Taxonomy, phylogeny and divergence times of *Polyporus* (Basidiomycota) and related genera

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Abstract

*Polyporus* is a taxonomically controversial genus which includes species belonging to six infrageneric groups. Recently, many species of *Polyporus* have been transferred into other related genera viz. *Cerioporus*, *Favolus*, *Lentinus*, *Neofavolus* and *Picipes* based on the phylogenetic and morphological analyses. To ascertain the relationships of *Polyporus* and its allied genera, eight DNA fragments viz. the internal transcribed spacers 1 and 2 with the 5.8S rDNA (ITS), the nuclear ribosomal large subunit (nLSU), partial translation elongation factor 1-α gene (EF1-α), the mitochondrial small-subunit (mtSSU), the β-tubulin gene (TUB), the gene for RNA polymerase II largest subunit (RPB1), the gene for RNA polymerase II second largest subunit (RPB2) and the nuclear ribosomal small subunit (nSSU), are used in the molecular systematic studies. Phylogenetic analyses were carried out based on two combined datasets (ITS+nLSU) and (ITS+nLSU+EF1-α+mtSSU+RPB1+RPB2+nSSU+TUB), and the results indicated that species of *Polyporus* and its related genera fell into six well supported clades: the picipes clade, the favolus clade, the neofavolus clade, the lentinus clade, the core polyporus clade and the squamosus clade. Moreover, the conserved regions of six DNA fragments (5.8S, nLSU, EF1-α, RPB1, RPB2 and nSSU) were used to analyze the divergence times and evolutionary relationships of *Polyporus* and its related genera by using BEAST v1.8. Bayesian evolutionary analysis revealed that the ancestor of Polyporales split at about 141.81 Mya, while the mean stem ages of the six major clades of *Polyporus* and its allied genera were 49–63 Mya. Based on the combined analyses of morphology, phylogenies and divergence times, species in the picipes clade formed the genus *Picipes* by the coriaceous (fresh) to hard (dry) basidiomata and strongly branched skeleto-binding hyphae; species nested in the favolus clade and the neofavolus clade were separately treated as two distinct genera *Favolus* and *Neofavolus*; the polyporoid species in the lentinus clade with central and light-colored stipe and inflated hyphae were transferred into *Lentinus*, and the core polyporus clade was treated as *Polyporus* s. str. The squamosus clade contained species belonging to several different genera viz. *Datronia*, *Datroniella*, *Echinochaete*, *Mycobonia*, *Neodatronia*, *Polyporus* s. lat. and *Pseudofavolus*, but there are no enough efficient morphological evidence to combine all species in the squamosus
clade into a specific genus. In addition, three new species of *Polyporus* and seven new species of *Picipes* are described and illustrated.

**Key words** – molecular clock – morphology – multi-gene phylogenies – new species – Polyporaceae

**Introduction**

*Polyporus* P. Micheli ex Adans. was firstly used by Micheli (1729) to define 14 polypores with pore layers can hardly be peeled off from the context. But the name was invalid until Adanson (1763) restored Micheli’s concept. Linnaeus (1753) treated *Polyporus* as a synonym of *Boletus* L., while Fries (1821) accommodated most polyporoid species into *Polyporus*. After that, many mycologists revised the definition of *Polyporus*, and the definition provided by Gilbertson & Ryvarden (1987) was widely accepted. They characterized *Polyporus* by the features of annual stipitate basidiomata, a dimitic hyphal system with generative hyphae and skeleto-binding hyphae, hyaline, thin-walled, and cylindrical basidiospores, and causing white rot.

Most *Polyporus* species grow on different kinds of dead woods, especially on dead hardwoods. But several species can also grow on living hardwoods or other substrates, for examples, *P. squamosus* (Huds.) Fr. always grows on living hardwoods and causes stem rot (Schwarze et al. 2000), *P. rhizophilus* Pat. grows with the grass roots, *P. umbellatus* (Pers.) Fr. only rises on the ground from sclerotia, and *P. phyllostachydis* Sotome, T. Hatt. & Kakish. is limited to bamboo roots (Ryvarden & Gilbertson 1994, Núñez & Ryvarden 1995a, Sotome et al. 2007, Sotome et al. 2008). Several species of *Polyporus* are known as medicinal fungi (Dai et al. 2009), and the most famous one is *P. umbellatus*.

Because Micheli (1729) initially did not select the type species of *Polyporus*, there is no consensus on the type selection. Murrill (1903, 1904) first selected *P. ulmi* Paulet, which is the synonym of *P. squamosus*, as the nomenclatorial type of *Polyporus*, but it was rejected by others according to the “First Species Rule” (Krüger & Gargas 2004). The first acceptable type for *Polyporus* is *P. brumalis* (Pers.) Fr., proposed by Clements & Shear (1931) who argued that the best known or important one should be selected as the correct lectotype. This selection was supported by Krüger & Gargas (2004), but, this lectotypification was refused by Donk (1933) and ICBN (Greuter et al. 2000) because it was not identified by Micheli. In addition, *P. arcurarius* (Batsch) Fr. is another candidate which is supported by Cunningham (1948). Since Donk (1933) chosen *P. tuberaster* (Jaq. ex Pers.) Fr. as the type species, this lectotype has been followed by most succeeding researchers (Cunningham 1965, Singer 1986, Niemelä & Kotiranta 1991, Ryvarden 1991, Núñez & Ryvarden 1995a, Sotome et al. 2008, Dai et al. 2014, Zhou et al. 2016a).

*Polyporus* is a widespread genus that includes many species belonging to six morphological groups, *Polyporus* group, * Favolus* group (= *Favolus* Fr.), *Melanopus* group (= *Melanopus* Pat.), *Polyporellus* group (= *Polyporellus* Karst.), *Admirabilis* group and *Dendropolyergus* group (= *Dendropolyergus* (Pouz.) Jülich) described by Núñez & Ryvarden (1995a). According to the morphological analyses, 32 species were divided into those groups, although several of them had been removed and many other species were added (Dai 1996, 1999, Buchanan & Ryvarden 1998, Popoff & Wright 1998, Hattori 2000, Thorn 2000, Dai et al. 2003, 2007, 2009, 2014, Ryvarden & Iturriaga 2003, Zheng & Liu 2005, Sotome et al. 2007, 2013, 2016, Drechsler-Santos et al. 2008, Xue & Zhou 2012, 2014, Hyde et al. 2016, Runnel & Ryvarden 2016, Zhou et al. 2016a, Palacio et al. 2017, Tibpromma et al. 2017, Zhou & Cui 2017, Zmitrovich et al. 2017, Cui et al. 2019, Xing et al. 2020).

Phylogenetically, *Polyporus* was proved to be a polyphyletic genus according to the mtSSU analysis (Ko & Jung 2002), and this attitude has been demonstrated by others (Krüger & Gargas 2004, Krüger et al. 2006, Sotome et al. 2008, Dai et al. 2014, Zmitrovich & Kovalenko 2016, Zhou et al. 2016a, Tibpromma et al. 2017). The phylogenetic analyses of basidiomycetes revealed that *Polyporus* clusters in the core polyporoid clade with *Echinochaete* Reid, *Pseudofavolus* Pat., *Datronia* Donk, *Lentinus* Fr., * Dichomitus* D.A. Reid and several other genera (Binder et al. 2005,
Based on molecular analyses, *Polyporus* was mainly divided into six major clades, but these clades did not conform to the six morphological groups (Sotome et al. 2008, Zhou et al. 2016a). Species of *Polyporellus* always cluster with *Lentinus* (Krüger & Gargas 2004, Sotome et al. 2008, Binder et al. 2013, Dai et al. 2014, Seelan et al. 2015, Tibpromma et al. 2017), while several species of *Polyporus* and *Melanopus* always gather together with *Datronia*, *Echinochaete*, *Mycobonia* Pat. and *Pseudofavolus* (Krüger & Gargas 2004, Sotome et al. 2008, Binder et al. 2013). When studying group *Favolus*, species of this group were divided into two genera viz. *Neofavolus* Sotome & T. Hatt. typified by *N. alveolaris* (DC.) Sotome & T. Hatt. and *Favolus* typified by *F. brasiliensis* (Fr.) Fr. (Sotome et al. 2013). Based on multi-gene phylogenetic analyses, species in *Melanopus* were proved to be distributed in two different clades viz. picipes clade and squamosus clade (Zhou et al. 2016a). The picipes clade has been described as *Picipes* Zmitr. et Kovalenko (Zmitrovich & Kovalenko 2016), and sixteen species with hard basidiomata in dried condition, brownish to black stipes and strongly branched skeleton-binding hyphae were included in this genus (Zhou et al. 2016a). While the *Polyporus* and *Datronia* species in the squamosus clade were combined into *Cerioporus* Quél. by Zmitrovich & Kovalenko (2016). Moreover, species of *Polyporellus* were recently treated as members of *Lentinus* (Krüger 2002, Seelan et al. 2015, Zhou et al. 2016a, Zmitrovich & Kovalenko 2016). Although the above opinions have been phylogenetically supported, species in the squamosus clade and the lentinus clade are morphologically diversified. More valuable information to confirm the above taxonomic researches are needed.

To recognize different taxonomic ranks, Hennig (1966) proposed the divergence time that can be used as a universally standardized criterion in the systematics of all known organisms. This conception was firstly used in the study of fishes, anthropoid primates and fruit flies at the end of 20th century (Avise & John 1999). For fungi, Zhao et al. (2017) confirmed that the mean stem ages of Basidiomycota and Entorrhizomycota are ca. 530 million years ago (Mya), subphyla of Basidiomycota are 406–490Mya, while the most classes and orders of Agaricomycotina are separately about 358–393Mya and 120–290Mya.

Nowadays, as more fungal fossil specimens being found and DNA fragments being used in analyzing the relationships between different fungal groups, molecular divergence time analyzing has been widely used in estimating evolutionary times of different fungi, for example, mycorrhizal fungi (Hibbett & Matheny 2009, Kohler et al. 2015), white and brown rot lineages (Eastwood et al. 2011, Garcia-Sandoval et al. 2011), porcino (Feng et al. 2012), amanitas (Cai et al. 2014, Sánchez-Ramírez et al. 2014), *Heterobasidion* Bref. (Chen et al. 2015), Caliciaceae Chevall. (Prieto & Wedin 2017), *Bondarzewia* Singer (Song et al. 2016), *Agaricus* L. (Zhao et al. 2016), *Laetiporus* Murrill (Song & Cui 2017), Basidiomycota (Zhao et al. 2017) and *Sanghuangporus* Sheng H. Wu, L.W. Zhou, and Y.C. Dai (Zhou et al. 2019). However, there is no study focused on the evolutionary times of *Polyporus* and its allied genera.

In the present study, we investigated the taxonomy and phylogeny of *Polyporus* and related genera (including *Favolus*, *Lentinus*, *Neofavolus* and *Picipes*). Six DNA fragments viz. the 5.8S, nLSU, EF1-α, RPB1, RPB2 and nSSU, were used to estimate the evolutionary time of *Polyporus* and its related genera. Besides the above genes, ITS, mtSSU and TUB were also used in the phylogenetic analyses. Multigene phylogenetic analyses of ITS+nLSU and ITS+nLSU+EF1-α+mtSSU+RPB1+RPB2+nSSU+TUB were provided to reveal the phylogenetic relationships between *Polyporus* and its allied genera.

**Materials & Methods**

**Morphological studies**

All specimens tested in this study are deposited in the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC, Beijing, China) and the Institute of Applied Ecology, Chinese Academy of Sciences (IFP, Shenyang, China). Macro-morphological characteristics were described based on the field notes and the herbarium specimens. Color
descriptions were based on Petersen (1996). Micro-morphological features were obtained from dried specimens under light microscopes, the proceedings were followed previous studies (Zhou et al. 2016a, b, Zhou & Cui 2017). Free-hand sections were observed and measured in 5% potassium hydroxide solution after staining with 1% Congo Red solution. Cotton Blue and Melzer’s reagents were respectively used to examine whether the tissues have cyanophilous and amyloid reactions or not. All the microscopic characteristics were inspected and photographed at a magnification of up to ×1000 by Nikon Eclipse Ni microscope (Nikon Corporation, Tokyo, Japan). All the sizes of basidiospores, basidia, cystidia and hyphae were measured using the Image-Pro Plus 6.0 software (Media Cybernetics, Silver Spring, USA). To represent variation in the size, no less than 30 basidiospores were measured from each specimen. The following abbreviations were used in this study: IKI− = neither amyloid nor dextrinoid, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous, CB− = acyanophilous, L = mean spore length ± standard deviation, W = mean spore width ± standard deviation, Q = variation in the L/W ratios between the specimens studied, Qm = mean L/W ratio ± standard deviation, n (a/b) = number of spores (a) measured from given number (b) of specimens.

DNA extraction and amplification

Total DNA were extracted from dried specimens using CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) and FH plant DNA kit II (Demeter Biotech Co., Ltd., Beijing, China) according to the manufacturer’s procedures. The primer pair ITS4 and ITS5 (White et al. 1990) was used to amplified ITS regions while LR0R/LR7 (Vilgalys & Hester 1990), EF1-983F/EF1-1567R (Rehner & Buckley 2005), Bt-1a/Bt-1b (Glass & Donaldson 1995), PNS1/NS41 (Hibbett 1996), MS1/MS2 (White et al. 1990), RP1-Af/RP1-Cr (Matheny et al. 2002) and fRPB2-5F/bRPB2-7.1R (Liu et al. 1999, Matheny 2005) were used to amplified nLSU, EF1–α, TUB, nSSU, mtSSU, RP1 and RP2 regions, respectively. The primers RP1-2.2f (Binder et al. 2010) and bRPB2-6F (Matheny 2005) sometimes were seperately used as alternatives to RP1-Af and fRPB2-5F. 50 μl PCR volume with 2×1.5 μl primers (10 pM), 2 μl DNA extract, 20 μl ddH2O and 25 μl 2×EasyTaq PCR Supermix (TransGen Biotech Co., Ltd., Beijing, China) was used each tube. All the polymerase chain reactions (PCRs) were performed on S1000™ Thermal Cycler (Bio-Rad Laboratories, California, USA). The PCR procedures for different genes were as Zhou et al. (2016a):

a) PCR conditions for mtSSU, ITS, nSSU, TUB and EF1–α were (i) 2 min initial denaturation at 94°C, (ii) 36 cycles of 45 s denaturation at 94°C, 45 s annealing at 52°C (for mtSSU)/53°C (for ITS, nSSU and TUB)/54°C (for EF1–α) and 1 min extension at 72°C, (iii) 10 min final extension at 72°C.

b) PCR condition for nLSU was (i) 5 min initial denaturation at 94°C, (ii) 36 cycles of 1 min denaturation at 94°C, 1min 20 s annealing at 50°C and 1 min 30 s extension at 72°C, (iii) 10 min final extension at 72°C.

c) PCR condition for RP1 and RP2 was (i) 2 min initial denaturation 94°C, (ii) 9 cycles of 45 s denaturation at 94°C, 45 s (minus 1°C per cycle) annealing at 60°C and 1min 30 s extension at 72°C, (iii) 36 cycles of 45 s denaturation at 94°C, 1 min annealing at 53°C and 90 s extension at 72°C for, (iv) 10 min final extension at 72°C.

All PCR products were directly purified and sequenced in the Beijing Genomics Institute (BGI), China, with the same primers. Newly generated sequences were submitted to GenBank and listed in Table 1.

Divergence time estimation of Polyporus and related genera

Two fossil calibrations, Archaeomarasmius leggetti Hibbett, D. Grimaldi & Donoghue and Quatsinoporites cranhamii S.Y. Sm., Currah & Stockey, were used in the divergence time estimating. Archaeomarasmius leggetti, an agaricoid fungus dated to 94–90 Mya (Hibbett et al. 1997), was treated as the representative of the minimum age of Agaricales. While the other fossil,
Q. cranhamii, was considered to be the minimum divergence time of Hymenochaetales at 113 Mya (Smith et al. 2004).

Table 1 Names, voucher codes, locations and corresponding GenBank accession numbers of the taxa used in this study.

| Species                        | Specimen No. | Country    | GenBank accession No. | ITS     | nLSU    | EF1-α   | mtSSU   | TUB     | RPB1    | RPB2    | nSSU    |
|-------------------------------|--------------|------------|-----------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| Agaricus campestris           | LAPAG370     | –          | KM657927              | KR006607| KR006636| –       | –       | –       | –       | KT951556| –       |
| Amylocorticium cebennense     | CFMR:HHB-2808| USA        | GU187505              | GU187561| GU187675| –       | –       | –       | –       | GU187439| GU187770| GU187612|
| Antrodia tanakae              | Cui 9743     | China      | KR605814              | KR605753| KR610743| –       | –       | –       | –       | KR610833| KR605914| –        |
| Aphanobasidium pseudotsugae   | CFMR:HHB-822 | USA        | GU187509              | GU187567| GU187695| –       | –       | –       | –       | GU187455| GU187781| GU187620|
| Athelia epiphylla             | CFMR:FP-100564| USA    | GU187501              | GU187558| GU187676| –       | –       | –       | GU187440| GU187771| GU187613| –        |
| Boletopsis leucomelaena       | AFTOL-ID 1527| USA        | DQ484064              | DQ154112| GU187763| –       | –       | –       | GU187494| GU187820| DQ435797| –        |
| Boletus edulis                | HMJAU4637     | –          | JN563894              | KF112455| KF112202| –       | –       | –       | KF112586| KF112704| –       | –        |
| Bondarzewia sp.               | Yu 56         | China      | KT693203              | KT693205| KX066148| –       | –       | –       | KX066158| KX066165| –       | –        |
| Callistosporium graminicolor  | AFTOL-ID 978 | USA        | DQ484065              | AY745702| GU187761| –       | –       | –       | GU187493| KJ424369| AY752974| –        |
| Clavulicium macounii          | GB:KHL12129   | Sweden     | KC203494              | KC203494| KC203514| –       | –       | –       | –       | –       | KC203494| –        |
| Coriolopsis trogii            | RLG4286sp     | USA        | JN164993              | JN164808| JN164898| –       | –       | –       | JN164820| JN164867| –       | –        |
| Cotylidia sp.                 | MB5           | –          | AY854079              | AY629317| AY885148| –       | –       | –       | AY864868| AY883422| AY705958| –        |
| Daedalea modesta              | Cui 10151     | China      | KP171205              | KP171227| KR610716| –       | –       | –       | –       | KR610806| KR605883| –        |
| Daedaleopsis septentrionalis  | H6035         | Finland    | HG973499              | HG973499| HG973507| –       | –       | –       | –       | HG973516| –       | –        |
| Datronia mollis               | RLG6304sp     | USA        | JN165002              | JN164791| JN164901| –       | –       | –       | JN164818| JN164872| –       | –        |
| Datronia stereoides           | Holonen       | Finland    | KC415179              | KC415196| –       | –       | –       | –       | –       | –       | –       | –        |
| Dationillea scutellata        | RLG9584T      | USA        | JN165004              | JN164792| JN164902| –       | –       | –       | JN164817| JN164873| –       | –        |
| Dationillea tropica           | Dai 13147     | China      | KC415181              | KC415189| –       | –       | –       | –       | –       | KC477838| –       | –        |
| Echinocincla brachypora       | TFM:F 24996   | Japan      | AB462321              | AB462309| –       | –       | –       | –       | –       | –       | –       | –        |
| Echinocincla ruficeps         | TFM:F 15716   | Japan      | AB462310              | AB368065| –       | –       | –       | –       | –       | AB368123| –       | –        |
| Echinocincla russiceps        | TFM:F 24250   | Japan      | AB462313              | AB462301| –       | –       | –       | –       | –       | –       | –       | –        |
| Favolus acervatus             | Cui 11053     | China      | KU189774              | KU189805| KU189920| KU189956| KU189864| KU189889| KU189994| KU189835| –       | –        |
| Favolus acervatus             | Dai 10749b    | China      | KX548953              | KX548979| KX549043| KX549018| KX549033| KX549065| KX549073| KX549000| –       | –        |
| Favolus philippinensis        | Cui 10941     | China      | KX548976              | KX548998| KX549062| KX549032| KX549042| –       | –       | KX549016| –       | –        |
| Species                          | Specimen No. | Country     | ITS    | nLSU   | EF1-α  | GenBank accession No. |
|---------------------------------|--------------|-------------|--------|--------|--------|-----------------------|
| Favolus philippinensis          | Cui 10926    | China       | KX548977 | KX548999 | KX549063 | –                      | –                     | –                     | –                     | –                     | KX549017               |
| Favolus brasiliensis            | INPA241452   | Brazil      | AB735953 | AB735977 | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Favolus emerici                 | Cui 11129    | China       | KX548955 | KX548980 | KX549044 | –                     | –                     | –                     | –                     | –                     | KX549001               |
| Favolus niveus                  | Dai 13276    | China       | KX548956 | KX548982 | KX549046 | –                     | –                     | –                     | –                     | –                     | KX549003               |
| Favolus pseudobetulinus         | TFMF:27567   | Japan       | AB587644 | AB587639 | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Favolus roseus                  | TFM:F 20589  | Malaysia    | AB735975 | AB368099 | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Favolus septatum                | Zhou 287     | China       | KX548968 | –       | KX549054 | –                     | –                     | –                     | –                     | –                     | KX549008               |
| Favolus spathulatus             | Cui 8290     | China       | KX548969 | KX548991 | KX549055 | –                     | –                     | –                     | –                     | –                     | KX549009               |
| Favolus spathulatus             | Dai 13615A   | China       | KU187977 | KU189006 | KU189921 | KU189865             | –                     | –                     | –                     | –                     | KU189836               |
| Favolus gracilisporus           | Cui 4292     | China       | KX548970 | KX548992 | KX549056 | –                     | –                     | –                     | –                     | –                     | KX549010               |
| Favolus gracilisporus           | Li 1938      | China       | KX548971 | KX548993 | KX549057 | –                     | –                     | –                     | –                     | –                     | KX549011               |
| Favolus sp.                     | MEL 238296   | Australia   | KP012829 | KP012829 | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Fomitopsis pinicola             | AFTOL-ID 770 | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Ganoderma lingzhi              | Dai 12574    | China       | KJ143908 | –       | KX029977 | –                     | –                     | –                     | –                     | –                     | JX029985               |
| Ganoderma tsugae                | AFTOL-ID 771 | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | JX029981               |
| Geastrum recoligens             | OSC41996     | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Gloeophyllum septarium           | Wilcox-3BB   | USA         | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Grifola frondosa                | AFTOL-ID 701 | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Grifola sordulenta              | AFTOL-ID 562 | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | –                     |
| Hexagonia glabra                | Dai 10691    | China       | JX569733 | JX569750 | –       | –                     | –                     | –                     | –                     | –                     | KF274649               |
| Hexagonia tenuis                | Cui 8468     | China       | JX559277 | JX559302 | –       | –                     | –                     | –                     | –                     | –                     | JX559311               |
| Hydrochaete dupontii            | AFTOL-ID 666 | –           | DQ404386 | AY635770 | DQ435793 | –                     | –                     | –                     | –                     | –                     | AY662669               |
| Hyphoderma praeternissum         | AFTOL-ID 518 | –           | –       | –       | –       | –                     | –                     | –                     | –                     | –                     | AY684717               |
| Jaapia argillacea               | CBS:252.74   | Netherlands | GU187524 | GU187581 | GU187711 | –                     | –                     | –                     | –                     | –                     | GU187788               |
| Lactarius deceptivus            | AFTOL-ID 682 | USA         | AY854089 | AY631899 | AY885158 | –                     | –                     | –                     | –                     | –                     | AY864883               |
| Lentinus arcularius             | Cui 10998    | China       | KX548973 | KX548995 | KX549059 | KX549029             | KX549071             | KX549077             | –                     | –                     | KX549013               |
| Lentinus arcularius             | Cui 11398    | China       | KU189766 | KU189797 | KU189911 | KU189947             | KU189984             | KU189980             | KU189826             | –                     | –                     |
| Species                | Specimen No. | Country     | GenBank accession No. |   |   |   |   |   |   |
|------------------------|--------------|-------------|-----------------------|---|---|---|---|---|---|
| Lentinus badius        | JS0094       | Malaysia    | KP283478              | KP283512 | – | – | – | – | KP325691 | – | – |
| Lentinus brumalis      | Cui 7188     | China       | KX851591              | KX851646  | KX851771 | – | KX851575  | KX851747  | KX851758 | KX851723 |
| Lentinus brumalis      | Cui 10750    | China       | KU189765              | KU189796 | KU189910 | – | KU189857 | KU189883 | KU189979 | KU189825 |
| Lentinus crinitus      | DSH92N43C    | Costa Rica  | KP283495              | KP283523 | – | – | – | – | KP325687 | – | – |
| Lentinus flexipes      | TENN56491    | USA         | AF516553              | AJ488115 | – | – | – | – | – | – | – |
| Lentinus flexipes      | TENN56503    | USA         | AB478884              | AB368100 | – | – | – | – | – | – | – |
| Lentinus longiporus    | DAOM:229479  | Canada      | AB478880              | LC052217 | – | – | – | – | – | – | – |
| Lentinus longiporus    | WD2579       | Japan       | AB478879              | LC052218 | – | – | – | – | – | – | – |
| Lentinus polychrous    | KM141387     | Thailand    | KP283487              | KP283514 | – | – | – | – | – | – | – |
| Lentinus substrictus   | Wei 1582     | China       | KU189767              | KU189798 | KU189912 | KU189948 | KU189858 | – | KU189981 | KU189827 |
| Lentinus substrictus   | Wei 1600     | China       | KC572022              | KC572059 | – | – | – | – | – | – | – |
| Lentinus thailandensis| Dai 6722     | China       | KX851590              | KX851645  | KX851770 | KX851698 | – | – | KX851757 | KX851722 |
| Lentinus thailandensis| MSUT_6734    | Thailand    | LC052221              | LC052219 | – | – | – | – | – | – | – |
| Lentinus tigrinus      | MUCL22821    | Belgium     | AB478881              | AB368072 | – | – | – | – | – | AB368130 | – |
| Leptosporomyces raunliaeri | CFMR:HBB-7628 | USA | GU187528 | GU187588 | GU187719 | – | – | GU187471 | GU187791 | GU187640 | – |
| Lignosus rhinocerotis  | PEN94        | Malaysia    | JQ409359              | AB368074 | – | – | – | – | – | AB368132 | – |
| Microporus affinis     | Cui 7714     | China       | JX569739              | JX569746 | – | – | – | – | – | – | – |
| Microporus vernicipes  | KUC20130711-23 | South Korea | KJ668503              | KJ668355 | – | – | – | – | – | – | – |
| Microporus xanthopus    | Cui 8284     | China       | JX290074              | JX290071 | – | – | – | – | – | JX559313 | – |
| Mycobonia flava        | CuiTENN10256 | Costa Rica  | AY513570              | AJ487934 | – | – | – | – | – | – | – |
| Neodatronia gaoligongensis | Cui 8055    | China       | JX559269              | JX559286 | – | – | – | – | – | JX559317 | – |
| Neodatronia sinensis   | Dai 11921    | China       | JX559272              | JX559283 | – | – | – | – | – | JX559320 | – |
| Neofavolus alveolaris  | Cui 9900     | China       | KX548974              | KX548996  | KX549060 | KX549030 | KX549040 | KX549072 | KX549078 | KX549014 |
| Neofavolus americanus  | Dai 12761    | USA         | KX900072              | KX900186 | – | – | – | – | – | – | – |
## Table 1 Continued.

| Species                        | Specimen No. | Country | ITS   | nLSU  | EF1-α | mtSSU | TUB   | RPB1 | RPB2 | nSSU   |
|--------------------------------|--------------|---------|-------|-------|-------|-------|-------|------|------|--------|
| *Neofavolus cremeoalbidus*     | Cui 12412    | China   | KX900067 | KX900182 | KX900368 | –     | –     | –    | –    | KX900315 |
| *Neofavolus cremeoalbidus*     | TUMH:50009   | Japan   | AB735980 | AB735957 | –       | –     | –     | –    | –    | –      |
| *Neofavolus mikawai*           | Cui 11152    | China   | KX900068 | KX900183 | KX900369 | KX900248 | –     | –    | –    | KX900316 |
| *Neofavolus mikawai*           | Dai 12361    | China   | KC572002 | KX900069 | KX900183 | KX900369 | KX900248 | –   | –    | KX900294 |
| *Neofavolus squamatus*         | Cui 12175    | China   | KX900060 | KX900176 | KX900363 | –     | –     | –    | –    | KX900286 |
| *Neofavolus suaviissimus*      | DSH2011      | USA     | KC572003 | KX900069 | KX900183 | KX900369 | KX900248 | –   | –    | KX900271 |
| *Neofavolus suaviissimus*      | LE202237     | USA     | KC572003 | KX900069 | KX900183 | KX900369 | KX900248 | –   | –    | KX900270 |
| *Neofavolus suaviissimus*      | MA672        | USA     | KC572003 | KX900069 | KX900183 | KX900369 | KX900248 | –   | –    | KX900289 |
| *Neolentinus adhaerens*        | DAOM 214911  | –       | HM536096 | HM536071 | HM536117 | –     | –     | –    | –    | KX900290 |
| *Panus lecomtei*               | HHB-11042-Sp | USA     | KX900064 | KX900180 | KX900366 | KX900246 | –     | –    | –    | KX900280 |
| *Phanerochaete chrysosporium*  | HHB-6251-Sp  | USA     | KX900064 | KX900180 | KX900366 | KX900246 | –     | –    | –    | KX900281 |
| *Picipes ailaoshanensis*       | Cui 12578    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes ailaoshanensis*       | Cui 12585    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes americanus*           | JV 0509-149  | USA     | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes americanus*           | JV 0809-104  | USA     | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes annularius*           | Cui 10123    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes atratus*              | Cui 11289    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes atratus*              | Dai 13375    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes auriculus*            | Cui 13616    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes auriculus*            | Yuan 4221    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipess australindus*         | MR10472      | Argentina | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipess australindus*         | MR10701      | Argentina | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes badius*               | Cui 10853    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes badius*               | Cui 11136    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes baishanzuensis*        | Cui 11395    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes baishanzuensis*        | Dai 13418    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes brevistipitatus*       | Cui 11345    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes brevistipitatus*       | Cui 13652    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes conifericolor*         | Cui 9950     | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |
| *Picipes conifericolor*         | Dai 11114    | China   | AF516568 | AF516568 | –       | –     | –     | –    | –    | –      |

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| Species                  | Specimen No. | Country     | ITS          | nLSU          | EF1-α         | mtSSU        | TUB          | RPB1        | RPB2        | nSSU        |
|-------------------------|--------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| *Picipes cf. dictyopus* | Cui 11109    | China       | KX900025     | KX900145     | KX900347     | KX900220     | KX899934     | KX900380     | KX900303     | KX900267     |
| *Picipes cf. dictyopus* | Cui 11092    | China       | KX900026     | KX900146     | KX900348     | KX900221     | –             | –             | –             | –             |
| *Picipes dictyopus*     | TENN 59385   | Belize      | AF516561     | A478945      | –             | –             | –             | –             | –             | –             |
| *Picipes fraxinicola*   | Dai 2494     | China       | KX572023     | KX572062     | KU189932     | KU189966     | –             | –             | –             | –             |
| *Picipes fraxinicola*   | Wei 6025     | China       | KX572024     | KX572063     | –             | –             | –             | –             | –             | –             |
| *Picipes melanopus*     | H 6003449    | Finland     | JQ964422     | KX572064     | –             | –             | –             | –             | –             | –             |
| *Picipes melanopus*     | MJ 372-93    | Czech       | KX572026     | KX572065     | –             | –             | –             | –             | –             | –             |
| *Picipes pumilus*       | Cui 5464     | China       | KX851628     | KX851682     | KX851785     | KX851710     | KX851581     | KX851753     | KX851765     | KX851735     |
| *Picipes pumilus*       | Dai 6705     | China       | KX851630     | KX851684     | KX851787     | KX851711     | –             | –             | –             | KX851737     |
| *Picipes rhizophilus*   | Dai 11599    | China       | KX572028     | KX572067     | KU189933     | KU189967     | KU189874     | KU189896     | KU189992     | KU189847     |
| *Picipes rhizophilus*   | Dai 16082    | China       | KX851634     | KX851687     | KX851788     | KX851713     | –             | –             | –             | KX851738     |
| *Picipes nigromarginatus* | Cui 8113 | China       | KX900062     | KX900178     | KX900365     | KX900244     | –             | –             | –             | KX900288     |
| *Picipes subdictyopus*  | Cui 11220    | China       | KX900057     | KX900173     | KX900360     | KX900240     | –             | KX900390     | KX900314     | KX900283     |
| *Picipes subdictyopus*  | Cui 12539    | China       | KX900058     | KX900174     | KX900361     | KX900241     | –             | –             | –             | KX900284     |
| *Picipes submelanopus*  | Dai 13294    | China       | KU189770     | KU189801     | KU189915     | KU189951     | KU189860     | KU189886     | KU189984     | KU189830     |
| *Picipes submelanopus*  | Dai 13296    | China       | KU189771     | KU189802     | KU189916     | KU189952     | KU189861     | –             | –             | KU189831     |
| *Picipes subtrropicus*  | Cui 2662     | China       | KU189759     | KU189791     | KU189905     | KU189943     | –             | –             | –             | KU189821     |
| *Picipes subtrropicus*  | Li 1928      | China       | KU189758     | KU189790     | KU189904     | KU189942     | KU189854     | KU189881     | KU189976     | KU189820     |
| *Picipes subtubaeformis* | Cui 10793 | China       | KU189753     | KU189785     | KU189900     | KU189938     | KU189851     | KU189875     | KU189973     | KU189816     |
| *Picipes subtubaeformis* | Dai 11870 | China       | KU189752     | KU189784     | KU189999     | KU189937     | KU189850     | KU189876     | KU189972     | KU189815     |
| *Picipes taibaiensis*   | Dai 5741     | China       | JX489169     | KX572071     | –             | –             | –             | –             | –             | –             |
| *Picipes taibaiensis*   | Dai 5746     | China       | KX196783     | KX196784     | KX196785     | KX196786     | –             | –             | –             | KX196787     |
| *Picipes tibeticus*     | Cui 12215    | China       | KU189755     | KU189787     | KU189902     | KU189940     | KU189853     | KU189879     | KU189975     | KU189818     |
| *Picipes tibeticus*     | Cui 12225    | China       | KU189756     | KU189788     | KU189903     | KU189941     | –             | KU189880     | –             | KU189819     |
| *Picipes tubaeformis*   | Niemela 6855 | Finland     | KX572036     | KX572073     | –             | –             | –             | –             | –             | –             |
| *Picipes tubaeformis*   | JV 0309-1    | USA         | KX572034     | KX572072     | –             | –             | –             | –             | –             | –             |
| *Picipes ulleungus*     | Cui 12410    | China       | KX900022     | KX900142     | KX900344     | KX900217     | KX899932     | –             | –             | KX900302     | KX900266     |
| *Picipes virgatus*      | CulTENN11219 | Argentina   | AF516581     | A488122      | –             | –             | –             | –             | –             | –             |
| *Picipes virgatus*      | CulTENN11406 | Argentina   | AF516582     | A488122      | –             | –             | –             | –             | –             | –             |
| *Picipes wuyishanensis* | Dai 7409     | China       | KX900061     | KX900177     | KX900364     | KX900243     | –             | –             | –             | KX900287     |
| *Podoserpula*           | ZJL2015015   | China       | KU324484     | KU324487     | KU324494     | –             | –             | –             | –             | KU324491     |
| *Polyporus auratus*     | Dai 13665    | China       | KX900056     | KX900172     | KX900359     | KX900239     | –             | –             | –             | KX900313     | KX900282     |
| Species                      | Specimen No. | Country    | GenBank accession No. | ITS       | nLSU      | EF1-α   | mtSSU     | TUB | RPB1  | RPB2  | nSSU  |
|-----------------------------|--------------|------------|-----------------------|-----------|-----------|---------|-----------|-----|-------|-------|-------|
| *Polyporus austrosinensis*  | Cui 11140    | China      | KX900046              | KX900162  | KX900352  | KX900230 | –         | –   | –     | –     | –     |
| *Polyporus austrosinensis*  | Cui 11126    | China      | KX900045              | KX900161  | KX900351  | KX900229 | KX899936  | KX900386 | KX900309 | KX900273 |
| *Polyporus cuticulatus*     | Cui 8637     | China      | KX851614              | KX851668  | KX851777  | KX851702 | –         | –   | –     | –     | –     |
| *Polyporus cuticulatus*     | Dai 13141    | China      | KX851613              | KX851667  | KX851776  | KX851701 | KX851576  | KX851749 | –     | KX851727 |
| *Polyporus guianensis*      | TENN 58404   | Venezuela  | AF516566              | AJ487948  | –         | –       | –         | –   | –     | –     | –     |
| *Polyporus guianensis*      | TENN 59093   | Argentina  | AF516564              | AJ487947  | –         | –       | –         | –   | –     | –     | –     |
| *Polyporus hapatolopus*     | Yuan 5809    | China      | KC297219              | KC297220  | KU189918  | KU189954 | –         | –   | –     | –     | KU189833 |
| *Polyporus hematicapnodes*  | Cui 11259    | China      | KX851625              | KX851679  | KX851782  | KX851707 | KX851580 | –   | KX851763 | KX851733 |
| *Polyporus hematicapnodes*  | Dai 13403    | China      | KX851627              | KX851681  | KX851784  | KX851709 | KX851579 | –   | KX851764 | KX851734 |
| *Polyporus lamelliporus*    | Dai 15106    | China      | KX851623              | KX851677  | KX851781  | KX851706 | KX851578  | KX851752 | KX851762 | KX851732 |
| *Polyporus lamelliporus*    | Dai 12327    | China      | KX851622              | KX851676  | KX851780  | KX851705 | KX851577 | –   | –     | –     | KX851731 |
| *Polyporus lepricurii*      | TENN 58579   | Costa Rica | AF516567              | AJ487949  | –         | –       | –         | –   | –     | AB368150 | –     |
| *Polyporus mangshanensis*   | Dai 15151    | China      | KX851796              | KX851797  | KX851802  | KX851798 | KX851795 | KX851800 | KX851801 | KX851799 |
| *Polyporus parvovarius*     | Yuan 6639    | China      | KX900049              | KX900165  | KX900354  | KX900232 | KX899937  | KX900388 | KX900311 | KX900275 |
| *Polyporus parvovarius*     | Dai 13948    | China      | KX900050              | KX900166  | KX900355  | KX900233 | KX899938  | KX900389 | KX900312 | KX900276 |
| *Polyporus radicatus*       | DAOM198916   | Canada     | AF516584              | AJ487955  | –         | –       | –         | –   | –     | –     | –     |
| *Polyporus radicatus*       | TENN 58831   | USA        | AF516585              | AJ487956  | –         | –       | –         | –   | –     | –     | –     |
| *Polyporus squamosus*       | Cui 10394    | China      | KX851635              | KX851688  | KX851789  | KX851714 | KX851582  | KX851754 | KX851766 | KX851739 |
| *Polyporus squamosus*       | Cui 10595    | China      | KU189778              | KU189809  | KU189925  | KU189960 | KU189868  | KU189892 | KU189988 | KU189840 |
| *Polyporus subvarius*       | WD2368       | Japan      | AB587643              | AB587638  | –         | –       | –         | –   | –     | –     | –     |
| *Polyporus subvarius*       | Yu 2         | China      | AB587632              | AB587621  | KU189924  | KU189959 | –         | –   | –     | KU189839 |
| *Polyporus tuberaster*      | Dai 11271    | China      | KU189769              | KU189800  | KU189914  | KU189950 | –         | –   | KU189983 | KU189829 |
| *Polyporus tuberaster*      | Dai 12462    | China      | KU507580              | KU507582  | KU507590  | KU507584 | KU507588 | –   | KU507586 | KU507586 |
| *Polyporus umbellatus*      | Pen 13513    | China      | KU189772              | KU189803  | KU189917  | KU189953 | KU189862  | KU189887 | KU189985 | KU189832 |
| *Polyporus varius*          | Cui 12249    | China      | KU189758              | KU507583  | KU507591  | KU507585 | –         | –   | KU507589 | KU507592 | KU507587 |
| *Polyporus varius*          | Dai 13874    | China      | KU189777              | KU189808  | KU189923  | KU189958 | KU189867  | KU189891 | KU189987 | KU189838 |
| *Polyporus sp.1*            | Cui 11071    | China      | KX851642              | KX851695  | KX851794  | KX851719 | KX851584  | KX851755 | KX851768 | KX851744 |
| *Polyporus sp.1*            | Cui 11045    | China      | KX851643              | KX851696  | –         | –       | KX851720  | KX851753  | KX851769  | KX851745 |
### Table 1 Continued.

| Species               | Specimen No. | Country     | GenBank accession No. | GenBank accession No. |
|-----------------------|--------------|-------------|-----------------------|-----------------------|
| **Species**           | **Specimen No.** | **Country** | **ITS** | **nLSU** | **EF1-α** | **mtSSU** | **TUB** | **RPB1** | **RPB2** | **nSSU** |
| *Polyporus sp.2*      | Dai 13585A   | China       | KX900055              | KX900171              | KX900358              | KX900236  | –       | –       | –       | KX900279  |
| *Pseudofavolus*       | Dai 13584A   | China       | KX900071              | KX900185              | KX900371              | KX900251  | –       | –       | –       | –        |
| *Pseudofavolus*       |              |             |                       |                       |                       |           |         |         |         |          |
| *cucullatus*          |              |             |                       |                       |                       |           |         |         |         |          |
| *Pseudofavolus*       | WD2157       | Japan       | AB587637              | AB368114              | –                     | –         | –       | –       | –       | –        |
| *Russula emeticicolor*|              |             |                       |                       |                       |           |         |         |         |          |
| *Serpula himantioides*|              |             |                       |                       |                       |           |         |         |         |          |
| *Schizopyllum*        |              |             |                       |                       |                       |           |         |         |         |          |
| *radiatum*            |              |             |                       |                       |                       |           |         |         |         |          |
| *Stereopsis radicans* |              |             |                       |                       |                       |           |         |         |         |          |
| *Tomentella*          |              |             |                       |                       |                       |           |         |         |         |          |
| *sp.*                 |              |             |                       |                       |                       |           |         |         |         |          |
| *Trametes conchifer*  | FP106793sp   | USA         | JN164924              | JN164797              | JN164887              | –         | –       | –       | JN164823 | JN164849  |
| *Trametes elegans*    | FP105679sp   | USA         | JN164944              | JN164799              | JN164899              | –         | –       | –       | JN164833 | JN164861  |
| *Trametes polyzona*   | Cui 11040    | China       | KR605824              | KR605767              | KR610760              | KR606029  | –       | –       | KR610849 | KR605932  |

Newly generated sequences are shown in black bold.

Fifty-one species of *Polyporus* on the six main clades proposed in our previous study (Zhou et al. 2016a) were added into the multiple DNA data (5.8S+nLSU+EF1-α+RPB1+RPB2+nSSU). Four species of Agaricales viz. *Agaricus campestris* L., *Aphanobasidium pseudotsugae* (Burt) Boidin & Gilles, *Callistosporium graminicolor* Lennox and *Schizopyllum radiatum* Fr. were used to represent the Agaricales clade while *Hydnochaete duportii* Pat., *Hyphoderma praetermissum* (P. Karst.) J. Erikss. & Å. Strid and an undescribed species of *Cotylidia* were used to represent Hymenochaetales clade. Based on the analyses of Zhao et al. (2017), Amylocorticiales was treated as sister clade of Agaricales. Moreover, members of Atheliales, Boletales, Russulales, Thelephorales, Stereopsidales and other three orders were also included in our dataset. Divergence times were estimated by using BEAST v1.8.0 (Drummond et al. 2012).

All the DNA sequences were aligned separately using Clustal Omega (Sievers et al. 2011) and manually adjusted in BioEdit 7.2.5 (Hall 1999). Introns of EF1-α, RPB1 and RPB2 sequences, and poorly aligned regions of nLSU and nSSU were removed from the analysis. The best substitution models were selected by using jModelTest 2.1.7 (Darriba et al. 2012). The XML file was executed in BEAUti v1.8.0. Six DNA datasets were set as different partitions, with substitution and clock models unlinked while the trees linked. The HKY+Gamma+Invariant model was chosen as the substitution model of 5.8S while GTR+Gamma+Invariant was selected for other five genes. The clock model was set to uncorrelated lognormal relaxed clock (Drummond et al. 2006, Lepage et al. 2007). Yule process speciation was used as the tree prior (Gernhard 2008). Gamma priors distribution was used for fossil node calibrations, set shape = 1.0, scale = 50.0, offset = 90.0 for Agaricales clade and 113.0 for Hymenochaetales clade (Sánchez-Ramírez et al. 2014). All the ucld.mean parameters for different genes were set to gamma priors distribution, shape = 1.0, scale = 0.001 and
Four independent Markov chain Monte Carlo (MCMC) chains of 100 million generations were conducted and saving trees every 5000th generation. The resulting log file was inspected with Tracer v1.6 (http://tree.bio.ed.ac.uk/software/tracer/) to confirm that the estimated effective sample size (ESS) ≥ 200. 20000 ultrametric trees from each run were summarized using TreeAnnotator v1.8.0 to estimate the 95% credible node intervals referred to as highest posterior densities (HPD), discarding 10% of states as burn-in and setting posterior probability limit 0.80.

**Phylogenetic analyses of Polyporus and related genera**

*Trametes conchifer* (Schwein.) Pilát, *T. elegans* (Spreng.) Fr. and *T. polyzona* (Pers.) Justo were selected as outgroups in the phylogenies. Totally 735 DNA sequences, which belonging to 122 isolates of *Polyporus* and 28 isolates of allied genera, were used in the phylogenetic analyses, procedures were done as in our previous studies (Zhou et al. 2016a, Zhou & Cui 2017, Zhu et al. 2019).

Eight gene regions were initially aligned separately using Clustal Omega (Sievers et al. 2011) and then manually adjusted to maximize alignment and minimize gaps in BioEdit 7.2.5 (Hall 1999). Sequence alignments were deposited at TreeBase (http://purl.org/phylo/treebase; submission ID: 29005).

One thousand partition homogeneity test (PHT) replicates of the combined datasets (ITS+nLSU and ITS+nLSU+EF1-α+mtSSU+RPB1+RPB2+nSSU+TUB) were tested using PAUP 4.0 beta 10 (Swofford 2002) to determine whether the partitions are homogeneous. PHT results revealed that all the DNA sequences displayed congruent phylogenetic signals (P values were 0.866 and 0.994 for ITS+nLSU and the eight-gene dataset, respectively).

The best-fit evolutionary models were selected by hierarchical likelihood ratio tests (hLRT) and Akaike information criterion (AIC) in MrModelTest 2.2 (Nylander 2004) after scoring 24 models of evolution using PAUP 4.0 beta 10. Analyzing results revealed that GTR+I+G was the best-fit model for both ITS+nLSU and the eight-gene dataset.

The best maximum likelihood (ML) topology obtained from 1000 maxtrees was performed using PAUP 4.0 beta 10. All characters were equally weighted and gaps were treated as missing. ML bootstrap values (ML-BS) obtained from 1000 replicates were performed using RAxMLGUI 1.31 (Michalak 2012) with the GTRGAMMA and GTRCAT models to assess the reliability of the nodes.

The maximum parsimony (MP) topology and bootstrap values (MP-BS) obtained from 1000 maxtrees were performed using PAUP 4.0 beta 10. Trees were inferred using the heuristic search option with tree-bisection-reconnection (TBR) branch swapping algorithm and 1000 random sequence additions. Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each MP tree generated.

Bayesian phylogenetic inference and Bayesian posterior probabilities (BPPs) were performed with MrBayes v3.2 (Ronquist et al. 2012). The analyses were run with four Markov chains for 5 000 000 (ITS+nLSU) and 8 000 000 (eight-gene dataset) generations to make the average standard deviation of split deviation frequencies less than 0.01, and sampled every 100th generation. The first 25% of the sampled trees were discarded as burn-in and the remaining ones were used to reconstruct a majority rule consensus and calculate BPPs of the clades.

Trees were viewed in FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) and edited by using Adobe Illustrator CS5 and Adobe Photoshop CC (Adobe Systems Inc., California, USA). The best topologies from ML analyses were shown in this study with ML-BS (≥50), MP-BS (≥50) and BPPs (≥0.95).

**Results**

**Divergence time estimation**
The MCMC tree (Fig. 1) shows that the ancestor of Polyporales evolved during the early Cretaceous, approximately 141.81 Mya (95% HPD = 102.35–191.91Mya), while the mean estimated stem ages of the four main clades of Polyporales proposed by Hibbett & Donoghue (2001) and Binder et al. (2013) are between 123.74 and 88.81 Mya. In addition, the mean stem ages of the six major clades of Polyporus recognized by Zhou et al. (2016a) are approximately 47–60Mya. Among the six clades, the lentinus clade diverged at 46.9 Mya contained gilled species of Lentinus and several poroid species which previously treated as Polyporus (Polyporellus group), and this clade is sister to Microporus P. Beauv. and Lignosus Lloyd ex Torrend. The favolus clade and the neofavolus clade grouped together and evolved from the same anceser dated to 60.01 Mya. The squamosus clade, which dated to 58.09 Mya, contains species of Polyporus, Datronia, Neodatronia B.K. Cui, Hai J. Li & Y.C. Dai, Datroniella B.K. Cui, Hai J. Li & Y.C. Dai, Pseudofavolus and Echinochaete. The core polyborus clade, which including the lectotype of Polyporus, is sister to the picipes clade, and both of them diverged at 56.33 Mya but with low support.

Phylogenetic analyses

The ITS+nLSU dataset was composed of 2160 total characters (770 bp ITS and 1390 bp nLSU), of which 1362 characters were constant, 696 variable characters were parsimony-informative. The best ML tree scored 26414.12589 was obtained after trying 518348 rearrangements. Sixty-six equally most parsimonious trees (tree length = 5168, CI = 0.286, RI = 0.756, RC = 0.217, HI = 0.714) were retained after trying 4.2288×10^10 rearrangements in the MP analyzing. Bayesian analysis presented essentially the same topology with the best ML tree and the best ML topology was presented along with ML-BS, MP-BS and BPPs in Fig. 3.

In the eight-gene based phylogeny, 7512 total characters (770 bp ITS, 1390 bp nLSU, 607 bp EF1-α, 743 bp mtSSU, 1292 bp RPB1, 1110 bp RPB2, 1118 bp nSSU and 482 bp TUB) were equally weighted. Among these characters, 4521 bp characters were constant and 2651 bp characters were parsimony-informative. The best ML tree scored 81741.75120 was achieved after trying 489289 rearrangements. In the MP analyzing, 56 best parsimonious trees (tree length = 17298, CI = 0.316, RI = 0.721, RC = 0.228, HI = 0.684) were saved after trying 1.5844×10^10 rearrangements. Bayesian analysis presented essentially the same topology with the best ML tree and the best ML topology was presented along with ML-BS, MP-BS and BPPs in Fig. 3.

In our current study, both ITS+nLSU and the eight-gene dataset analyses support the existence of the six major clades of Polyporus proposed in our previous study (Zhou et al. 2016a). Both datasets have the similar topology but with discrepant bootstrap values.

1. The picipes clade is composed of 27 species, which including 7 undescribed ones, with high supports in the eight-gene analyzing (100/98/1.00) but with low supports in the ITS+nLSU analyzing (72/66/-). It reveals that P. dictyopus Mont., P. subdictyopus H. Lee, N.K. Kim & Y.W. Lim and P. ulleungus H. Lee, N.K. Kim & Y.W. Lim has much closer relationships with Picipes spp. than other Polyporus species. As is shown in Fig. 3, four major lineages are presented in the picipes clade. Twelve species are included in the lineage A and most of them are restricted to the temperate region. Unlike lineage A, species of lineage B are limited in the tropical and subtropical regions. Picipes submelanopus (H.J. Xue & L.W. Zhou) J.L. Zhou & B.K. Cui is the only species of lineage C, it is merely collected in temperate and Pleteau zones of China. Lineage D includes two subtropical species, Pi. baishanzuensis J.L. Zhou & B.K. Cui and P. ulleungus, the former one is only reported in Baishanzu Nature Reserve of China (Zhou et al. 2016a), while the later one was originally described from Korea (Tibpromma et al. 2017).

2. The core polyborus clade, which contains the lectotype of Polyporus and other five species, is strongly supported in both datasets (94/83/1.00 for ITS+nLSU and 96/96/1.00 for the eight-gene phylogeny). In this clade, P. tuberaster is mainly found from temperate zone, but it can also be found in tropical and subtropical regions according to our collections. For other species, P. umbellatus is mainly collected from temperate areas, P. hapalopus H.J. Xue & L.W. Zhou is limited to subtropical areas, while other three specie are restricted to tropical regions.
Figure 1 – Divergence time estimation of *Polyporus* and related genera from Bayesian evolutionary analysis sampling tree based on 5.8S, LSU, EF1-α, RPB1, RPB2 and nSSU multiple
dataset. Posterior probabilities not less than 0.80 and the mean ages of each node are annotated. The 95% highest posterior densities of divergence time estimation are marked by horizontal bars.

Figure 2 – Phylogeny of *Polyporus* and related genera inferred from ITS+nLSU data. Topology is from ML analysis with maximum likelihood bootstrap support values (≥50, left), parsimony bootstrap support values (≥50, middle) and Bayesian posterior probability values (≥0.95, right). New species are indicated in black bold.
3. Both ITS+nLSU and eight-gene based phylogenies support the division of the squamosus clade. In this clade, twelve Polyporus spp. nested with species of Datronia, Datroniella, Echinochaete, Mycobonia, Neodatronia and Pseudofavolus, species in this clade is very diverse in morphology, for the time being, we prefer to remain the different genera names for species in this clade.

4. The favolus clade is comprised of twelve Favolus species with high supports in both ITS+nLSU and eight-gene dataset analyses (Figs 2 and 3). Most of these species are distributed in tropical and subtropical areas. However, F. pseudobetulinus (Murashk. ex Pilát) Sotome & T. Hatt. has a boreal distribution in northern hemisphere (Sotome et al. 2011). Based on our own collections, few samples of F. acervatus (Lloyd) Sotome & T. Hatt. can also be found in temperate areas.

5. Six species are included in the neofavolus clade with high supports (Figs 2, 3). Among these species, N. squamatus J.H. Xing, J.L. Zhou & B.K. Cui is only collected in Tibet (plateau zone), N. americanus J.H. Xing, J.L. Zhou & B.K. Cui is merely found in the temperate area of America (Xing et al. 2020), while N. cremeoalbidus Sotome & T. Hatt. is limited in subtropical regions of China and Japan. Neofavolus suavissimus (Fr.) J.S. Seelan, Justo is mainly distributed in warm to cold temperate areas, but several subtropical collections can also be found in Japan (Seelan et al. 2015). Based on our own collections, both N. alveolaris and N. mikawai (Lloyd) Sotome & T. Hatt. can be collected in temperate, subtropical and tropical regions, the former one mainly distributes in temperate areas while the later mainly in subtropical areas.
6. Six species in group Polyporellus of Polyporus clustered in the lentinus clade and showed closer relationships with Hexagonia Fr., Lentinus and Microporus than other Polyporus spp. This clade is strongly supported in both ITS+nLSU and multi-gene analyses (Figs 2, 3). Three well-supported lineages are recognized in the lentinus clade (Fig. 3). Lineage I is composed of four poroid species (*P. arcularius*, *P. brumalis*, *P. ciliatus* Fr. and *P. longiporus* Audet, Boulet & Sirard). These four species mainly distribute in temperate areas though *P. arcularius* and *P. brumalis* can also be found in subtropical, tropical and plateau zones. Lineage II is formed by gilled species of *Lentinus*, and almost all the species in this lineage distribute in the tropical areas. *Polyporus thailandensis* Sotome and *P. tricholoma* Mont. nested in the lineage III are tropical species with poroid hymenophores. All poroid species in the lentinus clade were treated as members of the genus *Lentinus*.

Figure 3 – Phylogeny of *Polyporus* and related genera inferred from the combined dataset ITS+nLSU+EF1-α+mtSSU+TUB+RPB1+RPB2+nSSU. Topology generated by ML analysis with
maximum likelihood bootstrap support values (≥50, left), parsimony bootstrap support values (≥50, middle) and Bayesian posterior probability values (≥0.95, right) are indicated on the nodes. New species are indicated in black bold. The colored dots indicate four different climate zone distributions.

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**Taxonomy**

*Picipes ailaoshanensis* B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559395; Facesoffungi number: FoF 10644

**Etymology** – *ailaoshanensis* (Lat.): referring to the locality (Ailaoshan) of the type specimen.

**Basidiomata** – Annual, laterally stipitate, solitary, woody hard when dry. Pileal surface yellowish brown to chestnut when dry, glabrous or covered with protuberances towards the stipe, azonate, frequently with radially aligned stripes; margin straight or incurved when dry. Pore surface grey beige when dry; pores angular, 3–7 per mm; dissepiments thin, entire. Context buff to festucine when dry, woody hard upon drying, up to 3.5 mm thick. Tubes concolorous with pore surface, decurrent on one side of the stipe, up to 1.5 mm thick. Stipe short, upper portion concolorous to the pileal surface and bearing a black cuticle at the base, up to 9 mm long and 1.2 cm in diam.

**Hyphal structure** – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

**Context** – Generative hyphae frequent, colorless, thin-walled, occasionally branched, 2–8 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid,
frequently branched, strongly interwoven, 1.2–5.5 μm in diam.

Tubes – Generative hyphae frequent, colorless, thin-walled, frequently branched, 1.5–5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide lumen when young and with a narrow lumen to solid when mature, with dendroid branches, strongly interwoven, 1.5–5 μm in diam. Cystidia absent; cystidioles frequent, subulate and clavate with an acerate head, 15.5–20 × 5–6.8 μm. Basidia not observed.

Stipe – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 2–4.3 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, with arboriform branches, strongly interwoven, 1.8–6.1 μm in diam. Hyphae in cuticle with brown inclusion inside, thick-walled with a wide lumen, bearing clamp connections, 2.5–8 μm in diam.

**Figure 4** – Basidiomata of four new species: *Picipes ailaoshanensis* (A and B: Cui 12578); *Picipes annularius* (C: Cui 10123); *Picipes atratus* (D: Dai 13375, E: Cui 11289); *Picipes auriculatus* (Cui 13616). Scale bars = 1 cm.
Basidiospores – Basidiospores infrequent, cylindrical, rarely oblong, colorless, thin-walled, smooth, frequently bearing one or more guttules, IKI–, CB–, (5.9–)6–7.3(–8) × (2.5–)2.6–3.6 μm, L = 6.71 ± 0.52 μm, W = 3.06 ± 0.29 μm, Q = 1.91–2.67, Qm = 2.22 ± 0.17 (n = 44/2).

Rot type – A white rot.

Known distribution – Subtropical regions of China.

Materials examined – China, Yunnan Province, Jingdong County, Ailaoshan Nature Reserve, on fallen angiosperm branch, 10 Sep 2015, B.K. Cui, Cui 12578 (BJFC, holotype), Cui 12585 (BJFC, paratype).

Notes – *Picipes ailaoshanensis* is a subtropical species with greyish pore surface, laterally short stipe with a black base, and clavate cystidioles with an acerate head. *Picipes taibaiensis* (Y.C. Dai) J.L. Zhou & B.K. Cui resembles *Pi. ailaoshanensis* by having yellowish brown to chestnut pileus and laterally short stipe, but *Pi. taibaiensis* has brownish pore surface upon drying, larger basidiospores (7.5–10.5 × 3.2–3.8 μm), fusoid cystidioles and temperate distribution (Dai et al. 2009).

Figure 5 – Basidiomata of six species: *Picipes brevistipitatus* (A: Cui 13652); *Picipes nigromarginatus* (B: Cui 8113); *Picipes wayishanensis* (C: Dai 7409); *Polyporus auratus* (D: Dai 7909).
Polyporus austrosinensis (E: Cui 11123); Polyporus lamelliporus (F: Dai 15103). Scale bars = 1 cm.

Figure 6 – Microscopic structures of Picipes ailaoshanensis. A Basidiospores. B Cystidioles. C Hyphae from context. D Hyphae from trama. E Hyphae from stipe. F Hyphae from cuticle of stipe. Scale bars = 10 μm.

Picipes annularius B.K. Cui, Xing Ji & J.L. Zhou, sp. nov. 

Index Fungorum number: IF559396; Facesoffungi number: FoF 10659

Etymology – annularius (Lat.): referring to the annularly arranged squamae on the pileal surface when fresh.

Basidiomata – Annual, laterally stipitate, solitary, coriaceous when fresh and hard when dry. Pilei fan-shaped, projecting up to 1.8 cm long, 2.1 cm wide and 3 mm thick at base. Pileal surface pinkish buff to buff yellow when fresh, becoming buff upon drying, with radially aligned stripes when dry; margin yellowish brown when dry, covered with beige to cinnamon-buff small squamae,
annularly arranged, straight. Pore surface pinkish buff when fresh, becoming buff to yellowish brown when dry; pores angular, 3–5 per mm; dissepiments thin, entire. Context white when fresh, becoming buff to ivory when dry, corky upon drying, up to 1.5 mm thick. Tubes concolorous with pore surface, not decurrent and has an obvious boundary with stipe, up to 2 mm thick. Stipe short, white when fresh and pinkish buff when dry at the upper parts towards the tubes, grey to black when fresh and greyish buff to dark brown when dry at the low parts, tomentose, up to 4 mm long and 3.5 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, slightly CB+; tissues unchanged in KOH.

Context – Generative hyphae frequent, colorless, thin-walled, rarely branched, 2–5.6 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen, frequently branched, interwoven, 1.2–4.6 μm in diam.

Tubes – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 1.3–3.3 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen, with dendroid branches, strongly interwoven, 1.1–2.9 μm in diam. Cystidia and cystidioles absent. Basidia clavate, with a basal clamp connection and four sterigmata, 13–17 × 7–8.6 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 3.2–6.9 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen, frequently branched, interwoven, 1.5–4.9 μm in diam.

Basidiospores – Basidiospores cylindrical, rarely oblong, colorless, thin-walled, smooth, occasionally bearing one or two guttules, IKI–, CB–, (5.9–)6.1–7.2(–7.9) × 2.6–3.3(–3.4) μm, L = 6.65 ± 0.46 μm, W = 2.95 ± 0.2 μm, Q = 1.88–2.67, Qm = 2.27 ± 0.2 (n=38/1).

Rot type – A white rot.

Known distribution – Subtropical regions of China.

Materials examined – China, Guangdong Province, Heyuan, Daguishan Forest Park, on fallen angiosperm branch, 18 Aug 2011, B.K. Cui, Cui 10123 (BJFC, holotype), Cui 10120 (BJFC, paratype).

Notes – Picipes annularius is a special species has buff pileus covered with annularly arranged beige to cinnamon-buff small squamae and obvious boundary between tubes and stipe. Its buff pileus, cream pore surface and short stipe are similar to those of P. varius (Pers.) Fr. But phylogenetically, P. varius belongs to the squamosus clade, while Pi. annularius clusters with Picipes spp. Morphologically, P. varius differs in having glaborous pileal surface, smaller pores (5–9 per mm), lager basidiospores (7.5–9 × 2.5–3.3 μm) and basidia (18–30 × 7–9 μm) according to the Chinese specimens.

Picipes atratus B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559397; Facesoffungi number: FoF 10645

Etymology – atratus (Lat.): referring to the black pileal surface when mature.

Basidiomata – Annual, centrally to laterally stipitate, scattered to gregarious, coriaceous to hard leathery when fresh, hard woody when dry. Pilei fan-shaped to irregularly semicircular, occasionally circular with a depressed center, projecting up to 5.8 cm long, 8.7 cm wide and 3 mm thick at base. Pileal surface white when fresh, becoming orange brown and finally black when dry, glabrous, occasionally zonate and with radially aligned stripes; margin straight. Pore surface white when young, becoming white to pale mouse-grey when mature; pores suborbicular, 7–9 per mm; dissepiments thin, entire. Context white when fresh, becoming buff when dry, up to 1 mm thick. Tubes concolorous with pore surface, decurrent on one side of the stipe, up to 2 mm thick. Stipe white with a black base when young, becoming entirely black when mature, bearing a black cuticle, glabrous, up to 1.5 cm long and 1 cm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.
Figure 7 – Microscopic structures of *Picipes annularius*. A Basidiospores. B Basidia and basidioles. C Hyphae from context. D Hyphae from trama. E Hyphae from stipe. Scale bars = 10 μm.

Context – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 1.2–4.3 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, with arboriform branches, strongly interwoven, 1.5–6.5 μm in diam. Hyphae in cuticle with olivaceous buff to light black inclusion inside, slightly thick-walled with a wide lumen, simple-septate, 3–4.5 μm in diam.

Tubes – Generative hyphae frequent, colorless, thin-walled, frequently branched, 1.5–5.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid,
with arboriform branches, strongly interwoven, 1–5 μm in diam. Cystidia absent; cystidioles subulate, 13.5–19.5 × 4–5 μm. Basidia clavate, with a basal clamp connection and four sterigmata, 11.2–18.5 × 6.1–8.2 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 1–3.7 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, with arboriform branches, strongly interwoven, 1–5 μm in diam. Hyphae in cuticle with olivaceous buff to light black inclusion inside, slightly thick-walled with a wide lumen, frequently branched, simple-septate, 1–5.6 μm in diam.

Basidiospores – Basidiospores cylindrical, colorless, thin-walled, smooth, frequently bearing one or more guttules, IKI–, CB–, (5.2–)5.6–7(–7.3) × (2.3–)2.4–3(–3.1) μm, L = 6.21 ± 0.39 μm, W = 2.74 ± 0.15 μm, Q = 2–2.63, Qm = 2.27 ± 0.14 (n=144/2).

**Figure 8** – Microscopic structures of *Picipes atratus*. A Basidiospores. B Basidia and basidioles. C Cystidioles. D Hyphae from context. E Hyphae from trama. F Hyphae from stipe. Scale bars = 10 μm.
Rot type – A white rot.

Known distribution – Subtropical regions of China.

Materials examined – China, Fujian Province, Wuping County, Liangyeshan Nature Reserve, on living angiosperm tree, 25 Oct 2013, B.K. Cui, Cui 11289 (BJFC, holotype); Anhui Province, Qimen County, Gunujiang Nature Reserve, on rotten angiosperm wood, 9 Aug 2013, Y.C. Dai, Dai 13375 (BJFC, paratype).

Notes – *Picipes atratus* is a special subtropical species with a black pileus and stipe in mature specimens. It is morphologically similar to *P. blanchettianus* Berk. & Mont. for the black pileus, black short stipe and similar pore size (7–10 per mm), but the absence of cystidioles, smaller basidia (10–11 × 5–6 μm) and basidiospores (5–6.2 × 2.2–2.5 μm) of *P. blanchettianus* are different from *Pi. atratus* (Ryvarden & Johansen 1980). Based on our own specimens, *Pi. badius* (Pers.) Zmitr. et Kovalenko also has blackish basidiomata when old, but it’s simple-septate generative hyphae, absence of cystidioles, larger pores (5–6 per mm) and basidia (20–30 × 7–9 μm) are different from *Pi. atratus*.

**Picipes auriculatus** B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559398; Facesoffungi number: FoF 10646

Etymology – *auriculatus* (Lat.): referring to the auricular basidiomata.

Basidiomata – Annual, laterally stipitate, solitary, coriaceous when fresh, woody hard when dry. Pilei auricular to fan-shaped, about 1.7–5 cm long, 1–3 cm wide, and up to 4.5 mm thick at base. Pileal surface blackish red to black towards the stipe when fresh, becoming brownish red to yellowish brown towards the margin when dry, glabrous, with radially aligned stripes; margin incurved upon drying. Pore surface light ivory to honey buff when dry; pores circular to subcircular, 4–6 per mm; dissepiments thin, entire. Context light ivory to buff when dry, woody hard upon drying, up to 3 mm thick. Tubes concolorous with pore surface, up to 1.5 mm thick. Stipe very short or forming a flattened base, bearing a black cuticle, up to 3 mm long and 4.5 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

Context – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 1.8–6 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, frequently branched, interwoven, 1.3–8.2 μm in diam, rarely inflated at the branching area. Hyphae in cuticle towards the stipe with buff yellow to reddish brown inclusion inside, thick-walled with a wide lumen, bearing clamp connections, 2.2–7.5 μm in diam.

Tubes – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 1.3–5.9 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, with dendroid branches, strongly interwoven, 1.3–7.1 μm in diam. Cystidia and cystidioles absent. Basidia infrequent, clavate, with a basal clamp connection and four sterigmata, 13.3–17.6 × 5.5–7.5 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 1.6–4.8 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen, frequently branched, interwoven, 1.6–6 μm in diam. Hyphae in cuticle with buff yellow to brown inclusion inside, thick-walled with a wide lumen, bearing clamp connections, 4–8.8 μm in diam.

Basidiospores – Basidiospores cylindrical, rarely oblong, colorless, thin-walled, smooth, frequently bearing two guttules, IKI–, CB–, (5.4–)5.8–6.8(−7) × (2.4–)2.5–3.2(−3.4) μm, L = 6.27 ± 0.35 μm, W = 2.82 ± 0.21 μm, Q = 1.8–2.69, Qm = 2.24 ± 0.18 (n=72/2).

Rot type – A white rot.

Known distribution – Tropical regions of China.

Materials examined – China, Hainan Province, Baisha County, Yinggeling Nature Reserve, on fallen angiosperm branch, 17 Nov 2015, B.K. Cui, Cui 13616 (BJFC, holotype); Changjiang County, Bawangling Nature Reserve, on fallen angiosperm branch, 12 Nov 2007, H.S. Yuan, Yuan 4221 (IFP, paratype).
Figure 9 – Microscopic structures of *Picipes auriculatus*. A Basidiospores. B Basidia and basidioles. C Hyphae from context. D Hyphae from trama. E Hyphae from cuticle of stipe. F Hyphae from stipe. Scale bars = 10 μm.

Notes – *Picipes auriculatus* is a tropical species with an auricular basidiomata, yellowish brown to black pileus and a very short black stipe. *Picipes subtubaeformis* J.L. Zhou & B.K. Cui resembles *Pi. auriculatus* by sharing similar pores (4–6 per mm) and basidiospores (5.7–6.8 × 2.7–3.1 μm, Zhou et al. 2016a), but its central to lateral stipe, subulate cystidioles, longer basidia (15.7–29 × 5.1–6.2 μm) and subtropical distribution are different from *Pi. auriculatus*. *Picipes subtropicus* J.L. Zhou & B.K. Cui also has blackish pileal surface towards the stipe, a very short black stipe, similar basidiospores (5.1–6.2 × 2.2–2.7 μm) and subtropical distribution; however, the fan-shaped to semicircle basidiomata and subulate cystidioles (Zhou et al. 2016a) are different from *Pi. auriculatus*.

*Picipes brevistipitatus* B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559399; Facesoffungi number: FoF 10647
Etymology – *brevistipitatus* (Lat.): referring to the basidiomata rising from a very short stipe.

Basidiomata – Annual, laterally stipitate, solitary, woody hard when dry. Pilei fan-shaped to irregularly semicircular, projecting up to 2 cm long, 3.1 cm wide and 4.5 mm thick at base. Pileal surface cream, buff to olivaceous buff when dry, glabrous, occasionally zonate and with radially aligned stripes; margin straight. Pore surface pale mouse-grey when dry; pores suborbicular, 3–6 per mm; dissepiments thin, entire. Context buff when dry, woody hard upon drying, up to 2.5 mm thick. Stipe very short or forming a flattened base, concolorous with pileal surface, glabrous, up to 4 mm long and 8.5 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

Figure 10 – Microscopic structures of *Picipes brevistipitatus*. A Basidiospores. B Basidia and basidioles. C Cystidia. D Hyphae from context. E Hyphae from trama. F Hyphae from stipe. Scale bars = 10 μm.
Context – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 1.5–3.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen or solid, with arboriform branches, strongly interwoven, 1.5–4 μm in diam.

Tubes – Generative hyphae frequent, colorless, thin-walled, occasionally branched, 1.5–5.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen or solid, with arboriform branches, strongly interwoven, 1–6 μm in diam. Cystidia absent; cystidioles subulate, 15–25.5 × 4.5–5.8 μm. Basidia oblong to clavate, with a basal clamp connection and four sterigmata, 12.5–15.5 × 4.8–9.6 μm; basidioles clavate, slightly smaller than basidia.

Stipe – Generative hyphae frequent, colorless, thin-walled, rarely branched, 1.5–3.6 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen or solid, moderately branched, interwoven, 1–4.5 μm in diam.

Basidiospores – Basidiospores cylindrical, rarely oblong, colorless, thin-walled, smooth, frequently bearing one or more guttules, IKI–, CB–, (5.7–5.9–7.1(7.7) × (2.6–2.7–3.4(3.8) μm, L = 6.54 ± 0.39 μm, W = 2.98 ± 0.22 μm, Q = 1.84–2.73, Qm = 2.2 ± 0.15 (n = 85/3).

Rot type – A white rot.

Known distribution – Tropical and subtropical regions of China.

Materials examined – China, Hainan Province, Qiongzhong County, Limushan Forest Park, on fallen angiosperm branch, 18 Nov 2015, B.K. Cui, Cui 13652 (BJFC, paratype); Fujian Province, Xiamen, Xiamen Botanical Garden, on fallen angiosperm branch, 27 Oct 2013, B.K. Cui, Cui 11345 (BJFC, paratype).

Notes – Picipes brevistipitatus is a species collected from subtropical and tropical regions of China, it is characterized by the very short stipe that concolorous with pileus, cream to buff pileal surface, festucine to honey yellow when dry. This species is similar to Pi. pumilus (Y.C. Dai & Niemelä) J.L. Zhou & B.K. Cui, both of them have light colored pileus, pale porus surface and similar basidiospores; however, Pi. pumilus has smaller pores (8–10 per mm), lacks radially aligned stripes on the pileal surface and absence of cystidioles (Dai et al. 2003). Polyporus gayanus Lév. also has a very short stipe, but its larger pores (2–3 per mm), orbicular basidiomata, light brown pileus with dark fibrils towards the margin and larger basidia (17.5–20 × 6.5 μm, Núñez & Ryvarden 1995a) are different from Pi. brevistipitatus.

**Picipes nigromarginatus** B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559400; Facesoffungi number: FoF 10648

Etymology – nigromarginatus (Lat.): referring to the black margin of the basidiomata when dry.

Basidiomata – Annual, laterally stipitate, solitary, coriaceous when fresh and hard corky when dry. Pilei fan-shaped to semicircular, projecting up to 2.2 cm long, 3.4 cm wide and 3 mm thick at base. Pileal surface festucine to honey-yellow when fresh, becoming reddish brown when dry, glabrous, zonate, with radially aligned stripes; margin black, straight. Pore surface greyish buff when dry; pores subcircular, 7–9 per mm; dissepiments thin, entire. Context buff and woody hard corky upon drying, up to 2 mm thick. Tubes clay brown and hard corky upon drying, less than 1.5 mm thick, decurrent on one side of the stipe. Stipe short, concolorous with pileal surface, glabrous, up to 5 mm long and 4 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

Context – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 2–6.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, moderately branched, interwoven, 1.5–4.8 μm in diam.

Tubes – Generative hyphae frequent, usually present near hymenium, colorless, thin-walled, 1.8–4.2 μm in diam; skeleto-binding hyphae dominant, thick-walled with a wide to narrow lumen, with dendroid branches, strongly interwoven, 1.2–6.6 μm in diam. Cystidia absent; cystidioles...
frequent, subulate, 14.2–17.2 × 4.7–5.5 μm. Basidia clavate, with a basal clamp connection and four sterigmata, 11.4–18.7 × 6.2–7.9 μm; basidioles in shape similar to basidia, but slightly smaller.

**Figure 11** – Microscopic structures of *Picipes nigromarginatus*. A Basidiospores. B Basidia and basidioles. C Cystidioles. D Hyphae from context. E Hyphae from trama. F Hyphae from stipe. Scale bars = 10 μm.

Stipe – Generative hyphae infrequent, colorless, thin-walled, rarely branched, 1.8–5.1 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, moderately branched, interwoven, 1.3–5.1 μm in diam.

Basidiospores – Basidiospores cylindrical, colorless, thin-walled, smooth, frequently bearing one or two guttules, IKI−, CB− or slightly CB+, (5.2−)5.6–6.9(−7.4) × 2.3–3(−3.2) μm, L = 6.31 ± 0.55 μm, W = 2.64 ± 0.22 μm, Q = 2.03–2.87, Qm = 2.4 ± 0.2 (n=37/1).

Rot type – A white rot.

Known distribution – Subtropical regions of China.
Materials examined – China, Yunnan Province, Baoshan, Gaoligongshan Nature Reserve, on fallen angiosperm branch, 25 Oct 2009, B.K. Cui, Cui 8113 (BJFC, holotype), 26 Oct 2009, B.K. Cui, Cui 8191 (BJFC, paratype).

Notes – *Picipes nigromarginatus* is a subtropical species that lacks a brown to black cuticle on the stipe. It can be identified by the reddish brown pileal edge and laterally short stipe. *Picipes nigromarginatus* phylogenetically clustered with *Pi. brevistipitatus* (Figs 2, 3), they sharing similar pileus and basidiospores, but the larger pores (3–6 per mm) and buff pileal margin of *Pi. brevistipitatus* are different from *Pi. nigromarginatus*. *Picipes fraxinicola* (L.W. Zhou & Y.C. Dai) J.L. Zhou & B.K. Cui also has a laterally short stipe without a black cuticle, but it differs from *Pi. nigromarginatus* in the larger pores (2–4 per mm), larger basidiospores (5–8 × 2.8–3.7 μm), absence of cystidioles and temperate distribution (Dai 1999).

*Picipes wuyishanensis* B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559401; Facesoffungi number: FoF 10649

Etymology – *wuyishanensis* (Lat.): referring to the locality (Wuyishan) of the type specimen.

Basidiomata – Annual, laterally stipitate, solitary, hard corky when dry. Pilei semicircular, projecting up to 2.9 cm long, 3.9 cm wide and 6 mm thick at base. Pileal surface buff towards the stipe and darker towards the margin when dry, glabrous; margin brownish red to black, with radially aligned stripes, straight. Pore surface beige grey to pearl beige when dry; pores angular, 3–5 per mm; dissepiments thin, entire. Context buff to buff yellow when dry, hard corky, up to 3 mm thick. Tubes concolorous with pore surface, up to 4 mm thick. Stipe short, concolorous with the pileal surface, bearing a black cuticle at the base, up to 5 mm long and 1 cm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeletal-binding hyphae IKI–, slightly CB+; tissues unchanged in KOH.

Context – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 2–6.5 μm in diam; skeletal-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, frequently branched, strongly interwoven, 1.3–7.4 μm in diam.

Tubes – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 2–4.2 μm in diam; skeletal-binding hyphae dominant, colorless, thick-walled with a narrow lumen to solid, with dendroid branches, strongly interwoven, 1.5–5.5 μm in diam. Cystidia absent; cystidioles frequent, subulate, 12.3–24 × 4–6.9 μm. Basidioles infrequent, oblong to clavate, with a basal clamp connection and four sterigmata, 11–14.5 × 6.2–8.9 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae infrequent, colorless, thin-walled, occasionally branched, 2.5–5 μm in diam; skeletal-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, frequently branched, strongly interwoven, 1.5–4.8 μm in diam. Hyphae in cuticle with brown inclusion inside, slightly thick-walled with a wide lumen, simple-septate, 2.2–5.4 μm in diam.

Basidiospores – Basidiospores cylindrical, colorless, thin-walled, smooth, frequently bearing two guttules, IKI–, CB–, (5.6–)6–6.9(–7.4) × (2.4–)2.5–3(–3.4) μm, L = 6.42 ± 0.37 μm, W = 2.76 ± 0.2 μm, Q = 2–2.77, Qm = 2.33 ± 0.17 (n = 72/2).

Rot type. A white rot.

Known distribution – Subtropical regions of China.

Materials examined – China, Fujian Province, Wuyishan, Wuyishan Nature Reserve, on dead angiosperm tree, 22 Oct 2005, Y.C. Dai, Dai 7409 (IFP, holotype), on fallen angiosperm branch, 21 Oct 2013, B.K. Cui, Cui 11246 (BJFC, paratype).

Notes – *Picipes wuyishanensis* is well characterized by its buff pileus with radially aligned stripes, broad and short stipe with a black base. It has a close relationship with *Pi. annularius* according to the phylogenetic analyses (Figs 2, 3). Morphologically, both of them have laterally stipitate basidiomata, similar pore size and basidiospores, but the beige to cinnamon-buff small squamae on pileus and absence of cystidioles in *Pi. annularius* are different from *P. wuyishanensis*.
Figure 12 – Microscopic structures of *Picipes wuyishanensis*. A Basidiospores. B Basidia and basidioles. C Cystidioles. D Hyphae from context. E Hyphae from trama. F Hyphae from stipe. Scale bars = 10 μm.

*Polyporus auratus* B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.  
Index Fungorum number: IF559402; Facesoffungi number: FoF 10650  
Etymology – *auratus* (Lat.): referring to the golden yellow basidiomata when dry.  
Basidiomata – Annual, centrally stipitate, gregarious, fleshy when fresh, becoming fragile and light in weight upon drying. Pilei flat with a depressed center when fresh, occasionally becoming infundibuliform upon drying, 1.7–6 cm in diam, up to 4 mm thick. Pileal surface cream to buff when fresh, becoming golden yellow when dry, glabrous, azonate, shining when dry; margin straight when fresh, in-curved upon drying. Pore surface white when fresh, becoming cinnamon when dry; pores angular, 3–4 per mm; dissepiments thin, entire to lacerate. Context white to cream when fresh, becoming buff when dry, up to 3.5 mm thick. Tubes concolorous with pore surface, fragile, decurrent, up to 1 mm thick. Stipe cylindrical, cream when fresh, buff to beige upon drying, up to 4 cm long and 6.5 mm in diam.
Hyphal structure – Hyphal system dimitic in trama and stipe, monomitic in context; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

Context – Generative hyphae colorless, slightly thick-walled, occasionally branched, with tapering ends, 3.8–12.1 μm in diam, occasionally inflated up to 19 μm in diam.

Tubes – Generative hyphae frequent, colorless, slightly thick-walled, occasionally branched, 1.5–6.8 μm in diam; skeleto-binding hyphae frequent, colorless, thick-walled with a wide lumen, occasionally branched, interwoven, 2–12.1 μm in diam, occasionally inflated up to 18 μm in diam. Cystidia and cystidioles absent. Basidia infrequent, clavate, with a basal clamp connection and four sterigmata, 15.3–26.7 × 6–9.1 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae frequent, colorless, slightly thick-walled, occasionally branched, 3.5–7.8 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, occasionally branched, interwoven, 2.5–24.5 μm in diam, occasionally inflated up to 34.5 μm in diam.

Basidiospores – Basidiospores cylindrical, rarely oblong, colorless, thin-walled, smooth, frequently bearing two guttules, IKI–, CB–, (6.9–)7.7–10 × 3–3.9 μm, L = 8.66 ± 0.67 μm, W = 3.45 ± 0.24 μm, Q = 2.1–2.93, Qm = 2.52 ± 0.2 (n = 57/1).

Rot type – A white rot.

Known distribution – Tropical regions of China.

Materials examined – China, Hainan Province, Changjiang County, Bawangling Nature Reserve, on rotten angiosperm wood, 16 Jun 2014, Y.C. Dai, Dai 13665 (BJFC, holotype), on fallen angiosperm branch, 18 Jun 2016, B.K. Cui, Cui 13878a (BJFC, paratype).

Notes – Polyporus auratus is characterized by its golden yellow and fragile basidiomata in dried condition. According to the phylogenetic analyses (Figs 2, 3), P. auratus is strongly clustered in the core polyporus clade with P. tuberaster and other four species. Morphologically, P. auratus is similar to P. corylinus Mauri for their glabrous and cream to buff pileal surface, circular pileus, white to cream pore surface and central stipe, but the later has larger pores (1 per mm; Núñez & Ryvarden 1995a) and smaller basidiospores (6–7.5 × 2–3 μm; Núñez & Ryvarden 1995a). Polyporus craterellus Berk. & M.A. Curtis resembles P. auratus by sharing centrally stipitate, flat pileus, fragile basidiomata upon drying and inflated skeleto-binding hyphae, but its basidiospores (10–14 × 4–6 μm; Núñez & Ryvarden 1995a) are much larger than P. auratus.

Polyporus austrosinensis B.K. Cui, Xing Ji & J.L. Zhou, sp. nov. Figs 5E, 14

Index Fungorum number: IF559403; Facesoffungi number: FoF 10651

Etymology – austrosinensis (Lat.): referring to the species geographically distributed in southern China.

Basidiomata – Annual, centrally stipitate, solitary, fleshy to soft leathery when fresh, becoming fragile when dry. Pilei horn-shaped or flat with a depressed center, up to 6.3 cm in diam and 2 mm thick. Pileal surface cream, beige, buff yellow to orange when fresh, becoming buff to honey yellow when dry, glabrous, usually azonate; margin sharp, straight when fresh, incurved upon drying. Pore surface white when fresh, becoming yellow when bruised, turning to light ivory to buff when dry; pores angular, 4–7 per mm; dissepiments thin, entire. Context white, fleshy to soft leathery when fresh, becoming cream to ivory, fragile when dry, up to 2 mm thick. Tubes concolorous with pore surface or slightly lighter, decurrent, very thin, fragile when dry, less than 0.5 mm. Stipe white to ivory at the upper part and brown at the lower part when fresh, becoming ivory to buff at the upper part and beige brown to brown at the lower part when dry, glabrous, 1.5–3 cm long and 2.5–10 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI–, CB+; tissues unchanged in KOH.

Context – Generative hyphae frequent, colorless, thin-walled, frequently branched, 2–8.8 μm in diam, occasionally inflated up to 14.8 μm in diam; skeleto-binding hyphae dominant, colorless,
thick-walled with a wide lumen, moderately branched, interwoven, 1.5–10 μm in diam, occasionally inflated up to 19 μm in diam.

Figure 13 – Microscopic structures of *Polyporus auratus*. A Basidiospores. B Basidia and basidioles. C Hyphae from context. D Hyphae from trama. E Hyphae from stipe. Scale bars = 10 μm.

Tubes – Generative hyphae frequent, colorless, thin-walled, frequently branched, 2–5.5 μm in diam, occasionally inflated up to 8.7 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide lumen, moderately branched, interwoven, 1.5–7 μm in diam. Cystidia absent; cystidioles infrequent, bacciliform, 33–45 × 5.4–6.5 μm. Basidia clavate, with a basal clamp
connection and four sterigmata, 22–45 × 7.5–9.8 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae frequent, colorless, thin-walled, occasionally branched, 3–8.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, infrequently branched, interwoven, 1.5–9 μm in diam, occasionally inflated up to 12.2 μm in diam. Hyphae in cuticle with brown beige to light brown inclusion inside, thick-walled with a wide lumen, bearing clamp connections, 2.3–5.6 μm in diam.

Basidiospores – Basidiospores cylindrical, colorless, thin-walled, smooth, occasionally bearing one small guttule, IKI–, CB–, (6.7–)7.5–10.6(–11.2) × (2.9–)3.3–4.4(–4.9) μm, L = 9.05 ± 0.87 μm, W = 3.82 ± 0.42 μm, Q = 2–2.86, Qm = 2.4 ± 0.21 (n = 69/2).

Figure 14 – Microscopic structures of *Polyporus austrosinensis*. A Basidiospores. B Basidia and basidioles. C Cystidioles. D Hyphae from context. E Hyphae from trama. F Hyphae from stipe. Scale bars = 10 μm.
Rot type – A white rot.

Known distribution – Tropical and subtropical regions of China.

Material examined – China, Yunnan Province, Nanhua County, Dazhongshan Nature Reserve, on fallen angiosperm branch, 15 Jul 2013, B.K. Cui, Cui 11126 (BJFC, holotype), Cui 11123 (BJFC, paratype), Cui 11140 (BJFC, paratype); Hainan Province, Wuzhishan, Wuzhishan Nature Reserve, on angiosperm stump, 19 Nov 2015, B.K. Cui, Cui 13675 (BJFC, paratype).

Notes – *Polyporus austrosinensis* was found in subtropical to tropical regions of China, it is characterized by the fleshy to soft corky basidiomata when fresh, glabrous and cream to orange pileal surface, white pore surface which changed to yellow when bruised. Phylogenetic analyses (Figs 2 and 3) revealed that *P. austrosinensis* has a close relationship with *P. mangshanensis* B.K. Cui, J.L. Zhou & Y.C. Dai; morphologically, *P. austrosinensis* and *P. mangshanensis* share similar basidiospores and pores sizes, brown to dark brown stipe, glabrous pileal surface and inflated hyphae; however, *P. mangshanensis* has both clamped and simple-septate generative hyphae, eccentrical to almost lateral stipe, smaller basidia (16.5–24 × 7–10 μm) and corky basidiomata when dry (Hyde et al. 2016). *Polyporus auratus* is similar to *P. austrosinensis* in having similar basidiomata of similar shape, white pore surface, inflated skeleto-binding hyphae, and basidiospores; however, *P. auratus* has larger pores (3–4 per mm), light colored stipe and lacks cystidioles.

*Polyporus lamelliporus* B.K. Cui, Xing Ji & J.L. Zhou, sp. nov.

Index Fungorum number: IF559404; Facesoffungi number: FoF 10652

Etymology – *lamelliporus* (Lat.): referring to the pores elongate and lacerate to form a lamellae-shaped structure.

Basidiomata – Annual, centrally stipitate, gregarious or clustered, corky to slightly fragile when dry. Pilei flat with a depressed center or infundibuliform, up to 5.2 cm in diam and 2 mm thick. Pileal surface cream to buff yellow when dry, glabrous and azonate; margin sharp, incurved upon drying. Pore surface cream buff yellow to light brown when dry; pores angular, usually elongate and lacerate to form lamellae-shaped hymenophores, 0.5–1 per mm, occasionally elongated to 3 mm long and 1.5 mm wide; dissepiments thin, entire to lacerate. Context cream to light ivory when dry, corky upon drying, up to 0.5 mm thick. Tubes lighter than pore surface, fragile when dry, decurrent, up to 1.8 mm thick. Stipe white to cream towards the tubes, brown to black at the lower part, glabrous, 1–3.5 cm long and 2.5–6 mm in diam.

Hyphal structure – Hyphal system dimitic; generative hyphae bearing clamp connections; skeleto-binding hyphae IKI−, slightly CB+; tissues unchanged in KOH.

Context – Generative hyphae frequent, colorless, thin-walled, frequently branched, 2–6 μm in diam, occasionally inflated up to 15.3 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide lumen, moderately branched, interwoven, 1.5–8 μm in diam, occasionally inflated up to 19 μm in diam in branching area.

Tubes – Generative hyphae frequent, colorless, thin-walled, frequently branched, 2–5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, moderately branched, interwoven, 1.5–5 μm in diam. Cystidia and cystidioles absent. Basidia clavate, with a basal clamp connection and four sterigmata, 27–40 × 8–9.8 μm; basidioles in shape similar to basidia, but slightly smaller.

Stipe – Generative hyphae frequent, colorless, thin-walled, rarely branched, 2–11.5 μm in diam; skeleto-binding hyphae dominant, colorless, thick-walled with a wide to narrow lumen, moderately branched, interwoven, 1.3–8.5 μm in diam, occasionally inflated up to 12 μm in diam in branching area. Hyphae in cuticle with olive yellow to light brown inclusion inside, thick-walled with a wide lumen, bearing both clamp connections and simple-septa, 2.5–8 μm in diam.

Basidiospores – Basidiospores cylindrical, colorless, thin-walled, smooth, frequently bearing one or more guttules, IKI−, CB−, (7.9–)8.4–10.7(–11.5) × (3.3–)3.7–4.7(–4.7) μm, L = 9.42 ± 0.71 μm, W = 4.2 ± 0.25 μm, Q = 2–2.67, Qm = 2.25 ± 0.15 (n = 103/3).
Figure 15 – Microscopic structures of *Polyporus lamelliporus*. A Basidiospores. B Basidia and basidioles. C Hyphae from context. D Hyphae from trama. E Hyphae from stipe. F Hyphae from cuticle of stipe. Scale bars = 10 μm.

Rot type – A white rot.

Known distribution – Tropical and subtropical regions of China.

Material examined – China, Hunan Province, Yizhang County, Mangshan Nature Reserve, on fallen bamboo, 15 Aug 2014, Y.C. Dai, Dai 15106 (BJFC, holotype), Dai 15103 (BJFC, paratype); Yunnan Province, Menghai County, Mangao Nature Reserve, on fallen angiosperm branch, 8 Jun 2011, Y.C. Dai, Dai 12327 (BJFC, paratype).

Notes – *Polyporus lamelliporus* was collected on both bamboo and hardwoods, it is characterized by centrally stipitate basidiomata with light-colored pileus, lamellae-shaped hymenophores, and brown to black stipe. *Polyporus meridionalis* (A. David) H. Jahn is similar to *P. lamelliporus* by sharing central and brown stipe, flat to infundibuliform pileus, large pores and inflated hyphae; but, the white pore surface and ellipsoid to amygdaliform basidiospores (7–9 ×
3.5–4 μm, Núñez & Ryvarden 1995a) are different from *P. lamelliporus*. *Polyporus phyllostachydis* Sotome, T. Hatt. & Kakish. was also collected from bamboo, its central stipitate basidiomata, brown to black stipe, glabrous pileus, and thick-walled skeleto-binding hyphae with a wide to narrow lumen are similar to *P. lamelliporus*; however, the former has both smaller pores (3–4 per mm) and basidiospores (5–7 × 2.5–4 μm), and simple-septate generative hyphae (Sotome et al. 2007). *Polyporus lamelliporus* resembles *P. guianensis* Mont. by sharing black stipe, light brown pore surface and yellowish pileal surface, but the later has somewhat smaller pores (1–2 per mm), shorter basidia (21–27 × 8–10 μm) and solid skeleto-binding hyphae (Núñez & Ryvarden 1995a, b).

**New combinations**

**Picipes dictyopus** (Mont.) B.K. Cui, Xing Ji & J.L. Zhou, comb. nov.

Index Fungorum number: IF559405; Facesoffungi number: FoF 10653

Basionym – *Polyporus dictyopus* Mont., Annales des Sciences Naturelles Botanique 3: 349. 1835.

≡ *Melanopus dictyopus* (Mont.) Pat., Essai taxonomique sur les familles et les genres des Hyménomycètes: 80. 1900.

Notes – In our previous study, *Picipes dictyopus* was clustered in the squamosus clade but with low supports (Zhou et al. 2016a). But, after adding more species collected from China, the sequence of *Pi. dictyopus* from type locality (Chile, Palacio et al. 2017) strongly clustered in the picipes clade (Figs 2, 3).

**Picipes subdictyopus** (H. Lee, N.K. Kim & Y.W. Lim) B.K. Cui, Xing Ji & J.L. Zhou, comb. nov.

Index Fungorum number: IF559406; Facesoffungi number: FoF 10661

Basionym – *Polyporus subdictyopus* H. Lee, N.K. Kim & Y.W. Lim, Fungal Diversity 83: 228. 2017.

Materials examined – China, Shaanxi Province, Zhashui County, Niubeiliang Forest Park, on living tree of *Prunus*, 16 Sep 2013, B.K. Cui, Cui 11220 (BJFC); Yunnan Province, Binchuan County, Jizu Mountain, on fallen angiosperm branch, 8 Sep 2015, B.K. Cui, Cui 12539 (BJFC); Jingdong County, Ailaoshan Nature Reserve, on fallen angiosperm branch, 10 Sep 2015, B.K. Cui, Cui 12593 (BJFC).

Notes – *Polyporus subdictyopus* was originally described from Korea (Tibpromma et al. 2017). Our specimens have almost the same micro-features and ITS sequences with the holotype, SFC20130719-53. However, our specimens have larger pores (4–6 per mm) and slightly shorter basidiospores (6.4–8.1 × 2.4–3.5 μm) than those given in the original description (pores 8–10 per mm, basidiospores 6.8–9.1 × 2.2–2.8 μm, Tibpromma et al. 2017).

**Picipes ulleungus** (H. Lee, N.K. Kim & Y.W. Lim) B.K. Cui, Xing Ji & J.L. Zhou, comb. nov.

Index Fungorum number: IF559407; Facesoffungi number: FoF 10654

Basionym – *Polyporus ulleungus* H. Lee, N.K. Kim & Y.W. Lim, Fungal Diversity 83: 229. 2017.

Material examined – China, Zhejiang Province, Qingyuan County, Baishanzu Nature Reserve, on fallen branch of *Cyclobalanopsis*, 12 Aug 2015, B.K. Cui, Cui 12410 (BJFC).

Notes – *Polyporus ulleungus* was originally described from Korea (Tibpromma et al. 2017). Our specimen has very similar character and almost the same ITS sequences with the holotype, SFC20120814-41. However, our specimen has larger basidiospores (7.5–9.7 × 3–3.7 μm) than that given in the original description (6.8–8 × 2.3–3.3 μm, Tibpromma et al. 2017).

**Lentinus thailandensis** (Sotome) B.K. Cui, Xing Ji & J.L. Zhou, comb. nov.

Index Fungorum number: IF559408; Facesoffungi number: FoF 10655

Basionym – *Polyporus thailandensis* Sotome, Mycoscience 57: 86. 2016.
Material examined – China, Yunnan Province, Xishuangbanna, Jinghong, Lvshilin Forest Park, on fallen bamboo, 4 Aug 2005, Y.C. Dai, Dai 6722 (BJFC).

Notes – *Lentinus thailandensis* was originally collected on hardwood from northeast Thailand (Sotome et al. 2016). But the specimen we collected from Xishuangbanna, located in tropical areas of China, grows on fallen bamboo. Our specimen has almost the same macro-features and ITS and nLSU sequences with the holotype, MSUT_6734. However, the basidiospores (6.3–7.8 × 2.9–4.0 μm) of our specimen are much smaller than those given in the original description (7–10.5 × 3–4.5 μm; Sotome et al. 2016).

**Discussion**

**Divergence times**

Because of lacking enough fossils, molecular clocks calibrated by the existing fossils are the only available tools to estimate timing of evolutionary events in fungi (Berbee & Taylor 2010). Based on the calibrations of two fossils of Agaricales and Hymenochaetales, we obtained the diverging relationships between *Polyporus* and its allied genera. Moreover, the divergence times of the main clades of Polyporales were also proved here.

Hibbett & Matheny (2009) considered that the Agaricales is significantly older than the rosids while Boletales appears to be young enough to have been primatively associated with Pinaceae. Previous results confirmed that the origin of crown group rosids ranged from 110 to 93 Mya (Wang et al. 2009) while the crown group Pinaceae diverged 184 or 136 Mya (Gernandt et al. 2008). Our results well conformed to the analyses provided by Hibbett & Matheny (2009).

Hennig (1966) first proposed that taxonomic ranking should represent its geological age. Then, Avise & John (1999) presented a scaling of taxonomic ranks by using the gene-specific molecular clocks, and proposed that each taxonomic genus might signify membership in a clade whose lineages shared a most recent common ancestor in the Pliocene (ca. 2–5 Mya), and each taxonomic order could indicate a clade whose coalescent node fell in the Jurassic (ca. 145–205 Mya). But these scales are not applicable to all the organisms (Zhao et al. 2016). Recently, Zhao et al. (2016, 2017) proposed a series of divergence time scales for different group of fungi.

In the present study, Polyporales is estimated to have a common ancestor evolved during the early Cretaceous. This result matched the divergence time ranges of orders proposed by Zhao et al. (2017). Although there are many species of Polyporales growing on gymnosperm substrates, most members of this order are limited on angiosperms or both on angiosperms and gymnosperms. So, we compared the divergence times of different clades of Polyporales with the originating and diversifying times of angiosperms (Fig. 1). The oldest fossil of angiosperms was dated to 136 Mya, and previously many botanists considered that angiosperms originated during the early Cretaceous (ca. 140–135 Mya; Brenner 1974, Gübeli et al. 1984, Hughes & McDougall 1987, Thusu et al. 1988), and rapidly diversified and dominated in the world during the early to middle Cretaceous (ca. 130–83 Mya; Lidgard & Crane 1988, Crane et al. 1995, Grimaldi 1999). But, based on the analysis of a three-gene dataset, Wikström et al. (2001) proved that the origin of the crown group of extant angiosperms dated to the early to middle Jurassic (ca. 179–158 Mya). Recently, many other botanists also confirmed the crown age for the angiosperms was at least 160 Mya (Moore et al. 2007, Smith et al. 2010, Bell et al. 2010, Magallón 2010, Doyle 2012, Zhang et al. 2012, Magallón et al. 2013, Zeng et al. 2014). According to the analysis of plastid genomes, Moore et al. (2007) confirmed that a rapid diversification of angiosperms occurred between 143.8 and 140.3 Mya. Our analysis indicates that the Polyporales originated at the beginning of the period when angiosperms rapidly diversifying, and then occurred a rapid diversification during the period when angiosperms dominated in the world. The inferred origination and rapid diversification of Polyporales corresponded with the variety and rapid rise of angiosperm-dominated forests may explain why most Polyporales spp. prefer to grow on the angiosperm woods.

As the saprotrophic wood-decay fungi, Polyporales spp. play a key role as decomposers and habitat creators in forest ecosystems (Binder et al. 2013, Norros et al. 2015). The great majority
members of Polyporales can be divided into two major groups: white-rot and brown-rot (Binder et al. 2013). According to our analysis (Fig. 1) based on the 5.8S+nLSU+EF1-α+RPB1+RPB2+nSSU dataset, it seems that species of Polyporales evolved from a common ancestor during the beginning of the Cretaceous, and then parallel diverged into the white-rot group and the brown-rot group at about 124 Mya and the core polyporoid clade, which is now treated as the Polyporaceae (Justo et al. 2017), diverged during the middle Cretaceous.

According to the divergence time estimation of Polyporus s. lat. in the current study, the six major clades of Polyporus are well supported as allied lineages originated during the early to middle Paleogene period. The divergence times of the picipes clade, the favolus clade, the neofavolus clade and the lentinus clade could effectively support the existence of the four specific genera, Picipes, Favolus, Neofavolus and Lentinus. In the squamosus clade, Datronia and several other genera are included, while most of them diverged less than 30 Mya. On the basis of the view proposed by Zhao et al. (2016), Datronia and other genera should be treated as subgenera of Cerioporus for their stem ages ca. 30 Ma. But, species in this clade is not monophyletic taxa and the genera gathered in this clade are morphologically different from each other. Though Zmitrovich & Kovalenko (2016) support the view combine species in squamosus clade into Cerioporus, we prefer not to treat this clade as a specific genus before more comprehensive phylogenetic and morphologic evidences are provided.

**Phylogenetic analyses**

Phylogenetic analyses of the genus Polyporus and related genera based on 8-gene loci (ITS, nLSU, nSSU, mtSSU, EF1-α, RPB1, RPB2 and TUB) were reconstructed in this study. The combined datasets of ITS+nLSU and ITS+nLSU+EF1-α+mtSSU+RPB1+RPB2+nSSU+TUB showed similar topologies although the later analysis has higher supports.

**Core polyporus clade**

Core polyporus clade, which diverged during the early Paleogene, is strongly supported in divergence time estimation, ITS+nLSU and the eight-gene mutiple dataset analyses (Figs 1–3). In this clade, the lectotype of Polyporus and five other Polyporus spp. are included. Among these species, P. umbellatus merely grows from a black sclerotium underground where close to stumps of hardwoods, P. tuberaster can grow both on hardwoods and on the ground from a blackish sclerotium (Núñez & Ryvarden 1995a), while others are restricted to hardwoods (Xue & Zhou 2014, Si & Dai 2016). As is shown in Fig. 3, P. auratus, P. cuticulatus Y.C. Dai, Jing Si & Schigel and an undescribed species are merely collected in the tropical area, P. hapalopus only distributes in subtropical region, P. umbellatus is limited in circumpolar zone while P. tuberaster can be found from temperate to tropical regions.

As the lectotype species of Polyporus, P. tuberaster was put into group Polyporus with P. australafrcanus Núñez & Ryvarden, P. craterellus, P. radicatus Schwein., P. squamosus and P. udus Jungh (Núñez & Ryvarden 1995a). Krüger (2002) proposed that group Polyporus is polyphyletic taxa, and this conclusion has been proved by others (Sotome et al. 2008, Dai et al. 2014, Zmitrovich & Kovalenko 2016). In our present study, P. radicatus has closer relationships with species in squamosus clade. Polyporus australafrcanus, P. craterellus and P. udus are not included in our phylogenetic analyses for lacking enough DNA sequences. But according to the analyses obtained by previous scholars, P. craterellus always clustered with P. umbellatus (Krüger 2002) while P. udus had an unclear phylogenetic position (Sotome et al. 2008). Recently, P. udus was combined into genus Favolus as F. udus (Jungh.) Zmitr. et Kovalenko (Zmitrovich & Kovalenko 2016).

Polyporus umbellatus was morphologically put into group Dendropolyporus for its sclerotia (Núñez & Ryvarden 1995a). Sotome et al. (2008) considered P. umbellatus as a phylogenetically distinct lineage from other species for its phylogenetic placement was not clarified. Recently, this species was treated as the type species of genus Cladomeris Qué. (Zmitrovich & Kovalenko 2016). Based on our analyses, P. umbellatus is strongly supported as a member of the core polyporus clade.
The core polyporus clade was treated as a natural group of *Polyporus* (Zhou et al. 2016a). Based on our own specimens collected from China, all species in this clade have fleshy basidiomata when fresh and brittle upon drying, inflated skeleton-binding hyphae, generative hyphae dominant to almost monomitic in trama or context and light-colored stipes (Zhou et al. 2016a). Based on the steam age, phylogenetic relationships and morphological features, here we prefer to treat the core polyporus clade as a specific group, *Polyporus* s. str., and characterize it with the following features: basidiomata annual, centrally to laterally stipitate or substipitate, fleshy when fresh, becoming brittle and light in weight when dry, pore surface white to cream in fresh condition, stipe light colored and without a blackish cuticle, a dimitic hyphal system with generative hyphae and skeleton-binding hyphae, generative hyphae dominant to almost monomitic in trama or context, skeleton-binding hyphae thick walled with a wide lumen and inflated, basidiospores cylindrical, hyaline and thin-walled, on hardwoods or developing from sclerota buried in the ground, causing a white rot. Based on the above characters, we think *P. craterellus* and *P. udus* should be kept in *Polyporus* s. str. while *P. austroafricanus* and *P. radicatus* should not.

**Polyporus indigenus** I.J. Araujo & M.A.de Sousa, *P. minutosquamosus* Runnel & Ryvarden and *P. sapurema* Möller are not analyzed in our present study for lacking specimens. All the above three species are described from tropical areas of South America, and both *P. indigenus* and *P. sapurema* grow on the ground from a sclerotium while *P. minutosquamosus* grow on dead hard wood (Gomes-Silva et al. 2012, Runnel & Ryvarden 2016). Based on the analyses proposed by Runnel & Ryvarden (2016), *P. minutosquamosus* is phylogenetically closely related to *P. tuberaster* and *P. hapalopus*. Morphologically, according to the description of Gomes-Silva et al. (2012) and Runnel & Ryvarden (2016), we think all the above three species should also be kept in *Polyporus* s. str.

**Picipes clade**

Picipes clade is sister taxa to the core polyporus clade but with low supports. Twenty-seven species, which include seven new species collected from tropical to subtropical areas of China, are contained in this clade (Figs 2, 3). Several species in this clade were initially treated as members of genus *Melanopus* Pat. for their black stipes (Patouillard 1887), then they were combined into genus *Polyporus* and treated as members of group *Melanopus* (Núñez & Ryvarden 1995a). Recently, this clade was treated as an individual genus according to the phylogenetical and morphological characters (Zmitrovich & Kovalenko 2016, Zhou et al. 2016a). In the present study, the diverged time also support this clade as an individual genus. So, in this article, we follow the views Zmitrovich & Kovalenko (2016) and Zhou et al. (2016a) proposed.

Núñez & Ryvarden (1995a) previously treated *P. centroafricanus* Núñez & Ryvarden, *P. guianensis*, *P. leprieuri* Mont., *P. mikawai* Lloyd, *P. nigrocristatus* Núñez & Ryvarden and *P. varius* as members of group *Melanopus*. But, based on the present analyses, *P. guianensis*, *P. leprieuri* and *P. varius* are strongly clustered in the squamosus clade (Fig. 3). Moreover, *P. mikawai* is now combined into genus *Neofavolus* and treated as *N. mikawai* (Sotome et al. 2013). Because of lacking specimens and DNA sequences, *P. centroafricanus* and *P. nigrocristatus* are not included in our present phylogenetic analyses.

Lineage A of picipes clade is strongly supported by both mutiple genes analyses (Figs 2, 3). This lineage contains twelve species of *Picipes*, including the type species, *P. badius*. Among these species, *P. badius*, *P. subtropicus* and *P. subtubaeformis* can be collected from subtropical area or tropical area, while other nine species are restricted to the regions with lower temperature. *Picipes badius* was previously put into *Royoporus* A.B. De (De 1996) for its simple septa, then it was included in the clade /Tubaeformis– “Phaeopodi” with *P. melanopus* (Pers.) Zmitr. & Kovalenko and *P. tubaeformis* (P. Karst.) Zmitr. & Kovalenko based on ITS+nLSU analysis (Krüger et al. 2006). Recently, Zmitrovich & Kovalenko (2016) defined the genus *Picipes* to substitute this clade, they characterized this genus by lignicolous, numerous branched skeletons with uninflated axial elements, numerous subsolid fibrohyphae in combination with small pores and dark-colored stipe cuticle. But as the *P. rhizophilus* (Pat.) J.L. Zhou & B.K. Cui and *P. fraxinicola*
were included in phylogenetic analysis, it made the lignicolous and dark-colored stipe not sufficient features to define genus *Picipes* (Zhou et al. 2016a).

Lineage B is tropical to subtropical taxa that merely supported by Bayesian analysis of the eight-gene multiple dataset (Fig. 3). Seven new species and four previously described ones are included in this lineage. Among these species, *Pi. brevistipitatus*, *Pi. nigromarginatus* and *Pi. pumilus* are subtipitate and without a black cuticle on the stipe. *Picipes dictyopus* was initially described from temperate forest in Juan Fernández archipelago (Chile) (Pulgarin 2016, Palacio et al. 2017). But in the latest monographic about *Polyopus*, it was reported as a pantropical species (Núñez & Ryvarden 1995a). Based on morphological characters and mating type results, *Pi. dictyopus* was considered as a complex species (Núñez & Ryvarden 1995a, 2001). Recently, on the basis of the specimens collected from South America and the type specimens, Palacio et al. (2017) divided specimens of *Pi. dictyopus* complex into five species: *Atroporus diabolicus* (Berk.) Ryvarden (≡ *Polyopus diabolicus* Berk.), *Atroporus rufoatratus* (Berk.) Palacio, Reck & Robledo (≡ *Polyopus rufoatratus* Berk.), *Neodictyopus atlanticus* Palacio, Grassi & Robledo, *Neodictyopus dictyopus* (Mont.) Palacio, Robledo & Drechsler-Santos (≡ *Polyopus dictyopus* Mont.) and *Neodictyopus gugliottiæ* Palacio, Robledo, Reck & Drechsler-Santos. Though these species were not added in our phylogenetic analyses, according to the phylogenetic analysis and morphological descriptions Palacio et al. (2017) provided, we think genera *Atroporus* Ryvarden and *Neodictyopus* Palacio, Robledo, Reck & Drechsler-Santos should be treated as synonyms of *Picipes*, and species in the former two genera should be transferred into *Picipes*.

Lineage C merely contains *Pi. submelanopus* in our analyses (Figs 2, 3). *Picipes submelanopus* was originally described from northeast of Qinghai-Tibetan Plateau and reported as a terraneous species that grows on the ground in *Picea* forest (Xue & Zhou 2012). But based on our own specimens, *Pi. submelanopus* can also be found in temperate region of China. Moreover, this species can also be collected both on hardwoods (e.g. *Berberis*) and softwoods (e.g. *Picea*).

Lineage D is well supported by the analyses using ITS+nLSU and the eight-gene multiple datasets (Figs 2, 3). The only two species clustered in this lineage were recently described from China and Korea (Zhou et al. 2016a, Tibpromma et al. 2017), both of them are limited in subtropical region. Morphologically, their black stipe, hard basidiomata in dried condition, uninflated hyphal and strongly branched skeleto-binding hyphae in trama are typical characteristics of *Picipes*.

**Favolus clade and neofavolus clade**

Favolus clade and neofavolus clade, which were divided from *Polyopus* group *Favolus*, are sister taxa that diverged at about 60 Mya from a common ancestor (Fig. 1). The divergence times can well support the above two clades as specific genera. Núñez & Ryvarden (1995a) initially put *P. alveolaris* (DC.) Bondartsev & Singer, *P. grammacephalus* Berk., *P. philippinensis* Berk. and *P. tenuiculus* (P. Beauv.) Fr. into the group *Favolus* according to morphological analyses. While *P. pseudobetulinus* (Murashk. ex Pilát) Thorn, Kotir. & Niemelä and *P. mikawai* were put into group *Admirabilis* and group *Melanopus*, respectively (Núñez & Ryvarden 1995a). Phylogenetically, it revealed that *P. pseudobetulinus* had closer relationships with *P. grammacephalus* and *P. tenuiculus* while *P. mikawai* closely related to *P. alveolaris* (Krüger 2002, Sotome et al. 2011). Recently, group *Favolus* was divided into two distinct genera viz. *Favolus* and *Neofavolus* based on the morphological studies and phylogenetic analyses of ITS+nLSU (Sotome et al. 2013). Based on the analyses of Sotome et al. (2013), the *P. grammacephalus* complex was divided into two distinct species viz. *F. acervatus* and *F. emericci* (Berk. ex Cooke) Imazeki while *P. tenuiculus* complex was divided into three viz. *F. brasiliensis*, *F. roseus* and *F. spatulatus* (Jungh.) Lév. This conclusion has been widely accepted by subsequent mycologists (Dai et al. 2014, Seelan et al. 2015, Sotome et al. 2016, Zmitrovich & Kovalenko 2016, Zhou et al. 2016a, Tibpromma et al. 2017, Zhou & Cui 2017). In our present study, eleven species and an undescribed one are included in the favolus clade while six species are contained in the neofavolus clade.
Almost all the species in favolus clade are restricted in tropical to subtropical regions except *F. acervatus* and *F. pseudobetulinus*. *Favolus pseudobetulinus* is a temperate species distributed in boreal areas of North America, East Asia and Europe (Thorn et al. 1990, Núñez & Ryvarden 1995a, Schigel & Toresson 2005, Stome et al. 2011, Dai 2012). It was once treated as a member of *Piptoporus* P. Karst. and then combined into *Polyergus* by Thorn et al. (1990). Later, De (1998) put it into genus *Royopus* with *P. badius* by the character lacking clamp-connections. But phylogenetic results revealed that the lack of clamp-connections is not a sufficient character to define a genus but can be used only at the species level (Sotome et al. 2011). *Favolus acervatus* was mainly collected from tropical and subtropical areas (Núñez & Ryvarden 1995a), but it was recently reported in warm-temperate areas of China and Japan (Sotome et al. 2013, Zhou & Cui 2017). Sotome et al. (2013) considered that there may be more additional species of *Favolus* in tropical areas, and this conclusion had been recently proved. Five new species viz. *F. gracilisporus* H. Lee, N.K. Kim & Y.W. Lim, *F. niveus* J.L. Zhou & B.K. Cui, *F. pseudoemerici* J.L. Zhou & B.K. Cui, *F. septatum* J.L. Zhou & B.K. Cui and *F. subtropicus* J.L. Zhou & B.K. Cui collected from tropical and subtropical areas of East Asia were described and illustrated based on the morphological and phylogenetical analyses (Tibpromma et al. 2017, Zhou & Cui 2017). But, after comparing the ITS sequences and morphological descriptions, we find that *F. subtropicus* is a synonym for *F. gracilisporus*. Because the former one was published after the later, so, we should use *F. gracilisporus* as the correct name of this species.

Neofavolus clades is well supported in all trees and contains six species mainly collected from temperate and subtropical areas (Figs 1–3). Sotome et al. (2013) previously considered that all the known species of genus *Neofavolus* are known from temperate regions and unknown from the tropics. However, several samples of *N. mikawai* and *N. alveolaris* distributed in tropical areas of Hainan Province and Yunnan Province of China were collected (Zhou & Cui 2017). *Neofavolus squamatus* collected from Tibet is much different from other *Neofavolus* spp. by its yellowish orange squamae on the pileus and plateau distribution (Xing et al. 2020). For *N. americanus*, a temperate species collected from Connecticut of America, it has larger basidiospores (10.4–12 μm) than other species in the *Neofavolus* clades. The specimen MA672 collected from Massachusetts state of America has almost the same ITS and nLSU sequences to our present species, but because of lacking its morphological descriptions, we could not confirm whether they are the same species or not. *Neofavolus cremeoalbidus* is a subtropical species originally described from Japan, it is distinct from other *Neofavolus* spp. in its thin and pale-colored basidiomata (Sotome et al. 2013). But when analyzing the samples collected from Zhejiang, located in subtropical areas of China, our specimens has somewhat smaller basidiospores (8–10.7 × 3.8 μm) than those given in the original description (8–12 × 3–4 μm, Sotome et al. 2013). *Neofavolus suavissimus* is a special one with gilled hymenophores. It was previously treated as a member of *Lentinus* and named *L. suavissimus* Fr. for a long time (Pegler 1983, Hibbett & Thorn 1994, Knudsen & Vesterholt 2012). Phylogenetical analyses revealed that it has much closer relationships with *Neofavolus* spp. than *Lentinus* spp. (Seelan et al. 2015, Zmitrovich & Kovalenko 2016, Zhou & Cui 2017).

**Lentinus clade**

Lentinus clade, evolved during the mid-Paleogene, is well supported in all trees and contains both poroid and gilled species (Figs 1–3). Six polyporoid species, which were previously treated as members of *Polyergus* group *Polyoepeolus*, and members of genus *Lentinus* are included in this clade (Figs 2, 3). It reveals that species in group *Polyoepeolus* have much closer relationships with *Lentinus* than other *Polyergus* spp. Krüger (2002) proposed to combine species in the group *Polyoepeolus* into genus *Lentinus*, but the new combinations were illegally published. Therefore, we accept the names Zmitrovich (2010) and Zmitrovich & Kovalenko (2016) provided.

Phylogenetically, three subclades were presented in the lentinus clade. All the four species clustered in lineage I are with poroid hymenophores. Among these species, *L. brumalis* (Pers.) Zmitr. has circular pores while other three species have angular pores. Geographically, *L.
Species in lineage II are with lamellate hymenophores and morphologically treated as members of genus *Lentinus*. Among these species, *L. tigrinus* (Bull.) Fr. morphologically has sub-poroid hymenophore between lamellae and angular pores across the entire width of the pileus, while others are lamelled (Hibbett et al. 1993, Seelan et al. 2015). *Lentinus* spp. occur from boreal to tropical regions and are widely documented in southeastern Asia (Seelan et al. 2015). Although *L. tigrinus* was reported in tropical areas, Grand et al. (2011) proved *L. tigrinus* merely has an Eurasian and northern temperate distribution based on an ITS phylogeny and mating studies. Besides, Seelan et al. (2015) considered *L. tigrinus* as a sister group of *Polyporellus* in their four-gene phylogeny, but with low supports. According to our phylogenetic analyses, *L. tigrinus* reveals closer relationships with other gilled species than polyporoid ones, even though this conclusion is merely supported in the eight-gene phylogeny (Fig. 3).

Morphologically, almost all the species in this clade have central stipe without dark-colored cuticle, dimitic hyphal systems with generative hyphae and skeleton-binding hyphae, inflated hyphae and cylindrical basidiospores (Pegler 1983, Krüger 2002). *Lentinus* was previously considered to be derived from polyporoid species (Pegler 1983, Singer 1986), and this conclusion was subsequently validated according to the phylogenetic analyses (Hibbett & Vilgalys 1993, Hibbett & Donoghue 1995, Ko & Jung 2002, Krüger 2002, Krüger & Gargas 2004). Recently, Seelan et al. (2015) estimated that the ancestral hymenophoral configuration for species of *Lentinus* and *Polyporellus* group is circular pores, with independent transitions to angular pores and lamellae. Based on our present analysis (Fig. 3), the ancestral state for the *lentinus* clade is estimated to be tropical organisms, with a dissemination to temperate and boreal regions.

**Squamosus clade**

Species belonging to seven distinct genera viz. *Datronia*, *Datroniella*, *Echinochaete*, *Mycobonia*, *Neodatronia*, *Polyporus* and *Pseudofavolus* are included in the squamosus clade, and this clade is well supported in all trees except parsimony analyses (Figs 1–3). Bayesian evolutionary analysis (Fig. 1) indicates that all these genera are congenetic and have a common ancestor evolved during the early Paleogene. Morphologically, most members in this clade share more or less crustate pileus or stipe although they have various morphologies of basidiomata and distribution patterns (Sotome et al. 2008).

Nine previously described *Polyporus* species and two undescribed ones are contained in this clade (Figs 2, 3). Among these species, *P. hemicapnodes* Berk. & Broome was initially described from Dolosbagey (Sri Lanka) by Berkeley & Broome, and then it was treated as a synonymy of *P. leprieurii* (Núñez & Ryvarden 1995a). Based on our specimens collected from China, though both of them have greyish pore surface, similar pore size and black stipe, *P. leprieurii* has flabelliform to sparsulate pileus, azonate pileal surface, larger basidia (20–30 × 8–10 μm; Núñez & Ryvarden 1995a) and narrower basidiospores (4.5–7 × 2–2.5 μm; Núñez & Ryvarden 1995a), while *P. hemicapnodes* has flat pileus with a depressed center or infundibuliform basidiomata, zonate pileal surface, smaller basidia (17–21 × 6.4–8.8 μm) and rounder basidiospores (5.4–7.6 × 2.9–3.8 μm). *Polyporus guianensis*, *P. leprieurii* and *P. varius* were morphologically put into group *Melanopus* while *P. radicans* and *P. squamosus* were put into group *Polyporus* (Núñez & Ryvarden 1995a). But the phylogenetic analyses reveal that they have much closer relationships with *Datronia* and other five genera than species in core polyporus clade and picipes clade. Morphologically, unlike species in the core polyporus clade, almost all the *Polyporus* species in the squamosus clade have brown to black cuticles on the stipes. Based on our present specimens collected from China,
Polyporus species in squamosus clade have brittle tubes and more or less brittle basidiomata when dry. These features are much different from those of species in the picipes clade.

Datronia was established based on the type species D. mollis (Sommerf.) Donk. (Donk 1966). This genus was previously proved to have a close relationship with Polyporus (Krüger 2002, Binder et al. 2005, Sotome et al. 2008, Ghobad-Nejhad & Dai 2010, Justo & Hibbett 2011, Sotome et al. 2013, Dai et al. 2014, Seelan et al. 2015, Zmitrovich & Kovalenko 2016). Recently, Li et al. (2014) divided this genus into three distinct genera viz. Datronia, Datroniella and Neodatronia based on the taxonomic and phylogenetic analyses. Although Datronia, Datroniella and Neodatronia produce resupinate to sessile basidiomata, brown context, tissues becoming black in KOH and brownish skeletal hyphae (Li et al. 2014), their dimitic hyphal system with clamped generative hyphae and dextrinoid arboriform hyphae, thick-walled skeleto-binding hyphae, cylindrical basidiospores and white rotting habit are similar to those of Polyporus (Nuñez & Ryvarden 1995a, 2001, Sotome et al. 2008, Li et al. 2014). Sotome et al. (2008) considered that the presence of the stipe alone might not be a sufficient character to morphologically characterize a phylogenetically differentiated polypore genus.

Pseudofavolus is a distinct genus characterized by the dimidiate basidiomata with a contracted base, tessulate upper surface, thin context, basidiomata becoming hard and brittle upon drying, cylindrical basidiospores longer than 13 μm and tropical distribution (Nuñez & Ryvarden 1995a). However, Corner (1984) rejected Pseudofavolus as a segregate genus for its dextrinoid hyphae, dendrolyphidia, large basidiospores and thin context could also be found in Polyporus. Phylogenetic analyses also revealed Pseudofavolus is closely related to Polyporus (Krüger 2002, Sotome et al. 2008, Krüger & Gargas 2010). In our present study, Pseudofavolus nested in the squamosus clade with moderate support (Figs 2, 3). Pseudofavolus cucullatus (Mont.) Patouillard was transferred into Polyporus as a variety under P. miquelii Mont. (Corner 1984). Krüger (2002) and Krüger & Gargas (2010) also supported the opinion that Pseudofavolus should be included in Polyporus, but they prefer to choose Polyporus curtipes (Berk. & M.A. Curtis) Ryvarden as the valid name for Ps. cucullatus in Polyporus.

Mycobonia is a genus with hydnoid hymenium that established by Patouillard (Jülich 1976). It was previously treated as a member of Thelephoraceae (Donk 1957) and then put into family Polyporaceae (Singer 1986). Corner (1984) considered that Mycobonia has a close relationship with Pseudofavolus and treated M. flava (Sw.) Pat. (the type species of Mycobonia) as a variety of Ps. miquelii without pores. Krüger & Gargas (2010) proposed that the hymenophore of M. flava is reduced to a flat surface as in corticioid and thelephoroid fungi, and the pore walls appear to have become isolated hyphal peg fascicles. While the brittle basidiomata in dried condition, basidiospores and basidia sizes of M. flava are similar to those of P. squamosus and several other species in squamosus clade (Krüger 2002, Krüger & Gargas 2010). Recently, M. flava was transferred into Polyporus as a subspecies of P. curtipes (Krüger 2002, Krüger & Gargas 2010). But, according to the phylogenetic analyses, M. flava seems to be a distinct species far from Ps. cucullatus. Hence, we prefer to treat M. flava and Ps. cucullatus as two different species.

Echinochaete is a genus described by Reid (1963) based on the type species E. megalopora (Mont.) Reid (= E. brachypora (Mont.) Ryvarden). This genus is characterized by basidiomata with a laterally short stipe-like base,pileus velutinate especially near the attachment, angular to hexagonal pores, dimitic hyphal system with clamped generative hyphae and dextrinoid arboriform skeleto-binding hyphae, spinulose setoid elements on pileal surface and hymenium, cylindrical basidiospores, tropical to subtropical distribution and white rotting habit (Ryvarden & Johansen 1980, Nuñez & Ryvarden 1995a, 2001). Phylogenetic analyses proved that Echinochaete spp. always cluster with species of Datronia, Mycobonia, Polyporus and Pseudofavolus (Krüger 2002, Sotome et al. 2008, Krüger & Gargas 2010, Binder et al. 2013). Morphologically, Echinochaete is similar to Polyporus with laterally stipitate basidiomata becoming brittle upon drying, similar hyphal characters and cylindrical basidiospores. Both Corner (1984) and Singer (1986) previously treated Echinochaete as a synonym of Polyporus.
In this study, species in squamosus clade reveals to have a common ancestor and rapidly diversified into different forms of basidiomata with poroid or hydnoid hymeniums during Paleogene. Recently, Zmitrovich & Kovalenko (2016) and Zmitrovich (2018) transferred species of *Datronia, Datroniella* and *Mycobonia* in squamosus clade into *Cerioporus*, a genus established by Quélet based on the type species *C. squamosus* (Huds.) Quél. They characterized this genus by polyporoid to trametoid hymenium, dimitic hyphal system with inflated axial skeletals and arboriform branching, fusoid basidiospores with navicular or humpbacked tendency (Zmitrovich & Kovalenko 2016). Though the evolutionary time supports the suqmosus clade as an individual genus, Zhao et al. (2016, 2017) declared that divergence times should be not used on polyphyletic groups. Moreover, species in this clade are morphologically different from each other. So, in this study, we suggest retaining the genera *Datronia, Datroniella, Echinochaete, Mycobonia* and *Neodatronia* and keeping *Polyporus* species in the squamosus clade in genus *Polyporus* until more evidences are found.

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