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A re-examination of *Sanango racemosum*. 4. Its new systematic position in *Gesneriaceae*

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Summary

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The investigations of a research team show clearly that *Sanango racemosum* is a member of the *Gesneriaceae*. Special emphasis is placed on the following features found in this odd species: the woody habit, the stomata grouped into "islands", the node with split-laterals, the solid siphonostele of the petiole, the pair-flowered cymes of the terminal inflorescence, the semi-inferior ovary position, the (axile)-parietal placentation, the oddly shaped nectary, and the presence of the chemical compounds conandroside and sanangoside. All of these are features found in the *Gesneriaceae*, and most of them are unknown in the rest of the *Tubiflorae* or *Scrophulariales*. *Sanango* may not look like a typical gesneriad at first glance, but it fits best into the Caribbean tribe *Gesnerieae*, as a companion for the genus *Gesneria* L. sensu lato.

The studies of *Sanango racemosum* (Ruiz & Pav.) Barringer by Norman (1994), Dickison (1994), and Jensen (1994) have revealed a whole series of unusual taxonomic features which point very clearly to novel familial affinities of this monotypic genus. Does this taxon belong to the *Gesneriaceae*? To a long-time student of this family who recently viewed live and dried material of this treelet, the arboreal habit, the terminal inflorescences borne above the foliage and the tiny white flowers seem initially foreign. Even though I can usually recognize even a sterile gesneriad in the field at first glance, I would have walked past this shrub or tree without a second thought. However, the evidence leads one to conclude that *Sanango* G. S. Bunting & J. A. Duke has the genera of the neotropical *Gesneriaceae* as its closest relations.

The most salient anatomical, floral and chemical features described by Dickison, Norman and Jensen which claim *Sanango* for the *Gesneriaceae* are the following: (1) the woody habit; (2) the anisocytic stomata grouped into islands; (3) the occurrence of split-laterals in the vasculature of the node; (4) the solid siphonostele of the vasculature of the petiole; (5) the terminal inflorescence a pair-flowered gesneriaceous thyrse; (6) the semi-inferior ovary position; (7) the (axile-)parietal placentation, typical for *Gesneriaceae*; (8) the well-developed, cup-shaped nectary; (9) the presence of the rare compounds conandroside and sanangoside in both *Sanango* and *Gesneria* L. These points will be discussed in sequence, and elaborated when necessary.

Tree habit and vegetative morphology. – While most of the 3700 species of *Gesneriaceae* are herbaceous or suffrutescent, a small number are treelets or even trees. *Solenophora calycosa* Donn. Sm. from Panama and Costa Rica is a tree up to 12 m tall, with a trunk diameter of up to 30 cm. Other species in this genus are herbs or subshrubs. The tree *Gesneria onacaënsis* Rusby from the Santa Marta mountains in coastal Colombia reaches a height of 14 m (Wiehler, 1993), while its companion species, *G. cumanensis* (Hanst.) Kuntze from coastal Venezuela, grows up to 3.5 m

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tall. *Besleria variabilis* C. V. Morton in Peru is a treelet up to 5 m tall. In the newly established austral subfamily *Coronantheroideae* Wiehler there are at least four trees: *Coronanthera grandis* G. W. Gillett from the Solomon Islands, to 15 m tall, the monotypic *Depanthus glaber* (C. B. Clarke) S. Moore from New Caledonia, to 11 m tall, the monotypic tree *Lenbrassia australiana* (C. T. White) G. W. Gillett from Queensland, Australia, to 13 m tall, and the monotypic *Negria rhabdothamnoides* F. Muell. from Lord Howe Island off Australia, up to 9 m tall. So *Sanango* with its tree-like habit is in good company in the versatile pantropical *Gesneriaceae*.

Sanango fits into the *Gesneriaceae* because of the following attributes: leaves simple (leathery, looking like those of many species of *Gesneria*), opposite-decussate; stipules absent; trichomes unbranched, uniseriate, with either pointed end cells or capitate-glandular end cells; stomata of the anisocytic type; petioles united by an interpetiolar line, as they occur fairly frequently in the gesneriad family, for instance in *Drymonia* Mart., *Gloxinia* Nees, *Nautilocalyx* Hanst. and *Paliavana* Vand. Interpetiolar lines do not occur in *Gesneria* s. l. because almost all species in this group have a (secondarily) alternate leaf arrangement.

Stomata in groups. – This feature (Fig 1B; see also Dickison, 1994: fig. 3B) is of major interest for a more appropriate disposition of *Sanango*. Stomata grouped into “islands” are a rare feature among the angiosperms. It is found only in the dicotyledons, in 17 unrelated families (Wilkinson, 1979), representing 14 different orders in Cronquist’s (1968) system. It does not occur in the families *Loganiaceae*, *Buddlejaceae* or *Scrophulariaceae*. Stomata aggregated into “islands” are present, though, in the versatile *Gesneriaceae* (Wiehler, 1970; 1983: 94-98): four neotropical genera, with a total of over 100 species, exhibit stomata gathered into groups. In *Gasteranthus* Benth. and *Napeanthus* Gardner they represent a generic character, and in *Gesneria* and *Reldia* Wiehler they occur frequently.

Dickison (1994) reports the presence of a one or two-layered adaxial hypodermis in the leaf lamina of *Sanango racemosum*. This feature occurs also in the neotropical *Gesneriaceae*; in fact, it is typical for most of the 21 genera in the tribe *Episcieae* Endl., appears sporadically in other genera (Wiehler, 1970; 1983: 68-78), and more frequently in *Gesneria* (Skog, 1976: 13). Dickison reports leaf parenchyma cells

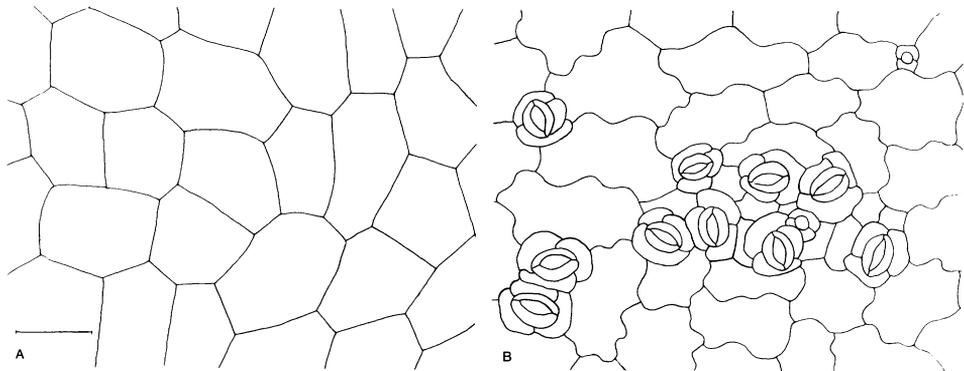


Fig. 1. Epidermis of the leaf of *Sanango racemosum*, drawn from epidermal peels of live material of Neill 9458, growing at the greenhouse of the Gesneriad Research Foundation. – A, adaxial surface; B, abaxial surface, with the stomata grouped into islands raised above the surface level. – Bar = 50 μ m.

containing crystals in the form of needles and prisms in *Sanango*, and Skog (1976: 13) mentions crystals and raphides in species of *Gesneria*.

Split-lateral vascular bundles and stem anatomy. – The multi-trace multilacunar nodes (7 : 7) with split-lateral bundles found by Dickison (1994: fig. 4G) in the nodal anatomy of *Sanango* are likewise of major taxonomic significance. Split-lateral traces in the nodal anatomy are unusual, occurring scattered among nine unrelated angiosperm families: *Chloranthaceae*, *Rhizophoraceae*, *Zygophyllaceae*, *Myrothamnaceae*, *Rubiaceae*, *Gentianaceae*, *Caprifoliaceae*, *Asteraceae*, and *Gesneriaceae* (Howard, 1970; pers. comm., 1993). The *Gesneriaceae* make up the largest contingent of split-laterals among the angiosperms, mostly in the form of three-trace trilacunar nodes (3 : 3). This is the normal condition in the neotropical tribe *Episcieae* (over 730 species). The same split-laterals occur also in some (but not all) species in the palaeotropical gesneriad genera *Chirita* D. Don, *Cyrtandra* J. R. Forst. & G. Forst., *Saintpaulia* H. Wendl., and *Streptocarpus* Lindl. In the *Episcieae* and in the genera just cited, there are also species with multilacunar nodes (5 : 5) with split-laterals, one of the many indications of the evolutionary versatility of this tropical plant family. The other four tribes in the neotropical *Gesneriaceae* (*Gesnerieae*, *Gloxinieae*, *Napeantheae*, and *Beslerieae*) are characterized by unilacunar nodes with one trace per leaf (1 : 1), which is still the most common nodal condition in this large family of over 3700 species (Wiehler, 1970; 1983: 49-67).

The presence of multilacunar nodes with split-laterals in *Sanango* provides another linkage of this genus with the *Gesneriaceae*. Other features of *Sanango* do not associate it with any of the other eight families in Howard's list above, and split-laterals are not known to be present in the three families into which this treelet was placed previously. However, *Sanango* does not fit into the split-lateral *Episcieae*, and there are no split-laterals known in the *Gesnerieae*. In fact, this tribe is an oddity within the opposite-leaved family *Gesneriaceae*, because most of its over 90 species have alternate leaves. Alternate leaves and split-laterals are mutually exclusive. Only two species of *Gesneria* show an opposite-decussate leaf arrangement. A third species, *Gesneria fruticosa* (L.) Kuntze, with typically alternate leaves, has one population on the island of Hispaniola with opposite leaves. Since the inflorescence in all species of the tribe has an opposite-decussate arrangement, there is good reason to assume that their alternate leaves are not a primitive but a secondary or derived feature. Placing *Sanango* with its multilacunar nodes and split-laterals in the so far unilacunar tribe *Gesnerieae* would create a parallel situation with what one finds in the Old World *Gesneriaceae*, typically unilacunar, where tri- and multilacunar nodes with split-laterals occur sporadically within several tribes and genera (Wiehler, 1983: 63).

The presence of cortical vascular bundles in the internodes of the stem of *Sanango racemosum*, as found by Dickison (1994: fig. 4A, H), is of some concern to a gesneriad specialist. Such an anomalous structure, considered by Metcalfe & Chalk (1979: 207) as a diagnostic feature for some genera among 47 otherwise unrelated plant families, is not found in the cortex of the stem of any species of *Gesneriaceae* examined so far, except in the Asiatic gesneriad *Rhynchoglossum obliquum* Blume in which Solereder (1908) discovered a single centric cortical bundle. Dickison (1994) shows that in *Sanango* the cortical vascular bundles, originating from the stele at node level, are joined by branches of the lateral vascular traces arising at the next

node. One branch travels to the petioles, the other moves upwards through the cortex of the stem. It may be justifiable to attribute such a sporadic presence of cortical vascular bundles in the *Gesneriaceae* to the almost legendary evolutionary versatility of this family.

Dickison (1994) cites “scalariform perforation plates in the majority of vessel elements” in *Sanango*. Metcalfe & Chalk (1950) and Carlquist & Hoekman (1986) report simple perforation plates for the family *Gesneriaceae*. But during a rather tentative and incomplete study of the gesneriad genera *Kohleria* Regel and *Moussonia* Regel I (Wiehler, unpubl.) found scalariform perforation plates in some vessels of *Kohleria warszewiczii* (Regel) Hanst. *K. spicata* (Kunth) Oersted, and *Moussonia hirsutissima* (C. V. Morton) Wiehler. Carlquist & Hoekman (1986: fig. 16-20) regarded the occasional scalariform perforation plates in *Moussonia elegans* Regel as exceptional, but the truth is, anatomical investigations of the *Gesneriaceae* are still very scanty. Yet, scalariform perforation plates do occur in this family.

Petiole anatomy. – Dickison (1994: fig. 4J-K) discovered a thick, flattened cylinder forming the vascular tissue in the petiole of the leaf of *Sanango*. The shape of the vascular supply of the petiole is a feature of extreme diagnostic importance in the *Gesneriaceae*, a character employed to separate the five tribes of the neotropical subfamily *Gesnerioideae* (Wiehler, 1983: 64). As illustrated there, the vascular bundles of the petiole at midpoint, seen in cross-section, form a thin arc of varying shape in four of the tribes, but in the *Gesnerieae* the same vascular supply shows a thick, almost closed arc or a complete ring. The vascular tissue in the *Gesnerieae* is a solid or slightly opened siphonostele. The petiole cross-sections of *Sanango* by Dickison are strikingly similar to those found in the tribe *Gesnerieae*. I am unfamiliar with the configurations of the petiolar vascular supply in the *Loganiaceae*, *Buddlejaceae*, and *Scrophulariaceae*, except as published by Metcalfe & Chalk (1950). The petiolar cross-sections of *Sanango* are a good match for those in the *Gesnerieae*.

Inflorescence and floral morphology. – How does the terminal, compound, thyrsoid inflorescence of *Sanango* conform with the distinctive gesneriaceous inflorescence, which is based on the pair-flowered cyme (Weber, 1973; Wiehler, 1983: 21-27)? This unique type of inflorescence is a key character for the whole family *Gesneriaceae*. If *Sanango* did not show this peculiar inflorescence pattern, any attempt to place the taxon in the *Gesneriaceae* would be futile. Fig. 2, from pickled material of *Sanango racemosum* (Neill 9458) studied recently by Anton Weber (Vienna), illustrates beautifully that the *Sanango* inflorescence is composed of the gesneriaceous, pair-flowered cyme units. The inflorescence in the illustration of Bunting & Duke (1961: fig. 1) does not clearly depict this unique pattern. Furthermore, the specific epithet, “*racemosum*”, coined by Ruiz & Pavón (1798), is a misnomer, for the inflorescence of *Sanango* is not a raceme but a thyrse.

The descriptions of the floral morphology by Ruiz & Pavón (1794), Bunting & Duke (1961), Norman (1994) and Dickison (1994) point to a gesneriaceous flower and fruit. The *Sanango* flower may be unusually small (corolla length: 1.2 cm), even puny among the often large, showy and stately gesneriad flowers, but all the features as described in the above investigations are gesneriad: calyx and corolla 5-merous, corolla slightly zygomorphic, aestivation of the corolla lobes imbricate, androecium epipetalous; stamens typically 4, plus one staminode, the filaments adnate to the base of the corolla, then free, bent, thickened, densely white-barbate (as in *Gesneria* sect.

Rhytidophyllum Mart.), anthers versatile (but apparently not syngenesious at anthesis, as is typical for many but not all *Gesneriaceae*), thecae divergent at the base, confluent distally (as in *Besleria* L., etc.); pollen 3-colporate (according to Erdtman in Bunting & Duke, 1961); ovary semi-inferior, placentation axile at lower level, parietal at mid-level (typical for *Gesneriaceae*; Weber, 1971); ovules anatropous. Fruit a dry capsule with loculicidal and septicidal dehiscence, (as in *Gesneria*); seeds fusi-form (as in *Gesneria* and many other genera, Beaufort-Murphy, 1983: 323).

Ovary position. – The semi-inferior ovary of *Sanango* reported by Dickison (1994) is worthy of some further comment. In the *Scrophulariales*, the neotropical subfamily *Gesnerioideae* is the only group showing a strong tendency towards the development of an inferior ovary (Wiehler, 1983: 35-36). Two tribes, the *Gesnerieae* and *Gloxinieae*, with 24 genera and about 380 species, have an ovary position ranging from almost superior through semi-inferior to completely inferior.

Nectary. – The prominent, ring-shaped nectary of *Sanango*, elongated into a cup surrounding the ovary, also calls for some reflection. Such a pronounced development of nectariferous tissue within the flower is not found in the *Loganiaceae*, *Buddlejaceae*, *Scrophulariaceae*, nor in any of the other families of *Scrophulariales*, except in the versatile *Gesneriaceae*. In the neotropical subfamily *Gesnerioideae* the nectary has exploded into a great variety of shapes, as an adaptation to different modes of cross-pollination (Wiehler, 1983: 36-41). The pollinators in this subfamily are, in order of frequency, hummingbirds, female euglossine bees, bats, male euglossine bees (nectary non-functional, replaced by an osmophore), butterflies, moths, and flies, each preferring a different kind of nectar consistency. There are also “buzz” bees searching for pollen, with no nectary being developed. The original annular gesnerioid nectary (an organ that originated de novo), which surrounds the base of the ovary, develops into either an enlarged ring, or half-ring, or five-lobed

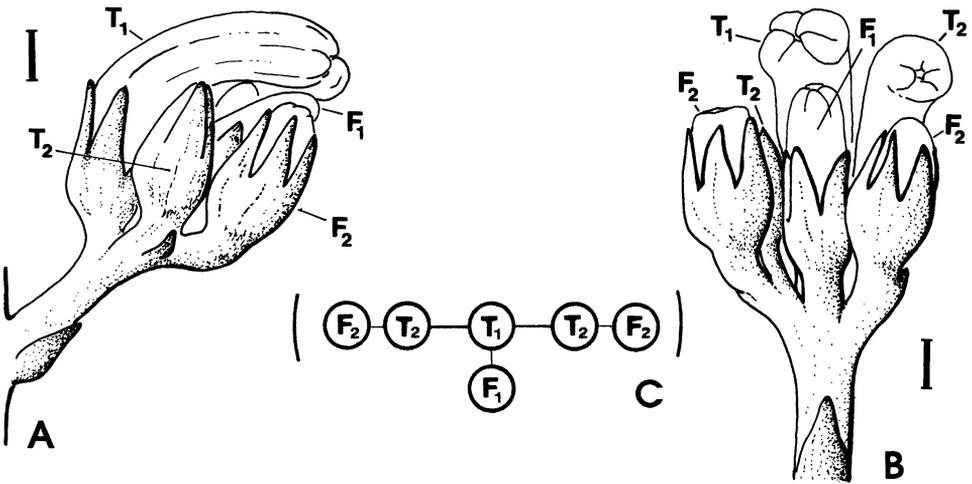


Fig. 2. Structure of partial inflorescence of *Sanango racemosum*. – A, B, six-flowered cyme in bud stage, seen from aside (A) and from below (B); C, corresponding diagram. – T 1-2 = terminal flowers of successive cyme units; F 1-2 = front flowers. – Bar = 1 µm. (Drawing by A. Weber.)

ring, which in many genera has evolved into five separate, free glands which in turn may become reduced to three or two separate glands. In many ornithophilous genera the two (dorsal) glands become united and enlarged. Indeed, the American *Gesneriaceae* show more evolutionary change in nectary shape than any other angiosperm family.

The nectary of *Sanango* fits well into this scheme. The basic ring has been enlarged or stretched into a cup, as an adaptation to pollinators in need of comparatively large amounts of nectar. The bulk of glandular tissue, the white colour of the corolla, and the inflorescences borne above the foliage bring night-time bat pollination to mind. One herbarium label (Dwyer 6228, from Tingo Maria, Peru) notes that the white flowers are fragrant. Masses of white, fragrant flowers carried high above the foliage, with an ample supply of nectar, certainly points towards chiropterophily. Similar adaptations to bat pollination can be seen in many species of the Caribbean genus *Gesneria* [*G. auriculata* (Hook.) Kuntze, *G. leucomalla* (Hanst.) Kuntze, *G. pedunculosa* (DC.) Fritsch, *G. tomentosa* L.]. Here the typically axillary inflorescences are placed above the foliage by an extreme elongation of the peduncles. Axillary and terminal inflorescences may fulfil the same function.

It could be argued that nectarial tissue elongated into a cup is an odd phenomenon in the neotropical *Gesneriaceae*, but even here there is a precedent. In the little known genus *Anetanthus* Hiern ex Benth. the nectary is a stretched out, five-pronged sheath covering the lower half of the ovary, looking like a cup with a defective longitudinal slit.

Conandroside and sanangoside. – The chemotaxonomical investigation of *Sanango* by Jensen (1994) sheds some additional light on the disposition of this genus. He found that *Sanango* contains no iridoid glucosides as would have been expected if it were related to *Buddlejaceae*. On the other hand, it does contain verbascosides specifically found in the *Gesneriaceae*. Such a compound, conandroside, was first discovered in the Japanese gesneriad *Conandron* Siebold & Zucc. and has since been isolated from *Sanango racemosum* as well as from *Gesneria leucomalla* and *G. ventricosa* Sw. (Jensen, 1994). The leaves of *G. pedicellaris* Alain from Hispaniola yielded both conandroside and sanangoside, a compound discovered by Jensen in *Sanango*. Traces of sanangoside were also found in *G. christii* Urb. (tribe *Gesnerieae*), *Koellikeria erinoides* (DC.) Mansf. (tribe *Gloxinieae*) and in *Episcia cupreata* (Hook.) Hanst. (tribe *Episcieae*), all neotropical *Gesneriaceae*.

Conclusions. – The many striking similarities between *Sanango* and the genera of the *Gesnerioideae* speak in favour of the inclusion of this monotypic genus in the *Gesneriaceae*. Among the counter-arguments one might name the long, aseptate trichomes inside the corolla, which have no counterpart as yet among the *Gesneriaceae*; but, then again, not too many gesneriad flowers have been thoroughly examined. Long, aseptate trichomes do occur in the closely related family *Scrophulariaceae* (Raman, 1987), but such a minor feature of still unknown function presents no mayor obstacle to the inclusion of *Sanango* in the *Gesneriaceae*.

Thus placed, *Sanango* would fit best into the otherwise monogeneric tribe *Gesnerieae*, as a second genus. The peculiar vascular pattern of the petiole, the stomata grouped into “islands”, and the phytochemical data argue for such inclusion. The delimitation of this tribe could be stretched to include multilacunar nodes with split-

laterals (paralleling the situation within the Old-World subfamily *Cyrtandroideae* C. B. Clarke, where split-laterals occur sporadically within several tribes and individual genera). The *Gesnerieae* would then contain plants with either terminal or axillary inflorescences, just as both kinds of inflorescences occur in the neotropical tribe *Gloxinieae*.

The inclusion of *Sanango* in the *Gesnerieae* would add an interesting feature to the pattern of distribution of this tribe. The over 90 species of *Gesneria* are restricted to the islands of the Caribbean Sea, with the exception of two woody species growing in the coastal mountains of Colombia and Venezuela. *Sanango* has been found in at least 14 different localities on the eastern slope of the Andes of Ecuador and Peru. Most if not all of the species of *Gesneria* grow on limestone rocks, and *Sanango* in Ecuador likewise grows on calcareous outcroppings (Neill, pers. comm.); for the sites from Peru, no such information is available. The remaining species of the New World *Gesneriaceae* do not appear to have a preference for limestone.

Michael Kiehn (Vienna) has counted the chromosome number of *Sanango racemosum* as $n = 16$ (Kiehn, pers. comm.). While this is not an exact match of the number known for *Gesneria* ($n = 14$), it fits within the tribal pattern of New World *Gesneriaceae*.

Sanango, a genus first collected over 200 years ago, has been shifted from one family to another, because its many unusual features were not sufficiently investigated. Its tree habit and small flowers no doubt confounded its earlier classifiers. It is my firm belief that it has now found its definitive home among the versatile *Gesneriaceae*.

Acknowledgements

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Literature cited

- Beaufort-Murphy, H. T. 1983. The seed surface morphology of the *Gesneriaceae*. *Selbyana* 6: 220-442.
- Bunting, G. S. & Duke, A. 1961. *Sanango*: new Amazonian genus of *Loganiaceae*. *Ann. Missouri Bot. Gard.* 48: 269-274.
- Carlquist, S. & Hoekman, D. A. 1986. Wood anatomy of *Gesneriaceae*. *Aliso* 11: 279-297.
- Cronquist, A. 1968. *The evolution and classification of flowering plants*. Boston.
- 1988. *The evolution and classification of flowering plants*, ed. 2. New York.
- Dickison, W. C. 1994. A re-examination of *Sanango racemosum*. 2. Vegetative and floral anatomy. *Taxon* 43: 601-618.
- Howard, R. A. 1970. Some observations on the nodes of woody plants with special reference to the problem of the “split-lateral” versus the “common gap”. Pp. 195-214 in: Robson, N. K. B., Cutler, D. F. & Gregory, M. (ed.), *New research in plant anatomy* [Bot. J. Linn. Soc. 63, Suppl. 1]. London.
- Jensen, S. R. 1994. A re-examination of *Sanango racemosum*. 3. Chemotaxonomy. *Taxon* 43: 619-623.
- Metcalf, C. R. & Chalk, L. 1950. *Anatomy of the dicotyledons*, 1-2. Oxford.
- & – 1979. *Anatomy of the dicotyledons*, ed. 2, 1. Oxford.

- Norman, E. M. 1994. A re-examination of *Sanango racemosum*. 1. Morphology and distribution. *Taxon* 43: 591-600.
- Raman, S. 1987. A code proposed for the classification of trichomes as applied to the *Scrophulariaceae*. *Beitr. Biol. Pflanzen* 62: 349-367.
- Ruiz, H. & Pavón, J. 1794. *Florae peruviana, et chilensis prodromus*. Madrid.
- & – 1798. *Systema vegetabilium florae peruviana et chilensis*. Madrid.
- Skog, L. E. 1976. A study of the tribe *Gesnerieae*, with a revision of *Gesneria* (*Gesneriaceae: Gesnerioideae*). *Smithsonian Contr. Bot.* 29: 1-182.
- Solereder, H. 1908. *Systematic anatomy of the dicotyledons*, 1. Oxford.
- Weber, A. 1971. Zur Morphologie des Gynoeceums der Gesneriaceen. *Oesterr. Bot. Z.* 121: 234-305.
- 1973. Die Struktur der paarblütigen Partialfloreszenzen der Gesneriaceen und bestimmter Scrophulariaceen. *Beitr. Biol. Pflanzen* 49: 429-460.
- Wiehler, H. 1970. Studies in the morphology of leaf epidermis, in vasculature of node and petiole, and in intergeneric hybridization in the *Gesneriaceae - Gesnerioideae*. Thesis (M. Sc.), Cornell University, Ithaca, NY.
- 1983. A synopsis of the neotropical *Gesneriaceae*. *Selbyana* 6: 1-219.
- 1993. Gesneriad trees in Colombia. *Gesneriad Res. Found. Bull.* 4(4): 2.
- Wilkinson, H. 1979. The plant surface. Pp. 97-165 in: Metcalfe, C. R. & Chalk, L. (ed.), *Anatomy of the dicotyledons*, ed. 2, 1. Oxford.