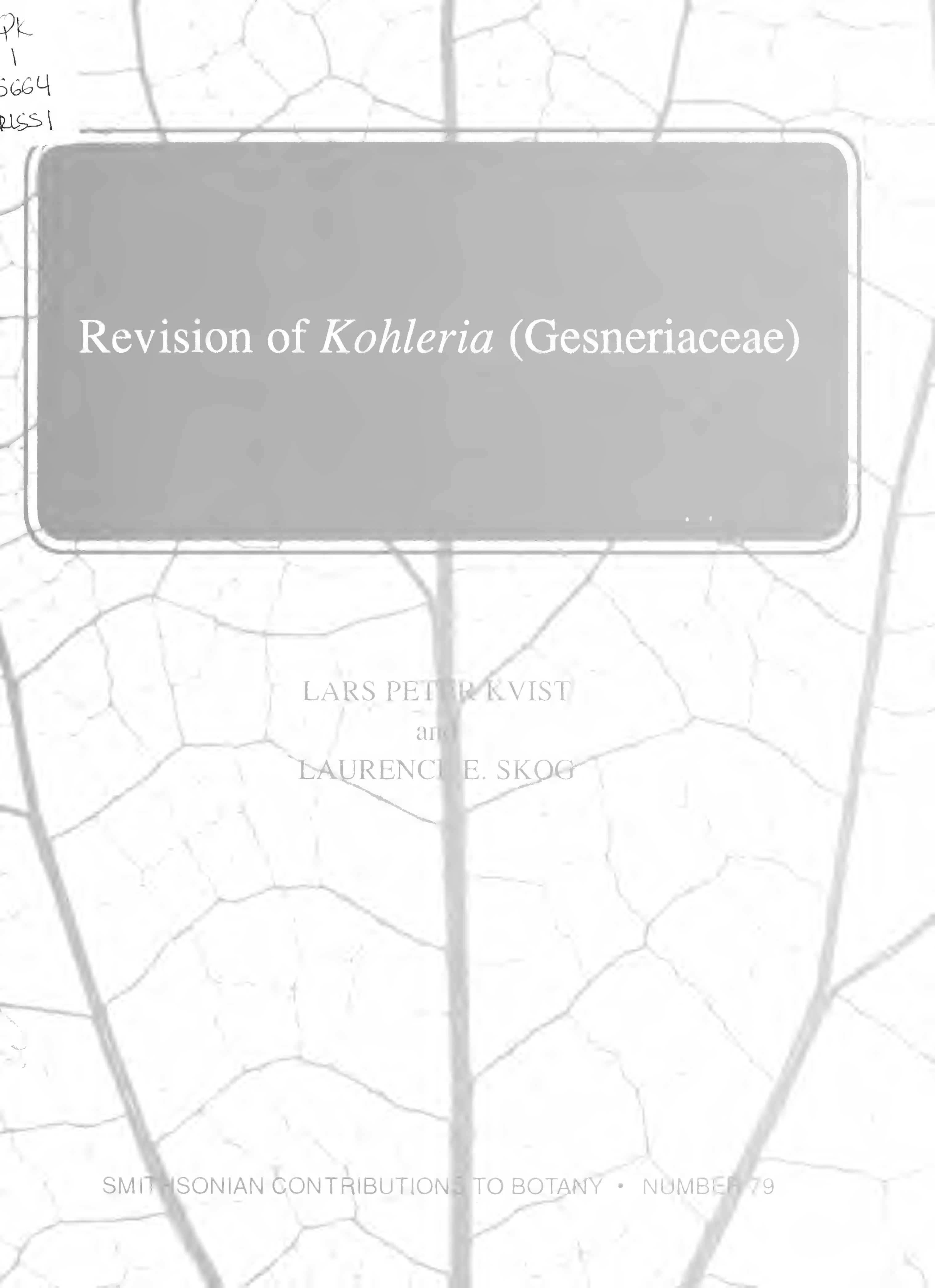

Revision of *Kohleria* (Gesneriaceae)

LARS PETER KVIST
and
LAURENCE E. SKOG

SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 79

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ABSTRACT

Kvist, Lars Peter and Laurence E. Skog. Revision of *Kohleria* (Gesneriaceae). *Smithsonian Contributions to Botany*, number 79, 83 pages, 37 figures, 4 tables, 1992.—The genus *Kohleria* (Gesneriaceae: Gloxinieae) ranges from Mexico to Peru and east to Surinam, and from sea level to about 2500 meters altitude, but most commonly grows between 800 and 2000 meters. About 100 species have been described in *Kohleria*, but in the present work only 17 are recognized. Fourteen species occur in Colombia, with 9, including four newly described species, *K. diastemoides*, *K. grandiflora*, *K. longicalyx*, and *K. neglecta*, being endemic to this country.

Eleven *Kohleria* species occur in exposed, disturbed habitats along rivers, roads, etc. These species have capsular fruits that split apically into two valves and have wind-dispersed seeds. In contrast, the remaining species are found in shaded, humid forest understory, and have capsules that split by a slit from the apex to the base to expose a sticky mass of seeds that apparently are animal-dispersed. These latter species also usually lack the scaly rhizomes that enable exposed-habitat species to survive dry spells.

Some *Kohleria* species are stable in most features even over wide distribution ranges, e.g., *K. spicata* and *K. tubiflora*. In contrast, a few species are surprisingly variable. To circumscribe this variation the following varieties are recognized: *K. amabilis* var. *bogotensis*, *K. hirsuta* var. *longipes*, *K. villosa* var. *anisophylla*, *K. inaequalis* var. *ocellata*, and var. *lindenii* (none of these are new taxa). *Kohleria hirsuta* and *K. trianae* hybridize in the Central Colombian Cordillera. In the Eastern Colombian Cordillera, var. *longipes* of *K. hirsuta* may be a formerly well-separated semi-species that has hybridized extensively with the typical variety. The most variable species *K. inaequalis* apparently is a complex of three extensively hybridizing semi-species, and pure breeding populations still are found in the periphery of its range. Generally, the main mode of speciation of *Kohleria* appears to be the geographical isolation of peripheral populations, while hybridization breaks down species limits rather than creating new ones.

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Contents

Revision of *Kohleria* (Gesneriaceae)

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Introduction

The genus *Kohleria* has for many years needed revision. Species of *Kohleria* are among the most well-known members of New World Gesneriaceae, partly because they are frequently cultivated in Latin America, Europe, and in the United States, and partly because the most common *Kohleria* species, especially *K. spicata* and *K. tubiflora*, are somewhat weedy and among the most frequently collected New World Gesneriaceae. Since 1847, when *Kohleria* was established by Regel, about 100 species names have been added to the genus, mostly by European workers who never visited the New World but based their descriptions to a great extent on garden material. Some of the common and widespread species were repeatedly newly described. In addition, many species names were added to several synonymous genera. By the early 20th century *Kohleria* was in a seemingly hopeless taxonomic and nomenclatural mess, and most workers avoided the group. Wiehler (1975, 1978a) split off *Moussonia* Regel and *Parakohleria* Wiehler distributed from Panama to Mexico and along the eastern Andean slopes, respectively. In the present work the remaining approximately 70 species names remaining in *Kohleria* are reduced to 17. The taxa are distributed from southern Mexico to Peru and east to Surinam. The center of diversity is in the Colombian highlands, where 14 species occur (including nine endemics).

ACKNOWLEDGMENTS.—We greatly appreciate the assistance of Ximena Londoño during field work and her continued collections and observations of *Kohleria* in Colombia, the excellent drawings of Alice Tangerini, the help of Marie Uehling and Leslie Brothers in manuscript and plate preparation, the EPR-spectroscopic investigations undertaken by Jens Arne Pedersen, the careful and critical reading of the manuscript by Susanne S. Renner and three anonymous reviewers, and the herbaria listed below for the loan of their specimens for study.

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MATERIALS AND METHODS

The revision is based on studies of herbarium material (1762 collections from the following herbaria: A, AAU, BH, BM, C, CGE, CM, COL, E, EAP, ECON, F, FAUC, G, GB, GH, HBG, JAUM, K, L, LE, MA, MANCH, MEDEL, MEXU, MO, NY, P, PORT, QCA, QCNE, S, SEL, TULV, U, UC, US, USM, VEN, W, WU, WIS), as well as living plants in the field and in cultivation. A complete list of collections studied is available from the second author. During fieldwork in Ecuador and Colombia (L.P. Kvist) and Peru and Panama (L.E. Skog) 13 of the 17 recognized species were studied in their native habitats: *Kohleria amabilis, K. hirsuta, K. hondensis, K. longicalyx, K. neglecta, K. trianae, K. warszewiczii* in Colombia, *K. inaequalis* and *K. spicata* in Colombia and Ecuador, *K. villosa* in Ecuador, *K. peruviana* in Peru and *K. spicata* and *K. tubiflora* in Panama. During the time of the study the following species have been in cultivation in the greenhouses of the Smithsonian Institution and Botanical Institute of the University of Aarhus: *K. allenii, K. hirsuta, K. hondensis, K. inaequalis, K. peruviana, K. rugata, K. spicata, K. trianae, K. villosa*, and *K. warszewiczii*.

TAXONOMIC HISTORY

Until Regel published the name *Kohleria* in 1847, the species now referred to *Kohleria* were included in *Gesneria*

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Linnaeus or in *Gesnera* Martius. The first species described was *Kohleria tubiflora* (as *Gesneria tubiflora* Cavanilles, 1801). In 1818 Kunth added six species of *Gesneria* that currently are placed in *Kohleria: K. hirsuta* (as *Gesneria hirsuta, G. longiflora,* and *G. mollis*), *K. hondensis* (as *G. hondensis*), *K. spicata* (as *G. spicata*), and *K. trianae* (as *G. elongata*). Toward the middle of the 19th century interest in New World Gesneriaceae increased. Additional species were described, mainly in *Gesneria,* which are, for the most part, synonyms of the current species *Kohleria hirsuta* (as *Gesneria vestita* Bentham, 1845b, *Gesneria eriantha* Bentham, 1846, *G. longipes* Bentham, 1846, and *Gesneria rubricaulis* Kunth & Bouché, 1847), *Kohleria spicata* (as *Gesneria longifolia* Lindley, 1841, *Gesneria schiedeana* (DC.) W.J. Hooker, 1845, and *Gesneria petiolaris* Bentham, 1845a), and *Kohleria tubiflora* (as *Gesneria incurva* Bentham, 1845a, *G. rhynchocarpa* Bentham, 1845a, and *Gesneria hondensis* W.J. Hooker, 1846). The earliest descriptions of the following accepted species also come from this period: *Kohleria amabilis* (as *Achimenes picta* W.J. Hooker, 1844, *Kohleria inaequalis* (as *Gesneria inaequalis* Bentham, 1846), *Kohleria rugata* (as *Gesneria rugata* Scheidweiler, 1847) and *Kohleria villosa* (as *Nematanthus erianthus* Bentham, 1846). Thus, even at this early point most of the taxa described were synonyms of a few widespread species. From the turn of the 20th century this trend accelerated dramatically with new species named by Fritsch and new species based on hybrids. In addition, the species that currently are placed in *Kohleria* were simultaneously assigned to several synonymous genera, *Brachyloma* Hanstein, *Isoloma* (Bentham) Decaisne, *Tydaea* Decaisne, etc. The main workers in New World Gesneriaceae during this period (E. Regel, first in Zürich and later in St. Petersburg (formerly Leningrad), J. Decaisne in Paris, G. Bentham and W.J. Hooker at Kew, and especially J. Hanstein in Berlin) described the same few species again and again, mainly from plants cultivated in Europe.

The name *Kohleria,* with *K. hirsuta* as the type species, appeared for the first time in 1847 with a short diagnosis in a seedlist from the botanical garden in Zürich, where Regel was at that time head gardener. In April of the following year Regel described *Kohleria* more fully and added *K. triflora* (now *K. hondensis*). He noted that *Gesneria hondensis* Kunth (1818) would belong to *Kohleria,* but Regel never published a new combination in the genus for the species. Hanstein, however, crediting Regel (1848) for the combination *K. hondensis,* actually published it in 1859. In December 1848 another paper, by Decaisne, appeared that dealt with the splitting of *Gesneria.* In this paper Decaisne elevated the taxon *Isoloma,* earlier established in 1846 as a section of *Gesneria* by Bentham, to generic rank. Decaisne transferred most of the above-mentioned species of *Gesneria* and *Kohleria* to *Isoloma.* However, he did not select a type species, and it is remarkable that one of the species he did not transfer was *G. hirsuta* (the type species of *Kohleria*). Regel (1851) later followed Decaisne in believing that *Isoloma* had priority over *Kohleria.* He stated that Bentham chose the same type species for *Isoloma* as he himself had chosen for *Kohleria* in 1847, viz. *K. hirsuta.* This is incorrect, as Bentham (1846) chose no type species and only mentioned *K. hirsuta* in the description of *K. eriantha.* Much later, Morton (1973) finally lectotypified *Isoloma* with *Kohleria hirsuta. Isoloma* was actually illegitimate when elevated by Decaisne, because the name had been used previously for a fern genus by Smith (1841), and, in addition, the later published generic name *Kohleria* would have priority over the sectional name *Isoloma.* Unfortunately this error confused the nomenclature of *Kohleria* for the remainder of the 19th century. To add to the confusion Regel (1851, 1852a) described another new genus that he again named *Kohleria* but this time based on *K. ignorata* (described by Kunth and Bouché in 1848 as *Gesneria ignorata*) as the sole species. This species, based on material from Central America, is another synonym of *K. spicata.* This second genus established by Regel is obviously a later homonym.

In addition to *Isoloma,* Decaisne (1848b) also established the monotypic genus *Tydaea* to include *T. picta,* first described by W.J. Hooker (1844) as *Achimenes picta* (now *Kohleria amabilis* var. *bogotensis*). Shortly thereafter, Regel (1849) based *Giesleria,* another new monotypic genus, on the same species. But he soon realized (1851) that *Tydaea* had priority. In the same paper Regel added by transfer a second species, *T. ocellata,* originally described by W.J. Hooker (1848) as *Achimenes ocellata* (now *Kohleria inaequalis* var. *ocellata*). In 1853 Regel added another genus, *Sciadocalyx,* with *S. warszewiczii* as the sole species. The latter genus was expanded with *S. digitaliflora* by Linden and André in 1870. Both species are currently synonyms of *Kohleria warszewiczii.*

Hanstein (1854, 1856, 1859, 1865) studied the taxa currently placed in *Kohleria* and published a large number of new species names and combinations. In 1854 he realized that the name *Isoloma* (Bentham) Decaisne was illegitimate, replaced the generic name with *Brachyloma* (with *B. hirsutum* as type species), and included *B. hondense* as a second species. Unfortunately, Hanstein (1854) did not realize that the later (1851) *Kohleria* of Regel, based on *K. ignorata,* was also illegitimate as a later homonym. He took up this later Regel genus and added to it another synonym of *K. spicata, K. seemannii.* Oersted (1858) also accepted both the second *Kohleria* based on *K. ignorata,* as well as *Brachyloma,* and described a number of new species, especially in *Brachyloma.* These are all currently reduced to synonyms of *K. spicata* or *K. tubiflora.* In 1858 Oersted transferred *Gesneria spicata* to *Kohleria,* but because he accepted the genus *Brachyloma* with *B. hirsutum* as type species, he actually transferred *Gesneria spicata* to the illegitimate *Kohleria* genus that Regel (1851) based on *K. ignorata.* Hanstein (1856, 1859), well aware of the work of Oersted, included the latter's new species and established two more genera, *Calycostemma* and *Cryptoloma. Calycostemma* was monotypic and based on *C. lindenii,* treated herein as the variety *lindenii* of the variable *Kohleria inaequalis.* Hanstein split off *Cryptoloma* from *Brachyloma* and included 10 species in that genus, but only *Cryptoloma* *hondense* was transferred from *Brachyloma* to *Cryptoloma*. He did not choose any type species, and *Cryptoloma hondense* is herein selected as the lectotype. Besides the 10 species in *Cryptoloma*, Hanstein (1859) included 11 species in *Kohleria* and 15 species in *Brachyloma*. In the current work all 11 species Hanstein referred to *Kohleria* are synonyms of *K. spicata*, 8 of the 10 species referred to *Cryptoloma* are synonyms of *Kohleria tubiflora* (the remaining two are synonyms of *K. hondensis*), and 12 of the 15 species referred to *Brachyloma* are synonyms of the correct *Kohleria* type species, *K. hirsuta* (two of the remaining are synonyms of *K. trianae* and one of *K. spicata*). Thus, the genera accepted by Hanstein in 1859 basically represent the three most widespread species in the current concept of *Kohleria*.

After a few years Hanstein apparently recognized that his generic concepts were extremely narrow, and in 1865 he fused *Brachyloma*, *Cryptoloma*, *Calycostemma*, and *Sciadocalyx* with *Kohleria*. The only genus currently synonymized with *Kohleria* that he preserved was *Tydaea*. Into the latter genus Hanstein (1859) had placed four species, treated herein as synonyms of *Kohleria amabilis* and *K. inaequalis*.

At the time of the original establishment of *Kohleria*, Regel (1847, 1848) also established the genus *Moussonia*. There remains some doubt regarding the identity of the type species *M. elongata* selected by Regel, because no authority other than "Auct." was given after the basionym. If this is the species described as *Gesneria elongata* by Kunth in 1818 from Colombia, the name *Moussonia* evidently becomes a synonym of *Kohleria*. According to Wiehler (1975) plants originally collected in Mexico by Deppe were distributed in Europe under the name *Gesneria elongata*, and Regel probably had these plants in mind as *Moussonia elongata*, since they match his diagnosis of *Moussonia* more closely. The Mexican plants are *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, while the Colombian plants of *Gesneria elongata* Kunth represent *Kohleria trianae*.

The most recently described genus synonymous with *Kohleria* is *Synepileana* established by Baillon (1888a). The genus only included one species, *S. granatensis*, and was based on the same Linden collection number upon which Hanstein (1859) based his monotypic genus *Calycostemma*. It is now included in the variety *lindenii* of *Kohleria inaequalis*.

Although Hanstein (1854) pointed out that *Isoloma* (Bentham) Decaisne was an illegitimate name, Bentham (in contrast to Regel) continued to use the name. The use by Bentham of *Isoloma*, in *Genera Plantarum* (1876) for example, resulted in *Isoloma* virtually replacing *Kohleria* in the literature (see works of Hemsley, 1882; Baillon, 1888b; Voss, 1894; Rusby, 1896, 1900; Bailey, 1900, 1915; and Smith, 1916). Finally, through the works of Fritsch (1894, 1898, 1913a) *Kohleria* became generally accepted as the correct name. Fritsch (1894) also included *Tydaea* and *Moussonia* in *Kohleria* and treated these groups as two of the seven sections into which he divided *Kohleria* (the other sections were *Sciadocalyx*, *Calycostemma*, *Cryptoloma*, *Isoloma*, and *Eukohleria*). Apparently, Fritsch also did not realize that Regel (1851) had established a second *Kohleria*, being an illegitimate genus name based on *K. ignorata*. He placed the correct type species *K. hirsuta* in the section *Isoloma*, and *Kohleria spicata* (of which *K. ignorata* is a synonym) in the section Eukohleria. In later papers Fritsch (1913a, 1916) described many additional new species and varieties of *Kohleria*, of which only *K. peruviana* and *K. stuebeliana* are currently accepted. Two species that he described in *Diastema* Bentham (Fritsch 1913a) were transferred by Wiehler (1978b) to *Kohleria* as *K. villosa* and *K. anisophylla* and are herein treated as *K. villosa* var. *villosa* and var. *anisophylla*.

After the work of Fritsch (1894, 1913a, 1916) half a century passed with little work being done on *Kohleria* until Wiehler (1975, 1978a) split off *Moussonia* and his new genus *Parakohleria*. The most important investigations during this extended period were those of Moore (1953, 1954) and Morton (1967a), but the only currently accepted new species described between 1916 and the present is *K. allenii* named by Standley and L.O. Williams (L.O. Willams, 1968).

Wiehler (1975) re-elevated *Moussonia* to generic rank. This taxon had been treated by Bentham in 1876 as a synonym of the series *Brachyloma* in the genus *Isoloma*, and Fritsch (1894) had treated it as a section of *Kohleria*. The group does not belong in the present concept of *Kohleria;* among other characters it has a different basal chromosome number (11 versus 13 in *Kohleria*). However, as already mentioned, the name *Moussonia* published by Regel (1847) may actually be a synonym of *Kohleria*. Therefore, in order to stabilize the usage, we choose to accept the genus *Moussonia* based on *Gesneria elongata* of cultivation, originally from Mexico, and now *Moussonia deppeana*.

In his *Moussonia* paper Wiehler (1975) sorted out a species group denoted as "*Kohleria* group three" from the eastern Andean slopes. Later (1978a) he formally split off these plants from *Kohleria* as the new genus *Parakohleria*. His belief that this group was misplaced in *Kohleria* seems justified. During fieldwork we discovered that the fruits of *Kohleria* and *Parakohleria* (Kvist, 1991) are fundamentally different, and we consider this difference to be the primary distinguishing feature (see section below under "Related Genera"). The species transferred to *Parakohleria* by Wiehler (1978a) came from several genera: *Kohleria* (including several that had never been transferred from *Isoloma*), *Diastema* Bentham, *Moussonia* Regel, and *Pearcea* Regel.

Kohleria belongs to the tribe Gloxinieae sensu lato, which Wiehler (1983) established by fusing five tribes of Fritsch (1894): Bellonieae, Gloxinieae sensu stricto, Kohlerieae, Sinningieae, and Solenophoreae. Gloxinieae includes all the Gesneriaceae with perigynous to epigynous flowers, except for the Caribbean Gesneriaceae that are, for the most part, easily recognized by having an alternate leaf arrangement (Skog, 1976). Wiehler (1983) included 24 genera and more than 300 species in the reformed Gloxinieae. Recent revisions, e.g., *Achimenes* Persoon (Ramírez-Roa, 1987), *Heppiella* Regel

(Kvist, 1990), and other so far unpublished studies indicate the number to be smaller and probably about 200.

Delimitation of *Kohleria* Regel

As is often the case in genera of neotropical Gesneriaceae, no single feature distinguishes the genus *Kohleria* from related and similar genera in the tribe Gloxinieae, but the genus is set apart by a suite of characters: species of *Kohleria* are herbs, subshrubs, shrubs, or rarely scandent shrubs, but never lianas or epiphytes; the subtending leaves of the axillary inflorescences often become gradually reduced to bracts toward the shoot apex, but there never is a sharp gap between subtending leaves and bracts (Figure 3c,g); the corollas are mostly tubular often with a conspicuous limb and the tube is red or lavender outside; the nectary is usually reduced to free glands (Figure 10b-f) but consists occasionally of a five-lobed ring (Figure 10a); the stamens are included to subincluded with coherent anthers; the style is also included or subincluded and is conspicuously bilobed; the haploid chromosome number is 13; scaly rhizomes are often present but tubers never occur; and the capsules split apically into two valves (in species found in exposed habitats) or less commonly with a longitudinal slit to the base (in species found in the understory) (Figure 13c-e). The affinities with other genera in the tribe Gloxinieae are discussed in the section below, "Related Genera."

LEAVES

The leaf arrangement in *Kohleria* is opposite or less commonly whorled (three or four leaves at one node). The latter condition is always found in *K. allenii* (Figure 29a) and *K. neglecta* (Figure 32a) and usually in *K. spicata*. However, even these species may have opposite leaf pairs intermixed with whorls. In addition, several other species occasionally have leaves in whorls of three, e.g., *K. stuebeliana* (Figure 35a). The leaves, when in a pair, are normally equal or subequal, but unequal pairs characterize the rare *K. villosa* var. *anisophylla* (Figure 37a). The shape of the blades is usually ovate to elliptic and shows little variation. Thus, leaf characters have obviously little taxonomic value.

STOMATA

Stomata are restricted to the lower leaf surfaces and are often raised on mounds. This feature is known from many other New World Gesneriaceae, both in genera related to *Kohleria*, e.g., *Heppiella* (Kvist, 1990), and in more distantly related genera, e.g., *Reldia* Wiehler in the tribe Beslerieae (Kvist and Skog, 1989). In *Kohleria* (Figure 1) stomatal mounds are taller in species with a dense indumentum; the mounds are conspicuous in *K. spicata* (Figure 1c), but absent in *K. amabilis* (Figure 1a). This indicates that the mounds may improve the transpiration by raising the stomata above the calm air-layer created by the indumentum. There is no correlation between permanently humid habitats and the presence of stomatal mounds, in conflict with Wiehler's (1983) statement that "stomatal mounds occur only in terrestrial species in humid, rainforest habitats." Understory species, e.g., *K. inaequalis* and *K. villosa*, do possess stomatal mounds, but these are not as well developed as in the exposed-habitat *K. spicata* (Figure 1b-d).

INDUMENTUM

Kohleria has four main types of trichomes, all exclusively uniseriate: (a) slender, eglandular trichomes of 3-15 cells; (b) bristle-like eglandular trichomes of 1-3 cells; (c) glandular trichomes with a slender stalk of 5-10 cells; and (d) tiny glandular trichomes with a stalk of 1-2 cells.

The prevalent indumentum of stems, leaves and inflorescences consists of slender, eglandular trichomes (Figures 2a, 30b). The up-to-10 mm long trichomes of 10-15 cells that cover the stems of *Kohleria longicalyx* are among the longest known in New World Gesneriaceae, and those of *K. grandiflora* (Figure 31a) and *K. peruviana* (Figure 33a) are only slightly shorter.

The bristle-like trichomes mainly are found on upper leaf surfaces (Figure 2b). The species of *Kohleria* can be sorted out into two groups; one with a pilose to velutinous upper-leaf surface that is soft and pleasant to touch, and another with a hispid upper leaf surface that feels very scabrous, each exemplified by *K. hirsuta* and *K. hondensis*, respectively (Figure 2). This difference is more conspicuous in dried than in living material.

Glandular trichomes with a 1-7 mm long slender stalk are rare, but occur consistently on *Kohleria allenii*, frequently on *K. grandiflora*, and on *K. hirsuta* collections coming from elevations below 500 meters in the Río Magdalena valley of Colombia. The glandular spheres of these latter plants often bear curiously branched appendages. This same phenomenon was illustrated by Wiehler (1983) from *Rhytidophyllum auriculatum* W.J. Hooker (as *Gesneria auriculata* (W.J. Hooker) O. Kuntze, 1891) and from *Achimenes dulcis* C. Morton.

The throat of corollas of *Kohleria* and numerous other Gesneriaceae always possess at least a few approximately 0.2 mm long glandular trichomes. In addition, these often occur on the style and stigma, and occasionally on vegetative parts such as the stems. Wiehler (1983) illustrated both uni- and multicellular glandular spheres from the throat of *K. villosa*. According to Steiner (1985), working with *Drymonia serrulata* (Jacquin) Martius (tribe Episcieae), the multicellular nature of the glandular spheres is not revealed in SEM-micrographs due to a thick, surrounding, cuticular layer. Steiner also reported that the glandular spheres of *D. serrulata* exude substances that cause the pollen to stick to flower visitors.

INFLORESCENCES

Inflorescence characters are important both to distinguish species of *Kohleria* and to set the genus apart from related

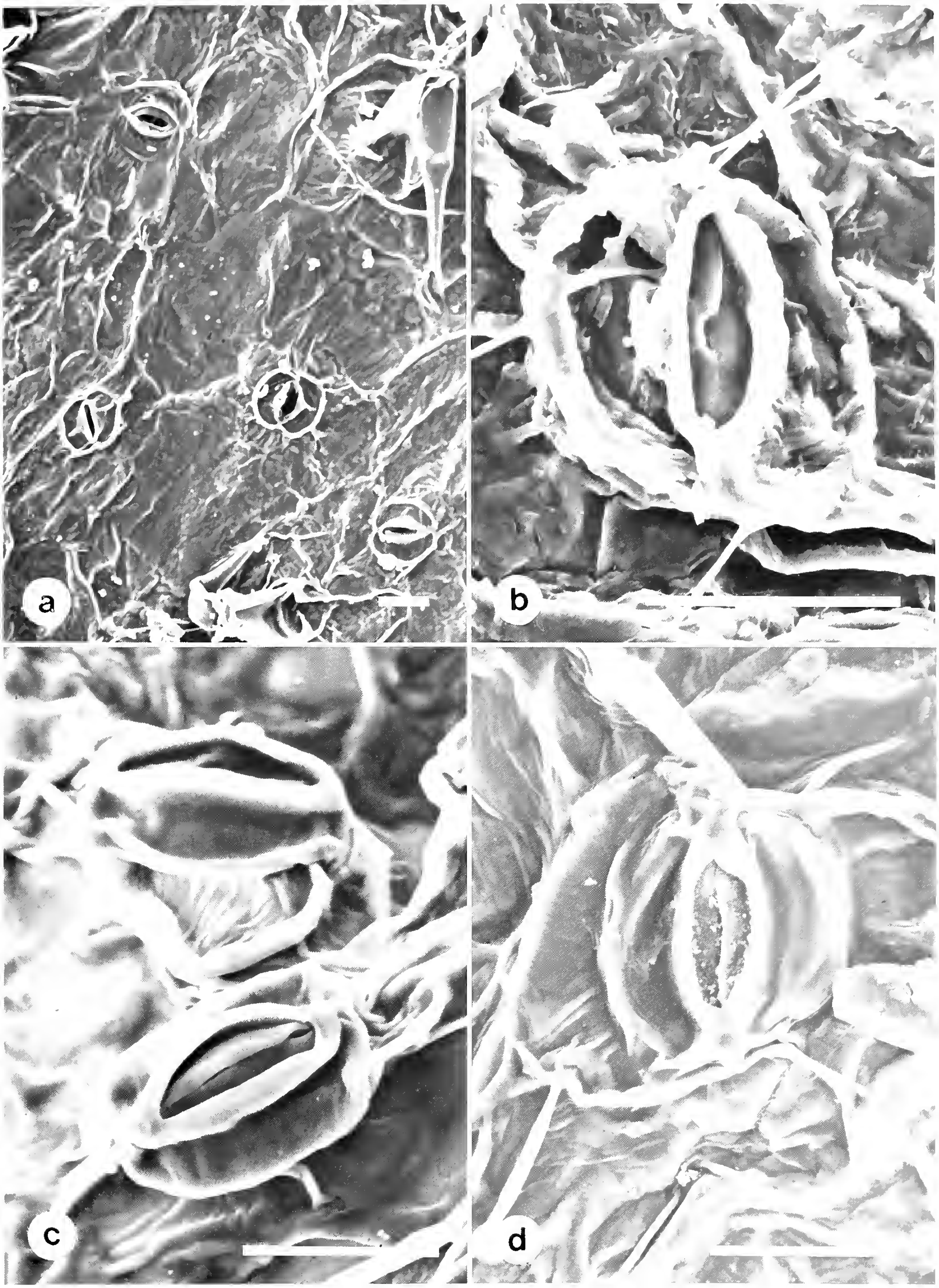


FIGURE 1.—Stomata of *Kohleria* (scale length = 20 µm): a, *K. amabilis* var. *amabilis;* b, *K. inaequalis* var. *inaequalis;* c, *K. spicata;* d, *K. villosa* var. *villosa*. Micrograph a of *Killip et al. 38338* (US); b of *Balslev 1939* (US); c of *Davidse et al. 29560* (MO); d of *Harling & Andersson 23222* (US).

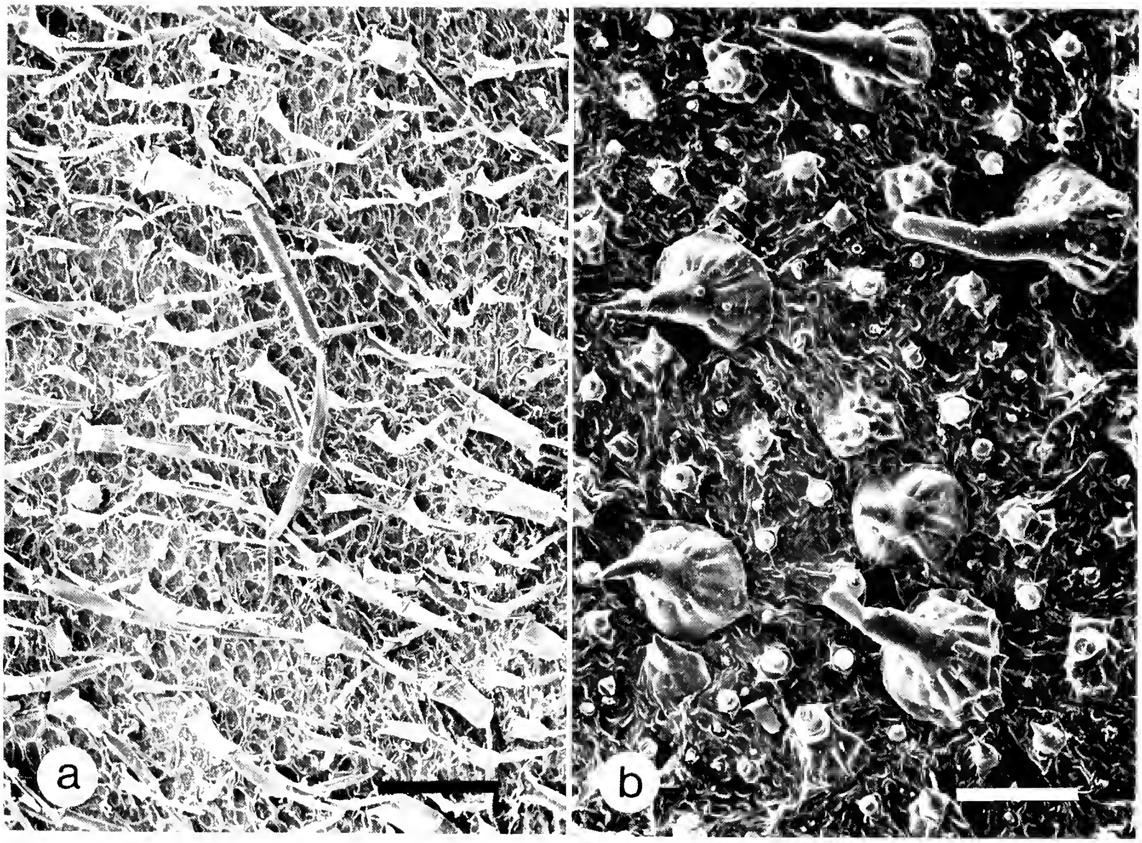


FIGURE 2.—Upper leaf surfaces of *Kohleria* (scale length = 250 μm): a, *K. hirsuta* var. *hirsuta;* b, *K. hondensis.* Micrograph a of *Plowman & Berry 13356* (US); b of *Pennell 3578* (US).

genera. Gesneriaceae have open (monopodial) flowering shoots with closed (sympodial) inflorescences in the axils of the individual subtending leaves or bracts (Figure 3). The terminology applied to describe the inflorescences of the Gesneriaceae has often been inconsistent. The term "inflorescence" is alternately used for the flowers located in the axil of a single subtending leaf, and for flowering shoots with few to many subtending leaves each with one to several flowers in their axils. Troll (1964) classified the inflorescences of Gesneriaceae as indeterminate, designated the closed inflorescences located in the axils of the single subtending leaves as "partial florescences" (Figure 3d–f), the open flowering shoots with several to many partial florescences as "florescences" (Figure 3b,c,g), and the complex systems made up of several florescences as "synflorescences" (Figure 3a). Furthermore he designated florescences with un-reduced subtending leaves and reduced subtending leaves (bracts) as "frondose" and "bracteose," respectively (Figure 3b,g). Finally, he designated synflorescences with subtending leaves that gradually are reduced to bracts toward the apex as "frondo-bracteose" (Figure 3c). The partial florescences of Gesneriaceae were described by Weber (1973, 1978, 1982) as "pair-flowered cymes," cymes in which each regular flower is accompanied by an additional bractless flower in frontal-median position ("front-flower").

The number of flowers in the partial florescences of *Kohleria* varies from 1 to 10. Only few species have a constant number of flowers, e.g., *K. rugata* (Figure 3b) with one flower and *K. trianae* (Figure 3d) with four flowers, including three regular flowers and the front-flowers of the central flower. In many species the partial florescences mostly produce 1–2 flowers, although they occasionally produce four to six flowers including up to three front-flowers, e.g., *K. spicata* (Figure 3c) and *K. stuebeliana* (Figure 35a). Only three species, *K. neglecta, K. peruviana,* and *K. warszewiczii,* may produce up to 10 flowers, including three or four front-flowers, although in most cases their partial florescences only develop six or fewer flowers. The latter two of these species have pedunculate partial florescences (Figure 3e, f), while the up-to-10 flowers of *K. neglecta* (Figure 32a) are densely congested in the axils of the subtending leaves. Nine species always lack peduncles, and the remaining eight species either always have pedunculate partial florescences (4 species) or both states occur (4 species) (Figure 4). The bracts subtending the regular flowers of the

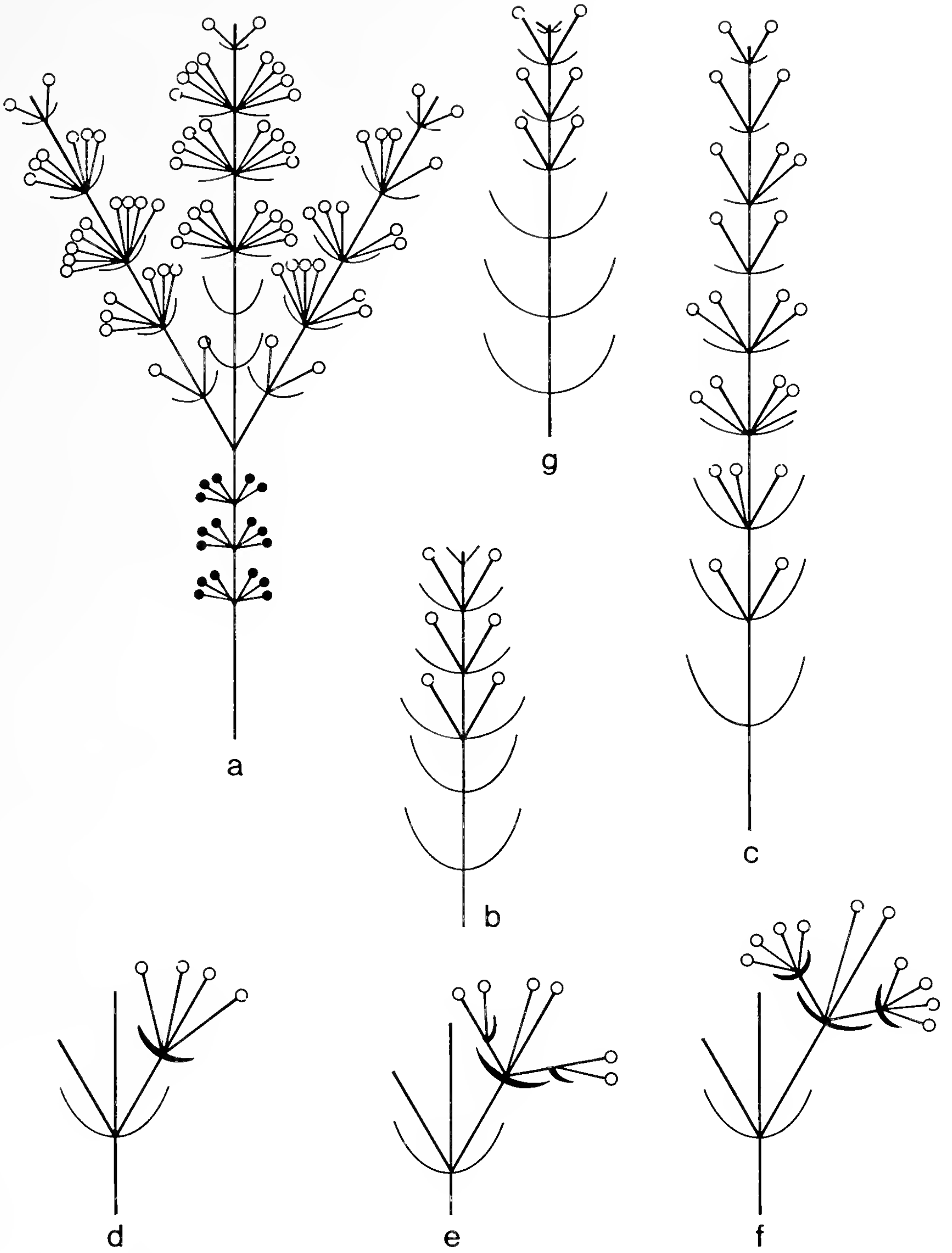


FIGURE 3.—Inflorescences of *Kohleria* and *Diastema* (open circle = flowers and buds, solid circle = old capsules, thick crescents = bracts, thin crescents = leaves and leaves reduced to bracts): a, biennial flowering shoot of *K. hirsuta;* b, frondose florescence of *K. rugata* with partial florescences of single, axillary flowers; c, frondo-bracteose florescence of *K. spicata* with partial florescences of often several axillary flowers; d, partial florescence of *K. trianae*, pair-flowered cyme with three regular flowers and one front-flower; e, partial florescence of *K. warszewiczii*, pair-flowered cyme with 5 regular flowers and one front-flower; f, partial florescence of *K. peruviana*, pair-flowered cyme with seven regular and three additional bractless flowers; g, bracteose florescence of *Diastema affine* Fritsch.

partial florescences often are reduced and caducous, and are even absent in a few species (Figure 3f). The flowering shoots of *Kohleria* are frondose, apart from *K. allenii* (Figure 29c), *K. spicata* (Figure 3c), and *K. stuebeliana* (Figure 35a), which are frondo-bracteose. *Diastema* is set apart from *Kohleria* by having only bracteose florescences (Figure 3g).

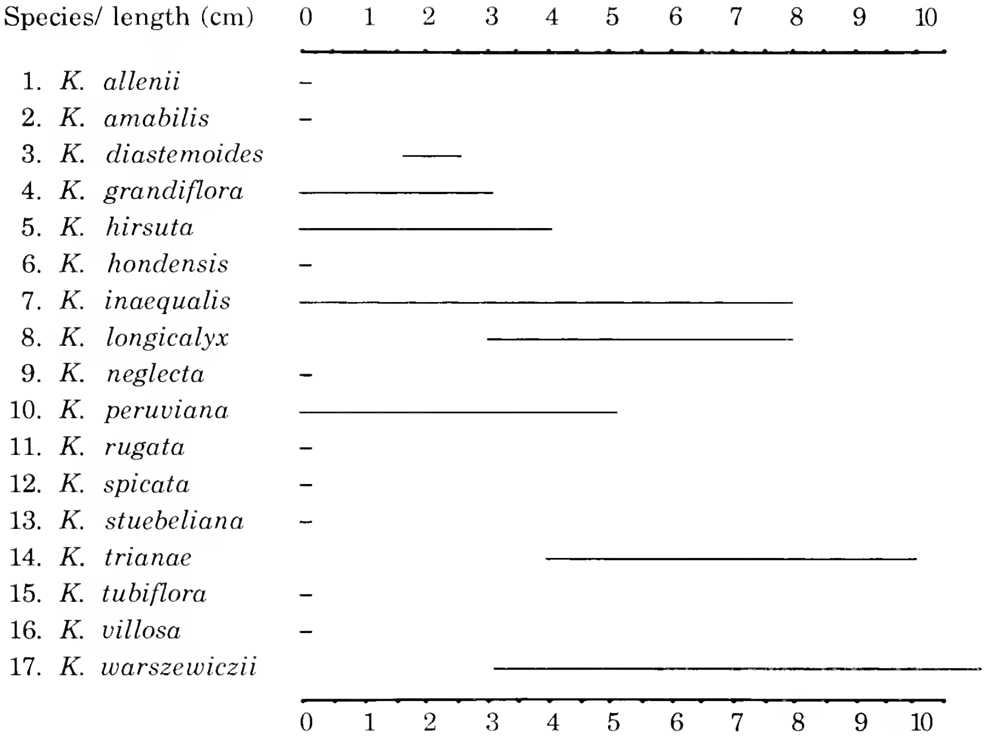


FIGURE 4.—Peduncle length variation (in cm) in the 17 *Kohleria* species. Nine species are always epedunculate.

In biennial or perennial shoots, the apex continues to grow at the end of the flowering period (Figure 3a). However, in this study the flowering shoots or florescences of one flowering season are treated as the basic inflorescence-unit, as they are separated by periods of vegetative growth.

SEEDS

Seeds in the tribe Gloxinieae rarely exceed 0.6 mm in length. Ivanina (1965) illustrated seeds from *Kohleria bogotensis* (probably a hybrid). Beaufort-Murphy (1983) included SEM-micrographs of seeds from *K. brachycalyx* (= *K. hirsuta*) and *K. digitaliflora* (= *K. warszewiczii*). For the present study SEM-micrographs were taken of seeds from all *Kohleria* species except *K. longicalyx* (Figures 5, 6). Light-microscope studies show the seeds to be brown or tawny.

The seeds of exposed-habitat and understory *Kohleria* species differ. The first group has narrowly ellipsoid to ellipsoid seeds with longitudinally, or to some extent, transverse striations (Figures 5a,e, 6a–c,e,f, and can also be seen in the seeds of *K. allenii, K. hondensis, K. rugata, K. stuebeliana,* and *K. trianae,* which not are illustrated). All of these seeds are typical of most wind-dispersed genera and species in the tribe Gloxinieae judged from the illustrations in the paper by Beaufort-Murphy (1983).

The seeds of the understory species *Kohleria diastemoides* (Figure 5c), *K. inaequalis* (Figure 5f), *K. longicalyx* (only studied with light-microscope), and *K. villosa* (Figure 6d) differ by being sub-globose, and by having irregularly rather than longitudinally striated surfaces. The seeds of *K. amabilis* (Figure 5b) are intermediate between these two seed types. The seeds of the last understory species, *K. grandiflora* (Figure 5d), have the combination of the two seed types: ellipsoid shape (as in exposed-habitat species) and an irregular surface (as in understory species). The striations are narrow in this species.

The understory Gesneriaceae have seeds similar to those found in the genera *Diastema, Monopyle,* and *Parakohleria* as illustrated by Beaufort-Murphy (1983). All these genera mostly occur in the calm understory, and have types of capsule dehiscence (and probably dispersal) different from the wind-dispersed *Kohleria* species (Figure 13).

POLLEN

Few studies of Gesneriaceae pollen exist, and the only one that included species of *Kohleria* was that of Williams (1978) with SEM-micrographs of pollen from *K. allenii, K. digitaliflora* (= *K. warszewiczii*), and *K. spicata.* During this study SEM-micrographs were taken of pollen from 12 *Kohleria* species, and apart from *K. peruviana* and *K. trianae,* these are all illustrated (Figure 7). Neither size, shape, nor surface of the pollen shows much variation among the species of *Kohleria.*

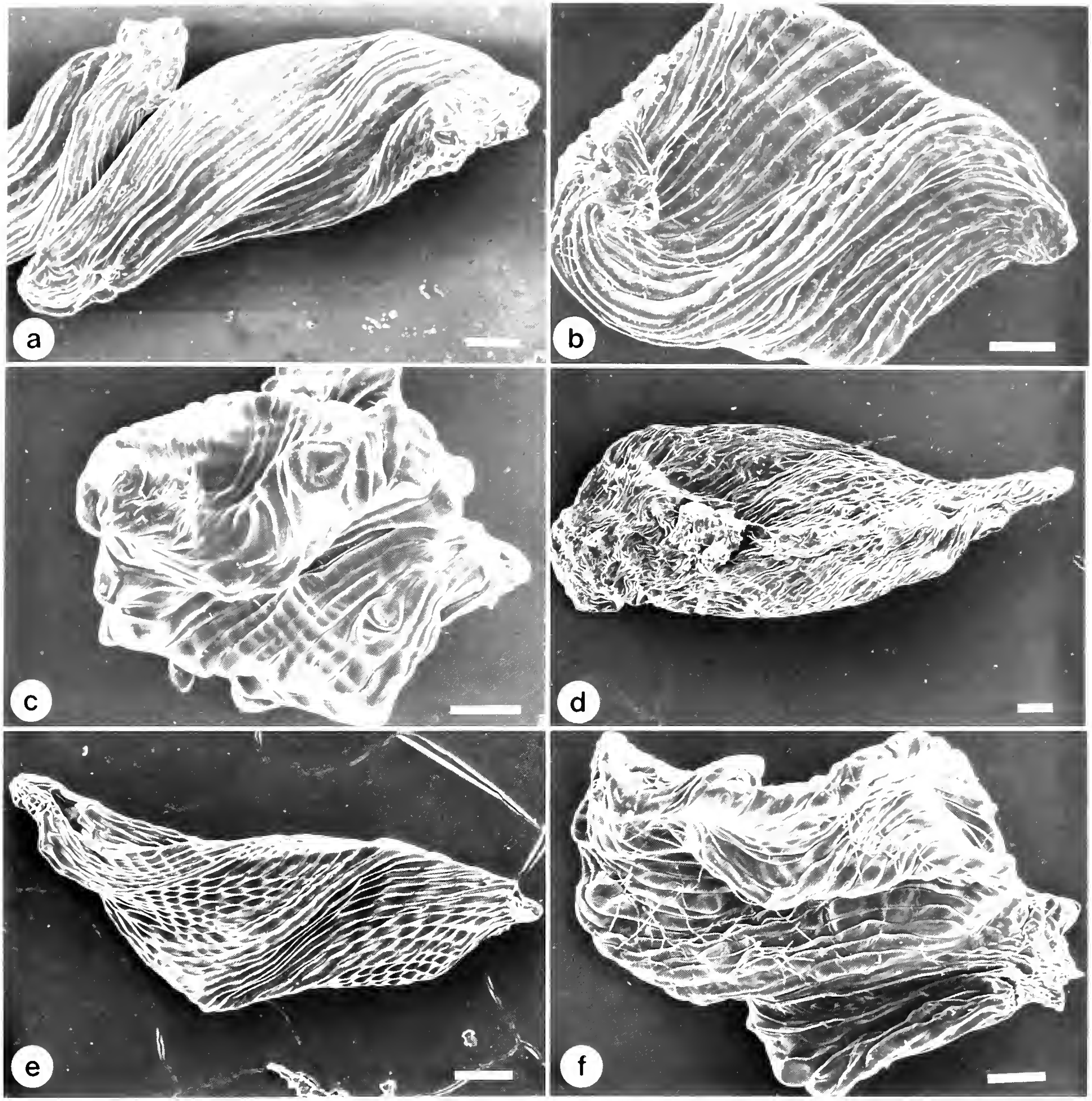


FIGURE 5.—Seeds of *Kohleria* (scale length = 50 µm): a, *K. neglecta;* b, *K. amabilis* var. *bogotensis;* c, *K. diastemoides;* d, *K. grandiflora;* e, *K. hirsuta* var. *hirsuta;* f, *K. inaequalis* var. *inaequalis.* Micrograph a of *García-Barriga 10737* (US); b of *Purdie s.n.* (K); c of *Lehmann 8892* (NY); d of *Cuatrecasas 11683* (US); e of *Barkley 35221* (NY); f of *Lehmann 1236* (NY).

The size of the grains is 19-25 µm along the polar axis and 15-18 µm along the equatorial axis. The sexine is reticulate and only *K. rugata* (Figure 7l,m) is set apart by having a verrucose surface. Skog (1976) found the same feature in a few *Gesneria* species, and suspected that this was a morphological modification for bat pollination. *Kohleria rugata*, however, is

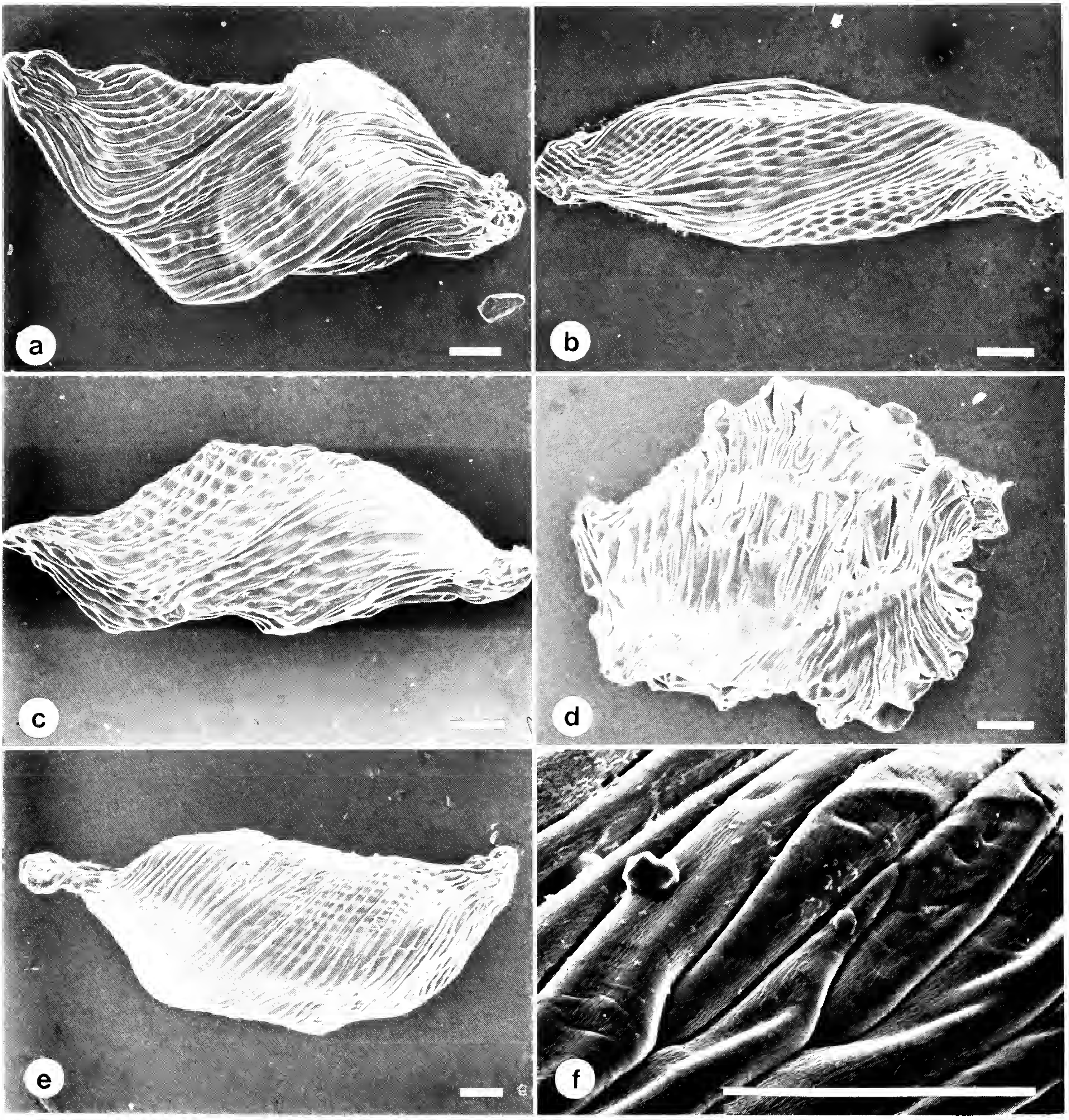


FIGURE 6.—Seeds of *Kohleria* (scale length = 50 μm): a, *K. peruviana;* b, *K. spicata;* c, *K. tubiflora;* d, *K. villosa* var. *villosa;* e, f, seed and seed surface of *K. warszewiczii*. Micrograph a of *Schunke 1472* (F); b of *Gutiérrez 35* (US); c of *Davidse & González 19038* (US); d of *Harling & Andersson 23222* (US); e, f of *Pérez-Arbeláez & Cuatrecasas 5865* (US).

likely not bat pollinated, although the identity of its pollinators is unknown.

Williams (1978) also illustrated pollen from other genera of the tribe Gloxinieae, viz., species of *Bellonia* Linnaeus, *Gloxinia* L'Heritier, *Moussonia* and *Sinningia* Nees, and Kvist (1990) illustrated pollen from *Heppiella,* another close relative of *Kohleria.* All these genera have pollen very similar to those of *Kohleria,* and pollen characters apparently have little taxonomic value in the Gloxinieae.

ANATOMY

Very little work has so far been published on the anatomy of New World Gesneriaceae, but see Weber (1971), Wilson (1974), Skog (1976), and Wiehler (1983). The first two publications include sections of the gynoecium morphology of *Kohleria.*

CYTOLOGY

The chromosome numbers of the comparably sized genera *Kohleria, Diastema,* and *Parakohleria* have been reported 37 times, five times, and once, respectively (Skog, 1984). This difference reflects that *Kohleria* is much more commonly cultivated than the other two genera. The 37 counts of *Kohleria* represent 9 of the currently accepted species and some hybrids. Since all species have a haploid chromosome number of 13, tetra- or polyploidy is unimportant or even absent in the evolution of *Kohleria.* A majority of the genera in the tribe Gloxinieae also have 13 haploid chromosomes, and tetraploids are not common (Skog, 1984).

CHEMISTRY

The chemistry of the Gesneriaceae is little known. Morley included some chemical data in Stearn (1969), and Harborne (1966, 1967) included some *Kohleria* species in his work on the flavonoids. As in most other New World Gesneriaceae the leaves and the petals of *Kohleria* contain an unusual class of flavonoids, 3-deoxyanthocyanins, responsible for the intensely red and orange colors of many members of the Gesnerioideae. Kvist and Pedersen (1986) included six species of *Kohleria* in their EPR-spectroscopic study of dihydric phenolic compounds in the Gesneriaceae. Additional EPR-studies were undertaken during this study (see Kvist and Pedersen for methods) and all the 17 recognized *Kohleria* species have now been investigated.

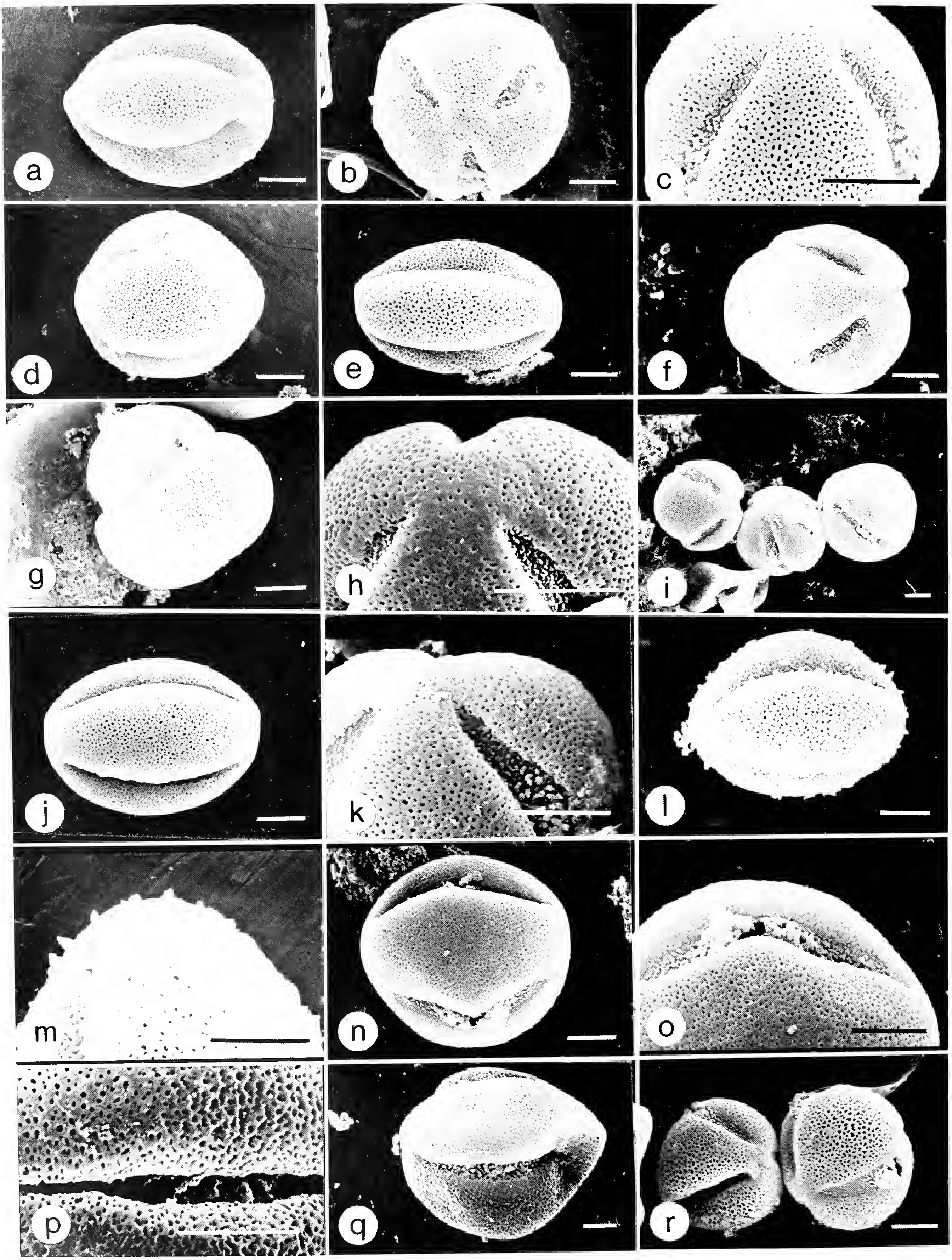
The occurrence of 3-4 dihydroxy-phenylethoxy glycosides (probably Acteoside) have been demonstrated from all *Kohleria* species apart from *K. tubiflora.* In this species another phenolic compound, Aesculetin, appears to replace Acteoside; the phenomenon was demonstrated by Kvist and Pedersen (1986) in a number of Gesneriaceae. In addition to Acteoside, a related compound Conandroside apparently was recorded from *K. hondensis.* Until now Conandroside had been isolated only from *Conandron ramondioides* in the Old World subfamily Cyrtandroideae (Nonaka and Nishioka, 1977), and Kvist and Pedersen (1986) recorded both compounds only from *C. ramondioides.*

SCALY RHIZOMES AND STOLONS

"Scaly rhizomes" is the phrase used for the subterranean, creeping stems with scale-like leaves densely congested into a somewhat cone-like structure (Figure 8b–d). In *Kohleria* their diameter typically is about one cm and their length up to five cm, but in native habitats the scaly rhizomes of *K. hirsuta* occasionally attain a length of 15 cm and a diameter up to two cm (pers. obs.). The scaly rhizomes allow the plants to survive unfavorable dry spells or seasons in dormancy and to re-sprout from the axils of the scale-like leaves when conditions improve. The majority of the *Kohleria* species produce scaly rhizomes in their native habitats, but this feature was not found in populations of *K. inaequalis, K. longicalyx,* and *K. villosa.* These latter species mostly occur in permanently humid understory and scaly rhizomes may not provide an advantage in this environment. Most exposed-habitat species, e.g., *K. hirsuta* (Figure 8b) and *K. warszewiczii* (Figure 8c), nearly always possess well-developed scaly rhizomes, but in *K. neglecta* and *K. trianae* (pers. obs.), and possibly *K. allenii* (Figure 29b), these are weakly developed. The possible explanation is that the roots of these species are the stoutest and the deepest found in the genus, probably supplying water to counteract the effects of dry periods.

The dormant organs densely covered with scales are called rhizomes, whereas stolons are the actively growing organs often with scales widely separated. The latter may be subterranean (Figures 8a, 36a, 37a). They are typically 10–30 cm long, and serve for vegetative propagation by giving rise to new shoots at the tips. They may also branch and thus give rise to several shoots. Stolons are nearly always present at least in species growing on soil substrate, and only epilithic plants, e.g., *Kohleria hondensis* (Figure 8d), growing in confining rock-crevices lack this feature (pers. obs.).

The transition between scaly rhizomes and stolons actually is gradual as the two features display the extremes of a continuum. The tips of stolons may form scaly rhizomes from which new plants later arise or conversely, dormant scaly rhizomes often re-sprout with stolons from which shoots arise. As a consequence, populations of *Kohleria* often occur in clones with few to many shoots linked together by stolons and scaly rhizomes. In *K. warszewiczii* the flowering of the individual clones, often consisting of many shoots, was found to be synchronized (pers. obs.).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PHENOLOGY

Species or hybrids of *Kohleria* cultivated in temperate regions tend to flower during the northern summer, the shoots then die back and the plants survive the winter as dormant rhizomes. However, most scaly-rhizomed *Kohleria* species in their natural habitats are not strongly seasonal. The only exception is *K. rugata* (Figure 9) from Mexico, which flowers exclusively during the humid period from September to December; it apparently never has been collected during the dry season, indicating that during that time the species is dormant and probably existing only as rhizomes. In Ecuador and Colombia not only the shaded-habitat species but also more surprisingly the exposed-habitat ones flower throughout almost the entire year (Figure 9; pers. obs.). Exposed-habitat species, however, often only have a few flowers during the driest period.

In native habitats the shoots of several *Kohleria* species may become biennial or even perennial (pers. obs.). The age of a shoot (the number of flowering seasons) can be easily determined. First-season shoots never branch apically, and shoots that continue growth after flowering and fruiting typically branch right above the old capsules, or at least possess a vegetative section of stem between the old capsules and the new buds or flowers (Figure 3a). *Kohleria hirsuta* is frequently biennial; also numerous shoots of *K. warszewiczii* and *K. neglecta* are at least biennial and some may grow three to four seasons, but the most fruticose, much-branched, and long-lived species is *K. trianae*. The shoots of the understory species *K. inaequalis*, *K. longicalyx*, and *K. villosa*, do not show any obvious seasonality (pers. obs. and data from herbarium sheets).

Observations in the Department of Cundinamarca, Colombia, demonstrated that the size, longevity, and branching of *Kohleria hirsuta* shoots (and the size of flowers) are correlated with the precipitation and the elevation. Two populations were studied at about 1000 meters altitude in a dry region with a sparse and degraded vegetation (*Londoño & Kvist 81*), and the second in a more humid area with a more luxuriant vegetation (*Londoño & Kvist 72*). At the first locality the shoots rarely exceeded 30 cm; these were all unbranched with no remnants of old capsules, but all had well-developed scaly rhizomes. According to the local inhabitants the plants flowered in the rainy season. At the second locality many plants exceeded a meter in height and were branched. Many plants had buds toward the apex and numerous degraded capsules or at least pedicels left from previous flowers below (Figure 3a).

FIGURE 7 (left).—Pollen of *Kohleria* (scale length = 5 μm): a,b, *K. allenii;* c,d, *K. amabilis* var. *bogotensis;* e, *K. hirsuta* var. *hirsuta;* f, *K. hondensis;* g,h, *K. inaequalis* var. *ocellata;* i–k, *K. neglecta;* l,m, *K. rugata;* n–p, *K. stuebeliana;* q, *K. villosa* var. *villosa;* r, *K. warszewiczii.* Micrographs a,b, of cultivated material, US acc. 2469223; c,d, of *Purdie s.n.* (K); e, of *Aymard C. 2191* (US); f, of *Mason 13806* (US); g,h, of *Tomas 2447* (US); i–k of *García-Barriga 10737* (US); l,m, of *Breedlove 11885* (US); n–p of *Cuatrecasas 3511* (US); q, of *Harling & Andersson 23222* (US); r, of *Agredo 119* (US).

FLOWERS AND POLLINATION

The nectary morphology shows considerable variation in *Kohleria*. The dominant type consists of five free glands (Figure 10b). Fritsch (1894) characterized the tribe Kohlerieae as having five nectary glands (Figure 10b–d), in contrast to the annular nectaries in his tribe Gloxinieae. However, *K. allenii* (Figures 10a, 29g) apparently always has annular, but usually shallowly to deeply five-lobed nectaries; this feature has also been observed in populations of *K. hirsuta*, *K. neglecta* (Figure 32e), *K. peruviana* (Figure 33f), *K. rugata*, *K. tubiflora*, and *K. warszewiczii*. The arrangement and the shape of nectary glands also varies; *K. amabilis* and usually *K. warszewiczii* (Figure 10c) have three free glands while the two dorsal are basally fused, *K. inaequalis* (Figure 10d) has five free glands, but often two of these are placed closely together, and *K. villosa* (Figures 10e, f, 36f, 37e) and *K. diastemoides* (Figure 30e) have glands that are two to four times as long as wide at the base. These glands are similar to those found in *Diastema*, while those of other *Kohleria* species are at most 1.5 times as long as wide at the base.

The size of the flowers of some *Kohleria* species is unusually variable (Figure 11). The shape of the corolla tube varies from narrow to broadly tubular (Figure 12) or less commonly campanulate (Figure 29c). The size of the limb varies from very small in *K. hondensis* and *K. tubiflora* (Figure 12g,h) to large and conspicuous in *K. longicalyx* (Figure 12f), and in *K. inaequalis* var. *inaequalis* (Figure 25f). The tube has some shade of red outside and frequently yellow basally and ventrally. The limb usually is yellow or red with a pattern of darker red, violet, or purple dots or lines. The four anthers are coherent by their apices and sides (Figure 33d) and included or subincluded, and a dorsal staminode is always present (Figure 35c).

Virtually all Gesneriaceae, including *Kohleria*, have protandrous flowers. A brief apparently bisexual stage has been recorded in *K. hirsuta*, *K. hondensis*, *K. spicata*, *K. trianae*, and *K. warszewiczii* (pers. obs.). During this stage the process of style elongation causes the stigma to be temporarily located near the anthers, and these may shed pollen onto a stigma that may already be receptive. Thereupon the filaments coil and pull the anthers away from the stigma, and later in the female stage the anthers are found back into the flowers as a collapsed fungus-infested mass. The temporary bisexual stage indicates that self-pollination is a possibility. However, both personal experiences, mostly with *K. hirsuta*, and discussions with other growers support the idea that at least the commonly grown and therefore well-known *Kohleria* species require cross-pollination.

Weihler (1975, 1976) considered the genera *Kohleria*, *Moussonia*, and *Parakohleria* to be adapted to hummingbird

FIGURE 8.—Stolons and scaly rhizomes of *Kohleria*: a, stolons of *K. amabilis* var. *bogotensis;* b, scaly rhizome of *K. hirsuta* var. *hirsuta;* c, seedling of *K. warszewiczii* with scaly rhizome; d, scaly rhizomes and habit of *K. hondensis,* clone of plants from rock-crevice. a of *Londoño & Kvist 78* (AAU); b of *Londoño & Kvist 75* (AAU); c of *Londoño & Kvist 62* (AAU); d of *Londoño & Kvist 69* (AAU).

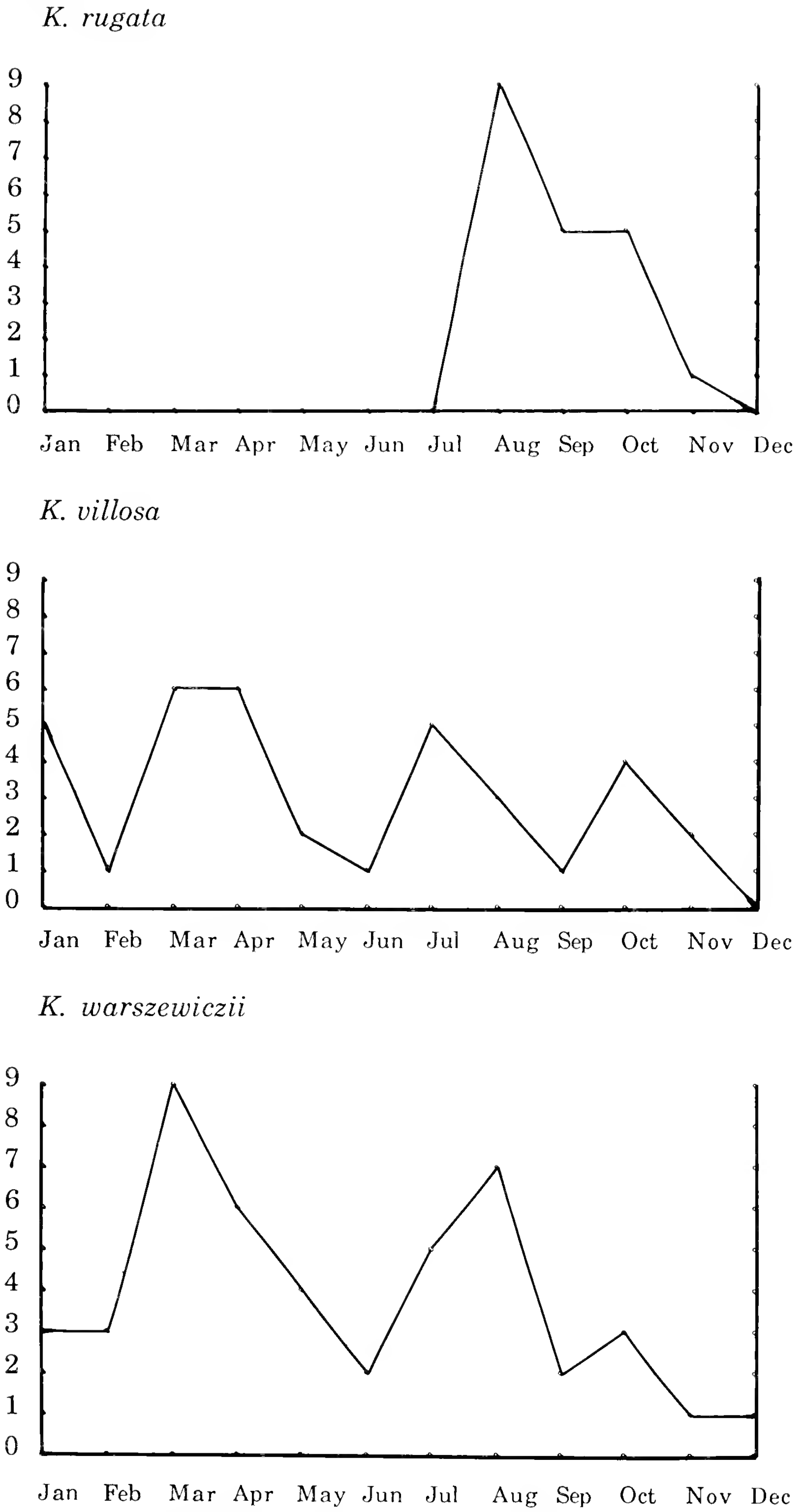


FIGURE 9.—Flowering phenology of *Kohleria* species. The number given is that of specimens with flowers recorded from each month.

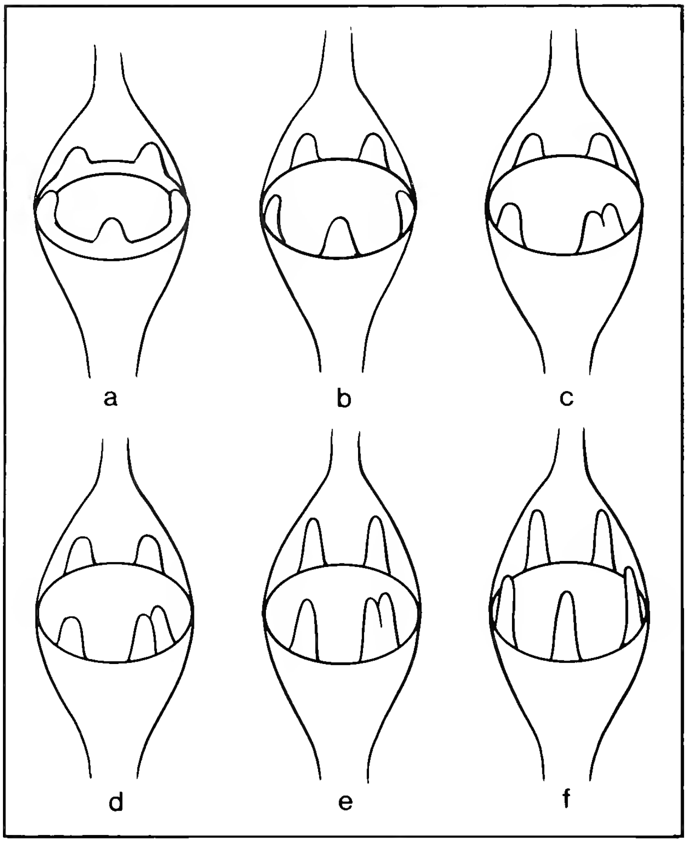
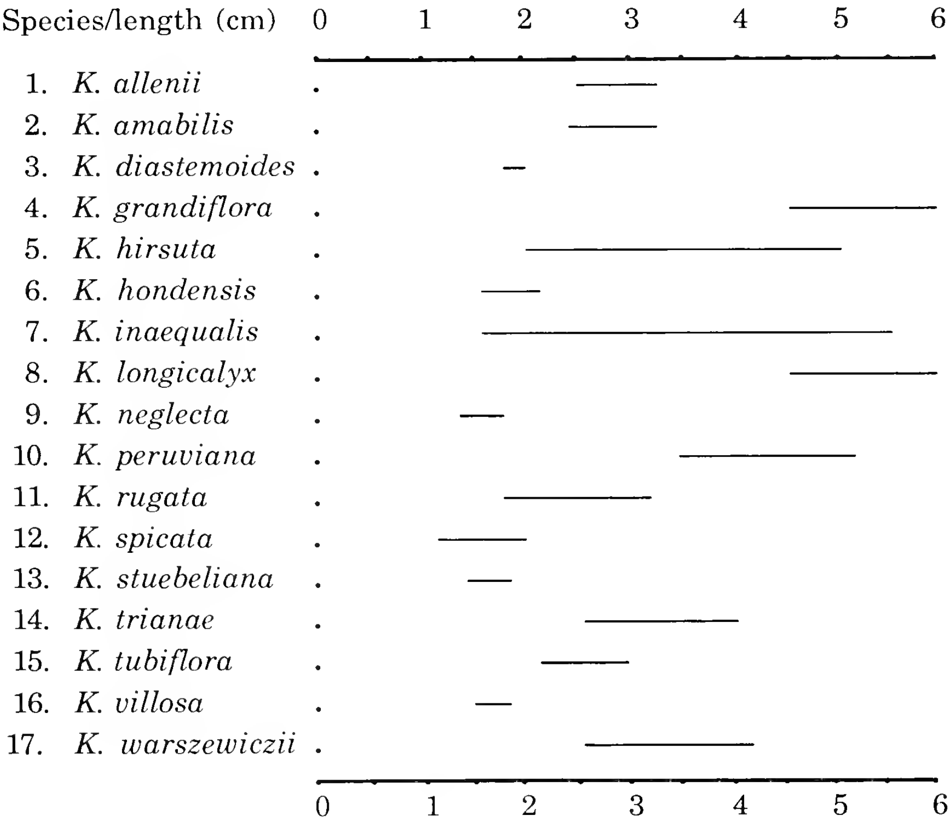
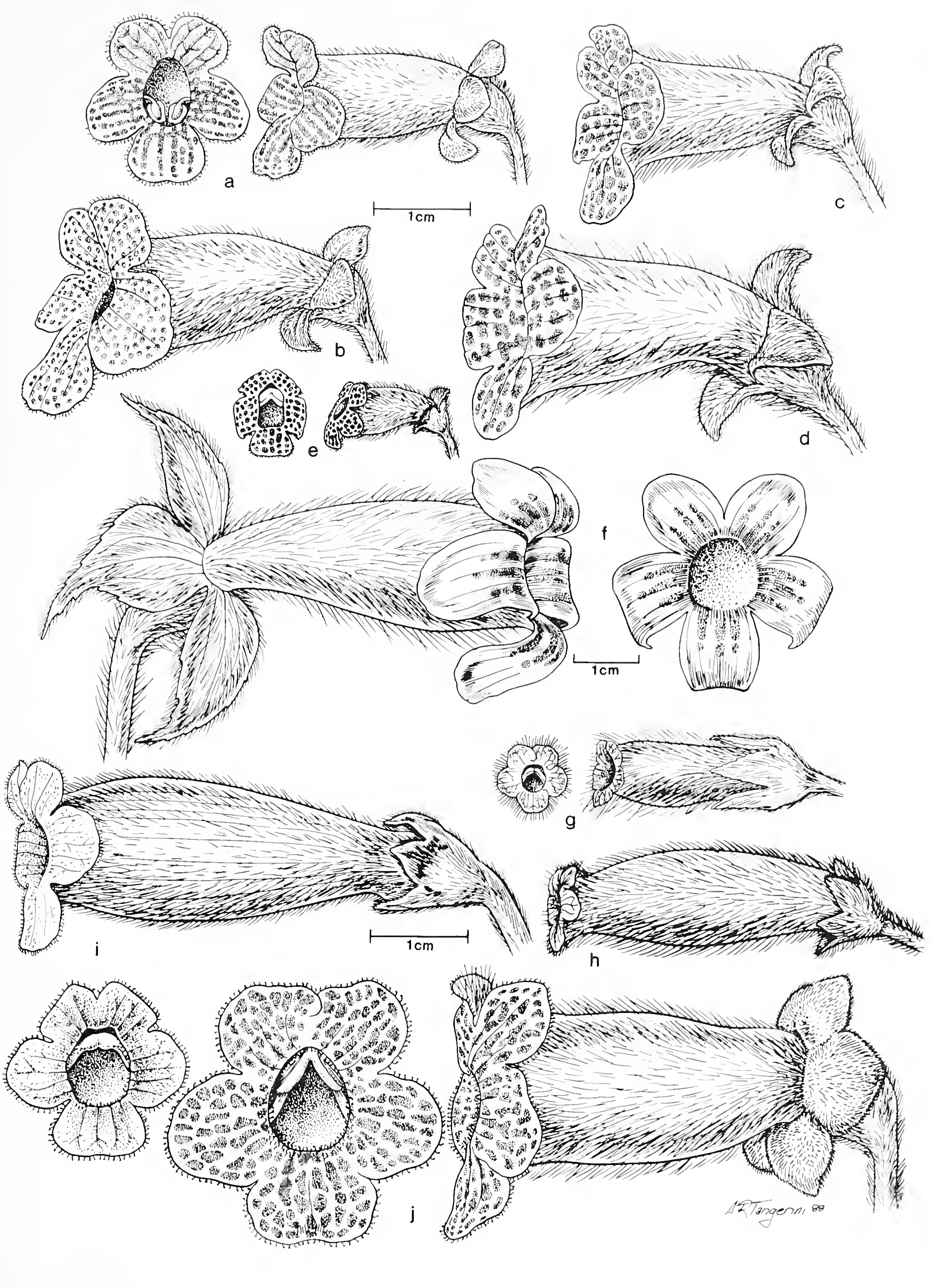


FIGURE 10 (left).—Nectary types of *Kohleria*: a, five-lobed ring as found in *K. allenii;* b, five free glands as found in *K. spicata;* c, three free and two basally fused glands, the usual state found in *K. warszewiczii;* d, five free glands with two of these placed close together, the usual state found in *K. inaequalis;* e, three free and two basally fused narrow glands, a rare state found in *K. villosa;* f, five free narrow glands, the usual state found in *K. villosa.*

FIGURE 11 (below).—Corolla length variation (in mm) found in the 17 *Kohleria* species. Two of the four most frequently collected species, *K. spicata* (762 collections) and *K. tubiflora* (260 collections), show little variation, in contrast with the two other commonly collected species, *K. hirsuta* (255 collections) and *K. inaequalis* (153 collections).

FIGURE 12 (right).—Flowers of *Kohleria*: a, *K. amabilis* var. *bogotensis*, lateral and front views; b, *K. amabilis* var. *amabilis*, lateral view; c, *K. rugata*, lateral view; d, *K. rugata*, lateral view; e, *K. spicata*, lateral and front views; f, *K. longicalyx*, lateral and front views (note the scale is reduced compared with that of the other flowers); g, *K. hondensis*, lateral and front views; h, *K. tubiflora*, lateral view; i, *K. trianae*, lateral and front views; j, *K. warszewiczii*, lateral and front views. a of *Londoño & Kvist 78* (AAU); b of *Haught 2422* (US); c of *Ton 2934* (US); d of *Nelson 2890* (US); e of *Haught 4634* (US); f of *Londoño & Kvist 153* (AAU); g of *Londoño & Kvist 69* (US); h of *Nee 8598* (US); i of *Londoño & Kvist 51* (US); j of *Londoño & Kvist 62* (US).

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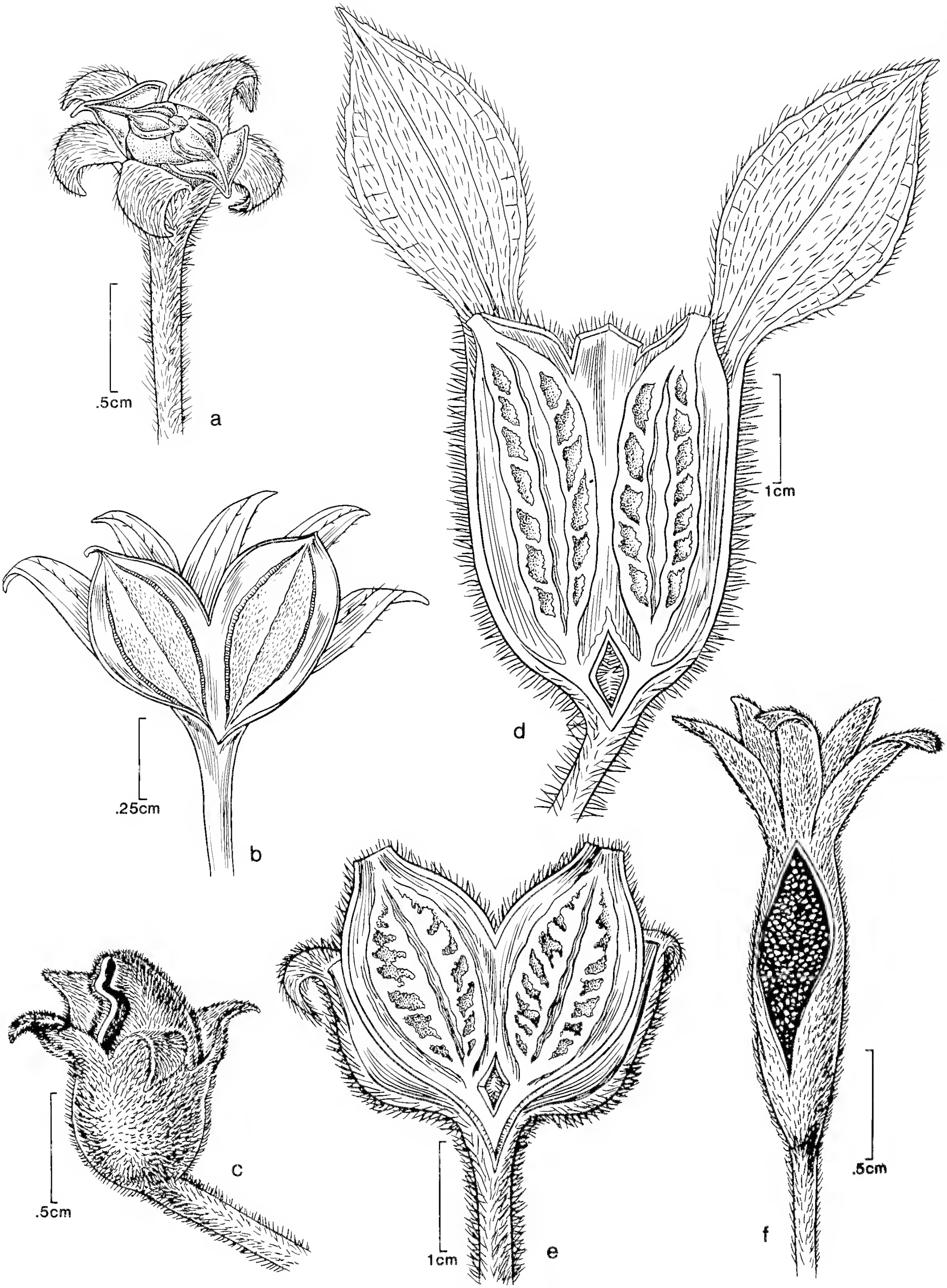
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pollination, which promoted their superficial similarity through parallel evolution. Their red, often funnel-shaped flowers conform to the "bird-pollination syndrome." However, many populations of *Kohleria*, as well as *Parakohleria*, were observed in Ecuador and Colombia, without seeing hummingbirds or other visitors to their flowers (pers. obs.). The few observations reported on herbarium labels do not identify a single group of visitors, as hummingbirds, bees, wasps, and butterflies have all been reported to visit *Kohleria* flowers (Table 1).

Some *Kohleria* species, especially *K. hirsuta*, may be pollinated by a series of unspecialized pollinators. Both the flowers and the habitats are extremely variable, making it unlikely that a single agent or even a few will function as pollinators. The length of *K. hirsuta* corollas ranges from two to five cm (Figures 11, 24), and in central Colombia the species occurs from 200 meters to 2700 meters elevation. The small-flowered populations occur at low elevations in hot, dry, open scrubland, and the large-flowered ones in chilly, humid, high-montane forest. The flower variation in *K. inaequalis* is even more extreme, as the corolla length ranges from 1.5 to 5.5 cm (Figures 11, 25), but in this species there is no correlation between flower size, precipitation, habitats, and elevations.

FRUITS AND DISPERSAL

Kohleria has unilocular capsules with parietal placentation and loculicidal dehiscence. Exposed-habitat, wind-dispersed species and understory, probably animal-dispersed species have capsules that split by two apical valves and by a slit from the apex to the base, respectively. However, the capsules of some understory species have intermediate features.

The 11 exposed-habitat *Kohleria* species all have ovoid capsules that dehisce into two apical valves and persist in this stage for weeks or months, during which several hundred minute seeds are dispersed by wind (Figures 13c, 33h). A row of stiff trichomes located at the edges of the valves further restricts the relatively narrow opening and probably extends the period during which dispersal occurs. Herbarium sheets often have numerous bivalved capsules. In contrast, open capsules are rare on sheets of understory species. The capsules mostly are oblong (Figure 30f) rather than ovoid (Figure 13c).

TABLE 1.—Observations of potential pollinators visiting *Kohleria* flowers (^{1} = two different species seen, ^{2} = *Lampornis calolaema*, ^{3} = three different species seen, ^{4} = documented with photos).

Species	Pollinator	Country	Reference
K. spicata	Bees^1	Colombia	*Folsom 10437*
	Hummingbirds^2	Guatemala	*Atwood 7737*
K. tubiflora	Butterflies^3	Panama	*Davidse & Pohl 1321*
	Hummingbirds	Panama	Croat (1978)
K. warszewiczii	Wasps^4	Colombia	Londono (pers. comm.)
	Hummingbirds	Colombia	Londono (pers. comm.)

FIGURE 13 (left).—Capsule dehiscence in species of *Kohleria* and in some other genera in the tribe Gloxinieae: a, *Parakohleria abunda* Wiehler, two fleshy valves that split from apex to base and reflex completely; b, *Diastema racemiferum* Bentham, two apical valves (2 slits) with one of the slits continuing to the base (similar to the capsules of *Kohleria villosa*); c, *Kohleria allenii*, two apical valves; d, *Kohleria longicalyx*, a single longitudinal slit from apex to base; e, *Kohleria inaequalis*, a single longitudinal slit from apex to base, but in this case possibly first forming two apical valves (most *K. inaequalis* capsules usually are more oblong and similar to those of *K. longicalyx*); f, *Monopyle macrocarpa* Bentham, a single longitudinal slit from the middle of the capsule toward the apex and base. a of *Kvist et al. 60450* (AAU); b of *Steyermark & Rabe 97441* (US); c of *Liesner 2106* (US); d of *Londoño & Kvist 153* (AAU); e of *Londoño & Kvist 190* (AAU); f of *Churchill et al. 4735* (US).

During fieldwork in Colombia it was discovered that the oblong capsules of the understory species *Kohleria inaequalis* (Figure 13e) and *K. longicalyx* (Figure 13d) dehisce by a single slit from the apex to the base, exposing the glutinous seed mass. The edges of the slit have no row of trichomes as seen in the exposed-habitat species. The rarity of open capsules both on herbarium sheets and in natural habitats indicates the capsules to be soon shed (and consequently the seeds quickly dispersed). The oblong capsules of *K. diastemoides* (Figure 30f) are similar, and their dehiscence is probably also unilateral.

The capsules of another understory species, *Kohleria villosa*, were found to have features intermediate between the bivalved and the unilaterally dehiscing fruits. The ovoid (Figure 36g) capsules first split apically into two valves, but one of the two slits continues to the base (Figure 13b). The valves have a few trichomes at the edge. The capsules of *K. amabilis* apparently are similar to those of *K. villosa*, but open capsules have only been observed on herbarium sheets. The dehiscence of the last understory species, *K. grandiflora*, is unknown as no mature fruits were seen.

The understory *Kohleria* species probably have switched from wind- to animal-dispersal. The mode of seed presentation presumably is an adaptation to attract animals that actively search the exposed glutinous seed-mass. Unfortunately no dispersing animals have so far been observed, but insects may prey on the seed-masses and become covered with the seeds, thus dispersing them. Burtt (1970, 1976) mentions that water-dispersal and the casual passive transportation by adherence of the tiny seeds to animals contribute to the dispersal of understory Gesneriaceae. However, these vectors are hardly the primary ones for species exposing a glutinous seed-mass.

Numerous seedlings are often found close to plants of exposed-habitat species, e.g., *Kohleria hirsuta*, *K. hondensis*, and *K. warszewiczii* (pers. obs.). These seedlings develop scaly rhizomes very early. Seedlings only a few cm tall of *K. warszewiczii* have tiny, scaly rhizomes (Figure 8c). The seedlings apparently must establish scaly rhizomes before they flower or form stolons. This may explain why *K. hirsuta*, *K. spicata*, and *K. tubiflora*, although they thrive in disturbed habitats, are never true annual weeds.

Animal-dispersal is often considered more efficient over longer distances than wind-dispersal (see, for example, Stebbins, 1971), but in *Kohleria*, with its numerous dust-like seeds, the situation may be quite the opposite. The exposed-habitat species have a much larger distribution than understory species (Figure 14), and the occurrence of *K. spicata* and *K. tubiflora* on many coastal islands (Figures 15, 16), and the former even on Cocos Island, ~500 km southwest of the nearest mainland in Costa Rica, demonstrates that long-distance wind dispersal must occur.

PHYTOGEOGRAPHY

Kohleria ranges from Mexico to Peru and east to Surinam (Figure 14). The 11 exposed-habitat species occur widely throughout the range, while the ranges of the six understory species are restricted to near the diversity center of *Kohleria* in Colombia and northwestern Ecuador (Figure 14). The entire ranges of all 17 *Kohleria* species are first discussed below, followed by the distributions within Colombia (14 species) in more detail.

Three exposed-habitat species are widely distributed, and to each of these a locally distributed, allopatric species appears to have close affinity. The most common species, *Kohleria spicata* (Figure 15), occurs from Mexico to Peru, and is replaced by *K. stuebeliana* on the eastern Andean slopes of Colombia. The second most common species, *K. tubiflora* (Figure 16), is widespread in Central America and northern South America, and is replaced by *K. hondensis* in the Río Magdalena valley of Colombia. The third widespread species, *K. hirsuta* (Figure 17), ranges from the Colombian highlands through Venezuela to Surinam. Further to the south, in Peru, the species is replaced by *K. peruviana* (Figure 17). Two species, *K. allenii* and *K. rugata* (Figure 18), are endemic to Costa Rica and adjacent Panama, and southern Mexico, respectively. The remaining three exposed-habitat species, *K. trianae*, *K. neglecta*, and *K. warszewiczii* (Figure 19), are endemic to Colombia. The only common understory species, *K. inaequalis*, is widespread in the Colombian highlands and northwestern Ecuador (Figure 28). The five other understory species, *K. amabilis*, *K. diastemoides*, *K. grandiflora*, *K. longicalyx*, and *K. villosa*, are rare and local endemics in the same region, although the latter species is locally common in Ecuador (Figure 20).

The valleys of the south- to north-flowing Ríos Cauca and Magdalena divide the Colombian highlands into three Cordilleras, delimiting and isolating the ranges of the 14 Colombian *Kohleria* species (Figure 21). On the eastern slopes of the Eastern Cordillera (the upper Amazon and Orinoco watersheds) six *Kohleria* species occur (Figure 21) including three endemics, *K. grandiflora*, *K. longicalyx* (Figure 20), and *K. stuebeliana* (Figure 19). In the Río Magdalena watershed eight species occur, making this the area of greatest species diversity (Figure 21). Among these are three endemics, *K. amabilis* (Figure 20), *K. hondensis* (Figure 16), and *K. neglecta* (Figure 19). In the Río Cauca watershed six species occur (Figure 21) but only the rare *K. diastemoides* (Figure 20) is endemic. Finally five species also occur in the area draining to the Pacific Ocean (Figure 21), but only *K. villosa* (Figure 20) is restricted to the western Andean slopes. *Kohleria trianae* is endemic to the Central Cordillera, including both the eastern and western slopes (draining to Río Magdalena and Río Cauca, respectively (Figures 21, 22)). The related *K. hirsuta* (Figures 21, 22) mostly is found in the Eastern Cordillera. *K. inaequalis* (Figure 28), *K. spicata* (Figure 15), and *K. warszewiczii* (Figure 19) are widespread in the Magdalena and Cauca watersheds as well as in the Pacific area (Figure 21). Finally *K. tubiflora* (Figure 16) is widespread but absent from the Magdalena watershed (where *K. hondensis* occurs).

Kohleria species often have a broad altitudinal distribution range, e.g., *K. hirsuta* and *K. spicata* (Figure 21). However, even the species concentrated within a specific altitudinal belt are often represented by a few collections from much higher, e.g., *K. stuebeliana* and *K. tubiflora*, or much lower altitudes, e.g., *K. inaequalis* and *K. warszewiczii*. The latter two species only reach the lowland in the extremely humid Pacific Colombia (Figure 21).

POPULAR NAMES AND MEDICINAL USES

Popular names have been recorded for species of *Kohleria* in Venezuela, Colombia, and Central America (Table 2). In the Central and Western Cordilleras of Colombia the most frequent name for *Kohleria* species that possess scaly rhizomes is "caracola," a name that is likewise used for *Heppiella ulmifolia*, which also has scaly rhizomes (Kvist, 1987). Pérez-Arbeláez (1947) confirmed that the name "caracola" referred to the scaly rhizomes. In the Eastern Colombian Cordillera and Venezuela an often-used name for *Kohleria hirsuta* is "tusilla" (Table 2). García-Barriga (1975) reported that both "caracola" and "tusilla" refer to a drug produced from the scaly rhizomes.

In Colombia and Venezuela, the scaly rhizomes of *Kohleria* are boiled for a beverage drunk as a treatment for kidney afflictions. This use has been recorded for *K. hirsuta* in the Colombian Dept. Tolima (*Londoño & Kvist 72, 81*), from Venezuela by Steyermark and Huber (1978), and for *K. spicata* in the Colombian Dept. Valle (*Herrera 975*). The latter species was also claimed to be useful for treatment of venereal disease. In Guatemala *K. spicata* is said to be an astringent (*Ruana 393*). This effect is confirmed by García-Barriga (1975) in Colombia, and the above-mentioned applications may very well also be based on the astringent properties. Pérez-Arbeláez (1947) reported that *Kohleria spp.* were used to regulate liver and kidney functions in Colombia. In addition, label data of an apparently Colombian *K. tubiflora* collection (collector unknown, at K) indicate the plant was used "in cases of dysentery with effect (as a decoction)."

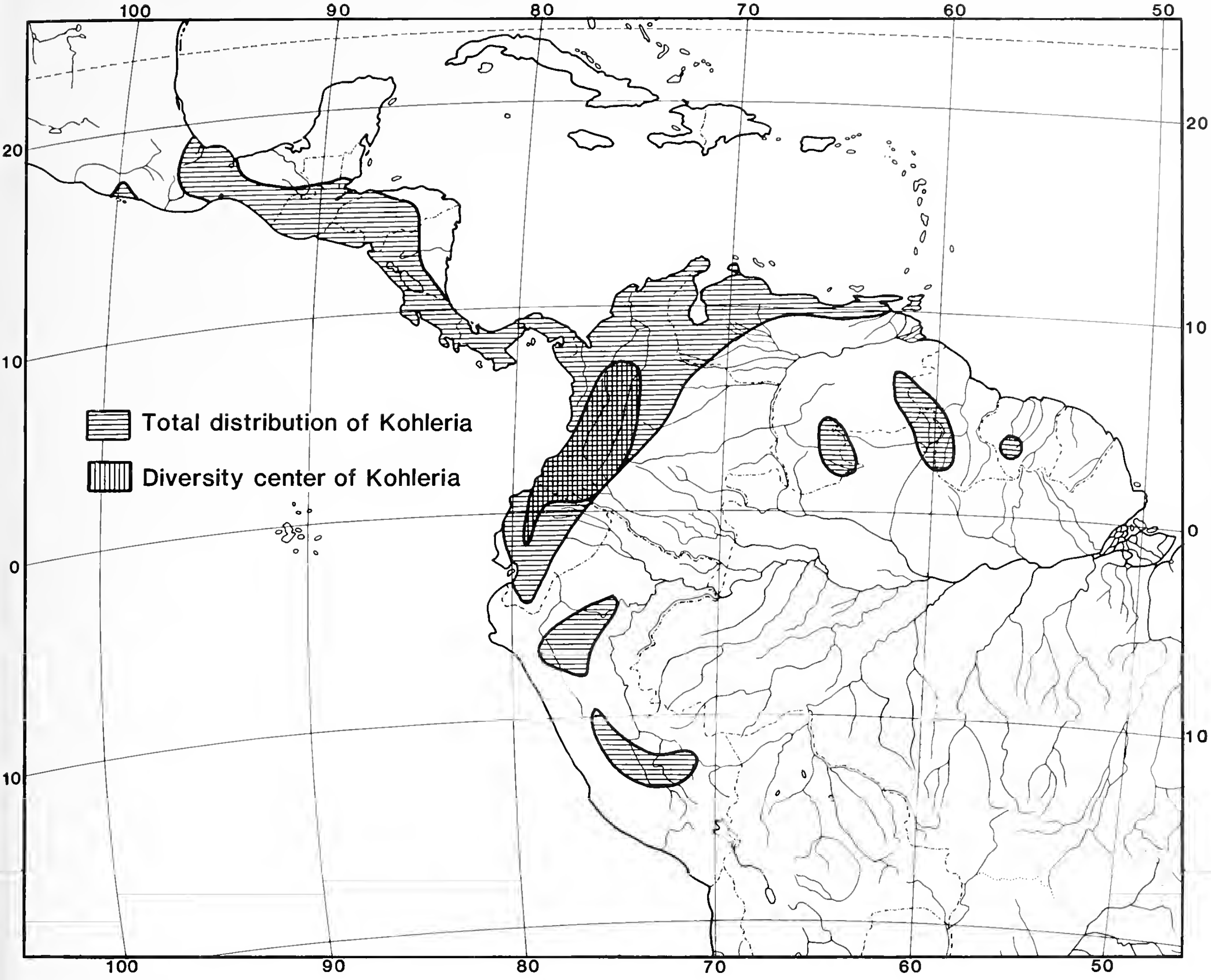


FIGURE 14.—Entire range of *Kohleria* and the diversity center of the genus where 19 of the 22 accepted taxa occur. The latter area is also the approximate range of the *Kohleria* species that have capsules splitting all the way to the base as an apparent adaptation to animal-dispersal.

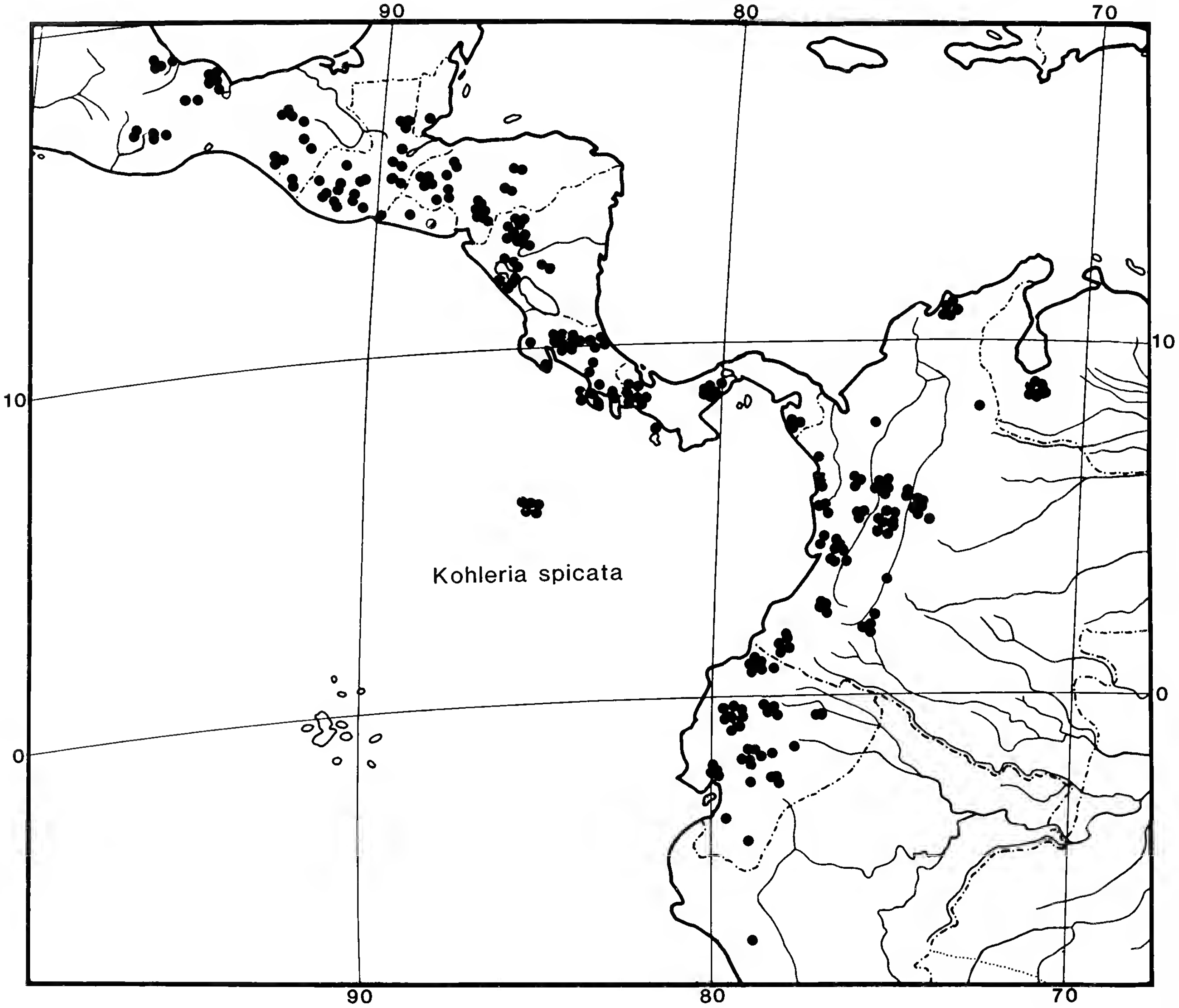


FIGURE 15.—Distribution of *Kohleria spicata*. Note the occurrence on Cocos Island.

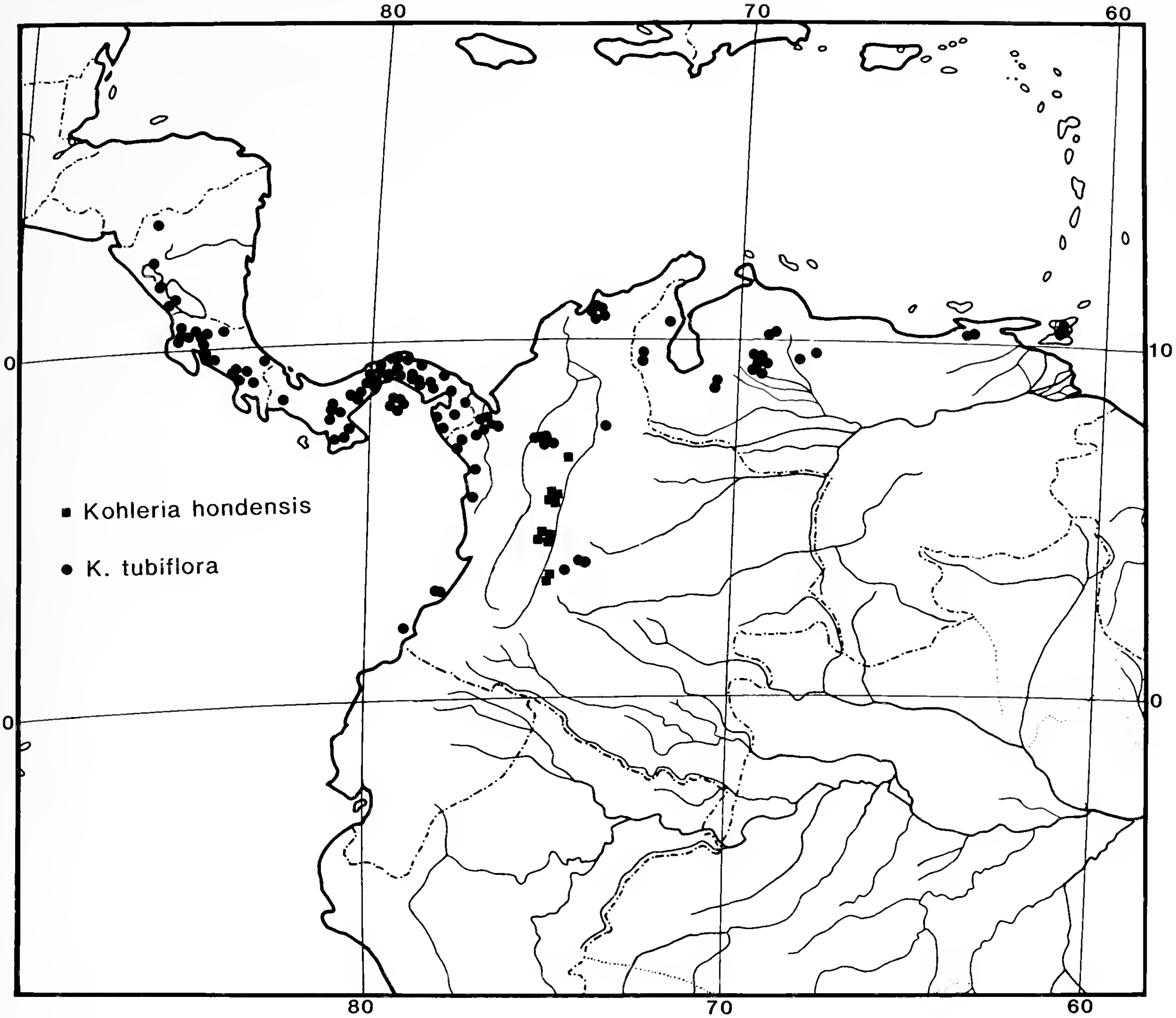


FIGURE 16.—Distributions of *Kohleria tubiflora* and *K. hondensis*. The barriers formed by the Central and Eastern Colombian Cordilleras appear to isolate the two related species.

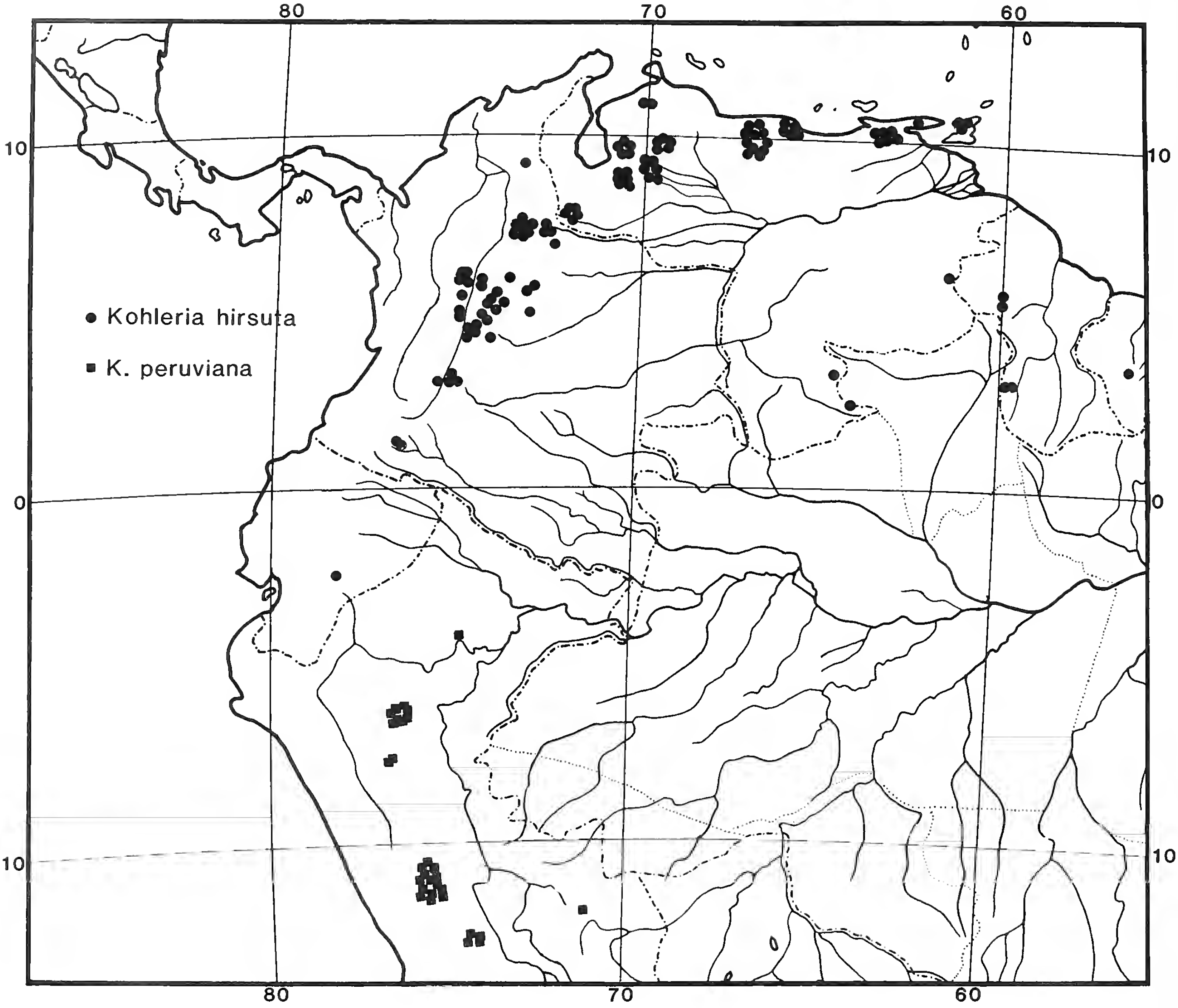


FIGURE 17.—Distributions of *Kohleria hirsuta* and *K. peruviana*. (Figure 22 shows the distribution of *K. hirsuta* in Colombia, including var. *longipes* endemic to that country.)

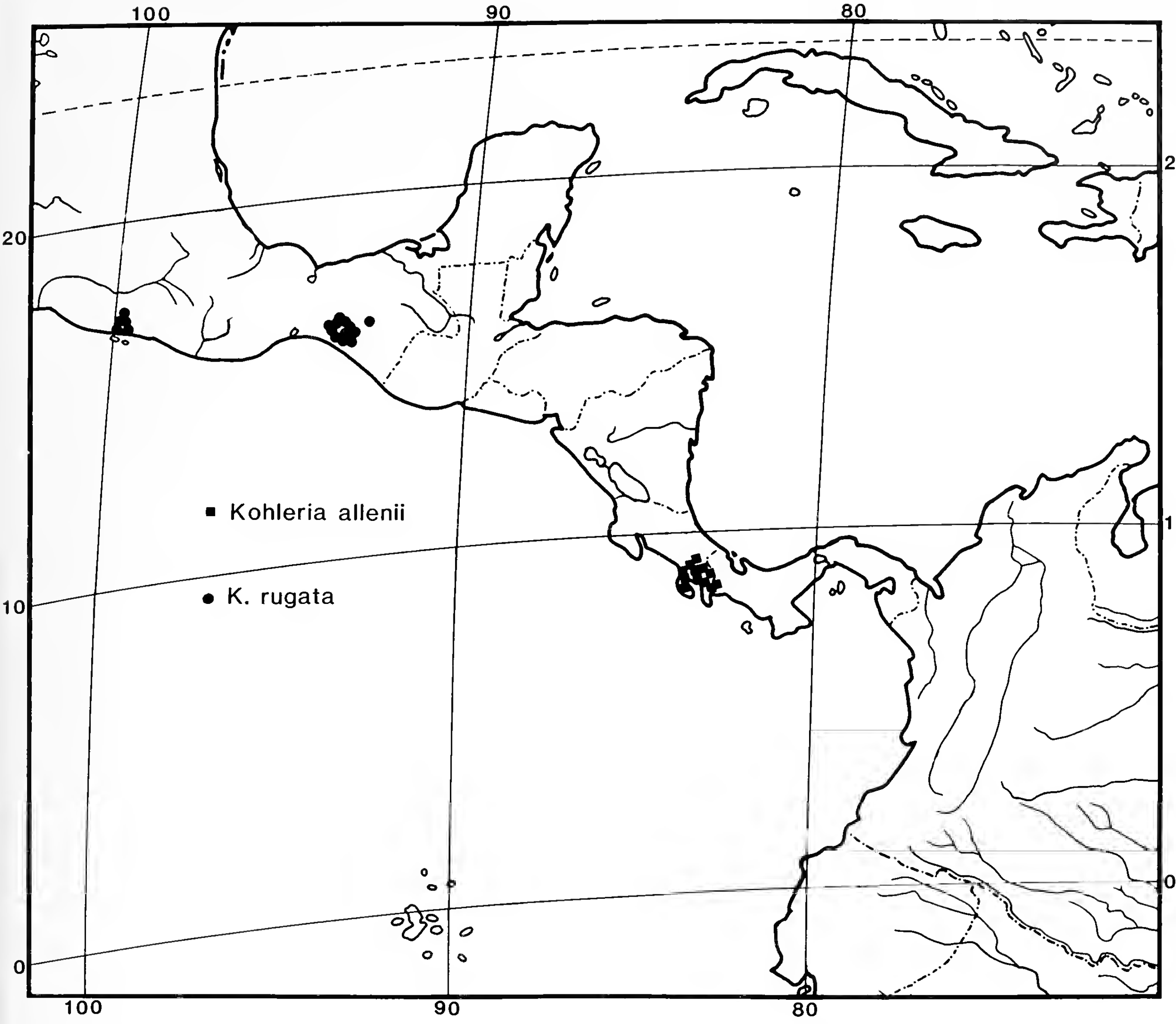


FIGURE 18.—Distributions of the two Mexico and Central American endemics, *Kohleria allenii* and *K. rugata*.

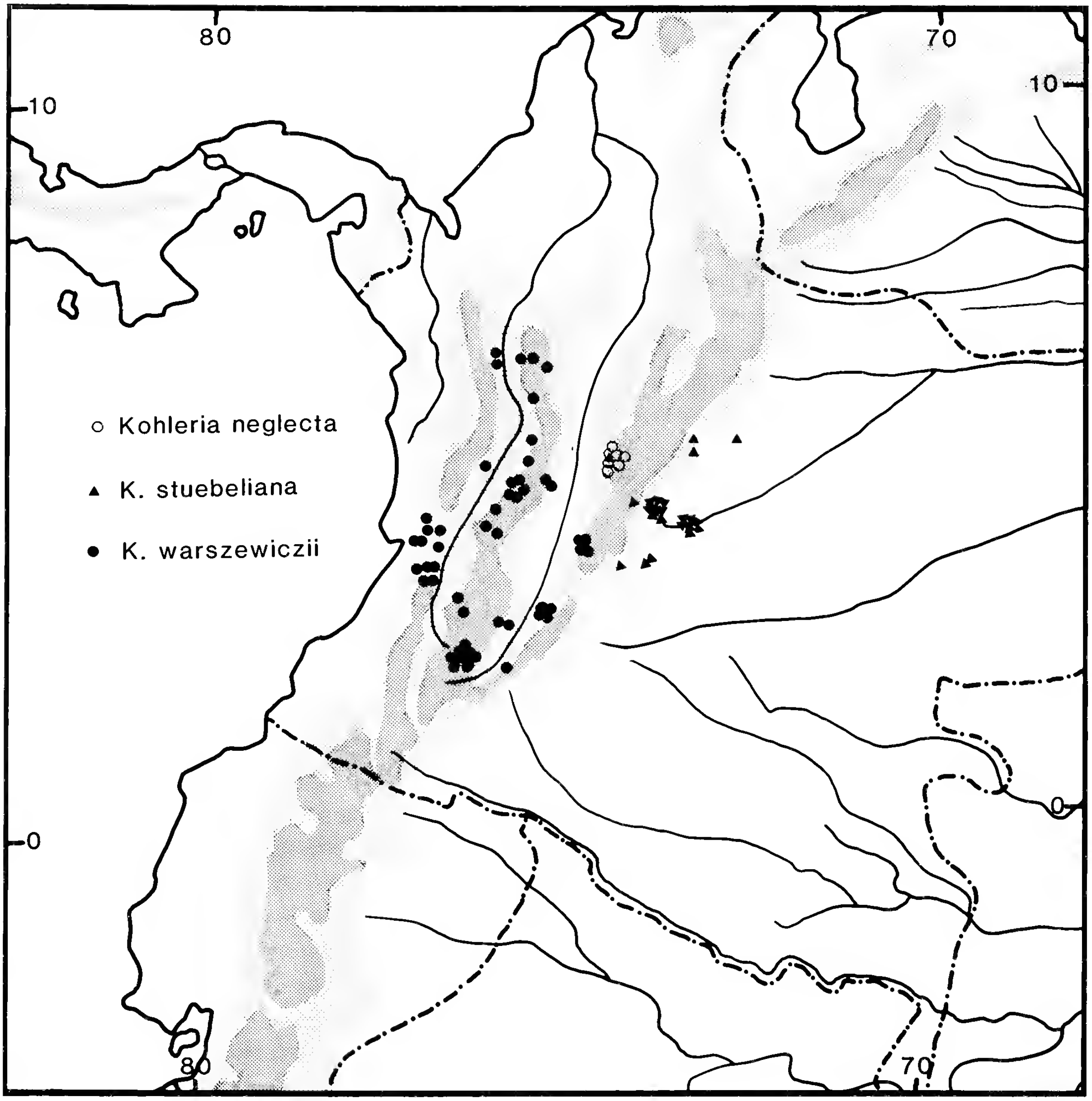


FIGURE 19.—Distributions of *Kohleria neglecta*, *K. stuebeliana*, and *K. warszewiczii* (note the single collection of *K. stuebeliana* from the western slopes of the Eastern Cordillera within the limited range of *K. neglecta*).

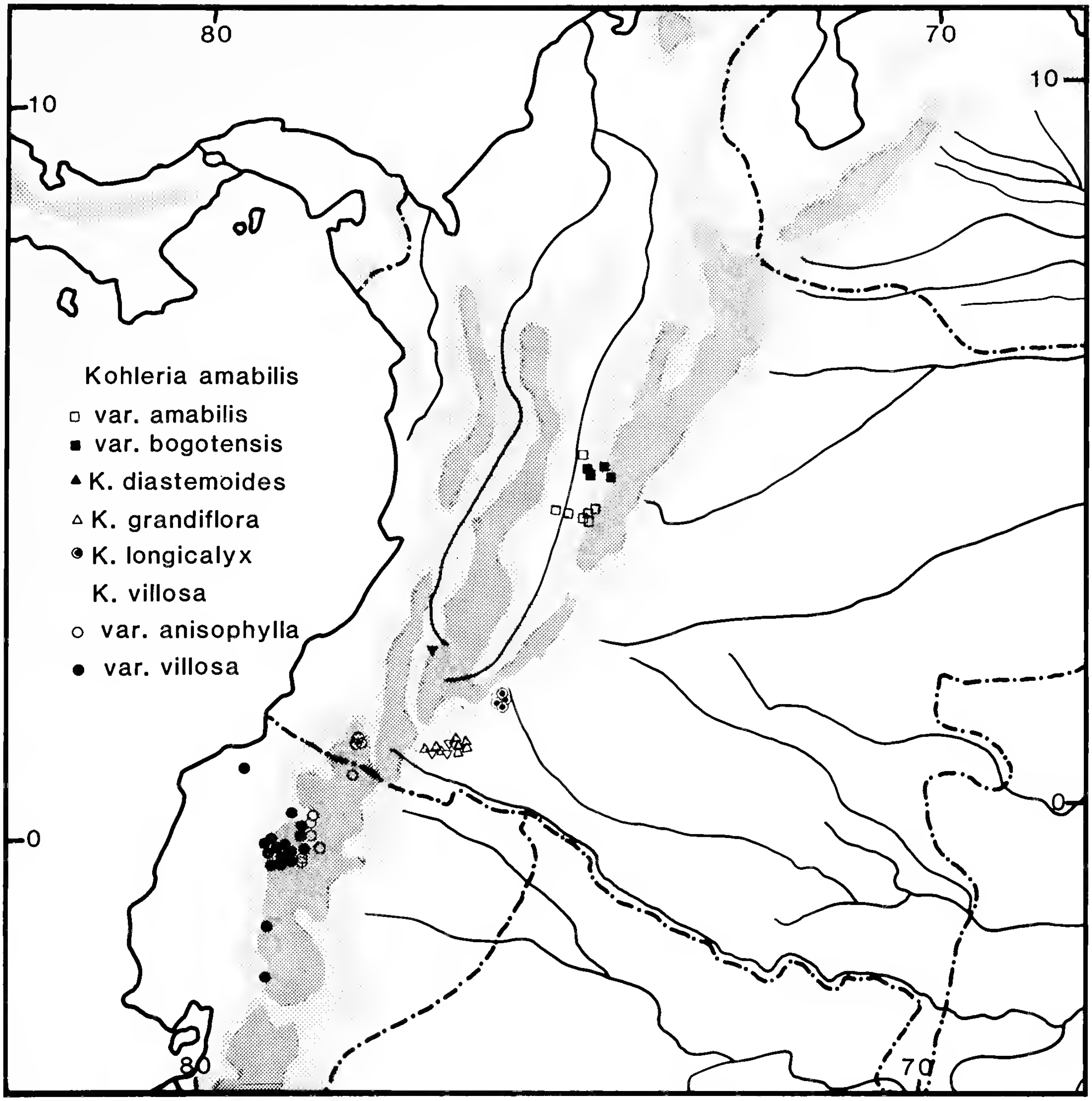


FIGURE 20.—Distribution of all *Kohleria* species and varieties (except *K. inaequalis;* see Figure 28) having capsules that split all the way to the base.

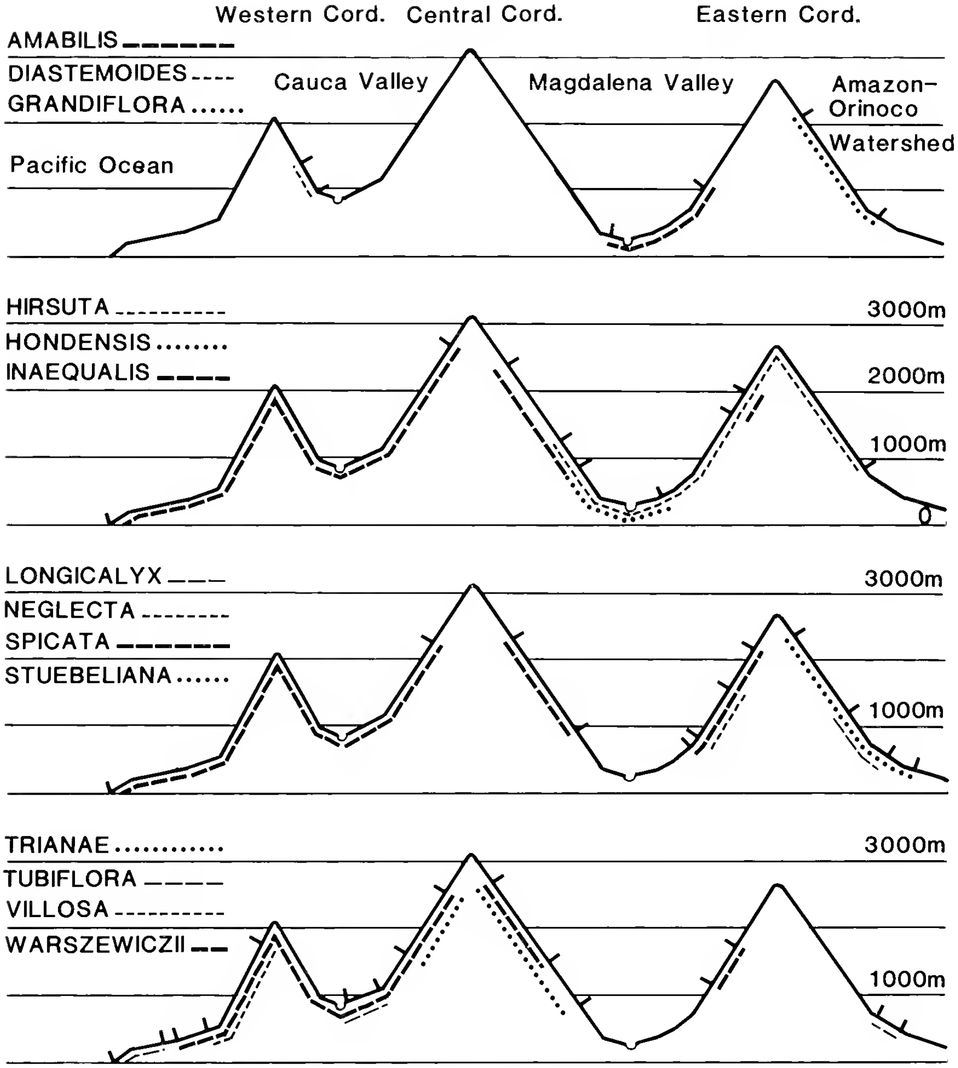


FIGURE 21.—Distributions and altitudinal ranges of the 14 *Kohleria* species that occur in the Colombian highlands. The three Colombian Cordilleras have been transected east-west, and the ranges of the individual species within each of the four watersheds are shown.

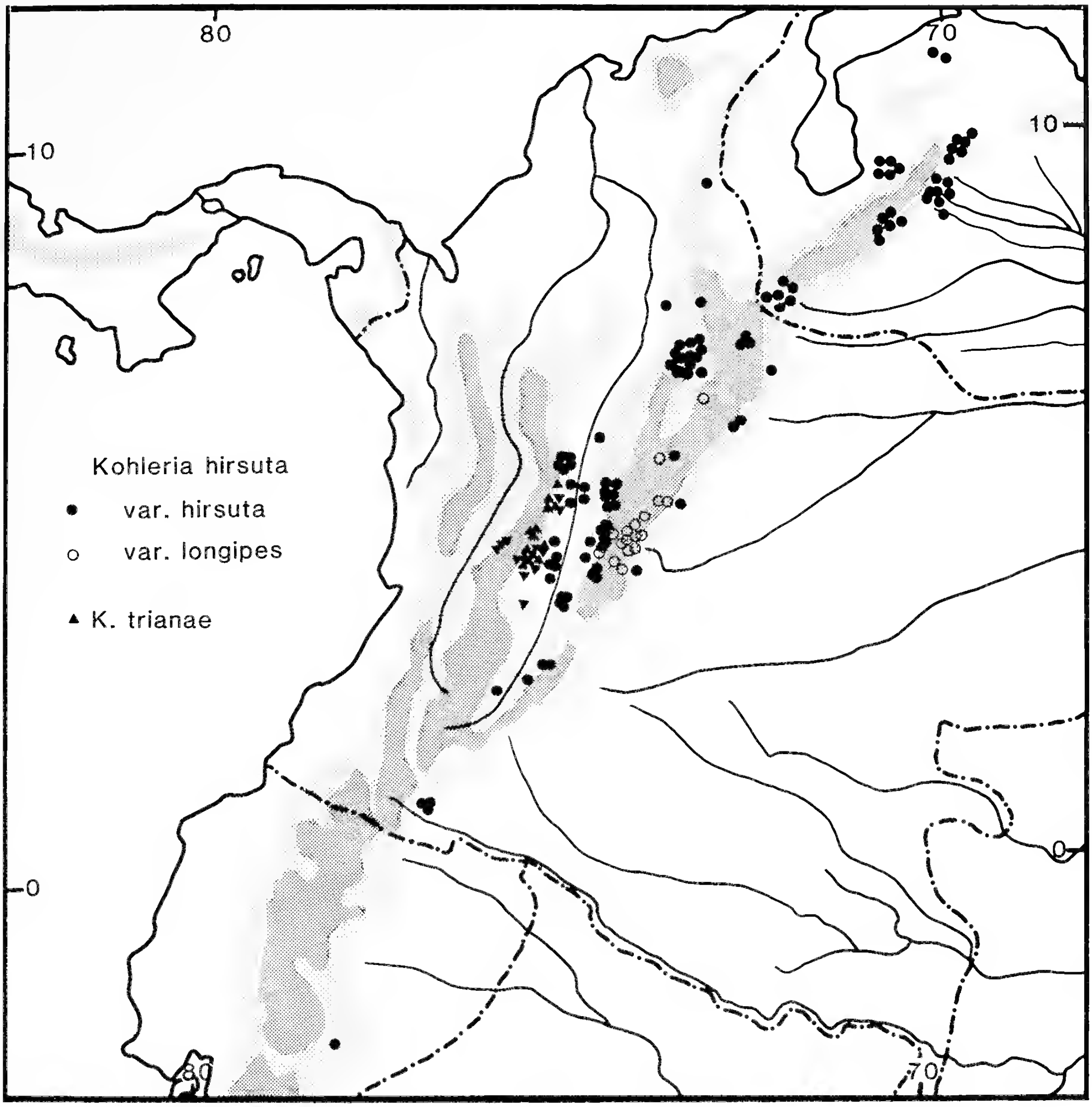


FIGURE 22.—Distributions in Colombia and adjacent Venezuela of *Kohleria trianae*, *K. hirsuta* var. *longipes*, and *K. hirsuta* var. *hirsuta* (see Figure 17 for the entire distribution of the variety *hirsuta*).

TABLE 2.—Vernacular names of *Kohleria* species given on herbarium labels and on a Venezuelan stamp.

Species/Country	Province	Collector	Vernacular name
K. grandiflora			
Colombia	Putumayo	*Lehmann 4018*	Flor de Bolivar
K. hirsuta			
Colombia	Cundinamarca	*Cuatrecasas 13578*	Tusilla
	Cundinamarca	*Fernández 1309*	Tucilla
	Cundinamarca	*Forero 139*	El buen cuidadano
Venezuela	Dist. Federal	*Elias 411*	Caljois del Diablo
	Miranda	*Fernández 4*	Tusilla
	unknown	from a stamp	Calzoncito del diablo
	(Dist. Federal?)	Steyermark & Huber (1978)	Tusilla
K. hondensis			
Colombia	Tolima	*André 1949*	Yerba de almorran
K. spicata			
Colombia	Antioquia	*Daniel 809*	Caracola
	Antioquia	*Daniel 1355*	Caracola
	Antioquia	*Daniel 3921*	Caracola roja
	Antioquia	*Rodriguez 24*	San Juanita
	Antioquia	*Tomas 977*	Caracola
	Valle	*Cuatrecasas 22568*	Caracola
	Valle	*Figuieras 8198*	Caracola
	Valle	*Herrera 975*	Caracola
El Salvador	El Salvador	*Calderón 174*	Digital Montes
	San Vicente	*Standley 21462*	Diente de Perro
Guatemala	Guatemala	*Ruana 393*	Mazorco
Honduras	Tegucigalpa	*Hagen et al. 1211*	Sulfatillo
K. stuebeliana			
Colombia	Meta	*Fosberg 19468*	Pana silvesto
K. trianae			
Colombia	Antioquia	*Daniel 2327*	Caracola
K. tubiflora			
Colombia	unknown	unknown	Sangremaria
Panama	Canal area	*Paul 161*	Perrito
K. warszewiczii			
Colombia	Antioquia	*Daniel 3917*	Caracola
	Antioquia	*Tomas 612*	Caracola
	Caldas	*Tomas 1919*	Caracola
	Cauca	*Cabrera R. 7869*	Chande, Yute
Cultivated hybrid			
Honduras	Morazán	*Molina R. 14581*	Flor de Peña

A hybrid, possibly between *Kohleria amabilis* and *K. hirsuta*, is cultivated in Ecuador and used by the Cayapa (Chachí) and Colorado (Tsatchela) Amerindian tribes for treating snake bite (Kvist, 1986). Other Gesneriaceae have the same utility (Holm-Nielsen et al., 1983; Kvist, 1989; Kvist and Holm-Nielsen, 1987). In Carchi province of Ecuador *K. inaequalis* (*Boeke 838*) was used to "provoke menstrual flow," probably by the local Coaiquer (Awa) Indians who often rely on the "doctrine of signatures" in their use of plants (Holm-Nielsen and Barfod, 1984). In this case, the red flowers and brown-red pubescence are probably associated with blood.

INTERSPECIFIC HYBRIDIZATION

Until now few interspecific hybrids have been reported from Gesneriaceae in native habitats. Morley (1971) described a *Columnea* hybrid-swarm, Kvist and Skog (in press) mention extensive hybridization between *C. ericae* Mansfeld and *C. guttata* Poeppig, and Wiehler (1983) mentions introgression between *Kohleria spicata* and *K. villosa* in northwestern Ecuador. On the other hand numerous *Kohleria* hybrids have been produced by hand-pollination in cultivation since the middle of the 19th century. All *Kohleria* species may potentially be able to interbreed, and the hybrids normally are partially fertile. The parentage of many early hybrids is unknown, but the following species were in cultivation in the last century and have probably been involved in artificial hybridization: *K. amabilis*, *K. hirsuta*, *K. hondensis*, *K. inaequalis*, *K. rugata*, *K. spicata*, *K. trianae*, *K. tubiflora*, and

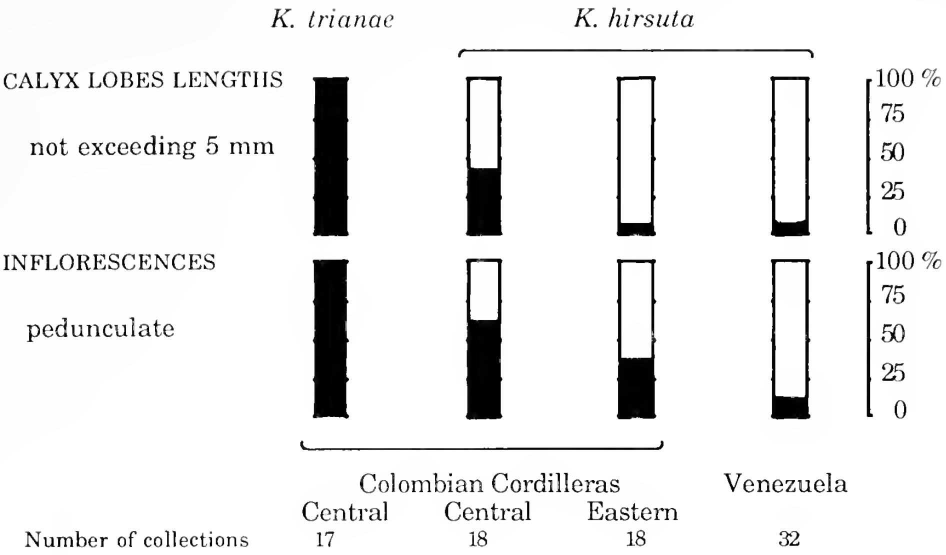


FIGURE 23.—Introgression between *Kohleria hirsuta* and *K. trianae.* The frequencies of pedunculate inflorescences and calyx lobes being shorter than five mm in populations of *K. trianae*–a species restricted to the Central Colombian Cordillera–and in populations of *K. hirsuta* in the Central Colombian Cordillera, in the Eastern Colombian Cordillera, and in Venezuela. Both characters characterize *K. trianae* but are only common in *K. hirsuta* populations sympatric with *K. trianae* indicating introgression.

K. warszewiczii. Some species, e.g., *K. hondensis* and *K. trianae,* died out in cultivation early and were reintroduced into cultivation only during this study. *Kohleria* hybrids still enjoy widespread horticultural popularity. The currently available hybrids and cultivars were discussed by Batcheller (1985).

Interspecific hybridization is a fairly common phenomenon in native populations of *Kohleria.* Three cases are discussed below; the first describes first generation hybrids between two apparently distantly related *Kohleria* species; the second, local hybridization between two widely distributed sympatric species; and the third, hybridization and introgression between two closely related species whose ranges mostly are allopatric separated by a topographic barrier. Hybridization between subspecific taxa (varieties) and between *Kohleria* and related genera are discussed in the sections below, "Intraspecific Hybridization" and "Intergeneric Hybridization."

In northwestern Ecuador, where both the understory species *Kohleria inaequalis* and the exposed-habitat species *K. spicata* are common, a putative hybrid between them, growing in a large clonal population, was studied (*Kvist et al. 48659*). Its indumentum, inflorescences, and flowers (Figure 25b) were intermediate between the parent species (Figures 12e, 25d–f). A specimen from adjacent Colombia is similar (*Soejarto 942*), and both these specimens apparently are first generation hybrids, while another Ecuadorian collection may be a backcross with *K. inaequalis* (*Játiva & Epling 843*).

The two exposed-habitat species, *Kohleria hirsuta* and *K. tubiflora,* are sympatric throughout much of their ranges, but hybridization only has been recorded from Trinidad. Specimens of the putative hybrids (e.g., *Adams 14358, Simmonds 275*) have tubular, ventricose corollas with a reduced limb resembling those of *K. tubiflora* (Figure 12h), although the throat is wider, but the calyx lobes are lanceolate like those of *K. hirsuta* (Figure 24). The hybrid differs from both parents in having red or purple lower leaf surfaces. Hybrid material was introduced into cultivation and considered to be true *K. hirsuta* by Raymond (1968), Stone (1978, with photo), and Bornstein (1986, with photo).

In Colombia, the main ranges of *Kohleria hirsuta* and the related *K. trianae* are separated by the low, hot, and dry Río Magdalena valley (Figure 22). *Kohleria trianae* is endemic to the Central Cordillera between 900 and 2500 meters elevation but is only common between 1700 and 2200 meters (Figure 21). Plants of *Kohleria hirsuta* mainly are found in the Eastern Cordillera, but also occur on the eastern slopes of the Central Cordillera at elevations between 400 and 1200 meters (Figure 21). The latter populations frequently have features that characterize *K. trianae* and almost certainly indicate hybridization and introgression with this species; e.g., pedunculate partial florescences (but their lengths do not exceed the length of the pedicels as in *K. trianae*) and less than five mm long triangular calyx lobes rather than longer, lanceolate ones (Figures 23, 24). *Kohleria hirsuta* may only have been able to colonize the lower slopes of the Central Cordillera where *K. trianae* is rare or absent (Figure 21). At higher elevations extensive hybridization with *K. trianae* may "eliminate" occasional *K. hirsuta* plants. *Kohleria hirsuta* populations in the Eastern Cordillera have a smaller frequency of *K. trianae* attributes than those in the Central Cordillera but a higher frequency than in the more distant populations of Venezuela indicating introgression (Figure 23). *Kohleria trianae* may occasionally wind-disperse across the Río Magdalena valley

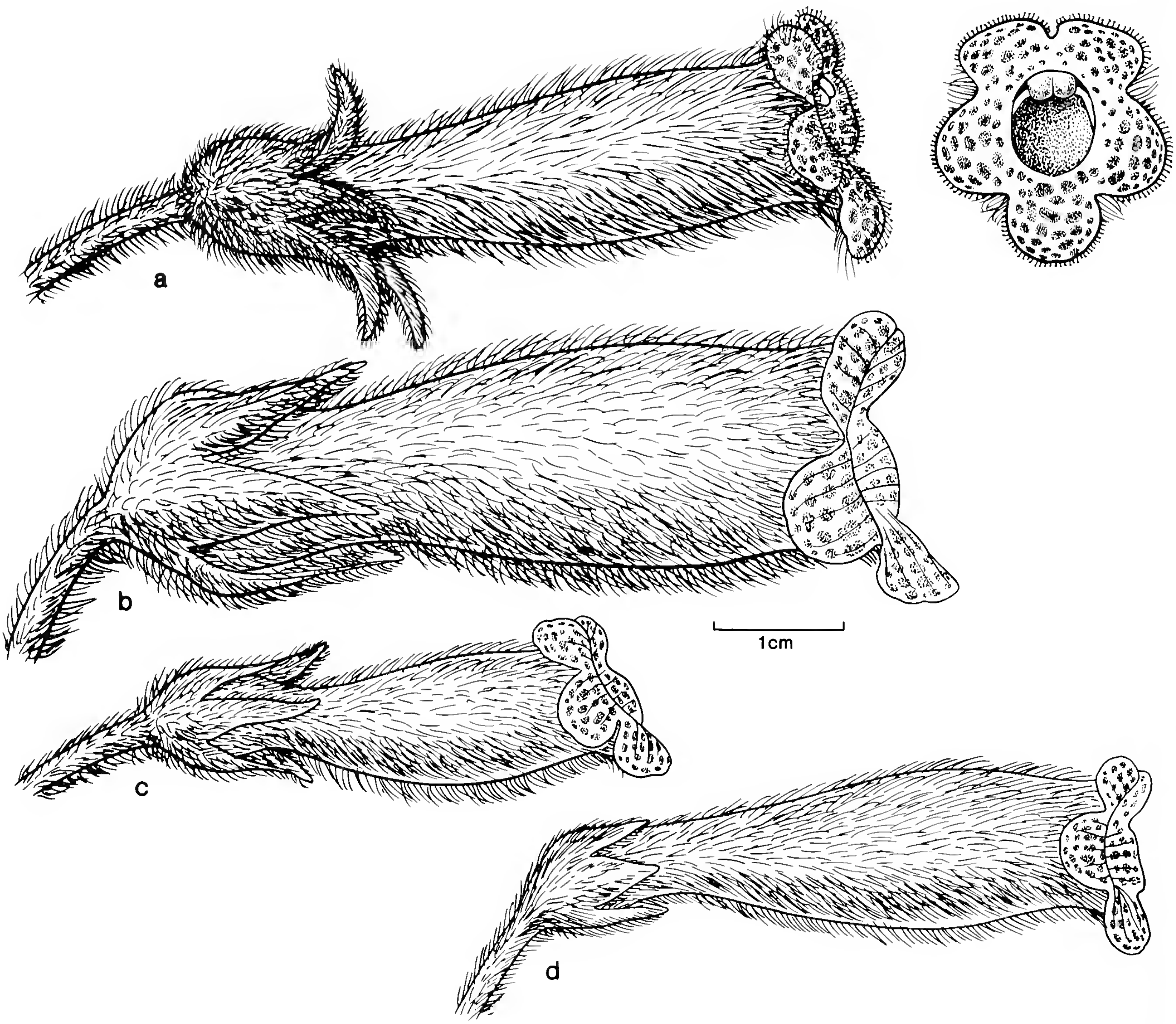


FIGURE 24.—Flowers of *Kohleria hirsuta*: a, var. *hirsuta*, lateral and front views; b, var. *longipes*, lateral view; c, var. *hirsuta*, lateral view; d, var. *hirsuta*, lateral view (example showing introgression with *K. trianae*). a of *Kvist 416* [cultivated material of *Londoño & Kvist 72*] (AAU); b of *Schultes 5692* (US); c of *Kvist 417* [cultivated material of *Londoño & Kvist 81*] (AAU); d of *André 1967* (NY).

and hybridize with *K. hirsuta*. A single old collection of *K. trianae* actually came from the Eastern Cordillera (*Holton 611A*).

INTRASPECIFIC HYBRIDIZATION

Kohleria hirsuta and *K. inaequalis* (Figures 4, 11) are extremely variable when compared with the 15 other species in the genus. Both "species" apparently are complexes of formerly well-delimited semi-species that have hybridized extensively and broken down their limits.

In Colombia and Venezuela *Kohleria hirsuta* is sympatric with 10 and 2 other *Kohleria* species, respectively. The species is only unusually variable in the former country. Introgression from *K. trianae* (see "Interspecific Hybridization" section above) obviously adds to this variation (Figure 23). In addition, two semi-species apparently are fusing in the Eastern Colombian Cordillera. In this region the populations found above 2000 meters elevation usually are distinct by having larger flowers (Figure 24b) and scandent shoots. These plants are

TABLE 3.—Variation in width of calyx lobes at base, and in width of corolla limb in *Kohleria hirsuta* populations at different elevations (m) in Eastern Colombian Cordillera and in Venezuela (Tachira, Aragua, Federal District). Colombian high-elevation populations referred to var. *longipes* have calyx lobes at least 3 mm wide, and corolla limbs at least 12 mm wide.

	Lobe width (mm)				Limb width (mm)						
Locality	-2	2-3	3-4	4-	-8	8-10	10-12	12-14	14-16	16-18	18-20
Colombia											
2000-2700	1	4	18	7	-	2	2	7	6	5	5
1500-2000	6	4	4	1	1	2	2	4	2	1	1
1000-1500	10	2	-	-	2	2	4	4	-	-	-
0-1000	5	5	-	-	2	1	3	-	2	-	-
Venezuela	26	6	-	-	14	17	7	-	-	-	-

herein referred to *K. hirsuta* var. *longipes*, as there is a continuous variation from pure breeding large-flowered var. *longipes* at high elevation to typical smaller-flowered var. *hirsuta* below 1500 meters (Table 3). The variety *longipes* possibly has a common ancestor with the species *K. peruviana* from the Peruvian highlands, making the evolution truly reticulate (in contrast to a single species diverging into two species in isolation followed by hybridization after renewed contact). Both taxa have similar unusually large flowers (Figures 24b, 33c) and leaves. Annular nectaries (Figure 33g) also occur in both taxa (in contrast to the typical variety of *K. hirsuta*). The Colombian populations may have diverged from the putative ancestor, developing a climbing habit in contrast to *K. peruviana*. The rather weedy, smaller-flowered, typical form of *K. hirsuta* later may have become more common in the Río Magdalena valley (possibly promoted by the disturbances of man) and have started to interbreed with the scandent populations from higher elevations—a process that has reduced the former semi-species to its current status as var. *longipes* of *K. hirsuta*.

Kohleria inaequalis shows a variation unmatched in any known New World Gesneriaceae, e.g., in peduncle length, corolla length, limb size, indumentum, etc. (Figures 4, 11, 25). The variation of the former two characters within Ecuador and several departments of Colombia (Figures 26, 27) indicates that *K. inaequalis* is a complex of three extensively hybridizing semi-species. The pure breeding populations are still found at the periphery of the "species" range (Figure 28); viz., the large-flowered, pedunculate var. *inaequalis* (Figures 25f, 27) in Ecuador and adjacent Colombia, the small-flowered, pedunculate var. *ocellata* (Figures 25a, 27) in the Colombian Río Cauca valley northward from Pereira, and the large-flowered, epedunculate var. *lindenii* (Figures 25c, 27) on the western slopes of the Western Cordillera in the Colombian Depts. Chocó and Antioquia. If Dept. Antioquia alone were considered, the isolated populations of *K. inaequalis* probably would be treated as two well-segregated species, since both var. *ocellata* and var. *lindenii* (but no intermediate forms) occur in the department (Figure 27). In Depts. Tolima, Risaralda, Valle, and Cauca (Figure 26), all three varieties blend together (Figure 27), but these plants mostly are referred to var. *inaequalis* (Figure 28). The indumentum, inflorescences, and corolla shapes of these populations mostly are intermediate between var. *inaequalis* and var. *lindenii*, but their flowers are considerably smaller than those of both of these varieties, indicating introgression from var. *ocellata* (Figure 25d,e).

During glacial periods the three semi-species of *Kohleria inaequalis* may have speciated in isolation. The cooler and drier climate in those periods extended the size of the paramos (Simpson, 1975), with the montane forests occuring lower on the slopes. Consequently, from the perspective of montane forest species, the Andean Cordilleras were more formidable barriers, restricting the dispersal compared with the present situation. The relatively low Western Cordillera presumably isolated the small-flowered variety, *ocellata*, in the Cauca valley from the large-flowered varieties, *inaequalis* and *lindenii*, to the southwest and the northwest respectively. Currently the Western Cordillera mostly is covered with montane forest and hardly restricts the dispersal of *K. inaequalis* significantly (Figure 21). The elevation is lowest west of Cali in Dept. Valle (Figures 26, 28). This is precisely the region where all three *K. inaequalis* semi-species interbreed extensively.

The extreme variation in *Kohleria inaequalis* may also in part reflect a faster speciation in isolated populations of understory species compared to wind-dispersed, exposed-habitat populations, possibly due to the fact that the seeds of the former species only are dispersed locally by understory insects. This theory is supported by the fact that, in the tribe Gloxinieae, the species delimitation apparently is more problematic in the presumably animal-dispersed understory genera *Diastema*, *Monopyle*, and *Parakohleria* (pers. obs.) than in the wind-dispersed genera *Achimenes* (Ramírez-Roa, 1987), *Heppiella* (Kvist, 1990), and *Sinningia* (A. Chautems, pers. comm.). The species delimitation has also proven to be difficult in understory genera belonging to other New World Gesneriaceae tribes; e.g., *Cremosperma* (Kvist & Skog, 1988) and *Reldia* (Kvist & Skog, 1989).

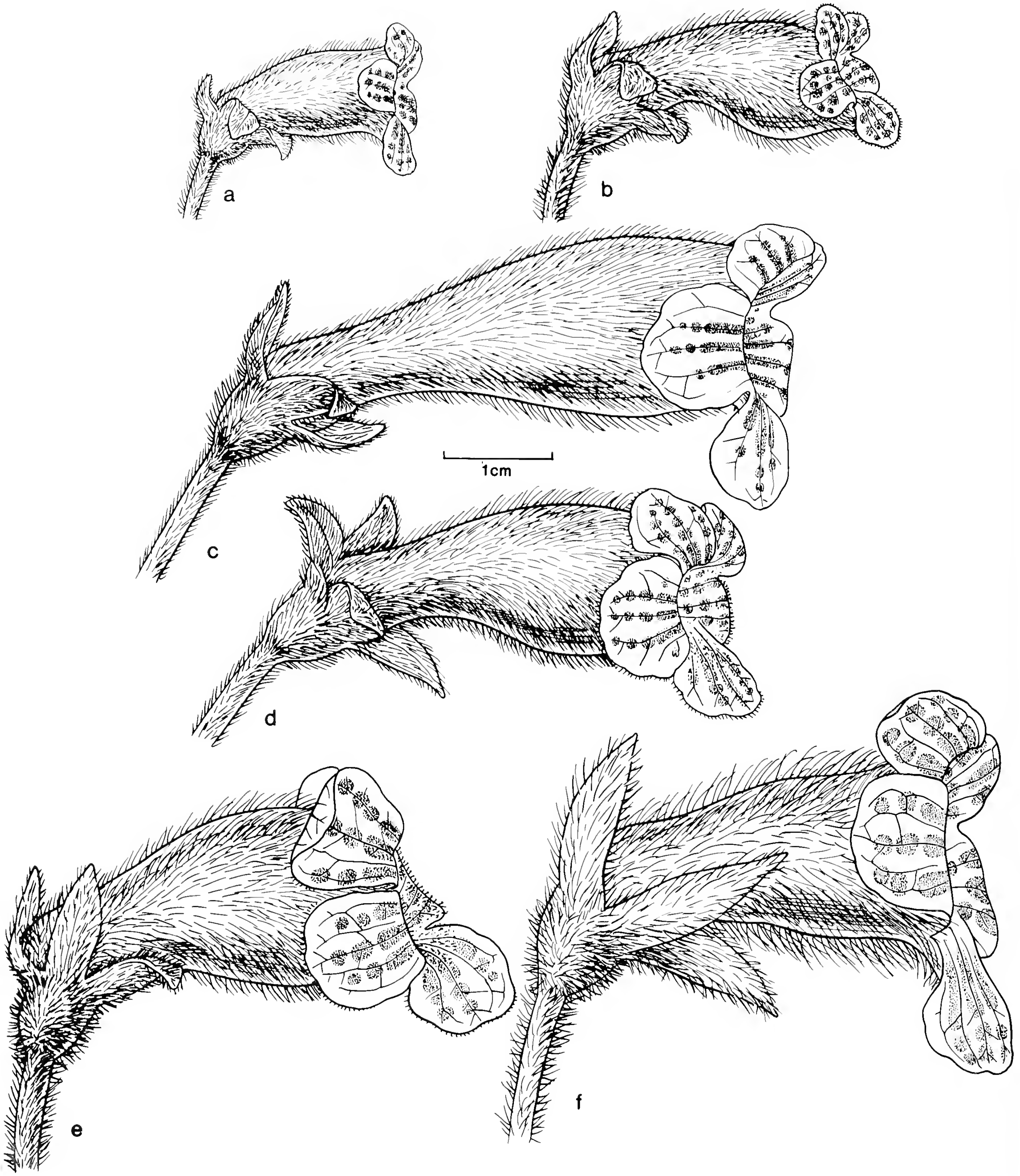


FIGURE 25.—Flowers of *Kohleria inaequalis*: a, var. *ocellata;* b, var. *inaequalis* x *Kohleria spicata;* c, var. *lindenii;* d, var. *lindenii;* e, var. *inaequalis;* f, var. *inaequalis.* a of *Juncosa 1971* (US); b of *Kvist et al. 48659* (AAU) and *Soejarto 942* (GH, SEL); c of *Forero et al. 2138* (US); d of *Londoño & Kvist 68* (AAU); e of *Londoño & Kvist 190* (AAU); f of *Balslev 1939* (AAU) and *Kvist et al. 48619* (AAU).

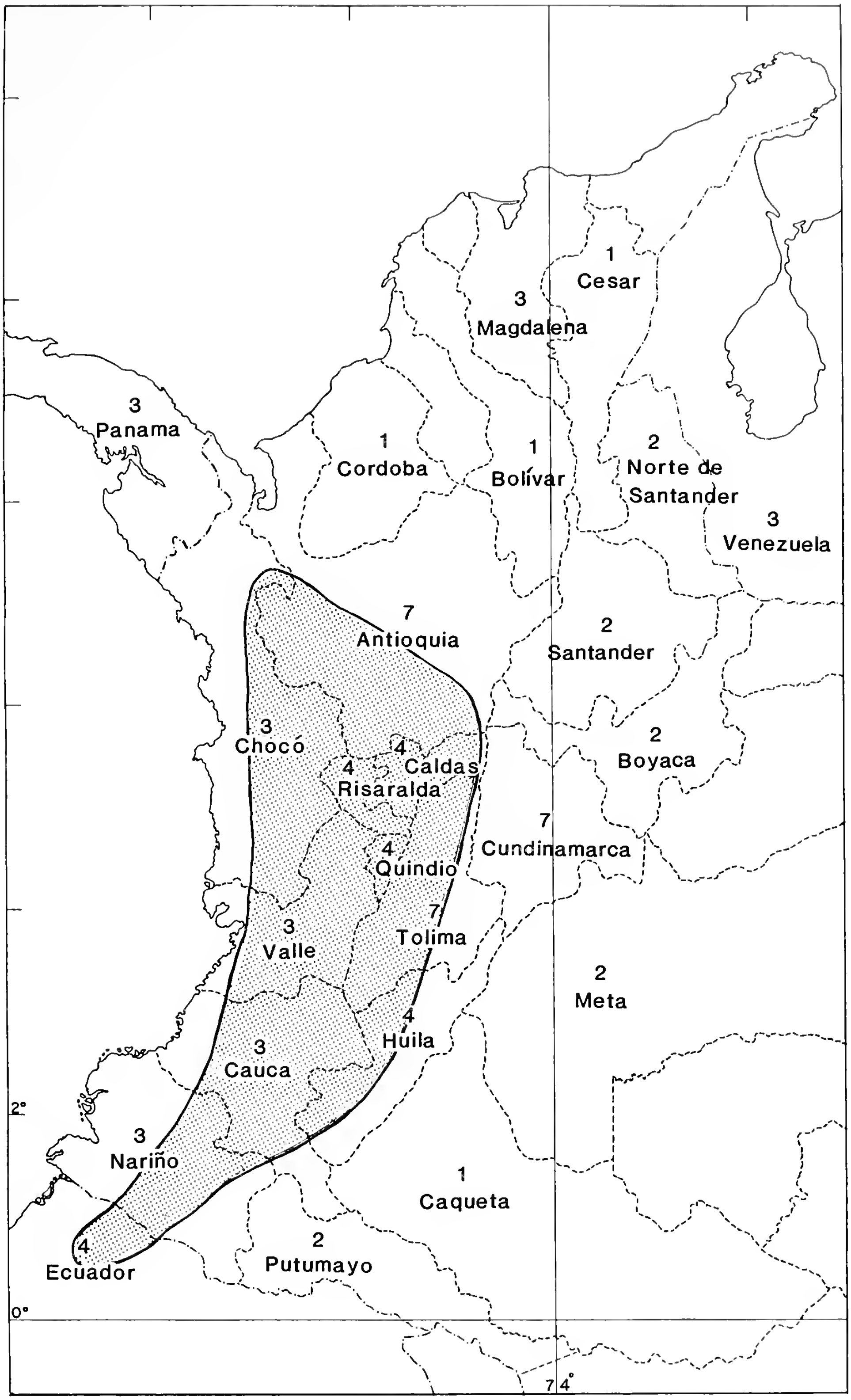


FIGURE 26.—Departments of Colombia in which species of *Kohleria* occur, and the number of species that occur in each department (and in Ecuador, Panama, and Venezuela). The approximate range of *K. inaequalis* is indicated by hatching.

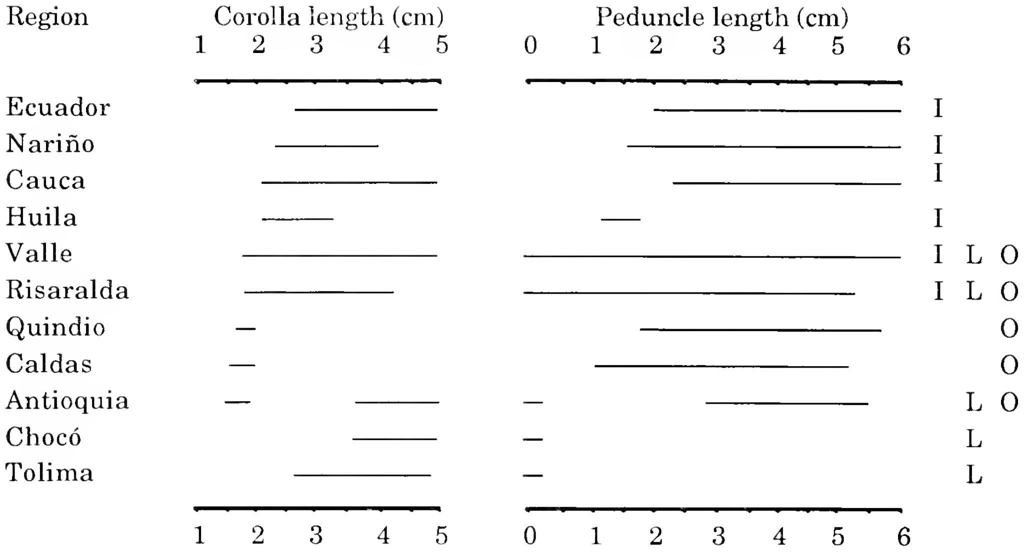


FIGURE 27.—The variation in corolla length and peduncle length (in mm) of *Kohleria inaequalis* in Ecuador and in the Colombian departments where the species occurs (epedunculate populations are illustrated as having very short peduncles). In addition, the varieties that occur in the single areas are indicated (I = var. *inaequalis*, O = var. *ocellata*, and L = var. *lindenii*).

INTERGENERIC HYBRIDIZATION

Intergeneric hybrids have been produced between *Kohleria* and species of *Koellikeria* Regel (Wiehler, 1968), *Parakohleria* (Wiehler, 1976a), *Diastema, Gloxinia,* and *Moussonia* (Wiehler, 1976b). No intergeneric hybrids with *Kohleria* are known from natural habitats. The possibility that *K. diastemoides* (newly described below) is a hybrid between a species of *Diastema* and *Kohleria inaequalis* has been considered. The fact that the only known *K. diastemoides* collection shows a combination of features characterizing these two taxa rather than intermediate features (Table 4), and that the seed production of *K. diastemoides* apparently is abundant, argues against the plant being an intergeneric hybrid. Intergeneric hybrids usually are entirely sterile. However, Wiehler (1976b) reported that hybrids between *K. spicata* and both *Diastema vexans* H.E. Moore and *Koellikeria erinoides* (DC.) Mansfeld were weakly fertile, which may indicate a close affinity with these genera. *Diastema* is related to *Kohleria* (see "Related Genera" section below) but the affinities of *Koellikeria* are uncertain. The habit, inflorescences, and flowers of *Koellikeria* do not suggest an affinity with *Kohleria.* The unusual inflorescences with alternate subtending prophylls are similar to those found in the small Mexican genus *Smithiantha* O. Kuntze, but the two genera differ in other respects. *Koellikeria* is monotypic and occurs in montane forests from Mexico to Argentina.

RELATED GENERA

The following genera are discussed: *Moussonia* and *Parakohleria,* both recently split off from *Kohleria; Diastema* and *Capanea,* genera that possibly have evolved from ancestors that might fit into the current concept of *Kohleria*; and *Heppiella* and *Vanhouttea* as collections of these genera often look very similar to *Kohleria. Achimenes, Eucodonia,* and *Gloxinia* are discussed in the section on "Evolution" below because these genera may be close to the ancestors of *Kohleria.*

The Central American genus *Moussonia* was until recently placed in *Kohleria* due to its similar tubular flowers and inflorescences. *Moussonia* (Wiehler, 1975) differs from *Kohleria* by having the basic chromosome number of 11 (rather than 13), a capitate stigma, and an annular nectary. Wiehler (1978b) split off the genus *Parakohleria* from *Kohleria* based on the following characters: capitate stigmas, absence of scaly rhizomes, basally bent corolla tubes, and congested inflorescences. Only the first of these characters separates the two genera consistently, but the two genera also are set apart by their very different capsule dehiscence. *Parakohleria* capsules differ from both the bivalved and the unilaterally dehiscing capsules of *Kohleria* (Figure 13c-e) by splitting from the apex to base into two fleshy valves that reflex completely to expose the glutinous seed mass (Figure 13a). *Parakohleria* (Kvist, 1991) is an understory genus, ranging along the eastern Andean slopes from Colombia to Bolivia (and locally on the western slopes in Ecuador).

Diastema, an understory genus of small herbs ranging from Mexico to Bolivia, shares many attributes with *Kohleria,* especially with the understory species *K. villosa* (Figures 36, 37). This species shares the following features with *Diastema*: long narrow nectary glands, capsules that dehisce by a slit down to the base, and sub-globose seeds with an irregular surface. However, *Diastema* is consistently set apart from

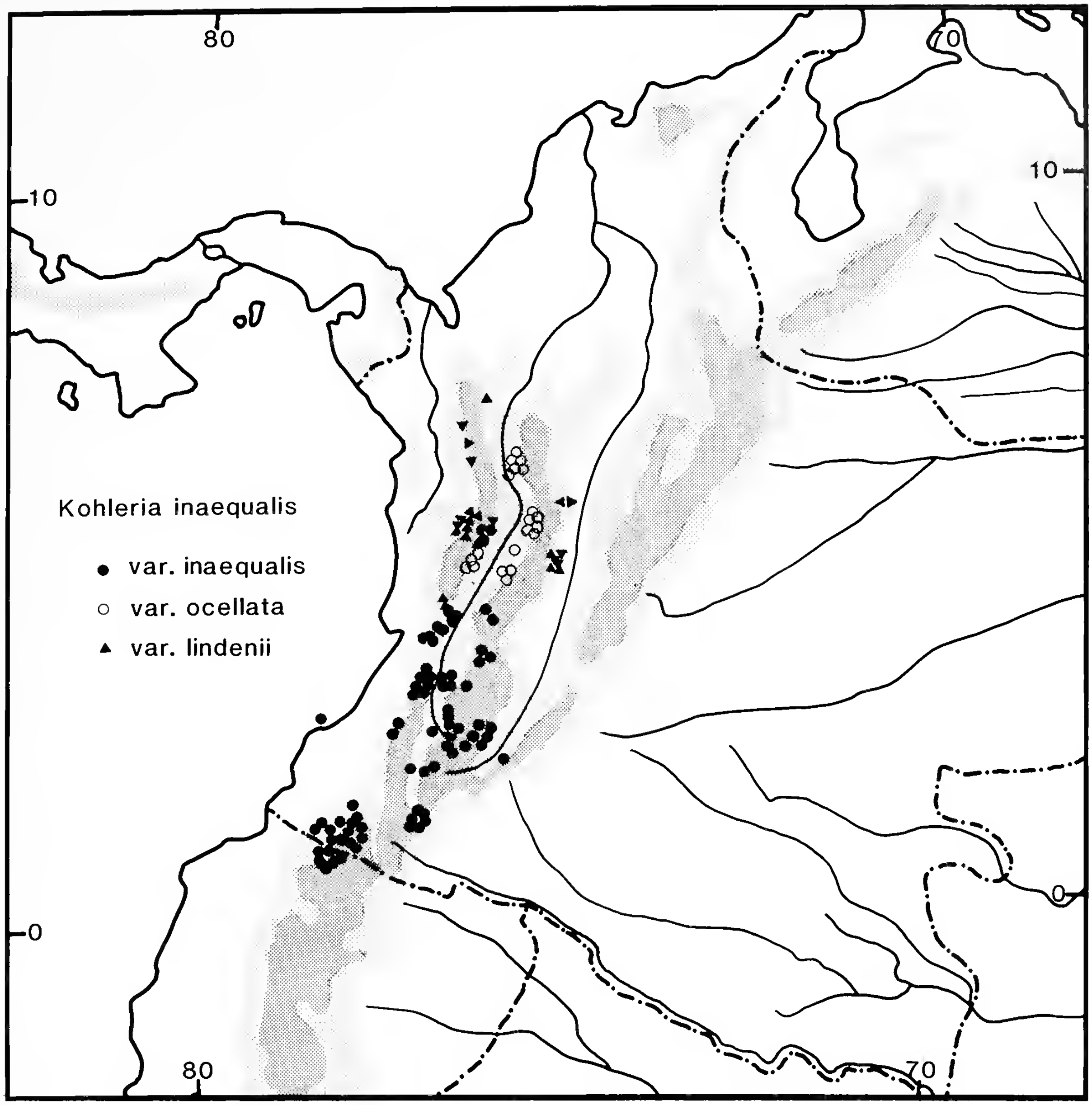


FIGURE 28.—Distributions of the varieties of *Kohleria inaequalis*: var. *inaequalis*, var. *ocellata*, and var. *lindenii*. The Pacific coast collection is from Gorgona Island in the Dept. Cauca of Colombia (*Guzano & Rangel 5280*).

Kohleria by having bracteose inflorescences (Figure 3g), and by mostly having small white or yellowish flowers often with blue or purple spots or lines on the limb. In addition, *Diastema* has scaly rhizomes (in contrast to the most similar *Kohleria* species), and the stigma is not conspicuously bilobed. *Diastema* possibly is a satellite genus derived from *Kohleria*, but additional studies are needed. The two *Capanea* species mostly are epiphytic climbers with capitate stigmas, exserted stamens, and capsules that split with four apical valves. The tubular to campanulate corollas, as well as the pedunculate axillary inflorescences and the rotundate calyx lobes of *Capanea affinis* Fritsch and *Kohleria warszewiczii*, are

TABLE 4.—Comparison of *Kohleria diastemoides* with *Kohleria inaequalis* and the genus *Diastema*. In size and habit *Kohleria diastemoides* resembles *Diastema* rather than *Kohleria inaequalis*.

Character	*K. diastemoides*	*K. inaequalis*	*Diastema*
Inflorescence	frondose	frondose	bracteose
Inflorescence	pedunculate	pedunculate	epedunculate
Corolla shape	narrowly tubular	broadly tubular	narrowly tubular
Corolla color	red or purple	red to purple	white
Corolla inside	villous	villous	glabrous
Filament base	villous	villous	glabrous
Capsule	oblong	oblong	ovoid/oblong
Nectary glands	narrow and high	broad and short	narrow and high
Stigma	bilobed	bilobed	bilabiate

strikingly similar. *Capanea grandiflora* (Kunth) Decaisne ex Planchon, has campanulate corollas similar to those of *Kohleria allenii*, but the latter species has different frondose-bracteose inflorescences. The similarity between *Capanea* and *Kohleria* probably reflects a parallel adaptation to pollinators, e.g., bats, but the possibility that *Capanea* has descended from *Kohleria* still exists.

The four species of *Heppiella* from the Andean highlands and the approximately five species of *Vanhouttea* from Brazil all have tubular red flowers making them superficially similar to *Kohleria*. *Heppiella* differs from *Kohleria* by having free anthers, capitate stigmas, annular nectaries, and the plants are often climbing or even epiphytic. *Heppiella* has scaly rhizomes and is probably a close relative of *Kohleria* (Kvist, 1990). The resemblance of *Vanhouttea* and *Kohleria* is likely caused by parallel evolution, as *Vanhouttea* occasionally develops tubers, suggesting a close affinity with *Sinningia* (A. Chautems, pers. comm.). *Vanhouttea* also differs from *Kohleria* by having annular nectaries, capitate stigmas, and by being woody shrubs.

EVOLUTION

Originally it was the intention to present a cladistic analysis of *Kohleria*. This has been abandoned for two reasons: (1) The relationships among the 24 genera currently included in the tribe Gloxinieae are little understood, making the selection of an outgroup unreliable; and (2) Populations of *Kohleria* speciate in isolation and hybridize after renewed contacts making the evolution reticulate. The following aspects are discussed below: the hypothetical ancestor of *Kohleria*, as well as the diverging of the understory species from exposed-habitat ancestors and the reticulate evolution of *Kohleria*.

The species with fewest advanced features among the current *Kohleria* species may be the wind-dispersed *K. rugata* from Mexico. The only conspicuous feature that separates *K. rugata* populations with annular nectaries from all species in the genus *Gloxinia* (from South America) and most species of *Achimenes* and *Eucodonia* (from Mexico and Central America) is the presence of bilobed rather than capitate stigmas (the latter two genera differ from *Kohleria* and *Gloxinia* by having 11 and 12 rather than 13 basic chromosomes). *Achimenes*, *Eucodonia*, and *Gloxinia* (except some advanced species that may fit better into *Monopyle*) possibly are the most primitive members of the Gloxinieae, being seasonal herbs with scaly rhizomes, bivalved capsules, annular nectaries, usually capitate stigmas, epedunculate partial florescences with 1 or 2 flowers, and frondose florescences. Consequently, wind-dispersal and occurrence in exposed habitats are primitive states in Gloxinieae. The understory groups, e.g., *Parakohleria*, *Diastema*, *Monopyle*, and some *Kohleria* species have individually advanced from exposed-habitat to understory habitats. During this process the scaly rhizomes have been reduced and the plants have apparently switched to animal-dispersal, evolving different types of capsule dehiscence in the different genera (Figure 13). *Kohleria amabilis* apparently has some features intermediate between exposed-habitat and understory *Kohleria* species, e.g., the capsules (Figure 13b–d) and the seeds (Figure 5a–c). In addition, the species is at least superficially similar to both the exposed-habitat species *K. rugata* and the understory species *K. villosa*.

The main mode of speciation in *Kohleria* seems to be geographical isolation; this is evident in the diverging of *K. hondensis* from *K. tubiflora*, and *K. stuebeliana* from *K. spicata*. None of the 17 species apparently has evolved by interspecific hybridization. This is surprising as hybridization seems to be a common phenomenon in *Kohleria*, and hybrids usually are fertile. One explanation may be that hybrids never become stabilized by chromosome doubling, as tetraploids are unknown in *Kohleria*. On the contrary, the effect of hybridization has been seen to weaken or even break down the species limits. The two most variable species, *K. hirsuta* and *K. inaequalis*, apparently consist of extensively interbreeding semi-species herein taxonomically treated as varieties. The variety *longipes* of *K. hirsuta* may share a common ancestor with a third semi-species, *K. peruviana*, making the evolution truly reticulate. *Kohleria* has evolved in the dynamic environment of northwestern South America. The climate changed, becoming cooler and drier during glacial periods, and volcanic eruptions and earthquakes occasionally have caused massive destruction of the vegetation cover. Populations of *Kohleria* must recurrently have been isolated during extended periods succeeded by new contacts. The current cases of speciation in isolation and hybridization after renewed contacts may be the most recent examples of an evolutionary pattern that has characterized the evolution of *Kohleria*, possibly during millions of years in the rising Andean highlands.

Kohleria Regel

Kohleria Regel, 1847:(4). [Type: *K. hirsuta* (Kunth) Regel (*Gesneria hirsuta* Kunth).]

Gesneria sect. *Isoloma* Bentham, 1846:230. [Lectotype: *Kohleria hirsuta* (Kunth) Regel (selected by C. Morton, 1973:317) = *K. hirsuta* (Kunth) Regel var. *hirsuta*.]

Isoloma (Bentham) Decaisne, 1848a:465 [not *Isoloma* J. Smith, 1841:414]. [Lectotype: *Kohleria hirsuta* (Kunth) Regel (selected by C. Morton, 1973:317) = *K. hirsuta* (Kunth) Regel var. *hirsuta*.]

Tydaea Decaisne, 1848b:468. [Type: *T. picta* (Bentham ex J.D. Hooker) Decaisne = *Kohleria amabilis* (Planchon & Linden) Fritsch var. *bogotensis* (Nicholson) Kvist & L. Skog.]

Giesleria Regel, 1849:181. [Type: *Achimenes picta* Bentham ex J.D. Hooker = *Kohleria amabilis* (Planchon & Linden) Fritsch var. *bogotensis* (Nicholson) Kvist & L. Skog.]

Kohleria Regel, 1851:893 [not *Kohleria* Regel, 1847:(4)]. [Type: *K. ignorata* (Kunth) Regel = *Kohleria spicata* (Kunth) Oersted.]

Sciadocalyx Regel, 1853a:257. [Type: *S. warszewiczii* Regel = *Kohleria warszewiczii* (Regel) Hanstein.]

Brachyloma Hanstein, 1854:303. [Type: *B. hirsutum* (Kunth) Hanstein = *Kohleria hirsuta* (Kunth) Regel var. *hirsuta*.]

Cryptoloma Hanstein, 1859:506, 578. [Lectotype: *C. hondense* (Kunth) Hanstein (selected herein) = *Kohleria hondensis* (Kunth) Hanstein.]

Calycostemma Hanstein, 1859:506, 556. [Type: *C. lindenii* Hanstein = *Kohleria inaequalis* (Bentham) Wiehler var. *lindenii* (Hanstein) Kvist & L. Skog.]

Synepileana Baillon, 1888a:725. [Type: *S. granatensis* Baillon = *Kohleria inaequalis* (Bentham) Wiehler var. *lindenii* (Hanstein) Kvist & L. Skog.]

Herbs, subshrubs, or shrubs, terrestrial or epilithic, most parts usually with conspicuous indumentum, scaly rhizomes and stolons often present, adventitious roots occasionally present; stems decumbent to erect, rarely pendant or scandent, terete (usually bisulcate or subquadrangular in dried material), (5-) 20-150 (-400) cm long, green to yellow or purplish, indumentum usually pilose to villous or sericeous towards the apex, basally often glabrescent, shoots annual and unbranched, less commonly biennial or perennial and branched. Leaves opposite, less commonly whorled (3 or 4 at each node), equal to subequal or rarely unequal in pairs or whorls, petiolate; blades usually ovate, elliptic or lanceolate, less commonly cordate or oblanceolate, base oblique, often acute or rounded, apex acute to acuminate, margin crenate to serrate, often hispid or pilose-hirsute above, green to dull green, often pilose or tomentose below, lighter green to purple or variegated, secondary veins (5-) 7-9 (-11) per side, above obscure, below emersed, villous or sericeous, often yellow-green. Florescences frondose or frondose-bracteose, partial florescences with 1 to 6 (-10) flowers, congested in leaf axils or less commonly pedunculate; peduncles and pedicels sericeous, villous or hispid, often purplish, bracts (0-) 2-3 (-6), sessile, lanceolate or scaly, often caducous. Flowers protandrous; floral tube often villous, green, yellow-green or purple; calyx lobes equal to occasionally somewhat unequal, usually erect, occasionally reflexed, often connate ~1/3 of length, or less commonly free nearly to base, the 5 lobes with margin entire, often sericeous outside and appressed pilose inside, with 3-5 sometimes prominent, longitudinal veins; corolla usually oblique in calyx, zygomorphic, occasionally subactinomorphic, tubular to campanulate, often subventricose, 1.2-6.0 cm long, tube outside villous to sericeous, red, often ventrally yellow, rarely yellowish red, inside glabrous or sparsely glandular-hairy, less commonly basally pilose to villous, lighter red, cream, or yellow, often with purple or red dots, base occasionally saccate, often dorsally gibbous, never spurred, outside cream to yellow, glabrous, throat often constricted, inside sparsely glandular-hairy, limb subregular to bilabiate, of 5 ovate to rotundate lobes, outside usually red, rarely orange, yellow, or yellowish green, villous or sericeous to glabrous along the margin, inside usually with red or purple dots and/or lines on a paler red, orange, or yellowish green background, rarely entirely red; stamens 4, didynamous, filaments never connate but adnate to the base of the corolla tube for 0.3-0.8 mm, usually glabrous, occasionally pilose to villous, yellowish, anthers included or subincluded, oblong, coherent at apices and sides, glabrous, cream or yellowish, thecae distinct, dehiscing by longitudinal slits, the filaments coiling in the later female flowering stage to pull the anthers deeper into the flower; one dorsal staminode present, 1-2 mm long; nectary fleshy, yellow and glabrous, usually of 5 free glands, less commonly with 3 free and 2 dorsal basally united glands or a 5-lobed ring; ovary half-inferior to almost completely inferior, sericeous to villous, style usually pilose and often glandular-hairy, rarely glabrous, cream or yellow-white, stigma included or subincluded, bilobed. Fruit a capsule, ovoid or less commonly oblong, apex conic or rostrate, dehiscing apically and loculicidally into 2 valves (by 2 apical slits), less commonly by 1 slit from apex to base (splitting the ovary and the floral tube) or by 2 apical slits with 1 of these continuing to the base; seeds numerous, 0.3-0.6 mm long, often narrowly ellipsoid to ellipsoid, less commonly subglobose, surface longitudinally to transversely reticulate striate, less commonly irregularly striate, tawny to brown.

Key to the Species and Varieties of *Kohleria* Regel

Fertile material is essential for identification, and fully developed flowers are often important. Any key is of little use for cultivated material, even within the native range of *Kohleria*, as cultivars are mainly hybrids of partly or completely unknown parentage. Putative natural hybrids usually have either *Kohleria hirsuta* or *K. inaequalis* in their ancestry, and tend to sort out with those species in the following key. Within the key the terms "partial florescences" and "florescences" are used for the closed inflorescences in the axils of subtending leaves and bracts, and for the open flowering shoots with several to many partial florescences, respectively (see Figure 3 for illustration of inflorescence terminology).

1. Corolla campanulate, outside yellow with a flush of red trichomes, 25-32 mm long, diameter at throat 15-20 mm; styles glabrous; subtending leaves of florescences (flowering shoots) gradually reduced to bracts toward the apex, partial florescences epedunculate, with 1 or 2 flowers; leaves 3 at a node, glandular-hairy (plants of Costa Rica and Panama) . . . . 1. *K. allenii*

Corolla tubular or tubular to campanulate, outside usually red, 12–60 mm long, diameter at throat 2–21 mm; styles pubescent; subtending leaves of florescences (flowering shoots) mostly not reduced to bracts toward the apex and only in combination with 12–20 mm long corollas, partial florescences epedunculate or pedunculate, with 1–10 flowers; leaves opposite or less commonly 3 at a node, rarely glandular-hairy (plants of Mexico, Central America, and South America) 2

2. Subtending leaves of florescences (flowering shoots) gradually reduced to bracts toward the apex, partial florescences epedunculate; corolla 12–20 mm long, diameter of limb 5–10 mm; calyx lobes triangular to ovate, 1.5–3.5 mm long 3

Subtending leaves of florescences (flowering shoots) not reduced to bracts toward the apex, partial florescences epedunculate or pedunculate; corolla 14–60 mm long, diameter of limb 3–35 mm; calyx lobes triangular, ovate, rotundate, lanceolate, or subulate, 2–40 mm long 4

3. Limb orange-red with red to purple dots/lines, nearly glabrous; upper leaf surface usually hispid, leaf arrangement frequently 3 at a node; widespread and common . . . . 12. ***K. spicata***

Limb yellow-green with brown to black dots, appressed pilose and glandular-hairy; upper leaf surface velutinous, leaf arrangement rarely 3 at a node (plants of Colombia) . . . . 13. ***K. stuebeliana***

4. Corolla 16–30 mm long, diameter in throat 1.5–4 mm, diameter of limb 3–7 mm, length of lobes 1–1.5 mm; calyx lobes triangular, ovate or lanceolate, 2–8 mm long; partial florescences epedunculate; upper leaf surface usually hispid to extremely hispid 5

Corolla 14–60 mm long, diameter in throat 3–21 mm, diam. of limb 5–35 mm, length of lobes 2–12 mm; calyx lobes triangular, ovate, rotundate, lanceolate or subulate, 2–40 mm long; partial florescences epedunculate or pedunculate; upper leaf surface hispid or velutinous 6

5. Calyx lobes ovate to lanceolate, 5–8 mm long; corolla 16–20 mm long; upper leaf surface extremely hispid (plants of Colombia) . . . . 6. ***K. hondensis***

Calyx lobes triangular to ovate, 2–4 mm long; corolla 20–30 mm long; upper leaf surface usually hispid; widespread and common . . . . 15. ***K. tubiflora***

6. Limb red with white edge (diameter at throat 3–5 mm) or yellow-green with purple dots (diameter at throat 7–13 mm); corolla narrowly tubular or tubular to campanulate, 25–42 mm long; partial florescences with peduncles 2–3 times as long as pedicels; calyx lobes triangular or rotundate, 2–6 mm long; upper leaf surface velutinous 7

Limb yellow to red with darker red or purple dots/lines, occasionally uniformly red, diameter at throat 3–21 mm; corolla narrow to broadly tubular, 15–60 mm long; partial florescences epedunculate or pedunculate; calyx lobes rotundate, ovate, lanceolate or subulate, 3–40 mm long; upper leaf surface velutinous or hispid 8

7. Limb red with white edge; corolla narrowly tubular, tube red outside; partial florescences with 4 flowers . . . . 14. ***K. trianae***

Limb yellow-green with purple dots; corolla tubular to campanulate, tube lavender outside; partial florescences with 3–10 flowers . . . . 17. ***K. warszewiczii***

8. Partial florescences always of single flowers, epedunculate; calyx lobes ovate, 3–8 mm long; corolla 18–32 mm long, limb yellow with red dots; leaf pairs equal, upper surface velutinous, lower surface uniformly colored (plants of Mexico; only sympatric with *K. spicata*) . . . . 11. ***K. rugata***, new combination

Partial florescences with 1 to several flowers, epedunculate or pedunculate; calyx lobes ovate, rotundate, lanceolate or subulate, 3–40 mm long; corolla 14–60 mm long, limb yellow to red with darker red or purple dots/lines; leaf pairs equal or rarely unequal, upper surface velutinous or hispid, lower surface uniformly colored or with a pattern of purple and green (plants of South America) 9

9. Calyx lobes subulate, 8–11 mm long; corolla 14–18 mm long, 3–4 mm wide at throat; partial florescences epedunculate, of 5–6 (–10) flowers; leaf arrangement 3 at a node, upper surface hispid (plants of Colombia) . . . . 9. *K. neglecta,* new species

Calyx lobes ovate, rotundate or lanceolate, 3–40 mm long; corolla 15–60 mm long, 3–21 mm wide at throat; partial florescences epedunculate or pedunculate, of 1–4 (–10) flowers; leaf arrangement rarely 3 at a node, upper surfaces hispid or velutinous (plants of South America) 10

10. Corolla 15–20 mm long, limb uniformly red or red with purple lines; nectary glands often 2–4 times taller than broad at base; calyx lobes 3–5 mm long 11

Corolla 20–60 mm long, limb yellow to red with darker red or purple dots/lines; nectary glands less than 2 times taller than broad at base; calyx lobes 3–40 mm long 14

11. Partial florescences usually pedunculate; leaves equal or subequal in pairs, upper leaf surface often hispid, lower surface uniformly colored; inside base of corolla and base of filaments villous 12

Partial florescences epedunculate; leaves equal, subequal or unequal in pairs, upper leaf surface never hispid, lower surface often with a pattern of purple and light green; inside base of corolla and filaments glabrous (but corolla toward the throat and apical part of filaments usually villous) 13

12. Partial florescences with 1 or 2 flowers; corolla narrowly tubular, 3–4 mm wide at throat; nectary glands 2–4 times taller than broad at base; upper leaf surface velutinous . . . . 3. *K. diastemoides,* new species

Partial florescences usually with 4 flowers; corolla broadly tubular, 5–9 mm wide at throat; nectary glands equally tall and broad at base; upper leaf surface hispid . . . . 7c. *K. inaequalis* var. *ocellata*

13. Leaves ovate with acute apex, equal or subequal in pairs; corolla tube not with long villous trichomes outside, limb 12–19 mm wide . . . . 16a. *K. villosa* var. *villosa*

Leaves ovate to lanceolate with acute to acuminate apex, most leaf pairs conspicuously unequal in pairs; corolla tube with villous trichomes outside, limb 9–13 mm wide . . . . 16b. *K. villosa* var. *anisophylla,* new status

14. Calyx lobes ovate, 3–5 mm long; corolla 24–32 mm long; upper leaf surface velutinous; partial florescences epedunculate (plants of Colombia) 15

Calyx lobes usually lanceolate, rarely ovate, occasionally rotundate to spathulate (but then in combination with 45–60 mm long corollas), 3–40 mm long; corolla 20–60 mm long; upper leaf surface hispid or velutinous; partial florescences epedunculate or pedunculate (plants of South America) 16

15. Diameter of limb 20–27 mm, ventral lobe up to 10 mm long, all lobes inside with a pattern of red dots on a paler pink background; lower leaf surface with a conspicuous pattern of light green blotches on a purple background . . . . 2a. *K. amabilis* var. *amabilis*

Diameter of limb 13–18 mm, ventral lobe up to 6 mm long, lateral and ventral lobes with red or purple lines on a yellow background and dorsal lobes red; lower leaf surface without a conspicuous purple and green pattern . . . . 2b. *K. amabilis* var. *bogotensis,* new status

16\. Calyx lobes rotundate to spathulate; corolla 45-60 mm long, tube 38-46 mm long, inside glabrous, limb red with purple lines; partial florescences with 1 flower . . . . 4. ***K. grandiflora,*** new species

Calyx lobes lanceolate, rarely ovate; corolla 20-60 mm long, tube 18-50 mm long, inside glabrous or especially basally pilose to villous, limb orange-red with purple dots or red with purple lines; partial florescences with 1-10 flowers 17

17\. Calyx lobes 2-25 mm long, usually reaching half of corolla length; corolla 45-60 mm long, tube 40-50 mm long, inside glabrous; upper leaf surface velutinous; partial florescences pedunculate . . . . 8. ***K. longicalyx,*** new species

Calyx lobes 3-25 mm long, rarely reaching half of the corolla length; corolla 20-52 mm long, tube 18-45 mm long, inside glabrous or especially basally pilose to villous; partial florescences pedunculate or epedunculate; upper leaf surface velutinous or hispid 18

18\. Limb red with purple lines, 9-32 mm wide; mature capsules 2-3 times as long as wide; corolla basally villous to pilose inside; upper leaf surface usually hispid 19

Limb orange-red with purple dots, 6-22 mm wide; corolla glabrous inside; mature capsules 1-2 times as long as wide; upper leaf surface soft-velutinous 20

19\. Partial florescences of several flowers, usually pedunculate; corolla 22-52 mm long, tubular to broadly tubular, not subventricose; upper leaf surface usually hispid . . . . 7a. ***K. inaequalis*** var. ***inaequalis***

Partial florescences of single epedunculate flowers; Corolla (25-) 35-52 mm long, narrowly tubular to tubular, often subventricose; upper leaf surface occasionally hispid . . . . 7b. ***K. inaequalis*** var. ***lindenii,*** new status

20\. Base of corolla saccate and sharply delimited, corolla 35-52 mm long; stems and lower leaf surfaces densely villous, whitish; length of leaves usually 8-18 cm (plants of Peru) . . . . 10. ***K. peruviana***

Base of corolla not saccate, corolla 22-52 mm long; stems and lower leaf surfaces pilose, greenish or purplish; length of leaves usually 4-12 cm (plants of northern South America) 21

21\. Width of calyx lobes at base 1-2 mm; length of corolla 20-50 mm, diameter 3-8 mm at throat, limb 6-12 mm wide; rarely above 2000 meters . . . . 5a. ***K. hirsuta*** var. ***hirsuta***

Width of calyx lobes at base 2-6 mm; length of corolla 32-50 mm, diameter 8-15 mm at throat, limb 12-22 mm wide; rarely below 1800 meters . . . . 5b. ***K. hirsuta*** var. ***longipes,*** new status

1. *Kohleria allenii* Standley & L.O. Williams

Figures 7a,b (pollen), 13c (capsule dehiscence), 29 (habit and floral features); L.O. Williams, 1968:293 (photo).

Kohleria allenii Standley & L.O. Williams in L.O. Williams, 1968:291. [Type: Costa Rica, Puntarenas, near Palmar Sur, rocky railroad cuts, *Allen 6300* (F, holotype; EAP, GH, US, isotypes).]

Herbs or subshrubs, often epilithic, scaly rhizomes weakly developed or absent, stolons not seen; stems erect, rarely branching, glandular-hairy, purplish, 50-150 cm long, basal diameter 5-8 mm. Leaves ternate or whorled (4 at each node), internodes 4-11 cm; the blades ovate to elliptic, less commonly lanceolate to oblanceolate, 6-15 × 3-7 cm, above pilose and usually hispid, often glandular-hairy, below pilose and usually glandular-hairy, veins below villous, yellow-green or purplish; petioles 1-5 cm. Florescences frondose-bracteose, partial florescences with 1 or 2 flowers, the subtending leaves toward the apex reduced to subsessile, ovate to obovate prophylls; pedicels 2-5 cm long, villous and glandular-hairy, bracts scaly, caducous. Floral tube villous and glandular-hairy; calyx 6-8 mm long, glandular-hairy, lobes erect, occasionally reflexed, ovate to triangular, 4-5 mm long and 3-4 mm wide at base, outside pilose to villous, inside sericeous, veins prominent; corolla 25-32 mm long, campanulate, tube 20-25 mm long, diameter 6-8 mm at base and 15-20 mm at throat, outside sericeous and glandular-hairy, yellow with a flush of red trichomes, inside glabrous, yellow with red blotches, the base dorsally gibbous, limb 22-30 mm wide, lobes 7-9 mm long and 7-9 mm wide at base, inside sparsely glandular-hairy, ventral and lateral lobes green with purplish dots and lines, dorsal lobes yellow-red; filaments 18-22 mm, glabrous, anthers ~3.2 × 3.0 mm, included; nectary a 5-lobed ring, up to 1 mm tall; ovary half-inferior, 5-6 mm tall, diameter 4-5 mm, style 15-20 mm long, glabrous, stigma subincluded. Capsule

FIGURE 29.—*Kohleria allenii*: a, stem and leaves; b, sturdy root with small scaly rhizome; c, frondose-bracteose florescence; d, flower; e, ventrally opened corolla showing parts of androecium; f, calyx and gynoecium; g, capsule. a,b,g, from *Davidse & Pohl 1401* (MO); c, from *Allen 5339* (MO); d,e,f, from *Allen 6300* (MO).

ovoid, 10–12 mm long, diameter 6–7 mm, bivalved; seeds ellipsoid, longitudinally striate, ~0.40 × 0.15 mm. Chromosome number $n = 13$ (Wiehler, 1975).

DISTRIBUTION.—*Kohleria allenii* is endemic to the Prov. Puntarenas in southwestern Costa Rica, and the Prov. Chiriquí of adjacent Panama (Figure 18). The species ranges from sea level up to 1000 meters altitude.

OTHER COLLECTIONS.—COSTA RICA: PUNTARENAS: Golfito de Golfo Dulce, *Allen 5339* (BM, COL, F(2), G, GH, MO(2), NY(2), US(2)); Palmar Sur, *Allen 6300* (EAP, F, GH, US); between Agua Buena and Villa Neily, *Burger & Matta 4595* (F, NY); Golfito, *Burger & Matta 4753* (NY); Río Catarata along Carretera Interamericana, canyon of Río Terraba, *Davidse & Pohl 1401* (F, MO, US); 8 km N of Villa Neily, *Gillis & Plowman 10074* (GH); road from San Vito to Ciudad Neily, *Grayum 3393* (MO); Rincón de Osa, *Grayum 4020* (BM, US); between Agua Buena and Villa Neily, Golfito, *Jimenez M. 2445* (BM, F, MO); Rincón de Osa near Riyitos, *Kennedy 1917* (MO); 5 km W of Rincón, *Liesner 2106* (MO, NY, US(2)); *Liesner 2115* (MO); between Río Neily and Palmar, Río Coto, *McKee 11190* (US); Rincón de Osa, *Utley & Utley 1150* (F, SEL). LOCALITY UNKNOWN: *Laskowski 1402* (F).

PANAMA: CHIRIQUÍ: Burica Peninsula, 19 km W of Puerto Armuelles, *Busey 609* (MO, NY); Río Escárrea, Buenavista, *Butcher s.n.* (SEL). Total of 16 collections seen.

DISTINGUISHING FEATURES.—The combination of long spicate inflorescences (frondose-bracteose synflorescences) and large campanulate flowers makes *Kohleria allenii* a very distinctive species (Figure 29). Glandular trichomes are more prevalent in *K. allenii* than in any other *Kohleria* species. *Kohleria allenii* is the only species that has glabrous styles.

HABITAT.—*Kohleria allenii* occurs in calcareous areas, possibly the original habitat, and on roadsides. Most plants apparently grow on steep slopes.

PHENOLOGY.—*Kohleria allenii* has been collected with flowers from October to February and in July.

NOTES.—The species may survive drought by having well-developed roots rather than scaly rhizomes. The latter feature has only been observed on one herbarium sheet (*Davidse & Pohl 1401*; Figure 29b). However, scaly rhizomes may be more common in natural habitats. Plant collectors could easily fail to collect rhizomes deeply buried in rock crevices.

The corollas of *Kohleria allenii* are similar to those of other presumably bat-pollinated species of New World Gesneriaceae, e.g., *Capanea grandiflora* (Vogel, 1958), species of *Paliavana* and *Lietzia* (A. Chautems, pers. comm.), and some species of *Gesneria* (Skog, 1976).

2. *Kohleria amabilis* (Planchon & Linden) Fritsch

Kohleria amabilis (Planchon & Linden) Fritsch, 1913a:413.

Herbs, often epilithic, scaly rhizomes rarely observed, stolons abundant; stems decumbent to erect, branching not observed, pilose to villous near apex, 15–30 cm long, basal diameter 1.5–3.0 mm. Leaves opposite, internodes 0.5–8.0 cm; the blades ovate to rotundate, 4–9 × 3–7 cm, above pubescent and sparsely pilose, below pubescent and sparsely pilose, green or purplish with a pattern of light green blotches, veins below pilose to villous; petioles 0.5–4.0 cm. Florescences short, frondose, with 1 to 6 (-numerous) flowers, partial florescences with 1 (-5) flower(s); pedicels 4–8 cm, pilose to villous, yellow to purple, bracts absent. Floral tube villous; calyx 5–7 mm long, lobes reflexed, ovate, 3–5 mm long and 3–7 mm wide at base, outside pilose, inside appressed pubescent; corolla 24–32 mm long, broadly tubular, sometimes subventricose, tube 17–25 mm long, diameter 3–4 mm at base and 6–12 mm at throat, outside pilose, red, ventrally and basally often yellow, inside glabrous, yellow, limb 13–27 mm wide, lobes 3–10 mm long and 3–9 mm wide at base, inside glabrous, yellow to pink with red dots; filaments 14–20 mm long, glabrous, anthers ~1.8 × 1.3 mm, included; nectary of 3 free and 2 dorsal basally united glands, each ~1.2 mm high and 1 mm wide at base; ovary half-inferior, 4–5 mm long, diameter 2–3 mm, style 15–18 mm long, sparsely pubescent, stigma subincluded. Capsule ovoid, 6–8 mm long, diameter 4–6 mm, apically dehiscing into 2 valves (by 2 slits) and 1 of these slits appears to continue to the base; seeds sub-globose, longitudinally to transversely striate, ~0.4 × 0.3 mm.

DISTRIBUTION.—*Kohleria amabilis* is a rare endemic of the Río Magdalena valley in central Colombia (Figure 20), where it occurs below 1100 m altitude (Figure 21). Apparently the species has become rarer, since nearly all collections are at least 50 years old. However, in 1987 populations of the variety *bogotensis* were discovered on the banks of Río Dulce between Villeta and Sasaima in the Dept. Cundinamarca (*Londoño & Kvist 78*). *Kohleria amabilis* may disappear due to the advanced deforestation of the Río Magdalena valley. An old locality near Tocaima (*Killip et al. 38338*) was visited, but here the species has disappeared.

DISTINGUISHING FEATURES.—Specimens of *Kohleria amabilis* from Colombia and *K. rugata* from Mexico are difficult to distinguish, e.g., the flowers are similar (Figure 12a–d). The former has an often conspicuous pattern of purple and light green blotches on the lower leaf surfaces, in contrast to the uniformly colored lower leaf surface of the latter. However, *K. amabilis* occurs in relatively humid and shaded habitats, whereas *K. rugata* is a hardy exposed-habitat species. *Kohleria rugata* has bivalved capsules, while those of *K. amabilis* apparently split to the base similar to *Diastema racemiferum* shown in Figure 13b.

Another similar species is *K. villosa* (Figure 13b), which also has a lower leaf surface pattern of purple and light green (Figure 36a) and the same capsule dehiscence as *K. amabile* but differs in having smaller corollas that are villous inside, villous filaments (Figures 36e, 37d), a uniformly red limb and long narrow nectary glands (Figures 36f, 37e). *Kohleria amabilis* and *K. villosa* both have an abundance of stolons not seen in other species (Figures 8a, 36a, 37a).

HABITAT.—*Kohleria amabilis* occurs on calcareous rocks, steep slopes along streams, etc. The populations along Río Dulce grow down to the highest water level on steep, fragile, slippery, and mostly shaded cliffs (*Londoño & Kvist 78*). The label of the type collection of *Achimenes picta* (now *K. amabilis* var. *bogotensis*) relates that the plants occur in shade.

PHENOLOGY.—The few collections have flowers during the first half of the year. However, very few flowers but many immature capsules were present along Río Dulce late in January 1987 (*Londoño & Kvist 78*).

NOTES.—No open capsules were found in the field (*Londoño & Kvist 78*), but herbarium sheets show that the capsules split to the base (*Karsten s.n.*, *Pennell 3552*). Wiehler (1983) stated that *Kohleria amabilis* capsules split by a longitudinal slit, but his observation may have been based on a hybrid.

Scaly rhizomes of *Kohleria amabilis* have not been observed on herbarium specimens or in the field. Their presence may have been overlooked in the populations along Río Dulce because of the difficult collecting conditions (Kvist, 1987). However, the label of one collection relates that the plants possessed "peculiar scaly rhizomes" (*Haught 2422*), and André (1876) in describing *Tydaea ceciliae* also mentions the presence of scaly rhizomes.

2a. *Kohleria amabilis* var. *amabilis*

Figures 1a (stomata), 12b (flower); Planchon and Linden, 1856a, pl. 1070; Lescuyer, 1861, pl. 20; André, 1876, pl. 260.

Kohleria amabilis (Planchon & Linden) Fritsch, 1913a:413; *Tydaea amabilis* Planchon & Linden, 1856a:237, 1856b:4; *Achimenes amabilis* (Planchon & Linden) Van Houtte, 1856:253; *Isoloma bogotense* Nicholson var. *amabile* (Planchon & Linden) Voss, 1894:793; *Isoloma amabile* (Planchon & Linden) Hortorum ex Bellair & Saint-Léger, 1899:951 [not seen]. [Type: Illustration in Planchon and Linden, 1856a, pl. 1070, drawn from cultivated material, originally collected by Triana in Colombia.]

Tydaea ceciliae André, 1876:178; *Isoloma ceciliae* (André) Nicholson, 1885:201; *Isoloma ceciliae* (André) Hortorum ex Bellair & Saint-Léger, 1899:952 [not seen]. [Type: *André 1838*, Colombia, Cundinamarca, close to Tocaima, Alto de Limba (K, holotype; NY, isotype).]

Tydaea venosa Lescuyer, 1861:248. [Type: Illustration in Lescuyer, 1861, pl. 20, drawn from cultivated material.]

Stems and inflorescences villous. Lower leaf surface green to purplish with a conspicuous pattern of light green blotches. Limb 20–27 mm wide, inside pink with red or purple dots, corolla lobes unequal, ventral lobe up to 10 mm long.

DISTRIBUTION.—The variety occurs only in Colombia both east and west of the Río Magdalena in the Depts. Cundinamarca and Tolima, respectively (Figure 20). In addition, garden-collections from the Dept. Antioquia in Colombia (*Sandeman 5561*), from Cuba (*Morton 10753*) and from Puerto Rico (*Britton & Britton s.n.*) show that *Kohleria amabilis* var. *amabilis* is in cultivation in Latin America outside its native range. There are no indications that cultivated plants have naturalized.

OTHER COLLECTIONS.—COLOMBIA: CUNDINAMARCA: Between Tocaima and Pubenza, Quebrada Cabaña, Hacienda el Cucharo, *Killip et al. 38338* (US); Alto de Limba, *Triana 2525* (P); *Triana 4164-1* (BM). TOLIMA: Guataquicito, *Haught 2422* (COL, US); Honda, *Pennell 3552* (GH, NY, US). Total of 6 collections seen.

NOMENCLATURE AND TYPIFICATION.—*Tydaea amabilis:* Planchon and Linden (1856a) wrote that Triana had introduced the living material, on which they based their description of *Tydaea amabilis* from the Colombian department of Cauca. However, no Triana collections have been seen from Cauca, but there do exist two from the Dept. Cundinamarca (*Triana 2525, 4164-1*). Consequently, Triana may have collected the live material from which *Tydaea amabilis* was described in the Magdalena valley within the current range of the species. Unfortunately, the possibility also exists that *Tydaea amabilis* was described from a hybrid collected by Triana in the Dept. Cauca; a later collection from the Dept. Cauca is probably a hybrid (*García-Barriga 6492*). The type drawing of *Tydaea amabilis* provides inconclusive evidence, but we accept it as the type to stabilize the name.

Tydaea venosa: The species was possibly described from hybrid material, but there only exists an inconclusive illustration for evidence.

2b. *Kohleria amabilis* var. *bogotensis* (Nicholson) Kvist & L. Skog, new status

Figures 5b (seed), 7c,d (pollen), 8a (stolons), 12a (flower); Bentham ex W.J. Hooker, 1844, pl. 4126; Linden, 1845, pl. 42; Hanstein, 1854, pl. 1: fig. 13; Bailey, 1900, pl. 1184; 1915, pl. 1997.

Isoloma bogotense Nicholson, 1885:201; *Kohleria bogotensis* (Nicholson) Fritsch, 1894:178 [based on *Achimenes picta* Bentham ex W.J. Hooker, 1844: pl. 4126, not *Kohleria picta* (W.J. Hooker) Hanstein, 1865:442]; *Tydaea picta* (Bentham ex W.J. Hooker) Decaisne, 1848b:468; *Diastema pictum* (Bentham ex W.J. Hooker) Walpers, 1849:472; *Giesleria picta* (Bentham ex W.J. Hooker) Regel, 1849:182; *Isoloma tydaea* L.H. Bailey, 1900:836. [Type: Colombia, Cundinamarca, close to Guaduas, Hacienda de Palmar, *Hartweg 1263* (K, holotype; BM, CGE(2), E, G, K, NY, P, W(2), isotypes).]

Stems and inflorescences pilose. Lower leaf surface green, not with a conspicuous pattern of light green blotches. Limb 13–18 mm wide, corolla lobes subequal, inside yellow with purple lines, dorsal 2 lobes red, ventral lobe up to 6 mm long.

DISTRIBUTION.—The variety is endemic to Colombia in a small area in the Dept. Cundinamarca east of the Río Magdalena (Figure 20). Pure-breeding var. *bogotensis* is apparently not cultivated in Latin America as is var. *amabilis*.

OTHER COLLECTIONS.—COLOMBIA: CUNDINAMARCA: Close to Villeta, *Goudot s.n.* (W); Guaduas, *Karsten s.n.* (LE, W); between Villeta and Sasaima, steep banks of Río Dulce, *Londoño & Kvist 78* (AAU, COL, QCA, TULV, US). LOCALITY UNKNOWN: *Purdie s.n.* (GH, K(3)). Total of 5

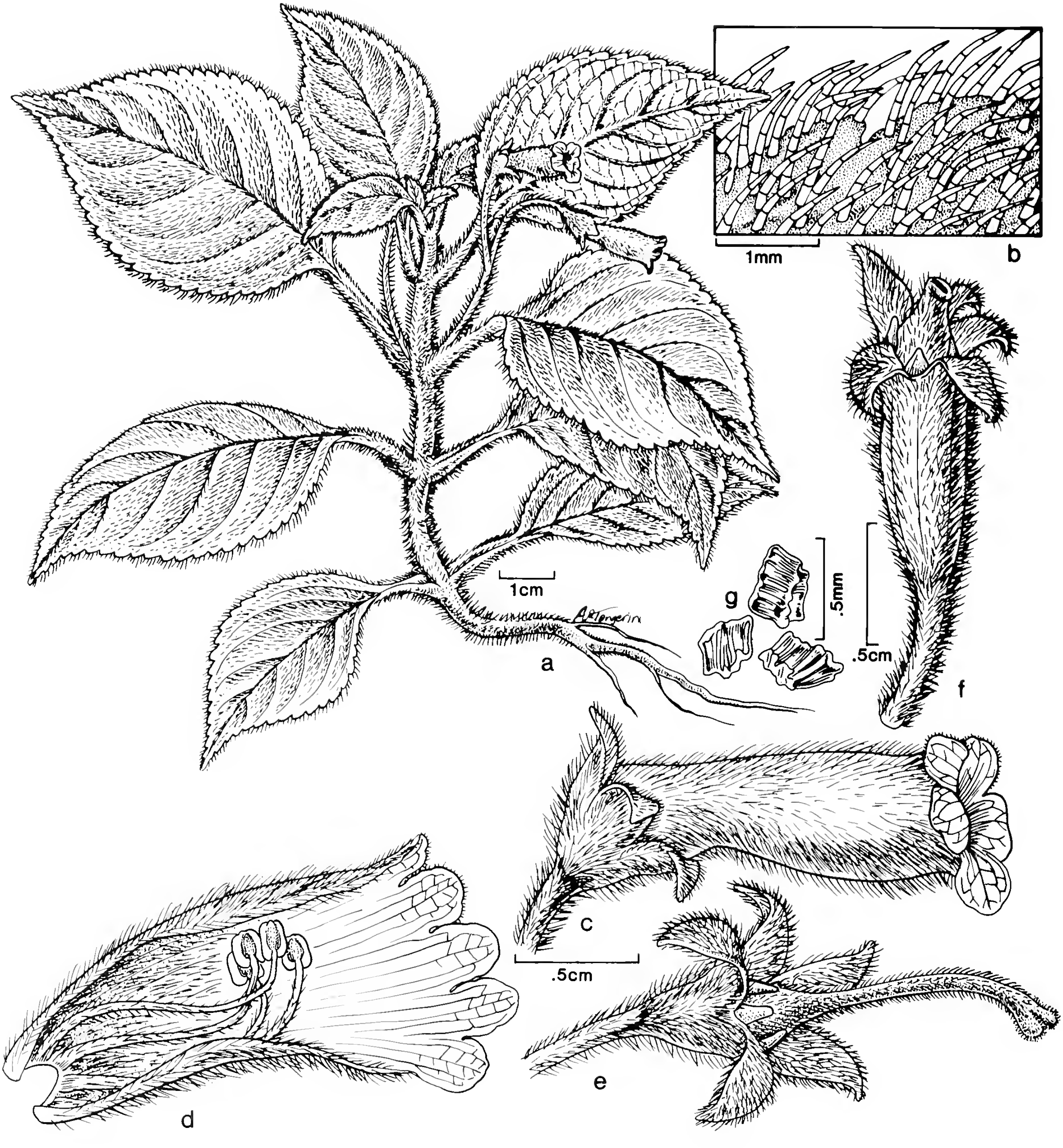


FIGURE 30.—*Kohleria diastemoides*, new species: a, habit and inflorescence; b, indument of upper leaf surface; c, flower; d, laterally opened corolla showing androecium; e, calyx, nectary, and gynoecium; f, capsule; g, seeds. All from *Lehmann 8892* (GH, NY).

collections seen.

NOMENCLATURE AND TYPIFICATION.—*Achimenes picta:* The two isotypes cited from CGE may be later clonal cultivated material of the type collection.

NOTES.—The most popular *Kohleria* in cultivation is known as "*K. bogotensis*." This is apparently a hybrid between *K. amabilis* var. *bogotensis* and *K. hirsuta*. It may have originated as a natural hybrid brought into cultivation first in Latin

America and later introduced from there to Europe, or it may have been produced in Europe. This hybrid is cultivated in Latin America, and occasionally naturalizes from cultivation, especially in Jamaica (e.g., *Lunden & Nilssen 26*; *Stearn 265; Sucker 17418*) and also in Brazil (*Ball s.n., Moroes 2232*). However, no collections are known from the small Colombian range of true *K. amabilis*. The features of the hybrid are variable, and the delimitation toward both parent-species are somewhat arbitrary. The hybrid produces scaly rhizomes, and its haploid chromosome number has been reported to be 13 (Eberle, 1956; Fussell, 1958). *Kohleria amabilis* may also hybridize with *K. warszewiczii* (see *K. warszewiczii*).

3. *Kohleria diastemoides* Kvist & L. Skog, new species

Figures 5c (seed), 30 (habit and floral features).

Differt a *Kohleria inaequalis* (Bentham) Wiehler et *K. villosa* (Fritsch) Wiehler corollis parvis anguste infundibuliformibus.

Herbs, scaly rhizomes, or stolons not seen; stems erect, branching not observed, villous, 5–10 cm long, basal diameter 1–3 mm. Leaves opposite, internodes 0.5–2.5 cm long; the blades ovate, 3–7 × 1.5–4.0 cm, above appressed pilose, below purplish, pilose, veins below villous; petioles 1.5–3.5 cm long. Florescences frondose, partial florescences with 1 or 2 flowers; peduncles 1.5–2.5 cm long, pedicels 1.5–2.5 cm long, villous, bracts absent. Floral tube villous; calyx 4–5 mm long, lobes erect to somewhat reflexed, ovate to lanceolate, 3–4 mm long and 1.5–2.0 mm wide at base, pilose; corolla 18–20 mm long, narrowly tubular, subventricose, tube 16–18 mm long, diameter 1.5–2.5 mm at base and 3–4 mm at throat, outside villous, deep purple (?), inside basally villous, glabrous toward the 4–6 mm wide limb, lobes 1.5–2.0 mm long and 1.5–2.0 mm wide at base, inside glabrous, deep purple (?); filaments 12–14 mm long, basally villous, apically glabrous, anthers ~1.2 × 1.0 mm, included; nectary of 5 separate glands, each ~1 mm high and 0.3 mm wide at base; ovary inferior, 2–3 mm long, diameter 2.0–2.5 mm long, sericeous, style 10–12 mm long, pilose, stigma included. Capsule oblong, 10–14 mm long, diameter 2.0–3.5 mm, probably dehiscing from apex to base by a single slit; seeds subglobose, irregularly striate, ~0.3 × 0.3 mm.

TYPE.—COLOMBIA: CAUCA: Western slopes of the West-Andes near Popayán, 900–1300 m, Dec 1899, *Lehmann 8892*, (NY, holotype; GH, K, isotypes).

DISTRIBUTION.—Only known from the type collection from Dept. Cauca, Colombia (Figure 20).

HABITAT.—Plants only found on slopes in dense, humid forest.

PHENOLOGY.—The type collections show flowers in December.

DISTINGUISHING FEATURES.—The oblong capsules, the pedunculate partial florescences, and the basally villous filaments and corollas are shared with *Kohleria inaequalis*, and the long, narrow, nectary glands, the velutinous leaves, and the habit and size of the shoots are shared with *K. villosa*. The small narrowly tubular corollas set *K. diastemoides* apart from both *K. inaequalis* and *K. villosa*. *Kohleria diastemoides* is sympatric only with the former species (Figures 20, 21).

NOTES.—The possibility that *Kohleria diastemoides* may be an intergeneric hybrid between *K. inaequalis* and a species of *Diastema* was discussed in the section above (see "Intergeneric Hybridization" and Table 4).

No dehiscing capsules have been seen, but the shape of the capsules (Figure 30f) is similar to those of *K. inaequalis* and *K. longicalyx* (Figure 13d,e), which dehisce by a slit from the apex to base. Scaly rhizomes may be absent (as in *K. inaequalis* and *K. villosa*), while stolons very likely are present.

4. *Kohleria grandiflora* Kvist & L. Skog, new species

Figures 5d (seed), 31 (habit and floral features).

Differt a *Kohleria longicalyx* Kvist & L. Skog lobis calycum rotundis ad spathulatis, inflorescentiis partialibus 1-floribus, a *K. inaequalis* (Bentham) Wiehler corollis glabris intus, filamentibus glabris basalibus, foliis paginis superioribus velutinis.

Herbs to subshrubs, scaly rhizomes not observed, stolons present; stems erect, rarely branching, villous with yellow-brown 3–5 mm long trichomes and smaller glandular trichomes, 50–150 cm long, basal diameter 5–8 mm. Leaves opposite, internodes 3–15 cm long; the blades ovate, 6–18 × 4–12 cm, above puberulent and sparsely pubescent, below pilose, light green to yellow-green, veins below pilose to villous, yellow; petioles 2–8 (–15) cm long. Florescences frondose, flowers single in leaf axil, often pedunculate but appearing epedunculate due to reduced bracts and buds; peduncles 0–3 cm long, pedicels 4–8 cm long. Floral tube villous; calyx 8–14 mm long, lobes erect, free nearly to base, rotundate to spathulate, basally 3–7 mm wide, ampliate above to 4–15 mm, puberulent and pilose to villous, with 5 prominent veins; corolla 45–60 mm long, tubular, tube 38–46 mm long, diameter 5–6 mm at base and 10–16 mm at throat, outside sericeous, red, inside glabrous, limb 23–35 mm wide, lobes 6–11 mm long and 8–13 mm wide at base, inside glabrous, red with purple-black dotted lines with white edges; filaments 30–35 mm long, apical half with a few trichomes, anthers ~2.5 × 2.0 mm, included; nectary of 5 free glands, each ~2.5 mm high and 1.5 mm wide at base; ovary inferior, 6–8 mm long, diameter 4–5 mm, villous, style 35–42 mm long, villous, stigma subincluded. Capsules ovoid to oblong, 16–20 mm long, diameter 8–12 mm, probably dehiscing apically into 2 valves (2 slits) and one of these slits later continues to the base; seeds ellipsoid, irregularly striate, ~0.35 × 0.15 mm.

TYPE.—COLOMBIA: PUTUMAYO: Mocoa-Pasto road, 1320 m, 6 Mar 1987, *Londoño & Quintero 215* (COL, holotype; AAU (2), TULV, US, isotypes).

DISTRIBUTION.—All collections are from Colombia and near

FIGURE 31.—*Kohleria grandiflora*, new species: a, habit and flowers; b, indument of upper leaf surface; c, indument of lower leaf surface; d, flower; e, laterally opened corolla showing parts of androecium; f, calyx and gynoecium. All from *Fosberg 20369* (US).

the roads toward Mocoa on the eastern slopes of the Eastern Cordillera in Dept. Putumayo (Figure 20) at altitudes 450 to 2200 meters (Figure 21).

COLLECTIONS.—COLOMBIA: PUTUMAYO: Between Achipayaco and Mocoa, *Cuatrecasas 11273* (COL, F(2), US); Valle de Sibundoy, *Cuatrecasas 11683* (F(2), US); 17 km W of Mocoa, below Sachamates, *Fosberg 20369* (US); by Putumayo, *Lehmann 522a* (BM, LE); Mocoa-Pasto road, 3 km from Río Pepinito, *Londoño & Quintero 216A* (AAU, COL); road to Mocoa, between El Pepino and Mirador, *Idrobo & Ospina-Hernandez 2404* (COL); N of Mocoa, *Schultes & Smith 2013* (COL, GH, US); Mocoa, *Vogel 316* (US). LOCALITY UNKNOWN. *Lehmann 4018* (BM, LE). Total of 10 collections seen.

DISTINGUISHING FEATURES.—*Kohleria grandiflora* differs from *K. longicalyx* by having rotundate to spathulate calyx lobes instead of lanceolate lobes (Figures 12f, 31d), partial florescences with one rather than two to three flowers, and ellipsoid rather than subglobose seeds (and possibly a different fruit dehiscence). *Kohleria grandiflora* and *K. longicalyx* both differ from *K. inaequalis* by having corolla tubes that are glabrous inside instead of basally villous, filaments that are basally glabrous instead of villous to pilose, considerably longer corolla tubes, and by having puberulous or velutinous instead of usually hispid upper leaf surfaces.

HABITAT.—*Kohleria grandiflora* occurs in shaded, humid forest understory.

PHENOLOGY.—The species has been collected with flowers from January to April and in July.

NOTES—The capsules of *Kohleria grandiflora* apparently are considerably shorter than those of *K. longicalyx* (or the capsules that have been seen are not mature). They may split into two valves apically with one of these slits continuing to the base (Figure 13b), rather than only having a single longitudinal slit as in *K. longicalyx* (Figure 13d).

Scaly rhizomes are absent according to X. Londoño (pers. comm.).

5. *Kohleria hirsuta* (Kunth) Regel

Kohleria hirsuta (Kunth) Regel, 1848:250.

Herbs or shrubs, frequently epilithic, scaly rhizomes and stolons usually present; stems erect, occasionally decumbent, pendent or scandent, branching variable, villous, less commonly tomentose or lanate, rarely glandular-hairy, erect part 30–150 (–200) cm long, scandent shoots occasionally reaching 400 cm, basal diameter 3–8 mm; internodes (1–) 2–7 (–14) cm long. Leaves opposite, occasionally ternate; the blades elliptic, less commonly ovate to elliptic, rarely appearing cordate due to an oblique base, 4–12 (–18) × 2–6 (–10) cm, above pubescent to sericeous, occasionally purplish especially along the margin, below villous to tomentose, lighter green to red or purplish, veins below sericeous or villous, yellow-green to purplish; petioles 1–4 (–8) cm long. Florescences frondose, partial florescences of 1 to 4 (–6) flowers, epedunculate or less commonly pedunculate; peduncles 0–2 (–4) cm long, always shorter than the 2–6 (–10) cm long pedicels, villous, yellow-green to purple, bracts usually scaly, occasionally lanceolate and up to 2 cm long, often caducous. Floral tube villous; calyx (4–) 7–12 (–20) mm long, lobes erect, lanceolate to subulate, rarely triangular, (3–) 6–10 (–15) mm long and 1–6 mm wide at base, outside villous or sericeous, green or purplish, inside appressed pubescent to sericeous; corolla (20–) 27–40 (–50) mm long, tubular, occasionally subventricose, tube (18–) 25–38 (–45) mm long, diameter 2–6 (–10) mm at base and 3–15 mm at throat, outside villous, red, less commonly yellow-red or orange-red, inside glabrous, yellow, with purple dots, the base usually saccate but not sharply delimited, limb 6–22 mm wide, lobes 3–6 mm long and 4–7 mm wide at base, inside glabrous, rarely sparsely glandular-hairy, yellow with numerous purple dots; filaments 18–35 mm, glabrous, anthers 2.5–4.0 × 1.5–2.5 mm, subincluded; nectary often of 5 free glands, each ~1 mm tall and 0.8 mm wide at base, less commonly a 5-lobed 1–2 mm tall ring or irregularly lobed; ovary half-inferior, 5–7 mm long, diameter 3–4 mm, style (22–) 27–33 (–37) mm long, sparsely pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 10–14 mm long, diameter 5–9 mm, bivalved; seeds narrowly ellipsoid to ellipsoid, longitudinally striate, ~0.50 × 0.15 mm. Chromosome number $n = 13$ (Davidse, 1971, 1981; Wiehler, 1972).

DISTRIBUTION.—Plants of *Kohleria hirsuta* occur in Venezuela, Guyana, Surinam, Trinidad, and in Colombia (Figure 17) in the Eastern Cordillera and Río Magdalena valley (Figure 22). Collections from Venezuela and Guyana close to the Brazilian territory of Roraima make it likely that *K. hirsuta* also occurs in Brazil. The lowland along the Río Orinoco apparently isolates the Guayana shield populations (the collections from southeastern Venezuela and western Guyana) from the main range of *K. hirsuta* (Figure 17). A few recent collections from south of its Colombian main range may represent plants escaped from cultivation; viz., from the Dept. Putumayo in southern Colombia (*Londoño 203, 212*), and from the Prov. Morona-Santiago in southeastern Ecuador (*Holm-Nielsen 20472*). Collections from the state of Chiapas in Mexico (*Schauffer s. n.*), and from the island of Guadeloupe in the Lesser Antilles (*Questel 3840*) must have escaped from cultivation. Garden-collections from Puerto Rico (*Britton & Britton 9048, 9819, 9939*) and the Dominican Republic (*Jiménez 5483*) show the species to be elsewhere cultivated in Latin America outside its native range. *Kohleria hirsuta* occurs from sea level to above 2600 meters altitude (Figure 21).

DISTINGUISHING FEATURES.—True to the species epithet, *Kohleria hirsuta* never has hispid nor scabrous leaves. A constant feature of this variable species is its pilose or hirsute leaves and stems that distinguishes *K. hirsuta* (Figure 2a) vegetatively from species with hispid or scabrous leaves (Figure 2b). *Kohleria trianae* and *K. warszewiczii* are vegetatively indistinguishable, but their long-pedunculate inflorescences set fertile plants apart. *Kohleria peruviana* (Figure 33) differs by having conspicuously saccate corolla bases, larger leaves, and a dense gray-white pubescence.

HABITAT.—The species is hardy and is often seen on exposed, dry, rocky slopes. The habitats of *Kohleria hirsuta* in Dept. Cundinamarca, Colombia, are described above (see "Phenology" section).

PHENOLOGY.—*Kohleria hirsuta* definitely is seasonal at lower elevations in the Colombian department of Cundinamarca (pers. obs., Jan–Feb 1987). However, data from herbarium labels do not show this seasonality. The species has been collected with flowers throughout the year, possibly because there is some reduced flowering throughout the dry season. The conspicuous flowers of *K. hirsuta* and the frequent occurrence on roadsides make it likely to be collected even during periods of reduced flowering.

NOTES.—The extreme variation of *Kohleria hirsuta* in Colombia is discussed above (Figures 4, 11, 24) The species has adapted to very different habitats (see "Phenology" section), and is hybridizing with other species, especially *K. trianae* (Figure 23; see "Interspecific Hybridization" section). In addition, the variety *longipes* apparently is a previously isolated semi-species that has hybridized extensively with the typical variety (Table 3; see "Intraspecific Hybridization" section).

The scaly rhizomes of *Kohleria hirsuta* have medicinal uses (see "Popular Names and Medicinal Uses" section above).

5a. *Kohleria hirsuta* var. *hirsuta*

Figures 2a (indument of upper leaf surface), 5e (seed), 7e (pollen), 8b (scaly rhizome), 24a,c,d (flowers); Kunth, 1818, pls. 189, 191; W.J. Hooker, 1841, pl. 3815; Regel, 1852c, pl. 7; Hemsley, 1903, pl. 7907; Hoehne, 1970, pls. 164, 173, 176.

Kohleria hirsuta (Kunth) Regel, 1848:250; *Gesneria hirsuta* Kunth, 1818: qto. ed. 394, fol. ed. 317; *Isoloma hirsutum* (Kunth) Regel, 1851:893; *Brachyloma hirsutum* (Kunth) Hanstein, 1854:203. [Type: Venezuela, Monagas (on border with Sucre), Caripé, Cumaná, *Bonpland 330* (P-BO, holotype; B-W, P, isotypes).]

Gesneria mollis Kunth, 1818: qto. ed. 395, fol. ed. 317; *Isoloma molle* Decaisne, 1848a:465; *Brachyloma molle* (Kunth) Hanstein, 1859:530, 571; *Kohleria mollis* (Kunth) Hanstein, 1865:441; *Isoloma molle* (Kunth) Nicholson, 1885:201. [Type: Probably collected in the Río Magdalena valley of Colombia, *Bonpland s.n.* (P, holotype).]

Gesneria longiflora Kunth, 1818: qto. ed. 396, fol. ed. 317; *Isoloma longiflorum* (Kunth) Regel, 1854c:108; *Brachyloma longiflorum* (Kunth) Hanstein, 1859:530, 572; *Kohleria longiflora* (Kunth) Hanstein, 1865:442. [Type: Probably collected by Bonpland in the Río Magdalena valley of Colombia but no specimen has been located; Colombia, Tolima, New Quindio trail, Río Coello, 1000–1500 m, 7 Aug 1922, *Hazen 9651* (NY, neotype, selected herein).]

Gesneria vestita Bentham, 1845b:19; *Isoloma vestitum* (Bentham) Decaisne, 1848a:465; *Brachyloma vestitum* (Bentham) Hanstein, 1859:530, 573; *Kohleria vestita* (Bentham) Hanstein, 1865:442. [Type: Colombia, Cundinamarca, Tena, *Hartweg 1259* (K, holotype; CGE, K, isotypes).]

Gesneria eriantha Bentham, 1846:228; *Isoloma erianthum* (Bentham) Decaisne, 1848a:465; *Brachyloma erianthum* (Bentham) Hanstein, 1859:530, 573; *Kohleria eriantha* (Bentham) Hanstein, 1865:442. [Type: Colombia, Cundinamarca, between Villeta and Guaduas, *Hartweg 1256* (K, holotype; BM, CGE, G, K, isotypes).]

Gesneria rubricaulis Kunth & Bouché, 1847:12; *Isoloma rubricaule* (Kunth & Bouché) Regel, 1851:893; *Brachyloma rubricaule* (Kunth & Bouché) Hanstein, 1859:526, 569; *Kohleria rubricaulis* (Kunth & Bouché) Hasskarl, 1860:97. [Type: Venezuela, Distrito Federal, "Caracas" *Moritz 1127* (B, holotype not extant; BM, lectotype selected herein).]

Brachyloma leucomallon Hanstein, 1859:528, 570; *Kohleria leucomallos* (Hanstein) Hanstein, 1865:441. [Type: Colombia, Cundinamarca, "Bogotá," *Karsten s.n.* (W, holotype).]

Brachyloma moritzianum Bouché & Hanstein in Hanstein, 1859:524, 568; *Kohleria moritziana* (Bouché & Hanstein) Hanstein, 1865:441. [Type: Described from cultivated material collected by Moritz in Colombia (B, no longer extant); Colombia, Santander, close to Bucaramanga, 1500 m, 27 Aug 1948, *Barkley & Araque M. 316* (US, neotype selected herein).]

Brachyloma rhodomallon Hanstein, 1859:526, 570; *Kohleria rhodomallos* (Hanstein) Hanstein, 1865:441. [Type: Venezuela, Distrito Federal, "Caracas," *Moritz 414* (LE, lectotype selected herein; BM, BR, CGE, G(3), HBG, L, NY, P, isolectotypes).]

Brachyloma ventricosum Hanstein, 1859:428, 572; *Gesnera* [sic] *ventricosa* Hortorum ex Hanstein, 1859:529 [nom. nud. pro syn.]; *Kohleria ventricosa* (Hanstein) Hanstein, 1865:441. [Type: Described from cultivated material, *Regel s.n.* (LE, neotype selected herein).]

Kohleria longipedunculata Hanstein, 1865:441; *Isoloma longipedunculatum* Hortorum ex Hanstein, 1865:442 [nom. nud. pro syn.]. [Type: Apparently described from cultivated material, no specimens located; Venezuela, Miranda, Parque Nacional de Guatopo, slopes between Río San Lorenzo and ridge leading to Aguaramal, 600–700 m, 25 Nov 1961, *Steyermark 90076* (US, neotype selected herein).]

Kohleria brachycalyx Fritsch, 1913a:424. [Type: Colombia, Tolima, Ibague, *Triana 2519* (W, holotype; G, isotype).]

Kohleria lanigera Fritsch, 1913a:423. [Type: Colombia, Antioquia, Aguadas, *Lehmann 4620* (B, holotype not extant; K, lectotype selected herein).]

Kohleria straussiana Fritsch, 1913a:34. [Type: Described from cultivated material (B, holotype not extant); Colombia, Cundinamarca, Guaduas to Palmar and road to Guaduero, 1040–1150 m, 6 Nov 1945, *García-Barriga 11775* (US, neotype selected herein).]

Isoloma pycnosuzygium J.D. Smith, 1916:382; *Kohleria pycnosuzygia* (J.D. Smith) Badillo in Pittier et al., 1947:397. [Type: Venezuela, Distrito Federal, Los Chorros, *Eggers 13078* (US, holotype).]

Herbs or subshrubs; stems not scandent, 30–150 cm long. Stems, pedicels, peduncles and calyces rarely purple, pedicels rarely exceeding 7 cm long. Diameter of floral tube 3–6 mm; calyx 4–20 mm long, lobes 3–15 mm long, width at base 1–2 mm; corolla 22–50 mm long, diameter of throat 3–8 mm, diameter of limb 6–12 mm; nectary of 5 free glands.

NOMENCLATURE AND TYPIFICATION.—*Gesneria mollis:* Kunth (1818) only gave the locality as "Regno Novogranatensi ?" and no additional information appears on the type specimen sheet. However, the type collection has features indicating introgression with *K. trianae*, a phenomenon restricted to the Río Magdalena valley (see "Interspecific Hybridization" section above). Thus, the species apparently was collected during Humboldt and Bonpland's sojourn through the Magdalena valley in 1801. When Decaisne published the name *Isoloma molle* in 1848, he probably intended to transfer the Kunth (1818) species, *Gesneria molle*, to *Isoloma*, but neglected to add the author of the basionym. However, the possibility also exists that *Isoloma molle* is an unidentified cultivar.

Gesneria longiflora: Kunth (1818) said that *Gesneria longiflora* came from the same locality as *Gesneria mollis* and that these two species were similar. Consequently, a Río

Magdalena valley collection showing introgression with *Kohleria trianae* is selected as neotype (see *Gesneria mollis*).

Gesneria eriantha: This species has features intermediate between *Kohleria hirsuta* var. *hirsuta* and var. *longipes,* but is here referred to the former, as the latter usually occurs above 1800 meters. Hartweg collected the type of *Gesneria eriantha* at about 1200 meters altitude. The large-flowered, high-elevation plants currently referred to the variety *longipes,* have often been called *Kohleria eriantha.*

Brachyloma moritzianum: No specimens annotated with this name have been located, but Bouché and Hanstein in Hanstein (1859) wrote that the species was similar to *Brachyloma rhodomallon.* According to the description there also are similarities with *Gesneria vestita.* A neotype similar to these species has been selected.

Brachyloma rhodomallon: Hanstein (1859) cited two specimens but selected no type (B, LE). The former is no longer extant.

Brachyloma ventricosum: The only specimen seen annotated with this name was cultivated by Regel in Saint Petersburg (formerly Leningrad). This specimen was selected as neotype, because Hanstein received the material on which he described *Brachyloma ventricosum* (1859) from Zürich, where Regel worked before he went to Saint Petersburg. Thus, it is likely that the name *Brachyloma ventricosum* and the material from which Hanstein described *Brachyloma ventricosum* came from Regel.

Kohleria longipedunculata: The species epithet apparently refers to the occurrence of long pedicels, because Hanstein's (1865) description demonstrates the partial florescences consist of single, axillary flowers. *Kohleria longipedunculata* was described from cultivated material of apparently unknown origin. Hanstein suspected *K. longipedunculata* was identical with *K. lanata* (now *K. rugata*), but the species was described as having lanceolate-lineate calyx lobes, while those of *K. rugata* are always ovate. Hanstein (1865) referred *K. longipedunculata* to the subgenus *Brachyloma* together with 13 other current synonyms of *K. hirsuta.* In addition, the description of *K. longipedunculata* supports the idea that the species is a synonym of *K. hirsuta* var. *hirsuta.*

Kohleria brachycalyx: Fritsch (1913a) described *K. brachycalyx* from *K. hirsuta* plants showing introgression with *K. trianae.* Consequently, a Río Magdalena valley collection has been selected as neotype (see *Gesneria mollis*).

Kohleria lanigera: The single specimen of this species has pedunculate inflorescences and ternate calyx lobes, but is rather poor in having no fully developed flowers. It seems to have some features of *K. warszewiczii* (or possibly *K. trianae*), which may be due to introgression with one of these species.

Kohleria straussiana: Fritsch (1913a) described *Kohleria straussiana* from cultivated material possibly of hybrid origin (he reported the pollen quality to be low). He mentioned four species he considered to be the closest relatives of *K. straussiana,* all currently synonyms of *K. hirsuta. Kohleria straussiana* apparently was described on plants similar to the material on which *Brachyloma rhodomallon* was based.

DISTRIBUTION.—The variety occurs throughout the range of *Kohleria hirsuta* (Figures 17, 22), and is common between 1000 and 2000 meters elevation.

SELECTED COLLECTIONS.—COLOMBIA: ANTIOQUIA: Below San Luis, Río Clara, *Folsom & Rentería 10342* (US). BOYACA: Region of Mt. Chapon, El Umbo, *Lawrance 469* (BM, F, GH(2), MO, NY, S). CUNDINAMARCA: Honda-Guadua road, *Londoño & Kvist 72* (AAU, COL, QCA, TULV, US). HUILA: La Plata, *Lehmann 478* (GH(2), NY). SANTANDER: Ocaña, *Schlim 93* (BM, CGE, G(3), K). TOLIMA: Ibague, *André 1967* (F, K, NY).

GUYANA: UPPER TAKUTU REGION: Kanuku mountains, *Goodland & Maycock 456A* (NY, US). MAZARUNI REGION: Upper Mazaruni river basin, Kamarang, *Tillett & Tillett 45809* (NY, US).

SURINAM: Wilhelmina Mts., Julianatop, *Schulz-LBB 10315* (U).

TRINIDAD: Between La Vache and Maracas Bay, *Davidse 2565,* (MO, NY).

VENEZUELA: ARAGUA: Colonia Tovar, *Fendler 793* (G(2), GH(2), K, MO, NY). BOLÍVAR: SE Bolívar, Cerro Venamo, *Steyermark 92776* (F, G, NY, US). DISTRITO FEDERAL: Old Caracas-La Guaira road, Río Grande, *Pittier 9864* (GH, NY, US). MÉRIDA: Mérida-Carbonera road, km 35, *Breteler 3128* (G, NY, S, US). MIRANDA: Los Teques, *Pittier 11251* (GH, NY, US). TACHIRA: San Juan de Colón, *Bruijn 1341* (MO, NY, S, US). TERR. FED. AMAZONAS: Along the Brazilian border, Sierra Parima, *Steyermark 106137* (SEL). Total of 211 collections seen.

5b. *Kohleria hirsuta* var. *longipes* (Bentham) Kvist & L. Skog, new status

Figure 24b (flower); Karsten, 1860, pl. 50.

Gesneria longipes Bentham, 1846:229; *Isoloma longipes* Decaisne, 1848a:465; *Brachyloma longipes* (Bentham) Hanstein, 1859:530, 572; *Kohleria longipes* (Bentham) Hanstein, 1865:442. [Type: Colombia, Cundinamarca, Tequendama Falls, *Hartweg s.n.* (K, holotype; K, isotype).]

Brachyloma karstenianum Hanstein, 1859:532, 573; *Kohleria karsteniana* (Hanstein) Hanstein, 1865:442. [Type: Colombia, Cundinamarca, Tequendama Falls, *Karsten s.n.* (W, lectotype selected herein; F, LE, isolectotypes).]

Subshrubs or climbing shrubs; stems often scandent, 100–250 (–400) cm long. Stems, petioles, peduncles, pedicels and calyces usually deep purple, length of pedicels often exceeding 7 cm. Diameter of floral tube 5–9 mm; calyx 12–20 mm long, lobes 6–12 mm long, width at base 2–6 mm; corolla 32–50 mm long, diameter of throat 8–15 mm, width of limb 12–22 mm; nectary usually a 5-lobed ring.

DISTRIBUTION.—The variety is almost completely restricted to the Dept. Cundinamarca in the Eastern Colombian Cordillera (Figure 22) and to elevations above 1800 meters (Table 3).

SELECTED COLLECTIONS.—COLOMBIA: BOYACA: Sierra del Cocuy, Bachira, *Grubb 616* (K, US). CUNDINAMARCA: Salto de Tequendama, *Cuatrecasas 71* (F(3), US); between El Salto and El Colegio, *Cuatrecasas 8202* (F, US); Mosquera-La Mesa road, km 18, *Gentry 17047* (MO, US); Salto de Tequendama, *Killip 33996* (BM, S, US); Boyaca-Siveria road, 2580 m, *Londoño & Kvist 80* (AAU, COL); Canasuca, *Triana 2520* (G, K, US(2)). Total of 44 collections seen.

NOMENCLATURE AND TYPIFICATION.—*Gesneria longipes:* When Decaisne (1848a) established the genus *Isoloma* and included the species *I. longipes,* he apparently forgot to add its basionym. If he truly did not intend to transfer the Bentham species, then the taxonomic status of *I. longipes* Decaisne is currently unknown.

Brachyloma karstenianum: Hanstein (1859) cited two collections but selected neither as type. The Karsten collection was selected as lectotype because Karsten (1860) based his illustration of *B. karstenianum* on his own material. The syntype is *Linden 394* at W.

6. *Kohleria hondensis* (Kunth) Hanstein

Figures 2b (indument of upper leaf surface), 8d (scaly rhizomes and habit), 12g (flower); Kunth, 1818, pl. 190; W.J. Hooker, 1847, pl. 4342; Hanstein, 1854, pl. 1: fig. 17; Fritsch, 1894, pl. 77: fig. L; Kvist, 1987:19 (photo from type locality).

Kohleria hondensis (Kunth) Hanstein, 1865:442; *Gesneria hondensis* Kunth, 1818: qto. ed. 395, fol. ed. 317; *Isoloma hondense* (Kunth) Decaisne, 1848a:465; *Brachyloma hondense* (Kunth) Hanstein, 1854:203; *Isoloma hondense* var. *chloranthum* Regel, 1854a:2; *Cryptoloma hondense* (Kunth) Hanstein, 1859:534, 579. [*Kohleria hondensis* Hanstein, 1859:535 (cf. Regel, 1848:250) (nom. nud. pro syn.)]. [Type: Colombia, Tolima, Honda, *Bonpland 1707* (P-BO, holotype, F, fragment; P, isotype).]

Gesneria triflora W.J. Hooker, 1847, pl. 4342; *Kohleria triflora* (W.J. Hooker) Regel, 1848:250; *Isoloma triflorum* (W.J. Hooker) Decaisne, 1848a:465; *Cryptoloma triflorum* (W.J. Hooker) Hanstein, 1859:534, 581. [Type: Illustration by Hooker, 1847, pl. 4342, originally described and drawn from cultivated material, collected by Purdie in Colombia.]

Herbs or subshrubs, usually epilithic, with scaly rhizomes, stolons not seen; stems decumbent to erect, occasionally pendent, rarely branching, appressed pilose to sericeous near apex, erect shoots 5–120 cm long, basal diameter 3–5 mm. Leaves opposite, internodes 0.1–1.5 cm long; the blades elliptic, 3–9 (–12) × 2–4 (–6) cm, above hispid, below tomentose, grayish white, veins below sericeous, yellow-green; petioles 0.5–2.0 cm long. Florescences frondose, partial florescences congested with 1 to 4 flowers; pedicels 1.5–3.0 cm long, sericeous, light green, bracts scaly, caducous. Floral tube sericeous; calyx 7–12 mm long, lobes erect, ovate to lanceolate, 5–8 mm long and 3–5 mm wide at base, outside sericeous, inside appressed pubescent; corolla 16–22 mm long, tubular, subventricose, tube 15–20 mm long, diameter 3–4 mm at base, above widened to 4–8 mm, diameter 1.5–2.5 mm at throat, outside sericeous, orange-red, inside glabrous, yellow, basally saccate, yellow, limb 5–7 mm wide, lobes ~1 mm long and 1.5 mm wide at base (the indument exceeding the length of the lobes), inside glabrous, yellow with 2 or 3 dots at each lobe; filaments 15–17 mm long, glabrous, anthers ~2.5 × 2.0 mm, included; nectary of 5 free glands, each ~1 mm high and 1 mm wide at base; ovary half-inferior, 5–6 mm long, diameter 2–4 mm, style 11–13 mm long, glandular-hairy, stigma included. Capsule ovoid, 7–9 mm long, diameter 5–6 mm, bivalved; seeds narrowly ellipsoid to ellipsoid, longitudinally striate, ~0.40 × 0.15 mm.

DISTRIBUTION.—*Kohleria hondensis* is endemic to the Río Magdalena valley in Colombia. The distance from the northernmost to the southernmost locality is about 350 km. *Kohleria hondensis* is restricted to elevations below 700 meters (Figure 21). The distributions of *Kohleria hondensis* and the related *K. tubiflora* are allopatric, with the latter occurring east, west, and north of *K. hondensis* (Figure 16).

OTHER COLLECTIONS.—COLOMBIA: ANTIOQUIA: Caracoli, *André 509* (K, NY). CALDAS: La Dorada, *Haught 2109* (BH, COL, NY, UC, US). HUILA: 5 km N of Villavieja, *Mason 13806* (COL, GH, UC, US); Villavieja-Baraya road, km 11, Cabrera Lajas, *Smith 1161* (COL, UC, US). TOLIMA: Piedras, *André 1949* (F, GH, K, NY, US); between Honda and Maraquita, *García-Barriga 8168* (US); Chicoral, *Haught 6268* (COL, US); Honda, *Karsten s.n.* (LE); Honda, *Linden 1162* (BM, CGE, G(3), K, LE, P); 2 km N of Honda toward La Dorado, *Londoño & Kvist 69* (AAU(3), COL, NY, QCA, TULV, US, USM, VEN); Honda, *Pennell 3578* (GH, MO, NY, US); Cuamo to Río Saldaña, *Pennell & Rusby 211* (NY); *Pennell & Rusby 212* (GH, NY, US); Maraquita, *Schneider 479* (COL, S); Piedras to Ibague, *Triana 2516* (G); Palmilla to Piedras, *Triana 4165* (COL); Mariquita, Río Gualí, *Uribe 2628* (COL). LOCALITY UNKNOWN. *Holton s.n.* (NY). Total of 19 collections seen.

DISTINGUISHING FEATURES.—The very small limb distinguishes *Kohleria hondensis* (Figure 12g) from all species except *K. tubiflora* (Figure 12h). The latter species has longer corolla tubes, and the calyx lobes are triangular instead of lanceolate. *Kohleria hondensis* is also characterized by the very hispid upper leaf surface.

HABITAT.—*Kohleria hondensis* is hardy, and most collections come from dry, rocky, overgrazed areas or from steep, exposed slopes, often along roads.

PHENOLOGY.—The species has been found with flowers from November to February and in July.

NOMENCLATURE AND TYPIFICATION.—*Kohleria hondensis:* Regel (1848) transferred *Gesneria triflora* to *Kohleria* and added that *Gesneria hondensis* also belonged here. However, Regel never made the new combination, and Hanstein (1859) listed *Kohleria hondensis* as a synonym of *Cryptoloma hondense*. By 1865 Hanstein fused *Cryptoloma* with *Kohleria* and finally made the valid combination.

Isoloma hondense: Decaisne (1848a) cited W.J. Hooker, 1846, pl. 4217, which actually shows a plant of *Kohleria tubiflora*. However, the Hooker description cites the Kunth publication of *Gesneria hondensis*. Thus, *Isoloma hondense* is included here as a synonym by indirect reference to the type.

NOTES.—*Kohleria hondensis* shoots show a striking variation in size. In a population near the type locality at Honda the height of flowering shoots ranged from 5 to 120 cm. Small plants were epilithic, and larger ones were growing in porous soil. All plants had an abundance of scaly rhizomes often deeply buried in rock crevices, but no stolons were observed (Figure 8d; *Londoño & Kvist 69*).

The anthers of *K. hondensis* shed a considerable pollen quantity in the throat as a possible reward to visitors (*Londoño & Kvist 69*)

7. *Kohleria inaequalis* (Bentham) Wiehler

Kohleria inaequalis (Bentham) Wiehler, 1978a:62.

Herbs or subshrubs, scaly rhizomes not observed, stolons often present; stems erect or decumbent, rarely branching, villous to hispid and puberulent or less commonly only puberulent, (15-) 30-60 (-100) cm long, basal diameter 3-9 mm. Leaves opposite, internodes 2-6 (-10) cm long; the blades ovate to elliptic, less commonly lanceolate, (3-) 6-10 (-20) × (1.5-) 3-6 (-9) cm, above hispid, less commonly sparsely pilose, rarely pilose, hispid or puberulous, below puberulous or glabrous, veins villous and puberulous, rarely sericeous, yellow-green; petioles (0.5-) 2-5 cm long. Florescences frondose, partial florescences with 1 to 4 flowers; peduncles (0-) 2-5 (-8) cm long, single flowers may appear epedunculate due to reduced additional flowers and bracts, pedicels 2-5 cm long, often villous to hispid with tawny, purple or blackish trichomes, less commonly with shorter appressed pubescence, bracts lanceolate, 4-13 × 1-3 mm, caducous. Floral tube villous to hispid, trichomes purple-black or yellow-green; calyx (3-) 6-11 (-25) mm long, lobes erect, free nearly to base, lanceolate, rarely ovate, base (1-) 2-5 mm wide, upwards occasionally widened to 5-10 mm, outside scabrous and hispid, less commonly puberulous, inside appressed pubescent, veins occasionally prominent; corolla 16-38 (-55) mm long, broadly tubular to narrowly tubular, occasionally subventricose, tube (12-) 20-35 (-50) mm long, diameter 3-5 mm at base and 5-21 mm at throat, outside villous, red to purple, inside basally villous, upwards pilose to glabrous, lighter yellow-red, the base dorsally gibbous, the limb 9-32 mm wide, lobes (3-) 5-7 (-15) mm long and (3-) 5-7 (-12) mm wide at base, inside glabrous, red with purplish or black dotted lines, these often surrounded by a white edge; filaments (12-) 20-25 mm long, basally pilose to villous, apically pilose to glabrous, anthers 2-3 × 1.5-2.0 mm, included, rarely subincluded; nectary of 5 free glands, the two dorsal often located appressed to each other, each ~1 mm high and 1 mm wide at base; ovary inferior, 4-7 mm long, diameter 2-4 mm, style 12-20 mm long, pilose, occasionally glandular-hairy, stigma subincluded. Capsule oblong, 9-15 (-20) mm long, diameter 4-6 (-8) mm, dehiscing by 1 slit from apex to base; seeds subglobose, irregularly striate, ~0.4 × 0.3 mm. Chromosome number $n = 13$ (Wiehler, 1975, as *K. magnifica*).

DISTRIBUTION.—*Kohleria inaequalis* occurs on the western Andean slopes of northern Ecuador, and in Colombia mainly in the Western and Central Cordilleras (Figures 21, 28). The species is frequent between 1000 and 2200 meters altitude, but occurs occasionally down to sea-level and up to 2600 meters. The collections from below 1000 meters come from Pacific coastal Ecuador and Colombia, the most humid part of the range (Figure 21).

DISTINGUISHING FEATURES.—*Kohleria inaequalis* is extremely variable (Figures 4, 11, 25, 27), but most specimens are recognized by the combination of hispid upper leaf surfaces, pedunculate inflorescences, oblong capsules, and a brown-red villous to hispid indument that especially covers the inflorescences and the floral tube. In addition, more subtle but stable features set this species apart. The corolla and the filaments are always basally villous to pilose, a feature shared with *K. diastemoides* (Figure 30d), but this latter species has very long, narrow nectary glands and small, narrowly tubular corollas (Figure 30c,e).

HABITAT.—*Kohleria inaequalis* mainly occurs in forest understory, and often along ravines with small streams. The species sometimes occurs along roads, but here usually under the cover of shrubs and protected from direct sun (*Londoño & Kvist 190*).

PHENOLOGY.—The species produces flowers throughout the year with little seasonality.

NOTES.—The extremes in the "*Kohleria inaequalis* complex" are so diverse that it seems justifiable to give the variations taxonomic recognition, although the majority of the collections have intermediate features. These plants mainly come from the central part of its range, and are here mostly referred to var. *inaequalis* (Figures 25d,e, 28). The pure breeding varieties occur in the southern and the northern parts of the range (Figures 25a,c,f, 28). The extreme variation of *K. inaequalis* (Figures 4, 11, 25, 27) is discussed above (see "Intraspecific Variation" section). A hybrid between *K. inaequalis* and *K. spicata* (Figure 25b) also is discusssed above (see "Interspecific Hybridization" section).

Scaly rhizomes are apparently never formed in native habitats but may occasionally develop in cultivation. Hooker (1848) wrote that the roots of var. *ocellata* (as *Achimenes ocellata*) were "tuberous, by which it is easily increased," and Lindley (1856) noted that var. *inaequalis* (as *Achimenes magnifica*) had scaly rhizomes. Thus, scaly rhizomes may arise, for example, under stress in cultivation.

7a. *Kohleria inaequalis* var. *inaequalis*

Figures 1b (stomata), 5f (seed), 7g,h (pollen), 13e (capsule dehiscence), 25d-f (flowers); Regel, 1854b, pl. 79 (as 76); Regel, 1855b, pl. 120; Planchon and Linden,1855, pl. 1013.

Kohleria inaequalis (Bentham) Wiehler, 1978a:62; *Gesneria inaequalis*

Bentham, 1846:230; *Isoloma inaequale* (Bentham) Bentham ex Jackson, 1895:1238 (cf. Bentham, 1876:1002). [Type: Colombia, Cauca, slopes of the Andes of Popayán toward the Pacific, *Hartweg s.n.* (K, holotype).]

Tydaea warscewiczii [sic] Regel, 1854b:73 [not *Kohleria warszewiczii* (Regel) Hanstein, 1865:442] [*Capanea warscewiczii* [sic] Warscewicz [sic] ex Regel, 1854b:73 (nom. nud. pro syn.)]; *Isoloma bogotense* Nicholson var. *warscewiczii* [sic] (Regel) Voss, 1894:794; *Kohleria ferruginea* Fritsch, 1913a:413. [Type: Illustration by Regel, 1854b, pl. 79 [as pl. 76], described from cultivated material, originally collected by Warszewicz (?) in Colombia.]

Tydaea ocellata (W.J. Hooker) Regel var. *formosa* Regel, 1855b:181. [Type: Illustration by Regel, 1855, pl. 120, described from cultivated material, originally collected by Warszewicz at St. Martha, Colombia.]

Locheria magnifica Planchon & Linden, 1855:117; *Achimenes magnifica* (Planchon & Linden) Lindley, 1856:116; *Tydaea magnifica* (Planchon & Linden) Hanstein, 1865:440; *Kohleria magnifica* (Planchon & Linden) H.E. Moore, 1954:383. [Type: Illustration by Planchon and Linden, 1855, pl. 1013, described from cultivated material, originally collected by Triana at Cauca, "Popayan," Colombia.]

Kohleria lehmannii Fritsch, 1913a:419. [Type: Colombia, Valle, West-Cordillera near Cali, *Lehmann 3762* (B, holotype no longer extant; K, lectotype selected herein; BM, LE, US, isotypes).]

Stems usually hirsute to villous, the length of the trichomes often exceeding 2 mm. Upper leaf surface hispid, rarely nearly velutinous. Partial florescences pedunculate, of 2 to 4 flowers, rarely epedunculate. Calyx lobes 6–25 mm long, corolla broadly tubular to tubular, tube 20–35 mm long, throat 9–21 mm wide, not constricted, limb 12–32 mm wide, lobes 5–15 mm long and 5–12 mm wide at base.

DISTRIBUTION.—The variety occurs on the western slopes of the Andes in northern Ecuador and in Colombia in the Central and Western Cordilleras northward to Dept. Risaralda (Figure 28). Var. *inaequalis* is only common between 1000 and 2000 meters, but ranges from the lowland to 2500 meters (Figure 21).

SELECTED COLLECTIONS.—COLOMBIA: CAUCA: Popayán, *Agredo 130* (COL, F, US); Río Pulacé, *Lehmann 1236* (F, GH, K, NY); Gorgona Island, road to Playa Gorgonilla, *Guzano & Rangel 5280* (COL). HUILA: Popayán-La Plata road, Santa Leticia, *García-Barriga & Hawkes 12870* (COL(2), US); Guadalupe-Florencia road, pass by Resinas, *Vogel 205* (US). NARIÑO: Near Ricaurte, *Alston 8425* (BM, F, S, US); road from Chucunes to Reserva La Planada, km 6, *Londoño 239* (AAU, COL, NY, TULV, US). RISARALDA: La Selva, *Sneidern 5263* (AAU, COL, F, MO, US(2)). VALLE: Valley of Río Digua, La Elsa, *Cuatrecasas 15301* (AAU, F(3), US); Cali-Buenaventura road, km 51, *Londoño & Kvist 190* (AAU(3), COL, QCA, NY, TULV, US, VEN, USM).

ECUADOR: CARCHI: Maldonado, *Balslev 1939* (AAU, NY, QCA, US); Chical W of Maldonado, *Kvist et al., 48619* (AAU, QCA, QCNE, US). ESMERALDAS: Lita, *Játiva & Epling 844* (AAU, BM, MO, NY, UC(2), US). IMBABURA: El Achiotal, *Acosta-Solis 12345* (F). Total of 114 collections seen.

NOMENCLATURE AND TYPIFICATION.—*Gesneria inaequalis:* Bentham (1876) noted that *Gesneria inaequalis* belonged to *Isoloma*, but he never made a new combination.

7b. *Kohleria inaequalis* var. *lindenii* (Hanstein) Kvist & L. Skog, new status

Figure 25c,d (flowers)

Calycostemma lindenii Hanstein, 1859:516, 557; *Kohleria lindenii* (Hanstein) Hanstein, 1865:441. [Type: Colombia, Tolima, Mariquita, *Linden 955* (W, holotype; BM, GH, K, LE, P(2), W, isotypes).]

Synepileana granatensis Baillon, 1888a:725. [Type: Colombia, Tolima, Mariquita *Linden 955* (P, holotype; BM, GH, K, LE, P, W(2), isotypes).]

Stems villous, trichomes up to 1.5 mm long. Upper leaf surface usually puberulous, rarely hispid. Partial florescences of single axillary, epedunculate flowers. Calyx lobes (5–) 7–12 mm long; corolla narrowly tubular to tubular, often subconstricted, tube (25–) 30–50 mm long, throat 6–12 mm wide, limb 10–25 mm wide, lobes 4–8 mm long and 3–8 mm wide at base.

DISTRIBUTION.—The variety has mainly been collected on the western slopes of the Western Cordillera in Dept. Chocó and Antioquia (the most pure-breeding populations), and on the eastern slopes of the Central Cordillera in Dept. Tolima and Antioquia (Figure 28). The few collections from the Cauca valley are difficult to set apart from var. *inaequalis*. The altitude ranges from 400 to 2100 meters.

OTHER COLLECTIONS.—COLOMBIA: ANTIOQUIA: W of Argelia, *Core 803* (US); trail from Encarnación to Parque Nacional de los Orchideas, *Gentry & Rentería 24579* (COL, MO, US); Santa Rita de Ituango, *White s.n.* (K). CHOCÓ: Río Ingará, between La Italia and Conrundó, *Forero et al. 2138* (MO, US); San José de Palmar, valley of Río Torito (tributary of Río Hábita), *Forero et al. 6807* (COL, US); *Forero et al. 7204* (COL); *Forero et al. 7556* (COL); Ansermanuevo-San José de Palmar road, *Luzano C. 3226* (COL). RISARALDA: Pueblo Rico, *Sneidern 5470* (F). TOLIMA: Líbano, *Londoño & Kvist 68* (AAU, COL, QCA, TULV, US, USM, VEN). VALLE: NW of Darién, Río Bravo, *Robinson 84* (K, US). DEPARTMENT UNKNOWN: Road toward Quibdo, *White s.n.* (K). LOCALITY UNKNOWN: *White 13* (K). Total of 14 collections seen.

NOTES.—The collections by White are, unfortunately, rather poor, but have considerably larger limbs, and a pattern of purple and green on the lower leaf surfaces.

7c. *Kohleria inaequalis* var. *ocellata* (W.J. Hooker) Kvist & L. Skog, new status

Figures 7g,h (pollen), 25a (flower); W.J. Hooker, 1848, pl. 4359 (as 4357); Linden and André, 1873, pl. 152; Hoehne, 1970, pl. 179.

Achimenes ocellata W.J. Hooker, 1848, pl. 4359 [as 4357]; *Tydaea ocellata* (W.J. Hooker) Regel, 1851:894; *Tydaea ocellata* (W.J. Hooker) Regel var. *confluens* Regel, 1854b:74; *Isoloma ocellatum* (W.J. Hooker) Bentham ex Jackson, 1895:1238 (cf. Bentham, 1876:1002); *Kohleria ocellata* (W.J. Hooker) Fritsch, 1894:178; *Isoloma bogotense* Nicholson var. *ocellatum* (W.J. Hooker) Voss, 1894:793. [Type: Illustration by W.J. Hooker, 1848, pl. 4359 (as 4357), described and drawn from cultivated material, originally collected by Purdie at El Roble, Dept. Valle, Colombia.]

Tydaea ocellata (W.J. Hooker) Regel var. *picta* Regel, 1854b:74 [*Achimenes klotzschii* Warscewicz [sic] ex Regel, 1854b:74 (nom. nud. pro syn.)]. [Type: Described from material from cultivation, collected by Warszewicz in Colombia; Colombia, Dept. Quindio, Salento, Río Boquia, 1600–1900 m, 27 Jul 1922 *Killip & Hazen 8836* (US, neotype selected herein; GH, NY, isoneotypes).]

Tydaea pardina Linden & André, 1873:212. [Type: Illustration by Linden & André, 1873, pl. 152, described from cultivated material, originally collected by Roezl in Colombia.]

Kohleria scabrida Fritsch, 1913a:420. [Type: Colombia, Dept. Valle, El Roble, *Triana 2531* (W, lectotype selected herein; G, K, MANCH, P, isolectotypes).]

Kohleria kalbreyeri Fritsch, 1916:33. [Type: Colombia, Dept. Antioquia, San José, *Kalbreyer 1506* (B, holotype not longer extant; K, lectotype selected herein).]

Stems sericeous to villous, length of trichomes not exceeding 1 mm. The upper leaf surface hispid. Partial florescences pedunculate, usually of 4 flowers. Calyx lobes 3–6 mm long; corolla broadly tubular, tube 12–15 mm long, throat 5–9 mm wide, not constricted, limb 9–12 mm wide, lobes 2–4 mm long and 3–5 mm wide at base.

DISTRIBUTION.—The variety occurs in Colombia in the Río Cauca valley from Armenia in the south to Medellín in the north (Figure 28). The collections come from the eastern slopes of the valley, except for the southernmost collection from Dept. Valle. The altitude ranges from 1600 to 2300 meters.

SELECTED COLLECTIONS.—COLOMBIA: ANTIOQUIA: Road between Medellín and El Retiro, Las Palmas, *Barkley et al. 64* (AAU, US); Río Medellín, below Alto de Morrogil, *Juncosa 1971* (US). CALDAS: Manizales, road to Neira, *Cerón 159* (FAUC, US), Manizales, Monteléon, *Fraume et al. 201* (FAUC, US). QUINDIO: Boquia, *Holton 608* (K, US). RISARALDA: Pereira, *Tomas 2447* (US). VALLE: El Roble, *Purdie s.n.* (K(4)); close to El Roble, *Triana 2523* (G); *Triana 2532* (NY); *Triana 4166* (BM(2)). Total of 25 collections seen.

NOMENCLATURE AND TYPIFICATION.—*Achimenes ocellata:* Bentham (1876) treated *Achimenes ocellata* in *Isoloma* but he never made a new combination. Hooker (1848) reported incorrectly that Seemann collected this species in Panama. *Kohleria inaequalis* does not occur in Panama, and var. *ocellata* does not occur along the Pacific coast of Colombia, but only in the Río Cauca valley from where Purdie sent seeds to Hooker.

Tydaea ocellata var. *picta:* The brief description of the small corollas by Regel (1854b) demonstrates that the species can only belong to *Kohleria inaequalis* var. *ocellata*. The neotype was selected according to this criterion.

Kohleria scabrida: Fritsch (1913a) did not select a type, but cited both Triana (*2531*), herein selected to represent the name, and Triana (*2523*), a syntype currently represented at G and W (and by a fragment at F).

8. *Kohleria longicalyx* Kvist & L. Skog, new species

Figures 12f (flower), 13d (capsule dehiscence); Hoehne, 1970, pl. 171 (as *Kohleria ferruginea*).

Differt a *Kohleria inaequalis* (Bentham) Wiehler corollis glabris intus, foliorum paginis superioribus velutinis, a *K. grandiflora* Kvist & L. Skog lobis calycum lanceolatis, inflorescentiis partialibus 2-3-floribus.

Herbs or subshrubs, scaly rhizomes not observed, stolons present; stems erect, rarely branched, villous, with yellow-brown, 6–10 mm long trichomes, 50–150 cm long, basal diameter 5–8 mm. Leaves opposite, internodes 4–8 cm long; the blades ovate, 8–20 × 5–12 cm, above appressed pubescent, below pilose, light green to purplish, veins below villous, yellow; petioles 6–12 cm long. Florescences frondose, partial florescences with 2–3 flowers; peduncles 3–8 cm long, pedicels 2–6 cm long, villous, bracts lanceolate to subulate, up to 20 mm long. Floral tube villous; calyx 24–40 mm long, lobes erect, free nearly to the base, lanceolate, basally 2–3 mm wide, ampliate above to 6–15 mm, sericeous to villous on both sides, with 5 prominent veins; corolla 45–60 mm long, tubular, tube 40–50 mm long, diameter 5–6 mm at base and 12–17 mm at throat, outside villous, red, ventrally yellow-red, inside glabrous, yellow with purple dots, the base saccate, yellow, limb 23–35 mm wide, lobes 8–12 mm long and 10–14 mm wide at base, inside glabrous, yellow with purple-dotted lines and red margin; filaments 30–35 mm long, apically with a few trichomes, anthers ~2.5 × 2.0 mm, subincluded; nectary of 5 free glands, each ~2.5 mm tall and 1.5 mm wide at base; ovary inferior, villous, 6–8 mm long, diameter 4–5 mm, style 40–50 mm long, pilose and glandular-hairy, stigma subincluded. Capsule oblong, 28–32 mm long, diameter 8–12 mm, dehiscing by a single slit from apex to base; seeds subglobose, irregularly striate, ~0.4 × 0.3 mm.

TYPE.—COLOMBIA: CAQUETA: Florencia-Guadalupe road, km 26, 750 m, 2 Feb 1987, *Londoño & Kvist 153* (COL, holotype; AAU, QCA, TULV, US, isotypes).

DISTRIBUTION.—Plants of *Kohleria longicalyx* are found on the eastern slopes of the Andes in the Colombian Dept. Caquetá (Figure 20). The few collections come from near the Guadalupe-Florencia road, and from altitudes between 500 and 1200 meters (Figure 21).

OTHER COLLECTIONS.—COLOMBIA: CAQUETA: Sucre, *Cuatrecasas 9100* (CM, COL, F, US); Florencia-Guadalupe road, km 23, *Davidse et al. 5763* (COL, MO, US); Florencia-Guadalupe road, km 21, *Luteyn 4943* (COL). Total of 4 collections seen.

DISTINGUISHING FEATURES.—*Kohleria longicalyx* differs from *K. grandiflora* mainly by having lanceolate instead of rotundate to spathulate calyx lobes (Figures 12f,13d), and from *K. inaequalis* mainly by having corollas that are glabrous inside (see "Discussion" under *K. grandiflora* and *K. inaequalis*).

HABITAT.—*Kohleria longicalyx* occurs in humid forest understory, often in ravines along streams. Occasionally some plants were seen in direct sun on roadsides, but only shaded plants seem to flower (*Londoño & Kvist 153*).

PHENOLOGY.—The few collections were seen flowering during the first four months of the year.

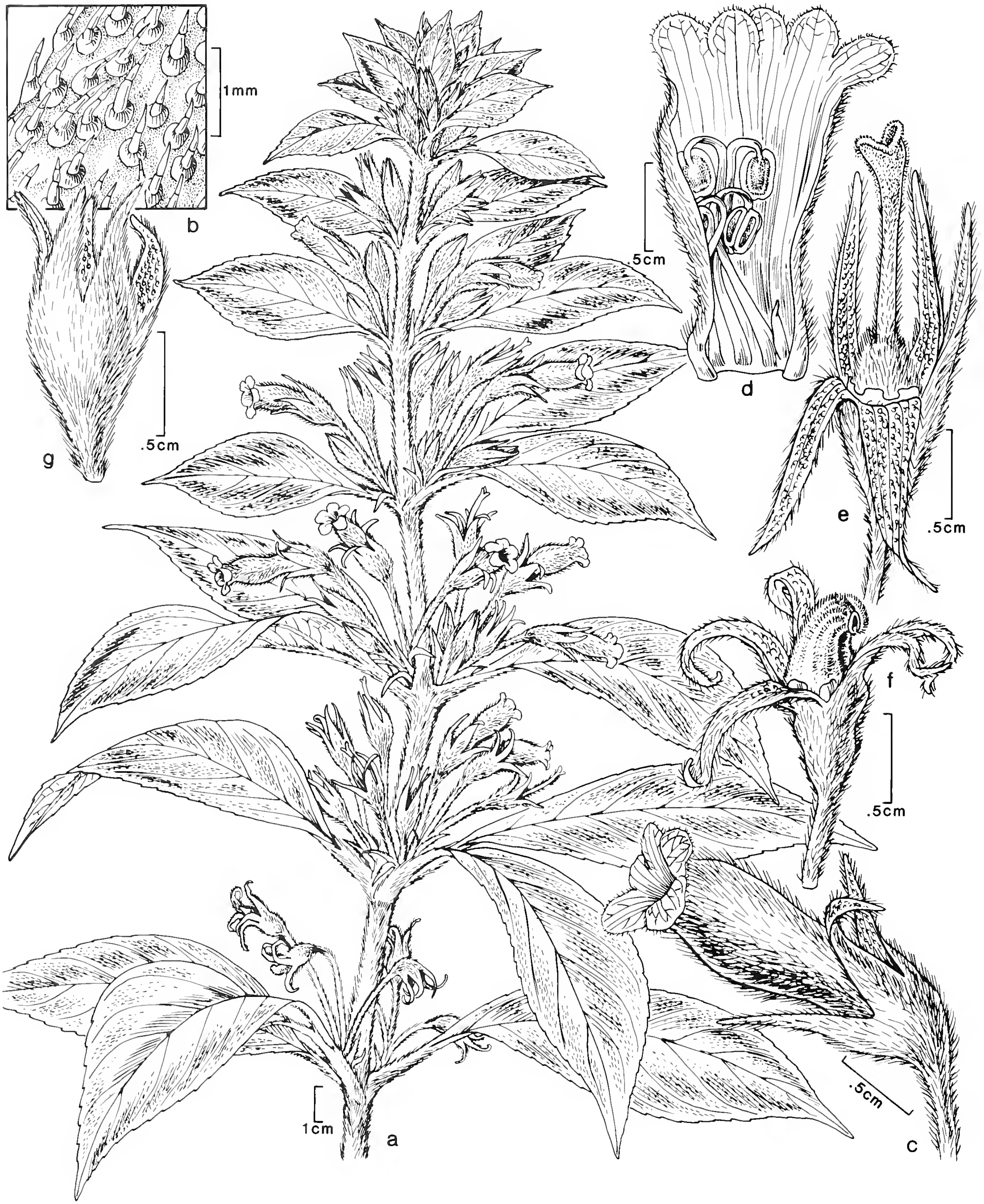


FIGURE 32.—*Kohleria neglecta*, new species: a, habit and inflorescences; b, calyx and calyx lobe indument of the inner side; c, flower; d, laterally opened corolla showing the androecium; e, calyx and gynoecium; f, capsule. All from *Uribe 3155* (US).

9. *Kohleria neglecta* Kvist & L. Skog, new species

Figures 5a (seed), 7i-k (pollen), 32 (habit and floral features).

Differt a *Kohleria spicata* (Kunth) Oersted et *K. tubiflora* (Cavanilles) Hanstein lobis calycum subulatis multo longioribus.

Herbs or shrubs, often epilithic, scaly rhizomes absent or weakly developed, stolons present; stems erect, often branching, sericeous to villous, 50–150 cm long, basal diameter 5–15 mm. Leaves 3 at a node, internodes 2–8 cm long; the blades lanceolate, 5–15 × 1.0–3.5 cm, above hispid, below tomentose, veins below sericeous; petioles 1–3 cm long. Florescences frondose, partial florescences of 5–6 (–10) flowers; pedicels 0.8–3.0 cm, villous to sericeous, yellow-green, bracts subulate, 5–20 × 1–3 mm. Floral tube sericeous; calyx 9–14 mm long, lobes erect, subulate, 8–11 mm long and 1–2 mm wide at base, outside sericeous, inside hispid; corolla 14–18 mm long, narrowly tubular to tubular, subventricose, tube 13–17 mm long, diameter 2.5–3.5 mm at base, above widened to 3–5 mm, diameter 3–4 mm at throat, outside sericeous, orange-red, inside glabrous, yellow, the base dorsally weakly gibbous, limb 5–7 mm wide, lobes 2–3 mm long and 2–3 mm wide at base, inside glabrous, dorsal lobes reddish, lateral and ventral lobes yellow with red dots; filaments 13–16 mm long, glabrous, anthers ~2.5 × 1.8 mm, included; nectary of 5 free glands, each ~0.8 mm high and 1.2 mm wide at base, rarely a 5-lobed ring; ovary half-inferior, 6–7 mm long, diameter 4–5 mm, style 9–11 mm long, pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 8–9 mm long, diameter 4–5 mm, bivalved; seeds narrowly ellipsoid, longitudinally striate, ~0.5 × 0.15 mm.

TYPE.—COLOMBIA: CUNDINAMARCA: Sasaima, towards Villeta, 900 m, 16 May 1958, *Uribe 3155* (COL, holotype; US, isotype).

DISTRIBUTION.—The few collections come from a small area in Dept. Cundinamarca west and northwest of Bogotá (Figure 19); the altitude ranges from 900 to 1600 meters (Figure 21).

OTHER COLLECTIONS.—COLOMBIA: CUNDINAMARCA: Sasaima-Villeta road, km 4, banks of Río Dulce, *Barclay 3675* (COL, US); Sasaima-Villeta road, Santa Cruz bridge across Río Dulce, *Dumont & Idrobo 36* (G); Pacho-Río Negro road, *García-Barriga 10737* (COL, US); La Palma, road to Pacho, Río Murca, *García-Barriga 12421* (COL, US); Villeta-Guaduas road, *Humbert 27121* (COL); Villeta-Guaduas road, close to Alto de Trigo, *Londoño & Kvist 79* (AAU, COL); Villeta, between town and Río Dulce, *Lozano C. & Torres C. 211* (AAU, COL); Villeta, Alto del Trigo, canyons close to the road, *Uribe 3706* (F, NY), *Uribe 3707* (COL). Total of 10 collections seen.

DISTINGUISHING FEATURES.—*Kohleria neglecta* is vegetatively similar to, although often more sturdy and fruticose than *K. spicata* and *K. tubiflora;* it differs from both by having longer subulate calyx lobes instead of triangular to ovate lobes. The corollas are rather similar to those of *K. spicata*, but differ by having a smaller limb and by being subventricose. In addition, the average pedicel length is considerably longer. The partial florescences of *K. neglecta* produce a higher average number of flowers (~6) than any other *Kohleria* species.

HABITAT.—*Kohleria neglecta* has been collected from slopes of canyons, river banks, and roadsides.

PHENOLOGY.—The species has been collected with flowers during much of the year, although no plants were seen flowering in late January, 1987 (*Londoño & Kvist 79*).

NOTES.—Scaly rhizomes are usually absent, but sometimes weakly developed, while the roots are stout and deeply rooted (*Londoño & Kvist 79*).

10. *Kohleria peruviana* Fritsch

Figures 6a (seed), 33 (habit and floral features).

Kohleria peruviana Fritsch, 1913a:421. [Type: Peru, Junín, Prov. Tarma, La Merced, *Weberbauer 1869* (B, no longer extant); Peru, Junín, near La Merced, E of Quimiri Bridge, 800–1300 m, Jun 1929, *Killip & Smith 23936* (US, neotype selected herein; NY, isoneotype).]

Kohleria peruviana Fritsch var. *pallida* Fritsch, 1913a:422. [Type: Peru, Junín, Prov. Tarma, Huacapistana, 1600–1800 m, *Weberbauer 2328* (B, no longer extant); Peru, Junín, Prov. Tarma, Utcayacu, 1800 m, 22 Feb 1948, *Woytkowski 35366* (US, neotype selected herein; F, MO, UC, isoneotypes).]

Herbs to subshrubs, often with scaly rhizomes, stolons not observed; stems erect, rarely branching, lanate, (40–) 60–120 (–200) cm long, basal diameter 5–12 mm; internodes 1–9 cm long. Leaves opposite; the blades elliptic to obovate, (5–) 8–18 (–25) × (2.5–) 4–8 (–12) cm, above pubescent, below tomentose, yellow-green to gray or whitish, veins below lanate, yellow-green; petioles (0.5–) 1.5–3.0 (–4.5) cm long. Florescences frondose, partial florescences in most cases pedunculate with 1–4 (–10) flowers; peduncles (0–) 2–5 cm long, pedicels (0.5–) 2.5–4.0 (–7.0) cm long, villous to lanate, yellow-green, bracts lanceolate, 2–10 × 1–3 mm. Floral tube lanate; calyx 10–15 mm long, lobes erect, lanceolate, rarely ovate, 5–12 mm long and 1–4 mm wide at base, outside villous to sericeous, inside appressed pubescent; corolla 35–52 mm long, tubular, tube 28–45 mm long, diameter 4–5 mm at base and 8–17 mm at throat, outside sericeous, orange-red or yellow, inside glabrous, cream to yellow, the saccate base sharply delimited, yellow, limb 15–25 mm wide, dorsal lobes 4–5 mm long and 5–6 mm wide at base, lateral and ventral lobes 7–8 mm long and 6–8 mm wide at base, inside sparsely appressed glandular-hairy, cream to yellow, with red dots; filaments 28–35 mm long, glabrous, anthers ~3.5 × 2.0 mm, subincluded; nectary often of 5 free glands, each ~2 mm high and 1.5 mm wide at base, less commonly a 5-lobed ring; ovary half-inferior, 5–7 mm long, diameter 2–4 mm, style 25–32 mm, pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 12–18 mm long, diameter 6–12 mm, bivalved; seeds ellipsoid, longitudinally striate, ~0.5 × 0.2 mm. Chromosome number $n = 13$ (Wiehler, 1972).

DISTRIBUTION.—*Kohleria peruviana* is endemic to Peru (Figure 17). Most collections come from Dept. San Martín in northern Peru and from Dept. Junín in central Peru, while the species is absent from the intervening Dept. Huánuco. In

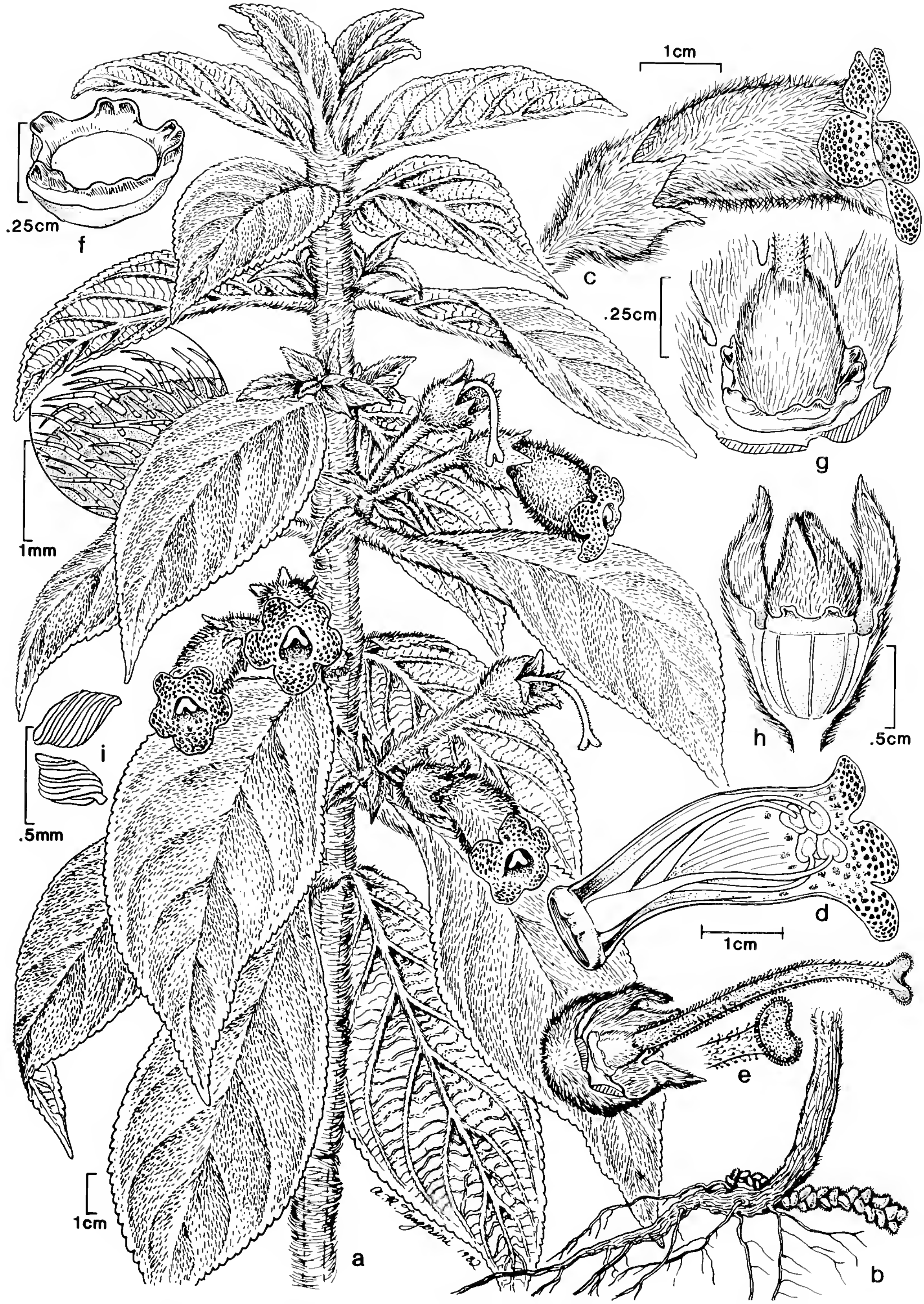


FIGURE 33.—*Kohleria peruviana*: a, habit; b, stem base with roots and scaly rhizome; c, flower; d, laterally opened corolla showing androecium; e, calyx and gynoecium; f, nectary; g, ovary and nectary; h, capsule; i, seeds. All from *Skog et al. 5003* (US).

addition, two apparently isolated collections from unusually low altitudes come from Depts. Loreto (*Williams 7768*) and Madre de Díos (*Foster 5759*). *Kohleria peruviana* occurs from (300–) 800 to 1700 (–2300) meters altitude.

SELECTED COLLECTIONS.—PERU: AYACUCHO: Between Huanta and Río Apurimac, Carrapa, *Killip & Smith 22454* (NY, US). JUNÍN: Between Tarma and San Ramón, Huacapistana, *Ferreyra 410* (US, USM); 8 km S of Vitoc, Río Tulumayo, Chilpes, *Gentry et al. 40166* (MO, US); La Merced, *Killip & Smith 23544* (NY, US); San Ramón, *Petersen & Hjerting 1325A* (C); Utcuyacu, *Woytkowski 35366* (F, MO, UC, US). LORETO: San Roque, *Williams 7768* (F). MADRE DE DÍOS: Parque Nacional de Manu, Río Manu, Cocha Cashu Station, *Foster 5759* (F). PASCO: N of Puente Paucartambo, *Gentry et al. 39848* (MO, US). SAN MARTÍN: Tarapoto-Yurimaguas road, km 12, *Rimachi Y. 3882* (F, MO, NY(2), US); road from Caserio de Santa Rosa to Mishollo, 4 km from Puerto Pizana, *Schunke V. 4915* (COL, F(2), G, GH, K, MO, NY, P, US). Total of 45 collections seen.

DISTINGUISHING FEATURES.—*Kohleria peruviana* may easily be confused with *K. hirsuta*, especially with the variety *longipes*. In contrast to *K. peruviana*, shoots of *K. hirsuta* var. *longipes* are usually branched and often scandent. In addition, the sharply delimited saccate base of the corolla, the larger leaves, and the whitish tomentose lower leaf surface and stems distinguish *K. peruviana* (Figure 33).

HABITAT.—*Kohleria peruviana* occurs on rocky slopes along rivers, roads, etc.

PHENOLOGY.—The species flowers during the first eight months of the year.

NOMENCLATURE AND TYPIFICATION.—*Kohleria peruviana* var. *pallida:* Fritsch (1913a) distinguished the variety *pallida* from the typical variety solely on its paler yellowish instead of red corollas. This difference also exists between the neotypes selected herein. Both the type and the neotype of var. *peruviana* come from about 1000 meters altitude, while the type and the neotype of var. *pallida* come from about 1800 meters.

NOTES.—About two-thirds of the collections have pedunculate partial florescences, and the epedunculate plants come mainly from Dept. San Martín. Otherwise the Junín and San Martín populations are similar.

Kohleria peruviana is closely related to *K. hirsuta*, and could possibly be reduced to a subspecies of this variable species. The possibility that *K. peruviana* and *K. hirsuta* var. *longipes* have diverged from a common ancestor was discussed above (see "Intraspecific Hybridization" section).

11. *Kohleria rugata* (Scheidweiler) Kvist & L. Skog, new combination

Figures 71,m (pollen), 12e,d (flower); Lemaire, 1861, pl. 287.

Gesneria rugata Scheidweiler, 1847:226 ("Gesnera"). [Type: Described from cultivated material, originally collected by Ghiesbreght in Guerrero (?), Mexico; Mexico, Guerrero, cutover hillside with limestone outcrops at km 338 beyond Acahuizotla on highway to Acapulco, 1000 m, 20 Aug 1948, *Moore & Wood 4685* (US, neotype selected herein; BH, MEXU, GH, isoneotypes).]

Gesneria maculata Mociño & Sessé ex A.P. de Candolle, 1839:532 [not *Kohleria maculata* C. Morton, 1938:1180]. [Type: Icon. fl. Mex. ined., pl. 721 (G); an original duplicate in the Torner Coll., Acc. No. 6331.242 (Hunt Institute for Botanical Documentation).]

Kohleria lanata Lemaire, 1861, pl. 287. [Type: Illustration in Lemaire, 1861, pl. 287, described from cultivated material, originally collected by Ghiesbreght in Guerrero (?), Mexico.]

Gesneria maculata Sessé & Mociño, 1889:97 [not *Kohleria maculata* C. Morton, 1938:1180, illegitimate name]. [Type: Mexico, Guerrero (?), *Royal Botanical Expedition (Sessé & Mociño) 2435* (MA, lectotype).]

Herbs, often epilithic, with scaly rhizomes and occasionally with stolons; stems decumbent, rarely branching, villous to basally pilose, (5–) 10–30 (–50) cm long, basal diameter 2.0–3.5 mm. Leaves opposite, rarely ternate, internodes 1–9 cm long; the blades ovate, 2–8 (–22) × 1–5 (–8) cm, above appressed pilose, less commonly villous or tomentose, below pilose to villous or tomentose, veins below pilose to villous, less commonly sericeous; petioles 1–3 cm long. Florescences frondose with 1–6 (–12) flowers, partial florescences with single flowers; pedicels 2–20 cm long, villous, yellow-green, bracts absent. Floral tube villous; calyx 4–8 mm long, lobes often reflexed, ovate with acute apex, 4–6 mm long and 2–4 mm wide at base, both sides sericeous; corolla 18–32 mm long, broadly tubular, tube 16–28 mm long, diameter 3–4 mm at base and 7–15 mm at throat, outside sericeous, orange-red or pink, inside glabrous, yellow, mottled with rose dots or blotches, limb 11–20 mm wide, lobes 3–8 mm long and 4–8 mm wide at base, inside sparsely glandular-hairy, yellow with red dots; filaments 15–20 mm long, glabrous, anthers ~2.2 × 1.5 mm, included; nectary of 5 free glands, each ~1.2 mm long and 0.8 mm wide at base, less commonly a 5-lobed ring; ovary half-inferior, 4–6 mm long, diameter 2–3 mm, style 12–15 mm long, pilose and glandular-hairy, stigma included. Capsule ovoid, 8–11 mm long, diameter 5–7 mm, bivalved; seeds narrowly ellipsoid to ellipsoid, longitudinally to transversely striate, ~0.6 × 0.3 mm. Chromosome number $n = 13$ (Wiehler, 1975, 1976a).

DISTRIBUTION.—*Kohleria rugata* is only known from the states of Chiapas and Guerrero of southern Mexico, with most collections from the former state. The species is absent from the intervening state of Oaxaca and thus occurs in two disjunct populations (Figure 18). *Kohleria rugata* ranges from 600 to 1500 meters altitude.

SELECTED COLLECTIONS.—MEXICO: CHIAPAS: Highway 190, El Chorreadoro 8 km E of Chiapas de Corzo, *Breedlove 11885* (F, US); 22 km N of Tuxtla Gutierrez, El Sumidora, *Breedlove 14687* (F, US); 15 km NW of Suchiapa along road to Villa Flores, *Breedlove 28259* (MEXU (2), MO); Tonala, *Nelson 2890* (GH, US); N of Arriaga on highway 195, *Roe et al. 851* (WIS(2)); Chorreadero, *Ton 2934* (F, US). GUERRERO: 2 km from Petaquillas on road to Colotlipa, *Moore & Bunting 8827* (BH, GH, MEXU, US); S of Chilpancingo, *Paxson et al. 17M785* (BH, BM, MEXU, NY, US). Total of 27 collections seen.

DISTINGUISHING FEATURES.—*Kohleria rugata* is at least superficially similar to *K. amabilis* (Figure 12a–d; see the latter species).

HABITAT.—*Kohleria rugata* occurs mainly in calcareous areas, possibly the original habitat, but also on rocky roadsides.

PHENOLOGY.—The flowering of *Kohleria rugata* seems to be restricted to a shorter period than that of any other *Kohleria* species, viz., August to November (Figure 9). During the dry months of the year *Kohleria rugata* probably survives as dormant rhizomes. The species is difficult to cultivate, because it demands a longer dormancy period than most *Kohleria* species (Batcheller, 1978, and pers. obs.).

NOMENCLATURE AND TYPIFICATION.—*Gesneria rugata:* Scheidweiler (1847) described this species on material collected by Ghiesbreght in Mexico in 1844. Later Lemaire (1861) described *Kohleria lanata* from cultivated plants probably derived from the same Ghiesbreght collection.

Gesneria maculata: A specimen at MA of *Kohleria rugata* and collected by the Sessé and Mociño expedition is herein selected as the lectotype because it closely resembles the description of the species and the illustrations (Fl. Mex. Ic. 330 [*Icones florae mexicanae ineditae*, pl. 721 in G and Torner coll. acc. no. 6331.242 in Hunt Institute for Botanical Documentation both labeled "Gesneria maculata Sp. N."]) cited by Sessé and Mociño, 1889.

Kohleria lanata: See *Gesneria rugata*.

NOTES.—*Kohleria rugata* shows a considerable variation in the length of the corolla tube and the size of the limb. The large-flowered specimens have longer florescences, while the small-flowered specimens have only a few flowers in apical leaf axils. The specimens from the state of Guerrero are all large-flowered, while both forms and intergradations occur in the state of Chiapas. For this reason, no varieties are established. Apparently both Ghiesbreght and the Sessé and Mociño expedition collected large-flowered plants in Guerrero.

Scheidweiler (1847) described and Lemaire (1861) illustrated the nectary of *K. rugata* as a five-lobed ring (Figure 10a), but the flowers we have examined have a nectary of five free glands (Figure 10b).

12. *Kohleria spicata* (Kunth) Oersted

Figures 6b (seed), 12e (flower); Kunth, 1818, pl. 188; Lindley, 1842, pl. 40; W.J. Hooker, 1845, pl. 4152; W.J. Hooker, 1850, pl. 4504; Regel, 1852a, pl. 1; Hanstein, 1854, pl. 1: fig. 18; Regel, 1854e, pl. 103; Oersted, 1858, pl. 4: figs. 25–29; Fritsch, 1894, pl. 77: fig. K; Hoehne, 1970, pl. 181; Skog, 1979, fig. 22.

Kohleria spicata (Kunth) Oersted, 1858:27; *Gesneria spicata* Kunth, 1818: qto. ed. 393, fol. ed. 316; *Isoloma spicatum* (Kunth) Decaisne, 1848a:465. [Type: Colombia, Tolima, close to Ibague, *Bonpland 1815* (P, holotype; P(3), isotypes).]

Gesneria spicata Kunth var. *schiedeana* A.P. de Candolle, 1839:531; *Gesneria schiedeana* (A.P. de Candolle) W.J. Hooker, 1845, pl. 4152; *Kohleria schiedeana* (A.P. de Candolle) Hanstein, 1859:518, 561; *Isoloma schiedeanum* (A.P. de Candolle) Hemsley, 1882:479. [Type: Mexico, Veracruz, Hacienda de la Laguna, *Schiede 185* (presumed to be at B, no longer extant); Mexico, Chiapas, near Tumbala, 1300–1800 m, 20 Oct 1895, *Nelson 3367* (US, neotype selected herein; GH, isoneotype).]

Gesneria longifolia Lindley, 1841: misc. 92 ("Gesnera"); *Isoloma longifolium* (Lindley) Decaisne, 1848a:465; *Brachyloma longifolium* (Lindley) Oersted, 1858:30; *Kohleria longifolia* (Lindley) Hanstein, 1859:524, 565. [Type: Described from cultivated material, originally collected by Hartweg in Guatemala; later clonal material of the Hartweg collection (K, neotype selected herein).]

Gesneria petiolaris Bentham, 1845a:131; *Isoloma petiolare* (Bentham) Decaisne, 1848a:465; *Brachyloma petiolare* (Bentham) Oersted, 1858:30; *Kohleria petiolaris* (Bentham) Hanstein, 1865:442; *Kohleria longifolia* (Lindley) Hanstein var. *petiolaris* (Bentham) C. Morton, 1938:1180. [Type: Panama or Costa Rica, "Veragua, island along the coast," *Sinclair s.n.*(K, holotype).]

Gesneria ignorata Kunth in Kunth & Bouché, 1848:13 [*Gesneria mollis* Hortorum ex Kunth in Kunth & Bouché, 1848:14 (nom. nud. pro syn.)]; *Kohleria ignorata* (Kunth) Regel, 1851:893; *Isoloma ignoratum* (Kunth) Hemsley, 1882:478. [Type: Illustration in Regel, 1852a, pl. 1, described from cultivated material, originally probably collected by Warszewicz in Central America.]

Gesneria linkiana Kunth & Bouché, 1848:13; *Kohleria linkiana* (Kunth & Bouché) Hanstein, 1854:160, 213; *Isoloma linkianum* (Kunth & Bouché) Hemsley, 1882:478. [Type: Described from cultivated material, originally collected by Warszewicz in Guatemala; Guatemala, Izabal, 2000 m, 25 Feb 1908, *Kellerman 7358* (US, neotype selected herein).]

Gesneria breviflora Lindley, 1848:165 ("Gesnera"); *Isoloma breviflorum* (Lindley) Lindley, 1850:63. [Type: Described from cultivated material, originally collected by Seemann in Panama (CGE, holotype).]

Gesneria seemannii W.J. Hooker, 1850, pl. 4504; *Kohleria seemannii* (W.J. Hooker) Hanstein, 1854:203; *Isoloma seemannii* (W.J. Hooker) Bentham, 1876:1002. [Type: Described from cultivated material, originally collected by Seemann in Panama (K, holotype).]

Kohleria wageneri Regel, 1853b [not seen]; 1854e:347; *Kohleria spicata* (Kunth) Oersted var. *wageneri* (Regel) Fritsch, 1913a: 417. [Type: Illustration in Regel, 1854e, pl. 103, described and drawn from cultivated material, originally collected by Wagener in Mérida, Venezuela.]

Isoloma kramerianum Lehmann, 1854:458 [*Gesneria mollis* Hortorum ex Lehmann, 1854:459 (nom. nud. pro syn.)]; *Kohleria krameriana* (Lehmann) Hanstein, 1859:524, 566. [Type: Described from cultivated material, originally collected by Warszewicz in Central America; Guatemala, Alta Verapaz, Cacao, Finca Trece Aguas, 300–400 m, 30 Sep 1905, *Goll 25* (US, neotype selected herein).]

Kohleria tetragona Oersted, 1858:27; *Isoloma tetragonum* (Oersted) Hemsley, 1882:480. [Type: Costa Rica, Aguascaliente, *Oersted 9309* (C, holotype).]

Kohleria incana Klotzsch & Hanstein in Hanstein, 1859:522, 564; *Isoloma incanum* (Klotzsch & Hanstein) Hemsley, 1882:478. [Type: Costa Rica or Panama ("Veragua"), *Warszewicz 29* (B, no longer extant); Costa Rica, Prov. Cartago, Turrialba, 600 m, 10 Oct 1949, *León 1871* (US, neotype selected herein).]

Kohleria tomentosa Hanstein, 1859:522, 561. [Type: Colombia (?), *Warszewicz* (B, no longer extant); Colombia, Antioquia, Medellín, 1800 m, Aug 1945, *Medina s.n.* (US, neotype selected herein).]

Kohleria rupestris Seemann, 1871:611; *Isoloma rupestre* (Seemann) Hemsley, 1882:479. [Type: Nicaragua, Chontales, Chontales Mountains, *Seemann s.n.* (BM, holotype).]

Kohleria spicata Kunth var. *hispida* Fritsch, 1913a:417. [Type: Ecuador, *Sodiro 119/11* (B, no longer extant); Ecuador, Chimborazo, between Huigra and Naranjapata, 600–1200 m, 17 Jul 1923, *Hitchcock 20648* (US, neotype selected herein; GH, NY, isoneotypes).]

Kohleria chiapensis T.S. Brandegee, 1914:66. [Type: Mexico, Chiapas, Finca Mexiquito, *Purpus 7049* (UC, holotype; BM, F, GH, MO, NY, US, isotypes).]

Herbs or subshrubs, often epilithic and with scaly rhizomes and stolons; stems erect, rarely branched, basally pilose to sericeous or villous toward the apex, (20–) 50–100 (–200) cm long, basal diameter 4–7 (–10) mm. Leaves ternate, less commonly opposite or whorled (4 leaves at nodes), internodes

2–8 cm long; the blades elliptic to lanceolate, (3-) 5–10 (-15) × 2.0–4.5 (-6.5) cm, above hispid, rarely velutinous or nearly glabrous, below tomentose, less commonly pubescent, veins below sericeous to villous, yellow-green; petioles 0.5–3.0 cm long. Florescences frondo-bracteose, partial florescences with 1–3 (-6) flowers, epedunculate but occasionally with a 1–3 mm long peduncle, subtending leaves toward the apex reduced to sessile ovate to lanceolate prophylls; pedicels 3–30 mm long, sericeous to villous, yellow-green to purple, bracts scaly, caducous. Floral tube sericeous to villous; calyx 4–8 mm long, lobes erect, 1.5–3.0 mm long and 2–3 mm wide at base, ovate to triangular, outside sericeous, inside appressed pubescent; corolla 12–20 mm long, tubular, tube 10–18 mm long, diameter 2–3 mm at base and 5–7 mm at throat, outside sericeous, red, inside glabrous, yellow-red, limb 5–8 mm wide, lobes 2–3 mm long and 2–3 mm wide at base, inside glabrous, yellow-red, with darker red to purplish dots, partly arranged in lines; filaments 10–15 mm long, glabrous, anthers 1.5–2.5 × 1.2–1.7 mm, included; nectary of 5 free glands, each ~1.2 mm high and 0.8 mm wide at base; ovary half-inferior, 5–6 mm long, diameter 3–4 mm, style 7–12 mm long, pubescent and usually glandular-hairy, stigma included. Capsule ovoid, 7–10 mm long, diameter 4–6 mm, bivalved; seeds ellipsoid to narrowly ellipsoid, longitudinally striate, ~0.50 × 0.15 mm. Chromosome number $n = 13$ (Davidse, 1970; Rogers, 1954; Wiehler, 1975).

DISTRIBUTION.—*Kohleria spicata* ranges from southern Mexico to northern Peru (only one collection) and east to northwestern Venezuela (Figure 15). The species is common throughout its range, but is especially abundant in Guatemala, Costa Rica, and western Colombia. In Colombia the species is absent from the eastern slopes of the Eastern Cordillera where *K. stuebeliana* occurs (Figure 21), in contrast to Ecuador where *K. spicata* occurs along the eastern foothills of the Andes. *Kohleria spicata* is the most frequently collected species of New World Gesneriaceae.

Kohleria spicata is found from sea-level up to 2500 meters altitude, but is most common between 1000 and 2000 meters. In Colombia, the species mainly occurs above 1000 meters, and lower altitude collections come from the Pacific coast (Figure 21). In Central America and Ecuador *K. spicata* often occurs down to sea-level.

An ecotype of *Kohleria spicata* has adapted to salt-influenced coastal rocks, occurring on the Pacific coasts of Costa Rica and Panama and the Cocos Island in the Pacific Ocean about 500 km southwest of Costa Rica (Figure 34). The label from one of the Cocos Island collections relates that "these plants are extremely rare, and are found on cliff faces on the northwestern shores" (*Gómez 3296*).

SELECTED COLLECTIONS.—MEXICO: CHIAPAS: Near Tumbala, *Nelson 3367* (GH, US). OAXACA: Between Puerto Eligio and Comaltepec, *Calderón 369* (F, GH, US). VERACRUZ: Mirador, *Liebman 9300* (AAU, C(2), GH, US).

BELIZE: TOLEDO: Lower part of Maye mountains, Richardson Creek, *Davidse & Brant 31928* (US).

GUATEMALA: ALTO VERAPAZ: Cobán, *von Tuerckheim 1083* (ECON, F, G(2), GH, LE, MO, NY, US(2)). PETEN: Road to Poptún, km 67, *Ortíz 1662* (BM, F, MO, S). QUEZALTENANGO: Finca Helvetia, *Skutch 1374* (GH, US).

EL SALVADOR: SAN SALVADOR: Vicinity of San Salvador, *Standley 19166* (GH, NY, US).

HONDURAS: EL PARAÍSO: Near Yuscarán, *Williams & Molina R. 11201* (F, GH, MO, UC). SANTA BARBARA: Río Sisicapa, *Molina R. 13456* (BM, F, GH, MO, US).

NICARAGUA: CHONTALES: Santo Domingo, *Narvaez S. 3374* (BM, GH, MO, UC, US). GRANADA: W slope of Mumbacho Volcán, *Stevens & Krukoff 4342* (BM, MO, US). MATAGALPA: 10 km E of Matagalpa, *Williams & Molina 42558* (BM, F, US).

COSTA RICA: ALAJUELA: 7 km S of Villa Quesada, *Molina R. et al. 17481* (F, GH(2), NY, US). CARTAGO: 3 km SE of Turrialba, *Holm & Iltis 67* (BM, G, MO, US). SAN JOSÉ: Vicinity of El General, *Skutch 2899* (GH, MO, NY, S, US).

PANAMA: CHIRIQUÍ: 4 km NW of Boquete, *Skog 4013* (AAU, MO, US). COCLÉ: 3 km from El Valle on road to La Mesa, *Croat 13315* (F, MO, NY).

COLOMBIA: ANTIOQUIA: Dabeiba, *Barkley & Gutiérrez V. 1794* (BM, NY, S, UC(2)). HUILA: Guadalupe-Florencia road, km 14, *Londoño & Kvist 98* (AAU, COL, QCA, TULV, US). MAGDALENA: Santa Marta, Manganares, *Smith 2604* (F, GH, K, NY). TOLIMA: W of Santa Isabel, *Londoño & Kvist 60* (AAU, COL, TULV, US). VALLE: Old Cali-Buenaventura road, km 51, *Londoño & Kvist 179* (AAU, COL, QCA, TULV, US).

ECUADOR: MORONA-SANTIAGO: Macas, *Kvist 60449* (AAU, QCA, QCNE, US). PASTAZA: Puyo-Tena road, Santa Clara, *Kvist et al. 60350* (AAU, NY, QCA, QCNE, US). PICHINCHA: Santo Domingo-Quito road, km 45, *Holm-Nielsen et al. 7185* (AAU, F, NY, MO, S, US). TUNGURAHUA: E of Baños, *Kvist 60311* (AAU, NY, QCA, QCNE, US).

PERU: CAJAMARCA: Río Tabaconas valley, *Weberbauer 6263* (F).

VENEZUELA: MÉRIDA: Tabay, *Gehriger 356* (F, MO, NY, US). Total of 762 collections seen.

DISTINGUISHING FEATURES.—*Kohleria spicata* is easily distinguished from all other species except for the local *K. stuebeliana* (Figure 35; see discussion under *K. stuebeliana* for differences) by its frondose-bracteose florescences (Figure 3c), the small tubular flowers (Figure 12e), the ovate to triangular calyx lobes (Figure 12e), and the usually ternate and hispid leaves. Vegetative plants are nearly impossible to distinguish from those of *K. tubiflora* or the rare and local *K. neglecta* (Figures 19, 32).

HABITAT.—*Kohleria spicata* occurs in exposed places of canyons, river banks, coastal cliffs, and roadsides. The disturbances caused by man promote the continued dispersal of this rather weedy species; e.g., in the Ecuadorian Amazon region, *K. spicata* colonizes along new roads into deforested areas (*Kvist et al. 60350*). Plants on coastal rocks occur in an

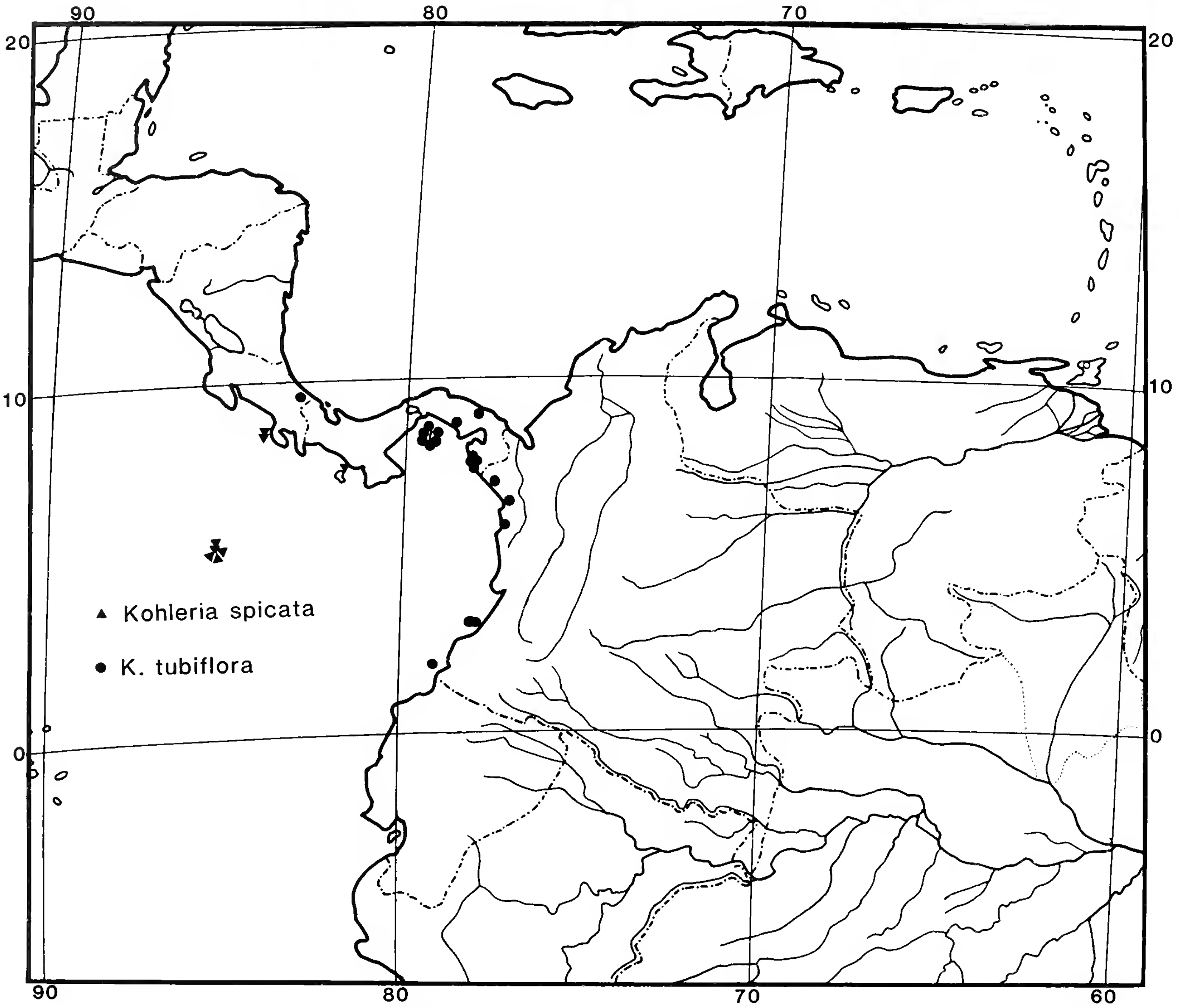


FIGURE 34.—Distributions of *Kohleria spicata* and *K. tubiflora* salt-influenced ecotypes from coastal cliffs (the entire distributions of the two species appear in Figures 13 and 14, respectively). Note the occurrence of *K. spicata* on Cocos Island.

especially harsh environment.

PHENOLOGY.—Based on data from herbarium sheets *Kohleria spicata* flowers with almost constant intensity throughout the year. However, field observations show that the intensity actually is reduced during dry periods, but there were always some flowers found.

NOMENCLATURE AND TYPIFICATION.—*Gesneria spicata:* An unusual nomenclatural problem results from the Oersted transfer of *Gesneria spicata* to *Kohleria* in 1858. In the section above, "Taxonomic History," we discussed that Regel in 1851 established a second illegitimate *Kohleria* with *K. ignorata* (currently a synonym of *K. spicata*) as type species. Although Oersted did not specifically state that he was transferring *K. spicata* to the second *Kohleria* genus, he made this transfer in practice. In the same work, Oersted accepted the genus *Isoloma* and included the type species of the legitimate *Kohleria, K. hirsuta.* However, according to the discussion by Nicolson (1975) and the response by Price (1976) on pseudo-isonymy, the transfer of *K. spicata* made by Oersted is available.

Gesneria spicata var. *schiedeana:* A.P. de Candolle (1839) only gave the Mexican type locality but no collector's name. However, the short description shows the variety to be a synonym of *K. spicata* rather than the other Mexican species *K. rugata*. According to Hanstein (1859) there was a Schiede collection from this locality (later destroyed in Berlin). No duplicates of this collection have been traced.

Gesneria petiolaris: The typification of the species by Bentham (1845a) is problematic due to fact that he gave neither collectors' names nor collection numbers but only type localities. In the case of *G. petiolaris* the description reads "island off the coast of Veragua," which is identical to data given on the label of a Sinclair collection assumed to be the type. The label of a Barclay collection at MANCH reads Atacamas (Veragua), but the specimen is not considered to be type material. The species was described from plants belonging to the coastal cliffs ecotype.

Gesneria longifolia: Lindley originally described the species in 1841, illustrated the species in 1842, but the type specimen came from cultivation in 1843, and is consequently at most a neotype of possibly clonal material.

Gesneria ignorata: This species, like *Gesneria linkiana* and *Isoloma kramerianum*, was apparently described from live material introduced by Warszewicz from Central America, while *Kohleria incana* and *K. tomentosa* were based on original herbarium specimens of the same Warszewicz collections. Kunth and Bouché (1848) did not credit Warszewicz as the collector of *Gesneria ignorata*. However, the material on which *G. ignorata* was based had previously been cultivated under the name *G. mollis*. According to Lehmann (1854), the material cultivated under this latter name was collected by Warszewicz in Central America. Regel (1852a) apparently illustrated *Kohleria ignorata* from clonal material of the Warszewicz collections.

Gesneria linkiana: Kunth & Bouché (1848) credited Warszewicz for having collected the species in Guatemala. Hanstein (1854:160) wrote that *Gesneria linkiana* belonged to *Kohleria*, but the combination *K. linkiana* only appears in the legend to his plate 1 (p. 213).

Gesneria breviflora: According to Lindley (1850) both this species and *G. seemannii* were based on material from the same Seemann collection "Veragua" (Panama or Costa Rica).

Gesneria seemannii: See *Gesneria breviflora*.

Isoloma kramerianum: See *Gesneria ignorata*.

Kohleria rupestris: According to Hemsley (1882) the type of this species was located at K, but only a specimen from BM has been located. Apparently Hemsley erred, as the first set of Seemann's collections was deposited at BM.

Kohleria spicata var. *hispida:* Judged from the description no major differences exist between the variety *hispida* and the typical variety; most *K. hirsuta* specimens have hispid or scabrous leaves.

NOTES.—*Kohleria spicata* is surprisingly uniform throughout its range, but lowland collections often have less hispid or even velutinous upper leaf surfaces. The plants from salt-influenced rocky cliffs have more succulent leaves with nearly glabrous upper surfaces. The coastal ecotype of *K. tubiflora* has similar leaf characteristics.

Hybrids with *Kohleria inaequalis* are discussed above (see "Interspecific Hybridization" section; Figure 25b). *Kohleria spicata* is sympatric with many other *Kohleria* species (Figure 21), but the limited variation in *K. spicata* indicates that hybrids with other species are rare.

The scaly rhizomes of *Kohleria spicata* have medicinal uses (see "Popular Names and Medicinal Uses" section above).

13. *Kohleria stuebeliana* Fritsch

Figures 7n-p (pollen), 35 (habit and floral features).

Kohleria stuebeliana Fritsch, 1913a:417. [Type: Colombia, Meta, Los Llanos de San Martín, Toquisa, *Stübel 178f* (B, holotype no longer extant); Colombia, Meta, Sabanas de San Juan de Arama, left bank of Río Güejar, "los Micos," 500 m, Dec 1950, *Idrobo & Schultes 562* (GH, neotype selected herein; COL(2), US, isoneotypes).]

Herbs, often epilithic, often with scaly rhizomes and stolons; stems decumbent to erect, rarely branching, sericeous to villous, (3-) 20–50 (-70) cm long, basal diameter 2–4 mm. Leaves opposite, less commonly ternate, internodes (1.0-) 1.5–5.0 (-10) cm long; the blades elliptic to lanceolate, 5–8 × 1.0–2.5 cm, above velutinous, below pilose, veins below sericeous, green to reddish; petioles 0.3–1.5 (-4.0) cm long. Florescences frondo-bracteose, partial florescences with 1–2 (-4) flowers, subtending leaves toward the apex reduced to subsessile lanceolate to ovate prophylls; pedicels 7–12 mm long, sericeous to villous, green to purple, bracts scale-like, caducous. Floral tube villous; calyx 3–6 mm long, lobes erect, ovate, 2.0–3.5 mm long and 1.5–2.0 mm wide at base, outside sericeous, inside pubescent; corolla 15–18 mm long, tubular, subventricose, tube 12–15 mm long, diameter 2–3 mm at base, above widened to 4–8 mm, diameter 4–6 mm at throat, outside villous, red, inside glabrous, sparsely glandular-hairy, yellow-red, the base dorsally gibbous, limb 6–10 mm wide, lobes 1.5–2.5 mm long and 2–3 mm wide at base, inside appressed pilose and glandular-hairy, yellow-green with numerous brown-black dots; filaments 12–15 mm long, glabrous, anthers ~1.4 × 1.0 mm, included; nectary of 5 free glands, each ~1 mm high and 0.8 mm wide at base; ovary half-inferior, 3–4 mm long, diameter 2–3 mm, style 7–10 mm, pilose and glandular-hairy, stigma included. Capsule ovoid, 6–8 mm long, diameter 4–5 mm, bivalved; seeds narrowly elliptic, longitudinally striate, ~0.50 × 0.15 mm.

DISTRIBUTION.—*Kohleria stuebeliana* is locally common in the region around Villavicencio, Dept. Meta, Colombia, and the adjacent areas of Depts. Cundinamarca and Boyacá (Figure 19). In addition, a single collection came from the western slopes of the Eastern Cordillera in Dept. Cundinamarca (*García-Barriga 10706*). *Kohleria stuebeliana* evidently is very rare on the western slopes as this region is botanically well explored; the species may have gotten there casually by

FIGURE 35.—*Kohleria stuebeliana*: a, habit and frondo-bracteose florescence; b, partial florescence with bud and flower; c, ventrally opened corolla showing androecium; d, calyx, nectary, and gynoecium; e, capsule. a,b,d,e, from *Idrobo & Schultes 562* (US); c, from *Fosberg 19468* (US).

wind-dispersal across the barrier of the mountains (the collection has not been added to Figure 21). *Kohleria stuebeliana* occurs on the Andean slopes and on the flat lowlands of Los Llanos, and has been collected from 300–1500 (-2500) meters altitude (Figure 21).

SELECTED COLLECTIONS.—COLOMBIA: BOYACÁ: Guateque-Santa María road, Piedra Campana, *García-Barriga 17231* (AAU, COL, NY, US); on border with the Dept. Casanare, Pajarito, *Uribe 4516* (COL, F, NY). CUNDINAMARCA: Villavicencio-Bogotá road, km 20, *Davidse & Llanos 5524* (COL, NY, US); between Pacho and Río Negro, *García-Barriga 10766* (COL, US); SW of Quetame, "Sucumuco," *Pennell 1357* (NY); *Pennell 1728* (GH, NY, US). META: Villavicencio, *Cuatrecasas 3511* (COL, F(2), US); Villavicencio, *Haught 2456* (AAU, BH, COL, NY, US). Total of 25 collections seen.

DISTINGUISHING FEATURES.—*Kohleria stuebeliana* is the closest relative of *K. spicata*, but the yellow-green, dark-dotted, appressed pilose and glandular-hairy limbs, the delicate, soft-velutinous leaves, and the slender shoots distinguish *K. stuebeliana* (Figure 35). Occasionally, tiny *K. stuebeliana* plants flower when only 3–5 cm tall (e.g., *Pennell 1357*), a condition never found in *K. spicata*.

HABITAT.—*Kohleria stuebeliana* grows in exposed places along rivers, roads, etc.

PHENOLOGY.—*Kohleria stuebeliana* flowers relatively constantly throughout the year, but less in the months April-July.

NOTES.—One specimen label states that the dark glands on the corolla lobes are sticky and trap small insects (*Uribe 4516*).

Kohleria stuebeliana apparently speciated from *K. spicata* when geographically isolated by the eastern Andean Cordillera. *Kohleria stuebeliana* could possibly be reduced to a subspecies of *K. spicata*, but is distinctive as a species.

14. *Kohleria trianae* (Regel) Hanstein

Figure 12i (flower); Kunth, 1818, pl. 192; Graham, 1840, pl. 3725; Regel, 1854c, pl. 82; Lemaire, 1855, pl. 57; Planchon, 1855b, pl. 1057; Hérincq, 1863, pl. 4.

Kohleria trianae (Regel) Hanstein, 1865:442; *Isoloma trianaei* [sic] Regel, 1854c:107; *Brachyloma trianae* (Regel) Hanstein 1859:532, 577. [Type: Illustration in Regel, 1854c, pl. 82, described and drawn from cultivated material, originally collected by Warszewicz in Colombia at St. Martha.]

Gesneria elongata Kunth, 1818: qto. ed. 396, fol. ed. 318 [not *Kohleria elongata* Regel, 1855a:4]; *Gesneria elongata* Humboldt in Maund, 1837, no. 27 [*Gesneria velutina* Willdenow ex A.P. de Candolle in A.P. de Candolle, 1839:528 (nom. nud. pro syn.)]; *Brachyloma elongatum* (Kunth) Hanstein, 1859:532; *Kohleria elongata* (Kunth) Hanstein, 1865:442. [Type: "Ecuador" (locality probably incorrect as plants only known from Colombia), *Bonpland s.n.* (P, holotype; B-W, P(2), isotypes).]

Gesneria elongata Kunth var. *fruticosa* Graham, 1840, pl. 3725 [not *Kohleria fruticosa* T.S. Brandegee, 1914:67; *Gesneria oblongata* Hortorum ex Graham, 1840, pl. 3725 (nom. nud. pro syn.)]. [Type: Illustration in Graham, 1840, pl. 3725, originally described from cultivated material.]

Gesneria trianaei Hérincq, 1863:30. [Type: Illustration in Hérincq, 1863, pl. 4, described from cultivated material, originally collected by Triana in Colombia.]

Herbs or shrubs, with stolons, scaly rhizomes occasionally present but weakly developed; stems erect, branching, sericeous, 50–150 (–250) cm long, basal diameter 4–10 (–15) mm. Leaves opposite; internodes 3–8 cm long; the blades ovate to lanceolate, 6–10 × 2–4 cm, above pilose, below tomentose, yellow-green, veins sericeous, often purplish; petioles 1.5–4.0 cm long. Florescences frondose, partial florescences of 4 flowers; peduncles 4–10 cm long, always longer than the 4–6 cm long pedicels, sericeous, purplish, bracts 2, lanceolate to ovate, 2–5 (–8) × 1–2 mm. Floral tube sericeous; calyx 3–5 mm long, lobes erect, triangular, 2.0–3.5 mm long and 2.0–3.5 mm wide at base, both sides sericeous; corolla 26–40 mm long, narrowly tubular, subventricose, tube 25–37 mm long, diameter 3–4 mm at base, above widened to 6–9 mm, diameter 3–5 mm at throat, outside villous, red, inside glabrous, yellow, limb 6–10 mm wide, lobes 3–4 mm long and 2–3 mm wide at base, inside sparsely pilose and glandular-hairy, appearing red, but actually yellow with numerous red dots; filaments 25–35 mm long, glabrous, anthers ~2.5 × 2.0 mm, subincluded; nectary of 5 free glands, each ~1 mm high and 1 mm wide at base; ovary half-inferior, 3–4 mm long, diameter 1.5–2.5 mm, style 20–33 mm long, glandular-hairy, stigma subincluded. Capsule ovoid, 9–14 mm long, diameter 5–8 mm, bivalved; seeds narrowly elliptic, longitudinally striate, ~0.5 × 0.2 mm.

DISTRIBUTION.—*Kohleria trianae* is endemic to the Central Cordillera in Colombia (Figures 21, 22). The species is known from the eastern slopes in Depts. Quindio, Risaralda, and Caldas and from the western slopes in Depts. Tolima and Antioquia, but is only common in Quindio and Tolima. In addition, a single old *K. trianae* collection came from Tequendama in Dept. Cundinamarca (*Holton 611A* (not shown in Figures 21, 22)). Numerous *K. hirsuta* var. *longipes* collections also come from Tequendama, and *K. trianae* possibly got there by wind-dispersal, and later disappeared due to hybridization with *K. hirsuta* (see "Interspecific Hybridization" section above).

Kohleria trianae has been collected from 900 to 2500 meters altitude (Figure 21), and is locally common between 1700 and 2100 meters (pers. obs.).

SELECTED COLLECTIONS.—COLOMBIA: ANTIOQUIA: San Felix, *Daniel 2327* (US). CALDAS: Manizales, *Yepes-Agredo 827* (COL). CUNDINAMARCA: Cataracts of Tequendama, *Holton 611A* (K). QUINDIO: Armenia-Cajamarca road, secondary road on the right toward Salento, *Londoño & Kvist 51* (AAU, COL, QCA, TULV, US, USM); Salento, *Pennell et al. 8750* (GH, K, NY, S, US). RISARALDA: Road to Herraduro, between El Cedral and Otún, *Salamarca 208* (COL). TOLIMA: Líbano-Murillo, km 16, Alto de Pones, *García-Barriga 12272* (COL(2), US); Trail Ibague-Salento, La Palmilla, *Hawkes 474* (BM, COL, K, US), *Hawkes 479* (COL, K); Cajamarca-Armenia road, before summit of divide, *Killip & Varela 34635* (BM, COL, GH, MO, US); Santa Isabel, *Londoño & Kvist 63* (AAU, COL, NY, QCA, TULV, US, USM, VEN). Total of 35 collections seen.

DISTINGUISHING FEATURES.—*Kohleria trianae* is easily recognized by its four-flowered, long-pedunculate florescences (Figure 3d) with entirely red, narrowly tubular, sub-ventricose flowers (Figure 12i). The species is vegetatively similar to, although often more fruticose than, *K. hirsuta* and *K. warszewiczii.*

HABITAT.—As the tallest and most fruticose species, *Kohleria trianae* thrives in denser and taller vegetation than any other species of *Kohleria.* In Dept. Quindio, the species was observed on steep slopes covered with low montane forest (*Londoño & Kvist 51*). *Kohleria trianae* also is common in hedges along roads and between fields (*Londoño & Kvist 51, 63*).

PHENOLOGY.—The species flowers relatively constantly throughout the year, but the flowering intensity seems reduced from mid-March until mid-June.

NOMENCLATURE AND TYPIFICATION.—*Gesneria trianaei:* Hérincq (1863) based *Gesneria trianaei* on plants introduced in cultivation by Triana, while Regel (1854c) based *Isoloma trianaei* on material brought into cultivation by Warszewicz. According to Regel, Warszewicz asked him to name the species after his friend Triana.

NOTES.—Many shoots of *Kohleria trianae* are strongly branched and certainly are several years old. However, even this fruticose species has shoots that die back after a single flowering. *Kohleria trianae* rarely possesses well-developed scaly rhizomes, but the roots are sturdy and deep-reaching (pers. obs.).

15. *Kohleria tubiflora* (Cavanilles) Hanstein

Figures 6c (seed), 12h (flower); Cavanilles, 1801, pl. 584; W.J. Hooker, 1846, pl. 4217; 1849, pl. 4431; Planchon, 1850, pl. 586; Raunkiaer, 1905:418; Regel, 1854a, pl. 74A,B; Oersted, 1858, pl: 4, figs. 9–24; Hoehne, 1970, pls. 163, 175, 180.

Kohleria tubiflora (Cavanilles) Hanstein, 1865:442; *Gesneria tubiflora* Cavanilles, 1801:61; *Isoloma tubiflorum* (Cavanilles) Decaisne, 1848a:465; *Brachyloma tubiflorum* (Cavanilles) Oersted, 1858:31. [Type: Panama, *Née s.n.* (MA, holotype, F (fragment).]

Gesneria incurva Bentham, 1845a:131; *Brachyloma incurvum* (Bentham) Oersted, 1858:31; *Isoloma incurvum* (Bentham) Hemsley, 1882:478. [Type: Colombia, Cauca, Gorgona Island, *Sinclair s.n.* (K, holotype; K, isotype).]

Gesneria rhynchocarpa Bentham, 1845a:131; *Isoloma rhynchocarpum* (Bentham) Decaisne, 1848a:465; *Brachyloma rhynchocarpum* (Bentham) Oersted, 1858:29; *Cryptoloma rhynchocarpum* (Bentham) Hanstein, 1859:538, 586. [Type: Panama, Darién, Isthmus of Darién, *Barclay s.n.* (K, holotype; MANCH, isotype).]

Gesneria hondensis sensu W.J. Hooker, 1846, pl. 4217 [not *Gesneria hondensis* Kunth; *Isoloma hondense* sensu Decaisne, 1848a:465 (excluding the type of *Gesneria hondensis* Kunth)]; *Isoloma hondense* var. *hookeri* Regel, 1854a:2; *Cryptoloma hookerianum* (Regel) Hanstein, 1859:536, 581; *Kohleria hookeri* (Regel) Hanstein, 1865:442. [Type: Illustration in W.J. Hooker, 1846, pl. 4217, described and drawn from cultivated material, originally collected by Purdie in Colombia).]

Gesneria picta W.J. Hooker, 1849, pl. 4431; *Isoloma pictum* (W.J. Hooker) Planchon, 1850:165; *Isoloma pictum* (W.J. Hooker) Regel, 1854d:110; *Brachyloma pictum* (W.J. Hooker) Oersted, 1858:29; *Cryptoloma pictum* (W.J. Hooker) Hanstein, 1859:536, 582; *Kohleria picta* (W.J. Hooker) Hanstein, 1865:442. [Type: Described from cultivated material, originally collected by Seemann in Colombia (or possibly in Panama) (K, holotype).]

Gesneria picta W.J. Hooker var. *minus-hirsuta* W.J. Hooker 1849, sub pl. 4431; *Isoloma pictum* (W.J. Hooker) Planchon var. *minus-hirsutum* (W.J. Hooker) Planchon, 1850:165. [Type: Described from cultivated material, originally collected by Lobb in Colombia; Colombia, *Lobb s.n.*, (K, neotype selected herein).]

Cryptoloma coloratum Hanstein, 1859:536, 583 [*Gesneria picta* Hortorum ex Hanstein, 1859:537, 583 (nom. nud. pro syn.)]; *Kohleria colorata* (Hanstein) Hanstein, 1865:442. [Type: Described from cultivated material, origin of original collection unknown; Panama, Canal Area, Ancón Hill, 100–200 m, 17 Oct 1922, *Killip 12065* (US, neotype selected herein).]

Isoloma hondense var. *uniflorum* Regel, 1852b:326; *Isoloma hondense* var. *wageneri* Regel, 1854a:2. [Type: Described from cultivated material, originally collected by Wagener in Colombia (or possibly by Warszewicz in Panama) (LE, neotype selected herein).]

Isoloma hondense var. *warszewiczii* Regel, 1854a:2. [Type: Described from cultivated material, originally collected by Warszewicz at Chagras, Panama; Panama, Canal Area, Balboa, 15 Sep 1936, *Melt 13* (US, neotype selected herein).]

Brachyloma pilosum Oersted, 1858:29; *Cryptoloma pilosum* (Oersted) Hanstein, 1859:538, 586; *Kohleria pilosa* (Oersted) Hanstein, 1865:442; *Isoloma pilosum* (Oersted) Hemsley, 1882:479. [Type: Costa Rica, Aguacate, *Oersted 9304* (C, holotype; C(2), US, isotypes).]

Brachyloma strictum Oersted, 1858:29; *Cryptoloma strictum* (Oersted) Hanstein, 1859:538, 585; *Kohleria stricta* (Oersted) Hanstein, 1865:442; *Isoloma strictum* (Oersted) Hemsley, 1882:479. [Type: Costa Rica, Aguacate, *Oersted 9308* (C, holotype; US, isotype).]

Cryptoloma anonymum Hanstein, 1859:536, 584; *Kohleria anonyma* (Hanstein) Hanstein, 1865:442. [Type: Described from cultivated material (LE, holotype).]

Cryptoloma cordifolium Hanstein, 1859:538; *Kohleria cordifolia* (Hanstein) Hanstein, 1865:442; *Isoloma cordifolium* (Hanstein) Hemsley, 1882:478. [Type: Costa Rica, *Hoffmann 672* (B, holotype no longer extant); Costa Rica, San José, Basin of El General, 700–950 m, Jul-Aug 1943, *Skutch & Barrantes 5152* (US, neotype selected herein; F, isoneotype).]

Herbs or subshrubs, occasionally epilithic, often with scaly rhizomes and stolons; stems decumbent to erect, occasionally pendent, branching rare, pilose, 20–200 cm long, basal diameter 2-7 mm. Leaves opposite, less commonly 3 at a node, internodes 2–7 cm long; the blades ovate to lanceolate or elliptic, (1.5-) 3-10 (-22) × (0.5-) 1.5-7 (-12) cm, above hispid to strigose, less commonly pilose, below pilose, occasionally purplish, veins below sericeous, yellow-green or purplish; petioles 1-6 cm long. Florescences frondose, partial florescences with 1-2 (-6) flowers; pedicels 1-3 cm long, pilose to villous, purplish, bracts usually present, scaly, caducous. Floral tube sericeous to villous; calyx 3-5 mm long, lobes erect, triangular to ovate, 2-4 mm long and 1.5-3.5 mm wide at base, outside sericeous to villous, inside appressed pubescent to sericeous; corolla 22-30 mm long, cylindric, subventricose, tube 20-28 mm long, diameter 3-5 mm at base, above widened to 6-10 mm, diameter 3-4 mm at throat, outside sericeous, inside glabrous, yellow to red, limb 3-5 mm wide, lobes 1.0-1.5 mm long and 1.5-2.5 mm wide at base, inside glabrous, yellow, with red to purplish dots; filaments 20-25 mm long, glabrous, anthers ~2.0 × 1.8 mm, included; nectary usually of 5 free glands, each ~1.2 mm tall and 1.0 mm wide at base, less commonly a 5-lobed ring; ovary half-inferior, 5-7 mm long, diameter 3-5 mm, style 18-25 mm, pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 10-12 mm long, diameter 6-7 mm, bivalved; seeds narrowly elliptic, longitudinally striate, ~0.50 × 0.15 mm. Chromosome number

$n = 13$ (Davidse, 1970, 1981; Lee, 1962; Wiehler, 1975).

DISTRIBUTION.—Plants of *Kohleria tubiflora* are found from Nicaragua to Colombia and east along the Caribbean coast through Venezuela to Trinidad (Figure 16). Isolated populations occur in the Colombian Amazon region in Serranía de la Macarena, an isolated mountain range in Dept. Meta close to the Eastern Andean Cordillera but geologically the extreme western part of the Roraima sandstone.

In Pacific Colombia, *Kohleria tubiflora* is apparently only represented by the ecotype restricted to coastal cliffs (Figures 16, 34). These plants are known from the Pacific coast of Panama south to Gorgona Island in the Dept. Cauca of Colombia. In addition, two collections come from the Caribbean coast from Prov. San Blas of Panama (*Garwood 1190*), and the Prov. Limones of Costa Rica (*Quirós 513*) (Figure 34). In western Costa Rica, adjacent Panama, and on Cocos Island the coastal ecotype of *K. spicata* apparently replaces that of *K. tubiflora* (Figure 34; see also "Discussion" under *K. spicata*).

Most *Kohleria tubiflora* collections come from near sea level (Figure 21), and the species is rarely collected above 1000 meters altitude. In Panama *K. tubiflora* is the most frequently collected of all Gesneriaceae (Skog, 1979).

SELECTED COLLECTIONS.—COLOMBIA: ANTIOQUIA: Cauca valley, 10 km N of Valdivia, *Gentry & Fallen 17946* (COL, MO, US). CAUCA: Gorgona Island, *Fernandez 418* (COL, US). CHOCÓ: W of Mutatá, Pavarandó Grande, *Gentry & León 20245* (AAU, COL, MO, US). CORDOBA: Río Uré, *Espina 660* (COL). MAGDALENA: Santa Marta, near Jiracasaea and Oñaca, *Smith 380* (BM, F, G(2), GH, MO, NY, UC, US, WIS). META: Río Mico, S of El Mico airstrip, *Philipson et al. 1348* (BM, COL, F, NY, US). NARIÑO: Isla de Gallos, *Dryander 2593* (US).

COSTA RICA: ALAJUELA: Close to Río Poás, *Brenes 17275* (F, NY). GUANACASTE: 33 km N of Cañas, *Frankie 266A* (F, MO). PUNTARENAS: 8 km NW of junction of Highway 17 (to Puntarenas) and Carretera Interamericana, *Davidse & Pohl 1321* (F, MO, US). SAN JOSÉ: 3 km from Rivas and 7 km from San Isidro del General, *Whitmore 80* (F, NY, MO).

NICARAGUA: RIVAS: 3 km NE of San Juan del Sur, La Cuesta, *Davidse & Pohl 2284* (MO(2), NY, US).

PANAMA: CANAL AREA: Barro Colorado Island, *Croat 4174* (F, MO, NY), *Croat 12441* (F, GH, MO(2)). CHIRIQUÍ: Cerro San Cristobal-David, *Caballero 4* (US). COCLÉ: Vicinity of El Valle, *Allen 743* (GH, MO, NY). COLÓN: Portobelo, *D'Arcy & D'Arcy 6687* (F, GH, MO, NY). DARIÉN: Vicinity of Santa Fé, Río Sabana, *Duke 4134* (GH, MO, US). LOS SANTOS: Headwaters of Río Pedregal, *Lewis 2909* (MO, UC). PANAMA: 3 km S of Accalda Diaz, Cerro Penon, *Nee 8598* (AAU, MO, US). SAN BLAS: Ustupo, *D'Arcy 9487* (MO, US). VERAGUAS: 3 km S of Cañitas, *D'Arcy 15153* (MO, US).

VENEZUELA: BARINAS: Baranitas-Apartaderos road, km 2, *Breteler 4198* (F, G, MO, NY, US). CARABOBO: Between Valencia and Yuma, *Alston 5667* (BM). LARA: NE of Barquisimeto, Guaremal River, *Meijer & Smith 65* (MO, SEL). PORTUGUESA: 30 km NNE of Guanare, NE of Boca de Monte, *Steyermark 127050* (US), *Steyermark 127073* (US). SUCRE: Sucre district, dam site on the Río Neverí, *Davidse & Gonzáles, 19038* (MO, NY, US). ZULIA: Valley of Río Guasara, *Bunting et al. 11970* (NY, US).

TRINIDAD: ST. ANN'S, Jades Amandes, *Broadway 7900* (BM, K, MO). Total of 260 collections seen.

DISTINGUISHING FEATURES.—The tubular ventricose flowers with a small limb and a narrow throat distinguish *Kohleria tubiflora* (Figure 12h) from all species except *K. hondensis* (Figure 12g). The latter species has lanceolate calyx lobes (see discussion under *K. hondensis*). *Kohleria tubiflora* and *K. spicata* are vegetatively almost indistinguishable.

HABITAT.—*Kohleria tubiflora* is a rather weedy species of disturbed, open habitats, e.g., along rivers, on coastal cliffs, and roadsides and other man-created disturbances. Johnston (1949) wrote about the coastal cliff ecotype on San José Island of the Pearl Archipelago in the Gulf of Panama: "Here it grows on the barren islets and exposed tops of large rocks along the shore."

PHENOLOGY.—According to Croat (1978) and observations on herbarium sheets, the species is strongly seasonal in Panama, flowering from September to January in the rainy season. In contrast, in Panama *Kohleria spicata* continues to flower during the dry season.

NOMENCLATURE AND TYPIFICATION.—*Gesneria incurva:* Bentham (1845a) described *Gesneria incurva* and *G. rhynchocarpa* from plants adapted to salt influence on coastal rocks.

Gesneria rhynchocarpa: Barclay, Hinds, and Sinclair all collected plants on the voyage of the H.M.S. *Sulphur.* The typification is problematic because Bentham (1845a) gave localities but neither collectors' names nor collection numbers. In the case of *Gesneria rhynchocarpa* the type locality was given as "Isthmus of Darien," and there exists one Barclay collection labeled with this locality at K. In addition, a specimen at MANCH apparently is a duplicate (here the label reads "Panama [Darien]"). The specimen at K is annotated as *Gesneria rhynchocarpa* var. *oppositifolia*, but no varieties have been published in *G. rhynchocarpa.* Two Sinclair specimens at K also annotated as *G. rhynchocarpa* come from the Pacific coast of Colombia. They have a ternate leaf arrangement in accordance with the description of *G. rhynchocarpa.* Thus, it appears that Bentham (1845a) originally intended to describe two *G. rhynchocarpa* varieties with opposite and ternate leaves, respectively, but ended with the specimen from Darien cited as the type, even though this collection has opposite leaves in conflict with the description.

Gesneria hondensis: W.J. Hooker (1846) assumed he was undertaking a more detailed description based on live material of *Gesneria hondensis* of Kunth (1818) (now *Kohleria hondensis*), but W.J. Hooker was actually describing material of *Kohleria tubiflora.*

Gesneria picta var. *minus-hirsuta:* W.J. Hooker (1849) described the variety from live material introduced by Lobb from Colombia, but no material called *G. picta* var. *minus-hirsuta* has been located. Consequently, the only Lobb collection of *K. tubiflora* seen from Colombia has been selected as neotype.

Cryptoloma coloratum: Hanstein (1859) described *C. coloratum* from cultivated material received from England. He suspected the species to be identical with W.J. Hooker's (1849) *Gesneria picta* var. *minus-hirsuta*. However, the description of the variety *minus-hirsuta* was brief and poor, and did not give sufficient evidence to conclude the two taxa to be identical. The description of *Cryptoloma coloratum* demonstrates that the species is a synonym of *Kohleria tubiflora*, and that the species apparently was based on material not particularly distinct from typical *K. tubiflora* plants.

Isoloma hondense var. *uniflorum:* Regel (1852b) mainly distinguished the variety by its single flowers in the leaf axils, in contrast to several axillary flowers in *Gesneria hondensis* sensu W.J. Hooker (1846). However, he soon realized that his variety occasionally would develop several axillary flowers, and for the same material he created the name var. *wageneri* (1854a). Regel named the plant after Wagener despite his mentioning both Wagener in Colombia and Warszewicz in Panama as possible collectors of the material on which he based var. *uniflora* (1852b). The neotype selected herein was annotated several years later with the name *Isoloma hondense* var. *wageneri* by Regel in St. Petersburg (formerly now Leningrad).

Isoloma hondense var. *warszewiczii:* The description by Regel (1854a) is brief. However, no major differences apparently exist between the variety *warszewiczii* and typical *K. tubiflora* specimens.

Cryptoloma cordifolium: The description indicates no major differences between *Cryptoloma cordifolium* and typical *Kohleria tubiflora* specimens. A similar Costa Rican neotype has been selected.

NOTES.—*Kohleria tubiflora* is stable in most characters throughout its range. The ecotype of salt-influenced rocky coasts differs from typical *K. tubiflora* plants by having more succulent and less hispid leaves.

Kohleria tubiflora hybridizes with *K. hirsuta* on Trinidad (see "Interspecific Hybridization" in section above).

16. *Kohleria villosa* (Fritsch) Wiehler

Kohleria villosa (Fritsch) Wiehler, 1978b:63.

Herbs, rarely subshrubs, scaly rhizomes not observed, stolons abundant; stems decumbent to erect, pilose to villous, erect part 8-35 (-100) cm long, basal diameter 1.5-4.5 mm; lateral branches rare. Leaves opposite, internodes 2-7 cm long; the blades ovate, less commonly lanceolate, 2-8 (-13) × 1-5 (-9) cm, above hispid, individual trichomes often located on small bullae, below pilose, usually purplish with a pattern of light green blotches, veins villous, yellow-green; petioles (0.3-) 1-3 (-5) cm long. Florescences frondose, partial florescences with 1 (-6) flower(s); pedicels 2-4 cm, villous, yellow-green to purple, bracts scale-like, caducous. Floral tube villous; calyx 4-6 mm long, lobes erect, ovate to lanceolate or spathulate, 3-4 mm long and 1-2 mm wide at base, outside pilose, inside basally glabrous to apically pilose; corolla 15-18 mm long, broadly tubular, less commonly merely tubular, medially often sharply arcuate downward $^1/_3$ of length from base, tube 12-15 mm long, diameter 2-3 mm at base and 7-10 mm at throat, outside sericeous or villous, dorsally deep red, ventrally yellow, inside pilose to villous but basally glabrous, glandular-hairy, yellow, ventrally with red spots, the base dorsally gibbous, limb 9-19 mm wide, inside glabrous, red, dorsal lobes 4-5 mm long and 4-5 mm wide at base, lateral and ventral lobes 3-5 mm long and 5-7 mm wide at base; filaments 8-11 mm long, basally glabrous, apically pilose to villous, anthers ~1.8 × 1.5 mm, included; nectary of 5 separate glands, each 2.0-2.5 mm high and 0.5-1.2 mm wide at base, rarely 3 free and 2 basally fused glands; ovary half-inferior, 3-4 mm long, diameter 1.5-2.5 mm, style 7-10 mm long, pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 6-8 mm long, diameter 3-5 mm, dehiscing apically into 2 valves (by 2 slits) and later opening by one of the slits continuing to the base; seeds sub-globose, irregularly striate, ~0.25 × 0.25 mm. Chromosome number $n = 13$ (Wiehler, 1975, as *K. platylomata*).

DISTRIBUTION.—*Kohleria villosa* is restricted to the western slopes of the Andes in Ecuador and Colombia (Figure 20), where it ranges from (500-) 900-2100 meters altitude (Figure 21). The variety *anisophylla* occurs at higher elevations than does var. *villosa*. When Fritsch (1913a) described *Diastema villosum* he cited a Sodiro collection *(119/7)* from Napo in eastern Ecuador. *Kohleria villosa* is otherwise unknown from the Eastern slopes of the Andes, and the specimen was probably misidentified. The collection was apparently destroyed at B.

DISTINGUISHING FEATURES.—The purple and green mottled lower leaf surfaces (not conspicuous in var. *anisophylla*), the epedunculate inflorescences, the uniformly red corolla lobes, the weakly bullate upper leaf surfaces (Figures 36b, 37b), the long and narrow nectary glands (Figures 36f, 37e), the globose seeds (Figure 6d) and the ovoid capsules (Figure 36g) that dehisce into 2 apical valves with one of the slits continuing to the base (Figure 13b), make *K. villosa* distinctive. The latter four characters are shared with the genus *Diastema*, to which *K. villosa* thus shows an affinity (see "Related Genera" section above).

HABITAT.—The species may require less light than any other *Kohleria* species. Flowering plants were seen in deeply shaded, very humid forest understory, e.g., along small streams, and below steep rocks (*Kvist et al. 60308*). However, the species also thrives and flowers in low vegetation exposed to the sun, at least in permanently humid montane forest regions (*Kvist et al. 60307*). Plants growing in shade are more robust and have darker leaves than sun-exposed plants.

PHENOLOGY.—The flowering intensity is relatively stable throughout the year (Figure 9).

NOTES.—Some specimens, especially from the area around

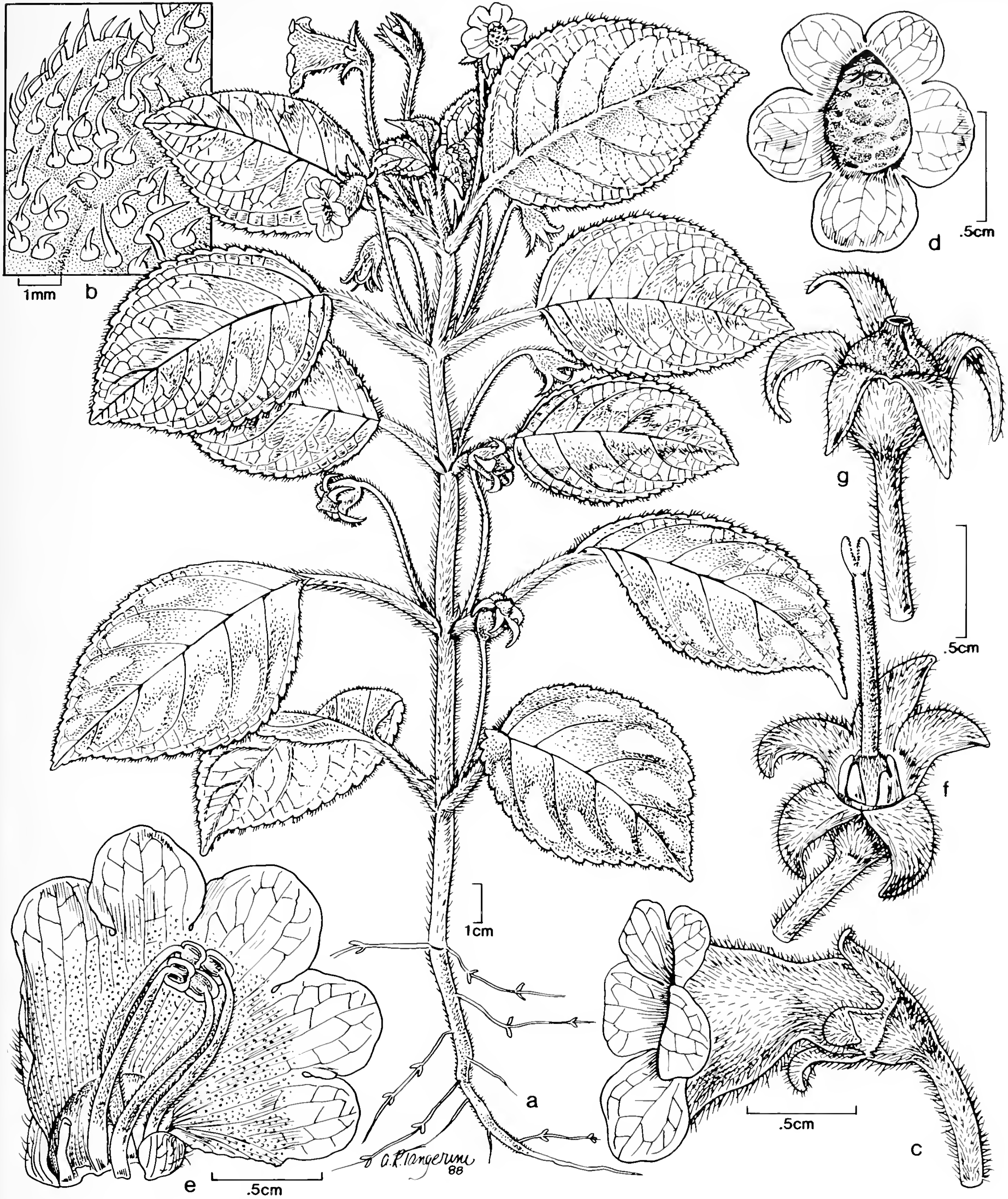


FIGURE 36.—*Kohleria villosa* var. *villosa;* a, habit and inflorescences; b, indument of upper leaf surface; c, flower; d, limb and throat; e, laterally opened corolla showing androecium; f, calyx, nectary, and gynoecium; g, capsule. a–f, from *Harling & Andersson 23222* (US); g, from *Holmgren 820* (S).

Nanegal in the Prov. Pichincha of Ecuador (e.g., *Harling & Andersson 11600*) have features intermediate between the two varieties. However, because var. *villosa* and var. *anisophylla* are usually easily distinguished (Figures 36, 37) and differ in geographical (Figure 20) and altitudinal ranges, we find taxonomic recognition justifiable.

16a. *Kohleria villosa* var. *villosa*

Figures 6d (seed), 7q (pollen), 36 (habit and floral features).

Kohleria villosa (Fritsch) Wiehler, 1978b:63; *Diastema villosum* Fritsch, 1913a:407. [Type: Ecuador, *Jameson s.n.* (W, lectotype selected herein; W, isolectotype (?)).]

Diastema platylomatum J.D. Smith, 1916:381; *Kohleria platylomata* (J.D. Smith) Wiehler, 1973:327. [Type: Ecuador, Pichincha, Río Pilatón, *Lehmann 409a* (US, lectotype selected herein; BM, LE, isolectotypes).]

Herbs up to 40 cm tall; leaves equal to subequal in pairs, blades ovate with acute apex, below usually conspicuously purplish with a pattern of light green blotches. Corolla broadly tubular, outside sericeous, sharply arcuate downward $^{1}/_{3}$ of length from base, limb 12–19 mm wide, lobes 3–5 mm long.

DISTRIBUTION.—*Kohleria villosa* var. *villosa* is restricted to the western slopes of the Andes in Ecuador (Figure 20), and ranges from 900–1600 meters altitude. The variety is locally common in Prov. Pichincha. A single collection from Esmeraldas province (*Balslev & Steere 1312*) apparently comes from much lower elevations; according to the label it came from 500 meters elevation, but the locality (located by coordinates given on the label) must be below 200 meters.

SELECTED COLLECTIONS.—ECUADOR: BOLIVAR: Tablas valley, Balsapamba, *Acosta-Solis 6157* (F). COTOPAXI: 2 km S of El Corazón, *Harling & Andersson 19193* (US). ESMERALDAS: 20 km SE of San Mateo, Zapallo, *Balslev & Steere 1312* (AAU, NY). PICHINCHA: Old Quito-Santo Domingo road, 3 km from bridge over Río Pilatón, *Harling & Andersson 23058* (GB, US); 1 km above Tandápi on Quito-Santo Domingo road, *Harling & Andersson 23222* (GB, US); Tandápi, *Holmgren 820* (S(2)); new Quito-Santo Domingo road, La Union del Toachí, *Kvist et al. 60307* (AAU, COL, NY, QCA, QCNE, US); *Kvist et al. 60308* (AAU, COL, NY, QCA, QCNE, US); SW of Chiriboga, *Ljtnant & Molau 15662* (AAU); 3 km from La Armenia, *Ilgaard et al. 37851* (AAU). Total of 38 collections seen.

NOMENCLATURE AND TYPIFICATION.—*Diastema villosum:* Fritsch (1913a) cited several collections but selected no type. Three Sodiro collections (119/2, 119/3, 119/7) were destroyed in Berlin, although (119/3) apparently is represented at BP and thus is a syntype. Another syntype at W is a Karsten collection.

Diastema platylomatum: J.D. Smith (1916) cited two Lehmann collections but selected no type. The syntype (*Lehmann 481a*) is represented in the same three herbaria as the lectotype (*Lehmann 409a*).

16b. *Kohleria villosa* var. *anisophylla* (Fritsch) Kvist & L. Skog, new status

Figure 37 (habit and floral features).

Diastema anisophyllum Fritsch, 1913a:408; *Kohleria anisophylla* (Fritsch) Wiehler, 1978b:62. [Type: Colombia, Nariño, W of Tuquerres, Piedra Ancha, *Lehmann 5843* (B, holotype not extant, K, lectotype selected herein; K, isolectotype).]

Nematanthus erianthus Bentham, 1846:231 [not *Kohleria eriantha* (Bentham) Hanstein, 1865:442]; *Columnea eriantha* (Bentham) Hanstein, 1865:391. [Type: Ecuador, Pichincha, Nanegal, *Hartweg s.n.* (K, holotype).]

Diastema anisophyllum Fritsch var. *quitense* Fritsch, 1913a:408. [Type: Ecuador, Pichincha, "Quito," *Jameson s.n.* (W, holotype).]

Herbs to subshrubs, up to 1 m tall; leaves unequal in pairs, blades ovate to lanceolate with acuminate apex, below not with a conspicuous purplish and green pattern. Corolla tubular, outside densely villous, not arcuate downward ventrally, limb 9–13 mm wide, lobes 2–3 mm long.

DISTRIBUTION.—*Kohleria villosa* var. *anisophylla* comes from the western slopes of the Andes in Provinces Pichincha and Carchi of Ecuador and Dept. Nariño of Colombia (Figure 20). The few collections come from altitudes between 1800 and 2100 meters.

OTHER COLLECTIONS.—COLOMBIA: NARIÑO: Near Chucunes, Finca La Planada, *Libenson et al. 30538* (COL, US); *Libenson et al. 30554* (COL, US); *Libenson et al. 30555* (COL).

ECUADOR: CARCHI: Toward Maldonado from Tulcán, 1800 m, *Luer et al. 2672* (SEL). PICHINCHA: Nanegal, *André K39* (K); Andes near Quito, *Couthouy s.n.* (GH); above Mindo, *Luer et al. 4744* (SEL); old Quito-Santo Domingo road, km 59, *Zak & Jaramillo 578* (MO, US). LOCALITY UNKNOWN: *Jameson 111* (BM, K). Total of 12 collections seen.

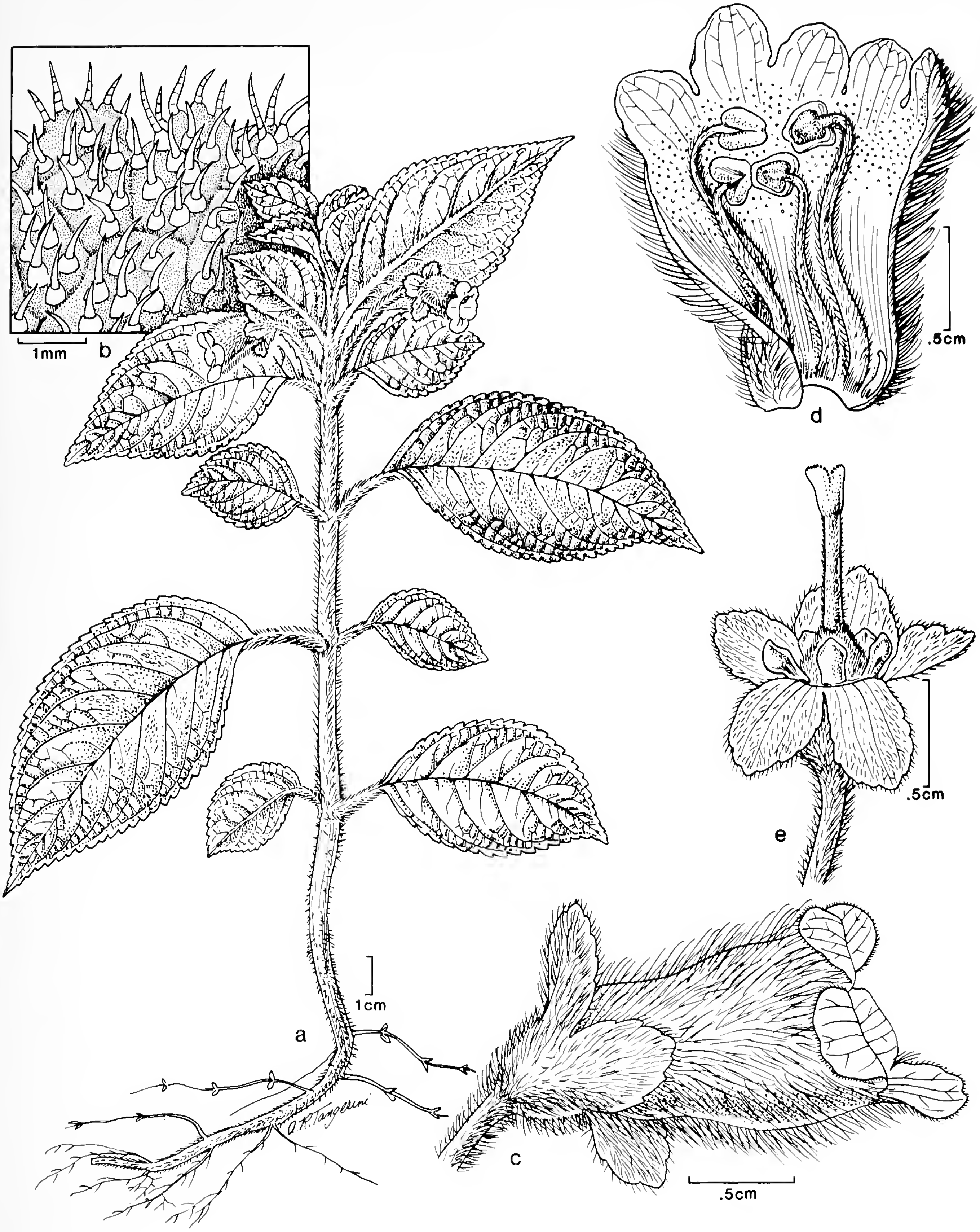
17. *Kohleria warszewiczii* (Regel) Hanstein

Figures 6e,f (seed and seed surface), 7r (pollen), 8c (seedling with scaly rhizome), 12j (flower); Regel, 1853a, pl. 61; Planchon, 1853, pl. 941; Linden and André, 1870, pl. 17; Fritsch, 1894, pl. 77: fig. J; Kvist, 1987:18 (photo).

Kohleria warszewiczii (Regel) Hanstein, 1865:441; *Sciadocalyx warszewiczii* Regel, 1853a:257; [*Gesneria regeliana* Warscewicz [sic] ex Planchon, 1853:213 (nom. nud. pro syn.)]; *Isoloma regelianum* Voss in Siebert & Voss, 1894:793 (nom. illeg., included *Sciadocalyx warscewiczii* [sic] Regel in synonymy); *Isoloma warszewiczii* (Regel) Bailey, 1917:3115. [Type: Illustration in Regel, 1853a, pl. 61, described and drawn from cultivated material, originally collected by Warszewicz in Colombia at St. Martha.]

Sciadocalyx digitaliflora Linden & André, 1870:95; *Isoloma digitaliflorum* (Linden & André) Voss in Siebert & Voss, 1894:793; *Kohleria digitaliflora* (Linden & André) Fritsch, 1894:178. [Type: Illustration in Linden and André, 1870, pl. 17, described and drawn from cultivated material, originally collected by Wallis in Antioquia, Colombia.]

FIGURE 37 (right).—*Kohleria villosa* var. *anisophylla;* a, habit and flowers; b, indument of upper leaf surface; c, flower; d, dorsally opened corolla showing androecium; e, calyx, nectary, and gynoecium. a,b, from *Libenson et al. 30554* (US); c,d,e, from *Libenson et al. 30538* (US).


b
1mm
d
.5cm
e
.5cm
1cm
a
D.R. Tangerini
c
.5cm

Kohleria violacea Fritsch, 1913a:414. [Type: Colombia, Cauca, Popayán, 1700-2500 m, *Lehmann 4495* (B, holotype not extant, K, lectotype selected herein; F, GH, US, isolectotypes).]

Herbs or shrubs, often epipetric, with scaly rhizomes and stolons; stems erect, occasionally decumbent, usually branching, villous, covered with violet trichomes, 30-200 cm long, basal diameter 4-15 mm. Leaves opposite, less commonly ternate or whorled (4 at each node), internodes (1.5-) 3-9 cm long; the blades elliptic to ovate, occasionally lanceolate, 7-20 × 2-9 cm, above pubescent to tomentose, below tomentose, less commonly villous or pilose, veins below villous, yellow-green, occasionally violet; petioles 0.5-3.0 cm. Florescences frondose, partial florescences with 3-6 (-10) flowers; peduncles (3-) 5-9 (-13) cm, pedicels 1-3 (-6) cm, yellow-green, villous, trichomes violet, bracts lanceolate to ovate, 5-10 × 2-3 mm, caducous. Floral tube tomentose; calyx 5-8 mm long, lobes often reflexed, triangular to rotundate, 5-6 mm long and 5-8 mm wide at base, outside villous, green suffused with red trichomes, inside sericeous; corolla (25-) 30-42 mm long, campanulate, subventricose, tube 22-40 mm long, diameter 4-6 mm at base, above widened to (6-) 9-12 (-16) mm, diameter 7-13 mm at throat, outside pilose to villous, lavender, ventrally lavender to cream, inside glabrous, lavender to cream, ventrally with purple dots, basally white, the limb 12-24 mm wide, lobes 5-7 mm long and 4-6 mm wide at base, inside sparsely glandular-hairy, yellow-green with numerous purple dots; filaments 25-40 mm, white, sparsely pubescent, anthers ~2.5 × 1.5 mm, subincluded; nectary often of 3 free and 2 dorsal basally united glands, each ~1 mm high and 1.5 mm wide at base, less commonly a 5-lobed ring; ovary 5-6 mm long, diameter 3-4 mm, style 24-32 mm, pilose and glandular-hairy, stigma subincluded. Capsule ovoid, 10-15 mm long, diameter 6-10 mm, bivalved; seeds elliptic, longitudinally to transversely striate, ~0.6 × 0.3 mm. Chromosome number $n = 13$ (Wiehler, 1975, as *K. digitaliflora*).

DISTRIBUTION.—*Kohleria warszewiczii* is widespread in the Colombian highlands (Figure 19). The species occurs in all three Cordilleras, but is apparently absent from the eastern slopes of the Eastern Cordillera (Figure 21). *Kohleria warszewiczii* ranges from 1300 to 2500 meters altitude, with a few collections from the Pacific lowlands of Dept. Cauca down to 300 meters altitude (Figure 21). The species is locally common between 1500 and 2100 meters altitude (pers. obs.).

SELECTED COLLECTIONS.—COLOMBIA: ANTIOQUIA: Medellín-Antioquia road, km 20, *Metcalfe 30033* (GH, MO, UC, US). CALDAS: Salamin, *Tomas 1919* (US). CAUCA: Tímbio, Hatoviejo, *Arbeláez & Cuatrecasas 6079* (COL, F, US); Popayán, *Lehmann 9092* (G(2), GH(2), K, NY). CUNDINAMARCA: Caqueza to Río Sananie, *Pennell 1337* (GH, MO, NY, US). HUILA: La Plata-Popayán road, km 25, *Londoño & Kvist 166* (AAU, COL, QCA, TULV, US, USM, VEN); km 42, *Londoño & Kvist 167* (AAU, COL, QCA, TULV, US). QUINDIO: Above Calarca, *Alston 7784* (BM, S, US). RISARALDA: Apia-Pueblo Rico road, km 32, *Luteyn et al. 7336* (COL, NY, SEL). TOLIMA: Below Santa Isabel, *Londoño & Kvist 62* (AAU(2), COL, NY, QCA, TULV, US, USM, VEN). VALLE: Río Cali, Pichindé, *Cuatrecasas 18231* (F(3), US). Total of 72 collections seen.

DISTINGUISHING FEATURES.—*Kohleria warszewiczii* is set apart by the long-pedunculate inflorescences of 3-6 (-10) flowers (Figure 3e,f), the tubular to campanulate corolla with a usually lavender tube and purple-dotted, yellow-green limbs and the rotundate, often reflexed calyx lobes (Figure 12j). *Kohleria trianae* and *K. hirsuta* are vegetatively similar. *Capanea affinis* has flowers similar to those of *Kohleria warszewiczii* but its habit is scandent. However, the latter two species frequently are confused in herbaria (see "Related Genera" in Introduction).

HABITAT.—*Kohleria warszewiczii* is found on exposed, often dry slopes along rivers, roads, etc. The species is light demanding, but can survive in fairly tall and dense vegetation due to its often fruticose habit.

PHENOLOGY.—The flowering intensity is greatest from March to September, but it is usually possible to find at least a few plants with flowers (Figure 9).

NOTES.—The coloration and the size of the corolla vary considerably. Small-flowered, epipetric *Kohleria warszewiczii* plants may look rather similar to *K. amabilis*. This is especially true in Dept. Cundinamarca where the two co-occur (Figures 19-21) and possibly hybridize. However, *K. amabilis* always differs from *K. warszewiczii* by having epedunculate inflorescences.

Appendix 1

List of Excluded Names

Isoloma bulbosum Baillon, 1888b, pls. 50, 51. [= *Sinningia* sp.]

Isoloma costaricense (Klotzsch ex Oersted) Hemsley, 1882:478. [= *Moussonia elegans* Decaisne, 1849:489]

Isoloma deppeanum (Schlechtendal & Chamisso) Hemsley, 1882:478. [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein 1865:284]

Isoloma elatior Decaisne, 1848a:465. [= *Sinningia incarnata* (Aublet) D. Denham, 1974:126]

Isoloma elegans (Decaisne) Hemsley, 1882:478. [= *Moussonia elegans* Decaisne, 1849:489]

Isoloma flexuosum Rusby, 1900:28. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Isoloma hahnii Hortorum ex Baillon, 1888a:719. [= *Moussonia* sp.]

Isoloma hypocyrtiflorum (W.J. Hooker) Bentham ex Jackson, 1895:1238 (cf. Bentham, 1876:1002). [= *Pearcea hypocyrtiflora* (W.J. Hooker) Regel, 1867:388]

Isoloma jaliscanum S. Watson, 1890:159. [= *Moussonia elegans* Decaisne, 1849:489]

Isoloma lasianthum (Zuccarini) Decaisne, 1848a:465. [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, 1865:284]

Isoloma lindenianum (Regel) Nicholson, 1885:201. [= *Gloxinia lindeniana* (Regel) Fritsch, 1913b:66]

Isoloma oblanceolatum J.D. Smith, 1916:383. [= *Capanea affinis* ("Campanea") Fritsch, 1913a:434]

Isoloma parviflorum Rusby, 1896:97. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Isoloma patentipilosum O. Kuntze, 1898:242. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Isoloma purpureum (Poeppig) Bentham, 1876:1002. [= *Parakohleria purpurea* (Poeppig) Wiehler, 1978a:8]

Isoloma sprucei Britton in Rusby, 1896:97. [= *Parakohleria sprucei* (Britton) Wiehler, 1978a:9]

Isoloma urticifolium Rusby, 1900:28. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Isoloma vulcanicolum J.D. Smith, 1916:382. [= *Capanea affinis* ("Campanea") Fritsch, 1913a:434]

Kohleria avilana Cuatrecasas, 1935:256 (reprint page 53). [= *Parakohleria avilana* (Cuatrecasas) Wiehler, 1978a:5]

Kohleria baezana Cuatrecasas, 1935:257 (reprint page 54). [= *Parakohleria baezana* (Cuatrecasas) Wiehler, 1978a:6]

Kohleria collina T.S. Brandegee, 1914:66. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria deppeana (Schlechtendal & Chamisso) Fritsch, 1894:179. [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, 1865:284]

Kohleria deppeana var. *lasiantha* (Zuccarini) Fritsch, 1913a:425. [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, 1865:284]

Kohleria elegans (Decaisne) Loesener, 1899:574. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria elegans var. *pedunculata* (T.S. Brandegee) C. Morton, 1967a:75. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria elongata Regel, 1855a:4. [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, 1865:284]

Kohleria filisepala Standley, 1940:107. [= *Omiltemia filisepala* (Standley) C. Morton, 1968:98] [Rubiaceae])

Kohleria fruticosa T.S. Brandegee, 1914:67. [= *Moussonia fruticosa* (T. S. Brandegee) Wiehler, 1975:25]

Kohleria hirsutissima C. Morton, 1967a:65. [= *Moussonia hirsutissima* (C. Morton) Wiehler, 1975:25]

Kohleria jamesoniana Fritsch, 1913a:429. [= *Parakohleria jamesoniana* (Fritsch) Wiehler, 1978a:6]

Kohleria lindeniana (Regel) H.E. Moore, 1954:380. [= *Gloxinia lindeniana* (Regel) Fritsch, 1913b:66]

Kohleria martensii Fritsch, 1913a:428. [= *Moussonia triflora* (Martens & Galeotti) Hanstein, 1865:286]

Kohleria papillosa (Oersted ex Hanstein) Fritsch, 1913a:427. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria papillosa var. *pendula* C. Morton, 1967a:72. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria papillosa var. *sericea* Fritsch, 1913a:428. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria papillosa var. *solitaria* C. Morton, 1967a:73. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria patentipilosa (O. Kuntze) Schumann, 1898:386. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Kohleria pedunculata T.S. Brandegee, 1914:67. [= *Moussonia elegans* Decaisne, 1849:489]

Kohleria regelii Hanstein, 1865:442 (nom. nud.). [= *Moussonia deppeana* (Schlechtendal & Chamisso) Hanstein, 1865:284]

Kohleria reticulata Fritsch, 1913a:428. [= *Parakohleria sprucei* (Fritsch) Wiehler, 1978a:9]

Kohleria rupicola Standley & L.O. Williams, 1952:62 [= *Moussonia rupicola* (Standley & L.O. Williams) Wiehler, 1975:25]

Kohleria sancti-josephi Cuatrecasas, 1935:258 (reprint page 55). [= *Parakohleria sancti-josephi* (Cuatrecasas) Wiehler, 1978a:8]

Kohleria saxicola T.S. Brandegee, 1914:66. [= *Achimenes flava* C. Morton, 1936:13]

Kohleria septentrionalis D. Denham in C. Morton, 1967a:70. [= *Moussonia septentrionalis* (D. Denham) Wiehler, 1975:25]

Kohleria serrulata C. Morton, 1939:309. [= *Moussonia serrulata* (C. Morton) Wiehler, 1975:25]

Kohleria skutchii C. Morton & D. Gibson in D. Gibson, 1972:336. [= *Moussonia skutchii* (C. Morton & D. Gibson) Wiehler, 1975:25]

Kohleria sprucei (Britton) Fritsch, 1913a:429. [= *Parakohleria sprucei* (Britton) Wiehler, 1978a:9]

Kohleria strigosa C. Morton, 1938:1181. [= *Moussonia strigosa* (C. Morton) Wiehler, 1975:25]

Kohleria urticifolia (Rusby) Fritsch, 1913a:430. [= *Parakohleria parviflora* (Rusby) Wiehler, 1978a:8]

Kohleria viminalis T.S. Brandegee, 1915:194. [= *Moussonia viminalis* (T.S. Brandegee) Wiehler, 1975:26]

Kohleria weberbaueri Fritsch, 1913a:430. [= *Parakohleria weberbaueri* (Fritsch) Wiehler, 1978a:10]

Tydaea elegans (Decaisne) Planchon & Linden in Linden, 1855:4 (not seen). [= *Moussonia elegans* Decaisne, 1849:489]

Tydaea lindeniana Regel, 1868:257. [= *Gloxinia lindeniana* (Regel) Fritsch, 1913b:66]

Tydaea lindenii Regel ex André, 1873:183, pl. 147. [= *Gloxinia lindeniana* (Regel) Fritsch, 1913b:66]

NOTES ON NOMENCLATURE.—*Isoloma elatior:* Decaisne (1848a) probably intended to transfer *Gesneria elatior* Kunth (1818) to *Isoloma*, but neglected to include the basionym or the author. The possibility that *Isoloma elatior* is a currently unknown cultivar also exists.

Appendix 2

Names Based on Hybrids

Only those taxa described as hybrids are marked as such (×). Types have not been selected herein and only those mentioned in the original descriptions are included. Moore (1954, 1957) gives the parentage of the majority of the hybrids included here. In many cases other hybrids constitute at least one of the parents.

Gesneria oblongata Paxton, 1839:103.

Isoloma bogotense Nicholson var. *giganteum* Voss, 1894:793. [*Tydaea gigantea* Van Houtte ex Voss, 1894:793 (nom. nud. pro syn.).]

Kohleria bella C. Morton, 1967b:79. [Type: *H.E. Moore 7556 bis*, Described from cultivation, originally collected by Horich in San José, Costa Rica, (US, holotype).]

Kohleria behnickii Fritsch, 1916:32. [*Tydaea decaisneana* Hortorum ex Fritsch, 1916:32 (nom. nud. pro syn.); *Tydaea grandiflora* Hortorum Behnick ex Fritsch, 1916:33 (nom. nud. pro syn.).] [Type: Described from cultivation (B, no longer extant).]

Kohleria dubia Fritsch, 1916:31; *Isoloma giganteum* Hortorum Bentham ex Fritsch, 1916:32. [Type: Described from cultivation (B, no longer extant).]

Kohleria maculata C. Morton, 1938:1180. [Type: Costa Rica, San José, *Morana 40* (F, holotype).]

Sciadocalyx × *lucianii* André, 1874:151; *Kohleria* × *lucianii* (André) Fritsch, 1894:178; *Isoloma lucianii* (André) Voss, 1894:793.

Tydaea × *decaisniana* Regel, 1858:374.

Tydaea × *gigantea* Planchon, 1855a:21; *Kohleria* × *gigantea* (Planchon) Fritsch, 1894:178; *Tydaea* × *hybrida* Hortorum ex H.E. Moore, 1954:384.

Tydaea × *hansteinii* Ortgies, 1858:65; *Isoloma bogotense* Nicholson var. *hansteinii* (Ortgies) Voss, 1894:794; *Kohleria* × *hansteinii (Ortgies) H.E. Moore, 1954:385.*

Tydaea hillii Regel, 1854b:73. [*Achimenes hillii* Hortorum ex Regel, 1854b:73 (nom. nud. pro syn.); *Achimenes kewensis* Hortorum ex Regel, 1854b:73 (nom. nud. pro syn.)]; *Isoloma bogotense* Nicholson var. *hillii* (Regel) Voss, 1894:794; *Kohleria* × *hillii* (Regel) H.E. Moore, 1954:386.

Tydaea × *lenneana* Ortgies, 1857:2; *Isoloma bogotense* Nicholson var. *lenneanum* (Ortgies) Voss, 1894:794; *Kohleria* × *lenneana* (Ortgies) H.E. Moore, 1954:386.

Tydaea × *lenneana* var. *viridis* Ortgies, 1857:2.

Tydaea × *lenneana* var. *rutilans* Ortgies, 1857:3; *Isoloma bogotense* Nicholson var. *rutilans* (Ortgies) Voss, 1894:794.

Tydaea × *meyendorffii* Regel, 1858:374.

Tydaea × *meyendorffii* var. *rubra* Regel, 1858:375.

Tydaea × *ortgiesii* Hortorum Van Houtte ex Planchon, 1856:213; *Isoloma* × *ortgiesii* (Hortorum ex Planchon) Voss, 1894:793; *Kohleria* × *ortgiesii* (Hortorum ex Planchon) H.E. Moore, 1954:387.

Tydaea picta (Bentham ex W.J. Hooker) Decaisne var. *karsteniana* Hortorum ex Hanstein, 1865:439. [*Tydaea karsteniana* Hortorum ex Hanstein (nom. nud. pro syn.).]

Tydaea × *pulchra* Hérincq, 1856:98; *Isoloma bogotense* Nicholson var. *pulchrum* (Hérincq) Voss, 1894:794; *Kohleria* × *pulchra* (Hérincq) H.E. Moore, 1954:387.

Tydaea × *pulchra* var. *argyroneura* Hérincq, 1856:98.

Tydaea × *pulchra* var. *chloroneura* Hérincq, 1856:98.

Tydaea × *pulchra* var. *concolor* Hérincq, 1856:98.

Tydaea × *pyramidalis* Regel var. *multiflora* Regel, 1861:193.

Tydaea × *regelii* Hérincq, 1856:97; *Kohleria* × *heeriana* H.E. Moore, 1954:386.

Tydaea × *regelii* var. *argentea* Hérincq, 1856:97.

Tydaea × *regelii* var. *chlorophylla* Hérincq, 1856:98.

Tydaea × *regelii* var. *erythrichina* Hérincq, 1856:98.

Tydaea × *robert-le-diable* Van Houtte, 1869:151.

Tydaea × *rossiana* Ortgies, 1857:1; *Kohleria* × *rossiana* (Ortgies) H.E. Moore, 1954:387.

Tydaea × *rossiana* var. *concolor* Ortgies, 1857:2.

Tydaea × *rossiana* var. *lucida* Ortgies, 1857:2.

NOTES ON NOMENCLATURE.—*Gesneria oblongata:* Paxton (1839) probably described this species from hybrid material, with *Kohleria trianae* as part of the parentage of this hybrid. *Gesneria elongata* Kunth var. *fruticosa* Graham (1840) was stated to be a synonym of *Gesneria oblongata*. The illustration of this variety, however, shows a different plant similar to typical *Kohleria trianae,* and the variety *fruticosa* is herein treated as a synonym of *K. trianae.*

Isoloma bogotense var. *giganteum:* This hybrid variety is probably identical to *Tydaea* × *gigantea* Planchon. Apparently Voss (1894) incorrectly credited Van Houtte as author of *Tydaea* × *gigantea* instead of Planchon (1855a); Van Houtte never published any *Tydaea gigantea.*

Kohleria behnickii: Fritsch (1916) described *K. behnickii* from cultivation, and added that the plant was known as *Tydaea decaisniana,* but had apparently never been described under this name. However, Regel (1858) published this name for a hybrid between *Achimenes picta* (now *Kohleria amabilis* var. *bogotensis*) and *Sciadocalyx warszewiczii* (*Kohleria warszewiczii*). The plant described by Fritsch as *Kohleria behnickii* has according to the description features intermediate between these two taxa, and *K. behnickii* is herein considered to be of hybrid origin. This condition is based on the Fritsch description, as no type material has been located.

Kohleria bella: see *Kohleria maculata.*

Kohleria dubia: Fritsch (1916) suggested that *K. dubia* might be a hybrid. Only minor differences distinguish *K. dubia* from *Tydaea* × *gigantea* Planchon (1855a), a hybrid between *Kohleria amabilis* var. *bogotensis* and *K. warszewiczii.*

Kohleria maculata: Morton (1938) described *K. maculata* on material collected close to San José, Costa Rica, and later (1967b) he added the similar *K. bella* (mainly set apart by having larger flowers); the species was based on cultivated material originally collected in San José. A few additional collections from Costa Rica (*Davidse & Pohl 1310*), Honduras (*Molina R. 14581*), Ecuador (*Valverde 23*) and Colombia (*Sandeman 639:39*) are similar; these latter collections are all from gardens. In addition, a hybrid cultivated at Cornell University in the 1950s under the name "Sunrise" has characteristics similar to *K. maculata* and especially the larger-flowered *K. bella* (*Moore 7689*). According to Batcheller (1985) "Sunrise" is unknown in origin and now believed to be extinct. Consequently, both *K. maculata* and *K. bella* apparently were described from a neotropical cultivated hybrid of unknown origin and parentage. *Kohleria warszewiczii* is probably part of the parentage.

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Index to Scientific Names of Genera and Species

(Currently accepted names, apart from hybrids, are in italics.)

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