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The genus is a holophyletic (strictly monophyletic) group of species, real and objective in its historical relations (common genealogy) but not otherwise. In several cases, due to their common origin, it is a group of species more similar to each other than to the species of any related genera: a more or less clear *hiatus* between genera *may* be present. In other cases 'overall similarity' (or dissimilarity) is misleading due to convergence, parallelism, quasi-homologous characters, inequality in speed of development of different characters, lack of objective measures of similarity and undisputable methods of clustering. Most of the taxonomic work in establishing the genera of fungi has been done using artistic-intuitive methods; consequently, the limits and scope of genera, and their classification depend on the individual nature of a taxonomist. Their methods may be described as intuitively phenetic ones with usually quite subjective *ad hoc* (over)weighting of characters. Conventionality in genus limits (scope) caused by their relative unreality may not be interpreted as freedom in genus splitting. A case study of *Hyphoderma, Hypochnicium* and the related genera (Basidiomycetes: Corticiaceae) demonstrates that in most cases a new segregate genus is in the same cluster with the related species of *Hyphoderma* or *Hypochnicium* when using phenetic methods. When the cladistic study was employed, the segregate new genera caused paraphyletic grouping of the 'leftover species' of the 'parent' genus. Genus splitting is usually unfounded not because the resulting genera are too small and uncomfortable for a user of the classification; but because they are created subjectively, therefore they are artificial and not in accordance with any methodology or methods. The phenetic approach in taxonomy is sometimes unavoidable (e. g., in the classification of a taxon when there are no qualitative characters which may be polarized). In that case a (small, splitted) genus may be acceptable when its species form a distinct cluster in a phenogram and/or is characterized by a combination of rare character states. To turn taxonomy from a kind of art of questionable scientific value to a science, subjective *ad hoc*

weighting of characters and subjective evaluation of 'overall similarity' must be avoided as well as fruitless attempts to find an impossible 'objective' compromise between phenetic and cladistic methods ('evolutionary taxonomy') .

Introduction

Taxonomy is a changing science as all the other branches of biology are developing. Nevertheless, it has lost much of its former authority, and 'crisis in taxonomy' is a term widely used. New approaches and methods introduced during the last decades have been accomplished with instability in both nomenclature and classification, and the situation seems to change worse in near future. That is why non-taxonomists as well as "the majority of professional taxonomists probably have secret conservative sympathies" (Jardine & Sibson, 1971: 135). Two serious diseased developments have infected taxonomy: nomenclatural *terrorist tactics* in taxonomy resulting in numerous formally legitimous but disturbing name changes, and *schizotaxia* realizing in the splitting of genera, families and other taxa.

Many mycologists are obviously ill disposed towards splitting but only a few papers have been published on this subject; the one by H. Romagnesi (1977) is brilliant in its style even if somewhat disputable in details. In several other papers splitting has been described as a "modern tendency to make each family contain only a few genera and each genus only a few species.." (Sneath & Sokal, 1973: 61). B.L. Turner (1985) has said: "I tend to believe that the predilection for "schizotaxia," especially where new phyletic insights are not apparent, is largely a phenomenon of the personality: a belief that, somehow, future workers will esteem generic erections (and hundreds of new combinations..)." He may be right that personality plays an important role in splitting. However, more than personality, 'splitting tendencies' depend on general trends in the taxonomy of one or another fungal group, i. e., on different approaches prevailing in groups of taxonomists. The average number of species in a genus is much higher in Agaricales (sensu latissimo) than in Aphyllophorales, and the number of genera in actual use has grown moderately for the last fifty years. This may be caused by the biological properties of the taxa, but surely also by the influence of R. Singer, H. Romagnesi and some other leading agaricologists. In lichenized fungi, the number of genera in use was 506 in 1943, up to 650 in 1984 (Hale, 1984: 12). In the studies of Aphyllophorales, the tendencies have been different. For example, the family Corticiaceae (Basidiomycetes: Hymenomycetes) in the sense used by Donk (1964) and Parmasto (1968, 1986) had 16 recognized

genera in 1928 (Bourdot & Galzin, 1928) and not many more until the 40-ies; near 70 forty years later (Parmasto, 1968), about 175 in 1987 (Hjortstam, 1987), and nearly two hundred today. Such a multiplication (more than 12 times) was partly the result of views and influence of M. A. Donk, J. Eriksson, E. Parmasto, W. Jülich, K. Hjortstam and some other mycologists. Such splitting was caused mainly by the quite understandable (but not quite successful) attempt to 'create' more or less homogeneous monophyletic genera derived from the highly heterogeneous ones. The splitting of the genera of 'macrofungi' or Aphyllophorales into more *natural* and *homogeneous* ones was favorably admitted, for example, by F. Kotlaba (1964) and M.A. Donk (1964: 200). As a rule, the new genera have been described as having a combination of rare character states, i. e. using phenetic approach without employing contemporary phenetic methods but applying subjective character weighting. Obviously, the 'splitting problem' is not only a question of personalities or their assemblages; it is also closely related to the fundamental problems of taxonomy. Three of these will be discussed below: are superspecific taxa real? how many 'natural' hierarchical categories may be distinguished? what is the aim of classification in general?

What is real?

What is a genus? Does it exist in nature, or in human mind only? Is it as real as are species, or it is a man-made taxonomic category? There are two different approaches to this problem. It seems to be widely accepted that the main aim of taxonomy is "to construct classes about which we can make inductive generalizations" (Gilmour, 1951; spaced by me. E. P.). According to the same author (p. 402), categories of genus and species are "human contrivances constructed for human purposes..." From the viewpoint of an evolutionist, "the relations between the members of the higher taxa are not biological, not dynamic, not causal, and in this sense not real and objective; they are historical relations (in so far as the taxa are based upon phylogeny) and relations of abstract morphological similarity" (Beckner, 1959: 68). The reality of genera was axiomatically accepted by pre-Darwinian authors. According to K. Linné, the species and genus are always creations of nature (Linnaeus, 1751 § 162); the same was asserted by E. Fries about the genera in his *Systema mycologicum* (Fries, 1821: Xll - "Genera in hoc systemate... ab natura ipsa fixa..."). However, there are also several modern authors who assert some kind of reality of genera. According to V.V. Chernykh (1986), to treat genera and other higher taxa as a sum of genealogically related species has no heuristic meaning. The related species have common features in their

coordinated evolution; we can speak about the assembled evolution of related groups. According to this, a genus may be considered to be an integrated system, but only in scale of geological time. Thanks to the genealogical relationship, there is a directed development of a higher taxon. According to this, higher taxa are in some correspondence with the criteria of reality (discretness, constancy, concreteness, integrity, etc.) (Chernykh, 1986: 115-118). A. Raitviir (1989: 60) asserts that "the genera are really existing discrete units of classification which could be described as subsystems of the system "family"." Some pages before this (p. 57) he writes: "It is really a difficult task to show the reality of higher taxa to those who do not like to beleive into this reality". (In both citations spaced by me. E. P.) However, until regarding oneself as a believer, one has to ask: what is reality? Is the reality that there are units of classification in taxonomy of the same value as is the reality of species as interbreeding groups of specimens? I have to repeat here Beckner's sentence: "The difficulty here is, of course, that the term "real" is suggestive of the intent, but hardly adequate for communicating precisely what systematists have in mind" (Beckner, 1959: 67). Indeed, the term reality does not design anything evident, and is unequivocal. Lyubischev (1982) has asserted, that there are different kinds or sorts of reality; there are different levels of reality. R.S. Karpinskaya (1984) has discussed the diversity of forms of biological reality and finds: obviously, a taxonomist operates with a different 'kind of reality' than an evolutionist, ecologist or ethologist. She asserts quite seriously (p. 87): "The term reality includes not only knowledge but also conviction". For me, the reality of genera is nothing more than the reality of the common origin of the species of a genus. This can be described in a sophisticated philosophical way (as has been done, for example, by Chernykh), but such an approach does not give any help in taxonomy. Speciation has obviously taken place not monotonously but ununiformly in the course of organic evolution. There have been periods of arogenesis when new structures have been formed during a relatively short time. These periods have been associated with the occupation of a 'new adaptive zone' or new 'macroniche'; in the following period of allogenesis (or adaptive evolution), smaller changes slowly took part and all available niches were occupied (Sewertzoff, 1931; see also Raitviir, 1989: 58-59). Based on this theory, an 'applied' hypothesis has been erected: macroarogenesis initiates the formation of genera, microarogeneses result in sections of genera. Between genera there is a hiatus which is more or less of the same size within a family (Raitviir, 1989: 59; see also Zavadskij, 1968). It may be questioned, whether all genera (and sections) have indeed arisen in the way described above. "If an ancestral species is surrounded by an array of

vacant niches on all sides, the speciation process may produce the initial stages of an adaptive radiation" (Grant, 1989: 605). Such a situation might be an exceptionally rare one - if we do not declare any habitat occupied by a (new) species to be a 'vacant niche'. Several genera of host-specialized fungal species may have originated by adaptive radiation in remote past; in mainly wood-inhabiting Aphyllophorales something similar to adaptive radiation is a rare phenomenon.

In phenetics, the groups of species may be treated as clouds of OTU points in the multidimensional character space. According to the arogenesis-hiatus hypothesis as expressed by Raitviir, a taxon (family) should be modelled as a complicated topological system of clouds and subclouds. Is any well-delimited (hiatus-surrounded) cloud a genus? Are there such clouds at all? Is it possible to measure the distances (hiatus) between clouds? Possibly sometimes not, sometimes yes, when we have some mutual agreement about the measures we are going to use when delimiting sections, genera and higher taxa. A.P. de Candolle asserted in 1844 that the distance that separates each taxon could be actually calculated, if not in an absolute manner, at least in a relative one (Cited after Nelson & Platnick, 1981: 103). Raitviir (1970, 1989) has shown that using the squared correlation coefficient as a measure of similarity between species, it is possible to group them into distinct genera. Maybe it is possible in the Hyaloscyphaceae and some other groups of fungi but obviously not in the Corticiaceae: the distinct hiatus between genera has disappeared together with simple artificial classifications. Such an approach may be (in some but not all cases) successful only if we believe that taxonomy may be based on the phenetic approach. In other words, if we believe that classification may be based on 'overall similarity'.

HIERARCHIAL CATEGORIES: NATURAL OR ARTIFICIAL?

The number of hierarchical categories used in systematics has been increasing during the last three hundred years. Pre-scientific, folk classification used 3-5 levels (Wattel, 1990); Linné only characterized the **genus**, order and *class* above the species (Linnaeus, 1751). **Familia** was for him a general term, and was introduced as a taxonomic category above genus (in botany) later by A.L. de Jussieu. E. Fries (1821) recognized **genera**, and seven orders in his class Hymenomycetes. But in 1838 already his **familia primaria** Hymenomycetes was divided into 'families', these in 'orders', and orders (= families!) into genera. The class Fungi had only three orders and altogether nine families in L. Rabenhorsts's *Kryptogamen-Flora* in 1844; however, these were divided to groups and subgroups (without category names indicated). In the Inter-

national Code of Botanical Nomenclature (Greuter et al., 1988), 18 supraspecific ranks of taxa are given, including some rarely used in mycology. Does such an increase in the number of categories mean that we have detected a complicated hierarchial structure of taxa which is made up of eighteen categories? Not at all. More than 30 years ago it was generally accepted that "the higher categories are not precisely definable at all" (Beckner, 1959: 72). There is nothing to add to this today. "The adoption of the Linnean Hierarchy is a convention, and not a biological necessity..." (Wiley, 1979: 316). In discussions on the reality of genera and the naturalness of hierarchial categories two different notions have been used under one term: the genus as a taxonomic category, and the genus as a taxon. As a category, the genus "...can only be defined by its position in the hierarchy; that is, it is defined with respect to the lower and higher levels in the hierarchy" (Scott, 1973: 406). In this sense, a genus (as a taxon, i. e. as a group of species) may be raised in its rank to a supergenus or any new category if pleased to 'create'; the group of species will remain the same. The increase in the number of categories is obviously a result of the growth of the number of species known. On the other hand, a subdivision of a genus sometimes has been raised to genus, subfamily, or even to family level by some specialized mycologist who is not dealing with all (or most) fungal groups - unlike L. Rabenhorst who was happy to put all European fungi in one book of some 600 pages one century and a half ago. There seems to be an absolute freedom to raise any taxa in its rank, and this freedom has been used with much pleasure. Alas, no information will be gained when the rank of a taxon is changed. Informational content of two classifications, one of a genus with seven subgenera, and another with a group of seven related genera, is equal (cf. Funk, 1985: 78). There seems to be an almost imperceptible, nevertheless existing limit of the easily acceptable number of categories (ranks) in the human mind. Most of the 18 supraspecific ranks are not in common use: it would be a too heavy psychological burden for our memory! Five to six seems to be the acceptable set of ranks for most mycologists except those who are studying a very limited group very carefully. Raising subgenera or genera to orders results in raising orders to phyla, etc. That means, further devaluation of categories (ranks) leads to the need for new additional, ranks unnamed so far, and this is hopefully unacceptable for most taxonomists.

THE AIM OF CLASSIFICATION is to store a certain kind of ordered information: it is a hierarchical database. A taxon (e. g., a genus) is a group of species closely related to one another. There are two different approaches with the different meaning of the word related: phenetic similarity, or common

origin. Similarity has been considered for a long time to be the main if not the only indicator of 'naturalness' of a taxon. But already in 1871 Ch. Darwin wrote: "I believe that the arrangement of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural..." (Cited after Nelson, 1974a: 457). Today every taxonomist admits that a phylogenetic classification, i. e. that based on genealogy, might be the aim of a system. Convergence and parallel evolution are common phenomena, and, as a rule, it is impossible to create a phylogenetic system when using only similarity data. Some thirty-forty years ago cladistic methods were in the very beginning of their development, and it seemed that it was unavoidable to use mainly phenetic methods in taxonomy. Simpson's (1945) classical sentence has been cited repeatedly: "Classification must be based on phylogeny but cannot express it". The same was said by Cain (1956: 105): "The most that the ordinary classification can do is avoid disagreeing with the phylogeny of a group as far as known". Even later, several authors avoided mentioning phylogeny altogether (McNeill, 1979: 475 - "The purpose of hierarchical classification in biology is to present phenetic relationships..."). After cladistic methods have became widely usable in the last decades, the situation has changed drastically. Systematics appeared to be on the horns of a dilemma: to continue using well-elaborated phenetic methods based on evaluation of 'overall similarity', or to adopt cladistic methodology based on generally accepted evolutionary ideas, but much less comfortable to use. One of the obstacles hindering the use of cladistic methods was and is the inadequacy of our knowledge of the taxa. Most species of fungi have been described without noticing the presence or absence of many taxonomically important characters: only the characters considered to be important from the essentialistic viewpoint of the author have been described. Another obstacle was the complicated way how cladograms were to be interpreted in the taxonomic hierarchy. It was soon surmounted by *phyletic sequencing convention* (Nelson, 1974; Wiley, 1979). There remained a serious doubt: is a classification based on genealogy as informative as is another based on 'overall similarity'? J.S. Farris (1980) has demonstrated that it is even more informative, but this study has been disregarded by many taxonomists. In such a controversial situation, baseless hopes to combine the two methodologies excluding each other have been expressed frequently. More than fifteen years ago R. R. Sokal hoped: "I have no doubt that combined methods of phenetics and cladistics will be the backbone of systematics in the years to come" (Sokal, 1975: 262). The hope to combine phenetic and genealogical characters to reach an 'ideal' general purpose system has been continuing

until recent days. *Evolutionary taxonomy* based on ideas of possibly fruitful compromise and propagated by such eminent biologists as E. Mayr (1969, 1982 and several subsequent papers) is quite popular as a system of general ideas among taxonomists - but it has shown itself to be almost unusable in practical systematics. The main influence of evolutionary taxonomy has resulted in the conviction that a genealogically founded (phylogenetic) classification scheme may be 'improved' by the measurement of similarity between taxa, i. e. by creating paraphyletic taxa. Such an approach has not diminished but increased subjectivity in taxonomy. The phenetic approach has been continuously followed in taxonomy, and the belief in practical usefulness of phenetic classifications has not disappeared. "General utility, albeit hard to define, lies at the base of the phenetic concept of natural classification" (Rohlf & Sokal, 1981: 467). Unsurprisingly, all new methods of (dis)similarity measurement and clustering made the phenetic methods more and more uncertain. "Each new technique, of course, had the potentiality of proceeding a different tree from the same data.... Therefore arose a new question for the computer to ask "what is the best procedure to construct a tree?" No answer was forthcoming.... And there it remains today, with a very uncertain future." (Nelson & Platnick, 1981: 134). I hope that my general preference of the phylogenetic methodology has been expressed unambiguously here. Nevertheless, there are several fields in practical taxonomy where we have to use phenetic methods today. There are groups of species distinguishable mainly by variable quantitative characters; of species poorly studied; of species with high degree of parallelism in character state changes. And, first and foremost, phenetic groups are the best first approximation of monophyletic groups (Thockmorton, 1968: 387). There are numerous genera and higher taxa created on *artistic intuitive* methods, i. e. using 'bad phenetics' with *ad hoc* character (super)weighting. And there is a sometimes propagated idea that two semiindependent classifications may exist side by side: the phenetic one for 'general purposes', and the phylogenetic one for specialists in evolutionary theory (Sokal, 1975: 260). Accordingly, we have to analyze the 'splitting problem' proceeding from both the phenetic and cladistic viewpoints.

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Proceeding from the theoretical standpoints shortly described above, one may conclude that the limits and scope of a(ny) genus is a question of convenience. It is not more than "a mandatory category to which every species must belong if binominal nomenclature is to be preserved" (Wiley, 1979: 318). "There are as yet no criteria for any absolute measure of taxonomic rank"

(Sneath & Sokal, 1973: 61). Nevertheless, one has to have in mind the practical side of the question. Phytopathologists, forest pathologists, amateur mycologists and other users of the 'taxonomists' production' do not recognize as practical a system with too many genera and other superspecific taxa (cf. Teixeira, 1988). Consequently, the splitting and lumping of genera might be carried on in the limits of decency, taking into consideration traditions and avoiding redundancy. Is it really so? Are there no theoretical grounds against splitting? A case study will demonstrate that splitting is not something which can be done freely.

A CASE STUDY: HYPHODERMOID FUNGI

Among Aphyllophorales there is a group of fungi with seemingly very simple basidiomata. These are usually closely adnated to wood - logs, fallen twigs, trunks. The hymenophore is more or less smooth, i. e. their basidiospore productivity might be quite low. One part of taxonomists (including the author of this paper) considers most of the species of this group to be ancient organisms, the other part - mostly reduced forms. The group was formerly a part of the family Thelephoraceae, then an independent family Corticiaceae. Nowadays we call the group usually *Corticioid fungi.* In the family Corticiaceae, a tribus Hyphodermeae was described by Parmasto in 1968. It contained six genera: *Radulomyces* M.P. Christ., *Irpiciporus* Murr., *Basidioradulum* Nobles, *Hyphoderma* Wallr. em. Donk, *Hypochnicium* J. Erikss. and *Metulodontia* Parm. Of these genera, *Irpiciporus* was later excluded, but numerous new genera closely related to the 'natural' genera *Hyphoderma* and *Hypochnicium* were described by several authors. The new genera are partly 'satellite genera', partly a product of the splitting of the two genera mentioned above. As a result, up to 22 genera are recognized in this group today. Usually modern phenetic or cladistic methods have been used for a taxonomic study with the aim to give a better classification scheme. Contrary to this, I have used these methods to analyse the classifications we have as a result of extensive genus splitting. I am not a supporter of the idea that two different classifications may be used in parallel: one all-purpose classification based on phenetics, and the other phylogenetical one based on cladistics. Nevertheless, both kinds of classifications are present in the contemporary taxonomy. Accordingly, splitting must be evaluated from both competitive sides.

Phenetic analysis

92 hyphodermoid species were described and coded using 43 qualitative and 7 quantitative characters; for Smirnov's dissimilarity measurement the

quantitative characters were previously ranged. Using A. Batko's program TYTAN, six different coefficients - (dis)similarity measures, and five methods of clustering were employed (Manhattan, Euclidean, Squared Euclidean, Canberra metric, Smirnov's distances and Arcsinus transformation; UPGMA, Ward's method, Complete-link and Singlelink clustering and Centroidal sorting). Smirnov's dissimilarity measure used among others is not widely known and needs some explanation here. It is generally accepted that all characters should be given equal weight in taxonomy. Smirnov's character weighting is based on a quite original approach. According to his ideas (Smirnov, 1960, 1969), a taxon is better characterized by rare character states than by a combination of common characters. The weight of a character state might be inversely proportional to its frequency and, consequently, depends also on the number of taxa in the group under study. Most interesting in Smirnov's method is the evaluation of species *originality/mediocrity* using the coefficient of similarity of a species with itself. This coefficient is an objective indicator demonstrating the extent of its difference from all other taxa under study. As a result of our analyses, more than 30 different phenograms were obtained (see figs. 1-4). In the phenograms where Smirnov's coefficient was used, originality/mediocrity of species is indicated; this is given in the beginning of the data on every genus below.

Results

Atheloderma Parm. (1 species).

A. mirabile Parm. is a very original species. The clusterings yield phenograms where *Atheloderma is* usually in one cluster with *Hyphoderma fouquieriae* Nakas. & Gilb., *H. rubropunctatatum* Warc. & Talb., sometimes also with *H. cremeo-album* (Hohn. & Litsch.) Jül., or with *H. assimile* (Jacks. & Deard.) Donk and *H. clavigerum* (Bres.) Donk.

Basidioradulum Nobles (1 species).

B. radula (Fr.: Fr.) Nobles is a species with a low originality index. In all phenograms it is clusterd with (other) *Hyphoderma* species, usually together with *H. litschaueri* (Burt) J. Erikss., *H. malenconii* Manj. & Moreno and *H. pilosum* (Burt) Gilb. & Bud.

Bulbillomyces Jül. (1 species).

B. farinosus (Bres.) Jül. is a very original species. In phenograms retrieved using UPGMA, complete and single clustering has an isolated position,

dissimilar to the other Hyphodermoid fungi. In phenograms resulting from Ward clustering not remarkably different, clustered with *Radulomyces sp. sp.*, *Hypochnicium lundellii* (Bourd.) J. Erikss. and *H. bombycina* (Sommerf.: Fr.) J. Erikss.

Conohypha Jül. (2 species).
Both species are of low originality. C. *terricola* (Burt) Jül. is in all phenograms clearly isolated from the type of *Conohypha, C. albocremea* (Hohn. & Litsch) Jül.; here only the position of the type is described. In different phenograms differently positioned, not remarkably different from other Hyphodermoid fungi; usually in one cluster with *Thujacorticium* and *Flavophlebia,* also with *Hyphoderma roseocremeum* (Bres.) Donk, *H. sibiricum* (Parm.) J. Erikss.

Cyanodontia Hjortst. (1 species).
C. spathulata Hjorts. is a species of low originality. In phenograms usually somewhat isolated but not clearly differentiated, mostly in one cluster with several *Hypochnicium* species.

Flavophlebia (Parm.) Larss. & Hjortst. (1 species).

F. sulfureo-isabellina (Litsch.) Larss. & Ryv. is a species of low originality. In all phenograms it is in one cluster with and closely related to *Hyphoderma lapponicum* (Litsch.) Ryv. and (with one exception) *H. roseocremeum* (Bres.) Donk. According to several phenograms, *Thujacorticium* and *Conohypha* may belong to the same group.

Globulicium Hjortst. (1 species).

G. hiemale (Laurila) Hjortst. is a species of low originality. In all phenograms it is clustered with (or near to) *Radulodon sp. sp.,* sometimes also with *Radulomyces fuscus* (Lloyd) Ginns or *Hyphoderma mucronatum* (Furukawa) S.H. Wu; the cluster is usually a subcluster of *Hyphoderma sp. sp.*

Gloeohypochnicium (Parm.) Hjortst. (1 species).

G. analogum is a moderately original species. In all phenograms clustered with *Granulobasidium* and several *Hypochnicium* species *(H. eichleri* (Bres.) J. Erikss., *H. geogenium* (Bres.) J. Erikss. a.o.).

Granulobasidium Jül. (1 species).

G. vellereum (Ell. & Crag.) Jül. is a very original species. In all phenograms clustered with *Gloeohypochnicium* and several *Hypochnicium* species *(H. eichleri, H. geogenium* a. o.).

Hyphoderma Wallr. (52 species).

All species except *H. arizonicum* Linds. & Gilb. are of low or moderate originality. The species are scattered in several clusters and subclusters

together with the segregate genera; however, *Hypochnicium* is usually in a quite different cluster (except when single-linkage clustering has been used, then the clustering is usually indistinct) which includes also *Hyphoderma nudicephalum* Gilb. & M. Blackw., sometimes also *H. setigerum* (Fr.) Donk, *H. deserticola* Gilb. & Linds. or *H. africanum* (Burt) Reid.

Hyphodermella J. Erikss. & Ryv. (1 species).

H. corrugata (Fr.) J. Erikss. is a moderately original species. In phenograms closely related to (other) *Hyphoderma* species (Manhattan / Ward, Canberra / Ward), or to *Radulomyces, Hypochnicium bombycina* (Somm.: Fr.) J. Erikss. (most other methods).

Hyphodermopsis Jül. (1 species).

H. polonensis (Bres.) Jül. is a species of low originality. In phenograms it is usually in one subcluster with *Nodotia aspera* and *Hypochnicium gomezii* among *Hypochnicium sp. sp.;* when Canberra metric is used, clustered with *Hypochnicium sp. sp.*

***Hyphoradulum* Pouz.** (1 species).

H. conspicuum Pouz. is a species of low originality. In most phenograms it is in one cluster with *Hyphoderma* species *(H. budingtonii* Linds. & Gilb., *H. baculorubrense* Gilb. & Blackw. or several others), sometimes with *Basidioradulum;* different methods give him a different place among other *Hyphoderma* species.

Hypochnicium J. Erikss. (11 species).

All species are *of* low or moderate originality. The species are in many cases in two groups: *H. bombycina* and *H. lundellii* together with *Radulomyces* in one cluster, the other species in a big cluster with *Gloeohypochnicium, Granulobasidium, Nodotia, Hyphodermopsis, Cyanodontia, Lagarobasidium.* In some other phenograms *H. bombycina, H. lundellii, H. eichleriana, H. erikssonii, H. geogenium* are clustered with *Gloeohypochnicium, Granulobasidium, Radulomyces confluens* and *R. molaris,* the other *Hypochnicium* in another cluster together with *Cyanodontia, Nodotia, Hyphodermopsis* and *Lagarobasidium.* In some phenograms all *Hypochnicium* species are together with *Cyanodontia, Gloeohypochnicium, Granulobasidium, Hyphodermopsis, Lagarobasidium, Nodotia, Radulomyces confluens* and *R. molaris.* In general, *Hypochnicium* and its segregate genera are more or less clearly separated from *Hyphoderma* and its segregate genera.

Lagarobasidium Jül. (2 species).

Both species are of low originality, in all phenograms clearly separated from each other. Only the position of the type species *(L. detriticum* (Bourd. & Galz.) Jül. is discussed below. - Depending on the methods used, this genus is

situated in very different clusters. Usually it is close to *Lyomyces* and *Hyphoderma clavigerum* (Bres.) Donk; when using Manhattan distance, it is in one cluster with *Hypochnicium longicystidiosum* (Rattan) Hjortst. & Ryv. and *H. subrigescens* Boid.; when Canberra metric has been used, *H. rickii* Hjortst. & Ryv. is also in the same cluster.

Lyomyces P. Karst. (1 species).

L. sambuci (Pers.: Fr.) P. Karst. is a species of very low originality. In phenograms situated quite differently depending on the methods used; usually in one cluster with *Lagarobasidium detriticum* (Bourd. & Galz.) Jül., *Cyanodontia* and/or *Hyphoderma clavigerum* (Bres.) Donk. - We did not include *Hyphodontia* J. Erikss. species into our data matrix, that is why it is not possible to say anything about their relations. The data given above demonstrate that *Lyomyces sambuci* does not belong to *Hyphoderma* (as *H. sambuci* (Pers.: Fr. Jül.).

Mutatoderma (Parm.) Gomez (4 species).

All species with low originality. *M. mutatum* (Peck) G.Gomez is far isolated from the other three species in most phenograms which form a close subcluster in a cluster of very similar *Hyphoderma* species *(H. cinnamomeum* Jül., *H. odontioides* (Burt) Donk, *H. rude* (Bres.) Hjortst. & Ryv., also *H. deserticola* Gilb. & Linds.).

Metulodontia Parm. (1 species).

M. nivea (P. Karst.) Parm. is quite an original species. In phenograms it has an isolated position distinct from other Hyphodermoid fungi. In phenograms resulting from Ward clustering not remarkably different, in one cluster with many *Hyphoderma sp. sp.* or (Euclidean distance) with *Radulodon* sp. sp. and *Globulicium hiemale.*

Nodotia Hjortst. (1 species).

N. aspera Hjortst. is a species of low originality. In phenograms in one cluster with closely related *Hypochnicium* species, always close to *H. gomezii* Lopez & Wright, usually also to *Hyphodermopsis;* in Canberra / Ward or Complete phenograms in one cluster with *Hyphoderma setigerum* (Fr.) Donk and *H. nudicephalum* Gilb. & M. Blackw.

Radulodon Ryv. (3 species).

All three species are of low originality. In all phenograms they form a subcluster hardly distinct from other taxa, usually together with *Radulomyces molaris* and *R. fuscus.* In many phenograms *R. licentii* (Pil.) Ryv. is far isolated from the other two *Radulodon* species.

Radulomyces M.P. Christ. (3 species).

All three species are of low originality. *R. confluens* (Fr.: Fr.) M.P. Christ. and *R. molaris* (Chaill.: Fr.) M.P. Christ. are in all phenograms in one subcluster with *Hypochnicium bombycina* (Somm.: Fr.) J. Erikss. and *H. lundellii* (Bourd.) J. Erikss., in a cluster with *Radulodon sp. sp.* among Hypochnicioid fungi. *R. fuscus* (Lloyd) Ginns is always separated from the other two *Radulomyces* species, usually it is related to *Radulodon.*

Thujacorticium Ginns (1 species).

T. mirabile Ginns is a species of low originality. Usually it is in one subcluster with *Conohypha albocremea* (Hohn. & Litsch.) Jül. in a cluster of *Hyphoderma sp. sp. (H. roseocremeum (Bres.)* Donk, *H. sibiricum* (Parm.) J. Erikss. & Strid, *H. lapponicum* (Litsch.) Ryv., H. *cremeoalbum* (Hohn. & Litsch.) Jül. a.o.) and *Flavophlebia.*

Character weighting has been stated unadvisable by most contemporary taxonomists. Nevertheless, it has been widely used by the artistic-intuitive 'school' of taxonomists, usually without any explanation why such an approach has been used. I carried on a computer experiment to simulate a splitter's activities. The genera *Bulbillomyces* and *Metulodontia* as obviously unrelated to the others were excluded from the data matrix. The 'most important' characters used for distinguishing a segregate genus were given weight 3. Possibly the 'best', i. e. the most objective measure of dissimilarity is Manhattan distance; of the methods of clustering, Centroid clustering has been said to give artificial clusters, distinguished, however, more clearly than by other methods. After an analysis using these methods, the 'most important' characters of the next genus were given weight 3 and the analysis repeated. For five genera, different characters were *ad hoc* weighted, and a phenogram retrieved. According to these phenograms, the genera may be characterized as follows.

Globulicium **and** ***Hyphoradulum*** **-** both genera are clearly distinguishable from all the species of other genera.

Mutatoderma - *M. brunneocontextum* C. Gomez and *M. populneum* (Peck) C. Gomez form a very clear cluster; in the neighbouring but quite different cluster *M. heterocystidium* (Burt) C. Gomez and *M. mutatum* (Peck) C. Gomez are situated together with *Hyphoderma puberum* (Fr.) Wallr. and *H. macrosporum* S.H. Wu.

Nodotia - forms a very clear cluster together with the closely related *Hypochnicium gomezii* Lopez & Wright.

Radulodon - *R. americanus* Ryv. and *R. licentii* (Pil.) Ryv., *Radulomyces fuscus* (Lloyd) Ginns and *R. molaris* (Fr.) M.P. Christ. *form* a moderately distinguished cluster; in the neighbouring cluster, *R. erikssonii* Ryv. and *Hyphoderma mucronatum* (Furukawa) S.H. Wu are together. *Radulodon* is the only taxon not clearly distinguishable among the five genera studied. The use of complete link clustering did not distinguish the five genera mentioned above. For comparison a 11 the 25 characters used for distinguishing segregate genera were weighted 3. As a result, all genera except *Hyphoradulum* lose their clear distinguishability. Consequently, only *ad hoc* weighting enables us to segregate the genera under study as independent ones. Moreover, according to the descriptions of the small 'unneeded' genera, not characters but character *states* have been *ad hoc* weighted (e. g., not spore form but a more or less globose form of spores).

Conclusions

When using the phenetic methods, only two genera may be clearly distinguished from *Hyphoderma* and *Hypochnicium: Bulbillomyces* Jül. and *Metulodontia* Parm. According to *the* Smirnov's coefficient of originality, *Atheloderma* Parm. and *Granulobasidium* Jül. are genera characterized by a combination of rare character states, and accordingly may be distinguished as independent taxa by enthusiastic pheneticists who do not pay too much attention to clustering. The phenetic analysis supports (in general) the distinction of two genera, *Hyphoderma* and *Hypochnicium* while the segregate ones are included into these. *Ad hoc* weighting of 'leading character states' enables us to distinguish the segregate genera as independent ones.

Cladistic analysis

Cladistic parsimony analysis was carried out using D.L. Swofford's programs PAUP version 2.4.1 and CONTREE. 92 species is a too large set for this, that is why three different data sets were studied separately. 24 characters altogether were used including 11 multistate ordered ones. All analyses were run on a IBM XT compatible 8 MHz microcomputer (8088 processor, 8087-2 math-coprocessor). The following options were used: ADDSEQ = CLOSEST; SWAP = GLOBAL; MULPARS; OPT = FARRIS; ROOT = ANCESTOR; MAXTREE = 100. An additional swapping without MULPARS was done, too. A hypothetical ancestor was designated as having all character states 0. For interpretation of the cladograms retrieved, Adams consensus trees were used. The analyses were made with only one aim: to check the effect of splitting on the taxonomic structure as expressed in cladograms. To propose a new system

of Hyphodermoid fungi, much more work must be done using all possibilities of cladistic analysis including character analysis.

Result

All groups

All segregate genera (except *Bulbillomyces, Metulodontia* and *Lyomyces),* 8 sections of *Hyphoderma,* 5 sections of *Hypochnicium* and a hypothetic ancestor, altogether 33 OTUs were analyzed using 23 characters. 100 trees with length 67 and consistency index 0.463 were found, and a consensus tree retrieved. According to the consensus tree (fig. 5), Hypochnicioid genera *Cyanodontia, Gloeohypochnicium, Granulobasidium, Hyphodermopsis, Hypochnicium, Lagarobasidium* and *Nodotia* form together a holophyletic group. If the segregate genera are excluded, *Hypochnicium* will change into a paraphyletic genus. The position of *Hyphodermella is* somewhat unclear. All the other Hyphodermoid groups may be considered to form a second genus, *Hyphoderma s.l.,* or to represent six different taxa (genera or subgenera): *Atheloderma s.l.* (incl. *argillaceum, capitatum* and *orphanellum* groups of *Hyphoderma), Thujacorticium s.l.* (incl. *Hyphoderma cremeoalbum* group), *Flavophlebia s.l.* (incl. *Mutatoderma* and *guttuliferum, praetermissum, puberum* and *roseocremeum* groups of *Hyphoderma), Hyphoderma* (incl. *Basidioradulum, Hyphoradulum, Radulodon* and *setigerum* group of *Hyphoderma), Conohypha,* and *Radulomyces s.l.* (incl. *Globulicium).* If all segregate genera are excluded as independent ones, *Hyphoderma* will remain as a paraphyletic genus, or will have to be divided into several 'independent' genera.

Hypochnicioid species

All species studied of *Cyanodontia, Gloeohypochnicium, Granulobasidium, Hyphodermopsis, Hypochnicium, Lagarobasidium, Lyomyces, Nodotia,* and a hypothetic ancestor, altogether 20 OTUs were analyzed using 19 characters. 100 trees with length 61 and consistency index 0.492 were found, and a consensus tree retrieved. According to the consensus tree (fig. 6), *Lyomyces, Lagarobasidium* and *Cyanodontia* may be considered to be a group of species (genera?) separated from the other Hypochnicioid fungi. All the other species form a holophyletic group (*Hypochnicium* s.l.). If the segregate taxa *Gloeohypochnicium, Granulobasidium, Hyphodermopsis* and *Nodotia* are recognized as independent genera, *Hypochnicium* will be a paraphyletic genus.

Hyphodermoid groups

All Hyphodermoid segregate genera *(Atheloderma, Basidioradulum, Conohypha, Cyanodontia, Flavophlebia, Globulicium, Hyphodermella, Hyphoradulum,*

Mutatoderma, Radulodon, Radulomyces, Thujacorticium), all 8 sections of *Hyphoderma,* and a hypothetic ancestor, altogether 23 OTUs were analyzed using 24 characters. 100 trees with length 40 and consistency index 0.625 were found, and a consensus tree retrieved. According to the consensus tree (fig. 7), all taxa may be considered to belong to one holophyletic group *Hyphoderma s.l.* Another possibility is to recognize 7 sister taxa (subgenera or genera): *Athelo-derma s.l.* (incl. *argillaceum* and *orphanellum* groups of *Hyphoderma), Hyphoderma capitatum* group, *Hyphodermella s.l.* (incl. *Thujacorticium* and *cremeoalbum* group of *Hyphoderma), Flavophlebia s.l.* (incl. *Mutatoderma,* and *guttuliferum, praeter-missum, puberum* and *roseocremeum* groups of *Hyphoderma), Radulomyces s.l.* (incl. *Globulicium), Conohypha, Hyphoderma* (incl. *Basidioradulum, Cyanodontia, Hyphoradulum* and *Radulodon).* If all segregate taxa are recognized as indepen-dent genera, *Hyphoderma* will be a paraphyletic genus.

Conclusions

The cladistic analysis carried out demonstrates that recognizing segregate genera as independent ones turns the genera *Hyphoderma* and *Hypochnicium* into paraphyletic assemblages. To avoid this, it would be reasonable until more profound studies to recognize only four genera in this group of fungi: *Hyphoderma* s.l., *Hypochnicium* s.l., and their satellite genera *Bulbillomyces* and *Metulodontia.*

General conclusions

The analyses demonstrate that the result of excessive genus splitting in Hyphodermoideae is founded neither phenetically nor cladistically. How much may the results of one case study used for generalizations? A similar phenetic study of *Hymenochaete* Lev. and the segregated genera *Hydnochaete* Bres. and *Stipitochaete* Ryv. has given similar results: their segregation is unfounded phenetically. The authors of the small (splitted) genera in Hyphodermoid fungi are typical representatives of contemporary taxonomists in Aphyllophorales, and have described numerous genera in several groups of Aphyllophorales.

The hope to achieve a 'natural' classification of fungi by splitting hetero-geneous genera into numerous 'natural' and hopefully monophyletic ones has not justified itself; it is not the idea that has been false but the methods used for splitting. In some cases the new genera are really holophyletic, but at the same time it results in *non-convex groups':* the 'parent' genera have been made paraphyletic. This has been described above, and mentioned earlier by Kuyper (1988: 38) on agarics. The result is the increase of informational noise. A

system with enormous number of small genera, and numerous new obligate synonyms is burdening to most users of the system. My conclusions are far from optimistic, and surely not very operational. Mutual friendly agreement between mycologists is needed to avoid excessive splitting (as well as extreme lumping). For splitting (or describing new genera), systems theory approach is a 'must'; a cladistic (or, in extreme cases, a phenetic) study of the whole group is highly recommended. The word 'observation' might be replaced by 'taxonomic study' in the Stevens' (1984: 406) well-known aphorism: "...if one's theoretical framework is unclear, then it is unclear for what theory one's observations will be useful, or even that they can be useful at all..."

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Fig. 1

Phenogram of Hyphodermoid species

Manhattan distance (data standardized) / Method UPGMA. Scale relative,
0 = minimal distance between species. H = Hyphoderma, HN = Hypochnicium

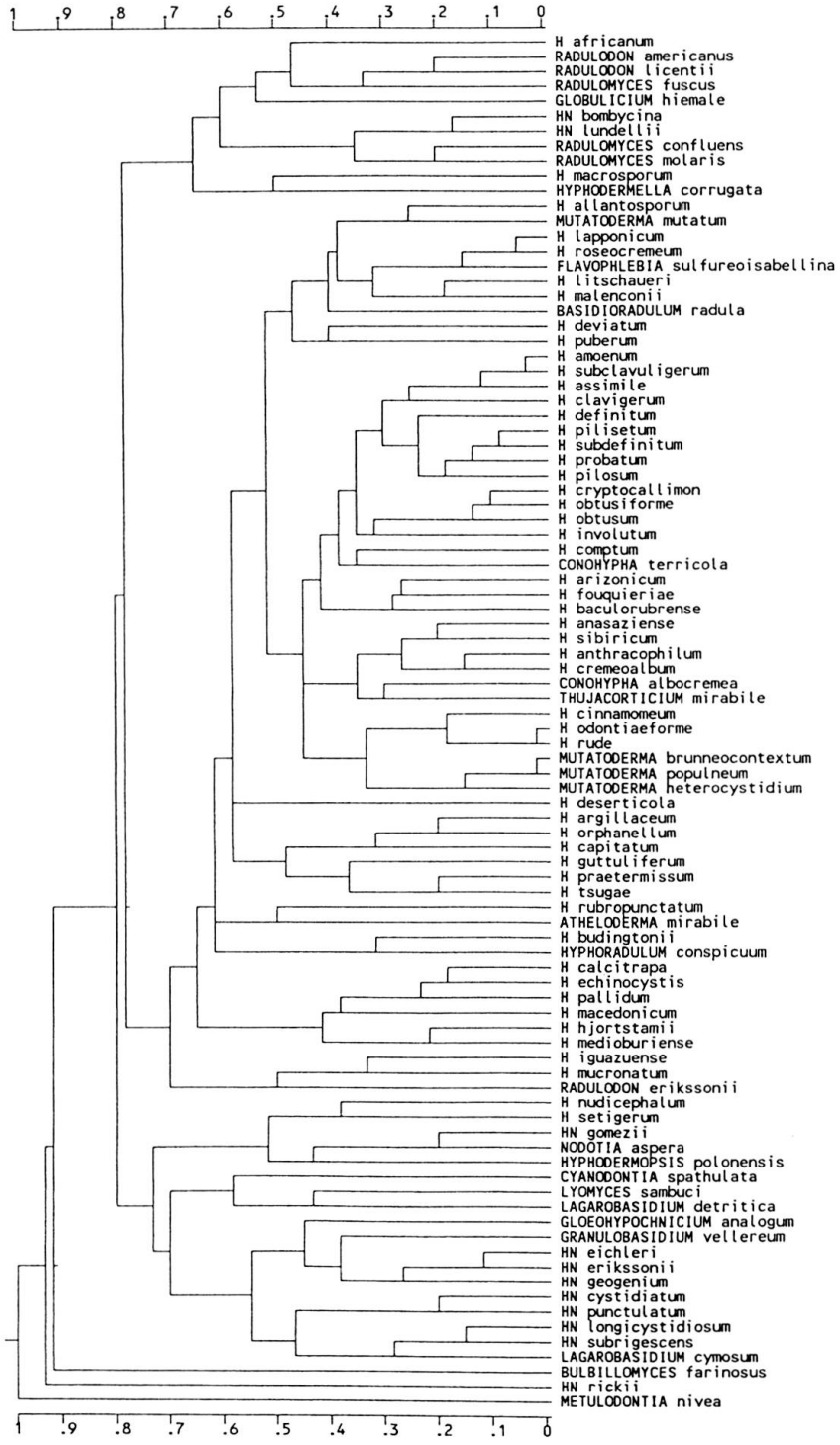


Fig. 2

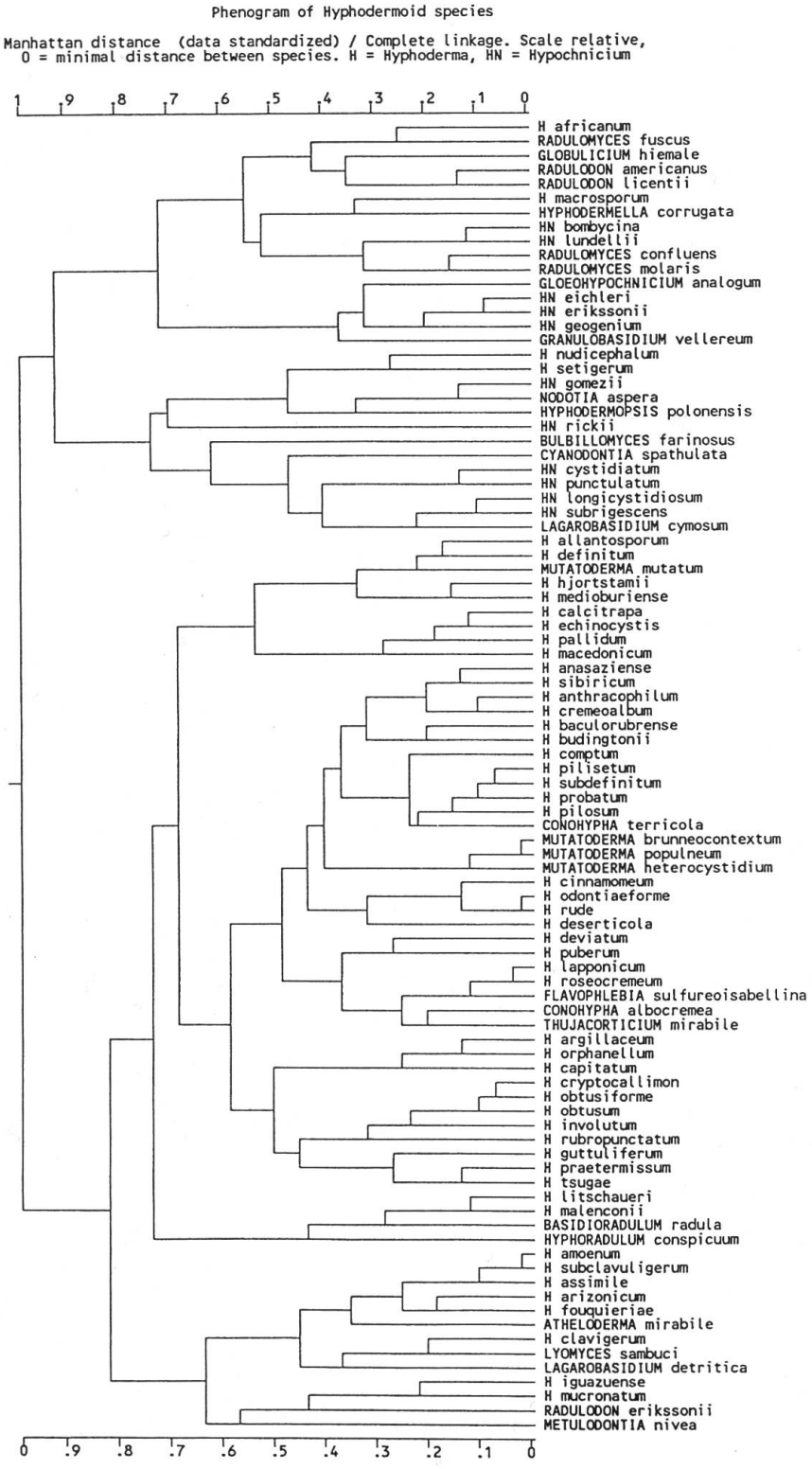

Phenogram of Hyphodermoid species
Manhattan distance (data standardized) / Complete linkage. Scale relative,
0 = minimal distance between species. H = Hyphoderma, HN = Hypochnicium
1 .9 .8 .7 .6 .5 .4 .3 .2 .1 0
H africanum
RADULOMYCES fuscus
GLOBULICIUM hiemale
RADULODON americanus
RADULODON licentii
H macrosporum
HYPHODERMELLA corrugata
HN bombycina
HN lundellii
RADULOMYCES confluens
RADULOMYCES molaris
GLOEOHYPOCHNICIUM analogum
HN eichleri
HN erikssonii
HN geogenium
GRANULOBASIDIUM vellereum
H nudicephalum
H setigerum
HN gomezii
NODOTIA aspera
HYPHODERMOPSIS polonensis
HN rickii
BULBILLOMYCES farinosus
CYANODONTIA spathulata
HN cystidiatum
HN punctulatum
HN longicystidiosum
HN subrigescens
LAGAROBASIDIUM cymosum
H allantosporum
H definitum
MUTATODERMA mutatum
H hjortstamii
H medioburiense
H calcitrapa
H echinocystis
H pallidum
H macedonicum
H anasaziense
H sibiricum
H anthracophilum
H cremeoalbum
H baculorubrense
H budingtonii
H comptum
H pilisetum
H subdefinitum
H probatum
H pilosum
CONOHYPHA terricola
MUTATODERMA brunneocontextum
MUTATODERMA populneum
MUTATODERMA heterocystidium
H cinnamomeum
H odontiaeforme
H rude
H deserticola
H deviatum
H puberum
H lapponicum
H roseocremeum
FLAVOPHLEBIA sulfureoisabellina
CONOHYPHA albocremea
THUJACORTICIUM mirabile
H argillaceum
H orphanellum
H capitatum
H cryptocallimon
H obtusiforme
H obtusum
H involutum
H rubropunctatum
H guttuliferum
H praetermissum
H tsugae
H litschaueri
H malenconii
BASIDIORADULUM radula
HYPHORADULUM conspicuum
H amoenum
H subclavuligerum
H assimile
H arizonicum
H fouquieriae
ATHELODERMA mirabile
H clavigerum
LYOMYCES sambuci
LAGAROBASIDIUM detritica
H iguazuense
H mucronatum
RADULODON erikssonii
METULODONTIA nivea
0 .9 .8 .7 .6 .5 .4 .3 .2 .1 0

Fig. 3

Phenogram of Hyphodermoid species

Euclidean distance (data standardized) / Ward's clustering. Scale relative,
0 = minimal distance between species. H= Hyphoderma, HN = Hypochnicium

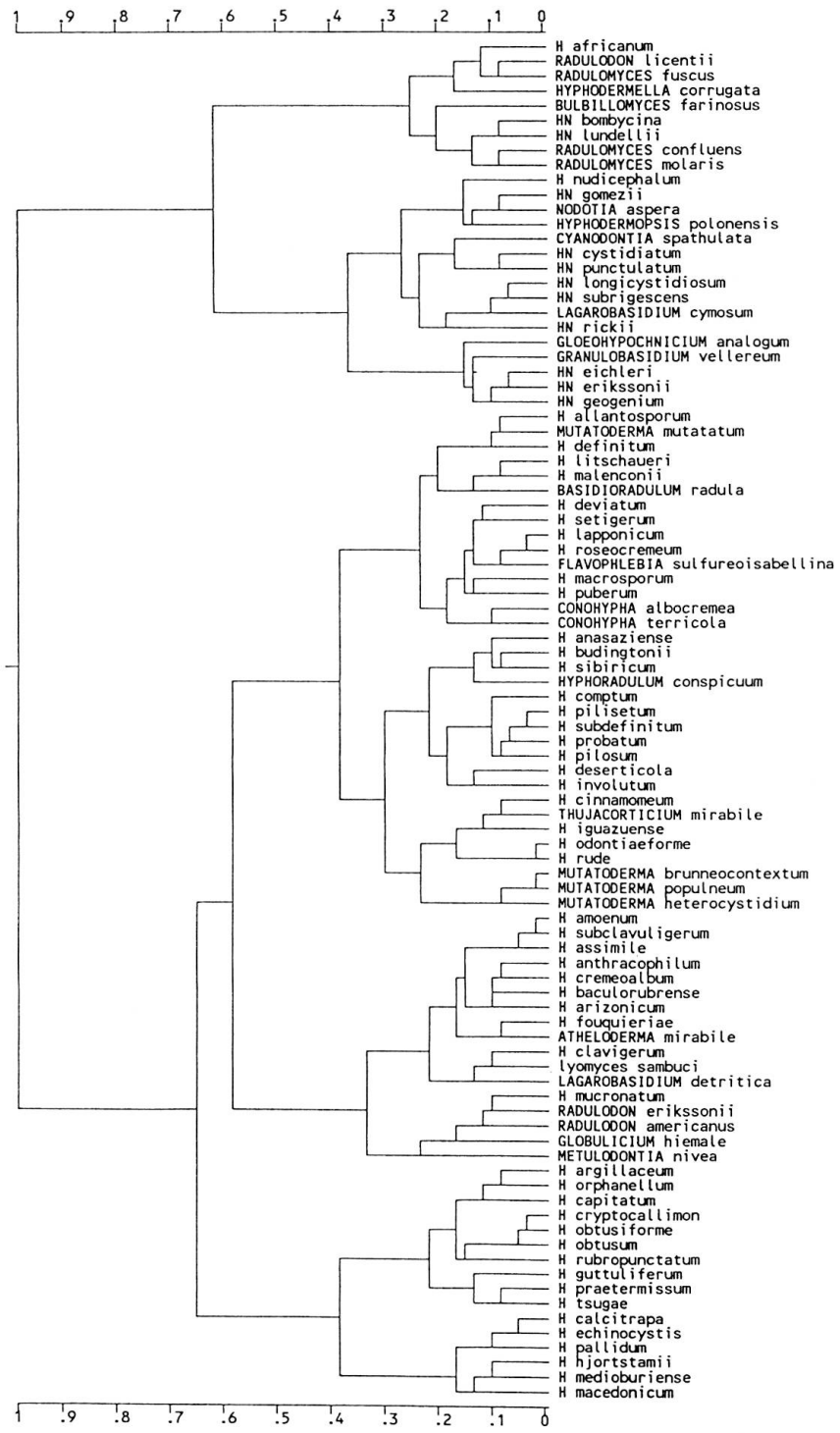
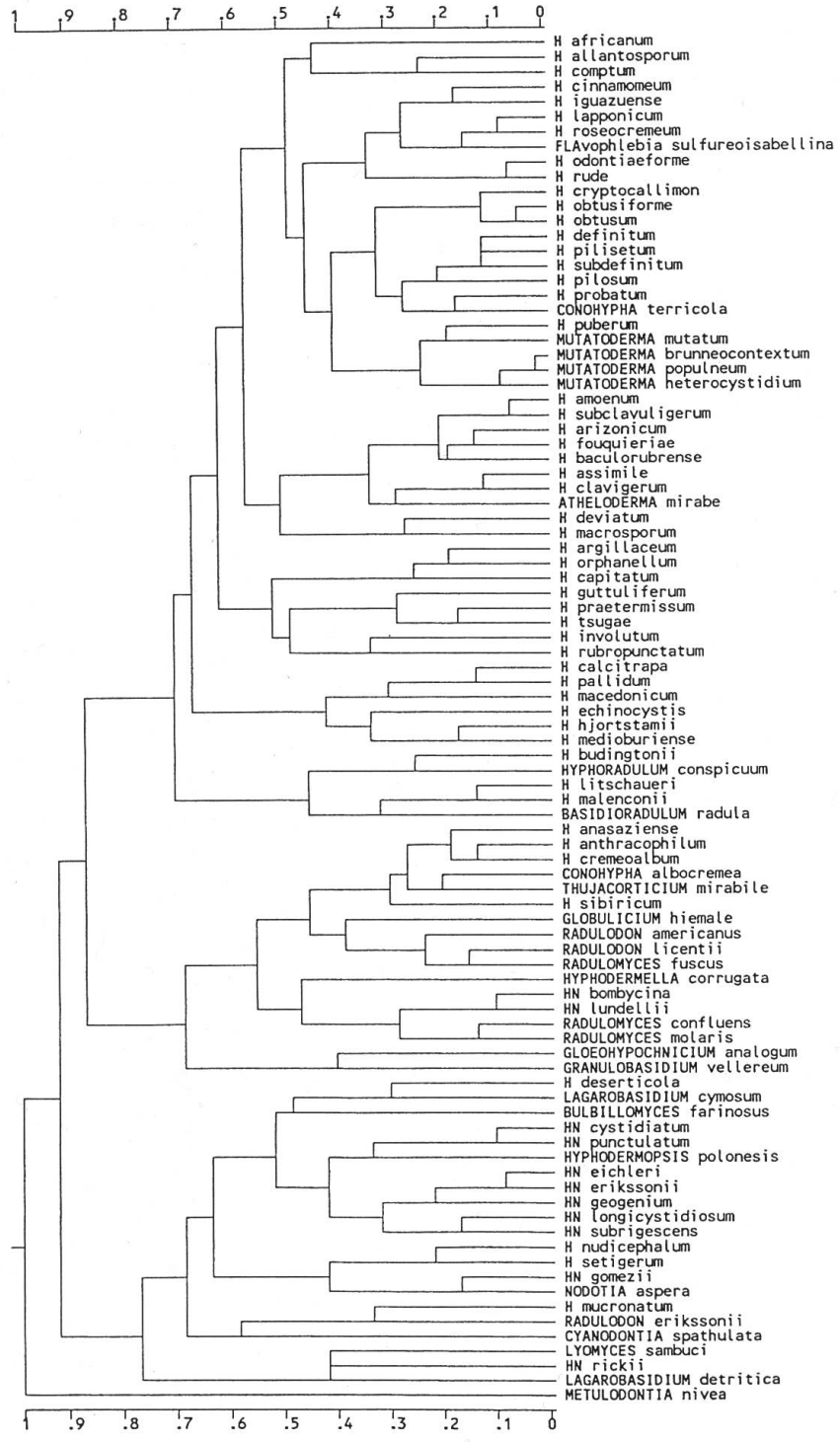


Fig. 4

Phenogram of Hyphodermoid species

Canberra distance (data standardized) / Complete linkage. Scale relative,
0 = minimal distance between species. H = Hyphoderma, HN = Hypochnicium



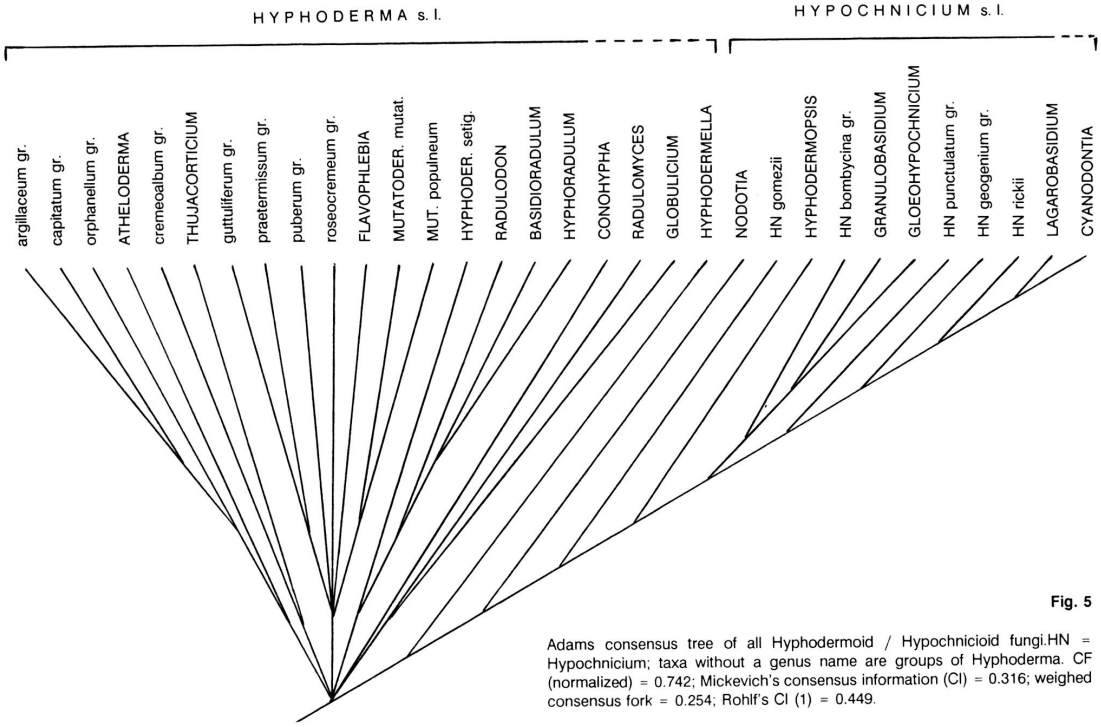


Fig. 5

Adams consensus tree of all Hyphodermoid / Hypochnicioid fungi.HN = Hypochnicium; taxa without a genus name are groups of Hyphoderma. CF (normalized) = 0.742; Mickevich's consensus information (CI) = 0.316; weighed consensus fork = 0.254; Rohlf's CI (1) = 0.449.

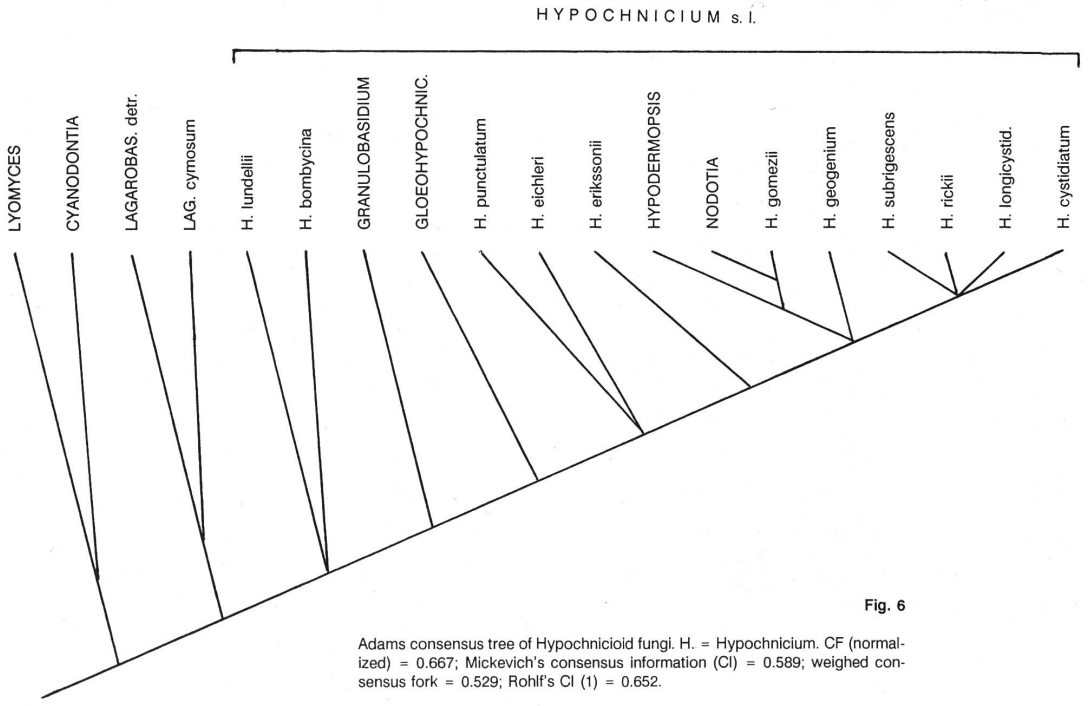


Fig. 6

Adams consensus tree of Hypochnicioid fungi. H. = Hypochnicium. CF (normalized) = 0.667; Mickevich's consensus information (CI) = 0.589; weighed consensus fork = 0.529; Rohlf's CI (1) = 0.652.

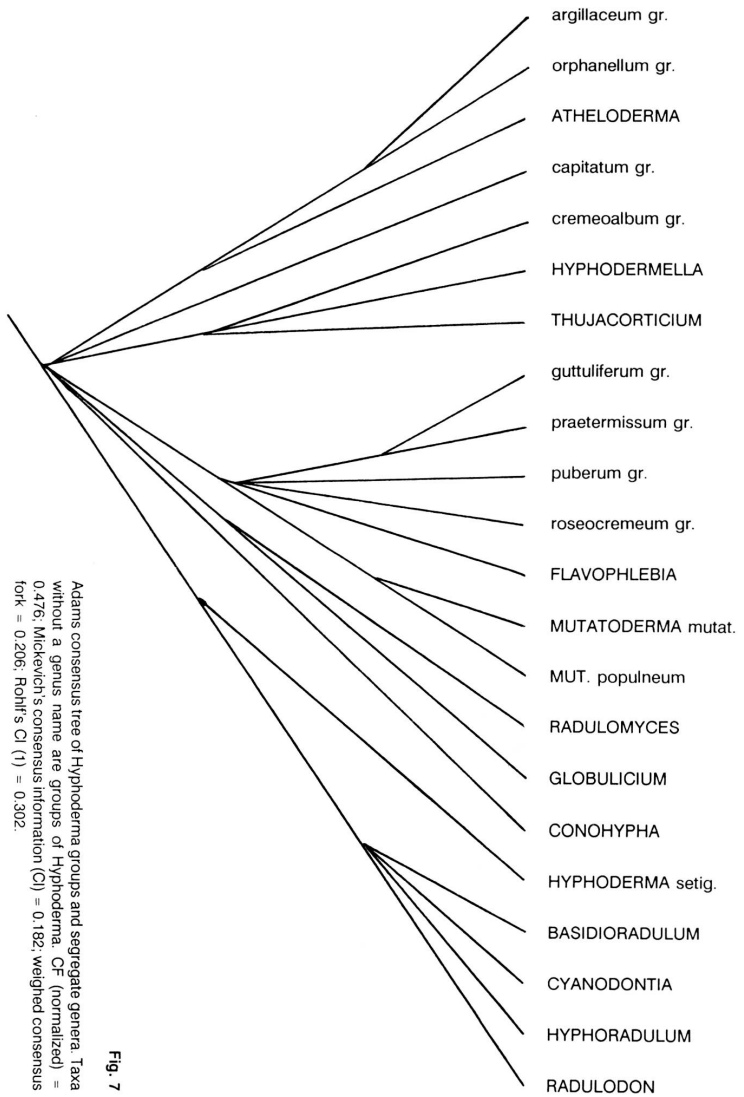


Fig. 7 Adams consensus tree of Hyphoderma groups and segregate genera. Taxa without a genus name are groups of Hyphoderma. CF (normalized) = 0.476; Mickevich's consensus information (CI) = 0.182; weighed consensus fork = 0.206; Rohlf's CI (1) = 0.302.