

NOTES ON BOLETE TAXONOMY—III

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Contributions involving bolete taxonomy during the last ten years have not only widened the knowledge and increased the number of species in the boletes and related lamellate and gastroid forms, but have also introduced a large number of new data on characters useful for the generic and subgeneric taxonomy of these fungi, resulting, in part, in new taxonomical arrangements. It is therefore timely to consider these new data with a view to integrating them into an amended classification which, if it pretends to be natural must take into account all observations of possible diagnostic value. It must also take into account all sufficiently described species from all phytogeographic regions.

I. CLAMP CONNECTIONS

Like any other character (including the spore print color), the presence or absence of clamp connections in the carpophores is neither here nor in other groups of Basidiomycetes necessarily a generic or family character. This situation became very clear when occasional clamps were discovered in *Phylloboletellus* and numerous clamps in *Boletellus fibuliger*. Kühner (1978-1980) rightly postulates that cytology and sexuality should be considered wherever at all possible. This, as he is well aware, is not feasible in most boletes, and we must be content to judge clamp-occurrence per se, giving it importance wherever associated with other characters and within a well circumscribed and obviously homogeneous group such as *Phlebopus*, *Paragyrodon*, and *Gyrodon*. (Heinemann (1954) and Pegler & Young (1981) treat this group on the family level.) *Gyroporus*, also clamp-bearing, is considered close, but somewhat more removed than the other genera. On the other hand, clamp connections observed by me in the stipe covering of *Leccinum*, a single species of *Boletellus* and the genus *Phylloboletellus* (mostly false or incomplete clamps) are no more than specific characters since the respective specimens do not differ by any other diagnostic character from their congeners. The best and most easily applicable character of the genera *Psilobolletinus* and *Boletinus* is the constant presence of numerous clamp connections in the carpophore hyphae and the base of the basidia, here generally linked with a hollow stipe. The fact that in some *Suillus* species clamp connections occur in mycelial cultures is, with this definition and application, just as in *Chroogomphus*, taxonomically irrelevant. However,

the occurrence of rare clamp-less carpophores in common species of *Gyroporus* such as *G. castaneus* (Heinemann & Rammeloo, 1979) or *G. subalbellus* (Singer, 1977) should be explained cytologically. Until that has been accomplished, my strictly tentative explanation suggesting parthenogenesis is perfectly valid inasmuch as the fact that Heinemann had difficulties in finding clamp connections in some Gyrodontoideae is no proof of their absence or rarity. (In a specimen of *P. sudanicus* described by Heinemann as having non-clamped hyphae, we have found numerous clamp connections as in all other specimens of that species.) Species described as *Gyroporus* but constantly clampless are in my opinion misplaced. Heinemann & Rammeloo (1979) quote Watling & Largent (1977) for their opinion that 'it has now been established that the occurrence of clamp connections has no value at the generic level in the case of *Gyroporus*' whereas what these latter authors really say is: 'It is true members of the genus *Gyroporus* possess clamp connections.' They dedicate a few paragraphs only to bolete anatomy without making any new contributions, but surprisingly in a (phylogenetic?) scheme (p. 594) put clamp-bearing genera at the end of each series (cf. Chapter 8).

This is not to say that in any genus generally characterized by the presence of clamp connections, clampless forms will never be discovered. But we can classify only what has been discovered. If, on the other hand, we go so far as to neglect clamp connections we are close to the point where Smith & Thiers (1977) seem to have arrived who include the clamped boletes (excluding *Gyroporus*) in *Suillus*, even *Gyrodon*. As soon as anybody gives some emphasis to an important character like clamp connections or amyloidity of the spores, there will always be those who deduce from the fact that the character is not important in other groups the license for dropping the character as generally unimportant.

2. DEVELOPMENTAL STUDIES

Thanks to the important and interesting studies on carpophore development from the primordium to the adult stages by Reijnders (1968) and discussed by Arpin & Kühner (1977), we have now some data on bolete development, especially for the genus *Suillus*. Reijnders describes for the one genus *Suillus* the development as either gymnocarpic (*S. bovinus*) pilangiocarpic (*S. variegatus*, *S. placidus*, *S. granulatus*, *S. americanus*, *S. spectabilis*), probably pilangiocarpic (*S. pictus*), mixangiocarpic (*S. luteus*, *S. aeruginascens*), probably mixangiocarpic (*S. grevillei*). Since these distinctions do not coincide with generic separations nor even with sectional characters in any modern treatment, nor with pigment-chemical investigations (see below), we can hardly give them more than specific significance inasmuch as all other boletes show, in one or another species, the same development as either one of the *Suillus* species or one of the *Xerocomus* species. In *Xerocomus*, we find in one section (*Parasitici*) an additional type of development viz. hypovelangiocarpic in Reijnders's terminology, as had already been pointed out by me 1945 (Singer, 1977), most or all of the others being gymnocarpous. Gomphidiaceae, in general, are metavelangiocarpic (in contrast to *Suillus* which many authors consider closely allied to *Gomphidius*), and *Strobilomyces* and *Gyroporus* are 'probably metavelangiocarpic' (Reijnders, 1968).

Unfortunately, one knows the type of development in only one species of *Boletellus*, viz.

B. zelleri which is gymnocarpic. The supposed marginal veil of *Boletellus ananas* (often spelled *ananas* by European authors), present only in the type section of the genus, and not as Arpin & Kühner suppose, in all species, does not necessarily reveal another type of primordial development. This is best illustrated by Corner's description and illustration of the development of *B. longicollis* Ces. (*Boletellus singaporensis* (Pat. & Baker) Sing.) where the glutinous layer in his youngest carpophore seems to be continuous and the membranous layer merely an extension of the margin of the pileus apparently attached to but easily separable from the stipe and sheathing only the apex. The same situation, but without the glutinous layer, seems to represent the development of *B. ananas* (Corner, 1972: 95) which, however, in the sense of Corner, is certainly related but not identical with the American type, provided it is described correctly. Although Corner may not have had the opportunity to study sufficiently young stages of *Boletellus*, it is rather probable that here we have development types ranging from gymnocarpous to partly pseudoangiocarpous or at least partially velangiocarpous ('angiocarpie primaire'). The development of *Strobilomyces* and *Gyroporus* seems to be not fully explored.¹ According to the drawing of *P. ravenelii* in Corner (1972: 201) one would add the latter to the species which are 'probably metavelangiocarpic.' Yet, this is not related to either *Strobilomyces*, or *Gyroporus*, or for that matter, to the Gomphidiaceae.

Neither is the development of the Paxillaceae (even if restricted to *Paxillus*) uniform or analogous with that of the Boletaceae inasmuch as the veiled species (sect. *Parapaxillus* and *Phyllobolites*) are still waiting for competent embryological research.

Ontogenetic data of Boletineae are therefore at present not automatically useful for generic and suprageneric taxonomy. On the other hand, I believe that a fuller investigation of this aspect of bolete studies will in the end be shown to have some significance in the taxonomy of the rough-spored genera of boletes, in the Gyrodontoideae including *Gyroporus*, in *Gastroboletus*, the sections of such genera as *Xerocomus* and *Pulveroboletus*, and *Paxillus* sect. *Parapaxillus*.

Supplementary to the developmental approach, a discussion of the situation in *Gyroporus* is necessary. Although we have no comparable data on *Paragyrodon*, *Gyroporus* would seem to stand out by its metavelangiocarpic development, which Kühner had previously assumed to be gymnocarpic (which would have approached *Gyroporus* to *Gyrodon*.) But there is another indication much exaggerated by some (Arpin & Kühner, 1977; Corner, 1972) that seemingly enhances the hiatus between *Gyrodon* and *Gyroporus*, viz. the structure of the stipe rind. This indication was originally an elaboration of Reijnders's finding that the stuffed interior of the stipe of *G. cyanescens* shows a surprising number of hyphae running horizontally. The rind itself is described as interwoven ('hyphes . . . emmêlées') in an early stage and remaining so for a long time. Reijnders (1968) explains this structure as a consequence of the hollowing by expansion observed in the stipe, accompanied by an outer veil layer strictly appressed to the cortex of the stipe and of similar structure. It is Corner (1972) who adds that he recognizes *Gyroporus* as a genus not (in contrast to Arpin & Kühner)

¹ But Heim assured us that *Strobilomyces* is 'Réellement angiocarpe' (*In Revue Mycol.* 30: 327. 1966), apparently judging from his observations on African material.

because of its spore color or the presence of clamp connections but because the stipe is not longitudinally fissile and not constructed by longitudinal hyphae but splitting transversely and being constructed by hyphae that have grown transversely round and across the longitudinal axis. This statement is apparently not based on Reijnders's careful observations but on observations on the Malaysian species *G. malesicus* (where the transversal fissibility of the stipe may have something to do with the series of vertically superimposed cavities in the specimen illustrated which is the smallest known in *Gyroporus*). The stipe sections (a and b, p. 55) do not prove transversal arrangement of the surface hyphae of the stipe. As for other species of *Gyroporus* Corner merely states that 'several species ascribed to *Gyroporus* may not belong because their stems appear to be longitudinally scissile e. gr. *G. atroviolaceus*', a species I have studied and find to belong to *Gyroporus* (Singer, 1977). Arpin & Kühner (1977) merely translate Corner's statement and imply that it is valid also for *G. cyanescens* and *G. castaneus*, not commenting on the extra-European species *G. malesicus* and *G. atroviolaceus*.

Do then the anatomical features of the type of *Gyroporus* really agree with Corner's characterization? According to my own observations, I agree with Arpin & Kühner that the consistency of the stipe rind is undoubtedly due to a special structure, but this structure is not the one described by Corner. In *G. castaneus*, for example, longitudinal and transverse sections of the stipe show that the interior layer of the stipe trama is influenced by the horizontal pull exercised by the widening of the stipe which leads to horizontal stretching of some hyphal strands. This stretching causes air spaces to appear between hyphal strands and single hyphae, and finally these dissociate to such a degree that the cavity results whereby many of the remaining hyphae collapse. Further towards the stipe surface we find a rather thin layer of tissue which is composed of two elements (1) longitudinally arranged hyphae and strands of hyphae running vertically and parallel with each other or almost so, intermingled with (2) strongly interwoven, irregularly arranged hyphae. This structure is a result of the intermingling of the interwoven hyphae (growing at first almost horizontally outwards as in most boleti) of the external velar layer with the longitudinal-vertical hyphae of the subjacent rind layer. For reasons of a somewhat different development as compared with other hollow-stemmed boletes (*Boletinus*, *Pulveroboletus*), this structure of *G. castaneus* is not exactly the same as in the other genera where in the stipe context longitudinal hyphae predominate. A supplementary analysis of the stipe anatomy in *G. cyanescens* and *G. purpurinus*, showed me an analogous picture, only that in *G. cyanescens*, with a more extensive original velar layer, the prevalence of interwoven hyphae is stronger. These data complement those given by Reijnders and contradict those provided by Corner. Whether the stipe is longitudinally fissile or not seems to depend on the prevalent stretching direction of the stipe tissue, the thickness of the rind layer compared with the velar layer, and possibly the extension of the cavity or cavities at a certain stage of development. The position of the genus *Gyroporus* side by side with *Strobilomyces* is highly unsatisfactory, even if the type of development in both genera is supposed to be the same.

3. CHEMOTAXONOMY

The recent studies on the chemistry of the bluing boletes and the various pigments found in Boletineae and related families represent a definite progress in chemotaxonomy and may serve, in many cases, for a better definition of taxa, and also for the discussion of affinities between families and orders (suborders). With Kögl & al. (1924–30) and Gabriel (1965) as fore-runners, Edwards and his collaborators (1967), especially Bresinsky and his collaborators (Besl, 1981; Besl & al, 1973, 1975, 1977, 1978; Bresinsky, 1974; Bresinsky & al. 1970, 1971, 1974, 1979; Steglich & al, 1968, 1969, 1970, 1971, 1977), and also Gaylord and collaborators (1971) have contributed a wealth of chemically and perhaps physiologically valuable data which are highly significant for the taxonomist, and provide new arguments for those interested in the phylogeny of the Boletineae and related groups.

On the other hand, a strict application of the principle that all Basidiomycetes — whether they are otherwise similar or not — which contain pulvinic acid derivatives are related, must be made with caution.

(1) The negative statement (i.e. absence of pulvinic acid derivatives) based until 1974 on 25 species examined (Boletineae excluded) might be considered insufficient evidence for the assumption of exclusivity of such substances in 'Boletales'.

(2) Other characteristic groups of pigments, such as carotenoid pigments, telephoric acid and related benzochinones, and muscoglavin have been found to exist much beyond any systematically definable fungus groups, e.g. in Ascomycetes, Phallineae, Cantharellineae, Tricholomataceae (in the case of carotenoids). May not such sporadic occurrences of pulvinic acid derivatives and other pigments thus far known only in the Boletineae also be expected (even though at present not postulated) in other suborders or orders?

(3) The existence of pigments in mycelial cultures but their absence in the carpophores may be interpreted as a biochemically different set of transformations when compared with cases where these same pigments exist in the carpophore alone or in both the carpophore and the mycelium. For a better appreciation of pigment studies in cultures, one may hope for a future interpretation of the transformations of assimilates in the transition phase from the vegetative to the reproductive part of an organism.

With these reservations, one may say that the relations of lamellate and gastroid forms to the boletes have been confirmed by chemotaxonomical data, and the generic taxonomy of the boletes proper should not be judged on anatomical bases alone.

The findings of the Bresinsky group show clearly that *Phylloporus* does not belong in the Paxillaceae but in the Xerocomoideae; this coincides with the chemical and morphological reasons which cause Arpin & Kühner (1977) emphatically to agree with me that *Phylloporus* is very close to *Xerocomus*, in contrast to the statements by Watling (1970) and Smith & Thiers (1971).

It seemed at first that *Boletinus cavipes* is chemically different from *Suillus* in the fact that the first contains large amounts of xerocomic acid, whereas the second does not (Bresinsky & Orendi, 1970). However later analyses showed that xerocomic acid occurs also in a few species of *Suillus*, *S. plorans*, *S. collinitus*, and *S. sibiricus* (Besl & Bresinsky, 1977), *S. spectabilis*, *S. serotinus*, *S. grisellus*, *S. grevillei*, *S. hirtellus* ssp. *thermophilus*, and *S. tomentosus*.

Likewise, there is no chemotaxonomic objection to or confirmation of the difference between *Suillus* and *Fuscoboletinus* although Bresinsky & Besl (1979) obviously tend to consider sect. *Larigni* as homogeneous and hope for more enlightenment from an exact determination of the spore print color. I can provide some data for *S. nueschii*: Fresh spore print chestnut with a slight rusty tinge (material from Moravia, *Singer C 5743*, (F) but this may be a further variety of *S. aeruginascens* since it differs from typical *S. nueschii* in unchanging context). *S. aeruginascens* var. *aeruginascens* and var. *bresadolae* have the fresh spore print between 'Vandyke br' and 'English oak', dehydrated 'teakwood' (Maerz & Paul). *S. tridentinus* and *S. grevillei* have an olive tinge when the spore print is quite fresh, e.g. 'buckthorn br' to 'citrine', but on dehydration near 'bure' (Maerz & Paul). This, in combination with the pigment analyses at hand, would indicate that subsection *Megaporini* is well separated from subsect. *Leptoporini* if *S. tridentinus* is transferred to *Leptoporini*, or, because of its intermediate position and the presence of tridentine it may be considered as typical for a third subsection. *Fuscoboletinus weaverae* and *S. caerulescens* belong in my opinion to sect. *Suillus*, the first showing that fuscoboletinoid spore colors occur also in species with glandular dots on the stipe, the second showing that the lack of known pigments (Bresinsky & Besl, 1979) also indicated for *S. borealis*, *S. cothurnatus*, and American *S. luteus* is apparently a characteristic of species of sect. *Suillus* (if indeed this finding is a final one). Since the pigment-spectrum of the species united in *Fuscoboletinus* (*F. paluster*, *spectabilis*) is more like that of sect. *Suillus* subsect. *Hirtellini* than that of *F. serotinus* (with gyroporin) or European *S. aeruginascens* we see no relation between dehydrated spore print color and pigments.

Bresinsky & Besl (1979: 260) owe no apology to taxonomists for not being able to show in all cases a clear support for one or the other of the different classifications proposed by Singer (1975) and Smith & Thiers (1971). No single approach will always be decisive. But there are numerous cases where the chemotaxonomical approach does give additional data. The absence of known pigments in *Xanthoconium affine* differentiates this genus from *Boletus* (except *B. griseus* and *B. ornatipes*, both obviously unrelated to *Xanthoconium*). Additional data on the type species of *Xanthoconium* (*X. stramineum*) are unlikely to give different results since the carpophores and mycelium are almost to quite white (pigmentless) in all parts but the spores.

With regard to gyroporin and gyrocyanin it may be said that it tends to support the relatively isolated position of *Gyroporus* at the same time as it shows the chemical affinity of *Chamonixia* since chamonixin differs from gyroporin only in the addition of an OH-group instead of an =O, and consequently confirms the affinity of some hymenogastraceous fungi with the Boletaceae. Gyroporin does however also occur in *S. serotinus*, in traces in *Tylopilus plumbeoviolaceus*, and in mycelial cultures of some species of *Leccinum*, including *L. eximium* recently transferred by me to *Leccinum*. *Leccinum* is undoubtedly another genus where the pigment approach does not lead to results fully parallel with the macro-morphological and anatomical approach. Chemically, *Leccinum* appears to represent a transition between *Boletus* and *Tylopilus* (see below).

I said (Singer, 1975: 744, 750) that 'I am certain that modern pigment analysis will confirm, however, that *Strobilomyces* and *Boletellus* are chemotaxonomically different' and that 'spore sections under E.M. and pigment analyses will eventually decide whether a subfamily

or a family Strobilomycetoideae or Strobilomycetaceae is preferable.' The first of these statements has been clearly decided (Bresinky & Besl, 1979) in the sense expected by me; the second will be discussed later (Chapters 4, 11). Chemotaxonomy would suggest that *Boletellus* is amply different from the other strobilomycetaceous genera except *Phylloboletellus* which seems to have a similar relationship to *Boletellus* as *Phylloporus* has to *Xerocomus*. The former pair has an olivaceous spore print, yellow colors in hymenophore and context, occurrence of clamp connections (one species with numerous clamps — *B. fibuliger*, few and often 'false' clamps in *Phylloboletellus*) as well as either gigantic or ornamented spores in common, aside from a predominantly tropical-subtropical distribution and a bilateral hymenophoral trama of the *Boletus*-type. This is in contrast to *Austroboletus* and *Porphyrellus*, as well as to *Strobilomyces* and *Xanthoconium*, *Tylopilus* and *Fistulinella*, one section or two of *Boletus*, and several species of *Leccinum*. In all these except the last two, the spore print is never olivaceous (fresh, not dehydrated), and all the data now available seem to indicate that there is a certain continuity here which cannot be expressed by separating the genera by spore ornamentation alone. Whether this reflects real affinity (a common ancestor) can now only be assumed, especially with the lack of positive identifications of pigments since the existing but unidentified pigments may in the end be found to be different in different genera.

In *Porphyrellus* sect. *Porphyrellus* tyrosine is converted to DOPA as in *Strobilomyces* and this puts *Porphyrellus* sensu stricto in an intermediate position between the Boletoidae (*Tylopilus*) and the Strobilomycetoideae (*Strobilomyces*), a situation foreseen by me because of the similar chemical color reactions of *Porphyrellus porphyrosporus* and *Strobilomyces floccopus*. 'This lends support to the placement, of *Porphyrellus* by Singer in the family Strobilomycetaceae' (Besl, 1981) inasmuch as before the S.E.M.-studies on the spores of *Porphyrellus*, the transition from smooth-spored Porphyrelli to *Austroboletus* (with ornamented spores) was difficult to break. It is still difficult for Corner (1980) who seems to resent my putting his subgenus *Austroboletus* in synonymy with *Porphyrellus* in 1975 when it was still defined in the wider sense. Since I had no first hand knowledge of *B. dictyotus* (Boedijn) Corner (*Porphyrellus* (!) *dictyotus* Boedijn), I could not insert this species into any of my sections and since Corner's (1972) drawings of the development stages (figs. 25-6) do not compare with the descriptions and photomicrographs by Reijnders and may illustrate other than 'pseudoangiocarpic' development (with truly primordial stages possibly missing, and other species indicated probably being gymnocarpic; about *B. mucosus* Corner see later), the development of the carpophores (Singer, 1975) was indicated as 'unknown'. While Corner indicates as type species of his subgenus *Austroboletus*: *B. dictyotus* (Boedijn) Corner (p. 77), he states on p. 8 'In the modern treatment of this genus [*Porphyrellus*] there are two sections, one with smooth spores (sect. *Porphyrellus*), and the other with ornamented spores (sect. *Graciles* Singer). The first I refer to *Tylopilus* . . . For the second I have made subgen. *Austroboletus* . . .' which would suggest that subgenus *Austroboletus* is based on sect. *Graciles*, and thus on *P. gracilis* (Peck) Sing. Since I now divide *Porphyrellus* sensu lato in *Porphyrellus* s.str. and *Austroboletus* and repress the family Strobilomycetaceae as such, it may seem an academic question to ask why Corner (1980) thinks that *B. dictyotus* does not fit my diagnoses (of *Porphyrellus*), and why *B. longipes* should not key out in Strobilomycetaceae (Singer, 1975: 166) once it is established that it has ornamented spores.

Another field for further chemotaxonomical studies is represented by the genus *Gastroboletus*. Most authors were quick in deciding that that genus is merely an assembly of 'gasteromycetation' forms arising from different bolete genera, yet data on the pigments are available in only one single species, not the type species, nor in any other species. The same holds true for spore analysis. In both cases, we should keep in mind that possibly not all species described are really congeneric with the type and may be retarded forms or misformations of known or unknown Boletaceae. This, however, is certainly not the case in the ecologically best known species, *G. laricinus* (cf. Chapter 11).

Within the Boletaceae we find the genera *Xerocomus*, *Pulveroboletus*, *Chalciporus*, and *Boletus* rather similar in their pigments — a situation to be expected. On the other hand, the separation of *Chalciporus* with variegatorubin as characteristic pigment (Besl, Bresinsky & al., 1975; Bresinsky, 1974; Bresinsky & Rennschmid, 1971; Singer, 1975) from *Suillus* appears justified. The identical pigments of *Pulveroboletus hemichrysus* and *P. auriporus* show that species with dry as well as viscid surfaces can be chemotaxonomically indistinguishable in this genus, justifying both Singer (1975) who put them in two sections of *Pulveroboletus* and Smith & Thiers (1971) who put them in the same section (*Subtomentosi*) of *Boletus*, the former as *B. sphaerocephalus*. This is not in support of Corner (1972) who puts *Pulveroboletus* in three different subgenera of *Boletus* and refers to *Pulveroboletus* (on the basis of frequently erroneous statements and misdeterminations) as a 'dump for species, mostly tropical, which do not fit the alliance of temperate species of subgenus *Boletus*.' May it just be stated here that of the 22 species referred to *Pulveroboletus* by me six are tropical. Chemotaxonomically, the split genera *Aureoboletus* Pouzar (based on *P. gentilis*, closely allied to *P. auriporus*) and *Buchwaldoboletus* Pilát (based on *P. lignicola* — twice misspelled by Corner — closely related to *P. hemichrysus*) should be abandoned unless microgenera are admitted for every section of *Pulveroboletus*. *Pulveroboletus* will be discussed further in Chapters 6 and 9.

There is still much room for chemical work on the species of *Pulveroboletus*. On the other hand, there is no sense in commenting on pigment-studies on rare, odd species which are insufficiently described, like *Phylloporus boletinoides* (spore print color? bluing?) which, if it had clamp connections and incrustated cystidia might well be a *Psiloboletinus*, or, if the anastomoses of the lamellae were less developed might approach *Phylloporus* sect. *Ma-naussenses*. Yet in either case would the chemotaxonomical support be moot. Further studies on *Leccinum* would also be welcome. *Leccinum* is rather easily separated from other boletes by macro- and microscopical as well as ecological-physiological characters, with uniform spore morphology as pointed out correctly by Pegler & Young (1981: 124) but not chemotaxonomically as discussed by Bresinsky & Besl (1979). Their data suggest that chemotaxonomy becomes important as a sectional character whereby for *L. subglabripes* (as the type species) a special section, closer to *Boletus*, should be separated from sect. *Luteoscabra*.

4. ELECTRON MICROSCOPY

Since the separation of the Strobilomycetaceae as a family from other boletes was strongly influenced by the ornamentation of the spores as seen in the light microscope (with only a

few smooth-spored species left in these genera where no other differences could be discovered), it was considered highly interesting to obtain not only scanning electron microscope (S.E.M.) pictures of strobilomycetaceous and related species but also spore sections under electron microscopy (E.M.). This approach has indeed helped to revise some of our earlier assumptions. Since the pigment analyses have shown, as expected, that *Boletellus* (and presumably *Phylloboletellus*) are chemically different from other boletes with ornamented spores (Bresinsky & Besl, 1979), the question comes up whether there are links between *Boletellus* and smooth-spored Boletaceae. Trying to answer this question, modern authors developed two hypotheses contradictory to each other, one attempting to link *Boletellus* with *Boletus*, the other with *Xerocomus*.

Pegler & Young (1971) were the first to show that under the scanning microscope certain Boletaceae have a weak striation on the spores. This refers to one collection of *Xerocomus subtomentosus* where in the basal region of the spore some ridges are visible, but this was not observed in other collections. In *X. truncatus* (= *X. porosporus*) the apex of the spore shows some truncation which reminded Perreau-Bertrand (1961, 1964) of the spore apex of *Boletellus betula*. The truncation of the spores is however visible in many specimens in only about half of the spores of a single carpophore (my own as well as Pouzar's observations) and this *Xerocomus* is so close to *X. chrysenteron* in all other regards that no affinity with *Boletellus* can be seen. Nevertheless, more recent S.E.M.-illustrations (Pegler & Young, 1981: fig. 52) show the *X. truncatus* spore finely longitudinally striate whereas *X. chrysenteron* spores (fig. 53) are shown to be smooth. The striation of the *X. truncatus* spores appears however much finer and lower than that of *X. zelleri* (figs. 50–51). Even if in these cases a misidentification (confusion with the macroscopically similar *B. intermedius*, for example) is excluded, the ornamentations of the Xerocomi are certainly on a different level as compared with those in *Boletellus*. Since the ornamentations of *B. zelleri* and *B. intermedius* are not only quantitatively different from those claimed for *X. subtomentosus* and *X. truncatus* — they are even visible in light microscopy — but are accompanied by a *Boletus*-type hymenophoral trama as opposed to a *Phylloporus*-type in *Xerocomus*, the present evidence points much rather to a hiatus between *X. truncatus* and *X. subtomentosus* on one hand and *B. zelleri* and *B. intermedius* on the other.

In *Boletus* sensu str. Pegler & Young (1971, 1981) show only smooth-spored replicas. The spores are 'remarkably uniform in appearance' which is remarkable inasmuch as *Boletus* shares with *Boletellus zelleri* and *B. intermedius* the structure of the hymenophoral trama. In macroscopical characters *Boletellus* comes close only to section *Subpruinosi* of *Boletus*.

Since Pegler & Young's (1981) classification is derived basically from spore morphology it is not surprising that a different ornamentation such as we have in *Boletellus* sect. *Retispori* (*Heimiella*) as compared with that of the remaining species, or the different ornamentation of *Afroboletus* as compared with that of sect. *Strobilomyces* has led the authors to recognize the genera *Heimiella* and *Afroboletus*, and to transfer *B. betula* to *Austroboletus*, which is classified in another family in Pegler & Young's scheme. Fortunately this transfer is modified by the remark 'The olivaceous tint of the spores raises the possibility that this species may have a closer relationship with Boletaceae than with Strobilomycetaceae.' Here, again, a different genus concept (i.e. smaller than mine and infinitely smaller than Kühner's) may permit the introduction of smaller generic split groups, but in the case of

Afroboletus and *Heimiella* the argument based on phytogeography does not hold since representatives of both have also been found in the neotropics (Singer & al., 1981). With regard to *B. mirabilis* and *B. projectellus*, the spore measurements given by different authors (Pegler & Young, 1981; Singer, 1977; Smith & Thiers, 1971) are in agreement and show spore sizes in these species that earned them the comment (Pegler & Young, 1981) that 'sect. *Mirabiles* differs . . . only in larger spores' (the word 'only' is an exaggeration), and a special subsection in Smith & Thiers's (1971) much emended section *Subtomentosi* of *Boletus* where it is combined with representatives of another subfamily (family for Pegler & Young). In reality sect. *Mirabiles* is intermediate between *Boletus* and *Boletellus* since it has spore size and wall thickness of many *Boletelli*, but the spores are smooth even under S.E.M. If one gives more emphasis to ornamentation, *Mirabiles* may be attached to *Boletus* as a section, but considering the projecting margin and lack of affinity to the species of *Boletus* sensu stricto, I prefer to maintain the section in *Boletellus*. Those who favor microgenera in Boletineae will probably come up with a third, new genus.

The other genera which I considered to belong to Strobilomycetaceae (*Porphyrellus*, *Fistulinella*, *Strobilomyces*) appear to have closer relations to *Tylophilus* than to *Boletus*. Thanks to the studies of Wolfe (1979a, b) it is now clear that the first three genera are sufficiently closely related to each other to be opposed to *Boletellus*, and that *Porphyrellus* can, in a restricted sense, be separated from *Austroboletus*. A large number of these decisions are now possible because of the S.M.-photos published by Wolfe (1979a) who showed that the genus *Austroboletus* can be defined by, among other characteristics, ornamented spores, including such species that under the light microscope seemed to be quite smooth. *Porphyrellus* is then restricted to *P. porphyrosporus* and related forms. Wolfe considered the spore differences between *Austroboletus* and *Porphyrellus* to be strictly accompanied by cystidial characters (cystidia, perhaps more precisely pseudocystidia, with optically discernible enclosures or pseudoamyloid contents in *Porphyrellus*, hyaline and inamyloid, optically 'empty' in *Austroboletus*).

These observations, in part confirmed by my own recent research (Singer & al., 1981), show that Strobilomycetaceae, in spite of a certain variability (just as in *Boletellus*) of ornamentation type even within a single otherwise homogeneous genus, consist of three groups (1) *Strobilomyces*; (2) *Porphyrellus*, *Austroboletus* and *Fistulinella* (= *Muciloporus* Wolfe, 1979b); (3) *Boletellus*, *Phylloboletellus*. The affinities of the first are unknown, those of the second are with *Tylophilus*, and the third with *Boletus*. As we have seen before, these groupings are confirmed by chemotaxonomy.

In some minor points we do not agree with Wolfe (or for that matter with Smith & Thiers). I believe that *Porphyrellus* is a small genus, not a section or subgenus of *Tylophilus*, an opinion I share with Moser (1978) and Pegler & Young (1981). Furthermore, *B. mucosus*, macroscopically and anatomically a *Fistulinella*, differs from the latter genus in the fact that the glutinous veil of the stipe covers a rather strong reticulation and, more important, the strongly (S.E.M. as well as light microscope) ornamented spores. Again, we have a choice of either considering the spore ornamentation decisive (the choice preferred by Wolfe and Pegler & Young) or considering the rest of the characters whereby *B. mucosus* enters a rough-spored section (still unnamed) of *Fistulinella*. Those who insert *Boletus* sect. *Mirabiles* in *Boletellus* will, like the present author, prefer to insert *B. mucosus* in *Fistulinella*, a

solution which imposes itself at the present time when the type species and some other species of *Fistulinella* have as yet not been studied with S.E.M. or E.M. techniques.

How different spore ornamentation types can be in *Austroboletus* becomes clear when available photomicrographs are compared (Moser, 1978: pl. 45; Arpin & Kühner, 1977: 29, figs. 131–139; Watling & Largent, 1977: figs. 20, 22, 23, 25–28, 31, 36). Why, then, should *Heimiella* and *Afroboletus* be separated from *Boletellus* respectively *Strobilomyces*? We see that here we have *Boletellus* spores ranging from smooth (if we admit sect *Mirabiles*) to faintly longitudinally veined, winged or reticulate. In *B. betula* we find the 'coalescence of the alveoli often producing the individualization of a pillar' (Perreau & Heim) while the light microscope shows what appears like pillars forming an ornamentation type XI (Singer, 1975). A similar ornamentation type is known in *B. alveolatus* (Heim & Perreau) Sing. Judging by the spore color and the yellow color of context and other parts of the carpophore, we may anticipate that all *Boletelli* are chemically similar to the species where pigment studies have already been made (cf. Bresinsky and collaborators).

Corner and some others seem to think that *Boletellus* if smooth-spored would be close to *Xerocomus*. This is correct as far as habitus is concerned, but incorrect with regard to the structure of the hymenophoral trama which is of the *Phylloporus*-type in *Xerocomus* and of the *Boletus*-type in *Boletellus* (see photomicrograph in 'Agaricales in Modern Taxonomy' (Singer, 1975: pl. 26), verified in nearly all species referred to *Boletellus* by me. The misinterpretation of the tramal structure by Corner may have to do with his method of using alcohol-formalin or, as with Heim, with studying a non-suitable stage of development of the carpophore. Thus smooth-spored species would not be like *Xerocomus* inasmuch as they often have small pores depressed around the apex of the stipe. They would rather be like *Boletus*, and in habit much like sect. *Subpruinosi* where, however, the species with stipes showing coarse elevated ridges forming alveoli as found in sections *Dictyopodes* and *Allospori* would be out of place, as would be clamp-bearing species as *B. fibuliger*.

A similar range of ornamentation types exists in *Austroboletus*, as we have seen before, and this range includes even longitudinally veined spores if we accept — as we must — Corner's fig. 24 as illustrating the spore variations of *A. dictyotus*, or accept Corner's statement that *B. nanus* has an 'endospore' becoming finely longitudinally striate.

In *Strobilomyces*, again, we have spore ornamentation which ranges from finely punctulate in the light microscope and 'coarsely rugose to irregularly verrucose' (Pegler & Young) under S.E.M. to an angular mesh, strongly projecting. Traces of the intercostal ridging seen in those species with longitudinal wings or ridges (sect. *Pterospori*) can also be seen in Pegler & Young (1981: fig. 117, *S. polypyramis*); these are therefore not exclusive of section *Pterospori*.

It is possible that more detailed studies on spore sections under E. M. rather than S.E.M. might add something to bolete taxonomy but data are still not available for enough species to draw conclusions. At any rate, Pegler & Young's figures (p. 143–144) do not support the idea that *Strobilomycetaceae* can be maintained as a family on the basis of wall differentiation, especially if *Austroboletus* and *Boletellus* are removed from the type genus *Strobilomyces*.

The so-called plage (in reality different from that in *Galerina* and merely a smooth to lower ornamented area in the superhilar region) is absent in section *Pterospori*. Since according to my observations the fresh spore print in both sections of *Strobilomyces* is identical (fuscous-

brown to chocolate brown or purple brown in thin, nearly or quite black in thick layers), the 'plage' in sect. *Strobilomyces* remains the only character supporting even a sectional subdivision of the genus, but it seems to be replaced, in sect. *Pterospori*, by a basal thickened rim. Arpin & Kühner (1977) rightly stress the frequent reddening and constant blackening (tyrosine – Dopa – melanines) as characteristic of *Strobilomyces*. This phenomenon holds sections *Strobilomyces* and *Pterospori* (*Afroboletus*) together.

Pegler & Young's well-documented observations which should be extended to other, particularly controversial species like *B. nanus*, are undoubtedly very valuable for the taxonomist as are those by Wolfe. Nevertheless, they cannot be a basis for a 'natural' classification, which, by definition, has to take all available characters into account.

There remain a few problems which spore morphology alone cannot solve. In the following I give a few examples.

PHYLOGENY.—Considering modern pigment chemistry, the relations demonstrated by many authors between hymenogastroid genera and Boletineae cannot any more be considered tenuous. The Corner hypothesis which can be read in the sense of Gomphaceae → Boletaceae → Gastroboletaceae or vice versa seems to me rather more tenuous, and cannot be discussed in the framework of Bolete spore characteristics alone (see also Chapter 8).

PAXILLACEAE.—This family is (p. 126) wrongly characterized. Even though spores are 'mostly' not elongated, some Paxilli not studied by Pegler & Young and even one studied by them have elongated 'boletoid' spores. Clamp connections are absent in an entire section (see below). As for spore ornamentation, a study of *Phyllobolites* (see Singer, in *Mycologia* 73: 507. 1981) should throw some more light on the matter. Obligatory ectomycorrhiza has been shown to exist in *Paxillus boletinoides* and *P. defibulatus* and is probable in *Phyllobolites*. *Paxillus defibulatus* is transferred to *Phylloporus* as *P. statuum* (Speg.) Pegler & Young on the strength of non-clamped hyphae, and so is *P. veluticeps*. This is in error because we know enough about *A. statuum* not to identify it with *P. defibulatus*. It is only known from material from Staten Island which is the type or a topotype and authentic. It has been suspected to be the same as *P. boletinoides* Sing. because it has clamp connections and cystidia (neither seen with certainty in the hymenophore); the clamps, however, are scarce but definitely present; the cystidia may be occasional projections of the numerous oleiferous ducts with rusty granular contents; the stipe is evelate as was stressed by Spegazzini, who describes his species as having ferruginous-fuscous to badious color and as being grossly squamose (both in contrast to *P. defibulatus*). *P. defibulatus* is a common edible (but because of the bitterish taste not exactly delicious) mushroom in Patagonia and is taken for chanterelles by local mushroom hunters which gives an idea of how unlike its appearance is in comparison to *Phylloporus*. Its spore print color is between 'tortoise' and 'cookie' Maerz & Paul, a color not occurring in *Phylloporus* spores. *Phylloporus* is totally absent from the temperate *Nothofagus* region of South America whereas *Paxillus* is particularly well represented there, so much so that it is supposed that the Paxillaceae have South American origin (Singer, 1964: 96).

BOLETINUS PICTUS.—This species has been transferred to *Suillus* by Smith & Thiers (1964). This transfer has been accepted by Singer (1965–7; 1975) because the species is neither clamp-bearing nor hollow-stemmed, nor is it associated with *Larix*, but its cystidia

are often clustered (see Smith & Thiers, 1971: fig. 25). The spore print of *S. pictus* when fresh, has an olive tinge but this is not a general character of *Suillus* or *Boletinus* since olive tinges are absent in spore prints of *Boletinus* subsection *Rubrini* and present in *Suillus*, subsection *Hirtellini*. I agree with Pegler and Young that *Boletinus* is a good, natural genus, but the above statements show clearly that it cannot be inserted in a different family from that of *Suillus*.

BOLETELLUS ANANAECEPS.—My findings (Singer, 1955: 423) are closely similar to those by Pegler and Young (1981). However, the supposed synonyms (*S. pallescens* and *S. ligulatus*) have in light microscopy striate longitudinal wings on their spores and are thus more similar to those of *B. ananas*. It may be that my specimens were not identical with the holotype or that the light microscopy does not give identical results with S.E.M.-studies. But the matter seems to be in need of further revision.

PHYLLOBOLETELLUS CHLOEPHORUS.—This species is not only known from the type locality but from three different stations in the same general region (Selva Tucumano-Boliviana).

XEROCOMUS ZELLERI.—This as well as *B. intermedius* has striate spores; the striation has been clearly visible to Snell, Dick, Pouzar, and myself under light microscopy. This is therefore a pair of species belonging in *Boletellus* according to definition inasmuch as the hymenophoral trama in both is of the *Boletus*-type, not the *Phylloporus*-type. Putting *Heimiella* and *Boletellus* in two different families, even if the former genus were recognized because of different ornamentation, seems highly artificial.

LECCINUM CROCIPODIUM, **L. VERSIPELLE**, and **L. CARPINI**.—See Chapter 10.

FUSCOBOLETINUS AERUGINASCENS.—Neither pigment analyses nor spore color justify the transfer of this species to *Fuscoboletinus* which, at least in the circumscription of Smith & Thiers (1971) cannot be accepted even as a subgeneric or sectional unit, although some of the species described in it may be separated as subsections or series of three different sections of *Suillus*.

5. ASIATIC SPECIES AND THE CURRENT TAXONOMIES

The boletineous species of the tropics and other extra-European regions have certainly helped to modify the early 'natural' classifications which were basically European classifications. The classification proposed by me in the first, and gradually improved in the following editions of 'Agaricales in modern taxonomy' is the first classification based on fresh material of and anatomical data on extra-European material, including tropical species. The adjustments based on pigment studies and electron microscopy discussed in the present paper are certainly not unimportant but are relatively minor so that new species described from the tropics in South America and Asia have been absorbed relatively easily into these classifications which, because of this, have found wide acceptance. The one exception seemed to be that of the Malaysian species introduced or redescribed by Corner (1972). The question imposes itself whether there is really a difference between the African and neotropical, temperate holarctic and south-temperate bolete flora on one hand, and the tropical Asian Boletineae on the other, a difference that caused Corner to comment that the Malay-

sian bolete flora contains many species which 'bridge the generic differences which have been proposed' up to 1972. It seems to me that Corner (1972) has done an excellent piece of work which is indeed very useful to taxonomists by giving mostly detailed descriptions of numerous Malaysian boletes. A final reclassification has been postponed rather than newly proposed because this would have involved a new interpretation of extraterritorial material including types that were not at his disposal. His reviewers have taken a different position. Thiers (1973) thinks — as I do — that little has been accomplished by returning to a large all-encompassing generic concept and reproaches Corner for misunderstanding several already described species. Watling (1973) uses twice the word 'refreshing' for Corner's supposedly 'conservative approach' (which was merely a practical approach when editing his valuable data). Watling also says that the information we have at hand is rather sparse and is based almost exclusively on north temperate groups. I find both statements rather surprising and unsupported. Could it be that Watling (1970) saw in Corner's book an approval of his own 'conservative approach'?

To relegate genera one step down the taxonomic hierarchy — and this is the basic difference I can see between Kühner's and my classification — is no solution for the question of affinities between and delimitation of the various genera and subgenera of Boletineae or for that matter of any taxonomic group. The question to be answered is: Can we or can we not, on the basis of available data on the known world flora, discover a hiatus between these taxa? If there is no hiatus, neither genera nor subgenera are justified; if there is a hiatus the matter rests with the personal concept of what is a genus, a concept which is not at all uniform among authors. Arpin & Kühner (1977) seem to have a broad generic concept but possibly for reasons different from Corner's (cf. the latter's enormously extended concept of *Trogia*). Horak and Pilát & Dermek have a generic concept narrower than mine, recognizing aside from other European genera of boletes such genera as *Buchwaldoboletus*, *Rubinoboletus*, and *Aureoboletus*, so that in this regard, I find myself frequently on the more conservative side.

But do the Malaysian boletes really fill any gaps between existing genera? It is, I believe, useful to indicate a few examples which show the contrary. I cannot do this for all species described by Corner and depend on Corner's descriptions for many. Some cases have been discussed elsewhere in this paper. Others follow here:

BOLETUS AUREOMYCELINUS Pat. & Baker.—A study of the type and material preserved at Kew reconfirms my own and Corner's disposition of this species in *Boletus* where it was placed in the neighborhood of *B. patouillardii* Sing. Together with the latter species it forms apparently a subsection or section of small tropical Boleti with short, small spores, with *B. guadelupae* marking the connection with the species around *B. rubellus*.

BOLETUS BALLOUI Peck.—This is different from *B. balloui* Corner non Peck. See below in connection with *B. spinifer*.

BOLETUS BORNEENSIS Corner.—Although the color of fresh spore prints is unknown, it is obvious that this is indeed, as Corner believes, a representative of *Leccinum* (at least in my circumscription).

BOLETUS LONGIPES Mass. sensu Corner.—This apparently combines two species (*A. longipes* and *A. tristis*), at least according to Wolfe's (1979a) type studies contested by Corner (1980).

BOLETUS MIRANS Corner.—In Corner's description I find nothing to exclude it from *Tubosaeta* Horak (1968) who does not, as quoted by Corner, indicate the hymenophoral trama as boletoid, but describes it so that one must infer that it has a *Phylloporus*-type of trama, just as Corner indicates it for *B. mirans* and Heinemann (by implication) for *B. goosensii* and *B. calocystis*. Corner says that *B. mirans* 'has short spores as in *B. spinifer* (thus destroying the prime character of *Tubosaeta*)'. In reality, the spores of *B. mirans* are 'ellipsoid $6.5-8(9) \times 4.5-5.3 \mu\text{m}$ ', i.e. longer than in *B. spinifer* (spores $5.5-7 \times 4-5 \mu\text{m}$) and *B. bicolor* Mass. ($5.5-7 \times 3.5-4.5 \mu\text{m}$) and slightly more elongated. Since there are short-spored forms in *Xerocomus*, there is no reason to assume that all *Tubosaeta* species must have strongly elongated spores. There are relatively short spores in some species of *Boletus*, *Chalciporus*, *Boletellus*, and *Tylophilus* which cannot be excluded from their respective genera if all other diagnostic characters are identical. It seems to me that Pegler & Young exaggerate the significance of the 'compressed' configuration of bolete spores whereas Corner (p. 23) states that 'sporographic analyses shows that subglobose spores are to be expected in any alliance of elongated spores.' However, *B. ascendens* Corner, also cited by Corner in his discussion of *Tubosaeta*, has extraordinarily large smooth spores ($17-25 \times 5.7-7 \mu\text{m}$) and 'subboletoid' hymenophoral trama, which, as stated by Corner himself, should place it in *Boletellus* sect. *Mirabiles*, differing only by lack of any reticulation on the stipe and by a non-projecting margin. The slightly thickened wall of the cystidia has (Smith & Thiers, 1971) been described in *B. projectellus*. A slightly thickened cystidial wall has also been observed in a variety of *Boletellus ananas* (Singer & al., 1981). It is therefore not considered to be worthy of generic significance in *Boletellus*. In some specimens of the species of sect. *Mirabiles* the sterile projection of the margin may be absent (Smith & Thiers, 1971). *Boletus ascendens* should therefore be placed in sect. *Mirabiles*. The placing of *B. olivaceoluteus* is somewhat more difficult since it is not fully described (mycelium and spore print color when fresh, chemical data). It is useless to discuss affinities of not sufficiently known species. Other species discussed by Corner in connection with *Tubosaeta* have thin-walled hymenial cystidia.

BOLETUS NANUS Mass.—This is a real puzzle for me, not because the species is suspect as 'bridging generic limits' but because the data I have on the type of *B. pernanus* Pat. & Baker do not agree with those given by Corner for *B. nanus* which according to Corner is the same as *B. pernanus*. I cannot see therefore whether the indication of a dirty pink spore print refers only to *B. nanus* in which no veil was seen and the hymenophore is described as pale leather colored with relatively wide pores. I suspect that two species have been mixed up. I have not seen any trace of longitudinally striped spores in *B. pernanus* which, if present in *B. nanus* would be extraordinary for a *Tylophilus*. As for *B. nanus* as described by Corner, I am strongly tempted to consider it an *Austroboletus* related to *A. dictyotus*. The *B. nanus-pernanus* assemblage needs further study, especially E.M.-studies of the spores.

BOLETUS PHAEOCEPHALUS Pat. & Baker.—In the sense of Corner, this is a *Boletellus* (cf. Singer & al., 1981). But the type of *B. phaeocephalus* is a *Xerocomus* sect. *Moravici*, and has completely smooth spores, at least under the light microscope. The fine longitudinal striation of the spores of *B. phaeocephalus* sensu Corner, non Pat. & Baker, discovered by Corner, and confirmed by me on the type of *B. umbrinellus* Pat & Baker proves that Corner is right in synonymizing the latter with his interpretation of *B. phaeocephalus* which is not a

Pulveroboletus, but *Boletellus*. A specimen cited by Corner for *B. phaeocephalus* (Borneo, K) is not a *Boletellus* and likewise not a *Xerocomus*, but probably a *Tylopilus* spec. In the case of *B. phaeocephalus*, while presumably one single species is discussed, three species of three different genera are involved. The citation of '*B. olivaceobrunneus* Zeller et Bailey' in the synonymy introduces a fourth species, unrelated and obviously misunderstood by Corner. It is quite clear that until this complex was unscrambled, no definite conclusion could be drawn.

BOLETUS PORTENTOSUS Berk. & Br.—We (Singer & al., 1981) have discussed this species. It is clearly a *Phlebopus* (= *Phaeogyroporus*).

BOLETUS RUBRIPORUS Corner.—This is obviously a good species of *Chalciporus*. Bluing species have been observed in *Chalciporus* (cf. *B. piperatoides* A. H. Sm. & Thiers). Although a slightly aberrant (more like the *Phylloporus*-type) hymenophoral trama is occasionally observed in certain stages of some species of *Chalciporus*, *C. rubinus* has, according to my own observations, a trama of the *Boletus*-type, which confirms an observation by Reid quoted by Corner. Corner's statement 'this complex proves the necessity of considering the world flora in mycological classification' can only be heartily applauded.

BOLETUS SPINIFER Pat. & Baker.—A revision of the thin- to thick-walled (in KOH) acute or subacute cystidia which reminded Patouillard and myself of setae (I called them later setiform cystidia) are in reality coscinocystidia. They are the only ones that occur both in *Linderomyces* (Gomphaceae) and *Boletochaete* (Boletaceae) and as such might have been an interesting item for those, like Corner (and perhaps Pegler) who look for links between the Gomphaceae and Boletaceae (*Clavaria*-hypothesis). Not knowing coscinocystidia when describing *Boletochaete*, I had no possibility to recognize these 'setiform cystidia' as coscinocystidia. Those of *B. spinifer* are ventricose below, with an outer thin to thickish wall (0.3–1.5 µm thick in KOH), unevenly thick and not well delimited from the spongy-chambered contents, appearing strongly metachromatic in toluidin-blue and cresyl blue (but it is not the outer wall which turns red; it turns blue!) with a subhyaline inner wall (both walls together in this medium appearing 0.5–3 µm thick). In KOH the color of these cystidia is dark ferruginous or olive to fulvous-brown. Aside from the coscinocystidia described, there are also thin-walled cystidia present which are mostly slightly narrower. Younger cystidial cells are less distinctly coscinoid and thinner walled. In *Linderomyces*, on the other hand, the coscinocystidia may be different insofar as they, according to Petersen (1971) are a stage of gloeocystidia (*Gloeoeantharellus*). The cystidial characteristics, combined with the late gelatinizing lateral trama and the pale spore print (pale cinnamon pink according to Corner) and the short spores leave no doubt but that *B. spinifer* is generically different from other *Tylopili*. The genus seems to be restricted to tropical and subtropical Asia. *Boletus balloui* Peck sensu Corner (which is different from *T. balloui* (Peck sensu Peck) Sing.!) and which I assume is *B. bicolor* Mass. is apparently another species of *Boletochaete* where the coscinocystidia are much more scattered (and only melleous in NH₄OH) than in *B. spinifer*. The bitterish taste may be an additional characteristic of the genus, as well as the adnate hymenophores (see Chapter 6).

Corner considers *P. viscidulus* (Pat. & Baker) Sing. as conspecific with specimens he describes as *B. balloui* var. *fuscatus*. The type of *B. viscidulus* has a shining and viscidulous, perfectly smooth pileus, an appearance much like that of other *Pulveroboletus* species,

unchanging context and spores $7.7\text{--}9.5 \times 4\text{--}5.3 \mu\text{m}$. Although I have not been able to study the cystidia, the above data suggest that it is not the same as *B. veluticeps* Pat. & Baker. The latter has somewhat more elongated spores ($7.5\text{--}8.7 \times 3.5\text{--}4.5 \mu\text{m}$) than var. *fuscatus* and, most important, short cells in chain-arrangement and erect on the pileus, with only occasionally cylindrical terminal cells, with the wall $1\text{--}1.3 \mu\text{m}$ thick (compare Corner's figure p. 194, fig. 66 with the above data). Corner has not seen the types of these species and 'can detect no difference in the original descriptions and in Singer's account of the microscopic details.' Yet here again we seem to be confronted with a group of species, all considered conspecific with each other by Corner, and therefore difficult to place without careful type studies.

BOLETUS VALENS Corner.—This species, unknown to me, does indeed not fit into any known genus, at least as described. However, this would be the only known species where both pinkish cinnamon and olivaceous-cinnamon (fresh?) spore prints occur in a single species. The comparison with *T. niveus* brings up the question of whether the spores are S.E.M.-smooth. The large spores exclude *Tylophilus*. If the spore print (fresh) is olivaceous and the spores really smooth, this may fit well into *Boletus* sect. *Grisei*.

BOLETUS VIRIDIS (Heinemann & Goos.) Corner.—This species seems to be a typical *Pulveroboletus* (section *Cartilaginei*) as originally stated by Heinemann (1954). The ferruginous spore print has also been observed for *P. curtisii*, the type of the section. The comparison with *Xanthoconium* (p. 17, 143) is unwarranted inasmuch as spore print color alone cannot be used as a single unifying character. But it may separate this section from the otherwise similar section *Glutinovelati* where the spore print as far as known has an olive tinge.

BOLETUS XYLOPHILUS Petch (identical with *P. viperinus* Sing.).—This species is not a *Phaeogyroporus* (*Phlebopus*), nor a *Gyrodon*, but quite obviously a *Pulveroboletus*, sect. *Sulphurei*, where the deterrent fibrillosity is seemingly or really lacking, and in this case a continuity between sect. *Sulphurei* and sect. *Duckeani* Sing. (Singer & al., 1981) can be established. I have studied the respective types and additional material from Asia.

6. GROWTH PATTERNS OF THE CARPOPHORES

A new aspect has been introduced by Corner (1972) who without special emphasis on the hymenophore development in the primordium has studied the growth patterns of several species of boletes from early stages to maturity. The shortcomings of this approach were enumerated by Corner himself (p. 28) and include also the following: Too few species have been studied in this regard and the patterns, elaborated in the field, could not be checked under fully identical conditions of humidity and temperature. In spite of all this, this approach is interesting and worthy of a follow-up under more controlled conditions. If we analyze the data obtained thus far by Corner on boletes, and if we substitute for the generic position attributed to them by Corner those we consider correct (see previous chapter), we have:

Fig. 5 — *Boletochaete* (slow-growing long-lived type),

Fig. 6 — *Austroboletus* (rapidly growing, short-lived type),

Fig. 7 — *Pulveroboletus* (rather slow-growing but shorter-lived type),

Fig. 8 — *Boletochaete* (slow-growing, long-lived type),

Fig. 9 — *Pulveroboletus* (rather slow-growing but shorter-lived type),

Fig. 10 — *Boletellus* (rapidly growing and short-lived type),

Fig. 11 — *Boletellus* (rapidly growing and short-lived type).

The coincidence of generic identity and growth pattern is here quite obvious, and is in full agreement with my classification. It is perhaps too much to hope that, generalized for the genera of boletes of all subfamilies and of all floral districts, this coincidence would still hold, but the existence of such correlations in a few genera and in a tropical environment may well suggest some taxonomic significance for the different growth patterns.

7. MYCORRHIZAL RELATIONSHIPS

Several authors, aside from the present, for instance Benedix (1963) have drawn attention to the fact that ectomycorrhizal relationships may be a useful tool for specific and supraspecific taxonomy and even for an attempt to determine the direction of evolutionary lines. Recent experiences in the tropics (Singer, 1973–1978; Singer & *al.*, 1981) tend to modify some earlier conclusions sufficiently to warrant a new survey of the various taxa.—

Paxillaceae:

Hygrophoropsis — Possibly some facultatively ectomycorrhizal.

Paxillus — Sect. *Parapaxillus*: At least one species constantly ectomycorrhizal;

Sect. *Atrotomentosi* and *Panuides*: Non-mycorrhizal, lignicolous;

Sect. *Paxillus*: Probably all (certainly *P. involutus*) facultatively ectomycorrhizal;

Sect. *Veluticipetes*: Perhaps; sect. *Defibulatie* certainly ectomycorrhizal.

Neopaxillus — Facultatively ectomycorrhizal.

Ripartites — No reliable studies available.

Phyllobolites — At least facultatively ectomycorrhizal, possibly obligatorily, but host not established.

Gomphidiaceae:

All genera ectomycorrhizal with conifers.

Boletaceae:

Gyroporus — Ectomycorrhizal, but not specialized. Mycorrhizae possibly facultative.

Phlebopus (*Phaeogyroporus*) — Facultatively mycorrhizal but not ectomycorrhizal in the species studied (a specialized form of peritrophic mycorrhiza in *P. tropicus*, with citrus).

Paragyrodon — Ectotrophically mycorrhizal with Fagales.

Gyrodon — Many species not mycorrhizal at all, others ecto- or ectendotrophically mycorrhizal with such genera as *Fraxinus*, *Alnus*, *Allophylus*.

Meiorganum — Apparently non-mycorrhizal, lignicolous.

Psiloboletinus — Ectomycorrhizal with *Larix*.

Boletinus — Ectomycorrhizal with *Larix*.

- Suillus* — All ectomycorrhizal particularly with *Pinus* and other conifers, quite exceptionally with Salicaceae.
- Phylloporus* — Ectomycorrhizal with various trees (excepting perhaps sect. *Manaussenses*).
- Xerocomus* — Some non-mycorrhizal (some parasitizing Gasteromycetes), some ectomycorrhizal with conifers (but some of these only facultatively so, or with combined endomycorrhiza with *Monotropa*), some with Salicales, Fagales, Tiliaceae, Leptospermataceae, Leguminosae etc.
- Tubosaeta* — Possibly non-mycorrhizal, or with ectomycorrhizae on leguminous trees (?).
- Chalciporus* — All ectomycorrhizal with conifers, Fagales, Leguminosae, etc.
- Pulveroboletus* — Some non-mycorrhizal or even lignicolous, some ectomycorrhizal with Fagales, Leguminosae, more rarely conifers.
- Boletus* — All species ectotrophically mycorrhizal (obligatorily), the majority with angiosperms (one apparently with Nyctaginaceae), fewer with conifers (none with Leguminosae, *Alnus*, *Fraxinus*), usually very strictly specialized.
- Xanthoconium* — All ectomycorrhizal with Fagales.
- Boletochaete* — No data available.
- Prophyrellus* — Ectomycorrhizal with conifers and Fagales, mostly rather specialized.
- Tylophilus* — Ectomycorrhizal with conifers and Fagales, Leguminosae, (Rutaceae).
- Leccinum* — All species ectomycorrhizal, mostly specialized, with Fagales and Salicales, fewer with conifers.
- Austroboletus* — Some non-mycorrhizal (saprophytic or parasitic), but many ectomycorrhizal with a wide range of Cormophyta.
- Fistulinella* — Probably some ectomycorrhizal (facultative?), but some apparently non-mycorrhizal.
- Boletellus* — Probably some at least facultatively ectomycorrhizal, others probably non-mycorrhizal.
- Phylloboletellus* — Possibly non-mycorrhizal, but perhaps ectomycorrhizal with Sapindaceae or Leguminosae (if so, probably facultatively).
- Strobilomyces* — Possibly all ectomycorrhizal but with a wide range of hosts.

Evaluating this list we find, as expected, that among the subfamilies only Suilloideae are reasonably homogeneous in their tree association. Other subfamilies and some genera (*Paxillus*, *Xerocomus*, *Pulveroboletus*) show a gradually increasing dependency on obligatory ectomycorrhiza and increasing specialization within the taxon. In the genera which one might characterize as mostly highly developed (*Boletus*, *Xanthoconium*, *Tylophilus*, *Leccinum*) all species are smooth-spored and associated predominantly with angiosperms, especially Fagales, and lacking clamp-connections. Here one finds the most constant association with the highest degree of specialization, except for the Suilloideae where the association is with conifers rather than angiosperms (which most authors derive from the Gymnospermae).

Ectomycorrhiza is (as compared with other symbioses with higher basidiomycetes and

with endomycorrhiza in general) a relative newcomer in the history of fungus-cormophyte associations. We should not be surprised to find those Boletineae with short, 'non-compressed' spores, or with ornamented spores, with veils or with hemiangiocarpous development, with lamellate hymenophore, clamps, and particularly those groups where such indications of supposedly early steps in the evolution of boletes and allies are shown simultaneously, are frequently the same that also show no or only sporadic (facultative) mycorrhizal association, or those where this association does not seem to be fixed in a single host species, i.e. ubiquitous, non-specialized species.

While there is then a definite pattern, showing the probable trends in the evolution of the boletes, there are indeed some inconsistencies (recent species with partly primitive, partly evolved characters). More important, no particular living boletoid organism shows all these characters at the same time. Rather, a number of species or groupings have been considered relatively ancient (Gyroporoideae, Gyrodontoideae, *Boletinus*, some *Xerocomi*, *Boletellus*, especially *B. fibuliger*, Paxillaceae, especially *Hygrophoropsis*, *Paxillus* sect. 1–3, *Phyllobolites*, *Phylloboletellus* and the Gomphidiaceae), with emphasis on some of these by some authors whose phylogenetic hypotheses have been supported by such assumptions.

It must therefore be assumed that either some of the presumed 'primitive' characteristics are not indeed primitive in the boletoid fungi or that one organism, either recent or fossil, combines them but has not yet been discovered.

On the positive side, the absence of *Leccinum* in neotropical lowlands, but its demonstrated presence in *Betula* plantations almost all over the world, and in native fagaceous forests in tropical Asia can now be explained by the absence of Fagales in the tropical lowlands of the neotropics and their abundance in the Asiatic tropics. Also, all *Larix*-connected boletes belong in the subfamily Suilloideae, a subfamily with an area coinciding with that of the ectomycorrhizal conifers.

What is remarkable is the fact that Boletineae are extraordinarily rich in ecological adaptation and that their mycorrhiza formation includes association with a particularly wide spectrum of hosts viz. conifers (Pinaceae), Fagales and Salicales, Oleaceae, Tiliaceae, Leptospermaceae (*Leptospermum* and *Eucalyptus*), leguminous families, Sapotaceae, Nyctaginaceae, Sapindaceae, Rubiaceae (some *Psychotria* sp.), and probably Polygonaceae (*Coccoloba*).

8. PARADOXES

Those who have criticized or amended my classification by defining families, subfamilies or genera differently, have not come out with solutions comparable with each other, even less with a common counter proposal. Authors who have published new classifications for all or some Boletineae, or with an interpretation of their phylogeny, have arrived at extremely divergent points of view. While Smith & Thiers (1971; but not Thiers, 1971) think of *Suillus* as the basic ('closest to the origin' of Boletaceae) genus, Pegler & Young (1981) strangely enough inserting *Suillus* in the Strobilomycetaceae, consider *Suillus* as a phylogenetically advanced genus (and we agree). Influenced by his 'Clavaria theory', Corner (1972) puts *Ixocomus* (= *Suillus*) near the end of his evolutionary line, considering *Heimiella*,

Boletellus, and *Strobilomyces* most primitive (scheme, p. 27). While he is right, to a certain degree, in that the 'Gasteromycete-theory' suffers from the fact that it can be read in different directions, his own suffers from his supposition that fungi necessarily derive from algal ancestors (but cf. Broda, 1975) and fruiting body similarities of Basidiomycetes with thallus shapes of algae indicate clavarioid fungi as the ancestral form of agarics, an argument we find unacceptable. As against the *Clavaria*-hypothesis we quote Donk's remarks (Thiers, 1971: 437). Pegler & Young, although offering their classification as a phylogenetic one (which it is only in part), do not elaborate on detailed evolutionary lines, merely indicating some genera as 'less advanced' (*Paxillus*), citing Corner's hypothesis (which they find attractive) and giving *Heimiella* relict status. Watling (Watling & Largent, 1977) says he is 'sympathetic' to the '*Clavaria*-theory' (p. 594).

All these modern hypotheses cannot be correct since they are mutually exclusive, unless, of course, we return to Heim's statements postulating polyphyletic origin of the boletes. We don't.

A few examples of contradictory statements in recent classifications.—

Species left in a single genus by Watling and Arpin & Kühner are classified in three different families by Pegler & Young. *Phylloporus*, relegated to the Paxillaceae by Smith & Thiers (1971) and Watling (1970) is congeneric with *Xerocomus* respectively *Boletus* (Boletaceae!) according to others (Arpin & Kühner, 1977; Kühner, 1978–1980). *Hygrophoropsis* whose position in the Paxillaceae has not been challenged by others, is placed in a family of its own together with *Omphalotus* by Kühner (1978–1980). This family, Hygrophoropsida-ceae, is considered to be transient between Tricholomatales and Boletales. *Pulveroboletus* (sensu lato, in my definition) is recognized as such by Pegler & Young while it is totally incorporated in *Boletus* (in various subgenera) by Corner and restricted to *P. ravenelii* by Smith & Thiers. *Boletinus* is transferred from the Suilloideae to the family Gyrodontaceae by Pegler and Young, but considered congeneric with *Suillus* by Smith & Thiers and Arpin & Kühner. *Meiorganum*, originally considered (by Heim) to belong in a family of its own, was inserted in the Gyrodontoideae by me, transferred to the Coniophoraceae (Aphyllophorales) by Pegler & Young. It must be stated here, however, that the 'minute, deep ferruginous spores' are neither the smallest in the Boletineae, nor are they deep ferruginous but gray-brown-lilac purple (Heim), dull vinaceous pink to fawn brown (Corner, 1971). Corner treats the genus in his 'Meruloid Fungi' but thinks that it is intermediate between Boletaceae or Paxillaceae and Meruliaceae, not Coniophoraceae. 'Its boletaceous affinity is clear' (Corner, l.c.: 357).

What seems to be more an error in identification than a taxonomic decision is Pegler & Young's insertion of *Boletinus pictus* with *B. cavipes*. The former, treated by Smith & Thiers and others as congeneric with *Suillus* (fam. Strobilomycetaceae according to Pegler & Young), differs from *Boletinus* and related species (family Gyrodontaceae according to Pegler & Young) by absence of clamp connections in the carpophore, ectomycorrhiza with *Pinus*, and solid stipe.

9. THE HIATUS BETWEEN GENERA

In most monophyletic, i.e. not artificial genera of Biota there are 'transitions' between genera. If we believe in evolution rather than creationism, this cannot be otherwise. But between genera and families (and all superspecific taxa) there must be a definable hiatus which is not always easy to describe or express in keys by a single character state alone (cf. Machol & Singer, 1971). As we study more thoroughly more and more species and newly introduced characters, our assumption about the position of the hiatus may change. Finding the position of the hiatus is among the main difficulties in the delimitation of taxa, especially the superspecific taxa. Much depends on the idea each author has about the size of the hiatus which, for him, justifies generic separation, but the problems do not just go away if we relegate a genus to subgeneric status.

In the Boletineae many authors, including the present author, have in their lifetimes transferred one or several species to a genus or family other than the genus or family it was originally attached to, mostly because of new evidence that has become available to them, e.g. regarding *Phyllobolites* (Singer, 1964; Singer & al., 1981). Some such cases have been discussed in the previous chapters. The remaining ones shall be discussed here.

Hygrophoropsis. After having redefined this genus and inserted it in the Paxillaceae, I at first admitted only species with pseudoamyloid spores, as have many Paxillaceae. These species were *H. aurantiaca* and *H. tapinia* (its identity with *Cantharellus flabelliformis* Berk. & Curt. cannot be accepted since the type has no spores and its description does not fit *H. tapinia*!). Only in 1975 I have added some species with inamyloid but cyanophilous spores. These species, with regard to their other characters, coincide with the type species. The spore wall of the latter was here described as simple (not 'thin-walled' and not 'mince et simple' as Kühner quotes me) and in my description of *H. aurantiaca* (Singer 1946, see Singer, 1977a) was described as thin-walled to somewhat thick-walled. Kühner states that after 30 hours at 60°, numerous spores showed a wall of three coverings, the middle one swollen, the endosporium not very thick but well characterized. This, according to him, is not the case in *H. olida* although the spores, as indicated by me, are cyanophilous as in *H. aurantiaca*. I have also observed rather thickish wall in *H. kivuensis* Heinemann (Singer & al., 1981) and we have weakly to strongly pseudoamyloid spores together with inamyloid spores in *H. panamensis*. Consequently there is a continuity of spore characters if extra-European species are considered. On the other hand, *Gerronema albidum* which differs not only by acyanophilous spores but by absence of clamp connections (in contrast to all *Hygrophoropsis* species), cannot be placed at the end of this series inasmuch as chemotaxonomy cannot be of much help here since *G. albidum* carpophores are almost pigmentless; however a pigment analysis of the closely related *G. alutaceum* and E.M. sections of their spores may possibly add some further evidence in the case. For the time being, the hiatus appears to be between *H. olida* and *G. albidum*, not between *G. albidum* and the rest of the *Gerronemas*, and the circumscription of *Hygrophoropsis* must remain the same (Singer, 1975; Pegler & Young, 1981).

Gyrodon.—It has been separated from a genus *Boletinellus*, a monotypic genus erected for *G. merulioides* (Smith & Thiers, 1971). There is no hiatus at all between the two genera, and I cannot go beyond my comment (Singer, 1975: 705) since Smith & Thiers (1971) who maintain

Boletinellus as a valid genus, have neither explained their reasons nor keyed out the genus in their book. This is a rather puzzling situation inasmuch as a genus much more different from *Gyrodon* than *G. merulioides*, viz. *Paragyrodon sphaerosporus* has been placed in *Suillus* by the same authors.

Pulveroboletus.—The continuity between the type species with a fibrillose veil and the other sections is difficult to understand for those who are not familiar with representatives of all sections. At first glance, the pulverulent-arachnoid veil of *Pulveroboletus ravenelii* sets this species apart but the veil hyphae may be present and forming a pulverulence, more or less deterrent, in other sections, and the gelatinization, present in the epicutis of *P. ravenelii* and related species, may become very strong in the ex-velar layer or even an indistinct velar layer leading to sections *Glutinovelati* and *Cartilaginei*. This gelatinized layer may be reduced to simply viscid pileus and stipe as in sect. *Auripori*, or else the gelatinization may be practically absent, as in sect. *Sulphurei*. I have added a new section (Singer & al., 1981), *Duckeani*, where both pulverulence and stipe viscosity are absent. The continuity between sect. *Sulphurei* and *Duckeani* has been discussed under *B. xylophilus* (Chapter 5). The genus as a whole consists of species unrelated to species of *Xerocomus*, *Chalciporus*, and *Boletus* but the pulverulent-arachnoid surfaces, which may be replaced by glutinous surfaces, or the habit, the tendency of the stipe to become hollow and/or cartilaginous, the absence of blue reactions of the fresh surfaces with ammonia are characters common to the species of *Pulveroboletus* even where one of these characteristics should be missing in a given specimen. The transition from dry to glutinous species is neatly illustrated by the fact that Corner (1972: 134) describes *P. umbilicatus* as having a cover on the surfaces which is originally a dry, piloso-fasciculate tomentum then becoming mucilaginous. This statement is turned by Corner (p. 10) into a fact supporting his contention that *Pulveroboletus* is not a natural genus in my circumscription, while, on the contrary, *P. umbilicatus* underscores the continuity of sections in this genus. As in other genera of mostly elongated-spored ('boletinoid') boletes, there is a tendency in *Pulveroboletus* towards short spores and, as in *Chalciporus*, there is a tendency of the hymenophoral trama to maintain a seemingly *Phylloporus* type of structure over longer periods, especially in species with reduced gelatinization or collected in dry periods.

It is understandable that it was European authors, unfamiliar with some sections of *Pulveroboletus*, who separated the split genera *Buchwaldoboletus* and *Aureoboletus* for the only two sections occurring in Europe. It goes by itself that Corner (1972) accepting an excessively wide circumscription of the genus *Boletus*, incorporated all *Pulveroboleti* in *Boletus*, but, following Smith & Thiers (1971) restricted the subgenus *Pulveroboletus* to *P. ravenelii* which, according to him is, in contrast to other sections, 'angiocarpic'. But this is neither proved nor necessarily diagnostic on a generic level (*Xerocomus* contains paravel-angiocarpic species), even if Corner's assumptions should turn out to be correct. Corner's further comments (p. 9–11) are partly based on misquotations. Neither do I say that the pores of the *Glutinovelati* are always golden yellow but they are described as 'golden yellow, cream color' (1962 as well as 1975) nor is *P. corrugatus* claimed to be angiocarpic, nor is the diagnosis of sect. *Glutinovelati* (1947!) taken from *P. lithocarpisequoiae* (1959!) nor is the latter a 'coniferous species' since no mycorrhiza with conifers was present. Another part of his comments is based on misinformation since species were referred to in the discussion

without knowledge of the types (*S. lithocarpisequoiae*, cf. Singer, 1975: 727) or were misdetermined (*B. olivaceobrunneus*, *B. balloui*, *B. phaeocephalus* and others). Since we know that some species of *Pulveroboletus* as well as the closely related *Chalciporus* either have or do not have resinous-incrusted cystidia, there is nothing strange or confusing about two species of section *Glutinovelati* being different in this regard. Considering all this, Corner's criticisms are not supported by convincing facts, and expressions like 'confusion of Malayan mycology' and 'dump for species' are uncalled for and misleading or at least a sample of Corner's frequently acid style (I prefer the second alternative because I believe that his opinions are sincere and open to new facts).

I admit that I may have contributed to misunderstandings about *Pulveroboletus* by referring there *B. ornatipes* and *B. phaeocephalus* although these mistakes have been corrected by me. Unless new evidence is presented, or a much smaller generic concept is admitted, there is no reason to change my circumscription of *Pulveroboletus* (Singer, 1975) as accepted by Snell & Dick (1970), Moser (1978), Pegler & Young (1981), and Bertault (*in Bull. Soc. mycol. Fr.* 95: 308–309, 1979).

10. NOMENCLATURE AND OTHER FORMALITIES

Kühner (1977; 1978–1980) removes the nomenclature of Kühner & Romagnesi (1953) from their own basic set of rules to internationally accepted nomenclature. This development will be met with applause by all those mycologists who at times have found it difficult to coordinate the names used in Kühner & Romagnesi and those that conform to the Code. It is unfortunate that those botanists most concerned with the continuity of botanical names and thus with the general acceptance and application of the Code of Nomenclature are often the same who discourage taxonomists by a continuing flood of new proposals and introduction of new examples and modifications of the rules. Kühner's historical merits in basidiomycete systematics make his exposé of the 'grandes lignes' of classification even if 'centred on European genera' and 'essentially critical and historical' an extraordinarily interesting and valuable source of information not only on characters introduced by him but for an exploration of the reasons behind his taxonomic thinking (but hardly as an alternative to Singer's or other systematists' classification as suggested by some reviewers). Thus, it is not without regret that I have to insist on some minor points of nomenclature and other formalities since they were brought up in recent papers (Arpin & Kühner, 1977; Kühner, 1977) critical of my own work (which Kühner at the same time called 'monumental'). By relegating several of the (nowadays mostly recognized as generic) taxa of Boletaceae to subgeneric status, Arpin & Kühner (1977) overlooked the fact that Fries and others had already subdivided *Boletus* into several infrageneric taxa which, applying the type principle, should be considered as having priority over the ones now proposed (Arpin & Kühner, l.c.) It is hard to imagine that Fries (1836) did not introduce, with Roman numerals, what he considered tribus and which are now to be treated as subgenera. If so, subgenus *Tylopilus* would have to be called *Boletus* subgen. *Hyporrhodius*. What is now the genus *Suillus* was apparently first treated as a subgenus by Kühner & Romagnesi (1953) under the name *Ixocomus* Quel.; by Schröter as II. *Leucocricos*, IV. *Cricunopus*, (V. *Boletinus*); *Leccinum* = *Krombholzia* (P. Karst.) Schröt. (subgenus).

Kühner (1977) finds it 'shocking' that the bibliography of my 'Agaricales in modern taxonomy' omits the works of E. M. Fries, and the '(Fr.)' in the citation of the genera proposed by Kummer is, for him, 'deeply regrettable' and 'a profound injustice'. It is hardly to be expected that a book called 'Agaricales in modern taxonomy' which does not even analyze most of the characters on which Fries's classification was based, would again (after an explicit account of the history of Agaricales-systematics provided in 1936, referred to in 1951, 1962 and 1977) enumerate and list all the classical works of Fries (or for that matter Persoon). Who, indeed, would at present feel that Fries himself whose name is attached to perhaps a majority of fungus taxa presently accepted in Europe, were injured in any way by the fact that his name is now omitted in some of the author citations — and that for good reasons. In the case of Kummer, this is a strictly formal question (in which, it is true, not all mycologists agree with me). This is based on Kummer's own words who, as I have explained before (Singer, 1951), says that he merely used the same name as Fries for what he introduced as 'new genera'. Few authors realize that this means more than a minor formality, and that it has rather far-reaching consequences in nomenclature. A new genus is not nomenclatorially based on the homonymous tribus name and therefore the type species does not have to be selected from the latter. If we consider Kummer's genera as merely elevations in rank, the designation of a lectotype would have to go back to the earliest use of the name at any rank, and the resulting choice would often be difficult or even embarrassing. Nomenclature rules have been made for the stated purpose of unification and continuity of nomenclature and not for historical justice. It is undoubtedly a historical 'injustice' that according to the new Code the family names Rhodogoniosporaceae Heim and Rhodophyllaceae Sing. had to be replaced by the nomenclatorially correct family name Entolomataceae or that *Calocybe carnea* (Bull. ex Fr.) Kühner was replaced by *Calocybe carnea* (Bull. ex Fr.) Donk. The case of *Armillariella* vs. *Armillaria* — where Donk (1962) says that under some conditions Singer's selection has to be respected — is another example for what has been said above. In a discussion of bolete taxonomy, however, I cannot enter into detailed discussions on other groups. But with all possible respect for the feelings of historical justice and taxonomical preferences, such feelings cannot be used as an argument against a nomenclatorial solution dictated by the rules, even if we tend to oppose it.

On Staude's so-called 'genera' the reader is again referred to my comments of 1951. Kühner's opinion that the so-called residue rule is an automatic rule like the 'first-species rule' is not well founded since the former is recommended in the present Code whereas the second is specifically rejected in the Code. What Kühner calls historical or scientific lectotypification is unfortunately something that does not exist in the rules. While it should in certain cases be a guide for new lectotypifications, it has no standing in 'correct' namegiving. Kühner's speculations with regard to the motive of taxonomists for a certain taxonomical or nomenclatorial solution are often incorrect and mostly irrelevant as they are in the case of my supposed motive for the lectotypification of *Armillaria*.

These minor points do not affect the taxonomy of boletes beyond the introductory remarks by Kühner cited above, nor is Kühner the only one who arrives at conclusions which are nomenclatorially unacceptable. The rejection of *Gyrodon* in favor of *Uloporus* by Watling (1970) is hardly convincing inasmuch as in the Fries Herbarium at Upsala, material determined by Fries himself is conserved. This material is the only authentic material

existing and is identified as *Boletus sistotremoides*. My own analysis of this specimen proves that it is *Gyrodon lividus*. *Boletus sistotremoides* is the type species of *Gyrodon* (cf. also Singer in Taxon 5: 30-33, 1956).

Furthermore, *Leccinum crocipodium* has an epithet not validly described and not very well (certainly without analysis) illustrated by Letellier. The correct name is *L. nigrescens* (Richon & Roze) Sing. *Leccinum versipelle* (Fr. ex Hök) Snell is neither demonstrably identical with *L. testaceoscabrum* nor is *B. testaceoscabrum* illegitimate since the example of the Leningrad Code (outlawing Secretan's names) is in contradiction with the main text of Art. 23 I.C.B.N. A proposal has been made to remove the respective example from the text of the Code. *Leccinum carpini* (R. Schulz) Moser ex Watling (1965) as cited by Watling (1970) is clearly a synonym of the earlier *Gyroporus griseus* Quél.=*Leccinum griseum* (Quél.) Sing.

11. CONCLUSIONS

The often divergent and to a certain degree contradictory results obtained by various authors and the few erroneous statements made by some cannot be an excuse for neglecting all but those that corroborate one's own earlier conclusions.

Far from minimizing Kühner's attempt to re-introduce the historical aspect which so often cannot be expressed satisfactorily in names or taxonomic schemes, I suggest that it would be useful and interesting to devote more time to the history of mycology (not only mycological taxonomy) than is now devoted to it. The rapid progress of science has not suppressed but rather spurred a renewed interest in the history of physics. A painstakingly detailed and unbiased reconstruction of the history of certain taxa and the role of mycologists involved in it would certainly put into perspective the progress thus far made in bolete taxonomy. It would also reintroduce the contributions by Snell & Dick whose works are too often forgotten where the history of bolete taxonomy is or should have been told.

One general tendency, especially justifiable on chemotaxonomical grounds, has manifested itself rather strongly in recent times: The boletes and bolete-like families should be united into a taxon above family level. There are however — as pointed out by me (Singer, 1975) — some difficulties involved in such a procedure. Added difficulties arise when we deal with families where gastromycetous affinities have been demonstrated. If Aphyllophorales or Gasteromycetes are involved, just how far back or how far ahead in evolutionary lines should this superfamily or order reach? While we now seem to agree that mammals are not necessarily monophyletic, we do not introduce additional taxa on the same level. If the gastromycetoid and hymenogastrineous groups related to the boletes, Gomphidii, and Paxillaceae are for the time being excluded, as I would prefer to do, the remaining groups do not pass order limits, and do not, therefore, require a taxon on the level of order unless Aphyllophorales, Agaricales, and Gasteromycetes are all split into orders (as proposed by Kühner, 1978-1980 for the Agaricales sensu lato). It is therefore proposed to accept, for the bolete-like families, the rank of suborder, Boletineae, such as it has been used before (Singer, 1977) and discussed by me as a possible solution (Singer, 1975: 152-153), leaving the Agaricales as such intact (non-aphyllophoraceous Higher Basidiomycetes with autobasidia). Nearly all proposals of orders within the Agaricales sensu lato have neglected the

suborder as an intermediate position in the taxonomic hierarchy as given in the Code. Its acceptance may also lead to the recognition of Kühner's new orders (Tricholomatales, Agaricales sensu stricto, Pluteales, Russulales, and Boletales) on the suborder level although the distribution of the families in these groups will hardly find immediate and wide acceptance among agaricologists. However this may be, Boletineae as a common denominator above family rank is now acceptable as well as Russulineae for Russulaceae (*Russula*, *Lactarius*).

What families should enter the suborder Boletineae? The following Table I will provide ample choice.

TABLE I. Families of Boletineae Gilbert

Snell, 1941	Moser, 1978	Pegler & Young	Kühner, 1977-80	Singer, 1936-75 Snell & Dick	Proposed readjustment
	Paxillaceae (incl. <i>Hygrophoropsis</i> , <i>Omphalotus</i>)	Paxillaceae (incl. <i>Hygrophoropsis</i>)	Paxillaceae Hygrophorop- sidaceae	Paxillaceae (incl. <i>Hygrophoropsis</i>)	Paxillaceae (incl. <i>Hygrophoropsis</i>)
	Gomphidiaceae	Gomphidiaceae		Gomphidiaceae	Gomphidiaceae
Boletaceae	Boletaceae	Boletaceae	Boletaceae (incl. Gomphidiaceae)	Boletaceae	Boletaceae
	Strobilomyce- taceae	Strobilomyce- aceae (sensu lato)		Strobilomyce- taceae	
		Gyrodontaceae			
		Xerocomaceae			
				(Gastroboleta- ceae)	(Gastroboleta- ceae)

As for the Paxillaceae, their recognition appears to be unanimous, and only Kühner (1978-1980) seems to favor a separate family for *Hygrophoropsis*. His decision is perhaps influenced by the uncertain position of *Omphalotus*. The latter is probably but not certainly related to the Paxillaceae (cf. Chapter 3), yet a Chinese species of what is obviously an *Omphalotus* has recently been published as *Paxillus* (Zang & Zeng, 1978).

The affinity of Gomphidiaceae to the Suilloideae is not evident since spore print color, hymenophoral configuration, carpophore development, and pigment occurrence (Besl & al., 1975; Bresinski & Besl, 1979) are not alike in any *Gomphidius* or *Chroogomphus* and any species of *Suillus*, even though some identical pigments or related substances may occur in both, as pointed out by Arpin & Kühner (1977) yet this is also true if we compare the Paxillaceae with certain other bolete genera. The one remarkable similarity between Gomphidiaceae and *Suillus* is their conifer specialization when forming ectomycorrhiza. It is however incorrect to say that oleocystidia in the sense of Corner and Kühner exist only in the Gomphidiaceae and *Suillus* (they occur in some *Chalciporus*, *Phylloporus*, *Pulveroboletus*, etc.) and the *Boletus*-type of bilaterality of the hymenophoral trama is even more widely

TABLE II. Arrangement of the genera in Boletineae

PAXILLACEAE	BOLETACEAE	
<i>Omphalotus</i> (tentatively)	Subfamily Gyroporoideae:	Subfamily Boletoidae:
<i>Hygrophoropsis</i>	<i>Gyroporus</i>	<i>Chalciporus</i>
<i>Paxillus</i>	Subfamily Gyrodontoideae:	<i>Pulveroboletus</i>
<i>Phyllobolites</i>	<i>Meiorganum</i>	<i>Boletus</i>
<i>Neopaxillus</i>	<i>Paragyrodon</i>	<i>Boletellus</i>
<i>Ripartites</i>	<i>Gyrodon</i>	<i>Phylloboletellus</i>
	<i>Phlebopus</i>	<i>Leccinum</i>
GOMPHIDIACEAE	Subfamily Suilloideae:	<i>Xanthoconium</i>
	<i>Boletinus</i>	<i>Tylopilus</i>
<i>Chroogomphus</i>	<i>Psiloboletinus</i>	<i>Boletochaete</i>
<i>Gomphidius</i>	<i>Suillus</i>	<i>Fistulinella</i>
<i>Cystogomphus</i>	Subfamily Xerocomoideae:	<i>Austroboletus</i>
	<i>Phylloporus</i>	<i>Porphyrellus</i>
	<i>Xerocomus</i>	Subfamily Strobilomycetoideae:
	<i>Tubosaeta</i>	<i>Strobilomyces</i>

distributed. These are the reasons why I cannot agree to place *Gomphidius* or other Gomphidiaceae next to *Suillus* in the Boletaceae.

There is obviously a necessity to revise the limits and status of the Strobilomycetaceae Gilbert, accepted by Singer, Moser, Snell & Dick (1977), and also (but in a strong, in my opinion exaggerated, emendation) by Pegler & Young (1981). There are however too few characteristics to hold the four genera together. I propose, therefore, to restrict this group to the genus *Strobilomyces* (including *Afroboletus*), with a characteristic spore print color, development type, and some minor spore characteristics, pigments, etc. and subordinate it as a subfamily to the Boletaceae. On similar grounds, and in spite of the obvious similarities, we may also separate the genus *Gyroporus* as a separate subfamily which must be placed in the immediate neighborhood of Gyrodontoideae.

Porphyrellus, *Fistulinella*, and *Austroboletus* should then be separated from the Strobilomycetaceae or Strobilomycetoideae and be placed along with the genera *Tylopilus* and *Boletochaete* in the Boletaceae. This leaves the ex-strobilomycetaceous genera *Boletellus* (incl. *Heimiella*) and *Phylloboletellus* which must be inserted close to *Boletus* and perhaps *Pulveroboletus*.

As for the two families Gyrodontaceae and Xerocomaceae it seems to me that the hiatus between them is not comparable with that admitted in other families of Agaricales. On the other hand, if a recognition of the orders Boletales, Tricholomatales, etc. comes close to a general uplifting of taxa by one step, it would not be entirely unreasonable to raise the bolete subfamilies to families. Most mycologists will however agree that such an attitude does not contribute to any visible progress of taxonomy.

With regard to position, recognition and circumscription of the genera, I refer to the respective discussions in previous chapters.

The proposed readjusted arrangement of the genera of Boletineae is shown on Table II, above. It does not take into account any gastroid forms which are at present better accom-

modated in the Hymenogastrineae, fam. Gastroboletaceae. The one exception can be seen in the boletes supposed to have arisen by 'gastromycetation' — the 'gastroid form (?) of ' *Suillus decipiens* and perhaps some species now inserted in the genus *Gastroboletus*. Where there is enough evidence to consider them as descendants of boletaceous genera, they should, of course, be attached to the respective genus in Boletaceae. But, as we have seen in Chapter 3, the final decision is by no means as easy as it may seem to some authors, inasmuch as little attention has been paid to the type, *G. boedijnii*. It was perhaps unfortunate that the family Gastroboletaceae Sing. (1962) was based on *Gastroboletus* and thus on *G. boedijnii*, but this type species has been revised (Singer, 1973–1978) anatomically if not ecologically. The presence of apobasidia (as in *G. laricinus*) indicates that it is probably congeneric with *G. laricinus* even though the spores are generally asymmetric-heterotropic. No generalized statement should be made without a careful study of our observations on *G. laricinus* (Singer & Both, 1977). It is here suggested that a possible approach to solving the *Gastroboletus* problem would be an attempt to see whether the primordial hymenophore is formed earlier in *Gastroboletus* than in supposedly related species of spore print producing boletes.

At any rate chamonixin and boviquinone have now been established as the links between Paxillaceae and Boletaceae on one hand, Gastroboletaceae and Rhizopogonaceae (secotioid and hymenogastrineous fungi) on the other, proving chemotaxonomically the affinity of the Boletineae with the Hymenogastrineae, an affinity which has been postulated for many years by Heim, Singer, Singer & Smith, Moser, Horak, and others. The evolutionary pattern, i.e. the direction of the evolutionary lines can be deduced in either way — from the gastroid to the agaricoid-boletoid side, or vice versa. Judging the entirety of the data and arguments involved, we still prefer the former without excluding the possibility of the opposite direction having prevailed, perhaps in more recent times and in certain instances (cf. Singer, 1975, especially pp. 19–20, 128–151). 'Proof' will only be provided by palaeontological data (but cf. Singer, 1977b).

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