A MANUAL AND SOURCE BOOK ON THE BOLETES AND THEIR ALLIES

ROY WATLING

Synopsis Fungorum 24

FUNGIFLORA

A MANUAL AND SOURCE BOOK ON THE BOLETES AND THEIR ALLIES

ROY WATLING

Synopsis Fungorum 24

FUNGIFLORA

This book can be ordered from :

FUNGIFLORA
P.O. Box 95, Blindern
N-0314 OSLO
NORWAY
FAX. 47-228 567 17
E.MAIL: leif.ryvarden@bio.uio.no

For information of other volumes of Synopsis Fungorum, see our homepage:
http://biologi.uio.no/Ascomycete/FungiFlora

Editors address:
L. Ryvarden, Dept. of Biology, Univ. of Oslo
P.O. Box 1066, Blindern, N-0316 Oslo, Norway
leif.ryvarden@bio.uio.no
Papers are accepted by invitation only.

Printed in PowerPrint A/S Steinkjer, Norway
Printing date 20 March 2008
ISBN 978-82-90724-36-3
ISSN 0802-8966

CONTENTS

PREFACE

I have over many years had the great privilege to collect in many countries of the world - the United States and Canada, India, Japan, Thailand, Malaysia [including Sabah], Australia, Zambia, Cameroon and Kenya, as well as a wide range of European countries. Sadly, the last do not extend to the Eastern European countries. I have, however, been able to make up some of the deficiencies in my understanding of the boletes and their allies by the examination of material from Eastern Europe, South America (Brazil & Argentina) and Central America. This publication is a condensate of my observations and examination of boletes and their allies from all these countries over more than forty years. It would not have been possible to undertake such a task without the cooperation and help of many people in the areas I have had good fortune to visit. It is in fact a tribute to those people that this publication has been prepared, and a 'thank-you' to them for their help and friendship. It is hoped that it will act as a base to the study of boletes and associated fungi from which to build their classical morphology, developmental, secondary metabolite, and molecular studies.

ABSTRACT

79 genera accepted in Boletales and their type species are described with information of their ecology, distribution and nomenclature and illustrated when appropriate. Generic synonyms (both taxonomic and nomenclatural) with their type species are indicated under the appropriate genera. A key to the accepted genera is provided together with a preliminary classification of the order based on recent investigations. There are two sets of references, one to useful illustrated mycofloras and one with general references relevant to Boletales. A glossary and an index are provided.

INTRODUCTION

The outline of the book is quite simple, in that all the genera currently placed in the Boletales E.-J. Gilbert (Binder *et al*., 2007) are arranged alphabetically, with the type species indicated, and linked to their morphological characteristics, ecology and distribution; illustrations to important characters are given. This grouping of fungi covers those genera which have been defined by molecular mycologists as the 'Bolete clade' (Hibbett & Thorn, 2001; Binder & Hibbett, 2006). Each generic account is completed with a short account of the history of the genus where appropriate, the various concepts adopted by different authorities and where difficulties have been experienced, or where changes have already been made. Accepted synonyms are listed in an appendix to each entry, again with the type species indicated, and where necessary some explanatory notes, useful references and an indication where keys to species may be found. All genera are keyed out and, where appropriate, line-drawings illustrate the main characteristics. The author commenced his early studies on boletes but because they could not be cultured, turned his attention to the Bolbitiaceae whilst keeping a watching brief on the boletes. It was only when he started work in the tropics that boletes took a more central position again in his activities. During the intervening period much knowledge he had slowly accumulated notes on the changing face of the bolete families, genera and species.

It might be a surprise to some to find that some resupinates, toothed fungi, gilled fungi (agarics) and even polyporoid taxa are included in this compilation. This is a result of careful examination of the field characters and micromorphological and developmental studies reaching back to the earliest parts of the 20th century. These attributes have been subsequently supported by evidence from the production of secondary metabolites and distribution of a series of specific chemical pathways exhibited by these fungi; in the last two decades molecular studies have reinforced the main relationships (Binder & Bresinsky, 2002; Larsson *et al.*, 2004). The choice of name for the clade emphasises the main core of the group, the boletes with soft putrescent hymenophore. However, there is a suggestion from ancestral state reconstruction that the ancestors of the boletes were either polyporoid or resupinate saprotrophic fungi producing a brown-rot. Ploidy levels give some indication of primitiveness and, linked with chemistry, are a very

potent tool for getting to grips with evolutionary relationships. The results from various threads of information have been incorporated in an attempt to summarize the genera.

Finally, all the genera accepted by the author are keyed out and no excuse is made for restricting certain genera to fewer species than previously accepted or, at the other extreme, transferring other species from one genus to another or merging one genus with another. In some cases, therefore, the approach will be rather different from that of other accepted texts. The procedure adopted herein will be tested by time, and the author has no doubt that changes will need to be made, especially when more taxa, especially tropical species, are analysed by molecular techniques. As the majority of genera have been defined around temperate species, the examination of tropical taxa may require amendment in the future to many of the traditional genera familiar to western mycologists

Genera considered synonymous appear at the end of the appropriate genus. Although this does not follow tradition so many of the synonymous genera are infrequently used, rarely appear in recent accounts and so old often lost in the literatures, the author did not want to detract the reader from the important identificatory information. As the genera are in alphabetical order no conventional index is offered, but an index to synonyms and specific references are provided to allow the reader to go further in his/her studies. Specific references applicable to the text are for convenience and user friendliness are included directly in the text. A preliminary classification ends the formal part of the book.

This is full circle for the author as his studies commenced on boletes in the 1960s and now, after 40 years, he considers that enough new information has been accumulated to attempt a synthesis, but such an activity is on-going. Even over the last 12 months of the preparation of the text new genera have been described and some taxa, previously considered boletaceous, have now found to reside elsewhere in classification. The book attempts to be as up-to-date as possible.

TAXONOMY

Abbreviations:

A positive reaction with Melzer's reagent, including the Imler reaction, where the reagent is placed on the flesh at the stipe-base = ME.

B/w indicates black & white photographs.

* Those genera for which the author has not seen fresh or herbarium material of the type species or an authentic member of the genus and, if a large genus, the type of its major sections.

"AGERER" refers to photographs and diagrams of mycorrhizas in *Atlas of Ectomycorrhizae*. Ploidy levels are taken from Wittmann-Meixner, 1989 & Bresinsky & Wittmannn-Bresinsky, 1995. For entries on chemistry see Gill & Steglich (1987).

@ Genera considered doubtfully related to the boletes.

AFROBOLETUS Pegler & Young, Trans. Brit. Mycol. Soc. 76: 130, 1981. Plate 1 A.

Type species (designated): *Strobilomyces pterosporus* Sing. (=*Afroboletus pterosporus* (Sing.) Pegler & Young)

Basidiome epigeal, pileate with tubulate hymenophore, centrally stipitate, metavelangiocarpic; putrescent. *Spore-print* dark fuscous brown.

Pileus hemispherical to convex, becoming applanate, dry, pustulate-squamulose, pale, soon fuliginous, often nigrescent to the touch, margin appendiculate from velar remnants. *Stipe* elongate, slender, cylindric, solid, smooth or slightly furfuraceous, concolorous with pileus, blackening with age or handling. *Tubes* adnate with decurrent tooth, ventricose, white soon greyish or pale pinkish at maturity, < 25mm long; *pores* concolorous, 1-2 per mm. diam. *Flesh* whitish, nigrescent on exposure to air.

Basidia pyriform, 4-spored. *Basidiospores* subglobose to broadly ellipsoid, ornamented with, prominent, longitudinal winged costae over 1µm or more deep, of which half extend to spore-apex, all abruptly truncated at thickened rim-like basal end, between costae secondary ornamentation of narrow, anastomosing veins, edges of costae retaining some remnants of mucilaginous myxosporium, inamyloid, acyanophilic. *Cheilocystidia* clavate to lanceolate, thin-walled, hyaline but soon with brown vacuolar pigment; *pleurocystidia* similar. *Tube trama* bilateral, divergent with gelatinised lateral strata. *Pileipellis* a trichoderm with short, cylindric or vesicular, brown cells forming palisade. *Clamp-connections* not seen.

Chemical reactions: None characteristic; blackening flesh of unknown chemistry, although Singer (1986), in support of his views of an infrageneric position cites Arpin & Kühner (1977), who discuss the chemical basis of reddening, and then blackening, flesh in *Strobilomyces*.
Ploidy level: 10x in *C. rutilus*.
Ecology: Terrestrial, probably facultatively mycorrhizal, but studies vague.
Distribution: Considered to be only of Equatorial African distribution, although there is evidence for at least one neotropical taxon (Singer 1986).

Afroboletus was first recognised as a distinct entity by Singer, as *Strobilomyces* Sect. *Pterospori*; *Farlowia* **2**: 114,1945), a position it retained in his later works. He considered that this section probably contained five species. Pegler & Young (1981) placed the genus in the Strobilomycetaceae, now considered a polyphyletic grouping. The basidiospore ornamentation is unusual amongst the boletes with the widely spaced longitudinal costae, intercostal ridges and thickened basal rim. Molecular studies have not been carried out on any species of this genus so far, so a final placement is wanting.

The basidiospores of the African *Strobolimyces costatispora* (Belli) Gilbert and *S. lepidellus* Gilbert ex Heineman indicate that these two species also belong here.

Although a small genus no single account dealing with the constituent species is available; African species are described and illustrated in colour in Heinemann - *Flore des Champignons du Congo* Fasc. **15**, 1966 and earlier works by this same author

***AMOGASTER** Castellano in *Mycotaxon* **55**: 186, 1995. Plate 1 B.

Type species (designated, only original species): *Amogaster viridigleba* Castellano
Basidiome gasterocarpic, subglobose to irregular, hypogeal, white or pale green, angiocarpic.

Peridium thin, evanescent, white, rubescent, bruising orange to pale red, finely tomentose. *Gleba* loculate, with round or irregular empty chambers pale green at first, drying pale to medium yellow with yellow-brown spore-mass. *Columella* small, cartilaginous, dendroid when fresh, inconspicuous on drying. *Odour* & *taste* not distinct.

Basidia clavate, hyaline, 4-spored. *Basidiospores* ellipsoid, subglobose or subfusiform with blunt apex, nearly all asymmetric, pale yellow-brown, smooth, some pseudoamyloid, sterigmatic appendage present. *Peridipellis* a single-layer of thin-walled, hyaline to pale brown, loosely interwoven to subpericlinal hyphae. *Trama* of thin-walled, hyaline, interwoven hyphae with some swollen elements. *Clamp-connections* absent.

Chemistry: Unknown.

Ecology: Terrestrial, probably ectomycorrhizal; in soil under *Populus*.

Distribution: Known only from North America (California).

The only member of the genus so far known has been compared with *Rhizopogon* q.v. and, therefore, *Suillus* q.v., but the spore colour is said to resemble that of Gyroporaceae – *Gyroporus* q.v.

Only b/w photographs of the spores accompany the original article.

ALPOVA C.W.Dodge, Ann. Miss. Bot. Gdn. **18**: 461, 1931. Plate 1 C.

Type species (designated, only original species,): *Alpova cinnamomeus* C.W.Dodge (= *A. diplophloeus* (Zeller & C.W.Dodge) Trappe)

Basidiome gasterocarpic, hypogeal to subhypogeal, globose to irregular, angiocarpic, mycelial attachment inconspicuous.

Peridium well-developed although variable in thickness resulting from separate chambers or groups of chambers intruding in some places into the subcutis but with gaps in outer chambers in other areas. *Gleba* solid, pale yellowish to yellowish pinky brown or even black, filled at first with both evanescent hyphae and basidia then with dark spore-mass embedded in gel, separated by pallid veins but columella absent. *Odour* mild or fruity; *taste* mild.

Basidia long, slender, attached to thin funicle, hyaline, 4-spored, collapsing into gelatinised mass *Basidiospores* hyaline to yellow or light greenish brown, oblong to ellipsoid, obovoid, allantoid, reniform or irregular, in some species truncate, lacking pore, relatively thin-walled, smooth, inamyloid, acyanophilic. *Hymenium* replaced by sterile palisade of long, narrow hyphae with irregularly arranged but evenly distributed basidia. *Peridipellis* a single layer of large cells almost forming a pseudoparenchyma. *Clamp-connections* present or absent.

Chemistry: Coloured contents of epicuticular layer leaking into solution in alkaline mounts. Strong colour reactions with KOH and iron salts, but chemistry unknown.

Ecology: Terrestrial, probably ectomycorrhizal with Pinaceae and with frondose trees, and especially associated with *Alnus*.

Distribution: Mainly North America, but also known from Southern and Central Europe, and at least one species in South East Asia.

A genus referred to the Rhizopogonaceae with some doubt and covering about a dozen species, some taxa only known from limited material. *Alpova* has been indicated as being intermediate between *Melanogaster q.v.* and *Rhizopogon q.v.,* some species sharing or exhibiting the characters of one or other genus. The close relationship with *Rhizopogon* is demonstrated by the fact that on morphological grounds Zeller & Smith (Mem. Bot. Gdn. New York **14**, 1962) erected subgenus *Rhizopogonella* A.H. Sm., which is now incorporated into *Alpova*. Subgenus *Antridium* Trappe may deserve generic rank when further critical studies are completed, and this might be confirmed when molecular studies are expanded, as the type species is indeed related to *Melanogaster* whilst other species so far studied nestle within *Rhizopogon* in the suilloid/gomphidioid branch.

A key is supplied by Trappe (Beih. Nova Hedw. **51**: 279, 1975) to the species then known. See Smith & Zeller (Mem. Bot. Gdn. New York **14**, 1962) & Smith

(Mich. Bot. **3,** 13-19, 1964). Trappe (1975) includes b/w photographs of sections and spores of type and related species; some species placed in *Rhizopogon* sect. *Rhizopogonella* are figured in Zeller & Smith in colour and the former author (Oregon State Monographs, 1939) has examined the development of Alpova. Presently placed in the Melanogastraceae.

ASTRAEUS Morgan, J. Cincinnati Soc. Nat. Hist. 12: 19, 1889 . Plate 1 D.

Type species (only original species): *Geaster hygrometricus* Pers. (viz. *Geastrum*) (= *Astraeus hygrometricus* (Pers.) Morg.

Basidiome sessile gasterocarp with basal tuft of mycelium, an earthstar with 2-layered peridium only at maturity outer layer breaking longitudinally to form the rays of a star which open and close, depending on the availability of water (hygroscopic), finally exposing subglobose or slightly compressed inner peridium, outer peridium hard, woody and persistent with age, subhypogeal finally epigeal. Known as the Barometer fungus in English.

Peridium thick, multi-structured, stratified, dry, tough, even harder when old; *exoperidium* pale buff or horn-colour to clay-buff or greyish ochre, smooth or slightly verrucose, often incorporating soil particles; *endoperidium* enclosed until maturity, subglobose generally pale, thin, paper-like, velvety or minutely roughened, becoming smooth on weathering, lacking peristome, simply opening by irregular apical tear. *Gleba* white at first divided into chambers by thin tramal plates, finally disintegrating into a powdery, dark brown spore-mass at maturity. *Odour* & *taste* very pleasant, the former often strong and almost nutty.

Basidia broadly clavate to almost capitate with 2-8 sterigmata. *Basidiospores* globose, echinulate to verruculose, thick-walled with 2-4 layers of alternating electron dense and electron transparent layers, inamyloid, acyanophilic. *Columella* absent. *Hymenium* replaced by hyaline, thick-walled, branched, long, interwoven paracapillitial hyphae originating from inner peridial wall, some intermixed with spore-mass at maturity. *Clamp-connections* present.

Chemistry: Not known; dark droplets exuded from cultures, which are probably pulvinic acid derivatives.

Ecology: Terrestrial, ectomycorrhizal with a range of arborescent plants; generally exposed on rather sandy soils.

Distribution: A widespread genus especially in the tropics and subtropics, although also known but less widespread in temperate-zone.

The mature basidiome in this genus, including the hygroscopic nature, resemble some members of *Geastrum*, where the type species was originally placed; it differs fundamentally, however, in its structure and development. This has led to it being placed in the Astreaceae. A small genus of half a dozen species although all collections at one time were thought to represent one, or at most two, cosmopolitan species. Molecular studies have demonstrated that there are several species looking very similar but with different geographical ranges and mycorrhizal associations. Fischer (1900) placed this genus in the Calostomatacaeae although this approach was not then followed; molecular studies indicate Fischer was more correct than many contemporary mycologists. Dring (1973) suggested that the genus is closely related to *Myriostoma q.v.*, a treatment not taken seriously until very recently. *Astraeus* spp. are considered delicacies especially in Thailand and China. Cherdchai Phosri and colleagues have separated out the Southeast Asian taxa (Mycotaxon **89**: 453-456, 2004 & Mycol. Res. **111**: 275-286, 2007); his researches are continuing.

Synonyms:
Diploderma Link, Mag. Ges. Naturwiss. Freunde Berlin **7**: 44, 1816; based on *Diploderma tuberosum* Link.
Endogonopsis Heim, Rev. Mycol. **31**, 150, 1966 – description of species and genus) & Rev. Mycol. **33**, 379, 1968 (description of new family - Endogonopsidaceae) both based on a single Indian species (*E. sacramentarum* Heim) from, Dumku Bihar, India; only one other record from near Indian border with Bangladesh, has been made. With the stratified peridial wall this is very likely to be based on immature or aberrant basidiomes of *Astraeus*; in herbaria there are many collections which are of immature, unexpanded basidiomes and these look very different from the final form because of the strongly adhering layered peridium. See Lloyd The Geastraceae, Ohio, 1902 for comments on collecting underdeveloped basidiomes and the snares that await the unwary mycologist. The author has been down that trail himself!!!!

Good line-drawings and colour illustration of the type species is presented in Pegler *et al*.,1995. B/w electron scanning micrographs appear in Phosri *et al* above.

AUREOBOLETUS Pouzar, Ceská Mykol. **11**: 48, 1957. Plate 1 E.

Type species (originally designated): *Boletus sanguineus var. gentilis* Quél. (= *Aureoboletus gentilis* (Quélet) Pouzar)

Basidiome epigeal, pileate with tubulate hymenophore, centrally stipitate, fleshy, putrescent, for type species velangiocarpic from gelatinised layer, possibly mix-angiocarpic? *Spore-print* ochraceous buff.

Pileus convex then expanding, brightly coloured, viscid, smooth but minutely wrinkled with age. *Stipe* slender, cylindrical, attenuated or swollen slightly in the middle, often more or less rooting, smooth to striate-fibrillose, viscid often with watery droplets on the gelatinised surface. *Veil* reduced to a gelatinous coating. *Tubes* & *pores* concolorous, rich chrome-yellow from start, unchanging on bruising, angular, relatively large. *Context* whitish or slightly pinkish in the pileus, yellowish above tubes and possibly in stipe-base, unchanging on exposure to air. *Odour* & *taste* pleasant, not astringent.

Basidia clavate, hyaline, 4-spored. *Basidiospores* subfusiform, inequilateral in side-view, smooth, inamyloid, acyanophilic. *Cheilocystidia* voluminous, irregularly clavate, filled with bright yellow sap, thin-walled; *pleurocystidia* similar, but many paler in aqueous ammoniacal solutions. *Pileipellis* a radially arranged cutis with gelatinised constituents intermixed with highly gelatinised viscous velar remnants? *Tube trama* bilateral, with gelatinised hyphae divergent from slightly darker central, gelatinised zone but soon loosing clear pattern. *Clamp-connections* not seen.

Chemistry: Negative ME. Yellow fluid leaches from hymenial mounts in ammoniacal solutions. Xerocomic and variegatic acids both known from constituent taxa.

Cytology: Ploidy level of 2x in type species (as *Pulveroboletus cramesinus*: Bresinsky & Wittmann-Bresinsky, 1994).

Ecology: Terrestrial, associated with members of Fagales or conifers; possibly facultatively ectomycorrhizal.

Distribution: North temperate but probably several in SE Asian tropics.

This presently rather small genus of about 6 species is of subtropical to warm

temperate distribution with probably many other tropical members still to be recognised. All members have been placed by Singer (Amer. Mid. Nat. **37**, 1947 *et subseq.*) in *Pulveroboletus q.v.*, which based on anatomy is patently unsupported; see Watling (Aust. Syst. Bot.: **14**: 407-416, 2001 & Mycol. Res. **105**: 1440-1448, 2001). Singer (loc. cit., 1947) erected the Sect. *Auripori* for this group within *Pulveroboletus*, a section that in 1942 he had attributed to *Xerocomus, q.v.* The distinguishing features are the gelatinised pileus and voluminous cheilocystidia containing yellow sap in aqeous ammoniacal solutions, coupled with the ochraceous buff spore-mass.

As a result of confusion the genus has not been monographed as an entity. Descriptions of individual taxa rely on those found in regional floras *e.g.*, Smith & Theirs (Boletes of Michigan, 1971: *B. auriporus* Peck), Watling & Hills (Enlarged edition British Fungus F1ora **1,** 2005: *A. gentilis*). Coloured illustrations of the type are found in European manuals, e.g. Alessio (Boletus, 1985) and Bessette, Roody & Bessette (North American Boletes, 2000) depict in colour related species. Corner (Boletus in Malaysia, 1972) illustrates *A. thibetianus* Pat.

AUSTROBOLETUS (Corner) Wolfe, Bibl. Mycol. **69**: 64, 1979. Plate 1 F.

Type species (originally designated): *Porphyrellus dictyotus* Boedijn (=*Austroboletus dictyotus* (Boedijn) Wolfe).

Basidiome epigeal, pileate with tubulate hymenophore, centrally stipitate, putrescent, stipitocarpous, gymnocarpic to pilangiocarpic where known. *Spore-print* flesh-pink to vinaceous brown to purple date or rust-cinnamon, loosing intensity of red or purple when dry, rarely with a slight olivaceous cast.

Pileus hemispherical to convex, dry especially when immature but often becoming viscid at maturity, with inrolled margin, becoming appendiculate when veil evident, generally in pale browns to rust-browns or darker in similar shades. *Stipe* generally elongate, attenuated upwards, reticulate to lacunose-lacerate, sometimes remarkably so, less frequently simply furfuraceous or smooth, generally dry or ornamentation slightly waxy to the touch, less frequently gelatinous and then usually from velar debris; *veil* present in some taxa as narrow annulus or gelatinised zone. *Tubes* at first white or cream-colour, then flushed pinkish and finally dark vinaceous pink and unchanging, adnate, adnexed to subdecurrent but depressed around the stipe-apex; tubes < 20mm long; *pores* small, concolorous. *Context* white or pallid sometimes yellow especially in stipe-base, generally

unchanging on contact with air, neither cyanescent nor vinescent, rarely blackening. *Odour* not distinctive; *taste* mild to slightly astringent.

Basidia clavate to broadly clavate even elongate-sphaeropedunculate, 4-spored. *Basidiospores* elongate- subfusiform, inequilateral in side-view, irregularly warted to irregularly reticulate from broad to narrow meandering ridges or from shallow meandering furrows, or irregularly pitted, or as if erumpent in a band restricted to the central region, generally easily observed under x 40 objective but obvious under x 100, inamyloid, acyanophilic. *Cheilocystidia* equal or elongate-clavate to narrowly sublanceolate, hyaline or with pseudoamyloid inclusions, sometimes sparse; *pleurocystidia* rare or sparse to prominent, fusoid ventricose to sublanceolate, hyaline, with or without yellowish contents in ME. *Tube-trama* divergent with non-pigmented, central gelatinised zone, yellowing only in ME or with dilute aqueous alkali solutions. *Pileipellis* a trichoderm or ixotrichoderm, gelatinising with maturity. *Stipitipellis* with strongly disrupted caulohymenium on ornamentation and caulocystidia either scattered and eroded from ornamentation or in depressions and on smooth stipe-surface as either clavate or elongate, thin-walled, hyaline cells. *Clamp-connections* not seen.

Chemistry: Not rubescent on application of KOH; neither cyanescent or viridescent with aq. ammoniacal solutions. Negative ME. Badione pigment isolated from *A. gracilis* (Peck) Wolfe. Some taxa known to be edible but of no major importance – fide Singer, 1986.

Developmental studies: For *A. dictyopus* & *A. longicollis* see Corner (1972).

Ecology: Terrestrial, probably forming sheathing mycorrhizas but poorly studied; some taxa thought to be saprotrophs or forming facultative associations.

Distribution: Mostly a tropical genus with extensions into temperate Australia, Asia (China) and North America.

This genus was recognised first by Corner (*Boletus in Malaysia*, 1972, p.76) as a subgenus of his large and unwieldy concept of *Boletus*. It was introduced to accommodate several tropical Malaysian boletes with ornamented basidiospores, but members of the genus are now known from several other countries, albeit those with a subtropical to tropical climate. The genus now contains about 30 taxa worldwide. This same grouping was in part recognised by Singer (Farlowia, **2**: 119, 1945) when he erected Sect. *Graciles* within his concept of *Porphyrellus q.v*. The type of this section was the North American *Boletus gracilis* Peck,

1872, and in addition he included *Tylopilus subflavidus* Murrill, 1938 also from N. America. At the same time (loc, cit. pp. 138) Singer erected Sect. *Allospori* within the genus *Boletellus* for *B. betula* Schw. - this is also referred to *Austroboletus* by Pegler & Young (1981), although molecular work does not support this placement. Singer (1986) later accepted an independent *Austroboletus*, although did not suggest then any infrageneric classification because of a general lack of knowledge of the species worldwide; he did not include *Boletellus betula* therein. Wolfe *et al.* (Mycologia **80**: 46-53, 1988) has discussed the neotropical species. The genus has been attributed incorrectly to the Strobilomycetaceae, based on similarities in basidiospore-form and ornamentation, these being thought to provide a link between *Porphyrellus* and *Strobilomyces q.v.*. The spore-colour on the other hand provided a link with both *Fistulinella (= Mucilopilus) q.v.* and *Tylopilus q.v.*. Molecular studies indicate, although quite separate, *Austroboletus* is closely related to *Tylopilus*; surprisingly the genus may have closer relationships with a consortium around the N. American *Boletus pallidus* Frost apud Peck, which has always been considered anomalous within *Boletus*.

Good accounts of *Austroboletus* are found in Corner (1972) where colour illustrations and figures are supplied and in Wolfe (Bibl. Mycol. **69**, 1979) in which supporting b/w photographs and line-drawings are offered. See also Singer in Farlowia **2**, 1945. Keys and line-drawings of neotropical species occur in Singer *et al.*, Beih. Nova Hedw. **77**, 1983. Horak (Sydowia **33**: 71-87, 1980) has re-examined many South East Asian species.

***AUSTROGASTER** Singer, Bol. Soc. Arg. Bot. **10**: 57, 1962. Plate 2 A.

Type species (only original species): *Austrogaster marthae* Sing.

Basidiome epigeal, opening or remaining closed - sequestrate, boletoid, centrally stipitate, putrescent, angiocarpic.

Pileus convex to conical, dry, pale brown, sometimes becoming rimose or areolate. *Stipe* nearly equal, for most part forming columella, attached to peridium, becoming somewhat lacerate. *Gleba* loculate, soft, fleshy, permanently enclosed or becoming exposed close to the stipe and then almost poroid, pale brown from spore-mass.

Basidia 4-spored, clavate, thin-walled, hyaline. *Basidiospores* ellipsoid to amygdaliform, cinnamon-brown, slightly thick-walled, orthotropic or nearly so with

central or asymmetric, broad hilar appendage, probably suggesting statismosporic dispersal, slightly roughened under SEM, inamyloid, acyanophilic. *Hymenophoral trama* gelatinised, bilaterally divergent. *Clamp-connections* present.

Chemistry: None known.

Ecology: Terrestrial, apparently mycorrhizal with *Nothofagus*.

Distribution: South America (Argentina) and New Zealand.

A genus related to *Gymnopaxillus q.v.* and to the lamellate *Paxillus* (Paxillaceae) *q.v*. Horak (see below) placed this genus with *Gymnopaxuillus q.v., Singeromyces q.v.* and *Paxillogaster q.v.* in subfamily Paxillogastroideae.

See Singer, 1962 for full description supported by line-drawings and Horak (Nova Hedw. **10**: 330, 1966) who provides b/w illustrations. Reid (Trans. Brit. mycol. Soc. **86**, 1986) supplies the description of the only other species with line-drawings.

AUSTROPAXILLUS Bresinsky & Jarosch apud Bresinsky, Jarosch, Fischer, Schonberger & Wittmann-Bresinsky, Plant Biology **1**: 33, 1999. Plate 2 B.

Type species (originally designated): *Agaricus statuum* Speg. (= *Austropaxillus statuum* (Speg.) Bresinsky & Jarosch).

Basidiome epigeal, pileate with lamellate continuously forked hymenophore, centrally to slightly excentrically stipitate, putrescent, probably gymnocarpic. *Spore-print* fulvous to fulvous with a slight olivaceous tinge.

Pileus convex but soon plano-convex to plane and with incurved margin becoming wavy with age, slightly tomentose then becoming smooth, dry, rust-brown to fulvous or even darker. *Stipe* cylindrical or slightly clavate, attenuated upwards, concolorous with pileus or slightly paler towards the apex, pruinose at apex becoming smooth downwards, spotted and streaked with brown on bruising. *Gills* decurrent, pale ochraceous at first then brown and finally rust-brown, crowded often branched and even anastomosing at stipe-apex. *Context* whitish to yellowish sometimes taking on slight pinkish hue when first exposed to the air, darkening and then becoming browner.

Basidia large, broad, hyaline, clavate to subclavate, 4-spored. *Basidiospores* relatively large, shortly subfusiform to elongate ellipsoid, smooth but, in those taxa examined, with scattered minute verrucae under SEM, broadly rounded apex, suprahilar depression present, pale yellow to straw-colour in aq. ammoniacal solutions, sometimes with olivaceous tint, inamyloid, acyanophilic. *Cheilo- and pleurocystidia* at most scattered and rare or the latter replaced by paraphyses-like cells. *Pileipellis* a repent cutis of slightly ornamented or smooth, filamentous hyphae with hardly differentiated, suberect end-cells, reddish brown in aq ammoniacal solutions. *Clamp-connections* absent or rare medallion-clamps present.

Chemistry: Contains 2,4,5-trihydoxyphenylglyoxylic acid (and several specific but unidentified pigments). No involutin detected. Also quinone methide tautomer isolated from *A. statuum* (Sing.) Speg.) Bresinsky *et al.*, 1999.

Ecology: Terrestrial, ectomycorrhizal with *Nothofagus* (Fagaceae) and probably also with *Eucalyptus* (Myrtaceae). See Agerer 151 *Austropaxillus boletinoides* (Sing.) Bresinsky & Jarlosch.

Distribution; South America, Australia and New Zealand.

A small genus of probably no more than ten species which resembles the north temperate *Paxillus q.v.*, a genus in which all the constituent species were formerly placed. This group of species was recognised as different by Pegler & Young (1981), who transferred them to a larger concept of *Phylloporus q.v*. The genus has been shown by molecular studies, however, to be more closely related to the resupinate *Serpula q.v.* and, therefore, the *Coniophora*-suite of genera. 8 species and an unidentified collection all show high ploidy levels, higher than for species of *Paxillus* or *Tapinella q.v.* The genus contains *Paxillus* sect. *Defibulati* as defined by Singer (1986).

Descriptions and key to Australian taxa in Watling & Gregory (Notes Roy. Bot. Gdn. Edinb.**48**: 353-391,1991) and in Watling & T.-H Li (*Australian Boletes; A Preliminary study*, 1999). Also see Horak, Pacific Mycogeography: a preliminary approach (Aust. J. Bot. Suppl. **10**, 1993) & (Sydowia **32**: 154-166, 1979). Line-drawings are provided by these authors and a colour portrait of *A. infundibuliformis* (Clel.) Bresinsky & Jarlosch appears in Young, *Common Australian Fungi*, 1982, Bougher & Syme, *Fungi of Southern Australia*, 1998 and Garrido (Biblio. Mycol. 120, 1988) under *Paxillus*. No illustrative material supports the erection of the genus.

Synonyms:
Parapaxillus Singer *ad int*., Ann. Mycol. **40**: 58, 1942 based on *Paxillus argentinus* Speg. but from 1951 onwards placed in synonymy with *Paxillus* by Singer. *P. argentinus* belongs to *Austropaxillus.*

BOLETELLUS Murrill, Mycologia **1**: 10, 1909. Plate 2 C & D.

Type species (only original species): *Boletus ananus* Curtis (= *Boletellus ananus* (Curtis) Murrill).

Basidiome epigeal, pileate with tubulate hymenophore, centrally stipitate, putrescent to fibrous and then rather persistent, either velangiocarpic or mixangiocarpic to gymnocarpic. *Spore print* deep olivaceous or olive-brown.

Pileus convex or even hemispherical then expanding to become plano-convex, scaly to smooth or minutely tomentose, dry or viscid, some species with appendiculate margin, generally in tones of brown but several, especially the more scaly taxa, with purple, maroon or reddish shades, rarely blood red. *Stipe* cylindrical or swollen towards the base, smooth or minutely pruinose to distinctly scaly from velar remnants, less frequently annulate from remnants of appendiculate pileus-margin, uniform or paler than pileus. *Tubes* yellow at first then olivaceous, cyanescent in some taxa; *pores* concolorous or in some constituent taxa reddish. *Context* whitish or pallid or flushed yellowish, more strongly coloured above tubes and in stipe-base where it may be flushed maroon, yellowish or brownish, cyanescent in some taxa. *Odour* & *taste* not distinctive or slightly acidulous.

Basidia clavate to pyriform, hyaline, 4-spored. *Basidiospores* with longitudinal ornamentation either as faint striae, or wings or ridged from prominent costae, often with distinct or indistinct cross-striae and at maturity with remnants of mucilaginous or membranaceous myxosporium, generally elongate-cylindric or subfusiform, less frequently ovo-ellipsoid, with suprahilar depression and prominent hilar appendix, inamyloid, acyanophilic. *Cheilocystidia* generally reduced to basidiole-like structures or ventricose, sometimes with a short prolonged apex, scattered; *pleurocystidia* similar and scattered and less obvious, hyaline. *Tube trama* of slightly gelatinised, slightly coloured central zone with divergent lateral strata. *Pileipellis* a cutis of appressed, filamentous hyphae loosely interwoven and many adhering together to form skeins that form squamules. *Clamp-connections* present but scattered in some species.

Chemistry: Atromentic, xerocomic and variegatic acids, and variegato-rubin have been isolated.

Cytology: Ploidy levels of 2x in *B. emodensis* (Berk.) Sing. and 4x in *B. dissiliens* Corner (Bresinsky & Wittmann-Bresinsky, 1994).

Developmental studies: For *B. ananus* & *B. emodensis*. see Corner (1972) and for the latter also Cleménçon (1997).

Ecology: Terrestrial, on logs, or on the lower parts of living or standing dead trees, or even fruiting up to shoulder height. Probably not obligately mycorrhizal, although some could form facultative associations.

Distribution: The genus is predominantly subtropical to tropical, and occurs in both warm and temperate climates world-wide.

Singer (1945 in Farlowia **2** *et subseq*.) has included several unrelated entities together under this name. Thus *Boletellus retisporus* is referable to *Heimioporus q.v.*; *B. mirabilis* (Murrill) Murrill & *B. projectellus* (Murrill) Murrill with exceedingly large, smooth basidiospores must be treated elsewhere and *B. betula* (Schw.) Gilb. (placed in Sect. *Allospori* by Singer, 1945) is referable to *Austroboletus q.v.* This means that three sections are then left in Singer's original treatment of *Boletellus* in addition to the type section (1945 *et subseq.*), Sect. *Chrysenteroidei,* with a range of species including *Boletus. zelleri* (Murrill) Singer & *B. obscureococcineus* (Höhn.) Singer, Sect. *Ixocephali* with *B. longicollis* (Ces.) Pegler & T.W.K. Young, and Sect. *Dictyopodes* with *B. russellii* (Frost) Gilb. There is no doubt that SEM studies of the basidiospores of those species with spores equipped with striae show that they are different from those exhibiting costate ornamentation, and the two groups should not be included in a single genus. *Boletellus* must be restricted to the consortium surrounding the type species, where the basidiospores are equipped with distinct structures built from a thickened wall; in other species the spores exhibit simple surface irregularities. Thus *Boletus zelleri* and *B. pruinatus* Fr. & Hök are more closely related to boletes placed amongst the xerocomoid consortium, indeed even some central members of the latter group have faintly striate spores. This separation is supported by molecular studies, where members of the type section associate with *Strobilomyces q.v.,* some with the xerocomoid boletes, and *B. russellii* and *B. chrysenteroides* Snell are, surprisingly, related to *Aureoboletus q.v*. Undoubtedly more work is required to resolve this issue. Pegler & Young (1981) place this genus in its widest sense in their Xerocomaceae. Patouillard & Baker (1918)

placed *B. singaporensis* Pat. & Baker (=*B. longicollis*) in *Boletopsis* a now rejected genus, *q.v*. Horak (Kew Bulletin **31**: 645-652, 1876) has discussed the species found in Papua New Guinea.

Synonyms:
Boletogaster Lohwag, Beih. Bot. Centralbl. **42** II: 274, 1926; type species *Ceriomyces jalapensis* Murrill based on the enveloping, widely appressed appendiculate pileus-margin (= sect. *Ixocephali* Singer, 1945); includes *Boletellus longicollis* (Ces.) Pegler & T.W.K.Young.
Frostiella Murrill, Florida Boletes. Contrib. Herb. Univ. Florida Exp. Station **1**: 6, 1942. Not validly published; based on the unusually reticulate-lacunose stipe ornamentation; proposed type species *Boletus russellii* Frost (= Sect. *Dictyopodes* Singer, 1945)
Strobilofungus Lloyd in Mycol. Writings 4: 538, 1915 refers to *B. ananus*; introduced to demonstrate the similarity to *Strobilomyces*, and because of the enveloping mixangiocarpic development a feature covered by the circumscription of *Boletellus*.

The genus has not been monographed on a world scale but good descriptions are available in regional floras e.g., Singer in Farlowia **2**, 1945, Smith & Thiers (*Boletes of Michigan*, 1971) and Corner (*Boletus in Malaysia*, 1972). Colour illustrations are found in Bessette, Roody & Bessette, *North Amercian Boletes*, 2000 and Imazeki *et al.*, *Fungi of Japan*, 1988.

BOLETINELLUS Murrill, Mycologia 1: 9, 1909. Plate 3 A.

Type species (only original species): *Daedalea merulioides* Schw., (in Trans. Amer. Phil. Soc. Ser. 2, **4**: 160, 1832) (=*Boletinellus merulioides* (Schw.) Murrill).

Basidiome epigeal, pileate with gyrose-tubulate hymenophore, excentrically or laterally stitipate, gymnocarpic and stipitocarpic with central to slightly excentric stipe; often associated with sclerotia and in some species forming complex associations with hemipteroid insects. *Spore print* olive-brown.

Pileus dry but becoming slightly tacky in wet weather, and then with lustrous appearance when mature, villose at margin, in shades of brown either with fulvous or olivaceous overtones. *Stipe* rarely central, cylindrical or slightly swollen

downwards, often quite tough, solid, concolorous with pileus or slightly paler especially at apex, smooth, base blackish, evelate. *Tubes* arcuate-decurrent, pale olivaceous brown at first, darkening with age; *pores* irregularly arranged, gyrose, as radiating ridges with cross veins which further divide to give an honey-comb appearance. *Context* pale olivaceous yellow or with a slight pinkish tinge under pileus-cuticle, unchanging, or when cyanescent blueing very slowly. *Odour* indistinct; *taste* of potatoes.

Basidia hyaline to straw-colour in aq. ammoniacal solutions, slightly darker in ME, 4-spored. *Basidiospores* shortly ellipsoid to subreniform or shortly phaseoliform, smooth, pale olivaceous or ochraceous yellow in aq. ammoniacal solutions, pseudoamyloid. *Cheilo- & pleurocystidia* poorly differentiated, scattered and often a few only at orifice of pores, smooth, fusoid ventricose. *Tube trama* divergent from a central, gelatinised strand but configuration loosening by maturity, hyaline throughout in aq. ammoniacal solutions. *Pileipellis* a poorly developed, interwoven, yellow-brown layer of filamentous, yellowish, smooth or encrusted hyphae from which issues yellow pigment in alkaline solutions in microscopic mounts. *Clamp-connections* present.

Chemistry: Variegatic acid has been isolated from *B. merulioides.*

Ecology: Terrestrial, but also on logs and rotten wood of deciduous trees. In the type species *B. merulioides* there is a close relationship with root-aphids feeding on their host *Fraxinus*, a phanerogamic genus not considered ectomycorrhizal; see Brundrett & Kendrick (1987). Thus associations with *Allophylus* (Sapindaceae) and *Quercus* (Fagaceae) require further investigation.

Cultural studies: see Pantidou (Can. J. Bot. **39**: 1149 –1162, 1961).

Distribution: Known from South America, and one taxon is widespread in temperate areas of the United States and southern Canada. Also in SE Asia.

A small genus with a handful of species which were once linked to *Boletus lividus* Bull.: Fr., and placed in *Gyrodon q.v.* but this is untenable from both structural and ecological points of view (Watling & de Meijer in Notes Roy. Bot. Gdn. Edinb. **54**: 231-251). Molecular studies support this separation and demonstrate that the true relationship is with some of the sclerodermatoid fungi. At least the transference of one of the species, *Phylloporus rompelii* Pat. & Rick, from its traditional placing in *Gyrodon* to *Boletinellus* has been confirmed by molecular studies (Louzan *et al*., 2007). The genus is placed in the Boletinellaceae; see Watling, Mycoscience **47**, 2006.

Synonyms:
Anastomaria Raf. in Ann. Nat. ou Ann. Synop. 16, 1820. A devalidated name according to Donk (Reinwardtia **3**: 276, 1955) with type *A. campanulata* Raf.; possibly refers to *Boletinellus* (*Daedalea merulioides* Schw.).
Campbellia Cooke & Mass., Grevillea **18**: 87, 1890; type species *Merulius infundibuliformis* Cooke & Mass. (selected). Replaced by *Rodwaya* because *Campbellia* had been used earlier for a genus of flowering plants – Orobanchaceae; see Singer, Taxon 5: 30-31, 1945. W.B. Cooke considered *M. infundibuliformis* as a species of *Serpula* but requiring re-study. Mycologia **49**: 221, 1957.
Rodwaya Syd. & P. Syd., Hedwigia 40: 2, 1901; based on the same type as *Campbellia, viz. M. infundibuliformis.*
Gilbertiella R. Heim, Rev. Mycol. **30**: 324 & 326, 1965; type species *Campbellia africana* Cooke & Mass.. This is an illegitimate name having been used for a member of the Anonaceae. Replaced by *Gilbertina*; see below.
Gilbertina R. Heim, Rev. Mycol. **31**: 151, 1966; based on *Campbellia aricana* – missplelt. Considered the same as *Gyrodon* by Pegler & Young, Trans. Brit. Mycol. Soc. **76**: 109. 1981.

The type species is described with supporting b/w photograph by Smith & Thiers (Boletes of Michigan 1971).Watling & de Meijer (Notes Roy. Bot. Gdn., Edinb. 54: 231-251, 1997) have discussed and described the S. American species with comments on their relationship with the type species; see also Watling, Notes Roy. Bot. Gdn., Edinb. **29**: 67-73, 1969. Colour illustrations are found in Bessette, Roody & Bessette *North American Boletes*, 2000.

BOLETUS Fr. in Syst. Mycol. **1**: 385, 1821. Plate 3 B & C.

Type species (selected): *Boletus edulis* Bull.: Fr.

Basidiome epigeal, sometimes quite massive, pileate, well-developed tubulate hymenophore, centrally stipitate, less frequently slightly excentric, variously coloured, gymnocarpic. *Spore print* olivaceous brown, bronze-colour or dark citrine.

Pileus convex then plano-convex or even plane and depressed in centre, smooth, tacky or even slightly viscid, or subtomentose to slightly velvety, in various shades of brown from pale buff to bronze and often darkening with age or on bruising, especially cyanescent species. *Stipe* evelate, frequently swollen downwards, generally clavate, sometimes cylindrical, either ornamented with a

distinct to rudimentary or poor network, or by clusters of furfuraceous granules or 'punctae', rarely totally smooth and glabrous, but never with glandulae or with scabrosities, concolorous or differently coloured perhaps with red, orange or yellow ornamentation and darkening when cyanescent, evelate. *Tubes* long, depressed about stipe or almost free, strongly gelatinised, whitish, yellow; *pores concolorous* or orange to red in some species. *Context* white or pale coloured, yellow sometimes with red blotches but less commonly rufescent, some strongly cyanescent. *Odour* indistinct or strong and rather unpleasant; *taste* mild or bitter; some species edible, especially those with white, unchanging context.

Basidia clavate, hyaline, 2-, 3- & 4-spored. *Basidiospores* elongate-fusoid to cylindrical, sometimes extremely large, rarely shortly fusoid, pale straw-yellow or honey-coloured to pale brown s.m., with pronounced suprahilar depression with or without a broad base or tapered apex, sometimes narrowed, smooth, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* variable, either rare and scattered or numerous, elongate fusiform or ventricose, hyaline to straw yellow or honey-coloured, thin-walled. *Tube trama* bilateral with distinctly coloured, gelatinised mediostratum and strongly divergent from lateral, highly gelatinised, less pigmented hyphae. *Pileipellis* generally a cutis or irregular trichoderm. *Stipitipellis* of cylindrical, longitudinally arranged hyphae supporting strongly developed caulohymenium in defined ridges or in islands of tissue scattered over surface. *Clamp-connections* not seen.

Chemistry: Xerocomic and variegatic acids are widely found in the genus but atromentic acid and variegato-rubin have also been isolated. Some species give a positive ME. Thelephoric acid isolated from speculative primitive members.

Cytology: Ploidy levels 1x in *B. frostii* Russell, occasionally 4x. 2x in *B. calopus* Pers., *B. luridus* Schaeff., *B. impolitus* Fr., *B. queletii* Schulzer & *B. radicans* Pers. (Wittmann-Meixner, 1989). Also 2x in *B. aereus* Bull., *B. appendiculatus* Schaeff. & *B. edulis* and varieties, and *B. aureomycelinus* Pat. & Baker & *B. gyrodontoides* Corner from Malaysia. Also 4x in *B. depilatus* Thoen & Heinem.& *B. rhodopurpureus* Smotl. and 1x in Malaysian *B. crassipedius* Mass. & *B. graveolens*.Corner (Bresinsky & Wittmann-Bresinsky, 1994).

Developmental studies: See Corner (1972) for *B. phaeocephalus*.

Ecology: Terrestrial, obligately ectomycorrhizal with Fagales and Pinaceae in the northern hemisphere and with eucalypts in Australia, and noted by Singer for Tiliaceae, Polygonaceae and Leptospermataceae. Also forms arbutoid mycorrhizas. See Agerer 36 *Boletus edulis* with *Picea abies*.

Distribution: The genus is mostly north temperate, although it is well represented in Australia; except for a few prominent species, the genus rarely occurs in tropical areas and undoubtedly introduced into some areas, e.g. *B. edulis* to South Africa. Apparently very poorly represented in South America. Members of the *B. edulis* group exported to many parts of the Western world being considered a great delicacy. Sought after for food especially by Italian communities

The limits of the genus at present are difficult to define as so many species have been assigned to the genus, and it remains for many species to be re-examined in the light of modern techniques before the limitations of a restricted *Boletus* can be made. Even in some modern understandings of the genus, members of *Xerocomus q.v.* are included within *Boletus*, emphasising that so little is known about the tropical species assigned to *Boletus* and those casually assigned to *Xerocomus*, so a true separation at present is not possible. The genus is well known from temperate areas but many tropical species, which might extend the character-set, have been added to cloud the description. In the restricted sense it is still a large genus with many important commercially edible species. Molecular studies support the idea that the genus, even in its restricted sense adopted today, may be heterogeneous, suggesting at least 3 distinct entities, a *B. edulis* group containing the type species, somewhat separated from the traditionally linked *B. satanus* group, and even further removed from a group centred on *B. luridus* Schaeff.: Fr. If *Boletus* is restricted to the *B. edulis* group then the number of species world-wide would probably be of the order of 25-20 distinct entities. *Xanthoconium q.v.*, a small genus covering a handful of species, is presently known only from temperate and subtropical North America. On spore-shape alone it appears distinctive from *Boletus* but molecular studies would suggest that this character is not significant; in such analyses the type species appears on a branch very close to the type of *Boletus* and its close allies. It is, therefore, distant from many other of the familiar boletes thought to be central to *Boletus*. Further studies are obviously required. Several authors *e.g.* Smith & Theirs (*Boletes of Michigan*, 1971), maintain *Boletus affinis* Peck in their expanded concept of *Boletus.*

Synonyms:
The genus has been variously typified. Selection of *Boletus bovinus* L.: Fr. or *Boletus cavipes* Opat. (= *Suillus* sect. *Boletinus*), the latter clearly an error, would give *Boletus* priority over *Suillus q.v.,* and selection of *Boletus subtomentosus* L.: Fr. would give it priority over *Xerocomus q.v. Tubiporus* was, therefore, used especially by continental European mycologists, for the *B. edulis* group of boletes as a replacement generic name. For an in depth discussion on all the problems

see Donk in Reinwardtia **3**: 275-313, 1955. *Boletus edulis* is now accepted as the type of *Boletus*. The boletes classified around the type are under molecular scrutiny by B. Dentinger & David McLaughlin, University of Minnesota, St Paul, US.

As many texts are devoted to the boletes in general they include members of the genus *Boletus* but there is no definitive contribution on the '*edulis*' group worldwide. The type species of *Boletus* and its European allies are discussed and illustrated in colour in Vassil'kov, *Belyy Grib*, 1966. Engel, Krieglsteiner, Dermek & Watling in *Die Gattung Boletus in Europa*, 1983 deal with those species which would have been placed in *Tubiporus* by many continental authorities, *viz*. 'edulis' and 'satanus' groups *etc*.; see below. Reference should be made to the general bibliography for publications which include *Boletus* in either a broad or restricted sense.

Ceriomyces Murrill, Mycologia **1**, 140, 1909; type species *Boletus crassus* Bat. = *B. edulis*. Used extensively by Murrill.
Dictyopus Quél. in Ench. Fung. 159, 1886; type species *Boletus edulis* (selected); therefore a synonym of *Boletus*
Oedipus Bat., Bull. Soc. Hist. Nat. Doubs **15**: 13, 1908; type species *Boletus edulis* (selected). Direct synonym of *Boletus*.
Tubiporus Paulet ex P. Karst., Rev. Mykol. **3(9)**, 16, 1881; type species *Boletus edulis* (selected). The preferred generic name for those species of *Boletus* allied to *B. edulis.* The genus has been widely used by French authorities. The type of Paulet's genus must be either *Boletus luridus* Schaeff.: Fr. or *B. bovinus* L.: Fr.(=*Suillus*) and so is at present superfluous. If *B. luridus* is found to characterise a separate group of species which is presently placed in *Boletus* the genus would automatically become available for use.
Suillellus Murrill, Mycologia **1**: 16, 1909; type species *Boletus luridus* Schaeff.: Fr.. Used by Murrill for some of the cyanescent species generally placed in *Boletus* Sect. *Luridi*. If *Boletus* is dissected in the future based molecular studies this name will become available for those currently placed in Sect. *Luridi*.
Suillus [Haller] O. Kuntze in Rev. Gen. Pl. **3(2)**, 534, 1898; see Donk (Reinwardtia **3**: 275-313, 1955) for discussion on typification of the type, which he considers to be a member of the *B. edulis* group. It therefore becomes a synonym of *Boletus*; *Suillus* is used today for a distinct group of boletes, *q.v.*

*** BONDARCEVOMYCES** Parmasto in Parmasto & Parmasto, Mycotaxon **70**: 219, 1999. Plate 3 D.
Type species (only original species): *Hapalopilus taxi* Bondartsev (= *Bondarcevomyces taxi* (Bondartsev) Parmasto & Parmasto

Basidiome pileate bracket fungus, non-stipitate, sessile, dimidiate, flabellate, thickening towards base, cheesy to fleshy or spongy, watery, drying brittle, annual. *Spore-print* yellow-ochre.

Pileus with slightly floccose surface, sometimes indistinctly zonate, orange-red, brownish orange, dark yellow near rounded or almost sharp margin, drying brick-colour. *Tubes* cheesy or fleshy, light orange or yellow, darkening on drying; *pores* angular to slightly irregular, with rather thick dissepiments, light to deep yellow, bruising olivaceous, drying olivaceous black. *Context* thick, indistinctly zonate or azonate, ochraceous to almost carrot-colour, viridescent when bruised, butter-yellow in herbarium material, sometimes darkening with alkali solutions. *Odour* sweetish, becoming stronger when dry.

Basidia 4-spored, clavate, with basal clamp-connection. *Basidiospores* ellipsoid with one flattened side or shortly cylindric, smooth, walls yellowish, pseudoamyloid. *Cystidioles or hyphidia* few. *Hyphal structure* monomitic; gloeoplerous hyphae present usually more abundant in tube trama.

Chemistry: presently unknown, although absorption spectra are given by Parmasto & Parmasto in the type description for aqueous and alkaloid extracts. Olivaceous incrustations soluble in alkali solutions present.

Ecology: On living and dead trunks of Cupressaceae, Pinaceae and Taxaceae, causing brown-rot.

Distribution: Europe (Caucasus) and Asia (Eastern Russia and China).

The type and only species in this recently described genus has held a rather isolated position amongst the bracket fungi, being placed by different authors in either *Tyromyces* or *Parmastomyces*; originally it was assigned to *Hapalopilus*. Similarities with *Phaeolus* have been demonstrated by Y-C. Dai & Niemela (Annales Botanici Fennici, **32**: 211, 1995), although it was not transferred to the Hymenochaetales. The true relationships were only finally clarified from the results of molecular analysis where it has been shown to have a high affinity with the *Coniophoraceae q.v.*; see Binder *et al*., 2005.

A full description accompanied by line-drawings of microscopic characters is given in Ryvarden & Gilbertson, European Polypores Vol. 2, 1994 as *Tyromyces taxi*.

BOTHIA Halling, Baroni & Binder, Mycologia 99: 311, 2007. Plate 4 D.

Type species (only original species): *Boletinus castanellus* Peck (= *Bothia castanella* (Peck) Halling *et al*.)

Basidiome epigeal, pileate with tubulate-sublamellate hymenophore, centrally or slightly excentrically stipitate, putrescent, cinnamon to chestnut colours prevailing throughout. *Spore-print* yellow-brown.

Pileus convex to plano-convex, becoming depressed at centre with age, dry, coarsely to granulate-tomentose and with or without adpressed, aggregated fibrils, dark red-brown, dark chocolate- or chestnut brown, even blackish at margin, appendiculate margin lacking. *Stipe* equal or tapering or sometimes broader downwards, coarsely or shallowly reticulate in upper part or reticulum confined to apex with ridges darker, vinaceous brown to spotted sooty brown back-ground, more irregularly ridged downwards, darkening to blackish brown with age and on handling. *Tubes* decurrent, although more depressed around stipe-apex with age, dull pallid brown; *pores* boletinoid in arrangement, coarsely angular to hexagonal, almost sublamellate towards stipe, dull cinnamon brown to pallid brown soon darkening and dark brown where bruised. *Context* soft, whitish, unchanging or becoming slowly pinkish brown, *Odour* & *taste* indistinct.

Basidia clavate, hyaline or sometimes with yellowish contents, 4-spored. Basidiospores ellipsoid to elongate-ovoid, hyaline to pale brownish yellow, smooth, thin-walled, inamyloid, acyanophilic. *Cheilocystidia* fusoid to fusoid ventricose or sometimes ventricose-rostrate, hyaline or sometimes with pale yellowish brown contents; *pleurocystidia* similar. *Tube trama* bilateral, divergent from a poorly differentiated central-zone, composed of hyaline or slightly yellowish, subgelatinized hyphae. *Pileipellis* a trichoderm with erect to suberect, cylindric, hyaline or brownish hyphae, which are smooth in water but possess spiral thickenings in alkaline solutions. *Clamp-connections* not seen.

Chemistry: No macroscopic reactions noted although all parts darken to some extent when bruised. Microscopically some coagulated brown material in basidia, anddark brown plaques on pileipellis hyphae found in mounts with ME.

Negative reaction with ammonia on pileipellis.
Ecology: Terrestrial, probably ectomycorrhizal with *Quercus* spp.

Distribution: Known from eastern United States of America.

The genus as presently circumscribed is restricted to a single species, *B. castanellus.* The recent erection of the genus *Bothia* for *Boletinus castanellus* is a welcome stabilization of what has been a long and involved history. Although the fungus has boletinoid pores and Peck placed it in *Boletinus*, in accordance with the thinking of his day, this fungus has found itself in six other bolete genera. A move to place it in *Boletinellus* by Murrill (1909) was instigated because *Boletinus* spp. are annulate, a feature lacking in Peck's fungus. Singer (1938) placed this same fungus in *Gyrodon* but the members of this genus have ovoid or broadly ellipsoid basidiospores unlike *B. castenellus*. Indeed this move was probably made because *Boletinellus* was considered by Singer (1950 *et subseq.*) a synonym of *Gyrodon*. Whilst treating *B. castanellus* in *Gyrodon* he also recognized an entity *Phylloporus squarrosoides* (Singer, 1938), based on *Boletinus squarrosoides* Snell & Dick, although later the same author preferred to include this latter species in *Xerocomus* (Singer, 1945), where it was later made the type of *Xerocomus* Sect. 2. *Pseudogyrodontes* (Singer 1950 & 1962); curiously this section in subsequent publications was abandoned, *e.g.* Singer, 1986. *Boletinus squarrosoides* is in fact a synonym of *Bothia castanellus* being a strongly sublamellate form. *Phylloporus carmineus* Heinemann described from West Africa was originally also housed in this section.

Recent DNA sequencing has shown that the type species of *Boletinus* nests neatly within the genus *Suillus*, a genus in which Smith & Thiers (1964) placed *B. castanellus*. The spore-print colour in *Suillus* is indeed similar being light brown and not olivaceous as in *Xerocomus*, but it is cinnamon (or purplish) and not yellow-brown as found in *B. castanellus*; also there are no fasciculate cystidia in *B. castanellus* and unlike *Suillus* the ectomycorrhizal host is not a member of the Coniferae. This unique fungus has similarities in hymenophoral trama structure to *Xerocomus* but the spore-print is differently coloured to that of this species. *Phylloporus* of which the type and its close relatives are considered by some authors to be purely lamellate taxa of *Xerocomus* have olivaceous spore-prints. On the combination of these divergent characters the genus *Bothia* was erected and its position close to *Xerocmus* demonstrated by DNA sequencing. A placement in *Chalciporus* proposed by Gomez (1)is not supportable. Reference should be made to all the genera mentioned above in order to see the reasons offered for the proposals for the various placements made over the intervening years.

Good colour illustrations are found in Snell & Dick (The Boleti of Northeastern North America, 1970) & Bessette, Roody & Bessette (North American Boletes, 2000). B/w photos in Coker & Beers (The Boletaceae of North Carolina, 1943) and Mycologia 99, 2007.

BRAUNIELLULA A. H. Sm. & Singer, Mycologia **50**: 928, 1958. Plate 3 E.

Type species (originally designated): *Brauniellula nancyae* A.H. Sm.

Basidiome epigeal, pileate, centrally stipitate, pileus generally strongly adhering to stipe even at maturity - sequestrate, obtuse to campanulate or convex sometimes depressed, sublamellate to loculate hymenophore, putrescent, veil present but poorly developed, angiocarpic. Resembles a squat or slightly contorted *Chroogomphus q.v.*

Pileus glabrous to fibrillose, sometimes at times slightly opening with the freeing of the lower margin. *Stipe-columella* thick, equal or narrowed below, exposed part solid, often quite short or almost absent, ochraceous with reddish purple or vinaceous fibrils, red fibrils at base. *Gleba* sublamellate to lacunose, cavities often elongate and irregular in outline, attached downwards to percurrent columella. *Context* yellowish ochraceous darkening downwards.

Basidia hyaline with granular contents yellowing in ME, long, fusiform, 4-spored. *Basidiospores* elongate-ellipsoid to broadly fusoid-cylindric with suprahilar depression, smooth, small hilar appendix, smoky yellow-brown in aqueous mounts, slightly darker in aq. alkaline solutions, strongly pseudoamyloid. *Cystidia* abundant, subventricose to subcylindric with obtuse or subacute apex, thin-walled and often covered by incrustations which become reddish brown in ME about the medial areas. *Hymenophoral trama* subparallel but curving outwards to interwoven subhymenium of thin-walled hyphae with incrustations some pseudoamlyoid in ME, others slightly amyloid. *Pileipellis* radially arranged cutis of heavily encrusted, narrow hyphae with amorphous material interspersed, some reddening in aq. alkaline solutions. *Clamp-connections* absent.

Chemistry: Strong amyloid reaction on context of columella and stipe; probably contains bovoquinones.

Ecology: Ectomycorrhizal with Pinaceae.

Distribution: North America (California).

A small sequestrate genus of no more than 3 temperate species, all of which will probably ultimately be united with *Chroogomphus q.v.*; *C. loculatus* O.K. Mill. comes very close to being an intermediate. Two sections were introduced by Smith & Singer (1958) in the original publication, but Sect. *Gomphidius* has been removed and forms the basis of *Gomphogaster q.v.* with affinities with *Gomphidius* q.v.

A key and descriptions are offered by Smith & Singer in Mycologia **50**, 1958 for all species including the single member now placed in *Gomphogaster q.v.* B/w photographs and line-drawings accompany the descriptions.

BUCHWALDOBOLETUS Pilát, Friesia 9: 217, 1959. Plae 4 A.

Type species (only original species): *Boletus lignicola* Kallenb. (= *Buchwaldoboletus lignicola* (Kallenb.) Pilát.

Basidiomes epigeal, pileate, tubulate hymenophore, centrally to excentrically stipitate, caespitose to fasciculate, pilei putrescent but stipes rather tough and fibrous and persistent, probably gymnocarpic. *Spore print* olivaceous snuff-brown.

Pileus almost spherical to hemispherical then expanding slightly, sometimes becoming convex, retaining inrolled margin even into maturity, dry, unpolished or becoming slightly silky tomentose and more minutely floccose towards margin, in shades of yellow-brown or rust-colour to tawny brown. *Stipe* central at first but frequently becoming slightly off-centre especially after pressure from accompanying basidiomes or position on substrate, cylindrical, frequently grouped together and then curved and slightly flattened towards the tapered base, concolorous with pileus or paler towards apex and more brown downwards, smooth or minutely granular floccose, evelate. *Tubes* adnexed to decurrent, almost arcuate, olivaceous; *pores* lemon- to sulphur-yellow when immature, darkening and flushed slightly olivaceous or greenish with age, bruising rusty tawny where damaged or pressed and irregularly in places cyanescent. *Context* cream-colour to buff or paler shades of pileus, rusty tawny towards the stipe-base, unchanging except for flush of blue or greenish blue immediately above the tubes. *Odour & taste* pleasant, slightly aromatic but also slightly acidic.

Basidia clavate, hyaline, 4-spored. *Basidiospores* ellipsoid in face-view, slightly elongate-ellipsoid to shortly subfusiform in side-view, straw-colour in aq. ammoniacal solutions and only slightly darker in ME, smooth, inamyloid, acyano-

philic. *Cheilocystidia* lageniform to fusiform sometimes slightly ampulliform, hyaline or yellowish to rusty tawny and producing lemon-yellow pigment in aq. ammoniacal solutions and red-brown globules in ME, smooth to asperulate, thin-walled; *pleurocystidia* sparse but when present similar to those at tube-orifice. *Tube trama* of slightly gelatinised central zone with divergent slightly paler lateral strata, laticiferous hyphae numerous. *Pileipellis* of smooth to scabrate hyaline or yellowish, filamentous hyphae forming a cutis with end-cells slightly to distinctly rounded. *Stipitipellis* composed of parallel hyphae supporting scattered clavate, thin-walled, hyaline to yellowish caulocystidia. *Clamp-connections* not seen

Chemistry: ME in flesh of stipe-base negative. Xerocomic and variegatic acids isolated.

Cytology: Plody level 2x in *B. lignicola* (Wittmann-Meixner, 1989).

Ecology: Lignicolous, on conifer stumps and sawdust piles in temperate species, and on xero-mesophytic trees in the tropics. A close relationship between *Buchwaldoboletus lignicola* and the polypore *Phaeolus schweinitzii* has been demonstrated; see Szczepka *et al*. (1984).

Developmental & *Cultural studies*: See Pantidou for *B. lignicola* and *B. sulphureus* (Can. J. Bot. **39**: 1163-1167, 1961 & **40**: 1313-1319, 1962).

Distribution: Predominantly temperate; known from the Caribbean and from Central Africa; one species is described from Australia and other unnamed species have been collected in Malaysia.

A genus of about ten species characterised particularly by the habitat preferences. For many years this genus was incorrectly placed within a wide circumscription of *Pulveroboletu*s *q.v.* (see *Aureoboletus* above). More recently Heinemann & Rammeloo (Mycotaxon **15**: 384-404, 1982) placed several of the constituent species in their understanding of *Phlebopus q.v.*, although the central species of this genus are not lignicolous but possibly putative ectomycorrhizal associates of tropical angiosperms. Singer (in Farlowia **2**, 1945) placed *B. sulphureus* and its allies in *Phlebopus* as Sect. *Sulphurei,* a section that he later (1961) transferred to *Pulveroboletus.* Pegler & Young (1981) accept this position, but molecular studies show that Sect. *Sulphurei* is neither related to *Phlebopus* nor closely related to *Pulveroboletus.* It demands its own separate genus. It would appear to be a member of a group including a consortium of blueing, yellow-pored boletes in

the *B. appendiculatus* Schaeff.: Fr. consortium on the one hand and *Chalciporus q.v.* on the other. The genus is placed in the Boletaceae. The S. American *Phlebopus beniensis* (Sing. & Digilio) Heinem. & Rammeloo, unlike other members of this genus, also belongs here.

The genus has not been monographed. Good descriptions, line-drawings of microscopic characters and colour illustrations of the two most widespread temperate species, often under *Pulveroboletus*, can be found in regional floras, *e.g*. Singer (*Die Pilze Mitteleuropas* Band VI: Die Röhrlinge, 1966); Pegler (*Agaric Flora of the Lesser Antilles*, 1983); Heinemann (*Flore Iconographique des Champignons du Congo*, Fasc. 3,1954); also see general bibliography.

CALOSTOMA Desv., J. Bot, Paris **2**: 94, 1809. Plate 4 C.

Type species (only original species): *Calostoma cinnabarina* Desv.

Basidiome epigeal, stalked gasterocarp with cartilaginous head, structurally complex endoperidium, centrally stipitate with complex rhizoidal stipe and at apex with parrot beak-ike peristome.

Peridium of four distinct layers, an outer exoperidium forming gelatinous layer which soon disappears, an inner evanescent, transparent, sticky or cottony exoperidium within volvate structure, breaking away before maturity to expose endoperidium; sac-like endoperidium coloured, tough, but papery dehiscing by a definite stellate stoma crowned with conspicuous, often coloured, tooth-like valves. *Stipe* equal, dry or covered in transparent gelatinous layer. *Gleba* pulverulent containing buff spore-mass and hyphal fragments from rapidly collapsing paracapillitium, true capillitium lacking or much reduced.

Basidia inflated, thin-walled, hyaline, evanescent, 4-12 spored. *Basidiospores* globose or ellipsoid, reticulate, punctate or pitted, thick-walled, straw-colour or pale brownish in aq. ammoniacal solutions, inamyloid, acyanophilic. *Cystidia* absent. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: Terrestrial; probably ectomycorrhizal; growing solitary or in groups on the ground or erumpent through soil at maturity.
Distribution: Species range from warm temperate climates to tropical, often rainforest areas.

A complex genus of about 15 species showing both microscopic and macroscopic diversity outside the general generic characters outlined above. Placed in the Calostomataceae; see Watling in Mycoscience **47**, 2006 and linked by Coker & Couch (1928) with *Astraeus q.v.* The wide range of spore-ornamentation found in the genus as it is presently understood may indicate that it is heterogeneous; molecular studies are desperately required on South East Asian species, as presently only data on N. American taxa are available to under-pin the genus. If it is found that the genus needs to be dissected then generic names are probably available. Hughey *et al.* (2000) have discussed the phylogeny of members of this genus. Molecular studies on *Calostoma* are being conducted by Andrew Wilson & David Hibbett, Clark University, Worcester, U.S.A.

Synonyms:
Mitremyces Nees in Syst. D. Pilz. U. Schw. 136, 1817; based on *Lycoperdon heterogeneus* Bosc (= *Mitremyces heterogeneus* (Bosc) Nees.), undoubtedly a *Calostoma* as presently understood.
Gyropodium E. Hitchc. in Silliman's Amer. J. Sci. **9**: 56, 1825; based on *G. coccineum* apparently a name said to be obtained from Schweinitz, although Coker and Couch are at a loss to know how. *G. coccineum* could probably be *Calostoma cinnabarina.*
Husseia Berk. in Hooker's J. Bot. London **6**: 508, 1847, often spelt *Husseya*; based on *H. insignis* Berk., a species now placed in *Calostoma*.

A key to world species appears in Lui, J. (Shansi Univ. nat. sci. ed. **1** 109, 1979). Also see Zeller (Mycologia **41**: 36-58, 1949) and for the tropical SE Asia species see Boedijn (Bull. Jard. Bot Buitenzborg, ser. 3, **16**: 64, 1938).

CHALCIPORUS Bat., Bull. Soc. Hist. Nat. Doubs. **15**: 19, 1908. Plate 4 E.

Type species (selected): *Boletus piperatus* Bull.: Fr. (= *Chalciporus piperatus* (Bull.: Fr.) Bat.).

Basidiome epigeal, pileate, reddish tubulate hymenophore, centrally stipitate, generally quite small to medium, putrescent, stipitocarpic and gymnocarpic. *Spore print* cinnamon-brown, in some with pinkish hues; never olivaceous.

Pileus convex then expanding to become plano-convex, glabrous or finely radially fibrillose, becoming slightly viscid or tacky at maturity. *Stipe* cylindrical slender rarely swollen, generally tapering, solid, dry, smooth throughout except for slightly pruinose-punctate apex when fresh, frequently with yellow basal

tomentum or mycelial attachments. *Veil* absent in type species. *Tube* cinnamon to reddish cinnamon or fulvous, decurrent or broadly adnate with decurrent tooth; *pores* concolorous, often with slight radial arrangement, small to medium, enlarging with age. *Context* firm, whitish to pallid with ochraceous tinges, and in some species bright yellow in stipe-base, sometimes flushing bluish on exposure to air. *Odour* mild; *taste* peppery in type species.

Basidia hyaline, clavate, 4-spored. *Basidiospores* generally relatively small, shortly ellipsoid, elongate to subfusiform, yellowish brown in aq. ammoniacal solutions, only slightly darker in ME, smooth with suprahilar depression or applanation and slightly tapered apex, inamyloid, acyanophilic. *Cheilocystidia* fusiform to lageniform, hyaline in aq. ammoniacal solutions, smooth or more frequently with apical mucilaginous cap which hardens and darkens to straw-yellow or honey-colour with age to form amorphous coating; *pleurocystidia* similar to those on pore orifice, scattered, never in fascicles. *Tube trama* with narrow mediostratum and often distinctly gelatinised divergent lateral strata. *Pileipellis* poorly developed and disrupted trichoderm or repent cutis of slightly to distinctly gelatinised, filamentous hyphae, which become intermixed with a filamentous subcutis. *Stipitipellis* of cylindric, hyaline hyphae overlaid in the upper portion with patches of caulohymenium containing cystidia similar to those at tube-orifice. *Clamp-connections* not seen.

Chemistry: No distinct chemical reactions; ME negative. Atromentic and variegatic acids present, with variegato-rubin.

Cytology: Ploidy level 2x in *C. piperatus* (Wittmann-Meixner, 1989).

Ecology: Terrestrial; possibly ectomycorrhizal associates of Salicales and Fagales in temperate areas and probably also capable of forming facultative associations with some conifers; hosts in the tropics have not been studied (see Pegler, *Agaric Flora of the Lesser Antilles*, 1983), which may suggest a non-mycorrhizal role.

Cultural Studies: See McLaughlin (Mycologia **56**: 136-139 & Mycologia **62**: 307-313) as both *Boletus* & *Suillus rubinellus* and by Pantidou & Watling (Notes Roy. Bot. Gdn., Edinb. **32**,1973) for *Boletus amarellus*.

Distribution: Although the genus is generally considered temperate and based on a temperate species, suspected members are found in the Neotropics including the Caribbean area, Australasia and Africa; a single species is known from New Zealand.

The hymenophore frequently shows a slightly radial arrangement, which has led to the early placement of members in *Suillus, q.v.* (or under its syn. *Ixocomus*) – Suilloideae; see Singer, 1938 as Sect. *Piperati*. This same author then linked the type species to *Pulveroboletus*, and even later accepted Bataille's genus within his somewhat modified concept of the Boletoideae, *i.e.* typical Boletaceae. Pegler & Young (1981) placed *Chalciporus* in the Suillaceae (Gomphidiaceae), suggesting a possible common ancestry with this group, although this is not supported by molecular studies. Members of *Rubinoboletus q.v.*, characterised by yellow tubes and pores, have been linked to *Chalciporus* through *Boletus rubinus* W.G. Sm. It should be noted than in Europe a yellow-pored variety of *C. amarellus* (Quél.) Moser has been described which demands further study.

Even with the additional tropical members, it is still a small genus, although we do not yet know its full extent. Many tropical species at present in *Pulveroboletus, q.v.* may belong here. The genus is related to *Buchwaldoboletus q.v.* Heinemann in *Flore Iconographique des Champignons du Congo* **3**, 1954 includes several taxa in *Pulveroboletus* with grey-green pores, which were assigned a position close to the Caribbean *Chalciporus trinitensis* (Heinem.) Singer; these also demand study, especially *P. annulatus* Heinem. and *P. croceus* Heinem. from tropical Africa, both of which possess an annulus.

As the circumscription of the genus is still in a state of turmoil no monographic treatment has been attempted. For the better known taxa good descriptions, supported by line-drawings of microscopic characters & habit and colour photographs, are available in regional studies, e.g. Pegler - *Agaric Flora of the Lesser Antilles*, 1983 and several European texts for the type species; see general references.

CHAMONIXIA Rolland, Bull Soc. Mycol. Fr. **15**: 73, 1899. Plate 4 F.

Type species (only original species): *Chamonixia caespitosa* Rolland

Basidiome gasterocarpic, hypogeous to subhypogeous, subglobose, ellipsoid to tuberous, sometimes in clusters, with or without rhizoids, attenuated downwards to form columella or reduced fleshy pad, gleba in small chambers, white at first then some shade of brown, pseudoangiocarpic.

Peridium dry, smooth with some rhizoids appressed to surface, horn-coloured or pallid at first then brown, olive-brown to ochraceous, in some species cyanes-

cent. *Gleba* in minute chambers adjacent to regularly branching columella which may reach the peridium, becoming irregularly tubulate in appearance, white or yellow then darkening to reddish, cinnamon- or chocolate- brown, darkening, only partially filled with rust-brown spore-mass at maturity.

Basidia developed in a true hymenium, clavate, thin-walled, hyaline, 2- or 4-spored, with distinct sterigmatic appendage. *Basidiospores* ellipsoid to ovoid with small apical pore, ornamented with longitudinal ridges or isolated warts, orthotropic, hilar appendix prominent, brown in aq. ammoniacal solutions, inamyloid, acyanophilic. *Cystidia* absent. *Hymenium* present along margins of chambers. *Clamp-connections* not seen.

Chemistry: Some species are cyanescent and chemical analysis has shown that chamonixin and two separate gyroporins, all cyclopentenones, are present in *C. caespitosa*. The colourless to blue reaction when exposed to air is the result of the transformation of chamonixin to the gyrocyanin anion.

Cytology: Ploidy levels 4-6x in the type species (Bresinsky & Wittmann-Bresinsky, 1994)..

Developmental Studies: Clémençon has described the development of *C. caespitosa* (Persoonia **18**: 499-504, 2005), which re-inforces its close affinities to the boletes.

Ecology: Terrestrial; in litter and leaf-mould, probably ectomycorrhizal associates of Pinaceae and Fagaceae in temperate northern hemisphere, and leguminous trees in tropics.

Distribution: Known from north temperate areas of North America and Europe and tropical SE Asia.

This is a small genus which, from molecular studies, is heterogeneous. Thus *C. pachydermis* sits with members of *Leccinum q.v.* (Sect. *Luteoscabra = Leccinellum q.v*), whilst the type is somewhat separated on a neighbouring branch.

For keys and species account, supported by line-drawings of microscopic characters see Smith & Singer in Brittonia **11**: 205, 1959.

***CHLOROGASTER** Laessøe & Jalink, Persoonia **18**: 422, 2004. Plate 5 A.

Type species (only original species): *Chlorogaster dipterocarpi* Laessøe & Jalink

Basidiome gasterocarpic, epigeal, centrally stipitate, head with truncate conical, green to blackish conspicuous warts, dehiscent.

Peridium dark olive-green, covered in conical, truncate warts, which are gradually lost to give a scar (similar to that seen in *Lycoperdon perlatum*), equipped only at maturity with pale green circular, fimbriate peristome. *Pseudostipe* buried in lower part in soil, upper portion exposed, base subbulbous or somewhat tapering, elongate, lacking mycelial rhizoids. *Endoperidium* and inner parts of pseudostipe vivid yellow-green, thin towards apex, darker and more olive towards base of pseudostipe. *Gleba* dark grey at first with white veins, very firm and non-gelatinised, becoming fluffy and dull olive at maturity. *Odour* absent; *taste* not tested.

Basidia probably 4-, 5-, 8-spored, some even 1-spored. *Basidiospores* globose to subglobose, dark brown, when immature covered in a solid, wide sheath, later ornamented with straight to undulating or slightly curved crests or spines < 9 µm high, of highly complex more or less distorted plates, some with a small short conical appendage, acongophilous, acyanophilous, although some embedded in cyanophilous and congophilous amorphous matter. *Endoperidium* gradually changing into exoperidium with amorphous aggregations of yellowish pigment which are persistent in aqueous mounts but dissolve rapidly in aq. alkaline solutions. *Paracapillitium* fairly elastic of narrow, thin-walled sparsely branched, hyaline hyphae with adhering yellow material. *Clamp-connections* not seen.

Ecology: Terrestrial, in heavy soil; probably ectomycorrhizal with Dipterocarpaceae.

Distribution: Known only from type locality in Malaysia (Sabah), although a probably similar un-named fungus has been found in Papua-New Guinea.

A genus with poorly known relationships. The type species has similarities to *Scleroderma q.v.* but the pigmentation and overall structure resembles *Pisolithus q.v.*, except no peridioles are found. The pseudostipe superficially resembles that found in *Calostoma q.v.,* although this is rather more complex in structure; similar structures are found in some species of *Scleroderma e.g. S. columnare* Berk. & Br..

In the original publication the authors give a very full account of the anatomy of the type supported by line-drawings of important features and colour photographs of the basidiomes.

CHROOGOMPHUS (Singer) O.K. Mill., Mycologia **56**: 529, 1964. Plate 5 B.

Type species (originally designated): *Agaricus rutilus* Schaeff. : Fr. (= *Chroogomphus rutilus* (Schaeff.: Fr.) O.K. Miller)

Basidiome epigeal, pileate, centrally stipitate, hymenophore lamellate, decurrent, thick and often veined, putrescent, metavelangiocarpic and stipitocarpic, tissues blue-black with ME. *Spore print* fuliginous or blackish, usually with a hint of dark green or olivaceous black, hues lost on drying to become rust-fuliginous.

Pileus convex to persistently umbonate with inrolled margin, dry or viscid, never glutinous, smooth or floccose-tomentose, in vinaceous shades, purplish brown or reddish brown to sienna, apricot- or peach-colour. *Stipe* fusiform to cylindrical, tapered or swollen downwards, concolorous with pileus or paler, pruinose to punctate at apex and with fibrillose-floccose annular zone or even a poorly developed annulus 1/3rd down, fibrillose-floccose downwards. *Gills* thick, waxy to subgelatinous, often with obtuse margins and often branched and interveined, paler or concolorous with stipe, arcuate-decurrent and running down stipe-apex to pass into pruinosity, at first concolorous with stipe then darkening to become rusty fuliginous often with olivaceous tinges but with base-colour of gill flesh prominent. *Context* peach- or apricot-coloured or yellowish, darker towards stipe-base, blue-black in ME.

Basidia distinctly elongate-cylindrical, thin-walled, hyaline, 4-spored. *Basidiospores* elongate, cylindrical to subfusiform, greyish honey-colour, smooth, lacking apical differentiation but with suprahilar depression, some slightly pseudoamyloid, cyanophilous. *Cheilo-* & *pleurocystidia* very prominent, scattered or numerous, some thick-walled, some with oleiferous contents, often slightly encrusted or with amorphous oily material attached. *Lamellar trama* of thin, central zone of parallel to subparallel hyphal organization which soon disrupts, accentuating divergent lateral hyphae, the divergence gradually less obvious as gills thicken, hyaline, gelatinised and supporting a dense, thick zone below the hymenium. *Veil* consisting of parallel to subparallel hyphae with amyloid encrustation, often covering the stipe-base and the pileus, especially at the margin. *Pileipellis* gelatinised, of hyaline, intertwined, narrow hyphae usually intermixed with amorphous amyloid material. *Clamp-connections* present.

Chemistry: Gomphic and xerocomic acids and several boviquinones (bovinone, helveticone & amitennonine) have all been isolated. The reaction with ME is significant. See Besl & Bresinsky (Plant Syst. Evol. **206**: 223-242, 1997) for review.

Cytology: Ploidy levels of 8x in *C. vinicolor* (Peck) O.K. Miller (Bresinsky & Wittmann-Bresinsky, 1994) and 10x for *C. rutilus* (Wittmann-Meixner, 1989); 4-6x in *C. helveticus* (Sing.) Moser (as var. *tatrensis*) (Bresinsky & Wittmann-Bresinsky, 1994).

Developmental studies: Development of basidiomes of *Chroogomphus rutilus* has been studied by Reijnders (1963).

Ecology: Ectomycorrhizal with conifers throughout their range. See Agerer 37 *Chroogomphus helveticus* subsp. *tatrensis* with *Picea abies*. See Agerer (1990) for ectomycorrhizal studies.

Distribution: Native to the northern temperate hemisphere. Introduced to Central America with exotic plantings; see Miller and Aime (2001) for a full analysis.

A genus of about 20 species assignable to the Gomphidiaceae and characteristic of conifer forests. This is the Sect. *Chroogomphus* in *Gomphidius* of Singer's earlier works (1951) and which was elevated to generic rank by Miller whilst monographing the species (Miller, Mycologia **56**: 526-549, 1964). Undoubtedly the genus *Brauniellula q.v.* will in the future be accommodated herein, especially as at least one intermediate is known, *viz*. *C. loculatus* Trappe & Miller; see those authors Mycologia **62**, 1970. *Gomphidius* (=*Chroogomphus*) *rutilus*, according to Kotlaba & Pouzar (1972) is the correct type of *Gomphidius*, making this name the correct one for what is herein called *Chroogomphus.* It has been proposed by Kotlaba & Pouzar that *Gomphidius* should be replaced by *Leucogomphidius* (see Kotlaba & Pouzar, Ceská Mykol. **26**: 219, 1972). Keys are available supported by b/w photographs, micrographs and line-drawings of microscopic characters in Miller, Mycologia **56**, 1964 and *subseq*. Also see Singer & Kuthanan in Ceská Mykol. **10**: 86, 1976

Synonym:
Gomphus (Fr.: Fr.) Weinm. in Syll. Pl. Nov. 2: 99, 1826; type species *Agaricus rutilus* Schaeff.: Fr. This is a synonym of *Chroogomphus. Gomphus* Pers. per S.F. Gray predates Weinemann's genus and must be retained to cover *Merulius clavatus* Pers. (=*Cantharellus clavatus* (Pers.) Fr.).

***CHRYSOCONIA** McCabe & G.A. Escobar, Mycotaxon **9**: 240, 1979. Plate 5 C.

Type species (only originally species): *Chrysoconia orthospora* McCabe & G.A. Escobar

Basidiome gasterocarpic, hemispherical or dendroid with basidia distributed all over surface.

Basidia clavate, 2-spored. *Basidiospores* ellipsoid, smooth, brown (Mar's yellow), orthotropic, pseudoamyloid ?, cyanophilous with thin-walled pedicel and apical pore. *Cystidia* absent. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Saprotrophic; on incubated decaying vegetable matter collected from lake-shore.

Distribution: Only known from North America (Washington, USA).

Only a single species known. The genus is placed in the Coniophoraceae as a gasteroid member by virtue of the smooth, brown spores with cyanophilic wall. It differs from all other members of the family in forming hemispherical to dendritic basidiomes composed of clamp-connected hyphae and the orthotropic basidiospores.

Supporting b/w photograph of basidiomes and micrographs accompany the type description.

CONIOPHORA DC. : Mérát in Nouv. Fl. Env. Paris. 2e, **Ed 1**, 36, 1821. Plate 5 D.

Type species (selected): *Coniophora membranacea* DC ex Mérat (= *C. puteana* Schum.: Fr.) P. Karst.

Basidiome effused crust, waxy, subcoriaceous or membranaceous, rarely other than strictly resupinate, gymnocarpic. *Spore print* dull reddish brown.

Hymenium effuse, smooth, undulate or tuberculate to papillose, granular to pul-

verulent from heavy spore-deposit, pallid to yellow when young and seated on a thin, dry, adnate to fleshy, separable layer, becoming brown to reddish brown, sometimes grey-brown, usually with hyphal strands. *Context* white to brown.

Basidia broadly clavate at first, then pedicel elongating to become cylindric, chiastobasidia in *C. marmorata*, 4-spored, rarely 2-spored. *Basidiospores* ellipsoid, obovoid or ovoid to nearly subglobose, or even subfusiform, thick-walled, pale yellow to brown with apical pore, smooth, dextrinoid, cyanophilous. *Cystidia* absent in most taxa or when present thick-walled, septate, brown; hyphidia usually present, hyaline. *Hyphal structure* monomitic, dimitic or trimitic, with hyaline or pale brown, thin to rather thick-walled, simple septate hyphae; skeletal hyphae when present pigmented, thick-walled, aseptate, infrequently branched; binding hyphae when present aseptate, frequently branched, pale brown or pale yellow, thick-walled hyphae. *Clamp-connections* present sometimes double or verticillate clamps on broader hyphae.

Chemistry: Xerocomic and variegatic acids isolated. See Besl & Kämmerer (1986) for further details.

Cytology: Ploidy 1x in *C. marmorata* (Wittmann-Meixner, 1989).

Developmental studies: see Clémençon (1997) for discussion.

Ecology: Saprotrophic lignicoles on rotten logs, fallen branches and stumps of conifers or hardwoods in forest, and even spreading onto soil and stones (and stonework when in houses). *C. puteana* forming a longitudinal rot in domestic buildings especially in garden out-houses, cold-frames, fences and door-stops exposed to the rain and known as **Wet Rot Fungus**; also in mines and glasshouses. Weakens timbers in service. Known to attack living trees in the forest

Distribution: Worldwide, known from most of Europe, North & South America, New Zealand and Australia, India and Sri Lanka and Japan; also Middle East and South East Asia.

A homogeneous genus of about 15 species and includes species with mono-, di- and trimitic hyphal systems. It is considered by Ginns (1982) that too much emphasis has been placed on separating out genera purely on their mitic system, as done by many polypore experts. *Coniophorella* P. Karst. is included despite the production of cystidia.

Type studies by Ginns appear in Can. J. Bot. **51**: 249, 1973 and a monograph of all known species with b/w photographs and line-drawings has been published by the same author in Opera Botanica **61**, 1982. Good colour photographs of *C. arida* (Fr.) P. Karst. *C. puteana* (Schum.: Fr.) P. Karst. and *C. olivacea* (Fr.: Fr.) P. Karst. (syn. *Coniophorella*) are found in Breitenbach & Kränzlin, *Pilze der Schweiz*, 1986. Hallenberg gives keys, full descriptions, b/w photographs and line-drawings in *Lachnocladiaceae and Coniophoraceae of Northern Europe*, 1985.

Synonyms:
Aldridgea Massee, Grevillea 20:121, 1892; type species *A. gelatinosa* Massee. Examination of the type found on sawdust proves it to be *Coniophora puteana* (Schum.: Fr.) P. Karst., type species of *Coniophora*. See Roberts, Kew Bull. **52**: 505, 1997.
Coniophorella P. Karst, based on *C. olivacea* (Fr.: Fr.) P. Karst., is now considered a good member of *Coniophora,* although characterised by the production of cystidia.

***CONIOPHOROPSIS** Hjortstam & Ryvarden, Mycotaxon **25**: 540, 1986. Plate 5 E.

Type species (only original species): *Coniophoropsis obscura* Hjortstam & Ryvarden

Basidiome crust-fungus, resupinate as in *Coniophora q.v.*

Hymenium effuse, brown-violet, in older parts brown with olive tints, seated on closely adnate, smooth, margin narrow, whitish or paler than fertile part, hyphal strands lacking. *Subiculum* well-separated from hymenium, whitish, fairly loose and soft.

Basidia cylindrical or more or less suburniform with median constriction, generally tapering downwards, thin-walled, 4-spored. *Basidiospores* subfusiform to subamygdaliform, verrucose, distinctly thick-walled, yellowish brown, inamyloid, strongly cyanophilous, with small hilar appendage, usually more or less hyaline and apparently with obscure apical-pore. *Cystidia* lacking, but protruding dendrophysoid elements present with a few, more or less, perpendicular short branches. *Context* monomitic of thin-walled, hyaline or slightly yellowish,

smooth to sparsely encrusted hyphae; subicular hyphae more or less closely packed. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Saprotrophic, presumably lignicolous, no substrate indicated in original description.

Distribution: Known only from South America (Argentina).

A genus based on a rather distinct crust-fungus and separated from other members of the Coniophoraceae by the ornamented, inamyloid basidiospores. The hilar appendage and apical pore are very difficult to discern, unlike in *Coniophora*, and the dendrophysoidal hyphae are more prominent and the distribution of clamp-connections in the tissue different. See original publication for full description.

Line-drawings of basidia, spores and hyphoids accompany the type description.

CORDITUBERA Henn. in Engl., Bot. Jahrb. **23**: 557, 1897. Plate 5 F.

Type species (only original species): *Corditubera staudtii* Henn.

Basidiome gasterocarpic, hypogeous, subglobose to irregularly elongate, rather smooth, few inconspicuous, adpressed rhizomorphs attached.

Peridium thick but soon reduced in drying, brown ochraceous, whitish in inner layer. *Gleba* black, compact, traversed by white veins. *Odour* weak; *taste* agreeable, slightly farinaceous.

Basidia ephemeral, not recorded. *Basidiospores* globose, brown, ornamented with delicate conical warts > 0.5 µm high, inamyloid, acyanophilic. *Cytstidia* absent. *Clamp-connections* not seen.

Chemistry: With phenol and phenolic reagents and ammonia no colour change; aq. potash solutions produces browning of inner peridium and olivaceous tints in outer layer.

Ecology: Terrestrial in the ground, possibly ectomycorrhizal.

Distribution: Known from tropical Africa, temperate north Europe and N. America; but see notes below.

A small genus of at least 5 taxa of which the type specimen *C. staudtii* has not been located; there is evidence for other species in rainforest communities in West Africa. A new species described by Dring & Demoulin is placed in this genus as the authors consider the characters are clear enough to assign it therein. The genus has been placed in proximity to *Melanogaster q.v.* but its characters fall closer to that of *Scleroderma q.v.*; if an intermediary genus was sought then this might be it, but molecular studies have always demonstrated these so-called intermediates are often in the imagination of the mycologists. One species, however, *C. bovonei*, was initially described as *Scleroderma* (*S. bovonei* Matt.). Although Guzmán rejected the fungus in his monograph of that genus, Dissing & Lange in *Flore Iconographie des Champignons du Congo* **13**, 1964) used the name for a collection from the Congo.

The African species have been discussed in Demoulin & Dring (Bull. Jard. Bot. Nat. Belg. **45**, 345, 1975) and line-drawings of the spores are included. However, Malençon (Crypt. Mycol. **4**: 1, 1983) described 2 new species from France,

viz. *C. gallicia* Malençon & *C. romagnesii* Malençon and emended the genus to include some species of *Leucophlebs* Harkness. The latter genus had already been monographed by Fogel (Canadian Journal of Botany **57**: 1718-1728, 1979) and considered a close relative of *Leucogaster*; photo-, transmission and scanning electron micrographs are supplied by Fogel. Also Malençon considered that *Cremeogaster* Mattiriolo was close to *Leucophlebs* and included it as a synonym of *Corditubera*. *Leucophleps* is now thought to be closely related not to the boletes but to the stipitate polypore *Albatrellus*; see Albee-Scott in Mycol. Research **111**, 2007. This may explain the uneasy position *Corditubera* formerly held within the Boletales, a placement probably based purely on its former link with *Scleroderma*.

CORNEROMYCES Ginns in Mycologia **68**: 970, 1976. Plate 6 A.

Type species (only original species): *Corneromyces kinabali* Ginns

Basidiome resupinate crust, effused, separable, firm, brittle, relatively thick, attached to strands that permeate substrate.

Hymenium snuff-brown, amber to grey-brown, smooth, shiny and soft to touch when young, velvety to the eye, then mealy to granulose, margin pale brown, tomentose, abrupt with prominent whitish to brownish strands. eventually with scattered to crowded, fine sterile hair-like processes. *Context* when fresh brownish umber, drying dull brown, darker than hymenium, coarsely granulose and appearing stratified in section from hymenial thickening.

Basidia clavate with narrow pedicel, hyaline, (2-) 4-spored. *Basidiospores* narrowly ellipsoid, straight in face-view, nearly cylindric, in profile similar with adaxial surface slightly flattened and with indistinct depression about narrow, small hilar appendage, smooth, thick-walled, hyaline at first then brownish, amyloid, cyanophilic. *Cystidia* absent but aborted and old slightly thick-walled, brown basidia embedded in thickened hymenium and projecting hair-like processes of loosely woven, with often irregular, hyaline- to brown-walled, encrusted hyphae interspersed with crystalline material present. *Context* of generative often branched hyphae some hyaline and thin-walled but mostly brown and rather thick-walled. *Clamp-connections* present.

Ecology: Saprotrophic, lignicolous, on fallen branches in rain forest.

Distribution: Known only from Malaysia (Sabah).

A genus related to *Coniophora* but differs in the spore characters, hair-like processes in the mature basidiome, shape of the basidia and simple clamp-connections. Julich (Persoonia **10:** 335-336, 1979) placed this genus in a new family Corneromycetaceae.

Excellent line-drawings of the microscopic characters accompany the type description.

***CYSTOGOMPHUS** Singer, Ann. Mycol. **40**: 51, 1942. Plate 6 B.

Type species (only original species): *Gomphidius tomentosus* Murrill sensu Humblot (=*Cystogomphus humblotii* Singer).

Basidiomes epigeal, pileate, hymenophore lamellate, centrally stipitate with veil composed of sphaerocysts, putrescent, velangiocarpic. *Spore print* blackish.

Pileus almost globose with incurved margin then convex, slightly flattened, cream-orange covered in cinnabar-red, granular veil, which forms small scales especially in centre of pileus, margin appendiculate. *Stipe* tapered downwards, concolorous with pileus, with distinct annulus, ornamented below with small scales as on pileus, smooth above, becoming cinnabar-red, mottled with black from spores. *Gills* decurrent, purple then blackish with white margins, broadly spaced. *Context* white in pileus blackening in stipe. *Odour* slightly of anise; *taste* mild.

Basidia clavate, 4-spored. *Basidiospores* ellipsoid-fusiform with hilar depression, apiculate but without pore, thick-walled, black. *Cheilocystidia* in clusters at margin, hyaline, non-encrusted, pyriform; *pleurocystidia* enormous, cylindric-stipitate, slightly encrusted towards apex. *Pileipellis* of rounded cells with rosaceous membrane. *Hymenophoral trama* divergent with broad hyphae at first compacted, then becoming floccose.

Chemistry: Not known; spore reactions unknown.

Ecology: Probably ectomycorrhizal with *Picea*.

Distribution: Known only from Europe (France); in plantations of exotic conifers

about Paris at the turn of the 20th century; otherwise unknown.

This genus is based on *Gomphidius tomentosus* Murrill as described by Humblot (Bull. Soc. Fr. Mycol. **42**: 75, 1926); it has not been re-found. *G. tomentosus (=Chroogomphus)* is well-known in North Western America and is very different from Humblot's interpretation; this led Singer to erect a new species and genus, based on the unusual veil composed of sphaerocysts. Fresh collections are urgently required for a re-evaluation. The genus is placed in the Gomphidiaceae.

An excellent colour illustration of this very distinctive agaric accompanies the original publication as *G. tomentosus* and a description with line-drawings of the type collection appears in Horak Beitrage Krypt. Schweiz **13**, 1968.

***DIPLOCYSTIS** Berk., J. Linn Soc. Botany **10(46)**, 344, 1868. Plate 6 C.

Type species (only original species): *Diplocystis wrightii* Berk. & Curtis apud Berk.

Basidiome epigeal, gasterocarpic, small, crowded together in large numbers on a common, fairly firm stroma c.1-2mm thick which superficially covers substratum; individual basidiomes touching each other or scattered here and there as much as 4mm apart, individual gasterocarps angiocarpic.

Peridium at maturity flattened, becoming pale and cracking into pieces which fall away; multi-structured. *Endoperidium* pale brown, thin, pliable, opening by small apical pore, collapsing gradually as yellowish brown spore-mass is revealed, finally on spore-dispersal leaving a firm deep brown, leathery sided cup only slightly lower than the original rounded structure.

Basidia ephemeral, not recorded. *Basidiospores* yellowish brown, globose, minutely warted, quite small, sometimes with hilar appendage visible. *Capillitium* very scarce, pale, thread-like, with long or fragmented, branching, interspersed with encrusted, thick-walled hyphae with narrow lumen and usually surrounded by collapsed hyphae.

Chemistry: not known; spore reactions not recorded.

Developmental studies: see Kriesel (Feddes Rep. **85**: 1974).

Ecology: probably ectomycorrhizal, on bare earth on hillsides or margins of ditches close to woodland. Potential hosts include *Coccoloba uvifera, Pinus cubensis, Neea buxifolia* & *Pisonia* (Louzan *et al*., Mycoscience **48**, 2007).

Distribution: Known only from the Caribbean (Cuba, Puerto Rico, American & British Virgin Islands, Guadeloupe), Bahamas and Central America (Mexico).

A currently monotypic genus resembling *Broomeia* (Broomieaceae: Lycoperdales) to which it has been frequently referred. *Broomeia,* however, is separated by the presence of a universal veil covering the crowded groups of small peridia, which are seated on a more or less elevated common base. Until fairly recently only known from early collections but Kriesel (Feddes Rep. **85** 1974) has examined many collections and described the anatomy and development. This genus is placed in its own family, the Diplocysticaeae in the sclerodermatoid fungi; see Watling, Mycoscience **47**: 25-35, 2006, a position confirmed by recent molecular studies by Louzan *et al*., 2007.

Good descriptive information supported by line-drawings and map of distribution have now been provided by Kriesel. B/w illustrations are found in Coker & Couch (*The Gasteromycetes of the Eastern United States and Canada*, 1928) and in Lloyd's Mycol. Notes 1 Plate 15; line-drawings are presented in the former and b/w photographs in the latter although the photomicrographs are of poor quality.

FISTULINELLA Henn. in Engl Bot. Jahrb. **30**: 43, 1901. Plate 10 E.

Type species (only original species): *Fistulinella staudtii* Henn.

Basidiome epigeal, pileate, hymenophore pinkish, tubulate, centrally stipitate, putrescent, probably gymnocarpic. *Spore print* light russet brown to ferrugineous.

Pileus convex then plano-convex when expanded, smooth at first or slightly innately and minutely fibrillose, sometimes scrobiculate, viscid or gelatinous, ranging from pale brown and buff to snuff- and tobacco-brown, often with purplish hue. *Stipe* cylindric, equal or tapering upwards, glabrous to subglabrous to finely pruinose, exannulate. *Tubes* & *pores* sordid greyish then with pinkish tints at maturity. *Context* whitish unchanging. *Odour* & *taste* not distinctive.

Basidia hyaline, clavate, 4-spored. *Basidiospores* dull honey-coloured or pinkish straw-colour, elongate-subfusiform or tapered to apex, smooth or with slight disruption at apex to form a thinning, with suprahilar depression, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* scattered, when present equal, subclavate to clavate, thin-walled, hyaline. *Tube trama* bilateral, divergent with well-developed central zone of slightly darker hyphae. *Pileipellis* an interwoven ixotrichodermium of gelatinised, hyaline hyphae, becoming more repent with age, with or without accumulation of gel, terminal cells poorly differentiated, slightly enlarged, obtuse, hyaline in aq. ammoniacal solutions, yellowish in ME. *Clamp-connections* not seen.

Chemistry: Not known.
Ecology: Terrestrial, apparently ectomycorrhizal with Pinaceae and Fagales.

Distribution: A small genus in the more southern states of North America and in Australia, New Zealand, South America (Venezuela) and Central America (Mexico).

This genus is synonymised with *Mucilopilus* Wolfe which is based on *Porphyrellus* sect. *Pseudotylopili* McNabb, and introduced for a group of New Zealand boletes because no specimen of the type, *viz. F. staudtii* Henn., 1901 was thought then to exist. However, Singer (Persoonia **7**, 1973) found the type and commented on its characteristics. This same genus has been synonymised with the African *Ixechinus* R. Heim, *q.v.* which Wolfe, with good supporting evidence, maintains as a separate entity. In molecular studies the type species is linked to *Retiboletus q.v.* Type-studies by Wolfe (1979) showed that the New Zealand taxa were related to the N. American *Boletus conicus* Ravenel apud Berk. & Curtis and subsequently expanded Mc Nabb's original concept. *B. conicus* was first separated by Singer as *Tylopilus* Sect. *Scrobiculati* (Amer. Midl. Nat., **37**, 1947) and later by the same author (Agaricales in Modern Taxonomy, 1975) as *Porphyrellus* Sect. *Scrobiculati*. Clearly a distinction was seen but not considered significant. Wolfe (Mycotaxon **10**,1979) has produced a well-argued case for the erection of this genus (ut *Mucilopilus*) and provides a key to the main species. The known species are listed by Singer (1986), although no formal monographic treatment is available. Guzmán (Bol. Soc. Mex. Micol. **8**, 1974), has provided a map of the world distribution. Descriptive data supported by line-drawings appear in Wolfe (1979). Colour illustrations of *Fistulinella mollis* R.Watl. appear in Bougher & Syme, *Fungi of Southern Australia*, 1998. Singer *et al*. (Beih. Nova Hedw. 77, 1983) supply keys and scant line-drawings to neotropical species under *Fistulinella*.

Synonym:
Mucilopilus Wolfe, Mycotaxon **10**: 117, 1979. For typification see above.
Gastrotylopilus T.-H. Li & R.Watl. in Edinburgh J. Bot. 56: 144, 1999. This genus is based on *G. brunneus* T.-H Li & R.Watl., which was later found to be purely a secotioid form of *Fistulinella mollis* R.Watl. (=*Mucilopilus*); see Trappe, Watling, Cázares & Claridge, Muelleria **18**, 2003.

GASTROBOLETUS Lohwag ex Kreisel & Lohwag in Handel-Mazetti Symb. Sinicae **2**: 54, 1937. Plate 6 D.

Type species (only original species): *Gastroboletus boedijnii* Lohwag

Basidiome epigeal-subepigeal, pileate, hymenophore tubulate-lacunose with lower part exposed - sequestrate, centrally to excentrically stipitate, putrescent, hemiangiocarpic.

Pileus convex but hardly expanding and margin often quite tightly adhering to stipe even at maturity, various shades of brown, velvety or subtomentose then smooth and soon becoming slightly to distinctly areolate. *Stipe* generally short, often tapered to a turnip-like base partially buried in litter and soil and extending into distinct columella upwards. *Hymenphore* free or less frequently broadly attached to columella, dirty yellowish to olivaceous; *pores* where present either yellow-orange or rich reddish, not vertically arranged but curved away from stipe, sometimes rather congested by the poorly to non-expanding pileus.

Basidia vesiculose-pedicellate to clavate, often voluminous, hyaline or yellowish, especially in aq. alkaline solutions, 1- or 2-spored or 1-, 2-, 3- or 4 spored, with prominent sterigmata. *Basidiospores* extremely variable, mostly fusoid cylindric to amygdaliform, with distinct suprahilar depression, pale honey-colour or brown, smooth, heterotropic with small hilar appendage, rather thick-walled, inamyloid, acyanophilic. *Basidioles* present, variable in size and shape. *Cheilocystidia* ventricose to mucronate, even ampullaceous, scattered, hyaline or yellowish with obtuse apex; *pleurocystidia* ventricose, seen only in recently formed chambers. *Tube trama* bilateral, divergent from a central zone. *Clamp-connections* not seen.

Chemistry: Not studied extensively. Xerocomic and variegatic acids have been isolated.

Ecology: Ectomycorrhizal; North American species appear to be associated with Pinaceae.
Distribution: Known from North and South America, Africa and from China; there does not appear to be any overlap in the species distribution.

Thiers (Mem. New York bot. Gdn. **49**, 1898) recognized 3 sections for the members of this genus. Sect. *Gastroboletelloides* for *G. fascifer* Singer & A.H.Sm. from Africa, because of its superficial resemblance to *Boletellus q.v.*; *Gastrosubtomentosi* for *Boletus turbinatus* Snell (=*G. turbinatus* (Snell) A.H. Sm. & Singer), *G. xerocomoides* Thiers & Trappe*, G. amyloideus* Thiers & allies with affinities to be sought amongst the xerocomoid boletes and the type section for *G. boedijni* and *G. subalpinus* Thiers, associated with *Boletus* Sect. *Boletus*. Two other groupings were recognized by Thiers as distinct but at generic level both based on previously described species of *Gastroboletus, i.e. Gastroleccinum q.v.* & *Gastrosuillus q.v. G. xerocomoides* has spores with thickened apical wall and so resembles *Boletus truncatus* Singer, Snell & E.A. Dick and *B. porosporus* Imler ex Redheuilh, suggesting a better assignment with some xerocomoid boletes.

The genus is probably artificial containing species of very mixed affinity drawn together by the fact that, although boletoid in pileus, stipe and hymenophore features, the tubes are not positively geotropic, which leads to a curvature covered or not by part of the pileal structure. The basidiospores are statismosporic and thus are supposedly non-ballistosporic, explaining why a spore print cannot be obtained. This has led to speculation that they are gasteroid relatives of the boletoid fungi and form a link between them and genera such as *Truncocolumella q.v.* currently housed in the Rhizopogonaceae and *Chamonixia q.v.* which Watling (Mycoscience **47**, 2006) referred to the sclerodermatoid fungi. The type species and its close relatives, *e.g. G. turbinatus* and *G. valdivianus* Horak are little more than sequestrate species within the wide concept of the genus *Boletus.* Both species have been studied by Pegler & Young (1981) and these authors have shown that the basidiospores in both taxa are ballistosporic and exhibit a small hilum subterminally placed on the hilar apex; there is also some evidence of adaxial applanation. Within the genus red-pored taxa and yellow-pored taxa are found, agreeing with sections within *Boletus*; see Watling (From Infancy to Maturity; Trans. & Proc. Bot. Soc. Edinb. **42** (Suppl.: 61-74, 1975). It is suggested that the genus cannot be upheld, indeed Pegler & Young transferred the African *G. fascifer* to a position close to the xerocomoid *Tuboseta, q.v.* and suggested a similar treatment for *G. xerocomoides*, which, as noted above, has a basidiospore with a thickened apex. Molecular work has demonstrated that *G. turbinatus* sits with members of *Boletus* Sect. *Luridellus*, such as *B. luridiformis* Rostk. (= *B. erythropus* Pers. s. auct.).

Sequestrate leccinoid boletes (=*Gastroleccinum*; see below) differ in the possession of scabrosities on the stipe and a pale, tubulate-loculate hymenium. Those parallel taxa with highly gelatinized pileipellis and fascicles of pleurocystidia are related to the suilloid fungi (=*Gastrosuillus*). *Gastrotylopilus* T. H. Li & Watling (type species *G. brunneus* T.-H. Li & R.Watl. from Victoria, Australia) houses pink-spored boletes with the same non-geotropically positioned hymenophore, although the type species has been found to have, like *G. fascifer*, symmetrically positioned spores, and has been demonstarted to be a syunonym of *Fistulinella mollis* R.Watl.. There is little doubt that even the core species of *Gastroboletus*, *i.e.* those exhibiting symmetrically placed spores, will ultimately be redistributed within the sections of the geotropically spored, classical boletoid genus. That intermediaries exist is demonstrated by *Tylopilus humilis* Thiers, which although giving a spore print, has the hymenium covered by the pileal cuticle and the basidiome often remains underground and could be equated with *Gastrotylopilus*. In a rather similar situation, *Suillus riparius* Thiers has labyrinthine pores, excentric stipe and variable pileus-expansion and equates with *Gastrosuillus.* The genus *Gastroboletus*, although covering a range of species-associations, can at present only be housed in the Boletaceae as presently conceived.

Re-examination of type material supported by line-drawings of microscopic characters and proposed circumscription of the genus is found in Smith A.H. & Singer, R. (Brittonia **11**: 205-233, 1959). Thiers & Trappe (Brittonia **21**: 244-254, 1969) and Thiers (Mem. New York Bot. Gdn **49**: 355-359, 1989) give keys, descriptions of species and b/w photographs of selected taxa.

Coloured microfiche of *G. subalpinus* Trappe & Thiers & *G. turbinatus* appear in Thiers (*California Mushrooms: a field guide to the boletes*, 1975). Coloured photographs of *G. citrinobrunneus* Theirs, *G. ruber* (Zeller) Cazares & Trappe, *G. subalpinus*, *G. turbinatus* (2 varieties) and *G. xerocmoides* appear in Bessette, Roody & Bessette *North American Boletes*, 2000.

GASTROLECCINUM Thiers, Mem. New York Bot. Gdn. **49**: 357, 1989. Plate 7 A.

Type species (only original species): *Gastroboletus scabrosus* Mazzer & A.H. Sm. (= *Gastroleccinum scabrosum* (Mazzer & A.H.Sm) Thiers)

Basidiome epigeal to subhypogeal, pileate, centrally stipitate, hymenophore tubulate-loculate - sequestrate, putrescent. Generic description as in *Leccinum q.v.,*

stipe scabrosities numerous, darkening, but spores not producing spore-print, tubes enclosed at maturity and not vertically disposed, hemiangiocarpic.

Pileus convex, broad convex at maturity, dry, unpolished or slightly tomentose, dingy yellow-brown with ochraceous tinges, slightly paler at margin. *Stipe* equal but for tapering base, yellow above, dull yellow-brown downwards, faintly striate to subreticulate, from fine, scurvy, yellow-brown then orange-brown, scabrosities enlarging downwards. *Tubes* flared to become almost horizontal; *pores* curved away from stipe, small, dull lemon-yellow becoming dingy olivaceous yellow and darkening when bruised. *Context* pale buff in pileus gradually and slowly becoming pinkish buff, mottled slightly olivaceous in places, pallid yellow in stipe and darkening to brownish where damaged.

Basidia hyaline, 4-spored. *Basidiospores* subfusiform, thin-walled, pale brown in aq. alkaline solutions, similar to those of *Leccinellum pseudoscabrum* (Kallenb.)Sŭtara, inamyloid, acaynophilic. *Pleurocystidia* fusoid-ventricose, thin-walled, hyaline; *cheilocystidia* similar. *Tube trama* bilateral with distinct, subgelatinous, hyaline, medial stratum. *Pileipellis* a trichoderm of loosely woven, septate, pale brown hyphae with slightly swollen end-cells. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: probably ectomycorrhizal with *Quercus* in oak-hickory forest

Distribution: North America (Michigan).

A currently monotypic genus undoubtedly closely related to members of *Leccinellum* q.v. where this species may finally rest. It was first described in *Gastroboletus*, where all gasterocarpic boletes were originally placed. Being present when the collection was made, the author has no doubts that this is a sequestrate member of *Leccinum* as then conceived, viz. Smith, Thiers & Watling, (Mich. Botanist **6(3A)**, 1967) – before the yellow-pored taxa had been assigned to *Leccinellum*. The genus should be placed in the Boletaceae. See discussion under *Gastroboletus.*

B/w photograph and line-drawings of microscopic features appear in the original publication.

GASTROSUILLUS Thiers, Mem. New York Bot. Gdn. **49**; 357, 1989. Plate 7 B.

Type species (designated): *Gastroboletus suilloides* Thiers (= *Gastrosuillus suilloides* (Thiers) Thiers)

Basidiome epigeal or subepigeal, pileate, centrally stipitate, as in *Suillus* but spores not forcibly ejected, hymenophore not vertically orientated and gleba not generally exposed, sequestrate, putrescent, hemiangiocarpic.

Pileus not fully expanding, margin clasping the stipe at maturity. *Stipe* ornamented with glandulae. *Gleba* tubulate-loculate, white or honey-coloured or slightly darker, not orientated vertically, with concolorous or paler pores with slight development of glandulae at margins.

Basidia clavate to subclavate or subcylindric, hyaline, 4-spored. *Basidiospores* smooth, brown, subellipsoid to subcylindrical as in *Suillus*, inamyloid, acyanophilic. *Cheilo- & pleurocystidia* in fascicles which darken in aq. alkaline solutions.

Chemistry: No widespread chemical analysis conducted. Grevillin-B has been isolated from *G. laricinus.*

Ecology: Terrestrial; ectomycorrhizal with Pinaceae.

Distribution: North America.

A small genus of 4 species, which undoubtedly will in the future be amalgamated into *Suillus* q.v., or a closely related genus. One species *G. laricinus* (Singer & Both) Thiers has recently been shown by molecular studies to be a recent mutant form of the familiar and widespread *Suillus grevillei* (Klotzsch) Singer (see Baura *et al.,* Mycologia **84**: 592, 1992); Grevilin-B has been isolated as might be expected from this discovery. *Suillus riparius* Thiers, a true boletoid fungus has a hymenium which in some collections is exposed as normal whilst in other members of the population the stipe is excentric, pores are more labrynthinal and the pileal cuticle covers the hymenium hindering the development of the tubes. The genus should be linked to *Suillus* and placed in the Suillaceae. See discussion under *Gastroboletus*.

A key and illustrations of the species is given in Thiers (Mem. New York Bot. **49**: 358, 1989).

GOMPHIDIUS Fr. in Flor. Scan. 339, 1835. Plate 7 C.

Type species (selected): *Agaricus glutinosus* Schaeff. : Fr. (= *Gomphidius glutinosus* (Schaeff.: Fr.) Fr.)

Basidiome epigeal, pileate, centrally stipitate, hymenophore lamellate, decurrent often thick and waxy-gelatinous with obtuse edges, pinkish grey and pale coloured, glutinous, flesh inamyloid, stipitocarpic, putrescent, metavelangiocarpic. *Spore print* fuliginous to olivaceous black.

Pileus convex to umbonate, viscid to gelatinous, from pink or pale coloured to greys and then washed with lilaceous or purplish, often smeared with darker colours and some species blackening where handled. *Stipe* cylindric to subfusiform or swollen downwards, white pruinose at apex but glutinous slimy from 1/3rd down, paler than the pileus, darkening and spotting with age or becoming distinctly black, in some species with hint of bright yellow at stipe-base. *Gills* arcuate-decurrent, running down stipe-apex, waxy, gelatinous and with obtuse margins, often forked and interveined, in some species spotting and blackening or vinescent, commencing white then becoming olivaceous black at maturity. *Context* white in pileus. *Taste* and *odour* indistinct.

Basidia distinctly elongate-cylindric, thin-walled, hyaline, 4-spored. *Basidiospores* elongate, cylindric to fusiform with tapering obtuse or subacute apex, slightly flattened in side-view, smooth, with suprahilar depression, inamyloid, cyanophilic, greyish honey-colour in aq. ammoniacal solutions. *Cheilo-* & *pleurocystidia* long, prominent, scattered to numerous with thickened wall and often encrusted or with oily material adhering to outer wall. *Lamellar trama* divergent with narrow, central zone of hyaline, gelatinised hyphae slightly divergent in lateral strata becoming disrupted with age, thick, with dense layer below hymenium. *Pileipellis* an ixocutis composed of narrow, flexuous hyphae in gelatinous matrix overlaying denser layer of less differentiated, hyaline hyphae. *Veil* similar to the outer most layers of the pileipellis. *Clamp-connections* not seen or rare.

Chemistry: Flesh in stipe-base gives negative ME. Gomphidic, xerocomic, variegatic and atromentic acids have been isolated as have compounds close to the

boviquinones. For review see Besl & Bresinsky (Plant Syst Evol. **206**: 223-242, 1997).

Cytology: Ploidy level 2x in *G. subroseus* Kauffman *& G. glutinosus*, 4x in *G. maculatus* Fr. and 6x in *G. roseus* (Fr.) Fr. (Wittmann-Meixner, 1989).

Developmental studies: Basidiome-development in *Gomphidius glutinosus* and *G. roseus* have been studied by Reijnders (1948).

Ecology: Terrestrial; ectomycorrhizal with conifers; also closely associated with members of the genus *Suillus* in a hemiparasitic relationship where the rhizomorphs of each species intermingle, *e.g.* relationship between *Gomphidius roseus* and *Suillus bovinus*; see Olsson *et al*. (2000). See Agerer 58 *Gomphidius glutinosus* with *Picea abies* and *G. roseus*. See Agerer (1991) for ectomycorrhizal studies.

Distribution: Apparently native to north temperate coniferous zone and where exotics have been planted; introduced to the southern hemisphere *e.g.* New Zealand.

A small genus of 9 species naturally confined to northern forests of the New and Old World; see Miller (Mycologia **63**, 1971). Easily separated from *Chroogomphus q.v.*, with which it was originally united by the lack of amyloid material in the tissues. Indeed this is Singer's *Gomphidius* sect. *Gomphidius* and might be the correct name for *Chroogomphus*. See Donk (Bibliotheca Mycol. **5**: 113,1962) for discussion on typification of *Gomphidius*. *Gomphogaster q.v.* will probably be shown to be purely a sequestrate member of this genus. Both *Gomphogaster* and *Gomphidius* are placed in the Gomphidiaceae.

Synonyms:
Gymnogomphus Fayod in Ann. Sci. nat. (Bot.) VII, **9**: 3835, 1889 might cover one or other of the gomphidioid agarics but is a confused concept: see Singer, 1951.
Leucogomphidius Kotl. & Pouzar Ceská Mykol. 26,1972; based on *Gomphidius glutinosus* (Schaeff.: Fr.)Fr. See discussion under *Chorogomphus*.

A key to the species with line-drawings, photomicrographs and b/w photographs appear in Miller (Mycologia **63**: 1129-1163, 1971).

***GOMPHOGASTER** O. K. Miller, Mycologia **65**: 227,1973. Plate 7 D.

Type species (only original species): *Brauniellula leucosarx* A.H. Sm. & Sing. (= *Gomphogaster leucosarx* A.H. Sm. & Sing.) O.K. Miller)

Basidiome epigeal, pileate, convex depressed, irregularly shaped, centrally stipitate, hymenophore sublamellate to loculate and protected by the unopening pileus with margin adhering to stipe – sequestrate, putrescent, hemiangiocarpic.

Pileus solid, pale vinaceous white within, soon tinted vinaceous buff. *Gleba* of small chambers developing semi-lamellate pattern, drab-grey, free from columella except at apex of peridium. *Stipe-columella* solid, percurrent, dull white, lemon-yellow at base. *Context* white in stipe and pileus but becoming tinged vinaceous buff, yellow at base.

Basidia clavate, 2-4 spored. *Basidiospores* ellipsoid in face-view, smooth, wall slightly thickened, smoky brown. *Cystidia* clavate to fusoid ventricose with thin or slightly thickened wall. *Trama* of peridial context and tramal plates of thin-walled, non-amyloid hyphae. *Clamp-connections* not seen.

Chemistry: ME negative on flesh at stipe-base. Spore reactions not recorded.

Ecology: Terrestrial; ectomycorrhizal with Pinaceae.

Distribution: Known only from North America (Idaho).

The single species in this genus probably will be accommodated in the future in *Gomphidius q.v.* after molecular analysis. It differs from *Gomphidius* only in the sequestrate characteristics. Recognized by Singer & Smith (Mycologia **50**: 927-938, 1958) as a separate section within their *Brauniellula q.v.*, a genus related to the agaricoid *Chroogomphus* but distinguished by lack of coloured pileus flesh and lack of amyloid flesh reaction. It was erected as a distinct genus by Miller (1973) and placed in close proximity to *Gomphidius* and not *Chroogomphus*.

Line-drawings of the type species accompany the original.

***GYMNOPAXILLUS** Horak apud Horak & M.M. Moser, Nova Hedwigia **10**: 335, 1966 Plate 7 E.

Type species (only original species): *Gymnopaxillus morchelliformis* Horak

Basidiome epigeal, rarely subhypogeous, ovate-conic to irregularly globose, pileate with contorted-gyrose hymenophore – sequestrate, centrally stipitate, putrescent, apparently almost angiocarpic.

Pileus lacking, replaced by exposed brain-like undulating, cavernous inner structures. *Stipe* diminutive, cylindrical, attenuated downwards, almost rooting, yellow or ochraceous brown, extending into ramose, dendriform, solid-spongy then hollow columella. *Gleba* morchelliform, yellowish to ferrugineous brown. *Context* spongy-watery, pale coloured; *odour* of scorched horn in type species.

Basidia elongate-clavate, hyaline, 4-spored. *Basidiospores* inequilaterally elliposid to subfusoid, smooth, lacking germ-pore, yellow-brown, inamyloid, prob. acyanophilic. *Cheilo- and pleurocystidia* apparently absent. *Tramal hyphae* filamentous, slender, smooth. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Probably ectomycorrhizal with *Nothofagus* and Myrtaceae.

Distribution: Known from South America (Argentina & Chile) and Australia.

A genus related, as the generic name implies, to the lamellate paxilloid fungi, but in fact more related to *Austropaxillus q.v.* (Austropaxillaceae) than *Paxillus q.v.* (Paxillaceae). Horak places this genus with *Austrogaster, Paxillogaster* and *Singeromyces* in the subfamily Paxillogastroideae, but this may be dismembered when molecular studies are undertaken.

Reference should be made to the original publication for line-drawings of habit and microscopic characters and a description of the species in the genus. Discussion, b/w photographs of basidiomes and micrographs of Australian species and key to species appear in Claridge *et al*., Aust. Syst. Bot. **14**, 2005.

GYRODON Opat. in Comm. Hist. Nat. fam. Fung. Bolet. in Weigmann's Archiv **2**: 5, 1836. Plate 8 A.

Type species (selected): *Boletus sistotrema* Fr. (= *B. sistotremoides* Fr. = *B. lividus* Bull.: Fr. = *Gyrdon lividus* (Bull.: Fr.) Opat.)
Basidiome pileate with shallow tubulate hymenophore, centrally or slightly excentrically stipitate, stipitocarpic with rather tough consistency, gymnocarpic. *Spore print* bronze-colour.

Pileus minutely tomentose but soon glabrous and often slightly viscid in damp weather, otherwise villose, dull coloured in shades of pale to dark brown, with or without ochraceous tints. *Stipe* evelate, central or slightly excentric, equal or slightly swollen downwards and frequently several stipes joined together, concolorous with pileus or paler, brown-vinaceous when excessively handled, smooth or minutely furfuraceous. *Tubes* arcuate-decurrent, pale sulphur-yellow when young then darkening to become olivaceous or with tinge of fulvous, greenish grey when bruised then fading to dirty brown; *pores* concolorous, irregularly arranged, almost subradial, rather elongate towards stipe-apex. *Context* pale lemon-yellow in pileus, sienna or rust-colour towards stipe-base, cyanescent especially above tubes and at stipe-apex. *Odour* slightly acidulous; *taste* indistinct or slightly nutty.

Basidia elongate-clavate, hyaline or yellowish especially in aq. ammoniacal solutions, 2- or 4-spored. *Basidiospores* ellipsoid to broadly ellipsoid in face- and side-views, adaxially applanate, smooth, straw-colour to olivaceous especially in aq. ammoniacal solutions, inamyloid, acyanophilic. *Cheilo- and pleurocystidia* fusiform to cylindrical, irregular in distribution and number, scattered and often infrequent at orifices. *Pileipellis* of suberect, filamentous, hyaline or yellowish hyphae soon collapsing to form irregular cutis with some darker amorphous material scattered amongst filaments. *Tube trama* regular at first then disorganized but showing some development of lateral strata, hyaline or slightly yellowish and becoming gelatinised. *Clamp-connections* present.

Chemistry: Xerocomic and variegatic acids isolated as well as the cyclopentenone chamonixin.

Developmental studies: Kühner's 1926 studies on *Gyrodon lividus* have been repeated by Reijnders (1963).

Ecology: Associated in temperate areas with *Alnus*; putative hosts of tropical

species not ascertained. See Agerer 76 *Gyrodon lividus*.

Distribution: North temperate hemisphere (Europe and eastern Asia) and from the African and SE Asian tropics; single site in N. America (California).

As presently conceived this very small genus of a handful of taxa is restricted to the type species and close relatives. It has been enlarged to include a morphologically similar but unrelated consortium of boletes centred around *Daedalea merulioides* Schwein. This is now placed in the genus *Boletinellus* q.v., a concept confirmed by molecular work. *Gyrodon* is placed along with the lamellate *Paxillus* in the Paxillaceae. With *Boletus lividus* (Bull. : Fr.) as its type *Uloporus* is a direct synonym, although it has been used even by the present author to house the type of *Gyrodon*.

Good descriptions of *G. lividus* can be found in regional studies often accompanied by colour illustrations, *e.g.* Singer in Die Pilze Mitteleuropas V: Die Röhrlinge 1, 1965; Alessio Fungi Europaei: *Boletus* Dill. ex L.,1985. See general references.

Synonyms:
Gilbertina R. Heim, Rev. Mycol. **31**: 151, 1966 based on *Campbellia aricana* – misspelling for *C. africana* Cooke & Mass. Considered the same as *Gyrodon* by Pegler & Young, Trans. (Brit. Mycol. Soc. **76**: 109, 1981) but see under *Boletinellus* above.
Uloporus Quél. in Ench. Fung. 162, 1886; type species *Gyrodon lividus* (Bull. : Fr.) Sacc. This is now considered an unnecessary replacement name for *Gyrodon* Opat., but when Quélet introduced the substitute for *Gyrodon* there was confusion in the interpretation of the name *Gyrodon*.

Developmental studies: Kühner's 1926 studies on *Gyrodon lividus* have been repeated by Reijnders (1963).

Ecology: Associated in temperate areas with *Alnus*; putative hosts of tropical species not ascertained. See Agerer 76 *Gyrodon lividus*.

Distribution: North temperate hemisphere (Europe and eastern Asia) and from the African and SE Asian tropics; single site in N. America (California).

As presently conceived this very small genus of a handful of taxa is restricted to the type species and close relatives. It has been enlarged to include a morpho-

logically similar but unrelated consortium of boletes centred around *Daedalea merulioides* Schwein. This is now placed in the genus *Boletinellus* q.v., a concept confirmed by molecular work. *Gyrodon* is placed along with the lamellate *Paxillus* in the Paxillaceae. With *Boletus lividus* (Bull. : Fr.) as its type *Uloporus* is a direct synonym, although it has been used even by the present author to house the type of *Gyrodon*.

Good descriptions of *G. lividus* can be found in regional studies often accompanied by colour illustrations, *e.g.* Singer in Die Pilze Mitteleuropas V: Die Röhrlinge 1, 1965; Alessio Fungi Europaei: *Boletus* Dill. ex L.,1985. See general references.

Synonyms:
Gilbertina R. Heim, Rev. Mycol. **31**: 151, 1966 based on *Campbellia aricana* – misspelling for *C. africana* Cooke & Mass. Considered the same as *Gyrodon* by Pegler & Young, Trans. (Brit. Mycol. Soc. **76**: 109, 1981) but see under *Boletinellus* above.
Uloporus Quél. in Ench. Fung. 162, 1886; type species *Gyrodon lividus* (Bull. :

Fr.) Sacc. This is now considered an unnecessary replacement name for *Gyrodon* Opat., but when Quélet introduced the substitute for *Gyrodon* there was confusion in the interpretation of the name *Gyrodon*.

GYRODONTIUM Pat. in Essai taxon. Hymen. 117, 1900. Plate 8 C.

Type species (selected): *Hydnum henningsii* Bres. (= *Gyrodontium henningsii* (Bres.) Pat.. Genus introduced with two species of which *G. versicolor* (Berk. & Br.) Maas Geest.) was selected by W. B.Cooke applying the first species rule, 1953, although either of the species cited by Patouillard are eligible.

Basidiome sessile or effuso-reflexed to mostly frequently imbricate brackets, sometimes solitary, or uncommonly entirely resupinate, hymenophore toothed. *Spore-print* fuscous olivaceous.

Pileus > 12cm - 21cm wide, often small, cottony, subfloccose to nearly smooth, pale yellowish white to clear primrose yellow, with obtuse then subacute, white, entire margin. *Hymenium* of crowded, discrete, conical or subacute to obtuse, even subtruncate, often angular, spines or somewhat rugulose, waxy, brittle, yellow then fuscous olive or olivaceous cinnamon. *Context* thick at base of pileus,

soft spongy, floccose, not gelatinised, pale to strong yellow. *Odour* aromatic, resembling caramel, slightly pungent.

Basidia 4-spored. *Basidiospores* ellipsoid, obtuse, smooth, with narrow, mucilaginous sheath, inamyloid. *Cystidia* absent. *Hyphal structure* monomitic, composed of scarcely or non-inflating, long-celled, thin-walled, flexuous hyphae without intermixed oleiferous hyphae; tramal hyphae longitudinally arranged, gelatinised. *Clamp–connections* not seen.

Chemistry: Not known. Spore reactions not recorded.

Ecology: On dead standing or fallen trees, bamboos, palms in both primary and secondary tropical forest systems.

Pathology: Ikeda *et al*. (Nihon Korkyuki Gakkai Zasshi, 2002) have reported a case of hypersensitivity pneumonia caused by *G. versicolor*.

Distribution: Known from Asia (Singapore and Malaysia) and Africa.

In his treatment of the genus Geesteranus (Persoonia **3**: 187, 1964) considered it to be based on a single taxon or at most two species *viz. G. versicolor*. Recent work suggests the genus, although still small, may contain about five taxa; see Gilbertson & Hemmes, 1997.

A good description of the type is provided by Corner (Garden's Bull. Singapore **25:** 367,1971), under the name *Merulius versicolor* (Berk. & Br.) Corner. This same author retains *Merulius* for species currently placed in *Serpula*. Full discussion of the genus with line-drawings appears in Maas Geesteranus; see above. B/w illustrations of microscopic characters of the W. African *G. boveanum* (Mont. Ex DC.) Maas Geest. are given by Douanla-Meli (Biblio. Mycol. **202**, 2007).

Synonym:
Boninohydnum S. Ito & S. Imai, Trans. Sapporo nat. Hist. Soc. **16**: 127, 1940; it is based on *B. pini* S. Ito & S. Imai.

GYROPORUS Quél. in Enchiridion Fungorum 161, 1886. Plate 8 B.

Type species (selected): *Boletus cyanescens* Bull. : Fr. (= *Gyroporus cyanescens* (Bull.: Fr) Quél.).

Basidiomes: epigeal, pileate, hymenophore tubulate, centrally stipitate with stuffed or hollowed centre, small to medium-sized, gymnocarpic, metavelangiocarpic or pileoangiocarpic, putrescent except for leathery stipe rind. *Spore-print* lemon-yellow.

Pileus convex then expanding, minutely to slightly velvety or floccose-scaly, often becoming slightly shaggy, rarely smooth, sometimes slightly tacky in wet weather. *Stipe* cylindrical or slightly attenuated upwards or swollen about the centre, villose-pruinose to minutely velvety becoming smooth and minutely radially cracked, stuffed at first then hollow. *Tubes* white to straw-colour then lemon-yellow, depressed around stipe-apex, quite long; *pores* minute to distinct, unequal to rounded, lemon-yellow, cyanescent or not. *Context* soft and spongy, denser in pileus and soon collapsing in the central parts of the stipe to form hollow tube stuffed with floccose 'pith', cyanescent or not.

Basidia clavate, hyaline, usually 4-spored. *Basidiospores* very pale yellow to straw-colour or subhyaline, distinctly shortly ellipsoid, adaxially applanate, rarely greater than 11µm long, smooth *s.m.* but denticulate beneath a mucilaginous sheath in electron micrographs, inamyloid, cyanophilic. *Cheilocystidia* lageniform to fusiform, hyaline, often infrequent; *pleurocystidia* scattered similar to those at orifice. *Tube trama* of gelatinised, hyaline to straw-coloured hyphae divergent from a darker central hyphal zone. *Pileipellis* a cutis of repent to ascendant, smooth or rough walled, elongate, sometimes shortened hyphae with cystidioid end-cells. *Stipitipellis* containing some horizontally arranged hyphae, sometimes predominantly so, amongst longitudinal hyphae of outer layers ('rind') and with strong demarcation from the inner zone; lacking differentiated caulohymenium or only scattered, differentiated cystidia present. *Clamp-connections* present.

Chemistry: No diagnostic chemical reactions, although flesh is cyanescent in some taxa; ME negative. Gyroporin and gyrocyanin, two cyclopentenones are described from *G. cyanescens.*

Developmental studies: Development of basidiomes of *Gyroporus cyanescens* has been studied by Reijnders (1963).

Ecology: Terrestrial, on ground in woods and copses; ectomycorrhizal or facultative associations with both conifers and angiosperms.

Distribution: Widely scattered throughout temperate and tropical areas; *G. cas-*

taneus (Bull.: Fr.) Quél. and *G. cyanescens* (Bull.: Fr.) Quél. are both distributed in several continents although future work may demonstrate cryptic speciation.

This is a small genus of about ten species, although there is evidence that several of the so-called widespread taxa are in fact species-complexes; see Watling (Mycoscience **47**: 18 – 24**,** 2006). The genus is placed in its own family, Gyroporaceae, which is less related to many of the familiar boletes than it is to the sclerodermatoid fungi.

The genus has not been monographed, although Heinemann & Rammeloo (Bull. Jard. Bot. Nat. Belg. **49**: 435-447, 1979) have examined in depth the *G. castaneus* complex. Descriptions and illustrations of individual species can be found in regional mycotas, e.g. Bessette, Roddy & Bessette, *North American boletes*, 2000; Heinemann, *Flore Iconographique des Champignons du Congo*, Part 3, 1954; Corner, *Boletus in Malaysia*, 1972 with key to 3 species; Imazeki *et al.*, *Fungi of Japan*, 1988 and several European texts listed in General References.

Synonyms:
Coleopus Bataille, Bull. Soc. Hist. Nat. Doubs **15**: 12, 1908; type species *Boletus cyanescens* Bull. : Fr. A synonym of *Gyroporus.*
Leucobolites Beck, Z. Pilzk **2**: 142, 1923; type species *Boletus castaneus* Bull.: Fr. (selected). The type is part of the genus *Gyroporus.*
Leucoconius (Reichert) ex Beck, Z. Pilzk. **2**: 146, 1923; type species *Boletus cyanescens* Bull.: Fr. This is a straight synonym of *Gyroporus.*
Suillus P. Karst., Bid. Karin Finl. Nat Folk **37(v)**: 1, 1882; type species *Boletus cyanescens* Bull.: Fr. Karsten's genus is a synonym of *Gyroporus*: see *Leucobolites* above. *Suillus q.v.* is presently used with a very different circumscription.

HEIMIOPORUS Horak, Sydowia, 56:237, 2004. Plate 8 D.

Type species (only original species): *Boletus retisporus* Pat. & Baker (=*Heimioporus retsiporus* (Pat. & Baker) Horak).

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, often quite massive in stature, putrescent, probably gymnocarpic. *Spore-print* olivaceous brown.

Pileus convex then expanding, dry or viscid, without appendiculate margin, in shades of brown or buff, crimson, magenta or purplish but infused with brown

with age. *Stipe* generally longer proportionally than the pileus, furfuraceous, squamulose or somewhat reticulate, lacking veil. *Tubes* deeply ventricose, yellow then olivaceous at maturity; *pores* relatively small, yellow or red. *Context* pallid to pale yellow, unchanging or cyanescent but never rufescent.

Basidia clavate to pyriform-clavate, hyaline, 2-4 spored. *Basidiospores* pale yellowish brown, ovoid to broadly ellipsoid, only slightly compressed in one view, with thin, hyaline myxosporium totally overlying reticulate exosporium, lacking adaxial patch, inamyloid, acyanophilic. *Cheilocystidia* absent or reduced to clavate cells resembling basidia; *pleurocystidia* subventricose to subcylindrical often with obtuse apex, rather sparse, hyaline, thin-walled. *Tube trama* with bilateral, hyphae divergent from a central strand. *Pileipellis* a trichoderm of inflated hyphal ends some almost forming moniliform chains. *Stipitipellis* of parallel filamentous hyphae giving rise to disrupted caulohymenium with subventricose to cylindric hyphae. *Clamp-connections* not seen.

Chemistry: No distinctive chemical reactions. Negative ME on stipe-base.

Cytology: Ploidy level 4x in *H. retisporus* (Bresinsky & Wittmann-Bresinsky, 1994).

Developmental studies: see Corner (1972) for *H. retisporus*.

Ecology: Terrestrial, ectomycorrhizal with Fagales and possibly Dipterocarpaceae.

Distribution: Only known from South East Asia.

A small genus of probably no more than fifteen species characterized under the microscope particularly by the distinctive spore-ornamentation. The genus is the same as *Boletellus* Sect. *Retispori* (Singer, Farlowia **2**, 1945); Corner indicates he thinks that the genus also should include Sect. *Allospori* (Singer, *ibid*), based on the N. American *Boletus betula* Schwein. The latter treatment is not supported by molecular studies. These same studies show that *Heimioporus* is distinct from *Boletellus* as generally conceived; see Pegler & Young (Trans. Brit. Mycol. Soc. 1981) under *Austroboletus q.v.*

Corner in *Boletus in Malaysia*, 1972 gives a key with line-drawings and colour illustrations to the Southeast Asian species.

HORAKIELLA Castellano & Trappe, Aust. Syst.. Bot. **5**: 641,1992. Table 8 E.

Type species (only original species): *Hydnangium clelandii* Rodway (= *Horakiella clelandii* (Rodway) Castellano & Trappe).

Basidiome gasterocarpic, hypogeous, subglobose to slightly irregular, brownish yellow, angiocarpic.

Peridium brownish yellow, tomentose with sulcate patches and/or encrusted with soil, one-layered, dirty pale yellow at first within, slowly staining reddish. *Columella* and sterile base absent. *Gleba* never exposed, solid, firm, dry, dark to blackish brown with white, pale yellow-white to pale brown tramal plates with irregular to isodiametric, persistent chambers completely filled with pale yellow spore-mass and some hyphae. *Odour* of fresh peanut butter paste in type species.

Basidia ephemeral, not recorded. *Basidiospores* subglobose to irregularly shaped, with inconspicuous sterigmatic attachment, slightly to moderate reticulate, some spores enclosed in nurse cells, basal pore absent, hyaline to pale brown in aq. alkaline solutions, aborted, darker coloured, rather small spores scattered throughout hymenium, dextrinoid, generally acyanophilic except when immature. *Tramal plates* narrow, composed of hyaline, thin-walled, compactly interwoven hyphae. *Cystidia* absent. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Probably ectomycorrhizal; under *Acacia melanoxylon* and *Eucalytpus globulus*.

Distribution: Known only from Australasia; South Australia & Tasmania, although there is reason to suggest the genus exists in Malaysia.

A currently monotypic genus is only known from a few collections, *viz.* the original and more recent ones from Tasmania; it has previously been placed in a whole array of gasteroid genera. The presence of nurse cells and the characters of the gasterocarp link this genus to the Sclerodermatinae and must be placed in the Boletales.

An undescribed hypogeous fungus collected in Malaysia under *Heriteria* (Sterculiaceae) may be referrable to the present genus. In parallel to the type species the gleba is dark brown to almost black and the chambers contain an exceedingly

high number of aborted spores. *Hydnagium mcalpinei* Rodway is also considered a member of the Boletales by Castellano & Trappe (Aust. Syst. Bot. **5**: 642, 1992) but it is not congeneric with *Horakiella* and undoubtedly requires a new quite separate genus.

HYDNOMERULIUS Jarlosch & Besl, Pl. Biol. 3(4): 447, 2001. Plate 9 A.

Type species (only original species): *Hydnum pinastri* Fr. (= *Hydnomerulius pinastri* (Fr.) Jarlosch & Besl).

Basidiome effused crust, separable, resupinate, hydnoid at maturity, waxy and translucent, especially towards matted-cottony margin, gymnocarpic. *Spore-print* pale buff or cream-colour.

Hymenium smooth at first then with low ridges which form net-work, finally with conical fluted spines 1-2mm long, yellow-brown when young then olivaceous yellow or tinged with brown with age, bruising red-brown when fresh and drying blackish brown; margin whitish to honey-colour, lacking or with pallid to brown and finally blackish hyphal strands at margin or on adjacent substrate below basidiome. *Sclerotia* numerous or rare, black, ovoid to broadly ellipsoid.

Basidia clavate to slenderly clavate, < 40µm long, 4-spored with long sterigmata. *Basidiospores* broadly ellipsoid, some ovoid or almost subglobose, slightly to distinctly flattened adaxially, pale yellow to yellow, distinctly thick-walled, smooth, slightly pseudoamyloid or a few spores distinctly so, cyanophilous. *Cystidia* replaced by numerous, hyaline, sometimes protruding, clavate to irregularly branched or forked cystidioles. *Tramal hyphae* hyaline, thin-walled, closely packed, parallel, forming a distinct core to the teeth. *Clamp-connections* present, frequent in contextual hyphae, less common in tramal hypae.

Chemistry: Involutin and flavomentin isolated suggesting a close relationship with *Paxillus involutus, q.v.*

Developmental studies: Wakefield (Kew Bull. (**1918)**: 229-233) has described the development of the characteristic hymenium.

Ecology: Saprotrophic, lignicolous on wood and bark of wide range of host trees but especially conifers and forming a brown, crumbly rot. Also known from soil in greenhouses, areas beneath domestic buildings and discarded timbers and wooden materials.

Distribution: Apparently world-wide; reported from North America, Caribbean, Europe, East Africa and New Zealand.

Currently a monotypic genus based on a fungus previously placed in *Leucogyrophana* by Ginns & Weresub (Mem. New York Bot. Gard. **28**: 96, 1976) but which differs from all other species in that genus in its olivaceous yellow, distinctly toothed hymenium. It is fully discussed with line-drawings and illustrations of basidiomes and cultures in Ginns & Weresub; see above and a further description in Ginns (Can. J. Bot. **56**: 1953-1873, 1978).

HYGROPHOROPSIS (J. Schröt.) Maire in Martin-Sans, L'Empoisonnement 99, 1921. Plate 9 B.

Type species (selected): *Agaricus aurantiacus* Wulfen, Jacq. Misc. Austr. 2: 107, 1781 = *Cantharellus aurantiacus* Wulfen: Fr. (= *Hygrophoropsis aurantiaca* (Wulf.: Fr.) Maire apud Martin-Sans).

Basidiome epigeal, pileate, centrally stipitate but may ultimately become excentric or even absent or lateral, hymenophore lamellate, decurrent and easily separable from context, stipitocarpic, gymnocarpic. *Spore print* whitish (ivory to cream-colour).

Pileus concave, depressed, often with wavy inrolled margin, which persists into maturity, subtomentose to velvety-tomentose, orange to sienna to fulvous or paler and then cream-colour or buff. *Stipe* elongate cylindric, curved or slightly swollen downwards sometime connate at base, sometimes lateral, absent or excentric, concolorous with pileus or paler. *Gills* decurrent, arcuate, narrow, with blunt edges, usually repeatedly forked and often interveined, especially towards the stipe, concolorous or paler than the pileus. *Context* soft, similarly coloured to outer layers of basidiome. *Odour* pleasant of cultivated mushrooms; *taste* pleasant.

Basidia small, clavate, thin-walled, hyaline, 4-spored. *Basidiospores* small to medium, hyaline or with very pale ochraceous tinge, subglobose to broadly ellipsoid or oblong ellipsoid, smooth, slightly thick-walled, usually pseudoamyloid but never amyloid, cyanophilic. *Cheilo- and pleurocystidia* absent. *Lamellar trama* vaguely bilateral at first, soon becoming subregular with a central zone of broad, often thickened, hyaline hyphae separating it from the thin-walled, loosely

arranged, subgelatinous lateral hyphae, finally appearing to run in all directions. *Clamp-connections* present.

Chemistry: Variegatic and xerocomic acids, variegato-rubin and a range of methylated variants of the latter isolated. Also demonstrated in mycelial cultures. ME negative. Electron micrograph of section of basidiospore in Clémençon, 1997.

Ecology: Terrestrial, non-obligatory ectomycorrhizal; on the ground in woodlands, in moss, on peat, amongst wood-chips, sawdust, herbaceous and grassy plants.

Distribution: Widespread in both north and southern hemispheres of New and Old Worlds.

A small genus of a handful of species, some species of which have a widespread distribution.

Key to Central American taxa in Singer *et al.* (Beih. Nova Hedw. **98**: 6, 1990). The European species are well-documented in regional mycobiotas with illustrations and descriptions and African species in Heinemann & Rammeloo (Flore Illustrée des Champignons d'Afrique Centrale **12**, 1986). Also see General references.

***IXECHINUS** R. Heim ex R. Heim, Rev. Mycol. **30**: 233, 1966. Plate 9 C.

Type species (selected, Donk, 1955): *Ixechinus majus* R. Heim.

Basidiome epigeal, pileate strongly gelatinised, often with shades of green, hymenophore tubulate and elements separating easily from each other and from context, centrally stipitate, putrescent, gymnocarpic. *Spore-print* ochraceous.

Pileus convex then plano-convex, smooth, viscid to glutinous in shades of pallid, grey- or olivaceous brown with hints of either purplish brown or with slight green tints. *Stipe* rather slender, cylindric, longitudinally and strongly striate to fibrillose, smooth and viscid, fibrillose, concolorous with pileus or paler and with tints of reddish brown. *Tubes* noticeably distinct from and depressed around stipe, greyish or rose, separating from pileus and from each other; *pores* concolorous, small, round. *Context* whitish or with yellowish tones especially in stipe-base, soft, not cyanescent. *Odour* indistinct; *taste* mild

Basidia clavate-pedunculate, 2- or 4-spored. *Basidiospores* elongate-amygdaliform, smooth, pale citrine-ochraceous, inamyloid, acyanophilic. *Cheilocystidia* clavate-pedicellate, hyaline, hardly differentiated; *pleurocystidia* similar, hyaline or slightly alutaceous in aq. alkaline solutions, pseudoamyloid. *Tube trama* of *Boletus* subtype, strongly gelatinized with central stratum but soon separating into separate units especially in alcoholic solutions. *Pileipellis* an ixotrichoderm with strong gelatinization of the constituent hyphae, end-cells not strongly differentiated, finally intermixed with thin-walled, hyaline hyphae in gelatinous matrix. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: Terrestrial; relationships not demonstrated. possibly ectomycorrhizal with *Uapaca*.

Distribution: The three species recognised in the genus occur in Africa, two in Madagascar but a single un-named taxon determined as *Boletus viridis* Heinem. & Gooss.-Font. by Corner (1972) from Malaysia belongs here (Wolfe, 1982; Watling, unpublished notes). Guzmán (1974) gives a distributional map under the name *Fistulinella*.

This very small genus has been synonymised with *Fistulinella q.v.* by Horak (1968), Gúzman (1974), Pegler & Young (1981) and by Singer (1986), a genus widely used to cover Wolfe's *Muciloporus* but, as Wolfe (1981, 1982 & 1983) has clearly demonstrated, the two genera, although closely related, are distinct. Wolfe erroneously attributed *Ixechinus* to Horak, 1968. The genus was first introduced by Heim (Rev. Mycol. 4: 20, 1939) for two boletes from Madagascar but the name was not validated according to the Botanical Rules of Nomenclature until much later (Heim, 1966). Wolfe (1982) added *Pulveroboletus viridis* (Heinem. & Gooss.-Font.) Wolfe to the genus. Fresh collections are required for molecular study to determine the position of the genus.

Horak (1968) gives a description with line-drawings of re-examined type material. See Singer (Sydowia **9**: 421, 1955). Wolfe (Mycologia **76**, 1984) has conducted statistical analyses on members of this genus.

ΦJAAPIA Bres., in Ann Myc. **9**: 428, 1911. Plate 9 D.

Type species (only original species): *Jaapia argillacea* Bres.

Basidiome resupinate crust with indefinite margin, whitish or pale yellowish, loose, floccose. *Spore-print* pale, dull yellow.

Hymenium effused, adnate, whitish becoming pale ochraceous, argillaceous or pale yellowish on drying, at first flocculose-porose then continuous, rather soft, with poorly differentiated margin, fluffy or pilose from emerging cystidia.

Basidia long, slightly sinuous and often constricted, 4-spored, sometimes secondarily septate. *Basidiospores* relatively large, smooth, fusiform with a very conspicuous more or less peg-like hilar appendage, after detachment becoming thick-walled (2-layered), inamyloid, inner part congophilic and cyanophilic; in one species inner layer finally surrounds a chlamydosporic-like body which fills part of the central area leaving empty spaces at each end, but in the other species there are generally no inter-membranal spaces. *Cystidia* long, thin, cylindric with obtuse apices, thin-or slightly thick-walled. *Context* of richly branched hyphae. *Clamp-connections* present.

Chemistry: Not known; pulvinic acids and their derivatives have not been traced in cultures.

Ecology: Saprotrophic; on dead branches *etc.* of various frondose and conifer trees, often in rather damp habitats.

Distribution: Known from temperate areas of Europe, Northern Asia and North America.

A very small genus well defined in one member by the unusual basidiospores; the two ends of the mature spores are hyaline and tend to collapse whereas the main body is rigid, becoming thick-walled, yellowish and filled with oily material. Wakefield & Pearson (Trans. Brit., mycol. Soc. **6**, 1920) & Rogers (Univ. of Iowa Studies in Nat. Hist. **17**, 1935) have discussed the development of the unusal basidiospores.

Following Nannfeldt & Eriksson (Svensk. Bot. Tids. **47**, 1953) the genus is currently placed in the Coniophoraceae but with more and more hesitation. Hallenberg (*Fungiflora Oslo*,1985) based on morphological differences, was one of

the first to question the placement of *Jaapia* in the Coniophoraceae. His opinion was later supported by Hibbett & Binder (Proc. Roy. Soc. London, Series B, **269**, 2002) using molecular techniques. This latter work has led to the recognition of *Jaapia* as a separate clade and sister group to the euagarics, boletes and athelioid fungi – see Binder *et al*., Syst.Biodiversity **3**: 149, 2005. The placement by Rogers (Farlowia **1**, 1943; Univ. of Iowa Studies in Nat. Hist., **17**, 1935 not 1938 as stated in Nannfeldt & Eriksson's references) of *J. ochroleuca* (Bres.) Nannf. & Erikss. in *Pellicularia* is not supportable.

See Eriksson & Ryvarden, *Corticiaceae of Northern Europe* Vol. 4, 1976 for description and line-drawings and photomicrographs. A key is also offered to the two currently known species. Colour photograph of *J. ochroleuca* in Breitenbach & Kränzlin, 1986 *Pilze der Schweiz* Band 2.

Synonym:
Coniobotrys Pouz. Ceská Mykol. **12**: 32, 1958; based on *Coniophora ochroleuca* Bres.

LECCINELLUM Bresinsky & Manfr.-Binder, Regensburg Mykol. Schriften **11**: 231, 2003. Plate 9 G.

Type species (originally designated): *Boletus nigrescens* Richon & Roze (= *Leccinum crocipodium* (Let.) Watl.).

Basidiomes epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, gymnocarpic. *Spore-print* ochraceous brown.

Pileus convex then plano-convex, smooth or slightly rugulose, never scaly but sometimes slightly tomentose-velvety when fresh, soon smooth especially in wet weather. *Stipe* evelate, cylindrical either attenuated upwards or slightly swollen towards the central area and then attenuated also downwards, scurfy throughout from fine, pallid or yellow scabrosities arranged in longitudinal lines down stipe, darkening as the stipe when handled. *Tubes* pale lemon-yellow or slightly ochraceous yellow when young, darkening when mature; *pores* concolorous, round and small, dark brown when bruised. *Context* white to pallid or yellow but soon darkening when exposed to the air. *Odour* & *taste* pleasant.

Basidia clavate, elongate, hyaline, thin-walled, 4-spored. *Basidiospores* subfusiform often elongate and slightly inequilateral in side-view, smooth, inamyloid,

acyanophilic. *Cheilo-pleurocystidia* hyaline, slightly darkening in aq. alkaline solutions, scattered, smooth, subfusiform to ampulliform. *Tube trama* with lateral, gelatinised hyphae divergent from central, slightly darker mediostratum. *Pileipellis* composed either of chains of erect, moniliform cells forming hymeniderm or with pedicellate-clavate cells creating a continuous layer, in some species at maturity collapsing and intermixed with some filamentous units. *Clamp-connections* absent.

Chemistry: The series of chemical reagents have been applied to this genus in parallel to *Leccinum – q.v.* Xerocomic and variegatic acids isolated from *L. rubropunctum* (Peck) Singer and *L. subglabripes* (Peck) Singer.

Cytology: Ploidy level of 2x in *Leccinum pseudoscabrum* (Kallenb.) Šuatara (as *L. griseum* (Quél.) Sing.) (Bresinsky & Wittmann-Bresinsky, 1994).

Ecology: Ectomycorrhizal with members of the Fagales, especially *Quercus* and with Betulaceae generally, except *Betula*.

Distribution: At present the genus appears to contain semi-thermophilous boletes associated with Mediterranean vegetation in both Europe and North America with outliers in the tropics and subtropics. A few species extend into north temperate areas.

Leccinellum is a small genus only recently separated from *Leccinum q.v.,* where the species can be sought in most texts. 8 species based on those formerly placed in *Leccinum* sect. *Luteoscabra* Singer, and sect. *Leccinum* subsect. *Albella* Singer (Amer. Mid. Nat. **37**, 1947). Molecular studies indicate the grouping is strongly supported. Also included is a series of boletes centred around *Boletus corsicus* Rolland, a bolete presently placed in the enlarged Boletaceae.

Keys to the species will be found incorporated into studies on *Leccinum*; see above. Smith, Theirs & Watling (Mich. Bot. **6(3A)** 107-154, 1966) deal with the N. Amercian taxa under *Leccinum* Sect. *Luteoscabra*. For colour illustrations but all under *Leccinum*, see Bessette, Roddy & Bessette, *North American Boletes*, 1999; Imazeki *et al*. *Fungi of Japan*, 1988 and for the handful of European species see Lannoy & Estades *Monographie des Leccinum d'Europe*, 1995. See also General References.

LECCINUM S. F. Gray in Nat. Arrang. British Plants **I**: 646, 1821. Plate 9 E & F.

Type species (selected): *Boletus aurantiacus* Bull. : Fr. (= *Leccinum aurantiacum* (Bull.) S.F.Gray)

Basidiomes epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, gymnocarpic, pileoangiocapic or stipiticarpic with or without marginal appendiculate flap to pileus. *Spore-print* ochraceous brown.

Pileus convex then plano-convex, smooth or slightly tomentose at first or with fine radiating fibrils which at maturity sometimes join to form adpressed, fibrillose scales, dry then tacky or greasy in wet weather, rarely truly viscid, ranging from pale brown, buff *etc*. to snuff-, tobacco-brown or fuliginous black to red-brown or even rich orange to fulvous. *Stipe* evelate, cylindrical, slightly swollen downwards, covered in minute to prominent dark or pale scabrosities which generally darken with age to become orange-brown, rust-brown, fuliginous or sepia or remain unchanged or only slightly discolouring. *Tubes* white or whitish, rarely with darkened orifices when young, becoming pallid with age and only darkening further when bruised or damaged and then flushed cinnamon, buff, ochraceous or even pinkish, free; *pores* concolorous, circular, generally small. *Context* white or pallid, either unchanging or becoming flushed pinkish or dull reddish, in some species cyanescent or viridescent, especially in the stipe-base. *Odour* & *taste* pleasant. slightly earthy.

Basidia hyaline, thin-walled, elongate-clavate, 4-spored. *Basidiospores* elongate-ellipsoid to elongate subfusiform and distinctly flattened on one side, often very long, smooth, outer wall separating in saturated aq. alkaline solutions, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* elongate-fusiform or ampulliform, hyaline, scattered on inner surface of tube or aggregated at margin, sometimes with darker contents. *Caulohymenium* strongly developed with caulobasidia and caulocystidia, which in most species darken with age to shades of pale or dark brown. *Pileipellis* a cutis of either shortened or elongate, narrow or slightly broad hyphal units with the end-cells slightly differentiated by narrowing to becoming torpedo-shaped. *Tube trama* with poorly coloured, lateral hyphae divergent from well differentiated, slightly darker, central strand of gelatinised hyphae. *Clamp-connections* absent.

Chemistry: Chemical reagents extensively used in the identification of species, although the reliability of some results remains doubtful. Use of phenol, iron

salts (aq. ferrous sulphate solutions and formulations) and formalin widespread. Gyrocyanin and gyroporin, two cylcopentenones, known from basidiomes; atromentic acid isolated from cultures. Atrotomentin isolated from *L. eximius*, a species placed in *Leccinum* by Pomerleau (Bol. Bull. du Cercle des Myc. Amat. de Quebec ***6****:* 117, 1959). Molecular studies, however, show that *Boletus eximius* Peck lies in an isolated position closer to *Boletellus q.v.* than either *Leccinum* or *Tylopilus* where Singer (Amer. Midl. Nat. **37**: 109, 1947) and Smith & Thiers, *The Boletes of Michigan* 106, 1971 place it. See Binder & Besl (2000) linking chemotaxonomic and molecular data.

Genetical studies: Den Bakker *et al*. (New Phytologist **163**, 2004, Mycologia **96**: 102-118**,** 2004 & Mycological Research **111**, 2007) have published on the molecular systematics of the temperate species and considered their evolution and host specificty.

Cytology: Ploidy level of 2x and 3x. 2x in *L. holopus* (Rostk.) Watl.*, L. rotundifoliae* (Sing.) Smith, Thiers & Watl. & *L. scabrum* (Bull.) S.F.Gray (Wittmann-Meixner, 1989). 2x & 3x in *L. piceinum* Pilát & Dermek & *L. subcinnamomeum* Pilát & Dermek respectively (Bresinsky & Wittmann-Bresinsky, 1994).

Ecology: Ectomycorrhizal with Salicales and Fagales, especially Betulaceae; also with Pinaceae and Cistaceae. Known to form arbutoid mycorrhiza. In Agerer 61 *L. scabrum* with *Betula pendula*.

Distribution: See Den Beker *et al.* (New Phytologist **163**: 201-215, 2004) for probable evolution of distribution. A large genus distributed mainly in boreal countries and across the northern hemisphere, with outliers in East Africa (single species), Malaysia (two species) and a handful in South and Central America. In Madagascar at least six undescribed species occurr simply with *Uapaca bojeri*.

Presently placed in an extended Boletaceae. Molecular studies have shown that the core species form an extremely tightly knit group. Some leccinioid boletes with a distinctly yellow hymenophore have been transferred to *Leccinellum q.v.*

Good keys supported by descriptions and line-drawings and b/w photographs are available for the North American and European members of the genus. See Smith, Theirs & Watling (Mich. Bot. **5**: 131-179, 1966) and Lannoy & Estades, *Monographie des Leccinum d'Europe*, 1995. This last publication has coloured illustrations and is a summary of several papers appearing in Bull. Soc. Mycol. Fr. & Documentes Mycol. Sutara (Ceská Mykol. **43**: 1-12.1989) has discussed

the delimitation and anatomy of members of *Leccinum.* Illustrations are also found in Vassil'kov *Conspectus Systematicus Krombholziae Aurantiacae*, 1956, Bessette, Roddy & Bessette *Boletes of North America*, 2000 and Imazeki *et al. Fungi of Japan*, 1988. Colour photographs in Thiers, *California Mushrooms; a field guide to the boletes*, 1975 and Halling & Mueller, *Common Mushrooms of the Talamanca Mountains, Costa Rica*, 2005. B/w photographs in Smith & Theirs, *Boletes of Michigan*, 1971. See Engel, Dermek & Watling, *Rauhstielröhrlige: Die Gattung Leccinum in Europa*, 1978.

Synonyms:
Krombholzia P. Karst., Rev. mycol. **3(9)**: 17, 1881; type species *Boletus versipellis* Fr. & Hök. (selected). This is a synonym of *Leccinum* but used earlier for a genus of grasses.
Krombholziella Maire, Pub. Inst. Bot. Barcelona **3(4)**: 41, 1937; type species *Boletus versipellis* Fr. & Hök. This is a direct replacement for *Krombholzia* because of the earlier homonym. It is a synonym of *Leccinum.*
Trachypus J. Bataille, Bull. Soc. Hist. Nat. Doubs **15**: 12, 1908; type species *Boletus rufus* Schaeff. (selected). The genus name has been widely adopted by many French authorities for *Boletus scaber* Bull. and allies. It has the same circumscription as the more familiar *Leccinum*, which predates it by 87 years.

Šutara (Taxon **324**: 678-686, 1985) has discussed at length the adoption of the name *Leccinum*.

LEUCOGYROPHANA Pouzar in Ceská Mykol. **12**: 32, 1958. Plate 10 A.

Type species (only original species): *Merulius molluscus* Fr. (= *Leucogyrophana mollusca* (Fr.) Pouzar).

Basidiome resupinate crust, effused, rarely reflexed and then pileus poorly developed, separable, membranous, hymenium on gyrose-plicate folds, fluted spines or tubercules, sometimes drawn into raduloid warts. *Spore-print* yellowish to pale brown.

Pileus often absent, thin, superficial, velvety on upper surface when present, whitish or pallid to apricot-colour or with pale orange tints, paler at margin and with white, scattered strands. *Hymenium* principally fawn, brownish, yellow-brown or with orange hues, sometimes tinted olivaceous, finely pruinose and waxy, shiny when fresh, with broad inflated ridges in brighter colours, soft

but hard and brittle when dry. *Context* cottony, white pallid or sometimes with brownish or olivaceous tints.

Basidia clavate-cylindric, hyaline, thin-walled, 4-spored. *Basidiospores* subhyaline to pale straw-yellow or honey-yellow, relatively small, broadly ellipsoid to slightly obovoid or oblong, smooth, slightly thick-walled, with broad hilar appendage, usually pseudoamyloid, cyanophilic. *Cystidia* clavate with or without prolongation or even finger-like extensions, thin-walled, hyaline. *Context* of interwoven, hyaline, thin-walled, relatively narrow hyphae; tramal hyphae generally in two strata, often embedded in rather gelatinised matrix. *Clamp-connections* present.

Chemistry: Atrotomentin and atromentic and xerocomic acids isolated and methyl variegatate found in cultures of *L. mollusca* (Fr.) Pouzar.

Cytology: Ploidy level 1x in *L. mollusca* (Wittmann-Meixner, 1989).

Ecology: Saprotrophic; lignicolous on coniferous wood, more rarely on angiosperm wood. Producing a brown rot.

Distribution: Widely distributed in both temperate and tropical environments. Known from Europe, N. America, India, South East Asia. Probably introduced in some areas on timbers.

Although the genus was introduced with a single species it has been expanded to cover nine additional taxa, three of which were assigned by Parmasto and Julich (Persoonia **8**: 51-58, 1974) and do not appear to be congeneric with the type; these species were omitted from the genus when it was monographed by Ginns (1973); see below. From molecular studies the genus is polyphyletic; see Jarosch & Besl (2001). The type species is assignable to the Hygrophoropsidaceae, whereas *L. arizonica* Ginns is more akin to *Coniophora q.v.* and two other species form a side branch from the *Austropaxillus/Serpula q.v.* consortium. In virtue of the differences in hymenial configuration and secondary metabolites *L. pinastri* (Fr.) Ginns & Weresub has been removed and placed in *Hydnomerulius q.v.*

See Ginns Can. J. Bot. **56:** 1953-1973, 1978 where a good key and list of epithets are offered accompanied by line-drawings and b/w photographs.

MEIORGANUM R. Heim, C. R. Acad. Sc. Paris **261**: 1720, 1965 see Rev. Mycol., Paris **31:** 157, 1965. Plate 10 B.

Type species (only original species): *Meiorganum neocaledonicum* R. Heim.

Basidiomes conical then ungulate to applanate, spathulate to flabellate, substipitate or excentric, dorsi-fixed, descending, hymenophore tubulate, solitary to subcaespitose and then imbricate, putrescent, gymnocarpic. *Spore-print* dark brown or fawn.

Pileus pallid fawn, bistre to light fulvous fawn or rufous, smooth or matt, somewhat adpressedly fibrillose towards pallid white to pallid yellowish, pruinose-velvety incurved margin, darker rugulose or villose towards basal attachment. *Stipe* reduced or simply a conical basal attachment, ferruginous. *Tubes* short, waxy, subgelatinous, dingy fawn orange or fuscous orange; *pores* small at first, developing in more or less radial rows, angular, compound, with uneven, entire edge, dull orange becoming fuscous orange or cinnamon fawn. *Context* spongy floccose, minutely lacunose, pallid dingy white to dingy buff, becoming pallid vinaceous on exposure. *Odour* of gas-tar and fenugreek.

Basidia 4-spored. *Basidiospores* broadly ellipsoid, dingy pinkish to dull vinaceous, smooth, quite small, darkening to fuscous ferrugineous in aq. alkaline solutions with small hilar appendage, inamyloid, slightly cyanophilic. *Cystidia* narrowly fusoid, obtuse to subacute, thin-walled, hyaline generally thickly encrusted in lower part embedded in hymenium. *Hymenophoral trama* of divergent hyphae with strongly mucilaginous walls, intermixed with some oleiferous hyphae. *Pileipellis* of more or less adpressed or slightly divergent, narrow, thin-walled hyphae with obtuse end-cells, not forming a palisade. *Clamp-connections* present.

Chemistry: Pigment in hymenium in orange-yellow granules which turn dark brown in aq. alkaline solutions and exude a yellow dye; in alcohol-formalin giving a dingy purplish colour.

Cytology: Ploidy level 1x in *M. curtisii* (Wittmann-Meixner, 1989).

Ecology: Saprotrophic; lignicolous on fallen rotting trunks, stumps and living trees.

Distribution: Known from Malaysian Peninsula, Indonesia, Borneo and New Caledonia.

A genus of two species referrable to the Serpulaceae with rather unusual field characters and in part fall intermediate between *Merulius* s. Corner (=*Serpula q.v.*) and *Gyrodon/Paxillus e.g. Paxillus panuoides* (Fr.) Fr. = *Tapinella* of this publication *q.v. Paxillus curtisii* Berk. apud Berk. & Br. has been placed by Singer *et al.*, (Beih. Nova Hedw. **98**, 1990) in the present genus.

See Corner (Garden's J. Singapore **25**: 355-381,1971) for discussion and description of genus and species. Colour photographs and line-drawings are given. Colour photographs of *M. curtisii* (Berk. & Broome) Sing. appears in Bessette, Roddy & Bessette, *North American Boletes*, 2000 and Imazeki *et al.*, *Fungi of Japan*, 1988.

MELANOGASTER Corda in J. Sturm, Deutschl. Fl. Abt. 3, **3** (Hefte 2): 1, 1837, nomen cons. Plate 10 C.

Type species (selected): *Melanogaster tuberiformis* Corda.

Basidiome gasterocarpic, hypogeous or subhypogeous, globose to tuberiform, when mature with dark brown or blackish spore-mass, putrescent, angiocarpic.

Peridium persistent, not separable, smooth, golden brown or ferrugineous to dull reddish brown but often blackening where bruised. *Gleba* white at first then marbled and darkening from deep olivaceous brown to black as spore-mass matures, mucilaginous and deliquescent with age with irregular rounded to angular chambers, largest towards the centre and with thin, pale coloured tramal plates. *Hymenium* discontinuous with irregularly arranged basidia maturing simultaneously. *Odour* strong and aromatic.

Basidia elongate-clavate, evanescent, 2- 4- (-6)-spored, with short or long sterigmata. *Basidiospores* orthotropic, symmetric, oblong-ovoid, ellipsoid, fusoid, to citriform, commencing honey-coloured soon darkening to fuscous black, thick-walled, slightly rugulose under SEM, with short, basal hilar appendage. *Peridiopellis* an indefinite epicutis of woven, non-inflated, brown, slightly thick-walled, sometimes encrusted hyphae.

Chemistry: Not known. Spore reactions indeterminate with strong pigmentation of spore-wall.

Ecology: Ectomycorrhizal, under fallen leaves and in superficial humus or on

upturned root plates of deciduous or coniferous trees.

Distribution: known from northern temperate areas of Europe and North America; introduced into the Southern Hemisphere.

A genus of about a dozen species the relationships of which, until molecular studies were conducted, were very speculative. The genus fits neatly into the paxilloid fungi, something not even considered possible from anatomical studies alone; see Besl, Dorsch & Fischer (1996). It is placed in the Melanogastraceae. Several unrelated hypogeous fungi have been associated with *Melanogster*, *e.g. Leucogaster* but these have been now shown to have quite different relationships.

For keys and analysis of species see Zeller & Dodge (Ann. Mo. Bot. Gdn. **23:** 639, 1936). Colour illustrations, SEM micrographs and line-drawings of British taxa appear in Pegler, Spooner & Young, *British Truffles*, 1993. Colour photographs of 2 European species in Breitenbach & Känzlin, *Pilze der Schweiz*, 1986. Known as Slime truffles.

Melanogaster is a conserved name. Hence the following genera all circumscribing the type species are synonymized.
Synonyms:
Argylium Wallr. in Fl. Crypto. Germ. **2**: 874, 1833; based on *Argylium liquaminosum* Wallr.
Bullaridia Jungh., Linnaea **5**: 408, 1830; based on *Bullardia inquinans* Jungh.
Hyperrhiza Fr. in Syst. Orb. Veg. **1**: 135, 1825; based on *Hyperrhiza tuberosa* Fr.,
Hyperhiza Spreng. apud L. in Syst. Veg. Ed 16. **4**: 416, 1827; based on *Hyperrhiza tuberosa* Fr.
Uperrhiza Bosc, Mag. Ges. Naturwi**ss** Freunde Berlin **5**: 88, 1811; introduced without naming species. Fries, 1825 used the name based on *Hyperrhiza tuberosa* Fr.

Octaviana Vitt., Monogr. Tuber, 15, 1831 based on 6 species with no type selected. The author emphasised the dark spore-mass and all but one of his species have been subsequently placed in *Melanogaser.* This left *O. asterosperma* aberrant in the genus and led Kuntze to erect a new genus with a confusingly similar name; see *Octavianina* below.

Hoehnelogaster Lohwag, Beih. Bot. Centralbl. 2 Abt. **42**: 325, 1926, based on

Corditubera microspora Höhn. (Frag. Z. Mykol., 1019, 1908) from Java but introduced with no formal description. It must be considered a *nomen dubium*, although the genus has been assigned to the Melanogastraceae.

MYCOAMARANTHUS Castellano, Trappe & Malajzcuk, Australian Systematic Botany **5**: 613, 1992. Illustration: See front page.
Type species (originally designated): *Mycoamaranthus auriorbis* Castellano et al. (= *M. cambodgensis* Tappe et al. syn. *Dendrogaster cambodgonese* Pat.).

Basidiome gasterocarpic, hypogeous to subhypogeous generally emergent, globose to subglobose, occasionally irregularly lobed, bright yellow or orange yellow, often in clusters, attenuated downwards to form a basal pad or short, stipe-like base with numerous emergent rhizomorphs, gleba with minute, irregularlty shaped locules.

Peridium dry, minutely scaly or felty, becoming smooth, brightly coloured. *Gleba* gelatinized, whitish at first, soon becoming a smoky lilaceous or greyish pink then blackish brown and accentuating white veins at maturity, filled with brownish yellow spore-mass..

Basidia clavate, hyaline, 4-spored. *Basidiospores* broadly fusiform to broadly void, symmetrical with distinct, persistent sterigmatic remnants, pale golden brown in aq. mounts, darkening in aq. ammoniacal solutions, minutely verrucose although sometimes appearing almost smooth, pseudoamyloid when immature. *Cystidia* not seen. *Peridial structure* of thin-walled coarsely or minutely roughened, compactly interwoven hyphae, possibly periclinal towards gleba, leaching coloured pigment in microsopic mounts. *Clamp-connections* not seen.

Chemistry: No reaction with potash solutions on peridium; leaching out bright yellow pigment in alkaline solutions.

Ecology: Ectomycorrhizal with Cassurianaceae, Dipterocarpaceae.and Myrtaceae.

Distribution: Known from northern Australia (Queensland) and from the Malaysian Peninsula northwards into Thailand and Cambodia.

This is a small genus at the moment of only two species, one not as yet formerly named. In addition to the account by Castellano *et al.* (1992) members of the

genus have been dealt with by Corner & Hawker (as *Dendrogaster*, Trans. Brit. Mycol. Soc. 36, 1953; see Patouillard, Bull. Soc. mycol. Fr. 39: 55-56, 1923) and by Lumyong et al. (Mycological Progress **2**, 2004). Line drawings are to be found in all articles mentioned.

OCTAVIANINA O. Kuntze in Rev. Gen. Pl. **3**: 501, 1898. Plate 10 D.

Type species (only original species): *Octaviania asterosperma* Vittad. (= *Octavianina asterosperma* (Vittad.) O. Kuntze).

Basidiome gasterocarpic, hypogeous, subglobose or globose to irregular in shape, with small, indistinct hyphal attachments to soil.

Peridium thin, white to pinkish but discolouring on bruising or where exposed, either cyanescent or rufescent but usually finally greyish brown, floccose but soon smooth, sometimes rimose, not separating. *Gleba* loculate with minute chambers filled with fuscous brown spore-masses, more or less radially arranged, sinuose or irregular, largest at centre and separated by thick, white tramal plates, pale yellow or white but soon discolouring to honey-colour and finally dark fuscous brown, soft and gelatinised. *Stipe* and *columella* replaced by basal pad. *Latex* present but scarce and may go unnoticed. *Odour* fruity.

Basidia clavate, 2- or 4-spored with short sterigmata. *Basidiospores* orthotropic, globose or nearly so with thick exosporial wall ornamented with coarse, conical, curved, inamyloid or at times pseudoamyloid spines with persistent, cylindrical hilar appendage exhibiting terminal tear. *Cystidia* absent. *Subhymenium* pseudoparenchymatic. *Hymenophoral trama* of parallel hyphae some with highly inflated segments, intermixed with scattered cells containing granular contents (lactiferous elements). *Peridipellis* an adpressed, non-agglutinate epicutis of loosely interwoven, yellowish brown, thin-walled hyphae. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: Probably ectomycorrhizal with Fagaceae and in South East Asia with Dipterocarpaceae (?). In Australia associated with Myrtaceae.

Distribution: Known from Australasia, North America, Europe and South East Asia.

A relatively small genus of hypogeous fungi covering about 15 species. The type species, because of the latex, has been placed with *Arcangieliella*, now in the Russulales and probably because of the spiny basidiospores in *Hydnangium*, which being related to the agaricoid *Laccaria* is now in the Tricholomatales. Both placements cannot be supported by critical anatomical examination. Some features relate the genus to the Melanogastraceae, itself a family close to *Paxillus q.v*. The dark spores with a pseudoamyloid reaction would suggest a placement in the Cortinariales, a position which Pegler, Spooner & Young (1993) adopted. Molecular studies have shown the type species at least sits clearly within a branch not only holding *Chamonixia q.v* but the leccinelloid boletes with yellow pores and tubes. *O. asterosperma* Vittad. is somewhat different from all other species placed by Vittadini in his *Octaviana*, which necessitated the erection of another genus. Sadly the similarity in names of the two genera has led to confusion, especially as each genus is assignable to different positions within the Boletales. At the moment Kuntze's genus belongs to an enlarged Boletaceae.

For further discussion on the name change see Singer & Smith (Mem. Torry Bot. Club **54**: 626, 1960) and Pegler & Young (Trans. Brit. Mycol. Soc. **72**: 353-388, 1979). See Singer & Smith (Mem. Torrey Bot. Club **54**, 1960) also for descriptions and line-drawings. Colour illustrations and line-drawings in Pegler, Spooner & Young, *British Truffles*, 1993.

PARAGYRODON (Singer) Singer, Ann. Mykol. **40**: 25, 1942. Plate 10 F.

Type species (only original species): *Boletus sphaerosporus* Peck (= *Paragyrodon sphaerosporus* (Peck) Sing.).

Basidiomes epigeal, pileate, hymenophore tubulate, centrally stipitate at first, entirely covered in a gelatinous sheath which becomes leathery and forms a volvate stipe-base, putrescent, hemiangiocarpic. *Spore-print* mustard to aniline yellow with an olivaceous tinge when dry.

Pileus convex to hemispherical, almost globose, then plano-convex and finally flattened with incurved margin, very fleshy and rather elastic, viscid to slimy especially in wet weather and on drying with leathery, shiny surface, ochraceous to tawny-colour darkening where handled and in age. *Stipe* central, equal or tapered to stipe-base, solid, pruinose or even reticulate at apex but from ¾ down enveloped in a thick, gelatinous membrane forming a skin stretching down to and usually enveloping the base, although often breaking up and then leaving an annulus

with pruinose upper surface, glabrous elsewhere and darkening with age and on handling. *Tubes* at first canary-yellow but soon darkening to dull gold-colour and finally with olivaceous tinge throughout, shallow, decurrent; *pores* concolorous, large, about 1 per mm. broad, angular, staining brownish when bruised. *Context* whitish or yellowish but soon becoming vinaceous brown. *Odour* not distinctive; *taste* indistinct or slightly unpleasant.

Basidia hyaline, clavate, 4-spored. *Basidiospores* globose to subglobose, smooth, pale yellowish in aqueous mounts but slightly darkening in aq. alkaline solutions, slightly thick-walled, inamyloid, acyanophilic. *Cheilocystidia* fusoid-ventricose with subacute apex, abundant at orifice, often with dingy brown contents, especially in aq. alkaline solutions; *pleurocystidia* scattered but abundant and similar in morphology to cheilocystidia. *Tube trama* highly gelatinised and divergent from brownish central hyphal strand. *Pileipellis* a thick layer of smooth, filamentous, highly gelatinised, appressed hyphae. *Stipitipellis* composed of cylindric, parallel hyphae supporting clusters or islands of caulocystidia similar in morphology to cheilocystidia and darkening with age or damage. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Terrestrial, ectomycorrhizal with *Quercus,* often in cleared hardwood forest and especially sites subsequently replanted by shade trees.

Distribution: North America (Great Lake states northwards into Quebec).

Paragyrodon was first considered a subgenus of *Gyrodon* by Singer (Rev. Mycol. **5**: 7, 1942), although very soon after, the same author made an independent genus. Subsequently it was placed as a section within the genus *Suillus q.v.* by Smith and Thiers (*Contribution toward a Monograph of North American Species of Suillus*, 1964). It is quite separate from both these placements and should be maintained as an autonomous genus within the Suillaceae.

See Smith & Thiers (*Boletes of Michigan*, 1971); Smith & Theirs (1964) in their preliminary account of N. American species of Suillus, noted above, offer b/w photographs. Also see Watling (Notes Roy. Bot. Gdn. Edinb. **29**: 67-73, 1969) who offers illustrations and descriptions of the single known species. Colour photograph in Bessette, Roddy & Bessette, *North America Boletes*, 2000.

***PAXILLOGASTER** Horak apud Horak & M. M. Moser, Nova Hedw. **10**; 323, 1966. Plate 10 G.

Type species (only original species): *Paxillogaster luteum* Horak.

Basidiome epigeal, pyriforme at first then expanding to become irregular, sequestrate, rudimentally stipitate, at first resembling a lycoperdaceous fungus – puffball.

Pileus an enveloping peridium which with age may break below to expose gleba within, depressed at centre with age, dry, densely tomentose, golden yellow to clear yellow then clay-colour or whitish with orange or brown radially arranged fibrils. *Gleba* loculate, irregularly sublamellate, whitish at first then ochraceous brown to ferrugineous brown. *Stipe* short but forming columella-like structure within, dry, cylindric with tapered base, yellow-brown. *Context* yellow. *Odour* aciduluous.

Basidia elongate-cylindric, hyaline, 4-spored. *Basidiospores* fusoid or ellipsoid, bilaterally symmetric, smooth, but exosporium indistinctly perforate, yellowish in aqueous mounts. *Cystidia* clavate, poorly differentiated. *Clamp-connections* rare.

Chemistry: Not known. Spore reactions not recorded.

Ecology: Terrestrial, ectomycorrhizal with *Nothofagus* (Fagaceae).

Distribution: Known only from South America (Argentina).

A currently monotypic genus whose type species is close to *Paxillus defibulatus* Singer, a species also found in Argentina. This is s a sequestrate member of a paxillliod series, although it is now necessary to conduct molecular studies in order to see its relationships with the recently described *Austropaxillus*.
For description and line-drawings of microscopic characters see original publication: Horak & Moser (Nova Hedw. **10**, 323, 1966).

PAXILLUS Fr. in Fl. Scan. 339, 1835. Plate 11 A.

Type species (selected): *Agaricus involutus* Batsch. (= *Paxillus involutus* (Batsch) Fr.)

Basidiome epigeal, small to large, pileate, centrally or slightly excentrically stipitate, hymenophore lamellate although often anastomosing towards the stipe and forming elongate pores which run down the stipe apex, pilangiocarpic in type species. *Spore-print* brown, when fresh, with either sienna or distinct purple-date tinge.

Pileus tomentose to velvety but soon smooth or retaining tomentosity at persistently inrolled, often grooved margin, rounded, convex at first but soon expanding, even to become depressed in centre, finally wavy, sometimes becoming slightly viscid in wet weather, ochraceous, fawn or red-brown darkening on bruising to dark red-brown. *Stipe* fleshy, cylindric or swollen downwards to become clavate or tapered downwards, paler or concolorous with pileus but soon darkening, especially where bruised to become spotty or streaked with red-brown, bay or chestnut. *Gills* decurrent, arcuate, easily separable from the pileus-context, obtuse at margin, narrow, pale ochre or even yellow at first with tinge of olivaceous or tinge of purple-date, finally fulvous or sienna, crowded, often branched and anastomosing, more so towards the stipe. *Context* pale ochre, buff in pileus, fulvous in stipe, darkening downwards and becoming chestnut or bay when exposed to air. *Odour* & *taste* acidulous.

Basidia clavate, hyaline, small, usually 4-spored. *Basidiospores* shortly ellipsoid to elongate-ellipsoid, adaxially applanate, smooth or very slightly rugulose under SEM, or in one species constantly rugose, yellowish brown, slightly thick-walled, with small conspicuous hilar appendage, inamyloid or pseudoamyloid, cyanophilic. *Cheilocystidia* absent or reduced to resemble basidia or lanceolate fusoid, hyaline, thin-walled; *pleurocystidia* scattered or rare and when present similar to those on margin. *Lamellar trama* divergent at first from central zone but at maturity subregular, mediostratum of interwoven hyphae some broad and then contrasting with thin-walled, loosely arranged, gelatinised lateral strata. *Clamp-connections* generally present.

Chemistry: Chemical reactions often quite distinct with aq. ferrous sulphate, ammoniacal and alkaline solutions, the last generally dark red-brown, reflected in the context changes when exposed to air, although in at least one species producing viridescent. Atromentin, atromentic acid, involutin & complexes and chamonixin isolated.

Ecology: Terrestrial, ectomycorrhizal with both conifers and frondose trees, sometimes fruiting on stumps and very rotten timber but not to be confused with *Tapinella*. Agerer 27 depicts the type species with *Picea abies*.

Distribution: Known from the north temperate areas and replaced in the Southern Hemisphere by *Austropaxillus q.v.* although *P. involutus* has been introduced to Australia.

Developmental studies: Basidiome development of *Paxillus involutus* has been described by Reijnders (1963).

Cultural studies: sclerotia formed in culture and also found amongst mycorrhizal root-systems.

Genetic studies: Fries (Mycotaxon **24**: 403-409, 1985) has recognized at least 3 intersterility groups within the taxon '*Paxillus involutus*'.

A small genus now reduced to 8 or 9 taxa after the wood-rotters have been removed and placed in *Tapinella q.v.* and the southern hemisphere species separated to form a distinct genus. *P. zerovae* Wasser from the Ukraine is an anomaly because of its unusual spore-morphology and may be closer to *Austrogaster q.v.*, although retained herein until further studies; see Wasser (Ukrayins'kyi Bot. Zhurnal **30**: 667-668, 1972). Zang & Zang (Acta Microbiol. Sinica **18**: 279-286, 1978) have attempted to unravel the species from Tibet and Yunnan, China, supported by colour illustrations and Heinemann & Rammeloo (*Flore Illsutrée des Champignons d'Afrique Centrale* 12, 1986) offer colour illustrations and electron micrographs of African taxa. See also Garrido (Biblio. Mycol. 120, 1988) for comparisons with S. American taxa.

Coloured illustrations, descriptions often supported by line-drawings are found in the majority of regional mycota e.g. Watling & Hills (British Fungus Flora Part I, 2006) and a key to the European *P. involutus* complex is provided by Hahn & Agerer in Nova Hedw. **69**, 1999.

Synonyms:
Ruthea Opat. in Arch. Naturgesch **2(1)**: 3, 1836; type species *Agaricus involutus* Batsch., making it a straight synonym of *Paxillus*.
Rylmoxis Pers. ex Rabenh. in Deutschl. Krypt.-Fl. **1**: 453, 1844, elsewhere as ***Rhymoxis***, with *Agaricus involutus* Batsch as type species. A straight synonym of *Paxillus*.

PHLEBOPUS (R. Heim) Singer, Ann. Mycol. **34**: 326, 1936. Plate 11 B.

Type species (only original species): *Boletus colossus* Heim. (= *Phlebopus colossus* (Heim) Singer).

Basidome epigeal, large to enormous, massive structured, pileate, centrally or excentrically stipitate, hymenophore tubulate, putrescent, gymnocarpic. *Spore-print* pale olivaceous brown.

Pileus convex but soon plano-convex to plane or even slightly depressed, finely tomentose but soon pruinose to smooth, glabrous or slightly darker fibrillose with age, dry, slightly greasy in damp weather, dry, possibly slightly cracking, margin not inrolled, often wavy and projecting beyond hymenium, brownish green, olivaceous brown, sometimes almost black. *Stipe* solid, stout, swollen downwards to form distinctly clubbed foot, stout, concolorous with pileus or pale at apex darkening downwards especially at maturity. *Tubes* adnexo-sinuate, pale yellowish to clear yellow, long; *pores* greenish yellow or with orange shades, not gyrose. *Context* soft-fleshy, yellowish, cyanescent or not.

Basidia short, clavate, 4-spored. *Basidiospores* shortly ellipsoid to broadly ovoid, adaxially applanate, brown, smooth, thick-walled, inamyloid, acyano-philic. *Cystidia* absent or inconspicuous. *Tube trama* loosely bilateral becoming subregular with age, with broad mediostratum of thin-walled hyphae and prominent pseudoparenchymatic subhymenium. *Pileipellis* a poorly developed cutis of interwoven, non-gelatinised or only slightly gelatinised hyphae with some end-cells erect to suberect to give impression of poorly differentiated trichoderm. *Context* of loosely interwoven, inflated, thin-walled hyphae. *Clamp-connections* present.

Chemistry: No chemical reactions reported. Variegatic acid isolated.

Ecology: Terrestrial probably ectomycorrhizal although in one South American species forms well-documented relationship with *Pseudococcus* (Hemiptera) root infections.

Distribution: Pan-tropical with wider distribution in Southern Hemisphere.

A small genus of a handful of species but is apparently, as presently conceived, a mixture of two elements one including the widespread Australasian *P. marginatus* (Berk.) Watling & N. M. Greg., which is related to the sclerodermatoid fungi, and another linked to *Chalciporus q.v.* The genus contains some of the largest single basidiomes of any fungus.

In the wide concept a key is offered by Singer *et al* (Nova Hedw. Beih. **77**: 40-47, 1983); see also monograph by Heinemann & Rammeloo (Mycotaxon

15: 384-404, 1990). Colour illustrations are found in Heinemann & Rammeloo, *Flore illustrée des Champignons d'Afrique Centrale* Fasc. 7, 1980.

Synonym:
Phaeogyroporus Singer, Mycologia **36**: 360, 1944; based on *Phaeogyroporus tropicus* Rick apud Rehm & Rick.

***PHYLLOBOLETELLUS** Singer apud Singer & Digilio, Lilloa **25** (1951): 438, 1952. Plate 11 C.

Type species (only original species): *Phylloboletellus chloephorus* Singer apud Singer & Digilio.

Basidiome epigeal, pileate, hymenophore lamellate, centrally stipitate, putrescent, gymnocarpic. *Spore-print* deep olivaceous.

Pileus convex, umbonate with acute, incurved margin. *Stipe* yellow, ornamented with brown fibrils, solid. *Gills* decurrent, broad, somewhat interveined, somewhat waxy, greenish, cyanescent. *Context* yellow, cyanescent when bruised and exposed to air.

Basidia elongate-cylindric with yellow vacuolar pigment in aq. alkaline solutions, 4-spored. *Basidiospores* shortly ellipsoid with suprahilar depression, lacking differentiated plage, ornamented with deep, often anastomosing, longitudinal costae extending beyond the broadly rounded spore-apex, brown, yellow-brown in aq. alkaline solutions. *Cheilo-*& *pleurocystidia* polymorphic, prominent, cylindric, elongate-fusiform, slightly enlarged at obtuse apex, hyaline but with yellow-brown, intracellular pigment in aq. alkaline solutions. *Pileipellis* a trichoderm of subregular, interwoven, filamentous hyphae, with yellow-brown pigment in aq. alkaline solutions. *Lamellar trama* bilateral with pale coloured lateral hyphae divergent from central mediostratum of gelatinised, cylindric, hyaline hyphae with yellowish contents in aq. alkaline solutions. *Clamp-connections* present, sometimes scarce.

Chemistry: Not known. Spore reactions unknown.

Ecology: Terrestrial, in tropical and subtropical, montane forest; apparently not ectomycorrhizal.

Distribution: Known only from South America (Argentina) and Central America (Mexico).

Only a single species known, very closely related on spore morphology alone to the boletoid *Boletellus,* but differs in its lamellate hymenophore; it superficially resembls *Phylloporus q.v.* or *Gomphidius q.v.*, in the presence of lamellate hymenophore.

The single species is described by Singer in the original paper and in Nova Hedw. **7**, 1964: an expanded description supported by line-drawings is provided by Horak (Beitrage zur Kryptogamenflora der Schweiz **13**, 1968) and by Petersen (J. Elisha Mitchell Sc. Soc. **90**: 53-54, 1974).

PHYLLOBOLITES Singer, Ann. Mycol. **40**: 59, 1942 – see rejected names. Plate 11 C.

PHYLLOPORUS Quél. In Flore Mycol. 409, 1888. Plate 11 D.

Type species (selected): *Paxillus pelletieri* Lév. apud Crouan (= *P. rhodoxanthus* (Schwein.) Bres. ssp. *europaeus* Singer).

Basidiome epigeal, pileate, hymenophore lamellate, centrally stipitate or slightly excentric, putrescent, gymnocarpic. *Spore print* olivaceous ochre.

Pileus convex but soon expanded and margin becoming wavy, velvety tomentose, becoming smooth and sometimes cracking, olivaceous brown or red-brown. *Stipe* cylindric or fusiform and then slightly attenuated upwards, or from halfway down tapered, sometimes becoming even rooting, pale at apex and some shade of yellow below or concolorous or paler than pileus and soon becoming streaked or spotted with pileus-colour. *Gills* thick, almost waxy, decurrent, with or without distinct interconnecting veins, sometimes almost elongate-poroid, rich yellow at first then more luteous and flushed sienna or rust-colour to chestnut where bruised, finally becoming tinged olivaceous. *Context* pale lemon-yellow or even white in stipe with pinkish colours under cuticle of pileus, unchanging or cyanescent and in some taxa nigrescent.

Basidia elongate-clavate, hyaline, usually 4-spored. *Basidiospores* fusiform to elongate-ellipsoid or ellipsoid, smooth, although slightly rugulose under SEM, with suprahilar depression, pale honey-colour in aqueous mounts and aq. ammo-

niacal solutions, inamyloid, acyanophilic. *Cheilocystidia* fusiform to cylindrical, some septate and many with elongated apex, some even pointed; *pleurocystidia* similar, prominent, some with yellow pigment in aq. ammoniacal solutions, thin-walled. *Tube trama* strongly divergent with poorly gelatinised lateral strata, divergent from scarcely darker central strand of hyphae. *Pileipellis* an intermingled layer of filamentous, smooth or slightly encrusted to granulate hyphae with swollen or rounded end-cells many of which are suberect to erect. *Stipitipellis* of parallel hyphae supporting an irregular layer of clavate, pyriform, yellowish or hyaline cystidioid elements. *Clamp–connections* not seen.

Chemistry: Most taxa become vivid blue-green with ammoniacal vapours. Variegatic acid and badione pigments isolated.

Cytology: Ploidy levels of 2x in *P. bellus* (Mass.) Corner*, P. rhodoxanthus* and *P*. cf. *rufescens* Corner (Bresinsky & Bresinsky-Wittmann, 1994).

Ecology: Terrestrial, ectomycorrhizal with Fagales in the temperate Northern Hemisphere and with Dipterocarpaceae and Myrtaceae in Australasia.

Distribution: A relatively small genus distributed in both hemispheres although probably best represented in Australia and in Malaysia.

In molecular studies it would seem that the type species falls neatly within the branch containing *Boletus subtomentosus* Fr.: Fr. and so the genus has by some been sunk in a restricted concept of *Xerocomus q.v.* as *X. rhodoxanthus* (Schwein.) Binder. It is very probable that not all *Phylloporus* spp. demonstrate the same molecular characters and the genus is polyphyletic; studies in this area are already underway by Maria-Alice Neves and Roy Halling, New York Botanical Garden New York, US. The single South American taxon requires further investigation.

For good keys to Malaysian and extralimital taxa with line-drawings and colour illustrations see Corner (Nova Hedwigia **20**: 793 – 822, 1970). Colour photographs are found in Bessette, Roddy & Bessette, *North American Boletes* 2000, Imazeki *et al*. *Fungi of Japan*, 1988 and for the single European species Breitenbach & Kränzlin, *Champignons de Suisse*, Vol. 3, 1991. In Engel *Schmeir- und Filzröhrlinge s.l. in Europa*, 1996 colour photograph, line-drawings and full list of world species are given. African species are described with coloured illustrations by Heinemann & Rammeloo, *Flore Illustrsée des Champignons d'Afrique Centrale* Fasc. 13, 1987. Useful key to *Phylloporus* in the neotropics appear in Singer (Persoonia **9**, 1978).

PISOLITHUS Alb. & Schwein. in Consp. Fung. Lusitiae 82, 1805. Plate 11 E.

Type species (selected): *Pisolithus arenarius* Alb. & Schwein. *(= Pisolithus arrhizus* (Scop.) Rauschert).

Basidiome gasterocarpic, epigeal or subhypogeal, one species totally hypogeal, subglobose, ellipsoid and almost sessile to clavate and elongated into a pseudostipe formed from coalescing thick, rhizoid-like structures, often incorporating soil particles; upper part forming swollen, smooth or slightly cracked to distinctly squarrose head, thinning and peeling away to expose pseudoperidioles and, at maturity, spore-mass.

Peridium very thin, pallid, buff to ochraceous or even fulvous or orange, often darkening on maturity and even nigrescent, especially where bruised, producing olive-black patches or smears, smooth to squarrose, cracking and disintegrating from apex downwards. *Stipe* absent or when present composed of fused rhizoidal structures with coloured, basal mycelial cords. *Gleba* divided by tramal plates to form many subspherical to ellipsoid and slightly compressed pseudoperidioles with gelatinised walls, whitish at first but rapidly ochraceous and breaking down forming pulverulent mass of ochraceous, fulvous or slightly olivaceous spore-mass; *pseudoperidioles* larger towards the apex of the basidiome. *Context* yellowish, orange etc. and in wet weather exuding yellow, brown or orange dye which stains objects with which it comes into contact.

Basidia clavate, hyaline, evanescent, surmounted with very short sterigmata, 2- to 6-spored. *Basidiospores* globose, thick-walled, distinctly ornamented with either isolated, long, curved spines, wavy ridges, coalescent conical warts or a crude, irregular reticulum, often < 2.5µm high, dark yellowish brown, inamyloid, acyanophilic. *Clamp-connections* present.

Chemistry: Norbadione-A, and small quantities of related pigments, isolated, some commencing yellow and turning salmon with ammonia and others brown and turning violet with ammonia. The coloured dye is a pulviquinone; see Gill & Watling (Plant Systematics & Evolution **154**: 225-236, 1986). Used on a commercial scale in the Middle Ages, hence the common name dye-ball, and the origin of the later epithet 'tinctorius.'

Ecology: Terrestrial, ectomycorrhizal with conifers, eucalypts and dipterocarps; the type species is an important source of ectomycorrhizal inocula and is found in the literature under the more familiar name of 'PT' *viz. Pisolithus tinctorius*

(P.Micheli: Pers.) Coker & Couch. It prefers mineral soils often in arid, even subdesert, conditions where it has gained the name Donkey dung fungus.

Distribution: Widely distributed in all but the coldest climates, and has undoubtedly been introduced in association with planting stock to some countries, e.g. South & East Africa. In Agerer 63 *P. tinctorius* (= *P. arhizus*) with *Picea abies* (Pinaceae): 80 *P. aurantioscabrosus* R. Watl. with *Shorea parvifolia* (Dipterocarpaceae).

A small genus with about 10 constituent taxa but which, for a long time, was thought to contain but one variable species. Although the macromorphology is variable it is not as variable as was once suggested; the spore-morphology is constant for certain well-differentiated populations which are supported by molecular data. The variability has led to the description of several species and by molecular techniques it has now been possible to unravel different species that appear to be geographically restricted and highly host specific. The picture has been made rather cloudy because several Australian species have been introduced to other parts of the world e.g. Africa and Thailand, with eucalypt plantings. Molecular studies have been carried out by Anderson *et al.*
(Mycol. Research **105**: 1304-1312, 2001) and Martin, F. *et al*. (New Phytol. **153**: 345-357, 2002)
Several authors have published molecular trees for this genus and Priest has carried out a monographic study of Australian species, yet to be published. The subterranean *P. hypogaeus* Thomas *et al.* is described in Mycotaxon **87**: 405-410, 2003. Tropical taxon have been described by Watling *et al*. (Nova Hedw. **61**: 417-429, 1995) and Kanchanaprayudh *et al.* (Mycotaxon **88**: 463-467, 2003). Burges *et al*., (Mycol Research **99**, 1995) link mycogeography with the results from molecular studies.

Colour illustrations of Australian taxa are found in Bougher & Syme *Fungi of Southern Australia*, 1998 and of the sole European species in Pegler *et al*. *British Puffballs, Earthstars and Stinkhorns*, 1995. B/w illustrations of so-called *P. tinctorius* are found in many texts but the identity of the subject may not be correct.

Synonyms:
Durosaccum Lloyd in Mycol. Writ. **7**: 1306, 1924; based on *Durosaccum pisiforme* Lloyd supported by very poor b/w photograph.
Favillea Fr. in Fung. Natal. 32, 1848; based on *Favillea argillacea* Fr., itself an unnecessary name change for *Polysaccum degenerans* Fr. (in Lehman, Pl. Preiss.

2: 139, 1846).
Endacinus Rof. in Precis dec. Deconu.et trav. semol 52, 1814.A synonym of *Pisolithus* fide Saccardo Syll. Fung **7**:148, 1888. The fungus is certainly a species of *Pisolithus* and Lloyd, amongst others, has suggested *Polysaccum pisocarpium* Fr. *(= P. arrhizus)* in its widest sense. For further information see May, T., Milne, J., Shingles, S. & Jones, R.H. Fungi of Australia **2B**: 238-240, 2003.
Lycoperdidodes P. Micheli in Nov. Pl. Gen 219, 1791; based on *Lycoperdoides tuberosum* P. Micheli.
Pisocarpium Link, Mag. Ges. Naturwissen. Freunde Berlin **3**:33, 1809; based on *Pisocarpium clavatum* Nees.
Polysaccum DC. & F. Desp., Rapp.Voy. Bot. L'Ouest Fr. **1**: 8, 1807; based on *Polysaccum crassipes* DC.
Polypera Pers. in Traité sur les Champignons comestibles (Paris), 116, 1818. Based on *Polypera crassipes* Ficinus & Schub. In Fl. Dresd 2: 306.

PODOSERPULA D.A.Reid, Kew Bull. **16**: 438, 1963. Plate 12 A.

Type species (only original species): *Craterellus pusio* Berk. (= *Podoserpula pusio* (Berk.) Reid.

Basidiome epigeal, complex, multistoried, divided into lobes spaced along a vertical column, either completely circular with stipe piercing centre or partially reduced and then on one side, rather tough, gymnocarpic. *Spore print* white.

Pileus as 4-8 tiered lobes, suede-like, dry, rust-coloured to fulvous, smooth. *Stipe* solid, terete or sometimes flattened, longitudinally fibrillose, sometimes divided near top lobe, diameter and distance between each inter-lobe varying, concolorous with hymenium. *Hymenium* on lower surface, subdecurrent ending abruptly at stipe, composed of low, blunt, bifurcating, soft ridges, radiating out from centre, divided into nodules especially near stipe-attachment, pinkish orange. *Context* pale pinkish orange, thin in lobes, unchanging on bruising.

Basidia narrowly clavate, hyaline, 4-spored. *Basidiospores* hyaline, small, broadly ellipsoid to subglobose, slightly thick-walled, hilar appendage very small, inamyloid, cyanophilic? *Cystidia* absent although poorly differentiated cystidiform cells found in some parts of hymenium and then cylindric, contorted and sometimes multiseptate. *Pileipellis* not strongly differentiated, composed of filamentous elements. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Saprotrophic on rotting wood or terrestrial amongst litter, particularly close to old stumps, in both native forest and plantations, including pine. Possibly obligately ectomycorrhizal.

Distribution: Known from New Zealand, Australia and South America (Venezuela) and possibly Malaysia.

A currently monotypic genus, although the constituent taxon is rather variable and several varieties based on minor characters have been recognised. This is a rather unusual genus assigned to the Coniophoraceae which includes the agaricoid *Hygrophoropsis q.v* and some species of *Leucogyrophana.q.v*

The species has been illustrated with line-drawings and documented with several varieties by Reid (Kew Bull. **16**: 438, 1963). Colour illustrations appear in Bougher & Syme, *Fungi of Southern Australia*, 1998.

PORPHYRELLUS E.-J. Gilbert in Les Bolets 99, 1931. Plate 12 B.

Type species (only original species): *Boletus porphyrosporus* Fr. & Hök (= *Porphyrellus porphyrosporus* (Fr. & Hök) E.- Gilb.

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, probably gymnocarpic. *Spore print* reddish brown to chocolate-colour.

Pileus convex then plano-convex, tomentose to velvety only rarely becoming gradually smooth, generally dark coloured or if not commencing so, ranging from horn-colour and sepia to olivaceous brown or snuff-brown to hazel, sometimes tinged purplish date or dark cinnamon, darkening with bruising in dark brown shades. *Stipe* equal or attenuated upwards, concolorous with pileus or slightly paler at the apex, soon darkening with olivaceous or purplish tints and even darker with handling, pruinose especially at apex or tomentose, even velvety downwards and sometimes slightly longitudinally ribbed, adhering to mycelial wefts at base which, at least in one species, are lilac. *Tubes* pale vinaceous buff, becoming ochraceous brown then olivaceous buff, finally with purplish cast, subdecurrent or depressed about stipe-apex; *pores*, concolorous but finally distinctly sienna, bluish green on bruising and finally black. *Context* pale, almost white or straw-colour but then flushing rubescent or vinacescent, or gradually cyanescent or not when exposed to air. *Odour* & *taste* slightly acidulous.

Basidia elongate-clavate, smoky grey in aqueous mounts, darkening further in aq. alkaline solutions, 4-spored. *Basidiospores* fusoid cylindric, obscurely inequilateral, with suprahilar depression, smooth, slightly purplish cast in aqueous mounts, darkening in aq. alkaline solutions, inamyloid, acyanophilic. *Cheilo- & pleurocystidia* scattered, clavate-mucronate to fusoid ventricose, often with dark brown contents, especially in aq. alkaline solutions. *Tube trama* bilateral, hyaline, lateral hyphae divergent from non-gelatinised, narrow, pale central zone. *Pileipellis* a trichoderm of hyaline, filamentous, smooth hyphae, slightly shortened towards end and end-cells tapered to become subacute, finally collapsing. *Stipitipellis* pruinose especially at apex from cells similar to cheilocystidia, although more clavate. *Clamp-connections* not seen.

Chemistry: On application of aq. alkaline solutions the basidiome darkens to become almost fuligineous black. In the type species the basidiomes turn white paper, or even the fingers, blue after handling.

Cytology: Ploidy level 3x in *P. porphyrosporus* (Wittmann-Meixner, 1989).

Ecology: Terrestrial, ectomycorrhizal especially with Fagales and conifers and in the tropics with Dipterocarpaceae and Myrtaceae.

Distribution: Known from temperate parts of the New and Old Worlds, but with several representatives in the tropics.

This genus has been maintained here in the original sense, although Smith & Thiers (*The Boletes of Michigan*, 1971) made it a subgenus of *Tylopilus q.v.*, a position supported by Wolfe & Petersen, (Mycotaxon **7**: 153-162, 1978 & Wolfe Biblio. Mycol. **69**, 1979). Such a move is not supported by molecular studies. In the sense of Singer (Farlowia **2**, 1945) the genus contained at least two elements each of which have subsequently been placed, even by Singer, in other genera. Originally classified with *Strobilomyces q.v.* in the Strobilomycetaceae the genus was later transferred to a place close to *Tylopilus*. In fact molecular studies have supported the original disposition. The spores are smooth although it has been reported by Singer that in a given spore-print there are a few spores which are ornamented; this has not been confirmed in material the author has examined; see also Pegler & Young, (Trans Brit. Mycol. Soc.: **76**, 1981). Wolfe (Nova Hedw. **43**, 1986) has applied numerical analysis to members of this genus under a wider concept of *Tylopilus*.

Descriptions of taxa can be found in regional mycota, with those for Malaysia,

supported by line-drawings and colour illustrations, are considered by Corner (*Boletus in Malaysia*, 1972) within his broad concept of *Boletus*. See Bessette, Roddy & Bessette, *Boletes of North America*, 2000 and Imazeki *et al*., *Fungi of Japan*, 1988. The sole European member is illustrated in Breitenbach & Kränzlin, *Champignons de Suisse*, Vol. 3 1991. Key to Central American species found in Singer & Gomez (Nova Hedw. **102**, 1991) accompanied by line-drawings.

Synonyms*:*
Phaeoporus J. Bataille, Bull. Soc. Hist. Nat. Doubs **35**: 11, 1908. This is a later homonym of *Phaeoporus* J. Schroet., 1888 placed in the Polyporaceae. Bataille's genus is based on *Boletus porphyrosporus.* Fr. & Hök., the type of *Porphyrellus*.
Porphyrosporus (Smotl.) ex Konrad & Maubl. in Icon. Selectae Fungorum **6**: 451, 1937; this genus although quoted appears to have never really been introduced at generic rank. It is based on the type of *Porphyrellus*.

PSEUDOBOLETUS Šutara in Ceská Mykol. **45**: 2, 1991. Plate 12 C.

Type species (only original species): *Boletus parasiticus* Bull.: Fr. (= *Pseudoboletus parasiticus* (Bull.: Fr.) Šutara).

Basidiome epigeal, pileate, tubulate hymenophore, centrally stipitate, attached to earthballs (*Scleroderma*) or barometer fungi (*Astraeus*), overall shape dependent on position taken on the host fungus, tough but finally putrescent, probably gymnocarpic. *Spore print* olivaceous snuff-brown.

Pileus convex to semiglobate, minutely tomentose but becoming smooth with age or slightly fibrillose-scaly and sometimes cracking, straw-colour or ochraceous, becoming flushed olivaceous or even sienna, dry, margin wavy. *Stipe* cylindric-curved, sometimes compressed, often tapering, paler or concolorous with pileus or ochraceous and becoming streaked rust-brown with age. *Tubes* adnate to subdecurrent, ochraceous lemon-yellow at first then ochreous to rust-colour; *pores* lemon-yellow then ochraceous flushed with rust-colour at maturity, non-cyanescent on bruising *Context* pale lemon-yellow or with rust-brown colours towards stipe-base, non-cyanescent.

Basidia clavate, hyaline, thin-walled, 4-spored. *Basidiospores* elongate-fusoid, cylindric with tapered apex, suprahilar depression present, pale honey-colour in aq. ammoniacal solutions, smooth although under SEM minutely longitudinally pitted in *P. parasiticus*, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* fusiform, cylindric to lageniform, often with apical swelling, numerous, hyaline

or pale straw-colour, cheilocystidia crowded at orifice. *Tube trama* with pale, hardly gelatinised hyphae divergent from pale central zone. *Pileipellis* of filamentous, hyaline or slightly pigmented, smooth hyphae forming a tangled layer but with poorly, only slightly swollen end-cells. *Stipitipellis* of parallel hyphae supporting scattered patches of caulohymenium. *Clamp-connections* not seen.

Chemistry: Not known.

Cytology: Ploidy level 2x in *P. parasiticus* (Witmann- Meixner, 1989).

Developmental studies: Development of the basidiomes of the type species has been studied by Reijnders (1948) & Kühner (1926) and by *S*utara (1991)– see above.

Ecology: Parasymbiont attached to sclerodermatoid stomach fungi and probably in a relationship with them and the host tree. Some evidence of parasitism; see Kavina, 1946. Apperntly not distributed as widely as the hosts.

Distribution: Known from temperate Northern Hemisphere, including Europe, North America and Japan.

A small genus of three species, previously placed in *Xerocomus*, which is well characterised by anatomical differences and unique ecological requirements. The genus is supported by molecular studies.

All species are thoroughly described in their regional mycotas. Colour illustrations and descriptions of *B. parasiticus* appear in N. American and many European texts; see General references. Line-drawings of microscopic characters and good colour photographs in Engel *et al. Schmeir- und Filzröhrlinge s.l. in Europa*, 1996. Colour photograph under *Xerocomus astraeicola* appears in Imaz., in Imazeki *et al.*, *Fungi of Japan*, 1988.

***PSEUDOGYRODON** Heinem. & Rammeloo, Bull. Jard. Bot. Nat. Belg. **53**: 295, 1983. Plate 12 C.

Type species (only original species): *Pseudogyrodon isabellinus* Heinem. & Rammeloo.

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent,

gymnocarpic. *Spore print* brown.

Pileus almost funnel-shaped, centre strongly depressed, margin lobed, grey-brown, darker at centre, probably dry. *Stipe* cylindric, concolorous with pileus, continuous with pileus, smooth, slightly velvety downwards with white basal mycelium. *Tubes* , probably concolorous, short, decurrent; *pores* polygonal, large and radially arranged, large. *Context* soft.

Basidia hyaline, pyriform with drawn-out base, 4-spored. *Basidiospores* subglobose or very shortly ellipsoid, smooth, very thick-walled, olive-brown containing a refringent central body, inamyloid, cyanophilic. *Cheilocystidia* absent or little differentiated; *pleurocystidia* similarly absent or poorly developed or represented by extremities of oleiferous hyphae. *Tube trama* slightly thickened, subregular with some elements divergent, with oleiferous hyphae and amorphous brown concretions. *Pileipellis* of interwoven, filamentous hyphae. *Stipitipellis* of parallel, cylindric hyphae some with brown contents and intermixed with brown amorphous material, supporting irregular claviform cells. *Clamp-connections* present.

Chemistry: Negative ME; basidiospores orthochromatic in Cotton blue solutions.

Ecology: Saprotrophic on rotten trunk in dried–up flood area.

Distribution: West Africa (Ghana).

A monotypic genus. *Pseudogyrodon* is closely related to *Boletinellus q.v.* but differs particularly in the thick-walled, rounded, cyanophilous basidiospores.

Line-drawings with original description and good illustration in Heinemann & Rammeloo, *Flore Illustrée des Champignons d'Afrique Centrale* Fasc. 14, 1983 but the basidiomes looks rather pale compared with the original description.

PSEUDOMERULIUS Julich, Persoonia **10**: 330,1979. Plate 12 F.

Type species (only original species): *Merulius aureus* Fr. (= *Pseudomerulius aureus* (Fr.) Julich).

Basidiome resupinate crust, effuse to effuso-reflexed, frequently confluent, coriaceous-membranous, adnate, lacking rhizomorphs, monomitic, putrescent, gymnocarpic. *Spore-print* yellowish brown.

Crust pale at first, white at extreme margin, becoming sulphur-yellow to bright greenish yellow, tomentose, abrupt. *Hymenium* distinctly merulioid when fresh, yellow to brownish, bright yellow towards margin, darker when dry, shallow, narrow folds continuous, radiating, frequently raduloid, sometimes anastomosing to form irregular pits. *Context* fragile, white when fresh, pallid when dry, homogeneous .

Basidia hyaline, suburniform or narrowly clavate, 4-spored. *Basidiospores* light yellowish, cylindrical or slightly curved, smooth, slightly thick-walled, inamyloid, acyanophilic. *Cystidia* absent. *Context* of hyaline, thin-walled hyphae or those towards base more thickened and distinctly swelling in aq. alkaline solutions. *Clamp-connections* present.
Chemistry: In aq. alkaline solutions exuding yellow pigment.

Ecology: Saprotrophic, lignicolous on wood and bark of Pinaceae, esp. *Pinus*; forms a brown rot.

Distribution: Know from north temperate forests in Europe and North America, and from Caribbean (St Vincent); also occurring in Australia.

A small genus of two or even three taxa, only two of which were transferred by Julich. Ginns in his analysis of *Merulius* spp. (Can J. Bot, **54**, 1976) did not consider *Merulius aureus* typical of the genus and although with some similarities to *Plicatura* he considered it also similar to *Paxillus panuoides* (Fr.) Fr. = *Tapinella q.v.* He refrained from making a new genus. The second species *Merulius elliottii* Mass., which is only known from the type collection, differs in its abundant, white rhizomorphs and *M. baileyii* Berk. & Broome has a thick context and dimidiate habit; the basidiospores of all three are similar. *M. baileyii* from Queensland is similar also to *Paxillus curtisii* Berk. apud Berk. & Curtis, which has been placed by Singer *et al*. in *Meiorganum q.v.*, although previously assigned to *Paxillus* sect. *Panuoides,* viz. *Tapinella q.v.*

The genus has not been monographed and descriptions of species are scattered in regional mycotas. Descriptions of *P. aureus* and *Merulius elliottii* are given in Ginns (Can, J. Bot. **54**, 1976) and of *M. baileyii* in an earlier publication (Mycologia **63**, 1971).

***PSILOBOLETINUS** Sing., Farlowia **2**: 250, 1945. No fig.

Type species (only original species): *Phylloporus larceti* Sing. (= *Psiloboletinus larceti* (Sing.) Sing.).

Basidiome epigeal, pileate, hymenophore lamellate, centrally stipitate, evelate, putrescent, gymnocarpic? *Spore-mass* burnt almond-colour or beige.

Pileus convex then plano-convex. depressed, dry, tomentose and at first with strongly incurved margin, tomentose but not breaking up into scales, alutaceous or pale fuscous. *Stipe* hollow, yellowish fuscous to olivaceous grey-fuscous at punctate apex to olivaceous umber-brown below, lacking glandular dots, becoming blackish on handling, velvety. *Gills* dilute brown to pale fuscous, cyanescent and finally browning, at stipe and margin, becoming radially arranged, decurrent and anastomosing, rather wide and somewhat compound, subvenose, seriate. *Context* orange-yellow then brownish, soft, fragile and spongy, cyanescent on bruising. *Odour & taste* mild, not distinctive then agreeable.

Basidia clavate (36-48 x 6-7 µm Horak, 1968), 4-spored. *Basidiospores* dilute fuscous yellow, cylindric to subclaviform to fusiform, thin-walled, smooth, elongate, smooth, light ochraceous brown, rather thin-walled, smooth, lacking apical pore, suprahilar applanation and depression, inamyloid, acyanophilic. *Cystidia* fusiform rarely constricted about middle or cylindric with apical prolongation, hyaline, smooth or with strong yellow encrustation, numerous. *Lamellar trama* mainly of the *Boletus* type, divergent from central strand. *Pileipellis* of radially arranged hyphae in outer layers forming trichoderm which collapses with age to form a cutis seated on filamentous, intertwined, smooth or encrusted, thin-walled, yellow-brown hyphae, with rounded terminal cells intermixed with hyaline elements roughened with darker material, some resembling oleiferous elements. *Clamp-connections* present.

Chemistry: With iron salts olivaceous; with aq. ammoniacal solutions yellow-brown.

Ecology: Terrestrial, ectomycorrhizal with *Larix sibirica.*

Distribution: Only know from North East Asia (Altai Mountains, Siberia).

A poorly defined genus superficially resembling *Phylloporus q.v.*, where the only known species was originally placed by Singer. Subsequently assigned close to *Boletinus* by the same author, which itself is now considered part of

Suillus. q v. Smith (Mycologia **68**, 332, 1966) has discussed the species at length without coming to any firm conclusion except that the genus may be congeneric with *Fuscoboletinus*, another genus now placed within *Suillus*.

The single species was not particularly well described originally but a good description is offered by Horak (Beitrag. Krypto. Schweiz **13**: 523, 1968). Fresh material is urgently required to make a final disposition.

PULVEROBOLETUS Murrill, Mycologia **1**: 9, 1909. Plate 12 E

Type species (only original species): *Boletus ravenelii* Berk. & M. A. Curtis (= *Pulveroboletus ravenelii* (Berk. & Curtis) Murrill).

Basidome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, hemiangiocarpic from enveloping pulverulent-arachnoid veil. *Spore print* smoky olivaceous brown.

Pileus almost hemispherical to obtusely convex then plano-convex, rarely plane, dry, surface with lanose or powdery coarse or fine particles, slightly viscid in wet weather after loss of powdery material, bright shades of yellow (sulphur-yellow, lemon-yellow, chrome-yellow, greenish yellow) throughout, brown showing through especially at disc as powdery particles disperse by erosion from abrasion with vegetation or soil, margin incurved and bordered with powdery or lanose veil material. *Stipe* equal or attenuated upwards, exannulate, solid, pale yellowish or even pinkish below dusty particulate matter, concolorous with pileus, more strongly coloured below with age, darkening when bruised, attached to whitish, yellow or pale pinkish mycelial strands. *Tubes* adnate or slightly depressed around the stipe-apex, lemon-yellow to luteous but soon with olivaceous tinge, cyanescent; *pores* small, round or nearly so, yellow with distinct olivaceous tint which strengthens with maturity, cyanescent, finally fuscous where bruised. *Context* whitish to yellowish, strongly or faintly cyanescent, finally becoming drab. *Odour* indistinct & *taste* acidulous.

Basidia clavate, thin-walled, hyaline to slightly yellowish especially in aq. ammoniacal solutions, 4-spored. *Basidiospores* slightly fusoid-cylindric to shortly ellipsoid, smooth, pale straw-colour in aqueous mounts and aq. ammoniacal solutions, with or without suprahilar depression, sometimes partly pseudoamyloid, acyanophilic. *Cheilocystidia* cystidioles or shortly fusoid-ventricose, hyaline to yellow in aq. alkaline solutions; *pleurocystidia* similar or often shortened and

inconspicuous or absent. *Tube trama* gelatinised throughout and lateral hyphae divergent from a slightly darker, central strand. *Pileipellis* of tangled, narrow, filamentous, yellow or hyaline hyphae with yellow encrustations intermixed with yellow amorphous material, reddish brown in ME. *Stipitipellis* of parallel hyphae covered in tangled mass of filamentous, yellow hyphae and detritus. *Clamp-connections* not seen.

Chemistry: No chemical reactions noted, except the elements of the pileipellis become red-brown in ME in the type species. Vulpinic acid isolated.

Cytology: Ploidy level of 1x in *P. icterinus* (Pat & Baker) Watl. Bresinsky & Wittmann-Bresinsky, 1994).

Developmental studies: For type species see Corner (1972).

Ecology: Terrestrial, ectomycorrhizal with Fagales and with Dipterocarpaceae.

Distribution: Known from North America, Australasia and India; possibly also East Africa.

This is a genus which has been hugely modified by Singer (Farlowia **2**, 1945 *et subseq.*) to include many disparate elements; see Watling (Mycol. Research **105**, 2001 & Aust. Syst Bot. **14**, 2001; 1988), Watling & Gregory (Proc. Roy. Soc. of Queensland **99**, 1988) and Smith & Thiers, *Boletes of Michigan*, 1971. *Boletus sulphureus* Fr*., B. retipes* Berk. & M. A. Curtis and *Ixocomus gentilis* (Quél.) Quél. have all been placed by Singer and others in *Pulveroboletus* but are now assigned to *Buchwaldoboletus, Retiboletus* and *Aureoboletus* respectively, *q.v.*. Such moves have been supported by the results from molecular analysis. The type species differs dramatically in its chemistry from the others in exhibiting vulpinic acid derivatives. Some species still require assessment, *e.g*. *Boletus curtisii* Berk. *apud* Berk. & M.A. Curtis. It is proposed to maintain the genus as originally conceived with close relationships with *Chalciporus q.v.*

Good descriptions and colour or b/w illustrations of the type species are found in North American and Japaneses regional mycotas and related tropical species in Corner, *Boletus in Malaysia*, 1972.

RETIBOLETUS Binder & Bresinsky, Feddes Repetorium **113**: 36, 2002. Plate 13 A.

Type species (originally designated): *Boletus ornatipes* Peck (= *Retiboletus ornatipes* (Peck) Binder & Bresinsky).

Basidome: epigeal, pileate, hymenophore tubulate, centrally stipitate with distinct yellow network, evelate, putrescent, gymnocarpic ? *Spore print* olive-brown.

Pileus dry, slightly tomentose at first but soon smooth and often with slight granular appearance at margin, convex to plano-convex or slightly wavy at margin, olivaceous, greyish with mustard-yellow, citrine and olive patches or tinged even with fuligineous black. *Stipe* attenuated upwards, not strongly clavate, strongly reticulate forming elongate net-work, more tightly meshed at stipe-apex and less obvious downwards, paler towards apex. *Tubes* & *pores* pallid at first, slightly greyish then rich lemon- or chrome-yellow, often browning on bruising or age and finally orange-brown in places or unchanging, non-cyanescent. *Context* pallid yellow at most flushing with vinaceous pink or intense chrome-yellow especially towards stipe-base, becoming orange- to orange-brown at maturity in patches or in stipe-base, non-cyanescent. *Odour* not distinctive & *taste* bitter.

Basidia clavate, hyaline to yellowish especially in aq. ammoniacal solutions, 4-spored. *Basidiospores* narrowly ellipsoid to subfusiform with slight suprahilar depression, smooth, pale yellowish, inamyloid or some partly pseudoamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* ventricose, slender, bottle-shaped to fusoid, hyaline in aq. alkaline solutions when fresh but when dry strongly yellow. *Pileipellis* of rather broad hyphae, ochraceous to bistre, with amorphous masses filling the central area, turning dark red-brown in ME. *Stipitipellis* of longitudinal hyphae with torpedo-shaped end-cells intermixed or supporting balloon-shaped, swollen elements with similar contents to cystidia and reacting in similar fashion. *Clamp-connections* not seen.

Chemistry: Retipolides frequently present, exceptionally absent; in addition pulvinic acid derivatives sporadically occur. In some taxa yellow compounds stain the fingers on handling.

Ecology: Terrestrial, ectomycorrhizal with frondose trees at least in North America, with members of the Fagales.

Distribution: Distributed in North and Central America and Thailand, with one additional species only known from South East Asia.

A small genus of five species corresponding to *Boletus* subsect. *Reticulati* of sect. *Boletus* in Smith & Thiers (*Boletes of Michigan*, 1971). This is also *Pulveroboletus* sect *Reticulati* of Singer (Amer. Midl. Nat. **37**, 1947), which is one of the several groupings within *Pulveroboletus* accepted in this genus but totally inappropriate. Although *B. retipes* Berk. & M.A.Curtis was maintained in *Pulveroboletus* by Singer the very closely related and often synonymised *B. ornatipes* Peck was placed in *Boletus* sect. *Ornatipedes* close to sect. *Grisei*. The latter housed *B. griseus* Frost apud Peck, which has now been shown to be in *Retiporus*. Singer suggested a possible relationship between these two last species and *Tylopilus q.v.* because of the similar reaction of the cystidial contents in aq. alkaline solutions and ME. Molecular studies, however, show conclusively that this group of species is closely related and should be separated into their own autonomous genus, which sits as a clearly independent branch relatively close to the *B.sensibilis/B. bicolor* consortium. Strangely in addition to what was called *Tylopilus nigerrimus* Heim, now *Retiboletus,* some other fungi assigned to a tylopiloid ancestory, *e.g. Mucilopilus mucidus* (McNabb) Wolfe should be sought within *Retiboletus.*

Descriptions of the individual members of this genus may be found in the appropriate local mycotas under *Boletus*! Colour photographs are found in Bessette, Roody & Bessette, *Boletes of North America*, 2000 and Imazeki *et al. Fungi of Japan*, 1988.

RHIZOPOGON Fr. apud Fr. & Nordholm in Symb. Gastromycetum **1**: 5, 1817. Plate 13 B.

Type species (selected): *Rhizopogn luteolus* Fr.

Basidiome gasterocarpic, hypogeal but often subhypogeal at maturity, subglobose, tuberiform to irregular, often attached to fine mycelial cords which may adorn the peridium, putrescent, angiocarpic.

Peridium well-developed, thick, not separable, pale coloured to yellowish or tinged with yellow-brown or red-brown or becoming rich yellow or lilaceous especially on bruising or becoming flushed pinkish. *Columella* absent. *Gleba* loculate, partially gelatinised, with small, irregularly arranged, hollow chambers which become filled with honey-coloured or straw-yellow spore-mass.

Basidia cylindrc-clavate to lageniform, often collapsing, from 2- to 8-spored.

Basidiospores statismosporic, orthotropic, small to medium, allantoid, cylindric or broadly ovoid, subhyaline or slightly honey-coloured in aqueous mounts and aq. ammoniacal solutions, slightly thick-walled, smooth, lacking any conspicuous myxosporium, with very short hilar appendage, inamyloid, acyanophilic. *Cystidia* absent. *Hymenophoral trama* narrow, regular with some divergence of lateral hyphae, often slightly gelatinised. *Context* with thin to slightly thickened generative hyphae. *Peridiopellis* a repent epicutis of narrow hyphae overlain with skeins of hyphae adhering together to form mycelial cords. *Clamp-connections* not seen or scarce

Chemistry: Chemical reactions not significant, although discussed by Smith & Zeller (Mem. New York Bot. Gdn. **14**, 1966). Several species contain thelephoric acid, whilst others contain atromentic and xerocomic acids, and variegato-rubin; also other less common pulvinic acid derivatives and boviquinone derivatives have been isolated.

Developmental studies: See Talbot (Persoonia **7**, 1973).

Ecology: Terrestrial, ectomycorrhizal with conifers, found in the upper levels of the duff and often at maturity showing the upper part of basidiome which may deeply crack to expose the gleba beneath. In Agerer 21 *R. luteolus* with *Pinus sylvestris*; 104 *R. subcaerulescens* A.H. Smith; 135 *R. melanogastroides* M. Lange; 136 *R. vulgaris* (Vittad.) M. Lange (var. *intermedius*). Molina and colleagues (New Phytol. **126** & **134**, 1994 &1997 respectively) have undertaken a study of the biology of the genus *Rhizopogon* conducting inoculation experiments to examine host specificity etc. Martin *et al*. (Phyton **40**: 135-141) have utilised molecular techniques to study *Rhizopogon* on root-surfaces.

Distribution: In Northern Hemisphere within the distribution of Pinaceae, but found extensively in Australia and New Zealand with plantings of introduced exotic conifers; some records from S. America.

A very large genus with upwards of a reported 150 species, of which sect. *Rhizopogonella* has been separated out and placed in *Alpova q.v.,* although this genus seems, from the little molecular data so far gathered, to be an incorrect placement. Talbot (Persoonia **7**, 1973) has expressed some doubt whether the genus is monophyletic based on basidial morphology alone. Grubisha *et al.* (2001) have discussed the biology of *Rhizopogon* and bolete relatives inferred from LSU rDNA.

Good keys with some line-drawings and colour illustrations are available in Smith & Zeller (Mem. New York Bot. Gdn. **14**, 1966). This work is expanded in Harrison & Smith (Can. J. Bot. **14**, 1966) and Hosford & Trappe (Tran mycol Soc Japan **29**, 63, 1988). For the genus in Europe see Svrcek in Pilát (*Flora CSR: Gasteromycetes*, 1958) who offers b/w photographs and line-drawings, and keys in English and Czech; for an expansion which includes molecular studies and colour photographs see Maria P. Martin (*Edicions especiales de la Soc. Catalana di Micol.*, 1996). Colour illustrations and line-drawings of British taxa are found in Pegler *et al*. (*British Truffles*, 1993).

Synonyms:
Anthracophlous Mattir. ex Lloyd, 1913; type species as herb. name *A. rhizopogonoides* Mattir. Based on a collection from Mauritius it was sanctioned but without formal description in Lloyd *Mycological Writings* Letter **42**: 4, 1913. For further discussion see Mycol.Writings **6**: 1100, 1921. This is *Rhizopogon rubrocorticus* Zeller & Dodge based on the same collection in Lloyd's Herb. and formally described in Ann. Miss. Bot. Gdn. **5**,1921.
Hysteromyes Vittad. in Nat. natur. e. civ. sulla Lomb. **1**: 341, 1844, based on *H. vulgaris* Vittad., the same as *Rhizopogon vulgaris.*
Splanchnomyces Corda in Sturm's Deutschl. Flora **3. Abt. 3**: 3, 1837, based on *Rhizopogon luteolus* Fr. A synonym of *Rhizopogon* but as this genus is probably a mixed entity it may be available for use depending on the typification adopted if *Rhizopogon* is further divided..

*** RHODACTINA** Pegler & T.W.K.Young, Opera Botanica **100,** 101, 1989.

Type species (only original species): *Rhodactina himalayense* Pegler & T.W.K.Young.

Basidiome gasterocarpic, subglobose to subpyriform, with purplish to violet-brown or pinkish gleba.

Peridium pale lilaceous, pale purple to pale pink, glabrous and smooth. *Stipe & columella* absent, reduced to small basal attachment. *Gleba* irregularly to angularly loculate, chambers < 1.5.mm. broad, with pink or purplish brown spore-mass.

Basidia clavate to subcylindric, 4-spored with long, rigid sterigmata. *Basidiospores* statismatosporic, orthotropic, broadly ellipsoid to subfusiform, ornamented with solid, longitudinally arranged ridges as high as 3µm high, base

truncate, appearing stellate end-on, purplish red to pinkish purple to purple, wall distinctly dextrinoid. *Cystidia* absent. *Tramal plates* thin-walled, non-gelatinised to gelatinised. *Peridiopellis* poorly differentiated, composed of interwoven, thin-walled hyphae with brown encrustations. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: Ectomycorrhizal with Dipterocarpaceae.

Distribution: As yet only known from India and South East Asia (Thailand).

Although recognizing some affinity with the Boletales, the authors when introducing the genus nevertheless assigned *Rhodactina* to the Gauteriaceae, which they placed in the Cortinariales. This was despite the fact that they had found one collection attacked by *Sepedonium chrysospermum* Tul., a hyperparasite restricted to the Boletales. Recent molecular studies, however, have demonstrated quite clearly that the genus is indeed in the Boletales and sits close to *Chamonixia.*

The two component species are compared in Yang *et al.* (Mycotaxon **96**, 2006) where line-drawings are available.

* **ROYOUNGIA** Castellano, Trappe & Malajczuk, Aust. Syst. Bot 5: 614, 1992.

Type species (only original species): *Royoungia boletoides* Castellano *et al.*

Basidiome gasterocarpic, hypogeal, flattened to subglobose, bright yellow and when dry, finely tomentose to almost glabrous, angiocarpic.

Peridium minutely tomentose to nearly glabrous, bright golden yellow with one or two concolorous rhizomorphs. *Columella* cartilaginous, abruptly truncate, stout, concolorous with peridium, slowly staining bright red on exposure to air. *Gleba* brown at first then dark chocolate-brown from spore-mass within sublamellate and irregularly shaped, empty chambers. *Odour* none; *taste* not determined.

Basidia clavate, hyaline, 4-spored. *Basidiospores* fusoid to suballantoid, smooth, apex obtuse and base mostly symmetrical, occasionally asymmetrical, pale brownish yellow in aq. alkaline solutions, darker in mass, inamyloid. *Peridiopellis* single-layered cutis with pale yellow-brown to hyaline, compactly interwoven, thin-walled hyphae with many sharply tapered, erect hyphal tips. *Clamp-connections* not seen.

Chemistry: Yellow pigment immediately leached into mounts with aq. alkaline solutions.

Ecology: Terrestrial, probably ectomycorrhizal in mixed woodland with Myrtaceae (*Eucalyptus, Leptospermum* and *Melaleuca*) and Casuarinaceae (*Allocasuarina*).

Distribution: Known only from North Eastern Australia (Queensland).

Royoungia is only known from the type collection. The original authors suggest it is analogous to *Truncocolumella q.v.* and has affinities with *Gastroboletus boedijini* Lohwag, based on the shape and size of the basidiospores, divergent trama, *Boletus*-like basidia and the yellow pigment which easily leaches from the peridium.

Reference should be made to the original publication for b/w photographs of basidiomes and photomicrographs of spores.

RUBINOBOLETUS Pilát & Dermek, Ceská Mykol. 23: 81, 1969. Plate 13 E.

Type species (only original species): *Boletus rubinus* W.G.Sm. (= *Rubinoboletus rubinus* (W.G. Sm.) Pilát & Dermek).

Basidome: epigeal, squat, pileate, hymenophore tubulate, centrally stipitate, putrescent, probably gymnocarpic. *Spore print* pale fulvous to cinnamon buff.

Pileus convex then plano-convex, even plane, smooth to slightly downy, sometimes cracking to become slightly scaly with age, slightly viscid when young, buff, leather-colour to horn-colour with or without ochraceous tints, often with pinkish flush towards margin. *Stipe* evelate, obconic, short in contrast to size of pileus, less frequently swollen, ochraceous apricot- to peach-colour with pink or reddish descending wings from the tubes, often becoming splashed with red, smooth. *Tubes* subdecurrent, coral-colour, ochraceous pink in lower part; *pores* small to medium-sized, rounded then slightly angular, coral-coloured then with carmine tints, finally ochraceous pink throughout with age. *Context* white in pileus, lemon-yellow in stipe-base and coral above tubes. *Odour & taste* not distinctive.

Basidia: clavate, hyaline, 4-spored. *Basidiospores* ellipsoid to broadly ellipsoid,

smooth, with suprahilar applanation, pale yellowish brown in both aqueous mounts and aq. ammoniacal solutions, slightly yellowish in ME, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* fusiform, hyaline to pale yellowish, thin-walled; many cheilocystidia adhering together with some interspersed oleiferous hyphae. *Tube trama* bilateral with lateral hyphae divergent from slightly darker central strand. *Pileipellis* of repent, filamentous hyphae and shorter elements intermixed with smooth, suberect to erect end-cells and pale ochraceous contents. *Stipitipellis* of cylindric hyphae with clusters of subcylindric, slightly coloured, thin-walled caulocystidia. *Clamp-connections* not seen.

Chemistry: Not known; ME negative.

Ecology: Terrestrial, temperate members ectomycorrhizal with Fagales; see below for African members.

In the original sense a small genus encompassing only a few species with rich red tubes and pores. The genus was expanded by Heinemann & Rammeloo (Bull. Jard. Bot. Belg. 53,1983) to include a series of Central African boletes. The same authors included in the genus the complex around the North American *Boletus balloui* Peck, which is widespread in many parts of both New and Old Worlds, and probably represents a complex of closely related taxa. Until further research is undertaken this species is at best maintained in *Tylopilus q.v*., where it is currently placed, although it remains anomalous there. It is proposed to retain *Rubinoboletus* in its original circumscription.

Good accounts of type species in Watling & Hills (*British Fungus Flora* Vol. 1 revised and enlarged edition, 2006) and in other regional mycota. Colour illustration in Pearson (*The Naturalist, London,* Suppl., 1946).

African species considered to be component species are described and illustrated in Heinemann & Rammeloo (*Flore Illustrée des Champignons d'Afrique Centrale*, Fasc. 10, 1983). For colour or b/w illustrations of North American taxa which have been associated with *Rubinoboletus* see Bessette, Roody & Bessette, *Boletes of North America*, 2000 and Smith & Theirs, *The Boletes of Michigan*, 1971. For discussion on the limits of the genus see Watling & T.-H., Li, (Australian Boletes : A Preliminary Survey, 1999) and Watling & Gregory (Proc. Roy. Soc. Queensl. 99, 1988).

SCLERODERMA Pers. in Synops. Method. Fung. 150, 1801. Plate 13F & G.

Type species (selected): *Scleroderma verrucosum* Pers.

Basidiome gasterocarpic, epigeal or subhypogeal but epigeal at maturity, globose, reniform to tuberiform or with well-developed, stout pseudostipe, often associated with numerous basal rhizomorphs, firm, fleshy and persistent, angiocarpic.

Peridium straw-yellow to ochraceous brown, smooth or squamose to verrucose or with velvety tomentum, dry, tough, dehiscing by irregular apical tears or by weathering. *Stipe* absent or often reduced but in some species with prominent pseudotstipe, composed of rhizoid-like cords, attached to strongly developed basal mycelium. *Gleba* initially firm and hard, whitish soon mottled purple and finally purplish brown with or without olivaceous tinge, interveined with very thin, white tramal plates which disintegrate and intermix with olivaceous to purplish brown spore-mass. *Capillitium* absent. *Odour* often strong and sometimes quite unpleasant.

Basidia clavate to pyriform, hyaline, 6-8 spored. *Basidiospores* globose or occasionally subglobose, brown, thick-walled, with coarse reticulation, wings or coarse isolated verrucae, inamyloid, acyanophilic. *Cystidia* absent. *Hymenium* not developed, basidia forming in small clusters, shedding spores into mixture of hyphae and nurse-cells. *Clamp-connections* present in some species.

Chemistry: Sclerocitrin – D has been isolated from *S. citrinum* Pers., which is a tetraphenylquinone analogue of the naphthalenoid pulvinic acids assignable to the badione group.

Ecology: Terrestrial, on sandy and highly mineral soils in woodland or under isolated trees along banks, sometimes on wood. Ectomycorrhizal with a range of trees in Fagales, Pinaceae and many tropical genera. In Agerer 80 *Scleroderma citrinum* Pers.: Pers. & 144 *S. bovista* Fr.

Distribution: Throughout the continents in temperate and tropical areas, ranging from rainforest to arid areas.

A relatively small genus of about 25 taxa worldwide. Molecular work has shown the integrity of the genus and that *Veligaster*, proposed to hold the velvety, stipitate forms, nestles tightly within the centre of the genus. The genus is placed in the Sclerodermataceae.

Guzmán (Darwiniana 16, 1970) has monographed the species supporting his descriptions and discussion by line-drawings and b/w photographs. See also European mycobiota for good accounts incl. Pegler, Laessθe & Spooner (*British Puffballs, Earthstars and Stinkhorns*, 1995). Also Sims *et al* for Philippine taxa and key to species (Mycotaxon 56, 1995). Demoulin (Bull. Jard. Bot. Nat. Belg. 37: 289-304, 1967) has discussed the typification of the genus. Good illustrations are also found in Coccia *et al.* (Bol. Assoc. Micol. Ecol. Romana 7: 3-59, 1990).

Synonyms:

Actigea Raf. in Précis déc. Découv. et trav. somiol. 52, 1814; based on *Actigea sicula* Raf. = *Scleroderma geaster* Fr. Also as *Actigena*.

Caloderma Petri, Malphigia 14: 136, 1900 based on *Caloderma echinatum* Petri which is a true *Scleroderma*; see Guzmán (Darwiniana 16, 1970). Records from South East Asia by Watling & Sims, 2003. The synonymy has been confirmed by molecular studies.

Lycoperdastrum P. Micheli in Nova Plant. Gen. 219, 1729?; based on *Lycoperdiastrum obscurum* P. Micheli = *Scleroderma verrucosum* Pers. fide Guzmán, 1970.

Sclerangium Lév., Ann. Sci. Nat. Bot. Ser. 3, 9: 130, 1848; based on *Lycoperdon polyrhizon* J.F. Gmelin: L.

Neosaccardia Mattir., Annali Fac. Med. Vet. Torrino 56: 32, 1921, based on *Tuber echinata* Sacc. & Paoletti in Atti R. Inst. Veneto Sc. Lett. Art 6 ser. 6: 27, 1888, non *Caloderma echinatum* Petri noted above; see Guzmán *et al.* (Mycologia 96: 1370-1372, 2004). Reported as being a synonym of *Scleroderma* but a recent collection from Thailand (Watling, Mycoscience 47, 2006) suggests that this may be an autonomous taxon.

Nepotatus Lloyd, Mycol. Writ. 7 - *Mycol Not*. 75: 1355, 1925; based on *Nepotatus stellatus* Lloyd = *Scleroderma geaster* Fr.

Phlyctospora Corda in Sturm's Deutschl. Flora. 2: 51, 1841; based on *Phlyctospora fuscum* Corda = *Scleroderma fuscum* (Corda) E. Fischer.

Pirogaster Henn., Hedwigia 40: 27, 1901 = *Scleroderma* fide Demoulin; see Dictionary of Fungi 9th edition.

Pompholyx Corda in Sturm's Deutschl. Flora. 3: 47, 1851; based on *Pompholyx sapidum* Corda = *Scleroderma citrinum* Pers.

Stella Massee, Journ. Mycol. 5: 185, 1889; based on *Scleroderma stella* Berk. = *Scleroderma geaster* Fr.

Sterrebeckia Link, Mag, Ges. naturwiss. Freunde, Berlin 7: 44, 1816; based on *Sterrebeckia sterrebeckii* Fr. = *Scleroderma geaster* Fr. = *Actinodermium*.

Veligaster Guzmán, Mycologia, 61: 1119,1969; based on *Scleroderma columnare* Berk. & Br. Based on morphology alone considered to be a synonym of

Scleroderma by Demoulin & Dring (Bull. Jard. Bot. Nat. Belg. 45, 1975), a placement subsequently supported by molecular studies.

SERPULA Pers.: S.F. Gray, Nat Arrang. Br. Plants 1: 637, 1821. Plate 14 A.

Type species (selected): *Merulius destruens* Pers, (= *Serpula lacrimans* Wulf.: Fr.).

Basidiome resupinate crust even effuso-reflexed, soft, often waxy-membranous to floccose especially at margin, hymenium of irregular folds and veins with obtuse margins, finally gryrose, some parts persistent especially marginal and substrate rhizomorphs, gymnocarpic.

Hymenium of irregular folds and veins with obtuse edges, gyrose in large, older specimens, yellow-ferrugineous at first, becoming rich orange then rust-red, surrounded by fibrous or membranaceous sterile zone with fimbriate grey margin often with lilaceous or lavender hues, weeping droplets of liquid when fresh, frequently emanating from obvious rhizomorphs radiating out to form mycelial fans.

Basidia slender clavate, < 70µm long, 4-spored, with basal clamp-connection. *Basidiospores* ovoid to subglobose or broadly ellipsoid, smooth, orange-brown, rich red-brown in mass, inamyloid, cyanophilic. *Cystidia* lacking. *Hymenial hyphae* yellowish but hyaline elsewhere, many thick-walled and some of the broader hyphae containing crystals, many covered in amorphous sheath, some secretory. *Clamp-connections* present, widespread.

Chemistry: Atromentic, xerocomic and variegatic acids all isolated and also isoxerocomic acid, xerocomorubin and a quinone methide are all known from the type species.

Ecology: Saprotrophic, lignicolous on coniferous wood.

Cutural studies: Well-studied. This is the destructive **Dry rot fungus** of European and North American dwellings. See Cartwright & Findlay (1958) & Coggins (1980).

Human pathology: Basidiospores in houses affected by dry rot fungus known to cause asthma in owners.

Developmental studies: *Serpula* is described as possessing '*Cantharellus* type' hymenophoral development (Reijnders & Stalpers, 1992).

Genetics: Kauserud *et al*. (Molecular Ecology 15, 2006) have discussed the cryptic speciation and long-distance dispersal found in *S. himantioides*.

Distribution: Known from Himalayan India and presumably adjacent countries; introduced into North America, Europe, Australia etc.

A very small but economically important genus easily recognized by the merulioid hymenium and the rich rust-coloured spores. Often only seen in the grey (tinged yellow, pink or lilac) rhizomorphic state covering wooden timbers or passing through plaster and porous brick and forming sheets, or attached to membranous sheets on flat surfaces. Often called '*Merulius lacrimans'* but *Merulius* Fr., Syst. Mycol. 1, 326; (type species: *Merulius tremellosus* Schrad .: Fr.) is not related to *M. lacrimans* and therefore *Serpula*. *Merulius* in the sense of Haller has also been used for some cantharelloid fungi, again unrelated to *Serpula*. The genus is placed in the Austropaxillaceae.

Illustrated in colour in a whole range of regional mycotas, timber preservation text-books and popular accounts. The type species is well illustrated by line-drawings and colour photograph in Breitenbach & Kränzlin, Pilze der Schweiz, Vol. 2, 1986.

Synonyms:
Gyrophana Pat. in Cat. Rais. Pl. cell Tunis, 53, 1897; type species *Merulius lacrimans* Wulf.: Fr. (selected). A replacement name for *Gyrophora*.
Gyrophora Pat., Hymen. Urp. 143, 1887; type species *Merulius lacrimans* Wulf.: Fr. A generic name replaced by the same author 10 years later because of the prior use of the name in the lichens.
Xylomyzon Pers. in Mycol. Europ. 2, 26, 1825; type species *M. destruens* Pers. (selected) =*M. lacrimans* Wulf.: Fr.
Xylophagus Link per Murrill, Torreya 3: 7, 1909; type species *Merulius destruens* Pers. (selected) = *M. lacrimans*. A printing error appears in the 2nd edition of the Dictionary of Fungi *viz. Xylophflgus.*

***SETOGYROPORUS** Heinem. & Rammeloo, Bull. Jardin Bot. Nat. Belg. 52: 481, 1982. Plate 14 B.

Type species (only original species): *Setogyroporus verus* Heinem. & Rammeloo.

Basidiome epigeal, pileate, hymenophore tubulate with setules, centrally stipitate, putrescent, gymnocarpic. *Spore print* ochraceous.

Pileus pulvinate, velvety, very finely granular under lens, brown to ochraceous, slightly viridescent on bruising, slowly more green towards margin. *Stipe* cylindric, slightly flexuous, slender, attenuated towards base, ochraceous with yellowish fibrils. *Tubes* shortly adnate, yellow, very slightly cyanescent; *pores* concolorous, small, round then larger and angular towards stipe and with narrow dissepiments. *Context* soft, yellow in pileus, brownish under disc, grey-yellowish and marbled white in stipe. *Odour* slightly disagreeable; *taste* acidulous.

Basidia clavate, 4-spored. *Basidiospores* nearly hyaline, thin-walled, ellipsoid slightly flattened in side-view, greyish yellow in ME and with red endosporium in cresyl blue. *Cheilocystidia* abundant, lanceolate or claviform, hyaline, thin-walled; *pleurocystidia* similar or slightly thickened in lower part; *setules* in hymenium fusoid, thick-walled, hyaline with ochraceous summit but also at pileus-margin and stipe-base. *Tube trama* subregular. *Pileipellis* poorly differentiated of cylindric, yellow hyphae with fine zebra-like ornamentation and exuding pigment in aq. ammoniacal solutions; end-cells sublanceolate with obtuse ends. *Stipitipellis* a disrupted, poorly developed hymeniform layer with pyriform and claviform cells but rarely with basidia. *Clamp-connections* not seen

Chemistry: Easily dispersed, yellow pigments in aq. ammoniacal solutions.

Ecology: Terrestrial, possibly ectomycorrhizal with caesalpinoid legumes.

Distribution: Known only from Central Africa (Burundi).

The only known species has connections to *Rubinoboletus* in the interpretation of that genus adopted by Heinemann & Rammeloo in 1983; see above. This genus is characterised by the presence of setules and therefore has been related to *Boletochaete* differing in its disjunct hymeniform stipitipellis and the poorly developed pileipellis. This last genus Corner (*Boletus in Malaysia*, 119, 1972) has demonstrated to be a tylopiloid bolete. This fits in with Heinemann &

Rammeloo's concept as *Boletus ballouii* Peck which was transferred by them to *Rubinoboletus q.v.,* and which these authors placed amongst the gyroporoid boletes. *Tuboseta q.v.* is another genus of African boletes with setules but the structure of the basidiome is very different and the basidiospores are clearly boletoid, *viz*. subfusiform. The present genus should be assigned to the Gyroporaceae.

*** SINGEROMYCES** M.M. Moser apud Horak & M.M Moser, Nova Hedwigia **10**: 231,1966. Plate 14 C.

Type species (only original species): *Singeromyces ferrugineus* M.M. Moser.

Basidiome gasterocarpic, hypogeal, stipitate, outer sheath absent or rudimentary and soon exposing spore-producing tissues - sequestrate, putrescent, commencing gymnocarpic.

Pileus replaced by enveloping evanescent outer sheath. *Stipe* short, cylindric, brown and percurrent in upper part to form an irregular surfaced columella. *Tubes* replaced by irregularly lacunose or loculate structures, rust-brown. *Context* white.

Basidia cylindric, 4-spored with long sterigmata < 8µm long. *Basidiospores* ellipsoid-cylindric, inequilateral, yellow, smooth but with subtle perforating punctae in exosporium, inamyloid, cyanophilic. *Cystidia* scattered, resembling undifferentiated basidia. *Clamp-connections* absent.

Chemistry: Not known.

Ecology: Terrestrial, ectomycorrhizal with Fagales (*Nothofagus*).

Distribution: Only known from South America (Argentina).

A currently monotypic genus related by Horak & Moser (1966) to *Paxillogaster q.v.* and *Austrogaster, q.v.*

Reference should be made to the original publication for description, habit sketch and line-drawings of microscopic characters.

SINOBOLETUS M. Zang, Mycotaxon **45**: 223, 1992. See rejected names.

STROBILOMYCES Berk. in Hooker's Journ. of Bot. Kew Gard. Misc. **3**: 77, 1851. Plate 14 D-E.

Type species (selected): *Boletus strobilaceus* Scop. : Fr. (= *Strobilomyces strobilaceus* (Scop.: Fr.) Berk.).

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, with persistent rather woody stipe, metavelangiocarpic. *Spore print* fuliginous black.

Pileus convex to almost hemispherical then shallowly convex to plano-convex, quite fleshy, dry, fluffy, velvety, tomentose-scaly to distinctly squarrose, soft, generally commencing quite pale and retaining these colours between surface-irregularities which otherwise darken quickly, often becoming sooty black, fuscous black or violaceous black, especially when bruised. *Stipe* cylindric or slightly swollen below, fluffy, tomentose from 2/3rds down, the upper part less pronouncedly fluffy but strongly and minutely floccose, concolorous with pileus beginning pale then nigrescent at maturity. *Tubes* adnate or even subdecurrent but depressed around the stipe, white then grey-olivaceous, finally fuligineous black; *pores* moderately wide, subangular, concolorous although often persistently white at very end, rubescent on bruising. *Context* whitish or pallid soon rufescent and then finally blackening. *Odour* indistinct; *taste* mild or slightly acidulous.

Basidia elongate-clavate, often filled with fuliginous black contents, 4-spored. *Basidiospores* subglobose to broadly ovoid with smooth, depressed suprahilar plage, ornamentation either complete or irregular, broken network or almost completely of isolated warts, darker in colour than main spore-wall, mesh of reticulum sometimes over 1 µm deep, some slightly pseudoamyloid, acyanophilic. *Cheilocystidia* numerous, mixture of hyaline and brown fusiform cells; *pleurocystidia* fusiform to lageniform, filled with fuligineous sap. *Tube trama* with hyaline, lateral hyphae divergent from a darker central zone intermixed with dark brown oleiferous hyphae. *Pileipellis* a loose, floccose mass of intertwined brown, sepia and hyaline, filamentous, flexuous or straight hyphae intermixed with ellipsoid and shortened elements. *Stipitipellis* of similar construction to pileipellis. *Clamp-connections* not seen.

Chemistry: Red with aq. alkaline solutions, and melanin-like compounds found in some taxa. The type species is able to convert tyrosine into L-3- (34,4-dihydroxyphenyl alanine) = L-Dopa.

Cytology: Ploidy level 2x in type species (Wittmann-Meixner, 1989).

Developmental studies: Development of the basidiomes of *Strobilomyces floccopus* (= *S. strobilaccus)* has been described by Reijnders (1948).

Ecology: Terrestrial, probably forming facultative associations with a series of arborescent plants in the Fagales, Myrtaceae etc.

Distribution: Widespread in South East Asia, Australia and Africa, but extending into temperate Europe and North America.

A medium sized genus that becomes most frequent in tropical and subtropical areas, with few representatives in temperate woodland. It is well-characterised by the rounded spores with strong ornamentation and the veil which is composed of hyphae from pileus, stipe and even tube orifices. The genus was split into two sections by Singer (Farlowia 2, 1945) of which Sect. *Pterospori* has been given generic rank as *Afroboletus q.v.* Presently placed in the Strobilomycetaceae but molecular studies show that the genus nestles as a branch close to the *Boletus chrysenteron* group!

The sole European taxa illustrated and described in regional texts e.g. Breitenbach & Kränzlin, *Champignons de Suisse*, Vol. 3, 1991. For the three North American species see Bessette, Roody & Bessette, *North American Boletes*, 2000; see also under general references. The South East Asiatic species are covered by Corner (*Boletus in Malaysia*, 1972) and Japanese species by Imazeki *et al.* (*Fungi of Japan*, 1988). African species are dealt with by Heinemann, (*Flore Iconographique des Champignons du Congo* Fasc. 3, 1954).

Synonym:
Eriocorys Quél. in Ench. Fung., 163, 1886; type species *Boletus strobilaceus* Vahl : Fr., the same as *Strobilomyces*.

SUILLUS Micheli ex Adans., Fam. Plantae. 2: 10, 1763. Plate 15 A & B.

Type species (selected): *Boletus luteus* L. (= Suillus luteus (L.) Roussel).

Basidiome epigeal, pileate, generally with viscid or even gelatinised pileus, hymenophore tubulate with small and angular pores often arranged in radial fashion (boletinoid), may become almost sequestrate, centrally stipitate with glandular dots, putrescent, veil annular or marginal and when present obvious, or totally

absent, pseudoangiocarpic -mixangiocarpic or gymnocarpic. *Spore print* ochraceous cinnamon to porphyraceous buff.

Pileus almost subglobose, convex then expanded, plano-convex, viscid or gelatinous less frequently simply tacky or humid, smooth and then sometimes streaky fibrillose below gluten or slightly fibrillose scaly and then scales superimposed above the gluten, margin naked or in some taxa at first with appendiculate velar remnants or marginal roll of veil which may be lost at maturity. *Stipe* cylindric or elongate-cylindric, not noticeably swollen towards base, either annulate or exannulate, the former a gelatinous ring or prominently membranous and then thick or thin, sometimes mobile, cuff-like structure or stipe naked, with pale 'glandular' dots which darken with age and frequently enlarge, densely distributed at stipe-apex and usually obvious under the velar remnants, sometimes exuding a cloudy liquid and often collapsing to form resinous smears with age, base attached to distinctly pigmented fans of mycelial cords. *Tubes* often rather shallow, generally yellowish, sometimes with olivaceous or grey aspect; *pores* at first small, enlarging, concolorous with tubes, darkening with age and on bruising, sometimes arranged radially (boletinoid), rich yellow, orange or with greyed aspect at maturity, in some species weeping. *Context* generally pale or concolorous with the tubes or sometimes rather more yellow downwards. *Odour* & *taste* various, indistinct to resinous or slightly acidulous.

Basidia clavate, often darkening with age, especially when in proximity to cystidia, 4-spored. *Basidiospores* rather narrow and sometimes quite small in comparison to other bolete genera, elongate- to cylindric-fusoid, smooth with suprahilar applanation, smooth, compressed, pale yellow to subhyaline, darkening when in presence of cystidia, inamyloid, acyanophilic. *Cheilo- & pleurocystidia* in most species in fascicles, clavate to elongate-clavate, hyaline at first but many darkening with age and progressively becoming covered in darkening, amorphous material which may finally become dark red-brown. *Caulohymenium* with numerous caulocystidia similar in shape and reaction to cheilocystidia and forming glandular-like dots. *Pileipellis* composed of a layer of amorphous, gelatinised material in which very narrow, thin-walled hyphae are dispersed or with narrow hyphae forming separate skeins of hyphae seated on more compacted and slightly broader hyphae. *Tube trama* bilateral and highly gelatinised with honey-coloured or subhyaline mediostratum from which divergent hyphae emanate but, because of gelatinisation, hardly touch. *Clamp-connections* absent or rare, sometimes in attached mycelium.

Chemistry: Some species cyanescent with gaseous ammonia on the pileus, but generally pink, grey or lilac with aq. ammoniacal solutions on the flesh. Pulvinic

acid derivatives present; thelephoric, atromentic, xerocomic and variegatic acids and variegato-rubin, pulvinones, boviquinones, bovilactone-4,4, suillin and grevillins present to some degree in different species. Also atromentin, gyroporin, chamonixin and involutin have all been isolated. Xerocomic acid is absent from some basidiomes but may be found in mycelial cultures, as is methyl bovinate in *S. bovinus.* See Besl & Bresinsky (Plant Syst. & Evol. **206**: 223-242, 1997) for review.

Cytology: Ploidy level of 2x in *S. flavidus* (Fr.) Singer & *S. placidus* (Bon.) Sing. and 4x in *S. plorans* (Rolland) Sing. & *S. sibiricus* (Sing. B resinsky & Wittmann-Bresinsky, 1994). In North American species 1x in *S. acidus* (Peck) Sing. (Wittmann-Meixner, 1989) & *S. pungens* Thiers & Smith and 2x in *S. caerulescens* Theirs & Smith & *S. pseudobrevipes* Smith & Thiers (Bresinsky & Bresinsky-Wittmann, 1994).

Genetics: Fries (New Phytol. **107**: 735-739, 1987) has studied incompatibility patterns in *Suillus luteus*. Population genetics of *Suillus bovinus* (L. : Fr.) O. Kuntze have been studied by Dahlberg and Dahlberg & Stenlid (New Phytol. **115** & **128,** 1971 & 1994 respectively) and genetic markers in *S. granulatus* (L.: Fr.) O. Kuntze by Jacobson *et al*. (Proc. Nat. Acad. USA **90**,1993).

Cultural studies: see Pantidou & Groves (Can. J. Bot. **44**: 1371-1392) & Pantidou & Watling (Notes Roy. Bot. Gdn., Edinb. **31**: 207-237). Under the generic name *Boletinus* see Laut (Can. J. Bot. **44**: 395-402, 1966) who studied 3 additional species.

Developmental studies: The following species have been studied in depth by Reijnders (1948) & Kühner, (1926) and *S. bovinus, S. grevillei*(Klotzsch) Sing. (as *elegans* Fr.), *S. luteus* and *S. variegatus* (Sow. ex Fr.) O. Kuntze and *S. viscidus* (L.) Roussel (as *aeruginascens* (Secr.) Snell) by Reijnders (1963). Also studies of *S. cavipes* (Opat.) Smith & Theirs (as *Boletinus*) by Kühner (Le Botaniste **18**, 1927). Elrod & Snell (Mycologia **32**, 1940) have studied *S. americanus* (Peck) Snell*, S., granulatus* (L.: Fr.) O. Kuntze*, S. placidus, S. pictus* (Peck) Smith & Thiers and *S. spectablis* (Peck) O. Kuntze, and Gentle & Snell (Mycologia, **45**, 1953) *S. paluster* (Peck) Kretzer & Bruns (as *Boletinus*)*.* Lange (Saetryk Bot. Tids. 68: 122-131,1973) has studied the development of basidiomes of *S. grevillei*. See also *S*utara (1987) when discussing *Boletinus* & *Mariaella* noted below under synonymy.

Ecology: Terrestrial, ectomycorrhizal with conifers, especially Pinaceae, very

rarely recorded with angiosperms and then usually (always?) in presence of conifers. Lists of species with hosts are given in Engel *et al*.; see below for reference. See Agerer 35 *S. cavipes* (Opat.) Smith & Thiers as *Boletinus* with *Larix decidua*: 81 *S. viscidus* (L.: Fr.) Roussel as *B. laricinus* Berk.: 45 *S. grevillei* (Klotszch) Singer with *Larix decidua*: 46 *S. placidus* (Bon.) Singer with *Pinus cembra*: 47 *S. sibiricus* (Singer) Singer with *Pinus cembra*. An interesting relationship between different *Suillus* spp. and *Gomphidius* spp. has been demonstrated, *e.g. Suillus bovinus* and *Gomphidius roseus*; see Olsson *et al.* (2000).

Distribution: Widespread in northern hemisphere and wherever the Pinaceae drifted south in the course of geological history; now known to be introduced to various southern hemisphere areas e.g. South America (Brazil), Australia and New Zealand. A list of world species is given in Engel *et al*.; see reference below.

A genus of nearly 50 taxa of great economic importance because of their ectomycorrhizal status. Easily separable from the other boletes by the fasciculate cystidia and generally viscid or gelatinised pileus and the intimate relationship with conifers. The genus now includes *Boletinus*, which was separated mainly on the boletinoid hymenophore and presence of clamp-connections; indeed it was this very character that led Singer (Farlowia **2**: 226,1945) to place *Boletinus* in the Gyrodontoideae. Molecular work has shown that *Boletinus* sits in amongst the core species of *Suillus*. Similarly molecular studies have shown that *Fuscoboletinus,* based on those species with a purple-brown spore-mass, is also superfluous and the species analysed sit within *Suillus* where the constituent species had been previously placed (- or maintained). Sequestrate members with parallel characters to *Suillus* have been assigned to *Gastrosuillus q.v.* but, as more work is carried, out it looks more and more likely that this genus will become untenable. Indeed, even within the main clusters of species in the genus there are taxa that have a poorly expanding pileus, leading to gasteroid characters, sitting close to expanding pileate species. *Gastrosuillus laricinus* Singer & Both has in fact been shown to be a recent mutant of *S. grevillei*. The genus *Suillus* is best placed in a separate family, the Suillaceae.

North American species well documented by Smith & Thiers (*A Contribution Toward a Monograph of North American Species of Suilus*, 1964) and expanded in Mycologia **58**, 1964, and again by Theirs (Beih. Nova Hedw. **51**, 1975). European species are dealt with in Engel *et al.* (*Schmier- und Filzröhrlinge s.l. in Europa*, 1996). The last publication includes colour illustrations and line-drawings.

For colour illustrations of N. American species see Bessette, Roody & Bessette, *North American Boletes*, 2000. Documentation of Chinese species may be found in Chui (Mycologia **40**, 1948) and Japanese species illustrated in Imazeki *et al.* (*Fungi of Japan*, 1988).

Synonyms:
Boletinus Kalchbr. in Bot. Ztg., 25: 1867. type species: *Boletus cavipes* Opat. Widely maintained based on the radially pored, hollow-stemmed basidiome and centred upon the European *B. cavipes,* which is now included in *Suillus*. Šutara (Ceská Mycologie **41**: 139-152, 1987) has discussed in full the limits between *Suillus* and *Boletinus*.
Boletium Clem., *Genera of Fungi* 108, 1909, based on *Boletus volvatus* Pers. and must be rejected as a *nomen nudum* being based on a monstrosity. See under *Volvoboletus* below.
Boletopsis Henn. in Engl. & Prantl, Nat Pfl Fam **1(1**)**: 194, 1898; type species: *Boletus luteus* (selected). A later homonym of *Boletopsis* Fayod which is based on a thelephoraceous polypore. Henning's genus has been used to cover several non-suilloid fungi, *e.g. Boletopsis icterinus* Pat. & Baker (J. Straits Br. Roy. Asiatic Soc. **78**; 68, 1918), which is a species of *Pulveroboletus q.v.*
Boletus L.: Fr. in Syst. Mycol. 1, 385, 1821. Restricted concept of name *Boletus* – 1) P. Karsten Rev. mycol. **3**: 17, 1881 - type species (selected) *Boletus bovinus* (L.) Roussel, currently considered a species of *Suillus.* 2). Murrill (Mycologia **1**: 10, 1909) – type species (selected) *Boletus luteus* – type of the currently circumscribed *Suillus.* 3) Maire (Publ. Inst. Bot. Barcelona **3**: 40, 1937) – type species (selected): *Boletus luteus* – type of *Suillus* and 4) W. Bridge Cooke (*Gen. Homobasid.* 14, 1953) – type species: *Boletinus cavipes* Opat., now placed within *Suillus*. Alternative type species *Boletus edulis* L.: Fr. See Donk (Reinwardtia **3:** 278-282,1955) and under *Boletus* above.
Cricunopus P. Karst. in Rev. mycol. **3(9)**: 16, 1881; type species: *Boletus luteus* (selected), the type of *Suillus*.
Euryopus Quél. in Ench. Fung. 163, 1886; type species: *Boletus cavipes* Opat. Therefore a synonym of *Boletinus* now placed in *Suillus*. Alternative spelling *Euriporus*
Fuscoboletinus Pomerl. & A.H. Sm. in Brittonia **14**: 156, 1962; type species: *Fuscoboletinus sinuspaulianus* Pomerl. & A.H. Sm. A recently introduced genus for those suilloid boletes with a slight purplish cast to the spore-print, *e.g,* European *S. aeruginascens* (Secr.)Snell = *Boletus viscidus* (L.) Roussel, a species placed in *Suillus* sect. *Larigni* subsect. *Megasporini* by Singer (Rev. Mycol. **3**, 1938). This genus is not supported by molecular studies and must be considered a synonym *Suillus.* See Smith & Pomerleau (Brittonia **14**: 156-172, 1962) and

Smith & Thiers, *The Boletes of Michigan*, 1971.
Gymnopus (Quél.) Quél. apud Moug. & Ferry in Champignons Fl. Vosges 476, 1887; type species *Boletus granulatus* (L.) Roussel, a species placed in *Suillus* sect. *Granulati* by Singer (Rev. Mycol. **3**, 1938). This generic name is a later homonym of a generic name now used for certain collybioid agarics.
Ixocomus Quél. in Flore mycol. Fr. 411, 1888; type species: *Boletus luteus*, the type of *Suillus*.
Mariaella *S*utara in Ceská Myol. **41**: 73,1987; type species: *Boletus bovinus* – see above. A genus introduced for those boletes in *Suillus* sect. *Fungosi* (Smotlacha) Singer (= Sect. *Bovini* in Rev. Mycol. **3**, 1938), *viz. Boletus bovinus* (L.) Roussel. It is not supported by molecular studies and is a synonym of *Suillus.* The anatomy of the constituent species is described by *S*utara (1987) in the original publication.
Peplopus (Quél.) Quél. apud Moug. & Ferry in Champignons Fl. Vosges 476, 1887; type species: *Boletus luteus* (selected), the type of *Suillus.*
Pinuzza S.F.Gray, Natural Arrangement of British Plants **I**, 646, 1821. Erected to contain *Boletus flavus* With. (= *Suillus grevillei* (Klotzsch) Singer), which must be taken as type. The genus is a synonym of *Suillus* as the type is based on a species which sits tightly amongst the other members of the genus. It probably would correspond to Singer's *Suillus* sect. *Larigni* subsect. *Leptoporini* Singer (Rev. Mycol. **3**, 1938 sub *Ixocomus*).
Rostokovites P. Karst., Rev. mycol. **3(9)**: 16, 1881; type species *Boletus granulatus* L. (selected). This is a synonym of *Suillus*; molecular studies demonstrate that this species sits within the genus. It would correspond to Singer's *Suillus* sect. *Granulati* (sub *Ixocomus* Rev. Mycol. **3**, 1938).
Solenia [Hill] O.Kuntze, Rev. Gen Pl. **3(2)**: 521, 1898; type species described as "Solenis pediculo crasso, punctato, brevi Hill' which is equated with *Boletus bellinii* Inzenga. This is a species of *Suillus* within *Suillus* sect. *Granulati* and thus the genus becomes a synonym of *Suillus*. *Solenia* is better known as being used for a genus of cyphellaceous fungi.
Suillus S. F. Gray, Natural arrangement of British Plants **1**, 646. 1821. With the change in starting point in fungal nomenclature this name no longer has status. See Palm & Stewart (Taxon **33**: 711-712).
Veloporus Quél. See Donk, 1955. Apparently not published but covers members of the genus *Suillus*.
Versipellis Quél. in Ench. Fung. 157, 1886; type species *Boletus variegatus* Sow.: Fr. Equivalent to *Suillus* Sect. *Fungosi* (Smotlacha) Singer and therefore becomes a synonym of *Suillus*; but see Donk, Taxon **12**: 122, 1963. It has also been considered to be the correct name for *Xerocomus q.v.* see Donk Taxon **12**: 122, 1963.

Viscipellis Quél. in Ench. Fung. 155, 1886; type species *Boletus luteus* (selected), the type of *Suillus*.
Volvoboletus P. Henn. in Engl. & Prantl, Nat. PflFam 1(1**) 196, 1898 based on *Boletus volvatus* Pers., which is considered a parasitised bolete or otherwise a monstrosity; see Donk, 1955.

TAPINELLA E.-J. Gilbert in Les Bolets 67, 1931. Plate 15 C.

Type species (only original species): *Paxillus panuoides* (Fr.: Fr.) Fr. (= *Tapinella panuoides* (Fr.) E.-J. Gilbert

Basidiome epigeal, pileate, excentrically stipitate, hymenophore lamellate although gryrose or elongate-poroid towards stipe-apex, ochraceous fulvous to rust-coloured, putrescent, pilangiocarpic ? or probably gymnocarpic. *Spore print* sienna.

Pileus convex then expanding and finally plano-infundibuliform, shell-shaped or fan-shaped (pleurotoid), dry, sienna to cinnamon-brown or rust-colour, then becoming tinged with sienna, snuff-brown or even olivaceous, minutely tomentose or velvety even at inrolled margin, sometimes becoming slightly to distinctly scaly. *Stipe* lateral, sometimes reduced or even absent, when present stout, fleshy and sometimes rooting, in at least one taxon covered in very fine buff to ochre or tinged olivaceous tomentum which becomes coarser with age and then velvety and cigar- to snuff-brown or even purplish black. *Gills* branched and frequently anastomosing especially at junction with stipe, crowded, pale yellowish or olivaceous buff at first then pale ochre and finally rust-colour with darker edge at maturity, often with olivaceous edge when drying, easily separable from context. *Context* cream-colour to pale ochre or buff with or without vinaceous flush and sometimes washed with lavender or purple. *Odour & taste* not distinct or slightly astringent.

Basidia elongate-clavate, hyaline, usually 4 spored. *Basidiospores* shortly ellipsoid to slightly ovoid, adaxially applanate, with slightly thickened wall, smooth and with short but distinct hilar appendage, pale yellowish brown in aq. ammoniacal solutions, darkening in ME, cyanophilic. *Cheilocystidia* poorly differentiated, clavate cells hardly larger than basidia; *pleurocystidia* absent. *Lamellar trama* of regular structure generally showing mediostratum and divergent hyphae linking with hymenium. *Pileipellis* a tangled mass of filamentous, hyaline, pale coloured to brown hyphae, some with slight encrustation, some adhering together

to form suberect scales, end-cells slightly differentiated either shortened and tapered, ampulliform or even capitate. *Stipitipellis* of cylindric hyphae overlaid by tangle of septate, hyaline to slightly coloured hyphae, some adhering together and intermixed with amorphous dark material. *Clamp-connections* present.

Chemistry: Reacts with aq. alkaline solutions to give strong red-brown colour. Contain atromentin, leuco- , flavo- & spiromentins, and xerocomic and variegatic acids.

Ecology: Saprotrophic, lignicolous on coniferous wood, either stumps or on wood-chips of coniferous origin; sometimes found in domestic buildings on timbers.

Distribution: Widespread throughout temperate North America, Europe and Asia and good collections from subtropical and tropical areas, to some of which it might have been introduced.

A genus containing a handful of species until recently included within *Paxillus q.v.*; Singer includes the species within his concept of *Paxillus* in two distinct sections sect. *Atrotomentosi* and sect. *Panuoides*. *Tapinia* (Fr.) Pat. in Hymen. Eurp. 130, 1887 has been used for this group of lignicolous paxilloid fungi but the type species of this genus is *Paxillus involutus* Batsch: Fr., the type of *Paxillus sensu stricto, q.v*. Thus a new genus, *Tapinella*, had to be erected to house *P. panuoides* Fr.: Fr. and its allies.

The species differ markedly from the ectomycorrhizal *Paxillus* in life-strategy and in producing a distinct brown-rot. It is placed close to the *Coniophora q.v*.

The European species are discussed by Šutara (Ceská Mykol. **46**, 1992). Species from southern United States and South America have been dealt with by Singer (Farlowia **2**, 1946) and (Beih. Nova Hedw. **29**, 1969) respectively as part of *Paxillus*. Colour illustrations of the two most widespread species appear in Imazeki *et al. Fungi of Japan*, 1982 and in Breitenbach & Kränzlin, *Champignons de Suisse*, 1991.

Synonyms:
Paxillopsis E.-J. Gilbert in Les Bolets, 86, 1931, nomen nudum but type *Paxillus atrotomentosus* (Batsch: Fr.) Fr. makes it a synonym of *Tapinella*. *Paxillopsis* has also been applied to a section of *Clitopilus* with its type *Clitopilus prunulus* (Scop.) Kumm.

Plicaturella Murrill in North American Flora **9**: 172, 1910; type species *Cantharellus olivaceus* Schwein. (=*Tapinella panuoides*).

***TREMELLOGASTER** E. Fisch., Mykol. Beitrage **28**. Mitt. Naturforsch. Ges. Bern (1923) 49, 1924. Plate 15 D.

Type species (only original species): *Tremellogaster surinamensis* E. Fisch.

Basidiome gasterocarpic, epigeal or hypogeal, rounded, clay-colour below, becoming bistre above, russet (-to Ridgway's Mars Brown') when dry, putrescent, angiocarpic.

Peridium > 1cm thick, coarsely flattened-tuberculate, more conspicuously rounded-tuberculate above, with thick outer zone and more gelatinised areas inwards. *Gleba* warm buff at first, becoming russet and powdery at maturity. *Pseudocapillitium* of variable length, much branched, hyaline, sparsely warty-spinulose. *Clamp-connections* present in some tissues.

Basidia narrowly clavate or cylindrical tapering towards base, forming palisade-like hymenium, 4-spored. *Basidiospores* globose, echinulate, hyaline at first then dark brown, occasionally minutely but inconspicuously pedicellate. *Exoperidium* of thick-walled, coloured, sclerotioid hyphae bordered internally by thin-walled, hyaline to subhyaline hyphae running approximately parallel to surface, inwards with brown, gelatinised zone reticulately divided by lighter coloured, non-gelatinised tissue; *endoperidium* white of non-gelatinised, intertwined hyphae with transverse thickenings running more or less parallel. *Clamp-connections* not seen.

Chemistry: Not known. Spore reactions not recorded.

Developmental studies: see Linder, 1930 below.

Ecology: Terrestrial on moist soil near decaying logs, at foot of a hill, bordering a swamp.

Distribution: Known only from South America (Surinam).

Tremellogaster was first considered a member of the Lycoperdales but the developmental structure revealed by Linder (Mycologia **22**, 1930) show a placement

closer to the sclerodermatoid fungi, It is probably best placed in the Tremellogastraceae as proposed by Zeller (Mycologia **40**, 662, 1948) until further collections are made and critical studies carried out. Zeller even suggested that the genus was best placed in its own order Tremellogastrales, which was later supported by Julich (Bibl. Mycol. **85**, 1981). Molecular work (Louzan *et al*., 2007) has demonstrated that this genus is referrable to the Sclerodermatineae. Julich also linked *Tremellogaster* with *Clathrogaster* Petri, 1900 from South East Asia but this has more affinities to *Gastrosporium* (see rejected genera below), a genus which probably has links to the stinkhorns - Phallales.

B/w photographs and description of only known species in Linder's original article.

TRUNCOCOLUMELLA Zeller, Mycologia **31**: 6, 1936. Plate 15 E.

Type species (selected): *Truncocolumella citrina* Zeller.

Basidiome epigeal to subhypogeal, pileate, obovate to irregular, centrally stipitate, stipe usually hidden beneath tightly attached pileus margin - sequestrate, putrescent, angiocarpic.

Peridium thick, smooth to slightly roughened, dry, greenish yellow, dingy yellow or with red-brown hues, fading with age. *Stipe* a columella, thickening and fleshy towards the base, white and with proliferating fine, radial branches extending towards pileus context. *Gleba* loculate with small, irregular chambers, gelatinous at first then tough with age, olivaceous grey or greyish brown from spore-mass. *Odour* & *taste* indistinct.

Basidia narrowly clavate, hyaline, pale yellowish in ME, 4-spored often with prominent sterigmata. *Basidiospores* narrowly ellipsoid to almost oblong, obscurely inequilateral with slight suprahilar depression, smooth, thin- or slightly thick-walled, yellowish in aq. ammoniacal solutions, with no apical pore and small hilar appendage, pseudoamyloid, acyanophilic. *Cystidia* absent or scattered, fusoid-ventricose with yellowish contents in aq. ammoniacal solutions and some slight encrustation, or replaced by clavate, hyaline pseudoparaphyses. *Peridiopellis* a single-layer of loosely, interwoven, thin-walled, non-encrusted hyphae. *Hymenophoral trama* with central zone of gelatinised, subparallel to interwoven, hyaline or slightly yellowish hyphae. *Clamp-connections* present.

Chemistry: No chemical reactions recorded. Xerocomic and variegatic acids isolated.

Ecology: Terrestrial, ectomycorrhizal with conifers.

Distribution: Known from Pacific Northwest America (United States & Canada).

A very small genus of gasteroid fungi apparently restricted in host preferences. The genus has been placed in the Hymenogastrales, a very unnatural placing but is presently assigned to the Rhizopogonaceae whose molecular relationships lie with the suilloid boletes.

See Smith & Singer (Brittonia **11,** 1959) for descriptions of species as then known and coloured illustration of the type species in Lincoff (*The Audubon Society Field Guide to North American Mushrooms,* 1981). A coloured photograph of *Truncocolumella rubra* Zeller, now considered *Gastroboletus ruber* (Zeller) Cázares & Trappe appears in Bessette, Roody & Bessette, *North American Boletes*, 2000.

Synonym:
Dodgea Malençon, Bull. Soc. mycol. Fr. **54** (1938): 194, 1939; type species; *Dodgea occidentalis* Malençon from British Columbia, probably the same as *T. citrina*. For discussion see Smith & Singer (Brittonia **11**: 215-216, 1959).

TUBOSAETA Horak, Bull. Soc. Bot. Suisse **77**: 362, 1967. Plate 16 A.

Type species (designated): *Boletochaete brunneosetosa* Singer (= *Tuboseta brunneosetosa* (Singer) Horak).

Basidiome epigeal, pileate, hymenophore tubulate with distinct setae within hymenum, centrally stipitate, probably gymnnocarpic. *Spore print* olivaceous brown.

Pileus pulvinate, hemispherical to convex then plano-convex, distinctly to slightly tomentose, slightly hairy under lens, cracking to expose context below, dry, rarely slightly tacky, brown with hints of purple-date, olivaceous or rust-colour, or reddish often with persistent yellow margin, cyanescent or not on bruising and if the former finally nigrescent, *Stipe* cylindrical, slightly fusoid, bulbose downwards, glabrous except at apex, slightly tomentose, solid, dry, smooth or

finely punctate or distinctly reticulate with elongate net-work, yellowish at apex, flushed carmine, red or rust-colour downwards, darkening on handling. *Tubes* adnato-decurrent, slightly emarginate; *pores* angular, cyanescent or not. *Context* fleshy, white, viridescent, rubescent or cyanescent when exposed. *Odour* none or acrid.

Basidia clavate-fusoid, 4-spored. *Basidiospores* fusoid-ellipsoid to fusoid cylindric, honey-colour to yellowish brown, smooth or slightly rugulose under SEM, lacking pore, with suprahilar depression, inamyloid, acyanophilic. *Cheilocystidia* clavate or fusoid, hyaline, thin-walled; hymenial setae thick-walled, conspicuous acutely fusiform, rarely multifurcate, with coloured wall, dextrinoid in apical area; *pleurocystidia* absent. *Tube trama* bilateral with gelatinised, compact central zone, boletoid, divergent from less pigmented, lateral hyphae. *Pileipellis* of chains of rounded, erect hyphae with coloured contents forming incomplete palisade. *Clamp-connections* not seen.

Chemistry: Not known.

Ecology: Terrestrial, probably ectomycorrhizal with caesalpinoid legumes.

Distribution: Central and Eastern Africa, in areas of miombo (*Brachystegia*) woodland and in rainforest in South East Asia.

A small Central African genus of six species, and probably further members in Malaysia, judging form collections made there. The necessary re-examination and taxonomic transfers, however, have not been made. Close to the bolete genus *Xerocomus q.v.* in its widest sense differing only by the presence of thick-walled cystidia; separable from *Boletochaete*, now placed in *Tylopilus q.v.*, in which *T. brunneosetosa* was originally part by the lack of brown cystidia with oily pigmented contents and pinkish ovoid basidiospores. The spore morphology separates this genus from *Setogyroporus. q.v*. also known from Africa. It has been placed in the Xerocomaceae.

Good descriptions and illustrations in Heinemann & Rammeloo (*Flore Illustrée des Champignons D'Afrique Centrale* Fasc.**14**, 1989).

TYLOPILUS P. Karst., Rev. Mycol. **3**: 16, 1881. Plate 16 B.

Type species: *Boletus felleus* Bull. : Fr. (= *Tylopilus felleus* (Bull.: Fr.) P. Karsten).

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, probably gymnocarpic, in one taxon pilangiocarpic and of restricted growth and then resembling a sequestrate fungus. *Spore print* some shade of vinaceous pink to pinkish buff when fresh, rarely with reddish or purple flush, pink aspect disappearing after drying to give uniform dull buff or honey-coloured print.

Pileus convex then plano-convex or even plane or with upturned margin, variously coloured in shades of light or dark brown or olivaceous, green, rust-colour or sienna *etc*., dry or very slightly viscid but not gelatinised, smooth to tomentose, lacking marginal flap. *Stipe* evelate, cylindric, attenuated upwards or swollen downwards, netted at apex or throughout, or smooth to pruinose, sometimes with punctiform-floccose ornamentation. *Tubes* whitish or pallid at first then some shade of pink to cinnamon- brown, adnate to usually depressed around stipe-apex; *pores* round, small, concolorous, rufescent to various degrees when bruised or even nigrescent, rarely cyanescent, and in one anomalous alliance presently housed in the genus red or orange. *Context* whitish or pallid, unchanging to rufescent or more rarely fuscescent, rarely cyanescent; intense orange in one tropical group. *Odour* indistinct, mild or slight acidulous & *taste* mild or bitter.

Basidia clavate, hyaline, 2-4 spored. *Basidiospores* elongate-fusoid to subcylindric, with suprahilar depression, or shortly ellipsoid, smooth (although Corner (1972) notes that some members have longitudinal striae), subhyaline or pale honey-colour SM, inamyloid, acyanophilic. *Cheilocystidia* less well differentiated than those on tube-face, clavate to almost subglobose with or without appendages or fusiform and ventricose; *pleurocystidia* ventricose-fusiform to obtuse, scattered, sparse or prominent, thin- or thick-walled, often distinctly pigmented in shades of brown or hyaline, or slightly coloured from vacuolar sap or oleiferous, sometimes pseudoamyloid contents. *Tube trama* of gelatinised, hyaline, lateral hyphae diverging from compacted, slightly darker, central zone. *Pileipellis* ranging from repent cutis to trichoderm or with rounded shortened cells almost resembling disrupted hymeniderm. *Stipitipellis*, especially in reticulate taxa, with a well-developed or reduced caulohymenium containing caulobasidia and caulocystidia. *Clamp-connections* not seen.

Chemistry: Chemical reactions known in two sections of *Tylopilus* which turn blue with ammoniacal solutions; in one species with red-purple crystals adhering to pileipellis constituents when in aq. ammoniacal mounts. Not yet analysed for secondary metabolites.

Cytology: Ploidy level 2x in type species (Bresinsky & Wittmann-Bresinsky, 1994) & 1x in *L. chromapes* (Frost) Smith & Thiers (Wittmann-Meixner, 1989). Also 2x in *Boletus tristiculus* Mass. which is a *Tylopilus s. l.*

Developmental studies: see Corner (1972) for *T. spinifer* (Pat. & Baker) Watl. and *Boletus ballouii* var. *fuscatus* Corner (= *T. viscidulus* (Pat. & Baker) Watl. & Lee).

Ecology: Terrestrial, ectomycorrhizal with coniferous and frondose trees, including caesalpinoid legumes and Sapotaceae. In Agerer 33 *Tylopilus felleus* with *Pinus sylvestris*.

Distribution: Predominantly southern hemisphere in distribution and tropical and subtropical. Widespread in South East Asia and in Australia where it can be the dominant bolete genus; good representation in North and Central America. A single taxon in Europe.

This is a large unwieldy and complex genus as presently circumscribed. Corner (*Boletus in Malaysia*, 1972) expanded the concept of *Tylopilus*, within what he termed *Boletus* subgenus *Tylopilus.* He recognised 8 alliances within the subgenus with spore-mass colours ranging from yellowish cinnamon, chocolate, pinkish brown and olivaceous pinkish cinnamon. As stated by Pegler & Young (Trans. Brit. Mycol. Soc. **76**: 134, 1981) 'if the genus is limited to the type species and its allies and defined as being gymnocarpic, ectomycorrhizal and producing pinkish, light greyish brown or pinkish orange brown spores not exceeding 15µm in length then a natural group may be recognized'. This probably would refer only to the type section (sect. *Tylopilus*) and a part of sect. *Oxydabiles* in the concept of Singer (1951 *et subseq.*). Wolfe (1981, 1983, 1986, 1990 – see specific refs. below) in Sydowia, Mycologia and Mycotaxon has studied many of the type species which have been assigned to *Tylopilus.* The genus is placed in the Boletaceae *pro tem*.

Molecular work has already indicated that *Tylopilus* as understood by both Singer (*Agaricales in Modern Taxonomy*, 1951 *et subseq*.) and Corner (1972) is a mixture of elements. Singer recognizes four sections of which two, sect. *Arenarii* Singer (*Agaricales in Modern Taxonomy* 4th ed., 1986) and sect. *Potamogetones* Singer (Persoonia **9**, 1978) are of tropical distribution, South America and Africa in the former and Amazonian South America in the latter. Section *Oxydabiles* includes not only close relatives of *T. felleus*, *e.g. T. ferrugineus* (Frost) Sing. but also *T. ballouii* (Peck) Sing., a species with a rather unusual suite of characters

(Watling *et al*., Bull. Soc. mycol. Fr. 122, 2007); future molecular studies may indicate that the members of this group, characterised as they are by frothy, oily cystidial contents and broadly ellipsoid, rounded almost hyaline basidiospores *s.m.* are worthy of generic rank.

A group of boletes around *T. chromapes* (Frost) A.H. Smith & Thiers forms a very distinct entity within *Tylopilus* and are thermophilic and mainly Australian in distribution; see Wolfe & Bougher (Aust. Syst. Bot. **6,** 1993). They were placed in subgenus *Rosescabra* (Sing.) Smith & Thiers by Smith & Thiers (The Boletes of Michigan, 1971) having been previously assigned to *Leccinum*; see Smith & Thiers (Mycologia **60,** 1968). Species of *Porphyrellus* were placed in *Tylopilus* by Smith & Theirs (*The Boletes of Michigan*, 1971) in subgenus *Porphyrellus* (E.-J. Gilb.) Smith & Thiers but this has been shown to be an incorrect placement both from developmental & morphological standpoint and molecular considerations. Numerical studies have been carried out by Wolfe (Nova Hedw. **43**, 1986) on this group; see *Porphyrellus* above.

Gastrotylopilus was erected for gasteroid forms but is based on a member of the genus *Fistulinella*, which although once merged with *Tylopilus* is now considered an independent genus. This sequestrate genus is, therefore, not available for true tylopiloid sequestrate boletes, although undoubtedly forms do exist. *T. humilis* Thiers is an intermediate with partial sequestrate form. *Boletochaete* Singer (Mycologia **36**: 358, 1944) has been separated out based on a species with thick-walled, brown cystidia but in fact these are thin-walled cystidia filled with brown contents which harden in the dried material to resemble setae.

Reference should be made to regional European descriptions of the type species. *Tylopilus felleus* and its close N. American allies are very well-known and can be keyed out in local mycobiota including Smith & Theirs (*Boletes of Michigan*, 1971) where descriptions are supported by line-drawings and b/w illustrations; Malaysian species are dealt with by Corner (*Boletus in Malaysia* 1972) and the African members by Heinemann (*Flore Iconographique des Champignons du Congo* Fasc.**15**, 1966). The descriptions in both the last publications are accompanied by coloured illustrations. Additional coloured photographs can be found in Bessette, Roody & Bessette, *North American Boletes*, 2000 and Imazeki et al., *Fungi of Japan*, 1988. Keys supported by scant line-drawings appear in Singer *et al*., (Beih. Nova Hedw. 78, 1983) for neotropical species, with some colour photographs and in Singer *et al.* Beih. Nova Hedw. **102**, 1991 for Central American species.

Synonyms:
Boletochaete Singer, Mycologia **36**: 358, 1944; type species: *Boletus spinifer* Pat. & Baker. Introduced for those species with oleiferous, brown, rigid cheilocystidia, erroneously compared with species of the *Hymenochaetales*. At present included in *Tylopilus* in the broad sense but would become available again if, as will be inevitable, future dismemberment of *Tylopilus* takes place.
Leucogyroporus Snell, Mycologia **34**: 408, 1942; type species *Gyroporus piscidorus* Murrill. The type is considered by Singer to be a synonym of *Boletus tabacinus* Peck, now placed in *Tylopilus* sect. *Oxydabiles* Singer (Amer. Mid. Nat. **37**, 1947). The genus was erected on the erroneous information that the spore-mass of the type species was white. It is a synonym of *Tylopilus* when taken in a wide sense but would become available when *Tylopilus* is dissected, a neccessity preliminary molecular studies seem to suggest.
Rhodobolites Beck, Z. Pilzk. **2**: 147, 1923; type species *Boletus roseus* G. Winter. The type is taken to be the same as *Boletus alutarius* Fr. sensu Rostk., which is itself considered to be a form of *B. felleus* Bull. : Fr., the type of *Tylopilus. B. alutarius* has in the past been interpreted erroneously as *B. porphyrosporus* Fr. & Hök.
Rhodoporus Quél. ex J. Bataille, Bull. Soc. Hist. Nat. Doubs **15**: 11, 1908; type species *Boletus felleus* Bull.: Fr.(selected) which is the type of *Tylopilus.*

VELOPORPHYRELLUS L.D.Gómez & Singer, Brinesia **22**: 293, 1984. Plate 16 C.

Type species(only original species): *Veloporphyrellus pantoleucus* L.D. Gómez & Singer.

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, probably velangiocarpic although reported as primarily angiocarpic which requires further study. *Spore print* chocolate-brown to fawn.

Pileus convex, expanding, with prominent, non-gelatinised, marginal flap which clasps stipe even into maturity, finally leaving appendiculate marginal extensions, pallid to whitish throughout or brick-coloured, dry, cracking slightly. *Stipe* elongate, attenuated upwards, buff-hazel, livid vinaceous at apex or pale, bruising ochraceous about centre, cyanescent or not. *Tubes & pores* free, hazel or pallid to whitish, hardly darkening or becoming tinged olivaceous. *Context* white, spongy, cyanescent or not.

Basidia hyaline, broadly clavate with granular contents, 4-spored. *Basidiospores* shortly fusoid to subfusiform, honey-colour in water mounts and in aq. ammoniacal solutions brownish with purple-red tinge, smooth, some pseudoamyloid, cyanophilic. *Cheilo-* & *pleurocystidia* hyaline, thin-walled, lacking coloured inclusions. *Tube trama* with central strand, which may be poorly differentiated, becoming very pale wine-red on bruising or not. *Pileipellis* a trichoderm of loose, intertwined, collapsing, hyaline to pale tawny brown, asperulate to minutely verrucose hyphae with rounded, blunt end-cells. *Clamp-connections* not seen.

Chemistry: Not known. One species cyanescent.

Ecology: Terrestrial, probably ectomycorrhizal with *Quercus* in Central America and with *Brachystegia* or *Marquesia* in central Africa.

Distribution: Single species known each from Central America (Costa Rica) and East Africa (Zambia).

A genus presently represented by only two species but perhaps with further studies in the tropics this may increase with the inclusion of newly found taxa and also the re-allocation of other bolete taxa. The significance of the velar flap needs to be reassessed in the light of several unrelated boletes having such a feature. The genus, apart from the shorter spores and the velar flap, comes close to *Fistulinella q.v.* Best assigned to the Boletaceae

Reference should be made to the original published descriptions.

WAKEFIELDIA Corner & Hawker, Trans. Brit. mycol. Soc. **36**: 130, 1953. Plate 17 A.

Type species (only original species): *Wakefieldia striaespora* Corner & Hawker.

Basidiome gasterocarpic, hypogeal, globose or irregular or lobate with depressed base, whitish, smooth or somewhat rimose, not separating.

Peridium thin, dingy white or pallid becoming yellowish when dry or exposed above soil surface, smooth. *Gleba* loculate with minute, numerous crowded chambers separated at first by pale grey tramal plates, becoming pink to pinkish brown then finally dark purplish brown from dark yellowish brown spore-mass.

Odour none at first but then unpleasant .

Basidia cylindrico-clavate, projecting into chamber, 2-spored, with prominent straight sterigmata. *Basidiospores* statismosporic, orthotropic, globose or almost so, hyaline to golden brown in aq. ammoniacal solutions, with disrupting exosporial ornamentation producing low, broad, truncate verrucae or short irregular ridges, at first overlain by often persistent, myxosporium which may give the impression of a smooth surface, hilar appendage and terminal pore distinct, inamyloid. *Tramal plates* homoiomerous with narrow, filamentous hyphae. *Peridiopellis* a poorly differentiated epicutis of thin-walled, hyaline, sometimes inflating hyphae. *Clamp-connections* present.

Chemistry: Not known.

Ecology: Terrestrial, the European taxon probably ectomycorrhizal with *Fagus*, and the South East Asian taxa with caesalpinoid legumes.

Distribution: Known from South East Asia and one species, originally placed in *Sclerogaster q.v.*, from Europe. See under rejected names.

A small genus of at present three taxa of which the European taxon has been related to *Hymenogaster* and even placed in the Hydnangiaceae, both untenable placements. The generic relationship to *Octavianina q.v.* needs to be reassessed carefully with fresh specimens of the type species, so that a link with the boletes can be assured. Presently assignable to the Octavianinaceae.

Colour illustrations and line-drawings of microscopic characters of the sole British species in Pegler *et al. British Truffles*, 1993. Line-drawings in original article by Corner & Hawker, 1953.

XANTHOCONIUM Singer, Mycologia **36**: 361, 1944. Plate 17 B.

Type species (designated): *Gyroporus stramineus* Murrill (= *Xanthoconium stramineum* (Murrill) Sing.).

Basidiome epigeal, pileate, hymenophore tubulate, centrally stipitate, putrescent, gymnocarpic. *Spore print* bright yellow-brown without any hint of olivaceous.

Pileus convex to broadly convex, dry to finely velvety, slightly rugulose at first,

vinaceous, purplish or olivaceous brown but paling with age to clay-colour, ochraceous etc., in some species becoming spotted whitish. *Stipe* evelate, slightly enlarged downwards and perhaps sometimes pointed, solid, infrequently reticulate, not strongly pruinose, except perhaps at very apex, streaked and lined with age, pallid at apex and whitish at base. *Tubes* depressed around stipe, white at first but then tan or buff finally infused with yellow; *pores* concolorous, small, rounded, becoming ochraceous yellow on bruising. *Context* white, unchanging. *Odour* & *taste* mild or faintly disagreeable.

Basidia hyaline, cylindric-clavate, 4-spored. *Basidiospores* narrowly ventricose to more or less cylindric with rounded ends, rod-shaped, inequilateral in side-view, with suprahilar depression or applanation, smooth, dingy yellow with golden tinge in both aqueous mounts and aq. ammoniacal solutions, tawny in ME, inamyloid, acyanophilic. *Cheilo-* & *pleurocystidia* fusoid-ventricose with acute apex, hyaline, thin-walled. *Tube trama* of parallel to obscurely divergent hyphae from gelatinised central zone. *Pileipellis* a trichoderm of shortened pale, brownish yellow cells compressed into hymeniform-like structure with clavate end-cells. *Clamp-connections* not seen.

Chemistry: No distinctive reactions noted although aq. alkaline solutions on cap form rusty tan spots and FeSo4 slowly becomes olivaceous grey on the flesh. The toxic protein, bolaffinine , has been isolated; see Razanamparany *et al.* (Biochemie **68**: 1217-1223, 1986).

Ecology: Terrestrial, probably ectomycorrhizal with wide host range in both deciduous and coniferous woodland.

Cultural studies: see Wolfe (Mycotaxon **35**: 75-84, 1989).

Distribution: Known from temperate and subtropical North America.

This is a small genus of a handful of species. On spore-shape alone it appears distinctive. Several authors, *e.g.* Smith & Thiers (*The Boletes of Michigan*, 1971) maintain *Boletus affinis* Peck in an expanded concept of *Boletus* and molecular studies would suggest that this is an appropriate placement; the type species sits on a branch very close to the type of *Boletus* and its close allies and therefore distant from many other, familiar boletes thought to be central to *Boletus*. Further studies are obviously required. At present the genus must take a position close to the centre of the Boletaceae.

Wolfe (Can. J. Bot. **65**, 1987 & Can. J. Bot. **66**, 1988) has examined type material of several constituent species and has adequately described the genus supporting his conclusions with line-drawings. Smith & Thiers (*The Boletes of Michigan*, 1971) offer b/w illustrations and Bessette, Roody & Bessette, *North American Boletes*, 2000, colour photographs. Colour photograph of the type species also in Imazeki *et al*. *Fungi of Japan*, 1988.

XEROCOMUS Quél. apud Mougeot & Ferry, Champignons Fl. Vosges 477, 1887. Plate 17 C-E.

Type species (selected): *Boletus subtomentosus* L.: Fr. (= *Xerocomus subtomentosus* (L.: Fr.) Quél.).

Basidiome epigeal, pileate, hymenophore tubulate although the orifices may be drawn out to become quite angular and may even be sublamellate at pileus margin and/or at stipe-apex, centrally or slightly excentrically stipitate, putrescent, stipitocarpic, gymnocarpic. *Spore print* olivaceous brown to bronze-colour.

Pileus convex, plano-convex and then plane to wavy, more or less tomentose or subtomentose, dry, sometimes torn into scales or the outer layers splitting to expose context below, in shades of brown from reddish or apricot to peach-coloured shades and purplish hues to species with olivaceous or sienna tints. *Stipe* evelate, usually subcylindrical or attenuated downwards to almost pointed or attached to a plate of mycelium or rhizomorphs, rarely bulbose but possibly subequal, comparatively narrow in comparison with the pileus and often twisted, dry, sometimes with distinct brown or reddish punctae, sometimes even forming a coarse ill-defined or irregular network, yellow or brown or with carmine or red infusions sometimes strongly so, occasionally cyanescent. *Tubes* yellow at first pale lemon- or pale sulphur-yellow, adnexed with wings of tube extending down stipe-apex and then often pulling free of the stipe with maturity; *pores* concolorous at first, darkening to become golden yellow or dark sulphur-yellow and often bruising rust-colour or darker golden, angular to sub-boletinoid, even irregularly sublamellate at stipe-apex, sometimes cyanescent. *Context* pallid or yellowish buff or slightly brownish, sometimes purple in stipe-cortex, unchanging or cyanescent. *Odour* & *taste* indistinct, earthy or unpleasant.

Basidia hyaline to slightly yellowish or honey-colour, elongate-clavate, 4-spored. *Basidiospores* subcylindric to elongate ellipsoid or fusoid, smooth, although some under SEM slightly longitudinally rugulose or finely verruculose,

some taxa with distinct thickening at apex and/or with apical pore, with suprahilar depression, inamyloid although in some cyanescent species taking on bluish hue in ME for a time, acyanophilic. *Cheilo-* & *pleurocystidia* hyaline or pale yellowish to honey-colour, thin-walled, scattered fusoid-ventricose sometimes quite prominent, not encrusted. *Tube trama* divergent, poorly differentiated from similarly coloured, non-gelatinised or poorly gelatinised central zone of hyaline elements. *Pileipellis* a trichoderm of elongate-cylindric hyphae or of shortened cells, either smooth or slightly asperulate or strongly encrusted which at maturity exhibit zebra-like ornamentation. *Stipitipellis* of cylindric hyphae supporting either clusters of a poorly developed caulohymenium or distinct ridges with caulocystidia similar to those at tube-orifices. *Clamp-connections* not seen.

Chemistry: Some species turn distinctly blue-green with the vapours of ammonia and this has been used for specific and subgeneric separation. In the type species atromentin has been isolated in addition to other compounds, some of which are found in other species, including atromentic, xerocomic and variegatic acids, and variegato-rubin in members of the *B. chrysenteron* consortium.

Cytology: Ploidy level 2x as exemplified by *X. badius* (Fr.) Kühn. apud E.-J. Gilbert*, X. chrysenteron* Bull. & *X. subtomentosus* (Wittmann-Meixner, 1989). Also 2x in *X. pruinatus* Fr. & Hök*,* (as *B. fragilipes*) *X. sylvestris* (Petch) Pegler & *X. truncatus* Sing., Snell & Dick (Bresinsky & Wittmann-Bresinsky, 1994).

Ecology: Terrestrial, probably all ectomycorrhizal, in temperate countries with Fagales and possibly Coniferae, but in the tropics with other arborescent plants the identity of which really need to be assessed; many species probably facultative. Also forms arbutoid mycorrhizas and is specifically involved in ectendomycorrhizal monotropoid forms. Particularly common in areas disturbed and modified by man. In Agerer 34 *X. chrysenteron* (Bull.: Fr.) Quél. with *Pinus sylvestris*; 49 *X. badius* with *Picea abies*; 90 *X. subtomentosus*; 149 *X. lanatus* (Rostk.) E.-J. Gilbert.
Cultural studies: Cultures of *Xerocomus badius* and *X. illudens* (Peck) Sing. have studied by Pantidou (Can. J. Bot. **42**: 1147-1149).and basidiome formation induced.

Developmental studies: Development of basidiomes of *Xerocomus zelleri* (Murrill) Snell has been studied by Zeller (Mycologia **6**, 1914), *X. badius* & *X. illudens* by Pantidou (Can. J. Bot. **42**, 1964) and of *X. subtomentosus* by Reijnders (1963). See also Clémençon, 1997.

Distribution: As presently conceived the genus is distributed throughout the southern and northern hemispheres in temperate and subtropical woodlands.

The genus is very large and, as presently understood, will undoubtedly be dismembered in the future simply from anatomical differences alone but supported by recent molecular studies. As it has been so difficult to unravel the different alliances within this complex genus little headway at the moment has been made. Binder (1999), who has studied these fungi from a molecular point of view, has made some progress and recognised a group, which he labelled *Paraxerocomus*, based on *B. chrysenteron* and its allies. Some mycologists, *e.g.* Watling (Field Mycologist **3**, 2002) have insisted that, although a good genus based on the type species is certainly a natural unit and then would be assigned to the Xerocomaceae, there are other generic groupings within the range of species presently included in *Xerocomus*. At the moment it is best to use the term 'xerocomoid bolete' for some of these

Agaricus pelletieri Lév., the type of the genus *Phylloporus q.v.*, is considered by some authorities to be just a lamellate member of the genus. Although this was suggested many years ago from basidiospore shape, pilleipellis structure and the presence of semi-lamellate xerocomoid boletes such as *B. tenax* Smith & Thiers, molecular work has shown that this is exceedingly likely. Whether all members of the genus *Phylloporus* can be so considered simply lamellate xerocomoid boletes is not proven. Corner (*Boletus in Malaysia*, 1972) expanded the concept of *Xerocomus,* as a subgenus within his expanded concept of *Boletus*, and introduced several rather divergent alliances, and in the Caribbean there is a group of boletes around *X. brasiliensis* (Rick) Singer with small spores, which also seem to form a distinct but different entity. Changes, if necessary, can be only made after the two major genera within the discussion are analysed carefully and fully intergrated with the many tropical species which have correctly, or not, been assigned to one or other genus.

Descriptions of the species presently assigned to this genus can be found in regional mycotas, often under *Boletus*. Many publications discuss the circumscription of various, especially European, members of this genus and more recently Engel *et al.* (*Schmeir- und Filzröhrlinge s.l. in Europa*, 1996) and Ladurner & Simonini (*Fungi Europaei* 8: *Xerocomus*) have monographed the European members with the descriptions supported by line-drawings and colour illustrations; the latter publication incorporates the discovery of a new hyphal type to be found in *X. pruinatus* (Fr. & Hök.) Quél. by Ladurner & Pöder (Oster. Z. Pilzk. **9**: 11-15, 2000). Molecular studies in the genus have been conducted by Taylor

et al. (Micol. e Vegetazione Mediterranea **16**: 171-192) and more recent studies by Taylor *et al*. (Mycol. Research **110**, 276-287, 2006) have started to unravel the species within the *X. subtomentosus* group. Asiatic species will be found under *Boletus*; see Chui (Mycologia **40**, 1948) and coloured illustrations in Corner (*Boletus in Malaysia*, 1972); also see Imazeki *et al., Fungi of Japan*, 1982 and General References. A key supported by scant line-drawings and some colour photographs of neotropical species appears in Singer *et al*. (Beih. Nova Hedw. **77**, 1983). Oolbekkink (Persoonia **14**: 245-273,1991) has examined the basidiospores structure of selected European species using SEM techniques.

Synonyms:

Boletus L.: Fr, in Syst. Mycol. **1**, 385, 1821; type species: *Boletus subtomentosus* L., selected by Clements & Shear in Genera of Fungi, 346, 1933. This move has not been supported universally; the type in fact is the same as that accepted for *Xerocomus*. See under *Suillus* and *Boletus* above.

Versipellis Quél. in Ench. Fungorum 157, 1886; type species: *Boletus subtomentosus* L. (selected) which is the type of *Xerocomus*. Murrill (Mycologia **1**: 140, 1909) selected *Boletus variegatus* Sow. for this genus and his proposal was followed by Maire (1937) and Singer (1945) but this would then make *Versipellis* a synonym of *Suillus*.

Xerocomopsis Reichert, Palest. J. Bot. Rehovot Series **3**: 229, 1940; type species: *Boletus subtomentosus* L. Reichert realized there were various elements within the xerocomoid fungi which needed separate generic status but on recognizing these differences separated for particular consideration *B. subtomentosus* which unfortunately had already been selected as the type of *Xerocomus*.

Rejected Names

Genera:

Boletium Clements in Gen Fungi. 108, 1909. Type species *Boletus volvatus* Pers. (= *Volvoboletus* Henn.) which is probably a species of *Amanita* fide Kuyper; see Kirk *et al.* Dictionary of Fungi 9th edition.

Boletus Tourn. ex Adans., 1763 = *Morchella* Ascomycotina fide Donk; see Reinwardtia 3: 275 1955.

Boletus Linn. In Species Plant. 1753 = *Phellinus* (Hymenochaetaceae) fide Donk; see Persoonia 1: 173, 1960.

Coniophorafomes Rick, Brotéria Ser. Ci. Nat. **3**: 167, 1934. Although considered a *nomen nudum* belonging to the Coniophoraceae in Hawksworth *et al*. Dictionary of Fungi 8th edition it has been shown in fact to belong to the Stereaceae with *C. stereoides* (Rick) Rick and *C. matsuzawae* (Yasuda) Rick as constituent species.

Lamyxis Raf. In Ann. Nat. ou ann. Synop. 16, 1820: Introduced by Rafinesque as a *nomen provisiorum* intermediate between *Sistotrema* & *Boletus,* based on *Sistotrema globularis* Raf. Found on beech tree in the Catskill Mts. North America. See Donk (Persoonia **1**: 201, 1960). Apparently not seen since!

Linderomyces Singer, Farlowia **3**: 157, 1947. Type species *Paxillus lateritius* Petch. This delimits a group of gomphaceous fungi. Probably a synonym of *Gloeocantharellus*.

Myriostoma Desv., J. Bot. (Paris) **2**: 103, 1809. Type species**:** *Lycoperdon coliforme* With.

Basidiome gasterocarpic, epigeal, subglobose or depressed with a basal tuft of mycelium, maturing to become star-shaped as in *Geastrum* but with inner endoperidium pierced by scattered simple openings.

Peridium splitting to about half-way to form 10-18, non-hygroscopic, arched and often recurved rays, consisting of outer whitish to dull yellow-brown, fibrous layer often longitudinally splitting, with a persistent mycelial layer of similar colour and an inner fleshy whitish to yellowish pseudoparenchymatous layer which is fleshy at first and then tends to peel away; *endoperidium* puff-ball like, subglobose to depressed and supported by up to 15, usually flattened and well-hidden stalks, linked to internal columellas, grey-brown, ornamented with numerous small warts and pits and with a few or several much larger slightly raised then flattened openings (stomata), with fimbriate margins. *Gleba* dark brown.

Basidia bladder-shaped when young or club-shaped, then ampulliform or lageniform, 6-8-spored, with basal clamp-connection. *Basidiospores* globose, yellow-brown, ornamented with irregular, curved often branched, anastomosing ridges reaching .1-2 µm high. *Capillitium* of slender, mostly 5-4 µm broad, smooth or some slightly encrusted, thick-walled hyphae with narrow, distinct lumen. Clamp-connections present.

Chemistry: Not known.

Ecology: terrestrial, on well-drained base-rich soils; in hedgerows and on banks, often amongst *Urtica* or in maritime areas. Extensive ecological data given in Sunhede, 1989; see below

Distribution: Widespread in Northern Hemisphere and in subtropical areas but nowhere common. Recorded from North and Central America, Asia, South Africa and Europe, including Caucasus.

A so-called monotypic genus, although judging from studies in *Pisolithus* and *Astraeus* this may be another so-called cosmopolitan taxon, which embraces a whole range of geographically and ecologically separate taxa. It has been linked with the Geastraceae because of the similar final phenotypic shape and molecular studies have confirmed this and not Dring's suggestion (The Fungi IV B, 1973) that it is a member of the Astreaceae. Descriptions of the only known species can be found in regional mycota including Pegler, Laessoe & Spooner, *British Puffballs, Earthstars and Stinkhorns*, 1995; line-drawings and colour photograph are supplied. See also Sunhede, Geastraceae: Synopsis Fungorum 1, 1989 for descripiton, line drawings, developmental data, b/w photographs and SEM micrographs.

Synonym:
Polystoma S.F.Gray in Nat Arr. Brit. Pl. **1**: 586, 1821; based on *Lycoperdon coliforme* With., described from England.

Neopaxillus Singer, Mycologia **40**: 262, 1948. Based on *Neopaxillus echinosporus* Sing. (= *N echinspermus* (Speg.) Singer) and placed in the Paxillaceae. However, the anatomical characters do not fit in with this grouping, and recent molecular studies have confirmed the authors opinion that it is a member of the Crepidotaceae.

Phyllobolites Singer, Ann. Mycol. **40**: 59, 1942. Type species: *Paxillus miniatus* Rick, although no type specimens were ever available for examination. Additional material of this species, authenticated by Rick, was later determined as a species of *Lentinus* (see Singer Farlowia **2**: 547, 1946) and subsequent specimens sent to Singer by Rick were found to be either *Tapinella panuoides* (Fr.) E.J. Gilb. or *Pleurotus ostreatoroseus* Sing.. In Farlowia (loc.cit.) Singer suggested that the type species should be replaced by *Paxillus russuloides* Peck and the genus maintained although this was never taken up, either by Singer or subsequent authors. Such a procedure is in fact illegal according to the Botanical Code, and it is doubtful whether the genus is legitimate. Indeed (Horak Beitr. Krypt.-fl. Schweiz **13**: 718, 1968) in his analysis of agaricoid generic, although making an entry, did not deal with the genus. In the last edition of his *magnus opus*, *Agaricales in Modern Taxonomy* (1986), Singer maintained the genus with the original type species.

Description as follows:

Basidiome: epigeal, hymenophore lamellate, centrally stipitate, velate, putrescent, with ornamented basidiospores.

Pileus similar to *Paxillus involutus* (Batsch) Fr. *Stipe* solid or soon becoming hollow, with narrow, somewhat fugacious, membranous apical annulus. *Lamellae* decurrent, some forked, with scattered veins, close to sub-close, rather broad, pallid at first then darkening.

Basidia 2-4 spored. *Basidiospores* fusoid to subfusoid-ovoid, with suprahilar depression or applanation, coarsely ornamented with longitudinally arranged verrucae and short ridges, thick-walled, ochraceous in aq. alkaline solutions brown in ME but not pseudoamyloid. *Pseudocystidia* conspicuous, numerous, becoming

somewhat coscionoid. *Lamellar trama* of a gelatinized mediostratum with broad, poorly or scarcely gelatinized lateral strata, somewhat divergent towards margin.

Ecology: Apparently ectomycorrhizal.

The genus is said to only occur in Tropical South America but Singer (Farlowia **2**: 547, 1946) suggested that *Paxillus lateritius* Petch of S.E Asian origin is possibly cogeneric. This latter species is now placed in *Gomphus* (Petersen, John E. Mitch. Sci. Soc. **84**: 380, 1968), although Singer had placed it in his paxillaceous genus *Linderomyces* (Farlowia **3**: 157, 1947), noted above. Although, Singer maintains *Phyllobolites* as a boletaceous genus its true affinities probably lie in the Gomphales, where Singer (1986) later placed *Linderomyces*. *Gomphus*, is a small genus widespread in both hemispheres and although commoner in the tropics has at least one species in northern coniferous woodland. Pegler in Agaric flora of Sri Lanka (Kew Bull. Series **12**, 1986) places Gomphaceae in the Boletales – see Beenakiaceae below. Colour photograph of *P. miniatus* is supplied in Ectomycorrhizal fungi of the Neotropical Lowlands, Beih. Nova Hedw. **77**, 1983.

Sclerogaster R. Hesse in Hypog. Deutschl. 1: 84, 1981. Although this genus was placed in the Octavianinaceae and therefore tentatively in the Boletales (Watling, 2006), molecular and anatomical studies have demonstrated that at least the type species and one other (*S. xerophilus*) are members of the gomphoid/phalloid consortium; see Hosaka *et al*., 2006; Clémençon *et al*., 2007. A description is offered, however, as the closely related genus *Wakefieldia* maintained in the main text is in need of careful reappraisal.

Type species: *Sclerogaster lanatus* R. Hesse (= *S. compactus* Tul. & C. Tul.) Sacc.

Basidiome gasterocarpic, hypogeal or subhypogeal, small and drying hard, embedded in extensive network of mycelium, soft and gelatinised within, putrescent, angiocarpic.

Perdium white, becoming slightly yellowish with age and on drying, separable or not and then weathering away, soft, tomentose within weft of mycelium. *Gleba* loculate with round or oblong, minute chambers, cream-colour to pale yellowish, darkening with age to become olivaceous from sulphur-yellow spore-mass, tramal plates of thick- or thin-walled hyphae. *Columella* present and extending at first half-way to apex but soon obliterated.

Basidia short, clavate, mostly 4-spored, sometimes 6- or 8-spored. *Basidiospores* orthotropic, globose to almost oviod, honey-yellow to straw-yellow in aq. ammoniacal solutions, inamyloid, with low, broad, truncate verrucae, cylindric hilar appendix with terminal tear but lacking myxosporium. *Cystidia* absent. *Tramal plates* homoiomerous, of filamentous hyphae. *Peridiopellis* thick, a poorly developed epicutis of loose, thin-walled, narrow, interwoven hyphae. *Clamp-connnections* absent.

Chemistry: Not known.

Ecology: terrestrial, ectomycorrhizal with both conifers and frondose trees.

Distribution: Known from Europe and North America.

A relatively small genus of ten or fewer species previously considered related to *Octavianina*, in which the original species was placed. Rather variable so that many so-called species are merely developmental stages of a handful of species.

For accounts of the species see Zeller & Dodge, Ann. Mo. Bot. Gdn. **23**: 565, 1936; Fogel, Mycologia **82**: 655, 1990. Colour illustrations and line-drawings of single British species in Pegler *et al., British Truffles* and b/w photographs of anatomical features in Clémençon *et al*. Mycotaxon **100**: 85-95, 2007. Has been linked with *Wakfieldia q.v.* in main text.

Sinoboletus Zang, Mycotaxon **45**: 223, 1992 A genus fairly recently described and based on two taxa, which from the descriptions look very different. The authors relate the genus both to *Boletus q.v.* and *Xerocomus q.v.* but without any discussion as to the development of the stratified tubes or even offering a hypothesis as to the way the basidiospores might be dispersed. More research is required on fresh material in all stages of development. The basidiospores do not resemble those of *Boletus* s.stricto and indeed it may be a coincidence that although the two species have had their tube structure interpreted in the same way; they may not be related one to the other. It would appear that the species depicted in the descriptions and illustrations are not conspecific, one resembling a xerocomoid bolete and the other a member the of the phlebopoid consortium; the position of the genus is debateable. This has been tentatively confirmed by recent Chinese collections agreeing with the type species of *Sinoboletus duplicatosporus* Zang and other taxa.

A generic description is offered based on the original account:

Basidome: epigeal, pileate, hymenophore tubulate. 2-layered, centrally stipitate, putrescent, probably gymnocarpic.

Pileus hemispherical, convex then plano-oconvex, dry, tomentose, rust-colour, reddish brown or in yellow browns. *Stipe* obclavate to clavate, cylindric or sub-equal to sub-bulbous, solid with striate apex, not reticulate, dry, attached to pale yellowish mycelium. *Tubes* adnate to sinuato-adnate with cross-veins prodoucing two definite layers, with superior layer irregular with age, reddish or yellowish brown and inferior tubes golden yellow to yellow; *pores* compound, boletinoid, round at first then angular. *Context* thick or thin, soft.

Basidiospores ovoid or ellipsoid, pale yellow to orange-yellow more orange in ME, smooth, thick-walled, sometimes with truncate apex or appearing slightly knotched and with small pore, with suprahilar depression. *Cheilocystidia* clavate to broadly clavate, hyaline, thin-walled; *pleurocystidia* elongate-fusiform, thin-walled, hyaline. *Pileipellis* an epicutis of tangled, filamentous hyphae with free tips. *Clamp-connections* not seen.

Ecology: terrestrial, associated with *Castanea* (Fagales) and Pinaceeae

Known only from China (Southwestern Yunnan) in vegetational zone bordering tropical monsoon forest.

Families

The following families have been previously linked to the Boletales:

Beenakiaceae Julich, 1982 based on *Beenakia* Reid with type species *Beenakia dacostae* Reid. It has been referred to the Boletales; see Hawksworth, Kirk *et al* in *Dictionary of Fungi*, 1995; see Reid, in Kew Bull. (1955): 635, 1956. The family was assigned to the Gomphales by Julich which is a better placement judging from the morphological characters. Molecular studies confirm this placement.

Basidiome: pileate, hymenophore hydnoid, dimidiate to laterally or centrally stipitate and equipped on the lower surfaces with teeth.

Pileus reniform to orbicular, tomentose but soon collapsing or matted to scrupose and finally smooth, pale to dark ochraceous, drying darker brown, often with olivaceous tints. *Stipe* excentric, central or lateral, or even lacking, tomentose cottony or felty and arising from basal tomentum, concolorous with pileus. *Hymenium* covering outside of beige to olivaceous spines. *Context* soft, spongy, homogeneous, not zoned, white, drying yellowish or pallid brown; taste and smell none or mild.

Basidia 4-spored, clavate, slender, with basal clamp-connection. *Basidiospores* broadly ellipsoid to pip-shaped or almost navicular, finely ornamented, hyaline to yellowish in aq. ammoniacal solutions, non-amyloid, cyanophilous. *Cystidia* absent. *Context* monomitic, of smooth to distinctly warted, filamentous or often inflated, thin-walled hyphae. *Clamp-connections* present.

Ecology: Saprotrophic, lignicolous, on hardwood and ferns, apparently in the former associated with white-rot.

Distribution: Known from New Zealand & Australia, from Zambia and Zaire, India, South America (Brazil, Bolivia) and Central America (Costa Rica). Single European species formerly placed in *Sarcodon*.

A small genus of 7 species 5 of which are monographed fairly recently by Nunez & Ryvarden in Sydowia 46: 321, 1994.

Gasterellaceae Zeller, 1948. Monotypic with *Gasterella* as the type genus and *G. luophila* Zeller & Walker found in North America (Nebraska) as the only spe-

cies. The gasterocarp is rather small, 200-700µm diameter, subglobose; peridium simple composed of fundamental hyphae, hollow, seated on sterile pulvinate to broadly conic base, gleba unilocular with smooth hymenium producing dark brown, citriform, verrucose, thick-walled, apiculate spores.
Because of the minute size it has been rarely found and Smith (1951) says 'not likely to recognize in the field'. It was originally found in a woodland soil brought into the laboratory. The genus has been associated with the boletes, although originally placed in the Hymenogastrales. As indicated in many places in the text above and the entries below the latter is a polyphyletic grouping. No molecular work has been undertaken to confirm the placement of *Gasterella*. See Zeller & Walker, Mycologia **27**: 573-579, 1937; also Routien (Mycologia **31**: 416-417, 1939) & Zeller (Mycologia **40**: 639, 1948).

Gastrosporiaceae Pilát, 1934 contains the genera *Leucorhizon* Vel. and *Gastrosporium* Matt. It is similar to the Gasterellaceae in that although it has been associated with the boletes no molecular work has been undertaken to show that such treatment is in fact correct; see main text under *Tremellogaster*. The type of *Gastrosporium* is *G. simplex* Matt., a hypogeal fungus associated with xerothermic Gramineae and prairie herbs. The basidiospores, 4-5.5 x 3.8-4.6 µm, are pallid ochraceous, subhyaline, globose to globoso-ovoid, thick-walled and slightly verrucose. The family is known from Europe, North America and India. Pilát (Bull. Soc. Mycol. Fr. **50**: 45-46, 1934) placed this genus in the Gastrosporiales in part based on the aculeate development, *i.e.* basidia formed on down-growing tissue from the upper regions of the inner peridium and then fragmenting to form locules. See Monthoux & Röllin, (Candollea **31**: 119, 1976). A good description of *Calvatia defodiodes* Lloyd (= *Disceda defodiodes* (Lloyd) Zeller) is given by Miller & Askew (1982); they demonstrated that this species is a synonym of *Gastrosporium simplex*. From recent studies this family could be related to the *Phallus/Gomphus* consortium.

Gautieriaceae Zeller, 1948 a family placed in the Gautieriales with 3 constituent genera; it has been linked to the boletes in virtue of the fact that at least *Gautieria morchelliformis* Vitt. (type of the genus) is often infected with *Sepedonium chrysospermum* Tul., a hyperparasite generally growing on boletes and relatives. However, many of the characters of the family fit more closely with the Cortinariales; molecular studies are required for a final decision. Indeed the *Sepedonium* associated with the type is in need of closer examination virtue of the rather more complex nature of this form genus than previously considered; see Rogerson & Samuels (1989). The basidiome is gasterocarpic, hypogeal with short to citriform, costate, golden to dark brown basidiospores with thickened wall; the

peridium is often lacking and gleba formed of independent cavities, separated by a cartilaginous, branched columella. Known from Europe, North America and Australia. See Zeller (Mycologia **40**: 666, 1948) Zeller (Ann. Miss Bot. Gdn., **29**: 625-708, 1934) in the monograph of *Hymenogaster* by Zeller & Dodge which also covers *Gautieria*. Also see discussion in main text under *Octavinana*. *Rhodactina q,v,* in main text*,* when first introduced was placed with *Gautieria*; it too has been found associated with the hyperparasite *Sepedonium*.

Glischrodermataceae Rea, 1913, based on the single constituent species, *Glischroderma cinctum* Fuckel, which has been included in the Sclerodermataceae. An excellent account of fresh material from the British Isles was published by Rea (Trans. Brit. Mycol. Soc. **4**: 64-65, 1912) and supported by a coloured illustration. Hennebert (Persoonia **7**: 183-185, 1973), however, has demonstrated that the fungus is a peridiolate coleomycete producing conidia.

Hymenogastraceae Vitt., 1831. This family traditionally has been associated with the boletes but in fact the relationships of the major sections of the genus are with the cortinarioid fungi. In fact species of *Hymenogaster* Vitt, are only united in their gasterocarpic, hypogeal basidiome with multiloculate gleba, differentiated peridipellis and brown basidiospores; the spores may be ornamented or verrucose indicating a wide range of relationships. Australasian taxa referred to the genus are now known to be a mixture of distinct genera including *Cortiomyces* Bougher & Castellano, *Descomyces* Bougher & Castellano, *Quadrispora* Bougher & Castellano and *Timgrovea* Bougher & Castellano, all undoubtedly cortinarioid. – see Bougher & Castellano (Mycologia **85**: 273-293, 1993). May & Wood (Mycotaxon **54**: 147-150,1996) has demonstrated that the first is in fact a synonym of *Protoglossum*.Mass. Some of the residual elements within *Hymenogaster* have been shown to have other well-defined lineages, *e.g. Braunia* Rick is referable to *Brauniella* placed in the Pluteaceae but others possess unknown affinities or the relationships are speculative. The Hymenogastrales as traditionally understood contains 5 families Gasterellaceae (see above), Gastropsoriaceae (see above), Octavianiaceae (see main text under *Melanogaster*), Protogastraceae (see below) and Hymenogastraceae. See Dodge & Zeller (Ann. Miss. Bot. Gdn. **21**: 605 -708, 1934).

Jugasporaceae (Kühn.) Singer Created by Singer (Ann. Mycol. **34**: 323, 1936) to cover *Clitopilus*, a pink-spored group of agarics whose basidiospores are longitudinally striate or grooved. The name was invalidly published. According to Singer (Farlowia **2**: 547-561,1946) this genus has many characters in common with the Paxillaceae, based on *Paxillus q.v.* The current position of *Clitopilus* is

in the Entolomataceae and so distantly related to the boletes and their allies, a placement agreed to in later works by Singer (*Agaricales in Modern Taxonomy*, 1951 *et subseq.*). A key to the species of this family are given by Singer in the reference above.

Leucogastraceae Moreau ex Fogel, 1979. With *Leucogaster* R. Hesse and *Leucophlebs* Harkness as consistuent genera this family has been associated with the boletes through the placement of *Leucogaster* in the Melanogastraceae. Both genera have been clearly demonstrated by molecular techniques as being hypogeal relatives of *Albatrellus*, a polyporaceous alliance and therefore not within the boletes (Albe-Scott, Mycol. Research **111**, 2007). Both have been linked to *Lycoperdellon* Heim by Zeller but this genus is now known to be a species of *Ostracoderma*. See Hennebert (Persoonia **7**: 183-185, 1973).

Omphalotaceae Bresinsky with *Omphalotus* Fayod as the type genus. The placement of this family close to the paxilloid agarics and therefore the boletes is based on the occurrence of specific secondary metabolite. See Kämmerer *et al.* (Plant Systematics & Evolution **150**: 113, 1985). Singer (1986) followed this placement but from anatomical and later molecular studies this does not appear to be the a true relationship; in these characters *Omphalotus* shows more connections to the tricholomataceous Marasmieae.

Protogastraceae Zeller, 1934 is based on a single species *Protogaster rhizophilus* Thaxter apud Zeller, 1934. It was found on the roots of *Viola* in North America (Maine) and has been associated with the boletes through its links with the Hymenogastrales; see above. This is increasingly doubtful. The genus is only known from North America and has been assigned to its own order Protogastrales; see Zeller (Ann. Miss. Bot. Gdn. **26**: 235, 1934).

Sphaerobolaceae J. Schroet., 1849 with *Sphaerobolus* Tode : Pers. as the type and only genus has been associated with the boletes through its supposed relationship with the *Sclerodermataceae*. Molecular studies demonstrate clearly that this genus is surprisingly related to a *Phallus/ Gomphus* consortium and not to the boletes. See Watling (Mycoscience **47**, 2000).

Classification:

The Boletales as here conceived is a natural grouping defined by molecular parameters and represents a major branch of the holobasidiomycetes, the Agaricomycotina, with strong boot strap support. For details see Hibbett (2006) and Binder & Hibbett (2006). For discussions on the boletiod genera included; see Snell (Mycologia **33**: 415-423, 1941) & Donk (Reinwardtia **3**: 75-313,955).

Basidiomycota
Basidiomycota: Agaricomycotina
Agaricomycetes
Agaricomycetidae

Boletales

Sclerodermatineae

Astreaceae: *Astraeus*

Boletinellaceae: *Boletinellus; Phlebopus*

Calostomataceae: *Calostoma*

? Diplocystacaeae: *Diplocystis*

Gyroporaceae: *Gyroporus; Setogyroporus*

Pisolithaceae: *Pisolithus*

Sclerodermataceae: *Corditubera Scleroderma; Horakiella ??*

? Tremellogastraceae: *Tremellogaster*

Incertae sedis: *Chlorogaster ?*

Suillineae

Gomphidiaceae: *Brauniellula; Chroogomphus; Cystogomphus; Gomphidius; Gomphogaster*

Suillaceae: *Gastrosuillus p.p,; Paragyrodon; Psiloboletinus; Suillus*

Rhizopogonaceae: *Alpova; Amogaster; Rhizopogon, Rouyangia; Truncolcolumella*

Paxillineae

Paxillaceae: *Gyrodon; Hydnomerulius; Paxillogaster; Paxillus; Pseudogyrodon ??*

Melanogastraceae: *Melanogaster*

Tapinellineae

Tapinellaceae: *Pseudomerulius; Tapinella*

C**oniophorineae**

Coniophoraceae: *Chrysoconia, Coniophora; Coniophoropsis; Corneromyces; Gyrodontium*

Hygrophoropsidaceae: *Bondarcevomyces; Hygrophoropsis; Leucogyrophana; Podoserpula ??*

Serpulaceae: *Austrogaster; Austropaxillus; Gymnopaxillus; Meiorganum; Serpula; Singeromyces*

Jaapia ??????????

Boletineae

Boletaceae *s. st.*

Boletus p.p. & Gastroboletus

Boletaceae *s. l.*: *Boletus p.p.; Xanthoconium*

Retiboletus; *Rubinoboletus;*

Porphyrellus p.p.; *Tylopilus p. p.; Veloporphyrellus*

Buchwaldoboletus; Chalciporus; Pulveroboletus

Xerocomus p.p.

Chamonixiaceae: *Chamonoxia p.p.*

Austroboletus: Gastroleccinum; Leccinellum; Leccinum

Octavaninaceae: *Octavaniana p.p.; Wakefieldia ??*

Xerocomaceae *s. st*: *Aureoboletus; Boletellus p.p.; Bothia; Gastroboletus p.p.; Hemiporus;Phylloporus; Tuboseta; Xerocomus p.p.*

Incertae sedis: *Hiemiella*

Xerocomaceae *s. l.*(Strobilomycetaceae?): *Afroboletus; Boletellus p.p.; Porphyrellus p.p.; Phylloboletellus; Strobilomyces, Rhodocatina*

Key to Genera

Specific hymenophoral configurations are no longer restricted to a single order. The hypogeous truffle-like species may be found in the Russulales, Cortinariales etc. see Dring in **The Fungi*** Chapter 24 -*Gasteromycetes*. Equally the poroid hymenophore which characterises the boletes is extensively found in the bracket fungi and their immediate relatives, constituting a large lignicolous group, e.g. Ryvarden & Gilbertson, 1993 & 1994 – see Pegler in **The Fungi*** Chapter 22 - *Aphyllophorales IV Poroid families*. The lamellate hymenophore traditionally associated with the mushrooms and toadstools, viz. agarics (Singer Agaricales in Modern taxonomy, 4th edition 1986), although widely expressed in that group occurs in other orders; see Smith **The Fungi *** Chapter 23 - *Agaricales and related Secotioid Gasteromycetes*. The hydnoid facies is rather rare in the Boletales, although it is expressed in several related orders. Thus only a handful of hydnoid genera are recognized with boleoid affinities whereas in the Thelephorales there are a whole series some with brown basidiospores and others with a white spore-print – see Harrison in **The Fungi*** Chapter 21 - *Aphyllophorales III: Hydnaceae and Echinodotaceae* & Talbot in Chapter 19 – *Aphyllophorales I general characteristics; Thelephoroid and Cupuloid Families*. The epigeous 'puff-ball' morphotype is again more extensively developed in the Lycoperdales, relatives of the true agarics but within the bolete-consortium several superficially similar types are found, *e.g. Pisolithus, Scleroderma*. The genera are often only represented by handful of species in each group; even the earth-star morphotype is represented by *Astraeus*, a relative of *Scleroderma*, although it is universally thought of as more representing *Geastrum* within a *Phallus/Gomphus* grouping – see Pilát (1958); Miller & Miller (1988). The resupinate crust-like basidiome is expressed in many orders including the Russulales and Polyporales, and there are reprsentatives amongst the bolete relatives also, two of which are economically important rotters of domestic timbers. Such morphotypes are dealt with in publications including Eriksson & Ryvarden and Hjörstram, Larsson & Ryvarden in 8 volumes of Corticiaceae of Northen Europe. Finally some basidiomes appear to be intermediate between the truffle-like-forms and the stipitate pileate forms in that the pileus does not expand and so by clasping the stipe encloses the hymenium. Such fungi are known as sequestrate and again are found not just in the boletes but Russulales etc.; see Smith Chapter 23 referred to above. They may be epigeal or hypogeal. Although based on macro-morphology, anatomy and chemical tests, many of these links were first suggested by Donk in the polyporaceous fungi, (Persoonia **3**, 1964) and in the gasteroid fungi by Heim (1971). They are

now largely supported, consolidated and extended by molecular studies; see Binder & Hibbett, 2006.

These chapters apply to **The Fungi An Advanced treatise. Vol IV B. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi**, 1973. eds. Ainsworth, G.C., Sparrow, F.K. & Sussman, A.S., Academic Press, London. 504pp.

As shown in the generic descriptions the hymenophore is still used as a major morphological character in defining genera but its significance is much reduced in modern treatments. However, the gross-morphology is a character, which can be ascertained in the field and must be used in any key to the group. Thus the hymenophore may be poroid, lamellate, corticioid or concealed within the fruit-body (gasteroid), stipitate or astipitate, hypogeous or epigeous. Spore-colour has always been used as a feature to define macromycetes, along with the reaction of the spores to solutions of iodine (Melzer's reagent) and this again is on the whole supported by molecular studies. The spore-mass colour is therefore another important character, which can be ascertained from working with fresh specimens. Generally microscopic examination is required to decide the spore-colour in herbarium specimens.

1. Basidiomes hypogeal or at most subhypogeal **2**
x Basidiomes epigeal **14**

2. Basidiomes developing below ground or in upper surfaces, erupting through soil surface **3**
x Basidiomes totally hypogeal **4**

3. Basidiospores smooth, hyaline at most honey-coloured **Rhizopogon** Plate13 B (if bright yellow see **Mycoamarantus**)
x Spores echinulate, becoming dark brown ..... **Tremellogaster** Plate 15 D

4. Basidiospores smooth **5**
x Spores ornamented **9**

5. Basidiospores brown s *m* or starting yellowish and darkening with age **6**
x Spores hyaline or pale honey-coloured *s m*. **7**

6. Basidiospores pseudoamyloid, commencing yellowish but darkening with age **Amogaster** Plate 1 B
x Spores not pseudoamyloid, brown to very dark brown from beginning..... **Melanogaster** Plate 10 C

7. Basidiospores fusoid to subbilateral, pale yellowish brown in ammoniacal solutions inamyloid ..... **Royoungia** Plate 13 D
x Spores ellipsoid with truncate to rounded base..... **8**

8. Hymenium present in palisadoderm with empty or spore-filled chambers .... **Rhizopogon** Plate 13 B
x Hymenium absent, chambers containing spores and gelatinizing basidia and hyphae ..... **Alpova** Plate 1 C

9. Basidiospores ornamentation composed of ridges and crests **10**
x Spore-ornamentation of punctae or spines, or reticulate **13**

10. Basidiospore with apical pore or distinctive hilar pore **11**
x Spore lacking such differentiation **12**

11. Basidiospore ellipsoid, ridged with small apical pore, brown in ammoniacal solutions ..... **Chamonixia** Plate 4 F
x Spores appearing smooth but verrucose below a smooth enveloping exosporium, distinct, broad hilar pore, hyaline to golden brown in ammoniacal solutions ..... **Wakefieldia** Plate 17 A

12. Basidiospores with solid, longitudinal ridges, pseudoamyloid and purple-red in ammoniacal solutions ..... **Rhodactina** Plate 13C
x Spores if with ridges then spore not so-coloured with coarse conical spines, inamyloid or some in time pseudoamyloid, hyaline to honey-coloured in ammoniacal solutions..... **Octavaniana** Plate 10 D

13. Basidiospores hyaline with low reticulum mixed with dark abhorted spores and nurse-like cells ..... **Horakiella** Plate 8 E
x Spores with delicate conical warts, brown in ammoniacal solutions..... ..... **Corditubera** Plate 5 F

14. Hymenium developing within an enclosed basidiome **15**
x Hymenium in tubes, on gills resupinate, sessile or reflexed and exposed at maturity **30**

15. Basidiome resembling a malformed agaric or bolete in section with contorted gill-like plates or curved tubes **16**
x Basidiome lacking such distinct internal structure **25**

16. Hymenium on curved or disorganized tubes.....**17**
x Hymenium on disorganised plate-like or gill-like structures.....**19**

17. Pileus gelatinous, viscid or greazy from an ixotrichoderm; cystidia in fascicles ..... **Gastrosuillus** Plate 7 B
x Pileus non-gelatinous at mosty humid to the touch **18**

18. Basidiome not cyanescent. Stipe covered in yellow or buff darkening scabrosities; tubes yellow..... **Gastroleccinum** Plate 7 A
x Basidiome cyanescent or not. Stipe if covered in scabrosities then these red or never yellow, and if tubes yellow then orifice red or orange, or cyanescent .....**Gastroboletus** Plate 6 D

19. Hymenium consisting of disorganised plates generally not exposed to environment or if so irregularly and never on well-defined gills **20**
x Hymenium on gills soon exposed to environment during development, hymenium finally exposed as irregular morchelloid honeystructure..... **Gymnopaxillus** Plate 7 E

20. Basidiospores rust- or yellow brown *s.m.*.....**21**
x Spores purple-brown *s.m* **24**

21. Basidiospores smooth, ellipsoid to subfusoid, hymenium only exposed by partially lifting cap-margin ..... **Truncocolumella** Plate 15 E
x Spores minutely roughened or punctate-perforate.....**22**

22. Basidiospores minutely roughened *s.m*..... **Austrogaster** Plate 2 A
x Spores perforate **23**

23. Basidiome resembling a puff-ball, spores yellow, indistinctly perforate ..... **Paxillogaster** 10 G
x Basidiome hypogeal, quickly exposing spore-surface, spores yellow perforate ..... **Singeromyces** Plate 14 C

24. Flesh in stipe white or yellow often chrome yellow at base, inamyloid ..... **Gomphaster** Plate 7 D
x Flesh pale yellowish or apricot, amyloid.....**Brauniellula** Plate 3 E

25. Basidiome in clusters on a common stroma, or either at maturity forming a star-shaped structure or with a prominent central sac with complex apical

peristome.....**26**
x Basidiome lacking any of the above.....**30**

26. Basidiomes clustered on a stroma..... **Diplocystis** Plate 6 C
x Basidiome single or if clustered then rarely and never on a common stroma **27**

27. Basidiome with prominent apical differentiation.....**28**
x Basidiomes star-shaped.....**Astraeus** Plate 1 D

28. Apical peristome fimbriate, vivid blue & yellow green. Spore-mass green on elevated stipe.....**Chlorogaster** Plate 5 A
x Apex more complex and resembling parrot beak. Spores ochraceous ....**Calostoma** Plate Plate 4 C

29. Basidiome containing several sacs of spores (peridioles)..... .....**Pisolithus** Plate 11 E
x Basidome lacking peridioles and having more or less uniform spore-mass; spore-mass olivaceous or brown and only pseudostipitate from interlocked rhizoidal structures.....**Scleroderma** Plate 13 F & G

30. Basidiome stipitate.....**31**
x Basidiome non-stipitate **75**

31. Hymenium smooth or wrinkled and on several tiers attached to lateral stipe .....**Podoserpula** Plate 12 A
x Basidiome lacking tiers of hymenia, either lamellate or tubulate..... **32**

32. Hymenium lamellate.....**33**
x Hymenium tubulate.....**42**

33. Basidiospores hyaline *s m* white or cream-colour in mass ..... **Hygrophoropsis** Plate 9 B
x Basidiospores coloured *s.m.* **34**

34. Basidiospore print rust-brown s m or burnt umber to beige **35**
x Spore print dark, blackish (fuligineous to violaceous) and never brown with slight porphyry tinge.....**39**
35. On wood..... **Tapinella** Plate 15 C
x Terrestrial **36**

36. Gills widely spaced waxy yellow ..... **Phylloporus** Plate 11 D
x Gills rust-brown or burnt umber **37**

37. Basidiospores dilute dull brown darkening in ammoniacal solutions; hymenophore in part boletinoid but lamellate in zone at margin
..... **Psiloboletinus** No figure
x Spores more richly coloured even when slightly tinged purplish; hymenophore distinctly lamellate even if with interconnecting forks..... **38**

38. Hymenial cystidia poorly or undeveloped; occurring with Soutrhern Hemisphere dicots..... **Austropaxillus** Plate 2 B
x Hymenial cystidia present: occurring with Northern Temperate dicots.
..... **Paxillus** Plate 11 A

39. Basidiospores longitudinally ridged ..... **Phylloboletellus** Plate 11 C
x Spores smooth..... **40**

40. Pileus covered in spherocytes ..... **Cystogomnphus** Plate 6 B
x Pileus lacking such structures although regularly with glutinous or wooly surface..... **41**

41. Basidiome with coloured, amyloid stipe and pileus flesh
..... **Chroogomphus** Plate 5 B
x Basidiome with white inamyloid stipe and pileus flesh.....
..... **Gomphidius** Plate 7 C

42. Basidiospor smooth..... **43**
x Spores ornamented with crests, wings or distinct striae **74**

43. Stipe central **44**
x Stipe lateral or almost absent **67**

44. Basidiospores in mass yellow, pinkish or purplish; coloured or hyaline *s.m.*. ..
..... **45**
x Spores olivaceous to cinnamon brown distinctly coloured although sometimes only faintly so *s.m.* **50**

45. Basidiospores hyaline *s.m* ellipsoid, yellow in mass ..... **Gyroporus** Plate 8 D
x Spores if hyaline *s.m* then elongate pinkish or purplish **46**

46. Basidiospores pinkish **47**
x Spores purplish **49**

47. Pileus surface never gelatinous or mucilaginous..... **Tylopilus** Plate 16 B
x Pileus gelatinous mucilaginous and basidiome rather soft and squidgy.....**48**

48. Hymenium intact..... **Fistulinella** Plate 10 E
x Hymenium especially pulling apart and collapsing..... **Ixechinus** Plate 9 C

49. With distinct appendiculate veil.....**Velvoporphyrellus** Plate 16 C
x Lacking such structure .....**Porphyrellus** Plate 12 B

50. Possessing setae or setules in hymenium or growing on wood, or on earth-balls (**Scleroderma**: see Plate 13 F & G) or earth stars (**Astraeus**: see Plate 1 D.) **51**
x Lacking setae and with different habit **54**

51. Setae or setules present in hymenium.....**52**
x Setae and setules absent.....**53**

52. Basidospores ellipsoid; hyaline or poorly pigmented setules present .....**Setogyroporus** Plate 14 B
x Spores elongate; darkly pigmented setae present.....**Tuboseta** Plate 16A

53. Growing on wood .....**Buchwaldoboletus** Plate 4 A
x Growing attached to gasteromycetes ..... **Pseudoboletus** Plate 12 C

54. Basidiome with distinct persistent pulverulent veil or with more or less distinct, dry, darkening or unchanging yellow, white or buff, or darker floccose scabrosities on stipe. If with peronate base to stipe see **62**.....**55**
x Basidiome lacking veil and if tubes yellow then not accompanied by darkening scabrosities **57**

55. Pulverulent veil present.....**Pulveroboletus** Plate 12 E
x Veil if present then purely an extension of the pileus margin to form appendiculate skirt **56**
56. Tubes yellow, pileus often palisadoderm or hymeniderm, blackening on damage; scabrosities yellow .....**Lecciniellum** Plate 9 G
x Tubes whitish; olivaceous or cinnamon coloured tubes when mature; pileus either a trichoderm or a cutis; scabrosities either commencing brown or blackish

or pale and then darkening to various shades of brown... **Leccinum** Plate 9 E & F

57 Basidiospores rounded **58**
x Spores elongate **61**

58. Basidiospores smooth *s.m.* **59**
x Basidiospores ornamented in some way, crested, ridged, costate *etc* **71**

59. Basidiome with rich red tubes & pores..... **Rubinoboletus** Plate 13 E
x Basidiome lacking red tubes **60**

60. Large fruiting body without distinct veil ..... **Phlebopus** Plate 11 B
x Rubbery basidiome with distinct peronate stipe-base
..... **Paragyrodon** Plate 10 F

61. Hymenium bright yellow with yellow contents in ammoniacal solutions in microscopic mounts **62**
x Hymenium if bright yellow then lacking such reactions although bluish green reaction may take place with ammoniacal vapours in very flesh state **63**

62. Hymenium with large, very prominent cystidia..... **Aureoboletus** Plate 1 E
x. Hymenium lacking distinctive cystidia..... **Retiboletus** Plate 13 A

63. Basidiospores coffin-shaped ..... **Xanthoconium** Plate 17 B
x Spores fusoid or subfusiform, inequilateral **64**

64. Basidiospores not greater than 11 µm with quotient ratio 2.3-2.8, pale cinnamon in mass..... **65**
x Spores larger **66**

65. Cystidia prominent either in fascicles at tube orifice or on tube surface and or as waxy or sticky punctae on stipe.or if separate then pores olivaceous and not cinnamon..... **Suillus** Plate 15 A & B
x. Cystidia when present at orifice and in tubes separate although sometimes with mucilaginous cap; tubes and pores cinnamon brown to red-brown.....
..... **Chalciporus** Plate 4 E

66. Network frequently strongly developed on stipe, comprising regular or reduced hymenial elements even when replaced to simple punctae. Hymenophoral

trama adhering together from gelatinization and separating entire when broken .....**Boletus** *s.l.* Plate 3 B & C

x Network if present poorly developed forming unorganized. elongate ribs, or replaced by similarly structured punctae or mixture of both. Hymenophoral trama separating down the middle when torn .....**Xerocomu**s Plate 17 C

67. Basidospores strongly coloured, very thick-walled..... ..... **Pseudogyrodon** Plate 12D

x Spores honey-coloured in aqueous ammoniacal soluions and lacking distinct thickened volvate stipe-base **68**

68. Hymenium sulphur yellow then olivaceous, composed of shallow tubes with subradial, angular orifices, more elongated towards margin; spores inamyloid, bronze-colour in mass .....**Gyrodon** Plate 8 A

x Hymenium olivaceous or cinnamon at first then flushed with olivaceous, gyrose tubuate, although sometimes with shortened tubes; pores honey-comb-like... **69**.....

69. Spore-print olivaceous; basidiome with olivaceous and ochraceous colours prevailing; spores pseudoamyloid..... **Boletinellus** Plate 3 A

x. Spore-print yellow-brown to amber.....**70**

70. Basidiomes with uniformly chestnut to cinnamon colours prevailing; lacking lamellate marginal zone to hymenophore ..... **Bothia** Plate 4 D

x Basidiomes with a distinct boletinoid confirguration except at lamellate margin ..... **Psiloboletinus** no figure

71. Basidiospores with longitudinal ridges or striae or distinct aveolae.....**72**

x Spores with crests, wings or ornamentation composed of punctae or wrinkles **73**

72. Basidiospore surfaces alveolate ..... **Hiemiella** Plate 8 D

x Basidiospore with distinct ridges or striae.....**73**

73. Basidiospores elliptic to elongate ellipsoid with longitudinal ridges or striae . ..... **Boletellus** Plate 2 C & D

x Spores broadly ellipsoid with longitudinally arranged ridges coalescing at ends .....**Afroboletus** Plate 1 A

74. Basidiospores punctate or wrinkled, the latter often medial ..... **Austroboletus** Plate 1 F
x Spores rounded or broadly ellipsoid with crests and wings and ridges ..... **Strobilomyces** Plate 14 D & E

75. Basidsospores smooth **76**
x Spores ornamented..... **Coniophoropsis** Plate 5 E

76. Hymenium smooth or composed of indistinct wrinkles and low folds **77**
x Hymenium distinctly folded , meruloid or toothed..... **81**

77. Hymenium distributed over small, pulvinate to hemispherical basidiomes ..... **Chrysoconia** Plate 5 C.
x Hymenium much more extensive, if commencing in small pulvinate patches then soon spreading often to several centimetres or even more **78**

78. Basidiospores hyaline *s. m.* only slightly coloured in mass ..... **Leucogyrophan**a Plate 10 A
x Spores distinctly coloured sm brown in mass..... **79**

79. Basidiospores elongate-fusoid, thick-walled sometimes sepate and with prominent stergmatic peg; cystidioles prominent ..... **Jaapia** Plate 9 D
x Spores ellipsoid and apiculus reduced **80**

80. Hair like processes in hymnenium ..... **Corneromyces** Plate 6 A
x Hair-like absent and cystidia rare..... **Coniophora** Plate 5 D

81. Hymenium distinctly toothed or poroid at maturity **82**
x Hymenium meruloid or strongly folded or honey-comb like **84**

82. Hymenophore distinctly poroid ..... **Bondarcevomyces** Plate 3D
x Hymenophore distinctly toothed..... **83**

83. Basidiome resupinate, crust-like..... **Hydnomerulius** Plate 9 A
x Basidiome rarely completely resupinate, sessile, effuso-reflexed and most frequently as imbricate brackets ..... **Gyrodontium** Plate 8 C

84. Hymenium honey-comb-like with or without a pileus ..... **Meiorangum** Plate 10 B
x Hymenium strongly folded **85**

85. With marginal thick border or even effuso-reflexed and irregularly pileate accompanied by long substrate strands ..... **Serpula** Plate 14 A

x Basidiome resupinate, thinner in over all appearance lacking rhizomorphs ... . **Pseudomerulius** Plate 12 F

Species recognition

This manual does not attempt to itemize species but the methods adopted for the identification of species may be helpful. Unlike 25 years or so ago, identification of species within the Boletales requires reference to several texts each referring to a particular growth-form (morphotype). Probably the most familiar group of macromycetes are the agarics and linked with these for many years have been the boletes, no doubt because of their putrescent nature and superficial resemblance, except for the tubulate hymenophore (see Singer 1950 *et subseq*.).

Thus species recognition here requires a rather more detailed knowledge of the hymenophore, whether poroid or lamellate, whether strongly attached to the stipe or totally free of the stipe or intermediates between, radially arranged or whether gill-like towards the pileus-margin (*viz.* semi-lamellate), angular or regular pored, colour differences between tube-walls and orifices, whether the tube layer is broad or narrow and finally the mature over-all colour. To this must be added the surface features of the pileus, whether smooth, hirsute *etc*., dry, humid or viscid and the type of stipe textures, whether hollow or solid, reticulate on the outer surface, smooth or scurfy-scabrous and degrees of each. Colour changes of the flesh when exposed to the air; odour and taste are useful as are a range of chemical tests listed in the texts.

Microscopically the spore-morphology is critical, not only the shape but the size and whether ornamented or not, and if ornamented what the patterns are, whether the basidia are 2- or 4-spored, whether clamp-connections are present on the hyphae or not, and the presence or absence of sterile cells (cystidia) and when present their morphology. The micro-structure of the outer layers of the pileus (pileipellis) are often critical. With this information married to developmental features, especially presence or absence of a distinct or fugacious veil and its structure a complete picture emerges. Useful illustrative descriptions of the terms are found in Josserand (1952), Snell & Dick (1957), Berger (1980) and various issues of the **Dictionary of the Fungi**. See also Singer (1950 *et subseq*.).

There are several books which focus entirely on the gasteroid fungi and within the Boletales there is a range of morphologies ranging from the false truffles, stromatic puffball *Diplocystis* to the earth-balls and earth-stars, and several other rather bizarre shaped taxa. Character definitions can again be sought in Snell & Dick (1957) but reference to Pegler *et al*. (1993) in their account of British truffles and Pegler *et al*. (1995) in their account of British gasteroid fungi is useful.

Not all the gasteroid morphologies, especially the sequestrate forms, are found in Britain so reference should also be made to Miller & Miller (1988).
Although the core of the order are boletes, viz. poroid, and to a lesser extent agarics, *viz.* lamellate (gilled) there are several corticioid forms. Again the configuration of the hymenial layer whether pseudoporoid, odontoid, raduloid, or greazy or dry, and its colour and colour changes with age or damage are paramount. As with the other Boletales spore-morphology and presence or absence of cystidia and presence or absence of clamp-connections are important. A good account of these structures are to be found in the first volume of the series **Corticiaceae of Northern Europe** by Hjortstam, Larsson & Ryvarden & Eriksson (1987). The same text can be used for the single polyporoid member and the small hydnoid fraction, although the two volumes on North American polypores by Gibertson & Ryvarden (1986-1987) will prove useful in providiong a handle to the terminology.
The results from molecular work have in many cases supported species which have been based on morphology alone, whilst in other cases what appear to be identical collections in the field turn out to be quite different after DNA sequencing. Generally in the latter examples differences, although often quite subtle, can be demonstrated after re-assessment of the field data, anatomy etc. Finally in other examples molecular work shows that what appeared to be separable in the field are simply variants of a single rather variable taxon. It cannot be over emphasised that it is essential to gather critical field data, especially ecological information, whenever possible and retain carefully dried exsiccata for later re-examination. A record of the location where the material was found is essential.

Glossary

Adaxial applanation patch: small flattened area around the hilar appendage of the basidiospore as in *Gyrodon lividus*.
Adnate: where tubes or gills are broadly attached to the stipe-apex as in *Suillus luteus*; adnato-decurrent where the attachment is equipped by a short decurrent tooth as in *Chalciporus piperatus*.
Adnexed: where the tubes or gills are narrowly attached to the stipe-apex; adnexo-sinuate with a small indentation before narrowly joining the stipe-apex as in *Xerocomus chrysenteron*.
Alkaline solutions: 10% aqueous solution of sodium or potassium hydroxide.
Ammoniacal solution: 10% aqueous solution of ammonia.
Ampullaceous: ampulliform: swollen below as in the shape of a flask – ampule-shaped as in cystidia of *Leccinum scabrum*.
Amyloid: basidiospores, hyphae, tissues becoming bluish grey or blue-black with Melzer's reagent (ME): see also inamyloid & pseudoamyloid
Anastomosing: where the tubes or gills are connected by veins or ridges as in *Phylloporus pelletieri*.
Angiocarpic (or –ous): with the hymenial tissue maturing within the basidiome.
Annulus or ring, annular zone: remnant partial veil left on the stipe as a distinct tissue or region as in several *Suillus* spp..
Appendiculate: expanded pileus with hanging fragments of partial veil or of pileal extensions, *e.g. Leccinum versipelle* & *Austroboletus.*
Applanate: flattened out.
Arcuate-decurrent: where the tubes or gills have a long arched extension at the attachment joining the stipe-apex as in *Chroogomphus rutilus*.
Areolate: of pileus or basidiospores divided by cracks into small areas as in the pileus of *Leccinellum crocopdium*. For illustrations in spores of *Austroboletus* see Clémençon (1997).
Aseptate: hyphae lacking separating walls (septa).
Bifurcate: divided or forked into two's as in the gills of *Hygrophoropsis aurantiaca*.
Basidiole: either immature basidium or aborted basidium, which maintains its basic shape but lacks sterigmata
Basidiome: correct name for the sexual structure of basidiomycetes variously called, carpophore, fruiting body, fruit-body and sporophore.
Bilateral: typical arrangement of the boletoid hymenophore consisting of three distinct zones, a central zone (mediostratum) with two lateral strata to each side. When hyphae curve away from the central zone see divergent. For full discussion see Singer (1986) For full discussion and illustrations see Clémençon (1997).

Binding hypha (pl. –ae): specialised hypha with many short, usually curved branches originating from generative hyphae and binding them and the skeletal hyphae together.
Boletinoid: when the pores are arranged in a radial pattern as in *Suillus cavipes*.
Boletoid: with a parasol shape – a pileus surmounting a stipe with tubes beneath. Can refer to the type of tube trama – see under divergent.
Caespitose: basidiomes aggregated into tufts as in *Pseudoboletus parasiticus* but not fused together; see fasciculate.
Caulobasidium: basidium produced on the stipe, either in a loose or well-organised hymenium-like tissue as in *Leccinum* spp.
Caulocystidium: -cystidia *q.v.* situated on stipe
Caulohymenium: surface of the stipe when forming a distinct layer of differentiated sterile cells resembling the hymenial tissue mixed with fertile or abhorting basidia as in *Leccinum* spp.
Chemical reactions: several reagents are used in the identification of boletes and their allies and they reflect the secondary metabolites therein. Melzer's reagent containing iodine, aqueous formulations of iron salts, strong or weak aq. alkali and akaline solutions etc. For full discussion see Clémençon (1997).
Cheilocystidium: cystidia *q.v.* at gill-margin or tube orifice.
Chambers: open areas within the gasterocarpic boletes in which the basidiospores form and collect.
Chlamydospore: thick-walled secondary spore formed in or on hyphae within or external to the basidiome as in the S.E. Asian *Boletus chlamydosporus*, or within the spore in *Jaapia argillacea*.
Chrysocystidia: cystidia q.v. with amorphous or crystalloid contents becoming yellow in ammoniacal solutions, *e.g. Tylopilus brachypus, T. ferrugineus* & *Fistulinella wolfiana* or yellow brown in aq. alkaline solutions, *e.g. Porphyrellus cyaneotinctus* & *P. zargovae*.
Clamp-connection or clamp-connexion:. Short hyphal branch associated with septum and appearing as a small arch across the septum or tightly adhering to the outer wall of the septum. Hyphae bearing clamp-connections often called nodose-septate.
Columella: persistent, sterile central tissue within gasterocarpic basidiomes; percurrent columella runs totally through basidome to join peridium *q.v.* and basal parts.
Congophilic: basidiospores and hyphae becoming red in an ammoniacal solution of congo red.
Confluent: running together.
Context or flesh: interior part of basidiome. Sometimes termed trama.
Coriaceous: basidiome of leathery texture; subcoriaceous slightly coriaceous as

in *Coniophora*.
Costae: ridge or rib; costate with costae as in basidiospores of *Afroboletus*.
Crust: resupinate basidiome as in *Leucogyrophana* spp. Crustose with form of a crust.
Cutis: layer covering pileus or stipe and composed of aggregated hyphae arranged in a periclinal way; separable into epicutis outermost layer and subcutis lowermost layer.
Cyanophilic: basidiospores and hyphae becoming blue when mounted in Aniline blue (cotton blue) in lactophenol as in *Coniophora* spp.: opposite acyanophilic. Also see orthochromatic.
Cystidiole: an obtuse or acuminate but poorly differentiated sterile basidium arising from hymenial layer.
Cystidium: (pl. -ia): sterile, differentiated cell of various forms (and functions) developing in a range of tissues. Includes those on the stipe (caulocystidia), on the pileus (pileocystidia), at tube orifice or gill-margin (cheilocystidium) or tube- and gill-faces (pleurocystidia). Those occurring on outer layers are termed dermatocystidia, those in the hymenium, hymenial and those deep in the tissues tramal. See also chrysocystidia, leptocystidia and metuloid. Cystidiform with some, but little differentiation and therefore resembling a cystidium.
Cyanescent: becoming blue when tissues are bruised or inner structures exposed to the air as in *Boletus luridus*.
Decurrent: where tubes or gills are strongly attached to the stipe-apex and run for some distance down the stipe as in *Paxillus involutus*.
Dendroid: resembling a branching tree; dendriform with the form of a tree as the columella in some gasterocarpic forms, *e.g. Amogaster*; also dendritic.
Dendrophysis: paraphysoid *q.v.* with warts, nipples or short branches on uppermost surface; dendrophysoid resembling a dendrophysis.
Dermatocystidium: cystidium *q.v.* on outer surface of basidiome.
Dextrinoid: becoming red-brown or purple-brown when mounted in Melzer's reagent (ME) as in *Hygrophoropsis aurantiaca*; more correctly termed pseudoamyloid.
Dichotomous: branched into pairs.
Dimidate: basidiome of semicircular shape or with one half distinctly smaller than the other as in *Bondarcevomyces.*
Dimitic: structure of a basidiome where two distinct types of hyphae are present in the tissues as in *Coniophora*.
Dissepiments: partitions or walls separating areas in the gasterocarpic basidiome or separating gills or tubes as in some xerocomoid boletes.
Divergent: where the tissues lateral to the central zone in the tube or gill trama curve away from the median line. A characteristic of the majority of boletoid

Boletales. The 'Boletoid type' refers to the strongly gelatinized, poorly pigmented and strongly curved lateral zonation which contrasts with the central core, *e.g. Boletus* & *Leccinum* and 'Phylloporus type' which refers to those taxa with lateral zones scarcely looser, slightly gelatinized, poorly curved and pigmented when compared with the medial tissues of the tube or gill, *e.g. Phylloporus* & *Xerocomus*.

Ectomycorrhizal: relationship between fungus and angiosperm or gymnosperm host where the fungus closely adheres to the root-surface forming a sheath. Often highly specific relationships as in *Suillus* associated with Pinaceae.

Effuso-reflexed: basidiome spread out over the substratum and curled at margin to form a rudimentary or distinct pileus as in *Serpula lacrimans* & *Gyrodontium*.

Endoperidium: innermost layer of peridium *q.v.* in gasterocarpic basidiome.

Encrusted or incrusted: hyphae covered with some development of amorphous or crystalline material, sometimes in distinct pattern as the zebra-like ornamentation in pilepellis-elements of some xerocomoid boletes..

Ephemeral: alternatives - fugacious or fleeting: short-lived, basidia in some gasterocarpic forms, or of velar tissues. Evanescent: only slightly developed and soon lost.

Epicutis: outermost layer of cutis *q.v.*

Epigeal (or epigeous): basidiome developing above the ground.

Epithelium: an outer layer of the basidiome composed of isodiametric cells as in *Leccinellum albellum*; a specialised palisadoderm *q.v*.

Evelate: lacking a veil.

Excentric: not attached to centre of pileus.

Exoperidium: outermost layer of the peridium *q.v*. in gasterocarpic basidiome. Alternative ectoperidium

Exosporium: outermost layer of the basidiospore.

Facultative: with the ability to form both ectomycorrhizas and exist in a saprotrophic state.

Fasciculate: crowded in bundles and with some fusion of parts of the basidiomes as in *Buchwaldoboletus sphaerocephalus*.

Filamentous: composed of thin threads.

Flabellate: fan-like; flabelliform with the form of a fan as in the basidiome of *Bondarcevomyces* and colonizing mycelial front in *Serpula lacrimans*.

Free: where the tubes or gills are not attached to the stipe-apex.

Gasterocarpic (gasterocarpous, gasteroid): having the hymenium enclosed in the basidiome and the spores only released at maturity. Sometimes lacking 'e'

Gasterocarp: basidiome within which basidiospores are developed.

Gelatinized: applied to tissues where mucopolysaccharides are produced from the hyphal wall. Produces a glutinous or gelatinous, or viscid surface depend-

ing on the degree of gel development as in many *Suillus* spp.. Often swelling in presence of water, viz. wet weather. Recognized in microscopic mounts as it becomes silvery when mounted in alkaline solutions.
Gills: blade or plate-like structures beneath the pileus in agaricoid (lamellate) boletes. Also termed lamellae.
Gleba: innermost tissue within the basidiome of gasterocarpic boletes; especially applies to the spore-mass.
Gloeocystidium: cystidium q.v. with oily, milky, resinous or granular contents which become blue in Aniline (cotton) blue in lactophenol mounts as in *Tylopilus spinifer* (=*Boletochaete*).. Sometimes spelt without first 'o'.
Gloeoplerous: hyphae with contents which become deep blue when mounted in Aniline (Cotton) blue in lactophenol as in *Bondarcevomyces.*
Gymnocarpic: where the hymenial tissues develop exposed to the elements from the beginning.
Gyrose: folded and wavy and convoluted; resembling the folds of a brain as in the pores of *Gyrodon* or teeth of *Gyrodontium*.
Hemiangiocarpic: basidiome in which the hymenial tissue is formed within a cavity but exposed at maturity after the dissolution or dehiscence of the enveloping tissues.
Heterotropic: basidiospore placed asymetrically on the basidium as in none-sequestrate gasterocarpic forms.
Hilar appendage: small attachment at the base of the dispersed basidiospore, which formerly connected it to the basidium – sterigmatal fragment.
Hydnoid: basidiome with hymenium composed totally or in part of tooth-like or spinulose projections as in *Gyrodontium*.
Hyaline: lacking colour under the microscope.
Hygrophanous: changing colour; usually paling of the pileus with loss of water, *viz*. on drying out.
Hygroscopic: changing shape with lack of water when fresh or with application of water when dry as in *Astraeus*.
Hymeniderm: layer resembling in its orderliness and construction the hymenium as in the pileipellis of *Leccinellum pseudoscaber* and frequenlty containing cystidiform cells. Also hymeniform.
Hymenium: basidiospore producing layer.
Hymenophore: the overall structure bearing the basidia: lamellate, tubulate, hydnoid etc.
Hymenophoral trama: tissue within the tube or gill and supporting the hymenium.
Hyphidium (pl. –ia): rsembling a hypha, *viz.* poorly differentiated in structure from hypha but a distinct and obvious element.

Hypogeal (Hypogeous): basidiome developing below the soil (substrate) surface as in *Rhizopogon* spp.. Sometimes spelt hypogeaous.
Imbricate: overlapping as the tiles of a roof as in basidiome groups of *Gyrodontium*.
Inamyloid: No reaction when mounted in Melzer's reagent. Same as non-amyloid.
Intervenose: having veins on the surface of the gill or tube, which extend down the face or even join up adjacent gills as in some *Phylloporus* spp.
Interwoven: where hyphae are intermingled and not showing any regular pattern.
Iron salts: various formulations of ferrous sulphate.
Irregular: tube or gill trama where there is no apparent organization of the medial hyphae.
Ixocutis: cutis *q.v.* with gelatinized components as in *Suillus luteus*.
Ixotrichoderm or ixotrichodermium: a trichoderm *q.v.* with gelatinized components as in *Xerocomus badius*.
Lacerate: torn as in *Austroboletus*.
Lacunose: with pits as in the basidiospores of *Austroboletus* spp. and in the stipe of *A. rostrupii*.
Lamellae: alternative for gills.
Lamellar trama: tissue between the two hymenial surfaces of the gill.
Lamellate: basidiome possessing plate- or blade-like structures on which basidia are borne; agaricoid resembling a mushroom by having lamellae or gills.
Lamprocystidium: thick-walled cystidia with refrigent walls, *e.g.Gomphidius*.
Lanose (or lanate): woolly.
Laticiferous: hyphae containing latex-like materials as in *Octavaniana asterosperma.*
Leptocystdidium (-ia pl.): thin-walled cystidia, often capitate.
Loculate: containing chambers or hollows in the basidiome as in several gasterocarpic taxa.
Medallion clamp: clamp-connections where there is a narrow gap between the outermost cell-component as in *Austropaxillus*.
Melzer's reagent (ME): 100gm. chloral hydrate, 5gm. potassium iodide & 1.5gm. Iodine made up in 100ml. distilled water. Used for basidiospores and trama. If turning some shade of blue termed amyloid, if red-brown termed pseudoamyloid and with no reaction termed inamyloid.
Membranaceous: thin and pliant as in the ring of *Suillus cothurnatus*.
Merulioid: basidiome composed of ribs and folds with gelatinous consistency as in *Serpula lacrimans*.
Metavelangiocarpic: development of basidiome in which tissues from pileus

and stipe fuse or intermingle with those of a universal veil as *Strobilomyces* spp.
Metuloid: thick-walled cystidia often encrusted and sometimes rooted below the hymenial layer as in the xerocomoid S.E. Asian *Boletus hastulifer* consortium.
Mixangiocarpic: development of basidiome where the enclosed nature of the development is a result of discrete growth of tissues from both pileus and stipe but which later break down to expose hymenium as in *Suillus grevillei*.
Moniliform: with the form of member of the genus *Molinia* (Fungi Imperfecti) and consisting of chains of cells as in a chain of beads, a structure termed a physalopalisadoderm. Exemplified in pileipellis of *Leccinellum albellum*.
Monomitic: basic tissue formed of a single type of hyphae.
Morchelliform: with the form of a morel (*Morchella*), viz. with longitudinal ridges stretching down basidiome as in *Gymnopaxillus*.
Multistoried: several layers (tiers) of individual hymenial surfaces as in a block of flats and exhibited in *Podoserpula.*
Mycorrhizal: association between the roots of a phanerogam and fungus; generally ectomycorrhizal *q.v.* in the Boletales. May be facultative or obligate q.v.
Myxosporium: a gelatinized outer layer found in some basidiospores.
Network: a reticulate pattern found on either stipe or pileus, or basidiospore; also known as reticulum.
Nigrescent: becoming black when bruised or when the inner tissues are exposed to the air.
Obligate: only able to live with the specific host or group of hosts, *e.g. Leccinum* spp. and *Suillus* spp.
Oleiferous: hyphae with oily or resinous contents as in *Tylopilus ballouii*.
Ornamentation: any projection, protuberance or depression, termed the ornament; usually applied to basidiospores. See Clémençon (1997) for full discussion.
Orthochromatic; where the inner and outer walls of the basidiospore are differently coloured when mounted in Cotton blue in lactophenol as in *Setogyroporus*.
Orthotropic: basidiospores symmetrically placed on basidium as in *Astraeus hygrometricus*.
Palisade or palisadoderm: a regular layer of erect cells as in the pileipellis of *Leccinellum crocipodium* & *Afroboletus*.
Paracapillitium (-llitial): hyphal components within the gleba *q.v.*, which do not become blue when mounted in Aniline (Cotton) blue in lactophenol.
Paraphyses: incorrectly applied to sterile cells separating basidia, although the term is incorporated into the definition of several other terms , *e.g.* dendrophysis. The term is correctly applied only to ascomycetous fungi and replaced in basidiomyctes with pseudoparaphyses.
Parasitic: living off another organism a suggested for *Pseuoboletus parasiticus*

or in the *Gomphidius/Suillus* relationships..
Parasymbiont: association of two organisms, which appears harmless and not detrimental to either partner as in *Buchwaldoboletus and Phaeolus schweinitzii.*
Pedicellate: with a small pedicel or tail.
Pellicle: outer most layer of a gelatinized pileus, which can be peeled away with ease.
Percurrent: extending for entire length referring to the columella *q.v.* in some gasterocarpic boletes.
Peridiopellis: layers constituting the peridium.
Peridium: outer enveloping tissue of gasterocarpic bolete; peridial - pertaining to the peridium.
Peristome: circular area variously adorned at apex of gasterocarpic basidiome as in *Calostoma* spp. and *Chlorogaster*.
Peronate: sheathed as the volvate stipe-base in *Paragyrodon sphaerosporus*.
Pilangiocarpic: hymenophore protected in early stages of development by downward growth of the pileal margin as in *Paxillus involutus*.
Pileate: possessing a pileus or cap shielding the hymenial layer.
Pileipellis: the entire structure of the outermost differentiated zone of the pileus seated on the context; may consist of a simple layer or up to 3 distinct layers with different chemical and anatomical features.
Pileocystidium (-ia pl.): cystidium *q.v.* on the pileus surface.
Pileus or cap: the upper portion of a tubulate or lamellate bolete, which surmounts the stipe and protects the hymenophore beneath.
Plage: a smooth area surrounding the hilar appendage in basidiospores.
Pleurocystidium (-ia pl.): cystidium *q.v.* on the tube- or gill-face.
Plicate: folded as in a fan.
Poroid: eqipped with tubes each of which ends in an orifice and collectively called the pores, e.g. putrescent forms *Boletus* and bracket fungus relatives as *Bondarcevomyces*..
Pseudoamyloid: synonym of dextrinoid. The latter term some authors have rejected as it was considered structures becoming red-brown or purple-brown in Melzer's reagant did not contain dextrin.
Pseudoangiocarpic: basidiome commencing gymnocarpic but then becoming enveloped with some kind of secondary veil. A general term: see metabelangiocarpic, bivelangiocarpic etc.
Pseudocystidium: tramal cystidium connected to vascular hyphae filled with frothy material as found in *Phyllobolites* and *Linderomyces* formerly thought to belong to the Boletales. Coscinoid is a synonym.
Pseudoparenchymatic: having the appearance of the parenchyma found in angiosperm leaves, *e.g*. *Alpova*.

Pseudoperidiole: a package of basidiospores in *Pisolithus* which superficially resembles the true peridioles found in the unrelated Bird's Nest fungi (Nidulariales).
Punctate: with small, dot-like elevations on pileus or stipe as in *Suillus* spp. or basidiospores as in some *Austroboletus* spp.
Putrescent: basidiome able to rot or putrefy rather rapidly.
Raduloid: hymenophore with the appearance of nutmeg grater as in the hymenial surface of some *Leucogyrophana* spp..
Ramose: branched or branchy.
Reflexed: turned up or back on itself.
Regular: tube- or gill trama showing distinct pattern of parallel hyphae in the median and lateral zones.
Repent: prostrate, non-ascending hyphae.
Reticulate: net-like pattern on basidiospores or stipe.
Rhizoid: finally branched, tapering extensions of skeins of hyphae as in *Suillus* luteus; rhizoidal with the appearance of rhizoids.
Rhizomorph: strand of compacted mycelium emenating from basidiome; rhizomorphic which implies presence of rhizomorphs as in *Serpula lacrimans*.
Rimose: possessing cracks or crevices.
Rubescent: becoming red when bruised or inner tissues exposed to the air.
Rufescent: as rubescent but changing to red-brown.
Rugose: wrinkled or creased as surface of *Leccinellum pseudoscaber*; rugulose diminutive of rugose
Saprotroph or saprobe: organism living on dead organic material; saprotrophic obtaining nourishment from dead organic material as in *Coniophora puteana*. Saprophyte is a term which cannot be used for fungi.
Scabrosities: irregularities on the stipe. Especially in *Leccinum* spp., the common name for which is rough-stalks.
Sclerotium (-tia pl.): a resting body composed of hardened mass of hyphae or central core of compacted hyphae surrounded by thickened hyphae as in *Hydnomerulius* & *Boletinellus*. A resting structure.
Sequestrate: with the characteristics of a boletoid or agaricoid fungus but where the pileus does not or hardly separates from the stipe to exopose the hymenium.
Sessile: without a stipe as in crustose Boletales.
Seta (-ae pl.): a long, coloured, bristle-like structure with thick walls and generally darkening in alkaline solutions as in *Tuboseta*.
Setule: as seta but thin-walled and generally hyaline and seen in *Setogyroporus* and several SE Asian xerocomoid boletes.
Sinuate: When there is a distinct upward curve of the tubes before their insertion with the stipe as in *Boletus badius*.

Skein: as in a skein of wool in knitting and exemplified in the hyphae constituting the scales on the pileus of many boletes.
Skeletal hyphae or skeletal fibres: rigid hyphae with thick walls, generally without contents and septae, and giving rigidity to the basidiome. Seen in some *Coniophora* spp. & *Serpula lacrimans*.
Spathulate: spoon-shaped as in the basidiome of *Meiorganum*.
Sphaerocyst: globular cell constituting the tissue of the basidiome or the veil as in *Cystogomphus*.
Spore-mass: contents of a mature gasterocarpic basidiome or for non-gasterocarpic forms when spore-print or deposit is scraped together to ascertain the colour.
Spore-print: pattern given by the cast basidiospores when the pileus is placed hymenophore face-down on a glass-slide or paper.
Sphaeropedunculate: almost spherical with a short stalk as in the basidia of *Austroboletus*.
Stellate: the shape of a star; end-on view of basidiospores of *Rhodactina.*
Sterigma (pl. -ata): small projection at apex of basidium on which the spore is borne. May remain attached to the spore as a sterigmatic or hilar appendage as in some gasterocarpic Boletales.
Stigmatospore: basidiospore with symmetric hilar appendage as found in many gasterocarpic Boletales, e.g *Alpova*, *Rhizopogon.*
Stipe: the structue elevating the pileus above the substrate-level.
Stipitate: those basidiomes equipped with a stipe, stalk or stem elevating the pileus above the level of the substrate.
Stipitocarpic: basidiome where the stipe is dominant in the early stages of development as in many xeromoiod and leccinoid boletes.
Stipitipellis: the layers making the outer surface of the stipe; may be simple or composed of more than one layer.
Strand: or rhizoid q.v.
Stroma: cushion-like mass of hyphae on which other structures, including basidiomes, may sit as in *Diplocystis*.
Subcutis: lower most layer of the cutis - pileipellis *q.v.*
Subdecurrent: having a small tooth of gill or tube running down the stipe but without any other indentations before reaching stipe-apex as in *Sullus bovinus*.
Subhypogeal (subhypogeous): a basidiome fruiting at soil level; may commence hypogeous q.v. but then working into the upper layers to become exposed at maturity as in *Rhizopogon*.
Subiculum: dense felt of hyphae covering a tissue.
Sublamellate: hymenophore dominantly with gills but various degrees of interveining and branching to form rudimentary pores.

Subpericlinal: partly curved in the direction of the surface; periclinal always curved in that direction.
Suprahilar: depression: a hollow around the hilar appendage (or apiculus) of a basidiospore.
Tomentum: clothing composed of long, soft hyphae or filamentous aggregates of hyphae often clothing the base of the stipe in many boletes.
Trama: the basic and supporting tissue of the basidiome.
Tramal plate: distinct plate-like structures bearing the hymenium within some gasterocarpic basidiomes.
Trimitic: structure of a basidiome where there are three distinct types of constituent hyphae, *i.e.* generative, skeletal and binding hyphae as in *Coniophora*.
Trichoderm or trichodermium: a turf-like structure of more or less erect filamentous units as in *Xerocomus subtomentosus* & *Pseudoboletus parasiticus*..
Tube-trama: the tissue within the two faces of the tube.
Tuberiform: with the shape of a potato tuber as in some hypogeous fungi.
Tubes: long or short, more or less cylindrical, hollow structures in which the basidiospores are produced; massed to produce a well-developed tissue each with an orifice characteristic of the boletoid basidiome.
Tubulate: a basidiome with definite tube layer.
Ungulate: with the shape of a horse's hoof.
Veil: covering to the basidiome, which might be membranous, filamentous, persistent or fugacious – the velar tissue; velar relating to the veil.
Velangiocarpic: development where the immature basidiome is enveloped or shrouded in velar tissue *q.v.*
Ventricose: swollen in the middle as in the tube-layer of *Afroboletus*.
Verticillate: whorled as the clamp-connections in *Coniophora*.
Vinescent: becoming the colour of red-wine.
Viridescent: becoming green when bruised or the inner tissues exposed to the air. Also when concentrated solutions of ammoniacal solutions are applied to the surface of the pileus in some xerocomoid boletes.

Viscid: where the pileus or stipe is covered in a sticky layer but not separable as a unit. Can be detected by placing suspected viscid surface on the lips where there will be adhesion or wetting slightly and rubbing with the finger tips.
Volvate: with the remains of a veil forming an obvious structure at the base of stipe as in *Paragyrodon*.

Acknowledgements

Over the forty years plus of my mycological 'upbringing' I have been grateful to many people in many different ways but especially my parents who encouraged me from an early age to take an interest in natural history and latterly look particularly at the fungi. They were tolerant enough to accompany me on field trips, encouragement which my wife continued with great understanding. From members of the Halifax Scientific Society and Ovenden Naturalists' I gained my basic field knowledge of not only fungi but also plants something further developed during my membership of the Yorkshire Naturalist' Union. Such amateur activities were set into a scientific, enquirying background by Profs. Roy Clapham and John Webster when I was a Sheffield University undergraduate. I was welcomed in Edinburgh for my PhD by Prof. Harold Fletcher, the then Regius Keeper, who, with Prof. Douglas Henderson moulded my mycological and botanical thoughts; all four were mentors to me and sent me on my future path of critical study and exploration.

Harold Fletcher also made it possible for me to travel abroad including joining up with Prof. A. H. Smith, University of Ann Arbor, who was instrumental in my understanding of North American fungi. This spawned a life long friendship with him and his wife and with many of his students particularly O.K.Miller, H. Thiers, H. Bigelow, J. Ammirati, D. Largent etc., and colleagues such as Ken Harrison and Dan Stuntz. Membership and various roles in The Botanical Society of Edinburgh (now Scotland) and the British Mycological Society provided many friendships and many valuable contacts which expanded my experiences.

Through the Royal Botanic Garden I was able to travel widely and until my retirement I was assisted in the laboratory and field by Evelyn Turnbull, and before that in the laboratory by Norma Gregory, Janice Sweeney, Celia Alden and Heather Mc Gilvray. Finally I would like to thank Mike Richardson for his companionship over many years and for agreeing to be subject to reading a draft of the manuscript and offering useful suggestions and Christopher Watling for his computer magic.

General References: Useful illustrative mycofloras

Breitenbach, J. & Kränzlin, F. (1986) *Pilze der Schweiz, Vol 2. Nichblätterpilze: Heterobasidiomycetes, Aphyllophorales & Gasteromycetes.* Mengis & Sticher AG, Lucerne, Switzerland, 416pp.

Ditto (1991). *Vol. 3. Strobilomycetaceae & Boletaceae, Paxillaceae, Gomphidiaceae, Hygrophoraceae, Tricholomataceae & Polyporaceae (Lamelleés)*. Sticher , Lucerne, Switzerland, 364pp.

Bougher, N. L. & Syme, K. (998). *Fungi of Southern Australia*. Univ. Western Australia Press, Perth, Australia, 391pp.

Cetto, B. (1971-1982). *I Funghi dal Vero*. Saturnia, Trento, Italy. 3 volumes. B. Cetto has published several other books with colour illustratians of boletes and their relatives.

Fuhrer, B. (2005). *A Field Guide to Australian Fungi*, Bloomings Books, Melbourne, Australia, 360pp.

Grgurinovic, C.A. 1997. Larger Fungi of South Australia. Botanic Garden Adelaide & State Herbarium Adelaide, Australia. 725pp.

Halling, R.E. & Mueller, G.M. (2005). *Common Mushrooms of the Talmanca Mountains, Costa Rica*. New York Bot. Gard., New York, USA, 195pp.

Härkonen, M., Niemelä, T & Mwasumbi, L. *Tanzanian Mushrooms*. University of Helsinki, Helsinki, Finland. 200pp.

Hongo, T. (1962 – 1980). Notulae mycologicae. *Memoirs of Shiga Univ. Natural Sciences*. Volumes 12-33.

Hongo, T. (1967 – 1984). Materials for the fungus flora of Japan. *Transactions of the Mycological Society of Japan*. Volumes 8-25.

Horak, E. (2005). *Röhrlinge und Blätterpilze in Europa*. Spektrum, Elsevier, Amersterdam, Netherlands, 555pp.

Imazeki, R., Otani, Y. & Hongo, T. (1988). *Fungi of Japan*, Shiba-daimon, Tokyo, Japan, 624pp.

Lincoff, G. H. (1981).*The Audubon Field Guide to North American Mushrooms*. Audubon Society, Knoft, New York, USA. 926pp.

Marchard, A. (1971-1974). *Champignons du Nord et du Midi*. Vol.1-3. Sociéte de Mycologique des Pyénées, Hachette, Perpignan, France. Contains several colour plates of boletes and allies.

Miller, O.K. (1972). *Mushrooms of North America*. Dutton, New York, USA, 360pp.

Pegler, D.N. (1977). *A Preliminary Agaric Flora of East Africa*. Kew Bulletin Additional Series VI. Royal Botanic Garden., Kew, Surrey, UK. 615pp.

Pegler, D.N. (1983). *Agaric Flora of the Lesser Antilles*. Kew Bulletrin Additional Series IX. Royal Botanic Garden,. Kew, Surrey, UK. 668pp.

Pegler, D.N. (1986). *Agaric Flora of Sri Lanka*. Kew Bulletin Additional Series XII. Royal Botanic Garden, Kew, Surrey, UK. 519pp.

Pegler, D.N., Spooner, B.M. & Young, T.W.K. (1993). *British Truffles*. Royal Botanic Garden, Kew, Surrey, UK. 216pp.

Pegler, D.N., Laessóe, T. & Spooner, B.M. (1995). *British Puffballs, Earthstars and Stinkhorns*. Royal Botanic Garden, Kew, Surrey, UK. 255pp.

Phillips, R. (1981). *Mushrooms and other fungi of Great Britain & Europe*. Pan Books, London, UK, 288pp. (There is a revised re-print dated 2006 but the colour production is not as good).

Phillips, R. (1991). *Mushrooms of North America*. Little Brown & co., London UK. 319pp.

Pilát, A. & Usak, O. (1961). *Mushrooms and other Fungi*, Peter Nevill, London, UK. 160pp.

Pilát, A. & Usak, O. (1961). *Mushrooms*, Spring Books, London, UK. 335pp.

Roux, P. (2006). *Mille et un champignons*. Sainte-Sigoléne, France. 1223pp.

Singer, R. (1951). Agaricales in Modern Taxonomy. Lilloa 22 (1949): 1- 832. Ditto 1962 2nd edition, J. Cramer, Weinheim, Germany. Ditto 3rd edition, Ditto 1975, J. Cramer, Vaduz, Germany Ditto 1986, 4th edition Koeltz Scientific Books, Koenigstein, Germany 981pp. Incorporates information including type studies published separately in range of journals.

Singer, R. (1969). Mycoflora Australis. *Beihefte Nova Hedwigia* **29**: 1-405.

Singer, R., Asaujo, I. & Ivory, M. (1983). *The Ectotrophically Mycorrhizal Fungi of the Neotropical Lowlands, especially Central America.* J. Cramer, Berlin-Stuttgart, Germany.

Smith, A.H. (1963). *The Mushroom Hunter's Field Guide*. Revised and enlarged. University of Michigan, Ann Arbor, Michigan, USA 264pp.

Smith A.H., (1975). *A Field Guide to Western Mushrooms*. University of Michigan, Ann Arbor, Michigan USA, 280pp.

Weber, N.S. & Smith, A.H. (1985). *A Field Guide to Southern Mushrooms*. University of Michigan, Ann Arbor, Michigan, USA, 280pp.

Young, Tony (1982). *Common Australian Fungi*. New South Wales University Press, Kensington, NSW, ustralia.156 pp.

Terminology

Josserand, M. (1952). *La description des champignons supérieurs*. *Encycl. Mycol*. **21**: 1-338.

Snell, W.H. & Dick, E.A. (1957). *A Glossary of Mycology*. Harvard University Press, Cambridge, Massachusetts, USA, 171pp.

Berger, K. (1980). *Mykologisches Wörterbuch*. VEB Gustav Fischer, Jena, Germany, 432pp.

General References: Bolete & Similar General works

Anatomical & Developmental: C Chemistry & histology: D Distribution E Ecological: G Genetic & Evolutionary: L Limited distributions: M Molecular S: Spores

Agerer, R. (1999). Never change a functionally successful principle: the evolution of Boletales s. l. (Hymenomycetes, Basidiomycetes) as seen from below ground features. Sendterina **6**: 5-91.

Alessio, C.L. (1985). *Fungi Europaei.2*, *Boletus* Dill. ex L. Giovanna Biella, Saronno. Italy, 710pp. Ditto (1991), Supplemento *Boletus* Dill. ex L., Fungi Europaei 2A.

Baroni, T. J. (1978). Chemical Spot-test reactions. *Mycologia* **70**: 1064-1076.

Beaton, G., Pegler, D.N. & Young, T.W.K. (1985). Gasteroid Basidiomycotina of Victoria State, Australia 5-7. *Kew Bulletin* **40**: 573-598.

Bertéa, P. (1989). *Catalogue Ecologique des Champignons Supérieurs médiiterranéens IV Bolets*. La Fédération des associations Mycologiques Méditerranénnes, Montpellier, France. 48pp.

Bessette, A., Roody, W.C. & Bessette, A.R. (2000). *North American Boletes. A Color Guide to the Fleshy Pored Mushrooms*. Syracuse Univ. Press, New York, USA, 396pp.

Binder, M. & Bresinsky, A. (1997). Agaricales oder Boletales? Molekularbiologische Befunde zur Zuordnung einiger umstrittener Taxa. *Zeitschrifte für Mykologie* **63**: 189-196.

Binder, M. & Bresinsky, A. (2002). Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. *Mycologia* **94**: 85-98.

Binyamini, N. & Avizohar-Hershenzon, Z. (1972). Boletaceae of Israel. I *Boletus* sect. *Luridi. Transactions of the British Mycological Society* **59**: 25-30. Ditto II *Gyroporus, Xerocomus* and *Boletus. Transactions of the British Mycological Society* **60**: 99-105.

Blum, J. (1962). *Les bolets*. Etude Mycologique 1, Lechvalier, Paris, France, 168pp.

Blum, J. (1965). Essai de Détermination des *Bolets* du Groupe g*ranulatus. Bulletin de la Société Mycologique de France* **81**: 450-491.

Blum, J. (1967). Essai de détermination de quelques *Bolets* du groupe *scaber*. *Revue de Mycologie* **32**: 135-161; ditto (suite) *Revue de Mycologie*.**32**: 336-367.

Blum, J. (1968 – 1969). Révision des Bolets. Series of 8 articles in *Bulletin de la Société Mycologique de France* **84**: 310-332 to **85**: 215-256.

Both, E. E. (1993). *The Boletes of North America. A Compendium.* Buffalo Museum of Science, New York, USA, 436pp.

Bresinsky, A. (1996). Abstammung, Phylogenie unde Verwandtschaft im Pilzreich. *Zietschrifte für Mykologie* **62**: 147-168.

Bresinsky, A. & Wittmann-Bresinsky, B. (!995). Ploidy levels and Evolution in Boletales. *Beihefte Sydowia* **10**: 35-47.

Bruns, T.D., Fogel, R., White, T.J. & Palmer, J.D. (1989). Accelerated evolution of a false-truffle from a mushroom ancestor. *Nature 339*: 140-142.

Burk, W. R., Flegler, S. L. & Hess, W. M. (1983). A Review of Ultrastructural studies of Gasteromycetes spores. *Revista de Biologie* **12**: 217-230.

Chui, W.F. (1948). The Boletes of Yunnan. *Mycologia* **40**: 199-231.

Clémençon, H. (1997). *Anatomie der Hymenomyceten*. University of Lausanne, Lausanne, Switzerland. 996 pp.

Coker, W.C. & Beers, A.H. (1943). *The Boletaceae of North Carolina*. Univ. North Carolina Press, Chapel Hill, North Carolina, USA, 89pp.

Corner, E.J.H. (1972). *Boletus in Malaysia*. Government Printing Office, Singapore, 263pp.

Cunningham, G.H. (1931). Sclerodermaceae of New Zealand. *Transactions of the New Zealand Institute* **62**: 1-6.

Cunningham, G.H. (1931). The Gasteromycetes of Australasia XII. The genus *Scleroderma. Proceedings of the Linnean Society of New South Wales* **56**: 277-287.

Cunningham, G.H. (1931). The Gasteromycetes of Australasia XIII. The genus *Pisolithus. Proceedings of the Linnean Society of New South Wales* **56**: 288-291.

Cunningham, G.H. (1934). The Gasteromycetes of Australasia XVI. Hymenogastraceae Part 1. The genera *Rhizopogon, Melanogaster* and *Hymenogaster. Proceedings of the Linnean Society of New South Wales* **59**: 156-172.

Dermek, A. (1979). *Fungorum rariorum icones coloratae. Pars IX Boletes I*. Cramer, Vaduz, Germany. *Ditto.* 1984 Pars XIII *Boletes II*. *Ditto* 1987. Pars XVI *Boletes III*.

Disbrey, B. & Watling, R. (1968). Histological & Histochemical techniques applied to the Agaricales. *Mycopathologia & Mycologia Applicata* **32**: 81-114.

Elrod, R.P. & Blanchard, D.L. (1939). Histological studies of the Boletaceae and related genera. *Mycologia* 31: 693-708.

Engel, E. Dermek, A & Watling, R. (1983). *Dichröhrlinge. Die Gattung Boletus in Europa*, H. Schneider-Druck, Weidhausen, Germany, 157pp.

Engel, E. Dermek A. & Watling, R. (1983). *Rauhsteilröhrlinge. Die Gattung Leccinum in Europa*. H. Scxhneider-Druck, Weidhausen, Germany, 76pp.

Engel, H., Dermek, A., Klofac, W., Ludwig, E. & Brückner, T. (1996). *Schmier- und Filzröhrlinge s.l. in Europa*. Schneider-Druck, Weidhausen b. Coburg, Germany, 268pp.

Fischer, M. (1995). On the systematics of the Boletales: isolation and characterization of DNA from fruitbodies and mycelial cultures. *Zeitschrift für Mykologie* **61**: 245-260.

Galli, R. (1998). *I Boleti, Edinatum*, Milan, Italy, 287pp.

Gilbert, E.J. (1930). *Les Bolets*, in les livres du mycologue. Encyclopédie Mycol., 3 Lechvalier, Paris,

Gomez, L. D. (1992). Los Basidiomicetes de Costa Rica IV. Revisión del género *Strobilomyces* Berk. (Agaricales, Boletaceae). *Brenesia* **38**: 95-103: V Paxillaceae (Agaricales, Boletaceae). *Brenesia* **38**: 105-113.

Gomez, L. D. (1996). Basidiomicetes de Costa Rica: *Xerocomus, Chalciporus, Pulveroboletus, Boletellus, Xanthoconium* (Agaricales: Boletaceae). *Revue Biologia Tropicana* **44** (Suppl. 4): 1-89.

Grand, L. (1970 et subseq.). Notes on North Carolina Boletes in *Journal of the Elisha Mitchell Science Society*. I Species of *Boletellus, Phylloporus, Strobilomyces, Tylopilus* & *Xanthoconium* **86**: 57-61; II. Species of *Gyrodon, Gyroporus, Xerocomus* and *Leccinum* **86**: 57-61; III Species of *Suillus.* **86**: 209-213 & IV New species and distributions of *Suillus*. **86**: 204-208.

Grand, L.F. & Moore, R.T. (1971). Scanning electron microscopy of basidiospores of species of Strobilomycetaceae. *Canadian Journal of Botany* **49**: 1259-1261.

Groves, J. W. & Thompson, S. C. (1955). Notes on Fungi from Northern Canada. II Boletaceae. *The Canadian Field naturalist* **69**: 44-51.

Grund, D.W. & Harrison, A.K. 1976. Nova Scotian Boletes. *Bibliotheca Mycologia* **47**: 1-283.

Halling, R. E. & Mueller, G. (2003). *Leccinum* (Boletaceae) in Costa Rica. *Mycologia* **95**: 488-499.

Heinemann, P. (1954) *Flore Iconographique des Champignons du Congo. Fasc. 3 Boletineae*. Jardin Bot. de L'Etat, Brussels, Belgium 49-80: Ditto *Fasc. 15 Boletineae II (complément)*. Jardin Bot. de L'Etat, 279-308. Incorporates information from earlier publications by Heimann in various journals.

Heinemann, P. (1961). *Les Bolètinèes. Les Naturalistes Belges*, Bruxelles, Belgium. 34pp. *Bulletin Nat. Belges* **42**: 333-362.

Heinemann, P. (1964). Boletineae du Katanga. *Bulletin du Jardin Botanique de l'État, Bruxelles* **34**: 425-478.

Heinemann, P. & Rammeloo, 1980. *Flore Illustrée des Champigonons d'Afrique*

Centrale.Fasc. 7 Gyrodontaceae p.p. (Boletineaea), Jardin Bot. Nat. de Belg., Meise, Belgium 128-131. Dittto *10 Gyrodontaceae p.p. (Boletineae*). Jardin Bot. Nat. de Belg. Meise, Belgium, 175-198. Dittto Fasc. 13 *Phylloporus (Boletineae)*. Jardin Bot. Nat. de Belg., Meise, Belgium.277-307. Ditto. Fasc. 14 *Suillus (Boletaceae, Boletineae)* & *Tuboseta (Xerocomaceae, Boletineaeae).* Jardin Bot Nat. de Belg. Meise, Belgium 312-333. Incorporates information from earlier publications by Heinemann in various journals.

Hibbett, D.S. & Binder, M. (2002). Evolution of complex fruting-body morphologies in homobasidiomycetes. *Proceedings of the Royal Society of London*, *Series B* **269**: 1963-1969.

Hóland, K. (1987). A new approach to the phylogeny of the order Boletales (Basidiomycotina). *Nordic Journal of Botany* **7**: 705-717.

S: Homola, R.L. (1981). The Use of the Scanning Electron Micoscope in Bolete Taxonomy. *Scanning Electron Microscopy* **111**: 611-616.

Hongo, T. (1960). The Agaricales of Japan I (–2). Rhodophyllaceae, Paxillaceae, Gomphidiaceae, Boletaceae & Strobilomycetaceae *Acta phytotax. Geobot.* **18**: 97-112.

Hongo, T. (1960). The Agaricales of Japan I (–4). Ecological Observations. *Memoirs of the Shiga University, Natural Sciences* **10**: 61-72.

Hongo, T. (1973). Mycological report. Enumeration of the Hygrophoraceae, Boletaceae & Strobilomycetaceae 1 *Bulletin National Science Museum, Tokyo* **16**: 537-557.

Hongo, T. (1975 – 1980). Notes on some boleti from Tottori. 1-5 *Reports from the Tottori Mycological Institute (Japan).* **12**: 31-40: ibid **14**: 85-89: ibid **15**: 50-54: ibid **16**: 50 – 58: ibid **18**: 133 –141.

Hongo, T. (1985). On some interesting boleti from the warm-temperate zone of Japan. *Memoirs of the Shiga University, Natural Sciences* **34**: 29-32

Horak, E. (1980). Indian Boletales and Agaricales. *Sydowia* **33**: 88-110.

M: Jarosch, M. (2001). Zur molecularen Systematik der Boletales: Coniophorineae, Paxillineae and Suillineae. *Bibliotheca Mycologia* 191: 1-158.

Kaillio, P. & Heikkila, H. (1978). The boletes of Finland. *Karstenia* 18: 1-19.
Kallenbach, F. (1962) see Singer below.

Klofac, W. & Krisai-Greilhuber, I. (1992). *Xerocomus chrysenteron* und ähnlich aussehende Röhrlinge. *Osterreichische Zeitschrift für Pilzkunde* **1**: 19-59.

Kretzer, A. M. & Bruns, T.D. (1990). Use of *atp*6 in fungal phylogenetics: an example from the Boletales. *Molecular Physiological Evolution* 13: 483-492.

Korhonen, M. (1995). New boletoid fungi in the genus *Leccinum* from Fennoscandia. *Karstenia* 35: 53-66.

Lannoy, G. & Estades, A. (1995). *Monographie des Leccinum d'Europe*. Fedération. Mycologique Dauphiné-Savoie, France, 229pp. Incorporates results from 4 publications in *Documents Mycologique* **21**: 11-25 to **24**: 1-29.

Lannoy, G. & Estades, A. (2001). Les Boletes. Mycologique d'Europe. *Documentes Mycologique* Mémoire Hors Série Boletaceae **6**: 1-63.

Lakhanpol, T.N. (1996). Mushrooms of India: Boletaceae. *Studies in Cryprtogamic Botany*. APH Publsihers Co. New Delhi, 169pp.

Leclair, A. & Essette, H. 1969. *Atlas Mycologiques Band 2 Les Bolets*. Lechvalier, Paris, 81pp.

McNabb, R.F. (1967). The Strobilomycetaceae of New Zealand. *New Zealand Jourtnal of Botany* **5**: 532-547.

McNabb, R. F.R. (1968). The Boletaceae of New Zealand. *New Zealand Journal of Botany* **6**: 137-176.

Merlo, E.G., Micheli, R. & Traverso, M. (1980). *I nostri funghi I Boleti*. Sagep Editrico, Genova, Italy, 127pp.

Miller, S.L. (1986). Hypogeous fungi from the southeastern United States 1. The genus Rhizopogon. *Mycotaxon* **27**: 193-218.

Munoz, J.A. (2005), *Boletus s. l. (excl. Xerocomus)*. Candussio, Alassio SV, Italy, 951pp.

Mu, Z. (1997). Taxonomic, Mycogeography and Ecto-mycorrhizal Association of the Boletales from China. I. Family Strobilomycetaceae. *Mycosystema* **16**: 192-196.

Murrill, W.A. (1910). *North American Flora (Boletaceae*). pp. 133-161. Incorporates observations published separately in *Mycologia*.

Noodeloos, M. E. (2000-2006). Hoe Raak ik Thuis in de Boleten – an illustrated series covering bolete genera in Nederland. *Coolia* **43**: 1-10 to **50**: 1-20.

Pearson, A.A. (1946). Notes on the Boleti, *Naturalist (1946*): 85-99. Reprinted and revised as British Boleti, 1946, The Naturalist, London. UK.

Peck, C.H. (1873). The genus *Boletus*. *Annual Report of the New York State Cabinet Natural History* **23**: 127-133.

Pegler, D.N. & Young, T.W.K. (1981). A natural arrangement of the Boletales with reference to spore morphology. *Transactions of the British Mycological Society* **76**: 103-146

Perreau-Bertrand, J. (1961). Recherches sur les Ornamentations Sporales et la Sporogenèse chez quelques Espèces des genres *Boletellus* et *Strobilomyces* (Basidiomycetes). *Annales des Sceances Naturelles Botanique* **12**: 399-489.

Perreau-Bertrand, J. & Joly, P. (1964). Sur quelques Boletales de la Flore du Viet-nam. *Bulletin de la Sociéte de Mycologique du France* **80**: 387-395.

Pilát, A & Dermek, A. (1974). *Hrîbovité huby*. Slov. Akad. Vied v Bratislava, Czechosloavkia, 207pp.

Redeuilh, G. (1985). Contribution a l'Étude des Boletes I. *Bulletin de la Sociète de Mycologique du France* **101**: 373-412.

Reijnders, A.F.M. (2000). A morphogenetic analysis of the basic characters of the gasteromycetes and their relation to other basidiomycetes. *Mycological Research* **104**: 900-910.

Reijnders, A.F.M. & Stalpers, J.A. (1992). The development of the hymenophoral trama in the Aphyllophorales and the Agaricales. *Studies in Mycology* **34**: 1-109.

Sartory, A. & Maire, L. (1931). *Les Bolets. Monographie du Genre Boletus* Dill., Nancy, France.

Singer, R. (1945). The Boletineae of Florida with notes on Extralimital species. I. Strobilomycetaceae. *Farlowia* **2**: 97-141. Ditto 1945b. Part II The Boletaceae (Gyroporoideae). *Farlowia* **2**: 223-303. Ditto 1947. Part 3 The Boletoideae with Notes on Extralimital species. *American Midland Naturalist* **37**: 1-135. Ditto 1946. Part IV *Farlowia* **2**: 527-567.

Singer, R. (1965). Die Röhrlinge Part 1 Die Boletaceae without Boletoideae), 131pp Ditto , 1966 Part 2 Boletoideae & Strobilomycetaceae. 151pp. as Die Pilze Mitteleuropas Band VI, Julius Klinkhardt, Bad Heilbrun Obb, Germany. This is a revised and enlarged edition of Die Plize Mitteleuropas Band 1 by F. Kallenbach 1926-1938.

Singer, R. (1969). *Mycoflora Australis*. J. Cramer, Lehre, germany, 405pp.

Singer, R. (1981). Notes on Bolete Taxonomy III. *Persoonia* **11**: 269-302.

Singer , R., Garcia, J. & Gomez, L.D. (1990-1992). The Boletineae of Mexico and Central America, Parts ! & 2. *Beihefte Nova Hedwigia* **98**: 1-70, 1990; Part 3 *Beihefte Nova Hedwigia* **102**, 1991 Part 4. *Beihefte Nova Hedwigia* **105**, 1992.

Skirgiello, A. (1960). Flora Polska. Grzyby (Fungi). Basidomycetes. Boletales. Warsaw, Poland, 130pp.

Smith, A.H. & Theirs, H.D. (1971). *The Boletes of Michigan*. University of Michigan, Michigan, USA, 428pp.

Smith, A.H., Theirs, H.D. & Watling, r. 1966. A Preliminary Account of the North American Species of *Leccinum*. Section *Leccinum. Michigan Bot*anist **5**: 131-179. Ditto. Sections *Luteoscabra* & *Scabra*. *Michigan Bot*anist **6**: 107-154. Ditto. Additions to Section *Leccinum. Lloydia* **31**: 252-267.

Snell, W. H. & Dick, E. A. (1970). *The Boleti of Northeastern North America*, J. Cramer, Lehre, Germany, 115pp. (incorporates information published in series of articles 1-XV by the authors in *Mycologia* **24**: 334-341 thru' **57**: 448-458 as 'Notes on Boletes'.

Sutara, J. (2005). Central European genera of the Boletaceae and Suillaceae with

notes on their anatomical characters. *Czech mycology* **57**: 1-50.

Thiers, H.D. (1964). The genus *Xerocomus* Quélet in Northern California. *Madröno* **17**: 217-249.

Thiers, H.D. (1975). *Californian Mushrooms: A Field Guide to the Boletes*. Hafner Press, New York, USA, 261pp. Incorporates results from 4 publications in *Mycologia* **57**: 524-534 thru' *Madrôno* **19**: 148-160 and *Mycologia 63*: 261-276.

Thiers, H. D. (1977). Species concept in the Boletes. In Clèmençon, H. (ed.) The Species Concept in Hymenomycetes. *Bibliotheca Mycologica* **61**: 55-78.c.

Watling, R. (1985). Hymenial surfaces in developing agaric primordia. *Botanical Journal of the Linnean Society* **91**: 273-293 – includes studies on 5 boletes.

Watling R. & Gregory, N.M. Observations on the Boletes of the Cooloola Sandmass, Queensland and Notes on Their Distribution in Australia Part 1. *Proceedings of the Royal Society of Queensland* **97**: 97-128. Ditto. Part 2a. Smooth spored Taxa- Introduction, Keys and References. ibid **99**: 45-63. Ditto. Part 2B Taxa of the Family Gyrodontaceae and the genus *Pulveroboletus*. ibid **99**: 65-96. Dittto. Part 2C Smooth spored Taxa – Strobilomycetaceae. ibid **100**: 13-30. Dittto. Part 2D Smooth-spored Taxa – Boletaceae, Xerocomaceae. Ibid **100**: 31-47. Ditto. Part 3 Lamellate Taxa. *Edinburgh Journal of Botany* **48**: 353-391.

Watling, R. & Hills, A.E. (2005) British Fungus Flora: Agarics and Boleti. Vol. 1 Revised and enlarged edition of the same title dated 1970, Her Majesty's Stationery Office, Edinburgh, Scotland, UK. Incorporates Watling's previous publications on British boletes appearing in Transactiona and Proceedings of the Botanical Society of Edinburgh. & Notes from the Royal Botanic Garden, Edinburgh.

Watling, R. & Li T-H. (1999). *Australian Boletes. A Preliminary Survey*. Royal Botanic Garden, Edinburgh, Scotland UK, 71pp.

Wittmenn-Bresinsky, B. & Bresinsky, A. (1989). Quantitative differences of nuclear DNA contents in Paxillaceae compared with other families of Boletales. *Mycological Research* **93**: 261-291.

General References: Indices etc.

Doi, Y. 1991. Type collection in the Herbarium of National Science. Musueum Tokyo (TNS). Agaricales named by Dr. T. Hongo (1). *Bulletin of the National Science Museum*, Tokyo, Series B. **17 (2)**: 49-58.

Fu, S.-Z., Wang, Q.-B. & Yao, Y.-J. (2006). An annotated checklist of *Leccinum* in China. *Mycotaxon* **96**: 47-50.

Gilbertson, R.L. (1962). Index of Species and Varieities of Fungi described by C.H. Peck from 1909 to 1915. *Mycologia* **54**: 460-465.

Halling, R.E. (1983). Boletes described by Charles C. Frost. *Mycologia* **75**: 70-92.

Halling, R.E. (1986). An Annotated Index of Species and Infraspecific Taxa of Agaricales and Boletales described by William A. Murrill, *Memoirs of the New York Botanical Garden* **40**: 1-120.

Halling, R. (1989). A synopsis of Colombian Boletes. *Mycotaxon* 34: 93-113.

Hansen, L. & Knudsen, H. (eds.) (1992). *Nordic Macromycetes Vol. 2 Polyporales, Boletales, Agaricales, Russulales*. Nordsvamp, Copenhagen, Denmark, 474pp. Ditto 1997 Vol. 3 *Heterobasidioid, Aphyllophorioid and gastromycetoid Basidiomycetes*. Nordsvamp, Copenhagen, Denmark, 444pp. (line-drawings only).

Homola, R. L. & Mistretta, P.A. (1977). *Ectomycorrhiza. A listing of Boletaceae with Associated Hosts*. University of Orono, Maine, USA.

Kriesel, H. (2001). Checklist of the gasteral and secotioid Basidiomycetes of Europe, Africa and the Middle east. *Osterreichische zur Pilzkunde* **10**: 213-313.

Kühner, R. & Romagensi, H. (1953). *Flore Analytique des Champignons Supérieurs (Agarics, Bolets, Chanterelles)*. Masson & Cie, Paris, France, 5556pp. (B/w sketches only).

Moser, M. (1978). *Basidiomycetes II: Röhrlinge und Blätterpilze, 4. Auflage*

(Teil IIb 2 der Kleine Kryptogamenflora), Gustav Fischer, Verlag Stuttgart, Germany. Translations have been made into Italian and into English, the latter published by R. Phillips, London UK, 535pp. (b/w illustrations only).

Mueller, G.M. & Wu, Q. (1997). Mycological Contributions of Rolf Singer: Field Itinerary, Index of New Taxa, and List of Publications. *Fieldiana* **38**: 1-124.

Nagasawa, E. (1975). New taxa of the Agaricales published by T. Hongo from 1951 to 1974. *Transactions of the Mycological Society of Japan* **16**: 378-386.

Nagasawa, E. (1982). A list of agaric and bolete taxa published by Dr. Sancshi Imai (1900-1976). *Reports of the Tottori Mycological Institute* **20**: 76-82.

Nagasawa, E. (1975). A preliminary checklist of the Japanese Agaricales I. Boletaceae. *Reports of the Tottori Mycological Institute* **35**: 39-78.

Zang, Mu, (1999). An annotated check-list of the genus *Boletus* and its sections from China. *Fungi Science* **14**: 79-87.

Specific references

Agerer, R. (1990). Studies on ectomycorrhizae XXIV. Ectomycorrhizae of *Chroogomphus helveticus* and *C. rutilus* (Gomphidiaceae, Basidiomycetes) and their relationships to those of *Suillus* and *Rhizopogon*. *Nova Hedwigia* **50**: 1-63.

Agerer, R. (1991). Ditto XXXIV. Mycorrhizae of *Gomphidius glutinosus* and of *G. roseus* with some remarks on the Gomphidiaceae (Basidiomycetes). *Nova Hedwigia* **53**: 127-170.

Albee-Scott, S. (2007). The phylogenetic placement of the Leucogastrales, including *Mycolevis siccigleba* (Cribbeaceae) in the Albatrellaceae using morphological and molecular data. *Mycological Resaearch* **111**: 653-662.

Anderson, I.C., Chambers, S.M. & Cairney, J.W.G. (2001). ITS-RFLP and ITS sequence diversity in *Pisolithus* from central and eastern Australian sclerophyll forests. *Mycological Research* **105**: 1304-1312.

Arpin, N. & Kühner, R. (1977). Les grandes lignes de la classification des Boletales. *Bulletin Societé Linn. de Lyon* **46**: 83-108 & 181-208.

Baura, G., Szaro, T.M. & Bruns, T.D. (1992). *Gastroboletus laricinus* is a recent derivative of *Suillus grevillei*. *Mycologia* **84**: 592-596.

Berger, K. (1980). *Mykologische Wörterbuch.* Gustav Fischer, Jena, Germany. 432pp.

Besl, H. & Bresinsky, A. (1997). Chemosystematics of Suillaceae and Gomphidiaceae (suborder Suillineae). *Plant Systematics and Evolution* **206**: 223-242.

Besl, H., Bresinsky, A. & Kämmerer, A. (1986). Chemosystematik der Coniophoraceae. *Zeitschrifte Mykologie* **62**: 195-199.

Besl, H., Dorsch, R. & Fischer, M. (1996). On the systematic position of the genus *Melanogaster* (Melanogastraceae, Basidiomycetes). *Zeitschrifte für Mykologie* **62**: 195-199.

Bessette, A.E., Roddy, W.C. & Bessette, A.R. (1999). *North American Boletes: A Color Guide to the Fleshy Pored Mushrooms*, Syracuse Unbiversity Press, New York. 396pp.

Binder, M. (1999). *Zur molecularen Systematik der Boletales: Boletineae and Sclerodermatineae subordo nov.* PhD thesis University of Regensburg, Regensburg, Germany.

Binder, M. & Bresinsky, A. (2000). 28S rDNA sequence data and chemotaxonomical analyses on the generic concept of *Leccinum* (Boletales). *A.M.B. Italy. Centro Studi Mycologici, Micologia 2000*: 71-82.

Binder, M. & Bresinsky, A. (2002). *Retiboletus*, a new genus for a species-complex in the Boletaceae producing retipeptides. *Feddes Repetorium* **113**: 30-40.

Binder, M. & Hibbett, D.S. (2006). Molecular systematics and biological diversification of Boletales. *Mycologia* **98**: 971-981.

Binder, M., Larsson, H-J, Larsson, E., Langer, E. & Langer, G. (2005) The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). *Syst. Biodiversity* **3**: 113-157.

Breitenbach, J. & Kränzlin, F. (1986). *Champignons de Suisse*, Tome 2. Edition Mykologia, Lucerne, Switzerland, 416pp.

Breitenbach, J. & Kränzlin, F. (1991). *Champignons de Suisse*, Tome 3. Edition Mykologia, Lucerne, Switzerland, 362pp. Vol2 & 3

M: 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 Biology* **1**: 327-333.

Brundrett, M.C. & Kendrick, B. (1987). The relationship between the ash bolete (*Boletinellus merulioides*) and an aphid parasite on ash tree roots. *Symbiosis* 3: 315-319.

Boedijn, K.B. (1938). The genus *Calostoma* in the Netherlands Indies (Fungi, Bas.). *Bulletin du Jardin de Botanique Buitenzorg,* ser. 3, 16: 64-75.

Bougher, N.L. & Castellano, M.A. (1993). Delimitation of *Hymenogaster s. s.* and four new segregate genera. *Mycologia* **85**: 273-293.

Bougher, N.L. & Syme, K. (1998). *Fungi of Southern Australia*, Univeristy of Western Australia, Perth, Australia, 390pp.

Burgess, T., Malajczuk, N. & Dell, B. (1995). Variation in *Pisolithus* based on basidiome and basidiospore morphology, culture characteristics and analysis of polypeptides using ID SDS-PAGE. *Mycological Research* 99: 1-13.

Cartwright, K.St.G. & Findlay, PK. (1958). *Decay of Timber and its Prevention*. Her Majesty's Stat. Office, London, UK. 215pp.

Castellano, M.A. & Trappe, J.M. (1992). Australasian truffle-like fungi III. *Royoungia* gen. nov. and *Mycoamaranthus* gen. nov. (Basidiomycotina). *Australian Systematic Botany* **5**: 613-636.

Chui, W.F. (1948). The boletes of Yunnan. *Mycologia* **40**: 199-231.

Claridge, A.W., Trappe, J.M. & Castellano, M.A. (2001). Australasian truffle-like fungi X. *Gymnopaxillus* (Basidiomycota, Austropaxillaceae). *Australian Systematic Botany* **14**: 273-281.

Clémençon, H. (2005). New Observations on the basidiome ontogeny of *Chamonixia caespitosa* (Sequestrate Boletaceae). *Persoonia* 18: 499-504.

Clémençon, H., Hosaka, K. & Taylor, A.F.S. (2007). Rhizomorph anatomy confirms the taxonomic position of *Sclerogaster* (Phallomycetidae, Basidiomycota). *Mycotaxon* **100**: 85-95.

Coccia, M., Migliozzi, V. & Lavarato, C. (1990). Studio sul genre *Scleroderma. Bollettino dell'Associazione Micologica* ed. Ecologica Romana.**7**: 3-59.

Coggins, C.R. (1980). *Decay of Timber in Buildings*. Rentokill Library, London, UK. 115pp.

Coker, W.B. & Beers, A.H. (1943). *The Boletaceae of North Carolina*. University of North Carolina Press, Chapel Hill, North Carolina, USA.

Coker, W.B. & Couch, J.N. (1928). *Gasteromycetes of Eastern United States*

and Canada, Chapel Hill, University of North Carolina Press, N. Carolina, USA. 201pp.

Cooke, Bridge, W. (1953). *The genera of the Homobasidiomyectes (exclusive of the Gastromycetes).* Special Publ. Div. Mycol. Dis. Survey. U.S. Dept. Agriculture, Beltsville, Maryland, U.S.A. 100pp.

Cooke, Bridge, W. (1957). The genera *Serpula* and *Meruliporia. Mycologia* **49**: 197-225.

Corner, E.J.H. & Hawker, L.E. (1953). Hypogeous fungi from Malaysia. *Transactions of the British Mycological Society* 36: 125-137.

Corner, E.J.H. (1970). *Phylloporus* Quél. & *Paxillus* Fr. in Malaya and Borneo. *Nova Hedwigia* **20**: 793-822

Corner, E.J.H. (1971). Merulioid Fungi in Malaysia. *Gardens' Bulletin, Singapore*. **25**: 355-381.

Corner, E.J.H. (1972). *Boletus in Malaysia*, Singapore Government Publisher, Singapore, 263pp.

Cunningham, G.H. (1944). *Gasteromycetes of Australia and New Zealand*. Dunedin, New Zealand. Privately published. 236pp.

Dai, Y.-C. & Niemelä, T. (1995). Changbai wood-rotting fungi 4. Some species described by A. S. Bondartsev & L. V. Lyubarsky from the Russian Far East. *Annales Botanici Fennici* **32**: 211-226.

Dalhberg, A. (1990). Population structure and dynamics in *Suillus bovinus* as indicated by spatial distribution of fungal clones. *New Phytologist* **115**: 487-493.

Dahlberg, A. & Stenlid, J. (1994). Size, distribution and biomass of genets in populations of *Suillus bovinus* (L.: Fr.) Roussel revealed by somatic incompatibility. *New Phytologist* **128**: 225-234.

Den Bakker, H.C., Gravendeel, B. & Kuyper, T.W. (2004). An ITS phylogeny of *Leccinum* and an analysis of the evolution of the minisatellite-like sequences within ITS1. *Mycologia* **96**: 102-118. *Mycological Research* 111, 663-672

Den Bekker, H.C., Zuccarello, G.C., Kuyper, T.W. & Noordeloos, M.E. (2004). Evolution and host specificity in the ectomycorrhizal genus. *New Phytologist* 163: 201-215.

Den Bekker, H.C., Zuccarello, G.C., Kuyper, T.W. & Noordeloos, M.E. (2007). Phytogeographic pattern in *Leccinum* sect. *Scabra* and the status of the arctic-alpine species *L. rotundifoliae.*

Demoulin, V. (1967).Typification et nomenclature de quelques espèces du genre *Scleroderma* Pers.(Gasteromycetes). *Bulletin du Jardin Botanique de l'Etat, Bruxelles* **37**: 289-304.

Demoulin, V. & Dring, D.M. (1975). Gasteromycetes of Kivu (Zaire), Rwanda and Burundi. *Bulletin du Jardin Botanique de l'Etat Bruxelles* 45: 339-372.

Dissing, H. & Lange, M. (1962). Gasteromycetes of the Congo. *Bulletin du Jardin Botanique de l'Etat Bruxelles* 32: 325-416.

Dodge, C.W. & Zeller, S.M. (1934). *Hymenogaster* and related genera. *Annals of the Missouri Botanical Garden* **21**: 639-655.

Donk, M.A. (1960). The generic names proposed for Polyporaceae. *Persoonia* **1**: 173-302.

Donk, M.A. (1964). A conspectus of the families of Aphyllophorales. *Persoonia* **3**: 199-324,

Donk M.A. (1955). The generic names proposed for Hymenomycetes – IV. Boletaceae. *Reinwardtia* **3**: 75-313.

Donk, M.A. (1960). The generic names proposed for Polyporaceae. *Persoonia* **1**: 173-302.

Donk M.A. (1962). The Generic Names proposed for Agaricaceae. *Beihefte zur Nova Hedwigia* **5**: 1-320.

Donk, M.A. (1963). The Generic Names proposed for Hymenomycetes – XIII. *Additions and Corrections to Parts I – X & XII*. Taxon 12: 113-123.

Dodge, C.W. & Zeller, S.M. (1936). *Hydnangium* and related genera. *Annals of the Missouri Botanical Garden* **23**: 565-598.

Douanla-Meli, C. (2007). Fungi of Cameroon. Ecological diversity with emphasis on the taxonomy of Non-gilled Hymenomycetes from the Mbalmayo forest reserve. *Bibliotheca Mycologica* 2002: 1-410.

Dring, D.M. (1973). Gasteromycetes. In Ainsworth, G.C., Sparrow, F.K. & Sussman, A.S. (eds.) *The Fungi*, Academic Press, London, UK. pp.451-478

Elrod, R.P. & Blanchard, D.L. (1939). Histological studies of the Boletaceae and related genera. *Mycologia* **31**: 683-708.

Elrod, R.P. & Snell, W.H. (1940). Development of the carpophores of certain Boletaceae. *Mycologia* **32**: 493-504.

Engel, H., Dermek, A. & Watling, R. (1978). *Dicksteilröhrlinge: Die Gattung Boletus in Europa*, Weidhausenh, Gewrmany. 84pp.

Engel, H., Dermek, A. & Watling, R. (1983). *Rauhstielröhrlinge: Die Gattung Leccinum in Europa*, Weidhausen-Coburg, Germany, 84pp.

Engel, H., Dermek, A., Klofac, W., Ludwig, E & Brückner, T. (1996). *Schmier- und Filzröhrlinge s.l. in Europa*, Weidhausen-Coburg, 268pp.

Eriksson, J. & Ryvarden, L. (1976). *The Corticiaceae of North Europe IV. Hyphodermella-Mycoacia*. pp.549-886. Fungiflora, Oslo, Norway

Fischer, E. (1900). Calostomataceae. In Engel, A. & Prantl, K. (eds.) *Die Nätürlichen Pflanzenfamilien* 1 Auf., teil Abt. 1**: 331 & 339-341.

Fries, N. (1985). Intersterility groups in *Paxillus involutus. Mycotaxon* **24**: 403-409.

Fries, N. (1987). Somatic Incompatibility and Field Distribution of the Ectomycorrhizal Fungus *Suillus luteus* (Boletaceae). *New Phytologist* **107**: 735-739.

Fogel, R. (1979). The genus *Leucophleps* (Basidiomycotina; Leucogastrales). *Canadian Journal of Botany* 57: 1718-1728.

Fogel, R. (1990). *Leucogaster columellatus* is a *Sclerogaster. Mycologia* 82: 655-657.

Garrido, N. (1988). Agaricales *s.l.* und ihre Mykorrhizen in den Nothofagus-Wöldern Mittelchiles. *Bibliotheca Mycologica* **120**: 1-528.

Geesteranus, Maas R. (1964). Notes on *Hydnum* II. *Persoonia* **3**: 155-198**.**

Gentile, A.C. & Snell, W.H. (1953). Development of the carporphore of *Boletinus paluster*. *Mycologia* **45**: 720-722.

Gilbertson, R.L. & Hemmes, D.E. (1997). Notes on Hawaiian Coniophoraceae. *Mycotaxon* **65**: 436-440.

Gill, M. & Steglich, W. (1987). Pigments of Fungi (Macromycetes). *Fortschritte der Chemie organischer Naturstoffe* **51**: 1-317.

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 Systematics and Evolution* **154**: 225-236.

Ginns, J. (1971). The genus *Merulius* IV. Species proposed by Berkeley, by Berkeley & Curtis and Berkeley & Broome types. *Mycologia* 63: 219-236.

Ginns, J. (1973). *Coniophora*: study of 22 type specimens. *Canadian Journal of Botany* **51**: 249-259.

Ginns J. (1976). *Leucogyrophana* (Aphyllophorales, Basidiomycetes: identification of the species. *Canadian Journal of Botany 56*: 1953-1973.

Ginns, J. (1976). *Merulius: s. s*. and *s. l*. Taxonomic disposition and identification of species. *Canadian Journal of Botany* 54: 106-167.

Ginns J. (1982). A monograph of the genus *Coniophora* (Aphyllophorales, Basidiomycetes. *Opera Botanica* **61**: 1-61.

Ginns, J. & Weresub, L. (1978). Sclerotium-producing species of *Leucogyrophana* (Aphyllophorales). *Memoirs of the New York Botanical Garden* **28**: 86-978.

Gomez, LD. (1996). Basidiomicetes de Costa Rica: *Xerocomus*, *Chalciporus*, *Pulveroboletus*, *Boletellus*, *Xanthoconium* (Agaricales: Boletaceae). *Revue Biologia Tropicana* **44** (Suppl. 4): 1-89.

Grubisha, L. C., Trappe, J. M., Molina, R. & Spatafora, J. W. (2001). Biology of the ectomycorrhizal genus, *Rhizopogon* V. Phylogenetic relationships in the Boletales inferred from LSU rDNA sequences. *Mycologia* **93**: 82-89.

Guzmán, G. (1974). El Genero *Fistulinella* Henn. (=*Ixechinus* Heim) y Las Relaciones Floristicas Entre Mexico y Africa. *Boletin Sociedad Micologia Mexico* **8**: 53-63.

Guzmán, G. (1970). Monografia del genero *Scleroderma* Pers. emend Fries. *Darwiniana* **16**: 233-407.

Guzmán, G., Ramírez-Guillén, F., Miller, O.K., Lodge, D. J. & Baroni, T. J. (2004). *Scleroderma stellatum* versus *S. bermudense*: the status of *Scleroderma echinatum* and the first record of *Veligaster nitidum* from the Virgin Islands. *Mycologia* **96**: 1370-1379.

Hallenberg, N. (1985). *The Lachnocladiaceae & Coniophoraceae of Northern Europe*. Fungiflora Oslo, Norway, 96pp.

Halling, R.E. & Mueller, G.H. (2005). Common Mushrooms of the Talamanca Mountains, Costa Rica, *Memoirs of the New York Botanical Garden* **90**: 1-195.

Hahn, C. & Agerer, R. (1999). Studien zum *Paxillus involutus* Formenkreis. *Nova Hedwigia* **69**: 241-310.

Harrison, K. A. & Smith, A.H. (1968). Some new species and distribution records of *Rhizopogon* in North America. *Canadian Journal of Botany* **46**: 881-899.

Heim, R. (1971). The interrelationships between the Agaricales and Gasteromycetes. In Petersen, R.H. (ed.) *Evolution in the Higher Basidiomycetes*, 505-534. University of Tennessee Press, Knoxville, Tennessee, USA.

Heinemann, P. (1954). Boletineae. *Flore Iconographique des Champignons du Congo* **3**: 49-80.

Heinemann, P. (1966). Hygrophoraceae, *Laccaria* & Boletineae II (complément). *Flore Iconographique des Champignons du Congo* **15**: 279-308.

Heinemann, P. & Rammeloo, J. (1979). Observations sur *Gyroporus castaneus s. l. Bulletin du Jardin Botanique Nationale Belgique* 49: 435-447.

Heinemann, P. & Rammeloo, J. (1980). Gyrodontaceae p.p. *Flore Illustrée des Champignons d'Afrique Centrale*. **7**: 128-131.

Heinemann, P. & Rammeloo, J. (1982). Observations sur le genre *Phlebopus* (Boletineae). *Mycotaxon* 15: 384-409.

Heinemann, P. & Rammeloo, J. (1983).Gyrodontaceae p.p. (Boletineae). *Flore Illustrée des Champignons d'Afrique Centrale* **10**: 173-198.

Heinemann, P. & Rammeloo, J. (1986). Paxillaceae (Boletineae). *Flore Illustrée des Champignons d'Afrique Centrale.* **12**: 263-271.

Heinemann, P. & Rammeloo, J. (1987). *Phylloporus* (Boletineae). *Flore Illustrée des Champignons d'Afrique Centrale* **13**: 277-309.

Heinemann, P. & Rammeloo, J. (1989). *Suillus* (Boletaceae, Boletineae) & *Tuboseta* (Xerocomaceae, Boletineae). *Flore Illustrée des Champignons d'Afrique Centrale* **14**: 313-335.

Hennebert, G.L. (1973). *Botrytis* and *Botrytis*-like genera. *Persoonia* **7**: 183-204.

Hibbett, D.S. (2006). A phylogenetic overview of the Agaricomycotina. *Mycologia* **98**: 917-925.

Hibbett, D.S. & & Binder, M. (2002). Evolution of complex fruiting body morphologies in homobasidiomycetes. *Proceedings of the Royal Society of London* **B. 269**: 1963-1969.

Hibbett, D.S. –lead author (2007). A higher-level phylogenetic classification of the fungi. *Mycological Research* **111**: 509-548.

Hibbett, D.S. & Thorn, R.G. (2001). *Homobasidiomycetes*. In McLaughlin, D.J. , McLaughlin, E..J.& Lemke, P. (eds.). The Mycota Vol. V11. Part B., *Systematics and Evolution*. Springer-Verlag, Berlin, Germany. 121-168.

Hjortstam, K., Larsson, K-L. & Ryvarden, L. (1987). *The Corticiaceae of North Europe*. Vol. 1, Fungiflora, Oslo, Norway. 59pp.

Hosaka, K., Bates, S.T., Beever, R.E., Castellano, M.A., Colgan, W., Dominguez, L.S., Nouhra, E.R., Geml, J., Giachini, A.J., Kenney, S.R., Simpson, N.B., Spatafora, J.W. & Trappe, J.M. (2006). Molecular phylogenetics of the gomphoid-phalloid fungi with establishment of the new subclass Phallomycetidae and two new orders. *Mycologia* **98**: 949-959.

Horak, E. (1968). Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). *Beitrage zur Kryptogamenflora der Schweiz* **13**: 1-739.

Horak, E. (1976). *Boletellus* and *Porphyrellus* in Papua New Guinea. *Kew Bulletin* **31**: 645-642.

Horak, E. (1979). Paxilloid Agaricales in Australasia. *Sydowia* **32**: 154-166.

Horak, E. (1980). Supplementary remarks to *Austroboletus* (Corner) Wolfe (Boletaceae). *Sydowia* **33**: 71-87.

Horak, E. (1983). Mycogeography in the South Pacific Region: Boletales. *Australian Journal of Botany* **Suppl. 10**: 1-41.

Horak, E. & Moser, M. (1966). Fungi Austroamericani VIII. *Nova Hedwigia* **10**: 329-338.

Hosford, D. P. & Trappe, J. M. (1988). A preliminary survey of Japanese species of *Rhizopogon*. *Transactions of the Japanese Mycological Society* 27: 63-72.

Hughey, B.D., Adams, G.C., Bruns, T.D. & Hibbett, D.S. (2000). Phylogeny of *Calostoma*, the gelatinous-stalked puffball, based on nuclear and ribosomal DNA sequences. *Mycologia* **92**: 94-104.

Humblot, M.R. (1926). Note sur deux espèces américanes récoltés aux environs de Paris. *Bulletin de Sociéte de Mycolgique de France* 42: 75-80.

Ikeda, T., Kuroda, M. & Ueshima, K (2002). A case of hypersensitivity pneumonitis caused by *Gyrodontium versicoor*. *Nihon Kokyuki Gakkai Zasshi* **40**: 387-391.

Imazeki, R., Otani, Y., Hongo & T. (1988). *Fungi of Japan*, Shiba-daimond, Tokyo, Japan. 622pp.

Jacobson, K.M., Miller, O.K. & Turner, B.J. (1993). Randomly amplified polymorphic DNA markers are superior somatic incompatibility tests for disconnecting genotypes in natural populations of the ectomycorrhizal fungus *Suillus granulatus*. *Proceedings of the National Academy of Sciences of the United States of America* **90**: 9159-9163.

Jarosch, M. & Besl, H. (2001). *Leucogyrophana*, a polyphyletic genus of the order Boletales (Basidiomycetes). *Plant Biology* **3**: 443-448.

Josserand, M. (1952). La descripiton des champignons supérieurs. *Encyclopédie Mycologique* **21**: 1-338.

Julich, W. (1974). Notes on the cyanophily of spores with a discussion of the genus *Leucogyrophana* (Corticiaceae). *Persoonia* **8**: 51-58.

Julich, W. (1979). Studies on Resupinate Basidiomycetes. VI. *Persoonia* 10: 335-336.

Julich, W. (1981). Higher Taxa of Basidiomycetes. *Bibliotheca Mycologica* **85**: 1-485.

Kämmerer, A., Besl, H. & Bresinsky, A. (1985). Omphalotaceae *fam. nov*. und Paxillaceae, ein chemotaxonomischer Vergleich zweier Pilzfamilien der Boletales. *Plant Systematics and Evolution* 150: 101-117.

Kanchasanaprayudh, J., Zhou, Z., Yomyart, S., Sihanonth, P., Hogestu, T. & Watling, R. (2003). A new species, *Pisolithus albidus*, an ectomycorrhizal fungus associated with dipterocarps in Thailand. *Mycotaxon* **88**: 463-467.

Kauserud, H., Stensrud,φ ., Decock, C., Shalchian-Tabirizi, K. & Schymacher, T., (2006). Multiple gene genealogies and AFLPs suggest cryptic speciation and long-distance dispersal in the basidiomycetes *Serpula himantioides*(Boletales). *Molecular Ecology* **15**: 421-431.

Kavina, K. Contribution à histologiie et biologie de *Boletus parasiticus*. *Rozpravy II Tr. Ceská Akademie*. **45**: 1-16.

Kirk, P.M., Cannon, P.F., David, J.C. & Stalpers, J.A. (2001). *The Dictionary of Fungi*, 9th edition. CABI, Wallyford, England, UK.

Kotlaba, F. & Pouzar, Z. (1972). Taxonomy and Nomenclatural notes on some Macromycetes. *Ceská Mycologia* 26: 217-222.

Kriesel, H. (1974). Die Gattung *Diplocystis* und ihre Stellung im System der Basidiomycetes. *Feddes Repetorium* 85: 325-335.

Kriesel, H. (2001). Check List of the gasteral and secotioid Basidiomycetes of Europe, Africa & the Middle East. *Österrische zur Pilz* 10: 213-313

Kühner, R. (1926). Le développement du *Boletinus cavipes* Kalch. *Le Botaniste* **ser. 17-18**: 177-181.

Kühner, R. (1926). Contribution à l'étude des Hyménomycètes et specialement des Agaricacés. Thesis Paris see Reijnders, 1963 below.

Ladurner, H. & Pöder, R. (2000). A new hyphal type found in *Xerocomus pruinatus*. *Österreiichische Zeitschrift für Pilzkunde* **9**: 11-15.

Ladurner, H. & Simonini, G. (2003). *Xerocomus. Fungi Europaei* 8. Edizione Candusso, Alassio, Italy. 527pp.

Laessóe, T. & Jaline, L. M. (2004). *Chlorogaster dipterocarpi*. A new peristomate gasteroid taxon of the Sclerodermataceae. *Persoonia* **18**: 421-428.

Lange, L. (1973). Development of fruiting bodies of the bolete *Suillus grevillei* under natural conditions. *Saetryk af Botanisk Tidsskrift* **68**: 122-131.

Lannoy, G. & Estades, A. (1955). *Monographie des Leccinum d'Europe*. Fédération Mycologique Dauphiné-Savoie, France. 229pp.

Laut, J. G. (1966). Cultural Charaacteristics of three Species of *Boletinus*. *Canadian Journal of Botany* 44: 395-402.

Linder, D.H. (1930). Notes on *Tremellogaster surinamensis. Mycologia* 22: 265-270.

Lincoff, G.H. (1981). *The Audubon Society Field Guide to North American Mushrooms*. Knoft, New York, USA. 926pp.

Lui, B. (1979). *Calostoma*. Journal of the Shanxi University. (Nat. Sci. ed.) 1: 109-118.

Lloyd, C. G. (1898-1905). *Mycological Writings* I. Plate 15. Cincinnata, Ohio, USA. Privately published

Lloyd, C.G. (1902). *Geastrae*. Cincinnati, Ohio, USA. 43pp. Privately published

Lloyd, C.G. (1913). *Mycological Writings* 4 – Letter 42. Cincinnati, Ohio, USA. Privately published

Lloyd, C. G. (1921). *Mycological Writings* 6: 877-1101. Cincinnati, Ohio, USA. Privately published

Lloyd, C.G. (1925). *Mycological Writings* 7: 1349-1364. Cincinnati, Ohio, USA. Privately published**.**

Louzan, R., Wilson, A., Binder, M. & Hibbett, D.S. (2007). Phylogenetic placement of *Diplocystis wrightii* in the Sclerodermatineae (Boletales) based on nuclear ribosomal large subunit DNA sequences. *Mycoscience* **48**: 66-69.

Lumyong, S., Sanmee, R., Lumyong, P , Zhu L. Yang & Trappe, J.P.(2004). *Mycoamaranthus cambodgonensis* comb. nov., a widely distributed sequestrate basidiomycete from Australia and Southeastern Asia. *Mycological Progress* 2: 323-325

Maire, R. (1937). Fungi Catalaunici, series altera. Publicaiones instituto. *Botanica Barcelona* **3**: 1-128.

Malençon, G. (1983). A propos de deux *Corditubera* nouveaux récoltés en France. *Cryptogamia Mycologia* **4**: 1-8.

Martin, M.P. (1996). *Rhizopogon* in Europe. *Speciales ediciones de la Societat Catalona de Micologia* **5**: 1-173.

Martin, M.P., Karen, O. & Nylund, J.-E. (2000). Molecular ecology of hypogeous mycorrhizal fungi: *Rhizopogon roseolus* (Basidiomycotina). *Phyton spec. issue ' Root-soil interactions'* **40**: 135-141.

Martin, F. Díez Jesús, Dell, B. & Delaruelle, C. (1994). Phylogeography of the ectomycorrhizal *Pisolithus* species as inferred from nuclear ribosomal DNA ITS sequences. *New Phytologist* **153**: 345-357.

May, T.W., Milne, J., Shingles, S. & Jones, R.H. (2003). *Fungi of Australia. Vol.2B Catalogue and Bibliography of Australian Fungi 2 Basidiomycota p.p. & Myxomycota p.p.* Australian Biological Resources Study, Canberra, Australia, 425pp.

May, T.W. & Wood, A.E. (1996). Nomenclatural notes on Australian macrofungi. *Mycotaxon* **54**: 147-150.

McLaughlin, D.J. (1964). Production of fruitbodies of *Suillus rubinellus* in Pure Culture. *Mycologia* **56**: 136-138.

McLaughlin, D.J. (1970). Environmental control of fruitbody development in *Boletus rubinellus* in axenic culture. *Mycologia* **62**: 307-331.

Massicote, H.B., Molina, R., Luoma, D.L. & Smith, J.E. (1994). Biology of the ectomycorrhizal genus , *Rhizopogon* II. Patterns of host-fungus specificity following spore inoculation of diverse hosts grown in monoculture and dual culture. *New Phytologist* **126**: 677-690.

Miller, O.K. (1964). Monograph of *Chroogomphus. Mycologia* **56**: 526-549.

Miller, O K. (1971). The genus *Gomphidius* with a revised description of the Gomphidiaceae and a key to the genera. *Mycologia* **63**: 1129-1163.

Miller, O.K (1973). A New gastroid genus related to *Gomphidius*. *Mycologia* **65**: 226-229.

Miller, O.K. & Aime, A.C. (2001). Systematics, ecology, and world distribution in the genus *Chroogomphus* (Gomphidiaceae). In Misra, J. & Horn, B.W. (eds.), *Trichomycetes and other fungal groups: R. Lichtwardt commemorative volume*. pp. 315-333. Sciences Publications Inc. Enfield, New Hampshire, USA.

Miller, O.K. & W.B. Askew (1982). The genus *Gasterosporium* in North America. *Canadian Journal of Botany* 60: 364-368.

Miller, O.K. & Miller, H. H. (1988).*Gasteromycetes. Morphological and development features with keys to the Orders, Families and Genera*. Mad River Press, California, USA. 157pp.

Miller, O.K. & Trappe, J. M. (1970). A New *Chroogomphus* with a loculate hymenium and a revised Key to Section *Floocigomphus. Mycologia* **62**: 831-836.

Molina, R. & Trappe, J.M. (1994). Biology of the ectomycorrhizal genus, *Rhizopogon* I. *New Phytologist* **126**: 653-675.

Molina, R., Smith, J. E., McKay, D. & Melveille, L.H. (1997). Biology of the ectomycorrhizal genmus *Rhizopogon* III. Influence of co-cultured conifer species on mycorrhizal specificity with the arbutoid hosts *Arctostaphlos uva-ursi* and *Arbutus menziesii. New Phytoloist* **137**: 519-528.

Monthoux, O. & Röllin, O. (1976). La flore fongique des stations xériques de la région de Genève III. Gastrosporealés. *Candollea* 31: 119-125.

Murrill, W. A. (1901). The Boletaceae of North America. *Mycologia* **1**: 4-18.

Nannfeldt, J. A. & Eriksson, J. (1951). On the hymenomycetous genus *Jaapia* and its taxonomical position. *Svensk Botanisk Tidsrift* **47**: 177-182.

Nunez, M. & Ryvarden, L. (1994). Notes on the genus *Beenakia. Sydowia*: 46: 321-328.

Olsson, P.A., Münzenburger, B., Mahmood, S. & Erland, S. (2000). Molecular and anatomical evidence for a three-way association between *Pinus sylvestris* and the ectomycorrhizal fungi *Suillus bovinus* and *Gomphidius roseus*. *Mycological Research* **104**: 1372-1378.

Oolbekkink G.T. (1991). The taxonomic value of the ornamentation of species in the *Xerocomus* group of *Boletus. Persoonia* **14**; 245-273

Palm, M.E. & Stewart, E.L. (1984). On the Typification of *Suillus* (Boletales, Basidiomycotina). *Taxon* **33**: 711-712.

Pantidou, M. (1961). Cultural studies of Boletaceae. *Gyrodon merulioides* and four species of *Boletinus. Canadian Journal of Botany* **39**: 1149-1162.

Pantidou, M. (1961). Carpophores of *Phlebopus sulphureus* in culture. *Canadian Journal of Botany* **39**: 1163-1167.

Pantidou, M. (1962). Cultural Studies of Boletaceae. Carpophores of *Phlebopus lignicola* in culture. *Canadian Journal of Botany* **40**: 1313-1319.

Pantidou, M. (1964). Cultural studies of Boletaceae: Carpophores of *Xerocomus badius* and *Xerocomus illudens* in culture. *Canadian Journal of Botany* **42**: 1147-1149

Pantidou, M. & Groves, J.W. (1966). Cultural studies of Boletaceae. Some species of *Suillus* and *Fuscoboletinus. Canadian Journal of Botany* **44**: 1371-1392.

Pantidou, M. & Watling, R. (1970). A contribution to the study of the Boletaceae – Suilloideae. *Notes from the Royal Botanic Garden, Edinburgh* **31**: 207-237.

Pantidou, M. & Watling, R. (1973). Fruit-bodies of *Boletus amarellus* in pure culture. *Notes from the Royal Botanic Garden, Edinburgh* **32**: 439-443.

Patouillard, N. & Baker, C.F. (1918). Some Singapore Boletineae. *Journal of the Straits Branch of the Royal Asiatic Society* **78**: 67-72.

Pegler, D.N. (1983). *Agaric Flora of the Lesser Antilles*, Royal Botanic Garden, Kew, England, UK. 668pp.

Pegler, D. N. (1986). *Agaric Flora of Sri Lanka*. Royal Botanic Gardens, Kew, England, UK. 518pp.

Pegler, D.N., Laessoe, T. & Spooner, B. M.. (1995). *British Puffballs, Earthstars and Stinkhorns.* Royal Botanic Garden Kew, England, UK.255pp.

Pegler, D.N., Spooner, B.M. & Young, T.W.K. (1993). *British Truffles*. Royal Botanic Garden Kew, England UK. 216pp

Pegler, D.N. & Young, T.W.K. (1981). A natural arrangement of the Boletales with reference to spore morphology. *Transactions of the British Mycological Society* **76**: 103-146.

Pegler, D.N. & Young, T.W..K. (1978). The Gasteroid Russulales. *Transactions of the British Mycological Society* **72**: 353-388.

Petersen, R. H. (1968). Notes on cantharelloid fungi I. *Gomphus* S. F. Gray and some clues to the origin of ramarioid fungi. *The Journal of the Elisha Mitchell Scientific Society* 84: 373-381.

Petersen, R. H. (1974). Notes on cantharelloid fungi V. Some fungi suspected of being gomphoid. *The Journal of the Elisha Mitchell Scientific Society* **90**: 53-54.

Phosri, C., Martin, M.P., Sihanonth, P., Whalley, A.J.S. & Watling, R. (2007). Molecular study of the genus *Astraeus*. *Mycological Research* **111**: 275-286.

Phosri, C., Watling, R., Martin. M.P. & Whalley, A.J.S. (2004). The genus *Astraeus* in Thailand. *Mycotaxon* **89**: 453-463.

Pilát, A. (1934). Sur le genre *Gastrosporium* Mattirolo (Gasteromycetes). *Bulletin de la Sociéte Mycologique de France* **50**: 37-46.

Pilát, A. (1958). *Flora CSR. Gasteromycetes*, Ceskoslovenske Akademie, Prague, Czechoslovakia. 862pp.

Pomerleau, R. (1980). *Flore des Champignons au Quebec*, Les Éditions la Presse, Ltée, Ottawa, Canada. 539pp.

Pomerleau, R. & Smith, A. H. (1962). *Fuscoboletinus*, a new genus of the Boletales. *Brittonia* **14**: 156-172.

Razanamparany, J.L., Creepy, E.E., Perreau-Bertrand, J., Boulanger, Y. & Dirheimer, G. (1986). Purification and characterization of bolaffinine, a toxic protein from *Boletus affinis* Peck (Boletaceae). *Biochiemie* **68**: 1217-1223.

Rea, C. (1913). *Glischroderma cinctum* Fckl. *Transactions of the British Mycological Society* **4**: 64-65.

Reid, D.A. (1956). New and Interesting Records of Australasian Basidiomycetes. *Kew Bulletin (1955)*: 631-648.

Reid, D.A. (1986). New and Interesting records of Australasian Basidiomycetes IV. *Transactions of the British Mycological Society* **86**: 429-440.

Reijnders, A.F.M. (1948) Le développement et l'organisation histologique des carpophores dans les Agaricales. *Rec. Travail Botanica Neerlandica* **41**: 213-396.

Reijnders, A.F.M. (1963). *Les problèmes du développement des carpophores des Agaricales et quelques groupes voisins.* W. Junk, Den Haag, The Netherlands

Reijnders, A.F.M. & Stalpers, J.A. (1983). Basal types of hymenophoral trama in the Aphyllophorales and the Agaricales. *Studies in Mycology* **34**: 1-109..

Roberts, P. (1997). *Aldrigea* (Fungi: Boletales). A synonym of *Coniophora. Kew Bulletin* **52**: 505-506.

Rogers, D. P. (1935). Notes on the Lower Basidiomycetes. *University of Iowa Studies in Natural History* **17**: 1-60-.

Rogers, D. P. (1943). The genus *Pellicularia. Farlowia* **1**: 95-118.

Rogerson, C. & Samuels, G. (1989). Boleticolous species of *Hypomyces. Mycologia* **81**: 413-432.

Routien, J. B. (1939). Observations on *Gasterella lutophila. Mycologia* 31: 416-417.

Ryvarden, L. & Gilbertson, R.L. (1994). European Polypores Part 2. *Synopsis Fungorum* **7**: 394-743

Sims, K., Watling, R. & Jeffries, P. (1995). A revised key of the Sclerodermataceae. *Mycotaxon* 56: 403-420.

Singer R. (1936). Das System der Agaricales I. *Annales Mycologici* 34: 286-378.

Singer, R. (1938). Sur les genres *Ixocomus, Boletinus, Phylloporus, Gyrodon* and *Gomphidius. Revue Mycologie* **3**: 35-53 & 157-177.

Singer, R. (1938). Notes sur quelques Basidiomycetes IV. *Revue de Mycologie* 4: 65-72

Singer , R. (1942). Das System der Agaricales. *Annales Mycologie* II 40: 1-132.

Singer, R. (1944). New genera of fungi. *Mycologia* **36**: 358-360.

Singer, R. (1945). The Boletineae of Florida with notes on extralimital species I. *Farlowia* **2**: 97-141.

Singer, R. (1945). The Boletinae of Florida with notes on extralimital species II *Farlowia* **2**: 223-302.

Singer, R. (1946). The Boletineae of Florida with notes on extralimital species IV. *Farlowia* **2**: 527-567.

Singer, R. (1947). The Boletineae of Florida with notes on extralimital species. III. *American Midland Naturalist* **37**: 1-135.

Singer, R. (1947). Coscinoids and coscinocystidia in *Linderomyces lateritius. Farlowia* **3**: 155-157.

Singer, R. (1951). Agaricales in Modern Taxonomy. *Lilloa (1949)* **22**: 1-832

Singer, R. (1955). Type studies on Basidiomycetes VIII. *Sydowia* **9**: 367-341.

Singer, R. (1956). *Campbellia africana* and *Versipellis variegata. Taxon* **5**: 30-33.

Singer, R. (1962). Monographs of South American Basidiomycetes especially those of the east slope of the Andes and Brazil V. *Boletin de la Sociedad Argentina Botánica* 10: 52-67.

Singer, R. (1962) *Agaricales in Modern Taxonomy*. Cramer, Weinheim, Lichenstein. 915pp.

Singer, R. (1964). Monograph of South American Basidiomycetes VI. *Nova Hedwigia* 7: 93-132

Singer, R (1965). *Die Pilze Mitteleuropas. Die Röhrlinge Part 1. Die Boletaceae (ohne Boletoideae).* J. Klinkhardt, Bad Heilbrunn, Germany. 131pp.

Singer, R. (1967). Ditto *Die Röhrlinge Part 2. Die Boletoideae and Strobilomycetaceae).* J. Klinkhardt, Bad Heilbrunn, Germany.151pp.

Singer, R. (1969). Mycoflora Australis. *Beihefte Nova Hedwigia* **29**: 1-405.

Singer, R. (1973). Notes on bolete taxonomy *Persoonia* **7**: 313-320.

Singer, R. (1975). *Agaricales in Modern taxonomy*. 3rd edition J. Cramer, Vaduz, Germany. 912pp.

Singer, R. (1978). Notes on bolete taxonomy. *Persoonia* **9**: 421-438.

Singer, R. (1981). Notes on bolete taxonomy. *Persoonia* **11**: 269-302.

Singer, R. (1986). *Agaricales in Modern taxonomy*. 4th and fully revised edition. Koeltz Scientific Books, Koenigstein, Germany.

Singer, R. Garcia, J. & Gomez, L. D. (1990). Boletineae of Mexico and Central America. I & II. *Beihefte Nova Hedwigia* 98: 1-70.

Singer, R., Garcia, J. & Gomez, L.D. (1991). Boletineae of Mexico and Central America III. *Beihefte Nova Hedwigia* **102**: 1-97.

Singer, R., Araujo, I. & Ivory, M. H. (1983).The ectotrophically mycorrhizal fungi of the Neotropal World especially Central America II. *Beihefte Nova Hedwigia* 77: 1-339.

Singer, R. & Kuthan, J. (1976). Notes on *Chrogomphus. Ceská Mycologia*. 10: 81-89.

Singer, R. & Smith, A.H. (1960). Studies on Secotiaceous fungi – IX. The Austrogastraceous series. *Memoirs of the Torrey Botanical Club* **21**: 1-111.

Smith, A.H. (1951). *Puffballs and their Allies in Michigan*, Michigan University Press, Ann Arbor, USA.131pp.

Smith, A.H. (1964). *Rhizopogon*. A curious genus of false truffles. *Michigan Botanist* **3**: 13-19.

Smith, A.H. (1966). A note on *Psiloboletinus*. *Mycologia* 68: 332-336.

Smith, A.H. & Singer, R. (1959). Studies on Secotiaceous Fungi – IV *Gastroboletus, Truncocolumella* and *Chamonixia. Brittonia* **11**: 205-223.

Smith, A.H. & Singer, R. (1958). Studies on Secotiaceous fungi - VIII. A New genus in the Secotiaceae related to *Gomphidius. Mycologia* **50**: 927-938.

Smith, A.H. & Thiers, H.D. (1964). *A Contribution toward a monograph of North American species of Suillus*. Ann Arbor, Michigan, USA. 116pp.

Smith, A.H. & Thiers, H.D. (1964). Further Notes on *Suillus*; the *S. granulatus* problem. *Mycologia* 58: 469-474.

Smith, A. H. & Thiers, H. D. (1968). Notes on Boletes I. 1. The generic position of *Boletus subglabripes* and *Boletus chromapes. Mycologia* **62**: 943-948.

Smith, A.H. & Thiers, H.D. (1971). *The Boletes of Michigan*. University of Michigan Press, Ann Arbor, USA. 417pp.

Smith, A.H., Thiers, H.D. & Watling, R. (1967). A Preliminary Account of North American species of *Leccinum* Sections *Luteoscabra* and *Scabra*. *Michigan Botanist* **6(3A)**: 107-154.

Smith, A.H. & Zeller, S.M. A preliminary account of the North American species of *Rhizopogon. Memoirs of the New York Botanical Gardens* **14**: 1-177.

Snell, W.H. (1941). The Genera of Boletaceae. *Mycologia* **33**: 415-423.

Snell, W.H. & Dick, E.A. (1970). *The Boleti of Northeastern North America*. Cramer, Lehre, Germany.

Sutara, J. (1985). *Leccinum* and the question of superfluous names (Fungi: Boletaceae). *Taxon* 34: 678-686.

Sutara, J. (1987). The limit between the genera *Boletinus* & *Suillus*. *Ceská Mykologie*. **41**: 139-152.

Sutara, J. (1987). *Mariaella*, a new boletaceous genus. *Ceská Mykologie* **41**: 73-84.

Sutara, J. (1989). The delimitation of *Leccinum. Ceská Mykologie* **43**: 1-12.

Sutara, J. (1991). *Pseudoboletus*, a new genus of Boletales. *Ceská Mykologie* **45**: 1-9.

Sutara, J. (1992). Rody *Paxillus* a *Tapinella* ve strední Europe. *Ceská Mykologie* **46**: 50-56.

Sunhede, S (1989). Geastraceae (Basidiomycotina). *Synopsis Fungorum* **1**: 534.

Szczepka, M.Z.,& Sokó. (1984). *Buchwaldoboletus lignicola* (Kallenb.) Pilát and *Phaeolus schweinitzii* (Fr.) Pat. – das Problems ihres gemeinsamenAuftretens. *Zeitschrifte für Mykologie* **50**: 95-99.

Talbot P. (1973). Basidial morpholgy and hymenophoral development in *Rhizopogon. Persoonia* **7**: 339-350.

Taylor A.F.S., Hills, AE., Simonini, G., Both, E.E., Eberhardt, U. Detection of species within *Xerocomus subtomentosus* complex in Europe using rDNA-ITS sequences *Mycological Research* **110**: 276-287.

Taylor, A.F.S., Jonsson, L., Jonsson, M., Rosling, A., Hills, A& Simonini, G. (2001). Species delineration within the European Species of *Xerocomus* using Internal Transcribed Spacer Sequence Data. *Micologia e Vegetazione mediterranes* 16: 171-192.

Trappe, J.M. (1975). A Revision of the Genus *Alpova* with notes on *Rhizopogon* and the Melanogastraceae. *Beihefte Nova Hedwigia* **51**: 279-309.

Theirs, H.D. (1969). Studies in the genus *Gastroboletus. Brittonia* **21**: 244-254.

Thiers, H.D. (1975). *California Mushrooms. A field guide to the Boletes*. Hafner Press, New York, USA, 261pp.

Theirs, H.D. (1975). The status of *Sullus* in the United States. *Beihefte Nova Hedwigia* **51**: 247-278.

Thiers, H.D. (1989). *Gastroboletus* revisited. *Memoirs of the New York Botanical Garden* **49**: 355-359.

Thiers, H.D. & Trappe, J. M. (1969). Studies in the genus *Gastroboletus. Brittonia* **21**: 244-254.

Thomas, S.R., Dunstan, W.A., Dell, B., Trappe, J.M. & Maljczuk, N. (2003). *Pisolithus hypogaeus sp. nov*.; a hypogeous representative of the genus *Pisolithus* from Western Australia. *Mycotaxon* **87**: 405-410.

Trappe, J. M., Watling, R., Cázares, E. & Claridge, A. W. (2003). Australasian Sequestrate Fungi 16: *Gastrotylopilus*, a synonym of *Fistulinella. Muelleria* **18**: 75-77.

Vasil'kov, B.P. (1956). Conspectus systematicus *Krombholziae aurantiacae* (Roques) Gilb. et huis formarum in URSS inventarum. *Proceedings of the Komarov Botanical Institute of the Academy of Sciences of the USSR* **10**: 369-373.

Vasil'kov, B. P. (1966). *Belyy Grib (Boletus edulis)*. Nauka Publishing House, Moscow-Leningrad, USSR. 132 pp.

Wakefield, E.M. (1918). New and rare British Fungi. *Kew Bulletin (1918)*: 229-233.

Wakefield, E. M. & Pearson, A. A. (1920). Records of Surrey Resupinate Hymenomycetes. *Transactions of the British Mycological Society* **6**: 317-321.

Wasser, S.P. (1972). *Paxillus zerovae* S.Wasser *sp.nov.* (Boletales) – A New Species from Steppe Zone of the Ukrainian SSR. *Ukrayins'kyi Botanichnyi Zhurnal* **30***:* 667-668.

Watling, R. (1969). The genus *Paragyrodon. Notes of the Royal Botanic Garden, Edinburgh* 29: 67-73.

Watling, R. (1975). From infancy to Adolescence: Advances in the study of Higher Fungi. *Transactions of the Botanical Society of Edinburgh* 42 (Suppl.): 61-74.

Watling, R. (2001). Australian boletes: their diversity and possible origins. *Australian Systematic Botany* **14**: 407-416.

Watling, R. (2001). The relationships and possible distributional patterns of boletes in south-east Asia. *Mycological Research* **105**: 1440-1448.

Watling, R. (2002). One Bolete genus or ?. *Field Mycologist* **3**:84-88

Watling, R. (2006). The Sclerodermatoid fungi. *Mycoscience* **47**: 18-24.

Watling, R. & de Mejer, A. (1997). Macromycetes from the State of Paraná, Brazil - 5. Poroid and lamellate boletes. *Edinburgh Journal of Botany* **54**: 231-251.

Watling, R. & Gregory, N.M. (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. Proceedings of the Royal Society of Queensland* **99**: 65-76

Watling, R. & Grgory, N.M. (1989). Ditto. Part 2C - Smooth-spored taxa of the Strobilomycetaceae. *Proceedings of the Royal Society of Queensland* **100**: 13-30.

Watling, R. & Gregory, N.M. (1991). Ditto. Part 3 - Lamellate taxa. *Edinburgh Journal of Botany* **48**: 253-281.

Watling, R. & Hills, A.E. (2005). *British Fungus Flora: Agarics and Boleti 1. Boletes and their allies*. New & Revised edition, Royal Botanic Garden. Edinburgh, Scotland, UK. 173pp.

Watling, R., Lee, S.-S & Turnbull, E. (2007). Notes Taxinomiques et Floristiques sur quelques Bolets tropicaux et groupes proches. *Bulletin de Sociéte mycologique de France* **122** (2006): 327-352.

Watling, R. & Sims, K. (2004). Taxonomic and floristic notes on larger Malaysian fungi. IV. Scleroderma. *Memoirs of the New York Botanical Garden* **89**: 93-96.

Watling, R., Taylor, A., Lee, S.S. & Alexander, I. J. (1995). A rainforest *Pisolithus*; its taxonomy and ecology. *Nova Hedwigia* **61**: 417-429

Wittmann-Meixner, B. (1989). Polyploidie bei Pilzen. *Bibliotheca Mycologica* **131**:

Wolfe, C.B. (1979). *Austroboletus* and *Tylopilus* subgenus *Porphyrellus*. With emphasis on North American Taxa. *Bibliotheca Mycologica* **69**: 1-136.

Wolfe, C.B. (1981). Type studies in *Tylopilus* I. Taxa described by Charles H. Peck. *Sydowia* **34**: 199-213.

Wolfe, C.B. (1981). Nomenclature and taxonomy of the tribe Ixechineae (Boletaceae). *Taxon* **30**: 36-38.

Wolfe, C.B. (1982). A taxonomic evaluation of the generic status of *Ixechinus* and *Mucilopilus* (Ixechineae, Boletaceae). *Mycologia* **74**: 36-43.

Wolfe, C.B. (1983). Type studies in *Tylopilus* II. Species described by William A. Murrill. *Mycologia* **75**: 699-706

Wolfe, C.B. (1983). Taxonomic and nomenclatural notes on Boletes. *Mycotaxon* **17**: 398-404.

Wolfe, C. B. (1984). Numerical taxonomic analysis of Tribe Ixechineae (Boletaceae). *Mycologia* **76**: 140-147.

Wolfe, C.B. (1986). Type studies in *Tylopilus* III. Taxa described by Walter H. Snell, Esther A. Dick and co-workers. *Mycologia* **78**: 22-31.

Wolfe, C.B. (1986). A numerical analysis of *Tylopilus* subgenus *Porphyrellus* (Boletaceae). *Nova Hedwigia* **43**: 515-523.

Wolfe, C.B. (1987). Studies in the genus *Xanthoconium* (Boletaceae). I. New species and a new combination. *Canadian Journal of Botany* **65**: 2142-2146.

Wolfe, C.B. (1988). Studies in the genus *Xanthoconium* (Boletaceae). II Type studies I. *Canadian Journal of Botany* **66**: 2134-2138.

Wolfe, C. B. (1989). Studies in the Genus *Xanthoconium* (Boletaceae). III. Cultural studies. *Mycotaxon* **35**: 75-84.

Wolfe, C.B. (1990). Type studies in *Tylopilus* IV. Taxa described by Rolf Singer. *Mycotaxon* **38**: 187-200.

Wolfe, C.B. & Bougher, N.L. (19934). Systematics, Mycogeography, and Evolutionary History of *Tylopilus* subg. *Roseoscabra* in Australia elucidated by comparison with Asian and American species. *Australian Systematic Botany* **6**: 187-213.

Wolfe, C.B. & Petersen, R.H. (1978). Taxonomy and nomencalature of the supraspecific taxa of *Porphyrellus. Mycotaxon* **7**: 153-162.

Wolfe, C.B., Singer, R. & Walsh, A. (1988). Notes on Neotropical *Austroboletus* species. *Mycologia* **80**: 46-53.

Yang, Z.L., Trappe, J.M., Binder, M., Sanmie, R., Lumyong, P. & Lumjong, S. (2006). The sequestrate genus *Rhodactina* (Boletales) in northern Thailand. *Mycotaxon* **96**: 129-132.

Zang, M & Zang, X. (1978). A Preliminary study of the family Paxillaceae of Yunnan and Tibet, China. *Acta Microbiologica Sinica* **18**: 279-286.

Zeller, S.M. (1914). Development of carpophores of *Ceriomyces zelleri*. *Mycologia* **6**: 235-239.

Zeller, S.M. (1934). *Protogaster* representing a new Order of the Gasteromycetes. *Annals of the Missouri Botanical Garden* 21: 231-240.

Zeller, S.M. (1939). Developmental Morphology of *Alpova. Oregon Monographic Studies in Botany* 2: 1-19.

Zeller, S.M. (1948). Notes on certain Gasteromycetes including two new orders. *Mycologia* **40**: 639-668.

Zeller, S.M. (1949). Keys to orders, families, and genera of the Gasteromycetes. *Mycologia* **41**: 36-58.

Zeller, S.M. & Dodge, C.W. (1918). *Rhizopogon* in North America. *Annals of the Missouri Botanical Garden* **5**: 1-36.

Zeller, S.M. & Dodge, C.W. (1937). *Melanogsster. Annals of the Missouri Botanical Garden* 23: 639-655.

Zeller, S.M. & Walker, L. B. (1937). *Gastrella*, a new uniloculate Gasteromycete. *Mycologia* **27**: 573-579.

PLATES:

Legends to Plates

Abb. h-s = habit sketch; sect. = section of basidiome; sp. = basidiospore; cheilo. = cheilocystidium (-a); pleuro. = pleurocystidium (-a); cystid. = cystidium (-a)

Plate 1. A. *Afroboletus luteolus* – Tanzania, East Africa: h-s, sect & sp. (10.5-14 x 8.5-11 µm; ridges , 1.5 µm high). B. *Amogaster* sp. (9-14 x 4-6 µm). after Castellano. C. *Alpova* – Oregon, Western North America: sp. (4-5.5 x 2-3 µm). D. *Astraeus hygrometricus* – Southern England, British Isles: h-s dry and moist & sp. (9-11.5 µm diam.). E. *Aureoboletus gentilis* – Berkshire, Southern England, British Isles: h-s., sect, sp. (10-14 x 4.5-6 µm) & cheilo. F. *Austroboletus* – all Australia: *A. dictyotus* h-s., sect., sp. (13-16 x 7-8.5 µm) compared with extreme forms.

Plate 2. A. *Austrogaster* sp. (12.5-15 x 6-7 µm) from Horak. B. *Austropaxillus infundibuliformis* – New South Wales, Eastern Australia: h-s., sect. & sp. (11-13 x 5-6 µm). C. *Boletellus* (1) *B. emodensis* – Queensland, Eastern Australia; h-s of 2 basidiomes in stages of development, sect. & sp.(17-19 x 6-7 µm) including *B. ananus*. D. *Boletellus* (2). *B. obscureococcineus* – Perth, Western Australia; h-s., sect. & sp. (14.5-17 x 6-7µm).

Plate 3. A. *Boletinellus merulioides* – Michigan, Mid-west, North America; h-s., sect. & sp. (7-10 x 6-7.5µm). B. *Boletus* (1) *B. edulis* – Peebles, Scotland, British Isles; h-s. showing reticulate stipe, sect. & sp. (14-18 x 4-5.5 µm). C. *Boletus* (2) *B. luridiformis*, Peebles, Scotland, British Isles; h-s showing punctate scurfy stipe & sp. D. *Bondarcevomyces* after Dai & Niemela; h-s. & sp. (4.5-5 x 2-3.5 µm). E. *Brauniellula nanycae* – Orgeon, North America; h-s., 2 sect. & sp. (16-20 x 6.5-9 µm).

Plate 4. A. *Buchwaldoboletus* (1) *B. lignicola* – Argyllshire, Scotland, British Isles; h-s., sect. & sp. (6.5-8 x 3-4.5 µm). B. *Buchwaldoboletus* (2) *B. sphaero-cephalus* – Hampshire, Southern England, British Isles; h-s., sect. & sp. (5.5-8 x 3-4.5µm). C. *Calostoma cinnabarina* h-s. & sp. (13-15 x 8-10 µm) Virginia, Eastern North America & *C. lutescens* h-s. & sp. (6-8µm diam.). D. *Bothia castanella* – Pennsylvania, Eastern North America; h-s., sect & sp. (7.5-10 x 4-5 µm). E. *Chalciporus piperatus* – Perthshire, Scotland, British Isles; h-s., sect., sp. (9-11 x 3.5-4 µm) and cheilo. F. *Chamonixia caespitosa* – Orgeon, Western North America; sp. (18-22 x 13-15 µm) & sect of primordia after Clémençon demonstrating early bolete-like structure.

Plate 5. A. *Chlorogaster*; h-s., sect. & sp. (14-17.5 µm diam.) after Jalink & Laessφe. B. *Chroogomphus rutilus* – Inverness-shire, Scotland British Isles; h-s, sect., sp. (15-22 x 5.5-7 µm). & pleuro. C. *Chrysoconia*; sp. (11-14 x 7-8 µm) after McCabe & Escobar. D. *Coniophora puteana* – Yorkshire, Northen England, British Isles; sp. (10-13 x 7-8 µm), multi-clamped & ornamented hyphae. E. *Coniophoropsis*; sp. (15-18 x 7.5-9µm) after Hjortstam & Ryvarden. F. *Corditubera* sp.– Cameroon, West Africa; sp. (7.5-10 µm diam.).

Plate 6. A. *Corneromyces*; hyphal peg & sp. (24-28 x 7-10 µm) after Ginns. B. *Cystogomphus*; h-s., sect., sp. (18-26 x 6-7 µm). & cyst. from Horak. C. *Diplocystis*; sp. (4-5.5µm diam.) & h-s. after Kriesel & Lloyd respectively. *Fistulinella*; see Plate 10E. *Gastroboletus turbinatus* – California, Western North America; h-s., sect. & sp. (13.5-18 x 6.5-9.5 µm).

Plate 7. A. *Gastroleccinum scabrosum* – Michigan, Mid-west North America; h-s., sect. & sp. (15-18.5 x 4-5 µm). B. *Gastrosuillus* – California, Western North America; h-s., sect. & sp. ((7-10 x 2.5-4 µm). C. *Gomphidius glutinosus* – Perthshire, Scotland, British Isles; h-s., sect., sp. (18-22 x 5-6.5 µm) & pleuro. D. *Gomphogaster*; sp. (17-22 x 8.5-10 µm) & cystid. after Miller. E. *Gymnopaxillus*; h-s., sect. & sp. (12-15 x 5-6 µm) after Horak.

Plate 8. A. *Gyrodon lividus* – Yorkshire, Northern England, British Isles; h-s., sect. & sp. (5-6.5 x 4-4.5 µm). B. *Gyroporus cyanescens* – Inverness-shire, Scotland, British Isles; h-s. showing hollow stipe, sect., sp. (8-11 x 5-6 µm). C. *Gyrodontium versicolor* – Selangor, Malaysia; h-s., sect. & sp. (4.5-6 X 3-3.5 µm). D. *Hiemisoporus retisporus* – Negri Sembilan, Malaysia; h-s., sect. & sp. (11.5-13 x 9-10 µm), one enlarged demonstrating ornamentation. E. *Horakiella* sp. – Negri Sembilan, Malaysia; sp. (30-35 x 25 –30 µm).

Plate 9. A. *Hydnomerulius* - h-s., sect. & sp. (5-6.5 x 3.8-4.5 µm) after Ginns & Weresub. B. *Hygrophoropsis aurantiaca* – Midlothian, Scotland, British Isles; h-s., sect. & sp. (5.5-7.5 x 3.5-4.5 µm). C. *Ixechinus viridis* s. Corner – Selangor, Malaysia; h-s., sect. & sp. (13-17 x 4-5 µm). D. *Jaapia ochroleuca* – herbarium material; cyst. & sp. (10-19 x 4.5-7 µm). E. *Leccinum* (1) *L. aurantiacum* - Aberdeenshire, Scotland, British Isles; h-s, sect. sp. & caulo. F. *Leccinum* (2) *L. scabrum* - Perthshire, Scotland, British Isles; h-s., sect., sp. (12-15 x 3.5-4 µm) & caulo. G. *Leccinellum crocipodium* – Berkshire, Southern England, British Isles; h-s, sect. & sp. (14-18 x 6-7 µm).

Plate 10. A. *Leucogyrophana mollusca* – Midlothian, Scotland, British Isles; h-s., sect. & sp. (6-7.5 x 4-5 µm). B. *Meiorganum neocaledonicum* – Selangor, Malaysia; h-s., sect. & sp. (3.7-4.3 x 2.7-3 µm). C. *Melanogaster ambiguus* – Orkney, Scotland, British Isles; sp. ((14-20 x 8-10.5 µm). D. *Octavaniana asterosperma*; sp. (10-12.5 x 9.5-11µm; spines < 3µm) herbarium material from SW Scotland, British Isles. E. *Fistulinella mollis* – Queensland, Australia; h-s., sect., & sp. (12.5-16 x 4-5 µm). F. *Paragyrodon sphaerosporus* – Michigan, Mid-west, North America; h-s., sect., & sp. ((7-10 x 6-8 µm). G. *Paxillogaster*; h-s., sect. & sp. (11-14 x 5-5.5 µm) after Horak.

Plate 11. A. *Paxillus involutus* – Midlothian, Scotland, British Isles; h-s., sect., sp. (8-10 x 5-7 µm). & pleuro. B. *Phlebopus marginatus* – Thailand, South East Asia; h-s., sect. & sp. (7.5-10 x 5-7.5 µm). C. *Phylloboletellus*; sp. (10.5-12.5 x 8.5-10 µm) after Horak. D. *Phylloporus pelleteri* – Yorkshire, Northern England, British Isles; h-s., sect. & sp. (10-13 x 3.5-4.5 µm). E. *Pisolithus arhizus* – Berkshire, Southern England, British Isles; h-s., sect. & sp. (8-12 µm diam.).

Plate 12. A. *Podoserpula pusio* – Perth, Western Australia; h-s., sect. & sp. (3.5-4 x 3-3.5 µm). B. *Porphyrellus porphyrosporus* – Yorkshire, Northern England, British Isles; h-s., sect. & sp. ((15-20 x 5.5-9 µm). C. *Pseudoboletus parasiticus* – Yorkshire, Northern England, British Isles; h-s., sect. & sp. (11-18 x 4-5 µm). D. *Pseudogyrodon*; h-s. & sp. (6-9.5 x 7.5-8 µm) after Heinemann & Rammeloo. E. *Pulveroboletus ravenelii* – Michigan, Mid-west North America; h-s., sect., sp. (9-11 x 4.5-5.5 µm) & young primordium enlarged. F. *Pseudomerulius aureus* h-s., sect. & sp. (3.5-4.5 µm) from herbarium material.

Plate 13. A. *Retiboletus ornatipes* – Michigan, Midwest North America; h-s., sect., sp. (11-14 x 3.5-4.5 µm) & caulo. B. *Rhizopogon luteolus* – Inverness-shire, Scotland, British Isles; h-s., sect. & sp. (5.5-7.5 x 2.5-3 µm).C. *Rhodactina*; h-s. & sp. (11-16 x7-10µm; ornament. < 4µm) after Pegler & Young. D. *Royoungia*; sp. (11-2.5 x 5-6 µm) after Castellano *et al.* E. *Rubinoboletus rubinus* – Berkshire, Southern England, British Isles; h-s., sect. & sp. (5.5-9 x 4-5 µm). F. *Scleroderma* (1). *S. citrinum*; h-s., & sp. (10-13 µm diam.), Midlothian, Scotland, British Isles. G. *Scleroderma* (2). *S. verrucosum*; h-s. & sp. (9-11 µm diam.), Yorkshire Northern England, British Isles..

Plate 14. A. *Serpula lacrimans* – Midlothian, Scotland, British Isles; h-s showing rhizomorphs, sect., sp. (11-13 x 5.5-8 µm) & cystid. B. *Setogyroporus*; h-s., sect., cystid., setae & sp. (5.5-7 x 3.6-4.8 µm) after Heinemann & Rammeloo. C. *Singeromyces*; h-s. & sp. (10.5-14 x 5.2-7 µm) from Horak. D. *Strobilomyces strobilaceus* – Perthshire, Scotland, British Isles; h-s., sect. & sp. (11-14 x 9-12 µm): E *S. confusus* – Pennsylvania, Eastern North America; sp. (10.5-12,5 x 9.5-10.5 µm) & *S. velutipes* – Selangor, Malaysia, South East Asia; sp. (8-10 x 6-8 µm).

Plate 15. A. *Suillus* (1). *S. luteus* – Inverness-shire, Scotland, British Isles; h-s., sect., sp. (7-9.5 x 2.5-3.5 µm), fasciculate cheilo. & caulo. B. *Suillus* (2) *S. granulatus* – Peebleshire, Scotland, British Isles; h-s showing absence of veil glandular & dottted stipe & *S. albovelatus* – Idaho, Western North America; sect. showing marginal velar roll. C. *Tapinella panuoides* – Aberdeenshire, Scotland, British Isles; h-s., sect. & sp. (4.5-6 x 3-4 µm). D. *Tremellogaster* h-s & sp. (5-6.5 x 4-5 µm) after Linder. E. *Truncocolumella citrina* – Orgeon, Western North America; h-s., sect. & sp. (6.5-9.5 x 3.5-5 µm).

Plate 16. A. *Tubosaeta calocystis* – Zambia, East Africa; h-s., sect., setae & sp. (10-13 x 4.5-5.5 µm). B. *Tylopilus felleus* – Yorkshire, British Isles; h-s., sect. & sp. (11-15 x 4-4.5 µm). C. *Veloporphyrellus africanus* – Zambia, East Africa; h-s., sect., sp. (11.5-13.5 x 3-4.5 µm) & section of young primordium of *V. pantoleucus* after Singer.

Plate 17. A. *Wakefieldia* sp. - Malaysia, South East Asia; sp. (12-15 µm diam.). B. *Xanthoconium affine* – Michigan, Midwest North America; h-s., sect. & sp. (12-16 x 3-5 µm). C. *Xerocomus* (1). *X. subtomentosus* – Perthshire, Scotland, British Isles; h-s., sect., pileal elements & sp. (9.8-14.8 x 3.9-6 µm). D. *Xerocomus* (2). *X. chrysenteron* – Peebleshire, Scotland, British Isles; h-s., sect., pileal elements & sp. (11.8-16.6 x 4.8-6.8 µm). E. *X. porosporus* – Midlothian, Scotland, British Isles –sp. (11.4-17.2 x 4.5-6.5) & *X. ripariellus* – Hampshire, Southern England, British Isles; sp. (11.3-14.5 x 3.5-5.2 µm).

INDEX

Families discussed in Notes; see classification for main families

Genera
(Generic and specific names in italics are considered synonyms or are rejected; those not in bold are accepted names. Those in bold are accepted genera and type species. Bold numerals indicate the site for the generic description)