Cacaoporus, a new Boletaceae genus, with two new species from Thailand

Santhiti Vadthanarat1,2,3, Saisamorn Lumyong1,3,6, Olivier Raspé4,5

1 Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, 50200, Thailand 2 PhD’s Degree Program in Biodiversity and Ethnobiology, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, 50200, Thailand 3 Center of Excellence in Microbial Diversity and Sustainable Utilization, Faculty of Science, Chiang Mai University, Chiang Mai, 50200, Thailand 4 Meise Botanic Garden, Nieuwelaan 38, 1860 Meise, Belgium 5 Fédération Wallonie-Bruxelles, Service général de l’Enseignement universitaire et de la Recherche scientifique, Rue A. Lavallée 1, 1080 Bruxelles, Belgium 6 Academy of Science, The Royal Society of Thailand, Bangkok, 10300, Thailand

Corresponding author: Olivier Raspé (olivier.raspe@botanicgardenmeise.be)

Academic editor: M. P. Martín | Received 30 March 2019 | Accepted 26 April 2019 | Published 10 June 2019

Citation: Vadthanarat S, Lumyong S, Raspé O (2019) Cacaoporus, a new Boletaceae genus, with two new species from Thailand. MycoKeys 54: 1–29. https://doi.org/10.3897/mycokeys.54.35018

Abstract

We introduce a new genus, Cacaoporus, characterised by chocolate brown to dark brown basidiomata and hymenophore, tubes not separable from the pileus context, white to off-white basal mycelium, reddening when bruised, amygdaliform to ovoid spores and dark brown spore deposit. Phylogenetic analyses of a four-gene dataset (atp6, tef1, rpb2 and cox3) with a wide selection of Boletaceae showed that the new genus is monophyletic and sister to the genera Cupreoboletus and Cyanoboletus in the Pulveroboletus group. Two new species in the genus, C. pallidicarneus and C. tenebrosus are described from northern Thailand. Full descriptions and illustrations of the new genus and species are presented. The phylogeny also confirmed the reciprocal monophyly of Neoboletus and Sutorius, which further support the separation of these two genera.

Keywords

3 new taxa, atp6, Boletales, cox3, Fungal Diversity, multigene phylogeny, Neoboletus, Pulveroboletus group, Taxonomy
Introduction

In the last decade or so, since molecular techniques and phylogenetic analyses have been used in taxonomy and systematics of the Boletaceae, many new species and genera have been described worldwide (e.g. Halling et al. 2012, 2016; Zeng et al. 2012; Arora and Frank 2014; Gelardi et al. 2014, 2015; Li et al. 2014, Zhao et al. 2014b, Zeng et al. 2014; Wu et al. 2015, 2016; Zhu et al. 2015). In Thailand, although the Boletaceae have been studied for a long time, only a few new Boletaceae species and a new genus have recently been described (Desjardin et al. 2009; Neves et al. 2012; Halling et al. 2014; Raspé et al. 2016; Vadthanarat et al. 2018). At the same time, many new species and genera have been described from southern and south-western China, an area with a climate and forests similar to Thailand (e.g. Li et al. 2011; Wu et al. 2015, 2016; Zhu et al. 2015). Similarly, a high number of new species and possibly new genera are expected to occur in Thailand (Hyde et al. 2018).

During our survey on the diversity of boletes in Thailand, several collections of brown to chocolate to dark brown boletes were obtained. Some collections bearing resemblance to *Sutorius* Halling, Nuhn & N.A. Fechner species, which typically have brown or reddish to purplish-brown basidiomata with reddish to purplish-brown hymenophore, reddish-brown spore deposit and narrowly ellipsoid to ellipsoid basidiospores (Halling et al. 2012). However, our chocolate brown bolete collections also showed differences, in particular in having a darker hymenophore, as well as in some microscopic characters like spore shape. We therefore performed a family-wide phylogeny, which showed that those brown to chocolate to dark brown boletes belong in a generic lineage, different from *Sutorius*. Consequently, we introduce the new Boletaceae genus *Cacaoporus* and describe two new species, *C. pallidicarneus* and *C. tenebrosus*, with full descriptions and illustrations.

Materials and method

Specimens collecting

Fresh basidiomata were collected in Chiang Mai Province, northern Thailand during the rainy season in 2013 to 2018. The specimens were photographed *in situ*, wrapped in aluminium foil and taken to the laboratory. After description of macroscopic characters, the specimens were dried in an electric dryer at 45–50 °C. Examined specimens were deposited in the herbaria CMUB, MFLU, BKF and BR (listed in Index Herbariorum; Thiers, continuously updated).

Morphological studies

Macroscopic descriptions were made, based on detailed field notes and photos of fresh basidiomata. Colour codes were taken from Kornerup and Wanscher (1978). Macrochemical reactions (colour reactions) of pileus, pileus context, stipe, stipe context and hy-
menophore were determined using 10% aqueous potassium hydroxide (KOH) and 28–30% ammonium hydroxide (NH$_4$OH). Microscopic structures were observed from dried specimens, using 5% KOH, NH$_4$OH, Melzer’s reagent or stained with 1% ammoniacal Congo red. A minimum of 50 basidiospores, 20 basidia and 20 cystidia were randomly measured at 1000× with a calibrated ocular micrometer using an Olympus CX51 compound microscope. The notation “[m/n/p]” represents the number of basidiospores “m” measured from “n” basidiomata of “p” collections. Dimensions of microscopic structures are presented in the following format: (a–)b–c–d(–e), in which “c” represents the average, “b” the 5$^{th}$ percentile, “d” the 95$^{th}$ percentile, “a” the minimum and “e” the maximum. Q, the length/width ratio, is presented in the same format. A section of the pileus surface was radially and perpendicularly cut to the surface at a point halfway between the centre and margin of the pileus. Sections of stipitipellis were taken from halfway up the stipe and longitudinally cut, perpendicularly to the surface (Hosen et al. 2013; Li et al. 2011). All microscopic features were drawn by free hand using an Olympus Camera Lucida model U–DA fitted to the microscope cited above. For scanning electron microscopy (SEM), a spore print was mounted on to an SEM stub with double-sided tape. The samples were coated with gold, then examined and photographed with a JEOL JSM–5910 LV SEM.

DNA isolation, PCR amplification and DNA sequencing

Genomic DNA was extracted from fresh tissue preserved in CTAB or about 10–15 mg of dried tissue using a CTAB isolation procedure adapted from Doyle and Doyle (1990). Portions of the genes atp6, tef1, rpb2 and cox3 were amplified by polymerase chain reaction (PCR) and sequenced by Sanger sequencing. The primer pairs ATP6-1M40F/ATP6-2M (Raspé et al. 2016), EF1-983F/EF1-2218R (Rehner and Buckley 2005) and bRPB2-6F/bRPB2-7.1R (Matheny 2005) were used to amplify atp6, tef1 and rpb2, respectively. Part of the mitochondrial gene cox3 was amplified with the newly designed primers COX3M1-F (5’-ATYGGAGCWGTAATGTWYATGC-3’) and COX3M1-R (5’-CCWACTAWTACRTGRATWCCATG-3’), using the following PCR programme: 2 min 30 s at 95 °C; 35 cycles of 25 s at 95 °C, 30 s at 48 °C, 30 s at 72 °C; 3 min at 72 °C. PCR products were purified by adding 1 U of Exonuclease I and 0.5 U FastAP Alkaline Phosphatase (Thermo Scientific, St. Leon-Rot, Germany) and incubated at 37 °C for 1 h, followed by inactivation at 80 °C for 15 min. Standard Sanger sequencing was performed in both directions by Macrogen Europe (The Netherlands) with PCR primers, except for atp6, for which universal primers M13F-pUC(-40) and M13F(-20) were used; for tef1, additional sequencing was performed with two internal primers, EF1-1577F and EF1-1567R (Rehner and Buckley 2005).

Alignment and phylogeny inference

The sequences were assembled in GENEIOUS Pro v. 6.0.6 (Biomatters) and introns were removed prior to alignment based on the amino acid sequence of previously
published sequences. All sequences, including sequences from GenBank, were aligned using MAFFT (Katoh and Standley 2013) on the server accessed at http://mafft.cbrc.jp/alignment/server/.

Maximum Likelihood (ML) phylogenetic inference was performed using RAxML (Stamatakis 2006) on the CIPRES web portal (RAxML-HPC2 on XSEDE; Miller et al. 2009). The phylogenetic tree was inferred by a single analysis with three partitions (one for each gene), using the GTRCAT model with 25 categories, two Buchwaldoboletus and nine Chalciporus species from sub-family Chalciporoideae were used as outgroup since Chalciporoideae always appeared as sister to the remainder of the Boletaceae in recent phylogenetic analyses (e.g. Nuhn et al. 2013; Wu et al. 2014, 2016). Statistical support of clades was obtained with 1,000 rapid bootstrap replicates.

For Bayesian Inference (BI), the best-fit model of substitution amongst those implementable in MrBayes was estimated separately for each gene using jModeltest (Darriba et al. 2012) on the CIPRES portal, based on the Bayesian Information Criterion (BIC). The selected models were HKY+I+G for atp6 and rpb2 and GTR+I+G for cox3 and tefl. Partitioned Bayesian analysis was performed with MrBayes 3.2 (Ronquist et al. 2012) on the CIPRES portal. Two runs of five chains were run for 15,000,000 generations and sampled every 500 generations. The chain temperature was decreased to 0.02 to improve convergence. At the end of the run, the average deviation of split frequencies was 0.008147.

**Results**

**Phylogenetic analysis**

A total of 325 sequences were newly generated and deposited in GenBank (Table 1). The alignment contained 1,013 sequences from four genes (186 for atp6, 358 for tefl, 326 for rpb2, 143 for cox3) from 362 voucher specimens and was 2946 characters long (TreeBase number 23886).

The four-gene analyses retrieved the six subfamilies (Austroboletoideae, Boletoideae, Chalciporoideae, Leccinoideae, Xerocomoideae, Zangioideae) as monophyletic (Fig. 1). The genera belonging to the Pulveroboletus group of Wu et al. (2014, 2016) did not form a monophyletic group. The new genus, Cacaoporus was monophyletic (BS=100% and PP=1) within a clade containing the genera Cupreoboletus Simonini, Gelardi & Vizzini and Cyanoboletus Gelardi, Vizzini & Simonini and one undescribed taxon, Boletus p.p. sp., clade 2 (specimen voucher JD0693) with high support (BS=94% and PP=0.99). The macromorphologically most similar genus, Sutorius, formed another clade (BS=100% and PP=1) sister to Neoboletus Gelardi, Simonini & Vizzini, with 67% BS and 0.97 PP support, in another clade of the Pulveroboletus group.

Our phylogeny also showed that thirteen Sutorius species including S. brunneissimus (W.F. Chiu) G. Wu & Zhu L. Yang, S. ferrugineus G. Wu, Fang Li & Zhu L. Yang, S. flavidus G. Wu & Zhu L. Yang, S. hainanensis (T.H. Li & M. Zang) G. Wu & Zhu L. Yang, S. junquilleus (Quél.) G. Wu & Zhu L. Yang, S. magnificus (W.F. Chiu) G. Wu &
Table 1. List of collections used for DNA analyses, with origin, GenBank accession numbers and reference(s).

| Species                          | Voucher     | Origin     | atp6     | cox3     | rps16 | rpb2     | Reference(s)      |
|---------------------------------|-------------|------------|----------|----------|-------|----------|-------------------|
| Afroboletus aff. multijugus     | JD671       | Burundi    | MH614651 | MH614794 | MH614700 | MH614747 | This study        |
| Afroboletus coquatiporus        | ADK4644     | Togo       | KT823958 | MH614795* | KT824024 | KT823991 | Raspé et al. 2016; *This study |
| Afroboletus lateralis           | ADK4844     | Togo       | MH614652 | MH614796 | MH614701 | MH614748 | This study        |
| Aureoboletus catarinarius       | HKAS54467   | China      | –        | –        | KT990711 | KT990349 | Wu et al. 2016    |
| Aureoboletus duplicatiporus     | HKAS50498   | China      | –        | –        | KFI12230 | KFI12754 | Wu et al. 2014    |
| Aureoboletus gentilis           | ADK4865     | Belgium    | KT823961 | MH614797* | KT824027 | KT823994 | Raspé et al. 2016; *This study |
| Aureoboletus mirabilis          | HKAS57776   | China      | –        | –        | KFI12229 | KFI12743 | Wu et al. 2014    |
| Aureoboletus monticulus         | VDK01120    | Belgium    | MG212528 | MH614798* | MG212573 | MG212615 | Vadtthanarat et al. 2018; *This study |
| Aureoboletus nephraporus        | HKAS67931   | China      | –        | –        | KT990720 | KT990357 | Wu et al. 2016    |
| Aureoboletus projectellus       | AFTOL-ID-713| USA        | DQ534604* | –        | AY879116 | AY878218 | Binder and Hilbert 2006; Binder et al., Unpublished |
| Aureoboletus shichimiens        | HKAS76852   | China      | –        | –        | KFI12237 | KFI12756 | Wu et al. 2014    |
| Aureoboletus sp.                | HKAS56317   | China      | –        | –        | KFI12239 | KFI12753 | Wu et al. 2014    |
| Aureoboletus sp.                | OR0245      | China      | MH614653 | MH614799 | MH614702 | MH614749 | This study        |
| Aureoboletus sp.                | OR0369      | Thailand   | MH614654 | MH614800 | MH614703 | MH614750 | This study        |
| Aureoboletus thibetanus         | HKAS76655   | Thailand   | –        | –        | KFI12236 | KFI12752 | Wu et al. 2014    |
| Aureoboletus thiobatus          | AFTOL-ID-450| China      | DQ534600* | –        | DQ029199 | DQ366279* | *Binder and Hilbert 2006; Unpublished |
| Aureoboletus tomentosus         | HKAS80485   | China      | –        | –        | KT990715 | KT990353 | Wu et al. 2016    |
| Aureoboletus vicinus            | OR0361      | Thailand   | MH614655 | MH614801 | MH614704 | MH614751 | This study        |
| Aureoboletus xanhui             | HKAS74766   | China      | –        | –        | KT990726 | KT990363 | Wu et al. 2016    |
| Austroboletus cl. dictyopus     | OR0045      | Thailand   | KT823966 | MH614802* | KT824032 | KT823999 | Raspé et al. 2016; *This study |
| Austroboletus cl. subvirens     | OR0573      | Thailand   | MH614656 | MH614803 | MH614705 | MH614752 | This study        |
| Austroboletus eburneus          | REH9487     | Australia  | –        | –        | JX889708 | –        | Halling et al. 2012b |
| Austroboletus olivaceoglutinosus| HKAS77576   | China      | –        | –        | KFI12212 | KFI12764 | Wu et al. 2014    |
| Austroboletus sp.               | HKAS59624   | China      | –        | –        | KFI12217 | KFI12765 | Wu et al. 2014    |
| Austroboletus sp.               | OR0891      | Thailand   | MH614657 | MH614804 | MH614706 | MH614753 | This study        |
| Bassoaria major                 | OR0209      | Thailand   | MG897421 | MK372295* | MG897431 | MG897441 | Phookamsak et al. 2019; *This study |
| Bassoaria pseudocaloporus       | HKAS63007   | China      | –        | –        | KFI12167 | KFI12677 | Wu et al. 2014    |
| Bassoaria pseudocaloporus       | HKAS75739   | China      | –        | –        | KJ184570 | KMG005497 | Wu et al. 2015    |
| Bassoaria pseudocaloporus       | HKAS75081   | China      | –        | –        | KFI112168 | KFI12678 | Wu et al. 2014    |
| Bassoaria raeforumculata        | BOTH4144    | USA        | MG897415 | MH614805* | MG897425 | MG897435 | Phookamsak et al. 2019; *This study |
| Bolellia ananas                 | NY814559    | Costa Rica | –        | –        | KFI12308 | KFI12760 | Wu et al. 2014    |
| Bolellia ananas                 | KMI123769   | Belize     | MH614658 | MH614807 | MH614707 | MH614754 | This study        |
| Bolellia aff. exomoides         | OR0061      | Thailand   | KT823970 | MH614806* | KT824036 | KT824003 | Raspé et al. 2016; *This study |
| Bolellia sp.                    | HKAS59536   | China      | –        | –        | KFI12306 | KFI12758 | Wu et al. 2014    |
| Bolellia sp.                    | OR0821      | Thailand   | MG212529 | MH614808* | MG212574 | MG212616 | Vadtthanarat et al. 2018; *This study |
| Boletus aureus                  | VDK01055    | Belgium    | MG212530 | MH614809* | MG212575 | MG212617 | Vadtthanarat et al. 2018; *This study |
| Boletus albobrunneicis          | OR0131      | Thailand   | KT823973 | MH614810* | KT824039 | KT824006 | Raspé et al. 2016; *This study |
| Boletus batyroides              | HKAS53403   | China      | –        | –        | KT990738 | KT990375 | Wu et al. 2016    |
| Boletus edulis                  | HMIJAU4637  | Russia     | –        | –        | KFI12202 | KFI12704 | Wu et al. 2014    |
| Boletus edulis                  | VDK00869    | Belgium    | MG212531 | MH614811* | MG212576 | MG212618 | Vadtthanarat et al. 2018; *This study |
| Boletus p.p. sp                 | JD0693      | Burundi    | MH645583 | –        | MH645591 | MH645599 | This study        |
| Boletus p.p. sp                 | OR0832      | Thailand   | MH645584 | MH645605 | MH645592 | MH645600 | This study        |
| Species | Voucher | Origin | apf6 | coz3 | tef1 | rpb2 | Reference(s) |
|---------|---------|--------|------|------|------|------|--------------|
| Boletus p.p. sp. | OR1002 | Thailand | MH645585 | MH645606 | MH645593 | MH645601 | This study |
| Boletus pallidus | BOTH4356 | USA | MH614659 | MH614812 | MH614708 | – | This study |
| Boletus pallidus | TBD-1231-Bruns | – | AF002142 | – | AF002154 | – | Kreutzer and Bruns 1999 |
| Boletus reticulocystis | HKAS7671 | China | – | – | – | – | Wu et al. 2014 |
| Boletus s.s. sp. | OR0446 | China | MG212532 | MH614813 | MG212577 | MK112703 | Vadtanarat et al. 2018; *This study |
| Boletus sp. | HKAS95660 | China | – | – | – | – | Wu et al. 2014 |
| Boletus sp. | HKAS63598 | China | – | – | – | – | Wu et al. 2014 |
| Boletus violaceofuscus | HKAS62900 | China | – | – | – | – | Wu et al. 2014 |
| Borodiniothyrium abominans | HKAS7749 | Bangladesh | – | JQ928576 | JQ928597 | – | Hosen et al. 2013 |
| Borodiniothyrium abominans | OR0345 | Thailand | MH614660 | MH614814 | MH614709 | MH614675 | This study |
| Butyriboletus appendiculatus | VDK0193b | Belgium | MG212537 | MH614816 | MG212582 | MG212624 | Vadtanarat et al. 2018; *This study |
| Butyriboletus cl. roseoflavus | OR0230 | China | KT823974 | MH614819 | KT824040 | KT824007 | Raspé et al. 2016; *This study |
| Butyriboletus fossii | NY815462 | USA | – | – | – | – | Wu et al. 2014 |
| Butyriboletus pseudoreguis | VDK03925 | Belgium | MG212538 | MH614817 | MG212583 | MG212625 | Vadtanarat et al. 2018; *This study |
| Butyriboletus pseudospeciosus | HKAS63513 | China | – | – | KT990743 | KT990380 | Wu et al. 2016 |
| Butyriboletus roseoflavus | HKAS54099 | China | – | – | KF739779 | KF739703 | Wu et al. 2014 |
| Butyriboletus roseopurpureus | BOTH4497 | USA | MG897418 | MH614818 | MG897428 | MG897438 | Phookamsak et al., 2019; *This study |
| Butyriboletus sp. | HKAS52661 | China | – | – | – | – | Wu et al. 2014 |
| Butyriboletus sp. | HKAS52525 | China | – | – | – | – | Wu et al. 2014 |
| Butyriboletus sp. | HKAS77774 | China | – | – | – | – | Wu et al. 2014 |
| Butyriboletus sp. | HKAS95814 | China | – | – | – | – | Wu et al. 2014 |
| Butyriboletus sp. | HKAS63528 | China | – | – | – | – | Wu et al. 2014 |
| Butyriboletus sp. | MHHN7456 | China | – | KT990741 | KT990378 | Wu et al. 2016 |
| Butyriboletus suboperculatus | HKAS50444 | China | – | – | KT990742 | KT990379 | Wu et al. 2016 |
| Butyriboletus yicichu | HKAS55413 | China | – | – | KF112157 | KF112674 | Wu et al. 2014 |
| Cacaoporus pallidicarnosus | OR0681 | Thailand | MK372259 | MK372296 | – | MK372283 | This study |
| Cacaoporus pallidicarnosus | OR0683 | Thailand | MK372260 | MK372297 | – | MK372284 | This study |
| Cacaoporus pallidicarnosus | OR1306 | Thailand | MK372261 | MK372298 | MK372272 | MK372285 | This study |
| Cacaoporus pallidicarnosus | SV0221 | Thailand | MK372262 | MK372299 | MK372273 | MK372286 | This study |
| Cacaoporus pallidicarnosus | SV0451 | Thailand | MK372263 | MK372300 | MK372274 | MK372287 | This study |
| Cacaoporus p.p. | SV0402 | Thailand | MK372270 | – | MK372281 | MK372293 | This study |
| Cacaoporus tenebricous | OR0054 | Thailand | MK372264 | MK372301 | MK372275 | MK372288 | This study |
| Cacaoporus tenebricous | OR1435 | Thailand | MK372265 | MK372302 | MK372276 | MK372289 | This study |
| Cacaoporus tenebricous | SV0223 | Thailand | MK372266 | MK372303 | MK372277 | MK372290 | This study |
| Cacaoporus tenebricous | SV0224 | Thailand | MK372267 | MK372304 | MK372278 | MK372291 | This study |
| Cacaoporus tenebricous | SV0422 | Thailand | MK372268 | MK372305 | MK372279 | – | This study |
| Cacaoporus tenebricous | SV0452 | Thailand | MK372269 | MK372306 | MK372280 | MK372292 | This study |
| Caloboletus aff. calopus | HKAS7439 | China | – | – | KF112166 | KF112667 | Wu et al. 2014 |
| Caloboletus calopus | ADK4087 | Belgium | MG212539 | MH614820 | KJ184566 | KP053030 | Vadtanarat et al. 2018; Zhao et al. 2014a, b; This study |
| Caloboletus inedulis | BOTH3963 | USA | MG897414 | MH614821 | MG897424 | MG897434 | Phookamsak et al. 2019; *This study |
| Caloboletus panniformis | HKAS55444 | China | – | – | KF112165 | KF112666 | Wu et al. 2014 |
| Caloboletus radicans | VDK01187 | Belgium | MG212540 | MH614842 | MG212584 | MG212626 | Vadtanarat et al. 2018; *This study |
| Caloboletus sp. | HKAS53353 | China | – | – | KF112188 | KF112668 | Wu et al. 2014 |
| Caloboletus sp. | OR0068 | Thailand | MH614662 | MH614823 | MH614711 | MH614757 | This study |
| Caloboletus yunnanensis | HKAS69214 | China | – | – | KJ184568 | KTO90396 | Zhao et al. 2014a; Wu et al. 2016 |
| Chaetiporus aff. piperatus | OR0586 | Thailand | KT823976 | MH614824 | KT824042 | KT824009 | Raspé et al. 2016; *This study |
| Chaetiporus aff. rubinlus | OR0139 | China | MH614663 | – | – | MH614712 | MH614758 | This study |
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

| Species                      | Voucher     | Origin          | atp6       | cox3        | tef1       | rpb2       | Reference(s)                        |
|------------------------------|-------------|-----------------|------------|-------------|------------|------------|-------------------------------------|
| Chacipora africana           | JD517       | Cameroon        | KT823963   | MH614825*   | KT824029   | KT823996   | Raspé et al. 2016; *This study       |
| Chacipora piperata           | VDK01063    | Belgium         | MH614664   | MH614826    | MH614713   | MH614759   | This study                           |
| Chacipora ruhius             | AF2835      | Belgium         | KT823962   | –           | KT824028   | KT823995   | Raspé et al. 2016                   |
| Chacipora sp.                | HKAS56400   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Chacipora sp.                | HKAS74797   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Chacipora sp.                | OR0363      | Thailand        | MH645586   | MH645607    | MH645594   | MH645602   | This study                           |
| Chacipora sp.                | OR0373      | Thailand        | MH645587   | MH645608    | MH645595   | MH645603   | This study                           |
| Chius sp.                    | OR0141      | China           | MH614665   | MH614827    | MH614714   | MH614760   | This study                           |
| China vires                  | OR0206      | China           | MG212541   | MH614828*   | MG212585   | MG212627   | Vadhyanathar et al. 2018; *This study|
| China vires                  | HKAS74928   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Crocinoboletus cl. laetissimus | OR0576    | Thailand        | KT823975   | MH614833*   | KT824041   | KT824008   | Raspé et al. 2016; *This study       |
| Crocinoboletus rubraeus      | HKAS53424   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Cuproboletus poikilochromus  | GS10070     | Italy           | –          | –           | KT157072   | KT157068   | Gelardi et al. 2015                 |
| Cuproboletus poikilochromus  | GS11008     | Italy           | –          | –           | KT157071   | KT157067   | Gelardi et al. 2015                 |
| Cyanoboletus brunneoceruber  | HKAS80579_1 | China           | –          | –           | KT990763   | KT990401   | Wu et al. 2016                      |
| Cyanoboletus brunneoceruber  | OR0233      | China           | MG212542   | MH614834*   | MG212586   | MG212628   | Vadhyanathar et al. 2018; *This study|
| Cyanoboletus instabilis      | HKAS59554   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Cyanoboletus pulvinellus      | RW109       | Belgium         | KT823980   | MH614835*   | KT824046   | KT824013   | Raspé et al. 2016; *This study       |
| Cyanoboletus sinopulverulentus| HKAS59609   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Cyanoboletus sp.             | HKAS52639   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Cyanoboletus sp.             | HKAS76850   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Cyanoboletus sp.             | OR0257      | China           | MG212543   | MH614836*   | MG212587   | MG212629   | Vadhyanathar et al. 2018; *This study|
| Cyanoboletus sp.             | HKAS90208_1 | China           | –          | –           | –          | –          | Wu et al. 2016                      |
| Cyanoboletus sp.             | OR0322      | Thailand        | MH614673   | MH614837    | MH614722   | MH614768   | This study                           |
| Cyanoboletus sp.             | OR0491      | China           | MH614674   | MH614838    | MH614723   | MH614769   | This study                           |
| Cyanoboletus sp.             | OR0961      | Thailand        | MH614675   | MH614839    | MH614724   | MH614770   | This study                           |
| Fuscumella prunicolor        | REH9880     | Australia       | MH614676   | MH614840    | MH614725   | MH614771   | This study                           |
| Gymnopaster boletoides       | NY01194009  | Australia       | –          | –           | KT990768   | KT990406   | Wu et al. 2016                      |
| Harrya atriceps              | REH4703     | Costa Rica      | –          | –           | JX889702   | –          | Halling et al. 2012b                 |
| Harrya chromopora            | HKAS50527   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Harrya moniliformis          | HKAS49627   | China           | –          | –           | KT990881   | KT990500   | Wu et al. 2016                      |
| Heimioporus cl. mandarinus    | OR0661      | Thailand        | MG212545   | MH614841*   | MG212589   | MG212631   | Vadhyanathar et al. 2018; *This study|
| Heimioporus japonicus        | OR0114      | Thailand        | KT823971   | MH614842*   | KT824037   | KT824004   | Raspé et al. 2016; *This study       |
| Heimioporus retioperus       | HKAS55237   | China           | –          | –           | KT990228   | KT990806   | Wu et al. 2014                      |
| Heimioporus sp.              | OR0218      | Thailand        | MG212546   | –           | MG212590   | MG212632   | Vadhyanathar et al. 2018; *This study|
| Hemileccinum depilation      | AF2845      | Belgium         | MG212547   | MH614843*   | MG212591   | MG212633   | Vadhyanathar et al. 2018; *This study|
| Hemileccinum impolitum       | ADK4078     | Belgium         | MG212548   | MH614844*   | MG212592   | MG212634   | Vadhyanathar et al. 2018; *This study|
| Hemileccinum indecorum       | OR0863      | Thailand        | MH614677   | MH614845    | MH614726   | MH614772   | This study                           |
| Hemileccinum vagum          | HKAS84970   | China           | –          | –           | KT990773   | KT990412   | Wu et al. 2016                      |
| Hortiboletus amygdalinus     | HKAS54166   | China           | –          | –           | KT990777   | KT990416   | Wu et al. 2016                      |
| Hortiboletus rubellas        | VDK00403    | Belgium         | MH614679   | MH614847    | –          | MH614774   | This study                           |
| Hortiboletus sp.             | HKAS50466   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Hortiboletus sp.             | HKAS51239   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Hortiboletus sp.             | HKAS51292   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Hortiboletus sp.             | HKAS76673   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Hortiboletus subpaludosus    | HKAS59608   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Houtania cl. parvula         | OR0762      | Thailand        | MH614680   | MH614848    | MH614728   | MH614775   | This study                           |
| Houtania cheni               | HKAS74744   | China           | –          | –           | –          | –          | Wu et al. 2014                      |
| Species                        | Voucher       | Origin      | atp6 | cox3 | tef1 | rpb2 | Reference(s) |
|-------------------------------|---------------|-------------|------|------|------|------|--------------|
| Hourangia cheni               | Zhu108        | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Hourangia nigropunctata       | HKAS 57427    | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Hymenobolus leptoasperatus    | HKAS46334     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Imleria bakia                 | VDKO0709      | Belgium     | KT823983 | MH614849² | KT824049 | KT824016 | Rapé et al. 2016; *This study |
| Imleria obscuribrunea         | OR0263        | China       | MH614681 | MH614850 | MH614729 | MH614776 | This study |
| Imleria subulipina            | HKAS4712      | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Lamarnia argyripunctata       | HKAS4759      | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Lamarnia argyripunctata       | HKAS4765      | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Lamarnia argyripunctata       | HKAS4752      | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Lamarnia asiatica            | HKAS4504      | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Lamarnia asiatica            | HKAS4516      | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Lanmaoa flavorubra           | BOTH4591      | USA         | MG897419 | MH614852² | MG897429 | MG897439 | Phookamsak et al. 2019; *This study |
| Lanmaoa flavorubra           | BOTH4432      | USA         | MG897417 | MH614853² | MG897427 | MG897437 | Phookamsak et al. 2019; *This study |
| Lanmaoa sp.                   | HKAS52518     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Lanmaoa sp.                   | OR0130        | Thailand    | MH614683 | MH614854 | MH614731 | MH614778 | This study |
| Lanmaoa sp.                   | OR0370        | Thailand    | MH614684 | MH614855 | MH614732 | MH614779 | This study |
| Leccinellum aff. crocepiodes  | HKAS76658     | Japan       | –    | –    | –    | –    | Wu et al. 2014 |
| Leccinellum aff. griecum      | KPM-NC-001783 | Japan       | KC552164 | JN378450² | –      | unpublished, *Orihara et al. 2012 |
| Leccinellum corvus            | Bu4507        | USA         | –    | –    | –    | –    | Nuhn et al. 2013 |
| Leccinellum crenenum          | HKAS90639     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Leccinellum crocepiodes       | VDKO1006      | Belgium     | KT823988 | MH614856² | KT824054 | KT824021 | Rapé et al. 2016; *This study |
| Leccinellum sp.               | KPM-NC-001804 | Japan       | KC552165 | –      | KC552094 | –      | Orihara et al. 2016 |
| Leccinellum sp.               | OR0711        | Thailand    | MH614685 | –      | MH614733 | MH614780 | This study |
| Leccinum monticolus           | HKAS76699     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Leccinum quercinum            | HKAS63502     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Leccinum scabrum              | RW105a        | Belgium     | KT823979 | MH614857² | KT824045 | KT824012 | Rapé et al. 2016; *This study |
| Leccinum scabrum              | VDKO0938      | Belgium     | MG212549 | MH614858² | MG212593 | MG212635 | Vadthanarat et al. 2018; *This study |
| Leccinum scabrum              | KPM-NC-0017840 | Scotland    | KC552170 | JN378455 | –      | Orihara et al. 2016, 2012 |
| Leccinum ochraceolens         | VDKO1128      | Belgium     | KT823989 | MH614859² | KT824055 | KT824023 | Rapé et al. 2016; *This study |
| Leccinum ochraceolens         | VDKO0844      | Belgium     | MG212550 | MH614860² | MG212594 | MG212636 | Vadthanarat et al. 2018; *This study |
| Macrolepiota castaneiceps     | HKAS75045     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Neobolus brunneainitius       | HKAS50538     | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Neobolus brunneainitius       | HKAS52600     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Neobolus brunneainitius       | HKAS57451     | China       | –    | –    | –    | –    | Wu et al. 2015 |
| Neobolus brunneainitius       | OR0249        | China       | MG212551 | MH614861² | MG212595 | MG212637 | Vadthanarat et al. 2018; *This study |
| Neobolus erythropus           | VDKO0690      | Belgium     | KT823982 | MH614864² | KT824048 | KT824015 | Rapé et al. 2016; *This study |
| Neobolus ferrugineus          | HKAS77718     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus ferrugineus          | HKAS77617     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS59443     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS58724     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS63515     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS47880     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS90209     | China       | –    | –    | –    | –    | Wu et al. 2016 |
| Neobolus flavida              | HKAS95469     | China       | –    | –    | –    | –    | Wu et al. 2014 |
| Neobolus flavidus             | AF2922        | France      | MG212552 | MH614862² | MG212596 | MG212638 | Vadthanarat et al. 2018; *This study |
| Species                  | Voucher   | Origin       | atp6   | cox3   | rpb2 | Reference(s) |
|-------------------------|-----------|--------------|--------|--------|------|---------------|
| Neoboletus magnificus   | HKAS54096 | China        | –      | –      | –    | Wu et al. 2014|
| Neoboletus magnificus   | HKAS47939 | China        | –      | –      | –    | Wu et al. 2014|
| Neoboletus multiplicatus| HKAS76851 | China        | –      | –      | –    | Wu et al. 2014|
| Neoboletus multiplicatus| OR0128    | Thailand     | MH614686 | MH614863 | MH614734 | This study     |
| Neoboletus obscuruspinus| OR0553    | Thailand     | MK372271 | –      | –    | This study     |
| Neoboletus obscuruspinus| HKAS6498  | China        | –      | –      | KT990791 | Wu et al. 2016|
| Neoboletus obscuruspinus| HKAS77774 | China        | –      | –      | KT990792 | Wu et al. 2016|
| Neoboletus obscuruspinus| HKAS89014 | China        | –      | –      | KT990793 | Wu et al. 2016|
| Neoboletus obscuruspinus| HKAS89027 | China        | –      | –      | KT990794 | Wu et al. 2016|
| Neoboletus rubriporus    | HKAS57512 | China        | –      | –      | KT990795 | Wu et al. 2016|
| Neoboletus rubriporus    | HKAS83026 | China        | –      | –      | KT990799 | Wu et al. 2016|
| Neoboletus sanguineodes  | HKAS57766 | China        | –      | –      | KT990900 | Wu et al. 2016|
| Neoboletus sanguineodes  | HKAS74733 | China        | –      | –      | KT990800 | Wu et al. 2016|
| Neoboletus sanguineodes  | HKAS55440 | China        | –      | –      | KT112145 | Wu et al. 2014|
| Neoboletus sanguineodes  | HKAS80823 | China        | –      | –      | KT990802 | Wu et al. 2016|
| Neoboletus tamentosus    | HKAS7756  | China        | –      | –      | KT990806 | Wu et al. 2016|
| Neoboletus tamentosus    | HKAS53369 | China        | –      | –      | KT112154 | Wu et al. 2014|
| Neoboletus sanguineodes  | HKAS57489 | China        | –      | –      | KT112158 | Wu et al. 2014|
| Neoboletus sanguineodes  | HKAS63355 | China        | –      | –      | KT990807 | Wu et al. 2016|
| Neoboletus sp.           | HKAS76660 | China        | –      | –      | KT112180 | Wu et al. 2014|
| Octavia australisipata    | KPM-NC-1782 | Japan     | KC552154 | – | JN378430 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia australisperpera  | AQUI3899  | Italy        | KC552159 | – | KC552093 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2016    |
| Octavia celatilifia      | KPM-NC-1777 | Japan     | KC552147 | – | JN378416 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia cyanecens         | PNW-FUNGI-5603 | USA | KC552160 | – | JN378438 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia decipens          | KPM-NC-1776 | Japan     | KC552145 | – | JN378409 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia taimanica         | MEL2128484 | Australia   | KC552157 | – | JN378437 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia taimanica         | MEL2341996 | Australia   | KC552156 | – | JN378436 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Octavia zelleri           | MES270     | USA          | KC552161 | – | JN378440 | Orihara et al.
|                          |            |             |        |        |        | 2016, 2012    |
| Pararexornis pseudoaquis  | OR0155     | China        | MG212553 | MH614865 | MG212577 | MG212639 |
| Phylloporus bellus        | OR0473     | China        | MHS80778 | MH614866 | MHS80798 | MHS80818 |
| Phylloporus brunniceps    | OR0050     | Thailand     | KT823968 | MH614867 | KT824034 | KT824001 |
| Phylloporus castanopidis  | OR0052     | Thailand     | KT823969 | MH614868 | KT824035 | KT824002 |
| Phylloporus imbricatus    | HKAS68642  | China        | –      | –      | KT112299 | KT112786 |
| Phylloporus luxentarios   | HKAS57077  | China        | –      | –      | KT112298 | KT112785 |
| Phylloporus maculatus     | OR0285     | China        | MHS80780 | –      | MHS80800 | MHS80820 |
| Phylloporus pelletieri    | WU18746    | Austria      | MHS80781 | MH614869 | MHS80801 | MHS80821 |
| Phylloporus palustris     | OR1158     | Thailand     | MHS80783 | MH614870 | MHS80803 | MHS80823 |
| Phylloporus rhodoxanthus  | WU17978    | USA          | MHS80785 | MH614871 | MHS80805 | MHS80824 |
| Phylloporus rubenoides    | OR0251     | China        | MHS80786 | MH614872 | MHS80806 | MHS80825 |
| Phylloporus rubiginosus   | OR0169     | China        | MHS80788 | MH614873 | MHS80808 | MHS80827 |
| Phylloporus sp.           | OR0896     | Thailand     | MHS80790 | MH614874 | MHS80810 | MHS80829 |
| Phylloporus subbacillisporus| OR0436   | China        | MHS80792 | MH614875 | MHS80812 | MHS80831 |
| Phylloporus subrubroviolus| BC022      | Thailand     | MHS80793 | MH614876 | MHS80813 | MHS80832 |

This study
| Species                          | Voucher | Origin       | atp6     | cox3     | rpb2    | Reference(s)                        |
|---------------------------------|---------|--------------|----------|----------|---------|-------------------------------------|
| *Phylloporus yunnanensis*       | OR0448  | China        | MG212554 | MH614877*| MG212598| Vadhanarat et al. 2018; *This study |
| *Porphyrellus castaneus*        | OR0241  | China        | MG212555 | MH614878*| MG212599| Vadhanarat et al. 2018; *This study |
| *Porphyrellus cf. nigroporphyra*| ADK3733 | Benin        | MH614687 | MH61479  | MH614735| This study                          |
| *Porphyrellus nigroporphyra*    | HKAS74938 | China       | –        | –        | KF112246| Wu et al. 2014                     |
| *Porphyrellus porphyra*         | MB97 023 | Germany      | DQ534609 | –        | GU187794| Wu et al. 2016                     |
| *Porphyrellus sp.*              | HKAS53366 | China       | –        | –        | KF112241| Wu et al. 2014                     |
| *Porphyrellus sp.*              | JD659   | Burundi      | MH614688 | MH614880 | MH614736| This study                          |
| *Porphyrellus sp.*              | OR0222  | Thailand     | MH614689 | MH614881 | MH614737| This study                          |
| *Pulveroboletus aff. ravenelii* | HKAS50203 | China       | –        | –        | KT990810| Wu et al. 2016                     |
| *Pulveroboletus aff. ravenelii* | ADK4360 | Togo         | KT823957 | MH614882*| KT824023| Raspé et al. 2016; *This study     |
| *Pulveroboletus aff. ravenelii* | ADK4650 | Togo         | KT823959 | MH614883*| KT824025| Raspé et al. 2016; *This study     |
| *Pulveroboletus brunneopunctatus* | HKAS52615 | China      | –        | –        | KT990813| Wu et al. 2016                     |
| *Pulveroboletus brunneopunctatus* | HKAS55369 | China      | –        | –        | KT990814| Wu et al. 2016                     |
| *Pulveroboletus brunneopunctatus* | HKAS74926 | China      | –        | –        | KT990815| Wu et al. 2016                     |
| *Pulveroboletus fuscus*         | OR0873  | Thailand     | KT823977 | MH614884*| KT824043| Raspé et al. 2016; *This study     |
| *Pulveroboletus macrosporus*    | HKAS57628 | China      | –        | –        | KT990812| Wu et al. 2016                     |
| *Pulveroboletus ravenelii*      | REH2565 | USA          | KU656355 | MH614885*| KU656357| *Raspé et al. 2016; *This study    |
| *Pulveroboletus sp.*            | HKAS4933 | China        | –        | –        | KF112262| Wu et al. 2014                     |
| *Pulveroboletus sp.*            | HKAS57605 | China      | –        | –        | KF112264| Wu et al. 2014                     |
| *Rhodactina aff. nigerrimus*    | OR0049  | Thailand     | KT823967 | MH614886*| KT824033| Raspé et al. 2016; *This study     |
| *Rhodactina griseus*            | HKAS52680 | China      | –        | –        | KF112179| Wu et al. 2014                     |
| *Rhodactina fuscus*             | HKAS59460 | China      | –        | –        | JQ282580| Hosen et al. 2013                  |
| *Rhodactina fuscus*             | OR0231  | China        | MG212556 | MH614887*| MG212600| Vadhanarat et al. 2018; *This study|
| *Rhodactina fuscus*             | HKAS63624 | China      | –        | –        | KT990829| Wu et al. 2016                     |
| *Rhodactina fuscus*             | HKAS74756 | China      | –        | –        | KT990830| Wu et al. 2016                     |
| *Rhodactina grisea*             | MB03 079 | USA          | KT823964 | MH614888*| KT824030| Raspé et al. 2016; *This study     |
| *Rhodactina grisea*             | HKAS65390 | China      | –        | –        | KF112178| Wu et al. 2014                     |
| *Rhodactina kauffmannii*        | OR0278  | China        | MG212557 | MH614889*| MG212601| Vadhanarat et al. 2018; *This study|
| *Rhodactina nigerrimus*         | HKAS53418 | China      | –        | –        | KT990824| Wu et al. 2016                     |
| *Rhodactina sinensis*           | HKAS59832 | China      | –        | –        | KT990827| Wu et al. 2016                     |
| *Rhodactina angolensis*         | HKAS59609 | China      | –        | –        | JQ282582| Hosen et al. 2013                  |
| *Rhodactina bimalayensis*       | CMU25117 | Thailand     | MG212558 | –        | MG212602, MG212605                  | Vadhanarat et al. 2018 |
| *Rhodactina rivulosa*           | SV170   | Thailand     | MG212560 | –        | MG212605| Vadhanarat et al. 2018             |
| *Rossbeevera cryptocephala*     | KPM-NC17843 | Japan     | KT581441 | –        | KC552072| Orihara et al. 2016                |
| *Rossbeevera cyanaeana*         | TNS-F-36986 | Japan      | KC552115 | –        | KC552068| Orihara et al. 2016                |
| *Rossbeevera griseoalutina*     | TNS-F-36989 | Japan      | KC552124 | –        | KC552076| Orihara et al. 2016                |
| *Rossbeevera pacificicus*       | KPM-NC23336 | New Zealand| KJ001064 | –        | KF222912| Orihara et al. 2016                |
| *Rossbeevera vittatissima*      | OSC61484 | Australia    | KC552109 | –        | JN378446| Orihara et al. 2016, 2012          |
| *Ryosynaga reticulata*          | HKAS52253 | China       | –        | –        | KT990786| Wu et al. 2016                     |
| *Ryosynaga rubina*              | HKAS53379 | China       | –        | –        | KF112274| Wu et al. 2014                     |
| *Ruhroboletus latipes*          | HKAS80358 | China       | –        | –        | KP055020| Zhao et al. 2014b                  |
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

| Species | Voucher | Origin | atp6 | cox3 | tef1 | rpb2 | Reference(s) |
|---------|---------|--------|------|------|------|------|---------------|
| Rubroboletus legitiae | VDK030936 | Belgium | KT823985 | MH614890* | KT824051 | KT824018 | Raspé et al. 2016; *This study |
| Rubroboletus rhodoangiogenus | BOTH4263 | USA | MG897416 | MH614891* | MG897426 | MG897436 | Phookamsk et al. 2019; *This study |
| Rubroboletus rhodoanthus | HKAS84879 | Germany | – | – | KT990831 | KT990468 | Wu et al. 2016 |
| Rubroboletus satanas | VDK030968 | Belgium | KT823986 | MH614892* | KT824052 | KT824019 | Raspé et al. 2016; *This study |
| Rubroboletus sinicus | HKAS86620 | China | – | – | KFI12146 | KFI11261 | Wu et al. 2014 |
| Rubroboletus sinicus | HKAS56304 | China | – | – | KF614983 | KP955031 | Zhao et al. 2014a; Zhao et al. 2014b |
| Rubroboletus sp. | HKAS86679 | China | – | – | KF112147 | KFI121662 | Wu et al. 2014 |
| Rugiboletus brunnescens | HKAS68586 | China | – | – | KF112197 | KFI121791 | Wu et al. 2014 |
| Rugiboletus brunnescens | HKAS83009 | China | – | – | KM605146 | KM605169 | Wu et al. 2015 |
| Rugiboletus brunnescens | HKAS83329 | China | – | – | KM605144 | KM605158 | Wu et al. 2015 |
| Rugiboletus extremiorientalis | HKAS76663 | China | – | – | KM605147 | KM605170 | Wu et al. 2015 |
| Rugiboletus extremiorientalis | OR0406 | Thailand | MG212562 | MH614893* | MG212607 | MG212647 | Vadhanarat et al. 2018; *This study |
| Singerocoma insindabili | TWH9199 | Guyana | MH645588 | MH645609 | MH645596 | LC043089* | *Henkel et al. 2016; This study |
| Singerocoma rubriflavus | TWH9585 | Guyana | MH645589 | MH645610 | MH645597 | – | This study |
| Spongiforma thailandica | DED7873 | Thailand | MG212563 | MH614894* | KF030436* | MG212648* | *Nuhn et al. 2013; Vadhanarat et al. 2018; **This study |
| Strobilomyces atrocauleanus | HKAS55368 | China | – | – | KT990839 | KT990476 | Wu et al. 2016 |
| Strobilomyces echinocephalus | OR0243 | China | MG212564 | – | MG212608 | MG212649 | Vadhanarat et al. 2018 |
| Strobilomyces mirandus | OR0115 | Thailand | KT823972 | MH614896* | KT824058 | KT824005 | Raspé et al. 2016; *This study |
| Strobilomyces strobilaceus | MB03 102 | USA | DQ534607* | – | AY883428 | AY786065 | *Binder and Hibbett 2006; Unpublished |
| Strobilomyces strobilaceus | RW103 | Belgium | KT823978 | MH614895* | KT824044 | KT824011 | Raspé et al. 2016; *This study |
| Strobilomyces verruculosus | HKAS55389 | China | – | – | KFI12259 | KFI12183 | Wu et al. 2014 |
| Strobilomyces sp. | OR0259 | China | MG212565 | MH614897* | MG212609 | MG212650 | Vadhanarat et al. 2018; *This study |
| Strobilomyces sp. | OR0319 | Thailand | MH614690 | MH614898 | MH614738 | MH614785 | This study |
| Strobilomyces sp. | OR0778 | Thailand | MG212566 | MH614899* | MG212610 | MG212651 | Vadhanarat et al. 2018; *This study |
| Strobilomyces sp. | OR1092 | Thailand | MH614691 | MH614900 | MH614739 | MH614786 | This study |
| Suillellus amygdalinus | 112605ba | USA | – | – | JQ327024 | – | Halling et al. 2012a |
| Suillellus luridus | VDK00241b | Belgium | KT823981 | MH614901* | KT824047 | KT824014 | Raspé et al. 2016; *This study |
| Suillellus queleti | VDK01185 | Belgium | MH645590 | MH645611 | MH645598 | MH645604 | This study |
| Suillellus subamygdalinus | HKAS57262 | China | – | – | KFI12174 | KFI12660 | Wu et al. 2014 |
| Suillellus subamygdalinus | HKAS53641 | China | – | – | KT990841 | KT990478 | Wu et al. 2016 |
| Suillellus subamygdalinus | HKAS74745 | China | – | – | KT990843 | KT990479 | Wu et al. 2016 |
| Sutorius aff. eacinus | HKAS52672 | China | – | – | KFI12207 | KFI12802 | Wu et al. 2014 |
| Sutorius aff. ecinus | HKAS56291 | China | – | – | KFI12208 | KFI12803 | Wu et al. 2014 |
| Sutorius austeraliensis | REPF9441 | Australia | MG212567 | MK386576* | JQ327032* | MG212652* | "Halling et al. 2012a; Vadhanarat et al. 2018; **This study |
| Sutorius ecinus | HKAS59657 | China | – | – | KT990887 | KT990505 | Wu et al. 2016 |
| Sutorius ecinus | REH9400 | USA | MG212568 | MH614902* | JQ327029* | MG212653 | "Halling et al. 2012a; Vadhanarat et al. 2018; **This study |
| Sutorius ecinus | HKAS50420 | China | – | – | KT990750 | KT990387 | Wu et al. 2016 |
| Sutorius sp. | OR0378B | Thailand | MH614692 | MH614903 | MH614740 | MH614787 | This study |
| Sutorius sp. | OR0379 | Thailand | MH614693 | MH614904 | MH614741 | MH614788 | This study |
| Species                              | Voucher         | Origin     | atp6 | cox3 | tef1 | rp2 | Reference(s)               |
|--------------------------------------|-----------------|------------|------|------|------|-----|----------------------------|
| Trogia boletus glutinosus            | HKAS53425       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Trogia boletus reticulatus           | HKAS53426       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Trogia boletus sp.                   | HKAS76661       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Turmalinea persicina                 | KPM-NC18001     | Japan      | KC552130 | –   | KC552082 | –   | Orihara et al. 2016       |
| Turmalinea yunnanensis               | KPM-NC18011     | Japan      | KC552138 | –   | KC552089 | –   | Orihara et al. 2016       |
| Tylascomium grieaudi                 | HKAS50281       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus alpinus                   | HKAS55438       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus atriporporens             | HKAS50208       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus balloni s.l.              | OR00039         | Thailand   | KT823965 | MH614905 | KT824031 | KT823998 | Raspé et al. 2016; *This study |
| Tylasporus brunneirubens             | HKAS53388       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus felleus                   | VDK00992        | Belgium    | KT823987 | MH614906 | KT824053 | KT824020 | Raspé et al. 2016; *This study |
| Tylasporus ferringineus              | BOTJ34369       | USA        | MH614694 | MH614907 | MH614742 | MH614789 | This study                 |
| Tylasporus otsurii                   | HKAS53401       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus sp.                       | HKAS74925       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus sp.                       | HKAS50229       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus sp.                       | JD938           | Gabon      | MH614695 | MH614908 | MH614743 | MH614790 | This study                 |
| Tylasporus sp.                       | OR0252          | China      | MG212569 | MH614909 | MG212611 | MG212654 | Vedanthanar et al. 2018; *This study |
| Tylasporus sp.                       | OR0542          | Thailand   | MG213530 | MH614910 | MG212612 | MG212655 | Vedanthanar et al. 2018; *This study |
| Tylasporus sp.                       | OR0583          | Thailand   | MH614606 | –     | MH614744 | –     | This study                 |
| Tylasporus sp.                       | OR1009          | Thailand   | MH614607 | MH614911 | –     | MH614791 | This study                 |
| Tylasporus vinaceipallidus           | HKAS50210       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Tylasporus vinaceipallidus           | OR0137          | China      | MG212571 | MH614912 | MG212613 | MG212656 | Vedanthanar et al. 2018; *This study |
| Tylasporus violaceobrunneus          | HKAS89443       | China      | –    | –    | –    | –   | Wu et al. 2016             |
| Tylasporus virens                    | KPM-NC-0018054  | Japan      | KC552174 | –   | KC552103 | –   | Unpublished                |
| Veloporphyrellus alpinus             | HKAS68301       | China      | JX984515 | –    | JX984550 | –   | Li et al. 2014b            |
| Veloporphyrellus concius             | REH8510         | Belize     | MH614698 | MH614913 | MH614745 | MH614792 | This study                 |
| Veloporphyrellus gniclioides         | HKAS55900       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Veloporphyrellus pseudorelatius       | HKAS94444       | China      | JX984519 | –    | JX984553 | –   | Li et al. 2014b            |
| Veloporphyrellus relatus             | HKAS63668       | China      | JX984523 | –    | JX984554 | –   | Li et al. 2014b            |
| Xanthoconium affine                  | NY00015399      | USA        | –    | –    | –    | –   | Wu et al. 2016             |
| Xanthoconium porphyllum              | HKAS90217       | China      | –    | –    | –    | –   | Wu et al. 2016             |
| Xanthoconium sp.                     | HKAS7651        | China      | –    | –    | –    | –   | Wu et al. 2016             |
| Xerocomellus chrysenteron            | VDK00821        | Belgium    | KT823984 | MH614914 | KT824050 | KT824017 | Raspé et al. 2016; *This study |
| Xerocomellus ciliaripes              | ADK51843        | Belgium    | KT823960 | MH614915 | KT824026 | KT823993 | Raspé et al. 2016; *This study |
| Xerocomellus communi                 | HKAS94067       | China      | –    | –    | –    | –   | Wu et al. 2016             |
| Xerocomellus corni                   | HKAS90206       | Philippines | –  | –    | –    | –   | Wu et al. 2016             |
| Xerocomellus poroportus              | VDK003011       | Belgium    | MH614678 | MH614846 | MH614727 | MH614773 | This study                 |
| Xerocomellus ripariellus             | VDK00404        | Belgium    | MH614697 | MH614916 | MH614746 | MH614793 | This study                 |
| Xerocomellus sp.                     | HKAS56311       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Xerocomus aff. macrobius             | HKAS56280       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Xerocomus fulvipes                   | HKAS76666       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Xerocomus magnipes                   | HKAS58000       | China      | –    | –    | –    | –   | Wu et al. 2014             |
| Xerocomus s.s.                       | OR0237          | China      | MHS80796 | –    | MHS80816 | MHS80835 | Chuannd et al. 2019        |
| Xerocomus s.s.                       | OR0443          | China      | MHS80797 | MH614917 | MHS80817 | MHS80836 | Chuannd et al. 2019; *This study |
| Xerocomus sp.                        | OR0053          | Thailand   | MH614975 | MH614918 | MHS80815 | MHS80834 | Chuannd et al. 2019; *This study |
| Xerocomus subrmoentouls              | VDK00987        | Belgium    | MG212572 | MH614919 | MG212614 | MG212657 | Vedanthanar et al. 2018; *This study |
| Zangia cirtina                       | HKAS52684       | China      | HQ326850 | –    | HQ326872 | –   | Li et al. 2011             |
| Zangia olivacea                       | HKAS5445        | China      | HQ326854 | –    | HQ326873 | –   | Li et al. 2011             |
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

| Species                  | Voucher     | Origin | Reference(s)           |
|--------------------------|-------------|--------|------------------------|
| Zangia olivaceobrunnea   | HKAS52272   | China  | HQ326857–HQ326876–Li et al. 2011 |
| Zangia roseola           | HKAS51137   | China  | HQ326858–HQ326877–Li et al. 2011 |
| Zangia roseola           | HKAS75046   | China  | KF112269–KF112791–Wu et al. 2014 |

**Figure 1.** Phylogenetic tree inferred from the four-gene dataset (atp6, cox3, rpb2 and tef1), including Cacaoporus species and selected Boletaceae using Maximum Likelihood and Bayesian Inference methods (ML tree is presented). The two Buchwaldoboletus and nine Chalciporus species in subfamily Chalciporoideae were used as outgroup. Most of the taxa not belonging to the Pulveroboletus group were collapsed into subfamilies. All genera clades in Pulveroboletus group that were highly supported were also collapsed. Bootstrap support values (BS ≥ 70%) and posterior probabilities (PP ≥ 0.90) are shown above the supported branches.

Zhu L. Yang, *S. obscureumbrinus* (Hongo) G. Wu & Zhu L. Yang, *S. rubriporus* G. Wu & Zhu L. Yang, *S. sanguineoides* G. Wu & Zhu L. Yang, *S. sanguineus* G. Wu & Zhu L. Yang, *S. tomentulosus* (M. Zang, W.P. Liu & M.R. Hu) G. Wu & Zhu L. Yang and
S. venenatus (Nagas.) G. Wu & Zhu L. Yang clustered in the Neoboletus clade with high support (85% BS and 0.95 PP), while the true Sutorius, including the typus generis S. eximius (Peck) Halling, Nuhn & Osmundson, formed a different well-supported clade (BS=100% and PP=1).

**Taxonomy**

*Cacaoporus* Raspé & Vadthanarat, gen. nov.
MycoBank: MB829655

**Etymology.** Refers to the dark, chocolate brown hymenophore and overall colour of basidiomata.

**Diagnosis.** Similar to the genus *Sutorius* in having brown basidiomata with brown encrustations in the flesh but differs from *Sutorius* in having the following combination of characters: brown to chocolate brown or greyish-brown to dark brown or blackish-brown basidiomata, without violet tinge, chocolate brown to dark brown hymenophore, tubes not separable from the pileus context, white to off-white basal mycelium which turns reddish-white to pale red when bruised, amygdaliform to ovoid with subacute apex in side view to ovoid basidiospores and dark brown spore deposit.

**Description.** Basidiomata stipitate-pileate with poroid hymenophore, small to medium-sized, dull, brown to greyish-brown to dark brown or blackish-brown. Pileus convex when young becoming plano-convex to slightly depressed with age, with deflexed to inflexed margin; surface even to subrugulose, minutely tomentose or slightly cracked at the centre; context soft, yellowish to greyish off-white then slightly greyish-orange to dull orange to greyish-brown when exposed to the air, patchy or marmorated with greyish-brown to dark brown, sometimes with scattered small dark brown to brownish-black encrustations, not or inconsistently reddening when cut. Hymenophore tubulate, adnate, subventricose to ventricose, slightly depressed around the stipe; tubes brown to greyish-brown to dark brown, not separable from the pileus context; pores regularly arranged, mostly roundish at first becoming slightly angular with age, sometimes irregular, elongated around the stipe, dark brown to greyish-brown at first, becoming brown to chocolate brown with age. Stipe central, terete to sometimes slightly compressed, cylindrical to sometimes slightly wider at the base; surface even, minutely tomentose, dull, dark brown to greyish-brown, basal mycelium white to off-white becoming reddish-white to pale red when touched; context solid, yellowish to orange white to yellowish-grey to pale orange to dull orange to reddish-grey, marmorated or virgated with brownish-grey to greyish-brown to dark brown, sometimes scattered with small reddish-brown to brownish-black fine encrustations, unchanged or inconsistently reddening when cut. Spore print dark brown.

**Basidiospores** amygdaliform to ovoid or ovoid with subacute apex in side view, thin-walled, smooth, slightly reddish to brownish hyaline in water, slightly yellowish to greenish hyaline in KOH or NH₄OH, inamylloid. **Basidia** 4-spored, clavate to nar-
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

rowly clavate without basal clamp connection. *Cheilocystidia* fusiform or cylindrical with obtuse apex, sometimes bent or sinuate, thin-walled, often scattered with small brownish-yellow to yellowish-brown crystals on the walls in KOH or NH₄OH. *Pleurocystidia* narrowly fusiform with obtuse apex or cylindrical to narrowly subclavate, sometimes bent or sinuate, thin-walled, densely covered with small reddish-brown to brownish dark encrustations on the walls when observed in H₂O, which are discoloured then dissolved in KOH or NH₄OH. *Pileipellis* a trichoderm becoming tangled trichoderm to tomentum, composed of thin-walled hyphae; terminal cells mostly slightly sinuate cylindrical to irregular with rounded apex or clavate to elongated clavate. *Stipitipellis* a trichoderm to tangled trichoderm or disrupted hymeniderm, composed of loosely to moderately interwoven cylindrical hyphae anastomosing at places. *Clamp connections* not seen in any tissue.

**Typus generis.** Cacaoporus tenebrosus

**Distribution.** Currently known from Thailand.

**Notes.** *Sutorius* most closely resembles the new genus. In the field, *Cacaoporus* is easily distinguished from the *Sutorius* by the following combination of characters: chocolate brown to dark brown to blackish-brown basidiomata, which are darker than in *Sutorius* and never purplish-brown like in *Sutorius* species; chocolate brown to dark brown hymenophore, which is much darker than in *Sutorius* and never reddish- to purplish-brown like in *Sutorius*; tubes that are not separable from the pileus context but can be separated in *Sutorius*; off-white basal mycelium that more or less turns red when bruised, which is never the case in *Sutorius*.

*Cacaoporus pallidicarneus* Vadthanarat, Raspé & Lumyong, sp. nov.

MycoBank: MB829657
Figs. 2a, 3a, 4a and 5

**Etymology.** Refers to the context, which is paler than in the other species, especially at the stipe base and in the pileus.

**Type.** THAILAND, Chiang Mai Province, Mae On District, 18°52′37″N, 99°18′23″E, elev. 860 m, 15 August 2015, Santhiti Vadthanarat, SV0221 (CMUB!, isotype BR!).

**Diagnosis.** *Cacaoporus pallidicarneus* is characterised by having a paler context than the other species and basidiospores that are amygdaliform or elongated amygdaliform to ovoid in side view, sometimes with subacute apex, shorter basidia and fusiform to narrowly bent fusiform to narrowly fusiform hymenophoral cystidia.

**Description.** *Basidiomata* small to medium-sized. *Pileus* (1.6)2.4–5.5 cm in diameter, convex when young becoming plano-convex with age; margin deflexed to inflexed, slightly exceeding (1–2 mm), surface even to subrugulose, minutely tomentose, dull, at first brown to greyish-brown to blackish-brown (8F3–4) sometimes paler (8C2) at places, becoming paler to greyish-brown (8E3–5) with age; *context* 4–9 mm thick half-way to the margin, soft, yellowish to greyish off-white then slightly
Figure 2. Habit of *Cacaoporus* species. a *C. pallidicarneus* (SV0221) b–d *C. tenebrosus* (b - SV0223, c - SV0224, d - SV0422). Scale bars: 1 cm (a–d).

Figure 3. Close-ups of hymenium/pileus context transition zone in *Cacaoporus* species, illustrating the non-separability of both tissues a *C. pallidicarneus* (OR0681) b *C. tenebrosus* (OR0654) c *C. tenebrosus* (SV0452). The transition between both tissues is particularly unmarked in *C. pallidicarneus* (a). Scale bars: 3 mm (a); 5 mm (b–c).

Pale orange to greyish-orange (6A3 to 6B3) when exposed to the air, with patchy or marmorated with greyish-brown (8E3) especially when young, scattered with reddish-brown to brownish-black of fine encrustations at places, slightly reddening when cut. **Stipe** central, terete or sometimes slightly compressed, cylindrical with slightly wider base, (2.0)2.8–3.7 × 0.4–0.7 cm, surface even, minutely tomentose, dull, greyish-brown to dark brown (8 E/F 3–4 to 8F2), basal mycelium white to off-white becoming pale red (7A3) when bruised; **context** solid, yellowish to greyish off-
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

white then orange white to pale orange (5A2–3) when exposed to the air, virgate to marmorate with brownish-grey (8F2), less so at the stipe base, at places scattered with brownish-black fine encrustations, unchanged to slowly slightly reddening when cut. **Hymenophore** tubulate, adnate, subventricose, slightly depressed around the stipe. **Tubes** (2)4–6 mm long half-way to the margin, brown to greyish-brown (8F3), not separable from the pileus context. **Pores** 0.4–1.5 mm wide at mid-radius, regularly arranged, mostly roundish to elliptical at first, becoming slightly angular with age, slightly elongated around the stipe, colour distribution even, dark brown to chocolate brown (9F4 to 10F3) at first, becoming chocolate brown to brown (10F4 to 7–8F4–5) with age. **Odour** rubbery. **Taste** slightly bitter at first, then mild. **Spore print** dark brown (8F4/5) in mass.

**Macrochemical reactions.** KOH, orange brown on cap, yellowish-black on stipe, yellowish-black on the pileus context and stipe context, brownish-black on hymenium; NH₄OH, yellowish-brown on cap, yellowish-orange on stipe, orangey yellow to yellowish-orange on the pileus context, stipe context and hymenium.

**Basidiospores** [437/7/5] (6.5–)6.7–7.7–8.6(–11.5) × (3.8–)4–4.6–5.1(–5.5) µm

\[ Q = (1.4–)1.48–1.68–1.9(–2.44). \]

From the type (3 basidiomata, \( N = 177 \)) (6.8–7–7.8–8.5(–9.1) × (4–)4.2–4.6–5(–5) µm, \( Q = (1.49–)1.5–1.69–1.9(–2.21), \) amygdaliform or elongated amygdaliform sometimes to ovoid with subacute apex in side view, ovoid in front view, thin-walled, smooth, slightly reddish to brownish hyaline in water, slightly yellowish to greenish hyaline in KOH or NH₄OH, inamyloid. **Basidia** 4-spored, (25.3–)25.4–29.7–33.8(–33.8) × (7.3–)7.3–8.4–9.8(–10) µm, clavate without basal clamp connection, slightly yellowish to brownish hyaline in KOH or NH₄OH; sterigmata up to 5 µm long. **Cheilocystidia** (16–)16.3–23.4–32.8(–34) × (5.5–)5.8–7.3–9(–9) µm, frequent, fusiform, thin-walled, yellowish to brownish hyaline to brown in KOH or NH₄OH. **Pleurocystidia** (44–)44.2–54.7–67.6(–68) × (5–)5–6–7(–7) µm, frequent, usually narrowly bent fusiform to narrowly fusiform with obtuse apex, thin-walled, yellowish to brownish hyaline in KOH or NH₄OH. **Hymenophoral trama** subdvergent to divergent, 62–175 µm wide, with 25–100 µm wide, regular to subregular mediostratum, composed of cylindrical, 4–7(11) µm wide.
Figure 5. Microscopic features of *Cacaoporus pallidicarneus* a basidiospores b basidia c cheilocystidia d pleurocystidia e caulocystidia f pileipellis g stipitpellis. Scale bars: 10 µm (a–b); 25 µm (c–e); 50 µm (f–g). All drawings were made from the type (SV0221).
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

hyphae, yellowish to brownish hyaline in KOH or NH₄OH. **Pileipellis** a trichoderm to tangled trichoderm at first, becoming a tomentum to tangled trichoderm with age, 65–110 µm thick, composed of firmly to moderately interwoven thin-walled hyphae; terminal cells 12–55 × 4–6 µm, slightly bent cylindrical with rounded apex, at places clavate to sub-clavate to elongated clavate, 16–34 × 8–10 µm, slightly dark to reddish to brownish in water, yellowish to brownish hyaline to yellowish-brown to slightly dark at places in KOH or NH₄OH. **Pileus context** made of moderately interwoven, thin-walled, hyaline hyphae, 6–12 µm wide. **Stipitipellis** a disrupted hymeniderm, 55–95 µm thick, composed of clavate cells, 11–37 × 5–8 µm, yellowish-brown to slightly dark in KOH or NH₄OH mixed with caulocystidia. **Caulocystidia** (17–)17–23.6–31(–31) × (5–)5–6.3–7(–7) µm, frequent, thin-walled, mostly yellowish-brown to slightly dark at places in KOH or NH₄OH. **Stipe context** composed of parallel, 3–7 µm wide hyphae, brownish hyaline to yellowish pale brown in KOH or NH₄OH. **Clamp connections** not seen in any tissue.

**Habitat and Distribution.** solitary to gregarious up to 4 basidiomata, on soil in hill evergreen forest dominated by Fagaceae trees, with a few *Dipterocarpus* spp. and *Shorea* spp. or in Dipterocarp forest dominated by *Dipterocarpus* spp. and *Shorea* spp. with a few *Lithocarpus* sp., *Castanopsis* sp. and *Quercus* sp. Currently known only from Chiang Mai Province, Northern Thailand.

**Additional specimens examined.** THAILAND, Chiang Mai Province, Mae Taeng District, 23 km marker (Ban Tapa), 19°08′50″N, 98°46′50″E, elev. 930 m, 2 August 2013, Olivier Raspé & Anan Thawthong, OR0681; Ban Mae Sae, 19°14′70″N, 98°38′70″E, elev. 960 m, 3 August 2013, Olivier Raspé & Anan Thawthong, OR0683; Muang District, Doi Suthep-Pui National Park, 18°48′37″N, 98°53′33″E, elev. 1460 m, 14 July 2016, Olivier Raspé, OR1306; Mae On District, 18°52′35″N, 99°18′16″E, elev. 860 m, 6 June 2018, Santhiti Vadthanarat, SV0451.

**Remarks.** We observed some small yellowish to reddish to brownish dark particles or crystals covering the cell walls in pileipellis, stipitipellis and on the hymenium, especially the cystidia and basidia when observed in water. The small particles or crystals were mostly dissolved in KOH.

*Cacaoporus pallidicarneus* differs from *C. tenebrosus* by its basidiomata context colour which is paler, especially at the stipe base. A combination of the following characters are also distinctive: spore shape which is amygdaliform or elongated amygdaliform or sometimes ovoid with subacute apex in side view and ovoid in front view, while *C. tenebrosus* has ovoid spores, shorter basidia and differently shaped hymenophoral cystidia (see note under *C. tenebrosus*). *Cacaoporus pallidicarneus* has a stipitipellis which is a disrupted hymeniderm composed of caulocystidia and clavate cells, while the other species has a loose trichoderm or tangled trichoderm. Interestingly, one collection (SV0402) had a slightly paler context than *C. tenebrosus* but not as pale as *C. pallidicarneus*. The phylogenetic analyses indicated that this collection might be a species different from *C. pallidicarneus* and *C. tenebrosus*. However, the specimen was immature and, therefore, more collections are needed before the species can be formally recognised.
**Cacaoporus tenebrosus** Vadthanarat, Raspé & Lumyong, sp. nov.
MycoBank: MB829656
Figs. 2b–d, 3b–c, 4b and 6

**Etymology.** Refers to the overall darkness of basidiomata, including the context.

**Type.** THAILAND, Chiang Mai Province, Mae On District, 18°52’37”N, 99°18’32”E, elev. 940 m, 15 August 2015, *Santhiti Vadthanarat*, SV0223 (holotype CMUB!, isotype BR!).

**Diagnosis.** *Cacaoporus tenebrosus* is characterised by having a darker context than the other species, longer basidia and cylindrical to narrowly subclavate hymenophoral cystidia.

**Description.** *Basidiomata* medium-sized. *Pileus* (2.3)3.1–5(9) cm in diameter, convex when young becoming plano-convex to slightly depressed with age; margin inflexed to deflexed, slightly exceeding (1–2 mm); surface even to subrugulose, minutely tomentose, slightly cracked at the centre, dull, greyish-brown (10F3) to dark brown to blackish-brown (8F4–5) to the margin; *context* 5–10 mm thick half-way to the margin, soft, marmorated, greyish-brown to dark brown (10F3–5) with greyish-brown (9B/D3), scattered with reddish-brown to brownish-black, fine encrustations at places, slightly reddening in paler spots when cut. *Stipe* central, terete, cylindrical to sometimes with slightly wider base, 4.3–7.0 × 0.7–1.4 cm, surface even, minutely tomentose, dull, dark brown to greyish-brown (9F4 to 10F3), basal mycelium white to off-white becoming reddish-white to pale red (7A3–4) when bruised; *context* solid, greyish-brown to dark brown (9–10F3–5) marmorated with reddish-grey (7/10B2), usually scattered with small reddish-brown to brownish-black fine encrustations, slightly reddening when cut. *Hymenophore* tubulate, adnate, subventricose to ventricose, slightly depressed around the stipe. *Tubes* (4)7–13 mm long half-way to the margin, brown to dark brown (8F3 to 9F4), not separable from the pileus context. *Pores* 0.8–2 mm wide at mid-radius, regularly arranged, mostly roundish at first, becoming slightly angular with age, sometime irregular, elongated around the stipe; colour distribution even, greyish-brown to dark brown (9F4) at first, becoming chocolate brown to brown (10F3 to 7–8F4–5) with age. *Odour* mild fungoid. *Taste* slightly bitter at first, then mild. *Spore print* dark brown (8/9F4) in mass.

**Macrochemical reactions.** KOH, yellowish then brown to black on cap, stipe, pileus context, stipe context and hymenium; NH₄OH, yellowish then orange to brown on cap, stipe, pileus context, stipe context and hymenium.

**Basidiospores** [290/8/6] (7.4–)7.7–8.4–9.2(–10) × (4.5–)5–5.3–5.7(–6.1) µm \( Q = (1.25–)1.44–1.57–1.77(–2) \). From the type (2 basidiomata, \( N = 134 \)) (7.5–)7.7–8.2–9(–9.9) × (4.9–)5–5.4–5.7(–5.9) µm, \( Q = (1.41–)1.43–1.54–1.71(–1.9) \), ovoid, thin-walled, smooth, slightly reddish to brownish hyaline in water, slightly yellowish to greenish hyaline in KOH or NH₄OH, inamyloid. **Basidia** 4-spored, (33.6–)34.3–38.8–45.8(–47) × (7.7–)7.8–9.5–10.8(–10.9) µm, clavate to narrowly clavate without basal clamp connection, yellowish to brownish hyaline to slightly dark in KOH or NH₄OH; sterigmata up to 5 µm long. **Cheilocystidia** (22–)22.1–28.7–37(–37) × (3–
**Figure 6.** Microscopic features of *Cacaoporus tenebrosus* **a** basidiospores **b** basidia **c** cheilocystidia **d** pleurocystidia **e** caulocystidia **f** pileipellis **g** stipitipellis. Scale bars: 10 µm (**a–b**); 25 µm (**c–e**); 50 µm (**f–g**). All drawings were made from the type (SV0223).
3.1–4.4–5(–5) µm, frequent, cylindrical with obtuse apex, sometimes bent or sinuate, thin-walled, yellowish-brown to dark brown in KOH or NH₄OH, often scattered with small brownish-yellow to yellowish-brown crystals on the walls in KOH or NH₄OH. **Pleurocystidia** (62–)62.5–81.5–99(–99) × (7–)7–8–9(–9) µm, frequent, cylindrical to narrowly subclavate, sometimes bent or sinuate, thin-walled, with yellowish-brown to slightly dark content in KOH or NH₄OH, densely covered with small reddish-brown to brownish dark encrustations on the walls when observed in H₂O, with some scattered small brownish-yellow to yellowish-brown crystals on the walls in KOH or NH₄OH. **Hymenophoral trama** subdivergent to divergent, 80–170 µm wide, with 60–80 µm wide of subregular mediostratum, composed of cylindrical, 4–8(11) µm wide hyphae, slightly yellowish to brownish hyaline in KOH or NH₄OH. **Pileipellis** a tangled trichoderm to tomentum at places, 70–110 µm thick, composed of moderately interwoven thin-walled hyphae; terminal cells 12–48 × 4–7 µm mostly slightly sinuate, cylindrical to irregular with rounded apex, at places clavate to elongated clavate terminal cells 18–33 × 7–9 µm, slightly dark to reddish to brownish dark in water, yellowish-brown to slightly dark in KOH or NH₄OH, scattered with small brownish-yellow to yellowish-brown crystals on the walls in KOH or NH₄OH. **Pileus context** made of moderately interwoven, thin-walled, hyaline hyphae, 7–12 µm wide. **Stipitipellis** a trichoderm to tangled trichoderm, 70–120 µm thick, composed of loosely to moderately interwoven cylindrical hyphae anastomosing at places, brownish dark to dark in KOH or NH₄OH. **Caulocystidia** (17–)17.6–29.4–46.3(–47) × (4–)4.1–5.5–6.9(–7) µm, clavate to cylindrical with obtuse apex, thin-walled, yellowish to brownish dark in KOH or NH₄OH. **Stipe context** composed of parallel, 4–6(12) µm wide hyphae, brownish hyaline to yellowish pale brown in KOH or NH₄OH. ** Clamp connections** not seen in any tissue.

**Habitat and distribution.** Gregarious (up to 9 basidiomata) to fasciculate or solitary, on soil in hill evergreen forest dominated by Fagaceae trees, with a few Dipterocarpus spp. and Shorea spp. or in Dipterocarp forest dominated by Dipterocarpus spp., Shorea spp. with a few Lithocarpus sp., Castanopsis sp. and Quercus sp. Currently known only from Chiang Mai Province, Northern Thailand.

**Additional specimens examined.** THAILAND, Chiang Mai Province, Mae Taeng District, 19°07'15"N, 98°43'55"E, elev. 910 m, 29 July 2013, Olivier Raspé & Benjarong Thongbai, OR0654; ibid. 19°7'29"N, 98°40'59"E, elev. 1010 m, 24 May 2018, Santhiti Vadthanarat, SV0422; Mae On District, 18°52'37"N, 99°18'19"E, elev. 850 m, 15 August 2015, Santhiti Vadthanarat, SV0224; ibid., 18°52'35"N, 99°18'16"E, elev. 860 m, 15 July 2017, Olivier Raspé, OR1435; ibid., 6 June 2018, Santhiti Vadthanarat, SV0452.

**Remarks.** There were many small yellowish to reddish to dark brown particles or crystals on the walls of pileipellis, stipitipellis and hymenium cells, especially on the cystidia and basidia when observed in water. The small particles or crystals are somewhat dissolved and discoloured in KOH.

Microscopically, *Cacaoporus tenebrosus* differs from *C. pallidicarneus* by having a darker context, longer basidia (33.6–47 µm vs. 25.3–33.8 µm, respectively), longer and larger...
hymenophoral cystidia, which also differ in shape (cylindrical to narrowly subclavate in *C. tenebrosus* but fusiform to narrowly fusiform in *C. pallidicarneus*). Phylogenetically, all *Cacaoporus* collections with a dark context formed a clade sister to *C. pallidicarneus* (BS = 85% and PP = 0.88), but some (SV0224 and SV0422) were genetically somewhat distant from the other collections. However, we could not find any difference in morphology. Consequently, we consider them as the same species (*C. tenebrosus*). Study of more collections is needed to confirm or infirm that they belong to the same species.

**Discussion**

Morphologically, *Cacaoporus* is most similar to *Sutorius*, with which it shares the overall brown colour of basidiomata and encrustations in the flesh. However, the genus *Cacaoporus* has darker basidiomata, especially the hymenophore and pore surface and is more chocolate brown, not reddish-brown or purplish-brown like *Sutorius*, tubes that are not separable from the pileus context whereas they are easily separable in *Sutorius*, white to off-white basal mycelium which becomes reddish when bruised, whereas in *Sutorius*, the basal mycelium is more or less white and unchanging. *Cacaoporus* also produces dark brown spore deposits whereas in *Sutorius*, spore deposits are reddish-brown (Halling et al. 2012). Microscopically, the two genera differ in the shape of basidiospores, which is amygdaliform to ovoid or ovoid with subacute apex in side view in *Cacaoporus*, whereas *Sutorius* produces narrowly ellipsoid to ellipsoid or subfusoid to fusoid basidiospores. Phylogenetically, *Cacaoporus* and *Sutorius* are not closely related - the two genera belong in two different clades of the *Pulveroboletus* group.

Some species in *Porphyrellus* E.-J. Gilbert also have brown to dark brown to umber basidiomata similar to *Cacaoporus*. However, *Porphyrellus* differs from the new genus in having white to greyish-white hymenophore when young, becoming greyish-pink to blackish-pink with age, white to pallid context in pileus and stipe variably staining blue and/or reddish when cut and white basal mycelium that does not turn red when bruised (Wolfe 1979; Wu et al. 2016). Some species in *Strobilomyces* Berk also share some characters with *Cacaoporus*, including dark brown basidiomata, white to off-white basal mycelium that turns red when bruised and the context turning red when cut. However, *Strobilomyces* species clearly differ from *Cacaoporus*, especially in the pileus surface, which is coarsely fibrillose or shows conical to patch-like scales, in the hymenophore, which is whitish-cream or greyish-brown or vinaceous drab and stains reddish then blackish when bruised and also basidiospores, which are subglobose to obtusely ellipsoid with reticulation or longitudinally striate (Gelardi et al. 2012; Antonín et al. 2015; Wu et al. 2016). Moreover, *Porphyrellus* and *Strobilomyces* were phylogenetically inferred to belong in subfamily Boletoideae (Wu et al. 2014, 2016; Vadthanarat et al. 2018) distinct from *Cacaoporus*.

Phylogenetically, *Cacaoporus* was monophyletic and clustered in a well-supported clade with the genera *Cyanoboletus* and *Cupreoboletus* and one undescribed taxon, *Boletus* p.p. sp. (specimen voucher JD0693), belonging to the *Pulveroboletus* group.
of Wu et al. (2014, 2016). *Cyanoboletus* and *Cupreoboletus*, however, differ from *Cacaoporus* in important morphological characters. The former two genera have a yellow hymenophore and yellowish context and tissues instantly discoloring dark blue when injured, and olive-brown spore deposits (Gelardi et al. 2014, 2015; Wu et al. 2016). The undescribed taxon represented by the voucher specimen JD0693, which clustered within the same clade as *Cacaoporus*, *Cyanoboletus* and *Cupreoboletus*, is also morphologically very different from *Cacaoporus*, in having yellow tubes, reddish pores, pale yellow to off-white context and reddish-brown pileus and stipe.

Our survey on the diversity of Boletes in the north of Thailand has been conducted since 2012 and no *Cacaoporus* has been found in the forests at elevations lower than 850 m. *Cacaoporus* was found only between 850 m and 1460 m elevation. However, more collections are needed to confirm that the distribution of the genus is restricted to mid- to high-elevation forests and does not occur in the lower elevation, drier forests. Most collections were made from Fagaceae-dominated, evergreen hill forests. The dominant trees in these forests belong to the Fagaceae, including *Lithocarpus*, *Castanopsis* and *Quercus*, but some Dipterocarpaceae may also occur. At the lower end of its elevation range, however, *Cacaoporus* was also found in Dipterocarpaceae-dominated forests (in which Fagaceae, especially *Quercus* spp., also occurs). The Dipterocarpaceae trees include *Dipterocarpus*, namely *D. tuberculatus*, *D. obtusifolius* and *Shorea*, namely *S. obtusa* and *S. siamensis*. The listed trees have previously been reported as ectomycorrhizal hosts of Boletaceae (Moser et al. 2009; Desjardin et al. 2009, 2011; Hosen et al. 2013; Arora and Frank 2014; Halling et al. 2014; Wu et al. 2018) and presumably are also the hosts for *Cacaoporus*.

Interestingly, our phylogeny indicated that the genera *Neoboletus* and *Sutorius* formed two different clades, both with high support (BS = 85% and PP = 0.95 for *Neoboletus*; BS = 100% and PP = 1 for *Sutorius*). Recently, Wu et al. (2016) synonymised *Neoboletus* with *Sutorius* because, in their phylogeny based on a four-gene dataset (28S+*tef1+rpb1+rpb2*), *Boletus obscureumbrinus*, a species morphologically more similar to *Neoboletus* than to *Sutorius*, seemed to cluster with *Sutorius* rather than with the *Neoboletus* species, although with neither ML nor BI support. Moreover, the *Neoboletus* clade was not supported either. Later, Chai et al. (2019) treated the two genera as different genetic lineages based on morphology and phylogeny (28S+ITS+*tef1+rpb2*), in which *B. obscureumbrinus* clustered with the other *Neoboletus* species in a well-supported clade. Our phylogenetic analyses, based on a different set of genes (*atp6+tef1+rpb2+cox3*), confirm the separation of the two genera *Neoboletus* and *Sutorius*. The differences in gene trees obtained could be explained by a long-branch attraction artefact in datasets with different taxon and gene samplings and/or problems in the dataset (e.g. suboptimal alignment). *Neoboletus obscureumbrinus* is quite atypical amongst *Neoboletus* species and its phylogenetic affinities within this genus remain unclear (Fig. 7).

*Cacaoporus* is the second novel bolete genus described from Thailand, the first one being *Spongiforma* Desjardin, Manfr. Binder, Roekring & Flegel, described in 2009 (Desjardin et al.). However, fungal diversity in Thailand is high and still poorly known (Hyde et al. 2018), with a large number of species and possibly genera that remain to be described.
Figure 7. Sub-tree of the phylogram in Fig. 1, showing the well-supported Sutorius and Neoboletus clades and the unsupported sister relationship of Neoboletus obscureumbrinus.
Acknowledgements

Financial support from the Graduate School, Chiang Mai University, is appreciated. The work was partly supported by a TRF Research Team Association Grant (RTA5880006) to SL and OR. OR is grateful to the Fonds National de la Recherche Scientifique (Belgium) for travel grants. The authors are grateful for the permit number 0907.4/4769 granted by the Department of National Parks, Wildlife and Plant Conservation, Ministry of Natural Resources and Environment for collecting in Doi Suthep-Pui National Park. Beatriz Ortiz-Santana (CFMR), Roy E. Halling (NY), and Terry W. Henkel are gratefully acknowledged for the loan of specimens.

References

Antonín V, Vizzini A, Ercole E, Leonardi M (2015) Strobilomyces pteroreticulosporus (Boletales), a new species of the S. strobilaceus complex from the Republic of Korea and remarks on the variability of S. confusus. Phytotaxa 219(1): 78–86. https://doi.org/10.11646/phytotaxa.219.1.6

Arora D, Frank JL (2014) Clarifying the butter Boletes: a new genus, Butyriboletus, is established to accommodate Boletus sect. Appendiculati, and six new species are described. Mycologia 106(3): 464–480. https://doi.org/10.3852/13-052

Binder M, Hibbett DS (2006) Molecular systematics and biological diversification of Boletales. Mycologia 98: 971–981. https://doi.org/10.1080/15572536.2006.11832626

Binder M, Larsson KH, Matheny PB, Hibbett DS (2010) Amylocorticariales ord. nov. and Jaa- piales ord. nov.: early diverging clades of agaricomycetidae dominated by corticioid forms. Mycologia 102: 865–880. https://doi.org/10.3852/09-288

Chai H, Xue R, Jiang S, Luo SH, Wang Y, Wu LL, Tang LP, Chen Y, Hong D, Liang ZQ, Zeng NK (2019) New and noteworthy boletes from subtropical and tropical China. MycoKeys 46: 55–96. https://doi.org/10.3897/mycokeys.46.31470

Chuankid B, Vadthanarat S, Hyde KD, Thongklang N, Zhao R, Lumyong S, Raspé O (2019) Three new Phylloporus species from tropical China and Thailand. Mycological Progress 18: 603–614. https://doi.org/10.1007/s11557-019-01474-6

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Desjardin DE, Binder M, Roekring S, Flegel T (2009) Spongiforma, a new genus of gasteroid boletes from Thailand. Fungal Diversity 37: 1–8.

Desjardin DE, Peay KG, Bruns TD (2011) Spongiforma squarepantsii, a new species of gasteroid bolete from Borneo. Mycologia 103(5): 1119–1123. https://doi.org/10.3852/10-433

Doyle JJ, Doyle JL (1990) Isolation of plant DNA from fresh tissue. Focus, 12: 13–15. https://doi.org/10.2307/2419362

Gelardi M, Vizzini A, Ercole E, Voyron S, Wu G, Liu XZ (2012) Strobilomyces echinocephalus sp. nov. (Boletales) from southwestern China, and a key to the genus Strobilomyces worldwide. Mycological Progress 12: 575–588. https://doi.org/10.1007/s11557-012-0865-3
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

Gelardi M, Simonini G, Ercole E, Vizzini A (2014) Alessioporus and Pulchroboletus gen. nov. (Boletaceae, Boletineae), two novel genera to accommodate Xerocomus ichnusanus and X. roseoalbidus from European Mediterranean basin: molecular and morphological evidence. Mycologia 106(6): 1168–1187. https://doi.org/10.3852/14-042

Gelardi M, Simonini G, Ercole E, Davoli P, Vizzini A (2015) Cupreoboletus (Boletaceae, Boletineae), a new monotypic genus segregated from Boletus sect. Luridi to reassign the Mediterranean species B. poikilochromus. Mycologia 107(6): 1254–1269. https://doi.org/10.3852/15-070

Halling RE, Desjardin DE, Fechner N, Arora D, Soytong K, Dentinger BTM (2014) New porcini (Boletus sect. Boletus) from Australia and Thailand. Mycologia 106: 830–834. https://doi.org/10.3852/13-340

Halling RE, Nuhn M, Fechner NA, Osmundson TW, Soytong K, Arora D, Hibbett DS, Binder M (2012a) Sutorius: a new genus for Boletus eximius. Mycologia 104(4): 951–961. https://doi.org/10.3852/11-376

Halling RE, Nuhn M, Osmundson T, Fechner N, Trappe JM, Soytong K, Arora D, Hibbett DS, Binder M (2012b) Affinities of the Boletus chromapes group to Royoungia and the description of two new genera, Harrya and Australopilus. Australian Systematic Botany 25: 418–431. https://doi.org/10.1071/SB12028

Henkel TW, Obase K, Husbands D, Uehling JK, Bonito G, Aime MC, Smith ME (2016) New Boletaceae taxa from Guyana: Binderoboletus segoi gen. and sp. nov., Guyanaporus albipodus gen. and sp. nov., Singerocomus rubriflavus gen. and sp. nov., and a new combination for Xerocomus inundabilis. Mycologia 108(1): 157–173. https://doi.org/10.3852/15-075

Hosen MI, Feng B, Wu G, Zhu XT, Li YC, Yang ZL (2013) Borofutus, a new genus of Boletaceae from tropical Asia: phylogeny, morphology and taxonomy. Fungal Diversity 58: 215–226. https://doi.org/10.1007/s13225-012-0211-8

Hyde KD, Norphanphoun C, Chen J, Dissanayake AJ, Doilom M, Hongsanan S, Jayawardena RS, Jeewon R, Perera RH, Thongbai B, Wanasinge DN, Witsirassameewong K, Tippromma S, Stadler M (2018) Thailand’s amazing diversity: up to 96% of fungi in northern Thailand may be novel. Fungal Diversity 93: 215–239. https://doi.org/10.1007/s13225-018-0415-7

Katoh K, Standley DM (2013) MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/msr010

Kornerup A, Wanscher JH (1978) Methuen Handbook of Colour (3rd edn). Eyre Methuen Ltd, London, 252 pp.

Kretzer AM, Bruns TD (1999) Use of atp6 in fungal phylogenetics: an example from the Boletales. Molecular Phylogenetics and Evolution 13: 483–492. https://doi.org/10.1006/mpve.1999.0680

Li YC, Feng B, Yang ZL (2011) Zangia, a new genus of Boletaceae supported by molecular and morphological evidence. Fungal Diversity 49: 125–143. https://doi.org/10.1007/s13225-011-0096-y

Li YC, Li F, Zeng NK, Cui YY, Yang ZL (2014a) A new genus Pseudoaustroboletus (Boletaceae, Boletales) from Asia as inferred from molecular and morphological data. Mycological Progress 13: 1207–1216. https://doi.org/10.1007/s11557-014-1011-1
Li YC, Ortiz-Santana B, Zeng NK, Feng B (2014b) Molecular phylogeny and taxonomy of the genus *Veloporphyrellus*. Mycologia 106(2): 291–306. https://doi.org/10.3852/106.2.291

Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). Molecular Phylogenetics and Evolution 35: 1–20. https://doi.org/10.1016/j.ympev.2004.11.014

Miller MA, Holder MT, Vois R, Midford PE, Liebowitz T, Chan L, Hoover P, Warnow T (2009) The CIPRES portals. CIPRES. http://www.phylo.org/portal2/home.

Moser AM, Frank JL, D’Allura JA, Southworth D (2009) Ectomycorrhizal communities of *Quercus garryana* are similar on serpentine and nonserpentine soils. Plant Soil 315: 185–194. https://doi.org/10.1007/s11104-008-9743-9

Neves MA, Binder M, Halling R, Hibbett D, Soytong K (2012) The phylogeny of selected *Phylloporus* species inferred from NUC-LSU and ITS sequences, and descriptions of new species from the Old World. Fungal Diversity 55(1): 109–123. https://doi.org/10.1007/s13225-012-0154-0

Nuhn ME, Binder M, Taylor AFS, Halling RE, Hibbett DS (2013) Phylogenetic overview of the Boletineae. Fungal Biology 117: 479–511. https://doi.org/10.1016/j.funbio.2013.04.008

Orihara T, Lebel T, Ge Z-W, Smith ME, Maekawa N (2016) Evolutionary history of the sequestrate genus *Rosseevera* (Boletaceae) reveals a new genus *Turmalinea* and highlights the utility of ITS minisatellite-like insertions for molecular identification. Persoonia 37: 173–198. https://doi.org/10.3767/003158516X691212

Orihara T, Smith ME, Shimomura N, Iwase K, Maekawa N (2012) Diversity and systematics of the sequestrate genus *Octaviania* in Japan: two new subgenera and eleven new species. Persoonia 28: 85–112. https://doi.org/10.3767/003158512X650121

Phookamsak R, Hyde KD, Jeewon R, Bhat DJ, Jones EBG, Maharachchikumbura SSN et al. (2019) Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Diversity. https://doi.org/10.1007/s13225-019-00421-w

Raspé O, Vadthanarat S, De Kesel A, Dreguef J, Hyde KD, Lumyong S (2016) *Pulveroboletus fragrans*, a new Boletaceae species from Northern Thailand, with a remarkable aromatic odor. Mycological Progress 15: 38. https://doi.org/10.1007/s11557-016-1179-7

Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97: 84–98. https://doi.org/10.3852/mycologia.97.1.84

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, et al (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Stamatakis A (2006) RAxML-vi-hpc: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Vadthanarat S, Raspé O, Lumyong S (2018) Phylogenetic affinities of the sequestrate genus *Rhodactina* (Boletaceae), with a new species, *R. rostratispora* from Thailand. MycoKeys 29: 63–80. https://doi.org/10.3897/mycokeys.29.22572
Cacaoporus, a new Boletaceae genus, with two new species from Thailand

Wolfe CB (1979) *Austroboletus* and *Tylopilus* subg. *Porphyrellus*, with emphasis on North American taxa. Bibliotheca Mycologica 69: 1–148.

Wu G, Feng B, Xu J, Zhu XT, Li YC, Zeng NK, Hosen MI, Yang ZL (2014) Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. Fungal Diversity 69: 93–115. https://doi.org/10.1007/s13225-014-0283-8

Wu G, Lee S ML, Horak E, Yang ZL (2018) *Spongispora temakensis*, a new boletoid genus and species from Singapore. Mycologia 110(5): 919–929. https://doi.org/10.1080/00275514.2018.1496387

Wu G, Li YC, Zhu XT, Zhao K, Han LH, Cui YY, Li F, Xu JP, Yang ZL (2016) One hundred noteworthy boletes from China. Fungal Diversity 81: 25–188. https://doi.org/10.1007/s13225-016-0375-8

Wu G, Zhao K, Li YC, Zeng NK, Feng B, Halling RE, Yang ZL (2015) Four new genera of the fungal family Boletaceae. Fungal Diversity 81: 1–24. https://doi.org/10.1007/s13225-015-0322-0

Zeng NK, Cai Q, Yang ZL (2012) *Corneroboletus*, a new genus to accommodate the southeastern Asian *Boletus indecorus*. Mycologia 104(6): 1420–1432. https://doi.org/10.3852/10-326

Zeng NK, Wu G, Li YC, Liang ZQ, Yang ZL (2014) *Crocinoboletus*, a new genus of Boletaceae (Boletales) with unusual polyene pigments boletocrocins. Phytotaxa 175: 133–140. https://doi.org/10.11646/phytotaxa.175.3.2

Zhao K, Wu G, Feng B, Yang ZL (2014a) Molecular phylogeny of *Caloboletus* (Boletaceae) and a new species in East Asia. Mycological Progress 13: 1127–1136. https://doi.org/10.1007/s11557-014-1001-3

Zhao K, Wu G, Yang ZL (2014b) A new genus, *Rubroboletus*, to accommodate *Boletus sinicus* and its allies. Phytotaxa 188: 61–77. https://doi.org/10.11646/phytotaxa.188.2.1

Zhu XT, Wu G, Zhao K, Halling RE, Yang ZL (2015) *Hourangia*, a new genus of Boletaceae to accommodate *Xerocomus cheoi* and its allied species. Mycological Progress 14: 37. https://doi.org/10.1007/s11557-015-1060-0