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Revision of *Heppiella* (Gesneriaceae)

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ABSTRACT. Four species are recognized in the Andean genus *Heppiella*: *H. ulmifolia* that ranges from Colombia to Peru, *H. viscida* from northwestern Venezuela, *H. verticillata* from the Eastern Cordillera of Ecuador and adjacent Colombia, and *H. repens* from Ecuador and southern Colombia. The former three species have allopatric distributions, occur in disturbed habitats, and are terrestrial. *Heppiella repens* is sympatric with *H. ulmifolia* and *H. verticillata*, occurs in mist forests, and is usually climbing and epiphytic. *Heppiella* has apparently developed from ancestors close to *Gloxinia*, and this latter genus was used as an outgroup in a cladistic analysis. The only derived features that the widespread and variable *H. ulmifolia* possesses are those that distinguish *Heppiella* from *Gloxinia*. The three more restricted species have no derived features in common, and have apparently evolved independently from geographically isolated populations of *H. ulmifolia*.

Heppiella Regel is a genus of Andean Gesneriaceae ranging from Venezuela to Peru. Nineteen species have been described, but in the present work only four are recognized: the widespread and common *H. ulmifolia* (Kunth) Hanst., and the three local species, *H. viscida* (Lindley ex Paxton) Fritsch, *H. verticillata* (Cav.) Cuatrec., and *H. repens* Hanst. This study was undertaken because the previous studies of *Heppiella* are outdated, and these works were based exclusively on a limited number of herbarium sheets.

MATERIALS

The revision is based on studies of herbarium material (439 collections) and field observations of *Heppiella repens* and *H. verticillata* in Ecuador and *H. ulmifolia* in Ecuador and Colombia. In addition, the latter two species have been studied in cultivation in the greenhouses of AAU.

TAXONOMIC HISTORY

Heppiella was established by Regel (1853) based on a single species cultivated in Europe, *H. atrosanguinea*. This species was believed to have come from Colombia, but it is endemic to northwestern Venezuela. Lindley and Paxton (1851) had previously described and illustrated the same plant under the name *Achimenes viscida*, and Fritsch (1894) reduced *H. atrosanguinea* to a synonym of *H. viscida*.

Another three species had previously been described in *Gesneria* L.: *G. verticillata* (Cavanilles 1801), *G. ulmifolia* (Kunth 1818) and *G. gua-*

zumaefolia (Bentham 1846), and were later transferred to *Heppiella* by Cuatrecasas (1935), Hanstein (1859), and Wiehler (1978), respectively.

In the middle of the last century, several Gesneriaceae in the horticultural literature, including both Old and New World species and characterized by having free stamens, were named *Chorisanthera* Oersted. Skog (1976b) reviewed the taxonomic history of *Chorisanthera* and its orthographic variants *Cheirisanthera* and *Corysanthera*. Some of these, published by Hérincq (1852), Lindley and Paxton (1851), and Regel (1852, 1853), are synonyms of *Heppiella viscida*.

Hanstein (1859) added seven species mostly based on weak characters such as leaf-shape, indumentum, etc. Fritsch (1913) added five species and stated that "these were at least as well-founded as those of Hanstein," and later (1916) he further described *Heppiella grandifolia*. In the present work all Hanstein and Fritsch species, apart from *H. repens* by Hanstein, are reduced to synonymy.

Two species from Jamaica and Cuba have been referred to *Heppiella*. Urban (1901) transferred *Gesneria corymbosa*, described by Swartz in 1788, to *Heppiella*, and Morton (1957) described *H. cubensis*. Wiehler (1971) included *H. corymbosa* and *H. cubensis* in *Gesneria* based on the fact that their haploid chromosome number is equal to that of *Gesneria* ($n = 14$) rather than that of *Heppiella* ($n = 13$), and that the clustered stomata arrangement and the vascular pattern of the petioles differ from *Heppiella*, but are in accordance with *Gesneria*. Skog (1976a) treated the

two taxa as subspecies of a newly established monotypic genus *Pheidonocarpa*, which among other characters differs from *Gesneria* by having opposite instead of alternate leaves.

Heppiella belongs to the group of New World Gesneriaceae with half to completely inferior ovaries. Fritsch (1894) placed *Heppiella* in the tribe Gloxinieae, together with *Gloxinia* L'Hér, *Achimenes* Pers., *Smithiantha* Kuntze, and *Seemannia* Regel, and most workers have followed this classification, e.g., Beaufort-Murphy (1983). The character that distinguishes Gloxinieae is its annular nectary elaboration. Wiehler (1983) united Gloxinieae s. str. with the tribes Bellonieae, Kohlerieae, Solenophorieae, and Sinnigieae, into Gloxinieae s.l. This latter classification is accepted here.

The combination of broadly tubular red corollas, stamens with free anthers, capitate stigmas, and annular or somewhat lobed nectaries set *Heppiella* apart from both the closely related genera *Gloxinia* and *Kohleria* Regel (table 1), and the superficially similar *Moussonia* Regel. *Heppiella* may be closely related to *Gloxinia*, but is most easily confused with *Kohleria spicata* (Kunth) Oersted and small-flowered specimens of the extremely variable *K. hirsuta* (Kunth) Regel. In Colombia the latter species frequently has a striking similarity to *Heppiella ulmifolia*, e.g., the nectary state often is annular as in *Heppiella*, instead of the usual free nectary glands of *Kohleria*. However, *Kohleria* always has a bilobed stigma (table 1). Most *Gloxinia* species differ from *Heppiella* by having larger flowers with different shapes and colors. *Gloxinia sylvatica* (Kunth) Wiehler from Peru is florally similar but is characterized by its 4-whorled leaves and the presence of large glandules in the corolla throat.

DISCUSSION OF CHARACTERS

Habit and Habitats. *Heppiella* comprises herbs, subshrubs, shrubs, and climbing shrubs arising from stolons or scaly rhizomes. The latter term is used for subterranean, creeping stems with scale-like leaves, densely congested in a somewhat conelike structure; a common feature in most genera in the tribe Gloxinieae. Scaly rhizomes are usually present in *H. ulmifolia*, *H. verticillata*, and *H. viscida*, and enable these species to survive unfavorable dry periods, but are frequently only weakly developed. Plants of *H.*

TABLE 1. Some features that distinguish *Heppiella* from the genera *Gloxinia* and *Kohleria*.

	<i>Heppiella</i>	<i>Gloxinia</i>	<i>Kohleria</i>
Anthers	Free	Coherent	Coherent
Filaments	Not coiling	Coiling	Coiling
Nectary	Annular	Annular	Five free glands
Ovary	½-¾ inferior	Inferior	½-¾ inferior
Stigma	Capitate	Capitate	Bilobed
Throat	Not glandular	Glandular	Glandular

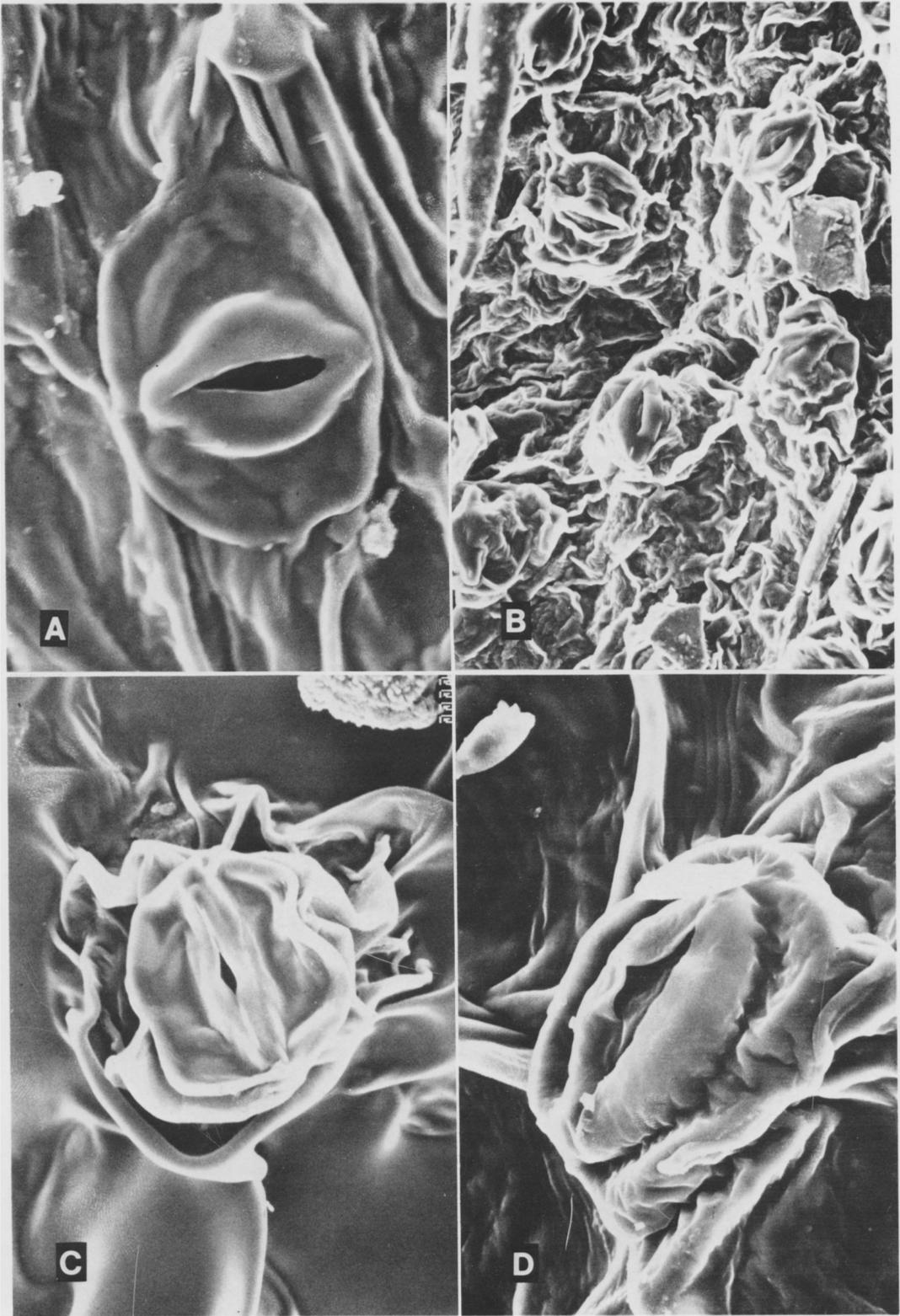
verticillata that grow exposed to desiccation often have well-developed scaly rhizomes, while nearby plants found in permanently moist places may lack these structures almost completely (pers. obs.).

The usual habitats of *Heppiella ulmifolia*, *H. verticillata*, and *H. viscida* are crevices of sun- and wind-exposed rocky slopes and disturbed areas along streams and roads. *Heppiella ulmifolia* may thrive in relatively dense, shrubby vegetation where the species develops a climbing habit (pers. obs.), but cannot survive in closed forest. The habitat influences the habit dramatically; e.g., *H. verticillata* was flowering when only a few cm tall growing exposed in crevices of rocks, while nearby plants from deep moist soil exceeded 50 cm (pers. obs.).

Heppiella repens is often epiphytic and occurs in permanently humid, low-stature mist forests. Here its stems may extend up to several meters appressed to moss-covered treetrunks or rocks, while the erect shoots with leaves and flowers only rise 10-20 cm high (pers. obs.; fig. 6D). *Heppiella repens* appears to lack scaly rhizomes. These may be of little adaptive value in a permanently humid environment.

The altitudinal range of *Heppiella* is broad; e.g., *H. ulmifolia* has been collected from 800-3700 m elevation. However, the genus is absent from the lowlands and is rare below 1500 m. *Heppiella repens* and *H. ulmifolia* reach higher elevations than other New World Gesneriaceae. The latter is among the very few Gesneriaceae common above 2500 m.

Leaves. The leaves of *Heppiella* usually are opposite, isophyllous, and decussate, but ternate leaves are frequent in *H. viscida* and occur in populations of *H. ulmifolia* in the Colombian Dept. Cauca and the Ecuadorean Prov. Chim-



barazo. However, opposite and ternate leaves may occur mixed even on the same shoot.

The size and shape of *Heppiella ulmifolia* leaves vary considerably. In most populations only ovate leaves occur, but in Ecuador plants with obovate or even oblanceolate leaves are widespread although relatively rare. These plants are usually climbing and occur below 2500 m elevation.

The upper leaf surfaces of *Heppiella repens*, *H. verticillata*, and *H. ulmifolia* are mostly bullate, and the veins are impressed. However, in Peru and parts of Colombia, especially in Dept. Cundinamarca, the leaves of most *H. ulmifolia* specimens have plane, tomentose upper leaf surfaces. Burt (1976) suggested bullate leaves to be an adaptation that improves the absorption of light in shaded habitats. However, *H. ulmifolia* plants of high-altitude, exposed-habitats usually have conspicuously bullate leaves, while many specimens from lush vegetation at lower altitudes have larger, less coriaceous, and fairly plane leaves.

In the Gesneriaceae stomata are restricted to the lower leaf surface. The individual stomata of *Heppiella* often are elevated above the level of the epidermis (fig. 1). This feature occurs consistently in *H. verticillata* (fig. 1C) and in most populations of *H. ulmifolia* (fig. 1B) and *H. viscida* (fig. 1D), but is absent from *H. repens* (fig. 1A). According to Wiehler (1983) stomatal mounds occur in terrestrial Gesneriaceae of the humid substory that mostly have thin velvety blades. This is in conflict with the occurrence of stomatal mounds on the coriaceous leaves of the exposed-habitat species; e.g., *H. verticillata* and *H. ulmifolia*.

Trichomes. Four types of trichomes, all uniseriate, occur in *Heppiella*. The stems, leaves, inflorescences, and flowers are covered with slender, eglandular trichomes, 0.5–1.5 mm long and of 5–8 cells. Short, stiff, bristle-like, nonglandular trichomes, 0.2–0.5 mm long and of 1–3 cells, mainly occur on the upper leaf surfaces located on the bullae of the leaves of *H. repens*, *H. verticillata*, and most populations of *H. ulmifolia*. Glandular trichomes with a terminal secretory sphere and slender stalk, 0.5–1.0

mm long and of 5–8 cells, cover the usually sticky *H. viscida*. These are common in populations of *H. ulmifolia* from Peru and parts of Colombia but rare in Ecuador, and occur on the corollas of *H. repens*. Finally, minute, 0.02–0.05 mm long, glandular trichomes with stalks of 1–2 cells often occur at the margins of the corolla lobes in all species.

Inflorescences. *Heppiella repens* has single, axillary, sessile, and ebracteate flowers. The inflorescences of *H. ulmifolia* and *H. verticillata* consist of (1)3–8(12) flowers and 2–6 scale-like bracts densely congested in the leaf axils. *Heppiella viscida* has pedunculate inflorescences, and only here is it fairly easy to discern the inflorescence morphology: a complex, axillary cyme with additional bractless flowers described by Weber (1973, 1978) as a “pair-flowered cyme.” According to the definition of Troll (1964) the flowering shoots or synflorescences of *Heppiella* usually are “frondose,” but the shoots of *H. verticillata* may become somewhat “bracteose.”

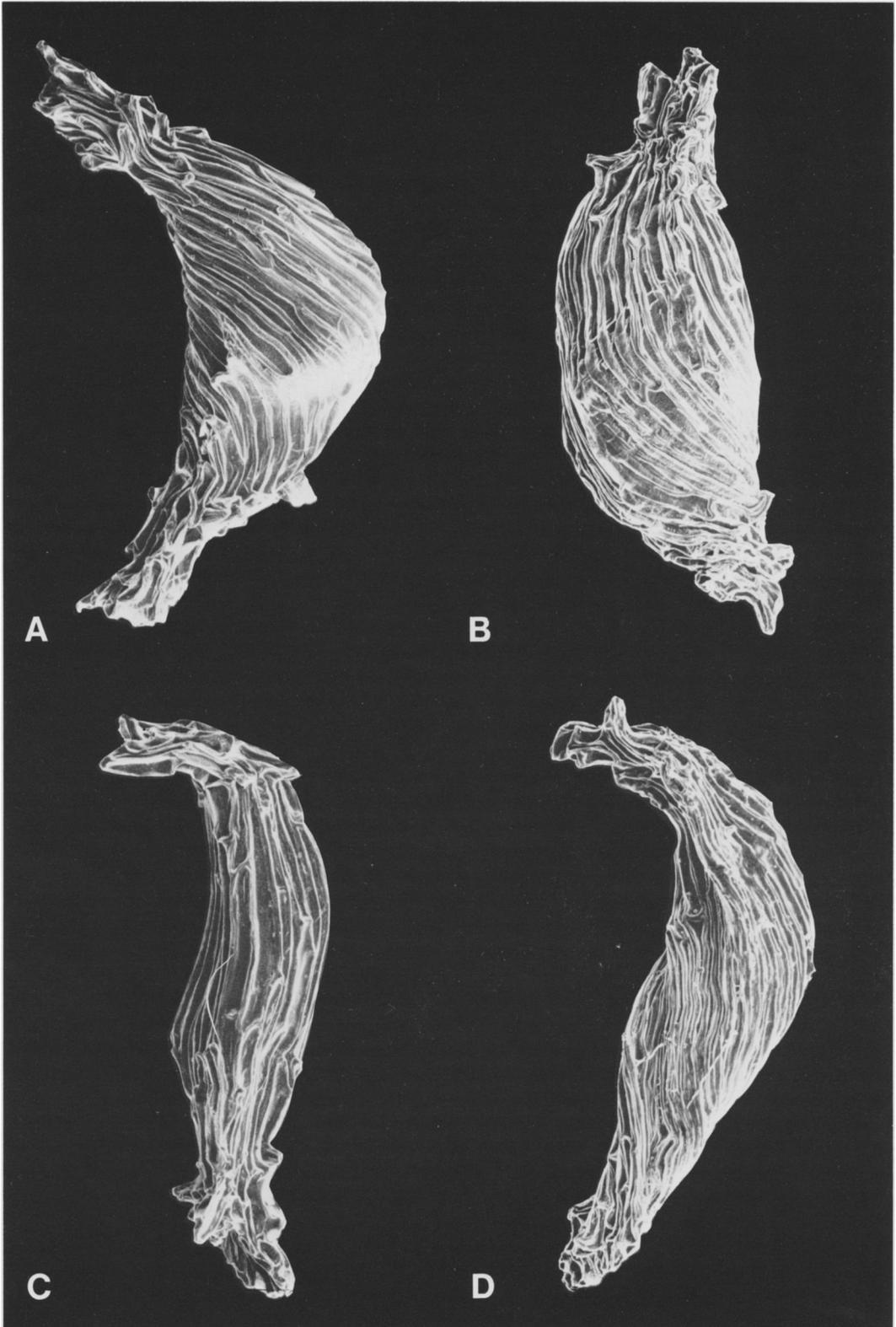
Flowers and Pollination. The broadly tubular, red corollas of *Heppiella* (fig. 6) are similar to those of many species in the genera *Kohleria*, *Parakohleria* Wiehler, *Moussonina*, and *Gloxinia*, but differ from all these by having free anthers and filaments that do not coil and pull the anthers back into the flower during the female phase (table 1). The anthers of the protandrous flowers continue to shed apparently viable pollen until after the style has elongated causing the receptive stigma to become placed close to the still fertile anthers in some species (in fig. 6B the style of *H. ulmifolia* is elongating).

The flowers of *Heppiella repens*, *H. ulmifolia* (fig. 6B, E), and *H. viscida* are rather similar but with some minor differences (table 2). The former species has been observed to be visited by the black-breasted puffleg hummingbird (*Eriocnemis nigrivestis*) in the Prov. of Pichincha of Ecuador (Bleiweiss 25). *Heppiella ulmifolia* and *H. viscida* may also be hummingbird-pollinated, but self-pollination may also occur.

In contrast to the former three species, *Heppiella verticillata* has much shorter corollas (length ca. 1 cm instead of ca. 2 cm) with included anthers and stigma (table 2; fig. 6C). Large flow-

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FIG. 1. Stomata in *Heppiella*. A. *H. repens*, Jaramillo & Cuello 2164 (AAU), ×1600. B. *H. ulmifolia*, Juncosa & Misas 1090 (US), ×700. C. *H. verticillata*, Barfod & Thomsen 49005 (AAU), ×1200. D. *H. viscida*, Alston 6543 (US), ×2200.



ering populations of *H. verticillata* were observed in Ecuador, but no flower visitors were seen, although the fruit- and seed-production were abundant (pers. obs). The occurrence of self-pollination in *H. verticillata* was demonstrated when a living collection flowered within a plastic bag in the greenhouse and produced fruits with numerous viable seeds (pers. obs.). In natural habitats the fruit- and seed-production of *H. ulmifolia* seem to be equally abundant, and in this species the anthers and the stigma also become located close together (pers. obs.; table 2). In *H. repens* (table 2; fig. 6E) the occurrences of excluded anthers and a subincluded style makes self-pollination less probable, as anthers and stigma are never located in close proximity (in contrast to *H. viscida* where the elongating style passes the anthers).

Populations of *Heppiella ulmifolia* and *H. verticillata* apparently flower throughout the year, but the intensity is strongly reduced in dry periods (pers. obs.; data from herbarium sheets). In Ecuador and Colombia the main flowering season of *H. ulmifolia* is May–August.

Heppiella viscida occasionally possesses a partly fertile fifth stamen, at least in the bud stage. During flowering this fifth stamen usually appears as an exceptionally long and straight staminode (9–11 mm long in contrast to the usual 2–3 mm). Only a few taxonomically scattered Gesneriaceae have five stamens, and Burt (1977) suggested that this is a reversion from the usual state with four stamens (or two in many Old World Gesneriaceae). The stamens of *Heppiella* differ from those of nearly all other New World Gesneriaceae by having free rather than coherent anthers. Such a reversion to five stamens in *Heppiella* may indicate that the fifth stamen does not cause the same "disorder" in flowers with free anthers as in flowers with joined anthers.

Fruits and Dispersal. *Heppiella* capsules are unilocular and contain several hundred minute seeds. The dehiscence in *H. ulmifolia*, *H. verticillata*, and *H. viscida* is bivalved and loculicidal. The capsules split from the apex, but the opening is rather narrow and partly closed by a row of stiff trichomes at the edge of the valves. The

TABLE 2. The location of the anthers and the stigma in *Heppiella* flowers.

	Anthers	Stigma
<i>H. repens</i>	exserted	subincluded
<i>H. ulmifolia</i>	exserted	exserted
<i>H. verticillata</i>	included	included
<i>H. viscida</i>	subincluded	exserted

capsules persist in this stage for weeks or months, during which the seeds are dispersed mainly by wind, as all three species grow in relatively open habitats. The trichomes at the edge of the valves may restrict dispersal during humid conditions unfavorable for wind-dispersal. The disjunct distribution of *H. ulmifolia* (fig. 4) between the highlands of Ecuador/Colombia and central Peru possibly is due to long-distance wind-dispersal. The minute seeds of Gesneriaceae occasionally are blown over long distances, as demonstrated by the occurrence of *Kohleria spicata* (with similar capsules and seeds) on Cocos Island ca. 500 km southwest of Costa Rica.

In contrast to the former three species, the capsules of *Heppiella repens* usually are secondarily septicidal, resulting in four partly-free valves. This feature was observed in Ecuador (pers. obs) and confirmed by herbarium specimens. Burt (1970, 1976) supposed that the small seeds of forest habitat Gesneriaceae are mainly dispersed by rainwash or by transport on the feet of animals. This is probably also true for *H. repens*. The capsules, of this mist-forest species, are borne on long erect stalks, and may act as splash-cups when struck by the rain-drops, thus spreading the seeds. The four-valved dehiscence possibly improves this mechanism. Splash-cup capsules are rare in New World Gesneriaceae, but are also known from *Gesneria* (Skog 1976a). Septicidal dehiscence is equally rare among the New World Gesneriaceae and according to Wiehler (1983) unknown in the tribe Gloxinieae. However, personal observations during fieldwork in Colombia and studies of herbarium sheets have indicated that another small genus in the Gloxinieae, *Capanea* Decne.

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FIG. 2. Seeds in *Heppiella*. A. *H. repens*, Dodson & Thien 2052 (US), ×119. B. *H. ulmifolia*, Juncosa & Misas 1090 (US), ×156. C. *H. verticillata*, Barfod & Thomsen 59005 (AAU), ×155. D. *H. viscida*, Alston 6543 (US), ×158.

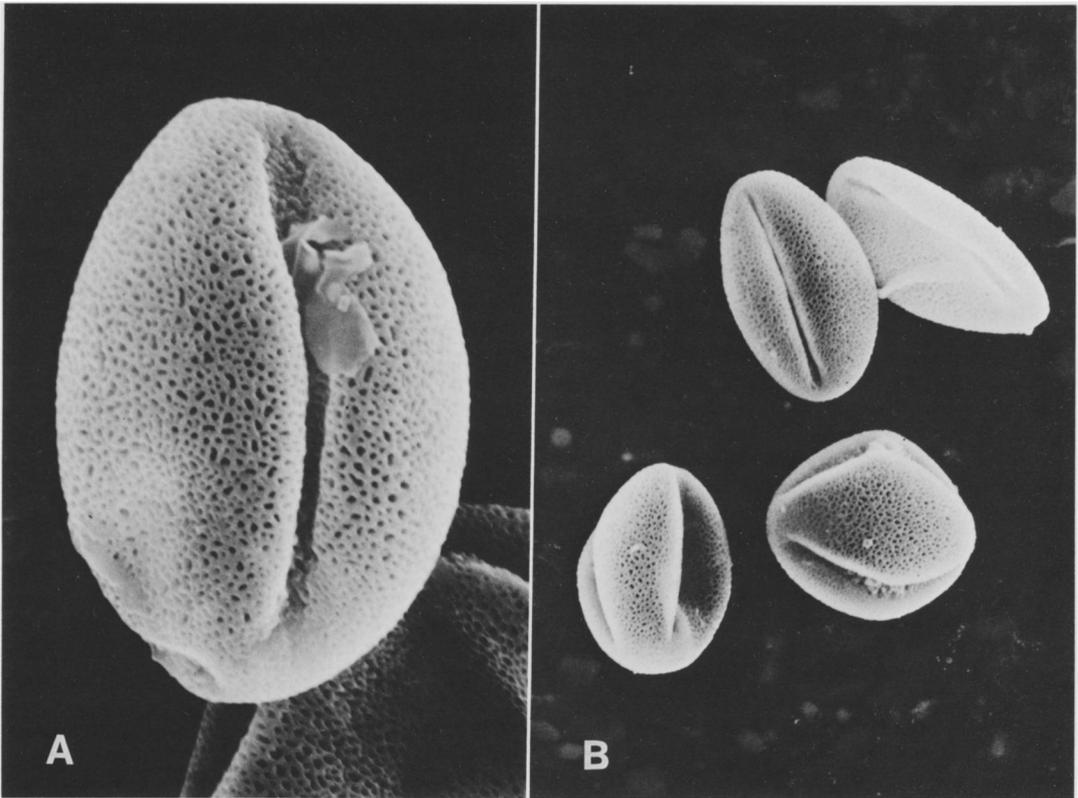


FIG. 3. Pollen in *Heppiella*. A. *H. ulmifolia*, Barclay et al. 7907 (US), $\times 4000$. B. *H. viscida*, Clements & Diaz-Miranda 2419 (US), $\times 1500$.

ex Planchon, has four-valved capsules. *Capanea* and *H. repens* both are climbing and frequently epiphytic inhabitants of the high montane forest.

Seeds. The small size (ca. 0.5×0.2 mm) and the shape (narrowly elliptic) of *Heppiella* seeds show little variation (fig. 2). Seeds of *H. ulmifolia* specimens from Ecuador and Peru are similar to those from Colombia (fig. 2B). The majority of the species and genera that constitute Gloxinieae have seeds similar to those found in *Heppiella* as shown in the SEM-micrographs of Beaufort-Murphy (1983). The seed surface in *H. viscida* (fig. 2D) has closer and narrower striations than that found in the remaining three species (fig. 2A, B, C).

Pollen. Fritze and Williams (1988), Kvist and Skog (1989), Skog (1976a), and Williams (1978) have published SEM-micrographs of New World Gesneriaceae pollen. The work of Williams (1978) indicated that the members of Gloxinieae have fairly uniform pollen of little systematic

value. Williams did not include *Heppiella*, but SEM-micrographs confirm that there is little variation among the species, and that *Heppiella* pollen are typical for the tribe (fig. 3).

Cytology and Hybridization. According to Wiehler (1972) the haploid chromosome numbers of *Heppiella viscida* and *H. repens* are 26 and 13, respectively (the latter species named *H. ampla* Hanst., Wiehler 7133). The haploid chromosome number for most members in the tribe Gloxinieae is 13, and tetraploids are relatively rare (Skog 1984).

Intergeneric hybrids are known between *Heppiella* and species of *Achimenes* (Batcheller 1978), *Gloxinia* (Wiehler 1976), and *Smithiantha* (Lemaire 1857; Moore 1954; Wiehler 1976). Lemaire described the hybrid between *Heppiella viscida* and *Smithiantha zebrina* under the name *Heppiella naegelioides* (now \times *Smithheppiella naegelioides* Lem. (Wiehler)). The pollen stainability in a hybrid between *Heppiella viscida* and *Gloxinia nematanthodes* (O. Ktze.) Wiehler was re-

ported as 0% indicating complete sterility (Wiehler 1976).

Interspecific hybrids have not been reported from *Heppiella*, but in most New World Gesneriaceae partially fertile hybrids are easily obtained by hand-pollination (Wiehler 1983). A collection from the Ecuadorean Prov. Pichincha may be a natural hybrid between *H. repens* and *H. ulmifolia* (Dodson & Thien 1077).

Chemistry. Six specimens representing the four currently accepted species of *Heppiella* were included in the phytochemical work on the phenolic compounds of the Gesneriaceae by Kvist and Pedersen (1986). There were no decisive differences between *Heppiella* and related genera.

DISTRIBUTION, VARIATION, AND EVOLUTION

Many genera of New World Gesneriaceae consist of a single or a few widespread species and a larger number of endemics, e.g., *Cremsperma* Benth. (Kvist and Skog 1988), *Reldia* Wiehler (Kvist and Skog 1989) and *Heppiella*. The widespread species, e.g., *H. ulmifolia*, are variable, while the local species, e.g., the three rarer *Heppiella* species, have fairly stable traits. *Heppiella ulmifolia*, *H. verticillata*, and *H. viscida* are allopatric, while *H. repens* is sympatric with the former two species (fig. 4), but this latter species occurs in a different habitat and has some advanced features, e.g., an epiphytic lifeform. This pattern suggests that *H. ulmifolia* is closest to the ancestor of *Heppiella*, and the other species speciated from geographically isolated populations close to or identical with present-day *H. ulmifolia*. To test this hypothesis, *Gloxinia* was selected as an outgroup. (In a forthcoming revision of *Kohleria* it will be argued that *Heppiella* and *Kohleria* have developed independently from ancestors close to the current genus *Gloxinia*.) The derived features (apomorphies) and the corresponding plesiomorphic features of *Heppiella*, polarized by comparison with *Gloxinia*, are listed in table 3, and the *Heppiella* species that possess the particular derived features are given. The absence of synapomorphies and reversions (character losses) make the cladistic analysis straightforward, and the cladogram illustrating the evolution of *Heppiella* is shown in figure 5.

Heppiella ulmifolia possesses no derived features beside the autapomorphies that set the genus as a whole apart from *Gloxinia*. The ab-

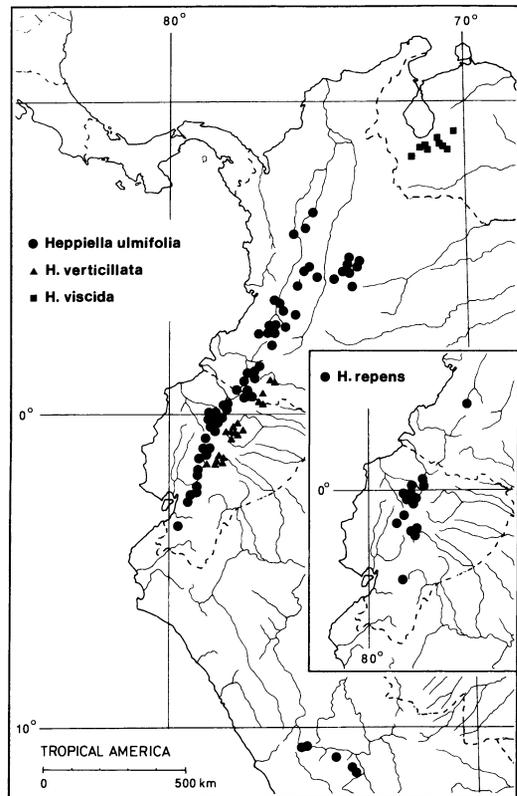


FIG. 4. Distribution of *Heppiella*. *H. ulmifolia*, *H. verticillata*, and *H. viscida* have allopatric distributions, while *H. repens* is sympatric with the former two species.

sence of synapomorphies indicates that the three rarer species probably speciated independently from *Heppiella ulmifolia*. The most distinct species is *H. repens*, while *H. verticillata* has fewer apomorphies but these are floral and may ensure reproductive isolation. The least distinct species is *H. viscida* (table 3; fig. 5).

Several features that characterize *H. viscida* are frequent in the Colombian *H. ulmifolia* populations closest to the range of *H. viscida*, but rare in the more distant Ecuadorean populations, e.g., plane and tomentose rather than bullate and hispid upper leaf surfaces and presence of glandular trichomes. This indicates that *H. viscida* probably speciated from plants related to current Colombian *H. ulmifolia* populations. These plants either became established in Venezuela by virtue of long-distance dispersal from central Colombia, or the range of *H. ulmifolia* was previously wider.

TABLE 3. Original or primitive features (plesiomorphies) and the corresponding derived or advanced features (apomorphies) in *Heppiella* polarized by using *Gloxinia* as the outgroup. *Heppiella* species that possess a particular derived feature are indicated: 1. *H. repens*. 2. *H. ulmifolia*. 3. *H. verticillata*. 4. *H. viscida*.

Character states	Species
1. Anthers coherent → free	1,2,3,4
2. Filaments coiling → not coiling	1,2,3,4
3. Throat glandular hairy → eglandular	1,2,3,4
4. Never epiphytic → often epiphytic	1
5. Shoots not arising from creeping rhizomes → arising from creeping rhizomes	1
6. Scaly rhizomes usually present → absent	1
7. Flowers in cymes → flowers single	1
8. Inflorescences bracteate → ebracteate	1
9. Capsule 2-valved → usually 4-valved	1
10. Corolla longer than 15 mm → shorter than 15 mm	3
11. Anthers not included → included	3
12. Stigma not included → included	3
13. Corolla lobes glabrous inside → pilose inside	3
14. Inflorescence sessile → inflorescence pedunculate	3
15. Fifth partly fertile stamen never present → occasionally present	4
16. Seeds with broad striations → narrow striations	4

TAXONOMIC TREATMENT

Heppiella Regel, Gartenflora 2:353. 1853.—*Cheirisanthera* Hort. ex Lindley et Paxton, Paxton's Fl. Gard. 2:59. 1851, pro syn.—*Chorisanthra* Hort. ex Hérincq, Horticulteur Franc. 2:1. 1852, nom. invalid.—*Corysanthera* Decne. ex Regel, Gartenflora 1:40. 1852, nom. illeg., non *Corysanthera* Wallich ex Bentham in Endl. Gen. Pl. 9:719. 1839.—**TYPE:** *Heppiella atrosanguinea* Regel = *Heppiella viscida* (Lindley et Paxton) Fritsch.

Herbs, subshrubs, shrubs or climbing, terrestrial, epipetric, or less commonly epiphytic; most parts of plants covered with uniseriate, eglandular trichomes, glandular trichomes less common; stems erect, decumbent, descending, or scandent, terete, often branching. Leaves opposite, less commonly ternate, isophyllous, the

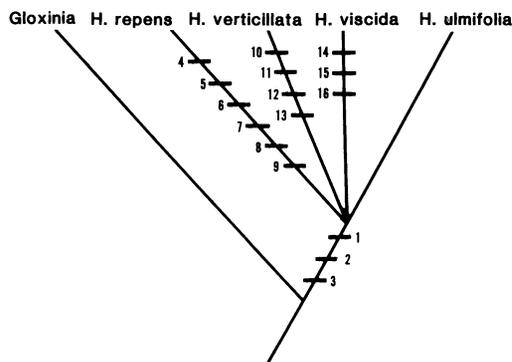


FIG. 5. Cladogram of *Heppiella* with *Gloxinia* as the outgroup. The derived features (apomorphies) indicated by the lines appear in table 3.

blades often ovate; base cordate and oblique; margin serrate to crenate; adaxial surface dull green, bullate and bristly or plane and pilose to tomentose, veins impressed; abaxial surface usually lighter green, pilose especially at the prominent veins, number of secondary veins (4)5–7(8) per side. Inflorescences axillary, pair-flowered cymes of 3–10(25) flowers, less commonly of single flowers, sessile or less commonly pedunculate; peduncles and pedicels pilose to villose; flowering shoots may appear racemose with reduced subtending leaves towards the apex. Calyx usually villous, the lobes equal, free for at least half of their length; corolla broadly tubular, tube red, basally yellow, often saccate, outside villous or sericeous, occasionally with glandular trichomes, inside white to yellow, glabrous, limb red, lobes subequal, rounded to truncate, outside villous to sericeous, often with glandular trichomes at the margin, inside glabrous or less commonly pilose; stamens 4, equal, filaments glabrous, anthers free, dehiscing by longitudinal slits, a dorsal staminode present; nectary annular, 0.3–0.7 mm high, usually shallowly 5-lobed, occasionally deeply lobed; ovary $\frac{1}{2}$ – $\frac{2}{3}$ inferior, sericeous to villous, style pilose, stigma capitate, glabrous. Fruit an ovoid, dry capsule, bivalved or less commonly 4-valved; seeds numerous, minute, ca. 0.5×0.2 mm, narrowly elliptic, surface longitudinally to somewhat obliquely striated, with grooves between striations usually wide.

Heppiella viscida is known as "Chivata" in Venezuela (Jahn 1139). A few popular names have been recorded for *H. ulmifolia* in Colombia,

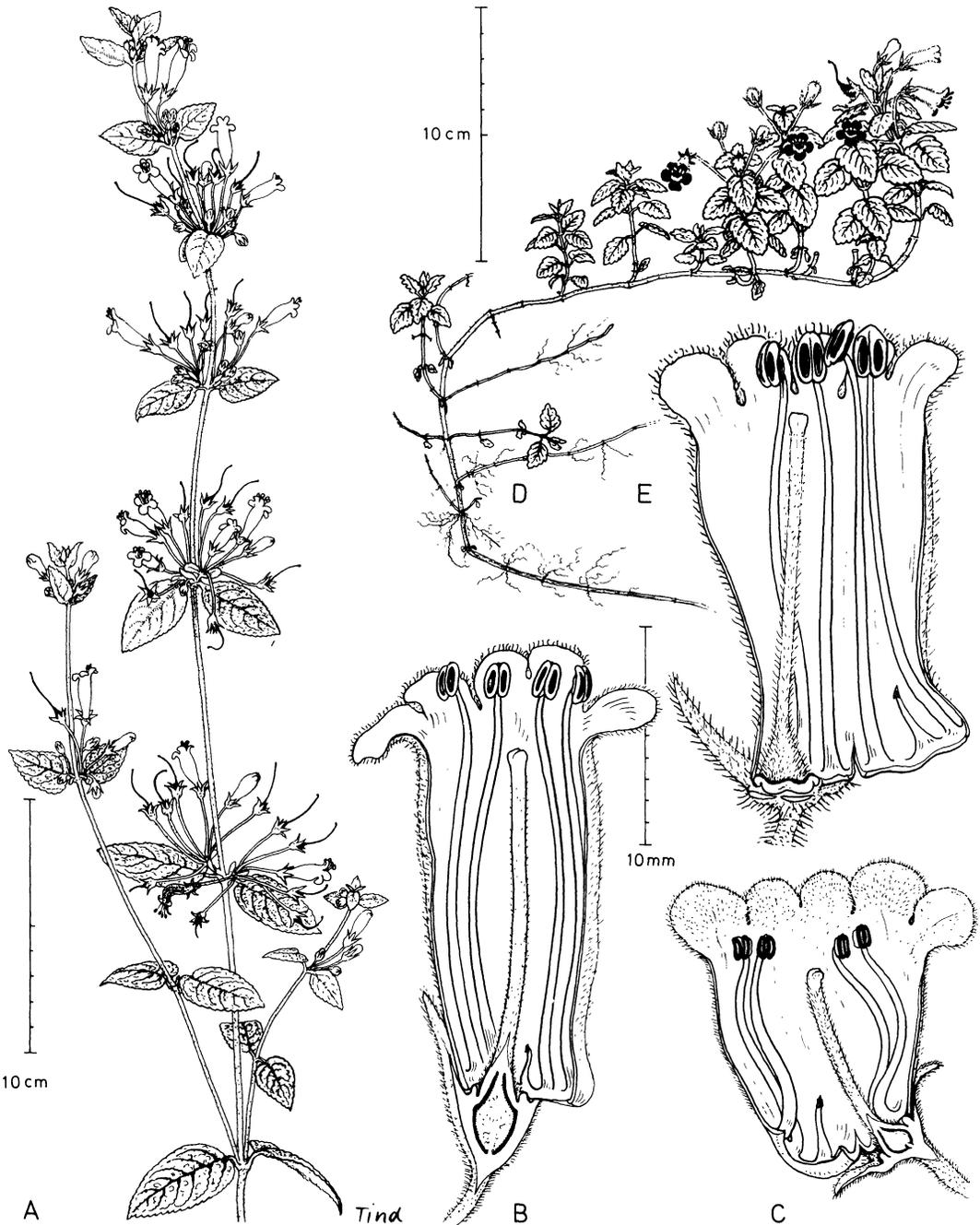


FIG. 6. Habit and floral features of *Heppiella*. A, B. *H. ulmifolia*. C. *H. verticillata*. D, E. *H. repens*.

viz., "Sunse" and "Ortiguilla" in Nariño (Vogelmann 2020), and "Caracola" in Antioquia (Daniel 1492). No popular uses of *Heppiella* have been recorded, but in Antioquia the name "Car-

acola" is also used for species of *Kohleria*, and the scaly rhizomes of the latter genus are here used for a decoction against kidney-afflictions (Kvist 1987). *Heppiella ulmifolia* probably has the

same application as Pérez-Arbelaez (1947) and García-Barriga (1975) relate that the name "Caracola" refers to the scaly rhizomes.

KEY TO SPECIES OF *HEPPIELLA*

1. Inflorescences sessile or occasionally with peduncles 1–4(10) mm long, number of flowers up to 12; leaves, stems, and inflorescences occasionally glandular hairy; Colombia, Ecuador, and Peru.
 2. Corolla 9–11 mm long, lobes pilose inside; anthers included, filaments 6–8 mm long
 3. *H. verticillata*
 2. Corolla 15–22 mm long, lobes glabrous inside; anthers exerted, filaments 15–22 mm long.
 3. Inflorescences usually with several flowers in the leaf-axils, bracteate, rarely exceeding the length of the leaves; flowering shoots not arising from creeping rhizomes, the length usually exceeding 20 cm; plants never epiphytic, occasionally climbing 2. *H. ulmifolia*
 3. Inflorescences single-flowered in the leaf axils, ebracteate, usually exceeding the length of the leaves; flowering shoots arising from creeping rhizomes, the length not exceeding 20 cm; plants often epiphytic and climbing 1. *H. repens*
1. Inflorescences with peduncles (15)30–60 mm long, the number of flowers up to 25; leaves, stems, and inflorescences always glandular hairy; Venezuela 4. *H. viscida*

1. *HEPPIELLA REPENS* Hanst., *Linnaea* 29:514, 553. 1859.—TYPE: Ecuador, Pichincha, western slopes of Mt. Pichincha, *Jameson* 646 (holotype: LE!; isotypes: BM—2 sheets!, CGE!, E!, G!, K!, W!).

Illustrations. Fig. 1A (stomata), 2A (seed), 6D, E (habit and flower).

Herbs or climbing shrubs, epiphytic or epipetric. Erect shoots arising from several meter long creeping rhizomes, 5–20 cm long, pilose to villous near apex, with adventitious roots and stolons, scaly rhizomes absent; internodes 0.5–2.5 cm long. Leaves opposite, the blades ovate to elliptic, (0.5)1–3(6) cm long, (0.4)0.7–1.5(2.2) cm wide, apex acute; base acute to rounded; adaxial surface bullate and bristly; petioles 2–4 mm long. Inflorescences axillary, single-flowered, usually exceeding the length of the leaves, ebracteate; pedicels 1–4 cm long. Calyx 6–10

mm long, lobes subulate, rarely lanceolate, 4–9 mm long, the base 1–2 mm wide; corolla red, 17–21 mm long, the tube outside pilose to villous, base yellow, saccate, 4–5 mm in diam., constricted above to 2.5–3.0 mm in diam., throat 4.5–6.0 mm. in diam.; the lobes 3–4 mm long and 2–3 mm wide at base, outside often sericeous with glandular trichomes at margin, inside glabrous; filaments 18–20 mm long, anthers 2.2–2.5 mm long, 1.5–1.8 mm wide, exerted, staminode 2–3 mm long; nectary annular, often deeply 5-lobed; style 13–17 mm long, stigma subincluded. Capsule 6–9 mm long, 4–6 mm in diam., often 4-valved, primarily loculicidal, secondarily septicidal; seeds with wide grooves between striations.

Representative collections examined (35 seen). COLOMBIA. **Cauca:** Mt. Trompo del Puerco, *Pennell* 7520 (GH, NY).

ECUADOR. **Azuay:** 1–8 km N of Sevilla de Oro, *Camp* 4300 (AAU, MO, NY, SEL, US—3 sheets). **Cotopaxi:** Corazón, *André* 3631 (F, NY). **Imbabura:** Mt. Cotacachi, *Kvist et al.* 45616 (AAU). **Pichincha:** Chillogallo-Chiriboga road, km 18, *Balslev & Steere* 3084 (AAU, QCA—2 sheets); W slope of Mt. Pichincha, ridge crest of Cerro Pugsí, *Bleiweiss* 25 (US); San Juan-Ventanilla-Las Comunas, *Jaramillo & Lascano* 2529 (AAU, MO, QCA). **Tungurahua:** Mt. Tungurahua, SW slope, *Heinrichs* 830 (G, NY, US); Trail from Baños to Mt. Tungurahua, *Lawesson et al.* 44185 (AAU); Tungurahua, *Spruce* 5312 (G, K—2sheets, NY).

Distinguishing features. *Heppiella repens* and *H. ulmifolia* are occasionally difficult to distinguish on herbarium sheets, but their different habits and habitats set them apart readily in the field (fig. 6A, E) (see *H. ulmifolia*).

Distribution. *Heppiella repens* (fig. 4) is a relatively uncommon species in Ecuador and most collections come from two intensely collected areas: the Andean slopes west of Quito and Mt. Tungurahua in the Eastern Cordillera. The distance between its Ecuadorean range and the apparently isolated Colombian occurrence in Cauca is considerable (fig. 4). *Heppiella repens* has been collected from 2000 to 3700 meters elevation, but is most frequent about 2800 meters.

2. *HEPPIELLA ULMIFOLIA* (Kunth) Hanst., *Linnaea* 29:512. 1859.—*Gesneria ulmifolia* Kunth in HBK Nov. Gen. Sp., qto. ed. 394, fol. ed.

316. 1818.—TYPE: Ecuador, Pichincha, between Chillo and Sangolqui, *Bonpland* 2274 (holotype: P!; isotypes: P—2 sheets!).
- Gesneria guazumaefolia* Benth., Pl. Hartw. p.147. 1846.—*Kohleria guazumaefolia* (Benth.) Regel, *Gartenflora* 3:347. 1854.—*Rechsteineria guazumifolia* (Benth.) O. Kuntze, *Revis. Gen. Pl.* 2:474. 1891.—*Heppiella guazumaefolia* (Benth.) Wiehler, *Selbyana* 5:62. 1978.—TYPE: Ecuador, El Oro, *Hartweg* 825 (holotype: K!; isotypes: BM!, CGE!, G!, K!).
- Heppiella ampla* Hanst., *Linnaea* 29:514, 554. 1859.—TYPE: Ecuador, Pichincha, *Jameson* 722 (holotype: LE!; isotypes: BM!, CGE!, G!).
- Heppiella pauciflora* Hanst., *Linnaea* 29:514, 552. 1859.—TYPE: Colombia, Cundinamarca, Salto de Tequendama, *Linden* 793 (lectotype here designated: W!; isolectotypes: BM!, G—3 sheets!, K!, LE!, P!, W!).
- Heppiella stenocalyx* Hanst., *Linnaea* 29:512, 552. 1859.—TYPE: Colombia, Cundinamarca, Bogota, *Karsten s.n.* (holotype: W!; isotype: LE!).
- Heppiella warszewiczii* Hanst., *Linnaea* 29:514, 552. 1859.—TYPE: Colombia (?), *Warszewicz* 35 (holotype: B!, no longer extant); Colombia, Antioquia, S. of Medellín, SE of Caldas, (Alto de?) Morrogil, *Juncosa & Misas* 1090 (neotype here designated: US!; isoneotype: MO!).
- Heppiella karsteniana* Fritsch, *Bot. Jahrb. Syst.* 50:402. 1913.—TYPE: Colombia, Quindío, *Karsten* 5373 (holotype: W!).
- Heppiella rosea* Fritsch, *Bot. Jahrb. Syst.* 50:400. 1913.—TYPE: (holotype at B no longer extant); Peru, Ayacucho, between Tambo and Río Apurímac, above Ayna, *Weberbauer* 5612 (lectotype here designated: F!; isolectotypes: G!, GH!).
- Heppiella scandens* Fritsch, *Bot. Jahrb. Syst.* 50:401. 1913.—TYPE: Ecuador, *Sodi* 119/8 (holotype: B!, no longer extant); Ecuador, Imbabura, Intag, Hacienda Tollo, *Heinrichs* 785 (neotype here designated: NY!; isoneotype: G!).
- Heppiella trianae* Fritsch, *Bot. Jahrb. Syst.* 50:402. 1913.—TYPE: (holotype at B no longer extant); Colombia, Cundinamarca, Bogota, *Triana* 2528 (lectotype here designated: US!; isolectotypes: G!, MANCH!, W!).
- Heppiella grandifolia* Fritsch, *Bot. Jahrb. Syst.* 54(Beibl. 119):29. 1916.—TYPE: (holotype at B no longer extant); Peru, Junín, Río Masamerich (Río Pontachuelo), *Weberbauer* 6651 (lectotype here designated: US!, isolectotypes: F!, GH!, S!).
- Notes on typification and nomenclature.* *Gesneria ulmifolia*: Skog (1976b) discussed *Chorisanthera atrosanguinea*.
- Heppiella pauciflora*: Hanstein (1859) cited the duplicates from LE and W but selected no holotype.
- Heppiella scandens*: The specimen selected as neotype is the only currently known collection that had been annotated as *H. scandens* in Berlin in the late 1930's, when the type of *H. scandens* was still extant. The collection matches the description of Fritsch, being a scandent shrub from a relatively dry area, and looks rather distinctive mainly due to its reduced indumentum.
- Heppiella warszewiczii*: It is with considerable uncertainty that *H. warszewiczii* is treated as a synonym of *H. ulmifolia* rather than *H. verticillata*. In favor of the latter possibility one might consider two collections of *H. verticillata* (*Heinrichs* 129; *Schimpff* 624) both identified in the 1930's as *H. warszewiczii* in Berlin, possibly by comparison with the later lost type. However, according to Hanstein (1859), *H. warszewiczii* has glandular trichomes, which never occur in *H. verticillata*, and is very similar to *H. stenocalyx* from central Colombia, here treated as a synonym of *H. ulmifolia*. In addition, the corolla length of *H. warszewiczii* given by Hanstein is within the range of that in *H. ulmifolia* while *H. verticillata* has smaller flowers. Finally, according to the itinerary given by Diels (1937), it is doubtful that *Warszewicz* ever collected within the distributional range of *H. verticillata*. Consequently, a Colombian collection of *H. ulmifolia* with glandular trichomes has been selected as the neotype.
- Illustrations.* Fig. 1B (stomata), 2B (seed), 6A, B (habit and flower); Hoehne 1970 (pl. 160, as *H. viscida*).
- Subshrubs to shrubs, occasionally climbing, terrestrial or epipetric. Stems erect, decumbent or pendulous, 20–200 cm long, frequently scandent, pilose, occasionally glandular hairy, the base usually with scaly rhizomes and stolons; internodes (0.5)2–7(15) cm long. Leaves opposite, less commonly ternate; blades ovate, less commonly elliptic, rarely oblanceolate, (1.5)3–8(14) cm long, (1)2–5(7) cm wide, apex acute;

base cordate to truncate or rounded; adaxial surface often bullate and bristly, less commonly plane and appressed pilose to tomentose, occasionally glandular hairy; petioles 2–12(25) mm long. Inflorescences axillary, of (1)2–7(12) congested flowers, rarely exceeding the length of the leaves, the bracts 2–6, ovate to lanceolate, 1–10 mm long, 0.5–4.0 mm wide, often caducous; peduncles usually absent but occasionally 1–4(10) mm long, pedicels 1–3 cm long. Calyx 5–9(12) mm long, lobes lanceolate, rarely subulate, 3–5(7) mm long, the base 1–2 mm wide; corolla red, 15–22 mm long, the tube villous outside, the base 2–4 mm in diam., throat 3–6 mm in diam., the lobes 2.0–3.0 mm long and 2.0–2.5 mm wide at base, outside villous, occasionally with glandular trichomes at margin, inside glabrous; filaments 15–22 mm long, anthers 1.5–2.0 mm long, 1.0–1.5 mm wide, exerted, staminode 1.5–2.0 mm long, nectary annular, often shallowly lobed; style 13–19 mm long, stigma exerted. Capsule 6–11 mm long, 4–7 mm in diam., bivalved, loculicidal; seeds with wide grooves between striations. $n = 13$ (Wiehler 1972).

Representative collections examined (230 seen). COLOMBIA. **Antioquia:** Jericó, *Daniel* 2442, 2449 (US). **Cauca:** Popayán-San Agustín road, close to Conuco, *Londoño & Kvist* 87 (AAU, COL, QCA, TULV, US, USM, VEN). **Cundinamarca:** 25 km NNW of Bogotá, Salto de Tequendama, *Smith & Idrobo* 1089 (F, GH, US). **Meta:** Between Susumuco and Villavicencio, *André* 789 (NY). **Nariño:** Ipiales, Las Lajas, *García-Barriga* 7759 (COL, US). **Putumayo:** Laguna de la Cocha, *García-Barriga* 7826 (US). **Quindío:** Old Quindío trail, Salento to "Laguneta," *Killip & Hazen* 9111 (GH, NY, PH, US). **Tolima:** Río Bugala Grande, Cerro de la Laguna, *Cuatrecasas* 20852 (F, US). **Valle:** Cali-Loboguerrero road, sideroad to San Antonio, km 16, *Luteyn & Lebrón-Luteyn* 6976 (NY, SEL).

ECUADOR. **Azuay:** Sanaguín, Río Patul, *Steyermark* 52579 (F, US). **Bolívar:** E of Echéandia, *Holm-Nielsen & Andrade* 18598 (AAU). **Cañar:** Road Cuenca-Guaquail, between Ducar and Cochancay, *Harling & Andersson* 14582 (GB, SEL). **Carchi:** Road El Carmelo-Tulcán, *Balsev et al.* 2637 (AAU). **Cotopaxi:** Along Río Toachi, Pilaló, *Holm-Nielsen* 23505 (AAU). **Chimborazo:** Huigra, *Camp* 3130 (AAU, NY, SEL, US—3 sheets). **El Oro:** Zaruma, *Espinosa* 1761 (US). **Imbabura:** 30 km W of Ibarra, Laguna Cui-cocha, *Holm-Nielsen et al.* 6335 (AAU, F, MO, NY, US). **Pichincha:** New Quito-Santo Domingo road, *Kvist & Barfod* 49062 (AAU—2 sheets, QCA, QCNE).

PERU. **Ayacucho:** Between Huanta and Río Apu-

rimac, *Ccarrapa, Killip & Smith* 22329 (NY, US). **Huancavelica:** Below Marcavalle, SE of Huachocolpa, *Tovar* 4735 (US). **Junin:** Agua Dulce, *Woytkowski* 35452 (F, MO—2 sheets, UC).

Distinguishing features. Although *Heppiella ulmifolia* is variable it is easily distinguished from the three rarer species. The long-pedunculate inflorescences set *H. viscida* apart, the small flowers with included anthers identify *H. verticillata* (fig. 6C), and the long creeping rhizomes with short erect shoots having single, long-pedicellate flowers in the leaf axils characterize *H. repens* (fig. 6E).

Variation. The many synonyms of *Heppiella ulmifolia* reflect the variable vegetative features, in contrast to the relatively stable floral features. Typical *H. ulmifolia* itself represents the dominant form of plants in Ecuador and western Colombia with ovate, eglandular leaves with bullate, hispid upper surfaces. The Ecuadorean synonyms *H. ampla* and *H. guazumaefolia* are based on plants with elliptic to oblanceolate leaves having plane surfaces with little indumentum. The Colombian synonyms *H. karsteniana*, *H. pauciflora*, *H. stenocalyx*, *H. trianae*, and probably *H. warszewiczii* (see notes on typification and nomenclature) are based on specimens with ovate leaves with plane, tomentose upper leaf surfaces. The Peruvian plants named *H. rosea* and *H. grandifolia* are rather similar to those from Colombia and like many of these have glandular trichomes. Finally *H. scandens* is apparently rather distinct (see notes on typification and nomenclature).

Distribution. *Heppiella ulmifolia* occurs in the western Andean Cordillera of Ecuador, the Colombian highland, and a disjunct area of central Peru (fig. 4). The species has been collected from 800 to 3700 meters, but is only common between 1700 and 3200 meters.

3. *HEPPIELLA VERTICILLATA* (Cav.) Cuatrec., *Anales Ci. Univ. Madrid* 4:259. 1935.—*Gesneria verticillata* Cav., *Icon.* 6:62, pl. 585. 1801.—*Isoloma verticillata* Decne., *Rev. Hort.* 20(Ser. 3,2):465. 1848.—TYPE: Ecuador, Chimborazo, between Guaranda and Chimborazo, *Nee s.n.* (holotype: MA!; isotypes: MA—3 sheets!).

Heppiella parviflora Fritsch, *Bot. Jahrb. Syst.* 50: 401. 1913.—TYPE: Ecuador, Tungurahua, Baños, *Spruce* 4975 (holotype: W!; isotypes:

C!, CGE!, E!, G!, GH!, K!, LE!, NY!, P!, W!, WAG!).

Illustrations. Fig. 1C (stomata), 2C (seed), 6C (flower); Cavanilles 1801 (pl. 585).

Herbs to subshrubs, terrestrial or epipetric. Stems decumbent or erect (2)10–100(200) cm long, occasionally branching, pilose, the base usually with scaly rhizomes and stolons; internodes 1–10 cm long. Leaves opposite, rarely ternate or appearing whorled due to short shoots in the leaf axils; blades ovate to elliptic, less commonly oblanceolate, 1.5–6(10) cm long, 0.8–3(4) cm wide; apex acute; base acute to rounded; margin often revolute; adaxial surface often bullate, bristly; abaxial surface often with a purple sheen; petioles 2–7 mm long. Inflorescences axillary, of (1)3–10 congested flowers, the bracts 2–6, 1–4 mm long, 0.5–2.0 mm wide, caducous; flowering shoots often appearing racemose with reduced bract-like subtending leaves towards the apex; peduncles usually absent, occasionally up to 5 mm long, pedicels 1.0–2.5 cm long. Calyx 4–8 mm long, lobes triangular to lanceolate, 2.5–5.0 mm long, the base 1.0–1.5 mm wide; corolla red, 9–11 mm long, tube sericeous outside, 1.5–2.0 mm in diam. at base, 3–4 mm in diam. at throat, lobes 1.5–2.0 mm long, 2.0–3.0 mm wide at base, outside sericeous, inside pilose; filaments 6–8 mm long, anthers 1.0–1.5 mm long, 0.6–0.9 mm wide, included, staminate node 2–3 mm long; nectary annular, sometimes shallowly lobed; style 4–5 mm, stigma included. Capsule 5–6 mm long, 3–4 mm in diam., bivalved, loculicidal; seeds with wide grooves between striations.

Representative collections examined (48 seen). COLOMBIA. **Nariño:** San Francisco-Mocoa road, *Mora* 4399 (COL). **Putumayo:** Between Sachamates and San Francisco de Sibundoy, Quebrada de Susunga, *Cuatrecasas* 11455 (F, US); Sibundoy, *Foster et al.* 1998 (COL, GH); Planado de Minchoy, *Londoño & Lozano* 223 (AAU, COL, TULV, US).

ECUADOR. **Chimborazo:** Road Riobamba-Baños, close to Puela, *Lugo* S. 566 (GB, SEL). **Napo:** Road Baeza-Lago Agrio, km 18, *Balslev & Madsen* 10547 (AAU, COL, F, MO, NY, SEL); 10 km E of Santa Bárbara, Sibundoy, *Kvist et al.* 60249 (AAU, QCA, QCNE, US); Road between Santa Bárbara and Sibundoy, *Kvist et al.* 60267 (AAU, NY, QCA, QCNE, US); Tena-Baeza road, 2 km S of Cosanga, *Kvist et al.* 60342 (AAU, QCA, US); Baeza, *Kvist et al.* 60395 (AAU, QCA, QCNE, US). **Tungurahua:** Río Verde, *Heinrichs* 129 (G, MA,

NY); Confluence of Río Pastaa and Río Ulva, *Kvist* 60310 (AAU, QCA, US); E of Baños, *Schimpff* 624 (G, MO).

Distinguishing features. The small flowers with included anthers and stigma characterize *Heppiella verticillata* (fig. 6C).

Distribution. *Heppiella verticillata* is fairly common in the eastern Andean Cordillera of Ecuador, while only the few cited collections are known from adjacent southern Colombia. *Heppiella verticillata* and *H. ulmifolia* basically have been collected in the eastern and western Andean Cordillera, respectively (fig. 4). The only exception is the type of *H. verticillata* as Nee apparently made this collection in the western Cordillera. According to the itinerary of Nee given by Diels (1937) the expedition actually did go to Prov. Chimborazo, which suggests the type locality is correct.

H. verticillata has been collected from 1200 to 2800 meters elevation, and is commonly found between 1500 and 2500 meters.

4. HEPPIELLA VISCIDA (Lindley et Paxton) Fritsch, *Nat. Pflanzenfam.* 4(3b):176. 1894.—*Achimenes viscida* Lindley et Paxton, *Paxton's Fl. Gard.* 2:59. 1851.—*Cheirisanthera atosanguinea* Hort. ex Lindley et Paxton, *Paxton's Fl. Gard.* 2:59. 1851 (nom. nud. pro. syn.).—*Corysanthera atosanguinea* Decne. ex Regel, *Gartenflora* 1:40. 1852.—*Achimenes populifolia* Wagner ex Regel, *Gartenflora* 1:40. 1852 (nom. nud. pro syn.).—*Heppiella atosanguinea* Regel, *Gartenflora* 2:353. 1853.—*Cheirisanthera coccinea* Hort. ex Regel, *Gartenflora* 2:353. 1853 (nom. nud. pro syn.).—TYPE: Horticultural material brought to England from continental Europa but the original (Venezuelan) locality not known (holotype: CGE!).

Chorisanthera atosanguinea Hort. ex Héring, *Horticulteur Franc.* 2:1. 1852.—TYPE: Described from cultivation, plate 4 in *Horticulteur Franc.* 2 (here designated) (incorrectly described as a synonym of *Gesneria ulmifolia* Kunth = *Heppiella ulmifolia* (Kunth) Hanst.).

Heppiella cordata Klotzsch et Hanst. in *Hanstein, Linnaea* 29: 512, 551. 1859.—TYPE: (holotype at B no longer extant); Venezuela, Merida, Mucuchies, *Moritz* 1129 (lectotype

here designated: K!; isolectotypes: BM!, BR!, CGE!, HBG!, K—3 sheets!, P!, W!).

Heppiella ovata Klotzsch et Hanst. in Hanstein, *Linnaea* 29:512, 551. 1859.—TYPE: (holotype at B no longer extant); Venezuela, Merida, Mucuchies, *Moritz 1128* (lectotype here designated: K!; isolectotypes: BM!, BR!, L!, W!).

Notes on typification and nomenclature. Skog (1976b) discussed *Corysanthera atrosanguinea* and *Chorisanthera atrosanguinea*.

Illustrations. Fig. 1D (stomata), 2D (seed), 3B (pollen); Lindley and Paxton 1851 (pl. 165); Hérisincq 1852 (pl. 1); Regel 1853 (pl. 70); Hoehne 1970 (pl. 159, as *Heppiella* sp.).

Herbs or subshrubs, terrestrial or epipetric, glandular hairy, sticky; stems erect, decumbent, or less commonly pendulous, 30–100 cm long, occasionally branching, the base with scaly rhizomes and stolons; internodes 2–10 cm long. Leaves opposite or ternate; blades ovate, occasionally elliptic, (2)3–7(10) cm long, (1.0)1.5–4.5(6.0) cm wide; apex acute; base acute to rounded; adaxial surface tomentose; petioles 5–20(30) mm long. Inflorescences pedunculate, of 3–10(25) flowers, the bracts 2–10, 1.5–10 mm long, 0.5–3.0 mm wide, caducous; peduncles (1.5)3–5(6) cm long, pedicels 1–2 cm long. Calyx 7–9 mm long, lobes lanceolate, 5–6 mm long, the base 2.0–2.5 mm wide; corolla red, 14–20 mm long, tube pilose to villous outside, 1.5–2.5 mm in diam. at base and 3–5 mm in throat, lobes 3–5 mm long and 3–4 mm wide at base, outside villous and usually glandular hairy, inside glabrous; filaments 15–18 mm long, anthers 1.7–2.0 mm long, 1.0–1.2 mm wide, subincluded, staminode usually 2–4 mm long, occasionally 9–11 mm and partly fertile; nectary annular, occasionally shallowly lobed; style 11–13 mm long, sigma exerted. Capsule 6–8 mm long, 3–4 mm in diam., bivalved, loculicidal; seeds with narrow, closely spaced striations. $n = 26$ (Wiehler 1972).

Representative collections examined (26 seen). VENEZUELA. **Barinas:** Santo Domingo-Baranitas road, *Boer 2003* (K). **Merida:** Between Timotes and Chachopo, *Alston 6543* (BM, F, US); 15 km NNE of Merida, La Mucuy, *Breteler 3458* (G, NY, US); Mucuruba, Quebrada del Pueblo, *Gehriger 281* (F, G, US). **Trujillo:** La Puerta to Timotes, *Jahn 1139* (US); Siliquieii, *Linden 288* (BM, G, K, W—2 sheets); Bocono, road to Cerro Guaramacal, around Laguna de "Los Cerros", *Stergios 1682* (US).

Distinguishing features. *Heppiella viscida* is closely related to *H. ulmifolia* and could possibly be reduced to a subspecies of this variable species. However, the allopatric distribution of the two taxa, and the fact that the long-pedunculate inflorescences easily distinguish *H. viscida* from *H. ulmifolia*, make it practical to preserve the specific rank of *H. viscida*. In addition, some minor differences exist: *H. viscida* has subincluded anthers and a relatively narrow corolla throat, while *H. ulmifolia* has exerted anthers and a wider throat (table 2), and the seed striations are narrower and closer in *H. viscida* (fig. 2B, D).

Distribution. *Heppiella viscida* is restricted to the highlands of northwestern Venezuela (fig. 4). The species ranges from 1500 to 3300 meters elevation, and is most frequent between 1900 and 2900 meters.

The closest occurrence of *H. ulmifolia* is in the region around Bogotá in Colombia (fig. 4). Lindley and Paxton (1851) stated that the origin of *Achimenes viscida* was unknown, but Regel (1852) claimed that Wagner had collected the plant in Colombia under the name *Achimenes populifolia*. Later Regel (1853) simply stated that *H. viscida* comes from Colombia. Hanstein (1859) cited both Venezuelan (*Moritz 1129*) and Colombian (*Linden 793*) collections, when he described *H. cordata* (synonym of *H. viscida*). In the same paper he published *H. pauciflora* (synonym of *H. ulmifolia*), using the same Linden collection as the type!

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