

Molecular phylogeny of *Trametes* and related genera, and description of a new genus *Leiotrametes*

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Abstract A phylogenetic analysis of *Trametes* and related taxa is proposed, based on a wide sampling of temperate and tropical species. Concatenate sequences of ribosomal DNA (ITS1-5.8S-ITS2) and RPB2 gene from mycelia cultures were analyzed by Maximum Likelihood and Bayesian methods, whilst morphological features were documented from the corresponding herbarium vouchers. Congruent results were obtained from analyses of ribosomal LSU sequences downloaded from Genbank. The Bayesian analysis of ITS + RPB2 sequences gave the best resolution for the phylogenetic reconstructions and revealed the existence of three main lineages in the *Trametes*-clade: 1) a monospecific lineage represented by *Artolenzites elegans* 2) a lineage including the genus *Pycnoporus* in its traditional sense and several species usually classified in the genus *Trametes* (*T. cingulata*, *T. lactinea*, *T. ljubarskyi*, *T. menziesii*) & 3) a lineage corresponding to the core genus *Trametes*, including type species of *Trametes*, *Corioloropsis* and *Lenzites*. The presence of a pseudostipe, aspect and structure of the abhymenial

surface, colour change with 5% aqueous solutions of potassium hydroxide and topography of pigments on skeletal hyphae gave relevant morphological support to these clades. When the structure of the hymenial surface, presence of a black line below the tomentum and color of context (except for genus *Pycnoporus*) usually used in traditional polypore-classifications did not reveal any phylogenetic significance. A partial systematic arrangement of the *Trametes* clade is proposed, with the introduction of a new genus: *Leiotrametes* Welti & Courtec. *gen. nov.*. Two new combinations: *Leiotrametes lactinea* (Berk.) Welti & Courtec. *comb. nov.* and *L. menziesii* (Berk.) Welti & Courtec. *comb. nov.* are proposed.

Keywords Basidiomycota · Polyporales · *Artolenzites* · *Corioloropsis* · *Lenzites* · *Pycnoporus* · Morphology · Biogeography

Introduction

Initially, the polyporoid genus *Trametes* Fr. was created by Fries (1835), in his ‘Tribe’ *Polyporei* to accommodate coriaceous species with poroid hymenophore characterized by a context continuously descending into the hymenial trama. In addition other genera were created based on other structures of the hymenophore: lamellate in *Lenzites* Fr., or daedalean in *Daedalea* Fr. for instance. Later, Quélet (1886) refined the systematics of the polypores (Fam. II *Polyporei*) and separated species with regular pores (Trib. II *Polypori*, including stipitate species such as *Caloporus* Quélet. or *Leucoporus* Quélet. and sessile or resupinate species: *Coriolus* Quélet. *Phellinus* Quélet. etc.), from species with alveoloid to daedalean pores (Trib. III *Daedalei*, including *Trametes gibbosa*, *T. suaveolens*, and *Daedalea* Pers., *Hexagona* Poll. etc.). *Lenzites*, with

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lamelloid hymenophore, was extracted from *Polyporei* and placed in the *Agarici* close to *Pleurotus* and allied genera despite of obvious natural affinities with *Daedalei*.

Later other morphological characteristics were considered relevant for defining new genera from the classical *Trametes*. For example, Quélet (1886) considered the presence of a tomentum on the abhymenial surface as a distinctive feature for *Coriolus*.

From this Friesian tradition the type of hymenophore, an easily observable and striking character, was considered the main distinctive feature at the generic level within the polypores. Pilát (*in* Kavina and Pilát 1936) first doubted its importance and considered hymenophoral morphology to be devoid of real systematic value. Thus, the genus *Trametes sensu* Pilát encompasses poroid, daedaleoid as well as lamelloid species and genera such as *Lenzites* or *Daedalea*, (e.g. *T. betulina* (L.: Fr.) Pilát; *T. quercina* (L.: Fr.) Pilát).

On the basis of the context pigmentation, *Corioloopsis* Murrill 1905 (based on *Trametes occidentalis* (Klotzsch) Fr., now *Corioloopsis polyzona*) and *Pycnoporus* P. Karsten 1881 (based on *Trametes cinnabarina* (Jacq. : Fr.) Fr.) were respectively created to distinguish trametoid specimens with brown or cinnabarin red color.

Considering as many genera as available, Patouillard (1900) recognized their affinities in his “série des *Trametes*”, in which he gathered poroid, daedaleoid as well as lamelloid genera. Considering a new character, the mitism of the context, Kotlaba and Pouzar (1957) restricted the genus *Trametes* to species with a trimitic hyphal system, but like Patouillard they gather in a same “*Trametes*-group” all genera with di- or trimitic hyphal system and colorless, smooth and inamyloid spores such as *Cerrena*, *Daedalea*, *Hexagona*, *Pycnoporus*, *Trametes* etc., whatever the aspect of hymenophore. At last the significance of the wood-rotting types (brown-rot *versus* white-rot types) was revealed by Nobles (1958) as a distinguishing feature between genera in the *Polyporaceae*. Thus, the white-rotting abilities become a new feature for the *Trametes*-group, excluding *Daedalea*, which causes a brown rot.

Once these characters were identified, controversies developed in their respective importance for generic delimitation. Corner (1989) weakened the value of rot-type, hymenophore configuration and context- colour, and came back to Kavina and Pilát’s (1936) enlarged *Trametes* concept. Indeed, he gathered all taxa showing trimitic hyphal systems with exception of three genera (*Daedalea*, *Lenzites* and *Trichaptum*) because of the presence of cystidiform ends of the hymenial binding hyphae. In contrast Ryvarden (1991), in a *Trametes*-group inspired from Kotlaba and Pouzar’s (1957) concept, accepted all white-rot genera such as *Corioloopsis* and *Pycnoporus*, with colored hyphal pigments, *Lenzites* with distinct pointed hyphal ends in the cathymenium and hymenial lamellate surface, and 16 others based on narrow

combinations of all the above mentioned characters (Ko and Jung 1999). In addition to the ability to produce a white-rot, all of these genera are characterized by di-trimitic hyphal system, clamped generative hyphae, hyaline, thin-walled, mostly cylindrical, smooth and non amyloid spores with no true hymenial cystidia.

The first molecular analysis on *Trametes* and related genera, by Hibbett and Donoghue (1995), and Ko and Jung (1999), contributed significantly to understand the phylogenetic structure of the family *Polyporaceae*, based on mitochondrial small subunit ribosomal DNA. Trimitism and white-rotting were confirmed as common features for all genera in a *Trametes*-clade within the “core *Polyporaceae* group”, which matched Ryvarden’s arrangement with only a few exceptions such as *Trichaptum*, which is related to the *Hymenochaetaeaceae* (Hibbett and Donoghue 1995; Ko and Jung 1999). An extensive work by Ko (2000) based on mt SSU rDNA and ITS sequences divided the core *Polyporaceae* group into 2 subgroups: the first (“A”) which gathers *Cryptoporus*, *Daedaleopsis*, *Datronia*, *Funalia* (including “*Corioloopsis*” *gallica* and “*Trametella*” *trogii*), *Ganoderma*, *Lentinus*, *Microporus*, *Polyporus* and the second (“B”) which gathers *Corioloopsis* (*C. polyzona* only), *Lenzites*, *Pycnoporus* and *Trametes*. Recently, Rajchenberg (2011) suggested a morphological and cytological support for a *Lenzites*-*Corioloopsis*-*Pycnoporus*-*Trametes* group (‘subgroup B’ of Ko 2000) on the basis of a normal nuclear behavior, tetrapolarity, white rot and trimitic hyphal system, consistent with the phylogenetic results described above. Moreover, heterocytic nuclear behavior with bipolar mating system separates *Funalia* and *Cerrena* from *Trametes* and *Corioloopsis* (David 1967). Although Tomšovský et al. (2006) already recognized a “main *Trametes*-clade” for a small group of tomentose species better matching the genus *Coriolus*, the question whether narrowly related genera in the ‘subgroup A’ (Ko 2000), such as *Corioloopsis*, *Coriolus*, *Lenzites*, *Pycnoporus*, should be recognized as independent monophyletic genera or included in an enlarged genus *Trametes* remains open. A more detailed analysis was required, taking into account more taxa (especially tropical), for defining a robust generic concept in coherence with morphological, chemical and ecological features.

On the basis of previous molecular data and taking into account all the above considerations and partial discrepancies or still questionable points, our study aimed: i) to examine the phylogenetic placement of species belonging to core *Trametes*, and to the related *Corioloopsis*, *Lenzites*, and *Pycnoporus*, with a focus on tropical taxa, and ii) to evaluate the taxonomic significance of the morphological characters traditionally used to discriminate the four genera. For these purposes 31 species including 16 tropical taxa were included in our molecular and morphological study. Phylogenetic analyses were performed using sequence data

from three nuclear ribosomal regions (internal transcribed spacers ITS1 and ITS2 and 5,8 S gene) and the protein-coding gene RPB2. An analysis of 41 NCBI nuc-ribosomal 28 s LSU sequences is also provided.

Materials & methods

Material studied A cluster of 50 dikaryotic isolates was used for DNA analyses: taxa and strains studied along with geographical origin and herbarium number are listed in Table 1. Twenty-nine strains were isolated from fresh basidiomes collected in Europe, French Guiana, and French West Indies (Guadeloupe and Martinique) between 2007 and 2010. They are deposited at the Banque de Ressources Fongiques de Marseille (BRFM) belonging to the Centre International de Ressources Microbiennes - Champignons Filamenteux (CIRM-CF). The source exsiccates were deposited at the herbarium LIP (Lille). Twenty-one additional strains were obtained from the culture collections at CBS (Baarn, NL), MUCL (Louvain-la-Neuve, B), and CIRM-CF (Marseille, F). *Daedaleopsis tricolor*, *Hexagonia nitida*, *H. mimites* and *Trametella trogii* were used as outgroups (Ko and Jung 1999; Tomšovský et al. 2006).

Sampling was enlarged with 6 sequences retrieved from GenBank: *Trametes elegans* JV021237J, *T. aff. junipericola* AY684171, *T. lactinea* GQ982887 and Damm 4703, *T. maxima* AB158315 and *Daedalea microsticta* FJ403209 (Table 1).

In addition, 41 nuc-ribosomal 28 s LSU sequences were downloaded from Genbank and were analyzed separately (Table 2).

Collection description The 29 collections of basidiomes and 2 specimens loaned from MUCL, corresponding to the strains MUCL 38443 *Funalia polyzona* and MUCL 38649 *Trametes socotrana*, were described on the basis of macro- and micro- morphological features. Fresh specimens were photographed then air dried. Microscopic features were observed on a Zeiss Axioscop light microscope. All observed elements and structures were described and hand-drawn from radial sections of exsiccata examined in Melzer's reagent (iodine 0,5 g, potassium iodine 1,5 g, hydrated chloral 20 g, for 22 cm³ of water), 1% Congo red in 10% aqueous ammonium hydroxide and 5% aqueous potassium hydroxide solution (abb. KOH).

DNA extraction, PCR and sequencing Strains were grown on Malt Agar medium (2% malt extract, 2% Bacto-agar DIFCO) at 25 ° C for 1 week. Genomic DNA was isolated from mycelial powder (40–80 mg) as described by Lomascolo et al. (2002). The primers bRPB2-6 F, bRPB2-7.1R (Matheny

2005), and ITS1, ITS4 primers (White et al. 1990) were used for PCR amplification and sequencing reaction. The ITS1-5.8S rRNA gene-ITS2 and RPB2 were amplified from 50 ng genomic DNA in 50 µl PCR reagent containing 1.5 U Expand™ High Fidelity PCR systems (Roche, France), with a protocol adapted from Lomascolo et al. (2002). Annealing temperatures and extension times were respectively 51°C and 1 min for ITS1/ITS4 amplification; 53°C and 1 min for RPB2 amplification. The PCR products were sequenced by GATC Biotech AG (Konstanz, Germany) or Cogenics (Meylan, France). All the nucleotide sequences were deposited in GenBank under the accession numbers given in Table 1. An additional gene (β -tubulin) was sequenced from a selection of the same strains but phylogenetic analysis gave a weak resolution and is not presented here.

Sequence alignments Sequences generated in this study and those obtained from GenBank were aligned under Clustal W (Higgins et al. 1994). They were carefully refined by eye on the editor in Mega 4.0 (Tamura et al. 2007). Several insertions in the ITS sequence of *Pycnoporus puniceus*, and another in the RPB2 sequences of several species in the *Trametes*-clade (see Discussion) were discarded before analyses.

Phylogenetic analysis Two methods of phylogenetic analysis were applied i.e. Maximum Likelihood (ML) and Bayesian. ML analysis was performed on the Phylogeny.fr platform with the following parameters : 1) the phylogenetic tree was reconstructed using the maximum likelihood method implemented in the PhyML program (v3.0 aLRT), 2) the default substitution model was selected assuming an estimated proportion of invariant sites (of 0.474) and 4 gamma-distributed rate categories to account for rate heterogeneity across sites, 3) the gamma shape parameter was estimated directly from the data (gamma=0.470), 4) reliability for internal branch was assessed using the ML bootstrapping method (500 ML bootstrap replicates), 5) transition weighted four times over transversion and log likelihood=-9403,75196. Estimated base frequencies were: f(A)=0.22636, f(C)=0.269792, f(G)=0.26798 and f(T)=0.23773. Sequence file: phymlla96ToTm4/input.phy.

Bayesian analyses were monitored by software Mr Bayes v3.1 (Ronquist and Huelsenbeck 2003). According to the Bayesian Information Criterium (BIC) score, SYM + G + I and K80 + G (K2P; Kimura 1980) were chosen respectively for combined (ITS + RPB2) and 28S sequences analyses as the optimal substitution model defined by TOPALi v2.5 (Milne et al. 2004). Bayesian analyses were conducted using four Metropolis-coupled Markov chain Monte Carlo (MCMC) with one tree sampled per 100th. The first 5000 trees were excluded of our analyses. For the both Bayesian

Table 1 List of Taxa and strains and Genbank accession numbers for RPB2 and ITS

Taxon	Origin	Culture	Herbarium number	Genbank Accession Numbers	
				ITS1-5.8S -ITS2	RPB2
<i>Trametes</i>					
<i>T. betulina</i>	Austria	CBS 695.94	–	JN645081	JN645126
<i>T. aff. meyenii</i>	French Guiana	BRFM 1121	GUY 08-152 (LIP)	JN645065	–
<i>T. aff. meyenii</i>	French Guiana	BRFM 1361	GUY 10-36 (LIP)	JN645083	JN645144
<i>T. gibbosa</i>	France	BRFM 1115	BEL 08-268 (LIP)	JN645064	JN645110
<i>T. hirsuta</i>	France	BRFM 994	MON 08-13 (LIP)	JN645100	JN645142
<i>T. junipericola</i>	Italy	–	–	AY684171	–
<i>T. aff. junipericola</i>	China	BRFM 25	–	JN645088	JN645143
<i>T. maxima</i>	Guadeloupe – FWI	BRFM 1367	RC/GUAD-10-87 (LIP)	JN645084	JN645146
<i>T. maxima</i>	Cuba	–	–	AB158315	–
<i>T. meyenii</i>	India	CBS 453.7	–	JN645067	JN645112
<i>'Daedalea' microsticta</i>	Costa Rica	–	–	FJ403209	–
<i>T. ochracea</i>	France	BRFM 632	–	JN645092	JN645133
<i>T. ochracea</i>	France	BRFM 884	CAR 29 (LIP)	JN645093	JN645134
<i>T. ochracea</i>	The Netherlands	CBS 257.74	–	JN645077	JN645122
<i>T. polyzona</i>	Zimbabwe	BRFM 1183 - MUCL 38443	–	JN645068	–
<i>T. polyzona</i>	–	CBS 319.36	–	JN645078	JN645123
<i>T. pubescens</i>	Austria	CBS 696.94	–	JN645080	JN645125
<i>T. socotrana</i>	Zimbabwe	BRFM 1293-MUCL 38649	–	JN645073	JN645118
<i>T. suaveolens</i>	France	BRFM 578	–	JN645090	JN645131
<i>T. versicolor</i>	France	BRFM 1219	B. Rivoire personal herbarium	JN645058	JN645113
<i>T. villosa</i>	Guadeloupe – FWI	BRFM 1375	RC/GUAD-10-201 (LIP)	JN645101	–
<i>T. villosa</i>	Argentina	CBS 334.49	–	JN645079	JN645124
<i>Artolenzites</i>					
<i>A. elegans</i>	Costa Rica	CBS 818.88	–	JN645060	JN645107
<i>A. elegans</i>	New Caledonia	BRFM 1280	CAL 09-201 (LIP)	JN645070	JN645115
<i>A. elegans</i>	Martinique	BRFM 1378	RC/MART-10-78 (LIP)	JN645105	–
<i>A. elegans</i>	Cuba	BRFM 1074 - MUCL 45380	–	JN645061	JN645108
<i>A. elegans</i>	French Guiana	BRFM 1122	GUY 08-145 (LIP)	JN645066	JN645111
<i>'Trametes elegans'</i>	Florida	–	–	JV021237	–
<i>Pycnoporus</i>					
<i>P. cinnabarinus</i>	Belgium	BRFM 146 -MUCL 30555	–	JN645087	JN645129
<i>P. cinnabarinus</i>	France	BRFM 945	MOU 129 (LIP)	JN645086	JN645128
<i>P. coccineus</i>	Australia	BRFM 939 - MUCL 38525	–	JN645094	JN645136
<i>P. coccineus</i>	China	BRFM 6	IMB H2180	JN645091	JN645132
<i>P. puniceus</i>	Cuba	BRFM 941 -MUCL 47087	–	JN645095	JN645137
<i>P. sanguineus</i>	French Guiana	BRFM 896	GUY 42 (LIP)	FJ234188	JN645135
<i>P. sanguineus</i>	Madagascar	BRFM 283-MUCL 29375	–	JN645089	JN645130
<i>Leiotrametes</i>					
<i>L. menziesii</i>	New Caledonia	BRFM 1281	CAL 09-202 (LIP)	JN645071	JN645116
<i>L. menziesii</i>	Martinique – FWI	BRFM 1368	RC/MART-10-212 (LIP)	JN645103	–
<i>L. menziesii</i>	Martinique – FWI	BRFM 1369	RC/MART-10-74 (LIP)	JN645085	JN645145
<i>'Trametes lactinea'</i>	Island of Mauritius	–	–	Damm 4703	–
<i>Leiotrametes sp.</i>	French Guiana	BRFM 1050	GUY 08-20 (LIP)	GU731566	JN645106
<i>Leiotrametes sp.</i>	French Guiana	BRFM 1056	GUY 08-225 (LIP)	JN645059	–
<i>Leiotrametes sp.</i>	French Guiana	BRFM 1080	GUY 08-167 (LIP)	JN645063	–
<i>Leiotrametes sp.</i>	French Guiana	BRFM 1078	GUY 08-156 (LIP)	JN645062	JN645109
<i>L. lactinea</i>	Taiwan	CBS 109427	–	JN645076	JN645121

Table 1 (continued)

Taxon	Origin	Culture	Herbarium number	Genbank Accession Numbers	
<i>L. lactinea</i>	French Guiana	BRFM 1251	GUY 09-110 (LIP)	JN645069	JN645114
<i>L. lactinea</i>	Guadeloupe – FWI	BRFM 1370	RC/GUAD-10-181 (LIP)	JN645102	–
<i>L. lactinea</i>	Guadeloupe - FWI	BRFM 1371	RC/GUAD-10-42 (LIP)	JN645104	–
<i>L. lactinea</i>	New Caledonia	BRFM 1282	CAL 09-206	JN645072	JN645117
<i>L. lactinea</i>	Thailand	–	–	GQ982887.1	–
<i>Incertae sedis</i>					
<i>Lenzites warnieri</i>	France	BRFM 972	ND 169 (LIP)	JN645098	JN645140
<i>T. cingulata</i>	Malawi	MUCL 40167	–	JN645075	JN645120
<i>T. ljubarskyi</i>	France	BRFM 957	MOU 139 (LIP)	JN645097	JN645139
<i>Others</i>					
<i>Hexagonia mimetes</i>	Zimbabwe	MUCL39660	–	JN645074	JN645119
<i>Trametella trogii</i>	France	BRFM974	ND 168 (LIP)	JN645099	JN645141
<i>Daedaleopsis tricolor</i>	France	BRFM 954	MOU 132 (LIP)	JN645096	JN645138
<i>Hexagonia nitida</i>	Corsica	BRFM 1327	COR 09-272 (LIP)	JN645082	JN645127

analysis, potential scale reduction factors (PSRF) were reasonably close to 1.0 for all parameters. Bayesian Posterior Probabilities (Bayesian PP) of each node were obtained with majority rules with all compatible partitions. Whatever the method, gaps were scored as missing and trees were rooted by Midpoint rooting application.

Selection of outgroups Initial analyses based on ITS sequences (not shown here) confirmed that several species fell outside of the core genus *Trametes* and of the related genera. Among these, *Hexagonia nitida*, *Daedaleopsis tricolor* and *Trametella trogii* (syn. *Funalia trogii*; for a comparison between *Funalia* and *Trametella* especially based on polarity: see (Pieri and Rivoire 2007) were selected as outgroups since all were shown to belong to the sister “subclade A” of Ko (2000). A strain identified as *Trametes mimetes* was found from our preliminary analysis to be closely related to *Hexagonia nitida*, as suggested earlier by Reid (1975), therefore the name *Hexagonia mimetes* (Wakef.) D. A.Reid is retained here assuming a correct identification of the strain (voucher specimen not seen). This species had not been included in previous phylogenetic works (e.g. Tomšovský et al. 2006). The corresponding sequences were also used as outgroups.

Results of the phylogenetic analysis

Morphological analysis All 31 collections have been observed, including the type material of *Lenzites acutus*, *Trametes cingulata*, *T. lactinea*, *T. menziesii*, *T. ochroflava*, *T. sclerodepsis* and *T. subectypus*, in order to confirm field identifications. European specimens from Marcel Bon’s collections (LIP herbarium) were studied to complete morphological

observations. For each collection the hymenophoral trama, hymenium, spores, pileus, structure of context, and structure on radial cuts were analyzed. Following various keys of neotropical species of *Trametes* (Ryvarden et al. 2009; Gomes-Silva et al. 2010; Læssøe and Ryvarden 2010) the KOH reaction was systematically investigated on abhymenial and hymenial surfaces of basidiomes (dry and also fresh specimens when possible).

Morphological analysis of 31 collections for which culture was successful resulted in the identification of 20 species, 10 being strictly tropical taxa (*‘Corioloopsis’ polyzona*, *Pycnoporus sanguineus*, *‘Trametes’ elegans*, *T. lactinea*, *T. maxima*, *T. menziesii*, *T. socotrana* and *T. villosa* (Table 1). Two species collected repeatedly in French Guiana remain unidentified: one showed morphological characters close to those of the paleotropical species *T. meyenii* (here called *‘Trametes aff. meyenii’*: GUY 08-152 and GUY 10-36, LIP), the other could not be compared to any well-defined species (here called *‘Leiotrametes sp.’*: GUY 08-20, GUY 08-225, GUY 08-167 and GUY 08-156, LIP).

ITS + RPB2 combined analysis Compared to separate gene analyses, the combination of ITS and RPB2 sequences produced the best resolved phylogeny and the highest number of strongly supported clades. A combined sequence dataset was thus constructed for 41 strains of *Trametes* and allied genera (24 being tropical areas, the others from Western Europe). The Bayesian 50% majority rule consensus tree is shown, in which 27 clades receive more than 95% Bayesian PP and 20 received more than 70% ML bootstrap support (Fig. 1). The ML analysis (not shown) was very similar in topology as the Bayesian analysis but differed by a lack of basal resolution for the main clades and revealed no more information.

Table 2 List of Taxa and Genbank accession numbers for nucLSU

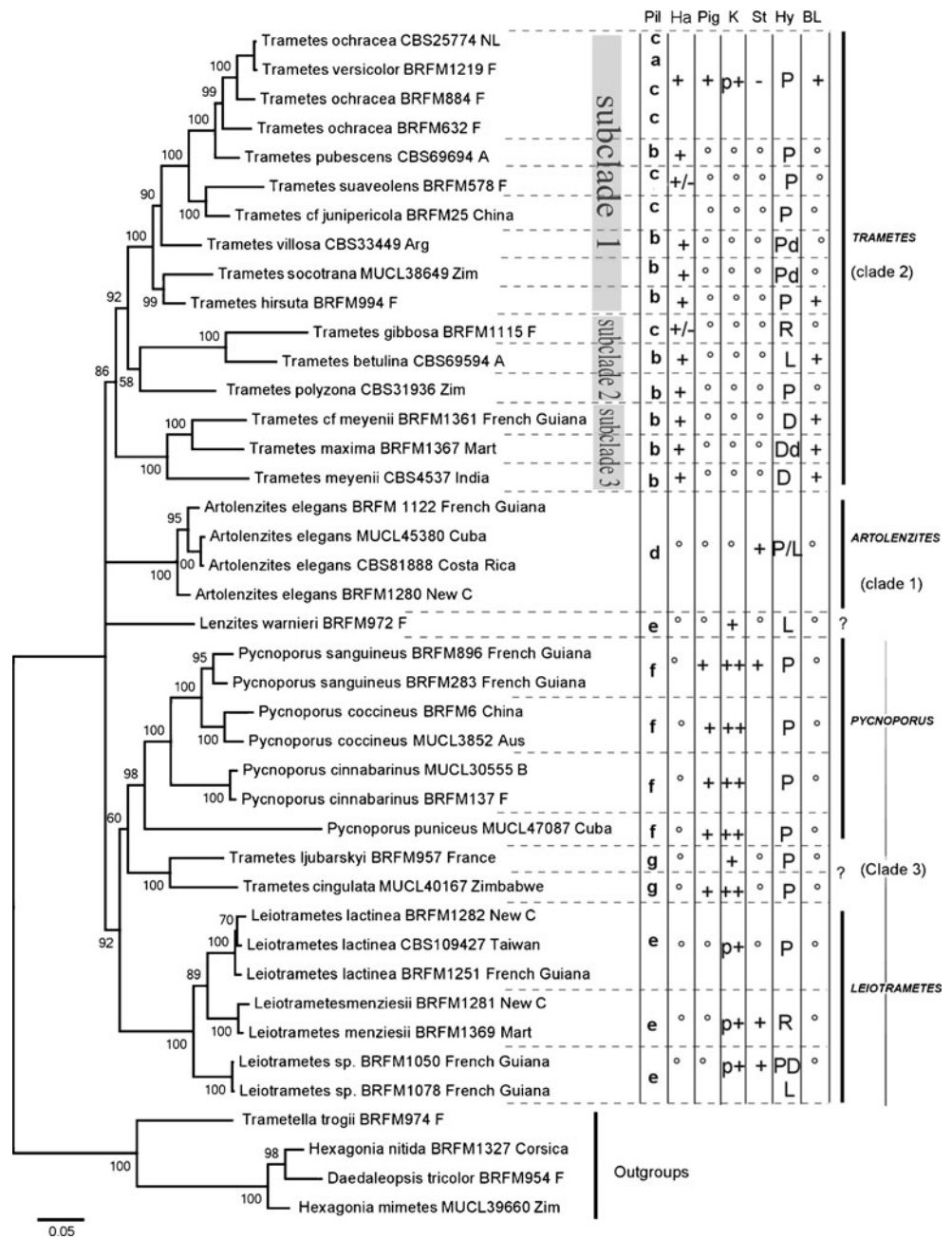
Taxon	Genbank Accession Number 28S rLSU
Trametes	
<i>L. betulinus</i>	AB368073.1
<i>T. conchifer</i>	AY515342.1
<i>T. gibbosa</i>	AY351924.1
<i>T. gibbosa</i>	AB368117.1
<i>T. gibbosa</i>	AY855905.1
<i>Pseudotrametes gibbosa</i>	AJ488127.1
<i>Pseudotrametes gibbosa</i>	AJ488126.1
<i>T. hirsuta</i>	AY855910.1
<i>T. hirsuta</i>	AY351922.1
<i>T. hirsuta</i>	AB368118.1
<i>T. junipericola</i>	AY855915.1
<i>T. maxima</i>	AB158315.1
<i>T. ochraceae</i>	AY855908.1
<i>T. ochraceae</i>	AY855914.1
<i>T. orientalis</i>	AY351920.1
<i>C. polyzona</i>	AY351951.1
<i>C. polyzona</i>	AY333817.1
<i>T. pocas</i>	AY351919.1
<i>T. pubescens</i>	AY515341.1
<i>T. pubescens</i>	AY855906.1
<i>T. suaveolens</i>	AY855909.1
<i>T. villosa</i>	AJ488131.1
<i>T. villosa</i>	AJ488130.1
Artolenzites	
<i>Trametes elegans</i>	GU048616.1
<i>Trametes elegans</i>	AY351925.1
<i>Lenzites elegans</i>	FJ372713.1
Pycnoporus	
<i>P. cinnabarinus</i>	AJ488128.1
<i>P. cinnabarinus</i>	AY586703.1
<i>P. cinnabarinus</i>	HQ891295.1
<i>P. puniceus</i>	FJ372707.1
<i>P. puniceus</i>	FJ372708.1
<i>P. sanguineus</i>	HQ891295.1
<i>P. sanguineus</i>	FJ372694.1
<i>P. sanguineus</i>	GQ982877.1
Leiotrametes	
<i>T. elegans</i>	AY855912.1
<i>T. lactinea</i>	AY351921.1
<i>T. lactinea</i>	GQ982880.1
Incertae sedis	
<i>T. ljubarskyi</i>	AY855911.1
Others	
<i>Trametes trogii</i>	AJ457810.1
<i>Corioloopsis gallica</i>	AY855913.1
<i>Laetiporus sulphureus</i>	EU232302.1

ITS and RPB2 sequences have an alignment of 594 and 697 bp, respectively, including gaps. After removing poorly aligned positions and divergent regions of DNA, ITS and RPB2 sequences had respectively an alignment of 532 bp with 178 variable regions and 131 parsimony informative characters, and 644 bp with 284 variable regions and 254 parsimony informative characters. 5.9% of gaps were maintained in the final combined alignment but were scored as missing.

As shown in Fig. 1, topology of the Bayesian tree is composed of three highly supported clades:

- 1) A strongly supported (Bayesian PP=1; ML bootstrap=100%) group of specimens that were identified as *Lenzites elegans sensu* Ryvardeen and Johansen (1980) (French Guiana, French West Indies, New Caledonia and Cuba).
- 2) A clade (Bayesian PP=0.92) of a groups specimens with glabrous upper surface. It comprises three distinct sub-clades:
 - *Pycnoporus* forms a strongly supported monophyletic group (Bayesian PP=0.98; ML bootstrap=0.78);
 - Sister sub-clade of *Pycnoporus*, moderately supported (Bayesian PP=0.60), comprising two close species of unclear systematic position: *Trametes ljubarskyi* (France) and *T. cingulata* (Southern Africa);
 - Third sub-clade, strongly supported, comprising 3 tropical species, *T. menziesii*, *T. lactinea* and an unidentified Guianese species that shows hymenial surface evolving from pored to more or less lamellate pattern while ageing (Bayesian PP=1; ML bootstrap=100%).
- 3) Third clade (Bayesian PP=0.86) comprising a group of specimens with pubescent to hirsute upper surface. Three distinct sub-clades are identified within this clade:
 - Firstly a strongly supported sub-clade comprising genuine *Trametes* species (i.e. with strictly poroid hymenophore): *Trametes versicolor*, *T. hirsuta*, *T. ochracea*, *T. suaveolens*, a chinese species close to *T. junipericola*, *T. socotrana*, *T. pubescens* and *T. villosa* (Bayesian PP=1; ML bootstrap=92%). Most of them excepting *T. socotrana* and *T. villosa* are from temperate areas.
 - Second sub-clade formed by a species with radially elongated pore surface (*T. gibbosa*), a lenzitoid species ('*Lenzites*' *betulinus*) and a strictly pored tropical species (*Corioloopsis polyzona*); the position of *C. polyzona* relative to the *T. gibbosa*-*L. betulinus* group is weakly supported (Bayesian PP=0.58)

Fig. 1 Phylogenetic reconstruction of the *Trametes*-clade based on the combined analysis of ITS1-5.8S-ITS and RPB2 (50% majority rule consensus tree). Interpretative features are figured on the right part of the figure: Pil = Pileus structure (letters a-g refer to type structures in Fig. 4); Ha = presence (+ to +/- if disappearing with age) or absence (°) of hairs (tomentum) on pileus; Pig: presence (+) or absence (°) of incrusting pigment (see Fig. 4); K = reaction to 5% KOH (°: none; +: brown; ++: black; p = only on pileipellis); St = presence (+) or absence (°) of a pseudostipe; Hy = morphology of hymenophore (P = poroid, Fig. 5d–f; D = daedaloid, Fig. 5a,c; L = lenzitoid, Fig. 5b right; d = with protruding dissepiments); BL = presence (+) or absence (°) of a “black line” under pileipellis



– Third strongly supported (Bayesian PP=1; ML bootstrap=0.92) sub-clade grouping 3 tropical species with intermediate hymenophore configuration, *Trametes maxima*, *T. meyenii*, and a Guianese species morphologically close to *T. meyenii*.

4) ‘*Lenzites warnieri*’ comes out as a single branch at the same phylogenetic level as the three main above-mentioned clades.

RBP2 analysis The alignment of RPB2 sequences revealed an interesting insertion area for some species (Fig. 2): most species of *Trametes* s.str. (*T. maxima*, *T. meyenii*, *T. ochracea*,

T. pubescens, *T. versicolor*) have a 15-nucleotide long insertion (21-nucleotide long in *T. ochracea* BRFM632), all of rather similar composition. *Trametes gibbosa* and ‘*Lenzites betulinus*’ show a much longer insertion, 51- and 69-nucleotide long respectively. This insertion (not included in the phylogenetic analysis) supports the inclusion of *Trametes meyenii* and *T. maxima* in the core *Trametes* group (a hypothesis already well-supported in the phylogenetic analysis, see above), and a further argument for considering the *Trametes gibbosa-Lenzites betulinus* clade as closely related. Interestingly enough this insertion is absent from all other lineages and suggests a basal origin of the “third clade” with an internal fast evolution; it might have disappeared in some derived lineages

Taxon	RPB2 seq (1)	Insert	RPB2seq (2)
<i>T. ochracea</i>	GAA CCC GAG	AAG GAT TCA GTG ATA CCT AAA	TTC GAG
<i>T. ochracea</i>	GAA CCC GAG	AAG GAT GCA ACC AAG	TC GAG
<i>T. versicolor</i>	GAA CCT GAG	AAG GAT GCA ACC AAA	TTC GAG
<i>T. pubescens</i>	GAA CCT GAG	AAG GAT GTA CCC AAA	TTC GAG
<i>T. suaveolens</i>	GAT CCC GAA		TAC GAT
<i>T. villosa</i>	GAC CCC GAG		TTC GAG
<i>T. hirsuta</i>	GAC CCC GAG		TTC GAA
<i>T. socotrana</i>	GAT CCC GAG		TTC GAA
<i>T. polyzona</i>	GAC CCC GAG		TTC GAG
<i>T. gibbosa</i>	GAA CGT GCG	GCG GAA GAA CGT GCG AAG GAG AAT GAT ACG TAC GAC CCT GAC GGC CCA CCG AGG	TTC GAC
<i>T. betulina</i>	GAG CGT GCG	GAG GAG GAG CGT AAG AAA GCG GAA GGT ATA GAA GAA CCG GAG GAC CCG GAT GAC CCC CCA CCA CCG AGG	TAC GAG
<i>T. cf. meyenii</i>	GAA GCG GGC	AAG GAA GAC CCC GCG	GTC ATA
<i>T. maxima</i>	GAG GCG GGC	AAG GAA GAT CCT GCC	GTC ATC
<i>T. meyenii</i>	GAT GCC GCC	CAC CAA GGA CCC GRA	TTC GCC
<i>A. elegans</i>	GAG CCG GAG		TTC GAC
<i>'Lenzites' warnieri</i>			
<i>L. warnieri</i>	GAC CCG ACR		TTC GAC
<i>P. cinnabarinus</i>	GAC CCG GAG		TTC GAG
<i>P. sanguineus</i>	GAS CCC GAC		TTC GAG
<i>P. coccineus</i>	GAT CCC GAC		TTT GAA
<i>P. puniceus</i>	GAC CCT GAA		TTC GAC
<i>L. cingulata</i>	GAC CCC AAG		TTC GAG
<i>T. ljubarskyi</i>	GAC CCG AAG		TTC ACT
<i>L. menziesii</i>	GAC CCC GAG		TTC GAC
<i>L. lactinea</i>	GAC CCC GAA		TTC GAC
<i>Leiotrametes sp.</i>	GAT CCG GAA		TTC GAC

Fig. 2 Distribution and composition of insert in RPB2 sequences in the *Trametes* clade; species are disposed according to the ITS + RPB2 phylogeny in Fig. 1

such as *Trametes suaveolens* or *Corioloopsis polyzona*, the alternative hypothesis (a multiple origin of this insertion) from an evolutionary point of view being less parsimonious.

28S rLSU analysis In order to obtain additional information, a 28S rLSU analysis was processed, independently from the former, by using sequences downloaded from GenBank (Fig. 3). A group of 41 reliable sequences of *Trametes* and allied taxa (incl. 8 tropical species) was considered (Table 2). Most of them have been previously published by Tomšovský et al. (2006), whose species concepts match those adopted here. No rLSU sequence of *Lenzites warnieri* or *T. cingulata* is available in public databases. *Laetiporus sulphureus*, *Trametella trogii* and *T. (Corioloopsis) gallica* were used as outgroups (Tomšovský et al. 2006).

This single-gene analysis using Bayesian methods gives a weak basal support, which does not contribute to a better definition of the clades defined with ITS + RPB2. Nevertheless a good support (Bayesian PP=0.94) is given to the “second clade” of the former analysis, including *Pycnoporus* and the *Trametes lactinea*-group. The displacement of *Corioloopsis polyzona*, *Lenzites betulinus* and *Trametes elegans* e.g., compared to the former analysis, is not supported and cannot be considered as consistent. It is assumed that the 28S rLSU sequences are not pertinent for reconstructing the phylogeny of the *Trametes*-clade, although easily aligned. The necessity of choosing a very distant outgroup (*Laetiporus sulphureus*) in

order to get a better ML bootstrapping suggests that the resolution power of rLSU is insufficient with the currently available data, as it is for the other gene studied by us (β -tubulin, data not shown). More taxa might partly improve this analysis.

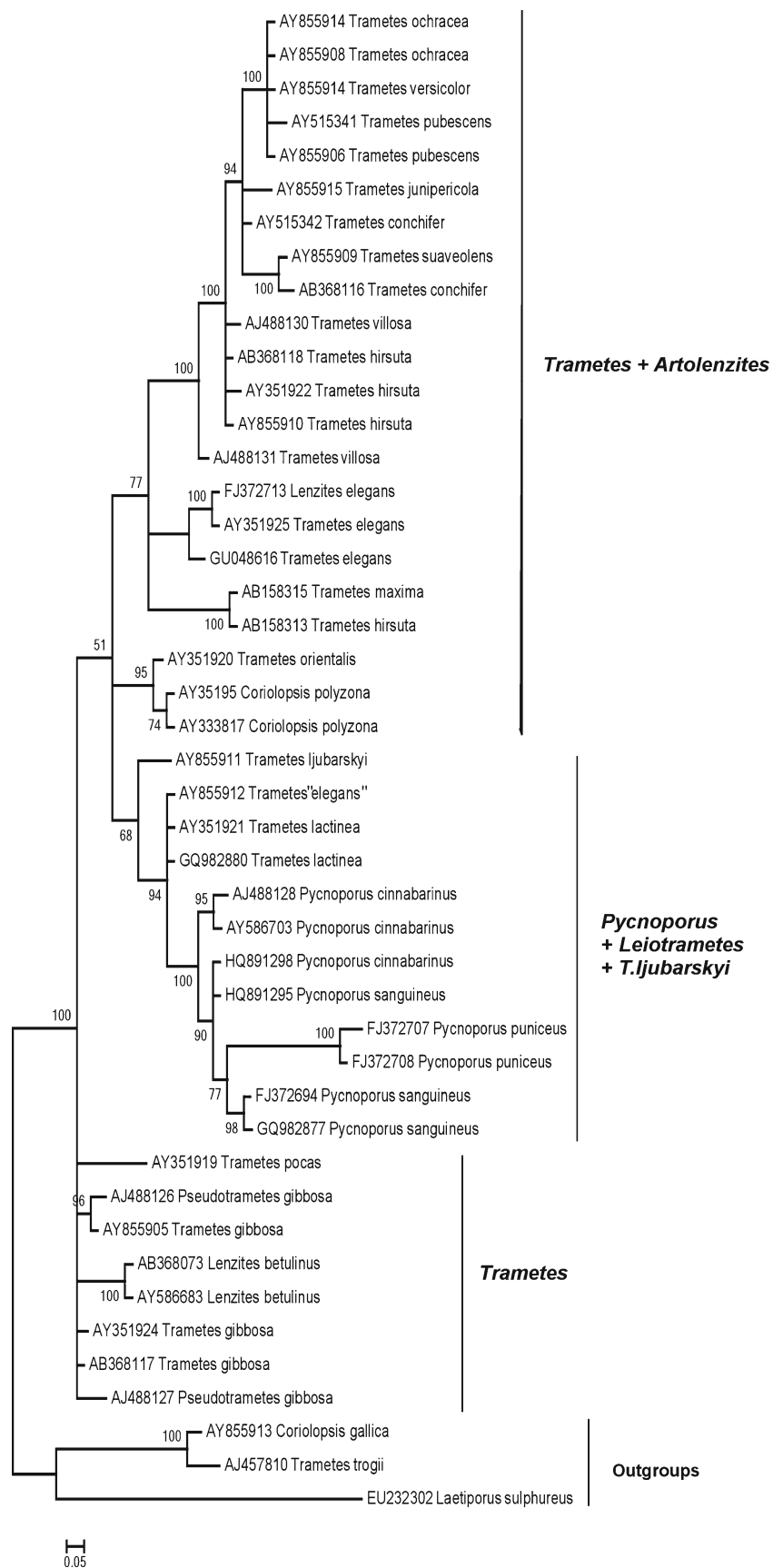
Discussion and new systematic arrangement of the *Trametes*-clade

General systematics in the *Trametes*-group

As expected, the close relationships between the genera *Pycnoporus*, *Lenzites*, *Corioloopsis* and *Trametes*, as previously described by Ko (2000), Garcia-Sandoval et al. (2011) and Rajchenberg (2011) were confirmed. Species such as *Hexagonia nitida*, *Daedaleopsis tricolor*, *Trametella trogii* with binucleate spores and heterocytic nuclear behavior, previously located in a sister clade position (Ko and Jung 1999; Tomšovský et al. 2006), and the newly positioned *Hexagonia (Trametes) mimetes*, represented convenient outgroups for our study.

However, relationships within the subgroup “B” *Trametes-Lenzites-Pycnoporus-Corioloopsis* (Ko 2000) of the core polyporoid group remained uncertain. Morphological features defining these four genera such as lamellate or pored hymenophore and colour of the hyphae have not yet proved their worth at the generic level.

Fig. 3 Phylogenetic reconstruction of the *Trametes*-group based on Bayesian analysis of rLSU (50% majority-rule consensus tree). Only the *Pycnoporus/Leiotrametes* clade including “*Trametes*” *ljubarskyi* shows a significant support compared to the ITS + RPB2 phylogeny (Fig. 1)



By addition of more tropical and rare temperate taxa, such a configuration is no more fully supported by our phylogenetic results, and three (ITS + RPB2 analysis, Fig. 1) well-supported monophyletic lineages can be identified, with some still uncertainly placed outstanding taxa such as *Lenzites warnieri* for which some molecular data are missing.

Although the basal resolution of the three main clades (1, 2, 3) remains relatively weak, whatever the data sets and analyses, each of them received a good support by the concatenate analysis as well as by the macro- and micro-characters (Fig. 1).

At this stage two possibilities can be considered according to such results: either recognizing an unique genus *Trametes*, enlarged to encompass the three traditional genera cited above; or, as far as some monophyletic clades can be supported by morphological features, split this clade into different genera, each of them defined by a thorough combination of characters. Morphology supplies strong information where molecular phylogenies provide weak support, and helped us propose a better systematic arrangement. Therefore, we propose separation and delimitation of four distinct genera in the *Trametes* group (Fig. 1; Table 3):

- 1) *Trametes*, corresponding to the species with pubescent to hirsute upper surface, including most temperate species fitting the traditional definition of the genus, in addition to '*Lenzites*' *betulinus* and '*Corioloopsis*' *polyzona*;
- 2) *Pycnoporus* to include species with red basidiomes, blackening with KOH;
- 3) *Artolenzites* to include the tropical '*Lenzites*' *elegans*;
- 4) *Leiotrametes* gen. nov., comprising three tropical species: '*Trametes*' *menziesii*, *T. lactinea*, '*Leiotrametes* sp.'

This classification is nevertheless incomplete, since some critical taxa from various tropical parts of the world were not accessible to us and might either add new lineages to the system, or illustrate more continuities between some of the proposed divisions. In the same way two still unplaced lineages not included in previous analyses: '*Lenzites*' *warnieri* and the '*Trametes*' *ljubarskyi*-*T. cingulata* group, cannot reasonably justify new genera according to their uncertain position in our analyses, nor can they be included in *Trametes* s.s. because of outstanding morphological features, and will deserve further studies. There are here provisionally maintained in their traditional genera.

Morphological characters in the four branches within the *Trametes* clade

Structure of upper surface Aspect and structure of the abhymental surface is a discriminating morphological feature of

Table 3 Morphologic characteristics of genera and species groups in the *Trametes*-group

Morphologic features	Upper surface	Hypohal Parietal Crystals	KOH reactivity	Attachment to the substrate	Hymenophore	Presence of a Black Line below the tomentum
<i>Trametes</i>	Pubescent to hirsute	None - except <i>T. versicolor</i> : blue soluble in KOH 5%	Context and abhymental surface sordid yellow - except <i>T. polyzona</i> and abhymental surface of <i>T. versicolor</i> which are deep brown black	Never contracted into a stem-like base	Regularly pored or radially elongated, daedaleoid to lamellate. Dentate when pored (<i>T. versicolor</i> - <i>T. maxima</i>)	Sometimes for <i>T. betulina</i> , <i>T. hirsuta</i> , <i>T. versicolor</i> ; Always into the <i>meyenii</i> subclade
<i>Pycnoporus</i>	Glabrous-dull	Orange to red soluble in KOH 5%	Context pale brown-abhymental surface deep brown	Contracted into a stem-like base - sometimes with a disc	Regularly pored	never
<i>Leiotrametes</i>	Glabrous-dull	none	Context pale brown-abhymental surface deep brown	Contracted into a stem-like base - sometimes with a disc (except for the sessile <i>L. lactinea</i>)	Regularly pored becoming daedalean to lamellate	never
<i>Artolenzites</i>	Glabrous-dull	None	Sordid yellow	Contracted into a stem-like base - sometimes with a disc	Pored, daedalean to lamellate often in a single specimen-irregular	never
<i>T. ljubarskyi</i> - <i>T. cingulata</i>	Glabrous-dull to semi glossy	Colorless, becoming black with KOH 5% for <i>T. cingulata</i>	Deep brown (<i>T. ljubarskyi</i>) to strongly black (<i>T. cingulata</i>)	Never contracted into a stem-like base	Regularly pored	never
<i>L. warnieri</i>	Glabrous-dull	none	Context pale brown-abhymental surface deep brown	Never contracted into a stem-like base	Regularly lamellate	never

major importance at the generic level in the core polyporoid clade, as already shown in *Ganoderma* (Steyaert 1980; Gottlieb et al. 1999; Moncalvo 2000; Welti and Courtecuisse 2010). In the *Trametes* group differences in pileus-structure (glabrous or tomentose) have already been described for each species studied here and are considered by Læssøe and Ryvarden (2010) as an essential feature for species recognition; they nevertheless never been used for phylogenetic interpretation. Taking our phylogenetic results, fundamental differences in structure (Fig. 4) and consequently in macroscopic aspect of the basidiome surface, explain the evolutionary history of the groups. Differentiation of hairs (pileus tomentum) is a synapomorphy of our redefined genus *Trametes* (Fig. 4a–c), without any known exception, although some species are only minutely pubescent when young and become somewhat glabrous whilst ageing (*T. gibbosa*, *T. ochracea*, *T. suaveolens*).

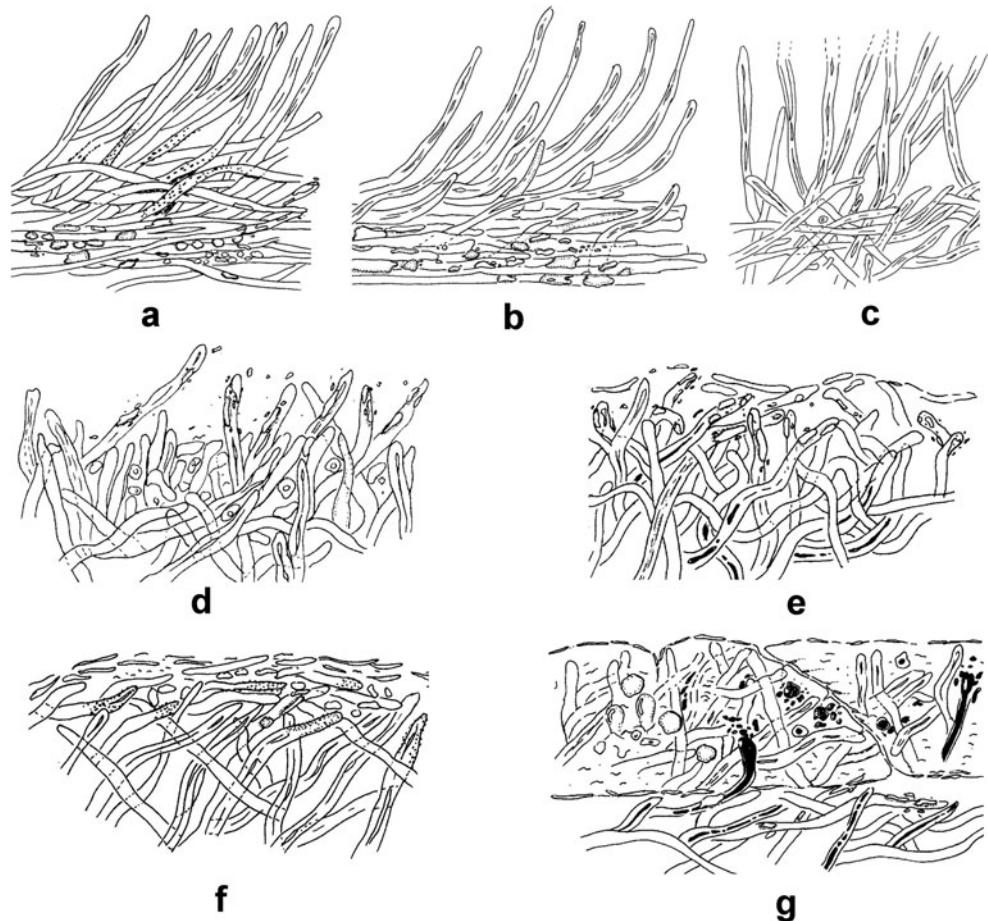
The most superficial layer in strictly glabrous species shows other architecture specificities (Fig. 4d–g): Thus in *Artolenzites* (Fig. 4d) and *Pycnoporus* (Fig. 4f) the pileipellis is made of a single cutis composed of a +/- gelatinized layer of undifferentiated hyphae, whilst in *Leiotrametes* and *Lenzites warnieri* (Fig. 4e) superficial hyphae are thick-walled and filled with brown, resinous material. In *Trametes ljubarskyi*

(Fig. 4g) the same kind of hyphae are overlapped by a 150–200 µm thick layer of colourless +/- resinous or mucilaginous substance soluble in KOH. In *Trametes cingulata* the brownish resinous layer from the accumulation of amorphous resinous material from damaged hyphae reminds one of the upper surface of the laccate *Ganoderma* species but lacks clavate pileocystidia.

All glabrous species have a dull superficial aspect, except *T. ljubarskyi* and *T. cingulata* which have a glossy surface due to the upper resinous layer.

Differentiation of subpellis (“black line”) The hairy-tomentose species *Trametes betulina*, *T. maxima*, *T. meyenii*, and *T. versicolor* – and often also *T. hirsuta* – typically differentiate a dark subpellis (“black line” or BL). When observed under the light microscope, the BL is very refractive and consists of a dense layer of radially arranged hyphae embedded in a mucus partly dissolving in 5% KOH. In *Trametes* species where the BL is not apparent this structure is not (*T. gibbosa*, *T. suaveolens*) or only weakly (*T. polyzona*, *T. socotrana*, *T. villosa*) developed. Contrary to Ryvarden (1991) and Tomšovský et al. (2006) who consider the BL as a characteristic of the whole “*Coriolus*-subclade” (our core *Trametes* clade) we failed to systematically

Fig. 4 Pileus structures in *Trametes* and allied species. **a**: trichoderm with differentiated subpellis, with incrustations (*Trametes versicolor*); **b**: idem, without incrustations (*T. villosa*); **c**: trichoderm without differentiated subpellis (*T. gibbosa*); **d**: intermixed structure without incrustations (*Artolenzites elegans*); **e**: idem, with brown pigment in skeletal hyphae (*Leiotrametes lactinea*); **f**: idem, with incrustations at hyphal apex (*Pycnoporus cinnabarinus*); **g**: idem, with brown intracellular pigment and resinoid matrix (*Trametes ljubarskyi*)



observe it in *T. hirsuta* and never in *T. gibbosa*, *T. ochracea*, *T. pubescens*, or *T. polyzona*. Thus the BL is not a synapomorphic feature in *Trametes* and does not support the distinction of a genus or subgenus (such as *Coriolus*) based on this character (Ryvarden 1991).

Such a differentiated subpellis is absent in glabrous species of the *Trametes* clade (*Pycnoporus*, *Leiotrametes*, *Artolenzites*, *L. warnieri*, *T. ljubarskyi*, *T. cingulata*). In the same way *Trametes* species without differentiated subpellis (especially *T. gibbosa* and *T. suaveolens*) tend to soon become glabrous whilst ageing.

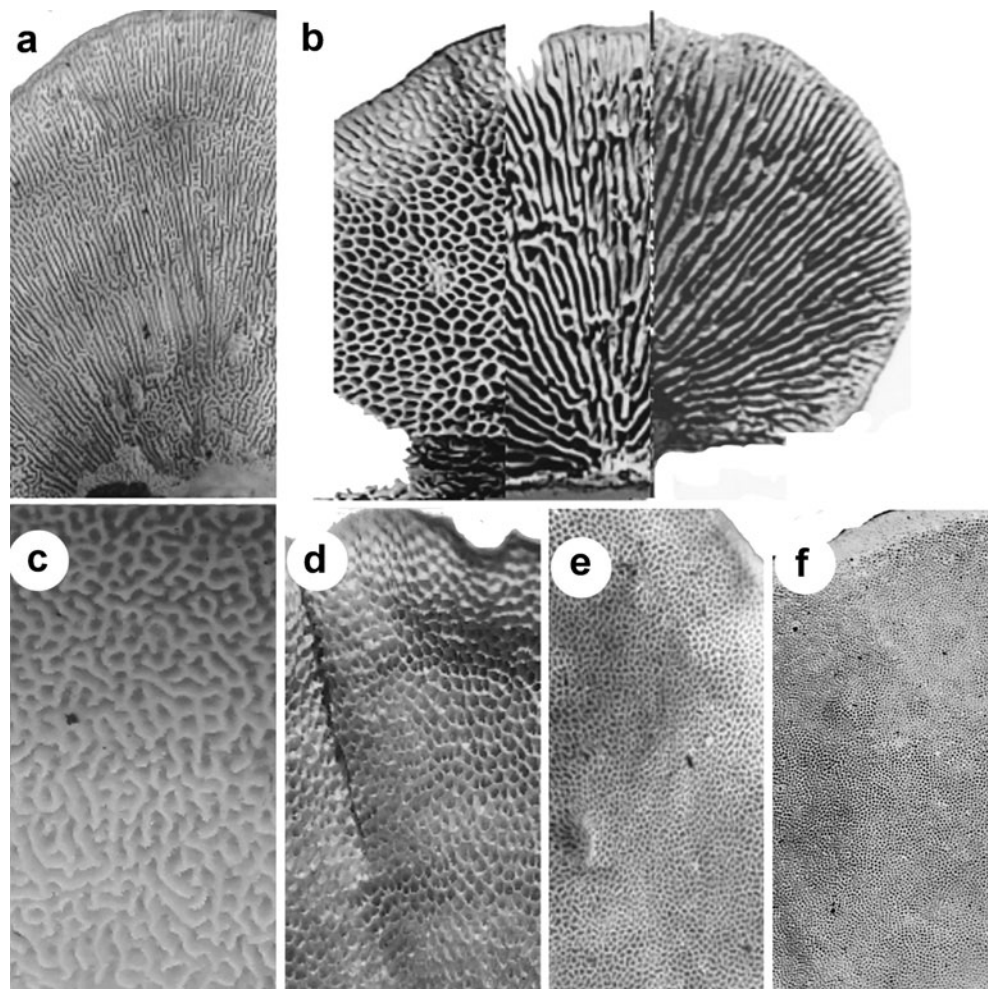
Parietal crystal pigment Red to orange parietal crystals located along skeletal hyphae, especially those quite close to the upper surface and hymenophore, is the main feature differentiating *Pycnoporus* species from those belonging in the genus *Leiotrametes* and more generally from the glabrous members of the *Trametes* group, where we never found the pigment. Although these crystals are very quickly soluble in 5% KOH and must be searched for carefully, such a feature is so far relatively significant to justify monophyly of the genus *Pycnoporus*. However, some species outside

this genus also showed relatively similar crystals located at the upper surface level: colorless and turning black with 5% KOH for *T. cingulata* or blue and incompletely soluble in 5% KOH for *T. versicolor*.

Hymenophore Despite its importance in traditional systematics, the phylogenetic analysis does not support a classification based on the type of hymenophore at generic level. All genera (*Artolenzites*, *Trametes*, and *Leiotrametes*) except the exclusively pored *Pycnoporus* contain some species with lamellate hymenophore. Although the type of hymenophore is usually stable at species level (Fig. 5), its structure is variable within the tropical *Artolenzites elegans* and even more in *Leiotrametes* sp. (Fig. 5a–b) according to the specimen (mainly daedalean, mainly lamellate, or a mixed pattern).

The origin of daedalean or heteromerous (mixture of rounded and elongate pores) hymenophore seems to species-correlated. On comparing the aspect of mature specimens of *T. gibbosa* the pores elongate irregularly from the origin. In contrast in *L. menziesii* young specimens show regular pores, of which only radial dissepiments develop

Fig. 5 Types of hymenophores of *Trametes* and allied species. **a**: daedaleoid (*Artolenzites elegans*); **b**: poroid (left), daedaleoid (middle) and lenzitoid (right), in three sporocarps of “*Leiotrametes* sp.”; **c**: secondarily daedaleoid (*L. menziesii*); **d**: poroid with protruding dissepiments (*Trametes villosa*); **e**: poroid with angular pores (*T. polyzona*); **f**: poroid with round pores (*Leiotrametes lactinea*). Pictures of S. Welte (b,f), R. Courtecuisse (c,d), P.-A. Moreau (a,e)



with age to give a secondarily false daedalean or somewhat lenzitoid structure, with the primary septa still visible in the bottom of the alveoli (Fig. 5c). Such development may be correlated to the inclination of the basidiomes on its substrate. When dimidiate and horizontally growing the hymenial surface remains pored, but when growing oblique or erect the continuous geotropic growth of the dissepiments from a regularly pored ground yields an irpicoid (*T. maxima* or *T. villosa*; Fig. 5d) or more or less lenzitoid (*L. menziesii*) aspect.

Presence of a pseudostipe A distinct and sterile base clearly delimited from the hymenophore, mostly attached to the substrate with a disc is found in various species: *Leiotrametes menziesii*, the Guianese *Leiotrametes sp.*, *Artolenzites elegans* and *Pycnoporus sanguineus*. All species of *Trametes* known to us are sessile, as well as *Leiotrametes lactinea*, *Lenzites warnieri* and *T. ljubarskyi* (*T. cingulata* having a contracted basal attachment). Despite great morphological variability within the *Trametes* group, this character is very stable in all studied collections of the above mentioned taxa.

KOH reaction Basidiomes were tested in both fresh and dry conditions with 5% KOH, on pileus, context and hymenophore. All species of *Pycnoporus* showed an immediate black reaction on all surfaces, in addition to *T. cingulata* (Table 3). The other species studied never showed such significant reactions (either nil to yellow or brownish and never in all parts of the basidiomes). Nevertheless, the upper surface in species belonging to the new genus *Leiotrametes* turned deep brown or even almost black with 5% KOH, but the colour of the context did not show a strong reactivity and remained pale yellow. Indeed, this KOH reaction was already used to distinguish *Leiotrametes lactinea* (turning to deep brown) from ‘*Trametes*’ *modesta* or *T. supermodesta* (becoming red to brownish) by Gomes-Silva et al. (2010).

Biogeography *Leiotrametes* and *Artolenzites* are common in all tropical areas, some species, such as *L. lactinea* and *A. elegans* being apparently pantropical (Neotropics and New Caledonia). Nevertheless *L. lactinea* has been recently collected by Vlasák and Kout (2011) in Eastern USA (especially Florida) and interpreted as a recent colonization. According to Gilbertson and Ryvar den (1987), *A. elegans* is common in South Eastern USA. However, since Vlasák and Kout (2011) “were able to find only one specimen of this species in ten year”, such a statement could result from a misidentification with either *L. lactinea* or *T. gibbosa* the introductions of which could possibly be recent in the North American continent. *Leiotrametes menziesii* (= *T. menziesii*) is so far known from Paleotropical area (Ryvar den and Johansen 1980; Corner 1989) and is reported here from the Neotropics for the first time.

Trametes and *Pycnoporus* are more widely distributed. Some species are commonly found in Northern temperate or Mediterranean areas, but they also include common tropical species such as *T. maxima*, *T. meyenii*, *T. villosa*, *P. sanguineus* or *P. puniceus*. Finally *Lenzites warnieri* and *Trametes ljubarskyi* are mainly Mediterranean species.

Taxonomy

Genus *Trametes* Fr., *Fl. Scand.*: 339 (1836), *emend.*

Synonyms : *Lenzites* Fr., *Fl. Scand.* : 339 (1836); *Coriolus* Qué!., *Enchir. Fung.*: 175 (1886); *Corioloopsis* Murrill, *Bull. Torrey Bot. Club* 32: 358 (1905).

Type species : *Trametes suaveolens* Fr. (Murrill 1905).

Species studied: *T. betulina* (L.: Fr.) Pilát (lectotype of *Lenzites*), *T. gibbosa* (Pers.: Fr.) Fr., *T. hirsuta* (Wulfen: Fr.) Pilát (lectotype of *Coriolus*), *T. junipericola* Manjón et al., *T. maxima* (Mont.) David & Rajchenberg, *T. meyenii* (Klotzsch) Lloyd, *T. ochracea* (Pers.: Fr.) Gilbertson & Ryvar den, *T. polyzona* (Pers.: Fr.) Corner (holotype of *Corioloopsis*), *T. pubescens* (Schum.: Fr.) Pilát, *T. socotrana* Cooke, *T. suaveolens* (L.: Fr.) Fr., *T. versicolor* (L.: Fr.) Lloyd and *T. villosa* (Swartz: Fr.) Kreisel.

Observations: The main feature which could characterize this genus is certainly the pubescent to hirsute upper surface of the pileus in all species (Fig. 4a–c). Although *T. suaveolens*, *T. ochracea* and *T. gibbosa* are characterized by a glabrescent abhymenial surface, they are in fact tomentose at early stages of their development (Fig. 4c). In contrast, species of *Artolenzites*, *Leiotrametes*, *Pycnoporus*, as well as ‘*Lenzites*’ *warnieri* and the ‘*Trametes*’ *cingulata*-*T. ljubarskyi* group, all excluded from *Trametes* in this study, are always glabrous, and the hyphae located at the far edge of the upper surface are bent or adpressed and never protruding (Fig. 4d–h).

As defined here, *Trametes* encompasses species with various types of hymenophore: typical from circular or angular pores (*T. versicolor* complex; Ko 2000; Fig. 5d–e) to also radially elongated to lamellate (*T. gibbosa* - *T. betulina* group; Tomšovský et al. 2006) or daedaleoid pores (*T. maxima* and *T. meyenii*, formerly classified in *Cerrena* by Hansen 1960 and *Sclerodepsis* by Ryvar den 1972). These results confirm that hymenophoral structures, although conspicuous and on which traditional systematics was mainly based (Fries 1835; Ryvar den 1991), is of low taxonomic value at generic level. However it represents a relevant morphological character for species delimitation. Moreover, except *T. polyzona* with strictly poroid hymenial surface, which moderately clusters (Bayesian PP=0,58; Fig. 1) with *T. betulina* and *T. gibbosa*, each type of hymenial surface corresponds to a monophyletic subclade of *Trametes*.

The Black line is frequent in *Trametes* but has no taxonomic value at subgeneric level, as it can be found in various subclades (Figs. 1, 4a–b) and shows no correlation with hymenophoral structures. In the *T. meyenii* subclade all species analyzed herein show a black line. However an ITS sequence of *Daedalea microsticta* deposited in Genbank clusters with *T. meyenii* and *T. maxima* (data not shown); for Ryvarden et al. (2009) *Daedalea microsticta* is a synonym of *T. ochroflava*, whose type specimen is glabrous, strictly pored and without black line (personal observation). More precision on this still confused group of species is required.

Trametes polyzona, a species with brown context, was incorporated into *Trametes* by the mttSSU and ITS rDNA analyses of Ko (2000), who also established a close relationship between *T. polyzona*, *T. gibbosa*, *T. hirsuta* and also *T. meyenii* (Ko and Jung 1999; Garcia-Sandoval et al. 2011). Consequently the brown color of the skeletal hyphae is not significant in excluding *T. polyzona* from the genus *Trametes* we propose. Morphological similarities between *T. hirsuta*, *T. betulina*, *T. socotrana*, *T. villosa*, *T. maxima* and *T. polyzona*, are especially significant regarding the upper surface with hirsute hairs along narrow sulcate zones (Gilbertson and Ryvarden 1987; Ryvarden and Gilbertson 1994). Finally, the effused-reflexed basidiome of *T. polyzona* is another characteristic of the genus *Trametes*, in contrast to the other clades mostly characterized by pseudostipe or contracted basis (Fig. 1).

Once compared morphological characters with phylogenetical results, we can deduce that the major characteristic distinguishing *Trametes* from the other genera of the core *Trametes*-clade is the pilose upper surface. As quoted above, Quélet (1886) was the first to emphasize the significance of this feature by separating the genus *Coriolus* from *Trametes* which was restricted to glabrous species (or supposed so, erroneously for *T. gibbosa* and *T. suaveolens*). However, as soon as *Trametes suaveolens* (type species of the genus *Trametes*, unless one of its less representative members) is considered congeneric with the type species of *Coriolus* (*C. versicolor*), the genus *Trametes* in this clade, *Trametes* keep priority on *Coriolus*.

Genus *Pycnoporus* P. Karst., *Rev. Mycol. (Toulouse)* 3 (9):18 (1881)

Type species: *Polyporus cinnabarinus* Jacq.:Fr.

Species studied: *Pycnoporus cinnabarinus* (Jacq. : Fr.) P. Karsten, and, *P. sanguineus* (L.: Fr.) Murrill.

Observations: In a large phylogenic study of *Pycnoporus*, Lesage-Meessen et al. (2011) clearly separated four species of *Pycnoporus* and defined the genetic intraspecific variability of each according to geographic distribution.

Monophyly of this genus is strongly supported by both of the phylogenetic methods (Bayesian PP=0,98; ML bootstrap=78%). This is correlated with the presence of red,

extracellular pigments soluble in 5% KOH, a relevant morphological character at generic level (Fig. 4f). In addition, black KOH reaction on all parts of the basidiomes clearly separates *Pycnoporus* from *Trametes* (Ryvarden and Johansen 1980)

Genus *Leiotrametes* Welti & Courtec., gen. nov.

Mycobank MB 563399

Basidiomata lignatilia, annua vel perennia, coriacea, sessilia vel pseudostipitata nonnunquam basi discoidea, dimidiata usque ad fere circularia; contextus albidus usque ad cremeum, homogeneous; superficies hymenialis porata ad aspectum labyrinthiforme vel lenzitoideum vertens sive ex incremento radiali dissepimentorum sive ex porrectione radiali pororum; superficies superior semper glabra, zonis concentricis angustis interdum tantum marginalibus; frequens proventus excrescentiarum verrucosarum in basi superioris partis pilei. Structura tramae trimitica; hyphae generativae fibulatae; hyphae skeleticae incolores usque ad pallide flavas, aliquot repletae pigmento resinideo specialiter sub zonis concentricis coloratis pileipellis. Pigmenta parietalia nulla. Basidiosporae cylindratae, incolores, laeves, nec amyloideae nec cyanophilae. Cystidia hymenialia nulla. Saprotropha, in ligno mortuo Angiospermarum; caries alba. Distributio pantropicalis.

Holotypus hic designatus : *Polyporus lactineus* Berk., *Ann. Nat. Hist.* 10: 373 (1843)

Species studied: *Leiotrametes lactinea* (Berk.) Welti & Courtec. *comb. nov.* (basionym: *Polyporus lactineus* Berk., *Ann. Nat. Hist.* 10: 373, 1843; Mycobank MB 563400), *L. menziesii* (Berk.) Welti & Courtec. *comb. nov.* (basionym : *Polyporus menziesii* Berk., *Ann. Nat. Hist.* 10: 378, 1843; Mycobank MB 563401) & *Leiotrametes* sp.

Observations: in all our phylogenetic analyses (Figs. 1 and 3) this group of three tropical species separates from all other clades with strong support; the Bayesian analysis includes it in the “second clade” and suggests a sister position to the *Pycnoporus* + ‘*Trametes*’ *cingulata*-*T. lju-barksyi* lineage.

Leiotrametes lactinea was recently documented from South America by Ryvarden (2000) and from Southern USA by Vlasák and Kout (2011); descriptions of this material match the morphological characteristics of our numerous Guianese and Caribbean collections. Our collections of *L. menziesii* are the first reported from the Neotropics and their morphological features match those of *Polyporus menziesii* as described by Ryvarden and Johansen (1980) and our personal observations (isotype – K).

The third species here mentioned as ‘*Leiotrametes* sp.’ from French Guiana does not match any species known to us nor described in the literature. Nevertheless hymenial surface of this species could evoke the temperate *Daedalea quercina* (L.: Fr.) Fr., a phylogenetically unrelated species producing a brown rot (also showing other morphological

discrepancies). Since *Daedalea quercina* was mentioned by Patouillard (*in* Duss 1903) after a collection by Duss in Guadeloupe and taking into account its unlikely occurrence in the Carribean (see Courtecuisse and Welti 2011) it is possible that Duss's material represents this still undescribed *Leiotrametes* sp.

The main characteristic separating *Leiotrametes* from *Trametes* and *Pycnoporus* is the glabrous upper surface, the lack of black line under the pileipellis and of parietal crystals (red in *Pycnoporus*, colorless in *T. cingulata* and blue in *T. versicolor*). Another interesting character is the brown resinous substance filling the lumen of the skeletal hyphae in the pileipellis, particularly those concentrated in the narrow grayish concentric zones (Fig. 4e). They were also found in some species of *Trametes*: *T. gibbosa* and *T. villosa*.

A comparable resinous content also appears in *T. cingulata* and *T. ljubarskyi* but differs by its conspicuous accumulation in uppermost level inducing cellular walls rupture (Fig. 4g) and so generating a glossy and brown, surface. '*Lenzites*' *warnieri*, of still unsolved phylogenetic position, also showed similar resinous hyphae; nevertheless, they appear less abundant in the upper surface level and did not show resinous accumulation at the surface (Fig. 4e).

'*Trametes*' *cingulata* and '*Trametes*' *ljubarskyi*

The position of *Trametes cingulata* and *T. ljubarskyi* has already been shown to be ambiguous according to our study. However the Bayesian analyses on ITS + RPB2 (Fig. 1) and to a lesser degree on 28S rLSU, suggest a sister-clade relationship between both species and *Pycnoporus*. As a support to this hypothesis we detected crystals darkening in 5% KOH under the upper surface of *T. cingulata*. Furthermore, the orange-brown, dry basidiomes of this species, as well as its tendency to turn blackish with 5% KOH 5%, at a lower degree the characteristic of *Pycnoporus* species (red basidiomes and KOH reaction).

So far a close relationship between *Trametes ljubarskyi* and *T. cingulata* has never been mentioned, probably because of their distinguishing morphological characteristics (Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1986; Ryvarden and Gilbertson 1994). The Asian and African distribution of *T. cingulata* versus Europe for *T. ljubarskyi*; the thickness of the basidiomes: 2–10 mm. for *T. cingulata* versus 30 mm. for *T. ljubarskyi*; the pore pattern and dissepiments: round and regular, 4–6 per mm., fairly thick dissepiments for *T. cingulata* versus circular to angular, 3–4 per mm., thin dissepiments for *T. ljubarskyi* and strikingly different upper surface: frequently concentrically sulcate and whitish to ochraceous becoming sooty black spreading from the base for *T. cingulata* versus azonate and whitish to ochraceous becoming pale grayish brown in

spots for *T. ljubarskyi*. Furthermore, according to our own observations, basidiomes of *T. ljubarskyi* are paler than those of the isotype of *T. cingulata* which is rather red brown.

Nevertheless these 2 species share several common features: somewhat broadly ellipsoid basidiospores (a very unusual character in this group) with similar sizes strictly pored hymenial surface remaining so during development of the basidiomes and glabrous and somewhat glossy upper surface.

'*Lenzites*' *warnieri*

As mentioned above, '*Lenzites*' *warnieri* creates a unique branch according to the topology of the Bayesian tree. This unresolved phylogenetic position is reflected in the fact that the species possesses many morphological features from other genera, and this ultimately would place *L. warnieri* in a separate genus.

This Mediterranean species is always glabrous and dull, with strictly lamellate hymenial surface (character in common with *T. betulina*), without parietal crystals on the hyphae (*Artolenzites*, *Leiotrametes*). *L. warnieri* shows superficial skeletal hyphae filled with a brown resinous content not accumulating at the apex (Fig. 4e) and its abhymenial surface turns deep brown with 5% KOH. These 2 features also characterize species of the genus *Leiotrametes*.

This supports one of the striking points emphasized in this study: there is no correlation at all between type of hymenial surface and phylogenetic position of a species within the *Trametes*-group. The lamellate *Lenzites warnieri*, *Artolenzites elegans* and *T. betulina* are not monophyletic and show no close relationship. *Lenzites* is therefore discarded.

Unfortunately, because of the absence or very weak development of the hymenium in most of our specimens, we cannot rule about the taxonomic significance of the hymenial sword-like pseudo-cystidia previously mentioned for *T. betulina*, *T. gibbosa* and *L. warnieri* (Ryvarden and Gilbertson 1993; Tomšovský et al. 2006). For the same reason, the basidiospores could not be properly analyzed in these species. Nevertheless, while Pieri and Rivoire (2007) revealed that pseudocystidia were not found in *T. gibbosa*, Ryvarden and Johansen (1980) mentioned the presence of such pseudocystidia in the hymenium of *Lenzites acutus* (with pored to lamellate hymenial surface) and *Trametes cubensis* (strictly pored) (Gilbertson and Ryvarden 1987; Ryvarden and Johansen 1980). Thus, further investigations should be undertaken to evaluate the relevance of pseudo-cystidia at generic level.

Although Ko (2000) showed recently on the basis of ITS sequences that *Daedaleopsis flavida* (Lév.) A. Roy & A. Mitra clustered with *Pycnoporus*, Ryvarden and Johansen

(1980) considered this taxon in the synonymy of *L. acutus*, a species closely related by several morphologic similarities to *L. warnieri* (Gilbertson and Ryvarden 1987). Morphologic description (Ryvarden and Johansen 1980) and molecular results of *L. acutus* remind us of our Guianese species named *Leiotrametes* sp. but thorough comparison of both species finally reveals no real morphological similarities.

Genus *Artolenzites* Falck, *Hausschwammforsh* 3: 37 (1909)

Type species: *Daedalea repanda* Pers. (= *A. elegans* (Spreng.: Fr.) Teixeira)

Species studied: *Artolenzites elegans* (Spreng.: Fr.) Teixeira, *Rev. Brasil. Bot.* 9(1):43 (1986).

Observations: So far only one species is recognized in this genus, with an abundant synonymy (Ryvarden and Johansen 1980). However, we noted several morphological and genetic differences between our collections from New Caledonia and French West Indies, and do not exclude that the type species of the genus - *Daedalea repanda* Pers., originally from New Guinea (Gaudichaud-Beaupré 1827) might be different from *L. elegans* from Guadeloupe (Fries 1821). Further comparisons within this cosmopolitan and polymorphic species are required.

The morphology of specimens in this clade matches those formerly described by Vlasák and Kout (2011) and Ryvarden and Johansen (1980). All basidiomes are white to cream-coloured, glabrous, of large size, spatulate to reniform with acute margin, sometimes with stipe-like base attached to the substrate with a disc. The hymenophore is narrowly daedaleoid to lamellate (Fig. 5a). All possess hyphal pegs.

As already stated above the hymenial surface cannot be considered as a separating character at generic level so that Ryvarden (1991) was right on this very point in considering *Artolenzites* as a taxonomic synonym of *Trametes*. However, since molecular results clearly separate *T. elegans* from the core *Trametes*, the type of abhymenial surface turns out to present the main feature for distinguishing *Artolenzites* from *Trametes*.

Thus, the aspect and structure of the upper surface are much more significant than the hymenial pattern to separate the genera from the *Trametes* group.

Finally, *Artolenzites* is distinguished from the other glabrous genera (*Pycnoporus*, *Leiotrametes*, '*Lenzites*' *warnieri* and the *T.cingulata*-*T. ljubarskyi* clade) by lack of both resinous accumulation in the upper surface skeletal hyphae and parietal crystals (Fig. 4d).

Key to genera of the *Trametes* group (see Table 3)

1. Upper surface pubescent to hirsute.....genus *Trametes*
1. Upper surface glabrous.....2
2. Basidiome red, incrusting pigment present as orange-red parietal crystals soluble in 5% KOHgenus *Pycnoporus*
2. Basidiome not red, lacking red incrusting pigment.....3

3. No part of basidiome darkening in 5% KOHgenus *Artolenzites*
3. Entire basidiome or at least upper surface darkening to black or dark brown with 5% KOH4
4. Entire basidiome initially orange-brown becoming black with 5% KOH. Upper surface glossy, hymenophore strictly pored.....*Trametes cingulata*
4. Only upper surface or context becoming deep brown with 5% KOH. Superficial layer of pileipellis with numerous skeletal hyphae filled with brown resinous contents.....5
5. Upper surface glossy. Hymenial surface strictly pored, context staining brown with 5% KOH.....*Trametes ljubarskyi*
5. Upper surface dull. Hymenial surface pored to lamellate, upper surface staining brown with 5% KOH.....6
6. Temperate to Mediterranean species. Hymenophore strictly lamellate. Basidiome never pseudostipitate, lacking narrow, coloured, concentric zones on the abhymenial surface.....*Lenzites warnieri*
6. Tropical species. Hymenophore pored or daedalean to lamellate. Basidiome sometimes pseudostipitate, with mostly numerous and narrow grayish or brownish, concentric zones on abhymenial surface.....genus *Leiotrametes*

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