Polyporaceae (Aphyllophorales, Basidiomycetes) from Southern South America: a mycogeographical view

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The 37 species of Polyporaceae so far recognized in the Nothofagus forests in southern South America may be clustered in 5 different distributional patterns, viz., cosmopolitan, endemic, paleoaustral (gondwanic and subantarctic) bipolar and pantropical. Thirteen taxa, representing 35% of the total produce a brown rot in wood. This is a relatively high value when compared with that found in other floras. The brown wood rotting species are concentrated in the groups with paleoaustral and bipolar distribution, a fact that may be correlated with the primitiveness of these groups. Brown wood rotting fungi in the area show less specificity for gymnosperm substrata than those in north temperate areas. The existence of high morphological conservatism and of ,sister' species are discussed. Postia grata (Berk.) RAJCH. is proposed as new combination.

The polyporaceous mycota of the South Andean Patagonian region have been intensively studied. First by Spegazzini (e. g. 1887, 1919, 1926) and, more recently, by such workers as Wright & Deschamps (1972, 1975), Rajchenberg (1983, 1987), Plank & Ryvarden (1982) and Hjortstam & Ryvarden (1985). These studies, and others, have given us a fairly good, however incomplete, knowledge of these mycota, at least of the eastern slope of the Andes. With these data, it is now possible to attempt a mycogeographic analysis.

PIROZYNSKI (1983) pointed out the tardiness of mycologists concerning biogeographical problems and presented the factors and misconceptions that have determined it. Nevertheless, from his own general analysis of the Pacific Mycogeography (PIROZYNSKI, 1983) and from other studies by DEMOULIN (1973), GAMUNDI (1977), TRAPPE (1977) and HORAK (1983), it becomes evident that studies on mycogeography may help to confirm and/or elaborate new approaches or possibilities on general biogeographical ideas. This is because mycogeography generally compels the student to integrate vascular plants into more complex evolutionary associations, e. g. the host-parasite or the plant-mycobiont units.

Obligate mycoparasites and ectomycorrhizal fungi offer par-

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ticular relationships with their hosts and have established correlative evolutionary trends of great biogeographical interest (Pirozynski, 1983). Some attempts have been made to elaborate coevolutionary schemes between fungi and their hosts, notably for *Cyttaria-Nothofagus* (Humphries & al., 1986) and Uredinales-Monocotyledons (Baum & Savile, 1985). Polypores, as saprobic organisms, present less specific relationships with their hosts. Nevertheless, the organisms here studied form part of the mycota from a region with a very specific and peculiar history: that of Gondwanaland and its "living fossils" *Nothofagus* (Van Steenis, 1971) which dominates its forests.

This paper provides a synthetic view of the polyporaceous mycota of southern South America and a mycogeographic analysis ot its components. Several problems still unsolved are also presented.

Materials and Methods

All species presented in this paper have been seen by the author, and their inclusion in the floristic check-list implis personal studies of living specimens and exsiccata. Many references found in the literature, many of which referred to Chile, were not included here due to the impossibility of tracing the materials on which determinations were made, or due to disagreement on the identification. Refer to the papers cited in the Introduction for detailed descriptions of most of the included species and for the indication of hosts and distribution in the area. All herbarium abbreviations follow Holmgren & Keuken (1974). Color notations were made in acordance to Munsell (1954).

Floristic Synthesis

The 37 species occurring in the phytogeographic region under study may be clustered according to 5 different distributional patterns. The following symbols are used below: "*" indicates those species associated or producing a brown rot in wood; "=" indicates those species morphologically very similar – if not identical – to species in other parts of the world.

Cosmopolitan species

Bjerkandera adusta (Willd: Fr.) Karst.

Ceriporia reticulata (Fr.) Dom.

Ganoderma applanatum (Pers.: Wallr.) Pat.

Lenzites betulina (L.: Fr.) Fr.

Schizopora paradoxa (Schrad.: Fr.) Donk

Trametes versicolor (L.: Fr.) Phil.

Perenniporia medulla-panis (Jacq.: Fr.) Donk

* $Gloeophyllum\ trabeum\ (Pers.:\ Fr.)\ Murr.$

Endemic species

- = Bondarzewia guaitecasensis (P. Henn.) Wright
- = Grifola sordulenta (Mont.) Sing.

Inonotus crustosus (Speg.) Wright & Desch.

Perenniporia pauciskeletalis Rajch.

Phellinus andinopatagonicus (WRIGHT & DESCH.) RYV.

Phellinus andinus Planck & Ryv.

Phellinus livescens (Speg.) Rajch.

Polyporus gayanus Lév.

Skeletocutis australis Rajch.

* Postia venata (Rajch. & Wright) Rajch.

Paleoaustral species

- A) Gondwanic (Southern south America, Australia, New Zealand and N India or E Africa)
 - * Macrohyporia dictyopora (Cke.) Johans. & Ryv.
 - * Postia dissecta (Lév.) Rajch.
 - * Postia pelliculosa (Berk.) Rajch.
- B) Subantarctic (Southern South America, Australia and New Zealand)
 - = Junghuhnia collabens (Fr.) Ryv. var. meridionalis Rajch. Tyromyces merulinus (Berk.) G. H. Cunn.
 - * Piptoporus portentosus (Berk.) G. H. Cunn. (also present in New Guinea and New Caledonia
- =? * Polyporus maculatissimus Lloyd (not cited for New Zealand)
 - * Postia campyla (Berk.) Rajch.
 - * Postia cretacea (LLOYD) RAJCH. (not cited for New Zealand)

Bipolar species

Phellinus inermis (Ell. & Everh.) G. H. Cunn.

Polyporus melanopus Fr.

Rigidoporus undatus (Fr.) Donk

- = * Antrodia stratosa (Wright & Desch.) Rajch.
 - * Fibroporia gossypia (Speg.) Parm.
 - * Fibroporia vaillantii (DC: Fr.) PARM.
- * Fistulina hepatica Schaef.: Fr. var. antarctica (Speg.) Wright and var. endoxantha (Speg.) Wright & Desch.

Pantropical species

Pycnoporus sanguineus (L.: Fr.) Murr.

Phellinus merrillii (Murr.) Ryv.

Cyclomyces tabacinus (Mont.) Pat.

Taxonomic notes on species

A) Cosmopolitan species

Ganoderma applanatum (Pers.: Wallr.) Pat.

Our concept of this species includes G. australe (Fr.) Pat. as there are no reliable morphological features to keep them separated. Certainly, G. applanatum seems to represent a species complex, but until experimental or more detailed morphological studies are carried out, we prefer to maintain a conservative attitude.

Trametes versicolor (L.: Fr.) Pil.

Morphological studies (RAJCHENBERG, 1982), as well as unpublished experimental data, have shown that the three varieties of the species present in this region, viz. var. *antarcticus* (Speg.) Rajch. & Wright, var. *azureus* Fr. and var. *versicolor*, do not merit specific rank.

B) Endemic species

Bondarzewia quaitecasensis (P. Henn.) Wright

This is microscopically identical with *B. berkeleyi* (Fr.) Bond. & Sing. and *B. montana* (Quél.) Sing. but is separated on account of its host (e. g. *Nothofagus*) and, macroscopically, by the light yellowish colour of the pileal surface (5 YR 7/8) with orange hues. *B. berkeleyi* seems to present a western circumpacific distribution with records in Australia, New Zealand, Japan, Borneo and Sumatra (Corner, 1984; Cunningham 1965) but is also present in east and central USA (Gilbertson & Ryvarden, 1986). Gilbertson & Ryvarden have distinctly shown the correspondance between host, macromorphological features, distribution and these two species. A critical re-evaluation of collections cited by Cunningham (1965), however, should be made.

 $Grifola\ sordulenta\ ({\tt Mont.})\ {\tt Sing.}$

This species is very similar to *G. frondosa* (Diks.: Fr.) S. F. Gray from the north temperate regions, varying mainly in its host (e. g. *Nothofagus dombeyi*) and macroscopical features such as a more fragile hymenophore, which is more lamellate and lacerate.

Postia venata (Rajch. & Wright) Rajch. (Fig. 1)

This species is characterized by its small, fibrous, flabelliform fruitbodies with pilei overrun by black veins (RAJCHENBERG, 1983), generative hyphae with irregularly thickened walls and an amyloid

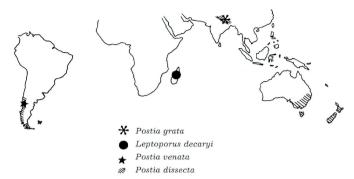


Fig. 1 – Distributional areas of Postia venata (RAJCH. & WRIGHT) RAJCH., Leptoporus decarui PAT., Postia grata (BERK.) RAJCH. and Postia dissecta (LÉV.) RAJCH.

reaction (in mass) in the dissepiments. It seems very closely related to *Polyporus gratus* Berk. and to *Leptoporus decaryi* Pat., mainly on account of the microscopic features. The former species was described from Nepal (Ryvarden, 1977; Hjortstam & Ryvarden, 1984) and has white, thin, dimidiate to circular, pendent fruitbodies with a small umbo at the attachment point, smooth pilei and soft to fragile, brittle consistency; an amyloid reaction is also present in the tramal hyphae. On account of its monomitic hyphal system and the positive metachromatic reaction in cresyl blue of its clamped generative hyphae, this species is herein transferred to the genus *Postia* Karst.

Postia grata (Berk.) Rajchenberg comb. nov.

Bas.: Polyporus gratus BERK., HOOK. J. Bot. 6: 163, 1854.

L. decaryi was described from Madagascar and was considered a synonym of P. grata by Ryvarden (1983) but, after studying the type collection (PC, sur bois mort à Ankaizniana à 1200–1500 m alt., leg. R. Decary) I have noted the following differences: fruitbodies are circular, ungulate and pendent, not attached by a small umbo but by a narrowing pileus, the pilear surface is velutinate; tramal hyphae exhibit an amyloid – though faded – reaction and the allantoid spores are $4-4.5 \times 1.2 \, \mu m$ (somewhat shorter and broader than in P. grata and P. venata, where spores are $4 \times 0.8-1 \, \mu m$) and are amyloid in Melzer's reagent. Recently, a most disconcerting specimen was found in our herbarium (BAFC 22470, Argentina, Neuquén, Los Lagos, Península Quetrihué, 850 m, ad truncum Nothofagi dombeyi, leg. R. Singer M 665 16. V. 52, obs. (R. S.) "woolly all over, white, with a blue zone, somewhat like Tur. (omuces)

caesius"). It presents a gossypine, dimidiate, horizontal fruitbody with a pileus narrowing toward the base and an areolate upper surface with black borders (incipient veins?) but it is gossypine-velutinate toward the margin, spores and amyloid reactions are like L. decaryi and it certainly seems closely related to that species.

All the taxa mentioned here seem to pertain to the *Postia caesia* (Schrad.: Fr.) Karst. species complex which is characterised by the amyloid reaction of tramal hyphae and spores. *L. decaryi* and BAFC 22470 are the more closely related to it; *P. venata* and *P. grata* differ in macromorphological features and in the lack of an amyloid reaction in the spores. In any case, all three taxa present a very peculiar geographic distribution suggesting speciation from a common ancestor after Gondwanian disruption, viz. allopatric speciation

Although morphologically differentiated and endemic, $P.\ venata$ could be included in the group of Gondwanic (Paleoaustral) species.

C) Paleoaustral, gondwanic species

Macrohyporia dictyopora (CKE.) Johans. & Ryv. and Postia pelliculosa (Berk.) Rajch.

M. dictyopora has been recorded from Argentina, Australia, Reunion Is. (David & Rajchenberg, unpublished) and Malawi (Fig. 2). Preliminary observations of exsiccata from all the three regions have shown some variability in spore size, but a statistical analysis should be undertaken to evaluate whether this implies taxonomic differences.

 $Postia\ pelliculosa$ has also been recorded from Tasmania and Rwanda.



Fig. 2 – Distributional area of Macrohyporia dictyopora (CKE.) Johans. & Ryv.

Postia dissecta (Lév.) Rajch. (Fig. 1)

Recorded from Chile, Argentina, Australia, New Zealand and Nepal. Ryvarden (1981) has already reported the similarities with the north-temperate *Postia floriformis* (Quél.) Jul. which remains white upon drying.

Polyporus exiguis Col. is here considered a synonym of this species as exsiccata at BAFC have fruitbodies with the typical features of the species – small, white, brittle and pendent fruitbodies – which intergrade with other typical fruitbodies of $P.\ dissecta$ – flabelliform, horny and chestnut. In any case, both species are very closely related, differing mostly on macromorphological features.

D) Paleoaustral, subantarctic species

Junghuhnia collabens (Fr.) Ryv. var. meridionalis Rajch.

This subantarctic variety exhibits ellipsoid-cylindric spores, angiospermic substrate, smaller pore size and lighter hymenial colour (RAJCHENBERG, 1987) which suggest a probable independent rank at the species level.

Piptoporus portentosus (Berk.) G. H. Cunn.

This species exhibits divergent morphological elements in the genus such as the subglobose spores with slightly thickened walls, the clampless generative hyphae and the much branched binding hyphae which totally dissolve in 5% KOH (a character only partially present in the north temperate species of the genus). As suggested by CORNER (1984) its affinities may be with *Buglossoporus* KOTL. & POUZ. but this statement requires further experimental data. Fruitbodies of this species are always found on live or dead standing trunks, 5–15 m above the ground (CUNNINGHAM, 1965) or higher on *Nothofagus* in Argentine forests.

Polyporus maculatissimus Lloyd

Though still included in *Polyporus* Fr., and currently related to the north temperate *Polyporus squamosus* Fr., this taxon seems totally unrelated to that genus. Preliminary data have confirmed this species to be associated with a brown rot, it has binucleate spores, bipolar sexuality, astatocoenocytic nuclear behavior and much branched generative hyphae with irregularly thickened walls (Rajchenberg, unpublished). Its proper generic position is still under consideration.

Postia campyla (Berk.) Rajch. and P. cretacea (Lloyd) Rajch.

These two related species have a monomitic hyphal system with some generative hyphae with thickened walls and thus appearing like skeletals and mainly so in the dissepiments. The hyphae do not exhibit a metachromatic reaction in cresyl blue and the spores are pip-shaped to subglobose with slightly thickened walls, thus differing in these respects from other species of the genus (cf. David, 1980, sub *Spongiporus* Murr.). Both species are found on dead fallen trunks but also on living standing trees, *P. campyla* at not more than 1 m and *P. cretacea* up to 5 m from the ground.

E) Bipolar species

Phellinus inermis (Ell. & Everh.) G. H. Cunn.

In a previous paper (Raichenberg, 1987) I have pointed out the differences between the north temperate specimens (USA) and those from southern Chile and New Zealand. Parmasto & al. (1980) have suggested that the south temperate specimen belong to a different taxon and the differences and distributional areas would suggest so. In this case we should include this taxon among the subantarctic species, with a "sister" species (very similar morphologically) in the north temperate regions. Nevertheless, we still prefer to leave this taxon under this epithet until more reliable studies can be carried out.

Polyporus melanopus FR.

This temperate species has been described as $P.\ dictyopus\ Mont.$ by Wright & Deschamps (1972, 1975). It has also been recorded from Vietnam (Parmasto, 1986).

Antrodia stratosa (Wright & Desch.) Rajch.

This species is very close to another south temperate taxon, viz. Poria subcrassa Rodw. & Clel., which is found in Australia and Tasmania, and to the north temperate Antrodia sordida Ryv. & Gilbn. (= Poria oleagina Overh.). All three taxa are resupinate, perennial, with a dimitic hyphal system with irregularly thickwalled clamped generative hyphae and skeletal hyphae, small, cylindric-ellipsoid to slightly allantoid spores, and there is an oily substance in the fruitbodies that fill the microscopical preparations. Poria subcrassa is different on account of its waxy fruitbodies and some of its skeletal hyphae being filled with a black pigment. Antrodia stratosa has a corky fruitbody, strata are differently coloured (from cream-white to dark chestnut), and it grows on fallen trunks of Nothofagus dombeyi. Antrodia sordida has more slender, typically cylindric spores and grows on gymnosperms.

Fibroporia gossypia (Speg.) Parm.

Among the bipolar species, this is the only one that has not been so far recorded from subantarctic regions other than southern Chile and Argentina.

Fibroporia vaillantii (DC: FR.) PARM.

Cunningham's (1965) description of the species does not fit the current concept of this taxon, and specimens at PDD filed under this name represent another taxon. Anyway, a specimen was found (PDD 19213, New Zealand, Auckland, Hamilton, leg. G. Cooper 30. III. 60, sub *Poria subcrassa* Rodw. & Clel.) which represents this species, differing in the presence of enlarged basidioles (22–26 \times 8–9 μm , cystidia?) among the current, smaller ones (14–18 \times 5–7 μm) which perhaps suggest a different, but related, taxon.

Fistulina hepatica Schaef.: Fr. varieties

According to the literature no fundamental distinction, other than macromorphological, can be established between the South American varieties and the typical north temperate one, in spite of Singer's (1969) opinion and Reid's (1963) enumeration of differences. Similarly, the Australian *Fistulina spiculifera* (Cke.) Reid also needs a critical analysis with more material before a clear distinction can be made between all these species.

Discussion

In spite of our fairly good knowledge of the polyporaceous mycota in the southern tip of South America (= Subantarctic biogeographical province, see Cabrera & Willink, 1973) many unsolved problems persist:

- A) Many species, mostly listed by Mujica & Vergara (1945) and Mujica & Oherens (1967) and reported for Chile have not yet been confirmed and thus, the present floristic sketch only include collections personally studied.
- B) Many species, including a few new ones (cf. Rajchenberg, 1987) were found only after repeated trips to the area and others are only known from very few or single collections. This fact suggests the peculiar and/or specific ecological requirements of many elements of these mycota and do not exclude the possibility that more taxa may be found in the future. Furthermore, the western slope of the Cordillera, more humid, and in the northern area (south in the Maulin District and north in the Valdivian District; see Cabrera & Willink, 1973) including neotropical vascular elements, has not yet been studied systematically. It is logical to assume that a more

specific diversity will be found in that area. A clue to this reasoning is the fact that some taxa, viz. the pantropical species reported here and *Phellinus inermis*, were so far found only in Chile, and that others, like *Postia venata* were found only in the westernmost, more humid areas on the Argentine side.

C) There remain many unsolved taxonomical problems, as is shown by the above commentaries. In some cases, like *Postia venata*, *Phellinus inermis* and *Antrodia stratosa*, the question remains whether their mycogeographical disposition is correct or not.

Provided that: — "on morphology stands taxonomy and on taxonomic monographs stands biogeography" (CORNER, 1963, in PIROZYNSKI, 1983); — that a phylogenetic scheme of the family is not yet accomplished; — and that many taxa and/or names are based on slight morphological differences still not (experimentally) evaluated, a biogeographical analysis is quite restricted. Nevertheless, some general remarks and/or conclusions may be pointed out.

The number of polypores in this region is relatively low, with only 37 accepted species. This is in accordance with the low specific number of other organisms (animals and vascular plants) as has been pointed out by Darlington (1965) who postulated the particular climatic conditions and the geographic narrowness to be the determining factors. Thirteen of these species (35%) produce a brown rot in wood. This percentage is relatively high when we compare it with other mycota where those values vary between 2% and 24% (cf. Gilbertson & Ryvarden, 1986). These data are not fully comparable, however, since the areas presented by Gilbertson & RYVARDEN are phytogeographically not homogeneous. When we take into consideration the USA and Canada Phytogeographical regions and we calculate the percentage of brown wood-rotting polypores in each region (Gilbertson & Ryvarden, 1986), higher values are reached, viz. 30.6% for the Pacific Coast Forest, 32% for the Rocky Mountain Forest and 29% for the Northern Hardwoods Forest. Nevertheless, in these regions, all or almost all the brown woodrotting polypores attack gymnosperms, which is not the case in the South Andean region (see below). In any case, the values here presented were calculated on the basis of the characteristic species of each region presented by the authors and not on the sum total. Eleven of the 13 brown wood-rotting species are concentrated in the groups with paleoaustral and bipolar patterns of distribution where they represent 69% (11 of 16 species) of the species with such a pattern. This value rises to 78% when only the paleoaustral species are taken into consideration. This seems to suggest a correlation between these taxa's probable old origin and the accepted fact that brown wood-rotting Hymenomycetes are primitive groups (Nobles, 1958; Gilbertson & Ryvarden, 1986).

There exists in this region a lesser affinity between the gymnosperm host and the brown wood-rotting species than that pointed out by Gilbertson & Ryvarden (1986) for the north temperate mycota. Postia venata and its related collection BAFC 22470 grow on angiosperms, whereas the Postia caesia complex of species grow mainly on gymnosperms. The same happens between Antrodia stratosa, occurring on N. dombeui, and its north temperate counterpart A. sordida which grows on gymnosperms. Other examples are: Fibroporia gossupia, found on Nothofagus in this area but only on gymnosperms in the northern hemisphere; and Postia dissecta, found on angio- and gymnosperms in southern South America whereas its north temperate counterpart, viz. Postia floriformis, is principally found on gymnosperms. Among the white wood-rotting species, Junghuhnia collabers var. meridionalis has angiospermous hosts, whereas the north temperate typical variety has always been found on gymnosperms. The relatively small number of gymnosperm taxa in this area may have "forced" the shifting from one type of host to another with time. Perhaps these data indicate a speciation process.

Another astonishing fact is the small amount or even lack of intraspecific morphological variation in most of the paleoaustral species. On this basis, and on the basis of their particular distribution, we may extend the origin of the gondwanic species to at least about 125 million years when, in the Middle Cretaceous, Africa and (later) India were detached from Gondwanaland. For the subantarctic species we should assume their existence (with their present morphology!) for at least about 65 M. y., when New Zealand separated during the Late Cretaceous. The subantarctic species absent in New Zealand can be assumed to be at least about 55 M. v. old, when Australia and East Antarctica were separated in the Early Eocene. This high morphological conservatism (stasigenesis), has been already pointed out for other groups of fungi, viz. Lycoperdon (Gasteromycetes: Demoulin, 1973), hypogeous Ascomycetes (Trappe, 1977) and also for some polypores (Parmasto, 1981). The present study suggests older ages for the species here involved. This is supported by the known old fossil records in this family (Tiffney & BARGHOORN, 1974) and by other mycogeographical studies in the southern hemisphere, notably those of Gamundi (1977) for Geoglossaceae and Horak (1983) for Agaricales.

Concerning the bipolar species, the present mycota of the Higher Andes remain to be studied so as to evaluate that region as an effective route through the tropics. Nevertheless, the Andes are relatively young and all the bipolar species (excepting *Fibroporia gossypia*) are also present in Australia and/or New Zealand, thus suggesting an earlier origin.

For some endemic species, viz. Bondarzewia guaitecasensis and

Grifola sordulenta, an older origin than that suggested by their present distribution may be assumed, given the existence of a "sister" species, a vicarious counterpart, either in the western Pacific region or in the northern hemisphere.

The morphological conservatism requires more studies before a proper evaluation of the concept can be made. In spite of the morphological features being the initial basis to key out different species, we must not equate them with biological separation. Recent works on biological species concepts and species delimitation give many examples of biological speciation without a correlative morphological differentiation (e. g., Anderson & Ullrich, 1979; Boidin, 1977, 1986; Bresinsky & al., 1987). Major experimental studies on intercompatibility tests between a number of similar or identical disjunct species remain to be undertaken (but see Boidin & al., 1980: BOIDIN & LANQUETIN, 1984; HALLENBERG, 1984). DAVID & DEQUATRE (1984, 1985). DAVID & RAJCHENBERG (1985) and BOIDIN (1977, 1986) have shown the existence of cryptic species in the Polyporaceae and Corticiaceae, which are discernible only by their sexuality and/or nuclear behavioral features. These studies have stressed the necessity to typify these biological species since they constitute marks of differentiation and evolution.

There is lack of information concerning the differentiation that the species here studied may have followed after the disruption of Gondwanaland. One probable exception is *Postia venata* and its related species, *Leptoporus decaryi* and *Postia grata*, which may be an example of allopatric speciation. Spore size differences verified in exsiccata of *Macrohyporia dictyopora* from different geographic areas may indicate ongoing speciation. If shown to be an uniparental reproductive taxon, the selection species concept (PARMASTO, 1985) could be applied to this species.

HJORTSTAM & RYVARDEN (1985) pointed out that the occurrence of different endemic poroid species of the family Hymenochaetaceae Donk (genera *Phellinus* Quél. and *Inonotus* Karst.) in southern South America and New Zealand could be an indication that the family evolved rather recently, after the break up of Gondwanaland. Nevertheless, the presence of *Phellinus inermis* in both areas contradicts, at least in part, this statement. *Phellinus* seems to be a genus with a high evolutionary rate, reflected in its large number of species, wide distribution, and requirement by many of its species of specific substrates, in spite of morphological similarities (cf. *Phellinus igniarius* (Fr.) Quél. complex of species; Niemela, 1975).

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