

BESLERIA L. AND THE RE-ESTABLISHMENT  
OF GASTERANTHUS BENTH. (GESNERIACEAE)

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The genus *Besleria* L. with over 170 species is the largest group in the neotropical Gesneriaceae. The herbaceous or suffrutescent terrestrial species occur from Mexico (Pueblo, Oaxaca, Chiapas) and the Caribbean Islands south to Bolivia and Sao Paulo in Brazil. The center of distribution lies in the Andes of Colombia and Ecuador. Many of the species are sharply defined local endemics, but some are widely distributed and somewhat variable, such as *Besleria laxiflora* Benth. and *B. solanoides* HBK. Most species with their orange, red, or yellow tubular corollas are apparently pollinated by hummingbirds. Until recently this taxon has been known to science only through the study of herbarium material. Mr. C. V. Morton described most *Besleria* species published in this century, and he also authored an excellent monograph of this large group (Morton, 1939).

Recent field studies in Ecuador, Colombia, Venezuela, Panama, and Guatemala, and observations of live material in greenhouse and laboratory have added some significant information on this group. Data on the fruit, for instance, is difficult to ascertain from pressed and dried herbarium specimens. The fruit in *Besleria* is a soft berry, either orange, red, or white, and apparently eaten by birds and fruit bats. It has now become clear that a more extensive knowledge of fruit characters is vital for a better understanding and classification of the neotropical subfamily Gesnerioideae. Fruit characters now help to separate the genus *Besleria* in the tribe Beslerieae Bartling & Wendland from the baccate genera in the tribe Episcieae Endlicher. Superficially both groups have very similar appearing berries, but the pulp of the *Besleria* berry consists of solid enlarged placental tissue, while the pulp in the episcoid genera *Codonanthe* (Mart.) Hanst., *Columnea* L., *Corytoplectus* Oerst., *Dalbergaria* Tussac, *Neomortonia* Wiehler, *Rufodorsia* Wiehler, *Pentadenia* (Planch.) Hanst., and *Trichantha* Hook. consists of enlarged and curled funicular tissue. With over 250 species, these baccate taxa comprise more than one third of the species in the large tribe Episcieae. *Besleria* is the only baccate genus in its tribe. While almost three fourths of the species in the revised tribe Beslerieae are berry-fruited, over 60 species in seven genera have capsular fruits (Wiehler, 1975b).

Another recent discovery concerns the nature of the florescence in the tribe Beslerieae. A study of live material and an extended survey of herbarium specimens from Europe and America have revealed that the florescence of *Besleria* and of all other taxa in the tribe Beslerieae is bractless, in contrast to the florescence of the other four tribes in the Gesnerioideae which has prophylls and subtending bracts.

The study of live plants and a subsequent examination of herbarium material indicate further that the genus *Besleria* includes a discordant element. A total of 27 described species, contained in the section *Gasteranthus* (Benth.) Fritsch and in five subsections of the section *Neobesleria* Morton, possess a definitely fleshy laterally compressed capsular fruit, quite different from the berry in *Besleria* (Fig. 1A-D). All these species with capsular fruit form a single, distinct unit.

A second major difference between *Besleria* and the discordant ele-

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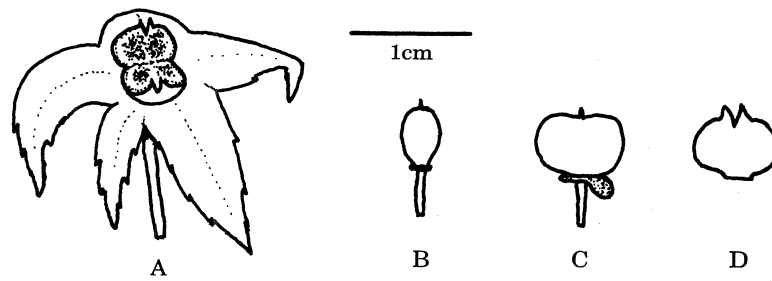


Fig. 1 A-D. Capsular fruit of *Gasteranthus allenii*, H. Wiehler & R. L. Dressler 71162 (SEL) from Rio Guanache, Colon, Panama (drawings natural size); A, recurved calyx lobes with split fruit and exposed seels; B, anterior-posterior view of laterally compressed ovary; C, broad-side view of same ovary, with posteriorly thickened nectary gland; D, one of the two loculicidally split carpel valves, showing the partial septicidal fissure.

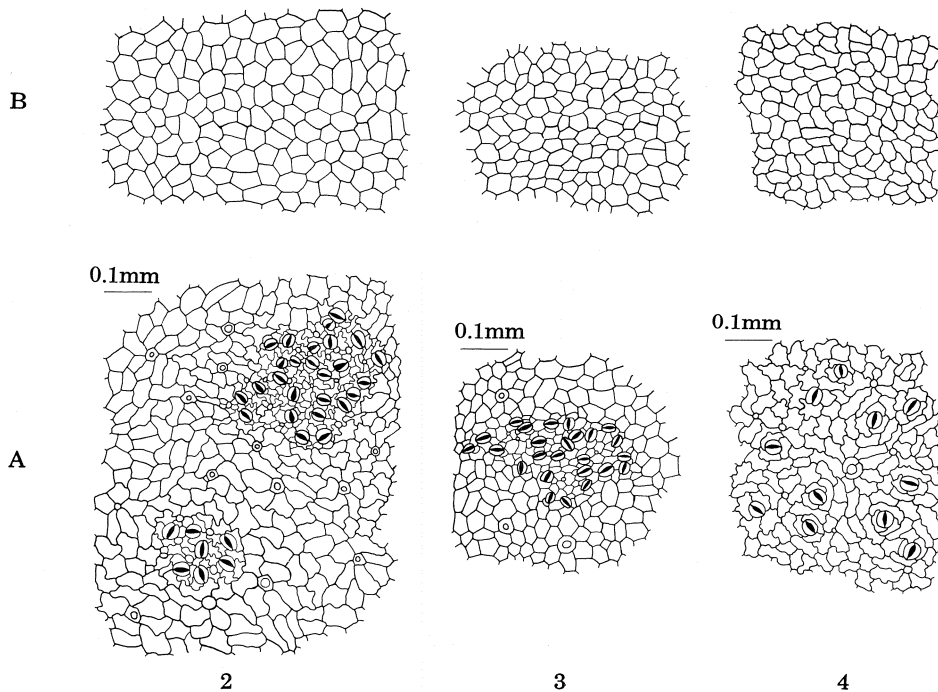


Fig. 2 A & B. Epidermis of the leaf *Gasteranthus pansamalanus*, H. Wiehler & P. Kunkel 7556 (SEL) from Riachuelo de Quecixibal, Alta Verapaz, Guatemala; A, abaxial leaf surface with clustered stomata. The typical number of stomata per island is between 90-185; B, adaxial leaf surface.

Fig. 3 A & B. Epidermis of the leaf of *Gasteranthus allenii*, H. Wiehler & R. L. Dressler 71270 (SEL) from El Valle, Cocolé, Panama; A, abaxial leaf surface with stomata in a cluster. The number of stomata per island varies between 15-40; B, adaxial leaf surface.

Fig. 4 A & B. Epidermis of the leaf of *Besleria pendula* Hanst., H. Wiehler & J. A. Steyermark 72456 (SEL) from Yacambu, Lara, Venezuela; A, abaxial leaf surface with the stomata irregularly scattered; B, adaxial leaf surface.

ment (labelled from now on as *Gasteranthus*) is expressed in an epidermal feature. The stomata on the abaxial leaf surface of *Gasteranthus* appear in definite clusters or islands (Figs. 2 and 3). The stomata in all *Besleria* species with baccate fruit are scattered irregularly over the abaxial lamina (Fig. 4). Clustered stomata also occur in other taxa of the Gesnerioideae: in all species of *Napeanthus* Gardner, in many species of *Gesneria* L., in a few species of *Rhytidophyllum* Mart., and in the two new species with alternate leaves of an undescribed genus in the tribe Beslerieae (Wiehler, 1970; Skog, 1972).

The floral nectary shows a third difference between the two groups. While the nectary is evenly ring-shaped in the majority of the species of *Besleria*, the nectary in *Gasteranthus* it is either reduced to a posterior gland, or semi-annular, or annular with a pronounced posterior enlargement.

This combination of characters suggests the exclusion of the discordant element from *Besleria* and the re-establishment of Bentham's genus *Gasteranthus* for the segregate. This generic re-alignment is part of a larger re-classification scheme and a new character evaluation of the Gesnerioideae (Wiehler, 1975b). *Besleria* and *Gasteranthus* can be separated by the following combination of characters:

<i>Besleria</i>	<i>Gasteranthus</i>
1. Fruit a berry.	1. Fruit a fleshy capsule.
2. Stomata of the abaxial leaf surface well-spaced.	2. Stomata of the abaxial leaf surface grouped into large clusters.
3. Nectary in the majority of species evenly ring-shaped.	3. Nectary never evenly ring-shaped, but either reduced to a posterior gland, or semi-annular, or annular with a pronounced posterior swelling.

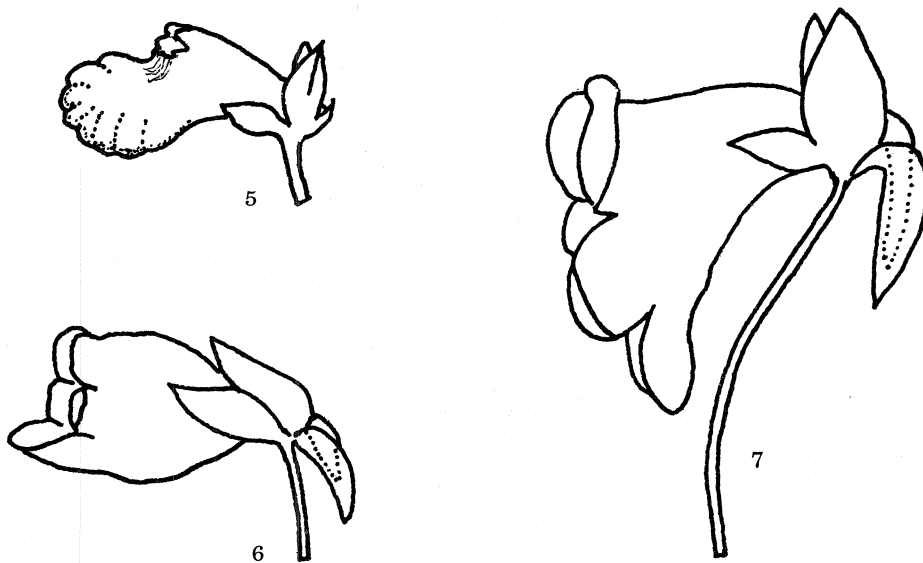
The monotypic genus *Halpophyllum* Mansf. also fits into the *Gasteranthus* complex and needs to be placed into synonymy. Mansfeld was the first to notice the peculiar stomatal grouping in his new genus (and thus in *Gasteranthus*), and rightly saw *Halpophyllum* as an entity distinct from *Besleria*.

The species of *Gasteranthus*, of which about one third of the collected material is still undescribed, are found from Peru north to Guatemala, along the Andes and the Central American mountain ranges. Most of these usually herbaceous species are local endemics, with the center of distribution in Ecuador and Colombia. Two species have a wider range of dispersal: *Gasteranthus rupestris* (Colombia, Ecuador, Peru), and *G. delphinioides* (Colombia, Panama, Cost 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.

About 35 species of *Gasteranthus* are presently known and these can be divided into two obvious groups. One of them has typical ornithophilous flowers, characterized by a red, orange, or pink *Hypocyrtia*-shaped corolla with a contracted entrance, narrow limb, and protruding pouch (Fig. 5). The Little Hermit hummingbird *Phaethornis longuemareus* (Lesson) has been observed as the pollinator of *Gasteranthus oncogastrus* at the Rio Palenque Biological Station in Los Rios Province, Ecuador (C. H. Dodson, personal communication), and I have watched an unidentified hummingbird visit

flowers of *Gasteranthus ecuadorensis* near Nono, Province of Pichincha, Ecuador (Wiehler & Diehl 71146, SEL). and another unidentified bird work flowers of an undescribed *Gasteranthus* species (Wiehler, Dressler, & Williams 7266, SEL) near Buenaventura, Dept. of El Valle, Colombia.

The second *Gasteranthus* group has typically white or cream-colored tubular-campanulate corollas with a wide entrance and broader limb (Figs. 6 and 7). This kind of flower, held in a horizontal or nodding position, is typically visited by female Euglossine bees. The shiny bees search these flowers for nectar. Dr. R. L. Dressler observed female bees of *Euglossa nigrosignata* Moure pollinate flowers of *Gasteranthus allenii* at Cerro Campana, Panama (Dressler 3520, SEL). In the absence of other differentiating characters it appears desirable to regard these two groups as sections, based quite clearly on pollination syndromes. Since, however, a switch from one type of pollinating agent to another is apparently only a matter of little genetic change in the Gesneriaceae (Wiehler, 1975b), it is entirely possible that some ornithophilous species of *Gasteranthus* may have a closer affinity to members of the euglossaphilous group than to other bird-pollinated species in the same section. The same division into euglossaphilous and ornithophilous species groups occurs in the recently enlarged genus *Sinningia* Nees, in which the *Rechsteineria* group represents the hummingbird flower element (Clayberg, 1968, 1970; Moore, 1973), and likewise in the recently amplified genus *Gloxinia* L'Heritier in which the red-flowered *Seemannia* complex is hummingbird-pollinated (Wiehler, 1975a).



Figs. 5-7. Flowers of *Gasteranthus* species (all drawings natural size). 5. *G. ecuadorensis*, H. Wiehler & S. Diehl 71146 (SEL) from Nono, Pichincha, Ecuador. 6. *G. allenii*, H. Wiehler & R. L. Dressler 72316 (SEL) from Almirante, Bocas del Toro) Panama. 7. *G. delphinioides*, R. L. Dressler 4277 (SEL) from El Llano, Prov. Panama, Panama.

**Gasteranthus** Benth., ampl. Wiehler

Folia chartacea vel coriacea, laminae abaxiales stomatibus conglomeratibus. Florescentiae ebractiatae; corollae calcaratae antice sub limbis insigniter saccato-inflatae, faucibus constrictis, limbis brevissimis 5-lobis, vel corollae calcaratae irregulares tubuloso-campanulatae, faucibus ampliatis, limbus latis subregularibus vel bilabiatis; nectaria in glandulas posticas reducta, vel semi-annularia, vel annularia postice incrassata. Fructus capsulae bivalves vel quadrivalves.

**Gasteranthus** Benth., Pl. Hartweg. 233. 1846.

*Besleria* L., subgen. *Gasteranthus* (Benth.) Hanst., *Linnaea* 34:334. 1865.

*Besleria* L., sect. *Gasteranthus* (Benth.) Fritsch, in Engler & Prantl) *Nat. Pflanzenfam.* 4(3b):159. 1894; cf. Morton, *Contr. U.S. Natl. Herb.* 26(9):417. 1939.

*Besleria* L., sect. *Neobesleria* Morton, subsections *Corallinae* Morton, *Imbricatae* Morton, *Wendlandianae* Morton, *Maculatae* Morton, and *Herbaceae* Morton, *Contr. U.S. Natl. Herb.* 26(9):414-416. 1939.

*Halpophyllum* Mansf., in Fedde, *Repert.* 41:145-146. 1937.

TYPE SPECIES: *Gasteranthus quitensis* Benth., Pl. Hartweg. 233. 1846. (*Hartweg s.n.*, HOLOTYPE: K).

ETYMOLOGY: From the Greek gaster = belly, pot-belly; anthos = flower.

THE ORNITHOPHILOUS SPECIES (SECTION *Gasteranthus*)

**Gasteranthus anomalus** (Morton) Wiehler, comb. nov. Colombia

*Besleria anomala* Morton, *Contr. U.S. Natl. Herb.* 26(9):471. 1939.

**Gasteranthus calcaratus** (HBK) Wiehler, comb. nov. Colombia, Ecuador

*Besleria calcarata* HBK, *Nov. Gen. et Sp. Pl.* 2:399. 1818.

*Gasteranthus pilosus* Benth., Pl. Hartweg. 233. 1846.

*Besleria sodiroana* Fritsch, in Fedde, *Repert.* 18:12. 1922.

**Gasteranthus calceolus** (Fritsch) Wiehler, comb. nov. Ecuador

*Besleria calceolus* Fritsch, in Fedde, *Repert.* 18:12. 1922.

**Gasteranthus caligula** (Morton) Wiehler, comb. nov. Peru

*Besleria caligula* Morton, *Contr. U.S. Natl. Herb.* 38(4):148. 1968

**Gasteranthus corallinoides** (Fritsch) Wiehler, comb. nov. Ecuador, Colombia

*Besleria corallinoides* Fritsch, in Fedde, *Repert.* 18:11. 1922.

**Gasteranthus corallinus** (Fritsch) Wiehler, comb. nov. Peru, Colombia

*Besleria corallina* Fritsch, in Fedde, *Repert.* 18:13. 1922.

**Gasteranthus crenatus** (Morton) Wiehler, comb. nov. Colombia

*Besleria crenata* Morton, *Contr. U.S. Natl. Herb.* 26(9):460. 1939.

**Gasteranthus crispus** (Mansf.) Wiehler, comb. nov. Ecuador

*Halpophyllum crispum* Mansf., in Fedde, *Repert.* 41:145-146. 1937.

**Gasteranthus ecuadorensis** (Fritsch) Wiehler, comb. nov. Ecuador, Colombia

*Besleria pansamalana* Donn.-Sm., var. *ecuadorensis* Fritsch, *Notizbl.*

*Bot. Gart. Berlin-Dahlem* 11(110):975. 1934. *Besleria ecuadorensis*

(Fritsch) Morton, *Contr. U.S. Natl. Herb.* 26(9):471. 1939.

- Gasteranthus imbricans** (Donn.-Sm.) Wiehler, comb. nov. Costa Rica  
*Besleria imbricans* Donn.-Sm., Bot. Gaz. 25:155. 1898.
- Gasteranthus lateralis** (Morton) Wiehler, comb. nov. Ecuador  
*Besleria lateralis* Morton, Contr. U.S. Natl. Herb. 26(9):469. 1939.
- Gasteranthus oncogastrus** (Hanst.) Wiehler, comb. nov. Ecuador  
*Besleria oncogastra* Hanst., Linnaea 34:335. 1865.
- Gasteranthus panamensis** (Morton) Wiehler, comb. nov. Panama  
*Besleria panamensis* Morton, Contr. U.S. Natl. Herb. 26(9):460. 1939.
- Gasteranthus pansamalanus** (Donn.-Sm.) Wiehler, comb. nov. Guatemala, Mexico  
*Besleria pansamalana* Donn.-Sm., Bot. Gaz. 16:197, pl. 17. 1891.  
*Episcia aurea* T. S. Brandege, Univ. Calif. Publ. Bot. 6(3):374. 1917.
- Gasteranthus perennis** (Morton) Wiehler, comb. nov. Ecuador  
*Besleria perennis* Morton, Contr. U.S. Natl. Herb. 26(9):470. 1939.
- Gasteranthus quitensis** Benth., Pl. Hartweg. 233. 1846. Ecuador  
*Besleria quitensis* (Benth.) Hanst., Linnaea 34:334. 1865.
- Gasteranthus sylvarum** (Morton) Wiehler, comb. nov. Colombia  
*Besleria sylvarum* Morton, Contr. U.S. Natl. Herb. 26(9):459. 1939.
- Gasteranthus timidus** (Morton) Wiehler, comb. nov. Ecuador  
*Besleria timida* Morton, Proc. Biol. Soc. Wash. 48:56. 1935.
- Gasteranthus tinctus** (Morton) Wiehler, comb. nov. Colombia  
*Besleria tinctoria* Morton, Contr. U.S. Natl. Herb. 26(9):470. 1939.
- Gasteranthus venustus** (Morton) Wiehler, comb. nov. Ecuador  
*Besleria venusta* Morton, Contr. U.S. Natl. Herb. 26(9):468. 1939.

## THE EUGLOSSOPHILOUS SPECIES

- Gasteranthus acropodus** (Donn.-Sm.) Wiehler, comb. nov. Costa Rica  
*Besleria acropoda* Donn.-Sm., Bot. Gaz. 54:240. 1912.
- Gasteranthus allenii** (Morton) Wiehler, comb. nov. Panama  
*Besleria allenii* Morton, Ann. Missouri Bot. Gard. 29:38. 1942.
- Gasteranthus colombianus** (Morton) Wiehler, comb. nov. Colombia  
*Besleria colombiana* Morton, Contr. U.S. Natl. Herb. 26(9):462. 1939.
- Gasteranthus delphinioides** (Seem.) Wiehler, comb. nov. Colombia, Panama,  
 Costa Rica  
*Drymonia delphinioides* Seem., Bot. Voy. Herald 186. 1854.  
*Besleria delphinioides* (Seem.) Lwbg., Acta Bot. Neerl. 8:49. 1959.  
*Besleria subcoriacea* Morton, Contr. U.S. Natl. Herb. 29(1):28. 1944.  
*Besleria callista* Standl. & L.O. Williams, Ceiba 1:248. 1951.
- Gasteranthus herbaceus** (Morton) Wiehler, comb. nov. Colombia  
*Besleria herbacea* Morton, Contr. U.S. Natl. Herb. 26(9):363. 1939.
- Gasteranthus rupestris** (Morton) Wiehler, comb. nov. Colombia, Ecuador,  
 Peru  
*Besleria rupestris* Morton, Contr. U.S. Natl. Herb. 26(9):462. 1939.

**Gasteranthus wendlandianus** (Hanst.) Wiehler, comb. nov. Costa Rica  
*Besleria wendlandiana* Hanst., *Linnaea* 34:318. 1865.

A complete generic revision of *Gasteranthus* will appear at a later date, when the biology of this group is better understood. The new combinations, however, are necessary for floristic work in progress and for a more adequate labelling of material recently brought into cultivation.

Postscript: One collection of *Gasteranthus delphinioides* from Darién, Panama, has the following medicinal note on the herbarium label: "Tea from the roots for coughs and TB." (*J.A. Duke 5458*, 1962. MO).

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