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# Arthroxylaria elegans, a new coprophilous anamorphic fungus allied with the Xylariaceae, with notes on the genus Bisporostilbella*)

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The new genus and species *Arthroxylaria elegans* is described for a synnematous hyphomycete isolated from pack rat dung. The fungus is characterized by the production of tall, lightly pigmented, indeterminate synnemata covered with a layer of unbranched or sparingly branched chains of 0–1-septate meristem arthroconidia. A synanamorph with sympodially-proliferating conidiogenous cells, producing minute aseptate conidia, is also produced. Phylogenetic analyses of partial small subunit ribosomal DNA sequences suggest that the fungus is related to the Xylariaceae, Xylariales, and analysis of internal transcribed spacer sequences places the fungus in *Xylaria*. The new species is compared with other anamorphs of the Xylariaceae, and a number of similar synnematous and mononematous hyphomycetes, including the poorly understood *Bisporostilbella fusca*, which is illustrated based on holotype material.

**Key words**: anamorph taxonomy, coprophilous fungi, hyphomycetes, biodiversity

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Je popisován nový druh synematických hyfomycetů *Arthoxylaria elegans* isolovaný z krysích exkrementů. Houba je význačná vytvářením vysokých světle pigmentovaných, indeterminovaných synemat pokrytých vrstvou nevětvených nebo řídce rozvětvených řetízků neseptovaných nebo septovaných meristemových artrokonidií. Tvoří se též synanamorfa se sympodiálně proliferujícími konidiogenními buňkami, které vytvářejí drobné, neseptované konidie. Fylogenetická analýza částečné podjednotky sekvencí ribosomální DNA naznačuje že houba je příbuzná čeledi Xylariaceae z řádu Xylariales. Analýza vnitřní prostorové transkribované sekvence zařazuje tuto houbu do rodu *Xylaria*. Nový druh je srovnáván a ostatními anamorfami čeledi Xylariaceae a s četnými podobnými synematickými a mononematickými hyfomycety včetně málo známé *Bisporosilbella fusca*, která je vyobrazena na základě holotypu.

*) We are pleased to dedicate this contribution to our friend and colleague Ludmila Marvanová on the occasion of her 70th birthday. We remember with fondness Ludmila's visits to CBS in Baarn and pleasant evenings of conversation in the Gams' home. We have admired her observant eye and patient coaxing of many aquatic hyphomycetes into pure culture for the first time, from both European and Canadian streams.

## Introduction

In 1977, Dr. R. K. Benjamin isolated a synnematous hyphomycete from the dung of pack rats (*Neotoma* sp.) in California, USA. The fungus produced spectacular synnemata that would grow as much as 6 cm tall if the lid of the Petri dish was removed to allow continued growth. The culture was circulated to several hyphomycete specialists, who were unable to assign the fungus to an appropriate anamorph genus. We began studying the fungus in 1981, including it in an as yet unpublished study of some nondescript, mononematous hyphomycetes with similar conidiogenesis. Our recent molecular results have convinced us that this fungus is unrelated to the mononematous species under consideration, and have stimulated the description of a new hyphomycete genus and species here.

## Materials and methods

Cultures. For morphological studies, the culture was grown on oatmeal agar (OA, Gams et al. 1998) and 2% Malt Extract Agar (MEA, using brewer's malt available at CBS) at room temperature under ambient light or in the dark at 25 °C for 14 days. For DNA extraction, cultures were grown on OA in the dark at 25 °C for 10 days.

DNA Sequencing. DNA was isolated using a FastDNA™ Kit and the FastPrep™ FP120 (BIO 101 Inc.) using synnemata removed from OA cultures. PCR and cycle sequencing reactions were performed on a Techne Genius thermocycler (Techne Cambridge Ltd.). PCR reactions were performed using Ready-To-Go™ Beads (Amersham Canada Ltd.) in 25 $\mu$L volumes, each containing 20–100 ng of genomic DNA, 1.5 units Taq DNA Polymerase, 10 mM Tris-HCl (pH 9.0), 50 mM KCl, 1.5 mM MgC12, 200 $\mu$M of each dNTP, 0.4 $\mu$M of each primer, and stabilizers including BSA. The reaction profile included an initial denaturation for 3 min at 94 °C, followed by 30 cycles of 1 min denaturation at 94 °C, 1.5 min annealing at 56 °C, 2 min extension at 72 °C, with a final extension of 10 min at 72 °C. Amplicons were purified using UltraClean™ PCR Clean-up™ DNA Purification Kit (MO BIO Inc.) following the manufacturer's directions. Amplification products were sequenced using the BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (ABI Prism/Applied Biosystems) system, and the ABI PRISM™ 310 DNA Sequencer (Applied Biosystems, Foster, CA) following the manufacturer's directions. A portion of the small ribosomal subunit (18S) DNA was amplified and sequenced using primers NS1 and NS4. The complete internal transcribed spacers and 5.8S rDNA were amplified using primers ITS1 and ITS4, and cycle-sequenced using primers ITS1, ITS2, ITS3 and ITS4 (primers from White et al. 1990).

Phylogenetic analysis. The partial small subunit sequence of *A. elegans* (GenBank AF432180) was subjected to a BLAST search on GenBank

(http://www.ncbi. .nlm.nih.gov/BLAST/), and then aligned with the closest matches. The ITS sequence of *A. elegans* (GenBank AF432179) was aligned with selected sequences for *Xylaria* and similar genera reported by Lee et al. 2000. GenBank accession numbers for these sequences are included on Fig. 3. Alignments were calculated using the pileup option of GCG 10.1 (Canadian Bioinformatics Resource http://www.cbr.nrc.ca/) with a gap weight of 5 and a gap length penalty of 1. Parsimony analysis of alignments were performed with PAUP *4.0b8 (Swofford 1999) using heuristic searches with uninformative characters removed, and further evaluated using bootstrap analysis with 1000 replications.

## Results

Phylogenetic analysis. Parsimony analysis of the partial nuclear small subunit sequence placed *A. elegans* clearly in the *Xylariaceae*, sister to *Xylaria carpophila* Z49785, and also closely related to *Poronia punctata* AF064052, *Xylaria curta* U32417 and *X. hypoxylon* U20378 with weak bootstrap support for the topology, which was otherwise robust based on the strict consensus (results not shown).

The complete ITS alignment was 586 characters. To create a data set that was comparable for all sequences, 28 bp at the beginning and 56 bp at the end of the alignment were omitted. Removal of uninformative positions left a remainder of 167 characters. Heuristic searches resulted in four equally parsimonious trees of 464 steps (CI 0.641, RI 0.586, RC 0.381 and HI 0.349). The ITS-based phylogenetic hypothesis placed *A. elegans* in the *Xylariaceae* with strong bootstrap support. The topology of the tree presented here (Fig. 3) compares well with the more detailed analysis of Lee et al. (2000), placing *A. elegans* basal to Groups A and B of *Xylaria*.

## Taxonomic Part

**Arthroxylaria elegans** Seifert et W. Gams, gen. et sp. nov. Figs. 1, 2

Synnemata indeterminata, ad 6 cm alta, albida vel cremea in parte sterili basilari, in parte fertili olivaceo-viridia et 300–1000 $\mu$m lata, apicem versus modice rosea, filiformia, sinuosa, rotunda in sectione, gregaria vel caespitosa, simplicia vel in quavis parte ramis aequalibus dichotoma vel trichotoma, in parte fertili tomentosa vel lanosa. Hyphae stipitis 1.5–3 $\mu$m latae, hyalinae, tenuitunicatae, septis simplicibus divisae. Arthroconidia catenis 50–280 $\mu$m longis adhaerentia, (0-)1(-3)-septata, 3.5–8 $\mu$m lata, conidia 0-septata 7.5–13 $\mu$m longa, 1-septata 12.5–21 $\mu$m, 3-septata 28–38 $\mu$m, quorum cellulae globosae, subglobosae vel oblongae ellipsoideae, aequales vel inaequales, ad septum constrictae an

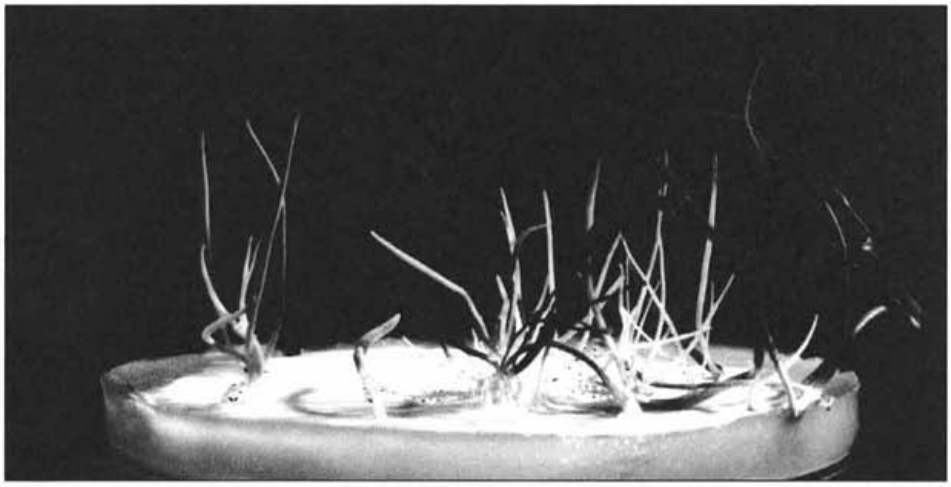

**Fig. 1.** *Arthroxylaria elegans*, ex-type culture on OA. Habit of synnemata growing on deep oatmeal agar with the lid replaced by a beaker to allow indeterminate growth.

non, tenuitunicatae vel modice crassitunicatae, nonnumquam asperulatae; conidia utrinque applanata et magis tenuitunicata, eximie cicatricata. Synanamorphosis polyblastica e catenis arthroconidiorum oriunda, cellulis conidiogenis 30–70 μm longis, hyalinis, denticulatis, conidiis 2–4.5 × 1.5–2.5 μm, ovoideis vel ellipsoideis. Chlamydosporae submersae, intercalares, hyalinae, 6.5–10 μm diam.

Holotypus: U.S.A., California, Cottonwood Springs, May 15, 1977, leg. R. K. Benjamin, dried culture of CBS 537.79 (Herb. CBS)

Synnemata indeterminate, up to 6 cm tall, white to cream-coloured in the basal sterile 1–2 mm, olive-green and 300–1000 μm wide in the sporulating area, slightly pink at the growing tip, filiform, sinuous, terete, gregarious or caespitose, unbranched or with dichotomous or trichotomous equivalent branches anywhere along the stipe, tomentose to lanose in the fertile zone. Hyphae of stipe 1.5–3 μm wide, hyaline, with smooth, thin walls and simple septa. Arthroconidia forming chains 50–280 μm long, (0-)1(-3)-septate, 0-septate conidia 7.5–13 μm long, 1-septate conidia 12.5–21 μm long, 3-septate conidia 28–38 μm long, all conidia 3.5–8 μm wide, individual cells globose, subglobose to oblong-ellipsoidal, with cells of equal size or one smaller, constricted or not at the septum, walls thin to slightly thickened, sometimes slightly rough, resulting in flattened poles with slightly thinner walls and a minute frill.

Secondary conidiophores sometimes developing from the apex of arthroconidial chains, hyaline, unbranched or with 1–2 lateral branches, up to 100 μm long, 1–2 μm wide. Secondary conidiogenous cells 30–70 μm long, hyaline, proliferating sympodially, with 1–15 proliferations forming a terminal conidiogenous zone

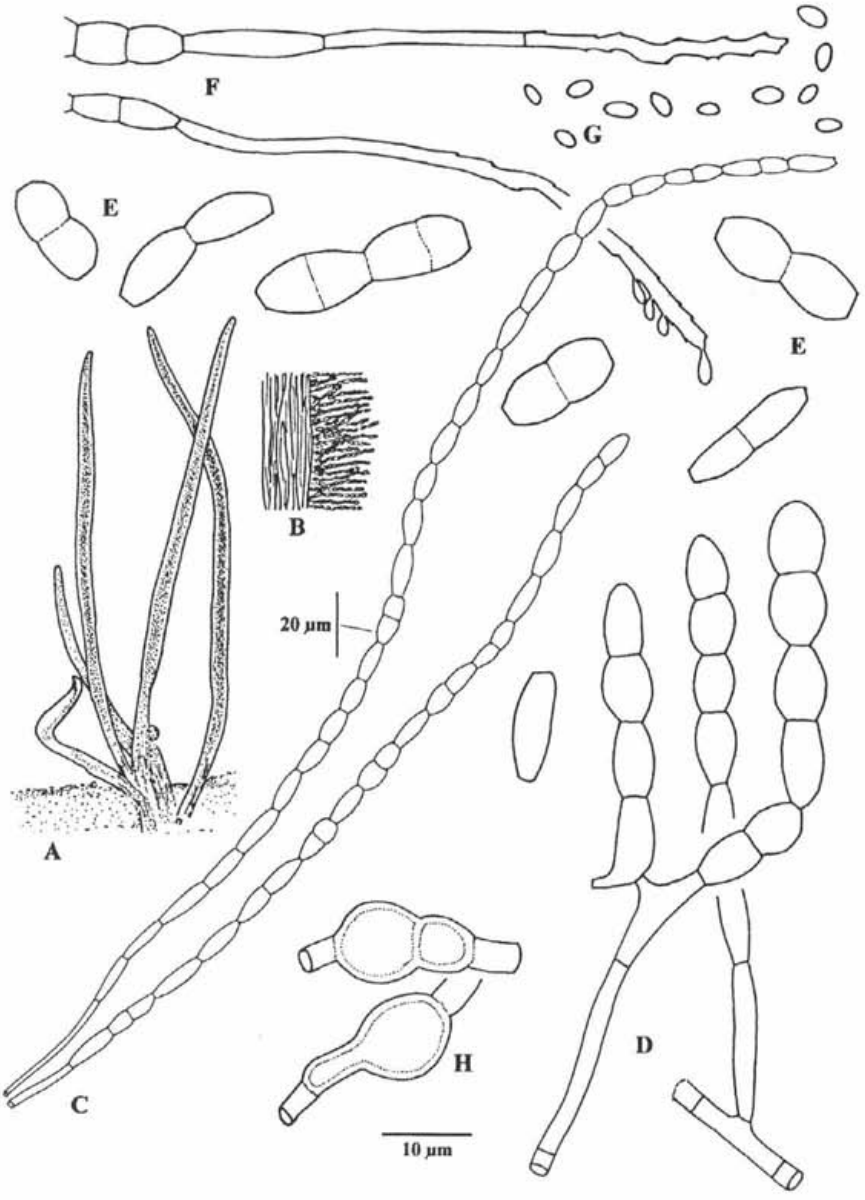


**Fig. 2.** *Arthroxylaria elegans*, ex-type culture on OA, habit sketches and camera lucida drawings. **A.** Habit. **B.** Diagramatic section of synnema showing arrangement of conidial chains. *C.* Complete conidial chains. **D.** Partial conidial chains. *E.* Seceded conidia. **F.** Sympodially-proliferating conidiogenous cells of the synanamorph. **G.** Conidia of the synanamorph. *H.* Chlamydospores imbedded in agar. Scale bar at bottom for all figures except A-C. A, B not to scale.

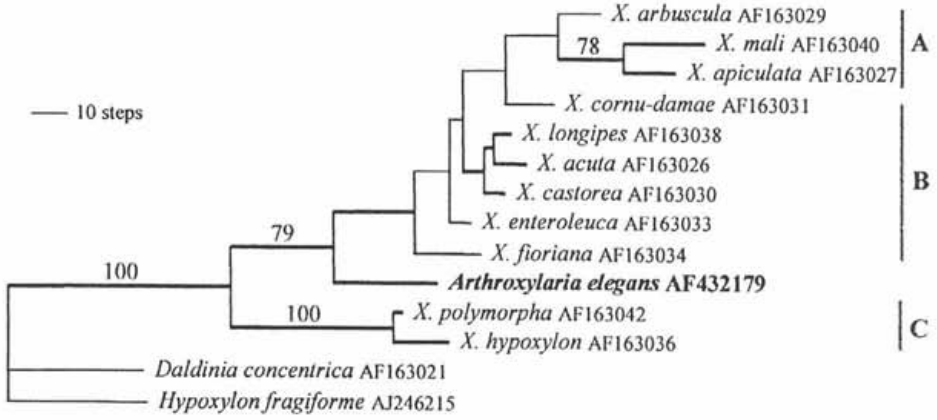


**Fig. 3.** One of four equally parsimonious phylograms showing postulated relationships between *Xylaria* species and *Arthroxylaria elegans* based on heuristic analysis of internal transcribed spacer (ITS) sequences. The groups A-C identified within *Xylaria* by Lee et al. (2000) are shown on the right of the figure. Branches in bold occur in all equally parsimonious trees. Bootstrap values above 50% are based on 1000 replicates. See Results for further details.

up to 30 μm long, 1–2 μm wide, proliferations visible as minute denticles or notches, sometimes with single denticles up to 1.5 μm on intercalary cells of the conidiophore. Secondary conidia 2–4.5 × 1.5–2.5 μm, ovoid to ellipsoidal.

Colonies on OA at 25 °C under ambient light 19–24 mm diam after 7 days, 32–37 mm diam after 14 days, covered with cottony to lanose white aerial mycelium about 1 mm deep, with vague concentric zonation, margin gnawed, reverse white to cream, mottled, with brown spots. Hyphae 2–3.5 μm wide, with swollen cells up to 9 μm wide, hyaline, with thin, smooth walls. Chlamydospore-like cells intercalary in submerged hyphae, hyaline, 6.5–10 μm diam, walls smooth, about 0.5 μm thick. Synnemata developing near the inoculum after 1 week. Colonies on MEA at 25 °C under ambient light 18–23 mm diam after 7 days, 34–37 mm diam after 14 days, with cottony to felty white aerial mycelium up to 2 mm deep near the inoculum and in patches elsewhere, surface light brown, wrinkled, margin gnawed, reverse cream to light orange-brown, wrinkled, with concentric zonation. Synnemata scattered over the colonies on OA and MEA, starting to develop within 2 weeks; if the Petri dish lid was left in place, the synnemata grew into it and spread rádially to form an arachnoid aerial growth.

Material examined: CBS 537.79 (= UAMH 4811 = IMI 286722 = DAOM 226684), ex-type culture, USA, California, San Bernadino Co., Cottonwood Springs, N. side of Mid Hills, New York Mountains, isol. from pack rat dung by R. K. Benjamin, # RSA 2455, 15 May 1977.

## Discussion

*Arthroxylaria elegans* is a coprophilous hyphomycete distinguished by the production of tall, lightly pigmented, indeterminate synnemata covered with long, dry chains of usually 0–1-septate conidia that sometimes terminate in a sympodially proliferating conidiogenous cell bearing minute, aseptate microconidia. Conidium ontogeny on the primary conidiophores of this fungus follow the meristem arthroconidium pattern (Hughes 1953). Contorted hyphae grow laterally and terminally from the growing synnema. These hyphae become septate as they grow, and the cells then swell in a retrogressive sequence, resulting in constrictions at the septa. Mostly 2-celled conidia mature while in the chain, giving the now fertile hypha a monilioid appearance. Conidia maturing near the base of the chain tend to be less swollen, cylindrical to clavate, and aseptate. Secession is schizolytic.

Parsimony analyses of partial small subunit and internal transcribed spacer ribosomal DNA sequences clearly place this fungus in the *Xylariales*, allied with species of *Xylaria*. The production of stipitate, anamorphic stromata is a common feature in this order, as is the production of a sympodially proliferating microconidial synanamorph (often referred to as selenosporella-like). Although synnematous anamorphs are relatively common in the *Xylariales* (classified in genera such as *Acanthodochium* Samuels, Rogers et Nagasawa, *Dematophora* R. Hartig, *Moelleroclavus* P. Hennings, *Nodulisporium* Preuss and *Xylocoremium* J. D. Rogers), these anamorphs all have sympodially-proliferating conidiogenous cells, each aperture producing a single, blastic conidium with a truncate base. The known anamorphs of *Xylaria* tend to be produced directly on the immature teleomorph stroma, or are known only from culture (eg. Callan & Rogers 1990, van der Gucht 1996, Ju & Rogers 1999). Although anamorphs are considered an important taxonomic character in *Xylaria* (Rogers 1985), most lack anamorph-generic names (Whalley 1996). Exceptions include the synnematous *Moelleroclavus* anamorph reported for *X. moelleroclavus* Rogers et al. (1997). *Xylocoremium flabelliforme* (Schw.) J. D. Rogers is the anamorph of *Xylaria cubensis* (Mont.) Fries (Rogers 1984), a species that is separate from the main groups of *Xylaria* according to the ITS analysis of Lee et al. (2000).

Apart from *A. elegans*, meristem arthroconidium production is unknown in the *Xylariales*. There are a few aberrant anamorphs in this order that do not always conform to the typical pattern, however. The *Lindquistia* anamorphs of *Poronia* species produce typically xylariaceous conidiogenous cells on a capillitium-like mass of interwoven conidiophores at the apex of synnematous conidiomata. The cells of the conidiophores sometimes disarticulate, resulting in hyphal fragments capable of germinating and acting as propagules (Rogers & Læssøe 1992).

There are a few synnematous hyphomycete genera with arthroconidia that warrant comparison with *Arthroxylaria*. None of these have known teleomorph

connections or available DNA sequence data, so their phylogenetic relationships remain unknown.

*Briosia ampelophaga* Cavara is most similar. This species causes lesions on leaves of *Vitis* vines, produces short (<500 μm tall) unpigmented synnemata terminating in branched chains of golden-brown, aseptate conidia. The conidia are meristem arthroconidia that mature in basipetal sequence and are cuboid when in the chain, but become globose after schizolytic secession (Sutton 1973).

*Arthrographis cuboidea* (Sacc. et Ellis) Sigler produces minute synnema-like conidiomata on wood, with dry, terminal heads of schizolytically-seceding, fission arthroconidia (Sigler & Carmichael 1983).

*Coremiella cubispora* (Berk. et M. A. Curtis) M. B. Ellis produces small (<1 mm tall) determinate synnemata on dying or dead plants, with dry, terminal capitula comprising divergent chains of alternate, cuboid arthroconidia (Ellis 1971). Separating cells in the conidial chains lose their cytoplasm and break, a type of rhexolytic conidial secession. The conidia have characteristic, doliipore-like occlusions at both ends, visible with light microscopy (Cole & Samson 1979).

The poorly understood soil hyphomycete *Bisporostilbella fusca* Brandsberg et E. F. Morris (1971) also warrants comparison with *Arthroxylaria*. Our examination of the dried agar cultures that comprise the holotype of *B. fusca* (WSP 58777) revealed radiating, feathery to funiculose dark olivaceous-brown colonies (Fig. 4). The feathery or funiculose bundles of hyphae, which are several mm long (Fig. 4a), are not synnemata in the usual sense of the term (Seifert & Okada 1990). Marginal hyphae of the bundles may be sterile and bear contorted short branches (Fig. 4e), or integrated, lateral or discrete, terminal conidiogenous cells may be produced (Fig. 4e). The bundles terminate in divergent, branching, dematiaceous hyphae that become frequently septate, and bear terminal or lateral conidiogenous cells (Fig. 4b, c). Conidiogenous cells are 3–7.5 μm long and 2–4.5 μm wide. The base of the conidium is truncate, lying flat against the conidiogenous aperture, but we saw no evidence of the percurrent proliferations of the conidiogenous cells described in the protologue, although percurrent regeneration of the conidiophore was observed (arrowhead in Fig. 4c). Indeed, the mechanism for the production of conidial chains could not be deduced from the specimen, and it was unclear whether conidium ontogeny is blastic or thallic. Conidial secession is clearly schizolytic. Chains of 2–4 conidia were noted. Each conidium is 5–6 × 3–4.5 μm, olivaceous-brown, ellipsoidal to somewhat doliiform, with a single thick, darkened septum, sometimes constricted at that septum, with lateral walls that are conspicuously thicker than the polar walls (Fig. 4d). Unfortunately, a culture derived from the holotype of *B. fusca* (CBS 253.72) is now a *Cladosporium* sp. and no longer represents the original fungus. Thus *B. fusca* remains an enigma, but our impression of the holotype is of a fungal culture expressing aberrant morphology that may be unrepresentative of the wild type of the fungus.

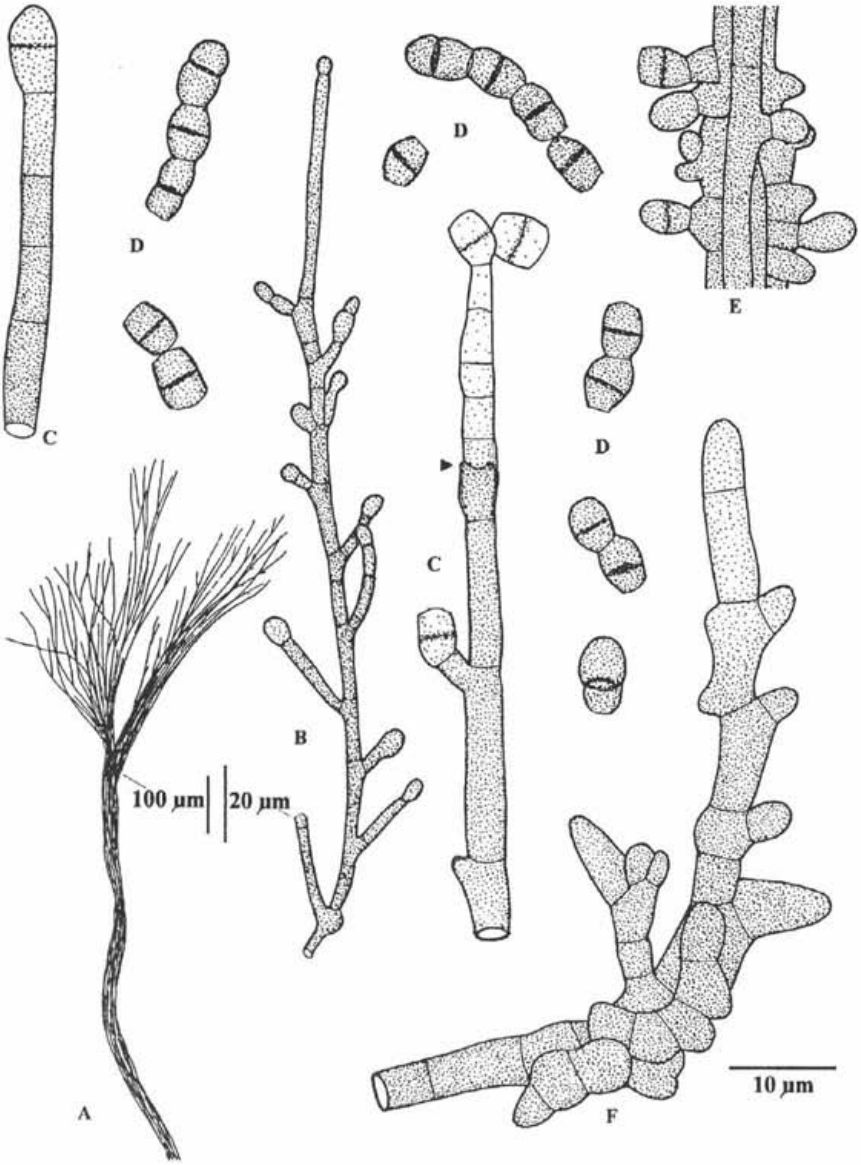


**Fig. 4.** *Bisporostilbella fusca*, holotype, camera lucida drawings, showing feathery hyphal aggregations, conidial chains and seceded conidia. **A.** Synnema-like bundles. **B, C.** Terminal hyphae bearing conidia; the arrow in C indicates percurrent regeneration of the conidiogenous hypha. **D.** Conidia. **E.** Part of hyphal bundle with lateral conidiogenous cells. **F.** Contorted, branched hypha from side of hyphae bundle. Scale in lower right for all figures except A, B.

If the synnematous nature of the conidiomata of *Arthroxylaria elegans* is discounted, there are some mononematous hyphomycetes producing similar chains of conidia of mixed arthric and blastic conidiogenesis. *Basipetospora chlamydosporis* Matsushima (1975), for example, produces erect, branching aerial hyphae that are converted into chains of 4–10 conidia, with the longest conidia generally near the middle of the chain. Like *A. elegans*, *B. chlamydosporis* also produces chlamydospores. Phylogenetic analysis of partial small subunit ribosomal DNA sequences of three cultures identical with or similar to this species [listed as *Monilia pruinosa sensu* Gilman CBS 249.68 (AF437893), CBS 217.74 (AF437894) and *Basipetospora variabilis* Mats. 995.87 (AF437892)] suggests that it is unrelated to the *Xylariales* and hence *Arthroxylaria*. It instead has affinities with the *Microascales* (Seifert & Louis-Seize, unpublished), and is consequently also unrelated to *Basipetospora rubra* Cole & Kendrick, the anamorph of *Monascus ruber* van Tiegham (*Eurotiales*). Similar undescribed anamorphs are found in the *Sporormiaceae* and *Onygenales*.

*Arthroxylaria elegans* illustrates the taxonomic and nomenclatural dilemma presently posed by anamorphic fungi (Seifert & Samuels 2000). No teleomorph is known but the fungus is clearly related to *Xylaria* based on parsimony analysis of rDNA sequences. Morphologically, the conidiogenesis of the fungus is dissimilar from other known anamorphs in this group, although the synnema may be a homologous structure to the erect, multiloculate perithecial stroma that characterizes *Xylaria*. Does this fungus really require the formal description of a genus? There are no provisions in the International Code of Botanical Nomenclature to allow the naming of an anamorphic species in a teleomorphic genus in the absence of the morphological manifestation of a sexual apparatus. We argue that a well-defined descriptor is necessary for such a distinctive anamorph, to facilitate its identification by morphological means when the teleomorph (if extant) is not seen.

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## REFERENCES

BRANDSBERG J. W. and MORRIS E. F. (1971): A new stilbellaceous fungus from Missouri soil. – Mycologia 63: 1076–1080.

CALLAN B. E. and ROGERS J. D. (1990): Teleomorph-anamorph connections and correlations in some Xylaria species. – Mycotaxon 36: 343–369.

COLE G. T. and SAMSON R. A. (1979): Patterns of Development in Conidial Fungi. – 190 p. Pitman, London.

ELLIS M. B. (1971): Dematiaceous Hyphomycetes. – 608 p. Commonwealth Mycological Institute, Kew.

GAMS W., HOEKSTRA E. S. and APTROOT A. (eds.) (1998): CBS Course of Mycology, $4^{th}$ ed. – 165 p. Centraalbureau voor Schimmelcultures, Baarn, Delft.

HUGHES S. J. (1953): Conidiophores, conidia, and classification. – Can. J. Bot. 31: 577–659.

JU Y. M. and ROGERS J. D. 1999. The Xylariaceae of Taiwan (excluding Anthostomella). – Mycotaxon 73: 343–440.

LEE J. S., KO K. A. and JUNG H. S. (2000): Phylogenetic analysis of Xylaria based on nuclear ribosomal ITS1–5.8S-ITS2 sequences. – FEMS Microbiol. Letters 187: 89–93.

MATSUSHIMA T. (1975): Icones microfungorum a Matsushima lectorum. – 209 p, 415 pl. Published by the author, Kobe, Japan.

ROGERS J. D. (1984): Xylaria cubensis and its anamorph Xylocoremium flabelliforme, Xylaria allantoidea, and Xylaria poitei in continental United States. – Mycologia 76: 912–923.

ROGERS J. D. (1985): Anamorphs of Xylaria: Taxonomic considerations. – Sydowia 38: 255–262.

ROGERS J. D., JU Y. M. and HEMMES D. E. (1997): Xylaria moelleroclavus sp. nov and its Moelleroclavus anamorphic state. – Mycol. Res. 101: 345–348.

ROGERS J. D. and LÆSSØE T. (1992): Podosordaria ingii sp. nov. and its Lindquistia anamorph. – Mycotaxon 64: 435–443.

SEIFERT K. A. and OKADA G. (1990). Taxonomic implications of conidiomatal anatomy in synnematous hyphomycetes. – Stud. Mycol. 32: 29–40.

SEIFERT K. A. and SAMUELS G. J. (2000): How should we look at anamorphs? – Stud. Mycol. 45: 5–18.

SIGLER L. and CARMICHAEL J. W. (1983): Redisposition of some fungi referred to Oidium microspermum and a review of Arthrographis. – Mycotaxon 18: 495–507.

SUTTON B. C. (1973): Hyphomycetes from Manitoba and Saskatchewan. – Mycol. Pap. 132: 1–143.

SWOFFORD D. (1999): PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b8. Sinauer Associates, Sunderland MA.

VAN DER GUCHT K. (1996): Xylaria species from Papua New Guinea: Cultural and anamorphic studies. – Mycotaxon 60: 327–360

WHALLEY A. J. S. (1996): The xylariaceous way of life. – Mycol. Res. 100: 897–922.

WHITE T. J., BRUNS T., LEE S. and TAYLOR J. W. (1990): Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – In: PCR Protocols: A Guide to Methods and Applications. In: Innis M. A., Gelfand D. H., Sninsky J. J. and White T. J. (eds). p. 315–322, Academic Press, New York.