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A SYNOPSIS OF THE NEOTROPICAL GESNERIACEAE

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Volume Six, planned about three years ago to be devoted entirely to the family Gesneriaceae, was to be published in conjunction with the First International Gesneriad Symposium held in July 1982. We apologize to our subscribers for the year delay. We regret that we are still unable to publish Dr. Wiehler's complete paper at this late date. The editorial committee and reviewers, however, believe that the bulk of the incomplete manuscript published herein is of sufficient botanical merit to warrant publication as it is. . . . Ed.

INTRODUCTION

The family Gesneriaceae consisting of about 126 genera and around 3000 species is one of the larger of the tropical plant families. It belongs to the order Scrophulariales of the dicotyledons (Cronquist, 1968), closely related to the Scrophulariaceae. The pantropical Gesneriaceae may be divided into three natural groups or subfamilies. The neotropical subfamily Gesnerioideae contains about 54 genera and more than 1300 species; the paleotropical subfamily Cyrtandroideae comprises about 63 genera and over 1550 species (Burtt, 1963, 1977, 1978, and personal communication); and the newly constituted subfamily Coronatheroideae from the South Pacific region consists of 9 genera and 20 species.

The following synopsis offers a new classification of the neotropical Gesneriaceae. It is based on surveys (both brief and extensive) of morphological, anatomical, and cytological features, and it is built on a critical evaluation of taxonomic characters. Because of the evolutionary plasticity of this advanced tropical dicot family, difficulties of the systematist holding concepts based on the northern-temperate flora have repeatedly arisen in the past. The only major treatment of the family, that by Hanstein, is well over one hundred years old, and the modifications of this system by Bentham &

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Part of this work is included in a doctoral dissertation submitted to the University of Miami, Miami, Florida, U.S.A.

Hooker (1876) and by Fritsch (1893-94) are likewise outdated. An outline of the subfamilies, tribes, and genera of Fritsch's classification is given in Table 1. Recently Burtt (1963) published a valuable new classification for the Gesneriaceae of the Old World, based on seedling morphology, which affected the position of a number of neotropical taxa previously placed in the predominantly paleotropical subfamily Cyrtandroideae (see Tables 1, 29). I fully agree with Burtt's new delimitation of the Cyrtandroideae which now contains only paleotropical taxa, with the exception of a single species of *Rhynchoglossum* (see page 51). Therefore, the present treatment includes all tribes and genera outside the Cyrtandroideae as interpreted by Burtt (1963).

The most critical problem in the Gesneriaceae of the New World is that of generic delimitation. There are very few problems on the species level. The initial concepts of most of the major genera in the Gesnerioideae had become blurred and confused, either through the subsequent addition of many new species which created discordant elements within these genera, or through some initial vagueness of definition caused by an overemphasis on certain floral characters and a concomitant neglect of other more essential features. Another factor contributing to the taxonomic confusion among neotropical Gesneriaceae was the lack of vital information concerning the new species sent to Europe as dried specimens. The best and often only solution to accommodate the considerable influx of novelties was to attribute them to several of the vaguely defined "catch-all" genera established between 1753 and 1850, such as *Achimenes* P. Browne, *Kohleria* Regel, *Gesnera* Martius, *Episcia* Martius, *Alloplectus* Martius, *Columnea* Linnaeus, *Hypocyrta* Martius, *Besleria* Linnaeus, *Gesneria* Linnaeus, and others.

That the Gesneriaceae of the New World have been shadowed for too long by a reputation of presenting unusual difficulties in generic delimitation can be attested to by the following comments of botanists working with this plant group. George Bentham (who authored the largest number of still valid genera among the Gesnerioideae) wrote as early as 1846:

> "Since the publication of the 7th volume of DeCandolle's *Prodromus* (1839), the number of Gesneriaceae known has nearly doubled, the forms assumed by the flower and fruit have been found to be much more varied than was supposed, the characters assigned to the genera are no longer sufficient to distinguish them clearly, either from one another, or from the new ones since proposed, . . . so that there is now scarcely any order (=family) which is more in want of a complete revision." (London J. Bot. 5:357. 1846.)

In 1876 Joseph Dalton Hooker commented, in describing a new species:

> "The American genera of Gesneraceae, however, present unusual difficulties in respect to their limitation . . ." (*Bot. Mag.* 102. sub t. 6233. 1876.)

Even after Karl Fritsch's revision of 1893-94, William Botting Hemsley complained in 1903:

> "The genera of the Gesneriaceae have been so diversely defined and limited by different botanists at different periods that it is difficult to understand what really constitutes a genus in this natural order." (*Bot. Mag.* 129: sub. t. 7907. 1903.)

The frustrations botanists have experienced with the genera of the neotropical Gesneriaceae are probably best summarized by B. L. Burtt's (hyperbolic) statement in 1956:

"There is probably no group of flowering plants whose generic classification is more in need of revision than the American Gesneriaceae." (*Bot. Mag.* 171: sub t. 278. 1956.)

Burtt, at the Royal Botanic Garden, Edinburgh, is today the foremost authority on the Gesneriaceae of the Old World. Since about 1950 this botanic garden has become the center of research for the paleotropical Gesneriaceae, housing a large greenhouse collection of the subfamily Cyrtandroideae. The parallel research on the neotropical Gesneriaceae, done by the workers listed below, has presently culminated in the proposed new classification of the American Gesneriaceae.

Since about 1950, many new neotropical species of Gesneriaceae have been introduced into the United States, either from horticultural sources in Europe or directly from the wild. The L. H. Bailey Hortorium at Cornell University, dedicated to research on cultivated plants, became the center of study for cultivated Gesneriaceae. Under the direction of Dr. H. E. Moore, Jr., there was a special emphasis on correct identification and nomenclature, more complete (or new) descriptions, and proper nurture of the newly introduced species (Moore, 1953a, 1953b, 1953c, 1954a, 1954b, 1954c, 1954d, 1954e, 1954f, 1955a, 1955b, 1957a, 1957b, 1958, 1960a, 1960b, 1962, 1963, 1965, 1972, 1973b) and a beginning to redefine generic delimitations (Moore, 1973a, 1973c). Of equal importance was the cytogenetic work done at Cornell at the same time, under the direction of Dr. Robert E. Lee. The establishment of chromosome numbers for the American Gesneriaceae (Rogers, 1954; Fussell, 1958; Lee, 1962a, 1962b, 1964-1967b; Lee & Grear, 1963; Clayberg. 1967; Wiehler, 1972), and the hybridization studies (Cooke & Lee, 1966; Lee, 1967a; Sherk & Lee, 1967; Wiehler, 1968, 1970) became an important cornerstone for the reconstruction of the genera. A valuable report by Moore & Lee (1967) summarized the work done of the Gesnerioideae up to that time and offered the beginning of a new basis for classification.

A morphological study of the epidermis of the leaf and of the vasculature of the node and petiole added further information on the relationships of the tribes and genera within the Gesnerioideae which became useful data for a new classification (Wiehler, 1970).

With my transfer in late 1970 from Cornell University to the University of Miami, Florida, another phase of research began in neotropical Gesneriaceae: field work in Central and South America to observe and collect the Gesnerioideae in their native habitats. The association with Drs. C. H. Dodson and R. L. Dressler, known for their work on the classification of the Orchidaceae, added another dimension: the application of the discoveries of pollination biology to the New World Gesneriaceae, especially concerning the problems of generic limitations. A duplicate live collection of Gesneriaceae transferred from Cornell University to the University of Miami was soon enlarged by many species new to science or cultivation.

I have observed and worked with the extensive greenhouse collections of Gesnerioideae and Coronantheroideae since 1966, first at Cornell University, then at the University of Miami and at the Marie Selby Botanical Gardens in Sarasota. I have grown and studied alive all but four genera (mostly monotypic) of Gesnerioideae and Coronantheroideae which contain together a total of 63 genera. Through continuing intensive field work at the center of distribution of the Gesnerioideae, (Colombia, Ecuador, Venezuela, Panama, Costa Rica, and Guatemala), my knowledge of this fascinating plant group has been enriched. I have so far observed the species of 43 (out of 54) genera of Gesnerioideae in their native habitats, collected 402 species of neotropical gesneriads, and published descriptions of 107 species new to science. The live collection has also been enriched through the efforts of Drs. R. L. Dressler, C. H. Dodson, T. C. Plowman, M. T. Madison, C. Luer, Mrs. E. Besse, and others.

Also studied were the most important herbarium collections of neotropical Gesneriaceae at the United States National Museum of Natural History in Washington, D. C. (US), the New York Botanical Garden (NY), the Harvard University Herbaria (A and GH), the Field Museum in Chicago (F), the Missouri Botanical Garden at St. Louis (MO), the L. H. Bailey Hortorium, Cornell University (BH), Duke University, Durham N. C. (Duke), the Instituto Botanico in Caracas (VEN), the Royal Botanic Gardens, Kew (K), the British Museum of Natural History (BM), the Museum National d'Histoire Naturelle, Paris (P), the Botanische Staatssammlung, München (M), the Naturhistorische Museum, Wien (W), the Botanische Museum, Berlin-Dahlem (B), the Jardin Botanique National de Belgique, Bruxelles (BR), the Botanisch Museum de Rijksuniversiteit, Utrecht (U), the Laboratorium voor Plantensystematick, Wageningen, Netherlands (WAG), the Systematisch-Geobotanische Institut, Universität Göttingen (GOET), the Institut für Allgemeine Botanik, Hamburg (HBG), and the Naturhistoriska Riksmuseet, Stockholm (S). The herbarium of the Marie Selby Botanical Gardens (SEL) held until recently over 14,000 sheets of Gesnerioideae on loan from 37 herbaria in Europe and North and South America for the construction of a new classification and in connection with monographic and floristic work. In fact, the new classification, featuring more clearly defined genera and tribes, is a necessary prerequisite for the beginning of floristic studies of the Gesnerioideae in Ecuador, Colombia, Panama, Costa Rica, Venezuela, the Guayana Highland, Brazil, Peru, and Bolivia.

The remodeling of the taxa of the New World Gesneriaceae is, therefore, based on the following factors:

1. The observation of live plant material in field and greenhouse.
2. Cytogenetic data obtained a) through chromosome counts for the majority of the genera of the Gesnerioideae (by other workers and by myself, see below); b) through hybridization work at the interspecific and intergeneric levels (Wiehler, 1976b).
3. An understanding of the vital importance of pollen and seed dispersal phenomena in the life cycle of the gesneriaceous species, and a subsequent re-interpretation of the significance of reproductive characters for the taxonomy of this tropical plant group.
4. A systematic study and a taxonomic evaluation of such characters as the inflorescence, the shape and color of the corolla, the varied structure and evolution of the nectary, the type of fruit (mostly unknown before for many species), as well as investigations of the vasculature of the node and petiole, and of the epidermis.
5. A new emphasis on certain vegetative characters, especially plant habit. Among some gesneriaceous genera, vegetative characters appear to have greater taxonomic import in generic delimitation than floral features.

This synopsis is divided into three parts: investigation, interpretation, and taxonomic application. A broad spectrum of the features of the New World Gesneriaceae is examined for its systematic value, with the exception of the ultrastructure of seed and pollen which will be treated later or is presently studied by other workers (cf. Williams, 1978, Fritze & Williams, 1981).

A complete character evaluation, absolutely essential for any new classification or generic revision, has not been produced previously for the neotropical Gesneriaceae. Hanstein attempted this in his scheme (1854-65), but it was necessarily limited in scope by material available. The result of this fifteen-year evaluation is a clearer delimitation of all of the problematic taxa of the New World Gesneriaceae and more precise generic diagnoses. This was effected through a sometimes drastic splitting up of the larger generic complexes into separate genera, or through a fusion of other genera or sections of several genera into new generic units. Names for these genera were already available in most instances, reflecting a residue of classification attempts in the last century. All of the generic reconstructions have been published in separate papers since 1971, during my stay at the University of Miami and at the Marie Selby Botanical Gardens. These papers form the basis for the present discussion on generic delimitations.

The character evaluation and the reconstruction of the major genera of the neotropical Gesneriaceae result also in a sharper delimitation of the tribes in the subfamily Gesnerioideae. Five tribes are united into a single unit, the Gloxinieae, partially as a consequence of artificial intergeneric hybridization; the new tribe Napeantheae is established; several genera are assigned to different tribes, or affiliated with a tribe for the first time; the tribe Coronanthereae (*sensu* Fritsch) is excluded from the subfamily Gesnerioideae and raised to a new status as subfamily Coronantheroideae (Tables 2, 33).

The broad scope of the task allows here only a basic restructuring of generic and tribal limits within the neotropical Gesneriaceae. Complete revisions of the genera of the subfamilies Gesnerioideae and Coronantheroideae will be published later.

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LIST OF CLASSIFICATION SCHEMES AND KEYS

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TABLE 1

THE LAST CLASSIFICATION OF THE FAMILY GESNERIACEAE BY FRITSCH, 1893-94

(Only neotropical genera are listed below)

I. Subfamily Cyrtandroideae:*

Tribes:	
1. Ramondieae	
2. Didymocarpeae	
3. Championieae	
4. Streptocarpeae	
5. Trichosporeae	
6. Klugieae	*Napeanthus*, *Rhynchoglossum*, and 3 paleotropical genera
7. Hemiboeeae	
8. Anetantheae	*Anetanthus*, *Goyazia*
9. Beslerieae	*Besleria*, and 9 paleotropical genera
10. Coronanthereae	
Subtribes:	
Coronantherinae	*Rhabdothamnus*, *Coronanthera*, *Negria*
Mitrariinae	*Fieldia*, *Asteranthera*, *Mitraria*, *Sarmienta*
11. Cyrtandreae	
12. Columneeae	
Subtribes:	
Columneinae	*Episcia*, *Drymonia*, *Chrysothemis*, *Alloplectus*, *Trichantha*, *Columnea*, *Nematanthus*, *Hypocyrta*
Codonanthinae	*Codonanthe*

II. Subfamily Gesnerioideae:

13. Bellonieae	*Bellonia*, *Niphaea*, *Phinaea*, *Monopyle*, *Anodiscus*
14. Gloxinieae	*Gloxinia*, *Achimenes*, *Koellikeria*, *Smithiantha*, *Heppiella*, *Seemannia*
15. Kohlerieae	*Diastema*, *Kohleria*, *Pearcea*, *Vanhouttea*, *Paliavana*, *Capanea*
16. Sinningieae	*Lietzia*, *Sinningia*, *Rechsteineria*
17. Solenophoreae	*Solenophora*, *Hippodamia*
18. Gesnerieae	*Gesneria*, *Rhytidophyllum*

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*The main character in Fritsch's system was ovary position, dividing the Cyrtandroideae (superior ovary) from the Gesnerioideae (inferior and semi-inferior ovary). All neotropical genera with a superior ovary were thus placed in the Cyrtandroideae. After the discovery that the seedlings in paleotropical Gesneriaceae are anisocotylous and in neotropical Gesneriaceae isocotylous, Burtt (1963) used seedling morphology as the principal character to divide the two major subfamilies which now also became geographical units. Burtt shifted all neotropical genera (with the exception of a neotropical species of the Asiatic genus *Rhynchoglossum*) listed here under subfamily Cyrtandroideae to the Gesnerioideae. Burtt's classification of the Cyrtandroideae is listed in Table 29.

TABLE 2. A NEW CLASSIFICATION OF THE AMERICAN GESNERIACEAE
(Base chromosome number at left of each genus;
number of species in each genus at right)

I. SUBFAMILY GESNERIOIDEAE — 54 genera, over 1300 species
Distribution: Neotropics

1. TRIBE GLOXINIEAE Fritsch

13	*Gloxinia* L'Heritier	15	13	*Sinningia* Nees	60+
13	*Monopyle* Bentham	23+		*Lietzia* Regel	1
13	*Kohleria* Regel	20+		*Lembocarpus* Leeuwenberg	1
13	*Anodiscus* Bentham	1		*Goyazia* Taubert	2
13	*Koellikeria* Regel	1	13	*Bellonia* Linnaeus	2
13	*Pearcea* Regel	1	13	*Phinaea* Bentham	10
13	*Parakohleria* Wiehler	20+	11	*Niphaea* Lindley	4
13	*Heppiella* Regel	15+	12	*Smithiantha* Kuntze	3
13	*Diastema* Bentham	21+	12	*Eucodonia* Hanstein	2
13	*Capanea* Decaisne	11	11	*Achimenes* Persoon	22
	Vanhouttea Lemaire	6	11	*Moussonia* Regel	11
13	*Paliavana* Vandelli	7	10	*Solenophora* Bentham	20+

2. TRIBE EPISCIEAE Endlicher

9	*Episcia* Martius	9	9	*Rufodorsia* Wiehler	4
9	*Nautilocalyx* Hanstein	50+		*Oerstedina* Wiehler	3
9	*Chrysothemis* Decaisne	7	9	*Pentadenia* Hanstein	30+
9	*Corytoplectus* Oersted	10+	9	*Dalbergaria* Tussac	90+
9	*Alloplectus* Martius	65	9	*Trichantha* Hooker	70+
9	*Cobananthus* Wiehler	1	9	*Bucinellina* Wiehler	2
	Rhoogeton Leeuwenberg	2	9	*Columnea* Linnaeus	75+
9	*Drymonia* Martius	110+	9	*Codonanthopsis* Mansfeld	6
9	*Paradrymonia* Hanstein	50+	8	*Codonanthe* Hanstein	20+
9	*Alsobia* Hanstein	2	8	*Nematanthus* Schrader	26
9	*Neomortonia* Wiehler	3			

3. TRIBE BESLERIEAE Bartling & Wendland

16	*Besleria* Linnaeus	200+
	Gasteranthus Bentham	40+
	Cremosperma Bentham	25+
	Reldia Wiehler	4
	Resia H. E. Moore	2
	Tylopsacas Leeuwenberg	1
	Anetanthus Bentham	1

4. TRIBE NAPEANTHEAE Wiehler

	Napeanthus Gardner	30+

5. TRIBE GESNERIEAE

14	*Gesneria* Linnaeus	69

II. SUBFAMILY CORONANTHEROIDEAE Wiehler — 9 genera, 20 species
Distribution: southern Chile,
South Pacific islands, Australia

6. TRIBE CORONANTHEREAE Fritsch

±37	*Mitraria* Cavanilles	1	(These 3 genera are native to temperate South America in Chile,where other gesneriads are absent. See Table 33.)
±37	*Sarmienta* Ruiz & Pavon	1	
	Asteranthera Hanstein	1	

III. SUBFAMILY CYRTANDROIDEAE Endlicher — 63 genera, over 1550 species
Distribution: Paleotropics

7. TRIBE KLIGIEAE Fritsch

20	*Rhynchoglossum* Blume	12	[One species, *R. azureum* (Schlechtendal) B. L. Burtt, of this paleotropical genus occurs from Mexico to Peru and Venezuela; the other 11 species are native to Southeast Asia from India to New Guinea, Taiwan and China.]

PART 1: THE BIOLOGY OF THE GESNERIACEAE IN THE NEOTROPICS: THE FOUNDATION FOR A NEW EVALUATION OF GENERIC, TRIBAL, AND SUBFAMILIAL CHARACTERS

The Gesneriaceae are a family rich in variation and full of exceptions to the norm. A description of the family will bring about a better appreciation of the problems involving its generic delimitations. There is a reason for the great diversity within this group of plants: diversity in habit (herb, bush, tree, liana), floral shape, structure of androecium, development of nectary, ovarian position, and types of fruit, and for the development of special features within the family: the phyllomorph system, trilacunar nodes in the vasculature, aggregate stomatal arrangement, epiphytism, tubers, rhizomes, and stolons. It has now become evident that the Gesneriaceae are a very plastic (and young) family, evolutionarily active and flexible; in fact, they are in many respects the most advanced family in the order Scrophulariales of Cronquist (1968), or among the larger grouping traditionally labelled Tubiflorae. They may possibly even be the most advanced family among all the dicotyledons (*see* Hilliard & Burtt, 1971).

No fossil pollen or macrofossil record has yet been discovered for the Gesneriaceae. The earliest pollen record for herbaceous families of the Scrophulariales dates from the lower Miocene to the Pliocene, 22.5 to 5 million years ago (Muller, 1981), thus suggesting that these families are among the latest to evolve within the angiosperms, even later than the Compositae.

Much of the information is presented here for the first time. It would not have been possible without extensive field work in the neotropics, and without the maintenance of a large live collection of Gesneriaceae at the Marie Selby Botanical Gardens and at the Gesneriad Research Foundation.

CHAPTER 1: DIFFERENTIATING FAMILIAL CHARACTERS

From other dicotyledonous families the Gesneriaceae are distinguished by the following combination of characters: plants chlorophyllous and nonparasitic (in contrast to the Orobanchaceae), the simple, undivided leaves (in contrast to the Bignoniaceae) mostly opposite-decussate, whorled, or secondarily alternate (in most species of *Gesneria*, and all of *Reldia* and *Rhynchoglossum*), the inflorescence typically a pair-flowered cyme (or reduced to 1-2 flowers, *see* chapter "Inflorescence"), the corolla sympetalous and zygomorphic (secondarily almost or completely actinomorphic in *Conandron*, *Depanthus*, and species of *Napeanthus*, *Phinaea*, and *Bellonia*), the placentation parietal (in contrast to the Scrophulariaceae), and 4 (or 2, rarely 5) stamens usually with connate anthers, the 2-carpellate fruit or a 2- or 4-valved capsule (dehiscing loculicidally or septicidally, or both) or a berry. The closest relative of the Gesneriaceae is the family Scrophulariaceae (2700 species). The affinities are further elaborated under the heading "Placentation." The Orobanchaceae (150 species), formerly regarded as another of the close relations of the Gesneriaceae, are now considered more distant relatives (Weber, personal communication).

CHAPTER 2: DISTRIBUTION, HABITAT, AND HABIT

The Gesneriaceae are a pan-tropical plant family, with the noteworthy exception of a few cold-tolerant, mostly rosette-forming species found on rock faces of the Pyrenees [*Ramonda myconi* (L.) Rchb., covered by snow in winter], in the mountains of the Balkan Peninsula [species of *Ramonda*, *Haberlea*, with *Jankaea heldreichii* (Boiss.) on Mount Olympus in Greece], in the Himalayas (*Briggsia*, *Corallodiscus*, *Lysionotus*), and in Japan (*Conandron*, *Lysionotus*, *Opithandra*). In the cool but humid forests of central and southern Chile the epiphytic and monotypic genera *Asteranthera*, *Mitraria*, and *Sarmienta* occur. They are the only Gesneriaceae native to Chile, members of the subfamily Coronantheroideae. To the same group belongs also *Rhabdothamnus solandri* A. Cunn., a small shrub endemic to the cool climate of New Zealand.

The more typical taxa of the Gesneriaceae, however, are found in the warm and humid tropical forests. The majority of the species are herbaceous or suffrutescent perennials, but a few species of the following genera are shrubs: *Besleria*, *Cyrtandra*, *Coronanthera*, *Paliavana*, *Pentadenia*, *Gesneria*, and *Vanhouttea.* A very few species are small trees, almost all belonging to subfamily Coronantheroideae: *Coronanthera grandis* G. W. Gillett, up to 15 m tall, *Depanthus glaber* (C. B. Cl.) S. Moore, up to 9 m tall, *Lenbrassia australiana* (C. T. White) G. W. Gillett, 12 m tall, *Negria rhabdothamnoides* F. Mueller, up to 9 m high, and *Solenophora calycosa* Donn. Sm. (tribe Gloxinieae) from Costa Rica and Panama, up to 12 m high, with a trunk to 30 cm in diameter.

Most of the soft-stemmed or sub-shrubby gesneriads grow terrestrially or on rocks in the tropical forest, exposed to a certain amount of direct daily sunlight. Preferred habitats are small sunny clearings in the forest, the banks of rivers and creeks, moisture-dripping vertical rock faces, steep slopes, and road-cuts. A few species thrive in deep shade and high humidity, with only occasional indirect sunlight: the genus *Napeanthus*, and some species of *Gasteranthus* and *Sinningia.* The first two genera have developed independently a special stomatal arrangement on the leaf surface (clustered stomata, discussed below).

CHAPTER 3: EPIPHYTISM

A significant number of the Gesneriaceae, however, have forsaken a terrestrial habitat in search of more light. A few have become lianas (many species of *Drymonia*, some species of *Alloplectus*, *Paradrymonia*, and *Capanea*), but the rest have evolved into true epiphytes. In fact, with over 598 species the Gesneriaceae have the second largest contingent of epiphytic species among the dicotyledonous plant families. The largest number of epiphytes are in the Piperaceae in which the genus *Peperomia* Ruiz and Pavon may have around 700 epiphytic species (Table 4). In the number of dicotyledonous epiphytic species, the Gesneriaceae are followed distantly by the Melastomaceae, Ericaceae, and Cactaceae; but the Piperaceae and Gesneriaceae are surpassed in numbers of epiphytic monocotyledonous taxa by the Orchidaceae, Araceae and Bromeliaceae. Table 3 lists the 28 genera containing epiphytes among the Gesneriaceae and Table 4 compares these numbers with epiphytes in other plant families. It is also of interest that epiphytism is a rare phenomenon in the groups related to the Gesneriaceae in the order Scrophulariales and the subclass Asteridae of Cronquist (1968), the Rubiaceae excepted. Within the Gesneriaceae, the development of epiphytism is most pronounced in the subfamily Gesnerioideae. The tribe Episcieae in this subfamily contains the second largest number of epiphytic species among the dicotyledons: about two-thirds (468 out of 670) species of the Episcieae live

TABLE 3
EPIPHYTIC GENERA AND SPECIES IN THE GESNERIACEAE

SUBFAMILY GESNERIOIDEAE (over 1300 spp.)

Tribe Gloxinieae Fritsch (300+ spp.)

			Epiphytic Species
Monopyle Benth.	(23+ spp.)	*M. macrocarpa* Benth.	1
Gloxinia L'Herit.	(15 spp.)	*G. purpurascens* (Rusby) Wiehler	1
Heppiella Regel	(15+ spp.)	*H. repens* Hanst.	1
Capanea Planch.	(11+ spp.)	*C. affinis* Fritsch *C. andina* Fritsch *C. grandiflora* (Kunth) Decne. *C. hansteinii* Fritsch *C. urceolata* Fritsch	5+
Sinningia Nees	(60+ spp.)	*S. bulbosa* (Ker-Gawler)Wiehler (incl. *Corytholoma micans* Fritsch) *S. cooperi* (Paxton) Wiehler (incl. *Gesneria reflexa* Knowl. & Westc.) *S. verticillata* (Vell.) H. E. Moore [incl. *Rechsteineria oligantha* (Malme) Hoehne] *S.* sp. nov. (from Peru)	4+
			12+

Tribe Episcieae Endl. (670+ spp.)

Alsobia Hanst.	(2 spp.)	2
Columnea L.	(75 spp.)	75+
Dalbergaria Tussac	(90+ spp.)	90+
Trichantha Hook.	(70+ spp.)	70+
Alloplectus Mart.	(65 spp.)	25
Pentadenia (Planch.) Hanst.	(30+ spp.)	27+
Paradrymonia Hanst.	(50+ spp.)	20+
Rufodorsia		
Rufodorsia Wiehler	(4 spp.)	4
Neomortonia Wiehler	(3 spp.)	3
Drymonia Mart.	(110+ spp.)	100+
Nematanthus Schrader	(26 spp.)	26
Codonanthe (Mart.) Hanst.	(20+ spp.)	20+
Codonanthopsis Mansf.	(6 spp.)	6
		468+

SUBFAMILY CYRTANDROIDEAE JACK (over 1550 spp.)

Tribe Trichosporeae Fritsch

Aeschynanthus Jack	(80+ spp.)	80+
Agalmyla Bl.	(50+ spp.)	15
Loxostigma C. B. Cl.	(4 spp.)	3
Lysionotus G. Don	(13 spp.)	2
		100+

Tribe Cyrtandreae Endlicher

Cyrtandra J. R. & G. Forst.	(600+spp.)	*C. oblongifolia* (Bl.) C. B. Cl. and species of section *Geodesme* in New Guinea (fide Burtt, personal communication)	4

TABLE 3 (Cont'd)
EPIPHYTIC GENERA AND SPECIES IN THE GESNERIACEAE

			Epiphytic Species
Tribe Didymocarpeae Endlicher			
Streptocarpus Lindley	(132 spp.)	about 10 species (fide Burtt, personal communication)	10
SUBFAMILY CORONANTHEROIDEAE WIEHLER (18 spp.)			
Tribe Coronantheroideae Fritsch (18 spp.)			
Asteranthera Hanst.	(1 sp.)	*A. ovata* (Cav.) Hanst.	1
Fieldia Cunn.	(1 sp.)	*F. australis* F. Mueller	1
Mitraria Cav.	(1 sp.)	*M. coccinea* Cav.	1
Sarmienta Ruĭz & Pavon	(1 sp.)	*S. repens* Ruĭz & Pavon	1
			4

SUMMARY:

Tribe Gloxinieae	12+ species
Tribe Episcieae	468
Tribe Trichosporeae	100
Tribe Cyrtandreae	4 (?)
Tribe Didymocarpeae	10 (?)
Tribe Coronanthereae	4

The Gesneriaceae contain over 598 epiphytic species.

TABLE 4
EPIPHYTISM IN SOME ANGIOSPERM PLANT FAMILIES

FAMILY	TOTAL NO. OF		NO. OF EPIPHYTIC		% OF EPI-PHYTIC SPP.
	GENERA	SPECIES*	GENERA	SPECIES**	
(Monocots)					
Orchidaceae	735	25-30000	500	20000	66
Araceae	115	2000	15	850	42
Bromeliaceae	45	1400	24	900	64
(Dicots)					
Piperaceae	8	3000	2	710	24
Gesneriaceae	126	3000	28	598	20
Moraceae	53	1400	3	521	37
Melastomataceae	240	4500	22	483	11
Ericaceae	75	2000	28	478	23
Rubiaceae	450	6000	21	217	4
Asclepiadaceae	130	2000	6	132	7
Cactaceae	50-150	2000	25	143	7
Marcgraviaceae	5	100	5	94	94
Solanaceae	90	2200	5	33	2
Lentibulariaceae	4	250	1	10	4
Scrophulariaceae	220	2700	2	5	0.1
Asteraceae	900	13000	2	3	0.02

* Many of these numbers were taken from Willis (1973).

** These numbers were worked out by or in cooperation with Dr. M. Madison, Selby Botanical Gardens.

on trees. The only other epiphytes in the subfamily Gesnerioideae occur in the tribe Gloxinieae, with a ratio of about 12 epiphytes to over 300 terrestrial species. The Old World subfamily Cyrtandroideae contains about 114 epiphytic species, most of them in southeastern Asia and in the tribe Trichosporeae. Four species are epiphytes among the 20 species of the small austral subfamily Coronantheroideae (Table 3).

CHAPTER 4: ADAPTATIONS FOR DRY SEASONS: RHIZOMES AND TUBERS

For periodic dry seasons some terrestrial gesneriad genera have evolved adaptations in the form of underground scaly rhizomes (specialization of the shoot, development of storage tissue in modified leaves) or tubers (development of storage tissue on the stem.) Scaly rhizomes are typical for the majority of the tribe Gloxinieae Fritsch, involving 14 genera and over 160 species (Table 5). The same feature also occurs in the Asiatic genera *Briggsia*, *Platystemma*, and *Titanotrichum*. Tubers are found in most species of *Sinningia*, the monotypic genera *Lembocarpus* and *Lietzia*, in all species of *Chrysothemis*, in many species of *Nautilocalyx*, and in some species of *Drymonia*, *Paradrymonia*, and *Rhoogeton.*

TABLE 5

THE GENERA WITH SCALY RHIZOMES IN THE TRIBE GLOXINIEAE FRITSCH

Gloxinia L'Heritier
Monopyle Bentham
Kohleria Regel
Pearcea Regel
Parakohleria Wiehler
Heppiella Regel
Diastema Bentham
Achimenes Persoon
Eucodonia Hanstein
Smithiantha Kuntze
Koellikeria Regel
Goyazia Taubert
Niphaea Lindley
Phinaea Bentham

CHAPTER 5: POLLINATION

An understanding of the fascinating phenomena of pollen transport in the neotropical Gesneriaceae is an essential prerequisite for any modern solution to the vexing problems of generic delimitations in this family. The pollination biology of the Gesnerioideae is intimately connected with speciation, and therefore also with the nature of the generic classification of the subfamily. I estimate that about 60% of the neotropical Gesneriaceae are hummingbird-pollinated. This is rather a high percentage of bird pollination for any large plant family, even for a neotropical plant family. It is not accidental that the center of distribution of the Gesnerioideae, Colombia and Ecuador, coincides with the center of distribution of the neotropical bird family Trochilidae. The hummingbird family contains over 320 species, or about 450 well-defined forms or subspecies (Thompson, 1964; Fisher & Peterson, 1964). Other modes of pollen transport in the Gesnerioideae include about 30% gynandro-euglossophily (pollination by iridescent neotropical male and female Euglossine bees in search of nectar), and the remaining 10% includes chiropterophily, psychophily, sphingophily, phalenophily, myophily, androeuglossophily (male Euglossine bees gathering fragrance compounds) and "melittophily". The honey bees, consisting of four species of *Apis*, are most closely associated with the phenomenon of melittophily. They are indeed prominent pollinators in the temperate zone of Europe and in tropical Asia, but they are not native to the New World. The introduced *Apis mellifera* is now abundant in the Americas, but no species of native New World flowering plants has adapted to it for specific pollination (Dodson, personal communication). Bumble bees (*Bombus*), also included in the syndrome of melittophily, are represented by a number of species in the New World. Except at higher elevations, they do not appear to play a significant role in the neotropical pollination scheme, at least when compared with the five genera of neotropical Euglossine bees. There is some indication that other small nectar-feeding bees of the families Andrenidae and Halictidae may pollinate neotropical gesneriads, but precise information is still lacking. The term "melittophily", as customarily used in the Old World does not readily apply to bee flowers in the New World. The term does not take into account the utterly different phenomenon of the male Euglossine pollination system, and it obscures the decisive flower specificity of the many species of Euglossini involved in the gynandro-euglossophilous pollination system. Although several species of both *Drymonia* and *Nautilocalyx* with gynandro-euglossine flowers exist sympatrically in Ecuador and Colombia and bloom at the same time (Wiehler, unpublished data), no intrageneric hybrids have been observed but these hybrids can be produced with ease artificially in cultivation.

Each type of pollinator, whether it be bird, mammal, or insect, has a corresponding flower-type. From the present state of field observations (Wiehler, Dodson, Dressler, N. H. Williams, unpublished data), it may be safely deduced that in the Gesnerioideae the pollinator-flower relationship is usually unique within a given species, and obligatory in a few cases. In fact, the plants have evolved effective devices against promiscuous nectar thieves which would squander their energy budget or disturb the gene pool unnecessarily through hybridization. The recent renewed interest of an increasing number of zoologists, ecologists, behaviorists, and botanists in the phenomena of pollination biology and of co-evolution of animal pollinators with families of flowering plants (Knoll, 1921-26, 1956; Grant, 1949; Kugler, 1963, 1970; von Frisch, 1960; Ziegenspeck, 1955; Baker, 1960; van der Pijl, 1960-61; Vogel, 1963; Dodson, 1962, 1965; Faegri & van der Pijl, 1966, 1979; Proctor & Yeo, 1973; Richards, 1978), should apply in a special way to the tropical Gesneriaceae where showy flowers of many shapes and colors are adapted to a wide range of pollinating agents. It cannot be overemphasized at this point that in the Gesneriaceae, speciation and evolution are most intimately linked with changes in the mode of pollination.

The extent of genetical fine-tuning accomplished by a plant species to effect cross-pollinization by attracting a specific pollen carrier has usually not been appreciated to the deserved extent by plant taxonomists and writers of botanical textbooks. The following features are directly or indirectly involved: the type, position, and length of the inflorescence; the mechanism for the synchronization of anthesis; the shape, size, color, and texture of the calyx and of the corolla; the position of the ovary; the presence or absence, shape, size, and position of the nectary or of the osmophore; fragrance compounds produced; the shape and positon of the stigma; the length of the style; the phenomena of protandry and protogyny; the shape and position of the anthers; the type of dehiscence of the anthers; the arrangement of the paired anther cells; the texture and degree of viscosity of the coat of the pollen grains; and the length of the pollen tube in relation to the length of the style. Even some strictly vegetative characters may become involved in the process of pollination. Some taxa of the Gesnerioideae develop bright red translucent designs on the leaves at the time of anthesis as an extrafloral attraction mechanism for hummingbirds (cf. Jones & Rich, 1972).

There is a strong correlation between epiphytism and ornithophily. In fact, in some advanced dicotyledonous families (Ericaceae, Gesneriaceae, Rubiaceae) the change from a terrestrial to an epiphytic habit evidently invites both pollen transport and seed dispersal (fruit = berry) by birds. In the Gesnerioideae, both epiphytism and ornithophily are strongly expressed in the large tribe Episcieae which contains over 670 species. At least 80 % of the more than 468 epiphytic species in this tribe are pollinated by hummingbirds.

Four different kinds of hummingbird corollas, typically colored red, orange or strong yellow, are found in the Gesnerioideae and Episcieae (Table 6): first, the tubular corolla with a narrow and more or less straight tube and a narrow, subregular limb (Figure 1); second, the columneoid corolla with a narrow but expanding tube and a strongly zygomorphic limb divided into a prominent galea (hood) consisting of the two enlarged dorsal lobes, with two triangular lateral lobes, and a long and narrow ventral lobe (Figure 2); third, the hypocyrtoid or urceolate corolla with an inflated tube and a very constricted throat and a very narrow regular limb [this type of corolla is labelled hypocyrtoid when the tube has a ventrally inflated pouch, as in the former genus *Hypocyrta* (=*Nematanthus*), a taxon based solely on the shape of the corolla] (Figures 3-4); fourth, the converted euglossine corolla with a moderately wide tube and a wide subregular limb. This type of corolla apparently represents a "recent" adaptation from euglossophily to ornithophily. The typical euglossine corolla is either white or light yellow, often with a purple, rose, or lemon nectar guide. The converted corolla is orange or red (Figure 5). Table 6 lists the genera in which these four types of hummingbird corollas occur. The large genus *Columnea sensu stricto* has only one type of corolla, the columneiod corolla, but the same type is also found in the three genera recently segregated from *Columnea* (*Dalbergaria*, *Trichantha*, and *Pentadenia*) and in the following tribes: in the monotypic genus *Asteranthera* (tribe Coronanthereae), and in the red-flowered species of *Sinningia* (tribe Gloxinieae). Yellow tubular corollas are characteristic of the genus *Dalbergaria.* Since these yellow corollas are usually fairly small and somewhat hidden in the foliage and from a distance unattractive to the potential pollinator, many species of *Dalbergaria* have evolved extrafloral attraction patterns for the inquisitive hummingbirds: bright red translucent spots on the lamina of the leaf which glow like a red-stained glass window in the sunlight, or red borders, dots, or spotting on the abaxial leaf surface. The reason for the differences in the shapes of the first three types of hummingbird corollas is not known at present, although the columneoid and hypocyrtoid corollas appear to be derived from the tubular type.

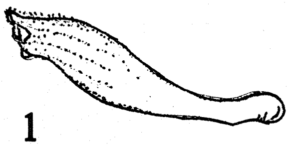
CHAPTER 6: THE INFLORESCENCE

Characters of the inflorescence have played a minor role in the taxonomy of the Gesnerioideae. In fact, only the unusual alternately bracted inflorescence in *Koellikeria* and *Smithiantha* has been employed in the keys of the neotropical Gesneriaceae. It is surprising that the special nature of the gesneriaceous inflorescence has for so long escaped deserved attention in the botanical literature, as well as in the description of the species and genera, and in previous classifications of the family. Illustrations and diagrams of

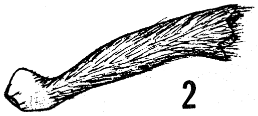
TABLE 6: FOUR DIFFERENT TYPES OF HUMMINGBIRD COROLLAS FOUND IN GENERA OF THE NEOTROPICAL GESNERIACEAE *

The corollas are typically red or orange, and when yellow (rarely white), they are associated with red calyces, or red bracts, or the leaves feature abaxial red extrafloral attraction patterns. Genera outside the tribe Episcieae are listed in parentheses.

1. THE TUBULAR COROLLA



1



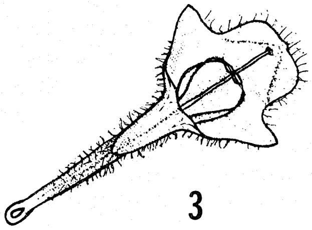
2

Dalbergaria
Pentadenia
Trichantha
Bucinellina
— found in the majority of species

Drymonia — in a few species
Cobananthus — monotypic
Paradrymonia — in *P. densa*

(Heppiella), *(Gesneria)*, *(Sinningia)*, *(Moussonia)*, *(Kohleria)*, *(Capanea)*, *(Solenophora)*, *(Achimenes)*.

2. THE COLUMNEOID COROLLA



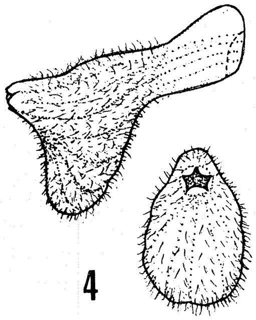
3

Columnea — typical for the whole genus

Dalbergaria
Pentadenia
Trichantha
— in a few species

(Sinningia) — in the *S. cardinalis* complex
(Asteranthera) — monotypic

3. THE HYPOCYRTOID AND THE URCEOLATE COROLLA



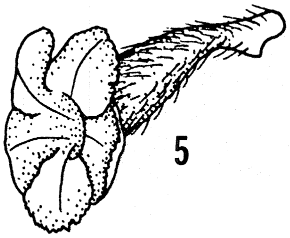
4

Nematanthus — in the majority of the species

Alloplectus
Drymonia
Corytoplectus
Pentadenia
Neomortonia
Paradrymonia
— in a few species

(Pearcea) — monotypic
(Besleria) — in many species
(Gasteranthus) - in many species

4. THE CONVERTED RED EUGLOSSINE COROLLA



5

Episcia — in *E. cupreata* and *E. reptans*
Nautilocalyx — in *N. kohlerioides*, *N. porphyrotrichus*, etc.
Paradrymonia — in undescribed species and probably in *P. hansteiniana*.
Drymonia — probably in *D. conchocalyx* and others.

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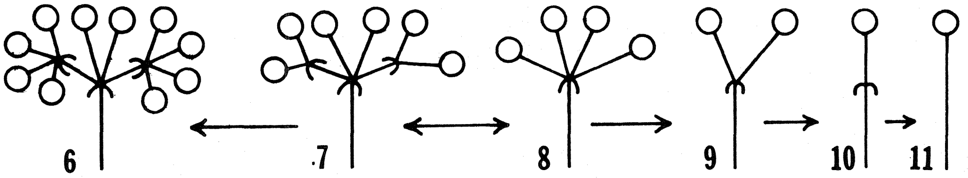
* First published in *Selbyana* 5(1): 16. 1978.

gesneriaceous inflorescences were often drawn incorrectly or misinterpreted (cf. Leeuwenberg, 1958, pp. 337, 345, 359, 362, 410, 419).

Awareness of the distinct nature of the gesneriaceous inflorescence has developed slowly. Hayek (1926) and Fritsch (1927, 1931) were the first to publish diagrams of pair-flowered cymes of species of the European genera *Jankaea*, *Ramonda*, and *Haberlea*. The conventional cyme has only one terminal flower per cyme unit. In a sequel to his famous "Organographie der Pflanzen", Goebel (1931) examined several other Old World Gesnericeae *(Streptocarpus*, *Ramonda*, *Saintpaulia*, *Monophyllaea)*, all with two terminal flowers per cyme unit. He interpreted the extra or second terminal flower as an accessory or adventitious flower, and Troll (1964) came to the same conclusion in his monumental study, "Die Infloreszenzen," which included several New World Gesneriaceae. In all these studies, however, the impression was left that these curious twin-flowered cyme units were somehow a special or side-line development within the Gesneriaceae.

With the accumulation of the largest collection of neotropical Gesneriaceae ever assembled in cultivation and through extensive field and herbarium study of this group, I became aware around 1971 that the pair-flowered cyme is the basic inflorescence unit in the subfamily Gesnerioideae. At the same time Burtt (1971, p. 34) recognized this type of inflorescence as the predominant pattern for the Gesneriaceae of the Old World as well. It is now evident that the twin-flowered cyme is typical for the whole family Gesneriaceae. This model can either be elaborated into a compound cyme or reduced to two or one flowers:



Figures 6-11: Patterns of the inflorescence in the Gesneriaceae

No morphological explanation for this peculiar cymal pattern in the Gesneriaceae was to be found in the American botanical literature on inflorescences (Rickett, 1944; Lawrence, 1951, 1955; Eames, 1961; Cronquist, 1968; Stebbins, 1973). Following the widespread acceptance of Rickett's dichasial theory in America, in which the three-flowered cyme is the fundamental element, I was under the erroneous impression that the four-flowered cyme (Figure 8) was the basic unit of the inflorescence in the Gesneriaceae. The four-flowered cyme occurs frequently in a number of genera (e.g.*Gesneria*, *Moussonia*, *Kohleria*, *Alloplectus*, *Besleria*, *Gasteranthus*). Skog (1976) interpreted the inflorescences in the tribe Gesnerieae as basically similar to each other, each species "a stage in a reduction series from a compound dichasium to a single flower" (p. 14), but he still tried to explain this special type of inflorescence in terms of Rickett's (1944) dichasial theory.

Anton Weber's (1973a) publication on the structure of the pair-flowered partial florescences in the Gesneriaceae and some Scrophulariaceae finally

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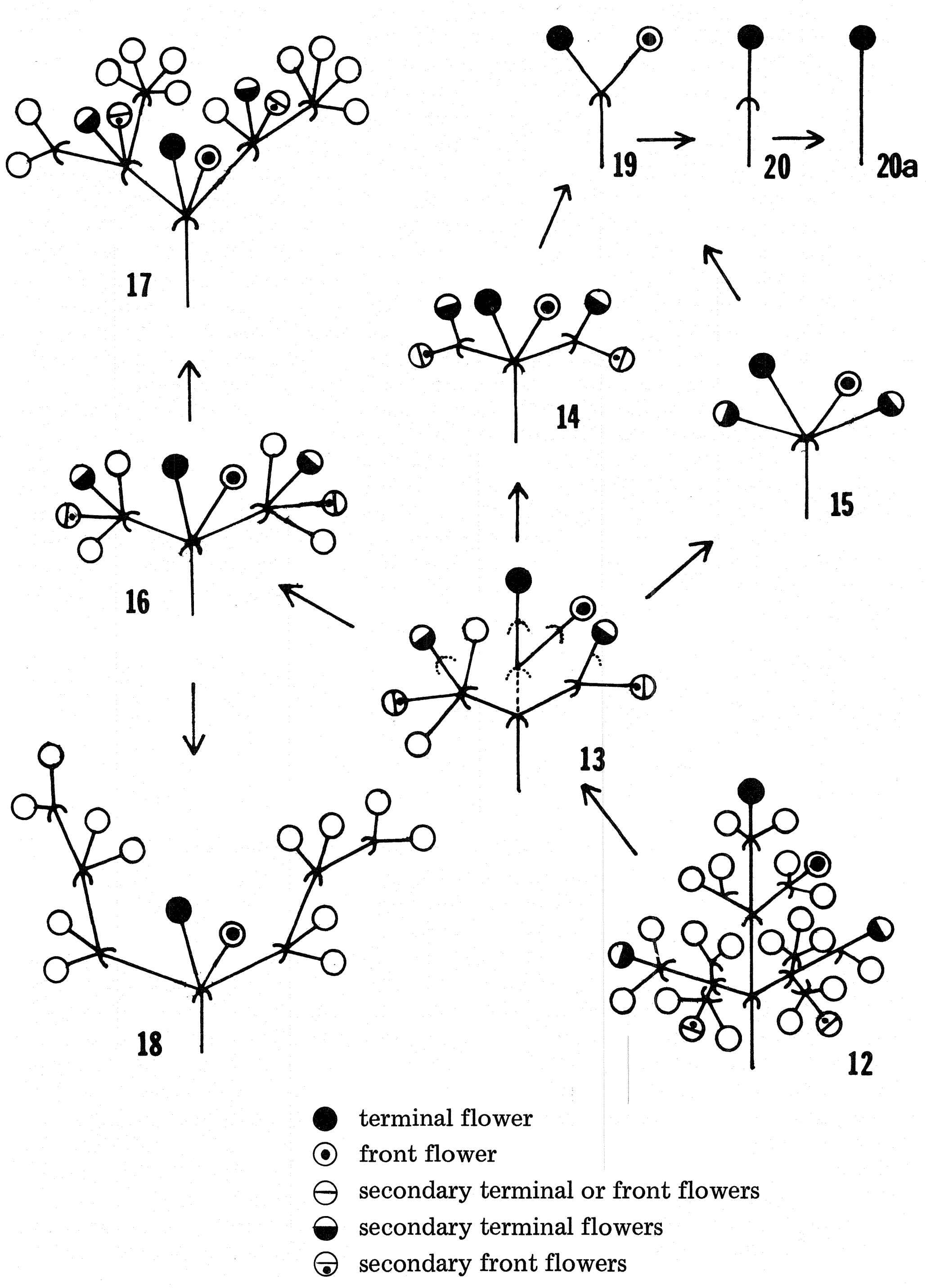
Figures 1-5: (Opposite page) Different types of hummingbird corollas found in genera of neotropical Gesneriaceae (within Table 6). 1. *Bucinellina paramicola* (Wiehler) Wiehler. 2. *Pentadenia ecuadorana* Wiehler. 3. *Columnea dressleri* Wiehler. 4. *Paradrymonia hypocyrta* Wiehler. 5. *Episcia cupreata* (Hooker) Hanst.



Figures 12-20: Schematic drawings of modifications of the inflorescences in the Gesneriaceae. Figure 12 is the hypothetical ancestral paniculoid model (after Weber, 1973).

brought a much-needed clarification and adequate morphological explanation of the gesneriaceous cyme. He demonstrated that the second terminal or front flower of the cyme is "a true axillary medium branch of the cyme unit." This branch, originally part of a larger hypothetical ancestral paniculoid inflorescence in the Scrophulariales, has become reduced to a pedicelled, but unbracted, single flower through internode contraction or condensation (Figures 12-16).

In an evaluation of familial relationships in the order Scrophulariales it is important to realize that this distinct pattern of pair-flowered cymes has become phylogenetically fixed for the family Gesneriaceae as a unit. The same pattern occurs also in a few genera of New World Scrophulariaceae, e.g., in all species of *Calceolaria*, in all thyrsic species of *Penstemon*, and in species of *Russelia* and *Tetranema* (Weber, personal communication). More typical for the Scrophulariaceae, however, is the conventional cyme unit with one terminal flower.

Some species of *Besleria* in my greenhouse collection (*B. affinis* Morton, *B. laxiflora* Bentham) show branched front flowers as a remnant of an apparently more primitive condition (Figure 21). Internodal contraction, a basic element in Weber's thesis, may also play a role in vegetative shoot development of the Gesnerioideae: it may serve as an explanation for the curious growth pattern of *Sinningia tuberosa* (Mart.) H. E. Moore. The mature plant consists only of a rooted tuber from which periodically sprouts a single large leaf (or several single leaves from different eyes of the tuber), followed by "partial florescences" (see Figure 22 for new terminology) arising from other eyes of the large tuber. I have not yet been able to obtain seed from my greenhouse collection of this Brazilian plant to study the development of seedlings and juvenile stages of this strange species so reduced in its vegetative habit. The same situation apparently applies also to the mono-

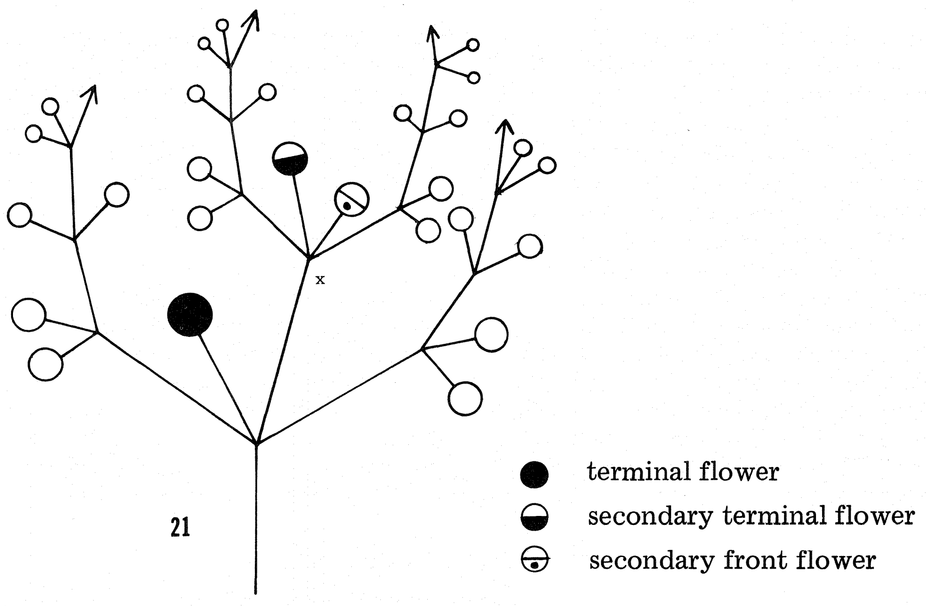


Figure 21: Ebracteate partial florescence of *Besleria affinis* Morton (GRF greenhouse acc. no. W-1829) with ramification replacing the front flower at x.

typic genus *Lembocarpus* from Surinam, in which *L. amoenus* Lwbg. is acaulescent, with the few leaves and partial florescences arising directly from the small tuber. This species appears to be closely related to *Sinningia* (see below). Efforts are presently being made to obtain live specimens from Surinam.

Weber's study of inflorescences is based on Troll's (1964, 1969) monumental work on inflorescences which has not yet been absorbed by the American school of botanical thought. The adoption of Troll's concepts and terminology for the Gesneriaceae appears to be rather logical since Troll's work represents the only unified and most thoroughly evaluated system available today. In Troll's terminology, the Gesneriaceae have polytelic (= indeterminate) synflorescences (= systems of inflorescences) of both bracteose or frondose forms. The indeterminate florescences (= the main branch or the side branches of the synflorescence) are thyrses consisting of determinate twin-flowered partial florescences (= pair-flowered cymes). Figure 22 explains Troll's terminology applicable for the Gesneriaceae (Troll, 1964, p. 539). Of special importance are the precise terms used for the various types of bracts occurring in the gesneriaceous partial florescence: bract, prophyll, and the subtending bract (Figure 22). Troll's system facilitates the recognition of homologous and non-homologous structures. Polytelic synflorescences are also typical for the families Scrophulariaceae, Orobranchaceae, Lentibulariaceae, Lamiaceae, and Asteraceae, contrasting with the completely monotelic (= determinate) synflorescences in such families as the Solanaceae, Boraginaceae, and the majority of the Rubiaceae. The overwhelming majority of the genera of the Gesnerioideae have frondose synflorescences; bracteose synflorescences occur only in the tribe Gloxinieae, in the genera *Diastema*, *Koellikeria*, *Monopyle*, and *Smithiantha*. Frondo-bracteose or intermediate situations occur in some species of *Kohleria*, *Heppiella*, and *Sinningia*.

The gesneriaceous partial florescence has an opposite-decussate phyllotaxy and presumably evolved from an ancestral inflorescence system that was opposite-decussate in structure. It is, therefore, noteworthy that the genus *Gesneria* (including *Rhytidophyllum*) has the same opposite-decussate twin-flowered cymes as the rest of the Gesnerioideae, even though the leaf arrangement in most of the species in *Gesneria* is alternate, a rare phenomenon in the Gesneriaceae. This indicates 1) that the fixation of the pair-flowered gesneriaceous cyme occurred phylogenetically *before* the shift to the alternate leaf arrangement, and 2) that the alternate leaf arrangement, usually considered a more primitive feature than opposite leaves, is a secondarily derived element in the advanced family Gesneriaceae.

It is further noteworthy that prophylls and subtending bracts are typically present in all members of the tribes Gesnerieae, Gloxinieae, Episcieae, and Napeantheae (except when the cyme is reduced to a single flower). The same bracts are, however, absent for all members of the tribe Beslerieae, including the genera *Anetanthus*, *Resia*, and *Tylopsacas*. The presence or absence of floral bracts thus becomes an important generic and tribal character in the Gesnerioideae. It becomes evident that comparative morphology of the inflorescences, based on a carefully researched system, has far greater importance to plant taxonomy and phylogeny than was realized previously.

CHAPTER 7: THE COROLLA

Most of the genera of the Gesnerioideae in need of reorganization were established one or two hundred years ago on the basis of the shape of the

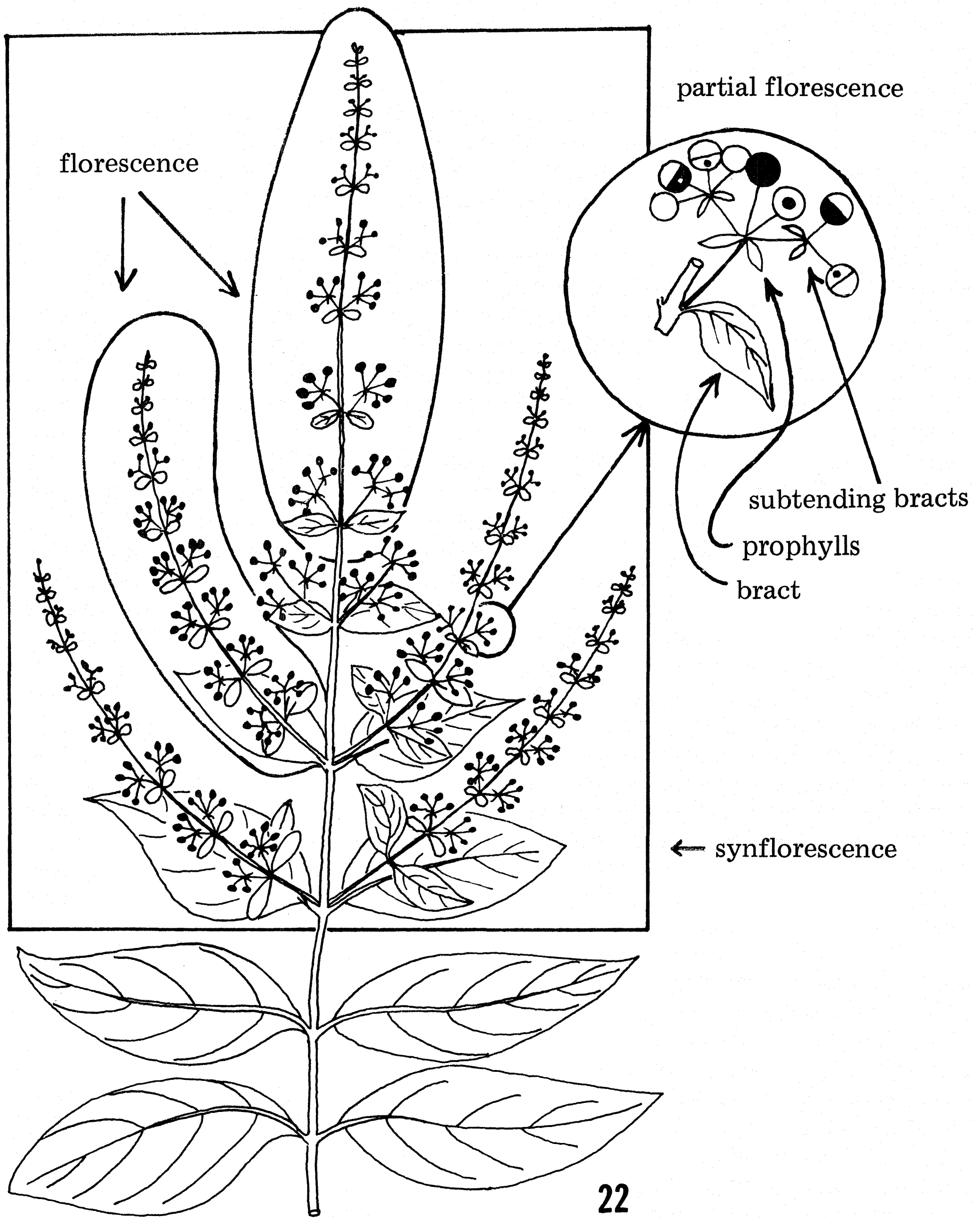


Figure 22: Schematic drawing of a typical pattern of a gesneriaceous inflorescence (e.g., *Sinningia aggregata*), with Troll's terminology of inflorescences).

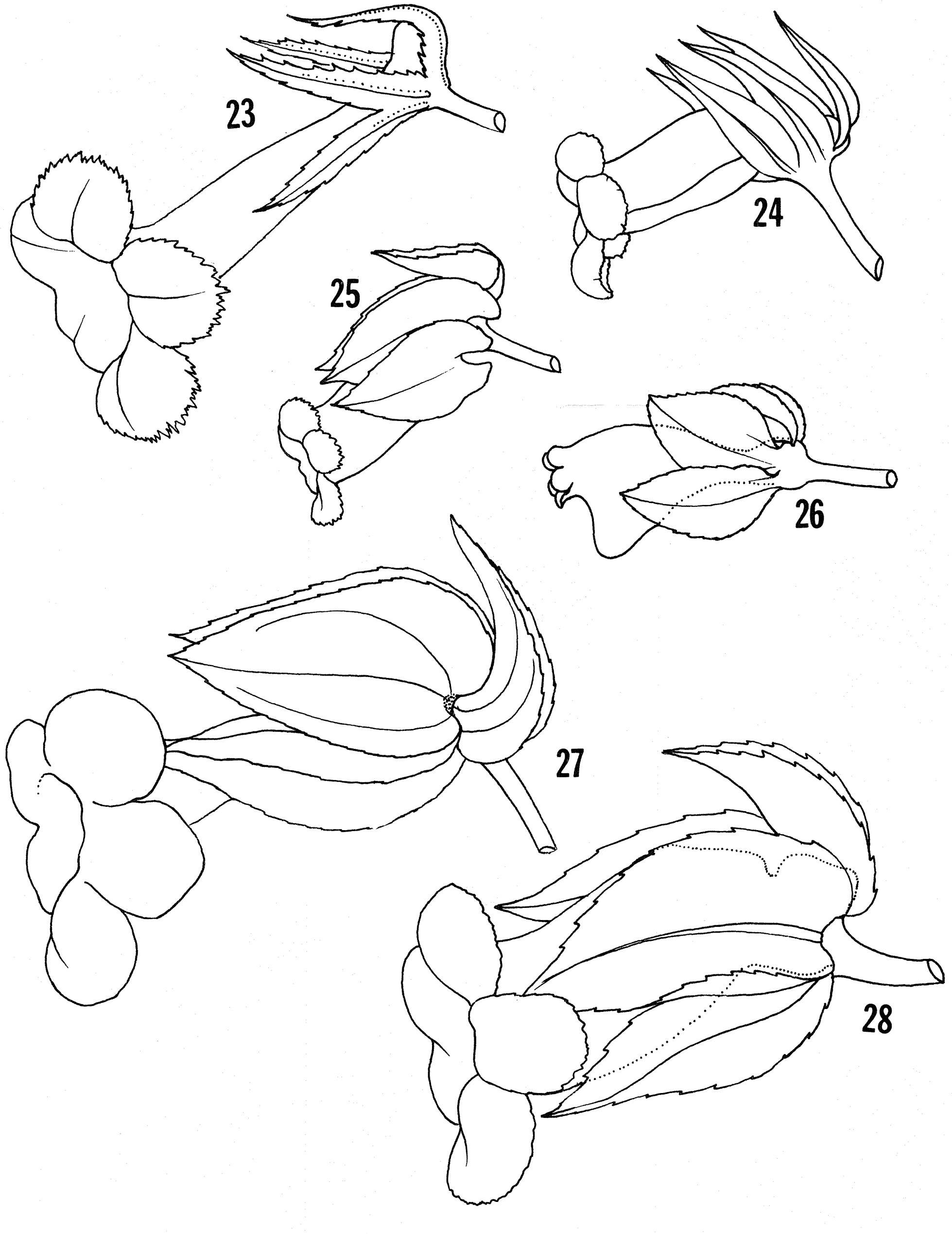
corolla and the calyx, without an understanding of the biology of pollination. The traditional classification of the New World Gesneriaceae by floral shapes often resulted in a pigeon-holing of types of pollinators. Such a scheme reveals little of the actual relationships among the plant taxa. It has now become evident that in the Gesnerioideae different species within the same genus may be pollinated by a diverse range of pollinating agents (Wiehler, unpublished data). The same phenomenon occurs in other plant families (Vogel, 1954; Straw, 1956; Sprague, 1962; Grant & Grant, 1965, 1966-67; Dodson, 1965). Closely related species can possess quite divergent shapes and colors of the corolla and can exist sympatrically without the occurrence of natural hybridization. The specificity of the divergent pollinators is, in fact, the only effective barrier against interbreeding.

One example may illustrate this point: In Colombia, between Cali and Buenaventura, I found six species of *Drymonia* flowering sympatrically within a range of less than 50 meters. The creeping and climbing vines of several of the species were intertwined in some instances. The flowers, especially the corollas, of these six species are very distinct from each other. The shapes and colors of the corollas indicate that two species are pollinated by hummingbirds, one by bats, another by moths, and two by Euglossine bees in search of food (Figures 23-28). The pollinators of four of the species had been identified during previous collections. It needs to be mentioned here that the pollination studies and observations still continue and that it is possible, after considerable field experience, to deduce the type of pollinator from the shape, color, texture, position, and odor of the corolla. Seven other species of *Drymonia* grew within a distance of five kilometers along the road, probably still in a sympatric relationship to the six aforementioned species, considering the mobility of the pollen carriers.

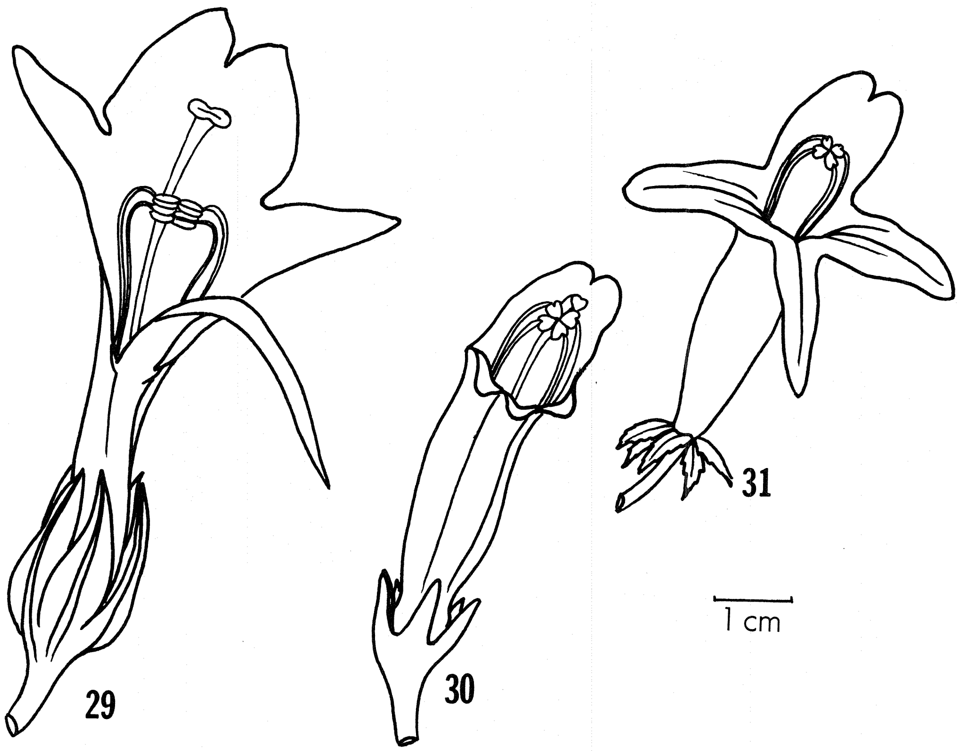
The close genetic relationship of species with different floral types and colors is shown by the usually high degree of fertility of their artificially produced hybrids, as in the genera *Achimenes* (Cooke & Lee, 1966; Wiehler, 1976a), *Sinningia* (including *Rechsteineria*, Clayberg, 1968, 1970), *Gloxinia* (including *Seemannia*, Wiehler, 1976a, 1976b), and *Nematanthus* (including *Hypocyrta*, Wiehler, unpublished data). The reconsideration of these and other genera is, however, based not only on pollination biology and cytogenetic data, but in each case series of important morphological characters unite the regrouped taxa.

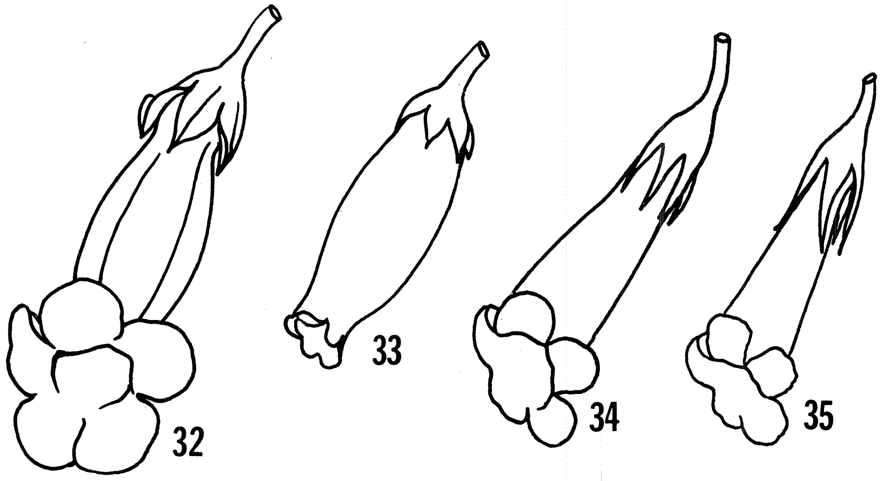
The absence of genetic barriers in closely related taxa has made hybridization experiments a useful tool in the study of the Gesnerioideae. Twenty-nine intergeneric hybrid combinations (based on the traditional classification) produced by the author during the last eleven years indicate that some previously held generic and tribal concepts may be invalid (Wiehler, 1976b). Species placed in different genera, distinguished mainly by strikingly different shapes and colors of the corolla, were found to be congeneric. In these cases the parents share important gross morphological features and the same chromosome number; their hybrids are completely or partially fertile. In those instances where parental species were not suspected of close relationship, hybrids revealed either complete sterility or a very low degree of pollen stainability (3-14%). The "intertribal" hybrids produced by the author between species of genera of five tribes are one of the reasons cited below for the proposed uniting of these tribes into a single unit.

Just as closely related species within the same genus may have diverse pollinators and varied shapes of corollas, the converse of this situation may



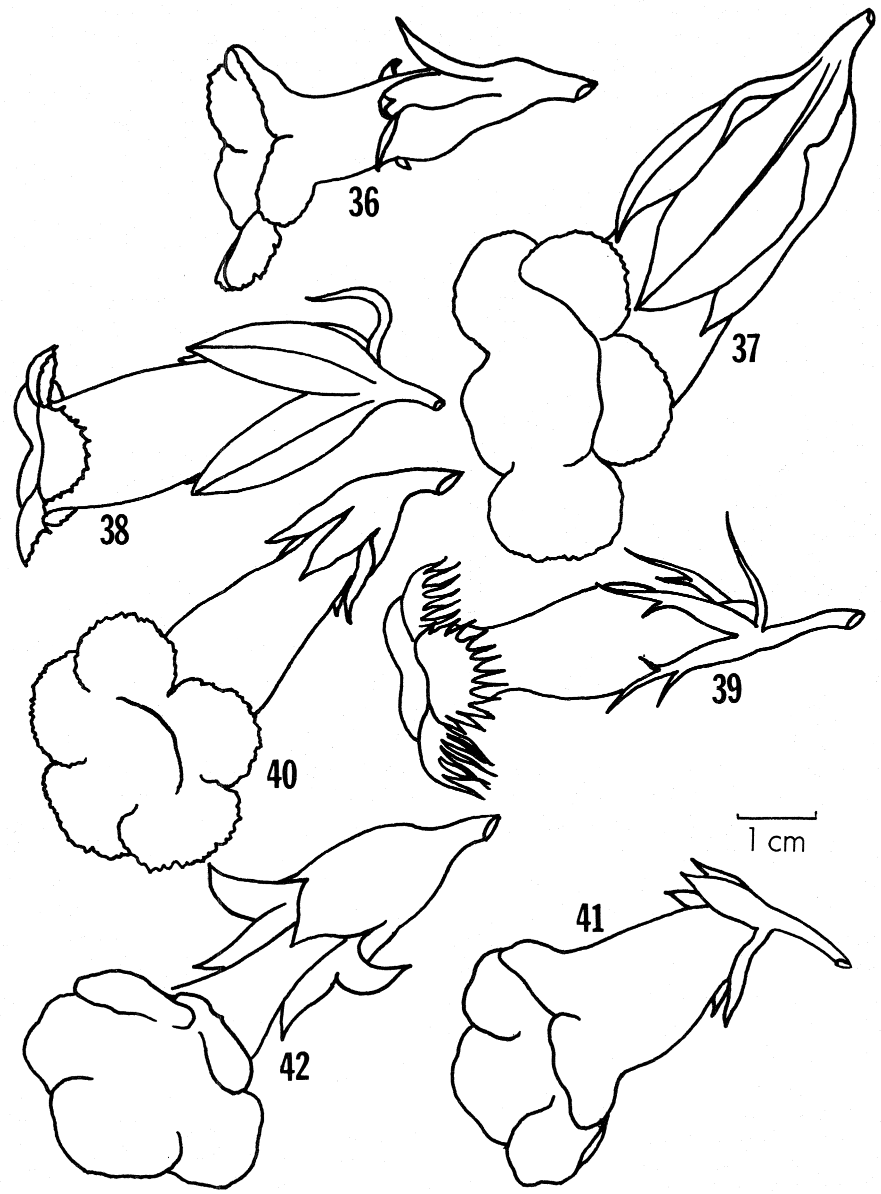
Figures 23-28: The flowers of six sympatric species of *Drymonia* from Colombia, varying in shape and size, and attracting different types of pollinators. (All illustrations natural size.) 23. *Drymonia luteola* Wiehler: corolla pale yellow, presumably pollinated by a moth. 24. *Drymonia warszewicziana* Hanst.: corolla pale yellow, with a maroon nectar-guide, pollinated by Euglossine bees elsewhere. 25. *Drymonia ornithantha* Wiehler: corolla tube and limb rose-red, tube inside red, hummingbird-pollinated. 26. *Drymonia coriacea* (Oersted) Wiehler: corolla red, hummingbird-pollinated. 27. *Drymonia killipii* Wiehler: corolla tube cream-white, the limb royal purple, the throat yellow, spotted with brown, a yellow nectar-guide inside; lemon-scented. probably pollinated by a Euglossine bee. 28. *Drymonia serrulata* (Jacq.) Mart.: corolla off-white, with faint red lines on the limb; cabbage-scented; bat-pollination observed elsewhere.





Figures 29-31: Hummingbird flowers with columneoid or hooded corollas found in different genera and tribes of neotropical Gesneriaceae. (All illustrations natural size.) 29. *Columnea nicaraguensis* Oersted. 30. *Sinningia cardinalis* (Lehm.) H. E. Moore 31. *Asteranthera ovata* (Cav.) Hanst.

Figures 32-35: The same kind of red hummingbird flowers with tubular corollas found in the genera *Kohleria* and *Moussonia.* 32. *Kohleria eriantha* (Benth.) Hanst. 33. *Kohleria tubiflora* (Cav.) Hanst. 34. *Moussonia elegans* Decaisne. 35. *Moussonia septentrionalis* (Morton) Wiehler.



Figures 36-42: Euglossine corollas found in different genera of neotropical Gesneriaceae. (All illustrations natural size.) 36. *Alsobia punctata* (Lindl.) Hanst. 37. *Drymonia macrantha* (Donn. Smith) Gibson. 38. *Nautilocalyx dressleri* Wiehler. 39. *Paradrymonia ciliosa* (Mart.) Wiehler. 40. *Achimenes glabrata* (Zucc.) Fritsch. 41. *Gloxinia sarmentiana* Gardner ex Hook. 42. *Sinningia guttata* Lindl.

also occur: the same type of shape and color of the corolla may appear in distantly related genera because their flowers are visited by similar types of pollinators. Examples of such parallelism are the characteristic red corollas with a long, narrow tube and a galea in species of *Columnea*, *Sinningia (Rechsteineria)*, and *Asteranthera*, all of which are pollinated by hummingbirds. Each of these genera belongs to a different tribe, in both the old and new systems. Yet because of the shape of the corolla, *Asteranthera ovata* was first described as a species of *Columnea* (Figures 29-31). Other examples of such parallel floral evolution are found in the red tubular corollas of *Kohleria* and *Moussonia* (Figures 32-35). For about one hundred years the latter has been joined to the former only on the basis of similar shape of the corolla (Bentham, 1876). We know now that these two genera differ in all decisive generic characters, including chromosome numbers (Lee, 1962-67). The funnelform corollas (Figures 36-42) in species of *Nautilocalyx*, *Sinningia*, *Achimenes*, *Alsobia*, *Drymonia* and other genera reveal the same trend of parallelism in floral development of genera not closely related. The corollas are usually white, with a broad limb, and represent co-adaptation to pollination by various taxa of female Euglossine bees. The interpretation of gesneriads with this type of flower has not infrequently been confused during the last century (Wiehler, 1976a). Even in recent treatments of the New World Gesneriaceae, the similarity of shapes of the corolla has been considered indicative of close affinity among taxa in different tribes (cf. Leeuwenberg, 1958, pp. 294-297, i.e., the relationship of *Sinningia* to *Nautilocalyx*).

The most striking example of parallel floral evolution within the Gesnerioideae is evident in the *Hypocyrta*-type corolla phenomenon (Figures 43-61). The *Hypocytra-Nematanthus* complex (these two genera have now been united under the name *Nematanthus*) is a distinct taxon in the Episcieae, separated from other genera of the tribe by geographical distribution (southeastern Brazil), chromosome numbers, and type of fruit. In this group the typically red corolla has a prominent pouch below the tightly constricted throat. This shape of the corolla is the principal characteristic of the genus *Hypocyrta* Martius (*sensu* Hanstein, 1854, 1864), but other shapes of the corolla also occur in this complex (cf. Figure 57). The red, orange, and sometimes yellow corollas attract hummingbirds as effective pollinators (Wiehler, unpublished data, for the extra-Brazilian genera, below; verification is still necessary for *Nematanthus* in Brazil). The reason for the existence of the inflated pouch is not fully understood. Such a structure may serve as target enlargement (cf. frontal view of flowers, Figures 53 and 55), aiding in more

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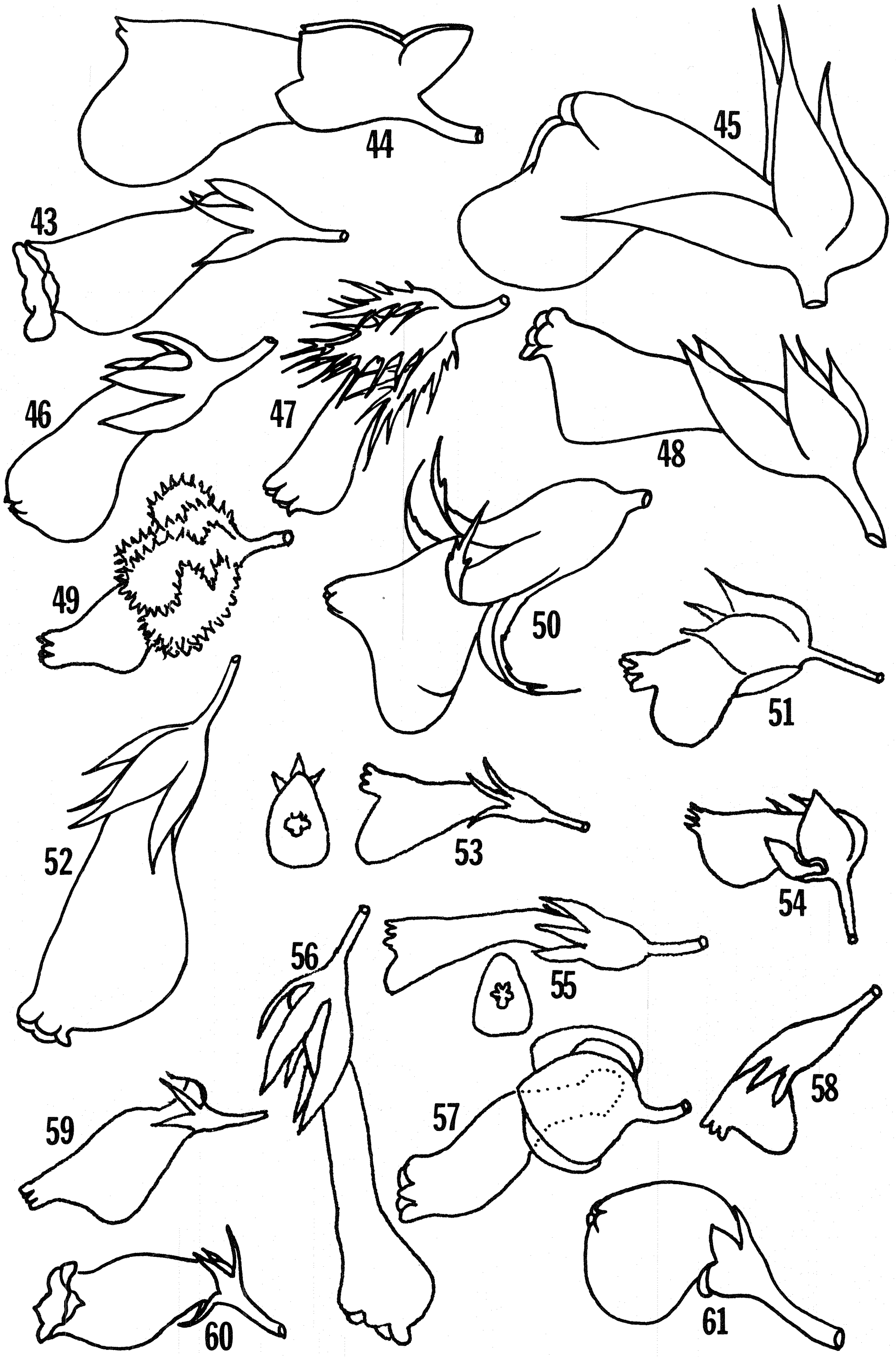
Figures 43-61: Hypocyrtoid or pouched corollas found in different genera and tribes of neotropical Gesneriaceae. (All illustrations natural size.) 43. *Besleria leucostoma* (Hook.) Hanst., first published as *Hypocyrta leucostoma* Hook. 44. *Gasteranthus crispus* (Mansf.) Wiehler. 45. *Gasteranthus macrocalyx* Wiehler. 46. *Alloplectus bolivianus* (Britton) Wiehler. 47. *Alloplectus hypocyrtiflorus* Wiehler. 48. *Alloplectus sp. nov., Pennell 14010.* 49. *Alloplectus teuscheri* (Raymond) Wiehler, first published as *Hypocyrta teuscheri* Raymond. 50. *Paradrymonia hypocyrta* Wiehler. 51. *Pentadenia hypocyrtantha* Wiehler. 52. *Pentadenia trollii* (Mansf.) Wiehler. 53. *Neomortonia nummularia* (Hanst.) Wiehler, first published as *Hypocyrta nummularia* Hanst. 54. *Corytoplectus congestus* (Lindl. ex Hanst.) Wiehler. 55. *Nematanthus fissus* (Vell.) L. Skog. 56. *Nematanthus fritschii* Hoehne. 57. *Nematanthus hirtellus* (Schott) Wiehler. 58. *Nematanthus hirsutus* (Mart.) Wiehler. 59. *Nematanthus wettsteinii* (Fritsch) H. E. Moore. 60. *Gloxinia sylvatica* (Kunth) Wiehler. 61. *Pearcea hypocyrtiflora* (Hook.) Regel.

See also Figure 26: *Drymonia coriacea* (Oersted) Wiehler.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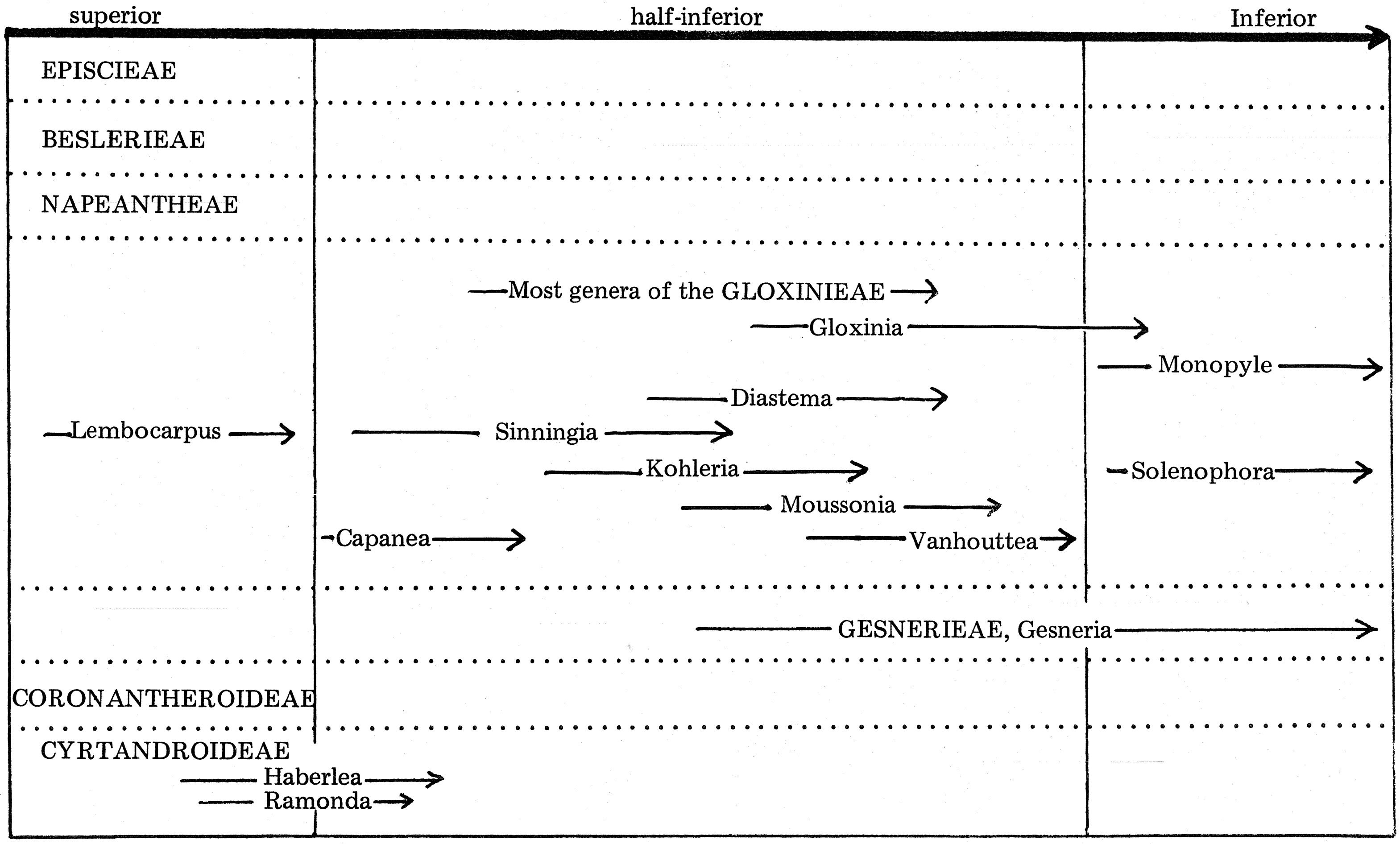


TABLE 7: TRENDS IN OVARY POSITION IN THE GESNERIACEAE

effective pollination, as opposed to the regular tubular corolla which offers very little of a showy surface in frontal view. The restricted aperture of the corolla may also be a device for sympatric isolation from species pollinated by larger insects such as Euglossine bees. The same *Hypocyrta*-type corolla occurs in other gesneriad genera: in *Alloplectus*, *Besleria*, *Drymonia*, *Gasteranthus*, *Gloxinia*, *Paradrymonia*, *Pearcea*, *Pentadenia* and *Trichantha*. Many of these species with pouched flowers are native to Ecuador, Peru, and Bolivia; some of these were originally attributed to *Hypocyrta* and will need to be transferred. The genus *Gasteranthus* has at least 19 species with *Hypocyrta*-shaped corollas (Wiehler, 1975g).

CHAPTER 8: OVARY POSITION

The evolutionary plasticity of the Gesnerioideae can further be demonstrated by the fact that in the large order Scrophulariales this subfamily is the only group which shows a strong tendency toward the development of an inferior ovary. Two tribes, the Gesnerieae and the Gloxinieae, with 25 genera and about 370 species, have an ovary position ranging from semi-inferior to completely inferior (Table 7). The Cyrtandroideae, traditionally characterized by a superior ovary position, also contain a few taxa with some degree of an inferior ovary (*Haberlea* Friv., *Ramonda* L. C. Rich.; see Weber, 1971). Hartl (1956a) reports an inclination toward an inferior ovary in some species of such scrophulariaceous genera as *Calceolaria* L., *Penstemon* Mitch., and *Buddleia* L. (also placed in the Loganiaceae or Buddleiaceae). In botany text books these taxa are supposed to have strictly superior ovaries.

The position of the ovary as a taxonomic criterion in the Gesneriaceae is currently being re-evaluated. A separation of subfamilies by ovary position, as was done by Fritsch (1893/94) and all previous workers in the Gesneriaceae, is no longer tenable. With a few exceptions, however, ovary position remains a reliable character at the tribal and generic levels in the Gesnerioideae. In this new classification I have placed the genera *Goyazia* and *Lembocarpus*, both characterized by a superior ovary in their original descriptions, in the tribe Gloxinieae in which all other genera have semi-inferior or completely inferior ovaries. *Goyazia*, a genus of two small species of rhizomatous plants with tiny flowers, had been attributed to the tribe Beslerieae in which no rhizomes occur. An examination of recently collected material of both species showed the ovary to be semi-inferior at anthesis.Since on herbarium sheets the pressed and dried ovaries at anthesis are somewhat less than one millimeter long, a misjudgment in the original description is entirely possible. In *Lembocarpus amoenus* Lwbg., a small species reduced to a tuber, single leaf, and inflorescence, the ovary is, however, superior. This monotypic genus has been without tribal affiliation. I have no hesitation in placing *Lembocarpus* next to the tuberous genera *Sinningia* and *Lietzia* in the tribe Gloxinieae. Two dwarf species of *Sinningia*, *S. concinna* (Hook.) Nichols. and *S. pusilla* (Mart.) Baill., have almost completely superior ovaries at anthesis. These ovaries become semi-inferior only in the matured fruiting stage. The same situation occurs in the dwarf species *Gloxinia villosa* (Gardner) Wiehler (Wiehler 1976a). Observation of living material and hybridization experiments with *Lembocarpus amoenus* recently brought into cultivation, may soon indicate the relationship of this species to *Sinningia*.

A correlation between the evolution of the inferior ovary and hummingbird pollination has been postulated by Grant (1950) who stressed the need for protection of the ovules from the pollinators. As stated before, the center of distribution of the subfamily Gesnerioideae, Colombia and Ecuador, coincides with the center of distribution of the hummingbird family Trochilidae. It has to be noted, however, that ornithophily predominates in the tribe Episcieae in which all species have a superior ovary (see Table 4). The ovary is likewise superior in the large, mostly ornithophilous genus *Besleria*. Conversely, only about half the species in the tribes Gloxinieae and Gesnerieae, marked by the development of the inferior ovary, are presently pollinated by hummingbirds. If indeed there is a relationship between ornithophily and the inferior ovary in the Gesnerioideae, it may be postulated that at one point in history the ancestral stock of the tribes Gloxinieae and Gesnerieae had shifted to hummingbird pollination which concomitantly triggered the development of the inferior ovary. The other modes of pollination in these two tribes (by female and male Euglossine bees, bats, butterflies, moths, and flies) may represent later evolutionary events which did not result in another reversal of ovary position. For reasons unknown, the tribe Episcieae has shown a different kind of response to hummingbird pollination. Enlarged, leafy calyces and waxy, thick-tissued corolla-tube bases envelop the ovary and nectary in many species, presumably as safeguards against hole-pecking or puncturing nectar thieves (= hummingbirds, bees, and wasps). In the tribes Gloxinieae and Gesnerieae small and narrow calyx lobes are more prevalent.

CHAPTER 9: THE NECTARY

Cross-pollination is a major feature contributing to the success of the angiosperms dominating the floras of the earth. The nectar of the angiosperm flower is one of the prime sources of attraction for the various pollinating agents, but the importance of the nectary in the process of flowering has not yet received the full attention of taxonomists and floral morphologists. Although the nectary is an important floral structure, it has often been labelled disinterestedly "the hypogynous disk," without reference to function or reason for existence. General and basic information on the nature and phylogeny of the nectary in angiosperm families is still scarce, spotty, and at times, speculative (Brown, 1938; Agthe, 1951; Fahn, 1952, 1953, 1967, pp. 413-422; Frei, 1955; Frey-Wyssling, 1955; Kugler, 1970, pp. 59-69; Rao, 1971). Detailed information on nectary development in individial families is still a rarity, and contemporary botanists specializing in a particular plant family are often ignorant about the nectary (and pollination) in their selected group.

Nectaries occur in various places on the angiosperm flower, and there has been speculation whether the nectary in some cases represents a fifth floral whorl, namely a transformation of an extra cycle of stamens, carpels, or perianth parts -- or whether it may be a *de novo* outgrowth on one of the four typical floral whorls. Wilson (1974a, 1974b) recently examined the vascularization of nectaries in some 130 species of Gesneriaceae and concluded that in this family the nectary is an enation, an outgrowth of the ovary wall or of the receptacle, "and not an alteration of some preexisting cycle of floral parts" (p. 256). After studying the floral ontogenesis of *Monophyllaea*, *Epithema*, and *Rhynchoglossum*, Weber (personal communication, 1979) agrees with this fundamental assessment. Rao (1971), impressed by the diversity of the origin of the vascular supply of the nectaries in the closely related family Acanthaceae, comes to a similar conclusion about the derivation of the nectary in the Acanthaceae: it is a newly arisen tissue. He also suggests a more functional approach to floral morphology by regarding the nectary, when present, as a fifth type of floral organ, regardless of its origin. The nectary "is an organ *sui generis* getting its vascular supply from whatever traces are conveniently located" (p. 449). This functional approach, namely treating the nectary as a type of floral organ on the same level with the calyx, corolla, stamens, and carpels, elevates the long-neglected nectary to its rightful place in floral biology.

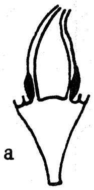
My own investigations and inquiries to specialists on some of the pertaining families indicate that the typical nectary in the order Scrophulariales and related groups is a ring-shaped structure around the base of the ovary, between the whorls of carpels and epipetalous stamens (cf. Figure 62b, c). Therefore, it seems logical to regard the annular nectary as basic for the Gesneriaceae. In the subfamily Cyrtandroideae the nectary is, when present, always ring-shaped (Wilson, 1974a), but in the genus *Dasydesmus* Craib this ring is deeply five-lobed (Burtt, 1963). In the subfamily Coronantheroideae the nectary structure is of a different type in all genera, distinct from the rest of the Gesneriaceae, and thus furnishing a valuable taxonomic key character for the separation of this austral group. The nectary tissue is adnate to or part of the outside ovary wall, forming a pulvinate ring at the base of the ovary (Figure 62a). There appears to be no variation from this pattern in the 9 genera and 20 species of this group.

In the subfamily Gesnerioideae an annular nectary, free from the ovary wall, occurs in the genera *Gesneria*, *Besleria*, *Cremosperma*, *Resia*, *Moussonia*, *Heppiella*, *Gloxinia*, *Koellikeria*, *Smithiantha*, *Eucodonia*, and *Achimenes* (Figure 62b, c, g,). The nectaries of all other genera in this subfamily are modifications of the annulus. Therefore, the Gesnerioideae have more variation in nectary shape than any other group in the Scrophulariales or Personales. In fact, the American Gesneriaceae apparently show more evolution in the structure of the floral nectary than any other family of the angiosperms.

There are two different lines of nectary development in the subfamily Gesnerioideae, both starting from the complete annulus, either around the base of the ovary in taxa with superior ovaries, or with the annulus above the point of adnation of the floral tube (joint tissue of calyx, corolla, and stamens) to the ovary in taxa with inferior or semi-inferior ovaries. In the tribe Beslerieae the trend of nectary evolution is from a complete, evenly shaped ring via a dorsally thickened annulus to a semi-annular structure, ending in a truly single dorsal gland (Figure 62 c-f).

In the tribes Gloxinieae and Episcieae the ring-shaped nectary evolves via a five-lobed ring to five separate glands of equal size (Figure 62 g-i). The next step is the enlargement of the two dorsal glands which then unite to form an apparently single structure with two or four lobes (rarely one lobe); the two lateral glands and the one ventral gland become less prominent and disappear (Figure 62 j-p). In this line of nectary development the apparently single large dorsal gland consists actually of two connate glands. The large, double, dorsal gland is the type of nectary occurring most frequently in the Gesnerioideae, namely in about 650 species [in all but two genera of the tribe Episcieae (ovary superior) and in the genus *Solenophora* (ovary inferior) in the tribe Gloxinieae]. In a few genera the nectary is a vestigial and non-functional structure, or has completely disappeared. Figure 62 shows the various nectary structures in the neotropical Gesneriaceae and lists the

Figure 62. Evolution of the nectary in neotropical Gesneriaceae

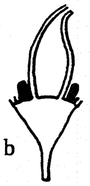


a

I. SUBFAMILY CORONANTHEROIDEAE

Nectary tissue part of ovary wall, adnate to base of ovary, always ring-shaped, pulvinate.

In temperate southern South America:	*Asteranthera* *Mitraria* *Sarmienta*



b

II. SUBFAMILY GESNERIOIDEAE

Nectary tissue, when present, free from ovary wall as a separate organ, either ring-shaped (='primitive') or composed of separate glands.

(The nectary is annular in the tribe Gesnerieae, absent in tribe Napeantheae. These taxa are thus not further treated here.)

A. THE BESLERIEAE LINE OF NECTARY DEVELOPMENT

c		Nectary ring-shaped.	most *Besleria* spp. *Cremosperma* *Resia*
d		Nectary ring-shaped, but ring thickened dorsally.	*Gasteranthus* *Cremosperma* few *Besleria* spp.
e		Nectary semi-annular.	*Gasteranthus*
f		Nectary a single dorsal gland.	*Reldia* *Besleria comosa*
g		Nectary ring-shaped, with 2 enlarged dorsal lobes.	*Tylopsacas*
h		Nectary an open ring, sheath-like, 5-lobed.	*Anetanthus*

B. THE GLOXINIEAE AND EPISCIAE LINE OF NECTARY DEVELOPMENT

i		Nectary ring-shaped.	*Achimenes* *Eucodonia* *Moussonia* *Koellikeria*	*Smithiana* *Gloxinia* *Heppiella*
j		Nectary a 5-lobed ring.	*Kohleria* *Goyazia*	*Gloxinia*

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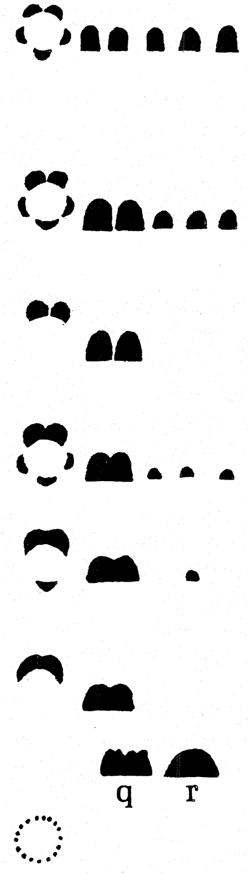
Figure 62. (continued from facing page)



k	Five separate glands of equal size.	*Kohleria* *Gloxinia* *Pearcea* *Paliavana* *Sinningia*	*Diastema* *Capanea* *Parakohleria* *Vanhouttea* *Pentadenia*
l	Five glands, the 2 dorsal ones enlarged.	*Kohleria* *Parakohleria*	*Sinningia*
m	Nectary reduced to 2 large, separate dorsal glands	*Sinningia*	
n	The 2 large dorsal glands connate, plus 3 small glands.	*Sinningia* *Corytoplectus*	*Kohleria* *Pentadenia*
o	The 2 large dorsal glands connate, plus 1 small ventral gland.	*Sinningia tubiflora* *Corytoplectus* some spp. of *Columnea* and *Dalbergaria*	
p	Nectary reduced to 2 large, connate, dorsal glands.	*Solenophora* most taxa of the Episcieae, except *Pentadenia* and *Corytoplectus*	
s	Nectary absent or non-functional.	*Monopyle* *Anodiscus* *Niphaea*	*Gloxinia* *Bellonia* *Phinaea*

genera involved. In the monotypic tribe Gesnerieae with about 69 species (ovary inferior or semi-inferior) the nectary is either an evenly shaped or five-lobed ring. The nectary is completely absent in the monotypic tribe Napeantheae with over 30 species (ovary superior). Osmophore tissue on the corolla tube has replaced the nectary tissue in a few species of *Gloxinia* (Wiehler, 1976a) and in the genus *Monopyle*. These taxa are pollinated by male Euglossine bees in search of fragrance compounds. Most of the other genera without a nectary (*Bellonia*, *Phinaea*, *Niphaea*, and *Napeanthus*) are characterized by the same solanoid type of corolla structure: rotate, almost flat, (secondarily actinomorphic in a few species), always white, and with four or five free or connate anthers in the center. The pollinators of this type of corolla, almost foreign in the Gesneriaceae, have not yet been observed. These flowers may belong to the vibratile ("buzz") pollination syndrome. The anthers in *Bellonia* are poricidally dehiscent (see Table 9).

In the American Gesneriaceae the nectary in its varied form is a prominent feature in the total floral structure. The reason for this proliferation of nectary shape in this neotropical plant group is not obvious at present, for there appears to be no close correlation between nectary structure, corolla structure, pollinator type, and ovary position. It is, however, possible that the reduction of the ring-shaped nectary to a large dorsal structure represents an adaptation to ornithophily. A dorsally located gland in a hummingbird-pollinated flower cannot be reached or injured by the long and sharp beak of a bird. Among the Gesnerioideae ornithophily is most prominent in the tribe Episcieae for which the dorsally located nectary gland is typical. Many species in this tribe with this kind of gland are not at all hummingbird-pollinated flowers, but are pollinated by female Euglossine bees, while a few are pollinated by bats, moths, and butterflies. Furthermore, the ornithophilous species in the genera *Gesneria*, *Besleria*, *Moussonia*, *Heppiella*, *Gloxinia*, and *Achimenes* have a ring-shaped nectary, without any tendency toward a dorsal thickening (except in some species of *Besleria*). Two-thirds of the species of *Gasteranthus* are ornithophilous while the other third is gynandro-euglossophilous, but all species of the genus have either a dorsally thickened nectarial ring or a half-ring located on the dorsal side at the base of the ovary (Figure 62 d-e). It is, however, possible that euglossophily in the Episcieae and Beslerieae is a secondary phenomenon, developed after ornithophily, with the nectary structure remaining fixed for ornithophily. Did the female euglossine mode of pollination in the neotropics arise after hummingbird pollination was widespread?

The development of the inferior ovary is another special feature within the American Gesneriaceae, but this does not seem to correlate with the proliferation of nectary structures: *Besleria* (ovary superior), *Heppiella* (ovary semi-inferior), and *Gesneria* (ovary usually inferior) have annular nectaries, while the double dorsal gland occurs in most of the genera of the Episcieae (ovary superior), in *Sinningia tubiflora* (ovary semi-inferior), and in all species of *Solenophora* (ovary inferior).

The shape of the nectary is a very conservative character in the subfamily Gesnerioideae, usually consistent for each genus. This makes this floral organ a reliable taxonomic criterion on the tribal, generic, and sectional levels, and even on the subfamilial level in the case of the Coronantheroideae. In fact, in the Gesnerioideae the shape of the nectary is a more important taxonomic character than the shape of the corolla or the structure of any other floral organ. Most of the genera in the tribe Gloxinieae have a nectary of one particular shape. More variation, however, occurs within the genera *Gloxinia*, *Kohleria*, and *Sinningia* where the nectary shape becomes a sectional feature.

While emphasizing the conservative nature of the nectary shape in the American Gesneriaceae and stressing its usefulness as a taxonomic character, it is also true that the Gesnerioideae abound in exceptions to the rule. In a few species the nectary shape is somewhat variable. In *Gloxinia lindeniana* (Regel) Fritsch, known only from a single collection (made in 1868) in cultivation, the nectary on different flowers of the same plant varies from five, separate, thin, triangular glands to a thin five-lobed ring. In different collections of *Goyazia rupicola* Taubert the annular nectary is either evenly ring-shaped or five-lobed. But these exceptions represent only minor variations of a major theme.

The taxonomic value of the shape of the nectary in the classification of the Gesnerioideae cannot be over-emphasized. The shape of the nectary helps the botanist to separate such frequently confused genera as *Besleria* and *Alloplectus*, *Drymonia* and *Besleria*, *Heppiella* and *Kohleria*, *Kohleria* and *Moussonia*, *Diastema* and *Achimenes*, *Sinningia* and *Gasteranthus*, *Nautilocalyx* and *Sinningia* and many others. The difference in nectary structure is also one of the reasons for separating *Pentadenia* from *Columnea* on the generic level. *Pentadenia* has the most "primitive" type of nectary found in the tribe Episcieae. It consists of either five separate glands (Figure 62i) or three glands of equal size plus the two dorsal glands enlarged and partially connate (Figure 62 l). The typical nectary in *Columnea* is shown in Figure 62n. Some species of *Dalbergaria* have a thin and narrow, vestigial, non-functional ring around the base of the ovary, in addition to the typical large, double, dorsal gland.

Noteworthy cases of special nectary development in families near the Gesneriaceae are the epistaminal nectaries in the genera *Penstemon* Mitch. and *Chionophila* Benth. in the Scrophulariaceae, the single elongated gland in *Physostegia virginiana* Benth. in the Lamiaceae, and the five separate glands in *Echites hirsuta* Ruíz & Pavon in the Apocynaceae.

CHAPTER 10: PLACENTATION, OVULE POSITION, AND FRUIT

A functional approach to floral morphology has to consider how the type of placentation and the kind of fruit and its mode of dehiscence relate to the successful production and dispersal of seed. Next to pollen dispersal, seed dispersal is seen here as the second critical stage for decisive evolutionary change in the life cycle of a tropical angiosperm. There seems to be no published information available on the kind of selection pressures which brought about the various types of placentation in the angiosperm gynoecia, and we do not know about the advantages, if any, of parietal placentation for the Gesneriaceae in terms of successful seed dispersal (cf. Cronquist, 1968).

A discussion of placentation is of prime importance in a modern systematic treatment of the Gesneriaceae. The type of placentation has been regarded traditionally as a very basic and reliable taxonomic character, usually on the familial level. Thus the main criterion for separation of the two large families Scrophulariaceae and Gesneriaceae has been the type of placentation, axile in the Scrophulariaceae, parietal in the Gesneriaceae. However, we have known for a long time that each of these families has some species with partially axile and partially parietal placentation within the same ovary (i.e., in *Sarmienta repens* Ruiz & Pavón), that some otherwise *bona fide* Scrophulariaceae have unilocular ovaries (*Rehmannia* Liboschitz), and that some Gesneriaceae have axile placentation [*Asteranthera ovata* (Cav.) Hanst., *Hemiboea* C. B. Cl., *Monophyllaea* R. Br., *Stauranthera* Benth.]. The investigations of Leinfellner (1950, 1951), Hartl (1956a), and Weber (1971) have now demonstrated that there is no fundamental difference between the axile placentation of the Scrophulariaceae and the parietal placentation of the Gesneriaceae. According to the above representatives of the German school of carpology, both families have the same basic plan of development of the bicarpellate gynoecium, with axile placentation in the lower portion of the ovary and parietal placentation above, and both families have a similar spectrum of variation within this basic plan. The decisive difference lies in the shift of the focal point. In the Scrophulariaceae the area of maximum development of the fertile part of the placentae is the "ascidiate" or axile part, and in the Gesneriaceae the fertile region is the "symplicate" or parietal part. In the latter, the lower part is typically abbreviated or has disappeared altogether.

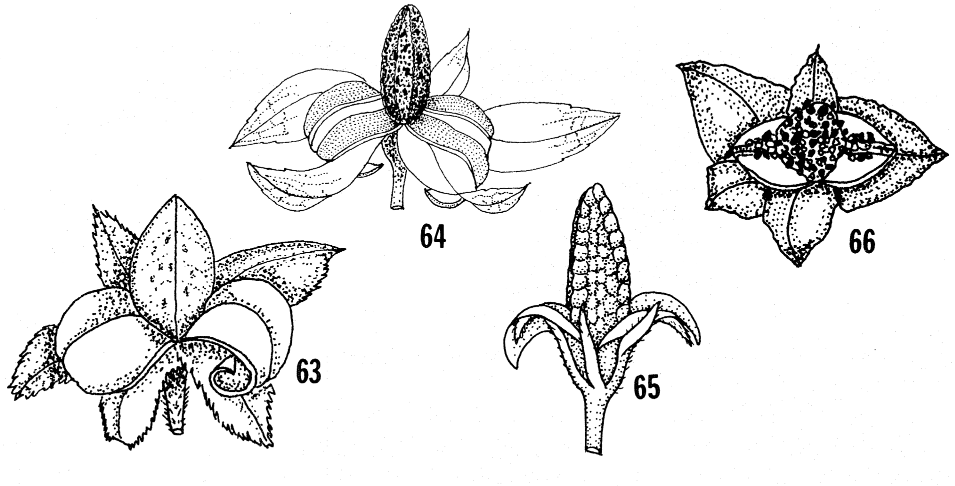
While these findings reveal once more the affinities between these two families, they also elucidate the difference. A cross-section of the middle of the ovary of the species in these two large plant groups will still reveal in about 96% of the cases whether one deals with a scroph or a gesneriad, and a combination of other characters (inflorescence, stamens, seed, seedling structure) places the rest of the taxa. One could, of course, argue for a merger of these two families since the placentation character (axile versus parietal) has lost part of its crucial value. But a systematic lumping of two large families to a total of over 5000 species may prove of little practical merit, especially if one considers that the relationship of the Scrophulariaceae to the Acanthaceae, Orobanchaceae, Bignoniaceae, and Lentibulariaceae appears to be equally close (cf. Hartl, 1956b, 1959). A study of the structure of the gynoecium with its axile, parietal, free-central, and apical types of placentation in the order Scrophulariales may best serve to give us a new appreciation for the close affinity of these comparatively recently evolved and advanced tubiflorous families, in contrast to the evolutionary isolation of many of the more primitive and "middle-aged" angiosperm families. A thorough understanding of the affinities between these tubiflorous families will have greater value than a taxonomic merger of these large groups into a single unwieldy unit or superfamily. A functional approach to this pseudoproblem will ask instead: what evolutionary forces brought about the different "types" of placentation among the Scrophulariales? Do these variations in placentation contribute now to the success of the species in this large order, in terms of pollination and seed dispersal (pollen tube growth, number and kind of seed produced, type of fruit, dehiscence and dispersal mechanisms, etc)? There are no answers as yet for the Gesneriaceae with their parietal placentation.

Some workers in the Gesneriaceae have emphasized that the position of the ovules on the placenta has taxonomic significance; Hielscher (1883), Sprague (1912), Leeuwenberg (1958, 1964, 1965, 1969), Ivanina (1965, 1966, 1967). The "outer" or "inner" surface of the placenta is then usually (and wrongly) equated with the abaxial or adaxial side of the carpel. Weber (1971) draws attention to this confusion and stresses that 1) only the adaxial side of the carpel can give rise to ovuliferous tissue, and that 2) the ovule-bearing placenta as a whole is an emergence, morphologically different from the carpel. It appears, therefore, of less vital importance on which portion of the placental arm the ovules are borne. Sprague and Leeuwenberg used ovule position on the placenta as a generic and sectional character in *Episcia* (*sensu lato*) and *Nautilocalyx*. A more extensive sampling of the species in these taxa, especially by using fresh greenhouse material in contrast to shrivelled and permanently distorted carpel structures from herbarium sheets, shows that the distinction between inner and outer surface of the placenta breaks down completely (Wiehler 1978b). Ovule position on the placenta has no taxonomic significance in the Gesnerioideae.

Until a few years ago the fruit of the neotropical Gesneriaceae was insufficiently known, mostly because of inadequate data on the labels of herbarium specimens.This pertains especially to the large tribe Episcieae and to some extent to the tribe Beslerieae. The fruit in these groups is hard to collect and to prepare as a dried permanent record; when present, it is difficult to evaluate. The new information, presented in Table 8, has come mostly from live material, namely, field work and greenhouse observations. A valuable pickled collection of fruit (and flowers) of the neotropical Gesneriaceae has been assembled in the laboratory of the Gesneriad Research Foundation.

The new information indicates that the various fruit types in the neotropical Gesneriaceae are, indeed, valuable taxonomic characters, especially on the generic and tribal levels. The fruit character, for instance, has helped to separate *Gasteranthus* from *Besleria*, *Cremosperma* from *Besleria*, *Corytoplectus* from *Alloplectus*, *Alloplectus* from *Columnea*, *Nematanthus*, *Paradrymonia*, and *Rufodorsia*, *Dalbergaria* from *Columnea*, and *Codonanthopsis* from *Codonanthe*. The berry-fruit in the tribe Episcieae is different from the berry-fruit in the tribe Beslerieae, and fruit characters separate the tribes Gloxinieae and Gesnerieae from the tribe Episcieae (see Table 8). In fact, the fruit has provided valuable criteria for the new classification of the neotropical Gesneriaceae.

As with other tropical fruit, some of the gesneriaceous fruit, especially in the taxa of the tribes Episcieae and Beslerieae, does not fit well into the conventional fruit classification. There seems to be no description in the literature of a rather common type of fruit in the Gesnerioideae, labeled here "display fruit," characteristic of the large genera *Drymonia*, *Alloplectus*, and *Nematanthus*, of the small genus *Codonanthopsis*, and of the subgenus *Codonanthella* of *Codonanthe*. It is a fleshy, bivalved capsule with loculicidal dehiscence whose valves separate at maturity from the placentae. These placentae, together with the mass of seeds and the enlarged, glistening funiculi, form an attractively colored cone-shaped structure or food body positioned upright on the receptacle. The two reflexed or convex carpel valves are usually strikingly colored on the inside (red, pink, yellow, or white) to offset further the food-body. This display is surrounded by contrastingly colored calyx lobes which have grown in size since anthesis (Figures 63, 64, and 66). This type of display fruit offers an outstanding visual target for the seed dispersal agents which are birds, fruit-eating bats, and possibly monkeys. In some collections of *Drymonia serrulata* I have noticed a distinct cabbage odor emanating from the cone-shaped food-body, indicating probable seed distribution by bats. A slight variation in this structure of the display fruit occurs in the genus *Nematanthus*. The cone-shaped food-body is usually absent here because the placentae remain attached to the two spread or reflexed valves.



Figures 63-66. Display fruit in neotropical Gesneriaceae. Figure 63. *Alloplectus dodsonii* Wiehler. Figure 64. *Drymonia rhodoloma* Wiehler. Figure 65. *Codonanthopsis dissimulata* (H. E. Moore) Wiehler. Figure 66. *Nematanthus hirtellus* (Schott) Wiehler.

TABLE 8: FRUIT TYPES IN THE GESNERIOIDEAE AND CORONANTHEROIDEAE

Type of fruit	No. of valves	Type of dehiscence	Taxa
1. Dry capsule (The seeds in dry capsules do not have enlarged funicular tissue.)	2	loculicidal	Tribe Gloxinieae Tribe Gesnerieae *Napeanthus* *Resia* *Rhynchoglossum azureum*
2. Dry capsule	2	septicidal	*Anetanthus* *Depanthus*
3. Dry capsule	4	loculicidal and septicidal	*Napeanthus apodemus* *N. bullatus* *N. primulinus* *N. spathulatus* *Coronanthera* *Negria* *Rhabdothamnus*
4. Dry capsule	0	irregular	*Cremosperma* *Tylopsacas*
5. ±fleshy capsule [Capsule, held at right angle to pedicel, splitting only along one side (=upper), offering seeds like in outstretched parallel hands.]	(2)	one-sided loculicidal	some *Diastema* spp. some *Monopyle* spp. *Gloxinia lindeniana* *Kohleria amabilis*
6. ±fleshy capsule (Valves convex, not reflexed, forming a cup which holds seeds with prominent funiculi.)	2	loculicidal	*Episcia, Alsobia, Nautilocalyx, Chrysothemis, Paradrymonia, Rhoogeton, Cobananthus, Gasteranthus, Reldia*
7. Fleshy capsule (Valves concave, reflexed, displaying moist, glistening, usually cone-shaped mass of funicular tissue, seeds, and placentae.)	2	loculicidal	*Alloplectus, Drymonia, Nematanthus, Codonanthopsis, Codonanthe* sect. *Codonanthella*
8. Berry (The pulp in the berries of the episcioid genera consists of funicular tissue, that of *Besleria* of enlarged placental tissue. After excessive rainfall, the berries split loculicidally in *Codonanthe crassifolia*, *C. gracilis*, and *C. uleana.* In the following species the mature, soft berries peel irregularly, or loculicidally and septicidally, with the bright-colored thin carpel walls reflexed or coiled above the hanging remainder of the fruit consisting of attractively colored placental tissue and seeds: *Besleria affinis* and *B. pendula* from Venezuela, and *B. pauciflora* Rusby in collections from Panama.)	0	none	*Corytoplectus, Rufodorsia, Neomortonia, Dalbergaria, Pentadenia, Trichantha, Columnea, Codonanthe, Besleria, Asteranthera, Fieldia, Mitraria, Lenbrassia, Sarmienta, Drymonia,* sect. *Drymoniella*

The mass of colored seeds and moist funiculi is torn apart, this offering a larger target (Figure 66).

The display fruit occurs in over 200 species (in four genera) of neotropical Gesneriaceae. An equally advanced type of fruit, the berry, occurs in eight genera or in over 430 species. Seven of these genera, all of them epiphytic, belong to the tribe Episcieae. The only non-episcioid group with berries in the Gesnerioideae is *Besleria*, a large genus of terrestrial shrubs or subshrubs. There is also an obvious difference in the nature of the berry in these two groups. The pulp of the berry in the episcioid genera consists of elaborated, plump and swollen funicular tissue, while the pulp of the *Besleria* berry is enlarged placental tissue. There is no proliferation of the funiculus in the tribes Beslerieae, Gloxinieae, Gesnerieae, and Napeantheae. In all genera of the tribe Episcieae, including those with capsular fruit, the funiculus is enlarged and thickened through the addition of extra cells, thus making this structure several times longer than the seed.

Among the berry-fruited genera, at least two unusual developments have occurred which are not cited in textbook classifications of fruits. *Codonanthe* is a genus of about 20 species of ant nest epiphytes with typical orange, red, deep purple, or magenta-pink berries. In three of the species, *Codonanthe crassifolia* (Focke) Morton, *C. gracilis* (Mart.) Hanst., and *C. uleana* Fritsch, the mature, soft berries split loculicidally occasionally, especially after excessive rainfall. Labeling as capsules these occasionally splitting "berries" seems inappropriate or missing the point, for, from a functional viewpoint, this occasionally split fruit represents an adaptation from diaspore dispersal by birds to dissemination by ants. The seeds of the above three species and a few other non-splitting species like *Codonanthe calcarata* (Miq.) Hanst. are the largest in the Gesneriaceae. They are shaped like ant eggs, about 3 mm long. Each berry contains only between 15 and 125 seeds (usually around 35), probably the lowest number of seeds in the gesneriaceous fruit. The seed is clad at its lower half (or in some species completely covered) by an aril-like cupule which is attached to the 8-11 mm long, many-celled, glistening, hyaline, and juicy funiculus. Actual field observations of ants carrying off these seeds with their food-bodies have not yet been made; I have found only the empty "berries" on the ant nest plants on trees, with other mature berries on the same plant not split. Excessive watering in the greenhouse on cultivated plants of the above species produces the same splitting effect.

A different type of berry-splitting occurs regularly in a few species of the large terrestrial genus *Besleria*. The berries in this group are usually orange or red, rarely white, and they are probably eaten mostly by birds. In three species, *Besleria affinis* Morton, *B. pendula* Hanst., both from Venezuela, and in Panamanian collections of *B. pauciflora* Rusby, the mature, soft berry always peels, either irregularly, or loculicidally and septicidally. The bright-colored, paper-thin carpel walls are reflexed or coiled above the glistening remainder of the fruit, consisting of attractively colored placental tissue and numerous small dark brown or black seeds. The possible advantages of such peeled berries, probably also eaten by birds, are not known. The human nose cannot detect any odor emanating from the skinned fruit. Whole berries wet from rainfall glisten similarly to the peeled berries.

Recently L. I. Ivanina (1965, 1966, 1967) published a fruit classification of the Gesneriaceae based on an examination of the fruit of 87 genera and of the seeds of 82 genera. She listed six different fruit types within the family and then proposed a reclassification of the Gesneriaceae based solely on this carpological approach. The main criteria in this approach are the degree of intrusion of the placentae into the cavity of the fruit, the forms of the placentae, the character of the seed arrangement on the placentae, and the methods of fruit dehiscence. The value of this classification appears diminished today becasue 1) it is based on one single criterion only, namely the fruit, thus neglecting other equally or even more important characters as essential input for a well balanced classification, and 2) it is founded on the dated assumption that the placentae represent "arms" of the original carpels (see Weber, 1971). The placentae are more generally considered today as new emergences (= non-carpellate tissue) and thus of less phylogenetic and taxonomic value. Because of this limited viewpoint, Ivanina's system of the Gesneriaceae differs in some essential elements from the classification by Burtt (1963) of the paleotropical group and from the new one proposed here for the neotropical group. Within this latter group Ivanina proposed the establishment of a new subfamily, the Episcioideae, for which the tribe Episcieae is equivalent in the present system. When using other information besides carpelogical data. it becomes evident that the tribe Episcieae is as distinct as the four other tribes in the group, but not more so. There are no bridging genera or species between these equally distinct tribes. Raising some or all of these tribes to subfamilial status represents no taxonomic gain. As seen elsewhere in this paper, our current knowledge of the neotropical Gesneriaceae does not support Ivanina's placement of the genera *Besleria*, *Cremosperma*, *Tylopsacas*, *Lembocarpus*, and *Napeanthus* in the tribe Episcieae, nor the erection of the tribe Rechsteinerieae (containing *Rechsteineria*, *Lietzia*, *Capanea*, and *Paliavana*). Ivanina dissolved the tribe Sinningieae (which comprised *Sinningia*, *Rechsteineria*, and *Lietzia* in Fritsch's system) by transferring *Sinningia* to the tribe Kohlerieae. In the present system *Sinningia* and *Rechsteineria* are united as a single genus in the tribe Gloxinieae (see Clayberg 1968, 1970; Moore, 1973c; Wiehler 1975c). Nevertheless, Ivanina's illustrations and descriptions of carpel structure for individual genera and species are of lasting value. Even more so is her beginning of a seed atlas for the family Gesneriaceae.

CHAPTER 11: THE ANDROECIUM

Compared with the typically five stamens of the actinomorphic corolla in many taxa of the Tubiflorae, the androecium of the neotropical Gesneriaceae has undergone some adaptation for various modes of pollination. As in the Lamiaceae and the Scrophulariaceae, the Gesneriaceae typically have five corolla lobes and only four or two functional stamens. The dorsal fifth stamen is usually reduced to a staminode or completely absent. All taxa in the subfamily Gesnerioideae typically have four stamens, with the exceptions of the genus *Bellonia* and some species of *Napeanthus* in which the corollas are nearly actinomorphic and the number of fertile stamens five (Table 9). Four stamens are also the norm in the subfamily Coronantheroideae, with the exception of the monotypic Chilean genus *Sarmienta* which has only two stamens (Table 10). A reduction of the androecium to two stamens occurs more often in the subfamily Cyrtandroideae. The four fertile anthers in the Gesnerioideae are typically connate, forming a flat rectangular or square surface and thus functioning as a unit in pollination (Figures 67-70). Sometimes the anthers are didynamous with the pairs connate (in some species of *Nautilocalyx*, *Codonanthe*, etc.). In a few instances the anthers are only coherent or even free (Tables 9 and 10). In *Conandron* the anthers are syngenesious.

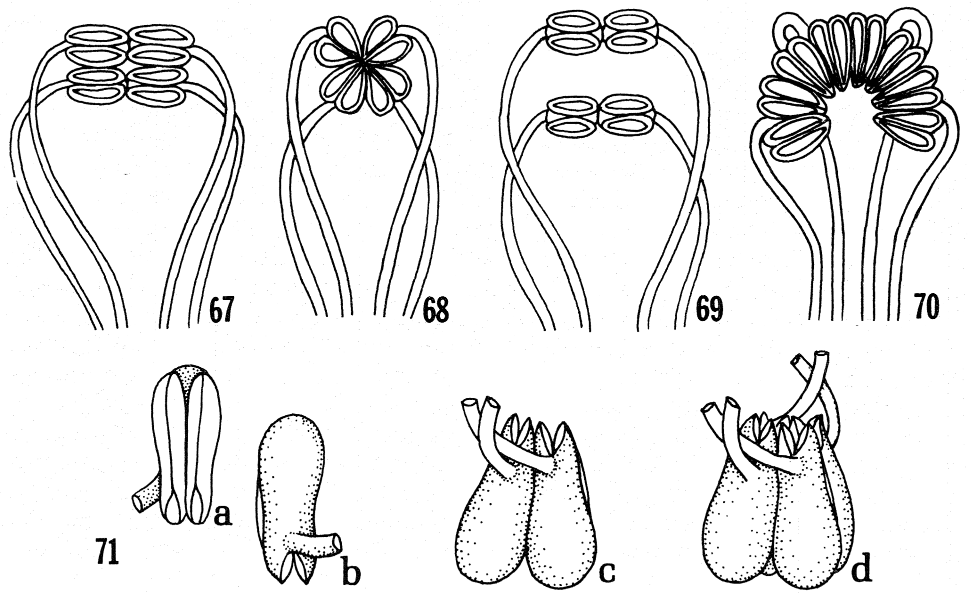
There appears to be an intriguing and unexplored relationship between the zygomorphy of the corolla in the Gesneriaceae, Scrophulariaceae, and Lamiaceae and the reduction of the number of stamens from five to four or two. The evolution of zygomorphy is a feature of advanced modes of pollination (by bee, bird, and bat). The reduction of stamens from an unequal number to four or two facilitates the functioning of the anthers as synchronized units of pollen transfer in these advanced pollination syndromes (Figures 67-71). Even the special nectary development in many taxa of the neotropical Gesneriaceae, namely the presence of a large dorsal gland, would "compete" spatially with the existence of a fifth stamen in the same area.

Among the four genera with rotate white corollas, *Bellonia, Niphaea, Phinaea*, and *Napeanthus*, and among the nine genera of the subfamily Coronantheroideae, the androecium is more varied in terms of the number of stamens and proximity of anthers, even within a single genus (Tables 9 and 10). There appears to be a correlation between the secondary actinomorphy in the corollas of *Bellonia, Depanthus*, and some species of *Napeanthus*, and the reversion to five stamens. There are, however, also actinomorphic corollas with four stamens and one staminode (in *Napeanthus*).

With the exception of the anthers in *Drymonia, Codonanthe*, and *Bellonia*, the androecium in the Gesnerioideae and Coronantheroideae is remarkably uniform and relatively unspecialized, thus possessing little taxonomic value below the family level. The anther cells usually dehisce by the conventional longitudinal slit. Theca dehiscence by a pore is characteristic for *Bellonia* and *Drymonia*, apical in the former, basal in the latter, and some species of *Paradrymonia* have bearded anther cells dehiscing by a central pore. The structure of the anthers and the corolla of *Bellonia* appears to fit well into the "buzz" flower syndrome. The pollen in the anther cells is dry and pourable in contrast to the sticky pollen grains, typical for most of the Gesneriaceae, caused by the presence of oil droplets. Unusually broad connectives separating the thecae are typical of the genus *Codonanthe*.

The most specialized anthers in the Gesneriaceae (and probably in all of the Tubiflorae) occur in the protandrous genus *Drymonia*. The unique, salt-shaker-like anthers are the trademark of this large group of vines, epiphytes, and very few terrestrials. The oblong and sagittate anthers are larger and longer than those in any other taxa in the tribe Episcieae. The shape of the individual anther (and anther cell with its mode of dehiscence) alone is sufficient to distinguish *Drymonia* from *Alloplectus*, two related taxa often confused in the past. The manner of anther connation and the resulting configuration of the composite unit of pollination (Figure 71) is novel enough to constitute the leading generic character for *Drymonia* (followed by the display fruit), although this was not mentioned in the original description of the genus by Martius in 1829. Martius had looked only at herbarium specimens for his description, or observed the flowers of his type collection from Amazonian Brazil (*Martius 3014*, M) only in the late phase of anthesis. The anthers unite only from about two days before anthesis (= late bud stage) until the beginning of the female phase of flowering when the style elongates and the stigma becomes receptive. At the onset of connation the four anthers are already grouped coherently around the much smaller gynoecium, with their thecae facing inside. As the anthers mature, they become connate by the length of the thecal margins and by their upper end, thus forming a single rectangular and columnar unit, with the connectives on the outside and the thecae inside. The individual theca actually dehisces halfway by the typical longitudinal slit from the base to the middle, but in the connate structure the only openings are four irregular pores at the base of the unit. A day before anthesis the pores are still basal, but as the filaments lengthen and the anther unit inside the corolla reaches its ultimate and strategical spot to effect cross-pollination, the curvature and the differential length of the pairs of filaments cause the anther unit to flip upside down, with the pores on the upper side. When the specific pollinator (bird, bat, moth or Euglossine bee in search of food) or simulating pencil in a greenhouse situation enters the corolla to obtain nectar, it must touch the apparent bottom of the strategically placed pendant anther unit which then tips over briefly like a salt-shaker and "rains" dry pollen grains on the visitor's head, thorax, or sternum. Not all of the pollen is shed at once; about five to eight visits are required to empty the anther unit.

The male period of flowering usually lasts about two days, followed by the female phase which lasts for a similar span of time. As the style elongates to place the stigma (not yet receptive) in the same spot the anthers occupied earlier, the filaments begin to coil and retract the anther unit toward the ovary, thus preventing self-pollination. In the process of coiling, the now defunct anther unit usually breaks up into individual anthers. The violent process of pressing and drying *Drymonia* flowers for herbarium specimens usually has the same effect, thus accounting for the annotation "anthers free" and for the absence of a description in the literature of this unique mechanism of pollination until 20 years ago. H. E. Moore, Jr. (1955a) gave the first account of *Drymonia* anthers as a biologically functioning unit, based on observation of live material in the greenhouse at Cornell University.



Figures 67-71. Variation in anther coherence in Gesneriaceae. Fig. 67. *Columnea*. Fig. 68. *Sinningia*. Fig. 69. *Nautilocalyx*. Fig. 70. *Rhabdothamnus*. Fig. 71 a-d. *Drymonia*; a-b: frontal and dorsal view of a single anther and the basal pores of the thecae; c-d: functional anther unit with the pores in the apical position.

Most of the taxa of the neotropical Gesneriaceae have separate male and female phases of anthesis, with protandry predominating overwhelmingly. Protogyny is known so far only in the isolated Caribbean tribe Gesnerieae in a few bat-pollinated species of *Gesneria: G. auriculata* (Hooker) Kuntze, *G. leucomalla* (Hanst.) Kuntze, *G. tomentosa* L., *G. vernicosa* (Urban & Ekman) Wiehler*, and *G. viridiflora* (Decne.) Kuntze. Determinations of protandry

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*comb. nov. for *Rhytidophyllum vernicosum* Urban & Ekman, Ark. Bot. 22A(10): 78. 1929.

or protogyny can usually be made only by observing live material. The coiling of the filaments, described above, is a typical phenomenon in the female phase of protandry in the Gesneriaceae. Yet straight versus contorted stamen filaments have been used in the gesneriad literature as distinguishing features between species. The first biological interpretation of stamen filament coiling was offered by Moore (1955a; cf. Moore & Lee, 1967, p.99).

The stamen filaments, typically adnate to the base of the corolla tube in the gesneriaceous flower, have acquired additional elaboration and function in the tribe Episcieae. In many species of this tribe the lower portion of the four filaments has become sheathlike and fused into a posteriorly split tube. (The split may be caused by the absence of the fifth filament.) The tube provides additional protection for the superior ovary against the probing beak or proboscis of the nectar-seeking bird or bee, and also channels the tongues of these animals toward the sweet liquid siphoned up from the reservoir of the corolla spur into the space between corolla and filament tube. In other species the flattened and bent filaments conduct the nectar for several millimeters upward along the sides of the corolla tube for easier access to the specific pollinator, thus leaving the ovary area untouched by the nectar. Sometimes the flattened individual filaments or the connate filament tube are also partially adnate to the lower portion of the corolla tube. This strengthens the protective corolla tissue against the ever present external nectar thieves which attempt to puncture or peck holes in the corolla tissue near the ovary, nectary gland, or spur for easier access to a good food source.

Fritsch (1893-94, p. 165) used the presence or degree of filament connation as an important generic character in his key to the taxa of the tribe Episcieae, but a larger sampling of the species and genera indicates now that stamen filament connation does not strictly follow along generic lines. There appears to be a direct correlation between the length of filament connation, corolla shape, and pollinator type, but this situation is without taxonomic significance in the Gesnerioideae (see Chapter 7, The Corolla). Differences in the degree of adnation of the anther filaments to the base of the corolla were considered by Fritsch (1893-94) and Morton (1957) as the sole distinction between the Caribbean genera *Gesneria* and *Rhytidophyllum*; they were recently cited again by Skog (1976) to warrant a separate existence for *Rhytidophyllum*. This character does not have any value on the generic level elsewhere in the neotropical Gesneriaceae, and a closer examination of the species of *Gesneria* and *Rhytidophyllum* (Wiehler, 1970; Skog, 1976, p. 18) has shown it to be inconsistent and therefore of little or questionable taxonomic import. When compared with the rest of the genera of the neotropical Gesneriaceae, the 69 species of the isolated Caribbean tribe Gesnerieae represent a very natural single generic unit.

CHAPTER 12: VEGETATIVE CHARACTERS: STEMS, NODES, LEAVES, PHYLLOTAXY, AND VASCULAR ANATOMY

With the beginning of concentrated field work and greenhouse study, vegetative characters have increased in importance for more precise generic limitations among the neotropical Gesneriaceae. The growth habit, for instance, is a prominent generic marker for *Napeanthus* and *Paradrymonia* (leaves rosette-forming), *Dalbergaria* versus *Columnea* (fern-frondlike shoots characteristic of the former), *Codonanthe* versus *Codonanthopsis* (extreme anisophylly in the latter), *Episcia* versus *Nautilocalyx* (presence and absence

TABLE 9: THE ANDROECIUM IN GESNERIOIDEAE WITH ROTATE COROLLAS

Taxa	No. of Stamens	Anther Proximity	Anther Cell Dehiscence
Bellonia aspera L.	5	coherent	apical pore
Bellonia spinosa Sw.	5	coherent	apical pore
Niphaea oblonga Lindl.	4	coherent	longitudinal slit (= l. s.)
Nipheae peruviana Wiehler	4	connate	l. s.
Phinaea divaricata (Poepp.) Wiehler	4	free	l. s.
Phinaea multiflora Morton	4	connate	l. s.
Phinaea repens (Donn. Sm.) Solereder	4	free	l. s.
Napeanthus (most species)	4	coherent	l. s.
Napeanthus subacaulis (Griseb.) Kuntze	4-5	free	l. s.
Napeanthus primulinus (Karsten) Jackson	5	free	l. s.

TABLE 10: THE ANDROECIUM IN THE CORONANTHEROIDEAE

Genera	No. of Stamens	Length of Stamens	Proximity of Anthers
Coronanthera	4	didynamous	connate
Lenbrassia	4	equal	coherent
Depanthus	5	equal	free
Rhabdothamnus	4	equal	connate
Negria	4	didynamous	free
Asteranthera	4	equal	connate
Mitraria	4	didynamous	free
Sarmienta	2	equal	free
Fieldia	4	equal	free

of stolons), and *Episcia* versus *Alsobia* (differences in stolon grown pattern). Other vegetative characters have been found to be of taxonomic value among the following genera: *Kohleria* versus *Moussonia* (presence and absence of scaly underground rhizomes), *Achimenes* versus *Goyazia* (peculiar leaf venation in the latter), and *Besleria* versus *Gasteranthus* (presence and absence of stomatal clustering on the leaves).

The leaves of the Gesneriaceae are always estipulate, simple, and usually devoid of lobing or deep sinuation, in contrast to the frequent occurrence of compound leaves in the related family *Bignoniaceae*. But since the Gesneriaceae abound in exceptions, such categorical statements often need to be qualified. Pseudostipules (remnants of an auriculate lamina) appear in several species of the *Rhytidophyllum* group in the genus *Gesneria*, such as *G. auriculata* (Hooker) Kuntze and *G. tomentosa* L. (cf. Weber, 1973b; Skog, 1976:9).Unusually deep laciniate leaves occur in isolated populations of *Tylopsacas cuneatum* (Gleason) Lwbg. on two tepuis in southern Venezuela (Figure 72), in *Paradrymonia lacera* Wiehler from Ecuador, in *Phinaea lacerata* Morton from Central America, and in a few other taxa.

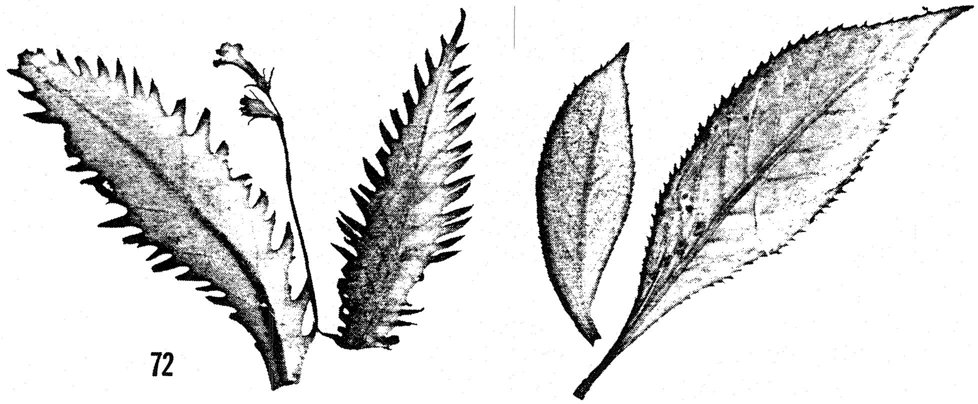

Figure 72. Xerograph of collections of *Tylopsacas cuneatum* (Gleason) Lwbg. from Amazonas, Venezuela. a. from a population with strongly laciniate leaves from base of Cerro Avispa, altitude 150 m, *G. C. K. Dunsterville s.n.*, 1972 (SEL, greenhouse acc. no. W-1791); b. from a more typical collection with normal serrate leaves from Cerro Sipapo. altitude 1000-1300 m, *B. Maguire & L. Politi 27502* (NY, US). Plants with deeply laciniate leaves have been found only at low altitudes at the southwest border of the geographical distribution of this species endemic in the Guayana Highland.

The phyllotaxy of the Gesneriaceae is predominantly decussate, sometimes verticillate, and rarely (= secondarily) alternate. All taxa in the Coronantheroideae have a decussate leaf arrangement; among the Gesnerioideae, alternate leaves occur only on the vegetative parts of most of the species of *Gesneria* and in the four species of the new small genus *Reldia* in the tribe Beslerieae. It is of interest that the inflorescences of both taxa have the typical decussate phyllotaxy. The only representative of the subfamily Cyrtandroideae in the neotropics, *Rhynchoglossum azureum* (Schlechtd.) Burtt, is also marked by alternate leaves, as are its congeners in the paleotropics.*

The genus *Codonanthopsis* in the tribe Episcieae was originally described as possessing an alternate leaf arrangement, but this concept was based on a misinterpretation of mature shoots on herbarium sheets. All six species of this epiphytic genus at first have opposite leaves of equal size, and then anisophyllous leaves in the young shoot stages. On mature

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*An examination of herbarium material of neotropical *Rhynchoglossum* reveals that the three named species from the New World represent only a single, somewhat variable species, *R. azureum,* occurring from Mexico to Peru.

Rhynchoglossum azureum (Schlechtd.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24(2): 168. 1962.
Klugia azurea Schlechtd., Linnaea 8: 248. 1833.
Glossanthus mexicanus R. Br. in Horsfield, Bennett & Brown, Plantae javanicae rariores 121. 1840.
Klugia violacea Fritsch, Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl., Abt. 1, vol. 135: 285. 1926.
K. granidflora Fritsch, ibidem, p. 287.
K. azurea var. *costaricensis* Fritsch, ibidem, p. 287.
Rhynchoglossum violaceum (Fritsch) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24(2): 171. 1962.
R. grandiflorum (Fritsch) B. L. Burtt, ibidem, p. 169.

shoots one of the leaves of the opposite leaf-pair is scalelike and often caducous. There is still a small, tell-tale leaf scar on the living branches; on shrivelled and dried herbarium material this leaf scar sometimes seems to have disappeared.

The occurrence of alternate leaves among almost all of the 69 species of the tribe Gesnerieae is a curious phenomenon deserving some attention. This tribal group, isolated from the rest of the Gesnerioideae, has proliferated on the Caribbean Islands. Because of the following factors, it may be stated that the alternate 2/5 phyllotaxy in *Gesneria* (and *Reldia*) is of secondary origin, namely derived from a decussate leaf arrangement, and not a primitive condition:

1. Decussate leaves are the norm for the subfamily Gernerioideae.
2. The inflorescence-systems in the tribe Gesnerieae have a decussate phyllotaxy and branching system, exactly the same as that of the rest of the Gesnerioideae; the opposite branching system is also present in most of the species of *Reldia* with a compound pair-flowered cyme (the one species has a more complex compound inflorescence-structure caused by the reduction of the peduncle), but in all species the prophylls and subtending bracts are absent. In the pair-flowered cyme of the Gesneriaceae (including the genus *Gesneria sensu lato*) the front flower is a remnant of a second branch whorl with a decussate position above the prophylls. According to Weber (1973a), this indicates that the pair-flowered cymes have evolved from a more complex ramification system with decussate phyllotaxy.
3. One species in the tribe Gesnerieae, *Gesneria corymbosa* Sw. from Jamaica and Cuba, has truly decussate leaves (Wiehler, 1970, 1971; Skog, 1976).
4. One population of *Gesneria fruticosa* (L.) Kuntze from Hispaniola has truly decussate leaves, while the type and other collections in this species have alternate leaves (Wiehler, 1970, 1971; Skog, 1976). Since every species in the tribe Gesnerieae has a decussate leaf arrangement in the inflorescence in the form of prophylls and subtending bracts, the consistent occurrence of decussate leaves on the entire plant body of one species, *Gesneria corymbosa*, does not seem to be so extraordinary as to warrant its isolation into a separate genus (*Pheidonocarpa*, Skog, 1976).

Anisophylly occurs in all three subfamilies of the Gesneriaceae, although in the small group of the Coronantheroideae it is only weakly expressed among three species, *Asteranthera ovata*, *Fieldia australis* A. Cunn., and *Rhabdothamnus solandri* A. Cunn. In the subfamily Gesnerioideae, extreme anisophylly occurs among all species of the genera *Monopyle*, *Dalbergaria*, and *Codonanthopsis*. The following genera have several to many anisophyllous species: *Gloxinia*, *Kohleria*, *Parakohleria*, *Capanea*, *Achimenes*, *Solenophora*, *Alloplectus*, *Pentadenia*, *Trichantha*, *Columnea*, *Nematanthus*, and *Cremosperma*. The rest of the taxa in the Gesnerioideae are isophyllous. Ternate or whorled leaves have been found among some species of the genera *Gloxinia*, *Kohleria*, *Anodiscus*, *Heppiella*, *Paliavana*, *Sinningia*, *Achimenes*, *Neomortonia*, *Trichantha*, *Pentadenia*, *Columnea*, and *Mitraria*.

In terms of function, anisophylly among the Gesneriaceae can be interpreted as an adaptation of the photosynthetic organs for a better utilization of the light available in the tropical rainforest. Plants with decussate or whorled leaves usually have upright or pendent shoots in which the photosynthetic tissue is three-dimensionally layered, resulting in shade-producing overlapping and less efficiency in energy production (Figure 73). Plants with strong anisophylly always have spreading or ascending two-dimentional shoots shaped like a fern frond, with none of the photosynthetic tissue overlapping, thus functioning as a very efficient unit of energy transformation (Figure 74).

Figures 73-74. Schematic drawings of gesneriad shoots with the characteristic decussate phyllotaxy, isophyllous in Figure 73, converted through extreme anisophylly into an apparent distichous system in Figure 74. The seedlings and young plants of *Codonanthopsis, Dalbergaria,* and *Monopyle*, among others, show the habit of Figure 73, but their mature shoots, the aspect of Figure 74.

In terms of numbers of species, there is more anisophylly among epiphytes than among terrestrials in the neotropical Gesneriaceae. The fernfrondlike branches of the species in the large genus *Dalbergaria* spread typically at almost right angles to the host tree trunk, thus exposing themselves to a maximum amount of light. The terrestrial genus *Monopyle* has adapted to a fern-frondlike habit on the dim forest floor for the same purpose.

Since many of the species of *Gesneria* (and all species of *Reldia*) are rosette-forming plants in the shade of the forest floor, it appears possible that the secondarily alternate leaf arrangement occurring in the majority of the species of these genera became fixed after going through an anisophyllous decussate stage. The secondarily alternate leaves in *Gesneria* and *Reldia* would thus be the most extreme form of (or the final step in) anisophylly.

Anatomical characters of plants, though not inherently more important than morphological features, are now used with increasing frequency in plant taxonomy (Davis & Heywood, 1963: 167). When basic or additional evidence is needed, the vascular structure of a plant may provide fairly reliable characters for the classifying botanist. Eames (1961: 724) stated that the rate of evolution in the morphology of reproductive organs has, generally speaking, been much faster than in the anatomy of the petiole, leaf, and the secondary xylem; changes in the vasculature are recognized by anatomists as very slow.

Four main types of nodal structure are now generally recognized in the dicotyledons: (1) the unilacunar, one-trace type; (2) the unilacunar, two-trace type; (3) the trilacunar type with three traces, one per gap; and (4) the multilacunar type with more than three traces, one per gap. Several other nodal structures, comparatively rare in occurrence, have been found in recent years, and are summarized by Howard (1974: 135). Since many plant families exhibit either one or the other of these conditions, nodal anatomy can play an important role in determining the relationship of hard-to-place genera and in phylogenetic considerations, mainly at the familial or ordinal level. Sinnott, who published the first major study of vasculature of the families of the dicotyledons (1914), concluded that the trilacunar node was the most primitive nodal condition in the angiosperms. In recent years there have been several major shifts of opinion concerning the primitiveness and derivation of these four nodal types. Marsden & Bailey (1955) and Bailey (1956) regarded the two-trace unilacunar node as the most primitive, while in still more current publications the odd-number trace, unilacunar one-trace or trilacunar (Benzing, 1967) or the one-trace unilacunar node alone (Philipson & Philipson, 1968) are considered as the most primitive in the angiosperms. The unilacunar one-trace node has been viewed as the primitive condition in the Coniferales (Namboodiri & Beck, 1968).

Following the pioneer work by Sinnott, nodal pattern was long considered a very conservative character, often stable in all members of large taxonomic groups within the dicotyledons. This view now requires some modification, since several investigators reported considerable variation in nodal structure within some families and even within genera (Saha, 1952; Post, 1958; Philipson & Philipson, 1968). It is now thought that cotyledonary nodal structure, at times differing from adult nodal anatomy, may possibly be of greater significance for phylogenetic interpretation (Post, 1958, p.12.).

The petiole was regarded by Hare (1944), Metcalfe & Chalk (1950), and Howard (1962) as of considerable taxonomic importance since its structure appeared to be but little affected by environmental change. The vasculature of the petiole of dicotyledons showed more basic types of variation than that of the node. Hare derived 24 different types from three basic and functional structure patterns, the **U**, **O**, and **I** shapes. Metcalfe & Chalk reduced these to nine principal types of vascular systems in the petiole.

Since the stem, the node, and the petiole of a plant are so intimately related, there has been a tendency within the last decade to combine nodal and petiolar vasculature into one unified taxonomic character. Carlquist (1961, pp. 85,87) suggests that "as a systematic feature, nodal anatomy is best used in combination with petiolar vascularization. . . .With our increased knowledge of both nodes and petioles, separation of one from the other becomes increasingly artificial." Howard (1959, 1962, 1974) has proposed a system of classification based first upon nodal types, then within these types upon distinctive configurations of the petiolar stele. He also found that the vasculature of the petiole appears to be most useful as a diagnostic character at the generic level. In a recent paper Howard (1974) emphasized again the structural unity of the stem, the node, and the leaf, and of finding the primitive type of node or leaf among the present-day dicotyledons. Howard's characterization of the node as "a locus of meristematic activity capable of producing one or more products" is a very useful new concept, especially for the Gesneriaceae (cf. Vegetative Reproduction, Chapter 13).

The vasculature of the node and petiole in the Gesneriaceae has never been exploited taxonomically or for phylogenetic considerations, and the references in the literature on the anatomy of this family are very few and scanty (treatments of the unifoliate *Streptocarpus* species being an exception, i.e., Hielscher, 1883). Metcalfe & Chalk (1950, pp. 996-999) do not comment on the nodal situation but quote Solereder that single leaf-traces occur "in numerous genera," three leaf-traces in species of *Alloplectus*, *Besleria*, *Columnea*, *Episcia*, *Nematanthus*, and a relatively large number of separate strands in *Rhynchoglossum (Klugia).*

Sinnott wrote in 1914, in characterizing the nodal structure for the order Tubiflorae:

> This immense order is characterized almost without exception by a nodal structure which is unilacunar. In the many genera from the sixteen families of this order investigated only *Cyrtandra*, one of the Gesneraceae, displayed other than this single-gapped condition. Three or five strands and gaps is typical for this genus. Such an exception may be regarded as merely one of the cases where the anatomy of the node is not conservative; or it may be taken as an indication that the Gesneraceae are relatively primitive among the Tubiflorae and connect such families as the Bignoniaceae and Scrophulariaceae with the Rubiales. (p. 317)

Solereder (English translation, 1908, pp. 600-601) and Fritsch (1893-94) refer to a certain study by Hollstein according to which the subfamily Gesnerioideae has single leaf-traces, and the tribe Episcieae — at that time in the subfamily Cyrtandroideae — and *Chirita urticifolia* D. Don, an Asiatic member of the Cyrtandroideae, have three separate leaf-traces. A search for Hollstein's publication, alluded to by Fritsch and Solereder but not mentioned by Sinnott and Metcalfe & Chalk, long proved fruitless (until well after the completion of my nodal study.) A copy was finally located at the Library of Congress in Washington, D.C., apparently the only copy in the United States. In this doctoral dissertation, on 40 small pages and without any illustration, Hollstein (1878) described very clearly and forthrightly three types of nodal structure in the Gesneriaceae. There is the "*Gesneria* type," a unilacunar node with one trace per leaf, applying to the larger part of the family; the "*Alloplectus* type," with a trilacunar three-trace node with splitting lateral bundles for another part of the Gesneriaceae; and lastly, the peculiar vascular structure in *Rhynchoglossum notonianum* (Wall.) Burtt (*Klugia notoniana* Wall.) with medullary vascular bundles, no proper vascular cylinder, and thus no proper nodal gaps. The genera and species examined and assigned to the two main groups are significant. In light of our present generic concepts they represent 22 genera (Table 11).

It is unfortunate that Hollstein's study has remained for so long in obscurity. Sinnott (1914) was aware of only one exception (*Cyrtandra*, three to five lacunae) in the otherwise uniformly unilacunar order Tubiflorae. A knowledge of much more frequent vascular deviation of the Gesneriaceae among the Tubiflorae might have encouraged Sinnott, Bailey, and others to investigate the vasculature of the family further. Metcalfe & Chalk do not even mention Hollstein in their references on the anatomy of the Gesneriaceae. The taxonomic and possible phylogenetic significance of Hollstein's findings have been overlooked. Mention has to be made also of a study in leaf-structure of over 80 species of the subfamily Gesnerioideae by Marie Sachs (1915). The data compiled in her dissertation has never been evaluated for taxonomic purposes.

Simultaneously with my initial investigation of the vasculature of the node and petiole in the neotropical Gesneriaceae at Cornell University between 1968 and 1970 (Wiehler, 1970), Richard A. Howard of Harvard University examined the vasculature of the tetraploid epiphyte *Trichanths am-*

TABLE 11: LIST OF 37 SPECIES OF GESNERIACEAE EXAMINED BY HOLLSTEIN (1878) IN HIS STUDY OF NODAL ANATOMY

Names used by Hollstein	Names changed, current status
The *Gesneria* type	
Achimenes Bodmeri Regel	*Achimenes* (extinct cultivar)
Achimenes Liebmanni Hort.	*Achimenes grandiflora* (Schiede) DC.
Aeschynanthus pulcher (Blume) G. Don	
Codonophora prasinata Lindl.	*Paliavana racemosa* (Vell.) Fritsch
Diastema quinquevulnerum Planch.	
Dicyrta candida Hanst. & Kl.	*Achimenes candida* Lindl.
Eucodonia Ehrenbergi Hanst.	*Eucodonia verticillata* (Martens & Gal.) Wiehler
Gesneria Sellowii Mart.	*Sinningia sellowii* (Mart.) Wiehler
Gesneria tubiflora Cav.	*Kohleria tubiflora* (Cav.) Hanst.
Gloxinia caulescens Lindl.	*Sinningia speciosa* (Lodd.) Hiern
Gloxinia maculata Herit.	*Gloxinia perennis* (L.) Fritsch
Guthnickia ignea Auct.?	Hybrid of *Achimenes erecta* (Lam.) H. P. Fuchs
Houttea calcarata Hort.	*Vanhouttea calcarata* Lemaire
Isoloma longipes Benth.	*Kohleria longipes* (Benth.) Hanst.
Kohleria ignorata Regel	*Kohleria spicata* (Kunth) Oersted
Koellikeria agyrostigma Regel	*Koellikeria erinoides* (DC.) Mansf.
Ligeria barbata Hanst.	*Sinningia barbata* (Nees & Mart.) Nich.
Locheria hirsuta Regel	*Achimenes skinneri* Lindl.
Mitraria coccinea Cav.	
Niphaea oblongata Lindl.	*Niphaea oblonga* Lindl.
Rechsteineria allagophylla Regel	*Sinningia allagophylla* (Mart.) Wiehler
Rhytidophyllum tomentosum Mart.	*Gesneria tomentosa* L.
Rosanovia conspicua Auct.?	*Sinningia conspicua* (Seem.) Benth. & Hook. f.
Scheeria mexicana Seem.	*Achimenes mexicana* (Seem.) Fritsch
and perhaps	
Streptocarpus polyanthus Hook.	
The *Alloplectus* type	
Alloplectus sparsiflorus Mart.	*Nematanthus hirtellus* (Schott) Wiehler
Alsobia punctata Hanst.	
Besleria melittifolia L.	*Nautiocalyx melittifolius* (L.) Wiehler
Columnea Schiedeana Schlechtd.	
Cyrtodeira cupreata Hanst.	*Episcia cupreata* (Hook.) Hanst.
Episcia bicolor Hook.	
Episcia pulchella G. Don	*Chrysothemis pulchella* (Donn ex Sims) Decaisne
Gonatostemon Boucheanum Regel	*Chirita urticifolia* D. Don
Houttea calcarata Hort.	? (cf. sub *Gesneria* type)
Paradrymonia glabra Hanst.	
Nematanthus longipes DC.	*Nematanthus crassifolius* (Schott) Wiehler
With completely different vasculature	
Klugia Notoniana DC.	*Rhynchoglossum notonianum* (Wall.) B. L. Burtt

bigua (Urban) Wiehler (then known as *Alloplectus ambiguus* Urban) from Puerto Rico. He coined the useful phrase "split-laterals" for the type of vascular bundles found in this gesneriad. Finding some interesting variation from the typical vascular pattern, he published two sets of illustrations of the nodal anatomy of *Trichantha ambigua* (Howard, 1970). This important paper, further referred to below, gives a ground-breaking perspective on the phenomenon of split-laterals by discussing the occurrence of this comparatively rare nodal type among the angiosperm families. Howard proposed the trilacunar node with split lateral traces as a separate nodal type.

My own investigation has continued since 1970 and now includes representatives of all genera of the Gesnerioideae and Coronantheroideae, or a total of 347 species. A unilacunar node with one trace per leaf (1:1) was observed in all species examined in the tribes Gesnerieae, Gloxinieae, Napeantheae, Beslerieae, and in the sole tribe Coronanthereae of the subfamily Coronantheroideae (Figure 75a-d). From each species five nodes were usually examined, originating on at least two different branches.

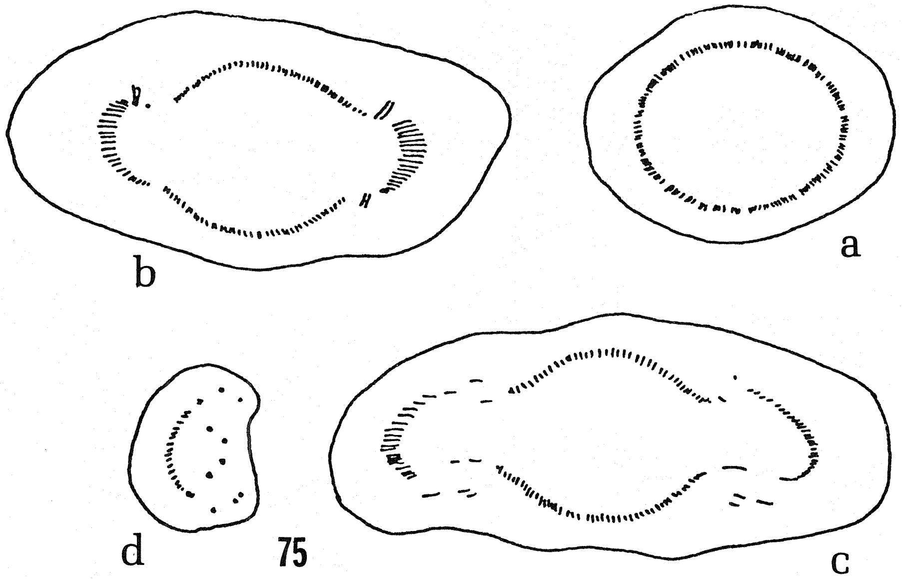

Figure 75. Cross-sections of internode, node, and petiole in a representative species of the tribe Gloxinieae: *Gloxinia perennis* (L.) Fritsch × 6; a. internode, with xylem cells in tiers of two or three; b. unilacunar node with (1:1) leaf-traces. The traces in pairs, leaving last, become free bundles in the petiole; c. node, more advanced; d. petiole near node.

A three-trace trilacunar node (3:3) with split lateral bundles was found to be the normal condition in the tribe Episcieae. The schematic illustration below (Figure 76) shows that this node in the Episcieae is not the conventional trilacunar node, but of a special type. It is the same as "the *Alloplectus* type" node of Hollstein (1878) and the node with "split-laterals" of *Trichantha ambigua* described and illustrated by Howard (1970). At each node of the decussate and estipulate leaves there are only four gaps in the stele: the two larger median lacunae (A), and two smaller lateral gaps (B). The lateral traces (C) leave the stele somewhat earlier than the median traces, split in the cortex and travel in opposite directions toward the petiole where they

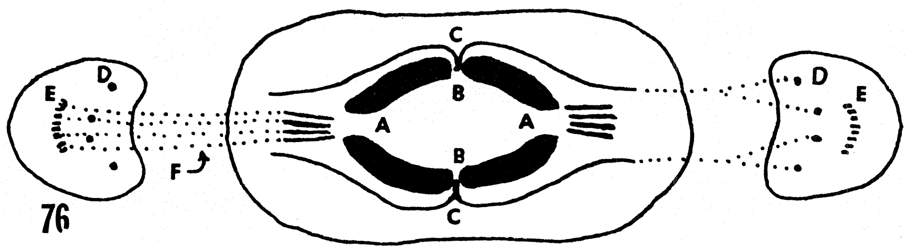

Figure 76. Typical node with split lateral traces of the species in the tribe Episcieae. Details explained in text.

form the vascular strands (D) adaxial to the crescent (E) which in turn is supplied by the larger median leaf-trace (F). The lateral lacunae are, therefore, shared by the opposite leaves, each of which has three traces. There is no relationship between anisophylly and split lateral nodes in the Episcieae; isophyllous taxa in this tribe have the same type of node (Figure 77 a-d).

The vascular anatomy of the tribe Episcieae is unique within the subfamily Gesnerioideae, comparatively rare among the angiosperm families (Howard, 1970), and thus warrants some special attention in this report. An investigation of the ontogeny of the vascular structure of seedlings in the Episcieae shows the three-trace trilacunar node in this tribe to be derived from the one-trace unilacunar situation (that is, if one considers the vascu-

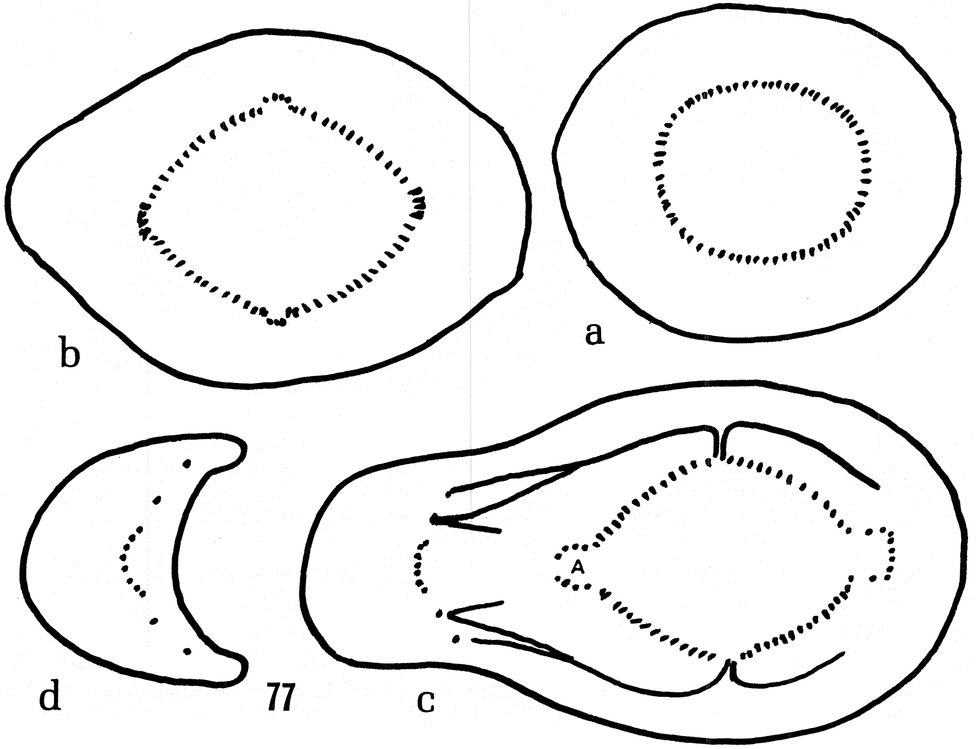

Figure 77. Cross sections of internode, node and petiole in a representative species of the tribe Episcieae: *Rufodorsia major* Wiehler (X 17); a. internode with stele of vascular bundles; b. internode, changing to node; c. trilacunar node with split lateral leaf-traces (3:3), and, at A, vascular supply for axillary shoot. The long, drawn out leaf-traces become free bundles in the petiole; d. petiole near node.

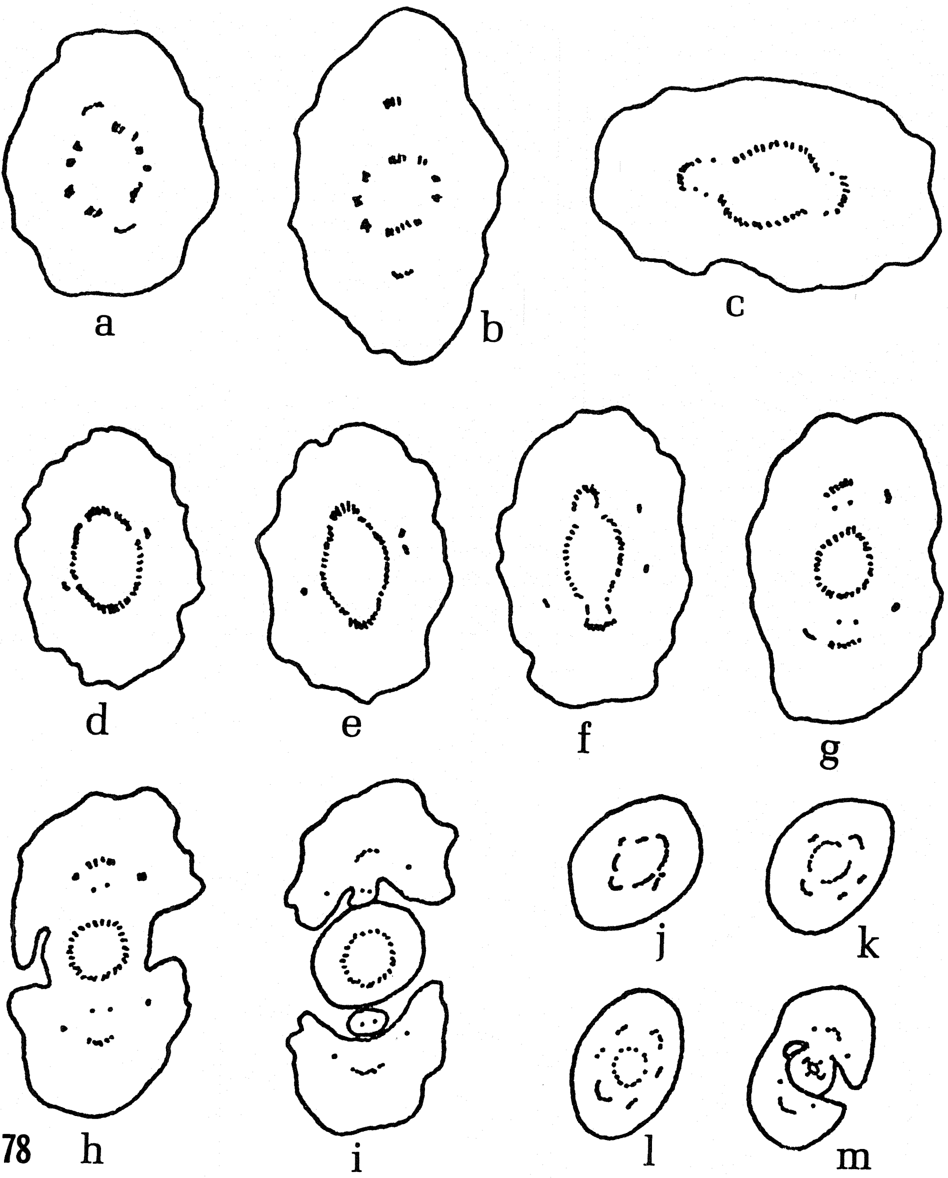

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Figure 78 a-m. Nodal ontogeny in the tribe Episcieae. Seedling of *Corytoplectus speciosus* (Poeppig) Wiehler, selected cross-sections from the same plantlet, starting with lowest node × 28; a-b. cotyledonary node, unilacunar 1:1; a. early stage, b. further advanced; c. first true leaf-node, unilacunar 1:1; d-h. second true leaf-node, transition to trilacunar 3:3 node. d. the lateral traces depart from stele ahead of the median traces; e. the median leaf-traces depart from the stele; one of the lateral traces does not divide; f-h. further advanced stages; i-l. third (true) leaf-node, trilacunar 3:3; i. stele of internode, with two petioles and axillary shoots. j-k. both lateral traces divide; m. fourth (true) leaf-node, trilacunar 3:3.

lature of the cotyledonary node to be more conservative than that of the following nodes of the seedling and the mature plant). In those seedlings examined, e.g., *Corytoplectus speciosus* (Poeppig) Wiehler, *Chrysothemis pulchella* (Donn. ex Sims) Decaisne, *Columnea erythrophaea* Decaisne, *Codonanthe crassifolia* (Focke) Morton, *Drymonia strigosa* (Oersted) Wiehler, *Paradrymonia decurrens* (Morton) Wiehler, *Episcia reptans* Martius, *Nematanthus perianthomegus* (Vell.) H. E. Moore and *Nematanthus crassifolius* (Schott) Wiehler, the cotyledonary and the first true leaf-nodes were found to be one-trace unilacunar. In the second true leaf-node a transition was noticed to the three-trace trilacunar condition; from the third or fourth true leaf-node onward the situation was uniformly three-trace trilacunar (Figure 78 a-m). The seedlings of representatives of unilacunar tribes had typically one-trace unilacunar nodes throughout: e.g., *Gloxinia perennis*, *Kohleria tubiflora* (Cav.) Hanst., *Smithiantha cinnabarina* (Linden) Kuntze, *Sinningia cardinalis* (Lehmann) H. E. Moore, *Besleria lutea* L., *Gesneria pedunculosa* (DC.) Fritsch, *Gesneria berteroana* (Mart.) Kuntze, and *Sarmienta repens* Ruíz & Pavón (Wiehler, 1970).

Exceptions seem to abound in the Gesneriaceae. While the trilacunar node can be regarded as typical for the tribe Episcieae, one-trace unilacunar nodes were found in a few species of *Alloplectus*, *Bucinellina*, *Codonanthe*, *Columnea*, *Nematanthus*, *Neomortonia*, and *Trichantha*, all of them pendant or scandent epiphytes with very thin stems (1-2 mm diam. *in vivo*). These species represent some of the most advanced elements in the Episcieae. They are *Alloplectus cristatus* (L.) Mart., *Bucinellina nariniana* (Wiehler) Wiehler, *Codonanthe devosiana* Lemaire, *C. gracilis* (Mart.) Hanst., *C. digna* Wiehler, *Columnea allenii* Morton, *C. arguta* Morton, *C. chiricana* Wiehler, *C. dodsonii*

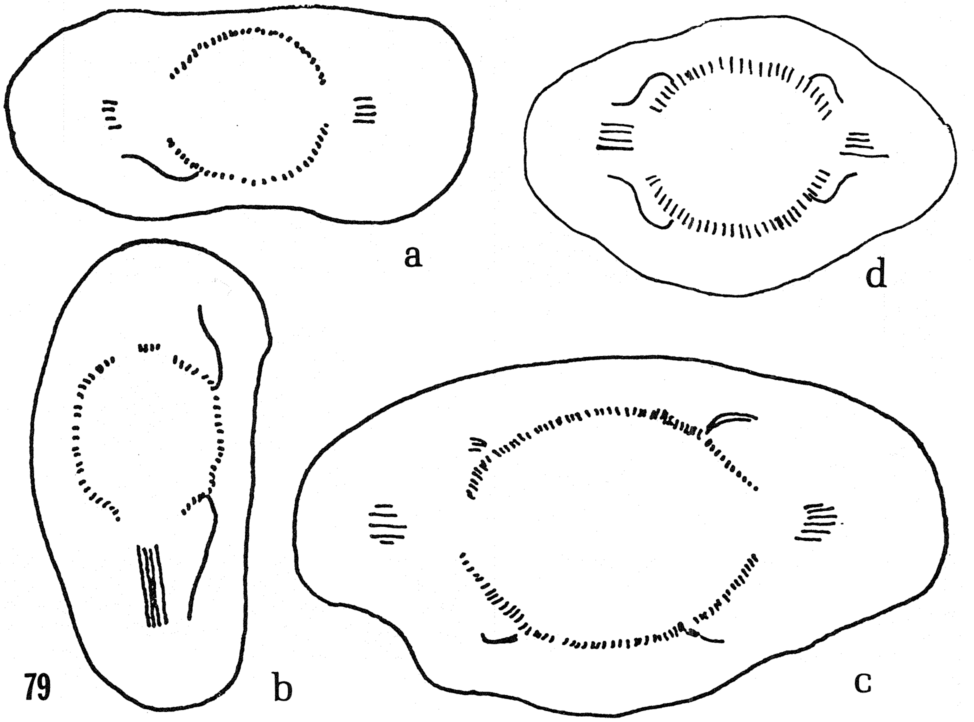

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Figure 79 a-d. Unusual nodes in the tribe Episcieae. a-b. *Columnea microcalyx* Hanst. (X 28); a. 1:1, but with one additional small lateral trace which does not leave a recognizable gap in the stele; b. as above, basically 1:1, but with two lateral traces; c. *Columnea salmonea* Raymond (X 28), a transitional stage between 1:1 and 3:3. The lateral traces leave practically no gap in the stele; d. *Bucinellina nariniana* (Wiehler) Wiehler (X 28), the same transitional stage between 1:1 and 3:3, as above.

Wiehler, *C. gloriosa* Sprague, *C. hirta* Hanst., *C. kienastiana* Regel, *C. microphylla* Oersted, *Nematanthus gregarius* Denham, *N. nervosus* (Fritsch) H. E. Moore, *N. hirsutus* (Mart.) Wiehler*, *N. wettsteinii* (Fritsch) H. E. Moore, *Neomortonia nummularia* (Hanst.) Wiehler, and *N. rosea* Wiehler (see Wiehler, 1970, Plate 15).

Other epiphytic species of *Codonanthe*, *Columnea*, *Nematanthus*, and *Trichantha* with somewhat thicker stems (2.5-4 mm diam. *in vivo*), either pendant or ascending, have the typical trilacunar nodes with three leaf-traces: *Codonanthe luteola* Wiehler, *C. uleana* Fritsch, *Columnea bilabiata* Seemann, *C. billbergiana* Beurl., *C. cobana* Donn.-Sm., *C. flaccida* Seemann, *C. hirta* Hanst. var. *mortonii* (Raymond) Morley, *C. scandens* L., *Nematanthus crassifolius* (Schott) Wiehler, *N. fissus* (Vell.) L. Skog, *N. fritschii* Hoehne, *N. perianthomegus* (Vell.) H. E. Moore, *Trichantha herthae* (Mansf.) Wiehler, *T. minor* Hooker, *T. moorei* (Morton) Morton, *T. purpureovittata* Wiehler, *T. sanguinolenta* (Oersted) Wiehler, and *T. tenensis* Wiehler (cf. Wiehler, 1970, Plate 15).

A curious intermediate or transitional situation was discovered in the following thin-stemmed species: *Columnea microcalyx* Hanst., *C. salmonea* Raymond, and in two nodes of the otherwise unilacunar 1:1 nodes of *Bucinellina nariniana* cited above. Here in the basically unilacunar nodes, one or two very small vascular traces departed from the stele near the lacunae to travel into the petiole. These small bundles created a space in the stele hardly large enough to be labelled a gap (Figure 79 a-d). In *Bucinellina paramicola* (Wiehler) Wiehler, the nodes were transitional from the unilacunar 1:1 to the trilacunar 3:3 condition. These nodes had only one small lateral gap, with the traces running in opposite directions. The opposite side of the stele had either a thin single trace without any obvious gap or no trace at all(Figure 80 a-b).

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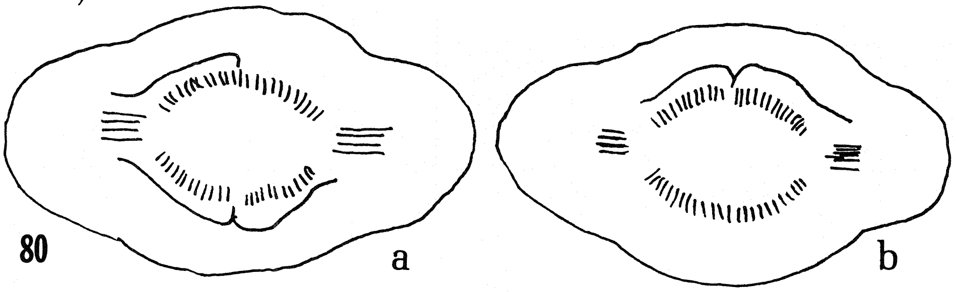

Figure 80 a-b. Unusual nodes in the tribe Episcieae. *Bucinellina paramicola* (Wiehler) Wiehler (X 28), transitional stage between 1:1 and 3:3, with one lateral gap and lateral traces running in opposite directions, but the opposite side of the stele without an obvious gap, with a single trace (a), without a trace (b).

The above examples and the nodal ontogeny in the tribe Episcieae indicate a degree of affinity between the unilacunar 1:1 node and the trilacunar 3:3 node in the evolutionarily flexible Gesneriaceae. The next step, from the trilacunar node to the multilacunar 5:5 node, occurs also in the Gesneriaceae. Most nodes of *Columnea repens* (Hooker) Hanst. from Jamaica have the typical trilacunar condition, but two nodes examined were multilacunar, one with four traces for one leaf and three traces for the opposite leaf, the other with five traces for one leaf and three for the opposite (Figure 81 a-c).

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*Nematanthus hirsutus (Mart.) Wiehler, comb. nov.
Hypocyrta hirsuta Mart., Nov. gen. et sp. pl. 3:52, t. 222. 1829.
Columnea martiniana Kuntze, Rev. gen. 2:472. 1891

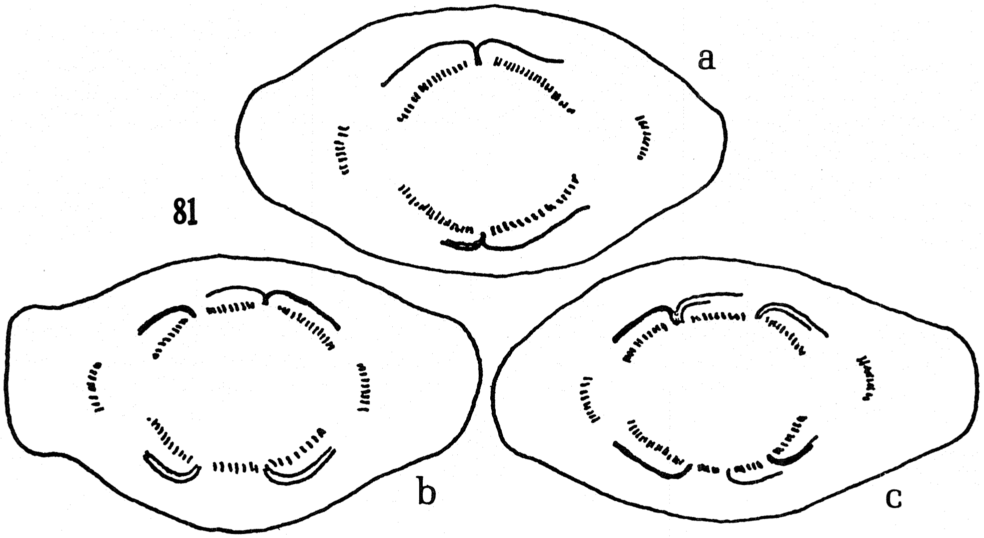
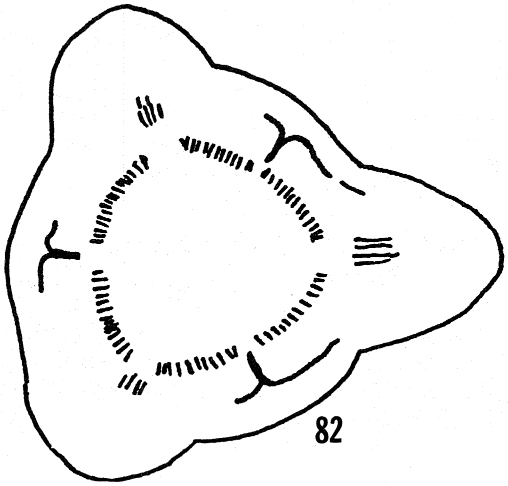


Figure 81 a-c. Multilacunar nodes in the tribe Episcieae. *Columnea repens* (Hook.) Hanst. X 15; all nodes are from the same stem; a. trilacunar 3:3, representative of most nodes of the plant examined; b. trilacunar 3:3 for one leaf, multilacunar 4:4 for the other leaf; c. trilacunar 3:3 for one leaf, multilacunar 5:5 for the opposite leaf.

Further examination will probably reveal more multilacunar nodes in the tribe Episcieae (cf. Howard, 1970). Two examples of nodes with ternate leaves and split lateral traces were found, one in one branch of *Pentadenia crassicaulis* Wiehler, the other in a branch of *Streptocarpus saxorum* Engler (Figures 82, 83). Most of the stems of these two species have nodes with decussate leaves.

The only member of the subfamily Cyrtandroideae in the neotropics, *Rhynchoglossum azureum* (Schlechtd.) B. L. Burtt, has a rather peculiar vascular structure for Gesneriaceae: the stems have medullary vascular bundles, secretory canals, no proper cylinder, and thus no proper lacunae at the nodes, and no distinct vascular crescent in the petiole in cross-section (Figure 84). This is typical for the genus *Rhynchoglossum* and all other members



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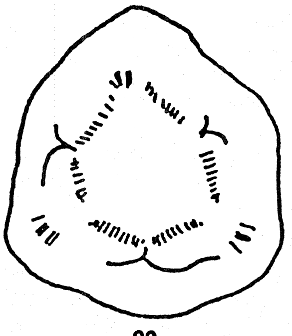

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Figures 82-83. Cross-sections of ternate leaf nodes with split lateral traces in the Gesneriaceae. Figure 82. *Pentadenia crassicaulis* Wiehler. Figure 83. *Streptocarpus saxorum* Engler.

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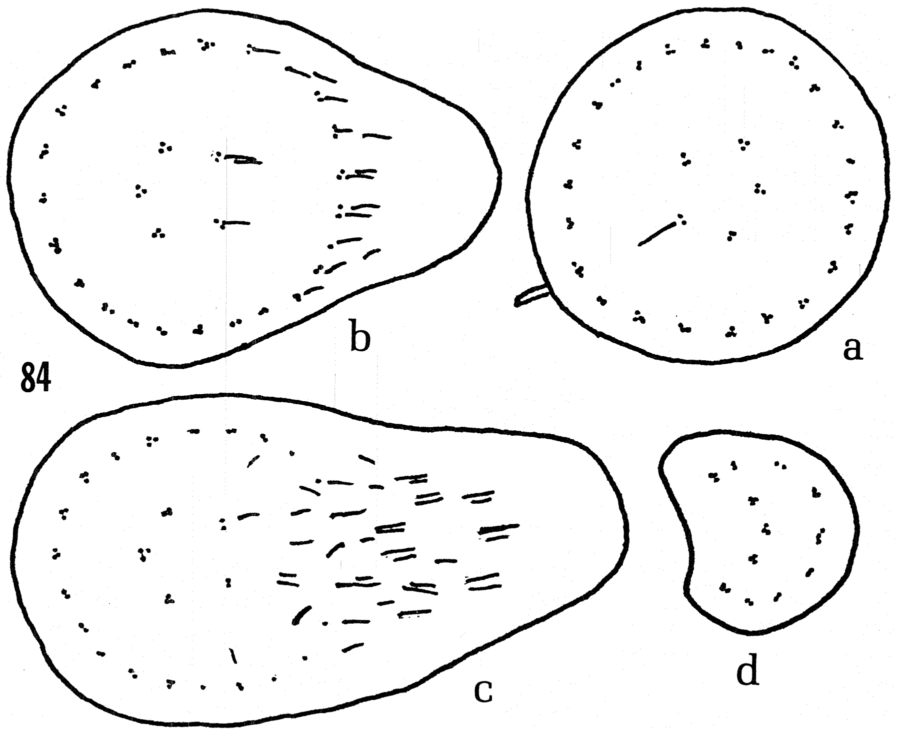

Figure 84 a-d. Cross-sections of the vasculature of stem-node-petiole of *Rhynchoglossum azureum* (Schlechtd.) B. L. Burtt, a species with alternate leaves; a. internode with medullary bundles and a root-trace; b-c. nodes; d. petiole.

of the tribe Klugieae, namely *Epithema*, *Monophyllaea*, and *Moultonia* (Wonisch, 1909; Metcalfe & Chalk 1950: 999. 1882).

The Episcieae are not the only group in the Gesneriaceae to possess a trilacunar node with split-laterals. Exactly the same type of node was found in the following cultivated species of the subfamily Cyrtandroideae: (1) in the tribe Didymocarpeae Endl. (*sensu* Burtt, 1963): *Streptocarpus caulescens* Vatke, *S. glandulosissimus* Engler, *S. holstii* Engler, *S. kirkii* Hook. f., *S. saxorum* Engler, *S. stomandrus* B. L. Burtt, *Chirita anachoretica* Hance, *C. pumila* D. Don, *Saintpaulia ionantha* Wendland, *S. magungensis* E. Roberts var. *occidentalis* B. L. Burtt; (2) in the tribe Cyrtandreae: *Cyrtandra oblongifolia* (Bl.) C. B. Cl., *C.* sp. G-1272, and *C.* sp. G-1273, all three species native to the island of Borneo (cf. Wiehler, 1970, plates 16, 17).

Whether the genera listed above are characterized throughout by trilacunar nodes with split-laterals could not be ascertained because of lack of material and the necessary limits of this study. The available unifoliate acaulescent species of *Streptocarpus* present a very specialized situation and were not examined. Species of *Aeschynanthus*, by some considered the Asiatic counterpart of the epiphytic American genus *Columnea*, showed one-trace unilacunar nodes (in *A. ellipticus* Lauterb. & K. Schum., *A. longicaulis* Wall., *A. micranthus* C. B. Cl., *A. obconicus* C. B. Cl., *A. parasiticus* (Wall.) Spreng., *A. parviflorus* (D. Don.) Spreng., *A. parvifolius* R. Br., *A. pulcher* (Bl.) G. Don, *A. speciosus* Hooker, and *A. tricolor* Hook. *Boea hygroscopica* F. Muell., the only other available representative of the tribe Didymocarpeae, had a one-trace unilacunar node (Wiehler, 1970).

The vascular bundles of the petiole as seen in cross-section form an arc or crescent in all the species of the family examined, except those of the tribe Gesnerieae (Figure 85e-f). The changes in the vascular pattern along the length of the petiole were generally found to be very minor (Wiehler, 1970, plate 20). Usually the shape of the crescent remained essentially constant in the petiole, and the free vascular bundles in a cross-section were very few in number.

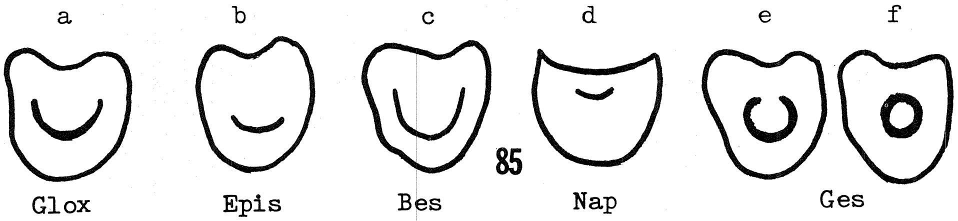

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Figure 85. Typical vascular patterns of the petiole in the tribes of the subfamily Gesnerioideae; a. Gloxinieae; b; Episcieae; c. Beslerieae; d. Napeantheae; e-f. Gesnerieae.

For the tribe Gloxinieae (Figure 85a) the arc is usually large, broad and deep, with the vascular strands fused. In the tribe Episcieae (Figure 85b), in contrast, the crescent is usually small, flat and narrow, with the traces mostly fused, but occasionally free. Larger and somewhat deeper arcs are found in species of *Nautilocalyx*, *Chrysothemis*, and *Alloplectus* (Wiehler, 1970, plates 23-25). The very deep crescent in the Beslerieae (Figure 85) contrasts nicely with that of the Episcieae (the taxa of these two tribes have often been confused in the past). The arc in the Napeantheae (Figure 84d) is small and flat, similar to that of the Episcieae, but located more adaxially. The most distinctive pattern of the vasculature of the petiole within the neotropical Gesneriaceae is found in the tribe Gesnerieae (Figure 85e-f). The crescent here is usually very thick and deep, with invaginated ends (Figure 85e) or the vascular bundles form a complete ring (Figure 85f). The distinct shape of the vascular crescent was one kind of evidence used to reunite *Heppiella corymbosa* (Sw.) Urban with *Gesneria* (Wiehler, 1970, 1971); the shape of the petiolar arc also separates such similar species as *Gesneria cuneifolia* (DC) Fritsch and *G. reticulata* (Griseb.) Urban (Wiehler, 1970). There are no differences in petiolar vascular pattern between the *Rhytidophyllum* group of *Gesneria* and the other sections of *Gesneria*.

The vasculature of the node and petiole in the neotropical Gesneriaceae is of taxonomic value primarily at the tribal level. The trilacunar node with split-laterals (with rare exceptions, commented on below) separates the large tribe Episcieae from the other tribes of the subfamily Gesnerioideae which have one-trace unilacunar nodes. Nodal anatomy and petiolar vasculature in combination similarly have taxonomic significance at the tribal level in segregating the Caribbean Gesnerieae from the other tribes. The anatomy of the node now offers a definite character for the separation of the tribes Beslerieae and Episcieae, species of which have often been confused before. For instance, the "*Besleria*" reported by Metcalfe & Chalk (1950, p. 997) as possessing three leaf-trace strands is not a member of this genus but a species in the tribe Episcieae, *Nautilocalyx melittifolius* (L.) Wiehler (cf. Solereder, 1908, p. 600; Hollstein, 1879, p. 29: "*Besleria melittifolia* L."). Except for the genus *Gesneria* in the monotypic tribe Gesnerieae, no single genus of the

Gesnerioideae can be conclusively characterized by nodal and petiolar vasculature alone. The same holds true on the species level.

The phenomenon of the trilacunar node with split lateral traces of the tribe Episcieae in the Gesnerioideae needs now to be placed into a clearer perspective. The same type of node occurs also in two tribes in the Old World subfamily Cyrtandroideae, in the genera *Cyrtandra*, *Chirita*, *Streptocarpus*, and *Saintpaulia*. The presence of the same distinct nodal type brings the two subfamilies, at times treated as separate families, closer together and suggests further studies in relationships. It appears likely, however, that this rare nodal type arose independently in the Episcieae and again in the Cyrtandroideae. To assume direct phylogenetic relationship between the Episcieae and the otherwise rather diverse taxa of the Cyrtandroideae seems implausible. We know today that the Gesneriaceae are a very plastic plant group, in it such elaborations of nodal anatomy can apparently be triggered easily and repeatedly.

The frequent occurrence of a special type of trilacunar nodes in the Gesneriaceae may seem surprising since this family belongs to an order characterized by one-trace unilacunar nodes. There is, however, one other known exception in the Scrophulariales: regular trilacunar nodes were found in *Crescentia* L. of the Bignoniaceae, but the leaves in this genus are in an alternate arrangement, and the aspect of the node differs accordingly (R. A. Howard, personal communication, 1969).

The scattered appearance of the trilacunar node with split lateral traces among the angiosperm families was recently shown by Howard (1970). He found this nodal type within three different subclasses of the dicotyledons (according to the system of Cronquist, 1968), and suggested that "split-laterals are usually associated with the presence of stipules" (cf. Esau, 1965: 424).

Subclass	Order	Family	Stipules
Magnoliidae	Piperales	Chloranthaceae	present
Rosidae	Cornales	Rhizophoraceae	present
	Sapindales	Zygophyllaceae	present
Asteridae	Rubiales	Rubiaceae	present
	Gentianales	Gentianaceae	absent
	Dipsacales	Caprifoliaceae (=*Sambucus* L.)	absent
	Asterales	Compositae	absent
	Scrophulariales	Gesneriaceae	absent

From the scattered ocurrence of the split-laterals within some genera of the families listed above one may safely deduce that this nodal type arose many times independently among the dicotyledons. From the viewpoint of the Gesneriaceae, the relationship of stipules to split-laterals appears questionable, especially since the estipulate Gesneriaceae make up the largest contingent of split-laterals (see below). Howard noted (1970, p. 213) that "the Gentianaceae are commonly reported to lack stipules but do possess a transverse line connecting the opposite leaf bases." Some of the taxa in the Episcieae exhibit the same transverse line, but in other genera it is absent.

The nodal development in the Gesneriaceae apparently shows a trend in the evolution of trilacunar and multilacunar nodes among the dicotyledons: (1) The one-trace unilacunar nodes of the cotyledonary leaf pair and the first set of true leaves in seedlings of the species of the tribe Episcieae point to a one-trace unilacunar origin of the trilacunar node with split lateral traces for this large tribe. (2) The rare occurrence of one-trace unilacunar nodes in very thin-stemmed epiphytes of the Episcieae represents a reduction from the trilacunar split lateral trace nodal type. The most likely explanation for this reversal in nodal development is that, from a structural viewpoint, there is just not enough space left in the small node for either lateral lacunae in the stele or lateral traces in the cortex. (3) On the pathway from one-trace unilacunar nodes to trilacunar nodes with split laterals, multilacunar nodes represent the next and ultimate step of nodal development. This progression from trilacunar to multilacunar nodes has been observed in *Columnea*, *Cyrtandra*, and *Trichantha* in the Gesneriaceae. The nodal development in the Gesneriaceae can be expressed in the following diagram:

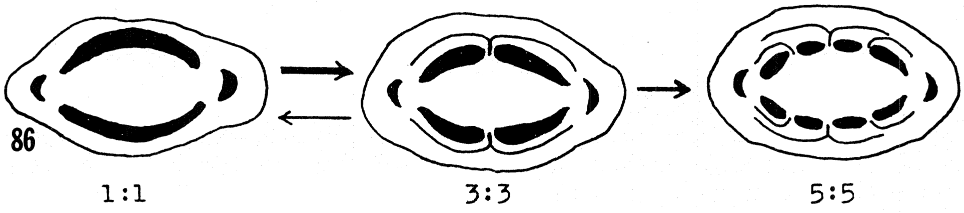

Figure 86. Nodal development in the Gesneriaceae.

Among the typically one-trace unilacunar families of the Tubiflorae, or the Scrophulariales of Cronquist, the Gesneriaceae present a much more varied nodal situation than Sinnott (1914) and Metcalfe & Chalk (1950) realized. Three of the four main types of nodal situations occur in the Gesneriaceae (even within a single species): the one-trace unilacunar, the trilacunar node with split-laterals, and the multilacunar node. According to Bailey & Nast (1944), a comparatively large number of families in the dicotyledons exhibit a combination of unilacunar and trilacunar, or trilacunar and multilacunar nodes, but it is relatively uncommon for a single family to possess three types.

The one-trace unilacunar node may still be the most common in the Gesneriaceae, but the numerical importance of the occurrence of the lacunar node with split lateral traces cannot be underestimated: the tribe Episcieae is the largest in its subfamily, with 21 genera and over 670 species. The nodal situation in the genus *Cyrtandra* is apparently known only from three species from Borneo, two from Hawaii (R. H. Howard, written communication), and the one mentioned by Sinnott (1914). All of these show a trilacunar or multilacunar node with split lateral traces, and there is at least a possibility that this may be the situation for the whole genus. *Cyrtandra* is the largest genus in the family, with over 600 species described (Gillett, 1967). The other genera in the Cyrtandroideae in which trilacunar nodes with split-laterals are reported (*Streptocarpus*, *Chirita*, *Saintpaulia*) are also comparatively large. Thus a nodal study of the Cyrtandroideae may reveal that species with trilacunar and multilacunar nodes with split-laterals either equal or outnumber species with one-trace unilacunar nodes in the Gesneriaceae.

The nodal situation in the Gesneriaceae parallels the evidence gathered by Philipson & Philipson (1968) in the Ericaceae where the trilacunar nodes are reportedly derived from the unilacunar condition.

If nodal anatomy is indeed a comparatively slowly changing or conservative character as our plant anatomy textbooks indicate, then the Gesneriaceae stand out again in their flexibility or plasticity in vascular anatomy. In this family three different nodal types can be found within a single genus such as *Columnea:*

Columnea erythrophaea Decaisne (representing the bulk of the species of this genus)	trilacunar node with split-laterals 3:3
Columnea dodsonii Wiehler (representing the species with thin, pendant stems)	unilacunar node 1:1
Columnea repens (Hook.) Hanst. (only a few nodes of this species are multilacunar)	multilacunar node 4:4, 5:5

If the typical one-trace unilacunar cotyledonary node for the tribe Episcieae is taken into consideration, the above three nodal types can be found within the same species, *Columnea repens*, in which most nodes of the mature plant are trilacunar with split lateral traces.

CHAPTER 13: VEGETATIVE REPRODUCTION

As an adjunct to the previous chapter, this topic deals with some special features of the Gesneriaceae, but it is not directly relevant to generic delimitation within the Gesnerioideae. The stems, nodes, leaves, and inflorescences of the Gesneriaceae often retain a residue of meristematic activity which assures the continuation of a species by asexual reproduction under adverse environmental conditions. This appears to be a special advantage to the precarious existence of the many epiphytic and saxicolous species in this group for which the long process of sexual reproduction (pollination, fruit maturation, seed dispersal, seed germination) may often be a bottleneck situation. A storm-broken shoot or leaf roots easily, given the right kind of substratum, and produces mature plants much faster than through seed production.

There are three kinds of asexual reproduction in the Gesneriaceae:

1) Vegetative regeneration by meristematic activity in the stems and especially in the nodes, exemplified by
    a) the emergence of adventitious roots near the sectioned basal end of the stem or at the node, leading to the fast establishment of a new plant (in most or all Gesneriaceae);
    b) the formation of callous tissue turning into a tuber at the sectional basal end of the stem (in species of *Chrysothemis*, *Lembocarpus*, and *Sinningia*);
    c) the production of plantlets by the formation of stolons arising from the node in the leaf axils (in all species of *Alsobia* and *Episcia*).
2) A residual meristematic potential in the leaves of Gesneriaceae speeds up the reproduction process by the formation of plantlets from
    a) the (accidentally) scattered scale-leaves of underground rhizomes (in all genera with rhizomes, cf. Table 3);
    b) leaves with petioles, with the plantlets arising from the base of the petiole (in many genera, including species of *Achimenes*, *Corytoplectus*, *Gloxinia*, *Nautilocalyx*, *Pearcea*, *Phinaea*, *Smithiantha*, *Aeschynanthus*, *Chirita*, *Saintpaulia*, and *Streptocarpus*);

c) the veins of severed pieces of the lamina of the leaf (in species of *Chrysothemis*, *Corytoplectus*, *Lembocarpus*, *Nautilocalyx*, *Sinningia*, *Chirita*, *Saintpaulia*, and *Streptocarpus*);

d) the teeth of the leaf margins of the small, terrestrial species of *Rhoogeton viviparus* Leeuwenberg from Guyana and adjacent Venezuela (Leeuwenberg, 1958:429).

3) Adverse conditions (seasonal drought, or lack of water in the greenhouse) trigger meristematic activity in axillary inflorescence shoots in some Gesneriaceae, causing the formation of various types of propagules instead of flowers:

a) Scaly rhizomes have been observed in the leaf axils of *Achimenes*, *Eucodonia*, *Gloxinia*, *Phinaea* and *Smithiantha*. Most of these rhizomes are brittle and scatter easily as the mother plant deteriorates.

b) Small tubers are formed on the inflorescence shoots of species of *Chrysothemis*. They break off easily, remain dormant on the dry soil for a long time and send out roots and shoots after the soil remains moist and the atmosphere humid.

c) In the monotypic rhizomatous Asiatic genus *Titanotrichum* from Taiwan and China, placed in the past with the neotropical Gesneriaceae because it does not seem to fit into any of the tribes of the subfamily Cyrtandroideae (Sealy, 1949; Burtt, 1963; Moore & Lee, 1967), the long, whiplike, bracteous inflorescence of culturally neglected plants produces plantletlike buds (Figure 87) in the axils of the numerous small bracts. These two-scaled plantlets, which differ from the much larger underground rhizomes of this species, detach themselves easily from the inflorescence at maturity, and produce roots and regular leaves when the soil is moistened. This species has apparently never produced seed in cultivation (since around 1850).

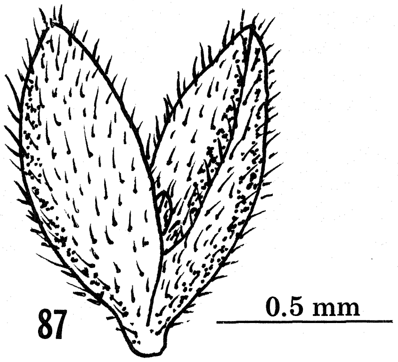

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Figure 87. One of the hundreds of vegetative propagules on an inflorescence of *Titanotrichum oldhamii* produced when the plant grows temporarily under adverse environmental conditions.

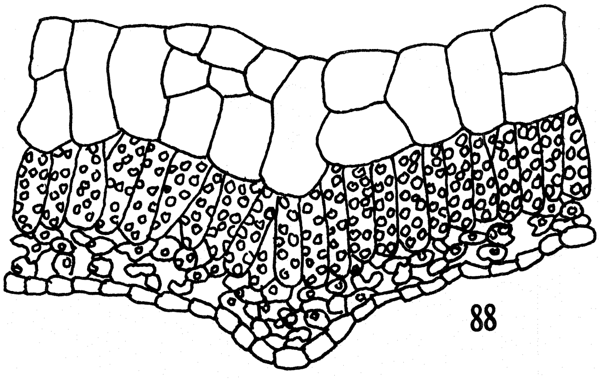
CHAPTER 14: EPIDERMIS AND HYPODERMIS, CELL SIZE, AND CELL WALL SINUATION

This chapter deals with the structure of the gesneriad leaf, with a special emphasis on the hypodermis, with the size and shape of epidermal cells, and the following chapters with stomata and trichomes. It is now generally accepted that the epidermis of the leaf has diagnostic value in the classification of plants. Cell size, cell wall sinuation, the ontogeny and arrangement of the subsidiary cells surrounding the stomata, and the types of trichomes have found increasing use in plant taxonomy, although the value of each of these characters may vary from family to family.

In all species of the Gesneriaceae examined, the leaf structure was found to be bifacial (dorsiventral). The abaxial epidermis consists always of a single layer of cells. This is usually the case with the adaxial epidermis of the lamina, except when a hypodermis (*sensu* Esau, 1960: 346) is present which is always of protodermal origin when it is located above the palisade cells. Such a hypodermis may be two to nine cells thick, or just form a single layer below the epidermis. The distinction between epidermis and hypodermis breaks down in the Gesneriaceae when the one-layered epidermis cells are all enlarged (= serving the same function as the hypodermis) and have a few scattered periclinal divisions, as in *Sinningia sceptrum* (Mart.) Wiehler (Figure 88) and *S. verticillata* (Vell.) H. E. Moore (the latter known to be epiphytic). The mesophyll tissue is separated into palisade and spongy parenchyma. Most of the chloroplasts occur in the palisade parenchyma cells which usually form a layer one cell thick. The cells of the adaxial epidermis are often large and seem to serve as water storage cells. In some species the abaxial epidermis cells are also enlarged and equal in size those of the adaxial leaf surface (*Napeanthus costaricensis* Wiehler, Figure 89; *Trichantha tenensis* Wiehler, Figure 90), but usually the abaxial epidermal cells are small.

The upper or adaxial external surface of the epidermis of the leaf in the Gesneriaceae is usually fairly even and flat. This is usually also the case for the abaxial or lower surface of the leaf in the tribes Episcieae, Beslerieae, Napeantheae, Coronanthereae, and in the majority of the species in the Gesnerieae (Figure 91), but there are some noteworthy exceptions, as in the genera *Episcia* and *Nautilocalyx* (Figure 92). In the tribe Gloxinieae and in most (but not all) species of the *Rhytidophyllum* group in *Gesneria* in the tribe Gesnerieae, the abaxial surface of the epidermis of the leaf appears contorted (Figure 93). Trichomes of various types, shapes, and sizes dominate the "landscape;" some are tall, with very large basal cells, others small, in the shape of a mushroom and with glandular head cells. Among this usually dense "forest" of trichomes, the stomata are located on elevated mounds of varying heights and diameters. It is difficult to trace cell outlines in such "landscapes." But here again are some exceptions that render the interesting surface of the abaxial epidermis of the gesneriaceous leaf almost devoid of any taxonomic value: the epidremis on the underside of the leaves is almost completely flat in *Gloxinia perennia*, *G. sylvatica*, *G. sarmienta*, in species of *Paliavana*, and others. The type of surface structure of the foliar epidermis in the Gesneriaceae appears to be mostly an ecological adaptation to the habitat of the species or genera. Gesneriad species with a contorted abaxial epidermal layer are terrestrials and lack a hypodermis; species with a fairly flat-lying epidermis and a hypodermis are usually epiphytes.

The hypodermis of the leaf in the Gesneriaceae is derived from two different kinds of tissue. The more frequently occurring type of hypodermis, here labeled "the hypodermis of the epiphytes," originates from the adaxial protodermis and is thus located above the chloroplast-bearing palisade cell layer. The second type of hypodermis in the Gesneriaceae is situated below the palisade cells and consists of a proliferation of spongy parenchyma tissue which is thicker than usual and has much enlarged cells. This type of hypodermis has been found only in terrestrial or saxicolous species, such as *Gloxinia lindeniana* (Regel) Fritsch, but this species also has large adaxial epider-



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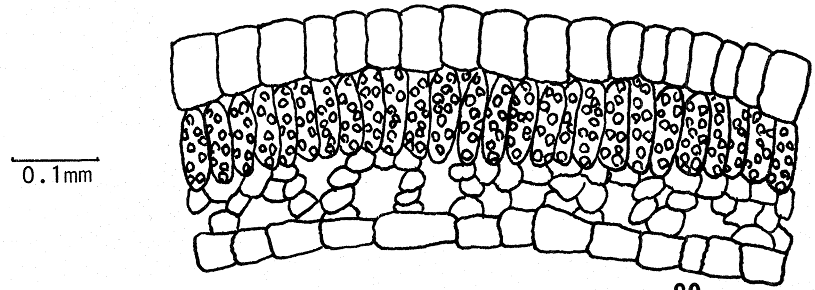

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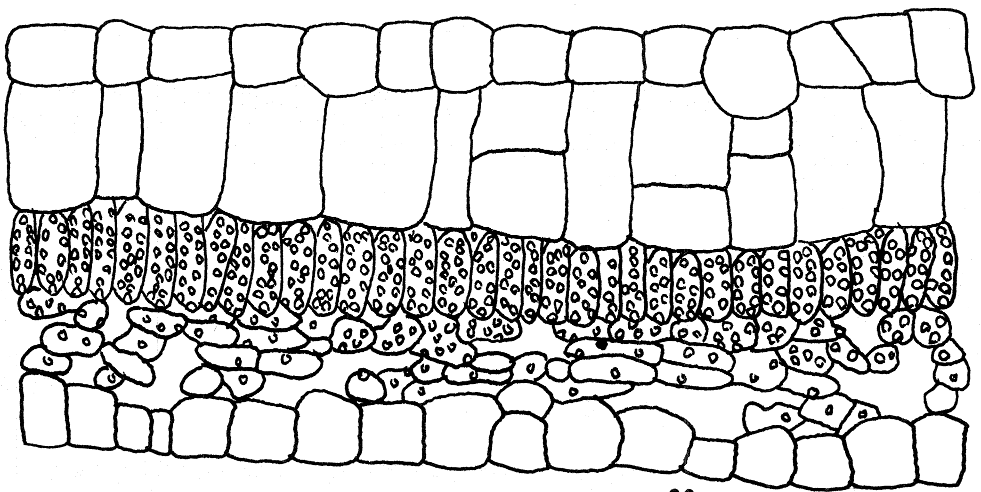

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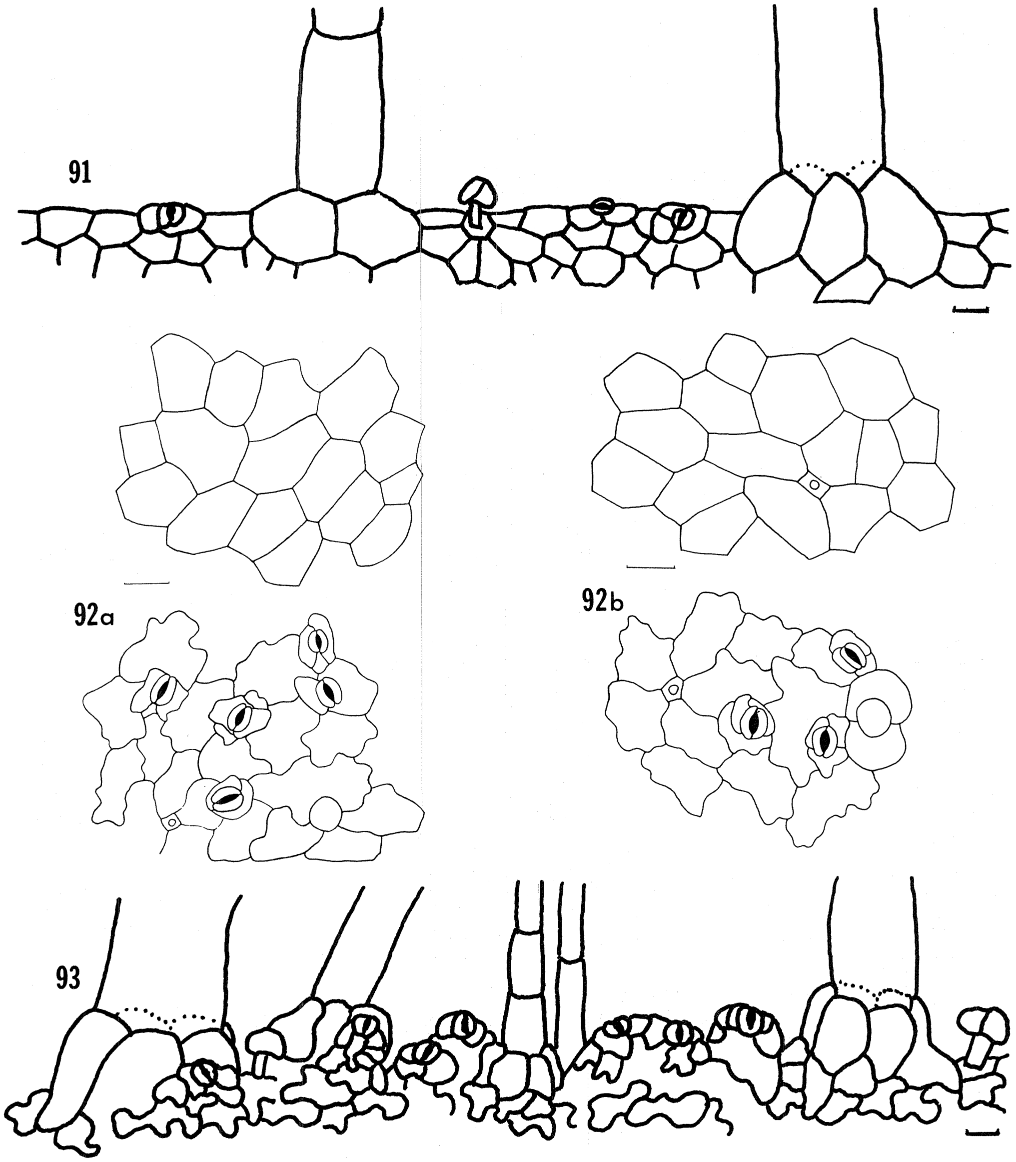
Figures 88-90. Cross-sections of leaves of species of Gesneriaceae with enlarged epidermal cells (X 130). Figure 88. *Sinningia sceptrum* (Mart.) Wiehler; the traditional distinction between (adaxial) epidermis and hypodermis is not applicable for this terrestrial, sun-loving species from Brazil. Figure 89: *Napeanthus costaricensis* Wiehler; large epidermal cells in a terrestrial species preferring deep shade and high humidity. Figure 90: *Trichantha tenensis* Wiehler; large epidermal and hypodermal cells in an epiphytic species of the rain forest, growing in filtered sunlight.



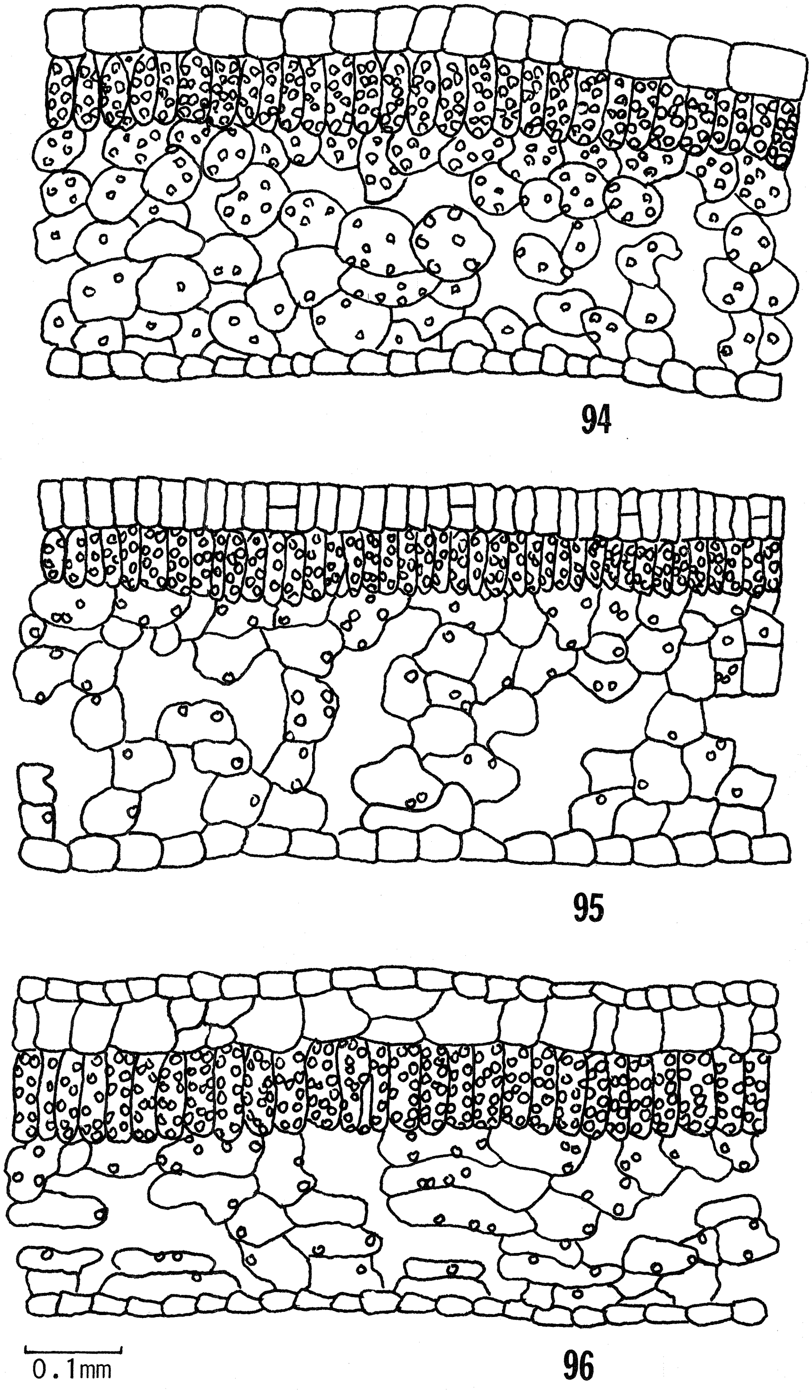
Figures 91-93. Abaxial surface of the epidermis of leaves. Scale: 50 microns. Figure 91. Tribe Episcieae. A typical flat or level leaf surface with straight cell margins; *Dalbergaria sanguinea* (Pers.) Steudel, G-71. Figure 92 a-b. Tribe Episcieae. Level abaxial leaf surface with rarely occurring wavy cell contours and slightly raised stomatal complexes; a. *Nautilocalyx panamensis* (Seem.) Seem., G-1095; b. *Neomortonia nummularia* (Hanst.) Wiehler, G-1040. Adaxial surfaces, without stomata, are added for comparison. Figure 93. Tribe Gloxinieae. A typical contorted abaxial leaf surface with the characteristic wavy cell margins; *Kohleria spicata* (Kunth) Oersted, G-331.

mis cells (Figure 94). In *Gloxinia perennis* (L.) Fritsch there is somewhat less spongy parenchyma tissue and the adaxial epidermis cells are still larger, with a few periclinal divisions present in the "single" layer (Figure 95). In *Gloxinia sylvatica* (Kunth) Wiehler the spongy parenchyma tissue equals in thickness the tissue above the palisade cells which consists of a single layer of small epidermis cells and another single layer of large hypodermis cells with a few periclinal divisions (Figure 96).

A multi-layered adaxial hypodermis occurs rarely outside the tribe Episcieae in the Gesnerioideae. Figure 97 illustrates such a hypodermis in *Sinningia sellovii* (Mart.) Wiehler. The predominance of such a hypodermis in the non-terrestrial species of the tribe Episcieae indicates a definite relationship in the neotropical Gesneriaceae between the phenomenon of epiphytism and the presence of an adaxial hypodermis in the leaf. The same kind of hypodermis located above the compact layer of palisade cells occurs in many epiphytes of other plant families (Madison, 1977), It still needs to be explored whether the function of such a prominent multi-layered hypodermis is merely water storage as plant physiology textbooks indicate (Haberlandt, 1914: 114, 124, 397; Strasburger et al., 1962: 74, 157; Gessner, 1956). Water conservation is a critical problem for many epiphytes without access to the moist forest floor.

A number of fleshy-leaved epiphytic Gesneriaceae store extra amounts of water in the hypodermis of old and yellowing leaves which then are swollen like balloons (Figure 98). The hypodermal tissue does not proliferate in such cases, but the individual cells enlarge greatly (Figure 102 a-b). Schimper (1888: 37) in his famous paper on epiphytism was the first one to observe and describe this phenomenon, citing the example of *Codonanthe devosiana* Lemaire from southeastern Brazil. He found through experimentation that cut-off, old, and swollen (control) leaves of this species, when placed in a light spot in his house in Blumenau, Brazil, were still alive and plump after four weeks, while the same kind of leaves left on stem cuttings were shriveled, wilted, and finally dried up after a short period. The regular succulent green leaves were also thinner after four weeks, but the stem cutting was still alive and producing new apical growth. Schimper concluded from this experiment that the swollen old leaves serve as water reservoir for the actively photosynthesizing younger leaves. I have found the same kind of swollen old leaves on *Codonanthe crassifolia* (Focke) Morton in Ecuador, Colombia, Venezuela, Panama, and Guatemala, on *C. luteola* Wiehler, *C. uleana* Fritsch, *Columnea arguta* Morton, and *Trichantha moorei* (Morton) Morton in Panama, and on cultivated plants of *Codonanthe caribaea* Urban cv. 'Paria,' *C. carnosa* (Gardner) Hanst., *C. gracilis* (Mart.) Hanst., *C. digna* Wiehler, *Nematanthus crassifolius* (Schott) Wiehler, *N. fissus* (Vell.) L. Skog, *N. wettsteinii* (Fritsch) H. E. Moore, and in species of *Aeschynanthus*. Schimper (1888) stated that the same adaptation to epiphytism occurs also in the large and successful genus *Peperomia* Ruiz and Pavon (Piperaceae), and Madison (1977) cited the same phenomenon in *Medinilla ledifolia* Hort. (Melastomataceae), *Psychotria guadelupensis* (DC.) Howard (Solanaceae), *Acanthostachys strobilacea* Link, Klotzsch & Otto (Bromeliaceae), and *Pleurothallis microphylla* A. Rich. & Gal. (Orchidaceae), all of which are epiphytic species.

The hypodermis is of taxonomic value in the Gesneriaceae. The presence or absence of this tissue separates such (often misidentified) genera as *Alloplectus* and *Nematanthus*, and *Alsobia* from *Episcia*. All species in the following genera of the New World Gesneriaceae in the tribe Episcieae have the adaxial "hypodermis of the epiphytes:" *Alsobia*, *Codonanthe*, *Codonanthopsis*, *Columnea*, *Nematanthus*, and *Rufodorsia*. The same hypodermis is also found in a few or many (but not all) species of *Dalbergaria*, *Drymonia*, *Paradrymonia*, *Pentadenia*, and *Trichantha*. In the rest of the genera of the Episcieae the hypodermis is absent: *Alloplectus*, *Bucinellina*, *Chrysothemis*,



Figures 94-96. Cross-section of leaves of species of *Gloxinia* (X 130). Figure 94. *Gloxinia lindeniana* (Regel) Fritsch. Figure 95. *Gloxinia perennis* (L.) Fritsch. Figure 96. *Gloxinia sylvatica* (Kunth) Wiehler.

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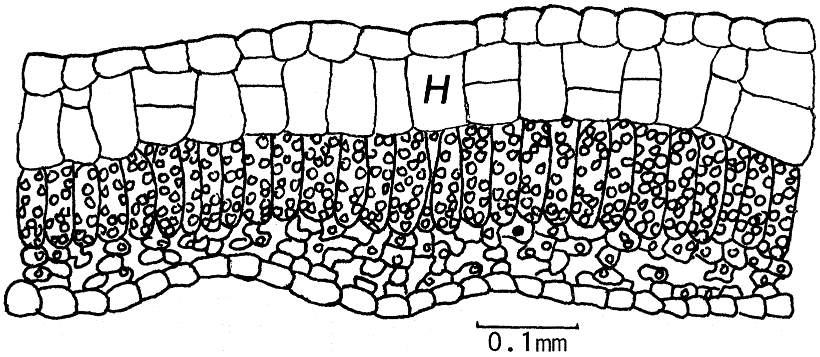

Figure 97. Cross-section of a leaf of *Sinningia sellovii* (Mart.) Wiehler, with a partially multilayered adaxial hypodermis (at H), a rare occurrence in terrestrial gesneriads (X 130).

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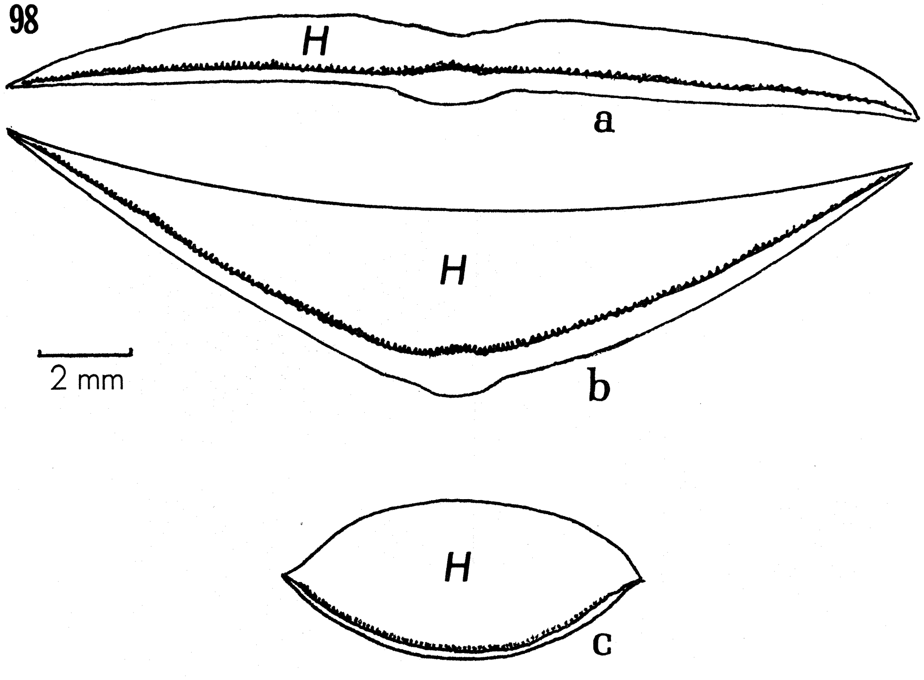
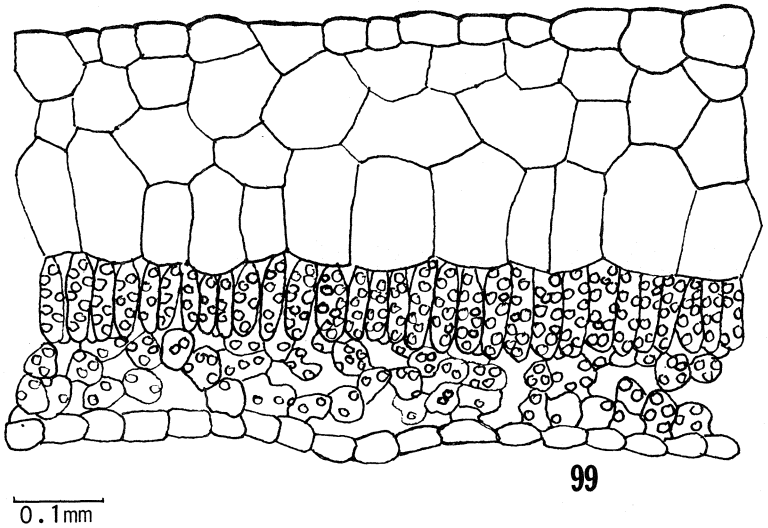


Figure 98. Cross-sections of whole leaves of species of the epiphytic genus *Codonanthe*(X 6). Figure 98a. A young, mature leaf of *Codonanthe luteola* Wiehler, with the normal, multilayered hypodermis at H, magnified X 6. (Figure 102a shows a section of the same leaf, magnified X 130.) Figure 98b. An old, yellowing leaf of *Codonanthe luteola*, functioning as a water storage organ, with enlarged hypodermal tissue at H, magnified X 6. (This leaf is shown again in Figure 102b, at a magnification of X 130.) The amplification of the hypodermal cells is not accomplished through cell proliferation by division but by cell enlargement. Figure 98c. An old, yellow leaf of *Codonanthe digna* Wiehler, a species with small leaves. The hypodermis (H) is swollen like a balloon (X 6).



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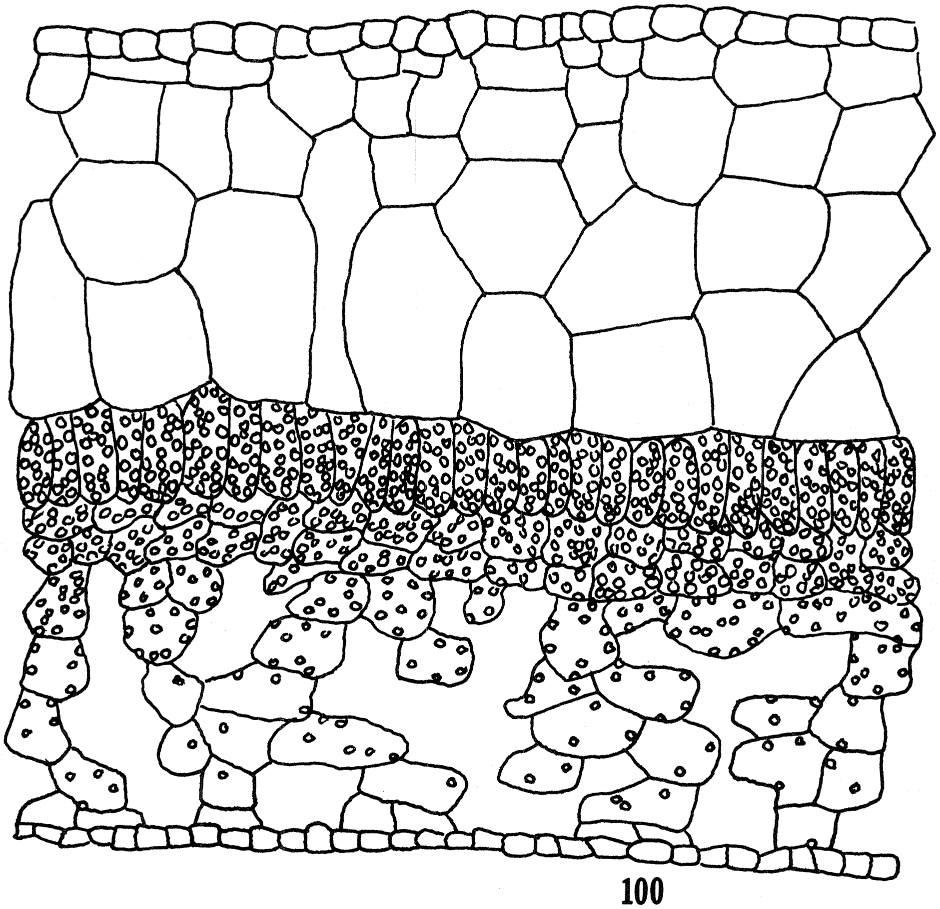

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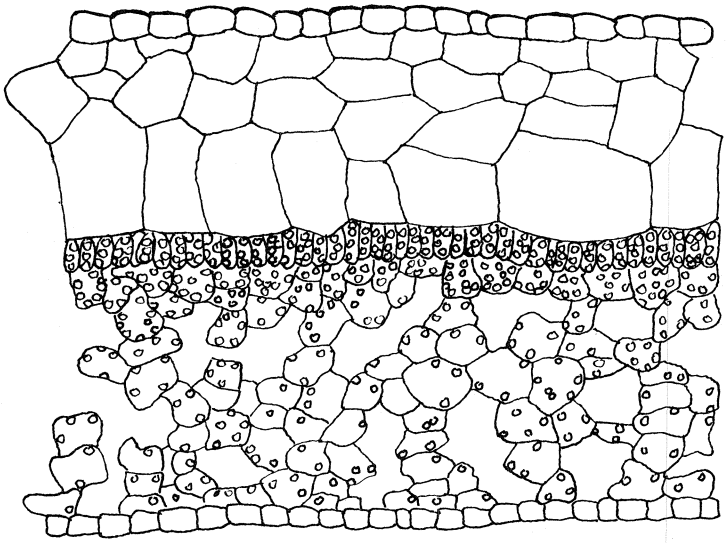
Figures 99-103. The hypodermis in epiphytes. Cross-sections of leaves of epiphytic species of the tribe Episcieae (X 130). Figure 99. *Columnea gallicauda* Wiehler. Figure 100. *Rufodorsia major* Wiehler.



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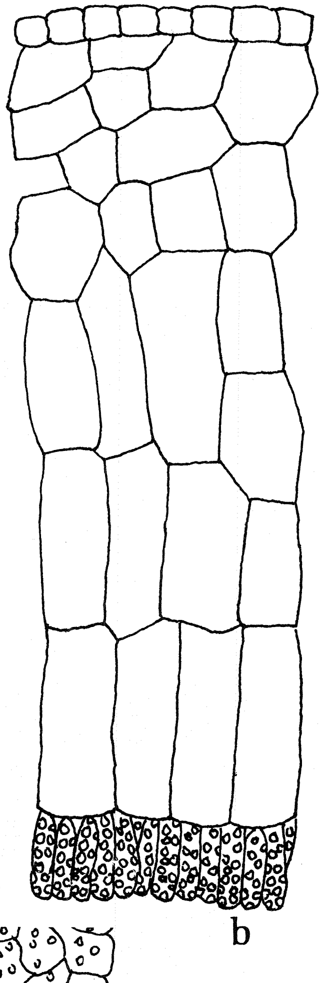

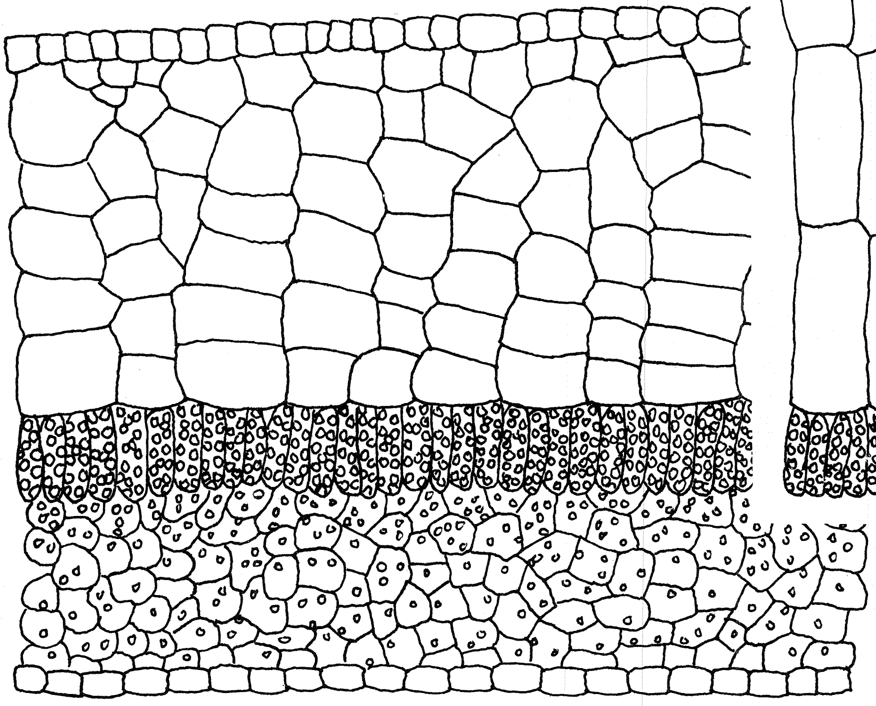

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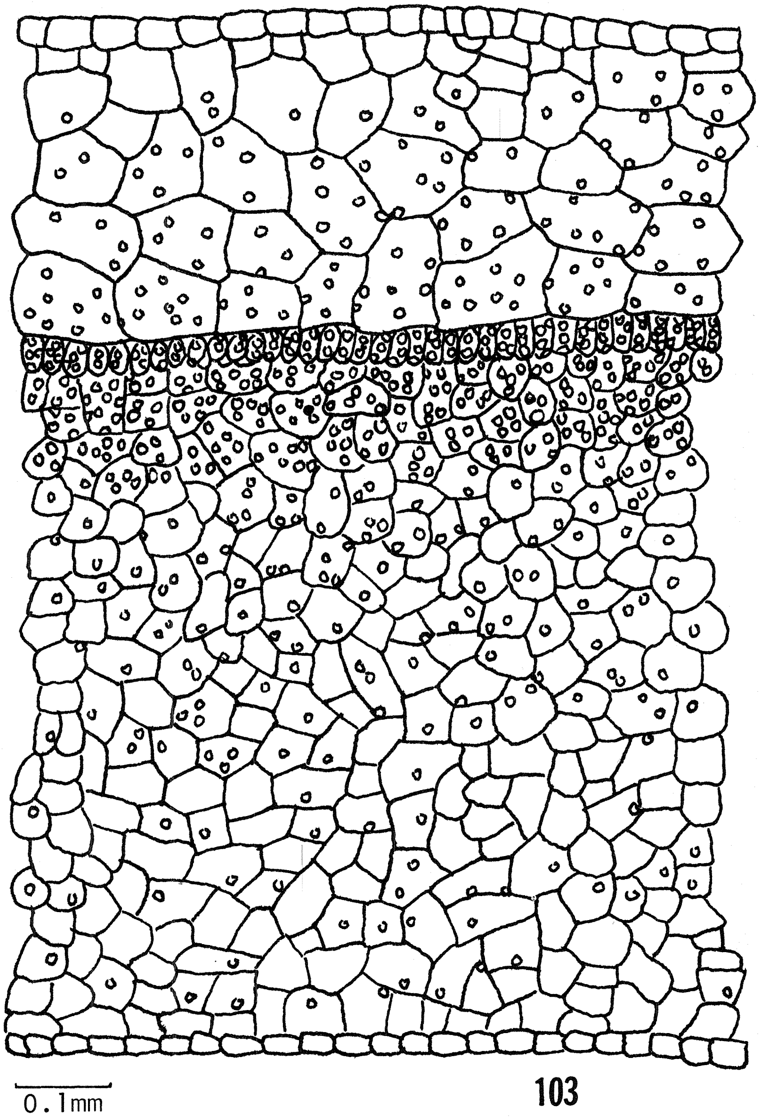
Figures 99-103 (continued). The hypodermis of epiphytes. Cross-sections of leaves of epiphytic species of the tribe Episcieae (X 130). Figure 101. *Nematanthus hirtellus* (Schott) Wiehler. Figure 102. *Codonanthe luteola* Wiehler (tetraploid form). a. young but mature leaf; b. old leaf, functioning as a water storage organ, with swollen hypodermal tissue (see Figure 98).



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Figures 99-103 (continued). The hypodermis of epiphytes. Cross-sections of leaves of epiphytic species of the tribe Episcieae (X 130). Figure 103. *Codonanthopsis ulei* Mansf. The succulent, leathery leaves (with a lamina to ca. 15 cm long) of this epiphyte from the Amazon River appear to function primarily as water storage tissue. The hypodermis is about 4 cells thick, and the spongy parenchyma below the narrow band of palisade cells is enlarged yet very dense, having lost most of its "spongy" quality.

Corytoplectus, *Episcia*, *Nautilocalyx*, *Neomortonia*, and *Rhoogeton*, but most species in these taxa have leaves with enlarged adaxial epidermis cells. Figures 99-103 illustrate the hypodermis in several epiphytic species of the tribe Episcieae.

Both Solereder (1908) and Metcalfe & Chalk (1950) refer to the hypodermis as a special character in the Gesneriaceae. The present investigation indicates that in the Gesneriaceae this tissue is correlated primarily with the phenomenon of epiphytism which, in turn, is a special feature within the tribe Episcieae.

Epiphytic Gesneriaceae have also evolved other methods for water storage: *Sinningia verticillata* (Vell.) H. E. Moore uses its large tuber for that purpose (cf. Schimper, 1888. 38), and *Pentadenia crassicaulis* Wiehler and *P. matudae* Wiehler have swollen stems, with the leaves mostly deciduous during the dry season.

The size of the epidermal cells of the leaf in the Gesneriaceae is usually consistent within a species, but varies greatly from species to species within the genera. For instance, among the 11 species of *Kohleria* examined, no evidence of any correlation between cell size and sectional disposition was seen (Wiehler, 1970: Table 4). The same situation was observed within all other genera investigated. Cell size in the Gesneriaceae is therefore of taxonomic value usually only at the specific level.

The cell size in the Gesnerioideae ranges from about 125 to 2700 adaxial cells per square millimeter. Using a classification of cell size adopted from Stoddard (1965), this is expressed here as follows, with the second numerical value representing the abaxial epidermal cells per square millimeter:

Koellikeria erinodes (DC.) Mansf.	125/450	(Figure 104)
Capanea grandiflora (Kunth) Decaisne	2700/4400	(Figure 105)

As among other plant families, the larger cells in the Gesneriaceae occur in the adaxial leaf epidermis, the smaller on the abaxial surface. There are, however, a few noteworthy exceptions, observed mostly among terrestrial species:

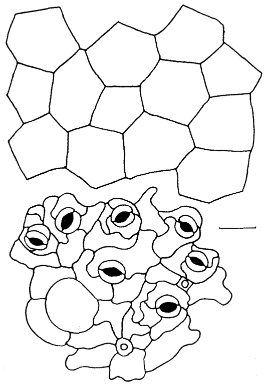
Columnea repens (Hook.) Hanst.	700/500	(Figure 106)
Coronanthera sp. G-1205	400/300	(Figure 144)
Cyrtandra oblongifolia (Bl.) C. B. Cl.	500/300	
Diastema vexans H. E. Moore	500/300	
Gesneria acaulis L. var. *acaulis*	900/500	(Figure 164)
Gesneria corymbosa Swartz	1800/700	(Figure 191)
Napeanthus subacaulis (Griseb.) Kuntze	1300/350	(Figure 209)
Parakohleria vinicolor Wiehler	1500/1300	
Parakohleria weberbaueri (Mansf.) Wiehler	1300/900	
Resia nimbicola H. E. Moore	1450/800	(Figure 107)

(Facing page)
Figures 104-112. Examples of large and small epidermal cells of the leaf in the subfamily Gesnerioideae. The upper drawing in each figure represents the adaxial epidermis, the lower drawing the abaxial leaf surface. Scale: 50 microns

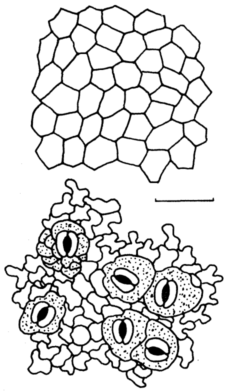
Figures 104-105. Examples of the largest and the smallest epidermal cells found.
Fig. 104. *Koellikeria erinoides* (DC.) Manfs. 125/450
Fig. 105. *Capanea grandiflora* (Kunth) Decaisne, 2700/4400
(stomatal mounds shaded; cells out of focus.)

Figures 106-107. Unusual examples of species in which the abaxial epidermal cells are larger than the adaxial cells of the epidermis.
Figure 106. *Columnea repens* (Hook.) Hanst. 700/400
Figure 107. *Resia nimbicola* H. E. Moore 1500/1000

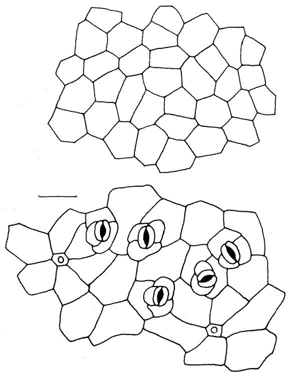
Figures 108-112. Examples of species with small leaves and large epidermal cells and congeneric species with large leaves and small cells of the epidermis.



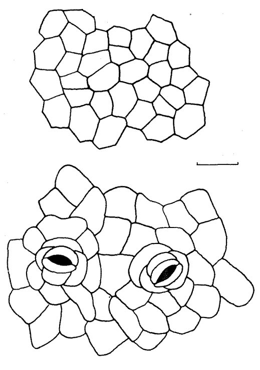
104 Koellikeria erinoides



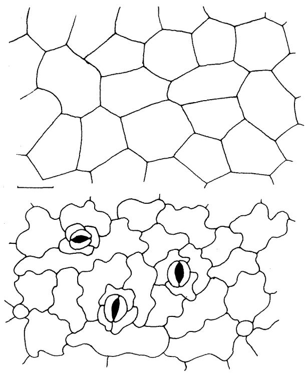
105 Capanea grandiflora



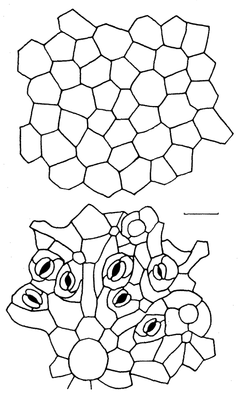
106 Columnea repens



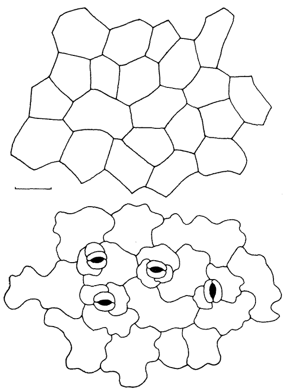
107 Resia nimbicola



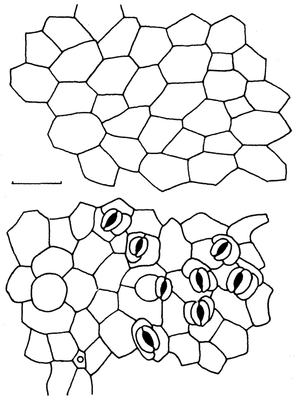
108 Alloplectus hispidus



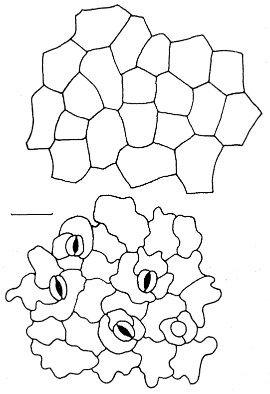
109 Alloplectus tetragonus



110 Sinningia pusilla



111 Sinningia eumorpha



112 Sinningia aggregata

Figure 108. *Alloplectus hispidus* (Kunth) Mart., a species with small leaves	200/350
Figure 109. *Alloplectus tetragonus* (Oersted) Hanst., a species with large leaves	750/900
Figure 110. *Sinningia pusilla* (Mart.) Baillon, leaves small	350/250
Figure 111. *Sinningia eumorpha* H. E. Moore, leaves large	850/900
Figure 112. *Sinningia aggregata* (Ker-Gawl.) Wiehler, leaves comparatively small	500/650

It was also observed that small-leaved species tend to have large epidermal cells and, conversely, large-leaved plants, small cells. A selective advantage for this phenomenon or a ready physiological explanation does not seem apparent. Examples are:

(Small leaves)	(Large leaves)
Alloplectus hispidus (Kunth) Mart. 200/350 (Figure 108)	*A. tetragonus* (Oersted) Hanst. 800/900 (Figure 109)
Columnea microphylla Oersted 250/300	*C. nicaraguensis* Oersted 400/800
Drymonia serrulata (Jacq.) Mart. 700/800	*D. macrantha* (Donn.-Sm.) Gibson 1900/2100
Gesneria citrina Urban 200/600	*G. grandis* Swartz 1400/1000
Moussonia strigosa (Morton) Wiehler 500/550	*M. hirsutissima* (Morton) Wiehler 1100/2900
Nematanthus wettsteinii (Fritsch) Moore 300/400	*N. hirtellus* (Schott) Wiehler 900/900
Sinningia pusilla (Mart.) Baillon 350/250 (Figure 110)	*S. eumorpha* H. E. Moore 850/900 (Figure 111)

Polyploidy among plants is usually correlated with enlarged cells in comparison with the original diploid species. Natural polyploids occur rather infrequently in the Gesnerioideae (see Chapter 17), and since this survey has revealed that many species in this subfamily have extraordinarily large epidermal cells, polyploids in this group are not easily recognized by enlarged cell size (Figures 113-123).

Plant morphologists still do not understand completely all the causes for the undulation of the anticlinal walls of the epidermal cells of the leaf (Esau, 1965: 150). The waviness of the cell walls is more pronounced in the abaxial leaf epidermis, and Gesneriaceae are no exception to this. Although there may be slight differences in sinuation and cell size between a very young and a mature leaf (somewhat deeper sinuation and larger cell size in a mature leaf, cf. *Gloxinia perennis*, Wiehler, 1970: pl. 7), and although there are reports that environmental conditions may at times affect the degree of undulation of epidermal cells (Watson, 1942), the consensus is that sinuation of epidermal cells is a genetically fixed character, and thus possesses diagnostic value (Linsbauer, 1930: 67; Metcalfe & Chalk, 1950; Metcalfe, 1961).

Most species in the tribes Gloxinieae and Beslerieae have rather wavy cell contours, while in the tribes Episcieae and Napeantheae the cell margins are predominantly straight (Wiehler, 1970). There are. however, enough exceptions to make this feature unreliable for taxonomic use. The whole range of cell undulation occurs in the tribe Gesnerieae, from "straight" to "very deep." Most species in *Gesneria* (*sensu stricto*) show either no or only very shallow sinuation while the majority of the species in the former genus *Rhytidophyllum* (now *sub Gesneria*) have deep cell sinuation. There are again exceptions, discussed below in Chapter 48, "The Genus *Gesneria.*" These

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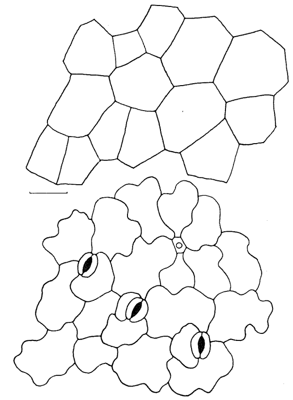
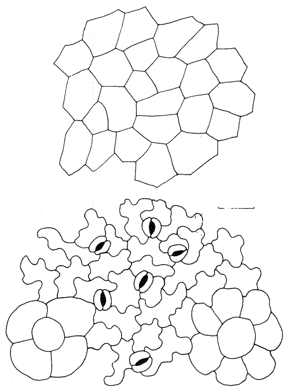
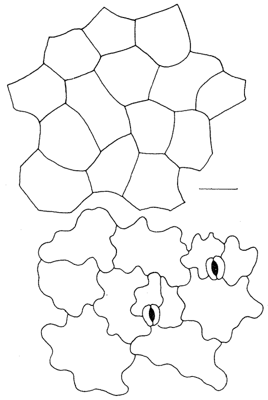
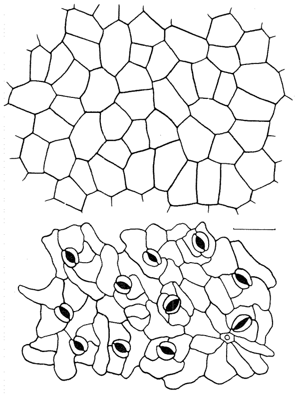
Figures 113-121. Examples of epidermal cells od diploid and tetraploid species or cultivars in the Gesnerioideae. Scale: 50 microns

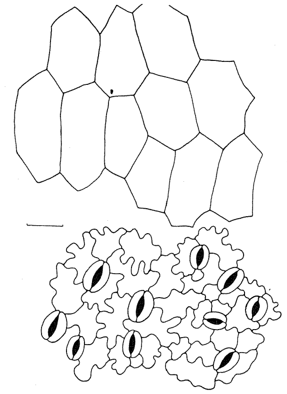
Fig. 113. *Achimenes flava* Morton, G-405, diploid	200/300
Fig. 114. *Achimenes erecta* (Lamarck) H. P. Fuchs G-182, tetraploid	500/500
Fig. 115. *Achimens misera* Lindl. G-431, tetraploid	300/200

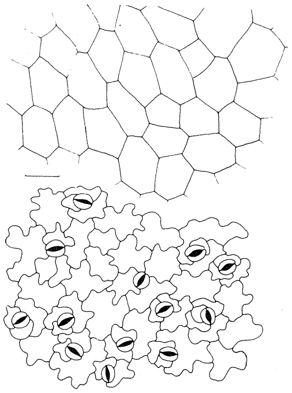

113 Achimenes flava

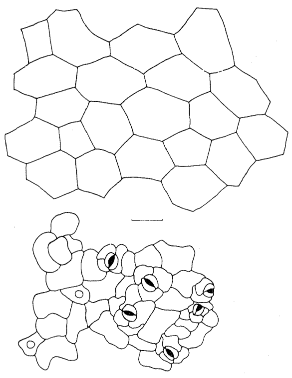

114 Achimenes erecta, tet.

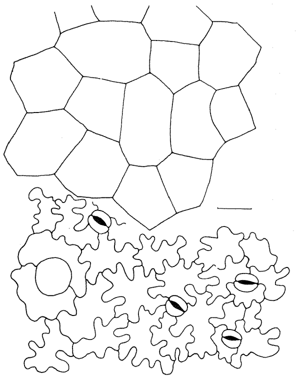

115 Achimenes misera, tet.


116 Gloxinia sylvatica, dip.


117 Gloxinia sylvatica, tet.


118 Gloxinia nematanthodes


119 Eucodonia verticillata, dip.


120 Eucodonia verticillata, tet.

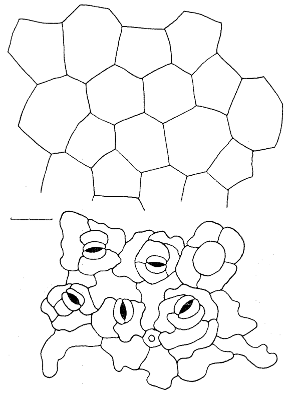
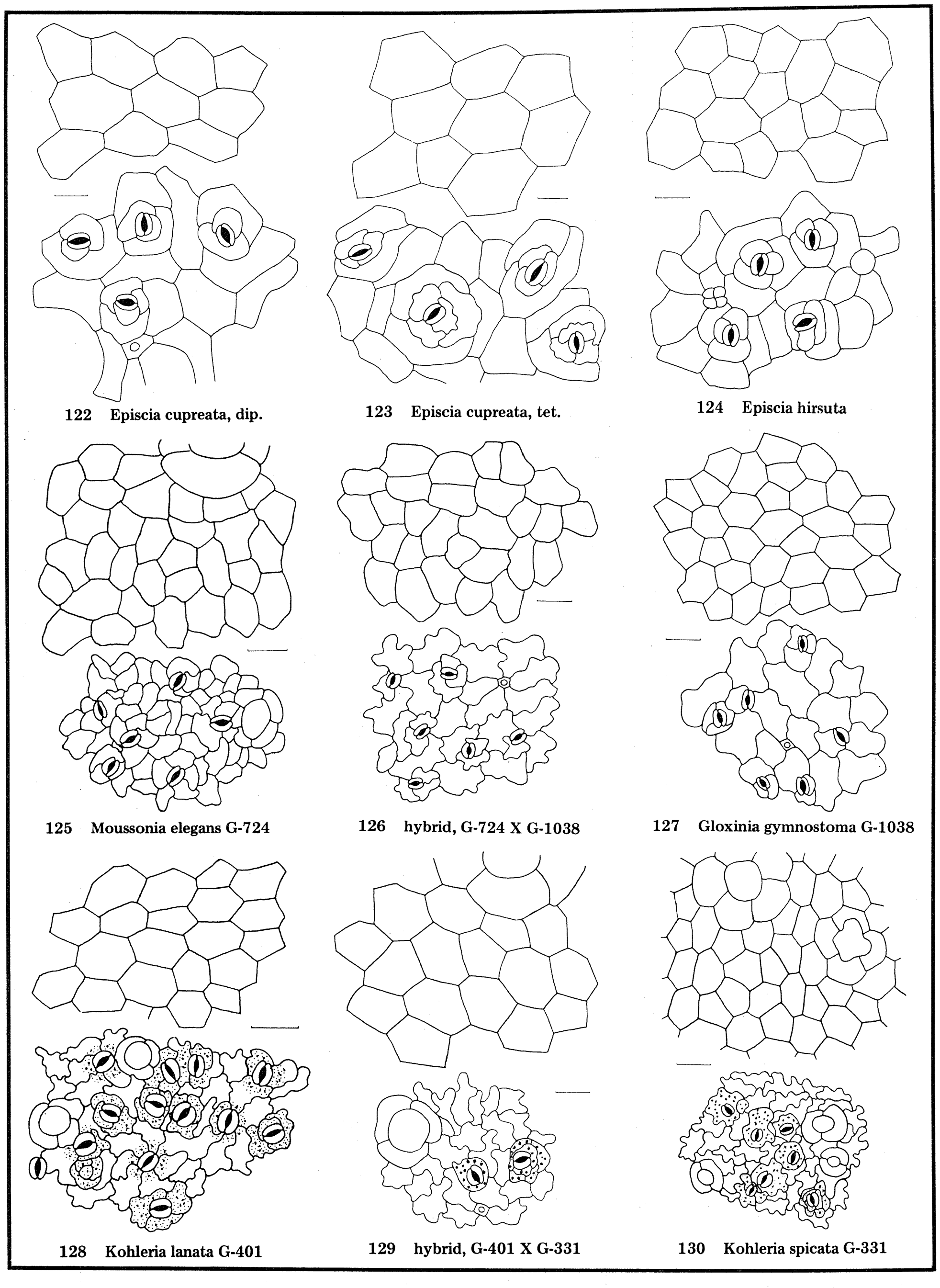

121 Eucodonia andrieuxii, dip.

Fig. 116. *Gloxinia sylvatica* (Kunth) Wiehler, G-990, diploid	750/950
Fig. 117. *Gloxinia sylvatica* G-990a, a tetraploid seedling of the species above	175/550
Fig. 118. *Gloxinia nematanthodes* (Kuntze) Wiehler G-1324, diploid	300/450
Fig. 119. *Eucodonia verticillata* (Martens & Gal.) Wiehler G-561, diploid	200/400
Fig. 120. *Eucodonia verticillata* 'Bella' G-706, tetraploid	150/250
Fig. 121. *Eucodonia andrieuxii* (DC.) Wiehler G-420, diploid	250/500



122 Episcia cupreata, dip.
123 Episcia cupreata, tet.
124 Episcia hirsuta
125 Moussonia elegans G-724
126 hybrid, G-724 X G-1038
127 Gloxinia gymnostoma G-1038
128 Kohleria lanata G-401
129 hybrid, G-401 X G-331
130 Kohleria spicata G-331

Figures 122-130. Examples of epidermal cells of the leaf of diploid and tetraploid cultivars of species and of hybrids in the Gesnerioideae. Scale: 50 microns (stomatal mounds shaded; cells out of focus.)

Fig. 122. *Episcia cupreata* (Hook.) Hanst., 'Variegata' G-109, diploid 200/200
Fig. 123. *Episcia cupreata* 'Amazon' G-1314, tetraploid, with undulating subsidiary cell margins 125/175
Fig. 124. *Episcia hirsuta* (Benth.) Hanst. G-1062, diploid 250/450

exceptions are clear evidence that the cell margin is not a generic character. On the contrary, these exceptions indicate forcefully that all the species in this tribe form a rather natural generic unit. A similar situation occurs in *Sinningia* (*sensu stricto*) which has quite a few species with either no or shallow sinuation of the cell margins, and *Rechsteineria* in which all species have rather deep cell contours. It is now generally accepted that these two taxa represent a single generic unit.

In general, there appears to be a correlation between velvety leaves with a paper-thin lamina and various degrees of sinution of the abaxial epidermal cells of such leaves, and conversely, leaves with a thick, succulent, tough or leathery lamina and straight cell margins (cf. Linsbauer, 1930: 65-69). Cell sinuation may thus be seen as a subordinate function of the general texture of the leaf. This texture, in turn, represents an adaptation to a particular habitat or environment to which a given species is limited (or has limited itself). The succulent leaves of many species in the Episcieae are for the bright and "dry" epiphytic environment; the papyraceous, hairy or glabrous leaves of the Gloxinieae and Beslerieae are adaptations for the darker terrestrial habitats of the moist rain forest; and the tough, smooth and leathery leaves (with the stomata often grouped together) of the Napeantheae, many Gesnerieae, and *Gasteranthus* and *Reldia* are fit for an even more shaded and wet environment in which thin leaves would rot.

There is also some correlation between deep sinuation of the abaxial epidermal cell margins of the leaf and polyploidy and hybridity in the Gesneriaceae (Wiehler, 1970). In a greenhouse-produced spontaneous tetraploid seedling of *Gloxinia sylvatica* (Kunth) Wiehler, the abaxial epidermis has deeply undulating margins, while in the parental plant and other collections of this species, the cell contours are almost straight (Figures 116-117). A natural tetraploid collection of *Eucodonia verticillata* (Mart. & Gal.) Wiehler differs in the same feature from a diploid collection of the same species (Figures 119-120). In a spontaeous tetraploid of *Episcia cupreata* (Hook.) Hanst., the subsidiary cells surrounding the stomates have wavy margins, while they are non-undulating in diploid collections (Figures 122-123). The same phenomenon also occurs along some interspecific and intergeneric (diploid) hybrids where the parental species may have fairly straight cell contours (Figures 125-127).

CHAPTER 15: STOMATES

In well over 400 species of Gesneriaceae examined, the stomata (guard cells plus aperture) were found only on the abaxial surface of the leaf. Stomata occur on both leaf surfaces in most families of the Scrophulariales, the Bignoniaceae excepted (Metcalfe & Chalk, 1950). In the Gesneriaceae the stomates are either randomly scattered on the lower epidermis of the leaf or grouped there into distinct islands (Figures 184-210). In some taxa they are located at the apices of stomatal domes (Figures 177-183). According to the

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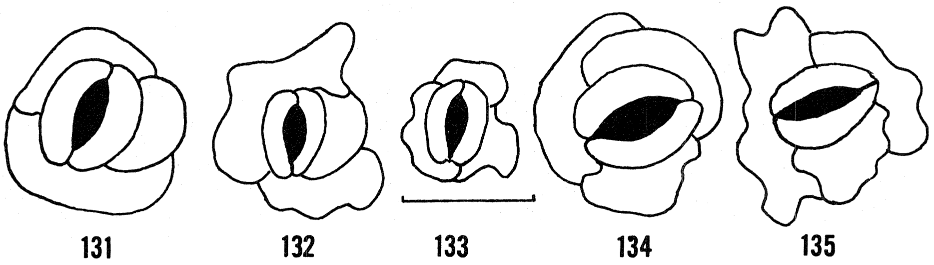
Fig. 125. *Moussonia elegans* Decaisne G-724	550/1900
Fig. 126. hybrid G-724 × G-1038	500/500
Fig. 127. *Gloxinia gymnostoma* Grieseb. G-1038	550/400
Fig. 128. *Kohleria lanata* Lemaire G-401	600/1300
Fig. 129. hybrid G-401 × G-331	200/800
Fig. 130. *Kohleria spicata* (Kunth) Oersted G-331	600/950

recent classification of the ontogenetic types of stomata by Fryns-Claessens & van Cotthem (1973), the stomatal complexes (stomata and their subsidiary cells) in the subfamily Gesnerioideae belong predominantly to the aniso-mesogenous type (Figures 131-135). In the new small subfamily Coronantheroideae most of the taxa have anomo-mesoperigenous (or aperigenous) adult stomata (Figure 136-142), while two of the three examined species of *Coronanthera* showed adult stomata of the para-mesogenous type only (Figures 143-144). Although the stomatal ontogeny in the Coronantheroideae has not yet been studied, the different types of stomatal complexes appear to be of high taxonomic value in the classification of the Gesneriaceae.

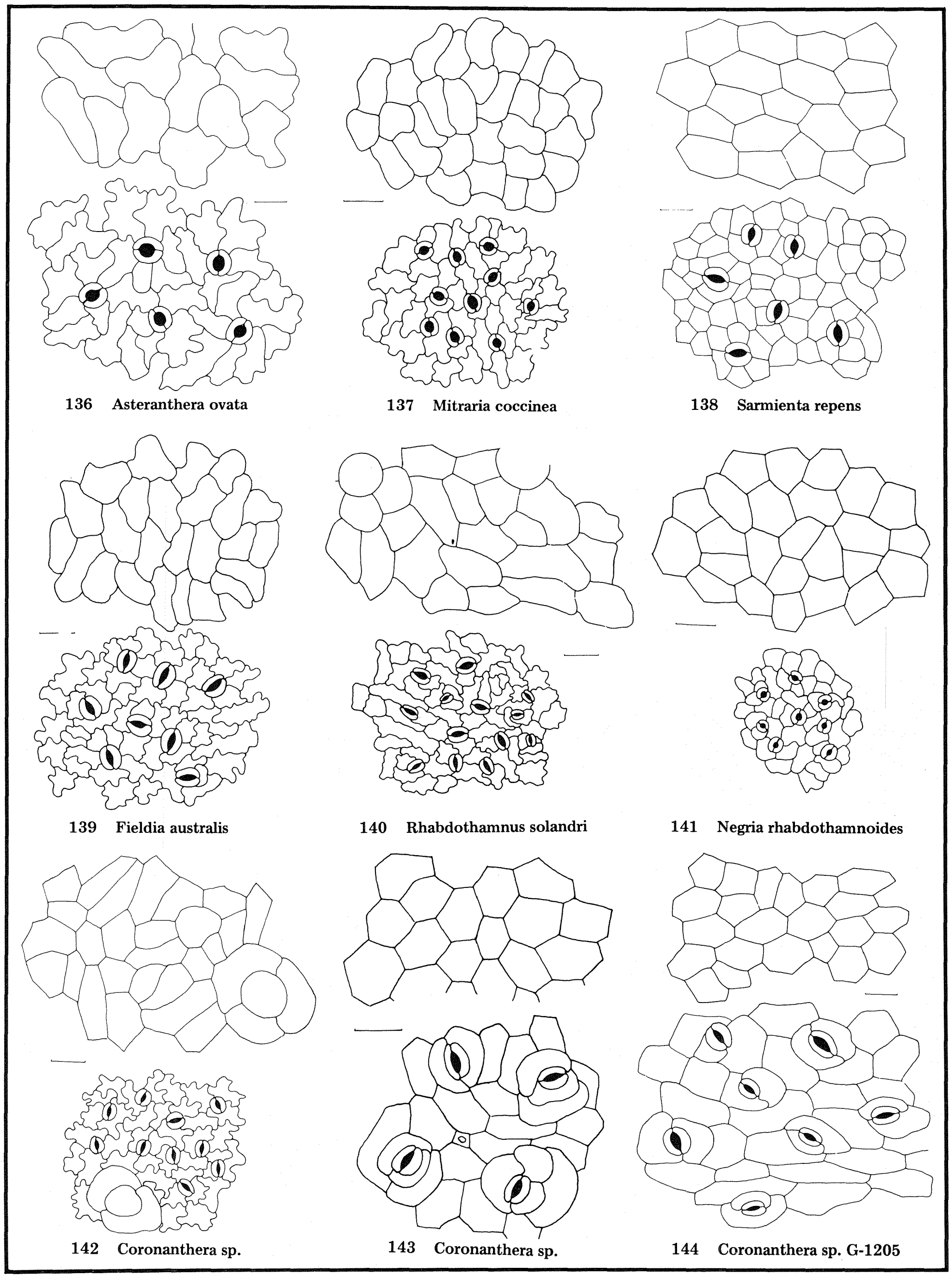


Figures 131-135. Representative aniso-mesogenous stomatal complexes in the five tribes of the Gesnerioideae. Scale: 50 microns

Figure 131. *Columnea microphylla* Oersted	Tribe Episcieae
Figure 132. *Gloxinia perennis* (L.) Fritsch	Tribe Gloxinieae
Figure 133. *Gesneria auriculata* (Hook.) Kuntze	Tribe Gesnerieae
Figure 134. *Napeanthus bullatus* Wiehler	Tribe Napeantheae
Figure 135. *Besleria maasii* Wiehler	Tribe Beslerieae

The ontogeny of the stomatal complexes in the subfamily Gesnerioideae was observed in leaf primordia and in examples of arrested stomatal development in mature leaves (Figures 145-151). The sequence of cell divisions is for the most part characteristic for the aniso-mesogenous stomatal pattern (Fryns-Claessens & van Cotthem, 1973; Payne, 1970; Pant, 1965). But as happens frequently in the Gesneriaceae, there are also exceptions here. Although the aniso-mesogenous type of stomatal complex predominates in the Gesnerioideae (and may be indeed the only basic stomatal type in this group) other "types" of stomatal complexes can be found scattered among the regular aniso-mesogenous stomata in a number of species. Some species in the tribes Gloxinieae and Beslerieae have mixed in several apparent anomo-mesoperigenous (or aperigenous) stomatal complexes (Figures 152-160). Apparent para-mesogenous, dia-mesogenous, and helico-mesogenous stomata have been observed scattered among the typical aniso-mesogenous stomatal complexes in a number of species in the tribes Episcieae and Gesnerieae (Figures 161-169).

From preliminary observations made of leaf primordia and of arrested stomatal development in mature leaves it appears that in most instances the scattered aberrant stomatal "types" in the Gesnerioideae have their origin in sporadic deviations in the sequence of cell divisions of the stomatal initial or meristemoid. In other instances the aberrant stomatal complex appeared to have had a complete aniso-mesogenous ontogeny but was then shifted about in the process of leaf maturation so as to appear of another stomatal type. Further investigation is necessary to prove this thesis, but examples of arrested stomatal development in *Alsobia dianthiflora* (H. E. Moore & R. G. Wilson) Wiehler Figure 170 a-i) indicate already fairly convincingly how



136 Asteranthera ovata

137 Mitraria coccinea

138 Sarmienta repens

139 Fieldia australis

140 Rhabdothamnus solandri

141 Negria rhabdothamnoides

142 Coronanthera sp.

143 Coronanthera sp.

144 Coronanthera sp. G-1205

Figures 136-144. Epidermal cell patterns of leaves in the subfamily Coronantheroideae.
Scale: 50 microns

Figures 136-142. Abaxial epidermis with anomo-mesoperigenous (or aperigenous) stomata. Figure 136. *Asteranthera ovata* (Cav.) Hanst. Figure 137. *Mitraria coccinea* Cav. Figure 138. *Sarmienta repens* Ruĭz & Pavon. Figure 139. *Fieldia australis* Cunn. Figure 140. *Rhabdothamnus solandri* Cunn. Figure 141. *Negria rhabdothamnoides* F. Muell. Figure 142. *Coronanthera* sp. *Bierhorst s.n.* (2) (SEL).

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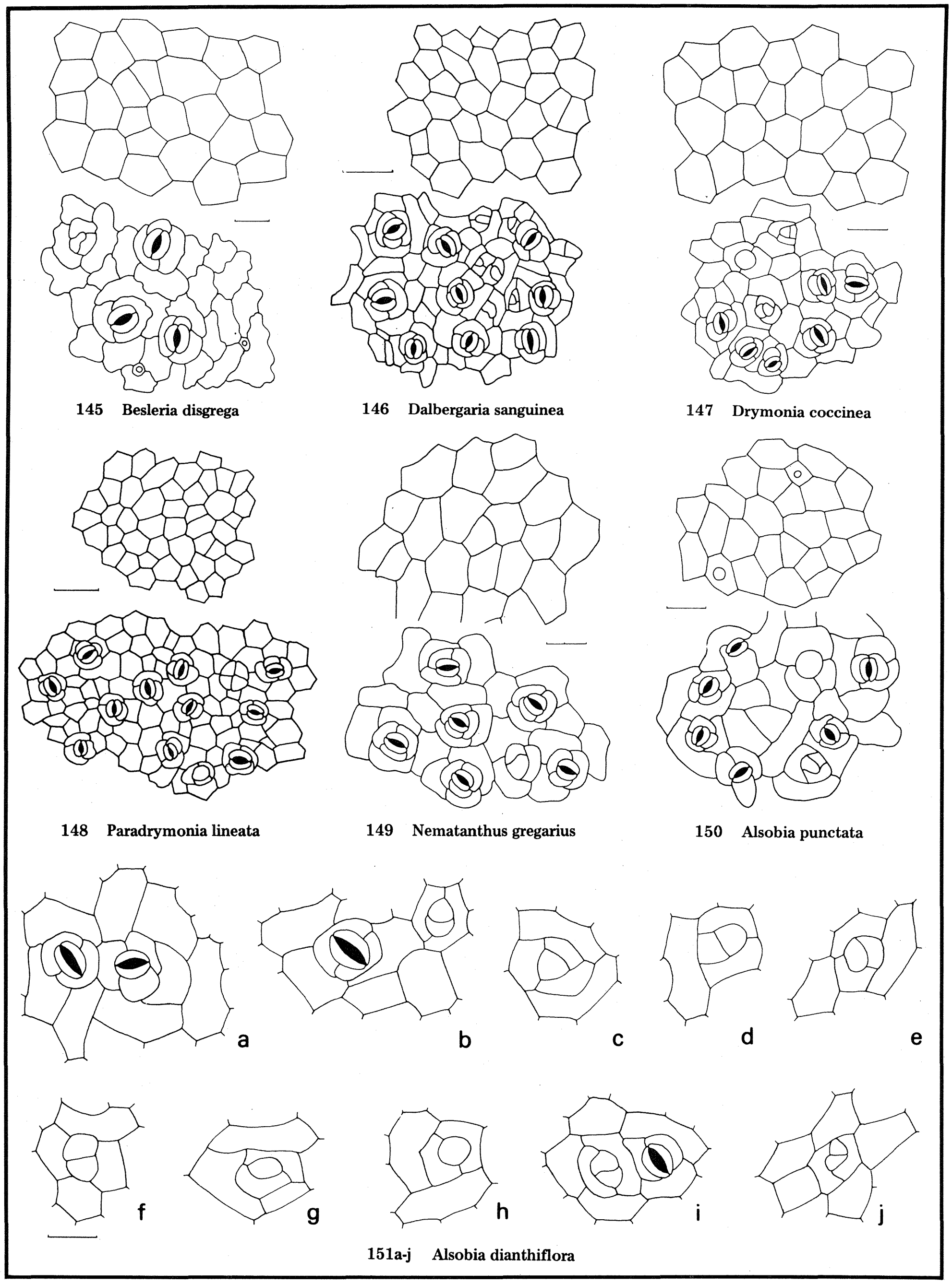
145 Besleria disgrega
146 Dalbergaria sanguinea
147 Drymonia coccinea
148 Paradrymonia lineata
149 Nematanthus gregarius
150 Alsobia punctata
151a-j Alsobia dianthiflora

Figures 145-151. Examples of arrested stomatal development on the abaxial epidermis of mature leaves of species of Gesneriaceae. Figure 145. *Besleria disgrega* Morton G-1065. Figure 146. *Dalbergaria sanguinea* (Pers.) Steudel G-71. Figure 147. *Drymonia coccinea* (Aubl.) Wiehler G-1210. Figure 148. *Paradrymonia lineata* (Morton) Wiehler G-944. Figure 149. *Nematanthus gregarius* Denham G-597. Figure 150. *Alsobia punctata* (Lindl.) Hanst. G-722. Figure 151 a-j. *Alsobia dianthiflora* (H. E. Moore & R. G. Wilson) Wiehler

Scale: 50 microns

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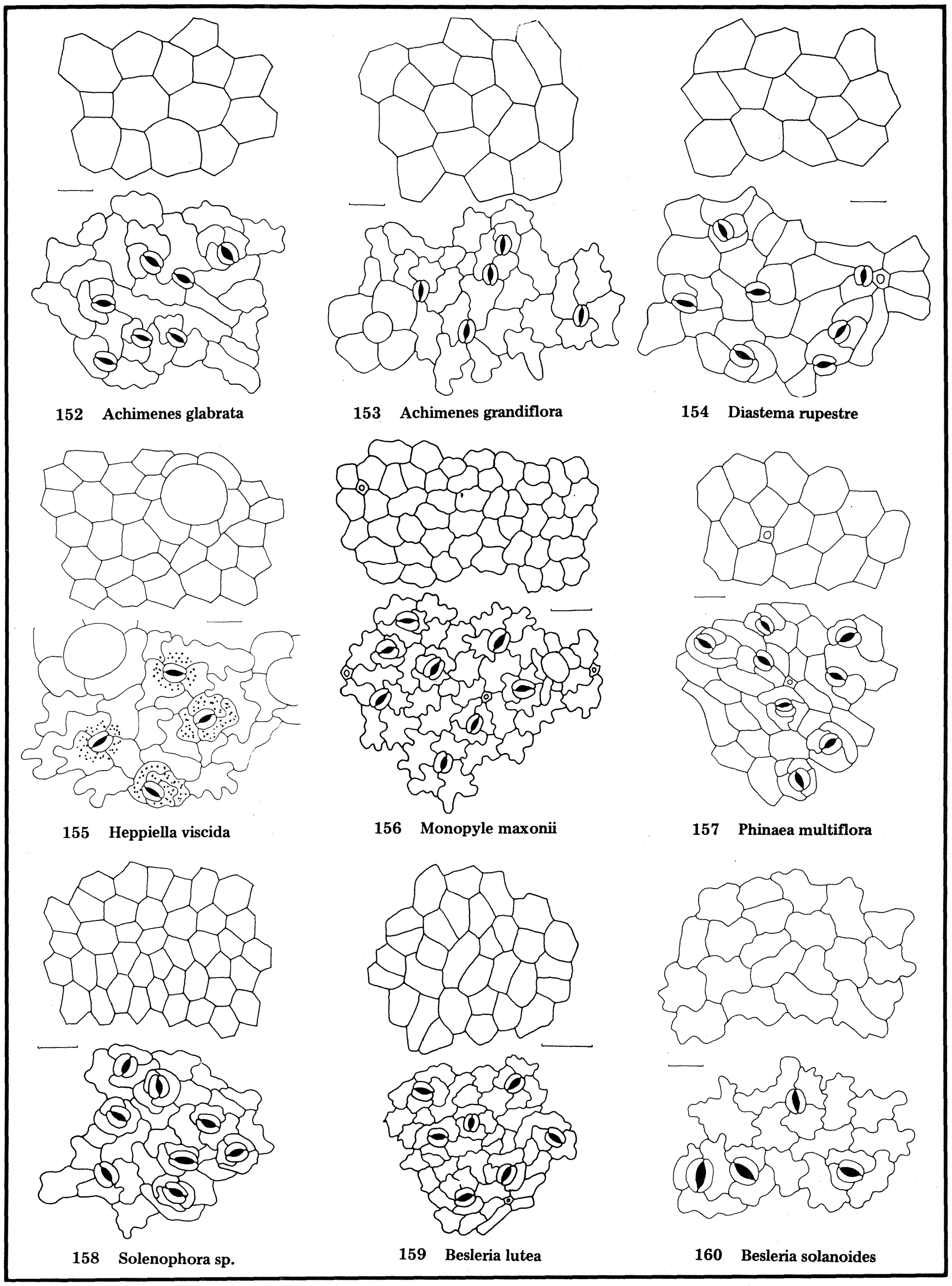
152 Achimenes glabrata
153 Achimenes grandiflora
154 Diastema rupestre
155 Heppiella viscida
156 Monopyle maxonii
157 Phinaea multiflora
158 Solenophora sp.
159 Besleria lutea
160 Besleria solanoides

Figures 152-160. Examples of occasional anomo-mesoperigenous (or aperigenous) stomatal complexes on the abaxial epidermis of mature leaves of species of Gesneriaceae.
Scale: 50 microns

Figure 152. *Achimenes glabrata* (Zucc.) Fritsch G-697. Figure 153. *Achimenes grandiflora* (Schiede) DC. G-390. Figure 154. *Diastema rupestre* T. S. Brandegee G-434. Figure 155. *Heppiella viscida* (Lindl. & Paxton) Fritsch G-1300, tetraploid, stomatal mounds shaded; cells out of focus. Figure 156. *Monopyle maxonii* Morton G-870. Figure 157.

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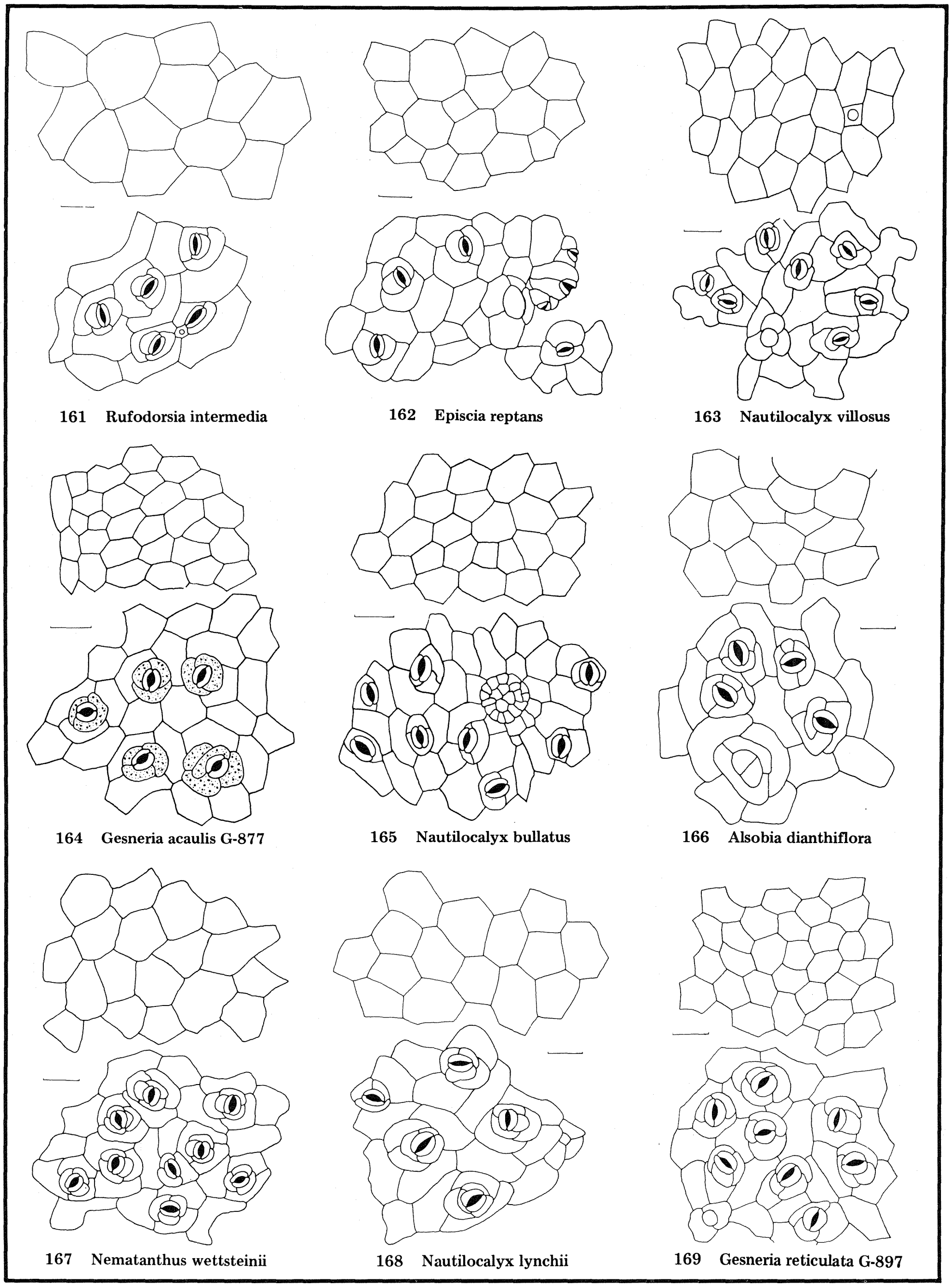

161 Rufodorsia intermedia
162 Episcia reptans
163 Nautilocalyx villosus
164 Gesneria acaulis G-877
165 Nautilocalyx bullatus
166 Alsobia dianthiflora
167 Nematanthus wettsteinii
168 Nautilocalyx lynchii
169 Gesneria reticulata G-897

Figures 161-169. Examples of occasional para-mesogenous, dia-mesogenous, and helico-mesogenous stomatal complexes on the abaxial epidermis of mature leaves of species of Gesneriaceae. Scale: 50 microns

Figures 161-162. Examples of para-mesogenous stomatal complexes. Figure 161. *Rufodorsia intermedia* Wiehler G-891. Figure 162. *Episcia reptans* Mart. G-811.

Figures 163-164. Examples of stomatal complexes intermediate between para-mesogenous

(Continued on page 89)

the occasional pseudo-dia-mesogenous stomatal complexes originate in this species. Figures 171-175 show a schematic representation of regular aniso-mesogenous stomatal ontogeny (Figure 171) and four alternate paths of cell development (via irregular cell divisions, Figures 172-175) leading to the four other (= occasional) "types" of stomatal complexes found in the subfamily Gesnerioideae.

Stomata elevated on mounds projecting above the plane of the epidermis are a special feature in the Gesnerioideae, occurring in many taxa of the tribe Gloxinieae and in about 18 species of *Gesneria* (Figures 176-183). These mounds include the subsidiary cells and adjacent regular epidermal cells. All cells of the mounds are typically smaller than the regular epidermal cells. The average height of the mounds lies between 30 and 40 microns above the level of the epidermis, but mounds as high as 70 microns were observed in *Kohleria tubiflora* (Figure 179) and in *Moussonia deppeana* (Figure 176). Usually each mound holds a single stoma.

There is a strong correlation between gesneriad leaves with a thin, velvety lamina, abaxial epidermal cells with deep sinuations, and the presence of stomatal mounds. All of the taxa possessing stomatal mounds are terrestrials inhabiting the humid tropical rain forest. The information on stomatal mounds in the literature is not very extensive. Haberlandt (1914, p. 474) offers an illustration of a raised stoma on the peduncle of *Cucurbita pepo* and notes that elevated stomata occur not infrequently in plants which inhabit shady places. The exposed situation of the stomata represents a device for accelerating transpiration. Biebl & Germ (1950: p. 105) state that the function of raised stomata on plants growing in a humid environment is to give

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(Continued from page 85 - **Legend for Figures 136-144**)

Figures 143-144. Abaxial epidermis with para-mesogenous stomata.
Figure 143. *Coronanthera* sp. *Bierhorst 646* (SEL). Figure 144. *Coronanthera* sp. G-1205

(Continued from page 86 - **Legend for Figures 145-151**)

G-111, selected configurations from several leaves: Figure 151a. Two fully developed stomatal complexes, one with a regular aniso-mesogenous pattern, the other with a dia-mesogenous subsidiary cell arrangement; Figure 151b. two dia-mesogenous stomatal complexes, one fully developed, the other aborted; Figure 151 c-f. aborted aniso-mesogenous stomatal complexes; Figure 151 g-j. aborted dia-mesogenous stomatal complexes.

(Continued from page 87 - **Legend for Figures 152-160**)

Phinaea multiflora Morton G-436. Figure 158. *Solenophora* sp. G-893 (*S. mortonii* Denham ined.). Figure 159. *Besleria lutea* L. G-840. Figure 160. *Besleria solanoides* Kunth W-1846.

(Continued from page 88 - **Legend for Figures 161-169**)

and dia-mesogenous. Figure 163. *Nautilocalyx villosus* (Kunth & Bouché) Sprague G-864. Figure 164. *Gesneria acaulis* L. var. *acaulis* G-877, stomatal mounds shaded.

Figures 165-166. Examples of dia-mesogenous stomatal complexes. Figure 165, *Nautilocalyx bullatus* (Lemaire) Sprague G-132. Figure 166. *Alsobia dianthiflora* (H. E. Moore & R. G. Wilson) Wiehler G-111

Figures 167-169. Examples of helico-mesogenous stomatal complexes. Figure 167. *Nematanthus wettsteinii* (Fritsch) H. E. Moore G-655 (the three stomatal complexes at top of lower illustration). Figure 168. *Nautilocalyx lynchii* (Hook. f.) Sprague G-288, tetraploid. Figure 169. *Gesneria reticulata*(Griseb.) Urban G-897

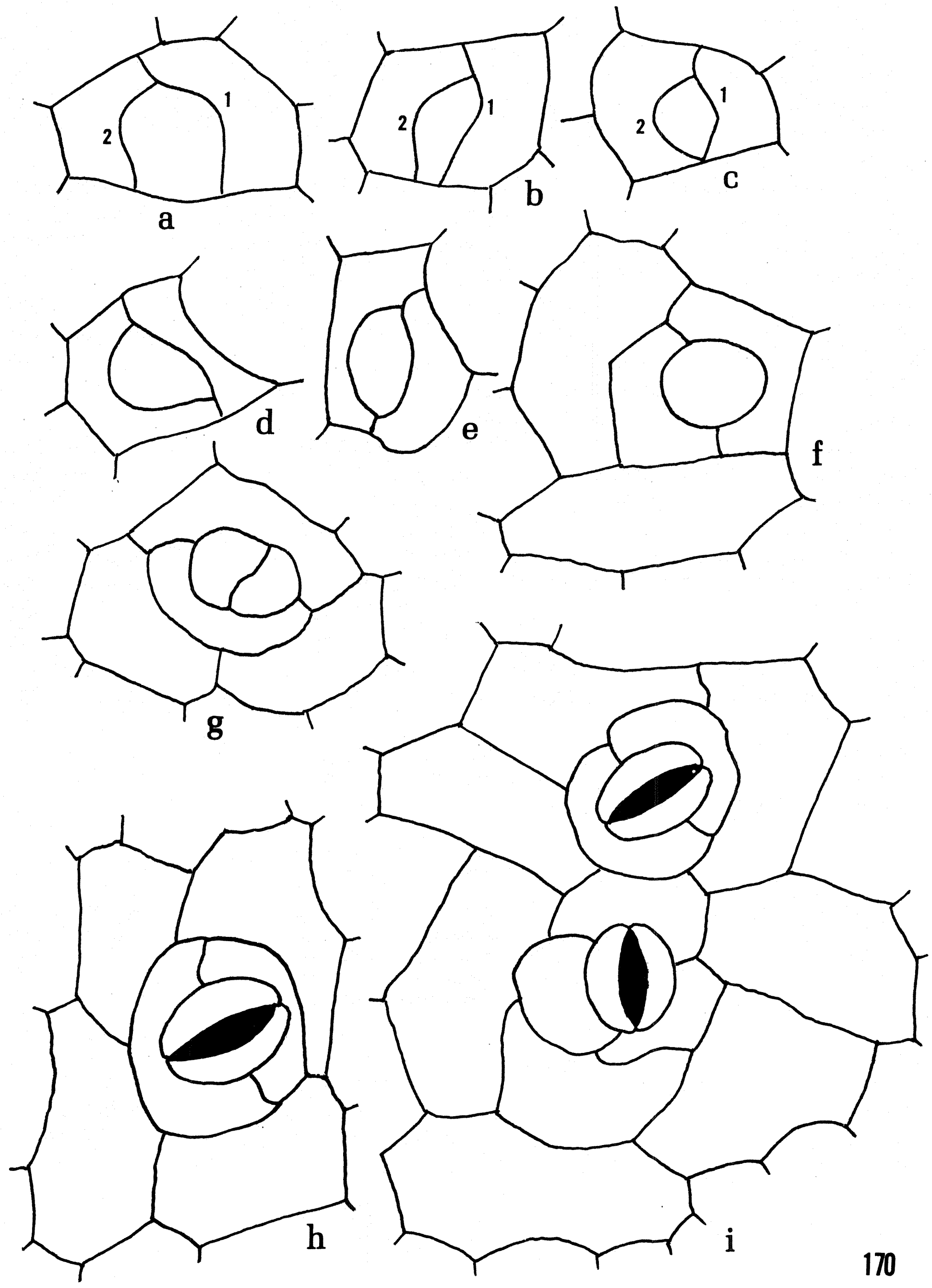
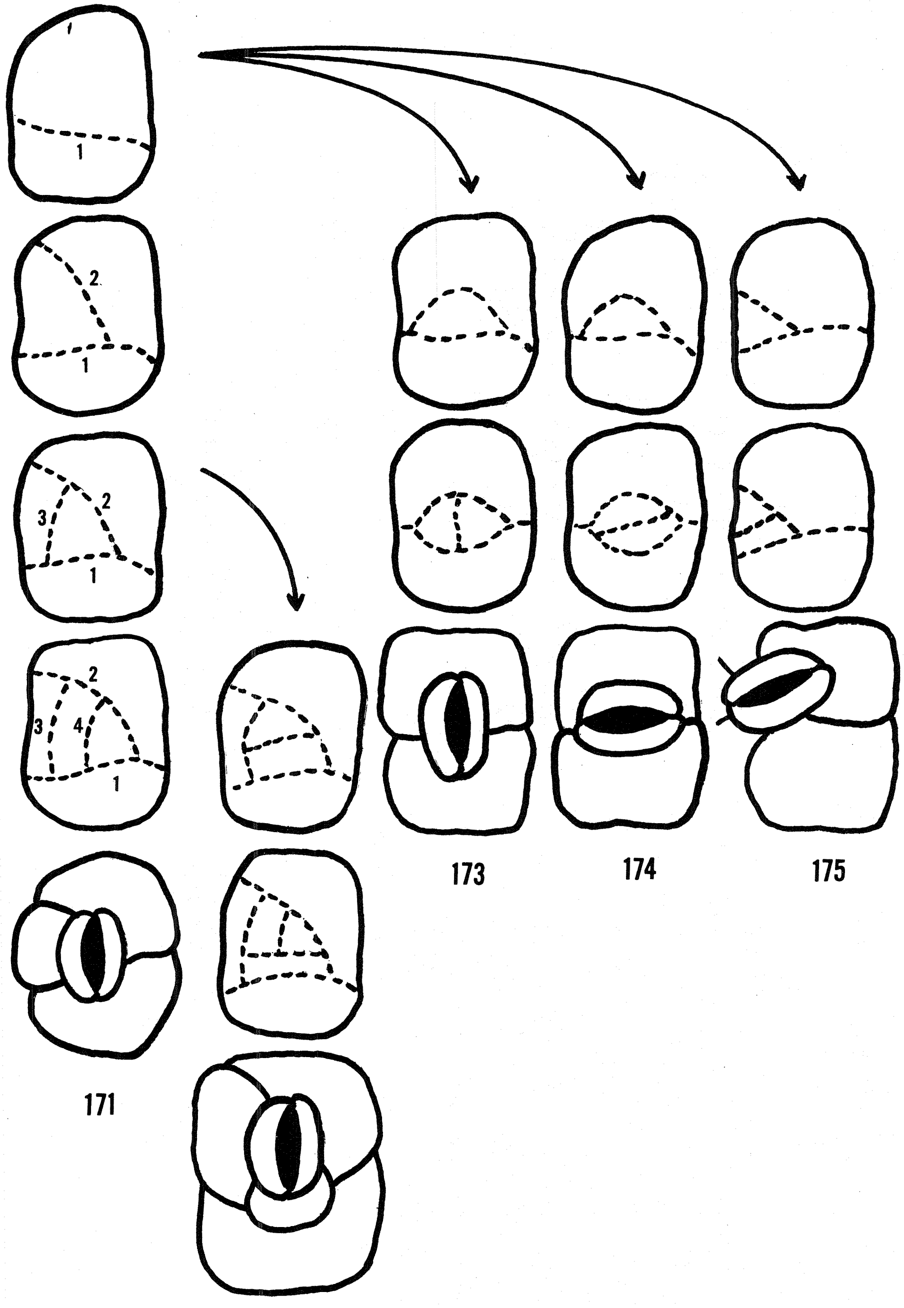


Figure 170 a-i. Abaxial epidermis of the leaf of *Alsobia dianthiflora* (H. E. Moore & R. G. Wilson) Wiehler, with patterns of arrested stomatal development and two pseudo-dia-mesogenous stomata; a-g. arrested stomatal development: a. with regular secondary division (at 2) leading to the typical aniso-mesogenous stomatal complex; b-f. examples of progressively aberrant secondary cell divisions; g. same, with the tertiary division; h. a fully developed, mature pseudo-dia-mesogenous stomatal complex; i. same, with a regular aniso-mesogenous stomatal complex (lower right) in close proximity.



Figures 171-175: Schematic representation of the ontogeny of the "types" of stomatal complexes found in the subfamily Gesnerioideae. Figure 171, the predominant aniso-mesogenous stomatal type from which the other four "types" (Figures 172-175) occasionally found scattered among the regular stomates of the Gesnerioideae appear to be derived through aberrant cell divisions. The presumably derived forms are: helico-mesogenous (Figure 172), dia-mesogenous (Figure 173), para-mesogenous (Figure 174), and anomo-mesoperigenous (Figure 175).

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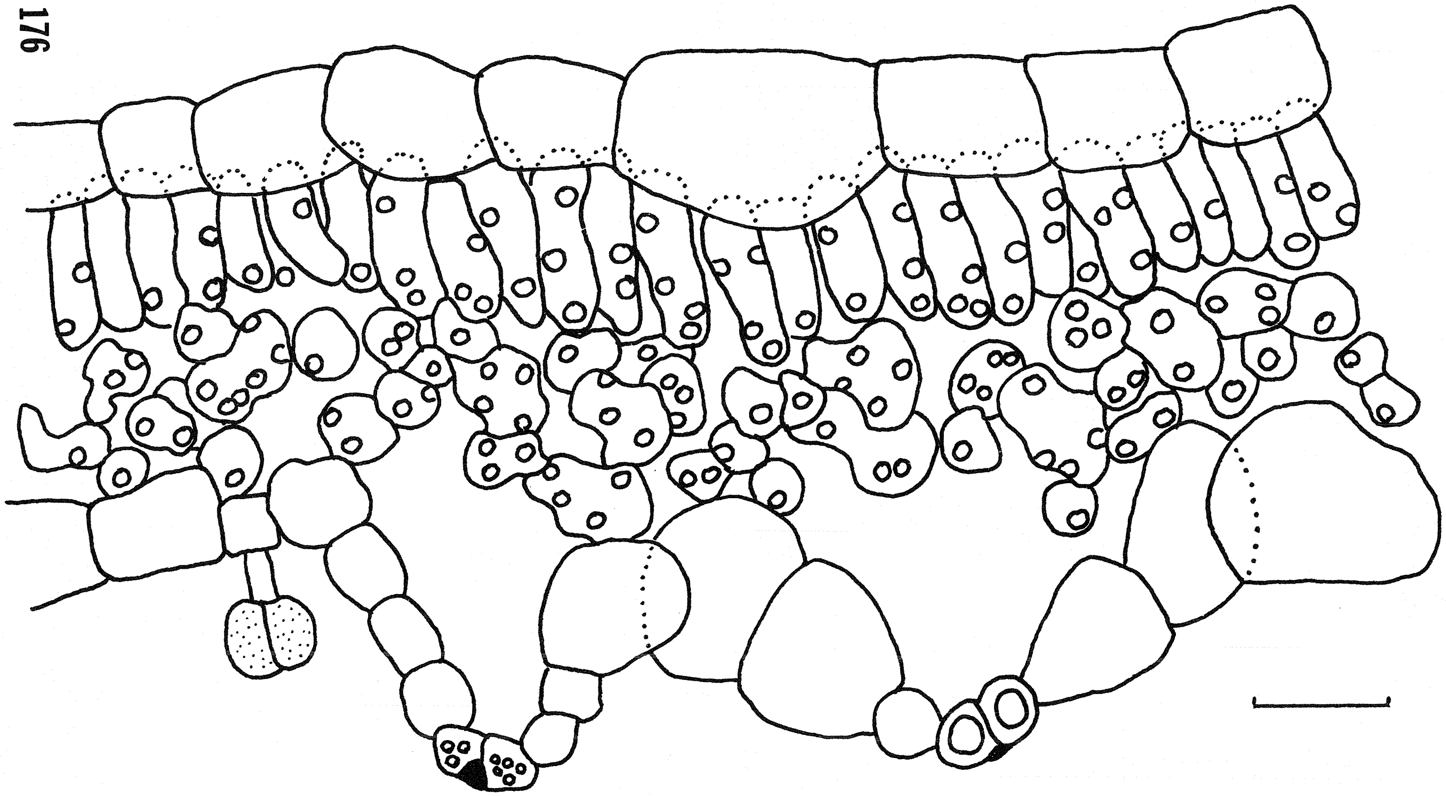
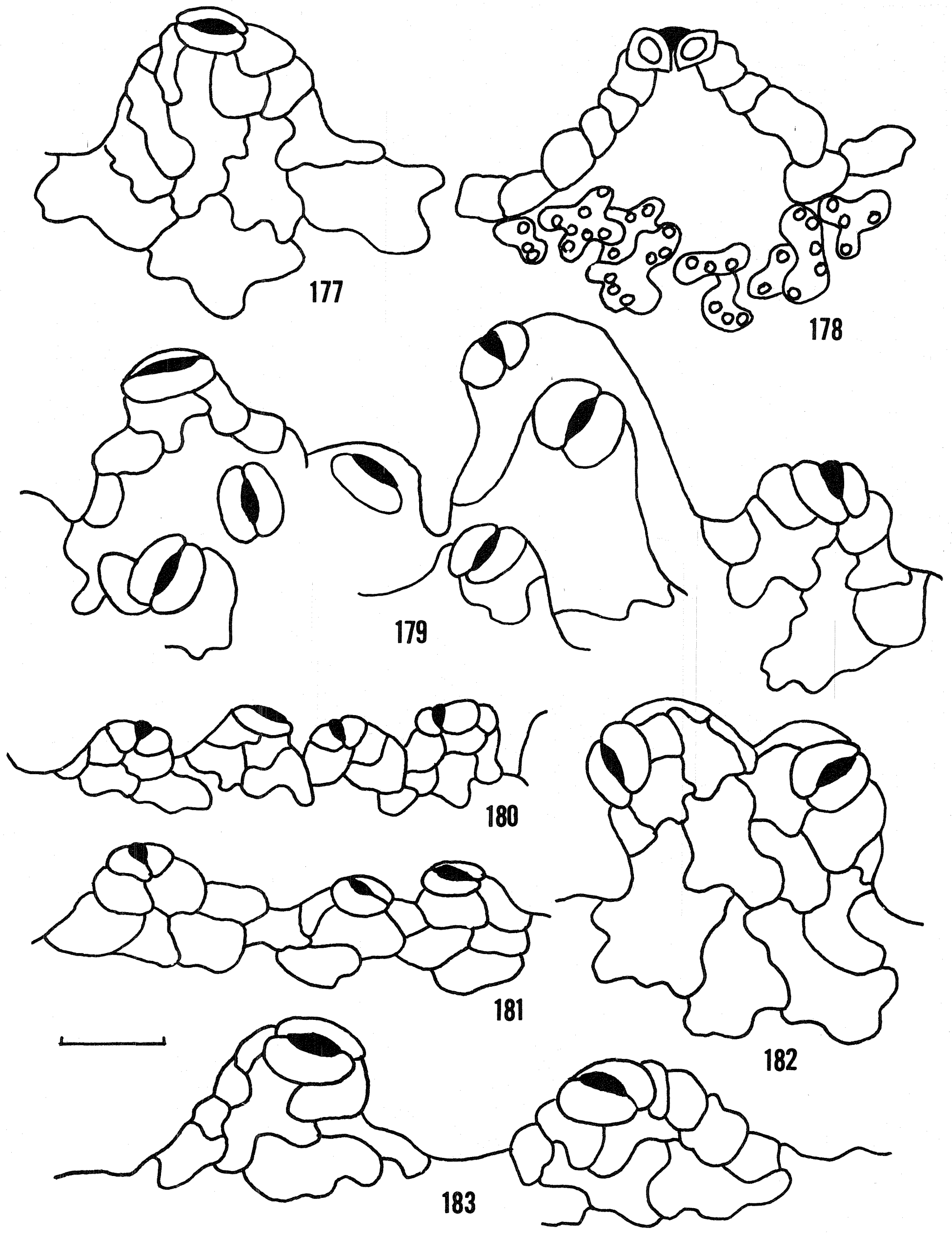


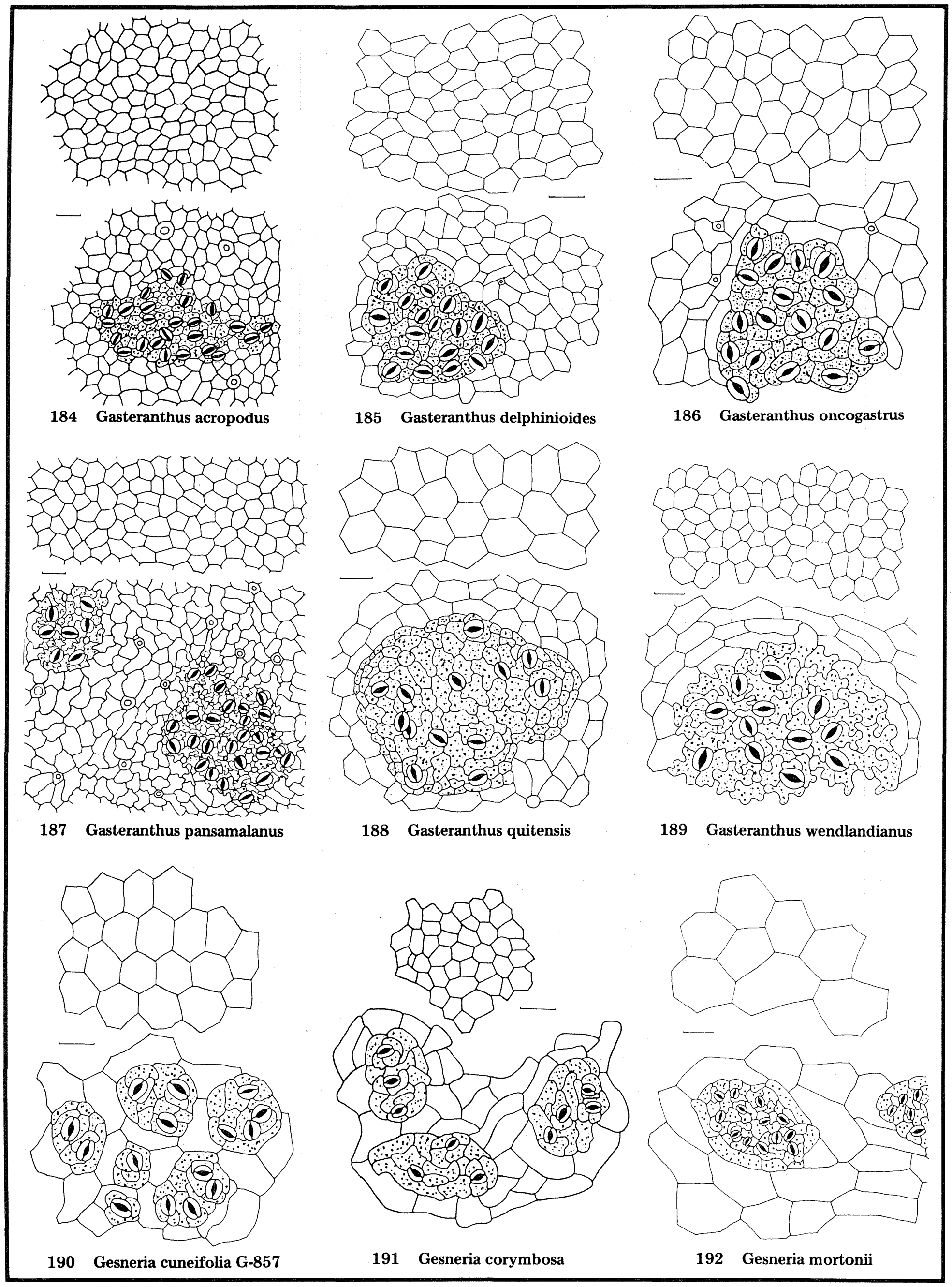
Figure 176. Cross-section of leaf of *Moussonia deppeana*, with stomatal mounds of the abaxial surface. Scale: 50 microns.



Figures 177-183. Stomatal mounds on the abaxial lamina in species of *Kohleria* and *Moussonia*. Scale: 50 microns

Figures 177-179. *Kohleria tubiflora* (Cav.) Hanst. Figure 177. External view of a stomatal mound, with stoma, subsidiary cells, and regular epidermal cells. Figure 178. Mound in cross-section. Figure 179. View of a larger area of the lamina, dominated by stomatal mounds of various sizes and shapes. Level areas are absent on the abaxial epidermis. Trichomes are not shown.

Figure 180. *Kohleria spicata* (Kunth) Oersted. Figure 181. *Kohleria bogotensis* (Nicholson) Fritsch. Figure 182. *Moussonia elegans* Decaisne. Figure 183. *Moussonia hirsutissima* (Morton) Wiehler 'Mexico White'.



184 Gasteranthus acropodus
185 Gasteranthus delphinioides
186 Gasteranthus oncogastrus
187 Gasteranthus pansamalanus
188 Gasteranthus quitensis
189 Gasteranthus wendlandianus
190 Gesneria cuneifolia G-857
191 Gesneria corymbosa
192 Gesneria mortonii

Figure 184-210. Examples of stomatal specialization in the Gesneriaceae: the aggregation of stomatal complexes into distinct groups elevated like islands above the plane of the abaxial epidermis of the leaf in *Gasteranthus, Gesneria, Napeanthus* and *Reldia.* Raised stomatal islands and stomatal mounds shaded. Scale: 50 microns

Figure 184. *Gasteranthus acropodus* (Donn.-Sm.) Wiehler, *Wiehler & Dressler 71271* (SEL). Figure 185. *Gasteranthus delphinioides* (Seem.) Wiehler, *Wiehler & Dressler 71161* (SEL). Figure 186. *Gasteranthus oncogastrus* (Hanst.) Wiehler, *Wiehler 7111* (SEL). Figure 187.

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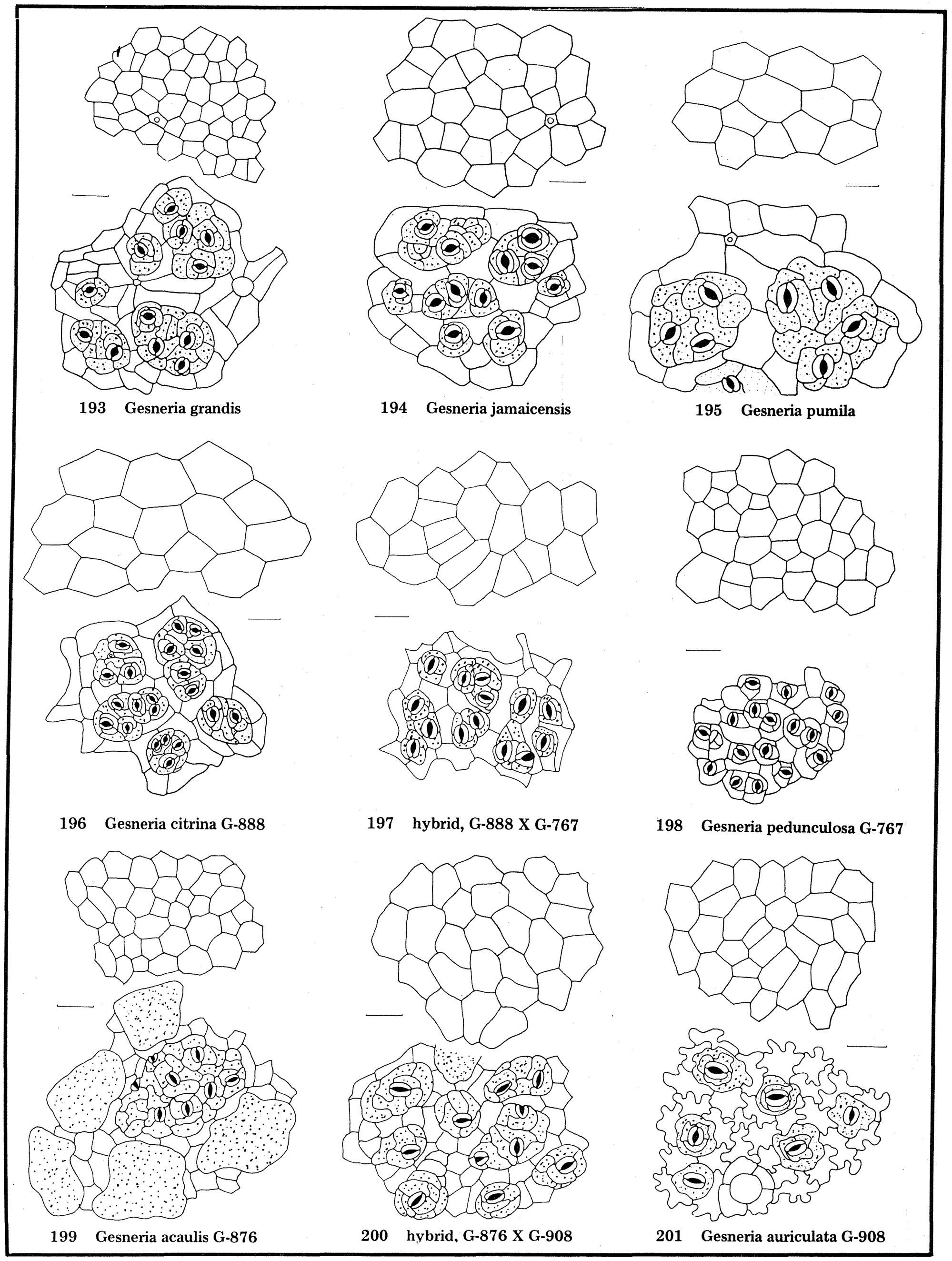
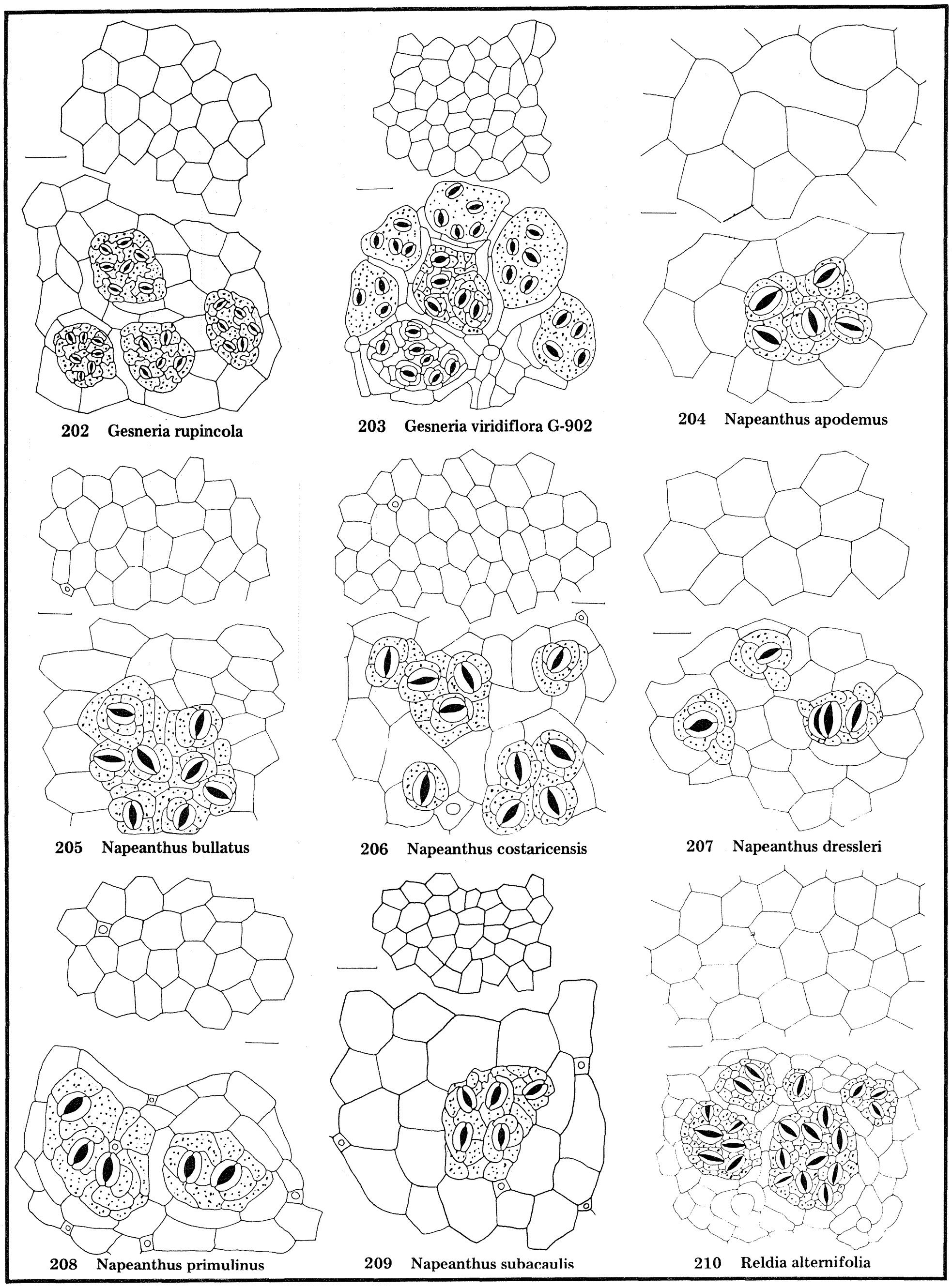


193 Gesneria grandis
194 Gesneria jamaicensis
195 Gesneria pumila
196 Gesneria citrina G-888
197 hybrid, G-888 X G-767
198 Gesneria pedunculosa G-767
199 Gesneria acaulis G-876
200 hybrid, G-876 X G-908
201 Gesneria auriculata G-908

Raised stomatal islands and stomatal mounds shaded. Scale: 50 microns

Figure 193. *Gesneria grandis* Swartz G-883. Figure 194. *Gesneria jamaicensis* Britton G-879. Figure 195. *Gesneria pumila* Swartz subsp. *pumila* G-873. Figure 196. *Gesneria citrina* Urban G-888. Figure 197. hybrid G-888 X G-767. Figure 198. *Gesneria pedunculosa* (DC.) Fritsch G-767. Figure 199. *Gesneria acaulis* L. var. *glabrata* L. Skog G-876. The stomatal arrangement of var. *glabrata* differs so strongly from that of *G. acaulis* var. *acaulis* (Figure 164) that the presumed conspecifity of these two collections representing

(Continued on page 97)



202 Gesneria rupincola
203 Gesneria viridiflora G-902
204 Napeanthus apodemus
205 Napeanthus bullatus
206 Napeanthus costaricensis
207 Napeanthus dressleri
208 Napeanthus primulinus
209 Napeanthus subacaulis
210 Reldia alternifolia

Raised stomatal islands and stomatal mounds shaded. Scale: 50 microns

Figure 202. *Gesneria rupincola* (C. Wright) Urban, *Britton et al. 7419* (US). Figure 203. *Gesneria viridiflora* (Decaisne) Kuntze subsp. *sintenisii* (Urban) L. Skog G-902. Figure 204. *Napeanthus apodemus* Donn.-Sm., *Wiehler & Dressler 71250* (SEL). Figure 205. *Napeanthus bullatus* Wiehler, *Wiehler & Dressler 71163* (SEL). Figure 206. *Napeanthus costaricensis* Wiehler W-1701. Figure 207. *Napeanthus dressleri* Wiehler, *Wiehler & Dressler 71248* (SEL). Figure 208. *Napeanthus primulinus* (Karsten) Benth. ex B. D. Jackson

Continued on page 97

passing air currents a chance to carry off the water vapor present in the stomatal chamber inside the mound, thus aiding the process of transpiration. Skog (1976: 13) suggests that the trichome covering of the leaf produces a humid microclimate in which transpiration is aided by raised stomatal domes. Stomatal mounds are absent from gesneriad taxa with leathery or succulent foliage and abaxial epidermal cells with straight anticlinal walls; no stomatal mounds have been found in the tribes Beslerieae, Episcieae, and Napeantheae, although many species in the first two tribes have a similar degree of indumentum as species in the tribe Gloxinieae and grow in a similar environment.

While stomatal domes represent a first specialized model of stomatal complexes among the Gesneriaceae, the grouping of stomata into definite islands marks a second distinct model (Figures 184-210). First known among the Begoniaceae, these stomata arranged in groups had previously been reported for the genus *Napeanthus* (Solereder, 1908-09; Fritsch, 1925) and for the monotypic genus *Halphophyllum* Mansf. (now united with *Gasteranthus*, Wiehler, 1975g). The same type of stomatal grouping has since then been reported for many species of *Gesneria* (Wiehler, 1970; cf. Skog, 1976), for all species of *Gasteranthus* (Wiehler, 1975g), and for the new genus *Reldia* in the tribe Beslerieae (Figure 210).

The plants with such stomatal arrangement are all terrestrials. Most of them have a rosette-like habit (except *Gasteranthus*) and prefer a humid and shaded environment on river banks or on moss-covered cliffs or boulders. The leaves are usually somewhat (or quite) coriaceous and often almost glabrous. The stomatal islands are always slightly (and sometimes considerably) elevated above the plane of the epidermis. Aside from the clustered guard cells, the cells of these islands consist mostly or entirely of subsidiary cells which differ strongly in size and sinuation from the rather straight-walled and larger regular epidermal cells. There are usually 3-15 stomata crowded on one island, but in some species of *Gasteranthus* an average island contains between 90-185 stomata (Figure 187). In this genus the stomatal islands are clearly visible without magnification as prominent white dots on the abaxial surface of the leaf.

The presence of stomatal islands is a generic character for *Gasteranthus*, *Napeanthus* and *Reldia*. In the genus *Gesneria* occur all three models of sto-

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(Continued from page 94 — **Legend for Figures 184-192**)

Gasternathus pansamalanus (Donn.-Sm.) Wiehler, *Wiehler & Kunkel 7556* (SEL). The typical number of stomata per island is between 90-185. Figure 188. *Gasteranthus quitensis* Benth W-2072. Figure 189. *Gasteranthus wendlandianus* (Hanst.) Wiehler W-2184. Figure 190. *Gesneria cuneifolia* (DC.) Fritsch G-857. Figure 191. *Gesneria corymbosa* Swartz 839. Figure 192. *Gesneria mortonii* Wiehler, *Leon & Victorin 17748* (US). This material from Cuba may be a subspecies of the above *G. corymbosa* from Jamaica, as indicated by Skog (1976: 43), A future study of live material from Cuba will help to clarify the relationship.

(Continued from page 95 — **Legend for Figures 193-201**)

different populations endemic to separate areas in Jamaica appears doubtful (cf. Skog, 1976: 103, 105; Wiehler, 1970). Figure 200. hybrid, G-876 × G-908. Figure 201. *Gesneria auriculata* (Hook.) Kuntze G-908.

(Continued from page 96 — **Legend for Figures 202-210**)

G-1280. Figure 209. *Napeanthus subacaulis* (Griseb.) Benth. ex Kuntze, *Bailey & Bailey s.n.* (BH). Figure 210. *Reldia alternifolia* Wiehler W-2188.

mata found in the Gesneriaceae: (1) irregularly scattered stomata lying nearly flat on the surface of the epidermis; (2) individual stomata on mounds; and (3) stomata grouped into islands. In interspecific hybrids between these models the stomatal complexes are intermediate (Figure 196-201).

A fourth stomatal model, with the guard cells sunken into the epidermis, has been reported briefly by Sachs (1915: 11) for the epiphytic species *Sinningia verticillata* [*Corytholoma douglasii* (Lindl.) Voss], but this report could not be verified after examining two collections of this species in cultivation at the Marie Selby Botanical Gardens. The irregularly scattered stomata of this species lie nearly flat on the surface of the epidermis (Figure 211).

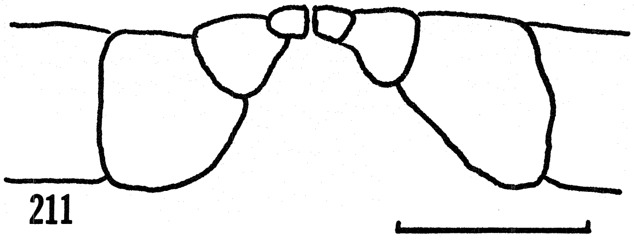


Figure 211. Abaxial epidermis of the leaf of *Sinningia verticillata* (Vell.) H. E. Moore, W-1980, in cross-section. The stomates of this epiphytic species (or at least of this collection) are not sunken into the epidermis, as reported by Sachs (1915). Scale: 50 microns

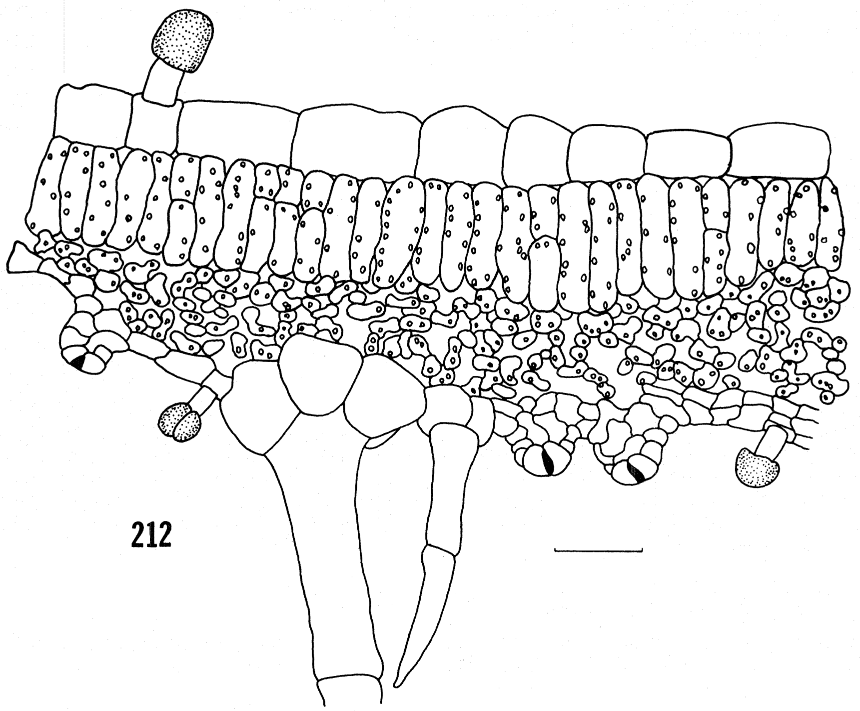
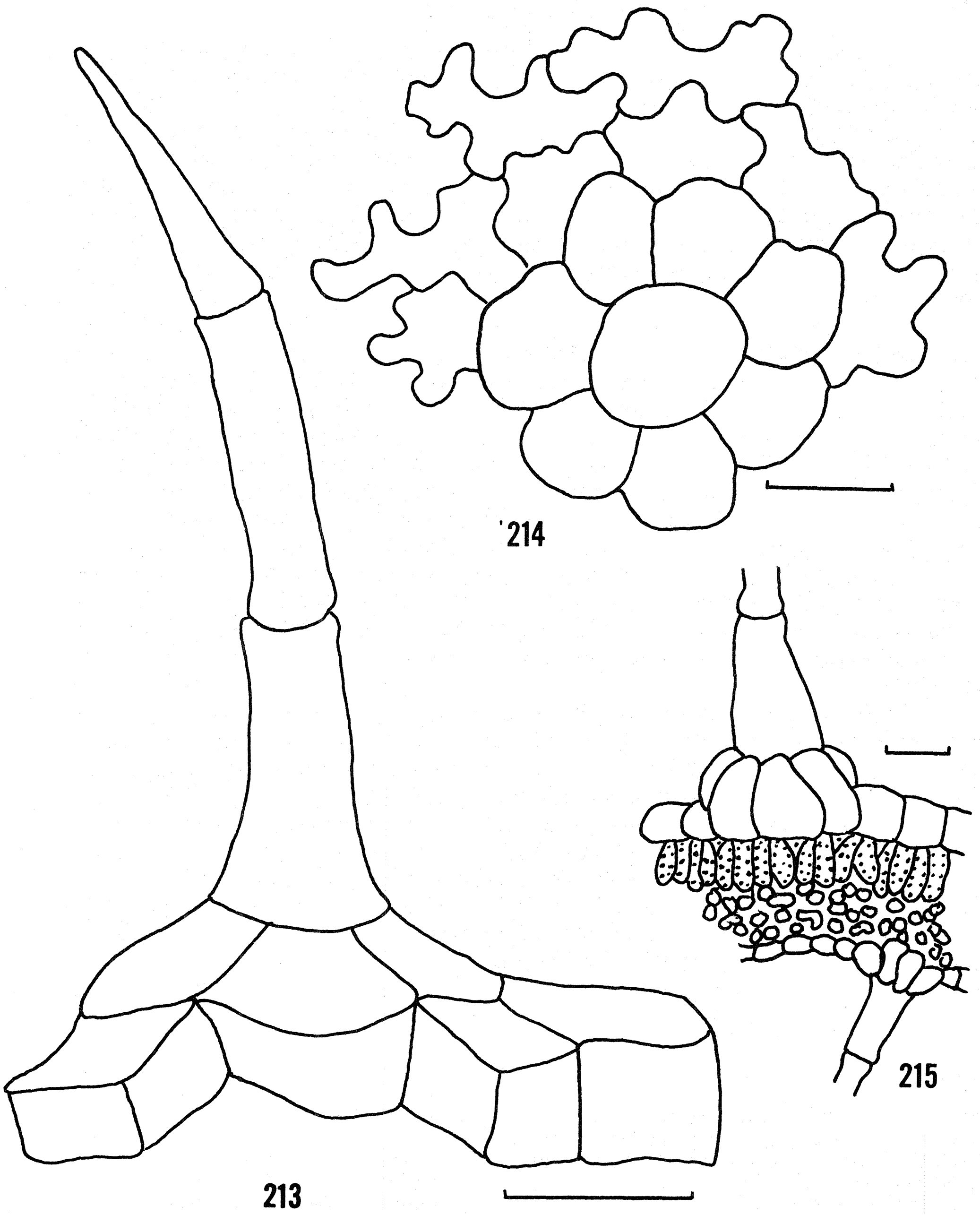


Figure 212. *Kohleria spicata* (Kunth) Oersted, G-718. Cross-section of the leaf showing the large basal cells of the non-glandular trichomes on the abaxial surface, and the relationship in size between non-glandular and mushroom-shaped glandular trichomes. Since the epidermal cells of the adaxial surface of the leaf are much larger than those of the abaxial surface, the glandular trichomes on the upper surface tend to be somewhat larger than those on the lower surface of the leaf. Scale: 50 microns



Figures 213-215. Basal cells of trichomes. Figure 213. *Moussonia elegans* Decaisne, G-444. Trichome on the adaxial surface of the leaf. The basal cells of this trichome do not differ in size from regular epidermal cells. Figure 214. *Achimenes erecta* (Lamarck) H. P. Fuchs, G-182. Top view of a trichome base from an abaxial epidermis peel. The basal trichome cells differ in shape from the regular epidermal cells. Figure 215. *Capanea grandiflora* (Kunth) Decaisne, G-987. Cross-section of the leaf. The elevated base cells of the trichomes are larger than the regular epidermal cells. Scale: 50 microns

CHAPTER 16: TRICHOMES

Four types of trichomes were observed among the Gesneriaceae examined. By far the more frequent ones are non-glandular hairs, either unicellular, or multicellular and uniseriate, ending in a pointed tip. Somewhat less frequent are small glandular trichomes shaped like a mushroom, with a short stalk and capped by a head of one to four cells containing glandular material. A third category consists of glandular trichomes with longer, uniseriate stalks, and the fourth type are multiseriate hairs. The last two categories are comparatively rare within the Gesneriaceae. Many of the trichomes in these two groups are unusual or specialized; they are therefore of particular interest and of some taxonomic value.

Non-glandular trichomes vary in length from species to species. Hairs three to four cells long (0.70 to 1.75 mm in total length) seem to occur most frequently. The longest trichomes were observed in *Sinningia hirsuta* (Lindl.) Nicholson (15 cells and about 8 mm long), *Nautilocalyx villosus* (Kunth & Bouché) Sprague (18 cells and about 8 mm long), *Kohleria peruviana* Fritsch (12 to 15 cells long), and *Gesneria leucomalla* (Hanst.) Kuntze (10 to 20 cells long). The basal cells surrounding and supporting these trichomes are often much larger than the regular epidermal cells, and are elevated quite considerably above the general level of the epidermis (Figures 212-215).

While the cell walls of most trichomes encountered were smooth-textured, in a few species some (but not all) of the cells had walls sculptured with wartlike protuberances [*Eucodonia andrieuxii* (DC.) Wiehler, *Nautilocalyx villosus.*] In closely related species no evidence of such sculpturing was found.

Vacuolar anthocyanin, varying in color from orange-red to deep purple, was present in some cells of non-glandular trichomes. At times adjoining cells showed differing shades of color. Some hairs had only one cell with this type of vacuolar pigment, others two or three; in other trichomes all cells were stained. In a few instances some of the raised basal cells at the foot of the trichomes also contained anthocyanin, as well as some of the parenchyma cells surrounding the vascular bundles on the abaxial side of the leaf. If the underside of a leaf appears deep purple-red, a large percentage of the abaxial epidermal cells may contain anthocyanin. On some functional leaves the trichomes had apparently lost their nuclei, and the anthocyanin had then crystallized into clusters of cubical or boxlike shapes. Some of these cells still contained liquid, others did not.

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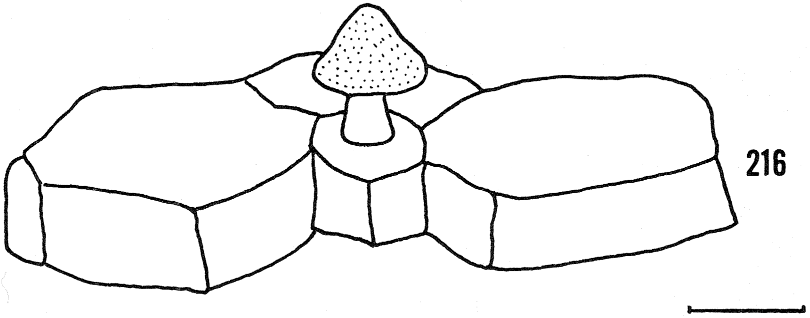
Figures 216-227. Mushroom-shaped glandular trichomes found on leaves in the Gesnerioideae. Figure 216. *Kohleria digitaliflora* (Linden & André) Fritsch, G-941. The single basal cell of the capitate glandular trichome is typically smaller in size than the regular epidermal cell. Figure 217. *Nematanthus wettsteinii* (Fritsch) H. E. Moore. On this epiphytic species with glabrate succulent leaves the glandular trichomes are sunken into the epidermis. Figure 218. *Sinningia incarnata* (Aubl.) Denham, G-463. The base of the glandular trichome in the single-layered epidermis was often observed divided into two cells. Figure 219-222. *Heppiella viscida* (Lindl. & Paxton) Fritsch. Top view of glandular head cells undivided (Figure 219) and subdivided. Figures 223-224. *Capanea grandiflora* (Kunth) Decaisne, G-539. A rare occurrence of a capitate glandular trichome with two stalk cells, horizontally divided. Figure 225. *Kohleria bogotensis* (Nicholson) Fritsch, G-127. Stalk cells horizontally and vertically divided. Figures 226-227. *Paliavana racemosa* (Vell.) Fritsch, G-732, a species with ovoid head cells.

Cells with glandular inclusions are shaded. Scale: 25 microns



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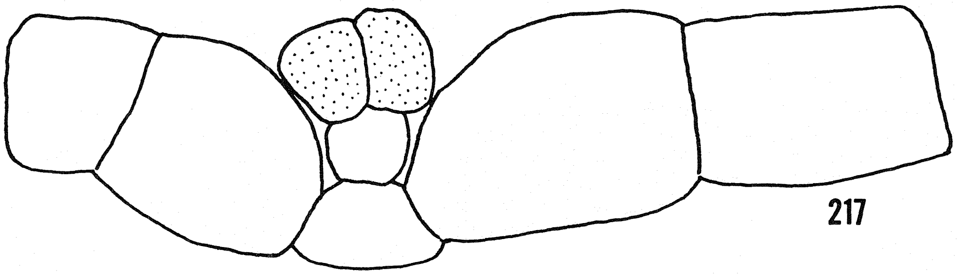

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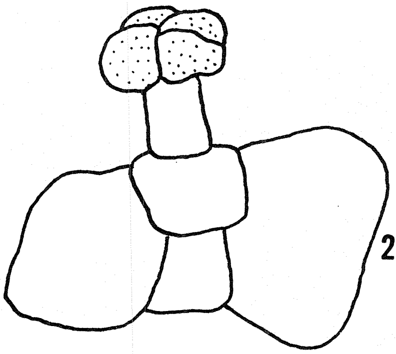

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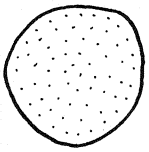

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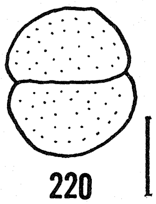

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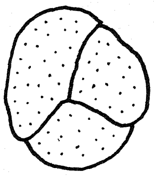

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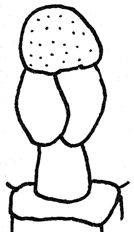

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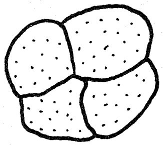

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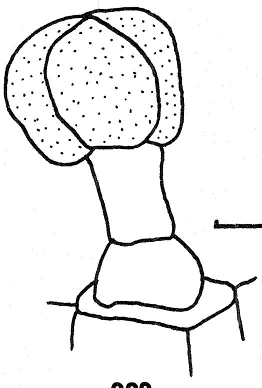

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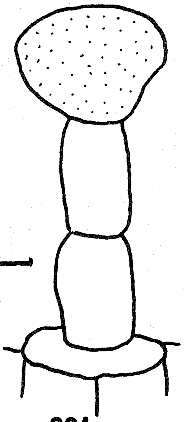

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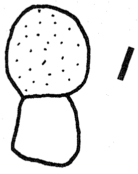

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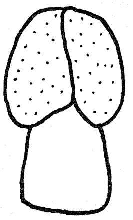

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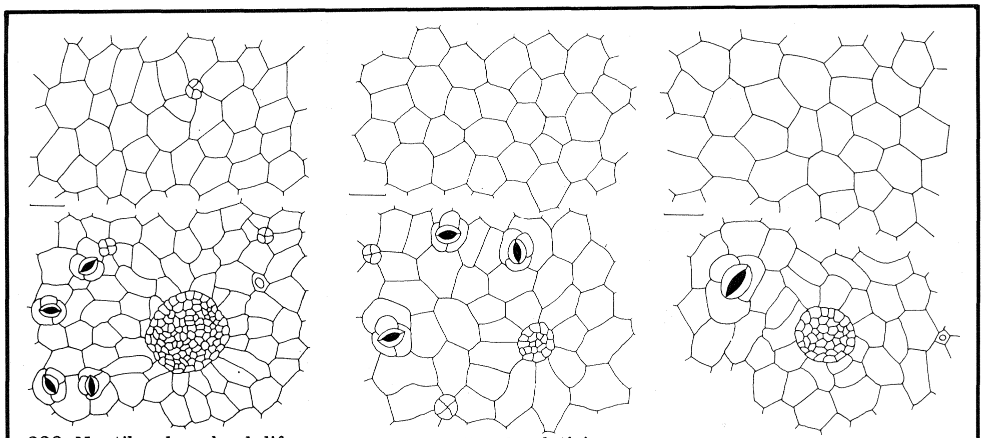


228 Nautilocalyx glandulifer

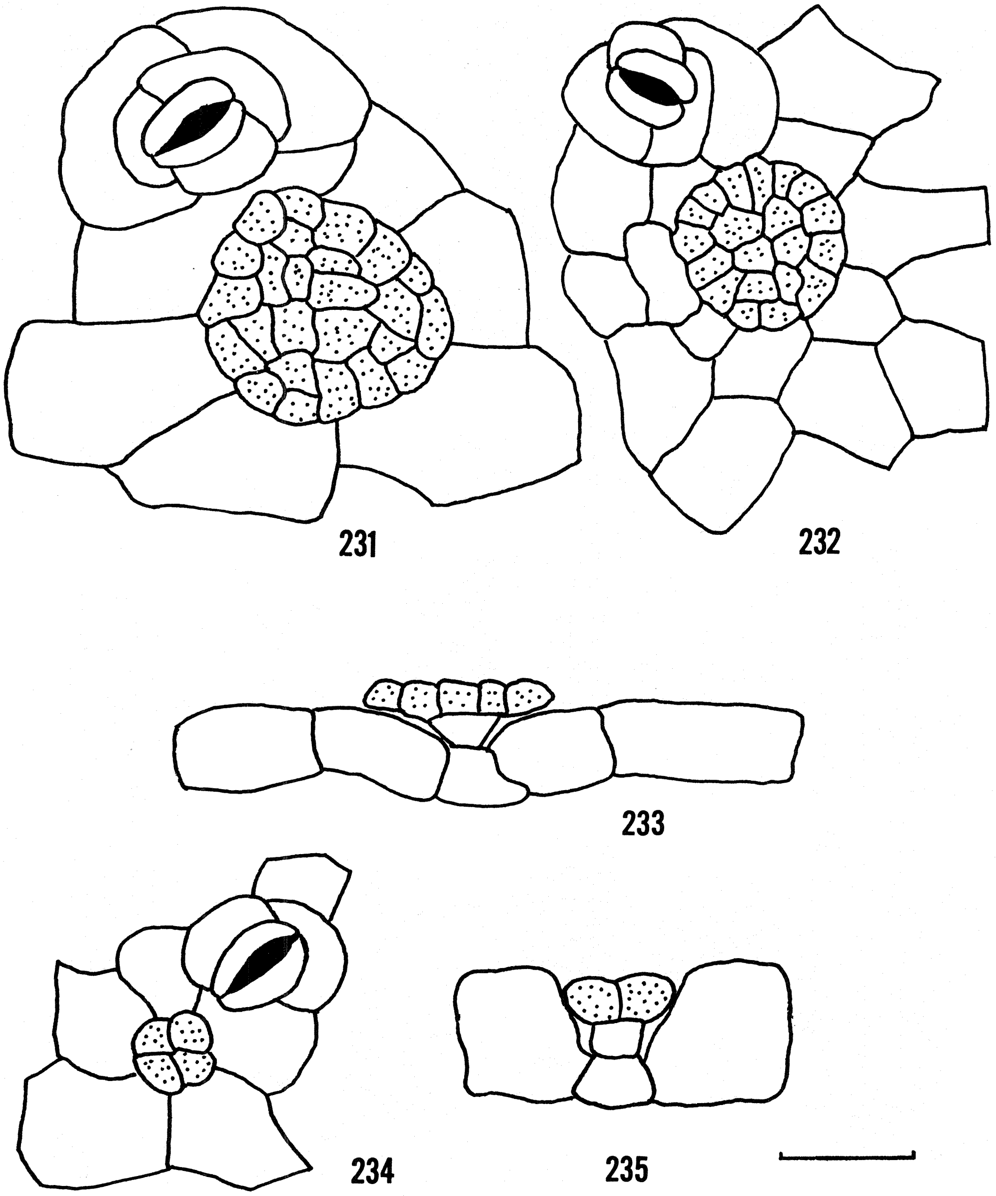
229 Nautilocalyx leticianus

230 Nautilocalyx punctatus

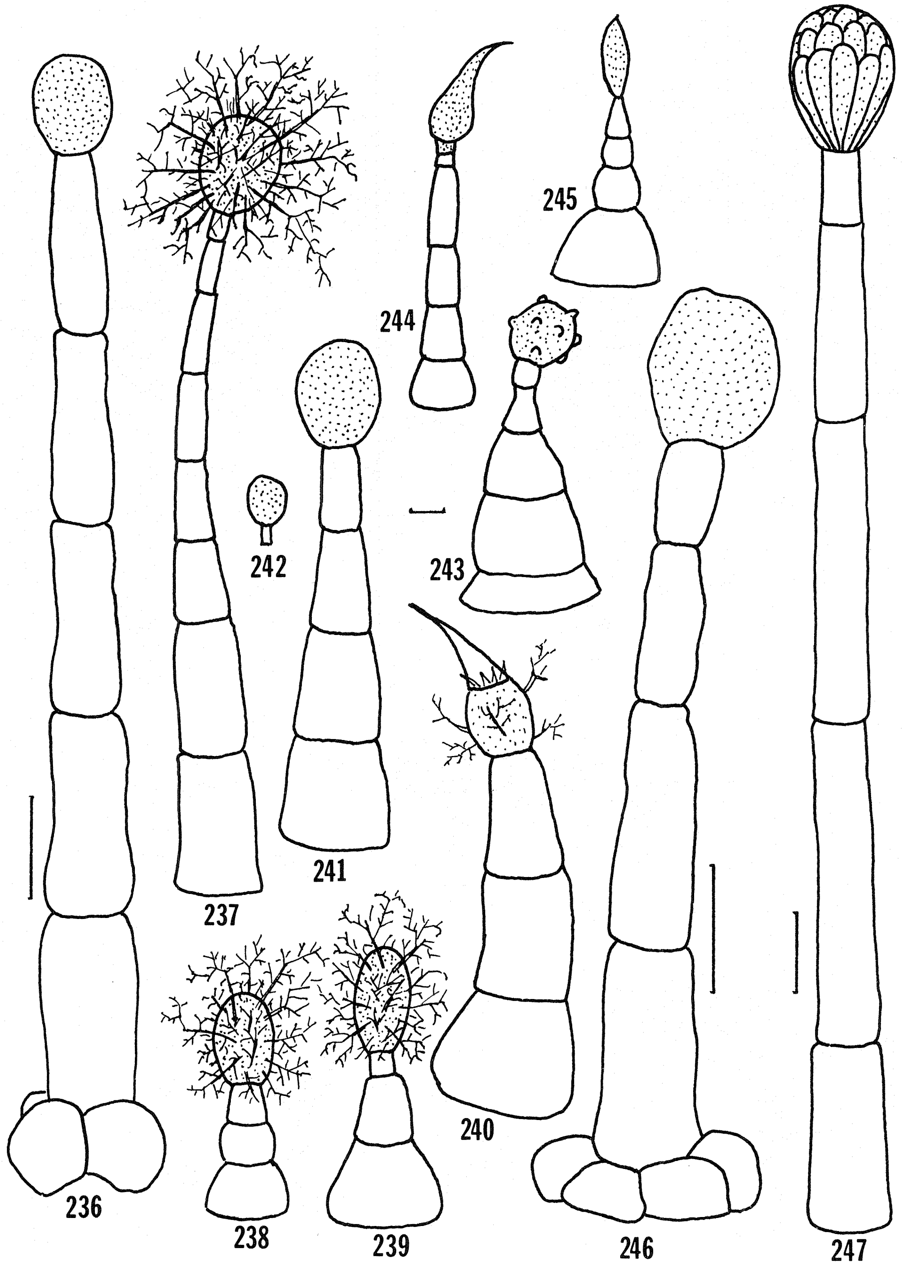
Figures 228-230. Unusual peltate glandular trichomes on the abaxial leaf surface of species of *Nautilocalyx*. Figure 228. *Nautilocalyx glandulifer* Wiehler, W-1537. The mound-like shield of these peltate glandular trichomes consists of usually more than 100 cells; the surrounding surface of the epidermis is somewhat depressed. These trichomes are abundant in this species from Tena, Ecuador. Figure 229. *Nautilocalyx leticianus* Wiehler, W-1995. The peltate trichomes in this species from Leticia, Colombia, are smaller and less frequent. Figure 230. *Nautilocalyx punctatus* Wiehler, W-1821. Some of the peltate glandular trichomes of this species from southern Venezuela carry a glandular excretion on the shield. A few of these peltate trichomes appear to have no glandular contents in the head cells. (These figures were first published in *Selbyana* 5:35, 1978.) Scale 50 microns

The absence or presence of anthocyanin in the leaves of Gesneriaceae has been used in the past as a diagnostic character at the specific and varietal levels. In some species where, exposed to the same light conditions, plants with and without anthocyanin occur in the same population, the absence or presence of this pigment seems to be genetically controlled. Examples are *Episcia hirsuta* Benth. and *Nautilocalyx porphyrotrichus* (Lwbg.) Wiehler. Observations in the greenhouse indicate that in other species the environment (light) influences the expression of anthocyanin. Experiments with such species as *Kohleria spicata*, *Moussonia elegans*, × *Koellikeria rosea* Wiehler, *Columnea arguta* Morton and *C. gloriosa* Sprague cv. 'Santa Fe', showed that exposure to full sunlight or fluorescent light furthers the development of anthocyanin in the trichomes and abaxial epidermal cells of new shoots and leaves. Control plants (cuttings and siblings) of the same species kept in shady situations had only very few epidermal cells and trichomes containing anthocyanin. When the shaded plants were later exposed to full sunlight, the new growth revealed an abundance of anthocyanin in trichomes and epidermal cells, while the leaves developed under shaded conditions remained plain green, covered with clear-celled trichomes. The reverse happened with plants transferred from sunlight to shade.

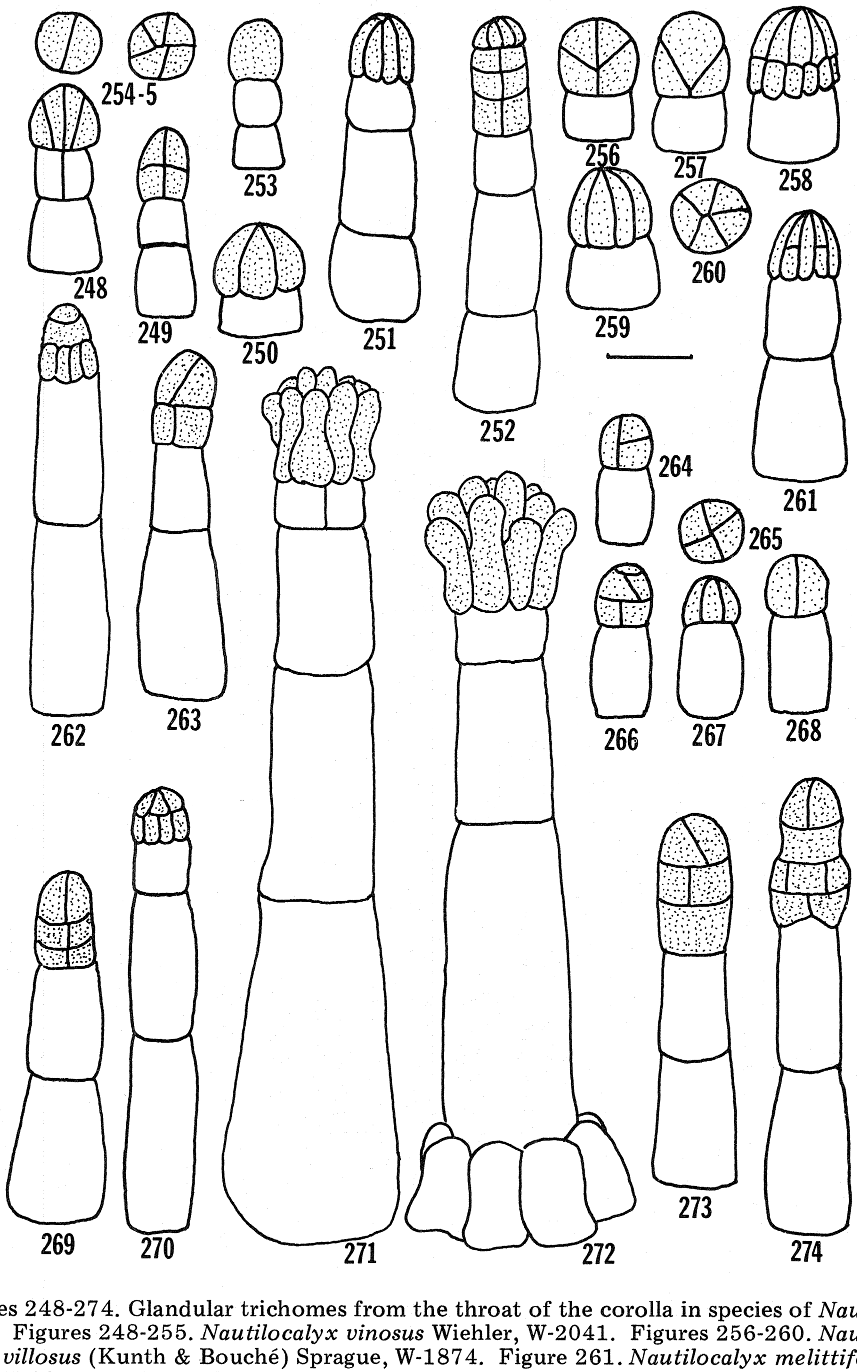
The much smaller capitate glandular trichomes are the second basic type of indumentum found in the Gesneriaceae (Figure 212). Their base consists of a single epidermal cell which is much smaller than the regular surrounding cells. The stalk of the trichome is usually one-celled, but two- or very rarely three-celled stalks occur. The glandular head is most frequently divided vertically into two cells but one-celled heads were also noted and three- and four-celled heads occur rarely. The color of the glandular inclusion of the cells of the head is orange-yellow in all species observed. Sometimes



Figures 231-235. Unusual peltate glandular trichomes on the abaxial leaf surface of species of *Nautilocalyx*. Figure 231. *Nautilocalyx whitei* Rusby, G-978. Top view of a peltate glandular trichome with many head cells. Figure 232. *Nautilocalyx bullatus* (Lemaire) Sprague, G-132. Same view. Figure 233. *Nautilocalyx bullatus*. Cross-section of the same kind of peltate glandular trichome showing the single stalk cell. Figures 234-235. *Nautilocalyx glandulifer* Wiehler. Top view of the typical kind of capitate glandular trichome with four head cells (Figure 234), and cross-section of the same type of trichome (Figure 235), for comparison with Figure 233. (These figures were first published in *Selbyana* 5:35, 1978). Scale: 50 microns

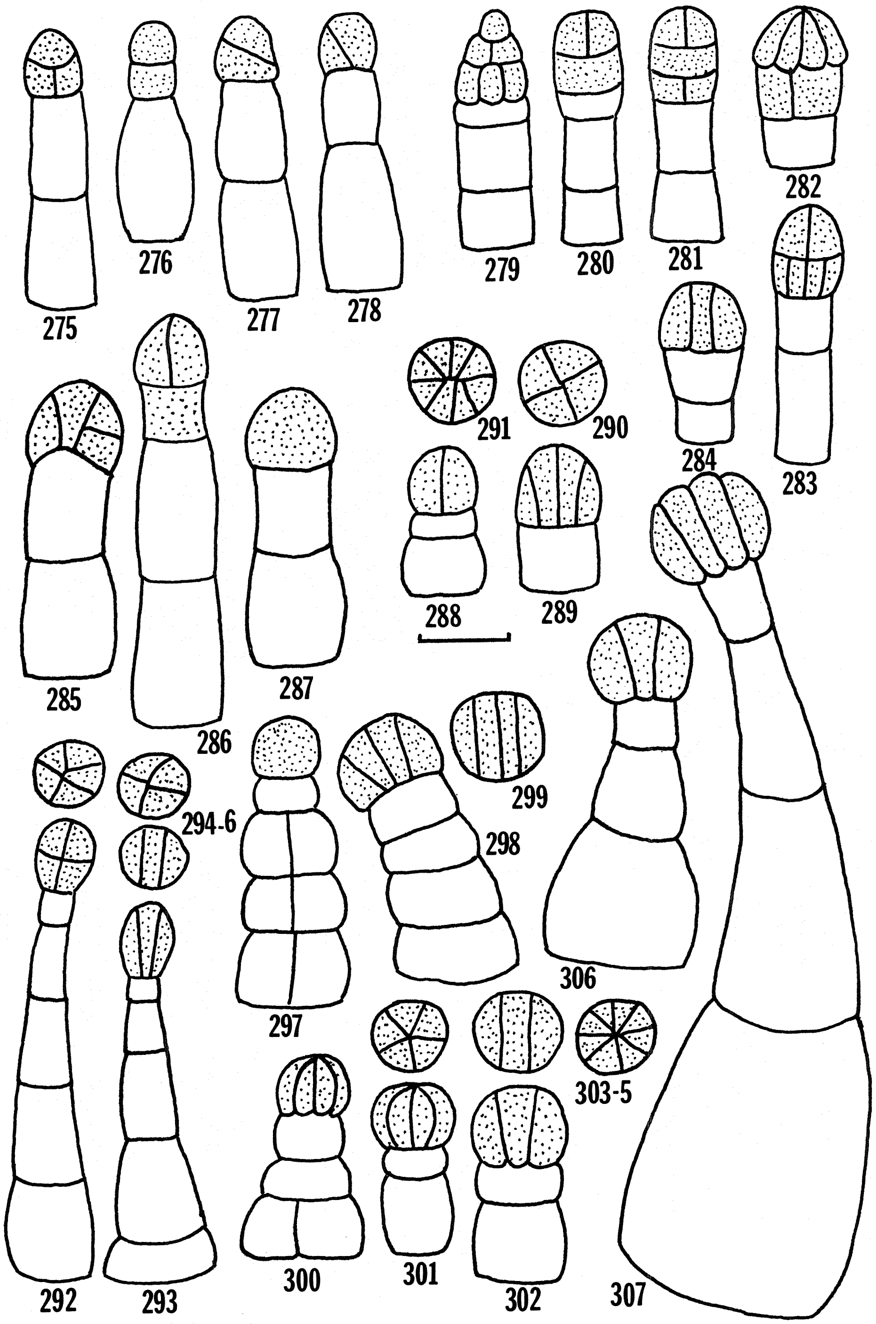


Figures 236-247. Glandular trichomes from leaves of species of *Diastema*, *Gesneria*, *Gloxinia*, and *Trichantha*. Figure 236. *Gloxinia lindeniana* (Regel) Fritsch. Long trichomes topped by a globular end cell are comparatively rare in the Gesnerioideae. Most of the leaf hairs of this species have the typical pointed, non-glandular end cells (cf. Figure 213). The globular end cell varies in size and shape. Figures 237-245. *Gesneria auriculata* (Hook.) Kuntze, G-1265. Glandular trichomes of various shapes from the abaxial leaf surface. The branched structures (Figures 237-240) appear to be either filigree-like crystallizations of emanations of the yellow glandular cell contents or the filamentous mycelia of a symbiotic fungus (see Figure 362). Figure 246. *Diastema vexans* H. E. Moore. Abaxial lamina: see Figure 236. Figure 247. *Dalbergaria polyantha* Wiehler, W-1154. Abaxial lamina, fairly common. Scale: 50 microns



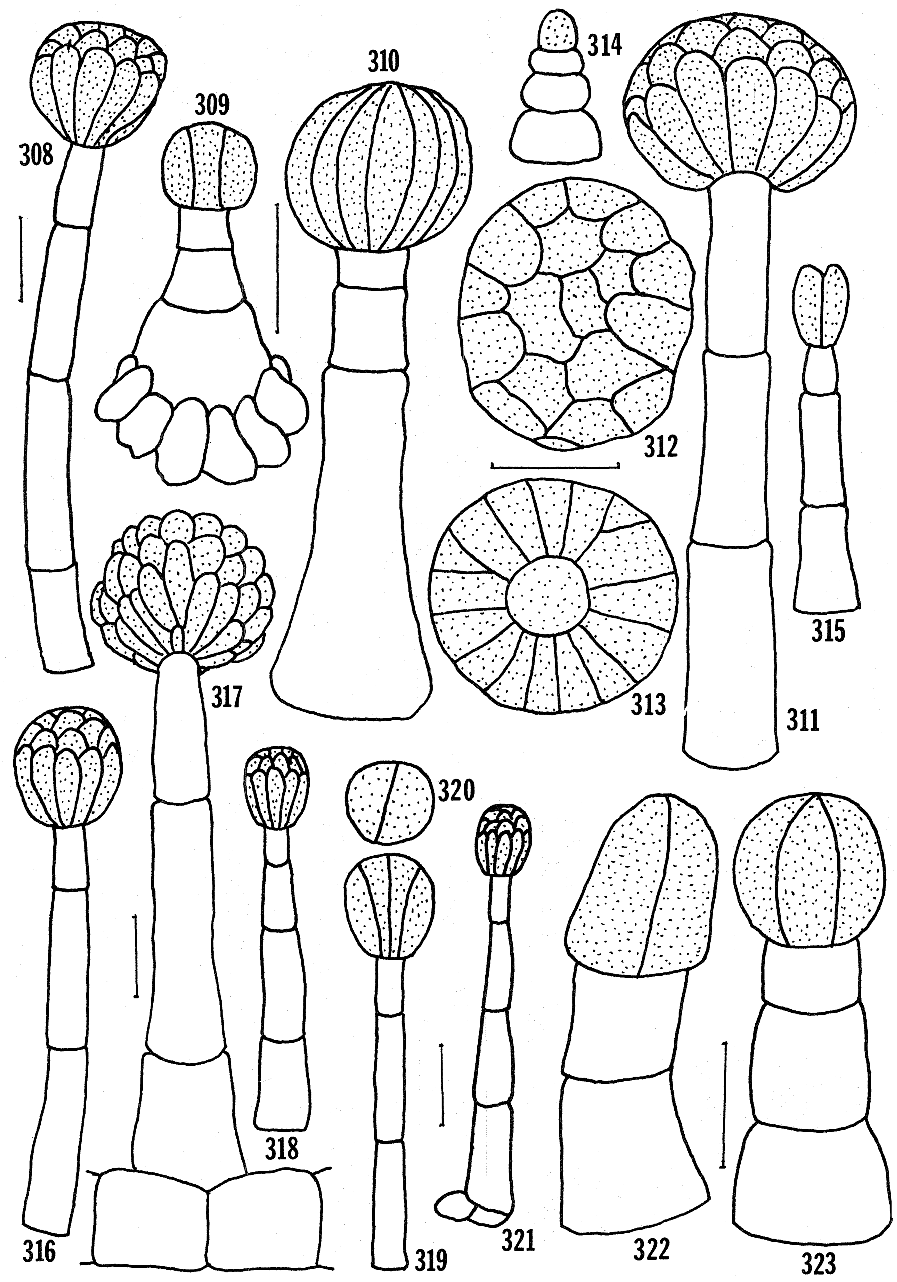
Figures 248-274. Glandular trichomes from the throat of the corolla in species of *Nautilocalyx*. Figures 248-255. *Nautilocalyx vinosus* Wiehler, W-2041. Figures 256-260. *Nautilocalyx villosus* (Kunth & Bouché) Sprague, W-1874. Figure 261. *Nautilocalyx melittifolius* (L.) Wiehler, W-1970. Figures 262-263. *Nautilocalyx colombianus* Wiehler, W-1109. Figures 264-268. *Nautilocalyx membranaceus* (Morton) Wiehler, W-1817, Figures 269-270. *Nautilocalyx aeneus* (Linden & André) Wiehler, cv. 'Stickland's Green,' W-2241. Figures 271-272, *Nautilocalyx porphyrotrichus* (Leeuwenb.) Wiehler, cv. 'El Dorado,' W-1812. Figures 273-274. *Nautilocalyx forgetii* (Sprague) Sprague, G-133.

Scale: 50 microns



Figures 275-307. Glandular trichomes from the throat of the corolla in species of *Nautilocalyx* and *Achimenes.* Figures 275-278. *Nautilocalyx dressleri* Wiehler, W-1974. Figures 279-284. *Nautilocalyx bullatus* (Lemaire) Sprague, G-132. Figures 285-287. *Nautilocalyx punctatus* Wiehler, W-1821. Figures 288-291. *Nautilocalyx panamensis* (Seem.) Seem., G-1095. Figures 292-296. *Achimenes grandiflora* (Schiede) DC., G-595. Figures 297-305. *Achimenes mexicana* (Seem.) Benth. ex Fritsch, G-678. Figures 306-307. *Achimenes skinneri* Lindl., W-1973. Scale: 50 microns

Figures 276-277, 294-296, 299, 300-302, top view of glandular head cells.



Figures 308-323. Glandular trichomes from the throat of the corolla in species of *Columnea, Pentadenia,* and *Trichantha.* Figure 308. *Trichantha minor* Hook. cv. 'Firebird', W-1685. Figures 309-310. *Pentadenia ecuadorana* Wiehler, W-1176. Figures 311-315. *Trichantha brenneri* Wiehler, W-2275, with top view (Figure 312) and bottom view (Figure 313) of glandular head cell. Figures 314-315. Glandular trichomes from the filaments of the stamens inside the corolla. Figure 316. *Trichantha mira* (Morley) Wiehler, W-1586. Figure 317. *Trichantha tenensis* Wiehler, W-1584. Figure 318. *Trichantha dissimilis* (Mor-

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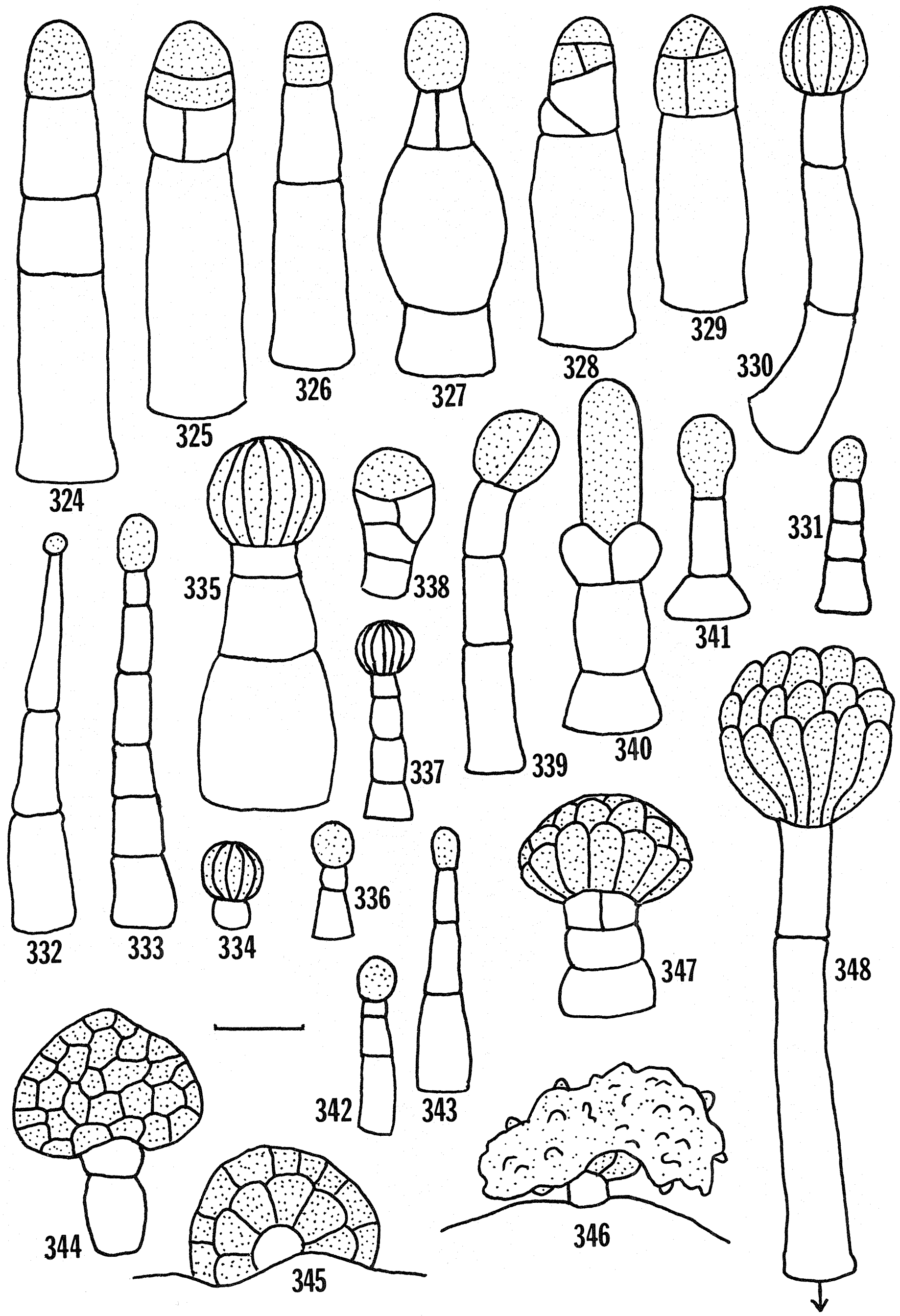

Figures 324-348. Glandular trichomes from the flowers of neotropical Gesneriaceae. Figures 324-329. *Nautilocalyx cataractarum* Wiehler, throat of the corolla. Figure 330. *Nematanthus wettsteinii* (Fritsch) H. E. Moore, inside of corolla tube. Figure 331. *Nematanthus perianthomegus* (Vell.) H. E. Moore, W-1718, from the ciliate lobe of the corolla. Glandular trichomes are absent inside the tube of the corolla. Figures 332-338. *Kohleria villosa* (Fritsch) Wiehler, W-2223, all from the style of the pistil except Figure 335 which is from the throat of the corolla. Figures 339-341. *Kohleria magnifica* (Planchon & Lin-

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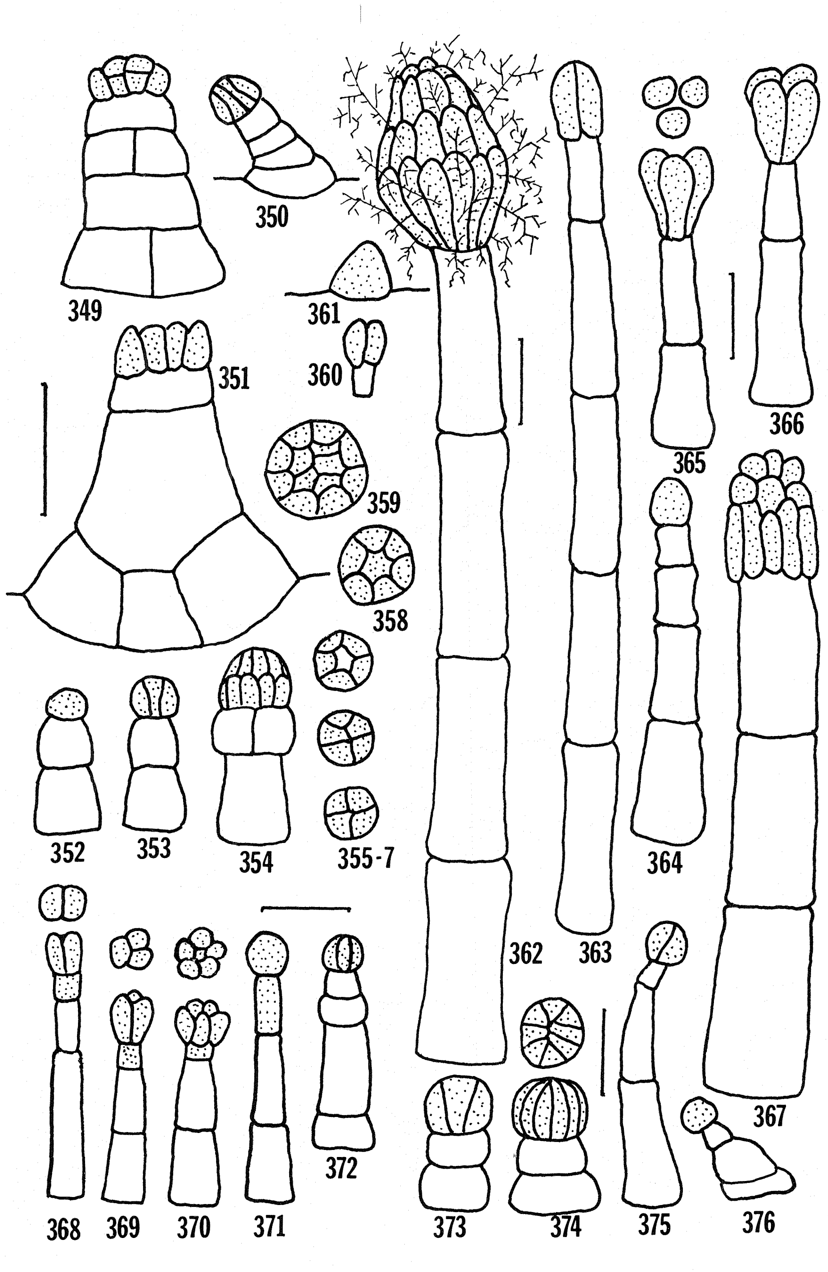

Figures 349-376. Glandular trichomes from the flowers of neotropical Gesneriaceae. Figures 349-359. *Drymonia pulchra* Wiehler, W-1567, inside of the corolla. Figures 360-362. *Bucinellina nariniana* (Wiehler) Wiehler, W-1642. Figure 360. inside corolla throat; Figure 361. on corolla tube outside; Figure 362. on the tip of the calyx lobes (see Figures 237-240). Figures 363-364. *Codonanthe carnosa* (Gardner) Hanst., W-2199, deep inside corolla tube. Figures 365-366. *Besleria maasii* Wiehler, W-2186, inside corolla. Figure 367. *Gasteranthus acropodus* (Donn.-Sm.) Wiehler, W-2164, inside corolla throat. Figures

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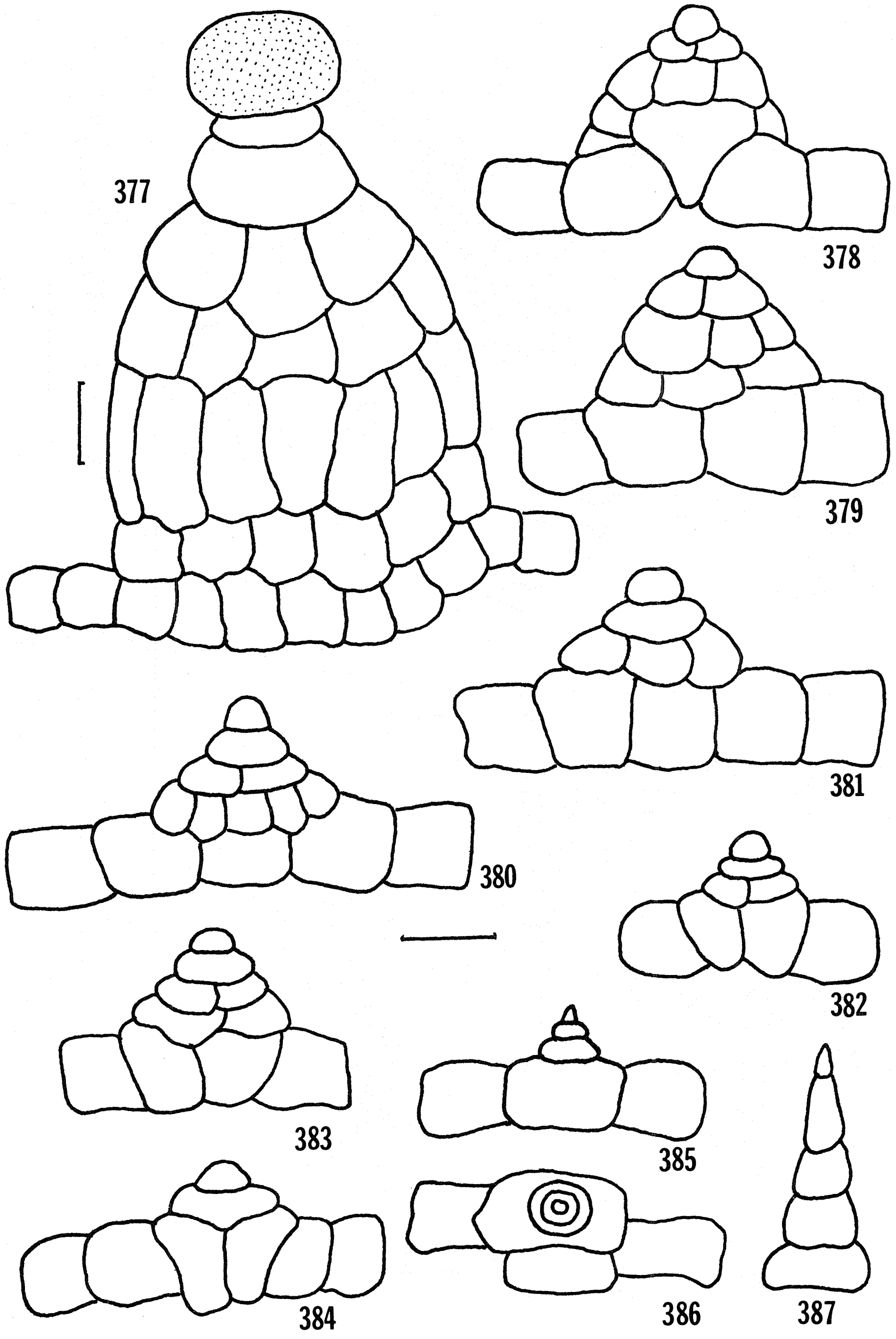

Figures 377-387. Multiseriate trichomes in the Gesnerioideae. Figure 377. *Gloxinia sylvatica* (Kunth) Wiehler cv. 'Broadleaf', G-990, inside the throat of the corolla; only the top cell contains a glandular inclusion of a yellowish brown color. The stalk cells are stained by wine-colored anthocyanin. Figures 378-384. Cone-shaped, non-glandular, and multiseriate trichomes in the genus *Columnea*, located inside the tube of the corolla along a narrow vertical band below the ventral corolla tube. Figures 378-379. *Columnea querceti* Oersted, W-2258; Figures 380-381. *Columnea gloriosa* Sprague cv. 'Santa Fé, W-2131;

(Continued on page 111)

the cell walls were blistered or broken, and the glandular substance was clustered on the outer surface of the head. The function of these fairly common mushroom-shaped capitate glandular trichomes is unknown at present (Figures 216-227).

A possible derivative of the mushroom-shaped glandular trichome is the peltate glandular trichome (Figures 228-235) discovered in several species of *Nautilocalyx* (Wiehler, 1970). The uni- or bicellular stalk is depressed into the epidermis (Figure 233), and the head consists of one layer of between 18 and 100 or more glandular cells, lying appressed to the epidermis. These peltate trichomes occur only on the abaxial side of the epidermis of the leaf, usually in the vicinity of veins. They are most numerous in *Nautilocalyx bullatus* (Lem.) Sprague and *N. glandulifer* Wiehler, and less frequently on *N. leticianus* Wiehler, *N. punctatus* Wiehler, *N. whitei* Rusby, and on *N.* sp. G-499 (Figures 228-232). Peltate trichomes were not found in 13 other cultivated species of *Nautilocalyx* examined, or in related genera. In those species with peltate glandular trichomes, the much smaller mushroon-shaped glandular trichomes were likewise sunken into the epidermis (Figures 234-235), indicating a possible relationship through proliferation of glandular tissue. The function of all of these glandular trichomes remains unknown. Some of the peltate trichomes in *Nautilocalyx punctatus* appeared to be free of glandular inclusion.

The first two categories of trichomes represent the typical indumentum of the taxa of the Gesnerioideae. A third and relatively infrequently occurring

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(Continued from page 107 - **Legend for Figures 308-323)**

ton) Wiehler, W-1177. Figures 319-320. *Columnea arguta* Morton cv. 'Iguanita', W-2195. Figure 321. *Columnea gloriosa* Sprague cv. 'Santa Fé', W-2131. Figure 322. *Trichantha pulchra* Wiehler, W-1910. Figure 323. *Trichantha calotricha* (Donn.-Sm.) Wiehler, W-2181. Scale: 50 microns

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(Continued from page 108 - **Legend for Figures 324-328)**

den) H. E. Moore, W-1657, from the style of the pistil. Figures 342-343. *Sinningia reitzii* (Hoehne) Wiehler, W-2250, from the style of the pistil; none present inside corolla tube. Figures 344-346. *Gesneria auriculata* (Hook.) Kuntze, G-1265, from the border of the limb of the corolla: Figure 344. lateral view; Figure 345. viewed from below, with stem of trichome attached to limb of corolla; Figure 346. glandular head covered with exudant. Figure 347. *Gesneria pedunculosa* (DC.) Fritsch, G-767, from the border of the limb of the corolla. Figure 348. *Dalbergaria vittata* Wiehler, W-2265, from the lacinae of the tips of the calyx lobes. The stem is seven cells long. Scale 50 microns

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(Continued from page 109 - **Legend for Figures 349-376)**

368-372. *Paradrymonia hypocyrta* Wiehler, W-2246, all from the style of the pistil except Figure 372, which is from inside the corolla. Figures 373-374. *Achimenes dulcis* Morton, G-696, from the style of the pistil. Figures 365-376. *Achimenes longiflora* DC., W-1762, inside corolla. Scale: 50 microns

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(Continued from page 110 - **Legend for Figures 377-387)**

Figure 382. *Columnea rubicaulis* Standley cv. 'Matagalpa', W-2328; Figures 383-384. *Columnea nicaraguensis* Oersted, W-1188. Figure 385-386. *Trichantha tenensis* Wiehler, W-1584, uniseriate trichomes shaped similar to the above found in the same area on the corolla; lateral view (Figure 385) and top view (Figure 386). Figure 387. *Columnea gloriosa* Sprague, W-2131, example of the elongated, cone-shaped trichomes found on the outside and inside of the corolla and on the style of the pistil in many species of *Columnea*; the multiseriate trichomes found in this genus are probably derived from these structures. The function of these epidermal hairs is still unknown. Scale: 50 microns

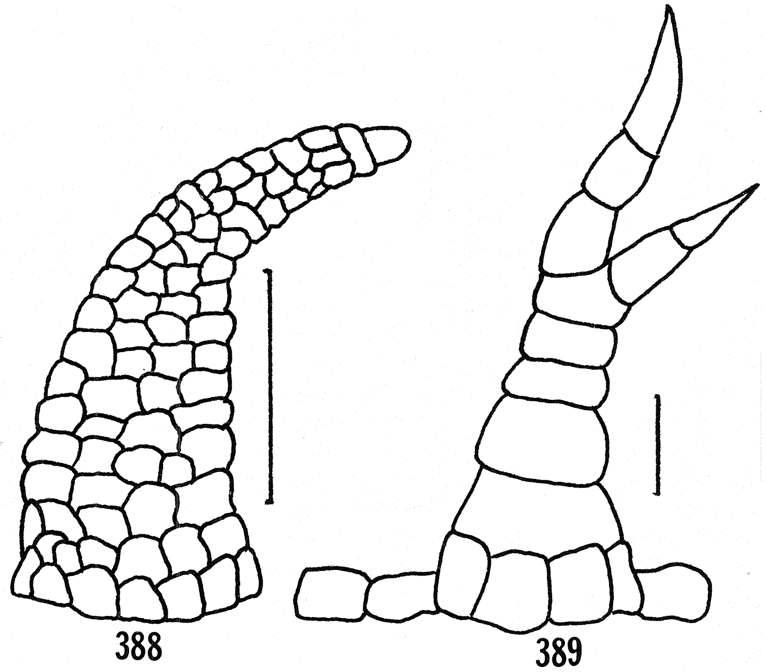
group of plant hairs have longer (compared with the mushroom category) uniseriate stalks of 1-10 cells topped by a glandular end cell of varying shape or by a glandular cell aggregate, all with orange-yellow content (Figures 236-376). These cells rupture when touched. In some species these glandular hairs are found mixed in with the regular indumentum of the stem, leaves, inflorescence axes, and flowers (calyx, corolla, pistil, and filaments). In other species this type of trichome predominates on a particular plant organ, such as on the leaves of *Heppiella ovata* Hanst., *H. viscida* (Lindl. & Paxton) Fritsch, *Sinningia aggregata* (Ker-Gawler) Wiehler, *S. tuberosa* (Mart.) H. E. Moore, or on the calices of *Monopyle maxonii* Morton and species of *Achimenes*, *Goyazia*, and *Gesneria*.

The most proliferation in the shape of trichomes within the Gesneriaceae occurs in the glandular hairs located in the throat, on the limb, or on the style of the corolla (Figures 248-376). This phenomenon appears to be connected with the biology of pollination, but the details are not yet understood. Glandular trichomes within the corolla may serve the purpose of coating the pollinators with a glue to facilitate the adherence of pollen grains. The intricate and exotic shapes of these glandular trichomes are in some cases at least species-specific (see Figures 271-272 and 306-307) and thus possess taxonomic value. There exists as yet no survey of this type of gesneriad trichome in the literature except for a brief reference by Pongracic (1931: Figures 1-5). These unusual trichomes cannot be studied from herbarium specimens but need to be observed *in vivo* or from pickled material.

Multiseriate trichomes, both glandular and non-glandular, appear to be very rare in the Gesnerioideae. They have been observed so far only in the corolla of species of *Columnea* and *Gloxinia* (Figures 377-387). In *Columnea* these trichomes are non-glandular and occur in a very restricted area within the corolla tube, namely ventrally along a narrow band below the slender ventral corolla lobe, and on the style. A similar but uniseriate type of trichome is found in the same areas in *Trichantha tenensis* Wiehler (Figures 385-386). It appears likely that the multiseriate trichomes in *Columnea* are elaborations of the elongated cone-shaped hairs found both inside and outside of the corolla tube and on the style in many species of *Columnea* (Figure 387). It should be noted that multiseriate stalks occur occasionally also among the variations of the tall, uniseriate glandular trichomes (Figures 274, 297, 303, 325-329, 338, 340, 347, 349, 351, 354), and that the glandular end-cells in many of these trichomes are subdivided. A strict classification of types of trichomes appears therefore impossible.

Multiseriate trichomes similar to those in *Columnea* occur also in the throat of the corolla of species of *Gloxinia* (Figure 377). But these barrel-shaped trichomes are topped by a single glandular cell with yellowish brown contents. The stalk cells are filled with wine-colored anthocyanin. A cross-section of such large multiseriate trichomes reveals that the barrel-shaped portion is not a protrusion of the epidermis with a hollow space inside; it consists of a solid mass of cells. As far as is known, this is the only occurrence of multiseriate glandular trichomes among the Gesneriaceae.

Multiseriate bullhorn-shaped non-glandular trichomes can be found on the adaxial side of the leaf of *Rhynchoglossum azureum* (Schlechtd.) Burtt, the only representative of the paleotropic subfamily Cyrtandroideae in the neotropics (Figure 388). A related species from India and Ceylon, *R. notonianum* (Wall.) Burtt, has branched foliar trichomes, a feature not found in the American Gesneriaceae (Figure 389).



Figures 388-389. Multiseriate and branched trichomes in the Asiatic genus *Rhynchoglossum*. Figure 388. *Rhynchoglossum azureum* (Schlechtendal) B. L. Burtt, *Dressler s.n.* Oaxaca, Mexico; from the adaxial leaf surface. Figure 389. *Rhynchoglossum notonianum* (Wall.) B. L. Burtt, G-658, a species from India and Sri Lanka. adaxial leaf surface.
Scale: 50 microns

Trichomes containing mucilaginous sap in their cells occur in several species of *Gesneria* (Wiehler, 1970; Skog, 1976). In *Gesneria auriculata* G-1265 from Hispaniola the indumentum of the total plant body consists of mucilaginous trichomes, irrespective of their type, non-glandular with pointed end-cells or glandular with a spheroid end-cell. In the glandular end-cells the viscid liquid has an orange-yellow color; in all other trichome cells the sticky liquid is clear. A slight touch ruptures or decapitates the end-cells, causing the viscous liquid to ooze out which, in turn, gives the plant body its tacky characteristic. Some of the spheroid end-cells of the trichomes on the underside of the leaf of this species exhibit odd-looking dendroid protuberances from the apparently still unruptured glandular cell. These branched structures appear to be either filigree-like crystallizations of emanations of the yellow glandular cell contents or the filamentous mycelia of a symbiotic fungus (Figures 237-240). The same phenomenon was observed on the glandular trichomes on the calyx lobes of *Bucinellina nariniana* (Figure 362).

The abundance of trichomes is an outstanding feature in many species and genera of the Gesneriaceae. This is reflected in the frequence of such specific epithets as *hirsuta*, *hirsutissima*, *hirta*, *hispida*, *lanata*, *pilosa*, *pilosissima*, *strigosa*, *tomentosa*, *velutina*, and *villosa*. Yet, with the exception of the floral trichomes, very little diversification of the indumentum has taken place in the evolutionary development of the family. No particular taxonomic significance may be attributed to the two main types of trichomes occurring among the Gesnerioideae — the long, uniseriate hairs, and the short, capitate glandular trichomes — not even on the familial level. Hummel & Staesche (1962) state that both types of hairs appear in each family of the Scrophulariales and related orders.

Small differences in the indumentum and in the coloration of the hairs have been used in the past in the classification of the Gesneriaceae, mostly on the specific and varietal levels. More careful observations of live material in field and greenhouse reveal that the systematic value of these features varies from species to species. The usefulness of small differences in the indumentum of Gesneriaceae for taxonomic evaluation depends on the familiarity of the classifying botanist with the given plant material. In many gesneriad species the development of anthocyanin in trichomes and epidermal cells can be influenced by the degree of exposure to light. In other species, as in *Nautilocalyx porphyrotrichus* (a species in which many plants have only clear-celled trichomes), the presence or absence of anthocyanin is genetically controlled. In another species named for the color of the indumentum, *Parakohleria rhodotricha* (Cuatrec.) Wiehler, all plants in several populations examined in Ecuador had only red trichomes. The paucity or abundance of indumentum and the degree of appressedness of the hairs to the surface of the epidermis within a given species may likewise vary between geographically separated populations or in plants found at different altitudes in the same region [*Sinningia canescens* (Mart.) Wiehler in Brazil, species of *Columnea* and *Drymonia* in Panama and Costa Rica].

CHAPTER 17: THE CYTOGENETIC DATA AND HYBRIDIZATION

The gradual establishment of chromosome numbers for species in most genera of the neotropical Gesneriaceae (Rogers, 1954; Fussell, 1958; Lee, 1962a, 1962b, 1964, 1966a, 1967b; Lee & Grear, 1963; Clayberg, 1967; Wiehler, 1972a, 1975b, 1975h, 1976a) and the interspecific and intergeneric hybridization work in this subfamily (Cooke & Lee, 1966; Sherk & Lee, 1967; Clayberg, 1968, 1970; Saylor, 1971; Wiehler, 1968, 1970, 1972a, 1973a, 1975b) have proved of immense value in arriving at better generic concepts and in the development of a new classification for this taxonomically difficult plant group.

One of the interesting factors to emerge from this biosystematic research is that the chromosome numbers for each genus of the Gesnerioideae appear to be constant (Table 2). This realization had three practical implications. 1) The validity of many of the traditional genera of the subfamily was confirmed by the constancy of the chromosome number of their species (as well as through a more thorough assessment of gross morphological characters). 2) Differing base chromosome numbers became valuable and decisive generic markers in the following pairs of taxa in which species look superficially similar and thus were often confused in the past:

Alloplectus	$n = 9$	*Nematanthus*	$n = 8$
Phinaea	$n = 13$	*Niphaea*	$n = 11$
Kohleria	$n = 13$	*Moussonia*	$n = 11$
Gloxinia	$n = 13$	*Achimenes*	$n = 11$

3) Constancy in chromosome numbers, in conjunction with hybridization data, became strong supporting evidence for either the fusion or division of genera, discussed below.

TABLE 12. "INTERTRIBAL" AND INTERGENERIC HYBRIDS IN THE GESNERIACEAE ACCORDING TO FRITSCH'S CLASSIFICATION

	Parental Genera	Hybrid Pollen Stainability	Hybrid Genus
1.	*Monopyle* X *Gloxinia*	0%	X *Gloxinopyle* Wiehler (1976b)
2.	*Gloxinia* X *Smithiantha*	0%	X *Gloxinantha* R. E. Lee (1967a)
3.	*Seemannia* X *Gloxinia*	19%	(= *Gloxinia*, in new classification)
4.	*Gloxinia* X *Achimenes*	79%	(= *Gloxinia*)
5.	*Achimenes* X *Smithiantha*	0%	X *Achimenantha* H. E. Moore (1973c) and X *Smithicodonia* Wiehler, (1976b)
6.	*Achimenes* X *Kohleria*	2%	(= X *Glokohleria* Wiehler and X *Glocodonia* Wiehler, 1976b)
7.	*Seemannia* X *Achimenes*	91%	(= *Gloxinia*)
8.	*Heppiella* X *Smithiantha*	?%	X *Heppiantha* H. E. Moore (1954a) synonym: X *Smitheppiella* Wiehler (1976b)
9.	*Heppiella* X *Seemannia*	0%	(= X *Heppigloxinia* Wiehler 1976b)
10.	*Seemannia* X *Kohleria*	0-8%	(= X *Glokohleria* Wiehler, 1976b)
11.	*Koellikeria* X *Kohleria*	0-11%	X *Koellikohleria* Wiehler (1968)
12.	*Kohleria* X *Smithiantha*	0%	(= X *Moussoniantha* Wiehler, 1976b)
13.	*Kohleria* X *Solenophora*	0%	(= X *Moussonophora* Wiehler, 1976b)
14.	*Diastema* X *Kohleria*	5-8%	X *Diaskohleria* Wiehler (1976b)
15.	*Heppiella* X *Achimenes*	0%	X *Heppimenes* Batcheller (1978)
16.	*Sinningia* X *Rechsteineria*	0-100%	("X *Gloxinera*" Weathers, 1895: = *Sinningia*)
17.	*Episcia* X *Nautilocalyx*	73-100%	(= *Nautilocalyx*)
18.	*Hypocyrta* X *Nematanthus*	45-100%	(X *Hypotanthus* Saylor, 1971; = *Nematanthus*)
19.	*Codonanthe* X *Nematanthus*	ca. 50%	X *Codonatanthus* Saylor (1978)
20.	*Gesneria* X *Rhytidophyllum*	0-36%	(X *Rhydidoneria* Katzenberger, 1976; = *Gesneria*)
21.	*Mitraria* X *Sarmienta*	?%	X *Mitramienta* Wiehler, gen. hybr. nov.*

* *Mitraria coccinea* Cav. X *Sarmienta repens* Ruíz & Pavon, reported by J. W. Besant (1937: 252).

The relative ease with which interspecific and intergeneric hybrids can be made among the New World Gesneriaceae is probably paralleled only by the family Orchidaceae. It is again a prodigious plasticity which places these two groups near the peak of one direction of evolution among the dicots and monocots. Until the recent hybridization experiments only few intergeneric hybrids were known within the New World Gesneriaceae: between *Achimenes* and *Smithiantha*, *Heppiella* and *Smithiantha*, *Rechsteineria sensu* Fritsch and *Sinningia*, and *Mitraria* and *Sarmienta*. The 21 new intergeneric hybrids and the numerous interspecific hybrids produced since 1960 have been a major factor in the fixation of generic and tribal limits in the Gesnerioideae (Tables 12-24).

TABLE 13: INTERGENERIC HYBRIDS IN THE GESNERIACEAE ACCORDING TO THE NEW CLASSIFICATION

Parental Genera	Hybrid Pollen Stainability	Hybrid Genus
1. *Monopyle* × *Gloxinia*	0%	× *Gloxinopyle* Wiehler (1976b)
2. *Gloxinia* × *Smithiantha*	0%	× *Gloxinantha* R. E. Lee (1967a)
3. *Achimenes* × *Smithiantha*	0%	× *Achimenantha* H. E. Moore (1973c)
4. *Achimenes* × *Eucodonia*	0%	× *Achidonia* Wiehler (1976b)
5. *Smithiantha* × *Eucodonia*	0%	× *Smithicodonia* Wiehler (1976b)
6. *Gloxinia* × *Eucodonia*	0%	× *Glocodonia* Wiehler (1976b)
7. *Gloxinia* × *Kohleria*	0-8%	× *Glokohleria* Wiehler (1976b)
8. *Heppiella* × *Smithiantha*	?%	× *Heppiantha* H. E. Moore (1954a)
9. *Heppiella* × *Gloxinia*	0%	× *Heppigloxinia* Wiehler (1976b)
10. *Koellikeria* × *Kohleria*	0-11%	× *Koellikohleria* Wiehler (1968)
11. *Moussonia* × *Smithiantha*	0%	× *Moussoniantha* Wiehler (1976b)
12. *Moussonia* × *Gloxinia*	0%	× *Moussogloxinia* Wiehler (1976b)
13. *Moussonia* × *Solenophora*	0%	× *Moussonophora* Wiehler (1976b)
14. *Moussonia* × *Kohleria*	0%	× *Moussokohleria* Wiehler (1976b)
15. *Parakohleria* × *Kohleria*	0%	× *Paleria* Wiehler, gen. hybr. nov.*
16. *Diastema* × *Kohleria*	5-8%	× *Diaskohleria* Wiehler (1976b)
17. *Heppiella* × *Achimenes*	0%	× *Heppimenes* Batcheller (1978)
18. *Niphaea* × *Achimenes*	?%	× *Niphimenes* Worley (1979)
19. *Columnea* × *Dalbergaria*	0%	× *Colbergaria* Wiehler (1976b)
20. *Columnea* × *Trichantha*	0%	× *Coltrichantha* Wiehler (1976b)
21. *Columnea* × *Pentadenia*	0%	× *Coltadenia* Wiehler (1976b)
22. *Dalbergaria* × *Trichantha*	6-9%	× *Daltrichantha* Wiehler (1976b)
23. *Dalbergaria* × *Pentadenia*	0%	× *Daltadenia* Wiehler (1976b)
24. *Trichantha* × *Pentadenia*	0%	× *Trichanthenia* Wiehler, nom. nov.
25. *Codonanthe* × *Nematanthus*	ca. 50%	× *Codonatanthus* Saylor (1978)
26. *Mitraria* × *Sarmienta*	?%	× *Mitramienta* Wiehler (see Table 12)

* Based on hybrids between *Parakohleria weberbaueri* (Fritsch) Wiehler × *Kohleria spicata* (Kunth) Oersted, and *P. sprucei* (Britton) Wiehler × *K. hirsuta* (Kunth) Regel. Hybrids produced by the author (see Wiehler, 1976b: 379).

** Replacing × *Trichadenia* Wiehler (1976b) which is a later homonym for *Trichadenia* Thwaites, a genus in the Flacourtiaceae.

This table is a summary and updating of Wiehler (1976b)

These hybridization experiments reveal five interesting facts related to the evolution, biology, and taxonomy of the Gesnerioideae. 1) The high degree of pollen stainability and fertility among many interspecific hybrids (within *Gloxinia sensu lato*, *Kohleria*, *Moussonia*, *Achimenes sensu stricto*, *Smithiantha*, *Columnea sensu stricto*, *Trichantha*, *Pentadenia*, *Nautilocalyx sensu lato*, *Nematanthus sensu lato*, and in *Sinningia)* indicates that the effective isolating mechanisms between the species are usually not genetic or internal barriers but external physiological, ethological, spatial, and ecological barriers. (In a sense, even some of these external barriers are often under genetic control.) The most important isolating mechanisms between species in the Gesneriaceae appear to be the phenomena of pollination, geographical

TABLE 14: INTERGENERIC HYBRIDIZATION AMONG FIVE TRIBES OF FRITSCH'S CLASSIFICATION (1893-94): THE BASIS FOR REDUCING THESE TAXA TO A SINGLE UNIT, THE TRIBE GLOXINIEAE

(Number values in circles refer to gametic chromosome numbers; lines between taxa represent artificial hybrids established.)

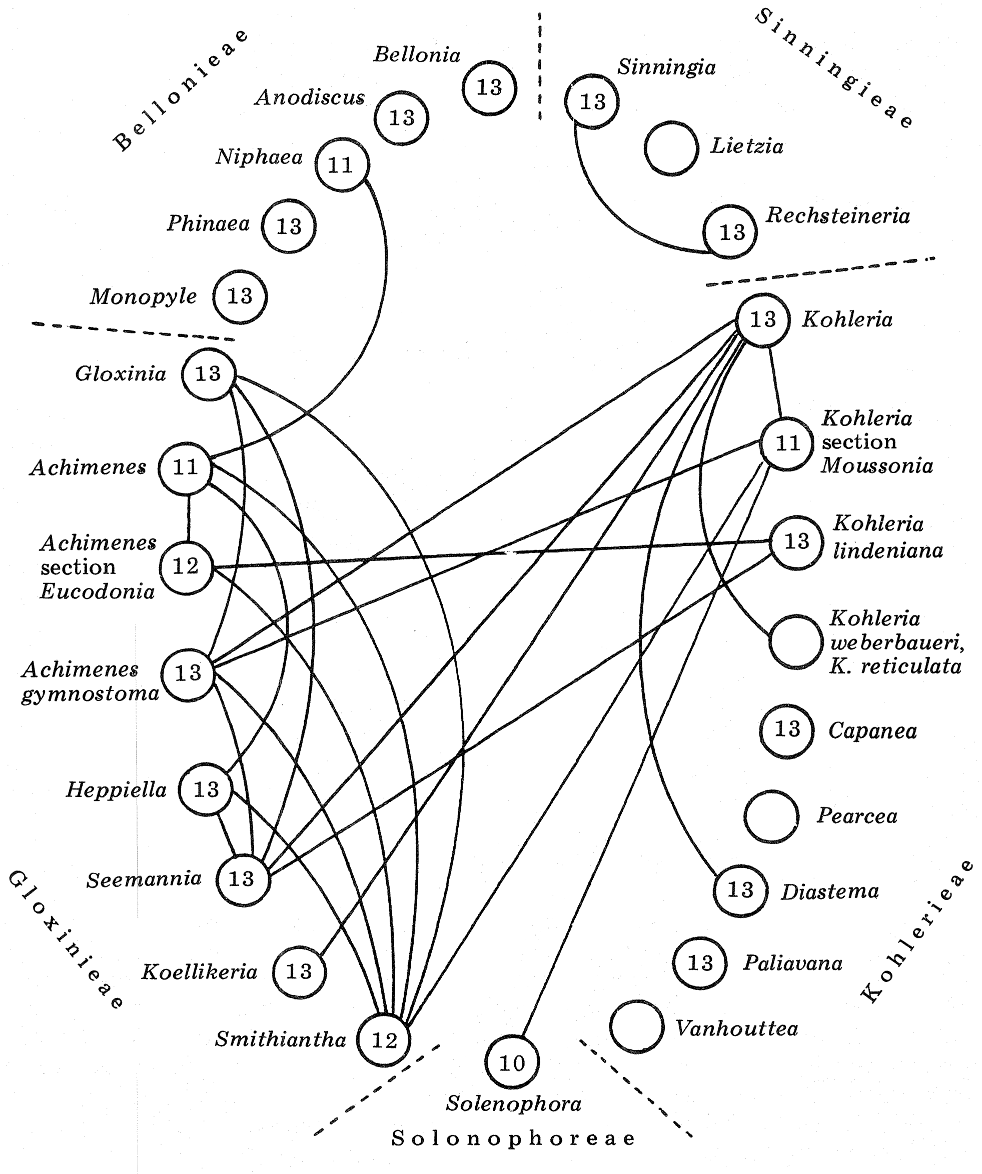


TABLE 15: INTERSPECIFIC HYBRIDS IN *MOUSSONIA**

				Hybrid Pollen Stainability
1.	*M. deppeana* G-1061	X	*M. elegans* G-724	100%
2.	Reciprocal cross			100%
3.	*M. elegans* G-444	X	*M. hirsutissima* G-826	100%
4.	*M. elegans* G-724	X	*M. hirsutissima* G-826	98%
5.	*M. elegans* G-724	X	*M. septentrionalis* G-1201	99%
6.	*M. hirsutissima* G-793C	X	*M. septentrionalis* G-1201	91%
7.	*M. hirsutissima* G-793A	X	*M.* species G-828	98%
8.	*M. septentrionalis* G-1201	X	*M. hirsutissima* G-826	100%
9.	Reciprocal cross			100%
10.	*M.* species G-828	X	*M. deppeana* G-1061	100%
11.	*M.* species G-828	X	*M. elegans* G-444	99%

* Summarized from Wiehler (1975b)

TABLE 16: INTERSPECIFIC HYBRIDS IN *KOHLERIA**

	Parental Species			Hybrid Pollen Stainability
1.	*K. spicata (schiedeana)* G-718	X	*K. digitaliflora* G-941	49%
2.	*K. hirsuta* G-1059	X	*K. eriantha* G-798	20%
3.	*K. spicata* G-331	X	*K. lanata* G-401	39%
4.	Recriprocal cross			41%
5.	*K. tubiflora* G-274	X	*K. spicata (longifolia)* G-834	62%
6.	*K. tubiflora* G-274	X	*K. spicata* G-331	39%
7.	Reciprocal cross			35%
8.	*K. peruviana* G-1208	X	*K. eriantha* G-1277	31%
9.	*K. allenii* G-1317	X	*K. spicata (longifolia)* G-834	55%
10.	*K. allenii* G-1317	X	*K. spicata* G-331	67%
11.	*K. digitaliflora* G-1278	X	*K. peruviana* G-1208	11%

* Summarized from Wiehler (1975b)

or ecological isolation, and time of flowering. This assumption is further substantiated by the fact that only very few natural gesneriad hybrids have been found in the neotropics, and those mostly in ecologically disturbed areas: H. E. Moore discovered in one locality in Mexico several hybrids between species of *Achimenes* (personal communication), and I found a single hybrid plant between *Dalbergaria perpulchra* and *D. sanguinea* in Panama, as well as evidence of limited introgression between *Kohleria spicata* and *K. villosa* in western Ecuador and adjoining Colombia. Two different natural hybrids between species of *Gesneria* are known from Jamaica (Table 25).

2) The second noteworthy fact was the complete sterility of all except one of the many intergeneric crosses produced (Tables 12-13), measured so far only in terms of hybrid pollen stainability and in the inability to produce

offspring through backcrossing, and not by a more time-consuming analysis of meiotic behavior of pollen mother cells of the F_1 generation. The sterility of these intergeneric hybrids ranged from the typical 0% pollen stainability to 8 and 9%, and in the case of the "intertribal" hybrid *Koellikeria* × *Kohleria*, from 0-11% in counts taken through several years and in different seasons (Table 13). There is thus a slight difference between these values for sterility and the three fertility classes suggested by Clayberg (1968) for hybrid Gesneriaceae: fully fertile, 85-100% pollen stainability; partially fertile, 5-85% pollen stainability; sterile 2-0% pollen stainability. From the male sterility data on hand (Table 13), coupled with the presumed female sterility of the intergeneric hybrids (unsuccessful selfing and backcrosses with pollen from either parent), the values for sterility in the Gesnerioideae (at least for intergeneric crosses) appear to be between 10-0%. Partial fertility would thus include values between 11-85%.

It has to be further noted that the fertility level of the intergeneric hybrids was not affected by either a difference or equality in parental chromosome numbers, as seen by the following examples (chromosome numbers underlined):

Monopyle	13	×	*Gloxinia*	13	0% h.p.s.*
Diastema	13	×	*Kohleria*	13	5-8%
Heppiella	13	×	*Gloxinia*	13	0%
Smithiantha	12	×	*Eucodonia*	12	0%
Columnea	9	×	*Trichantha*	9	0%
Niphaea	11	×	*Achimenes*	11	0%
Gloxinia	13	×	*Smithiantha*	12	0%
Moussonia	11	×	*Gloxinia*	13	0%
Moussonia	11	×	*Solenophora*	10	0%
Achimenes	11	×	*Smithiantha*	12	0%
Achimenes	11	×	*Heppiella*	13	0%

* h. p. s. = hybrid pollen stainability

The sterility of nearly all intergeneric hybrids is a major support for the validity of most of the traditional generic limits in the Gesnerioideae. The same hybrid sterility was also a major factor in the division of those genera (in Fritsch's system) with more than one base chromosome number: section *Moussonia* ($n = 11$) from the genus *Kohleria* ($n = 13$), and sections *Eucodonia* ($n = 12$) and *Mandirola* ($n = 13$, = *Gloxinia*) from the genus *Achimenes* ($n = 11$). The new classification system has the appeal of simplicity and uniformity in its generic divisions: a single base chromosome number for each genus, high fertility for many species within a genus, and complete sterility for intergeneric hybrids.

An intriguing problem for generic delimitations and cytogenetics in the Gesnerioideae present the recently produced hybrids between orange-berried species of *Codonanthe* (section *Codonanthe*, $n = 8$) from southeastern Brazil and at least 10 species and hybrids of *Nematanthus* ($n = 8$) from the same area in Brazil (Saylor, 1978). These intergeneric hybrids are partially fertile and have produced F_2 generations (Saylor, personal communication). The parental genera appear to be quite distinct one from another, and all attempts of hybridization between species of other sections of *Codonanthe* (none of them native to southeastern Brazil) and *Nematanthus* have failed. Two graduate students are presently examining this curious situation from differ-

TABLE 17: INTERSPECIFIC HYBRIDS IN *ACHIMENES**

	Parental Species			Hybrid Pollen Stainability
1.	*A. cettoana*	X	*A. longiflora*	63%
2.	*A. patens*	X	*A. grandiflora*	86%
3.	*A. candida*	X	*A. patens*	88%
4.	*A. flava*	X	*A. grandiflora*	55%
5.	*A. flava*	X	*A. patens*	27%
6.	*A. flava*	X	*A. candida*	88%
7.	*A. flava*	X	*A. obscura*	85%**
8.	*A. woodii*	X	*A. grandiflora*	84%
9.	*A. heterophylla*	X	*A. grandiflora*	65%
10.	*A. heterophylla*	X	*A. patens*	68%
11.	*A. mexicana*	X	*A. grandiflora*	78%
12.	*A. mexicana*	X	*A. patens*	37%
13.	*A. dulcis*	X	*A. grandiflora*	40%
14.	*A. dulcis*	X	*A. antirrhina*	38%
15.	*A. dulcis*	X	*A. mexicana*	75%

* Selected from Cooke & Lee (1966).
** Count made in 1970: *Wiehler 7045* (BH).

TABLE 18: INTERSPECIFIC HYBRIDS IN *SMITHIANTHA**

	Parental Species			Hybrid Pollen Stainability
1.	*S. multiflora* G-717	X	*S. cinnabarina (fulgida)* G-247	68%
2.	*S. cinnabarina* G-1225	X	*S. multiflora* G-717	21%
3.	*S. zebrina* hybrid G-167	X	*S. cinnabarina (fulgida)* G-247	83%
4.	*S. zebrina* hybrid G-167	X	*S. multiflora* G-717	87%

* Summarized from Cooke & Lee (1966). The genus *Smithiantha* contains only three species (Wiehler, 1981: 383).

ent aspects for their doctoral dissertations. Considering our present knowledge of intergeneric hybridization within the Gesnerioideae, the partially fertile hybrids between *Codonanthe* and *Nematanthus* have to be regarded as one of the many exceptions to the norm in the Gesneriaceae.

3) The partial or high fertility of some presumed intergeneric hybrids (according to Fritsch's system) with equal parental chromosome numbers [*Sinningia* (n = 13) X *Rechsteineria* (n = 13), *Gloxinia* (n = 13) X *Seemannia* (n = 13), *Episcia* section *Skiophila* (n = 9) X *Nautilocalyx* (n = 9), *Nematanthus* (n = 8) X *Hypocyrta* (n = 8), *Gesneria* (n = 14) X *Rhytidophyllum* (n = 14)] contrasts sharply with the sterility of the rest of the intergeneric hybrids. In each of these cases there was already sufficient gross morphological evidence on hand to unite (or suggest the union of) the taxa concerned (Clayberg, 1968, 1970; Wiehler, 1970, 1972a, b, 1973a, 1976a; Moore, 1973c).

TABLE 19: INTERSPECIFIC HYBRIDS IN *SINNINGIA* *

	Parental Species			Hybrid Pollen Stainability
	Section *Thamnocaula***			
1.	*S. macropoda (lineata)*	X	*S. canescens*	97-99%
2.	*S. macropoda (lineata)*	X	*S. macropoda (cyclophylla)*	90-95%
3.	*S. cardinalis*	X	*S. macrorrhiza*	90-99%
4.	*S. macropoda (cyclophylla)*	X	*S. canescens (leucotricha)*	85-100%
5.	*S. cardinalis*	X	*S. canescens*	50-70%
6.	*S. cardinalis*	X	*S. verticillata*	15-30%
7.	*S. cardinalis*	X	*S. eumorpha*	15-30%
8.	*S. eumorpha*	X	*S. verticillata*	10-15%
9.	*S. canescens*	X	*S. eumorpha*	15-30%
	Section *Corytholoma*			
10.	*S. aggregata*	X	*S. sceptrum ('sellovii')*	30-50%
11.	*S. sceptrum ('sellovii')*	X	*S. tubiflora*	98-100%
12.	*S. aggregata*	X	*S. allagophylla*	95%
13.	*S. incarnata (warszewiczii)*	X	*S. sceptrum ('sellovii')*	90-99%
14.	*S. incarnata (warszewiczii)*	X	*S. tubiflora*	60-80%
	Section *Ligeria*			
15.	*S. speciosa (discolor)*	X	*S. speciosa*	99-100%
16.	*S. speciosa (regina)*	X	*S. speciosa*	90-95%
	Section *Stenogastra*			
17.	*S. concinna*	X	*S. pusilla*	0-10%
	Intersectional (= intercenospecific) hybrids			
18.	*S. allagophylla*	X	*S. richii*	5-10%
19.	*S. pusilla*	X	*S. canescens (leucotricha)*	0.5-2%
20.	*S. speciosa (discolor)*	X	*S. richii*	0-0.1%
21.	*S. concinna*	X	*S. allagophylla*	0-0.2%
22.	*S. aggregata*	X	*S. richii*	7-20%
23.	*S. tubiflora*	X	*S. eumorpha*	0-1%
24.	*S. concinna*	X	*S. hirsuta*	0-0.1%
25.	*S. eumorpha*	X	*S. aggregata*	0-0.2%

* Selected from Clayberg (1970).

** Based on hybrid pollen stainability and a cytological analysis of meiosis in the hybrids, Clayberg regroups the traditional sections. The new sections correspond to cenospecies. Only the following species listed above were originally in *Sinningia: S. concinna, S. eumorpha, S. hirsuta, S. pusilla, S. richii, S. speciosa* and *S. tubiflora.* The rest of the species cited above have been transferred from *Rechsteineria,* mostly on the basis of Clayberg's hybridization studies (Moore, 1973c; Wiehler, 1975c, 1978c, 1981).

4) The establishment of six presumably intertribal hybrids (Table 12), according to Fritsch's system, is a strong indication that the genera in the five tribes Gloxinieae, Bellonieae, Kohlerieae, Sinningieae, and Solenophoreae are evidently more closely related than previously assumed. The tribal structure has therefore been revised to include all these taxa in a single tribe, the Gloxinieae.

TABLE 20: INTERSPECIFIC HYBRIDS IN *COLUMNEA* *

	Parental Species			Hybrid Pollen Stainability
1.	*C. gloriosa*	X	*C. glabra*	98%
2.	*C. hirta*	X	*C. arguta*	93%
3.	*C. hirta*	X	*C. crassifolia*	72%
4.	*C. hirta*	X	*C. gloriosa*	83%
5.	*C. lepidocaula*	X	*C. glabra*	94%
6.	*C. lepidocaula*	X	*C. gloriosa*	94%
7.	*C. lepidocaula*	X	*C. hirta*	85%
8.	*C. linearis*	X	*C. allenii*	73%
9.	*C. linearis*	X	*C. crassifolia*	90%
10.	*C. linearis*	X	*C. gloriosa*	97%
11.	*C. linearis*	X	*C. hirta*	90%
12.	*C. linearis*	X	*C. lepidocaula*	95%
13.	*C. microphylla*	X	*C. crassifolia*	90%
14.	*C. nicaraguensis*	X	*C. arguta*	84%
15.	*C. nicaraguensis*	X	*C. glabra*	90%
16.	*C. nicaraguensis*	X	*C. gloriosa*	97%
17.	*C. nicaraguensis*	X	*C. lepidocaula*	97%
18.	*C. querceti*	X	*C. linearis*	99%
19.	*C. querceti*	X	*C. nicaraguensis*	99%
20.	*C. schiedeana*	X	*C. linearis*	94%
21.	*C. verecunda*	X	*C. nicaraguensis*	97%
22.	*C. verecunda* 'F.C.'	X	*C. querceti*	99%
23.	*C. linearis*	X	*C. hirsutissima*	61% **
24.	*C. fawcettii*	X	*C. repens*	99% ***
25.	*C. hirta*	X	*C. zebrina*	38% **
26.	*C. purpusii*	X	*C. zebrina*	24% **
27.	*C. crassifolia*	X	*C. zebrina*	20% **

* Selected from Sherk & Lee (1967).

** Hybrids recently produced at the Marie Selby Botanical Gardens, vouchers at SEL and GES.

*** Hybrid produced by William Saylor, grown at MSBG.

5) The inability to obtain hybrids between certain critical taxa (Table 26) appears to have some taxonomic implications. Because flowers or pollen were readily available for extended periods of time, some of the crosses listed were tried at least 15-25 times or were repeated for several years (for instance, those involving *Gloxinia perennis*, *Bellonia spinosa*, *Sinningia speciosa (regina)*, and *Episcia cupreata*). Often fruit appeared to be setting, but after the maturation of the capsule the seed was shrivelled, abnormally twisted, and without (or with aborted) embryos. The seed of some crosses appeared to be fully developed (sometimes only 3-6 grains out of 100), but failed to germinate after sowing. However, this record should be balanced by the following report: I tried for two years without success to produce hybrids between *Gloxinia perennis* and *G. sylvatica* (at that time known as *Seemannia latifolia*). When the cross finally took, five capsules produced completely

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TABLE 21: INTERSPECIFIC HYBRIDS IN *TRICHANTHA*

	Parental Species			Hybrid Pollen Stainability
1.	*T. brenneri*	X	*T. tenensis*	91%*
2.	*T. purpureovittata*	X	*T. sanguinolenta*	23%
3.	*T. sanguinolenta*	X	*T. anisophylla*	29%
4.	Reciprocal cross			36%**
5.	*T. minor (teuscheri)*	X	*T. illepida*	42%**

* From Wiehler (1975d).
** From Sherk & Lee (1967).
All 27 intergeneric hybrids between *Columnea* and *Trichantha*, reported by Sherk & Lee (1967) and Wiehler (1976b) are completely sterile (= 0% hybrid pollen stainability).

TABLE 22: INTERSPECIFIC HYBRIDS IN *PENTADENIA*

	Parental Species			Hybrid Pollen Stainability
1.	*P. ecuadorana*	X	*P. angustata*	76%
2.	Reciprocal cross			73%

TABLE 23: INTERSPECIFIC HYBRIDS IN *NAUTILOCALYX**

	Parental Species			Hybrid Pollen Stainability
1.	*N. melittifolius***	X	*N. villosus*	73%
2.	*N. panamensis***	X	*N. villosus*	100%
3.	*N. villosus*	X	*N. membranaceus***	100%

* Summarized from Wiehler (1976a).
** These species were formerly placed in *Episcia* (Wiehler, 1973a).

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viable seed, with about 93% germination. This was an exceptional case, for most of the successful crosses came about with the first or second trial.

Noteworthy failures in the hybridization experiments were attempted crosses between species of *Episcia sensu stricto* and taxa formerly attributed to *Episcia* but now accepted as separate genera: *Alsobia*, *Paradrymonia*, and species of *Nautilocalyx* (see Table 26). So far no intergeneric hybrids have been established with species of the genus *Sinningia* which, together with the monotypic genus *Lietzia* comprised the tribes Sinningieae. This group appears to fit, nevertheless, into the enlarged concept of the tribe Gloxinieae by virtue of such taxonomic characters as base chromosome number, ovary position, nectary development, epidermal features, and vascular structure.

Clayberg (1970) applied the concept of cenospecies (Turesson, 1922) to his elegant cytogenetic study of the genera *Rechsteineria* and *Sinningia* (Table 25). He redefined the generic and sectional limits of these taxa, now

TABLE 24: INTERSPECIFIC HYBRIDS IN *NEMATANTHUS*

	Parental Species		Hybrid Pollen Stainability	Hybrid Cultivar Name
1.	*N. fritschii*	× *N. crassifolius (longipes, corticola)*	100%*	'Stoplight'
2.	*N. fritschii*	× *N. perianthomegus*	100%	'Ubatuba'
3.	Reciprocal cross		100%**	
4.	*N. perianthomegus*	× *N. hirtellus*	98%	'Sao Paulo'
5.	Reciprocal cross		99%	
6.	*N. fissus*	× *N. fritschii*	100%	'Santos'
7.	*N. wettsteinii*	× *N. hirtellus*	61%	'Corcovado'
8.	*N. perianthomegus*	× *N. gregarius*	59%**	'Tropicana'
9.	*N. perianthomegus*	× *N. hirsutus (strigillosus)*	90%**	
10.	*N. gregarius*	× *N. fissus*	61%**	'Rio'
11.	*N. perianthomegus*	× *N. nervosus*	81%**	
12.	*N. gregarius*	× *N. wettsteinii*	88%**	'Cheerio'
13.	*N. hirsutus (strigillosus)*	× *N. wettsteinii*	. . .**	'Encore'
14.	*N. wettsteinii*	× *N. fritschii*	44%	'Bijou'
15.	*N. nervosus*	× *N. wettsteinii*	. . .***	'Marianne W.'
16.	*(N. fissus* × *N. fritschii)*	× *N. hirtellus*	99%	'Curitiba'
17.	*(N. perianthomegus* × *N. gregarius)*	× *N. hirtellus*	62%	
18.	*N. hirtellus*	× *(N. fritschii* × *N. crassifolius)*	95%	'Petropolis'
19.	*N. wettsteinii*	× *(N. fritschii* × *N. crassifolius)*	57%**	'Black Magic'
20.	*(N. perianthomegus* × *N. fritschii)*	× *[N. wettsteinii* × *(N. fritschii* × *N. crassifolius)]*	74%**	'Castanet'

* Hybrid made by Robert E. Lee in 1966.
** Hybrids made by William Saylor since 1968.
*** Hybrid made by James Wyrtzen in 1967.

Of the species listed here, only *N. crassifolius* and *N. fritschii* were originally associated with the genus *Nematanthus*; the rest were attributed to *Hypocyrta*, now united with *Nematanthus* (Moore, 1973c), mostly on account of the hybridization data presented here for the first time. *Nematanthus hirtellus* was the lectotype of the conserved genus *Alloplectus* (Wiehler, 1972b).

united into a single genus (Moore, 1973c) on the basis of full or partial hybrid fertility and the meiotic behavior of the hybrids. The genus *Sinningia sensu lato* is a well-defined group within the tribe Gloxinieae, and the interpretation of the revised sections as cenospecies must be welcomed as an excellent approach to a better understanding of a highly evolved tropical plant group.

Although the large genus *Sinningia* is well-defined in the Gloxinieae and appears to be isolated from the other genera in the tribe (there are now many intergeneric hybrids in this tribe, but none involving *Sinningia*, despite numerous trials), this genus is nevertheless a morphologically diverse aggregate of species. This can be seen in such characters as plant habit, degree of tuber

TABLE 25: INTERSPECIFIC HYBRIDS IN *GESNERIA**

	Parental Species			Hybrid Pollen Stainability
1.	*G. scabra* var. *sphaerocarpa*	X	*G. tomentosa***	4-36%***
2.	*G. pedicellaris*	X	*G. grandis***	18%
3.	*G. leucomalla***	X	*G. pedunculosa*	9%
4.	*G. acaulis* var. *glabrata*	X	*G. auriculata***	6%
5.	*G. acaulis* var. *glabrata*	X	*G. tomentosa***	0.8%***
6.	*G. reticulata*	X	*G. auriculata***	0.1%
7.	*G. pedicellaris*	X	*G. viridiflora* ssp. *quisqueyana*	66%
8.	*G. citrina*	X	*G. acaulis* var. *glabrata*	64%
9.	*G. pedicellaris*	X	*G. pedunculosa*	47%
10.	*G. citrina*	X	*G. ventricosa* ssp. *ventr.*	33%
11.	*G. acaulis* var. *glabrata*	X	*G. ventricosa* ssp. *ventricosa*	13%
12.	*G. citrina*	X	*G. pedunculosa*	12%
13.	*G. acaulis* var. *acaulis*	X	*G. ventricosa* ssp. *ventricosa*	0.1%
14.	*G. cuneifolia*	X	*G. citrina*	0.1%****
15.	*G. cuneifolia*	X	*G. ventricosa* ssp. *ventricosa*	——*****
16.	*G. leucomalla***	X	*G. grandis***	——*****
17.	*G. tomentosa***	X	*G. fruticosa*	——******

* From Wiehler (1970: Table 12); hybrids produced between 1966-69.

** These species, here united again with *Gesneria*, were considered belonging to a separate genus, *Rhytidophyllum*, by Fritsch (1893-94). Both genera were treated as a single generic unit by Linnaeus (1753), Hanstein (1854-65), Bentham (1876), and Kuntze (1891).

*** Natural hybrids.

**** Hybrid produced by Michael Kartuz in 1971.

***** Hybrids produced by Wiehler in 1969, did not flower by 1970.

****** Hybrids produced by Katzenberger (1976).

Twelve additional hybrids were produced by Skog (1976: 35) after 1969, but most of these were apparently not brought to the flowering stage and cytologically evaluated.

development, leaf shape, inflorescence patterns, and corolla shape. The shape of the nectary is an excellent taxonomic character in the Gesnerioideae; it is usually constant for a genus. In *Sinningia*, however, the structure of the nectary is extremely diverse, but still constant for each section or cenospecies. From epiphytic species (*S. verticillata*) to terrestrials two meters tall (*S. tubiflora*, *S. sellovii*) to dwarf rock plants which can be grown in a thimble (*S. pusilla*), the genus *Sinningia* exhibits more evolutionary diversity and greater genetic differentiation than any other group in the tribe Gloxinieae. (A similar situation occurs in the Caribbean genus *Gesneria sensu lato*.)

It is precisely because the different sections within *Sinningia* are so highly evolved that the concept of cenospecies appears to apply rather well to this genus. One critical section of the group (containing the type species, *S. helleri*) has so far not been available for cytogenetic experimentation. It will be interesting to see how this section relates to the rest of this comparium.

Clayberg (1970) suggested in the same paper that the concept of cenospecies may also apply to other genera or groups of genera in the Gesnerioideae. He offered that *Achimenes* ($n = 11$) and *Smithiantha* ($n = 12$) may be-

TABLE 26. ATTEMPTED INTERGENERIC CROSSES WHICH DID NOT PRODUCE HYBRIDS*

1.	*Gloxinia perennis*	X	spp. of *Achimenes*, *Eucodonia*, *Kohleria*, *Moussonia*, *Sinningia*, *Solenophora*, and with *Gloxinia lindeniana*
2.	*Gloxinia gymnostoma*	X	spp. of *Achimenes*, *Eucodonia*, *Sinningia*
3.	*Gloxinia sylvatica*	X	spp. of *Achimenes*, *Eucodonia*, *Moussonia*, *Sinningia*
4.	*Bellonia aspera* and *B. spinosa*	X	*Niphaea oblonga*, *Phinaea divaricata*, *Ph. multiflora*, *Ph. repens*, spp. of *Monopyle*, *Gloxinia*, *Kohleria*, *Achimenes*, *Smithiantha*, *Moussonia*, *Sinningia*
5.	spp. of *Kohleria*	X	spp. of *Achimenes*, *Eucodonia*, *Smithiantha*, *Sinningia*, *Solenophora*
6.	spp. of *Moussonia*	X	spp. of *Achimenes*, *Eucodonia*, *Smithiantha*
7.	*Sinningia speciosa (regina)* and *S. cardinalis*	X	spp. of *Gloxinia*, *Kohleria*, *Palivana*, *Koellikeria*, *Monopyle*, *Bellonia*, *Niphaea*, *Achimenes*, *Smithiantha*, *Moussonia*, *Solenophora*
8.	*Episcia cupreata*, *E. lilacina*, and *E. reptans*	X	spp. formerly attributed to *Episcia: Nautilocalyx melittifolius*, *N. panamensis*, *N. adenosiphon*, *Alsobia punctata*, *A. dianthiflora*, *Paradrymonia decurrens*, *P. lurida*
9.	*Gesneria corymbosa*	X	spp. of *Gesneria*, *Kohleria*, *Koellileria*, *Smithiantha*, *Gloxinia*, *Phinaea*, *Diastema*

* Partially based on Wiehler (1970)

long in a single cenospecies, because the sterile hybrids between these genera, exhibiting zero percent pollen stainability, had a minimum of six bivalents per cell at metaphase I (Sherk & Lee, 1966). The cytogenetic study in *Rechsteineria* and *Sinningia* lead to a uniting of these morphologically somewhat diverse genera, but this does certainly not imply that the application of the cenospecies concept to other taxa in the Gesnerioideae has to lead to similar results. *Achimenes* and *Smithiantha*, in contrast to *Sinningia*, hybridize with a large number of other genera in the tribe Gloxinieae (and these, in turn, have been crossed with others, Tables 13, 14). The nature of meiosis has not yet been studied in the more recent sterile intergeneric hybrids, but it may be expected that the presence of some bivalents will reveal a certain degree of close relationship between the parental genera. Does this mean we have to unite all these genera into a single unwieldy and impractical supergenus? All these genera have well-defined gross morphological generic markers, and often differences in base chromosome numbers (Table 2). *Achimenes* and *Smithiantha* are separated by clear-cut differences in inflorescence structure. It seems therefore only logical and practical to leave the traditional generic limits of these taxa intact.

TABLE 27. POLYPLOID SPECIES OR COLLECTIONS OF SPECIES IN THE SUBFAMILY GESNERIOIDEAE

Species	Gametic Chromosome Number	Reference
1. *Achimenes erecta* (Lam.) H. P. Fuchs	22*	Lee (1962b); Lee, unpublished: *n* = 11
2. *Achimenes misera* Lindl.	22	Lee (1966)
3. *Achimenes pedunculata* Benth.	17**	Fussell (1958)
4. *Achimenes skinneri* Lindl.	17**	Fussell (1958)
5. *Codonanthe corniculata* Wiehler	16	Lee (1967)
6. *Codonanthe calcarata* (Miq.) Hanst.	16	Wiehler (1975h)
7. *Codonanthe crassifolia* (Focke) Morton	16	Morley (1967); Wiehler (1975h)
8. *Codonanthe gracilis* (Mart.) Hanst.	16	Wiehler (1975h)
9. *Codonanthe luteola* Wiehler	16*	Wiehler (1975h, also: *n* =8)
10. *Codonanthe macradenia* Donn.-Sm.	16	Lee & Grear (1963); Wiehler (1975h)
11. *Codonanthe uleana* Fritsch	16	Lee (1967); Morley (1967); Wiehler (1975h)
12. *Columnea crassifolia* Brongn. 'Stella Nova'	18*	Morley (1967); Fussell (1958: *n*=9)
13. *Dalbergaria consanguinea* (Hanst.) Wiehler	18*	Morley (1967); Sherk, unpublished, *n*=9
14. *Dalbergaria sanguinea* (Pers.) Steudel	18	Fussell (1958)
15. *Eucodonia verticillata* (Mart. & Gal.) Wiehler 'Bella'	24*	Lee (1966b), Cooke, unpublished, *n*=12
16. *Gesneria cuneifolia* (DC.) Fritsch	28	Lee (1964)
17. *Gloxinia sylvatica* (Kunth) Wiehler	26*	Wiehler (1970); Lee (1962b,1966b, *n*=13)
18. *Heppiella viscida* (Lindl. & Paxton) Fritsch	26	Wiehler (1972a)
19. *Nautilocalyx lynchii* (Hook. f.) Sprague	18	Rogers (1954)
20. *Phinaea repens* (Donn.-Sm.) Solereder	26	Lee (1966b)
21. *Trichantha ambigua* (Urban) Wiehler	18	Lee (1964), Morley (1967)

* Diploid collections are also known of this species.
** Triploid collection of horticultural (=hybrid?) origin.

The value of cytogenetic studies in the Gesnerioideae lies in the realization of the close affinity of many of their genera: closely related but separate. The genus *Sinningia* can be regarded as a comparium, but a more typical comparium in the American Gesneriaceae appears to include whole series of recognized genera, as in the grasses and Orchidaceae, two other highly evolved plant groups.

The same situation as in the tribe Gloxinieae applies also to the large and formerly unwieldy genera *Alloplectus*, *Columnea*, and *Episcia* (all *sensu* Fritsch) in the tribe Episcieae where the majority of the genera even share the same base chromosome number, $n = 9$ (Table 2). *Columnea sensu lato*, for instance, contained four morphologically diverse groups which produce sterile offspring when hybridized one with another (Table 13). The division of *Columnea sensu lato* into the four genera *Dalbergaria*, *Pentadenia*, *Trichantha*, and *Columnea*, of *Alloplectus sensu lato* into *Corytoplectus*, *Cobananthus*, *Drymonia*, and *Alloplectus*, and of *Episcia sensu lato* into *Alsobia*, *Paradrymonia*, *Nautilocalyx*, and *Episcia* is easily understood when the same reasoning that keeps the genera in the tribe Gloxinieae as separate entities is also applied to the taxa in the tribe Episcieae. *Dalbergaria*, *Pentadenia*, *Trichantha*, *Bucinellina*, and *Columnea sensu stricto* may very well all belong in a single comparium, but they are generically as distinct one from another as *Achimenes* is from *Smithiantha*, *Kohleria*, *Heppiella*, *Moussonia*, *Gloxinia*, *Eucodonia*, etc., the genera which appear to make up a comparium in the tribe Gloxinieae.

Polyploidy is a rare phenomenon among the neotropical Gesneriaceae. Only 19 cases of tetraploids are known among the well over 230 species of American Gesneriaceae with published chromosome numbers in 41 genera, out of a total of over 1300 species in about 54 genera (Table 27). Six of the 19 tetraploid collections of species have also diploid forms of the same species. As among other herbaceous tropical plant families (Stebbins, 1971), polyploidy does not play a vital role in the formation of new species among the neotropical Gesneriaceae, at least in recent times.

The evolutionary origin of the basic chromosome numbers in the tribes Episcieae, $n = 9, 8$, Gloxinieae, $n = 13, 12, 11, 10$, Gesnerieae, $n = 14$, and Beslerieae, $n = 16$ is still obscure. Since the majority of the genera of the tribe Episcieae has a basic chromosome number of $n = 9$, this value may very well represent the original number for this group which appears to be also monophyletic, with $n = 8$, occurring only in about 40 species in two genera as a reduction series. The genera with different base chromosome numbers in the tribe Gloxinieae can be intercrossed (Tables 13, 14), indicating that the origin of these basic numbers is probably also monophyletic. Since $n = 13$ is the most frequently occurring chromosome number in this tribe, it may represent the original number in this tribe from which the other numbers are derived by descending series of aneuploids. However, the mechanism for the shifts in chromosome numbers remains still unexplained. It is also possible that the value 13 itself is a derived number by ancient polyploidy, from an original basic number of 7. This number does not seem to occur in the tribe Gloxinieae at the present time. The basic chromosome number for the tribe Gesnerieae appears to be $n = 14$, judging from the numerous counts made of $x = 14$. The only count of $x = 7$ for a species from Puerto Rico (Nevling, 1969) needs to be reexamined before any evaluation of its possible significance (Skog, 1976: 35). There is not enough cytogenetic information available at present for the other two tribes.

PART 2: CHARACTER EVALUATION FOR A NEW CLASSIFICATION

A new classification of a family of organisms, and even the revision of a genus, must elucidate the characters used in the scheme. Hanstein did this remarkably well for the Gesneriaceae in 1854-1865, considering the scanty information then at hand. It has not been done since for the Gesneriaceae, and character evaluation becomes therefore imperative. If a classification is to reflect the probable relationships of the tribes, genera, sections, and species within a plant family, the phenomena of evolution have to be taken into consideration. Our knowledge of speciation and evolution of angiosperms in the tropics is, however, still limited, since most of the research in evolutionary processes has been conducted on the depauperate temperate floras (cf. the subject matter in Grant, 1971).

A good taxonomic character is one that is constant or resistant to change. In the classification of the angiosperms, especially those of the northern temperate zones, *floral* characters have played a primary role because of their consistency or lack of plasticity. However, when the conventional taxonomic standards were applied to the tropical Gesneriaceae, this family soon gained an unmerited reputation as a systematically difficult group. Because of similarity or diversity of corolla shape and because of a lack of knowledge about other decisive features, many of the newly discovered exotic species were attributed to the wrong genus. The conventional use of floral characters brought about taxonomic confusion in this family. Various authors described geographical variants of the same species as novelties, and even placed them in different genera, giving rise to long lists of synonyms. It is worthwhile to recall at this point the laments of numerous botanists about the perennial chaos of generic limits in the neotropical Gesneriaceae, cited in the introduction of this work. To many workers it seemed therefore safer to add the steady influx of new species to the already existing genera. The predictable result was that most of the early good generic concepts in the Gesnerioideae soon ballooned into large, meaningless, and confused wastebasket genera, exemplified foremost by *Gesneria*, *Besleria*, *Alloplectus*, *Columnea*, *Episcia*, *Hypocyrta*, *Achimenes*, and *Kohleria*. Another solution was the establishment of a multitude of new and often vaguely defined genera which did not withstand the test of time. The list of such genera is about as long as the catalogue of the taxa presently considered valid, and includes such names as *Calanthus*, *Centrosolenia*, *Collandra*, *Corytholoma*, *Crantzia*, *Cyrtodeira*, *Diplolegnon*, *Duchartrea*, *Eumolpe*, *Fiebrigia*, *Flueckigeria*, *Fritschiantha*, *Halphophyllum*, *Herincquia*, *Kohlerianthus*, *Macrochlamys*, *Mandirola*, *Orthanthe*, *Pterobesleria*, *Pterygoloma*, *Salisia*, *Scheeria*, *Tapina*, *Tydaea* and *Vireya*.

The influx of new species is continuing. At the time of writing, over 230 novelties await description, illustration, and publication; most of them were found on recent field trips. The neotropical rain forest and the montane cloud forest, although rapidly disappearing, are still largely unexplored.

CHAPTER 18: REPRODUCTIVE CHARACTERS

The present morphological survey of the neotropical Gesneriaceae reveals a measure of the evolutionary plasticity of this plant group, especially at the floral level. The comparatively rapid floral evolution of the Gesneriaceae is paralleled and surpassed only by that of the Orchidaceae, now recognized as the largest flowering plant family. Speciation in these groups apparently comes about mostly through changes in floral structure and concomitant adaptation to different modes of pollination. The methods of zygote (seed) dispersal in both of these families are genetically fixed and constant, because they are successful: the neotropical Gesneriaceae with berries and fleshy display capsules are distributed over wide areas by bats and birds, and the minute seeds of the capsular fruits of the Orchidaceae and the Asiatic epiphytic Gesneriaceae (*Aeschynanthus*, *Agalmyla*, etc.) are disseminated by wind and storm. The change from axile to parietal placentation in both of these advanced families appears to increase the number of zygotes available for dispersal (see Burtt, 1970: 2). In contrast to the constancy of zygote dispersal, both families have a "strategy" of flexibility and variation in gamete (pollen) dispersal. In fact, the greatest asset of these families at the apex of angiosperm evolution is precisely their plasticity at the floral level. A typical flower in these families is adapted for one particular species of pollinator. A shift from one pollinator to another appears to be the most prevalent method of speciation. Seemingly major changes in the shape, color, and scent of the corolla are here brought about by minor genetic restructuring (Clayberg, personal communication). A single genus in these families may therefore contain species with many radically different corolla shapes. But there are also series of genera without any decisive differences in floral features: the *Achimenes-Eucodonia-Gloxinia-Smithiantha* complex, and the *Alsobia-Episcia-Nautilocalyx-Paradrymonia* complex. There are usually no (or only weak) genetic barriers between the species of a genus in the Gesneriaceae and Orchidaceae: the pollinators provide the specific isolation. Both families are known for their showy or spectacular flowers (and for their artificial hybrids), but this proliferation of floral shapes and colors is actually only an indication of the unending flexibility in their "strategy" of gamete dispersal. That is, after all, the only function of these flashy corollas.

The key to a more natural classification of the Gesneriaceae is thus a better understanding of their floral evolution and their pollination biology. A reevaluation of the floral characters, a knowledge of the fruit characters, and a stronger emphasis on vegetative features appear to solve the perennial systematic problems among the neotropical Gesneriaceae.

The positon of the inflorescence on the plant appears to have some systematic significance in the Gesnerioideae. Both axillary partial florescences and terminal partial florescences occur in this subfamily, but terminal, partial florescences are found only in the tribe Gloxinieae. Even in this tribe the axillary partial florescences predominate, but terminal partial florescences (actually consisting of whole systems of partial florescences, either unreduced as thyrses or reduced as racemes) characterize the genera *Anodiscus*, *Koellikeria*, *Lietzia*, and *Smithiantha.* Both axillary and terminal partial florescences are found in the genera *Achimenes*, *Gloxinia*, *Diastema*, *Heppiella*, *Kohleria*, *Paliavana*, and *Sinningia*, and in some species of these genera there are also intermediates between these categories.

The erect axillary partial florescences of *Corytoplectus* contrast with the pendent partial florescences in *Alloplectus* from which *Corytoplectus* was recently split. Congested partial florescences (with the peduncle shortened or absent) characterize the genera *Oerstedina* and *Rufodorsia.* The length of the pendent pedicel gave the genus *Nematanthus* ("thread-flower") its name, but this character lost its generic value when this genus was united with the short-pedicelled genus *Hypocyrta.*

The calyx of the Gesnerioideae offers hardly any characters for generic diagnosis. Since winged calyx lobes were the sole feature separating *Pterobesleria* from *Besleria*, these taxa have been united. The connate calyx lobes of *Chrysothemis*, however, correlate well with other generic characters of this genus: presence of tubers, a distinct growth habit, succulent stems, corollas of similar shape and color. A large and "leafy" calyx was once considered an earmark of the genus *Drymonia*, since the type species, *D. calcarata* Mart. [= *D. serrulata* (Jacq.) Mart.] has large calyx lobes. Today the key feature of this large genus is the specialized androecium, unique in the plant kingdom. The shape and size of the calyx varies from species to species; in fact the calyx is often quite small and reduced. This feature is now of diagnostic value at the species level only. A similar case may be made for the genus *Nautilocalyx*, where the fancied resemblance of the calyx (or bracts of the partial florescence?) of the type species to a "nautilus" is not representative of the majority of the species in this genus.

Even after a reevaluation of the corollas as a diagnostic feature in the Gesnerioideae, this showy floral structure often retains its importance as an indicator of generic and sectional relationship -- provided the corolla is understood from the perspective of the biology of pollination.

There are apparently three different floral "strategies" at work in the evolution of the Gesnerioideae:

1. A single genus may contain species with two or more quite different corolla shapes and colors because of basic differences in the mode of pollination. Examples are the genera *Achimenes*, *Besleria*, *Capanea*, *Dalbergaria*, *Drymonia*, *Episcia*, *Gasteranthus*, *Gesneria*, *Gloxinia*, *Kohleria*, *Neomortonia*, *Paradrymonia*, *Pentadenia*, and *Trichantha*.

2. The same type of corolla may also occur in two or several distinct genera. This does not necessarily imply a close affinity of the taxa, but merely that they adapted to the same type of pollinator. The similar corollas in these genera are thus a case of parallel evolution. Examples are the tubular red corollas in *Heppiella*, in some species of *Kohleria*, and in *Moussonia*, all pollinated by hummingbirds. A similar infundibular-tubular, whitish corolla is found in the genera *Achimenes*, *Alsobia*, *Episcia*, *Nautilocalyx*, *Neomortonia*, *Paradrymonia*, and *Sinningia*, with female Euglossine bees as pollinators. The same type of rotate white corolla characterizes such diverse genera as *Bellonia*, *Napeanthus*, *Niphaea*, and *Phinaea*, where even the latter two taxa differ in base chromosome number and in details of the androecium. Red or yellow *Columnea*-type corollas with a galea occur in such genera as *Asteranthera*, *Columnea*, *Dalbergaria*, *Pentadenia*, *Sinningia*, *Trichantha*, and in other families of the Tubiflorae.

3. In some genera of the Gesnerioideae the shape of the corollas has remained remarkably constant, indicating the employment of only one type of pollinator. Examples are the genera *Alsobia*, *Bellonia*, *Bucinellina*, *Chrysothemis*, *Columnea*, *Cremosperma*, *Diastema*, *Heppiella*, *Monopyle*, *Moussonia*, *Napeanthus*, *Niphaea*, *Phinaea*, and *Rufodorsia*. The reason for this constancy in floral shape is still unknown.

However spectacular or modest the corolla of a gesneriad may be, from now on this plant organ can be interpreted and categorized meaningfully by students of this family only in the context of the phenomena of pollination and gamete dispersal.

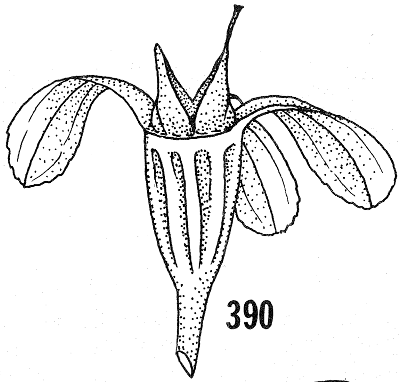
The androecium of the Gesnerioideae and the Coronantheroideae is, with a few exceptions, rather generalized. The filaments are usually joined to the base of the corolla tube, but adnate to the tube for a few millimeters in various species of the episcioid genera and in species of *Gesneria.* This type of adnation appears to have generic significance only in *Cremosperma*, where the filaments are adnate for about half of the length of the corolla tube. The connective tissue between the two anther cells is typically narrow, and the dehiscence is usually by longitudinal slits. The anther cells are confluent in almost all genera of the tribe Beslerieae, and predominantly parallel, or connivent in the other tribes of the Gesnerioideae. In contrast to earlier classifications, there is less reliance on this character in the present scheme. Of diagnostic value is the thecae dehiscence by pores, either basal, central, or apical, in *Bellonia*, *Drymonia*, in most species of *Codonanthe*, and in several species of *Nautilocalyx* and *Paradrymonia.* The latter has also several species with bearded anther cells. The number of stamens is usually four. The presence or absence of a rudimentary fifth structure, the staminode, appears to be without systematic value. Significant, however, is the occurrence of five stamens in *Bellonia*, *Depanthus*, and in several species of *Napeanthus* (Tables 9 & 10). As in some genera of the Old World Gesneriaceae, there are only two stamens in *Sarmienta* from Chile. The two or four anthers are typically coherent into a rectangular, square, or stellar formation, but sometimes they are coherent into pairs, and still less frequently they are free. The specialized coherence of the thecae into a "salt shaker" formation in *Drymonia*, the earmark of this genus, is unique among the angiosperms. The broad connectives of the stamens of *Codonanthe* are another specialization, a character of generic value.

The shape and texture of the pollen grains is a new and important feature in the catalogue of diagnostic characters. A preliminary pollen study of the Gesnerioideae (Williams, 1978) and another study in progress indicate that gesneriad genera may be recognized by the shape and texture of their pollen. The oblong-elliptic (prolate) pollen of *Columnea*, for instance, differs sharply from the pollen of the other genera in the *Dalbergia* alliance.

The nectary is one of the most important features in the classification of the New World Gesneriaceae. This should not be surprising, since this organ is of vital importance in the phenomenon of gamete dispersal in the Gesneriaceae. This plant family has the most highly developed floral nectaries among the Tubiflorae. The neutral term "disk," often used by botanists for this structure, does not do justice to it, since it does not convey its purpose or function. The nectary character is useful from the subfamilial level down to the sectional level. In the subfamily Gesnerioideae, the nectary is essentially free from the wall of the ovary, but in the subfamily Coronantheroideae the nectary is embedded like a pillow into the ovary wall, and may be an outgrowth of it (Figure 62). A ring-shaped nectary characterizes the tribe Gesnerieae, two connate dorsal glands earmark the great majority of the genera in the tribe Episcieae, while in the tribe Napeantheae the nectary is absent. The shape of the nectary is usually a generic character in the Gesnerioideae, and a sectional feature in the complex genera *Gloxinia* and *Sinningia.* The most primitive nectary in the tribe Episcieae, five separate glands, occur in *Pentadenia*, and this feature is thus the key character in this genus.

The position of the ovary is still a vital character in the classification of the Gesnerioideae, but the value of this feature is less absolute than in earlier classifications. In Fritsch's scheme (1893-94), all taxa of the subfamily Gesnerioideae had a half-inferior to completely inferior ovary. This same subfamily now contains three tribes with a completely superior ovary (Episcieae, Beslerieae, and Napeantheae). The ovary in the Gesnerieae is half-inferior to completely inferior, and that of the Gloxinieae likewise, except that this tribe also contains genera and species with almost completely superior ovaries (*Capanea*, *Sinningia barbata*, *S. richii*, etc.), and the monotypic genus *Lembocarpus* with a completely superior ovary (Table 7). The tribe Gloxinieae thus contains the whole range of ovary positions, from completely superior to completely inferior (*Monopyle*, *Solenophora*). Such a variation may be expected in a plant family characterized by evolutionary plasticity. The ovary position in the subfamily Coronantheroideae is superior (Table 7).

The fruit of the Gesnerioideae is now better known than in previous classifications and has become a valuable tribal, generic, and subgeneric character. The tribes Gesnerieae, Gloxinieae, and Napeantheae contain no berries, only dry capsular fruit. This statement has to be modified, however, for some species in the versatile tribe Gloxinieae in which the capsule is somewhat fleshy in the first few days after dehiscence (Figures 390-393). Most, but not all of these species have an inferior or nearly inferior ovary, such as species of *Monopyle*, *Solenophora*, *Diastema*, *Kohleria amabilis*, *Gloxinia dodsonii*, *G. lindeniana*, and *Sinningia speciosa*. The fruit in the tribe Episcieae is either a fleshy capsule (subdivided into a more or less cup-shaped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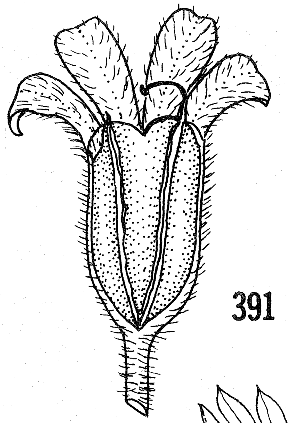
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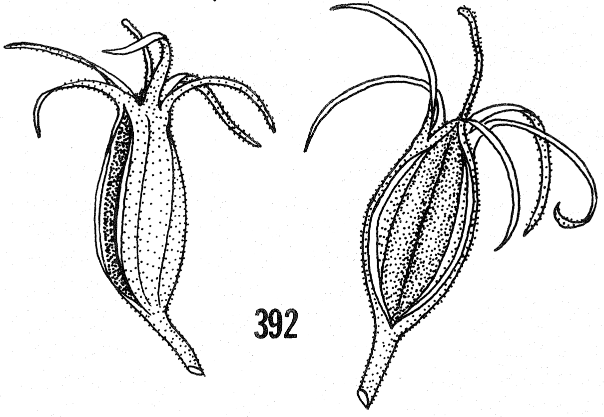
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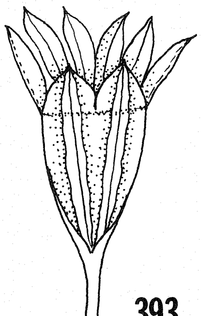
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Figures 390-393: Capsular fruit in the tribe Gloxinieae. Figure 390: *Gloxinia perennis* (L.) Fritsch, representing a typical bivalved, dry fruit, dehiscing above the hypanthium. Figures 391-393: Rare, univalved, fleshy capsules, dehiscing the total length of the fruit. Figure 391: *Gloxinia lindeniana* (Regel) Fritsch. Figure 392: *Monopyle grandiflora* Wiehler; two lateral views. Figure 393: *Diastema scabrum* (Poeppig) Walpers.

capsule and a display capsule) or a berry. The tribe Beslerieae contains three types of fruit, a dry capsule, a fleshy capsule, and a berry.

Several genera were recently segregated or established (Wiehler, 1973b; 1975g; 1977c) because of differences in fruit type: *Corytoplectus* and *Cobananthus* were separated from *Alloplectus*, and *Gasteranthus* divided from *Besleria*. Subgenera were created within two genera to accommodate differences in fruit type. The predominantly berry-fruited genus *Codonanthe* contains a few species with a pointed, fleshy, capsular fruit (=subgenus *Codonanthella*), and *Drymonia*, an epiphytic genus known for its fleshy, capsular display fruit, has also a few terrestrial species with a berry (subgenus *Drymoniella*). In both of these genera the peculiar androecial characters, present also in the subgenera, carried more weight in maintaining generic unity than the fruit characters.

Generic value has been assigned to the shape of the fruit, as in the difference between the display capsule in *Alloplectus* and the cup-shaped capsule in *Nautilocalyx*. In *Monopyle* the inferior capsule is quite elongated, in *Dalbergaria* the berry is pointed, which is not the case in *Columnea*, and in *Bucinellina* the berry is depressed.

The dehiscence of the capsule appears to have little systematic value in the Gesnerioideae, since it is predominantly loculicidal. Some species of *Napeanthus* have capsules with both loculicidal and septicidal dehiscence (= four valves), and the dehiscence in *Anetanthus* is septicidal.

There is presently little published information on seed morphology in the Gesnerioideae and Coronantheroideae (cf. Ivanina, 1965, 1966, 1967). This character needs to be more fully exploited for its systematic value. We are looking forward to the publication of the current investigation undertaken by Helen Beaufort-Murphy.

CHAPTER 19: VEGETATIVE CHARACTERS

A reevaluation of floral characters above the specific level brings about a greater reliance on vegetative features. Burtt (1963, 1970) showed the usefulness of seedling morphology at the subfamilial level: the Cyrtandroideae of the Old World have cotyledons that grow unequally after germination (anisocotyly), while in the Gesnerioideae of the New World (and in the austral Coronantheroideae) the seed leaves remain equal. Iso- and anisocotyly do not appear to be merely arbitrary taxonomic characters even though they have never before been used for higher plant categories. In the Cyrtandroideae anisocotyly or the occurrence of continued growth in one cotyledon (Burtt, 1970: 1) seems to have functional significance. A rapidly enlarging (accrescent) cotyledon compensated for the lack of endosperm in the small and numerous seeds of the Cyrtandroideae; the additional photosynthetic tissue provides the energy for the appearance of the shoot primordium. The accrescent cotyledon together with the suppression of the plumule produces such morphological curiosities as unifoliate plant species. In *Monophyllaea* and in species of *Streptocarpus* the entire photosynthetic tissue consists of a single, tremendously enlarged cotyledon (to 1 m long). This is anisocotyly developed successfully to its final potential. The concept of the phyllomorph, a new gesneriaceous growth pattern in plant morphology, was outlined by Jong (1970, 1973) and by Burtt (Hilliard & Burtt, 1971). Anisophylly occurs in many genera of the Gesnerioideae; it is a key character in the genera *Codonanthopsis*, *Dalbergaria*, and *Monopyle*.

The decussate leaf arrangement is the norm in the Gesnerioideae. Alternate leaves characterize the genus *Reldia* and predominate in the genus *Gesneria.* The inflorescence in both genera, however, has a decussate bract arrangement, indicating the secondary or derived origin of alternate phyllotaxy in the Gesnerioideae. The reverse situation has occurred in the genera *Koellikeria* and *Smithiantha* where the leaves remain decussate and the raceme-like terminal florescences have evolved, for reasons still not understood, into an alternate bract arrangement. It appears probable that the alternate leaf arrangement in the Gesnerioideae arose at least in primitive, rosette-forming stock of *Gesneria* via anisophylly. The presence of a few remnant species with decussate leaves in *Gesneria* does not therefore warrant their exclusion from the genus, especially when the same type of leaf arrangement occurs in all species of *Gesneria* on the inflorescence.

The absence of bracts on the inflorescence, another feature whose functional significance remains obscure, has been employed in this classification as the primary uniting factor for the taxa of the tribe Beslerieae. All genera of the Beslerieae are without bracts on the inflorescence. The process of bract loss through a reduction of the compound, bracteate inflorescences in the tribes Episcieae, Gloxinieae, and Napeantheae to a single (sometimes minute-bracted) but often ebracteate, epedunculate flower (or twin flowers), found in advanced species of these tribes, does not seem to explain the loss of all bracts on the well-developed, pedunculate, compound inflorescences of the genera of the Beslerieae.

Leaf venation in the Gesnerioideae has not undergone any special development, with one exception. The venation is usually pinnate with the lateral veins ending before reaching the margins. But in the Brazilian genus *Goyazia* the leaves have a pericraspedodromous type of venation (Wiehler, 1976a:394), with the lateral veins reaching and completely bordering the margin of the leaf. The diagnostic value of such an easily discernible feature is obvious.

Plant habit has now proven to be an excellent diagnostic character for several genera. Examples are the stolons in *Alsobia* and *Episcia*, the rosette habit of *Napeanthus* and most species of *Paradrymonia*, the fern-frond-like shoots of all species of *Dalbergaria*, the already cited anisophylly of the genera *Codonanthopsis*, *Dalbergaria*, and *Monopyle*, the succulent stems and petioles of *Nautilocalyx*, the vining habit of most species of *Drymonia*, the shrubby habit of *Bellonia*, (most species of) *Besleria*, *Paliavana*, and *Vanhouttea*, the herbaceous habit of most other genera, and the tree habit of such genera as *Lenbrassia* and *Negria.*

Adaptive features to periodical dry seasons in the natural habitat of certain taxa, used in past classifications, are still useful in generic delimitations. Underground tubers, which are enlargements of the main axis or stem at the hypocotyl level, are present in all species of *Chrysothemis*, in the monotypic genera *Lembocarpus* and *Lietzia*, in most (or all?) species of the large genus *Sinningia*, and in some species of *Drymonia*, *Nautilocalyx*, and *Rhoogeton.* Underground scaly rhizomes, which are stolon-like lateral shoots of the basal leaf axils (Troll, 1964:545), are still good generic markers for the taxa listed in Table 3. But in the Gesneriaceae one also has to be aware of the exceptions. The type section of *Sinningia* is supposedly without tubers, and some species of *Heppiella*, *Monopyle*, *Kohleria*, and *Parakohleria*, growing in very wet native habitats, were found to be (temporarily?) without scaly rhizomes.

Adaptive features to epiphytism which have diagnostic value at the generic level include the presence of a leaf hypodermis in all species of *Nematan-*

thus, versus its absence in *Alloplectus*. These two taxa have been confused in the past since both have similar corollas and similar types of fruit. A hypodermis occurs in most epiphytic species of the Gesnerioideae, but it is absent in the few epiphytic species of *Alloplectus*, for instance in *A. cristatus* and *A. hispidus*. *Alloplectus* is primarily a terrestrial genus. The presence or absence of water-storage tissue in the leaf distinguishes also the epiphytic genus *Alsobia* from the terrestrial genus *Episcia*.

The epidermis of the leaf has several features of taxonomic importance. In most species of the tribes Episcieae and Napeantheae the cells of the abaxial epidermis are without sinuation, while the majority of the species in the tribes Gloxinieae and Beslerieae have wavy abaxial cell contours on the lower leaf surface.

The stomatal complexes in the subfamily Gesnerioideae are predominantly of the aniso-mesogenous type, in contrast to the anomo-mesoperigenous or para-mesogenous stomata in the subfamily Coronantheroideae. Stomatal mounds are found in the tribes Gloxinieae and Gesnerieae, but are absent in the tribes Beslerieae, Episcieae, Napeantheae, and in the subfamily Coronantheroideae. Cell sinuation and stomatal types have not been employed in the following key to the tribes and genera, but these features may serve as an auxiliary in plant identification.

The presence of stomatal aggregations into "islands," however, is a welcome and useful marker for *Gasteranthus*, *Napeanthus*, and *Reldia*. The same feature also occurs in many species of the genus *Gesneria*, but is only of specific value in this taxon.

Our study of trichomes indicates that leaf hairs appear not to have any systematic value above the species level in the Gesnerioideae.

Vascular anatomy furnishes several good systematic characters for the Gesnerioideae at the tribal level. The tribe Episcieae is distinguished by 3:3 trilacunar nodes with split lateral strands, while the rest of the tribes of the Gesnerioideae and the single tribe of the Coronantheroideae have 1:1 unilacunar nodes. Nodal anatomy thus offers a clear-cut separation between taxa in the tribes Beslerieae and Episcieae, often confused in the past. The crescent (or annular) shape of the vascular bundles of the petiole as seen in cross-section is a good indicator of tribal affinity (Figure 85). The thick configurations of the species in the tribe Gesnerieae are especially noteworthy and unparalleled.

CHAPTER 20: CYTOGENETIC CHARACTERS

Although chromosome numbers are impractical for use in generic keys, their establishment has to rank as a great contribution to the classification of the Gesneriaceae. Table 2 shows the distinct chromosome number series for each tribe: Episcieae, x = 8, 9; Gloxinieae, x = 10, 11, 12, 13; Gesnerieae, x = 14; Beslerieae, x = 16; Napeantheae, still unknown.

The second important discovery was the constancy of the chromosome number for each genus (Table 2). This knowledge brought about a greater assurance for the traditional and new generic delimitations. It provided also the ultimate justification for uniting some genera (i.e., *Hypocyrta* and *Nematanthus*), and to divide others containing morphologically discordant elements (i.e., *Kohleria* and *Moussonia*).

Related to the idea of the constancy of a chromosome number for each genus is the assumption that in the Gesnerioideae there is only one base chromosome number per genus. This concept appears to be the best and safest solution to deal with such closely related genera of the tribes Episcieae and Gloxinieae. The alternative would be the establishment of unwieldy supergenera with vague boundaries. The small genus *Eucodonia* ($x = 12$) would probably not have been segregated from *Achimenes* ($x = 11$), were it not for the knowledge of the different base chromosome numbers, and the sterility of the hybrids of these taxa. *Eucodonia* was therefore separated from *Achimenes* for the sake of consistency in taxonomic treatment, with differences in indument as the only obvious, distinct character between the genera. But the same may be said for such look-alike genera as *Niphaea* ($x = 11$) and *Phinaea* ($x = 13$), *Moussonia* ($x = 11$) and *Kohleria* ($x = 13$), *Achimenes* ($x = 11$) and *Gloxinia* ($x = 13$), and *Alloplectus* ($x = 9$) and *Nematanthus* ($x = 8$). Had *Eucodonia* remained in *Achimenes*, even as a separate section or subgenus, there would have been little justification for maintaining *Smithiantha* ($x = 12$) as a genus separate from *Achimenes.* The hybrids among the latter three taxa are also sterile.

Along the same line of reasoning, the sterility of intergeneric hybrids (in the sense of the present generic classification), and the fertility of hybrids whose parents were once in separate genera (*Gloxinia* × *Seemannia; Episcia* section *Skiophila* × *Nautilocalyx; Hypocyrta* × *Nematanthus; Sinningia* × *Rechsteineria*) were often used as additional evidence for the separation or unification of genera. This does not imply, however, that all interspecific hybrids within a given genus of the new classification have to show various degrees of fertility, for some of these genera harbor several evolutionarily isolated sections or species within their boundaries. In such cases hybrids may be sterile, inviable, or may not be able to be established. The hybridization record for the Gesnerioideae indicates, however, that the majority of the interspecific hybrids reveal varying levels of fertility, and that all intergeneric hybrids are sterile. The recent establishment of apparently partially fertile hybrids between *Codonanthe* and *Nematanthus* (Saylor, 1978) is a rare exception to the rule.

PART 3

THE SUPRAGENERIC DELIMITATIONS IN THE GESNERIOIDEAE

CHAPTER 21: THE SUBFAMILY GESNERIOIDEAE

The present delimitation of the subfamily Gesnerioideae is the equivalent of the early concept of the family Gesneriaceae. The establishment of this family has been traced back to the Belgian botanist Barthelemy Charles Joseph Dumortier (b.1797, d.1878). In his *Commentationes botanicae*, 57, 1822, he published this group as a family, spelling the name "Gessneridiae" (= Gesneriaceae, nom. conserv.), and listing with it only the type genus *Gesneria* L. ("Gessneria"). He also added the cryptic reference: "Rich. et Juss. ann. mus. 5, p. 428."

This citation refers to a publication by the French botanist Antoine Laurent de Jussieu (b. 1748, d. 1836) in the *Annales du muséum national d'histoire naturelle*, volume 5, 1804. On pages 427 and 428, in a discussion on the distinguishing features among plant families, Jussieu stated that the German physician and botanist Joseph Gaertner (b. 1732, d. 1791) in his important publication *De fructubus et seminibus plantarum* (1788-1792) had found that the genus *Gesneria* differed from the family Campanulaceae by the unilocular fruit and parietal placentation. The same situation had been discovered in the genera *Besleria*, *Columnea*, *Achimenes*, and *Gloxinia*, and Jussieu suggested that *Paliavana*, *Orobanche*, and *Cyrtandra* may also belong to this group. The crucial passage is on page 428, with Jussieu commenting that one should not discount the opinion of Louis Claude Marie Richard (a French botanist, b. 1754, d. 1821), that this group constitutes a separate family, distinct by the unilocular fruit, parietal placentation, a fleshy nectary, the stamens adnate to the corolla, and by the number of stamens (usually 4) differing from the number of corolla lobes (=5).

The Cyrtandraceae were established as a separate, paleotropical family by the British physician and botanist William Jack (b. 1795, d. 1822) in a posthumous publication in 1825. Most of the classifying botanists subsequent to Dumortier regarded the neotropical Gesneriaceae and the paleotropical Cyrtandraceae as separate families: Martius (1829), Bartling & Wendland (1830), DeCandolle (1839), Colla (1849), Decaisne (1850), Hanstein (1854-1865), and Oersted (1858). George Don (1838) and Endlicher (1839) were the only early exceptions. Both treated the two groups as subfamilies (in present-day terminology) under the family name Gesneriaceae. George Bentham (b. 1800, d. 1884) was the first "modern" botanist to unite both families, preliminarily in 1846, completely in 1876, and his classification in the *Genera plantarum* has been generally accepted thereafter (Table 28). However, by applying ovary position as the primary criterion for the division of taxa, in hindsight Bentham brought about an unfortunate mixing of the tribes and genera: the majority of the neotropical Gesneriaceae, all those with a superior ovary, were shifted to the Cyrtandroideae (or to the tribe Cyrtandreae, in Bentham's system). In the last classification of the Gesneriaceae, in Engler & Prantl's *Pflanzenfamilien* (1893-94), Fritsch merely changed the ranks of the suprageneric structure of Bentham's system, including the nomenclatural adjustment to incorporate the long-neglected type genus *Gesneria* L. (versus *Gesnera* Mart. = *Rechsteineria*), as proposed by Kuntze in 1891; otherwise Fritsch followed Bentham's scheme very closely.

In Fritsch's concept, then, the subfamily Gesnerioideae comprised a comparatively small aggregate of neotropical genera, all with a semi-inferior or completely inferior ovary, grouped into six tribes: the Bellonieae, Gloxinieae, Kohlerieae, Sinningieae, Solenophoreae, and Gesnerieae. Since the first five tribes are now united into a single tribe (see below), the Gesnerioideae in Fritsch's system actually consisted of only two tribes (as here delimited), the Gesnerieae and the Gloxinieae. All American genera of Gesneriaceae with a superior ovary belonged to the subfamily Cyrtandroideae.

The most radical change in the classification of the Gesneriaceae as here presented, when compared with Fritsch's system of 1893-94, has taken place on the tribal and subfamilial levels. Burtt's revision of the subfamily Cyrtandroideae in 1963 (Table 29) also represented a major step toward a more natural classification of the New World Gesneriaceae. He defined the two subfamilies on the basis of seedling structure, with anisocotyly as the distinctive trait of the Cyrtandroideae, and isocotyly characterizing the rest of the Gesneriaceae, or the now much enlarged Gesnerioideae. Burtt's ingenious arrangement made the Cyrtandroideae again an exclusively Old World group (with the single exception of *Rhynchoglossum azureum*), and shifted all neotropical tribes of Fritsch's system, the Anetantheae, Beslerieae (minus the Old World genera), Columneeae (now Episcieae), and the genus *Napeanthus*

TABLE 28: CLASSIFICATION OF THE FAMILY GESNERIACEAE BY BENTHAM (1876)

Ordo Gesneraceae*

Tribus I. Gesnereae	
Subtribus 1. Bellonieae	*Bellonia, Niphaea, Phinaea, Monopyle, Anodiscus*
Subtribus 2. Gloxinieae	*Gloxinia, Achimenes, Naegelia, Heppiella, Seemannia, Koellikeria, Dicyrta*
Subtribus 3. Eugesnereae	*Diastema, Isoloma, Houttea, Paliavana, Campanea, Gesnera, Sinningia, Solenophora*
Subtribus 4. Pentarhaphieae	*Pentarhaphia, Rhytidophyllum*
Tribus II. Cyrtandreae	
Subtribus 1. Columneeae	*Tussacia, Episcia, Drymonia, Alloplectus, Trichantha, Columnea, Nematanthus, Hypocyrta, Codonanthe*
Subtribus 2. Eucyrtandreae	*Asteranthera, Negria, Rhabdothamnus, Fieldia, Mitraria, Sarmienta, Cyrtandra*
Subtribus 3. Aeschynantheae	*Aeschynanthus*, etc.
Subtribus 4. Beslerieae	*Besleria, Rhynchotechum*, etc.
Subtribus 5. Didymocarpeae	*Napeanthus, Klugia, . . . Anetanthus*, etc.

* All subtribes are listed here, but the majority of the Old World genera are omitted in the last three subtribes.

from the Cyrtandroideae back to the Gesnerioideae. Also included in this major shift was the austral tribe Coronanthereae, discussed below, which is now considered to be a separate subfamily. I agree fully with Burtt's delimitation of the two major subfamilies, for it brings all neotropical Gesneriaceae (except *Rhynchoglossum azureum*) together into a single, more natural unit. The three subfamilies are now also geographical units. Ovary position, although still a vital taxonomic character, has lost its importance on the subfamilial level in the Gesneriaceae, and on lower levels as well. The earlier static concept of ovary position in the Gesneriaceae has been replaced by the dynamic view that in many taxa of the family the position of the ovary has "recently" shifted from superior to partially inferior to completely inferior. This view leaves room for the inclusion of a few taxa with a superior ovary in the tribe Gloxinieae, which is characterized by an inferior or semi-inferior ovary.

On the basis of a fine carpological study of the family Gesneriaceae, the Russian botanist L. I. Ivanina (1965, 1966, 1967) recently proposed a new classification of the whole family, including a new subfamily Episcioideae which contains two tribes, the Episcieae and the Columneeae (Table 30). While Ivanina's morphological study remains an important addition to the store of knowledge of the Gesneriaceae, it seems questionable today that a single feature, the fruit (= carpel structure and seed morphology) can be successfully used singularly to reconstruct the suprageneric framework of such a complex family as the Gesneriaceae. The application of the carpological method by itself may be of value to the systematics of other, more "stable" plant families, but for the plastic, or evolutionarily flexible Gesneriaceae as many traits as are possibly available have to be employed to arrive at a satisfactory classification. The fruit is only one of the many vital characters in the systematics of this family. Taking all available diagnostic features into consideration, the Episcieae (or Episcioideae) stand indeed very isolated within the neotropical Gesneriaceae, but so do also each of the other groups, the Gloxinieae, Beslerieae, Gesnerieae, and Napeantheae. There are no bridging genera or species among them; in fact, all the groups of the neotropical Gesneriaceae appear to be about equally distantly related one to another. Overemphasizing a single feature can lead to some strange associations or divisions, such as the inclusion of the genera *Besleria*, *Pterobesleria*, *Tylopsacas*, and *Napeanthus* in the tribe Episcieae, or the separation of *Hypocyrta* and *Nematanthus*, today accepted as a single genus (Handro, 1964; Moore, 1973c; Wiehler, 1970, 1972b), into different tribes (Table 30). Comments on the tribal segregation of *Rechsteineria* and *Sinningia*, and on the establishment of the tribe Rechsteinerieae follow below. There is also the curious placement of the Asiatic genus *Jerdonia* (from southern India) in the otherwise completely American tribe Episcieae. This is probably better interpreted as a case of parallel evolution of carpel structure within dfferent taxa than an indication of actual affinity of *Jerdonia* to the Episcieae. Burtt (1977) transferred *Jerdonia* to the Scrophulariaceae. This example, and the cases of the recently merged genera cited above, highlight the fallibility of a one-character-system. Nonetheless, aside from some of the taxonomic implications deducted from too meager evidence, Ivanina's carpological study remains a valuable contribution to the knowledge of a tropical plant family.

In the present classification, the subfamily Gesnerioideae, with about 54 genera and over 1300 species, encompasses all of the New World Gesneriaceae, with the exception of a single American species of the Asiatic genus *Rhynchoglossum*, and the Chilean, temperate-zone, monotypic taxa *Asteranthera*, *Mitraria*, and *Sarmienta*, all of which are spatially far removed from the neotropical members of the family.

Subfamily Gesnerioideae

first established by Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4 (3b): 142, 143. 1893-94.*

Subfamily Columneoideae Morton, nomen nudum, in New Gesneriaceae from Panama, Ann. Missouri Bot. Gard. 29: 35. 1942.

Subfamily Episcioideae (Endl.) Ivanina, Bot. Žurn. (Moscow & Leningrad) 50(1): 37, 42. 1965; Notes Roy. Bot. Gard. Edinburgh 26 (4): 394, 401. 1966 (English translation).

Type genus: *Gesneria* L.

The subfamily Gesnerioideae is here emended to include the following characters: herbs, subshrubs, shrubs, vines, rarely trees, with isophyllous cotyledons. Nodal structure one-trace unilacunar, three-trace trilacunar with split lateral bundles, or rarely multi-lacunar. Leaves decussate, verticillate, or secondarily alternate. Stomata only on the abaxial surface of the leaf, with the stomatal complexes predominantly of the aniso-mesogenous type. Inflorescence typically a pair-flowered, single or compound cyme of 4-10 or more flowers, sometimes reduced to 1-2 epedunculate flowers. Corolla zygomorphic or secondarily actinomorphic, tubular, campanulate, or

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* All previous equivalents of the name Gesnerioideae or Gesnerieae were based on the genus *Gesnera* Mart. (= *Rechsteineria* Regel), not on *Gesneria* L.

TABLE 29: THE TRIBES AND GENERA OF THE SUBFAMILY CYRTANDROIDEAE IN BURTT'S CLASSIFICATION OF 1963, 1977, 1978 AND PERSONAL COMMUNICATION, AUGUST 1979

(Base chromosome number at left of each genus; number of species in each genus at right)
4 tribes, 63 genera, over 1500 species
Distribution: Old World, chiefly in tropics but 1 species in Neotropics.

1. TRIBE CYRTANDREAE C. B. Clarke

17	*Cyrtandra* J. R. & G. Foster	600+
10	*Rhynchotechum* Blume	12
	Sepikaea Schlechter	1

2. TRIBE TRICHOSPOREAE Fritsch

	Micraeschynanthus Ridley	1
	Oxychlamys Schlechter	1
15, 16	*Aeschynanthus* Jack	80+
	Agalmyla Blume	50+
	Lysionotus G. Don	13
	Loxostigma C. B. Clarke	4

3. TRIBE KLUGIEAE Fritsch

10,21,27	*Rhynchoglossum* Blume	12
	Epithema Blume	4
10	*Monophyllaea* R. Brown	32
	Whytockia W. W. Smith	2
	Loxonia Jack	3
	Stauranthera Bentham	4

4, TRIBE DIDYMOCARPEAE Endlicher

10	*Conandron* Siebold & Zucc.	1
	Tengia Chun	1
20,36	*Ramonda* L. C. Richard	3
	Bournea Oliver	1
	Jankaea Boissier	1
	Oreocharis Bentham	25+
	Dasydesmus Craib	1
	Tremacron Craib	5
17	*Briggsia* Craib	14
10	*Corallodiscus* Batalin	17
17	*Beccarinda* Kuntze	7
22	*Haberlea* Frivaldszky	2
	Cathayanthe Chun	1
	Isometrum Craib	6
17	*Ancylostemon* Craib	8
20	*Platystemma* Wallich	1
	Didissandra C. B. Clarke	30
17	*Hexatheca* C. B. Clarke	2
	Boeica C. B. Clarke	9
	Leptoboea Bentham	2
	Championia Gardner	1
	Anna Pellegrin	2
	Raphiocarpus Chun	1
17	*Opithandra* B. L. Burtt	5
	Petrocosmea Oliver	17
	Orchadocarpa Ridley	1
15	*Saintpaulia* H. Wendland	20
18	*Hemiboea* C. B. Clarke	8
4, 7, 9, 10, 14, 17, 18	*Chirita* D. Don	77
	Acanthonema Hooker	1
	Trachystigma C. B. Clarke	1
17	*Petrocodon* Hance	2
9, 11, 12, 14, 16, 18, 19	*Didymocarpus* Wallich	190+
	Schizoboea (Fritsch) B. L. Burtt	1
	Primulina Hance	1
18	*Trisepalum* C. B. Clarke	14
	Tetraphyllum C. B. Clarke	2
	Phylloboea Bentham	1
9	*Loxocarpus* R. Brown	15
	Linnaeopsis Engler	4
9,16, 17,18	*Paraboea* (C. B.Clarke) Ridley	55+
	Codonoboea Ridley	3
ca.16	*Ornithoboea* C. B. Clarke	10
	Rhabdothamnopsis Hemsley	1
8, 16,18	*Boea* Lamarck	17
15,16	*Streptocarpus* Lindley	132
	Platydenia B. L. Burtt	1

5. UNAFFILIATED GENUS

20	*Titanotrichum* Solereder	1

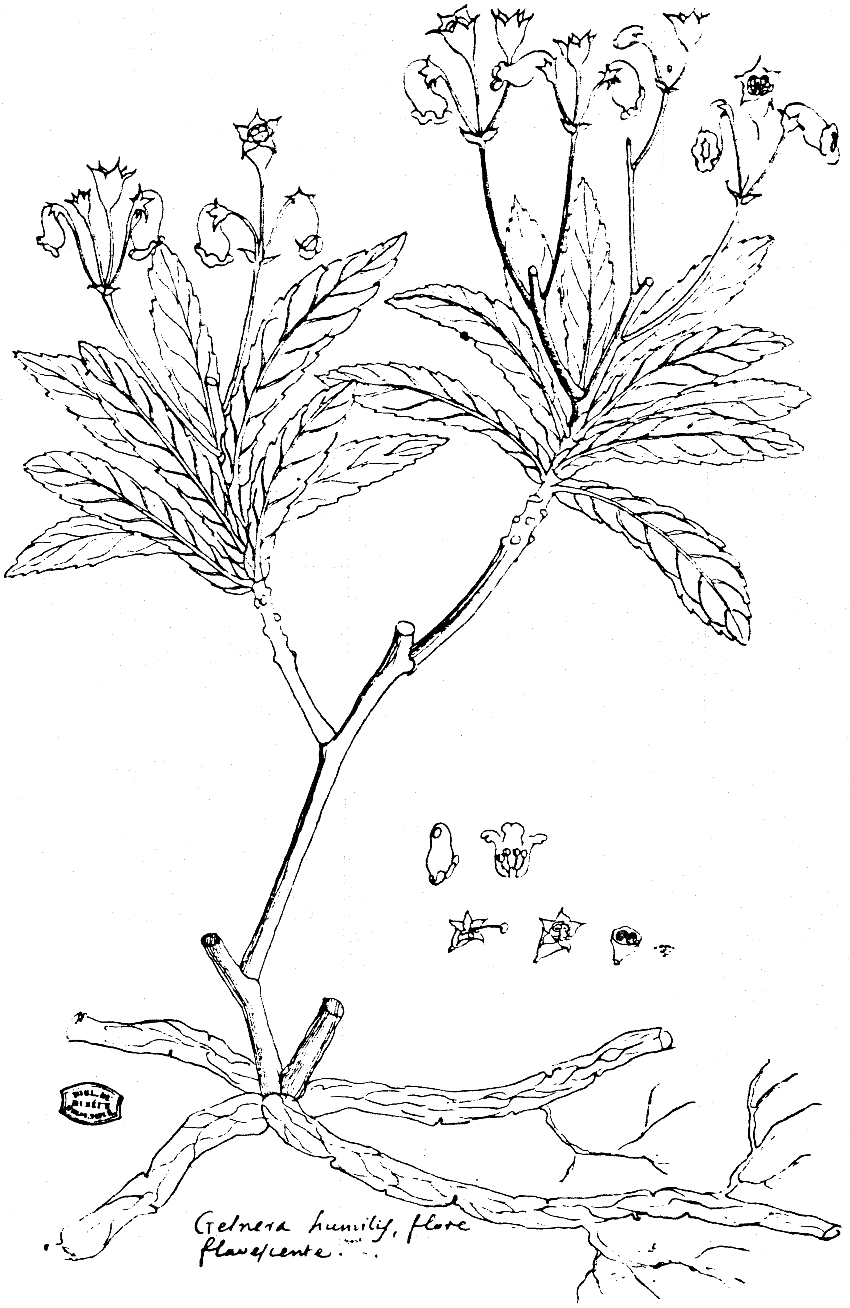

Figure 394. Charles Plumier's unpublished manuscript illustration of *Gesnera humilis, flore flavescente*, probably drawn in its native habitat in Haiti around 1690. As *Gesnera humilis* L. it became the type species of the genus *Gesneria* L. which, in turn, became the type genus of the family Gesneriaceae. Plumier's pen and ink drawings are deposited at the Bibliothèque Centrale of the Muséum National d'Histoire Naturelle in Paris. This is one of the earliest illustrations of a gesneriad. Only the inflorescence at the extreme left depicts the true nature of the gesneriaceous, pair-flowered cyme, here consisting of four flowers. The presence of a completely inferior ovary, as seen in the seed capsules, made *Gesneria* a hard-to-place taxon for the early botanists.

TABLE 30: CLASSIFICATION OF THE FAMILY GESNERIACEAE BY IVANINA (1965), BASED ON THE STRUCTURE OF THE CARPEL

Subfamily 1.	**Cyrtandroideae***	
Tribe 1.	Ramondeae	
Tribe 2.	Saintpaulieae	
Tribe 3.	Didymocarpeae	
Subtribe 1.	Conandrinae	
Subtribe 2.	Leptoboeinae	
Subtribe 3.	Roettlerinae	
Subtribe 4.	Streptocarpinae	
Tribe 4.	Trichosporeae	
Tribe 5.	Cyrtandreae	
Tribe 6.	Rhynchotecheae	
Tribe 7.	Klugieae	
Tribe 8.	Coronanthereae	*Coronanthera, Depanthus, Rhabdothamnus, ? Negria*
Tribe 9.	Mitrarieae	*Mitraria, Sarmienta, Fieldia, ? Asteranthera*
Subfamily 2.	**Episcioideae**	
Tribe 10.	Episcieae	*Episcia, Drymonia, Chrysothemis, ? Tylopsacas. Nautilocalyx, Besleria, Pterobesleria, Alloplectus, ? Diplolegnon, ? Trichantha, Hypocyrta, Napeanthus, ? Jerdonia*
Tribe 11.	Columneeae	*Columnea, Nematanthus, Codonanthe*
Subfamily 3.	**Gesnerioideae**	
Tribe 12.	Bellonieae	*Bellonia, Niphaea, Phinaea, Anodiscus, Scoliotheca*
Tribe 13.	Kohlerieae	*Diastema, Kohleria, Sinningia, Synepilaena, Pearcea, Vanhouttea, Koellieria, Smithiantha, Heppiella*
Tribe 14.	Gloxinieae	*Gloxinia, Achimenes, Seemannia, Monopyle*
Tribe 15.	Rechsteinerieae	*Lietzia, Rechsteineria, Paliavana*
Tribe 16.	Solenophoreae	*Solenophora, Hippodamia*
Tribe 17.	Gesnerieae	*Gesneria, Rhytidophyllum*

* The Asiatic genera of the subfamily Cyrtandroideae are here omitted.

secondarily rotate. Stamens 4, rarely 5 (in *Bellonia, Napeanthus*), never 2. Ovary superior, partially inferior, or completely inferior, hemiparacarpous (tribes Gesnerieae, Gloxinieae), or paracarpous (tribes Beslerieae, Episcieae, Napeantheae). Nectary at the base of the superior ovary, or at the apex of the hypanthium, but always free from the ovary wall, usually well-developed, rarely non-functional, or secondarily absent, ring-shaped or segmented into 1-5 separate (or secondarily connate) glands. Fruit a pointed or rounded, dry or fleshy capsule, with predominantly loculicidal dehiscence, or a berry. Seeds usually with endosperm. Base chromosome numbers: 8, 9, 10, 11, 12, 13, 14, and 16. Native to the neotropics.

The new tribal structure here proposed for the now much enlarged Gesnerioideae is a direct result of an intensive study of the 54 genera of the neotropical Gesneriaceae. The study has led to a more natural delimitation of many previously unwieldy genera and a simplified tribal system. Thus it became clear that the genera of five tribes in Fritsch's classification could be united into a single unit, the tribe Gloxinieae. It also became evident that there are clear-cut, decisive differences between the tribes Episcieae and Beslerieae, even though some of the taxa in these two groups show some superficial similarity (as in species of *Alloplectus* and *Besleria*). The Caribbean tribe Gesnerieae remains, as before, a very natural but isolated unit. The genera left without tribal affiliation in recent years, (Moore, 1962b; Moore & Lee, 1967), namely *Anetanthus*, *Cremosperma*, *Goyazia*, *Lembocarpus*, *Napeanthus*, *Resia*, and *Tylopsacas*, have been assigned to existing tribes, or, in the case of *Napeanthus*, necessitated the establishment of a new tribe, the Napeantheae.

CHAPTER 22: THE TRIBE GLOXINIEAE

The tribe Gloxinieae Fritsch emend. Wiehler comprises five tribes of Fritsch's system of 1893-94, the Bellonieae, Gloxinieae, Kohlerieae, Sinningieae, and Solenophoreae. The strongest evidence for uniting these tribes comes from the recent production of so-called intertribal hybrids (Tables 12, 14; Wiehler, 1968, 1976a, 1976b). The hybridization experiments indicate that the features employed to separate these tribes from one another have lost their value as tribal characters (Table 31). The "intertribal" hybrids actually involve only the Bellonieae, Gloxineae, Kohlerieae, and Solenophoreae, but the tribe Sinningieae has the same general characteristics as the other four tribes, and it is now known that the presence of tubers, the key feature for the Sinningieae, is no longer definitive. Tubers are supposedly absent from the type species of *Sinningia* and other species in the section *Sinningia.* In fact, a better knowledge of the genera of the above-cited five tribe complex has made it abundantly evident that most of the tribal characters employed by Fritsch for this group are no longer consistent. The tribe Bellonieae is marked by the absence of a nectary, but this structure is also lacking in species of the tribe Gloxinieae, namely in *Gloxinia perrennis* (L.) Fritsch, the type species of the genus, in *G. dodsonii* Wiehler, *G. planalta* Wiehler*, *G. racemosa* (Benth.) Wiehler, and in *G. reflexa* Rusby. In two other species of *Gloxinia* the nectary is present but apparently non-functional (Wiehler, 1976a). A ring-shaped nectary occurs in some species of *Capanea* in the Kohlerieae, a tribe otherwise characterized by individual glands (Table 31). Tubers are known to occur in quite unrelated genera in the neotropical Gesneriaceae such as *Chrysothemis*, *Drymonia*, *Lembocarpus*, *Nautilocalyx*, and *Rhoogeton.* Opposite leaves, a tribal character employed by Fritsch (Table 31), occur also in the tribe Gesnerieae (Wiehler, 1971; Skog, 1976).

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* *Gloxinia planalta* Wiehler, nom. nov. Based on:
Achimenes hirsuta DC., Prodr. 7: 536. 1839. [HOLOTYPE: Sylva de Manza, s.n. 1832 (G-DC)]
Gloxinia hirsuta (DC.) Wiehler, Selbyana 1(4): 386. 1976; non Lindley, Bot. Reg. 12: t.1004. 1826 = *Sinningia hirsuta* (Lindl.) Nicholson.

Further evidence for the unity of the five-tribe complex comes from a study of morphological-anatomical features and from cytological data. Strong sinuation of the anticlinal walls of cells of the abaxial epidermis of the leaf (Figure 93), the presence of stomatal mounds (Figures 176-183), and the same type of vascular crescent (Figure 85a) characterize the five-tribe complex as a whole, in contrast to the other tribes of the neotropical Gesneriaceae. No feature was found in this investigation which would set apart any of the five tribes from the others in the same complex. The diploid gametic chromosome numbers in the five-tribe complex range from $n = 10$ to $n = 13$, with $n = 13$ the most frequent value (Table 2). The same gametic chromosome numbers do not occur in the other tribes of the neotropical Gesneriaceae (Episcieae, $n = 8, 9$; Gesnerieae, $n = 14$; Beslerieae, $n = 16$; Napeantheae, unknown). Hybrids have been produced between genera representing the four different chromosome numbers ($n = 10, 11, 12, 13$) found in the five-tribe complex (Table 14).

All available evidence indicates that the five-tribe complex is best treated as a single entity. The oldest available name for the combined tribes Bellonieae, Gloxinieae, Kohlerieae, Sinningieae, and Solenophoreae is a choice of one of these five names. All five of them appeared first and simultaneously (on the tribal level) in Fritsch's classification of 1893-94. The name Gloxinieae is chosen here.

Tribe Gloxinieae Fritsch emend. Wiehler

Plantae vulgo terrestres, persaepe rhizomatibus squamatis vel tuberibus subterraneis; nodis univestigiatis unilacunatis; petiolis in sectione transversali luna crescenti vasculari profunda; lamina vulgo tenui velutina, cellulis abaxiali vulgo profunde sinuatis, stomatibus elevatis; ovario infero vel partialiter infero, vel raro supero; nectario annulari, vel constanti ex glandulis 2-5, vel absenti; fructu capsula bivalvis seca vel raro succulenta; chromosomatum numero $n = 10, 11, 12, 13$.

Type genus: *Gloxinia* L'Herit.

Tribe Gloxinieae Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 173. 1893-94.

Tribe Achimeneae Hanst., in Martius, Flora Brasiliensis 8(1): 345-348. 1864.

Nom. illegit. Later homonym of tribe Achimeneae Colla, Mem. Reale Accad. Sci. Torino ser. 2, 10: 203-216. 1849, based on *Achimenes* Vahl, Symbolae Botanicae 2: 71. 1791, type species *A. sesamoides* Vahl [=*Artanema sesamoides* (Vahl) Benth.], Scrophulariaceae; *Achimenes* Vahl = *Artanema* D. Don, Scroph. Colla meant his Achimeneae to be a tribe in the Gesneriaceae.

Tribe Bellonieae Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 171, 1893-94.

Tribe Kohlerieae Fritsch op cit., 143, 177.

Tribe Sinningieae Fritsch, op. cit., 144, 180.

Tribe Solenophoreae Fritsch, op. cit., 143, 182.

Tribe Rechsteinerieae Ivanina, Bot. Žurn. (Moscow & Leningrad) 50(1): 39, 42. 1965; Notes Roy. Bot. Gard. Edinburgh 26(4): 396. 1966 (English translation).

The emended tribe Gloxinieae, with about 24 genera and over 300 species, forms a very natural, single entity when compared with the other tribes in the new classification of the subfamily Gesnerioideae. A few comments on the tribe Rechsteinerieae are necessary at this point. Ivanina's decision to establish this tribe was based on study of a single feature, the structure of the carpel. Her tribe Rechsteinerieae, containing the genera *Lietzia*, *Rechsteineria*, and *Paliavana* (Table 29), is basically the same as Fritsch's tribe Sinningieae, but with the genus *Sinningia* transferred to the tribe Kohlerieae Fritsch. The biosystematic study of *Rechsteineria* and *Sinningia* by Clayberg (1968, 1970) stands in contradiction to Ivanina's taxonomic evaluation of her carpological work. The subsequent submersion of *Rechsteineria* in *Sinningia* (Moore, 1973c; Wiehler, 1975c) indicates that, at least in the Gesneriaceae, taxonomic reconstruction should be based on more than a single character. The very fact that the Gesneriaceae are the only group in the order Scrophulariales with a strong tendency toward the development of an inferior ovary should remind us that the structure of the carpel remains a flexible phenomenon in the biology of the Gesnerioideae.

CHAPTER 23: THE TRIBE EPISCIEAE

Containing about 21 genera and well over 670 species, the Episcieae are the largest tribe of the Gesnerioideae. With a primary center of distribution in Ecuador, Colombia, Panama, and Costa Rica, the Episcieae are also the most conspicuous members of the Gesneriaceae there, and probably also the most abundant and diverse ones. The special evolutionary developments of this tribe are a peculiar nodal anatomy, epiphytism, ornithophily and euglossophily.* The nodal structure of the Episcieae, three-trace trilacunar with split lateral bundles, is unique in the order Scrophulariales or among the Tubiflorae, all of which have one-trace unilacunar nodes. The same type of trilacunar node also occurs, however, among scattered taxa of the subfamily Cyrtandroideae, in the genera *Chirita*, *Cyrtandra*, *Didissandra*, *Hemiboea*, *Saintpaulia*, and *Streptocarpus* (See Chapter 12). Nodal anatomy thus provides a new link between the Cyrtandroideae and the Gesnerioideae.

TABLE 31: KEY TO THE TRIBES OF THE SUBFAMILY GESNERIOIDEAE
IN FRITSCH'S CLASSIFICATION OF 1893-94

1. Ovary superior .... Subfamily Cyrtandroideae
1. Ovary completely or partially inferior .... Subfamily Gesnerioideae
   2. Leaves opposite or verticillate
      3. Vegetative reproduction often by scaly rhizomes; tubers absent
         4. Nectary absent; corolla rotate or campulate .... Tribe Bellonieae
         4. Nectary present
            5. Nectary annular; corolla tube usually elongated .... Tribe Gloxinieae
            5. Nectary consisting of (2 or 5) separate glands
               6. Ovary partially inferior; calyx divided above hypanthium .... Tribe Kohlerieae
               6. Ovary completely inferior; calyx connate above hypanthium .... Tribe Solenophoreae
      3. Tubers present; scaly rhizomes absent .... Tribe Sinningieae
   2. Leaves alternate; nectary annular .... Tribe Gesnerieae

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* Adaptation to pollination by both male and female euglossine bees in search of nectar.

A second evolutionary specialization of the Episcieae is the large-scale colonization of the epiphyte habitat. The tribe Episcieae contains the second largest number of epiphytes among the dicotyledons, namely over 468 species, surpassed in this class only by the tribe containing the genus *Peperomia* (over 700 species) in the Piperaceae (see Chapter 3). This means, in teleological terms, that about two-thirds of the species of the Episcieae have left the floor of the forest and adapted to a more hazardous epiphytic environment in search for more sunlight and to achieve pollen and seed transport by birds.

A third earmark of the tribe Episcieae is ornithophily and euglossophily. More than two-thirds of its 670 species are pollinated by hummingbirds. In fact, it is the spectacular hummingbird flowers of such epiphytic genera as *Columnea*, *Dalbergaria*, *Trichantha* and *Nematanthus* which give a note of distinction to the Episcieae. It appears more than coincidence that both the Episcieae and the Trochilidae have about the same pattern of distribution density in the neotropics, with the highest concentration in Ecuador and Colombia (see Chapter 5). Gynandro-euglossine flowers, usually with white or yellow, funnel-shaped corollas of various sizes, are concentrated in such genera as *Codonanthe*, *Nautilocalyx*, *Alsobia*, *Drymonia*, *Codonanthopsis*, and *Paradrymonia*.

The development of the nectary is a vital aspect of the pollination biology of the Gesneriaceae. With the exception of the genera *Pentadenia* and *Corytoplectus* (and a few isolated species in other genera), the structure of the nectary is surprisingly uniform in this large tribe, in contrast to that of the Gloxinieae. The ancestral nectariferous ring around the base of the superior ovary is modified to two enlarged but connate glands (Figures 62n-r), probably in direct response to hummingbird pollination. The dorsally located double gland is protected from the probing beak of the hovering bird. The same tendency toward dorsal enlargement of the nectariferous tissue occurs also in *Corytoplectus* and *Pentadenia*, and in hummingbird-pollinated taxa in other tribes (*Kohleria*, *Sinningia*, *Solenophora*, and *Gasteranthus*), while in other large groups of ornithophilous genera (*Besleria*, *Gesneria*) the nectary remains annular. There is no indication that among the neotropical Gesneriaceae gynandro-euglossophily is connected with enlarged dorsal nectary glands which are present in all Euglossine flowers of the Episcieae. This suggests that gynandro-euglossophily is possibly a later phenomenon among the neotropical Gesneriaceae (or at least in the Episcieae) than ornithophily. In other words, the about 20% of the Episcieae presently pollinated by Euglossine bees may come from ornithophilous ancestral stock.

The Episcieae are a very natural taxon, but because they are a large group with many epiphytes (which are usually poorly botanized or collected), they were until recently much less known than the Gloxinieae. The nature of the fruit, for instance, was little understood, until live material was examined in field and greenhouse: the berry, different from the same fruit-type in *Besleria* (see below), the fleshy capsule, and the phenomenon of the display fruit. The Episcieae presented, therefore, more problems of generic delimitations than the Gloxinieae, in particular with such early-established taxa as *Alloplectus*, *Columnea*, and *Episcia* which became wastebasket genera as more and more discordant species were attributed to them.

The tribe Episcieae in the new classification is essentially the same (though enlarged) group as the tribe Columneeae in Fritsch's scheme, but it differs from Ivanina's subfamily Episcioideae and her tribe Episcieae by the absence of the genera *Besleria*, *Pterobesleria*, *Tylopsacas*, *Napeanthus*, and

Jerdonia. The Episcieae included only nine genera in Fritsch's system, and the equivalent of eleven genera in Ivanina's recent classification, in contrast to the 21 genera in the present scheme.

Tribe Episcieae Endl. emend. Wiehler

Plantae saepe epiphyticae, sine rhizomatibus squamatis; nodis trivestigiatis trilacunatis fasciculis lateralibus fissis; petiolis in sectione transversali luna crescenti vasculari parva non profunda; lamina saepe succulenta, cellulis abaxiali vulgo non sinuatis, stomatibus vulgo non elevatis; ovario supero; nectario vulgo constanti ex glandulis duabus dorsalibus connatis; fructu bacca vel capsula bivalvis carnosa; chromosomatum numero $n = 8, 9$.

Type genus: *Episcia* Mart.

Tribe Episcieae Endl., Genera plantarum 720. 1839.
Tribe Columneeae Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 165, 171. 1893-94.
Subfamily Episcioideae (Endl.) Ivanina, Bot. Žurn. (Moscow & Leningrad) 50(1): 37, 42. 1965; Notes Roy. Bot. Gard. Edinburgh 26(4): 394, 401. 1966 (English translation).
Tribe Episcieae Endl. *sensu* Ivanina, ibidem, p. 37, pro parte.
Tribe Columneeae Hanst. *s. str.*, *sensu* Ivanina, ibidem, p. 37.

CHAPTER 24: THE TRIBE BESLERIEAE

The tribe Beslerieae has contained a preponderance of foreign elements from its inception in 1830. It has never been clearly defined in terms of its type genus, *Besleria.* In fact, it was often used interchangeably for the Episcieae or Columneeae. The tribe Beslerieae included at first all or the majority of the then known episcioid genera, in all systems, from that of Bartling & Wendland (1830) to the last scheme of Hanstein (1865). In his major tribal reconstruction of the Gesneriaceae, Bentham (1876: see Table 28) was the first to withdraw the large episcioid group (as subtribe Columneeae) from his subtribe Beslerieae, which now contained only one New World genus, *Besleria* (with his genera *Cremosperma* and *Gasteranthus* as synonyms). However, Bentham also added a series of Old World genera to the Beslerieae: *Rhynchotechum*, *Isanthera*, *Stauranthera*, *Slackia*, *Epithema*, *Monophyllaea*, and doubtfully, *Loxophyllum.* Fritsch adopted Bentham's system wholesale in 1893-94; he merely raised the Beslerieae again to tribal rank, joined some more Old World genera to this group: *Cyrtandromoea*, *Siphoboea*, and *Hexatheca.* He deleted *Loxophyllum.* Burtt's decisive classification of the Cyrtandroideae (1963) separated the Old World taxa once more from the New World genera. It also left the Beslerieae virtually monotypic. Ivanina's carpological system (1965) deleted the tribe Beslerieae completely, and included *Besleria* and *Pterobesleria* in the subfamily Episcioideae, under the tribe Episcieae (Table 30).

With over 270 species, the tribe Beslerieae, as here constituted, is an important element of the subfamily Gesnerioideae. The genus *Besleria*, containing over 200 species, is the largest entity in the tribe. The other neotropical genera now placed in this tribe are: *Cremosperma*, *Gasteranthus*, *Reldia*, *Resia*, *Tylopsacas*, and *Anetanthus.* Some of these genera were previously without tribal affiliation. The Beslerieae differ from the other tribes of the Gesnerioideae and from the Coronantheroideae by the absence of prophylls and subtending bracts on the pair-flowered cyme. These features are readily discernible on any pedunculate inflorescence. Prophylls and subtending bracts may, however, be absent on any neotropical gesneriad with extremely reduced, 1-2-flowered inflorescences also lacking the peduncle, such as species of *Columnea, Bucinellina nariniana,* etc. The reason for the absence of prophylls and bracts on the inflorescence of all taxa of the Beslerieae is not known, but it constitutes the key character for the revised tribe.

It is now also impossible to confuse the Beslerieae with the Episcieae, for the former have one-trace unilacunar nodes and the petiole in cross-section with a large and deep vascular crescent, and the latter three-trace trilacunar nodes and the petiole with a small and shallow vascular crescent (Figure 85). The fruit in both *Besleria* and in many taxa of the Episcieae is a berry, and this was the primary reason in the past why these genera were placed in the same tribe. Examination of live material shows, however, that the nature of the beslerioid berry differs from that of the episcioid berry. The pulp of the berry of *Besleria* originates from enlarged lamellar or placental tissue, and the seeds are without fleshy funiculi. The pulp in the berry of the tribe Episcieae consists only of enlarged, fleshy funiculi.

The nectary in the Beslerieae is either ring-shaped or it is clearly derived from an annular structure (Figures 62c-h). Leeuwenberg (1958) stated in his description of the monotypic genus *Tylopsacas* that the nectary of *T. cuneatum* (Gleason) Leeuwenb. consists of "glands 5, one dorsal large, the others small." This is a structural impossibility in the Gesneriaceae. Ordinarily there are either two enlarged, connate, dorsal glands appearing as a single structure, with three additional glands (2 lateral, 1 ventral), typical for the nectary development in the tribes Episcieae and Gloxinieae (Figures 62i-s), or the nectary of *T. cuneatum* fits into the Beslerieae line of development (Figures 62 c-h). An examination of live material and of herbarium specimens from Venezuela and Guyana shows that the nectary in all specimens of *T. cuneatum* observed is ring-shaped, with two enlarged, dorsal lobes (Figure 62g). The ring is thin on the ventral side, and sometimes slightly lobed. This structure conforms perfectly, therefore, to the evolution of the nectary within the tribe Beslerieae. Carried a step further is the nectary development in the monotypic genus *Anetanthus* (Figure 62h). The nectary here is a thin, sheath-like, open ring with five pointed lobes.

Both *Tylopsacas* and *Anetanthus* stand somewhat isolated in the Beslerieae because of a special development of some features. The seed of *T. cuneatum* is subglobose and pustulate (Ivanina, 1966, Figure 4: 9), and the seed of *A. gracilis* Hiern is flat, discoid, and winged (Wiehler, 1976a, Figure 11; size = 0.25 mm). The dehiscence of the dry, bivalved capsule of *A. gracilis* is strictly septicidal, a feature otherwise unknown in the Gesnerioideae, but occurring in the Coronantheroideae, Cyrtandroideae, and in the Scrophulariaceae. This mode of dehiscence, the absence of placental lamellae, and the development of winged discoid seeds are aspects of a specialization in seed dispersal which may account for the wide distribution of *A. gracilis* in South America. The absence of the placental lamellae caused Ivanina (1965, 1966, 1967) to place *A. gracilis* outside the Gesneriaceae in the Scrophulariaceae (where it is even more isolated). Both Weber (personal communication) and I consider the monotypic genus *Anetanthus* as a bona fide member of the Gesneriaceae, in spite of some extra specialization (Wiehler, 1976a).

Tribe Beslerieae Bartling & Wendl. f., emend. Wiehler

Plantae terrestres numquam epiphyticae, sine rhizomatibus squamatis vel tuberibus subterraneis; nodis univestigiatis unilacunatis; petiolis in sectione transversali luna crescenti vasculari grandi et profunda; lamina vulgo tenui vel coriacei, cellulis abaxiali sinuatis vel rectis, stomatibus dispersis vel aggregatis in tumulis; ovario supero; nectario annulari, semi-annulari, ad lobos 2-1 dorsales redactos, vel vaginiformi; fructu bacca, vel capsula seca vel carnosa, loculicida, septicida vel uterque; chromosomatum numero $n = 16$ (*Besleria*).

Type genus: *Besleria* L.

Tribe Beslerieae Bartling & Wendl. f., Ordines naturales plantarum 175. 1830.
  Tribe Anetantheae Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 156. 1893-94.
  Tribe Beslerieae Bartling & Wendl. f., *sensu* Fritsch, ibidem, 143, 157.

CHAPTER 25: THE TRIBE NAPEANTHEAE

The genus *Napeanthus*, established by George Gardner (b. 1812, d. 1849) in 1843, was first placed in the family Cyrtandraceae, tribe Didymocarpeae, subtribe Loxonieae by A. P. de Candolle (b. 1778, d. 1841) in his *Prodromus*, vol. 7, in 1845. A year later Bentham united the Gesneriaceae and Cyrtandraceae of de Candolle's classification rather cursorily and assigned *Napeanthus* to the family Gesneriaceae, tribe Cyrtandreae (*London J. Bot.* 5: 357-365. 1846). Gardner's genus was not listed in the classifications by Colla (1849), Decaisne (1850), Hanstein (1854-1865), and Oersted (1858), but it surfaced again in Bentham's system of 1876, in the Old World Didymocarpeae, together with *Anetanthus*, *Rhynchoglossum*, and *Klugia* as a separate genus, and six other paleotropical genera (Table 28). Fritsch (1893-94) placed *Napeanthus* in a similar group, now renamed tribe Klugieae, together with *Jerdonia*, *Rhynchoglossum*, *Klugia*, *Primulina*, and *Acanthonema* (Table 1). Burtt's (1963) revision of the subfamily Cyrtandroideae (Table 29) left this neotropical genus without tribal affiliation, and in Ivanina's carpological classification (1965) *Napeanthus* is cited in the tribe Episcieae of the subfamily Episcioideae, in the company of eight episcioid genera, and *Besleria*, *Tylopsacas*, and *Jerdonia* (Table 30). Leeuwenberg (1958) produced a revision of the genus, then containing 12 species. He stated that *Napeanthus* occupies an isolated position among the New World Gesneriaceae, but that according to Fritsch and Burtt it is related to certain Old World genera (see Chapter 25). There are also two synonyms for *Napeanthus: Marssonia* Karsten (1860), a genus placed in the Gentianaceae, and *Hatschbachia* L. B. Smith (1953), assigned to the Scrophulariaceae. This brief taxonomic history of numerous affiliations indicates that there exists some basic unclarity and uncertainty about the affinities of the genus *Napeanthus*.

A study of live material in the field and greenhouse has improved our knowledge of this interesting taxon. *Napeanthus* is now known to include well over 30 species of low-growing, rosette-forming herbs found in humid areas on mossy rocks, in clay soil along river banks, and in cloud forests, usually in areas not frequented by botanical collectors. The genus has a wide neotropical distribution, from Bolivia and southeastern Brazil to the islands of Trinidad and Tobago, and in Central America north to Guatemala. All species are endemics of narrowly restricted geographical areas. Only one species was known from Panama until recently. Through more intense botanical explorations in this small country, this number has now increased to five well differentiated species (Wiehler, 1977a: 110-112 and unpublished data.)

There is no doubt that *Napeanthus* belongs in the Gesneriaceae, subfamily Gesnerioideae, because of the typically gesneriaceous, pair-flowered cymose inflorescence, the parietal placentation of the paracarpous gynoecium, the shape of the corolla, the anthers, the seeds, the aggregation of the stomata into distinct islands, and because of the distribution of the species. At the same time *Napeanthus* does not fit into any of the remodelled tribes of the Gesnerioideae (or into the tribes of the other subfamilies). It differs from the Episcieae by the absence of three-trace trilacunar nodes and by the presence of rotate corollas and strictly dry capsular fruits; from the Beslerieae by the presence of prophylls and subtending bracts on the inflorescence, the small vascular crescent of the petiole in cross-section (Figure 85d), and the rotate corollas; from the Gloxinieae and Gesnerieae by the superior ovary, the absence of the hemiparacarpous gynoecium (typical for the Gloxinieae and Gesnerieae), the presence of septicidal dehiscence of the fruit, and the small vascular crescent of the petiole in cross-section. Aggregate stomata do not occur in the Gloxinieae (but are found in the Gesnerieae), and rotate corollas are absent from the Gesnerieae (but characterize some genera of the Gloxinieae). The nectary is an important diagnostic feature in the Gesnerioideae: it is absent in all species of *Napeanthus*, but present in all four tribes of the subfamily, except in some taxa of the Gloxinieae.

This situation seems best treated by establishing a separate tribe for *Napeanthus* in the Gesnerioideae.

Tribe Napeantheae Wiehler, trib. nov.

Plantae terrestres humiles rosulares, numquam epiphyticae, sine rhizomatibus squamatis vel tuberibus subterraneis; folia decussata, nodis univestigiatis unilacunatis, petiolis in sectione transversali luna crescenti vasculari parva non profunda, lamina vulgo coriacea, cellulis abaxiali rectis, stomatibus aggregatis in tumulis; inflorescentia cyma axillaris bracteata geminiflora composita vel redacta ad 1-2 flores; corolla rotata; staminibus 4-5; ovario supero; nectario destituto; fructu capsula seca loculicida, vel loculicida at septicida.

Type genus: *Napeanthus* Gardner. The tribe Napeantheae is monotypic.

CHAPTER 26: THE TRIBE GESNERIEAE

The tribe Gesnerieae is a very natural taxon of about 69 species, all of which are native to the Caribbean islands, with the exception of two species from nearby coastal Colombia and Venezuela.

The nomenclatural history of the tribe Gesnerieae is problematic, representing a case where the rules of the International Code of Botanical Nomenclature cannot be applied strictly. The tribal name Gesnerieae is a reflection of the confusion about the application of the names *Gesneria* L. (1753) and *Gesnera* (or *Gesneria*) Mart. (1829) during most of the nineteenth century.

Linnaeus (1753) established the name *Gesneria* for two Caribbean species, *G. humilis*, and *G. tomentosa*, based on Plumier's description and illustration of these species under the name *Gesnera* in 1703. The slowly expanding botanical explorations into the New World brought a wealth of new Gesneriaceae to Europe. As with other early genera in this family (*Achimenes*, *Alloplectus*, *Besleria*, *Columnea*, *Episcia*, and *Gloxinia*), *Gesneria* L. soon became a depository for various groups of species foreign to the original concept of the genus. This became especially evident with Kunth's (1818) publication of many South American (mostly Colombian) taxa under *Gesneria.*

Lindley (1827) was the first to suggest a division of *Gesneria* (in *Bot. Reg.* 13: sub t. 1110):

> The genus *Gesneria*, as it presently stands, contains an assemblage of plants differing so much among each other, both in habit and parts of fructification, that it is probable a careful investigation of the species will lead to the establishment of more than one new genus. We are by no means in possession of sufficient materials to undertake such a task in the manner it deserves; but it may not be useless to offer a few remarks upon the subject, for the consideration of those who are more fortunately circumstanced.

He then suggested briefly that only red, tubular-flowered species from Brazil should belong to *Gesneria*, and he also proposed two new generic names for the Caribbean taxa then in *Gesneria*: *Codonophora* Lindl. and *Pentarhaphia* Lindl. ("*Pentaraphia*").

Martius (1829) proceeded a step further by redefining and emending the genus *Gesneria* L. He changed the spelling back to Plumier's *Gesnera*, and followed Kunth's (1818) example and Lindley's suggestions to include only South American species in it. Martius newly described or listed under *Gesnera* 11 Brazilian species transferred 62 years later to *Rechsteineria* (now *Sinningia*), and one species of the Brazilian genus *Paliavana.* Again following Lindley, he divided the Caribbean species of *Gesneria* L. into two groups. Martius, however, did not like Lindley's proposed names and chose two new ones: *Conradia* Mart. (honoring Conrad Gesner again), which included *Gesneria humilis* L., and *Rhytidophyllum* Mart. ("*Rytidophyllum*," corrected in his index), which contained *Gesneria tomentosa* L.

It is evident from the text that Martius did not intend to create a new genus with his emendation of *Gesneria* L.: there is no cross symbol (his indication of a new taxon) after *Gesnera*, as it is after *Conradia*, *Rhytidophyllum*, and his other new genera and species; in his key on page 67 he listed no author behind *Gesnera* (and *Besleria*) except "ex em. Mart.," while he cites authorities for the other 13 genera in the same key. Nevertheless, with the exclusion of the two original Caribbean type species of *Gesneria* L. (*G. humilis* L. and *G. tomentosa* L.) and by applying the same name in a different sense to South American taxa, Martius, in fact, published a new genus, *Gesnera,* according to Article 48 of the Code. *Gesnera* Mart. is a later homonym of *Gesneria* L.

There exists as yet no lectotype for *Gesnera* Mart. (see Morton & Denham, 1972: 669). The third species described by Martius appears to be more representative or typical of *Gesnera* than the first two described, and therefore *Gesnera sceptrum* Mart. [= *Sinningia sceptrum* (Mart.) Wiehler] is herewith chosen as lectotype.

Martius' concept of *Gesnera* (also cited as *Gesneria* Mart.) was subsequently generally accepted in the botanical literature until the 1890's. From 1829 until Fritsch's classification of 1893-94, all citations of the family name Gesneriaceae, the subfamily name Gesnerioideae, the tribal or subtribal name Gesnerieae were based on the illegitimate generic name *Gesnera* Mart. (or *Gesneria* Mart., or *Gesneria* L. ex emend. Mart.), and not on *Gesneria* L. The first citation of the tribal name Gesnerieae in the literature appeared in the classification of George Don (1838), based on *Gesneria* Mart., and the same concept was followed in the systems of Endlicher (1839), de Candolle (1839), Bentham (1846), Colla (1849), Decaisne (1850), Hanstein (1854-65), Oersted (1858), and Bentham (1876).

Baillon (1888) was the first to disagree with tradition by including *Conradia humilis* and *Rhytidophyllum tomentosum* again under *Gesneria* L. Kuntze in his *Revisio generum plantarum* (1891) then pointed out that *Gesnera* Mart. is an illegitimate name for *Rechsteineria* Regel, and that *Pentarhaphia* Lindl., *Conradia* Mart., and *Rhytidophyllum* Mart. are synonyms of *Gesneria* L. (which Kuntze spelled "*Gesnera*" L.).

Fritsch followed Baillon and Kuntze and incorporated the concept of *Gesneria* L. into his system of 1893-94. In this last classification of the Gesneriaceae, the subfamilial name is based again on *Gesneria* L. and the tribal name Gesnerieae is for the first time founded on *Gesneria* L. We have therefore the curious situation that the correct name for the tribe Gesnerieae (based on *Gesneria* L. and first employed by Fritsch in 1893-94) is a later homonym of Gesnerieae, established by G. Don in 1838, and based on *Gesnera* Mart. This situation was not clearly elucidated by Skog (1976: 3, 36) in his fine revision of the genus *Gesneria* L. Skog traced the establishment of the tribe Gesnerieae back to G. Don (1838). That Don's tribe Gesnerieae is based on *Gesneria* Mart. can be seen by the assortment of the 29 species he included in his concept of *Gesneria.* In present-day terminology, these 29 species consist of 15 species of *Sinningia*, seven species of *Kohleria*, two species each of *Heppiella* and *Moussonia*, and one species each of *Gloxinia*, *Paliavana*, and *Gesneria. Gesneria humilis* L., the type species of *Gesneria* L. (and thus the type of the tribe Gesnerieae, the subfamily Gesnerioideae, and the family Gesneriaceae) is submerged by Don in the genus *Conradia* Mart. as *Conradia humilis* (L.) Mart.

Tribe Gesnerieae,* Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 144, 183. 1893-94; *non* G. Don, Gen. Syst. 4: 643-44. 1837, and of subsequent authors.

Tribe Rhytidophylleae Oersted, Centralamericas Gesneraceer 10. 1858. *pro parte.*

Type genus: *Gesneria* L.

Terrestrial, perennial, acaulescent herbs, subshrubs, shrubs, and small trees; stems woody, the nodes one-trace unilacunar; leaves secondarily alternate with a 2/5 phyllotaxy, but then the bracts of the inflorescence decussate, or the leaves decussate; vascular trace of the petiole in cross-section thick, U-shaped and invaginated or cylindrical (Figure 85e-f); lamina often leathery, the cells of the abaxial epidermis usually with straight anticlinal walls (except in some species of section *Rhytidophyllum* of *Gesneria*), the stomata often aggregated into islands; ovary inferior or subinferior; nectary annular, sometimes 5-lobed; fruit a dry capsule with loculicidal, or loculicidal and septicidal dehiscence; base chromosome number $n = 14$.

Table 32 summarizes the diagnostic features used in the tribal reconstruction of the Gesnerioideae. A key for the tribes and genera is provided in the conclusion of this paper.

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* It is usually not customary to cite an authority for a suprageneric category based on a type genus but it is done here, nevertheless, for clarity's sake.

TABLE 32: DIAGNOSTIC FEATURES OF THE FIVE TRIBES OF THE GESNERIOIDEAE

	GLOXINIEAE	EPISCIEAE	BESLERIEAE	NAPEANTHEAE	GESNERIEAE
Character	24 gen./300+ spp.	21/670+	7/270+	1/30+	1/70
Growth form	herbs, shrubs, rarely trees	herbs, shrubs, vines	herbs, shrubs, small trees	herbs	herbs, shrubs, rarely small trees
Habitat	3% epiphytic 97% terrestrial	66% epiphytic 33% terrestrial	terrestrial	terrestrial	terrestrial
Storage organs	rhizomes and tubers often present	tubers (rare, in three genera)	none	none	none
Phyllotaxy	decussate, whorled	decussate, whorled	decussate, whorled, alternate 2/5, but then inflorescence decussate	decussate	alternate 2/5, rarely decussate, but inflorescence always decussate
Nodal structure	1:1 unilacunar	3:3 trilacunar	1:1 unilacunar	1:1 unilacunar	1:1 unilacunar
Vascular trace of petiole in cross-section					
Lamina of the leaf	usually velvety, thin	often succulent, leathery	thin or leathery	usually leathery	usually leathery
Epidermal cell contour of abaxial lamina	usually sinuate	usually straight	sinuate or straight	straight	straight or sinuate

TABLE 32 (cont.)

Character	GLOXINIEAE	EPISCIEAE	BESLERIEAE	NAPEANTHEAE	GESNERIEAE
Stomatal grouping	irregularly scattered	irregularly scattered	irregularly scattered or aggregated	aggregated	aggregated or irregularly scattered
Cyme of the inflorescence	bracteate	bracteate	ebracteate	bracteate	bracteate
Nectary structure	annular, 5-2 separate glands, or absent	2 dorsal, connate glands, or 5 glands	annular, semi-annular, lobed or sheathed, or reduced to 1 dorsal gland	absent	annular, sometimes lobed
Ovary position	semi-inferior, inferior, rarely superior	superior	superior	superior	inferior or semi-inferior
Carpel structure	hemiparacarpous	paracarpous	paracarpous	paracarpous	hemiparacarpous
Type of fruit	dry capsule	berry or fleshy capsule	berry, dry or fleshy capsule	dry capsule	dry capsule
Capsule dehiscence	loculicidal	loculicidal	loculicidal, loculicidal & septicidal, septicidal	loculicidal or loculicidal & septicidal	locucidal or loculicidal & septicidal
Base chromosome number	10, 11, 12, 13	8, 9	16	?	14

CHAPTER 27: THE NEW SUBFAMILY CORONANTHEROIDEAE

Burtt's (1963) revision of the subfamily Cyrtandroideae and the present generic and tribal reconstruction of the subfamily Gesnerioideae provide evidence that Fritsch's (1893-94) austral tribe Coronanthereae does not fit into either group. The Coronanthereae have isophyllous cotyledons and were therefore excluded by Burtt from the Cyrtandroideae. The Coronanthereae differ from the Gesnerioideae in the following features: 1) geographical distribution -- the taxa are native to the temperate zone of the Pacific coast of South America, the South Pacific islands, and the Pacific side of Australia; 2) the chromosome numbers of the genera ($x = \pm 37, \pm 40, \pm 45$; 3) the type of stomata (anomo-mesoperigenous or aperigenous stomata); 4) the nectary structure, with the annular and pulvinate nectary tissue imbedded in the basal part of the ovary wall, and the nectary thus adnate to the ovary; and 5) the occurrence of only two stamens in one genus (*Sarmienta*) of the Coronanthereae, a condition unknown in the Gesnerioideae, but fairly common in the Cyrtandroideae.

To add the austral tribe Coronanthereae to the Gesnerioideae strains the natural unity of that subfamily. The Coronanthereae seem to be just as distantly related to the Cyrtandroideae as to the Gesnerioideae. The establishment of a new subfamily, the Coronantheroideae, therefore, presents itself as logical.

Subfamily Coronantheroideae Wiehler, subfam. nov.

Differt a Cyrtandroideis cotyledonibus isophyllis, a Gesnerioideis distributione geographica, chromosomatum numeris, typo stomatum, et structura nectarii.

Type genus: *Coronanthera* Vieill. ex C. B. Clarke

The subfamily Coronantheroideae consists of nine genera and 20 species, native to Chile and adjacent Andean Argentina, both below the 38th parallel, the North Island of New Zealand, Lord Howe Island, New Caledonia, the Solomon Islands, and the provinces of New South Wales and Queensland in Australia (Table 32). Seven of the nine genera are monotypic. The two species of *Depanthus* and 10 of the 11 species of *Coronanthera* are endemic to New Caledonia. The small shrub *Rhabdothamnus solandri* is confined to several localities on North Island of New Zealand, and the tree *Negria rhabdothamnoides* is found only on two mountain peaks of the tiny Lord Howe Island near Australia. The high chromosome numbers (for Gesneriaceae) and the large percentage of monotypic genera endemic to isolated and restricted areas may indicate that the Coronantheroideae of today represent relics of a stock more abundant in the past.

The subfamily Coronantheroideae is delimited as follows: terrestrial and epiphytic herbs, vines, shrubs, or trees, with isophyllous cotyledons and a one-trace unilacunar nodal structure. Leaves opposite-decussate or whorled, stomatal complexes predominantly of the anomo-mesoperigenous type. Inflorescence typically a bracteate, pair-flowered (3-flowered in *Lenbrassia* and *Negria* ?), simple or compound cyme of 4-10 or more flowers, sometimes reduced to 1-2 flowers, and these often epedunculate and ebracteate. Corolla zygomorphic or secondarily actinomorphic (in *Depanthus*), tubular-campanulate. Stamens 4, rarely 5 (in *Depanthus*) or 2 (in *Sarmienta* -- see Table 10). Ovary superior, hemiparacarpous. Nectary annular, pulvinate, embedded in the basal part of the ovary wall. Fruit a pointed, dry capsule with loculicidal, or loculicidal and septicidal dehiscence, or a berry (in *Asteranthera*, *Fieldia*, *Mitraria*, and *Sarmienta*). Base chromosome numbers: $x = \pm 37, \pm 40, \pm 45$. Native to islands of the South Pacific Ocean and adjacent areas in Australia and South America.

In the present classification the subfamily Coronantheroideae contains only one tribe, the Coronanthereae. The nomenclatural history of the group is fairly simple. Before Hanstein (1854), the then existing genera *Mitraria*, *Sarmienta*, *Asteranthera* (as *Columnea ovata*) and *Fieldia* were scattered among various tribes (G. Don, 1838; Endlicher, 1839; de Candolle, 1839, 1845; Bentham, 1846). The first suprageneric names based on these taxa were established by Hanstein in 1854 with the subtribes "Sarmienteae" (comprising only *Sarmienta*) and "Mitrarieae" (monotypic with *Mitraria*), both belonging to the tribe Beslerieae. The genus *Asteranthera* appeared in the subtribe "Columneeae" on account of its *Columnea*-shaped corolla (Figures 29, 31). Oersted (1858) eliminated one subtribe by adding *Sarmienta* to the subtribe "Mitrarieae," but he left *Asteranthera* in the "Columneeae." In 1865 Hanstein eliminated the subtribal structure in his system and cited all three genera consecutively at the end of the tribe Beslerieae. Bentham (1876) placed the same three genera, plus *Fieldia*, *Negria*, *Rhabdothamnus*, and the central Pacific genus *Cyrtandra* in the Old World tribe Cyrtandreae, subtribe "Eucyrtandreae" (Table 28). Clarke (1883) left only the berry-fruited taxa (*Asteranthera*, *Fieldia*, *Mitraria*, *Sarmienta*, plus *Cyrtandra*, etc.) in the subtribe "Eucyrtandreae" amd moved the capsule-fruited genera *Coronanthera*, *Negria*, and *Rhabdothamnus* to the subtribe "Didymocarpeae" of the tribe Cyrtandreae. Fritsch (1893-94) used the same basic divisions for this austral group as Clarke (1883), but he created a new superstructure: subfamily Cyrtandroideae, tribe Coronanthereae, with the subtribes Coronantherinae and Mitrariinae (Table 1). While assigning the tribe Coronanthereae to the subfamily Gesnerioideae on account of the cotyledon structure, Burtt (1963) elevated the subtribe Mitrariinae to tribal rank because "these genera seem as close to Beslerieae and Columneeae in many respects as they are to Coronanthereae, . . ." (p. 206, 216). Ivanina (1965) used the same system.

The reason for the separation of the austral group into two subtribes or tribes is based on the two types of fruit found among them, dry capsules and berries. Burtt (1963) alludes to relationships between the Mitrariinae, Beslerieae, and Columneeae (*sensu* Fritsch), because these groups are berry-fruited. In fact, it was precisely because of the berry fruit that *Besleria* was associated for so long with the columneiod genera. The present classification emphasizes the profound differences between *Besleria* (with the whole tribe Beslerieae) and *Columnea* (with all the Episcieae), including the contrast in berry structure (see Chapter 10). The berry apparently evolved in each tribe independently from a capsular fruit. The presence of a berry fruit is therefore not a character for the indication of intertribal affinities. It should be self-evident that the berry-fruited genera in each of these tribes have a closer relationship to the genera with capsular fruit in the same tribe (*Besleria* - *Gasteranthus; Columnea* - *Alloplectus; Mitraria* - *Rhabdothamnus*) than to berry-fruited taxa in other tribes.

Parallel to the Beslerieae and the Episcieae in the Gesnerioideae, the tribe Coronanthereae in the Coronantheroideae contains both capsular-fruited and berry-fruited genera. This one-tribe thesis is supported by the geographical distribution of the taxa (*Fieldia* is separated by a large ocean from the three Chilean berry-fruited genera) and by the same chromosome number occurring in both capsular-fruited and berry-fruited genera ($n = +37$ for capsular-fruited *Rhabdothamnus* and for berry-fruited *Mitraria* and *Sarmienta*).

Tribe Coronanthereae Fritsch, in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 160. 1893-94.

Tribe Beslerieae Bartling & Wendl. f., subtribe Sarmienteae Hanst., Linnaea 26: 198-199, 206-207. 1854.

Tribe Beslerieae, subtribe Mitrarieae Hanst., ibidem, 198-199, 210-211. Oersted, Centralamericas Gesneraceer 11. 1858.

Tribe Beslerieae, pro parte, Hanstein in Linnaea 34: 233-235. 1865.

Tribe Cyrtandreae G. Don, subtribe Eucyrtandreae G. Don, pro parte, Bentham, in Bentham & Hooker f., Genera plantarum 2: 993-994. 1876.

Tribe Cyrtandreae, subtribe Eucyrtandreae (including *Fieldia*, *Asteranthera*, *Mitraria*, and *Sarmienta*), subtribe Didymocarpeae G. Don, (including *Rhabdothamnus*, *Coronanthera*, and *Negria*), C. B. Clarke in A. & C. DeCandolle, Monographiae phanerogamarum 5(1): 15-17. 1883.

Tribe Coronanthereae Fritsch, subtribes Coronantherinae Fritsch and Mitrariinae Hanst., in Engler & Prantl, Die natürlichen Pflanzenfamilien 4(3b): 143, 160-162. 1893-94.

Tribe Mitrarieae B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24(3): 216. 1963 ("1962").

A key to the three subfamilies concludes this section, and a key to the tribes and genera of the Cornantheroideae and Gesnerioideae follows as conclusion of this work.

Hybrids between the monotypic genera *Mitraria* and *Sarmienta* were produced at the National Botanic Garden, Glasnevin, Ireland, around 1937, according to a report by J. W. Besant (1937). The hybrid genus has been labelled × *Mitramienta* Wiehler (Table 11).

KEY TO THE THREE SUBFAMILIES OF THE GESNERIACEAE

1. Seedlings with equal cotyledons
    2. Nectary adnate to (= imbedded in) the basal part of the ovary wall; plants of the South Pacific region and adjacent Australia and temperate South America below the 38th parallel .... Subfamily Coronantheroideae
    2. Nectary free from the base of the ovary, or secondarily absent; plants of the neotropics .... Subfamily Gesnerioideae
1. Seedlings with unequal cotyledons; plants of the Old World .... Subfamily Cyrtandroideae

TABLE 33: THE GENERA AND SPECIES OF THE SUBFAMILY CORONANTHEROIDEAE

	Taxon	Fruit Type, Dehiscence; Chromosome No.	Habit; Habitat	Nativity
	Asteranthera Hanst., 1854			
1.	*A. ovata* (Cav.) Hanst., 1865 *Columnea ovata* Cav. 1797 *Asteranthera chiloensis* Hanst., 1854	berry	creeping & climbing vine; epiphyte; cool rain forest	Chile
	Coronanthera Vieill. ex C. B. Clarke, 1883			
2.	*C. aspera* C. B. Clarke, 1883	capsule: septicidal & loculicidal	small tree; montane forest	New Caledonia
3.	*C. barbata* C. B. Clarke, 1883	capsule; septicidal	shrub; montane forest	New Caledonia
4.	*C. clarkeana* Schlechter, 1906	capsule; dehiscence?	shrub; montane forest	New Caledonia
5.	*C. deltoidifolia* Vieill. ex C. B. Clarke, 1883	capsule; septicidal	small tree; montane forest	New Caledonia
6.	*C. grandis* G. W. Gillett, 1967	capsule; loculicidal & septicidal	shrub; montane forest	Solomon Islands
7.	*C. pancheri* C. B. Clarke, 1883	capsule; septicidal or sept. & loc.	small tree; montane forest	New Caledonia

(Continued on following page)

(Continued from preceding page)

TABLE 33 (cont.): THE GENERA AND SPECIES OF THE SUBFAMILY CORONANTHEROIDEAE

	Taxon	Fruit Type, Dehiscence; Chromosome No.	Habit; Habitat	Nativity
8.	*C. pedunculosa* C. B. Clarke, 1883	capsule; septicidal & loculicidal	small tree; montane forest	New Caledonia
9.	*C. pinguior* C. B. Clarke, 1883	capsule; dehiscence ?	?	New Caledonia
10.	*C. pulchra* C. B. Clarke, 1883	?	small tree	New Caledonia
11.	*C. sericea* C. B. Clarke, 1883	capsule; septicidal	small tree	New Caledonia
12.	*C. squamata* Virot, 1953	?	?	New Caledonia
Depanthus S. Moore, 1921				
13.	*D. glaber* (C.B. Clarke) S. Moore, 1921 *Coronanthera glabra* C. B. Clarke, 1883	capsule; septicidal	small tree; montane forest	New Caledonia
14.	*D. pubescens* Guillaumin, 1959	?	?	New Caledonia
Fieldia Cunn., 1825 *Basileophyta* F. Muell., 1853				
15.	*F. australis* Cunn., 1825 *Basileophyta frederici-augusti*	berry $n = \pm 40$	creeping & climbing vine; epiphyte; montane forest	Australia: New South Wales

TABLE 33 (cont.)

Lenbrassia G. W. Gillett, 1974			
16. *L. australiana* (C. T. White) G. W. Gillett, 1974	berry	tree, to 13 m tall, rain forest	Australia: Queensland
Coronanthera australis C. T. White, 1936			
Mitraria Cav., 1801			
Diplocalyx Presl, 1844			
17. *M. coccinea* Cav., 1801	berry $n = \pm 37$	subshrub; epiphyte cool rain forest	Chile & adjacent Argentina
Diplocalyx pallidus Presl, 1844			
Negria F. Muell., 1869-71			
18. *N. rhabdothamnoides* F. Muell., 1869-71	capsule loculicidal & septicidal; $n = \pm 45$	tree, 6-9 m tall, montane forest	Lord Howe Island
Rhabdothamnus Cunn., 1838			
19. *R. solandri* Cunn., 1838	capsule; loculicidal & septicidal $n = \pm 37$	shrub, 1/3-1 m tall; montane forest	New Zealand: North Island
Sarmienta R. & P., 1794, nom. conserv.			
Urceolaria Huth, 1758			
20. *S. repens* R. & P., 1798	berry; $n = \pm 37$	climbing or hanging, herbaceous or suffrutescent vine; epiphyte; cool rain forest	Chile
Urceolaria scandens J. D. Brandis, 1786			
U. chilensis Molina, 1810			
Sarmienta scandens (J. D. Brandis) Pers., 1805			

PART 4: GENERIC DELIMITATIONS IN THE SUBFAMILY GESNERIOIDEAE

The following chapters deal with the formerly problematic genera in the New World Gesneriaceae, with the rationale for their union with other genera or their division into separate taxa, with the recent establishment of a series of new genera, and with the genera left untouched by the new classification. The latter category includes, for instance, 13 genera of a present total of 24 in the tribe Gloxinieae and two genera of a present total of 21 in the tribe Episcieae.

The details of the generic reconstruction for the new classification have been published elsewhere (Wiehler, 1971; 1973a; 1973b; 1975a; 1975b; 1975c; 1975f; 1975g; 1976a; 1977a; 1978a; 1978b). The new delimitations of the genera are here either summarized, more fully explained, or cited verbatim to present a complete overview of all the changes in generic structure.

The alterations in the generic framework were brought about by three different processes:

1) The first was the uniting of genera, or the absorption of a section of one genus into another genus. In most of these cases the formerly separate taxa were founded on *differences in the shape of the corolla*, now seen as expressions of different modes of pollination within a single genus. Examples of united genera are: *Gloxinia* and *Seemannia; Sinningia* and *Rechsteineria; Nautilocalyx* and *Episcia* section *Skiophila; Drymonia* and *Alloplectus* section *Macrochlamys; Corytoplectus* and *Diplolegnon; Pentadenia* and *Kohlerianthus; Nematanthus* and *Hypocyrta; Besleria* and *Pterobesleria; Gasteranthus* and *Halphophyllum;* and *Gesneria, Rhytidophyllum* and *Pheidonocarpa.*

2) The second process of generic reconstruction of the Gesnerioideae was the division of large and unwieldy genera containing foreign elements. In most of these cases the recently separated taxa had *similar shapes of corollas.* All of these formerly large genera were established early in the history of the family and have thus suffered from the well-known waste-basket syndrome: as more and more species were dumped into these familiar genera, the delimitations of these taxa became increasingly vague and confused. This problem was solved by a completely new character evaluation of all the tribes and genera of the Gesnerioideae. Now *Eucodonia* is separated from *Achimenes* (which lost also some species to *Gloxinia* and *Goyazia*); *Moussonia* and *Parakohleria* are divided from *Kohleria* (which lost also a species to *Gloxinia*); *Alsobia* and *Paradrymonia* are split from *Episcia* (which lost also a section to *Nautilocalyx*); *Cobananthus* and *Corytoplectus* are parted from *Alloplectus* (which lost also some species to *Drymonia, Nematanthus, Paradrymonia, Pentadenia,* and *Trichantha*); *Dalbergaria, Pentadenia,* and *Trichantha* are detached from *Columnea*; and *Gasteranthus* is severed from *Besleria.*

3) The third process of generic construction involved the establishment of new genera for recently discovered species which fit neither into the old nor new generic schemes of the Gesnerioideae. The new genera are: *Bucinellina, Neomortonia, Oerstedina, Reldia,* and *Rufodorsia.*

The genera discussed below are grouped according to their tribal affiliation.

PART 4A: THE TRIBE GLOXINIEAE

CHAPTER 28: THE GENERA *ACHIMENES, EUCODONIA, GLOXINIA, MONOPYLE,* AND *GOYAZIA*

These genera share the following attributes: small herbaceous, terrestrial plants with scaly underground rhizomes and axillary, often showy flowers. The biological, historical, and nomenclatural details of these taxa are discussed by Wiehler (1976a). Plate 1 shows the transfer of species in the realignment of the genera for the new classification.

Achimenes Persoon

Achimenes was a typical case of a wastebasket genus, containing well over 30 species, presumably all with underground rhizomes, and initially all with the same type of infundibular corolla, but later consisting of four or five different corolla shapes, after Hanstein (1865), Bentham (1876), and Fritsch (1893-94) united the achimenoid taxa. The misplaced species included such diverse gesneriads as *Achimenes panamensis* (Seem.) Hemsl. [= *Nautilocalyx panamensis* (Seem.) Seem.] from Panama, *Achimenes picta* Benth. [= *Kohleria bogotensis* (Nicholson) Fritsch] from Colombia, *Achimenes gracilis* Britton [= *Gloxinia nematanthodes* (Kuntze) Wiehler] from Bolivia, and *Achimenes petraea* S. M. Phillips [= *Goyazia petraea* (S. M. Phillips) Wiehler] from central Brazil. These and many other species were attributed to the old and well-known genus *Achimenes* because of the infundibular shape of the corolla and the presence of rhizomes (except in *Nautilocalyx panamensis* which has tubers). Such a likeness of corolla structure was traditionally interpreted as a primary indicator of congeneric affinity; today it is understood as an expression of particular pollination syndromes found between either related or unrelated plant species.

With the study of many of these species in cultivation, with the determination of chromosome numbers, and through interspecific and intergeneric hybridization, the genus *Achimenes* has become more clearly defined. Containing 22 species of terrestrial herbs with scaly underground rhizomes, it is set apart from related genera by its chromosome number ($x = 11$) and geographical distribution. The majority of the species are native to central and southern Mexico, some are found throughout central America, and two of them occur also in Hispaniola, Jamaica, and Colombia (*A. erecta*), or in coastal Venezuela and Colombia (*A. pedunculata*; see Wiehler, 1976a: 375, Table 1). Four modes of pollination have arisen in *Achimenes*, each expressed by a different corolla shape: ornithophily, psychophily, gynandroeuglossophily, and melittophily. Most of the 22 species are in limited cultivation today and have been used in breeding programs. Many of the interspecific hybrids reveal a high degree of fertility, while all intergeneric hybrids (involving *Eucodonia, Heppiella, Niphaea,* and *Smithiantha*) are sterile. In spite of the different modes of pollination, most of the species of *Achimenes* have generalized floral shapes without special features to distinguish them from those of related genera. The leaves at a node are usually of equal size, or sometimes weakly anisophyllous or ternate.

The involved nomenclatural history of *Achimenes* is typical for a neotropical gesneriad genus. This taxon has eight synonyms, and the name *Achimenes* needed conservation. Patrick Browne established a genus *Achimenes* for two species from Jamaica in 1756. His generic description was based on his first species which later on turned out to belong to the Linnaean genus *Columnea*. Christiaan Hendrik Persoon transferred the first of Browne's species to *Columnea* in 1806 and furnished a new generic description for *Achimenes*, based on Browne's second species. This has become the traditional concept of the genus, but since its origin does not follow the rules, the name *Achimenes* Persoon was conserved in the International Code of Botanical Nomenclature of 1972 (p. 361; see *Taxon* 18((4): 469, 1969; 19(5): 817, 1970). The type species of the genus is *A. coccinea* (Scopoli) Persoon, but its correct name is *A. erecta* (Lamarck) H. P. Fuchs.

Achimenes Persoon, Syn. pl. 2: 164. 1806, *nom. conserv.* (*nom. rej. Achimenes* P. Browne, *Hist. Jamaica* 179. 1856, = *Columnea* L.)
Cyrilla L'Heritier, Stirp, nov. 147. 1791 ("1785").
Trevirana Willdenow, Enum. pl. hort. reg. bot. berolinensis 637. 1809.
Locheria Regel, Flora 31: 251. 1848.
Guthnickia Regel, Flora 32: 179. 1849.
Dicyrta Regel, Flora 32: 181. 1849.
Eumolpe Decaisne, in Jacques & Herincq. Manuel Général des Plantes 2: 575. 1850.
Scheeria Seemann, Bot. Mag. 79: t. 4743. 1853.
Plectoploma Hanstein, Linnaea 26: 201. 1854.

Type species: **Achimenes erecta** (Lamarck) H. P. Fuchs, Act. Bot. Neerl. 12: 15. 1963.
Columnea erecta Lamarck, Encycl. Method. Bot. 2(1): 66. Oct. 1786.
Achimenes minor, erecta, simplex . . . P. Browne, Hist. Jamaica 270. 1756.
Buchneria coccinea Scopoli, Deliciae florae et faunae insubricae 2: 10, pl. 5, Nov.-Dec. 1786.
Achimenes coccinea (Scopoli) Persoon, Syn. pl. 2: 165. 1806, *typ. conserv.*
Trevirana coccinea (Scopoli) Willdenow, Enum. pl. hort. reg. bot. berolinensis 638. 1809.
Gesneria pulchella Swartz, Prodr. 90. 1788.
Columnea humilis Meerburg, Pl. rar., ed. 2: 54, fig. 2. 1789.
Cyrilla pulchella L'Heritier, Stirp. nov. 147, pl. 71. 1791 ("1785").
Trevirana pulchella (L'Heritier) Martius, Nov. gen. 3: 66, tab. 226, fig. 4. 1829.
Achimenes pulchella (L'Heritier) Hitchcock, Missouri Bot. Gard. Report 4: 114. 1893.
A. tenella DC., Prodr. 7: 536. 1839.
A. rosea Lindley, Edward's Bot. Reg. 27: pl. 65. 1841.
A. pyropaea Lindley, J. Hort. Soc. London 2: 293, pl. 4. 1847.
?*A. autumnalis* hort. ex Hanst., Linnaea 27: 724, 744. 1854.

Eucodonia Hanstein

The genus *Eucodonia* was reestablished for two species placed until recently in *Achimenes*, although they or their synonyms were originally described in *Gloxinia*. These two species differ in chromosome number ($x = 12$) from both of the above genera, and their hybrids with species of *Achimenes sensu stricto*, *Smithiantha*, and with *Gloxinia lindeniana* are sterile. The constancy of chromosome numbers among the genera of the Gesnerioideae is one of the guiding principles of the present classification.

The two species of *Eucodonia*, *E. andrieuxii* (DC.) Wiehler and *E. verticillata* (Martens & Gal.) Wiehler, both in cultivation, are small terrestrial

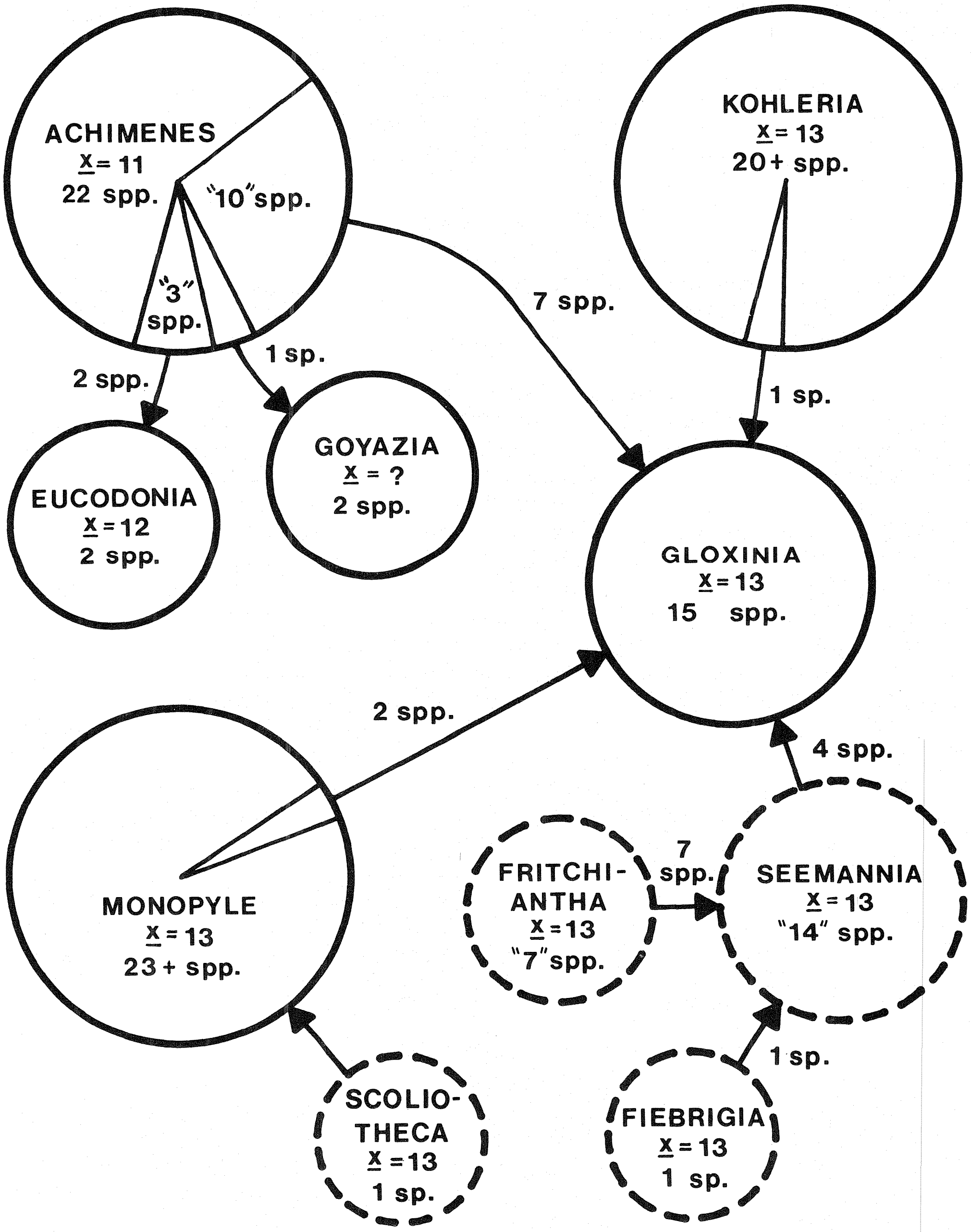

Plate 1. A revision of *Achimenes* and *Gloxinia* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

or saxicolous herbs with wooly stems and leaves, known only from a few localities in central and southern Mexico. The lanate indumentum appears to be typical for the genus. Again there are no floral characters to distinguish *Eucodonia* from some species of *Achimenes*, several species of *Gloxinia*, and from *Smithiantha*. The two species of *Eucodonia* are pollinated by male and female euglossine bees. The leaf pairs are more or less isophyllous.

A nomenclatural profile of the genus *Eucodonia* and its two species is given in *Selbyana* 1(4): 392 (Wiehler, 1976a). The type species is *E. ehrenbergii* Hanstein (= *E. verticillata*).

Gloxinia L'Heritier

The revised genus *Gloxinia* has three types of corolla shapes, corresponding to andro-euglossophily, gynandro-euglossophily, and ornithophily. The diversity of floral structure is similar to that in *Achimenes sensu stricto*, *Sinningia sensu stricto*, *Drymonia*, *Nematanthus*, *Besleria*, *Gasteranthus*, and *Gesneria sensu lato*.

As in other cases cited, it was the establishment of chromosome numbers (x = 13 for *Gloxinia*) and the hybridization of critical species which brought about the new delimitation of this genus. A certain degree of conformity in gross morphological characters and the same chromosome number led to hybridization of the following species in cultivation, at that time still placed in different genera: *Gloxinia perennis*, *Seemannia latifolia*, *S. sylvatica*, *Achimenes gymnostoma*, and *Kohleria lindeniana*. The partial or high fertility of the hybrids (cf. Wiehler, 1976a: 378, Table 3) provided the final impetus for the union of *Gloxinia* (represented mostly by andro-euglossophilous species) and *Seemannia* (with red-flowered ornithophilous species), to which were added the section *Mandirola* of *Achimenes* (containing *A. gymnostoma*), *Kohleria lindeniana*, and two species of *Monopyle*.

Gloxinia consists now of 15 species distributed throughout tropical South America, with two areas of concentration: Bolivia and central Brazil (Goias). The genus is characterized by the leaf pairs usually of equal size, the ovary almost completely inferior, and the nectary usually ring-shaped, or secondarily obsolete. Many of the species produce at times a profusion of threadlike rhizomes. Six species are presently in cultivation.

The intergeneric hybrids of *Gloxinia* are sterile, involving *Eucodonia*, *Heppiella*, *Kohleria*, *Monopyle*, and *Smithiantha*. The genera *Fiebrigia* Fritsch and *Fritschiantha* Kuntze are synonyms of *Gloxinia*. The nomenclatural history of the genus is outlined in *Selbyana* 1(4): 385-386 (Wiehler, 1976a). The type species is *G. perennis* (L.) Fritsch.

Monopyle Bentham

The transfer of two species of *Monopyle* to *Gloxinia* facilitates the circumscription of this genus: all of the remaining 23 or more species of *Monopyle* have strongly unequal leaf pairs (Figure 74), and an obsolete or undeveloped nectary. A faint fragrance and the presence of an osmophore near the base of the corolla in most or all of the species indicate andro-euglossophily, although this assumption has not yet been verified by field observation. The ovary is completely inferior, and the chromosome number is $x = 13$. The distribution is along the western Cordillera from Bolivia to Guatemala.

The species transferred to *Gloxinia* are *Monopyle racemosa* Bentham and *M. divaricata* Rusby (synonymized under *Gloxinia reflexa* Rusby). Baillon's monotypic genus *Scoliotheca* is a synonym of *Monopyle*, with *S. trianae* Baillon equalling *M. macrophylla* Bentham. Five species of *Monopyle* are presently in limited cultivation.

Monopyle Bentham (or Moritz ex Bentham), in Bentham & Hooker, Gen. pl. 2: 997. 1876.

See also *Monopyle* Bentham in Hooker's *Icones plantarum* 12: 85. 1876.
Scoliotheca Baillon, *Histoire des Plantes* 10: 84. 1888. Cf. Bull. Soc. Linn. Paris 1: 725-000. 1888.

Type species: *Monopyle subdimidiata* (Klotzsch & Hanstein) Mansfeld, in Repert. Spec. Nov. Regni Veg. 38: 28. 1935.
Koellikeria subdimiata Klotzsch & Hanstein, Linnaea 27: 736. 1854.
Monopyle leucantha Moritz ex Bentham, in Hooker's Icones plantarum 12: 87. 1876. (lectotype; cf. Morton & Bentham, 1972).

Goyazia Taubert

The genus *Goyazia* is the least known in this group and not yet in cultivation. It is native to the Planalto of central Brazil in the provinces of Goias and Mato Grosso. The two species of the genus, *G. rupicola* Taubert and *G. petraea* (S. M. Phillips) Wiehler, are small saxicolous, perennial herbs with scaly rhizomes. The floral structure is the same as that of *Achimenes*, *Smithiantha*, *Gloxinia*, etc. This explains why *G. petraea* was first attributed to *Achimenes*. But *Goyazia* differs from the other taxa in this group by its thin, stiff, wiry stems, its short, swollen petioles, and by its thick and leathery leaves with a pericraspedodromous venation pattern, not known elsewhere in the Gesneriaceae (Wiehler, 1976a: 392-395, Figures 5-7). The leaf pairs are somewhat anisophyllous, and the chromosome number is unknown. A nomenclatural profile of this small Brazilian genus is provided in *Selbyana* 1(4): 395 (Wiehler, 1976a).

CHAPTER 29: THE GENERA *KOHLERIA*, *MOUSSONIA*, *PARAKOHLERIA*, AND *DIASTEMA*

The first three genera share the following features: terrestrial herbs or sub-shrubs with scaly underground rhizomes (*Moussonia* excepted), usually with bell-shaped or tubular red corollas. The details of the biology, history, and nomenclature of these genera are discussed by Wiehler (1975b, 1978a). The genus *Diastema*, consisting of low-growing, shade-loving herbs, usually with white corollas dotted with blue, is quite distinct from the other genera listed here. But *Diastema* had its share of discordant elements which have been transferred either to *Kohleria* or *Parakohleria*. Plate 2 illustrates with a circlegraph the realignment of the species of *Kohleria*.

Kohleria Regel

Among the large number of species attributed to the old genus *Kohleria* (or its synonyms *Isoloma*, *Brachyloma*, etc.) were several groups of foreign elements, due to a false reliance on similarity of corolla shape. With the reestablishment of the genus *Moussonia* and the erection of the genus *Parakohleria*, *Kohleria* is now a very natural assemblage of about 21 species. They are native to the rain forests of the western Cordillera from central Peru north to Mexico (Oaxaca, Chiapas, and Vera Cruz), and eastward to coastal Venezuela, Trinidad, and the Guianas. Colombia is the center of diversity. The species grow in sun-exposed margins or glens of the forest. The leaves are usually isophyllous when paired, or ternate. The pollination syndromes include ornithophily, gynandro-euglossophily, and chiropterophily. The ovary is semi-inferior, and the nectary consists of five separate glands, or of four glands with the two dorsal ones connate. The base chromosome number is $x = 13$. Twelve species are in cultivation.

Many of the interspecific hybrids show a high degree of fertility (Wiehler, 1975b: 29, Table 4). The intergeneric hybrids, all sterile, involve the genera *Diastema*, *Gloxinia*, *Koellikeria*, *Moussonia*, and *Parakohleria* (Wiehler, 1976b).

Kohleria is another genus of the neotropical Gesneriaceae with an involved nomenclatural history:

Kohleria Regel, Flora 31: 250. April 1848.
Isoloma (Bentham) Decaisne, Rev. Hort. 20: 465. December 1848; *non Isoloma* J. Smith, J. Bot. (Hooker) 3: 414. 1841, a genus of ferns.
Gesneria Martius, sect. *Isoloma* Bentham, Plant. hartweg. 230. 1846.
Tydaea Decaisne, Rev. Hort. 20: 468. December 1848.
Giesleria Regel, Flora 32: 181. 1849.
Sciadocalyx Regel, Gartenflora 2: 257. 1853.
Brachyloma Hanstein, Linnaea 26: 203. 1854.
Calycostemma Hanstein, Linnaea 29: 506, 516, and 556. 1859.
Cryptoloma Hanstein, Linnaea 29. 506, 534, and 578. 1859.
Type species: *Kohleria hirsuta* (Kunth) Regel, Flora 31: 250. 1848.

Moussonia Regel

The genus *Moussonia* was described by E. Regel in 1847 and 1848, recognized by Oersted, Walpers, Decaisne, and Hanstein, submerged by Bentham (1876) in his genus *Isoloma* (= *Kohleria* Regel), and finally treated as a separate section of *Kohleria* by Fritsch (1893-94). An investigation of live material of this group in cultivation and in the field has accumulated sufficient evidence to warrant the exclusion of *Moussonia* from *Kohleria*. The features which separate the two taxa are consistent with generic characters among the rest of the genera of the tribe Gloxinieae:

Moussonia	*Kohleria*
1. Plants without scaly rhizomes	Plants with scaly rhizomes
2. Chromosome number $x = 11$	Chromosome number $x = 13$
3. Nectary ring-shaped	Nectary consisting of individual glands
4. Stigma capitate-stomatomorphic	Stigma bilobed

Six species are currently in cultivation. All attempts to produce hybrids between *Moussonia* and *Kohleria* have failed except in one instance where the progeny is completely sterile (Wiehler, 1976b: 407). All hybridization experiments among species of *Moussonia* produced completely fertile offspring (Wiehler, 1975b: 28, Table 1).

The approximately 11 species of *Moussonia* occur from north-central Mexico (Sinaloa, Nayarit, Jalisco, Hildago, Mexico, Puebla, Vera Cruz) to western Panama (Chiriqui). They are forest herbs or subshrubs, with equal leaf pairs, and long, tubular, usually red corollas, pollinated by hummingbirds. The ovary is semi-inferior to almost completely inferior. *Moussonia* has been involved in intergeneric hybridization with *Gloxinia*, *Kohleria*, *Smithiantha*, and *Solenophora* (Wiehler, 1975b: 28, Table 2). These hybrids are all sterile. The nomenclatural history of *Moussonia* is recorded in *Selbyana* 1: 22-31 (Wiehler, 1975b).

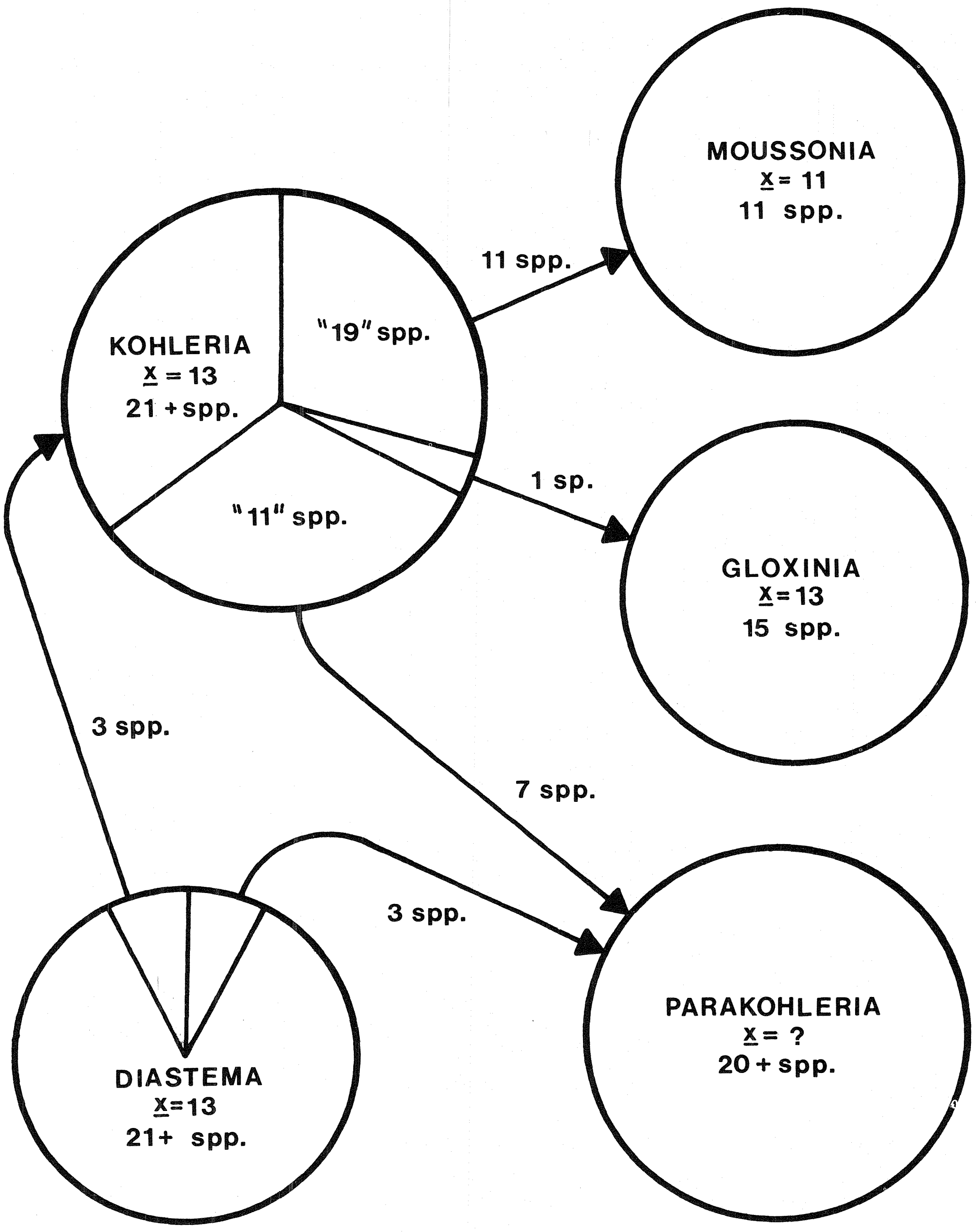

Plate 2. A revision of *Kohleria* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

Parakohleria Wiehler

This new genus (Wiehler, 1978a) has been established on the basis of field work, a study of species brought into cultivation, and herbarium research. *Parakohleria* consists of over 20 species. Some of them were formerly attributed to *Kohleria* or its synonym *Isoloma* (11 species reduced to 7), others to *Diastema* (3 species), or to *Rhytidophyllum* (2 species), *Pearcea*, *Moussonia*, and to *Kohleria* section *Moussonia*. Several species have been newly described, and a large number still await publication. The type species of the genus is *Moussonia hispidissima* Wiehler.

The species of *Parakohleria* are geographically separated from both *Kohleria* and *Moussonia*; they are native to the central and eastern slopes of the Andes from Bolivia north to Putomayo and Caquetá in southern Colombia. An exception is the weedy species *Kohleria spicata* which grows sympatrically with *Parakohleria sprucei* around and below Baños, Ecuador. Parakohlerias have a basally strongly bent corolla tube, a capitate-stomatomorphic stigma, and a nectary consisting of five separate glands of equal length, with the two dorsal glands often somewhat thickened. The inflorescence is typically a very hairy and congested corymb-like cyme, and the scaly underground rhizomes, typical for the genus *Kohleria*, are usually absent or only weakly developed. It is sometimes difficult to distinguish between herbarium material of *Moussonia* and *Kohleria* without floral dissection, but the species of *Kohleria* and *Parakohleria* can be separated at first glance. The base chromosome number for *Parakohleria* is $x = 13$.

Diastema Bentham

Diastema is a natural group without close affinity to other genera of the Gloxinieae. The species, low-growing herbs of the rain forest floor, are easily recognized. The salient features are scaly rhizomes, the inflorescence usually clustered at the end of branched stems, with the small prophylls and subtending bracts quite different from the large leaves below. The corolla has an almost completely straight, cylindric or funnel-shaped tube, and is usually white, rarely yellow or reddish, with a purple spot on each corolla lobe; the nectary, as in *Parakohleria*, consists of five elongate glands of equal length. The chromosome number is $x = 13$.

The 20 or more species are distributed along the western Cordillera from Mexico to Bolivia and in the coastal range of Venezuela, with a center of diversity in Andean Colombia, Ecuador, and Peru.

A sterile intergeneric hybrid has recently been produced between *Diastema vexans* and *Kohleria spicata* (Wiehler, 1976b). The species excluded from *Diastema* and transferred to *Kohleria* and *Parakohleria* differ in the shape of the corolla and in plant habit from *Diastema* (Plate 2; Wiehler, 1978a, 1978c).

Diastema Bentham, Bot. Voyage Sulphur 132. 1845.
  Diastemella Oersted, Centralamer. Gesner. 25. 1858.
  Diastemation Walpers, Annales. bot. syst. 5: 416, 426. 1858. *Nomen superfluum et illegitimum*, based on *Diastemella bracteosa* Oersted, an attempt to substitute the Latin diminutive suffix *-ella* in the Greek name *Diastema* with the Greek suffix *-ion.*

Type species: **Diastema racemiferum** Bentham, Bot. Voyage Sulphur 132. 1845 *("racemifera")*
  D. longiflorum Bentham, Plant. hartweg. 234. 1846.
  D. ochroleucum Hooker, Bot. Mag. 72: t. 4254. 1845.

D. caracasanum Klotzsch & Hanstein, Ann. Sci. Nat. Bot., Sér. 4, 6: 371. 1856.
D. cristatum Hanstein, Linnaea 34: 438. 1865.
D. exiguum Morton, Ann. Missouri Bot. Gard. 24: 202. 1937.
D. exiguum Morton, var. *lilacinum* Morton, ibidem.

CHAPTER 30: THE GENERA *SINNINGIA*, *LEMBOCARPUS*, AND *LIETZIA*

Sinningia Nees

The genus *Sinningia* stands somewhat isolated in the tribe Gloxinieae. In spite of numerous attempts, no intergeneric hybrids have to date been produced with *Sinningia.* The single feature which makes this genus unique in the tribe (with the exception of *Lembocarpus* and *Lietzia*, discussed below) is the type of underground storage organ evolved, the tuber, which is an enlargement of the stem. These tubers can be up to 20 cm in diameter. They are, like rhizomes, adaptations to periodic dry seasons (see Chapter 4, above). But even the presence of tubers does not represent an absolute in *Sinningia.* In species growing in wet habitats, as in *S. barbata* and *S. richii*, tubers are small or almost absent, and the type section of the genus, section *Sinningia* is said to be without tubers. This statement needs verification by the eventual examination of live material from Brazil. Definitely tuberous is a collection of *Sinningia guttata* Lindley brought into cultivation in 1977.

Sinningia was recently united (Moore, 1973c) with *Rechsteineria* (Plate 3), on the basis of the hybridization work of Clayberg (1968, 1970). Previously, the shape of the corolla had been thought to be decisive in the delimitation of these two large genera, but Clayberg's elegant breeding experiments showed that flower shape and color in this group are merely an expression of pollination syndromes. The typically white or blue-flowered species of *Sinningia sensu stricto* are pollinated predominantly by female and male euglossine bees in search of nectar, and the tubular red corollas of *Rechsteineria* indicate ornithophily. While it is possible to produce many partially fertile hybrids between gynandro-euglossophilous, ornithophilous, and sphingophilous sinningias *(sensu lato)*, the sterility of some hybrids and the apparent inability to produce others indicate that the genetic distance between some species and sections of *Sinningia* is more pronounced than in many other neotropical Gesneriaceae.

Although more than one hundred names in *Sinningia* or its synonyms are documented in the botanical literature, the genus is poorly collected and represented in herbaria. There exist probably over 60 species of *Sinningia*, spread throughout neotropical America, the Caribbean Islands excepted. The center of diversity is southeastern Brazil, while Central America has only two species, *S. incarnata* and *S. richii*. The base chromosome number of the genus is $x = 13$. There are presently 25 species of *Sinningia* in cultivation.

The extensive synonymy of *Sinningia* reflects some of the taxonomic difficulties botanists have had with this genus rich in variation of the shape of the corolla.

Sinningia Nees, Ann. Sci. Nati., Sér 1, 6: 296. 1825.
Gesnera (or *Gesneria*) Martius, Nov. gen. 3: 27. 1829; not *Gesneria* L. 1753.
Tapina Martius, Nov. gen. 3: 59. 1829.
Alagophylla Rafinesque, Flora Telluriana 2: 33. 1837.
Megapleilis Rafinesque, ibidem, 2: 57. 1837.

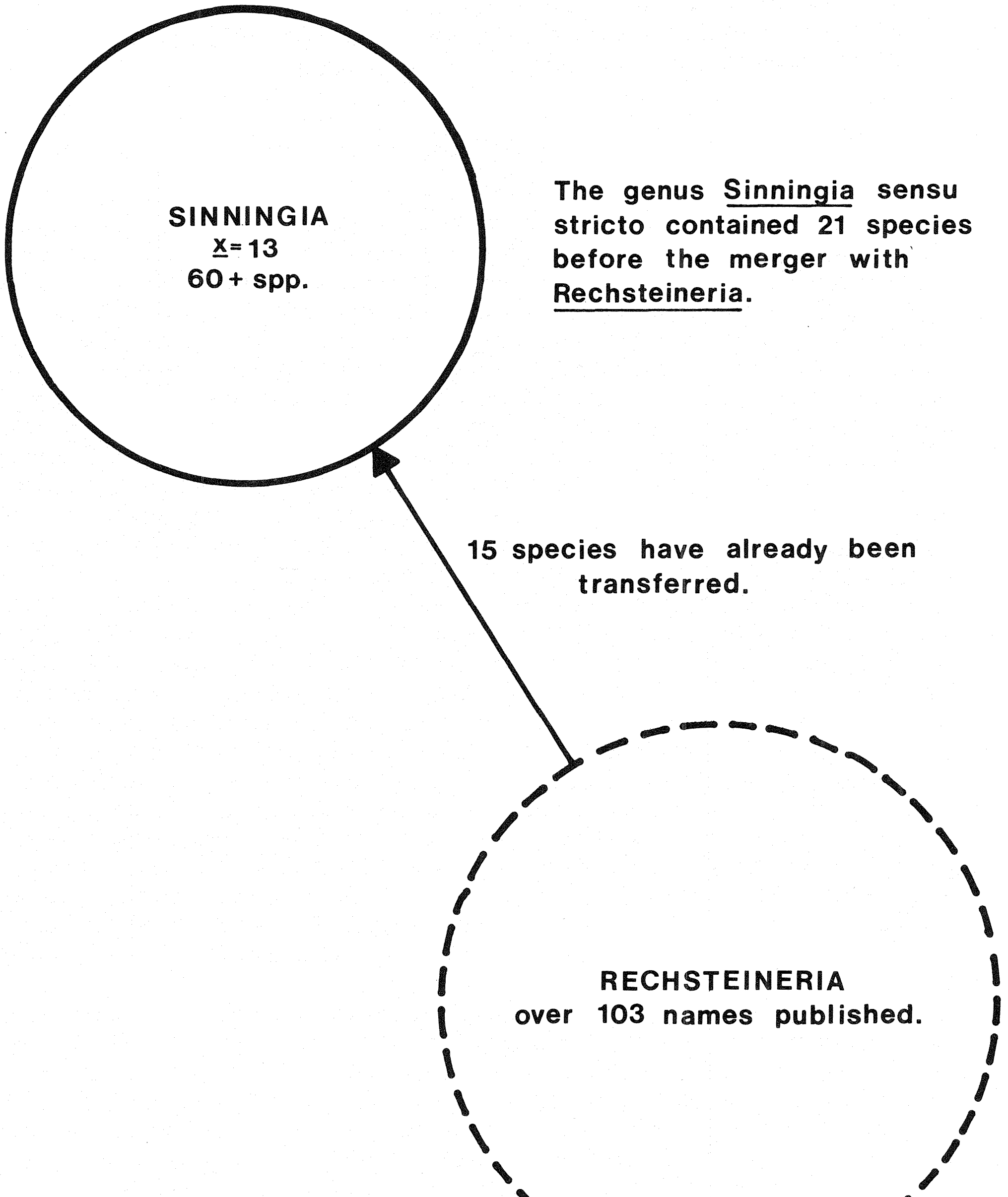

Plate 3. A revision of *Sinningia* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

Styrosinia Rafinesque, ibidem 2: 95. 1837.
Tusisma Rafinesque, ibidem 2: 98. 1837.
Fimbrolina Rafinesque, Sylva Telluriana 71. 1838.
Tapeinotes DC., Prodr. 7: 544. 1839.
Corytholoma (Bentham) Decaisne, Rev. Hort. 20: 466. 1848.
Gesneria Martius, sect. *Corytholoma* Bentham, Plant. hartweg. 230. 1846.
Dircaea Decaisne, Rev. Hort. 20: 466. 1848.
Ligeria Decaisne, Rev. Hort. 20: 463. 1848.
Rechsteineria Regel, Flora 31: 247. 1848.
Stenogastra Hanstein, Linnaea 26: 205. 1854.
Dolichodeira Hanstein, Linnaea 26: 205. 1854.
Orthanthe Lemaire, Ill. Hort. 3: pl. 81 in text. 1856.
Biglandularia Seemann, Gard. Chron. 29: 738. 1872; not *Biglandularia* Karsten
Rosanowia Regel, Gartenflora 21: 33. 1872.
× *Gloxinera* Weathers, Gard. Chron., ser. 3, 17: 144. 1895. An illegitimate combination for hybrids between *Gloxinia* hort. (= *Sinningia*) and *Gesnera* Martius (= *Rechsteineria*).

Type species: *Sinningia helleri* Nees, Ann. Sci. Nat. Sér. 1, 6: 297. 1826.

Lembocarpus Leeuwenberg and *Lietzia* Regel

These two monotypic genera are the only other representatives in the tribe Gloxinieae with underground tubers. *Lembocarpus amoenus* Leeuwenberg is native to the montane forests of Surinam and French Guiana. The stem is reduced to the tuber which produces usually only a single leaf and separate inflorescences per season, and the ovary is reported to be superior. This interesting species was recently brought into cultivation and appears to produce hybrids with *Sinningia* (Wiehler, unpublished data).

A collection of the apparently bat-pollinated *Lietzia brasiliensis* Regel & Schmidt from southeastern Brazil has recently been brought into cultivation in Europe. Breeding experiments should therefore soon establish whether or not these two genera belong within the limits of *Sinningia*. Both genera have an annular nectary, (nonfunctional in *Lembocarpus*), a condition so far unknown in *Sinningia*. But then again, the shape of the nectary is more variable in *Sinningia* than in other genera of the Gesnerioideae. The shape of the nectary is, nevertheless, the chief indicator of sections within *Sinningia*.

Lembocarpus Leeuwenberg, Acta Bot. Neerl. 7: 318. 1958.
L. amoenus Leeuwenberg, Acta Bot. Neerl. 7: 319, 418, Fig. 28. 1958. Ibidem, 14: 137. 1965.

Lietzia Regel, Gartenflora 29: 97. 1880.
L. brasiliensis Regel & Schmidt, Gartenflora 29: 97, pl. 1005. 1880.

Lietzia brasiliensis, native to the state of Espirito Santo in Brazil, is known only from very few collections.

CHAPTER 31: THE MONOTYPIC GENERA *ANODISCUS, KOELLIKERIA,* AND *PEARCEA*

All three of these monotypic taxa, known to science for over 100 years, are native to the rain-forested slopes of the Western Cordillera, and have scaly underground rhizomes.

Anodiscus Bentham

Anodiscus xanthophyllus (Peoppig) Mansfeld looks for all practical purposes like a species of *Kohleria* but with white corollas. The plants, from one-half to two meters tall, are native to the Andes of Peru, in the provinces of Cuzco, Ayacucho, Junin, Huanuco, San Martin, Loreto, and Amazonas. Originally described as *Gesnera xanthophylla* by Poeppig in 1840, this species differs from the rest of the tall-growing taxa in the tribe Gloxinieae by the absence of the nectary, a decisive feature in the American Gesneriaceae. There exists as yet no information concerning the pollinator of this Peruvian endemic. The isophyllous leaves, either decussate, ternate, or whorled, preclude the placement of *A. xanthophyllus* in *Monopyle*, in which the species are strongly anisophyllous and without a nectary. The chromosome number is $x = 13$. This species has been in limited cultivation for a few years. Its nomenclatural history has been as follows:

Anodiscus Bentham, in Bentham & Hooker, Genera plantarum 2: 998. 1876.

Anodiscus xanthophyllus (Poeppig) Mansfeld in Fedde, Repert. 36: 124. 1934.

Gesnera xanthophylla Poeppig, in Poeppig & Endlicher, Nova genera ac species plantarum 3: 7. 1840.

Rechsteineria xanthophylla (Poeppig) Kuntze, Revisio generum plantarum 2: 474. 1891.

Anodiscus peruvianus Bentham, in Hooker, Icones plantarum, t. 1199. 1876.

Koellikeria Regel

Koellikeria erinoides (DC.) Mansfeld is one of the most widely distributed gesneriads of the New World, ranging from the province of Salta in northwestern Argentina along the Western Cordillera northwards to Costa Rica, and eastwards to Venezuela and the States of Goias and Mato Grosso in Brazil. The reason for the success of this small terrestrial, rosette-forming species of the montane rain forest is not yet understood, for the local populations in any given area appear to be very small and scattered. The fruit is a dry, bivalved capsule with tiny seeds, but long-distance dispersal by wind or water hardly accounts for the pattern of distribution of this species.

The key feature of *Koellikeria* is its inflorescence with alternate bracts, a character shared with *Smithiantha.* The chromosome number is $x = 13$. Clones of collections from coastal Venezuela and from Puyo, Ecuador, are in cultivation in North America and Europe. A hybrid established with *Kohleria spicata* (Kunth) Oersted as × *Koellikohleria rosea* is still in cultivation (Wiehler, 1968).

Foreign elements attributed to *Koellikeria* in the past are *Monopyle subdimidiata* (Klotzsch & Hanstein) Mansfeld, first described as *Koellikeria subdimidiata*, and *K. mexicana* Matuda, conspecific with *Smithiantha cinnabarina* (Lindley) Kuntze. *Koellikeria major* Fritsch, described from a collection from Bolivia, is mainly a color variant, in spite of the somewhat larger size of the flower, as seen on the isotype at GH, *Fiebrig 2680*. The dorsal side of the corolla tube is pinkish instead of the more typical red-maroon. Similar color variants occur also in populations in Costa Rica and have arisen as mutations in seedlings of the cultivated collections from Venezuela (Wiehler, unpublsihed data). Fristch's species falls therefore within the range of variation within *K. erinoides* and is thus best regarded as a synonym of the latter. The nomenclature of the monotypic genus is as follows:

Koellikeria Regel, Flora 31: 249. 1848.

Koellikeria erinoides (DC.) Mansfeld, in Fedde, Repert. 38: 28. 1935.
Achimenes erinoides DC., Prodromus 7: 536. 1839.
Achimenes argyrostigma Hooker, Bot. Mag. 71: t. 4175. 1845.
Koellikeria argyrostigma (Hooker) Regel, Flora 31: 249. 1848.
Koellikeria argyrostigma (Hooker) Regel,
var. *ovalifolia* Oersted, Centralamericas Gesneraceer 15. 1858.
var. *moritziana* Hanstein, Linnaea 34: 431. 1865.
var. *chlorocaula* Hanstein, ibidem.
Koellikeria major Fritsch, in Engler, Bot. Jahrb. Syst. 50: 398. 1914.

Pearcea Regel

Pearcea hypocyrtiflora (Hooker) Regel is geographically the most restricted of the three monotypic genera treated here. It has been spottily collected within a 60 kilometer area north of Tena in the province of Napo, Ecuador. A single collection comes from a nearby region in the province of Pastaza. The almost globose, hypocyrtoid (orange-red) corolla, unusual in the Gloxinieae, set *Pearcea* traditionally apart from the rest of the genera of the tribe. Pouched corollas occur also in *Parakohleria*, but *Pearcea* differs from the latter by its epedunculate, 1-2-flowered inflorescence, and by the bilobed stigma. Even though *Pearcea* has been in cultivation since 1971, all hybridization attempts with species of *Kohleria*, *Parakohleria*, *Gloxinia*, and other taxa have failed so far. The base chromosome number is $x = 13$.

In 1936 Mansfeld attributed a second species to the genus, *P. schimpfii* from Mera, Pastaza province, Ecuador. This species fits well into the new genus *Parakohleria* and was transferred to it (Wiehler, 1978a). The nomenclature of *Pearcea hypocyrtiflora* is as follows:

Pearcea Regel, Gartenflora 16: 388. 1867.

Pearcea hypocyrtiflora (Hooker) Regel, ibidem.
Gloxinia hypocyrtiflora Hooker, Bot. Mag. 93: t. 5655. 1867.
Isoloma hypocyrtiflorum (Hooker) Bentham, in Bentham & Hooker, Genera plantarum 2: 1002. 1876.
Hypocyrta brevicalyx Hort., Gard. Chron. May 4: 458. 1867. Nomen nudum.

CHAPTER 32: THE BRAZILIAN GENERA *PALIAVANA* AND *VANHOUTTEA*

Both *Paliavana* and *Vanhouttea* are native to southeastern Brazil. Their species are shrubs or subshrubs without tubers or scaly underground rhizomes. The relationship between the two genera is not clear at present. Both of them are based mainly on differences in the shape of the corolla. The flowers of *Paliavana* fit into the pollination syndromes for bats and large bees, and the red tubular corollas of *Vanhouttea* indicate ornithophily. The affinity between these two Brazilian taxa may eventually turn out to be the same as that of *Rechsteineria* to *Sinningia* (Chapter 30).

Paliavana Vandelli

The corolla in *Paliavana* is comparatively large and campanulate, and its color either green with maroon dots, greenish yellow, blue-purple, or cream-white with a green tinge. The nectary consists of five separate, large and rounded glands, and the ovary position is semi-inferior. There are at least seven species of *Paliavana* in southeastern Brazil, but, with the exception of two of these, they are scantily represented in herbaria collections. Only four of the species have validly published names: *P. lasiantha* Wiehler, *P. racemosa* (Vell.) Fritsch, *P. tenuiflora* Mansfeld, and *P. werdermannii* Mansfeld.

There exists some doubt about the identity of the type species of the genus, and its nomenclature was until recently clouded by confusion. The generic name *Paliavana* was published by the Portuguese botanist Domingos Vandelli (b. 1735, d. 1816) on page 40 of his *Florae lusitanicae et brasiliensis specimen* . . . in 1788 and accompanied by an illustration of the flower ("Fig. 17," here reproduced as Figure 394). As in other botanical publications at the beginning of the scientific era, the ground rules for the naming of new genera and species were not yet well defined. Vandelli did not provide a generic diagnosis or circumscription for his new genus *Paliavana*. Instead, he gave a fairly detailed description of the floral character of the new species, aided by the illustration, but without supplying a specific epithet. Which species of *Paliavana* did Vandelli have in mind? A study of the genus and the distribution of its species narrows the choice down to two. *Paliavana lasiantha* and *P. racemosa* are the only two taxa occurring in the coastal and montane region around Rio de Janeiro. Both species were comparatively frequently collected since the beginning of botanical explorations in Brazil. *Paliavana racemosa* was described and illustrated by the Portuguese-Brazilian botanist José Vellozo (b. 1742, d. 1811) near the end of his life as *Orobanche racemosa* and published posthumously (Vellozo 1829; 1835). The somewhat stylized text figure of Vandelli bears a great resemblance to the flowers of the unrefined illustration of Vellozo's species. Both drawings are quite distinct from the shaggy appearance of the corolla of *Paliavana lasiantha* native to the same area. It appears, therefore, fairly certain that the type species of the genus *Paliavana* Vandelli is *P. racemosa* (Vellozo) Fritsch.

Is Vandelli the sole author for the genus *Paliavana*? Martius (1829:62), several editions of the *Index kewensis*, and the editors of the recent *Flora of Bahia* cite the authorship of *Paliavana* as "Vellozo in Vandelli" or "Vellozo ex Vandelli," while Bentham (1876), Fritsch (1893-94), and the *Index nominum genericorum* (Farr et al., 1979) attribute the authorship to Vandelli alone. Hanstein (1854-1865) does not employ the name *Paliavana* in his extensive work on the Gesneriaceae. Stafleu (1967) ascribes the authorship of *Florae lusitanicae* . . . exclusively to Vandelli. The internal evidence shows that about two-thirds of the taxa cited in *Flora lusitanicae* . . . are followed by the capital letter "B," and the others by the annotation "Vellozo." Sometimes the descriptions are initialled by "B" and the accompanying "observations" are authored by the letter "B," thus excluding Vellozo from the authorship. The letter "B" (or lower-case "b") stands traditionally for the Latin word *beatus* (blessed) and refers to deceased botanists. Its usage in *Florae lusitanicae* . . ., however, remains unexplained for Vandelli was 53 years old at the time of the publication of his work in 1788, and he lived to be 81 years old. Whatever the interpretation of the initial "B" may be, in the case of *Paliavana* it established Domingos Vandelli as the sole author. Martius and others could possibly have construed Vandelli's *Florae lusitanicae* . . . as co-authored by Vellozo because of the latter's contributions to the text, but then the authority for *Paliavana* would have been "Vandelli *et* Vellozo" or vice versa.

As if a problem of authorship and the identity of its type species were not enough of a burden for this small Brazilian genus, there existed also a nomenclatural confusion about the type species of *Paliavana*. The epithet *P. racemosa* is not the earliest name for the type species. Herbaria collections of this taxon and live material in cultivation have during the past 20 years been labelled as *P. prasinata* (Ker-Gawler) Bentham.

The story starts with the publication of *Gesneria prasinata* Ker-Gawler in *Bot. Reg.* 5:428 on 1 January 1820. The type specimen, "native of the Brazils," was a collection sent by Sir Abraham Hume from Wormleybury near London to Kew Gardens (K) in the summer of 1819. There is no such type material deposited at K. The Lindley Herbarium at the University of Cambridge (CGE) has a sheet in its type collection labelled as the holotype of *G. prasinata* Ker-Gawler, but with two different species pasted up on the same sheet (Figure 395).

Species A (stems and flowers glabrous) is labelled in Lindley's handwriting: "*G. prasinata*, *B. Reg.* 428." Species A agrees fully with the type illustration of plate 428. Species B (stem and flowers villous) is a collection of *Sellow (s.n.)* from Brazil, sent to England from the Herbarium at Berlin, and labelled in a German script: "*Gesnera prasinata* Ker." Species B represents the main element in the text of Ker-Gawler's publication. But there are also some elements of species A in the text: the ringed stem occurs only on species A, never on species B (both species A and B are represented in my live research collection in Sarasota). The leaves are described as decussate by Ker-Gawler, yet most collections of species B, including the Sellow collection on the type sheet at CGE, have ternate leaves. The leaves in species A are decussate.

Lindley thought several years later that Ker-Gawler's Brazilian material did not fit into the concept of the genus *Gesneria*. He not only established a new genus to accommodate it, but he also chose a new specific epithet for the same material: *Codonophora grandiflora* Lindley, *Bot. Reg.* 13: sub t. 1110, 1827. Lindley's superfluous and illegitimate epithet is based on the same mixed-up type and publication of Ker-Gawler. Lindley apparently regarded species A as the type of Ker-Gawler's *Gesneria prasinata* (we do not know whether the Sellow collection of species B was already pasted up on the type sheet in 1827), for Lindley wrote directly under the specimen of species A: "*Codonophora grandiflora* mihi in *B. R.* 1110" and also "*G. prasinata*, *B. Reg.* 428."

During the past 160 years, workers in neotropical Gesneriaceae have been divided almost evenly in their choice of either species A or species B as the type of *Gesneria prasinata* Ker-Gawler:

Lindley (1827)	Species A	Fritsch (1900)	Species B
Martius (1829)	B	Leeuwenberg (1957*)	B
Hanstein (1864)	B	H. E. Moore (1965*)	A
Bentham (1876)	A	Wiehler (1970-1980*)	A

*Dates of herbarium specimen determinations

Since it seems impossible to arrive at any satisfactory solution as to which of the two species, A or B, should bear Ker-Gawler's epithet, I propose to declare *Gesneria prasinata* Ker-Gawler a *nomen confusum* to be excluded from further consideration of the names of the two species involved (cf. articles 69 and 70 of the International Code of Botanical Nomenclature). Lindley's epithet *grandiflora* needs to be regarded in the same manner as it is based on the same mixed-up type and publication in *Bot. Reg.* 5.

The next available name for species A is *Orobanche racemosa* Vellozo, published in *Florae fluminensis* between September and November 1829 (*fide*

Species A

This is either the holotype or a clonotype of the plate (and the text pro parte)of the two very different species published in Bot. Reg. 5:428 as Gesneria prasinata Ker-Gawler. Based on conflicting elements, this combination has to be regarded as a nomen confusum. There is no type specimen for G. prasinata deposited at K. This sheet is, however, the holotype of Codonophora grandiflora Lindley, signed in Lindley's hand (mihi) on the cut-off portion of the sheet.

Species B on the left, with ternate leaves and without a ringed stem, represents the major element in the text of Bot. Reg. 5:428. This particular Sellow s.n. collection, however, could not have been the material Ker-Gawler used for his description, because it came from the Berlin Herbarium, labelled in a German script (see letter "s" and the absense of "i" in Gesneria) "Gesnera prasinata Ker, doubtlessly written after Ker's publication of the name. K has two sheets of the same Sellow collection from Berlin, labelled "Gesnera prasinata Ker, 1840." The Sellow collection of species B on this sheet appears to have been added later and thus could not be any type material. I did not find any type material of species B at K; apparently Ker-Gawler did not deposit any type of species B labelled Gesneria prasinata. Hans Wiehler, 1981

Paliavana racemosa (Vell.) Fritsch
Holo- or clonotype of plate of Gesneria prasinata Ker-Gawl. Holotype of Codonophora grandiflora Lindley. H.W. 1981
Determined by Hans Wiehler
THE MARIE SELBY BOTANICAL GARDENS

Figure 395: Sheet from the Lindley Herbarium labelled *Gesneria prasinata.*

Stafleu), with a plate published in 1831. In the absence of any herbarium material for *O. racemosa*, this plate is herewith designated as the type. The nomenclature and synonymy for species A is, therefore, as follows:

Paliavana racemosa (Vellozo) Fritsch, Bot. Jahrb. Syst. 29, Beiblatt 65: 18. 1900.

Orobanche racemosa Vellozo, Florae fluminensis 1:243. 1829; ibidem, 4: tab. 72. 1831.

Gesneria prasinata Ker-Gawler *pro parte*, Bot. Reg. 5: 428. 1820, *nomen confusum et rejiciendum.*

Paliavana prasinata (Ker-Gawler) Bentham, in Bentham & Hooker, Gen. plant. 2: 1003. 1876.

Codonophora grandiflora Lindley, Bot. Reg. 13: sub. t. 1110. 1827, *nomen superfluum et illegitimum*, based on the same confused type of *Gesneria prasinata* Ker-Gawler.

Prasanthea paniculata Decaisne, Rev. Hort. 20: 467. 1848, *nomen superfluum et rejiciendum*, based on the confused type of *Gesneria prasinata* Ker-Gawler.

Codonophora selloana Hanstein, in Martius, Flora bras. 8(1): 396. 1864.

Hanstein cited for his *Codonophora selloana* as syntypes the collections of seven persons: Sello(w), Houllet, Riedel, Gaudichand, Schott, Luschnat, and Lhotsky, without collection numbers and herbarium citations. There are three sheets of *Schott 6112* from "Rio-Janeiro" at W, and one of these bears the legend *Codonophora Selloana* Hanst. in Hanstein's handwriting. I designate this sheet as the lectotype of *C. selloana.* The collections used by Hanstein at Berlin were destroyed in 1943.

Species B was given the name *Paliavana sericiflora* by Bentham in Bentham & Hooker, *Gen. plant.* 2: 1003, 1876, but Bentham based this name on *Gesneria prasinata* Ker-Gawler, *sensu* Martius (1829:37) and Hanstein (1864: 395), or, in other words, on the same confused type and publication cited above. Bentham's new name was not accompanied by a diagnosis or description for species B.

I propose, therefore, a new name for species B: *Paliavana lasiantha* Wiehler, with a new type collection from Minas Gerais. The description and illustration are located at the end of this work. The synonymy is as follows:

Paliavana lasiantha Wiehler, nom. nov.

Gesneria prasinata Ker-Gawler *pro parte*, Bot. Reg. 5: 428. 1820, *nomen confusum et rejiciendum.*

Paliavana prasinata (Ker-Gawler) Bentham, in Bentham & Hooker, Gen. plant. 2: 1003. 1876.

P. sericiflora Bentham, ibidem, a name based on the confused and rejected type and description of *Gesneria prasinata* Ker-Gawler.

Paliavana racemosa occurs in southeastern Brazil in the States of Rio de Janeiro, Guanabara, Minas Gerais, and Bahia. *Paliavana lasiantha* has been collected in the states of Paraná, Río de Janeiro, and Minas Gerais. Among the rest of the named species, *P. tenuiflora* is native to the state of Bahia, and *P. werdermannii* is known from three collections in the state of Minas Gerais. *Paliavana lasiantha, P. racemosa*, and *P. tenuiflora* are in cultivation, and hybrids between them have been established (Wiehler, unpublished data).

The nomenclatural profile of the genus *Paliavana* is as follows:

Paliavana Vandelli, Florae lusitanicae et brasiliensis specimen . . . 40. 1788.
Codonophora Lindley, Bot. Reg. 13: sub. t. 1110. 1827.
Gesneria Martius, section *Prasanthea* DC., Prodromus 7: 532. 1839.
Prasanthea (DC.) Decaisne, Rev. Hort. 20: 467. 1848.

Vanhouttea Lemaire

The corolla in *Vanhouttea* is tubular and red, indicating pollination by hummingbirds. The nectary consists, as in *Paliavana*, of five separate, large, rounded glands (sometimes connected at the base by a narrow ring). The ovary is semi-inferior or almost completely inferior. The species of the genus are almost exclusively native to the state of Río de Janeiro. One collection is reported from Minas Gerais, another from Goias. The type species is *Vanhouttea calcarata* Lemaire, which is among its congeners, together with *V. gardneri* (Hooker) Fritsch, the most numerous represented in herbaria. There appears to be a certain amount of local or regional variation within both of these species, and their synonomy is extensive. The nomenclatural history of this group is as follows:

Vanhouttea Lemaire, Bull. Soc. Hort. Orleáns 1: 346. 1845.
Houttea
Houttea Decaisne, Rev. Hort. 20: 462. 1848, superfluous substitute name.

Vanhouttea calcarata Lemaire, Bull Soc. Hort. Orleáns 1: 346. Jan. 1845.
Houttea pardina (Hooker) Decaisne, var. *calcarata* (Lemaire) Decaisne, Rev. Hort. 20: 461. 1848.
Houttea calcarata (Lemaire) Decaisne, ibidem, 460 (plate).
Gesneria salviifolia Gardner, London J. Bot. 4: 129. 1845.
Houttea salviifolia (Gardner) Hanstein, in Martius, Flora bras. 8(1): 395. 1864.
Vanhouttea salviifolia (Gardner) Kuntze, Rev. gen. 2: 478. 1891.
Gesneria pardina Hooker, Bot. Mag. 74: t. 4348. 1848.
Houttea pardina (Hooker) Decaisne, Rev. Hort. 20: 461. 1848.
Gesneria aggregata "Ker," forma *depauperata* Wawra, Itinere principum S. Coburgi I, p. 79, 1883.

Vanhouttea gardneri (Hooker) Fritsch, Bot. Jahrb. Syst. 29, Beiblatt 65: 14. 1900.
Gesneria gardneri Hooker, Bot. Mag. 70: t. 4121. 1844.
Houttea gardneri (Hooker) Decaisne, Rev. Hort. 20: 462. 1848.
Gesneria leptopus Gardner, London J. Bot. 4: 129. 1845.
Houttea leptopus (Gardner) Hanstein, in Martius, Flora bras. 8(1): 393. 1864.
Vanhouttea leptopus (Gardner) Kuntze, Rev. gen. 2: 478. 1891.

Vanhouttea lanata Fritsch, Bot. Jahrb. Syst. 29, Beiblatt 65: 16. 1900.
Alloplectus tomentosus Glaziou, Bull. Soc. Bot. France 58, Mem. 3f: 515. 1911, *nomen nudum.* (This combination occurs on printed labels in herbarium collections.)

Vanhouttea mollis Fritsch, Bot. Jahrb. Syst. 37: 495. 1906. (This taxon may fit into the complex of *V. calcarata.*)

Vanhouttea bradeana Hoehne, Sellowia 9: 42. 1958. (= *V. gardneri?*)

CHAPTER 33: THE ANDEAN GENERA *CAPANEA* AND *HEPPIELLA* *

CHAPTER 34: THE MIDDLE AMERICAN GENERA *SMITHIANTHA* AND *SOLENOPHORA* *

CHAPTER 35: THE GENERA WITH A ROTATE COROLLA: *BELLONIA, PHINAEA,* AND *NIPHAEA* *

PART 4B: THE TRIBE EPISCIEAE

CHAPTER 36: THE GENERA *EPISCIA, ALSOBIA, NAUTILOCALYX,* AND *PARADRYMONIA*

These four genera possess no differentiating floral characters; they have the same type of nectary, the same subglobose capsular fruit, and the same base chromosome number, $x = 9$. Yet they differ decisively from one another in vegetative characters and appear to have no close generic affinity. In spite of numerous attempts, no hybrids have been established to date between *Alsobia* and *Episcia*, *Episcia* and *Nautilocalyx*, or between *Nautilocalyx* and *Paradrymonia.* In contrast, interspecific hybrids of these taxa are partially fertile. Recently a preliminary revision of this group was published (Wiehler, 1978b), and Plate 4 shows the new disposition of the four genera.

Episcia Martius

Episcia was one of the most vaguely defined genera of the neotropical Gesneriaceae, based solely on floral and fruit characters. By this traditional concept, *Episcia* would include over 100 species today, consisting of several groups of vegetatively strongly discordant elements: small terrestrial stoloniferous herbs with a sympodial shoot pattern and two stolons per node, epiphytic stoloniferous perennials with one stolon per node, succulent terrestrial herbs with a monopodial shoot pattern, lianas, and epiphytic rosette-forming plants with large and leathery, lanceolate leaves. But when examined from the viewpoint of pollination biology, it soon becomes evident that the only factor holding this diverse assembly of taxa together is their common euglossophilous flowers. The breeding evidence (Wiehler, 1970: 103, Table 14; 1976a), indicates that these so-called "episcoid" groups are apparently not even closely related. The occurrence of a fairly uniform floral structure among them is apparently a case of parallel or convergent evolution. The important generic markers for such taxa are therefore not floral characters but vegetative features, or specifically, plant habit.

Plate 4 illustrates the revision of *Episcia*: 19 species were transferred to *Nautilocalyx*, 16 species were set aside to constitute the reinstated genus *Paradrymonia*, and two species were segregated to reestablish *Alsobia. Episcia* and *Alsobia* are easily separated from *Nautilocalyx* and *Paradrymonia* by their stoloniferous habit, otherwise unknown in the Gesnerioideae, and by their sympodial shoot pattern. There are typically two stolons per node in the terrestrial or saxicolous genus *Episcia*, and one stolon per node, in alternating leaf axils, in the strictly epiphytic genus *Alsobia*. All attempts to produce hybrids between these two stoloniferous genera have failed, but the interspecific hybrids within these genera are partially fertile.

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* Manuscripts not received for publication.

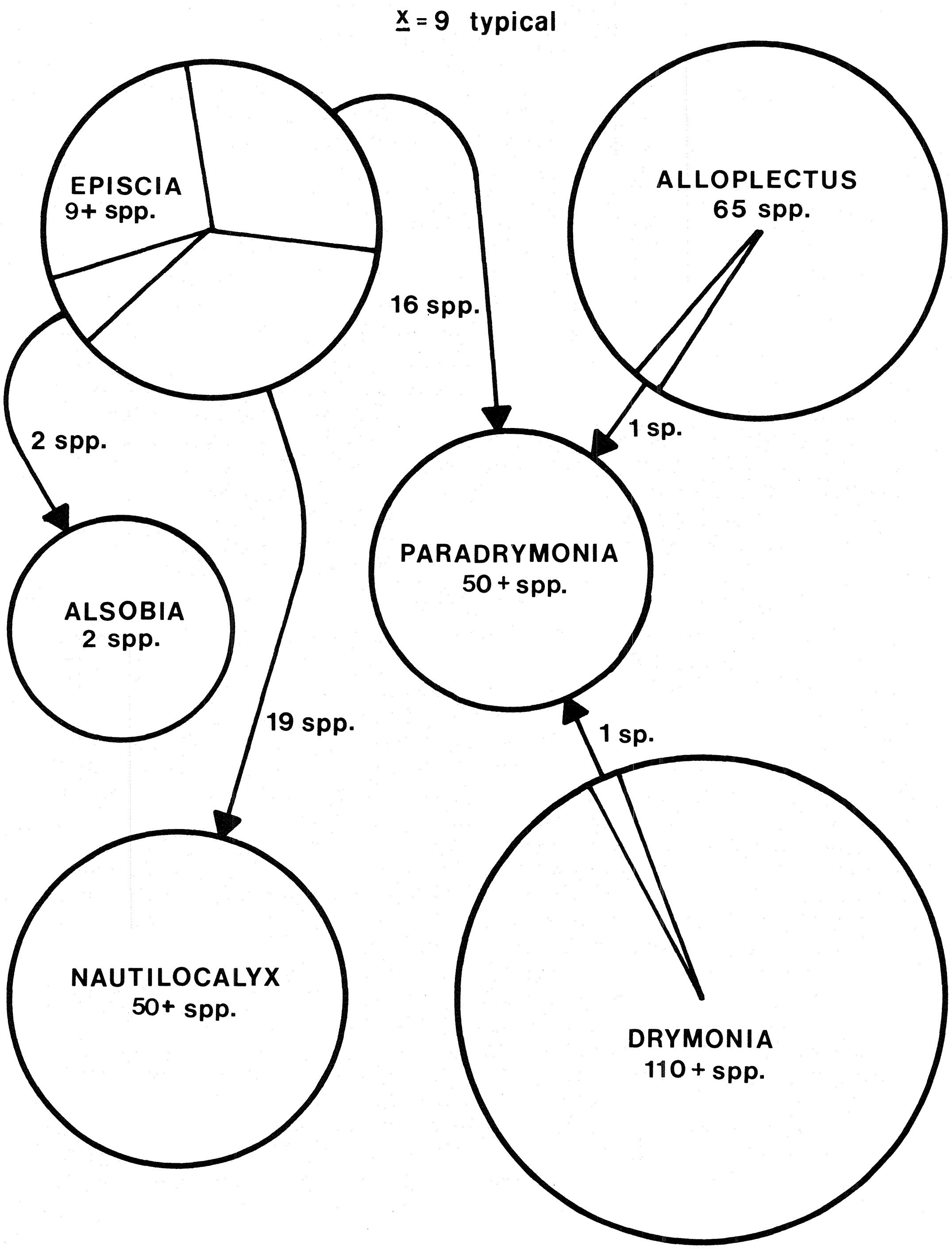

Plate 4. A revision of *Episcia* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

This drastic revision leaves *Episcia* as a small genus of nine or more species, distibuted from Peru north to Colombia, Venezuela, the Guianas, and the Amapa and Planalto regions of Brazil. The only psychophilous species in the group, *E. lilacina*, occurs from Antioquia and the Choco in Colombia north to Nicaragua. Two species, *E. cupreata* (Hooker) Hanst. and *E. reptans* Mart., have apparently changed from euglossophily to ornithophily (Wiehler, 1978b). Five of the nine species are in cultivation. Several species still await description. The placement of *E. hirsuta* (Benth.) Hanst. from the Guayana Highland is somewhat problematic: this species produces stolons in some collections in the wild (as seen in herbarium specimens), but not in the three collections in cultivation. The hybrids between *E. cupreata* and *E. lilacina* Hanst. and between *E. cupreata* and *E. reptans* are partially fertile.

Alsobia Hanstein

Alsobia is a strictly Middle American genus of two epiphytic species. The difference in stolon formation and sympodial shoot development between *Alsobia* and *Episcia* are illustrated in Figure 397. There is also a difference in leaf structure. While the adaxial epidermal cells of leaves of *Episcia* consist of a single layer of regular size, the same cells in *Alsobia* are enlarged as water storage tissue or comprise a multiple layer, a hypodermis.

The two species of *Alsobia* appear to have disjunct distributions although this may be attributed to the fact that epiphytes are usually poorly collected. *Alsobia dianthiflora* (H. E. Moore & Wilson) Wiehler is known only from two collections, one in the province of Guerrero in Mexico, the other from the province of Guanacaste in Costa Rica. *Alsobia punctata* (Lindl.) Hanst. has been found in the provinces of Jalisco and Oaxaca in Mexico and in an unknown locality in Guatemala. Both species are in cultivation, and their hybrid *A.* 'Cygnet' has a pollen stainability of 76%.

Nautilocalyx Linden ex Hanstein

The salient features of *Nautilocalyx* are: plants always terrestrial, the stems usually soft and sappy, erect, ascending, or creeping, rarely forming loose rosettes, the corolla infundibular, and the fruit subglobose and capsular.

The genus was established by Linden and Hanstein early in the 1850's, soon submerged into *Episcia*, but revived again by Sprague in 1912 for a few species. Recent hybridization experiments showed that the section *Skiophila* of *Episcia sensu lato* belongs with *Nautilocalyx* (Wiehler, 1970; 1976a, Table 3). The hybrids with *Nautilocalyx* are partially or completely fertile, while all attempts at crossing this section with the true species of *Episcia* failed. Several other sections of *Episcia* sensu lato (Wiehler, 1978b) fit easily into the concept of *Nautilocalyx*, which now appears to encompass a very natural assembly of plants. A total of 19 species were transferred from *Episcia* to *Nautilocalyx* (cf. Plate 4). Many new species remain to be described and published.

Nautilocalyx now contains over 50 species, distibuted throughout tropical America but absent from southeastern Brazil. There are 22 species of *Nautilocalyx* in cultivation.

Paradrymonia Hanstein

This genus is facultatively epiphytic. The plant habit is either a loose rosette on a low stem or a liana with suffrutescent stems. Many species are cauliflorous. Within the tribe Episcieae, *Paradrymonia* and *Episcia sensu stricto* appear to be among the more distantly related genera. As illustrated on Plate 4, 16 species were transferred from *Episcia* to *Paradrymonia* (Wiehler, 1978b).

There are now over 50 species in this very natural group; many of the species still await description. *Paradrymonia* is native to all of tropical America with the exception of southeastern Brazil and the Caribbean Islands. The center of diversity appears to be Colombia. While the majority of the species are endemic to very restricted areas, one species, *P. metamorphophylla* (Donn.-Smith) Wiehler, is disseminated along the western Cordillera from Peru to Costa Rica. Eleven species are presently in cultivation.

CHAPTER 37: THE GENERA *ALLOPLECTUS, CORYTOPLECTUS, COBANANTHUS, DRYMONIA, COLUMNEA, DALBERGARIA, PENTADENIA,* AND *TRICHANTHA*

This assemblage of genera is treated here as a unit because both of the drastically revised key genera, *Alloplectus* and *Columnea*, contributed species to the same segregate genera, *Pentadenia* and *Trichantha.* Plate 5 explains the somewhat complicated transfer of taxa.

Alloplectus Martius

Alloplectus and *Columnea*, like *Achimenes* and *Episcia* discussed above, have been wastebasket genera almost since their inception. In fact, the circumscription of *Alloplectus* was vague and confused from the start since the two new species which follow Martius' generic description later turned out to be heterotypic synonyms of *Nematanthus hirtellus* (Schott) Wiehler and *Drymonia coccinea* (Aublet) Wiehler. Of the five species cited by Martius as belonging to his new genus *Alloplectus*, only two fit into the traditional and present concept of this taxon, namely, *A. hispidus* (Kunth) Mart. and *A. cristatus* (L.) Mart. The other three are members of *Dalbergaria, Drymonia,* and *Nematanthus.* As later botanists added more species to *Alloplectus*, its definition gained in clarity. More than 100 species were attributed to this genus, including several foreign elements. A preliminary revision of *Alloplectus* maintains about 65 species in the genus (Wiehler, 1973b).

The name *Alloplectus* Martius was conserved in the International Code of Botanical Nomenclature in 1906 against older names for this plant group, with *A. sparsiflorus* Mart. [= *Nematanthus hirtellus* (Schott) Wiehler] as the lectotype. If the name *Alloplectus* is to be kept for nomenclatural stability, a new lectotype must be chosen. In a formal proposal, the species *Alloplectus hispidus* (Kunth) Mart. will soon be presented to the General Committee on Botanical Nomenclature to be published in *Taxon.*

The concept of the genus *Alloplectus* was recently clarified mainly 1) through the establishment of chromosome numbers for this group and related genera, 2) by an intensive study (of live material) of the type of fruit produced by these taxa, and 3) by a clearer definition of the genus *Drymonia* with its specialized anthers.

Alloplectus is now a genus of about 65 species of mostly terrestrial, upright plants, often with large foliage, but also containing some scandent or vining epiphytes with small leaves (Wiehler, 1973b).

A hypodermis is absent from the lamina of the leaves. The inflorescence is usually a pendent, simple or compound, pair-flowered cyme, often reduced to 1-2 flowers, usually with a shortened peduncle. The corolla has typically either a constricted throat with a nearly regular narrow limb and an inflated

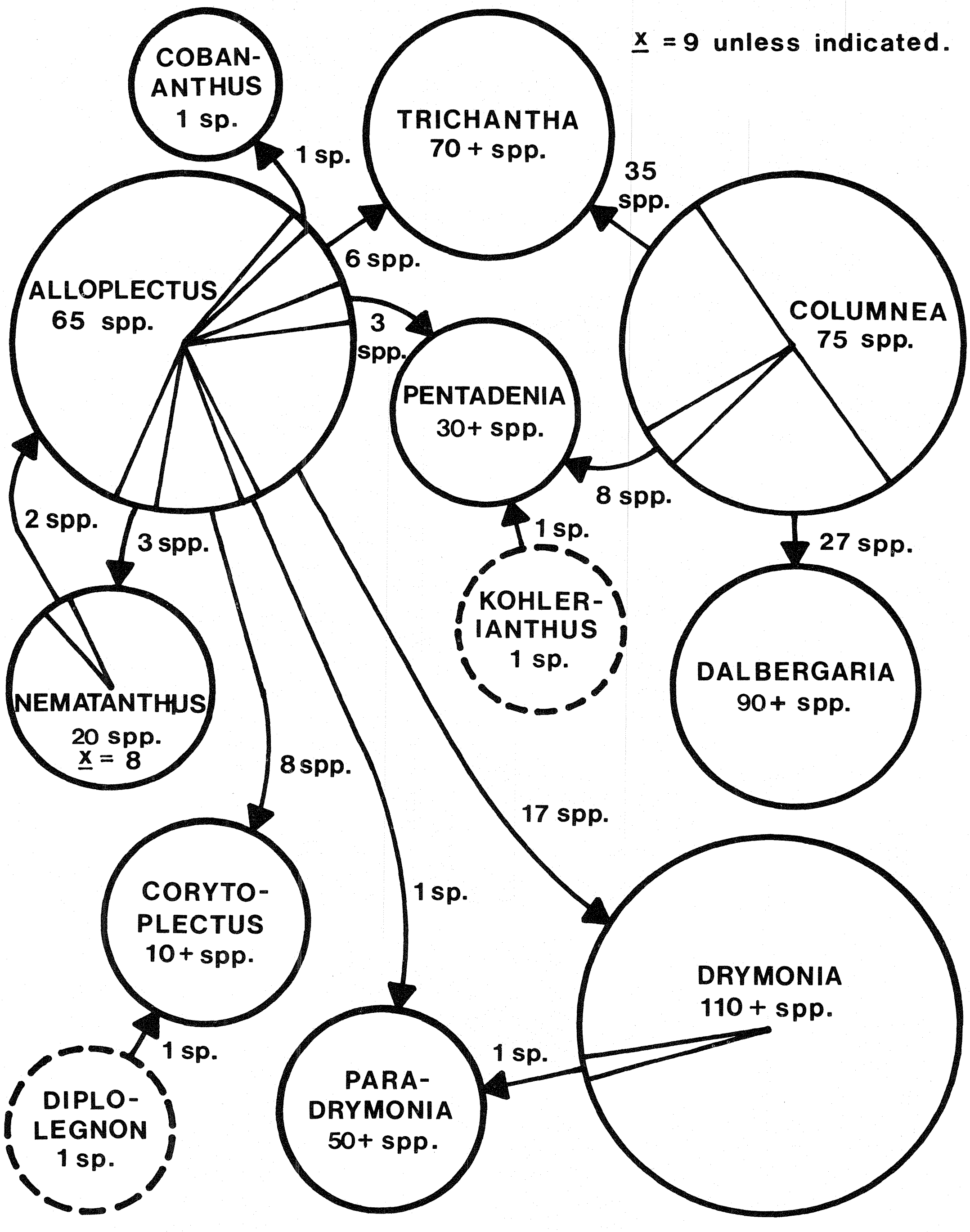

Plate 5. A revision of *Alloplectus* and *Columnea* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

pouch below the entrance (*A. ichthyoderma* Hanst.), or it is shaped like the *Nematanthus* corolla, with a widened throat laterally compressed, as in *A. tetragonus* (Oersted) Hanst. The fruit is a specialized display device, shared also by the genera *Drymonia*, *Nematanthus*, *Codonanthopsis*, and *Codonanthe* subgenus *Codonanthella*: a fleshy capsule in which two valves recoil at maturity, displaying a compact and pulpy cone-shaped mass of enlarged fleshy funiculi and seeds. The components of the fruit, the calyx, the inside of the carpel walls, and the soft cone, usually exhibit contrasting colors. The base chromosome is $x = 9$.

The genus is distributed over all of tropical America except in southeastern Brazil and the Greater Antilles. Eleven species are presently in cultivation.

The discordant elements excluded from *Alloplectus* comprise: 17 species with *Drymonia*-type anthers and a hypodermis; berry-fruited taxa, placed either in the reinstituted genus *Corytoplectus*, or into *Pentadenia* and *Trichantha*; three southeastern Brazilian species with a hypodermis and a chromosome number of $n = 8$, assigned to *Nematanthus*, and two species with a plain capsular fruit, one of which was placed into *Paradrymonia*, and the other into a new, monotypic genus *Cobananthus* (Plate 5).

Corytoplectus Oersted

Corytoplectus, recently reinstituted (Wiehler, 1973b), is a strictly terrestrial genus of the wet montane forest. The leaf arrangement remains decussate at maturity, and the leaf pairs are more or less of equal size. The inflorescence is always erect in the leaf axils, cymose, and pseudo-umbellate. The sepals are of equal length, and the corolla is almost erect in the calyx, tubular, with a constricted opening, often with a slight pouch. The nectary consists usually of 2-4 opposite separate glands, rarely reduced to a connate double gland. The fruit is a globose, shiny black berry, or transparent with the black seeds visible within. The base chromosome number is $n = 9$.

There are more than ten species of *Corytoplectus* distributed in the western Cordillera from Bolivia to Panama (Chiriquí), and in the coastal range and in the Guayana Highland in Venezuela. Seven species are in limited cultivation. The monotypic Bolivian genus *Diplolegnon* Rusby fits into the concept of *Corytoplectus* and has been synonymized. Its type species, *C. riceanus* (Rusby) Wiehler, is a close relative of the type species of *Corytoplectus*, *C. capitatus* (Hooker) Wiehler, from coastal Venezuela.

Cobananthus Wiehler

The single species of this genus has had the distinction of being associated with both *Alloplectus* and *Columnea*, yet fitting into neither (Wiehler, 1977a). It differs from both genera by its fruit, a thin, subglobose capsule of the episcioid type. Yet the floral characters place it outside the *Episcia* alliance and necessitated the establishment of a new genus.

Cobananthus is facultatively epiphytic. The leaf arrangement remains decussate at maturity, and the leaf pairs are subequal. The calyx of the axillary flowers is actinomorphic (a rare occurrence in the Gesnerioideae), and the corolla is tubular and narrow. The fruit is a subglobose, papyraceous, bivalved capsule. The only species of the genus, *C. calochlamys* (Donn.-Smith) Wiehler, is illustrated in Wiehler (1977a: 93, Plate 28B). The chromosome number is $n = 9$. This species is endemic to the region of Cobán, Alta Verapaz, Guatemala.

Drymonia Martius

The original concept of *Drymonia* was based on the leafy calyx and the large corolla of *D. serrulata* (Jacq.) Mart. [and its synonyms *D. calcarata* Mart. and *D. spectabilis* (Kunth) Mart.; cf. Figure 28], an ubiquitous neotropical species with considerable regional variation, pollinated by bats (and probably also by Euglossine bees). *Drymonia* is now a genus of over 110 species, consisting mostly of epiphytic lianas or subshrubs. The majority of the species are gynandro-euglossophilous, while others are ornithophilous and sphingophilous. The salient feature of *Drymonia* is therefore not the shape of the flower, as postulated by Martius, but the uniquely specialized anthers which all species have in common (Figure 71). The *Drymonia* anthers are, in fact, unique among all angiosperms. A second earmark of the genus is the display fruit, a fleshy capsule (Figure 64).

There is, however, a special development of the fruit within *Drymonia* which warrants the establishment of a separate subgenus, *Drymoniella.** Several species are strictly terrestrials with square, fleshy stems, and large, subequal leaves which remain decussate at maturity (rather than twisting to become isoplanar, as in the epiphytic species), and their fruit is a subglobose berry. The species are *D. sulphurea* Wiehler, *D. turrialvae* Hanst., *D. urceolata* Wiehler, and probably also *D. pulchra* Wiehler and *D. utuanensis* Wiehler. The fruit of the latter has not yet been observed. There is no difference in floral features between the new and the typical sections. Three species have gynandro-euglossophilous flowers, and the red-flowered *D. urceolata* appears to be pollinated by hummingbirds. These species also have the same anthers as the rest of *Drymonia*, and since these peculiar anthers are the key feature of the genus, it seems best to keep these few terrestrial species in *Drymonia.*

Drymonia occurs in moist forests throughout the neotropics, with a center of diversity in Colombia and Ecuador. Most of the species are local endemics, but some species are established successfully over large areas: *D. serrulata*, *D. alloplectoides*, *D. coccinea*, *D. coriacea*, *D. macrophylla*, *D. turrialvae*, and *D. warszewicziana.*

Columnea Linnaeus

The Linnaean genus *Columnea sensu lato* today would comprise over 270 species. This includes a large number of undescribed material soon to be published. However, a closer examination of this vast aggregation of species, in the field, in cultivation, and in the herbarium, made it evident that *Columnea* was just as much a wastebasket genus as were *Achimenes*, *Kohleria*, *Episcia*, and *Alloplectus* before their revisions. The concept of *Columnea* had become so vague in the last decades that almost any berry-fruited undescribed species (except *Codonanthe*) was given a provisional herbarium name under *Columnea*, including taxa published later as *Rufodorsia* and *Neomortonia*. Even *Cobananthus calochlamys* and *Alsobia punctata* (the latter newly described as *Columnea septentrionalis* Morton) were associated with *Columnea* in the 1960s.

The discordant elements within *Columnea* consisted of three large but homogenous and clearly delimited groups which were recently separated from *Columnea*, as the genera *Dalbergaria*, *Pentadenia*, and *Trichantha* Wiehler, 1973b, 1975c). The small, recently described genus *Bucinellina* rep-

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* Drymonia Mart. subg. Drymoniella Wiehler, subg. nov.
Differt a subgenere typico fructu bacca.
Type: *Drymonia turrialvae* Hanst.

resents a fifth element in this columneoid group (Wiehler, 1977a). Encountering a large degree of diversity within a genus, the classifying botanist has to decide whether these differences can remain on the sectional or subgeneric levels, or whether they merit separate generic status. The latter choice reflects more truly the situation in the columneoid complex. The tribe Episcieae is a fairly close-knit group of genera, and the distance or proximity in relationship between, for instance, *Dalbergaria* and *Columnea sensu stricto* is about the same as between *Paradrymonia* and *Episcia sensu stricto*. The most obvious distinctive character between these pairs of taxa is plant habit. The differences in plant habit between these genera are so clear-cut that these taxa can be distinguished one from another in the rain forest and in the greenhouse from a distance. Figure 74 illustrates the habit of *Dalbergaria. Pentadenia*, likewise, differs from the other columneoid genera, and in fact, from all other taxa in the tribe Episcieae, by its nectary structure, a generic character of primary importance in the subfamily Gesnerioideae (Figures 62k, 62n). The typical columneoid corolla shape (Figure 29) is absent from *Trichantha*, and *Columnea* differs from all other columneoid taxa (and from all other genera in its tribe) by the shape and morphology of its pollen grains (Williams, 1978) (Figure 398). While many interspecific hybrids within *Columnea*, *Dalbergaria*, *Pentadenia*, and *Trichantha* are either partially or completely fertile, their intergeneric hybrids are sterile. Hybrid sterility, in combination with other characters, is a good generic marker in the Gesnerioideae.

In terms of pollination biology and thus evolution and speciation, there is one major difference between the five columneoid genera and other large taxa in the American Gesneriaceae such as *Drymonia*, *Gesneria*, *Gloxinia*, *Kohleria*, and *Sinningia*. Each of the genera just cited contains a wide range of corolla shapes and colors because they employ different classes of pollinators. Much of the past taxonomic confusion in these groups resulted from the use of the corolla as the prime diagnostic trait for the definition of genera and sections. The columneoid genera, by contrast, are almost exclusively ornithophilous, the flower colors are limited to orange-red or yellow, rarely white, and the shape of the corolla shows little basic variation: it is either a narrow tube with a small subregular limb (Figure 1) or an inflated tube with a somewhat wider, subregular limb, or the typical *Columnea* corolla with a long and gradually widening tube, and the limb consisting of a galea, two small lateral lobes, and a long and narrow lower lobe (Figure 2). Here the similarity of the corolla (as in *Kohleria* and *Moussonia*) caused the lumping of all taxa with this flower type and with berries into a single genus *Columnea*, regardless of other differences. This difference in the mode of speciation between the columneoid genera and the other large taxa in the American Gesneriaceae needs to be considered in their taxonomic treatment.

The five columneoid genera, *Bucinellina*, *Columnea sensu stricto*, *Dalbergaria*, *Pentadenia*, and *Trichantha*, now constitute very natural generic units in the tribe Episcieae. They are similar to the new generic delimitations within the alloplectoid and episcioid complexes, and consistent with the concepts of the rest of the genera in the tribe Episcieae. This certainly was not the case with the unwieldy conglomerate of *Columnea sensu lato*. There is still abundant variation left within each of the four larger columneoid genera for the establishment of sections.

Columnea sensu stricto is now a genus of about 75 species of epiphytic herbs and subshrubs with ascending, spreading, or pendent stems. The flowers are borne either above or below the foliage; the corolla has a basally narrow, gradually widening (never inflated) tube, with a distinct galea, and a long and narrow, reflexed lower lobe. The pollen is oblong, with a pertectate sexine, and little differentiation around the apertures or colpi (Williams, 1978). The oblong shape of the pollen grain distinguishes *Columnea* from all other genera of the Gesnerioideae (Figure 398). The berry is globose or subglobose and usually white.

The species of *Columnea* are mainly native to Middle America and the Caribbean Islands with a center of diversity in Panama and Costa Rica (over 20 species in each country). Only five species occur in Colombia, one in Ecuador, and another five in Venezuela, the Guayana Highland and adjacent areas in northeastern Brazil. About 56 species and varieties of *Columnea* are in cultivation to date, and the number of named hybrids is about 140. The numerous intergeneric hybrids with the other columneoid genera are all sterile (× *Colbergaria*, × *Coltrichantha*, × *Coltadenia*, and × *Trichanthenia*, Wiehler, 1976b).

Dalbergaria Tussac

The genus *Dalbergaria* can be separated from the rest of the columneoid taxa by a combination of two characters: its distinct pattern of shoot growth, easily recognizable in field, greenhouse, and herbarium, and by the fruit, a usually colored, *ovoid* berry. The suffrutescent, thick stems of these epiphytes usually branch only near the base. The subsessile leaves are in close-set, imbricating, distichous pairs of which one is stipule-like, the other large and oblanceolate or elliptic, the pairs alternating in respect to their sizes, giving a fern-frond-shaped appearance to the branches. The underside of the lamina is often marked with species-distinct red patterns, a possible aid to pollination by hummingbirds. The axillary inflorescences are hidden from above. The corolla is either tubular with a subregular, narrow limb or somewhat inflated with an irregular, bilabiate limb, or somewhat *Columnea*-like in a few species (section *Cryptocolumnea*). The pollen grains of *Dalbergaria* are suboblate to prolate spheroidal with considerable differentiation around the colpi (Williams, 1978).

There are over 90 species in *Dalbergaria*, occurring in montane and rain forests from Bolivia to the Guianas and north to Mexico, and on the Greater Antilles. The center of diversity is Colombia and Ecuador. There are about 25 species in limited cultivation. One natural hybrid is known from Panama.

Pentadenia Hanstein

The salient feature by which *Pentadenia* is separated from related genera and from all other taxa in the tribe Episcieae is the presence of five individual nectary glands of which the two dorsal ones are sometimes connate. The plant habit of this epiphytic taxon varies from erect or ascending subshrubs (*P. matudae* Wiehler, *P. nervosa* Oersted) to scrambling lianas [*P. strigosa* (Benth) Hanst.] to scandent and pendent, thin-stemmed trailers with small leaves (*P. colombiana* Wiehler). The corolla is usually a narrow tube with a small limb with subequal lobes, but the corolla tube can also be somewhat or even strongly inflated, and the limb bilabiate, and the upper two lobes are fused into a galea in *P. strigosa*. The pollen grains are oblate spheroidal with a well-differentiated area around the colpi (Williams, 1978). The fruit is a globose or subglobose berry, usually white, in some species lavender.

There are about 30 or more species in *Pentadenia*, distributed from Bolivia along the Western Cordillera north to Mexico with one species in the coastal range of Venezuela. The center of diversity is Ecuador. Eleven species are in limited cultivation.

Trichantha Hooker

Trichantha is a genus of about 70 species of mostly vining, spreading, or scandent epiphytes with the opposite leaf pairs usually of unequal size. Some species such as *T. acuminata* (Benth.) Wiehler, *T. anisophylla* (DC) Wiehler, and *T. erythrophylla* (Hanst.) Wiehler, have *Dalbergaria*-like fern-frond shoots, but always in combination with long, thin, vining and scandent branches, a feature unknown in *Dalbergaria*. The flowers are usually borne below the spreading branches. The corolla is typically a straight and narrow tube [*T. ambigua* (Urban) Wiehler, *T. pulchra* Wiehler] or the tube is inflated, (*T. ciliata* Wiehler, *T. minor* Hooker), with a limb varying from subregular to strongly bilabiate. A galea is present in some species with a centrally strongly inflated but distally constricted corolla tube [several species in the *T. dictophylla* (Donn.-Smith) Wiehler alliance].The pollen grains are, as in *Pentadenia*, oblate spheroidal, with a well-differentiated area around the colpi (Williams, 1978). The globose or ovoid berry is usually pink, red, or purple, rarely white.

Trichantha is distinct from *Columnea* by the absence of the typical columneoid corolla and by the differently shaped and textured pollen grains; it differs from *Dalbergaria* by the distinct plant habit of the latter and by the shape of the pollen grains; it is separated from *Pentadenia* by the distinct nectary structure of the latter. *Bucinellina* differs from *Trichantha* by the distinctive shapes of the corolla and of the pollen grains. All intergeneric hybrids involving *Trichantha* are sterile.

Species of *Trichantha* occur from Bolivia along the Western Cordillera north to Guatemala and coastal Venezuela; four species are native to the Greater Antilles; one species, *T. calotricha* (Donn.-Smith) Wiehler, has a curious disjunct distribution from Colombia to Guatemala, and from Surinam and French Guiana to Brazil's Amapá and Pará; another species, *T. ulei* (Mansf.) Wiehler, is isolated in Ceará, Brazil. The center of diversity of *Trichantha* is in Colombia and Panama. Eighteen species are presently in cultivation.

CHAPTER 38: THE GENUS *NEMATANTHUS*

Nematanthus Schrader is now a natural genus of about 20 epiphytic, ornithophilous, perennial herbs and subshrubs, limited to southeastern Brazil. The salient features include two characters difficult to use in keys or ascertain from herbarium specimens: a restricted geographical range and a base chromosome number of $x = 8$, the latter shared only with the genus *Codonanthe* in the American Gesneriaceae. The leaves of all species of *Nematanthus* examined have a hypodermis. The orange, red, or yellow corollas are usually pouched below the constricted entrance with its small and narrow limb, or the throat is wide open but laterally compressed (in the type species of the genus). The fruit is a display capsule as in the genera *Alloplectus*, *Codonanthopsis*, and *Drymonia.*

The genus *Nematanthus* was recently merged with *Hypocyrta* Mart. (Moore, 1973c), as first suggested by Handro (1964: 339) and Wiehler (1970: 111, 220; 1972b). Both genera were originally based on the shape of the corolla (wide throat versus constricted throat with a pouch below, the latter

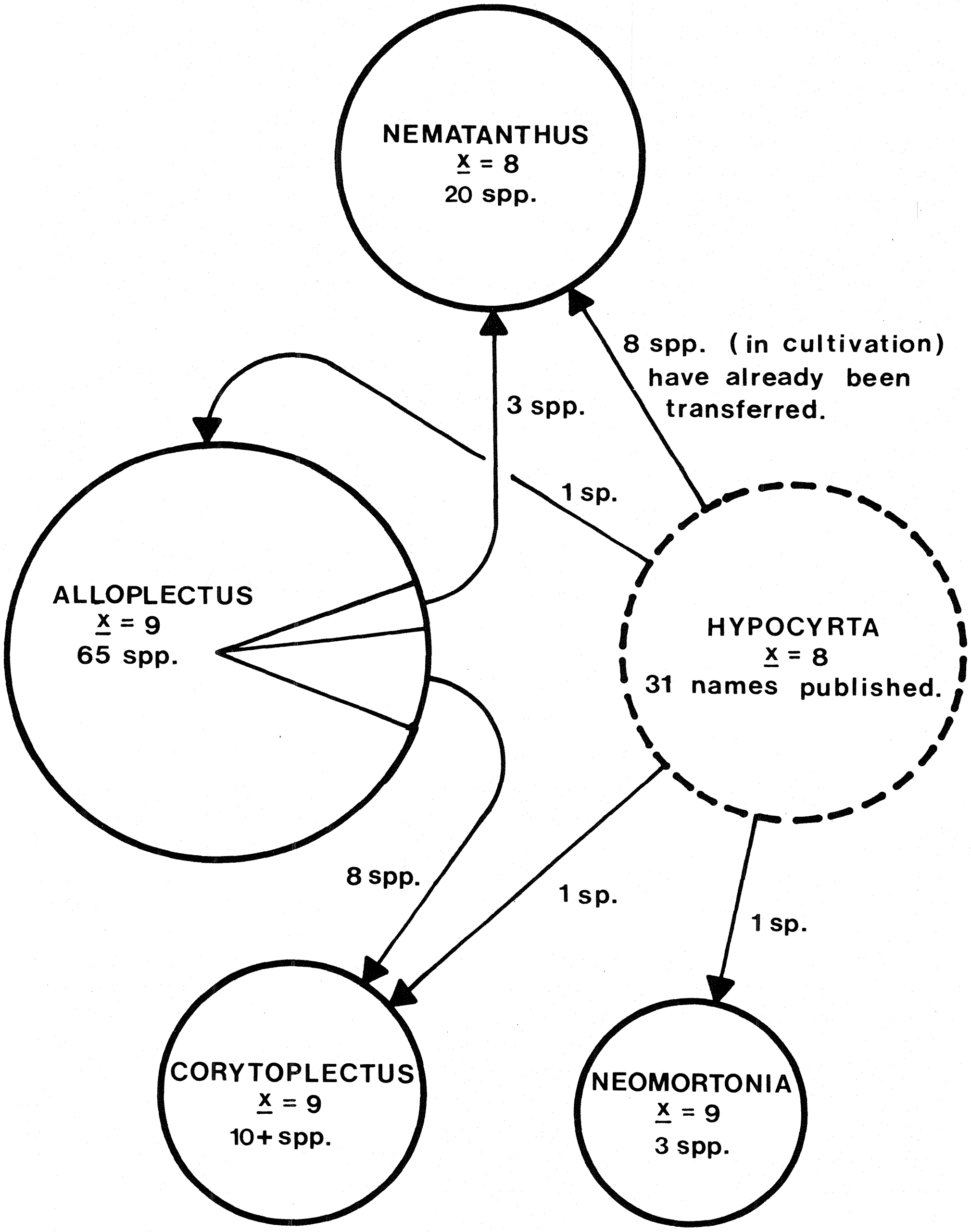

Plate 6. A revision of *Nematanthus* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

the trademark of *Hypocyrta*). Earlier systematists of the Gesneriaceae did not consider that both types of corollas exist also in other genera of this family (Chapter 7). The observation of species in cultivation, the establishment of chromosome numbers, and the production of many partially or completely fertile hybrids (Saylor, 1971; Wiehler, 1972a; and unpublished data) in the *Nematanthus-Hypocyrta* complex indicated a union of the genera.

Several species originally included in *Hypocyrta* have been shifted to other genera (Plate 6). They possessed pouched corollas but differed in chromosome numbers and other features from the *Nematanthus-Hypocyrta* complex. *Hypocyrta teuscheri* Raymond from western Ecuador and adjacent Colombia was transferred to *Alloplectus. Hypocyrta pulchra* N. E. Brown from eastern Ecuador and adjacent Colombia has been placed into *Corytoplectus. Hypocyrta nummularia* Hanst. from the Western Cordillera (Ecuador, Panama, Costa Rica, and Mexico) is now associated (with some reservations) with *Neomortonia* because of its plant habit and its bright orange berries*. This taxonomically problematic species was (after the dissolution of *Hypocyrta* and before the establishment of *Neomortonia*) temporarily placed in *Alloplectus* which has a capsular fruit.

Three species of *Alloplectus*, including its lectotype (see under *Alloplectus*), have been transferred to *Nematanthus* (Wiehler, 1972b, 1973b). The demarcation between these two genera, often confused with one another in the past, is now quite clear: *Alloplectus* does not occur in the territory of *Nematanthus* in southeastern Brazil, its base chromosome number is $x = 9$, and a leaf hypodermis is absent from all species examined, including the epiphytes.

Nine species of *Nematanthus* and about 20 registered hybrids are in cultivation. The flower shapes of the nine species were illustrated in Wiehler (1974).

CHAPTER 39: THE GENERA *CODONANTHE* AND *CODONANTHOPSIS*

Codonanthe (Martius) Hanstein

Codonanthe is an easily recognized genus of about 20 species of vine-like epiphytes, usually associated with ant nests. The salient features are, in order of their importance: the peculiar, broad connectives of the anther cells, unique in the Gesneriaceae (Figure 399), a base chromosome number of $x = 8$, the leaf pairs equal or subequal, and a trumpet- or funnel-shaped corolla, usually white.

There are two kinds of fruit in *Codonanthe*. In the majority of the species, including the type, *C. gracilis* (Mart.) Hanst., the fruit is a globose or subglobose, soft berry, colored either orange, pink, purple, or red (Figure 399). This plump berry may split at times in some species, especially when the plants are water-logged [as observed in *C. crassifolia* (Focke) Morton, *C. gracilis*, and in *C. uleana* Fritsch, Figure 400], but the same plants produce also non-split berries. Although such split berries defy our neat systems of fruit classification, they differ from the second type of fruit found in this genus. Four species in cultivation have a strictly bivalved capsular fruit with

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* The four different collections of this species grown in cultivation (hort.; from Costa Rica; from Chiriquí, Panama; and from Ecuador) produce plump ovoid, orange berries, ca. 13 cm × 10 cm, and not capsules as reported by Moore (1957: 207).

firm but fleshy carpel walls whose tips reflex at maturity (Figure 401). The immature fruits are either cone-shaped (in *C. chiricana* Wiehler and *C. macradenia* Donn.-Smith) or laterally compressed and pointed (in *C. caribaea* Urban and *C. luteola* Wiehler).

Codonanthe, like *Drymonia*, thus has two fruit types, a berry and a capsule. The erection of a subgenus (as in *Drymonia*) for the "aberrant" fruit in the species of *Codonanthe* cited above appears advisable.* Peculiar anther characteristics are the overriding diagnostic features for both genera (cf. Figures 71, 402).**

Species of *Codonanthe* are found in all regions of the neotropics. Three species are particularly widely distributed: *C. crassifolia*, *C. calcarata*, and *C. uleana.* The other species are regional endemics. There are probably several centers of diversity for the genus; both southeastern Brazil and the small country of Panama have at least five species each. Thirteen species are presently in cultivation.

Codonanthopsis Mansfeld

This genus of about six species, established by Mansfeld in 1934, is undoubtedly related to *Codonanthe* but differs from it in several important respects. 1) The most obvious feature is plant habit. The stiff and ascending branches have large (ca. 10-15 cm × 4-6 cm) and fleshy, strongly anisophyllous leaves of which the smaller of the pair is typically stipule-like and early caducous while the species of *Codonanthe* are usually vinelike, with small, equal or subequal leaf pairs. 2) The base chromosome number of *Codonanthopsis* is $x = 9$, but in *Codonanthe*, $x = 8$. 3) The connective of the anther cells in all species of *Codonanthopsis* is narrow as in the rest of the Gesnerioideae (Figures 403-404), but the trademark of *Codonanthe* is the peculiar broad connective spatially separating the pairs of thecae (Figure 402), as was stated by Fritsch (1893-94: 143, 171). 4) The fruit of *Codonanthopsis* is uniformly a pointed but laterally compressed display capsule with reflexed valves and a cone-shaped mass of funicular pulp and seed (Figures 405-406). The fruit in *Codonanthe* is either a round berry or rarely, a capsule, but without the dome of pulp and seed.

Moore (1973a) proposed a union of *Codonanthopsis* with *Codonanthe* for the following reasons: 1) *Codonanthopsis* does not have alternate leaves, as indicated in the generic description by Mansfeld. This feature was used to separate *Codonanthopsis* from *Codonanthe* and all other genera in its tribe. 2) Moore emphasized the aril-like extension of the funiculus, covering the seed, as a diagnostic character uniting these two genera, and apparently "unknown elsewhere in the family." Moore had to discount the traditional androecial key feature of *Codonanthe*, absent in *Codonanthopsis*, in his union of these genera.

A survey of all taxa of the tribe Episcieae supports the maintainance of *Codonanthopsis* as a valid genus. The plant habit alone sets these two genera easily apart in the field and greenhouse. The combination of such characters as extreme anisophylly, a chromosome number of $x = 9$, the narrow anther connective, and the capsular display fruit are here treated as generic markers between *Codonanthopsis* and *Codonanthe*. Aril-like extensions of the funiculi which cover the seeds occur also in other genera of the Episcieae. Arils cover the seeds completely in *Nematanthus hirtellus* (Schott) Wiehler, *Dry-*

Codonanthe

monia rhodoloma Wiehler, and partially in *Nematanthus strigillosus* (Mart.) H. E. Moore, *N. fissus* (Vell.) L. Skog, and other species of *Nematanthus*, in *Episcia reptans* Mart., in *Neomortonia rosea* Wiehler, and probably in many other neotropical gesneriads.

This treatment de-emphasizes the importance of the mode of thecae dehiscence as a generic feature, cited by Fritsch (1893-94) for *Codonanthe*. All species of *Codonanthe* examined have the same type of anther cell dehiscence by a pore near the apex of the cell instead of the longitudinal slit typical of the majority of the Gesnerioideae. But the same type of poral dehiscence also occurs in several (but not all) species of *Paradrymonia* and *Codonanthopsis*. It is clearly not a generic feature in these genera. *Codonanthopsis ulei* Mansf. and *C.* sp. nov. (*Prance et al. 24544*, NY, SEL) have anther cells with pores, but in all collections examined of *Codonanthopsis dissimulata* (H. E. Moore) Wiehler the anthers dehisce by the conventional longitudinal slit (Figure 392c). Basal pores of the thecae are typical for the genus *Drymonia*, but occur also in *Nautilocalyx dressleri* Wiehler (1977a: 111, Plate 32D).

The species of *Codonanthopsis* are distributed along the river systems of the Amazon. *Codonanthopsis dissimulata* apparently has the widest range from the province of Huanuco in Peru to the Kaieteur Plateau in Guyana. An ant nest association has not yet been established for this species, but it is known for *C. ulei.* Both species are in cultivation.

CHAPTER 40: THE NEW GENUS *NEOMORTONIA*

Neomortonia was published as a monotypic genus (Wiehler, 1975a). The funnel-form, fringed flowers of the thin-stemmed, scandent *N. rosea* Wiehler are reminiscent of *Alsobia dianthiflora* (Moore & Wilson) Wiehler, but the bright orange, laterally somewhat compressed berry matches neither the capsular fruit in the stoloniferous genus *Alsobia* nor the berry fruit in any other genus of the tribe Episcieae. Stolons are absent in *N. rosea* which is found from the province of Carchi in northwestern Ecuador north to Costa Rica. This species is also the closest match (in fruit, plant habit, and chromosome number) for a species with a similar geographic distribution (Ecuador to Mexico). It was originally described as *Hypocyrta nummularia* Hanst., and then temporarily placed in *Alloplectus* when the genus *Hypocyrta* was absorbed into *Nematanthus* (Wiehler, 1972b; Moore, 1973c). The presence of ornithophilous pouched flowers [*Neomortonia nummularia* (Hanst.) Wiehler] and gynandro-euglossophilous flowers (*N. rosea*) in the same genus occurs also in *Gasteranthus*, *Drymonia*, and *Paradrymonia*. *Neomortonia nummularia* is found from the province of Cotopaxi in Ecuador to the province of Chiapas, Mexico. A third species, *N. alba* Wiehler, is known from only two localities in Panama. All three species are in cultivation.

CHAPTER 41: THE NEW GENERA *BUCINELLINA*, *RUFODORSIA*, AND *OERSTEDINA*

Bucinellina (Wiehler) Wiehler

The genus *Bucinellina* Wiehler, 1977c; 1981) belongs to the *Dalbergia* alliance. The two epiphytic species in the genus differ in the peculiar trumpet-shaped corolla, in the oblate shape of the pollen grains, and in the depressed shape of the berry from the other columneoid taxa. Both species are from the province of Nariño, Colombia, and are in cultivation.

Rufodorsia Wiehler

Rufodorsia (Wiehler, 1975f) is a member of the tribe Episcieae, but the corollas of the four epiphytic species in this genus match in size, shape, and coloration that of the terrestrial *Koellikeria erinoides* (DC) Mansf. in the tribe Gloxinieae. This short corolla with a red back is therefore unique in the tribe Episcieae. The berry is globose or depressed. All four species are endemic to Panama and Costa Rica, and are in cultivation (Figure 407). The base chromosome number for the genus is $x = 9$ (Wiehler, 1975f).

Oerstedina Wiehler

The three species of *Oerstedina* (Wiehler, 1977c) are closely related to *Rufodorsia* but differ in the larger corollas which are not shaped and colored like that of *Koellikeria erinoides*, and in the pointed shape of the berry. The species have been found in cloud forests in western Panama and in south-central Mexico, and more material may be discovered at points in between.

PART 4C: THE TRIBE BESLERIEAE

CHAPTER 43: THE GENERA *BESLERIA* AND *GASTERANTHUS*

Besleria is the largest genus of the New World Gesneriaceae. The revision by Morton in 1939 was based only on herbarium collections. Until recently, containing about 170 species, this group stood isolated in the subfamily Gesnerioideae as the only genus left in the tribe Beslerieae after Burtt (1963) excluded the tribe and the genus from the Old World subfamily Cyrtandroideae. Field work, the influx of new species, and the cultivation of many species of *Besleria* and related genera have added to our knowledge of this group and delimited these taxa more clearly. The nature of the fruit, almost impossible to discern from herbarium material, proved especially valuable in the new classification.

Besleria Linnaeus

Besleria is a very natural genus in spite of its size (over 200 species). They are terrestrial herbs, subshrubs, shrubs, and a few small trees. The stomata on the underside of the leaves are scattered irregularly, and the vascular trace of the petiole in cross-section is deeply invaginated, in contrast to the taxa in the tribe Episcieae (Figure 85), with which *Besleria* has been confused or associated at times in the past. The typical *Besleria* flower is tubular, red, orange, or yellow, and ornithophilous, has a ring-shaped or semi-annular nectary, and a white (or orange or red) berry as its fruit. The pulp of the berry consists of placental tissue in contrast to the pulp of funicular origin in the berries of the tribe Episcieae.

The species of *Besleria* are native to the rain forests of the entire neotropics with a center of diversity in Colombia and Ecuador. As with many other New World gesneriads, the majority of the species of *Besleria* are local but sharply defined endemics. It is therefore curious that two species are rather widely distributed: *B. laxiflora* Bentham is found from Amazonian Brazil, the Guianas, Venezuela, and Colombia north to Mexico, and *B. solanoides* Kunth occurs from Peru north to Honduras and Andean Venezuela. Twelve species are in limited cultivation, but a systematic hybridization program has not yet been initiated.

A study of live material in the field, greenhouse, and laboratory resulted in the removal of two of Morton's (1939) sections of *Besleria*, and in the reestablishment of the genus *Gasteranthus*, with 27 transferred and many new species (Wiehler, 1975g). The differences in fruit structure and stomate formation are discussed below.

Morton's Venezuelan genus *Pterobesleria* has been submerged in *Besleria* (Wiehler, 1979). The two species of *Pterobesleria* agree in all vital aspects with *Besleria*, and the occurrence of winged calyx lobes, the single feature upon which the genus was founded, falls easily within the acceptable range of variation of floral shapes in *Besleria*. Plate 7 illustrates the recent revision of *Besleria*.

Gasteranthus Bentham

Established by Bentham in 1846, *Gasteranthus* was soon merged by Hanstein (1865) with *Besleria* as a subgenus, and by Fritsch (1893-94) it was further reduced to a section. This fascinating plant group was known until recently only from herbarium material. The species of *Gasteranthus* are, however, easily distinguished from those of *Besleria* in the field and greenhouse by their flower shapes and by their white dots on the underside of the leaves (= large stomatal islands). Since the two taxa differ in decisive fruit characters and epidermal features, *Gasteranthus* was recently reestablished as a genus (Wiehler, 1975g). The fruit in *Gasteranthus*, unknown from herbarium collections, is a fleshy, laterally compressed, bivalved capsule, and the stomates of abaxial leaf epidermis are grouped into large clusters or islands. These features are absent in *Besleria*. The monotypic genus *Halphophyllum* Mansfeld also fits into *Gasteranthus* and has been placed into synonomy (Wiehler, 1975g).

The species of *Gasteranthus*, of which about one-third of the collected material is still undescribed, are found along the Western Cordillera from Peru north to Guatemala. Most of the herbaceous species are local endemics with a center of diversity in Ecuador and Colombia. Two species have a wider range of dispersal: *G. wendlandianus* (Hanst.) Wiehler from Peru to Costa Rica and *G. delphinioides* (Seem.) Wiehler from Colombia to Costa Rica. All species are found in moist, humid, and shaded places at lower altitudes and in cloud forests, usually near waterfalls and streams. All gesneriaceous taxa with clustered stomata occur in the same type of shady and humid environment.

More than 40 species of *Gasteranthus* are presently known, and these can be divided into two obvious groups (which may, however, not correspond to sections). One group has typical ornithophilous flowers with red, orange, or pink *Hypocyrta*-shaped corollas with a contracted entrance, narrow limb, and protruding pouch. The second group has gynandro-euglossophilous flowers with white or cream-colored, tubular-campanulate corollas with a wide entrance and a broad limb, and often with a long spur. Twelve species of *Gasteranthus* are presently in limited cultivation.

CHAPTER 44: THE GENUS *ANETANTHUS*

The monotypic genus *Anetanthus* Hiern ex Bentham has been beset with nomenclatural and taxonomic problems since its inception. Bentham described the genus in 1876, based on a manuscript by Hiern, without citing a type and attributing several species in other genera to *Anetanthus* but not transferring them. A year later Hiern published his manuscript which con-

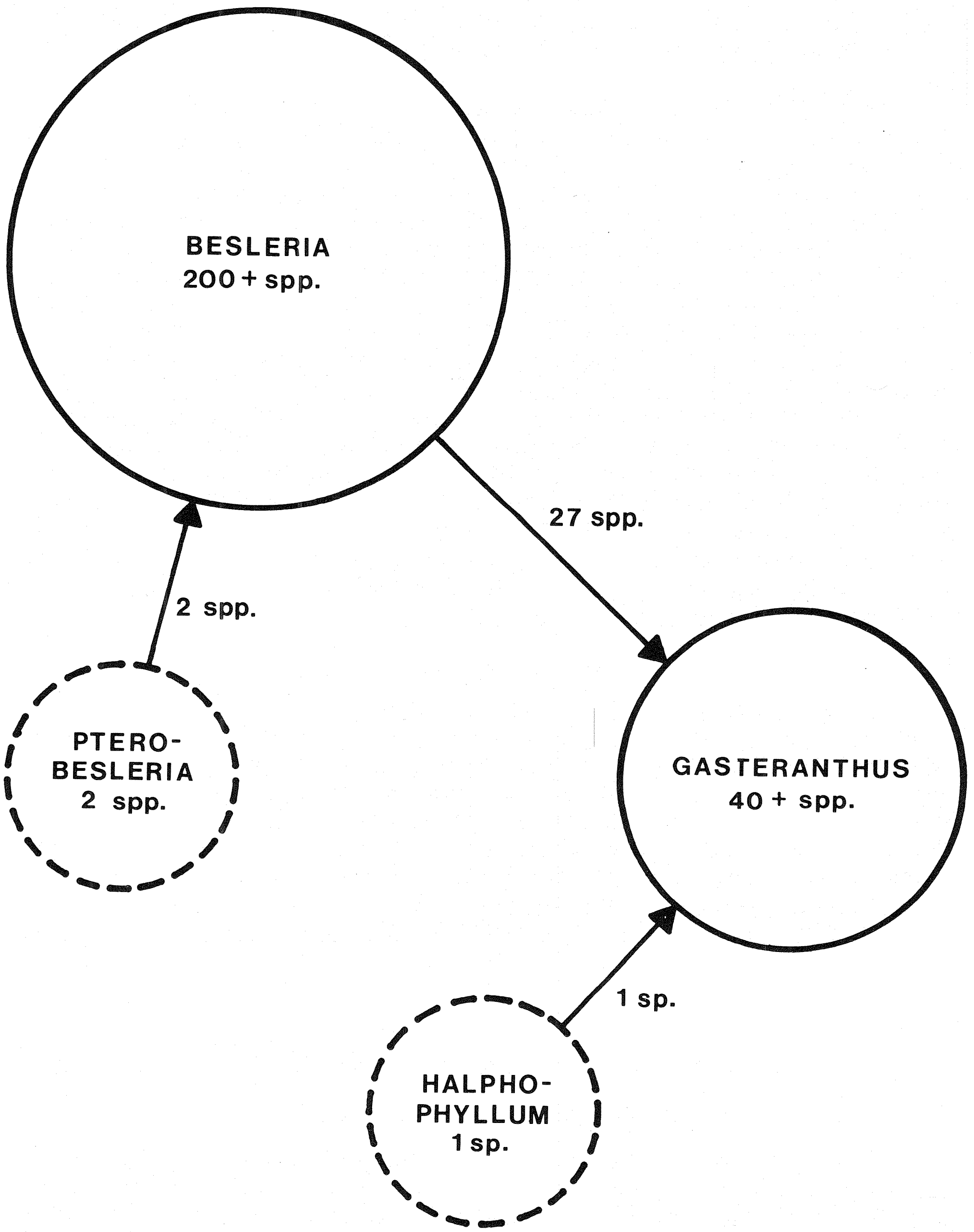

Plate 7. A revision of *Besleria* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

tained a more precise generic description and the new species *A. gracilis* Hiern. He cited Bentham's publication of *Anetanthus* in the Genera Plantarum and repeated Bentham's opinion that several species from other genera belonged to *Anetanthus*. A recent study of the same species indicates clearly that they are foreign to the concept of this genus (Wiehler, 1976a). *Anetanthus* thus remains a monotypic taxon as Hiern's original manuscript indicated.

Anetanthus has three novel features not found in other neotropical Gesneriaceae: 1) the nectary is a five-pronged sheath almost surrounding the superior ovary; 2) the dehiscence of the bivalved capsule is septicidal; and 3) the seeds are flat, discoid, and winged (Wiehler, 1976a: Figures 10, 11). These features, related to pollen and seed dispersal of this widely distributed species, are best interpreted as further indications of the plasticity of the neotropical Gesneriaceae and not as a case of intermediacy between two plant families. In her carpological review of the Gesneriaceae, Ivanina (1965) proposed the placement of *Anetanthus* in the Scrophulariaceae but it would stand there much more isolated than in the Gesneriaceae. The majority of its features are clearly gesneriaceous (cf. Wiehler, 1976a).

Fritsch (1893-94) established the tribe Anetantheae for this genus in the subfamily Cyrtandroideae but Burtt (1963) had to exclude this neotropical tribe in his revision of the Old World subfamily. The bractless inflorescence of *A. gracilis* aligns *Anetanthus* with the tribe Beslerieae, with *Tylopsacas* Leeuwenberg and *Cremosperma* Bentham as close relatives.

Anetanthus gracilis, a small herb growing on cliffs and rock faces, has a surprisingly wide distribution: southeastern Brazil, Bolivia, Peru, and central Colombia. It is not yet in cultivation.

CHAPTER 45: THE NEW GENUS *RELDIA*

The genus closest to *Reldia* Wiehler appears to be *Gasteranthus* with which it shares a similar habitat, the stomates grouped into islands, and a laterally compressed, bivalved (but dry) capsule (Wiehler, 1977a). *Reldia* differs from all other taxa in the tribe Beslerieae by its alternate leaves. One species of the genus, *R. alternifolia* Wiehler, has a cristate epiphyllous inflorescence, observed previously in several Gesneriaceae of the Old World (Weber, 1975). The same type of structure has now been found in *Gloxinia sylvatica* (Kunth) Wiehler (Wiehler, unpublished).

Four species are presently attributed to *Reldia*, all native to Panama and all in limited cultivation.

PART 4E: THE TRIBE GESNERIEAE

CHAPTER 48: THE GENUS *GESNERIA*

The type genus of the family Gesneriaceae and of the subfamily Gesnerioideae is isolated both geographically and developmentally from the rest of the New World Gesneriaceae. Its salient features are its exclusive distribution in the Caribbean region, a distinct base chromosome number of $n = 14$, a specialized vasculature of the petiole (Figures 85e-f), an alternate leaf arrangement in almost all of its species, and an annular nectary.

This Caribbean plant group was treated as a single generic unit by Linnaeus (1753) and Swartz (1788), but later authors (Lindley, 1827; Martius,

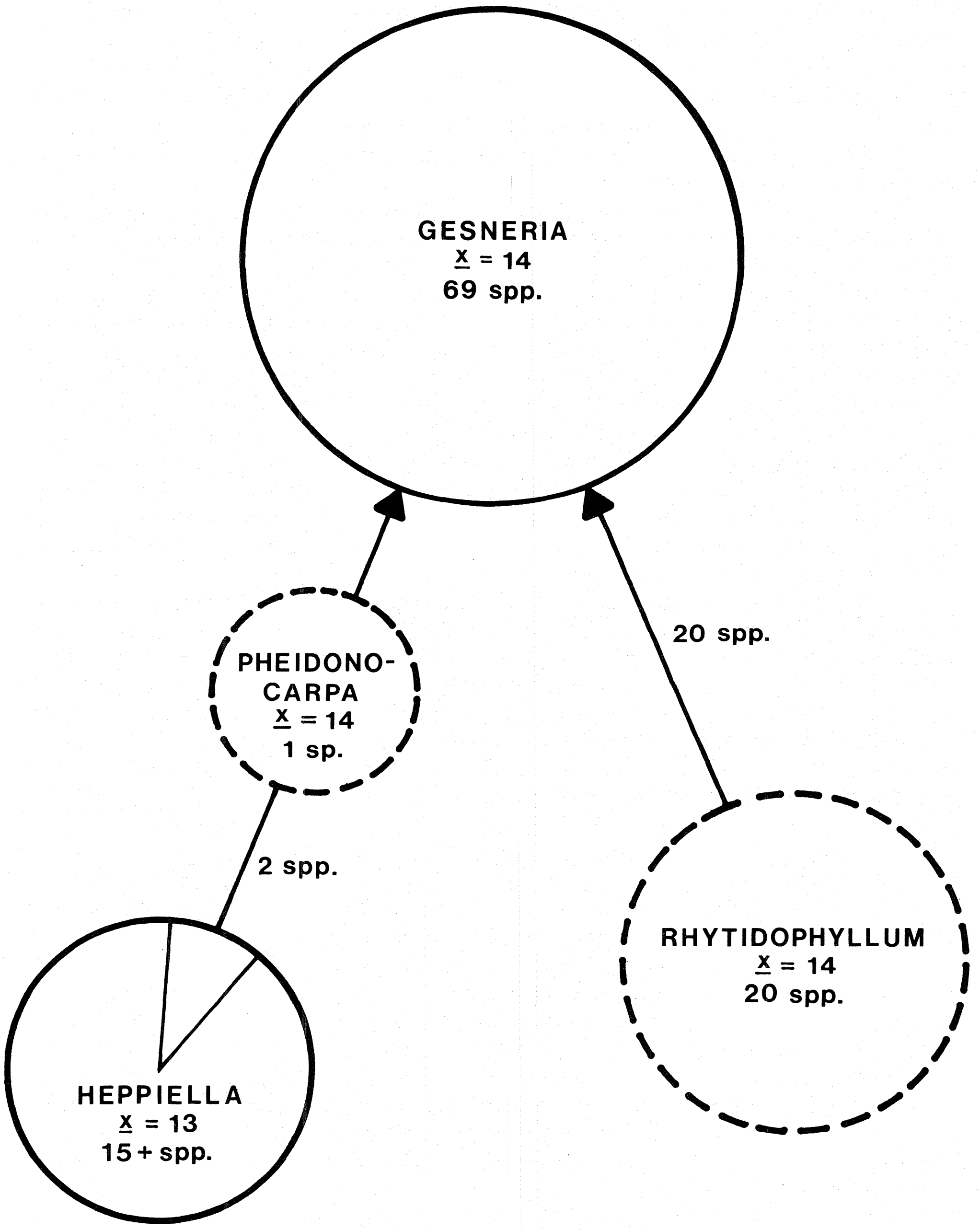

Plate 8. A revision of *Gesneria* with base chromosome number and number of species per genus. Broken circles indicate genera placed into synonymy. Values placed in quotation marks denote the total number of species described in a genus, before synonymization.

1829; Decaisne, 1846, 1847; Hanstein, 1854; Oersted, 1858; Grisebach, 1861) divided Linnaeus' genus into two or more genera, and lost the name *Gesneria* L. in the process. Hanstein (1865) merged most of the segregate genera under (the equivalent of) *Gesneria*, but maintained the genus *Rhytidophyllum* Martius, noting, however, that three species are intermediate between these two genera (*Gesneria corymbosa* Sw.; *G. calycina* Sw., and *G. scabra* Sw.). Bentham (1876) followed closely Hanstein's classification and stated again that the two genera are scarcely distinguishable. Baillon treated this Caribbean group as a single generic unit in 1888, and Kuntze (1891) resurrected the lost name *Gesneria* L. for this taxon while synonymizing *Rhytidophyllum* under *Gesneria*.

In the last major classification of the New World Gesneriaceae, Fritsch (1893-94) went back to the system of Hanstein and Bentham, with the tribe Gesnerieae consisting of *Gesneria* and *Rhytidophyllum*. Urban (1901) considered *Gesneria corymbosa* with its decussate leaf arrangement out of place in the Caribbean genus *Gesneria* and transferred this Jamaican species to the South American genus *Heppiella*. After an anatomical and morphological study of this puzzling group and of the rest of the Gesnerioideae, Wiehler (1970, 1971) recommended again the union of *Gesneria* and *Rhytidophyllum*, and transferred *Heppiella corymbosa* (Sw.) Urban and a companion species from Cuba back to *Gesneria*. Skog published an excellent monograph of *Gesneria sensu stricto* in 1976 but maintained the untreated *Rhytidophyllum* group of about 20 species as a separate generic entity and published a new genus, *Pheidonocarpa*, for *Gesneria corymbosa* (to which the second species from Cuba became a subspecies).

Skog provided a fine summary of the diagnostic characters of the tribe Gesnerieae. However, as his Table 1 (Skog, 1976: 25) indicates, there is no single feature to separate consistently the three genera maintained. It is also noteworthy that none of the characters used by Skog in his key to the tribe (p. 39) to distinguish among the three genera is of generic value in the rest of the genera in the subfamily Gesnerioideae in the present classification. As in the case of the numerous and varied but usually tuberous species of *Sinningia*, and in the form-rich genus *Drymonia* overridingly delimited by its specialized anthers, the 70 species of the Caribbean tribe Gesnerieae are best treated as a single generic unit, the genus *Gesneria*. The single-genus concept expresses best the uniqueness of this taxon as well as its developmental unity and avoids the pitfalls of setting up artificial delimitations which would be in discord with the rest of this classification.

The traditional feature separating *Gesneria sensu stricto* (ca. 50 species) from *Rhytidophyllum* (ca. 20 species) was the degree or length of adnation of the stamen filaments to the base of the corolla tube (filaments adnate for about ½ mm to the base of the corolla = *Gesneria;* filaments adnate for 2-6 mm = *Rhytidophyllum*; cf. Fritsch, 1893-94: 183). This trait is, however, not always consistent, and in *G. cumanensis* (Hanst.) Kuntze and in *G. onacaensis* Rusby, both transferred to *Rhytidophyllum* by Skog in 1976, the filaments are as in *Gesneria*. This character, related to pollination biology, has at best sectional value.

It is impossible to delimit *Gesneria sensu stricto* and *Rhytidophyllum* by a single feature because of a series of intermediate species cited below. Newly examined characters include the abaxial epidermis of the leaf. Wiehler (1970) showed that all species of *Gesneria sensu stricto* have either straight or very shallowly sinuate cell margins of the abaxial surface of the lamina

(Figures 190-203). The majority of the examined species of *Rhytidophyllum* have very deeply undulating cell contours except four species intermediate between the two genera. Many but not all species of *Gesneria sensu stricto* have the stomates grouped into clusters or islands (Figures 190-203) while the majority of the species of *Rhytidophyllum* have the stomates scattered irregularly but each stomate positioned on a mound (Figure 201). The same four species of *Rhytidophyllum* mentioned above (here cited under *Gesneria*), *G. earlei* Urban &Britton, *G. grandis* Sw., *G. lomensis* Urban, and *G. rupincola* (C. Wright) Urban, have the stomates aggregated into islands like species of *Gesneria.* Skog (1976) left these species in *Rhytidophyllum* but admitted that the section *Duchartrea* (Decaisne) Fritsch of *Gesneria* [containing *G. viridiflora* (Decaisne) Kuntze] may be more closely related to *Rhytidophyllum* than to any section in *Gesneria sensu stricto.* Just as the stamen feature discussed above is an expression of pollination syndromes, the epidermal characters are modifications of particular species to a particular environment. According to Skog (1976), many species of *Rhytidophyllum* are weedy species growing in comparatively dry places in full sun while most species of *Gesneria sensu stricto* have their root system in wet soil or rocks and prefer a high degree of humidity. The above epidermal features represent, therefore, adaptations of groups of species to certain types of environment. The epidermis of the species in the tribe Gesnerieae is therefore no indicator of generic delimitations.

Decussate leaves, a semi-inferior ovary position, and a slight curve or beak in the pointed capsular fruit are the generic markers assigned by Skog (1976) to his new genus *Pheidonocarpa*. In contrast, the leaves in *Gesneria sensu* Skog are alternate, the ovary position varies from less than semi-inferior to completely inferior, and the capsule is not beaked. The type of *Pheidonocarpa* is *Gesneria corymbosa* Sw. from Jamaica which contains either two subspecies (*fide* Skog) or has an allied species, *G. mortonii* Wiehler, in Cuba.

The occurrence of decussate leaves among the Gesnerieae is not such a strange feature that it warrants the exclusion of the above species from *Gesneria*, as was done by Urban (1901) and Skog (1976). Truly decussate leaves occur in one population of *Gesneria fruticosa* (L.) Kuntze as observed in cultivated material at Cornell University (Wiehler, 1970, 1971). More important, however, is the fact that truly decussate leaves are present in each species of the tribe Gesnerieae in the form of bracts of the inflorescence. While the sterile leaves in the vast majority of the species of *Gesneria sensu lato* have a truly alternate leaf arrangement with a 2/5 phyllotaxy, the inflorescence of these species is a pair-flowered cyme with decussate bracts, typical for the whole family Gesneriaceae (Figures 6-20, 22). The reverse situation occurs in the genera *Koellikeria* and *Smithiantha* in which the decussate leaves are topped by an inflorescence with alternate bracts. The distinctive nature of the gesneriaceous inflorescence itself provides further evidence. The evolution of the pair-flowered cyme of the family Gesneriaceae is, according to Weber (1973a, and personal communication), based on a complex ramification system with decussate phyllotaxy. The gesneriaceous inflorescence thus indicates the derived condition of alternate leaves in the Gesneriaceae. These considerations should influence our perception of the Caribbean genus *Gesneria*.

This peculiar mode of leaf arrangement in the tribe Gesnerieae indicates foremost that alternate leaves are not a primitive but a secondary or derived feature in this taxon. *Gesneria corymbosa* and *G. mortonii* have merely maintained their opposite leaf structure in all parts of the plant body. Both Skog (1976) and Wiehler (1970, 1971) agree that these species are members of the tribe Gesnerieae, and not of the genus *Heppiella* in the tribe Gloxinieae as stipulated by Urban (1901). Since decussate leaves are therefore not a foreign feature in the genus *Gesneria*, the above two species are here (as in Wiehler, 1971) regarded as somewhat more "primitive" members of *Gesneria*, in a new section *Pheidonocarpa.* *

The semi-inferior ovary position of the two species is merely one extreme of a continuum between semi-inferior to completely inferior. If the curved or beaked capsule in the two species warranted their generic separation from *Gesneria*, then the same treatment, for the sake of consistency, should be accorded to *G. calycina* Sw. from Jamaica [in the section *Dittanthera* (G. Don) L. Skog] which is the only species in the tribe with a curious elongated and linear capsule. Skog (1976) stated also that *G. corymbosa* was in many of its characters more closely related to *Rhytidophyllum* than to *Gesneria* sensu stricto (cf. Skog, 1976: 25, Table 1).

When the features that unite *Gesneria*, *Rhytidophyllum*, and *Pheidonocarpa* — the isolated geographical distribution, the unique chromosome number, the peculiar vasculature of the petiole, the occurrence of stomatal islands, the nectarial ring, etc. — are taken into consideration, and when the range of variation within this plant group due to differences in habitat and mode of pollen and seed dispersal are fully appreciated, then the generic unity of the Caribbean Gesnerieae becomes self-evident (Plate 8).

It appears possible that several of the species of *Gesneria* reduced by Skog (1976) to subspecies and varieties but possessing a distinct shape, size, or color of the corolla and thus possibly employing different pollinators, may turn out to be valid species (e.g., *G. acaulis* L., *G. pumila*, *G. shaferi* Urban, *G. viridiflora*). We need more field work to establish this. Pollinators often distinguish between similar appearing plant species more effectively than man (van der Pijl & Dodson, 1966).

Gesneria is a genus of over 70 species distributed almost exclusively on the islands of the Antilles with two species in adjacent coastal Venezuela (*G. cumanensis*) and coastal Colombia (*G. onacaensis*). Most of the species have a diploid chromosome number of $n = 14$, and a few are tetraploids. The only count of $n = 7$ for *G. viridiflora* subsp. *sintenisii* (Urban) L. Skog from Puerto Rico by Nevling (1969) appears questionable and needs to be repeated because of the implication of such a finding.

The Caribbean islands are known for the presence of many bat caves, and so it is not surprising that chiropterophily (and ornithophily) are the predominant modes of pollination in *Gesneria*. It appears possible that Euglossine bees, of which a few species occur in Cuba and Jamaica, are the pollen vectors of at least *G. gloxinioides* (Griseb.) Urban and the *G. pumila* Sw. complex.

About 25 species of *Gesneria* are in limited cultivation. Most of the interspecific hybrids show a fairly low percentage of pollen stainability (0-60%), in comparison with hybrids in other genera of the neotropical Gesneriaceae (Wiehler, 1970; Skog, 1976). Two natural hybrids are known from Jamaica.

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* Gesneria *L.* section Pheidonocarpa (L. Skog) Wiehler, stat. nov. genus *Pheidonocarpa* L. Skog, Smithsonian Contr. Bot. 29: 40. 1976.

The family Gesneriaceae is thus based on the Linnean genus *Gesneria* which commemorated the prodigious Swiss Renaissance scholar, humanist, linguist, philosopher, physician, botanist, and zoologist Conrad Gesner (b. 1516, d. 1565). Gesner's works in zoology and botany were utilized extensively by the Swede Carolus Linnaeus (b. 1707, d. 1778) in his classification systems for animals and plants. Linnaeus, however, did not actually establish the Caribbean genus *Gesneria.* This was done by the French missionary and botanist Charles Plumier (b. 1646, d. 1704) who explored the West Indies from 1689 to 1690 and illustrated and described many new taxa, among them *Gesnera humilis, flore flavescente (= Gesneria humilis* L.*)*, the type species of the genus *Gesneria* and the family Gesneriaceae (Figure 394). Plumier's *Nova plantarum americanum genera* was published in 1703 and contained eight gesneriads.

Figure 396: Flowers of *Paliavana* in Vandelli's *Florae lusitanicae* of 1788.

Figure 397: *Alsobia* and *Episcia* - shoot development.

Figure 398: Representative shapes and textures of pollen grains in genera of the tribe Episcieae. 1. *Episcia cupreata* (Hooker) Hanst., X 1306, polar-equatorial view. 2. *Nautilocalyx porphyrotrichus* (Lwbg.) Wiehler, X 1610, polar view. 3. *Drymonia serrulata* (Jacq.) Mart., X 1924, equatorial view. 4. *Rufodorsia major* Wiehler, X 2357, polar-equatorial view. 5. *Pentadenia spathulata* (Mansf.) Wiehler, X 1073, polar and equatorial views.. 6. *Dalbergaria aureonitens* (Hooker) Wiehler, X 1610, equatorial view. 7. *Trichantha filifera* Wiehler, X 1480, polar-equatorial view. 8. *Bucinellina nariniana* (Wiehler) Wiehler, X 1813, equatorial view. 9. *Bucinellina paramicola* (Wiehler) Wiehler, X 1813, equatorial view. 10. *Columnea maculata* Morton, X 1499, equatorial view. 11. *Columnea nicaraguensis* Oersted, X 1554, equatorial view. 12. *Columnea gloriosa* Sprague, X 1499, equatorial view. (Photos courtesy of Dr. Norris H. Williams).

Figures 399-401: The fruit in *Codonanthe.* Figure 396: *Codonanthe corniculata* Wiehler; typical berry. X 2. Figure 397: *Codonanthe gracilis* (Mart.) Hanst.; a) typical berry; b) split berry, both from the same plant. X 2. Figure 398: *Codonanthe luteola* Wiehler; a) immature, fleshy capsule, still unsplit; b) top view of mature fruit, split loculicidally; c) same, lateral view. X 1.

Figures 402-404: Anther connectives in *Codonanthe* and *Codonanthopsis* (all X 12). Figure 399: *Codonanthe chiricana* Wiehler. Figure 400: *Codonanthopsis dissimulata* (H. E. Moore) Wiehler. Figure 401: *Codonanthopsis ulei* Mansf.

Figures 405-406: The fleshy, display fruit of *Codonanthopsis* (all X 2). Figure 402: *Codonanthopsis dissimulata*, two lateral views. Figure 403: *Codonanthopsis ulei.*

Figure 407: The genus *Rufodorsia* Wiehler with the four species: 1) *R. major* Wiehler; 2) *R. minor* Wiehler; 3) *R. intermedia* Wiehler; 4) *R. congestiflora* (Donn.-Smith) Wiehler.

A. Habit. B. Leaf, abaxial side. C. Corolla, frontal view. D. Corolla, lateral view. E. Calyx. F. Prophyll(s). G-I. Anthers: ventral view (G), dorsal view (H), lateral view (I). J. Ovary, style, stigma, and nectary. K. Stigma. L. Berry-fruit. M. Seed and funicle. (All drawings from live material from Panama.),

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The above figures were not received for publication.

PART 6: A KEY TO THE TRIBES AND GENERA OF THE SUBFAMILIES GESNERIOIDEAE AND CORONANTHEROIDEAE*

1a. Plants of the neotropics; nectary free from the base of the ovary, annular, or composed of individual glands, or secondarily absent . . . . SUBFAMILY GESNERIOIDEAE . . . 2

1b. Plants of the temperate zone in Chile, or from islands of the South Pacific Ocean, or eastern Australia; nectary embedded in the basal part of the ovary, pulvinate, annular . . . . SUBFAMILY CORONANTHEROIDEAE and TRIBE CORONANTHEREAE . . . 60

2a. Inflorescence bracteate; if bracts absent (in some species with reduced, solitary or twin flowers), then plants with rhizomes, or tubers, or epiphytic, or with 3:3 trilacunar nodes, or with more than 3 separate nectary glands; nectary never semi-annular; ovary, fruit, and seed various 3

2b. Inflorescence ebracteate; ovary superior; nectary ring-shaped, or semi-annular, lobed, or sheathed, or reduced to one dorsal gland; fruit a berry, or a fleshy or dry capsule; seeds without obvious funicles; plants without tubers or rhizomes; nodes 1:1 unilacunar . . . . TRIBE BESLERIEAE . . . 54

3a. Leaves alternate 4

3b. Leaves decussate 5

4a. Ovary superior; stems succulent; flowers in terminal racemes, with a blue, bilabiate limb; nectary a high ring; vasculature of node and petiole composed of widely separate bundles; Peru to Mexico . . . . *Rhychoglossum azureum* (SUBFAMILY CYRTANDROIDEAE)

4b. Ovary semi-inferior or completely inferior; stems woody, flowers axillary, never blue or bilabiate; nectary ring-shaped; nodes 1:1 unilacunar; vasculature of the petiole in cross-section a thick, deeply invaginated arc or a thick ring; Caribbean region . . . . TRIBE GESNERIEAE with the genus *Gesneria*

5a. Vasculature of the petiole in cross-section a thick, deeply invaginated arc or a thick ring . . . . *Gesneria* spp. . . . . (*G. corymbosa*, *G. fruticosa*, *G. mortonii*)

5b. Vasculature of the petiole in cross-section a thin arc 6

6a. Ovary superior; plants predominantly fibrous-rooted, rarely with tubers (in *Chrysothemis*, *Lembocarpus*, and *Nautilocalyx*), never with rhizomes; nodes, nectary, fruit, and seeds various 7

6b. Ovary semi-inferior to completely inferior; plants fibrous-rooted, or with tubers, or underground, scaly rhizomes; nodes 1:1 unilacunar; nectary ring-shaped, or 2-5 separate glands, or absent; fruit a dry capsule; seeds without obvious funicles . . . . TRIBE GLOXINIEAE . . . 9

7a. Fruit a fleshy capsule or a berry; seeds with prominent fleshy funicles; nectary usually reduced to a large, double-connate, dorsal gland, rarely consisting of 2, 4 or 5 separate glands; nodes 3:3 trilacunar, or if rarely 1:1 unilacunar, plants epiphytic, with thin stems; vasculature of the

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* *Rhynchoglossum azureum*, the only species of the Old World subfamily Cyrtandroideae in the neotropics, is also keyed here.

petiole in cross-section a short, shallow, thin arc; stomates always irregularly scattered on the abaxial leaf surface .... TRIBE EPISCIEAE . . . 34

7b. Fruit a dry capsule; seeds without obvious funicles; nectary annular or absent; nodes 1:1 unilacunar; vasculature of the petiole and stomates various 8

8a. Plants fibrous-rooted; leaves in loose rosettes; nectary absent; stomates grouped into islands on the abaxial leaf surface; pan-neotropic .... TRIBE NAPEANTHEAE with the .... genus *Napeanthus*

8b. Plants with tubers and single leaf; nectary annular, lobed; stomates scattered irregularly on the abaxial leaf surface; endemic to Surinam and French Guiana .... genus *Lembocarpus* (Tribe Gloxinieae)

TRIBE GLOXINIEAE

9a. Nectary ring-shaped 10

9b. Nectary composed of individual glands or absent 19

10a. Plants with underground tubers 11

10b. Plants without tubers 12

11a. Small herbs, to 10 cm tall, with a single leaf; corolla campanulate, pale blue (or white, with a purple limb); ovary superior; endemic to Surinam and French Guiana .... *Lembocarpus*

11b. Plants to 50 cm tall, with decussate leaves; corolla campanulate, with an oblique limb and a galea, green, with wine-red dots; ovary almost completely superior; native to southeastern Brazil .... *Lietzia*

12a. Leaves leathery, with the lateral veins completely bordering the margins; small herbs with wiry stems; central Brazil (Planalto) .... *Goyazia*

12b. Leaves not leathery, with the lateral veins ending before reaching the margins; plants various, without wiry stems 13

13a. Inflorescence with alternate bracts 14

13b. Inflorescence with decussate bracts 15

14a. Corolla about 1 cm long; small herbs with leaves in rosettes, dotted white on upper surface; rhizomatous; tropical South America, Panama, Costa Rica .... *Koellikeria*

14b. Corolla about 3 cm long, or longer; herbs ¼-1 m tall, with plain or red, marbled leaves; rhizomatous; southern and central Mexico .... *Smithiantha*

15a. Anthers free; plants rhizomatous; corollas tubular, red; Andean America .... *Heppiella*

15b. Anther coherent; plants and corolla various 16

16a. Subshrubs or shrubs, without rhizomes; corolla tubular, red, rarely yellow or whitish; Middle America .... *Moussonia*

16b. Herbs with rhizomes; corolla various 17

17a. Stems and leaves densely lanate-villous; small, caulescent herbs or with leaves in rosettes; corolla campanulate, lavender and white; southern and central Mexico .... *Eucodonia*

17b. Stems and leaves without wooly indumentum; herbs with the leaf pairs equal, subequal, or leaves verticillate; corolla tubular or campanulate, of various colors 18

18a. Plants from Middle America, chiefly Mexico (*A. erecta* also from Jamaica, Hispaniola, and northern Colombia; *A. pedunculata* also from coastal Venezuela and Colombia); chromosome number $x = 11$ .... *Achimenes*

18b. Plants from South America and Panama to Canal Zone; chromosome number $x = 13$ .... *Gloxinia*

19a. Nectary composed of individual glands 20

19b. Nectary absent or non-functional 29

20a. Ovary inferior; nectary a large, double-connate, dorsal gland; herbs, shrubs, and 1 sp. a tree (*S. calycosa* in Costa Rica and Panama); corollas red, orange, or yellow; Middle America .... *Solenophora*

20b. Ovary semi-inferior; nectary 2 or more glands. herbs and shrubs; corolla various 21

21a. Plants with tubers; pan-neotropical .... *Sinningia*

21b. Plants without tubers 22

22a. Nectary glands 5, linear or club-shaped 23

22b. Nectary glands 4 or 5, wide and thick, the 2 dorsal ones sometimes larger or connate 25

23a. Corolla 4-6 cm long; plants with succulent stems, but without tubers, from southeastern Brazil .... *Sinningia*, section *Sinningia*

23b. Corolla less than 3 cm long; plants various 24

24a. Corolla usually white (rarely yellow or purple), with a long cylindrical tube, the wide, subregular limb often with a purple dot on each lobe; inflorescence often terminal, with distinct bracts, or flowers axillary; low herbs of the forest floor; Bolivia to Mexico, Venezuela .... *Diastema*

24b. Corolla red, inflated, constricted above the base and below the throat, the limb narrow; inflorescence usually an axillary, pedunculate, umbellate, congested, hairy cyme; herbs to 1 m tall; Bolivia to southeastern Colombia .... *Parakohleria*

25a. Ovary almost completely superior; corolla large, campanulate, but sometimes constricted in the throat; herbs and vines, sometimes epiphytic; Peru to Guatemala .... *Capanea*

25b. Ovary semi-inferior or almost completely inferior; corolla various; herbs and shrubs; terrestrial 26

26a. Calyx lobes in bud appressed to corolla 27

26b. Calyx lobes in bud patent 28

27a. Corolla cylindrical, red; ovary almost completely inferior; shrubs from southeastern Brazil .... *Vanhouttea*

27b. Corolla campanulate or funnel-shaped, green, blue, or greenish yellow; ovary semi-inferior; shrubs from eastern Brazil .... *Paliavana*

28a. Corolla spherically inflated, constricted at the throat, the limb practically absent, orange-red; low herbs of the eastern slope of the Andes in central Ecuador .... *Pearcea*

28b. Corolla tubular or campanulate, usually red, orange, yellow or pink, often with a wide, dotted or green limb; herbs and subshrubs; Peru to Mexico, Venezuela, the Guianas, and Trinidad .... *Kohleria*

29a. Corolla campanulate, often blue or white 30

29b. Corolla rotate, always white 32

30a. Leaves strongly anisophyllous; ovary in fruit inferior; corolla bluish, white, rarely rose or yellow; herbs to 1 m tall; Bolivia to Guatemala and Venezuela .... *Monopyle*

30b. Leaves isophyllous, or nearly so; ovary and corolla various 31

31a. Anthers coherent; ovary almost completely inferior; corolla more than 2 cm long, blue or white; herbs to 1 m tall; Bolivia to Panama, central and eastern Brazil . . . . *Gloxinia*, section *Gloxinia*

31b. Anthers free; ovary semi-inferior; corolla less than 1 cm long, white; herb to subshrub, 1-2 m tall; Peru . . . . *Anodiscus*

32a. Small shrubs, about 40 cm tall; anther thecae dehiscing by apical pores; Cuba and Hispaniola . . . . *Bellonia*

32b. Small herbs, to 15 cm tall; anther thecae dehiscing by longitudinal slits 33

33a. Anther filaments longer than anthers, chromosome number $x = 13$; Peru to Mexico, Venezuela, Cuba, Haiti . . . . *Phinaea*

33b. Anther filaments as long as or shorter than anthers, chromosome number $x = 11$; Peru, Venezuela, Guatemala, Mexico . . . . *Niphaea*

TRIBE EPISCIEAE

34a. Anthers specialized; thecae elongate, sagittate, dehiscing by basal pores, the 4 anthers coherent by their thecae facing inwards, forming a columnlike "salt-shaker" swinging back and forth on the filaments, with the pores upside, ready to spill some dry, non-sticky pollen on the pollinator tipping the elaborate structure (Figures 67-71); corolla various; epiphytic herbs, shrubs, or vines, or terrestrial herbs with succulent square stems; pan-neotropical . . . . *Drymonia*

34b. Anthers simple, not sagittate, coherent into flat rectangles, squares, or into pairs; pollen usually sticky; corolla and plant habit various 35

35a. Anther connective broad, the thecae widely separated, rounded; corollas funnel-shaped or campanulate, usually white; fruit a berry, rarely a fleshy capsule; epiphytic vines or small shrubs with equal leaves, usually on ant nests or associated with ants; pan-neotropical . . . . . *Codonanthe*

35b. Anther connective narrow, the oblong thecae touching, or nearly so; corollas, fruit, and plants various 36

36a. Fruit a capsule 37

36b. Fruit a berry 46

37a. Plants with stolons 38

37b. Plants without stolons 39

38a. Plants terrestrial, with 2 stolons per node; corollas red, white, or lilac; Peru and Brazil north to Nicaragua and the Guianas . . . . *Episcia*

38b. Plants epiphytic, with 1 stolon per node; corollas white; Costa Rica to Mexico . . . . *Alsobia*

39a. Fruit a display capsule, with the 2 fleshy valves reflexed, exposing a cone-shaped mass of fleshy funicles and seeds (Figures 63-66) 40

39b. Fruit a cup-shaped capsule, with the 2 valves opening about 45°, with the seeds and funicles inside the cup 42

40a. Leaves extremely anisophyllous, the smaller of the pair usually stipulelike and early caducous; corollas funnel-shaped, white, sometimes speckled with wine-red; ant nest epiphytes of the Amazon region and the Guianas . . . . *Codonanthopsis*

40b. Leaves isophyllous or weakly anisophyllous; corollas often with a pouch below the constricted entrance, or the entrance wide but laterally compressed; plants terrestrial or epiphytic 41

41a. Leaf lamina with a hypodermis; chromosome number $x = 8$; plants with succulent leaves, epiphytic; southeastern Brazil . . . . *Nematanthus*

41b. Leaf lamina without a hypodermis, also in epiphytic species; chromosome number $x = 9$; herbs, subshrubs, and vines with non-succulent leaves, mostly terrestrial; neotropics except southeastern Brazil . . . . *Alloplectus*

42a. Calyx lobes connate for at least 3/4 of their length; terrestrial herbs with succulent stems and underground tubers; corolla deep yellow; Ecuador to Guatemala, central Brazil, Guianas, Venezuela and Lesser Antilles . . . . *Chrysothemis*

42b. Calyx lobes free; plants terrestrial or epiphytic, without tubers (except in some spp. of *Nautilocalyx* and possibly *Rhoogeton*); corolla various 43

43a. Calyx actinomorphic, star-shaped, orange; corolla tubular, yellow; plants epiphytic and terrestrial; Guatemala . . . . *Cobananthus*

43b. Calyx zygomorphic, of various shapes and colors; corolla various 44

44a. Peduncles about 5 times as long as the red corolla; small, acaulescent, terrestrial herbs; Guayana Highland . . . . *Rhoogeton*

44b. Peduncles about as long as corolla, shorter, or absent; corolla various; plants caulescent 45

45a. Terrestrial herbs; stems succulent, either upright, or creeping and rooting by nodes; corolla tubular, with a large limb, usually white or yellow, rarely reddish; neotropical except southeastern Brazil . . . *Nautilocalyx*

45b. Epiphytic herbs or vines; stems usually firm; leaves often in rosettes (unless plant vining); corolla of various shapes and colors; neotropical except southeastern Brazil . . . . *Paradrymonia*

46a. Plants terrestrial, 1/3-2 m tall; inflorescence axillary, pedunculate, umbellate-cymose, erect; berries white-translucent, with the black seeds shining through; herbs and subshrubs with thick, somewhat fleshy stems; Bolivia to Costa Rica, Venezuela . . . . *Corytoplectus*

46b. Plants epiphytic; inflorescence and berries various 47

47a. Berries bright orange; stems thin, pendent; corolla either funnel-shaped, rose and white, or with a constricted entrance and a pouch below, orange-red; western Colombia and Middle America . . . . . *Neomortonia*

47b. Berries white, pink, red, purple, or lavender; stems and corolla various 48

48a. Corolla 8-20 mm long, campanulate, with a broad limb; inflorescence congested in the leaf axils, usually epedunculate 49

48b. Corolla longer than 20 mm, tubular, of if shorter, with a narrow limb; inflorescence various 50

49a. Corolla white, the back and upper lobes reddish; berries globose or depressed, white; Panama and Costa Rica . . . . *Rufodorsia*

49b. Corolla plain white, or reddish; berries pointed, white; Middle America . . . . *Oerstedina*

50a. Nectary composed of 5 separate glands, the 2 dorsal ones sometimes enlarged or connate (but nectary reduced to 2 large, connate, dorsal glands and a sterile ring in some, but not all, populations of *P. strigosa* in the province of Pichincha, Ecuador); corolla tubular, or somewhat inflated, with a narrow, subregular limb, rarely strongly inflated, with a bilabiate limb and a galea; berry globose, white, rarely pink, purple, or lavender; Bolivia to Mexico, Andean and coastal Venezuela . . . . *Pentadenia*

50b. Nectary a large, double-connate, dorsal gland (rarely an additional small ventral gland); corolla and berry various 51

51a. Berry lavender, subglobose-depressed; stems thin, pendent or scandent; the tubular corolla club-shaped, curved, spurred, with an oblique limb, the upper 2 lobes wine-red; pollen triangular-inflated (oblate); southwestern Colombia . . . . *Bucinellina*

51b. Berries white, pink, red, or purple, globose or ovoid; stems, corolla, and pollen various 52

52a. Pollen oblong-elliptic (prolate); stem thin and pendent, or thicker and ascending; corolla always with a narrow, gradually widening, never inflated tube, with a distinct galea, and a long and narrow, reflexed lower lobe; berry globose, white, (rarely pink or blotched with red); Ecuador to Mexico, Antilles, Venezuela and the Guianas . . . . *Columnea*

52b. Pollen nearly globose (oblate spheroidal and prolate spheroidal) 53

53a. Stems stout, short, ascending or spreading, never vining or thin or pendent, usually branching only from the base, with a distinct, fern-frond-shaped habit, with the subsessile leaves in close-set, imbricating, distichous pairs, one of which is stipule-like, the other large, narrow, and oblanceolate, the pairs alternating in respect to their sizes (the large leaves often with red extrafloral attraction patterns); corolla usually tubular or somewhat inflated, with a narrow, subregular limb, or bilabiate and *Columnea*-like in some species, but then the tube inflated; pollen prolate spheroidal; berry ovoid or pointed, yellow, orange, or red (rarely white); Bolivia to Mexico, Antilles, Venezuela, and the Guianas . . . . *Dalbergaria*

53b. Stems usually slender, pendent, scandent, or ascending, branching freely, the opposite leaf pairs of equal or unequal size (shoots like a fern frond only in a few species with slender, scandent, vining stems, bare except at the tip); corolla tubular or somewhat inflated, with a subregular limb (a galea present only in combination with a strongly inflated tube); pollen oblate spheroidal; berry globose or ovoid, usually a shade of red, rarely white; Bolivia to Guatemala, Antilles, Venezuela, the Guianas, and eastern Brazil . . . . *Trichantha*

TRIBE BESLERIEAE

54a. Fruit a berry 55

54b. Fruit a capsule 56

55a. Nectary ring-shaped and plain, or semi-annular (but in *B. comosa* Morton from Ecuador reduced to a single, dorsal gland); seeds rhombiform, striate; subshrubs, shrubs, and small trees; pan-neotropical . . . . *Besleria*

55b. Nectary a narrow ring, with 2 prominent dorsal lobes or teeth; seeds subglobose, pustulate; small herbs; Guayana Highland . . . . . *Tylopsacas*

56a. Capsule fleshy at maturity 57

56b. Capsule dry at maturity 59

57a. Stomata scattered irregularly on the abaxial surface of the leaf; stamen filaments adnate from the base to the middle of the corolla tube; corollas small, 2 cm long or less, white or yellow; small herbs; northern Andean Peru through Panama . . . . *Cremosperma*

57b. Stomata on the abaxial leaf surface in clusters; stamen filaments adnate at the base of the corolla tube; corollas and plants various 58

58a. Leaves decussate; corollas usually large and showy, either funnel-shaped or campanulate and white or yellow (often spotted), or oddly shaped, with a tightly constricted throat and a narrow limb, and a protruding, large pouch below, red, orange, or pink; herbs to 1 m tall; Peru to Guatemala . . . . *Gasteranthus*

58b. Leaves alternate; corollas small, 1-2 cm long, white; low herbs; endemic to Panama and Colombia . . . . *Reldia*

59a. Nectary ring-shaped; seeds ovoid, longitudinally striate; small subshrubs with long, cuneate, oblanceolate leaves; inflorescence long-pedunculate; corollas small, white or yellow; Colombia and Venezuela . . . . *Resia*

59b. Nectary a lobed sheath surrounding the ovary; seeds discoid, flat, winged; small herbs with elliptic leaves; inflorescence long-pedunculate; corollas small, white or bluish; tropical South America . . . . *Anetanthus*

TRIBE CORONANTHEREAE
(Subfamily Coronantheroideae)

60a. Fruit a capsule 61

60b. Fruit a berry 64

61a. Stamens 5; corollas actinomorphic; capsule dehiscence 2-valved, septicidal; trees; corolla small, yellow; New Caledonia . . . . *Depanthus*

61b. Stamens 4; corollas zygomorphic; capsule dehiscence 4-valved, loculicidal and septicidal; plants and corollas various 62

62a. Inflorescence epedunculate, 1-2 flowers per leaf axil; corolla orange-red; shrub, 0.5-1.5 m tall, with small betuloid leaves; North Island of New Zealand . . . . *Rhabdothamnus*

62b. Inflorescence with peduncles; corollas and plants various 63

63a. Anthers free at anthesis; tree with verticillate leaves; corollas large, yellow; Lord Howe Island . . . . *Negria*

63b. Anthers coherent at anthesis; shrubs and trees with decussate, leathery leaves; corollas small (red?); New Caledonia and Solomon Islands . . . . *Coronanthera*

64a. Trees to 13 m tall; corollas small, orange; stamens 4, anthers coherent; Queensland in Australia . . . . *Lenbrassia*

64b. Small shrubs and woody creepers; corollas and stamens various 65

65a. Stamens 2; woody creeper with succulent small leaves; often epiphytic; corollas orange-red; Chile . . . . *Sarmienta*

65b. Stamens 4; plants and corollas various 66

66a. Corolla red 67

66b. Corolla pale yellow-green; anthers free; small, scandent shrub; New South Wales in Australia . . . . *Fieldia*

67a. Corolla with a prominent galea and 3 lobes, each 2 cm long; anthers coherent, stellate; woody creeper or vine; flowers axillary, solitary, ebracteate; Chile . . . . *Asteranthera*

67b. Corolla with short, subequal lobes, 7 × 7 mm; anthers free or coherent into pairs; small shrubs; flowers axillary, solitary, bracts embracing calyx; Chile . . . . *Mitraria*

SUMMARY

The neotropical Gesneriaceae, now a group of five tribes, 54 genera, and over 1300 species, have presented problems to plant systematics for about 160 years, or ever since the time of the influx of large numbers of American gesneriads into Europe. For the past 25 years this fascinating plant group and its counterpart of about equal size in the paleotropics, have been studied intensively by several workers, in the greenhouse, laboratory, and through field work. Our understanding of this tropical family has increased accordingly, culminating in a new classification.

The Gesneriaceae turn out to be an evolutionarily very "active" and "probing" group in terms of habitat selection, morphological adaptations, pollen vectors, and seed dispersers. Parallel to the Orchidaceae among the monocotyledons, the Gesneriaceae appear to stand at the apex of evolution among the dicotyledons. In the neotropical Gesneriaceae is a high percentage of epiphytism, ornithophily, and berry-fruitedness as well as a fair percentage of chiropterophily. The subfamily Gesnerioideae is the only group among the Scrophulariales or in the Tubiflorae with a pronounced development of the inferior ovary (within two tribes), of the floral nectary, of the 3:3 trilacunar node (characteristic of one tribe), and of stomates grouped into islands (in genera of three tribes). The pair-flowered cyme, not catalogued or illustrated in botanical textbooks, categorizes the whole family.

The comparatively rapid speciation and the concomitant development of many closely related taxa, the phenomena of parallel evolution, and the biology of pollination and of seed dispersal have to be taken into account in any attempt to classify such an evolutionarily versatile and plastic tropical plant group. A character evaluation, and especially a revaluation of floral features are, therefore, essential in arriving at a more satisfactory classification of a plant family long plagued by vague generic and tribal delimitation.

This revision of the American Gesneriaceae contains a new subfamily, a new tribe, and several new genera as well as new tribal and generic realignments.

This biosystematic approach to a tropical plant family also demonstrates that such a study cannot be governed by concepts developed from studies of the impoverished flora of the temperate zones - which is the primary reason why the Gesneriaceae suffered for so long from a reputation as a taxonomically difficult group. The Gesneriaceae are a good example of the complexity of plant development in the tropics.

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