

THE SPECIES OF GIANT SENECIO (COMPOSITAE) AND GIANT LOBELIA (LOBELIACEAE) IN EASTERN AFRICA

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INTRODUCTION

The giant senecios and giant lobelias from eastern Africa have been cited as examples of adaptive radiation (Mabberley 1973, 1976; Carlquist 1974; Nordenstam 1978; Stott 1981; Beck 1986). Members of each group occupy a range of montane habitats on each of the tall mountains in eastern Africa. The giant lobelias have a more extensive geographical and ecological range than the giant senecios. The lobelias are found at higher latitudes and lower altitudes, and relatives are found elsewhere in the tropics (Knox et al., in press). There has been extensive convergent evolution within each group, a situation which Mabberley (1973) described as a “mosaic of variation.” There has also been extensive convergent evolution between the two groups, and with tropical alpine plants elsewhere (e.g., *Espeletia* in South America and *Argyroxiphium* in Hawaii), which provides compelling a priori evidence that the unusual features of these plants constitute adaptations to the peculiar climatic regime of “summer every day, winter every night” (Hedberg 1964).

My dissertation research has focused on the reconstruction of evolutionary history for the giant senecios and the giant lobelias. Each of these two case studies has been pursued using several lines of research including extensive fieldwork, phylogenetic analysis of morphology, restriction-site variation in chloroplast and nuclear DNA, chromosome counts, biogeographic analysis, and biochemical analysis of compounds in leaf tissue and secreted fluids. Monographic treatments for both of these groups are in preparation. In the interim, the need has arisen for revised taxonomies so that some facets of this project may be published with a consistent use of names prior to publication of the monographs. Presented below are brief discussions of the taxonomic history and problems within each group, along with a checklist of species and intraspecific taxa. Eleven species of giant senecio and twenty-one species of giant lobelia are recognized. Two new species and three newly recognized subspecies of *Lobelia* from Tanzania are described. Thirteen new combinations are proposed in *Dendrosenecio* and three new combinations in *Lobelia*.

THE GIANT SENECIOS

Hoffmann (1894) established *Senecio* section *Arborei* to accommodate the newly discovered *S. johnstonii* (Johnston 1886) along with woody species from Madagascar, Cameroon, Fernando Po, and St. Helena. Section *Arborei* was subsequently

purged of all but the East African species by Muschler (1909), independently emended by Humbert (1935), and renamed as subgenus *Dendrosenecio* by Hauman (1935). Hauman's description in French did not constitute valid publication after January 1 of that year, and so, Hedberg (1957) provided a Latin diagnosis to validate the name. Hauman distinguished subgenus *Dendrosenecio* primarily on life-form, and the inseparability of this group from the remainder of *Senecio* based on floral characteristics has been stated repeatedly (Cotton 1944; Hedberg 1957; Mabberley 1973, 1974a). Nordenstam (1977) revised the generic limits of *Senecio* and elevated *Dendrosenecio* to generic status (Nordenstam 1978), citing such features as "the pyramidal-paniculate synflorescence, the more or less biseriate involucre, and the continuous stigmatic surfaces of the disc styles." Jeffrey (1977) initially included the giant senecios in *Senecio*. He questioned Nordenstam's removal of the group (Jeffrey 1979), and classified the giant senecios as series *Arborei* in section *Crociseris* (Jeffrey 1986). In his most recent checklist, Jeffrey (1992) recognized the genus *Dendrosenecio* (Hauman ex Hedb.) B. Nord., and placed it in a primarily neotropical group of senecionoid genera in subtribe *Senecioninae*.

The segregation of *Dendrosenecio* is supported by evidence from DNA (Knox and Palmer, unpubl.) and biochemistry (Bohlmann & Knox, unpubl.) that demonstrates the lack of close relationship between the giant senecios and a narrowly delimited genus *Senecio*. The question concerning the origin of the giant senecios is currently unanswered, but the uniformly high chromosome number ($n = 50$) and the lack of meiotic irregularities (Knox & Kowal, in press) suggest that polyploidy in this group was not a recent event. Other segregate genera placed near *Dendrosenecio* (Jeffrey 1992) that include species with $n = 50$ may offer a starting point in the search for close relatives.

The taxonomic treatment of the giant senecios at the level of species and below is also complicated. The nature of colonial exploration in eastern Africa contributed to a proliferation of species descriptions such that most species were treated as narrow endemics. The size of the plants presented problems for collectors and resulted in many inadequate herbarium specimens (Hauman 1935; Hedberg 1957; Knox, in press). Adding to the confusion were erroneous descriptions of habit and habitat, and mixed collections such as those by J. W. Gregory from Mt. Kenya. E. G. Baker described Gregory's specimens as *Senecio keniensis* (Baker 1894a) and *Lobelia gregoriana* (Baker 1894b) with the leaves of the specimens switched (see Baker, 1894b, for an artist's reconstruction of one of these "species"). Fries and Fries (1922a, 1922b) rejected these names as *nomina confusa*, and from their own material renamed these species *S. brassica* and *L. keniensis*. As discussed by Thulin (1983a), the International Code of Botanical Nomenclature does not permit rejection of the original names, because satisfactory lectotypes can be selected from the original elements.

Hedberg (1957) discussed the taxonomic problems posed by the giant senecios, and reduced to synonymy several species based on minor vegetative differences or geographic separation. He also stressed the need for "comprehensive field studies by a botanist who has previously thoroughly mastered both the herbarium material available and the relevant literature." Mabberley (1973) addressed this problem as part of his dissertation and decided that the amount of differentiation was insufficient to maintain seventeen taxa of specific rank. His solution was to preserve the most distinctive species, *Senecio keniodendron*, to treat *S. brassiciformis* as a subspecies of *S. brassica*, and to submerge the remainder in a system of eight subspecies (and two varieties) in the highly polymorphic *S. johnstonii*.

Although Nordenstam (1978) disagreed with Mabberley's evolutionary interpretation based on Corner's (1949, 1954a, 1954b, 1964) Durian Theory, he considered Mabberley's taxonomic conclusions to be sound, and made no modification when he transferred the species to *Dendrosenecio*. However, Mabberley (1986) recognized earlier errors and reinstated *S. brassiciformis* at specific rank as *D. brassiciformis*, recognized *D. brassica* as a synonym of *D. keniensis*, and emended *D. johnstonii* subsp. *refractisquamatus* as *D. johnstonii* subsp. *adnivalis*. In the same year, Jeffrey (1986) retained the giant senecios in *Senecio*, and followed an alternative approach for *S. johnstonii* (discussed by Mabberley, 1973) by recognizing four geographic subspecies and twelve altitudinal varieties.

Jeffrey's (1992) acceptance of the segregate genus *Dendrosenecio* leaves us with the subgeneric classification of Mabberley (1973, 1986). Instead of reverting to Mabberley's classification in *Dendrosenecio*, or retaining Jeffrey's classification in *Senecio*, I offer below a provisional classification for *Dendrosenecio* for use in presenting my research results. This classification employs a synthetic approach similar to that defended by Nordenstam (1978) and Jeffrey (1979) and practiced by Mabberley (1973). Justification of this classification, along with any necessary refinement, will be presented in a full monographic treatment.

THE SPECIES OF GIANT SENECIO FROM EASTERN AFRICA

1. *Dendrosenecio adnivalis* (Stapf) E. B. Knox, comb. nov. *Senecio adnivalis* Stapf, J. Linn. Soc., Bot. 37: 521. 1906.

1a. *Dendrosenecio adnivalis* subsp. *adnivalis*.

1ai. *Dendrosenecio adnivalis* subsp. *adnivalis* var. *adnivalis*.

Distribution: Ruwenzori Mts., Zaire and Uganda.

1aii. *Dendrosenecio adnivalis* subsp. *adnivalis* var. *petiolatus* (Hedberg) E. B. Knox, comb. nov. *Senecio adnivalis* var. *petiolatus* Hedberg, Symb. Bot. Upsal. 15: 233. 1957.

Distribution: Ruwenzori Mts., Zaire and Uganda.

1b. *Dendrosenecio adnivalis* subsp. *friesiorum* (Mildbr.) E. B. Knox, comb. nov. *Senecio friesiorum* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 231. 1922.

Distribution: Ruwenzori Mts., Zaire.

2. *Dendrosenecio battiscombei* (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio battiscombei* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 1: 334. 1922.

Distribution: Aberdare and Mt. Kenya, Kenya.

3. *Dendrosenecio brassiciformis* (R. E. Fr. & T. C. E. Fr.) Mabb. in F. Vuilleumier and M. Monasterio, High Altitude Tropical Biogeography, 100. 1986.

Distribution: Aberdares, Kenya.

4. *Dendrosenecio cheranganiensis* (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio cheranganiensis* Cotton & Blakelock, Bull. Misc. Inform. 1937: 364. 1937.

4a. *Dendrosenecio cheranganiensis* subsp. *cheranganiensis*.

Distribution: Cherangani Hills, Kenya.

4b. *Dendrosenecio cheranganiensis* subsp. *dalei* (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio dalei* Cotton & Blakelock, Bull. Misc. Inform. 1937: 365. 1937.

Distribution: Cherangani Hills, Kenya.

5. *Dendrosenecio elgonensis* (T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio elgonensis* T. C. E. Fr., Svensk Bot. Tidskr. 17: 229. 1923.

5a. *Dendrosenecio elgonensis* subsp. *elgonensis*.

Distribution: Mt. Elgon, Uganda and Kenya.

5b. *Dendrosenecio elgonensis* subsp. *barbatipes* (Hedberg) E. B. Knox, comb. nov. *Senecio barbatipes* Hedberg, Symb. Bot. Upsal. 15: 230. 1957.

Distribution: Mt. Elgon, Uganda and Kenya.

6. *Dendrosenecio erici-rosenii* (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio erici-rosenii* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 330. 1922.

6a. *Dendrosenecio erici-rosenii* subsp. *erici-rosenii*.

Distribution: Mt. Muhi, Mt. Kahuzi, Virungas, and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

6b. *Dendrosenecio erici-rosenii* subsp. *alticola* (Mildbr.) E. B. Knox, comb. nov. *Senecio erici-rosenii* var. *alticola* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 230. 1922.

Distribution: Virungas, Zaire, Rwanda, and Uganda.

7. *Dendrosenecio johnstonii* (Oliv.) B. Nord., Opera Bot. 44: 42. 1978.

Distribution: Mt. Kilimanjaro, Tanzania.

8. *Dendrosenecio keniensis* (Baker f.) Mabb. in F. Vuilleumier and M. Monasterio, High Altitude Tropical Biogeography, 100. 1986.

Distribution: Mt. Kenya, Kenya.

9. *Dendrosenecio keniodendron* (R. E. Fr. & T. C. E. Fr.) B. Nord., Opera Bot. 44: 43. 1978.

Distribution: Aberdares and Mt. Kenya, Kenya.

10. *Dendrosenecio kilimanjari* (Mildbr.) E. B. Knox, comb. nov. *Senecio kilimanjari* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 229. 1922.

10a. *Dendrosenecio kilimanjari* subsp. *kilimanjari*.

Distribution: Mt. Kilimanjaro, Tanzania.

10b. *Dendrosenecio kilimanjari* subsp. *cottonii* (Hutch. & G. Taylor) E. B. Knox, comb. nov. *Senecio cottonii* Hutch. & G. Taylor, Bull. Misc. Inform. 1930: 15. 1930.

Distribution: Mt. Kilimanjaro, Tanzania.

- 11. *Dendrosenecio meruensis*** (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio meruensis* Cotton & Blakelock, Kew Bull. 2: 135. 1948.
Distribution: Mt. Meru, Tanzania.

THE GIANT LOBELIAS

The genus *Rhynchoptalum* was erected by Fresenius (1838; also 1839) to accommodate the discovery of the largest species of giant lobelia, the Ethiopian *R. montanum*, and was included the following year in the *Prodromus* by de Candolle (1839). This species was labeled by C. F. Hochstetter with the unpublished name *Tupa rhynchoptalum* in his distribution of W. G. Schimper's collections from Abyssinia. The genus *Tupa* had been recently described by Don (1834) for a group of Chilean species, and Richard (1850) published Hochstetter's name, along with his description of a second species, *T. schimperi*. A few years later, Ascherson (1869a, reported again in 1869b) presented another species, *T. deckenii* from Tanzania. Ascherson did not fully describe this species, but presented instead a table in which it was contrasted with *T. rhynchoptalum*. Vatke (1874) provided a more complete description when he illegitimately renamed this species *T. kerstenii*.

In *Genera Plantarum* (1873), Bentham submerged several allied genera into *Lobelia*. Section *Tupa* was restricted to the Chilean species, now known to be hexaploid (Lammers & Hensold 1992). Section *Rhynchoptalum* included African, Brazilian, Asian, and Pacific species now known to be tetraploid. Sections *Tylomium* and *Homochilus* also included robust (but not giant) tetraploid species, but each section contained at least one diploid species (Knox & Kowal, in press). Hemsley transferred the African species of giant lobelia to *Lobelia* in the *Flora of Tropical Africa* (1877). The names *L. montana* and *L. schimperi* were already in use for herbaceous species, and so *Rhynchoptalum montanum* (*Tupa rhynchoptalum*) was transferred as *L. rhynchoptalum*, and the Amharic vernacular was used to form *L. giberroa* for *Tupa schimperi*. As noted by Mabberley (1974b), *L. giberroa* was unfortunately presented in Hemsley's key, and later in *Index Kewensis*, as "*L. gibberoa*," an error that has been perpetuated (e.g., Baker 1898, 1908; De Wildeman 1922; Battiscombe 1926; Cotton 1944; Jex-Blake 1948; Dale & Greenway 1961; Coe 1967; Agnew 1974; Carlquist 1974). Schönland (1894) presented a broad concept of section *Tylomium* that included section *Rhynchoptalum*, an arrangement accepted by Fries and Fries (1922b) and Bruce (1934), but rejected by Hauman (1934). Fries and Fries, Bruce, and Hauman proposed various subsectional treatments to reflect the evolutionary relationships between the growing number of species described from eastern Africa.

Wimmer (1943, 1953, 1968) provided a treatment of Campanulaceae subfamily Lobelioideae for *Das Pflanzenreich*. Within the elevated subgenus *Tupa*, he restricted section *Rhynchoptalum* to species from eastern Africa, but excluded from this section one Tanzanian species, *Lobelia longisepala*. This he placed in section *Eutupa* subsection *Haynaldianae*, along with the Angolan *L. xongorolana*, the morphological sister-species of *L. stricklandiae*, which he retained in section *Rhynchoptalum*. The artificiality of Wimmer's classification was criticized by Mabberley (1974b) and is acknowledged by other workers (T. Ayers, T. Lammers, M. Thulin, pers. comm.).

Mabberley (1974b, 1975) retained Bentham's concept of section *Rhynchoptalum*, and proposed a subsectional treatment for the African species with suggestions concerning relationships with giant and herbaceous lobelias elsewhere in the

world. The most notable change with respect to specific treatment was his implementation (Mabberley 1974b) of Hedberg's (1957) suggestion that the six species of the *Deckenii* Group (Fries & Fries 1922b) be treated as subspecies. Thulin accepted this change in his treatment of Lobeliaceae for the *Flora of Tropical East Africa* (1984) and the *Flore d'Afrique Centrale* (1985), which are two parts of his regional treatment of this family (see also *Flora Zambesiaca*, 1983, and the *Flora of Ethiopia*, in press).

Since Thulin's treatment of the giant lobelias, three additional species from Tanzania have been recognized. *Lobelia morogoroensis* (Knox & Pócs 1992) had been previously collected as sterile material and was identified as *L. giberroa*. *Lobelia thuliniana* (proposed below; Fig. 2) had been previously collected as fertile material, but was identified variously as *L. giberroa* or *L. mildbraedii* (discussed in Knox, in press). The existence of the third new species, *L. ritabeaniana* (proposed below; Fig. 1), was predicted by Mabberley (1974b). During fieldwork in the Ukaguru Mountains, he discovered vegetative, but morphologically distinctive, plants (later named *L. sancta*; Thulin 1980), and he noted that "it is very likely that this or a similar species will be found on the upper slopes of the Nguru Mts., nearby."

In addition to the inclusion of new species, two other modifications of Thulin's treatment are made here. *Lobelia acrochila* has been elevated from varietal to species rank. This change was proposed in an unpublished manuscript by C. Puff in 1983, but Thulin (pers. comm.) considered the change unwarranted given the regional pattern of variation. Mabberley (1974b) treated *L. rhynchopetalum* var. *acrochilus* as a synonym of *L. rhynchopetalum* on the basis of the material available at the time, and his description of the variation reflects the fact that he was unable to inspect these plants in the field. In contrast, Thulin visited many of the sites that were accessible in the early 1980's and, with some reservation, felt that varietal treatment should be maintained. A specimen collected by J. Gillett (Gillett 5317) in 1933 from Gara Mulata, Harerge Region, that provided a distinctly intermediate combination of leaf and floral forms was considered of particular importance. This site has not been readily accessible, and the fieldwork needed to clarify the matter has not been conducted.

Some clarification was provided during a conversation with Mr. Gillett in 1989. Having promised to explain my reasons afterward, I asked him to recall any details concerning his collection of "a giant lobelia on Gara Mulata." After an initial disclaimer that memories fade with the passage of 56 years, he provided a very vivid and detailed account of the ascent, the vegetation, and his encounter with the giant lobelia. While describing the section of the inflorescence taken from a small plant growing on moist, flat ground, and the leaf taken from a "healthier" vegetative individual with the leaf-rossette borne on a well-developed trunk, growing among *Erica* shrubs on a nearby slope, Mr. Gillett interrupted himself with the conclusion that as a young botanist he had probably made a mixed collection. This anecdotal evidence provides insight into the origin of the most anomalous specimen. The prospect of peace in Ethiopia raises hope that the fieldwork needed to resolve this situation fully may be contemplated in the near future.

The final departure from Thulin's treatment is my classification of the *Lobelia deckenii* group. A conflict in the phylogenetic hypotheses suggested by morphology and chloroplast DNA evidence indicates a possible hybrid origin for *L. bequaertii* involving some ancestral member of the *L. deckenii* group and the

ancestor of the *L. wollastonii*-*L. stuhlmannii* species pair. The remaining members are classified as three species on the basis of comprehensive field studies. The three isolated (and formerly poorly known) populations of *L. burtii* are given subspecific rank to reflect the differentiation among them. Two altitudinal subspecies of *L. deckenii* on Mt. Kilimanjaro are recognized on the basis of ecological and morphological differentiation. The remaining members are treated as subspecies of *L. gregoriana*, the valid name for "*L. keniensis*" when treated at specific rank (Thulin 1983b).

THE SPECIES OF GIANT LOBELIA FROM EASTERN AFRICA

1. ***Lobelia aberdarica*** R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 403, figs. 5, 6a-d. 1922.
Distribution: Mt. Elgon, Cherangani Hills, Aberdares, and Mt. Kenya, Uganda and Kenya.
2. ***Lobelia acrochila*** (E. Wimm.) E. B. Knox, comb. nov. *Lobelia rhynchopetalum* var. *acrochilus* E. Wimmer, Ann. Naturhist. Mus. Wien 56: 368. 1948.
Distribution: Arsi, Bale, and Harerge Regions, Ethiopia.
3. ***Lobelia bambuseti*** R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 401, figs. 4, 6i-l. 1922.
Distribution: Aberdares and Mt. Kenya, Kenya.
4. ***Lobelia bequaertii*** De Wild., Rev. Zool. Africaines 8, Suppl. Bot.: 31. 1920.
Distribution: Ruwenzori Mts., Zaire and Uganda.
5. ***Lobelia burtii*** E. A. Bruce, Bull. Misc. Inform. 1933: 473. 1933.
- 5a. ***Lobelia burtii* subsp. *burtii***.
Distribution: Mt. Hanang, Tanzania.
- 5b. ***Lobelia burtii* subsp. *meruensis*** E. B. Knox, subsp. nov.—TYPE: TANZANIA, *Knox 1879* (holotype: MICH!; isotypes: BR! DSM! K! MO! UPS!).

Haec subspecies a *L. burtii* subsp. *burtii* internodiis elongatis, foliis grandibus, et corolla caeruleo-violacea differt.

Plant up to 2 m tall in flower, ascending or decumbent, suckering from the base with age to produce clumps of a few aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem 2–3 cm in diameter, terete, woody. Stem surface green, glabrous, developing with age a thin phellogen. Terminal leaf rosette of 35–90 leaves, spirally arranged, deciduous, each leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-lanceolate, ca. 35 cm long, 3.5–5.0 cm wide, obtuse at the apex, tapering at the base, glabrous with a smooth, waxy cuticle on both surfaces; margin entire, ciliate; hydathodes embedded; terminal hydathode sometimes appearing mucronate; venation not prominent; midvein ca. 1.5 cm wide at the base; lateral veins 25–30 pairs, straight at 30–45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, ca. 30 cm long, ca. 2 cm in diameter at the base, borne atop a leafy peduncle 30–50 cm long, with little modification from mature vegetative leaves to

pedunculate leaves, and a sharp transition from pedunculate leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly 6.5–8.0 cm long, 2.4–3.2 cm wide, ovate; apex acute; base rounded, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, bracts, pedicels, hypanthia, and calyx lobes glabrous except bracts and calyx lobes ciliate. Pedicel 8–12 mm long, elongating only slightly during fruit maturation, with two linear bracteoles, 1 mm long, not opposite, crowded to one side, inserted one-half of the distance from the base. Hypanthium ovoid, 6–8 mm long, 9–10 mm wide, distinctly 10-nerved; extending beyond distal face of ovary to form a nectiferous cup. Calyx lobes 8–10 mm long, 5–6 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla 27–37 mm long, strongly downcurved at the base, bluish purple; inner surface densely pubescent with wide, curly trichomes in the throat, elsewhere glabrous; two lateral petals splitting along one-half of their length; three middle petals generally not splitting. Filaments ca. 22 mm long, connate except basal one-half, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla. Anther-tube 7–8 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; distal face yellow or orange. Capsule ovoid, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 2.2–2.3 mm long, compressed and frequently contorted, asymmetrically winged on both sides, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Meru, Tanzania.

5c. *Lobelia burtii* subsp. *telmaticola* E. B. Knox, subsp. nov.—TYPE: TANZANIA, Knox 782 (holotype: MICH!; isotypes: DSM! K!).

Haec subspecies a *L. burtii* subsp. *burtii* caule crasso medulla lata, foliorum rosula robusta, inflorescentia grandi, et corolla longa differt.

Plant up to 2 m tall in flower, erect or ascending; with age, short rhizomes produce clumps of a few aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem ca. 6 cm in diameter, terete, woody. Stem surface obscured by densely packed leaf arrangement, developing with age a thin phelloderm. Terminal leaf rosette of 150–200 leaves, spirally arranged, deciduous, each leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-lanceolate, ca. 24 cm long, 2.7–3.0 cm wide, obtuse at the apex, phyllodic and slightly tapering at the base, glabrous with a smooth, waxy cuticle on both surfaces; margin entire, ciliate; hydathodes embedded; terminal hydathode appearing mucronate; venation not prominent; midvein ca. 1.0 cm wide at the base; lateral veins ca. 25 pairs, straight at 30–45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, ca. 100 cm long, ca. 4 cm in diameter at the base, borne atop a leafy peduncle 30–50 cm long, with little modification from mature vegetative leaves to pedunculate leaves, and a sharp transition from pedunculate leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly ca. 8.0 cm long, 3.5 cm wide, ovate; apex acuminate; base tapering, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, bracts, pedicels, hypanthia, and calyx lobes glabrous except bracts and calyx lobes ciliate. Pedicel 8–10 mm long, elongating only slightly during fruit maturation,

with two linear bracteoles, 1 mm long, not opposite, crowded to one side, inserted one-third of the distance from the base. Hypanthium obovoid, 11–13 mm long, 10–12 mm wide, distinctly 10-nerved; extending beyond distal face of ovary to form a nectiferous cup. Calyx lobes ca. 13 mm long, ca. 5 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla 33–42 mm long, strongly downcurved at the base, bluish purple; inner surface densely pubescent with wide, curly trichomes in the throat, elsewhere glabrous; two lateral petals splitting along one-half of their length; three middle petals generally not splitting. Filaments ca. 28 mm long, connate except basal one-half, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla. Anther-tube 8–10 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; color of distal face not known. Capsules ovoid, ca. 18 mm long, ca. 15 mm wide, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 1.9–2.2 mm long, compressed and frequently contorted, asymmetrically winged on both sides, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Loolmalassin, Tanzania.

6. *Lobelia deckenii* (Asch.) Hemsl., Fl. Trop. Afr. 3: 466. 1877.

6a. *Lobelia deckenii* subsp. *deckenii*.

Distribution: Mt. Kilimanjaro, Tanzania.

6b. *Lobelia deckenii* subsp. *incipiens* E. B. Knox, subsp. nov.—TYPE: TANZANIA, *Knox 2034* (holotype: MICH!; isotypes: BR! DSM! K! MO! UPS!).

Haec subspecies a *L. deckenii* subsp. *deckenii* caule gracili internodiis elongatis, foliis longis in rosula laxa, inflorescentia parva, et corolla alba differt.

Plant up to 2.5 m tall in flower, ascending, suckering profusely from the base with age to produce clumps of several aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem up to 3.7 cm in diameter, terete, woody. Stem surface green, glabrous, developing with age a thin phellogen. Terminal leaf rosette of 40–80 leaves, spirally arranged, deciduous or weakly marcescent, each eventually leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-oblongate, 29–36 cm long, 3.2–4.6 cm wide, acute or narrowly obtuse at the apex, tapering at the base, sparsely pubescent on both surfaces or sometimes glabrous; margin entire, ciliate; hydathodes embedded; terminal hydathode prominent; venation prominent below; midvein 2–3 mm wide at the base; lateral veins 40–45 pairs, straight at 45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 30–45 cm long, ca. 3 cm in diameter at the base, borne atop a leafy peduncle 20–40 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly 6.5–8.0 cm long, 2.5–2.7 cm wide, lanceolate; apex acuminate; base rounded, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, pedicels, and hypanthia glabrous. Bracts sparsely ciliate, glabrous or with sparse pubescence along the midvein on the upper surface; calyx lobes sparsely ciliate but otherwise glabrous. Pedicel 6–7 mm long,

elongating to 10–13 mm during fruit maturation; with two fleshy bracteoles, 2 mm long, subopposite, crowded to one side, inserted one-quarter of the distance from the base. Hypanthium campanulate, 5–7 mm long, 10–12 mm wide, distinctly 10-nerved, not forming a nectiferous cup. Calyx lobes 7–12 mm long, 4–5 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla ca. 36 mm long, not strongly downcurved except at the tip, white, glabrous; petals generally not splitting, but slits between petals not uncommon. Filaments ca. 30 mm long, connate except basal one-third, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla; scattered pubescence on inner surface. Anther-tube ca. 10 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; distal face yellow. Capsule globose, 15–16 mm long, 12–14 mm wide, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 1.8–2.0 mm long, compressed and frequently contorted, asymmetrically winged on one side, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Kilimanjaro, Tanzania.

7. *Lobelia giberroa* Hemsl., Fl. Trop. Afr. 3: 465. 1877.

Distribution: Ethiopia to Malawi, inland to Zaire.

8. *Lobelia gregoriana* Baker f., J. Bot. 32: 66. 1894.

8a. *Lobelia gregoriana* subsp. *gregoriana*.

Distribution: Mt. Kenya, Kenya.

8b. *Lobelia gregoriana* subsp. *sattimae* (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Lobelia sattimae* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 414. 1922.

Distribution: Aberdare Mts., Kenya.

8c. *Lobelia gregoriana* subsp. *elgonensis* (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Lobelia elgonensis* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 411, fig. 7a. 1922.

Distribution: Mt. Elgon and Cherangani Hills, Uganda and Kenya.

9. *Lobelia longisepala* Engl., Bot. Jahrb. Syst. 32: 117. 1902.

Distribution: Usambara Mts., Nguru Mts., Uluguru Mts., Uzungwa Mts., Mahenge Highlands, Tanzania.

10. *Lobelia lukwangulensis* Engl., Notizbl. Königl. Bot. Gart. Berlin 1: 107. 1895.

Distribution: Uluguru Mts. and Uzungwa Mts., Tanzania.

11. *Lobelia mildbraedii* Engl. in J. Mildbraed, Wiss. Erg. deut. Zentr.-Afr. Exped., Bot., 344. 1914.

Distribution: Several sites, disjunct between northern Malawi/southern Tanzania and Zaire, Burundi, Rwanda, and Uganda.

- 12. *Lobelia morogoroensis*** E. B. Knox & Pócs, Kew Bull. 47: 505. 1992.
Distribution: Morogoro Region, Tanzania.
- 13. *Lobelia petiolata*** Hauman, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8°) 2: 36, fig. 5. 1934.
Distribution: Mts. Kahuzi and Biega, Zaire and Nyungwe Forest, Rwanda.
- 14. *Lobelia rhynchopetalum*** Hemsl., Fl. Trop. Afr. 3: 465. 1877.
Distribution: Gondar, Gojam, Shewa, Arsi, Bale, and Harerge Regions, Ethiopia.
- 15. *Lobelia ritabeaniana*** E. B. Knox, sp. nov.—TYPE: TANZANIA, Pócs & Manktelow 91426 (holotype: UPS!; isotypes: BP! K! MICH! NHT!). Fig. 1.

Haec species a *L. sancta* inflorescentia non ramosa, bracteis angustis integrisque, et antheris thecis glabris differt.

Plants up to 4 m tall in flower, erect or ascending, not suckering from the base, not branching vegetatively; with an unbranched inflorescence. Stem 3–5 cm in diameter at the base, terete, woody. Stem surface green, glabrous, developing with age a thin phelloderm. Pith 1–2 mm in diameter at the base, 15–25 mm in diameter and hollow above. Terminal leaf rosette of 60–200 leaves, spirally arranged, deciduous, each with a conspicuous raised leaf-scar with a corky abscission layer. Leaves of mature non-flowering plant subsessile, narrowly oblanceolate, 25–40 cm long, 2–3 cm wide, acuminate at the apex, attenuate at the base, glabrous on both surfaces with a smooth, waxy cuticle prominent on the upper surface; margin often somewhat revolute, weakly or coarsely dentate with teeth up to 5 mm wide and 3 mm long, often appearing doubly dentate due to prominent hydathodes; terminal hydathode appearing mucronate; venation prominent beneath; midvein 2–3 mm wide at the base; lateral veins 25–30 pairs, arcuate at 60–90° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 50–100 cm long, 1–2 cm in diameter at the base, borne atop a leafy peduncle 55–150 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Lowermost bracts 30–35 mm long, 5–8 mm wide, with successive bracts more uniformly 25–30 mm long, 3–4 mm wide; margin entire or papillose; mucronate. Rachis, pedicels, and hypanthia sparsely puberulent or papillose. Pedicel 6–8 mm long, not elongating during fruit maturation, ebracteolate. Hypanthium campanulate, 6–7 mm long, 7–8 mm wide, distinctly 10-nerved; not forming a nectiferous cup. Calyx lobes uniformly 19–20 mm long, ca. 3 mm wide, subulate, glabrous; margin entire or papillose; mucronate. Corolla 40–44 mm long, strongly downcurved in the middle, pink to magenta; inner surface densely papillose along the throat, sparser toward the base, glabrous elsewhere; petal margin generally entire, with scattered papillae or longer trichomes, particularly at the tip; two lateral petals splitting along half their length, and also split up to 9 mm from the base; three middle petals split less than half their length. Filaments ca. 28 mm long, connate except basal 1 mm, forming a firm tube, flaring evenly toward the base; outer surface puberulent or papillose, particularly the basal portion of the lower two anthers. Anther-tube ca. 6 mm long, trichomes frequently found in small tufts along sutures at the base of the anthers, the two lower anthers barbate at the apex; bristles 1 mm long. Ovary subinferior; distal face not brightly colored. Capsule subglobose, 10–12 mm long, 8–10 mm wide, 10-nerved, puberu-

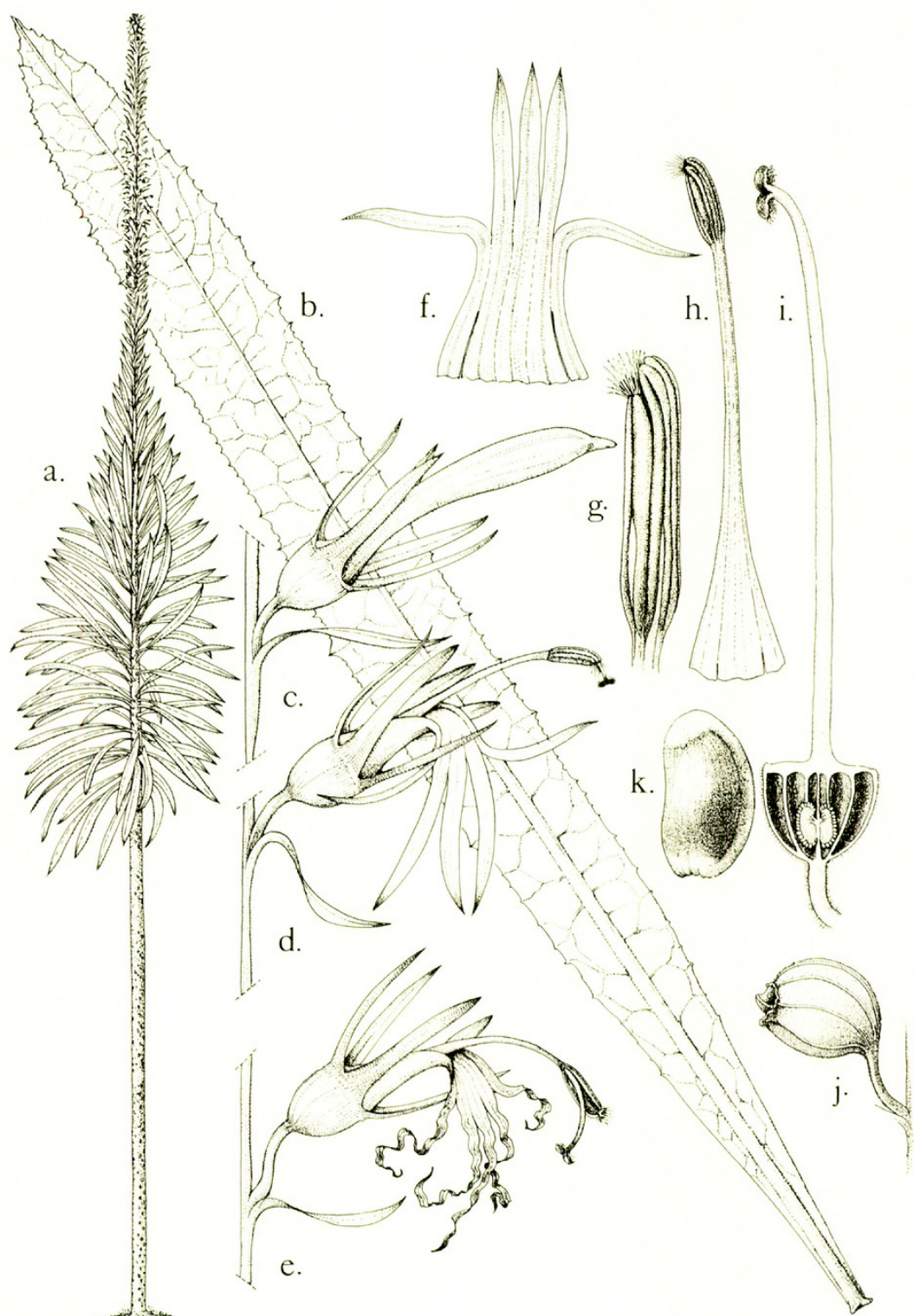


FIG. 1. *Lobelia ritabeaniana*. A. Habit, $\times 0.04$. B. Leaf, $\times 0.5$. C. Flower in bud, $\times 1$. D. Flower in female phase (male phase not shown), $\times 1$. E. Early stage of fruit development, $\times 1$. F. Corolla spread out, $\times 1$. G. Stamens (side view), $\times 2$. H. Anther-tube, $\times 6$. I. Ovary and style from female phase flower, $\times 1.5$. J. Mature fruit, $\times 1.5$. K. Seed, $\times 20$. Drawn by L. Bush.

lent, with two distinct valves. Bracts retained; calyx lobes frequently lost during fruit maturation; all other flower parts deciduous. Seed irregularly ovate in outline, ca. 1.1 mm long, somewhat compressed, lipped on one side, finely striate, dark brown with cream-colored margin. Seedlings found growing in shade with

slender stems, 3–4 mm in diameter, internodes 4–5 mm long, and leaves almost spathulate; in full light the growth-form is more robust with a wide hollow stem quickly produced and leaves characteristically oblanceolate.

Distribution: Nguru Mts., Tanzania.

16. *Lobelia sancta* Thulin, Kew Bull. 34: 815, fig. 1. 1980.

Distribution: Ukaguru Mts., Tanzania.

17. *Lobelia stricklandiae* Gilliland, J. Bot. 73: 248, as “stricklandae.” 1935.

Distribution: Several sites, Tanzania to NE Transvaal.

18. *Lobelia stuhlmannii* Stuhlmann, Mit Emin Pascha ins Herz von Afrika, 291, 295, and 300, excl. fig. 11. 1894.

Distribution: Mt. Muhi, Mt. Kahuzi, Virungas, and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

19. *Lobelia telekii* Schweinf. in L. von Höhnelt, Zum Rudolph- und Stephanie-See, 861, fig. 104. 1892.

Distribution: Mt. Elgon, Aberdares, and Mt. Kenya, Uganda and Kenya.

20. *Lobelia thuliniana* E. B. Knox, sp. nov.—TYPE: TANZANIA, *Knox & Butler* 2256 (holotype: MICH!; isotypes: DSM! EA! K! MO! UPS!). Fig. 2.

Haec species a *L. giberroa* rhizomate brevi, caule gracili et fere herbaceo, folio brevior, angustior et fere petiolato, insertione basali bracteolarum, et trichomatibus setaceis secus longitudinem 2 antherarum infernarum differt.

Plant up to 3 m tall in flower, erect; with age in favorable habitats, numerous short rhizomes produce dense stands of aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Rhizome 1–2 cm in diameter, rooting adventitiously, with pith 0.5–1.0 cm in diameter, surrounded by wood 3–5 mm thick. Aerial stem 2–3 cm in diameter throughout its length, terete, hollow or with occasional light pith. Stem surface green, glabrous, developing with age a thin phelloderm. Terminal leaf rosette of 30–80 leaves, spirally arranged, marcescent; lower leaves eventually deciduous, each leaving a small, raised leaf scar with a corky abscission layer. Leaves of mature non-flowering plant subsessile, oblanceolate, 25–45 cm long, 2.5–4.0 cm wide, acute at the apex, attenuate at the base; upper surface nearly glabrous with a smooth waxy cuticle and sparse, short pubescence; lower surface pubescent primarily along veins; margin finely serrulate due to prominent hydathodes; terminal hydathode appearing mucronate; venation prominent beneath; midvein 2–3 mm wide at base; lateral veins 15–25 pairs, mostly arcuate at 45–60° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 50–80 cm long, 1–2 cm in diameter at the base, borne atop a leafy peduncle ca. 40 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Lowermost bracts 45–65 mm long, 3–6 mm wide, with successive bracts more uniformly 27–48 mm long, 2–4 mm wide; margin entire; minutely mucronate. Peduncle, rachis, bracts, pedicels, hypanthia, and calyx lobes puberulent, pubescent, or tomentose. Pedicel 5–12 cm long, elongating only slightly during fruit maturation, with two subulate, pubescent bracteoles, 1 mm long, subopposite, inserted at the base. Hypanthium campanulate, 5–7 mm long, 6–8 mm wide, indistinctly 10-nerved; not forming a nectiferous cup. Calyx



FIG. 2. *Lobelia thuliniana*. A. Habit, $\times 0.05$. B. Leaf, $\times 0.5$. C. Flowers in bud and male phase, $\times 1$. D. Flower in female phase, $\times 1$. E. Mature fruit, $\times 1$. F. Corolla spread out, $\times 1.5$. G. Stamens (side view), $\times 2$. H. Ovary and style from female phase flower, $\times 1.5$. I. Seed, $\times 20$. Drawn by L. Bush.

lobes uniformly 15–20 mm long, ca. 3 mm wide, subulate; margin entire; mucronate. Corolla 28–35 mm long, not strongly downcurved, white or greenish; inner surface glabrous; outer surface densely pubescent distally, more sparse toward the base; two lateral petals generally splitting along half their length; three middle petals generally splitting less than a third of their length, but the pattern of splitting is variable. Filaments ca. 25 mm long, connate except basal one-third, forming a firm tube, glabrous; free sections of filaments with parallel margins, only slightly flaring and not becoming connate at the point of attachment with the hypanthium and corolla. Anther-tube ca. 10 mm long, the two lower anthers barbate at the apex, bristles extending along connectives and frequently found on the apices of the three upper anthers; bristles 1–2 mm long. Ovary subinferior; distal face yellow. Capsule subglobose, 10–11 mm long, 8–10 mm wide, 10-nerved, glabrescent, with two distinct valves. Seeds ovate in outline, ca. 0.8 mm long, somewhat compressed, slightly lipped on one side, finely striate, orange-brown. Seedling initially compact but rapidly developing an erect stem.

Distribution: Iringa Region, Tanzania.

21. *Lobelia wollastonii* Baker f., J. Linn. Soc., Bot. 38: 265, pl. 19, fig. 7. 1908.

Distribution: Virungas and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

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