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The Meaning of the Affinity of the Secotiaceae with the Agaricales

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I. Introduction.

Investigations into the affinity of certain *Secotiaceae* with certain *Agaricales* have long since proved beyond any reasonable doubt that a close and demonstrable affinity exists between these groups. These investigations were carried out either with the intention to prove the existence of and elaborate on the factual material concerning the affinity of certain taxonomic groups in both orders, or else they were done with the definite aim of showing that one group is ancestral to the other. The following genera of *Secotiaceae* (and allied *Gastromycetes*) exhibit demonstrable affinities with agarics and boletes; ***Hydnangium, Elasmomyces,*** the asterogastraceous (amyloid-spored) representatives of *Arcangeliella* respectively *Gymnomyces, Macowanites,* and some other genera of the same group as defined by Malençon (1931); *Gastroboletus, Truncocolumella; Galeropsis; Thaxterogaster*; *Endoptychum*; *Neosecotium, Secotium; Montagnea*; *Setchelliogaster, Nivatogastrium*; *Brauniella* and *Brauniellula*; *Weraroa.* Other examples which might be mentioned here in relation to the problem at hand and on a tentative basis are *Le Ratia* (according to some comments by Heim), *Lentodium* (according to Martin), perhaps *Richoniella* (according to Romagnesi); furthermore gastroid conditions, in cultures, of *Psilocybe* sp. (McKnight) and, in nature, of *Boletinus decipiens* (Dodge), and carpophoroids of *Acurtis.*

Taking all this evidence together — abstracting for the moment the phylogenetic conclusions or prejudices introduced by the various authors (Buchholtz, Malençon, Dodge, Lohwag, Conard, Singer, Heim, Martin, Romagnesi, Singer &

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[1] Paper read (in Spanish) on May 12, 1958 at the III South American Congress of Botany in Lima, Perú, with a summary in German.

Smith, McKnight, and others) who were involved in this particular subject — one may sum up the situation in the following way:

Very much factual material not considered in the early phases of the discussion on the phylogeny of the *Agaricales* and *Gastromycetes* has been added, particularly since the discovery of *Thaxterogaster, Brauniella,* and the latest taxonomical work of Singer & Smith [2]). It is therefore time to re-evaluate the data now at hand, based on a much more thorough knowledge of the species and genera involved. In spite of the fact that Singer and Singer & Smith have always emphasized that the interpretation of the direction of the evolutionary trends in this case as in many similar ones is not being investigated on the same level of scientific observation as descriptive and experimental data, Heim and others have drawn rash conclusions from incomplete facts and erroneously believed to have demonstrated the correctness of their views whereas, in reality, they have only added — valid or questionable: this is a controversial question — new arguments in favor of their own predilected way of looking at the whole problem. They have come out with a hypothesis, going far beyond — though in the same direction — of De Bary's original and now classical view that derived the *Gastromycetes* from the *'Hymenomycetes"*. They have developed a theory of degradation leading from certain agaric genera by a gradual process of degradational steps, deep into the *Gastromycetes*; just how deep is difficult to establish since some texts seem to indicate that Heim and Malençon are not fully agreed in their interpretation of further evolutionary development.

This being a largely academic problem, one of those that may rightly be called theoretical, and given the impossibility, at the present moment, to come to a clear-cut and absolutely valid conclusion, it may be asked whether it is worth our while to attempt to penetrate deeper into these problems, whether indeed we should go on interpreting the scientific facts in one way or another. It is my conviction that we should. We should go on for two reasons. In the first place, the problem has stimulated much valuable research in various phases of Basidiomycete morphology, anatomy, ontogeny, cytology, chemistry, habitat and area analysis, etc. and has uncovered such valuable "links" and "bridges" that this achievement — collective if I may call it so, by mycologists of different specialities and national schools, — seems worthy of being continued. Secondly, this interpretative controversy has stirred up a distinct interest in the mycological world because here we have one of the best documented affinity lines in the cryptogamic botany with the exception of the *Pteridophyta*, a

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[2]) Singer, R. & A. H. Smith. (1958) Studies on secotiaceous fungi I—VIII. (in print)

complex of questions touching on the basic problems of fungus phylogeny because of its profound implications regarding the origin of the *Eu-Mycetes* in general. And of all question complexes that might have some bearing upon the solution of such basic problems as this, the interpretation of the interrelationship of *Secotiaceae* and other *Basidiomycetes* seems to have the best prospects of being solved. Maybe this statement is overoptimistic but considering the rate at which material for the solution of the question is being unearthed, and judging by the possibilities of future palaeobotanical discoveries, it seems to me that the possible achievement in years ahead amply justifies a continuing effort to accumulate more facts and attempt their evaluation on a phylogenetic basis. By making it appear as though the problem were already solved, we do a disservice to this cause; but by evaluating from time to time the new and old facts at hand, we drive it forward.

II. Degradationalist Theories.

I shall refer to those who interpret the facts at their disposal by implying or stating that a degradational development has started in various families of agarics independently and leads into various orders of angiocarpous fungi called *Gastromycetes* which are in consequence of this hypothesis a heterogeneous assemblage of scarcely related groups, as „degradationalists“, in an attempt to have a relatively short expression at hand. Heim and Malençon seem to be the most vociferous of the degradationalist theoreticians at present. They see in a *„Secotium“*-type of Basidiomycete an agaric (or bolete) which has, in response to environmental factors, permanently lost its ability to open up its pileus to expose the hymenophore. The hymenophore has then become irregular instead of strictly geopetalous, the basidia and sterigmata have lost their capacity to discharge the spores in the Agaricales manner, and this is supposed to explain the phenomenon of axially symmetrical spores supposedly produced in all „true“ *Gastromycetes.* Usually passing through a secotioid stage, the evolutionary lines often lead into such groups a various *Hymenogastraceae,* while some specified or unspecified part of the other *Gastromycetes* is thought to have a different origin.

In support of their hypothesis, the degradationaliste have indicated that this development is usually or always accompanied (or induced) by a trend to adapt to more or less xerophytic or hypogeous conditions. Singer & Smith have shown that such is not the case. Thus, the contention that the failure of hymenophore exposure in primordia or young fruiting bodies is actually at least sometimes of advantage in the respective groups, cannot be maintained. The usefulness of the veil has been the subject of previous discussions which started with Lohwag's observations and which may now be supplemented by new facts. In the first place, the veil is not always a consequence and inheritance of — or a development destined to lead to — a generally gastroid condition or development, but it will rise and disappear according to the specific structure and development of certain groups. If we consider some forms of veil as very definitely reflecting developmental patterns of the *Gastromycetes* in the *Agaricales,* or of the *Agaricales* in the *Gastromycetes,* we may discard the idea of the veil being a fortunate adaptation to extreme conditions, least of all xerophytic conditions since it is now obvious that in xerophytic mycofloras (puna, Chaco, desert, etc.) the percentage of non-veiled agarics is incomparably higher than the share of the veiled ons. It is certainly impossible to show that a slow process leading to more angiocarpous development and more complex or more persistent veils has gradually led to the point where the degraded (gastroid) lines begin. It would have to be considered naive if anyone preferred to argue that the slow and gradual evolution of the more complete and intricate velar systems was initiated by a conformity of ancient fungus strains with the later arising degradationalist theories, anticipating the future need for enveloping material to produce an angiocarpous carpophore. But how else interpret the biological necessity of the rise of pseudoangiocarpous Russulas with annulus originating in the tropical forest as alleged forerunners of the hypogeous degradation? Or why would *Amanita rubescens* or *A. farinosa,* relatively primitive according to that view, gradually acquire a more robust general veil and, on the principle that double is better than simple, an additional „annulus superus" and in some species traces of a thick velar structure, all not in extreme climatic conditions but in temperate woods?

Heim has vaguely referred to an explanation of the apparent problem he has offered when studying *Termitomyces.* He makes two statements implying that the existence of a veil in *Termitomyces* is advantageous. Secondly, assuming that this has been satisfactorily proved, he goes on to generalize on the usefulness of veils in fungi. One may indeed be rather doubtful about the first statement inasmuch as it is always difficult to show that an organ is actually advantageous unless there is better proof than Heim's observation at hand. The development toward or away from strongly veiled forms to little veiled forms is just as marked in *Amanita,* another genus of the same family, as it is in *Termitomyces.* But even assuming that Heim's observations imply a usefulness for the development of the carpophore in these very special conditions of rising through termite nests up to the surface, a generalisation of such a unique situation is not warranted.

The truth of the matter, as we see it, is that another hypothesis — not a new one — explains all veil formations satisfactorily by assuming that they are inherited from similarly veiled *Secotiaceae,* unless the carpophore development which makes the veil take shape is as such a derivation of a corresponding gastromycetoid carpophore development.

The question whether or not a veil will be formed, in the *Secotiaceae,* and how, is a consequence of the combination of two factors (1) the rate of growth of the apex of the stipe in relation to other parts of the fruiting body (2) the structure of the peridium and its physical properties. It is possible that more factors enter some specific cases of volva formation. The volva is, under this aspect, not in principle different from all other veil formations, but merely a form of peridial remainder whereby the continuation of the columella enlarges and stretches so much more rapidly than the gastrocarp. especially the gleba, that there is a stipe portion between peridium attachment and columella proper where the stipe or columella — it is difficult to decide how to call this part — is not surrounded by the gleba yet still within the continuation of at least an outer layer of the peridium. We can see easily in the *Gyrophragmium* („*Longula*")-complex how a volva may be inserted above the base and then be considered an „annulus' as such the basis of generic separation (in our opinion a very artificial one).

This originally rather variable and polymorphous formation of veil structures in the *Gastromycetes* has been inherited by those agarics derived from veiled *Gastromycetes.* While the veil is definitely inconsequential for the purposes of dissemination or as impeding or jeopardizing any other function of the fruiting body in the *Gastromycetes,* it may be maintained as equally inconsequential or even useful (in *Termitomyces*?) in the Agaricales. But since the biological type represented by Agaricales is one in which there is a tendency to give free exit possibility to the spores at the time of their first maturing rather than later, there is, and must be, a reduction of those párts of the covering layers which are underneath the hymenophore, in other words this whole area tends to become reduced progressively earlier in the development of the carpophore, and this is why the volva is eventually reduced to an easily disappearing pulverulence in *Amanita farinosa* whereby the diminishing application of the edges of the lamellae to the apex of the stipe also reduces the possibilities of a membranous annulus superus. Where there are no corresponding ring-formations in secotiaceous related genera, these may nevertheless be induced through the characteristic development of the respective agarics or boletes — inherited from the Gastromycetes — as for example in the case of marginal veils acquired through pseudoangiocarpous development in *Russula annulata* (according to Heim) and *Boletinus cavipes* (according to Kühner). One has only to study the development of such species as *Hydnangium carneum* to see the origin of this type of development.

We see, then, that Heim's arguments in favor of a derivation of the *Secotiaceae, Hymenogastraceae* etc. from the *Agaricales* through reduction and degradation have lost their main attraction, viz. the easy explanation of the acquisition of velar formations as a step toward angiocarpy induced by special conditions (hypogeous carpophore development or xerophytic conditions).

We shall see further on that, likewise, all other arguments given in favor of degradationalist theories are either inconclusive, or can be countered by far better ones in favor of the opposite views. Nevertheless Morten Lange (1954) not only finds Heim's (1952) point of view „convincing" but attempts to add a new argument in its favor. He starts from the thesis that medallion clamps are a supposed „aphyllophoraceous" character. Since Lise Hansen (1954) has shown that numerous species of *Agaricales* have likewise medallion clamps, Morten Lange concludes that this is a significant argument in favor of affinity of the two groups. Since the *Aphyllophorales* with medallions cannot be considered descendants of the Agricales, it must then be concluded, always according to our Danish friend, that the *Gastromycetes,* undoubtedly related to the *Agaricales,* are descendants of the *Agaricales.* He adds other supposedly aphyllophoraceous characters such as allantoid spores, lignicolous habit, rudimentary stipe, oll found in the white spored pleurotoid agarics which are therefore thought to be of aphyllophoraceous origin.

All the characters enumerated can be found in secotiaceous fungi, including the medallions. I have seen medallion clamps in *Truncocolumella citrina.* If they were actually searched for, they would be found as commonly in other groups of *Basidiomycetes* as they are now in *Agaricales,* where I had long been aware of their occurrence — but not merely in the pleurotoid white-pink-spored species. The discovery of medallions in *Truncocolumella* should, with the same kind of logic, lead to the conclusion that *Truncocolumella* is related to *Paxillus* (which it is, at least indirectly), and to *Merulius* (which it is not). Without a thorough analysis of the tissues of not merely the *Agaricales* but the *Gastromycetes,* the medallion clamps will not add anything to the problem at hand.

It is true that allantoid spores are mainly found in those groups that are, always according to M. Lange, candidates for a closer relationship with Aphyllophorales, but then they are generally common in wood-inhabiting species where there is a tendency towards elongated hyaline spores. Wood as habitat does not necessarily express an affinity with the *Aphyllophorales* inasmuch as innumerable *Aphyllophorales* are not wood-inhabiting and numerous *Gastromycetes* (including *Weraroa, Secotiaceae)* are, not to mention the

Naematolomas, Naucorias, *Phlebopus sulphureus,* etc. Furthermore, it is not correct to introduce here, as M. Lange does, the metuloids as being a specifically aphyllophoraceous character (although the term was first employed for *Peniophora* cystidia and introduced into agaricology by me). Typical metuloids are found not only in those pleurotoid groups considered as close to the Aphyllophorales by some of our colleagues, but in *Marasmius* (where they also occur in correlation with narrow curved hyaline thin-walled spores), in *Pluteus* (e. gr. *P. amphicystis* Sing.), *Copelandia, Psathyrella, Inocybe, Galerina, Pseudohiatula, Xerula,* to mention only a few.

Lange mentions in his paper that Kühner (1948) suggests that *Paxillus* occupies a position intermediate between the *Boletaceae* and the *Aphyllophorales.* Although Kühner is not in favor or at least is on record of not having been in favor of my interpretation of the affinities existing between Agaricales and *Gastromycetes,* the paper quoted is, as usual in the case of this excellent and conscientious scientist, a perfectly objective and factual account and attempt at interpretation of the facts which are observed in the taxonomy of the *Paxillaceae, Gomphidiaceae, Boletaceae,* and *Strobilomycetaceae.* In fact the only difference in the final conclusions of our French friend and colleague seems to be that he does not give the veil as such a phylogenetic significance as a primitive character, but rather suggests that it might be an evolved character if only the European flora is considered. It is true that he considers the *Paxillaceae* as the probably most primitive group in the complex *Paxillus-Gomphidius-Boletus* sensu lato, and *Paxillus,* for him, is evelate. He gives, furthermore, a truly objective account of the reasons why the veil may also be interpreted as a primitive character. I wish to add at this point that my foregoing discussion of the significance of the veils in the *Basidiomycetes* represents rather an approach towards Kühner's point of view, insofar as the veil is here, and particularly in cases comparable to that of the *Boletaceae,* not any more considered an a priori primitive character but rather one with diminished phylogenetic significance or perhaps not necessarily primitive. On the other hand, Kühner was at that time not aware of the fact (neither was I) that *Paxillus* contains two strongly veiled species in Southern South America (by the way a center of distribution of that genus). If it is, therefore, clear that there are no major differences of opinion between the article quoted by Lange and my own present views, it is not equally clear to me which part of Kühner's article could have been so interpreted as to suggest an intermediate position of *Paxillus* between *Aphyllophorales* and *Boletaceae* since, in reality, it suggests an intermediate position between white-spored agarics and *Boletaceae* — a suggestion which had already been taken up by me in my treatment of ***Hygrophoropsis*** (***Cantharellus*** p. p.) and ***Cheimonophyllum*** (***Pleurotus*** p. p.) with the ***Paxillaceae***.

While Lange's misquotation or misinterpretation of Kühner's words is obviously an exception and an error easily explained by an author's wish to find other expressions of similar speculative thought, it must be mentioned here that Heim's discussions on the subject contain almost regularly quotations of my opinions which, in that form, have never been expressed. It is of course the easiest thing in the world to convince others by quoting an obviously wrong statement and then proving that it is wrong, or by quoting another scientist as having expressed the same views as those one wishes to expose. I have already mentioned this fact in previous papers. I have only to add that I have never said that the boletes have polyphyletic origin (since I share Kühner's opinion about their almost monophyletic origin), a question about which my earlier papers as well as Lilloa **22**: 642 1949 (1951) are quite eloquent. I have the impression that Heim's failure to understand them has a very simple and innocent reason: language difficulties [3]). Moreover, there might be, here and there, in literature, a bit of an isolationist tendency which leads to a certain disregard for foreign contributions in general [4]) However, while even a local flora suffers from a disregard of the work of extralimital writers, it is completely impossible to judge a complex phylogenetic problem without weighing with equal thoroughness all available facts wherever they may come from.

Under the circumstances, one is surprised to read that my Danish friend adds to the anatomical evidence provided and to a rather obscure quotation of Kühner a further, somewhat personal „argument": He finds Heim's (1952) point of view „convincingly advo-

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[3]) Misquotations can be found in Rev. Mycol. **10**:6. 1945 (1946); Trans. Brit. Mycol. Soc. **30**:174, 175. 1948; Rev. Mycol. **15**:9 (foot note 1). 1950; **16**:141, 151. 1951.

[4]) Thus, Heim consistently quotes my pre-thesis edition of the „Monographie der Gattung *Russula*" (Hedwigia 1926) instead of the later and completer edition of 1932; he omits in his newest works all reference to my role in the history of the study of the hallucinogenic mushrooms, or to my (with A. H. Smith) publication on *Kühneromyces* (proposing a new genus for it). This spirit is also well expressed in Romagnesi's —by the way very favorable — review of my *Agaricales in modern taxonomy* where he gives, aside from some useful suggestions which we have not hesitated to accept and adopt, the following example of the spirit of geographical limitation I have mentioned: „On ne manquera pas de lui reprocher d'avoir poussé trop loin l'esprit d'analyse ... en attribuant une place déterminée à beaucoup de genres et espèces exotiques encore mal connues". As I have explained in the work analysed by Romagnesi, only those genera and species which were completely known at the time have a definite place in the classification; those exotic forms Romagnesi does not like to see represented are merely the ones neglected and ignored by some Europe-centered mycologists.

cated". I cannot see why, in the evolution of plants or animals, a spiral evolution, starting from a point A and moving to a point B, should not lead back, on a higher level, to a point A; in other words, the tendency from the gymnocarpous to the hemiangiocarpous and angiocarpous development, provided it were proven, does not necessarily imply that it is irreversible, or that a contrary evolutionary trend is impossible in some other part of the history of fungi. Shortly, we do not find Heims argument as convincing as he or Malençon, or for that matter, Morton Lange[5]), since it overworks the analogy taken from the supposed evolution of the *Tuberales* from cup fungi and the „true" *Gastromycetes* from, apparently, some gymnocarpous ancestor, to such a degree as to deny the possibility of doubt in these cases, and the admissibility of a reversed trend in others.

Since most of the literature commented on in the preceding paragraphs goes back to the manner of thinking introduced by Malençon (1931) which is a reversal of the earlier by Buchholtz (1902) and an elaboration on the now classical one of De Bary and Fayod (1889), we may as well reconsider its main argument. For Malençon, his Asterosporés Quél. em. show only an apparent similarity with the „Agarics vrais" — here we have a forerunner of the division in *Gasteromycetes agaricoides* and *Gasteromycetes vrais* — while in reality they are sharply divided from the latter, first and principally by the „nature toute spéciale de la chair dont ils sont formés", i.e. their heteromerous tissues. Right away, we wish to interpolate here that we know now that this structure is also found in other *Gastromycetes,* a fact we shall not only demonstrate but explain later on. The singularity of the macrocystidia (not so called at that time by Malençon) is likewise debatable since pseudocystidia with corresponding reactions occur in the genus *Lentinellus.* Malençon, furthermore, insists on the ornamentation and chemical reaction with iodized liquids of the basidiospores which he believes to be a common character of the whole series from *Russula* to *Hydnangium* and *Octaviania* while, in reality, we know very similar spores in genera as far removed from the Asterosporés as the genus *Bondarzewia* (polypores) while *Hydnangium* has, at least taken in the sense as com-

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[5]) Reading the paper quoted by Lange, one cannot help wondering whether Malençon (1931) with his admirable paper on the *Série des Asterosporés,* has not started a chain reaction, convincing by his well presented thesis Heim who, in turn by the time the Torrendia paper — equally excellent — was ready for publication had again convinced Malençon (1955) whose strongest argument against derivation of secotiaceous *Gastromycetes* from *Gastromycetes* of the type *Torrendia,* is the fact that Heim showed this to be impossible. True to this merry-goround, we shall soon read that someone was convinced by Malençon „showing" that there are two phylogenetically completely different groups of so-called Gastromycetes, by studying the development of *Torrendia.*

monly interpreted, non-amyloid spores. The same is true for *Octaviania.*

Malençon proceeds then, arbitrarily, to call (rightly but without proof) the *Russulaceae* the „Asterosporés Supérieurs" which, allegedly have the following characters: Epigeous growth, a peridium (pileus), stipe, basal mycelium, lamellate hymenium (hymenophore) open towards below; spherocysts, lactifers (laticiferous hyphae), tetrasporous basidia, cystidia, subglobulose spores with asperities violet in iodine. As some of the characters here enumerated do not show up or are different in the „lower" groups, it is then assumed that the latter are members of a line of regression. The affinity of the series, enlarged by Malençon, but nevertheless mainly the same as studied by Buchholtz, Lohwag, and others before him, with the agaric genera *Russula* and *Lactarius* was nothing new. What was new and valuable in Malençon's treatment was the comparative anatomy approach. This approach helps arranging the various types in relation to the *Russulaceae* on one end and *Hydnangium* and *Octaviania* on the other, but it also helped create a phylogenetical dogma which I now call degradationalist although the latter term was created by Heim.

Which are the reasons given in 1931 which lead Malençon to accept a direction of an undoubted evolutionary trend which has later been generalized for all *Secotiaceae-Agaricales* relations as the direction more probable or less improbable than any other?

Malençon says that the spore regression takes place in four stages which are parallel with the embryology of the spore (but obviously in a reversed form, it being the *Russulaceae* which reproduce, in their sporogenesis, all four stages from *Octaviania* upwards as visualized by Malençon, viz the stage of a simple sphere, secondly an ovoid to subglobose spore symmetrically attached, thirdly piriform with the ventral region well developed but not recurved, finally the well-known shape of the eccentrically attached mature *Russula* spore). According to the Haeckel rule one might then assume a progressive differentiation. Malençon does not. He sees in the veined „plage" at the base of the peridium (or better gastrocarp) of *Arcangeliella* not the simple beginning of a zone of hymenophore or „a local absence of the peridium" revealing a structure reminiscent of the early configuration of the agaricoid hymenophore in the primordia of *Russula,* but „the homologon of the entirety of the lamellae edge of *Lactarius* and *Russula* whereby its upper limit corresponds to the margin of the pileus in these agariciform genera". While we do not doubt the existence of homology between this structure in *Arcangeliella* and some part or stage of the agaricoid hymenophore, this observation is *not* forceful for us as far as the direction of the evolution is concerned. Besides, we find structures much more similar to the glebal construction of the *Secotiaceae* in ***Russula*** (poroid and strongly anastomosing lamellae in ***Russula delica*** and other species) than the basal veins of some of the „asterogastraceous" genera are to the lamellae of the ***Russulaceae***. It would, on the contrary, appear that a regularly formed organ is the higher developed, thus more recent one as compared with the irregular one, particularly considering the biolgical advantage a tendency toward regularity bears for the ***Russulaceae***. But then, the term „degradation" would seem to take care of this common-sense argument and imply that the higher form deteriorates and regresses to a pseudo-primitive one.

There are, at every corner, in Malençon's paper such words as „still", „already", „lost" and „remained" which suggest a dynamism which has not convincingly been shown to exist but was merely implied. The most serious drawback of Malençon's paper is the incompleteness of the descriptive data for each of the authentic representatives of the genera studied. By hindsight, it is now easy to register some other shortcomings such as the indiscriminate use of the word cystidium since the macrocystidial type is not the only one found in asterogastraceous genera; consequently, here, we do not deal with a continuous series of degradation; indeed, the existence, in the Australian species *Cystangium sessile* of true cystidia of the leptocystidial type might be used as an argument for the non-acceptance of the degradationalist theory. The basidia, on the other hand, are not by any means, as assumed by Melançon „constantly tetrasporous" in ***Lactarius*** and ***Russula***. I have observed — and published on — two-spored (not mixed 2—3—4-spored forms which are common in certain sections) races of certain species of ***Russula***. This evidence — which, in part, had appeared after the publication of Malençon's paper — contradicts the hypothesis of a regression of the number of sterigmata (the only valid argument since a number smaller than a regular tetrad would have to be recognized as possible regression) inasmuch as *Macowanites* is not, as formerly assumed, different from ***Russula*** in this regard, and the frequent occurrence of mono-, and bi-sporous basidia in the more typically gastroid forms cannot be judged unless it is accompanied by studies of a cyto-taxonomical order which will show the significance of the various forms of sexuality for certain biological types, as for example the special condition of angicarpous hypogeous carpophores in relation to spore dispersal and chance meeting of primary mycelia with different polarities.

The most interesting, and by the way most quoted and original part of Malençon's work consists in the appraisal of the spore development types described and illustrated by him. Although (as partly recognized by Malençon himself in later papers) there is more variability and diversity in this regard — especially if considered as a whole: spore-sterigma-configuration — than anticipated in the paper of 1931, it gives a completer picture of the situation than in regard to the other aspects discussed by him. Nevertheless, there is not, as foreseen by Malençon any demonstrable parallelism between spore development and carpophore development, as soon as numerous forms of this series are studied. The level where, according to Malençon, an intermediate microchemical stage has been reached (*Hydnangium* with supposedly amyloid spores whereby the amyloid mass is restricted to the tips of the spinules) is at least debatable and may either be not a general character of the genus in question but an extraordinary, rare phenomenon, or else a mistake in observation. We have not been able to study authentic material of *Martellia mistiformis,* but the figure showing one spore of this species does not represent a case different from cases frequently seen in *Russula* and *Lactarius,* Crawshay, pl. 5, no. 7 a, and 6, no. 7 b being examples (whereby the more oblique covering of the amyloid substance or amylon mixture can be explained by the more irregular distribution of the ornamentation and the heterotropic character of the spore development). Consequently, the graduality of the „disappearance" of the amyloid reaction of the spore ornamentation or, expressed more correctly, the secondary ornamentation of the spores in the astrogastroceous series, may be doubted; but at any rate, even if demonstrated for the respective species, it would hardly be a proof of regression since with at least the same right we may assume gradual acquisition of this chemical character which would have to be studied with an eye on the questions of biophysics and spore growth mechanics first touched by Locquin (1948).

There is, however, in Heim (1937) the first attempt (p. 181, 9°) to use Malençon's data as support for the degradation theory conceived as such for the first time. In Heim (1952), somewhat later, the same hypothesis is developed with shorter words, with reference to three witnesses: Buchholtz, Malençon, Heim. As we know, Buchholtz was the first to suggest the affinity of *Russula* and *Elasmomyces* (etc.) — in the opposite direction; Malençon has merely given an *opinion* without forceful arguments, and Heim is only repeating himself in this regard.

It is not a pleasant task — and not one easily abbreviated and dealt with without at least an outward appearance of polemical writing — to go through the literature of phylogeny of *Basidiomycetes* with an endeavor of showing the absence of proof or claim to superior probability as far as a hypothesis is concerned which, in some of these papers, is presented as scientifically „refuting", excluding, or what not, any theory which does not appear to be compatible with that of its critic[6]). I had to emphasize repeatedly that a scientific proof or an accumulation of facts so overwhelmingly pointing towards one of the two main phylogenetic possibilities that it would be unreasonable to persist in giving any credit to the opposite one, cannot be hoped for at the present time. With the present methods and materials, any such claim would be unrealistic, exaggerated, and pretentious. The foregoing paragraphs were unfortunately necessary to show that the theory of Brefeld, Buchholtz, von Höhnel, Lohwag (in their general postulates rather than in detail) and the phylogeny worked out as the most probable by myself and supported by Dodge, Zeller, and to a certain point by Gäumann had not in the least been weakened by any facts discovered since 1931, or by any reasoning introduced lately.

As a supplement to the critical revision of the main degradationalist literature, it seems to be necessary to mention also some recent writings which, although they do not contribute new facts in favor of the degradationalist view-point, are presented as or may be interpreted as supporting it.

G. W. Martin (1956) has studied *Lentodium squamulosum* Morgan which, with a single exception, had until then been considered an aberrant form, abnormality, or mutation of *Panus tigrinus*. Martin, on the other hand, citing a paper by Lyman (1907) showed that the two genera — *Panus* and *Lentodium* — are not identical, and that *Lentodium* is often fertile, having a different area and being constant in its characters which are somehow gastroid — a conclusion which I (1951) had mentioned likewise although, not knowing the fungus from collections in nature or from fertile material, I had accepted the Berkeleyan tradition which considers *Lentodium squamulosum* and *Panus tigrinus* congeneric (if not conspecific). Martin goes on to state that *Lentodium* is another case which must be considered in the light of the strong evidence of relationship existing between various agarics and the gastromycete-like genera such as *Galeropsis, Endoptychum, Thaxterogaster.* So far so good. I am perfectly willing to admit that Dr. Martin who has had fresh wild material, fertile material and cultures of this species, has been able to show that I was wrong considering *Lentodium* a synonym of *Panus,* and did

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[6]) „... et la théorie de H. Lohwag-R. Singer est alors en défaut.“ (Malençon 1955) — „It seems under those conditions that the trial of the ascension theory must be closed and, as Heim (1952) has written ..., it is not possible any more to see in the *Gastromycetes* the origin of the *Agaricaceae* as H. Lohwag an R. Singer thought“ (translated from the same paper, p. 126). — „The hypothesis of our friend R. Singer seems to be refuted“ (Heim 1948). — „Rien ne nous semble autorizer notre excellent collègue Rolf Singer a maintenir l'hypothèse qu'il a soutenu jusqu'ici sur le sens vraisemblable de l'Évolution chez les *Basidomycetes*“ (Heim 1951).

not sufficiciently emphasize the gastroid character of the former. However, it seems to me that his further conclusions are entirely taken from the literature we have just shown to be inconclusive so that there is really no basis for his finding Heim's (1952) "answer" to the comments I had made regarding *Thaxterogaster* (Singer 1951) "convincing" and his final conclusion that "the existence [of *Lentodium*] furnishes an addition to the arguments favoring a derivation of the *Exogastrineae,* in Malençon's sense, from the agarics, as favored by Heim, rather than the reverse, as maintained by Singer"[7]).

McKnight (personal communication 1953, 1957) has been able to control the development of *Psilocybe* sp. in his cultures so that a gastroid aberration could be produced at will in laboratory conditions. This might be interpreted as a hint as to the origin of gastroid forms in response to environmental stimuli even in such families where no gastroid phylogenetic bridges had been discovered at the time. We shall see later that it is perfectly logical to consider such aberrations as atavistic and we shall also see that the negative proof based on the absence of a certain theoretically postulated organism in nature has, here as in many previous cases, turned out a dangerous tool in the hand of the phylogeneticist. As a matter of fact, Singer and Singer & Smith (1958) are now able to demonstrate that the *Strophariaceae* are closely related not to one but five different species of *Secotiaceae,* one of them particularly close to *Psilocybe.*

To think that the degradationalist hypothesis gains by showing that not all families of *Agaricales* can be linked with recent gastroid

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[7]) Unfortunately, even as quotations, the literature cited by Martin does not indicate what Martin states. Heim (1931) does not show that *Galera besseyi* was a gastromycete derived from *Galera* inasmuch as the species he calls *G. besseyi* (in reality not conspecific with the North American species) was described by him in a new subgenus *Cyttarophyllum* of *Conocybe,* an agaric. Velenovsky (1930) had not, independently, come to a similar conclusion since he did not comment on the position of the genus *Galeropsis* and, even less, on the phylogeny of this genus. The first author who recognized *Galeropsis* as a secotiaceous gastromycete was the writer of these lines (1936) when he — also for the first time — gave credit to Heim for his general statement regarding the affinity of some ocher-spored agarics with certain *Gastromycetes,* which had been shown to be correct through the example of *Galeropsis* as studied by Singer. Heim has actually linked what he considered a subgenus of *Conocybe (Galera)* with Podaxaceae or *Secotium,* an approximation where precisely the gastromycetous *Conocybe*-like link was missing. The fact that Heim later, much after my contribution recognized *Cyttarophyllum* (Heim) Sing. to be a synonym of *Galeropsis* and thus as a Gastromycete („agaricoide") cannot change the historical sequence of things.

Table I.

Families of *Agaricales*	Intermediate forms *	*Secotiaceae directly* linked with *Agaricales*	*Secotiaceae* indirectly linked.	Non-secotiaceous *Gastromycetes*
Hygrophoraceae				
Tricholomataceae	? *Lentodium*			
Amanitaceae *(Pluteeae)*	←	*Brauniella* ← *Brauniellula*	←	*Torrendia*
(Leucocoprineae)			← *Neosecotium* →	*Lycoperdon*
Agaricaceae *(Agariceae)*	*Agaricus* (poroid)	*Endoptychum*	*Secotium* ↑ ← *Gyrophragmium*	
Coprinaceae	? *Xerocoprinus*	←	*Montagnea*	
Bolbitiaceae		← *Galeropsis*		
— *(Pleuroflammula)*		← *Setchelliogaster* ← *Nivatogastrium*		*Hymenogastraceae* p. p.
(Pholiota)		←		
Strophariaceae *(Psilocybe)*	*Psilocybe* gastr. form.	← *Weraroa*		
(Melanomphalia)	←	*Setchelliogaster*	„*Secotium*" conei	*Hymenogastraceae* p. p.
Cortinariaceae *(Cortinarius)*	←	*Thaxterogaster*	←	
Crepidotaceae		*(Setchelliogaster)*		? *Hymenogastraceae* p. p.
Rhodophyllaceae	Acurtis forms		? *Chamonixia*	? *Richoniella*
Paxillaceae				
Gomphidiaceae	Secotioid *Gomphidius* leg. A. H. Smith)	← *Brauniellula*		
(Xerocomoideae)		← *(Brauniellula)*		
Boletaceae *(other groups)*	*B. decipiens,* gastr. form.		} *Truncocolumella*	? *Rhizopogonaceae*
Strobilomycetaceae *(Boletellus)*	←	*Gastroboletus*	*Chamonixia*	
(Russula)	←	*Macowanites*	← *Elasmomyces* & allied genera incl.	*Hydnangium soederstroemii*
Russulaceae *(Lactarius)*			← *Gymnomyces* ss. Dodge	↑ *Octaviania*
?			? *Le Ratia* ? *Rhopalogaster*	? *Rhizopogonaceae*

*) Gastroid formations and carpophoroids of *Agaricales* and incertae sedis.

ancestors can in the long run scarcely be of much use to the authors who prefer such hypotheses since the links become gradually more numerous (see table 1), and the still un-linked families may conceivably be linked secondarily — i.e. from inside the *Agaricales*. The interpretation of a laboratory experiment can only be given in correlation with facts observed in nature. If environmental factors induced the start of several phylogenetic degradational lines towards gastromycetous habit and development patterns, the supposed beginnings of such a trend in nature must have produced gastroid forms and carpophoroids together with normal agaricoid fruiting bodies at the same place according to certain (apparently light) conditions prevailing at certain times. This would assume a better adaptation to certain conditions on the part of the secotiaceous forms than on the part of the agarics. Since we know now that the *Secotiaceae* (e. gr. *Weraroa*) which — according to this way of thinking — would have evolved from a *Psilocybe* like the one studied by McKnight are neither hypogeous nor xerophytic, but on the contrary, more hygrophilous and generally lignicolous, the value of these cases as demonstration of a first rise of gastroid fructification by failure of hymenophore exposure, callapses. Many agaricologists will also be aware of the fact — from direct observations in field and laboratory — that diseases (other fungi, bacteria) can lead to a failure to open up. And such carpophoroids as those of *Acurtis giganteus (Rhodophyllus abortivus)* are not adaptations since they are either sterile or show reduced fertility, yet occur so regularly together with the „normal" agaricoid fruiting bodies that the existence of the carpophoroids is actually a character by which the species can be recognized in the field. The same is true for the carpophoroid, less regularly found, of *Boletus rubricitrinus,* which corresponds perfectly well with that of *Boletinus decipiens* except that the latter is fertile, the former sterile. All these facts are available for study by those unfamiliar with them, yet, it would be futile to ignore or misinterpret them in order to maintain a prejudice.

The behavior of the carpophoroids and the atavistic aberrations of *Psilocybe* are not as extraordinary phenomena among fungi as may be assumed. The capacity of some *Basidiomycetes* and *Ascomycetes* to reproduce sexually is often exclusively laboratory-induced and there is no indication that these forms are produced as phase of a regular life cycle under natural conditions, where asexual spore production is the only one known. Apparently, some gene-controlled functions are inhibited by other functions whose artificial suppression will bring the inhibited function to the surface; or else a minor mutation — loss of one gene — may lead to aberrations, often useless and wasteful, that appear as a reconstruction of an ancestral function (or lack of one). It seems to me that this way of interpreting phenomena of similar patterns is much more realistic than the illusion of having nature demonstrate, before your eyes, just how she has evolved to produce the Secotiaceae, or, for that matter the *Ascomycetes* (starting from *Hyphomycetes*), etc.

A further dogma of the degradationalist theoreticians is the gradual transformation of the morphology and function of the spore producing apparatus, the basidium-sterigma-spore configuration. If a single gene can regulate the transition from the agaricoid type of spore production with discharge to the gastroid spore production without discharge, it must be assumed that the same can be achieved in the reverse direction, i.e. by a single mutation. The stimulus favoring competition would be, in one case, dropping of an apparatus which has become useless, while in the other direction it would mean acquisition of an apparatus useful for spore-discharge and spore dispersal under conditions of hymenophores constructed so as to allow for free escape of the spores, or autodeliquescence. If it is permitted to think that this happened independently at several points of the ramified *Agaricales* system, it is also permitted to think that it happened more than once in different genera of the *Secotiaceae,* with reversed direction. However, this whole reasoning may be something of in oversimplification. The gradual transformation in some cases, and the incomplete transformation with a high degree of variability maintained in the gastroid forms, seems to point at a different possibility. There would indeed at first occur the omission of the drop of liquid formed in the Agaricales at the inner suprahilar region, then the sterigmata would straighten out and become more strictly apical, and the spores would at first still be eccentrically attached with an oblique hilar appendage which would eventually become straight and the spores axially symmetric. All this would happen in such a manner as to allow for the coexistence of different configurations in a single species or genus, often on a single basidium. This would happen not only in genera still close to the *Agaricales* but in such genera as *Torrendia* where the spores are by no means all symmetric and the sterigmata all gastroid but some sterigmata are less apical than others and these more than others show a tendency to be recurved to a vertical position and the spores arising from these might be eccentrically attached. This gradualness of development and variability of configurations makes it improbable that one loss of a gene regulates the whole process, and we may assume that the transformations after the initial loss of the capacity for discharge have been separately induced. But what is the biological basis of such an inducement? Is material to be saved, competition made more effective? An oblique hilar attachment of a globose spore as still seen in many *Gastromycetes* which have evidently no capacity of discharging basidiospores, does not seem to be a handicap of any sort. Looking at it, however, from the opposite point of view, we assume an originally inherited instable and somewhat variable basidium-sterigma-spore-configuration, not the loosening of an originally stable condition.

We do know that the *Lycoperdaceae* are related to the *Secotiaceae* (as we have mentioned above), and we know likewise that the *Tulostomataceae* cannot but be related to the *Lycoperdaceae* in spite of differences in the spore production. It must therefore be assumed that at a certain early stage of basidial evolution in the *Gastromycetes,* the apical position of the sterigma was not at all a fixed one, and the somewhat lateral sterigmata had a tendency to curve up. It is also possible that in certain *Gastromycetes,* in contrast to the *Agaricales* and the majority of the *Aphyllophorales,* basidia are frequently in a position so as to produce the sterigmata on the upper side (in the sense of away from the earth) which in the case of large heavy-walled spored which do not separate early could have induced a bending of the sterigmata (a hypothesis which might be considered not improbable since in the *Secotiaceae* the sterigmata are not always either straight or bent half-sickle-wise inward, but at times one or more of the strigmata are bent outward), a position which might have become stable through later adaptive compensation through reinforcement of the sterigma walls in a later stage of the sporulation process. A further inducement to curving may be seen in the fact that, in many *Gastromycetes,* the loculi or veins covered with the hymenium are at least in some portions of the carpophore so narrow that the long-straight-erect sterigma of the „typical" Gastromycete would interfere with its opposite hymenium; anyhow, less space needed through lowering of the spore in acystidiate forms would make it possible to achieve earlier maturing, and earlier maturing would necessarily take place in smaller cavities.

It is difficult to tell which of the three suggestions correspond to the historical reality of evolution in the *Gastromycetes,* but it is rather obvious that the curving of the sterigma is not necessarily to be considered a „hangover" of the free spore discharge mechanism in the *„Hymenomycetes".* But once originated by whatever the reasons, the curved sterigma will eventually become the „sine qua non" of free spore discharge in the *Agaricales.*

The spore development is closely linked with the shape of the sterigma, inasmuch as a mechanical explanation of the evolution of the shape of the latter would likewise take into consideration the fact that a spore, at maturity, whose longitudinal axis continues the direction of an oblique sterigma, will exercise a far greater tension upon the sterigma wall (in those cases-characteristic for *Gastromycetes,* when the basidium is not horizontally extended) than a spore recurved so that its axis becomes parallel with the axis of the basidium.

Furhermore, the denser the hymenium becomes in the highest forms of the *Secotiaceae,* the less mutual interference in sporulating basidia may be expected if the spores are recurved which will of necessity make them axially asymmetric or rather heterotropic.

If, then, the half-sickle-shape of sterigma and spore asymmetry are both chracters which may very well have arisen directly from a selective process deep in the gastromycete ascendency — and, it would seem, have done so not only possibly, but probably (since in *Torrendia* and other „true" *Gastromycetes* spore asymmetry and curved sterigmata do exist) — it would seem that only one step more is now needed to produce an agaric according to definition, i.e. a highly developed Basidiomycete which, in contrast to its ascendants has the capacity to discharge spores by separating them from the tip of the sterigmata by a certain force so that, if the pileus is placed on a horizontal surface a spore deposite is formed (the „spore print"). The constant and decisive difference between a secotiaceous Gastromycete and an agaric or bolete is the incapacity or capacity to deposite a spore print.

The capacity of producing a spore projection from the sterigma-basidium complex depends apparently on two conditions: (1) the sporulation time must be postponed (2) spore fall must be possible, i.e. the hymenophore must permit free spore fall to the outside at the time of maturity. The first of these conditions can occasionally be observed in the *Secotiaceae,* for example in *Macowanites americanus.* The second is often naturally present even in a relatively early stage of evolution. At any rate, it must exist in order to produce an agaric or bolete. Wherever these conditions are realized, only one, and this time a physiological — change is needed to make the virtual agaric or bolete a functional agaric or bolete. The biophysics of the phenomenon of spore discharge in agarics has not been studied sufficiently as to speculate on the conditions under which the exudation of the watery droplet at the suprahilar region of the spore (when still attached to the sterigma) takes place or under which conditions the osmotic forces act in such a way as to forcibly project the spore.

It is idle, at present, to theorize whether the exposure of the sporulating hymenium to the outside and its brusquer temperature and moisture changes, and/or the predominantly horizontal position of the basidium and/or the more advanced age of the fruiting body at the time of sporulation of the agaric have anything to do with this physiological change, and in which way.

It is then by a selective process, perhaps slow and little uniform, that we visualize the beginning of the anatomical-morphological basis of he spore discharge apparatus, still well within the Gastromycetes. The basidium will finally, by the logic of necessity, become stabilized in a constant and uniformly „hymenomycetous" type of development, and this will cause the same to happen to sterigma and spore. The final, most important step is dependent on a certain characteristic development of the overall morphology and ontogenesis of the carpophore, and where this is realized, a single mutation, physiological rather than morphological, will create the first agaric in the proper sense, i.e. not a morphological agaric as *Macowanites* or a morphological bolete like *Gastroboletus,* but a spore-shedding agaric like *Russula* or a spore shedding bolete like *Boletellus.*

This step-by-step progressive evolution of the basidium-sterigma-spore configuration and its development from basidiole to spore separation coincides in a reversed direction with Malençon's four-step „regression", except that the last phase, the globose *Sclerogaster* spore is not taken into consideration since we do not believe that the spore form is anything but a character of a definite line of evolution such as the astrogastraceous series, but not an integral part of any generalized evolutionary trend.

The foregoing hypothesis is the logical one to assume in order to explain the facts actually observed, facts that cannot be explained by the degradationalist school, or, in some cases, at least not any better. The theory which includes the thesis of ascendance from *Secotiaceae* to Agaricales does not, by any means, stand or fall with the correctness of this hypothesis. Furthermore, the hypothesis of sporogenesis evolution just developed above is not the only one which might possibly explain the facts supporting the ascendance theory. But at the present moment it seems as good a thesis, taken separately, as the thesis of regression in spore production types advocated by the degradationalist theory.

Our thesis covering sterigma-spore evolution has, moreover the great advantage that it starts at a point of evolutionary flux and instabilitiy which may logically lead to many types of basidial development, including the obviously highest — achieved in the Agaricales, white Heim and Malençon are handicapped by the manifest improbability of a basidium already stabilized from the primitive *Homobasidiales* upwards all through the *Aphyllophorales* and the *Agaricales* — far beyond the point where an instability is still demonstrable (as in *Tremellodendron* and related holobasidial groups) — only to degenerate into a new and repetitive instability in the „degraded" gastroid forms. By the time the „hymenomycetous" holobasidial basidium-sterigma-spore configuration, basically constant while passing through the evolutive process of two orders (always according to degradationalist theory), has reached the level of angiocarpy in the *Secotiaceae* and hymenogastraceous relatives of the latter, it is described as not only changing fundamentally to become increasingly „gastromycetoid", but it also falls back into types long since overcome, for example the up to 8-spored basidium in several of these fungi, and even the stichobasidium (in *Alpova*). To propose this thesis is, in my opinion, asking too much of the imagination of the mycologist. On the other hand, if we assume that in two separate but parallel cases the *Basidiomycetes* have passed through an initial phase of basidial instability in morphology and function, in a gastroid main branch as well as in a hymenomycetous main branch, and early in the former a further development towards the agaric basidium and sporulation type has taken place, we avoid trying the sense for the probable and remain in agreement with theory as well as facts.

III. Arguments in Favor of Ascension from the Gastromycetes to the Agaricales.

At this point — after having discussed the main contentions, as I see them, of the degradationalists — their and the opposed theory are perhaps on an equal footing, at least as far as we may go with rational means rather than with quoting of authorities or intuition.

But from this point onward, I propose to submit a number of additional arguments — some of them perhaps not strictly new, but not before made part of a concerted effort to interpret the facts observed in the *Secotiaceae* studies — which, taken isolatedly are not very persuasive, but taken as a whole should not fail to convince the unprejudiced that a certain amount of preference, arrived at by careful weighing of all the arguments, belongs to the view that the Agaricales are descendants of *Gastromycetes,* mostly *Secotiaceae.* This does not by any means im ply that Lohwag's theories on morphology and the whole of his views on veils and on the homologies of Basidiomycete structures should be accepted. It should also by no means imply that Brefeld or Buchholtz were reasoning in a similar way as the modern authors, and it shall not be denied that for example Malençon who has added a great deal to our knowledge in this field as early as 27 years ago, has actually given proof of very astute judgement. If we name the mycologists just mentioned we merely wish to identify, by their names a certain trend of phylogenetical thinking.

1. Taxonomical approach. Taxonomy can teach us a number of things about the probable direction of the evolutionary trend. Since conclusion of the studies on secotiaceous fungi by Singer and Smith, we are in the possession of new data which throw a new light on some of the issues. For example, one would justifiably expect a line of degraded units starting from certain points of the *Agaricales* system to remain within, at least, the pattern of the family, if not the genus from which they supposedly originated. If the projections of Agaricales groups into the *Gastromycetes* — such as a

degraded descendant from the *Bolbitiaceae* — is actually discovered, not once but twice, and shows characters not only of the *Bolbitiaceae* but of neighboring families, one is led to believe that what really has taken place is rather the development of a line of units leading from one intermediate position in the gastroid sphere to two recent taxa in the *Agaricales.* Concretely speaking, *Setchelliogaster tenuipes* has the external peridial layer of vesiculose elements which may be expected to be transformed, in the course of further evolution, into the hymeniform epicutis consisting of vesiculose bodies characteristic for the *Bolbitiaceae;* yet sporal ornamentation is of a type not found in the *Bolbitiaceae* but in the *Crepidotaceae* and *Cortinariaceae,* especially *Melanomphalia. Truncocolumella citrina* has a hymenophoral trama intermediate between the *Phylloporus* type of bilateral trama and the *Boletus* type. Thus, it becomes more probable that *Truncocolumella* is the common starting point of two subfamilies (*Xerocomoideae* and *Boletoideae*) than it is to assume that after having originated from either *Xerocomoideae* or *Boletoideae,* it has then changed so as to resemble the opposite type. *Endoptychum* is apparently a genus which during further development toward the *Agaricales* splits into a group we identify as the *Agariceae* and another which comes closer to the *Lepiota-Leucocoprinus* type. *Galeropsis,* strongly reminiscent of habit and spore characters of the Conocybes and Bolbitii has the peridial characters of an aberrant type such as would seem to correspond to a representative of the *Pholiotoideae (Strophariaceae)* rather than of the corticated Bolbitiaceae. *Brauniellula* is not merely close to *Pluteus* but may also be transient to *Gyroporus* and certainly is related to *Gomphidius.* Of course, we are always free to answer by claiming convergence — whatever this might mean in cases of this kind — but when „convergence" becomes as common as in the case of the *Secotiaceae,* the chances are that we are dealing with affinities rather than with convergence.

2. Statistical approach. In every reasonable, acceptable phylogenetic scheme, we will find that in the majority of the cases, representing the rule as against special and unusual cases, two genera in juxtaposition, with evolutionary lines linking them directly, one with the other, it is generally the smaller one (in species) that gives rise to the larger with the latter being richer in races, microspecies, transitional forms, recent speciation, and making the impression of an assemblage of closely allied units in evolutionary flux and active evolutionary processes. This is valid for fungi as well as for other plants, and the animal kingdom as well.

In the *Secotiaceae,* we find generally well defined small genera with the species not numerous and well separated from each other by strong hiatus. The number of individuals is generally not impressive, and on an average inferior to the most representative species of the corresponding genera of *Agaricales* which give us the impression of being at least partly of very recent origin. A comparison of good taxonomic treatments of *Setchelliogaster* and *Galeropsis* on one hand, and *Conocybe* on the other will prove the point. In table 2, some omparisons are made on a numerical basis.

Table II.

	Number of species *)	Infraspecific units **)
Montagnea	2	0
Coprinus & *Pseudocoprinus*	(200)	Many
Weraroa	4	0
Stropharia, Naematoloma, Psilocybe	38 (175)	Many
Nivatogastrium	1	0
Pholiota	33	Many
Setchelliogaster and *Galeropsis*	14	0—1
Conocybe and *Agrocybe*	15	Many
Thaxterogaster	6	0
Cortinarius	(400)	Many
Brauniella and *Brauniellula*	2	0
Volvariella and *Pluteus*	170	Many
Truncocolumella	2—3	0
Xerocomoideae, Boletoideae	113	Many
Astrogastraceous series	16	4—5
Russula and *Lactarius*	281	Many

3. Age and area. The „age and area hypothesis" is not a law that can be applied blindly in any given case, yet it is a rule for guidance which will hold true if used "cum grano salis", with a view on as large a number of phylogenetically significant aspects as possible. Genera with a nearly world-wide distribution are in principle more ancient than genera with compact though restricted areas if both are part of an evolutionary line. And as the large areas contract, they often become widely disjunct, and the pattern of disjunction may give interesting indications as to the flora the particular element belonged to. Specifically, *Thaxterogaster* still has an extremely wide area including Patagonia, New Zealand, Australia, and parts of North America. The disjunction between Patagonia and New Zealand which is in accordance with the area disjunction also observed in its geobotanical partner, *Nothofagus,* points unmistakably to its pertaining to the ancient Austral-Antarctic flora, and the minimum age can practi-

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*) Figures adapted from Fischer (in Engler & Prantl), Singer (*Agaricales*) and other sources supplementary to these, or Ainsworth & Bisby (in parentheses).

**) Estimated from available monographs.

cally be dated for the species of the Southern Hemisphere. On the other hand, *Cortinarius,* even though well represented in the areas of *Thaxterogaster,* is represented by a particularly large number of species (usually the largest single element in the flora) in those regions where a recent immigrant flora dominates. ***Gastroboletus boedijnii*** was found in a region with a flora notorious for numerous „living fossil" elements. ***Galeropsis*** — as many of the xerophytic fungi (and plants) — has still an almost universal occurrence although its representatives are rare and restricted to very definite habitats. ***Brauniella*** and ***Brauniellula*** with their widely disrupted area seems to have passed the point of general occurrence which its descendants, ***Volvariella*** and ***Pluteus*** are now gradually beginning to conquer. ***Elasmomyces*** and ***Arcangeliella*** apparently wiped off the cis-alpine Central European plains, is still found rarely in Italy where the ice age has not been able to reach it, and is likewise found in the Moscow area where it might have been able to return since the lack of east-west mountain ranges permitted it to retreat and progress freely according to the climatic conditions. ***Russula*** and ***Lactarius,*** on the other hand, are now widely distributed and apparently in progress; moreover they are favored by forestation and follow the pine plantations into the tropics, Australia, and South America. Even more pronounced is this contrast in the case of ***Truncocolumella*** vs. ***Boletaceae.***

3. The anatomical approach. The finer structure of hyphae and spores is often indicative fo the direction an evolutionary trend has taken. In the ***Basidiomycetes,*** Kühner has shown — and I do not believe that there are any dissenters — that the presence of clamp connections, where opposed to phylogenetically related groups without clamp connections, always indicates that the clamp-bearing group is relatively more ancient. Once the clamp connections have been lost completely, as in the entire family ***Russulaceae,*** there cannot be any possibility — without violating the law of irreversibility — to proceed to further descendant groups which again have clamp connections. Consequently, in the elaborate line of degraded genera leading off the ***Russulaceae*** in Malençon's scheme, a line generally called the astrogastraceous series, it is to be expected that all the genera remain clampless. This is actually the case as long as we are dealing with the first immediate steps of so-called degradation, i.e. ***Elasmomyces, Arcangeliella,*** etc. are consistently clamp-less as far as I could ascertain. However, precisely where we come to the terminal points of the series, in ***Hydnangium (Hydnangium carneum*** and ***soederstroemii***) clamp connections were again encountered by me. The same reversal of what the degradationalist would expect again appears in the neighborhood of the boletes. ***Gastroboletus,***

related to *Boletellus,* is clampless, just as all species of *Boletellus.* But *Truncocolumella,* one step further removed from the boletes, has abundant clamp connections (some taking the shape of medallion clamps). In the series leading from *Secotium* to *Neosecotium* and to *Endoptychum,* we find abundant clamp connections in the still far removed genus *Secotium* (volvate, gleba without sublamellar structure), some few in the genus *Neosecotium* which has gone one step further toward both *Leucocoprineae* and *Lycoperdaceae* according to the detailed comparative studies by Singer & Smith, and finally no clamps at all in *Endoptychum* in general as well as in *E. depressum,* the species so distinctly related to *Agaricus.*

Here again, these in my estimation very pertinent and important facts may be explained away by claiming that *Endoptychum* and *Neosecotium* as known today are only side branches of the main line leading to the *Agaricaceae* which may have had preserved their clamp connections and lost them only after reaching the agaricoid level. As a matter of fact, such a possibility exists inasmuch as we do not for a moment imply that the recent representatives of the *Secotiaceae* are themselves the actual ancestors of the respective agarics, and considering furthermore that there are some *Agaricaceae* which still have clamp connections (although it is only a small minority), a clamped series of ancestors may have to be assumed. But this does not remove the significance of the trend shown by comparison of *Secotium-Neosecotium-Endoptychum-Agaricus,* and the coincidence of parallel trends in the *Truncocolumella-Xerocomus-Boletus* series, and most convincing, the astrogastraceous series, cannot be brushed off lightly.

In the other groups, the existent data are insufficient or else, and this is the majority of the cases, the entire series maintain their either clamped or non-clamped condition throughout as might have been expected in the first place. This goes so far that the species of *Thaxterogaster* most related to the clamp-less minority of *Cortinarius* subgen. *Myxacium* are likewise clamp-less while the rest possesses clamp connections. But while all secotiaceous ancestors of the *Bolbitiaceae* have clamps, many species of the *Bolbitiaceae,* particularly *Bolbitius,* have none.

A less significant means of ascertaining the trend of evolution is the presence or absence of a germ pore. It is generally assumed that the possession of a germ pore is a sign of additional differentiation of a spore. It would therefore appear that the germ pore is either maintained where originally present, or remains absent throughout a series of related genera, and if any change should take place, it should take place in such a form as to allow the more evolved form to be the one with, the more primitive form the one without a germ pore. If we pass revue of the various series that interest us here, it becomes clear that the germ pore, where present, is maintained in both directions, and only one case is known where a gastroid genus is composed of primitive germ-pore-less species as well as species with germ pore. This is *Galeropsis*. Since it is true — assuming a relationship between all *Galeropsis* and all *Bolbitiaceae* — that there are two species of *Agrocybe* without a germ pore, this fact as observed by me on *Galeropsis allosperma* may not be forceful enough to be lined up together with the argument based on clamp connections.

4. The organographic approach. If it is permitted to use the word organographic as a heading for a study of comparative morphology of the loculus or tramal chamber, it may be said that the organographic approach has been used by this writer for many years in order to show that the transition from a loculate gleba into a sterile trama can lead to the formation of spherocyst nests. But the following lines are not a mere repetition of statements based on Lohwag's hypothesis, but based on recent observation of the structure of the tramal plates in astrogastraceous genera, in *Nivatogastrium, Setchelliogaster,* and even such remote groups as the Rhizipogonaceae. It has become clear to me that a common hymenophoral structure in the Hymenogastraceous and secotiaceous fungi shows a regular mediostratum accompanied on both sides by a layer of inflated hyphae transient into spherocysts, and this layer gradually becoming smaller (or rather as its elements develop, becoming larger in the older interior strata) and taking the place of a subhymenium from which eventually the basidia (and very commonly the pseudoparaphyses as hymenial outgrowths of the spherocyst-layer) are formed. Assuming now that under the pressure of a heavier development of the pileus trama vs. the thin gastroid peridium, the uppermost loculi are suppressed in favor of the glebal portions that will become free in the lower portion of the hymenophore, the uppermost loculi will be sterile and if allowed to develop to the point of forming the vesiculose lateral-stratum-subhymenium, a nest of spherocysts will be formed. Such sterility of the loculi near the peridium becomes more than an assumption if we remember that these are the ones that do not sporulate in *Gastroboletus* when the lower portion of the gleba has already passed the peak of sporulation. Driving this process a little further, the immature loculi will not have a chance any more during the life time of the fruiting body to develop spores at all, and will finally not develop basidia, or the basidioles will early be transformed into or replaced by pseudoparaphyses which, as we have seen in their origin, are merely hymenial spherocysts and will thus become another

type of endocystidia[8]). While it may appear from Malençon's account of the situation in the astrogastraceous series that the spherocyst nests of *Russula* are gradually lost after they had unaccountably appeared in that genus and *Lactarius,* we know now that the heteromerous structure of the trama is not anything quite special in the *Russulaceae* but is not even a phenomenon restricted to the *Agaricales.* In certain species of *Rhizopogon,* the peridial trama, quite obviously under the influence of the same transformations described above for *Elasmomyces-Russula,* is also forming sterile spherocyst nests, not only hymenium-less chambers but chambers completely filled in and solid with spherocysts exactly as in *Russula.* With this, I believe, the spherocyst nests of the *Russulaceae* have been satisfactorily explained. On the other hand, it will be up to the degradationalists to show that in one case a degraded line is losing the same structure which, in another, is formed not in the *Agaricales* but on the gastroid level, far removed from the Agaricales.

5. Developmental approach. In the comparative study of developmental types in the *Secotiaceae,* we are still in the beginning of a rational assemblage of dependable facts. Unfortunately, few species have been studied, and even those not always in sufficiently young primordia. There are two publications which seem to us of significance. One is the development study of *Secotium* carried out by Conard and actually dealing with what we now call *Endoptychum agaricoides.* We have already pointed out that *Endoptychum,* especially *E. depressum* and *melanosporum,* is the genus leading directly to *Agaricus,* and that *E. depressum* has not only the odor and taste but also the chemical reactions of *Agaricus,* section *Arvenses.* It is therefore not surprising to find that Conard's study of the development of *Endoptychum* finds complete agreement with what had been described by Atkinson for two species of *Agaricus.*

More significant for our present purpose is the fact that Cunningham, in his development study on *Weraroa erythrocephala (Secotium erythrocephalum)* observes that in the youngest stages a process of continuous and progressive carving-out of more cavities destined to become loculi is taking place in the direction toward the peridium. This is in complete agreement with my own observation regarding *Gastroboletus turbinatus* where, as indicated above, new chambers are continuously formed in the direction toward the upper portion of the gleba, not toward its lower margin. This continuous growth of the hymenophore is somewhat comparable with the

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[8]) This approach might also explain the *Amanita*-structure in many *Amanitaceae,* Cystidia of the *Brauniella* group buried in the trama as remainders of abandoned chambers would look — and do look — exactly like the swollen terminal bodies of tramal hyphae.

indefinite hymenophore which keeps developing further and further in some *Aphyllophorales,* and is in contrast to the pre-definition of the hymenopohre as generally observed in most *Agaricales,* and certainly in those from which *Weraroa* and *Gastroboletus* are supposed to be derived. This would suggest that on the contrary, the indefinite extension of the hymenophore into the peridium trama is a remainder of primitive Gastromycete development and makes place to predefined hymenophore only as the agaric-bolete level is reached. This is logical since the relative position of the hymenophore is now of more importance than its extension in order to use all available interior space for reproduction purposes.

It has been said that the pseudoangiocarpous development of some ***Boletaceae*** and ***Russulaceae*** is actually merely a subtype of gymnocarpous development (it is just that in Reijnders' scheme of developmental types) and as such does not link with the angiocarpous secotiaceous ancestors. This opinion does not take the facts into consideration but starts from easy text book generalisations. It is neither true that all non-gymnocarpic Russulae and boletes are pseudoangiocarpous. Especially as far as the boletes are concerned, I am inclined to believe that not only *Strobilomycetaceae* are hemiangiocarpous, but also some species of the genus *Xerocomus,* and probably others. Secondly, pseudoangiocarpy merely reflects an ancestral stage of pseudoendocarpous [9]) development, and the initial exposed position of the layer that is to form the hymenium will — as I have pointed out in 1936 — find its appropriate explanation in the fact that some hymenogastraceous species such as some Gautierias begin, according to Fitzpatrick, their development likewise with an external hymenial structure. The development of ***Hydnangium carneum*** is similar. This, in turn, would suggest that the original ancestors of such forms might have had at least a tendency to early gymnocarpy. But I shall come to that aspect later.

It is furthermore another text book fiction that *Gastromycetes* fail to open the peridium except to form defined or irregular outlets for the spore powder as in the Lycoperdaceae. As a matter of fact, many secotiaceous fungi break off the stipe-columella in a relatively early stage, sometimes even before the first spore maturation and expose the gleba from below, often assuming the shape of a pileate agaric or bolete. This is so much so that even Fischer, undoubtedly one of the finest specialists of the Gastromycetes, doubted whether ***Gyrophragmium*** and ***Polyplocium*** do not rather belong in the Agaricales because of this behavior.

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[9]) I have proposed this term for a type of gastromycetous development corresponding to agaric pseudoangiocarpy, and differing in that the spores mature in the closed phase.

What has been lost sight of is the fact that the sporulation before hymenium exposure is only one, and often a relatively little impressive feature of gastroid development. A very important and thus far neglected factor is the inability of spore deposite production. The Gastromycete refuses to give a spore print under whatever optimal spore discharge conditions offered. This criterion puts *Macowanites, Gastroboletus, Montagnea, Gyrophragmium, Longula*, and *Polyplocium* undoubtedly among the *Gastromycetes* even though their type of development cannot but be compared with hemiangiocarpy[10]) as observed in *Agaricus* or *Strobilomyces.*

When we consider the rare gastroid aberrations of *Agaricales,* we shall note that the failure to open around the stipe-columella to form a pileus and expose the gleba does not impair the spore discharge mechanism; it only makes its functioning useless or impossible. What keeps the carpophoroids from complete fertility is rather the incapacity to form continuous expanding glebal chambers in the trama, following up the pre-defined hymenophore formation. In other words, if the hymenium is too embryonal when the carpophore has become adult, the sterile corpophoroid will result. Generally speaking, sterile corpophoroids must be expected in gymnocarpous agarics or boletes rather than in those having a closed phase in their development during which the hymenium matures. Further insistence on this subject would, however, take us to far from the subject of this essay.

6. Cytological approach. Cunningham has described the cytology in terms of the nuclear behavior of the basidioles, basidia and spores of *Weraroa erythrocephala.* According to him, four nuclei ascend through the sterigmata and enter the spores, one nucleus per spore. Provided that this observation is correct it would compare "unfavorably" with the pattern described by Kühner and others whereby the four nuclei start the third division immediately after entering the spores so that each spore has two nuclei before discharge, a type of nuclear cytology which, according to Kühner, is to be considered more highly evolved than that of the *Agaricales* producing uninuclear spores, particularly as seen in the *Tricholomataceae.*

Another indication referring to the cytology of these species and genera is Ruhland's work on *Hydnangium carneum.* But the extraordinary variability of nuclear migration toward the one or two sterigmata of each basidium makes it difficult to draw any other comparative conclusion than to emphasize the instability of the division and distribution of the nuclei.

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[10]) The term hemiangiocarpy would be more adequate in order to emphasize the fact that here — even though the hymenophore becomes exposed — hymenial exposure is not prerequisite of spore formation.

In all fairness, the cytological results are too sketchy and far between to be of great value as an argument in favor of the theory which derives the Agaricales from the Gastromycetes by way of the *Secotiaceae.* While one single observation seems to favor this view, others, at least, do not favor the opposite view.

7. The biological approach. By a biological approach, I refer to arguments of phylogenetic significance which are based on the biological processes of the respective organisms in relation to their environment. Such relationships may include the means of dissemination by wind, animals, etc., parasitic and symbiotic relationships, and mere substratum-specialization. This form of argument has always been an attractive form of approach, yet its yield is relatively small. The rodents have been invoked who, according to observations by Singer and others play perhaps a major role in the dissemination of the spores of some *Secotiaceae,* particularly the hypogeous ones. It would seem logical, to assume that the respective fungi could not be more ancient than the rodents which, as mammals, cannot compete with polypore relicts found in carbonic deposits and other early fossil-bearing material.

This field is of course dangerous. Although it does not result that the Secotiaceae are more recent than the *Agaricales,* it shows that they are definitely more recent than the *Aphyllophorales* — leaving the *Agaricales* as the innocent bystanders but implying, naturally, that the more ancient group — the *Aphyllophorales* — is more likely to be ancestral of the *Agaricales* than the supposedly relatively recent *Secotiaceae.*

The argument is, however, fallacious. In the first place, there are even now Secotiaceae which have no biological relations with mammals, such as *Galeropsis*; secondly there might have been any number and kind of secotiaceous fungi before some few representatives of that family adapted themselves in a loose and still rather independent way to mammal-distribution, and there is no reason to assume that the actual ancestral forms of the *Agaricales* did depend on rodents for survival. Furthermore, the comparison is somehow incomplete since nothing can be said about the Agaricales generally, and any question about the "age of the *Agaricales*" must remain unanswered at present. The palaeobotanical relicts of *Aphyllophoraceae* are restricted to some woodinhabiting larger and very resistent (woody) forms, and their occurrence in carboniferous strata proves merely that fungi are a very ancient form of life.

On the other hand, although still not fully conclusive (since parasitism may be a unique adaptation in a single case between exceptional species), parasitism seems to be more indicative as a biological factor of significance. *Nyctalis (Asterophora)* parasitizes on *Russulaceae,* particularly *Russula-Nigricantinae*; *Xerocomus parasiticus* parasitizes on *Scleroderma,* and *Volvariella surrecta* on *Clitocybe nebularis* and *Cantharellus.* The latter example does not show much since both parasite and hosts are relatively ancient; but in the case of the second pair we have proof that at least parts of the genus *Russula* must have existed before the genus *Nyctalis* originated. In other words, it appears somewhat unlikely that the white spored *Tricholomataceae* and *Hygrophoraceae* had given rise to the *Russulaceae.* And in the case of the *Xerocomus-Scleroderma*-relationship it would appear that the primitive *Gastromycetes,* far from being an offspring of the *Boletaceae* and other Agaricales families, were ancient enough to offer themselves as hosts to *Xerocomus* species, or what others believe to be the origin of the *Gastromycetes.*

Nevertheless, here also, the deductions are not forceful since both the ancestral and the derived genera or families did continue to evolve and it cannot be denied that in the genus *Scleroderma* as well as in *Russula,* young side branches have been formed which participate very actively in the recent floras of this earth; thus we may also anticipate that it might be argued that both the respective parasites are merely very recent offsprings of a generally ancient family. Only the fact that the prima facie evidence in both cases points in favor of rejection of this explanation, will give it some limited value in the overall problem where it has to be weighed together with all the rest of the evidence.

It may also be attempted to bring up the question of mycorrhiza origin in the *Gastromycetes* or *Agaricales.* The contention that the relation with tree roots — undoubtedly existing in most hypogeous fungi — is a more primitive one *a priori* since the whole biological cycle takes place in the humus and where the root tips are, instead of showing a differentiation whereby an important part of the nutritional function is tied down to the root tips whereas the reduction division and spore dispersal takes place above the ground (as in the case of the epigeous mycorrhizal fungi), is a purely theoretical approach which does not provide any supporting facts. However, if some non-mycorrhizal gastroid forms could be shown to be close to some mycorrhiza-forming *Agaricales,* or vice versa, this would amount to an important argument in favor of one or the other theory. Unfortunately, this is not the case. Mycorrhiza is apparently maintained while evolution proceeds in all other regards, and it is not formed while organisms enter a degradation process or a phylogenetical ascent toward the Agaricales. The only case where such a possibility might have been realized is in the astrogastraceous series. *Hydnangium* may not or not always be mycorrhizal since it occurs in flower pots with usually non-mycorrhizal seedlings, and *MacOwanites* has allegedly been found under *Acacia,* also generally not considered a (ectotrophic) mycorrhizal host. However, in my recent travels in Bolivia and Brazil, I have come to the conclusion that certain *Leguminosae* such as probably *Inga* might be ectotrophic mycorrhiza formers, and on the other hand, *Russula* is only thoroughly mycorrhizal for the mycologist limiting his observations to the temperate regions while in the tropics the suggestion has been made that most species might be linked either with *Sapindaceae* or *Leguminosae,* but this is not more than a suggestion which is difficult to disprove except by experiment.

All together, it may be said that the biological approach has, thus far, not yielded much forceful evidence in either direction.

8. Reductio ad absurdum. While the preceding discussions were aimed at a test to show which theory would gain by application of all the possible rules and methods of research, we shall now use the negative method of showing that the contention of the degradationalists is not acceptable since they do not show a plausible way of deriving the Agaricales, after having rejected, arbitrarily, their origin in the *Gastromycetes*. It is of course a crucial question whether any of those groups which are by some believed to become degraded to gastroid stages could reasonably be derived from a "hymenomycetous" source. The important word here is the word "reasonably". It is undoubtedly possible to derive, on paper, almost any family from a "hymenomycete". Thus Heim has accepted a thesis, apparently going back to the year 1889, whereby the *Russulaceae* might be descendants from the *Hygrophoraceae,* or *Russula* from *"Hygrophorus"*. Unfortunately, this thesis which at Fayod's time must have looked better than now, will just not be adequate, and any mycologist who has acquainted himself sufficiently with modern methods of study in these families, will hardly go beyond acknowledging that there are two species in *Russula* which look somewhat like *Hygrophori* but are far from being hygrophoraceous by any stretch of the imagination. Some authors have quoted the reddening Hygrocybes as being counterparts of the *Russulae-Nigricantes,* but here again, the similarity stops at some vague external similarity. Dennis has discovered and Singer analyzed a species with echinate spores belonging to the *Hygrophoraceae.* Yet, the ornamentation of that species is not at all comparable with the charcteristic spore ornamentation of *Russula.* While all Russulas have some sort of cystidia, only few *Hygrophoraceae* have cystidia of any kind, and those which have them have inconspicuous cystidia of a type very different from that of the *Russulaceae.* Even assuming that those groups of *Hygrophoraceae* that lack clamp connections are better classified within this family than in the *Tricholomataceae* — a conclusion which I have lately accepted and published as acceptable — the clamp-less

Hygrophoraceae are precisely the ones least similar in other regards to the *Russulaceae*; they have no latex; they do not turn red or black; they do not have cystidia; and they are not forming mycorrhiza. Furthermore, there is an abrupt change in one of the most basic characters in *Agaricales,* in the structure of the trama. In all *Hygrophoraceae,* the trama is homoiomerous, and in all *Russulaceae* the trama (and in most Russulas even the hymenophoral trama) is heteromerous. We have already discussed the origin of the spherocysts in the trama of the Russulaceae. They are certainly not comparable with and cannot be derived from anything seen in any representative of the *Hygrophoraceae.* Chemically, the amyloid external layer of the spores so characteristic for the *Russulaceae,* is absent in *Hygrophoraceae;* only in one thus far monomorphic genus of the *Hygrophoraceae* have spores of a banal amyloid type been observed. These spores have a completely homogeneous non-ornamented wall, and their type of amyloidity is the one generally seen in agarics (*Amanita, Cantharellula, Catathelasma,* etc.), chemically and structurally far removed from that of the Russulaceae. In order to tentatively support the degradationalists hypothesis — merely in order to exhaust all the possibilities — I have mentioned in a previous paper that *Melanoleuca* would fill the degradationalists's bill much better than *Hygrophorus.* Even so, the *Russulaceae* being the only family in the *Agaricales* with spherocyst nests in the pileus trama, it will be difficult to encounter a satisfactory ancestor for the *Russulaceae* in the *Agaricales.*

The same difficulty as is found in search of an ancestor for the *Russulaceae* — unless the astrogastraceous forms are admitted as such —, is also met in the realm of boletineous groups. Heim has repeatedly stated, without making his idea plausible, that the *"Boletales"* are polyphyletic and that for example *Gyrodon* [11]) has polypore ancestry. While it is possible that biphyletism could be shown for the boletes as a whole insofar as *Gastroboletus* seems to be ancestral to the *Strobilomycetaceae,* and *Truncocolumella* to the *Boletaceae,* it is completely removed from reality to claim a polypore connection of any kind for *Gyrodon.* Neuhoff has once based his contention which also had to do with deriving boletes from polypores, on the non-existent white spored boletes which do seem to pop up from time to time in Agaricales systematics. The white-spored Gyrodons are a fairy tale; the white spored *Polyporoletus* turned out to be *Scutiger.* The white-spored *Boletus pyriodorus* turned out to be colored-spored *Tylopilus tabacinus* ("white-spored" only because Murrill had

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[11]) The situation is, if anything, worse for the pretended *Ixechinus-Fistulina* bridge. Singer (Sydowia **9**:421. 1955) has shown that *Ixechinus minus* is merely a species of *Tylopilus* (a homonym, if transferred) and that the tube-separation appears to be an artefact.

not obtained a spore print on white paper, and therefore claimed white spores for the species). There are no polypores with bilateral trama as *Truncocolumella* and *Gyrodon* have it; and the only fleshy polypores similar to *Gyrodon* are not colored-spored.There does not seem to be any formation of ectotrophic mycorrhiza in the polypores except probably in the *Scutiger*-group yet the *Scutiger* group is so different anatomically, chemically, in aspect, and in spore color that it takes as much imagination on the part of the mycologist to accept such an affinity as it takes to swallow the alleged affinity between *Hygrophorus* and *Russula.* In order to substitute again a better candidate for their needs, I offer the degradationalists the use of a bridge from the Boletaceae to the white-spored agarics and the "polypores" which they seem to have overlooked and which seems much more logical than the *Polyporus-Gyrodon* jump. I have several times had occasion to discuss the close relation existing between the Paxillaceae and *Gyrodon.* In the *Paxillaceae* I have placed two white-spored genera *Cheimonophyllum* and *Hygrophoropsis.* Although I personally do not believe that these two genera are very closely related with the *Tricholomataceae,* there are those who believe they are, and the totality of their characters makes it certainly possible, and a matter of individual opinion, at the present time, to argue in favor or against a closer relationship with some tricholomataceous groups. On the other hand, I have shown that the often pleaded affinity of *Polyporus* and *Lentinus* (with allies: *Panus, Pleurotus, Phyllotopsis* etc.) is anatomically demonstrable, but that not the *Lentineae* are part of the "polypores" but that *Polyporus* sensu str. (*Polyporellus*) with some satellites actually belongs to the *Agaricales.* I am not of the opinion that *Polyporus* sensu str. is in any direct or indirect way related and more than similar to the genus *Microporus,* yet if anyone needed a hypothesis by which a bolete should be linked with the *Aphyllophorales,* he might not hesitate to ignore the fact that *Microporus* is a *Coriolus* with a pseudostipe rather than an aphyllophoraceous projection of a *Polyporus* sensu stricto, and accept the bridge *Gyrodon-Hygrophoropsis-Clitocybe-Pleurotus-Polyporus-Microporus.*

After discussing the chances of the degradationalists to derive the gastromycete-near *Agaricales* from other *Agricales* or *Aphyllophorales* at this length, it might not be necessary to enter the question where *Volvariella* comes from if not from *Brauniella*; *Agaricus* if not from *Endoptychum; Cortinarius* — if not from *Thaxterogaster,* etc.

Instead, we may ask another question: If *Neosecotium* is sufficiently ancient to give rise, as we have shown it might have, to the Lycoperdaceae, would it not be slightly absurd to postulate that this general neighborhood — taxonomically speaking — is the result of repeated degradation starting at a point of the *Agaricales* system where a genus with numerous species difficult to classify, and vigorously defending their place in nature, *Agaricus,* is itself only the end product of a long series of gradually more and more differentiated agaric-forms which, in turn, have passed originally through the entire *Aphyllophorales* system? It turns out, then, that with a general statement saying that deeply colored agarics are more highly developed than whitespored groups (because of a number of reasons), no sensible phylogenetic answer can be found. The fact that the white-spored groups *are* more primitive in certain respects than colored-spored families in these same respects may easily be explained by the possibility that both groups are the result of evolutionary lines running parallel after a near-common or perhaps only similar start, whereby a certain set of characters has become quickly elevated to a highly differentiated standard in the colored-spored families and their white-spored allies (such as *Leucocoprinus* and the numerous cases of white-spored relatives of dark-spored genera, and their spore-albinos) while another set of characters has been found to evolve more rapidly in the typical white-spored families such as the *Hygrophoraceae* and *Tricholomataceae* (to which we might have to add the family *Polyporaceae* sensu str.). There is indeed an extraordinary development to be observed in *Mycena* and *Marasmius,* particularly as far as host specificity, rhizomorph production, or an intricate system of sexual and propagula-dissemination (as in *Mycena citriceps*) is concerned, not to speak of the differentiation of distinct cystidial types and the almost unlimited adaptability of the sexual reproduction forms and cytological types. The transition toward such interesting adaptations as the production of conidial fructifications on parts of or the entire macro-carpophore (*Armillariella*) or the only case of transition from normal sporulation to bulbillosis (in *Amparoina*) are exclusively or predominantly phenomena observed in the white spored agarics.

This may be the time to place bulbillosis into a new light. The first step in this regard is, as is shown by *Amparoina,* a transfer of sporulation to a much earlier stage of the fruiting phase than usual in agarics. This is accompanied by a strong development of the subhymenium. Only on this basis is it possible later on to reduce the spore bearing time or skip it entirely while some of the subhymenial cells, now replacing almost the entire trama of the pileus or at least the hymenophore, become sclerotized and take over the role of the gonotocont. It is obvious that both early sporulation and a broad vesiculose subhymenium are traits, reminiscences in my way of interpreting them, of gastroid origin, more particularly observed in most Secotiaceae. This would indicate that agaricoid development is not so much a transition to earlier hymenium exposure as it is later maturation. At any rate, only the gastroid ancestry makes bulbillosis phylogenetically understandable.

Likewise, on the physiological level, it may be said that white spored agarics are not, as a whole, of lower organization or simpler than the ones with colored spores.Specialized symbiosis with plants (endo- and ectotrophic mycorrhiza) and animals (coexistence with termites, ants, in tropical Asia, Africa and South America) exist in the colored-spored and the white-spored *Agaricales*, but for that matter did exist in other forms (lichenization, symbiosis with scale insects) at a morphologically and — no doubt — evolutionarily low level in the *Aphyllophorales* (Basidiolichenes, some *Clavariaceae*; *Septobasidaceae*).

As for the spore color in agarics, wherever a parallel development is unthinkable, there seems to be as much evidence fo the white spores originating from colored ones (as in Agaricaceae, *Inocybe, Psilocybe*) as there might be for the opposite. I have not the slightest doubt as to these contradictory trends having been realized, both almost coethaneously, in many evolutionary lines or side-branches during fungus evolution.

With the discovery of *Endoptychum depressum* and the reevaluation of *E. melanosporum* by Smith and Singer (Smith & Singer 1958), it might seem that in the *Agaricaceae* a trend from dark-spored to hyaline-spored genera leads by the way of pseudoamyloid spores and spore prints with a green tinge, an observation not without interest since it is paralleled by another hypothetical trend in the bolete-*Paxillus-Gomphidius* complex where those white spored agarics closest to *Paxillus* are characterized by frequently pseudoamyloid spores (*Hygrophoropsis*), and, within this complex („*Boletinaeae*") olive- spored groups are frequently encountered — an interesting phenomenon because of the fact that olive and greenish spores are generally rare in the Agaricales — except in these two cases. I do not know what significance it has — if any — that in the *Secotiaceae* and *Lycoperdaceae* (the latter to be derived from *Neosecotium*-like fungi [12]) both pseudoamyloid and greenish-olive spores are not unusual.

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[12] The similarity of habit, the spore characters including the pseudoamyloidity and ornamentation, and the characteristic pigmentation of the spores — with lack of characteristic pigmentation elsewhere —, the ecological requirements and the carpophore development make it very probable that *Lycoperdon*, as we know the genus today, is a descendant of *Neosecotium*, a secotiaceous genus with very definite affinity with *Endoptychum* which in its turn, is demonstrably close to *Agaricus*. Both Heim and Malençon have repeatedly insisted on the thesis that the *Lycoperdaceae*, among other gastroid groups, are completely isolated from the *Secotiaceae* and *Hymenogastraceae*, the so-called agaricoid *Gasteromycetes* of the degradationalists. The extraordinarily forceful demonstration of a link with one and the same secotiaceous genus on both sides, the side of the *Agaricaceae* and the *Lycoperdaceae*, should serve as one of the most important counter-arguments against the assumed hiatus between the

IV. Origin of the Gastromycetes.

Of course, a critical revue of the alternative possibilities may also be a method applicable in order to test the theory of those who derive the *Agaricales* from the *Gastromycetes*. The logical question in this case would be: Where do you believe the *Gastromycetes* originated?

The origin of the *Gastromycetes* takes us into the gray and indistinct past of fungus evolution without anything comparable to the bridging series, now at the diposal of the phylogenetic taxonomist in the *Secotiaceae-Agaricales*-complex. This problem is consequently much more difficult to answer than the hypothetical question regarding the origin of the *Agaricales* if they have not derived from the Gastromycetes.

While this is undoubtedly true, it does not mean that those who are in favor of deriving the *Agaricales* by an ascending line from the *Gastromycetes* would attempt to shirk the question.

It is my opinion — and here I speak about a pronouncement of a much vaguer status than my theory regarding the origin of the Agaricales — that there are among recent floras, hardly any species or genera which might illustrate what a really primitive Gastromycete looked like at the point of the origin of the *Gastromycetes* as an order or subclass. While illustrating the evolutionary trends and the traces they left in recent floras of the world, we may, as well as the degradationalists, safely refer to genera as representing as a whole (not necessarily any living species, or in the generic delimitation now accepted for the existing flora) a phase through which or by which evolution has passed. We may place the genera in our schemas in a certain distance from the corresponding genera of *Agaricales* wihtout being accused of the delusion that the taxa of the recent fungi are the actual ascendants of other taxa of recent fungi. However, this situation worsens, gradually but distinctly, as we ascend into the early phase of fungus evolution when the basic subdivisions of fungi first became differentiated.

It has become modish and sophisticated to say that the *Gastromycetes* as a natural taxonomic unit do not exist, that they are completely heterogeneous and break down or go back to a number of different sources. Classical Gastromycetologists were not of this opinion or were, at least, doubtful and openminded about such pronouncements. A group of plants may rightly and credibly be suspected of being heterogeneous only if at least a reasonably acceptable

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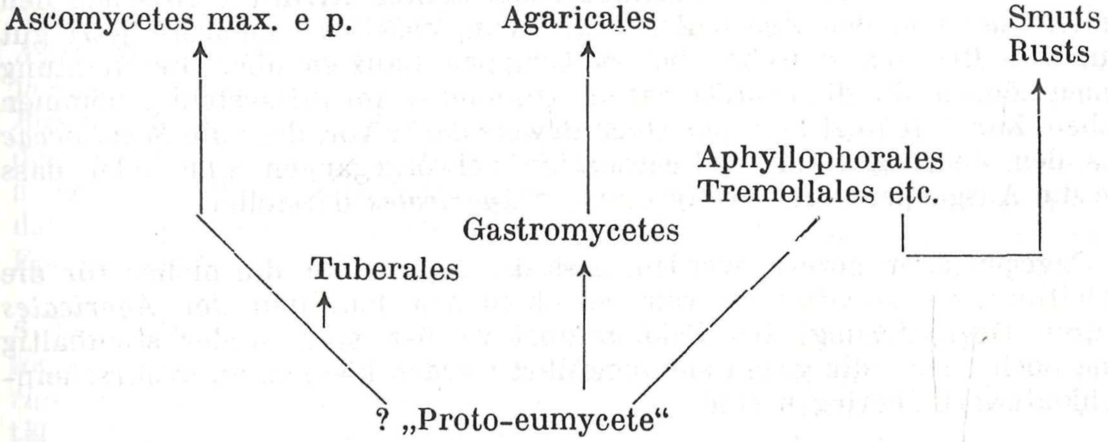
„true“ *Gastromycetes* (which, in Malençon 1955, pl. 10, p. 124, include, side by side, *Lycoperdaceae*, and „*Torrendiaceae*“ as *Endogastrineae*) and the agaricoid *Gastromycetes* or *Exogastrineae* in Malençon's terminology; in other words, the *Gastromycetes* are still phylogenetically-taxonomically a whole, and the *Secotiaceae-Hymenogastraceae-Phallaceae* are not separated from the rest of the *Gastromycetes*.

theory has been given which shows which other affinities besides the ones thus far assumed, might have some bearing on the phylogeny of such a group. In other words, admittedly strongly individualized groups with formidable hiatus separating them from the main group (or all other groups) of a large taxonomic entily like the Gastromycetes, cannot and should not be termed polyphyletic as a whole unless it is shown where the single main groups *did* originate. If we, like Malençon, derive several groups even within a — in my opinion homogeneous — family like the *Secotiaceae,* from starting points distributed all over the families of a neighboring order, we may very well speak about polyphyletic origin — to that extent. But Malençon has no plausible hypothesis and — if I understand his opinion correctly, no hypothesis at all about the origin of the „true" Gastromycetes of his scheme, i.e. the ***Plectobasidii*** and the other groups of gastroid forms which according to Malençon are not related to the Agaricales. Therefore, the claim that the *Gastromycetes* are heterogeneous and polyphyletic as a whole should be modified in the sense that they partly derive, always according to Malençon, from the Agaricales, and partly from some unknown source. Since, in view of the entire foregoing discussion and the play of probabilities involved, I reject Malençon's attempt to derive the *Gastromycetes* even partly from the *Agaricales,* I cannot convince myself that the Gastromycetes are necessarily heterogeneous and polyphyletic. There is merely the element of age: The origin of the various suborders constituting what is generally referred to as *Gastromycetes* is a very ancient one, and the bridging series of genera toward them is undoubtedly now partly extinct, partly so changed by further evolution that the respective forms are hardly recognizable as the original links or their relatives, particularly near the most primitive families.

Under the circumstances, it seems to me that the origin of the *Gastromycetes* must be sought in a hypothetic form which must be very close to the common origin of all *Eu-Mycetes* (*Asco-* plus ***Basidiomycetes***). It seems probable that the first appearance of a gonotocont which forms spores externally should be expected to have occurred not at a time when its counter-part, the ascus had already become fixed and unlikely to give off, phylogenetically speaking, a new structure with external spore production, as would be the case if *Ascocorticium* were really the original source of the ***Basidiomycetes.*** Assuming, however, that, using Schindelwolf's terms, the basidium had arisen while the formative period of the gonotocont was still in the phase of typogenesis rather than later when the ascus had arrived at a stage of typostasis, we assume implicitely that this will also lead to a series of vacillating and diversifying tendencies concerning the basidium itself which continue all through the first phase of an aphyllophoraceous and a gastroid branch of which the latter, after finally coming to a typostatic, „fixed" basidial type, the agaric-bolete-type, eventually reaches the level of the order *Agaricales.* On the other hand, having attained the state with exposed hymenium almost right away, the aphyllophoraceous type finally develops a similar type of basidium, which in its simplicity, and easy evolvement is inescapable, and actually becomes the rule where the higher chiastobasidial forms of the *Aphyllophorales* begin. This presupposes for the hypothetical „Proto-Eumycete" a tendency to form, possibly according to position or environmental variables, both an internal or an external basidial layer or basidium-producing layer, somehow indiscriminatingly and not genetically fixed as in later developments.

This is somewhat in contrast to my tentative acceptance in 1936 of the possibility of a derivation of the *Gastromycetes* from lower *Corticiaceae* which, in turn, might have come from *Ascomycetes* like *Ascocorticium.* This acceptance was merely the recognition of the existence of such a possibility as suggested before that by other writers, and has since been discarded as being just that, and not more than that: a bare possibility.

Table III.



Obviously a scheme as the one visualized by me here (see table 3), would lead to a certain symmetry between *Tuberales* on one hand, in the Ascomycete descendence, an the Gastromycetes on the other, in the Basidiomycete system. This, to me, explains better the certain similarities between the two groups, observed or compiled by Holm (1954) in order to show that the *Gastromycetes* originated with the *Tuberales,* than Holm's own thesis. If Holm were right, the acceptance of his thesis should almost automatically make the derivation of the *Agaricales* from the *Gastromycetes* still more probable to almost certain, yet, strangely enough, Holm himself did not realize this, and the arguments in favor of his thesis are not convincing enough although the suggestion is undoubtedly an interesting one.

This brings up for the second time the question whether the supposed derivation of the *Tuberales* from the *Pezizales* has any bearing on the question about the phylogenetic status of the *Gastromycetes.* In the first place, it seems to me that it is more probable to search for a common ancester of both *Tuberales* and *Pezizales* although I have to leave the details of this question to the specialists of the respective Ascomycete orders. But if the derivation of the *Tuberales* from the *Pezizales,* as mostly considered probable, should be verified upon further investigation, at least to the degree of probability to be expected in such questions, it would, in my opinion, not necessarily influence the direction of the evolutionary trend in the *Basidiomycetes.* While, in the *Basidiomycetes,* a tendence from gastroid to agaricoid in *Russula,* and coexisting with the first, another from agaricoid to gastroid in, e. gr., *Brauniella* seems to be unlikely in two almost parallel (yet reversed) branches, it is not difficult to imagine that at other occasions the trend might have been different, even opposite at different times, under different circumstances, and at different ends of the system of fungi.

Zusammenfassung:

1. Die Bedeutung der unzweifelhaft festgestellten Affinität zwischen den *Secotiaceae* und den *Agaricales* liegt darin, dass hier mehrere jetzt gut studierte Brücken zwischen beiden Gruppen Indizien über die Richtung geben können, die die evolutionären Strömungen im Pilzsystem genommen haben. Zur Zeit liegt kein positiver Beweis dafür vor, dass die *Secotiaceae* aus den *Agaricales* durch Degradation hervorgegangen sind, oder dass sie die Ausgangspunkte im System der *Agaricales* darstellen.

2. Dagegen kann gezeigt werden, dass die Argumente, die bisher für die Ableitung der *Secotiaceae* von verschiedenen Familien der *Agaricales* (durch Degradierung) ins Feld geführt worden sind, weder stichhaltig sind noch denen, die gegen sie angeführt werden können, an Wahrscheinlichkeitswert überlegen sind.

3. Andrerseits werden verschiedene Möglichkeiten die Frage zu lösen behandelt, unter denen besonders die taxonomische, die statistische, die Areal-und-Alter-, die anatomische, die organographische und die ontogenetische Methode wertvolle Hinweise auf die Entwicklungsrichtung in diesem Gebiet geben.

a) Die taxonomische Methode zeigt, dass durch ihre Stellung als Übergangsformen zwischen den Projektionen des *Agaricales*-Systems in die *Secotiaceae*-Taxonomie eine Ableitung der letzteren von den ersteren unwahrscheinlich ist.

b) Die statistische Methode zeigt, dass die mehr in Fluss und in aktiven Neubildungsprozessen befindliche Gruppe die der *Agaricales* ist, was sich durch Artenzahl und Varietätenzahl in jeder Gruppe durch Vergleich erweisen lässt.

c) Die „Age and Area Hypothesis“ und weitere Deduktionen und Additionen im Gebiet der historischen Pflanzengeographie begünstigen sehr deutlich die Thesis, dass die *Agaricales*, die irgendeiner Secotiazeengruppe nahestehen, älter sind als die abgeleiteten Agaricalesgruppen.

d) Der anatomische Hinweis auf das verhältnismässig grössere Alter der gasteralen Endglieder der evolutionären Ketten liegt ganz besonders darin, dass es möglich ist zu zeigen, dass schnallentragende Formen häufiger auf der Gastromycetenseite, schnallenlose auf der Agaricalesseite anzutreffen sind.

e) Durch die organographischen Methoden können wir zeigen, dass die Struktur von *Russula* und *Lactorius* nur dann zu erklären ist, wenn man annimmt, dass diese Gattungen von „Astrogastrazeen" (*Hydnangieae*) abstammen.

f) Ein Vergleich der Fruchtkörperentwicklung von *Secotiaceae* und ihnen nahestehenden*Agaricales* zeigt, dass diese Beobachtungen am besten erklärt werden können, wenn man die ontogenetischen Verhältnisse bei den letzteren aus ihrer Gastromyceten-Aszendenz heraus zu verstehen sucht.

4. Andere Methoden (die zytologische, biologische) geben keine klare Antwort auf die Frage nach der Richtung der Evolution, teils weil die Daten viel zu mangelhaft sind, teils weil sie entgegengesetzte Theorien gleichmässig unterstützen.

5. Der negative, aber sehr wichtige Hinweis auf die Unwahrscheinlichkeit einer Entstehung der *Secotiaceae* durch Degradation von den Agaricales liegt in der Unmöglichkeit eine überzeugende Aszendenz für die secotiazeennahen Gruppen der *Agaricales* unter anderen Gattungen oder Familien der *Agaricales*, oder unter gewissen Gattungen und Familien der *Aphyllophorales* zu finden; besonders unwahrscheinlich ist die Thesis, dass die *Russulaceae* von den *Hygrophoraceae* abzuleiten seien, und die Thesis, dass die *Boletaceae* polyphyletisch (teilweise von Porlingen) abzuleiten seien. Ebenfalls negativ aber wichtig ist der Nachweis, dass die Degradationshypothese annehmen muss, dass die Basidie nach einer sehr langen Epoche der Typostasis wieder in typische Typogenesis übergegangen sei.

6. Die Gattung *Neosecotium (Secotium macrosporum* Lloyd), die zweifellos den *Agariceae* und den *Lycoperdaceae* nahesteht, zeigt, dass die *Secotiaceae* nicht die einzige Gruppe unter den Gastromyceten ist, die Affinität mit den *Agaricales* hat. Infolgedessen ist es weiterhin erlaubt, von einer Ableitung der *Agaricales* von den Gastromyceten zu sprechen.

7. Die primitivsten und ältesten Gastromyceten sind wohl eher von einer heute nicht mehr klar zu identifizierenden und vielleicht ausgestorbenen Gruppe von Pilzen abzuleiten als von *Ascocorticium* über die *Corticiaceae*. Auf Tafel III gibt der Autor ein stark reduziertes Schema, wie er sich das Gesamtsystem der Pilze vom phylogenetischen Standpunkt im Lichte der Secotiazeen-Studien vorstellt.

8. Viele der Tatsachen, die der gegenwärtigen Arbeit zugrundeliegen, sind durch monographische Studien über verschiedene Triben der *Secotiaceae* ans Licht gekommen. Diese Studien wurden von Singer & A. H. Smith 1957—58 ausgeführt und sind gegenwärtig im Druck. Ein phylogenetischer Ausdruck der generischen Systematik, die in diesen Arbeiten enthalten ist, kann auf Tafel I meiner hier vorliegenden Arbeit (oben) eingesehen werden.

Literature.

Buchholtz, F. Zur Morphologie und Systematik der Fungi Hypogaei. Annal. Mycol. **1**: 152—174. 1902.

— Beiträge zur Morphologie und Systematik der Hypogaeen. 196 pp, 5 pls. Riga 1902.

Cunningham, G. H. The Gastromycetes of Australia and New Zealand. Dunedin, 1942.

Hansen, L. The phylogenetic position of *Agaricales* I. On the occurrence of clamp connections of the medallon type in the fruit body of some *Agaricaceae*. Bot. Tidskr. **51**: 185—187. 1954.

Heim, R. Le genre *Inocybe* ... Encycl. Mycol. **1**. Lechevalier, Paris 1931.

— Sur les liens phylétiques entre les agarics ochrosporés et certains gastéromycètes. C. R. S. Acad. Sc. **192**: 291—293. 1931.

— Sur la parenté entre *lactaires* et certain gastéromycètes. C. R. S. Acad. Sc. **202**: 2101. 1936.

— Sur la phylogénie des Lactario-Russulés. C. R. S. Acad. Sc. **203**: 108. 1936.

— Les Lactario-Russulés à anneau; Ontogénie et phylogénie. Rev. Mycol. **2**: 4—17; 61—75; 109—117. 1937.

— Les Lactaria-Russulés du domaine Oriental de Madagascar. Prodr. Fl. Madag. **1**: 1—96. 1937.

— Etudes descriptives et expérimentales sur les agarics termitophiles d'Afrique tropicale. Acad. Sc., Inst. Fr., Mém. **64**: 1—74, pl. 1—10. 1941.

— Phylogeny and natural classification of macro-fungi. Trans. Brit. Mycol. Soc. **30**: 161—178. 1948.

— Le Genre *Galeropsis* Velenovsky (*Cyttarophyllum* Heim), trait d'union entre agarics et *Gastérales*. Rev. Mycol. **15**: 3—28, 1 pl. 1950.

— Notes sur la flore mycologique des Terres du Pacifiques Sud III. Sur les *Secotium* de Nouvelle-Zélande et la phylogénie de ce genre. — IV. Le genre néo-calédonien *LeRatia*. Rev. Mycol. **16**: 129—158. 1951.

— Les voies de l'évolution chez les champignons. Colloque international, centre nat. rech. scient. évol. phyl. végét. Paris, mai 1952. Ann. Biol. **28**: C27—C46. 1952.

Holm, L. Some aspects on the origin of the *Gastromycetes*. Sv. Bot. Tidskr. **43**: 65—71. 1949.

— Classification et phylogénie des Gastéromycètes. VIII Congrès intern. Bot. Paris sect. **19**: 54—60. 1954.

Kühner, R. Le problème de la filiation des *Agaricales* à la lumière de nouvelles observations d'ordre cytologique sur les Agaricales leucosporées. Bull. Soc. Linn. Lyon 1945 (7&8): 160—169. 1945.

— Place des Bolets dans l'ensemble des Basidiomycètes et rapports des diverses espèces de Bolets entre elles. Bull. Soc. Natur. Oyonnax **2**: 37—48. 1948.

Lange, M. The phylogenetic position of *Agaricales*. II. Characters indicating derivation of some *Agaricales* from *Aphyllophorales*. Bot. Tidskr. **51**: 188—194. 1954.

Lohwag, H. Zur Stellung und Systematik der Gastromyzeten. Verh. zool. bot. Ges. Wien **74**: 38—55. 1924.

— Entwicklungsgeschichte und systematische Stellung von *Secotium agaricoides* (Czern.) Holl. Oesterr. Bot. Zeit. **73**: 161—174. 1924.

Malençon, G. La série des Astérosporés. Trav. crypt. dédiés à Louis Mangin, pp. 377—396. 1931.

— *Dodgea occidentalis* Malençon, nouveau genre et nouvelle espèce de *Rhizopogoneae*. Bull. Soc. Myc. Fr. **54**: 193—203. 1939.

— La sporogenèse chez les Basidiomycètes C. R. S. Acad. Sc. **215**: 434—486. 1942.

Martin, G. W. On *Lentodium squamulosum* Proc. Iowa Acad. Sc. **63**: 280—286. 1956.

Romagnesi, H. Le genre *Richoniella,* chainon angiocarpe de la série des Rhodogoniosporés. Bull. Soc. Mycol. Fr. **49**: 433—434. 1933.

Singer, R. Das System der *Agaricales*. Ann. Mycol. **34**: 286—378. 1936.

— Studien zur Systematik der Basidiomyzeten I. 2. *Galeropsis,* ein Gasteromyzet! Beih. Botan. Centralbl. 56 B: 147—149, Nachtrag, p. 150. 1936.

— Phylogenie und Taxonomie der *Agaricales*. Schweizer. Zeitschr. Pilzk. **17**: 1—25 (reprint pagination) 1939.

— O novykh dannykh dlya sistematiki i filogenii Agaricales kak potomkov *Gastromycetes* [On new data for the taxonomy and phylogeny of the Agaricales as descendants of the *Gastromycetes*]. Sov. Bot. 1939: 95—98. 1939.

— The *Boletoideae* of Florida (the *Boletineae* of Florida with notes on extralimital species III). Amer. Midl. Natur. **37**: 1—135. 1947 (esp. pp. 89—100).

— *Thaxterogaster* — a new link between *Gastromycetes* and *Agaricales* Mycologia **18**: 215—228. 1951.

— Type studies on *Basidiomycetes* VI. Lilloa **26**: 57—159. 1953 (esp. pp. 102—108).

— Four years of mycological work in southern South America. Mycologia **45**: 853—891. 1953.

— Type studies on Basidiomycetes VIII. Sydowia **9**: 367—430. 1955 (especially p. 421, pp. 427—431).

— & Walter H. Snell & Lawrence White. The taxonomic position of *Polyporoletus sublividus*. Mycologia **37**: 124—128. 1945.

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