

REVIEW

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## A review of the phylogeny and biology of the Diaporthales

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**Abstract** The ascomycete order Diaporthales is reviewed based on recent phylogenetic data that outline the families and integrate related asexual fungi. The order now consists of nine families, one of which is newly recognized as Schizoparmeaceae fam. nov., and two families are recircumscribed. Schizoparmeaceae fam. nov., based on the genus *Schizoparme* with its anamorphic state *Pilidella* and including the related *Coniella*, is distinguished by the three-layered ascomatal wall and the basal pad from which the conidiogenous cells originate. Pseudovalsaceae is recognized in a restricted sense, and Sydowiellaceae is circumscribed more broadly than originally conceived. Many species in the Diaporthales are saprobes, although some are pathogenic on woody plants such as *Cryphonectria parasitica*, the cause of chestnut blight, and agricultural crops such as canker diseases of soybean and sunflower caused by species of *Diaporthe-Phomopsis* in both temperate and tropical regions. Members of the Diaporthales such as *Apiognomonia-Discula* and *Diaporthe-Phomopsis* are commonly encountered as endophytes of woody plants.

**Key words** Ascomycetes · Canker disease · Endophytes · Systematics

### Introduction

The ascomycete order Diaporthales includes several plant pathogenic fungi, of which the most notorious is the chestnut blight fungus [*Cryphonectria parasitica* (Murrill) M.E. Barr] that altered the landscape of eastern North America (Anagnostakis 1988). Numerous other tree diseases are caused by members of the Diaporthales in either their ascomycetous or asexual states. These diseases include oak

dieback [*Apiognomonia quercina* (Kleb.) Höhn.], cherry leaf scorch [*A. erythrostoma* (Pers.) Höhn.], sycamore canker [*A. veneta* (Sacc. & Speg.) Höhn.], and ash anthracnose [*Gnomoniella fraxinii* Redlin & Stack, anamorph *Discula fraxinea* (Peck) Redlin & Stack] in the Gnomoniaceae. Diseases caused by anamorphic members of the Diaporthales include dogwood anthracnose (*Discula destructiva* Redlin) and butternut canker (*Sirococcus clavigignenti-juglandacearum* Nair et al.), both solely asexually reproducing species in the Gnomoniaceae. Species of *Cytospora*, the anamorphic state of *Valsa*, in the Valsaceae cause diseases on *Eucalyptus* (Adams et al. 2005), as do species of *Chrysosporthe* and its anamorphic state *Chrysosportheella* (Gryzenhout et al. 2004, 2005d). Many diseases of crop plants are caused by members of the Diaporthales. For example, species of *Diaporthe-Phomopsis* attack sunflower and soybean, causing stem cankers and seedling blights (Muntañola-Cvetkovi, et al. 1991; Black et al. 1996). The asexually reproducing fungus *Greeneria uvicola* (Berk. & M.A. Curtis) Punith., cause of bitter rot of grapes, belongs in the Diaporthales but is not affiliated with any family (Farr et al. 2001).

Molecular data support the Diaporthales as a distinct order within the Sordariomycetes, the class including ascomycetous fungi that produce their asci primarily in perithecial fruiting bodies (Zhang and Blackwell 2001; Castlebury et al. 2003; Zhang et al. 2006). In the latest multigene phylogeny of this class, the Diaporthales are a well-defined order in the subclass Sordariomycetidae, most closely related to the Magnaporthaceae and Ophiostomatales and allied with the Boliniales, Chaetosphaeriales, Coniochaetales, and Sordariales (Zhang et al. 2006). Castlebury et al. (2002) and Zhang et al. (2006) suggest that the Magnaporthaceae is sister to the Diaporthales. However, recent work by Mostert et al. (2006) places the Calosphaeriales even closer to the Diaporthales.

According to Kirk et al. (2001), the Diaporthales consists of about 94 genera with 500 species. The anamorphic species derived from within the Diaporthales, including such large genera as *Cytospora* (100+ species) and *Phomopsis* (100+ species), may at least double the estimated number

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of species. The Diaporthales are characterized morphologically by brown to black perithecial fruiting bodies immersed in a stroma or the substrata, lack of true paraphyses at maturity, and unitunicate asci that float free within the centrum at maturity and have a refractive ring in the apex (Barr 1978; Samuels and Blackwell 2001). The known asexual states of members of the Diaporthales are generally coelomycetous, producing phialidic, often annellidic conidiogenous cells, and usually non- or one-septate conidia in acervuli or pycnidia with or without a well-developed stroma.

Generic concepts in the Diaporthales have not been reevaluated since they were established, primarily on the basis of the Saccardoan system, which placed high value on ascospore characters. Characteristics of the stroma and the anamorph were combined with ascospore characteristics in the taxonomies proposed by Barr (1978, 1990), Kobayashi (1970), and Monod (1983; Gnomoniaceae only) that represent the most recent monographic accounts of the Diaporthales. The few molecular studies in the Diaporthales suggest that these generic concepts must be reevaluated (Zhang and Blackwell 2001; Castlebury et al. 2002, 2003). In these studies, many of the genera included were determined to be polyphyletic; thus, placement of the type species has been stressed.

Although for many years the genera *Magnaporthe* and *Gaeumannomyces* were included in the Diaporthales (Barr 1978; Yaegashi and Udagawa 1978; Monod 1983; Cannon 1988), these genera are now placed in their own family, Magnaporthaceae (Cannon 1994). In describing this family with six genera, Cannon (1994) reviewed its ordinal placement and concluded, based primarily on the biology of these fungi, that it should be excluded from the Diaporthales. Three recent studies of these taxa using molecular sequence data confirm the placement of *Gaeumannomyces* and *Magnaporthe* outside the Diaporthales (Zhang and Blackwell 2001; Castlebury et al. 2002; Zhang et al. 2006).

Within the Diaporthales, up to eight families have been recognized by various authors over the past 30 years. These familial classifications of the Diaporthales were summarized by Zhang and Blackwell (2001), comparing Barr (1978, 1990), Kirk et al. (2001), and Wehmeyer (1975). In the most comprehensive molecular study to date, Castlebury et al. (2002) analyzed nLSU rDNA sequence data and determined that there were six major lineages in the Diaporthales. Since then, an additional three lineages have been added such that nine families are now included in the order (Rossman et al. 2006). One of these families is named herein, and two families are redefined. Despite this expanded phylogeny of the Diaporthales, many genera are not affiliated with any of the lineages, and it is expected that additional families will be uncovered with increased taxon sampling. This was the case with the Sydowiellaceae. Initially, taxa now placed in the Sydowiellaceae were considered to be unaffiliated with any family but, with increased sampling and the addition of more taxa, these species have merged into a well-supported family (Rossman et al. 2006).

The phylogeny of each of the nine families currently recognized in the Diaporthales is reviewed here based on molecular data along with a summary of their biology. For some families, extensive data exist, while for others very little is known. Because of the polyphyletic nature of most of the genera as defined based on morphology, emphasis is placed on type species. At the end of the article, some genera in the Diaporthales are discussed for which data are insufficient to place them in any existing family.

## Gnomoniaceae

Figs. 1–4

Members of the Gnomoniaceae occur primarily on hardwood trees, although other hosts exist, such as conifers for the anamorph genus *Sirococcus*. Several diseases are caused by species in the Gnomoniaceae, as mentioned below, but these species fruit primarily on overwintered leaves (Stoykow 2005) and are also commonly isolated as endophytes (Kaneko and Kobayashi 1984; Barengo et al. 2000). This family includes at least ten known teleomorphic genera, namely, *Apiognomonia-Discula*, *Apioplagiostoma*, *Cryptodiaporthe*, *Cryptosporella-Disculina*, *Ditopella*, *Gnomonia*, *Gnomoniella*, *Ophiovalsa*, *Phragmoporthes*, and *Plagiostoma*, and the anamorphic genus *Sirococcus*, for which no teleomorph is known. Results of molecular studies (Castlebury et al. 2002) generally agree with the concept of the Gnomoniaceae as monographed by Monod (1983). This finding differs significantly from other concepts of this family based solely on morphology as proposed by Barr (1978, 1990, 1991), Kobayashi (1970), and Vasilyeva (1993).

The Gnomoniaceae is characterized by ascomata that are immersed, solitary without a stroma, or aggregated in a reduced prosenchymatous stroma in herbaceous plant material, especially in leaves or stems but also in wood. The ascomata are generally soft-textured, thin-walled, and prosenchymatous with either central or lateral beaks. The asci usually have a distinct apical ring. This family includes species having ascospores that are generally small, less than 25 µm long, although some are longer as in *Cryptosporella*, and range in septation from nonseptate to one-septate or multiseptate. The asexual states of members of the Gnomoniaceae are acervular or pycnidial with a broad opening. Conidiogenous cells are phialidic, and conidia are usually pallid and nonseptate (Monod 1983).

The genus *Gnomonia* is represented by the type species *G. gnomon* (Tode) J. Schröt. (Sogonov et al. 2005). Species of *Gnomonia* usually have beaked, thin-walled, solitary perithecia immersed in the substrata. Recent data show that *Gnomonia* may not be monophyletic (Sogonov et al. 2006). Numerous additional species of *Gnomonia* have been described but cannot yet be placed in well-defined genera. The genus *Apiognomonia* is distinguished from *Gnomonia* by unequally septate ascospores. Recent molecular data show that *Apiognomonia errabunda* and *Plagiostoma euphorbiae* (Fuckel) Fuckel, type of the genus *Plagiostoma*, are allied with a group that includes two species of *Cryptodiaporthe* including the type species *C. aesculi* (Fuckel) Petr. and *C. salicella* (Fr.) Petr. Monod (1983) placed *P. euphorbiae* in

*Gnomonia*. *Gnomoniella fraxinii* and its asexual state *Discula fraxinea* (Redlin and Stack 1988) is a non-type species of a genus similar to *Gnomonia* but having unicellular ascospores. *Gnomonia* also includes two morphologically similar species on *Corylus*, *Phragmoportha conformis* (Berk. & Broome) Petr. with polysporous asci and three-septate ascospores and *Ditopella ditopa* (Fr.) J. Schröt. with eight-spored asci and one-septate ascospores. Monod (1983) recognized *Ditopella ditopa* in the genus *Gnomonia*.

The genus *Cryptosporella* is a well-defined genus within the Gnomoniaceae, represented by the type species *C. hypodermia* (Fr.) Sacc. (Castlebury et al. 2002). The type species of *Ophiovalsa*, *O. suffusa* (Fr.) Petr., and a second species, *O. betulae* (Tul. & C. Tul.) Petr., are congeneric with *C. hypodermia*; thus, *Ophiovalsa* is considered a synonym of *Cryptosporella*. The genera *Cryptosporella* and *Ophiovalsa* were not included in Gnomoniaceae by Monod (1983) or any other authors. The genus *Winterella* has been confused nomenclaturally with *Ophiovalsa* (Reid and Booth 1987) and includes a number of species that were previously placed in the genus *Cryptospora* (Reid and Booth 1989). In contrast to members of the Gnomoniaceae, *Cryptosporella* is characterized by a distinctly valsoid arrangement of ascomata. *Cryptosporella* is similar to other members of the Gnomoniaceae in having stromatal tissues that are prosenchymatous, nearly lacking discs, or forming small ectostromatic discs that may be reduced to a brown disc between the erumpent ostiolar cluster and perithecia.

At least two groups of species in the Gnomoniaceae reproduce asexually and lack any known sexual state, as is the case for most plant-associated fungi (Rossman 1993). The cause of dogwood anthracnose, *Discula destructiva*, is such a species for which a sexual state is unknown. Despite use of molecular data, neither Zhang and Blackwell (2001) nor Castlebury et al. (2002) were able to infer the sexual state of *D. destructiva*. Its affinities to the Gnomoniaceae in the Diaporthales were hypothesized by Redlin (1991) and confirmed by Zhang and Blackwell (2001) and Castlebury et al. (2002). The anamorphic genus *Sirococcus*, typified by *S. conigenus* (DC.) P.F. Cannon & Minter, includes only species that occur on conifers. No teleomorph is known for these species, nor is one known for the noncongeneric species *S. clavignenti-juglandacearum*, cause of butternut canker in North America (Ostry et al. 1996).

### Melanconidaceae

Figs. 5–8

At present the only genus represented in this family is the type, namely, *Melanconis*, including the type species, *M. stilbostoma* (Fr.) Tul. & C. Tul., and two other species, *M. alni* Tul. & C. Tul. and *M. marginalis* (Peck) Wehm. (Castlebury et al. 2002). The anamorphs of *Melanconis* are placed in the genus *Melanconium*. The three species of *Melanconis* are restricted to hardwood trees in the Betulaceae, on which they appear to be endophytic and weakly pathogenic. This family is sister to the Gnomoniaceae, both of which have prosenchymatous stromatic tissues. The genus *Melanconis* sensu Wehmeyer (1941) included many

additional species, some of which have been studied but are not affiliated with any families in the Diaporthales (L.A. Castlebury, unpublished data). One of these has been segregated from *Melanconis* as *Melanconiella spodiæa* (Tul. & C. Tul.) Sacc., type of the genus *Melanconiella*, whereas *Melanconis desmazieri* Petr. appears to be affiliated close to the Sydowiellaceae (L.A. Castlebury, unpublished data).

### Schizoparmeaceae Rossman, fam. nov.

Figs. 9–11

Ascomata fusca vel nigra, collapsa, erumpentia, superficialia. Asci annulo apicali distincto praediti, ad maturitatem separati. Paraphyses nullae. Ascosporae non septatae. Anomorphi pycnidiales in *Coniella* Höhn. & *Pilidiella* Petr. & Syd.

Genus typicum: *Schizoparme* Shear

Ascomata brown to black, collapsed collabent, erumpent, becoming superficial. Asci with distinct apical ring, floating free at maturity. Paraphyses lacking. Ascospores nonseptate. Pycnidial anamorphs in *Coniella* Höhn. and *Pilidiella* Petr. & Syd.

Type genus: *Schizoparme* Shear, Mycologia 15: 121, 1923.

This new family includes the distinctive teleomorph genus *Schizoparme* and its asexual state *Pilidiella* and the closely related anamorph genus *Coniella*. Samuels et al. (1993) were the first to recognize the unique nature of *Schizoparme* and its relationship to *Coniella* and *Pilidiella*. These fungi were initially placed in the Melanconidaceae, but Castlebury et al. (2002) determined that these species constitute a distinct lineage within the Diaporthales, which they referred to as the *Schizoparme* complex, as did van Niekerk et al. (2004). Members of the Schizoparmeaceae have fruiting bodies that are often erumpent through the host epidermis, becoming superficial on living or decaying herbaceous and woody plants. Members of this family produce diseases such as white rot of grapes caused by *Pilidiella diplodiella* (Speg.) Crous & van Niekerk (Sutton and Waterston 1966, as *Coniella diplodiella*) and leaf and fruit diseases of strawberry caused by *P. castaneicola* (Ellis & Everh.) Arx (Maas 1998). Although known in temperate regions, species of the Schizoparmeaceae are most common in tropical areas.

Both the ascomata of *Schizoparme* and conidiomata of *Pilidiella* and *Coniella* are brown or black, occasionally pallid yellowish brown or gray. They have a distinctive wall layer that is irregularly thickened, often with plate-like ornamentation. They become collapsed cupulate upon drying, erumpent through the substromatal surface at maturity. The asci, which arise from the base of the fruiting body (Samuels et al. 1993), are typically diaporthalean with a distinct apical ring and float free in the centrum. The ascospores are one-celled, initially hyaline, but may become pale to dark brown, smooth, rarely with gelatinous appendages. The type species of *Schizoparme* is *S. straminea* Shear having the anamorph *Pilidiella castaneicola*. Seven species are included in *Schizoparme* (Samuels et al. 1993).



Until recently, *Pilidiella* was considered a synonym of *Coniella* (Sutton 1980; Nag Raj 1993); however, van Niekerk et al. (2004) demonstrated that these two anamorph genera should be distinct. Both produce one-celled conidia rarely with a longitudinal slit. *Pilidiella* includes species with hyaline to pale brown conidia having a length:width ratio of greater than 1.5, whereas conidia of *Coniella* are dark brown and much narrower. The pycnidia of both *Coniella* and *Pilidiella* are relatively thick-walled, often hyaline. They produce pale brown to dark brown conidial masses in which the conidiogenous cells develop from a basal pad described as a “pulvinate basal parenchyma” by Sutton (1980) and described in detail by Muthumary and Vaneja (1986) for *Coniella fragariae* (Oudem.) B. Sutton. This structure is morphologically similar to the basal pad from which the ascogenous hyphae develop in the ascomatal state. Species of *Schizoparme* have *Pilidiella* anamorphs; no teleomorph is known for *Coniella*.

### Cryphonectriaceae

Figs. 12–15

The Cryphonectriaceae was recently described to accommodate *Cryphonectria*, *Endothia*, and several segregate genera including *Amphilogia*, *Chrysosporthe*, and *Rostrareum* (Gryzenhout et al. 2004, 2005a–c, 2006), a group first recognized as the *Cryphonectria-Endothia* complex by Castlebury et al. (2002). All members of this family have microscopic characteristics typical of the Diaporthales with the addition of fruiting bodies with orange-reddish stromatic tissues that turn purple in 3% KOH. The genus *Cryphonectria* was recently conserved with a new type species, *C. parasitica*, thus ensuring that the name of this important fungus remains stable and serves as the basis for this family (Gryzenhout et al. 2005a). The anamorph states of members of the Cryphonectriaceae are pycnidial, often with the same orange-reddish KOH+ purple pigments, phialidic conidiogenous cells, and small, hyaline, nonseptate conidia, placed in the anamorph genera *Endothiella* and the recently described *Chrysosporthella*. Additional species in this family include *Wuestneia xanthostroma* (Mont.) J. Reid & C. Booth, type of the genus *Wuestneia* (L.A. Castlebury, unpublished data), and *Cryptodiaporthe corni* (Wehm.) Petr., a non-type species (Redlin and Rossman 1991). Both of these species have orange-reddish pigments in the stroma.

The Cryphonectriaceae includes virulent pathogens such as the well-characterized *Cryphonectria parasitica*, cause of chestnut blight (Anagnostakis 1988; Milgroom and Cortesi 1999; Breullin et al. 2006). In addition, *Chrysosporthe cubensis* (Bruner) Gryzenh. & M.J. Wingf. and several related species threaten eucalyptus trees throughout the world

(Gryzenhout et al. 2004, 2005d). Many members of this family occur primarily on woody plants as saprobes, e.g., *Endothia gyrosa* (Schwein.) Fr., *Cryphonectria nitschkei* (G.H. Otth) M.E. Barr, *C. macrospora* (Tak. Kobay. & Kaz.-Ito) M.E. Barr, and *C. radicalis* (Schwein.) M.E. Barr (Hoegger et al. 2002; Myburg et al. 2004) and are often observed in their *Endothiella* pycnidial states on the exposed roots of hardwood trees.

### Valsaceae

Figs. 16–19

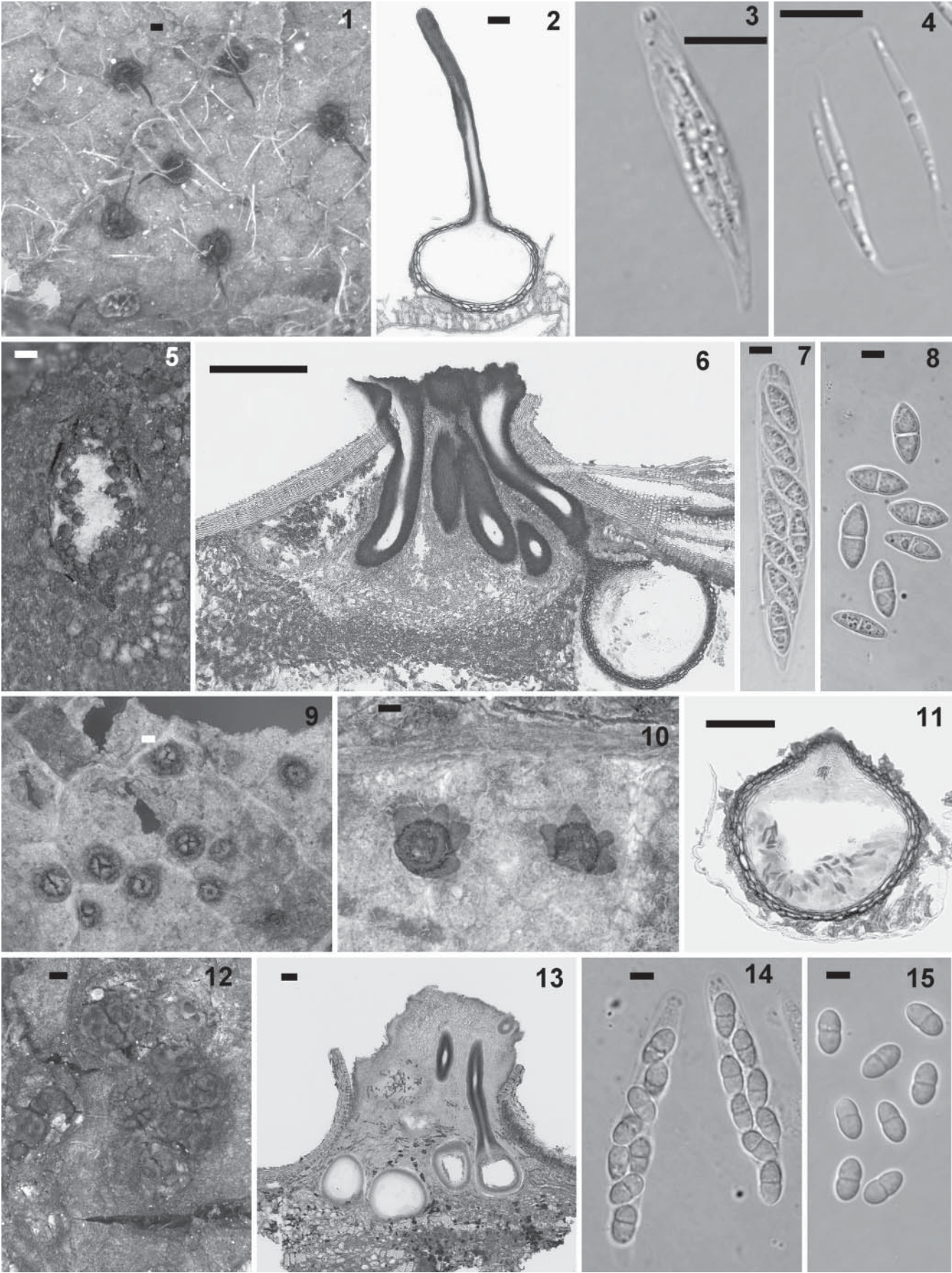
The Valsaceae is restricted to the genus *Valsa* and its segregates, including *Valsella* and *Leucostoma*, based on Castlebury et al. (2002). Previously, Barr (1978) had recognized the Valsaceae to include members of the Diaporthaceae such as *Diaporthe* as well as *Plagiostoma* and *Cryptodiaporthe*, now placed in the Gnomoniaceae, and *Cryphonectria*, now placed in the Cryphonectriaceae.

The genera *Leucostoma*, *Valsa*, and *Valsella* have been long recognized as closely related genera (Spielman 1985; Vasilyeva 1998; Castlebury et al. 2002), and the distinction between them is not clear. Traditionally they are separated based on the characteristics of having eight-spored asci (*Leucostoma* and *Valsa*) or polysporous asci (*Valsella*), with *Leucostoma* having a white to grayish-brown, ectostromatic disc, but this latter character appears to vary with specimen age. All three genera have anamorphs referred to as *Cytospora*. In Castlebury et al. (2002), the genus *Valsa* was represented by its type species *V. ambiens* (Pers.) Fr., which occurs on woody angiosperms in temperate regions throughout the world (Spielman 1985), and several other species. In the phylogenetic tree presented by Castlebury et al. (2002), the two species of *Valsella*, including the type species *V. salicis* Fuckel and *V. adherans* Fuckel, were intermingled with species of *Valsa* and *Leucostoma* such as *L. cincta* (Fr.) Höhn. and *L. nivea* (Hoffm.) Höhn. However, the type species *L. massarina* (De Not.) Höhn. was not included in this study. The genus *Leucostoma* is considered a synonym of *Valsa* by Vasilyeva (1998).

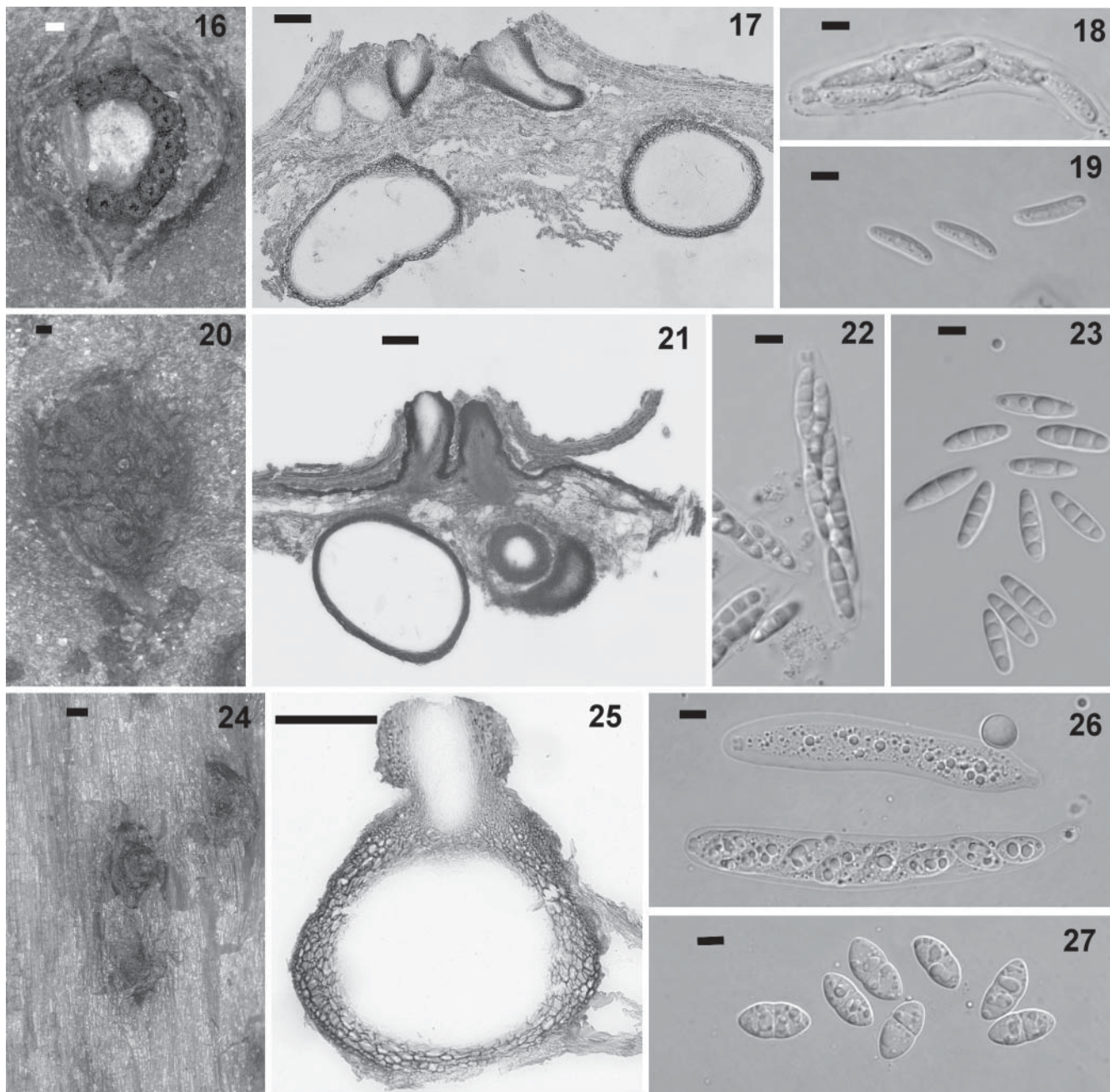
Members of *Leucostoma*, *Valsa*, and *Valsella* occur on hardwoods and occasionally on conifers throughout the world, often in their *Cytospora* anamorphic states. Species of *Valsa* on hardwoods in North America were delineated by Spielman (1985); three species of *Valsa* were reported from the eastern Himalayas by Dargan and Sharma (1991). Members of the Valsaceae cause canker diseases such as *Cytospora* canker or gummosis of peach and stone fruits caused by *Leucostoma persoonii* (Nitschke) Höhn. (Hayova and Minter 1998a) and other species of *Leucostoma* as described by Adams et al. (2002). Species of *Valsa* including *V. ambiens*, *V. ceratosperma* (Tode) Maire, *V. cypri* (Tul.)

**Figs. 1–15.** Representative species of four families in the Diaporthales. **1–4** Gnomoniaceae: *Gnomonium gnomon*. **1** Ascomata. **2** Section through ascomata. **3** Asci. **4** Ascospores. **5–8** Melanconidaceae: *Melanconis stilbostoma*. **5** Ascomata. **6** Section through ascomata. **7** Asci. **8** Ascospores. **9–11** Schizoparmeaceae: *Schizoparme straminea*. **9, 10** Ascomata. **11** Section through ascomata. **12–15** Cryphonectria-

ceae: *Cryphonectria parasitica*. **12** Ascomata. **13** Section through ascomata. **14** Asci. **15** Ascospores. **1–4** BPI 844237; **5, 6** BPI 748234; **8** BPI 872036; **9, 11** BPI 600008; **10** BPI 600023; **12, 13** BPI 749121; **14, 15** BPI 748234. Bars **1, 2, 5, 6, 9, 10, 11, 13** 100µm; **12** 400µm; **3, 4, 7, 8, 14, 15** 10µm







**Figs. 16–27.** Representative species of three families in the Diaporthales. **16–19** Valsaceae: *Valsa ambiens*. **16** Ascomata. **17** Section through ascomata. **18** Asci. **19** Ascospores. **20–23** Diaporthaceae: *Diaporthe eres*. **20** Ascomata. **21** Section through ascomata. **22** Asci.

**23** Ascospores. **24–27** Sydowiellaceae: *Sydowiella fenestrans*. **24** Ascomata. **25** Section through ascoma. **26** Asci. **27** Ascospores. **16–19** BPI 843602; **20, 21** BPI 841335; **22, 23** BPI 872076; **24–27** BPI 843503. Bars **16** 200µm; **17, 20, 21, 24, 25** 100µm; **18, 19, 22, 23, 26, 27** 10µm

Tul. & C. Tul., *V. eugeniae* Nutman & F.M. Roberts, *V. malicola* Z. Urb., *V. salicina* (Pers.) Fr., and *V. sordida* Nitschke cause canker diseases of hardwood trees, especially those that are stressed or damaged (Sivanesan and Holliday 1970; Hayova and Minter 1998b–h). Adams et al. (2005) described 27 species of *Valsa* and *Cytospora* causing diseases on *Eucalyptus* in Australia and South Africa.

#### Diaporthaceae

Figs. 20–23

The Diaporthaceae consists of the very large genus *Diaporthe* with 801 named taxa and its *Phomopsis* anamorph with more than 900 described species (Uecker 1988). Based on Castlebury et al. (2002), this family includes only *Diaporthe-Phomopsis* and the genus *Mazzantia* based on

the non-type species *M. napelli* (Ces.) Sacc. Wehmeyer (1933) recognized the relationship of *Mazzantia* to *Diaporthe*, especially as the anamorph *Mazzantiella* having “a stroma similar to the ascospore state with pycnidial locule containing comma-shaped conidia on filiform conidiophores . . . similar to the *Phomopsis* state of the genus *Diaporthe*.” At least one segregate genus, *Diaporthopsis*, on the basis of the presence of nonseptate ascospores, was determined to belong within *Diaporthe* based on a study of the type species, *Diaporthopsis angelicae* (Berk.) Wehm. (Castlebury et al. 2003). The genus *Allantoporthe*, based on the type species *A. tessella* (Pers.) Petr., was established for species similar to *Diaporthe* but having a short narrow appendage at the ends of the ascospores. Wehmeyer (1933) suggested that the presence of faint hyaline appendages was not a constant character. Barr (1978) segregated *Allantoporthe* from *Diaporthe* based on the prosenchymatous stromatic tissues in *Allantoporthe*. Molecular data suggest that both *A. tessella* and *A. decedens* (Fr.) M.E. Barr belong in *Diaporthe* sensu lato (L.A. Castlebury, unpublished data). Relationships within this genus and family have yet to be determined.

The proliferation of species names, especially in *Phomopsis*, has resulted from the assumption that these fungi are host specific. Some species of *Phomopsis* appear to be host-specific pathogens such as *Phomopsis amygdali* (Delacr.) J.J. Tuset & M.T. Portilla, cause of peach and almond canker (Farr et al. 1999; Kanematsu et al. 1999, 2000), although this species has recently been isolated from grape (van Niekerk et al. 2005). Other recently described, host-specific species of *Phomopsis* include *P. gossypii* (Sacc.) Palmateer et al., cause of boll rot of cotton (Palmateer et al. 2003), *P. vaccinii* Shear et al., cause of blueberry and cranberry canker (Farr et al. 2002a), *P. viticola* (Sacc.) Sacc. on grapes (Schilder et al. 2005), and *P. columnaris* Farr. & Castl. on lingonberry (Farr et al. 2002b). Recent studies suggest that many species of *Phomopsis* occur on a variety of plant host genera (Rehner and Uecker 1994) or, conversely, the same plant host may harbor several species of *Phomopsis* as exemplified by the six different species of *Diaporthe-Phomopsis* on *Vitis vinifera* (Phillips 1999; Kajitani and Kanematsu 2000; Mostert et al. 2001; van Niekerk et al. 2005).

Many plant diseases are caused by species of *Diaporthe* (Wehmeyer 1933) and *Phomopsis* (Uecker 1988), some of which have already been mentioned. The taxa causing diseases on soybean are difficult to separate, with at least four different taxa involved (Fernandez and Hanlin 1996). Northern soybean stem canker caused by *D. phaseolorum* (Cooke & Ellis) Sacc. var. *caulivora* Athrow & Cauldwell occurs on hosts in addition to soybean (Black et al. 1996), as does *D. ambigua* Nitschke, reported to cause a disease on rootstocks of rosaceous fruit trees (Smit et al. 1996) but also known on grapes (van Niekerk et al. 2005). For many disease-causing species of *Phomopsis*, host specificity is not known, as, for example, *P. limonii* I.C. Harv. et al. 2000 (non Vegh 1994), cause of stem canker on the cut-flower hybrid *Limonium* sp. (Harvey et al. 2000), *Diaporthe foeniculacea* Niessl on fennel (Phillips 2003), and *D. actinidiae*

N.F. Sommer & Beraha, cause of stem-end rot of kiwifruit (Lee et al. 2001).

*Phomopsis* is the most prevalent endophytic fungus isolated from both tropical and temperate woody plants (Fisher et al. 1994, 1995; Shamoun and Sieber 2000; Tomita 2003) and was present in the sapwood of almost all angiospermous trees examined (Boddy and Griffith 1989). Their potential role in protecting plants from fungal diseases such as Dutch elm disease has been explored (Brayford 1990). At least one endophytic *Phomopsis* from a woody tropical tree is known to produce toxins that affect the central nervous system in vertebrates (Bills et al. 1992), suggesting an adaptive advantage to plants that harbor these fungi.

Little is known about the mating systems in the *Diaporthe-Phomopsis* complex; however, Linders and van der Aa (1995) demonstrated that *D. adunca* (Roberge ex Desm.) Niessl was heterothallic with two mating types. Fertilization occurs in the fall when the alpha-conidia that function as both fertilizing agents and infective agents were splashed onto adjacent substrata, resulting in cross-fertilization and development of the *Diaporthe* sexual state the following spring (Linders and van der Aa 1995).

### Pseudovalsaceae

The Pseudovalsaceae was established by Barr (1978) in a broad sense to include members of the Diaporthales having upright, erumpent perithecia with central beaks. Based on Castlebury et al. (2002), many members of Pseudovalsaceae sensu Barr belong elsewhere, such as *Ditopella* and *Phragmoporthe*, now placed in the Gnomoniaceae, *Allantoporthe*, now placed in the Diaporthaceae, and *Chapeckia* and *Sydowiella*, now placed in the Sydowiellaceae (L.A. Castlebury, unpublished data). In fact, the only genus included in the Pseudovalsaceae at present is *Pseudovalsa* based on the type species *P. lanciformis* (Fr.) Ces. & de Not. and related species *P. longipes* (Tul.) Sacc., *P. modonia* (Tul. & C. Tul.) Höhn., and *P. umbonata* (Tul. & C. Tul.) Sacc., all species that have a *Coryneum* anamorph and occur on temperate hardwood trees in the Fagales.

### Sydowiellaceae

Figs. 24–27

The Sydowiellaceae is based on *Sydowiella*, type species *S. fenestrans* (Duby) Petr., with an assortment of genera and species that do not have any clear features in common (L.A. Castlebury, unpublished data). These taxa occur on herbaceous, dicotyledonous plants as well as hardwood trees. Genera in this family include the type species of *Chapeckia*, *C. nigrospora* (Peck) M.E. Barr, *Hapalocystis*, *H. berkeleyi* Fockel (the closely related *H. occidentalis* Jakl. & Voglmayr (Jaklitsch and Voglmayr 2004), *Rossmania*, *R. ukurunduense* Lar. N. Vassiljeva (Vasilyeva 2001), *Stegophora*, *S. ulmea* (Fr.) Syd. & P. Syd., and *Sillia*, *S. ferruginea* (Pers.) P. Karst. In addition, the Sydowiellaceae includes species previously placed in *Gnomonia*, such as *G. rostellata* (Fr.) Brefeld on herbaceous plants, a species potentially bet-



ter placed in *Sydowiella*. The biology of the Sydowiellaceae is also quite diverse, ranging from parasites of living leaves such as *Stegophora ulmea* on *Ulmus americana* and saprobes on herbaceous plants to *Hapalocystis berkeleyi* forming stromatic fruiting bodies on decaying woody plants.

## Togniniaceae

The Togniniaceae was established by Reblova et al. (2004) for species of *Togninia* and their *Phaeoacremonium* anamorphs that were removed from the Calosphaeriales and recognized in the Diaporthales along with the genus *Jobellisia* (Reblova et al. 2004; Mostert et al. 2006). This conclusion was based on small subunit (SSU) rDNA; however, analyses based on large subunit (LSU) rDNA are ambiguous about placement of this family (Mostert et al. 2006). The Togniniaceae and the Calosphaeriales are unique in having asci that develop in fascicles from short proliferating ascogenous hyphae and are morphologically quite unlike the Diaporthales. The phylogenetic data presented by Mostert et al. (2006) also suggest that *Jobellisia* may be allied with the Diaporthales. Except for the presence of a conspicuous ring in the ascus apex, this genus does not have characteristics of the Diaporthales, i.e., asci that float free and paraphyses lacking at maturity; rather, the long-stalked asci of *Jobellisia* remain attached among abundant straight paraphyses.

The genus *Togninia*, especially as the hyphomycetous anamorph *Phaeoacremonium*, is involved in two serious diseases of grapevine (esca and Petri disease) and other wilting and dieback diseases of plants (Mostert et al. 2003). These fungi also are opportunists that infect humans, causing phaeohyphomycosis. Ten species of *Togninia* and 22 species of *Phaeoacremonium* were monographed by Mostert et al. (2006) in a publication that also includes a review of the diseases caused by these fungi.

## Diaporthalean fungi of unknown affiliation

Several genera in the Diaporthales either are not affiliated with any family or have not been examined using molecular sequences. Only a few of the most important taxa are mentioned here.

The anamorphic genus *Harknessia* belongs in the Diaporthales with several species grouping together but outside of any recognized family (Castlebury et al. 2002). The teleomorph genus *Wuestneia* is linked to species of *Harknessia* (Crous et al. 1993; Crous and Rogers 2001); however, the type species of *Wuestneia*, *W. xanthostroma* (Mont.) J. Reid & C. Booth, with distinctive orange-red pigments, has affinities with members of the Cryphonectriaceae, whereas the remaining species of *Wuestneia* and species of *Harknessia* form a group outside this family (Lee et al. 2004). The similar-looking anamorph genus *Apotharknessia* lacks a known teleomorph and is phylogenetically distinct from

*Harknessia* (Lee et al. 2004) but also is not allied with any known family in the Diaporthales. Species of *Harknessia* and *Apotharknessia* are associated with diseases of primarily tropical plants, especially *Eucalyptus* (Yuan and Mohammed 1997; Yuan et al. 2000) and Proteaceae (Crous et al. 1993; Lee et al. 2004). The anamorph genus *Dwiroopa* with the non-type species *D. lythri* (D.F. Farr & Rossman) D.F. Farr & Rossman, initially described as *Harknessia lythri* D.F. Farr & Rossman, also could not be placed in any known family within the Diaporthales (Farr and Rossman 2001, 2003). The cause of bitter rot of grape, *Greeneria uvicola*, was determined to belong in the Diaporthales, but it is not affiliated with any recognized family, nor is any teleomorph known for this anamorph species (Farr et al. 2001).

*Hercospora* is a distinct genus in that the ostioles from individual fruiting bodies converge within the stroma and emerge as one ostiole. *Hercospora tiliae* (Pers.) Tul. & C. Tul., with its unusual anamorph, *Rabenhorstia*, groups with *Melanconis desmazieri*, also on *Tilia*, and is allied with the Sydowiellaceae but falls outside this family (L.A. Castlebury, unpublished data).

The genera *Lollipopaia* and *Phruensis* on *Licuala* (Areaceae) are described as members of the Diaporthales with unknown affinities, both having elongate ascospores and the latter producing a phialophora-like anamorph (Inderbitzin and Berbee 2001; Pinruan et al. 2004). *Phruensis* appears morphologically similar to *Melogramma* in the Melogrammataceae, Phyllachorales. The genus *Vismaya* was described from rotting wood in Hong Kong and appears to be a member of the Gnomoniaceae, but it lacks a distinct apical ring (Sarma and Hyde 2001). Without a culture, it will be difficult to determine the affinities of this genus.

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