

The Hymenochaetales: a revision of the European poroid taxa

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The relationships of the European poroid Hymenochaetales were assessed from an array of 20 characters: 14 morphological and microscopical features of the fruit body, cultural type and nuclear behaviour of the secondary mycelium, extractable styrylpyrone contents of the basidiocarp, electrophoretic protein patterns and type of enzymatic ability of the mycelium. Taxonomic information was retrieved in two ways: phenetic and phylogenetic.

As a result, the Hymenochaetales are divided into two suborders, Phaeolinae Fiasson & Niemelä and Hymenochaetinae Fiasson & Niemelä, the former comprising one family (Phaeolaceae Jül.) and the latter three (Hymenochaetaceae Donk, Inotaceae Fiasson & Niemelä and Phellinaceae Jül.). The following genera are accepted to accommodate the European species which were formerly included in the genera of *Inonotus* and *Phellinus*: *Inonotus* Karst., *Inocutis* Fiasson & Niemelä (formerly the *Inonotus rheades* complex), *Inonotopsis* Parm., *Phylloporia* Murr. (*P. ribis* complex), *Fomitiporia* Murr. (*P. robustus* complex), *Porodaedalea* Murr. (*P. pini* complex), *Ochroporus* J.Schroet. (*P. igniarius* complex), *Phellinidium* (Kotl.) Fiasson & Niemelä (*P. ferrugineofuscus* and its allies), *Phellinus* Quél. (*P. torulosus*), *Fuscoporia* Murr. (*P. ferreus* and its allies), and *Fulvifomes* Murr. (*P. rimosus* complex). Within these genera, 23 new combinations of species names are proposed. The concepts of the genera and families are emended, and the affinities of the Hymenochaetales to the other groups of fungi are discussed.

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The Hymenochaetales

The entity of the hymenochaetaceous fungi first arose as the *Série des Igniaries* of Patouillard (1900). This united genera which varied in their basidiocarp morphology and hymenial configurations, but all possessed setae. Actually this peculiar type of cystidia is missing in some species and even genera of the group, but the golden to brown colouration of the basidiocarp and its darkening in potassium hydroxide ('xanthochroic reaction') are shared by virtually all of them. It was as the Xanthochroic Series that Patouillard's *Igniaries* were finally acknowledged by Corner (1948), while Donk (1948) recognized the group as the family Hymenochaetaceae. They were raised to the rank of order as the Hymenochaetales by Oberwinkler (1977). Jülich (1981) merely raised some old dichotomies of the determination keys to family rank, without discussion and without any new information.

In its present scope, the order Hymenochaetales includes, e.g., *Asterodon* Pat., hydroid with both asterosetae and ordinary ones, the corticioid *Hymenochaete* Lév. and the irpicoid *Hydnochaete* Bres., which both lack the asterosetae, and various poroid genera. Of the poroid genera, those most often mentioned are *Phaeolus* Pat., *Coltricia* S.F.Gray, *Onnia* Karst., *Inonotus* Karst., *Phylloporia* Murr. and *Phellinus* Quél., the first three often being stipitate and growing mainly on roots of various trees, while the last three are dimidiate to resupinate and grow on trunks or branches. The distinction between *Inonotus* and *Phellinus*, based originally on the colour of the spores (Bourdote & Galzin 1928), then on the hardness and perenniality of the basidiocarp in *Phellinus* (Pilát 1936–1942), now rests (since Cunningham 1947) on the miticity. This in turn has led to a revival of *Phylloporia* Murr., which was accepted as the genus for the species widely known as *Phellinus ribis* (Schum.: Fr.) Karst., a perennial but monomitic polypore (Ryvarden 1978). The demarcation between the generative and skeletal hyphae is often vague to nonexistent in this group (Jahn 1981), and so the

distinction between *Inonotus* and *Phellinus* again appears to become a problem.

The naturalness of this order is underlined by the constant lack of clamp connections (Kühner 1950a) and, with the exception of *Phaeolus schweinitzii* (Fr.) Pat., whose taxonomical position has recently been discussed (Parmasto & Parmasto 1979, Jülich 1981), by the production of white-rot and the uniformity of the cultural characters (Nobles 1948, 1965).

A new approach

We approached the taxonomical problems of this group from diverse viewpoints, studying the styrylpyrone pigments of the basidiocarp (Fiasson et al. 1977, Fiasson & Bernillon 1977, Fiasson 1982), the enzymatic activities and proteinograms of the secondary mycelium (Fiasson & Bernillon 1983), and the morphological and anatomical features, especially those of the basidiocarp (Fiasson & David 1983). We also examined the nuclear behaviour of the secondary mycelium, a noteworthy evolutionary character (Boidin 1971, Kühner 1980). The basic material consisted of the European poroid taxa, and the observations published here deal mainly with them. To widen the scope of the study and allow us to place the results in a more general context, over one hundred exotic samples of the order were examined. Those results have not yet been published, but will be referred to in the following discussion. Some work on polypores other than the Hymenochaetales (David & Fiasson 1977) gave us personal acquaintance with some out-groups.

This paper is a synthesis of the studies of J.L. Fiasson. T. Niemelä joined in the project at its final stage, supporting the division of the genus *Phellinus*, and sharing the responsibility for this inevitable step.

The conclusions are mainly based on 20 characters, listed in Table 1. All these characters (except the nuclear behaviour: from Kühner 1950b and personal observations) have been previously described and discussed, and the relevant conclusions published (Fiasson 1982, 1983, Fiasson & Bernillon 1983, Fiasson & David 1983). This data matrix was analysed in two independent ways: by using a computerized taxometric analysis without weighting of the characters, and by drawing a phylogenetic groundplan in which a relative apomorphic value is attributed to each character state.

Materials and methods

The fungal material. The origin of the specimens studied was described by David, Dequatre and Fiasson (1982) and Fiasson (1982).

Nuclear behaviour. We followed the techniques of Kühner (1950b), in which the mycelium, in a drop of nutritive medium, was placed directly on a microscope slide and covered with a film of collodion, but Giemsa staining was used concurrently with the original ferric haematoxylin.

Mathematical treatment. Multiple correspondence analysis (Lebart et al. 1977) was followed by a TAXI automatic classification, using the computer programs of the Biometry Laboratory, University of Lyon-I, written by R. Fages.

The groundplan analysis was made according to Wiley (1981).

The data matrix

— Table 1

Characters 1—12 and 19—20 are features of the basidiocarp: the various character states were defined and discussed by Fiasson and David (1983). The hyphal system and perenniality practically coincided in an initial run with the morphological features alone and were merged here; the same goes for the size and wall thicknesses of the spores.

Character 13 is the 'type of culture'. At first we had 12 characters (32 character states) to describe the secondary mycelium, but it turned out to be unrealistic to treat them on a par with those of the basidiocarp, which are richer and more informative. The first analysis of the cultural characters distributed the species in four groups (Fiasson & David 1983), and it was decided to treat these as the four tentative character states of a single character. The 'type of culture' as a whole is thus given the same weight as a single feature of the basidiocarp (e.g., shape, miticity). This 'downgrading' of the mycelial characters is further justified by the reservations made about their reliability (Fiasson & David 1983).

Characters 14 and 15 are the 'proteinogram pattern' and the 'API' pattern of the secondary mycelium (Fiasson & Bernillon 1983). As each enzymatic activity (revealed here by API tests) and each individual protein (as seen in disc electrophoresis) can be coded by a single gene/allele, it would be inconsistent to put them on the same level as the morphological features, most of which have more complex determinants. So the two sets of data were submitted separately to clustering analysis. As regards the definition of their taxonomical significance (Fiasson & Bernillon 1983), it appears reasonable to treat the group to which each species belongs as a character state and each of the two arrays of data as a single character.

Character 16 is the type of nuclear behaviour in the secondary mycelium. Personal studies with hundreds of slides allow us to agree with the original observations of Kühner (1950b). The patterns distinguished can be regrouped in three classes:

Binucleate: Each cell constantly containing a dikaryon.

Oligonucleate: 4—8(—10) nuclei in the terminal cells, the number falling rapidly to (2—)3 (—4) in the following cells.

Coenocytic: Terminal cells with 16 to 40(—90) nuclei, this number decreasing slowly and progressively from cell to cell to (4—)8—12(—20) in those far from the hyphal apices.

Characters 17 and 18 refer, respectively, to the character and yield of the extractable styrylpyrones in the basidiocarp. Qualitatively, due to possible co-occurrence of hispidin and one or both of its two recognized dimers (3,14'-bishispidinyl and hypholomin B), five different pigment patterns were found (Fiasson 1982):

Hispidin and both dimers;

Hispidin and hypholomin B;

Hispidin and 3,14'-bishispidinyl;

Hispidin alone;

Absence of identifiable extractable styrylpyrones.

The quantitative viewpoint is often disregarded by phytochemists on the assumption that what counts is only the presence of the gene(s) of the biosynthetic pathway whose terminal products are observed. But the yield may be genetically determined, and the ability to accumulate secondary metabolites requires adaptations and processes possessing their own genes (Hegnauer 1976).

Phenetic analysis

Justification

When a systematist decides to give more weight to a certain character and considers it taxonomically critical, he makes his choice after survey of the whole array of available data. However, this choice cannot be free from subjectivity: it may be influenced by

Table 1. Discriminative description of 36 European poroid hymenochaetaceous fungi by 20 characters.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Species																				
<i>Phellinus chrysoloma</i>	3	1	3	3	1	1	3	2	2	2	1	2	1	2	3	3	2	3	2	1
— <i>onchatus</i>	3	2	3	3	1	4	3	6	1	1	3	1	1	2	2	3	3	1	2	1
— <i>contiguus</i>	1	2	2	2	1	4	3	6	1	1	3	1	1	2	2	1	3	1	2	1
— <i>erectus</i>	4	2	1	1	1	3	1	2	3	1	3	1	1	1	3	3	2	2	2	1
— <i>ferreus</i>	1	2	2	2	1	4	3	1	1	1	3	1	1	2	2	1	3	1	2	1
— <i>ferrugineofuscus</i>	1	1	2	2	1	3	1	7	1	1	3	1	1	2	2	2	1	1	2	1
— <i>ferruginosus</i>	1	2	2	2	1	4	4	5	1	2	1	1	2	1	1	3	1	2	2	1
— <i>hartigii</i>	5	1	1	1	1	1	2	1	2	3	1	3	1	1	1	3	2	2	2	1
— <i>igniarius</i>	4	2	3	3	3	4	3	3	1	1	2	2	2	2	3	3	1	2	2	1
— <i>laevigatus</i>	2	2	3	3	1	1	3	1	1	2	2	2	2	2	3	3	1	2	2	1
— <i>lundellii</i>	2	2	3	3	1	4	3	1	1	1	2	2	1	2	3	3	1	1	2	1
— <i>nigrolimitatus</i>	2	1	3	3	1	4	3	4	1	1	3	1	1	2	3	2	1	3	2	1
— <i>pini</i>	5	1	3	3	1	1	3	2	2	2	1	2	1	2	3	3	2	3	2	1
— <i>pseudopunctatus</i>	1	2	2	2	1	1	3	1	2	3	1	3	1	1	1	3	3	1	2	1
— <i>punctatus</i>	1	2	2	2	1	1	1	1	2	3	1	3	1	1	1	3	3	1	2	1
— <i>rhamnii</i>	1	2	2	2	1	1	3	1	1	2	1	3	1	2	3	3	4	1	2	1
— <i>robustus</i>	5	2	1	1	1	1	1	2	3	1	3	1	1	1	1	3	2	2	2	1
— <i>torulosus</i>	5	2	3	2	1	1	3	1	1	1	2	2	1	1	2	1	2	3	2	1
— <i>tremulae</i>	5	2	3	3	2	1	3	3	1	2	2	2	2	2	3	2	2	1	2	1
— <i>trivialis</i>	5	2	3	3	2	4	2	3	1	1	2	2	2	2	3	3	1	2	2	1
— <i>tuberculosis</i>	4	2	3	2	3	1	3	3	1	2	2	2	1	2	3	3	1	3	2	1
— <i>viticola</i>	2	2	2	2	1	4	3	1	1	1	3	1	1	2	2	1	3	1	2	1
<i>Phylloporia ribis</i>	3	2	4	3	1	1	1	1	2	1	2	2	2	1	3	3	3	2	1	2
<i>Onnia tomentosa</i>	7	1	4	1	1	1	3	1	2	1	1	1	1	1	2	3	3	1	1	1
— <i>triquetra</i>	6	1	4	1	1	1	4	2	1	2	1	1	1	1	2	3	2	1	1	1
<i>Inonotus cuticularis</i>	5	2	3	1	1	1	5	3	3	2	2	3	3	1	1	3	4	1	1	2
— <i>dryadeus</i>	5	2	3	1	1	1	4	2	2	3	1	3	1	1	1	3	4	1	1	2
— <i>dryophilus</i>	5	2	3	1	3	1	1	1	3	2	2	3	3	1	3	3	3	1	1	2
— <i>hispidus</i>	5	2	3	1	1	1	2	1	3	1	2	3	1	1	2	3	2	3	1	2
— <i>nidus-pici</i>	1	2	2	2	1	1	3	4	3	1	2	3	1	1	2	3	3	1	1	2
— <i>obliquus</i>	1	2	2	2	1	1	3	1	2	1	2	3	1	1	2	3	4	1	1	2
— <i>radiatus</i>	4	2	3	1	1	1	4	2	2	3	2	2	3	1	1	2	3	3	1	2
— <i>rheades</i>	4	2	4	1	3	1	1	1	3	2	2	3	3	1	3	3	3	1	1	2
— <i>tamaricis</i>	5	2	4	1	3	1	1	1	3	2	2	3	3	1	2	3	3	1	1	2
<i>Coltricia perennis</i>	7	4	3	1	1	1	1	1	3	3	2	3	1	1	1	3	4	1	1	3
<i>Phaeolus schweinitzii</i>	6	3	3	1	1	5	1	1	2	1	1	2	4	3	2	3	5	3	1	3

Characters and character states: 1 **Habit** of the basidiocarp (1 resupinate, 3 effused, 5 dimidiate, 7 stipitate). 2 **Host** (1 gymnosperms only ... 4 angiosperms only). 3 **Trichoderm**, built up by anticalinal hyphae (1 lacking, 2 weak or variable incl. resupinate specimens, 3 well-developed, 4 at least as thick as the flesh, i.e., duplex). 4 **Crust** built up by periclinal hyphae aggregated by an amorphous secretion, appearing as a black line in section if overlain by a thick trichoderm (1 none or very weak, 2 average or variable incl. resupinate species, 3 well-developed). 5 **Core** in the basidiocarp (1 none, 2 variable, 3 well-developed). 6 **Orientation of hyphae** (1 parallel throughout, 2 parallel in the context but subinterwoven in the trama, 3 interwoven in the context but parallel in the trama, 4 interwoven in the context but subinterwoven in the trama, 5 interwoven throughout). 7 **Hymenial setae** (1 lacking, 2 rare or malformed, 3 moderately developed, 4 strongly developed and abundant, 5 slightly hooked, 6 strongly hooked). 8 **Extrahymenial setae** (1 lacking, 2 rare, 3 abundant, 4 extremely abundant, 5 giant, 6 tramal and giant setae occurring, 7 setoid skeletal hyphae). 9 **Colour of the spore wall** (1 hyaline, 2 faintly, 3 deeply yellow). 10 **Staining** of the spore wall (1 negative, 2 slightly cyanophilous, not dextrinoid, 3 strongly cyanophilous and dextrinoid). 11 **Spore shape** (1 globose [$L/1 \leq 1.2$], 2 oval, 3 allantoid [$L/1 > 2$]). 12 **Spore size** (1 small [$L+1 \leq 4 \mu\text{m}$], 2 average, 3 large [$L+1 > 6 \mu\text{m}$]). 13 **Type of mycelial culture** (Fiasson & David 1983). 14 **Group according to the protein pattern** (Fiasson & Bernillon 1983). 15 **Group according to the enzymatic activities** (Fiasson & Bernillon 1983). 16 **Nuclear behaviour** of the secondary mycelium (1 binucleate, 2 oligonucleate, 3 coenocytic). 17 **Nature of the styrylpyrones** in the basidiocarp (1 hispidin + 3,14'-bishispidinyl, 2 hispidin+hypholomin B + 3,14'-bishispidinyl, 3 hispidin + hypholomin B, 4 none, 5 hispidin alone). 18 **Amount of styrylpyrones** in the basidiocarp (1 large [hundreds of μg per g, dry weight], 2 average, 3 low [some $\mu\text{g/g}$]). 19 **Perenniality** of the basidiocarp (1 annual, 2 perennial). 20 **Honeycomb hymenium** (1 no, 2 indistinct, 3 prominent network).

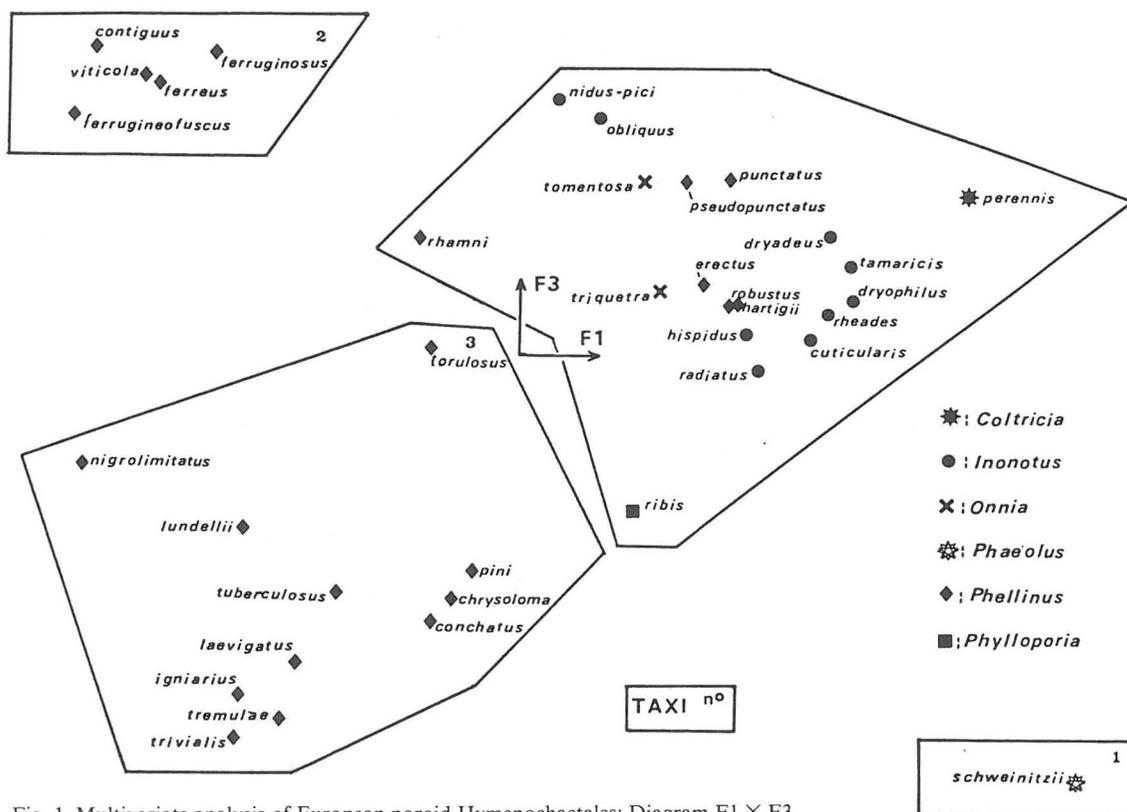


Fig. 1. Multivariate analysis of European poroid Hymenochaetales: Diagram F1 x F3.

factors such as tradition and the convenience of determination keys. As the distributions of the characters we studied — botanical and biochemical — did not support the current generic concepts, and as the value of the miticity as a criterion within the Hymenochaetales is now questioned (Jahn 1981), it seemed interesting here to subject the whole of our results to a neutral numerical analysis. That taxometrics is the phenetist's tool does not preclude its use by other taxonomists (Wiley 1981): a phenogram can be an approximation of a cladogram (G nermont 1980).

Our study group seemed specially propitious, because it is a homogeneous and natural order. Here the choice of generic characters is rather easy and far from the somewhat caricatural conditions presented by Kendrick and Weresub (1966). It is well known that some similarities (e.g., the resupinate growth habit) represent convergence, but this possibility must be considered in most characters (spore wall pigmentation, hyphal construction, etc.). All in all, the fact that the characters receive no *a priori* weighting here need not be considered shocking.

Mathematical tool

An objective analysis, in which all the characters are taken equally into account, computes out the 'taxonomic-phenetic real distances' between the

individuals, clusters them and extricates the more significant characters (Lebart et al. 1977). Each individual (species, in our case) is represented by a point in a space that has as many dimensions as the characters used. The whole sampling forms a 'cloud' and its principal axes (factors) are determined by the analysis. These main axes are the differences giving the best characterization. The analysis in turn reveals the position of each individual in relation to each factorial axis.

In practice, a plane representation generally visualizes most of the relationships between the analysed individuals. It is made up by the first two factorial axes (F1 x F2) as Cartesian coordinates. A certain amount of information, carried by the following factors, is then lost. Therefore such a two-dimensional figure must be completed with the abscissae on F3, F4, etc. and/or with an automatic clustering process, such as TAXI. This regroups the individuals according to their positions on all significant factors. The TAXI process splits up the sampling progressively, not hierarchically, but taking all the characters into account.

As a drawing of the clusters on the two-dimensional diagram reflects only the first two factors, the groups obtained by TAXI may look very different. However, they are far more significant than those discernible on F1 x F2.

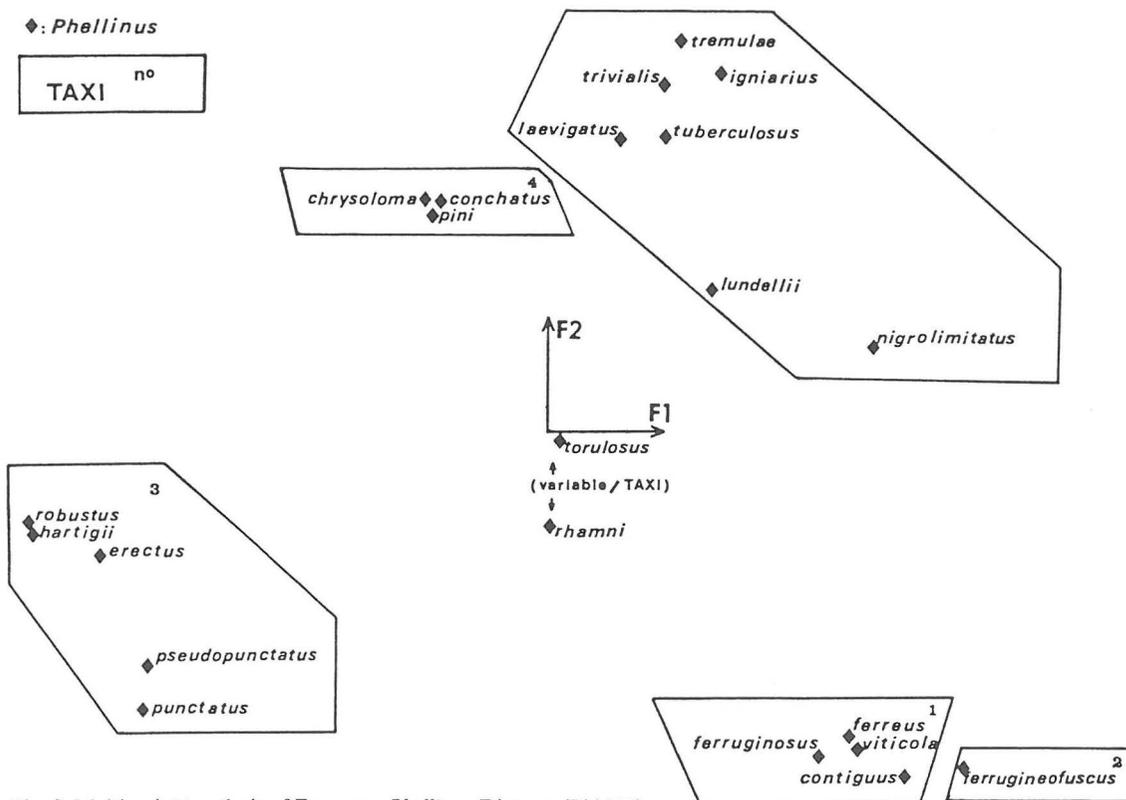


Fig. 2. Multivariate analysis of European *Phellinus*: Diagram F1 × F2.

Analysis of the poroid Hymenochaetales

Some of the characters appear to be of negligible taxonomical weight and none are determinative. On F2, the isolation of *P. schweinitzii* and of the associated character states generally outweighs the other features. Apart from this, the more important characters turn out to be the colour of the spore print, the styrylpyrone patterns, the hyphal disposition within the context and dissepiments, the extra-hymenial setae (though this may be partly an artifact, because of the number of character states, some appearing only once), and the structure of the cortical layers (artificially weighted by the partial coincidence of the 'medium' state with the resupinate habit). Then come the shape of the basidiocarp, spore size, and the type of culture.

Sharing no correlation with other characters, and so totally deprived of taxonomical significance are (at the level of the poroid Hymenochaetales as a whole) the host, the core of the basidiocarp and the amounts of styrylpyrone. The dimitic structure, which in classical keys isolates *Phellinus*, bears only moderate taxonomical significance (the same as the mere presence of hymenial setae!), for want of a high correlation with any other feature.

Figure 1 shows the distribution of 36 species of the F1 × F3 plane. F3 carries almost as much information as F2, on which distortion is caused by the extreme position of *P. schweinitzii*. At first glance,

two things are evident: The isolation of *Phaeolus* and the discrimination of *Phellinus* (except mainly the *P. robustus* group). But the TAXI automatic classification based on the information of the first six factors leads to a very different conclusion. Here the first group to be isolated (after *Phaeolus* alone) is that of the resupinate *Phellinus* with small, allantoid spores: *Fuscoporia* (sensu Fiasson 1982) with the addition of *P. ferrugineofuscus*. *P. nigrolimitatus* accompanies them at first, then falls back to the next group. This means that, according to their overall phenotype, they differ more from the remainder of *Phellinus* than the latter from, e.g., *Inonotus*.

This leads to the same conclusion as the taxometric analysis of the botanical features of the basidiocarp (Fiasson & David 1982): *Phellinus* shows phenetic diversity far larger than that of all the other undiscussed poroid Hymenochaetales put together. This casts doubts on its generic status. The question is not new to the polyporologists (Donk 1964), but the taxometric analysis indicates clearly which groups are to be separated and quantifies their relative degree of originality.

The analysis of *Phellinus*

The 24 representatives of *Phellinus* were submitted to a new analysis, which excluded characters 19 and 20. At this level, the more important characters are: size

of the spore, nature of the upper layers (again, weighted somewhat artificially because of its partial coincidence with the shape of the basidiocarp), and staining and shape of the spore. Then come the API enzymatic pattern and the extrahymenial setae. The nature of the styrylpyrones, nuclear behaviour, orientation of the hyphae and colour of the spore wall also have some weight.

The distribution of the 24 species on the F1 × F2 plane is shown in Fig. 2. The TAXI automatic classification corroborates the clustering apparent in the figure, and yields some interesting additional information: The first group to be isolated (level 2 classification) consists of *Fuscoporia* (as defined before) and *P. ferrugineofuscus*, but this latter segregates immediately afterwards (level 3). *P. torulosus* and *P. rhamni* are the only ambiguous species, though for very different reasons. *P. torulosus* appears to be undifferentiated, 'ancestral', as shown by its central position on all factorial planes; it combines features each of which elsewhere characterizes a different group. *P. rhamni* lacks the peculiar styrylpyrone pattern that anchors the other resupinate members of the *P. igniarius* complex, and therefore has some tendency to wander about.

Concluding remarks

The reader may wonder why we did not use the 'taxonomical distances' computerized between the species and between the clusters. First, their value is sensitive to the expression of data and calculation algorithms, and we lack the proficiency to choose those most appropriate to the problem in hand. Then, any calculator can give a result with six digits, but this is of no benefit if the initial data were accurate to one decimal place. Such apparent precision would be dangerously misleading with basic data as rough as are the morphological features, and probably often even the quantitative biochemical data of uncertain evolutionary value (Pasteur & Pasteur 1980, Fiasson & Bernillon 1983).

The phylogenetic groundplan

Principles

Wagner's classical method of groundplan divergence analysis proceeds in the following manner (Wiley 1981):

1) Determine which of the character states in a series of character transformations is the apomorphic one, i.e., derived, advanced, etc.

Table 2. Wagner divergence analysis of 36 European poroid Hymenochaetales, using 20 transformation series. Each character of Table 1 (No. 2 Host omitted) is treated as a transformation series, coded from 0 (plesiomorphy) to 1 (apomorphy), the numbering of the column being unchanged. DI is for total divergence index of the species.

Transformation series	1	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	DI
Species																				
<i>Phellinus chrysoloma</i>	0.6	0	1	0	0	0	0.2	0	0.5	1	0	0	1	1	1	0	0	1	1	8.3
— <i>conchatus</i>	0.6	0	1	0	0.25	0	0.2	0	0.5	1	0	0	1	1	1	0.5	0.5	1	1	9.55
— <i>contiguus</i>	1	0.5	0.5	0	1	0	0.75	1	0	1	1	0	1	0	0	0.5	1	1	1	11.25
— <i>erectus</i>	0.45	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0.5	0.5	1	1	9.45
— <i>ferreus</i>	1	0.5	0.5	0	1	0	0	1	0	1	1	0	1	0	0	0.5	1	1	1	10.5
— <i>ferrugineofuscus</i>	1	0.5	0.5	0	0.75	1	1	1	0	1	1	0	1	0	0.5	0.5	1	1	1	12.75
— <i>ferruginosus</i>	1	0.5	0.5	0	1	0.5	0.6	1	0	0	1	0	1	1	0	0.5	1	1	1	11.6
— <i>hartigii</i>	0.3	1	0	0	0	0.5	0	0	1	1	1	0	0	1	1	0	0.5	1	1	9.3
— <i>igniarius</i>	0.45	0	1	1	1	0	0.3	1	0	0	0	1	1	1	1	0.5	0.5	1	1	11.75
— <i>laevigatus</i>	0.75	0	1	0	0	0	0	1	0.5	0	0	1	1	1	1	0.5	0.5	1	1	10.25
— <i>lundellii</i>	0.75	0	1	0	1	0	0	1	0	0	0	0	1	1	1	0.5	1	1	1	10.25
— <i>nigrolimitatus</i>	0.75	0	1	0	1	0	0.4	1	0	1	1	0	1	1	0.5	0.5	0	1	1	11.15
— <i>pini</i>	0.3	0	1	0	0	0	0.2	0	0.5	1	0	0	1	1	1	0	0	1	1	8
— <i>pseudopunctatus</i>	1	0.5	0.5	0	0	0	0	0	1	1	1	0	0	1	1	0.5	1	1	1	10.5
— <i>punctatus</i>	1	0.5	0.5	0	0	1	0	0	1	1	1	0	0	1	1	0.5	1	1	1	11.5
— <i>rhamni</i>	1	0.5	0.5	0	0	0	0	1	0.5	1	1	0	1	1	1	1	1	1	1	12.5
— <i>robustus</i>	0.3	1	0	0	0	0.5	0	0	1	1	1	0	0	1	1	0	0.5	1	1	9.3
— <i>torulosus</i>	0.3	0	0.5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	3.8
— <i>tremulae</i>	0.3	0	1	1	0	0	0.3	1	0.5	0	0	1	1	1	0.5	0.5	0.5	1	1	10.6
— <i>trivialis</i>	0.3	0	1	0.5	1	0.5	0.3	1	0	0	0	1	1	1	1	0.5	0.5	1	1	11.6
— <i>tuberculosis</i>	0.45	0	0.5	1	0	0	0.3	1	0.5	0	0	1	1	1	0.5	0	1	1	1	9.25
— <i>viticola</i>	1	0.5	0.5	0	1	0	0	1	0	1	1	0	1	0	0	0.5	1	1	1	10.5
<i>Phylloporia ribis</i>	0.6	0.5	1	0	0	1	0	0	0	0	0	1	0	1	1	0.5	0.5	0	0.5	7.6
<i>Onnia tomentosa</i>	0	0.5	0	0	0	0	0	0	0	1	1	0	0	0	1	0.5	1	0	1	6
— <i>triquetra</i>	0.15	0.5	0	0	0	0.5	0.2	0	0	0	1	0	0	0	1	0.5	0.5	0	1	5.35
<i>Inonotus cuticularis</i>	0.3	0	0	0	0	0.5	0.3	1	0.5	0	1	1	0	1	1	1	1	0	0.5	9.1
— <i>dryadeus</i>	0.3	0	0	0	0	0.5	0.2	0	1	1	1	0	0	1	1	1	1	0	0.5	8.5
— <i>dryophilus</i>	0.3	0	0	1	0	1	0	1	0.5	0	1	1	0	1	1	0.5	1	0	0.5	9.8
— <i>hispidus</i>	0.3	0	0	0	0	0.5	0	1	0	0	1	0	0	0	1	0	0	0	0.5	4.3
— <i>nidus-pici</i>	1	0.5	0.5	0	0	0	0.4	1	0	0	1	0	0	0	1	0.5	1	0	0.5	7.4
— <i>obliquus</i>	1	0.5	0.5	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0.5	6.5
— <i>radiatus</i>	0.45	0	0	0	0	0.5	0.2	0	1	0	0	1	0	1	0.5	0.5	0	0	0.5	5.65
— <i>rheades</i>	0.45	0.5	0	1	0	1	0	1	0.5	0	1	1	0	1	1	0.5	1	0	0.5	10.45
— <i>tamaricis</i>	0.45	0.5	0	1	0	1	0	1	0.5	0	1	1	0	0	1	0.5	1	0	0.5	9.45
<i>Coltricia perennis</i>	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	0	0	8
<i>Phaeolus schweinitzii</i>	0.15	0	0	0	0.5	1	0	0	0	1	0	1	1	0	1	1	0	0	0	6.65

2) Assign to the plesiomorphic (primitive, ancestral, etc.) character state in each transformation series the score of 0, and to each apomorphic state the score of 1. If more than two homologues are present, the 'intermediate apomorphies' are scaled between 0 and 1.

3) Construct a table of the taxa and the coded characters. This has been done in Table 2 from the data of Table 1, excluding the host.

4) Determine the divergence, by totalling the values for each taxon from the whole transformation series. This is the total divergence index (DI) in Table 2.

5) Plot the taxa on a graph, by placing each taxon on one of a number of concentric semi-circles. The radius of a taxon equals its divergence index.

6) The lines connecting the taxa are determined by the shared synapomorphies. Ancestral species (indicated by open circles) of progressively higher levels are reconstructed step-by-step from the shared synapomorphies and symplesiomorphies of their supposed descendants.

Poroid Hymenochaetales:

Coded character data matrix

Table 2 shows the experimental data of Table 1 translated into steps of a transformation series, one for each character. Assessing what is the plesiomorphic (primitive, ancestral, archaic) character state and what is the apomorphic (derived, advanced) one was in some cases straightforward and in others required some subjective 'guesswork' with distribution within the poroid Hymenochaetales and also in outgroups (*Hymenochaete*, Polyporaceae) as background evidence.

For the *shape* of the basidiocarp, we considered the pileate habit to be primitive and the resupinate derived. A primitive saprophytic fungus at ground level has to be pileate to have its hymenial layer facing downward, as is generally the case among the Homobasidiomycetes. It remains so when evolving toward mycorrhizal symbiosis. When turning to parasitism and 'climbing up' its host, it becomes dimidiate when on the side of the trunk or main branches, then ultimately resupinate when under the twigs (Donk 1971). As a group, the Hymenochaetales are an advanced taxon. Their common ancestor should not be envisaged as a mycelial mat, but as a lignicolous fungus with an already well-differentiated basidiocarp. The possibility of parallel evolution was not taken into account here, though one may perhaps consider it for the dimidiate *Inonotus*, the basidiocarp of which is simpler in construction than that of *Phellinus*.

Owing to their distribution, the differentiated *trichoderm* and *crust* are considered primitive and derived, respectively. The *core* of some dimidiate species was treated as an apomorphy, while the lack of it in the resupinate members of the *P. igniarius* complex would theoretically have to be scored as surevolution.

Of the other characters, the more widespread character state (for the *hyphal orientation* and the *setae*), or the less differentiated character (for *spore*

features and the *mycelial characters*, except the nuclear behaviour) are considered plesiomorphic.

In the *nuclear behaviour* progress is assumed to have been from binucleate to coenocytic.

The distribution of the *styrylpyrones* strongly suggests that, within the poroid Hymenochaetales, the primitive character state is the co-occurrence of hispidin and its two dimers (3,14'-bishispidinyl and hypholomin B) and the ultimate state was considered to be total loss of extractable styrylpyrones. *Quantitatively*, as evolution worked towards reduction of extractable styrylpyrones, richness was seen as primitive.

Perenniality, strongly correlated with dimiticity, was seen as apomorphic. Lack of definite evidence forbade us to differentiate perenniality from miticity in order to distinguish primitive from reappeared monomiticity. The difficulties of using miticity as a criterion are much more evident now than when it was raised to the rank of generic criterion (Jahn 1981, Fiasson & David 1983).

In the configuration of the *interbasidial secretion*, best seen in front view, progress is suggested to have been towards a distinct honeycomb structure (Niemelä 1975).

Poroid Hymenochaetales: A groundplan

Figure 3 shows the phylogenetic diagram obtained from the criteria described above. Some comments are needed: First, as most divergence indices are not whole numbers, the traditional concentric semicircles representing the degrees of anagenetic divergence were omitted. Second, the figure is not a normal phylogenetic groundplan, i.e., the projection of a phylogenetic tree on the 'Present' plane. The sampling being limited to Europe, it is a projection of the extremities of the branches nowadays represented in Europe, with their past insertion extrapolated. Therefore artificial precision was avoided, trichotomies were not resolved into successive dichotomies, and the present-day species were not excluded from ancestral nodes. Reciprocally, when an ancestral species is plotted very close to an extant one, this may well reflect anagenesis rather than speciation.

The cladogram has been built up centripetally and is therefore easier to read from the centre outwards. The first dichotomy is between the genera without a neat interbasidial network (*Phaeolus*, *Coltricia*) and those with a more or less distinct honeycomb structure in their hymenium (*Inonotus*, *Phylloporia*, *Phellinus*, *Onnia*). This corresponds to the distinction between the proposed suborders Phaeolinae and Hymenochaetinae (the tribes Phaeolae and Phellinae as defined by Fiasson 1982: 25). This receives remarkable support from the septal ultrastructure, which was not taken into account in our data matrix, and of which we were unaware when proposing the two tribes in 1982. *C. perennis* and *P. schweinitzii* have normal perforate parentheses, while at least the type species of *Inonotus*, *Phellinus* and *Onnia* have nonperforate ones, generally associated with the Heterobasidiomycetes (Moore 1980). Now it has turned out that *Asterodon* also belongs to the non-perforate parentheses type (Moore, in litt. 1983).

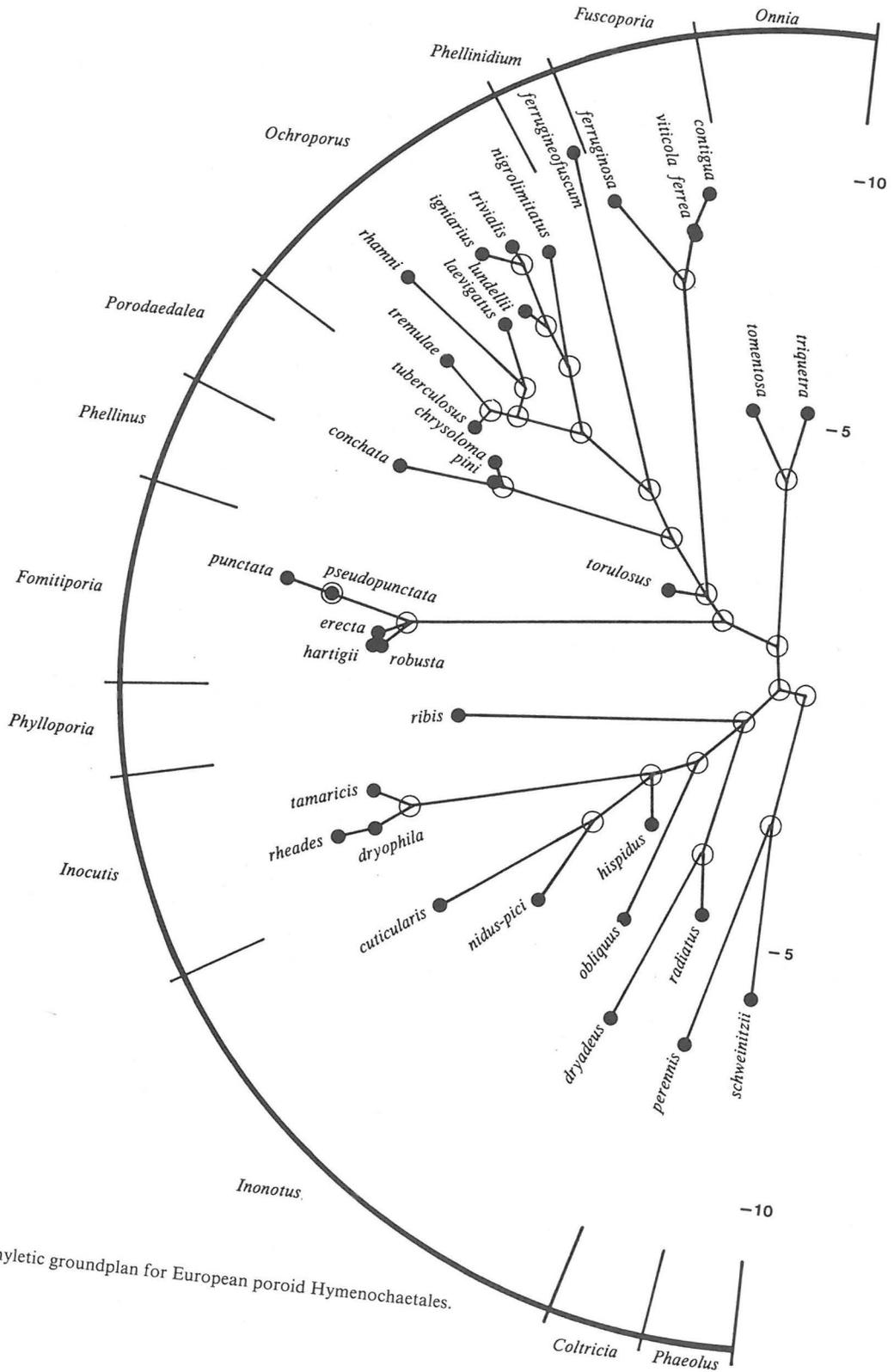


Fig. 3. Wagner phyletic groundplan for European poroid Hymenochaetales.

More evidence is needed, however, before further conclusions are made.

Among the Hymenochaetinae, the next dichotomy is between the genera with blurred interbasidial networks (*Inonotus*, *Phylloporia*) and those with a neat honeycomb hymenium (*Phellinus*, *Onnia*), a division strongly correlated with different hyphal systems. In *Inonotus*, the best isolated group is *I. rheades* and its allies (*Inonotus* sect. *Phymatopilus* Donk) and for this reason we propose its separation in a new genus.

In *Phellinus*, the first group to emerge is that of *P. robustus* (*Phellinus* subg. *Cyanovosporus* Fiasson). This is mostly due to the difference we found between its covering layers and those of the rest of *Phellinus*. Besides, the hyphae intermediary between generative and skeletal are especially conspicuous here (Jahn 1981), and so this group is 'the least *Phellinus*-like within *Phellinus*'. The next group segregated in *Phellinus* is *Fuscoporia* (sensu Fiasson 1982), which has retained the binucleate state though many of its other characters are advanced. The group of *P. pini* is more closely related to *P. torulosus* than it appears, if the loss of the binucleate state did not occur as a separate step, but during the passage from *P. 'pretorulosus'* (or *P. torulosus* itself) to *P. pini*. The remainder of *Phellinus* (*Ochroporus* sensu Fiasson 1982 and *Phellinidium*) is characterized by the occurrence of 3,14'-bishispidinyl without hypholomin B. *Ochroporus* itself is dichotomized according to two congruent characters: hyphal orientation in the basidiocarp (Cunningham 1965, Niemelä 1972) and colourability of the spore wall (Fiasson & David 1983).

Conclusion

As mentioned earlier, we consider that the most reliable results are those for which agreement exists between the two approaches — phenetic and phylogenetic. Both approaches show:

- 1) Relative isolation of *Phaeolus schweinitzii*.
- 2) Clustering of the species in *Inonotus* and especially *Phellinus* into infrageneric entities that appear natural — perhaps even more so that the large genera themselves.

These points have been familiar to mycologists for a long time, but they are defined and demonstrated more clearly here. They form the basis for all the following conclusions.

The major division of the Hymenochaetales

Although *P. schweinitzii* shares many features with *Coltricia*, some mycologists exclude it from the Hymenochaetales, mainly because it produces brown-rot (Parmasto & Parmasto 1979). As we discussed earlier (Fiasson 1982), even from the viewpoint of the wood-decaying metabolism, *P. schweinitzii* is not far from typical Hymenochaetales. In any case its styrylpyrone production is a very strong argument in favour of its inclusion in this order. As its pigmentary metabolism also shows peculiarities separating it from the *Inonotus-Phellinus* group, we propose its separation in a suborder of its own.

If the non-poroid Hymenochaetales are also taken into account, the rest of the order (apart from the *Phaeolus* group) shows two groups of taxa. *Hymenochaete* and the other non-poroid taxa are characterized by the ability to accumulate hispidin and sometimes leucohymenoquinone, but neither hypholomin B, nor 3,14'-bishispidinyl. The other group is the poroid one: these taxa can accumulate hispidin, hypholomin B and/or 3,14'-bishispidinyl, but not leucohymenoquinone, and their hymenium shows a more or less distinct honeycomb structure. As seen already here, the last group is the most heterogeneous.

When deciding the major division of the order, we first intended to separate three main groups, as defined above. This, however, would not emphasize sufficiently the originality of the *Phaeolus* group, and besides the last group would be much more heterogeneous than the others. On the other hand, we wished to achieve a simple system in preference to a complicated hierarchy. As a compromise between these partly opposite requirements, we propose the following division of the hymenochaetaceous fungi:

Order Hymenochaetales Oberwinkler

Suborder Hymenochaetinae Fiasson & Niemelä

Fam. Hymenochaetaceae Donk (genera *Hymenochaete* Lév., *Asterodon* Pat., *Hydnochaete* Bres.)

Fam. Inonotaceae Fiasson & Niemelä (genera *Inocutis* Fiasson & Niemelä, *Inonotus* Karst., *Phylloporia* Murr.)

Fam. Phellinaceae Jülich (genera *Phellinus* Qué., *Fomitiporia* Murr., *Fulvifomes* Murr., *Fuscoporia* Murr., *Inonotopsis* Parm., *Ochroporus* J.Schroet., *Onnia* Karst., *Phellinidium* Kotl., *Porodaedalea* Murr.)

Suborder Phaeolinae Fiasson & Niemelä

Fam. Phaeolaceae Jülich (genera *Phaeolus* Pat., *Coltricia* S.F. Gray)

Hymenochaetales Oberw. 1977 emend. Fiasson & Niemelä (Oberwinkler 1977: 89): Homobasidiomycetes with poroid, smooth or spiny hymenophore; hyphae golden to brown, xanthochroic and consistently simple-septate (in addition, hyaline simple-septate hyphae may occur); setae present in most species; parentheses nonperforate in most species; capable of synthesizing styrylpyrones; producing white-rot or seldom imperfect brown-rot. Typus: Hymenochaetaceae Donk. — These fungi do not manifest true dimiticity at all: the coloured hyphae, present in all the species, are septate and therefore cannot be regarded as skeletal hyphae proper; intermediaries are also common. The presence of the styrylpyrones could not be confirmed in *Asterodon*, but the nonperforate parentheses, presence of setae, hyphal characters, etc. support its inclusion. By the 'imperfect brown-rot' we mean *Phaeolus*, which does not react to some tests as a true brown-rot fungus (Gilbertson et al. 1975), and whose basidiocarp has the triterpene content of a white-rot species (Yokoyama et al. 1975).

Hymenochaetinae Fiasson & Niemelä, subordo nov. *Hymenochaetales hymenophoro poroso, glabro vel spinoso; setae in speciebue plurimis adsunt; parenthesesomata non-perforata. Hispidinum et unum vel plura ex sequentibus procreant: leucohymenoquinum, hypholominum B, 3,14'-bishispidinylum. Cariem albam producunt.* Hymenochaetales with poroid, smooth or

spiny hymenophore; setae present in most species; parentheses nonperforate; synthetizing hispidin and one or more of the following: leucohymenoquinone, hypholomin B, 3,14'-bishispidinyl; producing white-rot. Typus: Hymenochaetaeaceae Donk. — This suborder is best understood, when contrasted with Phaeolinae. The presence of setae and the lack of perforation in the parentheses are diagnostic of this suborder. The morphology varies greatly, and the first family (containing the non-poroid taxa) differs distinctly from the other two.

Hymenochaetaeaceae Donk 1948 emend. Fiasson & Niemelä (Donk 1948: 474): Hymenochaetinae with smooth or spiny hymenophore; hymenium not forming a honeycomb structure; setae present; accumulates hispidin and leucohymenoquinone, but neither hypholomin B nor 3,14'-bishispidinyl. Typus: *Hymenochaete* Lév. — This family and its accurate delimitation fall outside the scope of the present study. *Hydnochaete* Bres. most probably belongs here (cf. Ryvarden 1982). The inclusion of *Asterodon* Pat. is provisional. This group particularly needs a more thorough study with extra-European material.

Inonotaceae Fiasson & Niemelä, fam. nov. *Hymenochaetinae hymenophoro poroso; sporocarpia reflexa vel resupinata; annuae vel raro imperfecte perennes; structura hypharum monomitica; setae adsunt vel nullae; sporae ellipsoideae, dextrinoideae, valde cyanophilae; reticulum faveolatum hymenii indistinctum.* Hymenochaetinae with porous hymenophore; fruit bodies bracket-shaped or resupinate; annual or seldom imperfectly perennial; hyphal structure monomitic; setae present or absent; spores ellipsoid, dextrinoid and strongly cyanophilous; honeycomb structure in hymenium indistinct. Typus: *Inonotus* Karst. — The species can accumulate hispidin, hypholomin B and/or 3,14'-bishispidinyl, but not leucohymenoquinone. The spore characters are good for separating this family from the following, and so is the monomitic hyphal system. Most species are distinctly annual: *Phylloporia ribis* is perennial, or rather reviving because old parts of its sporocarps start to disintegrate after one or two winters. The taxonomy of the genus *Phylloporia* Murr. needs closer study. *Phymatopilus* of Donk (1974, as sect.) was erected as a genus (*Inocutis*) because it was most clearly separated from the rest of *Inonotus*. The remainder is a heterogeneous group; more knowledge of the extra-European species is needed before proposals for further division can be made.

Phellinaceae Jül. 1981 emend. Fiasson & Niemelä (Jülich 1981: 384): Hymenochaetinae with porous hymenophore; fruit bodies stipitate, bracket-shaped or resupinate; perennial or seldom annual; hyphal system dimitic in appearance, with thin-walled hyaline hyphae besides the pigmented ones; setae mostly present; honeycomb structure in hymenium distinct. Typus: *Phellinus* Quéél. — The species of this family can accumulate hispidin, hypholomin B and/or 3,14'-bishispidinyl, but not leucohymenoquinone. The spore characters vary greatly among the genera; the best character differentiating this family from the Inonotaceae is the distinct honeycomb struc-

ture, with the basidia and basidioles cohering in one network. Perenniality, when present, is strongly indicative of this family. The dimitic appearance is mostly clear, but remains vague in *Fomitiporia*, and even more so in *Phellinidium* and *Onnia*. The inclusion of *Inonotopsis* Parm. is provisional; see the discussion of Niemelä & Kotiranta (1983). The generic division will be presented in a separate section. Apart from its name, the family in our sense has little in common with that of Jülich (1981).

Phaeolinae Fiasson & Niemelä, subordo nov. *Hymenochaetales hymenophoro poroso; setae nullae; parenthesesata perforata; hispidinum procreant, nullum autem ex sequentibus: leucohymenoquinonum, hypholominum B, 3,14'-bishispidinylum; cariem albam vel cariem brunneam imperfectam producunt.* Hymenochaetales with poroid hymenophore; setae absent; parentheses perforate; synthetizing hispidin but none of the following: leucohymenoquinone, hypholomin B, 3,14'-bishispidinyl; producing white-rot or imperfect brown-rot. Typus: Phaeolaceae Jülich. — The perforation of the parentheses is the greatest difference from the Hymenochaetinae. The constancy of the lack of setae needs further investigation in *Coltricia*.

Phaeolaceae Jül. emend. Fiasson & Niemelä (Jülich 1981: 348): Phaeolinae with porous hymenophore; fruit bodies with tendency to stipitate habit; annual; monomitic; no honeycomb structure in hymenium. Typus: *Phaeolus* Pat. — Here again, the name of the family is adopted from Jülich, but not the concept: he also included the genus *Pycnoporellus* Murr., which is a very distant taxon (Fiasson 1982), better placed in the vicinity of *Laetiporus* Murr. (Niemelä 1980). *Coltricia* is included in the family by us; Jülich kept it in the vicinity of *Onnia*, *Inonotus*, etc.

Notes on *Inonotus* and *Phellinus*

The only character in the data matrix that seems to support the current generic distinction between *Inonotus* and *Phellinus* is the hyphal system (actually isolates *Phellinus* from all other genera). The other characters cut across the genera or isolate smaller entities within them. Four such groupings appear at first glance. Within *Inonotus*, the group of *I. rheades* emerges, which has a core and a characteristic chromatogram (Fiasson 1982). In *Phellinus*, the three clearest groups are that of *P. robustus* (with globose, cyanophilous and dextrinoid spores), that of *P. igniarius* (with a characteristic styrylpyrone pattern) and that of *P. ferreus* (mainly resupinate species with generally small, allantoid spores and binucleate secondary mycelium).

But what rank do these entities deserve? The first clusters isolated in TAXI analysis are the most 'original' judged on purely phenetic criteria. Here at least the *P. robustus* and *P. ferreus* groups seem to deserve generic ranking, rather than *Phellinus* as a whole. The phylogenetic approach is less straightforward, less automatic. Some of the well-defined genera may be monospecific while others embody a very large number of species, so that it is impossible to lay down a rule-of-thumb about how many dichot-

tomes above the extant species are needed to make up a genus.

In Fig. 3 we drew both *Inonotus* and *Phellinus* as monophyletic. The limited data at hand did not justify any other treatment. However, this does not imply that they are good genera: any natural taxon, regardless of its rank in the hierarchy, is monophyletic. Phylogenetically, a genus can be recognized in a well-defined branch arising not far above the (sub)tribal level: Then, by analogy with *Onnia*, *Phellinus* appears to deserve to be kept as a genus as well. From a less theoretical viewpoint, if the number of species and the importance of the hiatuses between the groups are considered, each of the lines (i.e., the sectors in Fig. 3) within *Phellinus* should be accorded generic rank. As mentioned above, our groundplan should not be considered absolutely exact; in fact we have a tetramerous division of a hypothetical ancestor very close to extant *P. torulosus*, leading to the groups of *P. robustus*, *P. igniarius* (from which the group of *P. ferrugineofuscus* may be further separated), *P. ferreus* and *P. pini*. Accordingly, we previously suggested for the first three groups the subgeneric names *Cyanovosporus*, *Ochroporus* and *Fuscoporia*, respectively (Fiasson 1982, Fiasson & David 1983). Being rather poorly differentiated, *P. torulosus* is situated somewhere in between the groups of *P. pini* and *P. ferreus*. We first connected it with the *P. pini* complex, but new observations (especially the presence of the crystal hyphae) also reveal affinities with the latter group. After repeated consideration, we find that the only solution is to separate *P. torulosus* from both complexes. This point is important, because *P. torulosus* is the type of the genus *Phellinus*, and so determines the future destiny of the name.

Singer (1975) states that a serious attempt at reorganisation on the generic level requires a thorough knowledge of the world flora. In practice, this demand is often exorbitant and would postpone such revisions until a very distant future. Of course, the wider the material, the more reliable the results. Actually, for the various characters used here, we studied more than a hundred tropical collections and our observations will be published as soon as the botanical determinations of the specimens have been confirmed. However limited these studies may be, they nevertheless allow us to be sure that a profound knowledge of *Phellinus* at global level will not seriously alter the concepts of the groups distinguished by us in the European collections. For instance, we never encountered a specimen combining the styrylpyrones of *Ochroporus* and the spores of *Fomitiporia* (*Cyanovosporus*). The extra-European material will rather make it possible to recognize other groups in the remainder of *Phellinus*.

Taking all these matters into account, we propose the recognition of the following genera within the fungi earlier included in *Inonotus* and *Phellinus*. In the difficult questions of the generic typification, we followed Donk (1960, 1962).

Inonotus Karst. 1879. Type: *Polyporus hispidus* Bull.: Fr. — For details of the nomenclature, typification and possible future division, see Donk (1974). In the present sense this is still a heterogeneous genus.

Inocutis Fiasson & Niemelä, gen. nov. *Sporocarpium medulla marmorata praeditum, hymenium sine setis*. Sporocarp with marmorate core, hymenium without setae. Type: *Polyporus rheades* Pers. 1825. — This is the *Inonotus rheades* complex, discussed earlier, or *Inonotus* sect. *Phymatopilus* Donk (Donk 1974: 228). We changed the name proposed by Donk to a shorter one that accords with the old genus. Meaning a fibrous cutis, it fits the European species well.

Phylloporia Murr. 1904. Type: *Phylloporia parasitica* Murr. — We have adopted this genus in the sense of Ryvar den (1978), containing *P. ribis* (Schum.: Fr.) Ryvar den as the only European representative. The type of the genus, *P. parasitica*, is epiphyllous, and therefore very different from the other species included by Ryvar den (1978) and Ryvar den & Johansen (1980: four pileate, epixyloous, tropical species). We have not studied the type, but the evidence given by Ryvar den points to a homogeneous genus. Jahn (1981) casts some doubts on this solution. If *P. ribis* is to be separated from *Phylloporia*, an available genus is *Cryptoderma* Imaz. 1943, with *P. ribis* as the type.

Fomitiporia Murr. 1907. Type: *Fomitiporia langloisii* Murr. = *Phellinus punctatus* (Karst.) Pilát. — Generally known as the 'Phellinus robustus complex' this is *Phellinus* subg. *Cyanovosporus* Fiasson (Fiasson 1983: 29). The genus is very well-defined, characterized by subglobose, strongly cyanophilous, dextrinoid spores; the context is brass-coloured, composed of hyphae which show very weak differentiation into the so-called skeletal and generative hyphae: hymenial setae do exist in most species, but are remarkably often very rare; in addition, the hymenium often possesses ampullaceous cystidioles. Of the groups of the traditional *Phellinus*, this is closest to *Inonotus*.

Porodaedalea Murr. 1905. Type: *Boletus pini* Brot. 1804 = *Daedalea pini* Brot.: Fries 1821 = *Phellinus pini* (Brot.) A. Ames. — The *Phellinus pini* complex. The spores are ellipsoid and rather thick-walled; they are not dextrinoid, but do possess moderate cyanophily. The reaction is not strong, and therefore depends on the quality of the dye. A positive reaction can be seen, for example, using the water-soluble aniline blue of Merck (Art. 1275), prepared according to Singer (1975: 94). The genus is further characterized by the pileus surface, which is pubescent or hirsute at first, later developing a rather weakly defined crust. The pores are round to labyrinthine, and without crystal hyphae in their mouths. Ungerminated spores often remain in old tubes, blocked by secondary mycelium: they swell and absorb brown pigments from the hyphae and are sometimes reported as chlamyospores (Ryvar den 1978). The hymenium possesses subulate setae, and in most species setae can also be found embedded in the tube walls.

Ochroporus J.Schroet. 1888. Type: *Polyporus igniarius* L.: Fr. — *Ochroporus* comprises the *P. igniarius* complex, as outlined by Niemelä (1972, 1974, 1975, 1977). The brown and thick-walled hyphae are well distinguished from the hyaline and thin-walled ones, and so the species are usually regarded as dimorphic. The hymenium shows a very well-developed honeycomb structure plus subulate setae. A rudimentary core is present in many of the pileate species. Apart from the hymenial and core setae, setal elements are absent, as are also crystal hyphae. The spores are rather thick-walled and indextrinoid; the cyanophily is as in *Porodaedalea*. The sporocarps are not hirsute but develop a regular crust. No chlamydospore-like spores remain in old tubes.

Phellinidium (Kotl.) Fiasson & Niemelä, stat.nov. Basionym: *Phellinus* subg. *Phellinidium* Kotl. (Kotlaba 1968: 29). Type: *Poria ferrugineofusca* Karst. 1887. — Kotlaba (1968) defined this group very well, and we need only repeat the main characters. The most striking are the macrosetae (also called the setoid skeletal hyphae) which predominate in both the trama and the context, overshadowing the true hyphae. The latter are very weakly differentiated. The spores are thin-walled, ellipsoid-cylindrical, without colour reactions in Melzer's reagent or Cotton Blue. This is a rather small, but characteristic genus. In our study it was long united with *Ochroporus*, but the microscopical characters alone are sufficient to justify separation.

Phellinus QuéL. 1886. Type: *Polyporus rubriporus* QuéL. = *P. torulosus* Pers. — We found it fairly difficult to define *Phellinus* in the strict sense. Being rather undifferentiated and ancestral, *P. torulosus* shares characters with several genera. The binucleate mycelium and crystal hyphae (the latter character is weakly developed) connect it with *Fuscoporia*, and the pigmentation with *Porodaedalea* and *Fomitiporia*. The genus is best defined by enumerating the characters that it does not possess: it lacks the cyanophilous-dextrinoid spores of *Fomitiporia*; the thick-walled and cyanophilous spore type of *Porodaedalea* and *Ochroporus* (also distinguished from them by the crystal hyphae); the macrosetae of *Phellinidium*; the allantoid spore type and the pigmentation of *Fuscoporia*. It is fortunate that the name *Phellinus* remains attached to an undifferentiated group. For the time being, this genus name can be used for species which do not find their natural place in the other genera. In the strict sense, *Phellinus* is represented in Europe only by *P. torulosus*, but the latter will be joined by many tropical species (e.g. *P. gilvus*, *P. licnoides*).

Fuscoporia Murr. 1907. Type *Boletus ferruginosus* Schrad. — In the present sense, *Fuscoporia* is a very homogeneous genus. The spores are extremely thin-walled and acyanophilous, and mostly allantoid in shape. The context is very soft-corky, and no crust or trichoderm develops on the pilei. Crystal hyphae are abundant in the tube mouths.

Fulvifomes Murr. 1914. Type: *Pyropolyporus robiniae* Murr. 1903 = *Phellinus robiniae* (Murr.) A.Ames — Often called the *P. rimosus* complex, this

group was not included in our study proper. Kotlaba and Pouzar (1978) have made a detailed examination of the group, and so the outlines of the genus are quite clear. Characteristic features are the large, coloured spores and complete absence of setae. For further details, the reader is referred to the revision of Kotlaba and Pouzar (1978).

Inonotopsis Parm 1973. Type: *Polyporus subiculosus* Peck 1879. — This genus could not be included in our study proper, because its sole representative, *I. subiculosa*, is extremely rare in Europe (Parmasto 1973, Niemelä & Kotiranta 1983). We accept the genus because of the microscopical characteristics, but cannot establish its relationships to the other genera. These questions were discussed by Niemelä and Kotiranta (1983).

New combinations and old accepted ones

Inocutis dryophila (Berk.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus dryophilus* Berk., London J. Bot. 6: 321, 1874.

Inocutis rheades (Pers.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus rheades* Pers., Mycol. Europ. 2: 69, 1825. Type of the genus *Inocutis* Fiasson & Niemelä. For the typification of *P. rheades*, see Kotlaba & Pouzar (1970).

Inocutis tamaricis (Pat.) Fiasson & Niemelä, n.comb. Basionym: *Xanthochrous tamaricis* Pat., Bull. Soc. Myc. France 20: 51, 1904.

Fomitiporia erecta (David, Dequatre & Fiasson) Fiasson, n.comb. Basionym: *Phellinus erectus* David, Dequatre & Fiasson, Mycotaxon 14: 165, 1982.

Fomitiporia hartigii (All. & Schn.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus hartigii* Allescher & Schnabl, Fungi Bavarici Exsicc. 48, 1890. See Jahn (1976).

Fomitiporia hippophaeicola (H.Jahn) Fiasson & Niemelä, n.comb. Basionym: *Phellinus hippophaeicola* H.Jahn, Mem. New York Bot. Garden 28: 105, 1976, 'hippophaecola'.

Fomitiporia pseudopunctata (David, Dequatre & Fiasson) Fiasson, n.comb. Basionym: *Phellinus pseudopunctatus* David, Dequatre & Fiasson, Mycotaxon 14: 171, 1982.

Fomitiporia punctata (Karst.) Murrill, Lloydia 10: 254, 1948. *Poria punctata* Karst., Bidr. Känned. Finlands Nat. Folk 37: 83, 1882. *Polyporus punctatus* Fries 1874 is a later homonym of *P. punctatus* Jungh. 1838. Syn.: *Fomitiporia langloisii* Murrill, North Amer. Flora 9(1): 9, 1907 (holotype: 12 Nov. 1897 Langlois 2525, NY, studied), type of the genus *Fomitiporia* Murrill.

Fomitiporia robusta (Karst.) Fiasson & Niemelä, n.comb. Basionym: *Fomes robustus* Karst., Bidr. Känned. Finlands Nat. Folk 48: 467, 1889.

Porodaedalea chrysoloma (Fr.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus chrysoloma* Fries, Öfvers. K. Vet.-Akad. Förh. 18: 30, 1861. The identity of the specific name was discussed by Donk (1971).

Porodaedalea conchata (Pers.: Fr.) Fiasson & Niemelä, n.comb. Basionym: *Boletus conchatus* Pers., Obs. Mycol. 1: 24, 1796. *Polyporus conchatus* Pers.: Fries, Syst. Mycol. 1: 376, 1821.

Porodaedalea pini (Brot.: Fr.) Murrill, Bull. Torrey Bot. Club 32: 367, 1905. *Boletus pini* Brotero, Flora Lusitana 2: 468, 1804. *Daedalea pini* Brot.: Fries, Syst. Mycol. 1: 336, 1821. The species was described already a year earlier, by the same name (*Boletus pini* Thore 1803), but having a separate type. Fries (1821) sanctioned the epithet of Brotero, which must be followed. See Donk (1974: 244). Type of the genus *Porodaedalea* Murrill.

Porodaedalea pilatii (Černý) Fiasson & Niemelä, n.comb. Basionym: *Phellinus pilatii* Černý, Česká Mykol. 22: 2, 1968.

Ochroporus alni (Bond.) Fiasson & Niemelä, n.comb. Basionym: *Fomes igniarius* (L.: Fr.) Fr. f. *alni* Bondarcev, Trudy Lesn. Opytn. Delu Ross. 37: 20, Fig. 1, Tab. 2, 1912. *Phellinus alni* (Bond.) Parm., Eesti NSV Tead. Akad. Toim. (Biol.) 25: 316, 1976. For the identity of the species, see Parmasto (1976).

Ochroporus igniarius (L.: Fr.) J.Schroet., Pilze Schles.: 487, 1888. For the typification of the epithet, see Niemelä (1975). Type of the genus *Ochroporus* J.Schroet.

Ochroporus laevigatus (Karst.) Fiasson & Niemelä, n.comb. Basionym: *Poria laevigata* Karst., Medd. Soc. Fauna Flora Fennica 6: 10, 1881. *Polyporus laevigatus* Fries 1874 is a later homonym of *P. laevigatus* (Pers.) Duby 1830. For the typification, see Niemelä (1972).

Ochroporus lundellii (Niemelä) Niemelä, n.comb. Basionym: *Phellinus lundellii* Niemelä, Ann. Bot. Fennici 9: 51, 1972.

Ochroporus nigricans (Fr.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus nigricans* Fries, Syst. Mycol. 1: 375, 1821. See Niemelä (1975).

Ochroporus nigrolimitatus (Rom.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus nigrolimitatus* Romell, Arkiv Bot. 11(3): 18, 1911.

Ochroporus populicola (Niemelä) Niemelä, n.comb. Basionym: *Phellinus populicola* Niemelä, Ann. Bot. Fennici 12: 94, 1975.

Ochroporus rhamnii (M.Bond.) Fiasson & Niemelä, n.comb. Basionym: *Phellinus laevigatus* (Karst.) Bourd. & Galz. f. *rhamnii* M.Bond. in Sinadskij & Bondarceva, Bot. Mater. Otd. Spor. Rast. Bot. Inst. Akad. Nauk SSSR 13: 230, 1960. *Phellinus rhamnii* (M.Bond.) H.Jahn, Westfäl. Pilzbriefe 6: 89, 1967.

Ochroporus tremulae (Bond.) Fiasson & Niemelä, n.comb. Basionym: *Fomes igniarius* (L.: Fr.) Fr. f. *tremulae* Bondarcev, Trudy Lesn. Opytn. Delu Ross. 37: 20, 22, 1912. *Fomes tremulae* (Bond.) Borisov, Sborn. Trudov Bol. Lesa ... 15: 85, 1940. See Niemelä (1974).

Ochroporus tuberculosus (Baumg.) Fiasson & Niemelä, n.comb. Basionym: *Boletus tuberculosus* Baumgarten, Flora Lipsiensis: 635, 1790. Syn.: *Ochroporus pomaceus* (Pers.: S.F. Gray) Donk. Discussed by Niemelä (1982).

Phellinidium ferrugineofusum (Karst.) Fiasson & Niemelä, n.comb. Basionym: *Poria ferrugineofusca* Karst., Medd. Soc. Fauna Flora Fenn. 14: 82, 1887. Type of the genus *Phellinidium* (Kotl.) Fiasson & Niemelä.

Phellinidium pouzarii (Kotl.) Fiasson & Niemelä, n.comb. Basionym: *Phellinus pouzarii* Kotlaba, Česká Mykol. 22: 24, 1968.

Phellinus torulosus (Pers.) Bourd. & Galz. Type of the genus *Phellinus* Quéil.

Fuscoporia contigua (Pers.: Fr.) Cunningham, New Zeal. Dept. Sci. Ind. Res. Bull. 73: 4, 1948. *Boletus contiguus* Pers., Syn. Fung.: 544, 1801. *Polyporus contiguus* Pers.: Fries, Syst. Mycol. 1: 378, 1821.

Fuscoporia ferrea (Pers.) Cunningham, New Zeal. Dept. Sci. Ind. Res. Bull. 73: 7, 1948. *Polyporus ferreus* Pers., Mycol. Europ. 2: 89, 1825.

Fuscoporia ferruginosa (Schrad.: Fr.) Murrill, North Amer. Flora 9(1): 5, 1907. *Boletus ferruginosus* Schrad., Spicil. Fl. Germ.: 172, 1794. *Polyporus ferruginosus* Schrad.: Fries, Syst. Mycol. 1: 378, 1821.

Fuscoporia viticola (Schw. ex Fr.) Murrill, North Amer. Flora 9(1): 4, 1907. *Polyporus viticola* Schw. ex Fries, Elenchus Fung. 1: 115, 1828.

Fulvifomes robiniae (Murr.) Murrill, Northern Polyp.: 49, 1914. Extra-European species, type of the genus *Fulvifomes* Murr. See Kotlaba & Pouzar (1978).

Fulvifomes rimosus (Berk.) Fiasson & Niemelä, n.comb. Basionym: *Polyporus rimosus* Berkeley, London J. Bot. 4: 54, 1845. For the identity of the species and its typification, see Kotlaba & Pouzar (1978).

Comparison of the results of the two methods

The results obtained from the same data matrix by these two different procedures largely coincide. The agreement was better than could theoretically be expected. The main weakness of the phenetic analysis turns out to be that some characters were incorrectly evaluated, i.e., used at the wrong level of universality (Wiley 1981), so that they masked other, more significant, characters. For instance, dextrinoid spores, presence of a core, and most styrylpyrone patterns arise in various genera and so lack good correlation with other characters (hyphal system, interbasidial secretion). They receive little significance when used at the polygeneric level, though they are actually valuable in defining some new genera. These non-generic characters create artificial links between species of different genera, introducing 'noise' into the analysis. All in all, the safest approach appears to be to use the two methods to check each other.

The comparative analysis made here helped to sort the species into groups, most of them now regarded as genera. After this rough division, the true 'face' of each genus will emerge and be refined as new species are included, more accurate comparisons are made, etc. The best diagnostic characters will be revealed by experience, and new ones are sure to be found, too. An example is the presence of the crystal hyphae in *Fuscoporia*: This character was found by Jahn (1967) but it was some time before its true value was appreciated by other authors. On the other hand, some characters must be treated with more caution. The cyanophily of the spores depends on the dye applied; strong cyanophily (in *Fomitiporia*) is always evident, and then mostly connected with dextrinoid

spores. The weak cyanophily recently observed in *Porodaedalea* and *Ochroporus* needs further study.

Affinities of the Hymenochaetales

The last question to be considered here is that of the affinities of the Hymenochaetales. When Donk (1948) erected the family, he included both the *Séries des Igniaires* and *des Astérostromes* of Patouillard. The linking genera, *Asterodon* and *Asterostroma*, have proved to lack affinity to each other (Boidin et al. 1980). The *Astérostromes* have now been included in the Lachnocladales (Reid 1965, Oberwinkler 1977), the affinities of which are totally different (Gluchoff-Fiasson & Kühner 1982).

In the search for related taxa, the best characteristics of the Hymenochaetales — the setae and the styrylpyrones — are of course promising clues. Structures resembling the setae are known in other groups (e.g., *Marasmius*), but they are now thought to be of a totally different origin (Donk 1971).

As for the styrylpyrones, their only other occurrence in fungi is in the Strophariaceae of the Agaricales (Gluchoff-Fiasson 1979). Compared with our group, the biosynthesis in the Strophariaceae shows two peculiarities. First, the accumulation of bis-noryangonine (hispidin minus one hydroxyl group) besides hispidin itself; accordingly, when hispidin engages in dimerization in more evolved genera, the 'dimer' hispidin + bis-noryangonine = hypholomin A appears besides hypholomin B. Second, hispidin in some cases 'dimerizes' with arylpyrones, giving colourless fasciculins. Nevertheless, these special features do not make the styrylpyrone pattern of Strophariaceae more distant from that of poroid Hymenochaetales than the latter is from that of *Hymenochaete*. Another similarity exists between the Hymenochaetales and Strophariaceae: some members of the latter show darkening in KOH (Kühner 1980), which resembles the xanthochroic reaction of the former. In both cases this may merely reflect the occurrence of styrylpyrones (or some of their precursors), and so these two features may be linked rather than independent and correlated.

The styrylpyrone-producing Strophariaceae are lignicolous and cause a white-rot, just like the Hymenochaetales. The agaricoid habit, requiring less hardening of the fruit body (Donk 1971), could be seen as accounting concurrently for the simplicity of the hyphal system and the low yield of highly polymerized styrylpyrones ('fungal lignin'). Nevertheless, it appears less plausible that a phyletic relationship exists between the Hymenochaetales and an ochrosporous (and clamped) family of Agaricales, than that there is a 'sulfo+' evolutionary series from the Lachnocladales and *Peniophora* to the Russulales (Gluchoff-Fiasson & Kühner 1982). In the latter case, the occurrence of styrylpyrones in both the Hymenochaetales and Strophariaceae would have to be understood as mere convergence, probably arising from their shared xylophagous metabolism.

It was first believed that fungi derive their

styrylpyrones from the lignin of the host. Now we know that they can produce them in cultures having glucose as the sole source of carbon. The Hymenochaetales and some Strophariaceae may have, independently, acquired the ability to mimic an aspect of the anabolism of the plant they prey upon. This would agree with the fact that the most primitive of the extant Strophariaceae (*Galerina* etc., Kühner 1980) lack styrylpyrones. If these pigments appeared within the family, then of course they cannot be used as clues to its external affinities. Nevertheless (and leaving aside the question of the naturalness of the Strophariaceae), a tendency to lose the ability to synthesize styrylpyrones is evident in all 'styrylpyrone+' genera and one cannot be sure that the ancestors of *Galerina* were not endowed with such pigments.

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