

**THE AMERICAN COLUBRINA CELTIDIFOLIA (RHAMNACEAE)
IS A MEMBER OF THE ASIAN GENUS HOVENIA**

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ABSTRACT

Colubrina celtidifolia, native to southern Mexico and Guatemala, has been acknowledged by previous Rhamnaceae students to be remarkably similar to the Asian tree *Hovenia dulcis*. The similarities are confirmed here, including the fleshy-swollen peduncles of the inflorescence, and the American species is recognized as ***Hovenia celtidifolia*** (Cham. & Schlecht.) Nesom, **comb. nov.** A taxonomic summary of *Hovenia* is provided, following the most recent Flora of China in recognizing 3 species, but treating *H. kiukiangensis* as a separate species (in the FOC as *H. acerba* var. *kiukiangensis*; here as *H. pubescens*). Formal typifications and photos of associated type specimens are provided. The Asian species accepted here are *Hovenia dulcis* Thunb. (without formal varieties), *H. acerba* Lindl. (without varieties), *H. pubescens* Sweet, and *H. tomentella* (Makino) Nakai ex Kimura (published one month earlier than the synonymous name *H. trichocarpa*; without formal varieties).

Colubrina celtidifolia is a tree species of southern Mexico and Guatemala (Map 1), scattered and rare south to Honduras and Nicaragua. Johnston (1971) noted that specimens of *C. celtidifolia* "closely resemble those of the *Hovenia dulcis* Thunb. of Japan, China, and Korea. Flowering and early fruiting specimens of these two species are nearly indistinguishable except by examination of the style base, which is glabrous in the Mexican plant but pubescent in the Asiatic one. ... The similarities of these two species are so numerous and striking that one can confidently assert a close relationship." Johnston alluded to the possibility that *Colubrina* and *Hovenia* could be merged, apparently with the assumption that *C. celtidifolia* represents *Colubrina*.

Colubrina celtidifolia, however, is singular among *Colubrina* species in its fleshy-swollen peduncles, a diagnostic feature of *Hovenia*, and indeed there is no morphological feature that would exclude it from *Hovenia*. It is transferred here to *Hovenia*. In the key below to *Hovenia* species, *C. celtidifolia* is more similar to *H. dulcis* and *H. acerba* in its glabrous fruits and shorter style branches; it differs from both in its larger fruits and from all the Asian species in the villous hypanthial cup.

Geography

The disjunction between plants of Mexico-Central America and southeast Asia is seen in other vascular plants, as noted by Wendt (1988).

- * *Chiangiodendron* (trees, Flacourtiaceae) – Most closely related to genera in southeast Asia (Wendt 1988).
- * *Ormosia* (trees, large shrubs, Fabaceae) – The genus is divided between eastern Asia/northeastern Australia and America; about 10 species are in Mesoamerica (Zamora 2006).
- * *Lasianthus* (shrubs, small trees, Rubiaceae) – *Dressleriopsis panamensis* is a member of the Asian genus *Lasianthus* (Robbrecht 1982).
- * *Pollia* (herbs, Commelinaceae) – *Pollia americana* of Panama is the only American member of the otherwise southeast Asian and African genus (Faden 1978).
- * *Mitchella* (herbs, Rubiaceae) – One of the two *Mitchella* species occurs in eastern Asia, the other in eastern North America, with a disjunct extension to Central America (Huang et al. 2013).
- * *Leibnitzia* (herbs, Asteraceae) – Two species are Mexican, the others Asian (Nesom 1983; Baird et al. 2010).
- * *Sageretia* (shrubs, Rhamnaceae) – Five species are American, the others Asian (Yang et al. 2019; Nesom 2023).

Fossil wood similar to *Hovenia palaeodulcis* (Oligocene) from Japan has been found in late Eocene or earliest Oligocene Florissant Formation, Colorado (Wheeler & Meyer 2012). *Ziziphus* and *Colubrina* are known as fossil leaves from the same Florissant assemblage. *Hovenia oregonensis* has been described from leaves in the early Oligocene Bridge Creek Flora of Oregon (Meyer & Manchester 1997). Manchester et al. (2009) reviewed Tertiary occurrences of *Hovenia* — fossil leaves also occur in the Middle Miocene Shanwang flora of Shandong Province, China, and wood of *Hovenia* has been described from the Oligocene of northern Kyushu and Lower Miocene of southwestern Honshu, Japan.

Phylogeny

Richardson et al. (2000) noted that "*Hovenia* appears to have a close relationship with *Ziziphus* and *Paliurus* in that these genera all have palmately veined leaves, cymose inflorescences, a base number of $x = 12$, and a similar pollen exine structure." They placed *Hovenia* in tribe Paliureae with *Paliurus* and New World and Old World *Ziziphus* — *Hovenia* is sister to the rest of the tribe. Richardson et al. (2004) estimated that the evolutionary divergence of *Paliurus* and *Hovenia* occurred in early Oligocene. *Hovenia* and *Colubrina* are phylogenetically distinct, but the evolutionary affinities of *Colubrina* are not clearly resolved (Hauenschild et al. 2016) and it is represented so far in molecular analyses only by *C. asiatica*, *C. glandulosa*, *C. oppositifolia*, and *C. reclinata*.

Recent studies have analyzed chloroplast genomes of individual *Hovenia* species (e.g., Yin et al. 2020; Liu et al. 2021). An estimate of phylogeny has been made by Wanichthanarak et al. (2023), based on chloroplast genomes, but relationships among the three *Hovenia* species were unresolved. Asaf et al. (2022), presumably using chloroplast genome data from the National Center for Biotechnology Data (as alluded to by the authors), showed a resolved phylogeny with *H. dulcis* as sister to *H. acerba* and *H. trichocarpa*.

Taxonomy

Three species of *Hovenia* are currently recognized in the Flora of China (Chen & Schirarend 2007), all native to southeast Asia — the same entities plus one additional Aisan species are recognized here. A formal nomenclatural summary is provided here for context in joining the American *Colubrina celtidifolia* to the genus. I have examined images of Chinese collections available via the Chinese Virtual Herbaria (2004-2020), iPlant.cn Plant Intelligence (2009-2022), and other digital sources, as well as the collections at TEX-LL, MO, and PH. Comments on variation within *Hovenia* species and the significance of type specimens are given within the nomenclature. Each species is treated without varietal taxa, but a more definitive and convincing assessment needs first-hand study and mapping of a large number of collections, including naturalized plants.

Identifications of naturalized plants are consistently as *Hovenia dulcis* (e.g., Bergamin et al. 2022), but given the inconsistency in distinguishing it from *H. acerba*, the latter may be represented among non-native occurrences.

Pharmacological studies have been made of *Hovenia* species (e.g., Kim et al. 2023) but vouchers and comments on identification have not been included and there are no comparative data. A study of *Hovenia* chemistry (Xu et al. 2003) did not attempt to search for phylogenetic patterns. A review and summary of traditional uses and current knowledge of the pharmacology and phytochemistry of *H. dulcis* has been published (Hyun et al. 2010).

The chromosome number of *Hovenia* has been reported as $2n = 24$ (*H. dulcis* — Gadella et al. 1969 and Guidini et al. 2017, from Brazil; *H. pubescens* — Kumar & Subramaniam 1987, from "the Indian subcontinent," as *H. dulcis*; Oginuma et al. 1994, from Yunnan, as *H. acerba* var. *kiukiangensis*).

A detailed overview of *Hovenia* taxonomy was provided by Kimura (1939, his key reproduced below). In a study of Indian *Hovenia*, working from the Central National Herbarium of India (CAL), Sen Gupta and Safui (1984, key below) observed that "many of the diagnostic characters used by Kimura

are more quantitative rather than qualitative in nature and variations in the lead to blurring of differences between *H. dulcis* and *H. acerba*" — they specifically noted variability in leaf shape, apex, and margins, inflorescence morphology, sepal nervation, petal shape, and style morphology. They treated *H. acerba* at varietal rank within *H. dulcis*, but the two appear to have broad region of sympatry within China (see Map 2), indicating their probable genetic distinction. Characterizations in the Flora of China do not suggest they are ecologically distinct. From the present study, however, all of the plants from Himalayan India are *Hovenia pubescens*, thus Sen Gupta and Safui apparently sought to find discontinuities within a single species.

Key from Kimura (1939)

1. Fruits and sepals densely brownish-tomentose; petals ca. 3–3.3 mm long; styles divided to the base.
 2. Leaves most 8–15 cm long; petal apex rounded, base short unguiculate **H. TOMENTELLA**
 2. Leaves mostly 15–20 cm long; petal apex emarginate, base narrowly unguiculate **H. ROBUSTA**
1. Fruits and sepals usually glabrous, rarely tomentose; petals less than 2–2.5 mm long; style deeply divided or merely with a 3-fid apex.
 3. Flowers ca. 6 mm wide; calyx lobes 1.5–2 mm long **H. PARVIFLORA**
 3. Flowers ca. 9 mm wide; calyx lobes 2.2–2.6 mm long.
 4. Leaf margins shallowly obtusely serrulate to crenate-serrulate; inflorescence symmetrical, terminal and axillary; petals orbiculate-elliptic; style branched at least half its length; mature fruits yellow, 5–6.5 mm in diameter **H. ACERBA**
 4. Leaf margins irregularly or coarsely serrate; inflorescence asymmetrical, often terminal, rarely axillary; petals broadly oblong; style apex slightly 3-fid; mature fruits black, 6.5–7.5 mm in diameter **H. DULCIS**
- 4a. Plants in flower shrubs or tall bushes, up to 3–5 m high, trunk diameter up to 20 cm wide (habitat in Korea) var. **koreana**
- 4a. Plants in flower trees 15–20 m high, trunk diameter up to 60–80 cm wide.
 - 4b. Leaves ovate to broadly ovate, ca. 8–15 cm long, 5–8 cm wide var. **glabra**
 - 4b. Leaves elliptic-ovate to cordate, ca. 11–14 cm long, 8.5–11 cm wide var. **latifolia**

Key from Sen Gupta & Safui (1984)

1. Leaves 15–20 cm long; sepals and fruits densely brown tomentellous; petals 3–3.5 mm long; style arms free from base **H. ROBUSTA**
1. Leaves up to 15 cm long; sepals and fruits glabrous; sepals 2–2.5 cm long; style arms not free from base **H. DULCIS**
2. Inflorescence mostly terminal and asymmetrical, occasionally axillary; sepals without prominently anastomosing nerves; style arms divided up to 1/4 the style var. **dulcis**
2. Inflorescence terminal and axillary and the latter symmetrical; sepals usually with more or less anastomosing nerves; style arms divided from 1/4–2/3 of the style var. **acerba**

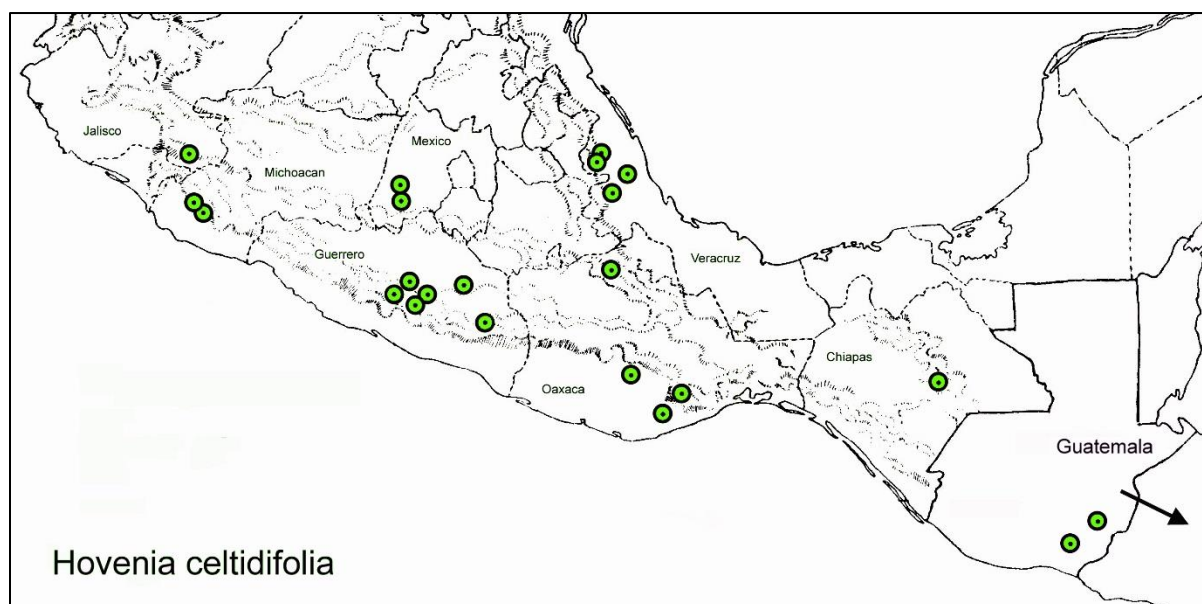
Key from Flora of China (Chen & Schirarend 2007)

1. Sepals and fruit densely ferruginous-tomentose **H. TRICHOCARPA**
 - 1a. Leaves densely yellow-brown or yellow-gray tomentose adaxially var. **trichocarpa**
 - 1a. Leaves glabrous on both surfaces or pilose on veins adaxially var. **robusta**
1. Sepals and fruit glabrous, rarely pilose.

2. Flowers in terminal, or rarely axillary, asymmetrical cymose panicles; style undivided to short-branched; fruit black at maturity, 6.5–7.5 mm in diam.; leaf margin irregularly or coarsely serrate **H. DULCIS**
2. Flowers in terminal or axillary, symmetrical, dichasial cymose panicles; style deeply branched to at least half of its length; fruit yellow at maturity, 5–6.5 mm in diam.; leaf margins shallowly obtusely serrulate **H. ACERBA**
- 2a. Fruit and style glabrous var. **acerba**
- 2a. Lower part of fruit and style pilose var. **kiukiangensis**

Key to species as recognized the the present account

1. Disc, hypanthium, and calyx lobes (within) conspicuously and persistently villous **H. CELTIDIFOLIA**
1. Disc, hypanthium, and calyx lobes glabrous, within and without. [this couplet modified 1 Nov 2023]
2. Inflorescence axis, sepals, and fruits tomentose; style arms free halfway or nearly from the base; leaf blades abaxially rusty-tomentose on major veins, epidermis variably tomentose to glabrate.
3. Leaves thickened, strongly bicolor; inflorescence terminal, usually from the distal 1-2 nodes, primary axis (peduncle) mostly 2–5 cm long **H. TOMENTELLA**
3. Leaves relatively thin, weakly bicolor or not at all; inflorescence terminal and axillary, usually from the distal 4-8 nodes, primary axis (peduncle) 1.5–3 cm long **H. PUBESCENS**
2. Inflorescence axis, sepals, and fruits glabrous; style either short-branched or deeply divided; leaf blades abaxially glabrous or pilose on veins or in vein axils.
4. Inflorescence mostly terminal and asymmetrical, occasionally axillary; style divided 1/5–1/4 of its length; rachis strongly thickened and fleshy; fruits dark purple or black at maturity, 6.5–7.5 mm in diam. **H. DULCIS**
4. Inflorescence terminal and axillary, the axillary symmetrical; style divided 1/4–2/3 of its length; rachis weakly thickened and fleshy fruits yellow at maturity, 5–6.5 mm in diam. **H. ACERBA**



Map 1. Distribution of *Hovenia celtidifolia* — Mexico and Guatemala (and Honduras and Nicaragua, as indicated by the arrow). Records are from collections cited below in the text.

HOVENIA Thunb., Nov. Gen. Pl., 7. 1781. **TYPE:** *Hovenia dulcis* Thunb.

1. HOVENIA CELTIDIFOLIA (Cham. & Schlecht.) Nesom, **comb. nov.** *Ceanothus celtidifolius* Cham. & Schlecht., Linnaea 5: 602. 1830. *Colubrina celtidifolia* (Cham. & Schlecht.) Schlecht., Linnaea 15: 471. 1842. **TYPE: MEXICO. Veracruz.** **Protologue:** "in sylvis Jalapensibus," Aug 1828, C.J.W. Schiede 722 (holotype: HAL; isotypes: BR image, F, W-photo at MO).

Trees (3–)4–15 m tall, rarely characterized as a shrub ("arbusto"), without short shoots or thorns; branches mostly glabrous, slightly zigzag, youngest stems slightly succulent. **Leaves** alternate, deciduous, petioles 7–12(–15) mm long, blades herbaceous (not thickened), ovate to lanceolate–ovate, 6–10(–14) cm long, 3.5–6(–8) cm wide, apex acuminate, base truncate to subcordate, dark and glossy adaxially, glabrous on both surfaces except main veins abaxially sparsely hairy with orangish hairs, venation brochidodromous but with 3 primary laterals originating from the very base, major abaxial veins raised but secondary reticulum dark and not raised, margins evenly serrulate-dentate from base to apex, each tooth glandular at the apex. **Inflorescence** axillary and terminal compound cymes at branch tips, repeatedly dichotomously branched, the central meristem usually suppressed, 4–25⁺-flowered; primary peduncles 7–12 mm long, ultimate peduncles swollen-fleshy, pedicels 2 mm long. **Flowers** bisexual; hypanthium glabrous inside and out, disk hemispheric, thick, glabrous, adnate to the ovary and hypanthium; sepals triangular, 2–2.5 mm long, glabrous, persistent into fruit maturity; petals white, 2–3 mm long, cucullate, enfolding the stamens; style branches 3, divided 1/8–1/3 the length of the style. **Fruit** globose, 9–12 mm wide, berrylike but only slightly fleshy, apparently reddish (from color seeping into hot water), glabrous, 3-locular, shallowly 3-lobed at maturity, breaking open irregularly. **Seeds** dark brown, shiny, 5–7 mm long.

Pine, oak, and pine-oak woods, selva mediana subperennifolia, mesophilic and subtropical deciduous woods, gallery forests, woods edges and within woods, arroyos, barrancas, river sides; 1200–2550 m. Southern Mexico, Guatemala, Honduras, Nicaragua. Map 1.

Collections examined.

HONDURAS. Present, fide Nelson Sutherland (2008).

NICARAGUA. **Jinotega.** Reserva Natural Mirafior, Comarca los Volcancitos, 13° 15' N, 86° 19' W, arbol 12 m, 1250 m, 25 Aug 1999, *Rueda 11686* (MO). **Nueva Segovia.** 0.7 km W of Hacienda Las Brisas, S slope of Cerro Mogotón, tree, disturbed cloud forest/pine forest interface, 1456 m, 31 Aug 2015, *Stevens & Montiel 36938* (MO).

GUATEMALA. [**Mpio. Cuilapa** (Dept. Santa Rosa)]: [Volcán] Jumaytepeque, 1200 m, Jan 1893, *E.T. Heyde* and *E. Lux 4331* (MO, US-sheets). **Mpio. Quezaltepeque:** Volcán Quezaltepeque, 14° 37' 21" N 89° 23' 26" W, 1500–2000 m, 8 Nov 1939, *Steyrmark 31420* (F, as cited by Pool 2015).

MEXICO. **Chiapas.** **Mpio. Las Rosas:** 3 km S of Aguacatenango along road to Las Rosas, tree 50 feet tall, moist grassy slope with *Pinus* and *Quercus* along deep ravine with seasonal evergreen forest, 1768 m, 4 Oct 1981, *Breedlove 53247* (MO, TEX).

Oaxaca. **Mpio. San Miguel del Puerto** (Dist. Pochutla): 16° 00' 32.2" N, 96° 06' 56.6" W, arbol 15 m, selva mediana subperennifolia, 1530 m, 27 Apr 2005, *Martínez 754* (MEXU); Oreja de León, 15° 58' 38.2" N, 96° 07' 18.4" W, arbol 12 m, selva mediana subperennifolia, 1382 m, 3 May 2005, *Pascual 1472* (MEXU). **Mpio. Teotitlán:** Puerto de la Soledad, 30 km NE de Teotitlán, 18° 10' N, 97° 00' W, arbol 8 m, bosque mesofilo, 2360 m, 18 May 1986, *Tenorio L. 11287* (MEXU). **Mpio. Zimatlán:** Transecto entre Aserradero-Pueblo Viejo, NE de La Cofradia, comunidad de San Pedro El Alto, arbol 4 m, terreno de cultivo en transición con bosque de *Quercus*, 2200 m, 12 Oct 1998, *Miranda & Hernández 354* (MEXU).

Veracruz. **Mpio. Coacoatzintla:** Arriba de Coacoatzintla, arbustito 6 m, veg. de encino, 1600 m, 11 Aug 1962, *Gómez Pompa 743* (MEXU-2 sheets). **Mpio. Huatusco:** 2 km W de Rio Seco, carr. Huatusco-Coscomatepec, 19° 08' 53" N, 96° 58' 02" W, *Avendaño R. y Vásquez B. 797* (MEXU, and ENCB, IEB, XAL as cited by Fernández N. 2010); Dos Puentes, Aug 1841, *Liebmann 1866* (US); camino a Las Trincheras, entrando por El Encino, 19.10889 N, -97.00028 W, arbol 3 m alto, bosque caducifolio, 1900 m, 17 Jun 1983, *Marquez R. JM-151* (UCR); fuera del Jardín Botánico del C.R.U.O., arbol 10-15 m alto, bosque

caducifolio, 1270 m, 28 Jun 1984, *Robledo M. 176* (MEXU). **Mpio. Teocelo:** Abajo de Coyopola, rumbo a Texin, arbol 10 m, bosque caducifolio, 1650 m, 3 Jul 1988, *Cházaro B. et al. 5534* (MEXU). **Mpio. Xalapa:** Salto del Gato, 4 km E de Xalapa, arbusto 4 m, bosque caducifolio, primaria, 1400 m, 29 Apr 1972, *Dorantes 577* (ENCB, LL, MEXU, MO-2 sheets, XAL, as cited by Fernández N 1986); Mirador [El Potrerillo], Aug 1841, *Liebmann 1829* (US); near Jalapa, 15 Aug 1901, *Rose 6141* (US); Colonia Zapata, matorral en cañada, 1300 m, arbusto 6 m alto, 19 Apr 1974, *Ventura A. 9904* (ENCB, MO, SD); Santa Rosa, arbol 15 m alto, orilla de arroyo, 1200 m, 3 Jun 1974, *Ventura A. 10073* (CHAPA, ENCB, MEXU, MO).

Edo. Mexico. [**Mpio. San Simon de Guerrero**]: Mina de Agua, 30 Mar 1932, *Hinton 658* (US); Mina de Agua, tree 15 m high, 1800 m, 24 Aug 1933, *Hinton 4458* (US); Mina de Agua, spreading tree 10 m high, 12 May 1935, *Hinton 7684* (CHR, LL-2 sheets, MO); Mina de Agua, 5 Aug 1935, *Hinton 7978* - same tree as 7684 (LL, MEXU, TEX, US). [**Mpio. Temascaltepec**]: Temascaltepec, tree 15 m high, by the river, 1800 m, 5 May 1935, *Hinton 7681* (US).

Michoacan. **Mpio. Coalcomán:** Puerto Zarzamora, slender tree 6 m high, oak forest, 1600 m, 26 Sep 1938, *Hinton 12251* (LL, US); Puerto Zarzamora, slender tree 5 m high, rare, oak forest, 1560 m, 4 Dec 1938, *Hinton 12703* - same tree as 12251 (US); Puerto Zarzamora, slender tree, forest, 1560 m, 1 Jul 1939, *Hinton 13866* - same tree as 12251 (LL, US, USF); S. Naranjillo, tree 6 m, forest, 1560 m, 14 Jul 1939, *Hinton 13929* (CHR, LL-2 sheets, US); Puerto Zarzamora 1 Jul 1939, *Hinton 15866* (LL)

Guerrero. **Mpio. Ahuacuotzingo:** 2 km de la desviación a Ajuatetla, arbusto 1.2 m, 17° 44' 47" N, 99° 02' 41" W, arroyo seco, bosque tropical caducifolio, 5 Sep 2002, *Diego & Santiago 9485* (MEXU). **Mpio. General Heliodoro Castillo:** Camino Yextla el Jiguero, 17.554944 N, -99.882166 W, arbol 10 m alto, bosque mesófilo de montaña, 2447 m, 5 Dec 2006, *Lozada 3317* (HUAP not seen); camino Carrizal de Bravo desviación a Yextla, 17.575302 N, -99.856136 W, arbol 6 m alto, bosque mesófilo de montaña, 2560 m, 30 Jun 2008, *Lozada 3449* (HUAP not seen). **Mpio. Leonardo Bravo:** 10.5 km SW of Tres Caminos, 17.541666 N, -99.911111 W, arbol 15 m alto, bosque de *Pinus*, 1850 m, 1 May 1998, *Mora J. 11* (HUAP not seen). **Mpio. Malinaltepec:** Cañada de Carrasco, Xochiatenco, arbol 15 m alto, bosque de galería, 25 Jun 2006, *Lozada 3115* (HUAP-2 sheets, not seen). **Mpio. Montes de Oca:** San Antonio-Buenos Aires, tree 10 m high, barranca, 28 Apr 1938, *Hinton 14058* (LL, US).

Jalisco. **Mpio. Tecalitlán:** KM 17 de la terracería a Jilotlán de Dolores, arbol 4 m, en una cañada, bosque de pino-encino, 2000 m, 16 Sep 1988, *González Casillas 136* (MEXU).

2. HOVENIA DULCIS Thunb. Nov. Gen. Pl. 1: 8. 1781. **TYPE: JAPAN.** "Crescit prope Nangasaki," [Aug 1775–Nov 1776], *C.P. Thunberg s.n.* (probable holotype: UPS-THUNB V-005733, Fig. 11; possible/probable isotype: LD 1731646 image). Sen Gupta & Safui (1984) cited the UPS specimen as the "Type." Kellerman (2019) regarded the UPS specimen as lectotype, selected by Sen Gupta & Safui, "since only one specimen of *H. dulcis* is present in Thunberg's herbarium." The existence of possible duplicates is discussed by Kellerman.

Hovenia dulcis var. *glabra* Makino, Bot. Mag. (Tokyo) 28: 155. 1914. **SYNTYPES: JAPAN. Musashi Prov. J. Matsumura s.n., T. Makino s.n., S. Matsuda s.n.; Iwashiro Prov. Ch. Onoda s.n.** None seen.

The protologue characterizes var. *glabra* as "Fruit (with the calyx tube), pedicel, fleshy and ordinary portions of the peduncles glabrous." Makino's name is listed here as legitimate, (regarding the cited specimens as syntypes) but, as noted by Sen Gupta and Safui (1984), it may have been intended as a homotypic name for the typical expression of the species (i.e., var. *dulcis*). Kimura's key (1939; reproduced above) appears to use var. *glabra* in the latter sense.

Hovenia dulcis var. *latifolia* Nakai ex Kimura, Bot. Mag. (Tokyo) 53: 476. 1939. **TYPE: JAPAN.** North Honshu. **Ugo Prov.** Yuzawamati, 22 Aug 1928, *Y. Satake s.n.* (holotype: TI, as cited, not seen).

The protologue notes that var. *latifolia* is similar to var. *glabra*, distinguished by the shape and size of the leaves (broadly elliptic-ovate to cordate, base truncate to subcordate, 11–14 cm long, 8.5–11 cm wide).

Hovenia dulcis var. *koreana* Nakai ex Kimura, Bot. Mag. (Tokyo) 53: 476. 1939. **TYPE: SOUTH KOREA. Tyuhoku Prov.** Zokurisan, circa Myohô, 14 Aug 1934, *T. Nakai s.n.* (holotype: TI, as cited, not seen).

The protologue's diagnosis: a shrub or tall bush ("arbuscula vel frutex elatus") up to 3-5 m high, trunk diameter up to 20 cm wide — otherwise like var. *glabra*. Kimura noted that "According to Prof. Nakai, the Korean *Hovenia* never grows large and blooms and fruits early in the small tree while the Japanese *Hovenia* grows large and tall before it begins to flower." Kim et al. (2005), however, characterized var. *koreana* as a narrow endemic with trees reaching 20 meters high.

FOC (Chen & Schirarend 2007): "Secondary forests, also cultivated in gardens; 200-1400 m. Anhui, Gansu, Hebei, Henan, NW Hubei, Jiangsu, Jiangxi, Shaanxi, Shandong, Shanxi, N Sichuan [Japan, Korea, Thailand]." *Hovenia* is not included in the checklist of the Taiwan flora (Huang 2003) but *H. dulcis* is listed in Taiwan Plant Names (www.eFloras.org) and its occurrence there is vouchered by Wang 4554 (PE). Plants from Thailand are identified here as *H. pubescens*. Map 2. Figures 11-27.

Hovenia dulcis Thunb. is native to China, Korea, and Japan (e.g., Chen & Schirarend 2007; Bergamin et al. 2022) — records as *H. dulcis* from Vietnam (voucher not seen) and Thailand (see comments below) almost certainly are *H. pubescens* — and has become sporadically naturalized in the USA (Goldman 1998; Nesom 2016; vouchers cited below) as well as in Australia, New Zealand, South America (Zenni & Ziller 2011), and Africa (Witt & Luke 2017). Kellerman (2019) noted that it is "introduced in Australia and occasionally adventive on rainforest margins in New South Wales and possibly Queensland." Plants of *Hovenia* in Tamil Nadu, southern India (Henry et al. 1983), presumably are naturalized *H. dulcis*. The species has not been reported as naturalized in Mexico or Central America (Pool 2015; Villaseñor 2016; searches in iNaturalista).

Trees of *Hovenia* have been documented in native habitats at two localities in northeastern Thailand (both within national parks) — Kopachon et al. (1996) have provided detailed observations on fruits, seeds, and seedlings pertinent toward accelerating natural forest regeneration on deforested sites. They identified the plants as *H. dulcis*, but judging from geography and their published photo of a fruiting branch (shown here as Fig. 59), the species instead is *H. pubescens*.

Vouchers for naturalized plants in the USA. North Carolina. Wake Co.: Stony Branch, S of NC State College campus, escaped in woods, 15 Oct 1949, *Fox s.n.* (GA, GH, MO, NCSC, NCU). **Texas. Travis Co.:** Austin, along the edge of Town Lake, directly across the lake from the boat ramp at the University of Texas Brackenridge Field Lab, with *Cornus drummondii*, *Platanus occidentalis*, and *Smilax bona-nox*, 30 Sep 1997, *Goldman 1105* (GAS, NY, TAES, TENN, TEX) and 29 May 1998, *Goldman 1200* (GH, LSU, TEX-2 sheets); Austin, cliffs on S side of Lady Bird Lake (formerly Town Lake), between Red Bud Trail and Loop 1 (Mopac), tree—the population here appears to be expanding, 22 Jun 2012, *Atha 11907* (NY, Fig. 24).

Hovenia dulcis (raisin tree) is used as an ornamental tree, for timber, fuel, shading, and windbreaks, and for its edible pedicels (which become swollen, succulent, and sweet when mature). Trees may reach at least 20 meters tall. A 45-year-old tree in the Morris Arboretum of Philadelphia grew to be 23 meters in 45 years, despite once being frozen back to within a few feet of the ground (Koller & Alexander 1979).

The species has been "introduced to parts of South America and Africa as an ornamental tree, as well as a source of fuel and a fast growing windbreak and shade tree for livestock, [and] it has become a problem in the seasonal deciduous forest of the Uruguay river basin (affecting Brazil, Paraguay, Argentina, and Uruguay). ... *Hovenia* has displaced sensitive native species in these

environments but is difficult to eradicate, resprouting vigorously from stumps and exhibiting a high success rate in germination" (Penny 2023). In southern Brazil, 18 bird species and 12 mammal species were observed to be involved in dispersal of *H. dulcis* (Müller de Lima et al. 2015).



Map 2. Distribution in China of *Hovenia dulcis* and *H. acerba*, based primarily on geography described in the Flora of China (Chen & Schirarend 2007). Symbols in blue are added from collections seen digitally (vouchers below), the identifications based mostly on inflorescence structure.

Hovenia dulcis — Guizhou: *Int. Team 128* (GZAC), *Int. Team 342* (GZAC), *Gongfan 100* (PE), *Ye 2-249* (PE). Hebei: Herb. 3565 (TIE), *Jinping 200602035* (HENU). Hunan: *Qigui 319* (HUFD), *Chen 735* (HUFD). Sichuan: *Dahai 662* (WCSBG). Zhejiang: *coll. 1878123* (PE), *Xianyu 20070* (WUK, Fig. 20). Taiwan: *Wang 4554* (PE). ***Hovenia acerba*** — Chongqing: many collections (PE). Hainan: *IBK 389961* (IBK). Shandong: *Dept. Biol. 96103175* (PE). Shanxi: *Weichan s.n.* (SXU). Zhejiang: *Qiugui 217* (PE), *Liu 218* (HITBC).

3. HOVENIA ACERBA Lindl., Bot. Reg. 6: t. 501. 1820. *Hovenia dulcis* var. *acerba* (Lindl.) Sen Gupta & Safui, Bull. Bot. Surv. India 26: 55. 1984 [1985]. **TYPE**: Lindley's plate 501. Figure 28.

From Sen Gupta & Safui (1984): "Type: (?) China (from a plant grown in Lambert's greenhouse in Boyton, England; raised from seeds obtained through Wallich, from Calcutta from a tree introduced in the Sibpur Garden by Buchanan-Hamilton in 1802-03 from Nepal derived originally from China), *Lindley s.n.*" (CGE, fide Sen Gupta & Safui, not seen). The protologue noted "pedunculis incrassatis." The illustration shows an inflorescence structure (all from uppermost nodes) more characteristic of *H. dulcis* than *H. acerba* as identified here, and the floral detail shows the style divided only at the apex, also a feature of *H. dulcis*. The name may prove to be misapplied, perhaps pending a search for preserved material of the illustrated plant.

Ziziphus esquirolii H. Lév., Repert. Spec. Nov. Regni Veg. 10: 148. 1912 [1911]. **TYPE**: CHINA. **Kouy-Tchéou [Guizhou] Prov.** No other collection information, *J. Esquirol 861* (holotype: E, Figs. 29, 30).

Hovenia parviflora Nakai & Kimura, Bot. Mag. (Tokyo) 53: 478. 1939. **TYPE**: CHINA: **Guangdong Prov.** Loh Kong Tung, Chuk Ko, tree 15 m, village commons, 22 May 1925, *F.A. McClure s.n.* (holotype: TI as cited, not seen; isotype: PE, Fig. 31).

Hovenia dulcis var. *montana* Rosanov, Bull. Appl. Bot. Moscov, 136. 1930. Not seen.

Hovenia dulcis forma *platyphylla* Rosanov, Bull. Appl. Bot. Moscov, 136. 1930. Not seen.

FOC (Chen & Schirarend 2007): "Sparse forests, forest margins, slopes, open places, also often cultivated in gardens or by houses; below 2100 m. Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Yunnan [Bhutan, India, Myanmar, Nepal]." Plants from Himalayan regions are identified here as *H. pubescens*. Map 2. Also native to northeastern Thailand but identified there as *Hovenia dulcis* (see comments above, p. 7). *Hovenia dulcis* is said to be native to Viet Nam (e.g., Witt & Luke 2017) but I have not seen a voucher — if native, the plants there probably are *H. pubescens*.

4. HOVENIA PUBESCENS Sweet, Hort. Brit. [Sweet] 91. 1826. **TYPE**: Protologue: "2 [Hovenia] pubescens. pubescent-1^d. Nepaul 1823. ... G. h. *dulcis*. D.P. [Don's Prodromus Florae Nepalensis] et F.I [Flora Indica] nec aliorum." Type specimen not seen.

David Don was in London during preparation of his Prodromus Florae Nepalensis (1825) — presumably the type may be there. Don's entry for *Hovenia* (as *H. dulcis*): "*Hab.* in Nepaliâ superiore, ubi in hortis colitur. *Hamilton. h* Floret Aprili. Moro Cowshi *Nawaricè*." I have not seen a collection by Sir Francis Hamilton, who collected around Kathmandu in 1802-1803 (Bhat 1964) but Nathaniel Wallich made collections in the same area in 1818 and 1821, as cited below. Only a single species occurs in Nepal.

Hovenia kiukiangensis Hu & Cheng, Bull. Fan Mem. Inst. Biol. Bot. ser. 2, 1: 195. 1948. *Hovenia acerba* var. *kiukiangensis* (Hu & Cheng) C.Y. Wu ex Chen & Chou, Bull. Bot. Lab. N.-E. Forest. Inst., Harbin. 5: 87. 1979. **TYPE**: CHINA. **Yunnan Prov.** Kiukiang Valley, Muhcouga, tree 30 ft high, among woods, 1150 m, 27 Sep 1938, *T.T. Yu 20476* (holotype: PE 23552, Fig. 50; isotypes: A-Figs. 48, 49, E image, KUN-Fig. 51, PE 23551 image). According to Lin and Yang (2022), this locality is Nu Jiang Valley in Nujiang Lisu Autonomous Prefecture, which is in northwest Yunnan where Yu collected other species at the same time.

Trees 30–80 feet tall, young stems and inflorescence axes densely puberulent. **Leaf blades** ovate to broadly ovate, 9–15 cm long, glabrous on both surfaces or puberulent on abaxial veins, marginal teeth gland-tipped. **Inflorescence** of compact axillary thyrses from the distal 4–8 nodes, primary axes (peduncles) 1.5–3 cm long. **Flowers** 3–9 (–14) in each thyrse; disc, hypanthium (inside cup), and calyx lobes (adaxial) persistently villous; style branches divided 1/3–1/2 the length.

Flowering mostly May–June. Forests and forest edges; (300–) 700–1800 (–2200) meters. China (Yunnan, Tibet), Bhutan, India (Himalayan states), Myanmar, Nepal, Thailand.

The young fruits of *Hovenia pubescens* are pubescent (glabrescent) and the peduncles, pedicels, and abaxial leaf surfaces are pubescent (in variable density, on the veins and epidermis) as in *H. tomentella*, and the style branches are deeply divided. The inflorescence structure, however, and the thinner leaves, are more like those of *H. acerba* and the Himalayan range is disjunct from *H. tomentella*. The relatively few-flowered thyrses on short peduncles at many nodes are characteristic. The Flora of China notes the distribution of *H. acerba* var. *kiukiangensis* as in "SE Xizang, NW and S Yunnan" and this species is abundantly represented in Chinese herbaria by collections from Yunnan and Tibet. Maps 3 and 4.

Long & Rae (1991) identified *Hovenia* in Bhutan as *H. acerba*, noting this (p. 145): "formerly confused with the Chinese and Japanese *H. dulcis* Thunberg, which is widely cultivated for its edible peduncles. No specimens of the latter have been located from the E Himalaya, nor has evidence been seen that *H. acerba* is eaten or cultivated." The Bhutan plants are identified here as *H. pubescens*.

Additional collections. **BHUTAN.** Kancham, Punakha, *Cooper s.n.* (E); Chumbi valley rd survey, Chummchi valley, *Searight 198* (CAL); "Samchi district (Chamarchi valley) and Deothang district (Deothang), Upper Mo Chu district (Kencho) – fide Long & Rae 1991. **CHINA** (representative). **Tibet.** Many collections, see Chinese Virtual Herbaria. **Yunnan.** Szemao, *Henry 12034A* (E, MO, US); many collections, see Chinese Virtual Herbaria. **INDIA. Arunachal Pradesh.** Abor expedition, Kobo, *Burkill 37090* (CAL); Siang (fide Hajra et al. 1996). **Assam.** Nowgong [Nagaon], Khasi & Garo Hills (fide India Biodiversity Portal); NE Frontier, Lakhimpur, *Goalpara s.n.* (fide India Biodiversity Portal); Namdapha National Park, 11 Nov 2017, photo by R. Naniwadekar (Wikimedia, here as Fig. 58). **Himachal Pradesh.** Bashahr, Kiaow to the Suttej, *Lace 667* (E-2 sheets); Chamba State, Gharosan Nala, Sao Valley, *Lace 750* (CAL, E-2 sheets); Chamba State, near Silla Grat [Sillagharat], *Lace 1975* (E). **Meghalaya.** Present, "Common in tropical forests of the state" (fide Sawian et al. 2007). **Nagaland.** Jaboca, *Prain's Collector 67* (CAL). **Sikkim.** Rungeet, *Care s.n.* (E); Birick, Darjeeling, *Care s.n.* (E); Tista, Darjeeling, *Care s.n.* (E, Fig. 57); Mal Forest, Kalimpong, Darjeeling, *Haines 1036* (E); Tista, *Ribu & Rhomoo s.n.* (E). **Uttar Pradesh.** No records seen. **Uttarakhand.** Kumaon, *Blinkworth 4274* (K); Nolarha, Ramganga River, Almora Div., Kumaon, *Bis Ram 2301* (E); Sat Tal, *Dudgeon & Kenoyer 411* (MO); Mussoorie, *Duthie 23092* (CAL, E); Garhwal, Lohba, *Hooper 38983* (CAL). **West Bengal.** Preng Cola, Munsong, *Craib 510* (CAL); Mangpo, *Prain's Collector 67* (CAL). **MYANMAR.** Shan State, around Pin Sein Pin village, Pindaya Township, *Shin et al. TS394*, sterile (MBK). **NEPAL.** Khebang-Bharomdin, *Hara et al. 6306653* (CAL); no other data, *Hooker s.n.* (E); Dharan-Sanguri, *Shrestha 12363* (KATH); Tatopani (E of Beni), *Stainton et al. 617* (E); E Napalia, 1818, *Wallich s.n.* (CAL, E); Napalia, 1821, *Wallich s.n.* (CAL, K). Collections from CAL are as cited by Sen Gupta and Safui (1984). **THAILAND.** Doi Suthep-Pui National Park, *Suriya s18b2* (CMU, see Fig. 59).

Hovenia dulcis occurs in Viet Nam (e.g., Witt & Luke 2017) but the plants there probably are *H. pubescens*. *Hovenia*, presumably *H. pubescens*, occurs in natural habitats in northeastern Thailand, but it has been identified there as *H. dulcis*.

5. HOVENIA TOMENTELLA (Makino) Nakai ex Kimura, Bot. Mag. (Tokyo) 53(329): 478. 1939 [May]. *Hovenia dulcis* var. *tomentella* Makino, Bot. Mag. (Tokyo) 28: 156. 1914. **SYNTYPES: JAPAN. Prov. Tosa, H. Yamamoto s.n.** (TI, as cited, not seen) and *T. Makino s.n.* (TI, as cited, not seen). Makino's protologue: "Peduncle: the fleshy portion pulverous, and the original portion

pulvereo-puberulent. Fruit pubescent-tomentose with fulvous hairs; endocarp thinner; calyx-tube densely pulvereo-puberulent; pedicel pulvereo-tomentose. Seed oval, subfulvous-black." ... "This variety is common in the western Japan."

Hovenia trichocarpa Chun & Tsiang, Sunyatsenia 4: 16, pl. 6, f. 3. 1939 [June]. **TYPE: CHINA. Kwangtung [Guangdong] Prov.** Yu-Yuen, Mo-Fung Shan, near summit of forested watershed, tree 12 m tall, 8 Sep 1935, *W.Y. Chun and Y. Tsiang 11010* (holotype: IBSC, Figs. 36, 37). The protologue notes that the collection was made by *Z.S. Chung* and deposited at SYSU, but the label for the IBSC specimen marked as type by Chun and Tsiang shows "*W.Y. Chun and Y. Tsiang 11010*."

Paratypes: Kwangsi Prov. Kwei-ling, Tzu Yuen District, tree, deep green glabrous above, pale green tomentose below, in woods, stream side, 3 Aug 1937, *Z.S. Chung [T.S. Tsoong] 83495* (A image, IBSC not seen, SYSU [or IBSC?] not seen); Chuen Yuen, no other collection information on the label, *Z.S. Chung 83330* (A, image, SYSU [or IBSC?] not seen).

Hovenia robusta Nakai & Kimura, Bot. Mag. (Tokyo) 53: 479. 1939. *Hovenia trichocarpa* var. *robusta* (Nakai & Kimura) Chen & Chou in Y.L. Chen, Fl. Reipubl. Popularis Sin. 48: 93. 1982. **LECTOTYPE** (designated here): **CHINA. [Anhui Prov.]** Wangshan [Huangshan], Oct 1933, *W.C. Cheng 3984* (PE, Fig. 40; isolectotypes: NAS 00071543-Fig. 41, NAS 00071542, NAS 00071544).

Also cited in the protologue as "Type" — **Anhui Prov.** Chu Hua Shan [Huangshan], dense forests on slopes, 2000 ft. 28 June 1925, *R-C. Ching 2802* (K, fide Kimura).

Hovenia merriliana Cheng, Science; an Illustrated Journal 2: 35. 1949 [protologue not seen]. **TYPE: CHINA. Hupei-Szechuan** (Metasequoia Area). No other locality information, 1948, *W.C. Cheng and C.T. Hwa 561* (holotype: ?; isotypes: A, K-Figs. 46 and 47, NAS). The label has this note: "Compared with paratype of *H. trichocarpa* Chun & Tsiang: identical ! — det. S.Y. Hu 1960").

Hovenia tomentosa Cheng, Science; an Illustrated Journal 32: 249. 1950. Noted in Tropicos to be a nomen nudum.

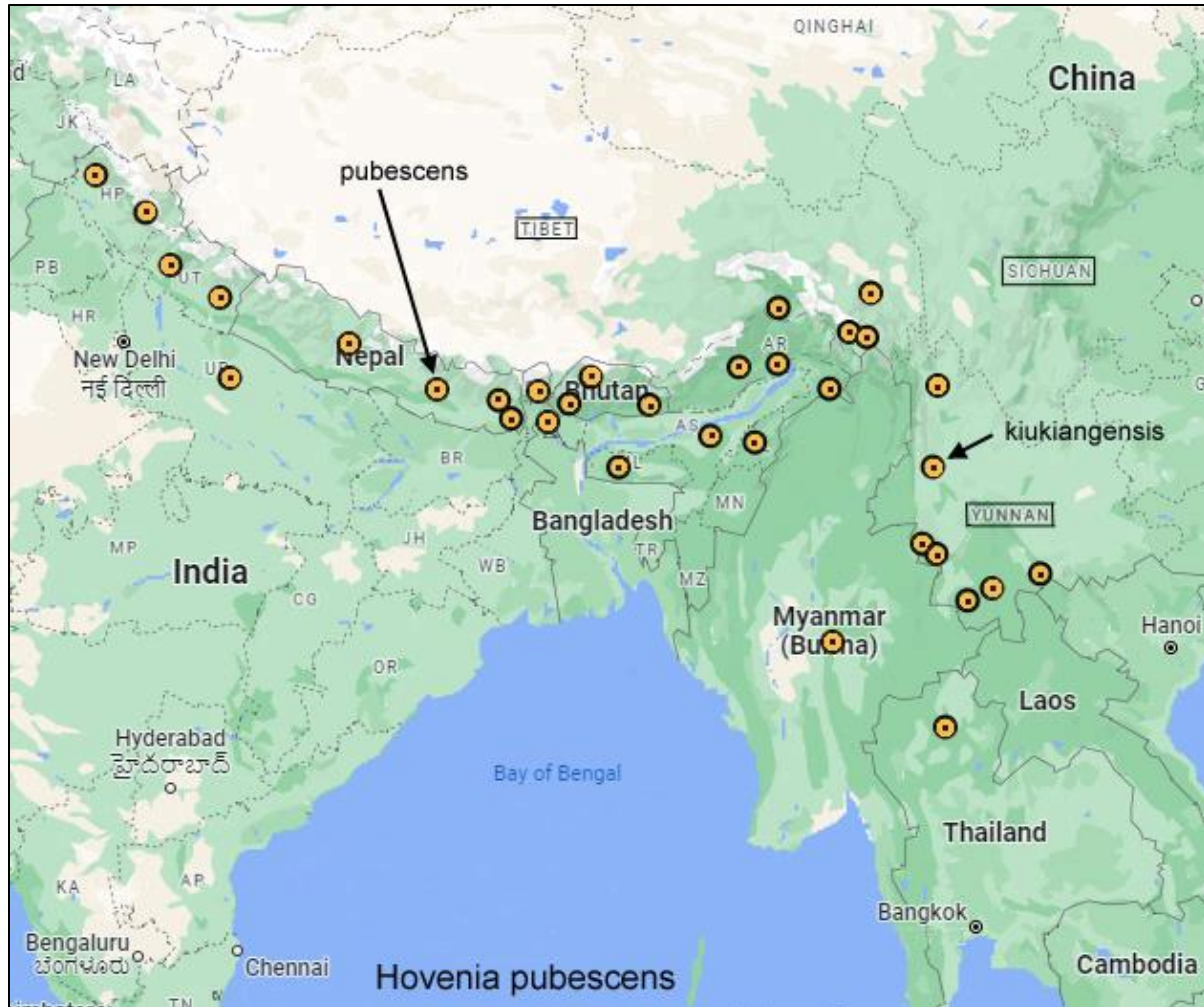
Hovenia fulvotomentosa Hu & Chen, Acta Phytotax. Sin. 1: 227. 1951. *Hovenia trichocarpa* var. *fulvotomentosa* (Hu & Cheng) Chen & Chou, Bull. Bot. Lab. N.-E. Forest. Inst., Harbin 5: 88. 1979. **TYPE: CHINA. Jiangxi Prov.** Xiushui Xian, Liushui-an, in ravine, 10 Sept. 1947, *Y.K. Hsiung 5833* (holotype: PE, Fig. 44; isotypes: LBG, Fig. 45).

Hovenia dulcis var. *crassifolia* Kōta, Bull. Natl. Sci. Mus., Tokyo, B. 31(4): 147. 2005. **TYPE: JAPAN. Honshu. Pref.** Shizuoka, Region VII, Shimoda City, Suzaki Peninsula, Kakisaki, tree 8 m high, 18 cm in trunk diameter, lvs very thick 0.25–0.33 mm thick, brown hairs at branching of mid vein and lateral ones on the abaxial side, among thickets by road, ca. 30 m alt., 14 Jul 2005, *F. Kōta 24448* (holotype: TNS, Kōta's Figs. 13 and 15-5). In distinguishing var. *crassifolia*, only this brief diagnosis was given: "Affinis *Hovenia dulci* var. *dulci*, sed folio crassa et lucida diversus."

Hovenia trichocarpa has been used as the name for this species, but *Hovenia tomentella* was published one month earlier. Most Japanese collections of *Hovenia* I have seen with hairy fruits and inflorescences have glabrate to sparsely hairy abaxial leaf surfaces, hairy most along the main veins — it seems likely that the type of *H. tomentella* (not seen) has similar leaf vestiture although some plants appear to be more densely invested (e.g., Fig. 42—from Aichi Pref., Japan).

Varieties of *Hovenia trichocarpa/tomentella* were distinguished by Chen & Schirarend (2007) with the following contrasts.

- a. Leaves densely yellow-brown or yellow-gray tomentose adaxially var. **trichocarpa**
 a. Leaves glabrous on both surfaces or pilose on veins adaxially var. **robusta**



Map 4. Distribution of *Hovenia pubescens*. Vouchers cited in the text, except for Yunnan and Tibet (see Chinese Virtual Herbaria, mostly as *H. acerba* var. *kiukianensis*). Type localities are indicated for *H. pubescens* and *H. kiukiangensis*.

The ecological characterizations by Chen & Schirarend (2007, as below, in **FOC**.) for var. *trichocarpa* and var. *robusta* are similar, but var. *robusta* was described with a wider geographical range. Intermediacy suggests that the two are arbitrarily distinguished.

The typical variety, presumably with the abaxial epidermis hairy:

"Mountain forests; 600-1300 m. N Guangdong, Guizhou, Hubei, Hunan, Jiangxi."

Var. *robusta*, with abaxial vestiture only along the veins:

"Dense forests on slopes; 600-1100 m. Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Zhejiang [Japan]."

Rejected names

Hovenia inaequalis DC., Prodr. 2: 40. 1825. **LECTOTYPE** (Sen Gupta & Safui 1984): **Protologue**: "Napauliâ 1821," *Wallich s.n.* (G-DC fiche 284-19, fide Sen Gupta & Safui; = G-DC 476590). Two other sheets at G-DC have labels as Wallich in 1821 (476565, 476586) — all appear to be a species of *Ziziphus* — probably *Z. oenoplia* (L.) Mill. 1768.

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Figure 1. *Hovenia celtidifolia*. Mexico, Chiapas, Breedlove 53247 (TEX).



Figure 2. *Hovenia celtidifolia*. Detail from *Breedlove 53247* in Figure 1.



Figure 3. *Hovenia celtidifolia*. Details from *Breedlove 53247* in Figure 1.



Figure 4. *Hovenia celtidifolia*. Detail from *Breedlove 53247* in Figure 1.



Figure 5. *Hovenia celtidifolia*. Details from *Breedlove 53247* in Figure 1.



Figure 6. *Hovenia celtidifolia*. Edo. México. Detail from *Hinton 7978*.



Figure 7. *Hovenia celtidifolia*. Mexico, Edo. Mexico, *Hinton 7684* (CHR).



Figure 8. *Hovenia celtidifolia*. Detail from *Hinton* 7684 in Figure 7.



Figure 9. *Hovenia celtidifolia*. Mexico, Veracruz, Avendabo & Vazquez 797 (MEXU).



Figure 10. *Hovenia celtidifolia*. Mexico, Veracruz, Ventura A. 9904 (SD).



Figure 11. *Hovenia dulcis*. Holotype of *Hovenia dulcis*, Japan, Thunberg s.n. (UPS).

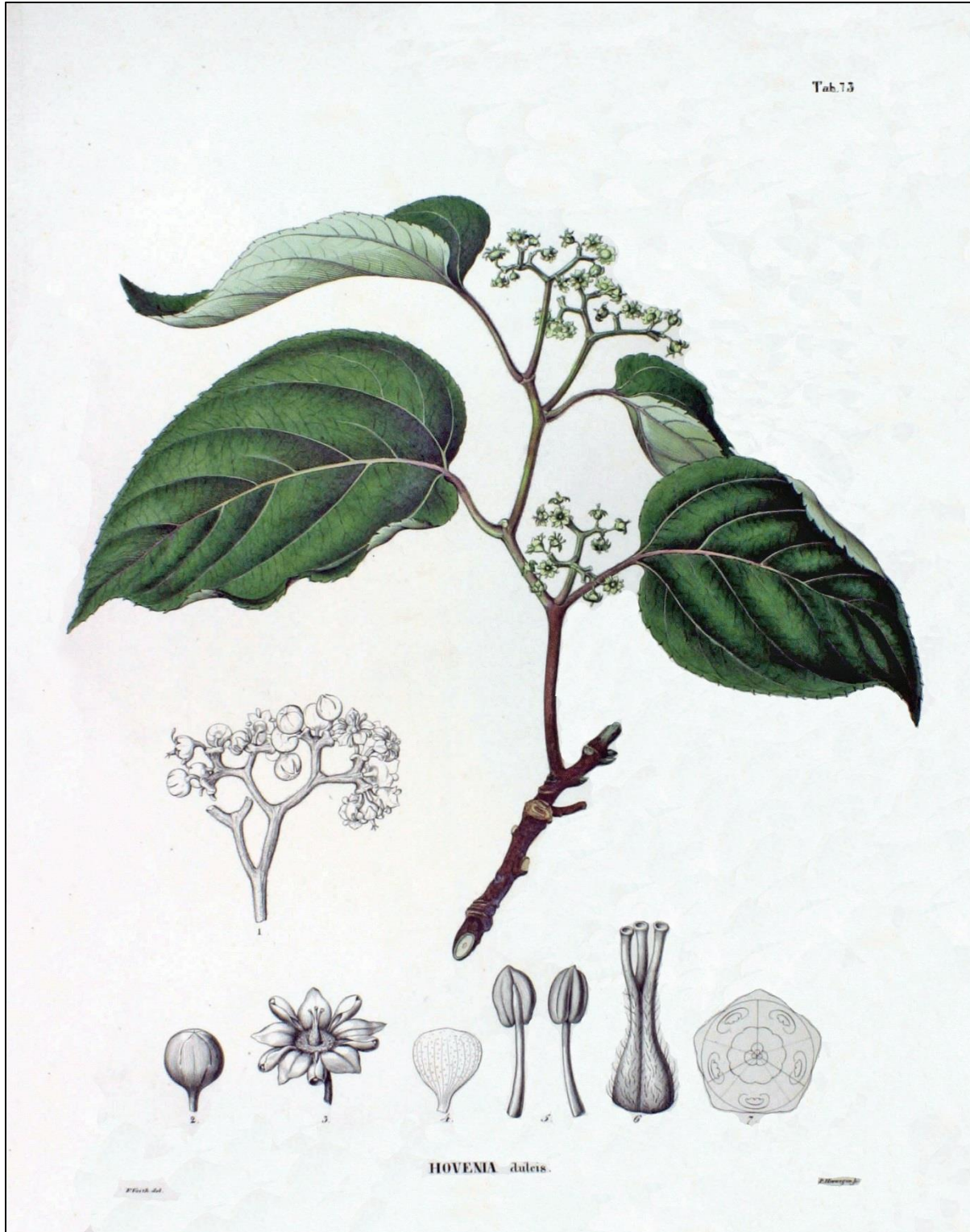


Figure 12. *Hovenia dulcis*. From Siebold & Zuccarini, *Flora Japonica*, Sectio Prima (Tafelband), t. 73. 1870.



Figure 13. *Hovenia dulcis*. From Siebold & Zuccarini, *Flora Japonica*, Sectio Prima (Tafelband), t. 74. 1870.



Figure 14. *Hovenia dulcis*. Japan, Sugawara 7071401 (E).



Figure 15. *Hovenia dulcis*. Japan, Matsumura s.n. (US).



Figure 16. *Hovenia dulcis*. Japan, *Matsumura s.n.* (US) — detail from Figure 15.



Figure 17. *Hovenia dulcis*. Korea, Meyer 81-548 (MOAR).

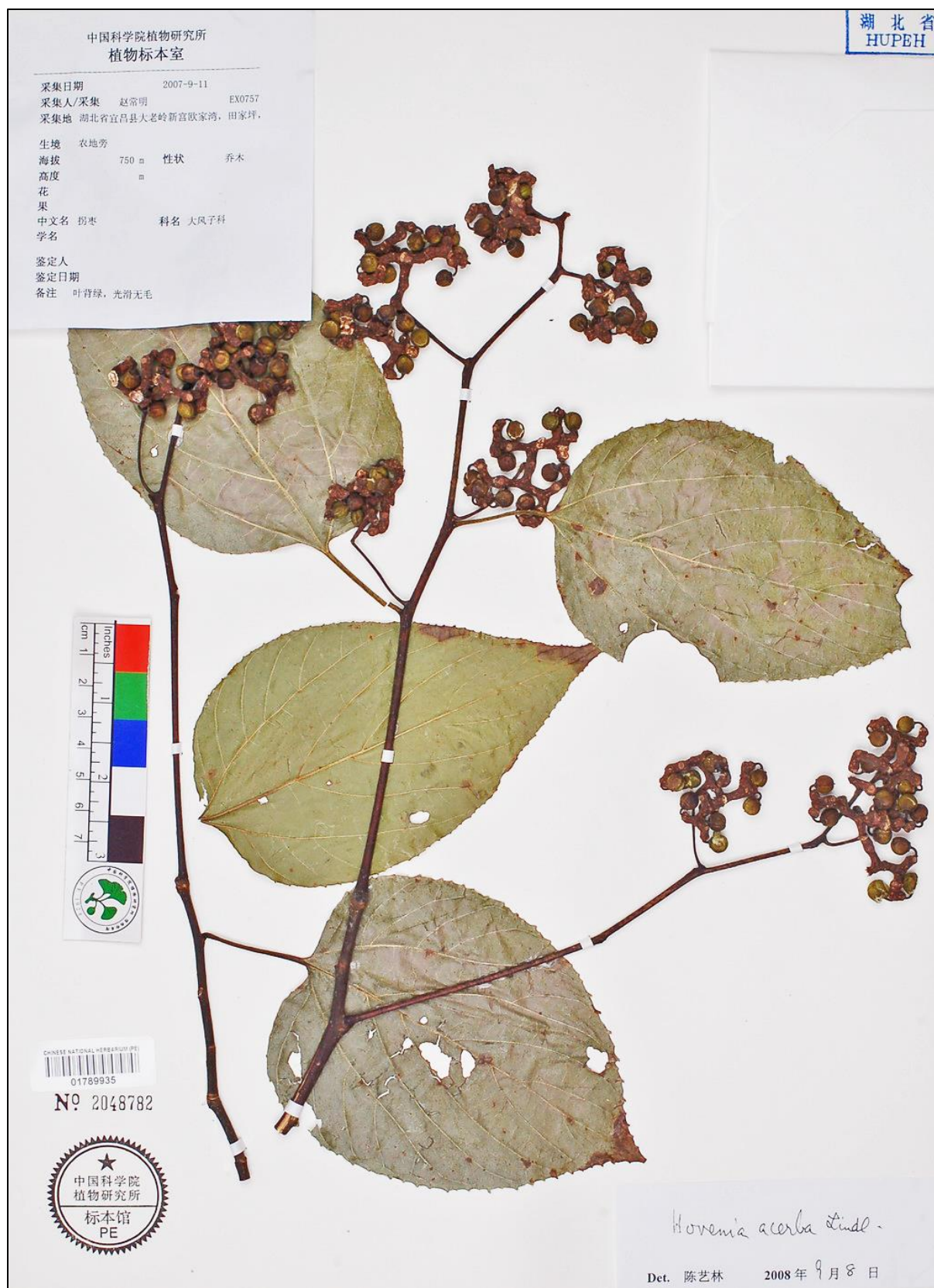


Figure 18. *Hovenia dulcis*. China, Hubei Prov., Changming EX0757 (PE).

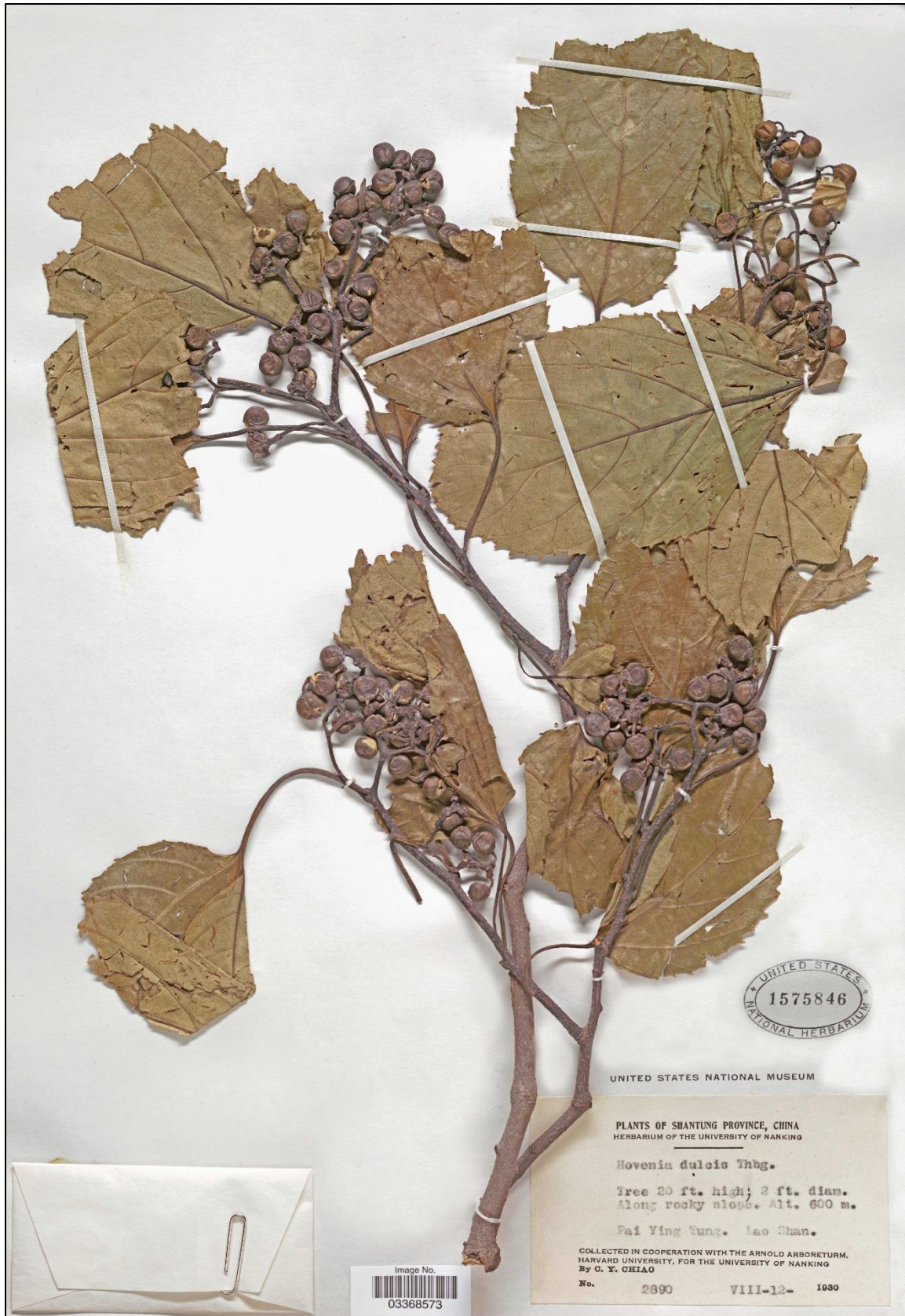


Figure 19. *Hovenia dulcis*. China, Shandong Prov., Chiao 2890 (US).



Figure 20. *Hovenia dulcis*. China, Zhejiang Prov., Xianyu 20070 (WUK).

Figure 21. *Hovenia dulcis*. China, Hebei Prov., Xinyuan 520 (PE).



Figure 22. *Hovenia dulcis*. Brazil (naturalized), *Hind et al.* H50280 (E).

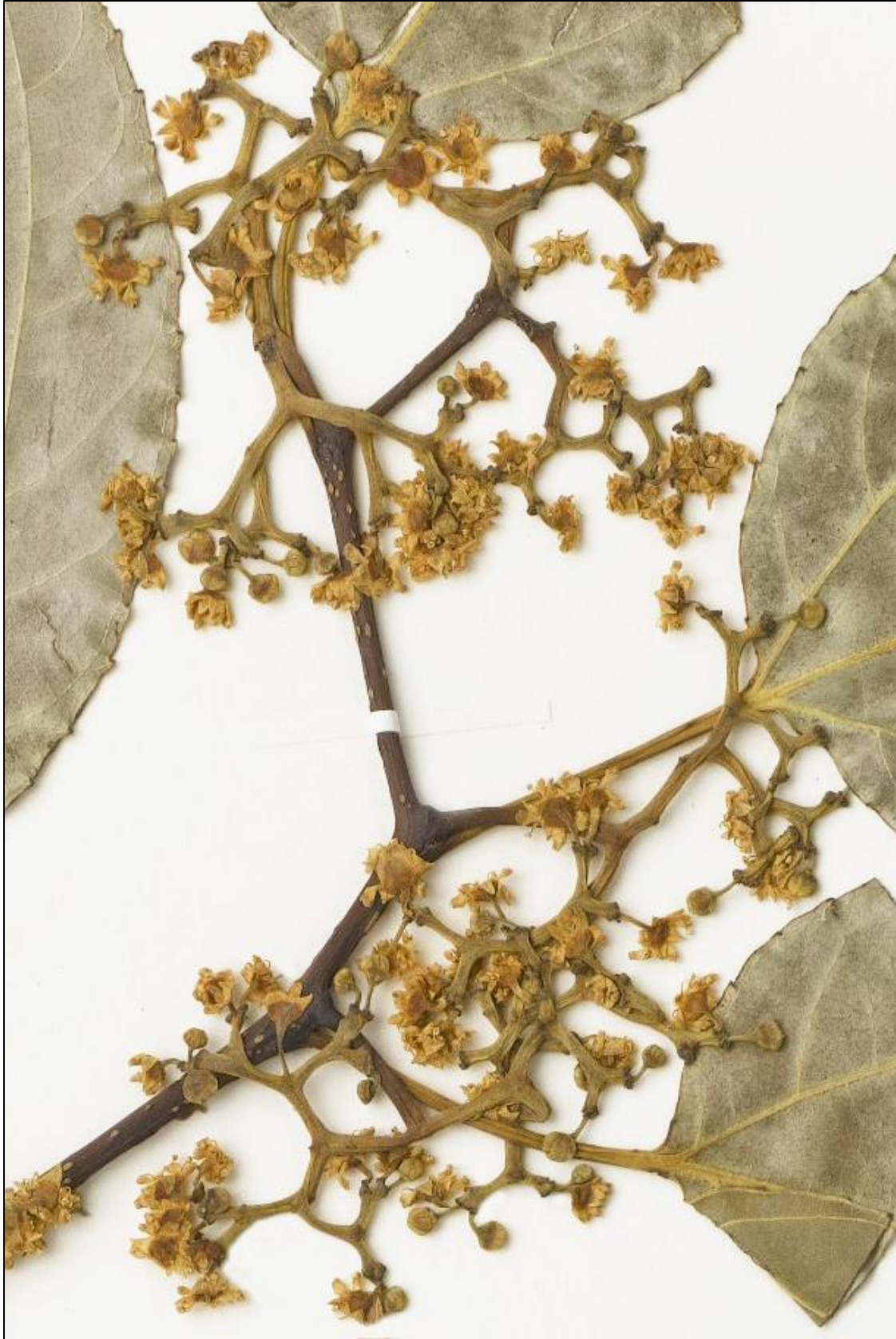


Figure 23. *Hovenia dulcis*. Brazil (naturalized), Hind et al. H50280 (E) – detail from Figure 22.



Figure 24. *Hovenia dulcis*. USA, Texas (naturalized), Atha 11907 (NY).

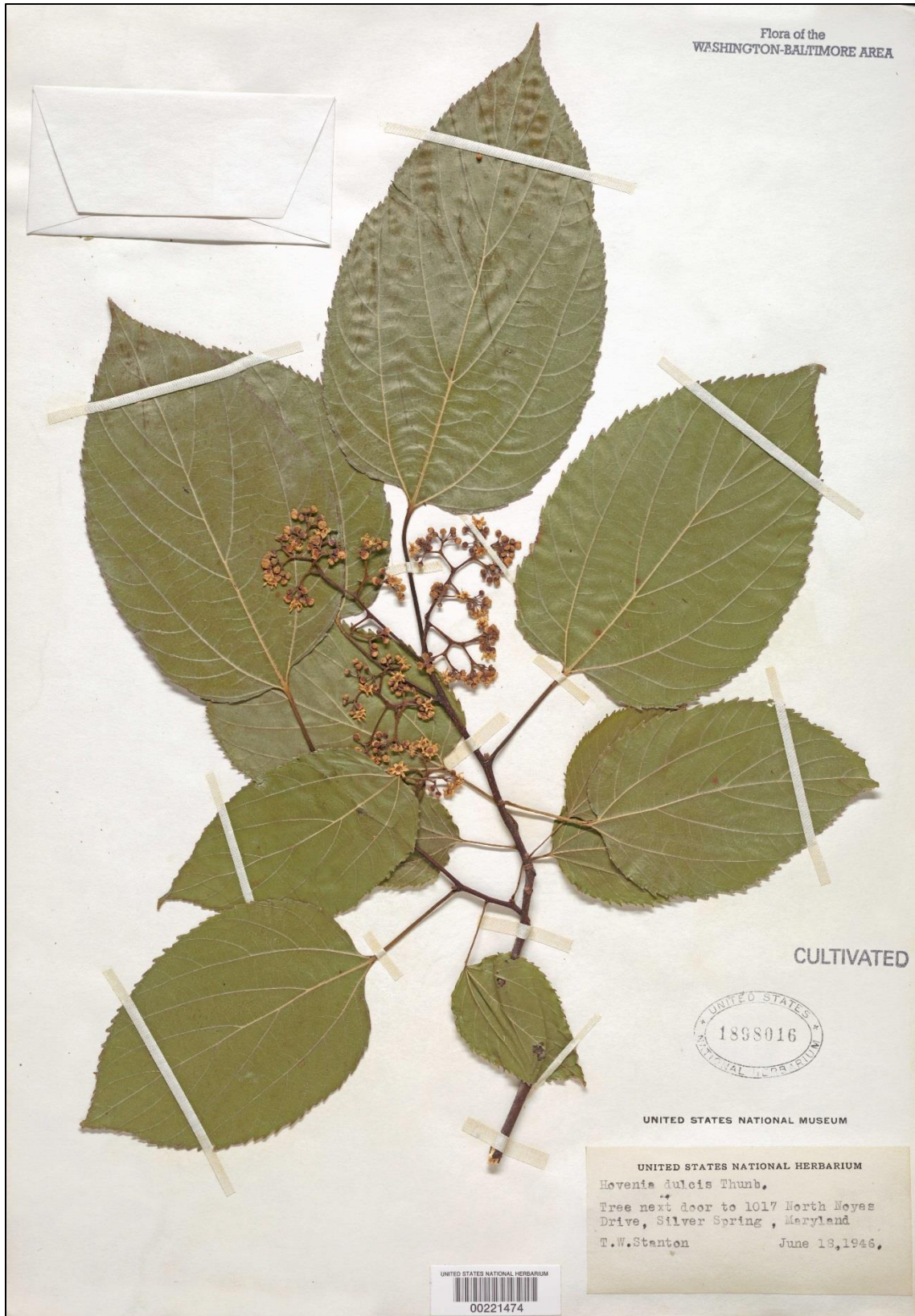


Figure 25. *Hovenia dulcis*. USA, Maryland (cultivated), Stanton s.n. (US).



Figure 26. *Hovenia dulcis*. USA, Maryland (naturalized), Stanton s.n. (US) — detail from Figure 25.



Figure 27. *Hovenia dulcis*. USA, Dist. of Columbia (cultivated), Wester and Sullivan s.n. (US).



Figure 28. *Hovenia acerba*. Type illustration from Lindley, Bot. Reg. 6: t. 501. 1820. From China or Nepal.



Figure 29. *Hovenia acerba*. Holotype of *Zizyphus esquirolii*, China, Guizhou Prov., Esquirol 861 (E).



Figure 30. *Hovenia acerba*. Detail from holotype of *Ziziphus esquirolii* (Fig. 29).



Figure 31. *Hovenia acerba*. Isotype of *Hovenia parviflora*, China, Guangdong Prov., McClure s.n. (PE).

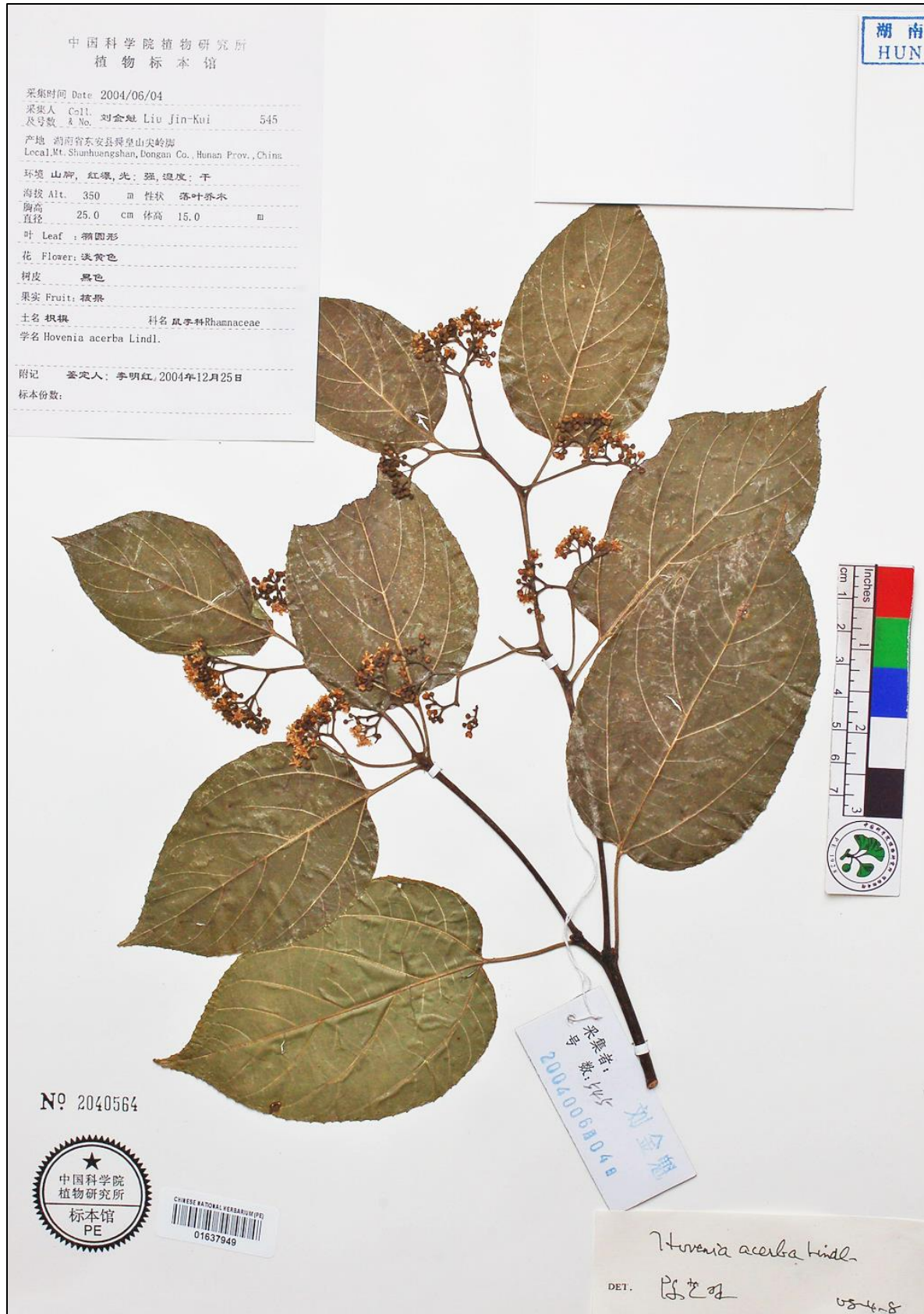
Figure 32. *Hovenia acerba*. China, Hunan Prov., Jin-Kui 545 (PE).



Figure 33. *Hovenia acerba* with exceptionally large axillary inflorescences. China, Guangxi Prov., Nandan Census team 451221180526012LY (GXMG).



Figure 34. *Hovenia acerba*. China, Xizang Prov. (Tibet), Deng 81-1413 (PE). Identified on the label as *H. dulcis* but out of range for that species. The exceptionally large inflorescence is similar to that shown for *H. acerba* from Guangxi Prov. — see Figure 33.

Figure 35. *Hovenia acerba*. China, Guangxi Prov., *Lingyun Census team* 451027121018009 (GXMI).



Figure 36. *Hovenia tomentella*. Holotype of *Hovenia trichocarpa*, China, Guangdong Prov., Chun & Tsiang 11010 (IBSC).



Figure 37. *Hovenia tomentella*. Detail from holotype of *Hovenia trichocarpa* (Fig. 36).

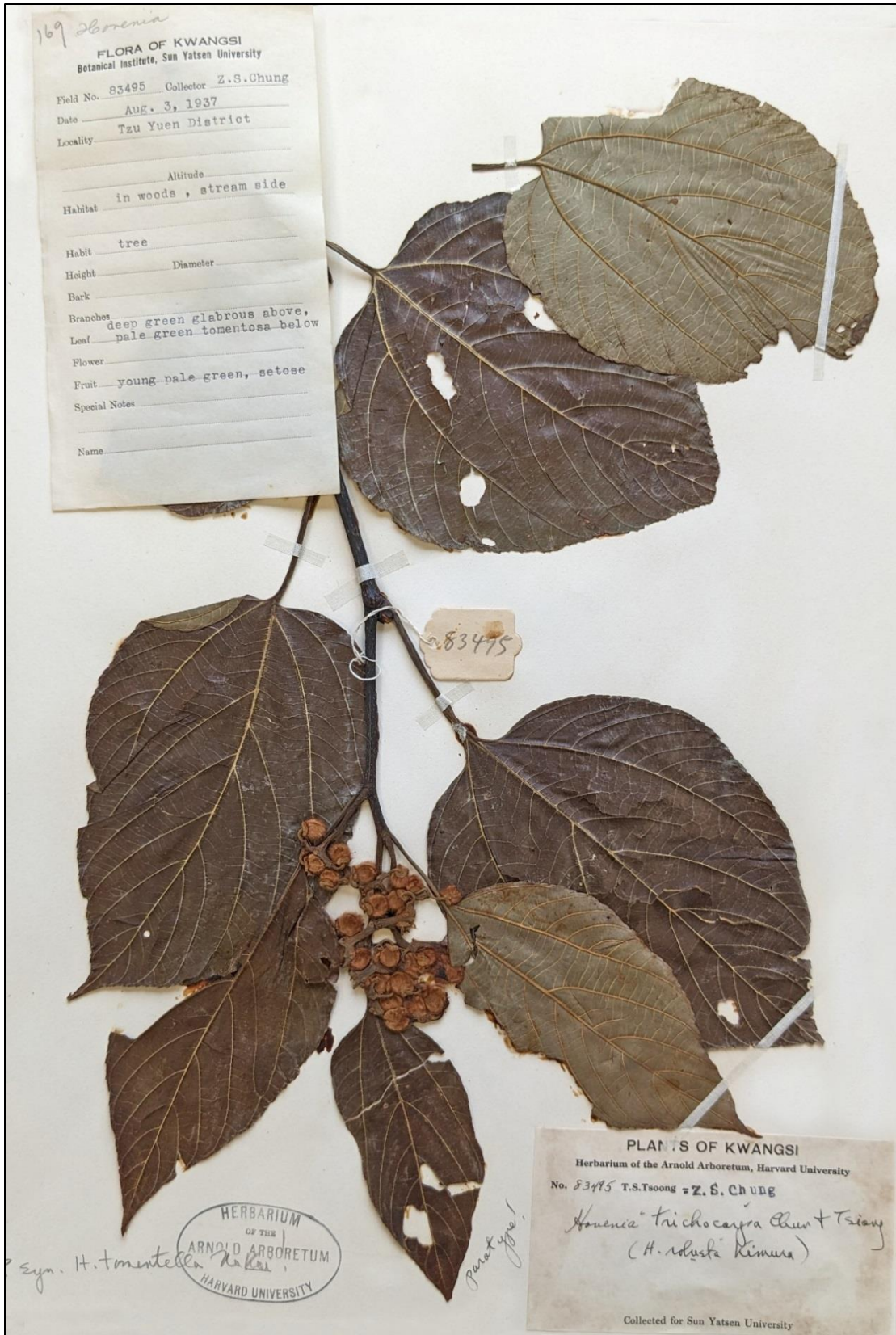


Figure 38. *Hovenia tomentella*. Paratype of *Hovenia trichocarpa*, China, Guangxi Prov., Chung 83495 (A).



Figure 39. *Hovenia tomentella*. Paratype of *Hovenia trichocarpa*, China, Guangxi Prov., Chung 83330 (A).



Figure 40. *Hovenia tomentella*. Lectotype of *Hovenia robusta*, China, Anhui Prov., Chen 3984 (PE).



Figure 41. *Hovenia tomentella*. Isolectotype of *Hovenia robusta*, China, Anhui Prov., Cheng 3984 (NAS).



Figure 42. *Hovenia tomentella*. Japan, Aichi Pref., Inami 367 (PE).

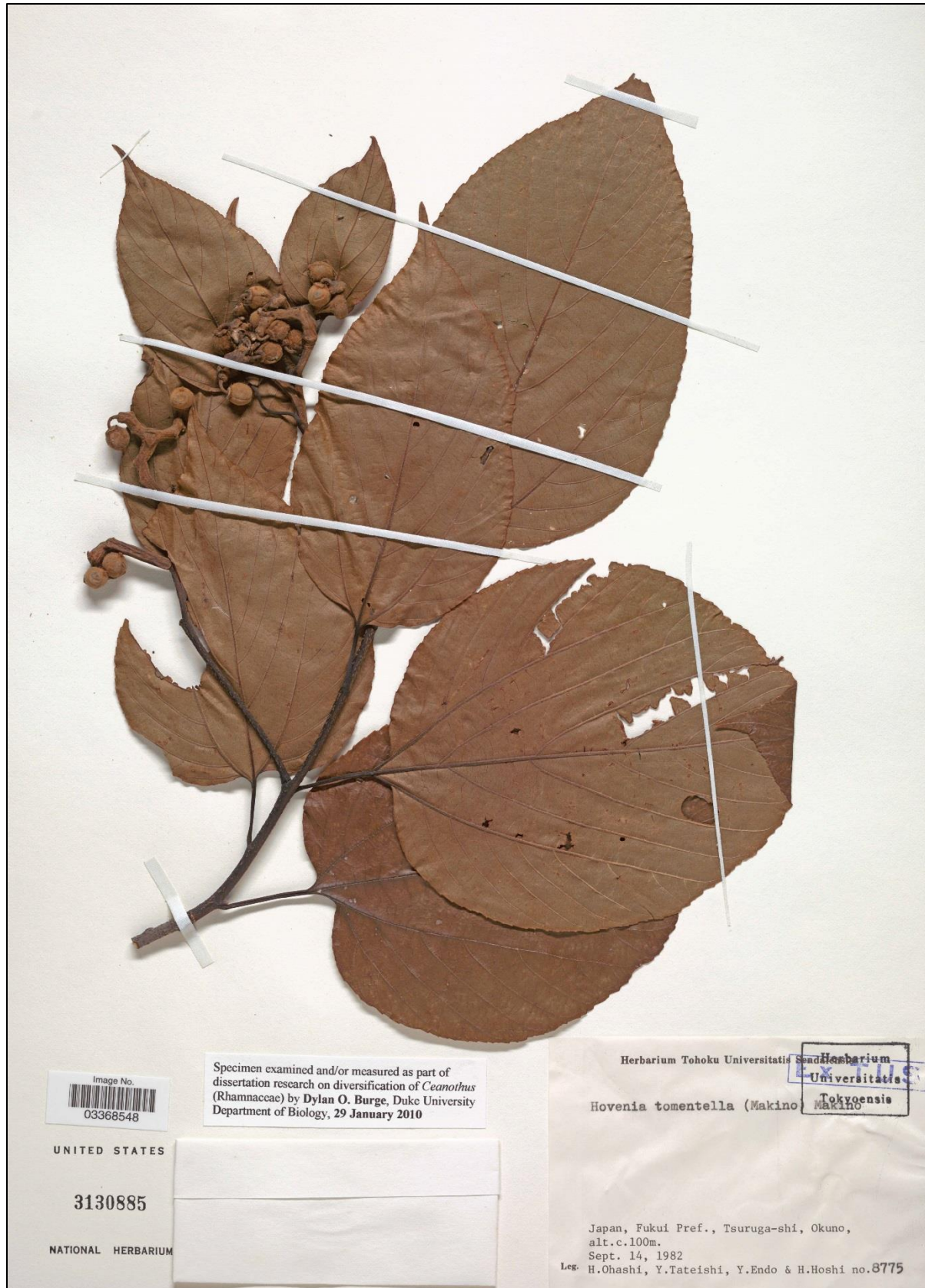


Figure 43. *Hovenia tomentella*. Japan, Fukui Pref., Ohashi et al. 8775 (US).

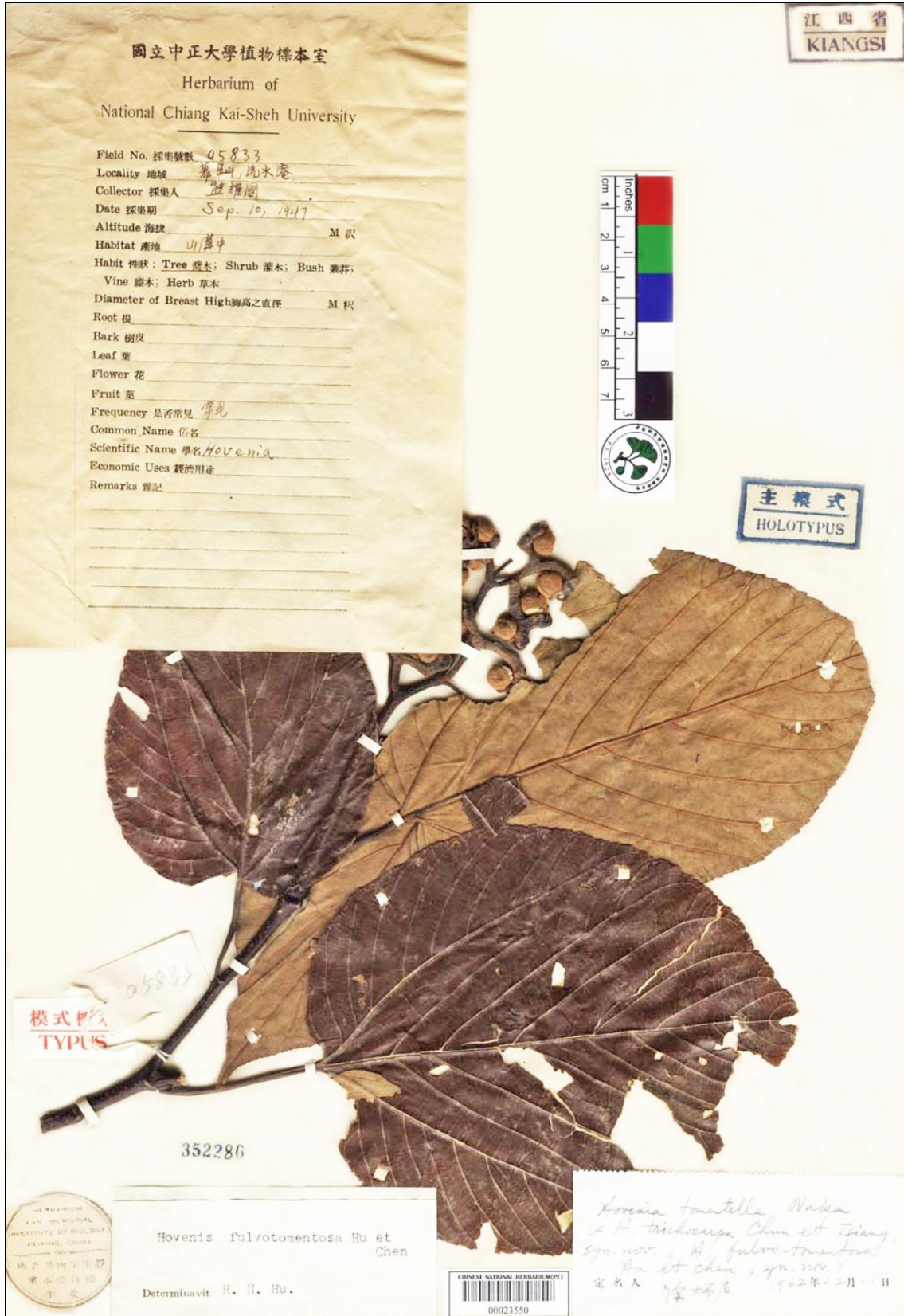


Figure 44. *Hovenia tomentella*. Holotype of *Hovenia fulvotomentosa*, China, Jiangxi Prov., Hsiung 5833 (PE).



Figure 45. *Hovenia tomentella*. Isotype of *Hovenia fulvotomentosa* (LBG).



Figure 46. *Hovenia tomentella*. Detail from isotype of *Hovenia merriliana*, China, Hupei-Szechuan Prov., Cheng & Hwa 561 (K).



Figure 47. *Hovenia tomentella*. Detail from isotype of *Hovenia merriliana*, China, Hupei-Szechuan Prov., Cheng & Hwa 561 (K).

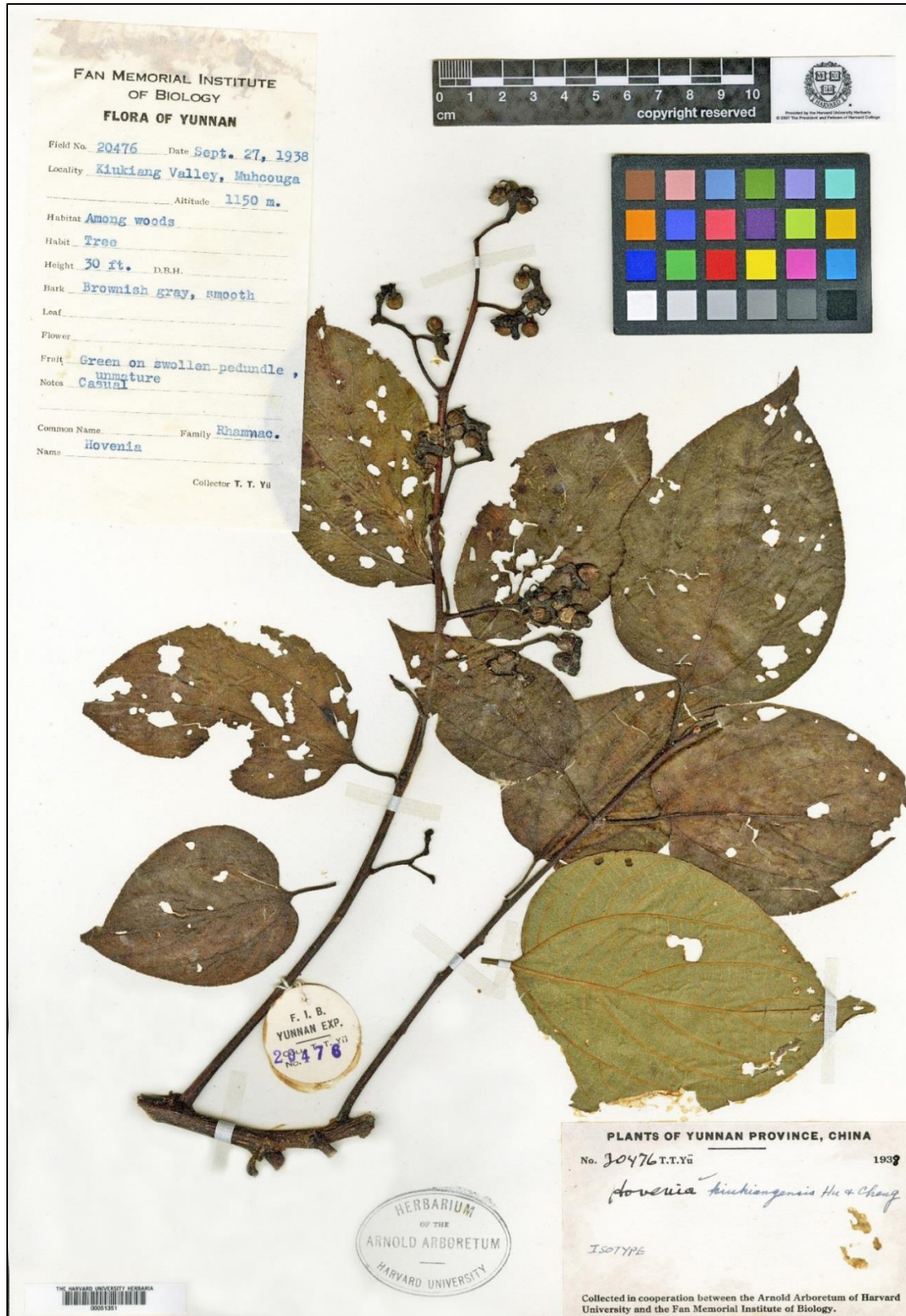
Figure 48. *Hovenia pubescens*. Isotype of *Hovenia kiukiangensis*, China, Yunnan Prov., Yu 20476 (A).



Figure 49. *Hovenia pubescens*. Detail from isotype (A) of *Hovenia kiukiangensis* (Fig. 48).



Figure 50. *Hovenia pubescens*. China, Yunnan Prov., holotype of *Hovenia kiukiangensis*, Yu 20476 (PE 23552). The sheet is stamped as "ISOTYPUS" but PE 23551 appears to be an isotype.



Figure 51. *Hovenia pubescens*. China, Yunnan Prov., isotype of *H. kiukiangensis*, Yu 20476 (KUN).



Figure 52. *Hovenia pubescens*. China, Xisang Prov. (Tibet), Zhang 09CS1598 (KUN).



Figure 53. *Hovenia pubescens*. China, Xisang Prov. (Tibet), Q-T team 749 (KUN).



Figure 54. *Hovenia pubescens*. China, Xisang Prov. (Tibet), Zhang 09CS1598 (KUN).

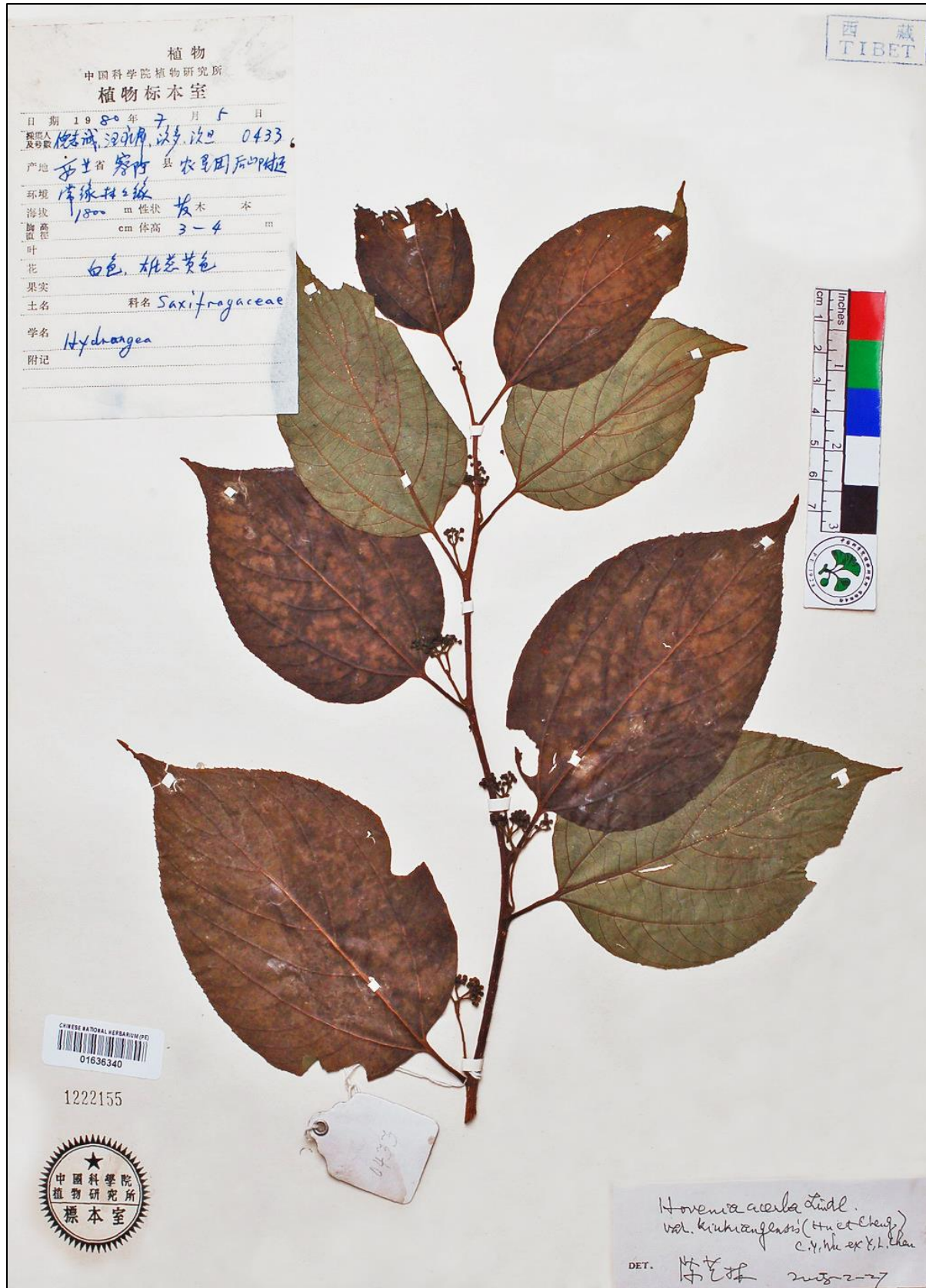
Figure 55. *Hovenia pubescens*. China, Xisang Prov. (Tibet), Zhicheng 433 (PE).

Figure 56. *Hovenia pubescens*. China, Yunnan Prov., Jianwu 3354 (KUN).

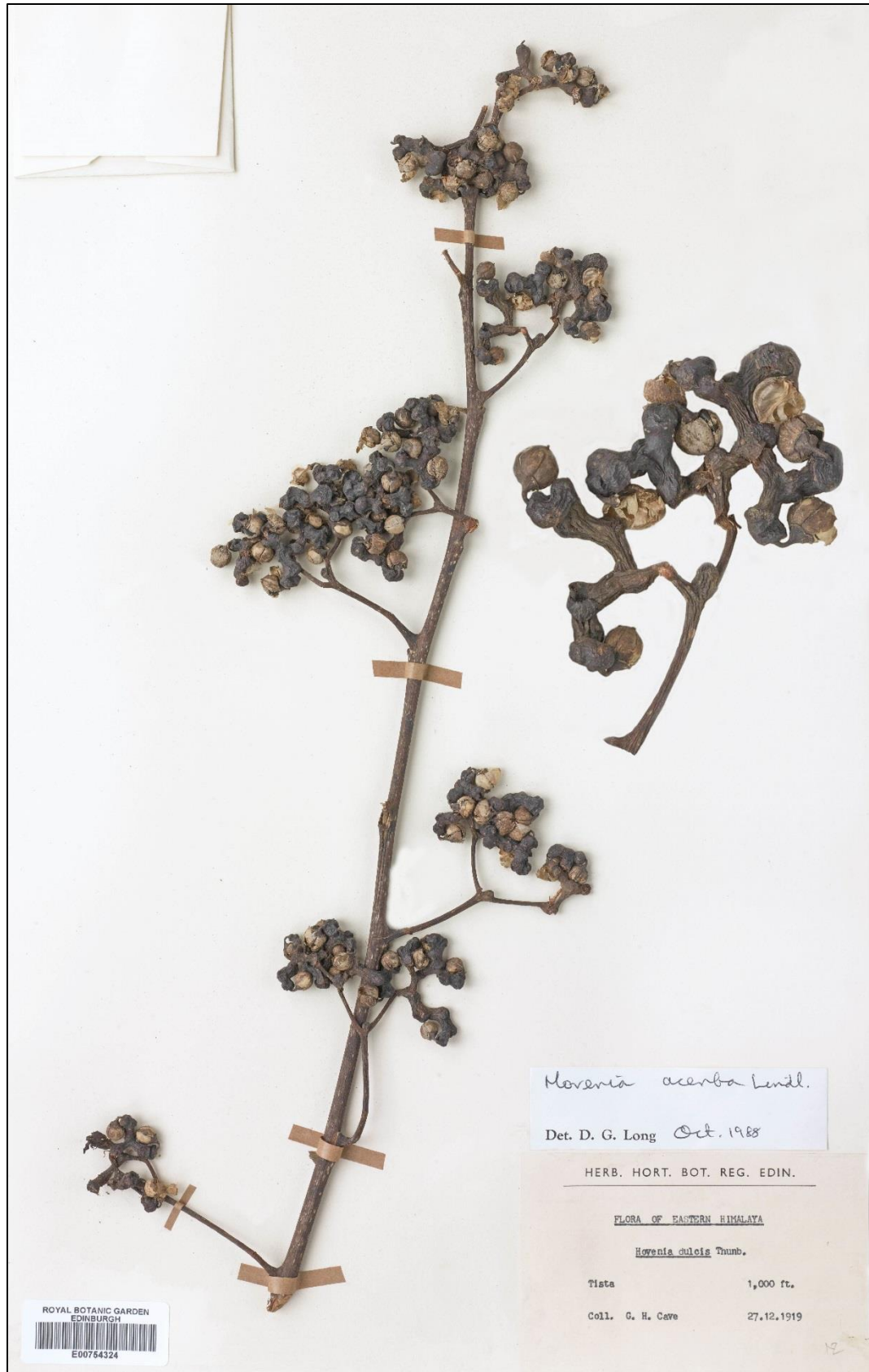


Figure 57. *Hovenia pubescens*. India, Sikkim, Cave s.n. (E).



Figure 58. *Hovenia pubescens*. India, Assam, Namdapha National Park, photo by R. Naniwadekar, 11 Nov 2017 (Wikimedia).



Figure 59. *Hovenia pubescens*. Thailand, Doi Suthep-Pui National Park, *Suriya s18b2* (CMU—Chiang Mai University Herbarium). Photo from Kopachon et al. (1996). The plant was identified by Kopachon et al. as *H. dulcis* but geography and inflorescence structure indicate that it is *H. pubescens*.