

Sylvainia, a new monospecific genus within the subtribe Cephalanthinae (Rubiaceae, Naucleaeae)

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Abstract

Background and aims – The genus *Cephalanthus* belongs to the tribe Naucleaeae together with 26 other genera. Members of *Cephalanthus* mainly grow in temperate and subtropical wetlands in the Americas and Asia, but there is a single African species that is associated with forest margins and rocky outcrops in moist temperate grasslands. The genus comprises six species and was historically known to have species with a markedly disjunct distribution: three species are from the Americas: *C. glabratus*, *C. occidentalis*, and *C. salicifolius*; two species are from tropical Asia: *C. angustifolius* and *C. tetrandrus*, and one species is from tropical Africa: *C. natalensis*. Recent molecular phylogenetic studies have supported the monophyly of the genus, however, most of the morphological synapomorphies are absent in the only African species, which is sister to the remaining species of the genus. This work aims to provide a short taxonomic revision of the genus *Cephalanthus*, taking into consideration morphological aspects previously underestimated or not considered, and to describe a new monospecific genus based on comparative morphological analysis.

Material and methods – Vegetative and reproductive material from all the species of *Cephalanthus* were analysed following conventional taxonomy techniques.

Key results – We transferred *C. natalensis* to a new genus, *Sylvainia*. Morphological similarities and differences between *Cephalanthus* and the new genus are discussed. *Cephalanthus glabrifolius*, a poorly known species and previously considered a synonym of *C. tetrandrus*, is resurrected as a valid species, bringing the number of species in *Cephalanthus* to six again. All species are described, illustrated, and their known distributions plotted on regional maps.

Conclusion – The subtribe Cephalanthinae now has two genera, its type *Cephalanthus* with six species, and a new monospecific genus *Sylvainia* endemic to south-eastern Africa. Based on the amended description of *Cephalanthus*, now absent from Africa, the generic concept is substantially modified, being represented now by three American and three Asian species.

Keywords

Cephalanthinae, Cinchonoideae, Naucleaeae, new genus, revision, taxonomy

INTRODUCTION

The genus *Cephalanthus* L. belongs to the subfamily Cinchonoideae of the Rubiaceae family (Bremer et al. 1999). It is a pantropical genus with species that inhabit temporarily flooded, humid, or moist habitats. This genus belongs to the tribe Naucleaeae together with 26 other genera. Haviland (1897) diagnosed the tribe by having globular inflorescences with numerous flowers, a narrow infundibuliform corolla with a long tube,

imbricate or valvate lobes, exerted style, capitate entire or bilobed stigma, bilocular ovary, linear placenta, and one to numerous ovules. Haviland's concept was taken over by Schumann (1889). Ridsdale (1976) considered the tribe Naucleaeae, as diagnosed by Schumann (1889) or Haviland (1897), as a heterogeneous group, the spherical multiflorous inflorescences being the only character in common. He evaluated this character and segregated *Cephalanthus* in its own monogeneric tribe Cephalantheae Kunth.

Razafimandimbison and Bremer (2002) redefined the Naucleaeae tribe as a monophyletic group supported by the globose multiflorous inflorescences and epigynous nectaries deeply embedded in the hypanthium. According to their molecular and morphological analyses, *Cephalanthus* is again placed within Naucleaeae. The genus is currently accepted as the subtribe Cephalanthinae, which is considered, with high support, as a sister group to the rest of the genera of the tribe (Razafimandimbison and Bremer 2002; Löfstrand et al. 2014).

According to Ridsdale (1976), *Cephalanthus* comprises six species, three in America: *Cephalanthus glabratus* (Spreng.) K.Schum., *C. occidentalis* L., and *C. salicifolius* Bonpl.; two species in tropical Asia: *C. angustifolius* Lour. and *C. tetrandrus* (Roxb.) Ridsdale & Bakh.f.; and one African species: *C. natalensis* Oliv. This disjunct geographic pattern of the genus also holds for the distribution of the American species: *C. occidentalis* is found in North America (from Canada to Mexico), *C. salicifolius* in southern North America and Mesoamerica, while *C. glabratus* occurs in the southern cone of South America.

The delimitation of *Cephalanthus* has never been questioned, although Ridsdale stated, without arguments, that “the single African species seems to occupy an isolated position”. Razafimandimbison and Bremer (2002) pointed to aberrant morphological features, as did Löfstrand et al. (2014), who resolved *C. natalensis* as sister to the rest of the genus. Most of the morphological synapomorphies are absent in the African species.

More than four decades after Ridsdale’s revision, the need for an update is apparent, especially due to the results of the recent molecular phylogenetic studies. Numerous new collections are available, and some species were scarcely studied before (e.g. *C. glabrifolius* Hayata).

The present work aims a) to update the taxonomy of the genus *Cephalanthus*, especially with regard to aspects newly available or previously underestimated or not addressed (e.g. colleter type and distribution, fruit dispersal, habitat); b) to describe, document, and illustrate all taxa.

MATERIAL AND METHODS

Vegetative and reproductive material from all the members of *Cephalanthus* were analysed following conventional taxonomic methods. Herbarium specimens and nomenclatural types were examined from the following herbaria (acronyms according to Thiers 2023): AS, AU, BR, C, CEPEC, COR, CTES, ESA, F, FCQ, FLOR, G, G-DC, HAL, HUEFS, ICN, INPA, K, LIL, M, MBM, NY, SI, SP, SPE, USZ (personally visited herbaria), MO, MEXU, P, R, RB (loans), and AMD, APA, ASU, BOTU, CGMS, COR, E, FLOR, FURB, FUEL, GH, HAS, HAST, HCF, HDCE, HN, HPL, HRB, HUCS, HUEFS, HUEM, ICN, INPA, IIAM, JOI, JRAU, L, LD, LE, LINN, MPUC, MU, PACA, PRE, RE, TAI, TAIF, TDC, TEX, TI, UNOP,

UPCB, UMO, UFG, U, US, WAG, and YU (online databases). For each species, at least one specimen is listed per major political subdivision.

The species were studied using a Leica MZ6 stereo microscope; their characters were recorded by drawings made with a camera lucida from dried, rehydrated, or FAA preserved material (FAA: formalin/ethanol/acetic acid). Measurements were taken using a Schwyz digital calliper. The morphological descriptions follow Stearn (1983), including macro- and microcharacters.

RESULTS AND DISCUSSION

The subtribe Cephalanthinae

The taxonomic position of the species currently recognized as the subtribe Cephalanthinae was debated for many years (de Candolle 1830; Haviland 1897) until the study carried out by Razafimandimbison and Bremer (2002). Ridsdale (1976) considered that the species belonged to a monogeneric tribe Cephalanthaeae, a concept that was broadly accepted (Robbrecht 1988). Based on a tribal phylogenetic study, Razafimandimbison and Bremer (2002) confirmed the monophyly of this group, and they recognized it as a subtribe Cephalanthinae of a broadly defined tribe Naucleaeae. In their study, the subtribe Cephalanthinae shows an early divergence and is accepted as a sister to the remaining members. This hypothesis was later confirmed by an even larger sampling by Löfstrand et al. (2014), supporting the basal position, which is always resolved with high support. According to Löfstrand et al. (2014), Cephalanthinae is characterised by the combination of the following characteristics: 1-ovulate locules, young inflorescences with absence of calyptra bracts, and infructescences formed by schizocarps that separate into two indehiscent mericarps when dry. In the present work, we follow the classification proposed by Razafimandimbison and collaborators (Razafimandimbison and Bremer 2002; Löfstrand et al. 2014), with minor additions.

Delimitation of *Cephalanthus*

When Ridsdale (1976), Razafimandimbison and Bremer (2002), or Löfstrand et al. (2014) defined the genus *Cephalanthus*, most of the morphological diagnostic characters were absent in only one species, *C. natalensis*. Indeed, Razafimandimbison and Bremer (2002) maintained *Cephalanthus* sensu Ridsdale (1976) as a separate genus because it forms a strongly supported monophyletic clade, however, they emphasised that there is not a single morphological synapomorphy that unites *C. natalensis* and the American and Asian species. In recent years, we performed macro- and micromorphological, ontogenetic, anatomical, and taxonomic studies in order to survey the probable synapomorphies of the genus. Below, a summary is given with the main diagnostic

features of what we consider *Cephalanthus* s.s., which is composed of five previously recognised species (*C. glabratus*, *C. occidentalis*, *C. salicifolius*, *C. angustifolius*, and *C. tetrandrus*) and *C. glabrifolius* (here considered as a valid species). Ecological, reproductive, and vegetative characteristics are uniform in this group, in contrast to *C. natalensis*, which is addressed below.

Habit and vegetative characters

In *Cephalanthus* s.s., plants are always erect and much-branched. The leaves are opposite in case of wider blades (length/width ratio 2–2.5:1; with the exception of *C. occidentalis*, which can also be 3-verticillate), while in case of narrow blades (ratio 4–5:1), there are 3–4 leaves per node, pseudopetiolate (fusion of petiole and the stipular sheath). The foliar domatia are tufts of hair, pockets (*C. occidentalis*), or domatia may be absent in *C. angustifolius* (presence and type still to be confirmed by field studies). The leaves of *Cephalanthus* show adaptations to seasonal environments; some have typical hydromorphic traits (i.e. thin cuticle and cell walls, mesophyll with large intercellular spaces, and few trichomes), while others reflect adaptations to sunny habitats and/or tolerance to dry periods (heterobaric leaves) (Romero et al. 2019).

Colleters

All species have standard colleters, but it is possible to differentiate light and dark colleters. Light colleters are translucent and are found inside the stipule and calyx tube. Dark colleters are on almost all parts of the plants (leaves, bracts, bracteoles, stipules, calyx, and corolla). Romero et al. (2022b) studied the colleters in almost all subtribes of Naucleae and confirmed that the dark colleters are exclusive to *Cephalanthus* s.s., being absent in other taxa of the tribe (i.e. Adiniinae, Breoniinae, Mitragnyninae, Naucleinae, Uncarinae), including *C. natalensis*.

Inflorescences

The characteristic inflorescence of *Cephalanthus* is also the most constant character for the tribe Naucleae. The partial inflorescence is a globose/spherical glomerule, with the flowers closely packed on a hard receptacle. Individual flowers are subtended by 1–2 bracteoles, papery or somewhat fleshy, with mostly truncate apex, and the base subtriangular, linear, or oblanceolate. According to field observations and herbarium material, the partial inflorescences are arranged in complex inflorescences of variable patterns (Fig. 1A–G). Each complex inflorescence is in a terminal or axillary position. Since they are perennial plants, their reproductive buds produce new inflorescences at the end of winter or in early spring. The whole complex inflorescence falls off when the fruits become mature. This can be seen in the field, since the axes and bracts that support the partial inflorescences gradually change from green, yellowish-green, to chestnut before falling off. The simplest pattern is represented by 2–3 axes (A1 and A2), in terminal or axillary position, ending in apical glomeruli, supported

by 2–3 basal foliaceous bracts (Fig. 1A). Then, the number of glomeruli increases, and the branching becomes more complex, with two basal dichasial cymes (up to 7 in Fig. 1B). Inflorescences can have several whorls, two or three are shown in Fig. 1C and Fig. 1D. In the schematic representations A to D, the foliaceous bracts are in a basal position, however, in E to F, two or three whorls of bracts are observed (in Fig. 1E, bracts are indicated by br). At the base of the flowering axes, small projections represent reduced bracts (indicated by re-br in Fig. 1E).

Flowers

They are sessile, actinomorphic, tetramerous or pentamerous, and heterochlamydeous, with stylar pollen presentation. Flowers of *Cephalanthus* s.s. were described as morphologically perfect, however, Romero et al. (2022b) described cryptic dioecy for *Cephalanthus glabratus*. Each inflorescence has a single type of flower, staminate or pistillate. Staminate glomeruli are 15–20 mm in diameter and have 100 to 150 flowers on average, while the pistillate ones are smaller (10–14 mm in diameter) and have 70 to 100 flowers. Morphologically, staminate flowers differ in having a thin band of puberulous hairs on the inner surface of the corolla lobes, while they are pubescent in pistillate flowers. In the remaining species, flowers are apparently perfect, at least on herbarium material. All species share an infundibuliform or hypocrateriform corolla, uniformly whitish. Based on our studies, the internal distribution of the hairs proved to have taxonomic importance, which was scarcely addressed by previous authors (see the dichotomous key of *Cephalanthus*).

Pollen grains and orbicules

The pollen grains of *Cephalanthus* s.s. are uniform in shape, size, ornamentation, and colpi disposition. They are very small to small, circular to subtriangular in polar view and spheroidal in equatorial view, while the sexine has a transitional pattern, from reticulate to microreticulate. Additionally, the presence of a protruding oncus was first observed in *Cephalanthus* on non-acetolised pollen grains. Regarding the orbicules, all species have orbicules, from spheroidal-sub-spheroidal to pyriform. Based on the accepted orbicule typology (Huysmans et al. 1998; Vinckier et al. 2000; Vinckier and Smets 2002), the orbicules found in Naucleae belong to type 3a (spheroidal and with smooth surfaces), which corresponds to the most common type in the subfamily Cinchonoideae.

Fruits and seeds

Fruits are described as indehiscent (Haviland 1897; Ridsdale 1976; Razafimandimbison and Bremer 2002), fleshy with two pyrenes opening by apical-marginal preformed slits (Robbrecht 1988), or as schizocarp that separates into two indehiscent mericarps (Löfstrand et al. 2014). Based on both fresh and herbarium material, we consider it as a schizocarp-type dry fruit (Romero

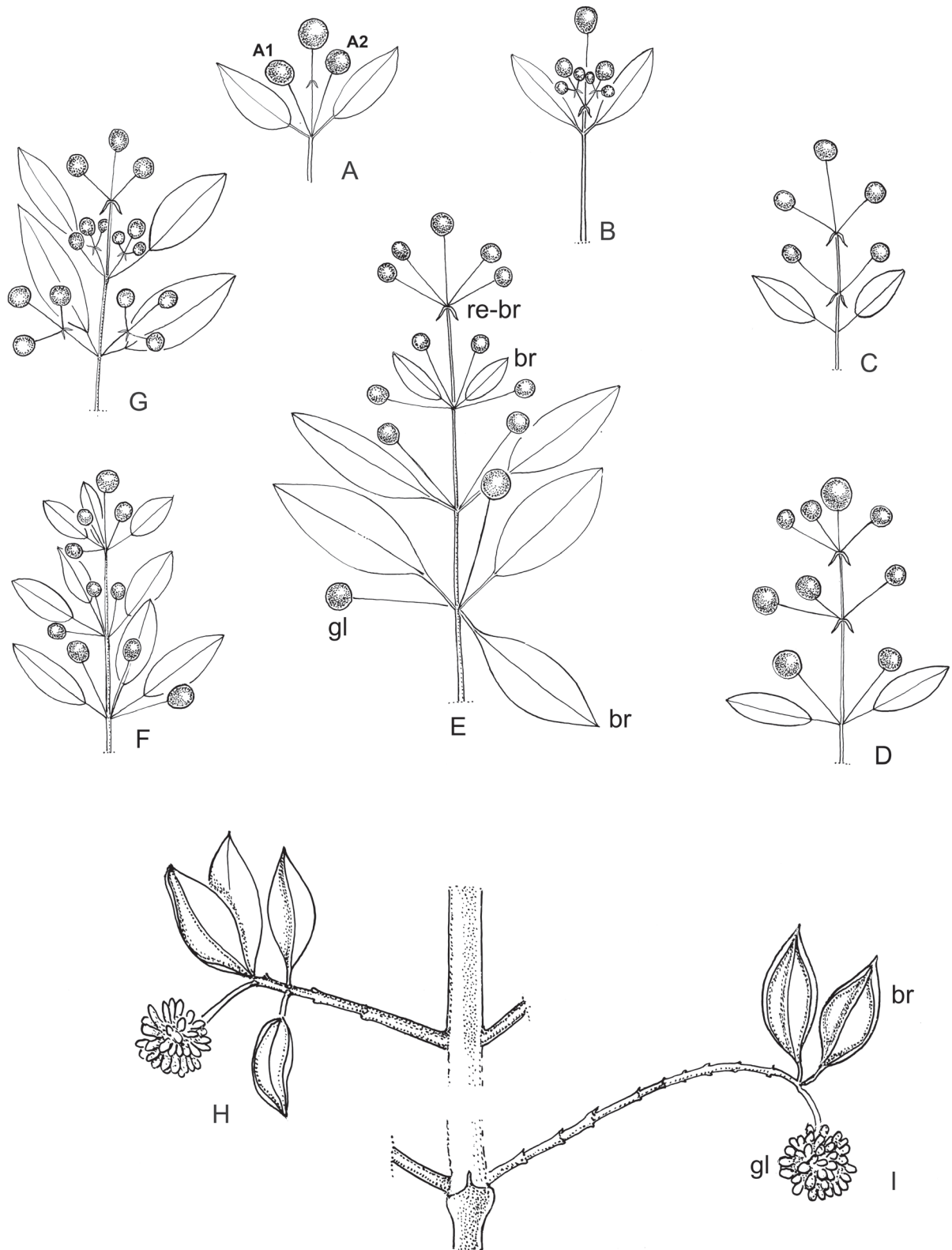


Figure 1. Inflorescences of *Cephalanthus* and *Sylvainia*. A–G. Inflorescences of *Cephalanthus* showing different arrangements of the complex inflorescences, with the circles representing glomeruli (gl). Each drawing represents an increase in the complexity of the branching. A–D. Inflorescences with foliaceous bracts (br) at the base and reduced bracts (re-br) above. A1 and A2 indicate glomeruli. E–G. The foliaceous bracts appear in two (G) or more whorls (E–F). H–I. Inflorescence of *Sylvainia*, only represented by an axis ending in an apical glomerule. H. A relatively young branch with a few older nodes. I. An old flowering branch with numerous old nodes of previous blooms. Drawn by Laura Simón.

et al. 2022b). The preformed apical slits observed by Robbrecht (1988: fig. 55E) were also noticed by us in the rest of *Cephalanthus* s.s., but it is absent in *C. natalensis*. Middleton (2000) mentioned for *C. occidentalis* that it has autochorous (gravity-dispersed) and/or hydrochorous (water-dispersed) fruits; the same condition was observed by us in natural populations of *C. glabratus*. Romero et al. (2022a) conducted an anatomical and developmental study of the fruits and seeds of all *Cephalanthus* species, and described these as having a well-developed whitish spongy aril, with a smooth exotesta (under stereo microscope) and reticulate (under scanning electron microscope). Robbrecht (1988) assumed an oily nature of the endosperm because the seeds are apparently hydrophobic (rapidly floating after being submerged); this character is not analysed here. The aril was not considered as a synapomorphy for subtribe Cephalanthinae by Löfstrand et al. (2014), however, here it is reaffirmed as such. In *C. glabratus*, the aril has a funicular origin; it develops from periclinal and anticlinal divisions of the epidermal cells of the funicle, originating in a pre-anthetic event (Romero et al. 2022a). Previously, Robbrecht (1988: 154–155) proposed a placentary origin for the aril (mentioned as stony arilloid tissue).

Geographic distribution and habitat

The species of *Cephalanthus* s.s. are found in subtropical and temperate areas in the Americas and Southeast Asia, being that in Asia, they also grow in tropical monsoon climates (South India and Indochina Peninsula). *Cephalanthus glabratus* is distributed in the Southern cone of America, while *C. salicifolius* and *C. occidentalis* are found in North America. The latter species has the most northern range, in Quebec, Canada. Of the Asian species, *C. angustifolius* grows only in the Indochina Peninsula (Laos and Vietnam), whereas *C. tetrandrus* and *C. glabrifolius* are widely distributed in Southeast Asia.

All species of *Cephalanthus* s.s. grow in habitats with mixed conditions, i.e. aquatic seasonal environments with occasionally long periods of drought. The aquatic environments can be lentic (lakes and lagoons) and lotic (rivers and small streams of variable water flow), and even in mixed environments, such as flooded river plains or in dammed reservoirs. They are obligate heliophilic plants that grow in saturated soils forming pure stands, in many cases representing the dominant woody element (Romero et al. 2019). The populations of *C. glabratus* are called “sarandisales” (Spanish) or “sarandisais” (Portuguese) in South America, and the *C. occidentalis* communities in the USA are known as “buttonbush wetlands” along the Mississippi river (Roberto M. Salas pers. obs.). The *Cephalanthus* species also occur with other woody species, e.g. *C. glabratus* in Argentina, Paraguay, and Brazil coexists with *Phyllanthus sellowianus* (Klotzsch) Müll.Arg. (red sarandi), *Sapium haematospermum* Müll.Arg., and *Erythrina crista-galli* L. (seibo). Similarly, *C. tetrandrus* (known in Thailand as “Chai Wan”) shares dominance with a species of bamboo

(Mikhama and Sirisant 2016), and *C. occidentalis* is part of the understory in forested wetlands (locally known as “bottomland hardwood forests”) in south-eastern United States (Hutchinson and Langeland 2010).

The position of *Cephalanthus natalensis*

This African species inhabits high, non-floodable habitats, which is in contrast to *Cephalanthus* s.s., whose species predominantly grow in wetlands. It is a much-branched shrub or small tree, and when it grows associated with forests, it can be a climbing tree. *Cephalanthus natalensis* also differs by the presence of crypt domatia. Its inflorescences are characterised by an axis ending in an apical glomerule. When the mature fruits fall off, a dormant bud at the base of the axis or immediately below the insertion point of the glomerule produces a new inflorescence in the following season. Figure 1H shows a relatively young branch with a few previous nodes, while Fig. 1I presents an old flowering branch with numerous old nodes representing previous blooms.

The pollen grains also have a transitional type of sexine, but in this case varies from perforate to microreticulate, while its orbicules are donut-shaped, which constitutes the only record for the tribe Naucleaeae. *Cephalanthus natalensis* is the only species of subtribe Cephalanthinae with fleshy fruits, a character already observed by Haviland (1897). The fruits are consumed by fruit-eating animals, notably birds, baboons, and monkeys (Boon 2010; Van Wyk and Van Wyk 2013). Seeds, in contrast to the other *Cephalanthus* species, have a reduced aril, smaller than half the length of the seed, and a foveolate exotesta (under stereo microscope and SEM). The presence of an aril was previously noted for all *Cephalanthus* species (Ridsdale 1976), with the exception of *C. natalensis*, which was confirmed by Razafimandimbison and Bremer (2002). The phylogenetic position of *C. natalensis* was always resolved as sister to the rest of the *Cephalanthus* species, indeed, in the first phylogenetic studies, it fell outside of *Cephalanthus* in a strict sense (based only on molecular data; Razafimandimbison and Bremer 2002). Based on recent morphological and molecular studies, we consider that *C. natalensis* deserves to be segregated into its own genus. The formal description of the new genus is given below in the framework of a taxonomic treatment of the subtribe Cephalanthinae.

TAXONOMIC TREATMENT

Subtribe **Cephalanthinae** DC. (de Candolle 1830: 538)

Tribe Cephalanthae Kunth (Humboldt et al. 1818: 379).

Tribe Cephalanthidae Havil. (Haviland 1897: 21).

Type genus. *Cephalanthus* L.

Description of the subtribe. Shrubs, rarely small trees, mostly erect, exceptionally scrambling or climbing, scarcely to much-branched. Stipules interpetiolar entire. Leaves opposite or 3- or 4-verticillate, pseudopetiolate.

Table 1. Morphological characters distinguishing *Cephalanthus* and the new genus *Sylvainia*.

Characters	<i>Cephalanthus</i>	<i>Sylvainia</i>
Habit	shrub or small tree	shrub in open environments to a climbing tree in forests
Leaves	commonly 3–4 verticillate, rarely opposite, up to 15–20 cm long	opposite, up to 5 cm long
Leaf domatia	absent in <i>C. angustifolius</i> and <i>C. glabrifolius</i> , tufts of hairs in <i>C. glabratus</i> and <i>C. tetrandrus</i> , and pockets in <i>C. occidentalis</i>	present, crypts
Colleters	Light	present on stipules
	Dark	absent
Inflorescences	thyrsoid, pleiochasia	terminal, on single branches
Corolla	infundibuliform or hypocrateriform, completely white, internally pubescent tube, internally glabrous or pubescent lobes	tubular, red tube, internally glabrous, greenish throat and nigrescent lobes, with margins inwardly plicate
Stamens	subsessile, sub-included at anthesis	filaments equal or longer than the anthers, included at anthesis, covered by a ring of trichomes of the corolla lobes
Stigma	capitate/bilobate	slightly claviform to inconspicuous
Pollen grains: exine pattern	perforate in <i>C. glabratus</i> and microreticulate in the remaining spp., unknown in <i>C. glabrifolius</i>	transitional, perforate to micro-reticulate
Orbicules	spheroidal, subspheroidal, pyriform and/or elongated	donut-shaped
Fruit	dry, schizocarp, autochorous and/or probably hydrochorous, greenish to reddish colour, mericarps with an apical preformed slit	fleshy, endozoochorous, white-green or pink, mericarps indehiscent
Exotesta (SEM)	smooth, minutely reticulate	rough, reticulate
Aril	longer than the length of the seed	shorter than half the length of the seed
Habitat	waterlogged or inundated habitat, from 0 to 250 m altitude	mountainous, humid forests, non-waterlogged, 1500 to 2000 m altitude
Distribution	Southeast Asia (tropical Asia) and America, North and Mesoamerica, and South America	Southeast Africa, subtropical

Inflorescences terminal and axillary, frondose-bracteate or bracteate; partial inflorescences congested. **Flowers** homostylous, perfect or functionally imperfect, with stylar pollen presentation; corolla aestivation imbricate, colleters in corolla located externally at the interlobular sinuses (*Cephalanthus*), or absent (*Sylvainia*). **Ovary** 2-carpellar, carpels 1-ovulate, each ovule pendulous.

Fruit dry (*Cephalanthus*), or fleshy (*Sylvainia*). **Seeds** with prominent or reduced aril, longer than the seed (*Cephalanthus*), with a reduced aril shorter than a third of the length of the seed (*Sylvainia*).

Genera. The subtribe Cephalanthinae comprises two genera: the type genus *Cephalanthus* and the new genus *Sylvainia* (Table 1).

Key to genera of the subtribe Cephalanthinae

- Plants erect, from floodable and/or waterlogged habitats; leaves 2–4-whorled, with domatia absent or present as tufts of hair or pockets; stipules with light colleters on the ventral (inner) face and dark colleters at the apex or along the margin; inflorescences thyrsoid, arranged in a pleiochasium; bracts, bracteoles, and calyx with dark colleters; corolla infundibuliform or hypocrateriform, uniformly whitish, dark colleters present at the interlobular sinuses; lobes glabrous or pubescent, with margin not plicate inwards; tube with a fringe of hairs internally; stamens subsessile; fruit dry, autochorous and/or hydrochorous; seeds with a prominent aril, longer than the length of the seed..... *Cephalanthus*
- Plants erect, in open areas on rocky outcrops in grasslands, to scrambling or climbing in forests, usually from high-lying periodically moist but non-floodable habitats; leaves opposite, with crypt domatia; stipules with light colleters on the ventral (inner) face; dark colleters absent; inflorescences in terminal glomeruli; bracts, bracteoles, and calyx without dark colleters; corolla tubular, tube internally glabrous, externally reddish, throat greenish, lobes blackish, colleters absent, lobes with margins plicate, internally pubescent; stamens with filaments equal to or longer than the anthers; fruits fleshy, endozoochorous; seeds with an aril smaller than half the length of the seed *Sylvainia*

Cephalanthus L. (Linnaeus 1753: 95)

Acrodryon Spreng. (Sprengel 1824: 386) – Type species: *Acrodryon angustifolium* (Lour.) Spreng. (lectotype designated by Merrill 1935) [= *Cephalanthus angustifolius* Lour.].

Axolus Raf. (Rafinesque 1838: 61) – Type species: *Axolus angustifolius* (Lour.) Raf. [= *Cephalanthus angustifolius* Lour.].

Eresimus Raf. (Rafinesque 1838: 60) – Type species: *Cephalanthus stellatus* Lour. [= *Cephalanthus angustifolius* Lour.].

Type species. *Cephalanthus occidentalis* L. (lectotype designated by Merrill 1915).

Description. Shrubs or small trees 3–5 m tall, much-branched. Stems with lenticels, fragile. Leaves opposite or verticillate, pseudopetiolate; blades narrowly elliptical, oblong to narrowly ovate, glabrous to pubescent, discolorous; veins slightly discolorous; leaf domatia generally present on the abaxial side; stipules interpetiolar, tardily deciduous, with dark colleters at the apex and along the margin, and light colleters on the ventral (inner) side, near the base. Inflorescences

terminal and axillary, thyrsoid, cymose, in pleiochasium, bracteose or frondobracteose, partial inflorescences in glomeruli, strongly congested, spherical, pedunculate, with synchronic anthesis; bracteoles spatulate, with dark colleters, pubescent. Flowers perfect or morphologically perfect, but functionally imperfect in *C. glabratus*, actinomorphic, sessile; calyx 4- or 5-lobed; corolla infundibuliform or hypocrateriform, 4- or 5-lobed; imbricated in bud; lobes rounded, internally pubescent or glabrous, externally with dark colleters at the interlobular sinuses; tube internally with a fringe of hairs or glabrous, externally glabrous; stamens 4 or 5, with filiform filaments, glabrous; anthers subsessile; hypanthium cupuliform, obovate or turbinate; ovary 2-carpellate, 2-locular, each locule 1-ovulate; ovules pendulous; style filiform; stigma capitate or shortly bilobate, exerted at the end of anthesis. Fruit a schizocarp, glabrous or pubescent; pericarp coriaceous and thin; seeds flat-convex, sub-rhomboid in outline, fragile, with surface almost smooth, microscopically papillose; aril prominent, dorsal, longer than the seed length, white, softly rough, and spongy.

Distribution. Pantropical, 6 species: 3 from the Americas and 3 from tropical Asia.

Key to species of *Cephalanthus*

1. Leaf lamina length/width ratio 4–5:1 2
- Leaf lamina length/width ratio 2–2.5:1 4
2. Calyx lobes widely triangular or widely ovate; corolla infundibuliform with tube gradually widening from the base towards the throat, which is 2–3 times wider than the base, 3.5–5.9 mm long, lobes internally pubescent up to the insertion of the stamens 2. *C. glabratus*
- Calyx lobes narrowly triangular or widely ovate; corolla hypocrateriform with a straight, thin tube at the basal two thirds and slightly widening towards the throat, 5–12 mm long, lobes internally glabrous 3
3. Leaf domatia present as tufts of hair; inflorescence with axis pubescent; hypanthium cupuliform; calyx lobes broadly ovate and pubescent, apex rounded; fruit pubescent (southern USA to Honduras) 5. *C. salicifolius*
- Leaves without domatia; inflorescence with axis glabrous; hypanthium turbinate; calyx lobes narrowly triangular and glabrous, apex acute; fruit glabrous (Cambodia, Laos, and Vietnam) 1. *C. angustifolius*
4. Leaf domatia present as hairy pockets; corolla densely pubescent inside, in the form of longitudinal lines from the apex of the lobes to the insertion of the stamens (Canada to Honduras and Cuba) 4. *C. occidentalis*
- Leaf domatia present as tufts of hair or absent; corolla lobes glabrous or sparsely pubescent inside, forming a fringe of hairs 5
5. Leaves glabrous; hypanthium obovate, 1.6–1.8 mm long; calyx lobes broadly triangular, 0.2–0.35 mm long, pubescent, often with a dark colleter at the apex; corolla lobes ovate or subtriangular, acute, 1.5–2 mm long, inside sparsely pubescent, with a fringe of hairs covering the tube from the apex to the upper third 3. *C. glabrifolius*
- Leaves pubescent above, puberulous or pubescent only on the veins beneath; hypanthium cupuliform, 1.3–1.5 mm long, glabrous; calyx lobes broadly ovate, 0.7–1 mm long, glabrous, margin puberulous, with dark colleters at the interlobular sinuses; corolla lobes oblong, obtuse, 1–1.3 mm long, inside glabrous, tube with a fringe of hairs from the base of the stamens to the base of the tube 6. *C. tetrandrus*

1. *Cephalanthus angustifolius* Lour. (Loureiro 1790: 67)

Figs 2, 3

Cephalanthus stellatus Lour. (Loureiro 1790: 68).

Acrodryon angustifolium (Lour.) Spreng. (Sprengel 1824: 386).

Nauclea stellata (Lour.) Wall. (Wallich 1832: 6102).

Axolus angustifolius (Lour.) Raf. (Rafinesque 1838: 61), non *Cephalanthus angustifolius* Dippel (Dippel 1889: 164).

Eresimus stellatus (Lour.) Raf. (Rafinesque 1838: 61).

Type. VIETNAM • Loureiro *s.n.*; holotype: BM [BM000606644]; probable isotype: K [K001123035].

Description. Shrub or small tree, up to 3 m tall. Leaves (2–)3-verticillate, pseudopetiolate; pseudopetiole subcylindrical, glabrous, 2–5 mm long; blade oblong to

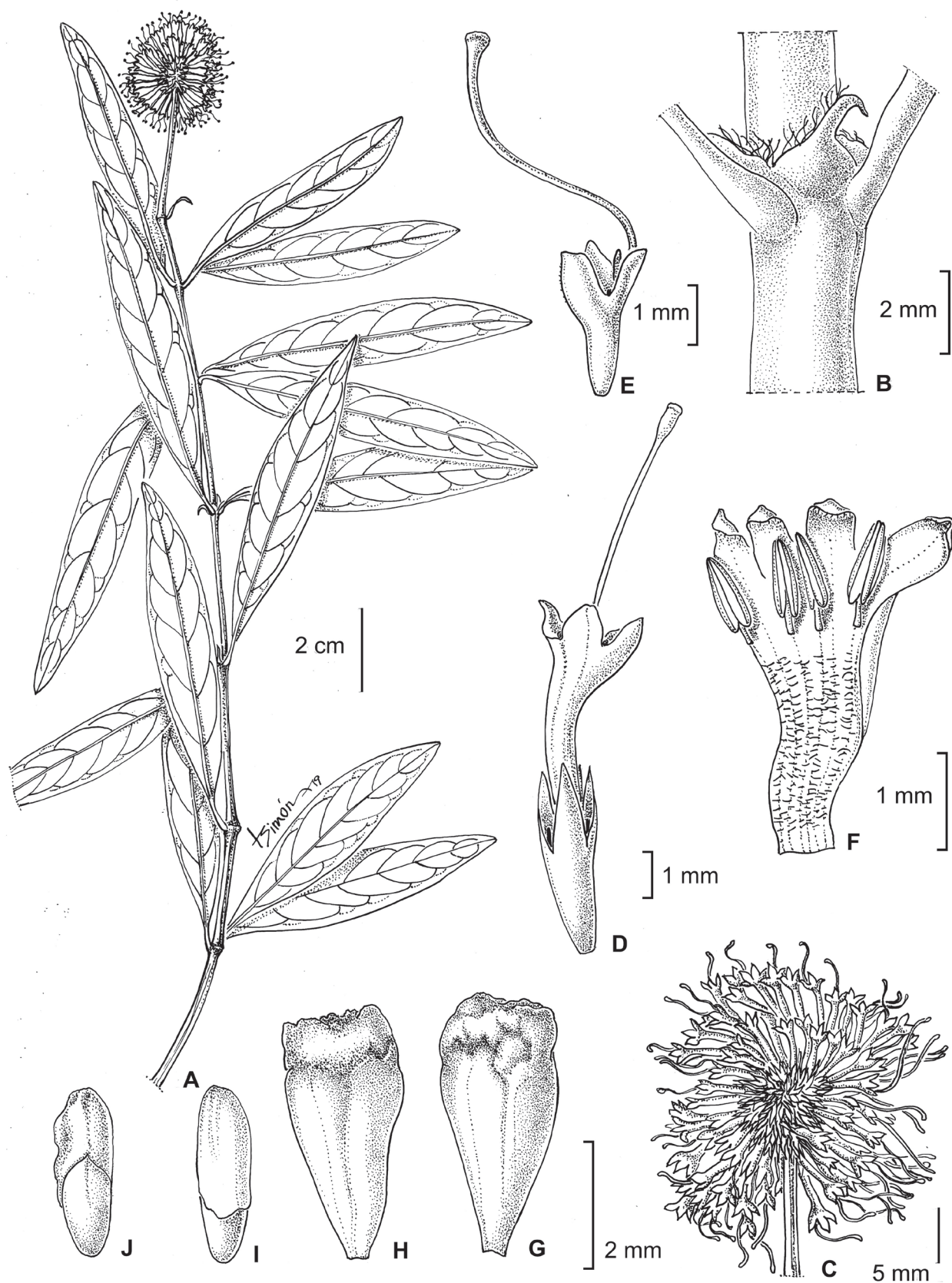


Figure 2. *Cephalanthus angustifolius*. A. Flowering branch. B. Stipule. C. Partial inflorescence. D. Flower. E. Hypanthium, style, and stigma. F. Corolla at anthesis. G. Ventral view of schizocarp. H. Dorsal view of schizocarp. I. Dorsal view of seed with aril. J. Subventral view of seed with aril. Drawn by Laura Simón.

narrowly ovate, glabrous, subcoriaceous, discolorous, (3–)5–13 × 1–5 cm, base acute, apex acute or acuminate; veins 3–6 on each side, slightly discolorous, leaf domatia absent; stipules triangular, pubescent on both sides, with dark colleters at the apex and margin, few light colleters on the ventral (inner) side intermingled with numerous trichomes. **Inflorescences** short pedunculate, peduncle 2–3 cm long, bracteoles spatulate, pubescent, with dark colleters at the apex. **Flowers** perfect; calyx 4- or 5-lobed, lobes narrowly triangular, pubescent on ventral (inner) side, 1.1–4.0 mm long, margin puberulous, with dark colleters at the interlobular sinuses, infrequent at the margin; corolla hypocrateriform to slightly infundibuliform, 4- or 5-lobed, 5–8 mm long, lobes oblong, 1–2 mm long, with dark colleters at the interlobular sinuses, tube externally glabrous and internally puberulous; stamens 4 or 5, filaments filiform, glabrous, 0.4–0.5 mm long; hypanthium turbinate, glabrous, 0.9–2.0 mm long; style filiform; stigma capitate and exerted at flower maturity. **Fruits** narrowly obovate, glabrous, 4–5 mm long. **Seeds** 1.5–2.0 mm long; aril 1.3–1.8 mm long.

Distribution. The species is found in the easternmost region of the Indochina Peninsula. According to Puff et al. (2021), it is found in Laos and Vietnam, and probably Thailand. However, in the latter country, no collections have been recorded so far. Puff et al. (2021) mentioned “It is not completely confirmed whether the species occurs

in Thailand or not. It is likely that a collection from the banks of the Mekong at 16°N (*Harmand s.n.* (W, P)) has originated on the Laos side of the river and no plants have been collected on the Thai side so far. However, being a rheophyte, it is very likely that it is not restricted to the E. banks of the Mekong”. Based on herbarium specimens (HN, F, K, L, NY, P, W), its presence was confirmed for Laos and Vietnam. According to studies of medicinal plants, several authors mentioned that *C. angustifolius* is present in Cambodia (Dy Phon 2000; Kham 2004; Ashwell and Walston 2008), however, it was not possible to see the herbarium specimens cited in these studies. The records for this country on the map are based on these citations (Fig. 3).

Habitat and ecology. *Cephalanthus angustifolius* is a rheophyte, typical of more or less rushing rivers and streams, surrounded by lowland forest, mostly in primary habitats. Some recent collections were made in secondary habitats.

Phenology. Based on the scarce material analysed, it flowers from November to January and produces fruit from April to June.

Vernacular name. Khtum kok (Cambodia; Dy Phon 2000); Rì lớn lá, Rì bông gạo, Vây lá hẹp (Vietnam).

Uses and ethnobotanical aspects. The leaves are used as an astringent in traditional medicine in Cambodia. The bark infusion is used as an analgesic for general aches and

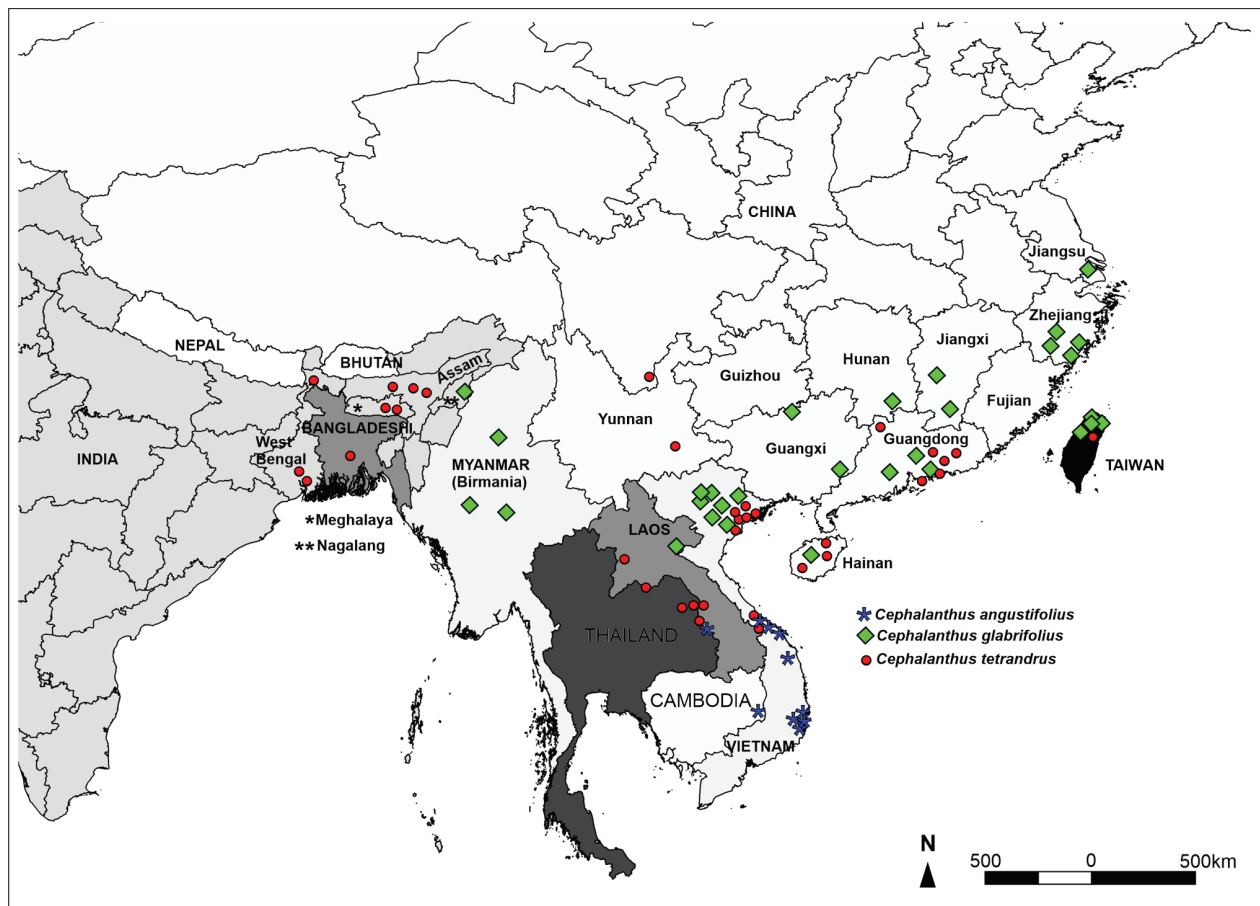


Figure 3. Distribution map of *Cephalanthus angustifolius*, *C. glabrifolius*, and *C. tetrandrus*.

pains. The plant is traditionally prescribed as an analgesic for childbirth pains (Dy Phon 2000; Kham 2004; Ashwell and Walston 2008).

Additional material examined. LAOS • Without precise locality, fluminis Mekong; Sep. 1877; *Harmand* 6270; P [P03820120, P03820119, P03820118], W.

VIETNAM • Tourane; 4–13 Jun. 1927; *J. Clemens & M.S. Clemens* 3588; P [P03820123]. – **Khanh Hoa** • *Krempf* s.n.; P [P03820121] • 20 Jan. 1913; *Krempf* s.n.; P [P03820124] • Nha Trang, cascades, au milieu du ruisseau (ilot); 2 Sep. 1953; *s.col. s.n.*; P [P04560861] • Dien Khanh district, road transact Suoi Cat-Hon Ba, at km 19 to Hon Ba, forest along rocky riverbank of Da Giang River; 12°06'53"N, 109°00'12"E; 22 Jun. 2004; *Soejarto* 13284; F, L, P • Hon Ba Mts, Suoi Village, road transect Suoi Village to peak a km markers 25–24, lowland tropical forest formation along Da Giang river; 12°7.97'N, 109°1.28'E; 110 m; 2 Nov. 2004; *Soejarto* 13537; F, L, P. – **Thua Thiên Huế** • Bên Du pro, Thua Thiên, Récolte sur le bord de Sông Bô; 16°31'40.8"N, 107°34'22.8"E; 13 May 1920; *Poillane* 1410; K, P [P03820122, P03820077] • [Annam], Thua Thien Hue, Nam Dong, Bach Ma N.P., Huong Loc; 16°8'22.99"N, 107°47'27.00"E; 137 m; 18 May 2016; *Hai* 1150; HN, NY.

Notes. According to Stafleu and Cowan (1981: 174), most of the collections of Loureiro are deposited in BM, while few specimens are also preserved at P and LINN. The remaining collections deposited in LISU were apparently destroyed, without explanation how it happened. After consulting the collections in BM, only one type specimen of Loureiro was found, which coincides with the results of the earlier *Cephalanthus* revisions (Haviland 1897; Ridsdale 1976). Loureiro (1790) described *C. angustifolius* and *C. stellatus* in the same treatment of Flora Cochinchinensis, separating the first by its opposite leaves (vs verticillate leaves in *C. stellatus*). Haviland (1897) noticed that the available type specimen in BM does not match in all aspects with the diagnosis of *C. angustifolius*, because the specimen has verticillate leaves, while the description mentions opposite. All available specimens of *C. angustifolius* have invariably verticillate leaves. Similar incongruence, in other taxa of Loureiro, was mentioned for *Stapelia cochinchinensis* Lour. and *S. chinensis* Lour. (Rodda 2016). Some morphological aspects of one type appeared in the description of the other name, and vice versa. As for the type of *C. angustifolius* and *C. stellatus*, we follow Haviland in considering them as homotypic synonyms.

2. *Cephalanthus glabratus* (Spreng.) K.Schum.
(Schumann 1889: 128)

Figs 4, 5

Buddleja glabrata Spreng. (Sprengel 1824: 431).

Cephalanthus sarandi Cham. & Schltdl. (Chamisso and Schlechtendal 1827: 610).

Type. URUGUAY • Montevideo; 1814–1831; *Sellow* s.n.; lectotype (designated by Romero et al. 2021): HAL [HAL0107358]; isoelectotypes: BR [BR0000005576456,

BR0000005576784], E [E00505359], HAL [HAL0097791], L [L.0000206], M [M0187150].

Description. *Shrub* 3–5 m tall, much-branched; trunk with smooth bark, slightly striated longitudinally. *Stems* smooth, sparsely covered by lenticels, fragile and brittle, glabrous distally, rarely pubescent. *Leaves* 3(–4)-verticillate; pseudopetioles subcylindrical, with puberulous margin, elsewhere glabrous, 3–9 mm long; blades narrowly ovate or narrowly elliptic, glabrous, sometimes puberulous below, attenuate at base and acute at apex, subcoriaceous, slightly discolorous, 5–8 × 1–2 cm; veins 3–6 at each side, visible abaxially; domatia present as tufts of hair; stipules ovate-acuminate, membranaceous, green or reddish green when young, chestnut when falling off, pubescent on both sides, with dark colleters present at the apex and margin and light colleters on the lower half of the ventral (inner) side, intermingled with numerous trichomes. *Inflorescences* pedunculate, with peduncle 2–6 cm long, usually frondose-bracteate; bracts with dark colleters at the apex and margin; terminal glomeruli usually wider in diameter; anthesis usually regular; bracteoles spatulate, pubescent, with dark colleters at the apex. *Flowers* morphologically perfect, functionally male and female, sessile, both with a slightly cinnamon aroma; calyx 4–5(–7)-lobed; lobes broadly ovate or broadly triangular, obtuse, with edges pubescent, 0.37–0.7 mm long, with dark colleters at interlobular sinuses or apex; tube 0.7–1 mm long; corolla infundibuliform, 4–5(–7) lobed; lobes externally glabrous, with tiny appendages at the interlobular angle ending in dark colleters, rounded, 3.5–5.9 mm long, internally puberulous in male flowers and densely pubescent from the base to the upper third in female flowers, glabrous externally; tube glabrous internally and externally; stamens 4 or 5 (6 or 7), with filaments filiform, glabrous, 0.4–0.7 mm long; anthers subsessile, sagittal at the base, 1–1.4 mm long; style filiform, 5–7.5 mm long; stigma exerted at the end of anthesis, capitate in male flowers, bilobate in female flowers; nectariferous disc bilobed. *Fruits* schizocarp, obpyramidal or turbinate, sometimes angular and more or less irregular, glabrous, with pericarp coriaceous, reddish at the apex, 6–7 mm long. *Seeds* flat-convex 2.5–3 mm long; aril 1.5–2.5 mm long.

Distribution. According to Romero et al. (2021), the species occurs in Argentina, Brazil, Paraguay, and Uruguay. It grows on low floodable land (lagoons, marshes, canyons, etc.), in flood plains of the main rivers in the region and their tributaries (Fig. 5).

Habitat and ecology. According to Persia and Neiff (1986), the environments near the Uruguay River where *Cephalanthus glabratus* grows can be characterized as a particular type of seasonal wetlands or “bañados”, which are exposed to an alternation of dry and wet periods. It is composed especially of herbaceous species with scattered trees and shrubs of *C. glabratus* and *Phyllanthus sellowianus* Mull.Arg. (“Sarandí blanco”, Phyllanthaceae). The authors called these environments “woody wetlands” or “bañados-bosques”. In coincidence with the seasonality

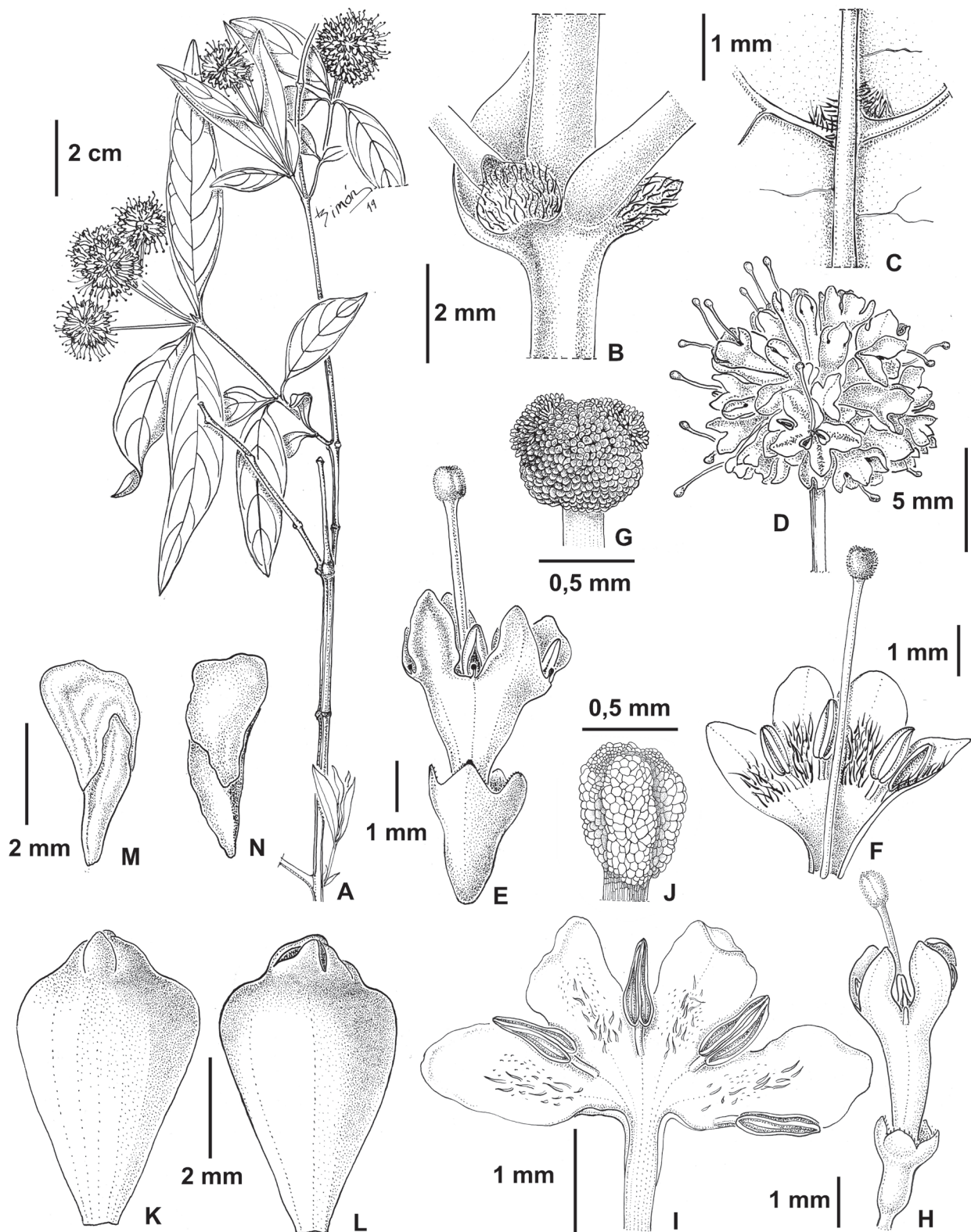


Figure 4. *Cephalanthus glabratus*. A. Flowering branch. B. Domatia as tufts of hair. C. Axils of the secondary veins showing domatia as tufts of hairs. D. Partial inflorescence. E–G. Functionally female flower details. E. Flower. F. Open flower showing pubescence. G. Bilobed stigma and apical portion of the style. H–J. Male flower. H. Flower. I. Open flower showing pubescence. J. Capitulate stigma and apical portion of the style. K. Dorsal view of schizocarp. L. Ventral view of schizocarp. M. Dorsal view of seed with aril. N. Subventral view of seed with aril. Drawn by Laura Simón.

and alternation of wet and dry periods, Romero et al. (2019) proposed that the structure of the leaf anatomy of *Cephalanthus* species shows adaptations to both hydromorphic (cuticle and thin cell walls, unistratified epidermis) and mesophilic habitats (large intercellular spaces and few trichomes), and tolerance to dry periods (heterobaric leaves).

Phenology. It flowers profusely from August to October, declines towards December, and also in isolated specimens until May. Fruiting from the end of October to January, declining towards March.

Vernacular name. Sarandí colorado (Cabrera and Zardini 1978).

Uses and phytochemical aspects. In traditional medicine, a decoction of the bark is a substitute for white sarandí (*Phyllanthus sellowianus*) and used for the treatment of diabetes. An infusion of the leaves is diuretic, depurative, and astringent (Martínez Crovetto 1981; Romero et al. 2021).

IUCN conservation assessment. The species should be considered as NT (Near Threatened) (Romero et al. 2021).

Additional material examined. ARGENTINA – **Buenos Aires** • Isla Martín García: Reserva Natural y Sitio Histórico, Isla Martín García, Talar de Arenal Central; 24 Nov. 2005; *Torres Robles* 2315; MO • Mun. Berisso, Isla Paulino; 1905; *Nianelli* 90; SI • Quilmes; Nov. 1910; *Jurado s.n.*; SI • Mun. Tigre, Delta, Puerto Mirú; 4 Dec. 1931; *Burkart* 4541; SI. – **Capital Federal** • Belgrano; 22

Nov. 1927; *Burkart* 1682; SI. – **Chaco** • 1 de Mayo, Campo Antequera, Laguna La Mora; 1 Sep. 1971; *Bacigalupo et al.* 9529; MO, SI. – **Corrientes** • Mun. Colonia Pellegrini, Isla de vegetación flotante en la laguna Iberá; 5 Nov. 1973; *Goodall & Tirel* 255; SI • Mun. Concepción, pastizales con parches de plantaciones de matorrales forestales; 30 Nov. 1978; *Renvoize* 3686; CTES, MO • Mun. Empedrado, Estación Agronómica Tres Marías, próximo al Río Paraná; 20 Mar. 1998; *Schinini* 34402; CTES, IAC. – **Entre Ríos** • Mun. Colón, Paraje La Calera, márgenes del Río Uruguay, desembocadura del arroyo Perucho Verna en Río Uruguay; 21–22 Dec. 1998; *Simón* 96; MO. – **Misiones** • Mun. Posadas, costas del Río; 16 Nov. 1905; *Bertoni* 1886; LIL • Mun. San Pedro, Parque Provincial Moconá; 27°08'00"S, 53°53'00"W; *Seijo* 849; CTES, G, MNES.

BRAZIL – **Mato Grosso do Sul** • Mun. Brasilândia, Rio Verde; 18 Oct. 1972; *Hatschbach* 30525; MBM, MO, NY; Mun. Rio Brillhante, Rio das Araras; 26 Oct. 1970; *Hatschbach et al.* 25247; NY, UEC • Mun. Mundo Novo, Porto Frangeli, Vargados de inundação do Rio Paraná; 13 Oct. 1984; *Hatschbach & Kummrow* 48386; MBM, MO, US [US02370589]. – **Paraná** • Alto Paraíso; 14 Aug. 2015; *Oliveira* 2551; FURB, RB • Mun. Foz do Iguaçu, Parque Nacional do Iguaçu; 16 Oct. 2015; *Caxambu* 7015; HCF • Mun. Guaíba, Entorno do Parque Nacional de Ilha Grande; 26 Aug. 2009; *Temponi* 547; FUEL, UNOP. – **Rio Grande do Sul** • Mun. Alegrete, ca 51 km S de Alegrete na estrada para Caverá; 19 Nov. 2006; *Queiroz* 12571; HUEFS • Mun. Gravataí, vicinity of Gravataí, 20 km E from Canoas; 20 m; 12 Dec. 1987; *Tsugaru et al.* B-2417; MO, NY. – **Santa Catarina** • Mun. Araranguá, Sombrio; Feb. 1946; *Rambo s.n.*; PACA [PACA31495] • Mun. Itapiranga, Forest above Rio Uruguai, Barra Macaco Branco; 27°10'S, 53°46'W; 150–250 m; 18 Dec. 1964; *Smith & Klein* 14118; FLOR, HRB, MO, NY, R, RB, P, US [US02370590]. – **São Paulo** • Mun. Porto Primavera, Margem do Rio Paraná, a montante da barragem de Porto Primavera; 22°27'43.3"S, 52°52'25.9"W; 17 Oct. 1998; *Bicudo* 265; CGMS, PACA, UPCB.

PARAGUAY – **Alto Paraná** • 14 km W de Itaquyry; 12 Oct. 1995; *Schinini & Caballero M.* 30213; CTES. – **Caazapá** • 7 km W of Tavaí, swamp and cerrado scrub; 26°10'40"S, 55°34'47"W; 25 Nov. 1997; *Zardini & Benítez* 47646; AS, MO. – **Canindeyú** • Jejuí-mí, después del puente Carona, 49500/29450UTM, bosque ribereño bajo; 13 Sep. 1997; *Marín* 622; MO. – **Central** • San Lorenzo, Ciudad Universitaria, arroyo; 24 Oct. 1974; *Arenas* 931; MBM, MO. – **Concepción** • Paso Horqueta, Río Aquidabán; 19 Oct. 1984; *Dure* 389; MO • Paso Horqueta, Río Aquidabán, gallery forest; 23°07'S, 57°20'W; 17 Mar. 1994; *Zardini & Guerrero* 39013; AS, MO. – **Cordillera** • Orillas del Lago Ypacaraí; *Hassler* 363; G. – **Itapúa** • Yacyretá Dam Island Reserve, eastern area, Aña Cua, clay soil with inundated savannas; 27°23'45"S, 56°39'08"W; 23 Oct. 1999; *Zardini & Gamarra* 51902; AS, MO. – **Misiones** • Santiago, Estancia La Soledad, Isla Corpiño; 21 Oct. 1957; *Lourteig* 2087; P, SI. – **Paraguarí** • Estero del Ypoá, 20 km W of Carapeguá, north of Pacheco, inundated savanna; 7 Jan.

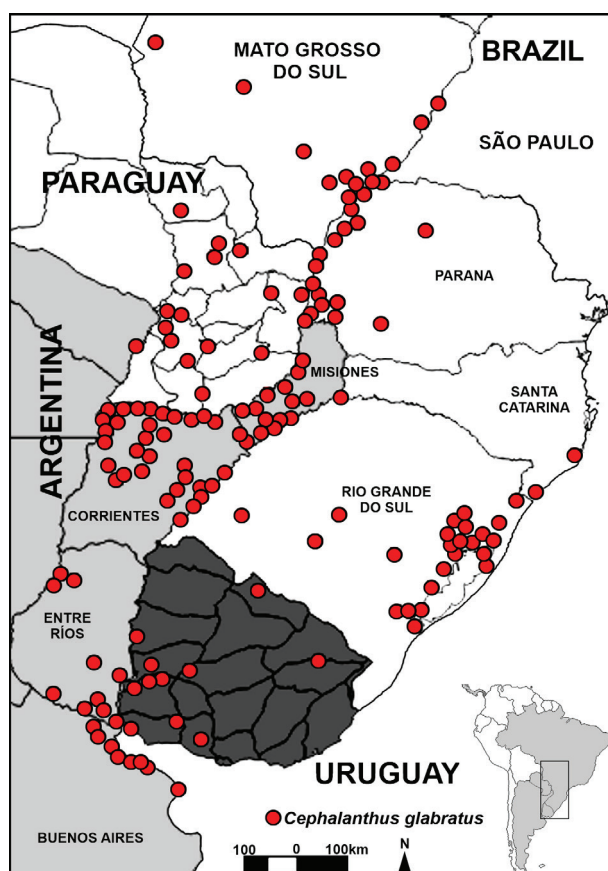


Figure 5. Distribution map of *Cephalanthus glabratus*.

1990; *Zardini & Velázquez* 17519; AS, MO. – **San Pedro** • Between Santa Rosa and Santa Barbara, inundated savanna; 23°50'26"S, 56°23'47"W; 29 Oct. 1996; *Zardini & Guerrero* 45505; AS, MO • Primavera, entre esteros y orillas húmedas; 11 Nov. 1957; *Woolston* 969; P, SI.

URUGUAY – **Cerro Largo** • Ruta 8, km 374, ayo. El Parao; 32°44'34"S, 54°13'14"W; *Seijo et al.* 2714; CTES, SI. – **Colonia** • Colonia, Colonia Punta Gorda próximo a confluencia del Río Uruguay con el Río de la Plata, E de Rincón de Darwin; 33°54'57"S, 58°24'49"W; 24 Nov. 2007; *Solis Neffa & Seijo* 2121; CTES, ICN. – **Rivera** • Mun. Rivera, [damp] Cuñapirú, in silvula paludosa; 12 Jan. 1941; *Rambo s.n.*; PACA [PACA3996]. – **San José** • *Herter* 520; MO • Barra; 10 m; Dec. 1926; *Herter* 769; MO. – **Soriano** • 17 Mar. 1940; *Gallinal H PE-4361*; MO.

Notes. Romero et al. (2015) mentioned that *C. glabratus* lacks domatia. Later, they found that it has domatia as tufts of hair (Romero et al. 2019).

3. *Cephalanthus glabrifolius* Hayata (Hayata 1920: 51)

Figs 3, 6

Type. TAIWAN • Koteisho [古亭庄]; 19 Jun. 1905; *s.col.* 532; holotype: TI [TI00080001].

Description. *Shrub* 3–5 m tall, much-branched. *Leaves* opposite, pseudopetiolate; pseudopetioles subcylindrical, glabrous, 5–8 mm long; blades ovate or elliptic, glabrous, base acute or rounded, apex acute or acuminate, subcoriaceous or papyraceous, discolorous, 6.5–10 × 2.3–4.5 cm; principal lateral veins 6–9 on each side, glabrous or sparsely pilose, slightly discolorous, leaf domatia absent; stipules ovate, apex acuminate, dark colleters present at the apex and margins, light colleters dispersed on the ventral (inner) side, intermingled with numerous trichomes. *Inflorescences* pedunculate, peduncles 2–6 cm long, glabrous; bracteate, bracts foliaceous, bracteoles spatulate, pubescent, with dark colleters present at the interlobular sinuses and apex. *Flowers* perfect; calyx 5-lobed, hypanthium pubescent, obovate, 1.6–1.8 mm long, lobes broadly triangular, pubescent on both sides, 0.2–0.35 mm long, margin pubescent, dark colleters at the interlobular sinuses and apex; corolla hypocrateriform, 5-lobed, 7–8 mm long, lobes ovate or subtriangular, 1.5–2 mm long, externally pubescent, internally with a fringe of sparse hairs from the apex of lobes to the upper third of the tube, with dark colleters at the interlobular sinuses, tube glabrous externally; stamens 5, filaments filiform; style filiform, 8–10 mm long; stigma capitate and exerted at flower maturity. *Fruits* obpyramidal, glabrous, 4.5–5 mm long. *Seeds* with an almost smooth surface, 2.5–2.8 mm long; with a large aril 1.5–2 mm long.

Distribution. *Cephalanthus glabrifolius* has been reported from southeast China, east India, Myanmar, Taiwan, and Vietnam (Fig. 3).

Phenology. Flowers from November to April and bears fruit from March to August.

Habitat and ecology. Occurs along streams and near lakes from sea level up to 1800 m. Occasionally growing on roadsides.

Additional material examined. CHINA • 1856; *Fortune* 1545; P [P05458899]. – **Guangdong** • Kwangtung, Hau T'ong Shan, Fuk Lung Monastery, Sin-fung District; 1–19 Jun. 1938; *Taam* 861; US [US02370626] • Kwangtung, Sha Lo Shan, Lo-Lo-ha Village, Sin-fung District; 6–25 Jul. 1938; *Taam* 1016; US, P [P05458901] • Kwangtung, near Fung Wan, North River Region; 14 Jul. 1924; *Canton Christian College* 12856; US [US02370639]. – **Guangxi** • Kwangsi, Bui Tung, NU bai, Border of Kweichow; 1158 m; 27 Apr. 1928; *Ching* 6258; US [US02370631]. – **Hainan** • 1889; *Henry* 8013; P [P05458905]. – **Hunan** • I-Chia-Ao, Changning Hsien; 3 Jul. 1935; *Fan & Li* 141; P [P05458902], L [L.2853483]. – **Jiangxi** • Kiangsi, Oo Chi Shan, near Lam Uk Village, Lungnan district; 1–25 Oct. 1934; *Lau* 4608; US [US02370636]. – **Zhejiang** • Southern Chekiang, Between Ping Yung and Tai Shan, 5 km, W. of Tai Suan, S. Chekiang; 579 m; 3 Aug. 1924; *Ching* 2222; US [US02370638] • Western Chekiang, Region, 130 km W. of Wenchow; 900 ft; 7 Jun. 1924; *Ching* 1852; US [US02370637].

INDIA – **Nagaland** • Naga Hills; 13 Sep. 1924; *Jagarmani* 497; US [US02370630].

LAOS – **Vientiane** • Ban Sa Phan Mo; 2 Apr. 1950; *Vidal* 1198; P [P03820113]. – **Xiangkhouang** • Plaine des Jarres; vers 1100 m; May 1931; *Colami* 4535; P [P03820116].

MYANMAR • *Lieut & Toppin* 2667; E [E00847463] • Birma and Malay Peninsula; 1835–1845; *Griffith* 3090 [Herbarium of the late East India Company, Herb. Griffith]; NY [2651078]. – **Sagaing** • Katha [city]; 28 Mar. 1912; *Lace* 5719; E [E00847465, E00847464].

TAIWAN – **Taipei** • 19 Jun. 1962; *Chao* 1065; HAST • Taipei City, at Academia Sinica campus (中研院院區), at pond border; 25°2'30"N, 121°36'47"E; 20 m; 8 Feb. 2013; *Huang* 6640; HAST • [City of] Taihoku; 2 Jun. 1929; *Sasaki-Syun'iti s.n.*; L [L.2853197, L.2853198], TAI. – **Ilan Hsien** • Ayushan (阿玉山); 24°46'60"N, 121°35'60"E; 10 Jul. 1996; *Cheng s.n.*; HAST [HAST-79561], TAIF • Tungshan Hsiang, Tungshan (冬山), in 平地水溝邊 [habitat]; 10 Jul. 1998; *Li* 595; HAST • Wuchieh Hsiang, Hsiaowei-Tapu (孝威-大埔), at roadside; 24°41'13"N, 121°48'25"E; 2–4 m; 12 Aug. 1995; *Wang & Lin* 1496; HAST • Wushiherhchia (五十二甲), on paddy ridges; 24°39'5"N, 121°48'17"E; 5 m; 9 Jul. 1998; *Kao & Huang* 575; HAST.

VIETNAM – **Bắc Giang** • Province de Bac Giang, bord d'une petite mare; 31 May 1936; *Pételot* 5674; P [P03820111]. – **Hòa Bình** • Route de Hansi à Hoa Binh; Mar. 1933; *Pételot s.n.*; P [P03820114, P03820115] • "Indochine"; 18–19 Apr. 1914; *Chevalier s.n.*; P [P03820070] • "French Indochina", Environs de Murang Chon, Province de Hva Binh; Mar. 1933; *Bonkin s.n.*; US [US02370641] • "Tonkin Occidental" [N Vietnam], in paludib.; 30 Apr. 1884; *Bon s.n.*; P [P03820095] • In nemore Ván Xa; 4 May 1886; *Bon* 3139; P [P03820096].

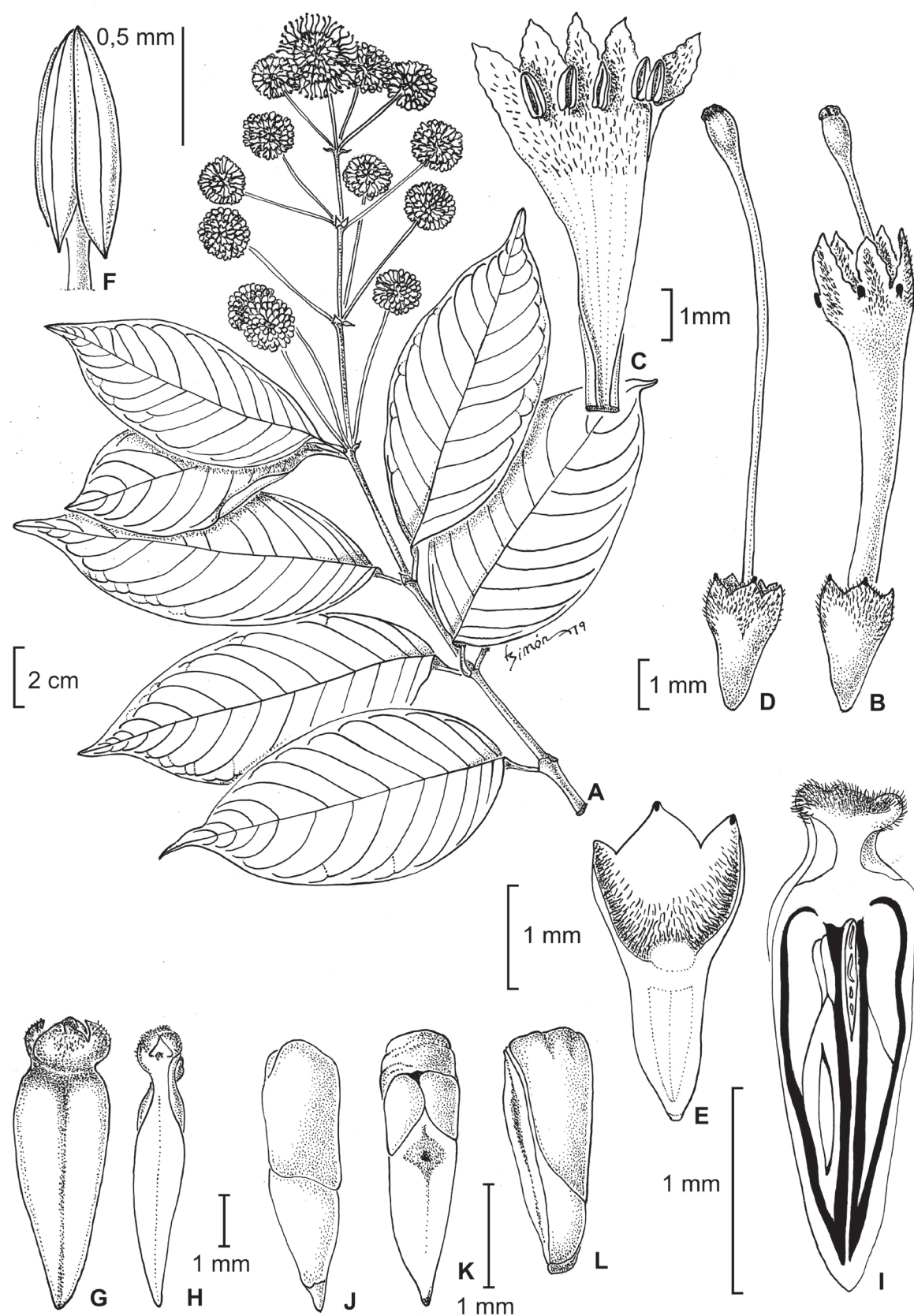


Figure 6. *Cephalanthus glabrifolius*. A. Flowering branch. B. Flower. C. Unfolded corolla. D. Hypanthium, style, and stigma. E. Longitudinal section through the hypanthium. F. Stamen. G. Dorsal view of schizocarp. H. Ventral view of the mericarp. I. Longitudinal section through the schizocarp. J. Dorsal view of seed with aril. K. Subventral view of seed with aril. L. Lateral view of seed with aril. Drawn by Laura Simón.

Table 2. Morphological characters distinguishing *C. glabrifolius* and *C. tetrandrus*.

Characters		<i>Cephalanthus glabrifolius</i>	<i>Cephalanthus tetrandrus</i>
Leaves		glabrous on both sides, exceptionally with sparse hairs along the veins	puberulous or pubescent on adaxial side, rarely glabrescent, notoriously pubescent on abaxial side
Domatia		absent	present, tufts of hairs
Hypanthium	shape	obovate	cupuliform
	size	1.6–1.8 mm long	1.3–1.5 mm long
Calyx lobes	shape	broadly triangular, acute	broadly ovate, obtuse
	size	0.2–0.35 mm long	0.7–1 mm long
	dark colleters	on the apex of the lobes	at the interlobular sinuses
	indumentum	pubescent externally and internally	margin glabrous or puberulous
Corolla lobes	shape	ovate-acuminate or subtriangular	oblong, obtuse
	size	1.5–2 mm long	1–1.3 mm long
	indumentum	pubescent	glabrous
Internal indumentum of corolla tube		with a fringe of hairs on the inner side of the corolla lobes reaching the upper third of the tube	with a fringe of hairs from the base of the stamens to the base of the tube

– **Phú Thọ** • Tonkin, prov. de Phú Thọ, reserve for Cham Wong; 8 Sep. 1916; *Chevalier* 3213; P [P3820101] • Réserve forestière de Chan-Mong; 16–17 Apr. 1914; *Fleury* 32135; P [P05459514, P05459515]. – **Hanoi** • Phan Đình Giót, sur le bord des marais; 2 Jul. 1889; *Balansa* 2679; P [P03820109].

Notes. *Cephalanthus glabrifolius* was described by Bunzō Hayata in 1920. The species was synonymized under *C. tetrandrus* by Ridsdale (1976) without analysis of the type specimen. Despite his exhaustive review, some morphological characters were underestimated, e.g. presence or absence of domatia, and floral features (shape of hypanthium, size and shape of calyx lobes, shape and indumentum of corolla lobes, and internal and external indumentum of corolla tube). Particularly, the pattern of the distribution of hairs inside of the corolla was not addressed in detail. For a summary of the differences between *C. glabrifolius* and *C. tetrandrus* see Table 2 and the key to the species of *Cephalanthus*. Based on our study, we consider *C. glabrifolius* as a valid species.

4. *Cephalanthus occidentalis* L. (Linnaeus 1753: 95)

Figs 7, 8

Cephalanthus occidentalis var. *brachypodus* DC. (de Candolle 1830: 539) – Type: USA – **Texas** • Entre el Río de la Trinidad y Bexar [San Antonio]; Jun. 1828; *Berlandier* 1737; holotype: G; isotypes: BM, YU [YU065576].

Cephalanthus occidentalis var. *californicus* Benth. (Benth. 1849: 314). – Type: USA – **California** • Sacramento; *Hartweg* 1765; holotype: LD [LD1361264]; isotypes: BR [BR0000005577118], GH [GH00104738].

Cephalanthus berlandieri Wernham (Wernham 1917: 175) – Type: USA [Mexico] – **Texas** • Bexar [Bejar]; *Berlandier* 1620; holotype: BM [BM000606675].

Cephalanthus hansenii Wernham (Wernham 1917: 176) – Type: USA – **California** • Amador Co., Crow Point; 1500 ft; Jul. 1895; *Hansen* 1163; lectotype (designated by Ridsdale 1976): BM [BM000606652]; isolectotypes: L [L.2583462], LE [LE00017272], US [US00130640]; syntype: MEXICO • Chihuahua, San Diego Canyon, Sierra Madre; 6400 ft; Sep.; *Jones s.n.*; BM.

Cephalanthus occidentalis f. *lanceolatus* Fernald (Fernald 1947: 181) – Type: USA – **Virginia** • Southampton, North of Courtland, upper border of sandy and peaty shore of Darden's Pond; 15–16 Nov. 1946; *Fernald, Long & Clement* 15357; holotype: GH [GH00092512].

Cephalanthus occidentalis subsp. *californicus* (Benth.) A.E.Murray (Murray 1982: 19) – Type: same as for *Cephalanthus occidentalis* var. *californicus*.

Cephalanthus naucleoides DC. (de Candolle 1830: 539) nom. illeg. – Type: same as for *Cephalanthus occidentalis*.

Type. COUNTRY UNKNOWN • *s.col. s.n.*; lectotype (designated by Reveal in Jarvis et al. 1993): LINN [LINN118.1].

Description. Shrub or small tree up to 3 m tall, much branched. Stems glabrescent or puberulous, with numerous lenticels. Leaves 2 or 3 per node, pseudopetiolate, pseudopetiole with pubescent margin, 7–26 mm long; blades elliptic, narrowly ovate, or oblong, base acute, apex acuminate, glabrous, puberulous or pubescent adaxially, sometimes only pubescent on mid-vein abaxially, discolorous, 5–18 × 2–8 cm; principal lateral veins 6–10 on each side, visible abaxially, leaf domatia present, pockets, internally pilose; stipules ovate-acuminate to narrowly triangular, tardily deciduous, dark colleters present at the apex and margins, light colleters on the ventral (inner) side, intermingled with trichomes. Inflorescences pedunculate; peduncle 3–10

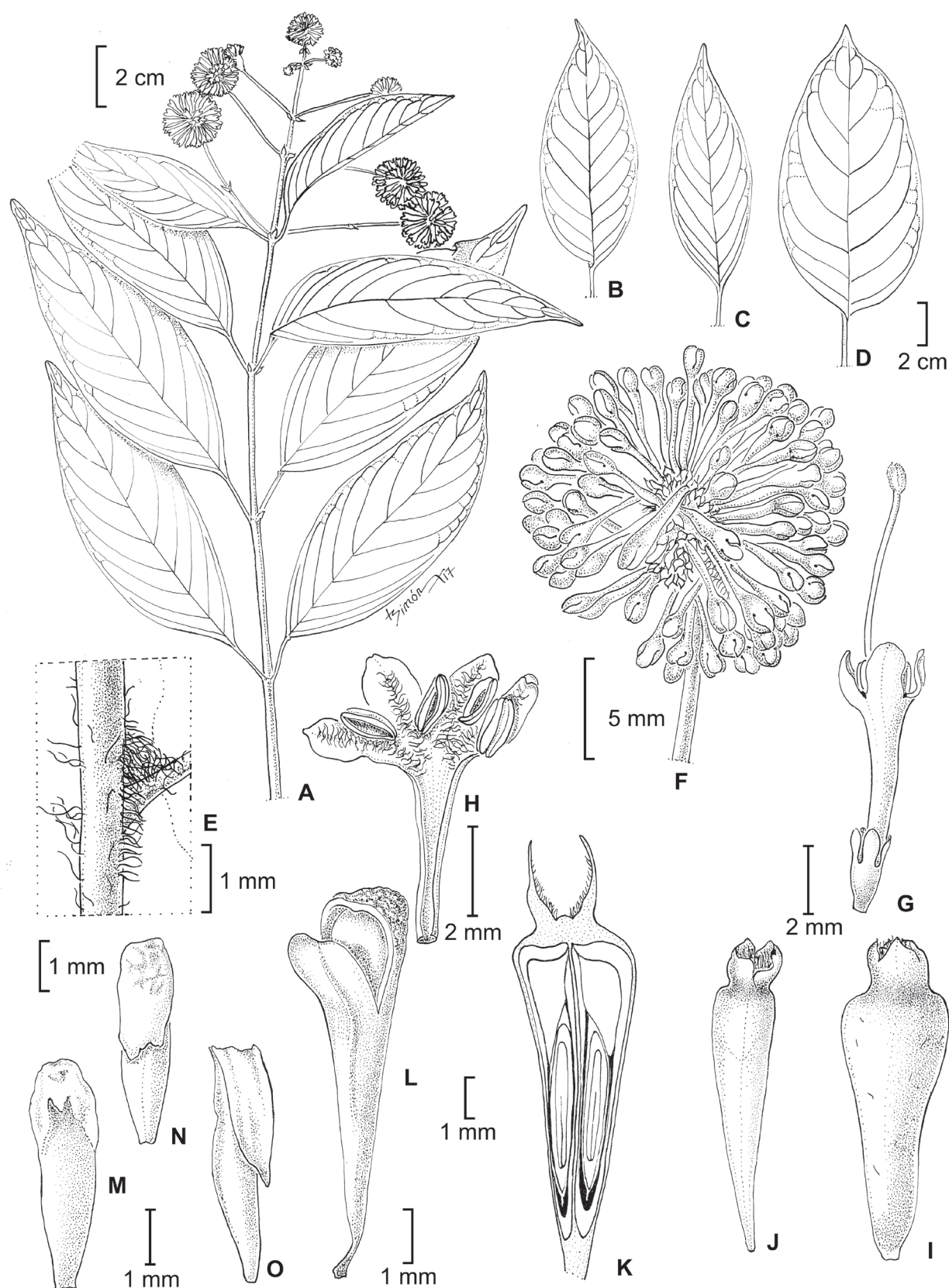


Figure 7. *Cephalanthus occidentalis*. A. Flowering branch. B–D. Variation in leaf form. E. Pocket with domatia as tuft of hairs. F. Partial inflorescence, in bud stage. G. Perfect flower. H. Unfolded corolla. I. Dorsal view of schizocarp. J. Ventral view of schizocarp. K. Longitudinal section through fruit and seed. L. Ventral view of mericarp with opening in apical region (slight manual pressure was exerted to provoke the opening). M. Subventral view of seed with aril. N. Dorsal view of seed with aril. O. Lateral view of seed with aril. Drawn by Laura Simón.

cm long, bracteate, dark colleters present at the apex and margin, bracteoles spatulate, puberulous, dark colleters present at the apex. Flowers perfect, calyx 4(–5)-lobed; hypanthium cupuliform, glabrous to densely pubescent at the base, 0.6–1.5 mm long; lobes obtuse, 0.3–0.6 mm long, externally puberulous, internally densely pilose, dark colleters present at the interlobular sinuses; corolla hypocrateriform, 4(–5)-lobed, 5–9(–12) mm long, lobes obtuse or ovate, internally with a longitudinal band of hairs, densely disposed, externally glabrous, 1–2 mm long, dark colleters present at the interlobular sinuses, tube internally and externally glabrous; stamens 4(–5), filaments filiform, glabrous, anthers large, sagittate, subsessile, 1–1.3 mm long; style filiform, 6–10 mm long; stigma capitate and exserted at flower maturity. Fruits narrowly obovate, glabrous, 5–7.5 mm long. Seeds 1.5–2.3 mm long; aril 1.4–1.8 mm long.

Phenology. Flowering from March to August, exceptionally from September to November. Fruiting from October to December. In its southernmost distribution (southern USA, Mexico, and Caribbean), it is possible to see flowers and fruit throughout the year.

Vernacular names. Buttonbush, common buttonbush, button-willow, buck brush, honey-bells, button ball, and riverbush.

Distribution. Native to the Northern Hemisphere, in Belize, Canada, Cuba, Guatemala, Honduras, Mexico, and USA (Fig. 8).

Habitat and ecology. *Cephalanthus occidentalis* occurs in places that are temporary flooded or waterlogged, such as the banks of rivers, streams, or wetlands. It has been cultivated in botanical gardens in Europe since colonial times for its profuse flowering and resistance to cold. In the USA and Mexico, it is common in gardens because of its rusticity and showy flowers.

Additional material examined. BELIZE • Maskall; 17°52'42"N, 88°18'47"W; 5–20 m; 10 Mar. 1934; *Gentle* 1254; MO • Stann Creek, ca 1 mile WSW of Hopkins, sea level, thickets in open marshland; 16°51'17"N, 88°17'51"W; 17 Apr. 1976; *Proctor* 35797; MO.

CANADA – **Quebec** • Ile Perrot; 1908; *Victorin s.n.*; AMD [AMD116817] • Missisquoi Bay Area, près Montreal; 23 Aug. 1959; *Hegnauer* 1959-775; L [L.2853429] • Rigaud, comté de Vaudreuil; 26 Jul. 1934; *Roy* 333 7; L [L.2853435], SI • Rigaud, comté de Vaudreuil; 23 Aug. 1935; *Roy* 4075; L [L.2853447]. – **Ontario** • Deep Bay, Sparrow Lake, wet shores, often in water; 7 Aug. 1935; *Kirk* 142; L [L.2853442]. – **Ottawa** • Pontiac Station, 30 miles west Hull, north shore of Ottawa river; 28 Aug. 1948; *Breitung* 7327; SI.

CUBA – **La Habana** • Border of Laguna Ariguanabo; 2 Jul. 1914; *A. León* 4337; US [US00794830, US00794844].

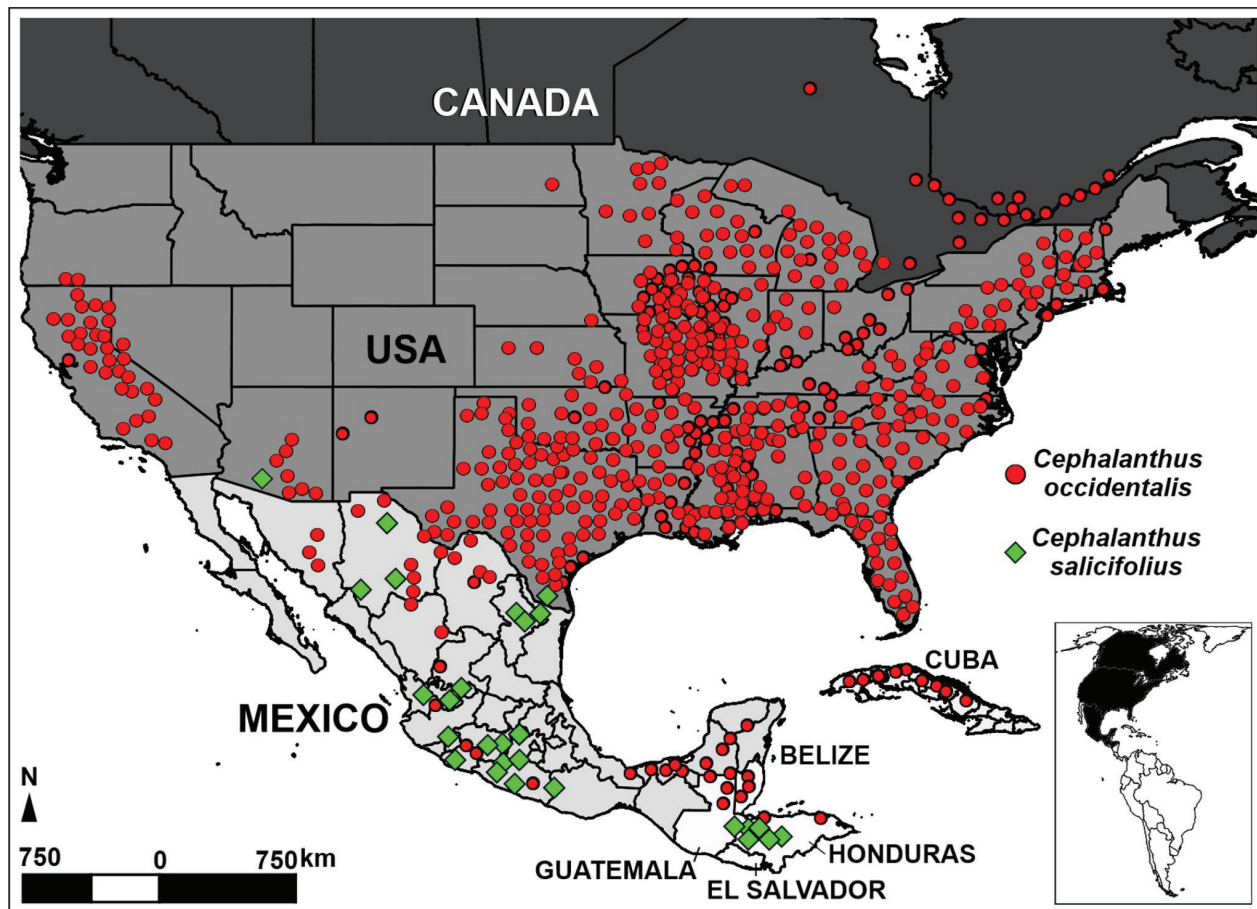


Figure 8. Distribution map of *Cephalanthus occidentalis* and *C. salicifolius*.

– **Las Villas** • On Gerhartz farm, 12 km E of Cascajal, shrub on edges of playa; Jun.–Aug. 1941; *Howard* 5584; MO, NY. – **Pinar del Río** • El Sablalo, Finca Sabanalamar; 22 Dec. 1937; *Killip* 32295; MO.

GUATEMALA – **Petén** • Quexil Turicentro, bordering the lake, in high forest; 16°55'10"N, 89°49'11"W; 5 Feb. 1970; *Contreras* 9596; MO • Sayaxche; 16°31'35"N, 90°11'22"W; 5 May 1942; *Steyermark* 46270; MO.

HONDURAS – **Atlántida** • Tela, Triunfo de la Cruz, 1.4 km N of the Tela-Ceiba Hwy. on the road to El Triunfo de la Cruz; 15°48'N, 87°24'W; 5 m; 17 Apr. 1994; *Brant & Hazlett* 2879; MO. – **Gracias a Dios** • Brus Laguna, Isla de Pájaros, Laguna Rapa, al sur[este] de Brus Laguna, nivel del mar; 15°43'36"N, 84°27'27"W; 5 m; 17–27 Apr. 1971; *Nelson & Hernández Meza* 1064; MO.

MEXICO – **Chihuahua** • Vicinity of Aldama; 15–17 May 1908; *Palmer* 234; K, MO, US [US00869798]. – **Coahuila** • Sierra Encantada at Rincón de María, about 5 miles S of Hacienda La Babia, with base camp at 1130 m, and going up canyon to the horizontal roadway that passes across the limestone rincón, these from the horizontal roadcut to 3.5 miles NE of the path up; 28°29'N, 102°01'W; 1700 m; 22 Aug. 1998; *Henrickson et al.* 20621; MO. – **Durango** • Jun.–Sep. 1896; *Palmer* 201; MO. – **Guerrero** • Juan R. Escudero, Tierra Colorada, carretera a la Presa Gral. Figueroa, antes de Puente Río; 17°07'40"N, 99°31'30"W; 350 m; 2 May 1965; *Kruse* 1479; MO. – **Michoacán** • La Huacana, presa Gral. Francisco J. Múgica, alrededores de la presa, puente de piedra; 19°03'35"N, 102°00'25"W; 333 m; 4 Sep. 2010; *Cortés Flores & Carmen Coba P.* 46; MEXU, MO. – **Tabasco** • Macuspana, Laguna El Gusano, aprox. 1 hora por lancha del sitio llamado el bordo Hormiguero, al norte de Cd. PEMEX, borde de la laguna; 18°05'48"N, 92°23'41"W; 7 m; 16 Mar. 1998; *Novelo R. & Ramos V.* 2293; MO. – **Veracruz** • Las Choapas, 11 km del entronque Las Choapas con la carretera Cardenas-Coatzacoalcos; 18°03'N, 94°06'W; 50 m; 14 Apr. 1973; *Orozco S.* 103; MO.

USA – **Arizona** • Maricopa Co.; 628 m; 6 Jul. 2012; *Markings & Butler* 3959; ASU, SI • Maricopa Co., Bosque Nacional de Tonto; 33°47.93'N, 11°29.49'W; 25 Jun. 1999; *Landrum* 9539; CTES. – **California** • Clear Lake, Goosenek point, in pebbly shore of lake; 1320 ft; 28 Jul. 1974; *Thorne* 45065; L. – **Illinois** • Jackson Co.; 37°35'08"N, 89°27'44"W; 110 m; 21 Oct. 2014; *Nee* 61696; MO, SI. – **Missouri** • Saint Louis City, Missouri Botanical Garden's Monsanto Research Center campus, by southwest corner of building, south of chiller equipment; 6 Sep. 2017; *Taylor* 12977; CTES, MO. – **New Jersey** • Burlington Co.; 23 Jul. 1981; *Ley* 42199; CTES. – **New York** • Bronx; 40°52'03"N, 73°52'34"W; 16 m; 6 Jun. 2006; *Nee* 54470; SI. – **North Carolina** • Biltmore, swamps and borders of streams; 19 Jul. – 30 Sep. 1897; *Biltmore herbarium* 1890; L [L.2853436]. – **Ohio** • Mantua, road 34, near old Coyle's Farm; 14 Sep. 1963; *Bruyne s.n.*; L [L.2853437]. – **Texas** • Aransas Pass Co., on N. Mc Campbell Road, between Rabbit Road and Jacoby Lane; 3 Jun. 1998; *Fryxell* 5137; CTES • Comanche Co., near Cache; 25 Jun. 1913; *Stevens*

1319; SI. – **Washington DC** • Potomac River bij Chain Bridge; 6 Sep. 1952; *Holthuis* 519; L [L.2853446]. – **Wisconsin** • Richland Co.; 210 m; 14 Jul. 1978; *Nee* 16308; SI • Richland Co., 2 miles NW OF Blue River, floodplain of the Wisconsin River, along the channel (usually with flowing water) flowing into Garner Lake; 43°11'55"N, 90°36'00"W; 204 m; 27 Sep. 2014; *Nee* 61662; SI.

Notes. *Cephalanthus occidentalis* has a profuse synonymy, especially with names published by Constantine S. Rafinesque between 1828 and 1838. Rafinesque published four new species (*C. acuminatus*, *C. obtusifolia*, *C. obtusifolius*, and *C. pubescens*) and four infraspecific taxa (*C. occidentalis* var. *macrophylla* Raf., var. *macrophyllus* Raf., var. *obtusifolius* Raf., and var. *pubescens* Raf.), all synonymized under *C. occidentalis* by Ridsdale (1976). As yet, no type specimens were found that support these names, and therefore, they were not included in the synonymy.

5. *Cephalanthus salicifolius* Bonpl. (Humboldt and Bonpland 1809: 63)

Figs 8, 9

Cephalanthus occidentalis var. *salicifolius* (Bonpl.) A.Gray (Gray 1884: 29) – Type: same as for *Cephalanthus salicifolius*.

Cephalanthus occidentalis subsp. *salicifolius* (Humb. & Bonpl.) Borhidi & Diego (Borhidi and Diego-Peréz 2008: 75) – Type: same as for *Cephalanthus salicifolius*.

Cephalanthus peroblongus Wernham (Wernham 1917: 176) – Type: MEXICO • Tepic; 31 May 1837; *Barclay* 1193; holotype: BM [BM000606674]; isotype: US [US00130642].

Type. MEXICO • Crescit juxta Acapulco Mexicanorum, in calidis; *Bonpland s.n.*; holotype: P [P00135084].

Description. Shrub or tree up to 6 m tall, much-branched. Stems glabrous, sparsely cover with lenticels. Leaves 2- or 3-verticillate, pseudopetiolate, pseudopetiole glabrous or puberulous, 1–10 mm long; blades narrowly ovate or linear-elliptic, glabrous, base acute, apex acute or acuminate, with a dark colletter at the apex when young, discoloured, 3–14 × 0.6–3 cm; principal lateral veins 8–10 on each side, leaf domatia present as tufts of hair; stipules broadly triangular, tardily deciduous, dark colletters present on the apex and margins, light colletters at the ventral (inner) side, intermingled with numerous trichomes. Inflorescences pedunculate, peduncle 2–5 cm long, bracteate, bracts foliaceous, with dark colletters at the apex and margins, bracteoles spatulate, puberulous, with dark colletters at the apex. Flowers perfect; calyx 4(–5)-lobed, hypanthium cupuliform, glabrous to densely pubescent at the base, 1.7–2.5 mm long, lobes oblong or rounded, pubescent on the external (dorsal) face, densely hairy on the internal (ventral) face, with dark colletters at the apex of the lobes, 0.3–0.6 mm long; corolla hypocrateriform, 4(–5) lobed, 5–12 mm long, on the external side with dark colletters at the interlobular sinuses,

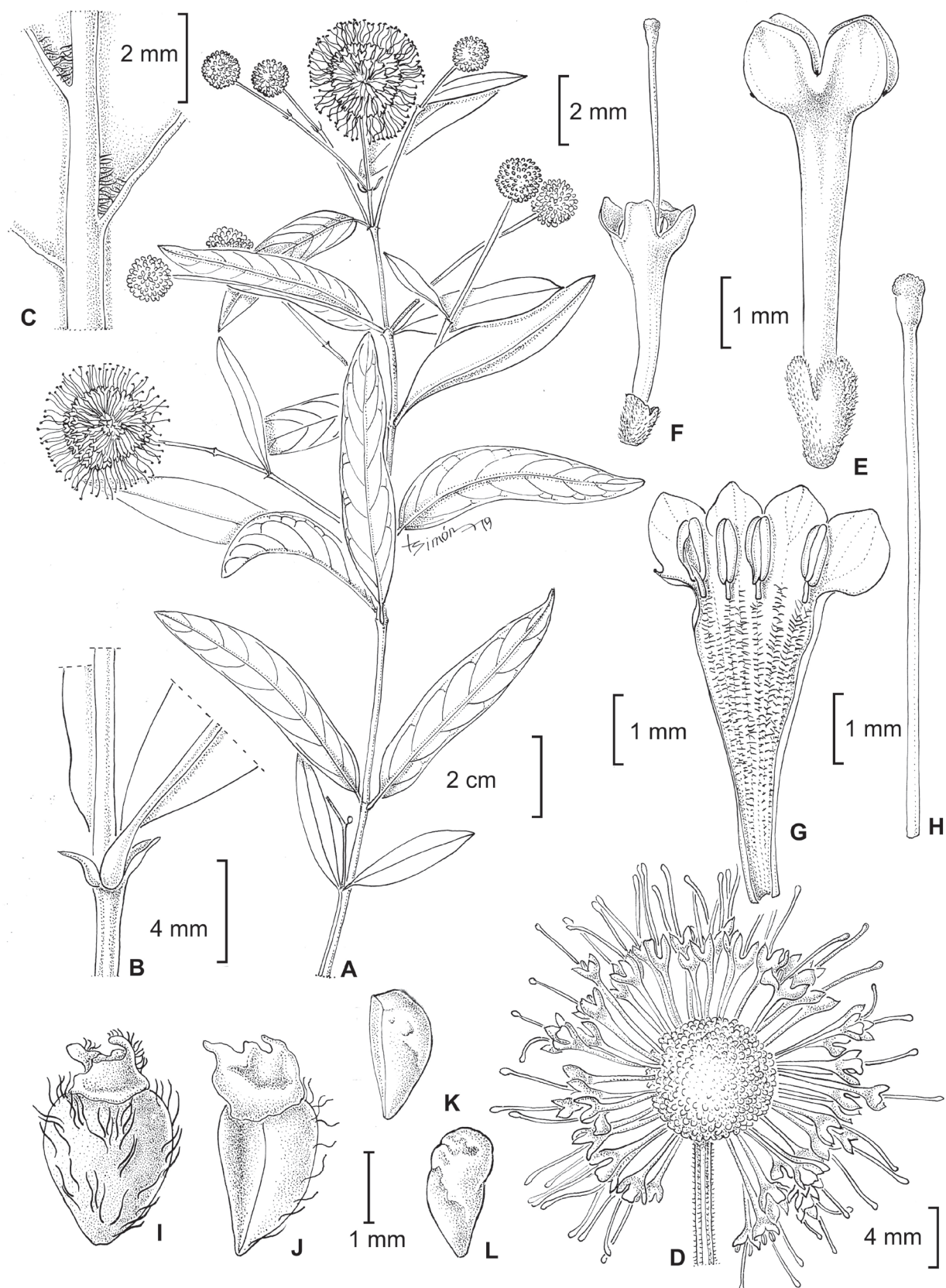


Figure 9. *Cephalanthus salicifolius*. A. Flowering branch. B. Stipule. C. Axils of the middle and secondary veins showing domatia as tufts of hairs. D. Partial inflorescence. E. Perfect flower. F. Flower with exerted style and stigma. G. Unfolded corolla. H. Style and stigma. I. Dorsal view of schizocarp. J. Lateral view of mericarp. K. Lateral view of seed with aril. L. Dorsal view of seed with aril. Drawn by Laura Simón.

lobes obtuse to ovate, internally with a pubescent band, externally glabrous; 0.8–1.5 mm long, tube internally and externally glabrous; stamens 4(–5), filaments filiform, glabrous, anthers subsessile, sagittate; ovary 2-carpellate, 2-locular, each locule 1-ovulate; style filiform, 3–6 mm long; stigma capitate and exerted at flower maturity. Fruits obpyramidal or turbinate, pubescent, 4.5–5 mm long. Seeds 1.2–2.2 mm long; aril 1.5–1.8 mm long.

Distribution. *Cephalanthus salicifolius* occurs in El Salvador, Honduras, Mexico (Colima, Chihuahua, Coahuila, Hidalgo, Nayarit, and Morelos), and USA (Texas and Arizona) (Fig. 8).

Habitat and ecology. Edges of streams, lagoons, or lakes, in flooded and waterlogged areas. Frequently forming dense populations, however, it is usually found scattered or as isolated plants along riverbanks.

Phenology. It flowers from March to July, and bears fruit in August to December. Flowers or fruits may be found throughout the year on isolated plants, especially in the southernmost populations.

Additional material examined. EL SALVADOR – **Morazán** • Río Sapo, area burnt ca 20 years prior; 13°55'47"N, 88°06'01"W; 678 m; 25 Mar. 2002; *Monro* 3808; MO.

HONDURAS – **Choluteca** • Common along Rio Pespire, vicinity of Pespire; 15 Mar. 1967; *Molina* 20620; US [US02370571]. – **El Paraíso** • Yuscarán, Aldea El Rodeo, quebrada Las Zarcas, road to Oropoli; 13°53'06"N, 86°46'47"W; 420 m; 3 May 2000; *Molina R. et al.* 34926; MO. • El Paraíso, common along river thickets, in pine forest area along fossil deposit of arenal river bed, 3 Kms East of Ojo de Agua; 25 Feb. 1969; *Molina* 23361; US [US02370569]. – **Francisco Morazán** • Yaguasire, campo abierto; 10 May 1981; *Midence* 117; US [US02370570]. • Lempira, Municipio San Miguelito, common along river, pine forest area El Comedero, road to Gracias; 4 Mar. 1969; *Molina* 24007; US [US02370567].

MEXICO – **Colima** • Ruta 110, Colima a Pihuamo, Km 215 a Río Salado; 19°11'32"N, 103°41'45"W; 300 m; 18 Jan. 1982; *Lorence et al.* 3798; MO. – **Chihuahua** • Allende, Valle de Allende, Balneario Ojo de Talamantes; 26.90°19'93"N, 105.45°73'49" W; 5400 ft; 29 Aug. 1990; *Swagel* 272; MO. – **Coahuila** • Castaños, San Lázaro, near the northern entrance of El Puerto de San Lázaro; 16 Jun. 1936; *Wynd & Muller* 118; MO. – **Hidalgo** • Jojutla; 31 Aug. 1902; *Pringle* 9822; SI. – **Nayarit** • San Blas, 3.8 Km al SE de Tecuitata sobre camino a tierra El Cora, carr. Jalcoctan-Miramar; 21°26'16"N, 105°08'13"W; 10 Nov. 1994; *Flores F. & Téllez V.* 3435; CTES, MEXU. – **Morelos** • Cuernavaca; 16 Jan. 1901; *Pringle* 8474; SI.

USA – **Arizona** • Pima Co., Coronado National Forest T16S, R18E, Sec. 1. Coronado National Forest along Forest Rd. 35, Ash Creek drainage; 32°04'36"N, 110°27'W; 1140 m; 12 Sep. 1998; *Brant & Stone* 3982; MO, UMO. – **Texas** • Starr Co., Santa Margarita Ranch, on W side of State Highway 83 via Santa Margarita Road, which branches from highway ca 9 miles N and W of Roma, Bank of Rio

Grande; 26°28'34"N, 99°05'29"W; 185 ft; 7 Oct. 2017; *Yatskievych et al.* 17-162; MO, TEX.

6. *Cephalanthus tetrandrus* (Roxb.) Ridsdale & Bakh.f. (Ridsdale and Bakhuizen in Ridsdale 1976: 182)

Figs 3, 10

Nauclea tetrandra Roxb. (Roxburgh 1824: 125) – Type: same as for *Cephalanthus tetrandrus*.

Cephalanthus ratoensis Hayata (Hayata 1920: 52) – Type: TAIWAN • Girancho; 1904; *Kawakami* 34; holotype: TI [TI00080002].

Type. INDIA – **Meghalaya** • Khasia, M. Sillet; 1832; *F. da Silva s.n. in Wallich Cat.* 6101A; first-step lectotype (designated by Ridsdale 1976): K; second-step lectotype (**designated here**): K [K001067160]; isolectotypes: BR [BR0000005585892], K [K001123031], K [K001123032], P [P03820092]; syntypes: INDIA • [Assam]; *s.col. s.n.*; K [K000265514] • *s.col. s.n.*; K [K000265513] • *s.col. s.n.*; K [K000265509] • Goalpara; 14 Apr. 1814; *F. da Silva s.n. in Wallich Cat.* 6101B • [Uttar Pradesh], “Goruckpore” [Gorakhpur]; 11 May 1808; *F. da Silva s.n. in Wallich Cat.* 6101C; K [K001123034].

Description. Shrub 3–6 m tall, much-branched. Stems pubescent or puberulous, sparsely cover by lenticels. Leaves opposite, pseudopetiolate; pseudopetioles subcylindrical, glabrous or puberulous, 9–13 mm long; blades ovate or elliptic, puberulous or pubescent on both sides, or glabrous above and pubescent beneath, base rounded or subcordate, apex acute, subcoriaceous, discolorous, 7–10 × 3–5 cm; principal lateral veins 6–9 on each side, slightly discolorous, leaf domatia present as tufts of hair; stipules ovate, tardily deciduous, with dark colleters at the apex and margins, light colleters on the ventral (inner) side, intermingled with numerous trichomes. Inflorescences pedunculate; peduncle 2–6 cm long, densely pubescent, bracts foliaceous, with dark colleters at the apex and margins; bracteoles spatulate, densely pubescent, dark colleters on the apex. Flowers perfect; calyx 4- or 5-lobed, hypanthium cupuliform, glabrous or glabrescent externally, 1.3–2 mm long; lobes broadly ovate, apex obtuse, internally pubescent, glabrous externally, margin puberulous, 0.7–1 mm long, dark colleters present at the interlobular sinuses; corolla hypocrateriform, 4- or 5-lobed, 5–9 mm long, lobes oblong, obtuse, 1–1.3 mm long, internally glabrous, dark colleters present at the interlobular sinuses, tube internally with a fringe of hairs from the insertion of the stamens to the base, externally glabrous; stamens 4 or 5, filaments filiform, glabrous, ca 0.3 mm long; style filiform, 8–13 mm long; stigma capitate and exerted at flower maturity. Fruits obpyramidal or turbinate, glabrous, 4–6 mm long. Seeds 1.3–2 mm long; aril 1.6–1.9 mm long.

Distribution. The species grows in Bangladesh, China (Guangdong, Hainan, and Yunnan), Hong Kong, India (Assam, East Bengal, and Meghalaya), Laos, Taiwan, Thailand, and Vietnam (Fig. 3).

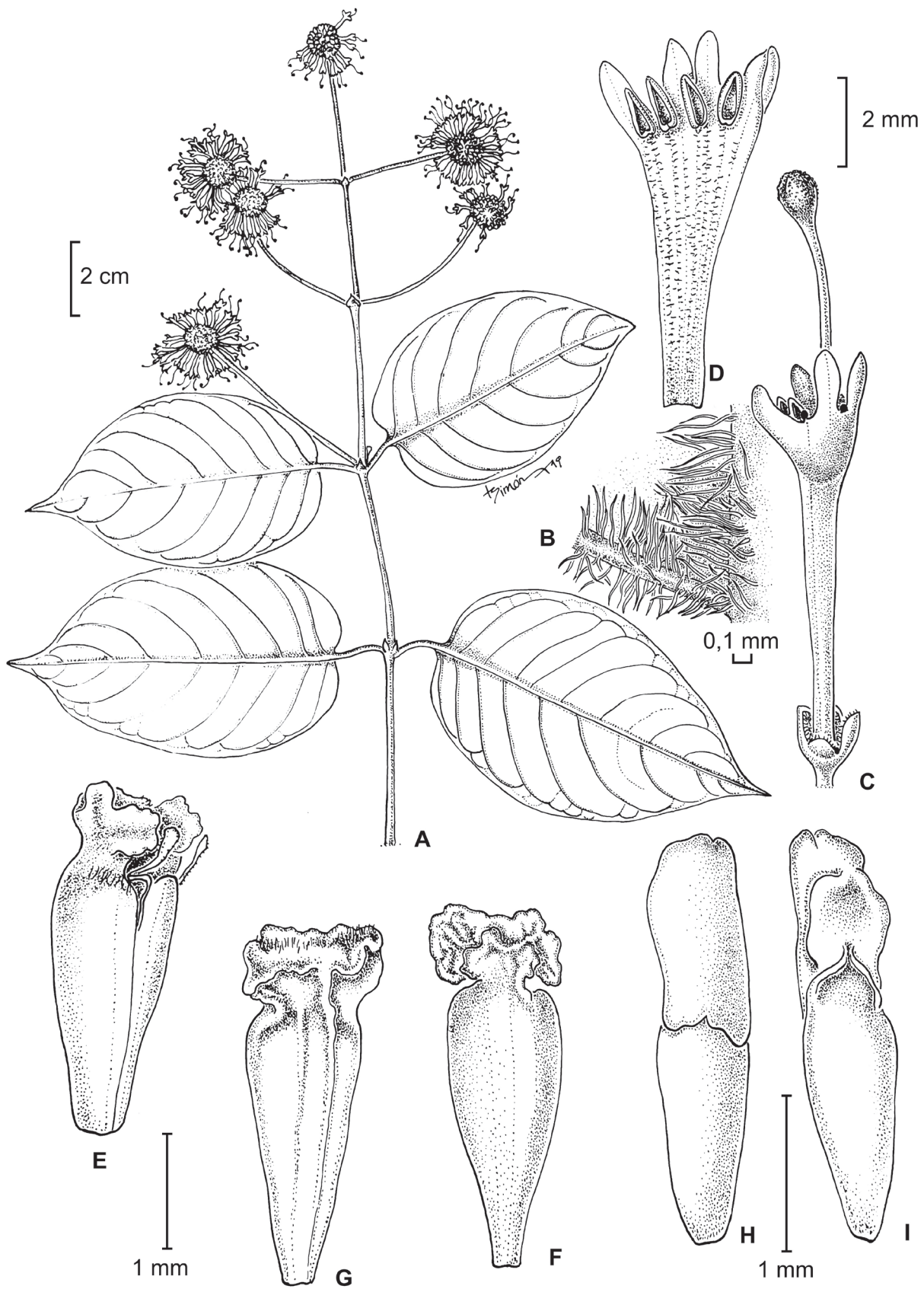


Figure 10. *Cephalanthus tetrandrus*. **A.** Flowering branch. **B.** Axil of the middle and secondary vein showing domatia as tuft of hairs. **C.** Perfect flower. **D.** Unfolded corolla. **E.** Side view of schizocarp. **F.** Ventral view of mericarp. **G.** Ventral view of schizocarp. **H.** Dorsal view of seed with aril. **I.** Subventral view of seed with aril. Drawn by Laura Simón.

Habitat and ecology. This species is typically associated with temporarily waterlogged areas, such as riverbanks, lakes, and lagoons. It forms especially dense populations in large lagoons. Mikhama and Sirisant (2016) considered the large populations of *C. tetrandrus* growing in lagoons as freshwater swamp forest (temporary inundated forest). Mikhama and Sirisant (2016) have studied natural populations in the north of Thailand (Nakhon Phanom province) and showed the important socio-cultural role and farming support for villagers that live in close proximity to these particular habitats. According to them, this interaction explains the good state of preservation of this species (at least locally) and its habitat. These waterbodies are the main source of water supply (for human consumption) and are also relevant in the water management for off-season rice farming.

Phenology. The species flowers from August to January and bears fruit from January to May.

Vernacular name. Kai chi muk (cock spur tree), Mak Tang Noi (*Spire* 327 (P)); Chai-wan (Kanlaya Mikhama, Nakhon Phanom University, Thailand, pers. comm.).

Additional material examined. CHINA • Habitat in provincia Cantoniensis Sinarum; *Loureiro* 67-1; P [P00150877]; wrongly cited as the holotype of *C. montanus* because it does not correspond with the protologue • Sep. 1845–1847; *Fortune* 15; P [P05458904] • Sep. 1845–1847; *Fortune* 15b; P [P05458910]. – **Guangdong** • Wan Tong Shan, (Ying Tak District); 6–24 Jun. 1932; *Tsui* 325; P [P05458909], US [US02370625] • Yang Shan and Vecinity, South of Linchow; 20 Oct. 1938; *Tsui* 615; P [P03820074] • Lung T'au Shan, along riverbank; 14 Jul. 1924; *Fungwanhui [To and Tsang]* 12856; P [P03820076]. – **Hainan** • Fung Muk Shan, (Taam Chau District), Sz Kai Taai Shue; 3 May 1928; *Tsang* 210; MO • Hainan Woh Ham Shi and Vicinity, Lam Ko District, Ma Yin Shu; 22 Apr. 1933; *Lei* 576; L [L.2853487], P [P05458903], US [US02370635]. – **Yunnan** • Du Yunnan, Arbres Kiao Kia [Qiaojia]; 400 m; Nov. 1910; *Maire* 6392; US [US02370640, US02369505]. HONG KONG • Lar Tai Shie, jardin de Hong-Kong; 1 May 1893; *s.col.* 396; P [P05458906]. INDIA • *Roxburg s.n.*; P [P03820106] • “Indes Orientalis”; 1859; *Hooker s.n.*; P [P03820102]. – **Assam** • “Nayaltia”; May 1902; *Chatterjee s.n.*; MPU [MPU1100692], P [P03820087] • Assam; *Jenkins s.n.*; P [P03820091], L [L.2853486] • *Jenkins s.n.*; P [P03820088]. – **[Bengal]** • East Bengal; *Griffith* 3090/1; K, P [P03820093] • Hortus suburbanus Calcuttensis, Bot. Gardens of Calcutta and Serampore; 1834–1841; *Voigt* 229; C, P [P05458908]. – **Meghalaya** • Shillong; May 1894; *King s.n.*; P [P03820085] • Phulbari, Garo Hills, near sea level, bush in swamp; 15 Apr. 1950; *Koelz* 25085; L [L.2853485]. LAOS • “Indo-Chine”; Dec. 1903; *Spire* 327; P [P3820103] • “Expedition du Me-Kong”, Sainyabuli; 1866–1868; *Thorel* 9199; P [P03820099, P03820100] • “Mekong Sani”, sur argile; 1080 m; May 1932; *Pételot* 4455; P [P03820110]. TAIWAN • Tomita-cho; 15 Dec. 1933; *Tanaka & Shimada* 13600; L [L.2853488, L.2853484], P [P05458900] • Taipeh; 6 Oct. 1897; *Yano* 36; LE.

THAILAND • “Siam”; Jan. 1924; *Kerr* 8337; TCD [TCD0017286].

VIETNAM • [North Vietnam], Tonkin Occidental, Khang Chúóng; 26 May 1882; *Bon s.n.*; P [P03820083, P05458911] • Khang Chúóng, ad oras aquarum; 26 May 1882; *Bon* 1593bis; P [P03820090] • “Tonkin”; 1909; *d'Alleizette* 219; P [P03820105, P03820094]. – **Hải Phòng** • Tonkin, dans les facies; 15 Jan. 1886; *Balansa* 637; P. – **Hanoi** • Pagode de Balny, près de Hanoi, bord des marais; Apr. 1891; *Balansa* 4802; P [P03820072]. – **Thừa Thiên-Huế** • 14 Apr. 1910; *Bauche* 72; P [P03820098] • 16 Apr. 1910; *Bauche* 33; P [P03820107].

Notes. Roxburgh (1824) described *Nauclea tetrandra* based on specimens deposited at the Kew herbarium and belonging to Wallich's catalogue (Stafleu and Cowan 1983; Wallich 1834). According to Charles Baron Clarke's notes on the “Khasia” localities of Wallich's catalogue, places labelled as “M. Sillet” belong to Meghalaya State (notes posthumously published in an anonymous text, Anonymous 1913). According to our observations, at the Kew herbarium, there are several specimens that can be considered as part of the original materials of *Nauclea tetrandra* (see type section). Ridsdale (1976) made the combination *Cephalanthus tetrandrus* (as “tetrandra”) mentioning as type material “Wallich Cat. 6101A” deposited in K; an action that is here considered an inadvertent lectotypification. However, in the Kew herbarium, there are duplicates of the same collections of *F.A. Silva* listed as belonging to Wallich's catalogue and also identified as “Wallich Cat. 6101A”. Duplicates of this collection can be found in the BR and P herbaria. Thus, a second-step lectotype must be designated following Turland et al. (2018: article 9.17).

Sylvainia M.F.Romero & R.M.Salas, **gen. nov.**
urn:lsid:ipni.org:names:77315541-1

Type species. *Sylvainia natalensis* (Oliv.) M.F.Romero & R.M.Salas.

Diagnosis. *Sylvainia* differs from *Cephalanthus* in the plants being erect in open areas to climbing in forests, usually in high lying non-floodable habitats (vs plants erect and associated with waterlogged or periodically inundated habitats); leaves opposite, with leaf domatia in crypts (vs leaves 2–4-verticillate, domatia mostly as tufts of hair, less common as crypts); plants without dark colleters (vs dark colleters present on leaves and stipules, bracts, bracteoles, calyx, and corolla); inflorescences in terminal glomeruli (vs inflorescences thyrsoïd, mostly in pleiochasia); corolla tubular, tube internally glabrous, externally reddish, throat greenish, with blackish lobes (vs corolla infundibuliform or hypocrateriform, uniformly whitish), lobes with margins rolled inwards, internally pubescent, tube internally glabrous (vs lobes with margin not rolled inwards, internally glabrous or pubescent, tube internally with a fringe of hairs), stamens with filaments equal or longer than the anthers (vs stamens subsessile); fruit fleshy, endozoochorous (vs fruit dry, schizocarpic,

autochorous or hydrochorous); seeds with an aril shorter than half the length of the seed (vs aril longer than the length of the seed).

Etymology. The genus is dedicated to Dr Sylvain G. Razafimandimbison, a specialist of Rubiaceae, especially of the tribe Naucleaeae.

Sylvainia natalensis (Oliv.) M.F.Romero & R.M.Salas, comb. nov.

urn:lsid:ipni.org:names:77315542-1

Figs 11A–M, 12

Cephalanthus natalensis Oliv., Hooker's Icones Plantarum 14: 22–23, t. 1331. 1881. (Oliver 1881).

Type. SOUTH AFRICA • Natal; *Gerrard* 1495; lectotype: first-step lectotype (designate by Ridsdale 1976): K; second-step lectotype (**designated here**): K [K000394935] (“Natal; *Gerrard* 1945; received 1865”); isolectotype: K [K000394934] (“Natal & Zulu-Land; Coll. *Gerrard*, purchased 1872”); syntype: SOUTH AFRICA • Transvaal, chiefly near Lydenburg; Dec. 1873; *Atherstone s.n.*; K [K000394933].

Description. Shrub or small tree 3–4 m tall, much-branched, occasionally climbing up to 12 m high or even reaching the canopy in forest. Stems pubescent, sparsely covered with lenticels. Leaves opposite, pseudopetiolate; pseudopetiole puberulous, 4–7 mm long; blades ovate or ovate-oblong, base rounded, cordate or acute, apex acute or obtuse, glabrous, 2–5 × 1–2.5 cm; principal lateral veins 4–6 on both sides, visible abaxially, leaf domatia present as crypts, internally pilose; stipules acuminate, tardily deciduous, dark colleters absent, only with light colleters on the ventral (inner) side. Inflorescences pedunculate; peduncle 2–5 cm long, pubescent, bracteate, bracteoles filiform or spatulate, puberulous, dark colleters absent. Flowers sessile; calyx 4- or 5-lobed, hypanthium cupuliform, puberulous, 0.9–1.9 mm long; lobes ovate, puberulous, 0.1–1 mm long; corolla tubular, 4- or 5-lobed, 6–11 mm long, without dark colleters, lobes oblong, with margin rolled inwards, internally pubescent, externally glabrous, 0.6–1.1 mm long, tube internally and externally glabrous; stamens 4 or 5, filaments filiform 1.2–1.4 mm long, glabrous, anthers subsessile, sagittate, 1–1.3 mm long; ovary 2-carpellate, 2-locular, each locule 1-ovulate; style filiform, 7–15 mm long; stigma slightly claviform to almost inconspicuous, exerted at flower maturity. Fruits fleshy, 3–4 mm long, obovate or ovate, glabrous, lilac, white to pink, with a coriaceous pericarp when dry. Seeds concave-convex, sub-rhomboid in outline, surface minutely reticulate, 1–1.5 mm long; aril 0.4–0.5 mm long, white, slightly rough and spongy.

Habitat and ecology. *Sylvainia natalensis* grows in humid forest, commonly found in forest edges and occasionally reaching the canopy of associated trees (of 12 m in height). It also grows in grassland and savanna, usually associated with fire-protected rocky outcrops, but as a much-branched shrub. It grows at elevations between 1500 and 2000 m. The fruits are endozoochorous; they are

consumed by fruit-eating animals, notably birds, baboons, and monkeys (Boon 2010; Van Wyk and Van Wyk 2013).

Phenology. Flowers from August to January, mainly in the middle of spring; bearing fruit mainly from December to March, extending to May and June.

Vernacular names. Strawberry bush, tree-strawberry, quinine berry (English); witaarbeibos, witpruim (Afrikaans); mothotwe, motlholobu (Northern Sotho); murondo, mutsanda (Tshivenda); umfomfo (Siswati); umfimi, isamfomfo, umfomamasi, umkhombe (isiZulu); morodwe (Balobedu); musipwe, umfunfu (Shona) (Nenungwi 2017).

Uses. The fruits are occasionally eaten by people, either fresh or made into a preserve; the flavour is bittersweet, with a slight touch of lemon peel, but extremely bitter when not ripe, or when bruised or stored for a long time (Fox and Norwood Young 1982). The specimen *Bull s.n.* (K000394931) mentions: “plant produces a good edible fruit”. A similar observation is mentioned on *Galpin* 534 (K000394932): “fruit said to resemble a strawberry in appearance and to be edible”. In traditional ethnoveterinary uses, the leaves are ground into powder and used to treat eye problems in cattle (Coates Palgrave 1997; Boon 2010; Van Wyk and Van Wyk 2013). In gardening, it can be used in pots or flower beds (Johnson et al. 2002).

IUCN conservation assessment. Categorized as LC (Least Concern) (Foden and Potter 2005).

Additional material examined. ESWATINI • Fortesberg [interpreted]; 7 Mar. 1964; *Bayliss* 2063; US [US02370618] • Mbabane, Forest arms, Red Hills, rocky hill in the forest plantation *c/Pinus* spp.; 26°26'59"S, 31°1'0"E; 20 Mar. 1983; *Groenendijk & Koning* 262; WAG [WAG.1543215]. MALAWI • Southern Mt Mulanje, Big Ruvo Valley; 1800 m; 3 Nov. 1988; *J.D. Chapman & E.G. Chapman* 9390; K, MO.

MOZAMBIQUE – **Manica** • Sussundenga Dist., Chimanmani mountains, Chindoro area, massif. wp125; 19°48'59"S, 33°06'17"E; 1593 m; 2 Nov. 2014; *Timberlake & Chipanga* 6042; BR [BR0000025607932V], K.

SOUTH AFRICA • Natal; 17 Mar. 1880; *Bull s.n.*; K [K000394931] • In colle saxoso Van Reenen, Natal; 1524–1829 m; 16 Nov. 1897; *Wood* 6621; BR [BR0000017839945], US [US02370622]. – **Limpopo** • [Soutpansberg] About 15 miles from Sibasa into Zoutpansberg Mountains toward Lake Funduzi; 1524 m; 12 Mar. 1948; *Rodin* 4109; US [US02370617] • Soutpansberg; 9 Aug. 1937; *Smuts* 3283; K. – **Mpumalanga** • Graskop, Diepdriest, Department of Forestry, *Eucalyptus* plantation; 11 Sep. 1975; *Balsinhas* 2771; PRE, WAG [WAG.1543224] • Badplaas (eManzana), Plaas Makatula, ca 6 km vanaf Badplaas-Machadodorp road; 3 Feb. 1987; *Behr & Crosby* 922; PRE • Transvaal orientalis, in regione civitatis Graskop, in collibus fruticosus et herbosis; 1200–1500 m; 10 Jul. 1962; *Bernardi* 8978; G, US [US02370619] • [Louwsburg] Ngotshe District, ca 55 km ESE of Vryheid and 31 km WNW of Nongoma, Farm Isihlengeni 689; 27°50'11.0"S, 31°20'22.6"E; 1186 m; 16 Feb. 2010; *Bester*

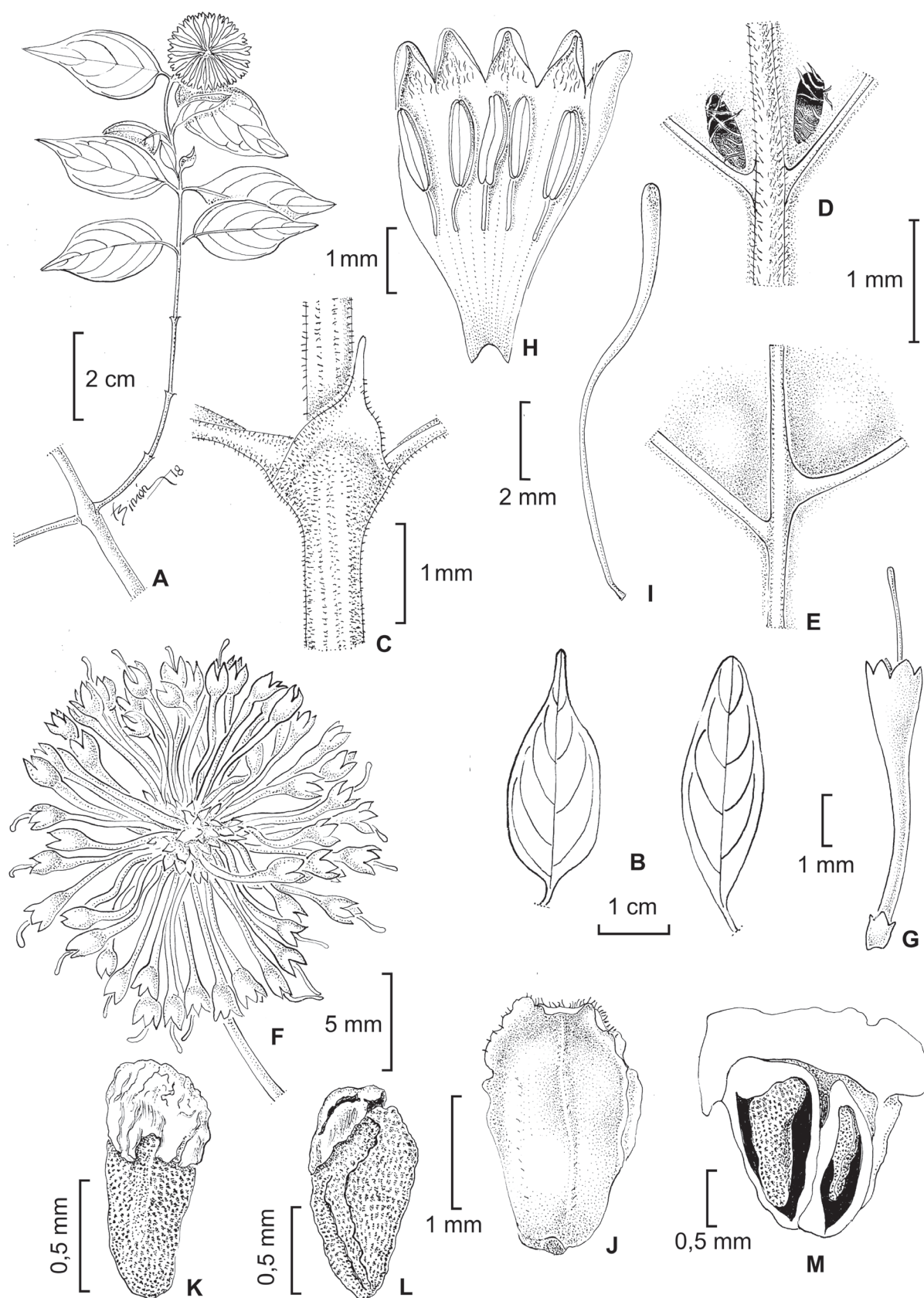


Figure 11. *Sylvainia natalensis*. A. Flower branch. B. Leaves. C. Stipule. D. Abaxial side of leaf with hairy crypt domatia. E. Adaxial side of leaf with bulges caused by domatia. F. Partial inflorescence. G. Perfect flower. H. Unfolded corolla. I. Style and stigma. J. Fruit, ventral side. K. Dorsal view of seed with reduced aril. L. Lateral view of seed with reduced aril. M. Longitudinal section through fruit and with one seed per locule. Drawn by Laura Simón.

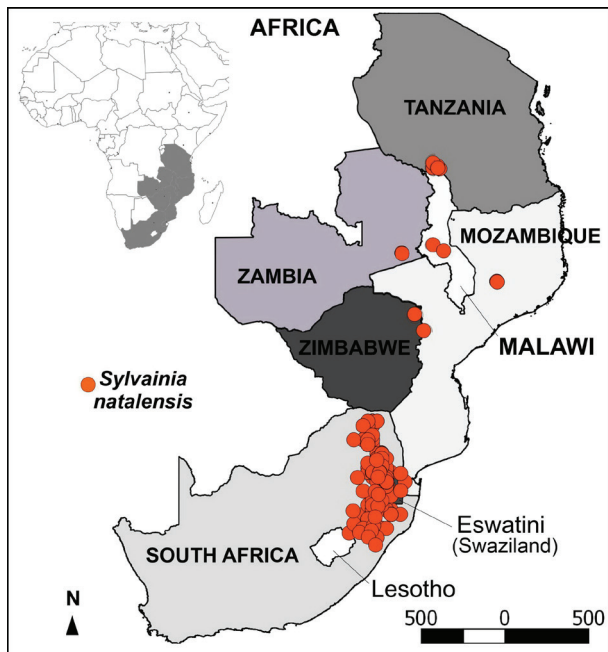


Figure 12. Distribution map of *Sylvainia natalensis*.

9869; PRE • Mountainsides Barberton; 914 m; Sep.–Oct. 1889; *Galpin* 534; K • 2 miles N of Potholes; 6 Mar. 1968; *Leistner & Mauve* 3261; K, PRE, WAG [WAG.1543221] • Sabie, Langverwag; 24 Aug. 1963; *Louw* 2836; AAU • Mariepskop, state forest; 24°34'57.9"S, 30°51'45.0"E; 1337 m; 6 Oct. 2007; *Maurin & Bank* 1583; JRAU, WAG [WAG.1488521] • Pilgrim's Rest; Nov. 1915; *Rogers* 14845; US [US02370620] • Barberton; 2 Feb. 1922; *Rogers* 21605; K • Waterval Onder; 1 Oct. 1979; *Ruprossev* 1227; K • east Transvaal, Sabie, Frankfort-plantasie; 13 Jan. 1963; *Sijde* 115; L [L.2853524] • Nkangala; 12 Jun. 1932; *Smuts* 21; K • Transvaal, District Lydenburg, bei der Stadt Lydenburg; Jan. 1886; *Wilms* 1815; AMD [AMD.116809].

TANZANIA– **Mbeya** • Rungwe Livingstone Mountains, foot trail from Bumbigi on steep ridge top N of Isalala River; 9°11'S, 33°52'E; 1900 m; 3 Mar. 1991; *Gereau & Kayombo* 4174; MO. – **Ruvuma** • Nyassa Hochland, Station Kymbila; 9°16'59"S, 33°37'0"E; Jan. 1912; *Stolz* 2164; L [L.2853522], U [U.1553392], WAG [WAG.1543216].

ZAMBIA • Klein Australe; Aug. 1930; *Hutchinson & Gillet* 4170; BR [BR0000017839884].

ZIMBABWE • Gazaland, Hills overlooking Jusitu R. on North, Rhodesia, raspberry-like fruits, making excellent preserves, common in mountain forests, especially in Mountain Pene; 5000 feet [1524 m]; 20 Sep. 1906; *Swynnerton* 654; US [US02370621] • District Melsetter, Jarka, in forest; 10 Oct. 1950; *Wild* 30393; BR [BR0000017839877] • District Umtali, Vumba Mountains, open grasslands; 5300 ft; 8 Feb. 1957; *Chase* 6740; BR [BR0000017839860] • S. Rhodesia, Vumba Mt. Insilimhumides; 10 Nov. 1938; *Lanjouw* 1312; U [U.1553393, U.1553394].

Notes. Schmidt et al. (2002) described the leaf domatia without any hairs inside. However, Romero et al. (2019), based on anatomical and micromorphological

examination, stated them to be crypt domatia, internally pilose. According to the protologue of *Cephalanthus natalensis*, this taxon was described from two specimens: *Gerrard* 1495 and *Atherstone s.n.*, both deposited in K. On the sheet of the type specimen, four branches were mounted; two of them correspond to the original material, *Gerrard* 1495 (K000394935 and K000394934), but the other branches do not and/or belong to other species. Ridsdale (1976) selected *Gerrard* 1495 as the lectotype, without distinguishing between the two specimens. He also mentioned that it is deposited in "CR", which corresponds to the National Herbarium of Costa Rica (acronym according to Thiers 2023), which can be interpreted as a clerical error, because all the type specimens studied by Daniel Oliver are deposited in K (Stafleu and Cowan 1981). The two collections of *Gerrard* 1495, mounted on the same sheet, can be identified as different specimens because they were incorporated in K at different times. One of the specimens was received in K in July 1865, and presents drawings made by the author of the species (K000394935), whereas the second specimen was acquired by the herbarium in March 1872 (K000394935). Although Ridsdale (1976) performed the lectotypification, he only mentioned "*Gerrard* 1495 (K)", without any mention that allows the two types to be differentiated. Thus, a second-step lectotype must be designated following Turland et al. (2018: article 9.17).

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