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Indoporus shoreae gen. et sp. nov. (Boletaceae) from tropical India

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Abstract – Tropical dry deciduous *Shorea* dominated forests in Jharkhand (India) harbour diverse groups of ectomycorrhizal macrofungi, including boletes. Repeated macrofungal explorations in different parts of this state followed by thorough investigation of collected samples uncovered a novel genus in the family Boletaceae subfamily Boletoideae. This genus is proposed here as *Indoporus* to include *I. shoreae*, a novel species. Detailed morphological description, a comparison table with closely allied genera, a distributional map, supporting illustrations and phylogenetic estimations based on nrITS sequence data and a combined analysis of nrLSU (28S) and *rpb2* sequence data are provided.

Boletales / nrITS / nrLSU / phylogenetic inferences / *rpb2* / taxonomy

INTRODUCTION

The family Boletaceae Chevall. (Boletales, Basidiomycota) is a large and immensely diverse group of mushroom producing Fungi. It contains about 70 genera and nearly 800 species (Bresinsky *et al.* 1999, Binder & Bresinsky 2002, Binder & Hibbett 2006, Drehmel *et al.* 2008, Desjardin *et al.* 2009, Orihara *et al.* 2010, Li *et al.* 2011, Nuhn *et al.* 2013, Gelardi *et al.* 2014a, Wu *et al.* 2014, Kirk *et al.* 2008, Farid *et al.* 2017) but several evidences revealed in recent past, particularly from Asia, suggest that the numbers of species and genera are likely to be higher because large parts of the tropics and the subtropics remain seriously under- or unexplored (Wu *et al.* 2016). Combined analyses of morphology and multigene phylogeny opened the avenue for a better delimitation of taxa and, consequently, made it possible to delimit a number of new genera (Arora and Frank 2014; Gelardi *et al.* 2014a,b,c; Li *et al.* 2014a; Vizzini 2014a,b; Zeng *et al.* 2014; Zhao *et al.* 2014, Gelardi *et al.* 2015, Wu *et al.* 2015, Henkel *et al.* 2016, Wu *et al.* 2018). In India *Boletaceae* is still poorly studied. Only some scattered work (Harsh & Bisht 1982, 1985; Lakhanpal 1996; Lakhanpal & Sagar 1989; Kumar and Sharma 2011; Pyasi

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et al. 2012; Das *et al.* 2013a, 2013b, 2015a, 2015b, 2016, 2017; Kaur *et al.* 2013; Parihar *et al.* 2014, 2018; Pradeep *et al.* 2015; Chakraborty *et al.* 2017a, 2017b, 2018) contributed to our knowledge about the diversity and systematics of boletes in India.

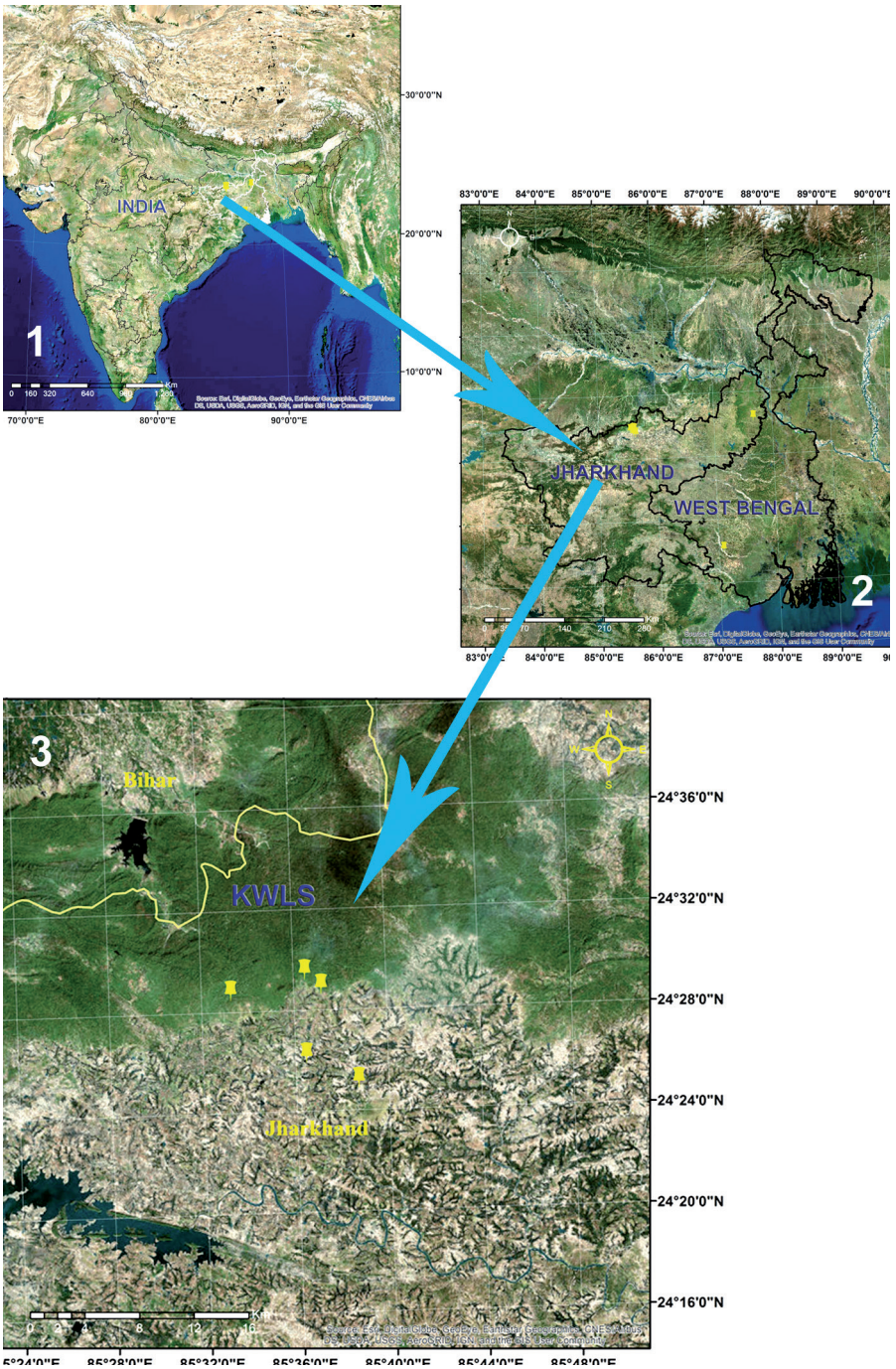
Jharkhand is an Indian state situated in the eastern part of India and comprising two distinct regions namely Chota Nagpur and Santhal Pargana. About 40% area of this state is covered with forest. These forests are mainly dry deciduous scrub forests that comprise a unique vegetation to support the diversity of different groups of fungi including ectomycorrhizal fungi. The diversity of macrofungi of this state is not yet well explored and systematic documentation of the macrofungal wealth from this state is not available. To fill this lacuna, two of us (AP and MEH) conducted several macrofungal survey tours to Koderma Wildlife Sanctuary and Rajmahal hills in Jharkhand respectively and a small part of West Bengal (Figs. 1-3).

During the course of their macrofungal surveys in monsoon to post monsoon periods from 2013 to 2018, several *Shorea robusta* C. F. Gaertn. (Dipterocarpaceae) dominated forested areas were explored and some remarkable collections were made. In order to establish their identity, detailed macro- and micro-morphological studies followed by phylogenetic analyses were carried out. Finally, thorough study of literature revealed that these samples with peculiar macro- and micro-morphological features do not belong to any known genera of Boletaceae. This taxon is proposed in the present communication as *Indoporus shoreae* gen. *et* sp. nov. Morphological details, phylogenetic analyses with (1) combined sequence data of nuclear ribosomal large subunit (given hereafter as nrLSU) and 2nd largest subunit of RNA polymerase II (given hereafter as *rpb2*) and (2) a separate sequence data of nuclear ribosomal internal transcribed spacer (given hereafter as nrITS) region, supporting illustrations, distributional map and comparison with the allied genera are given below for this novel taxon.

MATERIAL AND METHODS

Morphological studies

Macro-morphological features were recorded from fresh basidiomata in field or in basecamp. Field photographs of these basidiomata showing their habitat and distinguishing characters were taken with a Nikon D300s camera. Colour codes and terms used (mostly) in the text follow Methuen Handbook of Colour (Kornerup & Wanscher 1978). Micro-morphological features were observed with an Olympus CX-41 light microscope from several free hand sections obtained from dry basidiomata and mounted in a mixture of 3-5% KOH, Phloxin, Congo red and observed in 30% glycerol or directly under Melzer's reagent. Micro-photography was made with a dedicated camera Olympus PEN Lite E-PL6 attached with Olympus CX41 light microscope. Micro-morphological drawings were made using a dedicated drawing attachment with Olympus CX-41 microscope. Spore measurements were recorded in profile view from forty basidiospores and measurements are presented as (MIN) [KDx-2×SDx] - KDx - KDy - [KDy+2×SDy] (MAX) in which KDx = lowest mean value for the measured collections, KDy = greatest mean value and SDx/y = standard deviation of the lowest and greatest mean value respectively. MIN is the lowest value measured, MAX the highest value; MIN and MAX are only given when they exceed [KDx-2×SDx] or [KDy+2×SDy] respectively. Q stands for



Figs 1-3. **1.** Map of India showing location of Jharjhand and West Bengal. **2.** Map of Jharkhand and West Bengal showing Distribution of *Indoporus shoreae*. **3.** Map of Koderma Wildlife Sanctuary showing different collection sites of *Indoporus shoreae*.

Table 1. Taxa and GenBank accession numbers of nrLSU and rpb2 sequences used in the combined phylogenetic analysis (Fig. 2).

Taxon	*Specimen Voucher*	*Origin*	*GenBank accession number*	
			nrLSU	*rpb2*
Afroboletus luteolus	00-436	Africa	KF030238	-
Austroboletus fusisporus	HKAS 75207	China	JX889720	-
Austroboletus sp.	HKAS 57756	China	KF112383	KF112764
Austroboletus_gracilis	112/96	USA	DQ534624	-
Boletus aereus	REH 8721	USA	KF030339	-
Boletus aff. *aokii*	HKAS 52633	China	KF112379	KF112736
Boletus aokii	HKAS59812	China	KF112378	-
Boletus edulis	HMJAU 4637	Russia	KF112455	KF112704
Boletus edulis	Be 3	Germany	KF030282	GU187774
Boletus pallidus	JLF 2551	USA	KC812308	-
Boletus reticuloceps	HKAS 57671	China	KF112454	KF112703
Boletus sp.	HKAS 53426	China	KF112491	KF112828
Boletus sp.	HKAS 53425	China	KF112341	KF112800
Boletus sp.	HKAS 76661	China	KF112342	-
Boletus sp.	HKAS55393	China	JN563852	-
Boletus sp.	HKAS 55382	China	JN563851	-
Boletus subalpinus	27882	-	KF030340	-
Boletus variipes var. *fagicola*	4249	USA	JQ327014	-
Indoporus shoreae	**AP 6693, holotype**	**India**	**MK123973**	**MK243367**
Indoporus shoreae	**AP 6697**	**India**	**MK123976**	**MK243368**
Nigroboletus roseonigrescens	ZT13553	China	KT220589	KT220594
Nigroboletus roseonigrescens	GDGM 43238	China	KT220588	-
Nigroboletus roseonigrescens	MG 524a	China	KT220590	-
Porphyrellus brunneus	REH 9508	Australia	JX889646	-
Porphyrellus holophaeus	HKAS 74894	China	KF112474	-
Porphyrellus holophaeus	HKAS 50508	China	KF112465	-
Porphyrellus porphyrosporus	MB97-023	Germany	DQ534643	GU187800
Porphyrellus porphyrosporus	HKAS 76671	China	KF112482	KF112718
Porphyrellus sp.	KKAS 75078	China	KF112481	KF112717
Porphyrellus sp.	HKAS 53366	China	KF112480	KF112716
Porphyrellus sp.	HKAS 74938	China	KF112466	KF112763
Strobilomyces aff. *seminudus*	HKAS 59461	China	KF112479	KF112815
Strobilomyces aff. *verruculosus*	HKAS 55389	China	KF112604	KF112813

Strobilomyces echinocephalus	HKAS 59420	China	-	KX869529
Strobilomyces floccopus	Sf1	Germany	DQ534626	-
Strobilomyces latirimosus	HKAS74865	China	-	KX869539
Strobilomyces latirimosus	HKAS53348	China	-	KX869415
Strobilomyces montosus	HKAS 74809	China	-	KX869423
Strobilomyces parvirimosus	HKAS 74911	China	-	KX869428
Strobilomyces subnudus	HKAS59435	China	-	KX869445
Tylopilus aff. *balloui*	HKAS 59700	China	KF112458	KF112740
Tylopilus aff. *rigens*	HKAS 53388	China	KF112405	KF112688
Tylopilus badiceps	78206	USA	KF030335	-
Tylopilus felleus	HKAS 54926	Germany	KF112411	KF112737
Tylopilus ferrugineus	MB06-53	USA	JQ326994	-
Tylopilus microsporus	HKAS 59661	China	KF112450	KF112798
Tylopilus otsuensis	HKAS 53401	China	KF112449	KF112797
Tylopilus plumbeoviolaceoides	HKAS50210	China	KF112431	KF112738
Tylopilus plumbeoviolaceus	MB06-056	USA	KF030350	-
Tylopilus sp.	HKAS 74925	China	KF112473	KF112739
Tylopilus sp.	HKAS 55438	China	KF112404	KF112687
Tylopilus violatinctus	HKAS 50208	China	KF112472	KF112799
Xanthoconium affine var. *maculosum*	BD 217	USA	HQ161854	-
Xanthoconium purpureum	BD 228	USA	HQ161864	-
Xanthoconium sp.	MB06-49	USA	KF030292	-
Xerocomellus aff. *rubellus*	HKAS 51239	China	KF112425	KF112695
Xerocomellus cf. *rubellus*	MB03-033	USA	KF030294	-
Xerocomellus chrysenteron	HKAS 56494	China	KF112357	KF112685
Xerocomellus cisalpinus	PDD94421	New Zealand	JQ924322	KF112686
Xerocomellus cisalpinus	AT2005034	Finland	KF030354	-
Xerocomellus sp.	HKAS 76673	China	KF112370	KF112693
Xerocomellus sp.	HKAS 51292	China	KF112369	KF112692
Xerocomellus sp.	HKAS 59608	China	KF112371	KF112696
Xerocomellus sp.	HKAS 50466	China	KF112372	KF112694
Xerocomellus sp.	HKAS 50467	China	KF112489	KF112770
Xerocomellus zelleri	REH 8724	USA	KF030271	-
Xerocomus badius	MB03-098a	USA	KF030355	-
Xerocomus badius	Xb2	Germany	KF030357	-
Xerocomus badius	HKAS 74714	China	KC215212	-
Xerocomus sp.	HKAS 74712	China	KF112373	KF112706
Xerocomus sp.	HKAS 52557	China	KF112374	KF112707

Note: Newly generated sequences are shown in bold.

length/width ratio and is given as MINQ - Qx - Qy - MAXQ in which Qx and Qy stand for the lowest and the highest mean quotient for the measured specimens respectively. Herbarium acronym follows Thiers (continuously updated). SEM studies were undertaken with a FEI's Quanta FEG 250 model at the Central National Herbarium of Botanical Survey of India, Howrah. Dry basidiospores from spore print were directly mounted on a double-sided adhesive tape pasted on a metallic specimen-stub and then scanned with gold coating at different magnifications in high vacuum mode to observe patterns of spore ornamentation. Distributional map (Figs. 1-3) was prepared from the GPS data of the collection sites with the help of ArcGIS Software installed at the Central National Herbarium of Botanical Survey of India, Howrah.

DNA isolation, amplification and sequencing

Genomic DNA was extracted from dried herbarium specimens (10-50 mg) using the 'Fungal gDNA Mini Kit' (RGCB, RFDF, Thiruvananthapuram). PCR protocol for the amplification of ITS1, 5.8S and ITS2 regions (nrITS) and nrLSU (28S) followed those in Das *et al.* (2017). Primers used for the amplification of *rpb2* region were bRPB2-6F (TGGGGYATGGTNTGYCCYGC, forward primer sequence), bRPB2-7.1R (CCATRGCYTGYTTMCCCATDGC, reverse primer sequence) following Matheny (2005) and Matheny *et al. (*2007). PCR products were purified using a QIAquick Gel Extraction Kit (QIAGEN, Germany) and subjected to automated DNA sequencing on an ABI3730xl DNA Analyzer (Applied Biosystems, USA) using the same primers. The newly generated sequences were then deposited in GenBank.

Dataset preparation

Two separate datasets were prepared: 1) combined dataset of 65 nrLSU and 40 *rpb2* equences (including four sequences from the two collections of the new Indian species) (Tab. 1); 2) dataset of 53 nrITS sequences (including two respective sequences from the Indian collections). While preparing these datasets the sequences available in public databases like NCBI (GenBank) and UNITE were sampled based on BLAST search (Altschul *et al.* 1997) in NCBI GenBank or from recent research articles on allied genera (Wu *et al.* 2014, Gelardi *et al.* 2015, Tibpromma *et al.* 2017), covering almost all known boletes with blackening context reactions. Outgroup taxa for the *rpb2*-nrLSU combined dataset were three species of *Austroboletus* (subfamily Austroboletoideae, Boletaceae, Boletales), while two sequences of *Gyroporus ammophilus* (Gyroporaceae, Boletales) were used as outgroup in the nrITS dataset (Wu *et al.* 2014, Das *et al.* 2017).

Sequence alignment and phylogenetic analysis

Both datasets were aligned with the help of Muscle (default setting) using AliView (Larsson 2014). With these two aligned datasets phylogenetic estimation was performed using the Maximum likelihood approach (ML) in raxmlGUI 1.2 (Silvestro & Michalak 2012, Stamatakis *et al.* 2008) with 1000 bootstrap replicates. Bootstrap values (MLB) 70% and above are considered significant support for clades.

RESULTS

Phylogeny

The combined nrLSU/*rpb2* dataset was 4073 bp long. The ITS dataset was 514 bp long.

In our nrLSU/*rpb2*, combined phylogeny (Fig. 4), only few genera under subfamily Boletoideae are well resolved. The two collections (AP-6693 and AP-6697) of *Indoporus shoreae* appeared as monophyletic, being sister without support to a clade bearing *Boletus pallidus* (not in *Boletus* s.s.) and *Afroboletus luteolus* (Strobilomycetaceae).

In our nrITS phylogeny (Fig. 5), however, both collections (AP-6693 and AP-6697) of *I. shoreae* appeared as monophyletic but being sister (with low support) to a clade consisting of two established genera namely, *Chalciporus* and *Buchwaldoboletus* which are clustered together with strong support (MLB = 82%). However, our taxon appeared in an independent clade indicating its distinctiveness.

Taxonomy

Indoporus A. Parihar, K. Das, Hembrom & Vizzini, ***gen. nov.*** **Figs. 6-27**

MycoBank: MB 828965.

Diagnosis: Basidiomata epigeous; pileus grey with black squamules, non-glutinous, context yellowish white, quickly becoming dull red to greyish red then slowly becoming black to charcoal black; hymenophore tubulose, depressed at the juncture of stipe, reddish grey or paler brownish orange (6C4) on bruising, finally black after 5 minutes, pores angular, simple; stipe cylindrical to clavate, becoming narrow towards base, smooth, greyish violet at upper half, then grey (18F1) to blackish brown, context greyish violet to dark violet in upper half and dark blackish brown on lower half, slowly becoming black to charcoal black on exposure; basidiospores greyish brown in deposit, smooth, inamyloid; pileipellis a trichoderm, with irregular and inflated terminal cells with brownish-black intracellular pigmentations; pleurocystidia rare, lanceolate to ventricose, hyaline; cheilocystidia frequent, narrowly lanceolate with rounded to capitate apex, hyaline; hymenophoral trama parallel; occurrence under *Shorea robusta* in tropical dry deciduous forest.

Type species: *Indoporus shoreae* A. Parihar, K. Das, Hembrom & Vizzini

Etymology: 'Indo-' refers to country India from where it is discovered, and 'porus' refers to the poroid hymenophore.

Indoporus shoreae A. Parihar, K. Das, Hembrom & Vizzini, ***sp. nov.*** **Figs. 6-27**

MycoBank: MB 828966.

Genbank: MK123972 (AP-6693, holotype) & MK123977 (AP-6697) for nrITS, MK123973 (AP-6693, holotype) & MK123976 (AP-6697) for nrLSU, MK243367 (AP-6693, holotype) & MK243368 (AP-6697) for *rpb2*.

Diagnosis: Pileus initially convex, then plano-convex; surface dry, squamulose, grey with black squamules; margin entire, encurved. Hymenophore depressed near the juncture of stipe with age, reddish grey or paler when fresh, slowely becoming reddish grey with maturity, becoming brownish orange on bruising, black after 5 minutes, with KOH turning violet brown initially then black; pores angular, simple, 2-3 per mm. Context yellowish white on exposure, quickly

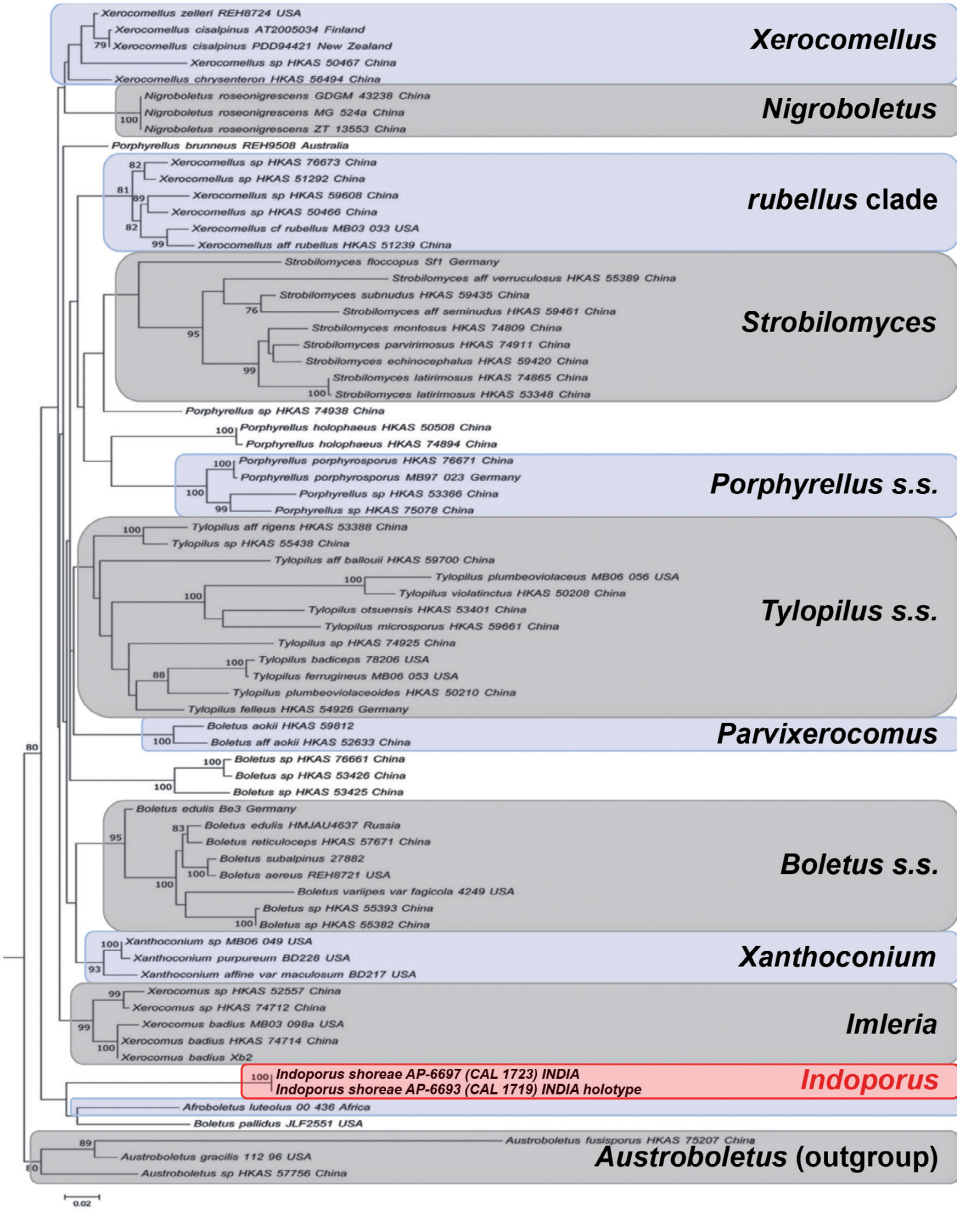


Fig 4. Phylogram generated from combined nrLSU and *rpb2* sequences: The evolutionary history was inferred by using the Maximum Likelihood method. Bootstrap support values (>70%) obtained from the ML analysis are shown above or below the branches at nodes.

becoming dull red to greyish red finally, black to charcoal black, turning reddish brown to brownish red (9D8-10D8) with KOH, stipe context in young basidiomata reddish white to reddish grey (9A2-9B2) in upper half, dark blackish brown on

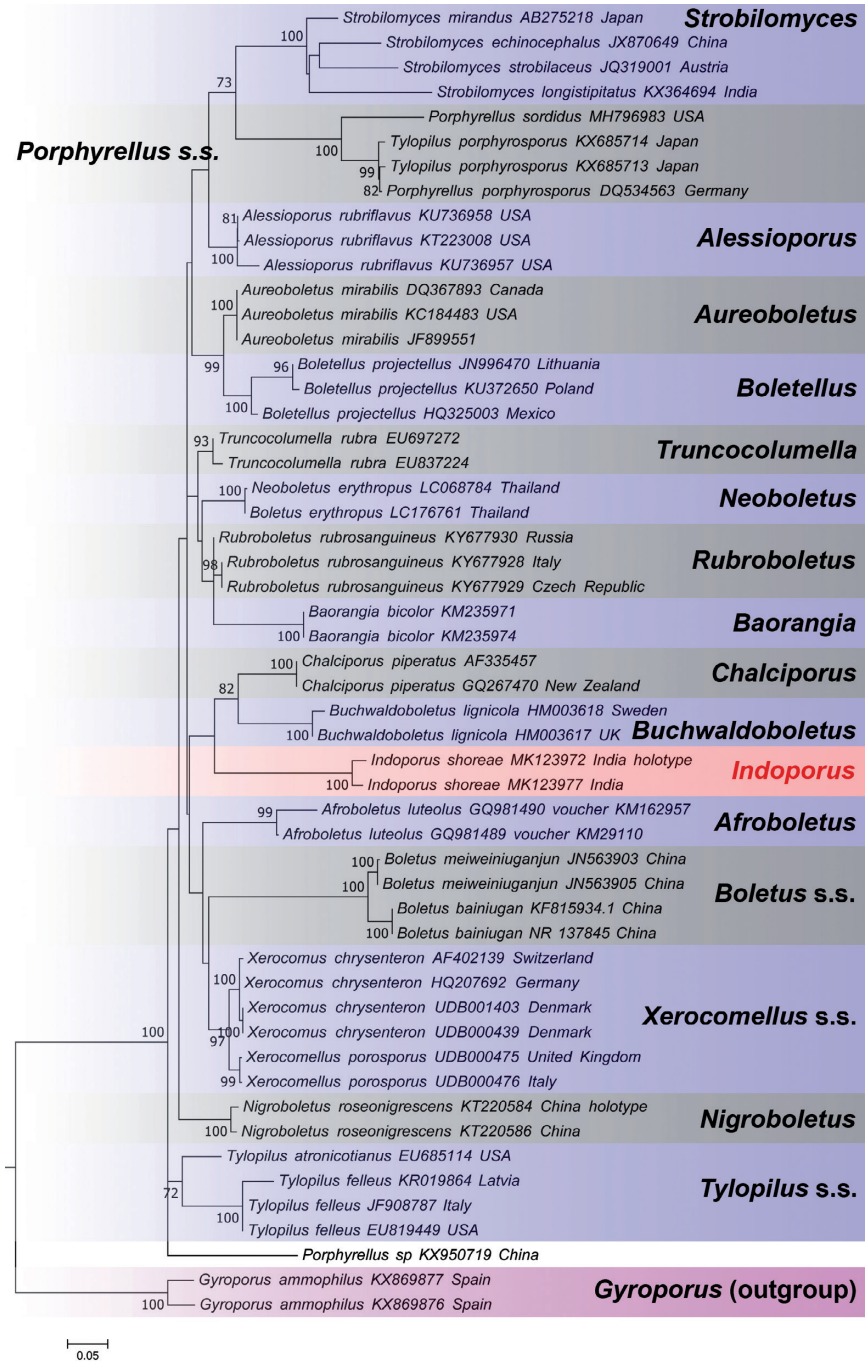


Fig 5. Phylogram generated from nrITS sequences: The evolutionary history was inferred by using the Maximum Likelihood method. Bootstrap support values (>70%) obtained from the ML analysis are shown above or below the branches at nodes.

lower half while in mature basidiomata greyish violet to dark violet (18E5-18F5) in upper half and dark blackish brown on lower half, becoming black to charcoal black on exposure, but turning coffee brown then blackish with KOH. Spore print greyish brown. Basidiospores 8.72-12.3-12.5-(18.4)-20 × 3.6-4.5-4.7-5.4 µm, cylindrical, subfusiform, inequilateral, thin-walled, smooth. Basidia four-spored, clavate. Pleurocystidia rare, lanceolate to ventricose, hyaline. Cheilocystidia frequent, narrowly lanceolate with rounded to capitate apex, hyaline. Hymenophoral trama divergent, hyphae septate, up to 10 µm wide. Pileipellis a trichoderm, composed of erect to suberect, loosely interwoven unbranched to rarely branched hyphae, mostly constricted at septa, moderately thick walled with dark brown to blackish pigment, mostly smooth, sometimes with faint zebroid incrustations. Caulocystidia, frequent, ventricose, lanceolate to obclavate, hyaline**.**

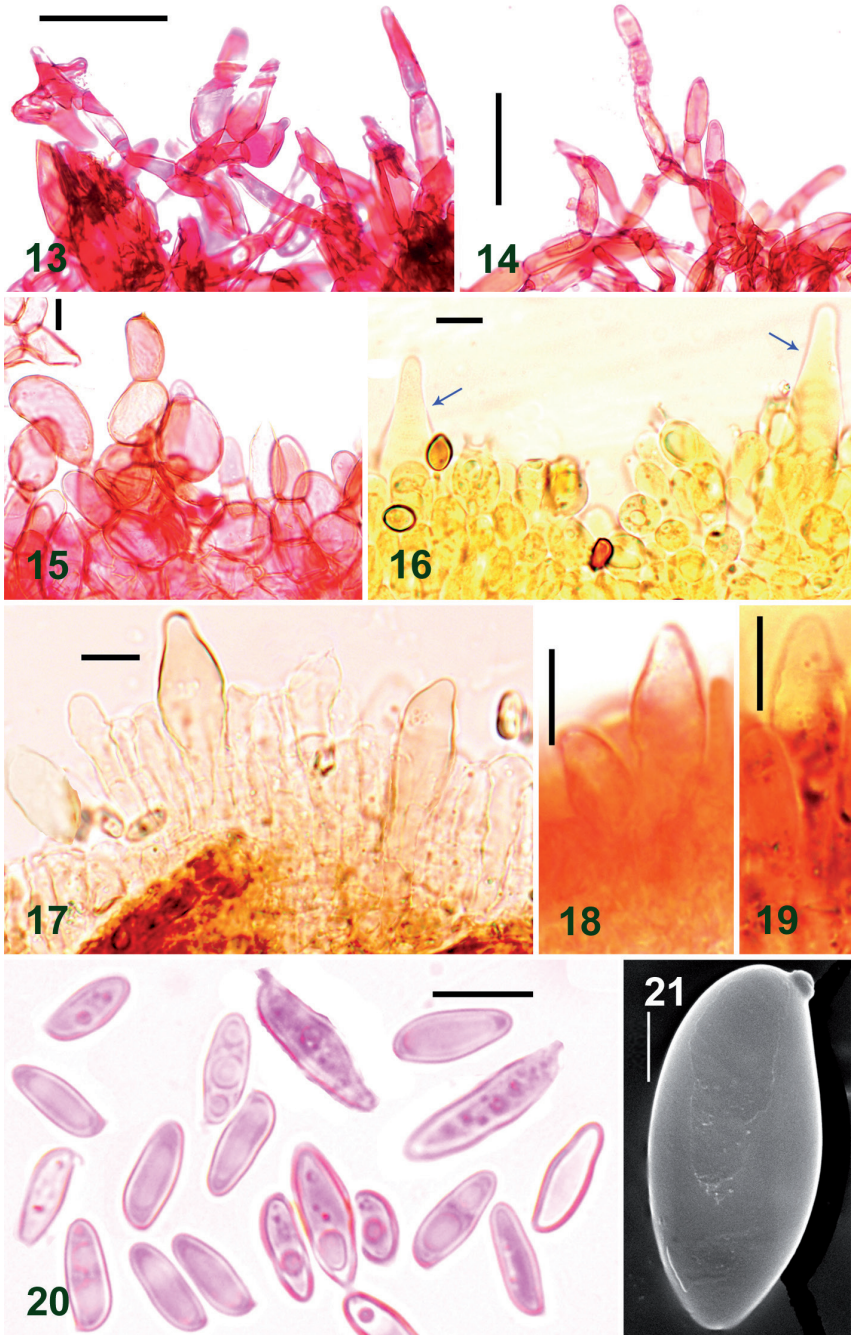
Holotype: INDIA: **Jharkhand**: Koderma district, Koderma Wildlife Sanctuary, near Chatarbar, N24º 25'16.9" E085º 38'42.1", 357 m asl., 22nd July 2017, *Arvind Parihar*, AP-6693 (CAL 1719.

Etymology: '*Shoreae*' refers to *Shorea robusta* (Dipterocarpaceae), the host tree.

Pileus 10-45 mm diam., initially convex, then plano-convex; surface dry, squamulose, grey (19-20B1) with black squamules, becoming black slowly when bruised or with age; margin entire, encurved. **Pileus surface** ruby (12C-D8) to blackish red with KOH but unchanging with $FeSO_4$. **Pore surface** depressed near the juncture of stipe with age, reddish grey (12B2) or paler when fresh, slowly becoming reddish grey (7B2) with maturity, becoming initially brownish orange (6C4) on bruising then brown (7E4-5) to dark violet (15F8) finally, black to charcoal black after 5 minutes but, turning violet brown (11E4-5) initially then black with KOH; pores 2-3 per mm angular, simple. **Tubes** adnate, 4-5 mm long, pinkish white to greyish red (8C4-5) becoming black on 5 minutes after exposure. **Stipe** 30-45 × 5-8 mm, cylindrical to clavate, becoming narrow towards base, smooth, reticulation absent, greyish violet (17D4) at upper half, then grey (18F1) to blackish brown, finally becoming black. **Context** up to 7 mm wide in pileus, yellowish white on exposure, quickly becoming dull red to greyish red (8B3-4) then greyish magenta (13E4) finally, black to charcoal black, turning reddish brown to brownish red (9-10D8) with KOH, unchanging with $FeSO_4$; stipe context in young basidiomata reddish white to reddish grey (9A2-9B2) in upper half, dark blackish brown on lower half while in mature basidiomata greyish violet to dark violet (18E-F5) in upper half and dark blackish brown on lower half, becoming black to charcoal black on exposure, but turning coffee brown then blackish with KOH. **Spore print** greyish brown (6D3).

Basidiospores 8.72-***12.3-12.5***-(18.4)-20 × 3.6-***4.5-4.7***-5.4 µm (Q = 2.1-***2.65-2.72***-3.5), cylindrical, subfusiform, inequilateral, thin-walled, smooth. Basidia 28-41 × 8-10 µm, four-spored, clavate. **Pleurocystidia** 29-38 × 12-17 µm, rare, emergent up to 20 µm, lanceolate to ventricose, thin-walled, hyaline. Subhymenial layer up to 10 µm thick, pseudoparenchymatous. Tube edge fertile with basidia and cystidia; cheilocystidia 28-37 × 8-9 µm, frequent, narrowly lanceolate with rounded to capitate apex, hyaline. **Hymenophoral trama** divergent, hyphae septate, up to 10 µm wide. **Pileipellis** a trichoderm, 250-350 µm thick, composed of erect to suberect, loosely interwoven unbranched to rarely branched hyphae, mostly with constriction at septa, moderately thick-walled with dark brown to blackish pigment, mostly smooth sometimes with zebroid incrustationss; terminal cells typically inflated, 10-45 × 5-12 µm, cylindrical to subcylindrical, sometimes subfusoid, content brown pigmented. **Stipitipellis** up to 50 µm thick, fertile near the apex of stipe, composed

Figs. 6-12. *Indoporus shoreae* (holotype). **6-7**. Fresh basidiomata in field. **8-9**. Pore surface showing colour change on bruising. **10-12.** Disected basidiomata showing different colour changes leading to charcoal black eventually.



Figs. 13-21. *Indoporus shoreae* (holotype). **13-15.** Transverse section through pileipellis showing terminal elements. **16.** Transverse section through stipitipellis showing caulocystidia. **17.** Pleurocystidia. **18-19.** Cheilocystidia. **20.** Basidiospores. **21.** SEM micrograph of basidiospores. Scale bars 13-14 = 50 µm; 15-20 = 10 µm; 21 = 2 µm.

of basidioles, basidia and cystidia in several clusters; caulobasidia 30-35 × 9-10 µm, 2- to 4-spored, clavate; caulocystidia 45-57 × 11-14 µm, frequent, ventricose, lanceolate to obclavate, hyaline.

Ecology: Solitary to gregarious on the soil in the dry deciduous forest under the *Shorea* tree; known from the Koderma Wildlife Sanctuary and Rajmahal hills of Indian state Jharkhand and Lalgarh block of another Indian state West Bengal.

Other collections examined: INDIA: **Jharkhand**, Koderma district, Koderma Wildlife Sanctuary, Lokai, alt. 380 m, N24°29'37.6" E85°36'29.60", 20 September 2013, Arvind Parihar, AP-6647 (CAL 1720); ibid., Chatarbar, alt. 382 m, N24°28'52.10" E85°33'16.30", 24 September 2013, Arvind Parihar, AP-6670 (CAL 1721); ibid., Chatarbar, alt. 382 m, N24°28'62.10" E85°32'18.10", 24 September 2013, Arvind Parihar, AP-6673 (CAL 1722) ibid., Koderma Wildlife Sanctuary, Chatarbar, alt. 361 m, N24°26'18.9" E85°36'28.5", 22 July 2017, Arvind Parihar, AP-6697 (CAL 1723); ibid., Lokai alt. 392 m, N24°29'01.9" E85°37'11.3", 23 July 2017, Arvind Parihar, AP-6698 (CAL 1724); ibid., Jharkahand, Rajmahal hills, Pakur district, Litipara block, Talphari and surroundings, alt. 91 m, N24°37'00.9" E87°40'48.1", 20 August 2014, M.E. Hembrom, MEH-66334 (CAL 1727); ibid., West Bengal, Jhargram district, Lalgarh block, Purnapani and surrounding forests, alt 91 m, N22°33'54.2" E87°05'05.1", 22 July 2018, M.E. Hembrom, MEH-18-03 (CAL 1728).

Comments: Phylogenetically *Indoporus shoreae* is a distinct lineage within the Boletaceae but its true relationships to other bolete genera remained unresolved. A comparison table of its main morphological features with other blackening bolete genera is provided in Tab. 2

Morphologically, *Indoporus* is somewhat similar to *Afroboletus* Pegler & T.W.K. Young and *Strobilomyces* Berk. Both these genera share the squamulose pileal surface and similar hymenophoral surface with *Indoporus*, but their ornamented basidiospores clearly separate them from our new genus (Pegler & Young 1981, Gelardi *et al.* 2013).

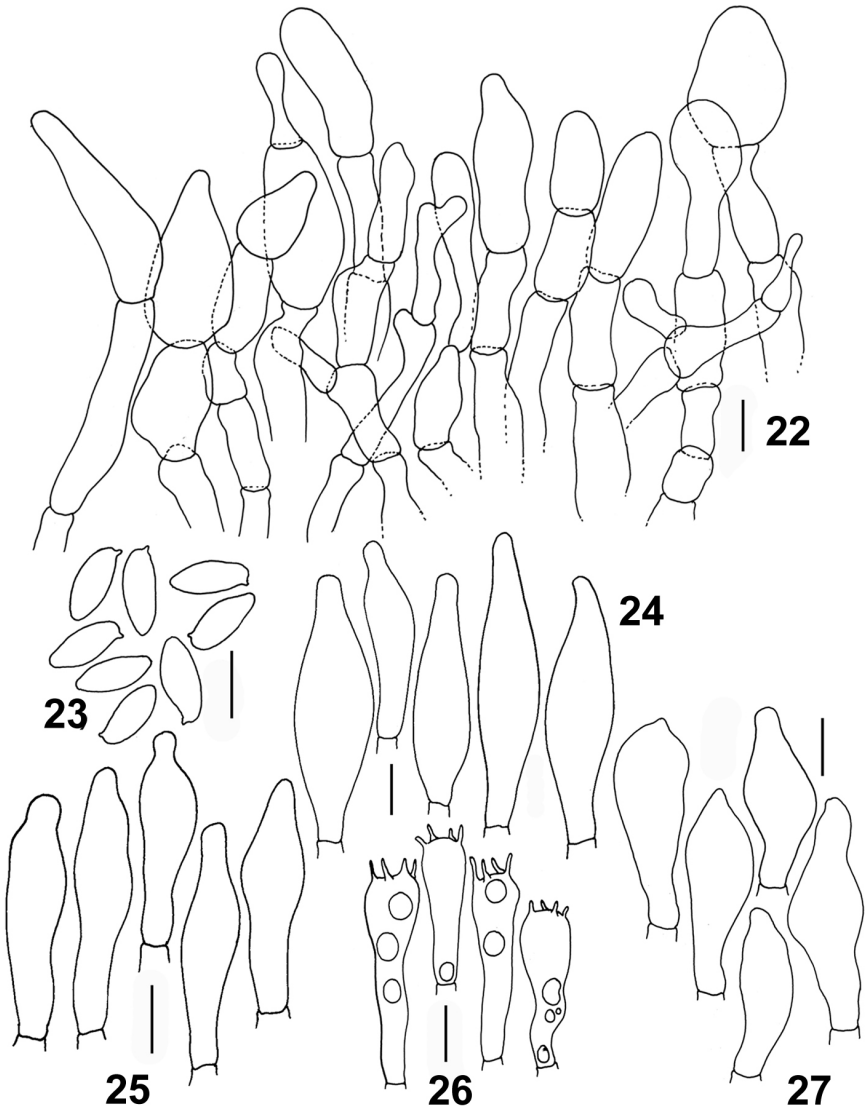
Porphyrellus E.-J. Gilbert and *Nigroboletus* Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang also show partial resemblance to the present novel genus because of the colour of pileus and smooth basidiospores, but the former can be separated by its white to pallid context, and bluish or reddish discoloration when cut (Gilbert 1931; Wolfe 1979), in comparison to reddish grey context which turns reddish brown to charcoal black when cut in *Indoporus*. *Nigroboletus* can be separated by its smooth pinkish pileus, yellowish to pinkish-orange stipe and yellowish context, moreover it is found to grow in forests dominated by Fagaceae and coniferous trees (Gelardi *et al.* 2015).

Tylopilus species can be distinguished (Chakraborty *et al.* 2018) by white to pallid context of the pileus, a hymenophoral (pore) surface white when young, and discoloring pinkish when mature (reddish grey or paler from very beginning in case of *Indoporus*). Two North American species, viz. *Tylopilus alboater* (Schweinitz) Murrill and *T. atronicotianus,* look quite similar to our novel species. However, both these *Tylopilus* species have robust basidiomata with a pileus 30-150 mm diam. and stipe 40-100 mm in *T. alboater*, and pileus 75-200 mm diam. and stipe 60-120 mm in *T. atronicotianus* (Bessette *et al.* 2010, 2016) as well as distinctively smaller basidiospores (8-12 × 3-4 µm in *T. alboater* and 7.5-10.5 × 4-5 µm in *T. atronicotianus*). Both these species are also genetically different (see Fig. 5 and suppl fig. 1). Further, *Indoporus shoreae* appears to be strictly associated with *Shorea robusta* in tropical broadleaf forests.

Table 2. Comparison table on the morphologically related genera to Indoporus

No.	Name of the genera	Pileus surface	Hymenophore	Stipe	Veil	Context	Pileipellis	Basidiospores	Habitat
1.	*Afroboletus* Pegler & T.W.K. Young (Pegler & Young, 1981)	Pustulate-squamose	Tubulate, adnate with a decurrent tooth, ventricose, white soon greyish or pale pinkish	Solid	Persistent, floccose, sometimes forming an annulus	Whitish, discolouring black on exposure	A trichodermal palisade, of short cylindric or vesicular, thick-walled elements with brown contents	Short ellipsoid, deep yellowish brown, with a complex eusporial ornament of 8-12 large, winged, longitudinal costae, intercostal ridging, and a basal thickened rim	Not known
2.	*Nigroboletus* Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang (Gelardi *et al.* 2015)	Subtomentose to glabrous	Very thin, poroid, adnate to subdecurrent, yellow to olive–yellow	Dry, smooth to minutely pruinose-punctate, reticulation absent	Absent	Firm, yellowish; tissues turning dull grayish to blackish throughout when injured or exposed	Consisting of subparallel to loosely interwoven erect hyphae	Broadly ellipsoid to subovoid, 5.2–10.1 × 4–6.4 µm, asymmetric, smooth, thin-walled straw yellow coloured in water and 5% KOH, inamyloid to slighty dextrinoid, acyanophilic	Gregarious or scattered, growing in clayey soil among litter in tropical montane and lowland mixed forests dominated by *Castanopsis, Lithocarpus, Schima, Litsea*
3.	*Porphyrellus* E.-J. Gilbert (Wu *et al.* 2016)	Subtomentose to glabrous	White when young, grayish pink to blackish pink when mature; pores angular or roundish; tubes	White to pallid with white basal mycelium	Absent	White to pallid, bluish or reddish discoloration when cut	A trichoderm composed of filamentous interwoven hyphae or erectly arranged inflated elements.	Subfusiform to oblong Smooth	Scattered on soil in forests dominated by Fagaceae and coniferous trees
4.	*Strobilomyces* Berk. (Singer 1970, 1986 and Wu *et al.* 2016)	Dry, densely covered with woolly, fibrillose, or rigid scale	Hymenophore whitish cream, grayish brown or vinaceous drab, staining reddish to rusty then blackish when injured; pores angular	Surface woolly or fibrillose scales, apical or upper part usually reticulate	Woolly or fibrillose scales, apical or upper part usually reticulate	Whitish to grayish or pale grayish cream, quickly staining reddish then slowly blackish when injured	Often an intricated trichodermium, composed of loosely branching hyphae	Globose to broadly ellipsoid basidiospores blackish brown, with reticulate, subcristate to verrucose ornamentation	Under coniferous or broadleaf trees

5.	*Tylopilus P.* Karst. (Wu *et al.* 2016)	Subtomentose or glabrous, dry to gelatinous	White when young, and becoming pinkish when mature	Glabrous or distinctly reticulate	Absent	context of the pileus and stipe without color change, or becoming rufescent in some species when injured	A subcutis to trichodermium	Ellipsoid to oblong, smooth	Under coniferous or broadleaf trees
6.	*Xerocomellus* Šutara, 2008	Dry subtomentose pileal surface red to purplish red tinged pileus and stipe	Olive-yellow to brownish yellow, becoming ochraceous with age, staining blue immediately when bruised	Red to brownish red, longitudinally fibrillose	Absent	Comparatively slender, red to brownish red, longitudinally fibrillose	A palisadoderm consisting of vertically arranged, yellowish brown, more or less broadened and often incrusted hyphal elements, terminal cells of which reach almost at the same level	Subfusiform to slender, brownish yellow, smooth (under SEM), rarely with indistinctly longitudinal ridges	Under coniferous or broadleaf trees
7.	*Indoporus* gen. nov.	Dry, matte, with black scales, never glutinous	Reddish grey (12B2) or paler when fresh, slowely becoming reddish grey (7B2) with maturity, becoming initially brownish orange (6C4) on bruising then brown (7E4–7E5) to dark violet (15F8) finally, black after 5 minutes pores angular	Cylindrical to clavate, becoming narrow towards base, smooth, greyish violet at upper half, then grey to blackish brown	Absent	Cylindrical, clavate to gradually tapering towards at base, sometimes tapering towards apex, yellowish white when exposed, quickly becoming dull red to greyish red (8B3–8B4), then greyish magenta (13E4), finally black to charcoal; black	A trichoderm, composed of erect to sub erect, loosely interwoven unbranched to rarely branched hyphae, moderately thick walled with dark brown to blackish pigment, mostly smooth sometimes with incrustations in zebroid pattern; terminal cells cylindrical to subcylindrical, sometimes subfusoid	Subfusiform, inequilateral, thin-walled, smooth 8.4–20 × 4.5–5.5 µm	Gregarious or scattered, growing in clayey soil among dry deciduous forests dominated by Shorea



Figs. 22-27. *Indoporus shoreae* (holotype). **22.** Pileipellis. **23.** Basidiospores. **24.** Caulocystidia. **25.** Cheilocystidia. **26.** Basidia. **27.** Pleurocystidia. Scale bars **22-27** = 10 µm.

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Online suppl. Fig 1.: ITS phylogeny showing the placement of the very similar *American Tylopilus alboater* and *T. atronicotianus*.