

REVIEW

Roy Watling

The sclerodermatoid fungi

Received: October 19, 2005 / Accepted: November 11, 2005

Abstract Those fungi that have been linked to the gasteroid genus *Scleroderma* by molecular techniques are discussed in relation to secondary metabolites, development, spore morphology, and anatomy. The group contains epigeous and hypogeous components and sequestrate and boletoid members. An intratribal classification is proposed to accommodate these life forms.

Key words Barometer earthstar · Boletoid · Devil's club · Earthballs · False truffles · Sclerodermatineae

Introduction

The sclerodermatoid fungi as an entity offer a window into the changes that are currently occurring in many groups of basidiomycetes where dissimilar morphologies are drawn together based on similarities in secondary metabolite production, development, geographical distribution, and molecular details.

Thus, in the sclerodermatoid fungi, the subject of this article, links have been found between the traditional gasteroid core members, generally called earthballs, and the boletes; several new species have been recognized, especially in the tropics, and distributions have been extended for many and other previously considered well-known species separated into more than one autonomous taxon.

What is meant by a sclerodermatoid fungus? The present study is based on the suborder erected by Binder (1999) in his dissertation wherein he strongly linked *Scleroderma* Pers.: Fr., 1821 to the genus *Gyroporus* Quéél., 1886 (Binder and Bresinsky 2002), in addition to consolidating the already suggested link with *Astraeus* Morg., 1889 and *Pisolithus* Alb. & Schwein., 1805. To everyone's surprise,

when a study by Hibbett et al. (1997) was published, a link was also demonstrated with the genus *Calostoma* Desv., 1809, a genus which until this work sat on the edge of most classifications. The survey by Binder and Bresinsky (2002) and others (Hibbett et al. 1997) also demonstrated that the sclerodermatoid fungi are a sister-group to the suilloid fungi, which includes the slippery jacks, viz. Suillaceae, and the nail heads, viz. Gomphidiaceae, and the bearded false truffles, viz. Rhizopogonaceae. Both are separate branches to the mainstream of boletes. All these fungi form sheathing mycorrhizae.

The sclerodermatoid fungi are also important commercially as mycorrhizal partners of many of our forest trees, and some, especially *Pisolithus* and *Scleroderma*, have been utilized for inocula in forestry practice, especially in developing countries such as the Philippines. There are some very good edible species contained in the group, and others have been used in dyeing. Herein the author wishes, based on molecular and developmental studies and the presence of specific secondary metabolites, to briefly discuss the group as a single unit, pointing out the exciting progress that has been made in understanding this group. It is an attempt to bring together a wide spectrum of features that will provide the reader with sufficient information to surf through all the available data to obtain a general overview of the earthballs and their relatives. Areas of possible further potentially fruitful research are indicated. For completeness and to assist this quest, dates of both genera and species are given.

Earthballs and devil's clubs

The Thai-Malaysian Peninsula has been a fruitful source of new species in both *Scleroderma* and *Pisolithus*. Thus, *S. cyaneoperidiata* Watl. & Sims, with its blue reaction in the flesh similar to that of the bolete *Gyroporus cyanescens* (Bull.: Fr.) Quéél., and *S. xanthochroum* Watl. & Sims, a member of *Scleroderma* section *Aculeati*, have recently been described from Malaysia (Watling and Sims 2004).

R. Watling (✉)
Caledonian Mycological Enterprises, 26 Blinkbonny Av., Edinburgh
EH4 3HU, Scotland, UK
Tel. +131-467-37-47
e-mail: caledonianmyc@compuserve.com

The latter is similar in color to *S. sinamariense* Mont., 1840, an earthball described from Guyana, and has been considered by Guzmán (1970) to have many synonyms, including *S. aureum* Mass., 1889, from New Guinea; *S. chrysastrum* Mart., 1954 from Panama; *S. endoxanthum* Petch, 1919 from Sri Lanka; *S. flavocrocatum* Sacc. & de Toni, 1887 from Malaya where it is widespread; *S. lutuem* Lloyd, 1914 from Sewarang; *S. pantherinum* Matt., 1931 from Indonesia, and *S. pisiforme* P. Henn., 1895 from Cameroon. As one can see, most epithets emphasize the yellow colors, and first impressions of this fungus would appear to indicate it has a pantropical distribution. If experience from the analysis of other species in this group of fungi can be taken as a guide, this species may very well turn out to be a cluster of closely related species hidden within this epithet as presently conceived by Guzmán, each with a different distribution, small morphological differences and totally different internal transcribed spacer (ITS) sequences. Reading the unpublished notes of Corner now in the Royal Botanic Gardens, Edinburgh, he certainly believed that there were several recognizable entities even in Malaysia, with which this author would concur. If so, it will be with great difficulty that the molecular “species” thus found could be connected to one or other of the names above, but we should try. Molecular studies of all the types that exist may come to the rescue depending on how well the material has been preserved!

Scleroderma echinatum (Petri, 1900) Guzmán, 1967 has been rarely collected since Petri (1900) described the species from Malaysia and made it the type of the genus *Caloderma* Petri. It was Guzmán (1967) who realized this fungus was in fact referable to *Scleroderma*, so relegating *Caloderma* to synonymy. Even when records for the suggested synonym *S. violaceum* Lloyd, 1924, described from the Congo are taken into account, there is still a paucity of records in existence. However, the author’s own studies in Malaysia indicate that it is a rather common member of the mycobiota of the seasonally dry tropical rainforests in the central parts of Malaysia (Sims et al. 1995). *Veligaster* Guzmán was a genus erected for those species of *Scleroderma* clustered around *S. columnare* Berk. & Br., 1875 (Guzmán, 1969), i.e., those species possessing a distinct stipitate basidiome and floccose velar tissue. However, based on molecular studies these same species cluster within the core species of *Scleroderma*, so the autonomy of this newly proposed genus cannot be upheld.

Other synonyms that have been indicated by various authors as synonyms of *Scleroderma* are *Actigea* Raf., 1814; *Goupilia* Mérat, 1834; *Lycoperdastrum* P. Micheli, 1729; *Mycastrum* Raf., 1813; *Sterrebekia* Link 1816; *Stella* Masee, 1889; *Sclerangium* Lév. 1848; *Pompholyx* Corda, 1834 · *Progaster*, P. Henn., 1901; *Nepotatus* Lloyd, 1925; *Phlyctospora* Corda, 1841; and *Pirogaster*, P. Henn, 1901. Most of these genera are poorly known or their original concept has been lost through time; none are used in modern texts today. For some of these more obscure genera, see Kirk et al. (2001).

At least two subhypogeous fungi have been linked to the sclerodermatoid fungi: (1) *Sclerogaster* R. Hesse, 1891 has

many of the characters of *Scleroderma* but it barely breaks through the soil surface; currently it is referred to the Octavianinaceae; and (2) *Neosaccardia* Mattir., 1921, which although synonymized with *Scleroderma*, based on recent Thai material is a genus that could well be distinct.

The genus *Favillea* Fr., 1848, based on a single Australian gasteromycete, is now lost in the mists of time and has been interpreted in different ways, sometimes referred to *Scleroderma* while on other occasions to *Pisolithus*. This last genus has often in this author’s opinion been incorrectly submerged in a united taxon, the Sclerodermataceae. In this genus, *P. aurantioscabrosus* Watl., 1999, with bright orange, cockatoo-like scales and diminutive stature, has been described from the dipterocarp rainforest in Central Malaysia and has now been seen on several occasions elsewhere in the same general vegetational type. If it is anything like *P. arhizus* (Scop.: Pers., 1801) Rausch., 1959 and is used as a mycorrhizal inoculum, this taxon might be exploited in tree nursery development for rainforest tree hosts. Several species of *Pisolithus* have been described previously but have all been too hastily relegated to synonyms of the so-called ubiquitous *P. tinctorius* (Mich.: Pers.) Coker & Couch, 1928 (= *Polysaccum tinctorium* (Mich.: Pers. 1801) Mont., 1840), correctly called *P. arhizus*; a further commonly used synonym in forestry practice is *P. arenarius* Alb. & Schwein., 1805.

Originally, “PT,” as this species is affectionately known and abbreviated in many general texts, was considered to have a wide range of arborescent hosts, but this fact did not sound any alarm bells in the minds of mycologists. However, studies of the spore morphology under the electron microscope alone soon showed there were differences between collections from different parts of the world. In Australia, molecular work indicated that there is indeed more than one species present on that subcontinent alone (Cairney et al. 1999; Martin et al. 2002). However, there remains some confusion because of the trade in arborescent plants, and the movement of plants about the world has muddled the true distribution if any clearly different entities were involved. Australian species have now been recognized in Thailand and South and East Africa, where they have been undoubtedly transferred on plant stock. Parallels are known for other fungi such as several Australian taxa including *Setchelliogaster tenuis* (Setch., 1907) Pouzar, 1958 on the Berkeley campus in California, *Hydnangium carneum* Wallr. apud. Dietrich, 1839, in as farflung places as the Falkland Islands and Mull off the west coast of Scotland, *Descolea* with *Nothofagus* in the Faeroes, and *Rodwayella* in North Africa. At least the different species of *Pisolithus* in Southeast Asia are now being unraveled by Thai mycologists with whom the author is collaborating. Naturally occurring Thai species, including the new *P. abditus* Kanchanaprayudh et al., and those introduced taxa mentioned above, have now been documented for that country (Kanchanaprayudh et al. 2003); at least one further species not yet formally described is known from Thailand.

Although producing such obvious basidiomes, *Pisolithus* spp. are still quite variable in morphology, especially as they mature, so it is understandable why it has been described

many times in the literature at both specific and generic levels. But do all the names really all refer to a single taxon? The author thinks not. Just as with *Scleroderma*, the genus *Pisolithus* also has many synonyms listed in the literature, e.g., *Durosaccum* Lloyd, 1924; *Endacinus* Raf., 1814 (= *Eudacnus* Merr., 1943); *Lycoperdodes* O. Kuntze, 1891; *Lycoperdoides* Micheli ex Kuntze, 1891; *Pisocarpium* Link, 1808; *Polypera* Pers., 1818; and *Polysaccum* F. Desp. & DC., 1807. Several of these genera have lost their credibility, but it is the last genus, *Polysaccum*, that is the most commonly seen, especially in herbaria, even in the main collections of the Royal Botanic Garden, Edinburgh.

Barometer earthstar

So, if *Pisolithus* contains a complex of species around *P. arhizus*, what does that mean for *Astraeus* (syn. *Diploderma* Link, 1816), with a supposed single worldwide component, viz. *A. hygrometricus* (Pers., 1801) Morgan, 1889, or at most two species. Is the same phenomenon seen in *Pisolithus* operating here also? Work linking Thailand, myself, and Liverpool's John Moore's University, UK, have looked carefully at the classical characters of *A. hygrometricus* in tandem with molecular and electron microscope studies. Certainly, as in *Pisolithus*, the spore morphology often varies from one collection to another, and the differences are supported by origin of collection and molecular studies of the ITS region. A culmination of these intensive studies has so far recognized one new species from Thailand, *A. odoratus* Phosri et al., 2004, and several other entities apparently introduced from other parts of the world all hiding under the epithet "hygrometricus," but each separable on their spore morphology and slight differences in peridial structure and in their geographical range (Phosri et al. 2004). Both *A. odoratus* and the Asiatic "hygrometricus" are widely sold as delicacies in Thai markets.

Astraeus hygrometricus, for which the synonym of *A. stellatus* (Scop., 1760) E. Fisch., 1900 is used, is a rare fungus in the British Isles, although a recent colony has been found in Devon, South West England (Brand and Finlay 1996). M.C. Cooke, however, when making up his British Fungal Exsiccata, and apparently under the impression, as most mycologists of the time, that the fungus was the same wherever it was collected around the world, appears to have added specimens from other parts of the globe to make up his numbers. By molecular techniques, it is now apparent that some of these specimens did not originate from Britain but almost certainly from somewhere in Southeast Asia. This realization shows how molecular studies can help to unravel not only species concepts but also the identity and probable origin of populations in an investigative approach.

The identity of the true "hygrometricus" remains a mystery, as unfortunately after several attempts it has been impossible to obtain DNA of suitable grade from Persoon's specimens. However, an instructive cladogram has resulted from these studies that has isolated a European morphotype, and two North American groupings, one of which

includes recent collections determined as *A. pteridis* Shearer. The last species can now be confirmed as a distinct North American taxon (Phosri et al. 2006). It would be interesting to examine in detail the Argentinian collections described by Nouhra and de Toledo (1998) and see if they are endemic and, if not, from whence they came.

Boleti

Gyroporus has always stood out as problematic within the overall classification of the boletes, especially in the unusual development of the stipe tissue, which instead of being composed of hyphae running the length of the stipe, the hyphae are arranged transversely, enveloping a stuffed, floccose area that gradually disintegrates, ultimately producing a central cavity. The spore print is also a deep lime-yellow, a color not found elsewhere in the boletes; the basidiospores are cyanophilic.

In the tropics, *G. atroviolaceus* (Hoehn., 1914) E.J. Gilb., 1931 is distinctive, and North America plays host to a handful of unique taxa. However, *Gyroporus* includes two widespread North temperate species that are found in all suitable areas of Asia, Europe, Australia, and North America, viz. *G. castaneus* (Bull.: Fr., 1821) Quél., 1886 and *G. cyanescens* (Bull.: Fr., 1821) Quél., 1886, with the former closely associated with fagaceous trees. Both species show a wide morphological range in their classical field characters; e.g., *G. lacteus* Lév., 1848, is considered a white form of *G. cyanescens*, *G. fulvidus* Fr., 1818, simply a pale form of *G. castaneus*, with *G. malesicus* Corner, 1972 and *G. heterosporus* Heinem., 1951, as very close relatives, the first from Malaysia and the latter most generally from Central Africa. Even in *G. cyanescens*, differences in color changes of the flesh when exposed to the air or whether the outer surfaces green as the basidiomes dry, have led to infraspecific recognition or even tentative species, e.g., var. *violaceotinctus* Watl., 1969 from North America. This variation has been shown by molecular studies to be more than "skin-deep" and represents real speciation (Vigalys, personal communication). More work is required, especially with *G. heterosporus* throughout its range, as it possesses a disjunct world distribution. The development of the basidiome in *G. castaneus* and in *G. cyanescens* differs, gymnocarpic in the former (Watling, unpublished) and metavelangiocarpic in the latter (Reijnders 1963). However, *Gyroporus* is not the only genus of boletes that shows a range of related developmental strategies; see members of the genus *Suillus* – gymnocarpic, pilangiocarpic, and mixangiocarpic (Reijnders 1963; Watling 1985).

Gyroporus is linked by molecular studies to two other groups of boletoid fungi that superficially have little in common. One group possesses a paxilloid/merulioid hymenophore (*Boletinellus* Murr.) and the other forms enormous, fleshy basidiomes (*Phlebopus* (Heim) Singer). The first group demonstrates once again that the same configuration of the hymenophore can be found in unrelated taxa. *Boletinellus merulioides* (Schwein., 1832) Murr., 1909,

the type of the genus, is also unusual in that in the field it is involved in a three-way association, viz. root–aphids and a member of the Oleaceae (*Fraxinus*), an arborescent group not generally considered to form sheathing mycorrhizae. This association has been so far demonstrated in North American populations (Brundrett and Kendrick 1987), but the same species is known from Japan. The author also has excellent collections from Thailand and one from Malaysia associated with *Scorodocarpus* (Oleaceae). All collections would appear to be slightly different to the North American *B. merulioides*, which again may demonstrate a similar situation as to that found in *Gyroporus* where considerable cryptic speciation has taken place. Investigations are presently well underway in attempting to unravel the elements involved.

Boletinellus has often been considered simply a segregate from *Gyrodon* Opat. (as *Uloporus* Quél.). However, some time ago the author emphasized the wide differences between these two genera, and this has been substantiated by molecular studies. *Gyrodon* has been shown to be a member of the Paxillaceae, yet another sister-branch in the Boletales. The support of the autonomy of *B. merulioides* in a separate genus for a short time left a range of South American taxa in limbo (Watling and de Meijer 1997), until it was demonstrated that they too were members of the genus *Boletinellus*. It would therefore be interesting to see what relationships these species have within the total ecology of the woodlands in which they fruit. Certainly de Meijer (personal communication), who is working under limiting circumstances in Brazil, requires help from the West to analyze his considerable amount of ecological data. Based on their unique suite of characters, a family has been erected for this group of fungi, viz. Boletinellaceae in Kirk et al. (2001).

A second root–aphid association is known in at least one neotropical member of the genus *Phlebopus* (Heim, 1936) Singer, 1936, as the genus is defined by Singer (1986). In the vegetative state of *P. tropicus* (Rick apud Rehm & Rick, 1906) Heinem. & Rammeloo, 1982 a crust, termed a crypta, forms around the otherwise endomycorrhizal roots of *Citrus*. On further investigation the fungus has been shown to envelop colonies of a root aphid (*Pseudococcus comstocki* Kuwana), individuals of which are “milked” by the ant *Solenopsis* for food. This is a very complex relationship (Gonçalves and Milanez in Singer, 1986), only known from a single South American representative. Until now, this association has yet to be explored in *P. marginatus* (Drummond, 1845) Watl. & Gregory, 1986, a species widespread in Australia and distributed northward, even into Sri Lanka, although some variation even in degree of cyanescence can be seen in collections from different countries. The fact that unlike most other boletes it has been successfully fructified in culture may indicate that there are some special characters in its growth pattern absent or lost in more familiar boletes. In Thailand, this species is sold in markets widely as food and because of this is currently demanding much research scrutiny.

This species is replaced by *P. colossus* (Heim, 1936) Singer, 1936, the type of the genus in Madagascar; *P.*

silvaticus Heinem., 1951 in the Cameroon and Congo; and *P. sudanicus* (Har. & Pat., 1909) Heinem., 1954 in East Africa, all placed in Sect. *Phlebopus* in Heinemann and Rammeloo (1982). In the Sect. *Tropici* these authors arrange *P. harleyi* Heinem. & Rammeloo, 1982 from Liberia, *P. latisporus* Heinem. & Rammeloo from Uganda, and *P. tropicus* from South America (see above), and in Sect. *Brunneorubri*, *P. brunneoruber* (Beeli, 1927) Heinem. & Rammeloo, 1982 from the Congo and *P. cystidiosus* Heinem. & Rammeloo, 1982, from Ethiopia. *Phlebopus beniensis* (Sing. & Digilio, 1960) Heinem. & Rammeloo, 1982, because of its hymenial pileipellis, was placed in its own subgenus, but subsequent molecular work has shown that Heinemann and Rammeloo (1982), although correct in separating it as unique, did not realize how different it really was. This species clusters in fact with more central members of the Boletineae (Binder, personal communication). The majority of species of *Phlebopus* have also been assigned to the genus *Phaeogyroporus*, which although recognizing the link with *Gyroporus* through its name, is in fact a superfluous name. All these species are noted for their massive basidiomes, but reliance on a single character lacking correlating features can lead to confusion. In the case of *Phaeogyroporus beniensis*, massive basidiomes resembling core members of the genus *Phlebopus* are really referable to *Boletus* s. st. as indicated earlier. Size of basidiomes is very variable especially in the tropics, where extremely small basidiomes are found in *Russula* and boletoid fungi, etc., basidiomes sometimes being scarcely bigger than a small fingernail. The development of those species of *Boletinellus* and *Phlebopus*, both identified and unidentified taxa, that the author has had the opportunity to study all appear to be gymnocarpic.

Buchwaldoboletus Pilät, erected to house *Boletus lignicola* Kallenb., 1929, and to which *B. sulphureus* Fr. 1838 was later added, is unrelated to *Phlebopus*, although placed there by some authorities. Discrepancies in morphology are emphasized by the fact that these same species earlier had been linked to *Gyrodon*. As a result of nomenclatural problems, the latter species is correctly known as *B. sphaerocephalus* (Barla, 1859) Watl. & T-H Li, 2004. These last two species have also previously been placed in *Pulveroboletus* by Singer (1951 et subseq.), a placement with which the author has been unhappy for many years, especially as the type of the genus *Pulveroboletus*, *P. ravenelii* (Berk. & Curt., 1853) Murr., 1909, and several Southeast Asian species all possess a pulverulent veil remnant from a mixangiocarpic development; for a commentary, see Watling (2001a,b) and Watling and Gregory (1988).

False truffles

The finding of false truffles in the tropics is very significant because 25 years ago laboratory-bound mycologists would have considered this group of fungi to be absent, or the exception, in rainforest communities. This conclusion is patently untrue for Southeast Asia and East and West Africa,

at least, and logically with the high diversity of faunal elements in these areas that feed on fungi, there should in fact be considerable diversification of taxa.

The recently erected Australian *Horakiella* Castellano & Trappe, 1992, from its anatomy is undoubtedly related to *Scleroderma*, and although based on a single species, the genus may be represented by an additional taxon from dipterocarp rainforest at Kepong in the Central Highlands of Malaysia; superficially, in gross morphology, the basidiomes resemble discarded golf balls. Other links between the Australian and Malaysian truffle-like fungi are now well established; e.g., records of *Zelleromyces malaiensis* (Corner & Hawker, 1953) A.H. Smith, 1962 (Beaton et al. 1984). The present author suggests that these fungi are prime candidates for molecular studies.

The truffle *Chamonixia caespitosa* Rolland, 1899, through its secondary metabolites, has been linked with the sclerodermatoid fungi, especially the bolete genus *Gyroporus* (Gill and Watling 1986), but from molecular studies it holds an isolated position in the Boletineae (Binder 1999). It is a European species, but other taxa are known from the New World, and *C. mucosa* Corner & Hawker, 1953 was described from Malaysia; it turns a spectacular blue-green color on collection, much the same as *Gyroporus cyanescens*. Recent collections of this species from the Highlands of Peninsula Malaysia were found to be associated with *Dryabalanops oblongifolia* Dyer (Dipterocarpaceae). *Chamonixia pachydermis* (Zeller & C.W. Dodge, 1934) Beaton, Pegler, & Young, 1985 in these same studies has been more strongly associated with *Leccinum* Sect. *Luteoscabra*, a group considered rather isolated from the core species of the genus, viz. *L. scabrum* (Bull.: Fr., 1821) S.F. Gray, 1821 and *L. aurantiacum* (Bull.: Fr., 1821) S.F. Gray, 1821, so much so that they are now placed in a separate genus, viz. *Leccinellum* Bresinsky & Besl., 2003. These could be seen as examples of convergent evolution, so it would be interesting to look at the molecular identity and chemistry of *C. mucosa*, especially as the basidiospores in this species are not pigmented, unlike *C. caespitosa* and *C. octospora* Corner & Hawker, 1953. Chemical pathways usually possess intriguing but defensible biochemical directions so are very indicative, as shown by Gill and Watling (1986).

It is of some interest to note that other hypogeous components formerly placed in the Octavianinaceae, viz. *Sclerogaster* R. Hesse, 1891 (10 species in Europe and North America, and mentioned earlier); *Wakefieldia* Corner & Wakef. 1953 (with 2 species in Malaysia), and *Octavianina* Kuntze 1893 with 15 widespread species, viz. *Octavianina asterolperma* (Vitt., 1831) O. Kuntze, 1898, have been linked with other tribes within the boletes; Octavianaceae: *Octaviania* Vitt., 1831 is considered a nomen confusum.

Misfits

Mention was made of *Calostoma* at the beginning of this account, enforced by the unusual stipe cortex composed of

interlaced rhizoidal structures exhibited by its members (Reijnders 2000). It is a genus on which much more work is required as, despite its placement within the ectomycorrhizal sclerodermatoid fungi in evolutionary trees, it is not certain whether it actually forms sheathing mycorrhizae. Miller and Miller (1988) think not, but although several collections are known from Southeast Asia on rotten trunks, material has been found on soil under *Tristania* (Myrtaceae). Molecular clustering usually is a much more potent indicator of ecological requirements than morphological similarities, and so the author would predict that *Calostoma* will be found to be ectomycorrhizal in character. The two taxa so far studied for their molecular profile are both from the New World, which gives bias to our overall information. However, there is an incredible range of spore ornamentation expressed in the genus, and generally such disparate spore morphologies are rarely found in a single genus. This observation alone may indicate some discrepancies in our present circumscription of *Calostoma* and that convergence between neo- and palaeotropical taxa is being experienced. This understanding may lead to recognizing fundamentally different taxa with Southern and Northern Hemisphere patterns similar to that exhibited between *Paxillus* and *Austropaxillus* (Bresinsky et al. 1999).

More in-depth studies such as that of Castro-Mendoza et al. (1983) and Miller and Cotter (1988) are required, especially as a wide range of morphologies, even almost hypogeous, are demonstrated by a series of undescribed taxa from Borneo, some fruiting in forests above 1615 m. If separation is required at generic level, then there are several names available, especially *Mitremyces* Nees, 1816. Less known suggested synonyms are *Husseia* Berk., 1847 and *Gyropodium* E. Hitchc., 1825.

Recently, a peculiar stipitate fungus has been found in Sabah and named *Chlorogaster dipterocarpi* Laessle & Jalink, 2004; it is characterized by a dark green exoperidium consisting of dehiscent, conical warts and a pale green circular peristome and dark brown spore mass held on the top of a stipe. The authors referred it with some hesitation to Sclerodermataceae from morphology alone (Laessle and Jalink 2004), but as in *Calostoma* it shows that the peristome has evolved several times and in different fungal groups, e.g., *Tulostoma* and some species of *Geastrum*. *Tremellogaster* E. Fisch., 1924 is an equally poorly understood member of this group described from Surinam and Guyana (see Reijnders 2000).

The genus *Diplocystis*, based on the single species *D. wrightii* Berk. & Curt., 1869, was originally described from the Caribbean but long remained a mystery as the basidiomes developed on a basal stroma. It has been recircumscribed in an extensive study by Kriesel (1974) based on several recent collections from Cuba and one from Mexico, and the genus can be now firmly linked to the sclerodermatoid fungi. The author has not had the chance to study any material, but this is really unnecessary with the highly explanatory and informative account given by Kriesel (1974); it appears to be a most extraordinary fungus, resembling in some ways members of the Broomeiaceae

(Lycoperdales), a family in which it was placed by Miller and Miller (1988), a further case of convergent evolution within molecularly unrelated groups.

Cannon fungi

Finally, mention must be made of the ubiquitous genus *Sphaerobolus* Tode, 1790, which has been linked by early classical authors, based on so-called developmental characters, to the sclerodermatoid fungi, although it is much better placed within the *Geastrum-Ramaria-Gomphus/Phallus* consortium (Hibbett et al. 1997). The genus has at least two species distributed in the world, the most common being *Sphaerobolus stellatus* Tode: Pers., 1801, growing widely on old woody debris, vegetable material, and dung. In this genus the members exhibit an unusual method of spore dispersal; the inner peridium everts to project a single globose peridiole as far as 4 m horizontally from the basidiome, leaving a stellate peridium behind on the substrate. This property was recorded from a very early time and has been the subject of many texts (Buller 1933). However, this fungus, for which we had a single name, albeit several varietal epithets, has been shown in recent molecular work to be composed of several closely related taxa, in parallel to many of the results described here.

Taxonomic summary

Although for the sclerodermatoid fungi we have a fairly substantial amount of information covering what is comparatively small group, there is much to do, especially among the gasteroid members. If these fungi are to be placed in the Boletales and in the Sclerodermataceae, as proposed by the eighth edition of *Ainsworth & Bisby's Dictionary of Fungi*, the differences in molecular details must in some way be expressed in the classification, a feature Binder (1999) recognized, based on his molecular studies, when he proposed the suborder Sclerodermatineae (Binder and Bresinsky 2002; see Hibbett and Binder 2002). The author wishes that the easily observable macro-morphological structures and inferred life strategies are reflected in the classification. The following intraordinal divisions therefore should be recognized to emphasize such features.

Sclerodermatineae Binder & Bresinsky, 2002

Astreaceae Zeller ex Jülich, 1982: *Astraeus*

Boletinellaceae Kirk et al. (Boletinellaceae Binder & Bresinsky, 2002 superfluous): *Boletinellus* (= *Plicaturella* Murr., 1910 fide Kuiper) and *Phlebopus*

Diplocystaceae Kriese, 1974: *Diplocystis*

Gyroporaceae (Singer) Binder & Bresinsky, 2002: *Gyroporus*

Sclerodermataceae Corda, 1842: *Scleroderma*

Pisolithaceae Ulbirsch, 1928: *Pisolithus*

Conclusion

The Sclerodermatineae is a small group of fungi, small enough to successfully tackle and understand the changing picture fairly comprehensively, so that indicators on how to approach much more complex families are possible. There are several areas in which research is urgently required and would not demand high expenditure, e.g., the composition of *Calostoma* and *Chamonixia*; indeed, an analysis of the sequestrate members in general could provide some interesting results. *Phlebopus marginatus* and *Boletinellus* from Southeast Asia are presently being analyzed with parallel thoughts in mind. In addition, careful analysis of *Gyroporus* spp., especially *G. castaneus* and *G. cyanescens*, which presently are thought to have a wide distribution, is suggested.

Studies should not be restricted to molecular analyses, but there should be a marriage between different approaches, such as secondary metabolites, electron microscope studies of the basidiospores, anatomical examination of the peridium and stipe, and development. However, judging from the work with *Astraeus* and *Pisolithus*, molecular examination of the circumtropical *Scleroderma sinnamariense* would be informative and undoubtedly reveal several distinct entities. The future looks very exciting.

As the reader will appreciate, the work described here has covered many years, small pieces to the jigsaw puzzle being interlocked one at a time over a long period. The work so far achieved in this suborder has not been possible without the collaboration of a series of mycologists. It has been a great pleasure to collaborate with these workers, and to continue to do so, and on many occasions to have their companionship while on field excursions sometimes under rather arduous conditions in the rainforest:

Binder, M., Clark University, Wisconsin, USA (formerly University of Regensburg, Germany) (molecular studies)

Gill, M., formerly Melbourne University, Australia (secondary metabolite studies) (deceased)

Hui, T.-H., Guangdong Microbiology Institute, Guandongzou, PR China (boletoid elements)

Kanchanasaprayudh, J., Chulalongkorn University, Bangkok, Thailand (*Pisolithus*)

Lee, S.-S., FRIM, Kepong, Malaysia (fieldwork in Malaysia; *Scleroderma* and *Pisolithus*)

Martin, M., Real Jardín Botánica de Madrid, Spain (molecular studies)

Phosri, C., Pibulsongkram Rajabhat University, Thailand (*Astraeus*)

Sihanonth, P., Chulalongkorn University, Bangkok, Thailand (support in *Astraeus* and *Pisolithus* studies)

Sims, K., Helsinki University, Finland (formerly University of Canterbury, Kent UK) (fieldwork in Philippines: *Scleroderma* and *Pisolithus*).

Acknowledgments I am particularly grateful to Manfred Binder for sharing his interests while on a visit to Regensburg, especially molecular data, information which later formed the basis of his thesis. Also, thanks are expressed to my longtime assistant, Evelyn Turnbull, for assistance in both the field and the laboratory, and finally to the late E.J.H. Corner, who encouraged me in my mycological studies and

placed his collections and notes, now housed in the Royal Botanic Gardens, Edinburgh, at my disposal.

References

- Beaton G, Pegler DN, Young T (1984) Gasteroid Basidiomycetes of Victoria State, Australia. 2. Russulales. *Kew Bull* 39:669–698
- Binder M (1999) Zur molekularen Systematik der Boletales: Boletineae und Sclerodermatineae subordo nov. PhD thesis, University of Regensburg, Regensburg
- Binder M, Bresinsky A (2002) Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. *Mycologia* 94:85–98
- Brand AW, Finlay J (1996) *Astraeus hygrometricus*, an uncommon earthstar. *Mycologist* 10:109
- Bresinsky A, Jarosch M, Fischer M, Schönberger I, Wittmann-Bresinsky B (1999) Phylogenetic relationships with *Paxillus s.l.* (Basidiomycetes Boletales): separation of a Southern Hemisphere genus. *Plant Biol* 1:327–333
- Brundrett MC, Kendrick B (1987) The relationship between the ash bolete (*Boletinus merulioides*) and an aphid parasitic on ash tree roots. *Symbiosis* 3:315–320
- Buller AHR (1933) *Researches in Fungi*. Longmans, Green, London
- Cairney JWG, Chambers SM, Anderson IC (1999) *Pisolithus* systematics – molecular methods provide fresh insights. *Mycologist* 13:31–35
- Castro-Mendoza E, Miller OK, Stetler DA (1983) Basidiospore wall ultrastructure and tissue system morphology in the genus *Calostoma* in North America. *Mycologia* 75:36–45
- Gill M, Watling R (1986) The relationships of *Pisolithus* (Sclerodermataceae) to other fleshy fungi with particular reference to the occurrence and taxonomic significance of hydroxylated pulvinic acids. *Plant Syst Evol* 154:225–236
- Guzmán G (1967) Taxonomía del género *Scleroderma* Pers. emend Fr. *Ciencia (Méx)* 2:195–208
- Guzmán G (1969) *Veligaster*, a new genus of the family Sclerodermataceae. *Mycologia* 61:1117–1123
- Guzmán G (1970) Monografía del genero *Scleroderma* Pers. emend Fr. *Darwiniana* 16:233–407
- Heinemann P, Rammeloo J (1982) Observations sur le genre *Phlebopus* (Boletineae). *Mycotaxon* 15:384–404
- Hibbett DS, Binder M (2002) Evolution of complex fruiting body morphologies in homobasidiomycetes. *Proc R Soc Lond B* 269:1963–1969
- Hibbett D, Pine EM, Langer E, Langer G, Donoghue M (1997) Evolution of gilled mushrooms and puffballs inferred from DNA sequences. *Proc Natl Acad Sci USA* 94:12002–12006
- Kanchanasaprayudh J, Zhou Z, Yomyart S, Sihanonth P, Hogestu T, Watling R (2003) A new species, *Pisolithus abditus*, an ectomycorrhizal fungus associated with dipterocarps in Thailand. *Mycotaxon* 88:463–467
- Kirk PM, Cannon PF, David JC, Stalpers JS (2001) *Ainsworth & Bisby's dictionary of Fungi*, 9th edn. CABI, Wallingford, UK
- Kriesel H (1974) Die Gattung *Diplocystis* und ihre Stellung in System der Basidiomycetes. *Feddes Repert* 85:325–335
- Laessle T, Jalink LM (2004) *Chlorogaster dipterocarpi*. A new peristomate gasteroid taxon of the Sclerodermataceae. *Persoonia* 18: 421–428
- Martin F, Diez J, Dell B, Delarulle C (2002) Phylogeography of the ectomycorrhizal *Pisolithus* species as inferred from ribosomal DNA ITS sequences. *New Phytol* 153:345–357
- Miller OK, Cotter VT (1988) Observations on tissue morphology and spore ultrastructure of *Calostoma junghuhnii* (Gasteromycetes). *Can J Bot* 66:2470–2473
- Miller OK, Miller HH (1988) Gasteromycetes. Morphological and development features with keys to the orders, families and genera. Mad River Press, Eureka
- Nouhra ER, de Toledo LD (1998) The first record of *Astraeus hygrometricus* from Argentina. *Mycologist* 12:112–113
- Petri L (1900) Descrizione di alcuni Gasteromyceti de Borneo. *Malphigia* 14:111–139
- Phosri C, Watling R, Martin MP, Whalley AJS (2004) The genus *Astraeus* in Thailand. *Mycotaxon* 89:453–463
- Phosri C, Watling R, Martin MP, Whalley AJS, Sinnanonth P (2006) Molecular studies of the genus *Astraeus*. *Mycotaxon* (submitted)
- Reijnders AFM (1963) Les problèmes du développement des carpophores des Agaricales et de quelques groupes voisins. *Junk, Den Haag*
- Reijnders AFM (2000) A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other basidiomycetes. *Mycol Res* 104:900–910
- Sims K, Watling R, Jefferies P (1995) A revised key to the genus *Scleroderma*. *Mycotaxon* 56:403–420
- Singer R (1951) Agaricales in modern taxonomy. *Lilloa* (1949) 22:1–832
- Singer R (1986) Agaricales in modern taxonomy, 4th (revised) edn. Koeltz, Koenigstein
- Watling R (1985) Hymenial surfaces in developing agaric primordia. In: Dick MW, Pegler DN, Sutton BC (eds) *Contributions to mycology*. Academic Press, London, pp 273–293
- Watling R (2001a) Australian boletes: their diversity and possible origins. *Aust Syst Bot* 14:407–416
- Watling R (2001b) The relationships and possible distributional patterns of boletes in south-east Asia. *Mycol Res* 105:1440–1448
- Watling R, de Meijer A (1997) Macromycetes of the State of Paraná. Poroid and lamellate boletes. *Edinb J Bot* 54:231–252
- Watling R, Gregory NM (1988) Observations on the boletes of the Cooloola Sandmass, Queensland and notes on their distribution in Australia. Part 2B. Smooth spored taxa of the family Gyrodontaceae and the genus *Pulveroboletus*. *Proc R Soc Queensl* 99:65–76
- Watling R, Sims K (2004) Taxonomic and floristic notes on larger Malaysian fungi. IV. *Mem N Y Bot Gard* 89:93–96