

REVIEW

E.B. Gareth Jones

Form and function of fungal spore appendages

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Abstract A wide variety of fungi have spores with appendages or mucilaginous sheaths, which are most elaborate in aquatic ascomycetes, especially marine species. The form and structure of a wide range of appendaged spores are documented from both taxonomic and ecological fungal groups, and their role in nature is discussed. The effect of environmental factors on appendage development and how ascospores are adapted for release from asci are reviewed. How fungi evolved such a variety of appendages in form and structure is also discussed.

Key words Appendaged spores · Attachment · Evolution · Role in nature

Introduction

At one time the study of form and function was in vogue, and for the fungi this reached its pinnacle with the publications of C.T. Ingold on fungal spore liberation and dispersal (Ingold 1965, 1971). A number of publications have focused on spore morphology, ultrastructure, and spore germination (Kendrick 1979). In this review I want to concentrate on appendaged and ensheathed spores, their release, dispersal, settlement, and attachment to surfaces. The major

part of the discussion is devoted to appendaged and ensheathed ascospores, their release from asci, and whether environmental conditions affect the development of these appendages. The primitive and advanced appendaged types, and how they evolved in aquatic and terrestrial habitats, are discussed.

The most intensively studied fungal groups with respect to appendaged spores are the coprophilous and marine taxa (Ingold 1971; Lundqvist 1972; Jones 1994, 1995). However, in recent years a wide range of fungi, both taxonomic and ecological groups, have been shown to possess appendaged spores: Rhytismatales (Canon and Minter 1986; Johnston 1994), palm fungi (Hyde 1994, 1995a,b; Hyde and Fröhlich 1995; Pinruan et al. 2002, 2004), coelomycetes (Nag Raj 1993), Trichomycetes (Lichwardt 1976; Lichwardt and Willimas 1983a; Moss 1998; Misra and Horn 2001), Microthyriaceae (Jones et al. 1999), and freshwater ascomycetes (Hyde et al. 1998a,b; Hyde and Goh 1999, 2003; Fallah and Shearer 2001; Tsui and Hyde 2003), to cite but a few examples. In the early mycological literature the presence of appendages or sheaths was often missed, not observed or reported for reasons of the optics available at the time. Improved optics and scanning electron microscopy (SEM) have revealed the elaborate morphology of appendaged and ensheathed spores. Another reason why appendaged spores may not have been reported was the practice of mounting fungi in glycerin or lactophenol; even lactophenol blue does not always stain appendages.

The form, possession of appendages or ensheathed spores, or the release of a drop of mucilage from the spores have arisen in response to environmental conditions, the result of parallel or convergent evolution (Shearer 1993, 2001; Moss 1990; Jones 1995). A similar observation has been made for tetra-radiate conidia on leaf surfaces in terrestrial habitats (Bandoni 1972; Ando and Tubaki 1984). This group is excluded from further discussion here, and the reader is referred to the studies of Webster (1987) and Descals (2005).

We can divide appendages, or elaboration of the spore wall, into five major groups (Jones 1994; Hyde and Goh 2003):

E.B.G. Jones (✉)

BIOTEC Central Research Unit, Phylogenetics Laboratory, National Center for Genetic Engineering and Biotechnology, National Science and Technology Development Agency, 113 Paholyothin Road, Khlong 1, Khlong Luang, Pathum Thani, 12120 Thailand
e-mail: bhgareth@yahoo.com

This article is dedicated to the late Professor Keisuke Tubaki for his invaluable contribution to mycology and for all his encouragement and support to the author over many years. I appreciate the invitation of the Japanese Mycological Society to write on the above subject, congratulate the society on their 50th anniversary, and wish it well in the coming years.

1. Outgrowths of the spore wall. Outgrowths of the epi- and mesosporium (e.g., in *Corollospora maritima* Werderm., *Halosphaeria appendiculata* Linder, Fig. 1), or of only the episporium [e.g., *Ondiniella torquata* (Kohlm.) E.B.G. Jones, R.G. Johnson, & S.T. Moss, Fig. 8], or exosporial extensions of the spore wall (e.g., in *Ceriosporopsis halima* Linder), or extrusion from a pore or pore fields [e.g., *Magnisphaera spartinae* (E.B.G. Jones) J. Campb., J.L. Anderson, & Shearer, Fig. 12; *Saagaromyces ratnagiriensis* (S.P. Patil & Borse) K.L. Pang & E.B.G. Jones, Figs. 10, 11; *Halosarpheia* sp., Fig. 14].
2. Sheaths that envelope the spore are usually exosporic [e.g., *Sordaria fimicola* (Roberge ex Desm.) Ces. & De Not., Figs. 23–25; *Massarina* and ascospores of bitunicate ascomycetes, Figs. 2, 5, 9). Ascospore sheaths may also be drawn out to form appendage-like structures [e.g., *Decorospora gaudefroyi* (Pat.) Inderb., Kohlm., & Volk.-Kohlm.].
3. Cellular, but not mucilaginous, as outgrowths of the spore wall and common in coelomycete conidia (e.g., *Chaetospermum camelliae* Agnitho., Fig. 4).
4. Mucilaginous drops, the origin of which is often unknown and little studied at the ultrastructural level (e.g., in the hyphomycetes *Sporidesmium*, *Ellisembia*, *Pseudoacrodictys dimorphospora* Somrithipol & E.B.G. Jones, Fig. 19; *Dictyosporium* sp., Fig. 20).
5. Elaboration of the spore wall, but not mucilaginous, e.g., fragmentation of an exosporic layer (e.g., *Groenhiella bivestia* J. Koch, E.B.G. Jones, & S.T. Moss, Fig. 7; *Carbosphaerella leptosphaerioides* I. Schmidt, Figs. 26, 27).

Appendages may be cellular, flexuous, rigid, exposed mucilaginous, or enclosed mucilaginous types (Kirk 1966). For marine fungi, limited information is available on the histochemistry of spore appendages (Kirk 1966, 1976, 1986; Lutely and Wilson 1972; Johnson 1982). Exosporic appendages of *Halosphaeriopsis mediosetigera* Cribb & J.W. Cribb T.W. Johnson are chitinous processes, whereas the mucilage in the end chambers of *Lulworthia medusa* (Ellis & Everh.) Cribb & J.W. Cribb is a mucoprotein. However, in other *Lulworthia* species, the mucilage contains only a carbohydrate moiety (Kirk 1966). In this review I use the term mucilaginous, whereas others refer to appendages as gelatinous or mucoid.

Review of taxonomic and ecological groups with appendaged spores

Marine Ascomycota

Marine Ascomycota greatly outnumber anamorphic fungi in marine habitats, 360/74 respectively, and of these approximately 50% have ascospores with appendages or sheaths (Hyde et al. 2000a).

Jones (1994) reviewed the different types of ascospore appendages in marine Ascomycota and recognized 12 onto-

genetic forms. However, no attempt was made to consider how these had evolved. Sequence analysis of various taxa suggests that appendages have evolved and then been lost during evolutionary times. The polyphyly of the genus *Lindra* (*Lindra thalassiae* Orpurt et al. and *L. obtusa* Nakagiri & Tubaki are placed distantly in sequence analysis of 28S rDNA) is an example of where the mucus-filled end chambers have been lost twice in the Lulworthiales (Campbell et al. 2005). Similarly, in *Saagaromyces* both appendaged [*S. abonnis* (Kohlm.) K.L. Pang & E.B.G. Jones] and nonappendaged [*S. glitra* (J.L. Crane & Shearer) K.L. Pang & E.B.G. Jones] ascospores are known (Pang et al. 2003a,b).

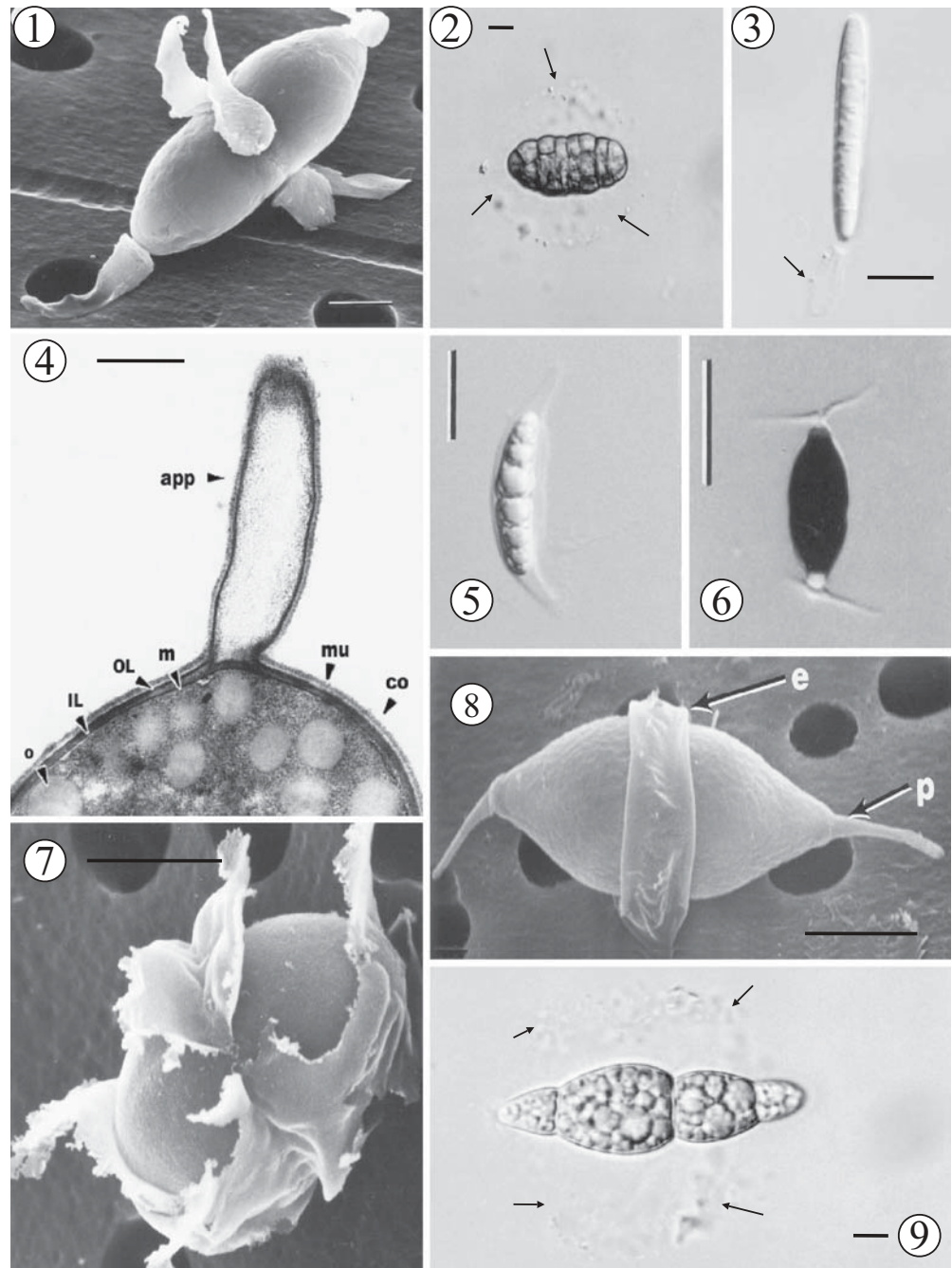
Sakayaroj (2005) mapped the different types of ascospore appendage ontogeny in 52 halosphaeriaceous species onto the most parsimonious tree using MacClade 3.0 and demonstrated there was no discernible pattern in their evolution within the order. For example, ascospores with unfurling bipolar appendages evolved in many distantly placed clades in the tree.

An assemblage of taxa that have a uniform pattern of spore appendage is the Lulworthiales (with the exception of the genus *Lindra*), with an extension of the episporium and mesosporium to form polar end chambers filled with mucilage (Jones et al. 1983; Yusoff et al. 1995). When immersed in water, the mucilage is released as a drop, which on contact with a surface spreads out to form an extensive adhesion pad (Figs. 32–34); this effects rapid attachment to the surface, and the spores are difficult to dislodge (Koch and Jones 1983, 1984; Jones 1995; Yusoff et al. 1995).

A morphological group of marine ascomycetes that appeared to form a coherent assemblage was those with polar hamate appendages that unfurl to form long thin strands: *Aniptodera*, *Cucullosporella*, *Halosarpheia*, *Tirisporella*. Campbell et al. (2003) suggested that at the light microscope level the appendages appeared to be produced in the same manner with little variation between genera and advocated studies at the transmission electron microscope (TEM) level. However, studies have shown there is variation in the way these appendages are formed. In *Aniptodera salsuginosa* Nakagiri & Tad. Ito, polar appendages initially are membranous like and only later differentiate into fine, intertwining filamentous threads (Nakagiri and Ito 1994). An undescribed freshwater *Halosarpheia* species has amorphous appendages with little evidence of a fibrillar component (Figs. 28–31; Jones, unpublished data). Although ascospores of some *Halosarpheia* species have a single long threadlike appendage [e.g., *Halosarpheia fibrosa* Kohlm. & E. Kohlm., *Nantantisporella retorquens* (Shearer & J.L. Crane) J. Campb., J.L. Anderson & Shearer], others appear to be branched (e.g., *A. salsuginosa*). In *Magnisphaera spartinae*, appendage material is extruded through an apical pore (see Fig. 12), while in other species they arise through discontinuities in the episporium (e.g., *Saagaromyces ratnagiriensis*, Figs. 10, 11; *Halosarpheia* sp., Fig. 14). In *Cucullosporella mangrovei* (K.D. Hyde & E.B.G. Jones) K.D. Hyde & E.B.G. Jones, the bipolar unfurling appendages differ in that they comprise two elements: bundles of fibrillar material in an amorphous matrix (Alias et

Figs. 1–9. Various appendaged ascospores.

1 *Halosphaeria appendiculata* polar and equatorial appendages. **2** *Julella avicenniae* with mucilaginous sheath (arrows). **3** *Flammispora bioteca* single polar appendage (arrow) (photograph, U. Pinuran). **4** Transmission electron microscopy (TEM) *Chaetospermum camelliae* section of conidium and appendage delimited from conidium by the inner wall layer, appendage lacks contents; *co*, conidium; *IL*, inner conidial wall separates the conidium from the appendage; *OL*, outer conidial wall that forms the appendage; *app*, appendage; *mu*, mucilage that surrounds the developing conidia and appendages; *m*, plasmalemma, *o*, oil globule (arrowheads) (photograph, N. Plaingam). **5** *Lophiostoma* cf. *armatispora* with the sheath drawn out to form polar appendages. **6** *Savoryella appendiculata* with tetradiate appendages formed after release from the ascus (photograph, Jones and Hyde 1992). **7** Scanning electron microscopy (SEM) of *Groenhiella bivestia* ascospore with a fragmenting sheath to form polar and equatorial appendages. **8** SEM of *Ondiniella torquata* with spinelike polar and a tubular annulus-like equatorial appendage derived from the episporium (photograph, Jones et al. 1983). **9** *Massarina velatospora* with diffuse mucilaginous sheath (arrows). Bars **1, 2, 7–9** 5 µm; **4** 1 µm; **3** 10 µm; **5, 6** 20 µm

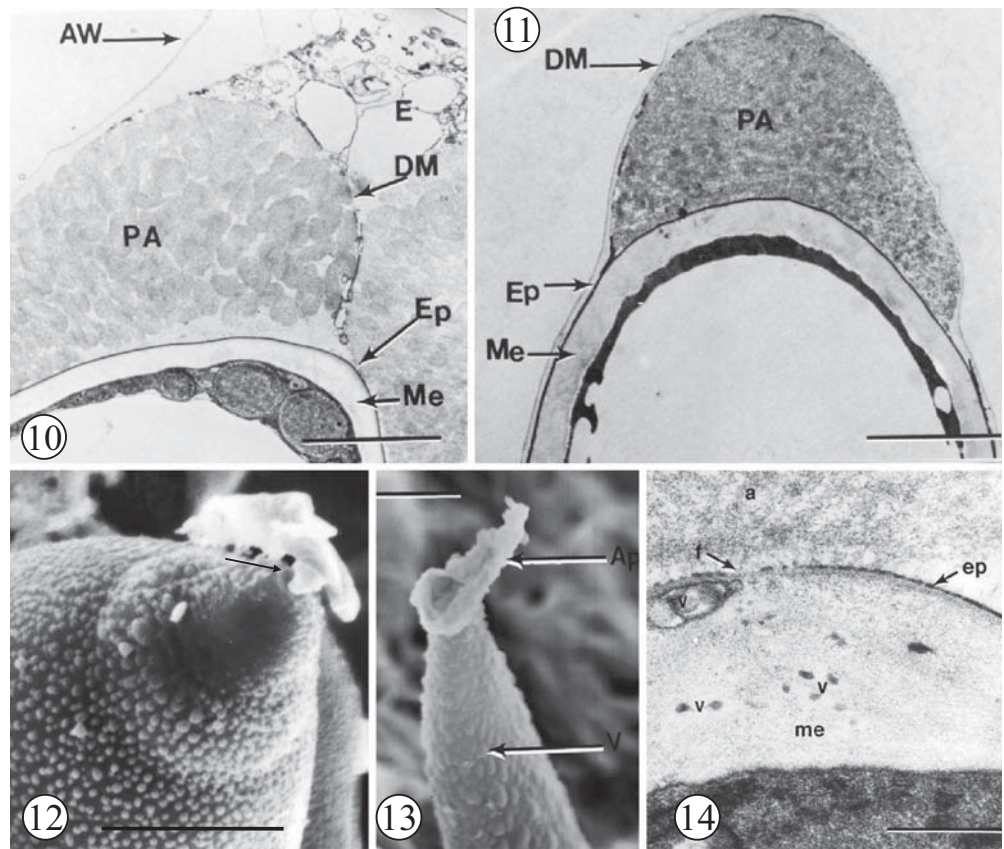


al. 2001). Molecular sequences confirm that *C. manvgrovei* is distinct from *Halosarphaea* and other more recently designated genera (*Natantisporea*, *Panorbis*, *Saagaromyces*). Taxa with unfurling bipolar polar appendages are often distantly placed within the Halosphaeriales, suggesting that this type of appendage has arisen many times during the evolution of the group (Campbell et al. 2003; Pang et al. 2003a,b; Pang and Jones 2004). This is an aspect that warrants further investigation at the ultrastructural level to determine if unfurling polar appendages are stable characters in the delineation of genera in this complex of species.

Marine bitunicate ascomycetes generally possess ascospores with sheaths, as documented for a wide range of

Massarina, *Lophiostoma*, *Phaeosphaeria* species, and other genera (Read et al. 1994, 1996, 1997; Yussuf et al. 1994; Kohlmeyer et al. 1995, 1996; Au and Vrijmoed 2002; Hyde et al. 2002). Occasionally some species also have polar appendages (e.g., *Massarina cystophorae* (Cribb & J.W. Herb.) Kohlm. & E. Kohlm.), or release a drop of mucilage from the spore wall but within the mucilaginous sheath [e.g., *Lophiostoma armatispora* (K.D. Hyde et al.) Liew, Aptroot & K.D. Hyde (Hyde et al. 2002)]. When ejected into water the sheath swells, often exceeding 6 µm in thickness (*M. ramunculicola* K.D. Hyde). However, within the ascus the mucilaginous sheath is highly condensed and surrounded by a delimiting membrane. The delimiting membrane prevents

Figs. 10–14. Transmission and scanning electron micrographs of marine ascospores. **10, 11** *Saagaromyces ratnagiriensis* TEM of polar region of an ascospore with the ascus showing delimiting membrane (*DM*), polar appendage (*PA*), epiplasm (*E*), episporium (*Ep*), and mesosporium (*Me*) (photograph, Baker et al. 2001). **12** SEM of *Magnisphaera spartinae* appendage exuded through a polar pore in the ascospore wall (arrow). **13** SEM of *Tirisporella beccariana* with appendage formed by fragmentation of an exosporic layer, with polar appendage (*Ap*) and verrucose ascospore wall (*V*) (arrows) (photograph, Jones et al. 1996). **14** TEM of *Halosarphaea* sp. with fibrillar (*f*) appendage material exuded through discontinuities in the episporium (*ep*), with appendage (*a*), vacuole (*v*), and mesosporium (*me*) (photograph, S.J. Read). Bars 10–12, 14 5 μ m; 13 20 μ m



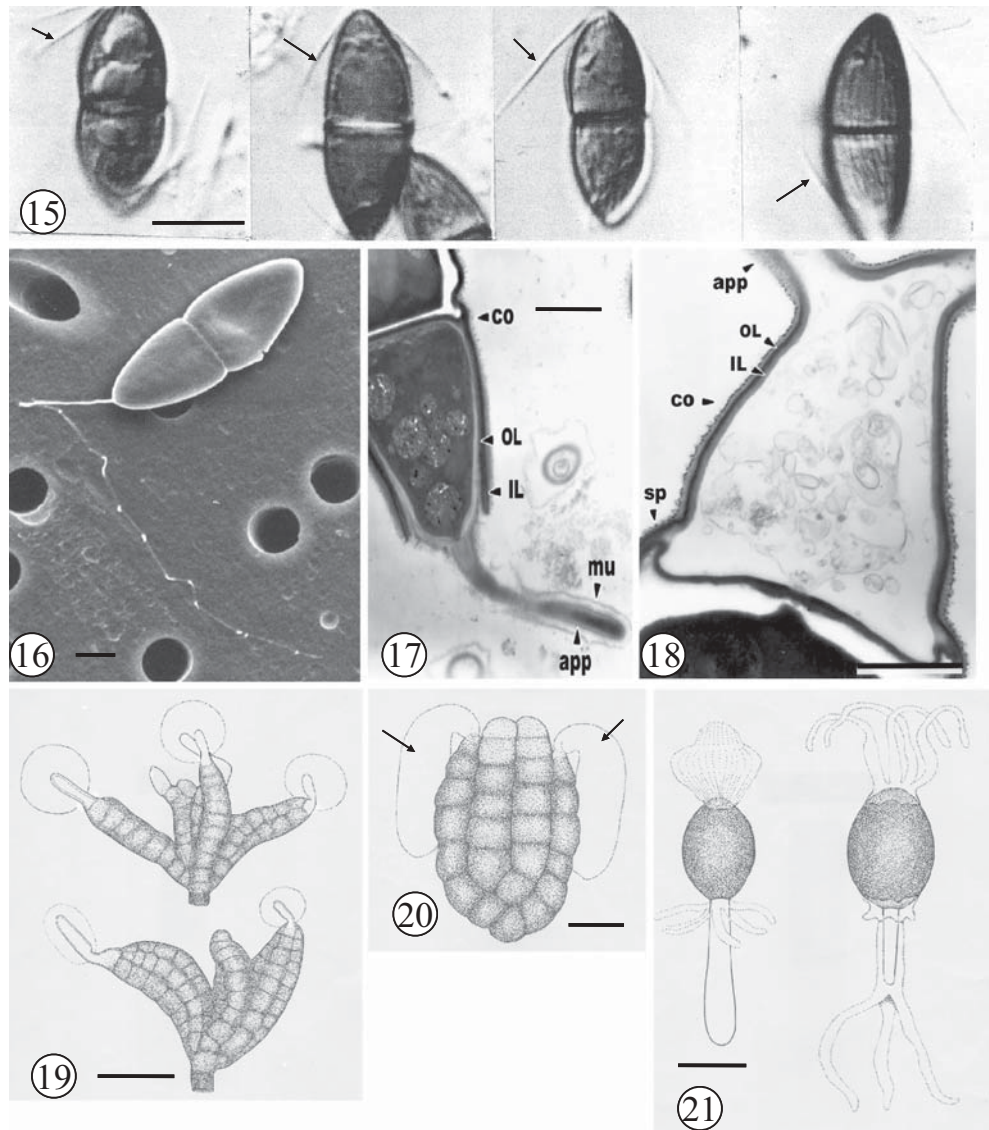
the sheath from swelling until it is ejected from the ascus (*Saagaromyces ratnagiriensis*, see Figs. 10, 11). In *Paraliomyces lentiferus* Kohlm., the ascospore has a gelatinous sheath and a single, gelatinous, lateral appendage adjacent to the central septum (Read et al. 1992). Appendages comprise electron-opaque fibrils that in immature ascospores are connected to the ascospore wall and larger electron-opaque aggregates of material (Read et al. 1992). In *Tirisporella beccariana* (Ces.) E.B.G. Jones, K.D. Hyde & Alias, a single polar appendage is formed by fragmentation of an exosporic ascospore sheath (Fig. 13; Jones et al. 1996).

Freshwater Ascomycota

More than 500 freshwater ascomycetes have been described growing on a variety of substrata, and of these many have ascospores with appendages or sheaths (Shearer 2001; Cai et al. 2003a). In contrast to the marine Ascomycota, most freshwater taxa actively eject their ascospores, although a few have deliquescent asci [*Ascococcus aquaticus* (K.D. Hyde) J. Campb., J.L. Anderson & Shearer (\equiv *Halosarphaea aquatica* K.D. Hyde), *Nais inornata* Kohlm.]. Hyde and Goh (2003) describe six types of ascospore appendages, and these follow the basic plan outlined for their marine counterparts:

1. Release of a drop of mucilage from ascospores; however, few have developed the special end chambers as described for *Lulworthia* species. An exception is *Cataractispora aquatica* K.D. Hyde, S.W. Wong & E.B.G. Jones, which has ascospores with polar chambers (or polar cells) within which fibrillar mucilage accumulates and is exuded to form long threadlike bipolar appendages in water (Hyde et al. 1999). In *Ophioceras* and *Pseudohalonectria* species an inconspicuous mucilage drop is released at the poles of the filamentous ascospores, but its origin has not been determined (Hyde and Goh 1999, 2003),
2. Hamate appendages that uncoil to form thin viscous threads are similar to those reported above for the marine ascomycete genera *Aniptodera*, *Ascococcus*, and *Phaeonectriella* (Halosphaerales). Two genera in the Annulatascaceae have polar appendages. In *Cataractispora bipolaris* (K.D. Hyde) K.D. Hyde, S.W. Wong & E.B.G. Jones, ascospores have padlike appendages that spread out in water to form long drawn-out strands (Ho and Hyde 2000). However, in *Diluvicola capensis* K.D. Hyde, S.W. Wong & E.B.G. Jones, the ascospore appendages are more complex. Ascospores have polar caps (filled with mucilage) that detach from the spore tip when in water, and a single sticky, thin, flexible filament unfurls from within the caps to form long threadlike polar appendages. At the TEM level the

Figs. 15–21. Ascospore and conidial appendages. **15** Undescribed lignicolous bitunicate ascomycete with 1-septate, brown ascospore with bristle-like polar appendages (*arrows*) (photograph, L.L.P. Vrijmoed). **16** SEM of undescribed bitunicate ascomycetes, with 1-septate hyaline ascospores with one polar uncoiling appendage. **17** TEM of *Pestalotiopsis* sp. basal conidial appendage formed as an outgrowth of the inner conidial wall (*app*); mucilage (*mu*), inner conidial wall (*IL*), outer conidial wall (*OL*), and conidium (*co*). **18** TEM of *Pestalotiopsis* sp. polar conidial cell with appendages (*app*) formed as outgrowth of the inner and outer conidial cell wall, with conidia and appendages enveloped by mucilage; septum (*sp*) (photograph, N. Plaingam). **19** Conidia of *Pseudoacrodactyls dimorphospora* with drops of mucilage released from the tips of the conidial branches (photograph, S. Somrithipol). **20** Conidium of *Dictyosporium* sp., with two appendages (*arrows*). **21** Ascospores of coprophilous ascomycetes (*Podospora pleiospora* and *P. dactylina* (redrawn from Bell 1983) with primary and secondary appendages. *Bars 15, 20, 21* 10 μ m; *16* 5 μ m; *17, 18* 1 μ m; *19* 20 μ m



- appendages comprise dense interlinked rodlike fibrils (Hyde et al. 1998b).
- Ascospores with sticky mucilaginous or gelatinous sheaths are frequently encountered in such genera as *Annulatasacus*, *Cyanoannulua*, *Fluviatispora*, *Jahnula*, *Lophiostoma*, *Massarina*, and *Vaginatisspora* (Hyde and Goh 2003; Raja et al. 2003). These sheaths are highly developed and elaborate in species such as *Lophiostoma ingoldianum* (Shearer & K.D. Hyde) Aptroot & K.D. Hyde, *Loramyces juncicola* W. Weston, *Massariosphaeria scirpina* (Wint.) Leichtm., *Patescospora separans* Abdel-Wahb & El-Sar., and *Aliquandostipite khaoyiensis* Inderb. (Inderbitzin et al. 2001; Pang et al. 2002). In *Submersisphaeria bambusicola* D.Q. Zhou & K.D. Hyde, the thin sheath is drawn out at each end (Zhou and Hyde 2000), while in *Jahnula appendiculata* Pinuran, growing on palm material from a peat swamp, ascospores not only have a prominent sheath, but also develop long polar appendages that extend beyond the gelatinous sheath (Pinruan et al. 2002).
 - Padlike appendages are to be found in species such as *Jahnula bipolaris* K.D. Hyde & S.W. Wong (Hyde and Wong 1999) and *Annulatasacus hongkongensis* W.H. Ho, Ranghoo, K.D. Hyde & Hodgkiss (Ho et al. 1999). In *Fluminicola bipolaris* S.W. Wong, K.D. Hyde & E.B.G. Jones, the bipolar appendages initially are appressed to the spore wall, but in water they expand and separate from the wall, but remain attached to it (Wong et al. 1999). They function in the same way as those reported for the marine ascospores in their attachment to substrata (Rees and Jones 1984; Jones 1994).
 - Adhesive spore walls can also aid in the attachment of propagules to substrata, although they may appear smooth at the light microscope level. However, ultrastructural studies of *Savoryella* species reveal the presence of an outer layer of fibrillar mucilage, and this has also been observed in *Rivulicola incrustata* Ranghoo & K.D. Hyde (Read et al. 1993; Hyde et al. 1997).
 - Hyde (1992) reported that *Ascosacculus aquaticus* (= *Halosarpheia aquatica*) ascospores have typical un-

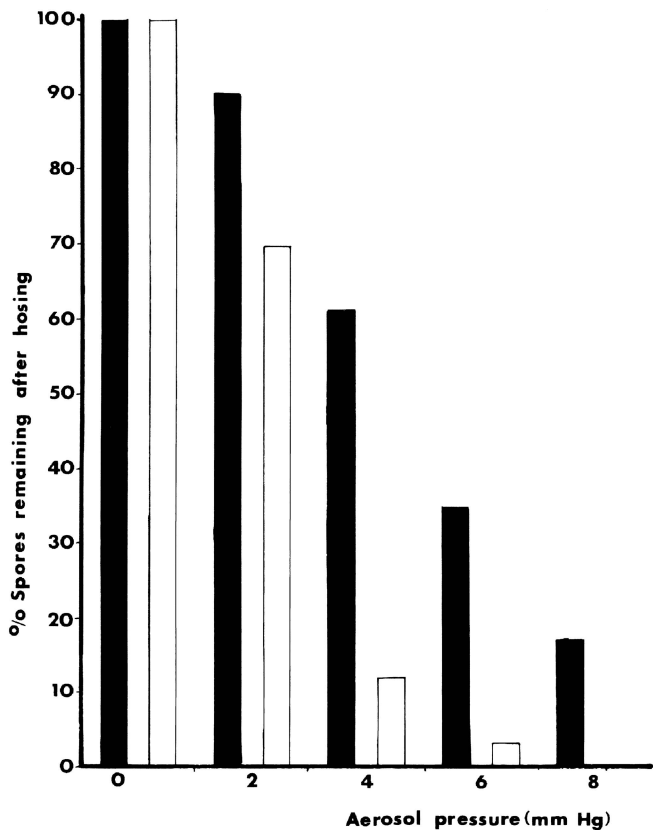


Fig. 22. Percentage attachment of *Sordaria fimicola* ascospores discharged through 1 cm (black column) and 10 cm (open column) after 3 h attachment, and subjected to hosing pressures of 2–8 mmHg

furling bipolar appendages. However, when released into water, they develop outgrowths at the spore apex, which in turn branch to form three or four radiating arms. A similar feature has also been described for the marine ascomycete *Savoryella appendiculata* K.D. Hyde & E.B.G. Jones (Jones and Hyde 1992; Read et al. 1993) (Fig. 6).

Terrestrial Ascomycota

Aptroot (2004) commented that an “increasing number of truly terrestrial ascomycetes with appendages that have recently been described” and proceeded to add a further two from dead leaves. *Funiliomyces biseptus* Aptroot (Amphisphaerales) has ascospores with two gelatinous appendages, one polar and the other median, while in *Munkovalsaria appendiculata* Aptroot (Pleosporales) ascospores possess two polar appendages. However, there is no indication as to the ontogeny of these ascospore appendages. In Figs. 15 and 16, two terrestrial bitunicate ascomycetes with appendages are illustrated, both undescribed taxa from Thailand: one with a single polar unfurling appendage (Fig. 16), the other with polar ciliate appendages (Fig. 15). Ensheathed mucilaginous ascospores are widely distributed in terrestrial ascomycetes [e.g., applanodictyosporus Pleosporales (Shoemaker and

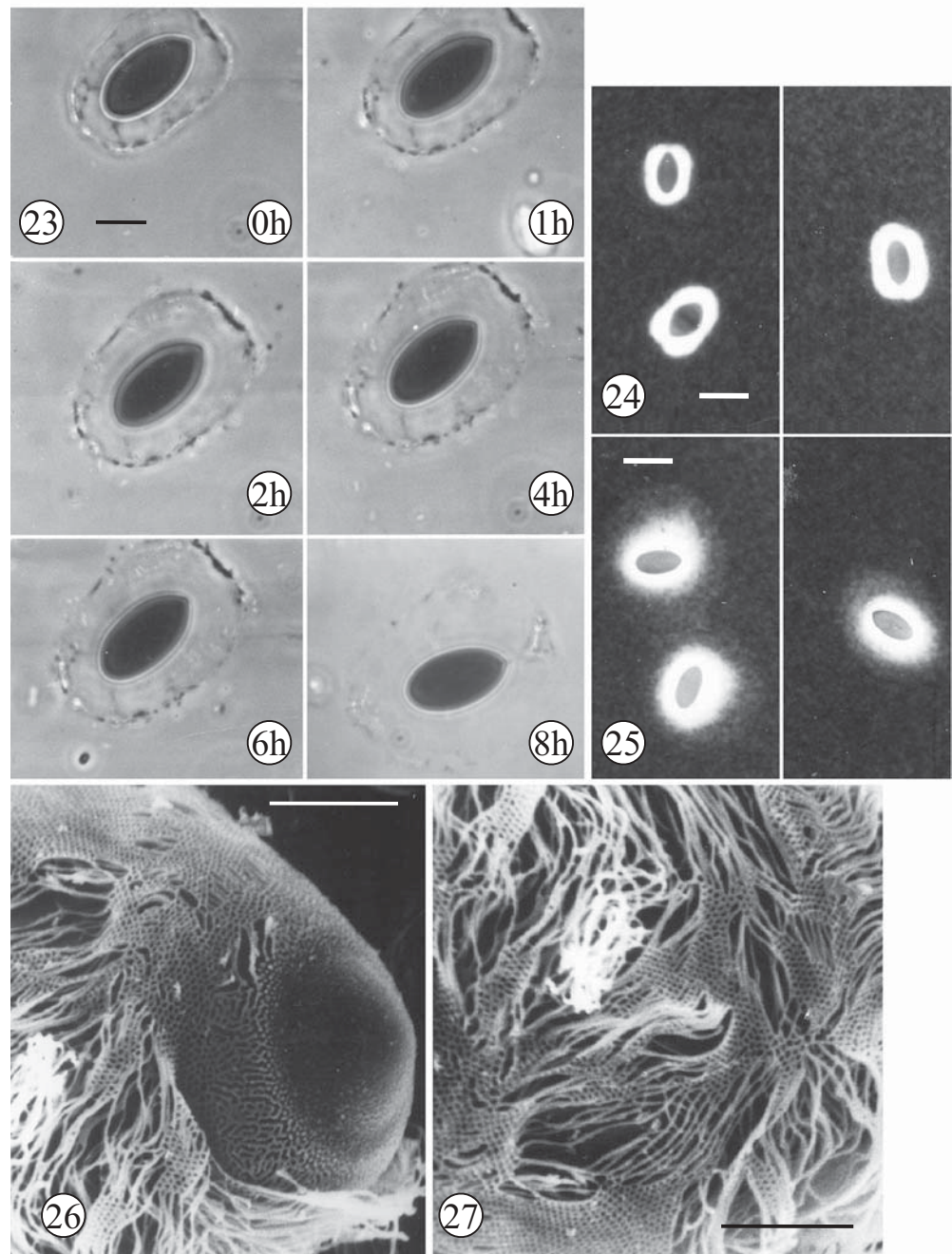
Babcock 1992), *Asteromassarina macroconidica* Kaz Tanaka, Y. Harada & M.E. Barr, *Splanchnoema argus* (Berk. & Broome) Kuntze (Tanaka et al. 2005), and *Katumotoa bambusicola* Kaz. Tanaka & Y. Harada (Tanaka and Harada 2005)].

Ascomycetes on palms have been shown to support a wide range of appendaged or ensheathed ascospores and spores with drops of extruded mucilage (Hyde 1994, 1995a,b; Hyde et al. 2000b; Fröhlich and Hyde 2000; Taylor and Hyde 2003; Duong et al. 2004). Aptroot (2004) expressed surprise that terrestrial ascomycetes on palms should possess appendaged ascospores. However, many of these are from rainforest palms, where there is high humidity with a film of water on the plants for most of the year, which facilitates spore dispersal and aids in the attachment of appendaged ascospores to substrata (Bandoni 1975). A similar observation has been made for the dispersal and attachment of tetradiate conidia on leaf surfaces in terrestrial habitats (Bandoni 1972; Ando and Tubaki 1984).

Hyde et al. (2000b) documented 100 palm fungi genera, the majority of which (67) have some kind of appendages or sheaths. Ascospores with mucilaginous sheaths predominated (52); 20 genera had appendages and 10 genera produced polar mucilaginous pads or a drop of extruded mucilage from the spore wall. Some genera possess species with both appendaged and ensheathed ascospores. Taylor and Hyde (2003) noted that 38% of the palm ascomycetes they listed had appendaged or ensheathed ascospores. Many palm ascomycetes have very thick mucilaginous ascospore sheaths (e.g., *Arecomyces*, *Arecophila*), or the sheath may be morphologically elaborate (e.g., *Carinispora*, *Fronidicola*). In *Durispora*, ascospores have a polar spine, and in *Niesslia* the ascospore sheath is drawn out at the apex (Bauer et al. 2003; Taylor and Hyde 2003). *Oxydothis* species are frequently saprobes of palms, and in *O. alexandrarum* K.D. Hyde the filiform ascospores have bipolar mucilaginous pads with the adhesive released through discontinuities in the episporium (Wong and Hyde 1999). In two *Gnomonia* species from decaying leaves in a tropical rainforest, ascospores have bipolar appendages, initially a gelatinous “pad,” but unfolding at maturity to become fibrillar, flexous, and nonbranching (Paulus et al. 2003).

Why do so many terrestrial ascomycetes have appendaged ascospores? This question applies equally to the Rhytismatales, another group of terrestrial ascomycetes with appendaged or ensheathed ascospores (Cannon and Minter 1986; Johnston 1994; Hou et al. 2005). Of 16 genera listed by Cannon and Minter (1986), only 3 lacked sheaths. Sheaths varied in thickness from 0.5 to 7 μm , depending on genus and species. Most rhytismataceous ascospores possess sheaths, which in *Bifusella seperba* P.F. Canon & Minter are thick and two-layered, whereas in *Meloderma desmazieresii* (Duby) Darker sheaths are clearly visible within the ascus (Cannon and Minter 1986). However, in the genera *Cyclaneusa* and *Propolis*, bipolar caps or gelatinous appendages are present. The possible significance of this is discussed later in this article. Johnston (1994) illustrated appendaged and ensheathed ascospores in selected genera in the Rhytismatales:

Figs. 23–27. Ascospores with sheaths. **23** *Sordaria fimicola* stages in the dilation of ascospore sheaths in water with time 0–8 h, when sheath area increased by 13% at 1 h to 59% at 32 h. **24** Ascospores of *S. fimicola* 3 h after ejection through a 10-cm cylinder, sheath compact. **25** Ascospores of *S. fimicola* ejected through a 1-cm cylinder, sheath wide-spread and diffuse (photographs, R. Healey). **26, 27** SEM micrographs of *Carbosphaerella leptosphaerioides* exosporic sheath, which fragments in water and is extremely sticky. Sheath composed of interlinked fibers. Bars **23–25** 10 μm ; **26, 27** 5 μm



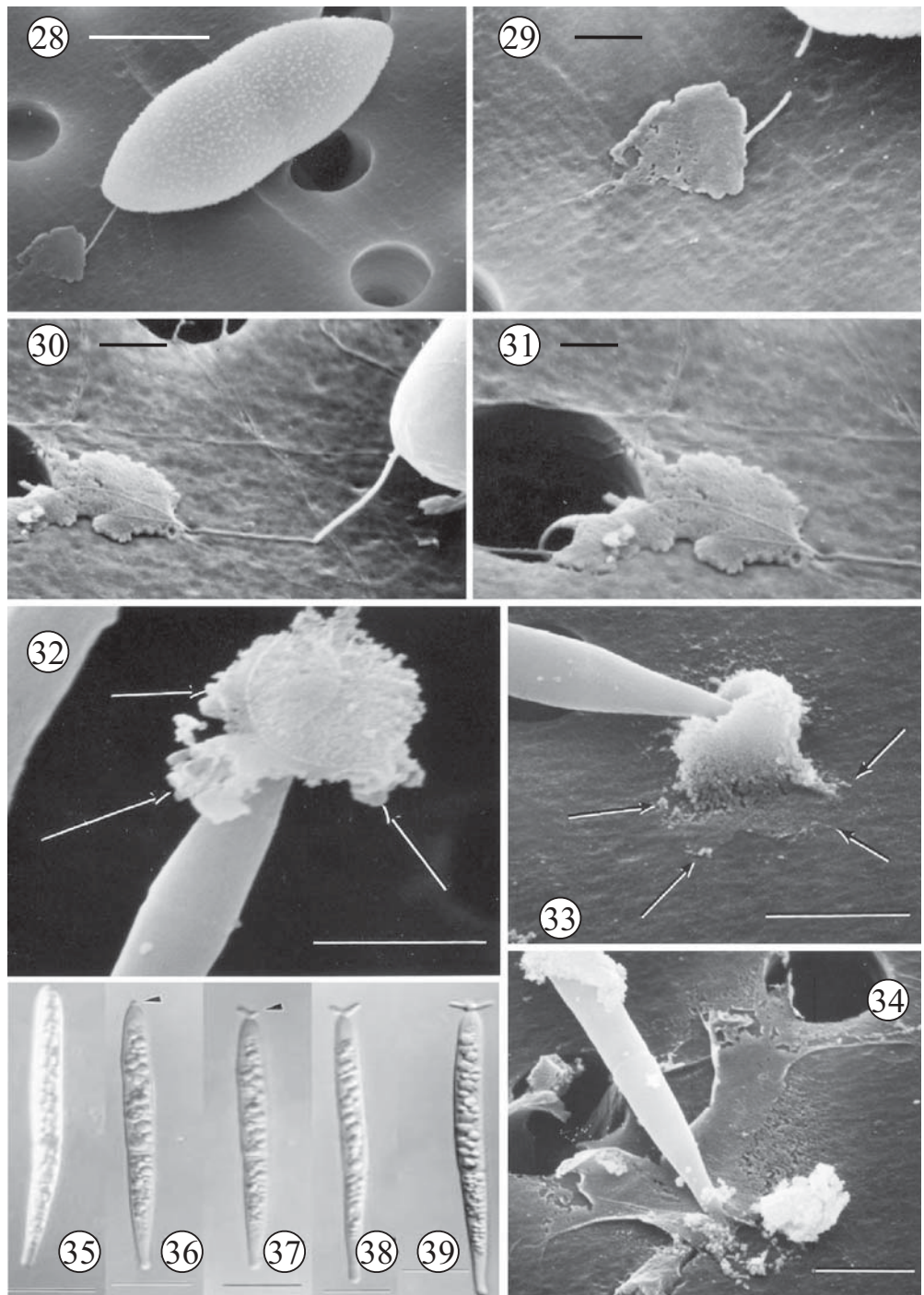
1. Uni- to bipolar gelatinous caps [*Coccomyces clusiae* (Lév.) Sacc., *Lophodermium mahuianum* P.R. Johnst.]
2. Barblike gelatinous appendages on the bend in the ascospore [*Lophodermium alpinum* (Rehm) Weese]
3. Well-developed sheaths (*Hypoderma cordylines* P.R. Johnst.)
4. Species with a combination of bipolar caps and sheaths (*Lophodermium medium* P.R. Johnst., *L. brunneolum* P.R. Johnst.). However, the role of appendages and ensheathed ascospores and their development was not discussed.

Coelomycetes

As for the marine ascomycetes, coelomycete conidia show infinite variation in the type of appendages produced and have been extensively illustrated and described by Nag Raj (1993). Currently some 7000 coelomycete species have been described, of which approximately 420 have appendaged conidia that can be characterized into 11 developmental patterns (Nag Raj 1993). They fall into two basic forms:

1. Cellular, which involves the outgrowth of the conidial cell wall, usually the outer layer, the inner layer forming

Figs. 28–39. Polar appendages of aquatic ascomycetes. **28–31** Undescribed freshwater *Halosarpheia* sp. with an undifferentiated polar appendage, connected to the spore by a fine thread, appendage material initially amorphous. **32** *Lulworthia* sp. with a drop of released mucilage (arrows). **33, 34** *Lulworthia* sp. mucilage spreads out onto substratum (arrows in **33**), greatly increasing the contact area with the surface (photograph, Jones 1994). **35–39** *Thalassiosira appendiculata* ascospores mounted in seawater form tetra- or radiate appendages (arrow head). Ascospores on release lack appendages (**35**), but over 1 h they form appendages, whereas those mounted in freshwater do not develop appendages (photograph, Jones et al. 2006). Bars **29–31** 1 μm ; **28** 5 μm ; **32–34** 10 μm ; **35–39** 20 μm



a delimiting septum (e.g., *Chaetospermum camelliae*; see Fig. 4). This type can be subdivided into two groups: those where the conidium is formed before the appendages (e.g., *Ch. camelliae*) and those formed before the conidium body [e.g., *Strasseria geniculata* (Berk. & Broome) Höhm].

2. Extracellular, when the conidial appendages are extruded and elaborated in various ways. Nag Raj (1993) recognized seven subtypes ranging from those with eversion and fragmentation of an exosporial sheath to extrusion of

a mucilaginous appendage to gelatinization of an end conidial cell. These, and other conidial appendage types in the coelomycetes, warrant further study at the TEM level, as so few have been studied in any detail (Nag Raj 1993; Plaingam 2002; Plaingam et al. 2004).

Few coelomycete conidia have mucilaginous sheaths or show the release of a drop of mucilage. However, in many species appendaged conidia are enveloped in mucilage, often early in conidiogenesis (see Figs. 4, 17, 18), and are

therefore regarded as slime spores (Gregory 1952; Nag Raj 1993). In some genera or species where conidia have both polar and basal appendages, they are not always formed in the same manner: *Infundibura adherens* Nag Raj & K.W. Kendr. (Nag Raj and Kendrick 1981) has a mucoid funnel-shaped, apical appendage and a terete, mucoid, basal appendage, while in *Libartania ischyrolepis* S.J. Lee & Crous there is a mucilaginous sheath and cellular polar appendage arising as a tubular extension of the conidium body (Lee and Crous 2003). Figures 17 and 18 illustrate the basal and polar appendages, respectively, of a *Pestalotiopsis* sp. (Plaingam 2002; Plaingam et al. 2004). The basal appendage arises from the inner wall of the conidium, while the polar appendage is formed by outgrowth of the outer and inner layers of the terminal cell of the conidium. The polar appendages are not delimited from the terminal cell as in *Chaetospermum camelliae* (see Fig. 4).

Hyphomycetes

Hyphomycetes, which often have dry conidia, rarely have appendages. Of 295 dematiaceous genera illustrated by Ellis (1971), less than 1% possess appendages. Most of these are cellular (setulae), although examples of conidia with a drop of extruded mucilage can be found in genera such as *Ellisemia*, *Linkosia*, *Sporidesmina*, *Sporidesmium*, *Stanjehughesia* (Wu and Zhuang 2005), and *Pseudoacrodactys dimorphospora* (see Fig. 19; Somrithipol and Jones 2003).

Appendaged conidia (e.g., *Dictyosporium* sp.; Fig. 20, mucilaginous?) have been reported for some dematiaceous hyphomycetes, e.g., *Dictyochoeta multisetula* Whitton, McKenzie & K.D. Hyde (Whitton et al. 2000), *Dictyosporium nigropice* Goh, W.H. Ho & K.D. Hyde (Goh et al. 1999), *D. canisporum* L. Cai & K.D. Hyde, and *D. tetraploides* L. Cai & K.D. Hyde (Cai et al. 2003b). In *Dichyochaetopsis brasiliensis* Caldusch, Gené, Stchigel & Guaró, the hyaline conidia possess a thin, undulating, single polar appendage (setula) (Caldusch et al. 2002). However, gelatinous sheaths are rare in the hyphomycetes (e.g., *Dactylaria tunicata* Goh & K.D. Hyde and *Delortia palmicola* Pat. & Gaillard) (Hyde and Goh 2003). Again, few of these have been studied at the SEM and TEM level, so that the origin of these appendages is not known.

Hyde and Goh (2003) documented lignicolous anamorphic fungi that produce conidia with modified appendages: setulae, or arms, that are functionally similar to those of "Ingoldian" Hyphomycetes. Setulae are produced by the genera *Dictyochoeta*, *Nawawia*, and *Obeliospora*, while conidial arms are formed by *Iyengarina* and *Sporidesmiella cornuta* Kuthub. & Nawawi (Goh and Tsui 2003).

Coprophilous fungi

Coprophilous ascomycetes are another ecological group with elaborate mucilaginous ascospore appendages for effecting attachment of the spores to substrata (Bell 1983, 2005; Lorenzo and Havrylenko 2001). Ascospores range

from those with sheaths to those with primary and secondary appendages [e.g., *Sordaria fimicola* Ces & De Not, see Figs. 23–25; *Podospora pleiospora* (G. Winter) Niessl and *P. dactylina* N. Lundq., see Fig. 21]. In *Podospora anserine* (Raberh.) Niessl, the primary appendage is formed by elaboration, or fragmentation, of the spore wall, whereas the secondary appendage forms by exudation through one or more pores in the spore wall (Beckett et al. 1968; Read and Beckett 1996). In the discomycete *Thecotheus formosanus* Yei Z. Wang, the ascospores have a sheath as well as small polar apiculi (?appendages) (Wang 1994).

Ascospores with elaborate appendages have to be ejected from the asci before they can dilate by the absorption of water. Ingold's (1971) studies indicated that in species such as *Saccobolous citrinus* Boud. & Torrend, and *S. glaber* (Pers.) Lamb., the ascospores stick together to produce a projectile that could be fired some distance from the ascoma (Brummelen 1967). However, in *Zygopleurage zygospora* (Speg.) Boedijn, each ascospore consists of two pigmented cells, linked by a hyaline intercalary cell, which can be seen within the ascus (Bell 1983). How these complicated structures are released is interesting!

The attachment of ascospores of coprophilous Ascomycota to herbage is well documented, as are the reasons for this (Ingold 1965, 1971). The gelatinous ascospore sheath swells in water (see Fig. 23), increasing in diameter and effecting greater adhesion to the surface.

Trichomycetes

Of the 255 Trichomycetes described, many have appendaged trichospores, with the exception of the taxa in the Amoebidiales (Lichtwardt 1976, 1984; Lichtwardt and Williams 1983a,b, 1984; Lichtwardt et al. 2001; Sato 2001). Sheaths or extrusion of a drop of mucilage have not been reported, although some may have adhesive spore cell walls. Appendages develop in two distinct ways within the subtending generative cell between the plasmamembrane and cell wall (Moss 1998). The appendages are attached either to the cross-wall separating the trichospore from the generative cell or to the lateral wall immediately below the cross-wall (Moss 1998). They also differ in development time; e.g., in *Trichozygospora chironomidarum* Lichtw. they are formed after septum formation whereas in *Harpella melusinae* L. Léger & Duboscq. they are formed before septum development.

Many trichospores have more than one appendage in a basal position, e.g., *Plecopteromyces leptoperlarum* Ferrington et al. and *P. trintoperlarum* Ferrington et al., both with two appendages (Ferrington et al. 2005). Moss (1999), Moss and Lichtwardt (1976) and Sato (2001) have studied appendage development in the group. The function of trichospore appendages appears to be for entrapment on suitable hosts whereas attachment of the spores is by the development of adhesive holdfasts (Moss 1998). Sato (2001) describes the various stages of trichospore attachment and the development of holdfasts.

Other groups

Many other fungi have appendaged spores, for example, the sporangiospores of the Choanephoraceae with their fine bipolar appendages (e.g., the genera *Blakeslea*, *Choanephora*, and *Poitrasia*) (Kirk 1984). How these are formed is not known, but could it be by fragmentation of an exosporic sheath?

Adaptation of appendaged ascospores for release from asci

One of the problems in the release of ascospores with sheaths or elaborate mucilaginous appendages is how the spores are ejected through the ascus apical pore without getting stuck there? for example, the elaborate sheathed ascospores of *Lophiostoma* (= *Massarina*) *ingoldianum*. Or, how are sticky appendaged ascospores in marine ascomycetes released without adhering or getting trapped within the ostiolar canal? In taxa we have examined at the ultrastructural level, a delimiting membrane surrounds appendaged ascospores, and this is evident in released ascospores where the appendages have yet to expand (Read et al. 1994, 1996; Wong et al. 1999; Alias et al. 2001; Baker et al. 2001) (e.g., *Saagaromyces ratnagiriensis*; see Figs. 10, 11). Clearly this thin membrane prevents appendage expansion until ascospores are released from the ascus or ascoma. In many ascomycetes referred to above, sheaths are often well developed within the ascus, but do not become sticky until released from the ascus or ascoma, when the delimiting membrane is ruptured or deliquesces. Many *Halosarpheia* species take a long time before the polar appendages uncoil, e.g., *Sagaaromyces abonnis* and *S. ratnagiriensis*. In others the salinity of the water may determine their rate of uncoiling (e.g., *A. salsuginosa*; Nakagiri and Ito 1994).

A delimiting membrane (also referred to as the membrane complex: Jones et al. 1986; Johnson et al. 1987; or the investing membrane: Furtado and Olive 1970), has been reported for a wide range of species. However, the function of the delimiting membrane has received little attention.

Effect of environmental factors on appendage development

Environmental conditions affect the absorption of water by appendages and degree of adhesion to a substratum. Read et al. (1991) demonstrated that hyphomycete conidia with the greatest contact area with a substratum were able to effect the best attachment. The spread of the mucilage spore drop on a surface has been well documented for *Lulworthia* species (see Figs. 32–34) and *Kohlmeyeriella tubulata* (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss (Rees and Jones 1984).

In *Halosarpheia* and *Aniptodera*, the salinity of the water has a profound effect on appendage morphology. In

Aniptodera salsuginosa, ascospores mounted in salinities of 0‰–30‰, differed in the rate of unfurling of the appendages (Nakagiri and Ito 1994). In seawater (20‰ or 30‰), appendages were firmly appressed to the spore wall after 10 min, began to separate from the spore wall after 15 min, and were fully expanded after 40 min. In brackish water (10‰), approximately 50% had partly or fully uncoiled within 5 min, and after 17–25 min both polar appendages had become detached. In 5‰ seawater they began to uncoil immediately and were fully uncoiled after 5 min. However, in distilled water, all appendages were detached immediately. Nakagiri and Ito (1994) suggested that the fungus is adapted to mangrove brackish water ecosystems because of the response of appendages to water salinity. In a freshwater *Halosarpheia* species, amorphous material was released, and connected to the spore by a fine thread, before its organization into filaments (Jones, unpublished data; see Figs. 28–31).

In some freshwater (*Ascococcus aquaticus*) and marine (*Thalespora appendiculata* Chatmala & E.B.G. Jones, see Figs. 35–39; *Savoryella appendiculata*, see Fig. 6) ascomycetes, tetrapolar polar appendages are formed once the ascospores are mounted in water. *Thalespora appendiculata* (Figs. 35–39) forms unipolar tetraradiate appendages in seawater, but these are not formed when mounted in freshwater (Jones et al., in press).

Function of appendaged spores and their role in attachment

Nag Raj (1993) reiterates the views of Gregory (1952) and Sutton (1986) that the possession of any structure is evidence that it has some function, in the case of conidia by the mechanisms for their liberation, dispersal, and deposition. Coelomycete conidia are predominantly slime-spores and thus not subject to dispersal by wind, and so splash liberation and insects are considered the primary method of dispersal. Water splash dispersal ensures that conidia scatter very rapidly and spread out on the surface of the film (Bandoni 1974). The water films then spread onto adjacent substrata and the conidia can make contact with the surface and effect attachment (Bandoni 1975). These water droplets can also be carried by wind currents and effect further dispersal of spores. Coelomycete conidia can attach rapidly to surfaces: e.g., *Infundibura adhaerens*, *Amarenographium metableticum*, and *Callistospora gaubae* Petr. (Nag Raj 1993). So what extra advantage do these appendages confer on dispersal and adhesion of coelomycete conidia, especially if they are not mucilaginous? Mucilaginous conidia may play a role in attachment to substrata while nonmucoid conidia with numerous setulae or appendages increase entrapment and contact with the host substratum. Cunnell (1958) suggested that the appendages of *Robillarda phragmitis* Cunnell aided conidial dispersal in surface water currents in the same way as tetraradiate propagules of hyphomycetes.

Jones (1995) suggested that all spores needed to attach to a substratum before they could begin to germinate. As a consequence, fungi have evolved a wide range of mechanisms to secure attachment, including the development of appendages and mucilaginous sheaths.

Cannon and Minter (1986) speculated as to the function of sheathed ascospores in the Rhytismataceae: (1) to seal the passage of spores through the ascus opening, thus preventing loss in hydrostatic pressure within it; (2) to provide water to facilitate germination of the spore under unfavorable conditions; or (3) to act as adhesive pads to anchor discharged spores to a substratum.

It is interesting to speculate where the development of a holdfast, the secretion of a polar or basal drop of mucilage, or formation of a mucilaginous sheath begins. As in the formation of polar appendages in the *Halosarpheia* sensu lato complex by extrusion of adhesive through discontinuities in the epispodium, a similar process occurs in the release of mucilage through well-formed pits in the inner wall of trichospores. However, in the latter, it is generally in response to a contact stimulus with the surface of a host. Such a process is evident in the release of a mucilage drop in *Mangnaporthe grisea* Sacc., triggered by a contact stimulus with the plant host (Jones 1995; Howard and Valent 1996; Howard 1997).

In *Lasiosphaeria alexandrae* Joanne E. Taylor, J. Fröhl. & K.D. Hyde, the ascospore has a single polar spur with a spatulate mucilaginous tip, forming a padlike structure on contact with the substratum. The origin of the mucilaginous drop was not determined, but was it released in response to surface contact? (Taylor et al. 2001).

Further evidence for the role of appendages in dispersal and attachment is provided by Rees (1980), who studied the effect of sonication of appendaged ascospores of selected marine fungi. Sedimentation rates ranged from 0.10 to 0.21 mm/s, with the slowest sedimentation in *Nia vibrissa* R.T. Moore & Meyers and the fastest in *Orbimyces spectabilis* Linder and *Nereiospora* (= *Corollospora*) *comata* (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss (0.35–0.41 mm/s). Sedimentation was shown to be affected by spore density, spore dimension, and appendage morphology. *Torpedospora radiata* Meyers had the slowest settlement rate, which was attributed to its low density and “parachute-type” descent facilitated by the arrangement of its appendages. Sonication to remove spore appendages resulted in an increased sedimentation rate. It was therefore concluded that spore appendages played a role in their dispersal in water.

Hyde et al. (1993) explored the loss of propagules of marine fungi from a spore suspension and their attachment to Kapok fibers in a rotating vessel. Species such as *Remispora pilleata* Kohlm. and *R. stellata* Kohlm. with large, appendaged ascospores tended to attach to the fiber extremely efficiently and to settle out rapidly in the absence of fiber. However, those of *Eiona tunicata* Kohlm. and *Nautosphaeria cristaminuta* E.B.G. Jones with smaller, appendaged spores attach less efficiently and were slower to settle in the absence of fiber, thus confirming the data from the sonication experiment reported above.

Rapid and efficient attachment of marine fungal spores is essential for the colonization (often under turbulent conditions) of substrata in the sea. Different species have different attachment abilities, but how this affects their local and geographical distribution remains a subject for further study.

Healey et al. (unpublished data) showed that sheath adhesion in *Sordaria fimicola* increased with time: after 3 h, 46.3% of the spores were attached to the substratum, and 83% at 12 h with a hosing pressure of 10 mmHg. There was an increase of 13.2% in the area of contact with the surface after 1 h, whereas at 32 h it was 59.4%. Increased attachment with settlement time has also been reported for a wide range of marine fungi (Rees and Jones 1984; Hyde et al. 1986a,b, 1989).

However, few have examined how successful coprophilous spores are attached to a surface. Healey et al. (unpublished data) examined this aspect by allowing *S. fimicola* ascospores to be ejected over a distance of 1 and 10 cm in an upright cylinder. The velocity at which ascospores impact on to a surface also affects the degree of adhesion; 90% of discharged spores up to 1 cm from the medium remained attached after 3 h at a hosing pressure of 2 mmHg (see Fig. 22). However, only 69.6% of the spores discharged through a 10-cm cylinder remained attached over a similar period. There was a 22.7% greater spore and sheath contact area in the spores discharged over 1 cm compared with those ejected through a 10-cm cylinder.

Another aspect important in the colonization of a substratum is the rate at which the spores become attached. Does the presence of an appendage confer an advantage over species without one? The conidia of the freshwater hyphomycetes *Mycocentrospora filiformis* (Greath.) S.H. Iqbal (filiform conidia) and *Lemonniera aquatica* De Wild. (tetradiate conidia) are attached to a surface within 5–30 min; however, we have no good data for how rapidly marine fungi attach to a surface. Personal observations indicate that appendaged ascospores of *Carbosphaerella* species (see Figs. 26, 27) and *Kohlmeyeriella tubulata* and *Lulworthia* sp. (see Figs. 32–34) attach very rapidly to glass slides. Experimental studies of the strength of attachment of ascospores of marine fungi show a range of responses (Rees and Jones 1984; Hyde et al. 1989). *Eiona tunicata* (ascospores $7.5\text{--}12 \times 3/5\text{--}5\ \mu\text{m}$ with small appendages) withstood higher shear stresses ($4.4\text{--}5.57\ \text{Nm}^{-2}$) than *Lautosporopsis* (= *Ceriosporopsis*) *circumvestita* (Kohlm.) E.B.G. Jones, Yusoff & S.T. Moss ($2.12\text{--}2.54\ \text{Nm}^{-2}$, ascospores $165\text{--}25 \times 9\text{--}13\ \mu\text{m}$ with well-developed appendages) (Hyde et al. 1989). The former species was therefore better adapted to attachment to a substratum.

Despite the importance of fungal spores securing attachment, there has been a singular lack of experimental studies of this topic. What is the internal trigger mechanism involved in spore attachment? For appendaged spores, is the process totally passive? Can spores select the surfaces they can colonize? What are the effects of hydrophobicity, surface roughness/topography, and surface energy on spore attachment? Although some of these issues have been researched for plant and human pathogenic fungi, saprobes

have fared poorly in comparison (Douglas 1987; Jones 1994).

Some fungi settle and adhere firmly to the substratum within 5–30 min, e.g., *Lulworthia* spp. and *Kohlmeyerella tubulata*. Here other questions arise: does this attachment preclude wider dispersal of the spores? What evidence is there that appendages help in the dispersal of spores by flotation? Thus a number of questions remain unanswered and there is much scope for further experimental studies, preferably with surfaces other than glass slides or perspex. If appendages/sheaths play such an important role in securing attachment of spores, why are so few examples to be found in the Basidiomycota (exceptions are the marine genera *Digitatispora*, *Mycaureola*, and *Nia*) and most anamorphic fungi (with the exception of the coelomycetes)?

A number of other factors play a role in the liberation, dispersal, and attachment of spores, e.g., their shape (tetradiate, filiform), density, and size. However, this is outside the scope of this review and must await another time (Ingold 1954; Jones 1994; Hyde and Goh 2003).

Evolution of appendaged ascospores

What is the most primitive type of ascospore appendage? This is a question that has rarely been raised or addressed. This brief review has demonstrated that fungi have evolved an interesting array of mechanisms for the dispersal, settlement, and attachment of spores to new substrata. Pang (2002) suggested that in marine fungi the most primitive type of appendage was a sheath, with those in ocean taxa the most advanced. He considered that taxa with unfurling ascospore appendages are intermediate in their development, and this view can be sustained by their occurrence in mangrove habitats. Nakagiri and Ito (1994) concluded that the unfurling of ascospore appendages of *Aniptodera salsuginosa* was better adapted to brackish water mangrove habitats rather than coastal marine habitats with a higher salinity range.

In Figs. 40 and 41 I outline the possible development of appendages in the Ascomycota, with particular emphasis on marine genera. This depiction is purely speculative but I hope it will generate an interest into how appendages arose and evolved. This aspect needs to be tested at the molecular level to determine their possible development (Sakayaroj 2005). As a starting point, spores with an adhesive cell wall (e.g., *Belizeana*) (Kohlmeyer and Volkman-Kohlmeyer 1987) might have given rise to those with a distinct mucilaginous sheath (*Massarina*, *Lophiostoma* species) (Fig. 40, route 1). Ascospores with sheaths are by far the most common within the Ascomycota, occurring in a wide range of taxonomic and ecological groups. Variation in the topography of sheaths led to the development of other forms:

1. Sheaths extended into folds (e.g., *Decorospora gaudefroyi*, *Lophiostoma ingoldianum*) (Shearer and Hyde 1997) (Fig. 40, route 5).
2. Fragmentation, or rupture of the sheath to form polar appendages [e.g., *Remispora maritima* Linder

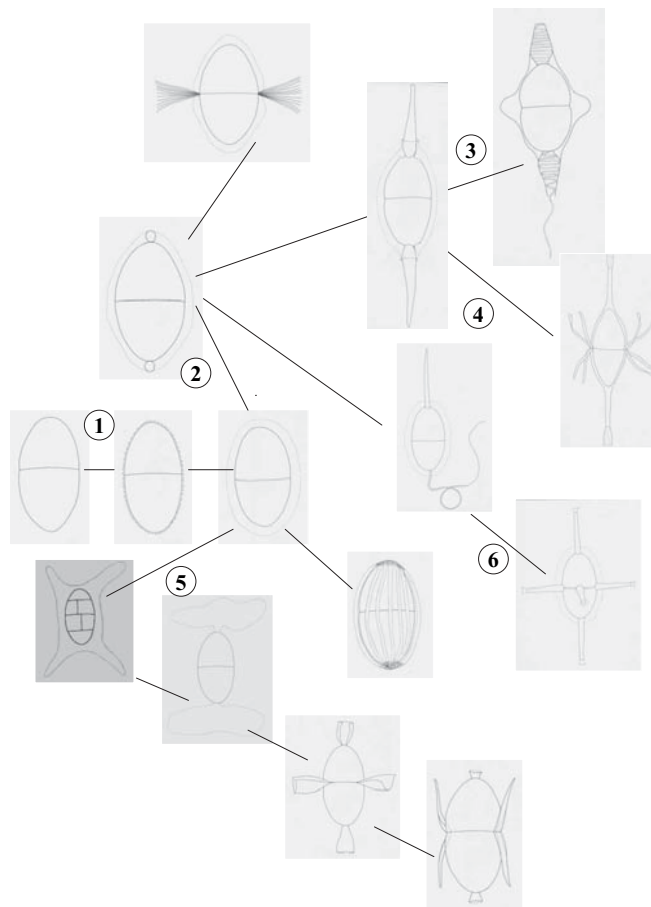


Fig. 40. Suggested evolutionary lines in the development of ascospore appendages: route 1, sticky spore walls leading to a distinct mucilaginous sheath; route 2, outgrowths from the spore wall, but within a sheath; route 3, extension of the polar outgrowths leading to the development of polar end chambers; route 4, fragmentation of the exosporic sheath to form secondary appendages; route 5, elaboration of mucilaginous sheaths, followed by fragmentation to form polar or equatorial appendages, or both; route 6, elaboration of the polar and equatorial mucilaginous appendages, the exosporic layer fragmenting (drawings, S. Somrithipol)

- (Manimohan et al. 1993), conidia of *Comatospora suttonii* Piroz. & Shoemaker, *Tiarosporella paludosa* (Pirozynski and Shoemaker 1971), *Tiriosporella beccariana* (Ces.) E.B.G. Jones, K.D. Hyde & Alias (Jones et al. 1996; see Fig. 13)], or equatorial [*Melaspilea mangrovei* Vrijmoed, K.D. Hyde & E.B.G. Jones (Vrijmoed et al. 1996)], or both polar and equatorial appendages (Fig. 40, route 5), e.g., *Groenhiella bivestita* Jørg. Koch, E.B.G. Jones & S.T. Moss; see Fig. 7).
3. Development of a polar appendage within the sheath [e.g., *Lophiostoma bipolare*, *Massarina ramunculicola*, *Thecotheus formosanus* (Wang 1994), *Lophodermium alpinum* (Johnston 1994), *Seynesia nobilis* (Hyde 1995b)] (Fig. 40, route 2).
 4. Polar mucilaginous appendage external to the sheath [e.g., *Ceriosporopsis halima* Linder (Johnson et al. 1987), *Hapalocystis occidentalis* Jakl. & Voglmayr (Jaklitsch and Voglmayr 2004)] (Fig. 40, route 3); leading to the

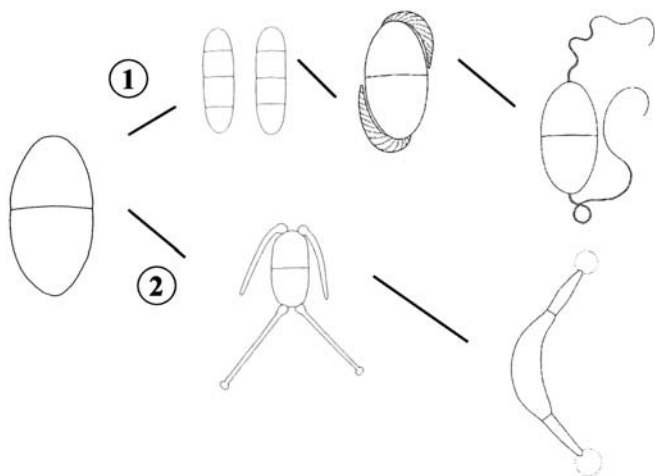


Fig. 41. Further hypothetical development of appendaged ascospores: route 1, release of mucilage from one or both ends of the spore, giving rise to unfurling bipolar appendages through a pore or discontinuities in the spore wall; route 2, outgrowths of the ascospore wall, and release of mucilage from an end chamber (drawing, S. Somrithipol)

formation of an end chamber with mucilage [e.g., *Ceriosporopsis tubulifera* (Kohlm.) P. Kirk (Johnson et al. 1987)].

5. The outgrowths of mucilage through the sheath [e.g., *Nimbospora bipolaris* K.D. Hyde & E.B.G. Jones (Hyde and Jones 1985)] (Fig. 40, route 2); or outgrowths of appendages through a sheath and fragmentation of an exosporium (e.g., *Marinospora calyprata* (Kohlm.) A.R. Caval.) (Fig. 40, route 6). By further elaboration of these forms others have developed.

Although most ascospore sheaths are mucilaginous and composed of amorphous material (acidic polysaccharides?), others are more complicated, as in the elaborate sheath in *Carbosphaerella* species (see Figs. 26, 27) and *Appendichorella amicta* (Kohlm.) R.G. Johnson, E.B.G. Jones & S.T. Moss (Johnson et al. 1987). Others are thin and sheetlike and do not appear to be mucilaginous [e.g., *Corollospora maritima* Werderm.; *Halosphaeriopsis mediosetigera* (Cribb & J.W. Cribb) T.W. Johnson]. Ultrastructural studies have shown that most sheaths are exosporic in origin (Au and Vrijmoed 2002; Hyde et al. 2002).

A second line in the development of appendages might be the release of a drop of mucilage from the spore: single pole (e.g., *Okeanomyces cucullatus* K.L. Pang & E.B.G. Jones) or bipolar (e.g., *Linocarpon bipolaris* K.D. Hyde, *Massarina phragmiticola* O.K. Poon & K.D. Hyde) (Fig. 41, route 1). The latter may have given rise to those with bipolar unfurling appendages, as illustrated by a variety of freshwater and marine ascomycetes (e.g., *Halosarpheia fibrosa*). This latter group may also show variation in ultrastructure from those with a single homogeneous thread (*H. fibrosa*) to appendages comprising a basal amorphous structure with fibrillar material [e.g., *Cucullospora mangrovei* (Alias et al. 2001)]. Other lineages comprise forms with outgrowths of the ascospore wall: mesosporium only (e.g.,

Arenariomyces trifurcates Höhnk), of the episporium (e.g., *Ondiniella torquata* (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss), and episporium and mesosporium (e.g., *Lulworthia* and *Kohlmeyeriella* species) (Fig. 41, route 2). The independent origin of these different forms is supported by molecular data (Sakayari 2005).

Kirk (1986) discussed evolutionary trends within the Halosphaeriaceae focusing on appendage form and structure, based on the limited data available at that time and before the advent of molecular data. Two evolutionary lines were proposed: one group with exosporic appendages, the other lacking such ornamentation. The latter group comprises *Lignincola* and *Nais*, genera lacking appendages, and *Halosarpheia*, *Haligena*, and *Trichomaris* (genera with only polar appendages) and *Ondiniella* with a polar and equatorial appendages arising as outgrowths of the episporium. The other group includes those with a wide variety of spore appendage morphology, including the genera *Kohlmeyeriella*, *Lindra*, and *Lulworthia*, now transferred to a new order, the Lulworthiales, based on small subunit (SSU) and large subunit (LSU) rDNA sequence data (Kohlmeyer et al. 2000).

Sakayari (2005) suggests there is no phylogenetic correlation between the types of appendage ontogeny found in the Halosphaeriaceae. Fungal spore appendages appear to have evolved independently many times within the marine environment, and this evolution would be in common with their pioneering role in that milieu. Pioneers generally are adapted to changing conditions in time and space by phenotypic plasticity (Margalef 1968) and this may account for the large number of monotypic genera (more than 50%) within the Halosphaeriaceae (marine ascomycetes). Confirmation by Spatafora et al. (1998) as to the terrestrial origins of marine higher fungi highlights their great adaptation to a new milieu, with the consequent elaboration in spore appendage morphology and structure, and the need to develop new strategies for the liberation, dispersal, and attachment of spores, often under turbulent conditions.

Conclusions

This review demonstrates the wide range of spore appendages to be found in all the major fungal taxa. Exceptions are the Basidiomycota (apart from the marine genera *Digitatispora*, *Mycaureola*, *Nia*) (Jones and Jones 1993) and anamorphic fungi (excluding many coelomycete genera, and those releasing a drop of mucilage). In marine and freshwater ascomycetes, appendaged ascospores clearly aid in their dispersal and attachment to substrata. The role of appendaged spores in terrestrial ascomycetes and coelomycetes is also associated with water, with splash liberation of spores and their spread in water films onto adjacent substrata, such as leaf litter and wood. Water is also vital for the attachment of coprophilous ascomycetes with the hydration of the mucilaginous ascospore sheaths. Although appendaged spores are well documented, much remains to be done to determine how they are formed.

For example, experiments to determine the role of appendages in spore attachment to various substrata and the factors that may influence this, such as surface energy, topography, surface chemistry, and electrical charges, need to be addressed. Furthermore, the evolutionary processes that gave rise to such variation in spore appendage morphology, particularly environmental conditions, need to be explored. We also have little information on the chemical nature of fungal spore appendages. Were initial appendages chitinous but later became mucilaginous and acidic?

Spore appendages and their attachment, although of academic interest, are especially relevant in plant and human pathology because they cause great economic losses. In bioremediation, they are of importance in developing fluidized bed systems for attachment of the fungi. Ecologically, they are vital in securing attachment of spores to new substrata and thus in the recycling of organic matter in nature. In the Trichomycetes, continued infection of the host is necessary, because the peritrophic membrane of the gut is cast at frequent intervals. Trichospore transmission from larva to larva within rivers is successfully achieved, despite the rapidity of water flowing over the larvae. How trichospores are carried from one drainage system to another remains unanswered (Lichtwardt and Williams 1983b; Moss 1998).

In his presidential address *Evolution of the Fungi*, Roy Cain (1972) drew attention to the fact that certain features appeared in many different groups of fungi, e.g., deliquescent asci, and staining of the ascus tip by Melzer's reagent. The only conclusion possible is that a repetition of the same feature has appeared in a number of different evolutionary lines, and arose as an adaptation to a particular environmental niche by different lines in fungal evolution. This conclusion is equally the case for the numerous examples of ascospore appendage development cited here.

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