A REPORT ON THE CLASSIFICATION OF *ACHIMENES*, *EUCODONIA*, *GLOXINIA*, *GOYAZIA*, AND *ANETANTHUS* (GESNERIACEAE)

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One of the last major genera in need of some reconstruction before the publication of a new classification of the neotropical subfamily Gesnerioideae (Wiehler, 1976) is *Achimenes* Persoon. The name has been conserved recently over *Achimenes* P. Browne (Stafleu et al., 1972; cf. Taxon 18(4):469. 1969; 19(5):817. 1970). The genus consists of lithophytic or terrestrial herbs with scaly rhizomes which perpetuate the plants through the dry seasons. The same kind of underground rhizome occurs, however, in a number of other genera in the tribe Gloxinieae Fritsch of which *Achimenes* is a member. The type species, *Achimenes erecta* (Lamb.) H. P. Fuchs is native to Jamaica, Hispaniola, Colombia, Costa Rica, Guatemala, and Mexico. The other 20 species of *Achimenes* sensu stricto have more limited distribution patterns in Central America and Mexico; 13 species are endemic to southern and central Mexico. These 21 species of *Achimenes* sensu stricto are listed in Table I. There are, however, several other groups of species which have been attribtuted to *Achimenes*. It is the purpose of this article to define these discordant elements and to propose their transfer to the genera *Eucodonia* Hanstein, *Gloxinia* L'Heritier, and *Goyazia* Taubert. These taxa within *Achimenes* sensu lato are labelled in the subsequent discussion as "the *Eucodonia* group," "the *Gloxinia* group," and "the *Goyazia* group."

The only extended treatment of the genus *Achimenes* sensu lato was done by Johannes Hanstein in 1854 and 1856 (Linnaea 26:145-216; 27:693-785). He gave detailed descriptions of 23 species and divided them into eight genera according to flower shape. He reduced these eight genera to three without detailed comment in 1865, basing his decisions primarily on the shape of the stigma (Linnaea 34:229-230). George Bentham (1876) divided the same group into two genera in a rather brief treatment, citing only six specific epithets. Karl Fritsch (1893-94) united these two genera under *Achimenes* with eight sections which correspond more or less with the former generic divisions. Several years later he added two monotypic sections. Fritsch's sectional arrangement is the last taxonomic treatment of the genus *Achimenes* sensu lato (Table II). Shortly afterwards, around 1900, H. H. Rusby, K. Fritsch, N. L. Britton, and O. Kuntze described a number of closely related species from Peru, Bolivia, and northern Argentina in the genera *Achimenes*, *Gloxinia*, *Seemannia* Regel, and *Fritschiantha* O. Kuntze. Several decades later, C. V. Morton published eight new species of *Achimenes* from Mexico, and in 1970 S. M. Phillips attributed to *Achimens* two more species from central Brazil.

The American Gesneriaceae have been known to be a taxonomically problematic group, and the genus *Achimenes* sensu lato is a good example of the systematic difficulties encountered. There are two reasons for this continuing confusion. First, the species of *Achimenes* sensu stricto have rather diverse but showy corolla shapes, ranging from tubular (*A. antirrhina*, *A. heterophylla* = hummingbird flowers) to funnelform-campanulate (*A. dulcis*, *A. glabrata*, *A. mexicana*, *A. pedunculata*, *A. skinneri* = euglossine bee flowers) to modified salverform (*A. longiflora*, *A. grandiflora*, *A. cettoana* = butterfly flowers). The stigma is either bilobed or stomatomorphic, the

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TABLE I. THE SPECIES OF *Achimenes* SENSU STRICTO ARRANGED ACCORDING TO POLLINATION SYNDROMES

	Species	Distribution
	THE ORNITHOPHILOUS SPECIES	
1.	*A. antirrhina* (DC.) Morton	Mexico
2.	*A. erecta* (Lamb.) H.P. Fuchs [*A. coccinea* (Scop.) Pers., type cons.; *A. pulchella* (L'Herit.) Hitchc.]	Jamaica, Hispaniola, Colombia, Panama to Mexico
3.	*A. heterophylla* (Mart.) DC.	Mexico
4.	*A. pedunculata* Benth.	Venezuela, Colombia, Panama to Mexico
5.	*A. skinneri* Lindl. (*A hirsuta* Lindl.; non *A. hirsuta* DC.)	Guatemala to Mexico
	THE PSYCHOPHILOUS SPECIES	
6.	*A. cettoana* H. E. Moore	Mexico
7.	*A. grandiflora* (Schiede) DC.	Costa Rica to Mexico
8.	*A. longiflora* (Sessé & Moc.) DC.	Panama to Mexico
9.	*A. patens* Benth.	Mexico
	THE GYNANDRO-EUGLOSSOPHILOUS SPECIES	
10.	*A. dulcis* Morton	Mexico
11.	*A. glabrata* (Zucc.) Fritsch	Mexico
12.	*A. mexicana* (Seem.) Benth. ex Fritsch	Mexico
	THE MELITTOPHILOUS SPECIES	
13.	*A. brevifolia* Morton	Mexico
14.	*A. candida* Lindl.	Panama to Mexico
15.	*A. fimbriata* Rose ex Morton	Mexico
16.	*A. flava* Morton	Mexico
17.	*A. misera* Lindl.	Honduras to Mexico
18.	*A. obscura* Morton	Mexico
19.	*A. occidentalis* Morton	Mexico
20.	*A. warszewicziana* (Regel) H. E. Moore	Honduras to Mexico
21.	*A. woodii* Morton	Mexico

nectary is annular, and the calyx is small with short and narrow lobes. There are no obviously distinguishing androecial characters. The eight genera established for *Achimenes* in Hanstein's time 120 years ago were based on the above differences in corolla shape and stigma shape. Second, the same generalized type of corolla (tubular or funnelform-campanulate) in combination with a small calyx and a bilobed or stomatomorphic stigma occurs also in the related genera *Smithiantha* O. Kuntze, *Gloxinia*, *Seemannia*, *Moussonia* Regel, and *Heppiella* Regel (all with annular nectaries), and in *Diastema* Bentham, *Kohleria* Regel, and *Sinningia* Nees (where the nectary consists of essentially five separate glands). In the absence of some decisive vegetative characters, a botanist often cannot determine the genus by the flower alone. This is the reason many species in this group of genera were assigned to the wrong genus: *Achimenes glabrata* was first described as *Gloxinia glabrata* Zucc., later as *Sinningia gloxiniflora* Scheidw.; the synonyms for *Achimenes candida* are *Diastema gracile* Regel and *Kohleria saxicola* Brandegee; *Kohleria bogotensis* (Nicholson) Fritsch has *Achimenes picta* Benth. and *Diastema pictum* (Benth.) Regel in its synonomy; *Kohleria magnifica* (Planch. & Lind.) H. E. Moore was first described as *Locheria*

TABLE II: THE SECTIONS AND SPECIES OF *Achimenes* SENSU LATO AS ARRANGED BY FRITSCH (1893-94), WITH ADDITIONS OR NOMENCLATURAL CHANGES BY MOORE (1960), MORTON (1962), PHILLIPS (1970), AND RECOMMENDATIONS BY COOKE & LEE (1966)

1. Sect. *Plectopoma* (Hanst.) Fritsch
    - *A. glabrata* (Zucc.) Fritsch
2. Sect. *Scheeria* (Seem.) Fritsch
    - *A. dulcis* Morton
    - *A. mexicana* (Seem.) Benth. ex Fritsch
3. Sect. *Guthnickia* (Regel) Fritsch
    - *A. antirrhina* (DC.) Morton
4. Sect. *Dicyrta* (Regel) Fritsch
    - *A. brevifolia* Morton
    - *A. burchellii* S. M. Phillips
    - *A. candida* Lindl.
    - *A. fimbriata* Rose ex Morton
    - *A. flava* Morton
    - *A. misera* Lindl.
    - *A. obscura* Morton
    - *A. occidentalis* Morton
    - *A. petraea* S. M. Phillips
    - *A. warszewicziana* (Regel) H. E. Moore
    - *A. woodii* Morton
5. Sect. *Mandirola* Decne.) Benth.
    - *A. gymnotoma* (Griseb.) Fritsch
    - *A. hirsuta* DC.
    - *A. ichthyostoma* (Gardner) Hanst.
    - *A. multiflora* Gardner
6. Sect. *Eucodonia* (Hanst.) Fritsch
    - *A. andrieuxii* DC.
    - *A. bella* Morton
    - *A. ehrenbergii* (Hanst.) H. E. Moore
7. Sect. *Achimenes* [Sect. *Trevirana* (Willd.) Benth.]
    - *A. cettoana* H. E. Moore
    - *A. erecta* (Lamb.) H.P. Fuchs
    - *A. grandiflora* (Schiede) DC.
    - *A. longiflora* (Sessé & Moc.) DC.
    - *A. patens* Benth.
8. Sect. *Locheria* (Regel) Benth.
    - *A. heterophylla* (Mart.) DC.
    - *A. pedunculata* Benth.
    - *A. skinneri* Lindl.
9. Sect. *Kohleriopsis* Fritsch
    - *A. heppielloides* Fritsch
10. Sect. *Tydaeopsis* Fritsch
    - *A. rusbyi* Britt.

magnifica Planch. & Lind. (*Locheria* Regel is a synonym of *Achimenes*); the correct name for *Achimenes ocellata* Hook. is *Kohleria ocellata* (Hook.) Fritsch; *Achimenes comifera* DC. belongs to *Diastema; Diastema maculatum* (Poepp.) Benth. was first published under *Trevirana* Willd., another synonym for *Achimenes;* the basionym for *Kohleria platylomata* (Donn.-Sm.) Wiehler is *Diastema platylomatum* Donn.-Sm.; *Heppiella viscida* (Lindl. & Paxt.) Fritsch was first published as *Achimenes viscida* Lindl. & Paxt.; *Smithiantha multiflora* (Martens & Galeotti) Fritsch was first known as *Gloxinia? multiflora* Martens & Galeotti, with *Achimenes amabilis* Decne. as a synonym; *Smithiantha zebrina* (Paxt.) O. Kuntze has *Gloxinia punctata* Martens & Galeotti in its synonymy; most of the species of *Moussonia* were originally described under *Kohleria;* the nomenclatural confusion between *Gloxinia* and *Sinningia* in the last century originated because of the similar generalized flower shape of some species in both genera (the florist's gloxinia actually belongs in *Sinningia*); and the names *Gloxinia* and *Seemannia* are involved in the *Gloxinia* group of *Achimenes* sensu lato.

In the last two decades 17 of the 22 species of *Achimenes* sensu stricto, the three species of the *Eucodonia* group, several members of the *Gloxinia* group, as well as many species of the other genera cited above have been brought into cultivation, at first mostly from the collections of H. E. Moore, Jr. of Cornell University which became a center for the study of cultivated neotropical Gesneriaceae. A systematic hybridization program was started and chromosome number reports were published intermittently (Rogers, 1954; Fussell, 1958; Lee, 1962a, 1962b, 1964, 1966a, 1967; Lee and Grear, 1963; Clayberg, 1967; Wiehler, 1972a, 1975a). The first cytogenetic study involved the genera *Achimenes* sensu lato and *Smithiantha*, but the results of these experiments (Cooke and Lee, 1966), although conclusive in themselves, need to be interpreted in the context of the subsequent generic and intergeneric hybridization work in the Gesnerioideae, listed here in chronological order (cf. Wiehler, 1970, p.106):

Achimenes sensu lato and *Smithiantha* (Cooke and Lee, 1966)
Columnea L. sensu lato (Sherk and Lee, 1967)
Rechsteineria Regel and *Sinningia* Nees (Clayberg, 1968, 1970)
Koellikeria Regel and *Kohleria* Regel (Wiehler, 1968)
Gesneria L. and *Rhytidophyllum* Mart. (Wiehler, 1970; Skog, 1972)
Gloxinia and *Seemannia* (Wiehler, 1970, 1972b)
Episcia Mart. and *Nautilocalyx* Hanst. (Wiehler, 1970, 1973a)
Hypocyrta Mart. and *Nematanthus* Schrader (Saylor, 1971; Wiehler, 1972b; Moore, 1973)
Kohleria Regel and *Moussonia* Regel (Wiehler, 1970, 1975a)

Table III presents a more inclusive and detailed list of intergeneric hybrid combinations (made by myself unless otherwise indicated), with parental chromosome numbers and hybrid pollen stainability. These cytogenetic studies have added to our understanding of speciation in a tropical plant family and given us new insight into generic definitions and affinities within the subfamily Gesnerioideae. The cytogenetic data has proved of immense value in the development of a new classification of the Gesnerioideae (Wiehler, 1976). One of the interesting factors to immerge from this biosystematic research is that the chromosome numbers for each genus of the Gesnerioideae appear to be constant. The validity of many of the traditional genera of the subfamily is confirmed by the constancy of the chromosome number of their species as well as through a more thorough assessment of vegetative or gross morphological characters of the cultivated material. Table IV lists the base chromosome numbers for *Achimenes* sensu stricto and for the rest of the genera in the tribe Gloxinieae.

The generic limits of the Gesnerioideae became more firmly fixed not only by the new information about the constancy of the chromosome numbers, but also through the hybridization experiments. The high degree of pollen stainability and fertility among many interspecific hybrids contrasted sharply with the complete sterility of the intergeneric hybrids. It became clear to me that experimental hybridization could be used to test generic affinities in the Gesnerioideae. This approach worked not only negatively (sterility between valid genera), but also positively: a high degree of hybrid pollen stainability in several cases where the traditional parental genera were suspected to be congeners on the basis of gross morphological character. The hybridization data was the final proof for the fusion of such genera as *Sinningia* and *Rechsteineria, Gloxinia* and *Seemannia, Nematanthus* and *Hypocyrta, and Nautilocalyx* with section *Skiophila* (Hanst.) Benth. of *Episcia.* The results of the experimental hybridization gave, thirdly, the final impetus to split several large genera believed to contain discordant elements: *Moussonia* was separated from *Kohleria, Paradrymonia* Hanst.

TABLE III: INTERGENERIC HYBRIDS IN THE SUBFAMILY GESNERIOIDEAE

Including combinations considered intergeneric in Fritsch's classification system (1893-94). Number values in ( ) = chromosome numbers; number values with % = percent of hybrid pollen stainability; C&L = hybrids produced by Cooke & Lee (1966); Cb = Clayberg (1968); L = Lee (1967a); Lem = Lemaire (1857); P = Planchon (1854-55); S = Saylor (1971); S&L = Sherk & Lee (1967); Sk = Skog (1972); W = Wiehler (1968, 1970, 1972b, 1973a, 1975a).

TRIBE GLOXINIEAE FRITSCH

1.	*Achimenes spp.*	(11)	X	*Smithiantha* spp.	(12)	C&L 0%
2.	*Achimenes spp.*	(11)	X	*Eucodonia* spp.	(12)	C&L 0%
3.	*Smithiantha spp.*	(12)	X	*Eucodonia* spp.	(12)	C&L 0%
4.	*Smithiantha spp.*	(12)	X	*Gloxinia perennis* (L.) Fritsch	(13)	L, W 0%
5.	*Gloxinia hirsuta* (DC.) Wiehler (as *Mandirola multiflora*)	(?)	X	*Smithiantha zebrina* (Paxt.) Kuntze (as *Naegelia zebrina*)	(12)	P
6.	*Smithiantha zebrina* [as *Gesneria (Naegelia) zebrina*]	(12)	X	*Heppiella viscida* (Lindl. & Paxt.) Fritsch (as *Heppiella atrosanguinea*)	(13)	Lem
7.	*Moussonia hirsutissima* (Morton) Wiehler	(11)	X	*Smithiantha multiflora* (Martens & Galeotti) Fritsch	(12)	W 0%
8.	*Koellikeria erinoides* (DC.) Mansf.	(13)	X	*Kohleria spicata* (HBK) Oerst	(13)	W 0-11%
9	*Gloxinia sylvatica* (HBK) Wiehler	(13)	X	*Gloxinia gymnostoma* Griseb. (as *Achimenes gymnostoma*)	(13)	W 91%
10.	*Gloxinia sylvatica* (as *Seemannia latifolia*)	(13)	X	*Gloxinia perennis*	(13)	W 19%
11.	*Gloxinia perennis*	(13)	X	*Gloxinia gymnostoma* (as *Achimenes gymnostoma*)	(13)	W 79%
12.	*Gloxinia sylvatica* (as *Seemannia latifolia*)	(13)	X	*Gloxinia lindeniana* (Regel) Fritsch (as *Kohleria lindeniana*)	(13)	W 20%
13.	*Gloxinia sylvatica*	(13)	X	*Kohleria lanata* Lem.	(13)	W 0%
14.	*Gloxinia sylvatica* (as *Seemannia latifolia*)	(13)	X	*Kohleria spicata*	(13)	W 8%
15.	*Gloxinia gymnostoma*	(13)	X	*Kohleria eriantha* (Benth.) Hanst.	(13)	W 2%
16.	*Gloxinia lindeniana*	(13)	X	*Eucodonia verticillata* (Martens & Gal.) Wiehler	(12)	W 0%
17.	*Heppiella viscida*	(13)	X	*Gloxinia nematanthodes* (Kuntze) Wiehler	(13)	W 0%
18.	*Moussonia elegans* Decne.	(11)	X	*Gloxinia gymnostoma*	(13)	W 0%
19.	*Moussonia hirsutissima*	(11)	X	*Gloxinia gymnostoma*	(13)	W 0%
20.	*Moussonia hirsutissima*	(11)	X	*Gloxinia nematanthodes*	(13)	W 0%
21.	*Moussonia hirsutissima*	(11)	X	*Solenophora insignis* (Martens & Gal.) Hanst.	(10)	W 0%
22.	*Moussonia hirsutissima*	(11)	X	*Solenophora* sp. (*S. tuxtla* Denham ined.)	(10)	W 0%
23.	*Moussonia elegans*	(11)	X	*Kohleria digitaliflora* (Lind. & André) Fritsch	(13)	W 0%
24.	*Monopyle maxonii* Morton	(13)	X	*Gloxinia perennis*	(13)	

25. *Diastema vexans* H. E. Moore	(13)	X	*Kohleria spicata*	(13)	W 5-8%
26. *Kohleria reticulata* Fritsch (to be transferred to gen. nov. = *Kohleria* group III, Wiehler, 1975a)	(?)	X	*Kohleria hirsuta* (HBK) Regel	(13)	W 0%
27. *Kohleria weberbaueri* Fritsch (= *Kohleria* group III)	(?)	X	*Kohleria spicata*	(13)	W 0%
28. *Sinningia* Nees spp.	(13)	X	*Rechsteineria* Regel spp. (submerged under *Sinnigia,* Moore, 1973)	(13)	Cb 0-100%

Tribe Episcieae Endl.

29. *Nautilocalyx melittifolius* (L.) Wiehler (as *Episcia melittifolia*)	(9)	X	*Nautilocalyx villosus* (Kunth & Bouche) Sprague	(9)	W 73%
30. *Nautilocalyx panamensis* (Seem.) Seem. (as *Episcia panamensis*)	(9)	X	*Nautilocalyx villosus*	(9)	W 100%
31. *Nautilocalyx villosus*	(9)	X	*Nautilocalyx membranaceus* (Morton) Wiehler (as *Episcia membranacea*)	(9)	W 100%
32. *Hypocyrta Mart.* spp. (submerged under *Nematanthus,* Moore, 1973)	(8)	X	*Nematanthus* Schrader spp.	(8)	S, W 45-100%
33. *Columnea* L. spp.	(9)	X	*Dalbergaria* Tussac spp.	(9)	W 0%
34. *Columnea* spp.	(9)	X	*Trichantha* Hook. spp.	(9)	S&L, W 0%
35. *Columnea* spp.	(9)	X	*Pentadenia* (Planch.) Hanst. spp.	(9)	S&L, W 0%
36. *Dalbergaria* spp.	(9)	X	*Trichantha* spp.	(9)	W 0-9%
37. *Dalbergaria* spp.	(9)	X	*Pentadenia* spp.	(9)	W 0%
38. *Trichantha* spp.	(9)	X	*Pentadenia* spp.	(9)	W 0%

Tribe Gesnerieae

39. *Gesneria* L. spp.	(14)	X	*Rhytidophyllum* Mart. spp.	(14)	W (1970) Sk (1972) 0-35%

from *Episcia,* and *Dalbergaria* Tussac, *Pentadenia* (Planch.) Hanst., and *Trichantha* (Hook.) from *Columnea.* In each case gross morphological features supported such generic reconstruction.

This brief review of recent cytogenetic developments in the Gesnerioideae is a prerequisite for an evaluation of the hybridization data and the generic limits of the genus *Achimenes* sensu lato. At the time of the hybridization work with *Achimenes* (Cooke & Lee), the small Mexican genus *Smithiantha* was included in this experimentation, because it was questioned whether *Smithiantha* should be united with *Achimenes* (cf. Moore & Lee, 1967, p. 106). The presumed affinity was based on the fact that many hybrids between these two genera had been produced in Europe in the last century (the more spectacular ones were illustrated in botanical magazines between 1840 and 1870), and that similar hybrid combinations were easily

TABLE IV: BASE CHROMOSOME NUMBERS FOR THE GENERA IN THE TRIBE GLOXINIEAE FRITSCH

Genus	*x*	*Genus*	*x*
1. *Solenophora* Benth.	10	13. *Diastema* Benth.	13
2. *Moussonia* Regel	11	14. *Kohleria* group III	—
3. *Achimenes* Pers.	11	15. *Capanea* Decne.	13
4. *Niphaea* Lindl.	11	16. *Paliavana* Vandelli	13
5. *Eucodonia* Hanst	12	17. *Vanhouttea* Lem.	—
6. *Smithiantha* Kuntze	12	18. *Sinningia* Nees	13
7. *Gloxinia* L'Herit.	13	19. *Lietzia* Regel	—
8. *Monopyle* Benth.	13	20. *Lembocarpus* Lwbg.	—
9. *Pearcea* Regel	13	21. *Goyazia* Taubert	—
10. *Heppiella* Regel	13	22. *Bellonia* L.	13
11. *Kohleria* Regel	13	23. *Phinaea* Benth.	13
12. *Koellikeria* Regel	13	24. *Anodiscus* Benth.	13

obtained in the early 1960's. The decisive factor, however, remains that all these integeneric hybrids were sterile, and that, in contrast, the interspecific hybrids among the four species of *Smithiantha* showed a high degree of pollen stainability, as did many interspecific hybrids among *Achimenes* sensu stricto. Since the base chromosome numbers between the two genera differ ($x=11$ in *Achimenes* sensu stricto, $x=12$ in *Smithiantha*), and since there is at least one good vegetative character to separate the two taxa (the florescence bracts and flowers are alternate in *Smithiantha*, opposite-decussate in *Achimenes*), there should be no question today that *Smithiantha* is a valid genus. If the hybridization data between *Achimenes* and *Smithiantha* is seen as a reason to unite these taxa, then almost all the genera of the tribe Gloxinieae must be merged into one unwieldy supergenus, on the basis of the current hybridization data.

THE *Gloxinia* GROUP

Species of the section *Mandirola* of *Achimenes* were not in cultivation at the time of the hybridization program of Cooke and Lee (1966). The type species of this section (or of the genus *Mandirola* Decne.) is *Achimenes multiflora* Gardner from the Province of Goias in Brazil. A second, very similar species from the same area was described by Gardner at the same time (1842) as *Gloxinia ichthyostoma*, but transferred by Hanstein in 1865 to *Achimenes*, subgenus *Mandirola*. The third species in Fritsch's section *Mandirola* comes from the Province of Tucumán in northwestern Argentina; it was first published by Grisebach in 1874 as *Gloxinia gymnostoma* (Figure 1), and transferred to *Achimenes* by Fritsch in 1894. Fritsch considered the section *Mandirola* as closely related to the genus *Gloxinia* ("Nahe verwandt mit der Gattung *Gloxinia*"). Nineteen years later, in 1913, Fritsch described a Bolivian collection of *Achimenes gymnostoma* as the type of a new genus, *Fiebrigia*. He characterized this genus as standing among *Gloxinia*, *Achimenes*, and *Seemannia* ("*Fiebrigia* steht in ihren Merkmalen zwischen *Gloxinia*, *Achimenes* und *Seemannia*, . . ."). In the same treatment of neotropical Gesneriaceae, two pages earlier, Fritsch established the monotypic section *Tydaeopsis* in *Achimenes* for the Bolivian species *A.*

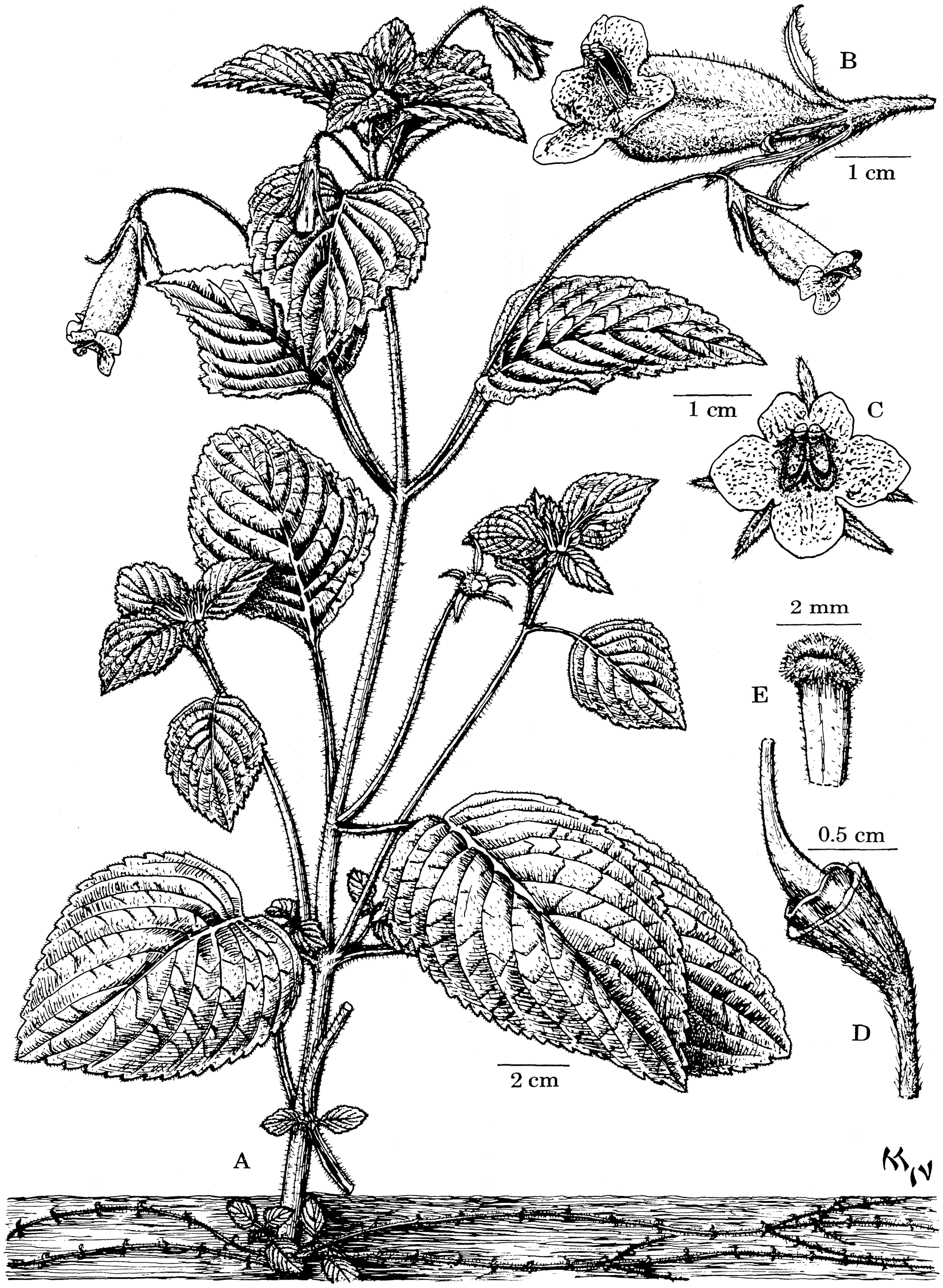


Figure 1. *Gloxinia gymostoma,* collected by T. Meyer, s.n., 1967, in Quedraba de los Sosa, alt. 940 m, Dept. Tafi, Prov. Tucuman, Argentina, and since then cultivated in North America. Illustration by Miss Mitsu Nakayama, 8 April 1969, at the L. H. Bailey Hortorium, Cornell University; greenhouse acc. no. G-1039. A, habit; B, flower at anthesis (male phase), lateral view; C, same flower, face view; D, ovary and nectary, with calyx lobes removed; E, distal part of style with stomatomorphic stigma.

rusbyi Britton. Sixteen years earlier, in 1897, he had erected the monotypic section *Kohleriopsis* in *Achimenes* to accomodate *A. heppielloides* Fritsch from Bolivia. After examining well over 80 collections of *Achimenes gymnostoma* and its close relatives, mainly at US, NY, GH, K, and P as well as the type material involved, I now consider *Achimenes heppielloides* and *A. rusbyi* to fall within the range of geographical variation found within *Achimenes gymnostoma,* an apparently fairly common species between Tucumán, Argentina, and Cuzco, Peru. Fritsch did not assign to sections several other Bolivian species related to *Achimenes gymnostoma* (described by Britton or Rusby under *Achimenes* around 1900), except that he transferred *Achimenes albescens* Rusby to *Seemannia.* After the establishment of the section *Tydaeopsis,* Fritsch commented that the limitations between the sections of *Achimenes* are rather tenuous and that they may be untenable with the finding of more new species ("Die Grenzen zwischen den *Achimenes*-Sektionen sind übrigens sehr schwache und werden bei weiterer Auffindung neuer Arten vielleicht gar nicht mehr haltbar sein"). The sections *Tydaeopsis* and *Kohleriopsis* are considered here as synonyms of the section *Mandirola* in *Achimenes* sensu lato.

Achimenes gymnostoma has been in cultivation since 1967 as the only representative of the section *Mandirola.* It was collected in the Province of Tucumán, Argentina (*T. Meyer s.n.,* 15 April 1967, BH, SEL). The chromosome number of this species is $n=13$ (Wiehler, 1972a), a value typical for the genus *Gloxinia,* but not found in *Achimenes* sensu stricto ($n=11$). I have used this critical species in hybridization experiments to help to determine generic relationships. *Achimenes gymnostoma* did not produce any hybrids with species of *Achimenes* sensu stricto, but formed partially fertile hybrids with other species of *Gloxinia* (including *Seemannia*) in cultivation: with the type species of *Gloxinia, G. perennis* (L.) Fritsch (79% hybrid pollen stainability = p.s.), with *Gloxinia sylvatica* (HBK) Wiehler [formerly *Seemannia sylvatica* (HBK) Hanst. and *S. latifolia* Fritsch, 86% p.s.], and with *Gloxinia nematanthodes* (O. Kuntze) Wiehler [formerly *Seemannia nemathanthodes* (O. Kuntze) K. Schumann, 91% p.s.]. *Achimenes gymnostoma* also produced sterile intergeneric hybrids with several species of *Kohleria* ($n=13$), *Smithiantha* ($n=12$), and with *Moussonia* ($n=11$). *Gloxinia nematanthodes* is illustrated in Figure 2.

The cytogenetic data indicates the removal of *Achimenes gymnostoma* (and thus the transfer of the complete section *Mandirola*) from the genus *Achimenes* sensu lato and suggests instead its placement in the genus *Gloxinia.* There are, however, no absolutely precise characters except chromosome numbers to separate *Gloxinia* from *Achimenes* sensu stricto. The fruit in *Gloxinia* is usually an almost or completely inferior, bivalved, elongated, and ridged capsule, while the capsule in *Achimenes* is semi-inferior, less elongated, and smooth-walled. The scaly rhizomes of *Gloxinia* (including the Brazilean species of the *Gloxinia* group) often produce long, threadlike runners, a feature usually not found in *Achimenes.* A planned investigation of pollen and seed morphology of the Gesnerioideae may result in sharper generic delimitation of these taxa. An elongated, inferior seed capsule is also typical of the genus *Monopyle* Benth., but in this genus the opposite-decussate leaves are strongly anisophyllous, while the leaf pairs in *Gloxinia* are of equal size. The florescence in *Monopyle* is usually elongated and compound, while that of Gloxinia is reduced to one flower per leaf axil (except

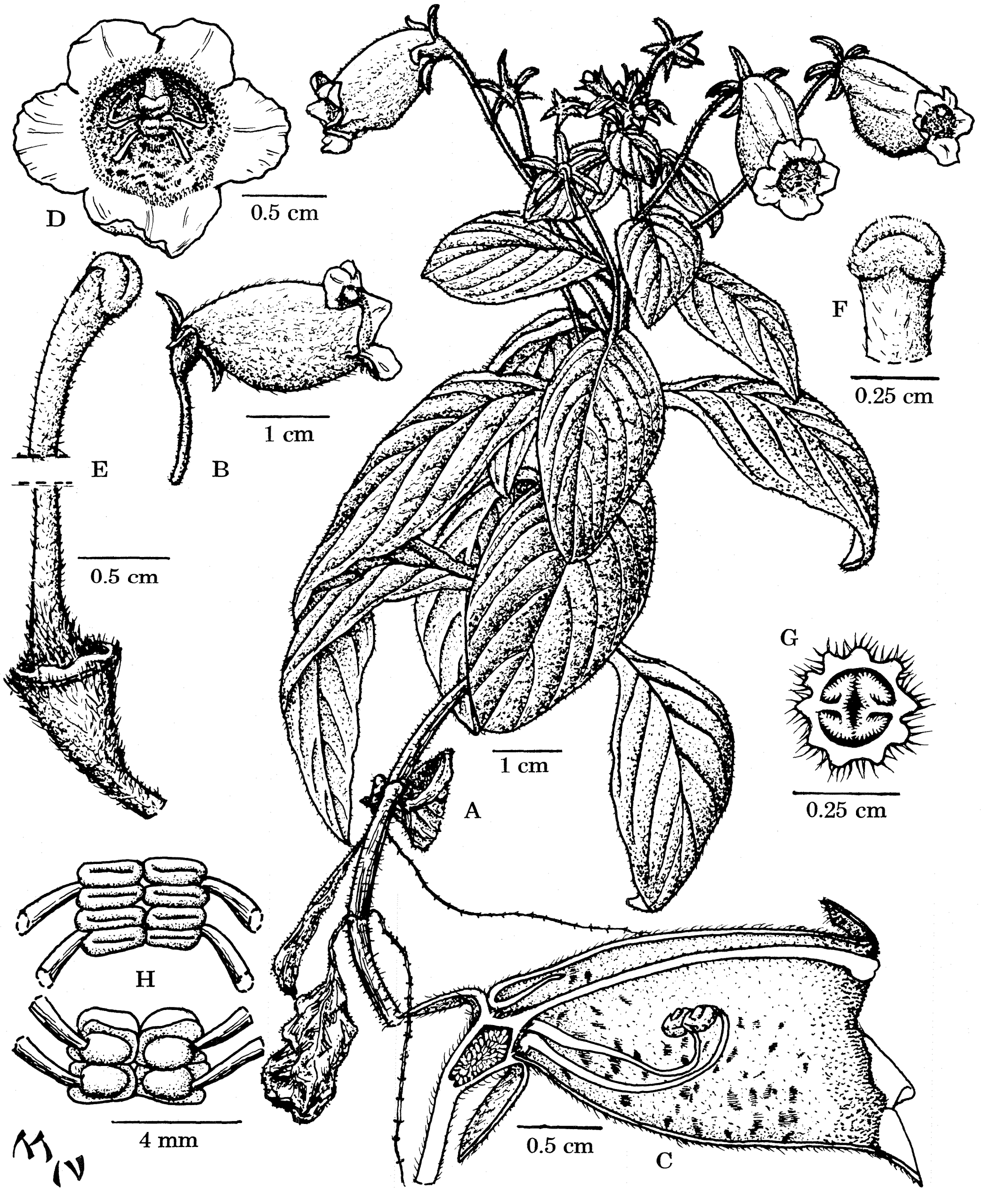


Figure 2. *Gloxinia nematanthodes.* Rhizomes collected in 1969 by C. Gomez Ruppel, of Mendoza, Argentina, in the region of Salta, Prov. Salta, Argentina, and sent to the author. Illustration by Miss Mitsu Nakayama, at first flowering, 9 March 1970, at the L. H. Bailey Hortorium, Cornell University; greenhouse acc. no. G-1324. A, habit; B, flower at anthesis, lateral view; C, same view, longitudinal section, showing gynoecium at female phase of anthesis with extended style and receptive stigma with stamens retracted; D, corolla, face view; E, gynoecium and nectary, calyx lobes removed; F, stigma; G, cross-section of ovary showing parietal placentation; H, anthers, ventral and dorsal views.

in a few collections of *G. sylvatica* which have 2-4 successive flowers per leaf axil). The stigma in *Gloxinia* is stomatomorphic or cup-shaped.

The nectary, important in the pollination of the neotropical Gesneriaceae, plays a decisive role in the classification of the gesneriaceous genera. A particular shape of the nectary is usually constant for a genus. There is, however, some variation in the structure of the nectary in the genus *Gloxinia.* It is a two-fold variation on a single theme, parallel to that found in the large genera *Kohleria* and *Sinningia.* In the majority of the species of *Gloxinia* the nectary consists of a thick ring surrounding the ovary just above the attachment of the calyx, corolla, and stamens. A nectary, however, is absent (or almost completely reduced and non-functional) in *Gloxinia perennis,* the widely distributed type species of the genus (Bolivia to Panama and the Guianas), in *G. racemosa* from northern Colombia, in *G. multiflora* from central Brazil, in *G. reflexa* Rusby from Bolivia and Peru, and in an undescribed species from Ecuador [*Mexia 8480* (GH, NY, K, BM), *Dodson & Thien 1173* (US, BH, WIS, K), Dodson 5244 (SEL)]. In other species *(G. sarmentiana, G. villosa)* the basically ring-shaped nectary has one dorsal or 4-5 paper-thin lobes, a condition still quite different, however, from the thick and swollen individual glands surrounding the ovaries in *Kohleria* and *Sinningia.* In *Gloxinia ichthyostoma* from central Brazil the nectarial ring is divided into four separate paper-thin glands (observed on isotypes at GH and NY, *Gardner 3304* but in the lectotype at K and isotypes at K, BM, and P the nectaries are annular although thin and somewhat irregular). In *Gloxinia lindeniana* the nectary of different flowers on the same plant varies from five separate, thin, triangular glands to a five-lobed ring. The presently cultivated material of this distinct species stems from the original collection of Jean Linden in 1868, apparently from Ecuador or northern Peru. It has not yet been rediscovered in its native habitat. The nectaries of both *G. lindeniana* and *G. ichthyostoma* appear to be non-functional; the flower of the former is fragrant, a rare phenomenon in the Gesneriaceae.

There is thus a definite trend towards a reduction of nectarial tissue and non-functioning nectaries in the genus *Gloxinia,* signifying a shift in the mode of pollination. In the most advanced (and most successful) species of the genus, *G. perennis,* the ovarian nectary is replaced by an osmophore near the ventral base of the corolla tube. This dark purple-colored tissue emits fragrance and attracts male euglossine bees of a single species, *Eulaema meriana* (Oliver), as pollinator (Vogel, 1966; Dressler, 1968a, 1968b; Dodson et al., 1969). It appears likely that all species of *Gloxinia* with non-functional nectaries are pollinated by male euglossine bees. The formation of an osmophore is not necessary for this advanced type of pollination syndrome since the fragrance exudant may be generally diffused from the corolla tissue. This is the case in most orchid species pollinated by male euglossine bees (Dodson, personal communication). Nectarial tissue is also absent from the 23 species of the closely related genus *Monopyle* where male euglossine pollination may be inferred from the shape and color of the corollas (white, pale blue, or yellow). Most Brazilian species of *Gloxinia* have a similar type of corolla as *Monopyle,* typical for euglossine bee pollination.

Most of the taxa in the subfamily Gesnerioideae show a certain degree of generic uniformity in flower types, as examplified by *Monopyle, Heppiella, Moussonia, Phinaea* Benth., *Columnea* L., *Dalbergaria* Tussac, *Nautilocalyx* Linden, *Chrysothemis* Decne., and *Napeanthus* Gardner. The same subfamily contains also a number of large genera with strongly divergent flower types. The situation in *Gloxinia* parallels that in *Sinningia* (including *Rechsteineria*), *Achimenes* sensu stricto, *Drymonia* Mart. (the most diverse group in flower shapes), *Nematanthus* Schrader (including *Hypocyrta* Mart.) *Besleria* L., *Gasteranthus* Benth., and *Gesneria* L. The species of *Gloxinia* have evolved along pollination syndrome lines, involving such pollinator types as: 1) euglossine bees (females and males in search of nectar = gynandro-euglossine pollination, visiting bluish or whitish corollas with wide entrances), 2) hummingbirds (in search of nectar, attracted by red, orange, or yellow corollas, more or less tubular, with a narrow entrance), and 3), male euglossine bees (in search of perfume = andro-euglossine pollination). In the Gesneriaceae the andro-euglossine flower is of the same type as the gynandro-euglossine flower, except that nectar production has shifted to fragrance production, either at a specific locus, the osmophore, or in a more diffused manner.

The main impetus to unite the genus *Seemannia* with *Gloxinia* came from the hybridization data, namely the high degree of hybrid fertility (Table II; cf. Wiehler, 1972b, 1975b). The similarity in vegative features and fruit type provided supporting evidence. The position of *Gloxinia lindeniana*, however, needs a few further comments. This species was originally placed in *Tydaea* Decne. (now a synonym of *Kohleria*), then transferred to *Gloxinia* by Fritsch, and shifted again to *Kohleria* by Moore two decades ago, mostly on account of the structure of the nectary which then seemed aberrant for the concept of the genus *Gloxinia*. The nature of the nectary of *Gloxinia lindeniana* has been clarified above. This species now fits well into the reconstructed genus *Gloxinia*, and is out of place in *Kohleria* where it needed a section of its own, *Gloxinella* H. E. Moore. The hybridization data was again suggestive. The only partially fertile hybrid of *Gloxinia lindeniana* is with *Gloxinia sylvatica* (Table II). It further produced a sterile (= intergeneric) hybrid with *Eucodonia verticillata* (Table II). I was unsuccessful in crossing it with species of *Kohleria*, although Dr. Carl Clayberg, then at the Agricultural Experiment Station at New Haven, Connecticut, obtained hybrids of *Gloxinia lindeniana* with *Kohleria amabilis* (Planch. & Lind.) Fritsch and *K. spicata* (HBK) Oersted. The hybrids were, however, too weak to produce flowers (Clayberg, personal communication, 1970). Clayberg has done extensive cytogenetic work in the genus *Kohleria* in which he originally included *Gloxinia lindeniana* and species of the section *Moussonia* (Regel) Fritsch (Clayberg, unpublished data). Both Clayberg and I agree now to exclude *Gloxinia lindeniana* and the section *Moussonia* from the genus *Kohleria* (Wiehler, 1975a).

The reconstructed genus *Gloxinia* consists of the following pollination groups (= sections?) and species:

Gloxinia L'Heritier, Stirp. Nov. 149. 1791. ("1785").

Mandirola Decne., Rev. Hort. 20:468. 1848.

Achimenes P. Br. subg. *Mandirola* (Decne.) Hanst., Linnaea 34-343. 1865.

Achimenes sect. *Mandirola* (Decne.) Benth., in Benth. & Hook., Gen. Pl. 2:999. 1876.

Salisia Regel, Flora 32:179. 1849.

Seemannia Regel, Gartenflora 4:183. 1855.

Achimenes sect. *Kohleriopsis* Fritsch, in Engler & Prantl, Nat. Pflanzenfam., Nachträge 1:299. 1897.
Fritschiantha Kuntze, Rev. Gen. Pl. 3(2):241. 1898.
Achimenes sect. *Tydaeopsis* Fritsch, Bot. Jahrb. Syst. 50:395. 1913 ("1914").
Fiebrigia Fritsch, loc. cit., p. 397.
Kohleria Regel sect. *Gloxinella* H. E. Moore, Gentes Herb. 8(5):382. 1954.

TYPE SPECIES: *Gloxinia perennis* (L.) Fritsch. HOLOTYPE: Cult., Hort. Cliffortianus (BM). (Hort. Cliff. t. 18. 1738).

ETYMOLOGY: Charles Louis L'Heritier de Brutelle (1746-1800) named this genus in honor of Benjamin Peter Gloxin (1765-1795), a German physician and botanist of Colmar, author of several botanical publications.

THE ANDRO-EUGLOSSOPHILOUS SPECIES (SECTION *Gloxinia*)

Gloxinia perennis (L.) Fritsch, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 174. 1894.

Martynia perennis L., Sp. Pl. 862. 1753.
Gloxinia maculata L'Herit., Stirp. Nov. 149. 1791; Bot. Mag. 29:t.1191. 1809.
Salisia maculata (L'Herit.) Regel, Bot. Zeitung (Berlin) 9:894. 1851.
Gloxinia trichotoma Moench, Suppl. 194. 1802.
Gloxinia heterophylla Poepp., in Poeppig & Endlicher, Nov. Gen. & Sp. Pl. 3:9. 1840.
Gloxinia pallidiflora Hook., Bot. Mag. 72:t. 4213. 1846.
Salisia pallidiflora (Hook.) Regel, Bot. Zeitung (Berlin) 9:894. 1851.
Gloxinia suaveolens Decne., Rev. Hort. 3(2):463. 1848.
Salisia gloxiniaeflora Regel, Flora 32:179. 1849.
Gloxinia trichantha Miq., Linnaea 22:473. 1849.

Gloxinia hirsuta (DC.) Wiehler, comb. nov.

Achimenes hirsuta DC., Prodr. 7:536. 1839; non *A. hirsuta* Lindl. (= *A. skinneri* Lindl.).
Achimenes multiflora Gardner, Hooker's Ic. Pl. 5:t. 468. 1842.
Mandirola multiflora (Gardner) Decne., Rev. Hort. 20:468. 1848.
Locheria multiflora (Gardner) Regel, Flora 31:252. 1848.

Gloxinia ichthyostoma Gardner, Hooker's Ic. Pl. 5:t. 472. 1842.

Mandirola ichthyostoma (Gardner) Seem. ex Hanst., in Mart., Fl. Bras. 8(1):348. 1864.
Achimenes ichthyostoma (Gardner) Hanst., Linnaea 34:434. 1865.
(It is possible that this species is merely a form of the variable and widely distributed *G. hirsuta* above, but this can only be ascertained through field study and hybridization work.)

Gloxinia lindeniana (Regel) Fritsch, Oesterr. Bot. Z. 63:66. 1913.

Tydaea lindeniana Regel, Gartenflora 17:257, t. 589. 1868.
Tydaea lindenii Regel? ex André, Ill. Hort. 20:183, t. 147. 1873.
Isoloma lindenianum (Regel) Nichols., Ill. Dict. Gard. 2:201. 1885.
Kohleria lindeniana (Regel) H. E. Moore, Gentes Herb. 8(5):380. 1954.

Gloxinia racemosa (Benth.) Wiehler, comb. nov.
Monopyle racemosa Benth., Hooker's Ic. Pl. 12:87. 1876; Bot. Mag. 102: t. 6233. 1876.

Gloxinia reflexa Rusby, Mem. Torrey Bot. Cl. 6:94. 1896.
Monopyle divaricata Rusby, Bull. N. Y. Bot. Gard. 8(28):119. 1912.

Gloxinia sp. nov., from western Ecuador [*Mexia 8480* (GH,NY); *Dodson & Thien 1173* (US,WIS); *Dodson 5244* (SEL)].

THE GYNANDRO-EUGLOSSOPHILOUS SPECIES

Gloxinia burchellii (S. M. Phillips) Wiehler, comb. nov.
Achimenes burchellii S. M. Phillips, Kew Bull. 24(1):225. 1970.

Gloxinia rupestris (Gardner) Wiehler, comb. nov.
Achimenes rupestris Gardner, Hooker's Ic. Pl. 5:t. 480. 1842.

Gloxinia sarmentiana Gardner ex Hook., Hooker's Ic. Pl. 4:t. 378. 1841.
Gloxinia attenuata Hanst., Linnaea 27:716. 1856.
Gloxinia stolonifera Fritsch, Bot. Jahrb. Syst. 37:493. 1906.

Gloxinia villosa (Gardner) Wiehler, comb. nov.
Tapina villosa Gardner, Hooker's Ic. Pl. 5:t. 469. 1842.
Ligeria villosa (Gardner) Hanst., in art., Fl. Bras. 8(1):240. 1864.
Anetanthus villosus (Gardner) Benth. ex Jackson, Ind. Kew. 1:113. 1893.
Goyazia villosa (Gardner) R. Howard, J. Arnold Arbor. 56(3):367.1975.

THE ORNITHOPHILOUS SPECIES

Gloxinia gymnostoma Griseb., Pl. Lorentz. 179. 1874.
Achimenes gymnostoma (Griseb.) Fritsch, in Engler & Prantl. Nat. Pflanzenfam. 4(3b):175. 1893-94.
Seemannia gymnostoma (Griseb.) Tours., Bol. Soc. Arg. Bot. 7(2):135. 1958.
Achimenes rusbyi Britton, Mem. Torrey Bot. Cl. 6:95. 1896.
Achimenes heppielloides Fritsch, Bull. Torrey Bot. Cl. 23:151. 1896; cf. Fritsch, in Engler & Prantl, Nat. Pflanzenfam. Nachträge 1:300. 1897.
Fiebrigia digitaliflora Fritsch, Bot. Jahrb. Syst. 50:397. 1913. ("1914").

Gloxinia nematanthodes (Kuntze) Wiehler, Baileya 18(4):137. 1972 ("1971")
Fritschiantha nematanthodes Kuntze, Rev. Gen. Pl. 3(3):241. 1898.
Seemannia nematanthodes (Kuntz) Schum., Just's Bot. Jahresber. 26(1):386. 1898.
Achimenes gracilis Britton, Bull. Torrey Bot. Cl. 27:27. 1900.

Gloxinia purpurascens (Rusby) Wiehler, comb. nov.
Seemannia purpurascens Rusby, Mem. Torrey Bot. Cl. 4:237. 1895.
Fritschiantha purpurascens (Rusby) Kuntze, Rev. Gen. Pl. 3(3):241. 1898.

Achimenes flaccida Rusby, Mem. Torrey Bot. Cl. 6:95. 1896.
Seemannia longiflora Fritsch, Bot. Jahrb. Syst. 50:404. 1913 ("1914").
Seemannia dioica Rusby, Mem. N.Y. Bot. Gard. 7:360. 1927.

Gloxinia sylvatica (HBK) Wiehler, Selbyana 1(1):33. 1975.
Gesneria sylvatica HBK, Nov. Gen. Sp. Pl. 2:393. 1818.
Seemannia sylvatica (HBK) Hanst., Linnaea 29:540, 587. 1859 *("silvatica")*.
Fritschiantha sylvatica (HBK) Kuntze var. coccinea Kuntze, var. aurea Kuntze, Rev. Gen. Pl. 3(3):241. 1898 *("silvatica")*.
Gesnera oxyphylla DC., Prodr. 7:531. 1839.
Seemannia ternifolia Regel, Gartenflora 4:183, pl. 126. 1855.
Seemannia benaryi Regel, Gartenflora 23:353, pl. 814. 1874.
Fritschiantha benaryi (Regel) Kuntze, Rev. Gen. Pl. 3(3):242. 1898.
Seemannia major Baillon, Bull. Bens. Soc. Linn. Paris 1:710. 1888.
Fritschiantha major (Baillon) Kuntze, Rev. Gen. Pl. 3(3):242. 1898.
Seemannia uniflora Baillon, Bull. Mens. Soc. Linn. Paris 1:710. 1888.
Fritschiantha uniflora (Baillon) Kuntze. Rev. Gen. Pl. 3(3):242. 1898.
Achimenes albescens Rusby, Mem .Torrey Bot. Cl. 6.94. 1896.
Seemannia albescens (Rusby) Fritsch, Bot. Jahrb. Syst. 50:403. 1913 ("1914").
Seemannia cuneata Rusby, Mem. Torrey Bot. Cl. 6:96. 1896.
Fritschiantha cuneata (Rusby) Kuntze, Rev. Gen. Pl. 3(3):242. 1898.
Seemannia regnelliana Fritsch, Bot. Jahrb. Syst. 29, Beiblatt 65:13. 1900.
Seemannia latifolia Fritsch, Meded. Herb. Leiden 29:52. 1916.

SPECIES EXCLUDED FROM *Gloxinia*

Gloxinia arborea Colla was described in 1824 from a sterile specimen of unknown origin in cultivation at the Botanical Garden in Turin, Italy. Twelve years later plant material with the same name flowered for the first time in Europe in the garden of Count Camaldoldi in Naples, Italy. Friedrich Dehnhardt, the gardner of the estate, could not find a published account of *Gloxinia arborea* in the botanical literature and thus decided to furnish a more complete diagnosis of the species which he renamed *Gloxinia fruticosa.* The description leaves no doubt that Dehnhard's and Colla's plant material with its green corolla dotted purple is *Paliavana prasinata* (Ker Gawler) Benth. from Minas Gerais, Brazil.

Paliavana prasinata (Ker Gawler) Benth., in Benth. & Hook., Gen. Pl. 2:1003. 1876.
Gesneria prasinata Ker Gawler, Bot. Reg. 5:t.428. 1819.
Gloxinia arborea Colla, Hortus Ripulensis 61. 1824.
Gloxinia fruticosa Dehnhardt, Memoire sopra alcune piante nuove 3-4. 1836.

The status of two Mexican species published by Martens and Galeotti as *Gloxinia micrantha* and *G. verticillata* is clarified below.

The *Eucodonia* Group

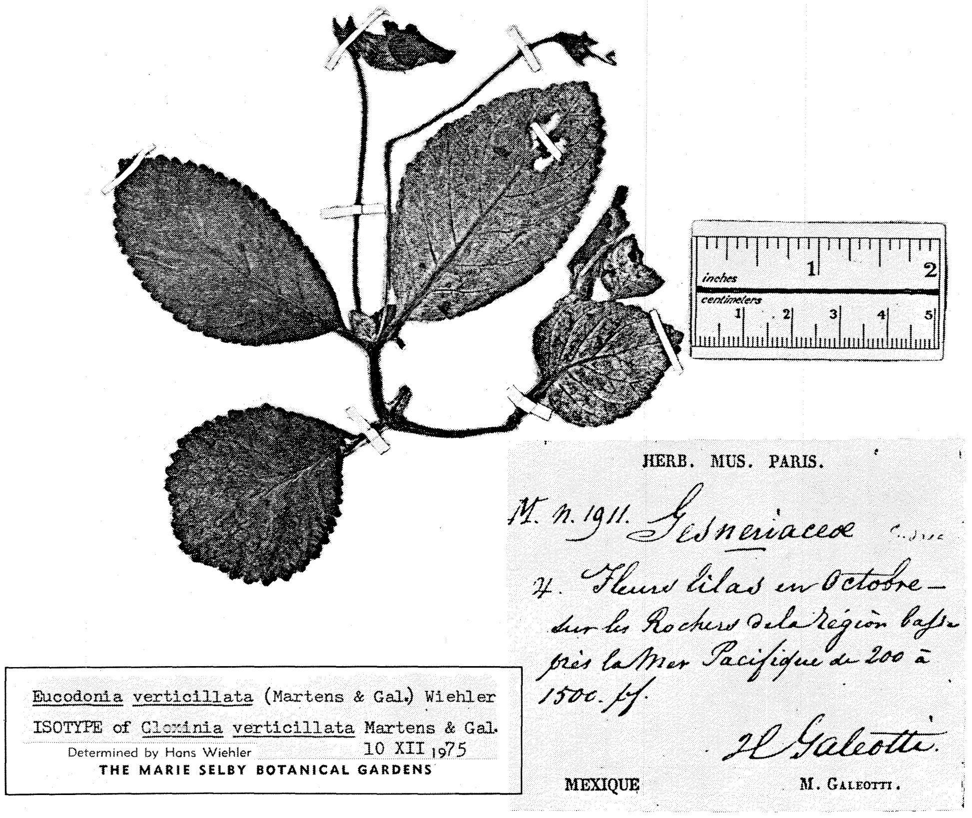
The cytogentic data of Cooke and Lee (1966) showed that *Achimenes ehrenbergii, A. andrieuxii*, and *A. bella* have a different base chromosome number ($x = 12$) from the species of *Achimenes sensu stricto* ($x = 11$), and that these species form only sterile hybrids with *Achimenes* sensu stricto and with species of *Smithiantha* ($x = 12$). The species in the *Eucodonia* group are very similar to general habit, in the wooly indumentum, and in the corolla shape and color, but they have been placed in different sections of *Achimenes*, on account of differences in the shape of the stigma. Hanstein founded the monotypic genus *Eucodonia* in 1854, based on *E. ehrenbergii* which had, according to his description, a bilabiate or bifid stigma, and reddish indumentum on the plant body. Two years later, in 1856, after a more detailed description of his new genus and species, he transferred a species just published by Lemaire as *Mandirola lanata* to *Scheeria*. This species had a whitish indumentum and, according to the generic definition, a stomatomorphic stigma. In 1865 Hanstein united both species under *Achimenes* (subgenus *Eucodonia*) but as *A. lanata* (Lem.) Hanst. instead of *A. ehrenbergii* (Hanst.) Hanst. The cultivated collection of this species at Cornell University (acc. nos. G-202 and G-561, of horticultural origin, apparently from England) had a bilobed stigma (Moore, 1957, p. 105; cf. Cooke & Lee, 1966, p. 99). A new collection at Selby Gardens (acc. no. W-1896, collected by *R. L. Dressler s.n.* in 1973 in the Province of Oaxaca, Mexico, in an open dry area on rocks) has a stigma intermediate between stomatomorphic and bilobed; it is actually both. The same condition exists in *Achimenes andrieuxii* (Cornell Univ. and Selby Gard. acc. no. G-420 and G-1001; cf. Cooke & Lee, 1966, p. 99). This species was never placed into a section. C. V. Morton described the stigma in *Achimenes bella* as stomatomorphic and placed it into the section *Scheeria*. A re-examination of the type material of *A. bella, Hinton 4512* (holotype at K, isotype at BM), reveals the stigma as intermediate between stomatomorphic and bilobed. In summary, the form of the stigma in the *Eucodonia* group is rather uniform; it can be interpreted as either mouth-shaped or bifid, a rare situation in the neotropical Gesneriaceae.

Cooke & Lee (1966) concluded that all three species should be placed into the same section *Eucodonia*. I concur in the opinion that the *Eucodonia* group forms a rather natural and distinct unit. However, in the context of generic structure in the revised subfamily Gesnerioideae (Wiehler, 1976), and in view of total cytogenetic data presently at hand, it appears more logical to propose once more generic status for the *Eucodonia* group. Otherwise *Achimenes* would be the only genus in the subfamily with two basic chromosome numbers. The cytogenetic information indicates that *Eucodonia* is as closely or as distantly related to *Achimenes* as *Smithiantha*; leaving *Eucodonia* in *Achimenes* would also imply the inclusion of *Smithiantha* in *Achimenes*. I have produced sterile hybrids between *Gloxinia lindeniana* and *Achimenes ehrenbergii, Gloxinia perennis* and *Smithiantha fulgida* (Ortgies) Siebert & Voss, *Moussonia hirsutissima* (Morton) Wiehler and *Smithiantha multiflora* (Martens & Galeotti) Fritsch, and other combinations between the above genera and other taxa in the tribe Gloxinieae, and Cooke & Lee (1966) report on hybrids (all sterile) between *Eucodonia* and *Smithiantha*. Therefore, one could either argue for uniting all these genera into one unwieldy entity, because the hybridization data reveals a certain degree of affinity among the parental genera in this plastic tribe—or one could leave the present generic limits intact wherever possible and advocate the re-establishment of *Eucodonia* as a genus. The latter is done here.

There is still a nomenclatural problem and a taxonomic problem to be considered which effect the names of *Achimenes ehrenbergii* and *A. bella.* In 1842 Martens and Galeotti published the combinations *Gloxinia verticillata* and *G. micrantha* for two gesneriad species collected by Galeotti in the State of Oaxaca, Mexico. I have seen isotypes of *G. verticillata (Galeotti 1911)* at K, P, and W, and an isotype of *G. micrantha (Galeotti 1912)* at P. The holo- or lectotypes at BR are presently on loan elsewhere. There is no question that *G. micrantha* is a later synonym of *Achimenes andrieuxii* DC., published in 1839 (*G. Andrieux 265,* holotype at G, isotype at K, also from the State of Oaxaca, Mexico). The true identity of *Gloxinia verticillata* has never been established, since Martens and Galeotti described this species as having glabrous leaves. Hanstein apparently did not see the type material, but he suggested nevertheless that *G. verticillata* may be conspecific with *Achimenes lanata* (= *A. ehrenbergii*) except for the statement of "folia glabra" which may have been an accidental error in the description of Martens and Galeotti ("An forte errore?" Linnaea 34:443. 1865). The isotypes of *Gloxinia verticillata* at P, K, and W show the typical lanate-villous indumentum on the abaxial leaf surface, and the campanulate lilac corolla is over 2.7 cm long. It is, therefore, evident that *Gloxinia verticillata* and *Achimenes ehrenbergii* are conspecific. We must now use the older epithet *verticillata* for this species (Figure 3).

Both *Eucodonia verticillata* and *E. andrieuxii* were until recently known only from collections in the States of Oaxaca and Chiapas in southern Mexico. Although the two species are clearly distinct by the shape and size of their corollas, there is a surprising degree of variation within each species in the size, color, and spotting of the corolla, in the degree and color of the indumentum on the plant body (white, rose-pink, and wine-red), and in the color of the underside of the leaves (green, wine-red, or purple). Between 1933 and 1938 George B. Hinton found seven other collections of *Eucodonia* in south-central Mexico, in the States of Michoacan and Mexico, and sent them to Kew and the British Museum. One of these collections (*Hinton 4512)* was described as *Achimenes bella* by C. V. Morton in 1936, but he compared the new species only with *Achimenes mexicana,* then the only member in the section *Scheeria* to which *A. bella* was also attributed. A comparison of *Achimenes bella* with the other six collections of *Eucodonia* by Hinton from this south-central Mexican area *(Hinton 8212, 9325, 10662, 12122, 12186,* and *12187)* and a comparison of these seven collections with material of *Eucodonia verticillata* from Oaxaca and Chiapas brings the specificity of *Achimenes bella* into question. When seen as a whole, there does not exist a single differentiating character among *A. bella,* the other six cited collections from Michoacan and Mexico, and the various collections of *Eucodonia verticillata* from Oaxaca and Chiapas. I regard, therefore, *Achimenes bella* as a synonym of *Eucodonia verticillata,* in spite of a difference in chromosome ploidy number. Two collections of *E. andrieuxii* and one collection of *E. verticillata* from southern Mexico are known to be diploids ($n=12$), while the only chromosome count of *A. bella,* from a collection near the type locality in south-central Mexico *(H. E. Moore 8803)*, is a tetraploid ($n=24$).

Eucodonia is a genus of small, saxicolous, perennial herbs with somewhat succulent stems, pseudoverticillate leaves, scaly underground rhizomes, a single long-pedicelled flower per leaf axil, with a small calyx and a bluish, purple or pink campanulate corolla. In cultivation and in the field the two species are easily distinguished from any species of *Achimenes*, *Smithiantha*, and *Gloxinia* by their conspicuous indumentum: dense lanate-villous hairs matt the stems, underside of the leaves, and sometimes the pedicels. Parallel to the *Gloxinia* group in relation to *Achimenes* sensu stricto discussed above, there appears to be no clear-cut generic character to separate the *Eucodonia* group from the true *Achimenes*. The type and degree of indumentum is at best a character at the specific level in the Gesnerioideae (Wiehler, 1970), and chromosome numbers are impractical characters in routine taxonomy, but these features are at present the only good criteria to separate *Eucodonia* ($x=12$) from *Achimenes* ($x=11$). *Eucodonia* is endemic to southern Mexico, from the States of Michoacan and Mexico to Oaxaca and Chiapas.



Eucodonia verticillata (Martens & Gal.) Wiehler
ISOTYPE of Gloxinia verticillata Martens & Gal.
Determined by Hans Wiehler 10 XII 1975
THE MARIE SELBY BOTANICAL GARDENS

HERB. MUS. PARIS.
M. n. 1911. Gesneriaceae
♃. Fleurs lilas en Octobre — sur les Rochers de la Région basse près la Mer Pacifique de 200 à 1500. p[illegible]
H Galeotti.
MEXIQUE M. GALEOTTI.

Figure 3. *Eucodonia verticillata.* Xerograph of isotype, *H. Galeotti 1911* (P), collected on rocks in lower regions (60-500 m) near the Pacific coast, Prov. Oaxaca, Mexico, in 1840. Corolla lilac.

Eucodonia Hanstein, ampl. Wiehler.

Herbae humiles saxicolae perennes, trichomatibus dense lanato-villosis adpressis, rhizomatibus squamatis subterraneis. Stigma stomatomorphum vel bifidum vel uterque. Chromasomatum numerus $x=12$.

Eucodonia Hanst., Linnaea 26:201. 1854; 27:698, 737. 1856.

Achimenes P. Br. subg. *Eucodonia* (Hanst.) Hanst., Linnaea 34:434. 1865.

Achimenes sect. *Eucodonia* (Hanst.) Fritsch, in Engler & Prantl, Nat. Pflanzenfam. 4(3b):175. 1894.

TYPE: SPECIES: *Eucodonia ehrenbergii* Hanst., Linnaea 26:201. 1854. 27:706, 737. 1856. [=*Eucodonia verticillata* (Martens & Gal.) Wiehler]

ETYMOLOGY: From the Greek *eu-* = true, and *codon* = bell, in reference to the bell-shaped corolla.

Eucodonia andrieuxii (DC.) Wiehler, comb. nov.

Achimenes andrieuxii DC., Prodr. 7:536. 1839.
Gloxinia micrantha Martens & Gal., Bull. Acad. Bruxelles 9(2):35. 1842.

Eucodonia verticillata (Martens & Gal.) Wiehler, comb. nov.

Gloxinia verticillata Martens & Gal., Bull. Acad. Bruxelles 9(2):35. 1842.
Eucodonia ehrenbergii Hanst., Linnaea 26:201. 1854; 27:706, 737. 1856.
Achimenes ehrenbergii (Hanst.) H. E. Moore, Gentes Herb. 8(5):375. 1954.
Mandirola lanata Planchon & Linden ex Lemaire, Ill. Hort. 3:pl. 80. 1856.
Scheeria lanata (Lem.) Hanst., Linnaea 27:757. 1856.
Koernickia lanata (Lem.) Regel, Ind. Sem. Hort. Petropolis 1857:48; Gartenflora 7:309. 1858.
Achimenes lanata (Lem.) Hanst., Linnaea 34:434. 1865.
Achimenes bella Morton, Kew. Bull. 1936:11.

KEY TO THE SPECIES OF *Eucodonia*

1. Corolla tube 1-2 cm long, 0.5-1.3 cm wide near the limb . . . *E. andrieuxii*
2. Corolla tube 2-5 cm long, 1.5-3.5 cm wide near the limb . . . *E. verticillata*

THE *Goyazia* GROUP

Paul Hermann Wilhelm Taubert (1862-1897) described in 1896 a new genus and species, *Goyazia rupicola*, based on a collection (*Ernst Ule 3180*, 1893) from the Serra Dourada in the southeastern part of the State of Goias in Brazil. Taubert placed the genus in the tribe Beslerieae Bartling & Wendland on account of the superior ovary position of the new species, but the new plant, a small herb inhabiting rock crevices at higher altitudes, also had rhizomes, a feature not found in the tribe Beslerieae but occuring frequently in the tribe Gloxinieae.

The genus *Goyazia* has not been mentioned again in the literature of the Gesneriaceae, because the Central Highland (Planalto) of Brazil has, until recently, not been very well explored botanically. Recent expeditions by the New York Botanical Garden have enriched our understanding of the flora of the Planalto do Brasil. I have seen two new collections of *Goyazia* *rupicola*, one found near the type locality at an altitude of 800 m [*Howard S. Irwin et al. 11751*, 18 Jan. 1966 (NY,US)] and another from the vicinity of the capital city Brasilia, from the summit of Pico de Pireneus, altitude 1000 m [*H. S. Irwin et al. 34102*, 14 Jan. 1972 (NY,SEL)]. On a recent visit to B, I could not find the holotype of *G. rupicola* (it was destroyed in the bombing of Berlin in 1943). Nor could I find isotype collections of *Ule 3180* in other European herbaria. The new collections cited above agree in all aspects with the detailed type illustration, except that in these collections the ovaries are semi-inferior and the nectaries evenly ring-shaped instead of a ring with five lobes. A small intraspecific variation in nectary shape is of minor importance (it apparently occurs also in the second species, see below), but a change from superior to semi-inferior ovary position is not so easily explained. Since the dried and pressed ovaries at anthesis are somewhat less than one millimeter long, a misjudgment of the ovary position is, however, a possibility. Even with a superior ovary in some collections of this species, the genus *Goyazia* belongs in the tribe Gloxinieae, and not in the Beslerieae. In the new classification of the subfamily Gesnerioideae less emphasis is placed on ovary position. The previously unplaced monotypic Surinamese genus *Lembocarpus* Lwbg. with a tuber, single leaf, sinningioid or gloxinioid (=generalized) flower, and a superior ovary has been assigned to the tribe Gloxineae which is traditionally characterized by a semi-inferior or completely inferior ovary position (Wiehler, 1976). In a second species of *Goyazia*, listed below, several single-flowered (reduced) florescences carry prophylls, a condition not found in the tribe Beslerieae, but present in the Gloxinieae and all other tribes of the Gesnerioideae (Wiehler, 1975c).

In 1970, S. M. Phillips described two new gesneriads from the Planalto do Brasil and assigned them to *Achimenes*. One of these, *A. burchellii*, is closely related to *Gloxinia villosa* and *G. hirsuta* from the same area in northern Goias; it has been transferred above to *Gloxinia*. The type collection (*Burchell 8615*, holotype: K, isotype: WAG) was found by Burchell at Porto Nacional in 1829. A recent collection, *H. S. Irwin et al. 21737*, 24 March 1968 (NY, SEL, WAG), comes from the same area in northern Goias, 20 km S. of Paraiso (Figure 4).

The other species, *Achimenes petraea* [*D. R. Hunt & J. Ferreira Ramos 6078*, 16 June 1966 (holotype: K, isotype: WAG), Serra Azul, 77 km W of Barra Garcas, Mato Grosso] is a close relative of *Goyazia rupicola* (Figure 5) and needs to be transferred to Taubert's genus. The expeditions of the New York Botanical Garden have yielded more herbarium material of *Goyazia petraea: H. S. Irwin et al. 17262*, 16 June 1966 (NY, US), from the summit of Serra Azul in Mato Grosso, and *H. S. Irwin et al. 19257*, 27 Jan. 1968 (NY, SEL, WAG), from the same Pico de Pireneus in Goias mentioned above, at an altitude of ca. 1400 m, "rooted in cracks and cavaties in sandstone cliffs" (Figure 6). *Goyazia rupicola* was found just 40 m further down the same mountain area four years later, so the two species occur here apparently sympatrically. On a recent visit to Kew I found another collection of *Goyazia petraea: D. Philcox & B. Freeman 4689*, 2 April 1968, Vale dos Sonhos, near Xavantina, Mato Grosso. *Goyazia petraea* thus appears to have a wider distribution (central Mato Grosso and south-central Goias) than *G. rupicola* (south-central Goias).

The genus *Goyazia* differs from *Achimenes* sensu stricto in the following features, all absent in *Achimenes:*

1. The thin stems are rather stiff and wiry.
2. The short petioles are swollen through tissue proliferation, but do not appear to have cavities.
3. The lamina of the leaf is thick and leathery.
4. The leaf venation is distinct from any other genus of the Gesnerioideae, in fact, it shows a venation pattern not recorded in the recent classification of dicotyledonous leaves (Hickey, 1973). The pinnate venation in *Goyazia* is neither craspedodromous (secondary veins terminating at the margins) nor camptodromous (secondary veins terminating before reaching the margins; Hickey, 1973, pp. 23-24. The term pericraspedodromous (from the Greek, peri-, surrounding, around; *kraspedon*, margin, edge; and *dromos*, a course, race running) is here proposed for the venation pattern in the leaves of *Goyazia*, meaning: the secondary veins reaching the margins, joining the superadjacent secondaries, surrounding the total lamina at the margins (Figure 7).

There appear to be no obvious floral differences between *Goyazia* and *Achimenes* (and *Smithiantha*, *Gloxinia*, etc., discussed above). In the Irwin collections of *Goyazia petraea* the nectary is evenly ring-shaped, while the type illustration and a syntype (at NY) of this species show a five-lobed ring. Taubert had no fruit available for his description of *Goyazia*. The fruit in the four Irwin collections is a loculicidal bivalved capsule, and seeds are ellipsoid with flattened surfaces, 0.1 mm long, and brown, not striate.

Figure 4. *Gloxinia burchellii.* Xerograph of herbarium material, *H. S. Irwin et al. 21737* (NY, SEL, WAG), found in 1968 on rocky slopes in soil-filled crevices, alt. 600 m, near Paraiso, Prov. Goias, Brazil. Corolla white, the tube tinged purple above, the nectar-guide spotted red, the limb with purple dots.

Figure 5. *Goyazia rupicola.* Xerograph of herbarium material, *H. S. Irwin et al. 34102,* found in 1972 in wet sandy crevices in rocks, alt. 1000 m, near the summit of Pico de Pireneus, Prov. Goias, Brazil. Corolla white, with brown-violet lines on the tube outside and inside.

Goyazia Taubert, emend. Wiehler.

Caules rigidi, petioli tumidi, laminae crassae et coriaceae venatione pericraspedodroma. Fructus capsula sicca bivalvis loculicida; semina ellipsoidea complanata brunnea, 0.1 mm longa.

Goyazia Taubert, Bot. Jahrb. Syst. 21:451. 1896.
TYPE SPECIES: *G. rupicola* Taubert, ibidem.
ETYMOLOGY: Named for the State of Goias in Brazil where the type species was found.

Goyazia petraea (S. M. Phillips) Wiehler, comb. nov.
Achimenes petraea S. M. Phillips, Kew Bull. 24(1):221. 1970.

Goyazia rupicola Taubert, Bot. Jahrb. Syst. 21:451. 1896.

KEY TO THE SPECIES OF *Goyazia*

1. Leaves serrate; calyx lobes linear-lanceolate, ca. 2.5 mm long; corolla tube at tips of calyx lobes narrow, ca. 1.8 mm in diameter .... *G. petraea*
1. Leaves entire (or subentire); calyx lobes broadly lanceolate, ca. 1.5 mm long; corolla tube at tips of calyx lobes broad, ca. 2.3 mm in diameter .... *G. rupicola*

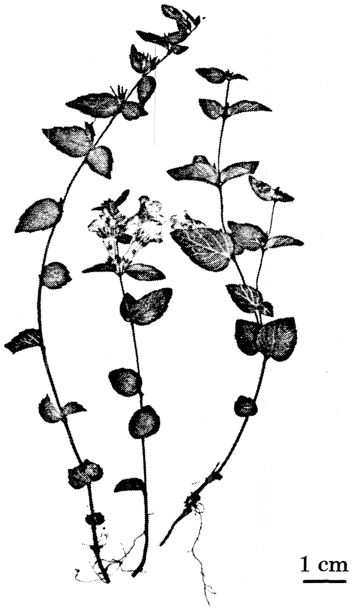


Figure 6. *Goyazia petraea.* Xerograph of herbarium material, *H. S. Irwin et al. 19257* (NY, SEL, WAG), collected in 1968; plants rooted in cracks and cavities in sandstone cliffs, alt. ca. 1400 m, on the same Pico de Pirineus where *Goyazia rupicola* was found. Corolla white with purple markings within.

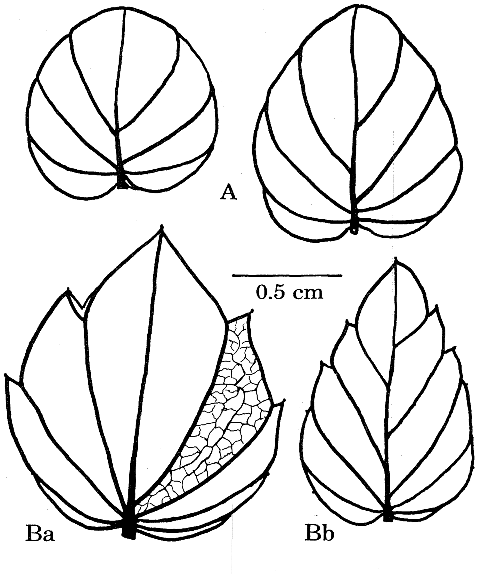


Figure 7. *Goyazia* leaves with pericraspedromous venation. A, *G. rupicola (Irwin et al. 34102);* B, *G. petraea*: a, (holotype); b, *(Irwin et al. 19257).*

SPECIES EXCLUDED FROM *Goyazia*

While considering whether a new and puzzling species from the Caribbean island of St. Vincent belongs to the little known genus *Anetanthus* Hiern ex Bentham, Dr. Richard A. Howard recently examined the other species attributed to *Anetanthus* and transferred one of them, *A. villosus* (Gardner) Benth. ex Jackson (*Tapina villosa* Gardner) to *Goyazia* (Howard, 1975a, 1975b). I agree with Howard that *Tapina villosa* is totally misplaced in *Anetanthus*, and he will probably concur with me that Gardner's species is also out of place in *Goyazia* when he studies the cited herbarium material of *G. rupicola* and *G. petraea*. *Tapina villosa* is so far known only from the type collection in northern Goias (*Gardner 3875*, Figure 8). I have studied the lectotype at K, and isotypes at BM, M, P, and W. The ovary position of this small herb with its tiny flowers is at anthesis almost semi-inferior, and distinctly semi-inferior in the fruit (Herbarium H. Baillon, P). The nectary is a thin but well-developed, sheath-like ring. The papyraceous leaves and their venation are like those of *Gloxinia* and other gesneriaceous genera, and totally unlike those of *Goyazia*. I did not find any evidence of scaly rhizomes on the mostly rootless stems of the about 12 plants examined, but Gardner explicitely cites rhizomes in his description of the saxicolous

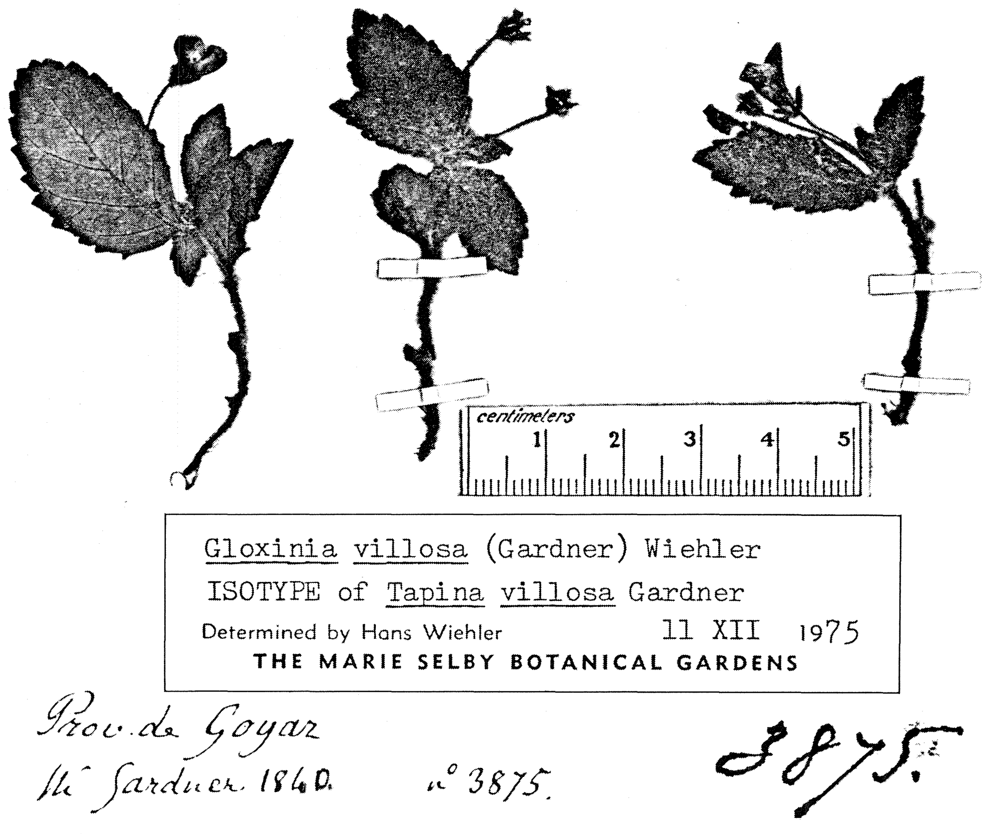


Figure 8. *Gloxinia villosa*. Xerograph of isotype, *G. Gardner 3875* (P), found in 1840 in dry clefts of rocks near the summit of the Serra de Natividade in the north of Prov. Goias, Brazil. Corolla tube with a pink-purple flush, the limb white.

species. Since such rhizomes occur in both *Gloxinia* and *Goyazia*, I feel no hesitation to assign *Tapina villosa* to *Gloxinia*. From a field trip to Brazil next year, I hope to bring back live material of this and other gesneriad species for further study.

COMMENTS ON *Anetanthus*

After the above notes on *Goyazia*, a few remarks need to be added to Dr. R. A. Howard's recent publication on the genus *Anetanthus* (Howard, 1975a). It is good that this obscure genus receives some attention in botanical research. I had become interested in *Anetanthus* in connection with a new classification of the neotropical Gesneriaceae, and in 1973 had asked Dr. Anton Weber (University of Vienna), who had just published important papers on the gynoecium and the inflorescence in the Gesneriaceae (Weber, 1971, 1973), to help in examining this genus. From Copenhagen he borrowed type material of *Anetanthus gracilis* Hiern, on which the genus is based (Figure 9). I found other collections, and we have since then exchanged several letters on this subject. We are now agreed to retain *Anetanthus* in the Gesneriaceae. It is probably more fitting to regard *A. gracilis* as a gesneriad with two scrophulariaceous features, than as a species on the borderline between the families Gesneriaceae and Scrophularicaeae. *Anetanthus gracilis* is a unique species, sufficiently distinct to maintain in a monotypic genus, and to cause the rejection of all other species transferred to it. Hiern's species is known only from a few herbarium collections (cited below) which show, however, a surprisingly wide distribution in the neotropical southeastern Brazil (Minas Gerais, D. F., Sao Paulo, Rio de Janeiro), Bolivia (La Paz), Peru (Puno, Huanuco; Cuzco and San Martin: fide Howard), and Colombia (Meta: Sierra Macarena; Cauca: fide Howard). The minor variations in these collections are too insignificant for specific recognition, and thus *Anetanthus hilarianus* Baillon, *A. weddellianus* Baillon, and *A. pusillus* Glaziou are listed below as synonyms of *A. gracilis*.

The distinctive features of *Anetanthus gracilis* include: 1. The florescence pattern is typical for the family Gesneriaceae, rarely found in the Scrophulariaceae (Weber, 1973). 2. The stamens are typical for the neotropical Gesneriaceae. 3. The nectary is a five-pronged sheath almost surrounding the superior ovary. This is a novelty among the Gesnerioideae but also unkown among the Scrophulariaceae. 4. The placentation is parietal, the conventional key character to separate the Gesneriaceae from the Scrophulariaceae which have axillary placentation. 5. The dehiscence of the bivalved capsule is septicidal, although there is often also a small loculicidal slit at the tip of the valves (Figure 10). Primary septicidal dehiscence is not known elsewhere in the New World Gesneriaceae, although it is of frequent occurrence in the Scrophulariaceae. All other members of the subfamily Gesnerioideae with capsular fruit dehisce loculicidally. Septicidal dehiscence is, in rare instances, an added feature to loculicidal splitting, thus making the capsule four-valved. This occurs in four species of *Napeanthus* Gardner [*N. apodemus* Donn. Sm., *N. dressleri* Wiehler, *N. primulinus* (Karsten) Jackson, *N. spathulatus* Lwbg.]. Ten other species dehisce loculicidally only, and in three the dehiscence is unknown. Four-valved capsules occur also in the subfamily Coronantheroideae Wiehler, in the monotypic genera *Negria* F. Mueller and *Rhabdothamnus* Cunn., and in the 10 species of *Coronanthera* C. B. Clarke. The dehiscence in the monotypic genus *De-*

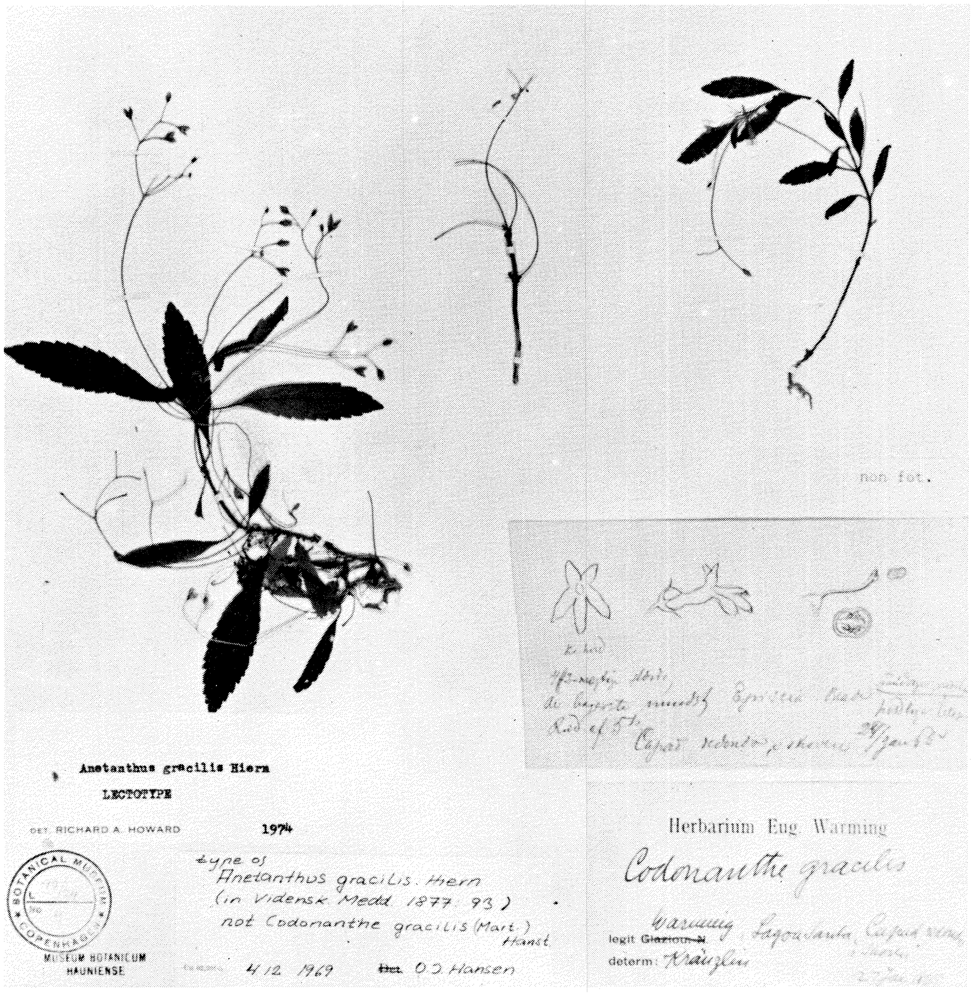


Figure 9. *Anetanthus gracilis*. Photo of lectotype by Dr. Anton Weber, *Warming s.n.* (C), found in 1865 in shaded woods near Lagoa Santa, Prov. Minas Gerais, Brazil. Corolla white, but bluish or violet in other collections.

panthus S. Moore is said to be septicidal. 6. The placentas of *Anetanthus gracilis* appear to be without lamellae. The seeds are arranged in almost straight vertical rows like stacks of coins. This condition, probably due to the shape of the seed, is otherwise unknown in the Gesneriaceae but found in the Scrophulariaceae. 7. Most unusual, however, are the flat, discoid, and winged seeds of *A. gracilis* (Figure 11). This type of seed is not found in the Gesneriaceae, but it occurs in some genera of the Scrophulariaceae [*Maurandya erubescens* (D. Don) Gray, *Paulownia tomentosa* Steud.]. Weber writes (personal communication, 1974) that winged seeds have developed several times independently in several tribes of the Scrophulariaceae. Such a feature is, therefore, no indicator of phylogentic relationship. He compares the emergence of wings on the seed of *Anetanthus gracilis* to the development of hairs as floating devices on the seed of the epiphytic genus *Aeschynanthus* Jack in the Old World Gesneriaceae. Most collections of

Anetanthus have been found on vertical rock faces or cliffs, and the winged seeds may help to account for the wide distribution of this apparently successful species. The round, flat, but pustulate seeds of the monotypic genus *Tylopsacas* Lwbg. from the Guayana Highlands may not prove a special relationship to *Anetanthus*, but the structure of these seeds is likewise unparalleled in the Gesneriaceae (illustrated in Ivanina, 1965, Figure 4:9). Nevertheless, *Tylopsacas* appears to be the genus most closely related to *Anetanthus*.

The above list of special features in *Anetanthus gracilis* shows the vast difference between this species and the other species attributed by Bentham as belonging to *Anetanthus*: *Trevirana parviflora* Hook. & Arn., *Russelia alata* Cham. & Schl., and *Tapina villosa* Gardner. Neither Bentham in 1876 nor Hiern in 1877 transferred these taxa to *Anetanthus*, and judging from the types at K, they were neither examined nor annotated when they were included in *Anetanthus* in the process of indexing Bentham & Hooker's Genera Plantarum for the Index Kewensis in 1893. Therefore, I support the exclusion from *Anetanthus* of *A. parviflorus* (Hook. & Arn.) Jackson by

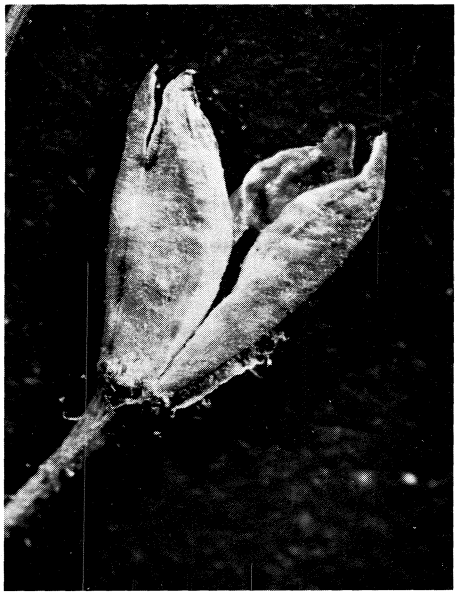


Figure 10. Fruit capsule of *Anetanthus gracilis*, showing the primary septicidal dehiscence and the secondary small loculicidal split of the upper part of the two valves. Photo of lectotype by A. Weber.

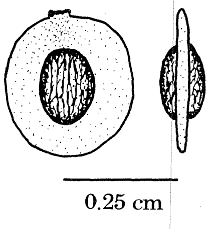
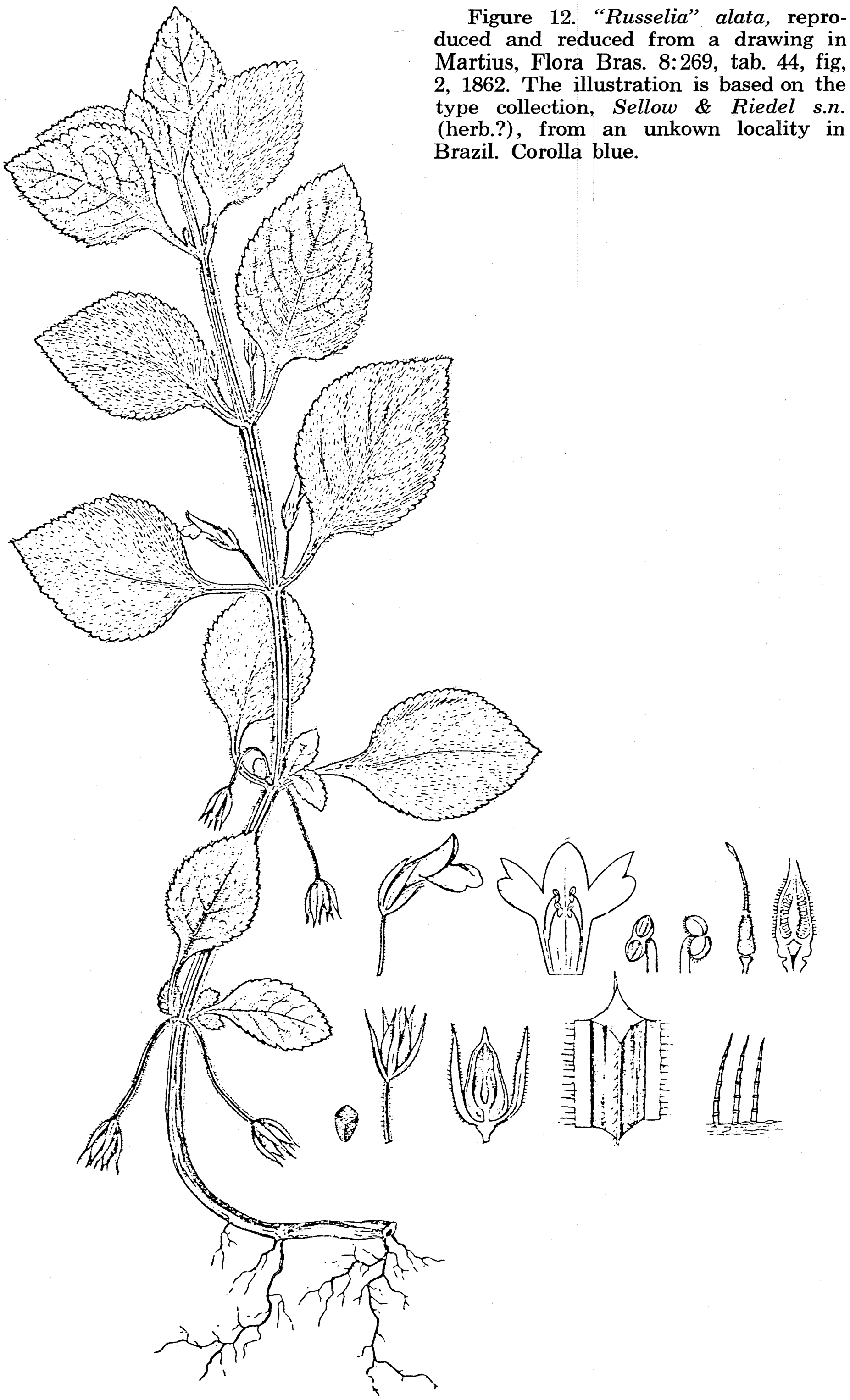


Figure 11. Winged seed of *Anetanthus gracilis (Allard 21646)*.

Figure 12. *"Russelia" alata,* reproduced and reduced from a drawing in Martius, Flora Bras. 8: 269, tab. 44, fig, 2, 1862. The illustration is based on the type collection, *Sellow & Riedel s.n.* (herb.?), from an unkown locality in Brazil. Corolla blue.



L. O. Williams (personal communication, March, 1973) and its transfer to the Scrophulariaceae as *Stemodia peduncularis* Bentham in Fieldiana Bot. 24, Part IX (3-4):406, April 1973. I also support Howard's exclusion of *Anetanthus villosus* (Gardner) Jackson (Howard, 1975a), but propose its transfer to *Gloxinia* instead of *Goyazia* as discussed above. I also propose the exclusion of *A. alatus* (Cham. & Schl.) Jackson from *Anetanthus.* This Brazilian species shows no other relationship to *A. gracilis* except septicidal dehiscence of the fruit capsule. The plant habit, winged stems, petioles, and peduncles, the one-flowered axillary florescence, the non-gesneriaceous stamens, the apparent absence of a nectary, and the small, ovoid-angular seeds are all foreign to the concept of the genus *Anetanthus.* I do not know, however, to which taxon in the Scrophulariaceae the species described as *Russelia alata* should be assigned. Except for the isotype sheet seen by Howard and myself at K, I have not found additional material of this species in European herbaria, including B where the holotype was destroyed in 1943 (Figure 12).

Anetanthus thus becomes a monotypic genus. In the new classification of the neotropical Gesneriaceae (Wiehler, 1976), this genus is placed in the tribe Beslerieae Bartling & Wendland, next to *Tylopsacas, Resia* H. E. Moore, and *Cremosperma* Bentham, and in the company of the larger genera *Besleria* L., *Gasteranthus* Bentham, and a new genus from Panama. All these taxa have bractless florescences.

Anetanthus Hiern ex Bentham, in Bentham & Hooker f., Genera Plantarum 2:1025. 1876. Hiern in Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhaven 1877-78: 93. 1877.

TYPE SPECIES: *Anetanthus gracilis* Hiern, ibiden (*Warming s.n.*, 17 Jan. 1865, LECTOTYPE: C: ISOTYPES: C, BM, K).

ETYMOLOGY: From the Greek *anethon* (Latin: *anethum*; old English: *anet*), the dill plant; and the Greek *anthos*, flower: the dill flower, probably an allusion to the florescences of *Anetanthus* resembling the linear or filiform leaf segments of dill, *Anethum graveolens* L.

Anetanthus gracilis Hiern, cited above.

A. hilarianus Baillon, Histoire des plantes 10:101. 1888. Nomen nudum.
A. wedellianus Baillon, ibidem. Nomen nudum.
A. pusillus Glaziou, Bull. Soc. France 58(Mem. 3):515. 1911 Nomen nudum.

MATERIAL EXAMINED: BRAZIL: MINAS GERAIS: Lagoa Santa (40 km N of Belo Horizonte), 27 Jan. 1865, *Warming s.n.* (Type collection: C, BM, K); Faria, près de Sabara, "fl. violettes," 27 Jan. 1891, *A. Glaziou 18413* (P, K); Serra do Ouro Preto, "in Felsenschluchten," Feb. 1892, *E. Ule 2666* (HBG); Ouro Preto, "fleur bleu-blanchatré," Dec. 1893, *A. Glaziou 20431* (P, K); Serra do Espinhasço, cut-over galery forest in deep valley at base of Pico de Itacolomi, ca. 3 km S of Ouro Preto, ca. 1600 m, 1 Feb. 1971, *H.S. Irwin, R.M. Harley, & E. Onishi 29527* (NY, SEL); DISTRITO FEDERAL: Gama: wet cliffs by Rio Gama, 16° 00' S, 48° 08' W, 7 March 1965, *L. B. Smith 15062* (P); Chapada da Contagem, wooded creek valley, Parque Municipal do Gama, ca. 25 km W of Brasilia, ca. 1100 m, 3 Feb. 1968, *H.S. Irwin, H. Maxwell, & D. C. Wasshausen 19470* (NY, SEL); Sao Paulo: “in rupibus secus verticum montis Guayrapurina,” (between Barretos and Uberaba), n.d., *R. Spruce s.n.* (K); Rio De Janeiro: Alto Macahé de Nova Friburgo, “herbacée, fl. violettes,” 1892, *A. Glaziou 19586* (K; not found at P); *“type” of A. pusillus* Glaziou, det. *A. gracilis* by Fritsch; without locality, “Brazil,” 1816-1821, *A. d'Saint-Hilaire 182* (P), “type” of *A. hilarianus* Baillon; BOLIVIA: La Paz: valleys between Tipuani and Apolobamba, May 1847, *H. A. Weddell s.n.* (P), “type” of *A. weddellianus* Baillon; Mapiri, San Carlos, 750 m, “nasser Wegabhang im Walde, Blüten weiss,” 29 Jan. 1927, *O. Buchtien 1338* (HBG); PERU: Puna: Tatanera, “in rupibus umbrosis,” Aug. 1854, *Lechler 2723* (GOET, K); Huanuco: Tingo Maria, 625-1000 m, “fls. white,” 30 Oct. 1949-19 Feb. 1950, *H. A. Allard 21646* (NY); COLOMBIA: Meta: Sierra de la Macarena, northern escarpment, 800 m, “habitat: scrub with deep leaf-mould on sandstone; creeping on rockface, 1 Feb. 1950, *W. R. Philipson 2313* (BM).

Epilogue on *Achimenes*

With the exclusion of the *Gloxinia*, *Eucodonia*, and *Goyazia* groups, the genus *Achimenes* presents now a more homogenous aspect. More hybridization experiments are necessary to explore the relationships of the 21 remaining species in *Achimenes*. The sectional arrangement, constructed in the last century, is completely artificial. It is based on corolla and stigma shapes and thus reflects only the various pollination syndromes. Cooke & Lee's (1966) hybridization chart shows, for instance, a much closer genetic affinity between the complex of *Achimenes grandiflora—A. patens* (two butterfly-pollinated species in the section *Trevirana*) and *A. heterophylla* (sect. *Locheria*), *A. mexicana*, *A. dulcis* (sect. *Scheeria*), *A. antirrhina* (sect. *Guthnickia*), *A. candida*, *A. flava*, and *A. woodii* (sect. *Dicyrta*), than between the same *A. grandiflora—A. patens* complex and *A. cettoana* and *A. longiflora*, the other two butterfly-pollinated species in the section *Trevirana*. Such cytogenetic information on the affinity of species agrees with the findings or axioms of pollination biology: 1) closely related species may have developed different modes of pollination (and thus possess different corolla and stigma shapes—the mode of pollination is often *the only* barrier between the closely related species); 2) the switch from on pollination syndrome to another requires only minor genetic change; and 3) species within the same pollination syndrome are not necessarily closely related since they may have evolved from different ancestral stock, but have converged on the same type of pollinator. A sectional revision of *Achimenes* may thus find species with different corolla and stigma shapes and with different types of pollinators within the same section. The red-flowered and presumably hummingbird-pollinated type species of the genus, *Achimenes erecta* belongs in the section *Achimenes*, but diploid collections of this species need to be hybridized with the four blue-flowered butterfly-pollinated species to establish the final sectional positions of the latter. The sterile hybrids obtained from the tetraploid collection of *A. erecta* available to Cooke and Lee (1966) do not portray accurate interspecific relationships. The genus *Achimenes* with its showy flowers and easy culture is likely to give us more insights into some aspects of angiosperm evolution in the tropics.

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