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Fomes: A comprehensive review of traditional and modern biotechnological applications in medicine, food, and materials

Fomes: Una revisión exhaustiva de las aplicaciones biotecnológicas tradicionales y modernas en medicina, alimentos y materiales

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ABSTRACT

Fomes fomentarius, commonly known as the tinder fungus, has been extensively studied for its potential in a wide range of medical and biotechnological applications and its ethnomycological significance. Research has predominantly focused on this species, the other three species accepted within the genus—*F. fasciatus* from the Neotropics, *F. inzengae* from Europe and Asia, and *F. graveolens* from North America—remain underexplored in terms of their applications. Furthermore, in previous studies, three distinct lineages within *F. fomentarius* have already been identified. Through maximum likelihood analysis of a concatenated ITS + LSU sequence dataset, we also discovered five additional clades of potential unnamed taxa in Asia and Europe, as well as three distinct clades within the Neotropical specimens of *F. fasciatus*. Additionally, we have compiled a comprehensive list of known applications of *F. fomentarius*, and considering the taxonomic discoveries, some of these medicinal applications could correspond to other

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species. This review highlights the urgent need for thorough taxonomic studies to precisely define species as we explore their chemical, biological, and biotechnological potentials, emphasizing the importance of including specimens from underexplored regions such as the Neotropics.

Keywords: Antioxidant properties; core polyporoid clade; lentinus clade; medicinal fungi; multigene phylogenetic analysis.

RESUMEN

Fomes fomentarius, conocido como el hongo de la yesca, ha sido ampliamente estudiado por su potencial en una vasta gama de aplicaciones médicas y biotecnológicas, así como por su importancia etnomicológica. El género comprende además otras tres especies: *F. fasciatus* distribuido en la región neotropical, *F. inzengae* en Europa y Asia y *F. graveolens* en América del Norte, que siguen estando poco exploradas en términos de sus aplicaciones. En este trabajo se realizaron análisis moleculares que muestran que dentro de *Fomes* hay al menos 5 clados adicionales que representarían especies diferentes de Norte América, Asia y Europa, así también muestran que *Fomes fasciatus* representa un complejo de especie con al menos tres linajes distintos. Se compilaron todas las aplicaciones conocidas de *F. fomentarius* y, considerando los descubrimientos taxonómicos, algunas de estas aplicaciones medicinales atribuidas a *F. fomentarius* podrían corresponder en realidad a otros linajes o especies del género. Esta revisión subraya la necesidad crítica de realizar estudios taxonómicos exhaustivos para definir con precisión las especies, mientras se investiga su potencial químico, biológico y biotecnológico; y además resalta la necesidad de incluir en los estudios a especímenes y especies de áreas poco exploradas como el neotrópico.

Palabras clave: Análisis filogenéticos multigen; clado lentinus; clado poliporoide principal; hongos medicinales; propiedades antioxidantes.

INTRODUCTION

Edible and medicinal mushrooms are important resources in both food and medicine, with a long tradition of use in various cultures around the world. Nowadays, mushrooms are becoming increasingly popular because they show a wide range of bioactivities and high nutritional quality (Boa, 2004; Lindequist *et al*., 2005). Polypore fungi, a diverse group characterized by developing a poroid hymenophore and distinctive growth habit, although not a natural group, are widely recognized (Robledo & Urcelay, 2009). Polypores are incorporated into the pharmacopeia and medicine of Indigenous people worldwide, these taxa play a key role as food, tinder, enzymes, commodities, and medicine, based on their important and potential applications in biomedical engineering and biodegradation (Dai *et al*., 2009;

Grienke *et al.*, 2014; Bankole *et al.*, 2020; Wang & Zhao, 2021). Among polypores, five species—*Laetiporus sulphureus* (Bull.) Murrill, *Fomes fomentarius* (L.) Fr., *Fomitopsis pinicola* (Sw.) P. Karst., *Piptoporus betulinus* (Bull.) P. Karst., and *Laricifomes officinalis* (Vill.) Kotl. & Pouzar—have been widely used in central European folk medicines to treat various diseases (Grienke *et al.*, 2014). In the Neotropics, *Hornodermoporus martius* (Berk.) Teixeira, *Stiptophyllum erubescens* (Berk.) Ryvarden and some species of *Ganoderma* P. Karst. have been analyzed for their chemical and biological properties (Mancuello *et al.*, 2022; Campi *et al.*, 2023a; Campi *et al.*, 2023b). Polypores possess significant biotechnological potential and are a promising component of healthcare biotechnology products (nutraceuticals, pharmaceuticals, and cosmeceuticals) are widely consumed in global markets (Badalyan *et al.*, 2015).

Fomes fomentarius, commonly known as the "tinder fungus", "hoof fungus", "tinder conk", "tinder polypore", "Mudi", "Agaric of the surgeons", "Iceman's fungus", and "Tsuriganetake" in Japan, has a long history of medicinal use in Europe, North America, and Asia (Grienke *et al.*, 2014; Wang & Zhao, 2021). This species was found in the pockets of Ötzi, a prehistoric mummy discovered in the Tyrolean Alps in 1991 (Pöder, 2005). The 5000-year-old Neolithic man is presumed to be the first to apply tinder material prepared from *F. fomentarius* basidiomata for medicinal purposes (Gáper *et al.*, 2016). Following the timeline, Hippocrates in the fifth century (460–377 B.C.) reported its topical use for cauterizing wounds (Peintner *et al.*, 1998; Gáper *et al.*, 2016). In medieval Europe and Western Siberia, *F. fomentarius* basidiome was used as a styptic and it was prescribed as a remedy for numerous diseases (Killermann, 1938; Wang & Zhao, 2021).

Recent research on the properties of *F. fomentarius* has validated much of the ancient knowledge. This species appears to be a source of potent antitumor, immunoenhancing, anti-inflammatory, antihyperglycemic, antimicrobial, and antiviral compounds (Roussel *et al.*, 2002; Roussel & Rapior, 2005; Gáper *et al.*, 2016; Maljurić *et al.*, 2018). Additionally, it has been used in different commodities such as raw materials for making caps, chest protectors, and other clothing articles or decorative elements such as flower pots (Grienke *et al.*, 2014).

Two species have been traditionally recognized in *Fomes* (Fr.) Fr., *F. fomentarius* and *F. fasciatus* (Sw.) Cooke. However, in the last ten years, research has shown that the traditional concept of *F. fomentarius* encompasses more than one taxon, with *F. inzengae* now recognized as an independent lineage (McCormick *et al.*, 2013; Peintner *et al.*, 1998; Garrido-Benavent *et al.*, 2020; Tomšovský *et al.*, 2023). Accurately delimiting species within the genus is essential, as medicinal polypore species within the same genus can exhibit markedly different chemical profiles (Hseu *et al.*, 1996; Lv *et al.*, 2012; Gáper *et al.*, 2016). It is important to consider that the ethnomycological uses and the biological and chemical properties reported pertain specifically to *F. fomentarius.*

In this context, we aim to know the progress in the study and knowledge of the genus *Fomes*, covering a review of 1) the taxonomic status, species diversity, and phylogenetic relationships, 2) the medicinal and cultural importance of *Fomes*, 3) the chemical composition and biological properties of *F. fomentarius*, and 4) the nutritional composition and ethnomycological information regarding uses.

TAXONOMY AND PHYLOGENY OF *FOMES*

Multigene phylogenetic analyses, including a broad sampling of either the order Polyporales or the core polyporoid clade, have placed *F. fomentarius* within the 'lentinus' clade of the core polyporoid clade (Binder *et al.,* 2013; Robledo *et al.,* 2020). Traditionally, two species have been accepted worldwide: *F. fasciatus* (Sw.) Cooke and *F. fomentarius* (L.) Fr. However, over the last decade, it has been demonstrated that *F. fomentarius* likely represents a species complex. So far, *F. inzengae* has been segregated and recognized as a sympatric, mostly cryptic species with *F. fomentarius* (McCormick *et al*., 2013; Peintner *et al*., 1998; Garrido-Benavent *et al*., 2020; Tomšovský *et al.,* 2023). Several other putative species are still represented by phylogenetic clades including specimens from Asia and North America (Garrido-Benavent *et al.,* 2020; Tomšovský *et al.,* 2023) that must be validated as species. However, to date, no comprehensive study of the diversity of the genus has been undertaken in a broad phylogenetic context.

To obtain an overview of phylogenetic relationships at the species and genus level, albeit preliminary, we performed a phylogenetic analysis based on ITS and LSU markers with representatives of the genera of the 'lentinus' clade (Binder *et al*., 2013; Robledo *et al*., 2020). We constructed a dataset with sequences available at GenBank (NCBI). Specimens and GenBank Accession Numbers of sequences are listed in Table 1. *Microporus* P. Beauv. was selected as the outgroup. Each region, ITS and LSU, were individually aligned using MAFFT 7 (Katoh *et al*., 2019) through the G-INS-I alignment method. Alignments were manually inspected and adjusted using MEGA 6 (Tamura *et al*., 2013). ModelFinder (Kalyaanamoorthy *et al*., 2017) as implemented in the IQ-Tree software (Nguyen *et al.*, 2014) was used to estimate the best-fit partitioning strategy and the best-fit model of nucleotide evolution for the dataset using 4 data blocks (ITS1; 5.8S; ITS2 and LSU). Maximum likelihood (ML) phylogenetic analyses were applied to the concatenated dataset using the partition scheme and evolutionary models defined in ModelFinder. Maximum likelihood searches were conducted with IQ-TREE. The analysis initially involved 100 ML searches, starting from one randomized stepwise addition parsimony tree. Branch supports were calculated using the UFBoot (ultrafast bootstrap approximation) (Hoang *et al*., 2017) implemented in IQ-TREE with 1000 replications. Nodes were considered strongly supported with BPP $\geq$ 0.95 or BS $\geq$ 95% (Hyde *et al*., 2013; Minh *et al*., 2020).

Table 1 (part 1 of 4). Voucher specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. Origin data are only presented for *Fomes* specimens. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 1 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. Los datos de Origen sólo se presentan para los especímenes de *Fomes*. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Species	Voucher / Isolate	Origin		Accession numbers	
		Country / Locality	Substrate	ITS	LSU
Microporus affinis	Cui 7714	Unknown	Unknown	JX569739	JX569746
Microporus flabelliformis	Dai 11574	Unknown	Unknown	JX569740	JX569747
Microporus vernicipes	Dai 9283	Unknown	Unknown	KX880618	KX880658
Microporus xanthopus	Cui 8284	Unknown	Unknown	JX290074	JX290071
Lentinus tigrinus	MUCL22821	Unknown	Unknown	AB478881	AB368072
Lentinus thailandensis	Dai 6722	Unknown	Unknown	KX851590	KX851645
Lentinus thailandensis	MSUT_6734	Unknown	Unknown	LC052221	LC052219
Lentinus substrictus	Wei 1582	Unknown	Unknown	KU189767	KU189798
Lentinus arcularius	Cui 10998	Unknown	Unknown	KX548973	KX548995
Lentinus arcularius	Cui 11398	Unknown	Unknown	KU189766	KU189797
Lentinus brumalis	Cui 7188	Unknown	Unknown	KX851591	KX851646
Lentinus brumalis	Cui 10750	Unknown	Unknown	KU189765	KU189796
Earliella scabrosa	PR1209	Unknown	Unknown	JN165009	JN164793
Earliella scabrosa	OAB0630	Unknown	Unknown	OR116231	OR116242
Earliella scabrosa	He31	Unknown	Unknown	KC867365	KC867484
Earliella scabrosa	CIRM-BRFM 1817	Unknown	Unknown	OL685338	OL685338
Earliella scabrosa	NTOU5882	Unknown	Unknown	MW940757	MW881468
Daedalopsis tricolor	Cui8301	Unknown	Unknown	KU892426	KU892468
Daedaleopsis nitida	LWZ 20210919-29a	Unknown	Unknown	ON897854	ON885318
Daedaleopsis confragosa	QHU20182	Unknown	Unknown	OM970931	OM942711
Daedaleopsis confragosa	Dai 7455	Unknown	Unknown	KU892428	KU892448
Daedaleopsis confragosa	Cui 6892	Unknown	Unknown	KU892417	KU892453
Daedaleopsis sinensis	Dai 11429	Unknown	Unknown	KU892444	KU892446
Neofomitella australiensis	Cui 16571	Unknown	Unknown	MK192443	MK192463
Neofomitella australiensis	Cui 16542	Unknown	Unknown	MK192438	MK192458
Neofomitella australiensis	Cui 16558	Unknown	Unknown	MK192440	MK192460
Neofomitella rhodophaea	TFRI 414	Unknown	Unknown	EU232216	EU232300
Neofomitella fumosipora	Cui 16750	Unknown	Unknown	MK192432	MK192452
Neofomitella fumosipora	Cui 16759	Unknown	Unknown	MK192433	MK192453
Neofomitella guangxiensis	Cui 14005	Unknown	Unknown	MK192436	MK192456
Neofomitella guangxiensis	Cui 14029	Unknown	Unknown	MK192437	MK192457
Funalia trogii	RLG4286sp	Unknown	Unknown	JN164993	JN164808
Funalia trogii	KUC3030	Unknown	Unknown	DQ912696	AY858359
Funalia trogii	Dai 11246	Unknown	Unknown	KC867380	KC867451

Table 1 (part 2 of 4). Voucher specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. Origin data are only presented for *Fomes* specimens. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 2 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. Los datos de Origen sólo se presentan para los especímenes de *Fomes*. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Species	Voucher / Isolate	Origin		Accession numbers	
		Country / Locality	Substrate	ITS	LSU
Funalia trogii	RLG7630sp	Unknown	Unknown	JN165013	JN164814
Funalia gallica	JV1407_1	Unknown	Unknown	OR911810	OR911804
Funalia gallica	FP91663T	Unknown	Unknown	JN165012	–
Funalia subgallica	Cui 6317	Unknown	Unknown	KC867384	KC867460
Funalia subgallica	Dai 10741	Unknown	Unknown	KC867385	KC867461
Funalia rigida	VRTO62	Unknown	Unknown	OR892710	OR896866
Funalia rigida	VRTO956	Unknown	Unknown	OQ702342	OR333971
Funalia rigida	BJFC12680	Unknown	Unknown	KC867381	KC867454
Funalia sanguinaria	Dai 9362	Unknown	Unknown	KC867391	KC867466
Funalia sanguinaria	Cui 14507	Unknown	Unknown	MK192428	MK192447
Funalia supina	JV0610	Unknown	Unknown	KF274645	KF274646
Funalia supina	Ryvarden 39027	For all specimens other than *Fomes*	Unknown	KF274643	–
Fomes graveolens	NRM11	USA	Unknown	MG663229	–
Fomes graveolens	iNat191131761	USA	Unknown	PP156218	–
Fomes graveolens	Mycomap7015	USA	Unknown	MK564554	–
Fomes fomentarius	NCSLG_18674	USA, North Carolina	*Betula alleghaniensis*	JX183720	–
Fomes fomentarius	HE21049	USA?		KC505546	–
Fomes fomentarius	CFMR 10193	USA: Wisconsin		KX065943	KX065978
Fomes fomentarius	209FT_AK	USA, Alaska	*Betula neoalaskana*	JX183717	–
Fomes fomentarius	124FT_JM	USA, Minesota	*Betula* sp.	JX183719	–
Fomes fomentarius	DAOM129034	Canada: British Columbia		JX183713	AF261538
Fomes fomentarius	NJB2011-KD3	USA	*Fagus grandifolia*	KU139199	KU139260
Fomes fomentarius	IB20130019 **Epitype**	Austria	*Picea abies stump*	KM360127	–
Fomes fomentarius	Ff/1	Armenia	*Quercus* sp.	KJ857248	–
Fomes fomentarius	Ffa/2	Armenia	*Fagus* sp.	KJ857249	–
Fomes fomentarius	Ff/11	Armenia	*Fagus* sp.	OL583666	–
Fomes fomentarius	IB20130011	Austria	*Picea abies stump*	KM360125	–
Fomes fomentarius	IB20130016	Austria	*Picea abies stump*	KM360126	–
Fomes fomentarius	7 FF007NA	Slovakia	*Negundo aceroides*	FJ865440	JX470537
Fomes fomentarius	ITS12 FF012FS	Slovakia	*Fagus sylvatica*	GQ184603	JX470535
Fomes fomentarius	BRNM 840283	Czechia		OQ474924	OQ474924
Fomes fomentarius	BRNM 840310	Czechia		OQ474930	OQ474930
Fomes fomentarius	BRNM 840314	Slovakia		OQ474932	OQ474932
Fomes fomentarius	BRNM 840294	Czechia		OQ474925	OQ474925

Table 1 (part 3 of 4). Voucher specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. Origin data are only presented for *Fomes* specimens. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 3 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. Los datos de Origen sólo se presentan para los especímenes de *Fomes*. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Species	Voucher / Isolate	Origin		Accession numbers	
		Country / Locality	Substrate	ITS	LSU
Fomes fomentarius	BRNM 840309	Czechia		OQ474929	OQ474929
Fomes fomentarius	ES2008-3	Sweden		JX109860	JX109860
Fomes fomentarius	13 FF013Tsp	Slovakia	*Tilia* sp.	FJ865443	JX470536
Fomes inzengae	IB20160343	Italy, **type locality**	*Quercus cerris*	MK184458	–
Fomes inzengae	IB20160342	Italy, **Epitype**	*Quercus cerris*	UDB034501	–
Fomes inzengae	Isolate 5704	Belgium	*Fagus silvatica*	OR473259	–
Fomes inzengae	Isolate 5711	Belgium	*Fagus silvatica*	OR473260	–
Fomes inzengae	IB20160349	Italy	*Castanea sativa*	MK184456	–
Fomes inzengae	IB20160351	Italy	*Carpinus betulus*	MK184457	–
Fomes fomentarius	IPAE-54	Crimea	*Juglans regia*	OP881549	–
Fomes fomentarius	LE-BIN 3809	Belarus	*Quercus robur*	OR892543	–
Fomes inzengae	Ff/15	Armenia	*Salix alba stump*	OL583668	–
Fomes inzengae	Ff/16	Armenia	*Salix alba stump*	OL583669	–
Fomes inzengae	BRNM 840274	Czechia		OQ474914	OQ474914
Fomes inzengae	BRNM 840275	Czechia		OQ474915	OQ474915
Fomes inzengae	BRNM 840278	Czechia		OQ474916	OQ474916
Fomes inzengae	BRNM 840289	Czechia		OQ474920	OQ474920
Fomes inzengae	BRNM 840301	Czechia		OQ474922	OQ474922
Fomes fomentarius	1 FF001AP	Slovakia	*Acer platanoides*	FJ865438	JX470534
Fomes fomentarius	9 FF009AH	Slovakia	*Aesculus hippocastanum*	FJ865441	JX470538
Fomes fasciatus	TH488	Guyana, Barima-Waini		PP102333	–
Fomes fasciatus	TH491	Guyana, Barima-Waini		PP102334	–
Fomes fasciatus	BRFM 1081	French Guiana, Kourou		JX082362	–
Fomes fasciatus	FP-1061048-T	USA, Mississippi	*Carya sp*	AM269766	AM269825
Fomes fasciatus	NCSLG 18643	Usa, Louisiana	*Platanus occidentalis*	JX126900	–
Fomes fasciatus	Miettinen 17907	USA, Florida		KY948730	–
Fomes fasciatus	FLAS-F-60214	USA, Florida		MF074787	–
Fomes fasciatus	JV 0610/7G2	Guatemala		KF605613	–
Fomes fasciatus	NCSLG_18645	USA, Georgia	*Quercus* sp.	JX126901	–
Fomes fasciatus	NCSLG_18639	USA, Florida		JX126902	–
Fomes fasciatus	NCSLG_18635	USA, Mississippi	*Carya illinoinensis*	JX126905	–
Fomes fasciatus	47FA_NCSLG_18633	USA, Mississippi	*Carya illinoinensis*	JX126906	–
Fomes fasciatus	NCSLG_18632	USA, Mississippi	*Carya illinoinensis*	JX126907	–
Fomes fasciatus	NCSLG_18633_49FA	USA, Mississippi	*Carya illinoinensis*	JX126908	–

Table 1 (part 4 of 4). Voucher specimens, geographic location and GenBank accession numbers of the samples included in the phylogenetic analyzes. Origin data are only presented for *Fomes* specimens. T= type specimen. New sequences generated in this study are in boldface.

Tabla 1 (parte 4 de 4). Vouchers, origen geográfico y número de acceso de GenBank de las muestras incluidas en los análisis filogenéticos. Los datos de Origen sólo se presentan para los especímenes de *Fomes*. T= especímenes tipo. Las nuevas secuencias generadas en este estudio se resaltan en negrita.

Species	Voucher / Isolate	Origin		Accession numbers	
		Country / Locality	Substrate	ITS	LSU
Fomes fasciatus	CFMR_FP-50332-T	Usa, Louisiana	*Celtis sp*	JX126904	–
Fomes fasciatus	CFMR_FP-57054-T	Usa, Louisiana	*Celtis sp*	JX126903	–
Fomes sp.	KUC20121123-35	South Korea		KJ668550	KJ668403
Fomes sp.	NAAS04711	South Korea		KP004978	–
Fomes sp.	IPAE-35	Japan	*Fagus* sp.	OP902262	–
Fomes sp.	IPAE-34	Japan	*Fagus* sp.	OP902261	–
Fomes sp.	XSD-29	Asia?		EU273503	–
Fomes sp.	CGMCC1658	Changbai Shan, China		DQ513402	–
Fomes sp.	ZF-51	China,environmental	*Cypripedium guttatum*	KM277628	–
Fomes sp.	B2SN036	Nepal	*Quercus* sp.	LC149605	–
Fomes sp.	CLZhao 4605	China, Ailaoshan Nature Reserve		MK795134	–
Fomes sp.	CLZhao 4393	China, Wuliangshan		MK343528	–
Fomes sp.	SWFU 004605	China, Ailaoshan Nature Reserve		MK809453	–
Fomes sp.	Cui8020	Asia?		JX290073	JX290070
Fomes sp.	CLZhao 1198	China, Ailaoshan Nature Reserve		MH114657	–
Fomes sp.	SWFU 006310	China, Ailaoshan Nature Reserve		MK809454	–
Fomes sp.	SWFU 006369	China, Ailaoshan Nature Reserve		MK809455	–

The dataset included sequences from 119 fungal specimens, encompassing 1794 characters, of which 1467 were constant, 283 parsimony-informative and 44 singleton sites. The partitions and evolutionary models selected were: GTR+F+G4 (ITS1 and ITS2) and K2P+I+G4 (5.8S and LSU). The ML tree is presented in Fig. 1. The topology recovered in our phylogenetic analysis showed seven clades at genus level with maximum support, congruent with previous multigen phylogenetic analyses including the 'lentinus' clade (Binder *et al*., 2013; Robledo *et al.*, 2020; Justo *et al*., 2017; Ji *et al*., 2019). In particular, within *Fomes,* the general topology recovers two main clades, consistent with previous findings (Garrido-Benavent *et al*., 2020; Tomšovský *et al*., 2023). One clade containing species with circumglobal north temperate distribution, here named as the 'fomentarius' clade, and a second clade including specimens identified as *Fomes fasciatus* from tropical and subtropical areas of America here named as the 'fasciatus' clade.

Within the 'fomentarius' clade, several lineages at the species level can be observed, including the three currently recognized species *F. fomentarius s.s.*, *F. inzengae,* and *F. graveolens* (Figs. 1, 2A, 2B, 2D-F), alongside several unnamed species from Asia and North America. Within the 'fasciatus' clade, at least three groups are identified, suggesting that the morphological concept of *F. fasciatus* (Fig. 2C) involves more than one taxon. *Fomes fasciatus* was described from Jamaica (Swartz *et al.*, 1788), with several heterotypic synonyms described from the Neotropical region as *Polyporus marmoratus* Berk. & M.A. Curtis (Nicaragua), *P. sclerodermeus* Lév (Guadeloupe), *Myriadoporus dussii* Pat. (Martinica) and *F. subfomentarius* Romell. A key question that remains is whether any of the recovered clades correspond to *F. fasciatus* in the strict sense, or whether the names of these heterotypic synonyms should be applied to the observed clades. Except for Guyana and French Guiana records, no sequences are available from South American specimens. *Fomes fasciatus,* in its current morphological concept, is a quite common species distributed in all of South America, the southern limit of its distribution being the north of Argentina (Robledo & Rajchenberg, 2007; Rajchenberg & Robledo, 2013).

The taxonomic and phylogenetic scenario presented here clearly underscores the need for more comprehensive taxonomic work at the genus level. Multigene analyses including coding markers from a larger sampling of specimens are needed to define and confirm at the species level the different clades of *Fomes* sp. recovered in our analysis. In particular, to resolve the 'fasciatus' clade, the sampling should include specimens from South America.

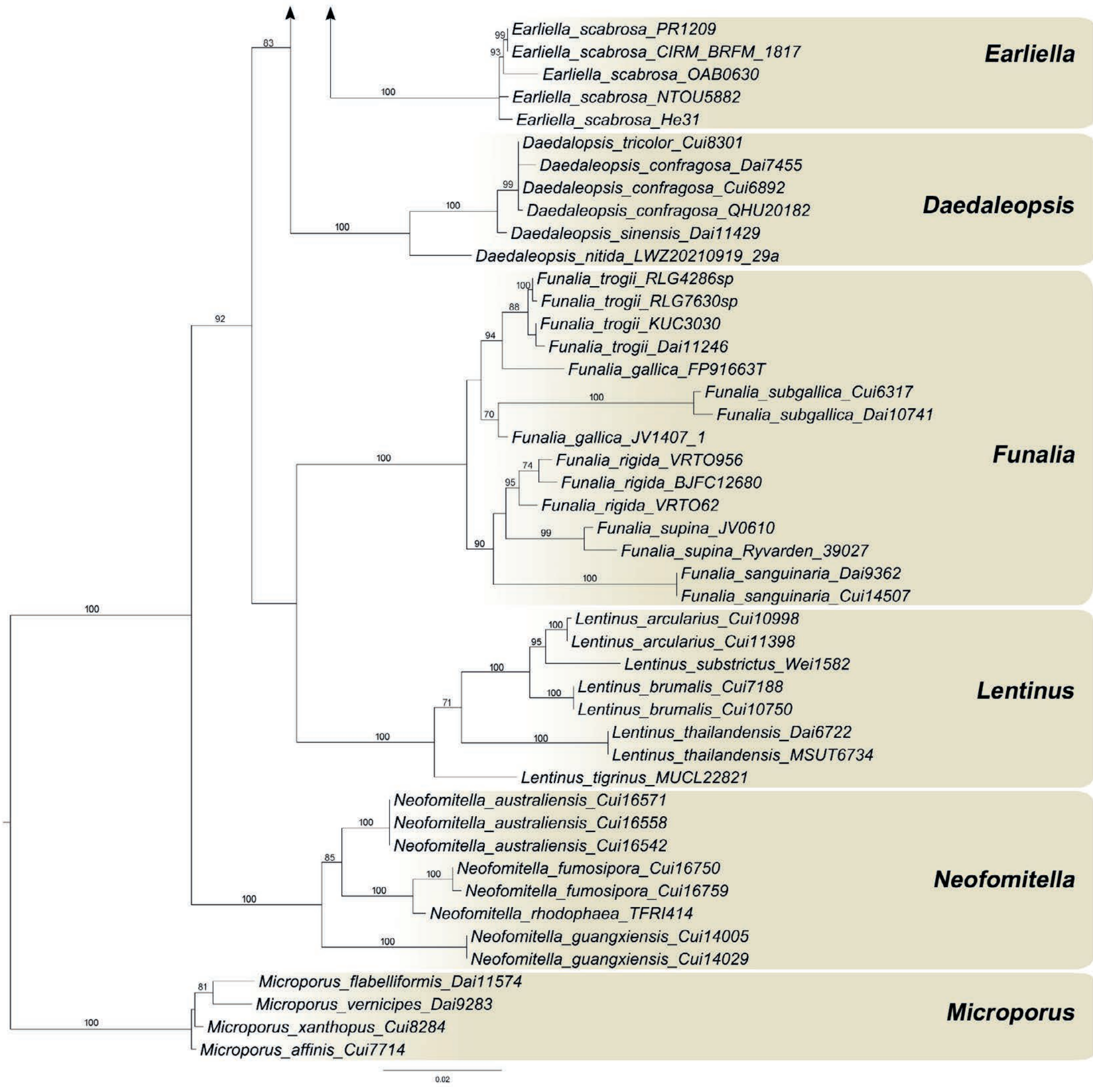

Fig. 1. Maximum Likelihood (ML) tree positioning *Fomes* within the 'lentinus' clade based on concatenated ITS + LSU sequence dataset and *Microporus* as outgroup. Branch support values are shown as Bootstrap values above 70%.

Fig. 1. Árbol de Maximum likelihood (ML) que posiciona a *Fomes* dentro del clado 'lentinus' basado en una matriz de secuencias de ITS+LSU concatenadas y *Microporus* como grupo externo . Los valores de soporte de las ramas se muestran como valores Bootstrap por encima del 70%.

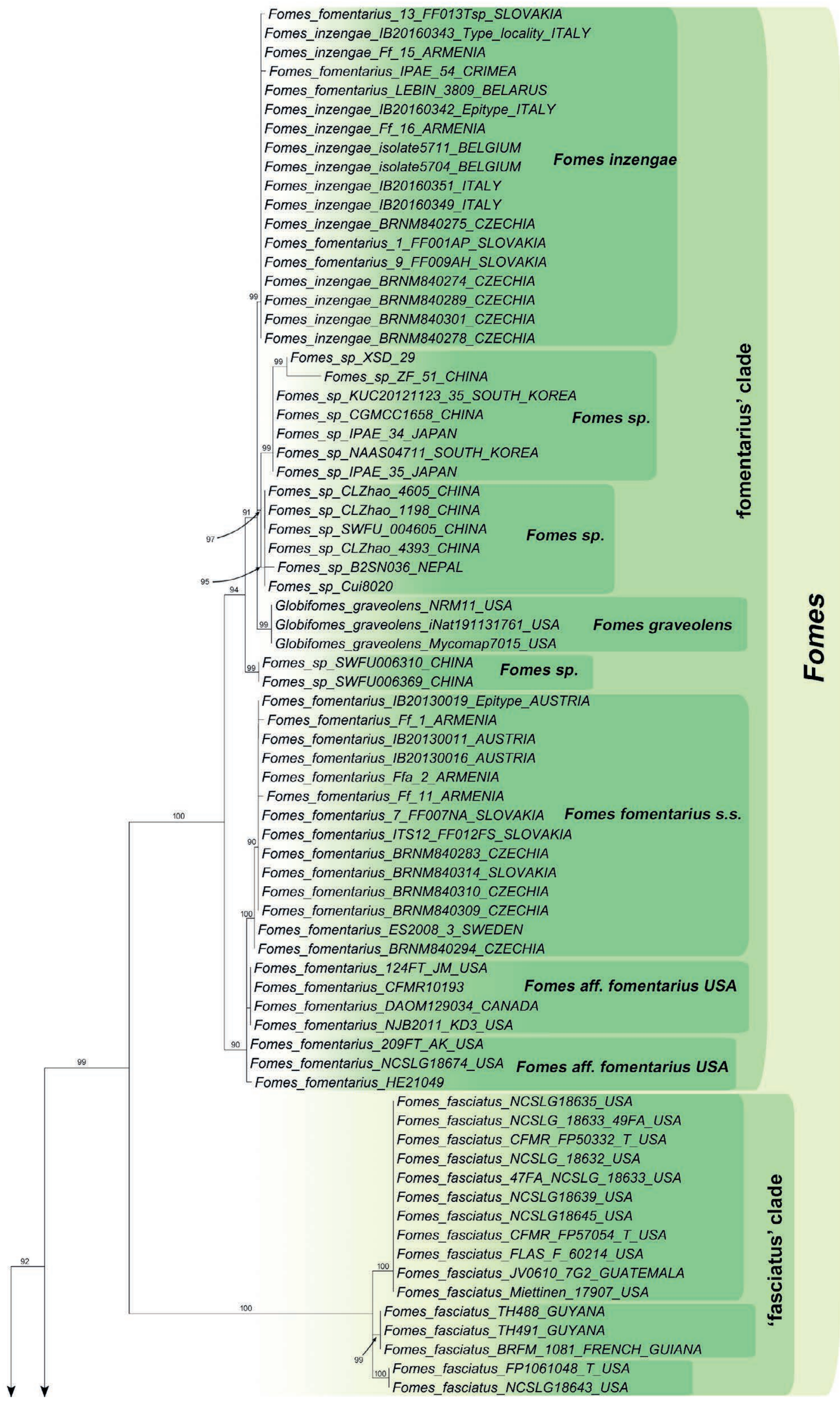
Fomes_fomentarius_13_FF013Tsp_SLOVAKIA
Fomes_inzengae_IB20160343_Type_locality_ITALY
Fomes_inzengae_Ff_15_ARMENIA
Fomes_fomentarius_IPAE_54_CRIMEA
Fomes_fomentarius_LEBIN_3809_BELARUS
Fomes_inzengae_IB20160342_Epitype_ITALY
Fomes_inzengae_Ff_16_ARMENIA
Fomes_inzengae_isolate5711_BELGIUM
Fomes_inzengae_isolate5704_BELGIUM
Fomes_inzengae_IB20160351_ITALY
Fomes_inzengae_IB20160349_ITALY
Fomes_inzengae_BRNM840275_CZECHIA
Fomes_fomentarius_1_FF001AP_SLOVAKIA
Fomes_fomentarius_9_FF009AH_SLOVAKIA
Fomes_inzengae_BRNM840274_CZECHIA
Fomes_inzengae_BRNM840289_CZECHIA
Fomes_inzengae_BRNM840301_CZECHIA
Fomes_inzengae_BRNM840278_CZECHIA
Fomes inzengae
Fomes_sp_XSD_29
Fomes_sp_ZF_51_CHINA
Fomes_sp_KUC20121123_35_SOUTH_KOREA
Fomes_sp_CGMCC1658_CHINA
Fomes_sp_IPAE_34_JAPAN
Fomes_sp_NAAS04711_SOUTH_KOREA
Fomes_sp_IPAE_35_JAPAN
Fomes sp.
Fomes_sp_CLZhao_4605_CHINA
Fomes_sp_CLZhao_1198_CHINA
Fomes_sp_SWFU_004605_CHINA
Fomes_sp_CLZhao_4393_CHINA
Fomes_sp_B2SN036_NEPAL
Fomes_sp_Cui8020
Fomes sp.
Globifomes_graveolens_NRM11_USA
Globifomes_graveolens_iNat191131761_USA
Globifomes_graveolens_Mycomap7015_USA
Fomes graveolens
Fomes_sp_SWFU006310_CHINA
Fomes_sp_SWFU006369_CHINA
Fomes sp.
Fomes_fomentarius_IB20130019_Epitype_AUSTRIA
Fomes_fomentarius_Ff_1_ARMENIA
Fomes_fomentarius_IB20130011_AUSTRIA
Fomes_fomentarius_IB20130016_AUSTRIA
Fomes_fomentarius_Ffa_2_ARMENIA
Fomes_fomentarius_Ff_11_ARMENIA
Fomes_fomentarius_7_FF007NA_SLOVAKIA
Fomes_fomentarius_ITS12_FF012FS_SLOVAKIA
Fomes_fomentarius_BRNM840283_CZECHIA
Fomes_fomentarius_BRNM840314_SLOVAKIA
Fomes_fomentarius_BRNM840310_CZECHIA
Fomes_fomentarius_BRNM840309_CZECHIA
Fomes_fomentarius_ES2008_3_SWEDEN
Fomes_fomentarius_BRNM840294_CZECHIA
Fomes fomentarius s.s.
Fomes_fomentarius_124FT_JM_USA
Fomes_fomentarius_CFMR10193
Fomes_fomentarius_DAOM129034_CANADA
Fomes_fomentarius_NJB2011_KD3_USA
Fomes aff. fomentarius USA
Fomes_fomentarius_209FT_AK_USA
Fomes_fomentarius_NCSLG18674_USA
Fomes_fomentarius_HE21049
Fomes aff. fomentarius USA
'fomentarius' clade
Fomes
Fomes_fasciatus_NCSLG18635_USA
Fomes_fasciatus_NCSLG_18633_49FA_USA
Fomes_fasciatus_CFMR_FP50332_T_USA
Fomes_fasciatus_NCSLG_18632_USA
Fomes_fasciatus_47FA_NCSLG_18633_USA
Fomes_fasciatus_NCSLG18639_USA
Fomes_fasciatus_NCSLG18645_USA
Fomes_fasciatus_CFMR_FP57054_T_USA
Fomes_fasciatus_FLAS_F_60214_USA
Fomes_fasciatus_JV0610_7G2_GUATEMALA
Fomes_fasciatus_Miettinen_17907_USA
Fomes_fasciatus_TH488_GUYANA
Fomes_fasciatus_TH491_GUYANA
Fomes_fasciatus_BRFM_1081_FRENCH_GUIANA
Fomes_fasciatus_FP1061048_T_USA
Fomes_fasciatus_NCSLG18643_USA
'fasciatus' clade
99
99
99
91
97
95
94
99
99
100
90
100
90
99
92
100
100
99
100

Fig. 1 (cont.).

Fig. 2. *Fomes* species. A-B) *Fomes fomentarius* (Finland, Photo By Gerardo Robledo). C) *Fomes fasciatus* (Paraguay, photo by Michelle Campi). D) *Fomes inzengae* (Czech Republic, photo by Michael Tomsovsky). E-F) *Fomes graveolens* (USA, photo by Danny Newman): E) Young specimen. F) Mature specimen.

Fig. 2. Especies de *Fomes*. A-B) *Fomes fomentarius* (Finlandia, foto por Gerardo Robledo). C) *Fomes fasciatus* (Paraguay, foto por Michelle Campi). D) *Fomes inzengae* (República Checa, foto por Michael Tomsovsky). E-F) *Fomes graveolens* (EE. UU., foto por Danny Newman): E) Espécimen joven. F) Espécimen maduro.

MEDICINAL AND CULTURAL IMPORTANCE OF *FOMES*

Although this section focuses on *F. fomentarius*, based on the results of the previous Taxonomy section, the uses and applications reported here may correspond to various species of *Fomes* from the Northern Hemisphere, either *F. inzengae* or one of the unnamed phylogenetic clades. Therefore, we suggest here that the properties and uses should be considered for the species of the 'fomentarius' clade. This applies equally to the other following sections.

Historicaly, *F. fomentarius* has been widely used in the field of medicine due to its perceived health benefits (Gupta *et al*., 2023). References of the medicinal value of *Fomes* span centuries and cultures worldwide, as summarized in Table 2, Fig. 3. The oldest report is possibly the Neolithic, with the discovery of Ötzi, the 5000-year-old man. This mummy was found in a glacier in the Ötztal Alps of Italy in 1991. Among Ötzi's belongings was the so-called "Black Matter", a mysterious material made from *F. fomentarius* that was likely used as tinder to obtain fire (Peintner *et al*., 1998; Kotowski, 2019). Moreover, it is estimated that it was probably the first to apply tinder

Table 2. Uses of *Fomes fomentarius* in Europe, Asia, and North America.
Tabla 2. Usos de *Fomes fomentarius* en Europa, Asia y América del Norte.

Ethnic Group / Country	Uses	Reference
Ötzi, 5000-year-old Neolithic man	Timber, insect repellent, ritual purposes	Peintner *et al*. (1998); Kotowski (2019)
Hippocrates (Ancient Greece)	Medicinal: anti-inflammatory, wound healer	Buller (1914); Emmons (1961); Molitoris(1994); Gáper *et al*., (2016); Gafforov *et al*. (2023)
Okanagan-Colville Indians of British Columbia and Washington State	Medicinal: treatment of arthritis	Hobbs (1995); Grienke *et al*. (2014); Gupta *et al*. (2023)
"The Khanty" European, West Siberian	Medicinal: absorbent bandage for wounds and burns Cultural: powdered and used as snuff; smoke rituals	Saar (1991); Hobbs (1995); Gupta *et al*. (2023)
Native American Indians	Medicinal: cauterizer and styptic	Hobbs (1995)
Germany and Austria	Medicinal: styptic bandages; smoking rituals	Grienke *et al*. (2014); Gupta *et al*. (2023); Kutalek (2002)
Hungary	Medicinal: treatment of headaches, hemorrhoids, bladder disorders, cough, and sweating	Gáper *et al*. (2016)
Northern Finland (Lapland) and Nepal	Medicinal: Cautery for moxibustion	Roussel *et al*. (2002)
Japan	Medicinal: anticancer effects in rats	Ito *et al*. (1976)
China	Medicinal: treatment of indigestion, esophageal cancer and gastric and uterine carcinomas.	Liu & Bau (1980); Ying *et al*. (1987)
India	Medicinal: diuretic, laxative and tonic effects.	Gáper *et al*. (2016)

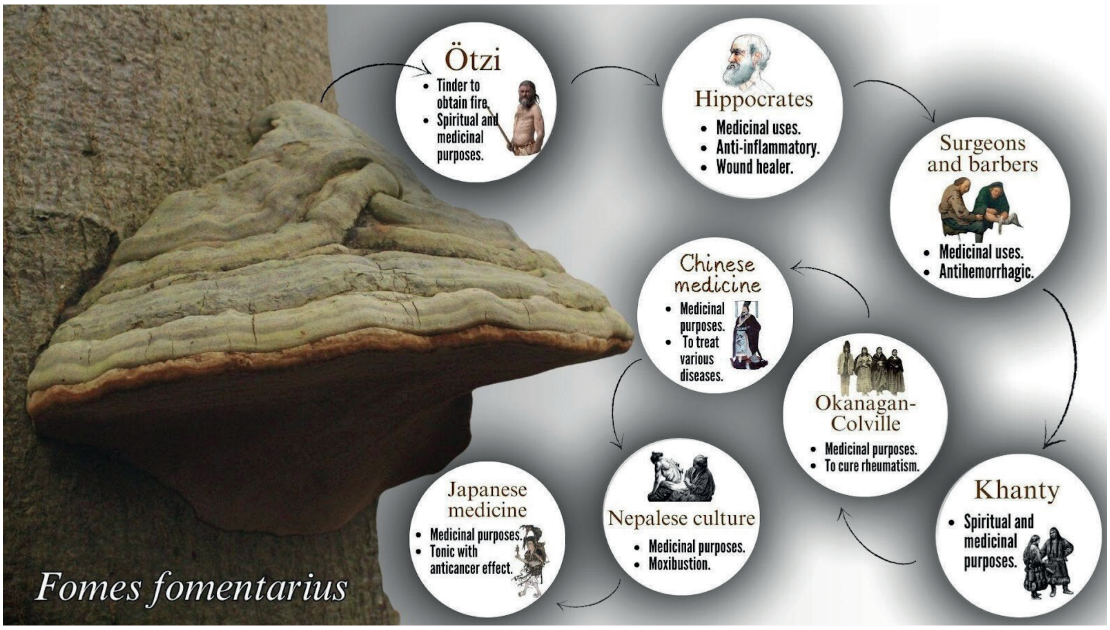

Fig. 3. Cultural use of *Fomes fomentarius* by various groups in the Northern Hemisphere.
Fig. 3. Uso cultural de *Fomes fomentarius* por varios grupos en el hemisferio Norte.

material prepared from *F. fomentarius* basidiomata for medicinal purposes in a first aid kit (Pöder, 2005; Gáper *et al*., 2016).

The first historical reference to the medicinal properties of *F. fomentarius* is attributed to Hippocrates, a Greek physician considered the "Father of Medicine" in the fifth century B.C. (Buller, 1914; Emmons, 1961; Molitoris, 1994; Peintner *et al.*, 1998; Gáper *et al*., 2016; Gafforov *et al*., 2023). Hippocrates described the Amadou mushroom (*F. fomentarius*) as a powerful anti-inflammatory and wound healer (Gupta *et al*., 2023). In writing on medicine, Hippocrates advised cauterization with a fungus to cure certain complaints (Buller, 1914). His writings include: "*One should cauterize the osseous and nervous parts with fungi* "*mykes*"; "*Quickly cauterize in eight places so as to intercept the extremities of the spleen*"; and "*When the liver has attained its greatest volume, one should cauterize with fungi*" (Buller, 1914).

Over time, *F. fomentarius* was widely used as a styptic by surgeons, barbers, and dentists, and therefore called "agaric of the chirurges" because it was used for stopping light hemorrhages (Buller, 1914; Neifar *et al.*, 2013; Grienke *et al*., 2014). Traditional European medicine cites the use of *F. fomentarius* by various groups. In West Siberia, the *Khanty*, a centuries-old ethnic group, used the *F. fomentarius* as smoke or cotton; smoke was used spiritually: "*The smoke was made when a person died and continued until the deceased had been taken out of the house. The people coming from the funeral also had to pass through smoke. The aim of the procedure was not to let the dead have any influence on the living*" (Saar, 1991). The cotton was used as an antiseptic bandage, this compress was made of the fungus flesh between the pileus cuticle and the tube layer (Saar, 1991).

In the German-speaking Alpine area, *F. fomentarius* was called "Wundschwamm" (sponge for wounds), "Chirurgenschwamm" (surgeon's sponge), or "*Fungus chirurgorum*" and until recently it was still official and available in many pharmacies as styptic bandages (Kutalek, 2002; Grienke *et al*., 2014; Gupta *et al*., 2023). In Hungary, it was used as a remedy against headaches, hemorrhoids, bladder disorders, coughs, and sweating (Gáper *et al*., 2016). In Northern Finland (Lapland), *F. fomentarius* was used in cautery for moxibustion in the treatment of rheumatism, abdominal pain, and paralysis until the 19th century (Roussel *et al*., 2002; Pöder, 2005; Gáper *et al*., 2016).

In North America, Indigenous groups from British Columbia and Washington State, the Okanagan-Colville and Shuswap, used *F. fomentarius* to cure rheumatism: "*A piece of the fungus (after pounding and softening) was put on the skin over the affected area with spittle and ignited*" (Hobbs, 1995).

In Asia, *F. fomentarius* has been used as a traditional Chinese medicine for centuries. The fruiting body is called "Mudi" and is used to treat various diseases such as oral ulcers, gastroenteric disorders, hepatocirrhosis, inflammation, and multiple cancers (Chen *et al*., 2008). In Nepal, it was used in moxibustion cautery (Gáper *et al*., 2016), and in Japan, it is brewed as a popular tonic drink believed to have anti-cancer effects (Ito *et al*., 1976).

CHEMICAL COMPOSITION AND BIOLOGICAL PROPERTIES OF *FOMES FOMENTARIUS*

Many civilizations have long used mushrooms, nevertheless, contemporary science has only recently explained the biological properties attributed to fungi by characterizing the chemical components. *Fomes fomentarius* has a broad spectrum of biologically active compounds summarized in Table 3.

In 1967, the Fomentaric acid, a novel type of alkyl succinic acid, was isolated from the petroleum ether fraction of *F. fomentarius* (Singh & Bangaswami, 1967). Fomentariol was isolated in 1974, and decades later the biological properties were analyzed, resulting in antioxidant, anti-inflammatory, and antidiabetic properties (Arpin *et al.*, 1974; Seo *et al*., 2015; Maljurić *et al*., 2018). Fomentariol inhibited nitric oxide production and intracellular reactive oxygen species triggered by lipopolysaccharides (Seo *et al*., 2015). Other bioactive molecules were the Fomentarols A-D isolated from ethanolic extracts of *F. fomentarius* that showed moderate cytotoxic effects against human cancer cell lines (Zang *et al*., 2013). Regarding alcohols, β-Sitosterol, 6-Epicerevisterol, Δ7-Ergostenol were reported (Feng & Yang, 2012; Huang *et al*., 2012; Zang *et al*., 2013).

Table 3. Chemical composition and biological properties of *Fomes fomentarius.*
Table 3. Composición química y propiedades biológicas de *Fomes fomentarius.*

Source	Fraction	Compound	Biological properties	Reference
Fruiting body	Petroleum ether extract	Fomentaric acid		Singh & Bangaswami (1967)
		1-octen-3-ol, 3-octanone, 3-octanol	Infochemicals for a specialist fungivore	Holighaus *et al*. (2014)
	n-hexane extract	Ergosta-7,22-dien-3-one	Anti-inflammatory	Rösecke & König (2000)
		5a,8a-epidioxyergost-6-en-3b-ol (ergosterol peroxide)		
	Ethanolic extract	Not isolated	Antitumor and immunomodulatory properties	Li *et al*. (2016)
		Fomentariol	Antioxidant activity, antidiabetic potential	Arpin *et al*. (1974); Seo *et al*. (2015); Maljurić *et al*. (2018)
		Ergosta-7,22-dien-3-ol, betulin	Antitumor activity	Huang *et al*. (2012)
		Fomentarols A–D	Moderate cytotoxic effects against human cancer cell lines	Zang *et al*. (2013)
			Antimutagenic activity	Park, & Lim (2024)
	Methanol extract	Methyl 9-oxo-(10E,12E)-octadecadienoate	Anti-inflammatory activity in murine macrophages	Choe *et al*. (2015)
		3-formyloxybetulin	Cytotoxic effect against cancer cell lines	Zhang *et al*. (2021)
		3-formyloxybetulinic acid	Activities against nitric oxide	Zhang *et al*. (2021)
	Methanol and aqueous extracts		Antibacterial activity	Kolundžić *et al*. (2016)
	Chloroform and methanol extracts	Phenyl-ethanediols	Antimicrobial activity	Zhao *et al*. (2013)
	Ethyl acetate and water extracts	Pyropolincisterols A and B, betulin, 28-formyloxybetulin erigosterols		Zhang *et al*. (2021)
		Polyporenic acid	Cytotoxicities against six human cancer cell lines	
		3-formyloxybetulin, 3-formyloxybetulinic acid, phellibarins A–C and volemolide	Inhibitory activities against nitric oxide (NO) production	
	Ethyl acetate and ethanol extracts		Antioxidant activity	Sveta (2022)
	Chloroform, ethyl acetate and ethanol extracts		Antimicrobial activity against *Staphylococcus aureus*	
	Aqueous extract		Antioxidant activity	Park & Lim (2024)
Mycelium	Aqueous extracts	Polysaccharide	Antimicrobial, antioxidant	Alvandi *et al*. (2020)

From the ethanolic extract of the fruiting bodies of *F. fomentarius*, 12 compounds were isolated and evaluated for their antitumor properties. The most effective compounds were ergosta-7,22-dien-3-ol, which showed activity against NCI-H460 cells, and betulin, which was effective against SGC-7901 cells (Huang *et al.*, 2012). In addition, recent studies have shown that the condition of 70% ethanol extract of *F. fomentarius* fruiting bodies, displayed the most robust antimutagenic activity and potent antioxidant properties (Park & Lim, 2024). Other compounds have been isolated, such as pentacyclic lupane-type triterpenes, 3-formyloxybetulin and 3-formyloxy-betulinic acid, two rare degraded ergosterols, pyropolincisterols A and B, along with ten known triterpenoids and four known ergosterols (Zhang *et al.*, 2021). Compounds such as 3-formyloxybetulin, 3-formyloxybetulinic acid, phellibarins A–C, and volemolide exhibited inhibitory activity against nitric oxide production, which may correspond to the anti-inflammatory effects of this fungus. These components could explain the ancestral medicinal folkloric use.

NUTRITIONAL PROFILE

Fomes fomentarius exhibits a high fiber content (Table 4) composed mainly of beta-glucans (approximately 39.5%) (Kalitukha & Sari, 2019). Beta-glucans are known for their immunomodulatory properties (Ahmad *et al.*, 2021). The primary structural components of these fibers include glucans, chitin, and melanin, with smaller amounts such as cellulose, mannans, galactans, xylans, arabinans, rhamnans, and uronic acid (Kalitukha & Sari, 2019). Regarding essential nutrients, *F. fomentarius* contains essential fatty acids (oleic and linoleic acid) and essential amino acids (threonine, phenylalanine, isoleucine, leucine, and lysine) (Kalitukha & Sari, 2019).

Table 4. Comparison of the proximate composition (% dry weight) of dried *Fomes fomentarius*.
Tabla 4. Comparación de la composición proximal (% peso seco) de *Fomes fomentarius*.

Dried Fruiting bodies	Sagar *et al.* (2009)	Kalitukha & Sari (2019)	Park & Lim (2024)
Moisture	–	–	11.04 ± 0.26
Crude carbohydrate	–	–	75.04 ± 1.44
Crude protein	25.16	–	5.82 ± 0.11
Crude fat	–	1.90 ± 0.88	–
Dietary fiber	–	74.93 ± 1.07	–
Ash	–	–	1.58 ± 0.18

OTHER USES

Fomes fomentarius is used for crafting various handmade accessories and is considered the most widely known mycotextile (Fig. 4) (Pegler, 2001; Blanchette *et al*., 2021). Traditionally, women create these products from the stretched parts of the tinder fungus species. Common products include hats, bags, tablecloths, brush-holders, and scarves (Papp *et al*., 2015). These items are primarily sold in markets across Transylvania, Romania, Hungary, and Germany, where they form an integral part of the regions' folkloric and ethnomycological traditions (Papp *et al*., 2015). Stretched strips that are not adequately used for medicinal or decorative purposes are frequently employed by beekeepers in Transylvania. This usage is consistent with previous regional findings, which suggest that the smoke from burning these strips acts as a sedative for bees (Papp *et al*., 2015).

Recent studies of other applied uses have demonstrated that fungal-based composites made from *F. fomentarius* partially meet or even exceed key performance parameters of currently used fossil fuel-based insulation materials and can also be used to replace particleboards (Schmidt *et al*., 2023). *Fomes fomentarius* is unquestionably a mushroom species of considerable economic importance, with a strong presence in the ethnomycological traditions of diverse cultures across the Northern Hemisphere.

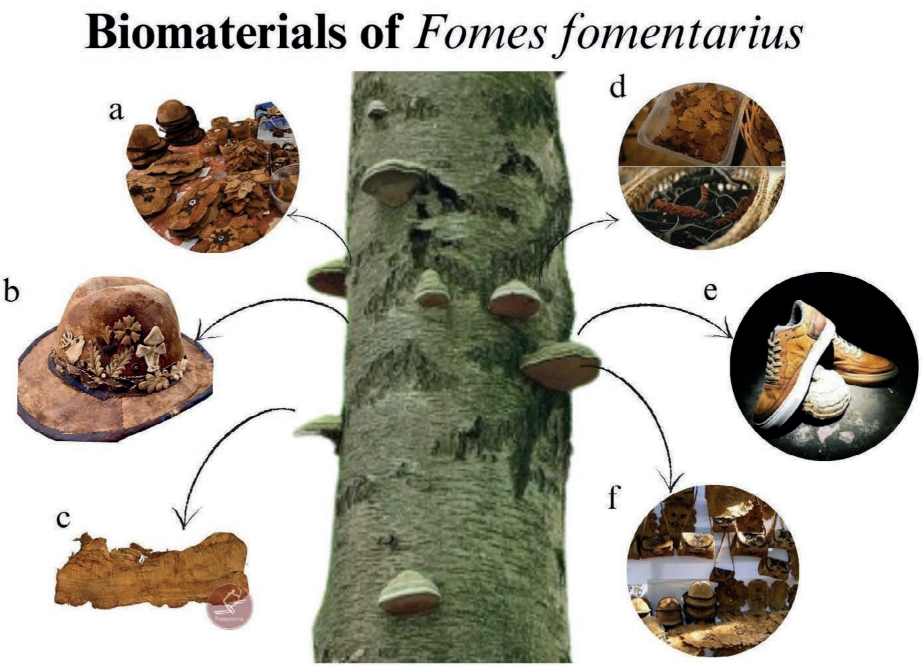

Fig. 4. Products made from tinder fungus. a, f) *Fomes fomentarius* leather products. b) Hat. c) Pieces of *Fomes* to light a fire. d) Decorations. e) *Fomes* leather shoes (Smith, 2018). Images used: a, c, e, f Zoltán, n.d.; b [Amadou hat], n.d.; d Transindex, 2020

Fig. 4. Productos hechos de hongo yesquero. a, f) Productos de cuero de *Fomes*. b) Sombrero. c) Piezas de *Fomes* para encender fuego. d) Decoraciones. e) Zapatos de cuero de *Fomes* (Smith, 2018). Imágenes extraídas de: a, f Zoltán, P. (s.f.); b [Sombrero de Amadou], s.f.

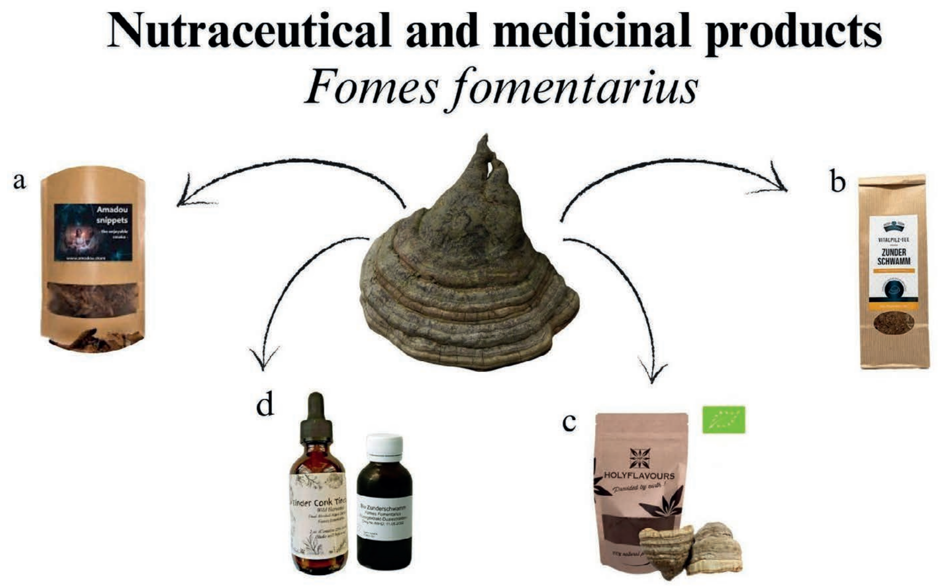

Fig. 5. Nutraceutical and medicinal products of *Fomes fomentarius* offered on the web. a-c) Fruiting body of the *F. fomentarius* for tea. d) Concentrated liquid dual extract. Images retrieved from a SlowToursTransilvania, (n.d.), b, d) MYKOTHEKE, (n.d.), c) La casa de la setas, (n.d.)

Fig. 5. Productos nutracéuticos y medicinales de *Fomes fomentarius* ofrecidos en la web. a-c) Cuerpo fructífero de *F. fomentarius* para té. d) Extracto líquido concentrado dual. Imágenes obtenidas de a) SlowToursTransilvania, (s.f.), b, d) MYKOTHEKE, (s.f.), c) La casa de las setas, (s.f.).

Regarding ethnomycological and ethnomedicinal uses of the fruit body of tinder fungus, the market for natural products features a variety of nutraceutical and medicinal products derived from *F. fomentarius*. These products encompass alcoholic extracts, fruit body powder, and various cosmetic formulations (Fig. 5). Current scientific research has confirmed the effectiveness of the medicinal use of *F. fomentarius*, a practice that remains prevalent in various cultures across the Northern Hemisphere. Advances in mycochemical techniques have played a crucial role in validating these traditional uses.

FOMES AND THE ELEMENTAL SPIRITS

With a long documented history of use, the tinder mushroom (*F. fomentarius*) has qualities that connect it to legends involving fire, the origin of fire, and mythological associations with this element (Niell, 2017).

In West Siberia, the Khanty, a centuries-old ethnic group, used *F. fomentarius* to incorporate smoke in spiritual practices: "The smoke was made when a person died and continued until the deceased had been taken out of the house. The people coming from the funeral also had to pass through smoke. The aim of the procedure was not to let the dead have any influence on the living" (Saar, 1991).

WHAT WE KNOW ABOUT *FOMES FASCIATUS*: PERSPECTIVES AND POTENCIAL USES

Despite the well-established relationship between *F. fasciatus* and *F. fomentarius* (McCormick *et al*., 2013), research on the chemical, biological, nutritional, and biotechnological (biomaterials) properties of *F. fasciatus* remains sparse in literature and conference presentations. Although a master's thesis from Brazil investigated the production of ligninolytic enzymes using residues from *Syagrus coronata* (Carneiro, 2014), this contribution highlights the general oversight of *F. fasciatus* by researchers. The impact of *F. fomentarius* on traditional medicine, food industry, and cosmetics underscores the potential value of exploring the endemic Neotropical species *F. fasciatus*.

Considering its ability to produce large basidiomata, grow on industrial waste substrates, and its relationship with *F. fomentarius*, a thorough evaluation of *F. fasciatus* for multidisciplinary applications is essential. In the present century, we have the tools and knowledge to elucidate the taxonomic status of Neotropical mushroom species and to explore their chemical, biological, and nutritional properties. Such insights will enable us to appreciate and utilize the endogenous resources of the region and address contemporary challenges. Traditional mushroom use has always offered solutions; our responsibility is to uncover and manage these valuable resources responsibly.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest between themselves or against third parties.

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