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Boggan 1991

A morphological study and cladistic analysis of Sinningia and associated genera with particular reference to Lembocarpus, Lietzia, Paliavana, and Vanhouttea (Gesneriaceae: Gloxinieae).

M.S.Thesis, Cornell University, Ithaca, New York, U.S.A. ix + 179 pages, 21 figures.

REFNO: 2233

KEYWORDS:

Capanea, Cladistics, Conradia, Diastema, Gesneria, Gloxinia, Kohleria, Lembocarpus, Lietzia, Morphology, Paliavana, Parakohleria, Pearcea, Rechsteineria, Rhoogeton, Rhytidophyllum, Sinningia, Solenophora, Vanhouttea

A MORPHOLOGICAL STUDY AND CLADISTIC ANALYSIS OF *SINNINGIA* AND ASSOCIATED GENERA WITH PARTICULAR REFERENCE TO *LEMBOCARPUS*, *LIETZIA*, *PALIAVANA*, AND *VANHOUTTEA* (GESNERIACEAE: GLOXINIEAE)

A Thesis
Presented to the Faculty of the Graduate School
of Cornell University
in Partial Fulfillment of the Requirements for the Degree of
Master of Science

by
John Kendall Boggan
May 1991

ABSTRACT

Sinningia and two other tuberous South American genera of Gesneriaceae, *Lembocarpus* and *Lietzia*, were transferred to tribe Gloxinieae by Wiehler (1983) with the note that further study may place the latter two genera within the circumscription of *Sinningia*. A morphological study of the species of these three genera, as well as two nontuberous genera, *Paliavana* and *Vanhouttea*, was undertaken. The objectives were to elucidate the relationships among these genera and critically examine their circumscriptions. *Lembocarpus* was determined not to share any synapomorphies with the other genera examined and was therefore excluded from Gloxinieae and referred to Episcieae near *Rhoogeton*. Cladistic analysis of the cultivated species of the other genera revealed that the present division of *Sinningia* into two subgenera, *Sinningia* and *Rechsteineria*, cannot be supported. Four well-defined clades can be recognized in *Sinningia*, but the relationships of these four clades to each other remain uncertain. The species of *Lietzia* share several synapomorphies with one of these clades, and their transfer to *Sinningia* is recommended. The species of *Paliavana* and *Vanhouttea* form a monophyletic group and may be members of another of the clades of *Sinningia*, but this placement cannot be considered conclusive. If further study supports this relationship of *Paliavana* and *Vanhouttea*

to *Sinningia*, it is recommended that *Sinningia* be divided into four genera, corresponding to the four clades discovered by cladistic analysis, as such an arrangement would allow a clearer definition of the genera.

BIOGRAPHICAL SKETCH

John Kendall Boggan was born 17 January 1962 to Martha D. and Martin E. Boggan in Syracuse, New York, but spent his formative years in the suburbs outside Buffalo. Surrounding his home were acres of old abandoned farmland which helped nurture his bent for natural history. His early interest in woodland wildflowers was later overshadowed by an interest in fossils and then insects, and he went on to graduate from Cornell University's College of Agriculture and Life Sciences with a Bachelor of Science in Entomology in 1984. He then spent four years working in the Cornell University Insect Collections. He finally got tired of rearranging dead bugs and decided to go back to school in 1988, returning to his earlier interest in plants by entering a graduate program in Systematic Botany in the L. H. Bailey Hortorium at Cornell University. After eleven wonderful years in Ithaca, he realizes it's time to move on and hopes to settle down permanently with his partner in life of the last eight years, Daniel Speck. He is a member of the American Gloxinia and Gesneriad Society and the American Horticultural Society.

For Dan, without whom I would never have made it

ACKNOWLEDGMENTS

First and foremost I must gratefully acknowledge the help of the members of my committee, Dr. Jerrold Davis and Dr. Dominick Paolillo, as well as the other members of the faculty, staff, and graduate students of the L. H. Bailey Hortorium for their help and advice. I must also thank KC Bennett, who took an active interest in the plants I placed in her care. For help and advice on matters scholastic, professional, and personal, I must thank Dr. Francesca Grifo, Dr. Karl Niklas, and Dr. Carolyn Eberhard.

My interest in systematics has been nurtured by many people, but I would especially like to acknowledge the influence of Dr. Quentin Wheeler, who piqued the interest of an undergraduate many years ago and started him down the road to cladistics.

I would like to thank the following people at their respective institutions, who went out of their way to make their Gesneriaceae collections available: Dr. Denis Barabé, Jardin Botanique de Montréal; Dr. Raymond Milewski, East Stroudsburg University; Dr. Laurence E. Skog, Smithsonian Institution; Elizabeth Varley, Longwood Gardens; and Dr. Hans Wiehler, Gesneriad Research Foundation.

I would like to thank the several commercial gesneriad growers who provided plants for this study: Judy Becker of

Lauray of Salisbury, David and Colleen Turley of Home-grown Gesneriads, and Jim and Barbara Roberts of Roberts' Gesneriads. Information, seeds, and fresh plant material were generously provided by many members of the American Gloxinia and Gesneriad Society, particularly Maryjane Evans, Al Wojcik, and Dave Zaitlin. I must especially thank Brazilian AGGS member Mauro Peixoto, who generously provided seeds from plants collected in the wild.

A special debt is owed to Dr. Alain Chautems, who was most generous with wild-collected material from his field work in Brazil, provided nomenclatural information about *Sinningia* and *Paliavana*, and verified identifications of plants used in this study.

Last, but not least, I must thank Dan Speck, who stood by me through thick and thin and encouraged me at every step along the way.

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CHAPTER I. INTRODUCTION.

The Gesneriaceae are a moderately large family of about 125 genera and over 3000 species (Wiehler 1983), whose economic value lies primarily in its cultivated ornamentals. The family, with zygomorphic sympetalous flowers, is agreed by most authors to belong in the Scrophulariales (Stebbins 1974; Heywood 1978; Goldberg 1986; Cronquist 1988) although its precise affinities are still unclear. It is distinguished from other members of the order by having unilocular ovaries with parietal placentation and an unusual axillary inflorescence often referred to as a "pair-flowered cyme," in which the terminal unit is a pair of flowers rather than a single flower. The members of the family are widely distributed throughout the tropics of both the New and Old World, with genera extending into temperate Asia. A few widely scattered, small genera are found in the mountains of Europe, China, Japan, and the Himalayas. Some of these hardy species are grown as ornamentals, but most cultivated Gesneriaceae are tropical or subtropical in origin. By far the best-known gesneriads are the african violet (*Saintpaulia*), florists's gloxinia (*Sinningia speciosa*), and cape primrose (*Streptocarpus*). Species and hybrids of these genera are important ornamentals in the florist trade. Other widely cultivated genera are

Achimenes, *Columnea*, *Aeschynanthus*, *Episcia*, and *Nematanthus*.

The Gesneriaceae are of great systematic interest as a nearly pantropical family of possible Gondwanan origin (Raven & Axelrod 1974), its members exhibiting a phenomenal ecological and morphological radiation. The family has been the subject of extensive systematic work in recent years. Significant studies at higher levels have involved floral anatomy (Ivanina 1965; Weber 1971; Wilson 1974a, 1974b), pigment types (Harborne 1966, 1967), inflorescence structure (Weber 1978, 1982), pollen morphology (Williams 1978), hybridization (Wiehler 1983), seed morphology (Beaufort-Murphy 1983), chromosome numbers (compiled by Skog 1984), wood anatomy (Carlquist & Hoekman 1986), and phenolics (Kvist & Pedersen 1986). An examination of chloroplast DNA is now being undertaken in tribe Episcieae (J. Smith, pers. comm.). With the large number of characters that have been studied in the family, the time would seem ripe to examine the current classification in a cladistic framework. Except for a revision of one small genus, *Heppiella* (Kvist 1990), no comprehensive cladistic analysis has yet appeared in the literature for the family.

At present, the family is divided into three subfamilies, as circumscribed by Burtt (1962) and Wiehler (1983). The 70+ genera of Cyrtandroideae are restricted to the Old World, ranging from Africa to China, Southeast Asia, Australia and the Pacific Islands, with species of one genus

(*Cyrtandra*) being found in the Hawaiian islands. One species of an otherwise Asian genus, *Rhychoglossum*, occurs in Mexico and Central America. Species of Gesnerioideae, distributed among five tribes and 54 genera, occur throughout South America, into Central America and Mexico, as well as the islands of the Caribbean. Coronantheroideae, separated as a subfamily only since 1983 (Wiehler), with one tribe, nine genera (seven of them monotypic), and twenty species, are restricted to eastern Australia and nearby islands and southern Chile. The anomalous monotypic genus *Titanotrichum*, from Taiwan and adjacent China, may belong to this group (Wilson 1974b). Several early classifications treated the two major subfamilies as separate families on the basis of geographical distribution (Martius 1829; Hanstein 1854, 1865).

The current circumscription of the subfamilies is based on both cotyledon morphology and geographic distribution, with other characters supporting this division. Another character which has been used in the past to separate the subfamilies is ovary position (Bentham 1876; Fritsch 1893). Many New World species have partially to fully inferior ovaries, a condition unknown in any Old World species. A division based on this character would place several New World genera in the Cyrtandroideae. Ivanina (1965) erected the subfamily Episcioideae to accommodate New World genera with superior ovaries, but this subfamily has not been accepted by subsequent authors. The superior-ovaried tribe

Episcieae shares with the two inferior-ovaried tribes an unusual anthocyanin type (Harborne 1966, 1967), which may support the monophyly of the New World species. Wiehler (1983) retained the tribes with superior ovaries in subfamily Gesnerioideae.

Species with inferior ovaries are currently placed in two tribes, Gloxinieae and Gesnerieae (Wiehler 1983). The tribes differ in distribution, chromosome number, and phyllotaxy. Most members of tribe Gloxinieae possess storage organs commonly referred to as scaly rhizomes. However, several members are tuberous rather than rhizomatous, and have been regarded by most authors as a distinct group, usually at the tribal level (Hanstein 1865; Fritsch 1893; Ivanina 1965). Tuberous genera which were placed in Gloxinieae by Wiehler are *Sinningia*, *Lietzia*, and *Lembocarpus*. Wiehler suggested that further study of *Lietzia* and *Lembocarpus* might place them within the boundaries of the much larger genus *Sinningia*. The tuberous genera of Gloxinieae have been the focus of the present study.

As now circumscribed (Clayberg 1968a, 1970a; Moore 1973), *Sinningia* is a genus of between 60 and 100 species. The majority are restricted to southeastern Brazil, but some species are found in Peru, Argentina, Bolivia, and Venezuela, and two species are found as far north as Mexico. Most of these species include Brazil within their ranges. The primary defining character of the genus is the tuber, a fleshy swollen stem which allows the plants to survive dry seasons, and which persists for several years. Species of *Sinningia* have flowers characteristic of pollination by either insects, or hummingbirds. The flowers can be red, orange, yellow, violet, or white. Until recently, the species with tubular red flowers typical of hummingbird pollination were placed in a separate genus, *Rechsteineria*.

Placement of *Sinningia* in a broadly-defined Gloxinieae is consistent with several characters: partially inferior ovaries (an unusual character in Scrophulariales), chromosome number of n=13 (although numbers of n=10, 11, and 12 also occur in the tribe), fruit usually a dry bivalved capsule, and seeds with spiral seed coat cell arrangment. *Sinningia* is also characterized by separate nectary glands, as are several genera of Gloxinieae (as opposed to the annular disc nectary characteristic of most other Scrophulariales). Although tuberous habit is unusual in the tribe, some *Sinningia* species also possess rhizomes which may or may not be homologous with the scaly rhizomes of most other Gloxinieae. A few small genera, such as *Capanea*, *Bellonia*, *Paliavana*, and *Vanhouttea*, are fibrous-rooted, often woody, shrubs. This distinction between three groups--tuberous, scaly-rhizomatous, and fibrous-rooted--has been the partial basis for tribal groupings by some authors. The distribution of *Sinningia* is also distinctive within the tribe. The scaly-rhizomatous genera are mostly restricted to Central America and northwestern South America (with

Goyazia and several species of *Gloxinia* in Brazil), whereas the members of the tribe in southeastern Brazil are either tuberous (*Sinningia* and *Lietzia*) or fibrous-rooted (*Paliavana* and *Vanhouttea*). The single species of *Lembocarpus* is restricted to Surinam and French Guiana.

Species which are now placed in *Sinningia* have been distributed among several genera in the past, but for most of this century were placed in only two, *Rechsteineria* and *Sinningia*. On the basis of the hybridization studies and recommendations of Clayberg (1968a, 1970a), Moore (1973) synonymized *Rechsteineria* under *Sinningia*. Adding the genera *Lietzia* and *Lembocarpus* would culminate the process whereby almost twenty tuberous genera have been consolidated into one. *Sinningia* now includes several subgroups which are very distinct from each other, and is arguably the most heterogeneous genus in the tribe. One of the primary goals of this study has been to examine the relationships of *Lietzia* and *Lembocarpus* to *Sinningia*, and to determine whether their synonymy under *Sinningia* could be justified. The present study used a cladistic analysis of morphological characters to determine the relationships of these genera to each other and to other genera in Gloxinieae, particularly two other Brazilian genera, *Paliavana* and *Vanhouttea*.

INITIAL QUESTIONS

The present study addressed several questions. One of the most important initial questions was whether the tuber is sufficient as a defining character for *Sinningia*. Aside from characters of the tribe, no other morphological characters have been suggested which define *Sinningia* as it is currently circumscribed. This is problematic for two reasons. First, herbarium specimens generally do not include tubers, and may not indicate if a tuber was present. This is understandable since the tuber is often buried and thus not visible, but lacking such knowledge can make identification of specimens difficult. Second, there are species of *Sinningia* which are not known to be tuberous, or have been specifically described as nontuberous. At least one species, *S. schiffneri*, is consistently nontuberous in cultivation. In fact, it was transferred to *Paliavana* by Handro (1962), although this action has not been recognized by subsequent authors. Another species, *S. barbata*, produces tubers in cultivation but has been described as occasionally nontuberous (Batcheller 1971; Elbert & Elbert 1984). Finally, the type species, *S. helleri*, has been reported to be nontuberous, along with other members of the type section (Burtt 1956; Wiehler 1983). The source of this information is unclear. Hanstein (1864) described *Sinningia*, then restricted to the type section, as "e tubere placentiformi prodeunte [produced from a round flattened tuber]" (p. 391). In addition to *Sinningia*, other New World genera of Gesneriaceae have tuberous species. Thus, particular emphasis was placed on examining all possible morphological characters in an attempt to improve the definition and circumscription of *Sinningia*. In addition, the placement of the tuberous genera in the primarily rhizomatous tribe Gloxinieae was examined. The cladistic analysis thus becomes a critical evaluation of the current taxonomy of the group.

A related question was whether the tuberous genera *Lietzia* and *Lembocarpus* belong within the present circumscription of *Sinningia*, and if the nontuberous *S. schiffneri* could be validly excluded. This question was approached by examining other morphological characters, as well as the tuber itself. Due to the possibility that some valid species of *Sinningia* are nontuberous, this raised the question of whether other nontuberous genera, particularly *Paliavana* and *Vanhouttea*, might represent nontuberous members of *Sinningia* as well. In fact, *Paliavana* has been described as tuberous by some authors, following Decaisne (1848). This led to the inclusion of these two genera in the analysis, and also their exclusion as possible outgroups. An additional hypothesis examined is that *Vanhouttea* and *Paliavana* together form a monophyletic unit, as suggested by Wiehler (1983).

One problem which has been given special consideration is the role of artificial hybridization in constructing a classification. Hybridization has been widely used as a tool to investigate relationships in the Gesneriaceae, particularly within subfamily Gesnerioideae. Hybridization led to the union of *Rechsteineria* and *Sinningia* (Clayberg

1968a, 1970a; Moore 1973), and *Seemannia*, *Achimenes* section *Mandirola*, and *Gloxinia* (Wiehler 1976). On the basis of hybridization between *Lietzia* and *Sinningia*, Wiehler (1988) has advocated the union of the two. Failure to hybridize and sterility of hybrids were factors in separating *Moussonia* and *Parakohleria* from *Kohleria* (Wiehler 1975a, 1978a) and *Eucodonia* from *Achimenes* (Wiehler 1976). The large number of intertribal hybrids led Wiehler (1983) to combine several tribes into Gloxinieae, including the tuberous tribe Sinningieae, although no hybrids were produced between *Sinningia* and any other members of Gloxinieae.

CONTRIBUTIONS TO THE SYSTEMATICS OF THE GESNERIACEAE

It is hoped that this study has made a significant contribution to the systematics of the Gesneriaceae. Contributions have been in several areas. First, this study represents a synthesis of information from several sources: the literature, herbarium specimens, and live material. It has demonstrated particularly the importance of using live material in systematic investigations. This has made possible a detailed and comprehensive survey of morphological characters and their variation, involving not only *Sinningia* but several other genera of the tribe. It is hoped that this information will be valuable to future researchers who investigate the systematics of the Gesneriaceae.

This study also presents the first comprehensive cladistic analysis in the Gesneriaceae. The analysis tested the current generic delimitations in the tribe, and provides a framework for future cladistic work in the family. It necessitated a critical investigation of characters in a large number of genera in Gloxinieae, and occasionally other tribes. It suggests which characters may be of greatest value in cladistic analysis at higher levels, and which may be too quantitative or too evolutionarily plastic to be of value. Perhaps most importantly, it has demonstrated the danger of examining only one or two species in a group when using that group in an analysis. Any such analysis must be broadly-based, and analyses at the level of tribe or family must take into account the high variability of many characters at lower levels.

CHAPTER II. TAXONOMY.

Tribal level: Gesneriaceae with inferior ovaries

Since early in the family's history, the species with partially to fully inferior ovaries have been given special recognition as a subgroup of the family, whether subfamily (Fritsch 1893; Ivanina 1965) or tribe (Hanstein 1854; Bentham 1876). How this group is subdivided has differed depending on the characters emphasized by the various authors. The characters given greatest weight in classifications have been growth habit, presence and type of storage organs, ovary position, corolla shape and color, and nectary gland configuration. The species with partially to fully inferior ovaries are now distributed among two tribes which are restricted to the New World. The following discussion is an examination of the major arrangements of these species, with an emphasis on genera treated by the present study. For further discussion, see Wiehler (1983).

Species with inferior ovaries were initially placed in only two genera, *Gesneria* Linnaeus 1753 and *Gloxinia* l'Heritier 1789. At the time these genera were created, very few New World Gesneriaceae were known to botanists. In the early 1800s the number of species in cultivation grew rapidly, and by 1827 Lindley had noted that several new genera could be based upon species which had been placed in *Gesneria*.

In 1829, Martius described several New World genera, placing them along with previously-described genera in three groups (Table 1). The first group, with half-inferior ovaries, consisted of *Trevirania* Willdenow, *Gloxinia*, and "*Gesnera* ex em. Martius." Martius' emended concept of *Gesnera*, using a pre-Linnaean spelling, did not contain Linnaeus' species, which were placed in the second group, with fully inferior ovaries, containing the new genera *Rytidophyllum* and *Conradia*. The third group contained species with superior ovaries. Martius' revised concept of *Gesnera* was reflected in several subsequent classifications, and was not rejected until sixty years later. The confusion surrounding the usage of *Gesnera* vs. *Gesneria* has been discussed by Skog (1976) and Wiehler (1983). Species of *Gesnera* were later assigned to several different genera, including *Sinningia*.

Table 1. New World Gesneriaceae as arranged by Martius (1829). Genera with species now placed in *Sinningia* are marked by an asterisk (*).

Group I. "Calyx ovario adnatus. Corolla semiinfera."
  Trevirania
  *Gesnera**
  *Gloxinia**
Group II. "Calyx ovario adnatus. Corolla supera."
  Rytidophyllum
  Conradia
Group III. "Calyx liber. Corolla infera."
  various genera, including:
  *Tapina**

The first comprehensive arrangement of Gesneriaceae was published in 1838 by Don (Table 2), largely following the arrangement of Martius. Unlike Martius and several subsequent authors, Don recognized Old World species as belonging to Gesneriaceae as well as New World species. He erected the tribe Gesnerieae to accomodate the New World gesneriads. Two subtribes, Gloxinieae and Conradieae, corresponding to groups I and II of Martius, consisted of genera with inferior ovaries.

In 1854, Hanstein published a preliminary outline for his treatment of the family (Table 3). This outline reflected a large number of new genera which had been published since Don's treatment. The family, again limited to New World species, was divided into two tribes. Tribe Gesnereae was limited to species with inferior ovaries; a new tribe, Beslerieae, was created for those with superior ovaries. Gesnereae was divided into six subtribes on the

Table 2. New World Gesneriaceae as arranged by Don (1838). Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

TRIBE GESNERIEAE
- Subtribe I. Gloxinieae
  - *Treverania*
  - *Gesneria**
  - *Gloxinia**
- Subtribe II. Conradieae
  - *Rytidophyllum*
  - *Conradia*
- Subtribe III. Beslerieae
  - 11 genera, including:
  - *Tapina**

basis of vegetative habit and corolla shape. Three subtribes consisted of scaly-rhizomatous genera. Two subtribes consisted of tuberous genera now synonymized under *Sinningia*. One subtribe, Rhytidophylleae, consisted of genera with neither tubers nor rhizomes.

Table 3. New World Gesneriaceae as arranged by Hanstein (1854). Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

- TRIBE GESNEREAE
    - Subtribe Niphaea
        - 1 genus
    - Subtribe Achimeneae
        - 12 genera, including:
        - *Gloxinia*
        - *Diastema*
    - Subtribe Brachylomateae
        - 5 genera, including:
        - *Kohleria*
    - Subtribe Eugesnereae
        - *Rechsteineria**
        - *Gesnera**
        - *Dircaea**
    - Subtribe Ligerieae
        - *Dolichodeira**
        - *Stenogastra**
        - *Sinningia**
        - *Ligeria**
    - Subtribe Rhytidophylleae
        - 11 genera, including:
        - *Houttea* (=*Vanhouttea*)
        - *Codonophora* (=*Paliavana*)
        - *Capanea*
        - *Rhytidophyllum*
        - *Pentarhaphia* (=*Gesneria*)
        - *Conradia* (=*Gesneria*)
- TRIBE BESLERIEAE
    - 6 subtribes, including:
    - subtribe Nematantheae
        - 3 genera, including:
        - *Tapina**

In Hanstein's more complete treatment of 1865 (Table 4), the number of genera had been greatly reduced, and the genera were distributed among four tribes, three with inferior ovaries and separated on the basis of absence or presence and type of storage organ. The two groups of tuberous species were combined into a single tribe, Eugesnereae, and all scaly-rhizomatous species were placed in one tribe, Achimeneae.

Bentham's treatment of 1876 (Table 5) once again included Old World species in the family. In this arrangement, however, ovary position, rather than geographic distribution, became the primary character dividing the family into two tribes. This placed several New World

Table 4. New World Gesneriaceae with inferior ovaries as arranged by Hanstein (1865). Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

TRIBE ACHIMENEAE
- 12 genera, including:
  - *Gloxinia*
  - *Diastema*
  - *Kohleria*

TRIBE EUGESNEREAE
- *Gesnera**
- *Dolichodeira**
- *Ligeria**
- *Sinningia**

TRIBE RHYTIDOPHYLLEAE
- 7 genera, including:
  - *Houttea* (=*Vanhouttea*)
  - *Codonophora* (=*Paliavana*)
  - *Campanea* (=*Capanea*)
  - *Pentarhaphia* (=*Gesneria*)
  - *Rhytidophyllum*

---

species in Cyrtandreae with all the Old World species. Gesnereae was restricted to species with inferior ovaries, with four subtribes separated by various floral and vegetative characters. Genera with rotate corollas and without nectaries were placed in Bellonieae. Genera with annular nectaries and scaly rhizomes were placed in Gloxinieae. The shrubby Caribbean species with fully inferior ovaries and alternate leaves were separated in their own subtribe, Pentarhaphieae, equivalent to Don's Conradieae. All genera with separate nectary glands were placed in subtribe Eugesnereae, regardless of vegetative habit.

Table 5. New World Gesneriaceae with inferior ovaries as arranged by Bentham (1876). Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

TRIBE GESNEREAE
- Subtribe Bellonieae
    - 5 genera
- Subtribe Gloxinieae
    - 7 genera, including:
    - *Gloxinia*
- Subtribe Eugesnereae
    - *Diastema*
    - *Isoloma* (=*Kohleria*)
    - *Houttea* (=*Vanhouttea*)
    - *Paliavana*
    - *Campanea*
    - *Gesnera**
    - *Sinningia**
    - *Solenophora*
- Subtribe Pentarhaphieae
    - *Pentarhaphia* (=*Gesneria*)
    - *Rhytidophyllum*

Fritsch's arrangement of 1893 for Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (Table 6) in many ways resembled Bentham's. However, he raised Bentham's two tribes to subfamilies, the difference between the two again being ovary position. Within Gesnerioideae he recognized six tribes, all with inferior ovaries, and relied heavily on nectary gland configuration as a diagnostic character. The most substantial difference was that he divided Bentham's Eugesnereae into three tribes. Tuberous genera were placed in Sinningieae, all others with glandular nectaries in

Table 6. New World Gesneriaceae with inferior ovaries as arranged by Fritsch (1893). Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

- SUBFAMILY GESNERIOIDEAE
  - TRIBE BELLONIEAE
    - 5 genera
  - TRIBE GLOXINIEAE
  - 6 genera, including:
    - *Gloxinia*
  - TRIBE KOHLERIEAE
    - *Diastema*
    - *Kohleria*
    - *Pearcea*
    - *Vanhouttea*
    - *Paliavana*
    - *Campanea* (=*Capanea*)
  - TRIBE SINNINGIEAE
    - *Lietzia*
    - *Corytholoma**
    - *Sinningia**
  - TRIBE SOLENOPHOREAE
    - 2 genera
  - TRIBE GESNERIEAE
    - *Gesneria*
    - *Rhytidophyllum*

Kohlerieae, and the shrubby Mexican genera *Solenophora* and *Hippodamia*, with neither rhizomes nor tubers, in Solenophoreae. A virtually identical arrangement was followed by Ivanina (Table 7), with some genera transferred to other tribes. Her arrangement was based on carpel anatomy only, resulting in some unconventional arrangements: *Sinningia* and *Rechsteineria* were placed in different tribes, as were *Paliavana* and *Vanhouttea*. She also proposed the subfamily Episcioideae to accommodate New World genera with superior ovaries.

Table 7. New World Gesneriaceae with inferior ovaries as arranged by Ivanina (1965) Only genera discussed in the text are included. Genera with species now placed in *Sinningia* are marked with an asterisk (*).

- SUBFAMILY GESNERIOIDEAE (all tribes with inf. ovaries)
  - TRIBE BELLONIEAE
    - 5 genera
  - TRIBE KOHLERIEAE
    - 9 genera, including:
    - *Diastema*
    - *Kohleria*
    - *Sinningia**
    - *Pearcea*
    - *Vanhouttea*
  - TRIBE GLOXINIEAE
    - 4 genera, including:
    - *Gloxinia*
  - TRIBE RECHSTEINERIEAE
    - *Lietzia*
    - *Rechsteineria**
    - *Paliavana*
  - TRIBE SOLENOPHOREAE
    - 2 genera
  - TRIBE GESNERIEAE
    - *Gesneria*
    - *Rhytidophyllum*

In the 1960s, chromosome number and artificial hybridization gained importance as systematic tools. It was found that a chromosome number of *n*=13 was widespread among, and restricted to, the genera with inferior ovaries in Gesnerioideae. It was also demonstrated that extensive hybridization was possible among these genera, regardless of tribal boundaries. Partially on the basis of this information, Wiehler (1983) combined all the species with inferior ovaries in one large tribe, Gloxinieae, with the exception of the Caribbean species of Gesnerieae (*Gesneria*, *Rhytidophyllum*, and *Pheidonocarpa*), which have a chromosome number of *n*=14 and could not be hybridized with the other genera. Although no crosses had been successfully made between *Sinningia* (*n*=13) and any other genus (except *Rechsteineria*, which had been synonymized by then under *Sinningia*), Wiehler included the two genera of the tuberous tribe Sinningieae in Gloxinieae. Wiehler also included *Lembocarpus*, a monotypic tuberous genus without any previous tribal affiliation, despite its superior ovary. Wiehler's transfers created a Gloxinieae which is variable in vegetative habit, chromosome number, ovary position, nectary configuration, and other morphological characters, tied together primarily by extensive intergeneric hybridization. Wiehler's arrangement of subfamily Gesnerioideae, now restricted to New World species, is presented in Table 8.

Lembocarpus aside (see discussion), it is probable that the species with inferior ovaries, i.e., tribes Gloxinieae and Gesnerieae, constitute a monophyletic group. Inferior ovaries are found only in these tribes in the family, and elsewhere in the Scrophulariales are found only in *Trapella* (Pedaliaceae) and *Columellia* (Columelliaceae). The monophyly of the species with inferior ovaries is also supported by their possession of 2,4-deoxyanthocyanins, which are common in ferns but very rare in the flowering plants (Harborne 1966, 1967); this character is shared with species of another New World tribe, Episcieae. Although the relationship between Gloxinieae and Gesnerieae is unclear, it is possible that one is paraphyletic if the other is excluded. Species of Gesnerieae are distinguished from

Table 8. Gesnerioideae as arranged by Wiehler (1983). Only genera discussed in the text are included.

- SUBFAMILY GESNERIOIDEAE
    - TRIBE GLOXINIEAE
        - 24 genera, including:
        - *Gloxinia* (incl. *Seemannia*)
        - *Kohleria*
        - *Pearcea*
        - *Parakohleria*
        - *Diastema*
        - *Capanea*
        - *Vanhouttea*
        - *Paliavana*
        - *Sinningia*
        - *Lietzia*
        - *Lembocarpus*
    - TRIBE EPISCIEAE
        - 21 genera
    - TRIBE BESLERIEAE
        - 7 genera
    - TRIBE NAPEANTHEAE
        - 1 genus
    - TRIBE GESNERIEAE
        - *Gesneria* (incl. *Rhytidophyllum* and *Pheidonocarpa*)

species of Gloxinieae by possessing alternate leaves, which within the subfamily are unique to this tribe (although one genus, *Pheidonocarpa*, has decussate leaves more typical of the family), and a chromosome number of *n*=14, which is also unique in the subfamily. Chromosome numbers found in Gloxinieae are *n*=13, 12, 11, and 10, and these numbers are restricted to this tribe. The last three counts are found only in Central American species, whereas species with n=13 are found in both Central and South America. Chromosome number is constant at the generic level in Gloxinieae, at least as the genera are now circumscribed. Within the tribe, a chromosome number of *n*=13 defines the largest subgroup, although whether this number is derived or plesiomorphic with respect to the numbers *n*=10, 11, 12, and 14 found in other species with inferior ovaries is still unclear. Finally, nested within the species with *n*=13 is a group of species with separate nectary glands; these are the genera involved in the present study. This group of genera is almost exactly equivalent to subtribe Eugesnereae of Bentham (1876) or tribes Kohlerieae and Sinningieae of Fritsch (1893), although its recognition as a tribe would almost certainly make Gloxinieae paraphyletic.

Lembocarpus Leeuwenberg

Lembocarpus was created in 1958 for the sole species *L. amoenus* (Leeuwenberg 1958), a small tuberous species from Surinam and French Guiana. Leeuwenberg wrote that

Lembocarpus is "related" to *Gloxinia* on the basis of its corolla shape (campanulate) and nectary (an annular disc), but is "related" to *Rhoogeton*, another Guyanan genus described by Leeuwenberg in 1958, on the basis of vegetative characters (tuber, calyx venation, inflorescence structure, acaulescent habit) and some floral characters (ovule placement on placentae and ovary position). It is not clear that Leeuwenberg meant "related" in a phylogenetic sense, but perhaps simply meant resemblance. At any rate, from his description it is clear that he considered its greatest resemblance to be to *Rhoogeton*.

Neither *Lembocarpus* nor *Rhoogeton* was treated by Ivanina (1965). These genera were not assigned to tribes until 1983. When Wiehler treated the subfamily Gesnerioideae, *Rhoogeton* was placed in tribe Episcieae, on the basis of its superior ovary (a plesiomorphic character) and single large dorsal nectary gland (a derived character). *Lembocarpus* was placed in tribe Gloxinieae next to *Sinningia*, although Wiehler noted that the superior ovary was unusual within this tribe. Wiehler's placement of *Lembocarpus* is rather puzzling in light of the fact that tuberous genera are known in tribe Episcieae (e.g., *Rhoogeton*, *Chrysothemis*, and *Nautilocalyx*), and that a superior ovary position is otherwise unknown in tribe Gloxinieae. As justification Wiehler offered that two *Sinningia* species, *S. concinna* and *S. pusilla*, have "almost completely superior ovaries at anthesis" (p. 35). He also wrote that *Lembocarpus* "appears to produce hybrids with *Sinningia*" (1983, p. 173), but later communicated that no such hybrids were produced (H. Wiehler, pers. comm.).

The taxonomic position of *Lembocarpus* was briefly discussed by Beaufort-Murphy (1983) in her study of seed surface morphology in the Gesneriaceae. She placed *Lembocarpus* in tribe Gloxinieae (sensu Fritsch, not Wiehler), while noting that "the seed shape of *L. amoenus* resembles that of some of the examined species of *Episcia*, but is not similar to any of the examined species of *Gloxinia*" (p. 366). It did share a similar cell shape with *Smithiantha zebrina*, also a member of Gloxinieae. Beaufort-Murphy concluded that "the anomalous combination of seed characters exhibited by *L. amoenus* suggests that the species may share an isolated position within the Gesnerioideae" (p. 367). Unfortunately, she did not study seeds of any species of *Rhoogeton*.

Lietzia Regel

Lietzia was created for the single tuberous Brazilian species *L. brasiliensis* (Regel, 1880). *Lietzia brasiliensis* differed from other tuberous species which were known at the time in its large, brown-spotted green corolla and annular (rather than glandular) nectary. Fritsch (1893) maintained *Lietzia* as a separate monotypic genus, placing it with *Sinningia* and *Corytholoma* (=*Rechsteineria*) in tribe Sinningieae. *Lietzia brasiliensis* enjoyed a brief popularity as a "remarkable and handsome stove plant" (Nicholson, 1885, vol. 2, p. 262), but then disappeared from cultivation. The large green flowers are typical of bat pollination.

Lietzia was treated briefly by Ivanina (1965), who placed it in tribe Rechsteinerieae with *Rechsteineria* and *Paliavana* (*Sinningia* being placed in tribe Kohlerieae). Wiehler (1983) transferred *Lietzia* to Gloxinieae next to *Sinningia*, noting that "breeding experiments should soon establish whether or not [this genus] belongs within the limits of *Sinningia*" (p. 173). Wiehler later (1988) recommended the union of *Lietzia* with *Sinningia* on the basis of hybrids produced between *L. brasiliensis* and *S. incarnata*.

One species of *Lietzia* used in the present study, obtained as "*Lietzia* sp.", was initially thought to be the sole described member of the genus, *L. brasiliensis*, but was later determined to be a new, undescribed species (A. Chautems, pers. comm.). The floral morphology of *L. glandulosa* Chautems (ined.) is very similar to that of *L. brasiliensis*; the two differ primarily in the narrow, deeply serrate, sticky and unpleasantly aromatic leaves of *L. glandulosa*.

Paliavana Vandelli

Species of *Paliavana* (and its synonyms) have generally been set apart from the other species with inferior ovaries on the basis of their woody, shrubby habit and lack of both rhizomes and tubers. The small genus is restricted to southeastern Brazil. Its species have large flowers typical of either insect or bat pollination. Now considered synonyms of *Paliavana* are *Codonophora* Lindley and *Prasanthea* (de Candolle) Decaisne.

Paliavana was described in 1788 by Vandelli, but this name, based on an illustration without a generic diagnosis or specific epithet, was not recognized for the next hundred years. No lectotype species has been designated as of this writing (April 1991). Adding to the confusion is the fact that two species have apparently been confused in the literature (see below).

The earliest published name of a species which is now regarded as *Paliavana* is *Gesneria prasinata* Ker-Gawler (1820). In 1827(a), Lindley, recognizing the heterogeneity of *Gesneria*, erected *Codonophora* to accommodate two species with campanulate, rather than tubular, corollas. The two included species were *Gesneria tomentosa* (now *Rhytidophyllum tomentosum*) and *Gesneria prasinata*. However, he created superfluous replacement names for them, *C. lanceolata* and *C. grandiflora*, respectively. Don (1838) did not recognize Lindley's genera, and listed *Codonophora grandiflora* as a synonym of *Gesneria prasinata* and *C. lancolata* as a synonym of *Rytidophyllum tomentosum*. *G. prasinata* therefore was placed in tribe Gesnerieae, subtribe Gloxinieae, on the basis of its half-inferior ovary.

Decaisne (1848) raised de Candolle's subgenus *Prasanthea* of *Gesneria* to generic status, replacing *Gesneria prasinata* with the superfluous name *Prasanthea paniculata*. He was apparently unaware of, or disregarded, Lindley's earlier generic name. Subsequent authors regarded *Prasanthea* as a synonym of *Codonophora*. Oddly enough, Decaisne (p. 467) described the single known species as "à rhizome tubereux," [with a tuberous rhizome], a fact noted but apparently not verified by subsequent authors (but see Fritsch's note below).

Hanstein (1854) recognized *Codonophora* as a distinct genus. He listed the "typical species" listed as *C. prasinata*, thereby effectively lectotypifying the genus. The genus was placed in tribe Gesnereae, on the basis of its half-inferior ovary, and in subtribe Rhytidophylleae, with other shrubby species which lacked storage structures. In his more complete treatment of 1865, the subtribe was raised to tribal status. Two species were listed, *C. prasinata* and *C. selloana*, which were not described as tuberous.

The name *Paliavana* was recognized by Bentham in 1876, with *P. prasinata* and a new species, *P. sericiflora*. He placed *Paliavana* and all other genera with separate nectary glands in subtribe Eugesnereae. Fritsch (1893) split this group up again, placing *Paliavana* in tribe Kohlerieae, a group with separate glands and scaly rhizomes, while noting that "wenn die Angabe Decaisne's, dass *P. prasinata* ein knolliges Rhizom hat, richtig ist, so müsste die Gattung in die folgende Tribus [Sinningieae] werden...." [If Decaisne's account of *P. prasinata* having a tuberous rhizome is correct, then the genus must be placed in tribe Sinningieae.] Ivanina, in her 1965 treatment, placed *Paliavana* in tribe Rechsteinerieae (with the tuberous genera *Rechsteineria* and *Lietzia*) on the basis of carpel characters. Finally, Wiehler (1983) combined all the tribes with inferior ovaries except Gesnerieae into one large tribe, Gloxinieae. In Wiehler's arrangement, *Paliavana* is associated with *Vanhouttea*, another genus of shrubby species from Brazil which lack both rhizomes and tubers.

Two species, *Paliavna tenuiflora* and *P. werdermannii*, were described by Mansfeld in 1935. While all the other described species have flowers typical of bat pollination, *P. tenuiflora* has large violet flowers quite similar to those of *Sinningia speciosa*, and are typical of insect pollination. One specimen at BH (*Bailey 1083*), annotated as *Paliavana* sp. and not agreeing with any described species, also has violet flowers.

The species-level nomenclature of *Paliavana* was reviewed by Wiehler (1983). He listed four described species: *P. lasiantha* Wiehler, *P. racemosa* (Vell.) Fritsch, *P. tenuiflora* Mansfeld, and *P. werdermannii* Mansfeld, and noted that there are several undescribed species. There has been widespread confusion between two species, to which he applied the names *P. racemosa* and *P. lasiantha*. Believing the type specimen and original description of *Gesneria* *prasinata* to be based on both these species, Wiehler took the illegitimate action of declaring *G. prasinata* a "*nomen confusum et rejiciendum.*" However, a live collection obtained as *P. prasinata* (SI 78-360) agrees well with Ker-Gawler's (1820) description and plate of *Gesneria prasinata*.

Rechsteineria Regel

Tuberous New World Gesneriaceae with tubular red flowers have been known variously as *Gesneria*, *Gesnera*, *Corytholoma*, and *Rechsteineria*, and finally came to rest in *Sinningia* (Moore 1973). The taxonomic history of *Rechsteineria* is here treated separately from that of *Sinningia* due to the long historical distinction between the two.

As new plants were being introduced to Europe from South America in the early 1800s, most gesneriads with tubular red flowers and inferior ovaries were placed in Linnaeus' *Gesneria*. It soon came to contain an assemblage of species which are now referred to various genera in Gloxinieae and Gesnerieae. This heterogeneity was recognized by Lindley in 1827(a), who noted that "it is probable a careful investigation of the species will lead to the establishment of more than one new genus." Lindley then erected two new genera, *Pentarhaphia* and *Codonophora*, to accommodate some of the "deviations from the normal structure of *Gesneria*." Unfortunately, into these he placed the species which had been included in the original concept of *Gesneria* by Linnaeus. A similar error was made by Martius (1829), who removed Linnaeus' species to *Conradia* and *Rytidophyllum*, emended *Gesneria* to *Gesnera*, and restricted it to tuberous species. Lindley's genera were not accepted by Don (1838), who followed Martius' circumscriptions of genera but added several nontuberous, scaly-rhizomatous species to "*Gesneria*." Following Lindley's lead, however, later authors carved several new genera out of *Gesneria/Gesnera*, notably *Rechsteineria* (Regel 1848), and *Corytholoma*, *Houttea*, *Isoloma*, and *Dircaea* (Decaisne 1848). These genera were recognized by Hanstein in 1854, who also accepted Martius' emended *Gesnera* and restricted it to tuberous species, but in his 1865 treatment, *Rechsteineria*, *Corytholoma*, and *Dircaea* were reduced to subgenera of *Gesnera*. *Gesnera* was now more sharply circumscribed than *Gesneria* sensu Don, including only tuberous species, and except for later name changes it retained this circumscription until 1973. Scaly-rhizomatous species which had earlier been placed in *Gesneria* or *Gesnera* remained in other genera. Recognition that the name *Gesnera* was illegitimate, and was not based on the Linnaean concept of *Gesneria*, did not come until many years later. The history of *Gesneria* vs. *Gesnera* has been discussed by Skog (1976) and Wiehler (1983). *Gesneria* is now placed in a different tribe, Gesnerieae, and is restricted to a group of fibrous-rooted Caribbean species with alternate leaves and *n*=14 (rather than decussate leaves and *n*=13 typical of tribe Gloxinieae).

The name *Gesnera* was finally discarded in 1893 by Fritsch, who substituted for it *Corytholoma*. He later (1913) accepted *Rechsteineria* Regel, an earlier name by several months, as the valid name, following Kuntze (1891). *Rechsteineria* has since been conserved against several older names by Rafinesque: *Alagophyla*, *Megapleilis*, *Styrosinia*, and *Tulisma* (Moore 1954a, 1954b). One Rafinesque name was overlooked, however, and for *Rechsteineria* to be recognized as a genus again, it would have to be conserved against *Fimbrolina* as well.

The division between *Rechsteineria* and *Sinningia* for the tuberous species, and their placement in a tribe separate from other genera with inferior ovaries, was accepted for much of this century (Ivanina 1965; Moore 1957; Hoehne 1958), although Ivanina placed the two genera in different tribes. *Rechsteineria* was finally synonymized under *Sinningia* by Moore (1973), primarily on the basis of the hybridization experiments and recommendations of Clayberg (1968a, 1970a). Based on the high fertility of their hybrids, Clayberg recommended that sections *Rechsteineria*, *Dolichodeira*, and one group of section *Thamnocaula* be combined with section *Corytholoma*, and that sections *Dircaea* and *Thamnocaula* be combined. These recommendations were also consistent with nectary gland configuration. However, Clayberg attached great significance to the fertility of hybrids between the two *Sinningia* species *S. eumorpha* (section *Hemiloba*) and *S. tubiflora* (section *Dolichodeira*) and several *Rechsteineria* species. On the basis of the high fertility of some of these intergeneric hybrids, Clayberg recommended that *Rechsteineria* and *Sinningia* be combined. Transfers to *Sinningia* have been made by Moore (1973), Wiehler (1975b, 1978b), and Chautems (1990). Most subsequent authors have accepted the union of *Rechsteineria* and *Sinningia* (Bailey 1976; Beaufort-Murphy 1983; Wiehler 1983; Kvist & Pedersen 1986), although the name *Rechsteineria* still can be found occasionally in the literature (e.g., Gibson 1974; Barraso 1986; Carlquist & Hoekman 1986). The names *Gesnera*, *Gesneria*, and *Corytholoma* still appear occasionally for *Sinningia* species in horticultural publications and catalogs. Additional comments on *Rechsteineria* can be found in the following section.

Sinningia Nees (exclusive of *Rechsteineria*)

The taxonomic history of *Sinningia* has been one of an initial proliferation of generic names followed by consolidation. Approximately twenty genera and one nothogenus described between 1825 and 1895 have been synonymized under *Sinningia* since its creation (Table 9). Some of these are now reflected in sectional names: *Corytholoma*, *Ligeria*, *Stenogastra*, and *Tapina*. The most recent synonymy added *Rechsteineria* (Moore 1973), which more than doubled the size of the genus. About 40 species are currently in cultivation (Appendix 1).

Sinningia was created for the single species *S. helleri* (Nees 1825). This species was cultivated until at least 1907 (Lynch 1907) but is now unknown in cultivation. Several more species were described by Lindley in 1827: *S. guttata*, *S. velutina*, and *S. villosa*. (A plant illustrated as *S. helleri* by Lindley (1826b) was later determined to be a new species, *S. lindleyi* Schauer.) In its narrowest circumscription, *Sinningia* consists of five species. Particularly distinctive of this group is the

Table 9. Genera synonymized under *Sinningia* and their type species. Information taken from Feuillet and Skog 1990.

Sinningia Nees 1825: *S. helleri* Nees
Gesnera Martius 1829 (not *Gesneria* L. 1753): no type designated
Tapina Martius 1829: *T. barbata* (Nees & Martius) Martius
Wildungenia Wender. 1831: *W. nobilis* Wender.
Alagophyla Rafinesque 1837: *A. dasyanthes* Rafinesque
Megapleilis Rafinesque 1837: *M. tuberosa* Rafinesque
Styrosinia Rafinesque 1837: *S. coccinea* Rafinesque
Tulisma Rafinesque 1837: *T. verticillata* (Hooker) Rafinesque
Fimbrolina Rafinesque 1838: *F. incarnata* (Aublet) Rafinesque
Tapeinotes De Candolle 1839 (replacement name for *Tapina*)
Houttea Heynhold 1846? (reference not seen, type unknown)
Rechsteineria Regel 1847: *R. allagophylla* (Martius) Regel
Rechsteineria Regel 1848 (April): *R. allagophylla* (Martius) Regel
Corytholoma (Bentham) Decaisne 1848 (December): *Gesneria stachydifolia* Bentham
Dircaea Decaisne 1848 (December): *D. bulbosa* (Ker-Gawler) Decaisne
Ligeria Decaisne 1848: *L. speciosa* (Loddiges) Decaisne
Dolichodeira Hanstein 1854: *D. tubiflora* (Hooker) Hanstein
Stenogastra Hanstein 1854: *S. hirsuta* (Lindley) Hanstein
Orthanthe Lemaire 1856: *O. fyfiana* (Lemaire) Lemaire
Biglandularia B. C. Seemann 1868: *B. conspicua* Seemann
Rosanowia Regel 1872 (replacement name for *Biglandularia*)
x*Gloxinera* Weathers 1895 ("*Gloxinia*" x "*Gesnera*"): no type designated

strongly angular, winged calyx with its large leafy lobes. Interestingly enough, none of these species was specifically described as tuberous, and the type species of the genus, *S. helleri*, has been described as nontuberous (Burtt 1956; Wiehler 1983). However, two species of the type section have recently proven to produce tubers in cultivation: *S. villosa* (Chautems, pers. comm.) and *S. guttata* (Wiehler 1983; verified by the present author). *Sinningia* remained sharply circumscribed until other genera began to be added to its synonymy in 1876.

One other species which is now placed in *Sinningia* had already been described when that genus was erected. *Sinningia speciosa*, by far the best-known member of the genus, was originally described in *Gloxinia* (Loddiges 1817), and it is still commonly known as the gloxinia or florist's gloxinia. This has often led to confusion between *Gloxinia* and *Sinningia*. Several other violet- and white-flowered *Sinningia* species were originally described as *Gloxinia* species as well. Although *S. speciosa* is now often considered the "typical" *Sinningia*, it was in fact not transferred to that genus until 1877 by Hiern. The taxonomic history of *Sinningia* and the other genera which came to be united with it is represented in Table 10.

When Don treated the family in 1838, he placed the species which are now in *Sinningia* in three genera, *Gesneria*, *Gloxinia*, and *Tapina*, following Martius (1829). *Gloxinia* contained mostly species which are now placed in

Table 10. The taxonomic history of *Sinningia*. Genera in CAPITALS.

Don 1838	Hanstein 1854	Hanstein 1865	Bentham 1876	Fritsch 1893	Clayberg 1970
GESNERIA	GESNERA -Cryptocaula -Thamnocaula -Eugesnera -Corytholoma -Microgesnera	GESNERA -Cryptocaula -Eugesnera -Corytholoma	GESNERA -Cryptocaula -Eugesnera -Corytholoma	CORYTHOLOMA -Cryptocaula -Thamnocaula -Eucorytholoma	SINNINGIA subg. Rechsteineria sect. Cryptocaula sect. Thamnocaula sect. Corytholoma
GESNERIA	RECHSTEINERIA	-Rechsteineria	-Rechsteineria	-Rechsteineria	
GESNERIA	DIRCAEA	-Dircaea	-Dircaea	-Dircaea	
GLOXINIA	DOLICHODEIRA	DOLICHODEIRA	ACHIMENES (1 sp.)	SINNINGIA -Dolichodeira	subg. Sinningia
GLOXINIA	SINNINGIA	SINNINGIA	SINNINGIA -Eusinningia	-Eusinningia -Thamnoligeria	sect. Sinningia sect. Thamnoligeria
GLOXINIA	LIGERIA	LIGERIA -Euligeria -Hemiloba	-Ligeria	-Ligeria -Hemiloba	sect. Ligeria sect. Hemiloba
GLOXINIA	STENOGASTRA	-Stenogastra	-Stenogastra	-Stenogastra	sect. Stenogastra
TAPINA	TAPINA	-Tapina		-Tapina	sect. Tapina

Sinningia, with one exception: *G. maculata* (now a synonym of *G. perennis*), the type species of *Gloxinia*. Nees' *Sinningia* was considered a section of the older genus *Gloxinia*. *Gesneria* also was subdivided, primarily on the basis of inflorescence characters, and included species which are now placed in various genera such as *Kohleria*, *Moussonia*, and *Paliavana*, as well as *Sinningia* (see previous discussion). The primary difference between *Gesneria* and *Gloxinia* was corolla shape: straight and tubular in *Gesneria*, "furnished with five gibbosities at the base," and "very oblique and campanulately ringent" in *Gloxinia* "with only one gibbosity at the base" (p. 644). This distinction between two floral forms was to retain its importance as the primary division in the tuberous species for the next century and a half. The third genus, *Tapina*, with its two species, *T. pusilla* and *T. barbata*, was placed in a separate subtribe, Beslerieae, which consisted of species with superior ovaries.

In 1848, Decaisne recognized that several species had been added to *Gloxinia* which did not correspond to l'Heritier's original concept of that genus. He recognized Nees' *Sinningia* as a genus once more and created *Ligeria* to accommodate *G. speciosa* and its tuberous relatives, retaining only scaly-rhizomatous species in *Gloxinia*.

Gloxinia, *Ligeria*, and *Sinningia* were accepted as separate genera by Hanstein when he outlined the family for a major treatment in 1854. *Gloxinia* was removed to subtribe

Achimeneae with other scaly-rhizomatous genera. The tuberous species were distributed among two subtribes and seven genera of tribe Gesnereae. Subtribe Eugesnereae, characterized by narrowly tubular flowers, consisted of three genera which had previously been treated as *Gesneria*: *Rechsteineria*, *Gesnera*, and *Dircaea*. Subtribe Ligerieae, characterized by campanulate to funnel-shaped flowers with a wide limb, consisted of four genera whose species had previously been placed in *Gloxinia*: *Dolichodeira*, *Stenogastra*, *Sinningia*, and *Ligeria*. Following Decaisne, details of the nectary glands were used to separate genera and subgenera. *Tapina* was still maintained in tribe Beslerieae, due to the apparently superior ovaries of the two included species.

Hanstein later (1865) modified this arrangement. *Stenogastra* became a subgenus of *Ligeria*. For the first time, the tuberous genus *Tapina* was recognized as a member of this group, also as a subgenus of *Ligeria* (although *Ligeria pusilla* was transferred to subgenus *Stenogastra*). All the tuberous genera were placed in tribe Eugesnereae. No subtribal classification was offered, but *Dolichodeira* was keyed with *Gesnera* on the basis of its narrow tubular corolla. *Sinningia* was separated from *Ligeria* on the basis of its winged calyx. Again, gland characters were used to separate genera and subgenera. Hanstein's treatment of Gesneriaceae in Martius' *Flora Brasiliensis* (1864) was virtually identical. All subsequent treatments of *Sinningia* and associated genera were relatively minor modifications of this arrangement.

Further consolidation of the genera followed. Species of *Ligeria* and *Dolichodeira* were transferred to *Sinningia* (Bentham & Hooker 1876; Hiern 1877; Nicholson 1885). With Bentham's (1876) treatment, only two tuberous genera, *Gesnera* and *Sinningia*, were recognized. This recognition of two major genera of tuberous species, based upon floral form and color, was to be followed until 1973.

A similar treatment of the genera was followed by Fritsch (1893), with the name *Gesnera* of Martius finally being discarded, replaced by *Corytholoma* (and later by *Rechsteineria*). In addition, *Rosanowia* Regel (a replacement name for *Biglandularia* Seemann, a later homonym of *Biglandularia* Karsten) was synonymized under *Sinningia*. A new tribal name, Sinningieae, was created for the tuberous genera *Corytholoma*, *Sinningia*, and the recently-described *Lietzia*. Fritsch later (1908) added a new section, *Thamnoligeria*, to *Sinningia* for the new species *S. schiffneri*.

Fritsch's treatment of the genera was accepted for most of this century, with tuberous species being distributed among three genera, *Lietzia*, *Sinningia*, and *Rechsteineria*. Several new species were described in the last two by Malme (1937) and Hoehne (1958). The size of *Sinningia* more than doubled when it absorbed *Rechsteineria* in 1973. The infrageneric classification of *Sinningia* used in this study reflects the recommendations made by Clayberg (1968, 1970). *Sinningia* was transferred to Gloxinieae in 1983 by Wiehler.

Vanhouttea Lemaire

Vanhouttea was erected in 1845 by Lemaire, but until 1893 was known by Decaisne's superfluous replacement name *Houttea* (see below). The small genus is restricted to southeastern Brazil, with a range similar to that of *Paliavana*, with which it has usually been associated in classifications. All described species are shrubs, with narrow tubular red to orange flowers typical of hummingbird pollination, with neither tubers nor rhizomes.

The earliest name attributable to *Vanhouttea* is *Gesneria gardneri*, described by Hooker in 1844. The following year, *Vanhouttea*, with its single species *V. calcarata*, was described by Lemaire (reference not seen). In 1848, Hooker described another species, *Gesneria pardina*. When Decaisne (1848) erected *Houttea* (as a more euphonic name than *Vanhouttea*) he believed *V. calcarata* to be a variety of *Gesneria pardina* and accepted the latter as the correct name for the type species. *Gesneria pardina* is now considered a synonym of *Vanhouttea calcarata*.

The genus (as *Houttea*) was placed by Hanstein (1854) in tribe Gesnereae, and in subtribe Rhytidophylleae with other shrubby genera with neither rhizomes nor tubers. Following Decaisne, Hanstein accepted *H. pardina* as the valid name for the type species. *Houttea* was similarly placed by Hanstein in his 1864 and 1865 treatments.

When the family was treated by Bentham in 1876, the genera with opposite decussate leaves, including *Houttea*, were transferred to Eugesnereae, Pentarhaphieae (=Rhytidophylleae) being reserved for those species with alternate leaves. *Houttea* was now associated with other genera with glandular (rather than annular) nectaries, e.g., *Sinningia*, *Paliavana*, and *Isoloma* (=*Kohleria*). Less emphasis was placed on plant habit. Fritsch (1893) followed Bentham closely, except that the tuberous genera were removed to a separate tribe and *Vanhouttea* finally replaced *Houttea* as the valid name for the genus. *Vanhouttea* was now in a tribe of various vegetative forms whose primary unifying characteristic was a nectary consisting of five separate glands. It was keyed with *Paliavana* on the basis of the valvate calyx lobes of the two genera.

Ivanina's treatment of 1965 placed *Paliavana* and *Vanhouttea* in separate tribes. The exact justification for this is not clear. In 1983 Wiehler placed *Vanhouttea* and *Paliavana* in Gloxinieae, with the note that "the affinity between these two Brazilian taxa may eventually turn out to be the same as that of *Rechsteineria* to *Sinningia*" (p. 175), implying that the two may constitute a single monophyletic taxon which is divided on a relatively superficial character or suite of characters, i.e., pollination syndrome.

The species synonymies were reviewed by Wiehler (1983). He listed three species, *Vanhouttea calcarata*, *V. gardneri*, and *V. lanata*, and two additional species which may be synonyms of other species, *V. mollis* and *V. bradeana*. At the time, no species were in cultivation. Two species have since been brought into cultivation in the United States, *V. calcarata*, and an unidentified species labelled *V.* sp. "mauroi". Other species are being cultivated in Brazil (M. Peixoto, pers. comm.), and may be expected to be introduced to cultivation in the United States shortly.

CHAPTER III. MATERIALS AND METHODS.

Ingroup vs. outgroup

For the purposes of this study, the South American species of Gesneriaceae with inferior ovaries, separate nectary glands, and chromosome number of n=13 have been considered a monophyletic unit within the family (see discussion of tribal taxonomy). The group with this combination of characters is equivalent to subtribe Eugesnereae of Bentham (1876) or tribes Kohlerieae and Sinningieae of Fritsch (1893), and its species are currently placed in tribe Gloxinieae without formal designation. The species of this group are distributed among *Sinningia*, *Paliavana*, *Vanhouttea*, *Kohleria*, *Parakohleria*, *Pearcea*, *Diastema*, and *Capanea*. *Lietzia* is unusual in that its nectary does not consist of separate glands, but otherwise agrees well with this group. The single species of *Lembocarpus* was also examined in this study, but it was determined not to share any of the apomorphies of this group or of the larger taxon of tribe Gloxinieae. It was therefore excluded from the analysis and its placement is discussed separately (see chapter 5).

The functional ingroup was initially considered to be the species of the tuberous Brazilian genera *Sinningia* and *Lietzia*. Later the nontuberous Brazilian genera *Paliavana* and *Vanhouttea* were added. The species of this group can be distinguished from the other members of the "separate gland" clade on the basis of both morphological characters and geographic distribution. Two characters were initially observed to distinguish the ingroup group from the outgroup. Members of the ingroup lack scaly rhizomes, which are ubiquitous in other South American members of the tribe (although some Caribbean and Central American genera also lack rhizomes, e.g., *Bellonia*, *Moussonia*, and *Solenophora*). Ingroup species also have distinctly larger seeds than outgroup species. Species of the ingroup, which with very few exceptions are restricted to southeastern South America, are geographically isolated from other members of the tribe, which are found in Central America and northwestern South America.

Species of the remaining genera with separate glands constitute possible outgroups for the analysis: *Kohleria*, *Parakohleria*, *Pearcea*, *Diastema*, and *Capanea*. Of these genera, species of *Kohleria* most nearly resemble species of *Sinningia*. *Parakohleria* and the monotypic *Pearcea* share several unusual floral characters, and are likely sister taxa within the outgroup. Otherwise, outgroup relationships are unresolved. Since no single genus could be identified as the probable sister taxon of the ingroup, representatives of all the potential outgroup genera but *Capanea* were included in the analyses. *Capanea* was omitted from the analysis because flowering material was not available, and herbarium specimens were inadequate for scoring several

Table 11. Species, acronyms, and distributions.

Outgroup species		
DRAC	*Diastema racemiferum* Bentham	Venezuela, Colombia, Ecuador to Mexico
DVEX	*Diastema vexans* H. E. Moore	Colombia
KERI	*Kohleria eriantha* (Bentham) Hanstein	Colombia
KHON	*Kohleria hondensis* (Kunth) Regel	Colombia
KINA	*Kohleria inaequalis* (Bentham) Wiehler	Colombia, NW Ecuador
KSPI	*Kohleria spicata* (Kunth) Oersted	Colombia to Mexico
PABU	*Parakohleria abunda* Wiehler	Ecuador
PHYP	*Pearcea hypocyrtiflora* (Hooker) Regel	Ecuador
Ingroup species		
LBRA	*Lietzia brasiliensis* Regel	S Brazil
LGLN	*Lietzia glandulosa* Chautems (ined.)	S Brazil
PPRA	*Paliavana prasinata* (Ker-Gawler) Bentham	S Brazil
PTEN	*Paliavana tenuiflora* Mansfeld	S Brazil
SAGG	*Sinningia aggregata* (Ker-Gawler) Wiehler	S Brazil, Paraguay
SBAR	*S. barbata* (Nees & Martius) Nicholson	S Brazil
SBUL	*S. bulbosa* (Ker-Gawler) Wiehler	S Brazil
SCAR	*S. cardinalis* (Lehmann) H. E. Moore	S Brazil
SCON	*S. concinna* (Hooker) Nicholson	S Brazil
SCSP	*S. conspicua* (Seemann) Nicholson	S Brazil
SDOU	*S. douglasii* (Lindley) Chautems	S Brazil, NE Argentina
SEUM	*S. eumorpha* H. E. Moore	S Brazil
SGLZ	*S. glazioviana* (Fritsch) Chautems	S Brazil
SGUT	*S. guttata* Lindley	S Brazil
SHIR	*S. hirsuta* (Lindley) Nicholson	S Brazil
SINC	*S. incarnata* (Aublet) Denham	E Brazil to Mexico
SKAU	*S. kautskyi* Chautems (ined.)	S Brazil
SLEU	*S. leucotricha* (Hoehne) H. E. Moore	S Brazil
SLIN	*S. lineata* (Hjelmqvist) Chautems	S Brazil
SMCP	*S. macropoda* (Dumont) Wiehler	S Brazil
SMCS	*S. macrostachya* (Lindley) Chautems	S Brazil
SPUS	*S. pusilla* (Martius) Baillon	S Brazil
SRIC	*S. richii* Clayberg	Mexico (Veracruz)
SRTZ	*S. reitzii* (Hoehne) L. E. Skog	S Brazil
SSCE	*S. sceptrum* (Martius) Wiehler	S Brazil
SSCH	*S. schiffneri* Fritsch	S Brazil
SSEL	*S. sellovii* (Martius) Wiehler	S Brazil, Paraguay, NE Argentina
SSPE	*S. speciosa* (Loddiges) Hiern	S Brazil
SSUL	*S. sulcata* (Rusby) Wiehler	Bolivia
STBF	*S. tubiflora* (Hooker) Fritsch	Paraguay, NE Argentina
STBR	*S. tuberosa* (Martius) Wiehler	S Brazil
SWAR	*S. warmingii* (Hiern) Chautems	S Brazil, Paraguay
VCAL	*Vanhouttea calcarata* Lemaire	S Brazil

characters (but see Appendix 3). Ingroup and outgroup species and their acronyms and distributions are listed in Table 11. Other members of the tribe (those with annular nectaries) were examined as possible outgroups, but with such a large number of genera, exhibiting such a wide range of morphological variation, identification of a genus or group of genera as a suitable outgroup was impossible. While the species with separate nectary glands may be considered a monophyletic group, the relationship of this group to the rest of the tribe must remain uncertain.

Sources of characters

Sources of the characters scored for each species are listed in Table 12. Only species which were available as live flowering material were included in the cladistic analyses. Characters were scored from fresh material whenever possible, with herbarium material and published descriptions providing a back-up to verify characters and supply otherwise missing data. Characters were scored from mature plants whenever possible, as character expression occasionally differs between immature and mature plants, particularly for inflorescence characters. For example, immature plants often produce fewer flowers on a less complex inflorescence. A mature plant was defined as one which was flowering for at least the second time. In most cases, characters for a species were scored from a single cultivated plant. Therefore some characters used in this

Table 12. Species examined and sources. Abbreviations: AGGS=American Gloxinia and Gesneriad Society; BH=Bailey Hortorium (cultivated greenhouse material); ESU=East Stroudsburg University (collection of R. Milewski); JB=John Boggan, personal collection; JBM=Jardin botanique de Montréal; GRF=Gesneriad Research Foundation; LG=Longwood Gardens; SI=Smithsonian Institution

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INGROUP SPECIES

Lietzia brasiliensis: LIVE MATERIAL: JB 8943 (seeds collected in wild by A. Chautems as AC 1314); JB 8944 (seeds collected in wild by A. Chautems as AC 1315); ESU s.n.; D. Zaitlin s.n.; LITERATURE: Regel 1880

Lietzia sp. nov. (*glandulosa* Chautems ined.): LIVE MATERIAL: BH 89-089 (JB 8602, plant obtained from A. Wojcik, orig. commercially obtained); voucher specimen, *Boggan 01*

Paliavana prasinata: LIVE MATERIAL: GRF G732 (as *P. racemosa*); JB 8920 (plant obtained from Smithsonian as SI 78-360); voucher specimen, *Boggan 02*; HERBARIUM MATERIAL: *Stone 233*, *Stone 1177*; LITERATURE: Ker-Gawler 1820 (as *Gesneria prasinata*) (despite Wiehler's assertion (1983) that the description contains elements of two species, the description as well as figure match well the material now cultivated as *P. prasinata*)

Paliavana tenuiflora: LIVE MATERIAL: JB 8916 (plant obtained from Smithsonian as SI 86-108); voucher specimen, *Boggan 03*; LITERATURE: Mansfeld 1935

Sinningia aggregata: LIVE MATERIAL: BH 89-004 (JB 8516, seeds obtained from AGGS seed fund); voucher specimen, *Boggan 04*; HERBARIUM MATERIAL: *Hatschbach 28201*, *Smith & Klein 14030*, *Wiehler W2125*; LITERATURE: Ker-Gawler 1827 (as *Gesneria aggregata*)

Sinningia barbata: LIVE MATERIAL: BH 89-083 (JB 8605, commercially obtained); voucher specimen, *Boggan 05*; HERBARIUM MATERIAL: *Moore 7544*, *Clark s.n.*, *Fussell 57-8-41*

Sinningia bulbosa: LIVE MATERIAL: JB 8933 (seeds collected in wild by A. Chautems as AC 1431); voucher specimen, *Boggan 06*; ESU s.n.; HERBARIUM MATERIAL: *Moore 7753*, *Wikoff 1409*, *Clayberg 20*, *Leva 36*, *Moore 7416*; LITERATURE: Ker-Gawler 1818 (as *Gesneria bulbosa*)

Table 12 (continued)

Sinningia cardinalis: LIVE MATERIAL: JB 9023 (seeds obtained from AGGS seed fund); JBM 1699-80; ESU s.n.; HERBARIUM MATERIAL: *Moore 6956, Peterson 5-636, Moore s.n., Stone 472, Clayberg 16, Moore 5869, Moore 7731, Hoog 38*

Sinningia concinna: LIVE MATERIAL: JB 8401 (source unknown); voucher specimen, *Boggan 07*; HERBARIUM MATERIAL: *Stone 128, Clayberg 5*; LITERATURE: Hooker 1861 (as *Stenogaster concinna*)

Sinningia conspicua: LIVE MATERIAL: JB 9007 (seeds obtained from M. Peixoto); D. Zaitlin s.n. (=JB 9007); LITERATURE: Seemann 1868 (as *Biglandularia conspicua*); Regel 1872 (as *Rosanowia conspicua*)

Sinningia douglasii: LIVE MATERIAL: JB 9004 (seeds obtained from AGGS seed fund); ESU s.n.; HERBARIUM MATERIAL: *Hatschbach 27579, Clayberg 23, Clayberg 3, Moore 7184*; LITERATURE: Lindley 1827 (as *Gesneria douglasii*)

Sinningia eumorpha: LIVE MATERIAL: BH 89-086 (JB 8518, seeds obtained from AGGS seed fund); voucher specimen, *Boggan 08*; HERBARIUM MATERIAL: *Moore 6470* (HOLOTYPE), *Clayberg 7, Moore 6936, Stone 409, Wikoff 1341*; LITERATURE: Moore 1954

Sinningia glazioviana: LIVE MATERIAL: JB 8905 (plant obtained from Frances Batcheller, seeds originally obtained from M. Peixoto); voucher specimen, *Boggan 09*; LITERATURE: Fritsch 1906 (as *Corytholoma glazioviana*m)

Sinningia guttata: LIVE MATERIAL: BH 89-084 (JB 8502, plant obtained from M. Mines); voucher specimen, *Boggan 10*; LITERATURE: Lindley 1827

Sinningia hirsuta: LIVE MATERIAL: BH 89-006 (JB 8403, seeds obtained from AGGS seed fund); voucher specimen, *Boggan 11*; HERBARIUM MATERIAL: *Stone 122, Clayberg 8, Clayberg 28*; LITERATURE: Lindley 1826 (as *Gloxinia hirsuta*)

Sinningia incarnata: LIVE MATERIAL: GRF W3336, W2724; JBM s.n.; HERBARIUM MATERIAL: *Stone 467, Moore 8058, Clayberg 24, Stone 179, Clark s.n., Wikoff 1290, Moore s.n., Fussell 57-8-6, Moore 6955, Haught 5250, Pittier 9553, Wiehler W1556*; LITERATURE: Leeuwenberg 1958 (as *Rechsteineria incarnata*), Skog 1979

Sinningia sp. nov. (*kautskyi* Chautems ined.): LIVE MATERIAL: JB 9002 (seeds obtained from M. Peixoto); voucher specimen, *Boggan 12*; LITERATURE: orig. description, manuscript supplied by A. Chautems

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Table 12 (continued)

Sinningia leucotricha (=*S. canescens* Hort): LIVE MATERIAL: BH 89-085 (JB 8517, seeds obtained from AGGS seed fund as *S. canescens*); voucher specimen, *Boggan 13*; ESU s.n.; HERBARIUM MATERIAL: *Moore 7547*, *Huttleston 1757*, *Clayberg 18*; LITERATURE: Hoehne 1956 (as *Rechsteineria leucotricha*)

Sinningia lineata (=*S. macropoda* Hort.): LIVE MATERIAL: JB 9028 (seeds obtained from AGGS seed fund); SI 77-188 (as *S. macropoda*); M. Evans s.n. (as *S. macropoda*); HERBARIUM MATERIAL: *Wiehler 7032*, *Dress 1838*, *Dress 1786*, *Moore 6846*, *Stone 1146*; LITERATURE: Hjelmqvist 1937

Sinningia macropoda: LIVE MATERIAL: JB 8939 (seeds collected in wild by A. Chautems as AC 1420); voucher specimen, *Boggan 14*; ESU s.n.; HERBARIUM MATERIAL: *Clayberg 17*; LITERATURE: Sprague 1908 (as *Corytholoma macropodum*), Watson 1908 (as *Corytholoma macropodum*)

Sinningia macrostachya: LIVE MATERIAL: JB 9001 (seeds obtained from M. Peixoto); D. Zaitlin s.n. (=JB 9001); voucher specimen, *Boggan 15*; HERBARIUM MATERIAL: *Hatschbach 272222*; LITERATURE: Lindley 1828 (as *Gesnera macrostachya*)

Sinningia pusilla: LIVE MATERIAL: JB 9011 (plant obtained from M. Mines); voucher specimen, *Boggan 16*; HERBARIUM MATERIAL: *Clayberg 9*, *Clark s.n.*; LITERATURE: Martius 1929 (as *Tapina pusilla*)

Sinningia reitzii: LIVE MATERIAL: JB 8940 (seeds obtained from AGGS seed fund); JB 8924 (plants obtained from Longwood Gardens s.n.); voucher specimen, *Boggan 17*; LG s.n.; ESU s.n.; HERBARIUM MATERIAL: *Wiehler W2250*; LITERATURE: Hoehne 1958 (as *Rechsteineria reitzii*)

Sinningia richii: LIVE MATERIAL: JB 9008 (plant obtained from D. Turley); HERBARIUM MATERIAL: *Clayberg 26* (HOLOTYPE), *Stone 236*, *Wiehler G1011*; LITERATURE: Clayberg 1968

Sinningia sceptrum: LIVE MATERIAL: JB 8903 (seeds obtained from M. Peixoto as *S.* sp. 'Ouro Preto'); JB 8941 (seeds collected in wild by A. Chautems as AC 1316); voucher specimen, *Boggan 18*; HERBARIUM MATERIAL: *Bailey 1261*, *Bailey 1154*; LITERATURE: Martius 1829 (as *Gesnera sceptrum*)

Sinningia schiffneri: LIVE MATERIAL: BH 89-002 (JB 8507, plant commercially obtained); voucher specimen, *Boggan 19*; SI 77-190; HERBARIUM MATERIAL: *Clark s.n.*, *Stone 187*, *Clayberg 11*, *Clayberg 4*, *Wiehler 7024*, *Wiehler G611*

Table 12 (continued)

Sinningia sellovii: LIVE MATERIAL: JB 8931 (seeds obtained from AGGS seed fund), voucher specimen, *Boggan 20*; GRF, W1197; ESU s.n.; D. Zaitlin s.n.; HERBARIUM MATERIAL: *Rosengurtt 4831*, *Wiehler W1197*; LITERATURE: Martius 1829 (as *Gesnera sellovii*)

Sinningia speciosa: LIVE MATERIAL: JB 8942 (seeds collected in wild by A. Chautems as AC 1319), voucher specimen, *Boggan 21*; GRF s.n. (as cv. 'Lavender Queen'); ESU s.n.; HERBARIUM MATERIAL: *Brade 160*, *Sucre 9731*, *Clayberg 13*, *Wikoff 1212*, *Moore 6950*, *Clayberg 6*, *Stone 104*, *Clayberg 59*, *Clayberg 10*, *Moore 7181*, *Moore 6975*

Sinningia sulcata: LIVE MATERIAL: JB 9019 (seeds obtained from AGGS seed fund), voucher specimen, *Boggan 22*; ESU s.n.; LITERATURE: Rusby 1895 (as *Gesnera sulcata*)

Sinningia tuberosa: LIVE MATERIAL: JB 9055 (seeds obtained from AGGS seed fund); D. Zaitlin s.n. (=JB 9055); HERBARIUM MATERIAL: *Clayberg 29*; plants cultivated as *S. tuberosa* match the description of *S. defoliata* (Chautems, pers. comm.; see also Malme 1937)

Sinningia tubiflora: LIVE MATERIAL: JB 8822 (plant obtained from A. Wojcik); L. Goodin s.n.; HERBARIUM MATERIAL: *Moore s.n.*, *Clayberg 14*, *Moore 7794*, *Arnold s.n.*, *Hoog 151*; LITERATURE: Hooker 1843 (as *Gloxinia tubiflora*)

Sinningia warmingii: LIVE MATERIAL: BH 89-005 (JB 8519, seeds obtained from AGGS seed fund as *S. sceptrum*); voucher specimen, *Boggan 23*; HERBARIUM MATERIAL: *Moore 7173*, *Moore 7658*, *Clayberg 22*, *Wiehler 7047*, *Stone 420*

Vanhouttea calcarata: LIVE MATERIAL: BH 89-209 (JB 8910), plant obtained from J. Becker as SI 81-068; voucher specimen, *Boggan 24*; LITERATURE: Lemaire 1845; Hooker 1848 (as *Gesneria pardina*)

OUTGROUP SPECIES

Diastema racemiferum: LIVE MATERIAL: JB 8614 (seeds obtained from AGGS seed fund); LITERATURE: Skog 1979

Diastema vexans: LIVE MATERIAL: JB 9032 (seeds obtained from AGGS seed fund), voucher specimen, *Boggan 25*; ESU s.n.; HERBARIUM MATERIAL: *Stone 214*, *Wikoff 1344*

Kohleria eriantha: LIVE MATERIAL: BH 89-206 (JB 8607, plant commercially obtained as "Selby collection"); voucher specimen, *Boggan 26*

Table 12 (continued)

Kohleria hondensis: LIVE MATERIAL: JB 8922 (plant obtained from David Turley as SI 87-174); ESU s.n.; voucher specimen, *Boggan 27*; LITERATURE: Hooker 1846 (as *Gesneria hondensis*)

Kohleria inaequalis: LIVE MATERIAL: BH 89-207 (JB 8601, plant obtained from A. Wojcik, originally from Mr. Kawasaka Nagahyde of Hiroshima Bot. Gardens, Japan); voucher specimen, *Boggan 28*; LITERATURE: Bentham 1846 (as *Gesneria inaequalis*)

Kohleria spicata: LIVE MATERIAL: JB 8816 (plant commercially obtained); voucher specimen, *Boggan 29*; HERBARIUM MATERIAL: *Moore & Bunting 8887*, *Moore 6606*, *Univ. Ct. 1244*, *Ramos 3557*, *Read 631*, *Jativa & Epling 846*, *Jative & Epling 318*, *Haught 2891*, *Haught 4634*, *Rowlee 247*, *Brenes 23242*, *Brenes 5063*, *Brenes 17275*, *Stone 175*, *Stone 184*, *Rogers 30*, *Lee 6319*, *Rowlee & Stork 689*, *Rowlee & Stork 845*, *Barrus 1036*, *Ewan 15848*, *Wiehler 7048*, *Lee 6319*, *Moore 8887*; LITERATURE: Skog 1978

Parakohleria abunda: LIVE MATERIAL: JB 8921 (plant obtained from Smithsonian as SI 87-032); voucher specimen, *Boggan 30*; LG s.n.; ESU s.n.; LITERATURE: Wiehler 1978

Pearcea hypocyrtiflora: LIVE MATERIAL: JB 8917 (plant obtained from Smithsonian as SI 77-432); M. Evans s.n.; HERBARIUM MATERIAL: *Stone 1159*, *Grubb et al 150*, *Grubb et al 1503*, *Peterson J-1831*; LITERATURE: Hooker 1867 (as *Gloxinia hypocyrtiflora*)

OTHER MATERIAL EXAMINED

Capanea grandiflora: LIVE MATERIAL: JB 9017 (plant obtained from R. Milewski at ESU); HERBARIUM MATERIAL: *Moore & Parthasarathy 9401*, *Lindsay 472*, *Norman 706*; LITERATURE: Skog 1978

Lembocarpus amoenus: LIVE MATERIAL: JB 8819 (plant obtained from J. Roberts); voucher specimen, *Boggan 31*; LITERATURE: orig. descr. & figures, Leeuwenberg 1958

Rhoogeton cyclophyllus: HERBARIUM MATERIAL: *Cowan & Soderstrom 2149*; LITERATURE: Leeuwenberg 1958

Rhoogeton viviparus: HERBARIUM MATERIAL: *Cowan & Soderstrom 2148*; LITERATURE: Leeuwenberg 1958

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analysis may prove to vary among individuals in wild populations. This is most likely to be true of two species examined, *Sinningia warmingii* and *S. incarnata*, which have very wide distributions (see Table 11) and thus may be morphologically variable over their respective ranges. Comparison with published descriptions and herbarium material showed intraspecific variation to be at a minimum in the characters examined.

All characters were scored either by the naked eye or with a compound or dissecting light microscope. Seeds of the Gesneriaceae were extensively surveyed by Beaufort-Murphy (1983) using SEM but despite her assertion that "the surface morphology can be seen only with the aid of the scanning electron microscope" (p. 229), a dissecting microscope proved quite adequate for studying seed characters, even of the smallest seeds. In some ways a light microscope provided more information; for example, seed appendages are translucent under a light microscope, but are opaque to SEM, making it difficult to distinguish them from the seed itself.

Plants were grown in the greenhouses of the L. H. Bailey Hortorium, and under fluorescent lights and outdoors in the personal collection of the author. Live plants were obtained from several sources as noted in Table 12. Seeds of some species were obtained from the seed fund of the American Gloxinia and Gesneriad Society (AGGS), and plants from AGGS members. The original sources of these seeds and plants are usually unknown, although many species in cultivation can be traced back to a single wild collection. Several species new to cultivation were also included in the cladistic analysis. These species were grown from seeds collected from wild plants in Brazil by Alain Chautems and Mauro Peixoto. Voucher specimens of plants cultivated for this study are deposited in the herbarium of the L. H. Bailey Hortorium at Cornell University. Live plants were also examined at the following institutions: East Stroudsburg University, East Stroudsburg, PA; Gesneriad Research Foundation, Sarasota, FL; Longwood Gardens, Kennett Square, PA; Jardin botanique de Montréal, Quebec, Canada; Smithsonian Institution, Washington, DC. Fresh flowers of some species were also provided by AGGS members.

All herbarium material came from the L. H. Bailey Hortorium at Cornell University. In some cases characters were scored from the literature; published descriptions (in most cases the original descriptions) were taken from various sources as noted in Table 12.

Notes on variation in cultivated species

Many species of *Sinningia* are fully interfertile, as has been demonstrated by the large amount of hybridization which has been done in the genus (Clayberg 1968a, 1970a; Arnold 1975; Boggan 1985a, 1985b; Dates 1989). This raises the possibility that some plants cultivated as species are actually of hybrid origin, particularly some of the more widely grown species. The most suspect are *S. cardinalis*, *S. macropoda*, and *S. lineata*. The latter two are particularly suspect because they have been grown under one name (*S. macropoda*) for several years, and individual plants may be misidentified or of hybrid origin (Boggan and Chautems, 1991). Plants of *S. macropoda* used in this analysis were from a wild collection.

Many other species do not form fertile hybrids with other species in cultivation (e.g., *S. richii*) and so are unlikely to be of hybrid origin. However, having been grown through several generations of self-pollination, they may not represent the variation which exists in wild populations. This is the case with several species in the present study. Plants grown from wild-collected seed (e.g., *S. macropoda*, *S. conspicua*, *S. kautskyi*, *S. macrostachya*) have exhibited variation in some characters (D. Zaitlin, pers. comm.). In addition, most of these newly introduced species have only been in cultivation for a short time. The plants used for scoring characters of these species were usually flowering for the first time and some vegetative differences could be expected in mature plants. Whenever possible, characters were verified from herbarium specimens and the literature.

Cladistic analysis

Cladistic analysis was performed on 33 ingroup species representing four genera using 36 binary and 10 multistate characters for a total of 46 characters (Table 13). All characters were unordered and equally weighted. Two of the characters (37 and 41) varied in the outgroups but not in the ingroup. Quantitative characters and autapomorphies of single species were excluded from the analysis. All tree calculations were performed using the cladistic software package Hennig86 (Farris 1988) on an IBM PC.

Hennig86 searches for most-parsimonious cladograms, applying global parsimony to find shortest possible trees with the least number of character state changes. It offers several options for data analysis. The implicit enumeration algorithm (ie), which examines all possible trees, proved too time-consuming to be useful; in its place the combination mhennig*;bb* was used to find multiple most parsimonious trees. Mhennig ("multiple hennig") is a more rapid approximation algorithm, and the resulting trees can then be passed to bb, "branch breaking," for extended branch-swapping to search for more parsimonious or additional equally parsimonious trees. According to the user's manual, "for many data sets bb gives the same results as ie, regardless of the input tree supplied" (Farris 1988: 14). This combination was tested by running the analysis with the order of terminal taxa rearranged. As suggested by Platnick (1989) the data were also analyzed using the combination tread;bb. This combination passes a completely unresolved tree from tread ("tree read") to bb. These two combinations of algorithms, mhennig*;bb* and tread;bb*, were demonstrated empirically by Platnick, using several data sets, to discover all known shortest trees; each combination found any trees the other had failed to find.

Cladograms were generated in three ways. First, the data were analyzed using multiple (all possible) outgroups. Second, analysis was performed using individual outgroups (see below). Finally, the data were analyzed using Hennig86's successive weighting option, again using multiple outgroups. This option calculates trees by assigning greater weights to "more reliable" characters as a function of the product of each character's consistency and retention indices. In all cases, strict consensus trees were calculated (using the command "nelsen").

Trees were rooted by outgroup comparison using eight species representing four genera. Because relationships among the outgroup genera are unresolved, all were included in the analysis. Trees were also calculated using each outgroup genus alone, except for *Pearcea* and *Parakohleria*. These two genera were together considered a single outgroup as they share several synapomorphies and remained together in all trees.

Table 13. Characters used in cladistic analysis. See text for explanations. Polarity of two characters, 20 and 25, could not be assigned. Otherwise 0 = plesiomorphic state, with polarity assignments based on results of analysis.

Vegetative characters

01 RHIZOMES
0=present
1=absent

02 TUBER
0=absent
1=present

03 TUBER EYES
0=few
1=densely clustered

04 SEEDLING HYPOCOTYL PIGMENTATION
0=unpigmented
1=pigmented

05 PLANT SIZE
0=mature plant 10 cm or more in diameter
1=plant less than 5 cm in diameter

06 PLANT HABIT
0=not suffruticose
1=suffruticose

07 FIRST INTERNODE LENGTH
0=short
1=long

08 BRANCHES
0=absent
1=present

09 PHYLLOTAXY
0=not verticillate (decussate)
1=verticillate

10 LEAF NUMBER
0=several pairs of leaves per stem
1=1 or 2 pairs of leaves

Table 13 (continued)

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11 **LEAF ABSCISSION LINE**
0=absent
1=present

12 LEAF TRICHOMES
0=long and erect, giving leaf a hairy appearance
1=short and appressed, giving leaf a glabrous appearance

Inflorescence characters

13 FLOWER PRODUCTION
0=flowers produced after vegetative growth
1=flowers precocious

14 HYPOPODIUM
0=absent
1=present

15 LATERAL HYPOPODIA
0=absent
1=present

16 PROPHYLLS
0=present
1=absent

17 FLOWER NUMBER
0=two or more in axil
1=solitary in axil

Floral characters

18 FLOWER ORIENTATION
0=not pendulous
1=pendulous

19 HYPANTHIUM SHAPE
0=round in cross section
1= winged

20 CALYX LOBE CONNATION
0=free or barely connate
1=connate 1/4 or more of length

21 CALYX LOBE AESTIVATION
0=distinct in bud
1=valvate in bud

Table 13 (continued)

22 **CALYX LOBE SIZE**
0=small
1=large and leafy

23 **CALYX LOBE ORIENTATION**
0=clasping corolla base
1=reflexed 90 degrees from corolla
2=strongly recurved

24 **COROLLA TEXTURE**
0= membranous
1=fleshy

25 **COROLLA ANTHOCYANIN COLOR**
0=red
1=violet
2=anthocyanin absent

26 **COROLLA EXTERIOR PIGMENTATION**
0=anthocyanin present
1=anthocyanin absent

27 **COROLLA EXTERIOR ORNAMENTATION**
0=unmarked
1=marked with speckles at base
2=marked with speckles throughout

28 **DORSAL NECTAR RESERVOIR**
0=absent
1=present

29 **DORSAL COROLLA GIBBOSITY**
0=absent
1=present

30 **GALEA**
0=absent
1=present

31 **COROLLA LOBE VESTITURE**
0=lobes glabrous
1=lobes with short capitate trichomes
2=lobes with elongate capitate trichomes

32 **NECTAR GUIDE**
0=various states
1=single large dark blotch

Table 13 (continued)

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33 COROLLA INTERIOR VESTITURE
0=without capitate trichomes over anthers
1=with capitate trichomes over anthers
2=capitate trichomes cover entire interior epidermis

34 STAMEN FILAMENT PIGMENTATION
0=without anthocyanin pigmentation
1=with uniform pigmentation
2=with mottled pigmentation

35 STAMEN FILAMENT VESTITURE
0=without capitate trichomes
1=with capitate trichomes

36 STAMEN FILAMENT VESTITURE
0=without noncapitate trichomes
1=with noncapitate trichomes

37 NECTARY GLAND DIMENSIONS
0=not more than twice as long as broad
1=4-5 times as long as broad

38 NECTARY GLAND FUSION
0=glands distinct
1=dorsal glands fused into a single large gland
2=all glands fused into annular ring

39 SIZE OF VENTRAL NECTARY GLANDS
0=equal in size to dorsal glands
1=less than half as large as dorsal glands
2=glands absent

40 NECTARY GLAND COLOR
0=glands yellow to orange
1=glands white

41 STIGMA SHAPE
0=entire
1=bilobed
2=bilabiate

42 OVARY POSITION
0=half-inferior
1=mostly inferior
2=mostly superior

Table 13 (continued)

Fruit and seed characters

43 CAPSULE TEXTURE
0=dry upon dehiscence
1=fleshy upon dehiscence

44 CAPSULE DEHISCENCE
0=dehiscence not splitting hypanthium
1=dehiscence splits hypanthium

45 SEED SIZE
0=less than .5 mm
1=greater than .75 mm

46 SEED COAT ORNAMENTATION
0=without warty protuberances
1=with warty protuberances

Character explanations

The terminology used to describe characters is for the most part consistent with the usage presented by Radford et al. (1974). The major exception is in inflorescence terminology. Inflorescence terminology follows the usage of Weber (1982), Wiehler (1983), and Weberling (1989).

VEGETATIVE CHARACTERS

01 Rhizomes (Figure 1)

Rhizomes in Gloxinieae are horizontal axillary stems with reduced leaves which are produced at or below ground level from the base of the plant. Most species of Gloxinieae reproduce vegetatively by rhizomes, while

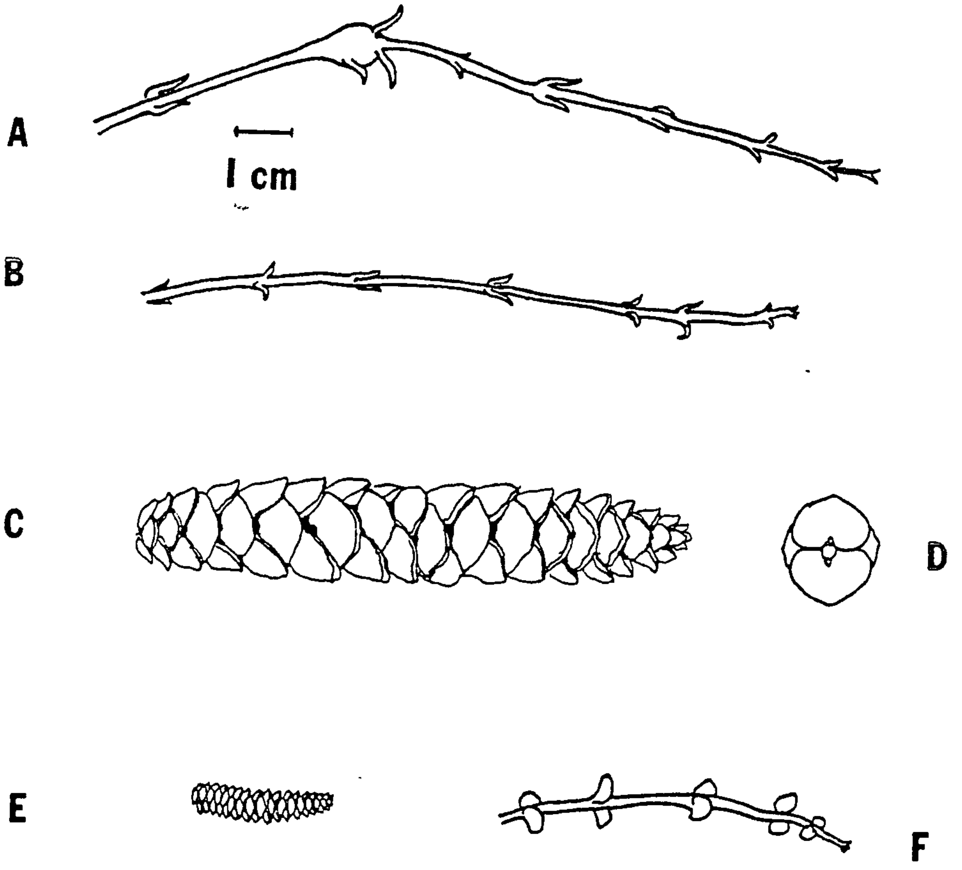


Figure 1. Comparison of rhizomes in Gloxinieae. All to same scale. A, *Sinningia curtiflora*; B, *Gloxinia nematanthodes*; C, *Kohleria eriantha*; D, transverse section of C; D, *Diastema vexans*; E, *Pearcea hypocyrtiflora*.

rhizomatous habit is rare outside the tribe. Presence or absence of rhizomes has been used in the past as a defining character at the tribal level (Fritsch 1893, Hanstein 1865). In most members of the tribe, the rhizomes are modified into scaly rhizomes, with short internodes and fleshy scales (Figure 1 C, E). Rhizomes are produced by some species of *Sinningia* as well (e.g., *S. tubiflora* and *S. richii*), in which case the scales are membranous rather than fleshy and tubers are usually produced on the rhizomes (Figure 1A).

02 Tuber

Tuberous habit was used as a defining character at the tribal level by Fritsch (1893) and Hanstein (1865). The tuber of *Sinningia* is a storage structure derived from the hypocotyl of the seedling, and it consists of large cells containing starch grains. It would probably be more accurate to refer to this structure as a corm, but the term "tuber" has been retained here to be consistent with historic usage. Tuber development and anatomy were described by Fritsch (1904). The tuber ranges in shape from nearly spherical to round or irregularly lobed and flattened, and ranges in size from 1 cm to over 30 cm in diameter. Although the tuber is occasionally described as woody (Heywood 1978), in actuality it is always a fleshy structure with the consistency of a potato. Tubers were not observed on cultivated material of *Paliavana*, although this genus has been described as tuberous (Decaisne 1848). Among species of *Sinningia* examined, only *S. schiffneri* is consistently nontuberous. Species which "occasionally" or "usually" produce tubers were scored as tuberous.

03 Tuber eyes

In most *Sinningia* species, new growth is initiated either from the base of the old stem or from relatively few "eyes" on the tuber at the base of the previous year's stem. In species of sections *Corytholoma* and *Cryptocaula*, and in species of *Lietzia*, however, the dorsal surface of the tuber has patches of numerous, often densely packed eyes with the leaves reduced to hairless scales; it is from among these that new stems arise. These eyes also give rise to rhizomes in some species (character 1). This character could not be scored in nontuberous taxa.

04 Seedling hypocotyl pigmentation

In species of *Sinningia* section *Thamnocaula*, the epidermis of the seedling hypocotyl, although initially green, turns purplish-red upon tuber initiation. The pigmented epidermis is then destroyed as the tuber continues to increase in size. This character was apparently first noted by Lubbock (reference not seen, cited by Fritsch, 1904), but its systematic value was not recognized. Seedlings of other taxa, both tuberous and non-tuberous, do not exhibit such pigmentation. Red-stemmed species which were grown from seed developed pigmentation in internodes above the hypocotyl.

05 Plant size

The extreme reduction in size of *S. pusilla* and *S. concinna* is unique within the family. No other taxa show a comparable reduction. These two species are tiny, nearly stemless rosulate herbs rarely exceeding 5 cm in diameter, and are proportionately reduced in all dimensions: tuber, stem, leaves, and flowers. The leaf blade rarely exceeds 2 cm in length, as opposed to 5 cm or more for the smallest leaves of other taxa. Other taxa examined exhibit a continuous range from small herbs to large shrubs.

06 Plant habit

Species of Gloxinieae typically have lignified stems with some degree of secondary growth. However, in most species new growth emerges from a storage organ (rhizome or tuber) each growing season. Suffruticose species (e.g., species of *Paliavana* and *Vanhouttea*) usually lack storage organs, which led Hanstein (1865) to place such genera in a separate tribe, Rhytidophylleae. In cultivation, at least, some *Sinningia* species also have persistent woody stems (e.g., *S. barbata*, *S. guttata*), with new growth emerging from the base of the old stem rather than the tuber. It is possible that species which have persistent stems under greenhouse conditions die back to the tuber in the wild.

For the purposes of this analysis, "suffruticose" denotes the possession of lignified stems which persist from one year to the next in cultivation, although some plants so scored are quite small (e.g., *S. hirsuta*).

07 First internode length (Figure 2)

Several species of *Sinningia* section *Thamnocaula* (e.g., *S. leucotricha*) have an unusual growth habit. Upon breaking dormancy, the first internode becomes very elongate before producing leaves, usually from only one or two nodes (see also character 10). These species are also unusual in that they usually bloom very soon after breaking dormancy, even before the leaves are mature (character 14). Other species produce several pairs of leaves which are more or less evenly spaced on the stem.

08 Branches

Branching is relatively rare in Gloxinieae, where it is typically associated with a suffruticose habit in species which lack storage organs. Most species of Gloxinieae produce inflorescences, rather than branches, in the leaf axils. Among the taxa included in the analysis, only species of *Sinningia*, *Lietzia*, *Paliavana*, and *Vanhouttea* regularly produce branches. Axillary stems produced at or near ground level were not considered branches.

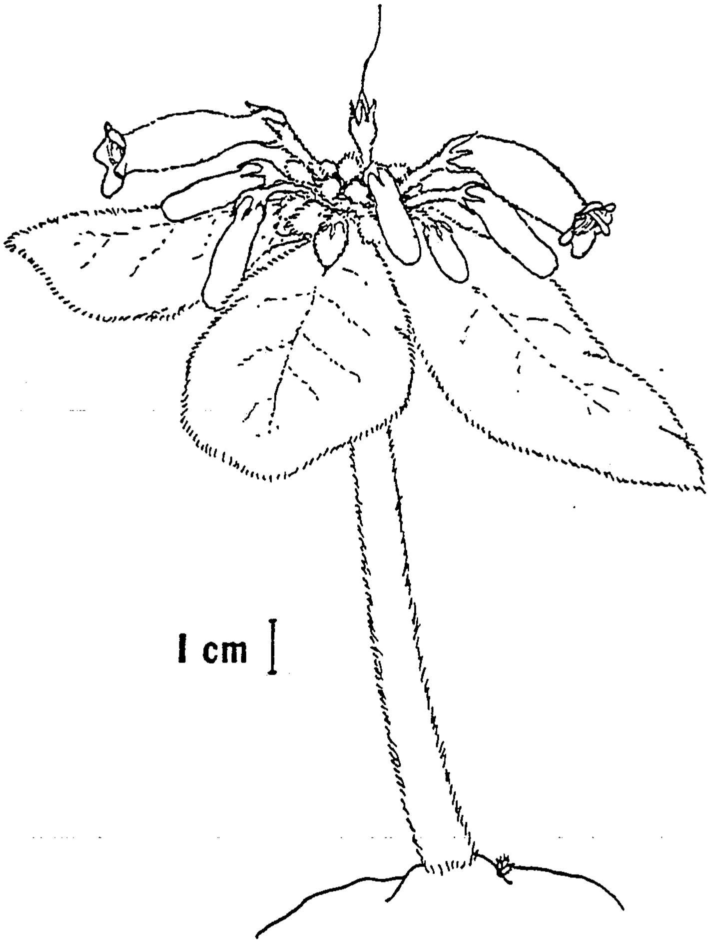


Figure 2. *Sinningia leucotricha*.

09 Phyllotaxy

The typical phyllotaxy among the taxa examined is decussate, with opposite leaves at each node. However, many members of *Sinningia* section *Corytholoma* have consistently ternate leaves (quadrate in *S. warmingii*) on the primary axis of mature plants. Axillary branches and immature plants invariably have a decussate arrangement. This character defined a section of Hanstein's subgenus *Corytholoma* (1864). Verticillate phyllotaxy is usually associated with a tall, many-leaved growth habit, but in section *Thamnocaula* it is associated with a very unusual growth habit (see next character). Verticillate phyllotaxy was rarely observed outside *Sinningia*. Although many species produce occasional stems with ternate nodes, only those which produce ternate nodes at least half the time were scored as having a verticillate phyllotaxy. The apparently whorled leaves of *S. leucotricha* have been scored as decussate (see chapter 5).

10 Leaf number (Figure 2)

Leaf number is highly variable in the tribe, with several nodes usually being produced by a plant before flowering. However, several species of *Sinningia* section *Thamnocaula* have a very unusual and distinctive growth habit. The vegetative axis produces only one or two pairs (or whorls) of leaves, usually at the top of a long internode (character 7), terminating abruptly without any decrease in leaf size (although there are occasionally one or two additional inflorescence-bearing nodes with the leaves reduced to bracts). *Sinningia richii* is the only species examined outside section *Thamnocaula* to have a similar reduction of leaf number, but in this species the leaves lie flat on the ground. Seedlings of all these species exhibit a decussate arrangement with several nodes.

11 Leaf abscission line (Figure 3)

This character has only been observed so far in species of *Paliavana* and *Vanhouttea*. A line at the base of the petiole is distinctly visible throughout the life of the leaf, and it is at this line that abscission eventually occurs. Leaves of these species often drop as soon as they begin to senesce (and thus are often absent or detached on herbarium specimens); in other taxa the leaves often turn brown and dry on the plant before falling, or do not fall at all. The abscission line is also found at the bases of prophylls (see character 16).

12 Leaf trichomes (Figure 4)

Although all species of Gloxinieae examined have trichomes on the adaxial surface of their leaves, there are a number of taxa in which the leaf surface appears glabrous. In species of *Sinningia*, e.g., *S. barbata* and *S. guttata*, this is due not to an absence of trichomes but to their being short (2-3 cells) and appressed (Figure 4I). The

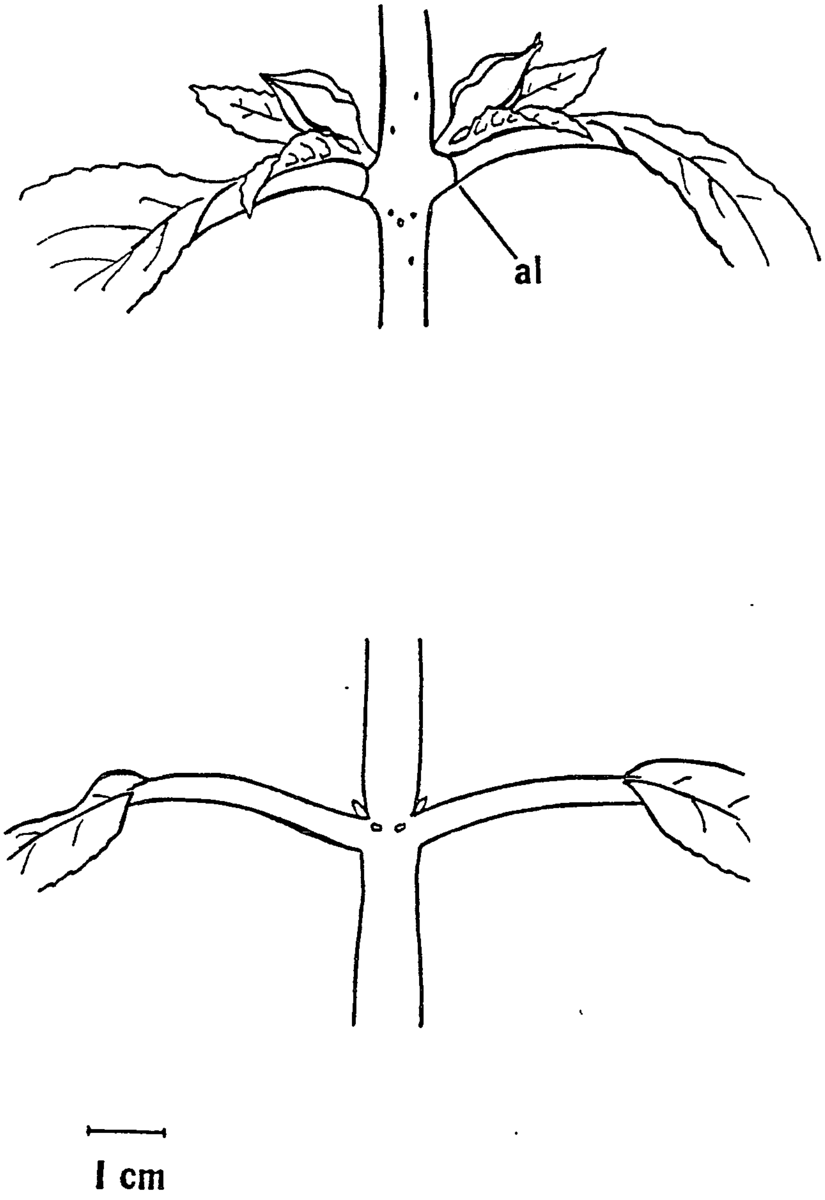


Figure 3. Nodes of *Paliavana tenuiflora* (top) and *Sinningia schiffneri* (bottom); al=abscission line.

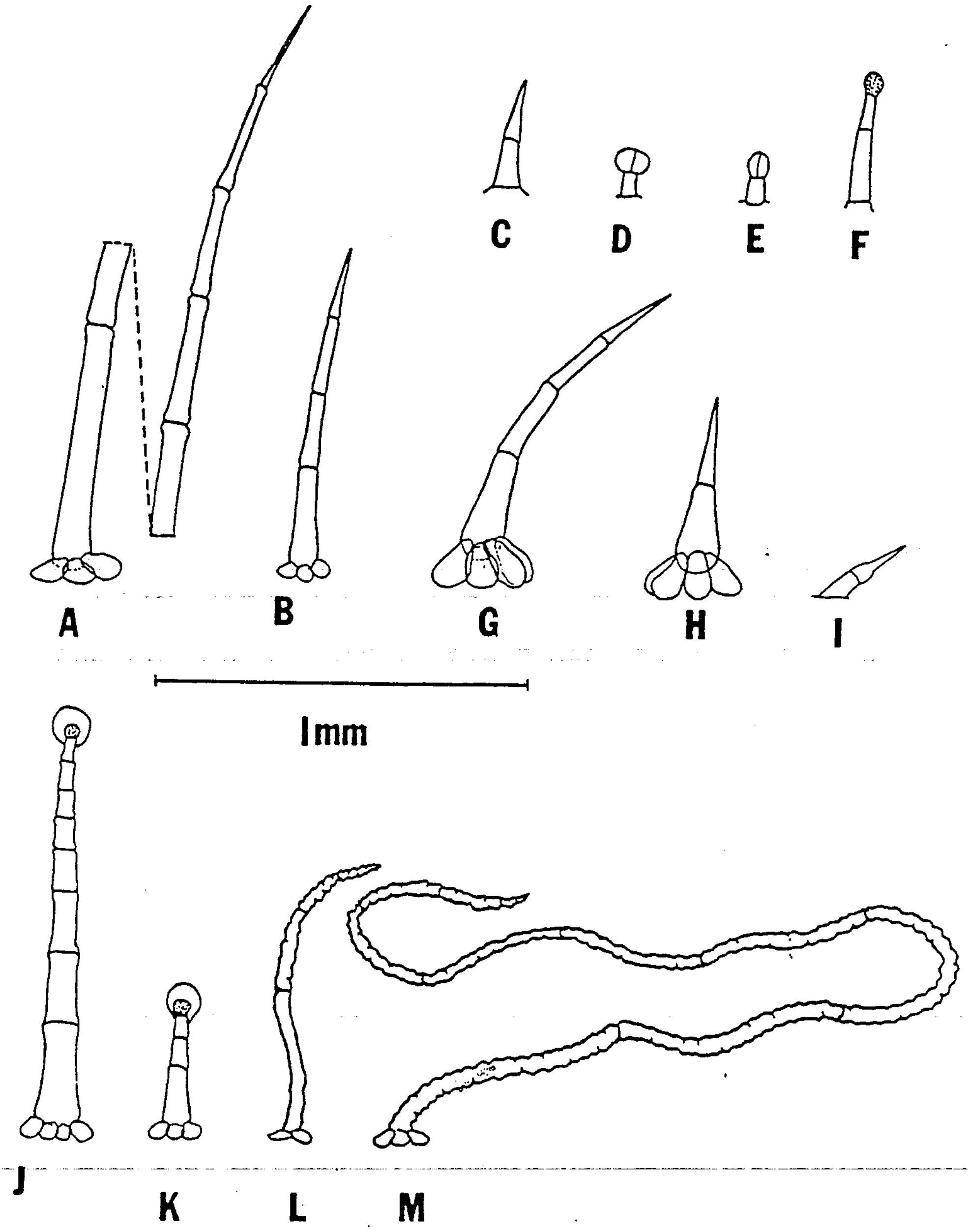


Figure 4. Trichomes on leaves of *Sinningia* species. All from adaxial surface unless otherwise noted. All to same scale. A-D, *S. hirsuta*; E, F, *S. hirsuta*, abaxial; G, H, *S. schiffneri*; I, *S. barbata*; J, K, *S. aggregata*, glandular trichomes with drop of exudate at tip; L, M, *S. leucotricha*.

trichomes are also slightly less densely distributed than those on "hairy" leaves, which have both short and long trichomes of various types (Figure 4 A-H, J-M). Other species with apparently glabrous leaves were not examined.

INFLORESCENCE CHARACTERS

The typical inflorescence of the family Gesneriaceae is an axillary cyme, subtended by a leaf or bract (the pherophyll in the terminology of Weberling, 1989), in which the terminal unit is two flowers rather than one. This has been termed the "pair-flowered cyme" by Weber (1982) and is diagnostic of the family with respect to other members of Scrophulariales. Inflorescence terminology is illustrated in figure 5.

13 Flower production

Most species of Gloxinieae produce various degrees of vegetative growth before flowering. However, some species of *Sinningia* do the opposite. In some species of section *Corytholoma* (e.g., *S. sulcata*, *S. aggregata*), a mature tuber produces flowers before mature leaves upon breaking dormancy. The primary axis produces flower buds immediately upon emerging, and then grows rapidly into a raceme-like florescence with only a few basal leaves (Figure 5A). Axillary branches grow from beneath the florescence as the flowers begin to open, often themselves producing

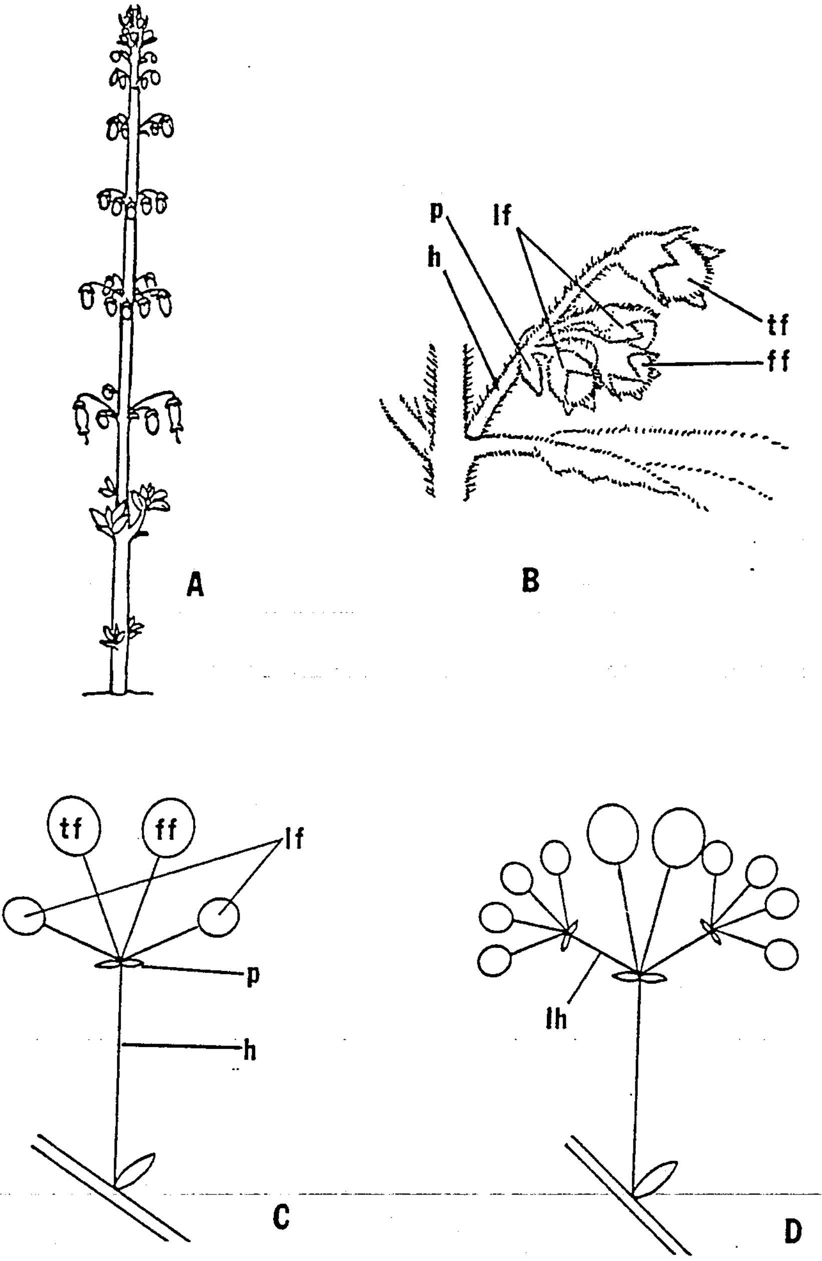


Figure 5. Inflorescence terminology. A, florescence of *Sinningia sulcata*, consisting of an axis with several axillary inflorescences; B, pedunculate axillary cyme of *Kohleria eriantha*; C, schematic diagram of B; D, cyme in which the lateral flowers are replaced by a secondary cyme unit; ff=front flower, h=hypopodium, lf=lateral flower, lh=lateral hypopodium, p=prophyll, tf=terminal flower.

coflorescences after a period of vegetative growth. Immature plants produce more typical growth, with axillary inflorescences being produced after a period of vegetative growth. The precocious florescence is taken to an extreme in *S. tuberosa*, which produces highly compressed, completely leafless florescences from eyes on the tuber and single leaves from separate eyes when the plant is not in bloom.

A different pattern of precocious flowering is found in some members of section *Thamnocaula*. In these species, only one or two pairs of leaves are produced (character 10), but reach maturity only after the inflorescences in their axils have begun to bloom. No branches or coflorescences are produced, although several individual flowering stems may be produced from one tuber.

14 Hypopodium (Figure 5 B, C)

The axillary inflorescence is produced on an elongate peduncle, or hypopodium, in species of several genera of Gloxineae (e.g., *Monopyle*, *Moussonia*, *Kohleria*, *Parakohleria*, and *Capanea*). Hypopodium length varies widely between species but its presence or absence is usually_ typical for a species. Immature plants or flowers produced solitarily usually lack hypopodia, even in taxa which normally produce pedunculate cymes. Species of *Sinningia* which consistently produce very short hypopodia (e.g., *S. glazioviana*, *S. schiffneri*), have been scored as possessing hypopodia. Expression of this character is variable in *S. speciosa*, but mature plants with numerous flowers usually produce short hypopodia, and have been so scored.

15 Lateral hypopodia (Figure 5D)

Lateral (secondary) hypopodia are occasionally produced at the first node of the cyme, replacing the lateral flowers, and then only if a primary hypopodium is also present. They are usually much shorter than the primary hypopodium, sometimes giving the inflorescence an umbellate appearance (e.g., *Parakohleria abunda*). In some species each lateral hypopodium gives rise in turn to two more hypopodia, repeating several times to produce a complex branching cyme. In *Sinningia* this pattern is found only in section *Thamnocaula*. Only production of the first set of lateral hypopodia was scored for analysis. As with the previous character, mature plants often produce lateral hypopodia whereas immature plants do not.

16 Prophylls (Figure 5 B, C)

The axillary cyme typically has a pair of laterally placed prophylls at the point where the pedicels or lateral hypopodia branch from the hypopodium. Prophylls are almost invariably present (but reduced to varying degrees) if the axillary cyme consists of more than one flower. Prophylls are usually absent from solitary axillary flowers, with some exceptions (e.g., *Lietzia glandulosa*). Prophylls are usually persistent, but those of *Vanhouttea* and *Paliavana* are often caducous, and are usually absent from herbarium specimens.

17 Flower number

The axillary cyme usually consists of four or more flowers, occasionally having the appearance of an umbel. It is sometimes reduced to a single flower, most commonly in species of *Diastema*, *Sinningia*, and *Lietzia*. Species with solitary axillary flowers usually lack hypopodia and prophylls as well. Although plants of *Kohleria inaequalis* cultivated for this study regularly produced solitary flowers, this species was not so scored; the flowers were often produced on hypopodia with prophylls (unusual for solitary flowers), the original description describes the inflorescence as umbellate (Bentham 1846), and a closely similar species listed as a synonym of *K. inaequalis* by Kvist (1987), *K. magnifica*, was observed to regularly produce two flowers per axil in cultivation.

FLORAL CHARACTERS

18 Flower orientation (Figure 6)

In most taxa, the flower is held horizontal or erect, on a stiff pedicel (Figure 6 C, D) In two species examined, *Sinningia sulcata* and *S. sellovii*, the flowers are pendulous (Figure 6 A, B). The pedicel has a weak spot, with the result that the flower flops over and dangles straight down, often being effectively resupinate. As the fruit matures, the pedicel straightens and attains a more typical appearance.

19 Hypanthium shape

The hypanthium of all outgroups examined is more or less round in cross section, as is that of most ingroup taxa. A strongly five-winged hypanthium is characteristic of *Sinningia* section *Sinningia*, and was one of the defining characters of the genus as originally circumscribed. A winged hypanthium is found in *S. barbata* and *Paliavana tenuiflora* as well.

20 Calyx lobe connation

If the hypanthium is assumed to be formed by adnation of the calyx lobes to the base of the ovary, then all taxa of Gloxinieae could be considered to have fused calyx lobes. "Fused" is taken here to mean connate at least one-quarter of their length past the point of attachment to the ovary. Species of Gloxinieae exhibit varying degrees of fusion of the calyx lobes, but the division between free and fused lobes is fairly clear-cut in the taxa examined. A third character state might be created for the fusion into a tube of the calyx lobes in *Sinningia* section *Sinningia* (Figure 7A), but variation between this and other degrees of fusion is continuous, even within that section.

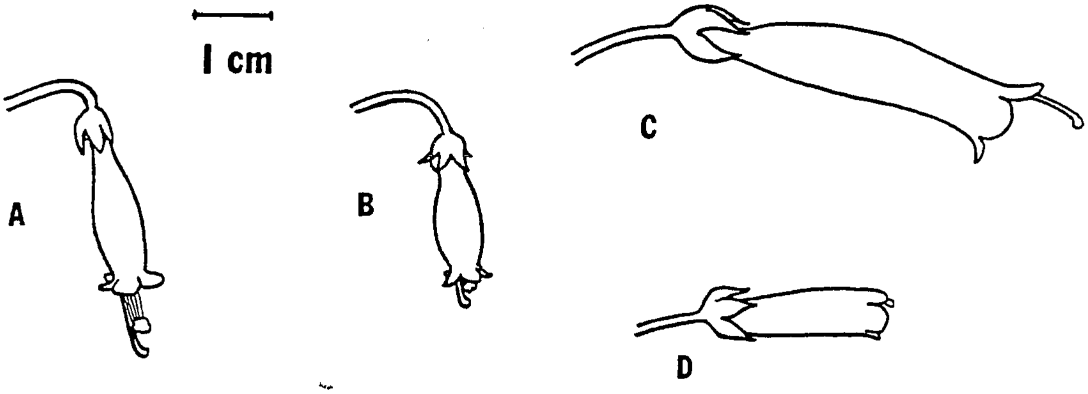


Figure 6. Flower orientation in some *Sinningia* species. A, *S. sulcata*; B, *S. sellovii*; C, *S. sceptrum*; D, *S. aggregata*.

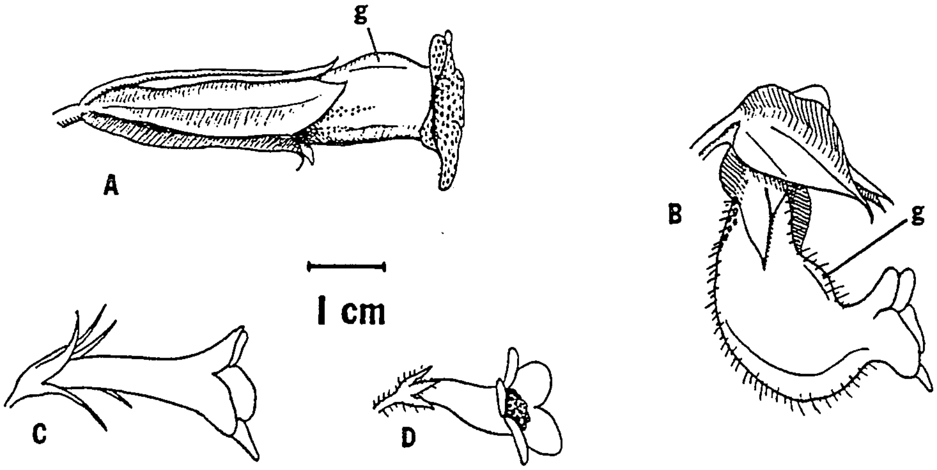


Figure 7. Flowers of some *Sinningia* species.. A, *S. guttata*; B, *S. barbata*; C, *S. schiffneri*; D, *S. hirsuta*; g=gibbosity.

21 Calyx lobe aestivation

In virtually all taxa examined, calyx lobes are separate in the developing bud. In species of only two genera, *Paliavana* and *Vanhouttea*, the calyx lobes are valvately sealed over the developing corolla. As the corolla matures and expands, the calyx lobes separate rather abruptly. This character was noted by Decaisne (1848) and Fritsch (1893).

22 Calyx lobe size (Figure 7)

Calyx lobes of species in Gloxinieae are generally small relative to the corolla. However, in *S. barbata* (Figure 7B) and members of section *Sinningia* (Figure 7A), the calyx lobes are greatly expanded, membranous, and leaflike, their length being 1/3 or more of that of the corolla and correspondingly wide. This was one of the defining characters of *Sinningia* as originally circumscribed.

23 Calyx lobe orientation

In most species examined, the calyx lobes clasp the base of the corolla. In two species, *Sinningia eumorpha* and *S. conspicua*, the lobes remain straight but are bent back 90 degrees from the corolla base. In two other species, *Paliavana prasinata* and *P. tenuiflora*, the calyx lobes are thick and fleshy, and curl back strongly upon or shortly after opening.

24 Corolla texture

In species of *Paliavana*, the corolla is thick, waxy in appearance, and somewhat brittle. Corolla texture in all other species examined is thin and membranous. The only exception was observed in cultivated material of *Kohleria hondensis*, although whether this is a normal condition for the species is doubtful.

25 Corolla anthocyanin color

Anthocyanin is usually present in the corolla, but may be restricted to markings in the throat. It is rarely completely absent (e.g., *Sinningia sulcata*, *S. tubiflora*), but when present exists in one of two states, red or violet. Corolla color is intimately linked to pollination syndrome; red anthocyanin is typical of hummingbird pollination, while violet anthocyanin is found in insect- and bat-pollinated flowers. Other characters which appear to be strongly linked to pollination syndromes (e.g., corolla shape, stigma shape) usually vary quantitatively and have been excluded (see chapter 5). Corolla shape and color were for a long time the basis for the separation of *Sinningia* from *Rechsteineria*.

26 Corolla exterior pigmentation

Most species of Gloxinieae have anthocyanin pigmentation in the outer epidermis of the flower, whether uniform or restricted to spots (character 28). When it is absent the flower may appear either yellow or white, depending on whether carotenoids are present or absent.

27 Corolla exterior ornamentation

In most species, corolla anthocyanin, when present, is uniformly distributed in the exterior epidermis. However, in some species the anthocyanin is aggregated into speckles. In some taxa, these speckles are limited to the base of the corolla (e.g., *Sinningia barbata*, *S. guttata*). In others, the speckles are randomly distributed all over the corolla. This is particularly marked in species of *Lietzia* and *Paliavana*, and appears to be linked to bat pollination.

28 Dorsal nectar reservoir (Figure 8)

A character which has been used to define *Sinningia* section *Corytholoma* is the nectar reservoir at the base of the corolla. It is a prominent, often deeply bilobed, dorsal inflation just above the two fused nectary glands (character 37), and the corolla is sharply constricted past this point. The copiously produced nectar accumulates in this reservoir (Figure 8 A, C). The species of *Lietzia* possess a very similar reservoir (Figure 8D). A nectar reservoir is found in some species of section *Thamnocaula*, but it is usually uniform around the base of the corolla and is highly variable within that section (Figure 8B).

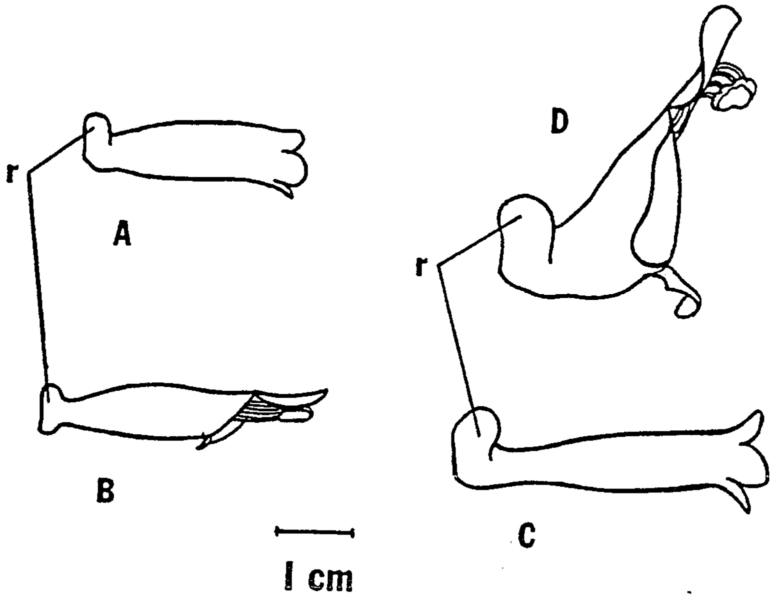


Figure 8. Nectar reservoirs (r) in some species of *Sinningia* and *Lietzia*. A, *S. aggregata*; B, *S. bulbosa*; C, *S. warmingii*; D, *L. glandulosa*.

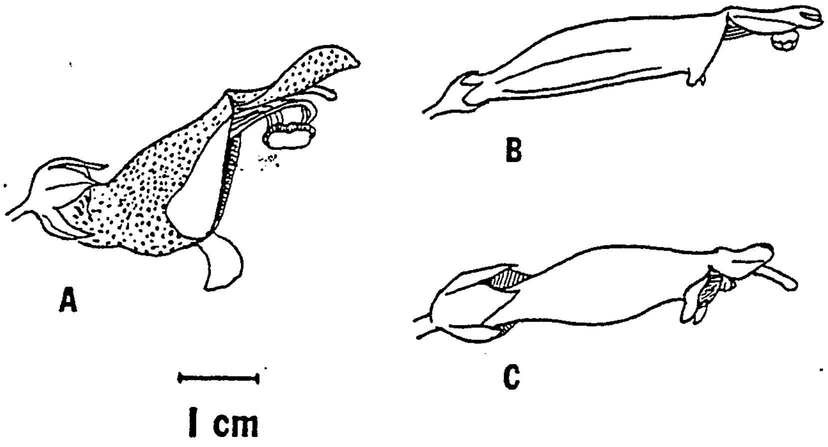


Figure 9. Galeate corollas in *Lietzia* and *Sinningia*. A, *L. glandulosa*; B, *S. glazioviana*; C, *S. incarnata*.

29 Dorsal corolla gibbosity (Figure 7)

The dorsal gibbosity, or bulge, of the tube behind the limb and above the anthers in the species of *Sinningia* section *Sinningia* has been noted by several authors and was part of Hanstein's (1854) generic diagnosis of *Sinningia* (then consisting only of the species of the type section, here represented by *S. guttata*, Figure 7A). The portion of the tube nearer the ovary is much narrower. A similar gibbosity which may or may not be homologous is found in *S. barbata* (Figure 7B) but not in species of other sections or any of the outgroups.

30 Galea (Figure 9)

Galeate ("hooded") corollas are found in *Lietzia* and two sections of *Sinningia*. The galea is formed by the fusion and expansion of the dorsal two corolla lobes, which are held horizontal rather than reflexed as in most other taxa. In one subgroup of section *Thamnocaula*, of which the best known member is *S. cardinalis*, the galea is associated with an unusually uniform floral morphology. A less-prominent galea is found in *S. incarnata* of section *Corytholoma*. Outside *Sinningia* and *Lietzia*, no species of Gloxinieae have galeate corollas, the corolla lobes being more or less equal.

31 Corolla lobe vestiture (Figure 10)

Trichomes are always found on the external epidermis of the corolla, but are less frequently found on the interior surface of the lobes, where they are capitate and at least sometimes glandular. Elongate capitate trichomes (Figure 10H), in which the the stalk consists of 3 to 5 long cylindrical cells and is approximately 1 mm in length, are unique to species of *Kohleria* among the taxa examined, often giving the limb a characteristic hairy appearance. Short capitate trichomes (Figure 10 F, G), with a stalk of only 2 or 3 short cells and less than .3 mm in length, are found on the lobes of several species of *Sinningia* and some of the outgroups. Occasionally they are so dense as to make the lobes appear velvety (e.g., *S. speciosa*). They are also found on the upper lobes only (galea) of the *S. cardinalis* group of section *Thamnocaula*. Other types of trichomes were not observed on corolla lobes.

Flowers of a species which was not included in the cladistic analyses, *Capanea grandiflora*, became available as writing was nearing completion (see appendix 3). The capitate trichomes on the corolla lobes of this species proved to be approximately intermediate between those observed on species of *Kohleria* and those of species of other genera. In future analyses, this character might be better scored simply as trichomes present or absent.

32 Nectar guide

The conspicuous markings on the flowers of most Gloxinieae species are assumed to be nectar guides. The nectar guides are highly variable in Gloxinieae, usually taking the form of spots or lines in the throat, often extending onto the lobes. Some types of guides appear to be associated with particular pollination syndromes (e.g., the guides of presumably insect-pollinated flowers are often lines extending into the throat). The nectar guides are unusually distinctive and uniform in the *Sinningia cardinalis* group of *Sinningia*. In this group the nectar guide consists of a single large, dark, almost black, blotch on the lower lip. The few species which lack nectar guides usually lack corolla anthocyanin entirely.

33 Corolla interior vestiture (Figure 10)

In most species of *Sinningia* subgenus *Sinningia*, there is a distinct patch of short capitate trichomes (Figure 10E) inside the corolla over the anthers (quite dense in *S. hirsuta* and *S. schiffneri*). Trichomes, when found in the corollas of other species of the genus, are either not capitate, or are very infrequent, and if present are usually distributed randomly throughout the corolla interior. The trichome distribution in the red-flowered species *Parakohleria abunda* and *Pearcea hypocyrtiflora* is very unusual among the species examined and must be considered a separate state. In these taxa the entire interior epidermis of the flower is covered with trichomes, both capitate and non-capitate.

34 Stamen filament pigmentation

Stamen filaments either lack anthocyanin, in which case they are white or yellow, or have anthocyanin whose color matches that of the corolla. When anthocyanin is present, it can be either uniformly distributed or irregularly distributed, giving the filaments a mottled appearance.

35 Stamen filament vestiture (Figure 10)

Stamen filaments in Gloxineae can possess both, either, or neither of two distinct types of trichomes. Although they are often found together, they appear to vary independently and so have been scored separately (see next character). Capitate trichomes on the stamen filaments (Figure 10 A, C) may be glandular. They may be dense or very sparse.

36 Stamen filament vestiture (Figure 10)

The second type of trichome found on stamen filaments is long, uniseriate, and multicellular, consisting of 3-6 elongate cells but without a capitate tip (Figure 10B). The trichomes are occasionally pigmented, and may be dense or sparse.

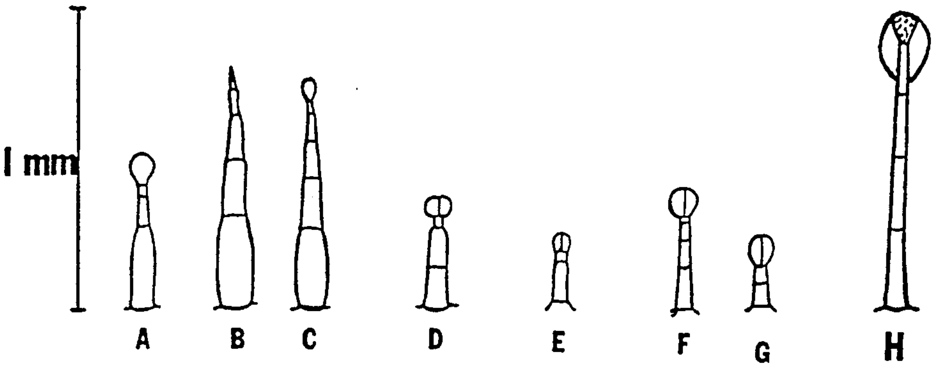


Figure 10. Floral trichomes. A-C, trichomes from stamen filament of *Sinningia bulbosa*; D, trichome from stamen filament of *S. eumorpha*; E, trichome from corolla interior epidermis of *S. hirsuta*; F, G, trichomes from corolla lobes of *S. speciosa*; H, glandular trichome from corolla lobe of *Kohleria eriantha* with drop of exudate at tip.

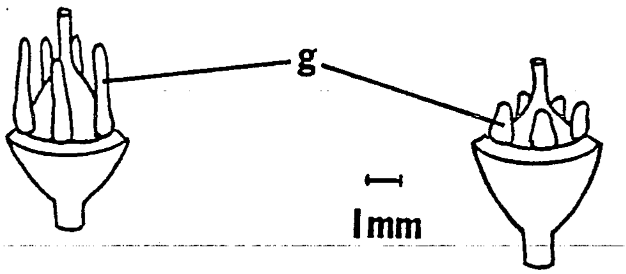


Figure 11. Nectary glands (g) of *Diastema vexans* (left) and *Sinningia hirsuta* (right). Corollas and calyx lobes removed.

37 Nectary gland dimensions (Figure 11)

The nectary glands of species of *Diastema* are unusual in that they are elongate and finger-like, and are approximately four or five times as long as broad. Glands observed in other species were, at most, twice as long as broad.

38 Nectary gland fusion (Figure 12)

The nectary in Gesneriaceae is typically a thin ring around the base of the ovary, and this pattern is found in other families of the Scrophulariales as well (Cronquist 1988, Goldberg 1986). Nectaries are occasionally absent, but are present in all species included in this analysis. By definition, the group examined is characterized by separation of the nectary into separate glands (with the exception of *Lietzia*, see below). In three groups examined, some or all of the glands were consistently fused. In all species of *Sinningia* sections *Cryptocaula* and *Corytholoma*, the dorsal two glands are fused into a single large, sometimes slightly bilobed, gland (Figure 12C); this fusion is one of the defining characters of these sections. Species of *Lietzia* are the only tuberous taxa with an annular nectary (Figure 12D), although in these species the nectary is thicker than that of other Gloxinieae with annular nectaries (see chapter 5). The annular nectary has been the basis for the separation of this genus from *Sinningia*, and is typical of the larger part of the tribe.

Occasional flowers of several species can have two or more glands joined at the bases only, particularly species of *Kohleria*. Such cases have been scored as separate glands, although the tendency of several *Kohleria* species to have the dorsal glands joined at the base only would probably merit scoring as a separate character or state in a more inclusive analysis.

39 Size of ventral nectary glands (Figure 12)

Size of the ventral three nectary glands was scored relative to that of the dorsal glands. Among the species examined, only species of *Sinningia* exhibit a marked tendency toward reduction (Figure 12C) or loss (Figure 12B) of the ventral glands. Glands were scored as reduced if they were present but less than half the size of the dorsal glands. Among species which typically lack the ventral glands, flowers occasionally can be found with the glands present (but usually minute).

40 Nectary gland color

Nectary gland color is either white or yellow to orange. The deep orange color of the nectary of the two *Lietzia* species was initially scored as a separate state, but intermediates between yellow and orange were found in *Sinningia*. In rare cases nectary glands were pigmented with anthocyanin as well and this character could not be scored, although it is possible that the carotenoids presumably

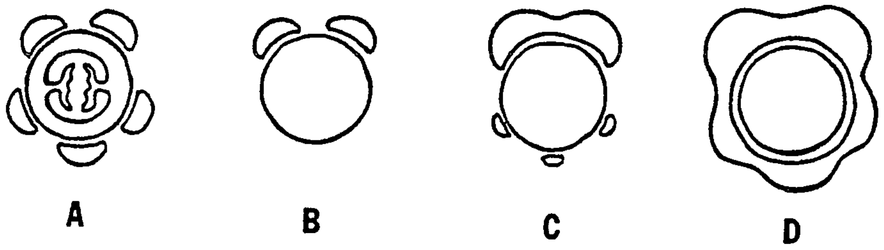


Figure 12. Nectary gland configurations. A, five free glands: all outgroup species and species of subgenus *Sinningia* (ovary in transverse section showing placentae); B, dorsal glands present, ventral glands absent: *S. barbata* and species of section *Thamnocaula*; C, dorsal glands fused, ventral glands present but reduced: species of sections *Cryptocaula* and *Corytholoma*; D, nectary a lobed annular disc: species of *Lietzia*.

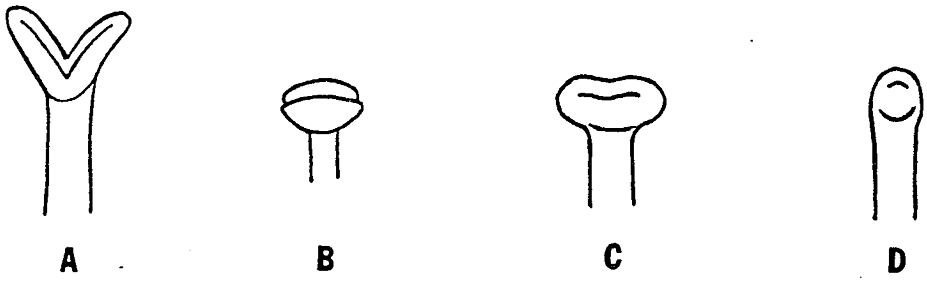


Figure 13. Stigmas of some representative species. A, *Kohleria eriantha*; B, *Diastema vexans*; C, *Sinningia eumorpha*; D, *S.bulbosa*.

responsible for yellow color were present but masked by the anthocyanin. In the two cases in which both yellow and white glands were found in the same flower (*Sinningia tubiflora* and *S. kautskyi*), the glands were scored as yellow. Nectary gland color was scored from newly-opened flowers or mature buds, as the glands often turn green or brown shortly after the flower opens.

41 Stigma shape (Figure 13)

Stigma shape is highly variable in Gloxinieae, and appears to be linked to the pollination syndrome. The most common states are narrowly stomatomorphic (the stigma not wider than the style, Figure 13D), which is usually associated with tubular red flowers, and broadly stomatomorphic (stigma enlarged and wider than the style, Figure 13C), usually associated with flowers typical of insect pollination. These states have not been considered separately as there is an almost continuous range of variation between the two. However, species of two outgroup genera have very distinctive stigmas which could be scored qualitatively. The stigma of species of *Kohleria* is distinctly divided into two lateral lobes (Figure 13A). Species of *Diastema* have a somewhat stomatomorphic stigma but with the lips broadly expanded and flattened (Figure 13B). These stigma types were universal in, and restricted to, all examined species of their respective genera.

42 Ovary position (Figure 14)

Ovary position has been given great weight in gesneriad systematics. Tribes Gesnerieae and Gloxinieae are defined by having fully to partially inferior ovaries, with the ovary embedded to varying degrees in the hypanthium. Although Cronquist (1988) suggests that inferior ovaries are frequent in the family, in actuality they are restricted to these two relatively small tribes.

Within Gloxinieae, the most frequent ovary position is half-inferior (Figure 14 A-C). Only two species included in this analysis have ovaries approaching fully inferior: *Kohleria inaequalis* and *Sinningia guttata* (Figure 14F). These species also have very elongate ovaries; both conditions are unusual in their respective genera. The only species examined with nearly superior ovaries were found in *Lietzia* and *Sinningia* (Figure 14 D, E). Even in these species the ovary is always at least partially inferior, however slightly. Throughout this thesis, "inferior ovary" is used to mean anything other than a completely superior ovary, unless elaborated further.

Although ovary position would probably exhibit a continous range of variation in a larger analysis, among the examined taxa it is usually unambiguous.

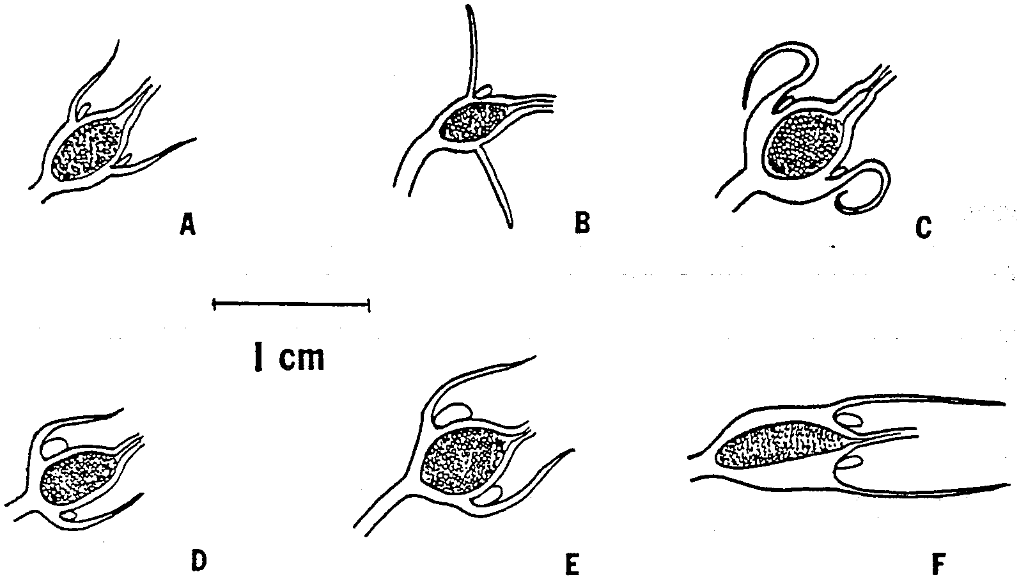


Figure 14. Ovary position in representative species (ovaries shown in longitudinal section). A, *Kohleria eriantha*; B, *Sinningia eumorpha*; C, *Paliavana prasinata*; D, *Sinningia aggregata*; E, *Lietzia glandulosa*; F, *Sinningia guttata*.

FRUIT AND SEED CHARACTERS

43 Capsule texture

The fruit in Gloxinieae is either a heavily lignified dry capsule or a poorly-lignified fleshy capsule. Fleshy capsules dehisce in one of two ways, whereas dry capsules have only one mode of dehiscence in the species examined (see next character). Fleshy capsules typically are green upon dehiscence and remain green and fleshy for several days afterward, shrivelling when they do dry. This type of capsule is rarely found on herbarium specimens. Dry capsules are generally dry upon or soon after dehiscence, and their shape is not deformed when they dry.

44 Capsule dehiscence (Figure 15)

Dehiscence of the capsule in Gloxinieae is loculicidal and occurs both dorsally and ventrally on the portion of the ovary above (superior to) the hypanthium (Figure 15 A-M). The only exceptions occur in fleshy capsules (see above), some of which dehisce along the dorsal surface only, with dehiscence splitting the hypanthium to its base (Figure 15 O). This type of dehiscence is usually, but not always, associated with almost fully inferior ovaries.

45 Seed size (Figure 16)

Although Beaufort-Murphy (1983) did not attach significance to seed size, the difference between ingroup and outgroup species in this character is striking, even to

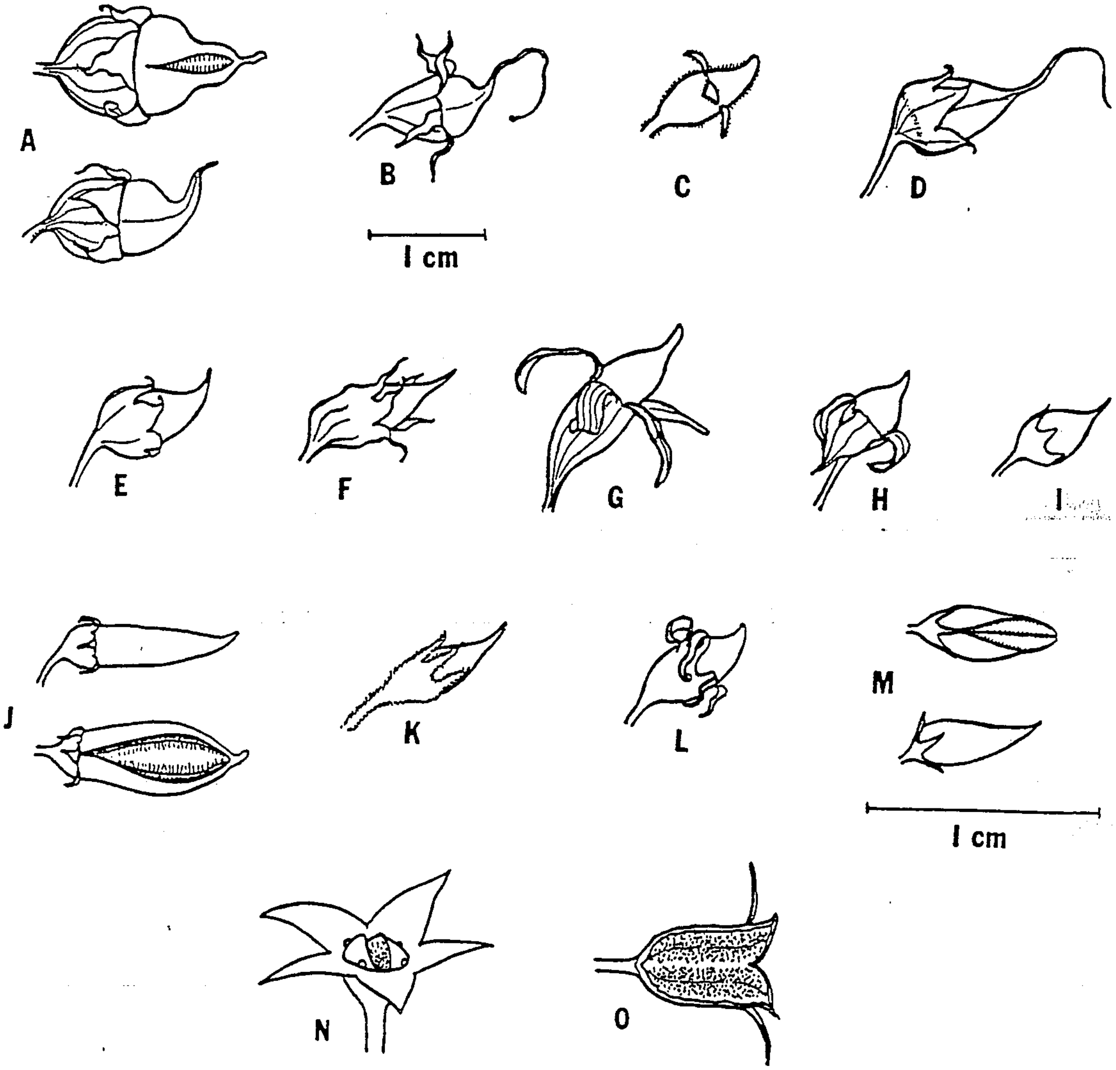


Figure 15. Seed capsules of representative species. Dry capsules, A-M; fleshy capsules, N and O. All to same scale except M. A, *Paliavana prasinata*, dorsal (top) and lateral view; B, *Vanhouttea calcarata*; C, *Kohleria eriantha*; D, *Lietzia glandulosa*; E, *Sinningia aggregata*; F, *S. warmingii*; G, *S. eumorpha*; H, *S. conspicua*; I, *S. bulbosa*; J, *S. glazioviana*; K, *S. leucotricha*; L, *S. reitzii*; M, *S. pusilla*; N, *S. speciosa*; O, *Kohleria inaequalis*.

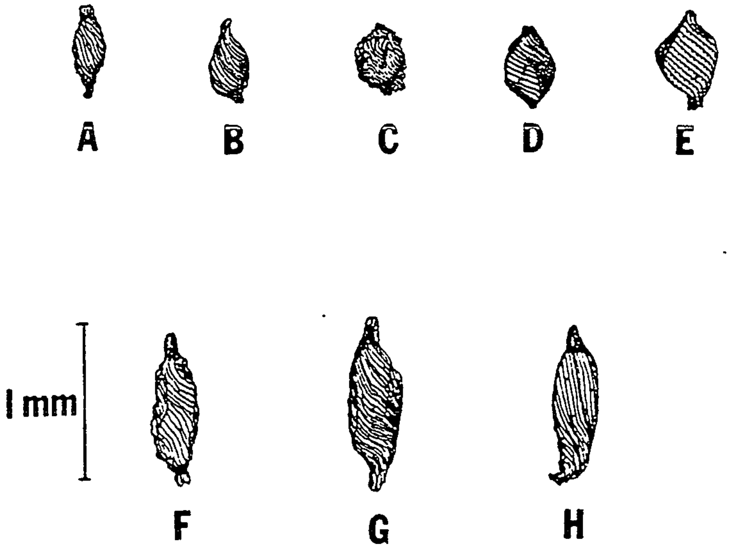


Figure 16. Seeds of representative outgroup (A-E) and ingroup (F-H) species. All to same scale. A, *Kohleria eriantha*; B, *K. hondensis*; C, *K. inaequalis*; D, *Diastema racemiferum*; E, *Parakohleria abunda*; F, *Lietzia glandulosa*; G, *Paliavana tenuiflora*; H, *Vanhouttea calcarata*.

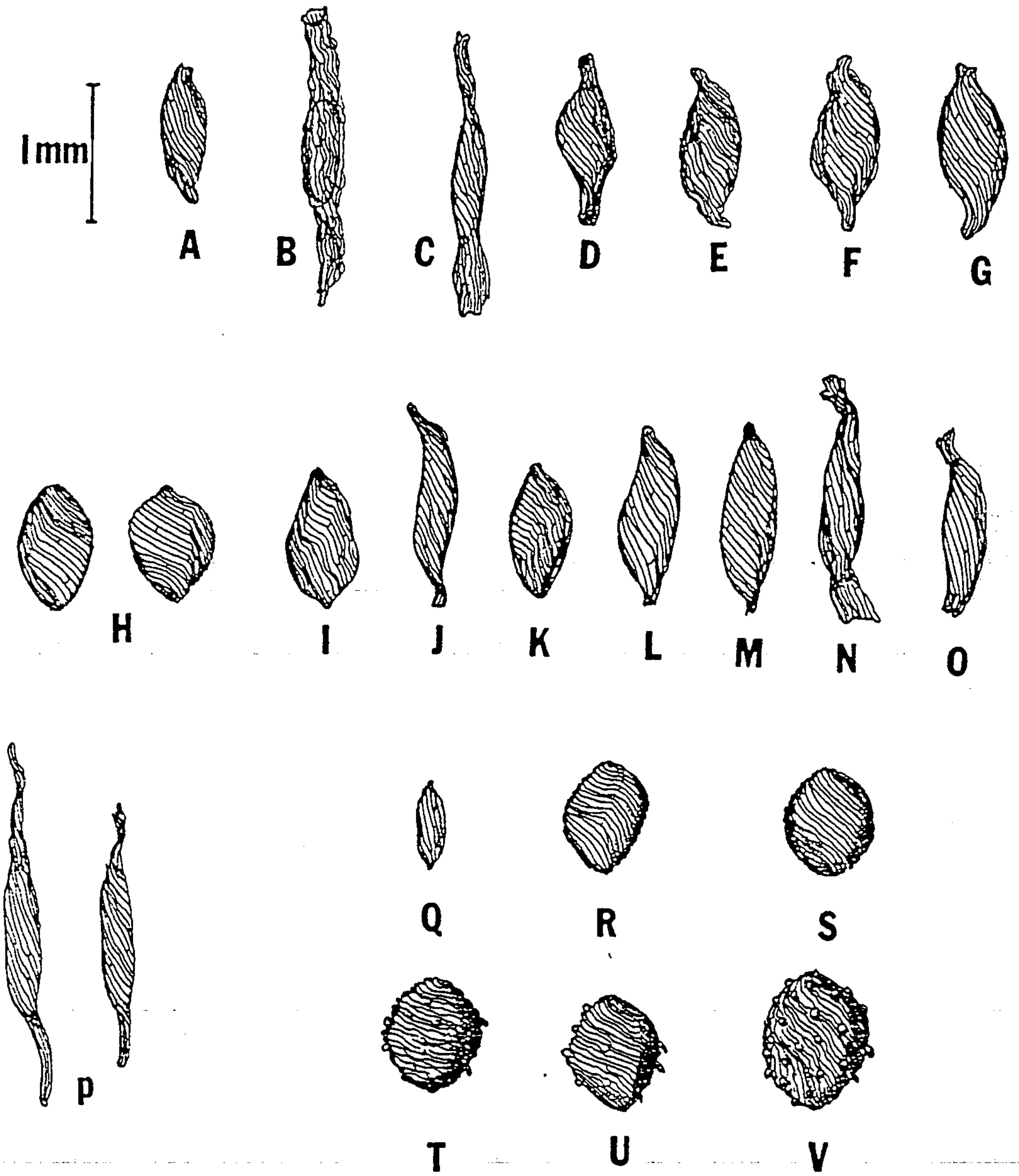


Figure 17. Seeds of representative *Sinningia* species, arranged by section. All to same scale. *Cryptocaula*: A, *S. tuberosa*; *Corytholoma*: B, *S. sceptrum*; C, *S. tubiflora*; D, *S. warmingii*; E, *S. sellovii*; F, *S. sulcata*; G, *S. aggregata*; *Thamnocaula*: H, *S. eumorpha*; I, *S. conspicua*; J, *S. reitzii*; K, *S. macrostachya*; L, *S. leucotricha*; M, *S. macropoda*; N, *S. douglasii*; O, *S. bulbosa*; P, *S. glazioviana*; *Stenogastra*: Q, *S. pusilla*; R, *S. kautskyi*; S, *S. hirsuta*; *Sinningia*: T, *S. guttata*; *Thamnoligeria*: U, *S. schiffneri*; unplaced: V, *S. richii*.

the naked eye. Gesneriad seeds are minute, usually less than 1mm in length. Gloxinieae seeds are especially small, usually less than .5 mm in length. Species of *Paliavana*, *Vanhouttea*, Lietzia, and Sinningia are unusual within the tribe for having relatively large seeds, approximately 1 mm in length or slightly smaller (exclusive of appendages). This was one of the initial characters used to define the ingroup. A difference in seed size was noted by Ivanina (1965) but it is not clear if this affected her tribal groupings.

46 Seed coat ornamentation (Figure 17 T-V)

Several species of *Sinningia* subgenus *Sinningia* have warty protuberances on the seeds (e.g., *S. guttata*, *S. barbata*). This character is unknown elsewhere in the genus, and was not observed on seeds of other members of the tribe.

Characters not used in cladistic analyses

Characters were excluded for several reasons. Characters were usually excluded because they proved to vary quantitatively. Variation in quantitative characters is described in the chapter 5. Others characters which were excluded were those which did not vary in the group under consideration, were autapomorphies of single species, or varied in parallel with another character in several groups (correlated characters).

Two characters of possible systematic value which were not examined in the present study are stamen filament coiling and wood anatomy. Stamen filament coiling was used as a character in a cladistic analysis of *Heppiella* by Kvist (1990). Wood anatomy was extensively surveyed in the Gesneriaceae by Carlquist and Hoekman (1986), but only two genera of Gloxinieae were examined, including only one member of the present study, *Sinningia reitzii* (as *Rechsteineria reitzii*). (The *Kohleria* species examined by Carlquist and Hoekman, *K. elegans*, is now considered a species of *Moussonia*, another genus of Gloxinieae.) Distribution of multiseriate and uniseriate rays, in particular, may prove to be of systematic value if more extensively surveyed in this group.

Invariant characters

Several systematic studies of Gesneriaceae have extensively surveyed particular characters in the family. However, in many cases these characters, while varying within the family, were found not to vary at the level of the present analysis. No substantial differences were found in floral vasculature (Wilson 1974b), chromosome number (Skog 1984), pollen morphology (Williams 1978), or phenolic chemistry (Kvist & Pedersen 1986). The chromosome number of *Lietzia glandulosa* is n=13 (Boggan, unpublished), as is that of all ingroup and outgroup species for which the chromosome number is known.

Autapomorphies of single species

Other characters which were excluded from the cladistic analyses are autapomorphies of single species. It is likely that some of these characters would take on greater significance in a more inclusive analysis. Two characters which may occur in species not included in the analysis are unifoliate habit (here restricted to *Sinningia tuberosa*) and trichomes with rugose cell walls (here restricted to *S. leucotricha*, see Figure 4 L, M). Two more autapomorphies involve phyllotaxy. The phyllotaxy of the tribe is opposite decussate with few exceptions, notably the verticillate phyllotaxy with ternate nodes found in some members of *Sinningia* and much less frequently in other genera. *S. warmingii* is very unusual among the verticillate species for having quadrate, rather than ternate, nodes. This was not scored as a separate character, not only because it is unique to this species, but also because S. warmingii is otherwise similar to species with ternate nodes and commonly produces ternate nodes as well, suggesting that the two nodal types are different expressions of the same character. Another exception to decussate phyllotaxy is S. concinna. The alternate leaves of this species are unique in Gloxinieae. All related species have opposite leaves, and so S. concinna has been scored as having opposite (i.e., not verticillate) leaves, the plesiomorphic condition, as well.

Correlated characters

Several characters were not included in the analysis due to their strong correlations with other characters, even in apparently unrelated groups. The most striking character correlations involve fruit and seed characters. Fruit type (dry or fleshy capsule) is highly correlated with valve trichome presence or absence, seed shape, and seed appendage presence or absence. The most common fruit type in Gloxinieae is a dry capsule, with heavily lignified valves which dehisce loculicidally down to the hypanthium, with stiff trichomes intermeshing along the edges. Almost all genera have at least some species with this type of fruit, several genera having only this type. Fleshy capsules, which are poorly lignified and remain green upon dehiscence, occur sporadically in Gloxinieae, although those found in Sinningia have a different type of dehiscence from those of other members of the tribe with fleshy capsules. In all species with fleshy capsules, regardless of the type of dehiscence, the valves lack trichomes along the edges; dry capsules always bear such trichomes. Fleshy capsules also have a characteristic seed shape. In all species with fleshy capsules, the seeds are nearly round and always lack appendages. Species with dry capsules almost invariably have spindle-shaped seeds, and often have appendages. Seed shape and appendage presence or absence were not included in the analyses not only because they are correlated with capsule type but also because they vary quantitatively (see Figures 16 and 17).

Another strong correlation was observed between corolla shape and color and stigma type. Tubular red, orange, or yellow corollas typical of hummingbird pollination invariably have narrowly stomatomorphic or slightly capitate stigmas, while violet or white flowers typical of insect pollination usually have broadly stomatomorphic stigmas (see Figure 13). (However, intermediates between the two occur in insect-pollinated flowers.) In species which are presumably bat-pollinated (characterized by large, open-mouthed green flowers covered with purple speckles), *Lietzia brasiliensis*, *L. glandulosa*, and *Paliavana prasinata*, the stigma is similar to that of hummingbird-pollinated flowers. However, the large violet flower of *P. tenuiflora*, which is presumably insect pollinated, has a narrow stigma as well.

Hybridizing relationships

Hybridizing relationships within and between the genera used in the cladistic analysis were another area of investigation. Hybridizing relationships within *Sinningia* have been well-documented by Clayberg (1968a, 1970a); additional hybrids were reported by Boggan (1985a). Several crosses were attempted during the course of this study using species of *Sinningia* which were not in cultivation at the time of Clayberg's research (e.g., *S. guttata*). However, primary emphasis was placed on intergeneric hybridization, as this was given great weight in formulating generic and tribal circumscriptions by Wiehler (1975a, 1976, 1978a, 1983).

Over 600 pollinations were carried out between 1988 and 1991. Flowers were always emasculated by removing the anthers before or shortly after opening, before the stigma was mature. Reciprocal crosses were attempted whenever possible. A total of approximately 80 crosses and their reciprocals, 30 of them intergeneric, were attempted using species (and occasionally hybrids) of *Kohleria*, *Paliavana*, *Vanhouttea*, *Lietzia*, and *Sinningia*. Species of *Parakohleria* and *Pearcea* were not available at the time the crosses were made. Seeds of all crosses but one were planted on soilless potting medium (PRO-MIX®) and placed under fluorescent lights. Seeds from one cross, *S. guttata* x *S. warmingii*, were planted on agar. Seeds from crosses involving species of *Vanhouttea* and *Paliavana* were not planted, as they were not produced until near the end of the project.

Expression in hybrids of some of the characters used in the cladistic analyses was also examined in both herbarium and live material. Hybrid material studied is listed in Table 14. All specimens are deposited in the herbarium of the L. H. Bailey Hortorium.

Table 14. Hybrid material examined. All specimens at BH. Seed parent is listed first in hybrid combination. Some of the plants listed as *S. macropoda* by Clayberg may have been *S. lineata* due to the confusion between these two species (see Boggan and Chautems, 1991).

Sinningia hybrids

aggregata x *allagophylla* ***Clayberg 35, Clayberg 72***
aggregata x *incarnata* ***Clayberg 30***
cardinalis x *douglasii* ***Clayberg 46***
cardinalis x *eumorpha* ***Clayberg 45***
cardinalis x *leucotricha* ***Clayberg 36***
concinna x *aggregata* (as *S.* 'Tinkerbells') *M. H. Stone 1218*
concinna x *eumorpha* (as *S.* 'Cindy') *M. H. Stone 1337*
concinna x *schiffneri* ***Clayberg 55***
cooperi x *magnifica* ***Clayberg 31***
douglasii x *cardinalis* ***Clayberg 43***
douglasii x *eumorpha* ***Clayberg 44***
douglasii x *macropoda* ***Clayberg 48***
douglasii x *magnifica*: ***Clayberg 37***
eumorpha x *aggregata*: ***Clayberg 71, Clayberg 72***
eumorpha x *cardinalis*: ***Clayberg 69***
eumorpha x *douglasii*: ***Clayberg 73***
eumorpha x *leucotricha*: ***Clayberg 61***
eumorpha x *macropoda*: ***Clayberg 60***
eumorpha x *schiffneri*: ***Clayberg 56***
eumorpha x *tubiflora*: ***Clayberg 53***
incarnata x *tubiflora*: ***Clayberg 32, Clayberg 38***
incarnata x *warmingii*: ***Clayberg 75***
leucotricha x *cardinalis*: ***Clayberg 42***
leucotricha x *eumorpha*: ***Clayberg 51***
leucotricha x *macropoda*: ***Clayberg 47***
macropoda x *bulbosa*: ***Clayberg 33***
macropoda x *cardinalis*: ***Clayberg 40, Clayberg 49***
macropoda x *douglasii*: ***Clayberg 39***
macropoda x *eumorpha* (as *S.* x*rosea*): *Moore 6825*
macropoda x *eumorpha*: ***Clayberg 41***
macropoda x *leucotricha*: ***Clayberg 50***
pusilla x *concinna*: ***Clayberg 67***
pusilla x *eumorpha* (as *S.* x*pumila*): ***Clayberg 1***
pusilla x *eumorpha* (as *S.* 'Dollbaby): *J. W. Peterson 5-761*
pusilla x *eumorpha*: ***Clayberg 62***
pusilla x *leucotricha*: ***Clayberg 54, Clayberg 64, Clayberg 68***
pusilla x *macropoda*: ***Clayberg 58***

Table 14 (continued)

Sinningia hybrids

pusilla x *schiffneri*: *Clayberg 65*
tubiflora x *eumorpha*: *Clayberg 70*
tubiflora x *cardinalis*: *Clayberg 57*, *Clayberg 74*
warmingii x *barbata*: *Clayberg 76*
warmingii x *eumorpha*: *Boggan 32*
warmingii x *incarnata*: *Clayberg 79*
warmingii x *tubiflora*: *Clayberg 78*

Other hybrids

Paliavana prasinata x *P. tenuiflora*: *M. H. Stone 1301*
Lietzia glandulosa x *Sinningia aggregata*: *Boggan 33*
(*Sinningia warmingii* x *S. sulcata*) x *Lietzia glandulosa*: *Boggan 34*

CHAPTER IV. RESULTS.

Cladistic analyis

Results using multiple (all) outgroups

The character state matrix resulting from scoring all characters for all taxa used in the cladistic analyses is presented in Table 15. The combinations mhennig*;bb* and tread;bb* produced identical results, as did rearranging the order of species in the matrix. Each of these combinations produced 30 trees of length 155 and consistency index of .36. Individual characters with the highest consistency indices are listed in Table 16; characters with the lowest consistency indices are listed in Table 17.

Each of the 30 trees exhibited one of only two alternatative topologies indicating relationships among four distinct ingroup clades (see below). Trees differed primarily in relationships among the outgroups and within two ingroup clades. Two representative trees, illustrating the two major branching patterns which were identified, are reproduced in Figures 18 and 19. In Figure 18, the clade *S. pusilla* + *S. concinna* is the sister group to all other members of the ingroup; in Figure 19, the clade *Corytholoma* + *Cryptocaula* + *Lietzia* is the sister group to the rest of the ingroup. Branching patterns within each of the four clades differed little between the trees. Two of the clades

Table 15. Character matrix used for cladistic analyses. See table 11 for species acronyms and table 13 for characters. "-" = inapplicable; "?" = unknown.

	000000000111	11111	1122222222223333333333444	4444
	123456789012	34567	8901234567890123456789012	3456
DRAC	00-000000000	00011	0000000100000?00000100020	1100
DVEX	00-000000000	00000	0000000110000101000100020	?000
KERI	00-000000000	01000	0010000000000200011000010	0000
KHON	00-000000000	00000	0010001000000200000000010	0000
KINA	00-000000000	01000	0000000000000200011000111	1100
KSPI	00-000001000	00000	0000000000000200011000010	0000
PABU	00-000000000	01100	0010020000000102011000100	0000
PHYP	00-?00000000	00000	0010000000000102011000000	??00
LBRA	111000010000	00001	0010000102101000211020002	0010
LGLN	111000010000	00001	0010000102101000211020002	0010
PPRA	10-?01010010	00000	0011021102000101000000000	0010
PTEN	10-?01010010	00000	0111021102000001200000000	0010
SAGG	111000011000	10000	0010000000100000000011002	0010
SBAR	110?01010001	00000	0111100101010001210002102	1011
SBUL	110100000000	01100	0000000000001110111002000	0010
SCAR	110100000000	00000	0000000000001110111002000	0010
SCON	110?10000000	00011	0000000100000000000000102	0000
SCSP	110?00000000	00000	0000010110000000010002100	0010
SDOU	110100101100	01100	0000000000000100000002?02	0010
SEUM	110100000000	00000	0000010110000000010002100	0010
SGLZ	110100000000	01001	0000000000001110111002002	0010
SGUT	110?01000001	00011	0110100101010101200000101	1?11
SHIR	110001000000	00011	0010000100000101200000100	1010
SINC	11??00010000	00000	0010000000101000111011002	0010
SKAU	11000-000000	00000	0010000100000000200000000	1010
SLEU	110100100100	11100	0000000000000000001002000	0010
SLIN	110100100100	11100	0000000000000000001002000	0010
SMCP	110100100100	11100	0000000000000000101002000	0010
SMCS	110?00000000	01000	0000000000000000001002?00	0010
SPUS	110010000000	00011	0000000100100000000000102	0000
SRIC	010000000100	00000	0000000101000101210000102	?011
SRTZ	110101000000	01000	0000000000000000000002000	0010
SSCE	011000001000	00000	0010000000100000100011000	0010
SSCH	10-001000000	01000	0010000110000101000000101	1111
SSEL	111000011000	00000	1010000000100000201011002	0010
SSPE	110000000000	01000	0010100100000101000000100	1011
SSUL	111000011000	10010	1010000210100000000011002	0010
STBF	011000000000	00011	0010000210100000000011002	0010
STBR	011000000100	10011	0010000000100000011011002	0010
SWAR	111000011000	00000	0010000000100000211011000	0010
VCAL	10-001010010	00000	0001000000000000000000000	0010

Table 16. Characters with highest consistency indices. Multistate characters may be listed more than once. P=paralellism, R=reversal.

03	Tuber eyes in dense clusters	1.0	
04	Seedling hypocotyl pigmented	1.0	
05	Plant size highly reduced	1.0	
07	First internode long	1.0	
11	Abscission line at base of petiole	1.0	
12	Leaves glabrous in appearance	1.0	
29	Corolla with dorsal gibbosity	1.0	
32	Nectar guide a large dark blotch	1.0	
37	Nectary glands 4-5 times as long as broad	1.0	
38_1	Dorsal nectary glands fused	1.0	
38_2	All nectary glands fused	1.0	
45	Seed size greater than .75 mm	0.5-1.0	R
46	Seed coat with warty protuberances	1.0	
18	Flowers pendent	0.5	P
19	Hypanthium winged	0.5	P
21	Calyx lobes valvate in bud	0.5	P
22	Calyx lobes large and leafy	0.5	P
23_1	Calyx lobes reflexed 90 degrees	1.0	
23_2	Calyx lobes strongly recurved	0.5	P
24	Corolla texture fleshy	0.5	P
27	Corolla with speckles at base	1.0	
28	Corolla with speckles all over	0.5	P
30	Corolla galeate	0.5	P
33_1	Sessile capitate trichomes over anthers	0.5	P
33_2	Corolla interior with capitate trichomes	1.0	
41_1	Stigma bilobed	0.5	R
41_2	Stigma bilabiate	1.0	

Table 17. Characters with lowest consistency indices. P=parallelism, R=reversal.

09	Phyllotaxy verticillate	.20-.25	P, R
14	Inflorescence pedunculate	.20	P, R
16	Prophylls absent	.16-.20	P
17	Flowers solitary	.14	P
20	Calyx lobe connation (polarity varies)	.20	P, R
26	Corolla exterior unpigmented	.20	P
35	Stamen filaments with capitate trichomes	.14	P
36	Stamen filaments with noncapitate trichomes	.20	P
40	Nectary glands white	.20	P
42	Ovary position	.22	P, R

Figure 18. One of thirty equally parsimonious trees produced using mhennig*;bb* (length 155, consistency index .36). Acronyms as in Table 11.

Figure 18. One of thirty equally parsimonious trees produced using mhennig*;bb* (length 155, consistency index .36). Acronyms as in Table 11.

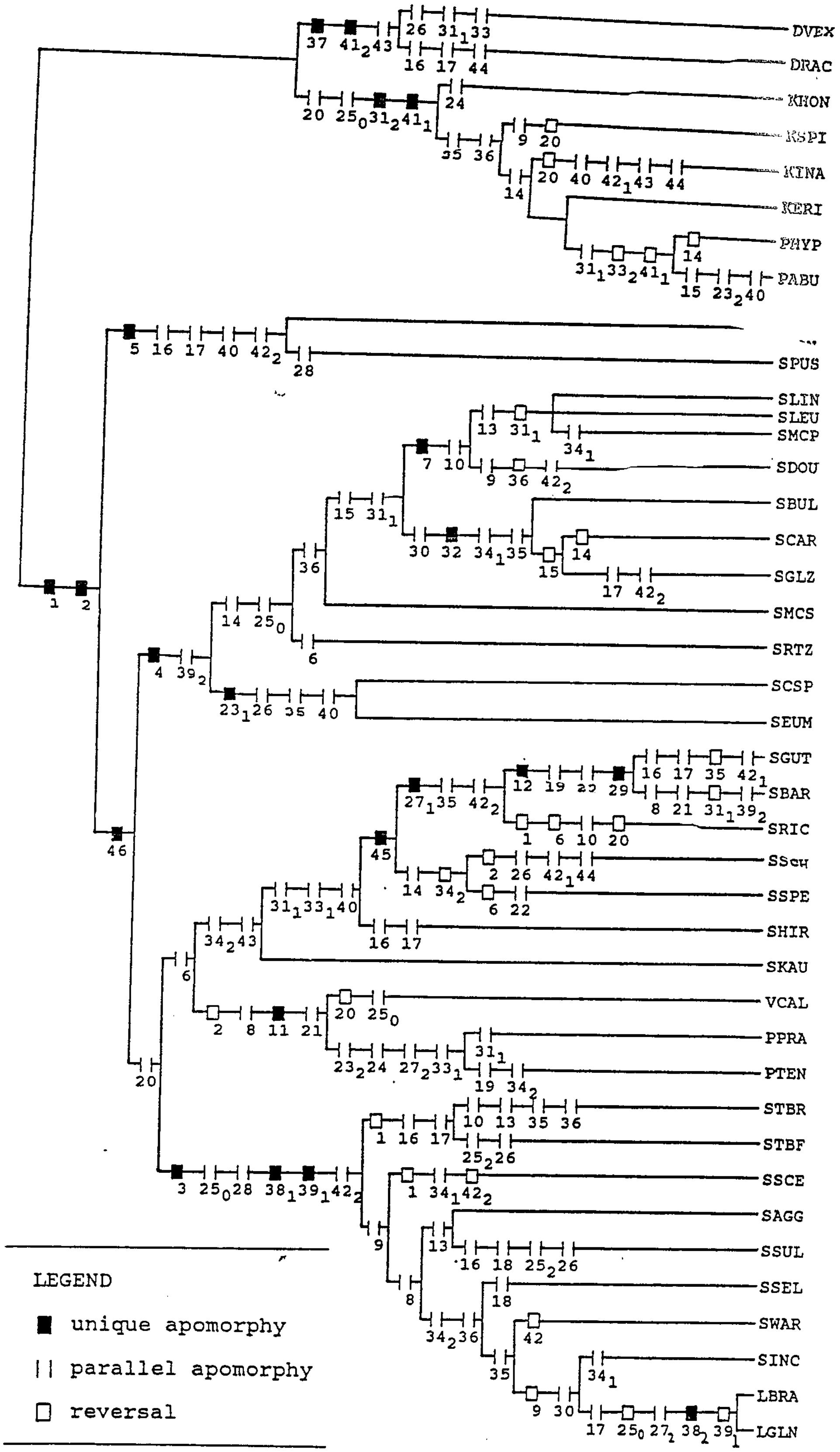
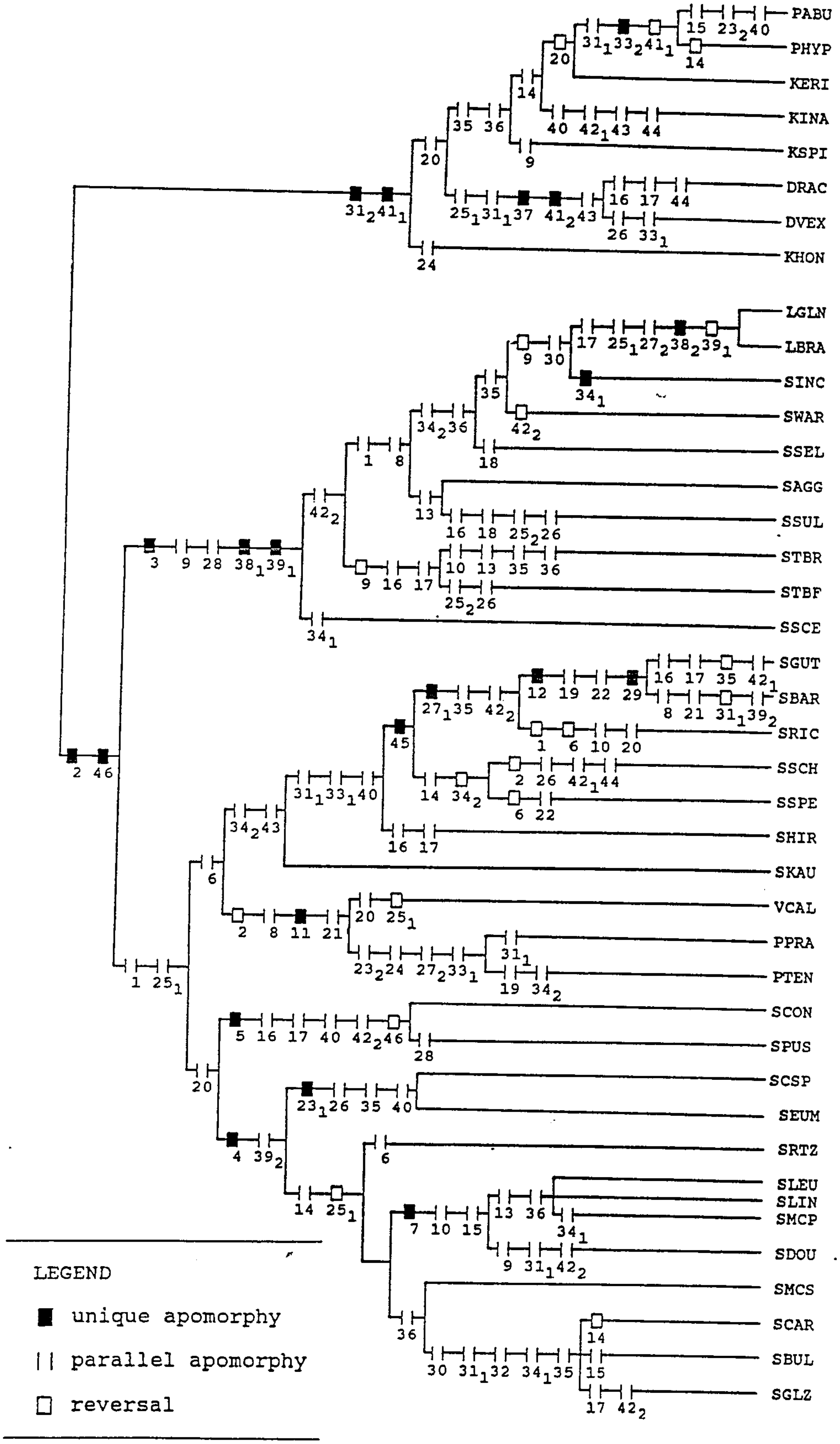

DVEX
DRAC
KHON
KSPI
KINA
KERI
PHYP
PABU
SPUS
SLIN
SLEU
SMCP
SDOU
SBUL
SCAR
SGLZ
SMCS
SRTZ
SCSP
SEUM
SGUT
SBAR
SRIC
SSCH
SSPE
SHIR
SKAU
VCAL
PPRA
PTEN
STBR
STBF
SSCE
SAGG
SSUL
SSEL
SWAR
SINC
LBRA
LGLN
LEGEND
■ unique apomorphy
|| parallel apomorphy
□ reversal

Figure 19. One of thirty equally parsimonious trees produced using mhennig*;bb* (length 155, consistency index .36). Acronyms as in Table 11.


PABU
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SBUL
SGLZ
LEGEND
■ unique apomorphy
| | parallel apomorphy
□ reversal

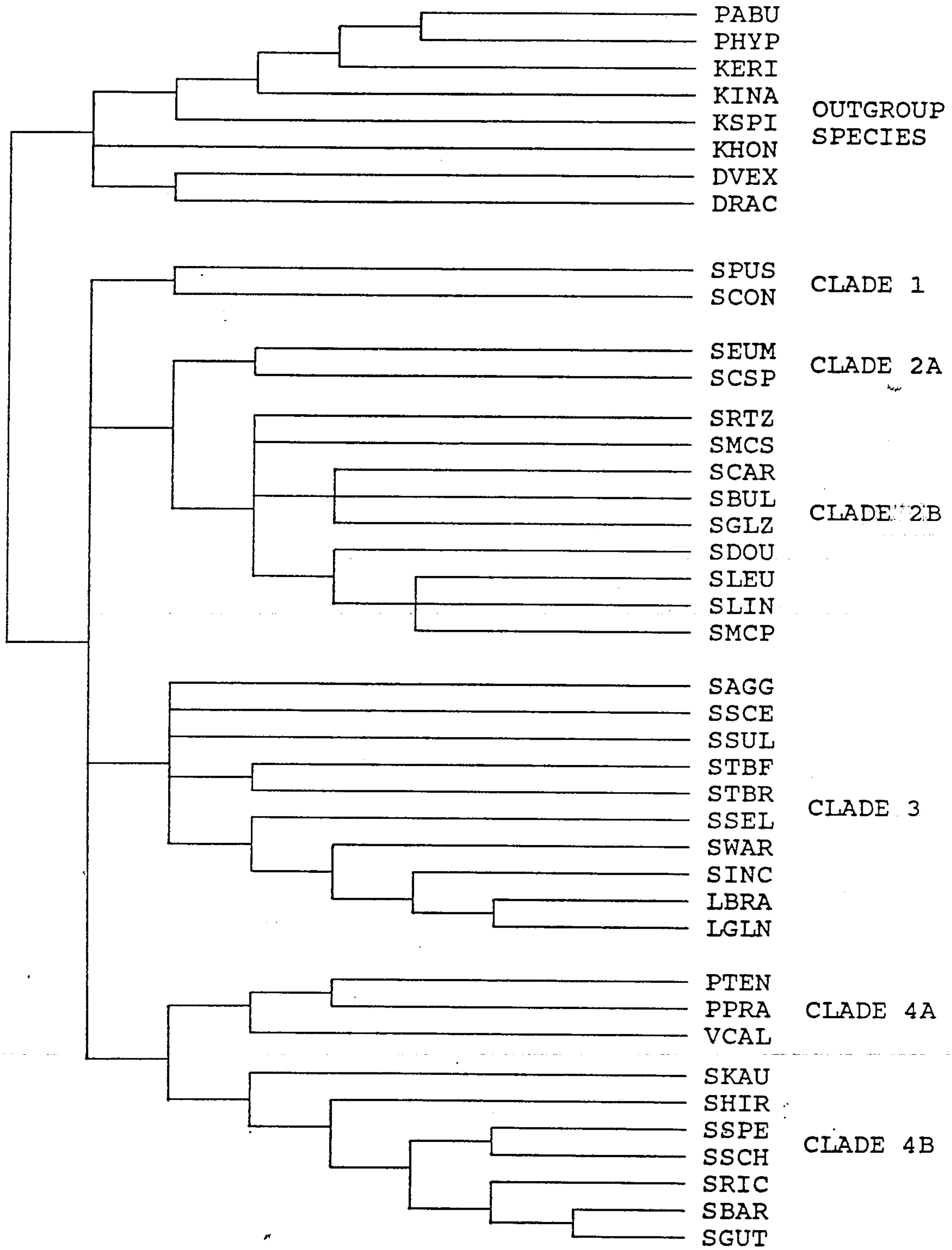

Figure 20. Strict consensus tree of 30 equally parsimonious trees from mhennig*;bb*. Acronyms as in table 11. See text for discussion of clades.

can each be further broken into two distinct subclades (see below). The strict consensus tree from all 30 cladograms is presented in Figure 20, with each of the four clades identified by number (see below). Relationships among these four clades cannot be resolved with certainty at this time.

Results using individual genera as outgroups

Using mhennig*;bb with individual genera as outgroups identified the same four major clades, and branching patterns within these clades were not substantially different than when all outgroup genera were included. Regardless of the outgroup used, no trees were produced which were not also produced when all outgroups were used together. In each case, the consensus tree exhibited a high degree of resolution, and each outgroup produced trees which were variations on only one of the two major topologies identified using all outgroups together. Using *Kohleria* (four species) as the outgroup produced 20 trees with length 138 and consistency index of .38. Using *Parakohleria* + *Pearcea* (two species) found 10 trees of length 133 and consistency index of .39. These outgroups only produced trees with the clade *Corytholoma* + *Cryptocaula* + *Lietzia* as the sister group to the rest of the ingroup (as in figure 19). Using *Diastema* (two species) produced 20 trees of length 134 and consistency index of .39, with the clade *S. concinna* + *S. pusilla* as the sister group to the rest of the ingroup (as in Figure 18). The trees thus produced will not be discussed further.

Results of successive weighting

Successive weighting produced a consensus tree with a higher degree of resolution than with fixed weighting, but did not find any trees which were not also found by the above methods. The trees produced by successive weighting were approximately twice the length of the trees produced by other methods. In all trees produced by successive weighting, the clade *S. pusilla* + *S. concinna* was the sister group to the rest of the ingroup, and the relationships among the four clades were the same as those indicated in figure 18. Successive weighting will not be discussed further.

Tree diagnosis

All trees indicate that *Sinningia*, as currently circumscribed, is paraphyletic if *Lietzia*, *Paliavana*, and *Vanhouttea* are excluded from it. Cladistic analysis grouped the two species of *Lietzia* with members of *Sinningia* section *Corytholoma*, whereas *Paliavana* and *Vanhouttea* were nested within *Sinningia* as the sister-group of subgenus *Sinningia*. Subgenus *Sinningia* is a monophyletic group only if *S. pusilla* and *S. concinna* are excluded from it. Subgenus *Rechsteineria* was found to be either paraphyletic or polyphyletic in all trees.

Clade 1. *S. pusilla* + *S. concinna*

There is no name available for this group. The two species have historically been associated with section *Stenogastra*, but are not associated with the type species of that section, *S. hirsuta*, or with other members of subgenus *Sinningia* in any cladogram. The group is defined by the following apomorphies in all trees: characters 5 (plant size highly reduced), 16 (prophylls absent), 17 (flowers solitary), 40 (nectary glands white), and 42 (ovary nearly superior). However, there are no conclusive synapomorphies linking this clade with any other. This clade occupies one of two positions in the trees: as the sister-group to the rest of the genus (as in Figure 18), or as the sister-group to section *Thamnocaula* (as in Figure 19).

Clade 2. Section *Thamnocaula*

This clade is well-defined but relationships among its species are partially unresolved, resulting in much of the variation between equally parsimonious trees. However, all trees indicate a division into two subclades. The first subclade (clade 2A in figure 20) consists of *S. conspicua* and *S. eumorpha*, and is supported by characters 23 (calyx lobes reflexed), 26 (corolla exterior lacking anthocyanin), 35 (stamen filaments with capitate trichomes), and 40 (nectary glands white). Clade 2B consists of all other members of the section. It is supported by characters 14 (inflorescence pedunculate) and 25 (corolla anthocyanin red). The entire clade is supported by characters 4 (seedling hypocotyl pigmented) and 39 (ventral nectary glands absent).

Clade 3. Section *Corytholoma*

This clade consists of species of *Lietzia* and *Sinningia* sections *Corytholoma* and *Cryptocaula*. It is defined by the following apomorphies in all trees: characters 3 (tuber eyes in dense clusters), 28 (flower with dorsal nectar reservoir), 38 (dorsal nectary glands fused), and 39 (ventral nectary glands reduced). The clade occupies one of two positions: as sister-group to the rest of *Sinningia* (Figure 19) or as sister-group to the clade *Paliavana* + *Vanhouttea* + *Sinningia* subgenus *Sinningia* (Figure 18). The two species of *Lietzia* occupy a position within section *Corytholoma* as sister-group to *S. incarnata*.

Clade 4. *Sinningia* subg. *Sinningia* + *Paliavana* + *Vanhouttea*

This clade consists of two distinct subclades, which are held together only by character 6 (suffruticose habit), a character that is homoplasious due to both parallelism and reversal. However, the association of these two subclades and the arrangement of species within them are uniform in all trees regardless of which outgroup or options of Hennig86 were used. Clade 4A consists of species of *Paliavana* and *Vanhouttea*. Species of these two genera form a clade that is supported by several characters: 2 (tuber absent), 8 (branches present), 11 (abscission line at base of petiole), and 21 (calyx lobes valvate in bud). The association of species of *Paliavana*, in turn, is supported by several apomorphies. Clade 4B consists of all species of *Sinningia* subgenus *Sinningia* except *S. pusilla* and *S. concinna* (see above). It is supported by characters 34 (stamen filaments mottled) and 43 (capsule fleshy upon dehiscence). Only the former is subject to reversal. Although its mature capsules were not available for examination, the problematic species *S. richii* occupies the same position within this group whether scored with a fleshy or dry capsule. Several other synapomorphies support the branching pattern within this subclade, for example 46 (seed coat with warty protuberances) and 27 (corolla marked at base).

Experimental hybridization

Of the approximately 80 distinct crosses attempted, 13 resulted in hybrid progeny. Many of the hybrid progeny which were produced were weak, poorly-growing plants which did not flower. Plants from only two crosses flowered (see below). Some hybrid progeny which were produced toward the end of this study may not have flowered due to insufficient growing time. Results of the hybridization attempts are summarized in Tables 17 and 18. The results fell into six categories:

1. Pollination resulted in high seed set, high seed viability, and vigorous plants which flowered.
2. Pollination resulted in high seed set, high seed viability, and weak plants which did not flower.
3. Pollination resulted in low seed set, low seed viability, and vigorous plants which flowered.
4. Pollination resulted in low seed set, low seed viability, and weak seedlings which died soon after germination.
5. Pollination resulted in ovary and ovule expansion, but seeds did not germinate.
6. Pollination resulted in no fruit or ovule development. No germination.

Table 18. Successful hybridizations. An asterisk (*) indicates the hybrid was produced late in the study and was not allowed sufficient time for evaluation.

SEED PARENT	POLLEN PARENT	RESULT (see text)
S. aggregata	*S. sulcata*	*
S. guttata	*S. warmingii*	4
S. pusilla	*S. conspicua*	*
S. warmingii	*S. eumorpha*	3
S. schiffneri	*Paliavana* hybrid	4
S. aggregata	*L. glandulosa*	1
L. glandulosa	*S. aggregata*	1
L. glandulosa	*S. barbata*	2
L. glandulosa	*S. eumorpha*	2
L. glandulosa	*S. richii*	2
L. glandulosa	*S. sulcata*	*
L. glandulosa	*S. tubiflora*	2
L. glandulosa	*S. warmingii*	2

Interspecific hybrids in *Sinningia*

Three seedlings were produced from the cross *S. guttata* x *S. warmingii*. The seedlings grew slowly and died while still small. Crosses between *S. guttata* and other species often produced seeds but which failed to germinate. This species is unusual in that it produces little pollen and is not known to have produced seeds by self-pollination in cultivation, despite numerous attempts. Other species of *Sinningia* self-pollinate readily.

A single seedling was produced from the cross *S. warmingii* x *S. eumorpha*. The resulting plant was approximately intermediate between the parents. The reciprocal cross did not result in hybrid progeny, although seeds were produced. This cross was attempted unsuccessfully by Clayberg (1968). All known hybrids between species of *Sinningia*, including those from the present study, are listed in Appendix 2.

Intergeneric hybridization

Several hybrids were produced between *Lietzia glandulosa* and species of *Sinningia*, but only the cross *S. aggregata* x *L. glandulosa* and its reciprocal flowered. The reciprocal hybrids were identical, and were approximately intermediate between the parents. Hybrids between *Lietzia glandulosa* and other species of *Sinningia* did not flower. Other hybrids between *Sinningia* and *Lietzia* have been reported (Boggan 1990; Wiehler 1988; Wojcik 1989; Zaitlin 1989, 1990).

Table 19. Unsuccessful hybridization attempts.

SEED PARENT	POLLEN PARENT	RESULT (see text)
SINNINGIA x SINNINGIA		
S. aggregata	*S. barbata*	5
S. aggregata	*S. eumorpha*	5
S. aggregata	*S. guttata*	6
S. aggregata	*S. leucotricha*	5
S. aggregata	*S. schiffneri*	6
S. aggregata	*S. speciosa*	5
S. barbata	*S. incarnata*	6
S. concinna	*S. barbata*	6
S. concinna	*S. guttata*	6
S. concinna	*S. speciosa*	5
S. eumorpha	*S. aggregata*	5
S. eumorpha	*S. barbata*	6
S. eumorpha	*S. schiffneri*	6
S. eumorpha	*S. speciosa*	5
S. eumorpha	*S. sulcata*	5
S. eumorpha	*S. warmingii*	5
S. guttata	*S. aggregata*	5
S. guttata	*S. barbata*	5
S. guttata	*S. eumorpha*	5
S. guttata	*S. leucotricha*	6
S. guttata	*S. schiffneri*	6
S. guttata	*S. speciosa*	5
S. hirsuta	*S. aggregata*	6
S. hirsuta	*S. barbata*	6
S. hirsuta	*S. eumorpha*	5
S. hirsuta	*S. schiffneri*	5
S. hirsuta	*S. speciosa*	5
S. pusilla	*S. barbata*	6
S. pusilla	*S. douglasii*	6
S. schiffneri	*S. aggregata*	6
S. schiffneri	*S. barbata*	6
S. schiffneri	*S. guttata*	6
S. schiffneri	*S. speciosa*	5
S. schiffneri	*S. warmingii*	6
S. warmingii	*S. barbata*	5
S. warmingii	*S. guttata*	6
S. warmingii	*S. schiffneri*	6

Table 19 (continued)

SEED PARENT	POLLEN PARENT	RESULT
SINNINGIA x LIETZIA		
L. glandulosa	*S. eumorpha*	5
L. glandulosa	*S. schiffneri*	6
L. glandulosa	*S. speciosa*	5
S. barbata	*L. glandulosa*	5
S. eumorpha	*L. glandulosa*	5
S. guttata	*L. glandulosa*	5
S. schiffneri	*L. glandulosa*	6
S. speciosa	*L. glandulosa*	6
SINNINGIA x PALIAVANA		
S. aggregata	*P. tenuiflora*	5
S. barbata	*P. tenuiflora*	5
S. pusilla	*P. tenuiflora*	6
S. schiffneri	*P. tenuiflora*	5
S. speciosa	*P. tenuiflora*	5
SINNINGIA x VANHOUTTEA		
S. bulbosa	*V. calcarata*	6
S. barbata	*V. calcarata*	6
S. pusilla	*V. calcarata*	6
SINNINGIA x KOHLERIA		
K. eriantha	*S. aggregata*	6
K. eriantha	*S. eumorpha*	5
K. eriantha	*S. warmingii*	6
K. 'Laura'	*S. schiffneri*	5
K. 'Longwood'	*S. barbata*	5
K. 'Longwood'	*S. eumorpha*	5
S. eumorpha	*K. eriantha*	5
S. glazioviana	*K. eriantha*	6
S. guttata	*K. eriantha*	6
S. warmingii	*K. inaequalis*	5
S. warmingii	*K. eriantha*	6
LIETZIA x KOHLERIA		
K. 'Longwood'	*L. glandulosa*	5
L. glandulosa	*K. inaequalis*	5
LIEZIA x PALIAVANA		
L. glandulosa	*P. tenuiflora*	5
LIETZIA x VANHOUTTEA		
L. glandulosa	*V. calcarata*	5
VANHOUTTEA x PALIAVANA		
V. calcarata	*P. tenuiflora*	5

A single seedling, which died soon after germination, was produced from the cross *Sinningia schiffneri* x *Paliavana* hybrid (*P. prasinata* x *P. tenuiflora*, obtained as *P. tenuiflora* from Longwood Gardens). No other intergeneric hybrids were produced, although several crosses resulted in capsule development and seed production. Unsuccessful hybridization attempts are summarized in Table 18.

CHAPTER V. DISCUSSION.

Variation in quantitative characters

Although quantitative characters were excluded from the cladistic analyses, they may prove to be informative when their variation is mapped against the trees produced by cladistic analysis. In many cases, these characters could be scored qualitatively at lower levels of cladistic analysis, or within a single taxonomic group, and only proved to be quantitative as more species were added. This would doubtless prove true for several characters which were retained as well, such as calyx lobe connation, ovary position, and seed size, if additional species were examined. In other cases one state of a character could be clearly defined while the alternative "state" was a continuous range of variation. These characters probably vary quantitatively in the tribe as a whole, yet could be scored qualitatively in the species included in the analyses. In general these characters proved to have very low consistency indices.

Clear trends can be seen within taxonomic groups for several quantitative characters. In many cases these trends concur with the phylogeny indicated by the cladograms.

VEGETATIVE CHARACTERS

The relationship between plant height, petiole length, and leaf dimensions (length:width) is complex and is outside the scope of this study. However, some generalizations can be made. There appears to be a negative correlation between plant height and petiole length. Petiole length (relative to leaf blade length) varies in the tribe from very long to effectively absent. While both extremes appear to be derived within the ingroup, and to a certain extent correspond to taxonomic divisions, exceptions occur and all intermediates can be found. Species with medium to long petioles are found in *Sinningia* section *Thamnocaula* and sections of subgenus *Sinningia*. Species with medium to short petioles are found in section *Corytholoma*. Species with long petioles are usually low-growing, more or less rosulate plants with broad, rounded leaves. In some cases, the petiole is nearly equal to the blade in length. Rosulate, long-petioled growth habit is not typical of any of the outgroup species examined, and is almost certainly derived within *Sinningia*. However, this growth habit results from the interaction of several characters and its appearance in several of the clades may indicate convergence. In cultivation, at least, these species usually grow better at low light levels than do taller species with short petioles and narrow leaves. Because of their more compact growth habit and lower light requirements, such species are more common in cultivation and are more popular among houseplant growers. Species with sessile leaves are most commonly found in section *Corytholoma*, but in this section every intermediate from medium-length to effectively absent petioles can be found.

Another quantitative leaf character which seems to follow taxonomic divisions is leaf base shape. Leaves of all examined species of *Paliavana* and *Vanhouttea* have cuneate bases, while those of *Sinningia* and *Lietzia* species usually have obtuse to cordate bases. *Sinningia* species with cuneate leaf bases are found almost exclusively in subgenus *Sinningia*, although the leaf base can vary from cordate to cuneate on a single plant in several species, e.g., *S. guttata*, *S. speciosa* and *S. schiffneri*. Two other species with cuneate leaf bases which are not in cultivation are *S. gracilis* (Martius) Bentham ex Fritsch and *S. gesneriifolia* (Hanstein) Clayberg. This may support a relationship between *Paliavana*, *Vanhouttea*, and *Sinningia* subgenus *Sinningia*, as suggested by the cladistic analyses. Cuneate leaf bases are more common in the outgroups (e.g., *Parakohleria*, *Kohleria*), but this character cannot be polarized with certainty. To some extent leaf base shape is correlated with petiole length, as species with elongate petioles almost invariably have cordate leaf bases. The leaf bases of the first few pairs of true leaves of seedlings have cuneate bases in all species examined.

Presence of sticky glandular hairs on the leaves was originally scored as a qualitative character, but it now appears that most Gesneriaceae, if not all, have such hairs, although in varying amounts. All Gesneriaceae have capitate trichomes, but it is not clear if they are always glandular. The texture of the secretion ranges from sticky (*Sinningia aggregata*, *Lietzia glandulosa*) to greasy (*S. tuberosa*). In most cases, plants with sticky leaves are also aromatic. The scent varies between species, although whether it is pleasant or not is quite subjective. The chemical compounds responsible are unknown.

INFLORESCENCE CHARACTERS

The architecture of the axillary cyme, as a function of hypopodium length, degree of branching, and flower number, is quite variable in Gloxinieae. A complete series can be observed from a pedunculate, many-flowered compound cyme to an epedunculate solitary flower in several groups. Such a series can be observed in *Sinningia*, particularly in section *Thamnocaula*. Although pedunculate inflorescences generally have been regarded as plesiomorphic (Skog 1976; Weber 1978, 1982; Wiehler 1983), the most parsimonious trees produced by cladistic analysis in this study were those in which epedunculate inflorescences were plesiomorphic.

Although the hypopodium can be scored qualitatively (present or absent) in section *Thamnocaula*, its length varies quantitatively from long (10+ cm) to short (.5 cm), and some members of this section have epedunculate inflorescences. Species with pedunculate inflorescences are rare in other sections of *Sinningia*, and the hypopodium is then invariably highly reduced. Such species may produce both pedunculate and epedunculate inflorescences on the same plant (e.g., *S. speciosa*).

Although flower number (one vs. two or more) can be scored unambiguously as a qualitative character, flower number might be better treated as continuous. The consistency index of this character is the lowest of any in the analysis (.14), and the cladograms indicate that reduction of the inflorescence to a solitary flower has happened independently at least six times. In most cases species with solitary axillary flowers (e.g., *Sinningia glazioviana*, *S. guttata*) have near relatives, as indicated by the cladograms, with several flowers per axil. In the case of the species of *Lietzia*, their nearest relative in *Sinningia*, *S. incarnata*, rarely has more than two flowers per axil, often only one. Species of *Lietzia* are unusual in that they have solitary axillary flowers with prophylls and often have a small abortive flower bud accompanying the flower, whereas most species with solitary flowers lack these structures.

Prophyll presence vs. absence is another qualitative character whose observed states may be extremes of a continuous range. While presence or absence is absolute among the species examined, among the species with prophylls the size of the prophylls ranges from large and leafy (particularly in species of *Paliavana* and *Sinningia* subgenus *Sinningia*) to barely evident. Species of section *Thamnocaula* are characterized by possessing small, scalelike prophylls, whereas prophyll size varies widely in section *Corytholoma*.

In almost all species of Gloxinieae, shoot morphology changes once flowering commences, with the florescence terminating the shoot. Some species examined, for example *Paliavana tenuiflora*, *Sinningia schiffneri*, *S. reitzii*, and *Kohleria eriantha*, have a more "generalized" mode of growth, with no substantial differences between flowering and non-flowering parts of the plant, but this could not be defined clearly as a distinct alternative state. The florescence, resulting from all the axillary inflorescences considered together as a unit, varies from a panicle-like organization to a true raceme, with all intermediates often occurring within a group. Species of section *Corytholoma*, in particular, have a distinctive florescence organization approaching a true raceme, with an elongate rachis on which the leaves are reduced to bracts. In *Sinningia tubiflora*, the florescence can be considered a true raceme.

FLORAL CHARACTERS

Although calyx lobe size (relative to flower size) varies widely in *Sinningia*, expansion of the lobes is so extreme in *Sinningia barbata* and members of section *Sinningia* that this character was scored qualitatively. In section *Thamnocaula* the lobes are usually very small, whereas members of subgenus *Sinningia* often have larger calyx lobes than the outgroup species. Both extremes are probably derived. Species of *Paliavana* also have large calyx lobes relative to the outgroup species, a fact which supports their relationship to subgenus *Sinningia*.

Although calyx fusion has been scored as a qualitative character, *degree* of fusion is quantitative. The relationship of the two species of *Lietzia* to *Sinningia incarnata* in section *Corytholoma* is supported by the extreme extent of fusion in these three species, whereas other members of the section exhibit lesser degrees of fusion. Members of section *Sinningia*, here represented only by *S. guttata*, also exhibit an extreme fusion of the calyx lobes.

A remarkable bimodality in corolla size, which appears to vary independently of overall plant size, occurs among species of subgenus *Sinningia* (see Figure 7). *Sinningia schiffneri*, *S. hirsuta*, and *S. kautskyi* have unusually small flowers which are less than half the size of those of the other members of the subgenus. Although this and other characters suggest a relationship among these three species, such a grouping would be paraphyletic if the phylogeny suggested by the cladograms is the true one. This character was excluded from analysis because it varies quantitatively in the genus as a whole.

Nectar guide pattern is an example of a character in which one state could be clearly defined, but an alternate state could not. While the nectar guide of the galeate members of section *Thamnocaula* is distinctive in the genus, other species exhibit a wide range in the size, organization, and distribution of nectar guide patterns in the flowers.

Pollen color ranges from white to orange-yellow among the species studied. Species with flowers typical of insect pollination invariably have white pollen, while that of flowers typical of hummingbird pollination is rarely white, and ranges from pale yellow to nearly orange. The darkest pollen was observed in the galeate species of section *Thamnocaula*.

Stigma shape (apart from the clearly autapomorphic states of *Diastema* and *Kohleria*) was excluded due to its being a quantitative character, but different stigma shapes appear to be associated with particular pollination syndromes (see chapter 3).

SEED CHARACTERS

Seeds of many species of *Sinningia* possess apical appendages. An entire range can be observed from appendages absent to appendages present and elongate, sometimes more than doubling the length of the seed (see Figures 16 and 17). Elongate appendages are most common in species of section *Thamnocaula* (e.g., *S. douglasii*, *S. cooperi*, *S. glazioviana*, see Figure 17), although species of other groups occasionally have elongate appendages as well (e.g., *S. tubiflora*, *S. sceptrum*, *Capanea grandiflora*). Species with fleshy capsules always have seeds which lack appendages. In addition, these species always have more or less round seeds, whereas species with dry capsules have seeds ranging in shape from round to elongate.

Notes on some character polarities

The presence of rhizomes in some species of *Sinningia*, and the nearly universally rhizomatous habit among *Sinningia*'s relatives, would seem to indicate that rhizomatous habit is plesiomorphic in *Sinningia*. In the trees with section *Corytholoma* basal, this is indeed the case, with rhizomatous habit being lost independently within *Corytholoma* and other sections of *Sinningia*. In the trees with *S. pusilla* + *S. concinna* basal, however, while rhizomatous habit is still plesiomorphic in the sense that all outgroup species are rhizomatous, the presence of rhizomes in some members of the ingroup represents a reversal from an ancestral *Sinningia* without rhizomes. In either case, the rhizomatous habit of *S. richii* represents a reversal from a nonrhizomatous ancestor.

Tuberous habit has retained its importance as a defining character of *Sinningia*. In fact, it is the only synapomorphy for *Sinningia* to appear in all trees. Even so, tuberous habit has been lost at least twice: in *S. schiffneri* and in the clade *Paliavana* + *Vanhouttea*. The rather surprising placement of these nontuberous genera relative to *Sinningia* is supported by few characters, but one species of *Sinningia* which is not currently in cultivation, *S. gesneriifolia*, is not definitely known to be tuberous and this and another species, *S. gracilis*, appear to be intermediate between *Paliavana* and *Sinningia*. The observation that cuttings of *Paliavana* develop copious callus tissue while rooting, much like the tuber initiation of *Sinningia* cuttings, supports the derivation of *Paliavana* from a tuberous ancestor. Cuttings of outgroup species (e.g., *Kohleria*) barely form callus tissue when rooting.

Calyx lobes connate vs. free is of questionable value as a supporting character at higher levels both because its consistency index is low and its polarity varies from tree to tree. In addition, this character probably varies quantitatively in the tribe as a whole (see above). However, connation is usually constant within clades. If fusion of calyx lobes is derived, then clades 3 (*Sinningia* sections *Corytholoma* and *Cryptocaula* + *Lietzia*) and 4 (*Sinningia* subgenus *Sinningia* + *Paliavana* + *Vanhouttea*) are supported as a unit within the trees. If free calyx lobes are derived, however, then clades 1 (*S. pusilla* + *S. concinna*) and 2 (section *Thamnocaula*) are supported as a unit within the trees.

It is likewise impossible to polarize anthocyanin color, another character which varies in polarity between the trees. However, in all trees the red-flowered members of section *Thamnocaula* (clade 2B) are derived from ancestors with violet anthocyanin within *Sinningia*, regardless of the polarity of this character. If red anthocyanin (always associated with hummingbird pollination) is primitive, then members of section *Corytholoma* (clade 3) are primitively hummingbird-pollinated, whereas the red-flowered species of *Vanhouttea* and *Thamnocaula* are secondarily hummingbird-pollinated within a primitively insect-pollinated group. If violet anthocyanin (typically associated with insect, occasionally bat, pollination) is primitive, then hummingbird pollination has arisen independently three times, in section *Thamnocaula*, section *Corytholoma*, and *Vanhouttea*. Whatever the polarity of anthocyanin color, the division of *Sinningia* into two subgenera, one with red flowers and the other with violet flowers, cannot be justified.

There can be little doubt that bat pollination represents a derived syndrome in the tribe, but it cannot be considered a single character any more than insect pollination or hummingbird pollination can. Species that are presumably bat pollinated, which are found in *Capanea*, *Lietzia*, *Paliavana*, and possibly *Kohleria*, are similar in that they have green, somewhat campanulate flowers, but are otherwise quite different in morphology. It is interesting to note that *Paliavana tenuiflora*, which has large, violet, presumably insect-pollinated flowers, shares several typical bat flower characters with *P. prasinata*, such as fleshy texture and external speckling.

Seed size was one of the characters initially used to separate the ingroup from the outgroup. Although this has remained a good character, its distribution and consistency index vary among the trees. The dwarf species (clade 1) alone among the ingroup have seeds as small as those of the outgroup species. Depending on the position of this clade relative to other members of the ingroup, the seeds may be either primitively small or a reversion to small seed size. Given the extremely reduced size of the entire plant in these two species, the latter possibility cannot be ruled out. In general, however, seed size (exclusive of appendages) is remarkably constant in the ingroup given the wide range in plant size from small herbs to large shrubs.

For some characters, the polarities established by the cladistic analyses were not those expected. For example, pedunculate inflorescences (character 14) have been considered primitive relative to epedunculate inflorescences by most authors (see above), but in the most parsimonious trees epedunculate inflorescences are plesiomorphic. Other characters which were polarized unexpectedly are the two types of stamen filament trichomes (characters 35 and 36). Although filaments with both types of trichome predominate in the outgroups, glabrous filaments were plesiomorphic in the most parsimonious trees. Running the cladistic analysis with a hypothetical outgroup which substituted subjective polarity assignments for the above three characters and accepted the polarities assigned by Hennig86 for all others did not yield substantially different trees, however. The trees found by this method were longer by only one step (156), and the strict consensus tree was identical to the one represented in figure 20 except with less resolution among the outgroups.

Notes on fruit characters

One of the more significant results of this study was the recognition that a subgroup of *Sinningia* can be clearly defined by fruit and seed characters. Although fleshy capsules are found in several genera, the fleshy capsule found in *Sinningia* is quite different and is likely to be independently derived.

Three basic fruit types were observed among species of Gloxinieae, and all three are found in *Sinningia*. By far the most common fruit type is the dry bivalved capsule which is very uniform in appearance among the genera in which it is found (see Figure 15 A-M). The fruit is slightly elongate, rostrate, and held horizontally or slightly erect. The strongly lignified valves dry upon dehiscence, splitting loculicidally on the dorsal and ventral sides of the capsule down to the hypanthium. The capsule functions somewhat like a salt shaker, the seeds sifting through a mesh of stiff trichomes between the valves.

The second kind of fruit apparently functions as a splash cup. The fruit is a poorly lignified capsule, is held erect, and has spreading calyx lobes forming a cup (Figure 15 N) It remains green and fleshy for several days or weeks after dehiscence. The valves dehisce like those of the dry capsule, but lack trichomes on the edges. In Gloxinieae, this type of fruit was observed only in species of *Sinningia*.

The third kind of fruit is quite different, but apparently also functions as a splash cup. The fruit is a fleshy capsule, usually poorly lignified, which is held horizontally and dehisces loculicidally along the dorsal side only, with the valves spreading broadly and tearing the hypanthium to the base as they do so (Figure 15 O) The fruit remains fleshy and green for several days after dehiscence. The valves lack trichomes. This type of fruit is usually associated with almost fully inferior ovaries. It has been noted previously in species of *Diastema* (Wiehler 1983), *Kohleria* (Wiehler 1983; Kvist 1987), *Monopyle* (Wiehler 1983), and *Heppiella* (Kvist 1990). In the course of the present study such capsules were observed on *Kohleria inaequalis*, *Diastema racemiferum*, *Gloxinia lindeniana*, and *Sinningia schiffneri*.

Lembocarpus

MORPHOLOGY

Although similar in their tuberous habit, *Lembocarpus* and *Sinningia* differ in many respects. The only character which appears to support a relationship between them is the tuber. However, tuberous habit is not restricted to *Sinningia* or even to tribe Gloxinieae; species of several genera of Episcieae are known to be tuberous: *Nautilocalyx*, *Chrysothemis*, and *Rhoogeton*. Comparison of the tuber of *Lembocarpus amoenus* to that of several *Sinningia* species indicated that the two are developmentally and morphologically different. In all known species of *Sinningia*, the tuber is a permanent structure which persists from year to year, gradually increasing in size. However, cultivation of *L. amoenus* through three growth cycles revealed that its tuber is not persistent. One or more new tubers form each year, each developing at the base of a leaf emerging from the old tuber (Figure 21A) The previous year's tuber then shrivels and dies. In addition, the surface of the tuber of *L. amoenus* is densely covered with trichomes, while the epidermis of the tuber of *Sinningia* invariably lacks trichomes. Study of the internal anatomy of the tuber of *L. amoenus* was inconclusive, revealing only that both genera store carbohydrate in the form of starch.

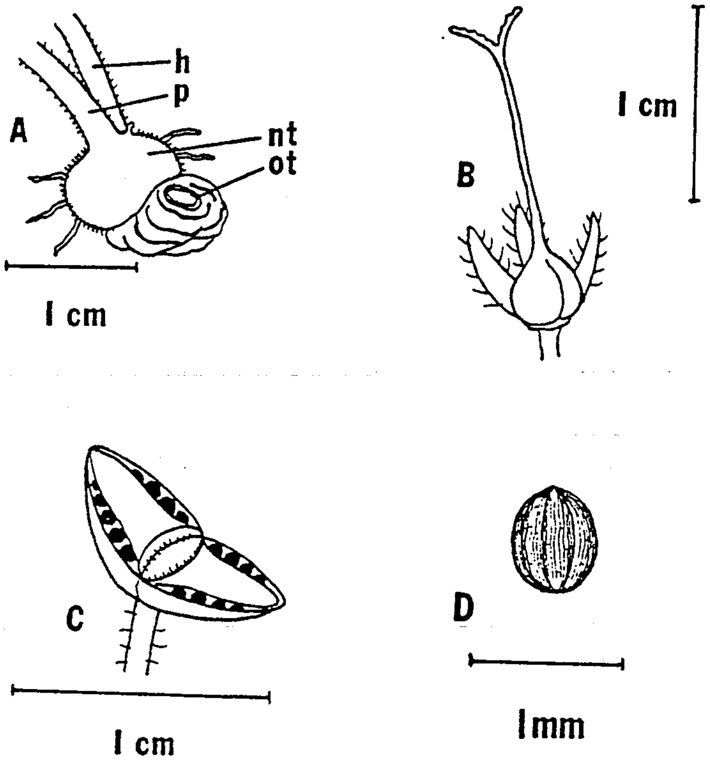

Figure 21. Morphology of *Lembocarpus amoenus*. A, base of plant, with new tuber (nt) forming on top of old tuber (ot), with leaf petiole (p) and inflorescence hypopodium (h) emerging from the tuber; B, ovary, style, and stigma (two calyx lobes removed to show ovary); C, mature capsule with seeds; D, seed.

Examination of young shoots emerging from tubers of *Lembocarpus amoenus* revealed its apparently unifoliate habit to be the result of extreme anisophylly. The single large leaf is derived from a pair of opposite leaves of which only one continues to develop. The pedunculate inflorescence emerges from the axil of this leaf (Figure 15A). In rare cases where more than one pair of leaves develops, the phyllotaxy of the later pairs is decussate. Seedlings exhibit a decussate arrangement, but anisophylly is established as early as the first pair of true leaves. A unifoliate *Sinningia* species, *S. tuberosa*, has seedlings with equal leaf pairs (although in this species the apparently unifoliate habit is derived from extreme anisophylly as well). In addition, *S. tuberosa* produces its leaves and inflorescences from separate eyes on the tuber, whereas *L. amoenus* produces both leaves and inflorescences from the same growing point.

Lembocarpus differs from *Sinningia* in several floral characters as well. Examination of the ovary of *L. amoenus* showed it to be completely superior (Figure 21B). No other species of Gloxinieae has a truly superior ovary. In all other species of Gloxinieae, at least a portion of the ovary is embedded in the hypanthium, even in species with apparently superior ovaries (e.g., *Sinningia pusilla*, *S. concinna*, and most members of section *Corytholoma*; see Figure 14). In addition, the flower of *L. amoenus* proved to lack a nectary, although it has been reported as possessing a nonfunctional nectary in the form of an annular disc (Leeuwenberg 1958; Wiehler 1983). Although some species of Gloxinieae lack a nectary (e.g., species of *Anodiscus*, *Bellonia, Monopyle*, and some species of *Gloxinia*), a nectary consisting of two or more separate glands is present in all known species of *Sinningia*. The stigma of *L. amoenus* is deeply divided into two lateral lobes (Figure 21B) unlike that of any *Sinningia* species (although bilobed stigmas are found in some other genera of Gloxinieae).

Finally, the fruit of *Lembocarpus* is unlike that of any member of Gloxinieae examined (Figure 21C). Upon dehiscence, the valves spread broadly, apparently pushed apart by the expansion of a cushion of tissue at the base between them. It was noted that when moved to an area of lower humidity, the valves began to close again. The capsule remains green and fleshy for several days after dehiscence. As noted with other species with fleshy capsules, the seeds are nearly round and lack any appendages (Figure 21D). Beaufort-Murphy (1983) noted that the straight cell orientation of the seed surface is anomalous in Gloxinieae, although she placed it in that tribe while noting that the seed was in some respects similar to that of *Episcia* (tribe Episcieae). *Sinningia* and *Lembocarpus* are compared in Table 20.

Table 20. Comparison of *Sinningia,Lembocarpus*, and *Rhoogeton*

	Sinningia	*Lembocarpus*	*Rhoogeton*
Number of species	60+	1	3
Distribution	primarily S Brazil	Surinam, French Guiana	Guyana, E Venezuela
Tuber duration	persistent	annual	?
Trichomes on tuber	absent	present	?
Trichomes over anthers	capitate if present	not capitate	?
Nectary	separate glands	absent	one dorsal gland
Stigma	entire	bilobed	bilobed or entire
Ovule placement on placentae	both surfaces	outer	outer
Ovary position	partly to almost fully inferior	superior	superior
Ovary vestiture	dense, not capitate	sparse, capitate	sparse, varies
Capsule valves at dehiscence	not spreading	spreading	?
Seeds	not ribbed	ribbed	?
Seed coat cell arrangement	spiral	straight	?

TAXONOMIC PLACEMENT

Although placed in Gloxinieae near *Sinningia* by Wiehler (1983), it would appear that *Lembocarpus* is misplaced in that tribe. *Lembocarpus amoenus* shares no synapomorphies with *Sinningia*, and several characters make its placement in Gloxinieae questionable. Wiehler's justification for his placement of *Lembocarpus* is unclear. In fact, *Lembocarpus* is keyed separately from any tribe in Wiehler's key. Morphological evidence does not support its placement in the tribe. Tuberous habit is not unique to Gloxinieae, and the superior ovary, while plesiomorphic in the family as a whole, is otherwise unknown in the tribe. While not addressing the homology of the tuber, Wiehler justified inclusion of a species with superior ovaries in Gloxinieae by citing the nearly-superior ovaries of *S. pusilla* and *S. concinna*. This evidence would seem circumstantial at best. Wiehler's other criterion for assessing tribal affiliations and generic relationships was hybridization. His statement that *L. amoenus* "appears to produce hybrids with *Sinningia*" (1983, p. 173) notwithstanding, no hybrids between the two genera have actually been produced, despite numerous attempts (H. Wiehler, pers. comm.; M. Belisle, pers. comm.). Finally, the distribution of *L. amoenus* is distinct from that of other members of Gloxinieae.

Although its inflorescence structure (an axillary pair-flowered cyme) and ovary anatomy (unilocular with parietal placentation) clearly place it in the Gesneriaceae, *L. amoenus* appears to lack any synapomorphies which would definitively support its placement in any tribe of Gesnerioideae as defined by Wiehler. *Lembocarpus* exhibits a combination of characters not found in any tribe of the subfamily: tuberous habit, "decussate" leaves without aggregated stomata, inflorescence with prophylls, flower zygomorphic, ovary superior, nectary absent, and seeds round with straight seed coat cell arrangement. This may indicate that the genus is rather isolated in the subfamily, as suggested by Beaufort-Murphy (1983). While its unique combination of characters may merit the creation of a new tribe, it is more likely that *Lembocarpus* is an anomalous member of one of the already-existing tribes. The tribe with which it appears to share the most characters is Episcieae. The two apomorphies for Episcieae, as defined by Wiehler, are an unusual nodal vasculature and single large dorsal nectary gland. Interpretation of these two characters was inconclusive for *Lembocarpus*. Absence of a nectary could conceivably be derived from any nectary type, and attempts to study the nodal anatomy of *L. amoenus* were unsuccessful due to limited availability of material and the acaulescent habit of this species. The members of Episcieae are characterized by chromosome numbers of n=8 or n=9, which are unknown in any other tribe of the subfamily. Unfortunately, the chromosome number of *Lembocarpus* is still unknown. None of the known characters of *Lembocarpus* is inconsistent with its placement in Episcieae, however.

Perhaps the best clue to *Lembocarpus*' affinities comes from Leeuwenberg's (1958) comparison of *Lembocarpus* to *Rhoogeton*, another genus described by Leeuwenberg. *Rhoogeton* was placed in Episcieae by Wiehler (1983) on the basis of its nectary configuration. As pointed out by Leeuwenberg, the two genera are quite similar both vegetatively and in geographic distribution (Table 20). Both include small, stemless, tuberous species endemic to the Guyanas. The pedunculate inflorescences of the two are similar. *Lembocarpus amoenus* is particularly similar vegetatively to *Rhoogeton cyclophyllus*. In fact, the only substantial differences between the two genera are in floral shape and color, characters given very little significance by Wiehler, and nectary configuration. Wiehler recognized that these characters are highly variable, even within a single genus (e.g., *Gloxinia*, *Sinningia*). This author has no hesitation in assigning *Lembocarpus* to Episcieae next to *Rhoogeton*.

Taxonomic implications of the cladistic analyses

PLACEMENT OF LIETZIA

The results of the cladistic analyses strongly support the transfer of the species of *Lietzia* to *Sinningia*. The two species share several synapomorphies with *Sinningia* section *Corytholoma*. Although the species of *Lietzia* would form a very distinctive group in *Sinningia*, they cannot be circumscribed as a genus without making *Sinningia* paraphyletic. Besides tuberous habit, the species of *Lietzia* share with this section (or some unit thereof) a distinctive eye organization on the tuber, branching stems, a similar type of nectar reservoir, and a nearly superior ovary. They also share a similar distribution. In addition, hybrids between *Lietzia* and *Sinningia* section *Corytholoma* have produced second-generation hybrid progeny (D. Zaitlin, pers. comm.; A. Wojcik, pers. comm.; Boggan, unpublished). Fertility of hybrids is a criterion which has been accepted by several authors as evidence of close relationship, although ability to hybridize must be considered a symplesiomorphy.

The most distinctive characters of *Lietzia* which are not shared by *Sinningia* are the green, purple-spotted corolla, and the annular nectary. The corolla coloration must be considered an apomorphy of *Lietzia* (although it has been paralleled by some species of *Paliavana*). Although an annular nectary is the plesiomorphic condition of the family as a whole, the nectary of *Lietzia* appears to be secondarily, rather than primitively, annular. Although its nectary configuration was scored as a separate state, the position of *Lietzia* in the cladograms suggests that its annular nectary is derived from the gland configuration typical of section *Corytholoma* (two fused, three separate). It is not unusual to find varying degrees of connation in occasional flowers of several species with normally separate glands. The annular nectary of *Lietzia* is much thicker than that of other members of the tribe, and in young buds it is deeply lobed This may indicate it has been derived from separate glands.

RELATIONSHIPS OF PALIAVANA AND VANHOUTTEA

There can be little doubt that *Vanhouttea* and *Paliavana* form a monophyletic unit, as suggested by Wiehler (1983). Their fibrous-rooted habit without storage organs and their persistent suffruticose stems are unusual within the tribe. They are also unique in having leaves with a distinct dehiscence zone at the base of the petiole. Perhaps the most unusual character shared by the two genera is the valvate aestivation of the calyx lobes, a character noted by Fritsch (1893) in his key to the genera of tribe Kohlerieae. However, an unidentified and probably undescribed species of *Paliavana* with acuminate calyx lobes in the herbarium of the L. H. Bailey Hortorium (*Bailey 1083*) appears to lack this synapomorphy.

Although *Vanhouttea* and *Paliavana* form a clade within *Sinningia* in all cladograms, as sister group to subgenus *Sinningia*, their placement in that genus is supported by few characters, all of which are homoplasious due to parallelism and reversal. A character which was most parsimoniously scored as a parallelism but which may prove to support a relationship to subgenus *Sinningia* is the mottled pigmentation of the stamen filaments of *P. tenuiflora*.

The primary character inconsistent with a placement of *Paliavana* and *Vanhouttea* in *Sinningia* is the nontuberous habit of these genera. However, they are otherwise vegetatively similar to species of *Sinningia* subgenus *Sinningia*, some of which have suffruticose stems in addition to tubers. Two species of *Sinningia* which were not available for study, *S. gracilis* and *S. gesneriifolia*, appear to be intermediate between *Paliavana* and *Sinningia*. In addition, there is some question as to whether *Paliavana* is strictly nontuberous; the genus has been described as tuberous (Decaisne 1848), a fact noted but not confirmed by Fritsch (1893). Although the plants cultivated for the present study did not form tubers, cuttings of both *P. tenuiflora* and *P. prasinata* were observed to form callus tissue over the cut end while rooting, much as cuttings of *Sinningia* do when initiating tubers. In addition, there is a plant which has recently been introduced to cultivation as *Vanhouttea* "mauroi" which clearly produces tubers (D. Zaitlin, pers. comm.).

Even if *Paliavana* is united with *Sinningia*, its species are not closely related to the nontuberous species *S. schiffneri*, which was transferred to *Paliavana* by Handro (1962). Despite its vegetative similarity, the capsule and seed of *S. schiffneri* are quite different from those of the species of *Paliavana*, and exhibit several synapomorphies shared by subgenus *Sinningia* but not *Paliavana*.

INFRAGENERIC CLASSIFICATION OF SINNINGIA

Leaving *Lietzia*, *Paliavana*, and *Vanhouttea* aside for the moment, it is clear that the division of *Sinningia* into two subgenera is untenable. The smallest number of units which can be clearly defined within *Sinningia* is four, corresponding to the four clades identified by cladistic analysis. These clades could be considered subdivisions (subgenera or sections) of *Sinningia*, or alternatively could be considered four (or more) distinct genera. Within a strictly cladistic interpretation, there is no circumscription or division of *Sinningia* which would allow *Lietzia* to remain a separate genus, and *Paliavana* and *Vanhouttea* can be maintained as separate genera only if *Sinningia* is split into four or more genera.

Taxonomic options

There are three options regarding the classification of *Sinningia*, *Lietzia*, *Paliavana*, and *Vanhouttea*, and to a certain extent which of these options is chosen is dependent upon one's taxonomic philosophy. The first option is the "lumping option," which would combine the several genera into one. The second option is the "splitting option," which would maintain *Vanhouttea* and *Paliavana* as separate genera (or perhaps combine them into one) but would also split *Sinningia* into several genera. The third option is to maintain the status quo, maintaining *Vanhouttea* and *Paliavana* but also retaining *Sinningia* as a single genus. The pros and cons of each of these options are discussed below. However, it must be stressed that maintaining *Lietzia* as an independent genus cannot be justified under any of these options. The cladistic analyses have conclusively shown that the species of *Lietzia* must be placed in section *Corytholoma*, whether this group remains in *Sinningia* or is circumscribed as a separate genus.

Lumping

To maintain *Sinningia* as a single genus would necessitate the addition of the species of *Paliavana* and *Vanhouttea*, which were shown to occupy a clade within *Sinningia* as it is currently circumscribed. The older name *Paliavana* would then have priority over *Sinningia*. The sixty or more species of *Sinningia* would have to be transferred to *Paliavana*, which now consists of only four described species, unless the name *Sinningia* were conserved over *Paliavana*. Transferring all *Sinningia* species to *Paliavana* is distasteful because of the taxonomic and horticultural confusion this would entail. It is unlikely that the name *Paliavana* would be accepted over *Sinningia* in horticultural circles. Conservation of *Sinningia* over *Paliavana* would be ill-advised (and would most likely be rejected) as both names are well-established in the literature, and the two groups have been recognized as separate entities throughout the history of the family. *Sinningia* as currently circumscribed could not even be maintained as a subgenus of *Paliavana*; it would have to be divided into four subgenera, corresponding to the four clades discovered by cladistic analysis. The combination of *Sinningia*, *Paliavana*, and *Vanhouttea* would result in a large, poorly-defined genus even more heterogeneous than *Sinningia*.

Splitting

To maintain *Vanhouttea* and *Paliavana* as independent genera (or to combine them in a single genus separate from *Sinningia*) would require splitting *Sinningia* into more than one genus. The former division into *Sinningia* and *Rechsteineria* is unacceptable, however, as it has been shown that in this arrangement *Rechsteineria* is either paraphyletic or polyphyletic. In addition, the species *S. concinna* and *S. pusilla* cannot be shown to be more closely related to subgenus *Sinningia* than to either of the *Rechsteineria* clades. *Sinningia* would therefore have to be split into at least four genera, corresponding to the four clades found by cladistic analysis. The name *Sinningia* would be retained for the species of subgenus *Sinningia*, consisting of sections *Ligeria*, *Sinningia*, *Stenogastra* (excluding *S. pusilla* and *S. concinna*), *Tapina*, and

Thamnoligeria. The name *Rechsteineria* could only be applied to a group containing the members of sections *Corytholoma* and *Cryptocaula* as well as those of the genus *Lietzia*. This matter is complicated by the fact that although the name *Rechsteineria* has been conserved against several older generic names by Rafinesque, it has not been conserved against *Fimbrolina* Rafinesque. Thus the name for this genus would have to be *Fimbrolina* unless *Rechsteineria* were conserved against this name as well. The oldest generic name available for the members of section *Thamnocaula* is *Dircaea*. For the miniature species *Sinningia pusilla* and *S. concinna* no generic name is available.

The major advantage of this arrangement is that it would allow the clear circumscription of several well-defined smaller genera rather than the large, poorly-defined, heterogeneous *Sinningia* that now exists. It would also be more consistent with the hybridization criteria employed by Wiehler in circumscribing genera in the tribe (see below). Many of the nomenclatural combinations which would be required in *Dircaea* and *Rechsteineria* already exist. On the other hand, it would require the creation of several nothogeneric names for the large number of plants now cultivated simply as interspecific hybrids of *Sinningia* rather than as intergeneric hybrids. It is likely that the substitution of several unfamiliar names for familiar ones would be resisted in horticultural circles, and would serve to confuse rather than stabilize the nomenclature of the group, especially since the submersion of *Rechsteineria* in *Sinningia* has been widely accepted in the taxonomic and horticultural literature.

Status Quo

The above options operate on the assumption that cladistic analysis has discovered the true phylogeny of the groups involved, and that *Paliavana* and *Vanhouttea* are clades within *Sinningia*. However, it has been shown that very few characters unite *Paliavana* and *Vanhouttea* with *Sinningia* in the cladograms, and these characters are not among the most reliable. It is possible that further examination will reveal that *Paliavana* and *Vanhouttea* occupy a position as sister-group of *Sinningia* rather than as a clade within that genus. The greatest advantage of maintaining the status quo is that it would retain a stable nomenclature in groups which are at least superficially distinct and whose circumscriptions are already widely accepted. It would also retain the useful division between nontuberous genera (*Paliavana* and *Vanhouttea*) and tuberous (*Sinningia*). This still leaves open the possibility that either of the two above options may be taken if further cladistic analysis or other research so indicates, while recognizing that the present circumscription of *Sinningia* may be paraphyletic. If *Paliavana* and *Vanhouttea* indeed prove to be derived from within *Sinningia* as it is currently circumscribed, the author would strongly recommend that

Sinningia be split into four genera, as described above, as this would allow the most precise definition of the taxa.

Artificial hybridization and its relationship to classification

Although artificial hybridization has been accepted by many authors as a tool to discover or clarify relationships in Gesneriaceae, whether it is a valid basis for constructing classifications will not be addressed here. One possible use of artificial hybridization may be to refine the scoring of characters (see below). This subject has been discussed with reference to hybrids in *Aphelandra* by McDade (1990). However, it cannot be denied that hybridization is of no use when the plants under consideration are known only from the literature or from herbarium specimens. Even when live material is available, hybridization experiments are time-consuming and the results are interpreted subjectively and applied inconsistently. Thus morphological characters and other intrinsic properties of the plants will continue to be of prime importance in classification. Perhaps most objectionable is when hybrization is the sole uniting "character" of a morphologically heterogeneous genus, as appears to be the case with *Gloxinia* as circumscribed by Wiehler (1976).

Artificial hybridization has had a particularly significant impact on the classification of subfamily Gesnerioideae. Wiehler (1975a, 1976, 1978a, 1983) accepted partially or fully fertile hybrids (as deduced from hybrid pollen stainability) as being indicative of congeneric status of the parent species, whereas sterile hybrids or inability to hybridize ruled out congeneric status. However, Wiehler maintained *Codonanthe* and *Nematanthus* (tribe Episcieae) as separate genera, despite the fertility of their hybrids. Wiehler also synonymized *Pheidonocarpa* under *Gesneria* (tribe Gesnerieae) despite the inability to form hybrids between these two genera.

Wiehler accepted ability to form intergeneric hybrids as being indicative of contribal status, leading him to combine several tribes in Gloxinieae. However, he transferred the tuberous genera *Lembocarpus*, *Lietzia*, and *Sinningia* to Gloxinieae without having produced any hybrids between these genera and other genera of the tribe as he circumscribed it.

Taxonomic placement of *Lietzia*

Hybrids between *Lietzia glandulosa* and several species of *Sinningia* were produced in the course of this study. Prior to this study, hybrids had been made between *L. brasiliensis* and *S. incarnata* (Wiehler 1988), and between *L. glandulosa* and two *Sinningia* hybrids (Zaitlin 1990). A hybrid from the former cross is being commercially distributed as *Sinningia* 'Adam Lietze', and a hybrid from one of the latter crosses is being distributed as *S.* 'King Midas'. Most, if not all, flowering hybrids between *Lietzia* and *Sinningia* section *Corytholoma* appear to be at least weakly fertile. The hybrids between *L. brasiliensis* and *S. incarnata* were shown by Wiehler to have a high pollen stainability, up to 54%, and second-generation hybrids have been produced from crosses between *L. glandulosa* and *Sinningia* species and hybrids (D. Zaitlin, pers. comm., A. Wojcik, pers. comm., and Boggan, unpublished). As of this writing (April 1991), none of these second-generation hybrids has bloomed. On the basis of the hybridization data, the species of *Lietzia* fall within *Sinningia* section *Corytholoma*, the species of which were considered a cenospecies by Clayberg (1968a, 1970a), and the union of the two genera was advocated by Wiehler (1988). Such a placement is supported by morphological evidence as well, as shown by the cladistic analyses.

The relationship between *Sinningia* and *Rechsteineria*

The current classification of *Sinningia* is inconsistent with Wiehler's criteria for delimiting genera. *Sinningia* now consists of several discrete and morphologically well-defined sections within which hybrids are fertile but between which hybrids are invariably sterile, a criterion used by Wiehler to maintain separate genera in other groups. Although Clayberg recommended the combination of

Rechsteineria and *Sinningia* on the basis of the many hybrids which were produced between the two genera, only two species of *Sinningia*, *S. tubiflora* and *S. eumorpha*, formed fertile hybrids with *Rechsteineria* species. Clayberg recognized that on morphological grounds as well, particularly nectary gland characters, these species were more properly placed within sections *Corytholoma* and *Thamnocaula*, respectively, of *Rechsteineria*. All other hybrids between *Rechsteineria* and *Sinningia* were sterile.

There are several cases, however, where morphological uniformity does not correspond with ability to hybridize. Although the species of subgenus *Sinningia* are united by several synapomorphies, few interspecific hybrids have been produced within this group, and those produced have all been completely sterile (Clayberg 1968a, 1970a; Boggan 1985a). Clayberg thus maintained the several small sections of subgenus *Sinningia* as separate entities. Another case in point is *S. tuberosa*, which was maintained in section *Cryptocaula* by Clayberg. This species, although highly specialized, shares several synapomorphies with section *Corytholoma* yet is difficult to cross with this section or any other species of the genus.

In some respects, artificial hybridization has proven to be a good indicator of relationship in *Sinningia*. With the exception of *S. tuberosa*, Clayberg's organization of the species of *Rechsteineria* into two large cenospecies, or groups of highly interfertile species, including two species formerly associated with *Sinningia*, conforms with the relationships of these groups later elucidated by cladistic analysis. Hybridization failed to elucidate relationships among species which failed to form fertile hybrids. In this context, ability to form fertile hybrids may be informative, whereas inability to form fertile hybrids must be considered uninformative.

Reticulate evolution in *Sinningia*

Despite the fact that many of its species are highly interfertile, the data do not suggest that hybridization has played an important role in the evolution of *Sinningia*. Ancient hybridization could conceivable account for the difficulty in determining relationships among the four clades. Only two species, *Sinningia sellovii* and *S. barbata*, appear to combine synapomorphies of two distinct groups. Although *S. sellovii* is very similar in morphology to *S. sulcata*, and shares with it an unusual apomorphic character, the dangling flower, this species is consistently grouped in cladistic analysis with another subclade of the same section with which it shares such floral characters as stamen filament pigmentation and vestiture. *Sinningia barbata* is unique among the members of subgenus *Sinningia* with its two nectary glands, the ventral glands being absent. Although this nectary configuration is characteristic of section *Thamnocaula*, *S. barbata* does not share any other characters with that section. This character led *S. conspicua* to be placed originally in section *Tapina* with *S. barbata*, although the two species are not otherwise similar.

Expression of characters in hybrids

Most characters, for example corolla anthocyanin color, proved to be intermediate in expression in hybrids. While anthocyanin can be scored easily in species as a qualitative character, either red or violet, crosses between species with red flowers and species with violet flowers produce hybrids with flowers intermediate in color, ranging from lavender-pink to magenta. The preponderance of intermediate states and the fact that neither primitive nor derived characters appear to predominate in expression in the hybrid progeny are consistent with the results of McDade's (1990) study of character expression in hybrids of *Aphelandra*. The fact that intermediates occur in hybrids between states which had been scored as qualitative in the parents may suggest that evolution of these characters has proceeded quantitatively, with extinction (or omission from analysis) of intermediates making qualitative scoring possible. It may also indicate that these characters will be less useful when more species are examined.

Comparison of the expression of possibly homologous characters in different hybrids revealed that for some characters, their expression is dependent upon parentage. These differences in expression may indicate that the characters are not homologous. One example of variable expression in hybrids is the production of solitary axillary flowers. This character is indicated as having arisen independently at least six times in the cladograms. However, solitary flowers appear to act as a recessive in some hybrids and as a dominant in others. For example, all hybrids with *Lietzia glandulosa* as one parent had solitary axillary flowers, regardless of the flower number of the other parent (e.g., *S. aggregata*). Similarly, the solitary flowers of *S. tubiflora* are apparently dominant in most crosses (although a single herbarium specimen of a hybrid with *S. eumorpha*, *Clayberg 53*, has two flowers per axil). On the other hand, crosses between either *S. concinna* or *S. pusilla* and other species with several flowers per axil (e.g., *S. eumorpha*, *S. schiffneri*, *S. aggregata*) yield hybrids with two or more flowers per axil. Hybrids of other species with solitary axillary flowers were unavailable for examination.

The galea is another character which varies in expression with different parents. Hybrids of *Lietzia glandulosa* all possessed galeate corollas, although the galea was slightly smaller in the hybrids than in the *Lietzia* parent. The galeate corolla of *S. cardinalis* and its close relatives, however, is apparently recessive in crosses. Although the upper corolla lobes are held horizontally in the hybrids, they do not show the expansion and fusion of the galeate parent. This supports what the cladograms have already indicated, that the genetic basis of the galea is different in these two groups; rescoring to reflect this fact could reduce the homoplasy in the analysis. It also suggests that the galea, which was scored as a single character, actually results from the interaction of two different characters, lobe orientation and lobe expansion.

One character for which hybridization aided interpretation is the apparently whorled leaves of *Sinningia leucotricha*. This species regularly produces a single whorl of four leaves atop a long bare stem. Most other species with whorled leaves produce three leaves at a node. A hybrid between *S. leucotricha* and *S. bulbosa* was observed to produce long stems with four large leaves, but in a decussate arrangement with a short internode of variable (0.5-3 cm) length between the two pairs. It appears likely that the apparently whorled leaves of *S. leucotricha* result from two pairs of leaves with the internode between them reduced and effectively absent. The phyllotaxy of the related *S. douglasii*, which produces a whorl of six leaves, may then be interpreted as two true whorls of three leaves each with a short, effectively absent internode between them. As all the leaves of these species are initiated immediately upon development of a shoot from a tuber, a test of this hypothesis may be to grow the plants in darkness, or to apply gibberellin, to discover if the internode between the leaves is revealed in etiolated plants.

CHAPTER VI. CONCLUSIONS.

Relationships among the tuberous Gloxinieae

It has been demonstrated that the species of *Sinningia* can be distributed among four well-defined clades. The relationships of these clades to each other are less certain, and there are few characters which define *Sinningia* as a monophyletic group. A division into two subgenera, *Sinningia* and *Rechsteineria*, cannot be justified. Any infrageneric classification of *Sinningia* would best divide it into four groups of equal rank, whether subgenera or sections, reflecting these four clades. A division of *Sinningia* into four genera could even be justified, and may be necessary if *Paliavana* and *Vanhouttea* are to be maintained as separate genera (see below). The species of *Lietzia* share several synapomorphies with one of the clades of *Sinningia*, and their transfer to that genus is strongly supported. The tuber of *Lembocarpus amoenus* is not homologous with that of the species of *Sinningia*, nor do these genera share any other synapomorphies. *Lembocarpus* most closely resembles *Rhoogeton* and its removal from Gloxinieae to Episcieae near that genus is recommended.

Relationships of some nontuberous species

The nontuberous species *Sinningia schiffneri* is a valid member of the genus as currently circumscribed, sharing several synapomorphies with one of the clades of *Sinningia*. A rather surprising result of the cladistic analyses was that the species of the nontuberous genera *Paliavana* and *Vanhouttea* may also belong in *Sinningia* as it is now circumscribed. It is recommended that these genera be maintained for now, although if future investigation supports the results of this study, it will be necessary to split *Sinningia* into four genera representing the four clades described above. In the opinion of the present author, this course of action would be preferable to combining *Sinningia*, *Paliavana*, and *Vanhouttea* into one large genus, as it would allow a clear circumscription of several small, well-defined genera, as opposed to a single large, poorly-defined genus.

Hybridizing and relationships

Although ability to hybridize is a symplesiomorphy, artificial hybridization may yield informative results when investigating relationships. The infrageneric classification of *Sinningia* based on hybridizing relationships parallels, in some groups at least, the classification suggested by cladistic analysis. One useful by-product of the creation of artificial hybrids is that it allows the study of character expression in hybrids, which may allow one to determine homology or nonhomology of some characters.

The Gesneriaceae have long been a family of interest to systematists, and will probably continue to be for years to come. Research in the family has followed a progression from classical morphology, to other types of investigation, such as chromosome numbers, biogeography, biochemistry, hybridization, and anatomy. With this cladistic analysis, it has come full circle, back to morphology. However, all areas of investigation have made valuable contributions to systematics, and it is hoped that a further synthesis of various systematic disciplines can continue to produce a classification which is broadly-based and evolutionarily sound.

APPENDIX 1. SPECIES OF SINNINGIA IN CULTIVATION*

Subgenus Sinningia
Section *Sinningia*
  S. guttata Lindley
  S. lindleyi Schauer
  S. villosa Lindley?
Section *Tapina*
  S. barbata (Nees & Martius) Nicholson
Section *Stenogastra*
  S. concinna (Hooker) Nicholson
  S. hirsuta (Lindley) Nicholson
  S. pusilla (Martius) Baillon
  S. kautskyi Chautems (ined.)
Section *Thamnoligeria*
  S. schiffneri Fritsch
Section *Ligeria*
  S. speciosa (Loddiges) Hiern ("Gloxinia". Hort.)
    syn. *S. discolor, S. regina*
Section *Hemiloba*
  No species in cultivation
Unplaced species
  S. richii Clayberg

Subgenus Rechsteineria
Section *Thamnocaula*
  S. bulbosa (Ker-Gawler) Wiehler
    syn. *S. macrorrhiza* (Dumont) Wiehler
  S. canescens (Martius) Wiehler
  S. cardinalis (Lehm.) H. E. Moore
  S. conspicua (Seem.) Nicholson
  S. cooperi (Paxton) Wiehler
  S. douglasii (Lindley) Chautems
    syn. *S. verticillata*
  S. eumorpha H. E. Moore
  S. gigantifolia Chautems
    syn. *Gesneria discolor*
  S. glazioviana (Fritsch) Chautems
  S. leucotricha (Hoehne) H. E. Moore (*S. canescens* Hort)
  S. lineata (Hjelm.) Chautems (*S. macropoda* Hort.)
  S. macropoda (Sprague) H. E. Moore
  S. macrostachya (Lindley) Chautems
  S. magnifica (Otto & Dietr.) Wiehler
  S. nivalis Chautems (ined.)
  S. reitzii (Hoehne) L. E. Skog
  S. rupicola (Martius) Wiehler

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*arrangement based on recommendations by Clayberg (1968a, 1970a)

Subgenus Rechsteineria, continued

Section *Cryptocaula*

- *S. defoliata* (Malme) Chautems?
- *S. tuberosa* (Martius) Wiehler

Section *Corytholoma*

- *S. aggregata* (Ker-Gawler) Wiehler
- *S.* sp. nov. aff. *aggregata*
- *S. allagophylla* (Martius) Wiehler
- *S. curtiflora* (Malme) Chautems
- *S. elatior* (Kunth) Chautems
- *S. incarnata* (Aubl.) Denham
    - syn. *S. warszewiczii*
- *S. sceptrum* (Martius) Wiehler
- *S. sellovii* (Martius) Wiehler
- *S. sulcata* (Rusby) Wiehler
- *S. tubiflora* (Hooker) Fritsch
- *S. warmingii* (Hiern) Chautems (*S. sceptrum* Hort.)
    - syn. *S. claybergiana*, *Rechsteineria lindleyi*

APPENDIX 2. INTERSPECIFIC HYBRIDS IN SINNINGIA

Hybrid	**Reference**
aggregata	
x *allagophylla*	Clayberg 1970a
x *concinna*	Arnold 1975
x *eumorpha*	Clayberg 1970a
x *incarnata* (as *R. warszewiczii*)	Clayberg 1968a
x *richii*	Clayberg 1970a
x *sulcata*	Boggan, unpublished
x *tuberosa*	Clayberg 1970b
x *tubiflora*	Clayberg 1968a
x *warmingii* (as *R. sellovii*)	Clayberg 1968a, 1970a
allagophylla	
x *aggregata*	Clayberg 1970a
x *concinna*	Clayberg 1970a
x *hirsuta*	Arnold 1975
x *richii*	Clayberg 1970a
x *speciosa*	Arnold 1975
barbata	
x *leucotricha*	Clayberg 1968a
x *pusilla*	M. Belisle, pers. comm.
x *speciosa*	Moore 1954c
x *warmingii* (as *R. sellovii*)	Clayberg 1968a
cardinalis	
x *douglasii* (as *R. verticillata*)	Clayberg 1968a
x *eumorpha*	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *lineata*	Clayberg 1968a
x *macropoda* (as *R. cyclophylla*)	Clayberg 1968a
x *macrorrhiza*	Clayberg 1970a
x *reitzii*	Conner 1982
x *speciosa*	Arnold 1975
x *tubiflora*	Clayberg 1968a
concinna	
x *aggregata*	Arnold 1975
x *allagophylla*	Clayberg 1970a
x *eumorpha*	Arnold 1975
x *hirsuta*	Clayberg 1970a
x *kautskyi*	D. Zaitlin, pers. comm.
x *pusilla*	Clayberg 1968a
x *richii*	Belanger 1985
x *schiffneri*	Clayberg 1968a
x *warmingii* (as *sceptrum*)	Belanger 1985

conspicua	
x *eumorpha*	D. Zaitlin, pers. comm.
x *pusilla*	Boggan, unpublished
x *speciosa*	Moore 1954
cooperi	
x *douglasii* (as *verticillata*)	Arnold 1975
x *tubiflora*	Moore 1954c
douglasii (=*S. verticillata*)	
x *cardinalis*	Clayberg 1968a
x *cooperi*	Arnold 1975
x *eumorpha*	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *lineata*	Clayberg 1968a
x *macropoda* (as *R. cyclophylla*)	Clayberg 1968a
x *macrorrhiza*	P. Conner, pers. comm.
x *pusilla*	Boggan 1985
eumorpha	
x *aggregata*	Clayberg 1970a
x *cardinalis*	Clayberg 1968a
x *concinna*	Arnold 1975
x *conspicua*	D. Zaitlin, pers. comm.
x *douglasii* (as *R. verticillata*)	Clayberg 1968a
x *glazioviana*	M. Peixoto, pers. comm.
x *leucotricha*	Clayberg 1968a
x *lineata*	Clayberg 1968a
x *macropoda* (as *R. cyclophylla*)	Moore 1957; Clayberg 1968a
x *macrorrhiza*	J. Steuerlein, pers. comm.
x *pusilla*	Clayberg 1968a Arnold 1975
x *reitzii*	Boggan 1985
x *richii*	Belanger 1977
x *schiffneri*	Clayberg 1968a
x *tuberosa*	Clayberg 1970b
x *tubiflora*	Clayberg 1968a
x *warmingii*	Boggan, unpublished
gigantifolia (=*Gesneria discolor*)	
x *speciosa*	Moore 1954c
glazioviana	
x *eumorpha*	M. Peixoto, pers. comm.
x *leucotricha*	M. Peixoto, pers. comm.
x *macropoda*	M. Peixoto, pers. comm.
guttata	
x *incarnata*	V. Pilloton, pers. comm.
x *warmingii*	Boggan, unpublished
x *speciosa*	Moore 1954c

hirsuta	
x *concinna*	Clayberg 1968a, 1970a
x *allagophylla*	Arnold 1975
incarnata (=*S. warszewiczii*)	
x *aggregata*	Clayberg 1968a
x *guttata*	V. Pilloton, pers. comm.
x *macropoda* (as *R. cyclophylla*)	Clayberg 1968a
x *richii*	Clayberg 1968a, 1970a
x *speciosa*	Arnold 1975
x *tubiflora*	Clayberg 1968a
x *warmingii* (as *R. sellovii*)	Clayberg 1968a
kautskyi	
x *concinna*	D. Zaitlin, pers. comm.
leucotricha	
x *barbata*	Clayberg 1968a
x *cardinalis*	Clayberg 1968a
x *douglasii* (as *R. verticillata*)	Clayberg 1968a
x *eumorpha*	Clayberg 1968a
x *glazioviana*	M. Peixoto, pers. comm.
x *lineata*	Clayberg 1968a
x *macropoda* (as *R. cyclophylla*)	Clayberg 1968a
x *macrorrhiza*	Boggan, unpublished
x *pusilla*	Clayberg 1968a
x *reitzii*	Boggan 1985
x *tuberosa*	Clayberg 1970b
x *warmingii* (as *R. sellovii*)	Clayberg 1968a
lineata (=*S macropoda* Hort.)	
x *cardinalis*	Clayberg 1968a
x *douglasii* (as *R. verticillata*)	Clayberg 1968a
x *eumorpha*	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *macropoda* (as *R. cyclophylla*)	Clayberg 1968a
x *pusilla*	Clayberg 1968a
macropoda (=*R. cyclophylla*)	
x *cardinalis*	Clayberg 1968a
x *douglasii* (as *R. verticillata*)	Clayberg 1968a
x *eumorpha*	Moore 1957, Clayberg 1968a
x *glazioviana*	M. Peixoto, pers. comm.
x *incarnata* (as *R. warszewiczii*)	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *lineata*	Clayberg 1968a
macrorrhiza	
x *cardinalis*	Clayberg 1970a
x *douglasii* (as *S. verticillata*)	P. Conner, pers. comm.
x *eumorpha*	Boggan, unpublished
x *leucotricha*	Boggan, unpublished
x *pusilla*	Belanger 1985

magnifica	
x *reitzii*	D. Zaitlin, pers. comm.

pusilla	
x *barbata*	M. Belisle, pers. comm.
x *concinna*	Clayberg 1968a
x *conspicua*	Boggan, unpublished
x *douglasii* (as *verticillata*)	Boggan 1985
x *eumorpha*	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *lineata*	Clayberg 1968a
x *macrorrhiza*	Belanger 1985
x *reitzii*	J. Steuerlein, pers. comm.
x *schiffneri*	Clayberg 1968a

reitzii (=*S.* 'New Zealand')	
x *leucotricha* (as *canescens*)	Boggan 1985
x *cardinalis*	Boggan 1985
x *eumorpha*	Boggan 1985
x *magnifica*	D. Zaitlin, pers. comm.
x *pusilla*	J. Steuerlein, pers. comm.

richii	
x *aggregata*	Clayberg 1970a
x *allagophylla*	Clayberg 1970a
x *concinna*	Belanger 1985
x *eumorpha*	Belanger 1977
x *incarnata* (as *R. warszewiczii*)	Clayberg 1968a, 1970
x *speciosa*	Clayberg 1968a, 1970
x *warmingii* (as *R. sellovii*)	Clayberg 1970a

schiffneri	
x *concinna*	Clayberg 1968a
x *eumorpha*	Clayberg 1968a
x *pusilla*	Clayberg 1968a

speciosa (=*S. discolor, S. regina*)	
x *allagophylla*	Arnold 1975
x *barbata*	Moore 1954c
x *cardinalis*	Arnold 1975
x *gigantifolia* (as *G. discolor*)	Moore 1954c

speciosa (continued)	
x *guttata*	Moore 1954c
x *incarnata* (as *warszewiczii*)	Arnold 1975
x *richii*	Clayberg 1968a, 1970
x *sulcata*	Belanger 1985
x *velutina*	Moore 1954c

sulcata	
x *aggregata*	Boggan, unpublished
x *speciosa*	Belanger 1985
x *warmingii* (as *sceptrum*)	P. Conner, pers. comm.
tuberosa	
x *aggregata*	Clayberg 1970b
x *eumorpha*	Clayberg 1970b
x *leucotricha*	Clayberg 1970b
x *tubiflora*	Clayberg 1970b
tubiflora	
x *aggregata*	Clayberg 1968a
x *cardinalis*	Clayberg 1968a
x *cooperi*	Moore 1954c
x *eumorpha*	Clayberg 1968a
x *incarnata* (as *R. warszewiczii*)	Clayberg 1968a
x *tuberosa*	Clayberg 1968a
x *warmingii* (as *R. sellovii*)	Clayberg 1968a
velutina	
x *speciosa*	Moore 1954c
warmingii (=*S. sceptrum* Hort., *S. claybergiana*, *R. lindleyi*, *R. sellovii* Hort.)	
x *aggregata*	Clayberg 1968a, 1970a
x *barbata*	Clayberg 1968a
x *concinna*	Belanger 1985
x *eumorpha*	Boggan, unpublished
x *guttata*	Boggan, unpublished
x *incarnata*	Clayberg 1968a
x *leucotricha*	Clayberg 1968a
x *richii*	Clayberg 1970a
x *sulcata*	P. Conner, pers. comm.
x *tubiflora*	Clayberg 1968a

APPENDIX 3. NOTES ON TWO SPECIES NOT INCLUDED IN ANALYSIS

The two species described below were excluded from the cladistic analysis because flowering material was not available at the time of the analysis. Cultivated material flowered as writing was nearing completion, and some observations are included here.

Capanea grandiflora (plant obtained from R. Milewski, East Stroudsburg University):

Capanea grandiflora is superficially similar, vegetatively, to some of the larger *Kohleria* species, but is reported to be an epiphyte (Skog 1979; Beaufort-Murphy & Stone 1984). There is conflicting information on whether this species produces rhizomes or not (Bentham 1876; Moore 1956; Skog 1978), but the material cultivated by the author produced rhizomes, although the rhizome scales were widely spaced and not fleshy as in scaly-rhizomatous species. *Capanea grandiflora* produces large, hairy green flowers on a long hypopodium. The stigma is not bilobed, as in species of *Kohleria*, but is broadly stomatomorphic. The corolla lobes have capitate trichomes which are intermediate in length between those of *Kohleria* species and those of other members of the tribe. The nectary consists of five glands which are joined at the base. Beaufort-Murphy (1983) noted that the seeds have elongate appendages. One of the more interesting characters which has not been noted in the literature is that the pedicel twists at the end near the flower, with the flower hanging upside-down (resupinate). The species has the following character states (characters and codings as in Table 13):

00-?00000000 01100 0000000110000200011000002 0000

Diastema comiferum (plant obtained from Hans Wiehler, Gesneriad Research Foundation, as W3268):

Diastema comiferum is unusual in *Diastema* for its showy, bright red flowers, but otherwise is consistent morphologically with that genus, particularly in the diagnostic long, narrow nectary glands and bilabiate stigma. The flowers are solitary in the axils, without prophylls, and the florescence is a true raceme. This species also produces a patch of short capitate trichomes on the interior corolla epidermis over the anthers, a character common in species with insect-pollinated flowers but which was not observed in any other species with red flowers. The species has the following character states (see Table 13 for characters and codings):

00-?00000000 00011 0010000010000001000100020 ????

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