Note



Resolving the taxonomic status of *Lithocarpus lycoperdon* (Fagaceae) and establishing a new synonym

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ABSTRACT: This study investigates the taxonomic status of *Lithocarpus lycoperdon* (Skan) A. Camus, *L. cinereus* Chun & C. C. Huang, and *L. pachylepis* A. Camus through extensive field observations, herbarium collections examinations, and detailed morphological comparisons. Our findings demonstrate that the type specimen of *L. lycoperdon* is an admixture, comprising an acorn from *L. pachylepis* mounted alongside a branchlet of *L. cinereus* on the same sheet. To resolve this taxonomic confusion, we designate the branchlet portion as the lectotype and select a specimen from the type locality with acorns attached to a branchlet as the epitype to provide a complete representation of *L. lycoperdon*. Furthermore, we reduce *L. cinereus* to a synonym of *L. lycoperdon*.

KEY WORDS: Admixture type, Flora, Lectotypification, Lithocarpus, Morphology, Nomenclature.

INTRODUCTION

Lithocarpus Blume (Fagaceae) is a large and morphologically diverse genus comprising approximately 330 to 347 species distributed across East and Southeast Asia (POWO, 2024). These trees are mostly dominant components of evergreen broad-leaved forests, playing critical roles in maintaining regional microclimates and biodiversity (Webb et al., 2008; Petit et al., 2013). Indo-China, recognized as a biodiversity hotspot for the Fagaceae family, harbors numerous Lithocarpus species, many of which form the upper canopy trees of these forests. The towering height of these trees makes it a pronounced difficulty to collect the intact specimens with reproductive (acorns and flowers) and vegetative parts well attached. As a result, taxonomic studies often rely on assembling fallen twigs and reproductive parts into a single specimen. However, this approach has often produced mixed specimens that contain elements from different taxa, leading to significant taxonomic confusion.

Lithocarpus lycoperdon (Skan) A. Camus exemplifies this taxonomic confusion. This species was initially described in the genus Quercus as Q. lycoperdon Skan (Skan, 1889), then it was later transferred to the genus Pasania as P. lycoperdon (Skan) Schottky (Schottky, 1912), and then to the genus Synaedrys as S. lycoperdon (Skan) Koidz. (Koidzumi, 1916) before eventually being placed in Lithocarpus by Camus (1931). Since the species was first described, there has been no discovery of reliably collected specimens that match the morphology of the type material. Huang and Zhang (1988) previously speculated that the type specimen of *L. lycoperdon* (*A. Henry 9069*) might be an admixture (Fig. S1), with the acorn originating from *L. pachylepis* A. Camus (Fig. S2). However, these suspicions remained uninvestigated. Consequently, the taxonomic status of *L. lycoperdon* has remained uncertain.

According to the protologue, the type specimen of L. lycoperdon was collected in "the southeastern region of Mengzi, Honghe, Yunnan, at an elevation of approximately 7000 feet" (Fig. S1), which presents a unique challenge. This specimen includes a foliage branchlet and a separated acorn (Skan, 1889). Historical records indicate that Pingbian was a district located in southeastern Mengzi County, with few mountains exceeding 7,000 feet (ca. 2,134 meters) (Mengzi County Chronicle Compilation Committee, 1995). The Da-Wei Mountain National Nature Reserve is the most plausible origin of the type specimen of L. lycoperdon based on the protologue. The reserve, located in southeastern Mengzi, contains one of the most intact vertical zonations of humid rainforests and tropical montane forests in the region, with altitudes ranging from 76.4 m to 2,363 m (Shui et al., 2018). Due to high productivity, primary forests outside the nature reserve have been severely disturbed by agriculture. As a biodiversity refuge minimally impacted by Quaternary glaciations, Da-Wei Mountain was designated a provincial nature reserve in 1986 and upgraded to a national nature reserve in 2001.

In 1988, Huang and Zhang (1988) described a new species, *L. cinereus* Chun & C. C. Huang, based on specimens bearing attached acorns on the branchlets (*C. C. Chang 12298*) (Fig. S3), which also occurs in southern



Fig. 1. Distribution of sampling sites of *Lithocarpus pachylepis* and *L. cinereus* in Da-Wei Mountain, Pingbian County, Yunnan Province, China. Red arrows represent *L. pachylepis*, while green arrows represent *L. cinereus*.

Yunnan. During a taxonomic revision of Chinese *Lithocarpus* species, incorporating herbarium and field surveys in the Da-Wei Mountain region, we found striking morphological similarities between the type material of *L. lycoperdon* (A. Henry 9069) and *L. cinereus*. Both species share key features, including glabrous branches and leaves, longitudinally grooved young branchlets, and leathery, oblong leaves with entire margins. Additionally, the abaxial leaf surfaces of both species are covered with gray scales that turn pale yellow-brown upon drying (Figs. S1, 3).

Our recent surveys in Da-Wei Mountain (2018–2023) confirmed the co-occurrence of *L. cinereus* and *L. pachylepis* within the primary forest of Da-Wei Mountain (Fig. 1), which is also documented in the comprehensive expedition reports on Da-Wei Mountain by Shui *et al.* (2018). These observations align with the protologues of *L. lycoperdon* suggesting that A. Henry might have inadvertently combined foliage from one species with a fallen acorn from another, thereby creating the type 354

specimen used to describe L. lycoperdon.

The middle elevations of Da-Wei Mountain harbors rich Lithocarpus species, including L. truncatus (King ex Hook.f.) Rehder, L. megalophyllus Rehder & E.H. Wilson, L. xylocarpus (Kurz) Markgr., L. dealbatus (Hook.f. & Thomson ex Miq.) Rehder, L. confinis S.H. Huang ex Y.C. Hsu & H.W. Jen, L. hancei (Benth.) Rehder, L. corneus (Lour.) Rehder, and L. gymnocarpus A. Camus, L. cinereus, L. lycoperdon, and L. pachylepis. We compared the key morphological characteristics of the eleven species and summarized the results in Table S1. It turns out that the acorn of L. lycoperdon is indeed similar to that of L. pachylepis, while its leaves resemble those of L. cinereus. The remaining eight species exhibit distinct differences from L. lycoperdon in either leaf characteristics-such as the color of both the abaxial and adaxial leaf surfaces, leaf size, leaf epidermal trichomes, and the abaxial waxy layer-or (and) in acorn traits. Therefore, we included only L. cinereus, L. lycoperdon, and L. pachylepis for further comparison.



Table 1. Morphological characteristics were observed andmeasured in 29 specimens.

Parameters	Туре	Coding		
Leaf blade length	Qt			
Leaf blade width	Qt			
Leaf texture	QI	Leathery (0)	Papery (1)	
Hairs of leaf	QI	Absence (0)	Presence (1)	
Leaf margin	QI	Entire (0)	Toothed (1)	
Lateral veins number	Qt			
Petiole length	Qt			
Cupule height	Qt			
Cupule diameter	Qt			
Nut height	Qt			
Nut diameter	Qt			
Cupule shape	QI	Hemisphericae (0)	Discoid (1)	
Nut shape	QI	Subglobose (0)	Depressed globose	

Qt: Quantitative; Ql: Qualitative

According to the protologue of *L. lycoperdon*, the acorn of the species resembles those of *L. corneus* and *L. pachyphyllus*, but differ in key features, including entire, leathery leaves, shallower and less symmetrical cupules (distinct from *L. corneus*), and the broad-topped pubescent acorn (distinct from *L. pachyphyllus*) (Skan, 1889). As the specimens of *L. lycoperdon* are quite rare, the taxonomic confusion over the name remains unresolved.

To address these taxonomic ambiguities, we conducted an extensive field survey in the Da-Wei Mountain National Nature Reserve. By collecting voucher specimens of regional fagaceous plants and systematically comparing them with type materials, we aimed to clarify the taxonomy of *L. lycoperdon*. Statistical analyses of key morphological traits in *L. lycoperdon*, *L. cinereus*, and *L. pachylepis* were conducted to delineate species boundaries. This study can resolve historical taxonomic confusion in regional fagaceous species, but also contributes to the biodiversity inventory and conservation management of this hotspot.

MATERIALS AND METHODS

Field survey and plant materials collection

To assess the diversity of Fagaceae species in the middle elevation ranges (1,000-2,200 m) of Da-Wei Mountain, we conducted a six-year field survey, systematically collecting fagaceous specimens. Specimens of Fagaceae were collected and deposited in the Herbarium of Yunnan University (YUKU). To validate species identification, delimitation and document key taxonomical significant characteristics, we examined 27 type specimens and representative morphological specimens from major herbaria in China and internationally (Table S1). These included the Herbarium of the Institute of Botany, Chinese Academy of Sciences (PE), the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), Guangxi Institute of Botany (IBK), The New York Botanical Garden (NY), the Museum National d'Histoire Naturelle (P), and the Royal Botanic Gardens, Kew (K). This comparative analysis validated species identification and facilitated the measurement of key taxonomically significant traits.

Morphological Analysis

Morphological analyses were conducted on the above-mentioned 29 specimens, focusing on fully developed, intact leaves and acorns. A total of 13 morphological traits were measured, including seven leaf and six acorn traits (Table 1). Images of specimens were measured using ImageJ software (Schneider *et al.*, 2012). To further investigate acorn morphology, X-ray scans were used to determine the size and shape of acorns from (1)*L. cinereus* and *L. pachylepis*. These traits were selected because of their rich variation and had long been applied in the taxonomy of identification practice in taxonomic relevance as identified.

Principal component analysis (PCA) and hierarchical cluster analysis were performed to identify statistically significant differences among the species. PCA was conducted on morphological traits of the 29 specimens to reduce dimensionality using the "dudi.pca" function in the R package "ade4" (version 1.7-22; Dray *et al.*, 2023). The results were visualized with the "ggplot2" package (version 3.5.1; Wickham *et al.*, 2024). Hierarchical cluster analysis based on Gower distance (Gower, 1971) was carried out using the "daisy" function from the R package "cluster" (version 2.1.6; Maechler *et al.*, 2023). Both methods can effectively handle mixed quantitative and qualitative data.

The *Kruskal-Wallis* test (Kruskal and Wallis, 1952) was applied to quantitative traits, while *Fisher's* exact test (Upton, 1992) was used for the qualitative traits to evaluate the differences among the 29 specimens. Differences were considered significant when a P value < 0.05 was obtained. All statistical analyses were conducted using R version 4.4.1 (R Core Team, 2024).

RESULTS

Lithocarpus species in Da-Wei Mountain National Nature Reserve

Field surveys and herbarium investigations confirmed the presence of 35 *Lithocarpus* species within the Da-Wei Mountain National Nature Reserve. These species predominantly occur at mid-elevations (1,000–2,200 m), with 10 species also extending into lower elevations.

The morphological traits of *L. lycoperdon*, *L. cinereus*, and *L. pachylepis* were systematically examined and summarized (Figs. 2, 3; Table 2). A morphometric comparison revealed significant differences across all 13 measured traits among the three species (P < 0.001, Table 4). These findings validated the inclusion of all variables in subsequent PCA and hierarchical clustering analyses.



Table 2. Important leaf architecture, acorn features of Lithocarpus lycoperdon (Type specimen), L. cinereus and L. pachylepis.

Characteristics	L. lycoperdon (Type specimen)	L. cinereus	L. pachylepis
Leaf texture	Leathery, abaxially rust-colored to tawny pulverulent-scurfy	Leathery, abaxially rust-colored to tawny pulverulent-scurfy	Papery, concolorous, abaxially covered with short stellate hairs along veins
Leaf size (L × W) cm	5.1–10.2 × 2.5–2.54	8.0–17.5 × 2.0–6.6	20.0–35.0 × 6.0–11.0
Number of secondary veins	8–12	8–12	25–30
Tertiary veins	Abaxially inconspicuous	Abaxially inconspicuous	Abaxially visible
Major secondary vein pattern	Eucamptodromous	Eucamptodromous	Semicraspedodromous
Leaf margin	Entire	Entire	Toothed
Cupule (H × diam.) cm	Discoid, ca. 2.5 × ca. 4.8, scaly	Hemisphericae, $1.6-2.2 \times 2.0-3.2$, scaly	Discoid, 1.5–3.0 × 4.5–6.0, scaly
Trichomes on outer cupule wall	Puberulent and scurfy	Puberulent and scurfy	Puberulent and scurfy
Concentric lamellae on the cupule wall	Bracts triangular-subulate, appressed	Bracts triangular-subulate, appressed	Bracts triangular-subulate, appressed
Size of mature nut (H \times W) cm	ca. 2.5 × ca. 5.0, enclosed base by cup	1.6–2.2 × 1.6–2.3, enclosed 2/3 by cup	$1.5-2.5 \times 4.0-6.5$, enclosed base by cup
Trichomes on outer nut wall	Tawny tomentose	Tawny tomentose	Tawny tomentose
Seed scar	Convex with clear edge	Convex with clear edge	Convex with clear edge



Fig. 2. Morphological characteristics of leaves and acorns of *Lithocarpus cinereus* (A, B) and *L. pachylepis* (C, D), scale bar = 1 cm. A & C. abaxial and adaxial sides of the mature leaf; B & D. acorns.



Table 3. Differences in morphological traits among the three Lithocarpus species.

Traits	L. pachylepis	L. cinereus	L. lycoperdon	Dyalua
	Mean ± SD/Coding	Mean ± SD/Coding	Mean ± SD/Coding	- P value
Leaf blade length	18.6 ± 5.46	13.6 ± 4.40	8.65 ± 3.11	<0.001
Leaf blade width	5.53 ± 2.03	3.08 ± 1.17	1.14 ± 0.399	<0.001
Number of lateral veins	20.7 ± 3.50 (12-27)	10.8 ± 1.06 (8-12)	10.6 ± 0.929 (9-12)	<0.001
Petiole length	1.72 ± 0.491	1.85 ± 0.451	1.47 ± 0.204	<0.001
Leaf texture	1	0	0	<0.001
Hairs of leaf	1	0	0	<0.001
Leaf margin	1	0	0	<0.001
Cupule height	1.64±0.366	1.75±0.183	2.3±0	<0.001
Cupule diameter	4.51±0.694	2.68±0.324	5±0	<0.001
Nut height	2.13±0.284	1.85±0.15	2.6±0	< 0.001
Nut diameter	4.38 ± 1.18	2.07 ± 0.213	4.89 ± 0	<0.001
Cupule shape	1	0	1	<0.001
Nut shape	1	0	1	<0.001



Fig. 3. X-ray scans of acorns of *Lithocarpus cinereus* (A, B, C, D) and *L. pachylepis* (E, F, G, H), bar = 1 cm. A, B & E, F. Lateral and frontal views of the mature acorn with cupule; C, D & G, H. Acorn without cupule.

Principal component analysis (PCA)

The detailed results of PCA are shown in Tables 2, 3, and Fig. 4. Since the first two components account for 89.32% of the variance in leaf traits and 86.65% in acorn traits, respectively, they capture the majority of the variance within the system; therefore these components were selected for further analysis.

PCA divided two distinct groups among the 29 specimens based on either acorn or leaf morphology, providing insights into the primary sources of morphological variation among the three species (Fig. 4).

Cluster analysis

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Hierarchical clustering analysis based on Gower distance supported the differentiation observed in the PCA. The samples of the 29 specimens were grouped into two well-defined clusters, showing clear separation (Fig. 5).

DISCUSSION

The field survey and integrative taxonomic study of three closely related and sympatric species (*L. lycoperdon*,

L. cinereus, and *L. pachylepis*) demonstrate that the type specimen of *L. lycoperdon* is an admixture, consisting of a branchlet from *L. cinereus* and an acorn from *L. pachylepis*. Whereas interspecific hybridization is commonly reported among closely related Fagaceae species, often resulting in intermediate morphological traits between parental taxa (e.g., Petit *et al.*, 2004; Song *et al.*, 2015; An *et al.*, 2017; Kremer and Hipp, 2020), our analyses provide no evidence for such morphologically intermediate individuals. Both PCA and cluster analyses consistently revealed two distinct morphological clusters for leaf and acorn traits, with no overlap (Figs. 4, 5).

Additionally, the leaf epidermal trichome type, a reliable taxonomic characteristic of *Lithocarpus*, supports this distinction. Based on the leaf epidermal trichome types, *L. cinereus* belongs to the APT (Appressed parallel tufts Group) and *L. pachylepis* to the BBT (Bubble Trichome Group) (Zhou and Xia, 2012; Deng *et al.*, 2013). These groups represent phylogenetically distinct lineages (Yang *et al.*, 2024), further reducing the likelihood of interspecific hybridization.

Table 4. Principal component analysis (PCA) of leaf characters of 29 specimens and their contribution to PC1, PC2, PC3, and PC4.

Principle component		PC1	PC2	PC3	PC4
Contribution of morphological traits to different components	Leaf blade length	8.998731965	4.372173963	0.28472084	0.180913378
	Leaf blade width	5.940349295	5.500668492	2.52616396	0.002298506
	Leaf texture	12.72888828	1.172805174	0.315825058	0.053831055
	Hairs of Leaf	12.72888828	1.172805174	0.315825058	0.053831055
	Leaf margin	12.72888828	1.172805174	0.315825058	0.053831055
	Number of lateral veins	12.97141033	0.073518107	0.067172276	1.139208698
	Petiole length	0.034469222	9.725965789	4.477309558	0.029696399
Eigenvalue	-	4.6292138	1.62335193	0.58119893	0.10595271
Variance explained		66.13162566	23.19074187	8.302841808	1.513610144
Cumulative variance explained		66.13162566	89.32236754	97.62520934	99.13881949

Table 5. Principal component analysis (PCA) of acorn characters of 29 specimens and their contribution to PC1, PC2, PC3, and PC4.

Principle component		PC1	PC2	PC3	PC4
	Cupule height	0.190215219	15.12981033	1.345390614	0.00018463
	Cupule diameter	14.62148704	0.036301002	0.051384802	1.823445514
Contribution of morphological traits to	Nut height	7.551062796	2.686267324	6.388840847	0.040456476
different components	Nut diameter	15.68346705	0.000217565	0.211953457	0.5316379
	Cupule shape	15.29892761	0.074641217	0.370488771	0.917316607
	Nut shape	15.29892761	0.074641217	0.370488771	0.917316607
Eigenvalue		4.11864524	1.08011272	0.52431284	0.25382146
Variance explained		68.64408733	18.00187866	8.738547262	4.230357735
Cumulative variance explained		68.64408733	86.64596598	95.38451324	99.61487098



Fig. 4. Principal component analysis (PCA) plot of seven leaf (A) and six acorn (B) traits of 29 specimens. Each species is represented by distinct markers: *Lithocarpus pachylepis* as violet rhombuses, *L. cinereus* as green circles, and *L. lycoperdon* as red triangles.



Fig. 5. Hierarchical cluster analysis plots based on morphological traits of seven leaf (A) and six acorn (B) traits of 29 specimens. 358



Our field survey revealed that L. cinereus and L. pachylepis frequently co-occur in the forests, with acorns of both species often found at the same site (Fig. 4). This ecological overlap makes it challenging to collect mature branchlets with attached acorns from these canopydominant Fagaceae trees. The holotype of L. lycoperdon consists of a disassociated acorn and branchlets (Fig. 1), while the isotype only includes the vegetative part without an acorn. Morphological and statistical analyses confirmed that these belong to different taxa (L. pachylepis and L. cinereus, respectively; Figs. 7, 8). Therefore, the type specimen represents an admixture of species components. According to Article 9 of the Shenzhen Code (Turland et al., 2018), the components of mixed specimens must be accurately identified before it can serve as a type specimen. Although Huang and Zhang (1988) attempted to re-designate the type specimen of L. *lvcoperdon*, they did not use the formal terms "lectotype" or "designated here", failing to meet the requirements of Article 7.11 (Turland et al., 2018). Considering the isotype deposited at NY (NY00253775) only contains the vegetative part and that the protologue uses a large paragraph to describe the vegetative parts, we designate the branchlet and leaves from A. Henry 9069, deposited at K (K000832338), as the lectotype of L. lycoperdon to resolve this ambiguity. However, as the lectotype lacks an acorn, a critical distinguishing feature for this species, we also designate an intact specimen with acorns attached to the branchlet from Da-Wei Mountain (DM27386), as the epitype (Fig. 9) in accordance with Article 9.9 of the Shenzhen Code (Turland et al., 2018). Meanwhile, following the priority established in Article F3 of the Shenzhen Code (Turland et al., 2018), L. cinereus is treated as a synonym of L. lycoperdon.

TAXONOMIC TREATMENT

Lithocarpus lycoperdon (Skan) A. Camus in Rivièra Sci. 18: 41 (1931). —Quercus lycoperdon Skan in J. Linn. Soc., Bot. 26: 518 (1899). —Pasania lycoperdon (Skan) Schottky in Bot. Jahrb. Syst. 47: 674 (1912). —Synaedrys lycoperdon (Skan) Koidz. in Bot. Mag. (Tokyo) 30: 197 (1916). —Lectotype (Designated here, only for foliage branch, the acorn was excluded) China, Yunnan, Mengtze, alt. 7000 feet, A. Henry 9069 (Lectotype: K [K000832338!]; Isolectotype: NY [NY00253775!]). [excl. the acorn on K (K000832338!) belongs to Lithocarpus pachylepis]. —Epitype (Designated here): China, Yunnan, Ping-Bian, alt. 2080 m, L. F. Yang & Y. Tu, DM27386 (Epitype: HITBC [HITBC0124992!]).

Lithocarpus cinereus Chun & C. C. Huang in Guihaia 8(1): 11 (1988), syn. nov. —Type: China, Guanxi, Shang-Si, alt. 1050 m, C. C. Chang 12298 (Holotype IBK [IBK00190905!]; Isotype: IBSC [IBSC35902!]).

Redescription: Trees, evergreen, 20–30 m tall, 50–80 cm in diameter. Branchlets of the current year sulcate, glabrous, dark brown when dry. Leaves alternate; petiole,

1.0-2.6 cm, glabrous, blackens upon drying; leaves coriaceous, oblong to elliptic, $5.1-17.5 \times 2.0-6.6$ cm, abaxially rust-colored to tawny, pulverulent-scurfy, adaxially glabrous, base cuneate and decurrent on petiole, margin completely entire, tip acute to blunt; midrib slightly prominent adaxially and strongly prominent abaxially; secondary veins 8-12 pairs, prominent abaxially, arcuate curvature disappearing near margin, tertiary veins inconspicuous or weak. Male inflorescences in a panicle, rarely solitary in leaf axils. Female inflorescences sometimes androgynous, 8-20 cm, flowers in clusters of three, styles ca. 1 mm. Infructescence to 16 cm, rachis 7-12 mm thick, glabrescent, lenticellate. Cupules clustered in sets of three, sessile, turbinate to cupular, $1.6-2.2 \times 2.0-3.2$ cm, broadest at the middle, enclosing most of the nut; wall woody, 2-3 mm thick; bracts triangular-subulate, appressed, puberulent and scurfy. Nut depressed globose to subglobose, $1.6-2.2 \times$ 1.6-2.3 cm, appressed puberulent and scurfy, apex narrowed; wall woody, 1-2 mm thick; basal scar convex and expanded to more than 1/3 of the nut.

Phenology: Flowers in May–June; acorns mature September –November of the following year.

Distribution and habitat: It is found in northern Vietnam, southwestern Guangxi Province, China (e.g., the Shi-Wan-Da-Shan area), and southeastern Yunnan Province, China (including Wenshan, Pingbian, Xichou, Jinping, and other regions). It thrives in evergreen broadleaved forests at elevations of 1,000 to 2,200 meters.

Additional specimens examined. CHINA. Yunnan: Jinping, Wu-Tai Mountain, Near Waterfall, alt. 2050m, 15 Oct. 1996, *S. K. Wu et al. 3790* (KUN [KUN0772445!]); Jinping, Wu-Tai Mountain, alt. 1400–2500m, 16 Oct. 2008, *J. Q. Wu et al. 2079* (HIB [HIB0178718!]); Mengtze, alt. 6000 feet, *A. Henry 9636* (A [00105384!]); Pingbian, Da-Wei Mountain, Shuiweicheng, alt. 2000 m, 25 Jun. 1956, *Anonymous 4461* (KUN [KUN0502546!]), alt. 2080 m, 24 Oct. 2023, *L. F. Yang & Y. Tu, DM27406* (YUKU!).

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