

Conidiomatal structures of the stilbellaceous and allied fungi*)

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Summary. – Conidiomatal anatomies of stilbellaceous and allied fungi were studied extensively mainly using freezing microtome sections. Conidiomatal structures varied considerably and were continuous among the fungi studied. Taxonomic systems of the Deuteromycotina based on conidiomatal morphology are discussed.

Introduction

Fruit-bodies, fructifications or sporocarps, which are spore-bearing organs of ascomycete and basidiomycete fungi, are referred to as ascocarps (ascomata) and basidiocarps (basidiomata), respectively. They may be subdivided into several categories (SNELL & DICK, 1957; HAWKSWORTH & al., 1983). Fructifications of the Fungi Imperfecti are generally categorized as pycnidia, acervuli, stromata, sporodochia, synnemata, or simple conidiophores. According to the nature of their fructifications, teleomorphic and anamorphic fungi may be classified into higher taxa; e. g., classes or orders. Following the Saccardoan system, the Deuteromycotina is now distributed into two classes and seven orders based on these fructifications (HAWKSWORTH & al., 1983).

As our knowledge of the fructifications of anamorphic fungi advances, it becomes clear that different kinds of fructifications are not always easily distinguishable and are in some instances continuous. MASON (1937) showed acervuli and pycnidia belonging to the same life-history in *Heteropatella antirrhini* BUDD. & WAKEF., and also discussed the overemphasis of fructifications in the classification of the Fungi Imperfecti. SUTTON (1973) mentioned the morphology and ontogeny of fructifications in his survey of Coelomycetes. He stressed that their variability leads to taxonomic difficulties, and suggested there was a close relationship between acervuli and sporodochia. Many unusual or intermediate fructifications have

*) This contribution is dedicated to Prof. Dr. E. MÜLLER (Zürich, Switzerland), on occasion of his 65th birthday (cf. SYDOWIA 38, 1985).

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been described particularly in Coelomycetes (e. g.: DiCosmo, 1978; Dyko & Sutton, 1979). NAG RAJ (1978) consequently coined the term conidioma (plural: conidiomata) for a specialized multi-hyphal, conidium-bearing structures. KENDRICK & NAG RAJ (1979) extended use of the term to embrace pycnidia, acervuli, sporodochia, synnemata and all intermediate forms and discussed some aspects of conidioma-morphology, particularly in the Coelomycetes. Conidiomatal structures as they relate to systematics in Coelomycetes are, moreover, well discussed by SUTTON (1980) and NAG RAJ (1981).

From the existing situation, SUTTON (1980) proposed an alternative system of classification for the Deuteromycotina. It is founded on the conidium-ontogeny based system (HUGHES, 1953; TUBAKI, 1958; COLE & SAMSON, 1979) and does not take a serious view of conidiomatal structures.

Apart from the study of SEIFERT (1985 a), who split synnemata into two broad categories, determinate synnemata and indeterminate synnemata, and recognized some anatomical types, no other studies have been done, as far as we know, on the conidiomatal anatomies of synnematous fungi. Therefore, it is the purpose of this study to reveal the conidiomatal structures of synnematous and related fungi, and also to discuss the taxonomy of the Stilbellales.

Materials and Methods

Fungi examined were mostly newly collected by the authors and other colleagues in Japan, and were immediately isolated by the senior author (G. O.). Most of the specimens and cultures are preserved in Japan Collection of Microorganisms (JCM).

Conidiomata developed on natural substrates or in culture were cryo-sectioned using a Yamato-koki freezing microtome (Yamato-koki Industrial Co., Tokyo, Japan) with a komatsu model EFM-101 thermo-electric freezing unit (Komatsu electronics Inc., Tokyo, Japan). Following the method of DiCosmo and Cole (1980), small pieces of the substrate or agar medium where conidiomata developed were embedded in drops of Tissue-Tek O.C.T. compound (Miles Scientific Inc., Naperville, IL, U.S.A.), frozen at ca. -15°C , and sectioned with a stainless steel microtome blade (Feather Inc., Osaka, Japan). The sections were mounted in lactic acid, 10% glycerol or distilled water on a slide and sealed with a cover slip.

Photomicrographs were taken on a Nikon XF-NT-21 Nomarski interference and phase contrast microscope, Nikon XF-21 microscope or Carl Zeiss Jena citoval stereomicroscope.

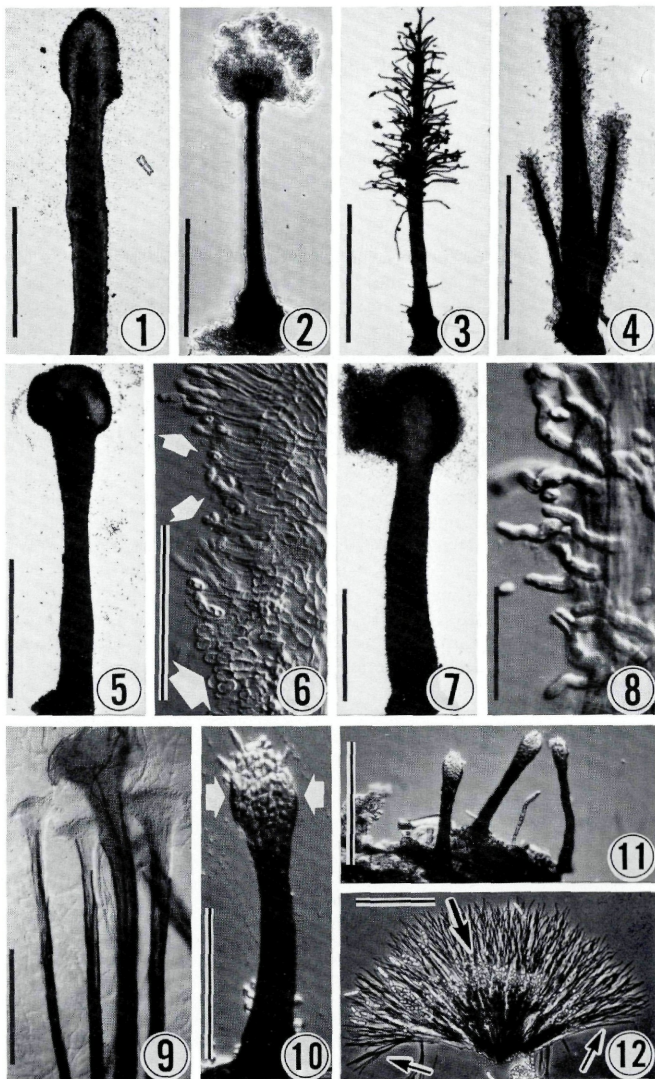
Results and Discussion

Our investigations of conidiomatal structures of synnematous and allied fungi reaffirmed that the conidiomata of synnematous fungi vary considerably in structure and some of them are closely related to conidiomata in the Coelomycetes as well as those in the Tuberculariales.

In most cases, the stipes of synnemata merely consist of aggregated conidiophores; e. g., *Arthrobotryum stilboideum* Ces., *Chalara*

paradoxa (de SEYNES) SACC., *Didymobotryum rigidum* (BERK & BR.) SACC., *D. verrucosum* HINO & KATUMOTO, *Doratomyces microsporus* (SACC.) MORTON & SMITH, *D. nanus* (EHRENB. ex LINK) MORTON & SMITH, *Graphilbum pleomorphum* OKADA & TUBAKI, *Graphium calicioides* (Fr.) COOKE & MASSEE, *Melanographium selenioides* (SACC. & PAOLETTI) M. B. ELLIS, *Penicillium vulpinum* (COOKE & MASSEE) SEIFERT & SAMSON (*P. claviforme* BAIN., SEIFERT & SAMSON, 1985), *Phaeoisaria clematidis* (FUCKEL) HUGHES, *P. magnifica* DEIGHTON, *Podosporium tjibodense* PENZ. & SACC., *Stilbella aciculosa* (ELLIS & EVERHART) SEIFERT, *Stilbella fusca* (SACC.) SEIFERT, *Trochophora simplex* (PETCH) MOORE, *Virgatospora echinofibrosa* FINLEY (Figs. 1, 2, 3, 4; HISAJIMA & al., 1983; OKADA & TUBAKI, 1984 b). Following the concepts of SEIFERT (1985 a), these synnemata can be further subdivided into determinate synnemata and indeterminate synnemata. Although both these synnemata are usually fertile at the head or along the whole surface, *Sarophorum palmicola* (HENN.) SAMSON & SEIFERT has unique synnemata where the conidiophores cover the entire surface except the apex (Fig. 33–h; PERSIANI & ONOFRI, 1982; SAMSON & SEIFERT, 1985). Some synnemata possess ornamenting cells or marginal hyphae often at upper part of the stipe: e. g., *Arthrobotryum hyalospora* OKADA & TUBAKI, *Myrothecium masonii* TULLOCH, *Stilbella clavulata* (MONT.) SEIFERT, *Tubercularia lateritia* (BERK.) SEIFERT (Figs. 5, 6, 7, 8; TULLOCH, 1972; OKADA & TUBAKI, 1984 b; SEIFERT, 1985 a). In *Pesotum piceae* CANE & SCHOKNECHT, young hyaline synnemata become wholly dark brown in age, as they are covered by an exterior cylinder of dark brown hyphae (Fig. 9). *Leptoxyphium* sp. and *Phialoarthrobotryum triseptatum* MATSUSHIMA have sterile hyphae at the top of synnemata that support and partly cover a conidial drop (Figs. 10, 11, 12).

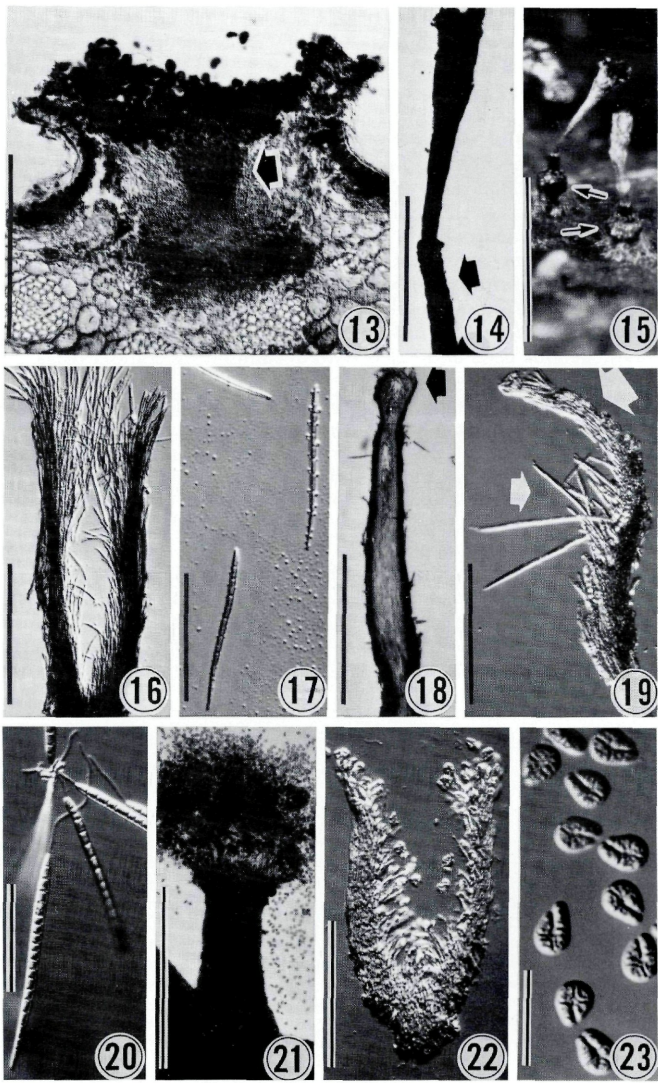
Plate 1: Fig. 1. *Graphilbum pleomorphum*. GO-254. Synnema, sectioned; scale = 200 μ m. – Fig. 2. *Graphium calicioides*. GO-273. Synnema, phase contrast; scale = 200 μ m. – Fig. 3. *Melanographium selenioides*. GO-168. Synnema; scale = 500 μ m. – Fig. 4. *Phaeoisaria clematidis*. GO-227. Synnemata; scale = 200 μ m. – Figs. 5, 6. *Stilbella clavulata*. GO-190. 5. Synnemata; scale = 500 μ m. – 6. Upper part of a synnema showing ornamenting cells (big arrow) and phialides (small arrows), sectioned, Nomarski; scale = 50 μ m. – Figs. 7, 8. *Tubercularia lateritia*. GO-188. 7. Synnemata; scale = 500 μ m. – 8. Ornamenting cells along the stipe of a synnema, sectioned, Nomarski; scale = 20 μ m. – Fig. 9. *Pesotum piceae*. OFC-1086. Synnemata covered with peripheral dark brown hyphae, Nomarski; scale = 100 μ m. – Figs. 10, 11. *Leptoxyphium* sp. GO-86. Synnemata in which sterile hyphae (arrows) partly cover a conidial drop at the head, Nomarski; scale = 50 μ m (Fig. 10), 100 μ m (Fig. 11). – Fig. 12. *Phialoarthrobotryum triseptatum*. MFC-2183. Conidial head in which conidigenous cells (big arrow) are embedded in sterile hyphae (small arrows), phase contrast; scale = 100 μ m.



Conidiomata of the genus *Endocalyx* BERK. & BR. are morphologically quite variable (OKADA & TUBAKI, 1984 a). In *E. melanoanthus* var. *melanoanthus*, *E. melanoanthus* var. *grossus* OKADA & TUBAKI, *E. indumentum* OKADA & TUBAKI, and *E. thwaitesii* BERK. & BR., conidiomata are superficially acervuloid to synnematosus, though they are covered with curious sterile peridial hyphae and have conidiogenous cells in much lower parts of the conidioma than those of other synnematosus fungi (Fig. 13). The base of the synnema-like conidioma of *E. cinctus* PETCH is further covered with a black carbonaceous hyphal cylinder which, in culture, often swells spherically, reminiscent of the base of pycnidium (Figs. 14, 15).

AS BRUBACHER & al. (1984) have already mentioned, it has been confirmed that some stilbellaceous fungi have synnema-like conidiomata with a terminal/apical cavity in which conidiogenous cells line the inner wall. An unidentified *Morrisographium* sp. possesses cupulate conidiomata (Fig. 16) in which annellidic conidiogenous cells and hyaline phragmoconidia are produced (Fig. 17). ILLMAN & WHITE (1985 b) recently presented a monograph of *Morrisographium* MORELET based mainly on conidial, conidiomatal morphology and host specificity. They mentioned "the exterior hyphae covering the enlarging conidial mass during early development (giving the conidiomata the appearance of a stalked pycnidium) . . ." The fact that some species of *Morrisographium* had formerly been disposed in some coelomycete genera (ILLMAN & WHITE, 1984, 1985 b) suggest a close relationship between *Morrisographium* and coelomycete fungi. Moreover, another unidentified *Morrisographium*-like fungus found in Japan also has cupulate conidiomata in which hyaline phragmoconidia with a distal appendage are produced (Figs. 18, 19, 20). This fungus is closely related to *Coniomyces transvaalensis* SIN-

Plate 2: Fig. 13. *Endocalyx melanoanthus* var. *melanoanthus*. TKBF-5014. Basal part of a conidioma, rupturing the epidermis of the host, in which conidiogenous cells and young conidia (arrow) exist in lower part, Nomarski; scale = 200 μ m. – Figs. 14, 15. *Endocalyx cinctus*. TKBC-1290. 14. Synnema-like conidioma covered with carbonaceous hyphal cylinder (arrow); scale = 500 μ m. – 15. Basal carbonaceous hyphae forming spherical structures (arrows); scale = 1 mm. – Figs. 16, 17. *Morrisographium* sp. 16. Cupulate conidioma at the apex, sectioned, GO-113, Nomarski; scale = 100 μ m. – 17. Phragmoconidia, GO-19, Nomarski; scale = 50 μ m. – Figs. 18–20. *Morrisographium*-like fungus. GO-287. 18. Conidioma with a cavity at the head (arrow), sectioned; scale = 500 μ m. – 19. A part of the covering hyphae (big arrow) and inner conidiogenous cells (small arrow), sectioned, Nomarski; scale = 100 μ m. – 20. Phragmoconidia with an appendage at the distal end, Nomarski; scale = 50 μ m. – Figs. 21–23. *Everhartia lignitalis*. GO-261. 21. Synnema-like conidioma; scale = 500 μ m. – 22. Eupulate conidioma in which conidiogenous cells lie along the cavity, sectioned, Nomarski; scale = 100 μ m. – 23. Helicoid conidia, Nomarski; scale = 20 μ m.

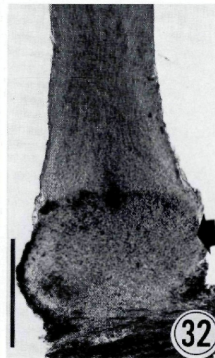
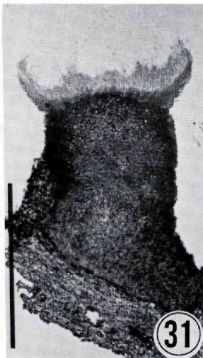
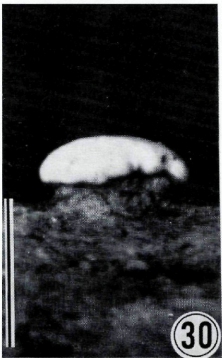
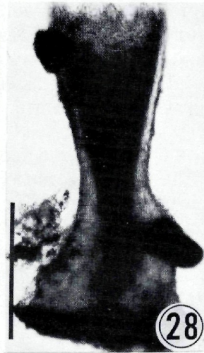
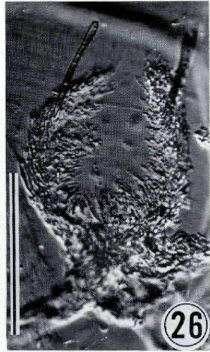
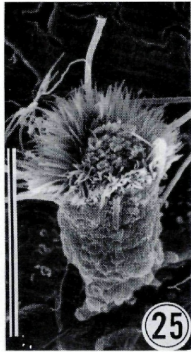
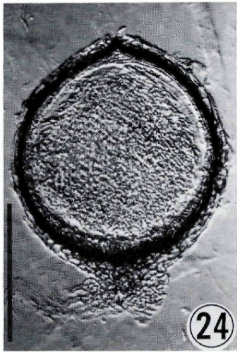


CLAIR & al. and *C. contortus* ILLMAN & WHITE. The vertical section of synnema of *C. transvaalensis* shown by SINCLAIR & al. (1983), illustrates a cupulate conidioma and ILLMAN & WHITE (1985 a) described the synnema of *C. contortus* as having a cup at the apex. Although conidiogenesis in the genus *Conicomycetes* SINCLAIR & al. is phialidic, the Japanese *Morrisographium*-like fungus seems to be annellidic. Further studies are required on the conidiogenesis of *Morrisographium* as CARMICHAEL & al. (1980) pointed out. As for *Everhartia lignitalis* THAXTER, conidiomata of this fungus (Fig. 21) have been interpreted as sporodochia (LINDER, 1929; TUBAKI, 1964; CARMICHAEL & al., 1980) or synnemata (MORRIS & FINLEY, 1967; as *Hyalotrichophora lignitalis* (THAXTER) FINLEY & MOORIS). The present study shows that the synnema-like (sometimes sporodochium-like) conidiomata of *E. lignitalis* have a cavity lined with conidiophores and conidiogenous cells and filled with accumulating conidia (Figs. 22, 23).

As mentioned below, some coelomycete fungi possess synnema-like or sporodochium-like conidiomata with a cavity in which conidia are produced. *Chaetomella raphigera* SWIFT produces dark brown pycnidia with a raphe and setae (the closed type) and white patellate sporodochia with setae (the open type), as described by DODGE (1930) (Figs. 24, 25, 26). This suggests that cupulate conidiomata are a transitional form between synnemata (or sporodochia) and pycnidia. Another unidentified coelomycete fungus, *Cornucopiella* sp., also has cupulate synnema-like conidiomata (Figs. 27, 28, 29). SUTTON (1980) and SEIFERT (1985 b) illustrated the similar conidiomatal structure of *Cornucopiella* species. Other conidiomata intermediate or transitional between typical conidiomata of coelomycetous and hyphomycetous fungi were described by SUTTON (1980).

Conidiomata of *Tubercularia vulgaris* TODE: FRIES, a representative species of the Tuberculariales (i. e., sporodochium-forming fun-

Plate 3: Figs. 24–26. *Chaetomella raphigera*. OFC-1053. 24. Pycnidium (the closed type) in which the peridial wall is composed of three layers, sectioned, Nomarski; scale = 100 μ m. – 25. Sporodochium-like conidioma (the open type) with setae, SEM; scale = 100 μ m. – 26. Cupulate sporodochium-like conidioma, sectioned, Nomarski; scale = 100 μ m. – Figs. 27–29. *Cornucopiella* sp. GO-111. 27. Stilboid conidiomata on the substrate; scale = 500 μ m. – 28. Conidioma under intense transmission; scale = 200 μ m. – 29. Cupulate conidioma in which phialoconidia are produced in the cavity, sectioned, phase contrast; scale = 200 μ m. – Figs. 30, 31. *Tubercularia vulgaris*. GO-115. 30. Sporodochium on the natural substrate; scale = 1 mm. – 31. Synnema-like conidioma in which the stipe is organized into pseudoparenchymatous tissue, sectioned; scale = 500 μ m. – Fig. 32. *Graphilbum pleomorphum*. GO-254. The base of a synnema in which fungal tissue consist of pseudoparenchyma (arrow), sectioned; scale = 200 μ m.



gi), often has synnema-like conidiomata, but the tissues of the stipe are generally differentiated to become a fairly good pseudoparenchyma (Figs. 30, 31). Because many synnematosus fungi also produce pseudoparenchyma at the base of synnemata (e. g.: *Graphilbum pleomorphum* OKADA & TUBAKI, Fig. 32; *Stilbella*, SEIFERT, 1985 a), no clear differences exist between sporodochia and synnemata with respect to the textura.

Following from the observations mentioned above, a scheme for conidiomata of synnematosus and allied fungi is shown in figure 33 with the representative species.

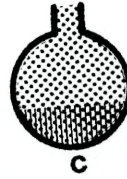
According to the morphology of fructifications, the subdivision Deuteromycotina is traditionally divided into two classes (Hyphomycetes, Coelomycetes) and seven orders (Agonomycetales, Hyphomycetales, Stilbellales, Tuberculariales, Melanconiales, Sphaeropsidales, Pycnothyriales). HAWKSWORTH & al. (1983) defined the Hyphomycetes and Coelomycetes as "mycelial forms which are sterile (Agonomycetes) or bear conidia on separate hyphae or aggregations of hyphae (as synnematosus or sporodochial conidiomata) but not within discrete conidiomata" and "forms producing conidia in pycnidial, pycnothyrial, acervular, cupulate or stromatic conidiomata", respectively.

On the other hand, SUTTON (1980) emphasized various aspects of conidiogenesis followed by the use of conidiomatal features at a lower taxonomic rank and introduced an experimental classification for the Deuteromycotina.

Although synnemata have been interpreted as merely aggregational stages of conidiomatal structures exist in the stilbellaceous fungi (Fig. 33) and also that some synnemata are very similar to pycnidia, acervuli or sporodochia (Figs. 13, 14, 15, 16, 18, 22, 32, 33). BRUBACHER & al. (1984) discussed stalked conidiomata with a pycnidoid cavity of *Crucellisporiopsis prolongatum* BRUBACHER & al. and stressed that the existence of a cavity in synnema-like conidiomata suggests an affinity with the Coelomycetes. However, we feel no clear distinction between the Hyphomycetes and the Coelomycetes seems to exist. SEIFERT (1985 a), moreover, included

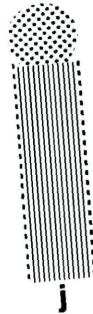
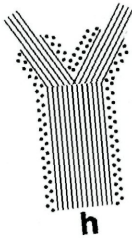
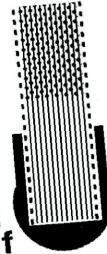
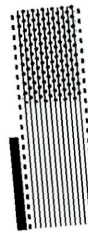
Plate 4: Fig. 33. Diagram of conidiomatal structures of the stilbellaceous and allied fungi and their traditional classification. a. *Cornucopiella* sp. b. *Chaetomella raphigera*: left; the open type: right; the closed type. c. common pycnidium. d. *Everhartia lignitalis* and *Morrisographium* sp. e. *Endocalyx melanozanthus* var. *melanozanthus*. f. *Endocalyx cinctus*: left; on the substrate: right; in culture. g. *Graphilbum pleomorphum*. h. *Sarophorum palmicola*. i. *Tubercularia lateritia*. j. *Pesotum piceae*. k. *Leptozyphium* sp. l. *Tubercularia vulgaris*..

Coelomycetes

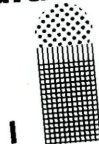
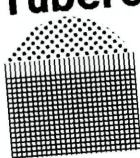


Hyphomycetes

Stilbelloales



Tuberculariales



sporodochial, synnematosus and pycnidial fungi in *Tubercularia* under the broad definition of conidiomata. Although the peridia of conidiomata are another important feature of the Coelomycetes, the yellow to brown sterile peridial hyphae were found in all species of *Endocalyx*, and peridium-like black carbonaceous hyphae in *E. cinctus*.

Studying conidiomatal structures is a useful way to reveal relationships among the synnematosus fungi as well as other anamorphic fungi. As our knowledge of conidiomatal structures advances, it may become clear that the different categories of conidiomata are continuous and indistinguishable from each other, as SUTTON (1980) stated. We feel it is safe not to follow the Saccardoan system. Although SUTTON'S classification of the Deuteromycotina has some advantages over the traditional classification, some problems still exist in the case of pleomorphic anamorphic fungi.

Acknowledgments

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Abbreviations: GO: Specimens of Gen Okada. – OFC: Cultures of Gen Okada. – MFC: Cultures of Takashi Matsushima. – TKBF: Specimens deposited in the herbarium of the University of Tsukuba. – TKBC: Cultures preserved in the Institute of Biological Sciences, the University of Tsukuba.

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