



Cellulariella warnieri (Basidiomycota, Polyporales) and its doubles

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Abstract

Species of *Polyporales* with a lamelliform hymenophore were traditionally classified in the genus *Lenzites*, until recent phylogenetic analyses revealed their affinities with various poroid lineages, leading to the re-classification of most of them. Nevertheless, the phylogenetic relationships of the lamellate *Lenzites warnieri* Durieu & Mont. have yet to be resolved. The recent erection of *Cellulariella* Zmitr. & V. Malysheva to encompass *L. warnieri* and *L. acuta* did little to disentangle the cross-synonymies between lamellate polypores of the *Trametes* group. To clarify the phylogenetic affinities of *L. warnieri*, we combined molecular data based on five markers (LSU, ITS, EF1- α , RPB1, RPB2) with morphological features of various collections belonging to the *Trametes* clade. In Bayesian phylogenetic reconstructions based on RPB1, RPB2 and EF1- α , *L. warnieri* has an unresolved position on globally poorly supported cladograms. Conversely, phylogenetic analyses of the combined (ITS+LSU) sequences support a monophyletic clade encompassing *L. warnieri* and *L. acuta*, which forms a sister group, within a broader clade encompassing *Leiotrametes*, *Pycnoporus* and the sub-clade *T. ljubarskyi* – *T. cingulata*. These phylogenetic results are also supported by micromorphological data. Here we redefine the genus *Cellulariella* based on the moderate amount of scarcely branched, not flagelliform binding hyphae in the context, the pointed and fusiform hyphal ends protruding through the hymenium and a strictly lamelliform (lenzitoid) hymenophore. A lectotype is designated for *Cellulariella warnieri*. The name *Lenzites acuta* has also been misapplied to a species of *Leiotrametes*, possibly identical to *Lenzites tenuis*. *Lenzites tenuis* is here recombined as *Leiotrametes tenuis* comb. nov.

Keywords – *Lenzites* – phylogeny – *Polyporaceae* – taxonomy – *Trametes*

Introduction

In the order *Polyporales* Gäum. (Basidiomycota, Agaricomycetes), most species with a lamelliform hymenophore were traditionally classified in the genus *Lenzites* Fr. (Fries 1835), until their affinities with poroid species led to the re-classification of most of them. Currently, as confirmed by molecular data, the type species of *Lenzites*, *Lenzites betulinus* (L.) Fr. is included in

the mostly poroid genus *Trametes* Fr. (Justo & Hibbett 2011, Welti et al. 2012). Consequently, all species formerly classified in *Lenzites* because of their lamelliform (or, by extension, daedaleoid) hymenophore have already been assigned to a genus in conformity with phylogenetic data, but for a small minority. Amongst them, the Mediterranean species *Lenzites warnieri* Durieu & Mont., originally described from Algeria, is easy to identify but has not yet found a natural place in modern systematics despite available molecular sequences. Vellinga et al. (2015) reported *Lenzites warnieri* forming an unsupported branch within the *Trametes s. lat.* clade, which makes its generic attribution undecidable, especially if *Trametes* were split into several genera as proposed by Welti et al. (2012). Meanwhile, exposing their personal interpretation of still unsupported phylogenetic reconstructions of *Trametes s. lat.*, Zmitrovich & Malysheva (2013) created *Cellulariella* Zmitrovich & V. Malysheva, based on *Lenzites acuta* Berk. along with *L. warnieri*, without further justification.

Before being confirmed as an autonomous species by David (1967), *L. warnieri* was often interpreted as a lamellate form of *Daedalea quercina* (Kavina & Pilát 1936). Microscopic features led David (op. cit.) to consider it (under the posterior synonym *Lenzites reichardtii* Schulzer) as a closer relative of *Lenzites betulinus*, a conclusion supported by phylogenetic results and physiology (Nobles 1958, Welti et al. 2012).

During our fungal surveys in the Neotropics (French Guiana and the Lesser Antilles), we learned about another unnamed species within *Leiotrametes* Welti & Courtecuisse. This species is characterized by a highly variable hymenophore and was probably identified as «*Daedalea quercina*» by Patouillard (in Duss 1904) from Guadeloupe (Welti et al. 2012). This confusion extends to *D. tenuis* Berk., a tropical Asian species also characterized by a variable hymenophore that was considered by Berkeley (1842) to be close “in many respects” to *D. quercina*.

Compared to *D. tenuis*, the lamelliform hymenophore of *Lenzites warnieri* is a constant feature, although the primordial zone may be locally daedalean in some specimens (Rivoire 2020). Conversely, Ryvarden & Johansen (1980) described *L. acuta* with a highly variable hymenophore, from lamellate to poroid. Further bibliographic investigations and comparisons with herbarium collections suggested that the long list of synonyms enumerated, e.g. by Ryvarden & Johansen (1980), Zmitrovich & Malysheva (2013) or MycoBank (www.mycobank.org, continuously updated) hides important morphological differences. Heterogeneity of both hymenophoral and microscopical features within *L. acuta s. lat.* required additional investigations.

This study aims at clarify the phylogenetic position of *Lenzites warnieri*, to discuss the legitimacy of *Cellulariella* within the *Trametes*-clade (Welti et al. 2012) and to refine its circumscription through the study of the type collections of *L. acuta*, *L. warnieri* and an additional collection of the latter from the Algerian type locality. This study aims also at disentangle the cross-synonymies between *L. acuta* and *D. tenuis*.

Materials & Methods

Microscopical observations

Thin radial and transversal sections were made on various exsiccata of molecularly confirmed collections of *L. warnieri*, holotype specimens of *L. acuta* and *Daedalea tenuis* Berk., and various species of *Trametes s.str.*, *Artolenzites* Falck, *Leiotrametes* and *Pycnoporus* P. Karst. A total of 29 specimens were analyzed (Table 1). Three staining processes were used to highlight the hyphal constitution: 1) stained with Congo red, then examined, 2) stained with Congo red before examination with KOH 5%, 3) stained 10 min in Congo red, washed in KOH 5%, stained again 10 min in Cotton blue lactophenol, observed in 1% Ruthenium red in aqueous solution.

DNA extraction and PCR amplifications

Genomic DNA was extracted from the context of 5 dry specimens and 2 dikaryotic isolates (Table 2). Each sample was incubated 1 h at 65°C in 500 µL extraction buffer (100 mM Tris/HCl pH 8.0, 20 mM EDTA, 1.4 M NaCl, 2% (w/v) CTAB, 0.2% (v/v) 2-mercaptoethanol and 0.1 mg

mL⁻¹ proteinase K). One volume of chloroform/isoamyl alcohol (24/1; v/v) was added after incubation. The mixture was gently mixed and centrifuged 10 min at 9500 g.

Table 1 List of specimens studied for morphology.

Genus	Species	Herbarium number
<i>Artolenzites</i>	<i>A. elegans</i>	SW/Mart10-91 (LIP)
	<i>A. elegans</i>	SW/Mart11-07 (LIP)
	<i>A. elegans</i>	SW/Mart10-78 (LIP)
<i>Cellulariella</i>	<i>C. warnieri</i>	ND169 (LIP)
	<i>C. warnieri</i>	Epitype 0001798 (LIP)
	<i>C. warnieri</i>	Neotype PC 0723637
	<i>Lenzites acuta</i>	Holotype K(M) 168874
<i>Leiotrametes</i>	<i>L. lactinea</i>	SW/Guad10-42 (LIP)
	<i>L. lactinea</i>	SW/Mart10-93 (LIP)
	<i>L. lactinea</i>	GUY/08-16 (LIP)
	<i>L. lactinea</i>	Guad/10-181 (LIP)
	<i>L. menziesii</i>	SW/Mart14-16 (LIP)
	<i>L. menziesii</i>	SW/Mart15-22 (LIP)
	<i>L. sp.</i>	SW/Guy12-78 (LIP)
	<i>L. sp.</i>	SW/Guy12-39 (LIP)
<i>Pycnoporus</i>	<i>Daedalea tenuis</i>	Holotype K(M) Cuming 2037
	<i>P. sanguineus</i>	SW/Mart08-02 (LIP)
	<i>P. sanguineus</i>	SW/Mart06-17 (LIP)
<i>Trametes</i>	<i>P. sanguineus</i>	SW/Mart06-18 (LIP)
	<i>T. versicolor</i>	SW/F_NSR16-02 (LIP)
	<i>T. betulina</i>	SW/F_NSR16-01 (LIP)
	<i>T. hirsuta</i>	SW/F_NSR16-03 (LIP)
	<i>T. maxima</i>	RC/GUAD10-87 (LIP)
	<i>T. maxima</i>	SW/Mart10-14 (LIP)
	<i>T. polyzona</i>	RC/Bali13-005 (LIP)
	<i>T. polyzona</i>	SW/Mart15-56 (LIP)
	<i>T. polyzona</i>	SW/Mart11-05 (LIP)
	<i>T. cingulata</i>	unknown
<i>T. ljubarskyi</i>	MOU139/957 (LIP)	

The upper phase was placed in a new tube and gently mixed with one volume of isopropanol before centrifugation. The resulting pellet was rinsed in 70% (v/v) ethanol and centrifuged. The ethanol was then removed and the pellet was air-dried in order to remove any remaining traces. The pellet was finally solubilized in TE buffer (10 mM Tris/HCl pH 8. 0.1 mM EDTA) at 4°C overnight. PCR reactions were performed in a final volume of 50 µL containing 1 µL of DNA, 80 mM Tris·HCl pH 9.4, 20 mM (NH₄)₂SO₄, 2.5 mM MgCl₂, 0.2% (w/v) Tween-20, 0.2 µM dNTPs, 0.2 µM of each primer and 1.25U Taq DNA Polymerase (Euromedex, Souffelweyersheim, France). Primers used for the ITS PCR amplification were ITS-1F (CTTGGTCATTTAGAGGAAGTAA) (Gardes & Bruns 1993) and ITS4 (TCCTCCGCTTATTGATATGC) (White et al. 1990). Primers used to amplify RPB2 were bRPB2-6F (TGGGGYATGGTNTGYCCYGC) and bRPB2-7.1R (CCCATRGCTGYTTMCCCATDGC) (Matheny et al. 2002). Primers used for the LSU region PCR amplification were LR0R (ACCCGCTGAACTTAAGC) and LR5 (TCCTGAGGGAACTTCG) (Vilgalys & Hester 1990). Primers used to amplify RPB1 were RPB1-Af (GARTGYCCDGGDCAYYTYGG) and RPB1-Cr (CCNGCDATNTRTTRTCCATRTA) (Matheny et al. 2002). To amplify the elongation factor EF1-α the primers were EF1-983F (GCYCCYGGHCAYCGTGAYTTYAT) and EF1-2218R (ATGACACCRACRGCACRGTYTG) (Rehner & Buckley 2005). PCR reactions for ITS and RPB2 were conducted as follows: an initial denaturation at 95°C for 2 minutes followed by 40 cycles of 30 s at 95°C; 30 s at 53°C for ITS or 50°C for RPB2; 1 min at 72°C followed by a final

step at 72°C during 5 min. 5 µL of PCR products were resolved at 8 V.cm⁻¹ on a 1.5% (w/v) agarose gel with 0.5 µg. mL⁻¹ ethidium bromide in TAE buffer (40 mM Tris/acetate pH 8.3, 1 mM EDTA). PCR reactions for LSU, RPB1 and EF1- α sequences were conducted as follows: an initial denaturation at 94°C for 3 min followed by 10 cycles of 30 s at 94°C, 60 s at 65 °C, 1 min 30 at 72°C decreasing the temperature by 1°C per cycle. Then 35 cycles of 30 s denaturation at 94°C, 60 s at 55°C and 1 min 30 at 72°C followed by a final step at 72°C during 10 min.

Regarding the strain BRFM 972, PCR reactions for LSU were conducted as follows: an initial denaturation step at 94°C for 2 min followed by 40 cycles of 15 s denaturation at 94°C, 30 s annealing at 51°C and 1 min elongation at 72°C. A final extension step at 72°C for 7 min was added at the end of the PCR. PCR products were then sequenced by the Sanger method with ITS-1F, RPB2-b6F, LR0R, RPB1-AF and EF1-983F as sequencing primers.

Table 2 List of the new sequences generated.

Species	Strain/Herbarium number	Country	ITS	LSU
<i>Cellulariella (Lenzites) warnieri</i>	BRFM 972	France	—	MW435560
<i>Cellulariella (Lenzites) warnieri</i>	LIP 0001798	Algeria	MW435553	—
<i>Trametes</i> sp.	SWMart14_15	Martinique	MW435554	MW435561
<i>Trametes membranacea</i>	SWMart15_15	Martinique	MW435555	—
<i>Trametes pavonia</i>	BRFM 1554	Martinique	MW435556	—
<i>Trametes polyzona</i>	SWMart15_56	Martinique	MW435557	—
<i>Trametes polyzona</i>	RC Bali 13005110	Indonesia	MW435558	—

Sequence alignments

Sequences generated for this study and those obtained from GenBank (Table 3) were aligned under Clustal W (Higgins et al. 1994) and carefully refined manually on the editor in Mega6 (Tamura et al. 2013). ITS, RPB2, RPB1, EF1- α , and LSU sequences have respectively an alignment of 560 bp with 173 variable regions and 121 parsimony characters, 700 bp with 310 variable regions and 261 parsimony characters, 705 bp with 298 variable regions and 240 parsimony characters, 456 bp with 155 variable regions and 121 parsimony characters and 821 bp with 112 variable regions and 80 parsimony characters. For the combined datasets, ITS and LSU sequences were aligned individually then concatenate. Combined sequences have an alignment of 1396 bp with 350 variable regions and 222 parsimony characters.

Phylogenetic analyses

For each marker a Bayesian analysis was monitored under Mr Bayes v3.1 (Ronquist & Huelsenbeck 2003). According to the Bayesian Information Criterium (BIC) score, SIM+I+G were chosen for RPB1, ITS, LSU and the combined sequences (ITS+LSU), GTR+I+G for RPB2 and K80+I+G for EF1- α sequence 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 sampled in every hundred trees. The first 5,000 trees were excluded from our analyses. For all Bayesian analyses, 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 50% majority rules with all compatible partitions. Each method gap was scored as missing and trees were rooted with *Lopharia cinerascens* (Schwein.) G. Cunn.

A Bayesian 50% majority rule consensus tree was shown for each gene. The alignments and phylogenetic trees were deposited in TreeBASE (Reviewer access URL: <http://purl.org/phylo/treebase/phyloWS/study/TB2:S28879?x-access-code=ec9ba09104ff2683885b1c168fb72efc&format=html>).

Table 3 Sequence list from GenBank.

Species	Source	No.	GenBank Accession No.		Country of origin
			LSU	ITS	
<i>Cellulariella warnieri</i>	voucher	MH72	–	MN909986	Pakistan
<i>Corioloopsis polyzona</i>	strain	OH-184-sp	AY333817	–	Taiwan
<i>Daedalea microsticta</i>	voucher	18612	–	FJ403209	Costa Rica
<i>Daedaleopsis flavida</i>	strain	5A	JF712849	–	India
<i>Leiotrametes</i> sp.	strain	CIRM-BRFM 1056	–	JN645059	French Guiana
<i>Leiotrametes</i> sp.	strain	CIRM-BRFM 1080	–	JN645063	French Guiana
<i>Leiotrametes menziesii</i>	strain	CIRM-BRFM 1369	–	JN645085	French West Indies
<i>Leiotrametes menziesii</i>	strain	CIRM-BRFM 1281	–	JN645071	French West Indies
<i>Leiotrametes menziesii</i>	strain	CIRM-BRFM 1368	–	JN645103	French West Indies
<i>Leiotrametes lactinea</i>	strain	CIRM-BRFM 1282	–	JN645072	French West Indies
<i>Leiotrametes lactinea</i>	strain	CIRM-BRFM 1371	–	JN645104	French West Indies
<i>Leiotrametes lactinea</i>	strain	CIRM-BRFM 1251	–	JN645069	French Guiana
<i>Lenzites acuta</i>	voucher	Cui 10091	KX900689	KX900642	China
<i>Lenzites acuta</i>	voucher	M0138338	–	KF573028	New Guinea
<i>Lenzites acuta</i>	voucher	Dai 13595	KX900691	KX900644	China
<i>Lenzites acuta</i>	voucher	Dai 13103	KX900690	KX900643	China
<i>Lenzites acuta</i>	voucher	Dai 11621	–	KC848333	China
<i>Lenzites betulinus</i>	strain	DAOM180504	AF261543	–	Canada
<i>Lenzites betulinus</i>	voucher	Cui 7234	KC848389	KC848304	China
<i>Lenzites vespacea</i>	voucher	Cui 8758	KC848339	–	China
<i>Lenzites vespacea</i>	voucher	M0138336	–	KF573027	New Guinea
<i>Lenzites vespacea</i>	voucher	Dai 13613	KX900692	KX900645	China
<i>Lenzites warnieri</i>	strain	CIRM-BRFM 972	–	GU731567	France
<i>Lenzites warnieri</i>	voucher	UOC_KAUNP _MK29	–	KP794599	Sri Lanka
<i>Lenzites warnieri</i>	strain	JZ27	–	MG719284	India
<i>Lenzites warnieri</i>	voucher	UOC_KAUNP _K05	–	KR867658	Sri Lanka
<i>Lopharia cinerascens</i>	strain	EL63_97	AY586687	–	USA
<i>Lopharia cinerascens</i>	strain	CBS 125884	MH875543	MH864085	New Zealand
<i>Lopharia cinerascens</i>	voucher	PDD_995857	–	JQ694103	New Zealand
<i>Pycnoporus cinnabarinus</i>	strain	KHL8557	AY586703	–	Sweden
<i>Pycnoporus cinnabarinus</i>	strain	MUCL-30555	–	AF363764	Belgium
<i>Pycnoporus cinnabarinus</i>	strain	DAOM72065	AF393074	–	Canada
<i>Pycnoporus coccineus</i>	strain	MUCL-38525	–	JN645094	Australia
<i>Pycnoporus coccineus</i>	voucher	Cui 7096	KC848414	KC848330	China
<i>Pycnoporus puniceus</i>	strain	MUCL-47087	–	FJ234199	Cuba
<i>Pycnoporus puniceus</i>	isolate	BCC27595	FJ372708	FJ372686	Thailand
<i>Pycnoporus sanguineus</i>	isolate	M66	HM595619	HM595574	China

Table 3 Continued.

Species	Source	No.	GenBank Accession No.		Country of origin
			LSU	ITS	
<i>Pycnoporus sanguineus</i>	strain	CIRM-BRFM 896		FJ234188	French Guina
<i>Pycnoporus sp</i>	isolate	ZW02-30	AY684160	–	–
<i>Trametes cingulata</i>	strain	MUCL-40167	–	JN645075	Zimbabwe
<i>Trametes cingulata</i>	strain	DMC814	KC589159	KC589133	Cameroon
<i>Trametes cinnabarina</i>	strain	CBS 375.34	MH867081	MH855576	Belgium
<i>Trametes cinnabarina</i>	strain	DAOM72065	AF261536	–	Canada
<i>Trametes conchifer</i>	voucher	Dai 8367	–	KC848276	China
<i>Trametes conchifer</i>	voucher	FP106793sp	JN164797	JN164924	USA
<i>Trametes cubensis</i>	voucher	AJ177	JN164787	JN164905	USA
<i>Trametes cubensis</i>	voucher	TJV93	–	JN164923	USA
<i>Trametes drummondii</i>	voucher	BJFC12708	KC848391	–	China
<i>Trametes duplexa</i>	voucher	Dai 12039	KC848348	KC848262	China
<i>Trametes ectypa</i>	voucher	FP106037T	JN164803	JN164929	USA
<i>Trametes ectypa</i>	voucher	FP103976sp	–	JN164961	USA
<i>Trametes elegans</i>	strain	CIRM-BRFM 1280	–	JN645070	New Caledonia
<i>Trametes elegans</i>	strain	CIRM-BRFM 1122	–	JN645066	French Guiana
<i>Trametes elegans</i>	strain	CIRM-BRFM 1378	–	JN645105	French West Indies
<i>Trametes elegans</i>	voucher	FP105679sp	JN164799	JN164944	USA
<i>Trametes elegans</i>	voucher	Dai 10748	JN048785	JN048766	China
<i>Trametes ellipsoidea</i>	voucher	Yuan 3453	KC848345	KC848259	China
<i>Trametes ellipsoidea</i>	voucher	Cui 8384	KC848337	–	China
<i>Trametes ellipsoidea</i>	voucher	Cui 6259	KC848335	JN048767	China
<i>Trametes gibbosa</i>	strain	Wu 9411-7	AY351924	–	Taiwan
<i>Trametes gibbosa</i>	voucher	Cui 7390	KC848387	KC848302	China
<i>Trametes hirsuta</i>	strain	CIRM-BRFM 994	–	GU731578	France
<i>Trametes hirsuta</i>	voucher	Dai 12319	KC848383	KC848298	China
<i>Trametes hirsuta</i>	strain	Wu 9410-39	AY351922	–	Taiwan
<i>Trametes junipericola</i>	voucher	HUBO 6916	–	AY684171	Italy
<i>Trametes junipericola</i>	voucher	145295 (O)	KC017763	KC017758	China
<i>Trametes aff. junipericola</i>	strain	BRFM 25	–	JN645088	China
<i>Trametes ljubarskyi</i>	voucher	Li 286	KC848415	KC848331	China
<i>Trametes ljubarskyi</i>	strain	CIRM-BRFM 957	–	JN645097	France
<i>Trametes ljubarskyi</i>	voucher	PRM_622107	–	AY684174	France
<i>Trametes ljubarskyi</i>	voucher	Wei 1653	KC848416	KC848332	China
<i>Trametes manilaensis</i>	voucher	Dai 10747	KC848398	KC848314	China
<i>Trametes cf manilaensis</i>	voucher	Cui 6240	–	KC848321	China
<i>Trametes marianna</i>	voucher	BJFC12714	KC848418	KC848334	China
<i>Trametes maxima</i>	voucher	Dai 12274	KC848394	KC848310	China
<i>Trametes maxima</i>	strain	CIRM-BRFM 1367	–	JN645084	French West Indies
<i>Trametes maxima</i>	voucher	UOC_KAUNP_MK78b	–	KR907875	Sri Lanka
<i>Trametes maxima</i>	voucher	Zhou 147	KC848393	–	China
<i>Trametes membranacea</i>	voucher	PRSC82	JN164805	JN164945	Puerto Rico

Table 3 Continued.

Species	Source	No.	GenBank Accession No.		Country of origin
			LSU	ITS	
<i>Trametes menziesii</i>	Voucher	Yuan 3555	KC848410	KC848326	China
<i>Trametes meyenii</i>	strain	CBS 453.76	MH872762	MH860991	India
<i>Trametes aff. meyenii</i>	strain	CIRM-BRFM 1121	–	JN645065	French Guiana
<i>Trametes aff. meyenii</i>	strain	CIRM-BRFM 1361	–	JN645083	French Guiana
<i>Trametes ochracea</i>	voucher	HHB13445sp	JN164812	JN164954	USA
<i>Trametes ochracea</i>	voucher	Dai 2005	KC848357	–	China
<i>Trametes ochracea</i>	voucher	Yuan 2477	KC848356	–	China
<i>Trametes ochracea</i>	strain	CBS 257.74	–	JN645077	Netherland
<i>Trametes orientalis</i>	strain	Wu 9708-190	AY351920	–	Taiwan
<i>Trametes pavonia</i>	voucher	FP103050sp	JN164806	JN164958	USA
<i>Trametes pocas</i>	voucher	Dai 11577	KC848340	KC848253	China
<i>Trametes pocas</i>	voucher	Dai 11577	–	KC848253	China
<i>Trametes pocas</i>	strain	Wu 9901-18	AY351919	–	Taiwan
<i>Trametes polyzona</i>	voucher	OAB0195	MK736961	MK736986	Benin
<i>Trametes polyzona</i>	strain	CBS 319.36	–	JN645078	Zimbabwe
<i>Trametes polyzona</i>	strain	WR710-1	–	JN848329	Thailand
<i>Trametes polyzona</i>	strain	RYNF13	–	KT281117	Thailand
<i>Trametes pubescens</i>	voucher	FP101414sp	JN164811	JN164963	USA
<i>Trametes pubescens</i>	voucher	Cui 7569	KC848377	–	China
<i>Trametes pubescens</i>	voucher	Cui 5904	KC848376	–	China
<i>Trametes pubescens</i>	voucher	Cui 7571	KC848375	–	China
<i>Trametes sanguinea</i>	voucher	PRSC95	JN164795	JN164982	Puerto Rico
<i>Trametes socotrana</i>	voucher	OAB0162	MK736963	MK736988	Benin
<i>Trametes socotrana</i>	voucher	OAB0131	MK736962	MK736987	Benin
<i>Trametes socotrana</i>	strain	MUCL-38649	–	JN645073	Zimbabwe
<i>Trametes socotrana</i>	voucher	BJFC12724	KC848397	KC848313	China
<i>Trametes sp</i>	voucher	Yuan 6455	KC848386	–	China
<i>Trametes sp</i>	voucher	Zhou 223	KC848346	–	China
<i>Trametes stipitata</i>	voucher	Yuan 3273	KC848360	KC848275	China
<i>Trametes suaveolens</i>	strain	CBS 296.33	MH866480	MH855012	Germany
<i>Trametes suaveolens</i>	strain	CIRM-BRFM 578	–	JN645090	France
<i>Trametes suaveolens</i>	strain	DAOM196328	AF261537	–	Canada
<i>Trametes subsuaveolens</i>	voucher	Cui 269	KC907404	–	China
<i>Trametes tephroleuca</i>	voucher	Wei 1518	KC848379	–	China
<i>Trametes tephroleuca</i>	voucher	Cui 7977	KC848381	KC848296	China
<i>Trametes thujae</i>	Voucher	Dai 4953	KC848373	KC848288	China
<i>Trametes thujae</i>	voucher	Dai 5055	KC848371	–	China
<i>Trametes velutina</i>	voucher	Dai 10149	KC848358	–	China
<i>Trametes versicolor</i>	strain	IUM00100	DQ208414	–	Korea
<i>Trametes versicolor</i>	strain	CBS 296.33	MH866900	MH855444	Netherlands
<i>Trametes versicolor</i>	strain	CIRM-BRFM 1219	–	JN645113	France
<i>Trametes villosa</i>	voucher	FP71974R	JN164810	–	USA
<i>Trametes villosa</i>	strain	CBS 334.49	MH868069	MH868069	Argentina
<i>Trametes_villosa</i>	strain	CIRM-BRFM 1375	–	JN645101	French West Indies

Results

Hyphal features and stains

Twenty-nine specimens were used to study representing 15 species of *Trametes s. str.*, *Artolenzites*, *Leiotrametes*, and *Pycnoporus* (Table 1). Different staining reactions were tested (data not shown) on thin sections of various orientations across the basidiome. The retained techniques (see Materials and Methods) were those providing the best resolution of hyphal systems, by differentially staining generative, skeletal, and binding hyphae.

Generative hyphae are always thin-walled and colorless in both water and KOH. When stained with method 3 (see Materials and Methods), their content strongly fixes Cotton blue (especially in clamps and around septa) while Congo red stains the wall surfaces.

Skeletal hyphae remain colorless in both Congo red and Cotton blue while binding hyphae strongly fix Congo red (wall and content) and sometimes show a red color gradient with KOH, lumen being more colorful. Ruthenium red and Cotton blue (CB) provide a global view of hyphal organization and reveal mucoid deposits.

Morphological inferences in the *Trametes*-clade

As shown in Table 4, the combination of four relevant micro-morphological characteristics allowed a clear-cut discrimination between the studied taxa.

Upper side pileus structure

Welti et al. (2012) described 7 types of abhymenial pileus structures within the *Trametes* clade. Among them, types “e” (illustrated by *Leiotrametes* spp., *Lenzites warnieri*, and *L. acuta*) and “g” (illustrated by *Trametes cingulata* Berk. and *Trametes ljubarskyi* Pilát) are characterized by a surface structures composed of superficial skeletal hyphae filled with brown resinous content, responsible for a resinoid matrix on mature specimens in type g. Observations of a specimen of *L. warnieri* (LIP 0001798), recently collected in Algeria, improved our understanding of the development of the upper side structure of this species, which evolves, either with aging or for still unknown reasons, from type “e” to type “g”. Such an intermixed structure with brown intracellular pigment is also found in species of the genus *Leiotrametes* and in “*Daedalea*” *tenuis*. However, in these species, it does not evolve into a resinoid matrix. Species in the genera *Trametes*, *Pycnoporus*, and *Artolenzites* do not produce resiniferous hyphae.

Hymenial hyphal ends

They arise either from binding hyphae (Ryvarden & Gilbertson 1993) or from subhymenial skeletal hyphae (Zmitrovich 2018). This feature associated with a lamelliform hymenophore distinguished *Lenzites sensu* Ryvarden & Gilbertson (1993) from the genus *Trametes s. str.* Only *T. betulina* (L.) Pilát and *L. acuta* show pointed fusiform hyphal ends, coming from the binding hyphae and protruding through the hymenium, comparable with those of *L. warnieri* (Figs 1-2). Other hymenial hyphal ends were also found in *Artolenzites*, *Leiotrametes*, and *D. tenuis*, but they showed morphological differences: they were either funnel-shaped, obtuse or rounded, coming from the binding hyphae and sometimes protruding through the hymenium such as in *Leiotrametes* and *D. tenuis* (Fig. 3), or full of gelled substances and clavate, arising from skeletal hyphae but not protruding or barely through the hymenium, such as in *Artolenzites*.

Binding hyphae of context – abundance and description

The hyphal system in the context is duplex (upper part dimitic with skeletal hyphae and lower part trimitic) for *L. warnieri*, and *T. ljubarskyi*, while it is uniformly trimitic in the other genera of the *Trametes* clade as well as in *T. cingulata*, *L. acuta*, and *D. tenuis*. Only *Leiotrametes* and *Trametes s. str.* show a significant amount of entangled binding hyphae, intricately branched with flagelliform ends. The moderate amount of scarcely branched binding hyphae without flagelliform ends makes the context of *Artolenzites* and *L. acuta* easy to cut, and even easier for *L. warnieri*.

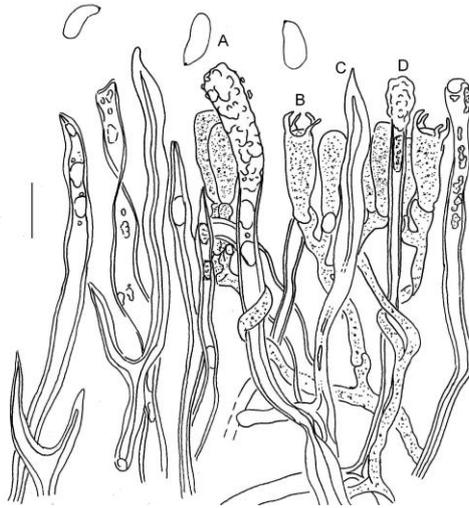


Fig. 1 – Hymenium of *Cellulariella warnieri* (neotypus and epitypus). A Basidiospores. B Basidia. C Hymenial pointed hyphal ends protruding from the hymenium. D Non-septate terminal segments with crystalline encrustation. Scale bar: 10 μ m.

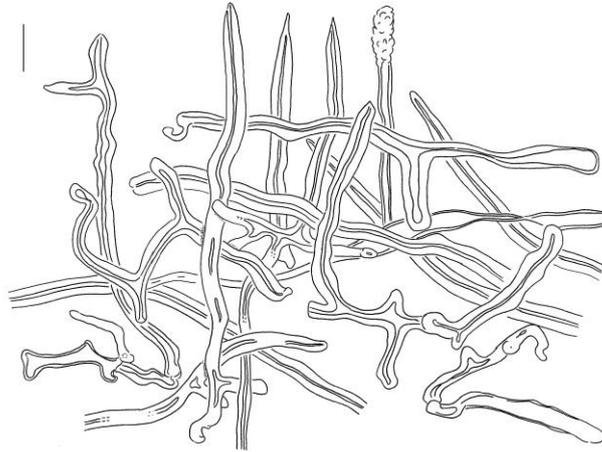


Fig. 2 – Trama of *Cellulariella warnieri* (neotypus). Scale bar: 10 μ m.

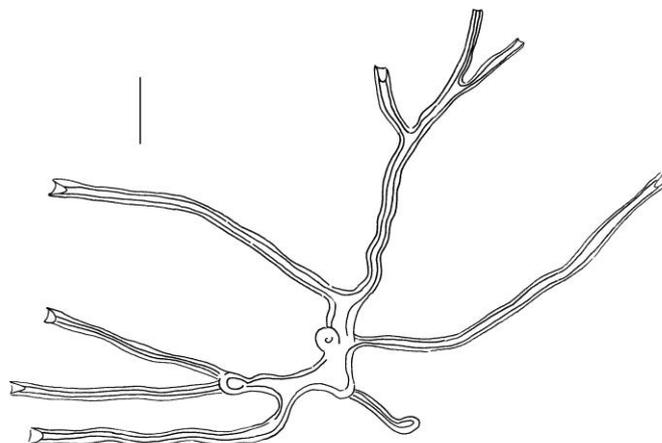


Fig. 3 – Binding hyphae from trama of “*Daedalea*” *tenuis* (holotypus). Scale bars: 10 μ m.

Table 4 Morphologic comparative studied between the lineage belonging to the *Trametes* clade.

Taxa of the <i>Trametes</i> clade	<i>Trametes s. str.</i>	<i>Artolenzites elegans</i>	<i>Cellulariella warnieri</i>	<i>Cellulariella acuta</i> (typus)	<i>T. ljubarskyi</i>	<i>T. cingulata</i>	<i>Pycnoporus</i>	<i>Leiotrametes</i> and <i>D. tenuis</i> (typus)
Upper side pileus structure	trichoderm with differentiated subpellis, with incrustations	intermixed structure without incrustations	intermixed structure with brown intracellular pigment with resinoid matrix	intermixed structure with brown intracellular pigment	intermixed structure with brown intracellular pigment and resinoid matrix	intermixed structure with brown intracellular pigment and resinoid matrix	intermixed structure with incrustations at hyphal apex	intermixed structure with brown pigment in skeletal hyphae
Hymenial hyphal ends	not found (pointed fusiform coming from binding hyphae and protruding in <i>T. betulina</i>)	clavate and full of gelled substances coming from skeletal hyphae and barely protruding	pointed fusiform coming from binding hyphae and protruding	pointed fusiform coming from binding hyphae and protruding	not found	not found	not found	obtuse, rounded to funnel-shaped coming from binding hyphae and not protruding (but for <i>Leiotrametes</i> sp.)
Abundance of the binding hyphae of the context	significant and tangled	moderate and isolate	moderate and mostly isolate only in the lower part of the context (duplex)	moderate and mostly isolate	moderate and mostly isolate only in the lower part of the context (duplex)	moderate and isolate	moderate and isolate	significant and tangled
Description of the main context binding hyphae	intricately branched with flagelliform ends	scarcely branched, with obtuse tips, sometimes antler-shaped or bifid	scarcely branched, sometimes with apex shaped sword	scarcely branched, sometimes with apex shaped sword	scarcely branched sometimes with flagelliform ends	frequently branched with flagelliform ends	frequently branched with flagelliform ends, sometimes hairpin-shaped	intricately branched, with flagelliform ends, sometimes hairpin-shaped

Phylogenetic results and position of *Lenzites warnieri*

On reconstructions based on RPB1, RPB2, and EF1- α , *L. warnieri* had an unresolved position on globally low-supported cladograms (data not shown). A multigene analysis was also intended (not shown) without conclusive result. To resolve the phylogenetic relationships of *L. warnieri*, a combined (ITS+LSU) data set provided more robust results.

In the phylogenetic analysis based on the ITS region alone (Fig. 4) or the combined (ITS+LSU) data set (Fig. 5), sequences identified as *L. warnieri* and some identified as *L. acuta* (vouchers Cui 10091 and Dai 11621) are clustered in a strongly supported monophyletic clade (Figs 4-5). The phylogenetic analysis based on the combined (ITS + LSU) data set resolve significantly this clade as sister to a broader lineage which encompasses three other clades: *Leiotrametes*, *Pycnoporus*, and the *T. ljubarskyi* - *T. cingulata* - *Trametes marianna* (Pers.) Ryvarden clade. Within this broad clade, the *T. ljubarskyi* - *T. cingulata* - *T. marianna* clade appears as sister to the *Leiotrametes*-*Pycnoporus* clade (Fig. 5). Other sequences from specimens identified as “*Lenzites acuta*” in GenBank are clustered in 2 other clades: 1) Dai 13103 and Dai 13595, closely related to *Leiotrametes* sp. (ITS, Fig. 4), belong to the *Leiotrametes* clade; 2) MO138336 clustered with *Lenzites vespacea* (ITS data only, Fig. 4) belongs to the sub-lineage of the genus *Trametes*.

The *Cellulariella* clade

To refine the taxonomy into this clade, pairwise comparisons were processed between available ITS sequences used in Fig. 4: *C. warnieri* from France (strain CIRM-BRFM 972) and Algeria (LIP0001798), Asian *C. warnieri* from India (strain JZ27), Sri-Lanka (vouchers UOC_KAUNP_MK29 and UOC_KAUNP_K05), and Pakistan (voucher MH-72) and *C. acuta* from China (vouchers Dai11621 and Cui 10091). The ITS-based *Cellulariella* clade (Fig. 4) showed weakly supported internal differences, leading us to question the autonomy between *C. acuta* and *C. warnieri*, which required deeper investigations.

On sequences of approx. 523 bp, for each pairwise alignment, internal variabilities (% identity) between collections of *C. warnieri* from France and Algeria, and from *L. acuta* from China are 99.4%. Among other Asian collections (India, Pakistan, Sri Lanka), the variability ranges between 99.4-99.8% (the sequence KAUNP_K05, from Sri Lanka, was discarded with the value of 99.2 % due to 7 suspect substitutions at the end of ITS2 region).

Similarities between *C. warnieri* (France, Algeria) and Chinese *C. acuta* range from 97.5 to 97.9%. Similarities between the first and other Asian collections range from 97.9 to 98.2%, whereas the similarities between Chinese and other Asian collections are from 99.2 to 99.8%.

With a significant ITS barcode gap of 0.8% between European-Algerian and Asian sequences, two species can be characterized, *i.e.* 1) *C. acuta* encompassing all sequences originating from Asia, and 2) *C. warnieri* from Europe and North Africa.

Taxonomy

Cellulariella warnieri (Durieu & Mont.) Zmitr. & Malysheva, Index Fungorum 180: 1 (2014)
[validation of *C. warnieri* (Durieu & Mont.) Zmitr. & Malysheva, Mikol. Fitopatol. 47(6): 376 (2013), inval., McNeill et al. 2013, art. 42.1 – no repository identifier indicated]

≡ *Lenzites warnieri* Durieu & Mont., Anns Sci. Nat., Bot., sér. 4 14: 182 (1860) (basionym)

≡ *Cellularia warnieri* (Durieu & Mont.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 452 (1898)

≡ *Trametes warnieri* (Durieu & Mont.) Zmitr., Wasser & Ezhov in Zmitrovich et al., Int. J. Medic. Mushr. 14(3): 182 (2012)

Typification:

Neotype (designated here): Algeria, Tipaza-Blideen Atlas, (1844); PC 0723637. MycoBank MBT 395712

Epitype (designated here): Algeria, Béjaia-Darguina, (2015-03-31); LIP 0001798, as support to the neotype designated above. MycoBank MBT 395713

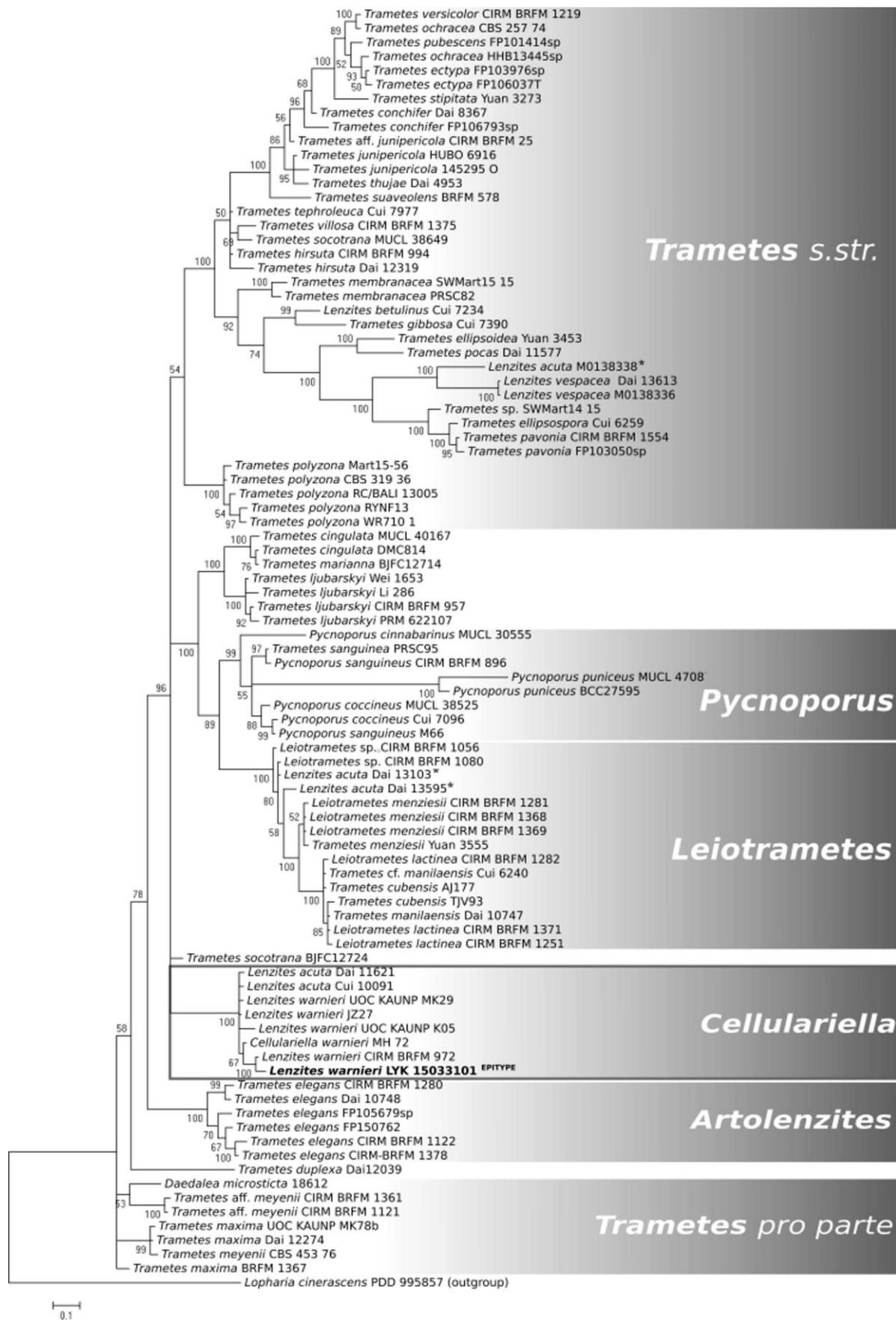


Fig. 4 – Phylogenetic relationships of *Cellulariella acuta* and *C. warnieri* within the *Trametes*-clade inferred from Bayesian analysis of the ITS rDNA dataset (50% majority rule consensus tree). Sequences of collections identified as “*Lenzites acuta*” in GenBank not belonging to *Cellulariella* clade are marked with a star (*).

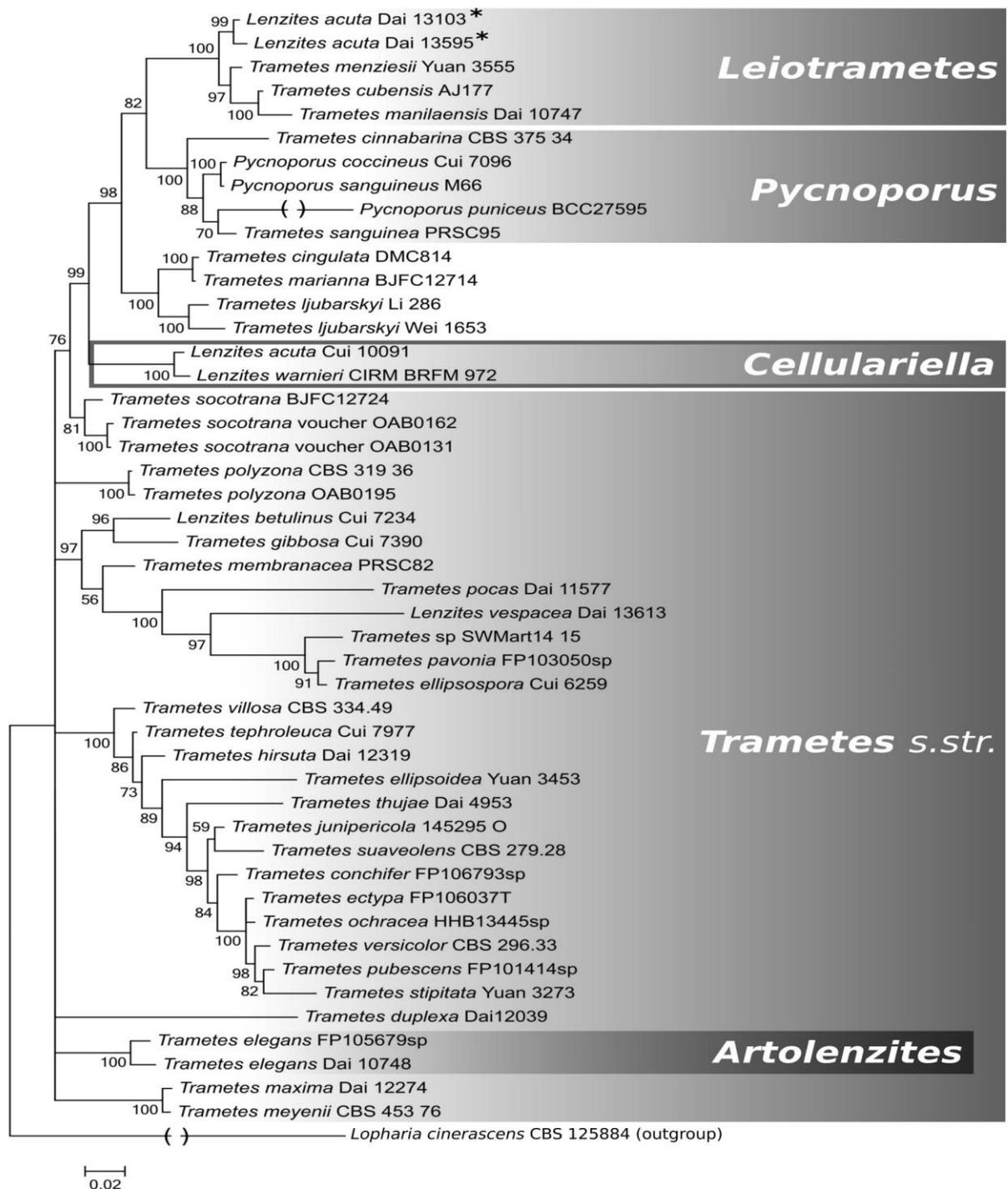


Fig. 5 – Phylogenetic relationships of *Cellulariella acuta* and *C. warnieri* within the *Trametes*-clade inferred from Bayesian analysis of the combined (LSU+ITS) rDNA dataset (50% majority rule consensus tree). Sequences of collections identified as “*Lenzites acuta*” in GenBank not belonging to *Cellulariella* clade are marked with a star (*).

= *Lenzites faventina* Caldesi, Nuovo G. bot. ital. 1: 133 (1869)

≡ *Cellularia faventina* (Caldesi) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 452 (1898)

≡ *Daedalea quercina* f. *lenzitoidea* Bres., Ann. Mycol. (Berlin) 14(3-4): 221 (1916) [as new name for *Lenzites faventina* Caldesi] ≡ *Trametes quercina* f. *lenzitoidea* (Bres.) Pilát in Kavina & Pilát, Atlas Champ. d’Europe, III, *Polyporaceae* (Praha) 1: 329 (1936).

= *Lenzites reichardtii* Schulzer, in Thümen, Mycoth. Univ., cent. 16: no. 1501 (1880)

≡ *Cellularia reichardtii* (Schulzer) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 452 (1898)

Description (based on neotype and epitype collections)

Basidiomata annual, pileate, solitary, sessile and broadly attached, thick and corky becoming tougher with age; pileus slightly convex, subtriquetrous, flabelliform, semi-circular to reniform, anterior part flattened along with the substrate insertion level, circularly gibbose at mid-radius, slightly projecting up to 130 mm, 200 mm wide and 30 mm thick at base; pileus surface initially pubescent, glabrous with age, first black grey sometimes with silvery bloom, then progressively becoming beige grey in concentric grey brown pigmentation zones, progressively indurated and wrinkled, anterior part radially veined and slightly concentrically sulcate, posterior part rather granulose, cracked, warty to nodular, sometimes with acute nodules; margin glabrous, cinnamon-brown, regular to slightly undulate and obtuse; Hymenophore lamelliform, lamellae yellow cream, gradually grey-brown towards edge, without sterile marginal zone, sometimes dichotomously branching, crowded (10 per cm), lamellae thick, regular and shallow (2 mm) at start, becoming sinuous, broader (10-13 mm), more spaced and thinner (4-7 per cm), then undulating towards the base and finally locally daedalean towards the insertion point to the substrate. Lamellulae variable in length, short and conspicuous at the margin, blending to lamellae from a certain length, edge yellowish cream, regular, faintly rounded in some parts; context corky, particularly soft towards surface, easily sectioned with a razor blade, thin, pale brown and fluffy under surface, corky towards hymenophore; trama cream to pale cream, in continuity with context; hyphal system duplex in the context, dimitic with skeletal hyphae in upper part, trimitic in lower part, trimitic in hymenophoral trama; generative hyphae 2-3 µm wide, hyaline, clamped, sparingly branched and anastomosing, isolated or inter-twisted, thin-walled; vegetative hyphae of two types: skeletal hyphae 3-6 (rarely up to 10) µm wide, longitudinal, straight or flexuous, sometimes bifurcate, never ramose, thin- to thick-walled or almost solid, congophobic; binding hyphae (2)3-4(5) µm wide, hyaline in water, often strongly congophilic, always distinctly swelling in KOH 5%, variably branched, either dichotomously branched or more frequently with alternate lateral branches, never flagelliform, tortuous but sometimes easily mingled with true skeletal hyphae, all thick-walled to almost solid; context made of basically tri-directional fibres, mostly radially oriented, others more or less vertically crossed in X, mainly composed of inter-twisted thin mediate hyphae, thick-walled skeletal hyphae, and barely branched generative hyphae, contextual binding hyphae scarcely branched, conspicuous only towards dissepiment; pileus surface made of dense adpressed fibers, radially inter-twined, crossed by short, 15 µm-wide vertically oriented fascicules arising towards margin through pileipellis and connected to others by horizontal skeletal hyphae, all covered by mucoid deposits soluble in KOH; generative hyphae also branched and abundant. In older parts a secondary pileipellis occurs as an intermixed structure with brown intracellular pigment in a resinoid matrix; trama made of a majority of binding hyphae, strongly polymorphic, all sparsely branched with diverticules and short or long branches, entangled, sometimes with apex shaped sword or fusiform, mixed with typical skeletal and generative hyphae (Fig. 2); basidia cylindro-clavate, 15-18 x 4-6 µm, 4-spored with sterigmata 3-4 µm long, clamped; basidioles cylindrical to shortly clavate, clavate at maturity (Fig. 1); leptocystidia absent, skeletocystidia abundant forming catahymenium, straight or fusiform, often bearing apical colorless amorphous secretions or crystals not dissolving in KOH or Melzer if originating from non-septate terminal segments that resemble thin-walled skeletal, bifurcate or sword shaped at apex (matching the hymenial pointed hyphal ends *sensu* Ryvarden & Gilbertson (1993) when originating from binding hyphae (Fig. 1); basidiospores 7-9 x 3-4 µm, cylindrical, slightly incurved, hyaline, inamyloid (Fig. 1).

Remarks

Montagne (1860) did not designate a holotype, and no original material matching the indications of the protologue could be located at PC (National museum of natural history of Paris). A contemporary collected specimen from Algeria (1844, Atlas, behind Blidah) exists in Montagne's

herbarium (PC), without indication of the collector. This specimen is here designated as neotype, as it was likely accepted by Montagne to represent his original species. An epitype (MBT 395713) originating from the locality, collected recently and for which molecular data were available, is also designated. Both types locally show a daedalean hymenophore at the point of insertion to the substrate.

Cellulariella warnieri is usually fully lamellate with the exception of rare specimens (Rivoire 2020). These exceptions are due to a physical constraint related to the mode of insertion on the substrate, also observed on specimens *Trametes betulina* (L.) Pilát [for instance LIP SW/F_NSR16-01, see table 1] in a more attenuated form.

Cellulariella acuta (Berk.) Zmitr. & Malysheva, Index Fungorum 180: 1 (2014)

[validation of *Cellulariella acuta* (Berk.) Zmitr. & Malysheva, Mikol. Fitopatol. 47(6): 376 (2013), inval., McNeill et al. 2013, art. 42.1 – no repository identifier indicated]

≡ *Lenzites acuta* Berk., London J. Bot. 1(3): 146 (1842) (basionym)

≡ *Cellularia acuta* (Berk.) Kuntze, Revis. Gen. pl. (Leipzig) 3(2): 451 (1898)

≡ *Trametes acuta* (Berk.) Imazeki, Bull. Tokyo Sci. Mus. 6: 73 (1943)

≡ *Artolenzites acuta* (Berk.) Mossebo & Ambit in Ambit & Mossebo, Index Fungorum 268: 1 (2015) [validation of *Artolenzites acuta* (Berk.) Mossebo & Ambit in Ambit & Mossebo, Mycosphere 6(3): 282 (2015), inval., McNeill et al. 2013, art. 41.5 – basionym not fully indicated]

Typification: Philippine Islands, Holotype K(M)168874; MBT 380721 (Berkeley, 1842: 146)

Holotype description

Basidiomata annual, pileate, solitary or laterally confluent, sessile to dimidiate, straightened from below by a discoid, sterile and oblique attachment, in some cases laterally substipitate when young, semi-circular to flabelliform, projecting up to 90 mm, 75 mm wide, flat to slightly convex, slightly depressed near the attachment zone; pileus surface “*of a beautiful grey umber or cinnamon, inclining toward the margin to tawny*” (Berkeley 1842), glabrous, sparingly granulose, scarcely radially striate, concentrically zonate by spaced concolorous furrows, less marked towards margin, more crowded around insertion; zones smooth, bumped, faintly marked by secondary furrows; margin acute, slightly undulate, flexuous; hymenophore strictly lamelliform, lamellae shallow if compared to *C. warnieri*, dark brown at the edge and zonally lighter until mid-length, radiating from base without daedaloid or poroid transient forms, approximately 10 per cm at margin, ‘*forked, truncate-dentate at the points of division, edge very acute, lacerato-dentate*’ (Berkeley 1842), faintly bifid towards margin; lamellulae occasional, inconspicuous due to the acute margin; context relatively thin but corky, easily sectioned with a razor blade; hyphal system trimitic in context and trama; binding hyphae rare and scarcely branched in the context, never flagelliform, sometimes with acute terminal hyphal ends, abundant, branched and entangled in the trama; hymenial crystal-bearing hyphal ends abundant; generative hyphae, basidia and basidiospores not observed. The pileipellis in radial section shows a vertically oriented structure more conspicuous toward margin, as well as a brown intracellular pigment but without a resinoid matrix.

Remarks

Most observed features, especially the vegetative hyphae and the hymenophoral structure, are similar to those of *L. warnieri*. Trimitic context (vs duplex in *C. warnieri*) thinner carpophore, acute margin, lacero-dentate edge of the lamellae as well as the lack of a resinoid matrix at the upper side level distinguish *C. acuta* from *C. warnieri*. Due to the variability of the 'resinoid matrix' character (see result part), analysis of the single isotype specimen did not allow us to fully evaluate this feature.

Leiotrametes tenuis (Berk.) Welty & P.-A. Moreau, comb. nov.

Mycobank number: MB 838542

≡ *Daedalea tenuis* Berk., London J. Bot. 1(3): 151 (1842), (basionym).

- ≡ *Lenzites tenuis* (Berk.) G. Cunn., Proc. Linn. Soc. N.S.W. 75(3-4): 244 (1950)
 ≡ *Striglia tenuis* (Berk.) Kuntze, Revis. Gen. pl. (Leipzig) 2: 871 (1891)
 ≡ *Trametes tenuis* (Berk.) Justo, in Carlson et al., Mycologia 106(4): 743 (2014)
 Holotype – Philippine Island, K(M), Cuming 2037; MBT 37440 (Berkeley 1842: 151)

Holotype description

Basidiomata annual, pileate, solitary; pileus dimidiate, broadly and laterally attached, flat and slightly convex towards the margin, hemi-circular with a reniform trend, projecting up to 101 mm, 64 mm wide, corky, thin and acute at margin level, gradually thickening towards the attachment; Pileus surface “wood coloured inclining to umber, especially towards the expanded, very acute margin” (Berkeley 1842), glabrous, initially flat, slightly depressed and partly reddened or blackened by resin, roughened by radial, irregular and discontinuous furrows, folds and small bump especially at margin, with 3 main concentric and narrow bumpy zones, delimited by deep furrows, and with discontinuous and not always apparent, concentric colored or slightly furrowed zones; margin narrow, acute, slightly wavy; hymenophore originally poroid and remaining so in places and at margin, lamellae developing radially as they furcate to somewhat irpicoid, deeper towards base and mostly interrupted by wedges; hyphal system trimitic in context and trama; context made of a majority of binding hyphae frequently hairpin-shaped (Fig. 6), branched with flagelliform ends, abundant and mostly tangled; pileipellis of hardly interpretable, intermixed filamentous structure with brown pigment in skeletal hyphae; basidia, basidiospores and hymenial cystidia not found; hymenial surface mainly made of vegetative hyphae usually funnel-shaped at apex (Fig. 3) arising from subhymenial binding hyphae.

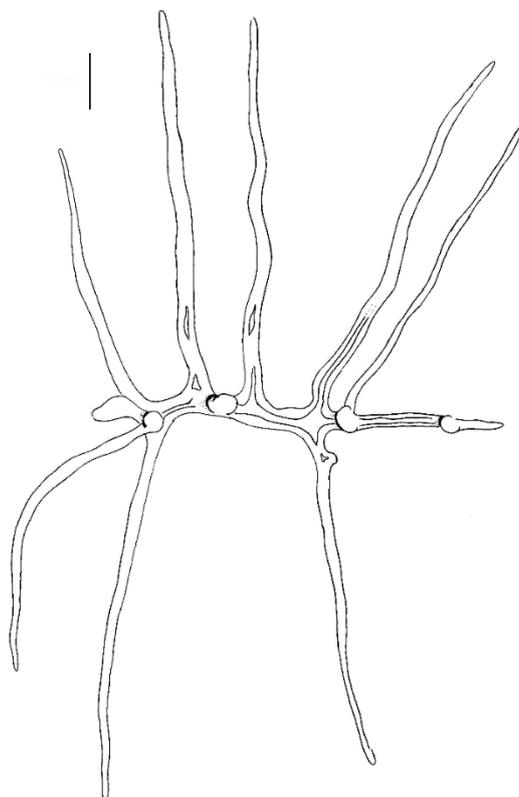


Fig. 6 – Binding hyphae from the context of “*Daedalea*”*tenuis* (holotypus). Scale bars: 10 µm.

Remarks

The branched, entangled binding hyphae with flagelliform ends within the context differs from the hyphal system of *Cellulariella* species, and refers to species of *Leiotrametes* Welti & Courtecuisse (Welti et al. 2012). The poroid hymenophore at margin, which evolves to a lamelloid

hymenophore with age and may vary from one to another specimen, is reminiscent of a species collected by Welti et al. (2012) from French Guiana and referred as "*Leiotrametes* sp." (SW/Guy12-39, SW/Guy12-78; Table 1). Perpendicular at lamellae or less frequently at lamellulae, the conspicuous and irregular anastomoses at the margin level distinguish *Leiotrametes tenuis*, as well as the *Leiotrametes* sp. (SW/Guy12-39, SW/Guy12-78) from French Guiana, from species of genus *Cellulariella*. We do not propose here to consider the East Asian and Neotropical collections as conspecific, but we propose to interpret the Asian *D. tenuis* as a *Leiotrametes* species and we introduce above the new combination.

Discussion

Phylogenetic affinities of "*Lenzites*" *warnieri*

In a previous phylogenetic analysis based on combined (ITS+RPB2) sequences, Welti et al. (2012) showed that the *Trametes*-lineage was composed of four highly supported clades, representing *Trametes* and *Artolenzites*, *Lenzites warnieri*, and a group of specimens with glabrous upper surface encompassing *Leiotrametes*, *Pycnoporus* and the sub-group *T. cingulata*-*T. ljubarskyi*. The phylogenetic relationships between these four clades remained unsolved.

Phylogenetic results based on RPB2 and EF1- α genes lack deep resolution in the *Trametes*-clade. According to the selected marker, *L. warnieri* is either supported as an isolated clade, or clustered without support within other genera of the *Trametes*-clade. Regarding the RPB1 gene, there is currently no publicly available sequence of *Trametes ljubarskyi* and *T. cingulata* at Genbank. We believe that the absence of these two species is a bias to the phylogenetic results. Conversely, the combined (ITS+LSU) analysis significantly placed *L. warnieri* as sister to the previously described large clade encompassing *Leiotrametes*, *Pycnoporus*, and the sub-clade *T. cingulata*-*T. ljubarskyi*. Within it, the subclade *T. ljubarskyi*-*T. cingulata* together with *T. marianna*, are placed as sister to the clade encompassing *Pycnoporus* and *Leiotrametes*. In many aspects, this topology of the Bayesian tree reflects the morphological characteristics (Table 4):

- the glabrous upper surface level is shared by *Lenzites warnieri* [(ND169 (LIP) and LIP0001798)] as well as all species of the *Leiotrametes*-*Pycnoporus* clade including *Trametes ljubarskyi* and *T. cingulata* (Welti et al. 2012). Such a character is therefore synapomorphic for these two clades

- the brown intracellular pigment is symplesiomorphic since it characterizes *L. warnieri* and all the species belonging to the *Leiotrametes*-*Pycnoporus* clade with the exception of *Pycnoporus*

- the resinoid matrix is only shared by *L. warnieri* as well as *T. ljubarskyi* and *T. cingulata*; since all of these species are glabrous, these two sublineages form a paraphyletic group

- with the exception of the resinoid matrix, *L. warnieri* as well as *L. acuta* share most of the morphological characters studied (see Table 4 and taxonomic part); these two species are consequently monophyletic.

Zmitrovich & Malysheva (2013) proposed to include *L. warnieri* into *Cellulariella*, typified by *L. acuta*, which is a paleotropical species. Some ITS and LSU sequences available in GenBank as well as micromorphological features of the isotype of *L. acuta* (Table 4) tend to confirm a close phylogenetic affinity between both species (Figs 4-5).

An emendation of the genus *Cellulariella*

With regard to the monophyly of the *L. acuta* - *L. warnieri* clade, we questioned the circumscription of *Cellulariella* provided by Zmitrovich & Malysheva (2013). *Cellulariella* is typified by *L. acuta*, and its delimitation is based on the following elements: "hymenophore daedaloid to lamellate; sclerohyphae hyaline, sympodially and rarely branched, inamyloid, without deposits; in some cases, with crystalline encrustation; context cream. Basidia clavate, basidiospores cylindrical".

We agree with these authors regarding “the sympodially and rarely branched sclerohyphae”, which are interpretable as scarcely branched binding hyphae. However, we emend and refine here the other elements of the definition as follows:

“Daedaloid to lamellate hymenophore”: our specimens (ND169, LIP0001798, lectotype of *L. warnieri* and isotype of *L. acuta*) showed a homogeneous lamelliform hymenophore with numerous and clearly distinct lamellulae. Lamellae are dichotomously branched and dividing points are truncate-dentate. Sometimes, this feature is so emphasized that the lamellulae appear free from lamellae. Such structured and homogeneous lamelliform hymenophore is mostly present in *L. warnieri* and frequent in *L. acuta*. It is also found in *Trametes betulina* (type of the genus *Lenzites*) and was defined by Ryvar den & Gilbertson (1993) as ‘lenzitoid’. We never observed any specimen identified as *L. acuta* or *L. warnieri* not strictly lenzitoid as defined above, i.e. without easily identifiable lamellulae and with frequent and disorganized forks as well as perpendicular anastomoses between lamellae. All specimens identified as “*L. acuta*” with heterogeneous hymenophore or with perpendicularly oriented anastomose are closely related or attributed to *Leiotrametes tenuis* (see Taxonomy part).

“Sclerohyphae without deposits and in some cases with crystalline encrustation”: we assume that the authors refer to skeletal hyphae of the context. In our previous observations (Table 4; Welti et al. 2012), we observed a parietal crystalloid pigment in *Pycnoporus* or *T. cingulata* for instance, but we did not find this characteristic in *L. warnieri* or *L. acuta*.

Although pointed hyphal ends protruding through the hymenium were not mentioned by Zmitrovich & Malysheva (2013), Zmitrovich (2018) adds them in a second description of *Cellulariella*. Previously described in *L. warnieri* by both Ryvar den & Gilbertson (1993) and Bernicchia (2005), this feature is rare in polypores and therefore is an interesting character to be included in the definition of *Cellulariella*. Many authors, including ourselves (Welti et al. 2012), pointed out the inconsistency of hymenophoral structure for a definition at generic level in the *Trametes*-clade. The type of *Lenzites*, *L. betulinus*, shows the rarely combined features “lamelliform hymenophore” and “hymenial pointed hyphal ends” (Ryvar den 1991) and has been shown to be phylogenetically nested into the *Trametes* *ss. str.* clade (Tomšovský et al. 2006, Justo & Hibbett 2011, Welti et al. 2012). In *Cellulariella*, the uniqueness of the association of lenzitoid hymenophore, pointed fusiform binding hyphal ends protruding through the hymenium, and scarcely branched contextual binding hyphae without flagelliform ends (intricately branched with flagelliform ends in *T. betulina*) characterizes both *L. acuta* and *L. warnieri* within the *Trametes*-clade and supports the recognition of *Cellulariella* in the trametoid complex of genera.

We therefore emendate the definition of *Cellulariella* to include hyphal system of the context trimitic with scarcely branched binding hyphae, never intricate and without flagelliform ends, pointed fusiform binding hyphal ends protruding through the hymenium, and strictly homogeneous lenzitoid hymenophore with, in some cases, numerous lamellulae mostly free from lamellae, instead of “daedaleoid to lamellate”.

Cellulariella* versus *Leiotrametes

Cellulariella in its original definition (Zmitrovich & Malysheva 2013) could match species belonging to other clades of the *Trametes*-clade, especially *Leiotrametes*.

Such a broadly formulated description could lead to an erroneous placement of various daedaloid polypores in this genus. The imprecision in hymenophoral structure might also affect species concepts, for instance too broad a morphological concept of *Lenzites acuta*.

In the combined (ITS+LSU) and ITS phylogenetic datasets (Figs 4-5), vouchers identified as “*L. acuta*” are spread within three distinct lineages, respectively close to *L. vespacea* (clade of the genus *Trametes*), *Leiotrametes* sp., and *L. warnieri*. *Daedalea tenuis* is a usual synonym of *Lenzites acuta* (Ryvar den 1976), likely confused by an approximatively similar morphology. Microscopical features clearly confirm the phylogenetic affinities of these taxa.

The study of the isotype of *L. acuta* revealed a strictly lenzitoid hymenophore, a trimitic context with scarcely branched binding hyphae, lacking flagelliform ends, and hymenial fusiform

pointed hyphal ends, that agree with the definition of *Cellulariella* (see description in the taxonomy part and Table 4). The examination of the holotype of *D. tenuis*, synonymized to *L. acuta* by Ryvar den (1976) for instance, revealed a poroid to daedaleoid hymenophore, locally lamelliform but never strictly lenzitoid, intricately branched binding hyphae with tapering flagelliform ends, sometimes hairpin-shaped, both within the context and hymenophoral trama (Fig. 6), and usually funnel-shaped (not pointed) hymenial ends originating from binding hyphae, that agree with the definition of *Leiotrametes* (see taxonomy part and Table 4). The same result was achieved with *Leiotrametes* sp. from French Guiana.

Given that these morphological observations are congruent with phylogenetic results, it is concluded that *D. tenuis* belongs to the *Leiotrametes* whereas *L. acuta* belongs to *Cellulariella*. Consequently, the synonymy between both species is rejected and each of them is transferred into its corresponding genus: *Leiotrametes tenuis* (Berk.) Welti & P.-A. Moreau, comb. nov. (see taxonomy part) and *Cellulariella acuta* (Berk.) Zmitr. & Malysheva. The species from French Guiana described as “*Leiotrametes* sp.” in a previous work (Welti et al. 2012), phylogenetically close to the vouchers “*L. acuta*” Dai 13103 and Dai 13595 from China, is comparable to *L. tenuis* in many aspects. Recent and reliably identified material from the original locality of *L. tenuis* (Philippines) is urgently needed, to confirm the molecular position of the species and compare more reliably Asian and neotropical collections.

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