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NOTE

Lectotypifications, new synonymizations, and a new distribution record in selected tropical Asian Fagaceae

Li-Fang YANG[1, 2], Yu-Ang XIONG[1, 2], Yun-Hong TAN[3], Yu TU[1, 2], Min DENG[1, 2,*]

1. *State Key Laboratory of Vegetation Structure, Function and Construction (VegLab), Ministry of Education Key Laboratory for Transboundary Ecosecurity of Southwest China, and Yunnan Key Laboratory of Biological Adaptation, Conservation and Utilization, School of Ecology and Environmental Science, Yunnan University, Kunming 650500, China.* ***2.*** *The key laboratory of Rare and Endangered Forest Plants of National Forestry and Grassland Administration & the Key Laboratory for Silviculture and Forest Resources Development of Yunnan Province, Yunnan, Academy of Forestry and Grassland, Kunming 650201, Yunnan, China.* ***3.*** *Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences & Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China.* [*]*Corresponding author's email: dengmin@ynu.edu.cn*

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ABSTRACT: Taxonomic confusion remains common among large Asian tropical Fagaceae, often due to inadequate understanding of diagnostic morphological traits and the presence of admixture-type specimens. Through a comprehensive literature review, critical examination of herbarium specimens and detailed morphological comparisons, we address several overlooked taxonomic issues. Lectotypes are designated here for *Castanopsis lanceifolia* (Oerst.) Hickel & A. Camus, *C. armata* (Roxb.) Spach, *C. tribuloides* (Sm.) A.DC., and *C. ferox* (Roxb.) Spach. Our study further reveals that the type specimens of *Quercus cepifera* H. Lév. and *Q. dussaudii* Hickel & A. Camus are admixtures: the former comprises the acorns and infructescence of *Lithocarpus litseifolius* (Hance) Chun mounted with a branchlet of *Castanopsis eyrei* (Champ. ex Benth.) Tutcher, while the latter contains acorns of *Q. kerrii* Craib along with a branchlet of *C. argyrophylla* King ex Hook.f.. We designate the infructescence and acorns portions as the respective lectotypes of *Q. cepifera* and *Q. dussaudii*, and reduce them to synonyms of *L. litseifolius* and *Q. kerrii*, respectively. We also document a new distribution record of *C. lanceifolia* in China. These taxonomic clarifications provide a refined basis for the identification, conservation, and sustainable management of ecologically and economically important Fagaceae species in tropical Asia.

KEY WORDS: Admixture type, *Castanopsis*, *Lithocarpus*, nomenclature, *Quercus*, taxonomy, typification.

INTRODUCTION

The family Fagaceae Dumort. is the most species-rich and widely distributed woody family within Fagales, comprising over 1,000 species across temperate, subtropical, and tropical regions of the Northern Hemisphere and parts of South America (Govaerts and Frodin, 1998; Huang *et al*., 1999). As a dominant component of forest ecosystems, Fagaceae plays a critical role in maintaining biodiversity and ecosystem functions, and serves as a model lineage for integrating ecology and evolution studies (Cannon *et al*., 2018; Cavender-Bares, 2019). Molecular phylogenetic studies recognize eight genera within the family: *Castanea* Daubenton, *Castanopsis* (D.Don) Spach, *Chrysolepis* Hjelmq., *Fagus* L., *Lithocarpus* Blume, *Notholithocarpus* Manos, Cannon & S.H.Oh, *Quercus* L., *Trigonobalanus* Forman (Manos and Stanford, 2001; Oh and Manos, 2008; Zhou *et al*., 2022; Liu *et al*., 2024).

East Asian tropics and subtropics are major biodiversity hotspots for Fagaceae. At the end of the 18th century and the beginning of the 19th century, botanical exploration in these regions began with the colonial expeditions of the British East India Company. These expeditions and efforts laid the foundation for the study of tropical Asian flora. William Roxburgh (1751–1815), the first superintendent of the Botanic Garden at Calcutta under the East India Company, made pioneering contributions to the study of plants in India and the surrounding regions (Sealy, 1956; Sanjappa *et al*., 1991; Forman, 1997). In collaboration with botanists such as John Gerard Koenig, he amassed a large collection of plant specimens from the Indian subcontinent, Nepal, Myanmar, and the Malay Peninsula. Based on these collections, Roxburgh described around 2,600 plant species, many of which were new to science. However, for most of these new species, no type was designated; instead, the accompanying illustrations were used as the basis for their names. Furthermore, Roxburgh's specimens are scattered across various herbaria, including those at the Natural History Museum, London (BM), Brussels (BR), Edinburgh (E), Geneva (G), Kew (K), and Liverpool (LIV), and there is no unified catalog of these specimens. This has complicated subsequent classification efforts and the designation of type specimens (Majumdar and Banerjee, 1976; Candolle and Radcliffe-Smith, 1981).

Many Fagaceae species are dominant canopy trees in evergreen broad-leaved forests of Asia, making the collection of reproductive material (e.g., flowers, cupules, and nuts) especially difficult. In another aspect, taxonomic research remains underdeveloped across much

Table 1. List of specimens that were used for morphological analysis.

Quercus cepifera: CHINA. Guizhou, Grand arbre au sud de Pin-Fa, *P. J. Cavalerie 2341* (E00275485, E00275486, A00034142).

Castanopsis eyriei: **CHINA**. Chongqing. Nanchuan, *G. F. Li 84070* (PE00224145); Guangdong (Kwangtung), Heyuan, *G. C. Zhang 94* (MO1071802), Hong Kong, Tai Mo Shan, *Tsang,W. T. s.n.* (P06851531) Hong Kong: *Eyre 301* (K000832604); Sin-fung, *Y. W. Taam 256* (BR0000030517783); Xingning, *X. G. Li 201783* (PE01659793); Guangxi, *Q. H. Lv 4110* (PE01658880); Guizhou, Anonymous *s.n.* (PE01506508), Libo, *Li Bo Team 81-6-0099* (PE01605782); Hunan, Henyang, Z. H. Hu & Y. Q. Kuang 015 (PE01458049), *P. P. Chen 11217* (PE01605032); Jiangxi, Guixi, *J. S. Yue et al. 5387* (PE00224067); Lushan, *C. M. Tan Lu088* (JJF00016744); Yunnan, Pin-fa, *P. J. Cavalerie 1268* (P00716222, P00716223); Zhejiang, Longquan, Z. L. Zhang 04279 (PE00273194).

Quercus dussaudii: **LAOS**. Ban Pac Sanane, Route de Vientiane à Luang-Prabang, *M. Dussaud 62* (P00753919).

Castanopsis argyrophylla: **CHINA**. Yunnan, Jinghong, *J. W. Li 2261* (HITBC0028018), Yunnan, Simao, *P. Y. Mao 5948* (PE00163110), *P. Y. Mao 6085* (PE00163132), *P. Y. Mao 6145* (PE00163133). **LAOS**. Phiang District, Sayaboury, *J. F. Maxwell 99-277* (L3793377). **MYANMAR**. Tenasserim and Andamans, *J. W. Helfer 4466* (K000395368), Arakan, *Hildebrand s.n.* (K000395370), Rangoon, *M. Lelland & Maingay1457/2* (K000395371), Paungbain Reserve, Upper Chiudein, *J. H. Lace 4216* (E00672020), Yangon, *R. W. Capt & I. M. S. MacGregor 810* (E00672024), Upper Burma, *B. Khan s.n.* (L1553086), Asia-Tropical, *B. Khan s.n.* (US39366). **THAILAND**. Nan, Doi Phu Kha National Park, *P. Srisanga 2164* (HITBC0027045), District Pahn, Chiang Rai, *P. Palee 443* (L3800447).

Quercus kerrii: **CHINA**. Hainan, Changjiang, *M. Deng et al. DM25264* (YUKU); Yunnan, Jingdong, *M. Deng et al. DM22418* (YUKU); Jinghong, *P. S. Zhang DM24486* (YUKU); Malipo, *R. Guo DM24486* (YUKU); Puer, *M. Deng et al. DM27841* (YUKU); Shuangbai, *M. Deng et al. DM23215* (YUKU); Yuanjiang, *M. Deng et al. DM18972* (YUKU).

Quercus rex: **CHINA**. Yunnan, Jinghong, *M. Deng et al. DM18934* (YUKU), *P. S. Zhang DM25163* (YUKU); Mengla, *Y. J. Zhou DM24490* (YUKU); Simao, *M. Deng et al. DM18930* (YUKU), *M. Deng & L. F. Yang DM26882* (YUKU), *M. Deng et al. DM27872* (YUKU); Xishuangbanna, *M. Deng DM1914* (YUKU).

of tropical Asia. Many taxa are known only from fragmentary or incomplete type material (often with fruits or branchlets alone). Admixture specimens, in which parts of different taxa are mounted together, further obscure species limits (Deng *et al*., 2015; Yang *et al*., 2025). Compounding these challenges, the flowers of Fagaceae are small and morphologically conserved, while traits such as leaf and acorn morphology vary markedly among populations, contributing to species misidentification and over-splitting. As a result, Fagaceae is widely considered a taxonomically difficult group, particularly in tropical Asia. Resolving these taxonomic uncertainties requires a rigorous approach that integrates detailed examination of herbarium specimens, critical evaluation of protologues, and targeted fieldwork.

From 2022 to 2025, we conducted an extensive survey of Fagaceae specimens housed in major herbaria in China and abroad. Based on extensive morphological comparisons and literature review, we aim to clarify long-standing taxonomic ambiguities within tropical Asian Fagaceae, particularly in the genera *Quercus*, *Castanopsis*, and *Lithocarpus*. By reassessing historical type materials, designating lectotypes when necessary, and critically evaluating species delimitation under modern taxonomic standards, this study seeks to stabilize the nomenclature and provide a reliable foundation for future phylogenetic, biogeographic, and ecological research on the family.

MATERIALS AND METHODS

Specimen examination

A large number of early collections of tropical Fagaceae were conducted by colonial expeditions of the British East India Company during the early 19th century (ca. 1800–1858), particularly through the efforts of botanists such as William Roxburgh, Nathaniel Wallich, and their associates. In addition, French colonial botanists like Jean-Baptiste Louis Pierre (active in Cochinchina and Cambodia during the late 19th century), and Dutch botanists such as Friedrich Anton Wilhelm Miquel and later Elmer Drew Merrill (working in the Dutch East Indies), also made significant contributions to the collection and documentation of tropical Fagaceae. These specimens are mostly deposited in BM, BR, K, E, G, L, LIV, and P, with duplicates distributed to other major herbaria worldwide (Sealy, 1956; Forman, 1997). To address potential taxonomic issues on these tropical Fagaceae, we conducted a comprehensive literature survey and meticulously examined specimens from major herbaria all over the world, including A, BM, BR, E, G, HITBC, IBK, IBSC, K, KUN, L, LIV, M, MO, NY, P, PE, SYS, US, and YUKU. The key specimens studied are listed in Table S1.

Protologue tracking

Most scientific names related to tropical Fagaceae plants were published successively in *Flora Indica: or, Descriptions of Indian Plants* (1751–1834), *Flora of British India* (1872–1897), and contemporaneous literature extending to the mid-20th century, such as *Flora van Nederlandsch Indië* (Miquel, 1855–1859), *Repertorium Specierum Novarum Regni Vegetabilis* (Fedde, 1910–1942), *The Cyclopædia; or, Universal Dictionary of Arts, Sciences, and Literature* (Rees, 1819), *A Bibliographic Enumeration of Bornean Plants* (Merrill, 1921), *Note sur les Castanopsis d'Indo-Chine* (Hickel and Camus, 1921a), *The Flora of the Malay Peninsula* (Ridley, 1922), and *Les Chênes* (Camus, 1934–1954). Accordingly, we conducted a systematic review of the relevant literature from this period and compiled the principal taxonomic studies on Fagaceae, tracing how

Table 2. Morphological characteristics of leaves or acorns were observed and measured in 48 specimens.

Parameters	Type	Coding	
Leaf blade length	Qt		
Leaf blade width	Qt		
Leaf shape	Ql	Ovata (0)	Elliptic (1)
Leaf apex	Ql	Acute (0)	Acuminate (1)
Leaf base	Ql	Symmetric (0)	Asymmetric (1)
Leaf base shape	Ql	Cuneate (0)	Acute (1)
Leaf texture	Ql	Leathery (0)	Papery (1)
Hairs of leaf	Ql	Absence (0)	Presence (1)
Leaf margin	Ql	Entire (0)	Toothed (1)
Lateral veins number	Qt		
Irregular intersecondary veins	Ql	Absence (0)	Presence (1)
Petiole length	Qt		
Cupule height	Qt		
Cupule diameter	Qt		
Hairs of Cupule	Ql	Absence (0)	Presence (1)
Cupule bracts number	Qt		
Nut height	Qt		
Nut diameter	Qt		
Hairs of Nut	Ql	Absence (0)	Presence (1)
Scar diameter	Qt		
Scar shape	Ql	Concave (0)	Slightly convex (1)

Qt: Quantitative; Ql: Qualitative

earlier researchers delineated species, and assessing whether nomenclatural typifications, lectotypifications, or taxonomic treatments have been applied to these names.

Morphological Analysis

To validate the species identification and delimitation, we examined 48 type specimens along with representative morphological specimens from major herbaria, including A, E, HITBC, K, L, MO, NY, P, PE, US, and YUKU (Table 1) to provide statistical evidence to reveal the possible identity. This comparative analysis not only confirmed species identification but also facilitated the measurement of key taxonomically significant traits.

Morphological analyses were conducted on the 48 specimens mentioned above, with a focus on fully developed, intact leaves and acorns. A total of 21 morphological traits were measured, including 12 leaf traits and 9 acorn traits (Table 2). For all specimens, leaf and acorn dimensions were measured using standardized criteria, with leaf length and width and acorn height and diameter recorded (in cm). Specimen images were analyzed using ImageJ software (Schneider *et al*., 2012). For *Q. cepifera*, *Castanopsis eyrei*, and *C. argyrophylla* specimens, leaf morphological traits were extracted; for *Q. kerrii* and *Q. rex* specimens, acorn traits were extracted; and for *Q. dussaudii* specimens, both leaf and acorn traits were examined. These traits were selected due to their significant variation, which has long been recognized and utilized in taxonomic identification practices.

Fig. 1. A. Type material of ***Quercus cepifera***, *P.J. Cavalerie 2341*(E00275485). The foliage branch is the lectotype of ***Q. cepifera***, inside the red (acorns) line belongs to ***Lithocarpus litseifolius***; **B.** Type material of ***Q. dussaudii***, *M. Dussaud 62* (P00753919). Inside the red line is the lectotype (acorns) of ***Q. dussaudii***, the foliage branch belongs to ***Castanopsis argyrophylla***; **C.** Lectotype specimen of ***C. lanceifolia*** (*W. Roxburgh s.n.,* P06856344); **D.** Epitype specimen of ***C. lanceifolia*** (*Hooker & T. Thomson s.n.*, O2163134).

To assess statistically significant differences among the species, principal component analysis (PCA) was performed on the morphological traits of the 48 specimens. Dimensionality reduction was carried out using the "dudi.pca" function from the "ade4" package in R (version 1.7-22; Dray *et al*., 2023). The resulting data were visualized with the "ggplot2" package (version 3.5.1; Wickham *et al*., 2024), which is capable of processing both quantitative and qualitative data. All statistical analyses were executed using R version 4.4.1 (R Core Team, 2024).

RESULTS AND DISCUSSION

1. *Quercus cepifera*

Quercus cepifera H. Lév. was described by Léveillé (1913) based on two specimens collected at different times (8 June 1905 and January 1906) under the same

gathering number (*P.J. Cavalerie 2341*), and no further specimens have been recorded ever since. Our examination reveals that the syntype dated 8 June 1905 (*P.J. Cavalerie 2341*, E00275485) and the isosyntype (*P.J. Cavalerie 2341*, A00034142) are mixed collections, comprising branchlets with foliage mounted together with unrelated acorns and infructescences (Figs. 1A, S1). In contrast, the other syntype collected in January 1906 (*P.J. Cavalerie 2341*, E00275486) consists solely of branchlets, lacking both acorns and infructescences (Fig. S2).

As the leaf of *Quercus* without shining abaxial leaf surface. Although the leaves of *Castanopsis* and *Lithocarpus* seem similar, but differ in that the leaves of *Lithocarpus* are usually arranged in a spiral manner; leaf base symmetrical, with secondary veins regular in space to the leaf margin, while leaves are arranged in a flat, asymmetrical leaf base, and not irregularly spaced secondary veins in *Castanopsis*. Therefore, the twigs of the type specimens of *Q. cepifera* actually belong to species in *Castanopsis*. In contrast, the infructescence of *Q. cepifera* is quite long with cupules/acorns in clusters of 3–5, demonstrating it is *Lithocarpus*. The type material of the species is collected from Guizhou "Grand arbre au sud de Pin-Fa" (present-day Pingba County, Anshun City, Guizhou Province). Within this region, the only *Lithocarpus* species whose acorn morphology matches that of the type material is *L. litesifolius* (Hance) Chun, with a glabrous, plate-shaped cupule covering only the nut base, bearing triangular, appressed, imbricate bracts, the cupules occurring in clusters of three; nut broadly conical, glabrous, with a concave scar. It differs markedly from other *Lithocarpus* species occurring in Guizhou, such as *L. elizabethae* (Tutcher) Rehder, *L. dealbatus* (Hook.f. & Thomson ex Miq.) Rehder, *L. fordianus* (Hemsl.) Chun, and *L. cleistocarpus* (Seemen) Rehder & E.H.Wilson, all with a convex scar; *L. fenestratus* (Roxb.) Rehder, with a cupule enclosing most of the nut; and *L. petelotii* A.Camus, with a puberulent cupule.

Rehder (1929), based on the fruiting spike of specimen *P.J. Cavalerie 2341*, reduced *Q. cepifera* to a synonym of *L. spicatus* (Sm.) Rehder & E.H. Wilson. However, he did not explicitly designate a lectotype using the formal terms "type," "lectotype," or "designated here," thus failing to meet the requirements of Article 7.11 (Turland *et al*., 2025). Furthermore, the size and shape of the fruit on specimen *P.J. Cavalerie 2341* (scar ca. 0.8 cm in diameter, cupule ca. 0.9 × 1.2–1.5 cm, nut broadly conical 0.4–0.6 × 1.0–1.2 cm) differ significantly from those of *L. spicatus* (scar 1.6–2.0 cm in diameter, cupule 0.6–1.0 × 2.2–2.8 cm, nut depressed globose 1.5–2.2 × 2.0–2.6 cm) (Huang *et al*., 1999). Therefore, Rehder's treatment is not justified.

The branchlet and leaf morphology of the type specimen is most consistent with *C. eyrei* (Champ. ex Benth.) Tutcher, which has glabrous branchlets and leaves; leathery, entire-margined, concolorous leaves, elliptic to narrowly elliptic, with a long acuminate apex often curved to one side, an oblique base, and male inflorescences spicate. It is clearly distinguishable from other sympatric *Castanopsis* species, including *C. carlesii* (Hemsl.) Hayata, with young leaves abaxially covered by reddish-brown to yellowish-brown waxy scalelike trichomes; *C. fissa* (Champ. ex Benth.) Rehder & E.H.Wilson, possessing serrate leaf margins; *C. hystrix* Hook.f. & Thomson ex A.DC., exhibiting leaves abaxially covered by reddish-brown to yellowish-brown waxy scalelike trichomes; and *C. kweichowensis* Hu, characterized by puberulent branchlets and leaves and serrate margins.

To further confirm the identity of the branchlet, we conducted morphometric analyses of leaf characters involving the type specimen of *Quercus cepifera*, the type specimen of *C. eyrei*, and a large series of morphologically and geographically representative *C. eyrei* specimens (Fig. 1A). The PCA explained 98.01% of the variance across the first four principal components, with the first two components alone accounting for 61.00% of the total variance in leaf traits (Table S2.1). These components capture the primary variation within the dataset and were therefore selected for further analysis. The PCA consistently revealed a single morphological cluster for leaf traits, with nearly complete overlap (Fig. 2A). Based on the combined morphological and statistical analyses, it is conclusively confirmed that the branchlets of *Q. cepifera* are taxonomically assigned to *C. eyrei* (Figs. 1A, 2A).

According to Article 9 of the Madrid Code (Turland *et al*., 2025), components of mixed specimens must be accurately identified before they can serve as a type material. Although Rehder (1936) informally treated *Q. cepifera* as a synonym of *C. eyrei,* he also did not explicitly designate a lectotype using the formal terms "type," "lectotype," or "designated here," and thus did not meet the requirements of Article 7.11 (Turland *et al*., 2025).

Given that Rehder described the epithet of *Q. cepifera* as referring to the term "glande cepiformi", and that the protologue provides an extensive description of acorn features (Léveillé, 1913), we designate the infructescence and acorns from *P.J. Cavalerie 2341*, deposited at E (E00275485), as the lectotype of *Q. cepifera* to resolve this ambiguity. Accordingly, *Q. cepifera* is here formally reduced to a synonym under *L. litesifolius.*

2. *Quercus dussaudii*

Quercus dussaudii Hickel & A.Camus was described based on a single collection (*M. Dussaud 62*) from Ban Pac Sanane, along the route from Vientiane to Luang-Prabang in Laos (Hickel and Camus, 1921b). The type specimen consists of detached acorns and leafy branchlets mounted on the same sheet (Fig. 1B). Since its original description, no additional specimens matching its morphology have been reported. In 1987, Thailand plant

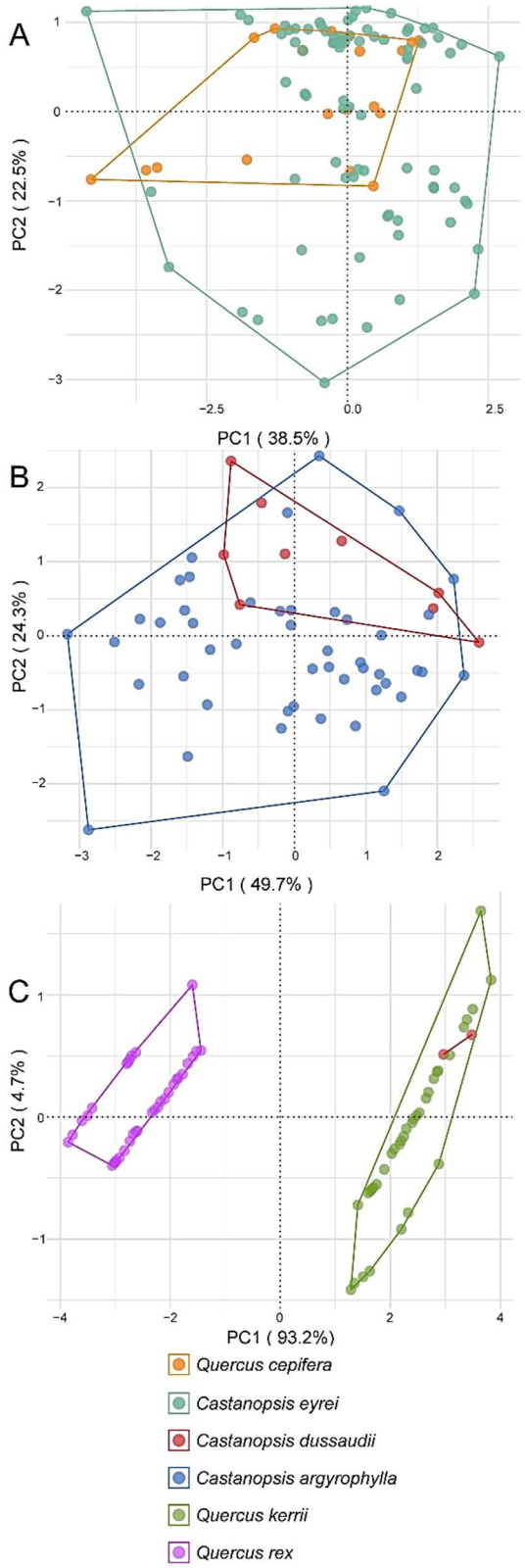

Fig. 2. Principal component analysis (PCA) plots of: (**A**) leaf characters from ***Quercus cepifera*** and ***Castanopsis eyrei***; (**B**) leaf characters from ***Q. dussaudii*** and ***C. argyrophylla*** specimens; and (**C**) acorn characters from ***Q. dussaudii***, ***Q. kerrii***, and ***Q. rex*** specimens.

taxonomist Tem Smitinand annotated the holotype, recognizing it as a mixed collection, with a note label on the sheet stating: "This sheet is a mixed collection; leaves belong to a *Castanopsis*; fruits, a *Quercus* (Sect. *Cyclobalanopsis*)" (Fig. 1B). We confirm Smitinand's observation that the flat leaf arrangement, asymmetric leaf base, and irregular secondary vein distribution indicate the foliage branchlet belongs to *Castanopsis*, while the oblate nut with four short styles and concentric ring-like structures at the base of the styles aligns it with the *Cyclobalanopsis* section, characterized by stellate trichomes (Deng, 2007). Despite Smitinand's accurate assessment, no formal taxonomic revision followed.

The glabrous branches and leaf blades, alternate and distichous leaf arrangement, lanceolate leaf blade (12–15 × 4–5 cm) with entire margin and acuminate apex, thick leathery texture, grayish-white abaxial surface, and approximately 10 pairs of secondary veins all indicate that the foliage branchlet traits are more consistent with *C. argyrophylla* King ex Hook.f., a widespread species in Indo-China.

Phengklai (2006) treated *Q. dussaudii* as a synonym of *Q. rex* Hemsl., but neither designates a lectotype nor explicitly indicates that it was being treated as a new synonym. Morphological comparison shows that the acorns of *Q. dussaudii,* collected in October (likely mature time), differ significantly from those of *Q. rex.* The cupules of *Q. dussaudii* measure 0.8–0.9 × 3.3–3.5 cm, with bracts arranged in 8–10 rings; the nuts are 1.2 × 2.5 cm with a scar ~1.5 cm in diameter. In contrast, *Q. rex* bears significantly larger acorns: cupules 1.5–1.8 × 3.3–5 cm with 7–8 rings and nuts 2.5–3.5 × 3.5–6 cm with a seed scar 2–2.5 cm in diameter. Moreover, as the specimen was collected roadside, its habitat differs from the typical ravine environment of *Q. rex*. Instead, the acorn characteristics of *Q. dussaudii* consistent with *Q. kerrii*, which has cupules 0.5–1 × 2–3.8 cm, with bracts arranged in 7–11 rings, and nuts measuring 0.7–1.2 × 2–2.8 cm, with seed scars 1–2 cm in diameter.

Therefore, we selected *Q. kerrii*, *Q. rex*, and the type specimen's acorns for comparative analyses, using the branchlets and leaves of *C. argyrophylla* as reference, to determine whether the morphological characters of the type specimen fall within the intraspecific variation range defined for these taxa.

The PCA analysis based on the type specimen of *Q. dussaudii* and a large number of typical *C. argyrophylla* leaf specimens supports our hypothesis. The first two principal components in the PCA accounted for 74.01% of the total variance (Table S2.2). The analysis consistently identified a single morphological group for the leaf traits, with near-complete overlap (Fig. 2B). Combining both morphological and statistical results, we confidently confirm that the branchlets of *Q. dussaudii* are taxonomically classified under *C. argyrophylla* (Figs. 1B, 2B).

Statistical analysis also supports the assignment of *Q. dussaudii* acorns to *Q. kerrii*. PCA analysis of the acorns from *Q. dussaudii*, *Q. rex*, and *Q. kerrii* explained a high proportion of the variance (PC1 = 93.2%; PC2 = 4.7%) and revealed two distinct groups among the three species based on acorn morphology (Fig. 2C; Table S2.3). Notably, *Q. dussaudii* and *Q. kerrii* clustered together (Fig. 2C).

As *Q. dussaudii* was originally placed in *Quercus* subgenus *Cyclobalanopsis* (Hickel and Camus, 1921b), a unique oak lineage characterized by concentric bract rings on the outer cupule wall, the acorn's characteristics carry greater diagnostic value than vegetation features. Following Article 9 of the Madrid Code (Turland *et al*., 2025), we designate the acorns on the sheet *M. Dussaud 62* (P00753919) as the lectotype of *Q. dussaudii*, excluding the detached foliage. Based on this typification, *Q. dussaudii* is here formally reduced to a synonym under *Q. kerrii*.

3. *Castanopsis lanceifolia*

Castanopsis lanceifolia (Oerst.) Hickel & A.Camus was originally described as *Quercus lanceifolia* Roxb. by Roxburgh (1832), an illegitimate later homonym of *Q. lancifolia* Schltdl. & Cham. (1830). The name was first validly published as *Pasania lanceifolia* Oerst. by Ørsted (1866), subsequently transferred to *Castanea* by Kurz (1875), and ultimately placed in *Castanopsis* by Hickel and Camus (1921a). However, none of these protologues, including Roxburgh (1832)**,** Ørsted (1866), Kurz (1875), and Hickel and Camus (1921a), designated a type species.

C. lanceifolia was originally described by Roxburgh (1832) in *Flora Indica*, based on material collected from Shingra (Garrow country) ، and accompanied by illustrations (Wight, 1840) (Fig. S3). De Candolle (1864) in *Prodromus Systematis Naturalis Regni Vegetabilis* mentioned that Roxburgh had collected specimens of this species in the Garrows (Meghalaya), and also listed additional specimens, including those collected by Hooker f. & Thomson from Meghalaya, Sillet, and Sikkim, as well as by W. Griffith from Bangladesh. Ørsted (1866) referenced both Roxburgh's illustration (Wight, 1840) and De Candolle's (1864) description, and also recorded the distribution of *C. lanceifolia* as "India orientali", referring to eastern India. The original description and accompanying illustrations (Fig. S3) clearly show the presence of both inflorescences and acorns, and the protologue states (Roxburgh, 1832): "*Leaves short-petioled, lanceolar, entire, obtusely acuminate, firm and lucid. Spikes panicled, terminal. Nuts oval; cup in some completely covering the nut, in others variously split and covering more or less of its lower part only.*"

We examined all *C. lanceifolia* specimens collected in 1832 and earlier that are available through GBIF and major herbaria. Among these, only a single specimen (Fig. 1C, P06856344) was collected by Roxburgh himself in India. This specimen exhibits branchlet and inflorescence characters fully consistent with the original description (Roxburgh, 1832) and the illustration (Fig. S3) provided in the protologue (Wight, 1840). We therefore designate the specimen *W. Roxburgh s.n.* (P06856344) at P (Fig. 1C), collected from India, as the lectotype of *C. lanceifolia*, although it lacks mature acorns. Since the protologue and its accompanying illustration provide detailed information on the male and female inflorescences, cupules, and nuts, we here designate O2163134 (Fig. 1D), J. D. Hooker & T. Thomson collected from Meghalaya, northeastern India, as an epitype. Among the many specimens listed by De Candolle (1864), this specimen from the type locality bears both inflorescences and acorns, and thus serves to supplement the diagnostic features—particularly those of the cupule and nut—and to ensure the nomenclatural stability of the name.

C. lanceifolia was previously recorded to occur in Assam, Bangladesh, the eastern Himalayas, Myanmar, Nepal, Thailand, and Vietnam (Phengklai, 2008; Aung *et al*., 2023; POWO, 2025). However, recent fieldwork has confirmed its presence in southwestern China (Tong-Bi Guan National Nature Reserve, Yingjiang County, Yunnan Province, 27 July 2022, based on a collection by P. Y. Wang *et al.* (*WPY37*; Fig. S4), representing a new national record for China.

4. *Castanopsis armata*

Castanopsis armata was originally described in 1820 as *Quercus armata* (Roxb.) Spach by Roxburgh in Plantae Coromandelianae (1820), but no specimens were cited, except for the protologue includes a detailed account of its distribution —"*A large timber tree, a native of the mountainous countries immediately east of Bengal; at Chittagong, it is called Kanta-lal-batana; at Tipperah Singahara; and in the forests near Golparah Kanta Singgur.*" —along with an illustration (Fig. S5) depicting a fruit characterized by a large globose cupule with short, clustered spines illustrated by (Wight, 1846), which are important diagnostic traits to the species.

To clarify the identity of this name, we surveyed all relevant Fagaceae specimens from Bangladesh and northeast India via GBIF and the main herbaria. Specimens collected on behalf of the British East India Company between 1802 and 1847 were largely deposited in BM, BR, CAL, E, G, LIV, and P (Sealy, 1956; Forman, 1997). Three collections under *F. Hamilton 3736* (Wallich no. 3736) (Fig. 3A: K001119915, Fig. S6: K001119916, and Fig. 3A: K00112088) were all collected from Goalpara, India, between 1802 and 1808, aligning with the protologue's locality and timeframe (predating the 1820 publication of *Quercus armata* Roxb.). The rest specimens were collected after 1820, ruling out the possibility of being the type materials.

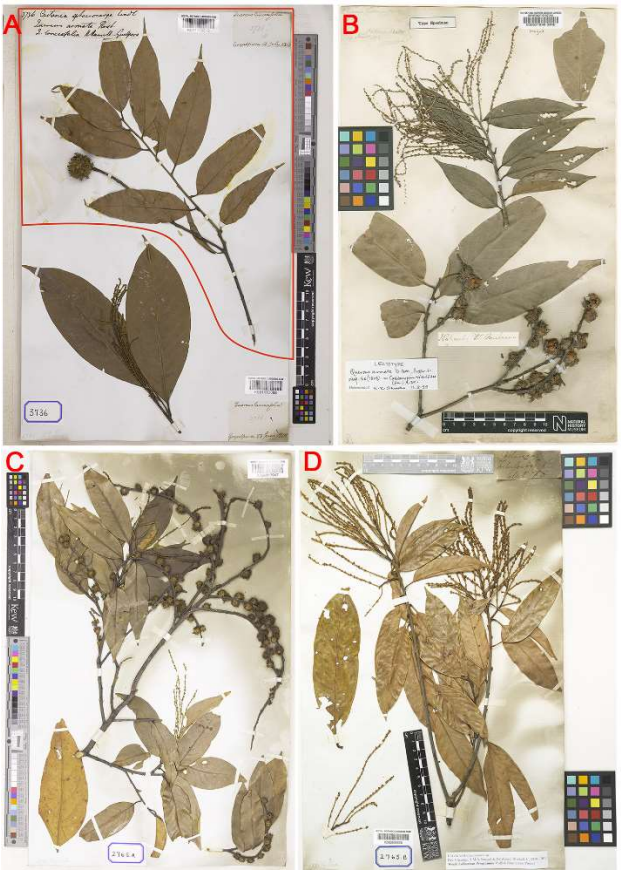

Fig. 3. A. Type material of ***Castanopsis armata***, *F. Hamilton 3736* (Wallich no. 3736, K001119915). The foliage branch within the red outline (K001119915) is designated as the lectotype of ***C. armata***, the material in the lower left corner (K001112088) corresponds to ***C. lanceifolia***; **B.** Lectotype specimen of ***C. tribuloides*** (*Buchanan s.n.*, BM000521899); **C.** Neotype specimen of ***C. ferox*** (*F. De Silva 2765B*, Wallich no. 2765A, K001117047); **D.** Lectotype specimen of ***C. ferox*** (*F. De Silva 2765B*, Wallich no. 2765B, K000639576).

Although these collections were originally collected by Francis Hamilton (F. Buchanan née), Roxburgh could have examined these specimens. According to historical records, Buchanan arrived in India in 1794 and left in 1815. During these twenty years, he was employed by the East India Company and frequently transferred his plant specimens to the company (Vicziany, 1986). During this time, William Roxburgh served as the first superintendent of the Botanic Garden at Calcutta under the same company. Given this overlap, William Roxburgh might have studied these specimens. Among the three collections, K001119915 (*F. Hamilton 3736*), collected on 16 July 1808, includes acorns that match both the morphological description and the illustration in the protologue, notably large, globose nuts totally enclosed by a cupule bearing short, clustered spines. This specimen is mounted on the same sheet as K001112088, which includes a branchlet with inflorescences collected from the same locality on 28 June 1808 (Fig. 3A). However, its larger and broader leaves (8–20 × 6–7.5 cm) suggest it represents *C. lanceifolia*. The third specimen (K001119916) under Wallich no. 3736 (Fig. S6), collected on 6 Nov. 1808, includes only branchlets with inflorescences, but shares similar leaf morphology (leaves 12–17 × 3.5–5 cm, lanceolate, acuminate, entire, smooth) with K001119915, indicating conspecificity. Because K001119915 is the only specimen that bears both diagnostic acorn and leaf characters fully consistent with the original description, illustration, and locality, we therefore designate K001119915 (*F. Hamilton* 3736) as the lectotype of the name *Castanopsis armata*.

5. *Castanopsis tribuloides and C. ferox*

Castanopsis tribuloides was originally described in 1819 as *Quercus tribuloides* Sm. in Rees's Cyclopaedia (1819), based on materials from "the forests of Upper Nepal", though no specimens were cited in the protologue, but it mentioned "Dr. Buchanan referred this remarkable plant", indicating these original materials might be studied or collected by Dr. F. Buchanan. The species was subsequently transferred to *Castanea* (*Castanea tribuloides* (Sm.) Lindl.) by Wallich (1830), and later to *Castanopsis* by Hance *et al*. (1863), and recorded in multiple regional floristic works and monographs later (e.g., Camus, 1929; Huang *et al*., 1998, 1999; Pusalkar *et al*., 2022), but none of these works designated the type of the name *Castanopsis tribuloides*.

To clarify the name application, we examined all available Fagaceae specimens from Nepal and the adjacent area deposited in GBIF and major herbaria. Four specimens attributed to Buchanan (Dr. F. Buchanan [Francis Buchanan-Hamilton]) *s.n.* and collected in Nepal in 1802 (Fig. 3B: BM000521899, Fig. S7: BM000521988, Fig. S8: BM000521989, and Fig. S9: BM000521895) match the protologue's locality and predate the publication of *Q. tribuloides* (1819), making them the possible original materials. Remarkably, the four specimens were collected at different times, although they represent the same taxa. Therefore, they are actually the syntypes. Among them, BM000521899 contains branchlets with attached infructescences and acorns, providing the most comprehensive morphological features. Therefore, we designate BM000521899 (*Buchanan s.n.*) as the lectotype of *C. tribuloides*.

It is worth noting that early botanical studies in the Indian region contained misinterpretations concerning the taxonomical status of *C. tribuloides*. In Prodr. Fl. Nepal. (1825: 56), the morphology of *Quercus armata* was described, then followed the *Quercus armata* cited as Roxburgh as the author of the name, along with the correct protologue: Pl. Coromandel 3: 92. However, D. Don (David Don) neither claimed authorship of the name *Q. armata* nor intended to publish it formally (Fig. S10A). Therefore, the entry in POWO (2025) lists *Q. armata* D. Don (1825) in Prodr. Fl. Nepal.: 56 (1825) appears to be

a misinterpretation. Meanwhile, Don mistakenly treated *Q. tribuloides* Sm. (1819) as a synonym of *Q. armata* Roxb. (1820), as *Q. tribuloides* was validly and effectively published earlier than *Q. armata*. Moreover, *Q. catungea* Buch.-Ham. ex D.Don, a name listed in the manuscript of Hamilton ("Hamilton MSS.") also under *Q. armata* as a presumed synonym (Fig. S10A). Following Art. 36.1 and 38.1(a) of the Madrid Code (Turland *et al*., 2025), the name *Q. catungea* is a nomen nudum (*nom. nud.*) and thus not validly published.

Later treatments by (Roxburgh and Carey 1832): 640 and (Wight 1846): 770 included illustrations (Fig. S5) and descriptions of *Q. armata* consistent with the original description from 1820, e.g., a large, globose cupule with clustered short spines scattered on the cupule wall. Whereas Prodr. Fl. Nepal. misapplied both the morphological concept and the nomenclature of *Q. armata*. Notably, neither Roxburgh and Carey (Roxburgh and Carey 1832) nor Wight (Wight 1846) included *Q. tribuloides* in their work, and both continue this confusion by treating *Q. tribuloides* as a synonym of *Q. armata* D. Don, thereby perpetuating the misclassification established in Prodr. Fl. Nepal.. Subsequently, *Q. tribuloides* was formally transferred to *Castanopsis*, resulting in the new combination *C. tribuloides* (Sm.) A.DC. by (Hance, 1863). It was not until (Hooker, 1888) that a clear distinction was made between *C. tribuloides* and *C. armata* (Fig. S10B), finally resolving a taxonomic confusion that had persisted for nearly 60 years!

Remarkably, Krishna Kumar Shrestha annotated the four specimens collected by Wallich from Nepal as "lectotype" or "syntypes" of *Quercus armata* D.Don (1825) in 1989. It is evident that he followed the erroneous taxonomic treatment and definition in Prodr. Fl. Nepal. Moreover, his lectotypification was never validly published (Figs. 2B, S7–S9).

The name "*Quercus ferox*" first appeared in William Roxburgh's *Hortus Benglensis* (1814: 104) as part of a list entry: "*Quercus ferox*, R., Hurineea batana, Cittagong", without any accompanying description. The name *Quercus ferox* Roxb. was validly published later in *Flora Indica*, accompanied by an illustration (Fig. S11), ed. 1832 (Roxburgh, 1832), and was subsequently transferred to *Castanopsis* by Spach (1842). Later, George King proposed the combination *C. tribuloides* var. *ferox* in an unpublished manuscript, which was eventually validly published by Hooker (1888) as *C. tribuloides* var. *ferox* (Roxb.) King ex Hook.f.. However, no specimen was cited or mentioned in the protologue of *Q. ferox*, which only included the locality note: "Chittagong Mountains" in southeastern Bangladesh. Subsequent regional floristic works and taxonomic studies of Fagaceae did not designate a type for the name either. Most of the voucher specimens that Roxburgh used to describe species were housed in the East India Company Herbarium (EICH), also known as the "Wallich Herbarium". According to the Wallich catalogue, *Castanea tribuloides*, with *Q. ferox* included as a synonym, was listed under entry no. 2765. Based on the cataloguing style of the Wallich Catalogue, entry no. 2765 should refer to *Q. ferox* (Wallich, 1828 – 1849). Three different collections are associated with Wallich no. 2765 and likely represent the same taxa: 2765A: collected by Wallich, N (NW) from Nepal in 1821, comprising four specimens (Fig. S12: E00301128; Fig. S13: K001117046; Fig. 3C: K001117047; Fig. S14: K000832665). Among them, specimen K001117047 bears a representative long infructescence and mature acorns (Fig. 3C). 2765C marked "H.B.C." indicating origin from the Calcutta Botanical Garden, consisting of two leaves and several female spikes. 2765B collected from Sylhet, Bangladesh by *F. De Silva* (K000639576; Fig. 3D), this specimen matches the morphological description, collection locality, and inflorescence features noted in the protologue (Roxburgh, 1832) and illustration (Wight, 1840). We hereby designate specimen K000639576 as the lectotype of *C. ferox*, although it lacks mature acorns. Since the protologue and illustration include a detailed description of male and female inflorescences, cupules, and nuts, we additionally designated K001117047 as an epitype to supplement the diagnostic features, especially those of the cupule and nut, and to stabilize the application of the name.

The taxonomic delimitation of *Castanopsis ferox*, *C. tribuloides*, and several closely related species (e.g., *C. wattii* (King ex Hook.f.) A.Camus, *C. longispina* (King ex Hook.f.) C.C.Huang & Y.T.Zhang) has long been problematic and confusing. These taxa have been treated inconsistently across various studies—sometimes as distinct species (Spach, 1842; Camus, 1929; Huang and Zhang, 1992) and at other times as infraspecific taxa of *C. tribuloides* (e.g., Hooker, 1888).

Morphologically, *C. ferox* shows striking similarity to *C. tribuloides*. Both species possess leathery leaves with entire margins, a grayish, compact indumentum of scalelike trichomes on the abaxial surface, and cupules that are globose to broadly ovoid, with spinelike bracts basally connate into bundles or arranged in discontinuous rings. Their nuts are subglobose, glabrous, and typically have pointed apices. Moreover, their geographic distributions largely overlap and are adjacent. Both species are widespread across the Southern Himalayan lowland montane areas and Indo-China (Huang *et al*., 1999; POWO, 2025).

Recent biogeographic and population genetic studies of East Asian Fagaceae suggest that several pronounced phylogeographic structures exist in the region. Notable geographic barriers, e.g., the Red River Fault (Zheng *et al*., 2016), the Nujiang–Irrawaddy River barrier (Sun *et al*., 2022), and the Tanaka Line (Zhao and Gong, 2015) have played critical roles in driving species differentiation in the subtropical regions of East Asia.

These barriers may have facilitated speciation despite limited morphological differentiation, leading to the emergence of cryptic species and species complexes in multiple areas (Hending, 2025). On the other hand, frequent interspecific gene flow, which is relatively common among Fagaceae, further complicates species delimitation. Although molecular phylogenetic studies of *Castanopsis* have made some progress, the genus remains understudied, particularly in Southeast Asia, where new species continue to be described in recent years. Both *C. ferox* and *C. tribuloides* are nearly ubiquitous across the tropical regions of the Indo-Chinese Peninsula. An integrated study that applied population concept to combine molecular phylogenetics and morphological analyses is crucial to clarify these taxonomic confusions over these names in the future.

TAXONOMIC TREATMENTS

1. *Lithocarpus litseifolius* (Hance) Chun in J. Arnold Arbor. 9: 152. 1928. —*Quercus litseifolia* Hance in J. Bot. 22: 228. 1884. —*Pasania litseifolia* (Hance) Schottky in Bot. Jahrb. Syst. 47: 668. 1912. —*Synaedrys litseifolia* (Hance) Koidz. in Bot. Mag. (Tokyo) 30: 196. 1916. —***Type*:** Hainan, Hung-mo, territori Lai, 22. 11. 1882, *B. C. Henry 22209* (Holotype: BM [BM015176768!]).

Quercus cepifera H. Lév. in Repert. Spec. Nov. Regni Veg. 12: 364 (1913), ***syn. nov.*** —***Type***: China, Guizhou, "Grand arbre au sud de Pin-Fa", 8 June 1905, *P.J. Cavalerie 2341* (Lectotype: E [E00275485!], designated here, infructescence and acorns only, branchlet excluded; Isolectotype: A [A00034142!]). (**Note**: The branchlet and leaves on sheets E00275485, E00275486, and A00034142 belong to *Castanopsis eyrei* (Champ. ex Benth.) Tutcher)

Distribution. Assam, China South-Central, China Southeast, Hainan, Laos, Myanmar, and Vietnam.

2. *Quercus kerrii* Craib in Bull. Misc. Inform. Kew 1911: 471 (1911). —*Cyclobalanopsis kerrii* (Craib) Hu in Bull. Fan Mem. Inst. Biol., Bot. 10: 106 (1940). —***Type*:** Thailand, Chiengmai, Doi Sootep, 300–600 m, *A.F.G. Kerr 550* (Lectotype: K [K000227636!]; Isolectotype: K [K000227634!; K000227635!; K000227637!], P [P00754003!], BM [BM001217650!], designated by Y. L. Menitsky (1976)); Doi Sootep, 1000 m, *C. C. Hosseus 438* (Isosyntype: M [M0168772!], BM [BM001217649!]).

Quercus dussaudii Hickel & A.*Camus* in Ann. Sci. Nat., Bot., sér. 10, 3: 384 (1921), ***syn. nov.*** —*Quercus rex* auct. non Heml. in Thai Forest Bull., Bot. 34: 151 (2006). —***Type***: Laos, Ban Pac Sanane, route de Vientiane à Luang-Prabang, *M. Dussaud 62* (Lectotype: P [P00753919!], designated here, acorns only, foliage branchlet excluded). (Note: the foliage branch on P00753919 belongs to *Castanopsis argyrophylla* King ex Hook.f.)

Distribution. Bangladesh, China South-Central, Hainan, Laos, Myanmar, Thailand, and Vietnam.

3. *Castanopsis lanceifolia* (Oerst.) Hickel & A.Camus in Bull. Soc. Bot. France 68: 394 (1922). —*Pasania lanceifolia* Oerst. in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1866: 84 (1866). —*Castanea lanceifolia* (Oerst.) Kurz in Prelim. Rep. Forest Pegu, App. A: cxxvii (1875). —***Type***: India, *W. Roxburgh s.n.* (Lectotype: P [P06856344!], designated here); Meghalaya, Khasias, 3000 ft, *J. D. Hooker & T. Thomson s.n.* (Epitype: O [O2163134!], designated here).

Distribution. Assam, Bangladesh, China, East Himalaya, Meghalaya, Myanmar, Nepal, Thailand, and Vietnam.

Notes. The distribution of *C. lanceifolia* extends from Nepal through Bangladesh and the Himalaya to Indochina. Hence, its occurrence in China is not unexpected.

Specimens examined. **BANGLADESH.** Sylhet, *J. D. Hooker 65* (P06856364!); East Bengal, *Griffith s.n.* (P06856346!). **CHINA.** Yunnan, Yingjiang, *P. Y. Wang et al. WPY37* (HITBC!). ***INDIA.*** Meghalaya, Cherrapunjee, *T. R. Chand 6170* (MICH1337333!); Pynursla, *T. R. Chand 2001* (MICH1337335!); Khasia Hills, *N. Young 4* (US150057!); Assam, *W. S. Kurz 20495* (BM000907540!). **MYANMAR.** *Anonymous s.n.* (E00908516!). **THAILAND.** Trang, *E. C. Abbe et al. 9695* (US3725779!).

4. *Castanopsis armata* (Roxb.) Spach in Hist. Nat. Veg. 11: 185 (1842). —*Castanea armata* (Roxb.) F.N.Williams in Bull. Herb. Boissier, sér. 2, 4: 1029 (1904). —*Castanopsis tribuloides* var. *armata* (Roxb.) Kurz in Forest Fl. Burma 2: 481 (1877). —*Quercus armata* Roxb. in Pl. Coromandel 3: 92 (1820). —***Type***: India, Goalpara, *F. Hamilton 3736* (*Wallich no. 3736*) (Lectotype: K [K001119915!], designated here).

Distribution. Assam, Bangladesh, East Himalaya, Myanmar, Thailand, and Vietnam.

5. *Castanopsis tribuloides* (Sm.) A.DC. in J. Bot. 1: 182 (1863). —*Quercus tribuloides* Sm. in A.Rees, Cycl. 29: n.° 13 (1819). —*Castanea tribuloides* (Sm.) Lindl. in N.Wallich, Pl. Asiat. Rar. 2: 6 (1830). —***Type***: Nepal, 19 November 1802, *Buchanan* (Dr. F. Buchanan [Francis Buchanan-Hamilton]) *s.n.* (Lectotype: BM [BM000521899!], designated here).

Quercus catungea Buch.-Ham. ex D.Don in Prodr. Fl. Nepal.: 56 (1825). *nom. nud.*

Quercus armata auto non Roxb. in Prodr. Fl. Nepal.: 56 (1825).

Distribution. Assam, Bangladesh, China South-Central, East Himalaya, Laos, Myanmar, Nepal, Thailand, Tibet, Vietnam, and West Himalaya.

6. *Castanopsis ferox* (Roxb.) Spach in Hist. Nat. Vég. 11: 185 (1842). —*Quercus ferox* Roxb. in Fl. Ind., ed. 3: 639 (1832). —*Castanopsis tribuloides* var. *ferox* (Roxb.) King ex Hook.f. in Fl. Brit. India 5: 623 (1888). —***Type*:** Bangladesh, *F. De Silva 2765B* (Wallich no. 2765B) (Lectotype: K [K000639576!], designated here); Nepal, 1821, *N. Wallich 2765A* (Epitype: K [K001117047!], designated here).

Distribution. Assam, Bangladesh, China South-Central, East Himalaya, Laos, Myanmar, Thailand, Tibet, and Vietnam

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