

Nuclear behavior of the mycelium and the phylogeny of Polypores (Basidiomycota)

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Abstract: This is a review of the available knowledge on nuclear behavior of the mycelium within polypore genera (Agaricomycetes, Basidiomycota). Information on 68 genera showed that nuclear behavior is a distinct and consistent feature at genus level and can be coupled with phylogenetic differentiation. The sole exception was found in *Polyporus*, where different species with normal, heterocytic and astatocoenocytic nuclear behaviors were found. Of the 68 genera treated 41 (60.3%) displayed a normal nuclear behavior, nine (13.2%) were heterocytic, nine (13.2%) were astatocoenocytic and another eight (11.8%) were holocoenocytic. In 95% of the genera a unique compatibility system was found, with the exceptions of *Antrodia*, which includes both homothallic and bipolar species all associated with a normal nuclear behavior, and *Spongipellis*, in which bipolar and tetrapolar species are found, all displaying an astatocoenocytic nuclear behavior. Normal and heterocytic nuclear behaviors were associated mostly with tetrapolarity, astatocoenocicity was associated mostly with bipolarity, and holocoenocicity was associated with either bipolarity or purported homothallism. The combination of nuclear behavior with mating system and brown or white rot capability appeared as a strong feature characterizing and distinguishing the genera of polypores, each combination being valuable to differentiate between apparently related genera, as is supported by phylogenetic studies. Several examples are presented to support this idea, as well as the cases of species that are problematic to this concept. Poroid genera of Hymenochaetaceae were treated apart because of the lack of knowledge regarding their nuclear behavior. In addition new information on the sexuality and/or nuclear behavior of 15 polyporoid taxa is given.

Key words: astatocoenocity, heterocity, holocoenocity mating systems, wood rots

INTRODUCTION

Polypores (Polyporaceae s.l., Agaricomycetes, Basidiomycota) are among the largest and most conspicuous fungi in all forests of the world. Although easily recognized in the field by large basidiomes and the poroid configuration of the hymenophore, they are a polyphyletic group of organisms, highly diverse regarding their micromorphology, cultural features and biology. Their main role in nature as wood decayers of standing trees, fallen wood and wooden products makes them key elements in the dynamics and health of any type of forest worldwide.

The morphology of polypores is well documented and well standardized thanks to many studies from different parts of the world. Features of the basidiomes such as detailed description of macro- and microcharacters are well established. Dimensions, coloration, pore size, pilear surface and general consistency for example are normally included in the descriptions. Also the hyphal system, as an expression of how the basidiomes are built, and characteristics of spores, basidia and sterile elements are incorporated regularly into descriptions (cf. Ryvardeen [1991] for a conspectus on polypore morphology, genera and taxonomy).

Morphology until the latter part of the last century was the main tool used to characterize fungi and to develop the taxonomy and putative phylogeny of different groups. The work by Nobles (cf. Nobles 1965 and 1971 for a summary of her work) made the first attempt to understand polypores (and other aphylloraceous wood-rotting or wood-associated fungi in general) on the basis of their cultural features studied in vitro and other biological features. Her work stressed the importance of (i) wood rotting abilities (brown vs. white rot types) as a key element when considering generic delimitation and taxonomy, (ii) detailed macro- and microscopic features of cultures in vitro as distinguishing characters between species and genera and (iii) mating system as a character of great importance that underlines the biology of each species. An ever increasing body of literature recording those features for each taxon was built by Nobles (1948, 1958, 1965), Stalpers (1978) and Nakasone (1990) among others. Modern floras on polypores were produced for North America and Europe (Gilbertson and Ryvardeen 1986–1987, Ryvardeen and Gilbertson 1993–1994) just before the widespread use of molecular techniques. Those floras stressed the

need of coherence between morphology, cultural features, mating capabilities and genus delimitation.

In the past two decades we have seen great advances in understanding the phylogeny of larger fungi, including the aphyllorphoraceous fungi (Hibbett et al. 2007). Molecular phylogenetics has certainly been the main research focus, and little effort has been invested in understanding other basic features of their life cycles. Critical factors, such as the nuclear behavior of the mycelium plus other “minor” features such as the number of nuclei in basidiospores and the germination rate of the latter, have remained neglected aspects of the biology of these fungi. Correspondingly key features such as the mating system and cultural features have been given progressively less and less importance, leaving a holistic picture of the taxa incomplete.

Nuclear behavior in the larger fungi was introduced by Kühner (1945a, b, c; 1948) in a series of articles that showed how nuclei of the basidia, basidiospores, germinating basidiospores, primary and secondary mycelia of agarics could be stained and studied. Boidin (1958) applied these techniques to the study of numerous species in the corticioid aphyllorphoraceous fungi. Nuclear behavior includes the number of nuclei present in a fungus at different phases of its life cycle, the production of basidiospores, the production of germinating basidiospores, production of the hyphal cells of the primary (monosporic) mycelium, production of the hyphal cells of the secondary (polyspore or tissue) mycelium and the variation in number of nuclei under different O₂ pressures. Boidin (1958) described and classified them (Boidin 1964, 1971) as follows.

Normal behavior: The uninucleate basidiospore germinates into a mycelium composed of uninucleate cells; the diplont is regularly binucleate.

Subnormal behavior: After the germination of the binucleate spore, a brief plurinucleate state precedes the appearance of mycelium which rapidly becomes uninucleate; the diplont is binucleate.

Heterocytic behavior: Binucleate or uninucleate spores germinate into primary mycelia that remain pluri- to multinucleate (at least within the growing cells); the diplont is regularly binucleate.

Astatocoenocytic behavior: The germinating uni- or binucleate spore is strongly coenocytic, and this state is maintained during the haplophase; the secondary mycelium is binucleate and clamped with sufficient aeration, but it turns coenocytic with progressive accumulation of CO₂, while clamps are partially or totally replaced by widely spaced simple septa. The basidiome is binucleate.

Holocoenocytic behavior: The spore with 1–2 nuclei germinates into a mycelium with plurinucleate

or coenocytic cells; secondary mycelium is also coenocytic. This condition may extend into the basidiome where in extreme cases the basidiole alone is binucleate.

The different nuclear behavior types were defined according to the increasing presence of a multinucleate state along the life cycle (TABLE I). A summary of data on nuclear behavior, mating system and main cultural features were published by Boidin and Lanquetin (1984 and literature referred to therein), mainly referring to the corticioid aphyllorphoroid fungi, which provided an overall scope of their importance in delimiting numerous genera from each other and integrating with morphology.

These aspects of polypores were studied mainly by David in a series of works (e.g. David 1966–1982) in which she characterized numerous species and genera. She demonstrated the correspondence among morphology, cultural features, nuclear behavior and polarity within several genera. In one of her last published works she summarized the knowledge up to 1982 (David 1988). Since then more data have been published on several taxa. Since the mid-1990s phylogenetic studies on different groups of polypores increased rapidly and enabled a fine comprehension of these organisms at several taxonomic levels (cf. the Deep Hypha project [Blackwell et al. 2006, Hibbett et al. 2007]).

In this paper a review of the knowledge of nuclear behavior of the mycelium, mating system and number of nuclei of the basidiospore in polypores (Basidiomycota) is presented as an aid to better understand the taxonomy and phylogeny of different genera. In addition I highlighted coincidences and mismatches between these data and the results of phylogenetic analyses of different groups within polypores.

NUCLEAR BEHAVIOR IN POLYPORES

A data matrix (TABLE II) was built containing genera accepted by the author as valid from a biological, morphological and phylogenetic points of view, excluding the poroid Hymenochaetaceae. Genera were organized according to three criteria: (i) rotting type (brown, white), (ii) nuclear behavior type (normal, heterocytic, astatocoenocytic, holocoenocytic) and (iii) mating system (homothallic, bipolar, tetrapolar). References were incorporated for the ensemble of these data, and species that have been studied for these features are specified (TABLE II last column). Information on the number of nuclei per spore and the hyphal system of the genera also was included. References are not provided for the hyphal system but they may be found in manuals such as those of Gilbertson and Ryarden (1986–1987) and

TABLE I. Nuclear behavior types classed according to the growing importance of the multinucleate phase (Boidin 1971)

Nuclear behavior type	Phases of the life cycle						
	Germination	Primary mycelium	Secondary mycelium	Subiculum	Subhymenium	Basidium	
Normal	—	—	==	==	==	==	==
Subnormal	—	—	==	==	==	==	==
Heterocytic	×××××	×××××	==	==	==	==	==
Astatocoenocytic	×××××	×××××	×××××	==	==	==	==
Holocoenocytic	×××××	×××××	×××××	×××××	×××××	==	==

—: uninucleate.
 ==: binucleate.
 ××: multinucleate.

Ryvarden and Gilbertson (1993–1994). I also provided information on the phylogenetic disposition of the genera according to literature based on molecular data and phylogenetic analyses (TABLE II). Data on species that have not been included in phylogenetic studies but whose biological features are well known, notwithstanding the fact that their placement in purported genera is disputable, are included as PROBLEMS TO BE DEALT WITH (TABLE II).

Poroid Hymenochaetaceae are included separately (TABLE III) because nuclear behavior in this group has been less investigated. Instead the number of nuclei in hyphal segments of the secondary mycelium were incorporated together with the mating system (Fischer 1987). Taxa at all levels are included without authorships for the sake of simplification and ease of reading.

The result generally affirms the fact that the type of nuclear behavior is consistent in all genera and therefore that it is a character of biological and phylogenetic significance at genus rank. Of 68 genera treated here 41 (60.3%) display normal nuclear behavior, nine (13.2%) are heterocytic, nine (13.2%) are astatocoenocytic and another eight (11.8%) are holocoenocytic. Only *Polyporus* (1.5% of total) is an exception because it includes species that can be either normal, heterocytic or astatocoenocytic, making it a rare, outstanding case within the polypores. The reasons for this single, exceptional case and its biological meaning are unknown. From the Sotome et al. (2008) phylogenetic study of *Polyporus* it is clear that this variability exists also within the clades, as detected in their research for clade 6 (see DISCUSSION). A subnormal nuclear behavior was not found in any of the polypore genera. Its presence among polypores (as well as in other groups) may be underestimated because few works have dealt with germinating basidiospores to establish the number of nuclei at that stage.

Nuclear behavior in relation to rotting types and mating types.—The distribution of nuclear behaviors are provided according to rot type (TABLE IV). The most evident feature is that white-rot type presents a high number of genera with normal nuclear behavior and is less represented by genera with other nuclear behavior types as compared with brown-rot type.

A single mating system also appeared to be highly characteristic and uniform at genus rank; in 95% of cases a consistent compatibility system was present (TABLE V). This also could be interpreted as a feature of great biological significance in the phylogeny of the aphylophoraceous fungi. Two important exceptions exist: (i) *Antrodia*, which includes homothallic and bipolar species (Gilbertson and Ryvarden 1986),

TABLE II. Polypore genera distinguished by their rotting type, nuclear behavior, mating system and number of nuclei per spore

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Antrodia</i>	Brown	normal	II/Homoth	1-2	2	David and Déquatre 1984, 1985; David and Tortić 1984	Antrodia clade	Binder et al. 2005	<i>albidoidea</i> , <i>subalbidoidea</i> , <i>malicola</i> , <i>ramentacea</i> , <i>serialis</i> , <i>sinuosa</i> ^f , <i>submalicola</i> , <i>subramentacea</i> , <i>variiformis</i> (1 nucleus/spore); <i>albida</i> , <i>heteromorpha</i> , <i>salicina</i> (2 nuclei/spore)
<i>Amylocystis</i>	Brown	normal	IV	1	1	David 1988	Antrodia clade	Binder et al. 2005	<i>lapponica</i> (T) ^g
<i>Anomophoria</i>	Brown	normal	IV	1	1	David and Gilles 1987	Euagarics clade ^h	Larsson et al. 2004	<i>ambigua</i>
<i>Daedalea</i>	Brown	normal	II	1	2-3	David 1967a, Rajchenberg 1986, Rajchenberg unpubl ⁱ	Antrodia clade	Hibbett and Donoghue 2001	<i>aethalodes</i> II', <i>quercina</i> (T) IV <i>vide</i> David (1967a) but II <i>vide</i> De (1981), Roy (1982) and Gilbertson and Ryvarden (1986)
<i>Echinochaete</i>	Brown	normal	IV	1(-2)	2	Wu and Ryvarden 2003	Core polyporoid clade	Sotome et al. 2008	<i>brachyporus</i> (T)
<i>Fibroporia</i>	Brown	normal	IV	1	2	David 1988	Antrodia clade?	Kim et al. 2001	<i>vaillantii</i> (T) ^g
<i>Fomitopsis</i>	Brown	normal	II	1	2-3	David 1988, David and Rajchenberg 1985, Rajchenberg 1995c	Antrodia clade	Hibbett and Donoghue 2001	<i>palustris</i> , <i>minutispora</i> , <i>cajanderi</i> , <i>pinicola</i> (T), <i>rosea</i> ^g
<i>Piptoporus</i>	Brown	normal	II	1?	2	Mac Donald 1937, Rajchenberg 1994	Antrodia clade	Hibbett and Donoghue 2001	<i>betulinus</i> (T)

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Postia</i>	Brown	normal	IV	1	1	David 1974, 1980, 1988; David and Malençon 1978; Rajchenberg and Greslebin 1995	Antrodia clade	Hibbett and Donoghue 2001	<i>subcaesia</i> , <i>simanii</i> , <i>inocybe</i> , <i>caesia</i> , <i>luteocaesia</i> , <i>balsamea</i> , <i>leucomalleus</i> ^g , <i>fragilis</i> ^g , <i>stipticus</i> , <i>tephroleucus</i> (T), <i>undulosus</i> , <i>pelliculosa</i> , <i>sericeomollis</i> ^g
<i>Amyloporia</i>	Brown	heterocytic	IV	1	2	David and Tortú 1986	Antrodia clade	Hibbett and Donoghue 2001	<i>crassa</i> , <i>xantha</i> (= <i>flava</i>) (T), <i>sordida sensu</i> David and Tortú (1984). See Discussion for alpina and oleracea, that display normality and, the latter, bipolarity
<i>Parmastomyces</i> (= <i>Sarcoporia</i>)	Brown	heterocytic	IV	1	1	David 1972a	Antrodia clade	Binder et al. 2005	<i>mollisimus</i> (= <i>transmutans</i> , = <i>kravtzevianus</i>) (= <i>Sarcoporia polyspora</i>) (T)
<i>Rhodonia</i>	Brown	heterocytic	IV	1	1	David 1988	close to <i>Antrodia</i> clade	Niemelä et al. 2005	<i>placenta</i> (T) ^g ; IV (David 1988), II (Nobles 1943)
<i>Auriporia</i>	Brown	astatocenocytic	II	2	1	David et al. 1974	Antrodia clade	Hibbett and Donoghue 2001	<i>aurulenta</i> , <i>aurea</i> (T)
<i>Gloeophyllum</i>	Brown	astatocenocytic	II	2	2-3	David 1968, 1970	Gloeophyllum clade	Hibbett and Binder 2002	<i>abietinum</i> , <i>sepiarium</i> (T), <i>striatum</i> , <i>trabeum</i> , <i>odoratum</i>
<i>Neolentiporus</i>	Brown	astatocenocytic	II	2	2	Rajchenberg 1995a	Antrodia clade	Hibbett and Donoghue 2001	<i>maculatissimus</i> (T)
<i>Ryvardenia</i>	Brown	astatocenocytic	II	1	1-2	Rajchenberg 1994			<i>cretacea</i> (T), <i>campyla</i>

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	No species specified ^g	Species
<i>Ceriporia</i>	Brown	holocenocytic	unknown	1	1	David 1988	Byssomerulius family (Phlebioid clade)	Miettinen and Larsson 2010		
<i>Laetiporus</i>	Brown	holocenocytic	II	2	2	Banik and Burdshall 1999, Ota et al. 2009, David unpubl ⁱ	Antrodia clade	Hibbett and Donoghue 2001, Binder et al. 2005, Lindner and Banik 2008		<i>sulphureus</i> (T), <i>cinnamatus</i> , <i>montanus</i>
<i>Leptoporus</i>	Brown	holocenocytic	unknown	1	1	David 1980	Phlebioid clade	Binder et al. 2005		<i>mollis</i> (T)
<i>Phaeolus</i>	Brown	holocenocytic	unknown	1	1	David 1969b	Antrodia clade	Hibbett and Donoghue 2001		<i>schweinitzii</i> (T)
<i>Pycnoporellus</i>	Brown	holocenocytic	Homoth?	2	1	David 1969b	Antrodia clade	Binder et al. 2005		<i>fulgens</i> (T), <i>albobuteus</i>
<i>Abortiporus</i>	White	normal	IV	1	1	David 1988	Residual polyporoid clade	Binder et al. 2005		<i>biennis</i> (T) ^g
<i>Antrodiella</i>	White	normal	IV	1	2	David 1988, David and Tortić 1986	Residual Polyporoid clade	Binder et al. 2005		<i>citrinella</i> , <i>semisuspina</i> (T)
<i>Climacocystis</i>	White	normal	IV	1	1	David 1988	Antrodia clade	Binder et al. 2005		<i>borealis</i> (T) ^g
<i>Coriopolopsis</i>	White	normal	IV	1	3	David 1970, David and Rajchenberg 1985	Trametes group	Ko and Jung 1999a,b		<i>polyzona</i> (= as <i>occidentalis</i>) (T), <i>caperata</i>
<i>Daedalopsis</i>	White	normal	IV	1	3	David 1967b	Core polyporoid clade	Binder et al. 2005		<i>confragosa</i> (T) (= <i>Trametes rubescens</i>)
<i>Datronia</i>	White	normal	IV	1	2	David 1967b, David et al. 1983, Rajchenberg unpubl ⁱ	Core polyporoid clade	Binder et al. 2005		<i>mollis</i> (T)
<i>Dichomitus</i>	White	normal	IV	1	2	David 1967b, David unpubl ⁱ , Wu 1996c	Core polyporoid clade	Vlasák et al. 2010		<i>campestris</i> , <i>squalens</i> (T), <i>leucoplacus</i> , <i>setulosus</i>

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Diplomitoporus</i>	White	normal	IV	1	2	David 1967b	Meruliaceae (Residual polyporoid clade)	Miettinen and Larsson 2010	<i>flavescens</i> (T)
<i>Earliella</i>	White	normal	IV	1	3	David unpubl ^{l,k}			<i>scabrosa</i> (T)
<i>Fomes</i>	White	normal	IV	1	3	David 1988, Rajchenberg 1995d	Core polyporoid clade	Binder et al. 2005	<i>fomentarius</i> (T) ^g , <i>hemilephrus</i>
<i>Fuscoerrena</i>	White	normal	IV	1	2	Rajchenberg unpubl ^l			<i>porticensis</i> (T)
<i>Grammothele</i>	White	normal	IV	1	3	David and Rajchenberg 1985	Core polyporoid clade ^l	Binder et al. 2005	<i>lineata</i> (T), <i>subargentea</i>
<i>Hexagonia</i>	White	normal	IV	1	3	David unpubl ^l			<i>cyclophora</i> , <i>hirta</i> , <i>pobequini</i> , <i>sacleuxii</i> <i>nitida</i> (T) ^g , <i>undigeri</i> ^l
<i>Jungkuhnia</i>	White	normal	IV	1	2	David 1988, David unpubl in David and Rajchenberg 1985, Rajchenberg unpubl ^l	Residual polyporoid clade	Binder et al. 2005	
<i>Lenzites</i>	White	normal	IV	1	3	David 1967a	Core polyporoid clade	Binder et al. 2005	<i>betulina</i> (T), <i>wamteri</i> (= <i>reichardtii</i>)
<i>Microporcellus</i>	White	normal	IV	1	2	David and Rajchenberg 1985			<i>dealbatus</i> (T)
<i>Microporus</i>	White	normal	IV	1	3	David unpubl ^l	Trametes group	Ko and Jung 1999b	<i>quarrei</i>
<i>Nigroporus</i>	White	normal	IV	1	2	David and Rajchenberg 1985			<i>vinosus</i> (T)
<i>Pachykytospora</i> (= <i>Haploporus</i>)	White	normal	IV	1	3	David 1972a, David and Rajchenberg 1985, Wü 1996c			<i>tuberculosa</i> (T), <i>alabamiae</i> , <i>papyracea</i>

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Perenniporia</i>	White	normal	IV	1	2	David and Malençon 1978, David and Tortić 1986, David and Rajchenberg 1985	Core polyporoid clade	Binder et al. 2005	<i>rosmarini</i> , <i>narymica</i> , <i>tephropora</i>
<i>Phaeotrametes</i>	White	normal	IV	1	2-3	Rajchenberg unpubl ^f			<i>decepiens</i> (T)
<i>Podofomes</i>	White	normal	IV	1	2-3	David et al. 1983			<i>trogii</i> (T)
<i>Porogramme</i>	White	normal	unknown	1?	2-3	David and Rajchenberg 1985			<i>albocincta</i> (T)
<i>Pouzaroporia</i>	White	normal	unknown	1	2	David and Tortić 1986	Residual polypore clade II	Tomšovský et al. 2010	<i>subrufa</i> (T)
<i>Pycnoporus</i>	White	normal	IV	1		David 1967b	Core polyporoid clade	Binder et al. 2005	<i>cinnabarinus</i> (T)
<i>Pyrofomes</i>	White	normal	IV	1	2-3	Rajchenberg unpubl ^f			<i>perlevis</i>
<i>Schizophora</i>	White	normal	IV	1	1	Hallenberg 1983, David and Rajchenberg 1985, Rajchenberg 1995d	Coltricia clade (Hymenoch-aetales)	Larsson et al. 2006	<i>radula</i> , <i>paradoxa</i> (T), <i>carneo-lutea</i> , <i>nothofagi</i>
<i>Sidera</i>	White	normal	IV	1	1-2	David 1982, Wu 1996b	Hymenochaetales Rickenella clade	Tomšovský 2010, Miettinen and Larsson 2010	<i>lenis</i> (T)
<i>Tinctoporellus</i>	White	normal	unknown	1	2-3	David and Rajchenberg 1985			<i>epimilitinus</i> (T)

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Trametes</i>	White	normal	IV	1	3	David 1966, 1967b; David and Rajchenberg 1985; Wu 1996a; Wu and Rywarden 2003	Core polyporoid clade	Binder et al. 2005	<i>Ijubarskyi</i> , <i>gibbosa</i> , <i>suaveolens</i> (T), <i>elegans</i> , <i>maxima</i> , <i>membranacea</i> , <i>pavonia</i> , <i>villosa</i> , <i>pocas</i>
<i>Trichaptum</i>	White	normal	IV	1	2-3	David 1970, Rajchenberg and Bianchinotti 1991	Coltricia clade, Hymenochaetoid clade	Larsson et al. 2006, Hibbett and Binder 2002	<i>sector</i> , <i>perrottetii</i> (= <i>trichomallum</i>) (T), <i>fumosoaevellanea</i> ,
<i>Wrightoporia</i>	White	normal	IV	1	1	David and Rajchenberg 1987	Russuloid clade	Miller et al. 2006	<i>flava</i>
<i>Bjerkandera</i>	White	heterocytic	II	2	1	David 1988	Phanerochaete family (Phlebioid clade)	Miettinen and Larsson 2010	<i>adusta</i> (T)? ^g
<i>Cerrena</i>	White	heterocytic	IV	2	2-3	David 1988	Meruliaceae (Residual polyporoid clade)	Miettinen and Larsson 2010	<i>unicolor</i> (T) ^g
<i>Erastia</i>	White	heterocytic	IV	1	1	David 1969b;	Antrodia clade?	Ko 2001, Niemelä et al. 2005	<i>sabniconcolor</i> (T) (as <i>Poria aurantiaca</i>)
<i>Funalia</i>	White	heterocytic	IV	2	3	David 1967b, 1970, unpubl; De 1989; David and Rajchenberg 1985, 1992	Trametes group	Ko and Jung 1999a,b	<i>trogi</i> , <i>gallica</i> , <i>fulvocinerea</i> , <i>tefarii</i> , <i>leonina</i> (T) ^{g,i}

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Skeletotitis</i>	White	heterocytic	IV	1	1–2	David 1971a, 1982; David and Keller 1984; Rajchenberg 1987	Residual polyporoid clade I	Tomšovský et al. 2010	<i>percandida</i> , <i>amorpha</i> , <i>albobremea</i> , <i>alutacea</i> , <i>carneogrisea</i> , <i>kuehneri</i> , <i>nivea</i> , <i>stramenticus</i> , <i>papyracea</i> , <i>portrosensis</i> , <i>stellae</i> , <i>subincarnata</i> , <i>odora</i> (= <i>tschulymica</i>), <i>lilacina</i> , <i>dilatata</i> <i>cervina</i> (T) ^g
<i>Trametopsis</i>	White	heterocytic	IV	2	2	David 1988	Byssomerulius family (Phlebioid clade)	Tomšovský 2006, 2008; Miettinen and Larsson 2010, Tomšovský et al. 2010	<i>lindbladii</i> (T)
<i>Cinereomyces</i>	White	astatocoenocytic	IV	1	2	David 1982 ^m , 1988	Core Polyporoid clade, Residual polypore clade III	Binder et al. 2005, Tomšovský et al. 2010, Miettinen and Larsson 2010	
<i>Hapalopilus</i>	White	astatocoenocytic	II	1	1	David 1969b, 1988; David and Rajchenberg 1985	Phlebioid clade	Binder et al. 2005, Wu et al. 2010	<i>nidulans</i> (= <i>nutilans</i>) (T), <i>croceus</i> , <i>albo-citrinus</i>
<i>Ischnoderma</i>	White	astatocoenocytic	II	1	1	David et al. 1983	Residual polyporoid clade	Binder et al. 2005	<i>benzoinum</i> , <i>resinosum</i> (T)
<i>Spongipellis</i>	White	astatocoenocytic	II–IV	1	1	David 1969a	Residual polyporoid clade	Binder et al. 2005	<i>spumeus</i> (II) (T), <i>unicolor</i> (IV), <i>pachyodon</i> (II), <i>delectans</i> (IV)
<i>Tyromyces</i>	White	astatocoenocytic	IV	1	1–2	David 1980	Residual polypore clade	Binder et al. 2005, Tomšovský et al. 2010	<i>chioneus</i> (T), <i>konetii</i>

TABLE II. Continued

Genus	Rotting type	Nuclear behavior ^a	Mating system ^b	Nuclei/spore	Miticity ^c	References ^d	Clade ^e	References	Species
<i>Gloeoporus</i>	White	holocenocytic	Homoth?	1	1	David 1972b			<i>theleporoides</i> (= <i>conchooides</i>) (T)
<i>Heterobasidium</i>	White	holocenocytic	II	2	2	Gluchoff-Fiasson et al. 1983	Russuloid clade	Hibbett and Binder 2002	<i>annosum</i> (T)
<i>Irpex</i>	White	holocenocytic	Homoth?	1	2	David 1969a	Phanerochaetaceae	Kim and Jung 2000	<i>lacteum</i> (T) (as <i>tulipiferae</i>)
<i>Polyporus</i>	White	normal, heterocytic, astatocoenocytic	IV	1	3	David and Romagnesi 1972, David and Déquatre 1982, David and Rajchenberg 1985	Core polyporoid clade	Binder et al. 2005, Tomšovský et al. 2010	<i>ciliatus, corylinus</i> (= <i>tumetanus</i>), <i>arcularioides, tricholoma; arcularius; brumalis, meridionalis</i>

PROBLEMS									
Genus	Rotting type	Nuclear behavior	Mating system	Nuclei/spore	Miticity	Reference	Clade	References	Species
<i>Antrodia stratosa</i>	Brown	heterocytic	II	1	2	Rajchenberg and Greslebin 1995			uncertain position, perhaps <i>Amyloporia Tyromyces spraguei</i>
<i>Fomitopsis spraguei</i>	Brown	heterocytic	II	1	2-3	David 1980	Antrodia clade or Plebioid clade	Kim et al. 2007	Not in the Laetiporus clade (cf. Hibbett and Banik 2008)
<i>Laetiporus portentosus</i>	Brown	holocenocytic	unknown	2	2	Rajchenberg 1995a	Antrodia clade or Plebioid clade	Hibbett and Donoghue 2001, Lindner and Banik 2008	Donoghue 2001 and Lindner and Banik 2008)

TABLE II. Continued

PROBLEMS									
Genus	Rotting type	Nuclear behavior	Mating system	Nuclei/spore	Mitoticity	Reference	Clade	References	Species
<i>Tyromyces wynneneae</i>	White	normal	IV	1	1-2(-3)	David 1980			genus disposition uncertain: <i>Heteroporos wynneneae</i> ? = <i>Lowomyces wynneneae</i> ?
<i>Gloeoporos B</i>	White	heterocytic	IV	1	1	David 1972b	Byssomerulius family (Phlebioid clade)	Wu et al. 2010, Miettinen and Larsson 2010, Tomšovský et al. 2010	<i>pannocinctus</i>
<i>Tyromyces fumidiceps</i>	White	heterocytic	IV	1	1	David and Duhem 1986			nuclear behavior different from <i>Tyromyces</i> s.s.
<i>Aurantiporus</i>	W	astatocenocytic	II	1	1	David 1969b, Rajchenberg 1995c		cfr. Ko et al. 2001, Tomšovský et al. 2006	<i>albidus</i> , <i>alborubescens</i> : uncertain position, not <i>Aurantiporus rivulosa</i> , <i>rivulosa</i> var. <i>valdiviana</i> : uncertain position
<i>Ceriporiopsis</i>	W	astatocenocytic	II-IV	1	1	David 1971b, Nakasone 1981, Rajchenberg 1995b	Residual polypore clade III or A close to <i>Sketelocutis</i> . Same as <i>S. jelicai</i> and <i>portcrossensis</i> but nuclear data absent	Tomšovský et al. 2010	
<i>Flaviporus venustus</i>	W	astatocenocytic	II	1	1	David and Rajchenberg 1985			<i>venustus</i>

TABLE II. Continued

PROBLEMS									
Genus	Rotting type	Nuclear behavior	Mating system	Nuclei/spore	Mitoticity	Reference	Clade	References	Species
<i>Jungkuhnia carneola</i>	W	astatocenocytic	II	1	2	David and Rajchenberg 1985			Nuclear behavior and polarity does not fit either with <i>Jungkuhnia</i> or with <i>Skeletocutis</i>
<i>Phaeolus albosordescens</i>	W	astatocenocytic	II	1	1	David 1969b		cfr. Ko and Ryvarden 2001	<i>Aurantiporus/Tyromyces fissilis</i> (as <i>albosordescens</i>)
<i>Skeletocutis sub-sphaerospora</i>	W	normal?	IV	1	1	David 1982	Residual polypore clade I or A close to <i>Skeletocutis</i> . Same as <i>S. jelicii</i> and <i>porterosensis</i> but nuclear data absent	Tomšovský et al. 2010	Nuclear behavior needs confirmation. Phylogenetic studies show it close to <i>Skeletocutis</i> spp.

^a Cfr. Introduction and TABLE I for explanation of nuclear behavior types.

^b II = bipolar heterothallic, IV = tetrapolar heterothallic, Homoth = homothallic.

^c 1 = monomitic, 2 = dimittic, 3 = trimittic (cfr. Ryvarden 1991 and literature thereof for explanation of terms).

^d References are provided for data on nuclear behavior; for mating systems refer to Stalpers (1978), Nobles (1965), Gilbertson and Ryvarden (1986–1987) or Ryvarden and Gilbertson (1993–1994).

^e References are provided when there exists an explicit placement by an author, if not cfr. text.

^f *Anbrodia sinuosa* is said to be bipolar by Stalpers (1978) but tetrapolar by David and Déquatre (1985); if the latter is true then it is the only case in the genus with such a mating system; it may be the materials represent a different brown-rot taxon. See text.

^g No detailed data given. T = type species.

^h Based on the assumption that *Anomophoria ambigua* (David and Gilles 1987) is a brown-rotting taxon according to cultural features.

ⁱ See Appendix online.

^j As *Megasporoporia setulosa*.

^k Wu (1996a) listed the species as bipolar, but the photograph does not seem to correspond to that taxon. In addition the number of confronted monospores (i.e. 8) is low

^l Based on *G. fuligo*, but its mating system and nuclear behavior are unknown.

^m Masked tetrapolarity according to David (1982, 1988); Nobles et al. (1957) listed this taxon as bipolar.

TABLE III. Poroid Hymenochaetales distinguished by the number of nuclei in their secondary mycelium, mating system and basic stage

Genus	Number of nuclei in secondary mycelium	Mating system ^a	Basic stage	Miticity ^b	Species	Clade	References
<i>Fuscoporia</i>	binucleate	Homoth to II	—	2	<i>contigua</i> , <i>ferrea</i> , <i>ferruginosa</i> , <i>viticola</i> , <i>torulosus</i>	Hymenochaetales family (Hymenochaetales)	Fiasson and Niemelä 1984, Fischer 1987, Larsson et al. 2006 ibid.
<i>Fomitiporia</i>	coenocytic ^c	Homoth	Diplophase	2	<i>hartigii</i> , <i>hippophaeicola</i> , <i>erecta</i> , <i>robusta</i> , <i>punctatus</i> , <i>pseudopunctatus</i>	ibid.	ibid.
<i>Inocutis</i>	coenocytic	—	—	1	<i>rheades</i> , <i>tamaricis</i> , <i>dryophila</i>	ibid.	ibid.
<i>Inonotus</i>	coenocytic	Homoth	Haplophase	1	<i>cuticularis</i> , <i>hispidus</i> , <i>nidus-pici</i> , <i>obliquus</i> (oligo)	ibid.	ibid.
<i>Onnia</i>	coenocytic	—	—	1	<i>tomentosa</i> , <i>triquetra</i>	ibid.	ibid.
<i>Phellinus</i>	coenocytic	II	—	2	<i>ignarius</i> , <i>laevigatus</i> , <i>lundelli</i> , <i>rhammii</i> , <i>trivialis</i> , <i>tuberculosus</i> , <i>tremulae</i> (oligo)	ibid.	ibid.
<i>Phylloporia</i>	coenocytic	Homoth	Haplophase	1	<i>ribis</i>	ibid.	ibid.
<i>Porodaedalea</i>	coenocytic	II	—	2	<i>chrysoloma</i> , <i>conchatus</i> , <i>pini</i>	ibid.	ibid.
<i>Pseudoinonotus</i>	coenocytic	—	—	1	<i>dryadeus</i>	ibid.	ibid.
<i>Coltricia</i>	coenocytic	—	—	1	<i>perennis</i>	ibid.	ibid.
<i>Mensularia</i>	oligonucleate	II	—	1	<i>radiata</i> , <i>nodulosa</i> , <i>hastifera</i>	ibid.	ibid.
<i>Phellinidium</i>	oligonucleate	—	—	2	<i>ferrugineofuscus</i>	ibid.	ibid.
<i>Phelolpitus</i>	oligonucleate	Homoth?	Haplophase	2-3	<i>nigrolimitatus</i>	ibid.	ibid.

^a Homoth = homothallic, II = bipolar heterothallic.

^b 1 = monomitic, 2 = dimitic, 3 = trimitic (cf. Ryvarden 1991 and literature thereof for explanation of terms).

^c Fiasson and Niemelä (1984) criterion on the hyphal segments being either coenocytic or oligonucleate was chosen vis à vis Fischer (1987, 1996) description when two options were available.

TABLE IV. Number and percentages (between brackets) of Polypore genera presenting a certain rotting type and nuclear behavior

Rotting type	Nuclear behavior type ^a				
	Normal	Heterocytic	Astatocoenocytic	Holocoenocytic	Mix ^b
Brown					
21 (31%)	9 (43%) ^c	3 (14%)	4 (19%)	5 (19%)	—
White					
47 (69%)	32 (68%)	6 (13%)	5 (11%)	3 (6%)	1 (2%)
68 genera (100%)					

^a Boidin (1971).

^b Genera including taxa with more than one nuclear behavior type

^c Percentages for the rotting type class.

all associated with a normal nuclear behavior; and (ii) *Spongipellis*, in which bipolar and tetrapolar species are found, all associated with an astatocoenocytic nuclear behavior (David 1969a). In *Antrodia* several morphologically almost identical species have been described that apparently differ only by their system of mating compatibility. This is the case for the species pairs *A. malicola*-*A. submalicola*, *A. ramentacea*-*A. subramentacea* and *A. albida*-*A. albidoides* (David and Déquatre 1984, 1985). When this occurs the populations with different mating systems are incompatible, representing different species. A phylogenetic study of these *Antrodia* taxa is needed and would provide much light on the role of mating systems and nuclear behavior in the phylogeny of these fungi. *Antrodia* also is peculiar in being the only polypore genus that includes species with either uninucleate or binucleate basidiospores (David and Déquatre 1984). To my knowledge only *Echinochaete brachyporus* has been described also as uninucleate but with a small proportion of binucleate basidiospores (Wu and Ryvarden 2003). At least for one species pair (*A. albida*-*A. albidoides*) this feature also

is coupled with different mating systems (David and Déquatre 1984).

It should be noted however that the different mating systems referred to here are between heterothallic (bipolar) and homothallic types. In this respect Nilsson et al. (2003) and Hallenberg et al. (2007) found when using phylogeny based on ITS sequences that homothallic specimens are mixed in terminal clades with heterothallic ones in two corticioid species complexes such as *Hyphoderma setigerum* and *Peniophorella praetermissa*. In those works homothallic and bipolar specimens were considered conspecific because there were no sequence differences at all between homothallic and heterothallic strains and therefore homothallism in such species could be considered a kind of surviving strategy, perhaps appearing at more or less regular occasions in otherwise heterothallic species. In the *Hypochnicium punctulatum* species complex on the other hand homothallism was coupled with species differentiation (Nilsson and Hallenberg 2003).

While reviewing the literature it was found that different mating systems have been recorded for the

TABLE V. Polypore genera according to nuclear behavior (NB) type and mating system

Mating system	Nuclear behavior type ^a			
	Normal	Heterocytic	Astatocoenocytic	Holocoenocytic
Homothallic	0	0	0	3?
Homothallic- bipolar	1	0	0	0
Bipolar	3	1	6	2
Bi- and tetrapolar	0	0	1	0
Tetrapolar	34	8	2	0
Unknown	3	0	0	3?
Total	41	9	9	8
Tetrapolar, several NB	1 ^b			0

^a Boidin (1971).

^b The number does not belong to any column in particular. It corresponds to genus *Polyporus*, see text.

same species in several cases (i.e. *Daedalea quercina* and *Ceriporiopsis rivulosa*) and generally the differences lie between bipolarity versus tetrapolarity. David (1971, 1980, 1988) explained some cases as being due to masked results (i.e. the formation of false clamps), but the existence of different, cryptic taxa that differ apparently only in their mating system, as shown above for *Antrodia*, also needs to be considered.

Relatedness of nuclear behavior with mating systems.—A normal nuclear behavior was related mostly to tetrapolarity and to a lesser degree with bipolarity. Among the white rot polypores it is apparently the rule; 29 of 32 genera displayed tetrapolarity with three genera, *Tinctoporellus*, *Porogramme* and *Pouzaroporia*, still in need of study. Among brown-rot genera with a normal nuclear behavior, tetrapolarity was present in five genera, bipolarity in three and one important genus (i.e. *Antrodia*, its importance determined on the basis of its high number of species) had both homothallic and bipolar species.

Heterocytism was distinguished by tetrapolarity (eight out of nine cases) in both white- and brown-rot genera, bipolarity being rarely associated with it as is the sole case of *Bjerkandera*, a white-rot genus. Astatocoenocytism was mostly associated with bipolarity (in six of nine cases), but it was associated with tetrapolarity in one genus (i.e. *Tyromyces* s.s. and *Cinereomyces*) and with both mating systems in still another (i.e. *Spongipellis*). Holocoenocytism was associated with bipolarity in two genera, purportedly homothallicity in three cases and unknown sexuality in an additional three cases.

The combination of a certain nuclear behavior with a certain mating system and rotting type appeared as strong features characterizing and distinguishing the genera of polypores, each combination expressing the difference between apparently related genera as shown by phylogenetic studies. The following discussion considers how these features highlight the distinctions between different genera.

DISCUSSION ACCORDING TO GROUPS OF GENERA

Skeletocutis (Residual Polyporoid clade, cf. TABLE I for references of clade names)

Species in this genus are heterocytic and tetrapolar. The genus belongs in the Polyporoid clade (Tomšovský et al. 2010) as part of the Residual Polypore clade.

Skeletocutis is characterized by a dimitic hyphal system, with hyphae incrustated by peculiar sharp-pointed crystals (Keller 1979). Trimitic or subtrimitic species with binding hyphae also were included without major rejection by specialists. The inclusion

of monomitic species by David (1982) (i.e. *S. azorica*, *S. jelicii*, *S. portrosensis* and *S. subsphaerospora*) was controversial from a morphological point of view and was rejected by several authors, mainly Ryvarden and Gilbertson (1993) and Bernicchia (2005), who transferred the species or accepted them in *Ceriporiopsis*. Nevertheless the combination of microscopic features (principally the presence of the sharp, thorn-like crystals on the hyphae) plus the nuclear behavior were more predictive than the hyphal systems. Tomšovský et al. (2010) showed that some of these monomitic taxa (i.e. *S. portrosensis*, *S. subsphaerospora* and *S. jelicii*) fall close to the *Skeletocutis-Tyromyces* s.s. group of species (polyporoid clade, or as residual polyporoid clade A or clade I by Tomšovský et al. 2010), closer to them than to the core of *Ceriporiopsis*, which belongs to the phlebioid clade, and which in fact is restricted to few taxa, *C. gilvescens* and *C. guidella* (Tomšovský et al. 2010, Miettinen and Larsson 2010 but cfr. Binder et al. 2005, who place *C. gilvescens* in the polyporoid clade). *Skeletocutis subsphaerospora* differs not only by its monomitic hyphal system but also by its apparently normal nuclear behavior, even though the latter needs confirmation because it was established with uninucleate monospermes obtained through a dikarionized mycelium (David 1982). No data is available so far on the nuclear behaviors of *S. jelicii* and *S. azorica*.

Contrary to the above cited cases, the inclusion of *Poria (Cinereomyces) lindbladii* in *Skeletocutis*, as suggested by David (1982) through “successive chaining” of characters, has been shown to be incorrect. *Cinereomyces lindbladii* produces a white rot in wood, it is dimitic with skeletal hyphae swelling in KOH, and it has an astatocoenocytic nuclear behavior and a tetrapolar mating system but lacks pyramidal, thorn-like encrustations on the hyphae characteristic of *Skeletocutis*. Nobles et al. (1957) and Nobles (1965) registered this taxon as bipolar but David (1982) said it had “masked bipolarity”. Phylogenetic studies have shown it to be more closely related to *Gelatoporia (Ceriporiopsis) subvermispora* (Tomšovský et al. 2010, Miettinen and Larsson 2010), and its placement in a genus of its own, *Cinereomyces*, might prove to be appropriate (Miettinen and Larsson 2010).

In relation to *C. lindbladii* and *Skeletocutis* the case of *Poria lenis* also should be mentioned. *Poria lenis* was included in *Skeletocutis* by Niemelä (Renvall et al. 1991) because of morphological similarities (i.e. dimitism, fusiform cystidioles, white rot, spore shape). David (1982) also sustained this connection. But the nuclear behavior of this species is normal, not heterocytic, and its position in the system has proved

to be far from *Skeletocutis*, in the Hymenochaetales in a new genus *Sidera* (Miettinen and Larsson 2010), which is placed in the Rickenella clade (Larsson et al. 2006, Larsson 2007). Its relationship with *C. lindbladii*, as proposed by Spirin (2005), was not supported by molecular studies.

Tyromyces s.s. (Residual Polyporoid clade)

Tyromyces species are astatocoenocytic and tetrapolar. In a restricted sense this white-rot genus is characterized by a monomitic hyphal system that lacks the peculiar incrustations present in *Skeletocutis*. Nevertheless these incrustations were developed in culture (David 1980) and David (1982) pointed out a close relationship between the two genera. This already was confirmed in the early work by Yao et al. (1999) and by Binder et al. (2005) and Tomšovský et al. (2010).

Within this picture the case of *T. fumidiceps* should be mentioned, which has been found to be heterocytic and tetrapolar and has been listed as problematic in this review because of discordant characters. Data on its phylogenetic placement are needed.

Funalia-Trametes-Coriolopsis (Core Polyporoid clade)-**Cerrena** (Residual Polyporoid clade)

Funalia is heterocytic and tetrapolar and has binucleate basidiospores. It belongs in the *Trametes* group (Ko et al. 1999a, b) (Polyporoid clade). Species included in this genus generally have been referred to *Trametes* or *Coriolopsis*. Those genera differ by normal nuclear behaviors, tetrapolar mating systems and uninucleate basidiospores. Niemelä et al. (1992) distinguished *Funalia* morphologically from other trametoid genera on the basis of the skeletal hyphae being cyanophilous and metachromatic. He made several combinations in the genus on this basis as that of *F. polyzona* (type species of *Coriolopsis* Murrill) and was followed by Dai (1996) vis à vis *Trametes cervina* (see discussion below under *Trametes*). I have been unable to confirm this feature in specimens of *F. trogii*, *F. gallica* and *Coriolopsis polyzona* (as *C. occidentalis*), which I studied from Argentina.

The biological differences between *Funalia* and *Trametes/Coriolopsis* were discussed many years ago by David (1967). Phylogenetically these differences later were expressed in Ko and Jung (1999) who showed that *F. trogii* and *F. gallica* cluster together, being more closely related to *Daedaleopsis* than to *Trametes* s.s. Both species in *Funalia* had been regarded as closely related on the basis of morphological similarities. However for a strict morphologist it has been hard to accept that a taxon with a white basidiome context was treated as congeneric with a species with a brownish context and both species therefore were treated classically as belonging to different genera, as

Trametes trogii and *Coriolopsis gallica* respectively, or considered both as belonging to *Trametes* or both to *Coriolopsis*. The context color within Polypores has been given little importance in recent years, and the character has been treated equivocally by some authors (Ryvarden 1991). Nevertheless its perceived importance was strong enough to keep both taxa separate in many manuals. Tomšovský et al. (2006) also confirmed that “*Coriolopsis trogii*” and “*Corio-Coriolopsis gallica*” cluster together but are separated at great distance from *Trametes* s.s., more closely related to *Daedaleopsis* and *Hexagonia*.

In this example nuclear behavior proved to be the most important biological character distinguishing *Funalia* among the Trametoid genera. Accordingly more research was done and more species have been included in the genus (viz. *F. telfarii* and *F. fulvocinerea* [David and Rajchenberg 1985, 1992]). Regarding the type species of the genus, *F. leonina*, it is noted that De (1986) established the binucleate condition of the basidiospores and Roy and De (1979) established the mating system as bipolar. On this basis De (1986) supported its transfer to *Cerrena*, but David (pers com in letter 18.VI.1990, cf. APPENDIX Online) studied the nuclear behavior of *F. leonina* and found it to be heterocytic and the mating system tetrapolar, thus confirming the homogeneity of this group of taxa. The mating system needs further confirmation because Roy and De used 20 monosporic cultures, enough to establish it on firm ground; David unfortunately did not provide details.

Cerrena also presents similar biological features (heterocicity, tetrapolarity, associated white wood rot, binucleate basidiospores) as does *Funalia*. Although the inclusion of *F. leonina* in *Cerrena* made sense considering biological features, it should be noted that *Cerrena* contains di- and trimitic species with sclerified generative hyphae; the latter being a feature not found in *F. leonina*. In fact Lee and Lim (2010) showed *Cerrena* to belong not in the “trametoid” or “polyporoid” clades but in the “phanerochaetoid” clade. Miettinen and Larsson (2010) also included the type species *C. unicolor* in the Meruliaceae family (Residual Polypore clade).

Trametes-Coriolopsis-Lenzites-Pycnoporus (Core Polyporoid clade)

These genera are normal and tetrapolar; they produce white rot and are characterized by pileate species with a trimitic hyphal system. Phylogenetically they are closely related (Tomšovský et al. 2006, Lee and Lim 2010). *Lenzites betulina*, type species of the genus, clusters within the *Trametes* s.s. group (Lee and Lim 2010). Tomšovský et al. (2006) said that the *Trametes* clade is paraphyletic with *Pycnoporus*

forming a monophyletic branch whereas *Lenzites* is found in an ambiguous position. The type species of *Corioloopsis*, namely *C. polyzona* (syn.: *C. occidentalis*), clusters with several species of *Trametes* s.s., as shown by Ko and Jung (1999), thus confirming the synonymy of *Corioloopsis* with *Trametes*.

The outstanding exception within *Trametes* s.s. is that of *T. cervina*, a species that for a long time has been included in the genus but recently was shown to fall outside the group (Tomšovský et al. 2006, Tomšovský 2008). The species is unusual within the genus because of its binucleate basidiospores, heterocytic nuclear behavior and lack of laccase production (David 1988), although its association with a white rot is without doubt (Tomšovský and Homolka 2004); in addition it has a peculiar dimittic hyphal system described as dimittic with a trimitic aspect (Jahn 1983) and not trimitic as in *Trametes* s.s. It should be noted that the inclusion of *Trametes cervina* in *Funalia* by Dai (1996) made sense, considering the nuclear behavior and number of nuclei in the basidiospores, but here the physiological and hyphal system made the difference. Certainly it does not belong in *Trametes*, and Tomšovský et al. (2006) created *Trametopsis* for its placement in the system, which fell in the “phlebioid clade” associated with some *Ceriporiopsis* spp. (Tomšovský et al. 2010).

***Antrodia-Fibroporia-Amyloporia-Daedalea-Neolentiporus* (Antrodia clade)**

The Antrodia clade was established by Hibbett and Donoghue (2001) within the Polyporoid clade and included several brown-rot polypores (viz. *Antrodia*, *Daedalea*, *Piptoporus*, *Fomitopsis*, *Postia* [incl. *Oligoporus*], *Laetiporus*, *Auriporia*, *Neolentiporus* and *Phaeolus*). The sole exception among brown-rot taxa was *Grifola*, a white-rot polypore. The nonpolyporoid *Sparassis*, also included in that work, later was omitted from the group (Binder et al. 2005).

Genus *Antrodia* was classically defined for annual to perennial, resupinate to pileate polypores with a dimittic hyphal system, cylindrical to ellipsoid basidiospores and producing brown rot. Despite this simple definition many authors have retained it as such and is now rich in species (Ryvarden and Gilbertson 1993, among others). Kim et al. (2001, 2003) made a detailed phylogenetic study of *Antrodia* s.l. and showed that the genus was not monophyletic but separated in three groups. One was represented by *Antrodia vaillantii* and *A. gossypium* (group A), a second by *A. serialis*, *A. sinuosa*, *A. heteromorpha* and *A. malicola* (group B), and a third by *A. xantha* and *A. carbonica* (group C). These differences already were reflected in Boidin et al. (1998) and later were shown

by Binder et al. (2005). Yu et al. (2010) confirmed the polyphyly of *Antrodia* and the validity of *Taiwanofungus*, a polypore genus including endemic species that originally were described or included in *Antrodia* s.l.

Group B here is considered the core group or *Antrodia* sensu stricto, which is formed by species presenting normal nuclear behavior with uni- or binucleate basidiospores that display homothallism or bipolarity in mating. In culture they are characterized by developing generative hyphae with irregularly thickened walls (code 9 in Nobles' system [Nobles 1965] cf. also Stalpers [1978]). *Antrodia* s.s. appears to belong to a group of genera that presents a normal nuclear behavior and displays bipolarity (i.e. *Daedalea*, *Piptoporus* and *Fomitopsis*) with the sole exception of *Neolentiporus* (see below).

Group C is represented by *A. crassa*, *A. xantha* (= *flava*) and *A. sordida* sensu David (David and Tortiç 1984) and is a distinctly different group, being heterocytic and tetrapolar with uninucleate basidiospores; some species also present skeletal hyphae that swell in KOH solution. Lombard (1990) described *A. sordida* as bipolar and there was doubt about the identity with European material, but Ryvarden and Gilbertson (1993) confirmed its presence there. Certainly the compatibility with specimens from North America needs to be worked out. Notwithstanding this group of species corresponds to *Amyloporia*, a name that was generally neglected in many works but received support from Niemelä and Penttilä (1992) and Renvall and Niemelä (1992). The genus was treated in detail by David and Tortiç (1984) as *Amyloporiella*, which is an illegitimate name (Ryvarden 1991). Hibbett and Donoghue (2001) included only species of group C (i.e. *Amyloporia*) in their phylogenetic analysis; therefore no lack of monophyly was detected in that study. When incorporating *A. serialis* in their analyses Hibbett and Binder (2002) and Binder et al. (2005) showed that this *Antrodia* s.s. taxon is clearly distinguished from *Amyloporia*. They also showed that *Antrodia* s.s. appears to be related to *Daedalea*, *Fomitopsis* and *Piptoporus*, and a similar relationship was shown by Kim et al. (2003). The validity of *Amyloporia* (type species *A. xantha*) was confirmed by Yu et al. (2010) but its monophyly was rejected; the relationship of different *Amyloporia* species needs to be worked out. For now it has been shown that *A. xantha* comes close to *Rhodonia placenta* (Kim et al. 2001, Binder et al. 2005) which, of note, also presents heterocytic nuclear behavior and tetrapolarity.

Group A, represented by *Fibroporia vaillantii*, corresponds to a group of species that has normal nuclear behavior, displays tetrapolarity and does not form generative hyphae with irregularly thickened

walls as in *Antrodia* s.s. and *Amyloporia* in basidiomes or in culture. Representatives of this group have been incorporated in phylogenetic studies by Kim et al. (2001, 2003), who included *F. vaillantii* and *F. gossypium*, and by Yu et al. (2010), who also included *F. radiculosa*. They have confirmed the independent position of this group of species. A preliminary report from Schigel et al. (2006) supports this view in an ongoing work on the *Postia-Oligoporus* species complexes. The three genera can be readily differentiated morphologically and biologically.

As stated by Rajchenberg (1995) some species purported to belong in *Amyloporia*, such as *Antrodia oleracea* and *Antrodia alpina* (David and Tortić 1984), displayed normal nuclear behavior and in the case of *A. oleracea* the mating system was shown to be bipolar (Lombard 1990). In these cases the evidence suggests that they should be kept in *Antrodia* s.s. as supported by Renvall and Niemelä (1992), who took into account morphological features as defining characters. Another conflicting example is that of *Antrodia stratosa*, a southern South American species that displays heterocyticity (a character that put it near *Amyloporia*) and bipolarity, a feature of *Antrodia* s.s. (Rajchenberg and Greslebin 1995). The case of *Antrodia carbonica* also needs to be mentioned. This taxon has been treated as close to *Amyloporia* because it has amyloid skeletal hyphae, but phylogenetic studies (Yu et al. 2010) did not support this disposition; also there is a total lack of information regarding its biological features. Still another case is that of *A. sinuosa*, whose mating system is tetrapolar according to David and Déquatre (1985); this is the single known case within *Antrodia* s.s. Stalpers (1978) cited Nobles (1943) and Sarkar (1959) as reporting bipolarity for *A. sinuosa* but, as stated by David and Déquatre (1985), there is no such a report in their work. For all the cases mentioned above the question persists on their appropriate placement. Confirmation of the mating systems is required but, research with molecular tools certainly is the challenge in placing them appropriately. We now know that there is no phylogenetic gradation between one genus and the other, as suggested by David and Déquatre (1985) and Rajchenberg (1995), and *Antrodia*, *Amyloporia*, *Fibroporia* and *Taiwanofungus* clearly belong to different clades.

Daedalea has long been regarded as a genus related to *Antrodia* (Aoshima 1967, van der Wethuizen 1971), differing in its trimitic hyphal system, daedaloid hymenophore with thick dissepiments and a catahymenium. It has normal nuclear behavior, uninucleate basidiospores and the mating system is bipolar, identical as that found in *Antrodia* s.s. Claims have been made on the purported tetrapolarity of *D.*

quercina (cf. Rajchenberg 1986, David 1988), but this needs further evaluation and confirmation. Several authors claim that *D. quercina* is bipolar (De 1981, Roy 1982, Gilbertson and Ryvarden 1986), but no precise data were given by them. *Fomitopsis* and *Piptoporus* also share the same types of biological features and appear closely related to *Daedalea* and *Antrodia* s.s.

Neolentiporus is a special case in this group of genera. It originally was proposed for an austral polypore that was purported to be associated both morphologically and biologically to the agaricoid *Neolentinus* (Rajchenberg 1995), differing mainly by its tubular hymenophore, and was considered the poroid counterpart of that genus. Both are characterized by binucleate basidiospores, astatocoenocyticity and bipolarity. Nevertheless Hibbett and Donoghue (2001) and Binder et al. (2005) showed that the type species, *N. maculatissimus*, clusters in the *Antrodia* clade and not in the *Gloeophyllum* clade (i.e. order *Gloeophyllales*) where *Neolentinus* pertains. Thus the introduction of *Neolentiporus* in the *Antrodia* clade adds an unusual element to this group. It should be noted that Rajchenberg (1995), when describing *N. maculatissimus*, stressed a relationship with *Antrodia*, but both the morphology and the biological features led him to a totally different group of organisms and conclusions.

Polyporus (*Polyporus* core clade)

The phylogenetic relationships within this genus were established by Ko and Jung (2002) and Sotome et al. (2008), the latter through the study of several DNA genes. They showed the genus to be polyphyletic, and Sotome et al. (2008) recognized six clades. One of them, clade 6, which corresponds to the infrageneric division *Polyporellus* (Núñez and Ryvarden 1995), includes *P. tricholoma*, *P. arcularius* and *P. brumalis*. All the mentioned species were studied by David and Romagnesi (1972) and David (1982b). They found that the nuclear behavior varied from being normal to heterocyticity and even astatocoenocyticity, while all of them are tetrapolar. Although pertaining to the same clade 6, this group of taxa presents completely different nuclear behavior, a fact that is strikingly different from what is known from other genera, where homogeneity in this feature is the rule (TABLE II). This group of taxa shows a plasticity regarding the nuclear behavior that is unknown in other genera, being the sole case among Polypores.

Ceriporiopsis (Phlebioid clade)

Ceriporiopsis is typified by *C. gilvescens*. Morphologically it has become a conglomerate of poorly related

species bound by their mitism (monomitic hyphal system) and their association with a white rot. Its heterogeneity has been validated by Tomšovský et al. (2010), who showed the genus to be markedly polyphyletic. In fact the type species occupied an isolated position, only related to *C. guidella* and other *Phlebia* spp. and the only group in the genus to cluster within the Phlebioid clade. The other species fell in different, so-called “residual polyporoid clades I to III”.

Unfortunately there is a large lack of knowledge regarding the cultural features, mating system and nuclear behavior of most of the taxa in this genus. Nevertheless the case of *Ceriporiopsis rivulosa* deserves to be highlighted. This taxon has been treated variously under *Physisporinus* (Gilbertson and Ryvar-den 1986) or *Rigidoporus* (David 1971), in any case always related to *P. sanguinolentus* and *P. vitreus*. These relationships were based on the macroscopically similar appearance of *C. rivulosa* and *P. sanguinolentus* and *P. vitreus*, which overemphasized the macroscopic watery to gelatinous aspect when fresh and its shrinking aspect when dry. But the major microscopic difference concerning septation (i.e. simple septate in *Physisporinus* or *Rigidoporus*, simple clamped in *C. rivulosa*) diminished the weight of the macroscopic features. Already Boidin et al. (1998) and Tomšovský et al. (2010) showed that *C. rivulosa* falls far from either *Physisporinus* or *Rigidoporus* and probably deserves a new genus to accommodate it. The species presents astotocoenocytic nuclear behavior and the mating system has been shown to be bipolar for USA specimens (Nobles et al. 1957, Nakasone 1981) or tetrapolar (David 1971b) for European specimens, although both are compatible (David 1971b). *Ceriporiopsis rivulosa* var. *valdiviana*, a taxon that possibly deserves species rank (cf. Rajchenberg 1995), is also astatocoenocytic. Niemelä (1985) suggested a possible relationship of *C. rivulosa* with *Gelatoporia* (type species *G. subvermispora*). This relationship was revealed by Tomšovský et al. (2006) but needs further treatment. *G. subvermispora* presents similar cultural characters and the same mating system as *C. rivulosa*, as shown by Nakasone (1981), but its nuclear behavior is still unknown. Miettinen and Rajchenberg (2011) have treated the problem and proposed a new genus to accommodate *C. rivulosa* and *C. rivulosa* var. *valdiviana*.

Gloeoporus-Gelatoporia (Phlebioid clade)

Gloeoporus is typified by *G. theleporoides*, a pansub-tropical to tropical species that has holocoenocytic nuclear behavior and is presumably homothallic. The species unfortunately has not been included thus far

in phylogenetic studies. Other well known species are *G. dichrous* and *G. pannocinctus*, but they display heterocytic nuclear behavior and are tetrapolar (David 1972b). In the phylogenetic studies by Binder et al. (2005), Tomšovský et al. (2010), Wu et al. (2010) and Miettinen and Larsson (2010) the two latter species come together with good jackknife support, suggesting a close relationship between them. Thus the combination of *G. pannocinctus* in *Gelatoporia* (Niemelä 1985) seems to be inappropriate. Moreover the type species *Gelatoporia subvermispora* falls far from both species within the Phlebioid clade in Binder et al. (2005) and Wu et al. (2010, group VI), whereas in Tomšovský et al. (2010) it is in the residual Polyporoid clade.

Postia-Oligoporus-Rhodonia placenta-Ryvardenia (An-trodia clade)

The bulk of monomitic, brown-rot polypores with metachromatic hyphae are placed in *Postia* or its purported synonym *Oligoporus*. Both names largely include the same taxa according to the authors' preference for one or the other name (cf. Gilbertson and Ryvar-den [1986, 1987] and Ryvar-den and Gilbertson [1993, 1994] for *Oligoporus*, or Donk [1960], Jülich [1982], Larsen and Lombard [1986], Renvall [1992] and Rajchenberg [2006] for *Postia*). Erkkilä and Niemelä (1986) proposed the use of *Oligoporus* for species with thick-walled basidiospores and *Postia* for those with thin-walled basidiospores. Preliminary results by Schigel et al. (2006) support the use of both names for different groups of species.

David (1980) established the biological features of the whole group (as *Spongiporus*), which has normal nuclear behavior and a tetrapolar mating system, with uninucleate basidiospores that are slow to germinate (3–4 wk or more). I note that David (1980: 47) in the summary table included *Postia tephroleuca* as tetrapolar, but in the text (p 39) she said that the poor germination of basidiospores prevents ascertaining the polarity of this species; Gilbertson and Ryvar-den (1986) described the mating system of this species as bipolar.

Rhodonia placenta had been included in *Postia* (or *Oligoporus*) until Niemelä et al. (2005) proposed the new genus *Rhodonia*. In addition to their own unpublished molecular analysis, but cf. Schigel et al. (2006) for preliminary results, Boidin et al. (1998) and Binder et al. (2005) had shown that this species is distinguished from species of *Postia*. David (1988) said the nuclear behavior of *R. placenta* is heterocytic, thus adding an important difference vis à vis its placement in *Postia*. Regarding the mating system David (1988) said it was tetrapolar, not bipolar

(Nobles 1943), adding that it has masked bipolarity through the formation of false clamps.

Rajchenberg (1994) proposed genus *Ryvardenia* for two southern hemisphere species with obscure monomitic hyphal systems, thick-walled basidiospores associated with a brown rot, namely *Polyporus cretaceus* (type species) and *Polyporus campylus*. Their association with tyromycetoid genera was suggested (i.e. in combinations with *Spongipellis*, *Grifola* or *Tyromyces* s.l.). However astatocoenocyticity coupled with a bipolar mating system supported its distinction from *Postia* and a new genus therefore was proposed. Molecular studies are needed to test his proposal.

Hapalopilus-Erastia salmonicolor (Polyporoid clade)

Erastia was created to accommodate *Polyporus salmonicolor* (Niemelä et al. 2005), which for many years was treated under *Hapalopilus*. Ko et al. (2001) showed that the species was not phylogenetically related to the type species *H. nidulans* or to other well known species in the genus such as *H. rutilans* and *H. croceus*. Instead the species had an isolated position. They proposed the use of *Sarcoporia* for the species but because of nomenclatural problems the name *Sarcoporia* is not available because it corresponds to *Parmastomyces* (Niemelä et al. 2005). The main issue here is that *E. salmonicolor* is very different from *Hapalopilus*, being heterocytic and tetrapolar, while species in *Hapalopilus* are astatocoenocytic and bipolar. Again gross biological differences have been validated by phylogenetic studies (see also Schiegel et al. 2006).

Poroid Hymenochaetaceae (Hymenochaetoid clade)

This is one of the most conspicuous groups within the Polypores of great importance to forest pathology. I refer to Larsson et al. (2006) for a summary of phylogenetic studies of the group. There is little knowledge regarding the nuclear behavior and mating systems in this group of genera due to the lack of clamped hyphae within the family, which could have enabled an easy recognition of secondary mycelium formation between compatible monosporous (i.e. primary) mycelia. Nevertheless Fiasson and Niemelä (1984) and Fischer (1987, 1996) provided most valuable data regarding the life cycles, polarity and number of nuclei of the secondary mycelium of some taxa (TABLE III). *Fuscoporia* is distinguished by being the single genus presenting a dikaryotic secondary mycelium, in contrast to other genera that present oligonucleate to coenocytic hyphal segments. *Fomitiporia* also is characterized by a different ploidy level (Fischer 1996).

PROBLEMS TO BE DEALT WITH

***Tyromyces* s.l. species**

Many molecular studies show the close relationship of *Tyromyces* s.s. (i.e. *T. chioneus*, *T. kmetii*) with *Skeletocutis* (Yao et al. 1999, Kim et al. 2001, Binder et al. 2005, Tomšovský et al. 2010) and validate ideas suggested by David (1982). Both genera differ in nuclear behavior, *Tyromyces* as astatocoenocytic and *Skeletocutis* as heterocytic, both being tetrapolar. However *Tyromyces* has relatively rapid germination of the basidiospores (within a week) while *Skeletocutis* basidiospores have long delay germination, 3–4 wk or more (David 1980). There are exceptions in this picture, such as the case of *S. stramenticus* (Rajchenberg 1987, 2006), which presents heterocytic nuclear behavior while its basidiospores germinate in 8–12 d.

Many *Tyromyces* species still await definite placement in the system. Ko et al. (2001) included *T. sambuceus* and *T. alborubescens* in their phylogenetic studies on *Hapalopilus*. These species remained isolated in their tree and need a deeper treatment to place them in a stable position. *Tyromyces alborubescens*, a taxon previously accommodated in different genera such as *Aurantiporus* and *Phaeolus*, has astatocoenocytic nuclear behavior and a bipolar mating system (David 1969b). The same occurs with other taxa such as *A. albidus* (a species similar to *T. pulcherrimus*, also combined in *Aurantiporus* [Buchanan and Hood 1992; Rajchenberg 1995c, 2006]), *Flaviporus venustus* (David and Rajchenberg 1985) and *T. fissilis* (David 1969b, sub *Phaeolus albosordescens*). Ko et al. (2001) considered *Aurantiporus*, with *A. pilotae* (= *Hapalopilus croceus*) as type species, a synonym of *Hapalopilus* leaving the genus name inapplicable to species such as *T. alborubescens*, *T. pulcherrimus*, *T. fissilis* and *A. albidus*. *Tyromyces* certainly does not seem to be the proper place, as shown by Ko et al. (2001), at least for some of them (i.e. *alborubescens*). Another *Tyromyces* species such as *T. fumidiceps* is heterocytic and tetrapolar (David 1986), and *T. wynnei* is normal and tetrapolar (David 1980), differing from other species in the genus. As in the other cases their positions need to be worked out. Many tropical, monomitic *Tyromyces* and obscurely mono- to dimittic taxa placed in *Antrodiella* (= *Flaviporus* sensu Ginns 1980) are largely unknown regarding their nuclear behavior and polarity, and there is a strong need of this type of knowledge if we want to enlarge our understanding of these tropical groups.

Fomitopsis-Pilatoporus-Rhodofomes (Antrodia clade)

The phylogeny of *Fomitopsis* taxa was studied by Kim et al. (2005, 2007). They showed that the genus is

heterogeneous, with three clades to be considered. The core group (i.e. including the type species *F. pinicola*) also includes *F. palustris* and *Fomes meliae*. Biological data are available only for *F. palustris*, which is normal and bipolar (David and Rajchenberg 1985). Another species displaying the same characters is *F. minutispora* (Rajchenberg 1995), but it so far has not been included in phylogenetic studies. *Fomitopsis iberica* was studied by David and Pieri (1991) who confirmed the bipolarity of this species, but the nuclear behavior was not fully studied.

Fomitopsis spraguei, an annual species with white basidiome context and subtrimitic hyphal system, is heterocytic and bipolar (David 1980) and either groups with several pink species, such as *F. cupreosea*, *F. lilacinogilva*, *F. feei* and *F. africana*, or has an isolated position according to analyses by Kim et al. (2005, 2007).

Whether the biological differences reflect phylogenetic paths that characterized these clades needs to be tested with more studies. The third clade recognized within *Fomitopsis* s.l. corresponds to *F. officinalis* (type species of *Laricifomes*), but the species has not been studied regarding its nuclear behavior and polarity.

Poria carneola

This species has been accommodated in *Junghuhnia* (Rajchenberg 1984), a genus distinguished by normal nuclear behavior and tetrapolarity (David 1988, David and Rajchenberg 1985) or in *Skeletocutis* (Ryvarden 1972, sub *Incrustoporia*), which is distinguished by heterocity and tetrapolarity. *Poria carneola* though is astatocoenocytic and bipolar (David and Rajchenberg 1985), and its cultural features are also very different from both genera; as in other astatocoenocytic taxa it develops wide, simple septate generative hyphae in the margin, while in *Junghuhnia* and *Skeletocutis* they are regularly clamped. Morphological features distinguish this species from taxa in both genera, from *Junghuhnia* by lacking apically heavily encrusted skeletocystida and from *Skeletocutis* by lacking the typical pyramidal, thorn-like incrustations on the hyphae and by lacking irregularly thickened walls in the generative hyphae, a feature that is well expressed in cultural studies (David 1982). Cultural features (David and Rajchenberg 1985) bring this species close to those in *Hapalopilus*, with which it shares nuclear behavior and compatibility, but this needs to be tested experimentally with molecular tools.

Laetiporus portentosus (Antrodia? Plebioid? clade)

Laetiporus sulphureus, type species of *Laetiporus*, has been shown to be characterized by binucleate basidio-

spores, a holocoenocytic nuclear behavior and bipolarity (Ota and Hattori 2008, Lindner and Banik 2008, Banik and Burdsall 1999). Rajchenberg (1995) combined the southern hemisphere polypore *Polyporus portentosus* in *Laetiporus* on the basis of morphological characters, cultural features, binucleate basidiospores and holocoenocytic nuclear behavior. In spite of these common characters, Hibbett and Donoghue (2001) and Lindner and Banik (2008) showed these two species to be separated when testing their affinities with molecular tools. The former kept both taxa in the Antrodia clade, while the latter kept *sulphureus* in the Antrodia clade but placed *portentosus* in the Plebioid clade. The reasons of this discrepancy are not evident and need to be determined.

FINAL COMMENTS

The primary problem when dealing with this type of study in which phylogenetic information is used as metadata is the fact that there is lack of information regarding who determines the basidiomes and the strains on which the sequences are based and whether there exist voucher herbarium specimens for each strain. Errors in identification may cause a part of the problems in phylogenetic trees. Nevertheless it is evident that inconsistencies will be resolved as information accumulates.

Boidin (1971) proposed that the evolution of nuclear behavior types proceeds from normal to holocoenocytic toward the full development of a multinucleate state. The phylogenetic tree of aphyllophoraceous fungi still needs much work before one can confront this hypothesis. Nevertheless Jeong et al. (2005) indicated for the Hymenochaetaceae that the ancestral karyotype might have been binucleate and the derived karyotype, oligonucleate, as theorized by Boidin (1971).

Polypores is a heterogeneous, polyphyletic group of organisms that has representatives in 11 out of the 19 major clades established within the Agaricomycetes (Hibbett et al. 2007, Binder et al. 2010). The analyses presented in this review do not address the phylogeny of the group. However I intended to show how nuclear behavior is indeed a crucial feature that characterizes each of the genera from which we have information. Because of its wide perspective this study can be taken as a good sample of the patterns that are found among the wood-decaying basidiomycetes in general and how they are related to their phylogeny. Larsson (2007) pointed out the importance of nuclear behavior in the phylogeny of corticioid basidiomycetes, but a review of this feature in the group is needed in spite of the quantity of literature available (Boidin and Lanquetin 1984, among others).

I concluded in this review that the combination of type of associated wood rot, type of nuclear behavior and mating system is a highly predictive character in the phylogeny of most polypores. There is only one case (i.e. *Grifola*, a white-rot genus) in which the type of rot does not match the clade in which the genus has been repeatedly associated, that is the *Antrodia* clade (Hibbett and Donoghue 2001), which is composed substantially of brown-rot genera. There is also only one case (i.e. *Polyporus*) in which several nuclear behavioral types are known within the same genus. There are only two cases (i.e. *Antrodia* and *Spongipellis*) in which two mating systems are known for a genus. From a practical point of view it is necessary to emphasize that nuclear behavior of the mycelium, together with other biological features, may explain the inconsistencies found between morphology and phylogenetics regarding the placement of species and the definition of genera.

The need of supporting a polyphasic taxonomy in fungi is evident; "...sequences are only a tiny part of the whole genome..." said Uilenberg and Goff (2006). For a satisfactory phylogeny and classification to be achieved there is a need to integrate sequence data to life cycle features (i.e. nuclear behavior), mating compatibility, decaying abilities and ecological strategies of the genera.

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