

**CARDIAGYRIS (ASTERACEAE: ASTEREAE),  
A NEW GENUS FOR THE DOELLINGERIA-LIKE SPECIES OF ASIA**

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**ABSTRACT**

Nine species of Asian *Aster* and one hybrid are placed in ***Cardiagyris* Nesom, gen. nov.**, typified by *Aster scaber* Thunb.: ***Cardiagyris dimorphophylla* (Franch. & Sav.) Nesom, comb. nov.**, ***Cardiagyris dolichophylla* (Y. Ling) Nesom, comb. nov.**, ***Cardiagyris huangpingensis* (W.P. Li & Z. Li) Nesom, comb. nov.**, ***Cardiagyris japonica* (Miq.) Nesom, comb. nov.**, ***Cardiagyris komonoensis* (Makino) Nesom, comb. nov.**, ***Cardiagyris marchandii* (Levl.) Nesom, comb. nov.**, ***Cardiagyris rugulosa* (Maxim.) Nesom, comb. nov.**, ***Cardiagyris scabra* (Thunb.) Nesom, comb. nov.**, ***Cardiagyris sohayakiensis* (Koidzumi) Nesom, comb. nov.**, and the hybrid ***Cardiagyris* × *sekimotoi* (Makino) Nesom, comb. nov.** Phylogenetic analyses based on molecular data place the *Cardiagyris* species at the base of the *Asterothamnus* branch of subtribe Asterinae, which includes other genera treated as separate from *Aster* sensu stricto. All species except *C. marchandii* have been included in molecular analyses, but a well-supported phylogeny is lacking. Morphological coherence of the genus is strong. Tentative evidence suggests that narrowly lanceolate leaves have evolved independently from cordate-petiole ones, once in China and once in Japan.

*Aster scaber* Thunb. and its close relatives have long been recognized as a distinctive natural group and the recent description of two species from southern China (Guangxi and Guizhou) have recalled attention to it. *Aster scaber* and *A. marchandii* Levl. were transferred to the American genus *Doellingeria* (by C.G.D. Nees in 1832, Y. Ling in 1975), and Nesom (1993) placed the remaining Asian species there. The similarities, however, are evolutionarily convergent, as molecular sequence data unequivocally show that the American species arose within a North American lineage (e.g., Noyes & Rieseberg 1999) while the Asian species are part of a lineage of Old World taxa (Ito et al. 1998; W.-P. Li et al. 2012; Z. Li et al. 2020; summary in Nesom 2020a).

The closest relatives (fide molecular analyses) to the doellingerioid Asian species include newly described genera *Yonglingia*, *Changchaochienia*, and *Sinobouffordia* (Nesom 2020b) as well as the more generally accepted genera *Arctogeron* DC. and *Asterothamnus* Novop. *Cardiagyris* species are distinct in karyotype from other Asian species (reviewed by Saito et al. 2007).

**CARDIAGYRIS** Nesom, **gen. nov.** **TYPE:** *Cardiagyris scabra* (Thunb.) Nesom

*Kalimeris* sect. *Cordifolium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B. 8: 312. 1937. *Doellingeria*

sect. *Cordifolium* (Kitam.) Nesom, Phytologia 75: 456. 1993. *Doellingeria* ser. *Cordifolium*

(Kitam.) Nesom, Phytologia 75: 456. 1993. **LECTOTYPE** (Nesom 1993): *Biotia japonica* Miq.

*Doellingeria* [sect. *Cordifolium*] ser. *Papposae* Nesom, Phytologia 75: 457. 1993. **TYPE:**

*Doellingeria scabra* (Thunb.) Nesom

*Aster* sect. *Teretachaenium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B, 8: 3357. 1937. **LECTOTYPE**

(Nesom 1993): *Aster scaber* Thunb.

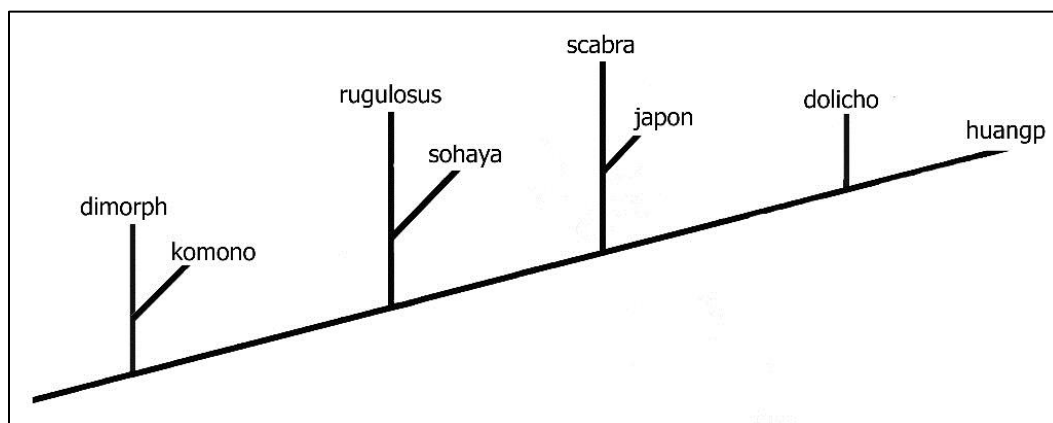
*Aster* ser. *Sohayakienses* Kitam., J. Jap. Bot. 12 722. 1936. **TYPE:** *Aster sohayakiensis* Koidz.

Distinct in its combination of herbaceous perennial habit from rhizomes, eglandular vestiture, either cordate- or ovate-petiolate or lanceolate-sessile to lanceolate-petiolate leaves, shallow involucre, thick-herbaceous phyllaries, heads on ebracteate peduncles in a loose corymb, rays few and white, achenes obovoid-cylindric and subterete, multinerved, elongating to equal or greater than the involucre height, and pappus of clavate-tipped bristles.

**Perennial herbs** from a compact, fibrous-rooted caudex, sometimes with short rhizomes or stolons. **Leaves** basal (usually withered by anthesis) and cauline, lanceolate-sessile to lanceolate-petiolate or cordate-petiolate to ovate-petiolate, glabrous, sometimes glaucous abaxially, margins serrate to crenate or dentate or subentire, venation weakly brochidodromous, basal actinodromous, or camptodromous. **Heads** in a loose corymb or panicle, rarely solitary, peduncles ebracteate or with 1 small bract (more in *C. dolichophyllus* and *C. huangpingensis*). **Involucre**s campanulate to broadly campanulate; phyllaries broadly elliptic to elliptic-oblong or narrowly triangular, evenly thickened (thin-herbaceous in *C. dolichophylla*), (2-)3-4-seriate, unequal to subequal, not keeled, margin scarious; receptacles epaleate. **Ray flowers** 4-20 in 1 series, ligules white, sometimes gradually becoming pink. **Disk flowers** fertile, lobes narrowly triangular, reflexing-coiling. **Achenes** obovoid-cylindric, very slightly compressed, variably 3-7-ribbed, 3-5 mm long, glabrous to sparsely short-strigose; pappus of barbellate bristles in 3-4 series of uneven length, innermost about as long as the disc corollas, clavate-tipped, outermost much shorter, or in *C. japonica* and *C. marchandii* all pappus elements much shorter than the disc corollas.  $2n = 18$ .

An apparent dichotomy in leaf morphology exists among the *Cardiagyris* species. Leaves of five species, including *Cardiagyris scabra* (the type, widespread) and four others (either Japan or China) have ovate to ovate-deltate blades with abruptly delimited petioles. Leaves of *C. rugulosa* – *C. soyahakiensis* (Japan) and *C. dolichophylla* – *C. huangpingensis* (China) have mostly narrowly lanceolate to elliptic-lanceolate blades long-attenuate to a gradually delimited petiolar portion. It is probable that *C. rugulosa/soyahakiensis* and *C. dolichophylla/huangpingensis* are paired evolutionarily as well as geographically, but preliminary evidence does not indicate that these pairs are most closely related to each other. As noted below, *C. scabra* (ovate leaves) and *C. rugulosa* (lanceolate leaves) are sympatric in Japan and occasionally hybridize to produce morphological intermediates. *Cardiagyris scabra* and *C. marchandii* (ovate) are sympatric in China with *C. dolichophylla* and *C. huangpingensis* (lanceolate), but there apparently is no overlap in ecology and hybrids have not been noted.

Cladograms have been published for phylogenetic studies with more than one species of *Cardiagyris* (Ito et al. 1994, 1998; Brouillet et al. 2009; Soejima & Hamashima 2019; Z. Li et al. 2020), but species included and molecular underpinning have varied. The diagram below attempts, intuitively, to summarize hypotheses of putative relationships but it should be interpreted only as speculative. *Cardiagyris marchandii* has not been included in molecular sampling.



**A. LEAF BLADES OVATE, PETIOLES ABRUPTLY DELIMITED**

1. ***Cardiagyris scabra*** (Thunb.) Nesom, **comb. nov.** *Aster scaber* Thunb., Fl. Jap., 316. 1784. *Doellingeria scabra* (Thunb.) Nees, Gen. Sp. Aster., 183. 1832. *Eucephalus scaber* (Thunb.) Gandoger, Bull. Soc. Bot. France 65: 40. 1918. **TYPE: JAPAN.** [No other collection data], *C.P. Thunberg s.n.* (holotype: S image).

*Biotia discolor* Maxim., Prim. Fl. Amur., 146. 1859. *Biotia corymbosa* var. *discolor* (Maxim.) Regel, Tent. Fl. Uss. 33. 1864. **TYPE MATERIAL: CHINA.** Manchuria, Amur, no date, *Maximowicz s.n.* (P 711746 [ex LE] image; P 711747 [gift from LE] image). Manchuria, Amur, 29 Aug 1855, *R. Maack s.n.* (GH 283649 [with LE label] image; GH 283650 [no label] image).

*Aster komarovii* H. Léveillé, Bull. Acad. Int. Géogr. Bot. 20(1): 142. 1909. **TYPE: SOUTH KOREA.** Jeju Island ["In silvis Quelpaert"], Oct 1906, *U.J. Faurie 1125* (holotype: E).

Eastern China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hebei, Heilongjiang, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Nei Mongol, Shaanxi, Shandong, Shanxi, Sichuan, Zhejiang), Japan, Korea, Manchurian region of Russia. Figures 1-4.

2. ***Cardiagyris marchandii*** (Levl.) Nesom, **comb. nov.** *Aster marchandii* Levl., Fedde Repert. Sp. Nov. 11: 306. 1912. *Doellingeria marchandii* (Levl.) Ling, Icon., Cormorph. Sin. 4: 423. 1975. **TYPE: CHINA.** [Guizhou]. Kouy-Tchéou, Col de Hong Kouan La sou, 28 Aug 1911, *J. Esquirol 2736* (holotype: E image; isotype: K image).

Southeastern China (Fujian, Guangdong, Guangxi, Guizhou, Hubei, Jiangxi, Sichuan, Zhejiang). Figure 5.

3. ***Cardiagyris japonica*** (Miq.) Nesom, **comb. nov.** *Biotia japonica* Miq., Ann., Mus. Bot. Lugduno-Batavum 2: 170. 1866. *Aster japonicus* (Miq.) Franch. & Sav., Enum. Pl. Japon. 2: 398. 1876 (not *Aster japonicus* Less. ex Nees 1832). *Aster miquelianus* Hara [nom. nov.], J. Jap. Bot. 12: 338. 1936. *Kalimeris miqueliana* (Hara) Kitam., Fl. Reipubl. Pop. Sin. 74: 108. 1985. *Doellingeria japonica* (Miq.) Nesom, Phytologia 75: 456. 1993. **TYPE: JAPAN.** Protologue: "In monte Fire Jama prope oppidum Karotsa ins. Kiusiu: PIEROT; aliis locis SIEBOLD et BUERGER legerunt. — Kon Gik iap."

Japan. Figures 6 and 10. *Cardiagyris japonica* is similar in overall appearance to *C. dimorphophylla*; the short pappus of the former led to its placement in *Kalimeris*.

1. Pappus 4 mm long ..... ***Cardiagyris dimorphophylla***  
 1. Pappus 0.5–1.5 mm long ..... ***Cardiagyris japonica***

4. ***Cardiagyris dimorphophylla*** (Franch. & Sav.) Nesom, **comb. nov.** *Aster dimorphophyllus* Franch. & Sav., Enum. Pl. Japon. 1: 224. 1875. *Doellingeria dimorphophylla* (Franch. & Sav.) Nesom, Phytologia 75: 457. 1993. **LECTOTYPE** (designated here): **JAPAN.** Hakone, in rupibus regionis montanae, 1866-74, *P.A.L. Savatier 602* (P 71659 image; isolectotype: P 711660 image). Protologue: "Hab. in rupestribus regionibus montanae: in jugo Hakone (Savatier, n. 602). Fl. Aug. Sept." The protologue also cites a collection by Tanaka (P-2 sheets images).

Japan. Triploid clones occur at low frequencies among diploids in Kanagawa Prefecture (Matsuda & Shibata 1978). Figures 7-9, 10.

5. ***Cardiagyris komonoensis*** (Makino) Nesom, **comb. nov.** *Aster komonoensis* Makino, Tokyo Bot. Mag. 12: 65. 1898. *Doellingeria komonoensis* (Makino) Nesom, Phytologia 75: 457. 1993. **TYPE: JAPAN.** Prov. Ise: Mt. Komono-yama, Aug 1889, *M. Miyoshi s.n.* (herb. Sc. Coll. Imp. Univ. Tokyo, not seen). Makino noted that "Prof. M. Miyoshi once figured and described in

this Magazine as above quoted, but with no scientific name." Bot. Magaz., Tokyo, II. p. 71, tab. V. 1888 (reproduced in Fig. 11).

Japan. Figures 11-13.

## B. LEAF BLADES NARROWLY LANCEOLATE, PETIOLES GRADUALLY DELIMITED

6. ***Cardiagyris rugulosa*** (Maxim.) Nesom, **comb. nov.** *Aster rugulosus* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 15: 226. 1871. *Doellingeria rugulosa* (Maxim.) Nesom, Phytologia 75: 456. 1993. **TYPE: JAPAN.** Yokohama, 1862, *C.J. Maximowicz 14501* (holotype: LE presumably, not seen; isotypes: GH, K, M, MO, NY, P-3 sheets, US; images of all). Only the MO sheet, with a handwritten label, has the number 14501.

*Aster rugulosus* var. *shibukawaensis* Kitam. & Murata, Acta Phytotax. Geobot. 19: 69. 1962. **TYPE: JAPAN.** Honshu, Prov. Totomi, Shibukawa, Inasatyo, Inasagun, 23 Sep 1959, *G. Murata 13105* (holotype: KYO, not seen but presumably the plant shown in Fig. 8 (photo) of the protologue).

Murata (1962) noted in the protologue that var. *shibukawaensis* is distinguished by hirsute and more branched stolons, more robust stems, and shorter and sometimes bracteate peduncles. Descriptions and photos of var. *shibukawaensis* are posted here: <<http://mikawanoyasou.org/data/sibukawasirogiku.htm>> and <<https://www.botanic.jp/plants-sa/sibuka.htm>>. The variety is included in lists of threatened Japanese plants but it is not clear that its taxonomy has been critically examined. It was not treated in the account by Ito and Soejima (1995), even in synonymy.

Japan. Figures 14, 15.

- Cardiagyris* × *sekimotoi*** (Makino) Nesom, **comb. nov.** *Aster sekimotoi* Makino, J. Japanese Bot. 7: 10. 1931. *Doellingeria sekimotoi* (Makino) Nesom, Phytologia 75: 457. 1993. **TYPE: JAPAN.** Prov. Shimotsuke, Mt. Kasakake, *H. Sekimoto s.n.* (holotype: KYO, not seen). The description has this: "Leaves elliptical-ovate to broadly lanceolate, ... cuneate towards the base," but Makino noted that "This species is very closely allied to *A. scaber* Thunb., having the non-cordate and depressed-dentate leaves."

*Aster* × *hashimotoi* Kitamura, Acta Phytotax. Geobot. 3: 130. 1934. **TYPE: JAPAN.** Prov. Ohmi, Hondo, Gamogun, Ichinebemura, Fuseno-tame, 10 Sep 1933, *Ch. Hashimoto s.n.* (holotype: KYO, not seen). Described by Kitamura as a hybrid, *Aster scaber* × *Aster rugulosus*.

*Cardiagyris* × *sekimotoi* is morphologically intermediate between *C. scabra* and *C. rugulosa*. Saito et al. (2007) showed that hybrids have low pollen fertility and exhibit additivity in ITS sequences, possessing nucleotide polymorphisms at 22 substitution sites, at positions where parents differ. Parents and hybrids are diploid. The hybrids occur at low frequency, hybrid swarms are absent, and they are "likely the result of repeated, reciprocal hybridizations."

7. ***Cardiagyris sohayakiensis*** (Koidz.) Nesom, **comb. nov.** *Aster sohayakiensis* Koidz., Tokyo Bot. Mag. 37: 56. 1923. *Doellingeria sohayakiensis* (Koidz.) Nesom, Phytologia 75: 456. 1993. **TYPE: JAPAN.** Wakayama (Kii), Doro-Haticho, 29 Jul 1922, *G. Koidzumi s.n.* (KYO, not seen).

*Aster ohtanus* Makino, J. Jap. Bot. 3: 18. 1926. **TYPE: JAPAN.** The protologue cited three collections from the same locality: Prov. Kii: Doro-hatchô, on rocks, Oct 1922 and Sep 1924", *U. Ôta s.n.* and 8-9 Sep 1924, *T. Makino s.n.* (not seen, photo of inflorescence in the protologue).

Japan, narrowly endemic to the Wakayama and Nara prefectures (Kii Peninsula). Figure 16. Makino noted in the protologue that "This species is closely allied to *Aster rugulosus* Maxim., and yet they grow at quite different localities." Distinctions in the couplet below are from Ito and Soejima (1995).

1. Peduncle 5–10 cm long, ebracteate; disc corollas 6–8 mm long ..... ***Cardiagyris rugulosa***  
 1. Peduncle 2–4 cm long, bracteate; disc corollas 4–5 mm long ..... ***Cardiagyris sohayakiensis***

8. ***Cardiagyris dolichophylla*** (Y. Ling) Nesom, **comb. nov.** *Aster dolichophyllus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 357. 1985. **TYPE: CHINA. Guangxi.** Longshenging Shan Village (25° 48'05" N, 110° 00'15" E), 830 m, 14 Oct 1955, *Guangfu Forest District Collecting Team 1056* (IBK image).

Guangxi, narrowly endemic. Illustrations: Fig. 516 in Flora of China (Chen et al. 2011); Fig. 6 in Zhang et al. (2019); Fig. 6 in Z. Li et al. (2020). Specimen images through Chinese Virtual Herbaria (website: National Plant Specimen Resource Center). Figures 18-20.

9. ***Cardiagyris huangpingensis*** (W.P. Li & Z. Li) Nesom, **comb. nov.** *Aster huangpingensis* W.P. Li & Z. Li, Phytotaxa 433: 242. 2020. **TYPE: CHINA. Guizhou.** Qiandongnan Miao and Dong Autonomous Prefecture, Huangping County, Grand Feiyun Canyon, 26° 55'06" N, 108° 01'53.10" E, riverbanks in a valley, 650 m, 13 Sep 2017, *LWP-LZ1709-015* (holotype HNNU, Fig. 17; isotypes: *LWP-LZ1709-006*, *LWP-LZ1709-007*, and *LWP-LZ1709-008*, all HNNU).

Guizhou, apparently known only from the type locality. Rocky stream banks at 650–680 meters. Illustrations: Fig. 5 in Z. Li et al. (2020). Figure 17.

1. Blades of proximal leaves lanceolate with acute to acuminate apex, 10–17 cm long, similar distally; phyllaries thin-herbaceous, loose and spreading, middle with ciliate-eglandular margins; disc flowers (26–)30–44, collecting appendages oblong-triangular ..... ***Cardiagyris dolichophylla***

1. Blades of proximal leaves obovate with rounded to obtuse apex, 3–7.5 cm long, becoming narrowly oblanceolate to lanceolate distally; phyllaries thickened, rigid and tightly appressed, middle with glandular margins; disc flowers 16–28, collecting appendages triangular-deltate ..... ***Cardiagyris huangpingensis***

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Figure 1. *Cardiagyris scabra*. Siberia. Shvedchikova s.n. (MW).





Figure 2. *Cardiagyris scabra*. Siberia. Dudov 2016\_S\_041 (MW).





Figure 3. *Cardiagyris scabra*. Japan. Photo by Masashi Igari, Plants Index Japan.





Figure 4. *Cardiagyris scabra*. Top: Japan, photographer unknown. Bottom: Manchuria, Amur, detail from type material of *Biotia discolor*, Maack s.n. (GH).

Figure 5. *Cardiagyris marchandii*. China (Guangxi). K.J. Yan 451029130912015 (GXMG).





Figure 6. *Cardiagyris japonica*. Japan. Murata 18654 (US).



Figure 7. *Cardiagyris dimorphophylla*. Japan. Collector not specified, s.n. (US). This plant is close in morphology to the type.





Figure 8. *Cardiagyris dimorphophylla*. Japan. Asai 7411 (US).



Figure 9. *Cardiagyris dimorphophylla*. Japan. Collector not specified, s.n. (US).





Figure 10. Involucres and flowers. Top: *Cardiagyris japonica*. Bottom: *Cardiagyris dimorphophylla*.

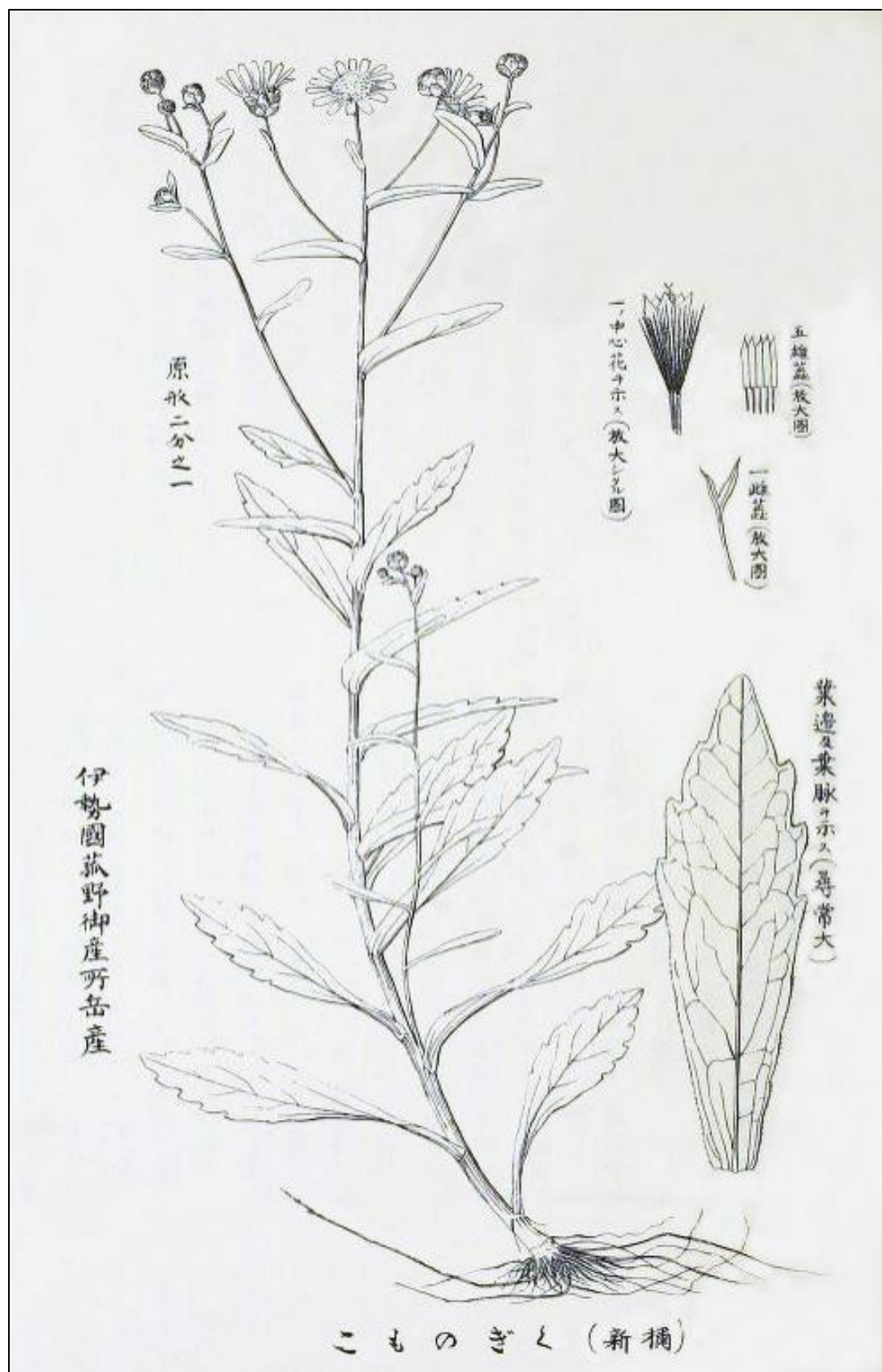


Figure 11. *Cardiagyris komonoensis*. Tokyo Bot. Mag. 2(15): 71, tab. 5. 1888.

Figure 12. *Cardiagyris komonoensis*. Japan. Saito 5533 (US).





Figure 13. *Aster komonoensis*. Mount Gozaisho, Komono, Mie Prefecture, Japan. Wikipedia.

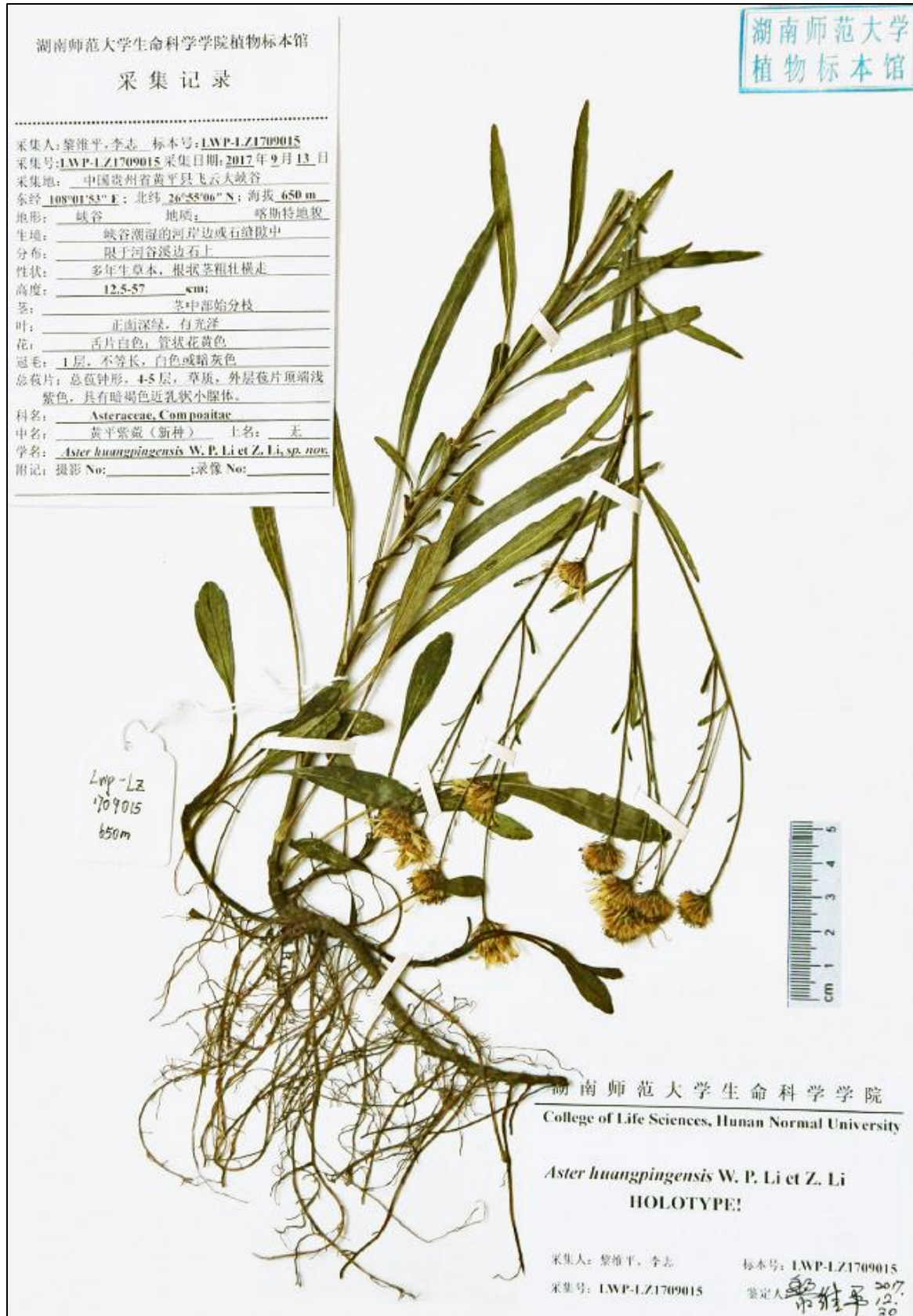
Figure 14. *Cardiagyris rugulosa*. Japan. Furuse 13044 (PE).



Figure 15. *Cardiagyris rugulosa*. Japan. Furuse 51333 (PE).

Figure 16. *Cardiagyris sohayakiensis*. Japan. Furuse 39493 (PE).



Figure 17. *Cardiagyris huangpingensis*. Holotype (HNNU), from Li et al. (2020).



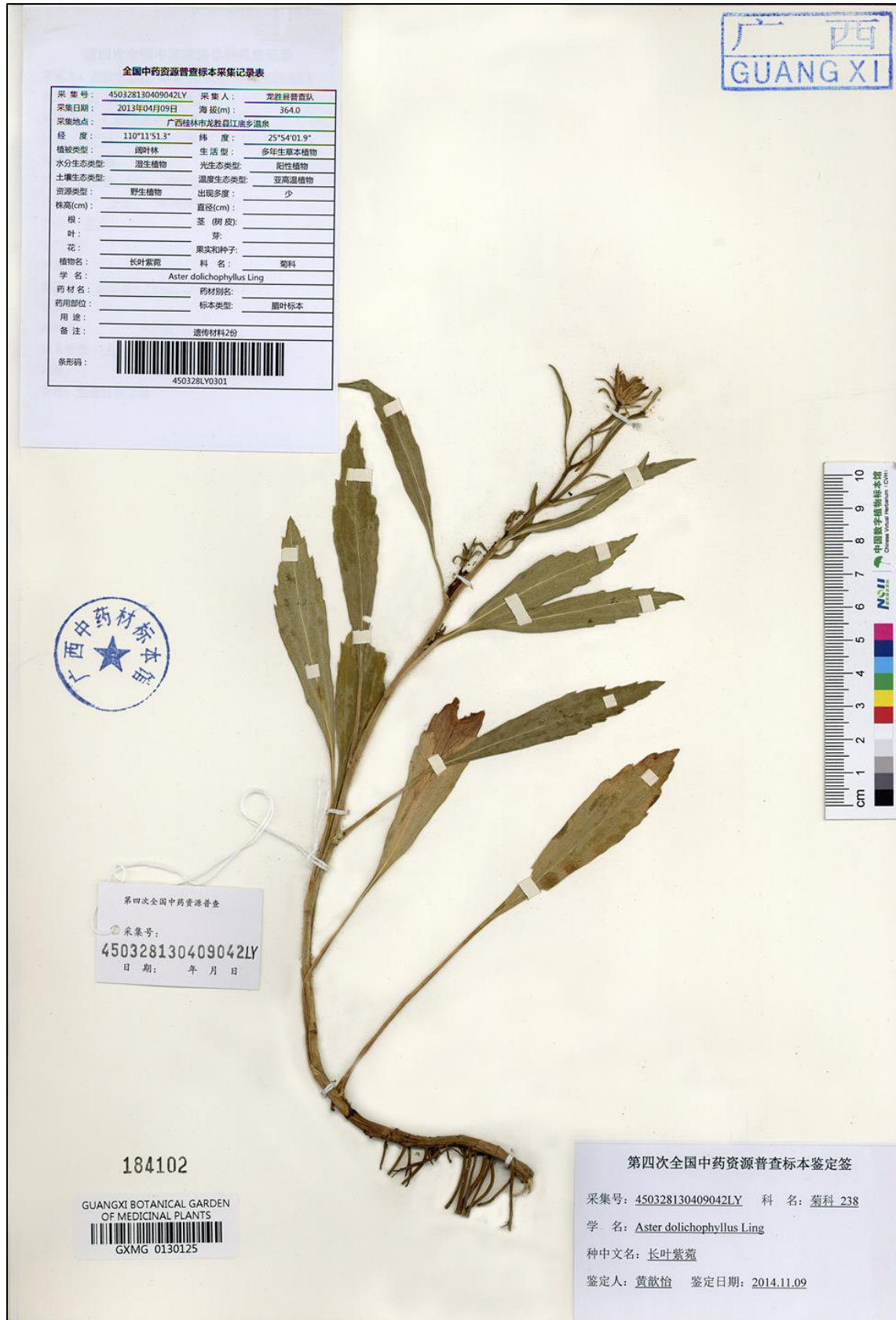
Figure 18. *Cardiagyris dolichophylla*. Guangxi. Longsheng County Census Team (GXMG).

Figure 19. *Cardiagyris dolichophylla*. Guangxi. Chen & Jiang EM271 (KUN).



Figure 20. *Cardiagyris dolichophylla*. PlantTong ZhiWuTong.com <<https://www.zhiwutong.com/latin/Compositae/Aster-dolichophyllus-Ling.htm>> The spreading, herbaceous, lanceolate phyllaries with sharply acute apices are unique among the species of *Cardiagyris*. See images contrasting involucre morphology of *C. dolichophylla* and *C. huangpingensis* in Z. Li et al. (2020, Fig. 6E).