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*Taxon*, Vol. 46, No. 1. (Feb., 1997), pp. 65-74.

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## Familial placement of *Cyrtandromoea*, *Titanotrichum* and *Sanango*, three problematic genera of the *Lamiales*

J. F. Smith, K. D. Brown, C. L. Carroll & D. S. Denton<sup>1</sup>

### Summary

Smith, J. F., Brown, K. D., Carroll, C. L. & Denton, D. S.: Familial placement of *Cyrtandromoea*, *Titanotrichum* and *Sanango*, three problematic genera of the *Lamiales*. – Taxon 46: 65-74. 1997. – ISSN 0040-0262.

Cladistic relationships among *Gesneriaceae* and related families are investigated using *ndhF* sequence data, to establish the affinity of three genera whose familial placement was uncertain on the basis of morphological evidence alone. A first analysis, including 18 outgroup species from the *Buddlejaceae*, *Scrophulariaceae*, *Bignoniaceae*, and *Acanthaceae* resulted in eleven most-parsimonious trees of 5740 steps each. Recent classifications had placed *Cyrtandromoea* in *Scrophulariaceae* or *Gesneriaceae*, *Titanotrichum* as a monogeneric tribe in *Gesneriaceae*, and *Sanango* in either *Scrophulariaceae*, *Gesneriaceae*, *Loganiaceae*, or *Buddlejaceae*. Sequence data from the chloroplast *ndhF* gene indicate that they are *Gesneriaceae*: *Cyrtandromoea* belongs to the *Klugieae*, the monogeneric *Titanotricheae* are perhaps sister to the remainder of the *Cyrtandroideae*, and *Sanango* is placed in the *Gesnerieae* as was predicted by recent morphological and chemical analyses.

### Introduction

The *Gesneriaceae* are a mid-sized to large plant family comprising approximately 3500 species in 150 genera, distributed primarily in the tropics with a few temperate species in Europe, China and Japan (Heywood, 1978; A. Weber, pers. comm.). The majority of species in the *Gesneriaceae* are herbaceous perennials, but some are annuals, shrubs, lianas, or trees.

The *Gesneriaceae* are a member of the *Lamiales* in the wide sense and are distinguished from other families in the order by a combination of five-lobed corollas, parietal placentation, and presence of endosperm in most taxa (Cronquist, 1981). They long have been thought to be a monophyletic family. However, several of the morphological features characteristic of the family also are found in species of the closely related *Scrophulariaceae*, *Acanthaceae*, and *Bignoniaceae*. Because of this character overlap, several genera traditionally placed in the *Gesneriaceae* are of uncertain familial affinity, among them *Cyrtandromoea* Zoll., *Titanotrichum* Soler., and *Sanango* G. S. Bunting & J. A. Duke.

*Cyrtandromoea* at one time was placed in the gesneriaceous tribes *Beslerieae* (Fritsch, 1893-1894) or *Loxonieae* (Burt, 1962), but later Burt (1965) moved it to the tribe *Mimuleae* of *Scrophulariaceae*. An analysis of floral nodal anatomy (Singh & Jain, 1978) supports the placement in *Scrophulariaceae*.

*Titanotrichum* is a monospecific genus from Taiwan, Fujian, and southern Japan (Wang & al., 1992), characterized by a terminal inflorescence of showy flowers often replaced by gemmae serving as vegetative propagules. Although *Titanotrichum* generally is considered a member of the *Cyrtandroideae*, Burt (1962, 1977) left its

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tribal affinity uncertain. Wang & al. (1992) recently placed it in its own monogeneric tribe, *Titanotricheae*.

*Sanango* is a small neotropical tree previously assigned to the *Loganiaceae* (tribe *Buddlejeae*), *Buddlejaceae*, or *Scrophulariaceae*. Recent investigations of floral and nodal anatomy (Dickison, 1994; Norman, 1994) and chemical constituents (Jensen, 1994) caused Wiehler (1994) to place *Sanango* in the *Gesneriaceae*, tribe *Gesnerieae*.

No cladistic analysis to date has included *Cyrtandromoea*, *Titanotrichum*, and *Sanango* to verify their positions. They deliberately were excluded from a cladistic analysis of morphological characters due to the potential difficulty in scoring homology (Smith, 1996). This study investigates the cladistic relationships of these three anomalous genera with other members of the *Gesneriaceae*, *Buddlejaceae*, *Scrophulariaceae*, *Bignoniaceae*, and *Acanthaceae*, based on sequences of the chloroplast gene *ndhF*. Comparison of gene sequences across divergent taxa does not pose the same difficulties of assessing homology as does morphology. The cladograms based on these data are likely to reflect evolutionary history and, thus, place the taxa in the correct family and tribe.

### Methods

The *ndhF* gene was amplified in two overlapping sections (positions 1-1350, and 972-2044). Amplification products were purified using PCR wizard purification preps (Promega) according to the manufacturer's instructions. The gene sequences were generated by thermal cycle sequencing (Innis & al., 1988) using the Silver Sequence method (Promega). This sequencing method resulted in sequences that could be read within six to eight hours after amplification was completed. The advantages of the silver staining procedure over radioactive methods are safety, minimal waste, and speed.

The focus of this analysis is on the relationships of *Cyrtandromoea*, *Titanotrichum*, and *Sanango* within the *Gesneriaceae* or other families. Therefore, we have included in our analysis taxa from nearly all tribes within the *Gesneriaceae* as accepted in current classification systems (Wiehler, 1983; Burt, 1962, 1977; Burt & Wiehler, 1995), along with 18 species of *Buddlejaceae*, *Scrophulariaceae*, *Bignoniaceae*, and *Acanthaceae*. Voucher information and Genbank accession numbers are given elsewhere (Smith & al., 1997). The *ndhF* sequence for *Sanango racemosum* (Ruiz & Pav.) Barringer is new in this analysis. Material of this species was obtained through Hans Wiehler from a plant in cultivation at the Gesneriad Research Foundation in Sarasota, Florida. The Genbank accession number for this sequence is U62144.

Phylogenetic relationships were reconstructed using PAUP version 3.1.1 (Swofford, 1993) to implement parsimony (Farris, 1970; Farris & al., 1970; Swofford & Maddison, 1987). This program allows parallelisms and reversals (homoplasy), and provides an option for missing data. Trees were generated using the heuristic option, saving minimal trees only, with the "collapse zero-length branches", and "ignore uninformative characters" options in effect. Because of the large number of taxa, the branch-and-bound and exhaustive search options would have consumed an excessive amount of time. Therefore, the trees presented here are best approximations and not

Table 1. Additional steps required to place *Cyrtandromoea*, *Titanotrichum*, and *Sanango* in positions other than those found in the most-parsimonious trees. Abbreviations as in Fig. 1.

Genus	Sc I	Sc II	Pa	Bu	KI	GE
<i>Cyrtandromoea</i>	56	48	36	19	0	29
<i>Titanotrichum</i>	50	46	39	23	5	24
<i>Sanango</i>	86	84	81	59	21	0

exact solutions. The manner in which the program reconstructs phylogenetic sequences is sensitive to the order in which taxa are presented in the data matrix, frequently finding different islands of equally parsimonious trees depending on the input order (Maddison, 1991). It is therefore important to repeat the analysis several times. To do this, the search option of Olmstead & Palmer (1994) was implemented searching for 1000 trees each in five subsequent analyses with the nearest neighbor interchanges (NNI) search option in effect and mulpars “off”. Each of the results from the five NNI searches was used as the starting tree for a search with tree bisection reconnection (TBR) and mulpars “on”. This strategy was used in the first analysis with all 18 non-*Gesneriaceae* taxa designated as outgroups, and with subsequent analyses with only *Buddlejaceae* as the designated outgroup.

Branch support analysis was performed to examine trees that were six or fewer steps longer than the most-parsimonious trees (Bremer, 1988, 1994; Donoghue & al., 1992). This type of analysis provides an indication of the robustness of the data by determining which clades persist in a consensus tree as parsimony is relaxed. The analysis was performed by searching for all trees six or fewer steps longer than the most-parsimonious trees, and then using the “filter trees” option of PAUP to find trees one, two, etc. steps longer than the most-parsimonious trees.

The cost, in terms of steps, required to place each of these three genera elsewhere in the cladograms was examined using the “constraints” option of PAUP.

## Results

Sequence analysis was initially performed with all 73 species from five families (*Gesneriaceae*, *Buddlejaceae*, *Scrophulariaceae*, *Acanthaceae*, and *Bignoniaceae*) with the outgroup designated as all taxa in the four outgroup families. This analysis resulted in eleven most-parsimonious trees of 5740 steps each, consistency index (CI) = 0.29, and retention index (RI) = 0.48, which indicated that *Gesneriaceae* were monophyletic and that *Buddlejaceae* were the closest outgroup to the *Gesneriaceae* (Fig. 1).

Subsequent analyses minimized computer time by using only *Buddlejaceae* as the designated outgroup. This reduced analysis resulted in a single most-parsimonious tree of 4678 steps (CI = 0.28, RI = 0.39; Fig. 2).

In order to place *Cyrtandromoea* in the *Scrophulariaceae* 56, 48, and 36 additional steps were required for the “Scroph I”, “Scroph II”, and *Paulownia* groups of Olmstead & Reeves (1995), respectively (Table 1). To place *Titanotrichum* in the same groups required an additional 50, 46, and 39 steps (Table 1). Likewise, to place

*Sanango* in the *Buddlejaceae* required an additional 59 steps, and to place *Sanango* in the *Scrophulariaceae* clades required 86, 84, and 81 additional steps (Table 1).

### Discussion

The results of this analysis clearly place *Cyrtandromoea*, *Titanotrichum*, and *Sanango* in the *Gesneriaceae* rather than in any of the other related families (Fig. 1-2). Forcing these genera elsewhere resulted in 19-56, 23-50 and 59-86 extra steps, respectively, to put *Cyrtandromoea*, *Titanotrichum*, and *Sanango* in the *Scrophulariaceae* or *Buddlejaceae* (Table 1). Within *Gesneriaceae*, our analysis places *Cyrtandromoea* in the *Klugieae*, *Titanotrichum* as a monogeneric tribe sister to the remainder of the *Cyrtandroideae*, and *Sanango* in the *Gesnerieae*.

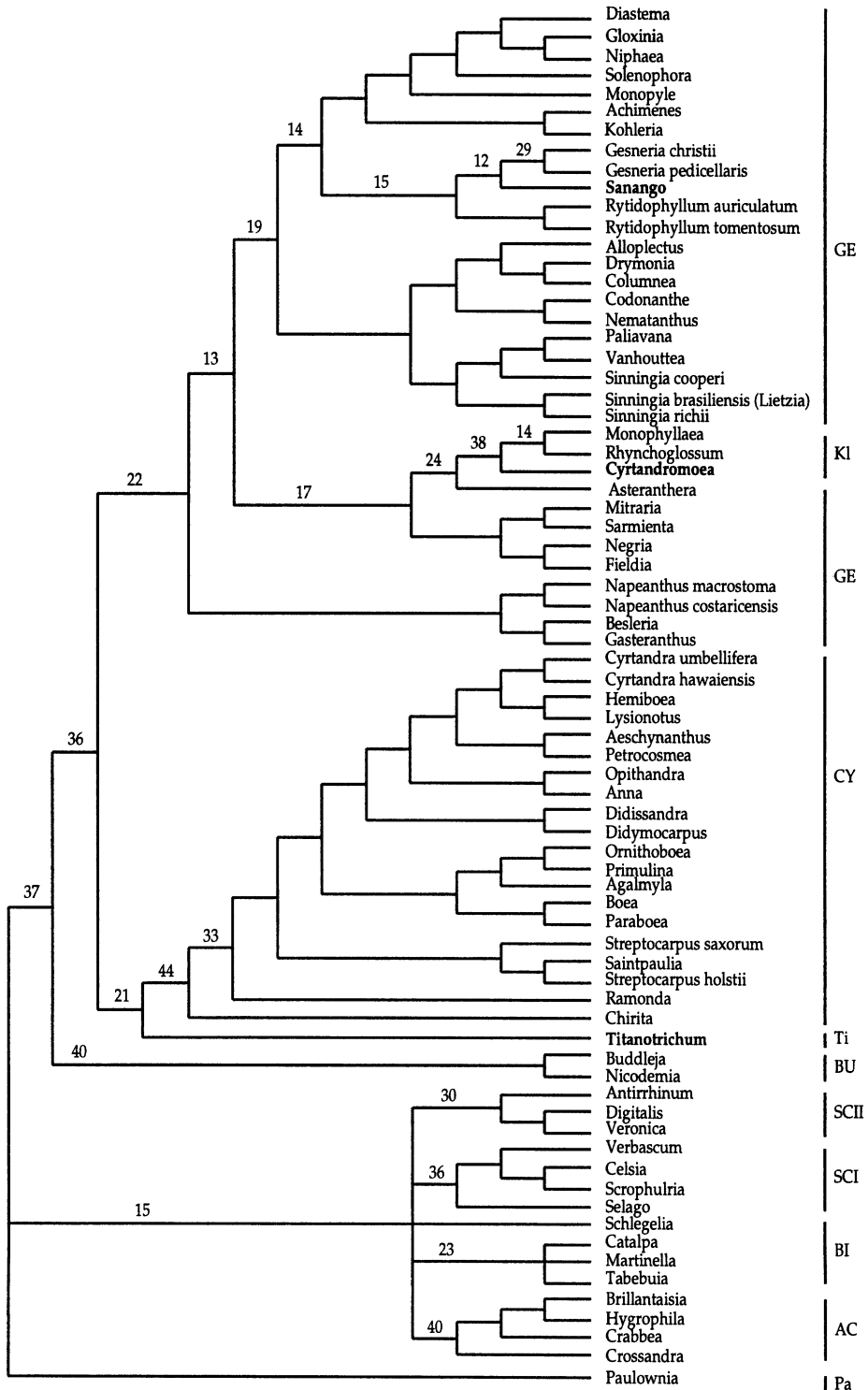
The tree resulting from the analysis of all taxa has *Klugieae* in the *Gesnerioideae*, an unusual result. A similar unusual placement of this tribe resulted from a previous analysis that did not include the *Buddlejaceae* (Smith & al., 1997) and is believed to be either the result of homoplastic characters between these taxa and the outgroups, or of the inability of the computer to find a shorter tree with these taxa in their expected positions. When only *Buddlejaceae* are used as the outgroup, this anomalous placement disappears (Fig. 2).

A similar discrepancy concerns the position of the *Beslerieae* and *Coronanthereae*. In a previous analysis that neither used the *Buddlejaceae* as the outgroup nor included *Sanango* (Smith & al., 1997), *Beslerieae* and *Coronanthereae* were sister taxa and as a whole were sister to the remainder of the *Gesnerioideae*. In this analysis (Fig. 2), the *Coronanthereae* are sister to the remainder of *Gesnerioideae*, with the exception of *Beslerieae* and *Napeantheae*, which are sister to the remainder of the subfamily. This is again likely due to the introduction of additional homoplasy by the inclusion of *Sanango*. The classification of Smith & al. (1997) can be obtained from the present data set with the addition of only three steps, but these relationships are only weakly supported, and no positive statements are permissible at this time.

*Cyrtandromoea*. – This genus was placed in the *Beslerieae* by Fritsch (1893-1894) and moved to the *Loxonieae* by Burt (1962) who, however, considered it to be anomalous there, and in the *Cyrtandroideae* as a whole, due to its isocotylous seedlings when nearly all other *Cyrtandroideae* are anisocotylous. Later, Burt (1965) rejected a placement of *Cyrtandromoea* in the tribe *Beslerieae* of *Gesnerioideae*, because the characteristic features of that tribe (confluent anther thecae, placentae ovuliferous on inner surfaces, bilobed or stomatomorphic stigma, thick verrucose exocarp, and spirally striate seeds) are lacking in *Cyrtandromoea*. Instead, he decided to move *Cyrtandromoea* to the *Scrophulariaceae*, due to its isocotylous seedlings,

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Fig. 1. Strict consensus of eleven most-parsimonious trees based on *ndhF* gene sequence analysis of 73 species of *Gesneriaceae* and outgroup families (5740 steps, CI = 0.29, RI = 0.48; numbers above clades are the number of character state changes that support that clade; not all values are reported on this tree). – AC = *Acanthaceae*, BI = *Bignoniaceae*, BU = *Buddlejaceae*, CY = *Cyrtandroideae*, GE = *Gesnerioideae*, KI = *Klugieae*, Pa = *Paulownia*, SCI = Scroph I (Olmstead & Reeves, 1995), SCII = Scroph II (Olmstead & Reeves, 1995), Ti = *Titanotricheae*.



presence of endosperm in the seeds, thin fruit wall, fleshy placenta, and bilocular ovary. Although none of these characteristics taken singly are sufficient to remove *Cyrtandromoea* from *Gesneriaceae* (in fact, character states such as endosperm presence and isocotylous seedlings are common among the *Gesnerioideae*), he felt that their combination and a strong resemblance of *Cyrtandromoea* to *Rehmannia* Libosch. ex Fisch. & C. A. Mey. and *Brookea* Benth., which had been moved previously from *Gesneriaceae* to *Scrophulariaceae*, justified the transfer.

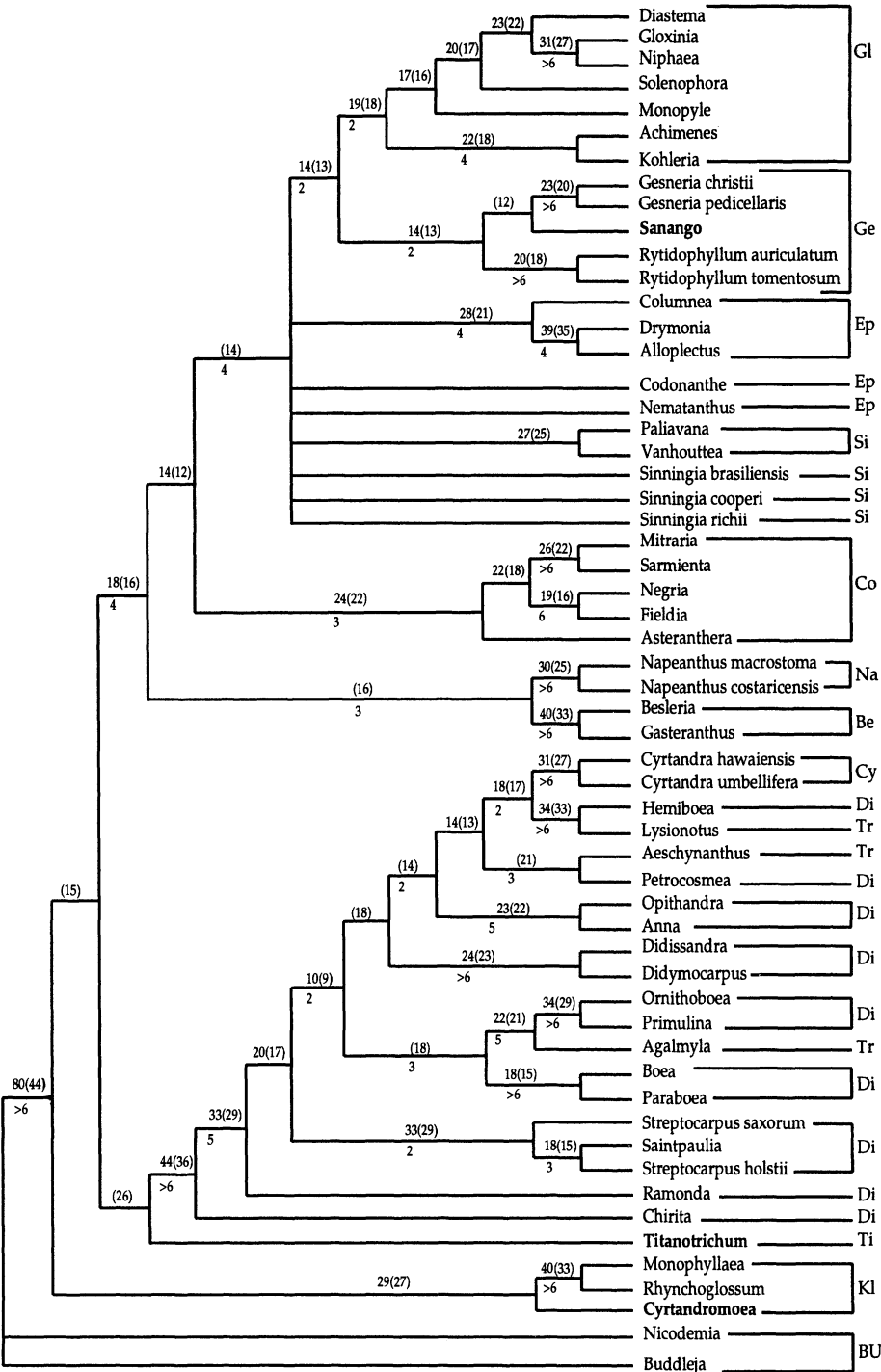
Searching the *Scrophulariaceae* for tribal affinity of *Cyrtandromoea* in the classification of Wettstein (1891-1893), Burt (1965) found a strong similarity of fruit characteristics between *Cyrtandromoea* and *Leucocarpus* D. Don in the *Mimuleae*. Since *Leucocarpus* is a Central American genus and *Cyrtandromoea* is Malaysian they would have been the first known examples of amphi-Pacific vicariance in the *Scrophulariaceae*, and the second such disjunction in the whole *Tubiflorae* along with *Rhynchoglossum* Blume of the *Gesneriaceae*.

Ivanina (1965) used carpel morphology to place *Cyrtandromoea* in the *Klugieae* in her analysis of the *Gesneriaceae*, but later analysis of floral vasculature indicated that *Cyrtandromoea* has little affinity to other members of *Gesneriaceae*, and is more appropriately placed in *Scrophulariaceae* (Singh & Jain, 1978) due to its sepal laterals arising independently from petal traces (they arise conjointly in *Gesneriaceae*), the presence of several lateral bundles (the *Gesneriaceae* have two or none), and collateral bundles (concentric in *Gesneriaceae*). Comparison with the *Gesneriaceae* (including members of *Klugieae*) was based on parallel studies by Wilson (1974a, b).

Ironically, the cladistic analysis of *ndhF* sequence data confirms Ivanina's (1965) suggestion by placing *Cyrtandromoea* in the tribe *Klugieae* of the *Gesneriaceae* [the same tribe to which amphi-Pacific *Rhynchoglossum* belongs] (Fig. 1-2). To place *Cyrtandromoea* in the *Scrophulariaceae*, an additional 19-56 steps beyond the most-parsimonious trees would be necessary (Table 1). No member of the *Mimuleae* has been included in our *ndhF* analysis, but the large number of extra steps required to remove *Cyrtandromoea* from the *Gesneriaceae* indicates that it is unlikely placed in a *Scrophulariaceae* tribe. Our results call for a reassessment of the characters that Burt (1965) used to move *Cyrtandromoea* to the *Scrophulariaceae*. Endosperm in seeds and isocotylous seedlings are unknown in the *Cyrtandroideae* but occur in the *Gesnerioideae*, as well as other families closely related to the *Gesneriaceae*. A placement of *Cyrtandromoea* in the *Gesnerioideae* would require 29 steps more than the most-parsimonious trees (Table 1) based on *ndhF* data. The bilocular ovary, traditionally characteristic of the *Scrophulariaceae*, also has been observed in other members of the *Gesneriaceae* (particularly in the *Klugieae*, e.g., *Monophyllaea* R. Br.), and therefore, can not be used to exclude *Cyrtandromoea* from the *Gesneriaceae* either.

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Fig. 2. Most-parsimonious tree based on the same data as Fig. 1 but with only two *Buddlejaceae* included as outgroups (4678 steps, CI = 0.28, RI = 0.39; numbers above the clade are character state changes that support that clade, numbers in parentheses are those character state changes that are homoplastic; numbers below the clade are decay values). – Be = *Beslerieae*, BU = *Buddlejaceae*, Co = *Coronanthereae*, Cy = *Cyrtandreae*, Di = *Didymocarpeae*, Ep = *Episcieae*, Ge = *Gesnerieae*, Gl = *Gloxinieae*, Kl = *Klugieae*, Na = *Napeantheae*, Si = *Sinningieae*, Ti = *Titanotricheae*, Tr = *Trichosporeae*.





*Titanotrichum*. – This monospecific genus is unusual among the *Gesneriaceae* in that it produces terminal inflorescences in which gemmae replace flowers, either in the apical portions or throughout. *Titanotrichum* has posed problems regarding its affinity within the *Gesneriaceae*, although it has traditionally been placed in the *Cyrtandroideae* (Burt, 1962; Wang & al., 1992). Wang & al. (1992) raised *Titanotrichum* to the status of a monogeneric tribe *Titanotricheae*, also recognized by Burt & Wiehler (1995).

The isolated position of *Titanotrichum* within the *Cyrtandroideae* is supported by our cladistic analysis of *ndhF* sequence data. The genus remains within *Cyrtandroideae*, but as sister to the remainder of the subfamily (Fig. 1-2). Placing *Titanotrichum* in the *Scrophulariaceae* requires 39-50 additional steps (Table 1). A placement within the *Gesnerioideae* would require only 24 additional steps (Table 1) and only five steps are necessary to place it in the tribe *Klugieae*, indicating that the exact position of *Titanotrichum* is still somewhat in doubt. The uncertainty regarding its placement as the sister to either *Cyrtandroideae*, *Gesnerioideae*, or *Klugieae*, indicates that *Titanotrichum* may have diverged early in the evolution of the *Gesneriaceae*.

*Sanango*. – *Sanango racemosum* is the single species of a genus endemic to South America. It is unusual among *Gesneriaceae* in its arboreal habit, terminal inflorescence, and small white flowers. However, as with the characters that had served to exclude *Cyrtandromoea* from the *Gesneriaceae*, none of these character states taken by itself would justify removal of a species from the *Gesneriaceae*. Some accepted members of the *Gesnerioideae* are woody (*Solenophora* Benth. and several members of the tribe *Coronanthereae*), whereas others are known to have terminal inflorescences and small white flowers.

Recent studies on floral anatomy, epidermal anatomy, and chemical constituents of *Sanango* (Norman, 1994; Dickson, 1994; Jensen, 1994) prompted Wiehler (1994) to move *Sanango* to the *Gesneriaceae*, specifically to the tribe *Gesnerieae*. Wiehler (1994) used several character states possessed by *Sanango* that are otherwise known in the families it had been placed in, *Loganiaceae*, *Scrophulariaceae*, and *Buddlejaceae*: anisocytic stomata in islands, split laterals in the nodal vasculature, solid siphonostele in the petiole, inflorescence of a pair-flowered thyrses, semi-inferior ovary, parietal placentation, cup-shaped nectary, and the presence of conandroside and sanangoside. Among these, the stomata, petiolar siphonostele, and chemical compounds are suggestive of the *Gesnerieae*, a tribe previously restricted to the Caribbean islands and nearby coastal mountains of Colombia and Venezuela whereas *Sanango* is found in the eastern montane forests of Ecuador and Peru. However, both *Sanango* and the other *Gesnerieae* are usually found on limestone, and are the only members of the *Gesnerioideae* to show such edaphic restrictions (Wiehler, 1994).

The cladistic analysis of *ndhF* sequences clearly supports Wiehler's (1994) assessment of *Sanango*. Its placement within the *Gesnerieae* is supported by 14 character state changes. 81 to 86 additional steps are required to place *Sanango* in the *Scrophulariaceae*, and 59 to place it in the *Buddlejaceae*. Inclusion of other members of the *Loganiaceae* in the analysis may modify the picture, but the large number of synapomorphies that place *Sanango* specifically in the *Gesnerieae* make its removal from the *Gesneriaceae* unlikely, especially since *Sanango* had been placed in the *Buddlejeae* of the *Loganiaceae* where both *Buddleja* and *Nicodemia*, used in our analysis, belong (Leeuwenberg, 1971).

### Acknowledgements

We are indebted to the following for sharing plant material: L. E. Skog, W. L. Wagner, J. K. Boggan, R. Dunn, H. Wiehler, D. Turley, Strybing Arboretum, M. Källersjö, B. Nordenstom, J. Katzenstein, B. Stewart, M. Evans, and the American Gloxinia and Gesneriad Society (AGGS) seed fund. Funding for this project was provided by NSF grant DEB-9317775 and the AGGS. The comments of Magnus Lidén, Anton Weber, and Elaine Norman have helped to make this a better publication.

### Literature cited

- Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795-803.
- 1994. Branch support and tree stability. *Cladistics* 10: 295-304.
- Burt, B. L. 1962. Studies in the *Gesneriaceae* of the old world XXIV: Tentative keys to the tribes and genera. *Notes Roy. Bot. Gard. Edinburgh* 24: 205-220.
- 1965. The transfer of *Cyrtandromoea* from *Gesneriaceae* to *Scrophulariaceae*, with notes on the classification of that family. *Bull. Bot. Surv. India* 7: 73-88.
- 1977. Classification above the genus, as exemplified by *Gesneriaceae*, with parallels from other groups. *Pl. Syst. Evol.*, Suppl. 1: 97-109.
- & Wiehler, H. 1995. Classification of the family *Gesneriaceae*. *Gesneriana* 1: 1-4.
- Cronquist, A. 1981. *An integrated system of classification of flowering plants*. New York.
- Dickson, W. C. 1994. A re-examination of *Sanango racemosum*. 2. Vegetative and floral anatomy. *Taxon* 43: 601-618.
- Donoghue, M. J., Olmstead, R. G., Smith, J. F. & Palmer, J. D. 1992. Phylogenetic relationships of *Dipsacales* based on *rbcL* sequences. *Ann. Missouri Bot. Gard.* 79: 333-345.
- Farris, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19: 83-92.
- Kluge, A. G. & Eckardt, M. J. 1970. A numerical approach to phylogenetic systematics. *Syst. Zool.* 19: 172-191.
- Fritsch, K. 1893-1894. *Gesneriaceae*. Pp. 133-185 in: Engler, A. & Prantl, K. (ed.), *Die natürlichen Pflanzenfamilien*, 4(3b). Leipzig.
- Heywood, V. H. 1978. *Flowering plants of the world*. Oxford.
- Innis, M. A., Myambo, K. B., Gelfand, D. H. & Brow, M. A. D. 1988. DNA sequencing and direct sequencing of polymerase chain reaction-amplified DNA. *Proc. Natl. Acad. Sci. U.S.A.* 85: 9436-9440.
- Ivanina, L. I. 1965. Application of the carpological method to the taxonomy of *Gesneriaceae*. *Notes Roy. Bot. Gard. Edinburgh* 26: 383-402.
- Jensen, S. R. 1994. A re-examination of *Sanango racemosum* 3. Chemotaxonomy. *Taxon* 43: 619-623.
- Leeuwenberg, A. J. M. 1971. Notes on American *Loganiaceae* V. Key to the genera represented in America. *Acta Bot. Neerl.* 20: 539-542.
- Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* 40: 315-328.
- Norman, E. M. 1994. A re-examination of *Sanango racemosum*. 1. Morphology and distribution. *Taxon* 43: 591-600.
- Olmstead, R. G. & Palmer, J. D. 1994. Chloroplast DNA systematics: a review of methods and data analysis. *Amer. J. Bot.* 81: 1205-1224.
- & Reeves, P. A. 1995. Evidence for the polyphyly of the *Scrophulariaceae* based on chloroplast *rbcL* and *ndhF* sequences. *Ann. Missouri Bot. Gard.* 82: 176-193.
- Singh, V. & Jain, D. K. 1978. Floral anatomy and systematic position of *Cyrtandromoea*. *Proc. Indian Acad. Sci.* 87: 71-74.
- Smith, J. F. 1996. Tribal relationships within the *Gesneriaceae*: a cladistic analysis of morphological data. *Syst. Bot.* (in press).

- , Wolfram, J. C., Brown, K. D., Carroll, C. L. & Denton, D. S. 1997. Tribal relationships in the *Gesneriaceae*: evidence from DNA sequences of the chloroplast gene *ndhF*. *Ann. Missouri Bot. Gard.* 200: 50-66.
- Swofford, D. L. 1993. *PAUP: Phylogenetic analysis using parsimony, version 3.1.1* Champaign.
- & Maddison, W. P. 1987. Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci.* 87: 199-229.
- Wang, W. T., Pan, K. & Li, Z. 1992. Keys to the *Gesneriaceae* of China. *Edinburgh J. Bot.* 49: 5-74.
- Wettstein, R. von, 1891-1893. *Scrophulariaceae*. Pp. 39-107 in: Engler, A. & Prantl, K. (ed.), *Die natürlichen Pflanzenfamilien*, 4(3b). Leipzig.
- Wiehler, H. 1983. A synopsis of the neotropical *Gesneriaceae*. *Selbyana* 6: 1-219.
- 1994. A re-examination of *Sanango racemosum*. 4. Its new systematic position in the *Gesneriaceae*. *Taxon* 43: 625-632.
- Wilson, C. L. 1974a. Floral anatomy of *Gesneriaceae*. I. *Cyrtandroideae*. *Bot. Gaz.* 135: 247-256.
- 1974b. Floral anatomy of *Gesneriaceae*. II. *Gesnerioideae*. *Bot. Gaz.* 135: 256-268.