Taxonomy and phylogeny of Resinicium sensu lato from Asia-Pacific revealing a new genus and five new species (Hymenochaetales, Basidiomycota)

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ABSTRACT

Resinicium, belonging to Hymenochaetales, Agaricomycetes, is a worldwide genus of corticioid wood-inhabiting fungi. To improve the knowledge of species diversity within the Hymenochaetales, two dozen specimens from Asia-Pacific preliminarily identified to be members of Resinicium sensu lato were carefully studied from morphological and phylogenetic perspectives. From these specimens, a new monotypic genus Skvortzoviella, and five new species, viz. Resinicium austroasianum, R. lateastrocystidium, Skvortzovia dabieshanensis, S. qilianensis and Skvortzoviella lenis are described; moreover, a new basal lineage of Resinicium represented by a Vietnam specimen and three Chinese specimens of S. pinicola are identified. The six newly proposed taxa are morphologically compared with related genera and species, while the family positions of Resinicium, Skvortzovia, and Skvortzoviella within the Hymenochaetales are still ambiguous. In addition, the ancestral geographic origin of Resinicium, even though inconclusive, is now thought to be Asia-Pacific instead of tropical America as previously assumed.

KEYWORDS: Corticioid fungi, Skvortzovia, Skvortzoviella, Wood-inhabiting fungi, Six new taxa

INTRODUCTION

Resinicium, a worldwide genus of corticioid wood-inhabiting fungi, was erected for Hydnum bicolor and Corticium furfuraceum with the former as the generic type (Parmasto 1968). Although this genus is treated as a member of Rickenellaceae within Hymenochaetales (He et al. 2019; Olariaga et al. 2020), the corresponding phylogenetic analysis did not have a comprehensive sampling throughout this order (Olariaga et al. 2020). Due to the ambiguous circumscription of families within Hymenochaetales, the taxonomic position of Resinicium at the family level was not fully clarified from the phylogenetic perspective.

A total of 22 species have been assigned to Resinicium at some stage (Index Fungorum: http://www.indexfungorum.org/Names/Names.asp). However, phylogenetic analyses have indicated that Resinicium is not a monophyletic genus (Larsson et al. 2006; Nakasone 2007). Within Hymenochaetales, R. aculeatum, R. bicolor, R. confertum, R. friabile, R. grandisporum, R. monticola, R. mutabile, R. rimulosum, R. saccharicola, and R. tenue were accepted to be members of Resinicium sensu stricto, whereas R. furfuraceum, R. furfurellum, R. meridionale and R. pinicola were included in the clade of Resinicium sensu lato and now are put in Skvortzovia (Larsson et al. 2006; Nakasone 2007; Telleria et al. 2008; Gruhn et al. 2017; Gruhn and Hallenberg 2018). Skvortzovia was originally erected as a monotypic genus for Odontia furfurilla (Hjortstam and Bononi 1987). Besides the above-
mentioned four species, *Phlebia georgica* was also combined into *Skvortzovia*, bringing the number of species in that genus to five (Gruhn and Hallenberg 2018).

Morphologically, *Resinicium* is characterized by resupinate, thin, soft basidiomes with smooth to odontoid hymenia, a monomitic hyphal system mainly with clamp connections or with simple septa in few species, the presence of astrocytidia, and thin-walled, smooth, ellipsoid to cylindrical basidiospores. *Skvortzovia* is quite similar to *Resinicium* but differs in the absence of astrocytidia.

In this study, we focus on *Resinicium sensu lato.* represented by specimens from the Asia-Pacific region including China, Vietnam, Malaysia, and Australia. Two new species are described in each of *Resinicium* and *Skvortzovia*, while a new monotypic genus typified by a new species without a confirmed position at the family level is introduced.

**MATERIALS AND METHODS**

**Morphological examination**

The studied specimens are deposited at the Fungarium, Institute of Microbiology, Chinese Academy of Sciences (HMAS), Beijing, China. The specimens were observed with Leica M125 (Wetzlar, Germany) and Nikon SMZ 1500 (Tokyo, Japan) stereomicroscopes and an Olympus BX 43 light microscope (Tokyo, Japan) at magnifications up to 1000×. Special color terms follow Petersen (1996). Microscopic procedures followed Wang et al. (2020). Specimen sections were mounted in Cotton Blue (CB), Melzer’s reagent (IKI), and 5% potassium hydroxide (KOH). All measurements were made from materials in CB. When presenting the variation of basidiospore sizes, 5% of the measurements were excluded from each end of the range and are given in parentheses. Drawings were made with the aid of a drawing tube. The following abbreviations are used in the descriptions: L = mean basidiospore length (arithmetic average of all measured basidiospores), W = mean basidiospore width (arithmetic average of all measured basidiospores), Q = variation in the L/W ratios between the studied specimens, and (a/ b) = number of basidiospores (a) measured from given number (b) of specimens.

**Molecular sequencing**

Crude DNA was extracted from dry specimens as templates for subsequent PCR amplification using CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies, Beijing, China). The primer pairs ITS5/ITS4 (White et al. 1990; Gardes and Bruns 1993) and LR0R/LR7 (Vilgalys and Hester 1990) were selected for amplifying ITS and nLSU regions, respectively. The PCR procedures were as follows: for ITS region, initial denaturation at 95 °C for 3 min, followed by 34 cycles at 94 °C for 40 s, 57.2 °C for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 10 min; for nLSU region, initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 47.2 °C for 1 min and 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR products were sequenced with the same primers used in PCR amplification at the Beijing Genomics Institute, Beijing, China. All newly generated sequences are deposited in GenBank ([https://www.ncbi.nlm.nih.gov/genbank/](https://www.ncbi.nlm.nih.gov/genbank/); Table 1).

**Phylogenetic analyses**

Besides the newly generated sequences, additional related sequences were also downloaded from GenBank (Table 1) for inclusion in the phylogenetic analyses. Firstly, the combined dataset of ITS and nLSU regions (1) was used to explore the phylogenetic positions of the newly studied specimens within *Hymenochaetales*. All vouchers of *Hymenochaetales* and *Polyporales* listed in Table 1, each with both ITS and nLSU sequences available, were included as ingroup taxa, while *Auricularia cornea* from *Auriculariales* was selected as an outgroup taxon (Hibbett et al. 2007). Due to previous phylogenetic studies focusing on *Resinicium* being mainly based solely on the ITS region, a voucher- and species-abundant ITS dataset of *Resinicium* (2), comprising all vouchers of *Resinicium* in Table 1, was used to further differentiate species identities within this genus. Finally, another combined dataset of ITS and nLSU regions (3) was used to perform a biogeographic analysis of *Resinicium*. All vouchers of *Resinicium* listed in Table 1, each with both ITS and nLSU sequences available, were included in this dataset. No outgroup taxa were selected for datasets 2 and 3.

All datasets were aligned using MAFFT 7.110 (Katoh and Standley 2013) under the G-INS-i option (Katoh et al. 2005). Regarding the combined datasets of the ITS and nLSU regions, each region was aligned separately and then the alignments of the two regions were concatenated as a single alignment. The best-fit evolutionary models of alignments for phylogenetic analyses were estimated using jModelTest (Guindon and Gascuel 2003; Posada 2008) under Akaike information criterion.

Regarding datasets 1 and 2, Maximum Likelihood (ML) and Bayesian Inference (BI) methods were utilized for phylogenetic analyses. The ML method was conducted using raxmlGUI 1.2 (Silvestro and Michalak 2012; Stamatakis 2006) with calculation of bootstrap (BS) replicates under the auto FC option (Pattengale et al. 2010). The BI method was conducted using MrBayes 3.2 (Ronquist et al. 2012). Two independent runs were employed, and each run had four chains and started from random trees. Trees were sampled every 1000th generation, and the first 25% of trees were
| Order               | Species              | Voucher | GenBank accession number |
|---------------------|----------------------|---------|--------------------------|
|                     |                      |         | ITS                      | LSU                      |
| Auriculariales      | Auricularia brasiliana | URM 85567 | NR151845                 | NG057066                 |
| Hymenochaetales     | Alloclavaria purpurea | T.Niskanen 01-053 | MF319053 | MF318894 |
|                     | Atheloderma mirabile  | TAA 169235 | DQ873592                 | DQ873592                 |
|                     | Basidioradulum radula | AFTOL-ID 451 | DQ234537                 | AY700184                 |
|                     | Blasphalia pseudogrisea | P.Hojer 4539 | MF319045                 | MF318896                 |
|                     | Bridgeaporus sinensis | Cui 10,013 | KY131832                 | KY131891                 |
|                     | Coltricia perennis   | Cui 10,319 | KU360687                 | KU360653                 |
|                     | Contumycetes rostellus | Redhead 7501 | U66452 | U66452 |
|                     | Fasciodonta brasiliensis | MSK-F 724Sa | MK575201 | MK598734 |
|                     | Fibricium rude       | CBS 339.66 | MH858815                 | MH870454                 |
|                     | Formitiporia hartigii | Cui 9914 | KY750527                 | MT319381                 |
|                     | Globulicium hiemale  | Hjm 19,007 | DQ873595                 | DQ873595                 |
|                     | Gyroflexus brevibasiatus | Lutzoni 930,826-1 | U66441 | U66441 |
|                     | Haplostichia halonata | HHB-17058 | MK575207 | MK598738 |
|                     | Hymenochaeta rubiginosa | He 1049 | JQ‘16407                 | JQ279667                 |
|                     | Hyphodontia alutaria  | KHL 11889 | DQ873603                 | DQ873603                 |
|                     | Kneiffiella abieticola | KHL 12498 | DQ873601                 | DQ873601                 |
|                     | Leucophellinus hobsonii | Cui 6468 | KT203288                 | KT203309                 |
|                     | Loreleia marchantiae  | Lutzoni 910826-1 | U66432 | U66432 |
|                     | Lyomyces grisellinaea | KHL 12971 | DQ873651                 | DQ873651                 |
|                     | Muscinupta laevis    | JJ 020909 | EU118621                 | EU118621                 |
|                     | Neaantrodia gypseae  | Cui 10372 | KT203290                 | MT319396                 |
|                     | Nigrofomes melanoporus | Vlasak 1704-39 | MF629835 | MF629831 |
|                     | Odonticium romellii  | KHL 1514b | DQ873639                 | DQ873639                 |
|                     | Peniophorea praeternissa | KHL 13164 | DQ873597                 | DQ873597                 |
|                     | Phellinidium ferrugineofuscum | Cui 10042 | KR350573 | MT319388 |
|                     | Repetobasidium conicum | KHL 12338 | DQ873647                 | DQ873647                 |
| Resinicium austroasianum | LWZ 20171014-3 | MW414503 | MW414449                 |
|                     |                       | LWZ 20180417-5 | MW414504 | MW414450 |
|                     |                       | LWZ 20180417-28 | MW414505 | MW414451 |
|                     |                       | LWZ 20180517-42 | MW414506 | MW414452 |
|                     |                       | LWZ 20180518-2 | MW414507 | MW414453 |
|                     | R. bicolor            | O.Miettinen 14049 | MF319079 | MF319009 |
|                     |                       | FP-133575 | DQ826533                 |
|                     |                       | HHB10731 | DQ826534                 |
|                     |                       | JLL13731 | DQ826535                 |
|                     |                       | FP-133695 | DQ826536                 |
|                     |                       | HHB 10108 | DQ826537                 |
|                     |                       | AFTOL-ID 810 | DQ218310 |             |
|                     |                       | O3 | JQ765682 |             |
|                     |                       | UC2022885 | KP814209 |             |
|                     |                       | TENNS7741 | AF518763 |             |
|                     |                       | GEL2071 | DQ340321 |             |
| Order | Species            | Voucher         | GenBank accession number |
|-------|--------------------|-----------------|--------------------------|
|       |                    |                 | ITS                      | LSU                       |
|       | R. confertum       | FP-102863       | DQ826538                 |
|       | R. friabile        | FP-102983       | DQ826545                 | DQ863690                 |
|       | R. friabile        | CBS 126043      | MH864058                 | MH875513                 |
|       | R. friabile        | FP-102803       | DQ826541                 |
|       | R. friabile        | PR-1380         | DQ826542                 |
|       | R. friabile        | FP-150153       | DQ826543                 |
|       | R. friabile        | ECCO-146        | DQ826544                 |
|       | R. friabile        | MS77            | KJ831948                 |
|       | R. grandisporum    | GGGUY13-008     | KY995325                 |
|       | R. grandisporum    | GGGUY13-030     | KY995326                 |
|       | R. grandisporum    | GGGUY13-031     | KY995327                 |
|       | R. grandisporum    | GGMAR12-326     | KY995329                 |
|       | R. lateastrocystidium | LWZ 20180414-13 | MW414508 | MW414454 |
|       | R. lateastrocystidium | LWZ 20180414-15 | MW414509 | MW414455 |
|       | R. lateastrocystidium | LWZ 20180416-10 | MW414510 | MW414456 |
|       | R. monticola       | FP-150360       | DQ826552                 | DQ863697                 |
|       | R. monticola       | FP-102832       | DQ826550                 |
|       | R. monticola       | FP-150061       | DQ826551                 |
|       | R. monticola       | FP-150355       | DQ826553                 |
|       | R. monticola       | FP-150407       | DQ826554                 |
|       | R. monticola       | FP-150332       | DQ826555                 |
|       | R. mutabile        | FP-102989       | DQ826556                 | DQ863699                 |
|       | R. mutabile        | PR-1366         | DQ826557                 |
|       | R. mutabile        | GGGUY12-087     | KY995322                 |
|       | R. mutabile        | GGMAR15-174     | KY995330                 |
|       | R. mutabile        | GGMAR15-175     | KY995331                 |
|       | R. rimulosum       | FP-150328       | DQ826546                 |
|       | R. saccharicola    | KUC20131022-12  | KJ668464                 |
|       | R. saccharicola    | FP-1502754      | DQ826547                 | DQ863691                 |
|       | R. saccharicola    | FP-102841       | DQ826548                 |
|       | R. saccharicola    | FP-102843       | DQ826549                 |
|       | R. saccharicola    | GGGUY12-118     | KY995323                 |
|       | R. saccharicola    | GGGUY12-158     | KY995324                 |
|       | R. saccharicola    | GGMAR12-230     | KY995328                 |
|       | R. tenue           | FP-150354       | DQ826539                 |
|       | R. tenue           | FP-150251       | DQ826540                 |
|       | R. sp.             | 026             | KC785591                 |
|       | R. sp.             | ASR-272         | GU973812                 |
|       | R. sp.             | ASR-290         | GU973828                 |
|       | R. sp.             | GSR1            | FJ79463                  |
|       | R. sp.             | LWZ 20171015-31 | MW414511 | MW414457 |
|       | R. sp.             | P.Salo 1882     | MF319088                 | MF319027                 |
|       | Rickenella fibula  |                 |                          |                          |
removed, while the other 75% of trees were retained for constructing a 50% majority consensus tree and calculating Bayesian posterior probabilities (BPPs). Tracer 1.5 (http://tree.bio.ed.ac.uk/software/tracer/) was used to judge whether chains converged.

A consensus tree for the alignment resulting from dataset 3 was generated by BI method using BEAST v1.10.4 (Suchard et al. 2018). Trees were sampled every 1000th generation from a total of 50 million generations and the first 10% of the sampled trees were removed as burn-in. Chain convergence recorded in the resulting log file was determined using Tracer 1.5. The consensus tree was used for biogeographic analysis using RASP 4.2 under the Bayesian Binary MCMC (BBM) analysis with default parameters (Yu et al. 2015, 2020). Six geographic origins, viz. Asia-Pacific, Europe, North America, South

### Table 1 Information of species used in phylogenetic analyses (Continued)

| Order | Species                        | Voucher  | GenBank accession number |
|-------|--------------------------------|----------|--------------------------|
|       |                                |          |                          |
|       | Rigidoporus corticola          | Dai 12652| KF111018 KF111020        |
|       | Sidera lunata                  | JS 15063 | DQ873593 DQ873593        |
|       | Skvortzovia dabieshanensis     | LWZ 20201012-22 MW414512 MW414458 |
|       |                                | LWZ 20201014-18 MW414513 MW414459 |
|       |                                | LWZ 20201017-55 MW414514 MW414460 |
|       | S. furfuracea                  | KHL 11738| DQ873648 DQ873648        |
|       | S. furfurella                  | KHL 10180| DQ873649 DQ873649        |
|       | S. georgica                    | KHL 12019| DQ873645 DQ873645        |
|       | S. pinicola                    | KHL 12224| DQ873637 DQ873637        |
|       |                                | LWZ 20180921-6 MW414515 MW414461 |
|       |                                | LWZ 2020111-18 MW414516 MW414462 |
|       |                                | LWZ 2020113-15 MW414517 MW414463 |
|       | S. qilianensis                 | LWZ 20180904-16 MW414518 MW414464 |
|       |                                | LWZ 20180904-18 MW414519 MW414465 |
|       |                                | LWZ 20180904-20 MW414520 MW414466 |
|       | Skvortziella lenis             | LWZ 20180921-7 MW414521 MW414467 |
|       |                                | LWZ 20180921-17 MW414522 MW414468 |
|       |                                | LWZ 20180921-25 MW414523 MW414469 |
|       |                                | LWZ 20180921-32 MW414524 MW414470 |
|       |                                | LWZ 20180922-39 MW414525 MW414471 |
|       |                                | LWZ 20180922-61 MW414526 MW414472 |
|       | Sphaerobasidium minutum        | KHL 11714 | DQ873652 DQ873653        |
|       | Trichaptum abietinum           | NH 12842  | AF347104 AF347104        |
|       | Tubulicrinis globisporus       | KHL 12133 | DQ873655 DQ873655        |
|       | T. hirtellus                   | KHL 11717 | DQ873657 DQ873657        |
|       | Xylodon asperus                | KG Nilsson 2004b DQ873606 DQ873607 |
|       | Polyporales                    | TFRI 274  | EU232187 EU232277        |
|       | Aboritiporus biennis           | FCUG 960  | EU232182 EU232266        |
|       | Antridiella semisupina         | PR1209    | JN165009 JN164793        |
|       | Earliella scabrosa             | Otto Miettinen 12388 JQ700297 JQ700297 |
|       | Formitopsis betulina           | Dai 13080  | KJ734260 KJ734264        |
|       | Fragiliporia fragilis          | Dai 13559  | KJ734261 KJ734265        |
|       | Melanoporia nigra              | X1735     | KC543172 KC543172        |
|       | Polyporus tuberaster           | Wei 2577   | AB474086 XX00131         |
|       | Radulodon aneinus              | MUAF 888  | EU340895 EU368503        |

The newly sequenced vouchers are in bold
America, tropical America and Africa were set according to voucher information.

RESULTS

A total of 24 specimens preliminarily identified to Resinicium sensu lato were studied further. ITS and nLSU regions were newly generated from all these specimens (Table 1).

The combined dataset of ITS and nLSU regions (1) from 78 collections generated a concatenated alignment of 2399 characters with GTR + I + G as the best-fit evolutionary model. The ML search stopped after 250 BS replicates. In BI, all chains converged after 50 million generations with an average standard deviation of split frequencies of 0.002644, which was indicated by all effective sample sizes (ESSs) above 13,600 and the potential scale reduction factors (PSRFs) close to 1.000. ML and BI methods generated similar topologies in main lineages, and thus only the topology generated by the ML method is presented along with BS values and BPPs above 50% and 0.8, respectively, at the nodes (Fig. 1). The phylogeny generated by this dataset well supported Hymenochaetales as an independent order (BS = 92%, BPP = 1). Within Hymenochaetales, the family rank was not resolved, whereas at the generic rank Resinicium was fully supported and Skvortzia was strongly supported (BS = 98%, BPP = 1). In the genera Resinicium and Skvortzia, three (one including a single specimen LWZ 20171015-31 from Vietnam) and two new lineages, respectively, emerged, and three studied specimens were grouped with Skvortzia pinicola with full support. Moreover, an independent clade from other sampled genera and species composed of six newly studied specimens was also fully supported.

The ITS dataset of Resinicium (2) from 58 collections generated an alignment of 645 characters with GTR + I + G as the best-fit evolutionary model. The ML search stopped after 300 BS replicates. In BI, after 10 million generations, all chains converged with an average standard deviation of split frequencies of 0.002680, which was indicated by all ESSs above 5500 and the PSRFs equal to 1.000. ML and BI methods generated similar topologies in main lineages. Therefore, the topology inferred from ML method was presented along with BS values and BPPs above 50% and 0.8, respectively, at the nodes (Fig. 2). The midpoint-rooted tree recovered nine known species of Resinicium, while the newly studied specimens formed three independent lineages (one including a single specimen LWZ 20171015-31 from Vietnam) as in the phylogeny inferred from dataset 1.

Taking both morphological characters and the phylogenies inferred from datasets 1 and 2 into consideration, two new species from each of Resinicium and Skvortzia, and a new monotypic genus typified by a new species within Hymenochaetales are described below. The new lineage with a single specimen LWZ 20171015-31 from Vietnam in Resinicium is treated as R. sp. instead of being described as a new species until more collections that group with LWZ 20171015-31 are available and carefully studied.

Dataset 3 from 15 collections generated a concatenated alignment of 1457 characters. The best-fit evolutionary model for this alignment was estimated as GTR + I + G. Chain convergence was indicated by all ESSs above 3500. The midpoint-rooted phylogeny successfully resolved the species relationships within Resinicium and the ancestral geographic origin of Resinicium was estimated to be Asia-Pacific (Fig. 3).

TAXONOMY

Resinicium austroasianum Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, sp. nov. (Figs. 4–5)

Mycobank: MB 840227.

Etymology: austroasianum (Lat.), refers to South Asia.

Diagnosis: Similar to R. monticola in the absence of halocystidia; however, R. monticola differs by its narrower basidiospores (2.8–3.2 μm in width) and rarely cracked basidioles (Nakasone 2007).

Type: Malaysia: Selangor: Kota Damansara Community Forest Reserve, on fallen angiosperm branch, 17 Apr. 2018, Li-Wei Zhou, LWZ 20180417-5 (HMAS– holotype).

Description: Basidiomes annual, resupinate, closely adnate, widely effused, not easily separable, thin, crustose, white to cream when fresh, pale yellow to curry-yellow with age, usually cracked into polygons. Hymenophore white to cream when fresh, pale yellow to curry-yellow with age, usually cracked into polygons. Hymenial hyphae obscured from numerous crystal clusters, frequently branched, often collapsed and indistinct, sometimes with denuded spines, 2–3 μm diam. Subhymenial hyphae obscured from numerous crystal clusters, frequently branched, hyaline, compact and agglutinated, 1.5–2.5 μm diam. Astrocytidia extremely abundant in hymenium and subhymenium, often developing both terminally and laterally on hyphae, hyaline, thin-walled, 7–20 × 1–3 μm, 1–1.5 μm diam at base, at apex a stellate cluster of hyaline crystals, up to 4–6 μm diam. Hymenial leptocystidia numerous, cylindrical with obtuse apex, 10–30 × 2–3 μm, with a basal clamp. Basidia cylindrical, often with a median constriction, four sterigmata, 10–20 × 4–6 μm, tapering to 2–3 μm diam with a clamp connection at base; basidioles similar in shape to basidia, but smaller. Basidiospores
Fig. 1 Phylogenetic positions of the newly studied specimens of *Resinicium sensu lato* within the *Hymenochaetales* inferred from the combined dataset of ITS and nLSU regions. The topology generated by the maximum likelihood method is presented along with the bootstrap values and the Bayesian posterior probabilities above 50% and 0.8, respectively, at the nodes.
Fig. 2 Species identities of *Resinicium* differentiated by ITS-based phylogeny. The midpoint-rooted tree generated by the maximum likelihood method is presented along with the bootstrap values and the Bayesian posterior probabilities above 50% and 0.8, respectively, at the nodes.
ellipsoid, hyaline, smooth, thin-walled, acyanophilous, non-amyloid, non-dextrinoid, (4.2–4.5–5.1(− 5.3) × (3.2–)3.3–4.2(− 4.3) μm, L = 4.8 μm, W = 3.7 μm, Q = 1.25–1.28 (n = 90/3).

Additional specimens examined: Australia: Queensland: Cairns: Cairns Botanic Gardens, on angiosperm stump, 17 May 2018, Li-Wei Zhou, LWZ 20180517-42 (HMAS); Mount Whitfield Conservation Park, on fallen angiosperm branch, 18 May 2018, Li-Wei Zhou, LWZ 20180518-2 (HMAS). – Malaysia: Selangor: Kota Damansara Community Forest Reserve, on angiosperm stump, 17 Apr. 2018, Li-Wei Zhou, LWZ 20180417-28 (HMAS). – Vietnam: Thac Mai Preservation Park, on fallen angiosperm branch, 14 Oct. 2017, Li-Wei Zhou, LWZ 20171014-3 (HMAS).

Resinicium lateastrocystidium Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, sp. nov. (Figs. 6–7)

MycoBank: MB 840229.

Etymology: lateastrocystidium (Lat.), refers to the wide astrocytida.

Diagnosis: Characterized in the genus by the presence of halocystidia and wide astrocytida (above 6 μm in diam).

Type: Malaysia: Kuala Lumpur: KL Forest Eco park, on fallen angiosperm trunk, 14 Apr. 2018, Li-Wei Zhou, LWZ 20180414-15 (HMAS – holotype).

Description: Basidiomes annual, resupinate, closely adnate, widely effused, not easily separable, thin, farinaceous, cream to buff-yellow when fresh, straw-yellow to olivaceous buff with age, not cracked. Hymenophore grandiniooid to odontoid, usually with small conical apex,
3–4 per mm, 300–500 μm long. Subiculum not stratified, straw-yellow to olivaceous buff, 100–200 μm thick. Margin gradually thinning out, white, occasionally with mycelia cords.

Hyphal system monomitic, generative hyphae with clamp connections. Subiculum composed of mostly indistinct hyphae; subicular hyphae hyaline, thin-walled, moderately branched, often collapsed, 2–3 μm diam. Subhymenial hyphae frequently branched, hyaline, compact and agglutinated, 1.5–2.5 μm diam. Astrocytidia rare, scattered, often developing both terminally and laterally on hyphae, hyaline, thin-walled, 10–20 × 1.7–3 μm, 1.5–3 μm diam at base, at apex a stellate cluster of hyaline crystals, to 6–15 μm diam. Halocystidia hyaline, thin-walled, 15–30 × 4–10 μm, tapering to 2–3 μm diam at base, the outer layer inflates to a bladder, 10–20 μm diam, formed a capitate cystidium. Basidia cylindrical, often with a median constriction, four sterigmata, 13–20 × 5–6 μm, tapering to 2–4 μm diam with a clamp connection at base; basidioles similar in shape to basidia, but
smaller. Basidiospores ellipsoid, hyaline, smooth, thin-walled, acyanophilous, non-amyloid, non-dextrinoid, (3.9–)4.1–5 × (2.8–)2.9–3.9 (–4) μm, L = 4.5 μm, W = 3.3 μm, Q = 1.35–1.36 (n = 90/3).

Additional specimens examined: Malaysia: Kuala Lumpur: KL Forest Eco park, on fallen angiosperm trunk, 14 Apr. 2018, Li-Wei Zhou, LWZ 20180414-13 (HMAS); Selangor: Kota Damansara Community Forest Reserve, on fallen angiosperm branch, 16 Apr. 2018, Li-Wei Zhou, LWZ 20180416-10 (HMAS).

Notes: Resinicium lateastrocystidium resembles R. friabile, R. rimulosum and R. saccharicola in the presence of halocystidia and astrocytidia; however, astrocytidia in the latter three species are much narrower (1.5–3 μm in width in R. friabile, Nakasone 2007; 3–4 μm in width in R. rimulosum, Nakasone 2007; 1.5–2 μm in width in R. saccharicola, Nakasone 2000). In addition, these three species differ from R. lateastrocystidium by narrower or longer basidiospores (4.5–5 × 2.8–3 μm in R. friabile, Hjortstam and Melo 1997; 4–4.8 × 2.8–3 μm in R. rimulosum, Nakasone 2007; 5–6.1 × 3.3–4.2 μm in R. saccharicola, Nakasone 2000). In addition, there are differences in shape and size to S. dabieshanensis.

Skvortzovia dabieshanensis Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, sp. nov. (Figs. 8–9)

Mycobank: MB 840228.

Etymology: dabieshanensis (Lat.), refers to the Dabieshan Mountains.

Diagnosis: Similar to Skvortzovia furfurella in the grey grandinioid basidiomes, capitate leptocystidia and lack of halocystidia, but S. furfurella differs by smaller allantoid basidiospores (3.5–4 × 0.8–1 μm, Gruhn and Hallenberg 2018).

Type: China: Anhui: Jinzhai County: Dabieshan Mountains: Tian Tangzhai National Nature Reserve, on fallen trunk of Pinus, 12 Oct. 2020, Li-Wei Zhou, LWZ 20201012-22 (HMAS – holotype).

Description: Basidiomes annual, resupinate, closely adnate, widely effused, not easily separable, thin, farinaceous, white to cream when fresh, ash-grey with age, not cracked. Hymenophore grandinioid, composed of small aculei, usually with round apex, 5–6 per mm, 200–300 μm long. Subiculum not stratified, white, 100–200 μm thick. Margin gradually thinning out, white, occasionally with mycelia cords.

Hyphal system monomitic, generative hyphae with clamp connections. Subiculum composed of indistinct generative hyphae; subicular hyphae hyaline, thin-walled, frequently branched, interwoven, 2–3 μm diam. Subhymenial hyphae hyaline, thin-walled, frequently branched, compact and agglutinated, 1.5–2.5 μm diam. Hymenial leptocystidia capitate, hyaline, thin-walled, with a basal clamp connection, 15–30 × 2.5–4 μm. Basidia clavate four sterigmata, 10–20 × 3.5–5 μm, tapering to 2–4 μm diam with a clamp connection at base; basidioles similar in shape to basidia, but smaller. Basidiospores cylindrical to allantoid, hyaline, thin-walled, smooth, acyanophilous, non-amyloid, non-dextrinoid, (3.5–)3.8–4.7 (–4.9) × 1.8–2.4 (–2.6) μm, L = 4.2 μm, W = 2.1 μm, Q = 2.05–2.08 (n = 90/3).

Additional specimen examined: China: Anhui: Yuexi County: Dabieshan Mountains: Yaoluoping National Nature Reserve, on fallen trunk of Pinus, 14 Oct. 2020, Li-Wei Zhou, LWZ 20201014-18 (HMAS); Shucheng County: Dabieshan Mountains: Wanfoshan National Nature Reserve, on fallen angiosperm trunk, 17 Oct. 2020, Li-Wei Zhou, LWZ 20201017-55 (HMAS).

Notes: Skvortzovia pinicola has similar basidiospores in shape and size to S. dabieshanensis but differs by the
presence of halocystidia in the apex of the aculei (Eriksson et al. 1981).

**Skvortzovia qilianensis** Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, sp. nov. (Figs. 10–11)
MycoBank: MB 840230.

*Etymology: qilianensis* (Lat.), refers to the Qilian Mountains.

*Diagnosis:* Characterized in the genus by the woody hard, buff-yellow to lemon-yellow and not cracked basidiomes, and odontioid hymenophores with relatively long aculei.

*Type:* China: Gansu: Zhangye: Qilian Mountains National Park: Sidalong Forest Farm, on fallen branch of *Picea*, 4 Sep. 2018, Li-Wei Zhou, LWZ 20180904-16 (HMAS – holotype).

*Description:* Basidiomes annual, closely adnate, widely effused, not easily separable, thin, woody hard, cream to pale yellow when fresh, buff-yellow to lemon-yellow with age, not cracked. Hymenophore odontoid, composed of small, cylindrical aculei, aculei rather distant, 2–4 aculei per mm, 400–500 μm long, the higher ones slightly attenuate with a short fimbriate sterile apex. Subiculum not stratified, buff to honey-yellow, 100–200 μm thick. Margin gradually thinning out, white, abrupt with short aculei.

Hyphal system monomitic, generative hyphae with clamp connections. Subiculum composed of indistinct generative hyphae; subicular hyphae hyaline, thin-walled, frequently branched, interwoven, 2–3 μm diam. Subhymenial hyphae hyaline, thin-walled, frequently branched, 1.5–2.5 μm diam. Hymenial leptocystidia tubular with obtuse apex, numerous, hyaline, thin-walled, with a basal clamp connection, 10–30 × 1.5–2.5 μm. Basidia not found; basidioles rare, clavate to cylindrical, 10–14 × 4.5–5.5 μm, tapering to 2–3 μm diam with a clamp connection at base. Basidiospores not found.

*Additional specimens examined:* China: Gansu: Zhangye: Qilian Mountains National Park: Sidalong Forest Farm, on fallen branch of *Picea*, 4 Sep. 2018, Li-Wei Zhou, LWZ 20180904-20 (HMAS), LWZ 20180904-20 (HMAS).

*Notes:* Basidiospores were not found in any of the three specimens of *S. qilianensis* studied. Traditionally, it is not a common practice to describe new species of wood-inhabiting fungi lacking basidiospores. However, if other morphological characters are taxonomically distinct, sometimes mycologists have ignored basidiospores and described the specimens as new species (Tchoumi et al. 2020).

**Skvortzoviella** Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, gen. nov.
MycoBank: MB 840231.

*Etymology:* Skvortzoviella (Lat.), refers to the similarity to *Skvortzovia*.

*Diagnosis:* Unique in *Hymenochaetales* being characterized by a combination of resupinate and cracked basidiomes, the smooth and light-colored hymenophore, a monomitic hyphal system, tubular leptocystidia with obtuse apex, and ellipsoid basidiospores.

*Type:* *Skvortzoviella lenis* Jia Yu et al. 2021.
Description: Basidiomes annual, closely adnate, widely effused, not easily separable, thin, membranous, rarely soft, usually with a few broad cracks or cracked extensively. Hymenophore smooth or irregular, cream to pale yellow. Margin gradually thinning out, white, filamentose.

Hyphal system monomitic, generative hyphae with clamp connections, hyaline, thin-walled, frequently branched. Hymenial leptocystidia tubular with obtuse apex, hyaline, thin-walled. Basidia cylindrical, often with a median constriction, four sterigmata. Basidiospores ellipsoid, hyaline, smooth, thin-walled, acyanophilous, non-amyloid, non-dextrinoid.

Notes: Morphologically, Skvortzoviella is closely related to Skvortzovia; however, Skvortzovia also accommodates species with grandinioid to odontioid hymenophores in addition to those with smooth hymenophores (Eriksson et al. 1981; Gruhn and Hallenberg 2018).

Skvortzoviella lenis Jia Yu, Xue W. Wang, S.L. Liu & L.W. Zhou, sp. nov. (Figs. 12–13) MycoBank: MB 840232.

Etymology: lenis (Lat.), refers to the smooth hymenium.

Diagnosis: Similar to Skvortzovia georgica in the smooth hymenium, but S. georgica has slightly larger leptocystidia (30–32 × 4–5 μm) and allantoid basidiospores (Gruhn and Hallenberg 2018).

Type: China: Yunnan: Baoshan: Gaoligong Mountains National Nature Reserve: Baihua Ridge, on angiosperm stump, 21 Sep. 2018, Li-Wei Zhou, LWZ 20180921-17 (HMAS – holotype).

Description: Basidiomes annual, closely adnate, widely effused, not easily separable, thin, membranous, rarely soft, usually with a few broad cracks or cracked extensively, 50–100 μm thick. Hymenophore smooth or irregular, white to cream when fresh, pale yellow to buff-yellow with age. Subiculum not stratified, white when fresh, light cream-coloured in dried material. Margin gradually thinning out, white, filamentose.

Hyphal system monomitic, generative hyphae with clamp connections. Subiculum composed of indistinct generative hyphae; subicular hyphae hyaline, thin-walled, frequently branched, 2–2.5 μm diam. Subhymenial hyphae hyaline, frequently branched, compact and agglutinated, 1.5–2.0 μm diam. Hymenial leptocystidia tubular with obtuse apices, hyaline, thin-walled, with a basal clamp connection, 15–30 × 1.5–3 μm. Basidia cylindrical, often with a median constriction, four sterigmata, 12–20 × 4.7–6 μm, tapering to 2.5–3.5 μm diam with a clamp connection at base; basidioles similar in shape to basidia, but smaller. Basidiospores ellipsoid, hyaline, smooth, thin-walled, acyanophilous, non-amyloid, non-dextrinoid, 4.8–5.8(–6.0) × (2.8–)2.9–3.5 μm, L = 5.1 μm, W = 3.1 μm, Q = 1.62–1.67 (n = 90/3).

Additional specimens examined: China: Yunnan: Baoshan: Gaoligong Mountains National Nature Reserve:
Baihua Ridge, on fallen angiosperm twig, 21 Sep. 2018, Li-Wei Zhou, LWZ 20180921-7 (HMAS); loc. cit., on fallen angiosperm trunk, 21 Sep. 2018, Li-Wei Zhou, LWZ 20180921-25 (HMAS); loc. cit., on fallen angiosperm twig, 21 Sep. 2018, Li-Wei Zhou, LWZ 20180921-32 (HMAS); loc. cit., on fallen angiosperm branch, 22 Sep. 2018, Li-Wei Zhou, LWZ 20180922-39 (HMAS), LWZ 20180922-61 (HMAS).

Notes: Skvortzovia furfuracea resembles Skvortzoviella lenis in the smooth to grandinioid hymenophore and ellipsoid basidiospores, but differs by the presence of halocystidia (Eriksson et al. 1981).

DISCUSSION
Previous phylogenies have shown the intraspecific ITS variations in Resinicium, such as those in R. friabile, R. grandisporum, and R. saccharicola (Nakasone 2007; Gruhn et al. 2017). Similarly, the newly described R. austroasianum formed intraspecific clades (LWZ 20180517-42 and the other four specimens; Figs. 1–2). However, these clades are short-branched and no morphological differences could be found corresponding to these clades. Therefore, we treated these genetic distances as intraspecific but not interspecific variations.

Resinicium was considered to originate in tropical America due to the high species diversity including basal lineages there (Nakasone 2007, Gruhn et al. 2017). However, the current study identifies two new species and more importantly a new basal lineage of Resinicium from tropical regions in the Asia-Pacific area (Figs. 1–2), which in part places doubt on the tropical American origin of this genus (Nakasone 2007, Gruhn et al. 2017). Moreover, the biogeographic analysis based on the combined dataset of ITS and nLSU regions also supported Asia-Pacific as the ancestral origin of Resinicium (Fig. 3). Comparing with the combined dataset (3), the ITS dataset of Resinicium (2) included more vouchers and species of Resinicium but failed to resolve species relationships with reliable statistical values in some lineages in biogeographic analysis (data not shown). Therefore, the current Asia-Pacific origin of Resinicium is not conclusive. A wider sampling around tropical regions in a multi-locus-based biogeographic analysis will clarify the geographic origin and evolution of Resinicium.

Like previous studies (Zhou et al. 2018; Liu et al. 2019), the current combined dataset of ITS and nLSU (1) does not resolve the relationships among families within Hymenochaetales (Fig. 1). Therefore, the family positions of Resinicium, Skvortzovia, and Skvortzoviella are still ambiguous. To solve this issue, a comprehensive phylogenetic study on the whole order with the help of multi-loci and a wider sampling should be performed, which is beyond the scope of the current study. However, the current study provides new materials for further reconstructing the phylogenetic backbone of Hymenochaetales.

CONCLUSION
The current study revealed one new monotypic genus, Skvortzoviella, typified by the new species, S. lenis, and four other new species, viz. Resinicium austroasianum, R. lateacrocidium, Skvortzovia dabieshanensis and S. qilianensis, from the Asia-Pacific region. Besides, a new basal lineage of Resinicium represented by one specimen...
LWZ 20171015–31 from Vietnam (Fig. 14), and three Chinese specimens of Skvortzovia pinicola (Fig. 15) are also identified. Phylogenetic analyses support the six new taxa and the new lineage of Resinicium as members of Hymenochaetales (Fig. 1) thereby adding to the knowledge of generic and species diversity within this order.

ABBREVIATIONS
BI: Bayesian inference; BPP: Bayesian posterior probability; BS: Bootstrap; CB: Cotton Blue; CTAB: Cetyl-trimethyl-ammonium bromide; ESSs: Effective sample sizes; IKI: Melzer reagent; ITS: Nuclear ribosomal internal transcribed spacer; KOH: 5% potassium hydroxide; ML: Maximum Likelihood; nLSU: Large subunit nuclear ribosomal RNA gene; PCR: Polymerase chain reaction; PSRFs: Potential scale reduction factors

Availability of data and materials
All sequence data generated for this study can be accessed via GenBank: https://www.ncbi.nlm.nih.gov/genbank/. All alignments for phylogenetic analyses were deposited in TreeBASE (http://www.treebase.org; accession number S27463).

DEclarations
Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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