

Global diversity and taxonomy of the *Inonotus linteus* complex (Hymenochaetales, Basidiomycota): *Sanghuangporus* gen. nov., *Tropicoporus excentrodendri* and *T. guanacastensis* gen. et spp. nov., and 17 new combinations

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Abstract Although *Inonotus linteus* complex is placed in the genus *Inonotus*, its perennial basidiocarps with a dimitic hyphal system, at least in the trama, distinguish the complex from other species in the genus, which have an annual habit and a monomitic hyphal system. The species number of *Inonotus linteus* complex has been increased in China and tropical America in recent publications. However, whether species in this complex belong to *Inonotus* has not specifically been addressed. To explore the phylogenetic placement of species of *Inonotus linteus* complex, we performed a comprehensive study using morphological and phylogenetic data based on

global samples. nLSU (53 with 13 new) and ITS (70 with 18 new) datasets were used to produce the phylogenetic results. Taking into consideration the phylogenies inferred from the nLSU and ITS datasets, *Inonotus* is a polyphyletic genus comprising at least three clades. Clade A, the core *Inonotus* clade, contains the generic type, *Inonotus hispidus*, while Clades B and C comprise species from the *Inonotus linteus* complex. Morphological and phylogenetic evidence indicates that Clades B and C are new genera, and *Sanghuangporus* and *Tropicoporus* are introduced in this study. Ten species are transferred to *Sanghuangporus* and seven to *Tropicoporus*. *Tropicoporus excentrodendri* and *T. guanacastensis* spp. nov. are described, and their distinctive characters are discussed. Keys to the two new genera and the *Inonotus sensu stricto*, and to species of each new genus are provided.

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Introduction

Inonotus P. Karst. (Hymenochaetaceae), was introduced by Karsten (1879) and *Inonotus hispidus* (Bull.) P. Karst. was later selected as its type species (Donk 1960). *Inonotus sensu lato* is traditionally characterized by annual basidiocarps and a monomitic hyphal system and includes more than 100 species (Ryvarden 2005). These morphological characteristics can distinguish *Inonotus* from *Phellinus* QuéL., another large genus within Hymenochaetaceae that often produces perennial basidiocarps with a dimitic hyphal system (Larsen and Cobb-Pouille 1990). Molecular studies have indicated that the delimitation between the two genera is weak, and several species of *Phellinus*, viz. *Phellinus baumii* Pilát, *P. linteus* (Berk. &

M.A. Curtis) Teng, *P. tropicalis* M.J. Larsen & Lombard, *P. vaninii* Ljub. and *P. weirianus* (Bres.) Gilb. were transferred to *Inonotus* (Wagner and Fischer 2002). Later Dai (2010), Wu et al. (2012) and Vlasák et al. (2013), respectively, combined *Phellinus lonicericola* Parmasto, *P. lonicerinus* (Bondartsev) Bondartsev & Singer and *P. dependens* (Murrill) Ryvarden to *Inonotus*. These are members of the *Inonotus linteus* (Berk. & M.A. Curtis) Teixeira complex.

Previous phylogenetic analyses (Wagner and Fischer 2002; Dai 2010) clearly indicated that *Inonotus sensu lato* had polyphyletic origins, and four more narrowly defined genera, namely *Inocutis* Fiasson & Niemelä, *Inonotopsis* Parmasto, *Mensularia* Lázaro Ibiza and *Onnia* P. Karst., were segregated from *Inonotus*. The *Inonotus linteus* complex was considered to belong to the reduced *Inonotus* (Wagner and Fischer 2002; Dai 2010). However, this opinion is questionable, because no comprehensive phylogeny study has specifically focused on the reduced *Inonotus*. Taxa in the *Inonotus linteus* complex also differ distinctively from other species of *Inonotus*. Several new taxa from East Asia and tropical America belonging to the *Inonotus linteus* complex have recently been introduced (Wu et al. 2012; Tian et al. 2013; Vlasák et al. 2013), which brings the number of species in this complex to 15 (Table 1). In our previous phylogenetic analyses, taxa of the *Inonotus linteus* complex formed two distinctly separate lineages (Tian et al. 2013; Vlasák et al. 2013). However, the phylogenetic relationships between the *Inonotus linteus* complex, especially those African members, as well as other species of *Inonotus* are poorly investigated.

The aim of this study is to investigate the diversity and taxonomy of the *Inonotus linteus* complex using a worldwide set of collections and to elucidate the phylogenetic position of the *Inonotus linteus* complex.

Table 1 Members of *Inonotus linteus* complex

| |
|---|
| <i>Inonotus alpinus</i> Y.C. Dai & X.M. Tian |
| <i>I. baumii</i> (Pilát) T. Wagner & M. Fisch. |
| <i>I. cubensis</i> Y.C. Dai, Decock & L.W. Zhou |
| <i>I. dependens</i> (Murrill) Vlasák & Y.C. Dai |
| <i>I. linteus</i> (Berk. & M.A. Curtis) Teixeira |
| <i>I. lonicericola</i> (Parmasto) Y.C. Dai |
| <i>I. lonicerinus</i> (Bondartsev) Sheng H. Wu, Y.C. Dai & T. Hatt. |
| <i>I. pseudolinteus</i> Vlasák & Y.C. Dai |
| <i>I. sanghuang</i> Sheng H. Wu, T. Hatt. & Y.C. Dai |
| <i>I. sideroxylicola</i> Vlasák & Y.C. Dai |
| <i>I. tropicalis</i> (M.J. Larsen & Lombard) T. Wagner & M. Fisch. |
| <i>I. vaninii</i> (Ljub.) T. Wagner & M. Fisch. |
| <i>I. weigela</i> T. Hatt. & Sheng H. Wu |
| <i>I. weirianus</i> (Bres.) T. Wagner & M. Fisch. |
| <i>I. zonatus</i> Y.C. Dai & X.M. Tian |

Materials and methods

Morphological studies

The studied specimens are deposited at the herbaria of the Institute Applied of Ecology, Chinese Academy of Sciences (IFP), the Institute of Microbiology, Beijing Forestry University (BJFC), the Botanical Museum, University of Oslo (O), the National Museum of Natural Science, Taichung, Taiwan (TNM), the Mycothèque de l'Université catholique de Louvain (MUCL), the Farlow Reference Library and Herbarium of Cryptogamic Botany, Harvard University (FH), and the private herbarium of J. Vlasák (JV). Microscopic procedures follow Dai (2010). Sections were prepared in Cotton Blue (CB), Melzer's reagent (IKI) and 5 % potassium hydroxide (KOH), and studied using a Nikon Eclipse 80i microscope at magnifications of up to 1000×. The measurements and drawings were made from sections stained with CB. When presenting the size range of basidiospores, 5 % of the measurements were excluded from each end of the range and are given in parentheses. Drawings were made with the aid of a drawing tube. Special colour terms follow Petersen (1996). The abbreviations are used as follows: L = mean basidiospore length (arithmetical average of all basidiospores), W = mean basidiospore width (arithmetical average of all basidiospores), Q = variation in the L/W ratios between the specimens studied, n = the number of basidiospores measured from given number of specimens, IKI− = neither amyloid nor dextrinoid, CB+ = cyanophilous and CB− = acyanophilous.

Molecular study

About 1 mm³ of the dried specimens collected from China and culture WD 1838 from the Forestry and Forest Products Research Institute, Ibaraki, Japan (FFPRI) were directly employed to PCR amplification using Phire® Plant Direct PCR Kit (Finnzymes Oy, Finland) according to the manufacturer's instruction. The PCR procedure included these steps: initial denaturation at 98 °C for 5 min, followed by 39 cycles denaturation at 98 °C for 5 s, annealing at 48 °C for 5 s for nLSU region/59 °C for 5 s for ITS region and extension at 72 °C for 5 s, and a final extension of 72 °C for 10 min. The primer pairs LR0R and LR7 (Vilgalys and Hester 1990), and ITS5 and ITS4 (White et al. 1990) were, respectively, used in the amplifications of nLSU and ITS regions, and also to sequence them in Beijing Genomics Institute, China. In addition, primers LR3R and LR3 (Vilgalys and Hester 1990) were sometimes used to sequence the nLSU region as well.

DNA was isolated from 0.02 to 0.2 g of the dried basidiocarps of non Chinese specimens using CTAB/NaCl extraction, followed by repeated extractions with chloroform

and isopropanol precipitation. Crude DNA was purified using Wizard Clean Up kit PROMEGA and was diluted as a template for subsequent amplifications. nLSU sequences were amplified with primers LR0R and LR7, while ITS sequences used primers ITS5 and ITS4. Annealing temperature is 55 °C for both regions. Amplified DNA sequences were sequenced with the same primers in the Genomics Laboratory of Biology Centre, Academy of Sciences of the Czech Republic, České Budějovice, on ABI 3730xl DNA analyzer, using BigDye Terminator 3.1 kit. All newly generated sequences were deposited at GenBank (<http://www.ncbi.nlm.nih.gov/>; Table 2)

Phylogenetic analysis

The new sequences generated for this study, and additional nLSU and ITS sequences (Figs. 1 and 2) retrieved from GenBank were assembled for phylogenetic analysis. The

nLSU dataset was first used to explore the phylogeny of *Inonotus sensu lato*. Besides *Inonotus* species, other representative species of *Inocutis*, *Inonotopsis*, *Mensularia*, *Fomitiporella* Murrill, *Fulvifomes* Murrill and *Phylloporia* Murrill were included in the dataset. ITS dataset, including more representatives of the *Inonotus linteus* complex, were used to further elucidate the phylogenetic relationship between *Inonotus linteus* complex and other species of *Inonotus*. *Phellinus laevigatus* (P. Karst.) Bourdot & Galzin and *P. populicola* Niemelä were selected as outgroup taxa for both datasets (Wagner and Fischer 2002). The two datasets were aligned using MAFFT 7 (Kato et al. 2002) with Q-INS-i option (Kato and Toh 2008). The resulting alignments are deposited at TreeBASE (<http://purl.org/phylo/treebase>; submission ID S16557).

When performing phylogenetic analyses of the alignments, all characters equally weighted and gaps were treated as missing. The maximum likelihood (ML) trees were constructed

Table 2 Information of the newly sequenced specimens

| Species | Voucher no. | Locality | GenBank accession no. | |
|-------------------------------|------------------|---------------------|-----------------------|----------|
| | | | nLSU | ITS |
| <i>Inonotus compositus</i> | Wang 552 (IFP) | Shaanxi, China | KP030768 | KP030781 |
| <i>I. henanensis</i> | Dai 12221 (BJFC) | Yunnan, China | – | KP030782 |
| <i>I. henanensis</i> | Dai 13157 (BJFC) | Yunnan, China | – | KP030783 |
| <i>I. latemarginatus</i> | Dai 9758 (BJFC) | Hainan, China | – | KP030784 |
| <i>I. pachyphloeus</i> | Wu 0407–6 (TNM) | Taiwan | KP030770 | KP030785 |
| <i>I. pruinosis</i> | Dai 2573 (BJFC) | Liaoning, China | KP030769 | – |
| <i>I. tricolor</i> | Dai 12228 (BJFC) | Yunnan, China | – | KP030786 |
| <i>Sanghuangporus alpinus</i> | Cui 9658 (BJFC) | Tibet, China | KP030771 | – |
| <i>S. lonicericola</i> | Dai 8376 (BJFC) | Heilongjiang, China | KP030772 | – |
| <i>S. microcystideus</i> | O 915609 | Tanzania | – | KP030787 |
| <i>S. sanghuang</i> | Wu 0903–2 (TNM) | Jilin, China | KP030773 | – |
| <i>S. weigela</i> | WD 1838 (FFPRI) | Japan | KP030774 | – |
| <i>S. zonatus</i> | Dai 10841 (BJFC) | Hainan, China | KP030775 | – |
| <i>Tropicoporus cubensis</i> | MUCL 47079 | Cuba | KP030776 | – |
| <i>T. cubensis</i> | MUCL 47113 | Cuba | KP030777 | – |
| <i>T. excentrodendri</i> | Yuan 6227 (IFP) | Guangxi, China | – | KP030788 |
| <i>T. excentrodendri</i> | Yuan 6229 (IFP) | Guangxi, China | – | KP030789 |
| <i>T. excentrodendri</i> | Yuan 6232 (IFP) | Guangxi, China | – | KP030790 |
| <i>T. excentrodendri</i> | Yuan 6234 (IFP) | Guangxi, China | – | KP030791 |
| <i>T. guanacastensis</i> | JV 1407-103 J | Costa Rica | – | KP030792 |
| <i>T. guanacastensis</i> | JV 1408-25 | Costa Rica | KP030778 | KP030793 |
| <i>T. guanacastensis</i> | MUCL 43130 | Costa Rica | KP030779 | – |
| <i>T. guanacastensis</i> | O 19228 | Costa Rica | – | KP030794 |
| <i>T. linteus</i> | JV 0904-140 | Florida, USA | KP030780 | – |
| <i>T. pseudolinteus</i> | O 906288 | Costa Rica | – | KP030795 |
| <i>T. rudis</i> | O 915614 | Rwanda | – | KP030796 |
| <i>T. rudis</i> | O 915617 | Tanzania | – | KP030797 |
| <i>T. cf. tropicalis</i> | Yuan 5898 (IFP) | Guangxi, China | – | KP030798 |

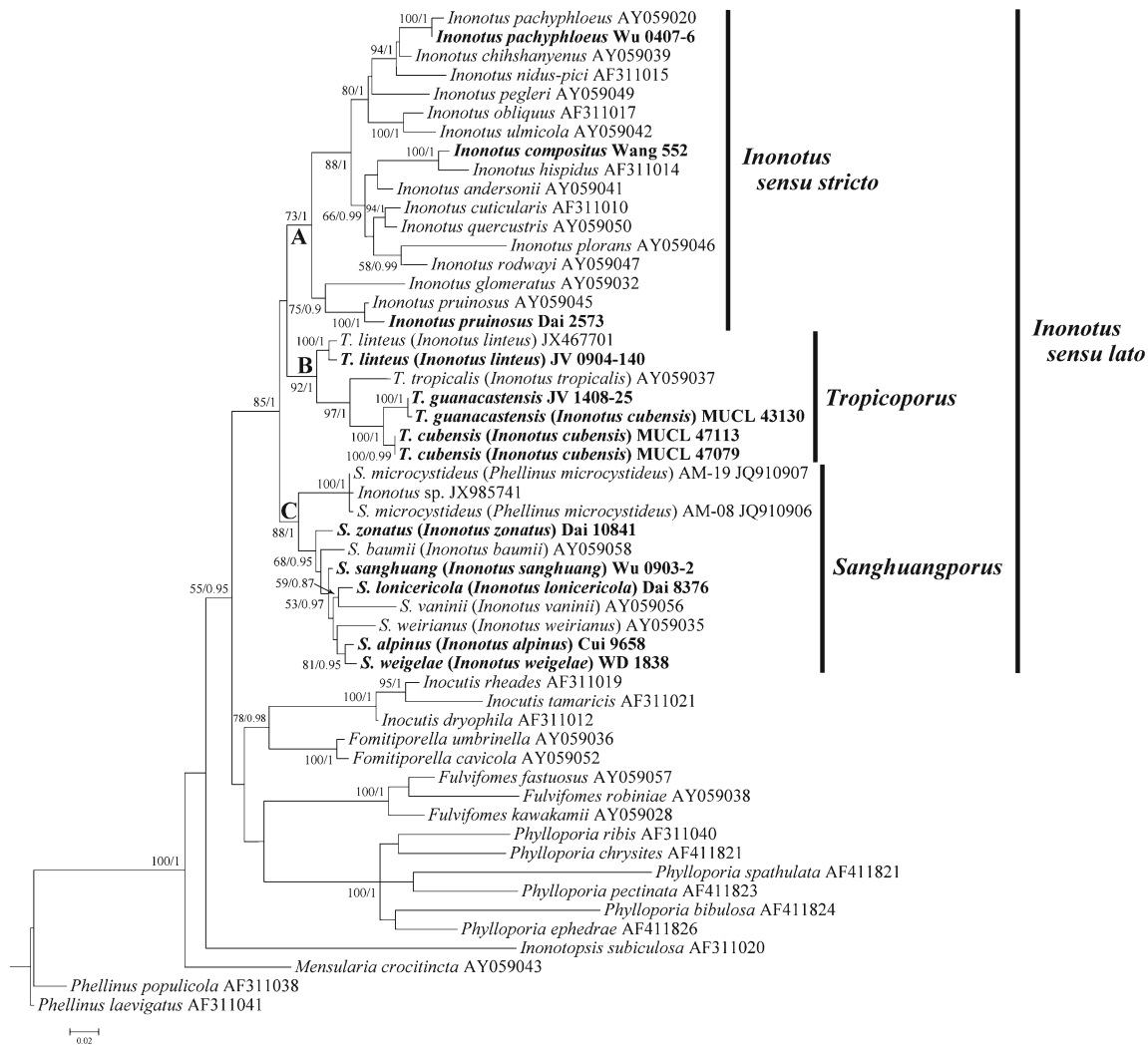


Fig. 1 Phylogeny of *Inonotus sensu lato* inferred from nLSU sequences. Topology is from maximum likelihood analysis, while bootstrap values from maximum likelihood analysis and Bayesian inference

using raxmlGUI 1.2 (Stamatakis 2006; Silvestro and Michalak 2012) with GTR+I+G model and auto FC option (Pattengale et al. 2010) in bootstrap (BS) replicates. Bayesian inference (BI) was conducted using MrBayes 3.2 (Ronquist and Huelsenbeck 2003) following the best-fit evolutionary model estimated by jModelTest 2.1.4 (Guindon and Gascuel 2003; Darriba et al. 2012). Two independent runs were employed and each run with four chains started from random trees. Trees were sampled every 1000th generation. The first 25 % of sampled trees was set as burn-in, while the other trees were used to produce a 50 % majority consensus tree and for calculating Bayesian posterior probabilities (BPPs). Chain convergence was determined with Tracer 1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>). The two phylogenetic methods resulted in similar topologies for each dataset. Therefore, only the ML tree is presented, and BS and BPP values simultaneously not below 50 % and 0.8, respectively, were indicated at the nodes.

(simultaneously not below 50 % and 0.8, respectively). The newly generated sequences for this study are in **boldface**. The species names in *brackets* were names before this study

Results

Molecular phylogeny

A total of 53 nLSU and 70 ITS sequences, including 13 nLSU and 18 ITS sequences newly generated in this study, were used in the phylogenetic analyses. The alignment, resulting from the nLSU dataset, contained 909 characters. Its best-fit evolutionary model for BI was estimated as GTR+I+G. All chains in BI converged after 10 000 000 generations, where the effective sample sizes (ESSs) of all parameters were greater than 2000 and the potential scale reduction factors (PSRFs) were equal to 1.000. The BS search for ML analysis stopped after 250 replicates.

The nLSU-based phylogeny (Fig. 1) recovered *Inonotus* as monophyletic with moderate support in ML and full support in BI. Within the genus *Inonotus*, *I. andersonii* (Ellis & Everh.) Nikol., *I. chihshanyenus* T.T. Chang & W.N. Chou,

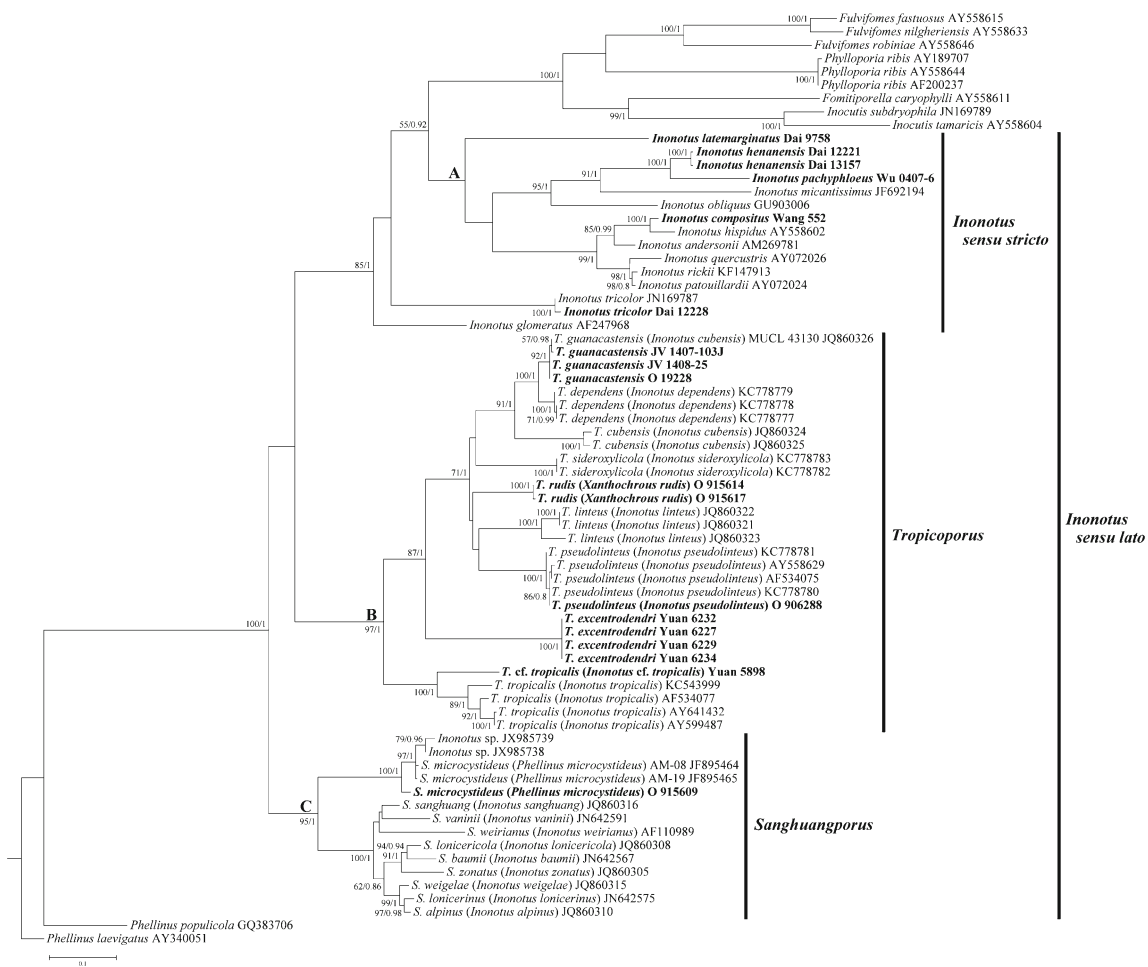


Fig. 2 Phylogeny of *Inotus sensu lato* inferred from ITS sequences. Topology is from maximum likelihood analysis, while bootstrap values from maximum likelihood analysis and Bayesian inference

(simultaneously not below 50 % and 0.8, respectively). The newly generated sequences for this study are in **boldface**. The species names in brackets were names before this study

I. compositus Han C. Wang, *I. cuticularis* (Bull.) P. Karst., *I. glomeratus* (Peck) Murrill, *I. hispidus* (the generic type), *I. nidus-pici* Pilát, *I. obliquus* (Ach. ex Pers.) Pilát, *I. pachyphloeus* (Pat.) T. Wagner & M. Fisch., *I. pegleri* Ryvardeen, *I. plorans* (Pat.) Bondartsev & Singer, *I. pruinus* Bondartsev, *I. quercustris* M. Blackw. & Gilb., *I. rodwayi* D.A. Reid and *I. ulmicola* Corfixen formed a clade that we term Clade A here. Species of *Inotus linteus* complex clustered in two other clades. The Clade B comprised *Inotus cubensis*, *I. linteus*, *I. tropicalis* and one unidentified collection, while the Clade C comprised *I. alpinus*, *I. baumii*, *I. lonicericola*, *I. sanghuang*, *I. vaninii*, *I. weigelae*, *I. weirianus*, *I. zonatus*, *Phellinus microcystideus* Har. & Pat., and one unidentified collection.

The ITS dataset resulted in an alignment of 1091 characters. The best-fit evolutionary model for BI was HKY+I+G. After 1 000 000 generations, the ESSs of all parameters were greater than 2000 and the PSRFs were close to 1.000, indicating all chains converged. The BS search for ML analysis stopped after 150 replicates.

The phylogeny inferred from the ITS dataset (Fig. 2), accommodating more representatives of the *Inotus linteus* complex than the nLSU dataset, clearly indicated that *Inotus* was a polyphyletic genus. The ITS dataset also showed that species of *Inotus* formed at least three clades. The Clade A, receiving low support (64 % in ML, 0.61 in BI), comprised *I. andersonii*, *I. compositus*, *I. henanensis* Juan Li & Y.C. Dai, *I. hispidus*, *I. latemarginatus* Y.C. Dai, *I. micantissimus* (Rick) Rajchenb., *I. obliquus*, *I. pachyphloeus*, *I. patouillardii* (Rick) Imazeki, *I. quercustris* and *I. rickii* (Pat.) D.A. Reid. Species of *Inotus linteus* complex clustered outside the Clade A; Clade B comprised *I. dependens*, *I. pseudolinteus*, *I. sideroxylicola*, *Xanthochrous rudis* Pat. and three unidentified lineages, besides *I. cubensis*, *I. linteus* and *I. tropicalis* also indicated in the nLSU-based phylogeny. Clade C additionally comprised *I. lonicerinus* and *Phellinus microcystideus*, and two unidentified collections compared with that in the nLSU-based phylogeny. In addition, *Inotus glomeratus* and *I. tricolor* (Bres.) Y.C. Dai clustered outside the three clades.

Based on the phylogenetic evidence and morphology, we introduced two new genera to accommodate species of the *Inonotus linteus* complex. In addition, two new species are described and 17 new combinations are proposed for these two new genera.

Taxonomy

Key to *Inonotus sensu stricto*, *Sanghuangporus* and *Tropicoporus*

1. Hyphal system monomitic in both context/subiculum and trama.....

Inonotus sensu stricto

1. Hyphal system monomitic to dimitic in context/subiculum, dimitic in trama.....2

2. Basidiocarps perennial, effused-reflexed to pileate; basidiospores when ellipsoid mostly <3.5 µm wide, when subglobose >3.5 µm wide; in boreal, temperate, subtropical to tropical zones.....

.....*Sanghuangporus*

2. Basidiocarps annual to perennial, resupinate, effused-reflexed to pileate; basidiospores when ellipsoid mostly >3.5 µm wide, when subglobose mostly <3.5 µm wide; exclusively in tropical zone.....

.....*Tropicoporus*

Sanghuangporus Sheng H. Wu, L.W. Zhou & Y.C. Dai, gen. nov.

Mycobank no.: MB 812143

Type species. Sanghuangporus sanghuang (Sheng H. Wu, T. Hatt. & Y.C. Dai) Sheng H. Wu, L.W. Zhou & Y.C. Dai (combined below).

Etymology. Sanghuangporus (Lat.): refers to the species of this genus called as ‘sanghuang’ in Chinese herbal markets.

Basidiocarps perennial, effused-reflexed to pileate. Pileal surface brown, dark greyish to black, hispid, tomentose, velutinate to glabrous with a radially cracked crust. Pore surface yellow to brown. Context homogeneous to duplex with a black line. Hyphal system monomitic to dimitic in context, dimitic in trama; generative hyphae simple septate; tissues darkening in KOH, hyphae unchanged in KOH. Hymenial setae present, hyphoid setae absent. Basidiospores ellipsoid, broadly ellipsoid to subglobose, yellowish, slightly thick- to thick-walled, smooth, IKI–, CB– or slightly CB+. On angiosperm wood, causing a white rot. In boreal, temperate, subtropical to tropical zones.

Sanghuangporus alpinus (Y.C. Dai & X.M. Tian) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812144

Basionym. Inonotus alpinus Y.C. Dai & X.M. Tian, in Tian et al., Fungal Diversity 58: 162. 2013.

Sanghuangporus baumii (Pilát) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812145

Basionym. Phellinus baumii Pilát, Bull. trimest. Soc. mycol. Fr. 48(1): 25. 1932.

Synonym. Inonotus baumii (Pilát) T. Wagner & M. Fisch., Mycologia 94(6): 1009. 2002.

Sanghuangporus lonicericola (Parmasto) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812146

Basionym. Phellinus lonicericola Parmasto, in Parmasto & Parmasto, Folia cryptog. Estonica 38: 59. 2001.

Synonym. Inonotus lonicericola (Parmasto) Y.C. Dai, Fungal Diversity 45: 276. 2010.

Sanghuangporus lonicerinus (Bondartsev) Sheng H. Wu, L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812147

Basionym. Fomes lonicerinus Bondartsev, Acta Inst. Bot. Acad. Sci. USSR Plant. Crypt., Ser. II: no. 500. 1935.

Synonym. Inonotus lonicerinus (Bondartsev) Sheng H. Wu, Y.C. Dai & T. Hatt., in Wu et al., Botanical Studies 53(1): 140. 2012.

Sanghuangporus microcystideus (Har. & Pat.) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812148

Basionym. Phellinus microcystideus Har. & Pat., Bull. Mus. Hist. Nat., Paris 15: 90. 1909.

Sanghuangporus sanghuang (Sheng H. Wu, T. Hatt. & Y.C. Dai) Sheng H. Wu, L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812149

Basionym. Inonotus sanghuang Sheng H. Wu, T. Hatt. & Y.C. Dai, in Wu et al., Botanical Studies 53(1): 141. 2012.

Sanghuangporus vaninii (Ljub.) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812150

Basionym. Phellinus vaninii Ljub., Bot. Mater. Otd. Spor. Rast. 15: 115. 1962.

Synonym. Inonotus vaninii (Ljub.) T. Wagner & M. Fisch., Mycologia 94(6): 1009. 2002.

Sanghuangporus weigelae (T. Hatt. & Sheng H. Wu) Sheng H. Wu, L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812151

Basionym. Inonotus weigelae T. Hatt. & Sheng H. Wu, in Wu et al., Botanical Studies 53(1): 143. 2012.

Synonym. Inonotus tenuicontextus L.W. Zhou & W.M. Qin, Mycol. Progr. 11(3): 793. 2012.

Sanghuangporus weirianus (Bres.) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812152

Basionym. *Fomes weirianus* Bres., Stud. Trent., Classe II, Sci. Nat. Econ. 7(1): 5. 1926.

Synonym. *Inonotus weirianus* (Bres.) T. Wagner & M. Fisch., Mycologia 94(6): 1009. 2002.

Sanghuangporus zonatus (Y.C. Dai & X.M. Tian) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812153

Basionym. *Inonotus zonatus* Y.C. Dai & X.M. Tian, in Tian et al., Fungal Diversity 58(1): 165. 2013.

Key to species of *Sanghuangporus*

1. Pores 4–5 per mm.....*S. lonicerinus*
1. Pores >5 per mm.....2
2. Pores 8–10 per mm.....*S. lonicericola*
2. Pores 5–8 per mm.....3
3. Context thin, <3 mm thick.....4
3. Context thick, > 10 mm thick.....5
4. Context duplex; distributed in the warm temperate zones.....*S. weigela*
4. Context homogeneous; distributed in alpine zones.....*S. alpinus*
5. Setae mostly <20 µm long.....6
5. Setae mostly >20 µm long.....8
6. Basidiocarps with a sharp edge.....*S. zonatus*
6. Basidiocarps with an obtuse edge.....7
7. Basidiospores broadly ellipsoid, mostly <4.5 µm long, < 3.5 µm wide.....*S. baumii*
7. Basidiospores subglobose, mostly >5 µm long, > 4 µm wide.....*S. microcystideus*
8. Basidiospores basically subglobose; restricted to *Juglans*.....*S. weirianus*
8. Basidiospores basically broadly ellipsoid; restricted to *Morus* or *Populus*.....9
9. Basidiocarps resupinate to pileate; basidiospores 3.8–4.4 × 2.8–3.7 µm; restricted to *Populus*.....*S. vaninii*
9. Basidiocarps distinctly pileate; basidiospores 4–4.9 × 3.1–3.9 µm; restricted to *Morus*.....*S. sanghuang*

Tropicoporus L.W. Zhou, Y.C. Dai & Sheng H. Wu, gen. nov.

Mycobank no.: MB 812154

Type species. *Tropicoporus excentrodendri* L.W. Zhou & Y.C. Dai (described below).

Etymology. *Tropicoporus* (Lat.): refers to a distribution of the genus exclusively in tropics.

Basidiocarps annual to perennial, resupinate, effused-reflexed to pileate. Pileal surface brown, dark greyish to black, hispid, tomentose, velutinate to glabrous with a radially cracked crust. Pore surface yellow to brown. Context homogeneous to duplex with a black line. Hyphal system monomitic to dimitic in context/subiculum, dimitic in trama; generative hyphae simple septate; tissues darkening in KOH, hyphae unchanged or swollen in KOH. Hymenial setae present, hyphoid setae absent. Basidiospores ellipsoid, broadly ellipsoid to subglobose, yellowish, slightly thick- to thick-walled, smooth, IKI–, CB–. On angiosperm wood, causing a white rot. In tropical zone exclusively.

Tropicoporus excentrodendri L.W. Zhou & Y.C. Dai, sp. nov. Figs. 3 and 4

Mycobank no.: MB 812155

Basidiocarps annual, resupinate, effused-reflexed to distinctly pileate, imbricate. Pileal surface tomentum to hispid, concentrically sulcate; margin obtuse, tomentose to hispid. Pores circular to angular, 7–8 per mm; dissepiments thick, entire. Context duplex with a black line. Hyphal system dimitic in both context and trama; hyphae unchanged in KOH. Hymenial setae occasionally present, 20–25 × 5–8 µm. Basidiospores broadly ellipsoid to subglobose, pale yellowish, slightly thick-walled, IKI–, CB–, 3.4–4 × 2.9–3.6 µm.

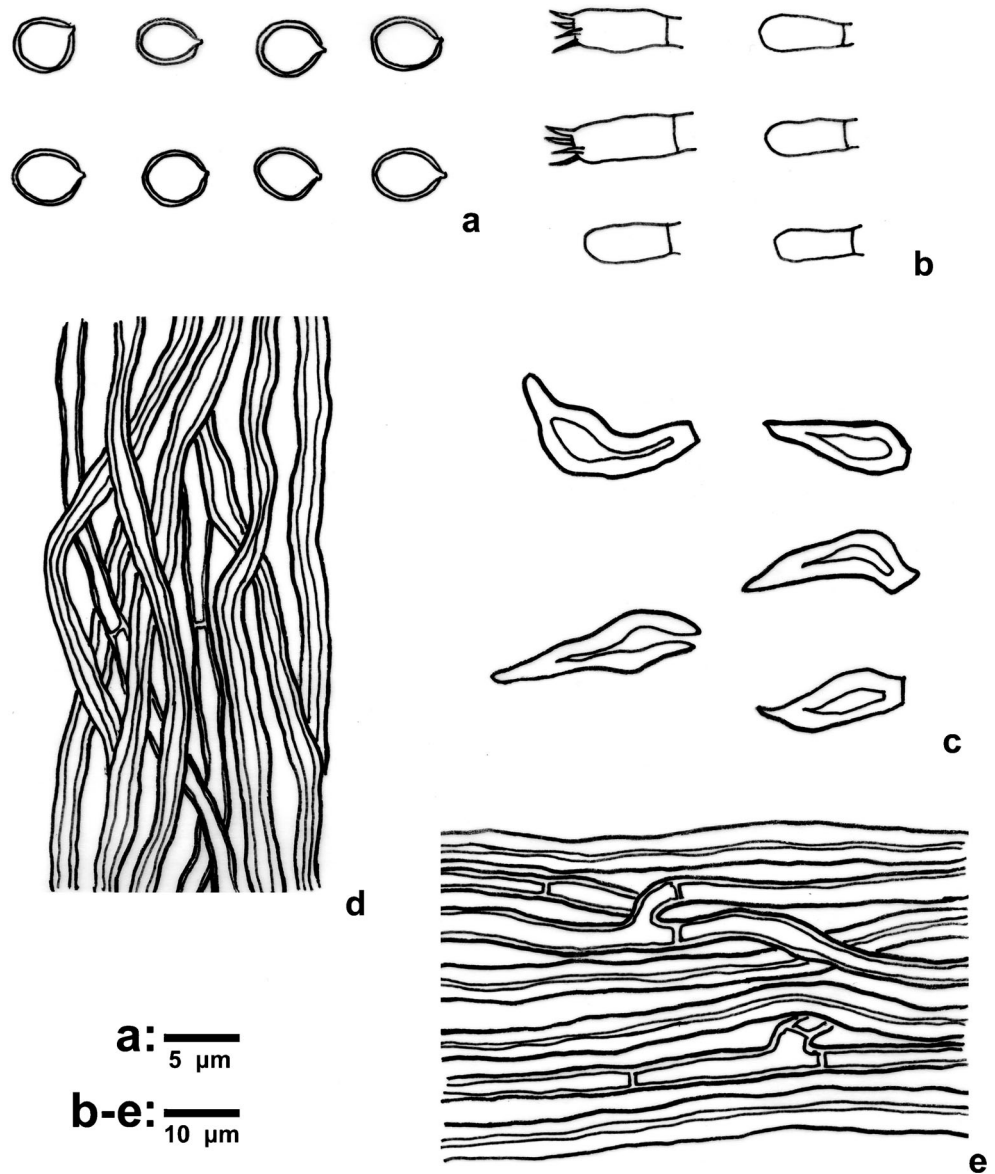
Holotype. CHINA. Guangxi, Longzhou County, Nonggang Nature Reserve, on stump of *Excentrodendron tonkinense*, 22 July 2012, Yuan 6232 (IFP).

Etymology. *excentrodendri* (Lat.): refers to the host genus *Excentrodendron*.



Fig. 3 A basidiocarp of *Tropicoporus excentrodendri* (holotype). — Scale bar=1 cm

Fig. 4 Microscopic structures of *Tropicoporus excentrodendri* (drawn from the holotype). **a.** Basidiospores; **b.** Basidia and basidioles; **c.** Hymenial setae; **d.** Hyphae from trama; **e.** Hyphae from context



Basidiocarps annual, resupinate, effused-reflexed to distinctly pileate, imbricate, without odour or taste and woody hard when fresh, woody hard and light in weight when dry. Pilei dimidiate, projecting up to 2 cm, 4.5 cm wide and 0.7 cm thick at base. Pileal surface vinaceous brown to fuscous, tomentum to hispid, concentrically sulcate; margin obtuse, hispid, yellow-brown to honey-yellow. Pore surface buff to honey-yellow, glancing; sterile margin distinct, honey-yellow, up to 3 mm; pores circular to angular, 7–8 per mm; dissepiments thick, entire. Context woody hard, up to 2 mm, duplex, with a black line between upper tomentum part and lower hard context, upper tomentum yellow-brown, soft, up to 1 mm thick, lower context cinnamon-buff, woody hard, up to 1 mm thick. Tubes curry-yellow, woody hard, up to 5 mm long; white mycelial strands occasionally present in old tubes.

Hyphal system dimitic; generative hyphae simple septate; tissue darkening but otherwise unchanged in KOH. *Context.* Generative hyphae pale yellowish, thick-walled, occasionally branched, frequently septate, straight, 2–3.5 μm in diam.; skeletal hyphae yellowish, distinctly thick-walled with a narrow lumen, unbranched, aseptate, straight, 3–5 μm in diam., more or less regularly arranged. Hyphae in the tomentum or hispid similar to those in context, but loosely interwoven. *Tubes.* Generative hyphae hyaline to pale yellowish, slightly thick-walled, unbranched, frequently septate, 2.5–3.5 μm in diam.; skeletal hyphae dominant, yellowish, thick-walled with a wide to narrow lumen, unbranched, aseptate, subparallel along the tubes, 3–4.5 μm in diam.

Hymenial setae occasionally present, ventricose, dark brown, thick-walled, with a sharp or obtuse tip, 20–25 \times 5–8 μm ; *cystidia* and *cystidioles* absent; *basidia* barrel-shaped,

with four sterigmata and a simple septum at the base, $10\text{--}15 \times 4\text{--}7 \mu\text{m}$; *basidioles* in shape similar to basidia, but slightly smaller; *rhomboid crystals* abundant.

Basidiospores broadly ellipsoid to subglobose, pale yellowish, slightly thick-walled, smooth, IKI–, CB–, $(3.2\text{--})3.4\text{--}4(-4.2) \times (2.7\text{--})2.9\text{--}3.6(-3.8) \mu\text{m}$, $L=3.74 \mu\text{m}$, $W=3.21 \mu\text{m}$, $Q=1.16\text{--}1.17$ ($n=60/2$).

Additional specimens (paratypes) examined. **CHINA.** Guangxi, Longzhou County, Nonggang Nature Reserve, on living *Excentrodendron tonkinense*, 22 July 2012, *Yuan 6227* (IFP); on dead branch of living *Excentrodendron tonkinense*, 22 July 2012, *Yuan 6229* (IFP); on stump of *Excentrodendron tonkinense*, 22 July 2012, *Yuan 6231 & 6234* (IFP).

Remarks. *Tropicoporus excentrodendri* is characterized by its annual, resupinate, effused-reflexed to pileate basidiocarps, and small pores and basidiospores within the genus *Tropicoporus*. *Tropicoporus tropicalis* (M.J. Larsen & Lombard) L.W. Zhou & Y.C. Dai (combined below) is the other species of *Tropicoporus* with annual, resupinate basidiocarps, and shares small pores (7–9 per mm) and basidiospores ($3\text{--}4.5 \times 2.5\text{--}4 \mu\text{m}$) with *T. excentrodendri*, but its basidiocarps are exclusively resupinate and grow on other angiosperms other than *Excentrodendron tonkinense* in Brazil (Larsen and Cobb-Pouille 1990).

Tropicoporus excentrodendri is similar to *Sanguangporus weigela* that has effused-reflexed to pileate basidiocarps, duplex context separated by a black line, 6–8 per mm of pores, a dimitic hyphal system in both context and trama, hymenial setae, and $3.8\text{--}4.2 \times 3\text{--}3.6 \mu\text{m}$ of basidiospores (Wu et al. 2012). However, *Sanguangporus weigela* has a perennial habit, obtuse pileal margin, and growth on *Weigela* in warm temperate zones (Wu et al. 2012; Zhou and Qin 2012).

Tropicoporus guanacastensis L.W. Zhou, Y.C. Dai & Vlasák, sp. nov. Figs. 5 and 6

Mycobank no.: MB 812156

Basidiocarps perennial, pileate, single. Pileal surface radially cracked, concentrically zonate and sulcate; margin sharp to obtuse. Pores circular to angular, 7–8 per mm; dissepiments thin to thick, entire. Context homogeneous. Tube layers distinctly stratified. Hyphal system monomitic in context and dimitic in trama; hyphae becoming swollen in KOH. Hymenial setae occasionally present, $12\text{--}25 \times 4\text{--}8 \mu\text{m}$. Basidiospores ellipsoid, pale yellowish, slightly thick-walled, IKI–, CB–, $4.1\text{--}4.9 \times 3.3\text{--}3.9 \mu\text{m}$.

Holotype. **COSTA RICA.** Guanacaste, Santa Rosa National Park, on dead standing angiosperm tree, 2 August 2014, *JV 1408–25* (holotype in IFP, isotype in JV).

Etymology. *guanacastensis* (Lat.): refers to the province name of type locality in Costa Rica.

Basidiocarps perennial, pileate, single, without odour or taste and woody hard. Pilei dimidiate, applanate, projecting up to 7 cm, 17 cm wide and 4 cm thick at base. Pileal surface black, radially cracked, concentrically zonate and sulcate,



Fig. 5 A basidiocarp of *Tropicoporus guanacastensis* (holotype). — Scale bar=1 cm

covered by mosses with age; margin sharp to obtuse, dark grey. Pore surface cinnamon-buff to honey-yellow, slightly glancing; sterile margin distinct, honey-yellow, up to 1 mm wide; pores circular to angular, 7–8 per mm; dissepiments thin to thick, entire. Context dark brown, woody hard, up to 5 mm. Tubes dark brown, woody hard, up to 3.5 cm long, tube layers distinctly stratified, annual layer about 2 mm long.

Hyphal system monomitic in context and dimitic in trama; generative hyphae simple septate; tissue darkening in KOH, hyphae becoming swollen in KOH. *Context.* Generative hyphae brown, slightly thick-walled with a wide lumen, unbranched, frequently septate, $3.5\text{--}6.5 \mu\text{m}$ in diam., regularly arranged. *Tubes.* Generative hyphae hyaline to yellowish, thin- to slightly thick-walled, unbranched, frequently septate, $2\text{--}4 \mu\text{m}$ in diam.; skeletal hyphae dominant, brown, thick-walled with a narrow lumen to subsolid, unbranched, aseptate, parallel along the tubes, $3\text{--}4.5 \mu\text{m}$ in diam.

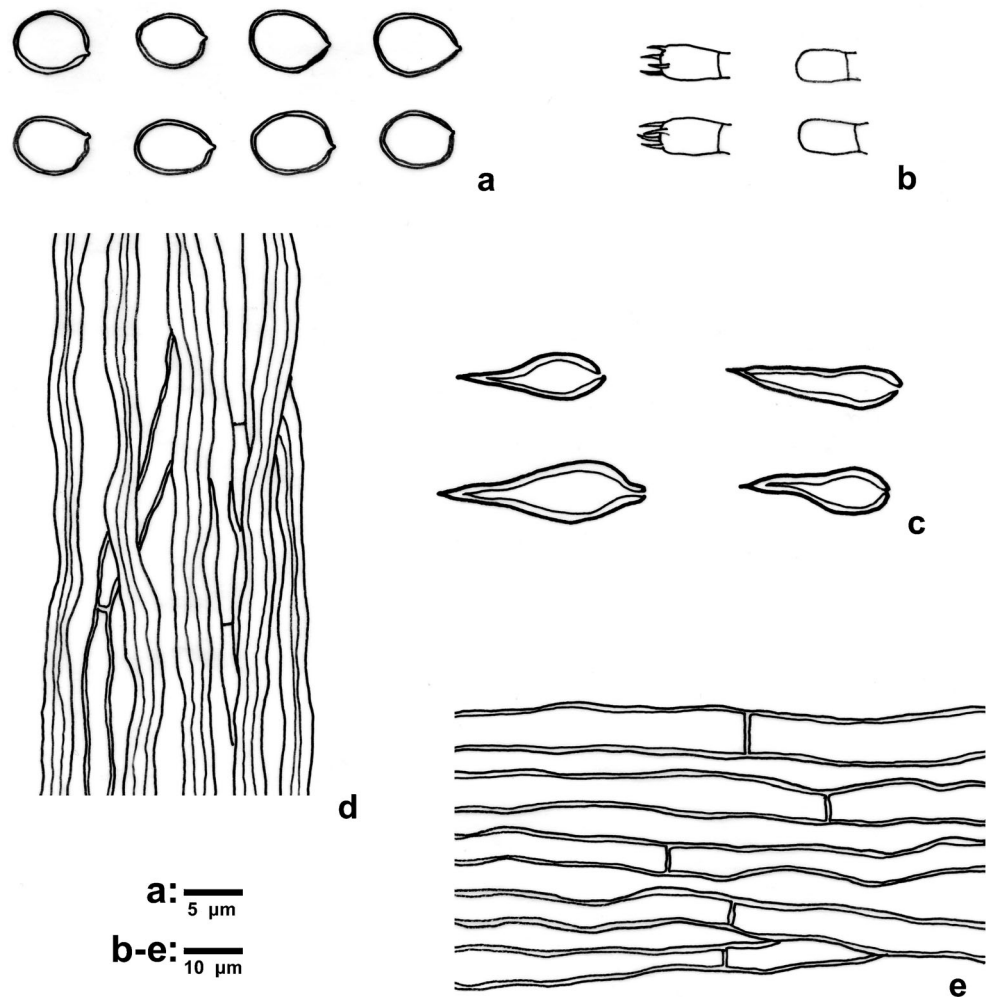
Hymenial setae occasionally present, mostly from skeletal hyphae, subulate to ventricose, dark brown, thick-walled, with a sharp tip, $12\text{--}25 \times 4\text{--}8 \mu\text{m}$; *cystidia* and *cystidioles* absent; *basidia* barrel-shaped, with four sterigmata and a simple septum at the base, $7\text{--}9 \times 4\text{--}5 \mu\text{m}$; *basidioles* in shape similar to basidia, but slightly smaller.

Basidiospores ellipsoid, pale yellowish, slightly thick-walled, smooth, IKI–, CB–, $4.1\text{--}4.9(-5) \times (3.1\text{--})3.3\text{--}3.9(-4) \mu\text{m}$, $L=4.47 \mu\text{m}$, $W=3.64 \mu\text{m}$, $Q=1.22\text{--}1.23$ ($n=60/2$).

Additional specimens (paratypes) examined. **COSTA RICA.** Guanacaste, Santa Rosa National Park, on angiosperm wood, 12 June 1997, *I. Lindblad 3101*, (O 19228); Guanacaste, Estacion Experimental Forestal Horizontes, on dead standing angiosperm tree, 31 July 2014, *JV 1407-103 J* (JV, IFP).

Remarks. *Tropicoporus guanacastensis* resembles *T. cubensis* (Y.C. Dai, Decock & L.W. Zhou) L.W. Zhou & Y.C. Dai (combined below) by similar hyphal structure with skeletal hyphae becoming swollen in KOH and basidiospores in shape and size. Both species have origins from Central

Fig. 6 Microscopic structures of *Tropicoporus guanacastensis* (drawn from the holotype). **a.** Basidiospores; **b.** Basidia and basidioles; **c.** Hymenial setae; **d.** Hyphae from trama; **e.** Hyphae from context



a: 5 μm
b-e: 10 μm

America; the former is from Costa Rica and the latter was described from Cuba (Tian et al. 2013). *Tropicoporus cubensis* differed from *T. guanacastensis* mainly in its indistinct tube layers, larger pores (5–6 per mm) and longer hymenial setae (27–43 \times 5–10 μm ; Tian et al. 2013).

Inonotus costaricensis Ryvarden was another species recently described from Costa Rica (Ryvarden 2002). This species is a typical member of *Inonotus*, producing annual basidiocarps and a monomitic hyphal system (Ryvarden 2002), and thus distinguish from *Tropicoporus guanacastensis*.

Tropicoporus cubensis (Y.C. Dai, Decock & L.W. Zhou) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812157

Basionym. *Inonotus cubensis* Y.C. Dai, Decock & L.W. Zhou, in Tian et al., Fungal Diversity 58(1): 163. 2013.

Tropicoporus dependens (Murrill) L.W. Zhou, Y.C. Dai & Vlasák, comb. nov.

Mycobank no.: MB 812158

Basionym. *Pyropolyporus dependens* Murrill, N. Amer. Fl. (New York) 9(2): 106. 1908.

Synonym. *Inonotus dependens* (Murrill) Vlasák & Y.C. Dai, in Vlasák et al., Phytotaxa 124(1): 27. 2013.

Tropicoporus linteus (Berk. & M.A. Curtis) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812159

Basionym. *Polyporus linteus* Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sci. 4: 122. 1860 (1858).

Synonym. *Inonotus linteus* (Berk. & M.A. Curtis) Teixeira, Revista Brasileira de Botânicas 15: 126. 1992.

Tropicoporus pseudolinteus (Vlasák & Y.C. Dai) L.W. Zhou, Y.C. Dai & Vlasák, comb. nov.

Mycobank no.: MB 812160

Basionym. *Inonotus pseudolinteus* Vlasák & Y.C. Dai, in Vlasák et al., Phytotaxa 124(1): 30. 2013.

Tropicoporus rudis (Pat.) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812161

Basionym. *Xanthochrous rudis* Pat., Bull. Soc. mycol. Fr. 23: 83. 1907.

Tropicoporus sideroxylicola (Vlasák & Y.C. Dai) L.W. Zhou, Y.C. Dai & Vlasák, comb. nov.

Mycobank no.: MB 812162

Basionym. *Inonotus sideroxylicola* Vlasák & Y.C. Dai, in Vlasák et al., Phytotaxa 124(1): 32. 2013.

Tropicoporus tropicalis (M.J. Larsen & Lombard) L.W. Zhou & Y.C. Dai, comb. nov.

Mycobank no.: MB 812163

Basionym. *Phellinus tropicalis* M.J. Larsen & Lombard, Mycologia 80(1): 73. 1988.

Synonym. *Poria rickii* Bres., Anns mycol. 18(1/3): 37 (1920); *Inonotus tropicalis* (M.J. Larsen & Lombard) T. Wagner & M. Fisch., Mycologia 94(6): 1009. 2002.

Key to species of *Tropicoporus*

1. Basidiocarps annual, resupinate, effused-reflexed to distinctly pileate.....2
1. Basidiocarps perennial, pileate.....3
2. Basidiocarps resupinate, effused-reflexed to distinctly pileate; on *Excentrodendron tonkinense*; in China.....
T. excentrodendri
2. Basidiocarps exclusively resupinate; on other angiosperms; in Brazil.....*T. tropicalis*
3. The binding alike hyphae (frequently branched and winding) present in trama.....4
3. The binding alike hyphae (frequently branched and winding) absent in trama.....5
4. Pores 5–7 per mm; basidiospores < 5 µm long, < 4 µm wide.....*T. dependens*
4. Pores 2–3 per mm; basidiospores > 6 µm long, > 4 µm wide.....*T. sideroxylicola*
5. Pores 4–5 per mm.....*T. pseudolinteus*
5. Pores > 5 per mm.....6
6. Basidiospores mostly < 4.5 µm wide; in tropical America.....7
6. Basidiospores mostly > 4.5 µm wide; in tropical Africa.....*T. rudis*
7. Pores 7–8 per mm, tube layers distinctly stratified; hymenial setae < 25 µm long.....
T. guanacastensis
7. Pores 5–7 per mm, tube layers indistinct; hymenial setae mostly > 25 µm long.....8
8. Dissepiments distinctly thick (≈ diameter of pores); basidiospores < 5 µm long, < 4 µm wide.....
T. cubensis
8. Dissepiments distinctly thin to slightly thick (< 1/4 diameter of pores); basidiospores mostly > 5 µm long, mostly > 4 µm wide.....
T. linteus

Other specimens examined.— *Sanghuangporus microcystideus*. CONGO. Oubangui, Grande Forêt (Holotype in FH). ETHIOPIA. Oromia Region, West Shewa, Menagesha National Forest, 11 July 2009, AM-08 (IFP); 26 March 2009, AM-19 (IFP). TANZANIA. Arusha Region, Arusha National Park, Mount Meru, on trunk of *Olea africana*, 18 February 1976, Harjula (O 915609).

— *Tropicoporus rudis*. NIGER. Maijirgui, 17 May 1906 (Holotype in FH). RWANDA. Eastern Province, Nyagatare District, Akagera National Park, Lake Hiema, 14 August 1976, J. Rammeloo (O 915614). TANZANIA. South High Province, Iringa District, Ruaha National Park, 21 May 1968, D.N. Pegler (O 915617).

Discussion

The traditional concept of *Inonotus* incorporated the poroid Hymenochaetaceae species with an annual habit and a monomitic hyphal system (Fiasson and Niemelä 1984). Using an nLSU-based phylogeny, Wagner and Fischer (2002) also treated some species with a perennial habit and a dimitic hyphal system, and several species bearing intermediate characters (an annual habit and a dimitic hyphal system, or a perennial habit and a monomitic hyphal system) in *Inonotus*. This opinion was accepted by Dai (2010), but Jeong et al. (2005) did not accept species without an annual habit and a monomitic hyphal system in *Inonotus*. Jeong et al. (2005) further considered taxa of *Inonotus linteus* complex to be a sister group of *Inonotus*. In this study, further samples of *Inonotus*, especially those from *Inonotus linteus* complex, were phylogenetically analyzed. Taking the phylogenies inferred from nLSU and ITS datasets, *Inonotus sensu* Wagner and Fischer (2002) and Dai (2010) was treated in a wide sense. *Inonotus andersonii*, *I. chihshanyenus*, *I. compositus*, *I. cuticularis*, *I. glomeratus*, *I. henanensis*, *I. hispidus*, *I. latemarginatus*, *I. micantissimus*, *I. nidus-pici*, *I. obliquus*, *I. pachyphloeus*, *I. patouillardii*, *I. pegleri*, *I. plorans*, *I. pruinus*, *I. quercustris*, *I. rickii*, *I. rodwayi*, *I. tricolor* and *I. ulmicola* (21 species) were considered to be members of *Inonotus sensu stricto* in this study. Species of *Inonotus linteus* complex clustered in two clades, deviating from *Inonotus sensu stricto*, and are respectively treated as two new genera, *Sanghuangporus* and *Tropicoporus*.

Species of *Inonotus sensu stricto*

Among the above-mentioned 21 species of *Inonotus sensu stricto*, *Inonotus glomeratus* and *I. tricolor* clustered outside the Clade A in the phylogeny inferred from ITS dataset (Fig. 2). However, the two species have key characters of *Inonotus sensu stricto*, such as a monomitic hyphal system, presence of hyphoid and hymenial setae, and coloured basidiospores (Ryvarden 2005; Dai 2010). The discrepancy between ITS-based phylogeny and morphology might be caused

by the low resolution of ITS region at the generic level. The nLSU-based phylogeny (Fig. 1) did confirm *I. glomeratus* as the members of *Inonotus sensu stricto*. Unfortunately, the nLSU region of *I. tricolor* was failed to obtain in this study. Further efforts to sequence the nLSU region from specimens of *I. tricolor* as well as of *I. henanensis* and *I. latemarginatus* might provide more insights into the delimitation of *Inonotus sensu stricto*, which is beyond the scope of this study.

All the 21 species of *Inonotus sensu stricto* produce annual basidiocarps with a monomitic hyphal system and coloured basidiospores, except that *I. pachyphloeus* and *I. tricolor* have a perennial habit and *I. henanensis* has hyaline basidiospores (Ryvarden 2005; Dai 2010; Dai et al. 2011). *Inonotus andersonii*, *I. chihshanyenus*, *I. henanensis*, *I. micantissimus*, *I. nidus-pici*, *I. obliquus*, *I. pegleri*, *I. pruinosis* and *I. ulmicola* produce resupinate basidiocarps, and *I. glomeratus* bears resupinate to effused-reflexed basidiocarps, while the other 11 species have pileate basidiocarps (Ryvarden 2005; Dai 2010; Dai et al. 2011). *Inonotus hispidus*, the generic type, and *I. plorans* has neither hyphoid nor hymenial setae, while the other 19 species has either one or both types of setae (Ryvarden 2005; Dai 2010; Dai et al. 2011).

Sanghuangporus and *Tropicoporus* differ from species of *Inonotus sensu stricto* mainly in having a dimitic hyphal system in trama. The two newly proposed genera are fairly similar in morphology, and it is hard to clearly separate them according to simple character differences (see the key for the features combined to separate them).

Sanghuangporus species

Nine species of *Sanghuangporus* are combined from *Inonotus linteus* complex. This group has recently been phylogenetically studied (Wu et al. 2012; Tian et al. 2013). Therefore, only one representative for each of the nine well-known species was sampled here for parsimony. Some of these species are medicinal fungi and have been subjected to pharmaceutical studies worldwide, but especially in East Asia (Dai et al. 2009, 2010; De Silva et al. 2012a, b, 2013). Previous studies in China, Japan and Korea have often dealt with all species as the important medicinal fungal species ‘Sanghuang’ (Jeon et al. 2011; Sun et al. 2014), and for several decades *Phellinus linteus* (or *Inonotus linteus*) was commonly used as the scientific binomial for species of this group. Recently, the species diversity of this group was clarified, and several new species and new combinations were added to the *Inonotus linteus* complex (Wu et al. 2012; Tian et al. 2013). *Inonotus sanghuang* (combined to *Sanghuangporus* above) was recognized as the genuine ‘Sanghuang’ species (Wu et al. 2012).

The nLSU-based phylogeny (Fig. 1) showed the two Ethiopian specimens, AM-08 and AM-19, clustering within *Sanghuangporus*. The African specimen O 915609 collected on *Olea* from Tanzania also nested within *Sanghuangporus* in

ITS-based phylogeny and formed a sister relationship with the other nine species of *Sanghuangporus* (Fig. 2). O 915609 was morphologically identified as *Phellinus microcystideus* by Dai and Xu (1998) through comparison with the holotype from Congo. In this study, besides the reexamination of holotype of *P. microcystideus*, we also morphologically checked AM-08 and AM-19, and confirmed that the two specimens represent *P. microcystideus*. Therefore, we combine *P. microcystideus* to *Sanghuangporus*. It is noteworthy that *P. microcystideus* was treated as a synonym of *P. linteus* (Ryvarden 1983) and Harjula (1980) reported that this species is used as a herb to cure headaches in Tanzania.

Tropicoporus species

Nine species are accepted in *Tropicoporus* in this study, including two new species and seven new combinations. Most are tropical American species, with the exception of *T. excentrodendri* from Guangxi, tropical China and *T. rudis* from tropical Africa.

Tropicoporus excentrodendri was only found on aged trees of *Excentrodendron tonkinense*, which is an endangered species in the IUCN red list of threatened species (<http://www.iucnredlist.org/>); mature trees are very scarce. It means *Tropicoporus excentrodendri* can be also a threatened species, if it has a strict relationship with its endangered host tree.

Another Chinese specimen within the *Tropicoporus* clade is Yuan 5898 from Guangxi. This specimen morphologically resembles *T. tropicalis* by its annual and exclusively resupinate basidiocarps, which can be distinguished from all other species of *Tropicoporus*. Specimen Yuan 5898 was closely related to four representatives of *T. tropicalis* in the ITS-based phylogeny (Fig. 2), and formed a basal lineage. The locality of Yuan 5898 (China) has a long geographic distance from type locality of *Tropicoporus tropicalis* (Brazil), and Yuan 5898 also has a relatively long branch in ITS-based phylogeny (Fig. 2), therefore we treat Yuan 5898 as *Tropicoporus* cf. *tropicalis*.

Tian et al. (2013) described *Inonotus cubensis* (combined to *Tropicoporus* above) based on the holotype and two paratypes from Cuba. However, one of the paratypes (MUCL 43130) is actually from Costa Rica. MUCL 43130 and JV 1408–25 also from Costa Rica formed a separated clade from *T. cubensis* in nLSU-based phylogeny (Fig. 1), and clustered together with another two Costa Rican specimens (JV 1407-103 J and O 19228) as a distinct clade in the ITS-based phylogeny (Fig. 2). These two clades are well-supported and clearly isolated from *Tropicoporus cubensis* and other species of *Tropicoporus*. The four Costa Rican specimens represent *Tropicoporus guanacastensis*, which is introduced in this paper.

Xanthochrous rudis was described from Maijirgui, Niger, West Africa (Patouillard 1907), and Ryvarden (1983) treated it as a synonym of *Phellinus linteus*. Two successfully

sequenced specimens from Rwanda (O 915614) and Tanzania (O 915617), both in East Africa, fit well with the morphology of *X. rudis* based on the current holotype study, and were considered to be *X. rudis*. *Xanthochrous rudis* formed a distinct clade from *Tropicoporus linteus* within *Tropicoporus* (Fig. 2). Therefore, *X. rudis* is transferred to *Tropicoporus* based on morphology and phylogeny.

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