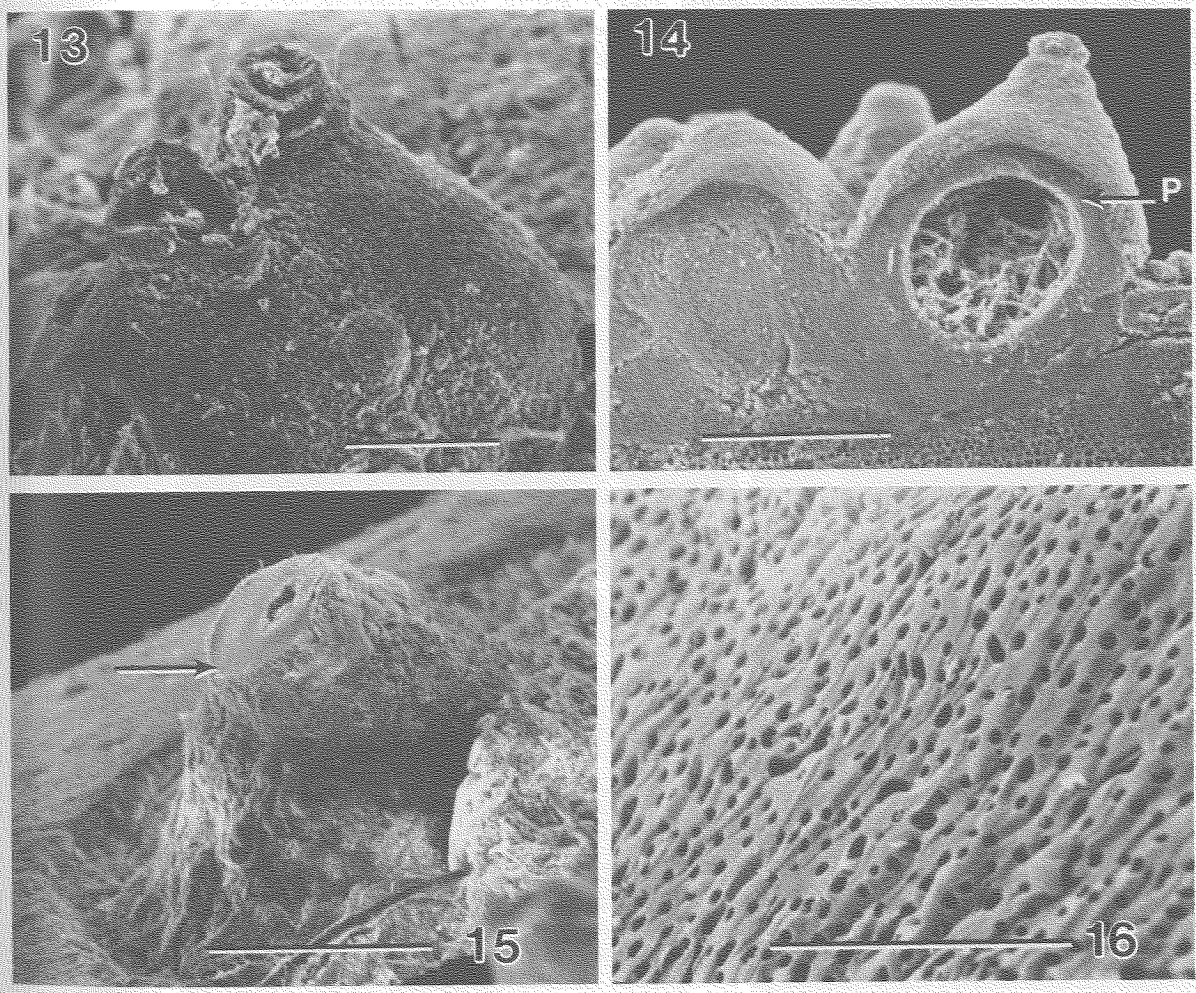
Figs. 1–12. *Tirisporella beccariana*. Light micrographs. Figs. 1–3. Ascospores with apical appendage around spore (arrowed). Scale bars = 10 μm. Figs. 4–6. Apical appendages recurved from spore wall (arrows). Scale bars = 10 μm. Figs. 7 and 8. Immature asci showing thick wall. Ruptured ectoascus (arrows). Scale bars = 50 μm. Fig. 9. Tip of mature ascus with ascospores. Scale bar = 25 μm. Figs. 10 and 11. Pseudoparaphyses. Scale bars = 10 μm. Fig. 12. Ascus cylindrical with apical apparatus. Scale bar = 100 μm.

Figs. 13–16. *Tirisporella beccariana*. Scanning electron micrographs. Fig. 13. Superficial, globose ascomata, carbonaceous, with ostiole. Scale bar = 1 mm. Fig. 14. Fracture of ascoma to show thick-walled peridium (P). Scale bar = 1 mm. Fig. 15. Fracture of thick-walled neck (arrow) of ascoma. Scale bar = 500 μm. Fig. 16. Thick-walled cells that comprise the neck of the ascoma. Scale bar = 25 μm.



Barr 1990) and is placed in Loculoascomycetes, Ascomycotina incertiae sedis.

Materials and methods

Specimens were collected on the cut decomposing rachides of the fronds of the mangrove palm *N. fruticans* at Morib, Malaysia, and Palsabangan, Philippines. The palm rachides were incubated in the laboratory (Jones and Hyde 1988) and examined periodically for ascomata. All measurements and micrographs were made from material mounted in water. All illustrations are from collections of the fungus from Morib, Malaysia.

Material for transmission electron microscopy (TEM) was embedded in 2% ion agar, prior to fixation in 2% (w/v) aqueous potassium permanganate for 10 min. Fixed material was washed in distilled water, dehydrated through a graded ethanol series, transferred to acetone, and embedded in Mollenhauer's resin (Mollenhauer 1964). Ultrathin sections were stained with lead citrate, poststained with uranyl acetate, and examined at 80 kV in a JEOL 100S TEM.

Material for scanning electron microscopy (SEM) was prepared as described by Moss and Jones (1977) and examined at 20 kV in a JEOL T20 SEM.

Type material of *G. nipae* from W and *M. cesatianum* from K were examined.

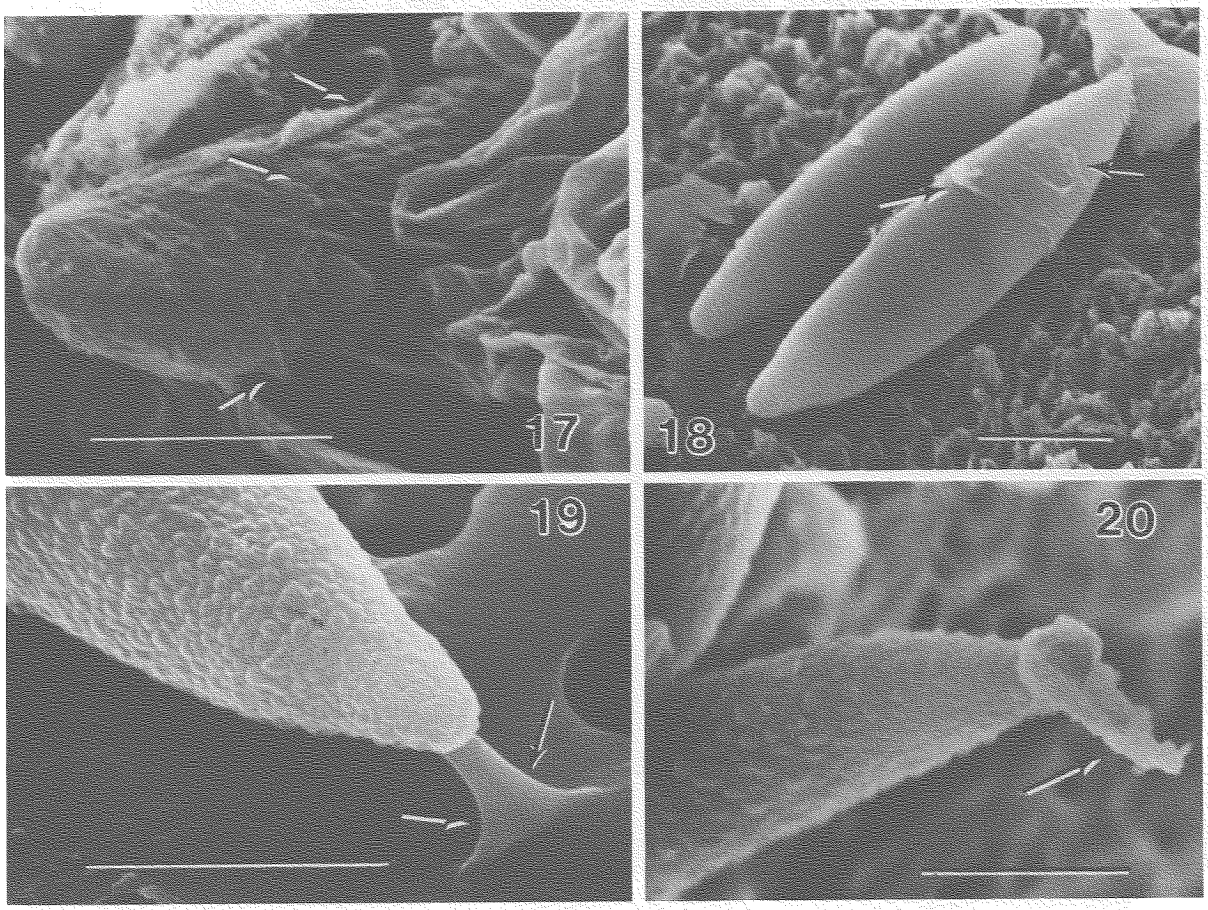
Taxonomy

Tirisporella E.B.G. Jones, K.D. Hyde et Alias gen.nov.

Ascomata subglobosa vel globosa, ostiolata, solitaria vel gregaria, superficialeia nigra, collis brevibus, periphysatibus, coriacei vel carbonacei. Peridium 3 cellularum crassitunicatum, crassum. Pseudoparaphyses fustae, solitares, septatae, hyalinae, ad septum constrictae. Asci octospori, cylindracei,

Figs. 21–26. *Tirisporella beccariana*. Transmission electron micrographs of asci and ascospores. Fig. 21. Longitudinal section through the ascus apex showing the electron-dense ectoascus (*ec*) and less electron-dense endoascus (*en*). Note the core of granular material (arrows) within the endoascus. Scale bar = 2 μm. Fig. 22. Longitudinal section through a dehisced ascus. Note the ruptured ectoascus (*ec*) and the extended endoascus (*en*). Scale bar = 2 μm. Fig. 23. Lateral region of ascus wall showing granular endoascus (*en*) and laciniated ectoascus (*ec*). Scale bar = 250 nm. Fig. 24. Wall layers at the base of the ascus. Note the ectoascus (*ec*), endoascus (*en*), and the corrugated layer between them (arrow). Scale bar = 1 μm. Fig. 25. Immature ascospore with episporium (*ep*), partially formed mesosporium (*me*), and outer delimiting membranes (*d*). Scale bar = 500 nm. Fig. 26. An unreleased mature ascospore. Note the mesosporium (*me*), episporium (*ep*), and appendage (*a*) adpressed to the spore pole. Note also the ascus wall with endoascus (*en*) and laciniate ectoascus (*ec*). Scale bar = 1 μm.

Figs. 17–20. *Tirisporella beccariana*. Scanning electron micrographs. Figs. 17 and 18. Apical appendage adpressed (arrows) to spore wall. Scale bars = 10 μm. Figs. 19 and 20. Note verrucose nature of ascospore wall and the apical appendage adhered to the substratum (arrows, Fig. 19) and recurved from the spore wall (arrow, Fig. 20). Scale bars = 10 μm.



pedunculati, breves, bitunicati, cum apparatu apicali. Ascosporae 5–7 septatae, brunneae, falcatae vel lunatae, cellula apicali acuta, hyalina vel pallida, verrucosa, apiculata.

Ascomata globose to subglobose, single or gregarious, superficial, black, ostiolate, coriaceous to carbonaceous, necks short and periphysate. Peridium comprising three layers: a thin inner layer of textura angularis, a wide middle layer of textura intricata, and an outer layer of black, small cells. Pseudoparaphyses solitary and tapering. Asci 8-spored, cylindrical, short peduncle, bitunicate, fissitunicate, thick-walled, apex flattened with an apical apparatus comprising a canal and pore. Ascospores 2–3 seriate, (4–)5–7 septate, brown, falcate to lunate, verrucose, appendaged, basal cell pointed and hyaline to pale brown.

TYPE SPECIES: *Tirisporella beccariana* (Ces.) E.B.G. Jones, K.D. Hyde et Alias.

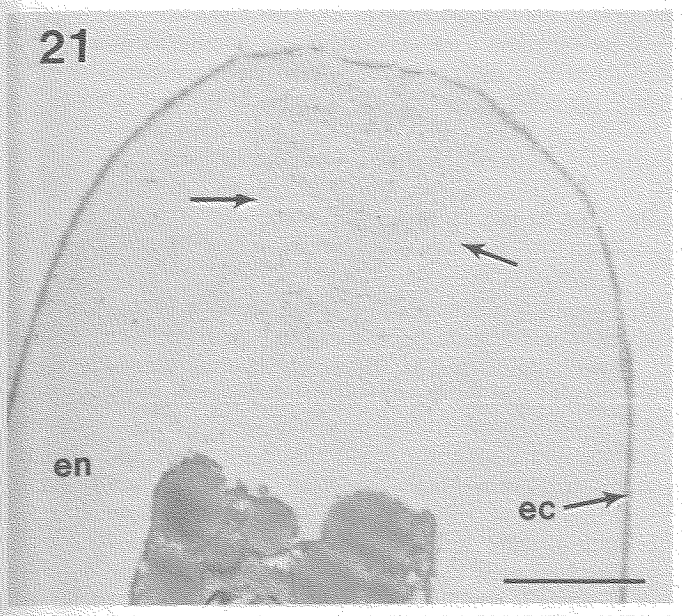
ETYMOLOGY: From the Polynesian *Tiri* meaning a mangrove and *sporella* meaning spore, in reference to the mangrove habitat of the fungus.

Tirisporella beccariana (Ces.) E.B.G. Jones, K.D. Hyde et Alias. comb.nov. Figs. 1–54

≡ *Sphaeria beccariana* Ces., Atti Accad. Sci. Fis. Mat. Napoli, 8: 20. 1880 (basionym).

≡ *Melanomma cesatianum* (Ces.) Sacc., Syllogeum Fungorum, 2: 113. 1883

= *Gibberidea nipae* Henn., Hedwigia, 47: 257. 1908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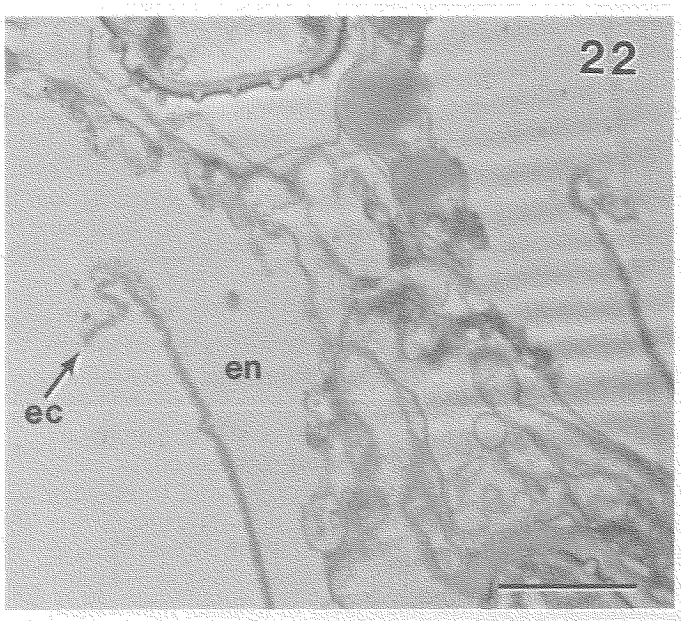
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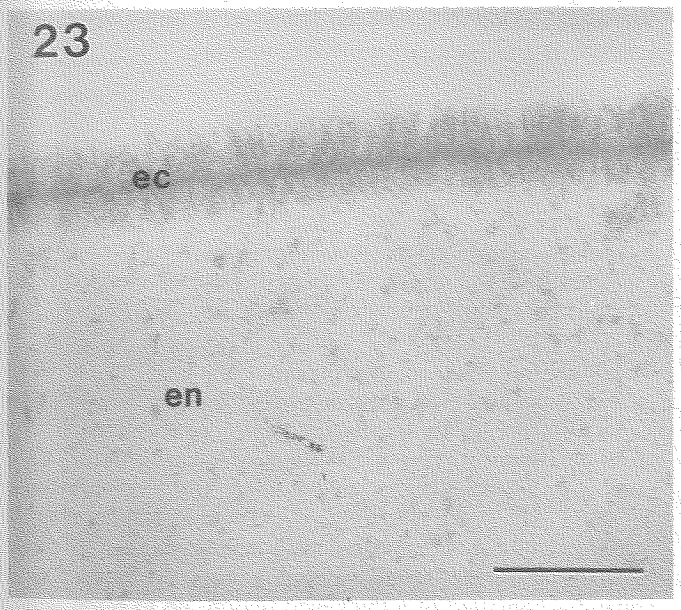
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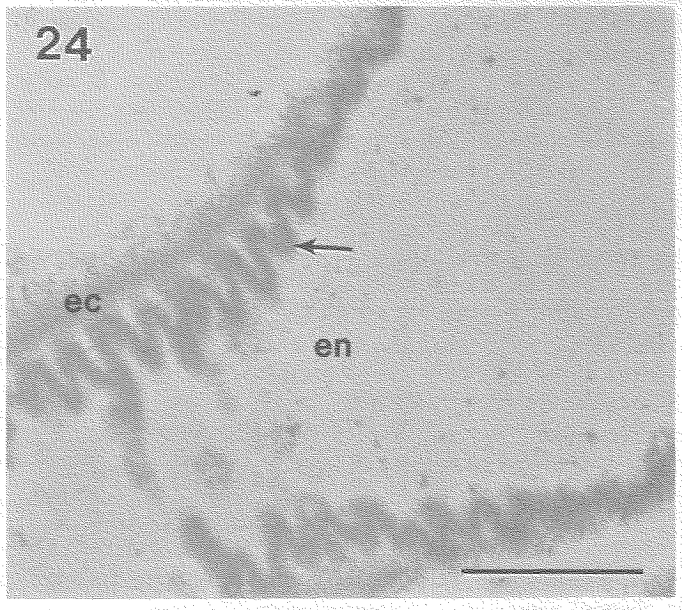
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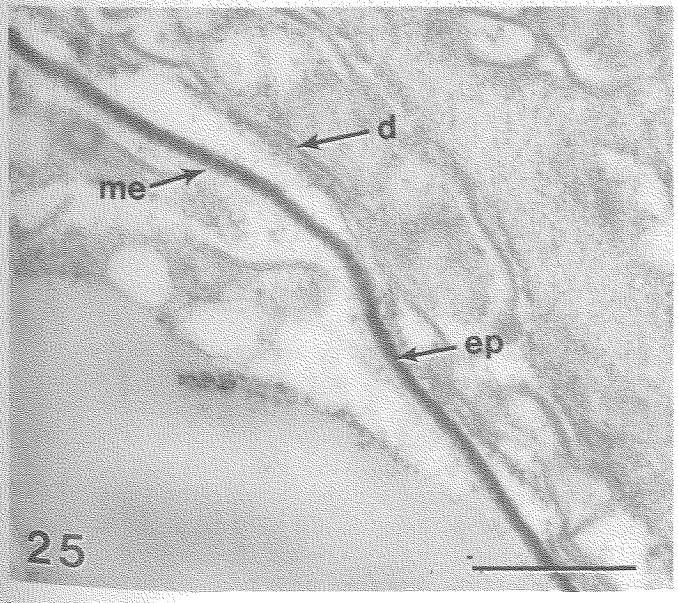
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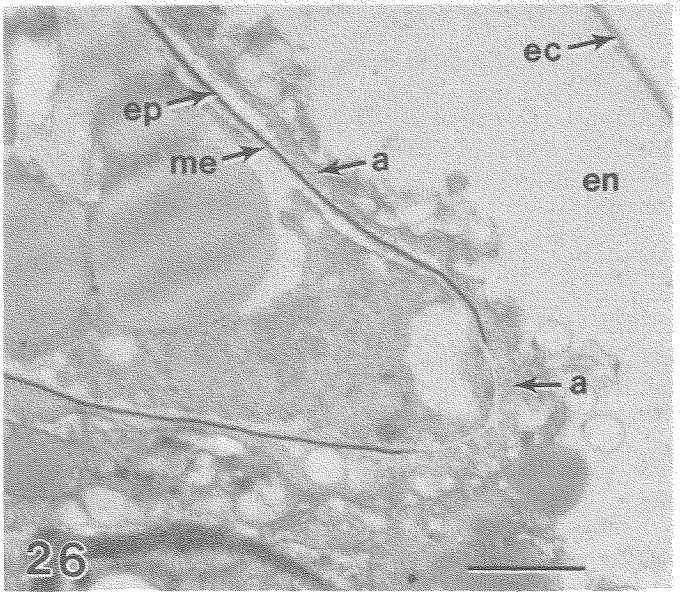
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Figs. 27–32. *Tirisporella beccariana*. Transmission electron micrographs of asci and ascospores. Fig. 27. Two adjacent ascospores (*Ac*) within the ascus. Note the outer delimiting membranes (*d*), mesosporium (*me*), episporium (*ep*), and the ascospore appendage (*a*). Scale bar = 500 nm. Fig. 28. Longitudinal section through the pole of an immature ascospore. The ascospore wall comprises a mesosporium (*me*) and episporium (*ep*). Note that the appendage (*a*) is continuous through a region of the wall in which the episporium is absent (arrow) and the mesosporium poorly defined. Scale bar = 500 nm. Figs. 29–32. Longitudinal sections through the apical regions of mature unreleased ascospores. Note the episporium (*ep*) with verrucose protrusions (arrows), mesosporium (*me*), apical appendage (*a*), and outer delimiting membrane (*d*). Note also the ascus wall with ectoascus (*ec*) and amorphous endoascus (*en*) in Fig. 29. Figs. 29 and 30. Scale bars = 1 μm. Figs. 31 and 32. Scale bars = 250 nm.

Ascomata: 1.3–2 mm in diameter × 1–2.2 mm high, globose to subglobose, crater-like at maturity, single to mainly gregarious, submerged becoming superficial as ascomata break through the epidermal layer of the host, ostiolate, coriaceous, becoming carbonaceous, necks short, periphysate (canal 39–54.5 μm wide, neck wall 83–235 μm thick), black (Figs. 13, 14). Peridium: thick (125–150 μm), comprising three layers (Figs. 14–16): an outer thick layer of textura angularis (60–85 μm) of thick-walled, small, melanized cells; a central layer of prosenchymatous cells (40–60 μm), slightly melanized; and a narrow inner layer of hyaline, thin-walled, elongate cells (35–45 μm). Outer layer of peridium appears to fragment or disintegrate. Pseudoparaphyses: 3.3–8.3 μm wide, single, unbranched, hyaline, septate, constricted at the septa and tapering (Figs. 10, 11). Asci: 122–230 × 16–38 μm ($\bar{x}$ = 204.7 × 20.6, n = 32), 4- or 8-spored, cylindrical, short peduncle, bitunicate, fissitunicate, thick-walled, apex flattened, with an apical apparatus comprising a canal and pore (Figs. 7–9, 12). Ascospores: 31–52.5 × 5–10.5 μm ($\bar{x}$ = 42.9 × 8.5, n = 80), brown, (4–)5–7 septate, falcate to lunate, verrucose, apical cell appendaged, basal cell pointed and hyaline (Figs. 1–6, 17–20). The first septum formed in the ascospore is near the base and delimits the light-coloured basal cell (Fig. 1). Appendage initially closely adpressed to the spore wall (Figs. 1–3, 17, 18); in water, separating from the wall and inverting to form a single, apical structure (Figs. 4–6, 19, 20).

LECTOTYPE (selected here): Malaysia, Sarawak on *N. fruticans*, 7 m, Aug. 1865, Beccari 361, Herb. Berk. 3144, K.

SUBSTRATUM: Decaying leaf bases of *N. fruticans*.

HABITAT: Brackish, 5–10‰, upper part of mangrove along the channel ways.

MODE OF LIFE: Saprobic.

DISTRIBUTION: Straits of Malacca, Matang, and Sarawak, Malaysia; Pampanga, San Esteban, Luzon, Philippines.

MATERIAL EXAMINED: MALAYSIA: Sarawak, on *N. fruticans*, 7 m, Aug. 1865, Beccari 361, Herb. Berk. 3144, K (LECTOTYPE); Morib, decaying bases of rachis of *N. fruticans*, June 1992, IMI 359654; Kuala Selangor, rachis *N. fruticans*, 9 Feb. 1993; Matang, rachis *N. fruticans*, Sept. 1994. PHILIPPINES: Luzon, Pampanga, San Esteban, in dead rachis of *N. fruticans*, Sept. 1905, Merrill No. 4255, W (lectotype of *G. nipae*); Quezon, Talipas, Palsabangan, decaying petioles of *N. fruticans*, July 1994, K.D. Hyde 2022.

ANAMORPH: Single spore isolations of *T. beccariana* yielded a dematiaceous anamorph morphologically similar to *Phialophora* cf. *olivacea* W. Gams. (CBS 735.94 isolated by K.D. Hyde; CBS 293.95 isolated by S.A. Alias ex PPCC 6937). Cultures grow well on seawater cornmeal agar, forming dark brown colonies. Phialides are 13.5–15 × 1.5–3 μm, conidia are 4.5–6 × 3 μm (Figs. 33–38). *Phialophora olivacea* is classified in section *Catenulatae* characterized by catenate phialoconidia (Gams and Holubová-Jechova 1976). The only difference is that our isolates form conidia in slimy heads.

Two specimens of *M. cesatianum* were provided by Kew, both marked as the type, Beccari 231 and 361. In the latter specimen, several solitary ascomata were present on the host surface and a diagram of the taxon was provided. In 231, there were no fungi, and therefore 361 is selected to represent this taxon. Unfortunately, this material is not in good condition; there are no asci or pseudoparaphyses. The ascospores, however, are identical to those found on the lectotype of *G. nipae* in which asci and pseudoparaphyses are preserved. We were unable to locate the holotype of either species in PAD or B and these are probably missing.

Ultrastructural observations

Scanning electron microscopy

Ascospores are verrucose (Figs. 17, 19, 20) with a single apical appendage (Figs. 17–20). This appendage initially surrounds the apex of the ascospore (Figs. 17, 18) but later separates from the subapical region of the spore wall to form the apically attached appendage (Figs. 19, 20).

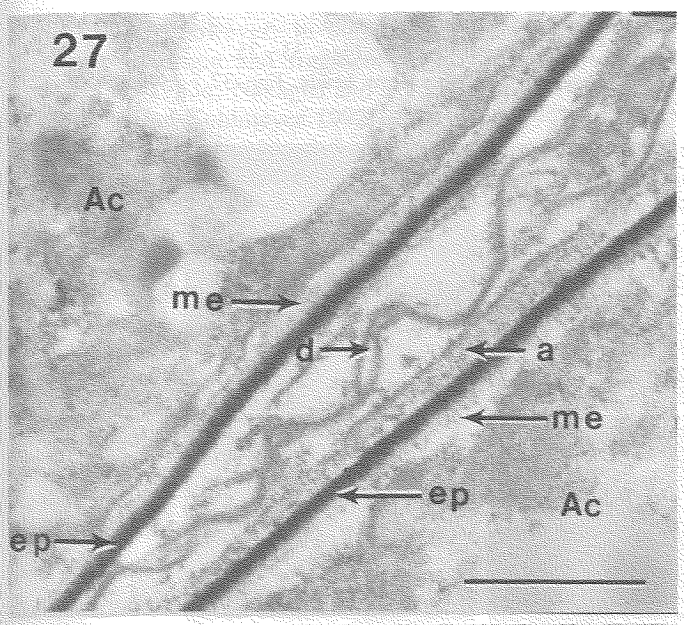
Transmission electron microscopy

In immature asci (not illustrated), the endoascus and ectoascus were not obviously discrete. In more mature asci, the ascus wall appeared two layered, with an inner, 2.2–2.75 μm thick region (endoascus), and an outer, 100–120 nm thick (Figs. 21, 22), more electron-dense layer (ectoascus) that, at higher magnification, appeared to be laciniated (Figs. 23, 24).

In early stages of ascosporogenesis, the ascus apical apparatus consisted of a thickened region, up to 6 μm deep, with a central core of a slightly more electron-dense granular material approximately 3 μm in diameter at its widest point (Fig. 21). Later in development, the ectoascus was discontinuous.

At maturity, the bitunicate nature of the asci was most apparent, the granular core of the ascus apex was lost, the ectoascus ruptured, and the endoascus extended through the ectoascus to release the ascospores (Fig. 22).

Early in ascosporogenesis, the ascospore wall was laid down between the outer and inner delimiting membranes (Figs. 25, 27, 30, 31) and comprised an inner, 65–75 nm thick layer, the mesosporium, and an outer, 60 nm thick, more electron-dense layer, the episporium. In some regions, a mucilage-like material appeared to be present between the episporium and the outer delimiting membrane (Fig. 31). At a later stage, but when the ascospores were still nonseptate, the episporium became more discrete and 50 nm thick, whereas the mature mesosporium was 100–110 nm thick. At the apex of the ascospores, a 0.9–1.1 μm diameter region of the episporium was absent and the mesosporium was less discrete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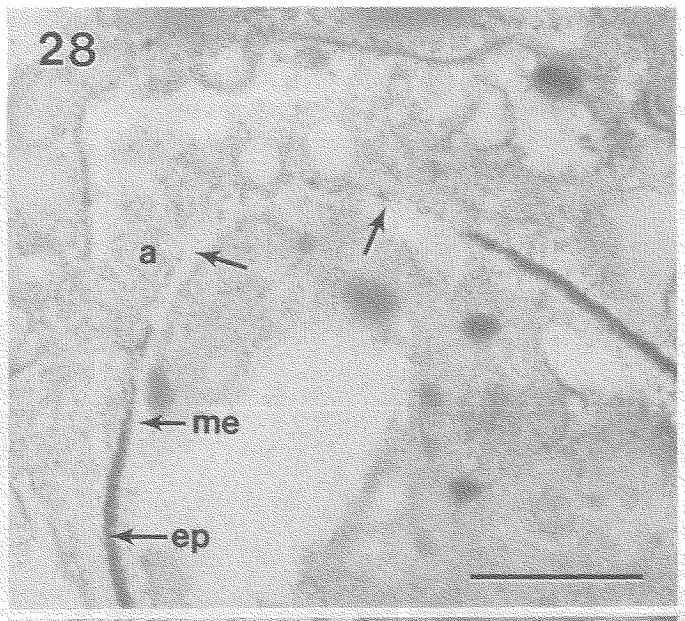
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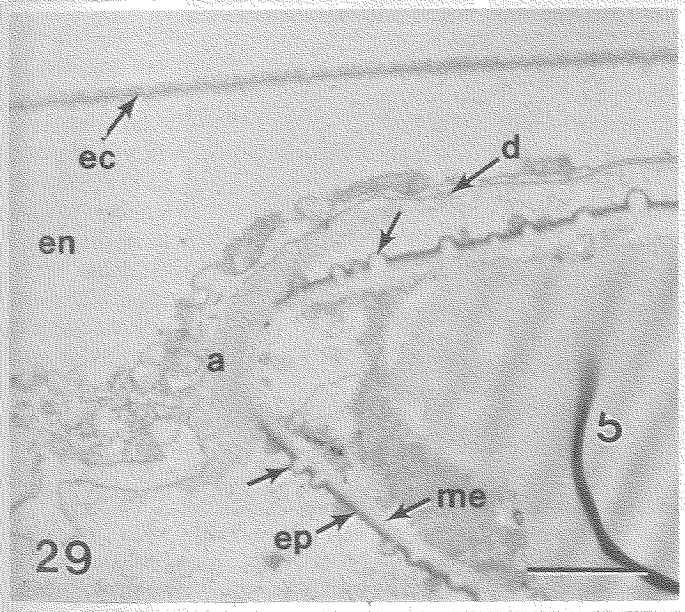
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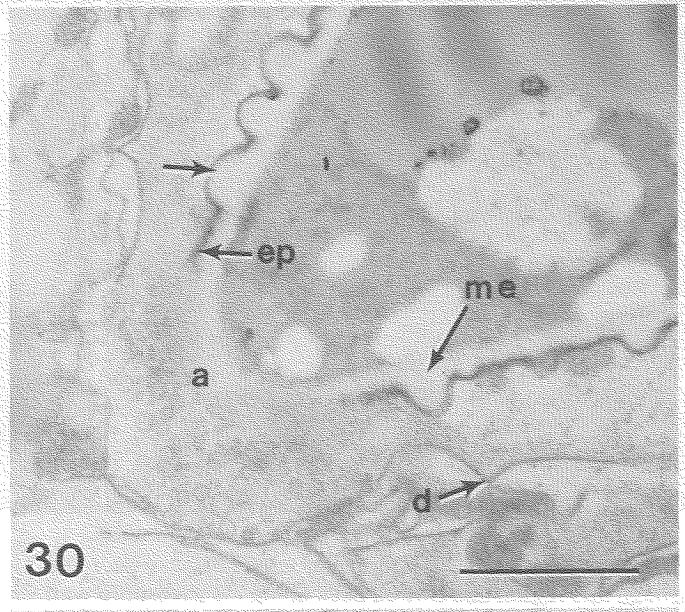
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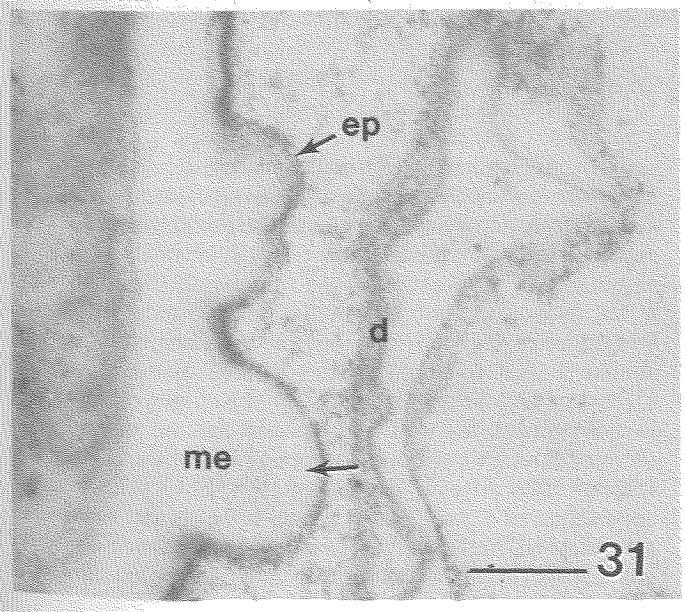
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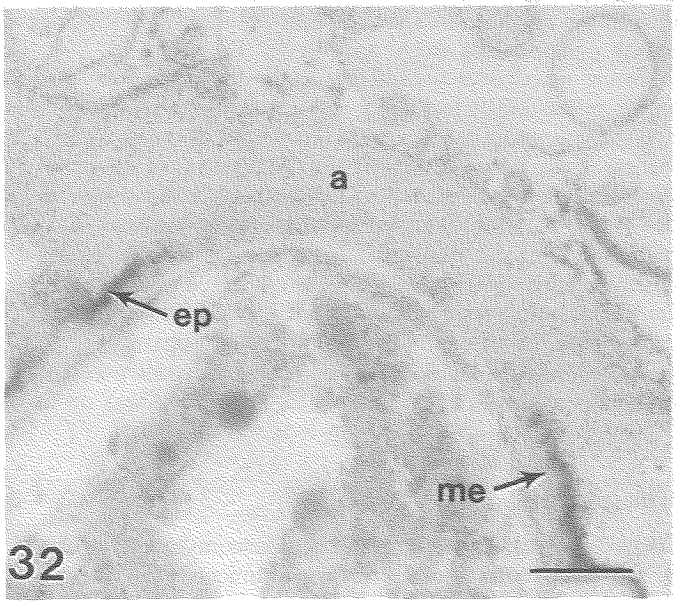
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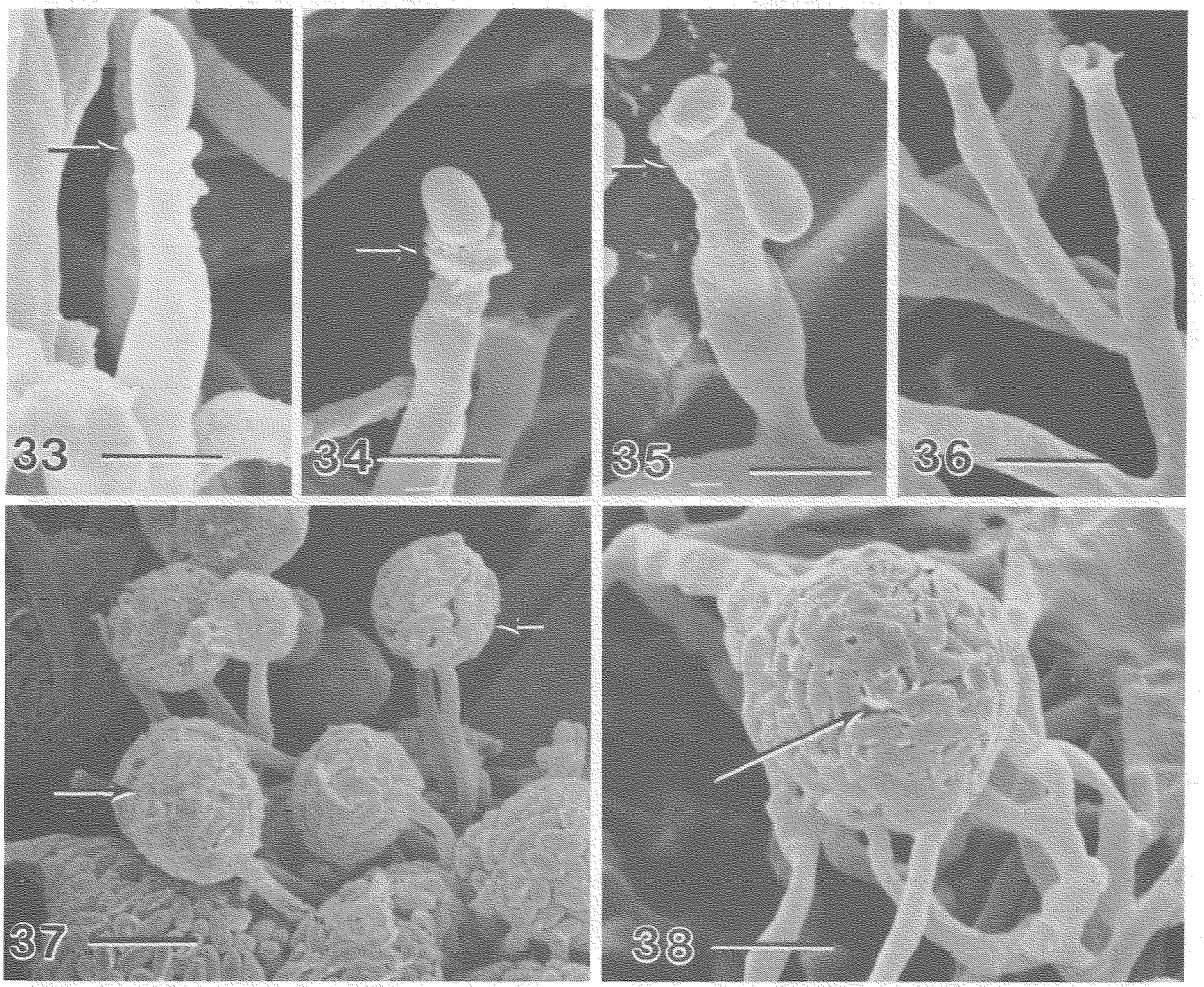
Figs. 33–38. *Tirisporella beccariana*, anamorph stage *Phialophora olivacea* in culture. Scanning electron micrographs. Figs. 33–36. Phialides with collarettes (arrows) and developing amerosporous conidia. Figs. 33–35. Scale bars = 3 μm. Fig. 36. Scale bar = 45 μm. Figs. 37 and 38. Conidia aggregated to form slimy heads. Fig. 37. Scale bar = 9.5 μm. Fig. 38. Scale bar = 6 μm.



(Figs. 26, 28–30, 32). A fibrillar material was secreted through this region and flowed back along the ascospore wall between the episporium and the outer delimiting membrane to form a sheath-like apical appendage (Figs. 26, 28, 29).

Mature ascospores within asci, or in the process of discharge, possessed up to 5 septa and were still retained within the outer delimiting membrane. The spore wall comprised an electron-dense episporium (50 nm thick) and an electron-transparent mesosporium (150–170 nm thick) that was verrucose (Figs. 29–31). The verrucations were hemispherical enlargements of the mesosporium, 250 nm across, scattered densely but irregularly over the entire surface of the spore. The episporium was continuous but less discrete over the verrucations. In water, the apical appendage separated from the spore wall (Figs. 19, 20). The ascospore wall was discontinuous at the pole, and the apical appendage was up to 270 nm thick and up to 12.5 μm long.

Discussion

Tirisporella is assigned to the Loculoascomycetes, incerta sedis, Ascomycotina because of the bitunicate asci. We are unsure of the familial placement of this taxon. The tapering pseudoparaphyses and the first ascospore septum formed near the base delimiting a hyaline or light-coloured basal cell is a characteristic feature of the genus. *Tirisporella* superficially resembles *Astrosphaeriella* (Hawksworth and Boise 1985), but this is a melanomataceous genus with trabecula in a gel matrix and with syroretric ascospores.

In *T. beccariana*, the most characteristic feature is the verrucose ascospore with the apical appendage. No other marine or mangrove species possesses such similarly appendaged ascospores. The appendage in *T. beccariana* arises as an outgrowth or secretion of the spore wall; the episporium at the ascospore apex is absent while the mesosporium is less discrete. This type of ascospore appendage ontogeny is similar to that found in species of *Aniptodera* Shearer et Miller and *Halosarpheia* Kohlmeyer et Kohlmeyer; however, in these genera, the wall layers persist and the appendage is secreted through a series of discontinuities of the episporium (Farrant 1986; Jones et al. 1994). At the SEM level, the apical appendages of *T. beccariana* appear to be similar to those of *Corollospora* Werdermann, *Corallicola* Volkmann-Kohlmeyer and Kohlmeyer (Halosphaeriaceae), and *Chaetosphaeria* (Jones

et al. 1983*b*); however, in these genera, appendages are exosporic in origin and fragment along precleaved zones (Jones et al. 1983*a*; Nakagiri and Tokura 1987; Volkmann-Kohlmeyer and Kohlmeyer 1992; Read et al. 1992*a*).

Ecologically, the species is known only from the decaying rachis bases of *N. fruticans* and has not been found on other parts of the frond. The ascomata are prominent on the rachis bases, easily detected by touch, and readily detached from the surface. These *N. fruticans* bases are frequently inundated by seawater, and the salinity at the collection area was in the range of 5 to 10‰. The fungus was first collected by us at Morib, Malaysia and was found to be abundant at this site on the cut rachis of *N. fruticans*. It has subsequently been collected on *N. fruticans* lining the banks of the river at Kuala Selangor, Malaysia, as before, on rachis bases that had been cut. More recently, the fungus was collected on *N. fruticans* rachis in Boracay, Philippines (E.B.G. Jones, S.A. Alias, and J. Torres, personal communication).

Acknowledgements

We are grateful to the British Council and the University of Malaya for financial support under the Consortium for International Cooperation in Higher Education (CICHE) programme, Mr. C. Derrick for photographic assistance, the Natural Environment Research Council for research grant No. GR3/7122, and the Curators of herbaria K and W for loan of material to study. We are grateful to Dr. Walter Gams, Centraalbureau voor Schimmelcultures, for the identification of the anamorph stage. Dr. K.D. Hyde is grateful to Helen Leung for technical assistance and Mr. A.Y.P. Lee for photographic assistance. Siti Aisyah Alias is grateful for a fellowship from the University of Malaya.

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