THE GENUS LINDENIA (RUBIACEAE)

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THE SMALL RUBIACEOUS genus *Lindenia* Bentham is probably better known to plant geographers than to other botanists. Its strikingly disjunct distribution was first noted by Seemann (1862), but no serious attempt to explain this phenomenon has been made. Indeed, the genus has never been reviewed on a worldwide basis, although as many as six species have been proposed by various authors since its establishment in 1841. As treated here, *Lindenia* consists of three species, of which one is endemic to Central America, one to Fiji, and one to New Caledonia. A new form of the American species (*L. rivalis* f. *glabra*) is described, and two other taxa, *L. acuminatissima* Wernh. and *L. radicans* Wernh., are excluded from the genus.

Appreciation is expressed to the administrators of the following institutions who have made their herbarium collections available: Arnold Arboretum of Harvard University (A); Amherst College Herbarium (deposited at University of Massachusetts) (AC); Bernice P. Bishop Museum (BISH); British Museum (Natural History) (BM); Field Museum of Natural History (F); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); Department of Botany, University of Massachusetts (MASS); Missouri Botanical Garden (MO); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); Departments of Agriculture and Forestry, Suva, Fiji (SUVA); University of California, Berkeley (UC); and U. S. National Herbarium (US).

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Lindenia Bentham, Pl. Hartweg. 84. 1841, in Hooker's Icon. Pl. **5**: *t. 476*. 1842; Endlicher, Gen. Pl. Suppl. **2**: 53. 1842; Bentham, Pl. Hartweg. 351. 1857; Hooker in Bot. Mag. **87**: *t. 5258*. 1861; Seem. in Bonplandia **10**: 33. 1862, Fl. Vit. 128. 1866; Hooker f. in Bentham & Hooker f., Gen. Pl. **2**: 51. 1873; K. Schum. in Engler & Prantl, Nat. Pflanzenfam. IV. **4**: 37. 1891; Standley in N. Am. Fl. **32**: 92. 1921, in Field Mus. Nat. Hist. Bot. Ser. **18**: 1325. 1938; A. C. Smith in Jour. Arnold Arb. **36**: 288. 1955; Standley & Williams in Fieldiana **24**(11): 118. 1975.

Siphonia sensu Bentham, Pl. Hartweg. 84. 1841, non D. Rich. ex Schreber (1791).

Riverine shrubs with stipulate, petiolate leaves; leaf blades chartaceous and drying dark, often red-brown above, paler beneath, acute to

attenuate at base and decurrent on petiole, acute to somewhat acuminate and often asymmetric at apex, with entire, revolute margin, the costa conspicuous, plane to somewhat raised and canaliculate above, prominent and rounded beneath, the secondary nerves 5–10 per side, plane to prominulous above, sharply elevated beneath, the tertiary nerves and veinlets immersed to somewhat prominulous beneath; inflorescences terminal, congested, appearing fundamentally cymose, invested with bracts and bracteoles, these conspicuous, puberulent on both surfaces, chartaceous; calyx limb with 5 essentially free lobes; corolla hypocrateriform, the tube elongate, the limb spreading, 5-lobed, the lobes sinistrorsely contorted in bud, entire; stamens 5, attached at corolla throat and alternate with lobes, the anthers exserted, subsessile, recurved, capped by the short apiculate connective, dehiscing longitudinally; hypanthium strongly 5-angled; ovary 2-celled, capped by a 2-lobed dome-shaped disk; ovules numerous, as many as one thousand in each locule, attached to an elongate central placenta; style filiform, the stigma exserted, clavate, bifid above middle; fruit an obovoid capsule surmounted by the persistent and narrowly decurrent calyx lobes, dehiscing septicidally along 2 sutures, the endocarp thin and bony; seeds small, essentially rhomboidal, the testa smooth.

The genus *Lindenia* was proposed by Bentham in *Plantae Hartwegianae* and was based on a K. T. Hartweg collection from Verapaz, Guatemala. Only one species, *L. rivalis*, was described; this is the type species. The name of this new American genus was first printed as *Siphonia*, but Bentham, shortly before the distribution of that fascicle of *Plantae Hartwegianae* (fascicle M, pp. 81–88), found that the generic name *Siphonia* had previously been employed in the Euphorbiaceae. Hooker (1873) and Standley (1921) have pointed out that the name *Lindenia* was holographically substituted in all copies of that fascicle of *Plantae Hartwegianae* before distribution, and their assumption that the name *Siphonia* was indeed scratched out in *all* copies is accepted here. In the copies consulted by me, this was found to be the case, and the effective publication of *Lindenia* by indelible autograph, as permitted by Article 29 of the *International Code of Botanical Nomenclature*, may be accepted. Standley (1921) suggested that there is no reason to cite "*Siphonia* Bentham" as a synonym of *Lindenia*, since the former name was never really published except as it has appeared in synonymy. However, if copies of *Plantae Hartwegianae* exist in which the name *Lindenia* was not substituted, then its effective publication on that date is questionable.[1] For this reason, *Siphonia* sensu Bentham is maintained in the present synonymy.

Even if *Lindenia* is not accepted as having been published by Bentham in 1841, it was described one year later by both Bentham and Endlicher. Their publications of *Lindenia* in the Rubiaceae predate the use of the same name by Martens and Galeotti in 1843 for a genus in the Nyctagi-

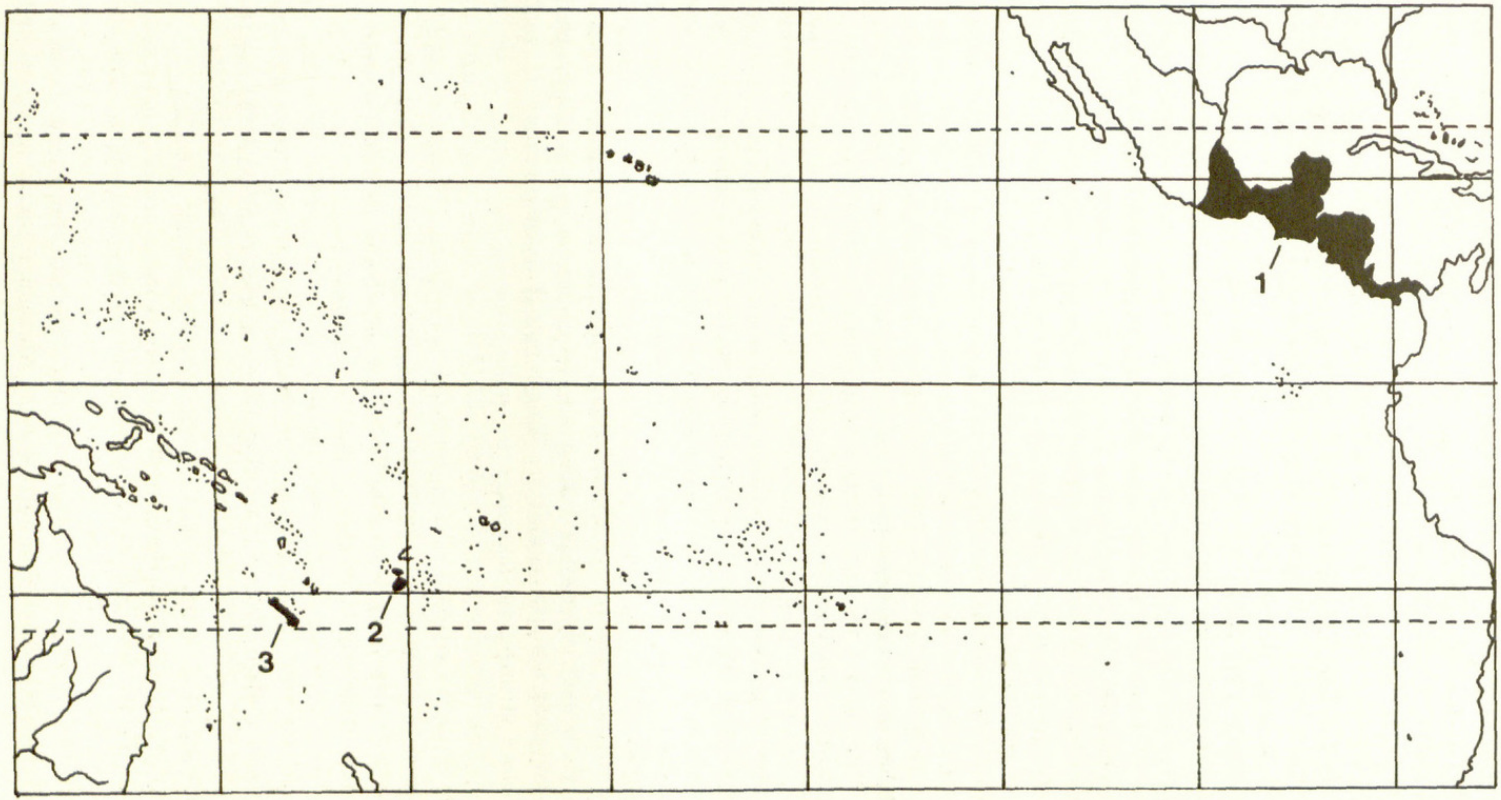
[1] It should be noted that in recent "facsimile" editions of *Plantae Hartwegianae* the handwritten name *Lindenia* has been removed and *Siphonia* restored.

naceae. The fascicle of *Plantae Hartwegianae* containing Bentham's printed correction of the name *Siphonia* to *Lindenia*, on page 351, did not appear until 1857.

As interpreted here, *Lindenia* comprises three species, *L. rivalis* Bentham (the type species), limited to tropical Central America, *L. vitiensis* Seem., endemic to Fiji, and *L. austro-caledonica* Brongn., endemic to New Caledonia (MAP 1). By previous authors the genus had been ascribed to the islands of Samoa and Tobago (Guppy, 1906; Hutchinson, 1969), but such reports are in error. *Lindenia* is most easily recognized by its exceptionally long corolla tubes, which are scarcely expanded at the throat (FIGURES 1, 13, 23). All of the species are characterized by occupying a strictly riverine habitat, or they are found growing in the middle of shallow watercourses.

Lindenia has been placed by all authors concerned with its taxonomy in the tribe Rondeletieae, and it agrees with other members of that tribe in a number of important characters. These include the capsular nature of the fruit (FIGURES 9, 10, 21, 31), the many ovules in each locule and their attachment to an elongate central placenta (FIGURES 6, 7), the nonalate seeds (FIGURES 11, 22, 32), the contorted aestivation of the corolla lobes (FIGURES 17, 27), and the subglobose, tricolporate pollen grains (FIGURES 8, 20, 30). Like other members of the Rondeletieae, *Lindenia* lacks raphid crystals, an important feature in the classification of the Rubiaceae according to Verdcourt (1958) and Bremekamp (1966). Significantly, *Lindenia* differs from certain other members of that tribe (*Rondeletia* in particular) by the contorted aestivation of its corolla. As usually interpreted, the tribe Rondeletieae contains genera with imbricate aestivation and genera with contorted aestivation. According to Bremekamp (1966), these two aestivation types are almost never encountered in closely related taxa, though imbricate and valvate aestivation are often closely associated. Further study may lead to the conclusion that the genera of the Rondeletieae with contorted corolla lobes should be removed from that tribe and placed elsewhere.

Although the association of *Lindenia* with the Rondeletieae may be uncertain, its closest relatives among extant genera are almost certainly American. Of the genera placed in the Rondeletieae by Schumann (1891), nearly all are American, and only a few extend into tropical and subtropical Asia. *Lindenia* is, however, the only member of the Rondeletieae with species indigenous in the Pacific. In general morphology, *Lindenia* approaches the Brazilian genus *Augusta* Pohl, but the latter genus, as pointed out by Bentham (1842), differs in its shorter, more expanded corolla tubes, shorter calyx lobes, more exserted stamens, axillary inflorescences, and loculicidally dehiscent fruits. A superficial resemblance is also shared between *Lindenia* and *Tocoyena* Aublet, a member of the Gardenieae. *Tocoyena*, however, with a baccate fruit and seeds embedded in a pulpy matrix, seems to be a firm member of the tribe Gardenieae and not closely related to *Lindenia*. A clarification of the relationships of *Lindenia* must await a detailed review of the tribe Rondeletieae.



MAP 1. Geographical distribution of *Lindenia* Bentham (Rubiaceae). 1 = *L. rivalis* Bentham; 2 = *L. vitiensis* Seem.; 3 = *L. austro-caledonica* Brongn.

The relationships of the Fijian flora are now fairly well known, owing primarily to the work of Dr. A. C. Smith. This flora is, in large part, derived from Indo-Malesian elements, and no transpacific migrations are thought to have been involved (Smith, 1955). The only exceptions to these observations occur in the predominantly American genera *Lindenia* and *Stillingia* L. (Euphorbiaceae). Similarly, *Lindenia* and *Epistephium* Kunth (Orchidaceae) form a puzzling American element in the New Caledonian flora (van Balgooy, 1971).

Concerning the widely disjunct distribution (MAP 1) of *Lindenia*, only two explanations seem possible. Either the disjunction is the result of chance long-distance dispersal, or the taxon was once continuous over an intervening land or insular area and has become restricted to now isolated populations. A third alternative, that human agency was involved, may definitely be excluded in the present case, since the New World and Old World portions of the genus have distinctive characteristics that could not have evolved in the immediate past.

There is little evidence to support the transpacific dispersal of *Lindenia* as an explanation of its present disjunct range. Although seeds of *Lindenia* are able to float in seawater by means of the crisp, air-filled outer tissues, it seems unlikely that these small seeds would be able to remain afloat for a sufficiently long time as to allow transportation over such a distance by ocean currents. Hypotheses have also been advanced (Guppy, 1906) that seeds of *Lindenia* may have become attached to the feet of migratory water fowl, but the smooth, rhomboidal seeds (FIGURES 11, 22, 32) show no obvious means by which they might become attached to the feet or plumage of such birds. Indeed, transpacific migrations must have been rare or nonexistent, since so few other genera have a pattern of disjunction like that of *Lindenia* (van Balgooy, 1971).

Unfortunately, nothing is known about the pollination biology of this genus. With such exceedingly long corolla tubes, it seems likely that flowers of *Lindenia* are visited by long-tongued lepidopterans. If such insects were at one time necessary for pollination in this genus, it seems unlikely that long-distance dispersal could have been possible without the concomitant dispersal of the required pollinators. However, certain moths already adapted to a pollination syndrome similar to that of *Lindenia* flowers may have been established in the Pacific before the arrival of *Lindenia* populations in Fiji or New Caledonia.

The most convincing argument against the transpacific dispersal of *Lindenia* is the fact that members of this genus are unknown from any intermediate archipelagoes. If its dispersal was the result of avian migrations, *Lindenia* might be expected to occur on other islands of the Pacific where appropriate habitats exist. Such, however, is not the case.

The hypothesis that *Lindenia* once occupied a much wider geographical area than it does today is more credible. It is easy to imagine that the small seeds were dispersed by wind, water, or even birds over short distances. After its origin somewhere on the American continent, *Lindenia* may have become established northward to Mexico and southward through

South America to the West Antarctic archipelago, and then westward to New Zealand, New Caledonia, Fiji, and possibly other islands of the southwestern Pacific, assuming that climatic conditions were favorable for such migration in the not too distant past. As mentioned above, all species of *Lindenia* are ecologically restricted to a habitat along the banks of rivers and streams. Such restriction was probably disadvantageous to *Lindenia* species as climatic changes and competition from other species were experienced. This strict habitat requirement, in conjunction with drastic climatic changes, was also probably in great part responsible for the extinction of *Lindenia* in South America, the West Antarctic archipelago, New Zealand, and other islands which at one time may have supported populations.

The Pacific and American species of *Lindenia* have so many characters in common, characters not shared with any other genus, that they seem to form a remarkably unified taxon in spite of their geographical disjunction. Such characters as the elongate, hypocrateriform corolla, the essentially free, subulate calyx lobes with glands near the base within, the frutescent habit, and the strict riparian habitat make *Lindenia* an easily recognized genus. It seems best, therefore, to maintain all three species within *Lindenia*, but to indicate their relationships by the recognition of two sections. As here interpreted, sectional distinctions are correlated with geographical distribution not because a long-distance-dispersed Pacific element was able to diverge rapidly from its American ancestor, but because the American and Pacific populations may represent the near-extreme ends of a once long, attenuate range. Divergence of the Pacific and American species would seem, therefore, to have been a slow process and the result of a gradual expansion of the area of *Lindenia* around the southern boundary of the Pacific. The similarity between the New Caledonian and Fijian species reflects their comparatively recent divergence at the younger end of this once continuous range.

Key to the sections

Stipules usually persistent, to 10 mm. long when mature, fused at base and forming a shallow cup surrounding the branchlet, gradually tapering toward apex into a sharply pointed acumen; style puberulent over basal half with thin, white, spreading hairs 0.3–0.7(–1.2) mm. long; valves of fruit often twisting strongly after dehiscence. ..... Sect. Lindenia.

Stipules caducous, 11–25 mm. long when mature, elliptic to lanceolate to oblanceolate, not obviously fused at base, acute to rounded at apex; style glabrous or with a few minute, scattered hairs about 0.1 mm. long; valves of fruit not twisting strongly after dehiscence. ..... Sect. Pacifica.

Lindenia Bentham sect. **Lindenia.**

This, the first of the two sections here recognized, is monotypic, containing only the type species of the genus.

1. **Lindenia rivalis** Bentham, Pl. Hartweg. 84. 1841.

Shrub to 2 m. high, generally puberulent with white to stramineous hairs or glabrous, the branchlets subterete, 1.2–2.8 mm. in diameter toward apex, brown or often black, smooth or swollen at nodes; stipules usually persistent, interpetiolar, membranaceous, entire, to 10 mm. long when mature, fused at base and forming a shallow cup surrounding the branchlet, gradually tapering toward apex into a subulate acumen up to 5 mm. long, puberulent within and without with appressed, white to stramineous hairs up to 0.6 mm. long, these sometimes few and restricted to base or acumen or adaxial surface only; petioles stout, semiterete to canaliculate, 2–16 mm. long, 1.4–2 mm. broad; leaf blades lanceolate to elliptic to oblanceolate, 3.2–17.6 cm. long, 1–3(–4.2) cm. broad, the upper and lower surfaces glabrous to puberulent with scattered hairs, or these restricted to base and costa; domatia absent; inflorescences 1–7-flowered, the peduncle up to 1 cm. long or essentially none, the bracts usually trifid, 4.2–9.2 mm. long, 1.8–2.8 mm. broad at base, acuminate at apex, the bracteoles subulate to lanceolate, 1.5–6.8 mm. long, 0.5–1.2 mm. broad at base, acuminate at apex, the pedicels slender, 3.6–8.6 mm. long, gradually broadening into the hypanthium; calyx lobes subulate to linear-lanceolate, (7.6–)10–22 mm. long, 0.8–1.8(–2.8) mm. broad, usually acute to long-acuminate at apex, entire, chartaceous to subcoriaceous, puberulent on both surfaces with scattered, stramineous hairs about 0.2 mm. long, these longer and denser at base of lobes within and partially concealing as many as 20 reddish, multicellular glands, each up to 0.3 × 0.1 mm.; corolla tube (8–)10.2–16.4 cm. long, 1.4–2.6(–3.4) mm. broad at middle, puberulent to tomentose without with white to stramineous hairs up to 0.7 mm. long, glabrous within, the corolla limb spreading, 2.6–6.8(–8) cm. broad, the lobes ovate to elliptic to lanceolate, 12–32(–38) mm. long, 4.8–14(–16) mm. broad, rounded to acute to acuminate at apex, densely puberulent to somewhat strigillose within with scattered hairs up to 0.3 mm. long, densely puberulent to tomentose without; anthers oblong-linear, 8.6–11.8(–14.2) × 0.9–1.3 mm., glabrous to glabrescent with a few scattered hairs; hypanthium 4–8.5(–10) mm. long, 2.6–4.6 mm. broad at apex, usually densely puberulent with spreading, stramineous hairs up to 0.3 mm. long; style 10.6–15.4 cm. long, about 0.5 mm. broad, puberulent over lower half with spreading hairs 0.3–0.7 (–1.2) mm. long, the stigma 5.4–9(–12.5) × 0.8–1.8 mm., up to 6 mm. broad when the lobes are spread apart; fruits (14–)18–26.2 mm. long, 9–12 mm. broad, drying brown, becoming black, the valves obviously twisting after dehiscence, the endocarp thin and bony; seeds 1–1.5 mm. long, 0.5–1.4 mm. broad.

Although *Lindenia rivalis* is variable in many characters, two forms based on features of indument are recognizable and appear to be reasonably distinct.

KEY TO THE FORMS OF LINDENIA RIVALIS

Indument consisting of white to stramineous hairs up to 0.6 mm. long variously present on young parts, branchlets, leaves, stipules, and inflorescences. . . . . 1a. f. *rivalis*.

Indument restricted to inflorescences and adaxial surfaces of stipules; all other parts glabrous. . . . . 1b. f. *glabra*.

1a. Lindenia rivalis f. rivalis. FIGURES 1–11.

Lindenia rivalis Bentham, Pl. Hartweg. 84. 1841, in Hooker's Icon. Pl. **5**: *t. 476*. 1842; Hooker in Bot. Mag. **87**: *t. 5258*. 1861; Hemsley, Biol. Centr.-Am. **2**: 26. 1881, in Ann. Mus. Nac. Rep. Costa Rica **1887**(2): 40. 1887; J. D. Smith, Enum. Pl. Guatemal. **2**: 30. 1891; Shannon in Intercont. Railway Commis. Rep. 1(2), Appendix **3**: 11. 1898; Pittier, Ens. Pl. Usual. Costa Rica, 109. 1908; Standley in N. Am. Fl. **32**: 92. 1921; Standley & Calderón, Lista Prelim. Pl. El Salvador, 210. 1925; Standley in Contr. U. S. Nat. Herb. **23**: 1358. 1926, in *op. cit.* **27**: 355. 1928; Standley & Record in Field Mus. Nat. Hist. Bot. Ser. **12**: 383. 1936, Standley in *op. cit.* **18**: 1325. 1938; Miranda, Veg. Chiapas Sec. Parte, 289. 1953; Pittier, Ens. Pl. Usual. Costa Rica. ed. 2. 147. 1957; Porter in Graham, Veg. & Veg. Hist. N. Latin America, 192. 1973; Standley & Williams in Fieldiana **24**(11): 119, *fig. 6*. 1975.

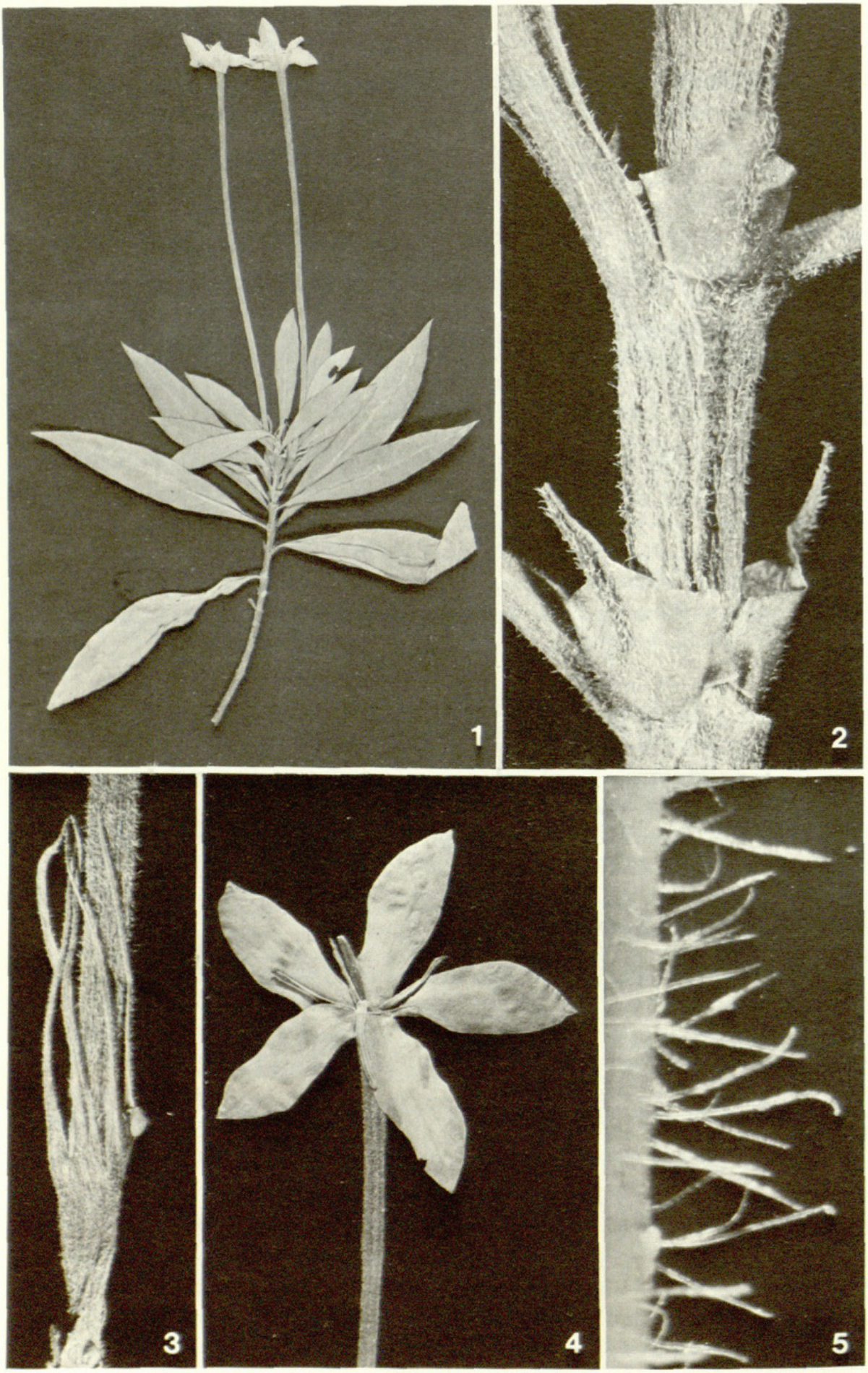
Siphonia rivalis Bentham, Pl. Hartweg. 84. 1841.

Lindenia acutiflora Bentham in Hooker's Icon. Pl. **5**: *t. 475*. 1842; Mart. & Gal. in Bull. Acad. Roy. Bruxelles **11**: 240. 1844; Hemsley, Biol. Centr.-Am. **2**: 26. 1881.

The typical form of *Lindenia rivalis* usually bears an obvious indument; at least the young parts, branchlets, leaves, and stipules are never glabrous all at the same time. The form includes nearly all of the neotropical collections of the genus.

TYPE LOCALITY. Bentham based the genus *Lindenia* solely on *Hartweg 581* from Guatemala, although Hooker was of the opinion that *L. rivalis* had been collected first by Linden on the banks of the Río Teapa, Mexico. One specimen, *Linden 331* (K), is labeled as having been collected at that locality in 1840, but since it was unmentioned in Bentham's original description, it cannot be considered a possible type of the species. Four examples of the Hartweg collection are known, two of these being at Kew. Only one of the two Kew specimens may be considered the holotype, the one bearing the stamp identifying it as having been a part of Bentham's own herbarium. The other Kew sheet was transferred from the Hooker herbarium in 1867. Only the "Bentham" sheet is labeled "Vera Paz, Guatemala" and bears the name "*Siphonia rivalis*."

The type of *Lindenia acutiflora* is *Linden 358*, the only collection cited by Bentham. This collection is known only from a single specimen at Kew labeled "Mexico. Vera Cruz. Puente nacional. 1838" and was originally part of the Hooker herbarium.



FIGURES 1–5. **Lindenia rivalis** f. **rivalis** (1 and 2 from *Tonduz 13947*, 3 from *Hinton et al. 13790*, 4 from *Deam 6124*, 5 from *Schipp 230*): 1, branchlet with

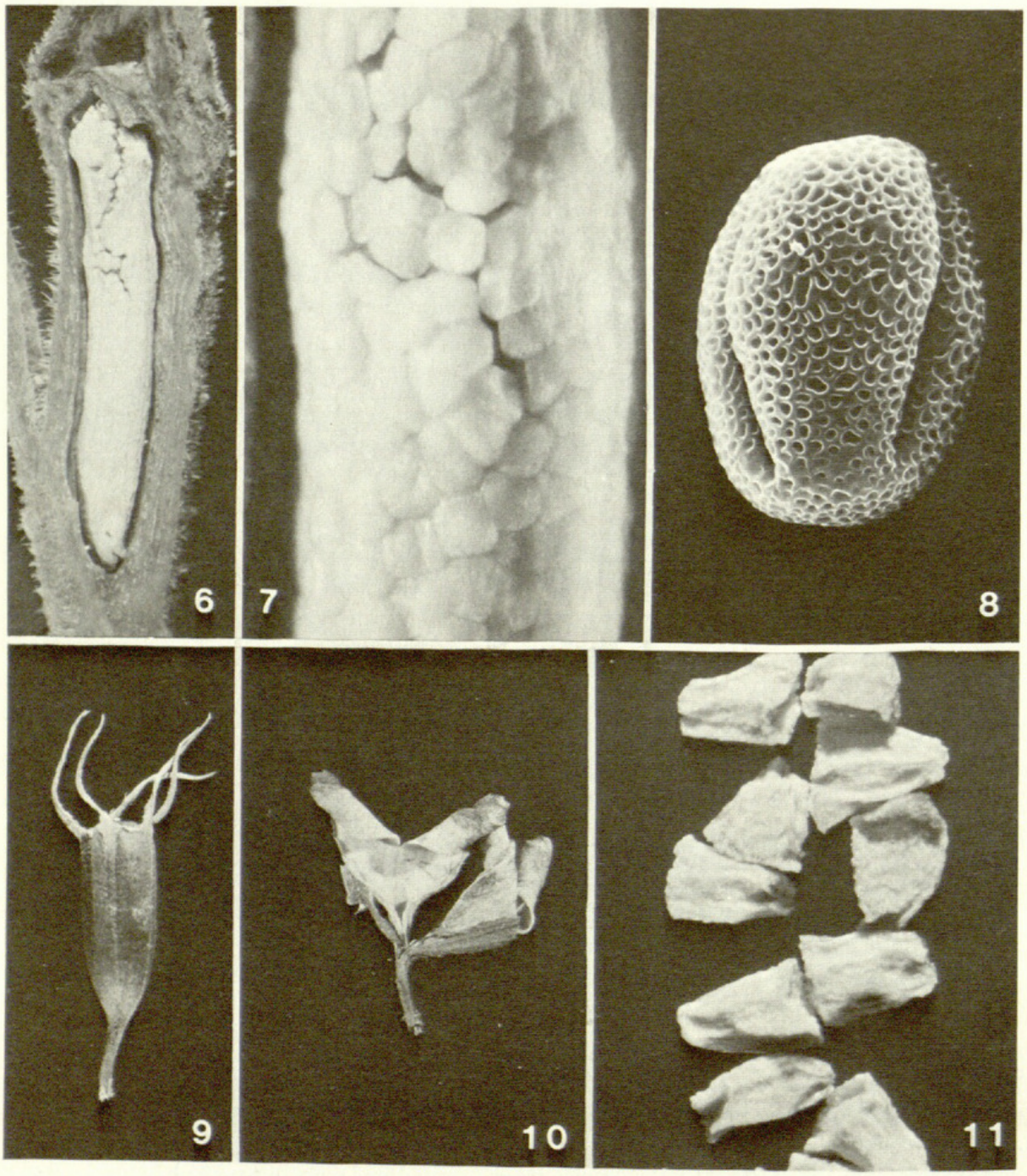
DISTRIBUTION. The typical form of *Lindenia rivalis* is restricted to tropical Central America and extends from northern Veracruz, Mexico, southward to Panama. It ranges in altitude from near sea level to 1500 m. Like other members of the genus, it is always found growing on the banks of rivers or, not uncommonly, directly in the waterways.

In habit, *Lindenia rivalis* f. *rivalis* is a shrub with leaves which are pale and silvery beneath. The plant is a showy one with long white corollas, these sometimes having a pinkish tube and white lobes. The flowers open in the morning and evening and are very fragrant. The fruits are also attractive; although at first green, they often become red and later brown. Flowering specimens of this form have been collected between April and July, rarely at other times of the year. Fruiting material is most commonly found between August and March.

LOCAL NAMES AND USE. The following names have been recorded: Mexico (Oaxaca), *pimenta de agua* (*Standley 1926*); Guatemala, *amalillo* (*Steyermark 42110*), *flore de Maria*, *mes-i-ha* (*Pittier 180*); Honduras, *chilca* (*Edwards 230*), *culebrita* (*Glassman 1553*), *lirio* (*Standley & Chacón 5606*); Costa Rica, *jarmincillo* (*Valerio 117*), *lirio de agua* (*Jimenez 507*); Panamá, *guabita de quebrada* (*Stern et al. 1788*). Herbarium specimens attest that this species was under cultivation as an ornamental shrub on the island of St. Vincent and at Kew in 1894. With its elongate, fragrant flowers and lush foliage, *Lindenia rivalis* probably has horticultural potential.

Mexico. MICHOACÁN: Pihuamo, *M. E. Jones 311* (MO, US); San José, Coalcomán, *Hinton et al. 13790* (F, GH, MO, NY, US); Las Minitas, Torrent de Chutá, *Langlassé 198* (GH, K, US). GUERRERO: Galeana, Atoyac, *Hinton et al. 14578* (K, NY, UC, US). OAXACA: Mogoñe, on F. C. N. T., *Orcutt 5206* (MO); Santo Domingo, *Nelson 2659* (GH, US); Paso Lagarto, Río Magdalena, Pochutla, *Conzatti, Reko, & Makrinius 3112* (GH). VERACRUZ: Río de los Pescados Baños del Carrizal, *Purpus 6099* (GH, MO, NY, UC); Colipa, *Karwinsky 1258* (F); Río Limón east of Paso de San Juan at Highway 140, *Maxwell 167* (MO); canyon 15 mi. southeast of Jalapa, *Barkley, Rowell, & Webster 2582* (F); Cavarrillo, *Pringle 8151* (AC, BM, F, GH, K, MO, NY, UC, US); Puente Nacional, *Linden 358* (K, holotype of *L. acutiflora*), *Purpus 13007* (F), *14240* (A, F); Barranca de Panoaya, *Purpus 8503* (UC); San Francisco, *C. L. Smith 1365* (F, NY, UC); vicinity of Veracruz, *Galeotti 1572* (K); Fortín, *Purpus 8483* (GH, MO, NY, UC, US); Orizaba, *Botteri* (GH); Cuitláhuac, *Matuda 1440* (A, K, MO, NY); Paso de Ingenio, *Calzada 323* (GH); Río de Santiago de Tuxtla, *Galeotti 2683C* (F); vicinity of Zacuapán, *Purpus 14270* (A, F); Los Tuxtlas, Ocotal, Chico, *Ross 208* (US); Dos Ríos, Río Grande de Cerro Gordo, *Ventura 2593* (NY); Paso del Correo, *Liebmann "Rubiaceae n. 5" (11419 or 11519)* (GH, K, MO, NY, US); Veracruz, without further locality, *Rosas 625* (A). TABASCO: Río Teapa, *Linden 331* (K). CHIAPAS: Sayula, *Juzepczuk 1353* (F); Javalinero, Palenque, Río Chacamax, *Matuda 3615* (A, F, K, NY); Río Despoblado near Comatitlán, *Matuda 17654* (F). MEXICO, uncertain locality ("Soledad"), *Wawra 156* (NY);

inflorescence, × ⅓; 2, branchlet showing stipules and petiole bases, × 4; 3, hypanthium, calyx, and base of corolla, × 2; 4, corolla limb with exserted stamens and stigma, × 1; 5, surface of style showing indument, × 40.



FIGURES 6–11. **Lindenia rivalis** f. **rivalis** (6 and 7 from *Calderon 2192*, 8 from *Pringle 8151*, 9 from *Lundell 6687*, 10 from *Bartlett 11767*, 11 from *Contreras 7047*): 6, longitudinal section of ovary showing elongate placenta, × 6; 7, portion of placenta showing ovules, × 30; 8, pollen grain, × 2000; 9, fruit prior to dehiscence, × 1; 10, dehisced fruit, × 1; 11, seeds, × 10.

without further locality, *Harris* (K), *"Herb. Pavon"* (BM), *Sartorius* (US). **Belize.** CAYO: Chiquibul Forest, east branch of Belize River at Guacamallo, *Brunt 2265A* (BM); between Benque Viejo and Melchor de Mencos, *Croat 24594* (MO); Río Mopan near Benque Viejo, 7 km. on Arenal Road, *Contreras 7047* (F, NY); vicinity of Cayo, *Lundell 6103* (F, GH, NY, US); vicinity of Vaca, *Gentle 2573* (A, F, K, MO); Mt. Pine Ridge, near Privation Creek, 12 mi. south of Cayo, *Burch 6255* (MO), Pinol Creek, *Proctor 30199* (BM), about 5 mi. south of Augustine Rd., 35 mi. south of San Diego, *Long 3237* (MO, NY), Río Frio, *Hunt 7063* (K), *Lundell 6687* (F, GH, NY, US); Mt. Pine Ridge, *Bartlett 11767*

(F, US); road to Augustine and San Luis, *Dwyer, Elias, & Maxwell 340* (MO); Hummingbird Highway, mi. 28, *Gentry 8587* (MO), mi. 30, *Gentry 8582* (MO), at Fairweather Creek, *Gentle 8833* (BM, F, NY, UC, US), at St. Margaret Creek, *Gentle 8722* (US); road to Church Yard, Beaver Dam Creek, *Campbell 109* (K); Big Creek, *Schipp 230* (A, BM, GH, K, MO, NY, UC, US). TOLEDO: Columbia Forest Station, *Dwyer 9846* (MO); San José, 1.5 mi. on road to Columbia Forest Station, *Gentry 8102* (MO); Moho River, *Peck 558* (GH, K); north side of Río Sarstún, *Harmon & Dwyer 2851* (MO). **Guatemala.** PETÉN: Dolores, 1 km. east of Río Ixcol, *Contreras 2409* (US). ALTA VERAPAZ: Chisaxte River below Secanquim, *Pittier 180* (US); vicinity of Finca Sepacuite, *Cook & Griggs 688* (US). BAJA VERAPAZ: 5 mi. southwest of Granados, *Harmon & Dwyer 3031* (NY); Verapaz, without further locality, *Hartweg 581* (K, holotype; isotypes at BM, K, NY). IZABAL: Jacoló, *H. Johnson 1137* (US); Lago Izabal between Punta dos Reales and Punta de Lechuga, *Steyermark 39616* (F); Montaña del Mico between mi. 49.5 and ridge 6 mi. from Izabal, *Steyermark 38603* (F); Río Oscuro, 0–8 km. southwest of Lake Izabal, *Jones & Facey 3492* (F, MO); Río Frio, *Steyermark 39921* (A, F, GH, NY). SAN MARCOS: Rodeo, Río Chol, *Lehmann 1452* (BM, F, US). RETALHULEU: Río Coyote, 4 km. west of Retalhuleu, *Standley 87425* (F, US), *87484* (F); road between Retalhuleu and Asintal, *Standley 87861* (F). QUICHÉ: without further locality, *Agilar 1244* (F). ESCUINTLA: Río Michatoya, *J. D. Smith 2051* (GH, K, US), *Standley 89095* (F), *89103* (F); Río Guacalate, *Shannon 3646* (GH, US). ZACAPA: Río Teculután, *Steyermark 42110* (F). SUCHITEPÉQUEZ: vicinity of Santo Domingo south of Mazatenango, *Standley 88908* (F, US). Guatemala, uncertain locality ("Agua Calientes"), *Deam 6124* (GH, MO, US). **El Salvador.** SANTA ANA: Río del Molino, *Calderón 2192* (NY, US). LIBERTAD: La Libertad, *Barclay 1130* (BM, US); Libertad, without further locality, *Barclay* (K). SAN VICENTE: vicinity of San Vicente, *Standley 21218* (GH, NY, US), *Standley & Padilla 3394* (F). **Honduras.** COMAYAGUA: vicinity of Siguatepeque, *Rodriguez 2684* (F), *Standley & Chacón 6117* (F); Rancho Grande, San Luis, *Edwards 230* (A, F, US); vicinity of Comayagua, *Standley & Chacón 5606* (F). FRANCISCO MORAZÁN: Santa Clara Creek, *Williams & Molina 10071* (F, GH, UC), *10348* (F); drainage of Río Yeguare, *Williams & Molina 15863* (BM, F, GH, US), *Glassman 1553* (F); vicinity of Zamorano, *M. & J. Hernández 5122* (F), *Rodriguez 166* (F); Río de la Orilla, Cerro Majicaran, *Molina 106* (F, GH, MO, UC, US); Río de la Orilla southeast of Zamorano, *Standley 22110* (F); Quebrada el Horno between Frijolar and Tabla Grande, *Molina 847* (F, GH). EL PARAÍSO: Quebrada de Dantas, 12 km. northeast of Yuscaran, *Molina 10044* (F, US); Río Choluteca near Oja de Agua, *Standley 4682* (F); 5 km. east of Oja de Agua, *Standley 4686* (F); Montaña Teupasenti between El Junquillo & Teupasenti, *Molina 11890* (F, NY); Sierra de La Villa Santa above Jacaleapa, *Williams 18162* (F, GH, US). OLANCHO: Río Wampú, Mata de Tarro, 18 km. northeast of Pisijire, *Nelson & Clewell 696* (MO). HONDURAS, without further locality, *Shakespear* (BM). **Nicaragua.** CABO GRACIAS A DIOS: Mosquito Coast, *Schramm* in 1924 (US); Río Sangsang, *Schramm 15* (F, US). MATAGALPA: Río Las Cañas 15 km. northeast of Matagalpa, *Williams, Molina, et al. 27531* (F, GH, NY, US). GRANADA: vicinity of Nandaime, Río Ochomogo, *Lévy 20* (F). NICARAGUA, uncertain locality ("Embarquito, Nialyo"?), *Seemann 111* (BM). **Costa Rica.** GUANACASTE: Sapoá, *Ørsted 11520* (US); between Sapoá and Tortuga, *"70"* (K); Las Cañas road 5 km. southeast of Liberia, *Harris 53* (F); Palo Verde research area E, *Frankie 168* (F, MO); Finca La Pacifica, Río Corubici 6 km.

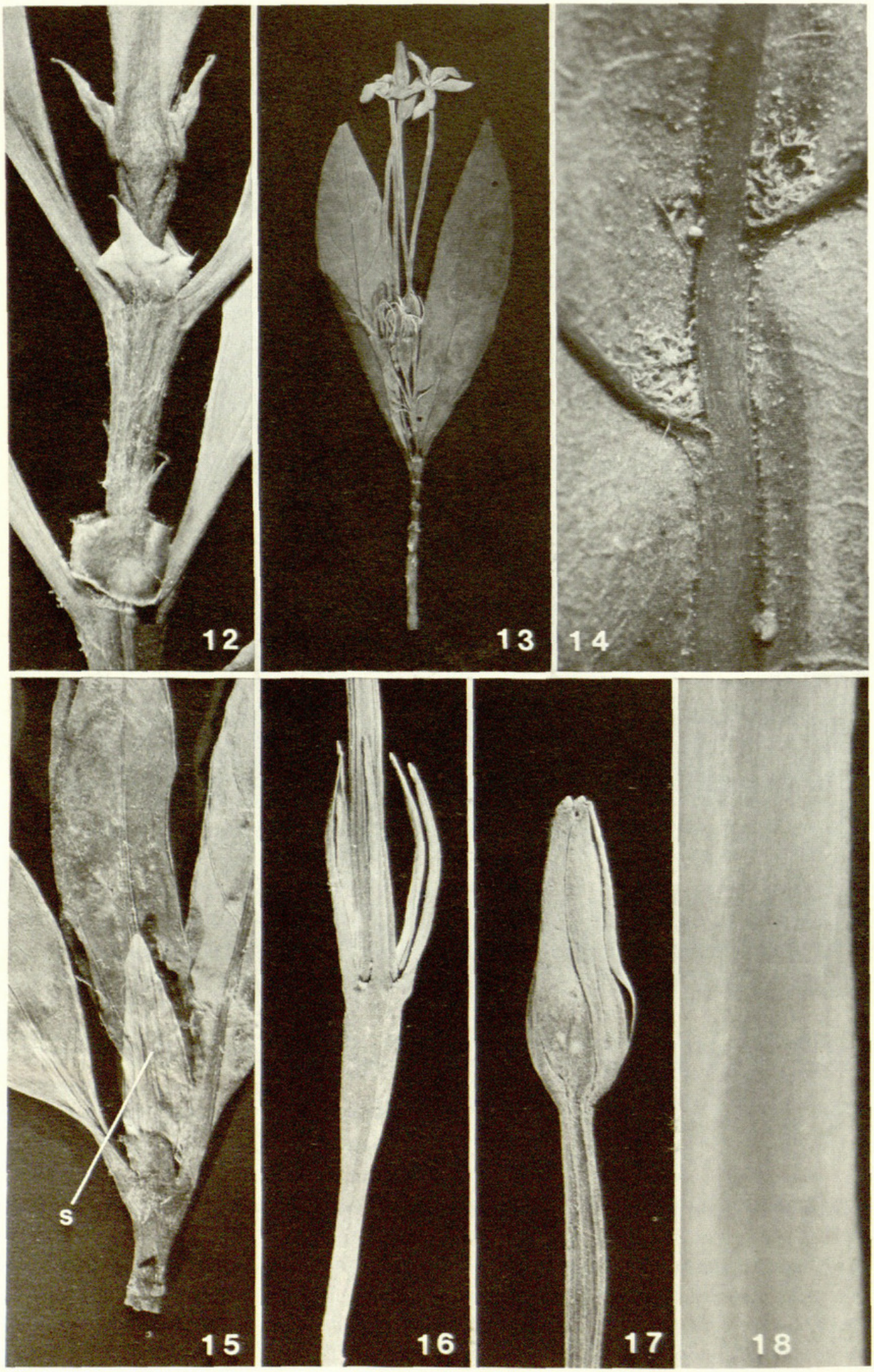


FIGURE 12. **Lindenia rivalis** f. **glabra:** branchlet with stipules and petiole bases, × 4, from *Steyermark 45966*. FIGURES 13–18. **Lindenia vitiensis** (13 from *Fiji*

northwest of Las Cañas, *Whitmore 20* (F, MO, NY); 22 km. along road to Finca Tenoria, *Croat 625* (MO); Hacienda Tenorio near La Pacifica, *Blum 366* (MO); Sandillal River north of Las Cañas, *Daubenmire 750* (F); Río Chiquito between Tilarán and Las Cañas, *Brenes 12702* (A, F, NY); vicinity of Tilarán, *Valerio 117* (US), *1144* (F), *Standley & Valerio 45678* (A, US); Nicoya, between Curime and Caimital, *Jimenez 507* (F); river at Nicoya, *Tonduz 13947* (BM, GH, K, US); La Colonia, Nicoya Peninsula, *Cook & Doyle 717* (US). PUNTARENAS: between Cascajal and Pigres, *Holm & Iltis 263* (BM, F, NY). **Panamá.** HERRERA: vicinity of Las Minas, Río Las Trancas, *Stern, Eyde, & Ayensu 1788* (MO, US). PANAMÁ: Río Bayano above confluence with Río Chepo, *Duke 3984* (MO); Chagres River, vicinity of Alhajuela, *Pittier 3521* (BM, GH, NY, US); Río Diablo, *Mayo 633* (MO); vicinity of Pacora, *Allen 3452* (BM, F, NY); upper Río Mamoni, *Pittier 4483* (BM, F, GH, NY, US); Río Canita near Jenine, *Duke 3842* (MO); Río Pasiga above waterfall on second main fork, *Gentry 2298* (MO); Río La Maestra, *Allen 24* (A, F); Utibé, *Maurice 759* (US). CANAL ZONE: Road K-6, east of Arriján, *Croat 15036* (GH, MO, NY); Road K-9, vicinity of Río Cocoli, *Stern, Chambers, Dwyer, & Ebinger 7* (GH, MO, UC, US); Road K-9, *Dwyer 3008* (MO); Río Aqua Salud between Frijoles and Pipeline Road, *Foster & Kiester 1951* (GH, NY). DARIÉN: Río Morti, Drill Site 7, *Duke 14208 (3)* (F, MO, NY). **Unknown locality.** "P. H. 23/8/12" (K). **Cultivated plants.** GUATEMALA: *"Stove — July — 1894"* (K). ST. VINCENT: cultivated shrub at Government House, *Powell 28* (K).

In the morphology of its vegetative and reproductive parts, the typical form of *Lindenia rivalis* is quite variable. Particularly noticeable is the range in the size and shape of the leaves and their indument, as well as the distribution of the leaves on the branchlets, i.e. whether they are crowded toward the tips of the branchlets or whether they are more equally spaced. Correlating with general robustness is the size of the inflorescences and the individual flowers. Bentham distinguished *L. acutiflora* from *L. rivalis* on the basis of such features, as well as the more densely pubescent lower surfaces of the leaves, the small size of the leaves, and the more acute apices of the corolla lobes. With many more collections now available for comparison, the type specimen of *L. acutiflora* readily falls within the continuum of variation ascribable to *L. rivalis* f. *rivalis* and cannot be satisfactorily separated from that taxon.

1b. Lindenia rivalis f. glabra S. Darwin, f. nov. FIGURE 12.

Lindenia rivalis sensu J. D. Smith, Enum. Pl. Guatemal. 3: 39. 1893; non Bentham.

Frutex idem ac forma typica sed indumenti restrictione ad inflorescentias et stipulae paginas interiores differt.

Dept. Agr. 2288, 14 from *Seemann 217*, 15 from *Fiji Dept. Agr. 2153*, 16, 17, and 18 from *Fiji Dept. Agr. 2288*): 13, branchlet with inflorescence, × ⅓; 14, abaxial surface of leaf blade showing axils of secondary nerves with domatia, × 10; 15, apex of branchlet showing stipule and young leaves, × 2; 16, hypanthium, calyx, and base of corolla, × 2; 17, corolla lobes in bud, × 2; 18, surface of style, × 40. (s = stipule.)

TYPE LOCALITY. Chicomucelo ("Chicomuselo"), Chiapas, Mexico; type, *Matuda 4449*.

DISTRIBUTION. This essentially glabrous form of *L. rivalis* is known from localities in Mexico, Guatemala, and Costa Rica. In its altitudinal range, habit, ecology, vegetative and floral morphology, and probable reproductive biology, the new form is similar to the typical form.

LOCAL NAMES AND USE. As far as is known, this taxon is not distinguished by Central Americans from *L. rivalis* f. *rivalis*, and the names and use ascribed to the typical form also pertain to f. *glabra*.

Mexico. TABASCO: Tenosique, *Matuda 3493* (A, F); Río Teapa (Río Morelia) at Teapa, *Gilly & Hernandez 273* (GH). CHIAPAS: Chicomucelo, *Matuda 4449* (US 2087017, holotype; isotypes at A, F, MO, NY); Santa Margarita, *Mell 2025* (NY, US); Chiapas, without further locality, *Ghiesbreght 860* (GH). **Guatemala.** PETÉN: Río Machaquila north of El Cambio, *Steyermark 45966* (F, US). QUEZALTENANGO: Río Ocosito, *Heyde & Lux 2753* (GH, K, MO, NY, US). **Costa Rica.** GUANACASTE: Los Conventillos, *Tonduz 2672* (US); vicinity of Las Cañas, Finca La Pacifica, Río Tenorio, *Daubenmire 647* (F); Finca La Pacifica, northwest of Las Cañas, Río Corobici, *Opler 945* (F, MO).

As stated above, *Lindenia rivalis* f. *glabra* is distinguished by the restriction of the indument to the inflorescences and inner surfaces of the stipules. Amid the wide range of variation encountered in the species as a whole, this feature may seem insignificant, but the glabrous specimens appear to be sufficiently distinct to warrant their recognition as comprising a separate form. In considering what rank to assign this taxon, one may note that the Mexican and Guatemalan collections come from a fairly discrete area within the range of the species as a whole, but the occurrence of essentially identical plants in Costa Rica suggests that the glabrous condition is likely to be encountered throughout the range of the species. Therefore, the rank of *forma* seems more logical than the rank of *varietas*, which might imply a degree of geographic isolation.

Lindenia Bentham sect. **Pacifica** S. Darwin, sect. nov.

Frutices stipulis caducis, demum 11–25 mm. longis, ellipticis vel oblanceolatis, basim versus non manifeste connatis, ad apicem acutis vel rotundatis; stylo glabro vel cum pilis paucis et dispersis plus minusve 0.1 mm. longis; fructu post dehiscentiam non valde torto.

Of the two species placed in *Lindenia* sect. PACIFICA, the Fijian species, *Lindenia vitiensis* Seem., is designated the type.

KEY TO THE SPECIES OF SECT. PACIFICA

Domatia consisting of tufts of stiff hairs always present on the lower surface of leaf blades in axils of secondary nerves; inflorescences 13- or 14-flowered; interior of corolla tube puberulent with scattered hairs; corolla lobes

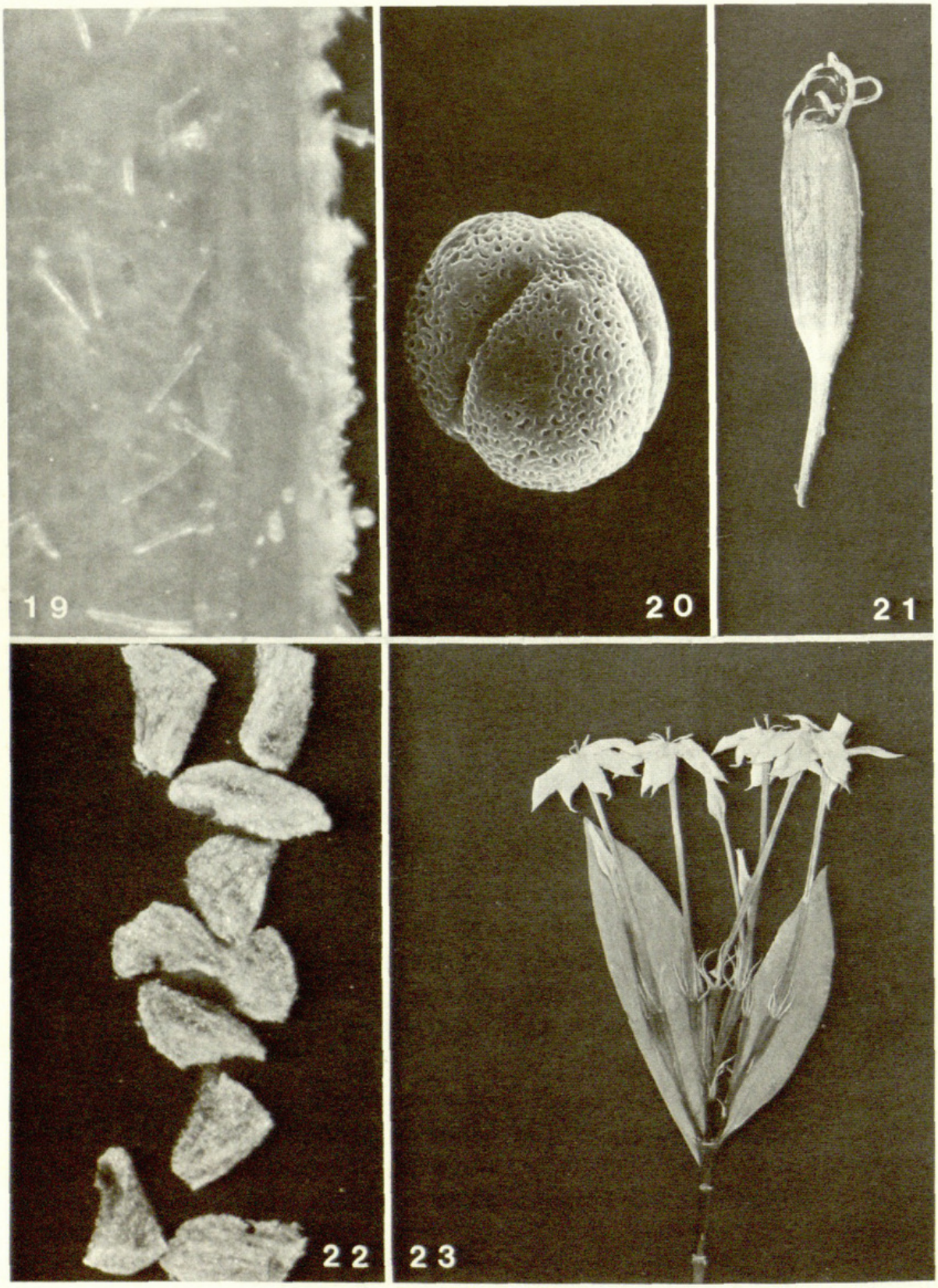
acute at apex; stipules usually more than 4.5 mm. broad when mature. . . . . 2. *L. vitiensis.*

Domatia rarely present on the lower surface of leaf blades; inflorescences 1–9-flowered; interior of corolla tube glabrous; corolla lobes sharply acute to acuminate at apex; stipules usually not more than 4.5 mm. broad when mature. . . . . 3. *L. austro-caledonica.*

2. **Lindenia vitiensis** Seem. in Bonplandia 9: 256. 1861. *nomen nudum*; A. Gray in Proc. Am. Acad. Arts 5: 318. 1862 (Jan.). *nomen nudum*; Seem. in Bonplandia 10: 33. *t. 8.* 1862 (Feb. 15); A. Gray in Bonplandia 10: 36. 1862; Seem. Viti, 438. 1862, Fl. Vit. 128. *pl. 24.* 1866, *op. cit.* 430. 1873; Drake, Ill. Fl. Ins. Mar. Pac. 186. 1890; A. C. Smith in Jour. Arnold Arb. 36: 288. 1955; J. W. Parham, Pl. Fiji Islands, 195. *fig. 71.* 1964, ed. 2. 276. *fig. 83.* 1972.

FIGURES 13–22.

Riverine shrub to 2 m. high, glabrous apart from the puberulent young parts and inflorescences, the branchlets subterete, 2.6–4.5 mm. in diameter toward apex; stipules soon caducous, interpetiolar, elliptic to oblanceolate, entire, 11–25 × 4.7–5.5 mm. when mature, broadly cuneate at base, obtuse to rounded at apex, finely puberulent with scattered hairs up to 0.2 mm. long or these slightly longer and persistent on branchlets above stipule scar; petioles stout, semiterete or canaliculate, 3–13 mm. long, 1.2–2.7 mm. broad; leaf blades lanceolate to narrowly elliptic, (6–)11–16 cm. long, (1.4–)2–3.8 cm. broad; domatia present, conspicuous on lower surface of leaf blades in axils of secondary nerves as tufts of stiff hairs 0.1–0.3 mm. long; inflorescences usually 3-branched, 13- or 14-flowered, the peduncle up to 1 cm. long or essentially none, the bracts usually paired at each node, trifid or divided to base and appearing whorled, 5.2–12.2 mm. long, 1–2 mm. broad at base, acute to acuminate at apex, the bracteoles undivided, linear-lanceolate to subulate, 2.8–8.1 mm. long, 0.3–1 mm. broad at base, acute to acuminate at apex, the pedicels slender, 1.2–2 cm. long and gradually broadening into hypanthium; calyx lobes subulate, 8–16 mm. long, 0.7–1.5 mm. broad at base, acuminate at apex, entire, chartaceous to subcoriaceous, puberulent without with hairs up to 0.1 mm. long and slightly longer ones within partially concealing as many as 10 yellowish, multicellular glands 0.2 × 0.1 mm. at base of each lobe, or glands absent; corolla tube 9.3–10.5 cm. long, 1.6–2.3 mm. broad at middle, puberulent without with hairs up to 0.2 mm. long, these more scattered within, the corolla limb 3–3.3 cm. broad, the lobes entire, ovate, 12–17 mm. long, 5–10 mm. broad, acute at apex, puberulent to tomentose within with densely matted, tangled hairs, densely puberulent without; anthers oblong, about 6 × 1.2–1.7 mm., glabrous; hypanthium 10–14 mm. long, 2.5–4 mm. broad at apex, strongly 5-angled, puberulent with short white to stramineous hairs; style 10–10.5 cm. long, about 0.5 mm. broad, glabrous or with occasional scattered hairs up to 0.1 mm. long, the stigma 3.2–4.1 × 1–1.6 mm., essentially glabrous; fruits 22–28 mm.



FIGURES 19–22. **Lindenia vitiensis** (19 and 20 from *Seemann 217*, 21 and 22 from *Horne 186*): 19, longitudinal section of corolla tube showing inner (left) and outer (right) indument, × 70; 20, pollen grain, × 2000; 21, fruit prior to dehiscence, × 1; 22, seeds, × 10. FIGURE 23. **Lindenia austro-caledonica:** branchlet with inflorescence, × ⅓, from *Buchholz 1290*.

long, 8–11 mm. broad, drying brown, becoming black, the valves not obviously twisting after dehiscence; seeds about 1.5 × 1 mm.

TYPE LOCALITY. Seemann's original description of *Lindenia vitiensis* was based entirely on his own collection, *Seemann 217*. The species was reported to occur on the islands of Ovalau and Viti Levu, but the holotype bears only the notation "Navua River," which is probably the correct locality of the type collection. It is possible that Seemann observed this species growing on Ovalau, although no collection of *L. vitiensis* can be unequivocally assigned to that island. The isotypes are labeled "Viti or Fiji Islands," without further locality.

DISTRIBUTION. Judging from the comparatively few collections available, *Lindenia vitiensis* is a relatively rare species known with certainty only from the islands of Viti Levu and Vanua Levu. It is found growing in forests from near sea level to an altitude of about 100 m. and, significantly, always along the banks of streams. Its habit is that of a shrub up to 2 m. high with sweet-scented, cream-colored flowers. Flowering specimens have been collected in December, fruiting material in March.

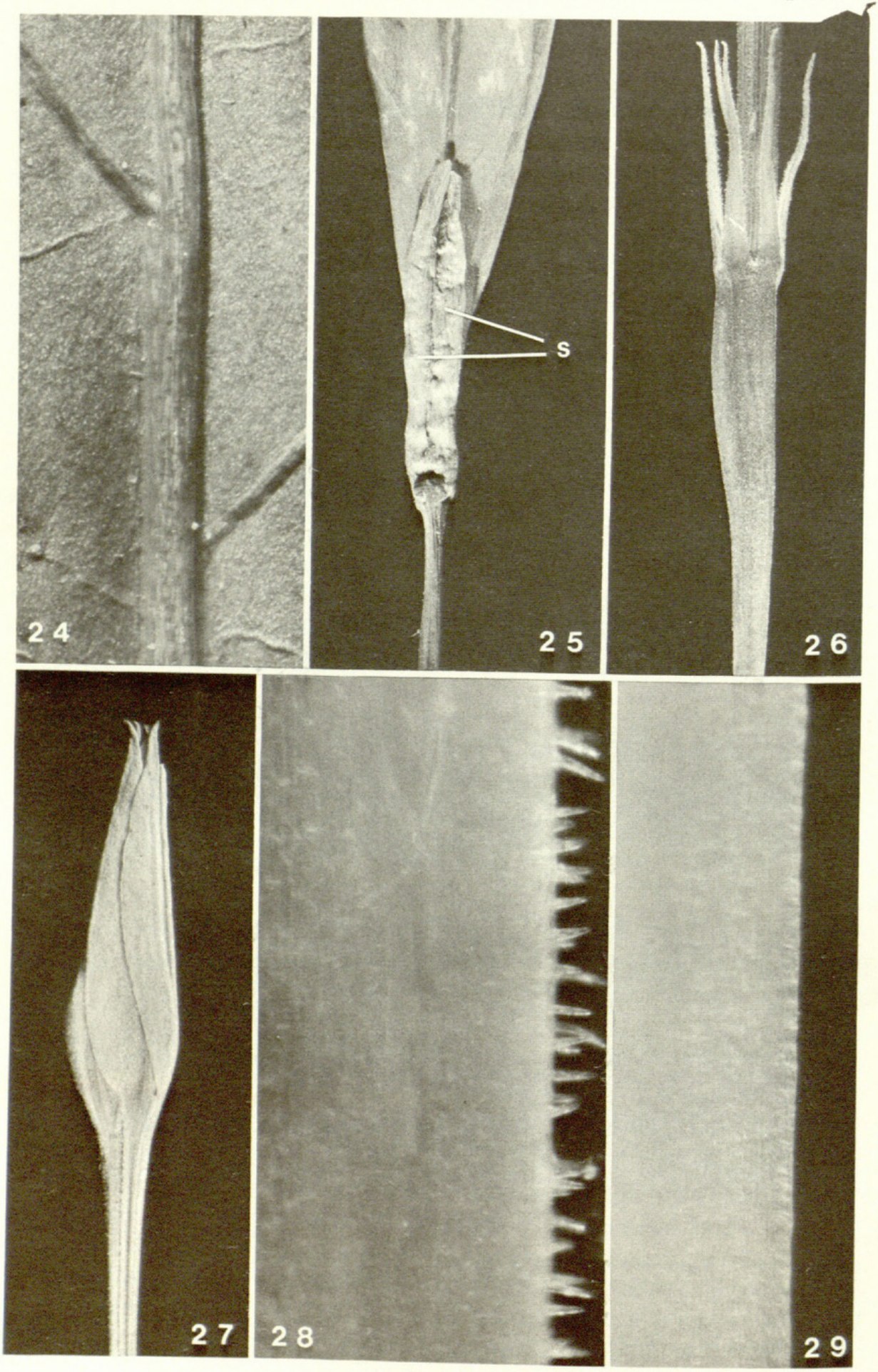
A single Graeffe collection of *Lindenia vitiensis* bears "Samoa" as a locality, but this species is otherwise unknown in that archipelago. It is likely that this Graeffe collection was mislabeled and is really of Fijian origin. Graeffe collected in southeastern Viti Levu, and in several other instances it is reasonably certain that specimens labeled "Samoa" actually came from Fiji (A. C. Smith, pers. comm.).

LOCAL NAMES. Seemann records the name *mbore ni wai*, a reference to the riverine habitat of this species. Variations include *mborewai* (*Fiji Dept. Agr. 2153*), *mbuarewai* (*Fiji Dept. Agr. 2288*), *mborewa*, and *mbua-siu*, the last two variants having been noted by Parham in the citations listed above.

Fiji. Viti Levu. SERUA: Navua River, *Seemann 217* (K, holotype; isotypes at BM, GH). NAITASIRI: Ndrauniwalai, Waindina River, *Fiji Dept. Agr. 1811* (BISH, SUVA), *2153* (BISH, K, MASS, SUVA, US). VITI LEVU, without further locality, *Graeffe* (K). **Vanua Levu.** MBUA: Nakorotiki, *Fiji Dept. Agr. 2288* (BISH, MASS, SUVA). FIJI, without further locality, *Horne 186* (K), *964* (GH, K). **Uncertain locality** ("Samoa"). *Graeffe* (BM).

The morphology of the stipules (FIGURE 15), the lack of a pronounced stylar indument (FIGURE 18), and the finely reticulate tectum of the pollen grains (FIGURE 20) indicate that this taxon is much more closely related to the New Caledonian species than to the American one. Seemann (1862) originally distinguished the Fijian species from *Lindenia rivalis* by the lack of pubescence on the lower surfaces of the leaf blades and by minute characters of the calyx lobes. Evidently he was unaware that the caducous stipules of *L. vitiensis* differ strongly from those of *L. rivalis*.

From *Lindenia austro-caledonica* the Fijian species is distinguished by the presence of domatia (FIGURE 14) on the lower surfaces of the leaf blades in the axils of the secondary nerves and by the blunter apices of the corolla lobes (FIGURE 17), a feature most easily seen when the flowers are in bud. In addition, the interior of the corolla tube (FIGURE 19)



FIGURES 24–29. **Lindenia austro-caledonica** (24 from *Schlechter 14992*, 25 from *C.B.I.B.S. 991*, 26 and 27 from *Buchholz 1290*, 28 and 29 from *Green*

is puberulent with scattered hairs in *L. vitiensis*, while it is glabrous in *L. austro-caledonica*.

3. **Lindenia austro-caledonica** Brongn. in Bull. Soc. Bot. France **12**: 407. 1865. FIGURES 23–32.

Lindenia vitiensis sensu Brongn. & Gris in Ann. Sci. Nat. Bot. V. **6**: 258. 1866; Zahlbruckner in Ann. K. K. Naturhist. Hofmus. **3**: 280. 1888; Guillaumin in Ann. Mus. Colon. Marseille II. **9**: 168. 1911; Schinz & Guillaumin in Sarasin & Roux, Nova Caledonia Bot. 234. 1921; Däniker in Mitt. Bot. Mus. Univ. Zürich **142**: 442. 1943; Guillaumin in Bull. Soc. Bot. France **91**: 12. 1944, Fl. Nouv.-Caled. 328. 1948, in Bull. Mus. Hist. Nat. (Paris) II. **21**: 118. 1949; non Seem.

Riverine shrub to 3 m. high, glabrous apart from the puberulent young parts and inflorescences, the branchlets subterete, 2.5–4.3 mm. in diameter toward apex; stipules caducous, interpetiolar, elliptic to lanceolate, entire, 13–22.6 × 1.2–4.5 mm. when mature, broadly cuneate at base or occasionally fused for about one-third their length and forming a sheath around the branchlet, acute to rounded at apex, finely puberulent with hairs up to 0.1 mm. long or these slightly longer and persistent on branchlets above the stipule scar; petioles stout, semiterete or canaliculate, 3–16 mm. long, 1.4–2.4 mm. broad; leaf blades lanceolate to narrowly elliptic to oblanceolate, (3.5–)7–14.8 cm. long, (0.7–)1.4–3.9 cm. broad; domatia only rarely present on lower surface of leaf blades in axils of secondary nerves as tufts of stiff hairs 0.1–0.3 mm. long; inflorescences usually 2- or 3-branched, 1–9-flowered, the peduncle up to 1.5 cm. long or essentially none, the bracts often paired at each node, somewhat to conspicuously trifid, 5.8–12.5 mm. long, 1.2–4.5 mm. broad at base, acute to acuminate at apex, the bracteoles undivided, subulate, 1.8–9.2 mm. long, 0.7–1.8 mm. broad at base, acute to acuminate at apex, the pedicels slender, 1.2–3 cm. long and gradually broadening into hypanthium; calyx lobes subulate, 9–15(–19) mm. long, 1–2.2 mm. broad at base, acuminate at apex, entire, chartaceous to subcoriaceous, finely puberulent without with hairs about 0.1 mm. long or glabrous, densely puberulent within with hairs up to 0.3 mm. long and partially concealing as many as 10 yellowish, multicellular glands about 0.2 × 0.1 mm. at the base of each lobe, or such glands absent; corolla tube 8.6–11.7(–12.3) cm. long, 1.4–2.5 mm. broad at middle, very finely puberulent without with hairs up to 0.1 mm. long, glabrous within, the corolla limb spreading, 2.9–5.3 cm. broad, the lobes oblong-elliptic to ovate, 15–27 mm. long, 4.2–10 mm. broad, sharply acute to acuminate at apex, densely puberulent to tomentose with matted, tangled hairs within, more finely puberulent without;

1317): 24, abaxial surface of leaf blade showing axils of secondary nerves, × 10; 25, apex of branchlet showing pair of stipules and basal portion of a young leaf, × 2; 26, hypanthium, calyx, and base of corolla, × 2; 27, corolla lobes in bud, × 2; 28, longitudinal section of corolla tube showing glabrous inner surface (left) and outer indument (right), × 70; 29, surface of style, × 40. (s = stipule.)

anthers oblong, 5.3–8 × 0.9–1.4 mm., glabrous; hypanthium 10–16 mm. long, 2.7–4.2 mm. broad at apex, puberulent with short white hairs; style 9.2–11.7 cm. long, about 0.5 mm. broad, glabrous, the stigma 2.5–5.4 × 1.2–1.8 mm., essentially glabrous or with minute, glandular hairs; fruits 20–32 mm. long, 8–10 mm. broad, drying dark brown, becoming black, not obviously twisting after dehiscence; seeds about 1–1.5 × 1–1.5 mm.

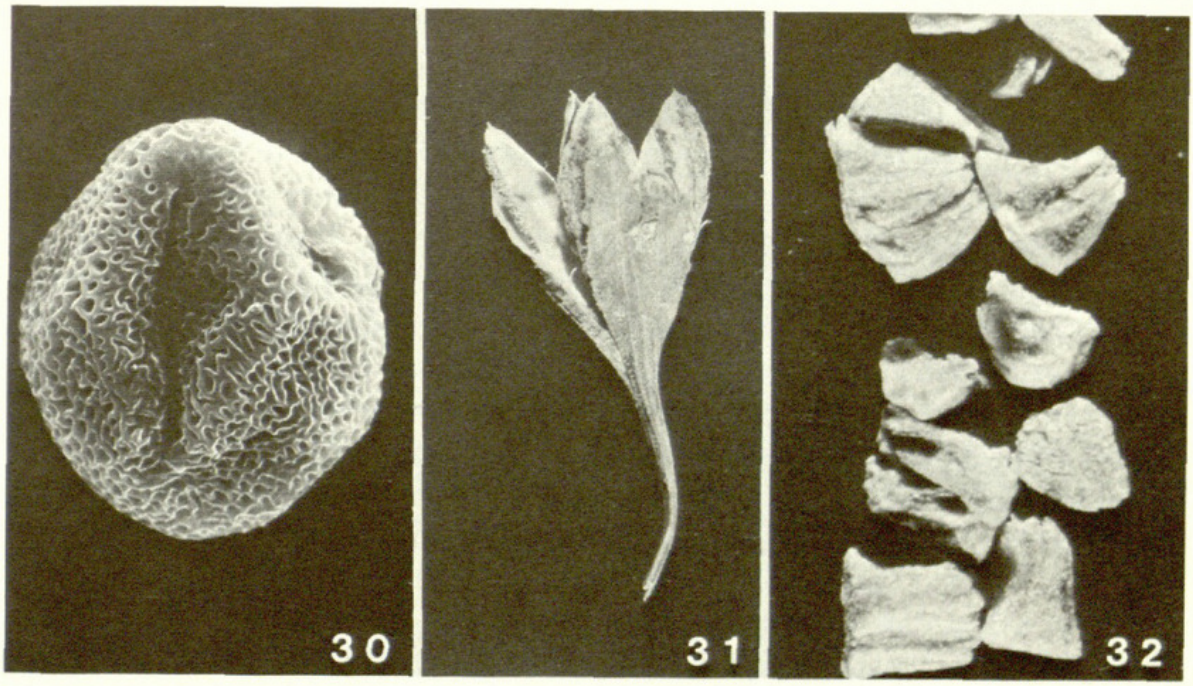
TYPE LOCALITY. Brongniart based *Lindenia austro-caledonica* on two collections which he cited as "habitat ad ripas rivorum Novae Caledoniae (Pancher, 1862); circa *Balade* (Vieillard, no. 651)." Of these two collections, specimens labeled *Vieillard 651* have been found scattered in European and American herbaria. It is important to note, however, that only two sheets (at K and P) are labeled as coming from the Balade locality cited by Brongniart. The remainder are labeled as having been collected at Wagap. In addition, the Balade sheets have the date "1855–1860" printed on their labels, whereas the Wagap labels read "1861–1867." It is probable, therefore, that *Vieillard 651* represents a mixed collection, the material having been gathered at different places and at different times. Evidently only the "Balade" specimens were available to Brongniart in 1865; these bear intact fruits, but the flowering material is poor.

The material collected by Pancher in 1862 is known definitely only from a single sheet (P), but because it consists of intact flowers as well as dehisced fruits, it seems the most appropriate lectotype and is here designated as such. Pancher's field label reads "Ourail — near (?) Kanala." Other Pancher specimens (at BM and K) are probably isolectotypes, although they are without collector's number and date.

DISTRIBUTION. Endemic to New Caledonia, but occurring throughout that island at elevations from sea level to about 375 m. Like the other taxa of *Lindenia*, this species is a shrub restricted to a riverine habitat. Flowering specimens have been collected between June and November; fruiting material has been found throughout the year.

New Caledonia. KOUMAC: Rt. 7, 16 km. north-northeast of Koumac, *Thorne 28117* (GH); road from Koumac to Balade, ascending first range of hills, *Green 1317* (A, K); 5 km. from Koumac on road to Ouégoa, *McKee 4715* (A, K). POUÉBO: Balade, *Vieillard 651*, 1855–60 (K, P); vicinity of Pouébo west of Colnett, near coast, *Webster & Hildreth 14804* (BISH). POINDIMIÉ: Wagap, *Vieillard 651*, 1861–67, (BM, F, GH, K, NY, P). CANALA: Canala, *Pancher* in 1862 (P, lectotype; probable isolectotypes at BM, K). MOINDOU: tributary of Rivière Boguen above waterfall at Tribu Katrikoin village on trail to Table Unio, *Buchholz 1290* (A, BISH, K, NY, UC, US). BOULOUPARI: Rivière Tahine, *Compton 1978* (BM). PAÏTA: mountains near Païta, *Schlechter 14992* (BM, K). DUMBÉA: Dumbéa Valley, north branch near river, *McKee 2480* (UC, US); Rivière Nondoué near airport, *Virot 312* (A); Rivière Nondoué, *Franc 629* (A, BM, K, NY, UC, US). NOUMÉA: near Nouméa, *Caldwell* (K). NEW CALEDONIA, without further locality, *C.B.I.B.S. 991* (K).

Brongniart, in the original description of this species, did not contrast it with the Fijian species which had been described by Seemann some



FIGURES 30–32. **Lindenia austro-caledonica** (30 from *Franc 629*, 31 from *McKee 2480*, 32 from *Vieillard 651* (1855–1860)): 30, pollen grain, × 2000; 31, dehisced fruit, × 1; 32, seeds, × 10.

three years earlier. Nor did Brongniart and Gris give any reason for the reduction of *Lindenia austro-caledonica* to *L. vitiensis* only one year after the publication of the former. As far as is known, all later authors have followed their example in considering the New Caledonian and Fijian *Lindeniae* as conspecific.

In fact, the magnitude of the differences between the two elements warrants the reinstatement of *Lindenia austro-caledonica* as a distinct species. The usual absence of domatia (FIGURE 24) in the New Caledonian species *versus* their presence in *L. vitiensis* is the most striking feature, although the occasional occurrence of domatia in New Caledonian plants may indicate that the presence or absence of domatia reflects the distribution of the presumed arachnid inhabitors rather than a genetic difference between the plant populations. However, the correlation of the usual absence of domatia in *L. austro-caledonica* with the glabrous interior of the corolla tube (FIGURE 28), the more acute corolla lobes (FIGURE 27), and the smaller stipules supports the conclusion that the New Caledonian and Fijian populations have diverged over a long period of time and should be considered distinct species.

EXCLUDED SPECIES

Lindenia acuminatissima Wernham in Jour. Bot. **52**: 227. 1914.

TYPE LOCALITY. Unknown.

Wernham based this species on a single specimen (K), which remains the only known collection. The type specimen bears a superficial resemblance to *Lindenia rivalis* in its somewhat elongate corolla tube and

sharply acuminate stipules, but in other characters it is quite different. Its corolla tube is not nearly as long as in true *Lindeniae*, and the calyx consists of six unequal lobes which are fused at the base into a distinct tube. The pubescence is also entirely different in that the hairs are much longer and stiffer. Wernham reported that the flowers are axillary, but in fact they are solitary and terminal on short axillary branchlets.

Although the limits of *Lindenia* might be extended to include Wernham's species, *Lindenia* is a much more uniform taxon if *L. acuminatissima* is excluded. The true taxonomic position of this collection is uncertain, and proper determination is difficult since its place of origin is unknown. The single specimen bears the notation "Gardenia mitis. Tobago Jasmine. Herb. Brown. (Barclay)?" The common name "Tobago Jasmine" hardly seems to be evidence that this plant was collected on the island of Tobago, and evidently there is also uncertainty as to whether or not it is a Barclay collection. Even if collected by Barclay, it may not be of Central American origin. Until more collections are available, it seems best to exclude this species from *Lindenia*.

Lindenia radicans Wernham in Jour. Bot. **52**: 226. 1914.

TYPE LOCALITY. This species is known only from the single type specimen, a Hartweg collection (K) made in 1839 but without a number. The holotype is labeled as having been collected at "Tocotepeque," Mexico; McVaugh (1970) has identified that locality as Jocotepec in the state of Oaxaca.

From other species of *Lindenia* this species differs in its long-petiolate, membranaceous leaves with much more broadly elliptic blades, the insertion of the anthers well within the corolla tube, the 4-parted corolla with a shorter tube, the unequal calyx lobes which may vary in number, and the much coarser indument consisting of longer, stiffer hairs. Unlike true *Lindeniae*, *L. radicans* is a recumbent shrub or woody vine. Wernham reported that elongate cystoliths are present in the membranaceous leaf blades. These are, however, the raised veinlets which give a rough texture to the surfaces of the leaves.

In the shape of the corolla and leaves, as well as in indument, *Lindenia radicans* is somewhat similar to *Tocoyena hirsuta* DC. from Brazil. In the latter species, however, the calyx is smaller and cupular. Until more collections are at hand, the position of this species cannot be assigned with certainty and it is best excluded from *Lindenia*.

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