A contribution to the ITS-LSU phylogeny of the genus *Leucopaxillus* (/tricholomatoid clade, *Agaricales*), with three new genera and notes on *Porpoloma*

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Phylogenetic analyses based on ITS-LSU rDNA sequences dataset indicate that *Leucopaxillus*, as currently defined, is a highly polyphyletic genus. The new genera *Giacomia*, *Notholepista* and *Pseudoclitopilus* are introduced to accommodate *Leucopaxillus mirabilis*, *L. subzonalis* and *L. rhodoleucus*, respectively. *Leucopaxillus* subg. *Aspropaxillus* also seems to represent an independent evolutionary line in the /tricholomatoid clade, for which we suggest resurrecting the genus *Aspropaxillus*. Furthermore, the morphologically allied genus *Porpoloma* is also polyphyletic.

**Key words** – *Agaricomycetes* – new combinations – ITS-LSU sequences – taxonomy

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**Introduction**

The basidiomycete genus *Leucopaxillus* Boursier, typified by *L. paradoxus* (Costantin & L.M. Dufour) Boursier and traditionally placed, together with *Melanoleuca* Pat., in the subtribus *Leucopaxillineae* Singer (tribus *Leucopaxillae* Singer, family *Tricholomataceae* R. Heim ex Pouzar of the *Agaricales* Underw., Singer 1986), consists of cosmopolitan species with usually terrestrial basidiomata. It is characterized by the following: clitocyboid to tricholomatoid habit; convex to slightly depressed pilei; adnate to decurrent lamellae easily separable from the pileus context; veils usually absent; white to pale yellowish spore print; cutis to trichoderm pileipellis; hyaline, smooth to verruculose spores, smooth spores weakly amyloid (subg. *Aspropaxillus* (Kühner & Maire) Bon = sect. *Aspropaxillus*), verrucose spores with strongly amyloid ornamentations and without a well differentiated plage (subg. *Leucopaxillus* = sect. *Leucopaxillus*); cheilocystidia absent or hyploid (not well developed); presence of clamp connections (Singer & Smith 1943, Pegler & Young 1973, Singer 1986, Bon 1991, Gulden 1992, Noordeloos 1984, 1995, Consiglio & Contu 2000, Horak 2005, Christensen 2008, Watling & Turnbull 2008, Vizzini 2009). Regarding its trophic status, Bryan & Zak (1961) reported on a ectomycorrhizal synthesis between *Leucopaxillus albissimus* var. *piceinus* and *Pinus* sp. but with a poorly developed mycocola and Hartig net. This taxon probably represents a *Tricholoma* sp. (Matheny et al. 2006). Stable isotopes (Kohzu et al. 1999, Hart et al. 2006) and synthesis experiments (Yamada et al. 2001) suggest that *Leucopaxillus* species are non-ectomycorrhizal but saprotrophic in forest and grassland (Tedersoo et al. 2010). Species of
Leucopaxillus subg. Aspropaxillus (L. candidus (Bres.) Singer, L. giganteus (Sowerby) Singer, L. lepistoides (Maire Singer) may produce very large fairy rings; Kaiser (1998) studied the relationships between L. giganteus, microfungi and herbaceous plants. Leucopaxillus species turned out to be easy to cultivate in vitro: mycelia of some species are characterized by forming chlamydoconidia (rhexolytically seceding conidia) in pure culture (Pantidou et al. 1983, Buchalo 1988, Ingaramo 2002).

Melanoleuca, a morphologically allied genus, differs from Leucopaxillus mainly in lacking clamp connections, by spores with a well differentiated plage area, and usually having well-developed hymenial thick-walled cystidia (Singer 1986, Bon 1978, 1991, Boekhout 1999). But, according to recent molecular analyses (Moncalvo et al. 2000, 2002, Matheny et al. 2006, Vizzini et al. 2011a), Melanoleuca and Leucopaxillus are not phylogenetically closely related: Melanoleuca species cluster within the Pluteoid clade (Pluteaceae Kotl. & Pouzar partim + Amanitaceae R. Heim ex Pouzar + Lymnoperdaceae G.A. Escobar + Macrocystidiaceae Kühner + Pleurotaceae Kühner) (Moncalvo et al. 2002, Vizzini et al. 2006, Matheny et al. 2006, Vizzini et al. 2011a) sister to a monophyletic group formed by Pluteus Fr. species and Volvopluteus Vizzini, Contu & Justo (Justo et al. 2011), whereas Leucopaxillus belongs to the /tricholomatoid clade, close to Porpoloma sp. + Tricholoma (Fr.) Staude (Moncalvo et al. 2002) or sister to Tricholoma (Matheny et al. 2006). Leucopaxillus, together with Clitocybe (Fr.) Staude, Collybia (Fr.) Staude, Lepista (Fr.) W.G. Sm., and Tricholoma (Fr.) Staude, forms the family Tricholomataceae s.s. (Moncalvo et al. 2002, Matheny et al. 2006). Therefore, morphological similarities between Leucopaxillus and Melanoleuca are due to evolutionary convergence.

Porpoloma Singer, typified by P. sejunctum Singer, differs in having a clear tricholomatoid habit, non-decurrent lamellae that are not separable from the pileux context, and always smooth amyloid spores (Raithelhuber 1980, Singer 1986, Bon 1991). The unique Porpoloma sequence (Porpoloma sp. AF261395) used in a phylogenetic analysis (Moncalvo et al. 2002), clustered sister to Leucopaxillus, forming with Tricholoma and Leucopaxillus the /tricholomatoid clade.

The genus Leucopaxillus is not yet well covered by DNA studies and only a few species have been sequenced. The present study, based on a wider ITS-LSU sequence dataset, sequences retrieved both from public databases (GenBank, www.ncbi.nlm.nih.gov/genbank/ and UNITE, unite.ut.ee/) and from newly sequenced collections, is the first to examine this genus extensively. The aim was to check whether Leucopaxillus is monophyletic as traditionally circumscribed.

Methods

Morphology

All Leucopaxillus collections were identified or redetermined using specific monographs (Singer & Smith 1943, Bon 1991, Consiglio & Contu 2000). Watling & Turnbull (1983), Horak (2005), and Christensen (2008) were also consulted. When not identifiable, collections are cited in Table 1 and Figs. 1–2 as Leucopaxillus sp. Author citations follow the Index Fungorum-Authors of Fungal Names (www.indexfungorum.org/authorsoffungalname s.htm) and the names of new taxa are deposited in MycoBank (www.mycobank.org/Default-Page.aspx). Herbarium acronyms follow Thiers (2011) except for “GC” that refers to the personal herbarium of Giovanni Consiglio.

DNA extraction, PCR amplification, and DNA sequencing

Genomic DNA was isolated from 1 mg of herbarium specimens (Table 1) by using the DNeasy Plant Mini Kit (Qiagen, Milan, Italy) following the manufacturer’s instructions. Universal primers ITS1F/ITS4 were used for the ITS region amplification (White et al. 1990, Gardes & Bruns 1993) and primers LR0R/LR7 (Vilgalys & Hester 1990, Vilgalys lab, unpublished, www.botany.duke.edu/fungi/mycol ab) for the LSU rDNA amplification. Amplification reactions were performed in PE9700 thermal cycler (Perkin-Elmer, Applied Biosystems) in a 25 µl reaction mixture using the following final concentrations or total amounts: 5 ng DNA, 1× PCR buffer (20 mM
Table 1 Leucopaxillus and Porpoloma new sequenced collection used in this study for the molecular analyses.

<table>
<thead>
<tr>
<th>Species</th>
<th>GenBank acc. Numbers</th>
<th>Source, country</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leucopaxillus alboalutaceus (F.H. Møller) F.H. Møller</td>
<td>JQ639147 —</td>
<td>GC 97076, Italy</td>
</tr>
<tr>
<td>Leucopaxillus cerealis (Lasch) Singer</td>
<td>JQ639148 JQ639149</td>
<td>TO AVL20112, Italy</td>
</tr>
<tr>
<td>Leucopaxillus giganteus (Sowerby) Singer</td>
<td>JQ639150 —</td>
<td>GC 94133, Italy</td>
</tr>
<tr>
<td>Leucopaxillus giganteus</td>
<td>JQ639151 JQ639152</td>
<td>GC 98046, Italy</td>
</tr>
<tr>
<td>Leucopaxillus mirabilis (Bres.) Konrad &amp; Maubl.</td>
<td>JQ639153 JQ639154</td>
<td>GC 94141, Italy</td>
</tr>
<tr>
<td>Leucopaxillus mirabilis var. nigrescens Fontenla &amp; Para</td>
<td>JQ639155 —</td>
<td>GC 07186, Italy</td>
</tr>
<tr>
<td>Leucopaxillus monticola (Singer &amp; A.H. Sm.) Bon</td>
<td>JQ639156 —</td>
<td>TO AVL20111, France</td>
</tr>
<tr>
<td>Leucopaxillus paradoxus (Costantin &amp; L.M. Dufour) Boursier</td>
<td>JQ639157 JQ639158</td>
<td>TO AVL20113, Italy</td>
</tr>
<tr>
<td>Leucopaxillus sp. 1</td>
<td>JQ639159 —</td>
<td>TO AVL20114, Italy</td>
</tr>
<tr>
<td>Leucopaxillus sp. 2</td>
<td>JQ639160 JQ639161</td>
<td>TO AVL20115, Italy</td>
</tr>
<tr>
<td>Porpoloma macrocephalum (Schulzer) Bon</td>
<td>JQ639162 JQ639163</td>
<td>GC 96016, Italy</td>
</tr>
<tr>
<td>Porpoloma metapodium (Fr.) Singer</td>
<td>JQ639164 —</td>
<td>TO AVL20116, France</td>
</tr>
</tbody>
</table>

Tris/HCl pH 8.4, 50 mM KCl), 1 µM of each primer, 2.5 mM MgCl₂, 0.25 mM of each dNTP, 0.5 unit of Taq polymerase (Promega). The PCR program was as follows: 3 min at 95°C for 1 cycle; 30 s at 94°C, 45 s at 50°C, 2 min at 72°C for 35 cycles, 10 min at 72°C for 1 cycle. PCR products were resolved on a 1.0% agarose gel and visualized by staining with ethidium bromide. PCR products were purified and sequenced by DiNAMYCODE srl (Turin, Italy). Sequence assembly and editing were performed using Geneious v5.3 (Drummond et al. 2010). The sequences are deposited in GenBank under the accession numbers given in Table 1 and Figs. 1–2.

Sequence alignment and phylogenetic analysis

Sequences included in the phylogenetic analyses were either generated in this study (Table 1) or retrieved from GenBank and UNITE databases, according to recent studies on Agaricales (Moncalvo et al. 2002, Matheny et al. 2006, Vizzini 2011b).

Two separate analyses of ITS and LSU sequences were carried out. Alignments were generated using MAFFT v6.814b (Katoh et al. 2002) with default conditions for gap openings and gap extension penalties. Alignments were slightly edited using MEGA 5.0 (Tamura et al. 2011). Molecular-phylogenetic analyses were performed using the Maximum likelihood (ML) and Bayesian inference (BI) approaches. ML estimation was performed through RAxML (Stamatakis 2006) with 1000 bootstrap replicates (Felsenstein 1985) using the GTRGAMMA algorithm to perform a tree inference and search for a good topology. Support values from bootstrapping runs (MLB) were mapped on the globally best tree using the -f a option of RAxML and -x 12345 as a random seed to invoke the novel rapid bootstrapping algorithm. BI of phylogeny using Monte Carlo Markov Chains (MCMC) was carried out with MrBayes (Huelsenbeck & Ronquist 2001). Four incrementally heated simultaneous MCMC were run over 10 000 000 generations, under GTR+G model assumption. Trees were sampled every 1000 generations resulting in an overall sampling of 10 001 trees. The “burn-in” value was evaluated using Tracer (Rambaut & Drummond 2007). The first 20% of trees was discarded as “burn-in”. For the remaining trees, a majority rule consensus tree showing all compatible partitions was computed to obtain estimates for Bayesian Posterior Probabilities (BPP). Branch lengths were estimated as mean values over the sampled trees.

Xeromphalina campanella (Hygrophoroid clade, GenBank accessions GU320006 and GU320009) was used in both datasets analysis as outgroup taxon. Only MLB and BPP values over 50% and 0.75, respectively, are reported in the resulting trees (Figs. 1–2). Pairwise % identity values of ITS sequences
Fig. 1 – Maximum likelihood phylogram obtained from the ITS sequence dataset of the /tricholomatoid clade. *Xeromphalina campanella* (Hygrophoroid clade) was used as outgroup. Support values (MLB, in bold and BPP) are given above branches. *Leucopaxillus* and *Porpoloma* sequences are in bold. * refers to samples sequenced in this work and reported in Table 1. The bar indicates number of substitutions per site.

**Results**

Maximum likelihood and Bayesian inferences were performed on a total of 81 sequences of the ITS dataset, including 69 sequences available from GenBank and UNITE public databases. Final alignment length was 916 bp. The LSU dataset consists of 60 sequences, including 54 available from GenBank and UNITE databases. Final alignment length was 1614 bp. Topology of Maximum likelihood and Bayesian phylogenies is congruent.

In the ITS phylogram (Fig. 1) *Leucopaxillus paradoxus* (the type species of the genus) clusters together with *L. monticola*, *L. cerealis*, *L. alboalutaceus*, *Leucopaxillus* sp. 1 and sp. 2 and “Tricholomataceae aff. Porpoloma” forming a monophyletic genus *Leucopaxillus* s.s. The genus is sister to *Porpoloma* sp. EF421106 (DUKE-PR3995). *L. giganteus*, *L. rhodoleucus*, *L. subzonalis*, *L. mirabilis* and *L. mirabilis* var. *nigrescens* fall outside *Leucopaxillus* s.s. *Porpoloma spinulosum*, *P. metapodium*, *Porpoloma* sp. EF421106, “Tricholomataceae aff. Porpoloma” and *P. macrocephalum* do not form a coherent group. The four *Leucopaxillus* tricolor
sequences from GenBank clearly do not represent a Leucopaxillus but a taxon very close to Lepista nebularis (pairwise % identity value 99.4). The two Porpoloma macrocephalum sequences and the Leucopaxillus nauseodulcis sequence showed a pairwise % identity value of 99.0, and are conspecific.

In the LSU phylogram (Fig. 2) L. paradoxus, L. cerealis, L. albissimus (Peck) Singer (= L. cerealis (Lasch) Singer, fide Singer 1986), L. gentianaeus and Leucopaxillus sp. 2 form a monophyletic group (Leucopaxillus s.s.). Leucopaxillus s.s., together with Porpoloma AF261395 (JLPR3395), is sister to Tricholoma. L. mirabilis and L. giganteus are independent from Leucopaxillus. Porpoloma AF261395 (JLPR3395) is not related to Porpoloma macrocephalum.

Discussion

Our molecular analyses clearly show (Figs. 1–2) that Leucopaxillus, as currently defined, is polyphyletic. Species traditionally ascribed to this genus (Singer 1986, Bon 1991, Consiglio & Contu 2000, Christensen 2008) do not form a monophyletic assemblage and are distributed over the /tricholomatoid clade. According to the LSU analysis (Fig. 2) Leucopaxillus s.s. and Porpoloma AF261395 (JLPR3395) are sister to Tricholoma, in agreement with Moncalvo et al. (2002) and with the multilocus phylogenetic overview by Matheny et al. (2006). The Leucopaxillus/Tricholoma connections were already highlighted, even if only on morphological bases, by Kühner (1980). So it is evident that the “leucopaxillloid” facies (basidiomata with a clitocyboid to tricholomatoid habit, clamp connections and spores with amyloid ornamentations) have arisen many times in more or less independent lines of evolution. Within Leucopaxillus s.s., Leucopaxillus sp. 1 and Leucopaxillus sp. 2 are collections representative of a yet undescribed taxon characterized by clampless basidiomata and mainly bisporic basidia. Leucopaxillus giganteus, L. mirabilis, L. subzonalis and L. rhodoleucus are not phylogenetically connected with Leucopaxillus s.s and are unrelated to each other (Figs. 1–2). They represent new genera in the /tricholomatoid clade.

Resurrecting the genus Aspropaxillus

Leucopaxillus giganteus is the type species of Aspropaxillus Kühner & Maire. Kühner & Maire (1934) established the genus to accommodate the smooth spored species, with a clitocyboid habitus and a perisporium characterized by a weak amyloid reaction. Singer & Smith (1943), in their monographic treatment of Leucopaxillus, maintained this separation but only at a sectional level. Bigelow (1982) considered it as a subsection of section Clitocybe within his heterogeneous definition of Clitocybe (Fr.) Staude. Finally, Bon (1990, 1991) accepted it as a distinct subgenus of Leucopaxillus. According to both ITS and LSU analyses (Figs. 1–2), we suggest using the genus Aspropaxillus for L. giganteus and allied species. Therefore, we propose the following new combinations:

Type: Aspropaxillus giganteus (Sowerby) Kühner & Maire

Aspropaxillus septentrionalis (Singer & A.H. Sm.) Vizzini, comb. nov.
Mycobank MB 564422

Aspropaxillus sainii (Singer) Vizzini, comb. nov.
Mycobank MB 564424

Aspropaxillus jageshwariensis (Dhan., J.C. Bhatt & S.K. Pant) Vizzini, comb. nov.
Mycobank MB 564426

Both A. sainii and A. jageshwariensis were described from India and are apparently known only from that region. We did not have

83
the chance to study authentic material of them but, judging by the protologues (op. cit.) they are well characterized and deserve specific rank on their own right.

On the taxonomic placement of *Tricholoma mirabile* Bres.: a new genus.

*Leucopaxillus mirabilis* is a striking European taxon easy to recognize in the field due to a dark brown pileus and stipe, a hairy pileus margin, a wrinkled stipe apex, an aranean partial veil forming a thin ring on stipe apex, abundant cheilocystidia (Moser 1963, Kühner 1977, Bon 1978, 1987a, 1991, Consiglio & Contu 2000), and heterogeneous spores variable in size, form and degree of ornamentation, which ranged from coarsely verrucose to smooth (Moser 1963). The type of ornament is composed of isolated, hemispherical verrucae, similar to that of *Melanoleuca cognata* (Fr.) Konrad & Maubl. (Pegler & Young 1973). It is not easily culturable in vitro (Moser 1963). Due to its peculiar features, Bon (1991) classified the species in the monospecific subsection *Mirabilini* (Bon) Bon (stipe with an arachnoid ring-like velum) of sect. *Mirabiles* Bon (presence of chelocystidia) of *Leucopaxillus*. *L. mirabilis* var. *nigrescens* differs only in having a darker pileus (Bresadola 1927, Bon 1991). The two *L. mirabilis* sequences and the one of *L. mirabilis* var. *nigrescens* are clearly identical (pairwise % identity value = 99.9). This variety is here reduced to a form. The species is not closely related either to *Leucopaxillus* s.s. or to other taxa of the *tricholomatoid clade*; consequently we accept this lineage to represent a distinct genus and establish the new genus *Giacomia* for accommodating *L. mirabilis*.

**Giacomia** Vizzini & Contu, gen. nov.
MycoBank MB 564428

Etymology – named in honour of Abbé Giacomo Bresadola, eminent Italian mycologist, and father of the species name.

A *Leucopaxillo differt basidioma velo araneoso ornato et in stuctura molecularis (ITS-spatius internis transcriptis et LSU DNA)*. Basidiomata agaricoid (with distinct pileus, lamellae and stipe), partial veil present as an arachnoid cortina, basidiospores with amyloid warts, chelocystidia often abundant, filamentous, pileal surface a cutis of repent to interwoven, cylindrical hyphae, clamp-connections present, no sarcodimitic texture in any part of the basidioma. On the ground, never on wood.

Type: *Tricholoma mirabile* Bres.

**Giacomia mirabilis** (Bres.) Vizzini & Contu, comb. nov.
MycoBank MB 564429

≡ *Tricholoma mirabile* Bres., Fungi Tridintini I: 16, 1881 (basionym).


≡ *Melanoleuca mirabilis* (Bres.) Singer, Lloydia 5: 121, 1942.

**Giacomia mirabilis** f. *nigrescens* (Bres.) Vizzini & Contu, comb. nov. et stat. nov.
MycoBank MB 564430

≡ *Tricholoma mirabile* Bres. var. *nigrescens* Bres., Iconographia Mycologica II: 92, 1927 (basionym).


**Notholepista** Vizzini & Contu, gen. nov.
MycoBank MB 564431

Etymology – refers to the habit being reminiscent of *Lepista* *gilva*.

A *Lepista differt sporis verrucis amyloides obtectis. A Leucopaxillo differt habitu clitocyboideo vel lepistoideo, Lepista
Fig. 2 – Maximum likelihood phylogram obtained from the LSU sequence dataset of the /tricholomatoid clade. *Xeromphalina campanella* was used as outgroup. Support values (MLB, in bold and BPP) are given above branches. *Leucopaxillus* and *Porpoloma* sequences are in bold. *#* refers to samples sequenced in this work and reported in Table 1. The bar indicates number of substitutions per site.

gilva in mente revocante et in structura molecularis (ITS-spatii internis transcrptis DNA).

Basidiomata agaricoid (with distinct pileus, lamellae and stipe), resembling those of *Lepista gilva* (Pers.) Pat., veils absent, basidiospores with amyloid warts, cystidia and pseudocystidia absent, pileal surface a cutis of repent to interwoven, cylindrical hyphae, clamp-connections present, no sarcodimitic texture in any part of the basidioma. On the ground, never on wood.

Type: *Agaricus (Clitocybe) subzonalis* Peck.

**Notholepista subzonalis** (Peck) Vizzini & Contu, **comb. nov.**

**Pseudoclitopilus** Vizzini & Contu, *gen. nov.*

MycoBank MB 564433

**Etymology** – refers to the habit being reminiscent of *Clitopilus prunulus*.


Basidiomata agaricoid (with distinct pileus, lamellae and stipe), resembling a stout and fleshy white *Clitopilus*, veils absent, basidiospores with amyloid warts, cystidia and pseudocystidia absent, pileal surface a cutis of repent to interwoven, cylindrical hyphae, clamps present, no saccodimitic texture in any part of the basidioma. On the ground, never on wood.

Type: *Clitocybe rhodoleuca* Sacc.

**Pseudoclitopilus rhodoleucus** (Sacc.) Vizzini & Contu, *comb. nov.*

MycoBank MB 564434


**Pseudoclitopilus salmonifolius** (M.M. Moser & Lamoure) Vizzini & Contu, *comb. nov.*

MycoBank MB 564435


**The status of Porpoloma Singer**

The genus *Porpoloma* seems also polyphyletic (Fig. 1). Singer (1952) erected the genus for three Argentinian species of *Nothofagus* forests, then combined the European *Tricholoma spinulosum* Kühner & Romagn, *Hygrophorus metapodius* (Fr.) Fr. and *Agaricus elytroides* Scop. in *Porpoloma* in 1962 and 1973, respectively. According to our analysis, the closely related *Porpoloma macrocephalum* and *P. spinulosum* are very distant from the other sequenced taxa of *Porpoloma*. According to the ITS phylogeny (Fig. 1) *P. metapodium* is sister to *Tricholoma*; this species was treated as *Hygrophorus* by Hesler & Smith (1963, as *Hygrophorus sect. Amylohygrocybe*), as *Hygrocybe* by Moser (1967), and as *Tricholoma* by Papetti (1999). Nevertheless, we refrain from erecting new genera until re-examination and sequencing of *P. sejunctum* Singer, the type species of *Porpoloma*, can better determine its characters and phylogenetic affinities.

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