Reinstatement of the corticioid genus *Leifia* (Hymenochaetales, Basidiomycota) with a new species *L. brevispora* from Hubei, Central China

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Abstract

The monotypic genus *Leifia* was previously considered to be a later synonym of *Odonticium*. With the morphological and phylogenetic evidence provided by an additional four East Asian specimens, we propose to reinstate *Leifia* as an independent genus in Hymenochaetales. *Leifia* morphologically differs from *Odonticium* by its grandinioid hymenophore with hyphal strands, numerous thick-walled cystidia with an invaginated apical end and narrowly and thick-walled basidia. The phylogeny generated from the current data set of ITS and 28S regions indicates that *Leifia* forms a sister clade to *Odonticium*. Besides the generic type *Leifia flabelliradiata* in the *Leifia* clade, two specimens, collected from Hubei, Central China, are newly introduced as *Leifia brevispora*. This new species is the second species of *Leifia* and differs from the generic type by its shorter basidiospores and distribution in warm-temperate to subtropical areas in East Asia. The additional two specimens, collected from Da Lat, Viet Nam, differ morphologically, both from each other and from known species of *Leifia*, but more samples need to be examined before further taxonomic decisions can be made.

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Keywords
Morphology, *Odonticium*, phylogeny, taxonomy, wood-inhabiting fungi, 1 new taxon

Introduction

*Leifia* Ginns is a monotypic genus of wood-inhabiting basidiomycetes introduced by Ginns (1998). The basionym of its type is *Phanerochaete flabelliradiata* J. Erikss. & Hjortstam that was described from Norway (Eriksson et al. 1981). Burdsall (1985) regarded *P. flabelliradiata* as a deviating element in *Phanerochaete* P. Karst. and transferred it to *Tubulicrinis* Donk. Hjortstam (1986) accepted the concept of *Phanerochaete* sensu Burdsall (1985), but he considered that *Tubulicrinis flabelliradiatus* (J. Erikss. & Hjortstam) Burds. did not fit the concept of *Tubulicrinis* or any other known genus and thus erected a new genus *Granulocystis* Hjortstam to accommodate this species. Unfortunately, *Granulocystis* is an illegitimate later homonym for *Granulocystis* Hindák, a genus of green algae (Code of Nomenclature Art. 53.1, Turland 2018). Therefore, Ginns (1998) introduced *Leifia* replacing *Granulocystis*. By examining Russian specimens of *Leifia flabelliradiata* (J. Erikss. & Hjortstam) Ginns, Zmitrovich (2001) combined this species to *Odonticium* Parmasto as *O. flabelliradiatum* (J. Erikss. & Hjortstam) Zmitr. that is the currently accepted name of this species in MycoBank and Index Fungorum. Correspondingly, *Leifia* is treated as a synonym of *Odonticium*.

Till now, Larsson et al. (2006) is the single paper which includes the species *Odonticium flabelliradiatum* in a phylogenetic analysis. Although *Odonticium flabelliradiatum* grouped with *O. romellii* (S. Lundell) Parmasto, the generic type of *Odonticium* and two species of *Repetobasidium* J. Erikss. with a full Bayesian posterior probability (BPP) support in the *Rickenella* Raithelh. clade of Hymenochaetales, Larsson et al. (2006) considered that this clade might not be reliable due to the lack of morphological similarities and still used the name *Leifia flabelliradiata* rather than *O. flabelliradiatum*. However, no further taxonomic opinion relating to *Leifia* was provided in Larsson et al. (2006).

In 2017, four specimens close to *Odonticium flabelliradiatum* were collected from Central China and Vietnam, which draw our attention to the taxonomic status and diversity of *Leifia*. Based on morphological and molecular evidence, we propose the reinstatement of *Leifia* and reveal a higher diversity of this genus.

Materials and methods

Specimens studied are deposited in the herbarium of Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Morphological photos were taken with a digital camera Canon E12 (Tokyo, Japan) in the field. Morphological observations were made with Nikon SMZ 645 and SMZ 1000 stereomicroscopes and a Nikon Eclipse 80i light microscope (Tokyo, Japan) at magnifications up to 1000×. Microscopic procedures followed Hjortstam et al. (1987). Basidiocarp sections were prepared in Melzer’s reagent, lactic acid Cotton Blue (CB) and 3% potassium hydroxide (KOH). All microscopic measurements were made in CB. When presenting the variation of basidiospore
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sizes, 5% of the measurements were excluded from each end of the range and are given in parentheses. The following abbreviations are used in the text: 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 specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens.

The four specimens newly collected were subjected to polymerase chain reaction (PCR) directly with the Phire Plant Direct PCR kit (Finnzymes Oy, Espoo, Finland), following the manufacturer’s instructions. The nucl rDNA ITS1-5.8S-ITS2 (ITS barcode) and 28S regions were amplified using the primer pairs ITS1-F (Gardes and Bruns 1993) or ITS5 and ITS4 (White et al. 1990) and LR0R and LR7 (Vilgalys and Hester 1990), respectively. The PCR procedure was as follows: initial denaturation at 98°C for 5 min, followed by 39 cycles at 98 °C for 5 s, 59 °C for 5 s (ITS region)/48 °C for 5 s (28S region) and 72 °C for 5 s, with a final extension at 72 °C for 10 min. The PCR products were sequenced at the Beijing Genomics Institute, China, with the same primers used for PCR. All newly generated sequences were deposited in GenBank (Table 1).

The current dataset for phylogenetic analysis was mainly adopted from Larsson et al. (2006), where, to avoid redundancy, taxa in the *Rickenella* clade including *Leifia flabelliradiata* were mostly referred to, while taxa in other clades were representatively selected (Table 1). *Sistotrema brinkmannii* (Bres.) J. Erikss. was selected as an outgroup taxon. Besides taxa in Hymenochaetales, *Protodontia piceicola* (Kühner ex Bourdot) G.W. Martin and *Exidiopsis calcea* (Pers.) K. Wells from Auriculariales were also included as additional ingroup taxa. The ITS and 28S datasets were separately aligned with MAFFT 7.110 (Katoh and Standley 2013) with the G-INI-I option (Katoh et al. 2005) and then the two resulting alignments were concatenated as a single alignment deposited in TreeBASE (study no. 23768). The best-fit evolutionary model for this concatenated alignment was estimated as GTR+I+G with jModelTest (Guindon and Gascuel 2003; Posada 2008). Maximum likelihood (ML) and Bayesian Inference (BI) methods were conducted to perform phylogenetic analysis, respectively, using raxmlGUI 1.2 (Silvestro and Michalak 2012; Stamatakis 2006) and MrBayes 3.2 (Ronquist et al. 2012). In the ML analysis, bootstrap (BS) values were tested under the auto FC option (Pattengale et al. 2010). In the BI analysis, two independent runs were employed. Each run had four chains of 10 000 000 generations and started from random trees. Chain convergence was determined with Tracer 1.5 (http://tree.bio.ed.ac.uk/software/tracer/). After sampling every 1000th generation, the first 25% of sampled trees was removed, whereas the other 75% was subjected to construction of a 50% majority consensus tree and calculation of BPPs. The ML and BI methods generated congruent topologies in main lineages. Therefore, the topology generated in the ML analysis is presented and the BS values and BPPs, simultaneously above 50% and 0.7, respectively, are shown at the nodes.

To further differentiate the taxa of *Leifia*, the distance matrix of the alignment of their ITS sequences (5.8S and ITS2 region) were estimated using MEGA5 (Tamura et al. 2011) under the parameters of maximum composite likelihood model, uniform rates amongst sites and pairwise deletion of gaps/missing data treatment.
Results

From four studied specimens, four ITS and four 28S sequences were newly generated (Table 1). These sequences were incorporated in the dataset of Larsson et al. (2006) with an emphasis of taxa in the *Rickenella* clade. The current dataset included 62 taxa, each with an ITS and a 28S sequence. The concatenated alignment had 2426 characters. The BS search in the ML analysis stopped after 350 replicates. In the BI analysis, all chains were converged as suggested by the effective sample sizes of all parameters above 3300 and by the potential scale reduction factors close to 1000.

The current phylogeny (Figure 1) recovered Hymenochaetales as a strongly supported clade (94%, 1.00). Amongst Hymenochaetales, the *Oxyporus* (Bourdot & Galzin) Donk clade, the *Kneifiella* P. Karst. clade, the *Hyphodontia* J. Erikss. clade and the Hymenochaetaceae clade were recovered like those in Larsson et al. (2006), although the latter two clades received no statistical support (Figure 1). The so-called *Coltricia* Gray clade in Larsson et al. (2006) here consisted entirely of corticioid species currently referred to *Lyomyces* P. Karst., *Palifer* Stalpers & P.K. Buchanan and *Xylodon* (Pers.) Gray, while *Coltricia perennis* (L.) Murrill nested within the Hymenochaetaceae clade (Figure 1). The *Rickenella* clade of Larsson et al. (2006), the focus group for this study, did not group together well, but *Odonticium romellii* and *Leifia flabelliradiata* formed a strongly supported clade (91%, 1.00; Figure 1) like that in Larsson et al. (2006). The four newly sequenced specimens, also in this clade, had a closer relationship with *L. flabelliradiata* (100%, 1.00; Figure 1) than with *Odonticium*. Besides the lack of morphological similarities between *Odonticium* and *Leifia*, the branch length separating *Odonticium* from *Leifia* and related taxa also indicated that the two genera should be treated as independent.

In the *Leifia* clade, four newly sequenced specimens formed two subclades: LWZ 20170820-46 and LWZ 20170820-48 (99%, 0.76) and LWZ 20171015-36 and LWZ 20171015-38 (58%, 0.86), which were both separated from *L. flabelliradiata*. The distance matrix of ITS sequences (Table 2) indicated that LWZ 20171015-36 and LWZ 20171015-38 represented two distinct lineages (4.4%), while LWZ 20170820-46 and LWZ 20170820-48 represented one lineage distinctly different from LWZ 20171015-36 (3.5%) and LWZ 20171015-38 (2.9%) and moderately from *L. flabelliradiata* (1.3%).

Table 1. Specimens used for the phylogenetic analyses.

| Species          | Voucher/strain number | GenBank accession number | Sequence reference | Origin   |
|------------------|-----------------------|--------------------------|--------------------|----------|
| *Abietoderma mirabile* | TAA 169235           | DQ873592 DQ873592       | Larsson et al. (2006) | Estonia |
| *Basidioradulum radula*   | AFTOL-ID 451         | DQ234537 AY700184       | Unpublished        | unknown |
| *Blasiphalia pseudogrisella* | Lutzoni 930728-3    | U66437 U66437           | Lutzoni (1997)     | unknown |
| *Coltricia perennis*       | DSH 93-198           | DQ234559 AF287854       | Hibbett et al. (2000) | unknown |
| *Conferraria weirii*       | JV 0407/8J           | KR350569 KR350557       | Zhou et al. (2016)  | USA      |
| *Cylindrosporus flavidus*   | Dai 13213            | KP875564 KP875561       | Zhou (2015)         | China    |
| *Cyphellostereum laeve*     | JJ 020909            | EU118621 EU118621       | Larsson (2007a)     | Sweden   |
| *Exidiopsis calceus*        | KHL 11075            | AY463406 AY586654       | Larsson et al. (2004) | Sweden   |
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| Species | Voucher/strain number | GenBank accession number | Sequence reference | Origin |
|---------|-----------------------|--------------------------|---------------------|--------|
| Fomitiporella caryophylli | CBS 448.76 | AY558611 | AY059021 | Wagner and Fischer (2002); Larsson et al. (2005); Jeong et al. (2005) |
| Fomitoporia bartigii | CBS 162.30 | AY558621 | AF311005 | Jeong et al. (2005) |
| Fulveszones fastuosus | CBS 213.36 | AY558615 | AY059075 | Jeong et al. (2005) |
| Fulvoderma scanorum | LWP 20130909-2 | MF860780 | MF860731 | Zhou et al. (2018a) |
| Globulicium biemale | Hjim 19007 | DQ873595 | DQ873595 | Larsson et al. (2006) |
| Hymenochaeta adusta | CBS 759.91 | AY585949 | AY385161 | Jeong et al. (2005) |
| Hypodermadetta capitatum | KHL 8646 (GB) | DQ677491 | DQ77491 | Larsson (2007b) |
| Hypodermadetta aurata | KHL 11889 | DQ873603 | DQ773603 | Larsson et al. (2006) |
| Hypodermadetta sp. | H Berglund 1117 | DQ873605 | DQ773605 | Larsson et al. (2006) |
| Koeffelina barbi-jovei | KHL 11730 | DQ873609 | DQ773610 | Larsson et al. (2006) |
| Koeffelina corvina | KHL | DQ873615 | DQ773616 | Larsson et al. (2006) |
| Koeffelina floccosa | Berglund 150-02 | DQ873618 | DQ773618 | Larsson et al. (2006) |
| Leifia brevipes | LWP 20170820-46 | MK343469 | MK343473 | This study |
| Leifia brevipes | LWP 20170820-48 | MK343470 | MK343474 | This study |
| Leifia flocculodipla | KG Nilsson 36270 | DQ873635 | DQ773635 | Larsson et al. (2006) |
| Leifia sp. 1 | LWP 20171015-36 | MK343471 | MK343475 | This study |
| Leifia sp. 2 | LWP 20171015-38 | MK343472 | MK343476 | This study |
| Lactulia marchantiae | Lutzoni 930826-1 | U66432 | U66432 | Lutzoni (1997) |
| Lyomyces crassatus | KHL 11731 | DQ873614 | DQ773614 | Larsson et al. (2006) |
| Lyomyces griseolae | KHL 12971 (GB) | DQ873651 | DQ773651 | Larsson et al. (2006) |
| Lyomyces prunii | Ryberg 021018 | DQ873624 | DQ773625 | Larsson et al. (2006) |
| Odonticium romellii 1 | H 6059319 | MF319073 | MF318929 | Korotkin (2017) |
| Odonticium romellii 2 | KHL s. n. | DQ873639 | DQ773639 | Larsson et al. (2006) |
| Palifera serecundus | KHL 12261 (GB) | DQ873642 | DQ773643 | Larsson et al. (2006) |
| Peniophora paetermusium | KHL 13146 (GB) | DQ873597 | DQ773597 | Larsson et al. (2006) |
| Peniophora paeternus | KHL 13154 (GB) | DQ873599 | DQ773599 | Larsson et al. (2006) |
| Protodonta piceicola | KHL 11763 (GB) | DQ873660 | DQ773660 | Larsson et al. (2006) |
| Reptobasidium conicum | KHL 12338 | DQ873647 | DQ773647 | Larsson et al. (2006) |
| Richenella fulva 1 | AD66093 | AY463464 | AY586710 | Larsson et al. (2004) |
| Richenella fulva 2 | TENV 071482 | MF319083 | MF318943 | Korotkin (2017) |
| Richenella mellicola | Lamoure 74-20h 1/9.91 | U66438 | U66438 | Lutzoni (1997) |
| Rigidosporus corticola | KHL 13217 (GB) | DQ873641 | DQ773641 | Larsson et al. (2006) |
| Sadeni lanata | JS 15063 | DQ873593 | DQ773593 | Larsson et al. (2006) |
| Sistotrema brinckmannii | KHL 14078 (GB) | KF218967 | KF218967 | Larsson and Kotiranta (2013) |
| Skvortzovia furfuracum | KHL 11738 (GB) | DQ873648 | DQ773648 | Larsson et al. (2006) |
| Skvortzovia furfurela | KHL 10180 (GB) | DQ873649 | DQ773649 | Larsson et al. (2006) |
| Skvortzovia georgica | KHL 12019 (GB) | DQ873645 | DQ773645 | Larsson et al. (2006) |
| Skvortzovia pincicola | KHL 12224 (GB) | DQ873657 | DQ773657 | Larsson et al. (2006) |
| Sphaerobasidium minutum | KHL 11714 | DQ873652 | DQ773653 | Larsson et al. (2006) |
| Sphagnumphalia revibasidiata | Lutzoni 930826-1 | U66441 | U66441 | Lutzoni (1997) |
| Trichaptum abietinum | NH 12842 (GB) | AF347104 | AF347104 | Larsson et al. (2004) |
| Tubulicrinis globularis | KHL 12133 | DQ873655 | DQ773655 | Larsson et al. (2006) |
| Tubulicrinis hirtellus | KHL 11717 (GB) | DQ873657 | DQ773657 | Larsson et al. (2004) |
| Tubulicrinis inornatus | KHL 11763 (GB) | DQ873659 | DQ773659 | Larsson et al. (2004) |
| Tubulicrinis sublactatus | KHL 11079 | AY463478 | AY586722 | Larsson et al. (2004) |
| Xylodon aspera | KG Nilsson s. n. | DQ873606 | DQ773607 | Larsson et al. (2006) |
| Xylodon brevissima | KHL 12386 | DQ873612 | DQ773612 | Larsson et al. (2006) |
| Xylodon detriticus | K.G. Nilsson 990902 | DQ677507 | DQ777507 | Larsson (2007b) |
| Xylodon neporii | B Nordon 030915 | DQ873622 | DQ773622 | Larsson et al. (2006) |
| Xylodon rimosissimus | Ryberg 021031 (GB) | DQ873627 | DQ773628 | Larsson et al. (2006) |

*Species names are adopted from recent taxonomic proposals.*
**Table 2.** Distance matrix of the alignment of ITS sequences (5.8S and ITS2 region) from *Leifia* specimens.

| Species                          | 1   | 2   | 3   | 4   | 5   |
|---------------------------------|-----|-----|-----|-----|-----|
| L. flabelliradiata              |     |     |     |     |     |
| L. brevispora (LWZ 20170820-46) | 0.013 |     |     |     |     |
| L. brevispora (LWZ 20170820-48) | 0.013 | 0.000 |     |     |     |
| L. sp. (LWZ 20171015-36)        | 0.043 | 0.035 | 0.035 |     |     |
| L. sp. (LWZ 20171015-38)        | 0.036 | 0.029 | 0.029 | 0.044 |     |

**Figure 1.** Phylogenetic relationship between *Odonticium romellii* and *Leifia*, based on the concatenated dataset of ITS and 28S regions. The topology was generated from the maximum likelihood analysis and the bootstrap values and Bayesian posterior probability, simultaneously above 50% and 0.7, respectively, are shown at the nodes. The clade names are adapted from Larsson et al. (2006) and the species names from recent taxonomic proposals.
Taxonomy

*Leifia brevispora* Gafforov, S.L. Liu & L.W. Zhou, sp. nov.
Figures 2 and 3
MycoBank MB829252

**Diagnosis.** The species is distinct from *Leifia flabelliradiata* by shorter basidiospores and by being distributed in warm-temperate to subtropical areas in East Asia.

**Typification.** CHINA. Hubei Province, Wudangshan Town, Wudangshan National Forest Park, on fallen angiosperm branch, 20 Aug 2017, *LWZ 20170820-46* (holotype in IFP 019239). GenBank: ITS = MK343469; 28S = MK343473.

**Etymology.** *brevispora* (Latin), referring to short basidiospores.

**Basidiomata.** Annual, resupinate, inseparable from substrate, effused, up to 0.6 mm thick. Hymenophore grandinioid to subodontioid. Margin white, smooth or minutely fibrous, sometimes bearing hyphal strands, thinning out, up to 2 mm wide. Aculei cream to buff in colour, rounded to ellipsoid, 2–3 per mm, up to 0.5 mm long, several being clustered together when dry. Subiculum white, up to 100 μm thick.

**Microscopic structures.** Hyphal system monomitic; generative hyphae without clamp connections. Subicular hyphae hyaline, thin- to thick-walled, occasionally branched, frequently septate, more or less parallel to substrate, 2–4 μm wide. Aculeus (subhymenial) hyphae hyaline, distinctly thick-walled, mainly vertically intertwined,

![Figure 2. Basidiocarps of *Leifia* in situ.](image-url)
Figure 3. Microscopic structures of *Leifia brevispora* (drawn from LWZ 20170820-46, holotype). A. basidiospores. B. basidia. C. basidioles. D. cystidia. E. subicular hyphae.

2–4 μm wide. Cystidia hyaline, thick-walled, tubular with an invaginated apical end, 60–100 × 5–7 μm, swelling in KOH. Basidia hyaline, thick-walled, clavate to cylindrical, with four sterigmata each 2–3 μm long and a simple septum at the base, 14–18 × 4.5–5.5 μm. Basidioles similar in shape to basidia, but smaller. Basidiospores ellipsoid, hyaline, thin-walled, smooth, inamyloid and indextrinoid, acyanophilous, 3.8–4.5(–5) × (1.8–)2–2.5 μm, L = 4.13 μm, W = 2.14 μm, Q = 1.92–1.96 (60/2).

**Other specimen examined.** CHINA. Hubei Province, Wudangshan Town, Wudangshan National Forest Park, on fallen angiosperm branch, 20 Aug 2017, LWZ 20170820-48 (IFP 019240).
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**Notes.** The grandinioioid hymenophore, simple-septate hyphae, distinctly thick-walled cystidia with an invaginated apical end and ellipsoid to subovate basidiospores with a straight or concave side, indicate that the new species is the second member of *Leifia*. Moreover, the phylogeny inferred from the ITS and 28S dataset also confirm the taxonomic position of *L. brevispora*. The generic type of *Leifia*, *L. flabelliradiata*, differs from *L. brevispora* by having longer basidiospores (4.5–5.5 × 2–2.5 μm) and a distribution in Europe (Eriksson et al. 1981).

**Discussion**

In this study, the newly generated ITS and 28S sequences were incorporated into the dataset of Larsson et al. (2006) and, in the resulting phylogeny (Figure 1), clades are labelled A-F as in Larsson et al. (2006). The differences of phylogeny observed between the current study and Larsson et al. (2006) might reflect that the ITS and 28S dataset itself is not enough to reliably resolve the relationships within Hymenochaetales. Similar to Larsson et al. (2006), *Leifia* formed a sister lineage to *Odonticium* with strong support in the current phylogeny (Figure 1). The five taxa of *Leifia* and the two of *Odonticium* were clearly separated and recovered as independent, fully supported clades. Morphologically, *Leifia* is well distinguished from *Odonticium* by its grandinioioid hymenophore with hyphal strands, numerous thick-walled cystidia with an invaginated apical end and narrowly and thick-walled basidia (Eriksson et al. 1981). Therefore, we propose to resurrect *Leifia* as an independent genus in Hymenochaetales.

Amongst the four newly sequenced taxa in *Leifia* clade, LWZ 20170820-46 and LWZ 20170820-48 represent the new species *L. brevispora*, while LWZ 20171015-36 and LWZ 20171015-38, both collected from Bidoup Nui Ba National Park, Da Lat, Viet Nam, seem to represent two undescribed taxa. LWZ 20171015-36 differs from *L. brevispora* and *L. flabelliradiata* by fairly thick basidiocarps and LWZ 20171015-38 differs by having basidia and basidioles that swell in KOH. Moreover, LWZ 20171015-38 grows on fallen branches of *Pinus*, while the other three specimens were all collected from angiosperm substrates. Although the morphological characters of LWZ 20171015-36 and LWZ 20171015-38 are unique in *Leifia*, we feel more samples need to be examined before describing them as new species.

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