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Anamorphs of *Xylaria*: Taxonomic Considerations

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Abstract. – *Xylaria* is divided into four sections on the following anamorphic characters: the presence of the anamorph on all parts of the immature teleomorphic stroma; the presence of the anamorph only on specialized appendages of the immature teleomorphic stroma; the presence of the anamorph on specialized and separate anamorphic structures and its total absence from the teleomorphic stroma; the production of pairs of dissimilar conidia which are forcibly discharged from the immature teleomorphic stroma. The usefulness of anamorphic features in delimiting *Xylaria* from *Hypoxyton*, *Poronia*, and *Podosordaria* is discussed.

Xylaria HILL ex SCHRANK is a complex and difficult genus for a number of reasons. Stromata of most species persist from several months to a year. During the period from initiation to maturation and subsequent disintegration, stromata of many species undergo profound changes. For example, immature stromata of some species bear conidia in a pinkish or whitish layer. As underlying perithecia develop, the conidial layer begins to shred or flake off, revealing a darker color beneath. The dominant color, however, might continue to be the same as the dehiscing outer layer. Eventually, these stromata become uniformly black. Some of these same species at first have a solid, white entostroma which, over time, deteriorates. The older stromata become hollow. Thus, depending upon their age and condition, stromata of a single species might be described as more or less white, or black with a white shredding outer layer, or black. The interior might be described as solid and white or hollow.

Stromata of many species or species complexes have different growth forms. For example, members of the *X. polymorpha* (PERS.: FR.) GREV. complex range from cylindrical or clavate and upright (xylarioid) to more or less hemispheric with short thin stipes (penzigoid or kretzschmarioid) to almost sessile (hypoxyloid). These various growth forms, taxa, and subtaxa range in size from ca. 1–2 mm high and 1–2 mm thick to 10 or more cm high and 2 cm thick. Various of them are found in almost every part of the world. Some of the more common members of the complex are *X. schweinitzii* BERK. & CURT., *X. anisopleura* (MONT.) FR., *X. tuberiformis* COOKE, *Kretzschmaria knysnana* van der BIL, and various *Penzigia* species.

Many *Xylaria* species have wide geographical distributions. For example, *X. feejeensis* (BERK.) FR. and *X. cubensis* (MONT.) FR. are found in various widely separated parts of the world. Cultural studies reinforce collection data to support the concept of cosmopolitan distributions of the above-cited species (ROGERS, 1984 b; unpublished data) and probably will do so in numerous other cases. It is probable that many *Xylaria* taxa were initially distributed during the rafting of continents and lesser land masses.

Because of the morphological manifestations of the life stages of most *Xylaria* species, the abundant polymorphisms of many complex species (or species complexes), and the wide distribution of many taxa, most taxa of *Xylaria* have been described more than once. Indeed, circumscribing taxa of *Xylaria*, applying legitimate names, and determining synonyms is fraught with difficulties. FRIES (1851) was the first to seriously attempt to organize *Xylaria* species into groups. He erected four tribes based primarily upon whether or not the stromatal apices bear perithecia and secondarily upon whether or not stromatal stipes are hairy. Many mycologists accepted FRIES' system, including that most perceptive student of pyrenomycetes, T. NITSCHKE (1867), SACCARDO (1882), ELLIS & EVERHART (1892) and WINTER (1887). Most contemporary mycologists still utilize it, at least in part.

MILLER (1942) separated *Xylaria* into two groupings primarily upon the absence or presence of a stromatal layer or pellicle distinct from the one encasing the perithecia. Each of these groupings was secondarily divided upon the absence or presence of sterile (non-perithecial) stromatal tips. DENNIS (1970) likewise emphasized the nature of the stromatal surface layer, including its persistence or nonpersistence and manner of dehiscence. MARTIN (1970) recognized two sections of *Xylaria* primarily on whether the stromatal surface is basically smooth or rough. Most recently, BERTAULT (1984), following in part JOLY (1968), recognized five stirpes based primarily on gross stromatal morphology.

All of the aforementioned schemes for dividing *Xylaria* into manageable units have considerable merit. They are all artificial to some extent, although related taxa are often clustered within subgroups. These systems all are difficult to use consistently, however, because of the polymorphic and often ambiguous nature of some of the major characters employed. Identification of species or species groups using any of the schemes can be accomplished more easily and confidently when more stable characters such as ascospore morphology – particularly the length and configuration of germ slits – and ascus tip ring morphology are also emphasized. CARROLL (1963, 1964), MARTIN (1970), and ROGERS (1984 a, 1984 b and papers cited therein) have utilized ascus and ascospore data in their studies.

Ascospore and ascus tip data, however, have not been published for many taxa.

It has long been known that many *Xylaria* species have anamorphs. Indeed, NITSCHKE (1867) included data on conidial states in his descriptions of European species. Since his time, however, comparatively few descriptions of *Xylaria* species have contained anamorphic data principally because most workers dealt entirely with mature specimens and because culturing was not often attempted. There are two aspects of *Xylaria* anamorphs that have great taxonomic importance – the location of the anamorph in the life cycle and the morphology of the conidiogenous apparatus. PETCH (1924) was among the first to realize that some *Xylaria* species produce anamorphic structures that are separate and distinct from teleomorphic structures, i. e., the young teleomorphic stroma does not produce conidia as do the species described by NITSCHKE (1867). PETCH was instrumental in convincing LLOYD of the separateness of anamorphic and teleomorphic states in certain *Xylaria* species (see ROGERS, 1984 b). LLOYD (1917) also came to realize that in a few of those species that produce the anamorph on young teleomorphic stromata, the conidial state is confined to special appendages, i. e., unlike the species that produce conidia over the entire stroma. It thus has become apparent that *Xylaria* can be divided into at least three groups on the location of the anamorph.

Modern studies have shown that most *Xylaria* anamorphs – regardless of their location in the life cycle – produce conidia holoblastically in a more or less sympodial sequence. The morphology of conidiophores and arrangement of conidiogenous cells have been useful in delineating species. Moreover, cultural characters – especially color of mycelial turf and morphology of stromata – have been useful in characterizing species and should become even more useful as additional species are cultured and compared (see JOLY, 1968; CHACKO & ROGERS, 1981; ROGERS, 1983; 1984 a; 1984 b). I know of only one case where the morphology of conidiogenous structures and discharge are primary characters worthy of consideration beyond the species level. The *Padixonia bispora* SUBRAMANIAN anamorph of *Xylaria furcata* Fr. [= *Xylospira furcata* (Fr.) DENNIS] produces dissimilar pairs of conidia which are forcibly discharged (DIXON, 1965; SUBRAMANIAN, 1972). This kind of anamorph is unlike any other described in *Xylaria* or allied genera and, indeed, DENNIS (1961) segregated *X. furcata* with *X. nigripes* (KLOTZSCH) COOKE and *X. tanganyikaensis* (DENNIS) D. HAWKSW. into subgenus *Pseudoxy-laria* (BOEDJIN) DENNIS on teleomorphic features. The conidial state of *X. tanganyikaensis* is uninvestigated and that of *X. nigripes* not well-understood (see below).

Based upon the foregoing discussion it seems possible to divide *Xylaria*, as follows:

Section I: Conidia produced from palisade of conidiogenous cells over entire young teleomorphic stromata or at least not limited to specialized appendages. Conidiogenesis holoblastic. Conidia produced in more or less sympodial sequence, seceding individually and passively.

A. *Xylaria polymorpha* group. Examples include *X. anisopleura*, *X. bulbosa* (PERS. : FR.) BERK. & BR., *X. curta* FR., *X. feejeensis*, *X. longipes* NITS., *X. obovata* (BERK.) FR., *X. polymorpha*, *X. schweinitzii*, *X. tuberiformis*, and probably, *X. castorea* BERK.

Some of these species can now be separated on conidial and cultural features (ROGERS, 1983; 1984 a; 1984 b).

B. *Xylaria hypoxylon* group. Examples are *X. acuta* PECK, *X. cornu-damae* (SCHW.) FR., *X. carpophila* (PERS. : FR.) FR., *X. digitata* (L. : FR.) GREV., *X. hypoxylon* (L. : FR.) GREV., *X. magnoliae* ROGERS, *X. mali* FROMME, *X. oxyacanthae* TUL., *X. persicaria* (SCHW. : FR.) BERK. & CURT. Some of these species can be separated on conidial and cultural features (CHACKO & ROGERS, 1981; ROE, 1974; ROGERS, 1983; 1984 a; 1984 b; STOWELL & ROGERS, 1983).

C. *Xylaria multiplex* group. Examples are *X. apiculata* COOKE, *X. arbuscula* SACC., *X. multiplex* (KUNZE) FR., *X. schreuderiana* van der BIJL.

D. *Xylaria pyramidata* group. Examples are *X. guaranitica* (SPEG.) DENNIS, *X. pyramidata* BERK. & BR.

E. *Xylaria pedunculata* group. Examples are *X. agariciformis* COOKE & MASSEE, *X. chardoniana* (TORO) J. H. MILLER, *X. pedunculata* (DICKS.) FR.

KRUG & CAIN (1974) considered these latter two species to be taxa of *Podosordaria*. Anamorphic data are required to resolve the disposition of these taxa, in my opinion (see later).

Section II: Conidia produced upon special and localized peg- or hair-shaped appendages on young teleomorphic stromata. Conidiogenesis apparently holoblastic. Conidia apparently seceding individually and passively.

A. *Xylaria comosa* group. Examples are *X. comosa* (MONT.) FR., *X. tentaculata* BERK. & BR.

Section III: Conidia produced upon special anamorphic stromata or coremia which usually are produced earlier in the year than teleomorphic stromata. Teleomorphic stromata never bear conidia. Conidiogenesis holoblastic. Conidia produced in more or less sympodial sequence, seceding individually and passively.

A. *Xylaria cubensis* group. Example is *X. cubensis* which has been shown by field observation and cultural studies to have a *Xy-*

locoremium flabelliforme (SCHW. : FR.) J. D. ROGERS anamorph (ROGERS, 1984 b). Other probable members of this group include *X. allantoidea* (BERK.) FR., *X. guyanensis* (MONT.) FR., and *X. poitei* (LÉV.) FR.

PETCH (1924) stated that in the commoner forms of *X. nigripes* „the perithecial stage does not, as a rule, develop from the conidial stage.“ PETCH, however, accepted as forms of *X. nigripes* fungi that I consider to be separate species. Until the taxonomy and biology of *X. nigripes* and its allies have been clarified I am reluctant to include it here. *Xylaria nigripes* is clearly unrelated to *X. cubensis* and its allies and, in any case, would have to be placed in a new group.

Section IV: Conidia produced upon young teleomorphic stromata. Conidiogenesis apparently holoblastic. Conidia produced in tandem, seceding forcibly.

A. *Xylaria furcata* group. Only known example is *X. furcata* with *Padixonia bispora* state.

The above system is only an outline which will be filled in and/or altered as anamorphic data are obtained and correlated with teleomorphic data. Nonetheless, the four sections probably represent natural assemblages of *Xylaria*. For example, sections I, III, and IV are probably only distantly related to each other. Sections I and II might be closely related, but section II taxa have not been investigated in modern times.

BROWN (1913) did a thorough study of the stroma and conidium-bearing appendages of *X. tentaculata*, but the details of conidiogenesis should be reinvestigated. There are many species that cannot yet be confidently assigned to a section. The groups within sections seem to be composed of more or less related species and, in most cases, only a few examples are given.

Can one predict anamorphic features for certain morphological types of teleomorph? There are as yet too few data to be certain, but the possibility seems promising. For example, it is probable that section III anamorphs of the *Xylocoremium* type will be correlated with teleomorphs featuring more or less smooth stromata devoid of peeling or flaking juvenile layers and tan, brown, or yellowish mature stromata. Section I anamorphs – undoubtedly the most numerous – will probably be correlated with teleomorphs featuring more or less wrinkled or otherwise roughened stromata with peeling or flaking layers and blackish adult colors. There are too few known examples of sections II and IV to speculate on anamorph-teleomorph correlations.

There are anamorphic features of *Xylaria* that seem of value in indicating relationships with other genera. The anamorphs of most

investigated *Xylaria* species have conidiogenesis and conidiophore proliferation reminiscent of *Nodulisporium* PREUSS or *Geniculosporium* CHESTERS & GREENHALGH. Many form-taxa of these genera are known anamorphs of *Hypoxyylon* BULL. : FR. and its allies, while many others are as yet unconnected with teleomorphs. *Xylaria* anamorphs – whether borne on young stromata destined to bear perithecia or borne on separate coremia – seem restricted to specialized structures, i. e., they probably do not grow as hyphomycetous molds on wood, leaves, etc. and in culture are usually not found free on the mycelial turf away from stromata or coremia. Anamorphs of many species of *Hypoxyylon*, although often produced on immature teleomorphic stromata, can grow as hyphomycetous molds on various substrates. Most *Hypoxyylon* and species of allied genera produce conidiogenous cells on more or less elaborately branched conidiophores that are not arranged in definite palisades as are those of most *Xylaria* species. The anamorph of *Hypoxyylon deustum* (HOFFM. : FR.) GREV. [= *Ustulina deusta* (HOFFM. : FR.) PETRAK] seems much more like those of *Xylaria* than of *Hypoxyylon* (JONG & ROGERS, 1972) and I regard the fungus as a resupinate *Xylaria*. Species of *Kretzschmaria* FR. have anamorphs similar to that of *H. deustum* and, indeed, MARTIN (1970) regards *H. deustum* as a *Kretzschmaria*, i. e., *K. deusta* (HOFFM. : FR.) Martin. KO & al (1982) present evidence that supports MARTIN's contention (1970).

Anamorphic criteria are among the most decisive in separating *Xylaria* from *Poronia* WILLD. and *Podosordaria* ELLIS & HOLWAY. Conidial states of *Poronia punctata* (L. : FR.) FR. and *P. oedipus* (MONT.) MONT. produce conidia from prostrate hyphae and, in the latter species, from more specialized conidiogenous cells; mycelial and conidiogenous cells often disarticulate and act as propagules (JONG & ROGERS, 1969; STIERS, ROGERS & WATTS, 1973). *Xylaria johorensis* G. MORGAN-JONES & LIM was shown to have an anamorph identical with that of *P. oedipus* and was subsequently transferred to *Poronia* as *P. johorensis* (G. MORGAN-JONES & LIM) G. MORGAN-JONES (MORGAN-JONES & HASHMI, 1973). KOEHN & COLE (1975) concluded that the anamorph of *Podosordaria leporina* (ELLIS & EVERH.) DENNIS is very much like those of *Poronia* species and, indeed, believed that it should be reinstated in *Poronia*. SUBRAMANIAN & CHANDRASHEKARA (1977) erected the genus *Lindquistia* to accommodate anamorphs of *Podosordaria*, the type species *L. indica* SUBRAMANIAN & CHANDRASHEKARA being the anamorph of *Podosordaria leporina*. This form-genus would accommodate the anamorphs of *P. oedipus*, *P. johorensis*, and, probably, *P. punctata*. Although the anamorphs of *P. oedipus* and *P. punctata* are listed by KENDRICK & DICOSMO (1979) as *Xylocladium* SYDOW ex LINDAU and similarities of *Lindquistia* and *Xylocladium* noted by von ARX (1982), these form-

genera are, in fact, highly distinctive and very different. *Xylocladium* has been connected only with applanate *Hypoxyylon* species (JONG & ROGERS, 1972), *Nummularia broomeiana* (BERK. & CURT.) H. MILLER (ROGERS, 1975) and some *Camillea* Fr. species (G. J. SAMUELS & J. D. ROGERS, unpublished). *Poronia pileiformis* (BERK.) Fr. has a *Nodulisporium*-like state (PADEN, 1978) and on this and other criteria might well be removed from *Poronia*, i. e., to *Xylaria*. BOISE (1982) correctly, in my opinion, assigned a newly described fungus to *Xylaria* rather than to *Poronia* partly on the basis of the anamorph. I am hopeful that anamorphic criteria will be utilized increasingly to make taxonomic decisions involving *Xylaria* at every level.

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