

# MYCOTAXON

AN INTERNATIONAL JOURNAL DESIGNED TO EXPEDITE PUBLICATION  
OF RESEARCH ON TAXONOMY & NOMENCLATURE OF FUNGI & LICHENS

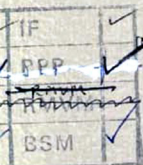
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October-December 1981

No. 3

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STUDIES IN THE LICHEN GENUS PSOROMA I  
PSOROMA TENUE AND PSOROMA CINNAMOMEUM

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## SUMMARY

The new species *Psoroma tenue* Henssen belongs to the *P. hypnorum*-group and is most closely related to *P. cinnamomeum*. Two varieties are described. *P. tenue* var. *tenue* is restricted to the Southern Hemisphere; the lichen has been collected in Tierra del Fuego and the South Shetland Islands. *P. tenue* var. *borealis* Henssen is a wide-spread northern taxon; localities are given for the Alps, Scandinavia, Iceland and North America. *P. tenue* is a species of snowbanks, glacial till and tundra heath. The lichen contains porphyrilic acid methyl ester and pannaric acid. The occurrence of these metabolites in other members of the *P. hypnorum*-group is mentioned. A short description of anatomical structures in *P. cinnamomeum* is included.

## INTRODUCTION

The lichen genus *Psoroma* Michx, a member of the Pannariaceae, occurs predominantly in the Southern Hemisphere, in South America and New Zealand. The type species *P. hypnorum* (Vahl) S.F. Gray (Synonyms: *P. bryantii* Dodge as "*Bryanti*" in Trans. Amer. Microscop. Soc. 84:511, 1965, holotype: hb. Dodge; and *P. follmannii* Dodge in Trans. Amer. Microscop. Soc. 84:510, 1965, isotype: KASSEL) only is known to be world wide distributed.

Our studies in *Psoroma* are mainly restricted to South American species, based on collections made by A. Henssen and G. Vobis in southern Chile and Argentina in 1973 / 74. P.W. James who was planning a monographic treatment of the genus encouraged us to collect *Psoroma* species intensively. The series of *Psoroma* papers, published in part together with P.W. James and K. Marton, may be regarded as preliminary studies for a world monograph. In this initial paper, A. Henssen is responsible for the taxonomic treatment; and B. Renner, for the identification of the lichen substances.

In its current circumscription *Psoroma* is a heterogenous genus, and affinities of certain species to *Pannaria* Del. in Bory have been suggested (James & Henssen 1976, Jørgensen 1978). The species of the *P. hypnorum*-group, for example, form a distinct assemblage of terricolous lichens of cold temperature or subalpine / alpine areas. They may be more closely related to *Pannaria pezizoides* (G.H. Web.) Trevis. than to the corticolous / saxicolous, squamulose or lobate species of *Psoroma* with which they are at present allied (James & Henssen 1976).

The new species *P. tenue* belongs to the *P. hypnorum*-group. The outstanding character of the species is a pattern of lichen substances not previously known to occur in *Psoroma* s.l. The specimens of *P. tenue* so far studied always contain pannaric acid and the new compound porphyritic acid methyl ester and some specimens contain an unknown substance ( $U_1$ ) (Renner et al. 1981). Specimens from the Northern Hemisphere differ slightly in morphology from the southern hemispheric ones and are included in the variety *borealis*.

In *P. hypnorum*, no lichen substances were found by TLC (Jørgensen 1978). We confirmed this observation in the type specimen (C) and in the types of the synonymous species *P. bryantii* (hb. Dodge) and *P. follmannii* (KASSEL) as well as in a number of our specimens from northern and southern



localities. All of these specimens were similar with regards to external and internal morphology. However, certain specimens, deviating to some extent in morphology, were found to contain one, two or all three of the compounds described from *P. tenue*. These specimens need further taxonomic investigation. Porphyrilic acid methyl ester and pannaric acid also occur in the new *P. rubromarginatum* P. James & Murray (Henssen et al. in manuscript), and the unknown (U<sub>1</sub>) occurs in a South American specimen of *P. paleaceum* (Fr.) Nyl. (? *P. hirsutulium* Nyl.) (Henssen 24353g: MB).

Within the *P. hypnorum*-group, several patterns in thallus anatomy may be recognized. *P. tenue* corresponds to *P. cinnamomeum* in external and internal morphology of the thallus and cephalodia. The two species, therefore, are regarded to be closely related. Although the South American species *P. cinnamomeum* was well-described by Malme (1952), additional information obtained by modern methods is included in the presented paper.

## MATERIAL AND METHODS

**MATERIAL.** The abbreviations of herbaria follows those given in *Index Herbariorum*; hb. Dodge means the private herbarium of C. Dodge, Burlington, Vermont, U.S.A., and hb. Henssen means the private herbarium of the senior author.

*Psoroma cinnamomeum*: Argentina, Tierra del Fuego, Rio Grande, 1896, Dusén 115 (holotype: S); Cabo San Pablo, on plant debris in a tundra heath, overgrowing a dead liverwort, 1973, Henssen & Vobis 24448t (MB). *P. hypnorum* (selected specimens): Norway, Vahl (lectotype by Jørgensen: C). Sogn og Fjordane, Nordfjordeid, on rock overgrowing mosses, 1959, Henssen 5339 (hb. Henssen). - Finland, Lapponia enontekiensis, Toskaljärvi, 1955, Henssen 6145 (hb. Henssen). - Argentina, Tierra del Fuego, Glaciar Martial, on rock overgrowing mosses, 400m s.m., 1973, Henssen & Vobis 24412a (MB); Laguna Escondida, Henssen & Vobis 24439h and 24460d (MB). - Antarctic Peninsula, Refuge Island, 1940, Bryant 30-2 (holotype of *P. bryantii*: hb. Dodge). - South Shetland Islands, Greenwich Island, Bahia Soberania, on mosses, 1963, Follmann 11843 (isotype:

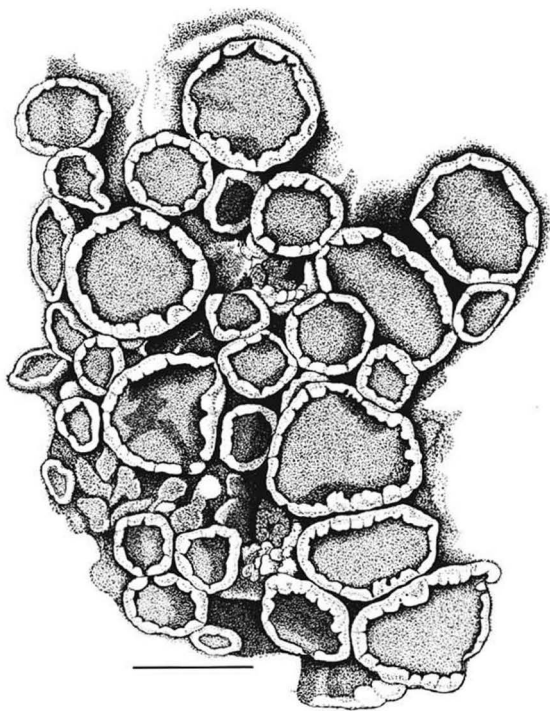


Fig. 1. *Psoroma tenue* var. *tenue* (paratype), young and mature densely aggregated apothecia; scale = 1 mm; drawn by H. Becker.

of *P. follmannii*: KASSEL). *P. paleaceum*: Argentina, Tierra del Fuego, between Ushuaia and Lapataia, on rock overgrowing mosses, 1973, Henssen & Vobis 24353g (MB). *P. tenue*: see below.

**MORPHOLOGY.** Samples were sectioned by freezing microtome and the sections mounted in lactophenol cotton-blue. Measurements of spores and anatomical structures were made from permanent preparations; measurements of gross morphology on air-dried specimens. For studying the ascus structure,  $KI_3$  solution was added directly to the squash preparation.

**CHEMISTRY.** Crude lichen extracts were chromatographed in solvent systems A, B, C of Culberson (1972), and D, E of Renner (1980). The methods of mass spectrometry and UV/VIS spectroscopy were used for the identification of the lichen substances; details are given in Renner et al. (1981).

### TAXONOMIC PART

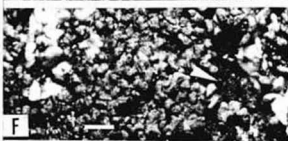
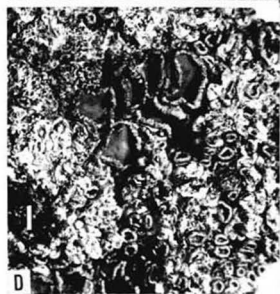
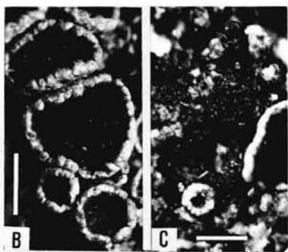
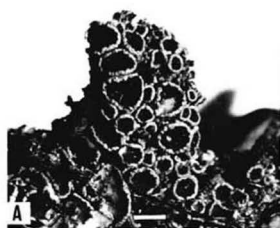
*Psoroma tenue* Henssen, sp. nov. var. *tenue*

Habit, Fig. 1, 2A-C; thallus anatomy, Fig. 3A-C, structure of the ascocarp, Fig. 4A-D.

**DIAGNOSIS.** Thallus granulatus vel subsquamulosus, pallidus vel fuscescens, e verrucis formatus semiglobosis, circiter 0.2 - 0.4 mm latis vel e squamulis plus minusve adscentibus, 0.4 - 0.8 mm latis, crassis, dispersis vel subcontiguis. Thallus corticatus, hyphae medullosae reticulum formantes, alga symbiotica laete viridis, ad familiam Chlorococcaceae pertinens. Cephalodia globularia vel ramosa, plus minusve aggregata, atropurpurea, corticata, alga ad *Nostoc* pertinens.

Apothecia usque ad 2 (-3)mm lata, disco plano vel subplano, atrofusco, margo thallinus vulgo pallidus, tenuis, subtiliter crenulatus. Hymenium 95-120 (-150) $\mu$ m altum. Asci subcylindrici, 80-110 x 8-12 $\mu$ m, 8-spori, annulo amyloidea in apice asci incrassato, Sporae eseptatae, incolores, polymorphae, ovoideae vel subfusiformes, 19-24 x (5-)7-10 (-12) $\mu$ m, superficie verruculosa. Pycnidia minuta, circiter 0.1-0.16 mm lata, conidiophora brevicellularia, conidia terminalia et lateralialia formantia. Conidia bacilliformia, circiter 2-4 x 1  $\mu$ m.

Chemistry: thallus and apothecia contain porphyrilic acid methyl ester, pannaric acid, in the holotype the unknown substance ( $U_1$ ) was found.

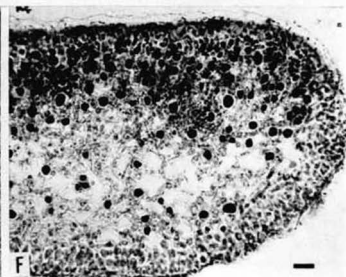
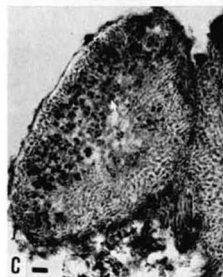
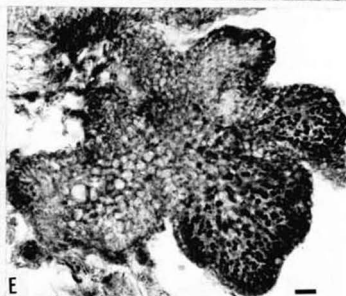
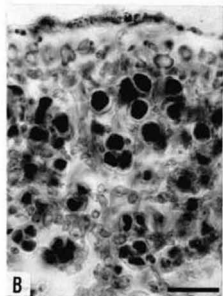
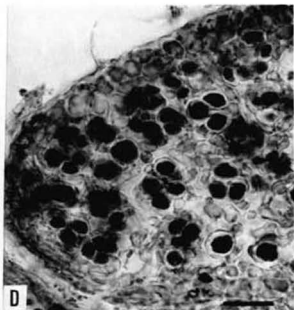
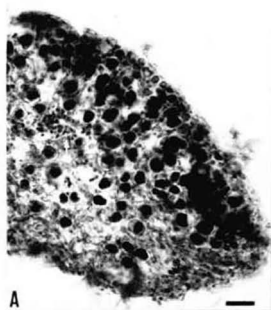


Holotype: Argentina, Tierra del Fuego, Parque Nacional de la Tierra del Fuego, Laguna Escondida, on loamy soil near the lake shore overgrowing *Cephaloziella* and plant debris, at c. 270m s. m. 1973 Henssen & Vobis 24439b (MB); isotypes: BM, LPS. Paratype: near the type locality at *Hosteria Petrel*, on soil overgrowing plant debris in a stand of *Nothofagus* at the lake shore, 1973 Henssen & Vobis 24460w (MB).

FURTHER SPECIMEN EXAMINED: South Shetland Islands, Greenwich Island, on earth and plant debris, 1963, Follmann 14065 (KASSEL).

Thallus of pale or more rarely brown colour, dull, composed of dispersed or aggregated minute granules and squamules, fastened by rhizoidal hyphae with colourless or brown thick walls. Granules up to 0.4 mm, squamules 0.4 - 0.8 mm broad, more or less ascending. Thallus sections (155-) 150-250 (450) $\mu$ m high, at least on the upper surface distinctly corticated. Upper cortex in young thalli composed by thin-walled cells (Fig. 3A), later on the walls gelatinizing, and the lumina in the gelatinous matrix up to 18 $\mu$ m broad, connected by pits (Fig. 3B). Lower cortex composed of isodiametric or elongated cells (Fig. 3C). Medullary hyphae (2.5-)4-6 $\mu$ m thick, orientated reticulately and enclosing single or several algal cells. Phycobiont a member of the Chlorococcaceae, cells c.6-10 $\mu$ m broad, distributed throughout the thallus but more numerous in the upper part. Crystals of lichen substances deposited in clusters in the medulla.

Fig. 2. Habit photographs of *Psoroma* species. A-B, *P. tenue* var. *tenue* (paratype); A, lichen overgrowing plant debris; B, enlarged apothecia. C, *P. tenue* var. *tenue* (holotype); dark colored, aggregated cephalodia between thallus squamules and apothecia. D, *P. cinnamomeum* (holotype). E-F, *P. tenue* var. *borealis* (holotype); E, mature apothecia; F, cephalodia (arrowed) between squamules. G, *P. cinnamomeum* (holotype), crowded apothecia surrounded by a thick thal-line margin; the black apothecia belong to a *Badicia* species. H, *P. tenue* var. *borealis* (hb. Henssen 6130), squamules and apothecia. A-H, scale = 1 mm.



Cephalodia granularly or coralloidly branched, dark purplish brown, singly or forming clusters up to 0.8 mm (Fig. 2C). Cephalodia corticated, cortex 4.5-12 $\mu$ m thick, formed by 1 to 2 rows of cells; medullary hyphae orientated in a network in young stages, later forming pseudoparenchyma (Fig. 5E). Alga a *Nostoc* species.

Apothecia dispersed or closely aggregated, up to 2(-3) mm broad, disc flat, dark brown, surrounded by a pale, finely crenulated margin (Fig. 1, 2A, B). Hymenium 95-120 (-150) $\mu$ m high; hypothecium - layer including the ascogenous hyphae - 20-25(-50) $\mu$ m; subhymenial layer of varying thickness, frequently extending into a stipe of adglutinated hyphae with enlarged cells towards the base. Margo thallinus corticated, basal part 100-120 $\mu$ m broad, composed of radiating hyphae with broad, up to 25 $\mu$ m wide cells; joint walls between the cell lumina 3.5-6 $\mu$ m thick (Fig. 4A, B). Crystals of lichen substances in clusters in the medulla of the margo thallinus.

Pycnidia inconspicuous, in sections 0.1-0.16 mm large. Conidiophores branched and anastomosing, conidiogenous cells short, the conidia terminally and laterally produced. Conidia rod-shaped, c.2-4 x 1 $\mu$ m.

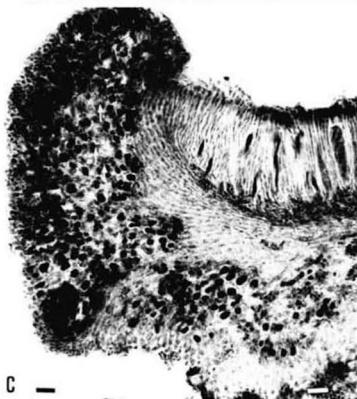
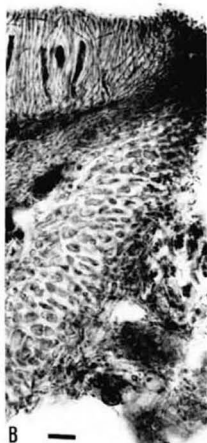
*Psoroma tenue* var. *borealis* Henssen var. nov.

Habit, Fig. 2E, F, H; thallus anatomy, Fig. 3D-F; structure of apothecium, Fig. 5C.

DIAGNOSIS. Differt a var. *tenue* thallo majori semper distincte corticato et colore cinnamomeo vel luteofusco.

Chemistry: thallus and apothecia contain porphyritic acid methyl ester and pannaric acid, in the holotype and in the specimens from Austria, Ost-Tirol and Canada the unknown substance (U<sub>1</sub>) was found.

Fig. 3. Thallus anatomy of *Psoroma* species (microtome sections). A-C, *P. tenue* var. *tenue* (holotype); A, l.s. of young thallus, crystals of lichen substances indicated by arrow; B, t.s. of upper cortex and algal zone; C, t.s. of thallus adjacent to an apothecium. D-E, *P. tenue* var. *borealis* (Henssen 22679g); D, l.s. of young thallus; E, l.s. of a cephalodium at the base of an apothecium. F, *P. tenue* var. *borealis* (Henssen 23157x), t.s. of corticated thallus. A-F, scale = 20  $\mu$ m.





Holotype: U.S.A., Colorado, Boulder Co., Niwot Ridge, on snowbank, between 3300 and 3750 m, 1961, Henssen 13030b (hb. Henssen). Paratype: Austria, Tirol. Samnaungruppe, Zebblasjoch, on snowbank at 2450m, 1975, Henssen 22679g (MB).

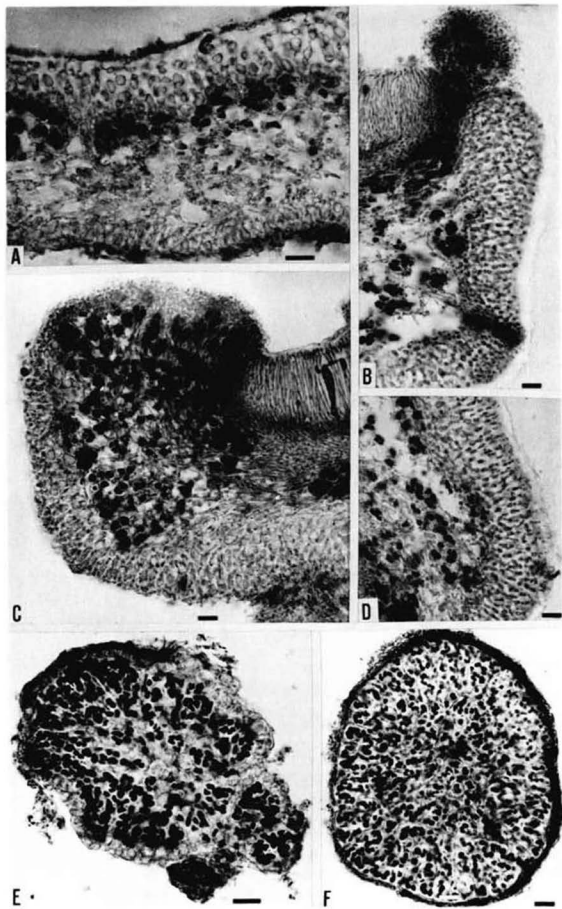
FURTHER SPECIMENS EXAMINED: Austria, Ost-Tirol, Matri, Johannishütte, in glacial till at c. 2200 - 2400 m, overgrowing mosses, 1938 F. & Koppe (hb. Henssen 6130). - Norway, Sør-Trøndelag, Dovrefjell, Knuthö, on snowbank at 1500 m, 1959, Henssen 4974 (hb. Henssen). - Sweden. Torne Lappmark, Abisko. Nuolja, on snowbank at 1160 m, 1954, Henssen 6127 (hb. Henssen). - Iceland, Bard, Kollsvik, overgrowing mosses in a lichen heath, 1972, Henssen & Kristinsson 23157x (MB). - Canada, Alberta, Banff National Park, Peyto Lake, *Dryas* heath at 2150-2250 m, 1962, Henssen & Cain 14471y (CAN, MB).

Thallus squamules up to 1 mm broad, brown or reddish brown, thick; thallus distinctly corticated on the upper and lower surface by isodiametric cells (Fig. 3D, F). Apothecial disc brown and margo thallinus of the same colour, or disc dark brown and margo thallinus slightly paler. Crystals of lichen substances deposited within the medulla of the thallus and apothecial margin or not.

In *P. tenue* var. *tenue* the lobes are smaller than in var. *borealis* (Fig. 2), and the cortex is usually less well developed since it is restricted to the upper surface. Broad cortical structures on both thallus surfaces have been observed in thalli closely attached to margins of apothecia (Fig. 3C). In such lobes the thallus corresponds exactly to that in *P. cinnamomeum* (cf. Figs. 3B with 5A).

The cephalodia occur either between the lobes or are produced in groups below the apothecia (Fig. 3E). The alga in the cephalodia is a

Fig. 4. Apothecial structure in *P. tenue* var. *tenue* (microtome sections of the holotype). A, median l.s. of young apothecium, note the numerous algal cells in the stipe; B, cortex structure in apothecial margin; C, upper part of apothecial margin, crystals of lichen substances indicated by arrows; D, ascus and spores. A-D, scale = 20  $\mu$ m.



species of *Nostoc* as is found in most *Psoroma* species.

The margin of the apothecia develops in the same way as in *Pannaria rubiginosa* (Ach.) Bury (Henssen 1969, 1981). The cortex in the margo thallinus is differentiated in part by the thallus cortex and in part by the medullary hyphae growing up between the hymenium and the thallus cortex (Fig. 4A, B). The cells formed by the medullary hyphae are considerable smaller in size (Fig. 4C, 5C). As seen from above the finely crenulated margin surrounding the relatively flat disc resembles that of certain *Pannaria* species. In very old apothecia the margin may bear granules and the disc becomes folded or medianly depressed. Young developing apothecia are at first urceolate.

The ascus wall and hymenial gelatine stain blue in iodine, and an amyloid ring structure is seen in the ascus apex of the same shape as that found in *P. hypnorum* (Keuck 1977).

In *P. tenue* var. *tenue* yellowish to brownish crystals of lichen substances are usually deposited in large amounts in the medulla of the thallus and apothecial margin. In var. *borealis* similar crystals have only been observed in the specimen collected in Canada (Henssen 14471y). These crystals are difficult to demonstrate in the sections by black and white photography but are rather impressive in microscopic examination of stained permanent preparations. The varying occurrence of the unknown substance ( $U_1$ ) in both varieties of the species is interesting.

Fig. 5. Anatomy in *Psoroma* species (microtome sections). A-B, *P. cinnamomeum* (holotype); A, l.s. of thallus; B, cortex structure in apothecial margin; C, *P. tenue* var. *borealis* (Henssen 22670g), apothecial margin; D, *P. cinnamomeum* (Henssen 24448t), cortex structure in apothecial margin; E, *P. tenue* var. *tenue* (holotype), l.s. of cephalodium; F, *P. cinnamomeum* (Henssen 24448t), l.s. of cephalodium. A-F, scale = 20  $\mu$ m.

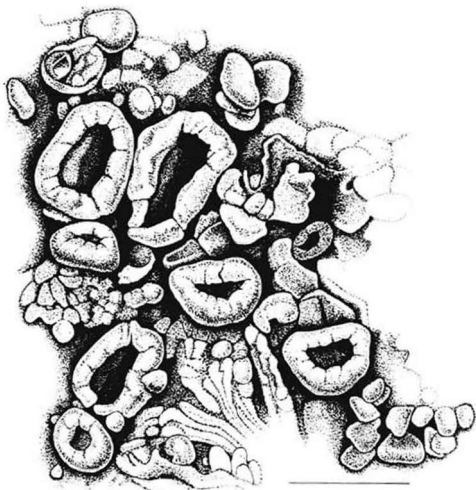


Fig. 6. *Psoroma cinnamomeum* (Henssen 24448t), young apothecia; scale = 1 mm; drawn by H. Becker.

*Psoroma tenue* is characterized by the presence of porphyritic acid methyl ester and pannaric acid in correlation with small, flat apothecia surrounded by a thin evenly crenulated margin, by dark purplish brown cephalodia, aggregated to clusters, and by an upper thallus cortex formed by periclinal hyphae with isodiametric cells.

In comparison to *P. tenue*, *P. cinnamomeum* has a similar anatomy and the same type of cephalodia but differs, apart from the lack of lichen substances, by having a very thick apothecial margin in the young, strongly urceolate apothecia

and by the smaller lumina in the cells forming the cortex in the margo thallinus (cf. Figs. 4C and 5C with B, D). *P. cinnamomeum* occurs in the same regions as *P. tenue* var. *tenue*. By the pale colour of the thallus and the abundant crystals in apothecial or thallus sections, *P. tenue* var. *tenue* is easily distinguished from *P. cinnamomeum*. Reddish brown specimens of *P. tenue* var. *borealis* resemble *P. cinnamomeum* but the variety is only known from the Northern Hemisphere at this time.

ECOLOGY. *P. tenue* var. *tenue* has been collected on soil, long covered by snow, together with *P. hypnorum* and *P. paleaceum*. *P. tenue* var. *borealis* has been found, hitherto, on snowbanks in glacial till and in tundra heath, where the lichen was growing together with *Leciophysma finmarkicum* Th.Fr. (23157x) or *L. furfurascens* (Nyl.) Gyeln. (14471y) respectively, among other lichens.

*Psoroma cinnamomeum* Malme 1925 P. 11, 12

The specimen studied in comparison to the holotype (Henssen 24448t) was growing on the same type of substrate. The prominent apothecial margin is especially distinct in younger apothecia (Fig. 1G, 6). The cortex was well developed in all sections studied. In the upper cortex the cell lumina are embedded in the gelatinous matrix of the cell walls. The lumina are roundish and connected by pits (Fig. 5A). In young thalli the cortex is formed only by periclinally arranged hyphae, later on cells are added by vertically growing medullary hyphae. In the lower thallus cortex the cell walls are less strongly gelatinized. The cortex in the margo thallinus is formed by radial or somewhat reticulately arranged hyphae with thick walls and relatively small lumina (Fig. 5B, D).

The cephalodia are dark purplish brown and form clusters between the squamules or they are produced in groups below the apothecia. They are surrounded by a brown pigmented cortex, composed of one or, in part, two rows of cells (Fig. 5F).

In young stages the hyphae are thin and form a network and later the enlarged cells become aggregated into a pseudoparenchyma.

### ACKNOWLEDGEMENTS

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### ZUSAMMENFASSUNG

Die neue Art *Psoroma tenue* Henssen, eine Flechte auf Schneeböden und in Tundra-ähnlicher Vegetation gehört zur *Psoroma hypnorum*-Gruppe und ist am nächsten mit *P. cinnamomeum* Malme verwandt. Morphologie und Anatomie der beiden Arten werden verglichen. Sie stimmen in der Wuchsform, der Struktur des Lagers sowie in der Gestalt und Anatomie der Cephalodien weitgehend überein. Zwei Varietäten der neuen Art *P. tenue* werden unterschieden. *P. tenue* var. *tenue* ist auf die südliche Hemisphäre beschränkt und wurde bisher in Tierra del Fuego und auf den South Shetland Islands gesammelt. *P. tenue* var. *borealis* ist anscheinend eine weit verbreitete Flechte der nördlichen Hemisphäre; Fundorte werden für die Alpen, Skandinavien, Island und Nordamerika angegeben. Beide Varietäten von *P. tenue* enthalten den neuen Flechtenstoff Porphyrilsäuremethylester und Pannarinsäure, sowie in einigen der untersuchten Proben zusätzlich eine unbekannte Substanz ( $U_1$ ). Das Vorkommen dieser Stoffe in anderen Arten der *P. hypnorum*-Gruppe wird erwähnt.

*Psoroma bryantii* Dodge und *P. follmannii* Dodge werden als Synonyme zu *P. hypnorum* (Vahl) S. F. Gray gestellt.

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# MYCOTAXON

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## AN UNDESCRIBED PLEOMORPHIC SPECIES OF *CODINAEA*

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In the course of an investigation of airborne fungi in Kobe, Japan, a hyphomycete was obtained in pure culture which proved to represent a previously undescribed species of *Codinaea* Maire. When grown on a variety of media such as cornmeal agar, malt extract agar, oatmeal agar, potato-carrot agar and potato-dextrose agar, sporulation is pleomorphic: It produces (a) polyphialidic, darker, thick-walled, and regularly septate conidiophores and allantoid, hyaline, 3-septate, and terminally setulate conidia characteristic of *Codinaea*, and (b) monophialidic, paler, and less septate conidiophores with fusiform non-septate conidia somewhat suggestive of *Chloridium*. Due to the latter features, the isolate superficially resembles *Chloridium codinaeoides* Pirozynski (1972), which produces monophialidic conidiogenous cells and narrowly fusiform-obclavate, aseptate conidia.

A recent account of the morphology and taxonomy of the genus *Codinaea* was given by Hughes and Kendrick (1968), who recognized 13 species and four anamorphic forms of *Chaetosphaeria* (Sphaeriaceae) and described in detail numerous collections from New Zealand. Subsequently the following 13 species have been added to the genus: *C. maharashtrensis* Pirozynski & Patil (1970), *C. novae-guineensis* Matsushima (1971), *C. eucalypti* Sutton & Hodges (1975), *C. septata* Sutton & Hodges (1975), *C. apiculata* Matsushima (1975), *C. lunata* Matsushima (1975), *C. britannica* M. B. Ellis (1976), *C. hughesii* M. B. Ellis (1976), *C. cylindrospora* Morgan-Jones & Ingram (1976), *C. unisetula* Morgan-Jones & Ingram



(1976), *C. clavulata* Holubová-Jechová (1976), *C. parkhalensis* S. M. & S. S. Reddy (1977), and *Codinaea* anamorph of *Striatosphaeria codinaeophora* Samuels & E. Müller (1978) (as '*S. codinaeaphora*'). *Dictyochoaeta fuegiana* Speg., the type species of the genus *Dictyochoaeta* Spegazzini that was considered as a possible earlier name for *Codinaea* (Hughes and Kendrick, 1968), has been re-described by Godeas et al. (1977). However, there are too few diagnostic features available on the type to properly define the type species of that genus.

Since none of the fungi of this genus are pleomorphic, the fungus from Kobe has been described here as a new species.

*Codinaea dimorpha* Toyazaki & Udagawa, sp.nov. (Figs. 1-6)

Coloniae in agaro "cornmeal" lente crescentes, tenuissimae, ex mycelio vegetativo submerso compositae; hyphae aerae sparsae; conidia abundantia, aggregata, brunneogrisea; reversum incoloratum. Coloniae in aliis agaris communibus celerius crescentes, planae vel rugosae, tenues, penitus auratae vel aurantiacae.

Mycelium immersum vel semi-immersum, ex hyphis hyalinis vel subhyalinis, ramosis, septatis, 1-3  $\mu\text{m}$  diam, laevibus compositum.

Setae steriles absentes.

Structurae conidiogenae macronematae, dimorphae: (a) polyphialidicae et (b) monophialidicae. (a) Conidiophora ex hyphis repentibus superficialibus orientia, singula vel 2-3 aggregata, simplicia, brunnea, cylindrica, 200-280  $\times$  6-8  $\mu\text{m}$ , laevia, incrassata, omnino diametro uniformia, apicem versus pallescentia, recta vel flexa vel plerumque geniculata, usque 6-8 septata, superne successive elongascentia. Cellulae conidiogenae elongatae, cylindricae, vulgo usque ad 40-60  $\mu\text{m}$  longae, polyphialidicae, raro discretiae, determinatae, pallide brunneae vel subhyalinae, multis collariibus conspicuis praeditae; collaria infundibuliformia, 3-4  $\times$  1.5-2.5  $\mu\text{m}$ , subhyalina vel pallide brunnea, postremo effracta. Conidia semi-endogena, acropleurogena, hyalina, allantoidea, ellipsoidea vel oblonga, parum curva, 22-28  $\times$  7-8  $\mu\text{m}$ , 3-septata, laevia, ad basim interdum hilo inconspicue et utrinque setula singula, simplici, hyalina, 5-6  $\mu\text{m}$  longa praedita, in massa mucida aggregata. (b) Conidiophora ex hyphis superficialibus singula oriunda, simplicia vel interdum irregulariter ramosa, 2-3 phialides ferentia, cylindrica, 45-100  $\times$  2.5-4  $\mu\text{m}$ , hyalina vel obscure olivaceo-brunnea, prope basin septata, laevia. Cellulae conidiogenae monophialidicae, integratae, determinatae, cylind-

ricae, superne gradatim angustatae, collari distincto 2-2.5  $\times$  1-2  $\mu\text{m}$  praedita. Conidia semi-endogena, acrogena, hyalina, cylindrica vel fusiformia, 10-18  $\times$  1-2  $\mu\text{m}$ , parum curva, aseptata vel raro uniseptata, utrinque plus minusve truncata, in massa mucida aggregata.

Chlamydosporae terminales, obscure olivaceo-brunneae, ellipsoideae vel pyriformes, laeves, incrassatae, 10-15  $\times$  6-10  $\mu\text{m}$ , aseptatae vel raro uniseptatae.

Holotypus: cultura NHL 2891 ex aere urbis Kobe in Japonia, in 12.vi.1980, a N. Toyazaki, isolata. In collectione fungorum "National Institute of Hygienic Sciences (NHL), Tokyo, Japan."

Etymology: lat. *dimorphus* = having two forms, referring to the dimorphic conidiogenesis.

Colonies on cornmeal agar (CMA) growing slowly, reaching 2.8 cm in diam after two weeks at 23 C, very thin, vegetative mycelium largely submerged; white aerial hyphae sparsely developed on the agar surface; conidia-bearing structures abundantly produced in central colony areas, "brownish grey" (Kornerup and Wanscher, 1978; pl. 6-E-2); reverse uncolored. Colonies on malt extract-yeast extract agar (MYA) growing rather restrictedly, consisting of a somewhat thick basal felt, wrinkled conspicuously, velvety to floccose, producing abundant aerial hyphae, "pastel yellow" (Kornerup and Wanscher, 1978; pl. 2-A-4); conidia slowly developed, not affecting the colony appearance within three weeks; reverse "orange" (Kornerup and Wanscher, 1978; pl. 6-B-7). Colonies on oatmeal agar (OA) or potato-dextrose agar (PDA) growing more rapidly, reaching 3.0-3.6 cm in diam after two weeks at 23 C, plane, thin, "deep yellow" or "deep orange" (Kornerup and Wanscher, 1978; pls. 4-A-8, 5-A-8).

Mycelium immersed or semi-immersed, composed of hyaline to subhyaline, branched, septate, 1-3  $\mu\text{m}$  wide, smooth-walled hyphae which often swell to knots of pale brown to brown cells up to 5.5-10  $\mu\text{m}$  wide.

Sterile setae lacking.

Conidia-bearing structures macronematous, of two types; (a) polyphialidic, and (b) monophialidic. Type (a) commonly developed on CMA and at later stages also on MYA, OA and PDA. Conidiophores arising singly from superficially repent hyphae or in groups of two or three from hyphal knots, simple, brown, cylindrical, 200-280  $\times$  6-8  $\mu\text{m}$ , smooth and thick-walled, uniform in width throughout, paler towards the apex, straight or flexuous, often markedly geniculate in the upper region, up to 6-8-septate, successively proliferating with age at short distances. Conidiogenous

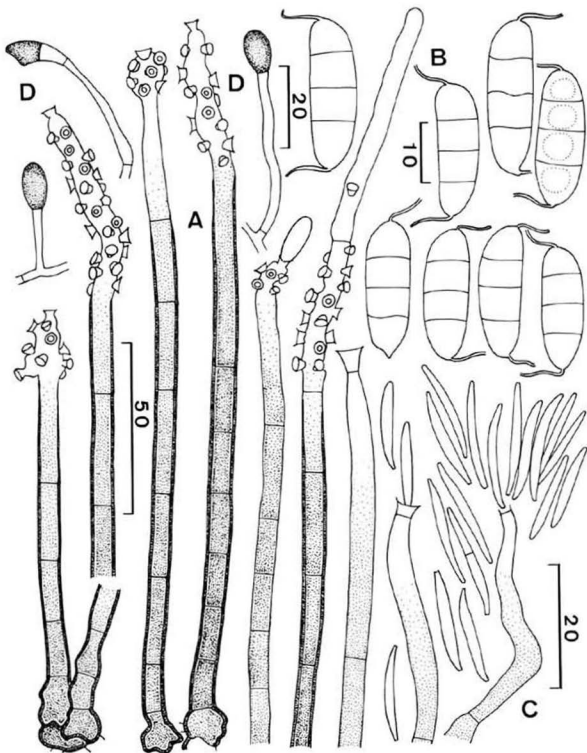
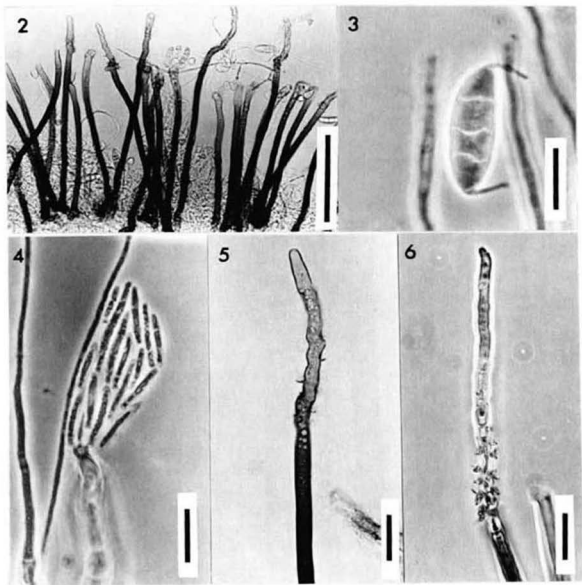


Fig. 1. *Codinaea dimorpha* (NHL 2891).  
 A. Conidiophores and polyphialides. B. Conidia (3-septate).  
 C. Monophialides and conidia. D. Chlamydospores. (All  
 measurements are in  $\mu\text{m}$ .)



Figs. 2-6. *Codinaea dimorpha* (NHL 2891).

2. Conidiophores. 3. Three-septate conidium. 4. Mono-phialidic conidiogenous cell and 0-1-septate conidia. 5 and 6. Polyphialidic conidiogenous cells. (Bars in 3-6 = 10  $\mu$ m and in 2 = 100  $\mu$ m.)

cells elongated, cylindrical, usually up to 40-60  $\mu$ m in length, polyphialidic, rarely discrete, determinate, pale brown to subhyaline, each phialide in turn becoming externally scarred with the persistent remains of the collarettes; collarettes funnel-shaped, 3-4  $\times$  1.5-2.5  $\mu$ m, subhyaline to pale brown, aged ones often broken off. Conidia semi-endogenous, acropleurogenous, hyaline, allantoid, ellipsoid or oblong, slightly curved, 22-28  $\times$  7-8  $\mu$ m, 3-sep-

tate, smooth-walled, sometimes with a basal hilum, provided at each end with a single, simple, hyaline setula 5-6  $\mu\text{m}$  in length, aggregated in a slimy mass. Type (b) developed at an early stage on MYA, OA and PDA. Conidiophores arising singly from superficial mycelium, simple or sometimes irregularly branching into two or three stalked phialides, cylindrical, 45-100  $\times$  2.5-4  $\mu\text{m}$ , hyaline to dark olive-brown, septate near the base, smooth-walled. Conidiogenous cells monophialidic, integrated, determinate, cylindrical, tapering gradually into a well-defined, terminal collarette measuring 2-2.5  $\times$  1-2  $\mu\text{m}$ . Conidia semi-endogenous, acrogenous, hyaline, cylindrical to fusiform, 10-18  $\times$  1-2  $\mu\text{m}$ , slightly curved, aseptate or rarely uniseptate, more or less truncate at both ends, aggregated in a slimy mass.

Chlamydospores often developed on MYA, OA and PDA, terminal, dark olive-brown, ellipsoid or pyriform, smooth, thick-walled, 10-15  $\times$  6-10  $\mu\text{m}$ , aseptate or rarely uniseptate.

At 37 C, no growth occurs.

Specimen examined: an isolate from air, at Kano-cho, Ikuta-ku, Kobe-shi, Japan, June 12th, 1980, N. Toyazaki, NHL 2891, holotype.

Of the species currently assigned to the genus, *C. dimorpha* somewhat resembles *C. fertilis* Hughes & Kendrick (1968) because of the crowded appearance of polyphialides which are produced at the portion where cylindrical conidiophores proliferate, and because it forms prominent phialide collarettes, as well as fusiform, curved and setulate conidia. It differs from *C. fertilis* in that it lacks sterile setae and has larger, 3-septate conidia and monophialidic conidiogenous cells.

*Chloridium codinaeoides* (*loc. cit.*) may be confused with the monophialidic fruiting structures of the present species, but in the former, conidia are smaller — 5-9  $\times$  1-1.5  $\mu\text{m}$  as opposed to 10-18  $\times$  1-2  $\mu\text{m}$  in *C. dimorpha*.

The another superficially similar hyphomycete, *Hyphodiscosia europaea* Hol.-Jech. & Borowska has recently been described by Holubová-Jechová and Borowska (1981). Both are characterized by cylindrical, setulate phragmospores produced acropleurogenously at the elongating part of simple, erect, pigmented conidiophores. *Hyphodiscosia europaea* is distinct from the present fungus in that the conidia are sympodial-polyblastic and dark-colored at maturity, and in lacking a monophialidic conidia.

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The Psilopezoid fungi. VIII.  
Additions to the genus *Pachyella*.

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SUMMARY

*A review of the genus Pachyella is given in view of recent collections from France and continued study by the senior author. One new species is proposed, P. peltata, and one new combination is made, P. pseudosuccosa. A key is given to the nine species now included in the genus.*

The senior author has revised the genus *Pachyella* (Pfister 1973) and emended its circumscription. The junior author has made significant new collections of species of the genus in France. This paper presents one new species of *Pachyella* from France, a report of *P. punctispora* from France, and a revision of the nomenclature of one species. A revised key to the genus *Pachyella* is given.

The literary history of the genus *Pachyella* was reviewed by Pfister (1973). Since that time several smaller contributions have been made (Pfister 1974, 1975). Pfister (1979) also added on species to the genus, *P. hydrophila* (Peck ex Sacc.) Pfister, and Berthet and Donadini (1978) described *Peziza aquatilis* which was later transferred to *Pachyella* by Donadini (1978). This species is discussed below.

A recent paper by Donadini (1980) should be mentioned. In it Donadini reduced *Pachyella* to the rank of a subgenus under *Peziza*. There is no indication that

specimens were studied. Unfortunately several bibliographical improprieties have occurred.

We feel that *Pachyella* should be maintained as a distinct genus. The species are not only morphologically and anatomically distinct from *Peziza* but they are ecologically quite different as was pointed out earlier by Pfister (1973).

The following is a synopsis of the species now placed in *Pachyella*. Complete synonymies may be found for previously treated species in Pfister (1973).

#### Synopsis of species

*Pachyella adnata* (Berk. & Curt.) Pfister, Canad. J. Bot. 51: 2010. 1973.

Earlier *Aleuria amantitica* Pat. was added to the synonymy (Pfister 1974). Few additional collections have come to light. The distribution is wide but disjunct. Additional collections deposited in FH have been examined from Ohio (W. B. Cooke 48304) and Connecticut (DHP). The species is unreported in Europe. Donadini (1980) listed the authors as "(Berk. et Currey)" [sic].

*Pachyella aquatilis* (Berthet & Donadini) Donadini, see *P. pseudosuccosa*.

*Pachyella babingtonii* (Berk. & Br.) Boud., Hist. Class. Discom. Eur. p. 51. 1907.

*Peziza exidiiformis* Berk. & Br. may be added to the already lengthy synonymy. Donadini (1980) listed the authors of *P. babingtonii* as "(Berk. et Bres.)" [sic].

*Pachyella clypeata* (Schw.) Le Gal, Prodr. Flore Mycol. Madagascar 4: 27. 1953.

This species is still known only from North America though the new species described below from France is quite similar.

*Pachyella hydrophila* (Peck ex Sacc.) Pfister, Mycotaxon 8: 335. 1979.

This species and *Pachyella punctispora* are quite similar anatomically. Detailed field studies of *P. hydrophila* should be made--it is thus far only known from dried material.



*Pachyella megalosperma* (Le Gal) Pfist., Canad. J. Bot.  
51: 2019. 1973.

No recent collections of this species have come to our attention. Comments on *Pachyella pseudosuccosa* should be seen below.

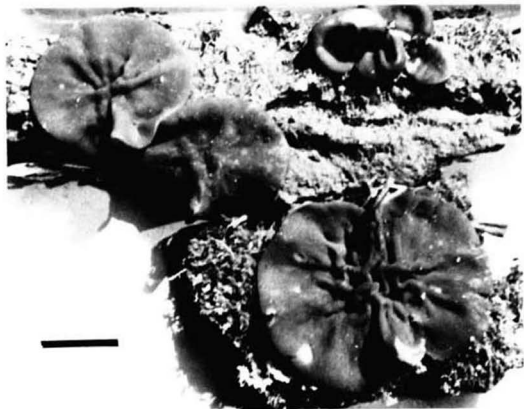


Figure 1. *Pachyella peltata*. Apothecia from the type collection. Scale = 2 cm.

*Pachyella peltata* Pfister & F. Candoussau sp. nov.

Figures 1 and 2

Apothecia 4-7 cm diam, planum, sessilia planae, similis *Pachyella clypeata*. Hymenium brunneum. Excipulum exterium ex hyphis 55 x 25  $\mu$ m compositum. Hyphis exteris rectis vel undulatis vel ramificans. Asci 4+, 500 x 20-22  $\mu$ m diam. Ascospori ellipsoidei, laevi biguttulati 27-30 x 13-15  $\mu$ m. Paraphyses rectae, brunnae.

Holotype: sur tronc de *Salix pourri*, à terre, endroit inondé périodiquement, avec *Psilopezia nummularialis* Pfist. & Candoussau et *Climacodon pulcherrimus* (Berk. & Curt.) Nikol. ainsi que sur *Alnus glutinosa* au même endroit. 14. IX. 1980. Forêt de Bugangue-Oloron, Pyrénées Atlantiques FH. Isotypes CUP and herb. Candoussau.

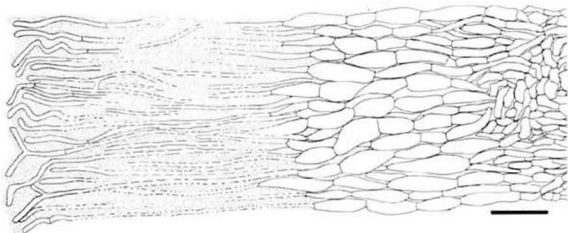


Figure 2. *Pachyella peltata*. Outer excipulum.  
Scale = 50  $\mu\text{m}$ .

Apothecia gregarious 4 to 7 cm diam, sessile, flat, toward the center undulating--plicate as far as the margin. External surface dirty-white. Hymenium brown (chatain), shining, slightly viscous. Flesh, dirty white up to 3 mm thick at the center, tinted yellowish where broken. In external features agreeing closely with *P. clypeata* (Schw.) Le Gal.

Outer excipulum of longitudinally elongate cells with their long axes oriented perpendicularly to the outer surface of the apothecium, 3-5 cells deep, the larger of the cells measuring 55 x 25  $\mu\text{m}$  or slightly larger. Cells tightly packed and only slightly swollen in width. The outer cells are uniformly embedded in a gelatinous matrix and give rise to hyphoid hairs of 5 to 7  $\mu\text{m}$  in width to more than 400  $\mu\text{m}$  in length, which often branch and anastomose or become moderately coiled.

Medullary excipulum of dense textura intricata, gel sparingly present, hyphae 6-12  $\mu\text{m}$  in diam.

Asci diffusely J+, nearly 500  $\mu\text{m}$  long and 20-22  $\mu\text{m}$  broad.

Ascospores at maturity hyaline, thin-walled, smooth or with some cytoplasmic granulation, biguttulate but often obscurely so, 27-30 x 13-15  $\mu\text{m}$ .

Paraphyses septate, enlarged above, exceeding the asci, of granular contents which become dark brown in fresh material when placed in iodine.

This species is quite similar to *Pachyella clypeata*; the spores are larger and the configuration of the hyphoid hairs differs. In habitat and growth form it is identical.



Figure 3. *Pachyella punctispora*. Apothecia from material collected in France. Scale = 1 cm.

*Pachyella punctispora* Pfister, Canad. J. Bot. 51: 2019. 1973.

Figure 3

= *Peziza punctispora* (Pfister) Donadini. Doc. mycologiques 11: 26. 1980.

Pierre Gabard, Guy Roux and the junior author have collected this species in France (Pont du Goa, Vallée du Soussuëou, 900 m alt. 15.VII.1979; Crampes de Piet, Vallée d'Ossau, 800 m alt. Leg. Guy Roux, Pyr. Atlantiques, environs de Pau, s/Betula et autres bois, 28.VII.1979). These collections constitute the first report of the species outside North America. Figure 3 shows apothecia of the French collection.

*Pachyella pseudosuccosa* (Le Gal) Pfister, comb. nov.

= *Galactinia pseudosuccosa* Le Gal, Rev. Mycol. (Paris) 10: 91-95. 1945.

? = *Peziza aquatilis* Berthet & J.-C. Donadini. Bull. Mens. Soc. Linn. Lyon 47: 205. 1978.

= *Pachyella aquatilis* (Berthet & Donadini) Donadini, Bull. Soc. Linn. Provence 31: 18. 1978.

When Le Gal described *Galactinia pseudosuccosa*, she did so in such a way as to introduce some ambiguities,

particularly in clearly stating the name in association with the Latin description. It seems to be validly published. One form she described, forma *macrospora*, was the form upon which *Galactinia megalosperma* (Le Gal 1953) was based. The typical form, material of which has been unavailable for study, was described from dried material in the Boudier herbarium and was collected by Barla in Nice in 1891.

A portion of the holotype specimen of *Peziza aquatilis*, kindly sent by M. Berthet, agrees closely with that described by Le Gal as *Galactinia pseudosuccosa*. Both have a reddish brown hymenium and both are said to produce a yellow juice when broken. Moreover, the Barla collection and those of Donadini are all from the same general area in S. W. France.

*Pachyella violaceonigra* (Rehm) Pfist., *Canad. J. Bot.* 51: 2021. 1973.

Previously the combination of this species in *Galactinia* by Boudier (*Hist. Class. Discom. Eur.* p. 47. 1907) was overlooked. Also to be added to the synonymy is the combination: *Peziza violaceonigra* (Rehm) Smits'Ka (Ret-sitsovi Gribi Ukrayini (Kiev) p. 78. 1975). Donadini (1980) also proposed the combination *Peziza violaceonigra*.

The junior author has made collections of *Pachyella violaceonigra* in France (Bois de St. Maur-Mirande, Gers, 13.VIII.1971; Forêt de Bugangue, Oloron, Pyr. Atlantiques 22.X.1973; FH, Herb. R. P. Korf, Herb. F. Candoussau). Other collections were made in Switzerland by A. Nyffenegger (near Kanton Bern; FH, Z) and by Bruno Erb and Stappung Erlinsback (automne 1980, Herb. F. Candoussau).

Key to species of *Pachyella*

1. Hyphoid hairs forming a palisade layer at the base of the apothecia . . . . . 2
1. Hyphoid hairs not forming a distinct palisade layer at the base of the apothecia . . . . . 7
  2. Ascospores smooth 13-16 x 18-25 (28)  $\mu\text{m}$ , apothecia umber to chestnut color, outer layer of excipulum of radially arranged globose cells, hyphoid hairs neither branched nor anastomosing, N. America. . . . . *P. clypeata*
  2. Ascospores or apothecial construction not as above . . . . . 3
3. Ascospores smooth 13-15 x 27-30  $\mu\text{m}$ , apothecia dark umber, outer layer of excipulum of tightly packed, only slightly swollen cells, hyphoid hairs branched and anastomosing, Europe. . . . . *P. peltata*
3. Ascospores variously ornamented . . . . . 4
  4. Ornamentations taking the form of large flat-topped warts, N. America, West Indies, and Japan. . . . . *P. adnata*
  4. Ornamentations smaller in the form of warts or interconnecting ridges. . . . . 5
5. Spores ornamented with anastomosing warts, hymenium reddish brown, known only from Madagascar . . . . . *P. megalosperma*
5. Spores ornamented with solitary warts . . . . . 6
  6. Hymenium dark brick to sepia, when damaged not producing a yellow juice, Europe . . . . . *P. violaceonigra*
  6. Hymenium reddish brown, when damaged producing a yellow juice, Europe . . . . . *P. pseudosuccosa*
7. Spores smooth or punctate, margin attached to the substrate, apothecia generally not greater than 1 cm in diam, worldwide . . . . . *P. babingtonii*
7. Spores ornamented with fine warts, margin free, apothecia generally larger than 1 cm . . . . . 8
  8. Spores 12-15 x 21-25  $\mu\text{m}$ , marked with small but discernable warts, paraphyses up to 9  $\mu\text{m}$ , N. America, Europe . . . . . *P. punctispora*
  8. Spores 13-16 x 22-26  $\mu\text{m}$ , marked with warts which can scarcely be seen with the light microscope, paraphyses up to 15  $\mu\text{m}$  in diam, N. America. . . . . *P. hydrophila*

## ACKNOWLEDGEMENTS

We wish to thank Richard P. Korf for his comments on this manuscript. Prof. Berthet kindly sent material of *Peziza aquatilis* for our study. We are grateful to Emile Jarias and Guy Roux for photographs. The senior author's work was supported in part by National Science Foundation Grant DEB 8023018.

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PITHOMYCES PAVGII, A NEW COMBINATION FOR  
TRICHOCLADIUM PAVGII AND PITHOMYCES FUNICULOSA

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*Trichocladium pavgii* Nath was published as a new species from India on 16 July 1979 (1). Additionally, a new dematiaceous hyphomycete from Swaziland was described as *Pithomyces funiculosa* Palm, Stewart, & Rossman on 19 October 1979 (2). We have determined that *T. pavgii* and *P. funiculosa* are conspecific. *Trichocladium pavgii* has priority according to the International Code of Botanical Nomenclature, Article 11.3 (3). However, based on conidium development and secession, *T. pavgii* can only be accommodated in *Pithomyces* Berk. & Br. *Trichocladium* Harz has been broadly circumscribed and at present contains a heterogeneous assemblage of species which produce transversely septate conidia holoblastically. *Pithomyces*, in contrast, is characterized by the holoblastic production of dematiaceous conidia which are usually both transversely and obliquely septate. Moreover, rhexolytic conidium secession leaves a characteristic denticle on the conidiogenous cell. *Trichocladium pavgii* must be transferred to *Pithomyces*. The new combination is herein made and the taxon redescribed based on additional studies of isolates from India and the United States.

- Pithomyces pavgii* (Nath) Palm, Stewart, & Rossman, comb.  
nov. Figs. 1-4  
= *Trichocladium pavgii* Nath, Sydowia 31: 122-125. 1978.  
(basionym)  
= *Pithomyces funiculosa* Palm, Stewart, & Rossman,  
Mycotaxon 10: 246-250. 1979.

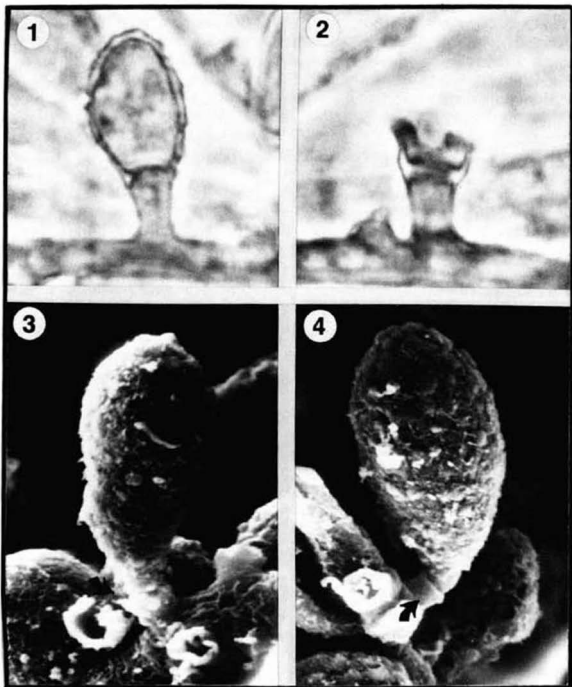
COLONIES on malt agar white to grey becoming brown to black, floccose to appressed, dark ropy strands of conidio-

phores frequently present. HYPHAE septate, branched, of two types, hyaline to subhyaline, smooth, 1.5-5 ( $\bar{x}$ =2.8)  $\mu\text{m}$  diam, and subhyaline to pale brown, sometimes finely roughened, 2.5-6 ( $\bar{x}$ =3.4)  $\mu\text{m}$  diam. CONIDIOPHORES micronematous to semi-macronematous, mononematous, frequently funiculose, infrequently branched, septate, subhyaline to pale brown. CONIDIOGENOUS CELLS holoblastic, monoblastic or polyblastic, integrated, intercalary, determinate or seemingly proliferating percurrently to produce one or more conidia, cylindrical to doliform, denticulate following secession of conidia, denticles short cylindrical to doliform, 1-4 ( $\bar{x}$ =2.4)  $\times$  1.5-4 ( $\bar{x}$ =2.3)  $\mu\text{m}$ . CONIDIA solitary, pleurogenous, mostly verrucose, pale to dark brown, clavate to obovate to obpyriform to broadly or fusiform ellipsoid to reniform, transversely (0-)1-3(-4)-septate, mostly 2-septate, may be slightly constricted at the septa, rarely with 1-2 oblique or longitudinal septa, 10-17 ( $\bar{x}$ =13.3)  $\times$  4.5-12 ( $\bar{x}$ =7.4)  $\mu\text{m}$  (1-septate), 13-20 ( $\bar{x}$ =17.2)  $\times$  5-12 ( $\bar{x}$ =7.8)  $\mu\text{m}$  (2-septate), 17-26 ( $\bar{x}$ =22.1)  $\times$  6-12 ( $\bar{x}$ =8.3)  $\mu\text{m}$  (3-septate), bases 2-4 ( $\bar{x}$ =2.6)  $\mu\text{m}$  diam, with a portion of the conidiogenous cell usually remaining as a basal frill.

Collections examined: India: Hyderabad, Rajendranagar, V. Ravindra Nath. From kernels of *Arachis hypogaea* L. 3 i 1973 (IMI 205718 [holotype] and living culture received from V.R.N.). Swaziland: Luyengo, A.Y. Rossman. From fungal comb of *Macrotermes ukuzii* Fuller. 15 ix 1977 (MPPD). United States: Alabama, Chambers Co., G. Morgan-Jones. From municipal industrial waste-water. v 1980 (AUAM 2405).

In addition to its occurrence in India and Swaziland, G. Morgan-Jones (personal communication) has isolated *P. pavgii* in the United States. Based on our observations using phase contrast and scanning electron microscopy, the conidiogenous cell either proliferates percurrently through the denticle, which remains as a short annellation, or the apparently inelastic outer wall ruptures and remains at the base of the exposed, elastic inner wall. Remnants of conidiogenous cells surrounding the possibly proliferating conidiogenous cell are seen infrequently and mainly in older cultures. Ravindra Nath's line drawings of *P. pavgii* indicate flared structures resembling annellations at the apex of some elongate conidiogenous cells which he described as "roughened". Examination of the type material (IMI 205718) and of a living culture indicate that the





FIGS. 1-4. *Pithomyces pavgii*. 1. Photomicrograph (phase contrast microscopy for Figs. 1 and 2) of a developing conidium with intact outer wall. X2000. 2. Photomicrograph of a conidiogenous cell following rhexolytic conidium secession showing remnants of either the inner and outer walls or the walls from two successively produced conidia. X2000. Figs. 3-4. Scanning electron micrographs of conidium and conidiogenous cell with inelastic outer wall beginning to rupture (Fig. 3) and conidium and conidiogenous cell with ruptured outer wall or a possible annellation (Fig. 4). X3000.

fungus sometimes appears to proliferate percurrently, but, a conidiogenous cell so long and with more than one "annellation" was never observed by us. Final elucidation of conidiogenesis requires ultrastructural or time lapse studies or both.

#### ACKNOWLEDGEMENTS

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VALIDATION OF THE HERPOMYCETINEAE AND  
HERPOMYCETACEAE IN THE LABOULBENIALES

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When the Euceratomycetaceae in the suborder Laboulbeniineae was described (Tavares, 1980), a comparison was made between the development of the perithecia in the Laboulbeniineae and the Herpomycetinae I. Tav. (*nom. nud.*). Inadvertently, I omitted a reference to the second volume of Thaxter's monograph (1908) of the Laboulbeniales, in which the tribe Herpomyceteae was described in the key to genera within the family Laboulbeniaceae. In addition, there was no mention of the family Herpomycetaceae, nor was a diagnosis of the Herpomycetinae included (Tavares, 1980). Consequently, a Latin diagnosis for the Herpomycetinae follows, for which I am indebted to Dr. William J. Dress, Bailey Hortorium, Cornell University.

Subordo Herpomycetinae *nom. nov.* Dioeciae. Thallorum femineorum perithecia uno vel pluribus axibus receptacularibus secundariis, qui una vel pluribus cellulis suprabasalibus in axe primario producti sunt, portata. Perithecii paries exterior ex seriebus quattuor verticalibus cellularum constans, serie quaque ex cellulis numerosis brevibus altitudine subaequis composita. Cellula infima in una serie verticali cellularum parietalium perithecii juvenalis et introrsum et sursum per medium perithecii crescens, carpoonium formans. Antheridia sunt phialides.

Familia Herpomycetaceae (Thaxter) *stat. nov.*

Tribus Herpomyceteae Thaxter. *Mem. Amer. Acad. Arts Sci.* 13: 237. 1908.

Family Herpomycetaceae: As in the suborder. Dioecious, occurring on cockroaches (Blattaria). The germinating spore becomes transformed into a primary axis of four or more cells. In the female, perithecia are produced

on secondary axes arising from the primary axis. Vertical septa are formed in the perithecial primordium, producing four cells, each of which divides into a vertical row of wall cells. When there are two tiers of wall cells, one of the four lower cells grows inward and upward and forms a central carpogonial upgrowth (Tavares, 1980). At maturity, there are many short outer wall cells, equal or subequal in height, in each vertical row. Four vertical rows of inner wall cells surround the passage in the perithecial neck through which the ascospores emerge (Tavares, 1966). Eight spores having median septa are formed in each ascus. Male thalli bear elongate, simple antheridia.

Thaxter's description (1908) of *Herpomycetaceae*, which was only a brief statement in his generic key, nevertheless served satisfactorily to distinguish the tribe, because *Herpomyces*, the solitary genus, is the only dioecious genus having secondary receptacles and simple antheridia. Although *Dimeromyces aberrans* Thaxter (1924) may have simple antheridia, additional receptacular cells in the female thallus are produced in the primary axis and do not form a secondary axis as they do in the closely related genus *Dimorphomyces*, in which all antheridia are compound.

In his poorly preserved material, Thaxter was unable to see the internal structure of the perithecium of *Herpomyces* (see Thaxter, 1931). Consequently, he (Thaxter, 1908) placed *Herpomyces* in the Laboulbeniaceae because of the simple antheridia, not realizing how strongly its perithecial development differed from that of the other genera in this family.

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## ERYNIA (ZYGOMYCETES: ENTOMOPHTHORALES):

## VALIDATIONS AND NEW SPECIES

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## SUMMARY

New specific names are proposed to validate three heretofore invalidly published species of *Erynia* Nowakowski (Entomophthoraceae): *E. bullata* Thaxter & MacLeod in Humber, *E. creatonoti* Yen in Humber, and *E. myrmecophaga* Turian & Wuest in Humber. *Erynia formicae* Humber & Bałazy in Humber, sp. nov., is proposed as a name for a fungus occurring on ants and differing from the incompletely characterized *E. myrmecophaga*.

During recent studies on the entomopathogenic Entomophthorales, *Erynia* Nowakowski and the closely allied or synonymous genus (depending on one's taxonomic opinion) *Zoophthora* Batko have received much attention (Remaudière and Hennebert 1980; Remaudière and Keller 1980; Humber 1981, 1982; Humber and Ben-Ze'ev 1981; Ben-Ze'ev and Kenneth 1981, 1982). Several species referable to *Erynia* sensu Humber & Ben-Ze'ev (1981) are not validly published under the International Code of Botanical Nomenclature. This paper vali-

dates three of these species and proposes a second new species of *Erynia* from ants.

*ERYNIA BULLATA* Thaxter & MacLeod, sp. nov.

*CORPORA HYPHALIA* variabilis per initium contagionis, hyphoidea postrem. *NUCLEI* persaepe conspicui, minimum 6-10  $\mu\text{m}$  in diametro, contentis granulatis autem sine nucleolo conspicuo ovoideo centrali. *CONIDIOPHORA* dichotome digitate ramosa ad apices, intertexta in hymenium continuum; in taeniis emergens et in integumenta super corpore hospitis coalescens. *CONIDIA PRIMARIA* uninucleata, bitunicata, ellipsoidea ovoidea, 23.0-37.5  $\mu\text{m}$  x 12.0-16.5  $\mu\text{m}$  (medio 29.5 x 14.0  $\mu\text{m}$ ), expulsa vehementer eversione papillae distinctae contra conidiophora. *CONIDIA SECUNDARIA* inobservata. *SPORAE PERDURANTES* hyalinae vel stramineae vel pallidae alutacae in massa in corpore hospitis; multinucleata ubi maturae; episporiis conspicue vel bullatis vel tuberculatis, 37-62  $\mu\text{m}$  (medio 50  $\mu\text{m}$ ) in diametro toto bullis inclusis. *RHIZOIDEA* numerosa, simplicia, hyphoidea, sine haptero disciformi terminali, ex abdomine et thorace emergentia; in praesentia vel conidiorum vel sporarum perdurantium formata. *CYSTIDIA* desunt.

*HYPHAL BODIES* variable in size and shape during early stages of development in host, becoming hypha-like at time of the host's death. *NUCLEI* easily distinguished in most vegetative or reproductive structures; large, usually 6-10  $\mu\text{m}$  or more in diameter; contents granular, without a prominent central ovoid nucleolus. *CONIDIOPHORES* branched digitately toward the apices, intertwining to form a continuous hymenium; emerging in bands from weak points of the host exoskeleton, coalescing to form more or less complete coverings over the abdomen and the junction of the neck and thorax. *PRIMARY CONIDIA* uninucleate, bitunicate, ellipsoid to ovoid, 23.0-37.5  $\mu\text{m}$  x 12.0-16.5  $\mu\text{m}$  (averaging 29.5 x 14.0  $\mu\text{m}$ ), forcibly ejected by the eversion of the conspicuous basal papilla against the conidiophore. *SECONDARY CONIDIA* not observed. *RESTING SPORES* forming a compact, hyaline to creamy-yellow or light tan mass inside the host body; multinucleate when mature; individual spores with prominent, rounded bullations up to 5  $\mu\text{m}$  in height on the epispore; 37-62  $\mu\text{m}$  (averaging 50  $\mu\text{m}$ ) in overall diameter (including the episporial bullations). *RHIZOIDS* numerous, unbranched, hypha-like, without any terminal disc-like holdfast, emerging principally from the abdomen and thorax; present whether the fungus produces conidia or resting spores.

*HOLOTYPE*: CUP 58970 (Cornell Univ., Plant Pathology Herbarium). Resting spores in *Sarcophaga aldrichi*. Coll.: D. Tyrrell, 23 June 1981.

*PARATYPE*: CUP 58971 (Cornell Univ., Plant Pathology Herbarium). Conidia on *Sarcophaga aldrichi*. Coll.: D. Tyrrell, 23 June 1981.

*TYPE HOST*: *Sarcophaga aldrichi* Parker (Diptera: Sarcophagidae).

*TYPE LOCALITY*: Birch Creek Road, Webwood, Ontario, Canada.

This species appears to be a relatively common pathogen of calliphorid and sarcophagid flies in North America. It was collected several times in the northeastern United States by Roland Thaxter (Riddle 1906, as *Entomophthora* "x") but never formally described. After Thaxter's death, Povah (1935) received permission from Dr. W. Weston at Harvard University to use Thaxter's unpublished herbarium name, *Entomophthora bullata*, for the fungus Povah found attacking bluebottle flies in Michigan. This name, attributed to Thaxter, was presented with scant details of the fungus's morphology except for the bullate nature of its resting spores (33-50  $\mu\text{m}$  diam. in Povah's collection) and the overall similarity of the primary conidia of this fungus with those of *Erynia americana* (Thaxter) Remaudière & Hennebert (1980). Unfortunately, *Entomophthora bullata* Thaxter in Povah appeared in print after 1 January 1935 and is, according to Article 36 of the International Code of Botanical Nomenclature, invalidly published without a Latin diagnosis or reference to any previously published Latin diagnosis. All subsequent combinations based on this name — *Zoophthora bullata* (Thax. in Povah) Batko (1966) and *Erynia bullata* (Thax. in Povah) Remaudière & Hennebert (1980) — are also invalidly published.

The most thorough study of *E. bullata* is that by MacLeod et al. (1973) who provide a complete morphological characterization. They suggest the host's age may affect whether conidia or resting spores are produced at the time of the fly's death. Kramer (1979) studied the time course of infection and the spore states produced in three species of calliphorid flies infected in the laboratory. He corroborated that the disease in younger flies does tend to produce only conidia while the probability for resting spore production increases with the age of the flies at the time of infection. In contrast to MacLeod et al. (1973), who state that the fungus never produced both conidia and resting spores in the same cadavers of field-infected *S. aldrichi*, Kramer (1979) found that, on rare occasions, both spore states may occur together in affected individuals of *Phormia regina* (Meig.) and *Phaenicia sericata* (Meig.). It is significant, then, to note that in the field-collected examples of *Sarcophaga aldrichi* in the holotype collection, tufts of conidiophores are apparent at the joints of the legs whereas the fly bodies are filled with resting spores. No bands of conidiophores are apparent on the abdomens of flies in the holotype collection.

Cytological studies by Riddle (1906) indicated that three-month-old resting spores of *E. bullata* are multinucleate. This condition was verified with resting spores from the holotype collection stained with either acetorcein or bismarck brown. Humber (1981a) discusses the implications of this multinucleate condition in entomophthorean resting spores.

### ERYNIA CREATONOTI Yen, sp. nov.

"CONIDIA pyriformia, uninucleata, med.  $32 \times 25 \mu\text{m}$ , basi papillata, muro tenui, cytoplasmatae granoso; NUCLEI med.  $12 \times 9 \mu\text{m}$ ; CONIDIOPHORI ramosi coalescentes tegimenta suffusco vel roseo super totum hospitis corpus. CORPORA HYPHALIA brevia, segmentis hypharum incompositis,  $8-28 \mu\text{m}$  latis  $20-24 \mu\text{m}$  longis. CYSTIDIA raro inveniuntur. SPORAE PERDURANTES azygosporae (zygosporae pauca inventae), globosae; episporio laevi atque crasso; cytoplasma granosum vel vacuolatus; diam.  $10-28 \mu\text{m}$ . Hospes substrato RHIZOIDEIS fixus." (Yen 1962)

TYPE: Latin and English descriptions and figure 1-4, *J. Insect Pathol.* 4, 88-94 (1962).

TYPE HOST: *Creatonotus gangis* (L.) (Lepidoptera: Arctiidae)

TYPE LOCALITY: Kun-Kuan, Taipei, Taiwan.

This species, originally proposed with the orthographically incorrect name *Entomophthora creatonotus* Yen (1962), was invalidly published since no type was designated. The combinations *Zoophthora creatonoti* (Yen) Batko (1964) and *Erynia creatonoti* (Yen) Remaudière & Hennebert (1980) are also, therefore, invalidly published. The choice of the description and figures of *E. creatonoti* to typify this species is motivated by the lack of any mention by Yen (1962) of the permanent deposition of either any specimens or the slides from which his photomicrographs were prepared. The English description of all morphological characters of this fungus is meticulously detailed even if the figures are of limited utility.

The placement of this species in *Erynia* is fully justified by its uninucleate (presumably bitunicate) conidia borne on digitately brached conidiophores. The large nuclei are readily detected, even in unstained material (Yen 1962), and correspond to those of all other *Erynia* species. The presence of fascicles of hypha-like rhizoids and of a few cystidia supports this generic assignment.



## ERYNIA FORMICAE Humber &amp; Bałazy, sp. nov.

CORPORA HYPHALIA irregularia per initium contagionis, 35-155  $\mu\text{m}$   $\times$  8-16(20)  $\mu\text{m}$ , et posterius manifestius hyphoidea et saepe parviter septata. NUCLEI persaepe conspicui, magni, contentis granulatis autem sine nucleolo ovoideo centrali. CONIDIOPHORA in taeniis distinctis emergentia, dichotome vel digitate ramosa ad apices. CONIDIA PRIMARIA uninucleata, bitunicata, obovata vel pyriformia, 18-25  $\mu\text{m}$   $\times$  10-16  $\mu\text{m}$ , expulsa vehementer eversione papillarum contra conidiophora; papilla basali aliquantum distincta. CONIDIA SECUNDARIA conidia primaria simulantia quanquam parviora, 16-19  $\mu\text{m}$   $\times$  10.5-13.5  $\mu\text{m}$ , expulsa vehementer in modum conidiorum primariorum. RHIZOIDEA sparsa crassa, haptera disciformia terminalia, ex junctura promesothoracica in fasciculum laxum emergentia. CYSTIDIA et SPORAE PERDURANTES ignotae.

HYPHAL BODIES irregular in length, diameter, and branching pattern inside host body during early stages of development 35-155  $\mu\text{m}$   $\times$  8-16(20)  $\mu\text{m}$ , later becoming infrequently septate and more obviously hyphal in appearance. NUCLEI conspicuous in most vegetative or reproductive structures, large, with granular contents but no central nucleolus. CONIDIOPHORES emerging in distinct bands from weak points on the insect exoskeleton, dichotomously or digitately branched at the apices. PRIMARY CONIDIA uninucleate, bitunicate, obovate to pyriform, 18-25  $\mu\text{m}$   $\times$  10-16  $\mu\text{m}$ , forcibly discharged by eversion of the more or less distinct papilla against the conidiophore. SECONDARY CONIDIA like the primary but smaller, 16-19  $\mu\text{m}$   $\times$  10.5-13.5  $\mu\text{m}$ , forcibly discharged as in the primary conidia. RHIZOIDS relatively few in number, stout, terminating in a discoidal holdfast; emerging from the ventral thorax just behind the head, forming a loose fascicle. CYSTIDIA may be present; if so, tapering to a point from a relatively broad base. RESTING SPORES not observed.

HOLOTYPE: CUP 58975 (Bałazy 1285a), coll: J. Wiśniewski and A. Sokołowski, 19 Sept. 1977, Tuchola pine forest, Poland

PARATYPES: CUP 58976 (Bałazy 1286), CUP 58977 (Bałazy 2074a) and specimens retained by S. Bałazy and R. A. Humber.

TYPE HOSTS: Ants of the genus *Formica* (Hymenoptera: Formicidae): *F. polyctena* and *F. rufa*.

TYPE LOCALITY: Pine forests near Tuchola, Poland.

A comparison of entomophthoraceous fungi reported to attack ants in Switzerland (Turian and Wuest 1969, 1977), the Federal Republic of Germany (Loos-Frank and Zimmermann 1976), and Poland (Bałazy and Sokołowski 1977) indicates the existence of two distinct species of *Erynia*. *Erynia formicae* is described for the better characterized fungus (Loos-Frank and Zimmermann 1976; Bałazy and Sokołowski 1977); these collections have been attributed to the inval-

idly published and less completely characterized *Zoophthora myrmecophaga* Turian & Wuest (which is validated below as *Erynia myrmecophaga* Turian & Wuest).

The conidia of the Swiss fungus are smaller (averaging 18 x 12  $\mu\text{m}$ ), considerably more ovoid, and have a less conspicuous papilla than those of *E. formicae*. The conidia of the Swiss fungus but not of *E. formicae* have a single large vacuole occupying most of the conidial volume. In addition to being held onto grass blades by the mandibles and clasped legs, *E. formicae* further secures the ant cadavers with a few stout rhizoids emerging in a loose fascicle from the ventral thorax (Loos-Frank and Zimmermann 1976; Bałazy and Sokołowski 1977). This sort of rhizoid generally terminates in a discoid haptor (Batko 1966; Humber 1981a); although Loos-Frank and Zimmermann (1976) refer to a holdfast disc ("Haftscheibe") on the rhizoids, neither they nor Bałazy and Sokołowski (1977) illustrate the morphology of this holdfast. *Erynia myrmecophaga* has no such fascicle of rhizoids; Turian and Wuest (1977) report the presence of a few very fine rhizoids emerging from all portions of the host body.

The presence or absence of cystidia in *E. formicae* remains uncertain. Loos-Frank and Zimmermann (1976) note the presence of isolated, broad cystidia tapering to a point, but do not state where these occurred on the host, or at what stage of development. Bałazy and Sokołowski (1977) observed no cystidia on any specimens allowed to develop and sporulate in damp chambers.

Loos-Frank and Zimmermann (1976) provide a detailed study of the effects of *E. formicae* on its host, and find the behavior of affected ants and fungus-mediated histopathology of the brain to be much like the effects in ants caused by the parasitic trematode *Dicrocoelium dendriticum*. Humber (1975, 1976) also found a marked tendency for hyphae of *Strongyloides magna* Humber to penetrate the thoracic ganglion and brain of affected flies, but without causing any obvious histopathology or changes in host behavior.

More complete information about the morphology and pathobiology of *E. formicae* is provided by Loos-Frank and Zimmermann (1976) and by Bałazy and Sokołowski (1977).

## ERYNIA MYRMECOPHAGA Turian &amp; Wuest, sp. nov.

*CONIDIOPHORA* parciter dichotome ramosa; in taeniis circum abdomen inter abdomen et occipitium et circum partes oris emergens. *CONIDIA PRIMARIA* uninucleata, bitunicata, late ovoidea vel pyriformia, medio  $18 \mu\text{m} \times 12 \mu\text{m}$ , vacuolam centraliam magnam conspicuam et guttulas oleosas sudanophilas numerosas continentia; papilla basali indistincta. *CONIDIA SECUNDARIA* conidia primaria simulantia sine vacuola quanquam parviora. Hospes ad substratum mandibulis et cruribus adhaerens.

*CONIDIOPHORES* sparingly dichotomously branched, emerging in bands on the abdomen, between the head and thorax, and around the mouth. *PRIMARY CONIDIA* uninucleate, bitunicate, broadly ovoid to pyriform, averaging  $18 \mu\text{m} \times 12 \mu\text{m}$ , containing a large central vacuole occupying most of the conidial volume and numerous sudanophilic oil droplets; basal papilla indistinct. *SECONDARY CONIDIA* similar to but smaller than primary conidia, but not containing the prominent central vacuole. Host attached to the substrate by the mandibles and clasped legs.

**HOLOTYPE:** Figs. 1, 2, and 4, *Mitt. Schweiz. Entomol. Ges.* 50:285-289 (1977).

**TYPE HOST:** *Serviformica fusca* L. (Hymenoptera: Formicidae).

**TYPE LOCALITY:** Sparse grasslands near Geneva, Switzerland.

This description of *E. myrmecophaga* is obviously fragmentary. There remains enough reasonable doubt about certain aspects included in the Latin description provided for *Zoophthora myrmecophaga* (Turian and Wuest 1977) that it was preferable to provide a wholly new description including only those characters which seem relatively well established.

Turian and Wuest (1969) found no rhizoids attaching ants affected by *E. myrmecophaga* to the substrate. These authors later described very fine rhizoids (Turian and Wuest 1977; Fig. 4) which are little distinguished from the epidermal hairs on the grass blades to which the ants are affixed. This characterization may actually note true rhizoids of *E. myrmecophaga*, but their appearance is not typical of other entomophthoralean rhizoids. The possibility remains that these structures, observed on insects collected in 1967 and 1968, might have been either strands of insect or spider silk or the fine hyphae of some saprobic deuteromycetous contaminant.

Similarly, it is so unlikely that the two different types of "resting spores" noted by Turian and Wuest (1969, 1977) actually represent any over-wintering spores which might be produced by *E. myrmecophaga* that these spore types were intentionally omitted from the description and typification of this fungus above. Turian and Wuest (1969; Fig. 3) first reported finding one solitary resting spore among the hyphal bodies in one ant; this globose spore has a single-layered, relatively thin, smooth-surfaced wall, was 20  $\mu\text{m}$  in diameter, and contained numerous oil droplets. If this was an entomophthoralean resting spore, it was immature and neither its size nor structure could be considered to be taxonomically significant. Turian and Wuest (1977; Fig. 3) later found a few globose resting spores with thick walls and rugose surfaces; the illustrated structure does not have the thick, two-layered wall which is characteristic of entomophthoralean resting spores. Neither were these rugose spores found in the numbers or aggregated mass in the abdomen that one might expect for naturally produced entomophthoralean resting spores. The best clue to the identity of these structures comes from the conspicuous furrows on the surface; this morphology is unprecedented in the Entomophthorales but is strongly reminiscent of tricolpate pollen grains like those produced by oaks and beeches (Fagaceae) (Faegri and Iversen 1975; Bassett et al. 1978).

*Erynia myrmecophaga* obviously requires further study from both any existing specimens and any future collections. Important differences between this species and the far better characterized *E. formicae* exist in the size and shape of the primary conidia, and the presence and nature of rhizoids. It should be noted, however, that the behavior and appearance of affected ants, the relatively low degree of conidiophore branching, absence of cystidia, and absence of verifiable resting spores are common characteristics of these species. None of the similarities is sufficiently important or convincing to suggest that *E. formicae* and *E. myrmecophaga* are not distinct species.

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## A REVIEW OF THE NONENTOMOGENOUS ENTOMOPHTHORALES

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### SUMMARY.

The characters used to define genera in the nonentomogenous Entomophthorales are evaluated and compared with those used for delimiting entomogenous genera. It is proposed that the host organism should be deemphasized. Five characters considered valid at the generic level are 1) spore karyology; 2) sporophore architecture; 3) method of spore discharge; 4) zygosporangium morphology and development; and 5) thallus development. These characters are applied to the fifteen nonentomogenous fungi reported to date, and two taxonomic realignments are proposed: Meristacrum pendulatum is transferred to Zygnemomyces and Entomophthora vermicola is transferred to Macrobiotophthora. The transfer of Tabanomyces milkoi to Meristacrum is accepted. Ancylistes netrii, originally described without a Latin diagnosis, is validated. The accepted genera are: Ancylistes (3 sp.), Ballocephala (3 sp.), Complectoria (1 sp.), Macrobiotophthora (2 sp.), Meristacrum (2 sp.), and Zygnemomyces (2 sp.). A key to the species of these genera is provided.

### I. INTRODUCTION.

Entomophthorales are separated from other orders of Zygomycotina by the forcible discharge of single spores and a tendency to parasitize insects. There are, however, a few saprobic species in Conidiobolus Brefeld and Basidiobolus Eidam, plus a small group of species parasitizing noninsect hosts. Humber (1981: p. 234) observes that ". . . it is inappropriate to argue about the choice of criteria used to define genera or about the correctness of one or another classification of the Entomophthorales without taking the non-entomogenous genera into full account." This paper attempts to render this accounting by reviewing published records, type and living material of these fungi, discussing the taxonomic criteria used to delimit the

TABLE 1.  
 REPORTS AND DESCRIPTIONS OF THE  
 NONENTOMOGENOUS ENTOMOPHTHORALES.

1872. Ancylistes closterii Pfitzer, Monatsb. Königl. Preuss. Akad. Wiss. Berl. 396.
1874. Completozia complens Lohde, Tagebl. Versamml. Deutsch. Naturf. Aertze 47: 206.
1896. Ancylistes pfeifferi Beck, Verh. Zool. Bot. Ges. Wien 46: 233.
1912. Macrobiotophthora vimariensis Reukauf, Centralbl. Bakt. Parasit. Infectk. 63: 390.
1940. Meristacrum asterospermum Drechsler, J. Wash. Acad. Sci. 30: 251.
1949. \*Ancylistes netrii Couch, J. Elisha Mitchell Sci. Soc. 65: 132.
1951. Ballocephala sphaerospora Drechsler, Bull. Torrey Bot. Club 78: 199.
1952. \*Botryobolus parasiticus Arnaud, Bull. Soc. Mycol. Fr. 58: 184. [=Ballocephala sphaerospora.]
1968. "A Conidiobolus-like fungus." Castaner, D. Mycologia 60: 440-443.
1970. †Ballocephala verrucospora Richardson, Trans. Brit. Mycol. Soc. 55: 308.
1973. Coelomyces milkoi Dudka & Koval, Novitates System Plantarum non Vascularium 10: 89.
1973. Zygnemomyces echinulatus Miura, Rep. Tottori Mycol. Inst. (Japan) 10: 520.
1977. †Entomophthora vermicola McCulloch, Trans. Brit. Mycol. Soc. 68: 173.
1977. †Meristacrum pendulatum McCulloch, Trans. Brit. Mycol. Soc. 68: 175.
1978. Ballocephala pedicellata Pohlád & Bernard, Mycologia 70: 131.
1980. "Conidiobolus sp." Amin, E. & J. Webster, Trans. Brit. Mycol. Soc. 74: 334.

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\* Invalidly published due to lack of Latin diagnosis.

† Type examined.

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nonentomogenous genera, and proposing taxonomic revisions where necessary.

There have been 14 entomophthoralean fungi reported since 1872 from noninsect hosts, primarily from small animals (nematodes, tardigrades) or plants in moist environments (fern gametophytes, desmid algae). These fungi, as well as the entomogenous Tabanomyces milkoii Couch et al. [= Coelomomyces milkoii] are listed in Table 1 in order of their publication. The useful data obtained from these published descriptions, illustrations and photographs, and from the original material are summarized in Tables 2-5. Three nematophagous fungi are excluded from further consideration in this paper. Two parasites of Heterodera Schmidt (cyst-nematodes) were recently transferred to the Lagenidiales: Catenaria auxiliaris (Kühn) Tribe ([=Tarichium auxiliare Kühn] MacLeod and Müller-Kögler 1970, Tribe 1980) and Nematophthora gymnophila Kerry & Crump ([='Entomophthora'-like fungus] Kerry 1974, Kerry and Crump 1980). Haptoglossa Drechsler was placed in the Entomophthorales by Ainsworth (1971), although Drechsler believed it belonged in the Saprolegniales, a disposition supported by Davidson and Barron (1973a) and Barron (1977).

## II. EVALUATION OF TAXONOMIC CHARACTERS.

### 1. HOST.

Host range is often valuable as a taxonomic character for delimiting nonentomogenous species since none have yet been found from more than one host. In addition, nonentomogenous genera such as Ancylistes Pfitzer, Balloecephala Drechsler and Completozia Lohde are restricted to one host (see Table 2). However, as will be seen with the species placed at various times in Meristacrum Drechsler (M. asterospermum, M. pendulatum, Tabanomyces milkoii), it is possible for natural relationships to be obscured if host characteristics are not tempered with an understanding of basic aspects of morphology and development. The following examination of these characteristics provide a better generic framework for the nonentomogenous Entomophthorales than can be obtained from host characteristics alone.

### 2. THALLUS DEVELOPMENT.

The initial stages of infection are similar in most nonentomogenous Entomophthorales, and involve the penetration of the cell wall or integument of the host by a thin penetration tube arising from a spore (especially a secondary spore) or appressorium formed at the tip of a sterile external hypha. Following penetration, the cytoplasmic contents of the infective propagule migrates into a swollen infection bladder. The thallus then matures from this bladder in one of three distinct patterns. In the nematode parasites (see Table 2), the thallus consists of long aseptate hyphae which more or less fill the host organism. These hyphae do not form short cells or fragment into

TABLE 2.  
HOST AND THALLUS CHARACTERISTICS IN THE  
NONENTOMOGENOUS ENTOMOPHTHORALES.

SPECIES	HOST	INITIAL THALLUS			MATURE THALLUS		
		form	length	x width	form	length	x width
<u>Ancylistes</u>							
<u>closterii</u>	D	AH	FH	x 7.5-11	SH	12.5-55	x 11-15
<u>pfeifferi</u>	D	AH	FH	x 7.5-14	SH	43-67	x 9.5-19
<u>netrii</u>	D	AH	FH	x 2.2-4.8	SH	15-30	x 8-15.5
<u>Completozia</u>							
<u>complens</u>	D	HC	15-30*	x 7-15	same		same
<u>Macrobiotophthora</u>							
<u>vimariensis</u>	TD	?	?	?	HB	?	?
<u>vermicola</u>	N	AH	FH	5-7	SH		same
Castaner (1968)	N	AH	FH	3-6.5	SH?		same
Amin & Web. (1980)	N	AH	FH	?	SH?	18-23	x 12-18
<u>Meristacrum</u>							
<u>asterospermum</u> †	N	AH	50-500	x 5-12	HB	25-60	x ?
<u>asterospermum</u> °	N	AH					
<u>milkoii</u>	TB	AH	> 120	x 5-7	HB	70-176x	28-56
<u>Zygnemomyces</u>							
<u>echinulatus</u>	N	AH	FH	2-5	same		same
<u>pendulatus</u>	N	AH	FH	5-12	same		same
<u>Ballocephala</u>							
<u>sphaerospora</u>	TD	AH	5-80	x 5-10	HB	40-80	x 5-10
<u>verrucospora</u>	TD	AH	?	?	HB	20-40	x 10-12
<u>pedicellata</u>	TD	AH	?	?	HB	20-31	x 13-16

All measurements in  $\mu\text{m}$ .

° Davidson and Barron (1973)

† Drechsler (1940)

\* measured from illustration

D=desmid algae

F=fern gametophyte

N=nematode

TB=tabanid larvae

TD=tardigrade

AH=aseptate hyphae

HB=hyphal body

HC=hyphal cluster

FH=filling host

SH=septate hyphae

hyphal bodies at maturity.

In Ancylistes, Ballocephala and Macrobiotophthora vimariensis, after an initial mycelial stage, the hyphae become regularly septate. The newly formed cells may remain attached, or fragment into freely floating hyphal bodies, depending upon the physical activity of the host.

In Completozia, the infection bladder germinates and forms numerous short hyphal lobes which form a radiating cluster of cells filling the host cell completely. This is reminiscent of growth patterns in some of the entomogenous Entomophthorales (Thaxter 1888).

TABLE 3.  
PRIMARY SPORE CHARACTERISTICS OF THE  
NONENTOMOGENOUS ENTOMOPHTHORALES.

SPECIES	PRIMARY SPORE						
	shape	ornam	length	width	base	disch	#spore devl
<u>Ancylistes</u>							
<u>closterii</u>	PYR	-	13.5-17.5	P	+	1	T
<u>pfeifferi</u>	PYR	-	21-23.5	P	+	1	T
<u>netrii</u>	PYR	-	16-25	P	+	1	T
<u>Completozia</u>							
<u>complens</u>	PYR	-	15-25	p	+	1	T
<u>Macrobiotophthora</u>							
<u>vimariensis</u>	OBV	-	18-21.5x10-11.5*	TR	?	1	T
<u>vermicola</u>	OBV	-	16-22 x 9-14	TR	+	1	T
Castaner (1968)	OV/B	-	6.5-9.5x6.5-8.5	TR	+	1	T
Amin & Web. (1980)	OBV	-	21-26 x 12-16	TR	+	1	T
<u>Meristacrum</u>							
<u>asterospermum</u> †	OBV	-	8-11 x 6-8	TR	+	5-15	B
<u>asterospermum</u> °	OBV	-	7-17.5x6-10	TR	+	2-8	B
<u>milkoi</u>	PYR	-	12-16 x 10-13	P	+	4(3-1)	B
<u>Zygnemomyces</u>							
<u>echinulatus</u>	SPH	ECH	5.7-7.2	U	-	10-20	A
<u>pendulatus</u>	SPH	ECH	5-7	U	-	1-3	A
<u>Ballocephala</u>							
<u>sphaerospora</u>	SPH	-	3.0-4.5	U	+	20-80	A
<u>verrucospora</u>	SPH	ECH	4.5-6.0	U	+	4-12	A
<u>pedicellata</u>	SPH	-	6.7-8.0	U	+	2-10	A

All measurements in  $\mu\text{m}$ .

\*Measured from published illustrations.

° Davidson and Barron (1973)

† Drechsler (1941)

ECH=Echinulate

OBV=Obovoid

OV/B=Ovate-Obovate

PYR=Pyriiform

SPH=Spherical

A=Acropetal

B=Basipetal

P=Papillate

T=Terminal

TR=Truncate

U=Unmodified

### 3. PRIMARY SPORES.

#### Morphology.

Shape. Three basic spore shapes are found in the non-entomogenous Entomophthorales; all spores are of the unitunicate type (Remaudière and Hennebert 1980, Remaudière and Keller 1980). Ancylistes, Tabanomyces, and Completozia have pyriform spores (i.e. globose spores with conical papillae (Berdan 1938, Couch 1949, Leitgeb 1881) and are similar to those found in Conidiobolus. Meristacrum has obovate spores with truncate bases (Davidson and Barron 1973). And finally, Ballocephala (Drechsler 1951, Richardson 1970, Pohlád and Bernard 1978), Zygnemomyces echinulatus (Miura 1973) and Meristacrum pendulatum (McCulloch 1977) have globose spores lacking basal modifications.

Ornamentation. Spore ornamentation is uncommon in the Entomophthorales. Some species of Massospora Peck emend. Soper have verrucose spores, and the primary spores of Conidiobolus coronatus (Cost.) Batko may become villose by the growth of appendages through the spore wall. Spore ornamentations consisting of small echinulations are also found in Ballocephala verrucospora, Zygnemomyces echinulatus, and Meristacrum pendulatum.

#### Karyology.

The morphological characteristics of nuclei are considered important by Humber (1981). The presence or absence of nucleoli and heterochromatin (and hence the staining ability of the nuclei) are taxonomically useful at the familial level (see §IV.3), and certain genera with similar spores (e.g. Conidiobolus, Entomophaga Batko) can best be distinguished using nuclear morphology. The number of nuclei per spore has been used to reveal the misplacement of individual species (e.g. Culicicola Nieuwland [Humber 1981]).

Unfortunately, few descriptions include karyological data, although there are a few exceptions among the fungi considered here. Hyphal bodies, gametangia and zygospores of Ancylistes closterii apparently have several nuclei with central nucleoli (Dangeard 1906). Couch (1949) was able to stain nuclei (weakly?) of A. netrii with lactophenol-cotton blue and confirmed Dangeard's earlier reports. Moorman (1976) also reported nucleoli in her study of mitosis in an unidentified species of Ancylistes. From these limited reports, it appears that Ancylistes is most similar to Conidiobolus in terms of karyology (Humber pers. comm.)

Two nonentomogenous fungi, Completozia complens (Humber pers. comm.) and Entomophthora vermicola, possess the heterochromatic nuclei lacking central nucleoli typical of Entomophthora Fresenius.

#### 4. PRIMARY SPOROPHORES.

##### Spore Number.

Most entomogenous species produce only one spore per sporophore. Species of the entomogenous genus Erynia Nowakowski, while having apically branched sporophores, still produce only one terminal spore per branch. The nonentomogenous members, however, can be divided into two groups. Single-spored sporophores are found in Ancylistes, Completozia, and Macrobiotophthora Reukauf. Pleuri- or multispored sporophores are found in Meristacrum, Tabanomyces Couch et al., Zygnemomyces Miura and Ballocephala.

The number of spores in the multispored genera is actually quite variable (see Table 3). Ballocephala has two to 80 spores per sporophore, with most of this range attributable to variation between individual sporophores of B. sphaerospora. Similarly, Meristacrum asterospermum usually produces five to 15 spores (Drechsler 1940) but was found to produce as few as two (Davidson and Barron 1973).

### Sporophore Septation and Spore Development.

Ballocephala produces sporophores with crosswalls at the base of lateral sporiferous branchlets. The main axis of the sporophore remains nonseptate, the spores are formed terminally, and then are pushed aside as the sporophore continues to elongate. Thus spores are formed and mature in acropetal succession. Acropetal spore formation is also observed in Zygnemomyces echinulatus and Meristacrum pendulatum (Figs. 1-2).

In Meristacrum asterospermum and Tabanomyces milkoi the sporophores become transversely septate, delimiting separate cells, each of which produces a single spore. Septum formation, and hence spore maturation, is basipetal.

### 5. PRIMARY SPORE DISCHARGE MECHANISM.

Ingold (1934, 1971) distinguished three types of spore discharge in the Entomophthorales: papilla-eversion (Conidiobolus), sporophore cannon (Entomophthora), and sporophore rocket (Basidiobolus). The method of spore discharge found in Ballocephala (see below) should be recognized as a fourth type, and fungi that have lost spore discharge could be placed in a fifth category.

The basic, and putative ancestral method of spore discharge (papilla-eversion) involves the separation of the wall layers of a columella which projects into the spore. The domeshaped columella that remains (more or less intact) after spore discharge and the everted conical or rounded papilla at the spore base are diagnostic for this release mechanism. Ancylistes, Completozia, and Entomophthora vermicola (with simple sporophores), Tabanomyces milkoi and Meristacrum asterospermum (with septate sporophores) have this type of spore discharge. The method of spore discharge was not seen in the "Conidiobolus-like fungus" (Castaner 1968) or Macrobotophthora vimariensis, but can be reasonably inferred from their spore shape. All other spore discharge mechanisms are modifications of this basic method.

The second type involves a sporophore having a more or less swollen apex, and which ruptures just below the spore. In Entomophthora s. str., the spore is campanulate, has a flat base, and is carried away in a stream of sap shot from the collapsing sporophore. It should be noted that in Entomophthora muscae (Cohn) Fresenius, the secondary spores are discharged by the papilla eversion method.

The third discharge mechanism, found in Basidiobolus, involves the rupture of the base of a subspore swelling. This swelling tapers apically to a point forming a minute columella within the spore. The spore rockets away as the swelling expels fluid from its torn end, and lands with or without the remnants of the vesicle still attached to the everted spore base. The claim that this is a two-stage rocket is probably more fanciful than accurate, as the decrease in turgor pressure within the sporophore must be accompanied by the simultaneous release of spore turgor by the eversion of the papilla.

TABLE 4.  
SPOROPOHORE AND SECONDARY SPORE CHARACTERISTICS IN THE  
NONENTOMOGENOUS ENTOMOPHTHORALES.

SPECIES	SPOROPOHORE		septr	SUBSPORE CELL		2° SPORES	
	length	width		length	width	replc	disch
<u>Ancylistes</u>							
<u>closterii</u>		3-7.5	-	-	-	++	+
<u>pfeifferi</u>		4-7	-	-	-	+	+
<u>netrii</u>	25-100 x	8	-	-	-	+	+
<u>Completozia</u>							
<u>complens</u>	60-80	?	-	-	-	+	?
<u>Macrobiotophthora</u>							
<u>vimariensis</u>		4-5	-	-	-	+	-
<u>vermicola</u>	27-50 x	6-8	-	-	-	+	-
Castaner (1968)	<60	x1.5-3	-	-	-	+	+
Amin & Web. (1980)	<60-90 x	?	-	-	-	+	+
<u>Meristacrum</u>							
<u>asterospermum</u> †	200-500x6-9(3-5)		+(S)	-	-	+	-
<u>asterospermum</u> °	60-500x5-9(3-5)		+(S,U)	-	-	+	-
<u>milkoii</u>	90-200x7-8(4-6*)		+(U)	-	-	+	-
<u>Zygnemomyces</u>							
<u>echinulatus</u>	100-750x2.7-5.7		-	1.5-3 x	.5-1.1	-	-
<u>pendulatus</u>	18- 71x2-3		-	1-3		-	-
<u>Ballocephala</u>							
<u>sphaerospora</u>	50-175x4-5		-	4-7 x	3-4.5	-	-
<u>verrucospora</u>	50-150x5-7		-	5-7 x	5-7	-	-
<u>pedicellata</u>	33- 73		-	2.1 x	1.6-2.6	-	-
					(1.1-1.6)		

All measurements in  $\mu\text{m}$ .

\* measured from published illustrations S=Spiralled sporophores

† Drechsler (1941)

° Davidson and Barron (1973)

++=produces 2°+ 3° spores

\*\*=produces microspores

§(narrowest width)

The sporophore discharge mechanism found in Ballocephala constitutes a fourth type. All species of Ballocephala have spherical spores lacking basal modifications, but are subtended by a special cell (separated from the sporophore by a crosswall) whose rupture discharges the spore. Drechsler (1951) proposed that this cell was, in fact, the undischarged primary spore which produces a premature secondary spore, a hypothesis which is consistent with the basic developmental patterns of the Entomophthorales. In B. sphaerospora and B. verrucospora, the spore bearing cells are utriculate, asymmetrical, curved upwards, and as large as the spore (Drechsler 1941, Richardson 1970). Ballocephala pedicellata has ovoid to broadly obpyriform pedicels which are much smaller than the spores. Spore discharge in this species is likely, although the evidence is circumstantial (Pohlad and Bernard 1978).

Spore discharge is lacking in Zygnemomyces echinulatus and Meristacrum pendulatum. In both species, the apex of the sporophore gives rise to a terminal spore lacking basal modifications, and then proliferates sympodially. The resulting pedicels are not delimited by a crosswall, although they may become devoid of cytoplasm. Thus, they are of distinctly different origin than the sporiferous cells of Ballocephala.

#### 6. 'SECONDARY' SPORES.

If forcible spore discharge is a key characteristic of the Entomophthorales, so too is the ability of the discharged spores to produce 'secondary' spores (Table 4). In almost every member of the order, primary spores that land on hostile substrates can produce replicative spores which are forcibly discharged. These spores are also called repetitive, or secondary (2°), tertiary (3°), etc. spores. Exceptions to this rule are Ballocephala spp., Zygnemomyces echinulatus, and Meristacrum pendulatum.

Two additional types of 'secondary' spores have been taxonomically useful. Microspores ("multiplicative spores" Drechsler 1952) are formed and discharged from single primary spores of various species of Conidiobolus. Basidiobolus microsporus Benjamin produces elongate passively detached "microspores" by a totally unrelated method (Benjamin 1962, Tucker unpubl.). Microspores are also found in the "Conidiobolus-like fungus" (Castaner 1968) but are otherwise absent in nonentomogenous species.

Capillisporos ("capilloconidia" Remaudière and Hennebert 1980; "elongated secondary conidia" Drechsler 1955) are usually slightly thick walled, ovoid, ellipsoid (or slightly irregular in shape), without modifications of the spore base and borne on long slender sporophores ("capillary conidiophores" Thaxter 1888). The loss of spore discharge is apparently counterbalanced by the increased infective potential or likelihood of dispersal by a passing host. True capillisporos are produced only by Basidiobolus. Nondischarged spores borne on tapering sporophores, are found in Meristacrum asterospermum, Macrobotophthora vimariensis, and Entomophthora vermicola.

#### 7. RESTING SPORES.

##### Morphology and Development.

Resting spores, whose function is one of perennation rather than dispersal, are usually thick walled and formed within the vegetative mycelium. The distinction between zygospores (developing following conjugation) and azygospores (developing without conjugation) has been questioned (Humber 1981), but is here considered provisionally useful (see below). Virtually all of the nonentomogenous Entomophthorales produce resting spores of one form or another (see Table 5).

Ancylistes, as in Conidiobolus, forms zygospores after scalariform or lateral conjugation of unequal gametangia

TABLE 5.  
RESTING SPORE CHARACTERISTICS OF THE  
NONENTOMOGENOUS ENTOMOPHTHORALES.

SPECIES	ZYGOSPORANGIUM			ZYGOSPORE / AZYGOSPORE			
	con	form	length width	shape	color	orn	diameter
<u>Ancylistes</u>							
<u>closterii</u>	U	GB	APPRESSED	SPH	BRN	none	14.5-20
<u>pfeifferi</u>	U	G	30-40	SPH	BRN	none	18.5-22
<u>netrii</u>	U	CT	APPRESSED	SPH	?	none	19-26
<u>Completozia</u>							
<u>complens</u>	E?	GB	APPRESSED	SPH	-	none	17-33*
<u>Macrobotophthora</u>							
<u>vimariensis</u>	-	-	-	-	-	-	-
<u>vermicola</u>	E	CT	APPRESSED	DDC	-	none	19-20
Castaner (1968)	-	-	-	-	-	-	-
Amin & Web. (1980)	-	-	-	-	-	-	-
<u>Meristacrum</u>							
<u>asterospermum</u> †	-	HB	LOOSE	SPH	YEL	UND	20
<u>asterospermum</u> *	-	HB	LOOSE	SPH	-	UND	15-20
<u>milkoi</u>	E	G	APPRESSED	OVD	-	none	12-20x23-30
<u>Zygnemomyces</u>							
<u>echinulatus</u>	E	HB/CT	22-28*	OCT	BRN	none	16-24
<u>pendulatus</u>	?	HB	-	POL	-	none	18-24*
<u>Ballocephala</u>							
<u>sphaerospora</u>	E	HB	28-33x14-16.5	DOL	BRN	none	17-20x13-16
<u>verrucospora</u>	-	-	-	-	-	-	-
<u>pedicellata</u>	E	HB	APPRESSED	DOL	BRN	PUNC	20.6-26.6 x 17.3-18.6

All measurements in  $\mu\text{m}$ .

\*Measurements from published illustrations.

†Davidson & Barron (1973)

\*Drechsler (1940)

orn=ornamentation

PUNC=punctate

UND=Undulate

con=conjugation

E=equal gametangia

U=unequal gametangia

dev=zygosporangia devel-

ope from or within:

CT=Conjugation tube

G=Gametangium

GB=Gametangial bud

HB=Hyphal body

(color)

BRN=Brown

YEL=Yellow

(shape)

DDC=Dodecahedral

OVD=Ovoid

POL=Polygonal

SPH=Spherical

(Pfitzer 1872). The presence of numerous protrusions on the zygosporangial wall is used to separate *A. pfeifferi* from other species of the genus (Berdan 1938, Couch 1949).

*Completozia* forms one to ten (or 20) round to oval, thick walled resting spores within the enlarged cells in the central portion of the hyphal mass. (The peripheral cells of the thallus are by this time emptied by the formation of primary sporophores or infective hyphae.) Conjugation has not been observed (Atkinson 1884, 1885).

*Zygnemomyces echinulatus* forms brownish, thick walled, octangular zygospores following scalariform conjugation. The octangular shape results from the position of the zygospore in the conjugation tube between the two parental hyphal bodies (Fig. 1E). The resting spores of *Meristacrum*



pendulatum are similar in shape (Fig. 2F), but the mode of development is unknown.

Entomophthora vermicola forms zygospores after scalariform or lateral conjugation (Fig. 3K-P). At maturity, these zygospores are dodecahedral, each face with 5 (4-6) raised edges and a central depression (Fig. 3P).

Conjugation in Ballocephala has not been proven, although its occurrence was inferred by Drechsler (1951) from the presence of two slightly inflated locules at either end of the zygospore. The zygospore itself is doliform or cylindrical, brown to dark-brown in color, smooth or punctate, and is preferentially formed at reduced temperatures (5° C) (Pohlad and Bernard 1978).

Meristacrum asterospermum was described by Drechsler (1940) as forming azygospores by the rounding up of the cytoplasm of a thalloid segment, laying down of retaining walls at either end, and deposition of a new undulate or scalloped wall around the cytoplasm. The star-shaped resting spore is colorless or slightly yellowish, is about 15-20  $\mu$ m in diameter, and contains a single large oil droplet.

Finally, in Tabanomyces milkoi, uninucleate, spherical gametangia fuse in pairs with the contents of one gametangium migrating into the other and forming a smooth, colorless ovoid zygospore with a single diploid nucleus (Couch et al. 1979, Nam and Dubitskii 1977).

#### Zygospores vs. Azygospores: A Different Perspective.

Resting spores have been used for taxonomic purposes to some extent, but recent treatments of the family (Remaudière and Keller 1980, Humber 1981) have cautioned against some traditional applications of resting-spore characteristics. In particular, the distinction between zygospores and azygospores (with respect to conjugation) was discussed at great length by Humber (1981), who dismissed it for two reasons. First, the development of (a)zygospores is often difficult to follow or interpret, and hence published accounts may be misleading. This objection is valid, and the presence or absence of conjugation must be used with caution. However, the second objection, that the nuclear events of karyogamy and meiosis are of more importance to the fungus than whether conjugation occurs, poses an interesting question.

Of what importance are the sexual events of conjugation, karyogamy and meiosis to the entomophthoralean fungi? It must first be noted that all "sexual" Entomophthorales are homothallic (automictic) and homomictic (i.e. no mating types exist). Conjugation, when it occurs, is between cells of the same branch or between hyphal bodies. Secondly, since most spores and hyphal bodies are multinucleate, genetic recombination may occur somatically rather than during meiosis. There are very few species in the Entomophthorales for which evidence of meiosis exists (exceptions include Conidiobolus thromboides Drechsler = Entomophthora virulenta Hall & Dunn, Tabanomyces milkoi). The lack of data on basic aspects of sexual events and genetics is a

great hindrance in attempts to assess the importance of zygospores or to understand evolution within the order.

Retaining the ability to coevolve with host organisms is likely to be important to these fungi, but it is also apparent that the presence or absence of conjugation or of karyogamy and meiosis do not seem to be as critical. Perennation and infective ability, however, continue to be important as a basic requirement of the entomophthoralean life cycle. The formation of the resting spore, whether induced by conjugation or not, involves the phenotypic expression of extensive portions of the genome, and thus the shape, size, or ornamentation of resting spores may ultimately be of more taxonomic significance than nuclear events.

## 8. SUMMARY OF TAXONOMIC CHARACTERS.

From the preceding discussion of morphological characters in the nonentomogenous Entomophthorales, it should be clear that character diversity within the order is greater than that encompassed by the entomogenous members alone. Nevertheless, the three characters which Humber (1981) proposed as most valuable in delimiting genera: "nuclear number and nature," "sporophore branching," and "method of spore discharge," apply as well to the nonentomogenous genera, and the assessment of these characters needs only minor revision.

1. Spore karyology, i.e. nuclear morphology and number per primary spore, remains important in distinguishing natural groups (i.e. families) within the Entomophthorales (see §IV.3). This may be of practical value for separating morphologically similar genera (e.g. Conidiobolus from Entomophaga; or Ancylistes from Completozia).

2. Spore discharge is virtually universal within the order and thus is presumably an ancestral character. The spore discharge "theme" has five variations: papilla-eversion (Entomophthoraceae, Ancylistaceae), sporophore-cannon (Entomophthoraceae), Ballocephala-type (Ancylistaceae), and sporophore-rocket (Basidiobolaceae), plus the loss of discharge (Entomophthoraceae [Massospora], Ancylistaceae [Zygnemomyces]).

3. Sporophore architecture now includes the presence or absence of sporiferous branchlets or transverse septations as well as branching of the sporophore. In addition, the mode of spore formation (basipetal, acropetal, or terminal) which is linked to sporophore septation, can be used to distinguish genera. It is presumed that the unispored sporophore is ancestral, and that multispored sporophores are derived.

4. Zygospore morphology, which Humber (1981) discounted but actually used as a secondary characteristic to delimit Triplosporium (Thaxter) Batko, is most appropriately used for delimitation of species or subgenera.

## III. GENERIC TAXONOMY AND REVISIONS.

ANCYLISTES Pfitzer,

Monatsb. Königl. Preuss. Akad. Wiss. Berlin. 396. 1872.

Type species: Ancylistes closterii Pfitzer, Monatsb. Königl. Preuss. Akad. Wiss. Berlin. 396. 1872.

## Other species:

Ancylistes pfeifferi Beck, Verh. Zool.-Bot. Ges. Wien 46: 233. 1896.

Ancylistes netrii Couch, J. Elisha Mitchell Sci. Soc. 30: 251. 1949. Validation of this species is here accomplished with the publication of the following Latin diagnosis:

Hyphae asumentes primum aseptatae 2.2-4.8  $\mu$ m crassae, tum ramosae et septatae, cellulis 15-30 X 8-15  $\mu$ m; hyphae exitibus unica in cellula una factae, 2-4  $\mu$ m crassae, parietem hospitis juxta tumidae usque ad 4-9  $\mu$ m emergentes et hyphas externas facientes, quae hospitem proximum obnoxium inficunt, aut si ex aqua emergunt sporophora 25-100  $\mu$ m faciunt; sporae primigenae 16-25  $\mu$ m crassae papillis conicis; zygosporae intra hospitem inter aliquot hyphas longitudinales seriales formatae, ut videtur conjugatione cellulis duabus hyphis oppositis, zygosporis intra tubum conjugentem, sphaericus vel subsphaericis 19-26  $\mu$ m crassis. Hospes: Netrium (Desmidiaceae).

Ancylistes is in many ways, similar to Conidiobolus, especially in spore shape and karyology (see §IV.2, IV.3). The species are divided on the basis of host (saccoderm or placoderm desmid algae), size of the primary spore, and zygosporangial morphology. See Berdan (1938) and Couch (1949) for a treatment of this genus.

BALLOCEPHALA Drechsler,

Bull. Torrey Bot. Club 78: 199. 1951.

Type species: Ballocephala sphaerospora Drechsler, Bull. Torrey Bot. Club 78: 199. 1951.

## Other species:

Ballocephala verrucospora Richardson, Trans. Brit. Mycol. Soc. 55: 308. 1970.

Ballocephala pedicellata Pohlád & Bernard, Mycologia 70: 131. 1978.

This genus, found only in tardigrades, is unique in the manner in which the spores are formed and discharged. As previously mentioned (see §II.4, II.5), the discharged spore may actually be a secondary spore developing neotenuously from the undischarged primary spore, which is present in the form of a utriculate vesicle or a reduced pedicel. The species are separated on the basis of spore ornamentation and the morphology of the sporiferous cell.

COMPLETORIA Lohde,

Tagebl. Versamml. Deutsch. Naturf. Aertze 47: 206. 1874.

Type species: Completoria complens Lohde, Tagebl. Versamml. Deutsch. Naturf. Aertze 47: 206. 1874.

This rare parasite of fern prothalli has been reported only twice since the original description (Leitgeb 1881, Atkinson 1884, 1885). The presence of large stainable nuclei lacking central nucleoli and a thallus composed of short hyphal branches indicate a distant relationship with most other nonentomogenous Entomophthorales. It is placed in the Entomophthoraceae (see §IV.3).

MERISTACRUM Drechsler emend. Tucker & Humber,  
J. Wash. Acad. Sci. 30: 250. 1940.

Type species: Meristacrum asterospermum Drechsler, J. Wash. Acad. Sci. 30: 251. 1940.

Vegetative hyphae developing within living animals, simple to somewhat branched, at first continuous, later dividing into disjointed segments which put forth a sporophore into the air, the terminal portion dividing basipetally, forming several to few cells, each of which produces a single spore forcibly discharged by papilla-eversion; secondary spores replicative or passively detached; resting spores azygospores formed from hyphal segments or zygospores formed from conjugation of spherical uninucleate gametangia.

## Other species:

Meristacrum milkoi (Dudka & Koval) Humber, Mycotaxon 13: 232. 1981.

Basionym: Coelomomyces milkoi Dudka & Koval apud Dudka, Koval & Andreeva, Novitates Systematicae Plantarum non Vascularum 10: 89. 1973.

Synonym: Pseudocoelomomyces milkoi Nam and Dubitskii, Inst. Zool. Alma Ata, Acad. Sci. Kazakh. SSR (VINITI no. 1309-77 Dep.). 1977. (Lacking Latin diagnosis.)

Synonym: Tabanomyces milkoi (Dudka & Koval) Couch, Andreeva, Laird, & Nolan, Proc. Natl. Acad. Sci. (U.S.A.) 76: 2300. 1979. (Deficient basionym cit.)

Tabanomyces milkoi was transferred to Meristacrum by Humber (1981) because of the similarity in their sporophore development. In M. asterospermum and M. milkoi, transverse septa are layed down in basipetal succession, with each of the newly formed cells producing a spore which is discharged by papilla-eversion. This mode of sporophore development is not found elsewhere in the Entomophthorales, and is the single most important character in delimiting the genus.

The difference in host organism is of questionable value at the generic level, and the non-helicoid sporophore

of M. milkoi is of no significance since Davidson and Barron (1973) observed a similar lack of spiralling in sporophores emerging from resting spores of M. asterospermum.

There are, however, three differences between these two species which may be used to divide Meristacrum into subgenera when a fuller understanding of these and other as yet undiscovered species is obtained.

<u>Character</u>	<u>M. asterospermum</u>	<u>M. milkoi</u>
1) Primary spore	obovoid, truncate base	globose basal papilla
2) Secondary spore	obovoid passively detached	globose replicative
3) Resting spores	azygospores spherical, undulate conjugation (-)	zygospores ovoid, smooth conjugation (+)

The resting spore characteristics are the most significant.

ZYGNEMOMYCES Miura emend.,  
Rep. Tottori Mycol. Inst. (Japan) 10: 520. 1977.

Type species: Zygnemomyces echinulatus Miura,  
Rep. Tottori Mycol. Inst. (Japan) 10: 520. 1977.

Vegetative hyphae developing within living animal, unsegmented, giving rise to sporophores; sporophores nonseptate, bearing spores on pedicels formed from the sporophore apex, proliferating sympodially at the apex or subapically; primary spores globose, echinulate, produced acropetally, not forcibly discharged; secondary spores absent; zygospores thick walled, forming after lateral or scalariform conjugation.

Other species:

ZYGNEMOMYCES PENDULATUS (McCulloch) comb. nov.,  
Basionym: Meristacrum pendulatum McCulloch, Trans.  
Brit. Mycol. Soc. 68: 175. 1977.

Body of the infested nematode containing unsegmented allantoid thalli, 2-5  $\mu$ m wide; sporophores erect, unsegmented, 18-71  $\mu$ m long, after penetrating the host cuticle forming an apical hook upon which a single terminal spore develops, growth continuing by sympodial proliferation; sterigmata formed from the sporophore hook, becoming emptied of cytoplasm, 2-3.5  $\mu$ m wide proximally, tapering to 0.8-1.2  $\mu$ m wide at the spore; spore spherical, echinulate, 5-8  $\mu$ m in diameter, adhering to the nematode when detached; resting spores 18-24  $\mu$ m, thick walled, with a single large oil drop, found within dead nematodes.

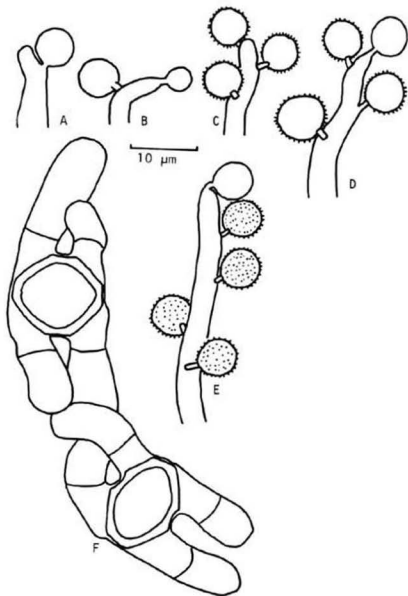


Fig. 1. ZYGNEMOMYCES ECHINULATUS Miura.

(A-E) Stages in sporophore development, showing acropetal maturation of the spores; (F) zygospores formed following scalariform conjugation. Redrawn from Miura (1973). Fig. 2E represents a portion of the iconotypus. Bar=10µm.

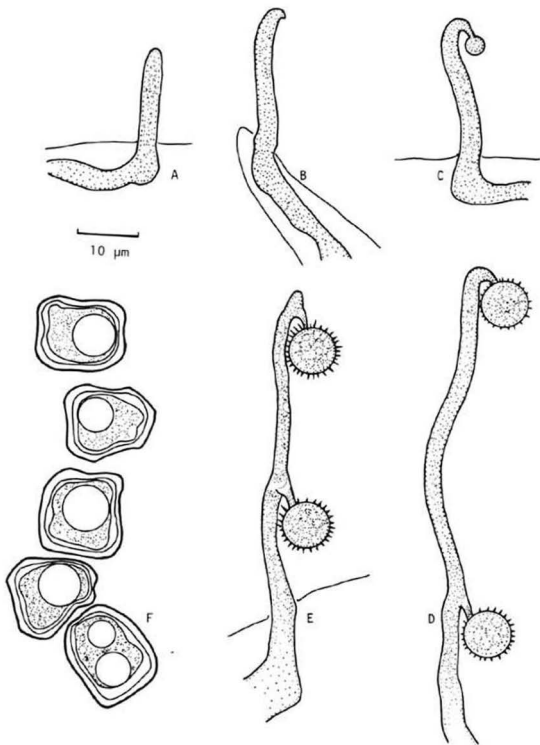


Fig. 2. ZYGNEMOMYCES PENDULATUS (McCulloch) Tucker.

(A-E) Stages in sporophore development, showing the apical hook that becomes the pedicel, and continued growth by sympodial proliferation; (D-E) mature echinulate spores, the pedicel making an acute angle with the sporophore base; (F) zygospores within the nematode. Drawn from type slide. Bar=10μm.

Zygnemomyces was established by Miura (1973) who distinguished Z. echinulatus from Ballocephala and Meristacrum by three characters: echinulate spores (though this is no longer valid with the discovery of Ballocephala verrucospora by Richards [1970]), spores borne on pedicels (and hence not discharged), and octangular zygosporangia formed by scalariform conjugation. The first two characters also are found in Z. pendulatus, and a careful reexamination of spore development has shown that both species have sympodially proliferating sporophores (Figs. 1 & 2). The two species can be distinguished on the basis of sporophore size (Table 4), spore number (Table 3), and orientation of the pedicel.

The three multisporous genera: Meristacrum, Ballocephala, and Zygnemomyces, as here treated are coherent genera, and each is quite easily distinguished from the others. Meristacrum, with basipetally septate sporophores contrasts with the nonseptate sporophores of Ballocephala and Zygnemomyces. While spores develop acropetally in both of these genera, the manner in which the spores are formed and discharged (i.e., borne on propulsive sporiferous cells vs. pedicels formed from the sporophore apex) is significantly different.

MACROBIOTOPHTHORA Reukauf emend.,

Centralbl. Bakt. Parasit. Infekt. Abt. 1 63: 390. 1912.

Type species: Macrobiotophthora vimariensis Reukauf. Centralbl. Bakt. Parasit. Infekt. Abt. 1 63: 390. 1912.

Vegetative thallus developing internally within host, giving rise to external hyphae and sporophores on which single terminal spores are borne; spores obovate, flat based, forming secondary spores or germinating vegetatively; conjugation scalariform or lateral forming zygosporangia, resting spores absent, or producing chlamydozoospores.

This genus was established by Reukauf (1912) for M. vimariensis, a fungus which he found parasitizing Hypsibius dujardini (Doyère) (= Macrobiotis lacustris Duj.) living near a spring in Belvederer Parks in Weimar, Germany. This fungus produced hyphal bodies which digested the fat bodies of the tardigrade and then gave rise to a multitude of sterile aseptate hyphae which penetrated the cuticle. Primary spores were obovoid, uninucleate and were produced terminally. These spores either germinated directly or gave rise to secondary spores on slender sporophores. While no other fungi similar to M. vimariensis have been isolated from tardigrades, the following nematode parasite is sufficiently similar to warrant transfer to this genus.

Other species:



MACROBIOTOPHTHORA VERMICOLA (McCulloch), comb. nov.,

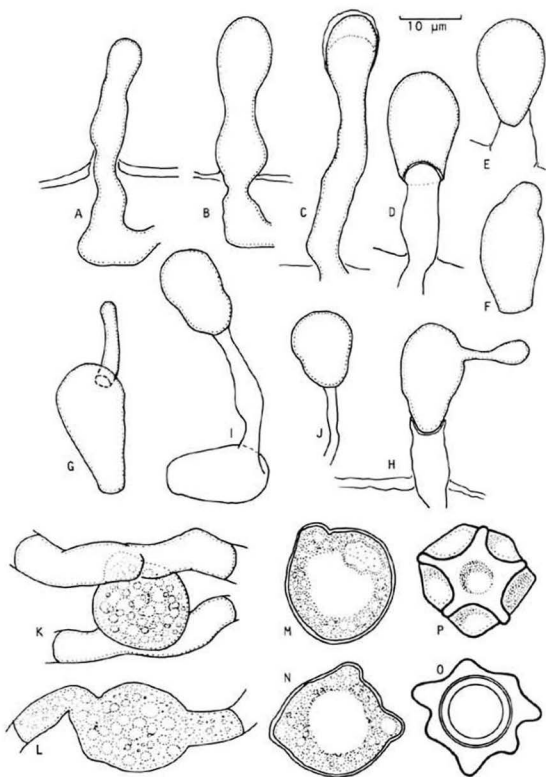
Basionym: Entomophthora vermicola McCulloch. Trans. Brit. Mycol. Soc. 68: 173. (Figs. 1-2). 1977.

Body of infested nematode filled with nonseptate hyphae, 5-7  $\mu\text{m}$  in diameter, developing erect hyphae which penetrate the nematode cuticle; external hyphae hyaline, unsegmented, flexuous (40-) 110-160 x 3-6  $\mu\text{m}$ ; sporophores 27-50 x 6-8  $\mu\text{m}$ , straight or bent at the point of emergence (110-120°), unbranched (branched according to McCulloch); primary spores terminal, obovoid, 16-22 x 9-14  $\mu\text{m}$  (rarely to 30 x 16  $\mu\text{m}$ ), pleurinuclate and unitunicate, discharged at maturity, adhering to the cuticle of a passing nematode and initiating new infections; secondary spores obovoid medially constricted, nonpapillate, 14.4-15.5  $\mu\text{m}$  long, 9-13.3  $\mu\text{m}$  in diameter narrowing at a neck to 7.4-8.9  $\mu\text{m}$ ; secondary sporophores 17-20  $\mu\text{m}$  long, 3.5-4.5  $\mu\text{m}$  at base, tapering to 1.8-2.2  $\mu\text{m}$  at spore; zygospores 17-22  $\mu\text{m}$ , dodecahedroid, faces centrally depressed with 4-6 edges.

Of the three type slides, only the one containing the nematode illustrated in McCulloch (1977: Fig. 1) remains intact (Figs. 3A-J). External hyphae are present, but these are not the morphologically modified cystidia found in species of Erynia (Remaudière and Hennebert 1980, Humber 1981). Figure 3C shows the appearance of several of the developing spores with a thin, hyaline outer wall layer separated from the spore wall proper, and the retraction of the cytoplasm from the spore apex. While the separated wall resembles the image seen in spores with bitunicate walls, these effects are probably due to the lactophenol mounting medium. The secondary spores are obovoid and medially constricted, with a distinct neck below a more globose region (Fig. 3H-J). A basal papilla is lacking making secondary spore discharge unlikely. The sporophores on which they are borne taper to a narrow point of attachment, but they are not the true capillary sporophores of other genera.

Macrobiotophthora vermicola was originally placed in Entomophthora, a genus to which it is no longer referable. Living material of this species obtained from E. Bernard, permitted additional characterization of the species, and the following observations are in conflict with the original description. The primary spores contain 4-9 Entomophthora-type nuclei and are forcibly discharged by papilla eversion. Secondary spores are medially constricted and passively detached. Dodecahedral zygospores are formed following scalariform or lateral conjugation.

Two Conidiobolus-like fungi reported from nematodes (Castaner 1968, Amin and Webster 1980) are probably species of Macrobiotophthora. However, nuclear morphology and number are unspecified, making placement of these two fungi provisional. The method of thallus and primary spore formation in all three nematophagous fungi is similar, but differences include the absence of zygospores (although these will probably be found), forcible discharge of secondary spores, production of microspores (?), and variation in



spore size (see Tables 2-5). Additional reports of parasites on terricolous animals may increase further the size of Macrobotophthora by at least two, if not more species.

#### IV. FAMILIES OF THE ENTOMOPHTHORALES.

At present, the order is variously divided, with one family, Entomophthoraceae (Waterhouse 1973); two families, Entomophthoraceae and Basidiobolaceae (Alexopoulos and Mims 1979, Benjamin 1979); or three families, Entomophthoraceae, Ancylistaceae, and Basidiobolaceae (Ubrizsy and Vörös 1966, Batko 1974). Although three characters: karyology, spore discharge mechanism, and conjugation might logically be used to delimit these families, only karyology results in a division consistent with current views of the order.

1. Separation of the genera on the basis of spore discharge method would result in four groups. The basic papilla-eversion method has been modified in Entomophthora to form a sporophore-cannon. The significance of this is reduced, since the secondary spores of E. muscae are still dispersed by the papilla-eversion method. Similarly, Basidiobolus has a vestigial spore papilla, although the propulsive force is provided by the rupture of a subsore swelling.

Less obvious is the origin of the Ballocephala discharge vesicle. The suggestion that the vesicle is homologous with the primary spore (Drechsler 1951), and gives rise directly to sessile secondary spores that (like capillispores) are not dispersed, is consistent with the basic developmental patterns of the Entomophthorales. It also should be noted that spore discharge was lost independently by Massospora and Zygnemomyces. From the above observations, it can be concluded that spore discharge mechanism cannot be used alone for family delimitation.

2. Details of gametangial conjugation and resting spore morphology are also possible criteria for family delimitation. Zygosporic characteristics have proven to be useful and conservative within the other orders of the Zygomycotina (Benjamin 1979). The Basidiobolaceae, with its beaked gametangia, is distinct from all other members of the order. The tendency of Conidiobolus and Ancylistes to form zygosporic in line with the unequal gametangia

Fig. 3. MACROBIOTOPHTHORA VERMICOLA (McCulloch) Tucker.

(A-H) Spores and sporophores drawn from the type slide. (A-B) Development of primary sporophores; (C) sporophore with retracted cytoplasm and separated outer wall layer; (D) primary spore with distinct columella; (E) spore with everted papilla; (F) germinating primary spore; (G-J) development of secondary spores, (I-J) medially constricted obovoid secondary spores on tapering secondary sporophore. (K-P) Conjugation and zygosporic from living culture. Scleriform (K) and lateral (L) conjugation; (M-N) developing zygosporic; Mature zygosporic in optical section (O) and surface aspect (P). Bar=10µm.

contrasts with the laterally budded zygospores of Entomophthora. Yet division of the order into families on this character alone is problematical due to the difficulties in interpreting zygospore development in many species, and the absence of conjugation in others. Until more research is done on Entomophthorales, the utility of zygospore characters will remain suspect.

3. Karyology is here regarded as the most useful character, and three distinct lines can be delimited within the Entomophthorales: Basidiobolus with large nuclei with central nucleoli; Entomophthora, Entomophaga, Erynia, Strongwellsea Datko & Weiser emend. Humber, Massospora, Completozia (Humber pers. comm.), and Macrobiotophthora have small, readily staining nuclei with heterochromatin but without a central nucleolus; and Ancylistes, Conidiobolus, Meristacrum, Ballocephala (?), and Zygnemomyces (?) have small, poorly staining nuclei with a central nucleolus. The elevation of these three groups to family status is not only consistent with the currently accepted segregation of the Basidiobolaceae, but also unites those genera which have similar spore discharge and zygospore characteristics and provides a logical framework for the perception of evolutionary trends within the Entomophthorales as a whole.

#### V. CONCLUDING REMARKS.

The taxonomic revisions proposed here are based upon the evaluation of basic morphological characteristics. Although important, the host organism is deemphasized at the generic level. While research in the Entomophthorales has been and probably will continue to be centered upon the parasites of insects, the nonentomogenous fungi must not be overlooked. It is hoped that as new reports of nonentomogenous fungi are forthcoming, they will include full descriptions of all aspects of nuclear morphology and number, method of spore discharge, sporophore architecture, zygospore development and morphology, and thallus characteristics. Only then will a fuller understanding of the order as a whole be obtained.

#### ACKNOWLEDGMENTS.

I would like to thank R. A. Humber and R. K. Benjamin for reviewing this article, and for their many comments, criticisms, and encouragements; J. Ammirati for reading the manuscript; and D. Stuntz for correcting the Latin diagnosis and proofreading the final draft. Types were lent by the following institutions: Commonwealth Mycological Institute (CMI) and Plant Pathology Herbarium, Dept. of Primary Industries, Queensland (BRIP). E. Bernard kindly supplied the new isolate of Macrobiotophthora vermicola.



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## ERYNIA (ZYGOMYCETES: ENTOMOPHTHORALES):

## EMENDATION, SYNONYMY, AND TRANSFERS

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## SUMMARY

The emended sense of *Erynia* Nowakowski (Entomophthorales: Entomophthoraceae) is limited to species having uninucleate, bitunicate primary conidia borne on (digitately and apically) branched conidiophores and forcibly discharged by the eversion of the basal papilla. This emendation specifically (1) rejects a separation of *Zoophthora* Batko from *Erynia* based on the presence of capilliconidia or any other criterion, (2) rejects any synonymy of *Strongwellsea* Batko & Weiser emend. Humber with *Erynia*, and (3) excludes from *Erynia* any species having conidia which are multinucleate, unitunicate, or borne on simple (or rarely or basally branched) conidiophores. *Zoophthora* Batko is rejected as a later synonym of *Erynia* Nowak., and the remaining species of *Zoophthora* not previously placed in *Erynia* are transferred. All recognized species of *Erynia* sensu Humber & Ben-Ze'ev are cited.

The recognition of two genera, *Zoophthora* Batko (1964a) and *Erynia* Nowakowski (1881), separated principally by the formation of capilliconidia (secondary conidia formed atop capillary conidiophores) by Remaudière and Hennebert (1980) has raised a problem in synonymies (Humber 1981a): If the type species of *Zoophthora*, *Z. radicans* (Brefeld) Batko (=



*Entomophthora sphaerosperma* Fres. sensu Thaxter 1888), and the type species of *Erynia*, *E. ovispora* (Nowakowski) Nowakowski, are accepted on any basis to be in distinct genera, then both of these generic names may stand. If, however, one accepts Batko's sense of *Zoophthora* for all species with uninucleate, bitunicate conidia borne on branched conidiophores (Batko 1964a-b, 1966a-b, 1974; Humber 1981a-b, 1982; Ben-Ze'ev and Kenneth 1981a-b, 1982a-b), then both of these species must be in the same genus. Further, the International Code of Botanical Nomenclature (ICBN) requires that Batko should have adopted the older generic name, *Erynia*, rather than propose a new name for this large group of species.

Humber (1981a-b; 1982), Ben-Ze'ev (1980), and Ben-Ze'ev and Kenneth (1981a-b, 1982a-b) find no basis for the separate and simultaneous usage of *Zoophthora* and *Erynia* espoused by Remaudière and Hennebert (1980) and Remaudière and Keller (1980). Among the possible resolutions of this synonymy, the only one that is both in accord with the ICBN and the prior transfer of most *Zoophthora* species to *Erynia* (Remaudière and Hennebert 1980; Humber 1981a-b) is now to take up *Erynia* Nowakowski as the correct name of the genus which includes *Entomophthora radicans* Brefeld. Accordingly, we present an emended circumscription for *Erynia*, and regard *Zoophthora* to be a younger synonym.

**ERYNIA** Nowakowski emend. Humber & Ben-Ze'ev, emend. nov.

- ≡ *Erynia* Nowakowski, 1881, *Dzienn. III Zjazdu Lek. Przynr. Polak. Kraków.*, *Sekc. Bot.* 6, 67-68.
- = *Zoophthora* Batko, 1964, *Bull. Acad. Polon. Sci. Sér. Sci. Biol.* 12, 323.

VEGETATIVE STRUCTURES usually hyphal bodies or mycelium, but exact form depends upon stage of development. NUCLEI easily observed, 4.5-15  $\mu$ m diameter; without a prominent central nucleolus; filled with conspicuous heterochromatic threads or granules. CONIDIOPHORES apically branched, forming a (usually digitate) cluster of conidiogenous cells; each branch basally septate, each conidiogenous cell usually uninucleate, producing a single apical conidium; some conidiophores unbranched, producing a single terminal conidiogenous cell and one conidium. PRIMARY CONIDIA uninucleate, bitunicate (with a separable outer wall layer except over the basal papilla); shape variable but usually ovoid, clavate, turbi-

nate, or elongate, radially symmetrical or curved; papilla centered on spore axis or displaced laterally; forcibly discharged by eversion of the papilla against the conidiophore. SECONDARY CONIDIA more or less similar to primary conidia (or with short radiate arms), formed singly on a short conidiophore arising from a primary conidium and forcibly discharged by eversion of the papilla or else amygdaliform to elongate, clavate, falcate, or lanceolate, usually curved, and borne on an extended, thin capillary conidiophore arising from a primary or secondary conidium. RESTING SPORES usually globose with two thickened wall layers; epispore colorless or variously colored, smooth or variously ornamented; budded laterally or terminally from parental hyphal body whether as zygospores or azygospores. RHIZOIDS present in most species, either (1) hypha-like, simple or branched, solitary or aggregated into pseudorhizomorphs, terminating in more or less branched (but only rarely discoid) holdfast of (2) stout, unbranched, solitary or loosely fasciculate (but not aggregated in pseudorhizomorphs), terminating in a richly branched discoid or irregularly expanded holdfast; rhizoids may not form when resting spores are produced. CYSTIDIA absent in most species; simple, usually aseptate, spear-like, extending slightly above level of conidiophores or else thick and columnar, aseptate, usually branching apically, extending far beyond level of conidiophores; cystidia usually absent when resting spores are formed in the host.

**TYPE SPECIES:** *Erynia ovispora* (Nowakowski) Nowakowski, 1881, *Dzienn. III Zjazdów Lek. Przycz. Polak. Kraków.*, *Sekc. Bot.* 6, 67-68. Basionym: *Entomophthora ovispora* Nowakowski, 1877, *Bot. Zeitg. (Leipzig)* 35, 20.

This emendation rejects *Zoophthora* as a separate genus for species forming passively detached secondary capilliconidia as advocated by Remaudière and Hennebert (1980). It also rejects a definition of *Erynia* based on conidial morphology (Remaudière and Hennebert 1980; Remaudière and Keller 1980), thereby excluding *Erynia caroliniana* (Thax.) Rem. & Henneb. (with unitunicate, plurinucleate conidia on simple conidiophores) and restoring *Strongwellsea* Batko & Weiser emend. Humber (with bitunicate, uninucleate conidia on unvaryingly simple conidiophores; cf. Remaudière and Keller 1980, Humber 1981a, 1982). This emendation also acknowledges the formation of multiradiate secondary conidia by some riparian species (Descals et al. 1981).

The formal adoption of *Erynia* as the nomenclaturally correct name for the genus circumscribed above requires the transfer of all remaining names placed in *Zoophthora* but not yet formally acknowledged as species of *Erynia*.

- ERYNIA APHIDIS (Hoffmann in Fresenius) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora aphidis* Hoffmann in Fresenius, 1856, *Abhandl. Senckenberg. naturf. Ges.* 2: 208 emend. Remaudière & Hennebert, 1980, *Mycotaxon* 11: 290, NON *Entomophthora aphidis* Hoffm. in Fres. sensu Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.* 4: 175.
- ERYNIA CANADENSIS (MacLeod, Tyrrell, & Soper) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora canadensis* MacLeod, Tyrrell, & Soper, 1979, *Canad. J. Bot.* 57: 2664.
- ERYNIA CRASSITUNICATA (Keller) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Zoophthora crassitunicata* Keller, 1980, *Sydowia Ann. Mycol., Ser. II*, 33: 170.
- ERYNIA COLEOPTERORUM (Petch) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora coleopterorum* Petch, 1932, *Trans. Brit. Mycol. Soc.* 17: 172.
- ERYNIA CRUSTOSA (MacLeod & Tyrrell) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora crustosa* MacLeod & Tyrrell, 1979, *Canad. Entomol.* 111: 1138.
- ERYNIA ELATERIDIPHAGA (Turian) Humber, Ben-Ze'ev, & Kenneth, comb. nov. BASIONYM: *Entomophthora elateridiphaga* Turian, 1978, *Mitt. Schweiz. Entomol. Ges.* 51: 398.
- ERYNIA GEOMETRALIS (Thaxter) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Empusa (Entomophthora) geometralis* Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.* 4: 170.
- ERYNIA HENRICI (Molliard) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora henrici* Molliard, 1918, *Compt. Rend. Hebd. Séances Acad. Sci. Paris* 167: 958.
- ERYNIA JACZEWSKII (Zaprometov in Jaczewski & Jaczewski) Humber, comb. nov. BASIONYM: *Tarichium jaczewskii* Zaprometov in Jaczewski & Jaczewski, 1931, *Opređelitel' gribov* 1: 225.
- ERYNIA LANCEOLATA (Keller) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Zoophthora lanceolata* Keller, 1980, *Sydowia Ann. Mycol., Ser. II*, 33: 133.
- ERYNIA NEBRIAE (Raunkiaer) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Entomophthora nebrae* Raunkiaer, 1892, *Bot. Tidskr.* 13: 108-111.
- ERYNIA OCCIDENTALIS (Thaxter) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Empusa (Entomophthora) occidentalis* Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.* 4: 171.
- ERYNIA ORIENTALIS (Ben-Ze'ev & Kenneth) Humber, Ben-Ze'ev, & Kenneth, comb. nov. BASIONYM: *Zoophthora orientalis* Ben-Ze'ev & Kenneth, 1981, *Phytoparasitica* 9: 35.
- ERYNIA PHALLOIDES (Batko) Humber & Ben-Ze'ev, comb. nov. BASIONYM: *Zoophthora phalloides* Batko, 1966, *Acta Mycol.* 2: 7.
- ERYNIA PHYTONOMI (Arthur) Humber, Ben-Ze'ev, & Kenneth, comb. nov. BASIONYM: *Entomophthora phytonomi* Arthur, 1886, *Bot. Gaz. (Crawfordsville)* 11: 14.
- ERYNIA RADICANS (Brefeld) Humber, Ben-Ze'ev, & Kenneth, comb. nov. BASIONYM: *Entomophthora radicans* Brefeld, 1870, *Bot. Zeitg. (Leipzig)* 28: 186.

*Entomophthora coleopterorum* Petch (1932) is included in the above list because of the conjunction of long, narrowly oval conidia (32-44 x 8-14  $\mu\text{m}$ ), two fascicles of stout rhizoids emerging from specific points on the ventral thorax, and cystidia (Petch 1944). This set of characters occurring together is known only from *Erynia* species although it must still be determined that *E. coleopterorum* has uninucleate, bitunicate conidia and branched conidiophores. Petch (1944) regarded this species to be a probable synonym of *Entomophthora carpentieri* Giard (1888) whose description was based wholly on the unique mode of rhizoidal attachment of affected elaterid beetles. Turian (1957) identified as *E. carpentieri* a fungus he found on beetles which died head-down and were attached to the plant by two fascicles of rhizoids; he claimed this fungus produced uninucleate, globose conidia. Humber (1981a) raised doubts about Turian's interpretation and discussed the possible synonymy of *E. carpentieri* and *E. coleopterorum*. Until any extant material of these collections can be re-examined, there is no doubt that the best characterized of these collections is *E. coleopterorum*, and that this species is more certainly a species of *Erynia* than of any other entomophthoralean genus.

*Entomophthora henrici* Molliard (1918), which was described from mosquitoes (*Culex pipiens*), is accepted here as an *Erynia* species by virtue of its much branched conidiophores, presence of cystidia (which Molliard stated were also produced in culture), and of rhizoids with discoid or irregularly ramified holdfasts. It remains to be established whether the conidia of this species are uninucleate and bitunicate as may be predicted from this constellation of other characters. *Erynia henrici* resembles *E. ovispora*, but insufficient information about the morphological plasticity of either species currently exists to support the proposition by Waterhouse (1975) of their synonymy.

*Entomophthora nebriae* Raunkiaer (1892), which attacks carabid beetles (*Nebria brevicolis*), has elongate conidia (28.0-37.0 x 10.0-13.0  $\mu\text{m}$ ) borne on richly branched conidiophores. Rhizoids are present, but their morphology is not described. No secondary conidial forms or cystidia are mentioned by Raunkiaer (1892). The resting spores of this species are formed outside of the host body, and are spherical, 36-50  $\mu\text{m}$  in diameter, with a pale brown, smooth, and rather thin wall. Batko (1966b) regarded this species to belong in *Zoophthora* subg. *Zoophthora*.

*Zoophthora jaczewskii* (Zaprometov in Jaczewski & Jaczewski) Batko (1964b) was not discussed by Remaudière and col-

leagues in their revision of entomophthoralean taxonomy. We have been unable to obtain the literature to confirm either the nomenclatural validity of *Tarichium jaczewskii* Zaprometov in Jaczewski & Jaczewski (1931; see also MacLeod and Müller-Kögler 1970) or the appropriateness of Batko's acceptance of *Entomophthora zabrii* Rozsypal (1951; an invalidly published *nomen nudum*) as the conidial state of *T. jaczewskii*. One of the present authors (RAH) feels that it is not unreasonable to accept both Batko's acknowledgement of *T. jaczewskii* to be validly published and of his synonymization of *E. zabrii* with this species.

Those species previously described as or transferred to *Erynia* and accepted according to the above emendation include the following:

- Erynia americana* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia aquatica* (Anderson & Ringo ex Anderson & Anagnostakis) Humber (1981a) non *Erynia aquatica* (Anderson & Ringo) Remaudière & Hennebert (1980)  
*Erynia blunkii* (Lakon ex Zimmermann) Remaudière & Hennebert (1980)  
*Erynia brahminae* (Bose & Mehta) Remaudière & Hennebert (1980) (possibly synonymous with *Erynia echinospora*)  
*Erynia bullata* Thaxter & MacLeod in Humber (1981b) non *Erynia bullata* (Thaxter in Povah) Remaudière & Hennebert (1980)  
*Erynia calliphorae* (Giard) Remaudière & Hennebert (1980)  
*Erynia conica* (Nowakowski) Remaudière & Hennebert (1980)  
*Erynia creatonoti* Yen in Humber (1981b) non *Erynia creatonoti* (Yen) Remaudière & Hennebert (1980)  
*Erynia curvispora* (Nowakowski) Nowakowski (1881)  
*Erynia delpiniana* (Cavara) Humber (1981a)  
*Erynia delphacis* (Hori) Humber (1981a)  
*Erynia dipterigena* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia echinospora* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia erinacea* (Ben-Ze'ev & Kenneth) Remaudière & Hennebert (1980)  
*Erynia formicae* Humber & Bałazy in Humber (1981b)  
*Erynia gloeospora* (Vuillemin) Remaudière & Hennebert (1980)  
*Erynia gracilis* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia montana* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia myrmecophaga* Turian & Wuest in Humber (1981b) non *Erynia myrmecophaga* (Turian & Wuest) Remaudière & Hennebert (1980)  
*Erynia neoaphidis* Remaudière & Hennebert (1980) [= *Entomophthora aphidis* Hoffmann in Fresenius sensu Thaxter (1888)]  
*Erynia nowyji* Remaudière & Hennebert (1980) [= *Entomophthora*

- exitialis* Hall & Dunn sensu Gustafsson (1965)]  
*Erynia ovispora* (Nowakowski) Nowakowski (1881)  
*Erynia phalangicida* (Lagerheim) Remaudière & Hennebert (1980)  
*Erynia rhizospora* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia sepulchralis* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia variabilis* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia virescens* (Thaxter) Remaudière & Hennebert (1980)  
*Erynia vomitoriae* (Rozsypal) Remaudière & Hennebert (1980)

Doubtful or excluded species:

- Erynia caroliniana* (Thaxter) Remaudière & Hennebert (1980)  
 ≡ *Entomophthora caroliniana* (Thaxter) Keller, 1978, *Sydowia Ann. Mycol., Ser. II*, 31: 88 ≡ *Empusa caroliniana* Thaxter, 1888, *Mem. Boston Soc. Nat. Hist.* 4: 167.  
*Erynia castrans* (Batko & Weiser) Remaudière & Keller (1980)  
 ≡ *Strongwellsea castrans* Batko & Weiser, 1965, *J. Invert. Pathol.* 14: 463 emend. Humber, 1976, *Mycologia* 68: 1056.  
*Erynia magna* (Humber) Remaudière & Keller (1980) ≡ *Strongwellsea magna* Humber, 1976, *Mycologia* 68: 1057.  
*Zoophthora exitialis* (Hall & Dunn) Batko, 1966, *Bull. Polon. Acad. Sci., Sér. Sci. Biol.* 12: 405 ≡ *Entomophthora exitialis* Hall & Dunn, 1957, *Hilgardia* 27: 163.  
*Zoophthora ferruginea* (Phillips in Houghton & Phillips) Batko, 1966, *Acta Mycol.* 2: 19 ≡ *Entomophthora ferruginea* Phillips in Houghton & Phillips, 1886, *Ann. Mag. Nat. Hist. Ser. 5*, 18: 6.  
*Zoophthora forficulae* (Giard) Batko, 1964, *Bull. Polon. Acad. Sci., Sér. Sci. Biol.* 12: 404 ≡ *Empusa forficulae* (Giard) Petch, 1944, *Trans. Brit. Mycol. Soc.* 27: 87 ≡ *Entomophthora forficulae* Giard, 1889, *Bull. Sci. France Belgique* 20: 211.

*Empusa caroliniana* and the two species of *Strongwellsea* are excluded from *Erynia* for reasons mentioned above and discussed extensively by Humber (1981a, 1982).

Remaudière and Hennebert (1980) provide strong reasons to regard both *Entomophthora exitialis* Hall & Dunn (1957) and *Entomophthora ferruginea* Phillips in Houghton and Phillips (1886) as *nomina confusa*; we agree with and accept these determinations. It is impossible to know exactly what fungus is described or illustrated by Hall and Dunn (1957); this situation is not eased by the fact that no type was declared for *E. exitialis* (nor did the ICBN require typification until the year after the publication of this species) or that the cultures deposited by the authors of this taxon in various major culture collections are found to be either *Conidiobolus*

*thromboides* Drechsler (= *Entomophthora virulenta* Hall & Dunn) or *Erynia radicans* (see Remaudière and Hennebert 1980). The fungus regarded to be *E. exitialis* by Gustafsson (1965) was redescribed by Remaudière and Hennebert (1980) as *Erynia nouryi*. Similarly, the real identity of *Entomophthora ferruginea* remains indeterminable in view of the three separate senses in which this name has been applied (see Remaudière and Hennebert 1980).

Batko (1964b) offered no explanation for his assignment of *Entomophthora forficulae* Giard to *Zoophthora*. Neither Remaudière and Hennebert (1980) nor Remaudière and Keller (1980) mentioned this species in their treatments of *Zoophthora* and *Erynia*, possibly because Giard (1889) mentioned no secondary conidia (the character used by Remaudière et al. to separate these two genera), and possibly because of the uncertainty which surrounds the identity of this fungus. The conidia of Giard's species are 20 x 6  $\mu\text{m}$  up to 25 x 8  $\mu\text{m}$ , with a length/width ratio of  $\geq 3$ ; the conidia in the only other collections attributed to this species are 18-21 x 8-10  $\mu\text{m}$  (Rostrup 1893) and 20-30 x 15-18  $\mu\text{m}$  (Petch 1944), with L/W ratios of  $\leq 2$ . Giard, who did not recognize the widely used distinction between *Empusa* (with simple conidiophores) and *Entomophthora* (with branched conidiophores), noted the conidiophores of *Entomophthora forficulae* to be only infrequently branched ("peu ramifiés"); those of the fungi reported by Rostrup and Petch could not have been prominently or digitately branched since Petch (1944) reassigned this species to *Empusa*. Rhizoids were not noted in any of these three collections (and note that Batko 1964a required rhizoids to be present in species of *Zoophthora*!). Despite the fact that L/W ratios of 3 or more are known only from *Erynia* species (with the sole exception of Balazy's undescribed species noted by Humber 1981a), the absence of information regarding the wall structure and nuclear number of the conidia, and of the actual nature of the conidiophores suggests that no definitive generic assignment for *Entomophthora forficulae* is advisable in the absence of other characters so frequently noted in species of *Erynia*. It seems doubtful that the collections of fungi by Rostrup (1893) and Petch (1944) are conspecific with *E. forficulae* Giard; the true identity of each of these fungi remains to be established by re-examination of any existing herbarium specimens.

At least two aspects of this emendation of *Erynia* deserve further comment. It is important to re-emphasize that this nomenclaturally required change from *Zoophthora* to *Erynia* has also necessitated the shift of the type species from

the very common *Erynia radicans* (= *Entomophthora sphaerosperma* Fres. sensu Thaxter) (see Batko 1964a; Remaudière and Hennebert 1980) to the less well known *Erynia ovispora*. Regardless of its nomenclator, the fungus which is still most widely known as *Entomophthora sphaerosperma* has served as the type for a genus distinguished primarily by the presence of rhizoids and branched conidiophores ever since Nowakowski (1883) affirmed a real taxonomic difference between *Empusa* and *Entomophthora*.

*Entomophthora aphidis* Hoffm. in Fres. was originally described only from its brown, roughened resting spores; the conidial state of this species was not found or described by Hoffmann. In his influential monograph, Thaxter (1888) applied the name *Empusa* (*Entomophthora*) *aphidis* to an exceptionally common fungal pathogen of aphids which produces conidia and whose resting spores may be assumed to exist but have never been found. Remaudière and Hennebert (1980) were successful in rediscovering Hoffmann's fungus and demonstrated unequivocally that Thaxter had misapplied Hoffmann's specific name: The conidia of *E. aphidis* Hoffm. are elongate-fusoid and produce secondary amygdaliform capilliconidia atop capillary conidiophores. The presence of capilliconidia in *E. aphidis* but not in Thaxter's fungus was used by Remaudière and Hennebert to place these two fungi into separate genera as *Zoophthora aphidis* (Hoffm. in Fres.) Batko and *Erynia neoaphidis* Rem. & Henneb. (the new name provided for Thaxter's misapplied sense of *E. aphidis*). The emended sense of *Erynia* provided here places both of these species together in the same genus. It will be especially important, then, for students of these fungi not to confuse these two similar specific names and to be certain that they do not apply the name *Erynia aphidis* (a very uncommon fungus with a seemingly narrow host range and localized distribution) when the fungus they refer to is actually *Erynia neoaphidis* (a very common species with a wide host range and occurring in most parts of the world).

In addition to the species of *Erynia* discussed above, we are aware of two additional new species awaiting publication: Kramer (1981) is proposing a new species of *Erynia* from snipe flies (Diptera: Rhagionidae). Ben-Ze'ev and Kenneth (1981b) are proposing a new species of *Zoophthora* which affects froghoppers (Homoptera: Cercopidae); this species will have to be transferred to *Erynia* after its formal publication.



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## REVUE DES LIVRES

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*THE COELOMYCETES, Fungi imperfecti with pycnidia, acervuli and stromata*, by Brian SUTTON, 696 p., 397 fig., 8°, hard cover, 1980. Commonwealth Mycological Institute publication, Commonwealth Agricultural Bureaux, Farnham, Slough SL2 3BN, England. Price UK £ 28.00, abroad £ 33.60.

*The Coelomycetes* by Sutton is the first comprehensive and modern contribution on that important wide spread group of fungi. After numerous publications on the Coelomycetes, including seven issues in the CMI Mycological Papers and the fundamental and synthetic chapter on Coelomycetes in *The Fungi IVA* (1973), we are really thankful for such a fine monograph covering 375 genera and 750 species.

The inestimable progress realized by Dr Sutton in the taxonomy of these fungi is the recognition of conidiogenesis as a basic taxonomical criterion to be used at the level of classes and orders, the conidiomatal structure (pycnidia, acervuli, sporodochia, etc.) and morphology being useful as a secondary criterion at the suborder level or lower. Although, in that concept of the taxonomy of conidial fungi, Hyphomycetes and Coelomycetes would ideally be and are close to being unified and classified according to the conidiogenesis, the conidioma from the pycnidium to the obsolete exposed conidial cell representing a *continuum*, the author still uses the term *Coelomycete* here for the practical reason of delimiting a workable field. Accepting the major modes of conidiogenesis as defined at the 1st Kananaskis Conference (1969), Sutton proposes two classes in the Deuteromycotina, the Thallodeuteromycetes and the Blastodeuteromycetes, and five orders, the Thallales, Enterothallales, Blastales, Phialidales and Tretales, instead of the traditional Sphaeropsidales, Melanconiales and Moniliales. The structure of the conidioma delimits eventually the suborders, f.i., in the Blastales, the Blastohyphineae (blastic Moniliales), the Blastopycnidineae (blastic pycnidial) the Blastopycnothyriineae (blastic Pycnothyriales) and the Blastostromatineae (blastic Melanconiales).

Notice that two orders, the Enterothallales and the Tretales, are not represented amongst the coelomycetous fungi so far but in the Hyphomycetes only. The Coelomycetes traditionally classified in the Pycnothyriales and now representing the Thallopycnothyriineae, the Blastopycnothyriineae and the Phialopycnothyriineae, are not treated for the simple reason that almost no information on their conidiogenesis is available.

Sutton discuss the hypothesis of Morgan-Jones, Nag-Raj and Kendrick (1972) that a distinction might exist between an anellidic conidiogenous cell and percurrently proliferating phialide but is not convinced. He prefers to base the distinction between anellidic and phialidic

percurrently proliferating conidiogenous cell on the single or repetitive conidium production by each of the successive cells. There is the reason why some fungi having conidiogenous cells looking like annellides are classified as repetitively proliferating phialidic fungi.

In regard of the amount of new information to be included, the author chose with reason to avoid any already published data and to refer to good descriptions, illustrations or comments published elsewhere when possible. Quite a number of genera are therefore not illustrated. But it would have been of great help to the users to reproduce, at least, an illustration of those genera, to give at once a full picture of the group. The text of the book is concise but clear. The paper, rather thin but of good quality and flexible, makes the size of the book reasonable and its manipulation easy. The book is completed with adequate indices and a glossary.

There is no need to say that the Coelomycetes are economically important plant pathogens and material deteriorogens. Not only should any mycologist welcome this major contribution to the systematics of fungi, so also should any plant pathologist, forest manager or microbiologist concerned with soil biology or material degradation be aware of it.

Furthermore, taxonomists will appreciate being stimulated in their investigations by an author who, at almost every page of his book, points out some ways of progress.

*A REVISION OF CHRYSOSPORIUM AND ALLIED GENERA*, by C.A.N. van OORSHOT, *Studies in Mycology* n° 20, 90 p., 36 fig., 3 pl., 8°, paper cover, 1980. CBS Publication, Baarn Nederland. Price HFL 25.-.

*Chryso sporium* Corda and the related genera *Myceliophthora*, *Emmonsia*, *Zymonema*, *Trichosporiella*, *Blastomyces*, *Glenosporella* and *Geomyces* are revised, including 38 species and varieties. The redescribed anamorphs have either thallic or blastic conidiation and rhexolytic dehiscence. Teleomorphs belong to the Gymnoascaceae, Onygenaceae, Ascosphaeraceae and Sordariaceae. The genus *Chryso sporium* Corda is quite an homogenous grouping now, *Sporotrichum pannorum* Link having a distinct position in *Geomyces*.

*COELOMYCETES. VII. STEGONSPORIUM*, by K.T. Van WARMELO and B.C. SUTTON, *Mycological Papers* n° 145, 46 p., 13 pl., 8°, paper cover, 1981. Commonwealth Mycological Institute, Kew Surrey, England. CAB Publication. Price £ 3.00.

The original spelling *Stegonsporium* from Corda in Opiz 1926 is accepted instead of Fries's spelling *Stegonosporium* 1849. Two species are maintained, *S. pyriforme* and *S. acerinum*. Sixty five species are excluded or questioned. The excluded species belong to *Stigmina*, *Myxocyclus*, *Coryneum*, *Camarosporium*, *Trimmatostoma*, *Dictyodesmium*, *Neohendersonia* and *Camaropellum*, with five new combinations. Two new genera, *Stegonsporopiopsis* and *Kaleidosporium* are proposed with two new combinations. *Stegonsporium* produces annellidic conidiophores with dictyoseptate conidia amongst filiform paraphyses.

*CONTRIBUTION TOWARDS A RATIONAL ARRANGEMENT OF THE CLATHRACEAE*, by D.M. DRING, 96 p., 27 fig., 8°, paper cover, 1981, reprinted from *Kew Bulletin*, 35(1), 1980. Royal Botanic Gardens, Kew, England. Price £ 5.00.

These are the conclusions of a long-term interest and research in the Clathraceae by the late Dr. Dring († 1978) and of his personal

observations in West Africa. It has been fortunate that the unfinished manuscript could be completed from the author's large collection of notes and drawings. Dring recognized 8 genera, *Azeroë*, *Blumenavia*, *Clathrus*, *Colus*, *Ideodictyon*, *Laternea*, *Lysurus* and *Pseudocolus*, and 36 species. These are fully described and illustrated, with synonymies and references to other valuable illustrations. The specimens examined are all cited, demonstrating the often restricted geographical distribution. The genus *Clathrus*, with 16 species, is the largest one and appears to the author as the ancestor of a diversifying evolution. All the species of the Clathraceae, the exception of *Clathrus ruber* and *C. hirudinosus* represented in Europe, West Asia and North Africa, are known from the other parts of the world and many are from tropical areas.

*THE GENERA OF FUNGI SPORULATING IN PURE CULTURE*, by J.A. von ARX, third edition, 424 p., 99 pl., 8°, hard cover, 1981. J. Cramer, Fl 9490 Vaduz, Lichtenstein. Price DM 120.-, for subscribers 100.-.

This third edition of Dr von Arx's book is a fully revised and expanded version of the previous ones. The classification of the fungi has been emended according to recent advances. The Dothideales include the Myriangiales, Dothiorales and Pseudosphaeriales. The Pezizales include the Tuberales. The Tilletiales are reintroduced. The Ustomycetes (Ustilaginales, Exobasidiales, Taphrinales, Sporobolomycetales and basidiomycetous yeasts) are distinguished from the Endomycetales on morphological grounds and wall composition. Basidiomycetes are not otherwise treated. All together 853 genera are accepted, of which only 370 are given an illustration, one third of these illustrations being new and based on recent studies. About 50 genera, some of them being recently described, are reduced into synonymy. Some genera rejected in recent years are reintroduced, e.g. *Endomycopsella*, *Karakulina* and *Bipolaris*. Illustrations and dichotomous keys result from studies of the fungi in pure culture, independent of their natural substrate. Keys have been adjusted to updated terminology. The 1100 literature titles include the most recent ones published in 1980. This edition, certainly like the previous ones, will be appreciated by those who have to identify fungi from sporulating cultures.

*MARINE MYCOLOGY, The Higher Fungi*, par Jan KOHLMAYER et Erika KOHLMAYER, xii + 690 p., 127 fig., 8°, relié toilé, 1979. Academic Press, N.Y. Price US \$ 71.50.

149 Ascomycètes, 4 Basidiomycètes, 56 Deuteromycètes filamenteux et 177 levures sont les champignons supérieurs récoltés à ce jour près de et dans la mer. Des 209 espèces filamenteuses rencontrées, 191 sont spécifiques au milieu marin. C'est dire qu'un ouvrage intitulé *Marine Mycology* ne saurait être de pure taxonomie sans aussi considérer l'écologie. C'est cette alliance qu'ont fort bien réussie les deux auteurs. Après un exposé des méthodes (chap. 2) l'écologie des champignons côtiers et marins met en évidence les relations champignon-substrat chez les espèces de pleine eau, d'estuaires, de sables, des écumes, des marais salés, des algues, des lichens, des mangroves et des débris animaux et végétaux (chap. 3-19 et 21). Dans les chapitres touchant la taxonomie (chap. 20, 22-28; 421 p.) les auteurs proposent d'abord des clés dichotomiques basées sur la morphologie sporale ou conidienne et finement illustrées par Erika Kohlmeier. Le principal chapitre 26 comporte la description taxonomique des 209 champignons filamenteux, avec synonymie, photographies et bibliographie. Une nouvelle espèce et 7 combinaisons sont proposées. 49 rejections de noms douteux ou invalides sont énoncées.

Dans le dernier chapitre, les levures sont répertoriées, sans description mais avec indication de leur habitat. Près de 1400 références bibliographiques complètent l'ouvrage. En mycologues avertis, les auteurs témoignent dans ce livre d'un sens aigu du détail et une manière esthétique de le mettre en valeur. Ce livre est une "somme" de ce domaine particulier de la mycologie. Sa qualité suscite l'admiration.

*MICROBIAL POLYSACCHARIDES AND POLYSACCHARIDASES*, par R.C.W. BERKELEY, G.W. GOODWAY and D.C. ELLWOOD édit., Publication de la Society for general Microbiology, xvi + 479 p., ill., 8°, relié, 1979. Academic Press, N.Y. Prix US \$ 47.00.

Ce livre est la synthèse de deux symposiums tenus à Aberdeen en 1978, l'un sur *The microbial extracellular Polysaccharides* du Groupe pour l'étude des surfaces et membranes de la Cellule microbienne, l'autre sur *The microbial Degradation of Polysaccharides* de la Society for general Microbiology.

Sans doute, cet ouvrage sort du champ habituel de la mycologie. Cependant la composition différente des parois des champignons suivant leur classe taxonomique est une raison de considérer cet ouvrage de portée aussi fondamentale qu'appliquée. La détection, l'analyse et la production de polysaccharides et des enzymes qui les dégradent sont les objectifs d'une recherche de plus en plus active. Ce sont surtout les polysaccharides extracellulaires, comme le pullulan de *Aureobasidium pullulans*, qui retiennent l'attention. La paroi fongique est donc un organe essentiel. Sa composition, sa structure microscopique fine, sa perméabilité, la structure biochimique, l'activité et la solubilité de ses polysaccharides sont autant d'aspects traités dans ce livre. La paroi se détruit autant qu'elle se construit. Les polysaccharidases produites par les champignons eux-mêmes ou les bactéries associées agissent au niveau de la paroi fongique et dans le milieu, transformant les polysaccharides en nutriments récupérables. Ainsi les cellulases, chitinases, amylases, glucanases, pullulanases des champignons ne sont pas les moins connues. Ce livre s'adresse non seulement au microbiologiste et biochimiste industriel, mais aussi le mycologue curieux de la nature exacte des champignons.

*STEREOLICAL METHODS. VOL. I. PRACTICAL METHODS FOR BIOLOGICAL MORPHOMETRY*, par E.R. WEIBEL, 515 p., ill., 8°, relié toilé, 1979. Academic Press. Price US \$ 66.50.

La première approche d'un être vivant est d'abord d'en saisir la forme. Au travers du microscope, où le relief disparaît, la forme est celle d'une image, d'un profil, d'une section. Le microscopiste, le biologiste, le mycologue traduit la vision de la forme (morphoscopie) en un tracé d'abord (morphographie), en une description ensuite (morphologie), en une mesure enfin (morphométrie). La promotion récente de la taxonomie numérique accentue la nécessité d'une morphométrie méthodique et traduisible en termes de réalité. La recherche de méthodes morphométriques valables est le but de la stéréologie. Ces méthodes sont mathématiques et visent à relier les paramètres tridimensionnels d'une structure spatiale aux mesures bidimensionnelles des sections de cette structure. Inversement, elles fournissent la réponse à la question: comment interpréter l'image vue au microscope comme expression de la réalité spatiale. L'auteur ne traite pas des fondements mathématiques des méthodes, les réservant au volume II. Le livre est donc d'un niveau mathématique accessible à qui possède des notions de mathématique moderne. Par voie d'exemples, de photos et de graphiques, l'auteur explique les méthodes d'échantillonnage des structures à mesurer et la réalisation de mesures

qui ne faussent pas la réalité. Il serait intéressant que des mycologues expérimentent les méthodes morphométriques proposées par la stéréologie au profit de la taxonomie des champignons.

*BULLETIN OF MYCOLOGY. VOL. I. N°1*, edited by Sultan AHMAD and S.H. IQBAL, Department of Botany, University of the Punjab, New Campus, Lahore, Autumn 1980.

We welcome the appearance of this new journal devoted to taxonomic mycology from Pakistan, a country where surely much waits to be discovered and described. The first issue of the *Bulletin of Mycology* contains interesting papers on freshwater Hyphomycetes, on coprophilous Ascomycetes, on Agaricales and other fungi from Pakistan. We hope that the new journal receives the attention that it deserves.

*SEXUALITY AND PATHOGENICITY OF FUNGI*, edited by R. VANBREUSEGHEM and Ch. DE VROEY, 250 p. ill., 8°, hard cover, 1981. Masson, 120 Bd. Saint Germain, 75280 Paris.

This is the Proceedings of the Third international Colloquium on Medical Mycology organized by the Prince Leopold Institute of Tropical Medicine, Antwerp, Belgium.

The question raised at the beginning of the colloquium "Is there a relationship between sexuality and pathogenicity to man in fungi?" received an answer far beyond any hope. That answer is that no relation between mating type and symptoms has been observed so far, but that a close relation between the mating type and the host or biotope is demonstrated and that that relation is determining particular geographical distribution. Beside the pathogenicity of mating types, serotypes, + and - types, sexual and asexual spores, many correlative aspects of the pathogenic fungi have been treated by the 32 contributors, like taxonomy and the relation anamorph-teleomorph, genetics, somatic hybridization, sexual stimulation, sexual test strains, filamentization of yeasts. The book answers a number of questions raised in the taxonomy and ecology of the fungi. It offers valuable readings for any mycologist and for plant pathologists.

*YEAST GENETICS AND MOLECULAR BIOLOGY 1980. Reports*, by A. GOFFEAU and J.M. WIAME. 102 p., 8°, paper back, 1980. Louvain-la-Neuve, Lab. Enzymology, Croix du Sud 1, 1348 Louvain-la-Neuve, Belgium. Price Workshop reports \$ 10, Abstracts book \$ 20.

This is the Workshop Reports of the tenth International Yeast Conference held at Louvain-la-Neuve, September 1980. It contains 24 plenary presentations covering the research progresses on *Saccharomyces cerevisiae* about its chromosome structure and replication, RNA, protein synthesis, cell cycle, sporulation, recombination, mutagenesis, radiation repair, expression of cloned genes, mating, regulation of C and N, metabolism, mitochondria, killers, genetics engineering, evolution and taxonomy. It certainly leads to conclude that *Saccharomyces cerevisiae* is a favorite model for studying the structure and the operation of eukaryotic cells. The Abstracts Book was distributed at the Conference but is still available, it reproduces the abstracts of each of the 200 posters presented.

*INTRODUCTION TO FUNGI*, by John WEBSTER, 2d edition, 669 p., 331 fig. 8°, paper or hard cover, 1980. Cambridge University Press. P.O. Box 110, Cambridge, England. Price h.c. £ 30, p.c. 9.95.

After the publication of the first edition, in 1970, advances have been made in all fields of mycology. Where necessary the text has been altered or expanded. The literature cited is twice in number now. The author adopts the Ainsworth, Sparrow and Sussman's system of the Fungi, as a separate kingdom. The Myxomycetes are more extensively treated. The anamorphic fungi, the Deuteromycotina, receive a special chapter with a description of their conidiogenesis. New and detailed accounts are added on three ecological groups of fungi, the aquatic, the predacious and the seedborne imperfect fungi. This reinforces the aim of the author to be not purely taxonomical but to describe the fungi in their life behaviour. The clarity of Webster's writing, the precision of the data, the excellent selection of original photographs and drawings are prominent characteristics of the book. The book is an excellent manual for the university level. For reaching constantly the present limits of knowledges, it concerns all students of mycology.

*HOW TO KNOW THE TRUE SLIME MOLDS*, by M.L. FARR, in Pictured Key Nature Series, 132 p., 159 fig., 23x17 cm, spiral binding, 1981. Wm. C. Brown Co. Publ., 2460 Kerper Bd., Dubuque, Iowa 52001, USA.

This "pictured key" to the Myxomycetes is intended to be introductory and practical. The introduction shortly explains what Myxomycetes are, how they live, where they growth, how to collect them, how to keep them alive, how to look at them, how to describe them, how to preserve them. The keys to orders, families, genera and species are all dichotomous. Specific descriptions, comments and illustrations are given at every species keyed out. Illustrations are mostly line drawings picturing fruiting bodies and, eventually, capillitium and spores. At every taxonomic level, indeed, the keys are constructed from both macroscopic and microscopic characters. They thus are not to be considered as field keys. They cover a selection of 276 common North-American species of Myxomycetes.

*TAXONOMY OF THE INDIAN MYXOMYCETES*, by T.N. LAKHAMPAL and K.G. MUKERJI. in *Bibliotheca Mycologica* vol. 78, 531 p., 40 fig., 8°, hard cover, 1981. J. Cramer, Fl 9490 Vaduz, Lichtenstein. Price: DM 120, subscription DM 96.

The authors have realised two aims. In the first part of the book, they describe, in a taxonomical order, all the species of Myxomycetes that they recorded in 1000 specimens from their respective collecting fields, i.e. Himalahal Pradesh and Delhi. The Taxonomy is that of Martin and Alexopoulos (1969) modified by Alexopoulos in Ainsworth, Sparrow and Sussman (1973). The illustrations are assembled in 28 full-page plates of black and white photographs of standard quality and 12 plates of rather poor line-drawings. In the second part of the book, the authors produce an updated index of all the Indian Myxomycetes records disposed in taxonomical order, with reference to the pertinent literature. The contribution is important. Out of the 450 presently known species of Myxomycetes, 293 are recorded in India and, out of those, 111 are recently recorded, by the authors mostly, after the publication in 1977 of Dr Thind's monograph.

*BIODEGRADATION ET HUMIFICATION, ATLAS ULTRASTRUCTURAL*, par G.M.OLAH, O. REISINGER et G. KILBERTUS, 334 p., 199 fig., 4°, cartonné, 1978. Les Presses de l'Université Laval, Québec. Librairie Vuibert, Paris.

En 1974, était organisé, à Nancy, le 1er Colloque international sur le thème "Biodégradation et Humification" (Mycotaxon IV(1):317, 1976).



Les auteurs, organisateurs de ce Colloque, ont rassemblé en un atlas leurs documents de microscopie électronique illustrant d'une part les agents de la biodégradation dans le sol (bactéries, champignons, algues bleues, et microfaune) et d'autre part les victimes, la matière organique vivante en déperissement (celle des algues, champignons, bryophytes et phanérogames). L'atlas est divisé en chapitres introduits par un texte et un schéma expliquant le processus de la biodégradation dans le sol. Les illustrations font face à une légende brève, à mon avis trop brève, mais suivie d'un grand nombre de références à la littérature. Les photographies sont de bonne qualité et suscitent l'intérêt par leur choix et leur originalité. On y voit des vues inattendues de bactéries du sol ou colonisant des hyphes fongiques. Des images en ombrage et en transmission illustrent la sporulation de divers champignons, un asque operculé béant, des annélides, des conidies en grappe, des pores septaux, la perforation bactérienne de parois fongiques, la désorganisation enzymatique de celle-ci, et la repousse interne d'une hyphe de régénération. Cet atlas est didactique et permettra de visualiser, dans l'enseignement, un des grands phénomènes de la biologie du sol, le "turn-over" de la matière organique.

*COMPENDIUM OF COTTON DISEASES*, par G.M. WATKINS, éd., in The Disease Compendia Series, n°5, 87 p., 45 fig., 59 ph. col., 4°, 1981. The American Phytopathological Society, 3340 Pilot Knob Road, St Paul Minnesota 55121. Prix US\$ 11.

Ce compendium, comme les précédents sur les maladies du soya, du froment, de la luzerne, du maïs, continue une série fort utile à la clinique des plantes cultivées. Plus de quarante spécialistes ont contribué à la rédaction et l'illustration de celui-ci. Près d'une cinquantaine de champignons responsables d'une pathogénèse fongique du cotonnier sont envisagés, la symptomatologie et l'épidémiologie décrites et le traitement indiqué. A côté des maladies fongiques, les autres maladies biotiques et abiotiques sont aussi décrites et illustrées. Une clé synthétique des symptômes permet l'identification rapide des maladies.

*THE CORTICIACEAE OF NORTH EUROPE. Vol. 6. PHLEBIA-SARCODONTIA*, par John ERIKSSON, Kurt HJORSTAM et Leif RYVARDEN, p.1051-1276, fig. 535-653, 8°, broché, 1981. Fungiflora, P.O. Box 95, Blindern, Oslo 3, Norway. Prix Nkr 120.

Sont déjà parus et recensés dans Mycotaxon les volumes 2 (*Aleurodiscus - Confertobasidium*), 3 (*Cornicium - Hyphoderma*), 4 (*Hyphodermella - Mycoacia*) et 5 (*Mycoaciella - Phanerochaete*). Dans le présent volume, les auteurs décrivent les genres *Phlebia* (31 espèces), *Repetobasidium* (8 espèces), *Piloderma*, *Resinicium* (3 espèces chacun), *Phlebiopsis*, *Radulomyces* (2 espèces) et *Physodontia*, *Plicatura*, *Plicaturopsis*, *Podoscypha*, *Pseudomerulius*, *Pseudoxenasma*, *Pulcherricium*, *Punctularia*, *Radulodon*, *Ramaricium*, *Repetobasidiellum* et *Sarcodontia* monospécifiques. Les auteurs proposent 1 nouveau genre (*Repetobasidiellum*), 9 nouvelles espèces dont 3 en *Phlebia*, 14 nouvelles combinaisons dont 5 en *Phlebia* et un nom nouveau. Certainement, ce volume est attendu, comme le sont aussi les suivants

*THE FISCHER-SMITH CONTROVERSY: ARE THERE BACTERIAL DISEASES OF PLANTS?*, par Erwin F. SMITH et Alfred FISCHER, introduit et traduit de l'allemand par C. Lee CAMPBELL, *Phytopathological Classics* n° 13, xviii + 65 p., 40 fig., 8°, broché, 1981. The American Phytopathological Society, St Paul, Minn., USA. Prix US \$ 8.50.

Erwin F. Smith, American plant pathologist, USDA, Washington, who has demonstrated experimentally the pathogenicity of bacteria to plants

refutes the assertion of Alfred Fischer, a German professor in Botany at the University of Leipzig, of the non-existence of bacterial diseases. It was in 1897. Fischer answered by unjustifiable critics about the Smith's observations and experiments. Smith then took his own defence, in a long and convincing paper (1902). As a result, the existence of bacterial diseases was accepted, and the rivals were both promoted, the one as director of the USDA Plant Pathological Laboratory, Washington, the other as professor and director of the Botanical Gardens at the University of Basel. "The facts are God's, the theories are human" (Lord Ripon, 1874).

*TROPICAL MYCORRHIZA RESEARCH*, par Peitsa MIKOLA édit., Oxford Science Publications, xii + 270 p., ill., 8°, relié, 1980. For the International Foundation of Science, Oxford University Press, Walton Street, Oxford OX2 6DP, England. Prix £ 15.

Ce volume est constitué des 31 communications présentées à l'International Workshop on Tropical Mycorrhiza tenu au Ghana, en 1978, par l'International Science Foundation (IFS). Elles se regroupent en quatre thèmes: les ectomycorhizes en région tropicale, les mycorhizes de la végétation naturelle, nutrition mycorrhizique des plantes tropicales et mycorhizes des plantes agricoles. Il est intéressant de constater le rôle grandissant des ectomycorhizes dans la reforestation des zones tropicales dénudées. D.H. Marx fait une revue très large des possibilités d'inoculation de champignons mycorrhizogènes, à travers le monde, et des méthodes utilisées. D'autres donnent les résultats particuliers obtenus en leur pays. La recherche explore aussi les mycorhizes naturelles des essences forestières et des plantes cultivées tropicales, en particulier de l'*Hevea*, de l'*Elaeis*, du cacaoyer, des *Citrus* et des graminées. Si on recherche les facteurs qui peuvent leur être favorables, on s'inquiète de plus en plus de l'effet néfaste sur les mycorhizes des fertilisations chimiques et des herbicides en forêt comme en agriculture. La mycorrhization est un phénomène tel qu'il importe de le connaître pour le maintien du monde végétal et du nôtre.

*DEVELOPMENTAL MICROBIOLOGY*, par John PEBERDY, in Tertiary Level Biology Series, 230 p., ill., 12°, paper back, 1980. Blackie & Son Ltd. Bishopbriggs, Glasgow G64 2NZ. Prix £ 8.50.

Ce petit livre de microbiologie est axé sur les phénomènes de croissance et de reproduction. Il en montre les aspects les plus fondamentaux de structure, de biochimie et de génétique cellulaires et les plus apparents de la morphologie, de l'accroissement et de la formation sexuée et asexuée de spores, avec le souci d'expliquer la relation entre ces aspects. Si dans un tiers du livre il est question de bactéries et virus vus sous les mêmes aspects, ce livre est particulier par le choix des champignons comme matériel privilégié d'étude du développement (levures, myxomycètes, champignons filamenteux, champignons sexués et asexués). Ce livre est destiné au niveau du baccalauréat ou "undergraduate".

*BIOLOGICAL MEMBRANES, THEIR STRUCTURE AND FUNCTION*, par R. HARRISON et G.G. LUNT, Tertiary Level Biology Ser., 2e ed., 288 p., ill., 12° 1980. Blackie & Son Ltd., Glasgow. Prix £ 7.95.

La structure de la membrane cellulaire, sa composition biochimique, les mécanismes fonctionnels de reconnaissance des macromolécules et de leur transport par la membrane cellulaire sont les sujets traités par les auteurs dans un langage clair et adapté au niveau universitaire. Cependant nous regrettons que ce livre n'envisage que la cellule animale et qu'il ne mentionne qu'en passant les membranes végétale et fongique.

## NOTICES

### XV PACIFIC SCIENCE CONGRESS

The XV Pacific Science Congress will be held February 1-11, 1983, in Dunedin, New Zealand. The Pacific Science Association is responsible for the program, which is sponsored by the Royal Society of New Zealand. A first circular may be obtained from The Secretary General, 15th Pacific Science Congress, P.O. Box 6063, Dunedin North, New Zealand.

### IMC<sub>3</sub>: ON HOUSING COSTS IN JAPAN

Though it is indeed true that Japan is currently a very expensive place to visit, the organizing committee of IMC<sub>3</sub> is well aware that most mycologists will not be able to spend great sums of money on housing for the congress. Dr. Keisuke Tubaki, a member of the Mycological Society of America's ad hoc committee on IMC<sub>3</sub> arrangements, has assured us that though the meetings are planned for a downtown Tokyo hotel-convention facility, there will be many hotel rooms available close by in less prestigious hotels in the \$15-20/night (1981 prices) range. There have apparently been rumors that housing costs would be substantially higher. Our Japanese hosts will do all they can to keep costs down for participants. The same concerns will be kept in mind for pre-congress and post-congress tours, workshops, and field trips. The Tokyo meetings will be from 28 August through 3 September, 1983.

- ALCORN, J. L. *Cochliobolus ravenelii* sp. nov. and *C. tripogonis* sp. nov. 339-345
- ALCORN, J. L. Ascus structure and function in *Cochliobolus* species 349-360
- ARENDHOLZ, WOLF-RÜDIGER & RICHARD P. KORF. The publication date of Arendholz's thesis on leaf-inhabiting Helotiales 187-190
- BAKER, JOHN G., IRA F. SALKIN, DAVID H. PINCUS & RICHARD F. D'AMATO. *Candida paratropicalis*, a new species of *Candida* 115-119
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### ERRATA, VOLUME TEN

Page 471, line 12: *for* 1094: La *read* 1094: La Palma.

### ERRATA, VOLUME TWELVE

Page 280, line 8: *for* Rossman, J. Wy- *read* Rossman, L. J. Spielman, J. Wy-

## ERRATA, VOLUME THIRTEEN

- Page 2, line 31: for gal read Gal  
 42, 14: for (Remaudière) Batko, read Remaud. & Henneb.,  
 47 12: for form read from  
 53 35: for *M. cicadina* read *Massospora cicadina*  
 60 44: for *immitabilis* read *immutabilis*  
 65 51: for *immutibile* read *immutabilis*  
 66 8: for *H. cauda-* read *Hymenoscyphus cauda-*  
 70 51: for *Hymenoscyphus fastidiosus* read *Helotium fastidiosum*  
 74 41: for sporen read spore  
 144 7: insert TYPE LOCALITY: Britain.  
 leg. l.1: for 4 read 5  
 176 36: for *P. phillipinensis* read *F. philippinensis*  
 38: for *brasilensis* read *brasiliensis*  
 177 2-3: for *P. phillipinensis* read *P. philippinensis*  
 7: for *brasilensis* read *brasiliensis*  
 43: for *berkeleyi* read *berkeleyi*  
 178 20: for *Phillipines* read *Philippines*  
 21: for *tenius* read *tenuis*  
 182 39: for *tabcinus* read *tabacinus*  
 183 43: for *supinus* read *supina*  
 185 14, 17: for *Phillipines* read *Philippines*  
 189 22: for *Arendholtz* read *Arendholz*  
 199 1: delete nuclei of  
 203 17: for *E.* read *Entomophthora*  
 18: for *E.* read *Erynia*  
 205 6: for *E. caoliniana* and *E. carpentieri*  
 read *Erynia caroliniana* and *Entomophthora carpentieri*  
 216 27: for *E.* read *Empusa*  
 28: for *E.* read *Entomophthora*  
 217 13, 17: for *E.* read *Entomophthora*  
 218 36: for *E.* read *Entomophthora*  
 220 3: for segregated read segregates  
 223 22: for *E.* read *Entomophthora*  
 228 10: for *E.* read *Entomophthora*  
 231 13: for *C.* read *Conidiobolus*  
 363 22: for *Maraconesian* read *Macaronesian*  
 370 13: for *Fusarium* read *Fusarium*  
 21: for *Steptomycetes* read *Streptomyces*  
 371 8: for *aspermum* read *asperum*  
 425 35: for *dengleyae* read *dingleyae*  
 434 18: for *P.* read *Psoroma*  
 445 21: for *P.* read *Psoroma*  
 450 30: for *C.* read *Codinaea*  
 451 1: for *parkhalen-* read *pakhalen-*  
 455 35: for *C.* read *Codinaea*  
 461 20: for *aquitilis* read *aquatilis*

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