

REORGANIZATION OF TRIBAL AND GENERIC BOUNDARIES IN THE GLOXINIEAE (GESNERIACEAE: GESNERIOIDEAE) AND THE DESCRIPTION OF A NEW TRIBE IN THE GESNERIOIDEAE, SPHAERORRHIZEAE

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ABSTRACT. Morphological and molecular studies in tribe Gloxinieae have led to the need to describe four new genera and one new tribe, with two historically recognized genera resurrected and three currently recognized genera submerged into other generic concepts. The new genera *Gloxinella*, *Gloxiniopsis*, *Nomopyle*, and *Sphaerorrhiza* include species previously treated in *Gloxinia*. The genus *Sphaerorrhiza* also is treated as a new tribe because of its distant phylogenetic relationship to the Gloxinieae. *Mandirola* and *Seemannia* have been resurrected to define monophyletic groups of species previously treated in *Gloxinia*. The genera *Anodiscus* and *Koellikeria* have been submerged into the new circumscription of *Gloxinia* to reflect phylogenetic relationships and morphological similarities among the species of these genera. The circumscription of *Kohleria* is here broadened to include *Capanea*. In all, seven generic transfers of already available names are made as well as 11 new combinations: *Gloxinella lindeniana*, *Gloxinia erinoides*, *G. xanthophylla*, *Gloxiniopsis racemosa*, *Kohleria affinis*, *K. tigridia*, *Mandirola rupestris*, *Nomopyle dodsonii*, *N. peruviana*, *Sphaerorrhiza sarmentiana*, and *S. burchellii*.

Key words: Gesneriaceae, Gesnerioideae, Gloxinieae, Sphaerorrhizeae

INTRODUCTION

Recent studies of phylogenetic relationships in Gesneriaceae subfamily Gesnerioideae (Zimmer et al. 2002) and tribe Gloxinieae (Roalson et al. 2003, Smith et al. 2004, Roalson et al. 2005, E. Roalson et al. unpubl. data) have suggested that tribal and generic boundaries in these groups require extensive reorganization. This paper begins the process of reorganizing generic boundaries in tribe Gloxinieae, reinstating old generic concepts for some groups, and creating new generic names where necessary. A characterization of the phylogenetic relationships of genera (as circumscribed here) within the Gloxinieae is presented in FIGURE 1. The currently accepted species for all genera of the tribe are enumerated below; complete synonymies for the species are listed by Skog and Boggan (2005). The placement of some species is tentative, as they have not been sampled in previous molecular phylogenetic studies. The species that have been sampled in these phylogenetic studies are denoted with an asterisk (*) in the species lists below. Where species identity is unclear or the

current generic placement of a taxon is clearly wrong, but there is not reasonable support for its placement in the generic concepts presented here, we have dealt with the taxon as *incertae sedis*. Further work will be necessary to determine the placement of these taxa. The problems associated with delimitation and polyphyly of *Phinaea* (Smith et al. 2004, Roalson et al. 2005) will be addressed in a separate publication (J. Boggan et al. unpubl. data). Finally, some taxa previously placed in the Gloxinieae, but for which there is now good evidence that they belong elsewhere, are discussed and their classification position is clarified. Among the most significant results of these studies are that *Gloxinia* sensu Wiehler (1976, 1983) is a polyphyletic assemblage that requires considerable reorganization, and that *Gloxinia sarmentiana* should not only be excluded from the genus *Gloxinia* but from tribe Gloxinieae. A key to genera of the recircumscribed Gloxinieae and a key to Gesnerioideae tribes with inferior or half-inferior ovaries are presented.

GLOXINIEAE FRITSCH

Achimenes C.H.Persoon, Syn. Pl. 2: 165. 1807
[Nov 1806], nom. cons. against *Achimenes*

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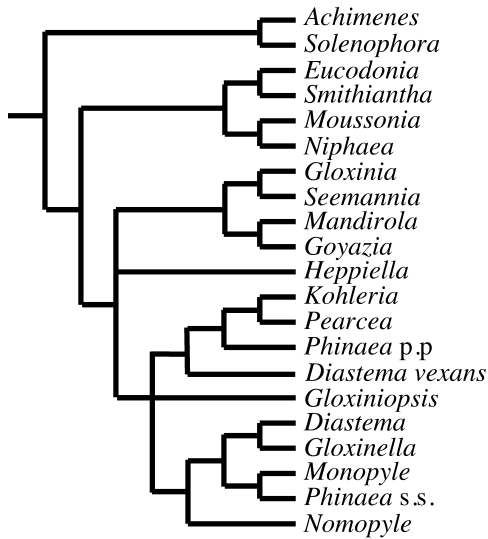


FIGURE 1. Hypothesis of phylogenetic relationships among genera based on the studies of Roalson et al. (2005) and E. Roalson et al. (unpubl. data).

P.Browne 1756, and Vahl 1791 (Scrophul.).
TYPE SPECIES: *Achimenes coccinea* (Scopoli) C.H.Persoon (= *A. erecta* (Lam.) H.P.Fuchs).

The genus includes **Achimenes admirabilis* Wiehler, **A. antirrhina* (DC.) C.V.Morton, **A. brevifolia* C.V.Morton, **A. candida* Lindley, **A. cottoana* H.E.Moore, **A. dulcis* C.V.Morton, **A. erecta* (Lamarck) H.P.Fuchs, **A. fimbriata* Rose ex C.V.Morton, **A. flava* C.V.Morton, **A. glabrata* (Zuccarini) Fritsch, **A. grandiflora* (Schiede) DC., **A. heterophylla* (C.F.P.Martius) DC., **A. hintoniana* A.Ramírez-Roa & L.E.Skog, **A. longiflora* DC., **A. mexicana* (B.C.Seemann) G.Bentham & J.D.Hooker ex Fritsch, **A. misera* Lindley, **A. nayaritensis* L.E.Skog, **A. obscura* C.V.Morton, **A. occidentalis* C.V.Morton, **A. patens* G.Bentham, **A. pedunculata* G.Bentham, **A. saxicola* (Brandegge) C.V.Morton, **A. skinneri* Lindley, **A. warszewicziana* (Regel) H.E.Moore, and **A. woodii* C.V.Morton.

Achimenes has undergone reorganization several times in the last 30 years (particularly Wiehler 1976, Ramírez-Roa 1987). Molecular phylogenetic tools recently have been used to explore phylogenetic relationships and floral evolution in the genus (Roalson et al. 2003). There appear to be three or four major lineages of *Achimenes* (Roalson et al. 2003, E. Roalson et al. unpubl. data), and the genus may not be monophyletic, with *Solenophora* possibly nested within *Achimenes* (E. Roalson et al. unpubl.

data), although currently we cannot exclude the possibility that *Achimenes* is monophyletic (E. Roalson et al. unpubl. data). *Achimenes* as currently circumscribed is morphologically heterogeneous, and if eventually shown to be paraphyletic with regard to *Solenophora*, it may be necessary to resurrect the genera *Dicyrta* Regel and *Plectopoma* Hanstein to include those species of *Achimenes* that may be more closely related to *Solenophora*. If this is the case, *Dicyrta* would likely include *Achimenes brevifolia*, *A. obscura*, and *A. misera*, and *Plectopoma* would include *A. glabrata*, as *Plectopoma fimbriatum* (W.J. Hooker) Hanstein. Further study of phylogenetic relationships will be needed to assess whether these generic recircumscriptions are necessary.

Diastema G.Bentham, Bot. Voy. Sulphur 132. 1844 [14 Apr 1845]. TYPE SPECIES: *Diastema racemiferum* G.Bentham.

The genus includes **Diastema affine* Fritsch, **D. comiferum* (DC.) G.Bentham ex Walpers, **D. eggerianum* Fritsch, **D. gymnoleuca* Gilli, **D. hispidum* (DC.) Fritsch, **D. kalbreyeri* Fritsch, **D. latiflorum* Rusby, **D. lehmannii* Regel, **D. maculatum* (Poeppig) G.Bentham ex Walpers, **D. micranthum* J.D.Smith, **D. purpurascens* Rusby, **D. quinquevulnerum* J.E.Planchon & Linden, **D. racemiferum* G.Bentham, **D. rupestre* Brandegge, **D. scabrum* (Poeppig) G.Bentham ex Walpers, **D. sodiroanum* Fritsch, **D. tenerrimum* (Poeppig) G.Bentham ex Walpers, **D. urticifolium* (Poeppig) G.Bentham ex Walpers, **D. vexans* H.E.Moore, **D. weberbaueri* Fritsch, and **D. williamsii* Rusby.

Although badly in need of revision, *Diastema*, as a genus, is morphologically well defined; and there is little doubt about its generic boundaries (but see below). Among its key characters are a racemose flowering axis consisting of solitary flowers in the axils of bracts on stems with (usually) condensed internodes; a nectary consisting of 5 long, finger-like glands; and a distinctive bilabiate stigma. In addition, most (but not all) species have small white flowers with a single purple blotch on each lobe. All of these are characters not found in other taxa of Gloxinieae, including *Gloxinella*, which is the probable sister-taxon of *Diastema*.

Although collections usually can be assigned easily to this genus, assigning them to a species is more problematic. Forty-six names have been described in *Diastema*, but it is unclear how many species should be recognized; several species are known only from their type collections and should probably be synonymized under other species, whereas the circumscriptions of some of the more common and widespread species (e.g., *D. racemiferum*) may be overly broad.

Diastema vexans H.E.Moore poses a particular problem. Although agreeing with other species of *Diastema* in several characters (nectary configuration, stigma type, fruit type, and a small white flower with a purple blotch on each lobe), *D. vexans* differs in its inflorescence structure (1–4 flowered, usually bracteolate, pair-flowered cymes in the axils of foliar leaves). Phylogenetic studies (Roalson et al. 2005) show *D. vexans* to belong to a clade including *Kohleria* and *Pearcea* rather than the clade with all other *Diastema*. In this case, the discrepancy between morphology and phylogeny is especially striking, and *D. vexans* and its relationship to the rest of the genus should be further investigated. One possibility is that *D. vexans* represents an ancient hybridization event between early members of the *Pearcea/Kohleria* and *Diastema* clades (or conversely, that the rest of *Diastema* had its origin in a hybrid between these two clades). As *Diastema* is in need of extensive revision, and we have not examined the type specimen of *D. vexans*, for now we retain this species as a dubious member of *Diastema*.

Eucodonia Hanstein, *Linnaea* 26: 200–201. 1853 [Apr 1854]. TYPE SPECIES: *Eucodonia ehrenbergii* Hanstein (= *E. verticillata* (Martens & Galeotti) Wiehler).

The genus includes **Eucodonia andrieuxii* (DC.) Wiehler and **E. verticillata* (Martens & Galeotti) Wiehler.

Molecular results (Zimmer et al. 2002, Roalson et al. 2003, Smith et al. 2004, Roalson et al. 2005, E. Roalson et al. unpubl. data) support the separation of this genus from *Achimenes* as discussed by Wiehler (1976, 1983).

Gloxinella (H.E.Moore) E.H.Roalson & J.K. Boggan, gen. nov., stat. nov. *Kohleria* sect. *Gloxinella* H.E.Moore, *Gentes Herb.* 8: 382. 1954. TYPE SPECIES: *Gloxinella lindeniana* (Regel) E.H.Roalson & J.K.Boggan.

Plants weak-stemmed herbs with scaly rhizomes, often produced at the tips of long stringy rhizomes; indumentum villous, lacking uncinat trichomes. **Leaves** opposite, equal, with 6–8 pairs of veins. **Flowers** epedunculate, ebracteolate, solitary in the leaf axils; corolla lavender, lobes subequal, entire; nectary annular, sometimes slightly 5-lobed; ovary inferior; stigma broadly stomatomorphic to obscurely bilobed. **Fruit** an ovoid to elliptic fleshy capsule, dehiscent along the dorsal side and splitting the hypanthium to the base. **Seeds** numerous, minute, rhombic to broadly ellipsoid, almost as broad as long.

The genus includes **Gloxinella lindeniana* (Regel) E.H.Roalson & J.K.Boggan.

Gloxinella lindeniana (Regel) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Tydaea lindeniana* Regel, *Gartenflora* 17: 257, pl. 589. 1868. Synonyms: *Gloxinia lindeniana* (Regel) Fritsch, *Oesterr. Bot. Zeit.* 63: 66. 1913. *Kohleria lindeniana* (Regel) H.E. Moore, *Gentes Herb.* 8: 380. 1954. TYPE: *Regel, s.n.* (LE, not seen).

Tydaea lindeniana Regel has been shuttled among several genera in its taxonomic history, suggesting that it fits well into none of them. Placed in *Gloxinia* by Fritsch (1913), it was later transferred to *Kohleria* by Moore (1954), who created the monotypic section *Gloxinella* to accommodate it. Wiehler (1976) transferred the species back to *Gloxinia* and listed *Kohleria* sect. *Gloxinella* as a synonym of *Gloxinia*. The species is here removed from both genera, and Moore's sectional name raised to generic rank, because this species does not belong to either of the clades containing the type species of these two genera (Roalson et al. 2005, E. Roalson et al. unpubl. data).

Fruit characters, in particular, set this species morphologically apart from *Gloxinia*, as defined here. Parsimony analyses (Roalson et al. 2005) weakly or moderately support *G. lindeniana*, sister to *Diastema*, or *Diastema* + *Gloxinia dodsonii* (= *Nomopyle dodsonii*, see below). Bayesian analyses moderately support the *G. lindeniana/Diastema* relationship (E. Roalson et al. unpubl. data). While the exact placement of *G. lindeniana* is somewhat variable depending on the analysis conducted, the species clearly is not closely related to *Gloxinia perennis*. We are here recognizing this species in its own genus rather than in its likely sister group, *Diastema*, since *G. lindeniana* does not share several apparent synapomorphies for *Diastema* (*Diastema*-type bilabiate stigma, nectary of 5 elongate, finger-like glands, flowering stems racemose). The general vegetative and floral aspect of *Gloxinella lindeniana* also is unlike that of any *Diastema*.

Gloxinia L'Heritier, in Aiton, *Hort. Kew* 2: 331. 1789. TYPE SPECIES: *Gloxinia maculata* L'Heritier, nom. illeg. (= *Martynia perennis* L.), *Gloxinia perennis* (L.) Fritsch, in A. Engler & Prantl, *Nat. Pflanzenfam.* 4(3b): 174. 1894.

Plants erect herbs with scaly rhizomes (rhizomes absent in *Gloxinia xanthophylla*), nearly glabrous to pilose, lacking uncinat trichomes. **Leaves** opposite (rarely ternate), with 5–9 (–12) pairs of veins. **Flowers** raceme-like flowering stems with leaves reduced to opposite or alternate bracts bearing solitary ebracteolate flowers;

corolla white, pink, purple, or brownish, lobes subequal to unequal, entire to toothed or fimbriate; nectary absent or annular; ovary half-inferior to inferior; stigma capitate to stomatomorphic. **Fruit** an ovoid to elliptical dry rostrate capsule, loculicidally dehiscent without splitting the hypanthium. **Seeds** numerous, minute, rhombic to ellipsoid.

The genus includes **Gloxinia erinoides* (DC.) E.H.Roalson & J.K.Boggan, **G. perennis* (L.) Fritsch, and **G. xanthophylla* (Poeppig) E.H.Roalson & J.K.Boggan.

Gloxinia erinoides (DC.) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Achimenes erinoides* DC., Prodr. 7: 536. 1839. Synonym: *Koellikeria erinoides* (DC.) R.Mansfeld, Repert. Spec. Nov. Regni Veg. 38: 28. 1935. TYPE: Venezuela—Districto Federal, Vargas, J. 1630 (holotype, G-DC).

Gloxinia xanthophylla (Poeppig) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Gesneria xanthophylla* Poeppig, in Poeppig & Endlicher, Nov. Gen. Sp. Pl. 3: 7. 1840. Synonym: *Anodiscus xanthophyllus* (Poeppig) R.Mansfeld, Repert. Spec. Nov. Regni Veg. 36: 124. 1934. TYPE: Peru—Chihuaneila, *E.Poeppig*, s.n. (holotype, W).

Wiehler (1976, 1983) favored a broad circumscription of *Gloxinia*, primarily on the basis of hybridization studies. Both molecular and morphological studies indicate that *Gloxinia* sensu Wiehler is polyphyletic and requires extensive reorganization.

Phylogenetic studies demonstrate that the type species of *Gloxinia*, *G. perennis*, is most closely related to *Anodiscus xanthophyllus* and *Koellikeria erinoides* (Zimmer et al. 2002, Roalson et al. 2005), and this relationship is reflected in their morphology. Although a relationship between *Anodiscus* and *Koellikeria* previously had been suggested (Wiehler 1983), the association of these genera with *Gloxinia perennis* (or with any species of *Gloxinia* s.l.) is novel. The most striking resemblance between these three species is the raceme-like flowering stem, with flowers solitary in the axils of strongly reduced bract-like leaves. Although similar arrangements are found in some other taxa in tribe Gloxinieae (notably the genera *Diastema*, *Gloxiniopsis*, and *Smithiantha*), we consider this general resemblance to reflect convergence rather than common ancestry. Given the close phylogenetic relationship and the distinctive morphological similarity, we here transfer *Koellikeria* and *Anodiscus* to a much restricted (but morphologically better-defined) *Gloxinia*.

For other species included in *Gloxinia* by

Wiehler (1976), see the genera *Gloxinella*, *Gloxiniopsis*, *Mandirola*, *Nomopyle*, *Seemannia*, *Sphaerorrhiza*, and *incertae sedis* species. Among these species, *Gloxiniopsis racemosa* is most similar to *Gloxinia perennis*, but differs in other key characters (most notably the fruit); and our phylogenetic analyses place it well outside the clade containing *G. perennis*.

Seemannia, *Mandirola*, and *Goyazia* are members of a clade including *Gloxinia* as defined by us, but we consider them to be morphologically distinct enough to merit recognition at the generic level. Although the *Gloxinia/Seemannia/Goyazia/Mandirola* clade could be partitioned in several ways, with anywhere from one to six monophyletic genera, we find that the generic circumscriptions proposed here best reflect the phylogenetic relationships and pattern of morphological variation. Given the shared inflorescence characteristics of *Gloxinia perennis*, *G. erinoides*, and *G. xanthophyllus*, this seems to be a cohesive generic unit. Similarly, the historically recognized *Seemannia* forms a monophyletic group and can be defined by several synapomorphies, including stringy aerial rhizomes, an elongated pointed stigma, and barrel-shaped trichomes in the corolla. The generic boundaries of *Mandirola* and *Goyazia* are somewhat more problematic as the species and generic boundaries of the included species are quite difficult to discern. We here have moved some *Gloxinia* species into *Mandirola* rather than combining them with *Goyazia*, which would require recognizing the entire group as *Mandirola* rather than *Goyazia*; and the *Mandirola* species do not share the *Goyazia* synapomorphies of pericraspedodromous-patterned leaf veins and a coriaceous leaf texture. While the exact boundaries of these genera require further study, we consider this organization to be the most reasonable, as inferred by the distribution of morphological characters and phylogenetic relationships (Roalson et al. 2005, E. Roalson et al. unpubl. data).

Gloxiniopsis E.H.Roalson & J.K.Boggan, gen. nov. TYPE SPECIES: *Gloxiniopsis racemosa* (G.Bentham) E.H.Roalson & J.K.Boggan.

Inter generes tribus Gloxinieae in fascibus vascularibus petiolorum profunde lunate dispositis differt; a *Diastema*, *Monopyle*, et *Phinaea* in corolla in calyce obliquo differt; a *Gloxinia*, *Goyazia*, *Mandirola*, et *Seemannia* fere omni in hypanthio dorsaliter secedenti et in costis capsulae non prominentibus differt.

Plants erect herbs with scaly rhizomes. **Leaves** opposite, equal, with 9–12 (–14) pairs of veins. **Flowers** raceme-like flowering stems with leaves reduced to opposite bracts bearing solitary ebracteolate flowers, white, campanulate,

lobes subequal, lower lobes toothed; ovary inferior; stigma stomatomorphic; nectary annular and strongly reduced or possibly absent. **Fruit** a subglobose fleshy capsule, dehiscent along the dorsal surface and splitting the hypanthium to the base. **Seeds** numerous, minute, almost as broad as long.

The genus includes **Gloxiniopsis racemosa* (G.Bentham) E.H.Roalson & J.K.Boggan.

Gloxiniopsis racemosa (G.Bentham) E.H. Roalson & J.K.Boggan, comb. nov. Basionym: *Monopyle racemosa* G.Bentham, Hooker's Icon. Pl. 12: 87. 1876; Bot. Mag. 102: pl. 6233. 1876. Synonym: *Gloxinia racemosa* (G.Bentham) Wiehler, Selbyana 1(4): 387. 1976. TYPE: cultivated, collector unknown (holotype, K).

Gloxiniopsis racemosa, previously *Gloxinia racemosa*, does not appear to be closely related to any species yet sampled in phylogenetic analyses. One analysis (maximum parsimony analysis of ITS + *trnL-F* + morphology) suggests, however, that it might be sister to a clade containing *Diastema*, *Gloxinella*, *Monopyle*, *Nomopyle*, plus a portion of *Phinaea* (Roalson et al. 2005). As with several other species previously treated in *Gloxinia*, *Gloxiniopsis racemosa* is clearly not closely related to the type of *Gloxinia*, *G. perennis* (Roalson et al. 2005, E. Roalson et al. unpubl. data), despite a superficial morphological resemblance to this species. The generic name *Gloxiniopsis* refers to this similarity.

Goyazia Taubert, Bot. Jahrb. Syst. 21: 451; 11 Feb 1896. TYPE SPECIES: *Goyazia rupicola* Taubert.

The genus includes *Goyazia petraea* (S.M.Phillips) Wiehler and **G. rupicola* Taubert.

Molecular analyses show that *Goyazia* is closely related to *Mandirola* (see below), the species of which have a similar distribution in Brazil. Future studies might support combining the two into a single genus under the older name *Mandirola*. We here maintain the two groups as separate (but closely related) genera, as they differ in numerous morphological characters.

One species formerly included in *Goyazia*, *G. villosa* (Gardner) R.Howard (basionym *Tapina villosa* Gardner) was later transferred in *Gloxinia* by Wiehler (1976) but also is misplaced in that genus; it is here considered *incertae sedis* and possibly related to *Phinaea*.

Heppiella Regel, Gartenflora 2: 353. Dec 1853. TYPE SPECIES: *Heppiella viscida* (Lindley & J.Paxton) Fritsch.

The genus includes *Heppiella repens* Hanstein, **H. ulmifolia* (Kunth) Hanstein, *H. verticillata* (Cavanilles) Cuatrecasas, and **H. viscida* (Lindley & J.Paxton) Fritsch.

Heppiella includes four species as circumscribed by Kvist (1990), but the phylogenetic position of *H. repens* and *H. verticillata* have yet to be tested; and these species need to be included in phylogenetic analyses to verify the circumscription of *Heppiella*. Molecular analyses confirm the placement of *Heppiella* in tribe Gloxinieae but do not suggest a close relationship to any other genus (Roalson et al. 2005, E. Roalson et al. unpubl. data).

Kohleria Regel, Index Sem. Turic. [4]. 1847, non Regel 1851. TYPE SPECIES: *Kohleria hirsuta* (Kunth) Regel, Flora 31: 250. 1848.

The genus includes **Kohleria affinis* (Fritsch) E.H.Roalson & J.K.Boggan, **K. allenii* P.C.Standley & L.O.Williams, **K. amabilis* (J.E.Planchon & Linden) Fritsch var. *amabilis*, *K. amabilis* var. *bogotensis* (G.Nicholson) L.P.Kvist & L.E.Skog, *K. bella* C.V.Morton, *K. diastemoides* L.P.Kvist & L.E.Skog, **K. grandiflora* L.P.Kvist & L.E.Skog, **K. hirsuta* (Kunth) Regel var. *hirsuta*, *K. hirsuta* var. *longipes* (G.Bentham) L.P.Kvist & L.E.Skog, *K. hondensis* (Kunth) Hanstein, *K. inaequalis* (G.Bentham) Wiehler var. *inaequalis*, *K. inaequalis* var. *lindenii* (Hanstein) L.P.Kvist & L.E.Skog, *K. inaequalis* var. *ocellata* (W.J.Hooker) L.P.Kvist & L.E.Skog, *K. longicalyx* L.P.Kvist & L.E.Skog, *K. maculata* C.V.Morton, *K. neglecta* L.P.Kvist & L.E.Skog, **K. peruviana* Fritsch, **K. rugata* (Scheidweiler) L.P.Kvist & L.E.Skog, *K. spicata* (Kunth) Oersted, *K. stuebeliana* Fritsch, **K. tigridia* (J.H.Ohlendorff) E.H.Roalson & J.K.Boggan, **K. trianae* (Regel) Hanstein, *K. tubiflora* (Cavanilles) Hanstein, *K. villosa* (Fritsch) Wiehler var. *anisophylla* (Fritsch) L.P.Kvist & L.E.Skog, **K. villosa* var. *villosa*, **K. warszewiczii* (Regel) Hanstein, **K. sp. nov.* c2446, and **K. sp. aff. villosa* c6152 (At least one, and possibly two, undescribed species: *K. sp. nov. Clark 2446* and *K. sp. aff. villosa Clark 6152*).

Kohleria affinis (Fritsch) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Capanea affinis* Fritsch, Bot. Jahrb. Syst. 50: 434. 1913. TYPE: Colombia—Antioquia, Triana, J. 2538 (holotype, W; isotypes, FI, G, K, MANCH, P, US).

Kohleria tigridia (J.H.Ohlendorff) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Gloxinia tigridia* J.H.Ohlendorff, in Otto & Dietrich, Allg. Gartenz. 13: 376. 1845. Synonyms: *Besleria grandiflora* Kunth, in

Humboldt, Bonpland & Kunth, Nov. Gen. Sp. Pl. 2: qto. ed. 401, fol. ed. 321. 1818; Colombia, A. Humboldt & A. Bonpland s.n. (holotype, P; isotype, P). *Capanea grandiflora* (Kunth) J. Decaisne ex J.E. Planchon, Fl. Serres Jard. Eur. 5: pl. 499–500. See Hanstein 34: 291. 1865. TYPE: described from cultivation (orig. coll. Moritz 1126: Merida, Venezuela) (holotype not seen).

Recent phylogenetic studies (Smith et al. 2004, Roalson et al. 2005, E. Roalson et al. unpubl. data) have strongly supported the position of *Capanea* nested within *Kohleria*, a possibility first raised in the revision of *Kohleria* by Kvist and Skog (1992), and it is therefore submerged into *Kohleria* here. Because of the existing combination *Kohleria grandiflora* L.P. Kvist & L.E. Skog, *Besleria grandiflora* Kunth cannot be transferred to *Kohleria*; and thus the next oldest epithet, *Gloxinia tigridia* J.H. Ohlendorff, must be used. *Kohleria tigridia* is a widespread and extremely variable species whose circumscription should be examined; it is possible that one or more taxa synonymized under this name should be recognized (J.L. Clark pers. comm.).

Capanea has been traditionally separated from *Kohleria* by having an epiphytic habit, capitate stigmas, and capsules that split with four apical valves (versus terrestrial habit, bilobed stigmas, and capsules splitting with usually two apical valves in *Kohleria*). Other characters of the calyx and corolla shape and inflorescence structure are extremely similar among *Capanea* and *Kohleria* species (Kvist & Skog 1992). These similarities in combination with the phylogenetic position of *Capanea* nested within *Kohleria* have suggested that the two species of *Capanea* are best treated as specialized epiphytic *Kohleria* species.

Mandirola J. Decaisne, Rev. Hort. 20 (ser. 3. 2): 468. 15 Dec 1848. TYPE SPECIES: *Mandirola multiflora* (Gardner) J. Decaisne. Synonyms: *Achimenes* subg. *Mandirola* (J. Decaisne) Hanstein, Linnaea 34: 343. 1865. *Achimenes* sect. *Mandirola* (J. Decaisne) G. Bentham, in G. Bentham & Hooker, Gen. Pl. 2: 999. 1876.

Plants erect herbs with scaly rhizomes. **Leaves** subsessile to short-petiolate, opposite or ternate, equal to subequal, rarely unequal, with 5–6 pairs of veins. **Flowers** in axillary bracteolate cymes, often with a short peduncle (sometimes solitary); corolla pink, lavender, or purple, lobes subequal, usually distinctly toothed to fimbriate; ovary half inferior; nectary annular; stigma distinctly bilobed. **Fruit** a dry rostrate cap-

sule. **Seeds** numerous, minute, rhombic to ellipsoid.

The genus includes **Mandirola ichthyostoma* (Gardner) B.C. Seemann ex Hanstein, **M. multiflora* (Gardner) J. Decaisne, and *M. rupestris* (Gardner) E.H. Roalson & J.K. Boggan.

Mandirola ichthyostoma (Gardner) B.C. Seemann ex Hanstein, in C.F.P. Martius, Fl. Brasil. 8(1): 348. 1864. Basionym: *Gloxinia ichthyostoma* Gardner, Hooker's Icon. Pl. 5: pl. 472. 1842.

Mandirola multiflora (Gardner) J. Decaisne, Rev. Hort. 20 [ser. 3, 2]: 468. 1848. *Achimenes multiflora* Gardner, Hooker's Icon. Pl. 5: pl. 468. 1842. Synonym: *Gloxinia planalta* Wiehler. *Achimenes hirsuta* DC., non *A. hirsuta* Lindley (= *A. skinneri* Lindley). *Gloxinia hirsuta* (DC.) Wiehler.

Mandirola rupestris (Gardner) E.H. Roalson & J.K. Boggan, comb. nov. Basionym: *Achimenes rupestris* Gardner, Hooker's Icon. Pl. 5: pl. 480. 1842. Synonym: *Gloxinia rupestris* (Gardner) Wiehler, Selbyana 1(4): 387. 1976. TYPE: Brazil—G. Gardner 3874 (holotype, K).

Phylogenetic studies clearly support a clade including *Gloxinia ichthyostoma* Gardner and *Gloxinia planalta* Wiehler and, presumably, *Gloxinia rupestris* (Gardner) Wiehler (Roalson et al. 2005, E. Roalson et al. unpubl. data). The oldest generic name for this group is *Mandirola* J. Decaisne. While material of *Gloxinia rupestris* has not been available for phylogenetic studies, we have placed this species in *Mandirola* based on strong morphological similarities and close geographical proximity to the other species here considered in *Mandirola* (Roalson et al. 2005, E. Roalson et al. unpubl. data). This genus was originally created to accommodate the Brazilian species *Achimenes multiflora* Gardner, and indeed the species included here in *Mandirola* are extremely similar to *Achimenes* morphologically. Phylogenetic studies, however, confirm that they are not closely related to that primarily Central American genus. Chromosome numbers are unknown for this group; but based on phylogenetic relationships, they are predicted to be $n = 13$ (as opposed to $n = 11$ in *Achimenes*). Despite the close resemblance of this group to *Achimenes*, their unknown chromosome numbers, and their absence from any hybridization studies, Wiehler (1976) transferred these species from *Achimenes* to *Gloxinia* on the basis of hybrids between *Gloxinia perennis* and *Gloxinia gymnostoma*, which he considered to represent *Achimenes* section *Mandirola*. We, however, have shown this species to belong to the *See-*

mannia group (all of whose members hybridize easily with *Gloxinia perennis*) rather than the *Mandirola* group. Although phylogenetic studies show this group to belong in the same major clade as the type species of *Gloxinia*, the species of this group are morphologically and biogeographically distinct from our recircumscribed *Gloxinia*. Therefore we here resurrect the genus *Mandirola* for this group to simultaneously recognize its sister group, *Goyazia*, as a similarly distinct genus. Species circumscriptions within *Mandirola* are difficult and need to be further explored.

Monopyle Moritz ex G.Bentham, in G. Bentham & J.D. Hooker, Gen. Pl. 2: 997. May 1876. TYPE SPECIES: *Monopyle leucantha* Moritz ex G.Bentham, Icon. Pl. 12: 87. 1876 (= *M. subdimidiata* (Klotzsch & Hanstein) R.Mansfeld).

The genus includes *Monopyle angustifolia* Fritsch, *M. divaricata* Rusby, *M. ecuadorensis* C.V.Morton, **M. flava* L.E.Skog, *M. grandiflora* Wiehler, *M. inaequalis* C.V.Morton, *M. iserniana* Cuatrecasas, *M. macrocarpa* G.Bentham var. *costaricana* W.B.Hemsley, *M. macrocarpa* var. *isophylla* G.Bentham, **M. macrocarpa* var. *macrocarpa*, *M. maxonii* C.V.Morton, *M. mexiae* C.V.Morton, *M. panamensis* C.V.Morton, *M. paniculata* G.Bentham, **M. puberula* C.V.Morton, *M. sodiroana* Fritsch, *M. stenoloba* C.V.Morton, *M. subdimidiata* (Klotzsch & Hanstein) R.Mansfeld, and *M. subsessilis* G.Bentham.

Monopyle reflexa (Rusby) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Gloxinia reflexa* Rusby, Mem. Torrey Bot. Cl. 6: 94. 1896. TYPE: Bolivia—La Paz, *M. Bang 1745* (holotype, NY; isotypes, A, BM, C, E, F, G, GH, K, M, MANCH, MO, NY, PH, US, W, WU). Synonym: *Monopyle divaricata* Rusby, Bull. N. Y. Bot. Gard. 8(28): 119. 1912.

The phylogenetic analyses of Roalson et al. (2005) have shown that one of the defining characters of *Monopyle*, the fruit a fleshy capsule splitting along the entire length of its dorsal surface including the inferior portion, is shared with several species previously classified in *Gloxinia* (*G. lindeniana*, *G. racemosa*, *G. dodsonii*); indeed some of these taxa (e.g., *G. racemosa*) previously have been included in *Monopyle*. A very similar fruit also is shared with two taxa not included in our analyses, *Gloxinia reflexa* and *Niphaea peruviana*. Apparently this fruit type is a synapomorphy for this entire clade (rather than a synapomorphy for *Monopyle*), but the precise relationship among these taxa requires further study.

Species of *Monopyle* can usually be distinguished from other members of the same clade by their anisophyllous leaves. Another character that was found to be restricted to *Monopyle* was the presence of uncinata (hooked) trichomes on the calyx and hypanthium (and frequently other parts of the plant as well). Such trichomes were not observed in any other taxa, and while they are apparently lacking in some *Monopyle* spp. (J. Boggan unpubl. data), uncinata trichomes may be a useful character in distinguishing this genus from its relatives.

We have here moved *Gloxinia reflexa* into *Monopyle*, as one of its synonyms was once treated, because it clearly does not belong to *Gloxinia* as here circumscribed, and it appears to have the greatest similarity to *Monopyle*. While it does not share the *Monopyle* characters of unequal leaves and uncinata trichomes, we believe this is a more reasonable place to treat the species, until more detailed studies of this species and *Monopyle* as a whole can be conducted. *Gloxinia reflexa* and *Monopyle* do share the combination of an absent nectary and distinctly unequal and oblique leaf bases, a combination exceedingly rare except in these taxa.

A thorough revision of *Monopyle* is badly needed. Rather than expand the circumscription of *Monopyle* (beyond moving *Gloxinia reflexa* back into *Monopyle*) to include several taxa that are clearly related and share some characters with this genus but are otherwise morphologically heterogeneous, we have retained a narrow circumscription to maintain the morphologically well-defined genera *Diastema* and *Phinaea*. Defining a monophyletic *Monopyle* necessitates creating several small genera (*Gloxinella*, *Gloxiniopsis*, and *Nomopyle*, based on *Gloxinia lindeniana*, *G. racemosa*, *G. dodsonii*, respectively). Phylogenetic analyses of this clade including *Diastema*, *Gloxinella*, *Gloxiniopsis*, *Monopyle*, *Nomopyle*, and *Phinaea* (in part) using nrDNA ITS, cpDNA *trnL-F*, and morphological cladistic data sets result in similar inferences of relationships as the analyses of the Gloxinieae as a whole. The suggestion is that morphological homoplasy in the large analyses are not confounding assessment of relationships within this clade of genera (E. Roalson unpubl. data).

Moussonia Regel, Index Sem. Turic. [4]. 1847. TYPE SPECIES: *Moussonia deppeana* (D.FL. Schlechtendal & Chamisso) Hanstein.

The genus includes *Moussonia ampla* L.E.Skog, **M. deppeana* (D.FL.Schlechtendal & Chamisso) Hanstein, **M. elegans* J.Decaisne, *M. fruticosa* (Brandege) Wiehler, *M. hirsutissima* (C.V.Morton) Wiehler, *M. rupicola* (P.C.Standley & L.O.Williams) Wiehler, **M.*

septentrionalis (D.L.Denham) Wiehler, *M. serulata* (C.V.Morton) Wiehler, *M. skutchii* (C.V.Morton & D.N.Gibson) Wiehler, *M. strigosa* (C.V.Morton) Wiehler, *M. triflora* (Martens & Galeotti) Hanstein, and *M. viminalis* (Brandege) Wiehler.

Molecular results (Zimmer et al. 2002, Roalson et al. 2003, Smith et al. 2004, Roalson et al. 2005, E. Roalson et al. unpubl. data) support the separation of this genus from *Kohleria* as discussed by Wiehler (1975, 1983). Species of *Moussonia* are unusual in tribe Gloxinieae, as they do not produce scaly rhizomes; but molecular and morphological analyses place this genus in tribe Gloxinieae and suggest that the taxa are secondarily arhizomatous (Roalson et al. 2005).

Niphaea Lindley, Bot. Reg. 27: Misc. 80; Oct 1841. TYPE SPECIES: *Niphaea oblonga* Lindley.

The genus includes *Niphaea mexicana* C.V.Morton and **N. oblonga* Lindley.

The circumscription of this genus and its relationship to the two elements of the polyphyletic genus *Phinaea*, will be discussed in a separate paper (J. Boggan et al. unpubl. data).

Nomopyle E.H.Roalson & J.K.Boggan, gen. nov. TYPE SPECIES: *Nomopyle dodsonii* (Wiehler) E.H.Roalson & J.K.Boggan.

A Gloxinieae fere omni in rhizomatibus non squamatis, fructo triplo vel quadruplo longiore quam latiore et in stomatibus aggregatis differt; a *Diastema* in stigmatate indiviso non didymo differt; a *Gloxinia*, *Goyazia*, *Mandirola*, et *Seemannia* in hypanthio dorsaliter secedenti differt.

Plants weak-stemmed erect to decumbent glabrescent herbs, lacking uncinat trichomes; scaly rhizomes present (*Nomopyle peruviana*) or apparently absent (*N. dodsonii*). **Leaves** opposite, equal, with 5–8 pairs of veins, undersides with stomata in indistinct groups. **Flowers** epedunculate, ebracteolate, solitary in the leaf axils; corolla campanulate to almost rotate, white to lavender, lobes subequal, entire; ovary inferior; stigma stomatomorphic; nectary absent or a reduced annular disc. **Fruit** a cylindrical fleshy capsule, dehiscing along the dorsal side and splitting the hypanthium to the base. **Seeds** numerous, minute, subglobose.

The genus includes **Nomopyle dodsonii* (Wiehler) E.H.Roalson & J.K.Boggan and *N. peruviana* (Wiehler) E.H.Roalson & J.K.Boggan.

Nomopyle dodsonii (Wiehler) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Gloxinia dodsonii* Wiehler, Selbyana 2(1): 80. pl. 24D. 1977. TYPE: Ecuador—Pichincha, C.

Dodson & L. Thien 1173 (holotype, SEL; isotypes, BH, K, UC, US, WIS).

Nomopyle peruviana (Wiehler) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Niphaea peruviana* Wiehler, Gesneriana 1: 65. fig. 18. 1995. TYPE: Peru—Huanuco, *R.L. Dressler 4935* (holotype, SEL).

Nomopyle dodsonii, previously *Gloxinia dodsonii*, clearly is not closely related to *Gloxinia perennis*, and appears to have affinities to a clade containing *Diastema*, *Gloxinella*, *Monopyle*, and a portion of *Phinaea*, or possibly the *Heppiella* lineage (Roalson et al. 2005, E. Roalson et al. unpubl. data). The exact affinities of this species are not entirely clear and need to be further explored, but it is not a *Gloxinia*, as defined here. *Nomopyle*, an anagram of *Monopyle*, is used here to reflect the similarities in morphology of these species to *Monopyle*.

Niphaea peruviana Wiehler, while not yet included in any molecular phylogenetic analyses, clearly shares several characteristics with *Nomopyle dodsonii*. Particularly, *Niphaea peruviana* has stomata aggregated in groups like *Nomopyle dodsonii*, a characteristic not found in any other Gloxinieae species. *Niphaea peruviana* also is consistent with the *Nomopyle dodsonii* character of solitary and ebracteate axillary flowers and similarly is lacking the *Monopyle* apomorphies of anisophylly and uncinat trichomes. We believe these similarities warrant inclusion of *Niphaea peruviana* in *Nomopyle* and therefore make the transfer here.

Pearcea Regel, Gartenflora 16: 388; Dec 1867. TYPE SPECIES: *Pearcea hypocyrtiflora* (J.D.Hooker) Regel.

The genus includes **Pearcea abunda* (Wiehler) L.P.Kvist & L.E.Skog, *P. bella* L.P.Kvist & L.E.Skog, *P. bilabiata* L.P.Kvist & L.E.Skog, *P. cordata* L.P.Kvist & L.E.Skog, *P. fuscicalyx* L.P.Kvist & L.E.Skog, *P. glabrata* L.P.Kvist & L.E.Skog, *P. gracilis* L.P.Kvist & L.E.Skog, *P. grandiflora* L.P.Kvist & L.E.Skog, *P. hispidissima* (Wiehler) L.P.Kvist & L.E.Skog, **P. hypocyrtiflora* (J.D.Hooker) Regel, *P. intermedia* L.P.Kvist & L.E.Skog, *P. purpurea* (Poeppig) L.P.Kvist & L.E.Skog, **P. reticulata* (Fritsch) L.P.Kvist & L.E.Skog, *P. rhodotricha* (Cuatrecasas) L.P.Kvist & L.E.Skog, *P. schimpfii* R.Mansfeld, *P. sp. nov.*, *P. sprucei* (Britton) L.P.Kvist & L.E.Skog var. *parviflora* (Rusby) L.P.Kvist & L.E.Skog, **P. sprucei* var. *sprucei*, and *P. strigosa* L.P.Kvist & L.E.Skog.

Some previous authors have recognized the genus *Parakohleria* as separate from a monotypic *Pearcea* (Wiehler 1978, 1983; Burt & Wiehler 1995). Phylogenetic studies have sup-

ported the position of the type species of *Pearcea*, *P. hypocyrtiflora*, as nested within the species separated as *Parakohleria* (Roalson et al. 2005, E. Roalson et al. unpubl. data). As the recognition of *Parakohleria* would result in the recognition of a paraphyletic genus, we recognize all of the species concerned as *Pearcea* here, as suggested previously on the basis of morphological characters (Kvist & Skog 1996).

Phinaea G.Bentham, in G. Bentham & J.D. Hooker, Gen. Pl. 2: 991, 997. 1876. TYPE SPECIES: *Phinaea albolineata* (W.J.Hooker) G.Bentham ex Hemsley.

The genus includes **Phinaea albolineata* (W.J.Hooker) G.Bentham ex Hemsley, **P. multiflora* C.V.Morton, and *P. pulchella* (Grisebach) C.V.Morton.

Phylogenetic analyses show *Phinaea* to be polyphyletic (Smith et al. 2004, Roalson et al. 2005, E. Roalson et al. unpubl. data), and morphological studies corroborate this. A separate paper (J. Boggan et al. unpubl. data) will clarify the circumscription of *Phinaea* (represented in our analyses by *P. albolineata* and *P. multiflora*) and will include the description of a new genus to accommodate *Phinaea* p.p. (represented in our analyses by *P. divaricata* and *P. sp. nov.* [96–336]).

Seemannia Regel, Gartenflora 4: 183. 1855. TYPE SPECIES: *Seemannia ternifolia* Regel (= *Seemannia sylvatica* (Kunth) Hanstein). Synonyms: *Fritschiantha* Kuntze, Rev. Gen. Pl. 3(2): 241. 1898. *Fiebrigia* Fritsch, Bot. Jahrb. Syst. 50: 397. 1913.

Plants erect to decumbent herbs with scaly rhizomes, often produced at the tips of long stringy rhizomes. **Leaves** opposite, ternate, or whorled, equal, with 3–9 pairs of veins. **Flowers** epedunculate, ebracteolate, usually solitary in leaf axils (except *Seemannia sylvatica* frequently with 2–3+ flowers per axil); corolla tubular or inflated, often constricted at the mouth, red, orange, purple (rarely yellow), with barrel-shaped multicellular trichomes at the mouth of the tube; lobes entire, subequal; nectary annular; ovary half to almost completely inferior; stigma pointed. **Fruit** a dry rostrate capsule. **Seeds** numerous, minute, ellipsoid.

The genus includes **Seemannia gymnostoma* (Grisebach) M.Toursarkissian, **S. nematanthodes* (Kuntze) J.Schumann, **S. purpurascens* Rusby, and **S. sylvatica* (Kunth) Hanstein.

Seemannia gymnostoma (Grisebach) M.Toursarkissian, Bol. Soc. Argent. Bot. 7(2): 135. 1958. *Gloxinia gymnostoma* Grisebach.

Seemannia nematanthodes (Kuntze) J.Schu-

mann, Just's Bot. Jahresber. 26(1): 386. 1898. Synonyms: *Fritschiantha nematanthodes* Kuntze; *Gloxinia nematanthodes* (Kuntze) Wiehler.

Seemannia purpurascens Rusby, Mem. Torrey Bot. Cl. 4: 237. 1895. Synonym: *Gloxinia purpurascens* (Rusby) Wiehler.

Seemannia sylvatica (Kunth) Hanstein, Linnaea 29: 540, 587. 1859. Basionym: *Gesneria sylvatica* Kunth. Synonym: *Gloxinia sylvatica* (Kunth) Wiehler.

We are here resurrecting the genus *Seemannia*, as it forms a monophyletic and morphologically well-defined group sister to an *Anodiscus*/*Gloxinia perennis*/*Koellikeria* clade (Roalson et al. 2005, E. Roalson et al. unpubl. data). Because of this close relationship, and because valid combinations for these species exist in the genus *Gloxinia*, an alternative classification would be to retain the *Seemannia* species in a still-monophyletic but more heterogeneous circumscription of *Gloxinia*. We have chosen to restore the generic status of *Seemannia*, as the species are distinctively different from the species we include in *Gloxinia*; and separating the two groups allows each genus to be defined more clearly (see discussion under *Gloxinia*). *Seemannia* can be distinguished from other genera of Gloxinieae by the presence of barrel-shaped multicellular trichomes in the corolla mouth and an unusual pointed stigma. *Seemannia* species also have long whip-like aerial rhizomes in addition to the typical Gloxinieae scaly rhizomes and non-racemose inflorescences, both present in some other genera of the Gloxinieae, but rarely in this combination.

Smithiantha Kuntze, Rev. Gen. Pl. 2: 977. 1891. Substitute name for *Naegelia* Regel 1847, not *Naegelia* Rabenhorst 1844, nor *Naegelia* Zollinger & Moritz 1845–1846, nor *Naegelia* Reinsch 1878. TYPE SPECIES: *Smithiantha zebrina* (Paxton) Kuntze.

The genus includes **Smithiantha aurantiaca* Wiehler, **S. canarina* Wiehler, *S. cinnabarina* (Linden) Kuntze, *S. laui* Wiehler, *S. multiflora* (Martens & Galeotti) Fritsch, and *S. zebrina* (Paxton) Kuntze.

The geographically restricted and morphologically well-defined Mexican endemic genus *Smithiantha* is easily distinguished by its showy flowers and racemose flowering stems with alternate bracts, a combination not found in any other member of Gloxinieae in the same geographic area.

Solenophora G.Bentham, Pl. Hartw. 68; Mar 1840. TYPE SPECIES: *Solenophora coccinea* G.Bentham.

The genus includes *Solenophora abietorum* P.C.Standley & Steyermark, **S. calycosa* J.D.Smith subsp. *australis* (C.V.Morton) Weigend & Förther, *S. calycosa* subsp. *calycosa*, *S. calycosa* subsp. *purpurascens* Weigend & Förther, *S. chiapensis* D.N.Gibson, *S. coccinea* G.Bentham, *S. erubescens* J.D.Smith, *S. glomerata* Weigend & Förther, *S. insignis* (Martens & Galeotti) Hanstein, *S. maculata* D.N.Gibson, *S. obscura* Hanstein, *S. pirana* C.V.Morton, *S. purpusii* Brandege, *S. schleehaufii* Weigend & Förther, *S. toucana* D.L.Denham & D.N.Gibson, **S. tuerckheimiana* J.D.Smith, *S. tuxtensis* Ramírez-Roa & Ibarra-Manríquez, and *S. wilsonii* P.C.Standley.

Solenophora recently has been revised, recognizing 18 taxa in 16 species (Weigend & Förther 2002). Although *Solenophora* seems to be a well-defined genus morphologically, its possible entanglement with *Achimenes* needs to be further explored (see discussion under *Achimenes* above). To date, only two of the 18 taxa have been included in phylogenetic analyses. More detailed phylogenetic analyses are necessary to verify the circumscription of this genus.

A KEY TO THE GENERA OF GLOXINIEAE

- 1. Shrubby herbs to shrubs or small trees with soft woody stems; scaly rhizomes never present; ovary half to fully inferior; plants of Mexico and Central America 2
- 1'. Plant habit various, usually herbs to shrubby herbs; scaly rhizomes usually present (absent in some South American taxa); ovary inferior to almost superior; plants of South America, Mexico, Central America, and West Indies 3
- 2. Calyx lobes usually connate at least half their length (rarely free almost to ovary); flowers large and showy with a broad limb; ovary inferior; nectary of one large (rarely 2–5) gland; fruit a globose (sometimes fleshy) capsule, rupturing irregularly; *n* = 10 *Solenophora*
- 2'. Calyx lobes free almost to base; flowers narrow and tubular with a small limb; ovary half inferior; nectary annular; fruit an ovoid, rostrate, dry bivalved capsule; *n* = 11 *Moussonia*
- 3. Flowering stems raceme-like with flowers solitary in the axils of small bract-like leaves 4
- 3'. Flowering stems not raceme-like, flowers in panicles, axillary cymes or rarely solitary in leaf axils 9
- 4. Bracts opposite; nectary consisting of 5 separate glands 5
- 4'. Bracts opposite or alternate; nectary an annular ring or absent 6
- 5. Robust strong-stemmed herbs; nectary glands about as long as broad; stigma bilobed; corolla mouth and lobes usually with long-stalked glandular trichomes *Kohleria* (in part)
- 5'. Small weak-stemmed herbs; nectary glands finger-like, longer than broad; stigma bilabiate; co-

- rolla mouth and lobes without stalked glandular trichomes *Diastema* (in part)
- 6. Leaves usually in distinctly unequal pairs; bracts opposite; hypanthium and calyx usually with uncinuate trichomes; fruit a fleshy capsule, dehiscing along the dorsal side and splitting the hypanthium to the base *Monopyle* (in part)
- 6'. Leaves in equal or subequal pairs; bracts opposite or alternate; hypanthium and calyx never with uncinuate trichomes; fruit a dry or fleshy capsule 7
- 7. Leaves with 3–5 pairs of leaf veins; bracts alternate; nectary annular; fruit a dry capsule; *n* = 12; plants of Mexico *Smithiantha*
- 7'. Leaves with 5 or more pairs of leaf veins; bracts opposite or alternate; nectary annular or absent; *n* = 13 (where known); plants of South America, Central America, (West Indies by introduction), not Mexico 8
- 8. Leaves with 5–9 (rarely to 12) pairs of veins; nectary annular or absent; fruit an ovoid, rostrate, dry capsule, dehiscing dorsally and ventrally but not rupturing the hypanthium; seeds longer than broad; *n* = 13; plants of Central and South America (West Indies by introduction) *Gloxinia*
- 8'. Leaves with 9–12 or more pairs of veins; nectary annular but strongly reduced (sometimes absent); fruit a subglobose fleshy capsule, dehiscing on the dorsal surface and splitting the hypanthium to the base; seeds about as broad as long; plants of Colombia *Gloxiniopsis*
- 9. Small weak-stemmed herbs; flowers white, (sub)rotate with a very short tube 10
- 9'. Plant habit various; flowers various colors, more or less zygomorphic with a distinct tube . . . 12
- 10. Plants of Mexico and Guatemala; fruit an ovoid, rostrate, dry capsule; filaments shorter than anthers; *n* = 11; plants of Mexico and Guatemala *Niphaea*
- 10'. Fruit a subglobose (rarely ovoid) dry or fleshy capsule; filaments longer than anthers; *n* = 13 or 26; plants of Central America, South America, or West Indies 11
- 11. Fruit a fleshy capsule, held on erect pedicel above leaves, valves opening widely; plants of Central America, South America, and West Indies *Phinaea* s.s.
- 11'. Fruit a dry capsule, often held on pedicel curving below leaves, valves opening slightly; plants of Central and South America *Phinaea* p.p.
- 12. Small herbs with wiry stems; leaves leathery, lateral veins reaching the margin and forming a marginal vein; plants of Brazil *Goyazia*
- 12'. Plant habit various, leaves not leathery, lateral veins ending before reaching leaf margins . . 13
- 13. Flowers tubular, red; anthers not coherent; fruit a dry capsule; plants of South America *Heppiella*
- 13'. Flowers various; anthers usually coherent; fruit a dry or fleshy capsule 14
- 14. Stigma distinctly bilobed 15
- 14'. Stigma various, but not distinctly bilobed . . 17
- 15. Nectary of separate glands (rarely united to some degree); corolla mouth and/or lobes usually with

- long-stalked glandular trichomes; fruit a dry or fleshy capsule *Kohleria* (in part)
- 15'. Nectary annular; corolla mouth and lobes without stalked glandular trichomes; fruit a dry capsule 16
16. Flowers usually in axillary cymes (rarely solitary in the leaf axils); corolla lobes usually distinctly toothed to fimbriate; plants of Brazil; chromosome number unknown *Mandirola*
- 16'. Flowers usually solitary in the leaf axils (sometimes in axillary cymes); corolla lobes usually entire; $n = 11$ or 22 ; plants of Central America and West Indies (elsewhere by introduction) *Achimenes* (in part)
17. Nectary of 5 separate glands 20
- 17'. Nectary annular or absent 18
18. Small weak-stemmed herbs; flowers small, white with a purple spot on each lobe; nectary of 5 long, finger-like glands; stigma bilabiate; plants of Colombia *Diastema vexans*
- 18'. Plant habit and flowers various; nectary glands about as long as broad; stigma not dilapidate 19
19. Plants terrestrial; rhizomes usually with widely spaced scales; flowers usually red or yellow; plants of South America *Pearcea*
- 19'. Plants usually epiphytic; rhizomes usually absent (if present, without fleshy scales); flowers usually green or purple; plants of Central and South America *Kohleria* (*Capanea* group)
20. Plants producing long stringy rhizomes in addition to scaly rhizomes; corolla with barrel-shaped multicellular trichomes at mouth; stigma pointed; fruit a dry capsule *Seemannia*
- 20'. Plants not usually producing long stringy rhizomes; corolla without barrel-shaped trichomes; stigma stomatomorphic or capitate, not pointed; fruit a dry or fleshy capsule 21
21. Fruit a dry capsule, not splitting the hypanthium at desiccance; seeds usually longer than broad; $n = 11, 12,$ or 22 ; plants primarily of Mexico and Central America 22
- 21'. Fruit a fleshy capsule, dehiscing along the dorsal surface, splitting hypanthium to base; seeds usually about as broad as long; $n = 13$; plants primarily of South America 23
22. Stems and leaves densely lanate-villous; $n = 12$; plants of Mexico *Eucodonia*
- 22'. Stems and leaves without woolly indumentum; $n = 11$ or 22 ; plants of Mexico and Central America (elsewhere probably by introduction) *Achimenes* (in part)
23. Leaves usually in distinctly anisophyllous pairs; flowers in axillary, often pedunculate, cymes (sometimes in panicles, rarely solitary in the leaf axils); hypanthium and calyx usually with uncinuate trichomes; plants of Central and South America *Monopyle* (in part)
- 23'. Leaves in (sub)equal pairs; flowers solitary (rarely 2 or more) in the leaf axils; uncinuate trichomes absent; plants of South America 24
24. Leaves nearly glabrous above, undersides with stomata in indistinct groups; nectary absent or a reduced annular disc; stigma stomatomorphic;

- fruit cylindrical; plants of Ecuador and Peru *Nomopyle*
- 24'. Leaves villous above, with stomata not in groups; nectary a slightly lobed annular disc; stigma obscurely bilobed; fruit ovoid to ellipsoid; plants of Peru *Gloxinella*

SPECIES INCERTAE SEDIS

Gloxinia mieliezii Regel, Ind. Sem. Hort. Petrop. 1865: 64. 1865.

This identity of the species is unclear, and the original publication and type material have not been seen.

Goyazia villosa (Gardner) R.Howard, J. Arnold Arbor. 56(3): 367. 1975. *Tapina villosa* Gardner, Hooker's Icon. Pl. 5: pl. 469. 1842. *Gloxinia villosa* (Gardner) Wiehler, nom. illeg., non (Lindley) Martius; Selbyana 1(4): 387. 1976.

Goyazia villosa (Gardner) R.Howard is here considered *incertae sedis* because it is morphologically distinct from the *Goyazia* and *Mandirola* groups. It is similarly out of place in *Gloxinia*. A relationship to *Phinaea* seems likely, but until the type can be examined, no transfer will be made.

GENERA EXCLUDED FROM THE GLOXINIEAE

The genus *Bellonia*, variously placed in the Gloxinieae (Wiehler 1983, Burt & Wiehler 1995) or its own tribe (Fritsch 1893–1894), is most closely related to members of tribe Gesnerieae (Roalson et al. 2005, E. Roalson et al. unpubl. data). While *Bellonia* is not a close morphological match to other genera of the Gesnerieae, neither is it very similar to any of the genera of the Gloxinieae, other than some superficial floral resemblance with *Niphaea* and *Phinaea* (Xu & Skog 1990). The primary morphological characters linking it to Gesnerieae are the absence of scaly rhizomes and habit as a woody shrub. *Bellonia* also shares a biogeographic distribution with the other genera of the Gesnerieae, as all but two or three species of this tribe are restricted to the Caribbean region. Given the molecular phylogenetic data and the shared biogeographic distribution, we consider *Bellonia* best treated as a member of the tribe Gesnerieae despite its lacking several key apomorphies of other members of tribe Gesnerieae (e.g., fully inferior ovary, spiral phyllotaxy, and chromosome number of $n = 14$).

Detailed studies of *Sinningia* and relatives, included in Gloxinieae by Wiehler (1983), are

underway by others (Perret et al. 2001, Perret et al. 2003). It is clear at this time from phylogenetic studies that these genera deserve to be recognized as a tribe separate from the Gloxinieae (Zimmer et al. 2002, Mayer et al. 2003, Perret et al. 2003, Weber 2004, Roalson et al. 2005).

The genus *Lembocarpus* Leeuwenberg was classified in tribe Gloxinieae by Wiehler (1983), and this placement was supported by Smith (2001). Although this paper does not address generic concepts in the Episcieae, it is clear at this time (Roalson et al. 2005) that *Lembocarpus* belongs in the Episcieae, as suggested by several authors (Beaufort-Murphy 1983, Boggan 1991, Feuillet & Skog 2003, Smith et al. 2004, J.L. Clark unpubl. data).

A NEW TRIBE OF GESNERIOIDEAE

Sphaerorrhizeae E.H.Roalson & J.K.Boggan, tribus nov. TYPE SPECIES: *Sphaerorrhiza sarmentiana* (Gardner ex W.J.Hooker) E.H.Roalson & J.K.Boggan.

A Gloxinieae Fritsch in lobis calyce in alabastro valvatis, rhizomatibus tuberiferis differt.

Sphaerorrhiza E.H.Roalson & J.K.Boggan, gen. nov. TYPE SPECIES: *Sphaerorrhiza sarmentiana* (Gardner ex W.J.Hooker) E.H.Roalson & J.K.Boggan.

A *Gloxinia* l'Heritier in lobis calyce in alabastro valvatis, rhizomatibus tuberifero differt.

Plants erect to decumbent glabrescent herbs producing rhizomes with tuber-like swellings, often breaking apart with each propagule giving rise to a new plant. **Leaves** short-petiolate to subsessile, opposite, equal, with 3–7 pairs of veins. **Flowers** calyx lobes valvate and sealed in bud; corolla broadly tubular, white, lavender, or purple; nectary annular; ovary half to almost completely inferior. **Fruit** a dry rostrate capsule. **Seeds** elliptic, numerous, minute.

The genus includes *Sphaerorrhiza burchellii* (S.M.Phillips) E.H.Roalson & J.K.Boggan and **S. sarmentiana* (Gardner ex W.J.Hooker) E.H.Roalson & J.K.Boggan.

Sphaerorrhiza burchellii (S.M.Phillips) E.H.Roalson & J.K.Boggan, comb. nov. Basionym: *Achimenes burchellii* S.M.Phillips, Kew Bull. 24(1): 225. 1970. Synonym: *Gloxinia burchellii* (S.M.Phillips) Wiehler, Selbyana 1(4): 387. 1976. TYPE: Brazil—Goias, *W. Burchell 8615* (holotype, K; isotypes, L, WAG).

Sphaerorrhiza sarmentiana (Gardner ex W.J.Hooker) E.H.Roalson & J.K.Boggan,

comb. nov. Basionym: *Gloxinia sarmentiana* Gardner ex W.J.Hooker, Icon. Pl. 4: pl. 378. 1841. TYPE: Brazil—*G. Gardner 2226* (holotype, K; isotypes, BM, CGE, K, L, P, W). Synonyms: *Gloxinia attenuata* Hanst., Linnaea 27: 716. 1856. *Gloxinia stolonifera* Fritsch, Bot. Jahrb. Syst. 37: 493. 1900.

Recently the tribal affinity of *Gloxinia sarmentiana* has been questioned (Zimmer et al. 2002). This species has been traditionally treated in the genus *Gloxinia* (Hoehne 1964, Wiehler 1976); but based on molecular phylogenetic studies (Zimmer et al. 2002, Roalson et al. 2005), it clearly is not related to the genus *Gloxinia*, nor does it even belong in tribe Gloxinieae. In its morphology, this species is consistent with members of Gloxinieae in some respects (rhizomatous habit, semi-inferior ovary, annular nectary, and distinctly rostrate dry capsular fruit). In one key character, however, it differs; rather than producing rhizomes with fleshy scales, it produces rhizomes with small tuber-like swellings. In this respect, it more closely resembles the genus *Sinningia* (tribe Sinningieae), and several of the characters it shares with tribe Gloxinieae also are consistent with tribe Sinningieae (e.g., semi-inferior ovary and rostrate dry capsular fruit).

From a phylogenetic perspective, this species does not share strong affinity with any other taxa sampled to date (Zimmer et al. 2002, Roalson et al. 2005), although it weakly groups with tribe Sinningieae in some phylogenetic analyses (Zimmer et al. 2002). *Gloxinia burchellii* appears to share several characters not found in the rest of *Gloxinia* s.l., and therefore tentatively is moved to *Sphaerorrhiza*, as *S. burchellii*, with *S. sarmentiana*. Generally, this new genus seems to be a distinct lineage with phylogenetic proximity to tribes Sinningieae and Episcieae (Zimmer et al. 2002, Roalson et al. 2005); and the production of small tubers on underground rhizomes, a character shared with some members of tribe Sinningieae, may provide a clue to the origin of tuberous habit in that tribe. For these reasons, we have erected a new tribe to deal with the lack of phylogenetic affinity of this genus to any current classification units.

Notably, Hoehne (1964) treated *Gloxinia attenuata* and *G. stolonifera* as valid species; determining whether the variation within *Sphaerorrhiza sarmentiana* represents a single variable taxon or two or more valid species will require further study. *Sphaerorrhiza* is here presented as the generic epithet to reference the distinctive rhizomes with tuber-like swellings found in the type species, *S. sarmentiana*.

**A KEY TO THE TRIBES OF GESNERIOIDEAE
WITH INFERIOR AND HALF-INFERIOR
OVARIES**

1. Plants producing rhizomes with small tuber-like swellings, but never with large perennial tubers or scaly rhizomes; nectary annular; plants of Brazil **Sphaerorrhizeae**
- 1'. Plants not producing rhizomes with tuber-like swellings (if tuber-producing rhizomes present, then in addition to a large perennial tuber); nectary absent, annular or consisting of individual glands; plants of Central America, South America and West Indies 2
2. Plants usually with large perennial tubers, never with scaly rhizomes; nectary present, usually consisting of 1–5 glands (if lacking tubers or with annular nectary, then plants of southern Brazil) **Sinningieae**
- 2'. Plants never with tubers; nectary absent, annular, or consisting of individual glands 3
3. Woody subshrubs, shrubs, or small trees, never with scaly rhizomes; leaves usually alternate, rarely opposite; ovary usually inferior (rarely half inferior); nectary annular (absent in *Bellonia*); fruit a dry capsule; plants of the West Indies; 2 or 3 rare species in Colombia and Venezuela **Gesnerieae**
- 3'. Herbs, rarely woody shrubs or small trees, usually producing scaly rhizomes (if lacking scaly rhizomes, then not plants of southern Brazil); leaves opposite (rarely whorled); ovary half inferior to inferior (rarely almost superior); nectary absent, annular, or consisting of individual glands; fruit a dry or fleshy capsule; plants primarily of Central and South America (if West Indies, then with scaly rhizomes) **Gloxinieae**

CONCLUSIONS

The classification changes proposed in this paper will bring generic circumscription more into line with our current knowledge of phylogenetic relationships in the Gesnerioideae subfamily, and particularly the Gloxinieae tribe, of Gesneriaceae. Several issues cannot be addressed here, including the proper generic affinity of some poorly understood species (e.g., *Goyazia villosa*). In addition, generic circumscription of species traditionally placed in *Phinaea* will be addressed elsewhere. We have made some assumptions about generic placement of species within genera. Many of the genera of the Gloxinieae need to be revised, including detailed infrageneric phylogenetic analyses, to have more confidence in generic circumscriptions. This is particularly needed for the *Achimenes/Solenophora* circumscription, *Diastema*, *Mandirola*, *Monopyle*, and *Moussonia*.

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