J.R. Clark, ed. Proceedings of the World Gesneriad Research Conference 2010. Selbyana 31: 65-253.

Soltis, D.E., S.A. Smith, N. Cellinese, K.J. Wurdack, D.C. Tank, S.F. Brockington, N.F. Refulio-Rodriguez, J.B. Walker, M.J. Moore, B.S. Carlsward, C.D. Bell, M. Latvis, S. Crawley, C. Black, D. Diouf, Z. Xi, C.A. Rushworth, M.A. Gitzendanner, K.J. Sytsma, Y. Qiu, K.W. Hilu, C.C. Davis, M.J. Sanderson, R.S. Beaman, R.G. Olmstead, W.S. Judd, M.J. Donoghue and P.S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. Am. J. Bot. 98: 704–730.

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A NEW FORMAL CLASSIFICATION OF GESNERIACEAE

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ABSTRACT. A new formal classification of Gesneriaceae is proposed. It is the first detailed and overall classification of the family that is essentially based on molecular phylogenetic studies. Three subfamilies are recognized: Sanangoideae (monospecific with *Sanango racemosum*), Gesnerioideae and Didymocarpoideae. As to recent molecular data, *Sanango*/Sanangoideae (New World) is sister to Gesnerioideae + Didymocarpoideae. Its inclusion in the Gesneriaceae amends the traditional concept of the family and makes the family distinctly older. Subfam. Gesnerioideae (New World, if not stated otherwise with the tribes) is subdivided into five tribes: Titanotricheae (monospecific, East Asia), Napeantheae (monogeneric), Beslerieae (with two subtribes: Besleriinae and Anetanthinae), Coronanthereae (with three subtribes: Coronantherinae, Mitrariinae and Negriinae; southern hemisphere), and Gesnerieae [with five subtribes: Gesneriinae, Gloxiniinae, Columneinae (=the traditional Episcieae), Sphaerorrhizinae (=the traditional Sphaerorhizeae, monogeneric), and Ligeriinae (=the traditional Sinningieae)]. In the Didymocarpoideae (almost exclusively Old World, especially E and SE Asia/Malesia) two tribes are recognized: Epithemateae [with four small, but morphologically and genetically very distinctive subtribes: Loxotidinae (monogeneric with *Rhynchoglossum*), Monophyllaeinae, Loxoniinae and Epithematinae (monogeneric)] and Trichosporeae (the earliest name at tribal rank for the ''Didymocarpoid Gesneriaceae''). The last is subdivided into ten subtribes: Jerdoniinae (monospecific), Corallodiscinae (monogeneric), Tetraphyllinae (monogeneric), Leptoboeinae, Ramondinae (Europe), Litostigminae (monogeneric), Streptocarpinae (Africa and Madagascar), Didissandrinae, Loxocarpinae and Didymocarpinae. Didymocarpinae is the largest subtribe (ca. 30 genera and >1600 species) and still requires intensive study. It includes the most speciose genera such as *Cyrtandra, Aeschynanthus, Agalmyla, Didymocarpus, Henckelia, Codonoboea, Oreocharis* and *Primulina* and the types of the traditional tribes Didymocarpeae, Trichosporeae and Cyrtandreae.

Key words: Gesneriaceae, classification, traditional classifications, molecular systematics

INTRODUCTION

The incorporation of molecular methods into plant systematics over the last two decades has dramatically changed our understanding of the phylogenetic diversification of angiosperms. Not unexpectedly, this applies also to the family Gesneriaceae. The last classification, based on morphological (and with respect to the Neotropical Gesneriaceae also cytological) characters was that of Burtt and Wiehler (1995). This was followed by the treatment of the family in Kubitzki's ''Families and genera of vascular plants'' by Weber (2004a). In the latter work, allowance was made for the molecular data then available (partly unpublished and published later by Möller et al. 2009). This resulted in an abandonment of the traditional tribes hitherto recognized in the Old World Gesneriaceae. For a provisional subdivision of the ''Didymocarpoid Gesneriaceae,'' informal group names (e.g., ''Basal Asiatic genera'') were used instead of formal names.

Since Weber's (2004a) treatment, many more molecular studies have been published (reviewed in Möller & Clark, 2013). In the New World Gesneriaceae a new tribe has been erected (Roalson et al. 2005b), and in the Old World Gesneriaceae a much more detailed picture of the informal groups previously recognized emerged through the work of M. Möller and his collaborators (e.g., Möller et al. 2009, 2011a; Weber et al. 2011a). This paper is the first to propose a comprehensive classification of the entire family based on molecular phylogenetic studies and to formalize a rank-based system from published phylogenies.

DO WE NEED FORMAL RANK-BASED CLASSIFICATIONS?

The answer is: not necessarily. Formal classifications with ranks indicated by name endings are simply a well-established custom. The modern language of our discipline consists of precise and easily comprehensible communication via phylograms

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or cladograms ("phylogenetic trees"). Trees are graphical representations (branching diagrams) of the relationships of taxa and can do without names that reflect the hierarchical order. Where complex diversification patterns exist, they provide more precise information than formal classifications (with a limited number of ranks) could ever do.

Traditional rank-based classifications date back to a time when nobody could imagine how precise phylogenetic reconstructions would ever be possible. Therefore, only few (three) formal ranks between family and genus have been established: subfamily, tribe and subtribe. Reveal (1995 onw, edition 2011; 2010) has suggested three additional ranks be implemented below the family level (supersubfamily, supertribe, supersubtribe). In earlier versions of this manuscript we attempted to introduce some of these new ranks. However, due to conflicting or incomplete molecular evidence, the relationships of the subtribes within the large tribes Gesnerieae and Trichosporeae (in the new sense, see below) proved ambiguous. Therefore, we refrain from establishing a complex hierarchical classification beyond the traditional ranks.

Systematics is a "never-ending synthesis" and time will perhaps never be ripe for an ultimate classification. However, at present we have molecular data of all major subgroups of Gesneriaceae and an updated classification along the lines addressed here appears meaningful. The classification of the neotropical Gesneriaceae seems to approach consolidation, and the recent phylogenetic analyses of the Old World Gesneriaceae without a doubt are a major step forward (see review of Möller & Clark 2013). Thus, the foundation is laid to synthesize a new and overall classification of the family.

WHAT TO DO WITH "ANOMALOUS" GENERA?

Inclusion of a number of genera in the Gesneriaceae has been debated (see Weber 2004a, under "Genera of uncertain familial affiliation" and "Excluded genera"). All may be, and some definitely are, of relevance for the classification of the family. In the following, the genera are listed (in alphabetical sequence) along with brief comments. The molecular aspects have been addressed in more detail by Möller and Clark (2013).

***Brookea* Benth.** This is a genus of four species of shrubs or small trees from Borneo. It was placed in Scrophulariaceae by Bentham (1876), but referred to Gesneriaceae by Hallier (1903). The flower has some similarity with a gesneriad flower, having a tubular-infundibuliform bilabiate corolla with two raised yellow ridges on the lower lip, but this type is found in several families of the Lamiales. The inflorescences are said to be racemose, and thus are abnormal in the Old World Gesneriaceae. Burtt (1963: 217) wrote that the genus "is at present best regarded as a slightly anomalous member of Scrophulariaceae, ... whose limits need a thorough overhaul." In the meantime, Scrophulariaceae have been split into many families of their own (e.g., Olmstead 2001, Albach et al. 2005, Oxelman et al. 2005, Tank et al. 2006, APG III 2009, Schäferhoff et al. 2010). Fischer (2004) referred *Brookea* to the Scrophulariaceae-"Stilbaceae." To the best of our knowledge there is no molecular data available for the genus (see also Wolfe et al. 2006). *Brookea* is clearly in need of a detailed morphological and molecular study. At present, there is no specific evidence that it does belong to Gesneriaceae.

***Charadrophila* Marloth.** The systematic position of this South African monotypic genus has been disputed since its establishment by Marloth (1899), having been moved between Scrophulariaceae and Gesneriaceae. Based on a detailed morphological and ontogenetical study, Weber (1989) reached the conclusion that *Charadrophila* should be removed from Gesneriaceae and placed in the Scrophulariaceae (s.l.). Fischer (2004) placed the genus in Scrophulariaceae (s.str.) tribe Alonsoeae. More recently, and based on molecular data, *Charadrophila* was placed in Stilbaceae, a segregate family of traditional Scrophulariaceae comprising mainly "scrophulariaceous" genera from the Western Cape (Oxelman et al. 2005, APG III 2009).

***Cubitanthus* Barringer.** From collections examined by the authors and photographs taken by A. Chautems (Genève), *Cubitanthus* [monotypic with *C. alatus* (Cham. & Schltdl.) Barringer, originally described as *Russelia alata* by Chamisso and Schlechtendal (1828: 3), and referred to Scrophulariaceae] is clearly a member of Scrophulariaceae (s.l.) and must be excluded from Gesneriaceae where the species was placed by Bentham (1876, as *Russelia alata*) and Barringer (1984, as *Cubitanthus alatus*). Recent molecular data (Perret et al. 2013) support the placement of *Cubitanthus* in or close to Linderniaceae and not in Gesneriaceae.

***Cyrtandromoea* Zoll.** The genus was established by Zollinger (1854–1855), with the name reminiscent of *Cyrtandra* J.R.Forst. & G.Forst., the largest genus of the Didymocarpoid Gesneriaceae. In early classifications (Bentham 1876, Clarke 1883, Fritsch 1893–1894, Ridley 1923), *Cyrtandromoea* was always retained in the Gesneriaceae. Likewise, Burtt (1963) attributed it to that family (placing it in tribe Loxonieae), but only "for want of a better place." Burtt later

(1965) transferred *Cyrtandromea* to Scrophulariaceae (tribe Mimuleae) based on a thorough morphological study and taxonomic revision of the genus. Analysis of the floral vasculature (Singh & Jain 1978) supported a placement in the Scrophulariaceae (s.l.).

The only published molecular-based phylogenetic study (Smith et al. 1997) placed *Cyrtandromoea* in the Gesneriaceae as the sister taxon to *Monophyllaea* R.Br. and *Rhynchoglossum* Blume (Klugieae, now Epithemateae). There is no morphological support for such a placement. According to Burtt (1965), the seedlings are isocotylous and thus lack the defining characteristic feature of Old World Gesneriaceae of anisocotylous seedlings. Studies of *Cyrtandromoea grandis* Ridl. (by AW, based on plants collected in Malaysia) showed that the plants have a ''scrophulariaceous'' bilocular ovary with axile placentation [see also Burtt 1965 for *C. subsessilis* (Miq.) B.L.Burtt] and that they possess cymes of the ordinary type rather than pairflowered cymes that characterize the Gesneriaceae (Weber 1973, 1982a, 1982b, 1995, 2004a, 2013). There are no morphological characteristics that suggest a placement in or near the Epithemateae (e.g., anisophylly, alterniphlly or alterniclady; Burtt 1977; Weber 1975–1982a). Preliminary, unpublished molecular data show that *Cyrtandromoea* is not related to Gesneriaceae (see Möller & Clark 2013). In view of these findings, *Cyrtandromoea* is refrained from being recognized as a member of Gesneriaceae.

***Jerdonia* Wight.** This is a monotypic genus of rosette plants that are locally endemic in southwestern India. Wight (1848, 1850), Bentham (1876), Clarke (1883) and Fritsch (1893–1894) treated the genus as a member of the Gesneriaceae. In contrast, Burtt (1977) treated the genus as a member of the Scrophulariaceae (s.l.) because of the presence of isocotylous seedlings. Some features such as broadly flattened filaments and four parietal placentae (reminiscent of *Orobanche* L.) are anomalous in the Gesneriaceae. Nevertheless, the inflorescences are comprised of pair-flowered cymes and thus match an important gesneriaceous criterion (Weber 1989) [outside Gesneriaceae and Calceolariaceae, pair-flowered cymes are only known from a single Asiatic species: *Pennelliantus frutescens* (Lamb.) Crosswh. (=*Penstemon frutescens* Lamb.), Plantaginaceae-Cheloneae, occurring in NE Asia and Japan (Weber 2013)]. Molecular data of Möller et al. (2009) placed the genus in the Gesneriaceae, falling in the ''Basal Asiatic genera'' as sister to all of the remaining Didymocarpoid Gesneriaceae. The present classification recognizes *Jerdonia* in the monospecific subtribe Jerdoniinae.

***Peltanthera* Benth.** This genus of small trees occurring in northern South and Central America is monotypic with *P. floribunda* Benth. Previous classifications placed it in Loganiaceae and Buddlejaceae (Leeuwenberg & Leenhouts 1980, Norman 2000). Molecular-based phylogenetic studies placed *Peltanthera* in different positions closely related with Calceolariaceae and *Sanango* G.S.Bunting & Duke, but always outside or as the sister taxon to Gesneriaceae (see Möller & Clark submitted, 2013). Recent collections in Costa Rica and a detailed morphological study of *P. floribunda* have revealed that the flowers and the inflorescences are not typically gesneriaceous. The flowers are small, urceolate, actinomorphic with 5 stamens, and the inflorescences are not pair-flowered cymes, but many-flowered panicles emerging from the axils of the foliage leaves (Weber 2013 and unpubl. obs.). The inclusion of *Peltanthera* in the Gesneriaceae is therefore not advocated.

***Rehmannia* Libosch. ex Fisch. & C.Mey.** This small genus from East Asia has been repeatedly shuttled between Scrophulariaceae and Gesneriaceae. Solereder (1909) placed it in Gesneriaceae, admitting that its features necessitated an extension of the family circumscription. Burtt (1963) excluded it from Gesneriaceae because of the inflorescence architecture (a strict raceme as in *Titanotrichum* Soler.) and the isocotylous seedlings. In contrast, the unilocular ovary is more similar to Gesneriaceae than Scrophulariaceae. The classification and phylogenetic placement of *Rehmannia* was recently settled by the molecular study of Xia et al. (2009) in which *Rehmannia* was strongly supported as closely related to *Triaenophora* Soler. (Solereder 1909) as the sister clade to the Orobanchaceae, and therefore not closely related to the Gesneriaceae.

***Sanango* G.S.Bunting & Duke.** This genus with a single species [*Sanango racemosum* (Ruiz & Pav.) Barringer] has a disjunct distribution on the lower Amazonian slopes of the Andes (Peru and SE Ecuador), where it grows as a small tree or shrub. It was first described more than 200 years ago by Ruiz and Pavon (1794, 1798), under the name *Gomara racemosa* Ruiz & Pav. It was considered a member of the broadly defined Scrophulariaceae by Ruiz and Pavon (1794, 1798) and Rauschert [1982, as *Gomaranthus racemosus* (Ruiz & Pav.) Rauschert]. In contrast, Bunting and Duke (1961), who were not aware of Ruiz and Pavon's description, described the plant anew as *Sanango durum* G.S.Bunting & Duke and assigned it to Loganiaceae-Buddlejoideae. Barringer (1986) and Norman (2000) placed it in the Buddlejaceae, a family then separated from Loganiaceae. Cronquist (1968, 1988) recognized

Sanango as an intermediate taxon between Buddlejaceae and Scrophulariaceae. At present, the Buddlejaceae are included as a tribe in Scrophulariaceae s.str. (APG III 2009).

It was unexpected when studies by Wiehler and collaborators (Wiehler 1994, and papers cited therein) suggested that *Sanango* belonged to Gesneriaceae, particularly to tribe Gesnerieae of subfam. Gesnerioideae (geographically centered in the Carribean). The molecular data of Smith et al. (1997) seemed in accordance with that position, but proved erroneous (J. Smith, pers. comm.). The embryological studies of Maldonado et al. (1998) confirmed that *Sanango* is not closely related to Loganiaceae s.l., but the authors could not decide ''what the most satisfactory assignment of the genus [Gesneriaceae/Scrophulariaceae s.l.] should be.''

In the meantime, there is unambiguous molecular data that supports a position of *Sanango* as sister to Gesneriaceae (see review of Möller & Clark 2013). Taxonomically, this leaves two options: (1) classify *Sanango* as separate from Gesneriaceae and place it in a family of its own, or (2) include *Sanango* in Gesneriaceae by broadening the circumscription of the family. After thorough consideration we decided to include *Sanango* in the Gesneriaceae as a monotypic subfamily, based on characters outlined under ''Notes on the proposed classification and on the particular groups.''

***Titanotrichum* Soler.** This monotypic genus (*T. oldhamii* Soler.) from SE China, Taiwan and S Japan has been systematically problematic until recently. After flowering, the inflorescence apex tails off into a long weak axis bearing numerous clusters of small propagules (often referred to as ''bulbils'' in the literature, e.g., Wang et al. 2004b, 2004c). These are capable of sprouting and serve (in most populations even exclusively) for vegetative reproduction (Wang et al. 2004d). Burtt (1963, 1977) referred to *Titanotrichum* as a ''genus anomalum'' of Gesneriaceae and Wang et al. (1990) accommodated it in the monogeneric tribe Titanotricheae in subfam. Cyrtandroideae. Various molecular studies included *Titanotrichum*, but with inconsistent levels of sampling and changing phylogenetic position (see Möller & Clark 2013). The most comprehensive molecular phylogenetic study devoted to *Titanotrichum* was carried out by Wang et al. (2004a) that included four gene regions and broad taxon sampling with a good representation of New and Old World Gesneriaceae. The Wang et al. (2004a) study strongly supported that the genus was nested within the New World Gesneriaceae (Gesnerioideae). This result was unexpected because it is the only example in the Gesneriaceae where a group that is geographically limited to the Old World is more closely related to members in the New World. More recently, the results of Wang et al. (2004a) were corroborated by Perret et al. (2013). In the present classification *Titanotrichum* is therefore treated as a monospecific tribe of Gesnerioideae.

Section conclusions. Of the nine genera discussed here, some (e.g., *Charadrophila, Cubitanthus, Cyrtandromoea, Rehmannia,* and probably *Brookea*) do not belong to the Gesneriaceae and are excluded from further consideration. The available molecular data place *Sanango* between Calceolariaceae and Gesneriaceae and sister to the latter family. Morphological features are discussed here that justify including *Sanango* in the Gesneriaceae. *Peltanthera* is not as close to Gesneriaceae as suggested by earlier molecular studies: according to the 17 gene analysis of Soltis et al. (2011) and a 10 gene analysis of Refulio and Olmstead (in prep.) it is sister to Calceolariaceae + Gesneriaceae, a position that is in accordance with morphology (Weber 2013 & unpubl. obs.). In contrast, *Jerdonia* and *Titanotrichum* are strongly supported as ingroup taxa of the family that occupy isolated positions in the Old and New World gesneriads, respectively.

HISTORY OF GESNERIACEAE CLASSIFICATION

The recent classification of the Gesneriaceae has resulted in major shifts relative to other angiosperm lineages. The family was recognized in 1804 by the French botanists L.C.M. Richard and A.-L. de Jussieu. They considered *Gesneria* L., *Besleria* L., *Columnea* L., *Achimenes* Pers., *Gloxinia* L'Hér. and *Eriphia* P.Browne [=*Besleria*] to be a distinct new family (de Jussieu 1804: 192: ''une famille particulière distincte des campanulacées''). De Jussieu (*l.c.*) discussed the characters of the group, mentioning for instance the unilocular fruit, the fleshy disc at the base of the ovary, and the insertion of the stamens on the corolla. However, neither de Jussieu nor Richard proposed a name for the new family. This was done by A.P. de Candolle 12 years later (1816, as ''*Gessnerieae*''). De Candolle did not give a description, but the name was validated by his reference to de Jussieu's paper. De Jussieu also discussed the possible inclusion of further genera such as *Paliavana* Vell. ex Vand., *Orobanchia* Vand. [=*Nematanthus* Schrad.], *Sanchesia* [=*Sanchezia* Ruiz & Pav., Acanthaceae] and, most remarkably, also *Cyrtandra* from the Old World (de Jussieu 1804: 428: ''Cette famille, ..., pourroit encore être enrichie par l'addition du *paliavana* et l'*orobanchia* de Vandelli, du *cyrtandra* de Forster, du *Sanchesia* de Ruiz et Pavon; mais cette réunion n'auroit lieu qu'après un nouvel examen de tout ces genres''). Thus, de Jussieu was the first to recognize the Gesneriaceae as a pantropical family, which has been overlooked by subsequent authors.

For the Old World genera, two families were established roughly at the same time: Didymocarpaceae (D. Don 1822) and Cyrtandraceae (Jack 1823). Didymocarpaceae has priority over Cyrtandraceae, but it was the latter name that was adopted by those who kept the Old World plants distinct from the American Gesneriaceae, most notably by de Candolle (1845). While it became immediately clear that Didymocarpaceae and Cyrtandraceae were identical, the relationship of Gesneriaceae and Didymocarpaceae/Cyrtandraceae was not (re-)discovered until Martius (1829) compared the two families. He concluded that they were closely allied, but decided to keep them distinct. Again, more or less at the same time (around 1830), David Don and Robert Brown reached the conclusion that the differences between these two groups did not warrant familial separation. Both authors announced their union (in obscure places, see Weber 2004b) and, again in close succession and independently, George Don (1838), the brother of David Don, and Brown (1839) formally united the two families into a single one, under the name Gesneriaceae. Both authors proposed a subdivision. G. Don divided his ''order Gesneriaceae'' into ''tribes'' and ''subtribes'' (tribe I. Gesnerieae, with subtribes Gloxinieae, Conradieae [=Gesnerieae] and Beslerieae, with all genera included therein occurring in the New World; and tribe II. Cyrtandreae, with subtribes Trichosporeae, Didymocarpeae, Cyrtandreae, and Loxotieae, with all genera from the Old World). R. Brown (1839) subdivided the family into three ''tribes'': (1) Beslerieae, (2) Gesnerieae, and (3) Cyrtandreae. He referred only to the latter group in some detail, in which he placed exclusively genera of the Old World, including *Fieldia* A.Cunn. and *Rhabdothamnus* A.Cunn. from Australia and New Zealand, respectively.

Though not referring to G. Don (1938), Endlicher (1839) proposed a similar, but less detailed classification. He divided the ''ordo Gesneraceae'' into ''subordo I. Cyrtandreae,'' with tribes Didymocarpeae and Eucyrtandreae, and ''subordo II. Gesnereae'' with tribes Beslerieae, Episcieae, and Eugesnereae.'' In contrast, in de Candolle's ''Prodromus,'' the first volume appearing in the same year as Endlicher's treatment, the families Gesneriaceae (in vol. I, 1839) and Cyrtandraceae (in vol. 2, published in 1845, four years after A.P. de Candolle's death) were still kept separate.

A more comprehensive treatment of the family was presented by Bentham (1876). He was the first taxonomist to give priority to morphological characters (e.g., ovary position) over phytogeographical relations as a basis for his classfication. Bentham divided the family into two ''tribes,'' the ''Gesnereae'' (ovary partly or fully inferior) and the ''Cyrtandreae'' (ovary superior). The Gesnereae comprised four ''subtribes'' (Bellonieae, Gloxinieae, Eugesnereae, Pentaraphieae), while the ''Cyrtandreae'' comprised five ''subtribes'' (Columneae, Eucyrtandreae, Aeschynantheae, Beslerieae, and Didymocarpeae). In the ''Cyrtandreae'' Bentham mixed New and Old World groups, and in the ''subtribes'' Eucyrtandreae, Beslerieae and Didymocarpeae he also included genera both from the New and the Old World.

Following Bentham (1876), the next comprehensive treatment was that of C.B. Clarke (1883), which was limited to the ''Cyrtandreae.'' He divided this group into the ''Trichosporeae,'' ''Didymocarpeae'' and ''Eucyrtandreae.'' In the latter group he included the New World genera *Besleria*, *Mitraria* Cav., *Sarmienta* Ruiz & Pav. and *Asteranthera* Hansl.

Fritsch (1893–1894) revised the family for Engler and Prantl's ''Die Natürlichen Pflanzenfamilien'' for his doctoral thesis. He followed Bentham (1876) and Clarke (1883) in essential respects, but worked out a much more detailed classification that recognized 18 tribes in two groups (newly treated as subfamilies), and subdivided the tribes into subtribes. Burtt (1954: 185) described Fritsch's treatment as a ''retrogression'' with ''little original work in it'' and ''negative in quality.'' In the authors' opinion here, Burtt's judgment is too harsh. It is true that Fritsch repeated errors of his predecessors, particularly in mixing Old and New World genera in some groups, but in many details Fritsch was correct and some of his work has been corroborated by recent molecular phylogenetic studies. For instance, Fritsch was the first to recognize and delineate correctly the Coronanthereae, and he placed the berry-fruited genus *Rhynchotechum* Blume correctly in the capsular-fruited alliance of *Leptoboea* Benth. and *Boeica* C.B.Clarke, while Burtt (1963) misplaced it in tribe Cyrtandreae.

After Fritsch's work (1893–1894), only regional treatments of Gesneriaceae were published for a long period of time. Burtt (1963) provided a classification that essentailly reverted to earlier systems (e.g., Don 1838, Brown 1839) that were based on geographical separation, clearly recognizing that the Old World Gesneriaceae share the uncommon feature of an anisocotylous seedling. It should be noted that the presence of anisocotyly in the Old World Gesneriaceae had been known for a long time (e.g., Crocker 1860), but its taxonomic significance had not been fully realized. Fritsch (1904) published a book that focused on seedling morphology in the Gesneriaceae. The major exception to the presence of anisocotylous seedlings in the Old World Gesnerieaceae were the genera occurring in the South Pacific. Therefore, Burtt (1963) recognized the South Pacific genera in the tribe Coronanthereae (tribal name first published by Fritsch) and subfamily Gesnerioideae. The Coronanthereae also included the newly described tribe Mitrarieae to accommodate three monotypic genera from temperate South America (i.e., *Asteranthera, Mitraria* and *Sarmienta*). Burtt (1963) reduced the 18 Old World tribes of Fritsch (1893–1894) to the following five tribes: Cyrtandreae, Trichosporeae, Klugieae, Loxonieae, and Didymocarpeae.

Ivanina (1967) was the next taxonomist to publish a classification of the entire family. Her work received little attention because it was published as a book in Leningrad and written in Russian (with the English subtitle ''The family Gesneriaceae – a carpological review''). The classification was almost exclusively based on fruit and seed characters which were previously described in Ivanina (1965a, in Russian). For this publication an English version is also available (Ivanina 1965b). Ivanina's classification (1967) contains the establishment of a new subfamily (Episcioideae) and several new tribes and subtribes. One of them, subtribe Streptocarpinae, is adopted here for the inclusion of the African and Madagascan genera of Didymocarpoideae.

The most recent classification of Gesneriaceae was published by Burtt and Wiehler (1995). Their classification is mostly based on morphology and for the neotropical members additional data were included from chromosome numbers and breeding experiments. In contrast to the preceding classifications the following three subfamilies were recognized: (1) Gesnerioideae, (2) Coronantheroideae, and (3) Cyrtandroideae. The Coronantheroideae was established by Wiehler (1983) on account of the subtropical distribution in the southern hemisphere and the nectary ''adnate'' to the ovary. In the Gesnerioideae, the following five tribes were recognized: (1) Gloxinieae, (2) Episcieae, (3) Beslerieae, (4) Napeantheae, and (5) Gesnerieae. In the Cyrtandroideae, Burtt and Wiehler (1995) combined the Klugieae and Loxonieae into a single tribe (Klugieae, mainly based on the investigations of Weber 1975 to 1982) and added the monospecific tribe Titanotricheae that had been described in the meantime by Wang et al. (1990). The list of tribes in the Cyrtandroideae thus reads: (1) Klugieae (now known as Epithemateae, see Burtt 1997), (2) Didymocarpeae, (3) Trichosporeae, (4) Cyrtandreae, and (5) Titanotricheae. The tribes Cyrtandreae and Trichosporeae contained fewer genera (e.g., Titanotricheae only one). In contrast, the Didymocarpeae contained 64 genera. Burtt and Wiehler (1995) listed the genera in alphabetical order and avoided arranging them according to conjectural relationships.

A preliminary classification by Weber (2004a) included results from recent molecular systematic studies. At the time of writing the account a good deal of molecular data was available for the New World Gesneriaceae, but only one paper (Mayer et al. 2003) was available for the Old World Gesneriaceae (Epithemateae). Molecular data for the Didymocarpoid Gesneriaceae were scanty and unpublished. Weber's treatment (2004a) was therefore presented as a mixture of formal and informal groups. The following four informal groups were recognized: (1) Coronantheroid Gesneriaceae, (2) Gesnerioid Gesneriaceae, (3) Epithematoid Gesneriaceae, (4) Didymocarpoid Gesneriaceae. No subdivisions were suggested for Coronantheroid and Epithematoid (groups 1 and 3, respectively). The Gesnerioid Gesneriaceae were subdivided into the following established traditional tribes: Beslerieae, Napeantheae, Gloxinieae, Gesnerieae, and Episcieae. The Didymocarpoid Gesneriaceae were subdivided into the following informal groups: (1) ''The Basal Asiatic genera,'' (2) ''The European genera,'' (3) ''The African and Madagascan genera,'' (4) ''The Advanced Asiatic and Malesian genera.'' In the last group, two lineages were outlined based on genera with predominantly twisted fruits, and genera with exclusively straight fruits. Both in the Gesnerioid and the Didymocarpoid Gesneriaceae some genera remained unplaced or were excluded from the family.

The last publication to be mentioned in the historical context is Reveals's ''Outline of a classification scheme for extant flowering plants'' (Reveal 2012). Regarding Gesneriaceae, it is an (incomplete) compilation of tribes recognized in recent molecular phylogenetic studies. Reveal's classification reads: a. Didymocarpoideae: a1. Didymocarpeae Endl., a2. Epithemateae Reveal. b. Gesnerioideae. b1. Napeantheae Wiehler. b2, Coronanthereae Fritsch, b3. Beslerieae Bartl., b4. Gloxinieae Sweet, b5. Gesnerieae Dumort., b6. Sinningieae Fritsch, b7. Episcieae Endl. Reveal's treatment has a number of shortcomings which are in need of rectification. Moreover, the available data allow a more detailed picture of the relationships between and within the particular groups. Last, but not least, *Sanango* was not included in the Gesneriaceae. In the light of the above, a new formal classification, as presented below, is justified.

TABLE 1. Synopsis of the proposed classification of Gesneriaceae. Species numbers based on Möller and Clark (2013).

Rank	Genera/Species	Notes
Gesneriaceae Rich. & Juss. in DC.		emended to include Sanangoideae / *Sanango* G.S.Bunting & Duke
1. Subfam. **Sanangoideae** A.Weber J.L.Clark & Mich.Möller	1/1	new (only *Sanango* G.S.Bunting & Duke)
2. Subfam. **Gesnerioideae** Burnett (1835)		remaining in traditional use, but including the tribes Titanotricheae and Coronanthereae
2.1. Tribe **Titanotricheae** Yamaz. ex W.T.Wang (1990)	1/1	remaining in current use, note placement in Gesnerioideae (only *Titanotrichum* Soler.)
2.2. Tribe **Napeantheae** Wiehler (1983)	1/20+	remaining in current use (only *Napeanthus* Gardner)
2.3. Tribe **Beslerieae** Bartl. (1830)		remaining in current use
2.3.1. Subtribe **Besleriinae** G.Don (1837/38)	4/239+	re-established
2.3.2. Subtribe **Anetanthinae** A.Weber & J.L.Clark	5/12+	trad. tribe Anetantheae Fritsch
2.4. Tribe **Coronanthereae** Fritsch (1893)		remaining in current use
2.4.1. Subtribe **Coronantherinae** Fritsch (1893)	2/14–21	remaining in current use
2.4.2. Subtribe **Mitrariinae** Hanst. (1854)	4/4	remaining in current use
2.4.3. Subtribe **Negriinae** V.L.Woo, J.F.Smith & Garn.-Jones (2011)	3/3	remaining in current use
2.5. Tribe **Gesnerieae** Dumort. (1829)		emended to comprise the following groups
2.5.1. Subtribe **Gesneriinae** Oerst. (1858)	4/100	trad. tribe Gesnerieae Dumort.
2.5.2. Subtribe **Gloxiniinae** G.Don (1837/38)	21/200+	trad. tribe Gloxinieae Sweet
2.5.3. Subtribe **Columneinae** Hanst. (1854)	26/525+	trad. tribe Episcieae Endl.
2.5.4. Subtribe **Sphaerorrhizinae** A.Weber & J.L.Clark	1/2	trad. tribe Sphaerorrhizeae Roalson & Boggan
2.5.5. Subtribe **Ligeriinae** Hanst. (1854)	3/91	trad. tribe Sinningieae Fritsch
3. Subfam. **Didymocarpoideae** Arn. (1832)		trad. subfam. Cyrtandroideae Burnett
3.1.Tribe **Epithemateae** C.B.Clarke (1874)		trad. tribe Klugieae Fritsch (incl. Loxonieae B.L.Burtt)
3.1.1. Subtribe **Loxotidinae** G.Don (1837/38)	1/10	re-established (only *Rhynchoglossum* Blume)
3.1.2. Subtribe **Monophyllaeinae** A.Weber & Mich.Möller	2/38+	new
3.1.3. Subtribe **Loxoniinae** A.DC. (1845)	2(3)/8+(9+)	re-established
3.1.4. Subtribe **Epithematinae** DC. ex Meisn. (1840)	1/20+	re-established (only *Epithema* Blume)
3.2. Tribe **Trichosporeae** Nees (1825)		emended to include all trad. Old World tribes excl. Epithemateae
3.2.01. Subtribe **Jerdoniinae** A.Weber & Mich.Möller	1/1	new (only *Jerdonia* Wight)
3.2.02. Subtribe **Corallodiscinae** A.Weber & Mich.Möller	1/3–5	new (only *Corallodiscus* Batalin)
3.2.03. Subtribe **Tetraphyllinae** A.Weber & Mich.Möller	1/3	new (only *Tetraphyllum* Griff. ex C.B.Clarke)
3.2.04. Subtribe **Leptoboeinae** C.B.Clarke (1884)	5(6)/42(43)	re-established
3.2.05. Subtribe **Ramondinae** DC. ex Meisn. (1840)	3(2)/5	re-established
3.2.06. Subtribe **Litostigminae** A.Weber & Mich.Möller	1/2	new (only *Litostigma* Y.G.Wei, F.Wen & Mich.Möller)
3.2.07. Subtribe **Streptocarpinae** Ivanina (1965)	9/157+	re-established
3.2.08. Subtribe **Didissandrinae** A.Weber & Mich.Möller	2/10	new
3.2.09. Subtribe **Loxocarpinae** A.DC. (1845)	12/171+	re-established
3.2.10. Subtribe **Didymocarpinae** G.Don (1837/38)	30(31)/1578–1744+	re-established
	Total: 147–148/3260–3435+	

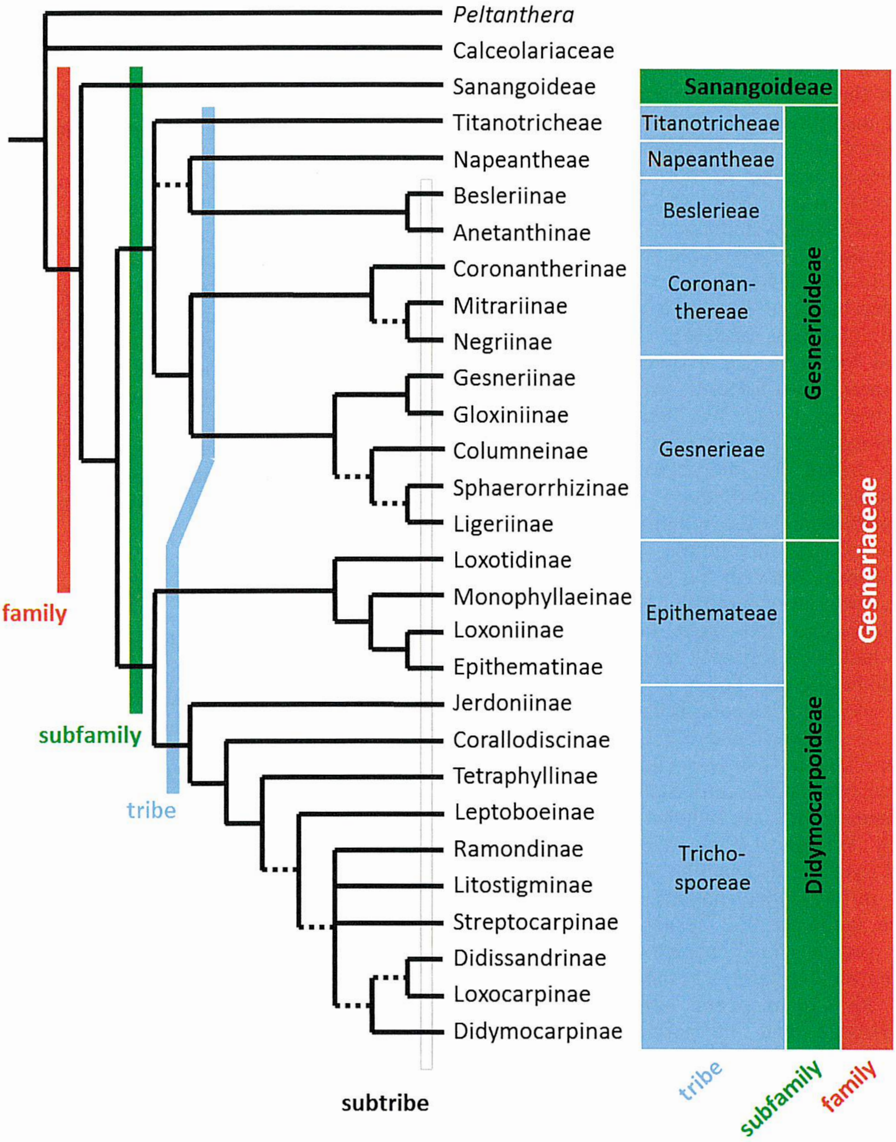

FIGURE 1. Diagrammatic representation of the formal classification proposed in the present paper. (see Möller & Clark 2013).

NOTES ON THE PROPOSED CLASSIFICATION AND ON THE PARTICULAR GROUPS

The classification advocated here is given in brief form in a synopsis (TABLE 1) and a diagrammatic representation of the phylogenetic tree (FIGURE 1). Comments are given in the following. By the inclusion of *Sanango* in the Gesneriaceae, and its accomodation in a distinct subfamily, three subfamilies are recognized: (1) Sanangoideae, (2) Gesnerioideae, and (3) Didymocarpoideae. The subfamilies established by Ivanina (1967: Episcioideae) and Wiehler (1983: Coronantheroideae) are kept in synonymy with Gesnerioideae.

SUBFAMILY SANANGOIDEAE

The first to include *Sanango* into Gesneriaceae was Wiehler (1994), with support from targeted morphological and phytochemical studies carried out by Norman (1994), Dickison (1994) and Jensen (1994). Wiehler (1994) placed *Sanango* in tribe Gesnerieae, though he was aware that the morphological characters and the geographical distribution did not fit well. Weber (2004a) was sceptical about this placement and treated *Sanango* as a genus of ''uncertain familial affiliation.'' In the meantime, molecular studies have provided unambiguous evidence that *Sanango* is closely associated with the Gesneriaceae. However, it is not an ingroup of that family, but holds a sister position (see Möller & Clark, 2013). This could be reflected systematically by the establishment of a distinct, monotypic family. *Sanango* is included in the Gesneriaceae to reflect the close relationship between the two taxa. *Sanango* shares a recent common ancestor from which all traditional Gesneriaceae evolved. It has clearly some gesneriaceous features, but, not surprisingly, is distinctive in others. We, therefore, establish a new, monotypic subfamily for its accommodation and thus widen the morphological concept of Gesneriaceae to some degree.

A morphological re-evaluation is needed, the more so as the taxonomic peripherals have changed considerably in the recent past. Wiehler and his collaborators compared *Sanango* only with the Gesneriaceae and those families to which *Sanango* had been formerly referred to (Loganiaceae, Buddlejaceae). Today we know that *Peltanthera* and the Calceolariaceae are the closest relatives of *Sanango* and the Gesneriaceae (see Möller & Clark, 2013). One character which was considered particularly important and ranked as a ''key character for the whole family Gesneriaceae'' by Wiehler (1994: 628) was the pair-flowered cyme. ''If *Sanango* did not show this peculiar inflorescence pattern, any attempt to place the taxon in the Gesneriaceae would be futile.'' Today, this character is no longer considered indicative of a gesneriaceous position, as it is known to occur ubiquitously in the Calceolariaceae and in parts of the family Plantaginaceae (Weber 2013). Features of *Sanango* that are distinctive from traditional Gesneriaceae include the large, cupular disc surrounding the ovary, the globose and slightly four-partite shape of the ovary, the style arising from a depression on the ovary top, the internal structure of the ovary, the shape of the placentae, and the hard (bony) capsular fruit exhibiting an apical depression (Bunting & Duke 1961, Wiehler 1994 and references quoted herein; Weber, pers. obs.). In this context, one must not forget that there is also considerable variation of floral and gynoecial characters within traditional Gesneriaceae. For instance, one of the classical characters defining the Gesneriaceae is the ''unilocular'' ovary (with parietal placentae). However, in a number of genera (e.g., *Sarmienta*, *Whytockia* W.W.Sm., *Monophyllaea*, *Allostigma* W.T.Wang, *Hemiboea* C.B.Clarke) the ovary is completely bilocular and the septum bears axile placentae (Weber 1971, 2004a; Wilson 1974a, 1974b). Nonetheless, no one would doubt their correct position in the Gesneriaceae.

SUBFAMILY GESNERIOIDEAE

Until Burtt (1963), this group was considered to be purely neotropical (e.g., Bentham 1976, Fritsch 1893–1894; however, *vice versa*, the ''Cyrtandroideae'' comprised both neo- and paleotropical taxa). Burtt (1963) was the first to transfer an Old World group (the Coronanthereae) to the Gesnerioideae. This has been confirmed by molecular data. Moreover, also *Titanotrichum* (Titanotricheae), from East Asia, must be referred to this subfamily (see review Möller and Clark 2013). In terms of geographical distribution and morphology, subfam. Gesnerioideae thus appears as a mixed and heterogeneous group. Therefore, the terms Gesnerioideae and ''New World Gesneriaceae'' are no longer equivalent.

Tribes and Subtribes in Subfamily Gesnerioideae

Tribal names that have been used during the last 30 years (from Wiehler 1983 onwards) are the following (in alphabetical order): (1) Beslerieae Bartl., (2) Coronanthereae Fritsch, (3) Episcieae Endl., (4) Gesnerieae Dumort., (5) Gloxinieae Sweet, (6) Napeantheae Wiehler, (7) Sinningieae Fritsch, (8) Sphaerorrhizeae Roalson and Boggan, and (9) Titanotricheae Yamaz. ex Wang. Monophyly has been confirmed for these distinct and well-supported groups.

It should be noted that the number of currently recognized tribes for the subfamily Gesnerioideae is relatively high compared to the Didymocarpoideae. The latter includes a strongly supported basal dichotomy that divides that subfamily into the tribes Epithemateae and Trichosporeae. The classification presented here reduces the number of tribes in the Gesnerioideae from nine to the following five: Beslerieae, Napeantheae, Gesnerieae, Coronanthereae, Titanotricheae. The tribe Gesnerieae is expanded to include five traditional tribes, here treated as subtribes. In size and content of subtribes it thus becomes comparable with the tribe Trichosporeae of subfamily Didymocarpoideae which includes ten subtribes. A description of the tribes and subtribes is outlined below.

Titanotricheae. This tribe and its monospecific genus *Titanotrichum* is distributed in S Japan, SE China and Taiwan. The placement of the Old World Titanotrichaeae in the New World Gesnerioideae is strongly supported by molecular data (Wang et al. 2004a, Perret et al. 2013). In the analysis of Perret et al. (2013), *Titanotrichum* is sister to and forming a clade with *Napeanthus*.

However, taxaon sampling in this work included relatively few samples from the Old World and from tribes of basal New World lineages and the support for the sister group relationship with *Napeanthus* Gardner is low (Bayesian posterior probability of 0.8). Morphologically, there are no known synapomorphies for *Napeanthus* and *Titanotrichum*. In conclusion, *Titanotrichum* is recognized as a distinct tribe.

Napeantheae. This tribe was established by Wiehler (1983) for the accommodation of a single genus, *Napeanthus* (>20 spp.) that is distributed throughout the Neotropics. These rosette plants lack nectaries and have nearly actinomorphic, truncate, white or pale pink or pale blue flowers. *Napeanthus* is strongly supported as a basal lineage within the Gesnerioideae and occupies a somewhat isolated position. Recent molecular data suggest that the Beslerieae and Napeantheae are not as closely related as previously thought (see Möller & Clark 2013). Therefore, the status of Napeantheae is left untouched (''in dubio pro reo'') and treated here as a distinct tribe. For the possible relationship with *Titanotrichum* see the preceding paragraph.

Beslerieae. This tribe is strongly supported by molecular data, but the relationship to tribe Napeantheae is tenuous (see Möller & Clark, 2013). Morphologically, Beslerieae is a heterogeneous alliance, both in vegetative habit, floral characters (with enormous floral variation and representation of pollination syndromes found even within particular genera, e.g., *Gasteranthus* Benth.) and fruit structure (dry capsules opening septicidally, loculicidally or both, fleshy capsules, or berries).

Taxonomic attention has been paid to the seeds of Beslerieae. *Besleria*, *Cremosperma* Benth., *Gasteranthus* and *Reldia* Wiehler exhibit a seed coat structure of the type found throughout the Gesnerioideae (see Beaufort-Murphy 1983) and in *Sanango* (Norman 1994): here the seed surface is reticulate (testa cells polygonal or quadrangular, with strongly thickened and raised adjacent cell walls) or, more frequently, ''striate'' (=basically reticulate, but with the testa cells strongly narrowed and elongated, and forming (rarely) straight or (frequently) spirally wound cell rows around the seed. In contrast, in *Anetanthus* Hiern ex Benth. & Hook.f., *Resia* H.E.Moore, and *Shuaria* D.A.Neill & J.L.Clark the adjacent walls of the testa cells are not thickened and straight, but strongly sinuate. The cells thus form a kind of jigsaw puzzle (*Anetanthus*: Beaufort-Murphy 1983: pl. 1b E, pl. 48: A–F, pl. 51 A; *Resia*: Beaufort-Murphy 1983: pl. 48 G–I; *Shuaria*: Weber, pers. obs.). The upper cell walls bulge faintly, the cells thus becoming slightly dome-shaped. In *Cremospermopsis* L.E.Skog & L.P.Kvist and *Tylopsacas* Leeuwenb. the contour of the cells cannot be made out in the available illustrations, but the seeds are clearly not reticulate or striate. The upper cell walls bulge out more prominently to very strongly, giving the seed surface a ''papillate'' (*Cremospermospis*, Skog & Kvist 2002) or ''pustulate'' (*Tylopsacas*, Leeuwenberg 1958, 1960; Beaufort-Murphy 1983: pl. 52 A, B) appearance. *Anetanthus*, *Shuaria* and *Tylopsacas* have been included in molecular analyses and were found to form a strongly supported clade (Clark et al. 2010). Based on the seed morphology and the molecular data (incomplete, as *Cremospermopsis* has not been included in molecular analyses yet), it is suggested here the tribe Beslerieae should be subdivided into two subtribes: (1) Besleriinae (*Besleria*, *Cremosperma*, *Gasteranthus* and *Reldia*) and (2) Anetanthinae (*Anetanthus*, *Cremospermopsis*, *Resia*, *Shuaria* and *Tylopsacas*). The latter subtribe has its origins in tribe Anetantheae Fritsch (Fritsch 1893, then monogeneric with *Anetanthus*). The tribe was not acccepted by Wiehler (1976, 1983) or Burtt and Wiehler (1995), but adopted by Beaufort-Murphy (1983), who added *Resia* as a second genus.

Coronanthereae. This group of SW Pacific–Australian and temperate South American Gesneriaceae, comprises nine genera and is included in the Gesnerioideae. Previous classifications have included it as a separate subfamily (cf. discussion above). The Coronanthereae is a group of polyploid origin with haploid chromosome numbers ranging from ±37 to ±45 (Möller et al. 2002 onw.). The recent study by Woo et al. (2011) has shown that the relationships are not fully congruent with the geographical pattern, but are more complex than previously thought. In this paper the following three subtribes are recognized: (1) Coronantherinae (*Coronanthera* Vieill. ex C.B.Clarke, *Rhabdothamnus*), (2) Mitrariinae (including not only the three South American genera *Asteranthera*, *Mitraria* and *Sarmienta*, but also *Fieldia* from Australia), and (3) Negriinae (*Depanthus* S.Moore, *Lenbrassia* G.W.Gillett, *Negria* F.Muell.).

Gesnerieae. As circumscibed here, this is the largest tribe of the Gesnerioideae, corresponding to the ''Core Gesnerioideae'' *sensu* Perret et al. (2013). It is here defined as comprising the following traditional tribes: Gloxinieae, Gesnerieae, Episcieae, Sinningieae, and the recently established monogeneric Sphaerorrhizeae (Roalson et al. 2005a). Morphological and karyological characteristics were provided by Wiehler (1983). All available molecular data suggest that the five tribes (here treated as subtribes) together form a monophyletic clade. Among these tribes, Gesnerieae and the Gloxinieae are sister. The relationships to and within the three remaining tribes are less clear. The data of Perret et al. (2013; based on *mat*K, *rps*16, and *trn*LF) are not congruent with previous studies (based on ITS; *trn*LF and partly *atp*B-*rbc*L spacer) (see Möller & Clark, 2013). Therefore, all groups are equally ranked in the following subtribes: (1) Gesneriinae, (2) Gloxiniinae, (3) Columneinae (selected name when the tribe Episcieae is reduced to subtribe), (4) Ligeriinae (correct name when the tribe Sinningieae is reduced to subtribe), and (5) Sphaerorrhizinae.

(1) *Gesneriinae.* This is a small group of four genera (*Bellonia* L., *Gesneria*, *Pheidonocarpa* L.E.Skog, and *Rhytidophllum* Mart.) primarily distributed in the Carribean and a few species in northern South America. The generic boundaries of *Rhytidophyllum* are weak, so that Wiehler (1983) suggested it be included in the genus *Gesneria*, while molecular data of Martén-Rodríguez et al. (2010) supports maintaining them as separate genera with at least one species of traditionally recognized *Gesneria* (*G. rupincola* Urb.) as a member of *Rhytidophyllum. Pheidonocarpa* was described by L.E. Skog, when revising *Gesneria* (Skog 1976). The basic chromosome number is x = 13 (*Bellonia*) and x = 14 (*Gesneria*, *Pheidonocarpa*, *Rhytidophyllum*), and the ovary is inferior. An exception is *Bellonia*, which has a superior ovary and actinomorphic flowers with poricidal anther dehiscence.

(2) *Gloxiniinae.* This subtribe comprises 21 genera and corresponds to the traditional tribe Gloxinieae. It should be noted that the Gloxinieae *sensu* Wiehler (1983) excluded the tribe Sinningieae. This was later segregated based on molecular data. Wiehler (1983) circumscribed this tribe from several alliances that are predominantly defined as having a basic chromosome number of x = 13. The plants are usually terrestrial, perennial herbs, with scaly rhizomes or fibrous roots serving for survival during adverse (dry) seasons. Their distribution is mainly in Central America and adjacent areas.

(3) *Columneinae.* This subtribe comprises 26 genera and corresponds to the tribe Episcieae (*sensu* Wiehler 1983). Morphologically, this is a heterogeneous alliance, with a high proportion of epiphytes. Their basic chromosome number is x = 9 or rarely x = 8. The distribution is mainly in Central and northern South America.

(4) *Sphaerorrhizinae.* This corresponds to tribe Sphaerorrhizeae, which was established by Roalson and Boggan (Roalson et al. 2005b) for the accommodation of the small and genetically isolated genus *Sphaerorrhiza* Roalson & Boggan (2 species, previously referred to *Gloxinia*). This is characterized by "stringy" rhizomes with tuber-like swellings, often breaking apart with each propagule giving rise to a new plant.

(5) *Ligeriinae.* This tallies with the traditional tribe Sinningieae and includes three genera: *Sinningia* Nees, *Paliavana*, and *Vanhouttea* Lem. However, none of the genera are monophyletic (see Möller & Clark, 2013) and the monography is a current work in progress (cf. Perret et al. 2003). The tribe was strongly supported as separate from Wiehler's tribe Gloxinieae based on molecular sequence data. The basic chromosome number is x = 13 (as in Gloxinieae). The plants are terrestrial herbs, often with conspicuous tubers for surviving adverse (dry) seasons. Their distribution is mainly in SE tropical South America (Brazil).

SUBFAMILY DIDYMOCARPOIDEAE

Until recently, the subfamily Didymocarpoideae had been generally referred to as the Cyrtandroideae (established by Burnett in 1835 as "Cyrtandridae," a subfamily of Acanthaceae). However, Reveal (1995) discovered that Arnott had already established the subfamily Didymocarpoideae (as "Didymocarpeae") in 1832, in a preprint of his botany account for Encyclopedia Britannica. Didymocarpoideae, therefore, has priority over Cyrtandroideae and has to be adopted. With the exception of a single species, *Rhynchoglossum azureum* (Schltdl.) B.L.Burtt, the members of this subfamily occur in the Old World in the following regions: Asia and Malesia, Africa and Madagascar, and Europe (where there are only three or two genera with 5 species). The morphological character that defines this group is an anisocotylous seedling (vs. isocotylous in the Gesnerioideae). Anisocotyly is not simply a size difference of the cotyledons due to a different growth tempo of the two structures (as misinterpreted for *Titanotrichum* in Wang et al. 2002), but involves a characteristic set of features (see Burtt 1970, Jong 1970). Size differences, even culminating in the complete reduction of one of the two cotyledons, do occur in other angiosperm families as well (e.g., Ranunculaceae, *Cyclamen* L., see Hill 1938), but the situation in Gesneriaceae is quite different (see also Nishii et al. 2004, Mantegazza et al. 2007). This character can be qualified as the most important synapomorphy of the subfamily. This character can be qualified as a most important synapomorphy of the subfamily. Even its extreme form, where the larger cotyledon ("macrocotyledon'') grows to be virtually the sole photosynthetic organ of these unifoliate plants, is found in both tribes of the Didymocarpoideae (Epithemateae: *Monophyllaea*; Didymocarpeae: *Acanthonema* Hook.f., *Streptocarpus* Lindl. p.p., *Trachystigma* C.B.Clarke). In other cases, the larger cotyledon grows into a leaf of similar size and shape as the foliage leaves (Epithemateae: *Epithema* Blume, *Rhynchoglossum*, Didymocarpeae: e.g., *Microchirita* (C.B. Clarke) Yin Z.Wang). In the Didymocarpeae there are also cases in which the size difference is not very marked, and possibly there are also cases in which anisocotyly has been secondarily lost. Current knowledge and documentation of Gesneriaceae seedlings is still lacking. The book on the seedlings of Gesneriaceae by Fritsch (1904) is incomplete and out of date.

Tribes and Subtribes in Didymocarpoideae

The molecular data of Mayer et al. (2003), Wang et al. (2004a), Möller et al. (2009, 2011a) show unequivocally that there is a dichotomy at the base of the subfamily, splitting into two statistically strongly supported clades. One is the Epithemateae and the other is Trichosporeae.

Epithemateae. As was noted already by Burtt (1977), the Epithemateae are morphologically set apart from the large remainder of Old World Gesneriaceae (now Trichosporeae). In some features (e.g., shape of placentae) they have retained symplesiomorphic characters of the New World Gesneriaceae. In others, they show derived morphological specialization not found in other groups of Gesneriaceae (see Weber 1975–1982, Möller et al. 2009). At present, the Epithemateae comprise seven genera. Molecular data are not available for the Chinese genus *Gyrogyne* W.T.Wang, the single species of which is only known from the type collection (and is possibly extinct; Wang 2003). The relationships of the remaining genera are well established (Mayer et al. 2003).

The unusual morphological features of Epithemateae (e.g., strong anisophylly in most taxa, monophylly and medullary vascular bundles in *Monophyllaea*, unilateral racemes in *Rhynchoglossum*, bilocular ovary in *Whytockia* and *Monophyllaea*), the strong morphological demarcations between the genera and the long branches in the molecular tree (high-levels of genetic distance!) indicate that the extant Epithemateae may be relicts of an originally large and highly diversified group that experienced high levels of extinctions with the surviving populations exposed to morphological and genetic drift. More detailed studies are needed here. The topology of the molecular tree, along with the marked morphology, supports a subdivision of the small tribe into the following four subtribes:

(1) *Loxotidinae*. This subtribe is comprised of a single genus, *Rhynchoglossum* (=*Loxotis* R.Br. ex Benth.). According to the molecular data of Mayer et al. (2003), this genus stands apart from the other genera of the tribe, which is consistent with its uncommon morphological characters (distichous-''alternicladic'' leaf arrangement, presence of truly ''racemose,'' unilateral inflorescences, personate flowers, etc.; for details see Weber 1978a, 1978b).

(2) *Monophyllaeinae*. This subtribe contains the unifoliate Malesian genus *Monophyllaea* and the caulescent, anisophyllous Chinese genus *Whytockia*. Though their outward appearance and distribution is quite different [which caused Burtt (1963) to refer them to different tribes, Klugieae, and Loxonieae, respectively], Weber (1976b) predicted a close relationship based on the recognition of a common ''bauplan'' and synapomorphic characters in their floral morphology (Weber 1975, 1976a, 1976b). Mayer et al. (2003) indeed found a sister relationship of the two genera.

(3) *Loxoniinae*. This subtribe is composed of another pair of closely related genera, *Loxonia* Jack and *Stauranthera* Benth.. As was shown by Weber (1977b), the two genera share (*inter alia*) conspicuous synapomorphies in their inflorescence structure (bracteose thyrses of pair-flowered or, in a single species of each genus, ordinary cymes). Based on the plicate calyx shared with *Stauranthera*, *Gyrogyne* may also belong to this alliance.

(4) *Epithematinae*. The only genus, *Epithema*, exhibits a unique morphology (a solitary leaf and equal leaf pairs following the extremely unequal cotyledons; inflorescence a thyrse which is reduced to a single, much condensed pair-flowered cyme embraced by its subtending leaf), which has no parallel in other Epithemateae or Gesneriaceae as a whole (see Weber 1977b, 1988).

Trichosporeae. Trichosporeae is the correct formal name for the ''Didymocarpoid Gesneriaceae'' *sensu* Weber (2004a) at the rank of tribe. This is the largest and taxonomically most difficult tribe of traditional Gesneriaceae. The 78 genera that were formerly accepted (Weber 2004a), were recently reduced to 65 (see Möller & Clark, 2013). For example, 15 Chinese genera were reduced to synonymy in *Petrocodon* Hance (Wang et al.

2011, Weber et al. 2011c) and *Oreocharis* (Möller et al. 2011b). Others have been newly described (e.g., *Litostigma* Y.G.Wei, F.Wen & Mich.Möller, Wei et al. 2010; *Somrania* D.J.Middleton, Middleton & Triboun 2012; *Tribounia* D.J. Middleton, Middleton & Möller 2012), or have resulted from splitting of larger genera (e.g., *Microchirita*, *Damrongia* Kerr ex Craib, *Liebigia* Endl., *Codonoboea* Ridl., *Loxocarpus* R.Br., Weber et al. 2011a).

Phylogenetically, the tribe is subdivided into distinct clades, but their relationships are not fully resolved and not consistently well supported (Figure 13 in Möller & Clark, 2013). There are only a few strongly supported clades, and these are often small (e.g., monogeneric or comprised of 3–5 genera) except for the advanced Asian and Malesian or African and Madagascan clade. The taxonomy for the African and Madagascan *Streptocarpus*-alliance is not settled. Traditional classifications based on morphology recognize genera to different alliances and geographical groups (e.g., Fritsch 1893–1894, 1908: *Saintpaulia* H.Wendl.—Ramondeae, *Streptocarpus*—Streptocarpeae, *Acanthonema*—Klugieae). In contrast to traditional-based classifications, the molecular data of Möller and Cronk (1997a, 1997b, 2001a, 2001b) and Möller et al. (2009) indicate that they are closely allied based on the straight-fruited genera thus far examined [e.g., *Acanthonema*, *Colpogyne* B.L.Burtt, *Hovanella* A.Weber & B.L.Burtt, *Linnaeopsis* Engl., *Saintpaulia*, *Schizoboea* (Fritsch) B.L.Burtt]. These genera have evolved from within *Streptocarpus* (no molecular data are available for *Nodonema* B.L.Burtt and *Trachystigma*). The available molecular data are incomplete (e.g., Möller et al. 2009), and whether the whole African-Madagascan alliance should be treated as a single genus will need to be examined with increased taxon sampling (see discussion in Streptocarpinae for additional details).

In view of the largely unsupported backbone structure of the Trichosporeae it is arbitrary to draw demarcation lines and define larger groups. However, the geographical patterns are helpful and are consistant with molecular results. Principally, the Trichosporeae is an Asiatic (-Malesian) group with two clades of different geography: the small group of European genera (monophyletic in the most comprehensive analysis with two chloroplast genes, Möller et al. 2009), and the African plus Madagascan genera. In the informal classification of Weber (2004a) the following four major groups were outlined: (1) The Basal Asiatic genera, (2) The European genera, (3) The African and Madagascan genera, and (4) the Advanced Asiatic and Malesian genera. The latter group was subdivided into a comparatively small group of genera with predominantly twisted fruits and a much larger group with straight fruits.

It would be relatively easy to apply formal names to these informal groups. However, for the following reasons formal ranks for an updated classification are not provided: (a) The position of the European genera is at present relatively weakly supported. In the most comprehensive analysis across the family (e.g., Möller et al. 2009) they fall into a polytomy with the Leptoboeinae and Streptocarpinae. This would not justify recognizing the Basal Asiatic genera as a monophyletic entity. (b) For the same reason, the Basal Asiatic plus European genera cannot be combined into a single entity (subtribe). This would also blur the conspicuous morphological differences of the (groups of) genera involved. The European genera and a couple of the Basal Asiatic genera are typical rosette plants with scapose inflorescences, while the remaining genera of the Basal Asiatics are tall, caulescent, lignescent plants with mostly opposite leaves and axillary, short-pedunculate inflorescences. (c) As outlined above, the formal classification should reflect branching patterns of the phylogenetic trees. Therefore, the basal splitting of the Basal Asiatics into apparently ancient and isolated grades is reflected in their taxonomic treatment. We thus split the Basal Asiatic plus European (''Eurasian'') genera into the following six subtribes: (1) Jerdonieae, (2) Corallodiscinae, (3) Tetraphyllinae, (4) Leptoboeinae, (5) Ramondinae, and (6) Litostigminae. These groups are followed by the African and Madagascan genera, as subtribe (7) Streptocarpinae. For the reasons given below, a subtribe (8) Didissandrinae is established for *Didissandra* C.B.Clarke & C.DC. and *Tribounia*, sister to the Advanced Asiatic and Malesian genera. The latter group is divided into subtribe (9) Loxocarpinae (predominantly genera with twisted capsular fruits and genera that include both straight and twisted fruits) and (10) Didymocarpinae [genera exclusively with straight capsular or (*Cyrtandra*) indehiscent fruits].

(1) *Jerdoniinae*. This subtribe comprises only the genus *Jerdonia*, which is addressed above. According to Möller et al. (2009), *Jerdonia* is sister to the rest of the ''Didymocarpoid Gesneriaceae'' (now tribe Trichosporeae). ''Basalmost'' does not equate to primitive, though some of the characters are uncommon for a member of Gesneriaceae or Trichosporeae, respectively: according to Wight's illustrations (1848, 1850), the ovary has four separate parietal placentae (as in *Orobanche*), flattened filaments, and, according to Burtt (1977), isocotylous seedlings. In contrast, the inflorescences are pair-flowered cymes (Weber 1989) and thus typical of Gesneriaceae. In agreement with a position in the Basal

Asiatic genera are the presence of four stamens and the septicidal dehiscence of the capsular fruits. A comprehensive morphological study that addresses the above features is urgently needed for this genus.

(2) *Corallodiscinae*. This newly established subtribe comprises a single genus, *Corallodiscus* Batalin. It was placed in tribe Ramondeae (''Ramondieae'') by Fritsch (1893–1894), which he regarded the most ''primitive tribe'' in the Gesneriaceae. He defined the group by the septicidally dehiscing capsules, and this seems to be a characteristic feature of the Basal Asiatic genera, together with the presence of a tetrandrous androecium and a clearly zygomorphic corolla.

(3) *Tetraphyllinae*. This monogeneric subtribe represents another basal lineage of the Trichosporeae. *Tetraphyllum* Griff. ex C.B.Clarke is distinguished by its habit of long erect (apparently monocarpic) stems bearing a tetramerous leaf whorl at the top. The inflorescences/flowers arising from the leaf axils form dense, subsessile clusters. The fruits are similar to the genera in the clade *Leptoboeinae*.

(4) *Leptoboeinae*. This subtribe comprises five to six genera. Samples of four genera of this tribe analysed molecularly represent a monophyletic clade on a basal lineage in tribe Trichosporeae. Their morphology is heterogeneous, though they share an inconspicuous or capitate stigma, which is uncommon in the other basal lineages. The core is formed by *Boeica*, *Leptoboea* and *Rhynchotechum*, all being caulescent and lignescent plants with tetrandrous flowers. In contrast, *Leptoboea* and *Boeica* (only distinguished from *Leptoboea* by alternate leaves) have capsular fruits with loculicidal dehiscence and *Rhynchotechum* has indehiscent berry-like fruits. Because of its fruit characteristics, *Rhynchotechum* was placed in Cyrtandreae by Burtt (1963) and Burtt and Wiehler (1995), but the classification of *Rhynchotechum* with *Leptoboea* and *Boeica* was already established by Fritsch (1893–1894). He combined *Platystemma* Wall., *Championia* C.B.Clarke, *Boeica*, *Leptoboea*, and *Loxonia* in tribe Championieae subtribe Championiinae, and *Tetraphyllum* and *Trisepalum* C.B.Clarke in subtribe Trisepalinae. The molecular data confirm the position of *Platystemma* despite its anomalous morphology relative to the other members of the group (e.g., rhizomatous plant with quasi-monophyllous aerial shoots). According to preliminary data of Möller (unpubl.) *Beccarinda* Kuntze also appears to belong in the Leptoboeinae. The presence of tetrandous flowers is a potential synapomorphy that *Beccarinda* shares with other members of the Leptoboeinae. *Championia* is similar in habit and fruit characters to *Leptoboea*, but no molecular data are currently available to test this phylogenetic placement. Thus, its position in the Leptoboeinae is therefore tentative.

(5) *Ramondinae*. This contains the three European genera *Haberlea* Friv., *Jancaea* Boiss. and *Ramonda* Rich. The sister group relationship of *Jancaea* and *Ramonda* is strongly supported and future taxonomies may treat them as a single genus. A closer link to Asiatic genera in some analyses may be an artefact of sampling or data paucity (Möller & Clark, 2013). More work is needed here.

(6) *Litostigminae*. This monogeneric tribe of the Basal Asiatic Gesneriaceae is based on the recently discovered and described genus *Litostigma* (Wei et al. 2010). Based on its molecular phylogenetic placement, it is a transitional genus that has symplesiomorphies such as septicidal and loculicidal dehiscence (shared with Basal Asiatic genera) and synapomorphies such as diandrous flowers and infundibuliform corolla (shared with Advanced Asiatic and Malesian and African and Madagascan Gesneriaceae).

(7) *Streptocarpinae*. This subtribe comprises all genera from Africa and Madagascar. It was previously noted that the available molecular studies suggest that all African and Madagascan genera with straight fruits are nested within *Streptocarpus*, which is a group traditionally defined as having twisted fruits. Molecular data are available for all genera in this tribe except *Nodonema* and *Trachystigma*. *Linnaeopsis* was recently included in *Streptocarpus* based on ITS sequence data (Darbyshire 2006).

The combination names proposed by Christenhusz (2012) are not accepted here. Christenhusz (2012) synonymized the following genera with *Streptocarpus*: *Colpogyne*, *Hovanella*, *Saintpaulia* and *Schizoboea*. Christenhusz's 2012 paper was a modest taxonomic exercise that overlooked currently available studies. It is presumed that Christenhusz based the new combinations on the datasets from Möller et al. (2009), but this study is not evaluated, discussed in the text, and it was not included in the Literature Cited. The Möller et al. (2009) study was limited and the matrix contained a significant amount of missing data. The combination names proposed by Christenhusz (2012) are therefore rejected until studies that include increased taxon sampling and additional markers are published.

(8) *Didissandrinae.* The phylogenetic position of *Didissandra* and *Tribounia* is not readily explained based on morphology. These two genera have straight capsular fruits. In *Didissandra* the tardily dehiscent fruits dehisce into separate strands (Weber & Burtt 1997a, 1997b). In *Tribounia* the fruits dehisce loculicidally with a long stipe (Middleton & Möller 2012). Their position outside of subtribe Didymocarpinae and between two clades of predominantly twisted-fruit genera of subtribes Streptocarpinae and Loxocarpinae was weakly supported in a study by Middleton and Möller (2012). The two genera are likely closely related to Loxocarpinae and are best accommodated in a subtribe of their own.

(9) *Loxocarpinae.* This is a morphologically distinct and well-supported clade that includes all genera in Asia and Malesia with predominantly twisted fruits (although there are species with straight fruits), often with a silky and silvery indumentum. Fruit morphology readily identifies three groups of genera that can be distinguished based on the following: (1) genera with twisted (*Streptocarpus*-like) fruits: *Boea* Comm. ex Lam., *Ornithoboea* Parish ex C.B.Clarke, ''*Streptocarpus*'' *orientalis* Craib and allies from Asia, and the monotypic *Rhabdothamnopsis* Hemsl., *Senyumia* Kiew, A.Weber & B.L.Burtt, *Emarhendia* Kiew, A.Weber & B.L.Burtt, and *Spelaeanthus* Kiew, A.Weber & B.L.Burtt (twisting sometimes slight and barely noticeable). (2) Genera with either twisted or straight fruits: *Paraboea* (C.B.Clarke) Ridl. (including the recently synonymized *Phylloboea* Benth. and *Trisepalum*; Puglisi et al. 2011) and *Kaisupeea* B.L.Burtt. (3) Genera with exclusively straight fruits: *Loxocarpus* (re-established by Middleton et al. 2013), *Damrongia*, *Somrania* and the monotypic genus *Orchadocarpa* Ridl. Currently available molecular phylogenies do not necessarily support these groups (see Möller & Clark, 2013). Though, the data and sampling in these studies is insufficient and future work will show whether any of the above groups represent natural entities.

(10) *Didymocarpinae.* This is the largest and least understood group of the Trichosporeae, and the whole family Gesneriaceae, respectively. It includes the traditional tribes Trichosporeae, Cyrtandreae and the remaining ''Didymocarpoid Gesneriaceae'' (=Trichosporeae in the new sense) not covered by subtribes 1–9. Nonetheless, the number of genera has been considerably reduced to about 30 by the new and expanded definitions of *Oreocharis* Benth. (Möller et al. 2011b) and *Petrocodon* (Weber et al. 2011c). A rank-based classification or further divisions of this large group are not recommended at this time for the following reasons: (1) the backbone structure of the molecular trees is still weak and several of the genera are difficult to place (e.g., the Chinese monotypic genera *Allostigma*, *Cathayanthe* Chun, *Conandron* Siebold & Zucc. and *Metapetrocosmea* W.T. Wang), (2) many of the clades are monogeneric and do not group with others, and (3) to date some traditional genera are highly polyphyletic (e.g., *Briggsia* Craib and *Raphiocarpus* Chun). Newly defined genera based on recent molecular phylogenies and the establishment of new genera are necessary for many of the clades in this subtribe.

TAXONOMIC TREATMENT

Precursory Notes

Descriptions. These are only provided for new suprageneric taxa. In the ''Content'' all genera are listed that were recognized in Weber (2004a) or were newly described since then. Those having been recently sunk into synonymy are given in brackets with relevant reference. Brief comments are given for genera which were newly and recently defined or which will be newly defined or synonymized in the near future.

Authorities in suprageneric names. All infrafamilial/suprageneric names are given with authorities, because autonyms (automatically created names, to be cited without authorities) are only relevant for infrageneric taxa (''Melbourne Code,'' McNeill et al. 2012, Articles 6.8, 22.1-3 and 26.1-3.). The long-standing question, whether or not parenthetical authors should be given in suprageneric names, has been settled by the ICN (see ''Melbourne Code,'' McNeill et al. 2012, Art. 49.2), which declares unambiguously: ''Parenthetical authors are not to be cited for suprageneric names.'' In practice, this means that reduction of Anetantheae Fritsch (1893) to subtribal rank must not read Anetanthinae (Fritsch) A.Weber & J.L.Clark, but Anetanthinae A.Weber & J.L.Clark, and the name at the new rank must be qualified as *status et nomen novum.* The same applies for Sphaerorrhizeae Roalson & Boggan, which becomes Sphaerorrhizinae A.Weber & J.L.Clark at subtribal rank.

Priority and available names based on synonyms. The priority rules of the ICN stipulate that (except names of any subdivision of a family that includes the type of the adopted, legitimate name of the family to which it is assigned, Art. 19.4, Ex. 2) the earliest name available at a given rank has to be adopted (Art. 11.3). For example, we therefore have to use ''Trichosporeae Nees'' for the ''Didymocarpoid Gesneriaceae'' *sensu* Weber (2004a), which is the earliest name available at tribal rank. This regulation also often necessitates name changes when the rank is changed. Therefore, the tribal name Episcieae Endl. cannot be simply altered into Episciinae, as earlier and different names at subtribal rank are available.

Still more uncomfortable is the situation when we are forced to adopt a name that is based on a synonym. This is the case with Ligeriinae (which is the available name for Sinningieae at subtribal rank; and Loxotidinae (based on *Loxotis*, a synonym of *Rhynchoglossum*).

Names with prefix Eu-. Rank names starting with the prefix Eu- (e.g., Eucyrtandreae Endl. 1839, Eudidymocarpinae DC. 1845) are not listed. By rule of the ICN, they are not validly published and, therefore, do not exist nomenclaturally.

Formal Classification

Fam. **Gesneriaceae** Rich. & Juss. in DC., Essai Propr. Méd. Pl., ed. 2: 192 (11 May 1816) (''*Gessnerieae*''), nom. cons. TYPE: *Gesneria* L. (1753)

= Belloniaceae Martinov, Tekno-Bot. Slovar: 67 (3 August 1820) (''*Bellonides*''). TYPE: *Bellonia* L. (1753)
= Didymocarpaceae D.Don, Edinburgh Phil. J. 7: 83 (1822) (''*Didymocarpeae*''). TYPE: *Didymocarpus* Wall. (1819), nom. cons.
= Cyrtandraceae Jack, Trans. Linn. Soc. 14(1): 24 (1823). TYPE: *Cyrtandra* J.R. & G.Forst. (1776)
= Besleriaceae Raf., Sylva Tellur.: 70 (October–December 1838) (''*Beslerides*''). TYPE: *Besleria* L. (1753)
= Ramondaceae Godr., in Grenier & Godron, Fl. France 2: 506 (1850). TYPE: *Ramonda* Rich. (1805), nom. cons.

Note. Until the turn of the millenium, the authorship of the family was incorrectly attributed to Dumortier (Commentat. Bot. 57, 1822). The authorities and the publication were given in the present form for the first time in the ''St. Louis Code'' (Greuter et al. 2000).

1. Subfam. **Sanangoideae** A.Weber, J.L.Clark & Mich.Möller, subfam. nov. TYPE: *Sanango* G.S.Bunting & Duke (1965).

Plants small, hard-wooded trees. ***Leaves*** opposite, petiolate, lamina elliptic to obovate. ***Inflorescence*** a terminal bracteose thyrse, with pair-flowered cymes emerging from the axils of bracts. ***Flowers*** 5-merous. ***Sepals*** connate in the lower part. ***Corolla*** tubular, tube curved, slightly gibbous, limb subactinomorphic. ***Stamens*** 4, included; staminode present. ***Nectary*** cup-shaped, ±as high as the ovary. ***Ovary*** 2-carpellate, superior, globose, incompletely divided in the upper part, completely divided (with axile placentae) in the lower part; style short. ***Stigma*** capitate-bilobed, the lobes laterally joined with the style and directing downwards. ***Fruit*** a bony capsule, depressed at the apex, style persisting, dehiscence septicidal plus loculicidal. ***Seeds*** small, numerous, narrow-elliptic, surface reticulate.

Content. *Sanango* G.S.Bunting & Duke (1965).

2. Subfam. **Gesnerioideae** Burnett, Outlines Bot.: 959, 1095, 1108 (February 1835) (''*Gesneridae*''). TYPE: *Gesneria* L. (1753)

= Beslerioideae Burnett, Outlines Bot.: 959, 960, 1095, 1108 (February 1835) (''*Bessleridae*''). TYPE: *Besleria* L. (1753)
= Episcioideae Ivanina, Bot. Zhurn. (Moscow & Leningrad) 50: 42 (1 February 1965). TYPE: *Episcia* Mart. (1829)
= Coronantheroideae Wiehler, Selbyana 6: 156 (31 August 1983). TYPE: *Coronanthera* Vieill. ex C.B.Clarke (1883)

Notes. Wiehler (1983) attributed the establishment of this subfamily to Link (Handbuch 1: 505, 4–11 July 1829, ''*Gesneriaceae*''), but Link's action is now considered as the establishment of a suborder (''Gesneriineae,'' Reveal 1995 onw., ed. 2011). Burnett (1835) divided the family Gesneriaceae (comprising the neotropical representatives only) into two subgroups, ''Besleridae'' and ''Gesneridae,'' which now have to be interpreted as subfamilies. The first to use explicitely the subfamily rank with the ending -oideae (Gesnerioideae) was Fritsch (in Engler and Prantl, Nat. Pflanzenfam. IV, 3b: 142, 143; 1893).

2.1. Tribe **Titanotricheae** Yamaz. ex W.T.Wang, Fl. Reipubl. Popularis Sin. 69: 577 (1990). TYPE: *Titanotrichum* Soler. (1909).

Content. *Titanotrichum* Soler.

2.2. Tribe **Napeantheae** Wiehler, Selbyana 6: 151 (31 August 1983). TYPE: *Napeanthus* Gardner (1843).

Content. *Napeanthus* Gardner.

2.3. Tribe **Beslerieae** Bartl., Ord. Nat. Pl.: 175 (September 1830) (''*Besleriea*''). TYPE: *Besleria* L. (1753).

= Anetantheae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Anetanthus* Hiern ex Benth. & Hook.f. (1876).

2.3.1. Subtribe **Besleriinae** G.Don, Gen. Hist. 4: 644, 651 (1837–8 April 1838) (''*Beslerieae*''). TYPE: *Besleria* L. (1753).

Content. ***Besleria*** L., ***Cremosperma*** Benth., ***Gasteranthus*** Benth., ***Reldia*** Wiehler.

2.3.2. Subtribe **Anetanthinae** A.Weber & J.L.Clark, nom. et stat. nov., based on Anetantheae Fritsch in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Anetanthus* Hiern ex Benth. & Hook.f. (1876).

Content. ***Anetanthus*** Hiern ex Benth. & Hook.f., ***Cremospermopsis*** L.E.Skog & L.P. Kvist, ***Resia*** H.E.Moore, ***Shuaria*** D.A.Neill & J.L.Clark (Clark et al. 2010), ***Tylopsacas*** Leeuwenbg.

2.4. Tribe **Coronanthereae** Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Coronanthera* Vieill. ex C.B.Clarke (1883).

= Mitrarieae B.L.Burtt, Notes Roy. Bot. Gard. Edinburgh 1962, 24: 216 (1962, publ. 1963).

2.4.1. Subtribe **Coronantherinae** Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Coronanthera* Vieill. ex C.B.Clarke (1883).

Content. ***Coronanthera*** C.B.Clarke, ***Rhabdothamnus*** Cunn.

2.4.2. Subtribe **Mitrariinae** Hanst., Linnaea 26: 198, 199 (1854) (''*Beslerieae* subtr. *Mitrarieae*''). TYPE: *Mitraria* Cav. (1801).

= Sarmientinae Hanst., Linnaea 26: 198, 199 (1854) (as ''Beslerieae subtr. Sarmienteae''). TYPE: *Sarmienta* Ruiz & Pav. (1794).

Content. ***Asteranthera*** Hanst., ***Fieldia*** Cunn., ***Mitraria*** Cav., ***Sarmienta*** Ruiz & Pav.

2.4.3. Subtribe **Negriinae** V.L.Woo, J.F.Smith & Garn.-Jones, Int. J. Pl. Sci. 172(3): 454 (2011). TYPE: *Negria* F. Muell. (1871).

Content. ***Depanthus*** S.Moore, ***Lenbrassia*** G.W.Gillett, ***Negria*** F.Muell.

2.5. Tribe **Gesnerieae** Dumort., Anal. Fam. Pl.: 30 (1829) (''*Gesnereae*''). TYPE: *Gesneria* L. (1753).

= Episcieae Endl., Gen. Pl.: 720 (January 1839). TYPE: *Episcia* Mart. (1829).
= Gloxinieae Sweet, Hort. Brit., ed. 3: 526 (late 1839). TYPE: *Gloxinia* L'Hér. (1785).
= Achimeneae Hanst., Linnaea 34: 229 (July 1864). TYPE: *Achimenes* Pers. (1806), nom. cons.
= Rhytidophylleae Hanst., Linnaea 34: 231 (July 1864). TYPE: *Rhytidophyllum* Mart. (1829).
= Bellonieae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893) TYPE: *Bellonia* L. (1753).
= Columneeae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Columnea* L. (1753).
= Kohlerieae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Kohleria* Regel (1847).
= Sinningieae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 144 (May 1893). TYPE: *Sinningia* Nees (1825).
= Solenophoreae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Solenophora* Benth. (1840).
= Pentaraphieae Kuntze, in Post & Kuntze, Lex. Gen. Phan.: 695 (20–30 November 1903). TYPE: *Pentaraphia* Lindl. (1827) = ***Gesneria*** L. (1753).
= Rechsteinerieae Ivanina, Bot. Zhurn. (Moscow & Leningrad) 50: 42 (1 February 1965). TYPE: *Rechsteineria* Regel (1848), nom. cons. = ***Sinningia*** Nees (1825).
= Sphaerorrhizeae Roalson & Boggan, Selbyana 25: 236 (2005). TYPE: *Sphaerorrhiza* Roalson & Boggan (2005).

2.5.1. Subtribe **Gesneriinae** Oerst., Centralamer. Gesner.: 10 (1858) (''*Gesnereae*''). TYPE: *Gesneria* L. (1753).

= Rhytidophyllinae Hanst., Linnaea 26: 198, 199 (April 1854) (*Rhytidophylleae*). TYPE: *Rhytidophyllum* Mart. (1829).
= Belloniinae Benth. & Hook.f., Gen. Pl. 2: 991 (1–16 May 1876) (''*Bellonieae*'') TYPE: *Bellonia* L. (1753).
= Pentaraphiinae Benth. & Hook.f., Gen. Pl. 2: 993 (1–16 May 1876) ''Pentarhaphieae''. TYPE: *Pentaraphia* Lindl. (1827) = ***Gesneria*** L. (1753).

Content. ***Bellonia*** L., ***Gesneria*** L., ***Pheidonocarpa*** L.E.Skog, ***Rhytidophyllum*** Mart.

2.5.2. Subtribe **Gloxiniinae** G.Don, Gen. Hist. 4: 644, 645 (1837–8 April 1838) (''*Gloxinieae*''). TYPE: *Gloxinia* L'Hér. (1785).

= Achimeninae Hanst., Linnaea 26: 198, 199. April 1854 (''*Achimeneae*''). TYPE: *Achimenes* Pers. (1806), nom. cons.

= Niphaeinae Hanst., Linnaea 26: 198, 199 (April 1854) (''*Niphaeeae*''). TYPE: *Niphaea* Lindl. (1841).

= Brachylaematinae Hanst., Linnaea 26: 198, 199 (April 1854) (''Brachylaemateae''), nom. illeg. TYPE: *Brachylaema* Hanst. (1854), nom. illeg.

= Heppiellinae Lem., Ill. Hort. 2: ad t. 57 (June 1855). Type: *Heppiella* Regel (1853).

= Moussoniinae Oerst., Centralamer. Gesner.: 10, 32 (1858) (''*Moussonieae*''). TYPE: *Moussonia* Regel (1847).

= Solenophorinae Oerst., Centralamer. Gesner.: 10 (1858) (''*Solenophoreae*''). TYPE: *Solenophora* Benth. (1840).

Content. ***Achimenes*** Pers., ***Amalophyllon*** Brandegee, ***Chautemsia*** A.O.Araujo & V.C.Souza, ***Diastema*** Benth., ***Eucodonia*** Hanst., ***Gloxinella*** (H.E.Moore) Roalson & Boggan, ***Gloxinia*** L'Hér., ***Gloxiniopsis*** Roalson & Boggan, ***Goyazia*** Taub., ***Heppiella*** Regel, ***Kohleria*** Regel, ***Mandirola*** Decne., ***Monopyle*** Benth., ***Moussonia*** Regel, ***Niphaea*** Lindl., ***Nomopyle*** Roalson & Boggan, ***Pearcea*** Regel, ***Phinaea*** Benth., ***Seemannia*** Regel, ***Smithiantha*** Kuntze, ***Solenophora*** Benth.

2.5.3. Subtribe **Columneinae** Hanst., Linnaea 26: 198, 199 (April 1854) (''*Columneae*''). TYPE: *Columnea* L. (1753).

= Drymoniinae Hanst., Linnaea 26: 198, 199 (April 1854) (''*Drymonieae*''). TYPE: *Drymonia* Mart. (1829).

= Nematanthinae Hanst., Linnaea 26: 198, 199 (April 1854) (''*Nematantheae*''). TYPE: *Nematanthus* Schrad. (1821), nom. cons.

= Hypocyrtinae Hanst., Linnaea 26: 198, 199 (April 1854) (''*Hypocyrteae*''). TYPE: *Hypocyrta* Mart. (1829).

= Codonanthinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Codonanthe* Mart. ex Hanst. (1854).

Content. ***Alloplectus*** Mart., ***Alsobia*** Hanst., ***Christopheria*** J.F.Smith & J.L.Clark (Smith & Clark 2013), ***Chrysothemis*** Decne., ***Cobananthus*** Wiehler, ***Codonanthe*** (Mart.) Hanst., ***Codonanthopsis*** Mansf., ***Columnea*** L. [including *Dalbergaria* Tussac, *Pentadenia* (Planch.) Hanst., *Trichantha* Hook.f. and *Bucinellina* (Wiehler) Wiehler], ***Corytoplectus*** Oerst., ***Crantzia*** Scop., ***Cremersia*** C.Feuillet & L.E.Skog, ***Drymonia*** Mart., ***Episcia*** Mart., ***Glossoloma*** Hanst., ***Lampadaria*** C.Feuillet & L.E.Skog, ***Lembocarpus*** Leeuwenb., ***Lesia*** J.L.Clark & J.F.Smith (Smith & Clark 2013), ***Nautilocalyx*** Hanst., ***Nematanthus*** Schrad., ***Neomortonia*** Wiehler, ***Oerstedina*** Wiehler, ***Pachycaulos*** J.L.Clark & J.F.Smith (Smith & Clark 2013), ***Pagothyra*** (Lwbg.) J.F.Smith & J.L.Clark (Smith & Clark 2013), ***Paradrymonia*** Hanst., ***Rhoogeton*** Leeuwenb., ***Rufodorsia*** Wiehler.

Notes. Subtribe Columneinae corresponds to the traditional tribe Episcieae Endl. With respect to the four earliest names available at subtribal rank, all published in the same paper of Hanstein (1854), we follow Fritsch (1893–1894), who used ''Columneinae'' and, though not formally synonymizing the other subtribes, included their type genera in that subtribe. The name is favorable as it refers to the most speciose genus of the subtribe. Moreover, it is based on an epiphytic genus and thus embodies the fact that epiphytism plays a major role in the group.

2.5.4. Subtribe **Sphaerorrhizinae** A.Weber & J.L.Clark, nom. et stat. nov., based on Sphaerorrhizeae Roalson & Boggan, Selbyana 25: 236 (2005) TYPE: *Sphaerorrhiza* Roalson & Boggan (2005).

Content. ***Sphaerorrhiza*** Roalson & Boggan.

2.5.5. Subtribe **Ligeriinae** Hanst., Linnaea 26: 198, 199 (April 1854) (''*Ligerieae*''). TYPE: *Ligeria* Decne. (1848) = ***Sinningia*** Nees (1825).

Content. ***Paliavana*** Vand., ***Sinningia*** Nees, ***Vanhouttea*** Lem.

3. Subfam. **Didymocarpoideae** Arn., Botany: 121 (9. March 1832) (''*Didymocarpeae*''). TYPE: *Didymocarpus* Wall. (1819), nom. cons.

= Cyrtandroideae Burnett, Outl. Bot.: 963, 1095, 1107 (February 1835) (''*Cyrtandridae*''). TYPE: *Cyrtandra* J.R.Forst. & G.Forst. (1775).

Notes. This is identical with the later synonym Cyrtandroideae (Jack) Burnett (1835), as used in Burtt (1997), and with its isonym Cyrtandroideae Endl. (1839), as used by Burtt (1963) and Burtt and Wiehler (1995). However, Reveal (1995) discovered that George A.W. Arnott, in a preprint of an article on botany for the seventh edition of the Encyclopaedia Britannica (the preprint appeared in 1832, the corresponding volume of E. B. ten years later) had established the ''Didymocarpeae'' (now to be interpreted as subfamily Didymocarpoideae) earlier than Burnett. This name thus has priority over Cyrtandroideae. Though formally irrelevant, this is fortunate, as it parallels the fact that the family Didymocarpaceae was established earlier (D.

Don 1822) than Cyrtandraceae (Jack 1823). Moreover (but also fomally irrelevant), the genus *Cyrtandra*, on which Cyrtandroideae is based, is exceptional in its indehiscent fruits, while *Didymocarpus* of Didymocarpoideae has dehiscent, dry capsules that are characteristic for almost all other genera of the subfamily.

3.1. Tribe **Epithemateae** C.B.Clarke, Commelyn. et Cyrtandr. Bengal. 67 (1874) (''Epithemeae''). Type: *Epithema* Blume (1826).

= Klugieae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). Type: *Klugia* Schltdl. (1833) = ***Rhynchoglossum*** Blume (1826).
= Loxonieae B.L.Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 210 (1962, publ. 1963). Type: *Loxonia* Jack (1823).
= Epithemateae Reveal, Phytoneuron 37: 216 (23 April 2012), nom. superfl.

3.1.1. Subtribe **Loxotidinae** G.Don, Gen. Hist. 4: 645, 664 (1837–8 April 1838) (''*Loxotieae*''). Type: *Loxotis* R.Br. ex Benth. (1835) = ***Rhynchoglossum*** Blume (1826).

Content. ***Rhynchoglossum*** Blume.

3.1.2. Subtribe **Monophyllaeinae** A. Weber & Mich.Möller, subtr. nov. Type: *Monophyllaea* R.Br. (1838).

Plants perennial or rarely annual herbs. ***Stem*** erect or decumbent. ***Leaves*** opposite, those of a pair strongly unequal, or stem (hypocotyl) with a single leaf (macrocotyledon). ***Inflorescences*** axillary, unilateral pair-flowered cymes, ebracteolate, arising from the axils of the large leaves of a pair or from small bracts following the single leaf. ***Flowers*** usually small, zygomorphic. ***Stamens*** 4. ***Nectary*** ring-shaped. ***Ovary*** bilocular. ***Fruit*** a capsule, opening by valves or rarely by an apical pore. ***Seeds*** small, numerous, surface reticulate.

Content. ***Monophyllaea*** R.Br., ***Whytockia*** W.W.Smith.

3.1.3. Subtribe **Loxoniinae** A.DC., in A.P. & A.L.P.P. de Candolle, Prodr. 9: 274 (1 January 1845) (''*Loxonieae*''). Type: *Loxonia* Jack (1823).

= Anomorhegmiinae Meisn., Pl. Vasc. Gen.: Tab. Diagn. 303, Comm. 212 (25–31 October 1840) (''*Anomorhegmieae*''), nom. illeg. Type: *Anomorhegmia* Meisn. (1840), nom. illeg. = ***Stauranthera*** Benth. (1835).

Content. ***Gyrogyne*** W.T.Wang (position uncertain), ***Loxonia*** Jack, ***Stauranthera*** Benth.

Notes. As *Anomorhegmia* Meisn. is an illegitimate name (through the inclusion in synonymy of *Miquelia* Blume in the ''Pars altera'' which was published simultaneously with the ''Pars prior'' of his work, Stearn 1967), the earlier subtribal name, Anomorhegmiinae Meisn., must also be considered illegitimate (ICN Art. 19.6) (D.J. Middleton, pers. comm.).

3.1.4. Subtribe **Epithematinae** DC. ex Meisn., Pl. Vasc. Gen.: Tab. Diagn. 303, Comm. 212 (25–31 October 1840) (''*Epithemeae*''). Type: *Epithema* Blume (1826).

Content. ***Epithema*** Blume.

3.2. Tribe **Trichosporeae** Nees, Flora 8: 143 (7 March 1825). Type: *Trichosporum* D.Don (1822), nom. rejic. = ***Aeschynanthus*** Jack (1823), nom. cons.

= Cyrtandreae Bartl., Ord. Nat. Pl.: 185 (September 1830) (''*Cyrtandrea*''). Type: *Cyrtandra* J.R.Forst. & G.Forst. (1775).
= Didymocarpeae Endl., Gen. Pl. 716 (January 1839). Type: *Didymocarpus* Wall. (1819), nom. cons.
= Ramondeae C.B.Clarke, Commelyn. et Cyrtandr. Bengal. 67 (1874) (''*Ramondiae*''). Type: *Ramonda* (1805), nom. cons.
(?) = Championieae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). Type: *Championia* Gardner (1846).
= Hemiboeeae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893), 148 (1894). Type: *Hemiboea* C.B.Clarke (1888).
= Streptocarpeae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 142 (May 1893). Type: *Streptocarpus* Lindl. (1828).
= Saintpaulieae Ivanina, Bot. Zhurn. (Moscow & Leningrad) 50: 31 (1 February 1965). Type: *Saintpaulia* Wendl. (1893).
= Rhynchotecheae Ivanina, Bot. Zhurn. (Moscow & Leningrad) 50: 42 (1 February 1965). Type: *Rhynchotechum* Blume (1826).

Notes. The tribal name Trichosporeae was traditionally used for a few genera characterized by appendaged seeds. However, in the molecular analysis of Möller et al. (2009) most of these genera proved unrelated and were scattered throughout the ''Didymocarpoid Gesneriaceae'' *sensu* Weber (2004a). Nonetheless, Trichosporeae is the earliest name for the whole group at tribal rank and, therefore must be adopted (ICN Art. 19.4, see particularly Ex. 4).

3.2.1. Subtribe **Jerdoniinae** A.Weber & Mich. Möller, subtrib. nov. Type: *Jerdonia* Wight (1848).

Plants perennial rhizomatous rosette herbs. ***Inflorescences*** (pair-flowered cymes) axillary, scapose, flowers several, in a subumbellate arrangement. ***Sepals*** free to base, narrow. ***Corolla*** infundibuliform, zygomorphic, tube inflated above the middle, limb with two upper lobes and three lower lobes. ***Stamens*** 4, with flattened filaments, the upper pair hooded at the top, the lower pair with a broad appendage above the insertion, all four anthers coherent. ***Disc*** cup-shaped. ***Stigma*** peltate, ovary unilocular, with four parietal placentae (*fide* Wight 1848, 1850). ***Fruit*** a dry, bivalved capsule, opening septicidally.

Content: ***Jerdonia*** Wight.

3.2.2. Subtribe **Corallodiscinae** A.Weber & Mich.Möller, subtrib. nov. TYPE: *Corallodiscus* Batalin (1892).

Plants perennial rhizomatous rosette herbs. ***Lamina*** broadly lanceolate, rhombic or suborbicular, rugose. ***Inflorescences*** axillary, scapose, 1- to several-flowered. ***Flowers*** in lax to subumbellate arrangement. ***Sepals*** free to base or fused halfway. ***Corolla*** tubular, zygomorphic, limb bilabiate, with two upper lobes and three lower lobes, lobes rounded, lower lip with dense beard inside of tube; colour blue to purple, rarely yellow or white. ***Stamens*** 4, included or slightly exserted, anthers dorsifixed, cohering in pairs. ***Nectary*** ring-shaped. ***Ovary*** with two parietal placentae. ***Stigma*** capitate. ***Fruit*** a dry, two- or four-valved capsule, opening septicidally or septicidally plus loculicidally. ***Seeds*** small, numerous, narrow-elliptic, surface reticulate.

Content. ***Corallodiscus*** Batalin

3.2.3. Subtribe **Tetraphyllinae** A.Weber & Mich. Möller, subtrib. nov. TYPE: *Tetraphyllum* Griff. ex C.B.Clarke (1854).

Plants terrestrial perennial caulescent herbs. ***Stem*** erect, bearing a tetramerous whorl (pseudowhorl?) of leaves on top. ***Flowers*** in axillary cymes, condensed, subsessile. ***Corolla*** widely funnel-shaped, limb bilabiate to subregular. ***Stamens*** 4, didynamous; anthers coherent at the tips, opening by longitudinal slits. ***Nectary*** largely reduced. ***Ovary*** ovoid, style slender. ***Stigma*** obscurely bilobed. ***Capsule*** splitting septicidally and/or loculicidally into 4 valves, leaving the two main ribs united to the style and 4 papery enrolled placentae.

Content. ***Tetraphyllum*** Griff. ex C.B.Clarke.

3.2.4. Subtribe **Leptoboeinae** C.B.Clarke, in J.D.Hooker, Fl. Brit. India 4: 337 (January 1884) (''*Leptoboeae*''). TYPE: *Leptoboea* Benth. (1876).

(?) = Championiinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May) 1893. TYPE: *Championia* Gardner (1846).

Content. ***Beccarinda*** Kuntze, ***Boeica*** C.B.Clarke, ***Championia*** Gardner (to be confirmed), ***Leptoboea*** Benth., ***Platystemma*** Wall., ***Rhynchotechum*** Blume.

3.2.5. Subtribe **Ramondinae** DC. ex Meisn., Pl. Vasc. Gen.: Tab. Diagn. 302, Comm. 212 (25–31. October 1840) (''*Ramondieae*''). TYPE: *Ramonda* Rich. (1805), nom. cons.

Content. ***Haberlea*** Friv., ***Jancaea*** Boiss. (according to the molecular data of Möller et al. 1999, 2009 and 2011a, likely to be synonymized with *Ramonda*), ***Ramonda*** Rich.

3.2.6. Subtribe **Litostigminae** A.Weber & Mich. Möller, subtr. nov. TYPE: *Litostigma* Y.G.Wei, F.Wen & Mich.Möller (2010).

Plants perennial acaulescent rhizomatous herbs. ***Leaves*** basal, petiolate. ***Cymes*** axillary, single-flowered, with two bracteoles. ***Calyx*** actinomorphic, 5-lobed. ***Corolla*** infundibuliform, ventrally slightly pouched, limb bilabiate, adaxial lip 2-lobed, abaxial lip 3-lobed, lobes orbicular to ovate. ***Stamens*** 2 fertile, inserted on abaxial side of tube, anthers coherent; staminodes 3, inserted on the adaxial side of the tube. ***Disc*** annular. ***Ovary*** narrowly ovoid, unilocular, with two parietal bifid intrusive placentae. ***Style*** elongate (4x longer than ovary). ***Stigma*** crateri- or disciform. ***Capsule*** elongate-ovoid, dehiscing by 4 valves. ***Seeds*** small, narrow-elliptic, surface reticulate.

Content: ***Litostigma*** Y.G.Wei, F.Wen & Mich. Möller.

3.2.7. Subtribe **Streptocarpinae** Ivanina, Bot. Zhurn. (Moscow & Leningrad) 50: 33 (1 February 1965). TYPE: *Streptocarpus* Lindl. (1828).

Content. ***Acanthonema*** Hook.f., ***Colpogyne*** B.L.Burtt, ***Hovanella*** A.Weber & B.L.Burtt, ***Linnaeopsis*** Engl., ***Nodonema*** B.L.Burtt, ***Saintpaulia*** Wendl., ***Schizoboea*** (Fritsch) B.L.Burtt, ***Streptocarpus*** Lindl., ***Trachystigma*** C.B.Clarke.

3.2.8. Subtribe **Didissandrinae** A.Weber & Mich. Möller, subtrib. nov. TYPE: *Didissandra* C.B.Clarke (1883).

Plants perennial-lignescent or annual (?) herbs. ***Stem*** caulescent, erect to creeping. ***Leaves*** decussate (rarely ternate), ±isophyllous, petiolate, lamina ovate or cordate. ***Cymes*** axillary, pedunculate, lax or epedunculate, condensed; flowers in pairs. ***Sepals*** free to base and persistent in fruit. ***Corolla*** white, or bluish, tube cylindrical, limb bilabiate, with a large or small boss on the upper side of the corolla, enclosing the anthers. ***Stamens*** 4, didynamous, or 2. ***Nectary*** cup-shaped or an annular ring. ***Fruit*** a straight capsule; erect, cylindrical, estipitate, ribbed, or pendulous, club-shaped, stipitate and not ribbed.

Content. ***Didissandra*** C.B.Clarke, ***Tribounia*** D.J.Middleton (Middleton & Möller 2012).

3.2.9. Subtribe **Loxocarpinae** A.DC., in A.P. & A.L.P.P. de Candolle, Prodr. 9: 277 (1 January 1845) (''*Loxocarpeae*''). TYPE: *Loxocarpus* R.Br. (1839).

= Trisepalinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Trisepalum* C.B.Clarke (1883).

Content [genera that have been recently synonymized in square brackets]. ***Boea*** Comm. ex Lam., ***Damrongia*** Kerr (re-established in Weber et al. 2011a), ***Emarhendia*** R.Kiew, A.Weber & B.L.Burtt, ***Kaisupeea*** B.L.Burtt, ***Loxocarpus*** R.Br. (included in *Henckelia* by Weber & Burtt 1997c, but restored on grounds of molecular data by Weber et al. 2011a & Middleton et al. 2013), ***Orchadocarpa*** Ridl., ***Ornithoboea*** Parish ex C.B.Clarke, ***Paraboea*** (C.B.Clarke) Ridl. (recently redefined and expanded by Puglisi et al. 2011 to include *Phylloboea* Benth. and *Trisepalum* C.B.Clarke), [*Phylloboea* Benth., see *Paraboea*], ***Rhabdothamnopsis*** Hemsl., ***Senyumia*** R.Kiew, A.Weber & B.L.Burtt, ***Somrania*** D.J.Middleton (Middleton & Triboun 2012), ***Spelaeanthus*** R.Kiew, A.Weber & B.L.Burtt, ***Streptocarpus*** p.p. (the Asian species), [*Trisepalum* C.B.Clarke., see *Paraboea*].

3.2.10. Subtribe **Didymocarpinae** G.Don, Gen. Hist. 4: 644, 658 (1837–8 April 1838) (''*Didymocarpeae*''). TYPE: *Didymocarpus* Wall. (1819), nom. cons.

= Trichosporinae G.Don, Gen. Hist. 4: 644, 658 (1837–8 April 1838). (''*Trichosporeae*''). TYPE: *Trichosporum* D.Don (1822), nom. rejic. = ***Aeschynanthus*** Jack (1823), nom. cons.

= Cyrtandrinae G.Don, Gen. Hist. 4: 644, 660 (1837–8 April 1838) (''*Cyrtandreae*''). TYPE: *Cyrtandra* J.R.Forst. & G.Forst. (1775).

= Liebigiinae A.DC., in A.P. & A.L.P.P. de Candolle, Prodr. 9: 259 (1. January 1845) (''*Liebigieae*''). TYPE: *Liebigia* Endl. (1841).

= Aeschynanthinae A.DC. in A.P. & A.L.P.P. de Candolle, Prodr. 9: 260 (1 January 1845) (''*Aeschynantheae*''). TYPE: *Aeschynanthus* Jack (1823), nom. cons.

= Lysionotinae A.DC., in A.P. & A.L.P.P. de Candolle, Prodr. 9: 263 (1 January 1845) (''*Lysionoteae*''). TYPE: *Lysionotus* D.Don (1822).

= Oreocharidinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893). TYPE: *Oreocharis* Benth. (1876).

= Conandrinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143 (May 1893), 145 (1894). TYPE: *Conandron* Sieb. & Zucc. (1843).

= Roettlerinae Fritsch, in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 143, 146 (May 1893), nom. illeg. TYPE: *Roettlera* Vahl (1804), nom. illeg.

Notes. Three subtribal names were published by G. Don in the same publication (Don 1838). We have chosen Didymocarpinae due to the fact that most of the genera listed below belonged to the traditional tribe Didymocarpeae.

Content [genera that have been recently synonymized in square brackets]. ***Aeschynanthus*** Jack (incl. *Micraeschynanthus* Ridl., Middleton 2007), ***Agalmyla*** Blume, ***Allocheilos*** W.T.Wang, ***Allostigma*** W.T.Wang, [*Ancylostemon* Craib, see *Oreocharis*], ***Anna*** Pellegr., [*Bournea* Oliv., see *Oreocharis*], ***Briggsia*** Craib p.p. – excl. type (see *Oreocharis*), ***Briggsiopsis*** K.Y.Pan, [*Calcareoboea* C.Y.Wu, see *Petrocodon*], ***Cathayanthe*** Chun, [*Chirita* Buch Ham. ex D.Don, see *Henckelia*], [*Chiritopsis* W.T.Wang, see *Primulina*], ***Codonoboea*** Ridl. (recently re-established by Kiew & Lim 2011, based on Möller et al. 2009 & Weber et al. 2011a), ***Conandron*** Sieb. & Zucc., ***Cyrtandra*** J.R.Forst. & G.Forst., [*Dayaoshania* W.T.Wang, see *Oreocharis*], [*Deinocheilos* W.T.Wang, see *Oreocharis*], ***Deinostigma*** W.T.Wang, ***Didymocarpus*** Wall., ***Didymostigma*** W.T.Wang, [*Dolicholoma* D.Fang & W.T.Wang, see *Petrocodon*], ***Gyrocheilos*** W.T.Wang, ***Hemiboea*** C.B.Clarke (incl. *Metabriggsia* W.T.Wang, Weber et al. 2011b), [*Hemiboeopsis* W.T.Wang, see *Henckelia*], ***Henckelia*** Spreng. (recently redefined by Weber et al. 2011a to include *Chirita* Buch Ham. ex D.Don, p.p., *Hemiboeopsis* W.T.Wang), ***Hexatheca*** C.B.Clarke, [*Isometrum* Craib, see *Oreocharis*], [*Lagarosolen* W.T.Wang, see *Petrocodon*], ***Liebigia*** Endl. (re-established by Weber et al. 2011a), ***Loxostigma*** C.B.Clarke, ***Lysionotus*** D.Don, [*Metabriggsia* W.T.Wang, see *Hemiboea*], ***Metapetrocosmea*** W.T.Wang, [*Micraeschynanthus* Ridl, see *Aeschynanthus*], ***Microchirita*** (C.B.Clarke) Yin Z.Wang (recently established by Wang et al. 2011 & Weber et al. 2011a), [*Opithandra* B.L.Burtt, see *Oreocharis*], ***Oreocharis*** Benth. (recently redefined and expanded by Möller et al. 2011b to include *Ancylostemon* Craib, *Bournea* Oliv., *Briggsia* Craib p.p. – incl. type, *Dayaoshania* W.T.Wang, *Deinocheilos* W.T.Wang, *Isometrum* Craib, *Opithandra* B.L.Burtt, *Paraisometrum* W.T.Wang, *Thamnocharis* W.T.Wang, and *Tremacron* Craib), [*Paraisometrum* W.T.Wang, see *Oreocharis*], [*Paralagarosolen* Y.G.Wei, see *Petrocodon*], ***Petrocodon*** Hance (redefined and expanded by Wang et al. 2011 and Weber et al. 2011c to include *Calcareoboea* C.Y.Wu, *Didymocarpus*

Wall. p.p. – excl. type, *Dolicholoma* D.Fang & W.T.Wang, *Lagarosolen* W.T.Wang, *Paralagarosolen* Y.G.Wei, *Tengia* Chun and *Wentsaiboea* D.Fang & D.H.Qin, p.p. – excl. type, see *Primulina*), ***Petrocosmea*** Oliv., ***Primulina*** Hance (recently redefined by Wang et al. 2011 and Weber et al. 2011c: expanded to include *Chirita* sect. *Gibbosaccus* C.B.Clarke, *Chiritopsis* W.T.Wang and *Wentsaiboea* D.Fang & D.H.Qin p.p. – incl. type, see *Petrocodon*), ***Pseudochirita*** W.T.Wang, ***Raphiocarpus*** Chun, ***Ridleyandra*** A.Weber & B.L.Burtt, ***Sepikea*** Schltr. (tentatively included in *Cyrtandra* J.R.Forst. & G.Forst. by Burtt 2001), [*Tengia* Chun, see *Petrocodon*], [*Thamnocharis* W.T.Wang, see *Oreocharis*], [*Tremacron* Craib, see *Oreocharis*], [*Wentsaiboea* D.Fang & D.H.Qin, see *Petrocodon* and *Primulina*].

CONCLUSIONS AND OUTLOOK

One of the most outstanding aspects of the present classification is the inclusion of *Sanango* and its accommodation as a distinct (third) subfamily. This inclusion not only widens the morphological concept of Gesneriaceae (especially with regard to ovary and fruit structure), but also influences the assessment of the age of the family. For traditional Gesneriaceae, Perret et al. (2013) suggest a late Paleocene/Eocene age between ~58 mya (stem age) and 45 mya (crown age). The inclusion of *Sanango* shifts the origin of the family into the Paleocene, between ~63 mya (stem) and ~58 mya (crown).

The classification of subfam. Gesnerioideae is well-established when compared to the Didymocarpoideae. Currently, there is still some disagreement between earlier and new work (e.g., Woo et al. 2011, Perret et al. 2013) as to whether Napeantheae is closely related to the Beslerieae. The strongly supported phylogenetic placement of *Titanotrichum* from the Old World as more closely related to the New World Genseriaceae (Wang et al. 2004a, Perret et al. 2013), is also remarkable and is recognized in the monospecific tribe Titanotricheae.

In the Didymocarpoideae, the division into two tribes is well supported, both by molecular data and morphological characters. The relationships between the genera of Epithemateae are well understood (Weber 1975 to 1982, Mayer et al. 2003). Molecular data are still lacking for the Chinese genus *Gyrogyne*, which is known only from the type collection and may be extinct (Wang 2003).

The most problematic group of Didymocarpoideae and Gesneriaceae as a whole is the tribe Trichosporeae because of its large size and the weakly supported backbone structure in phylogenetic trees (Möller et al. 2009, 2011b). The present subdivision into ten subtribes (with several of them being monogeneric, but Didymocarpinae remaining as a bulky, ill-understood group) is a first attempt to classify the tribe into natural entities. Some progress has been made in the recognition of groups falling on basal lineages (the monogeneric or small groups of Jerdoniinae, Corallodiscinae, Ramondinae, Tetraphyllinae, Leptoboeinae, an alliance collectively referred to as ''Basal Asiatic genera'' in Weber 2004a). Characteristic features are the tetrandrous flowers and the non-ornamented seeds. The monogeneric Litostigminae, with diandrous flowers form a link both to the African and Madagascan Streptocarpinae (having also diandrous flowers) and the ''Advanced Asiatic and Malesian genera'' *sensu* Weber (2004a). The justification of the Didissandrinae, which perhaps form the base of the Advanced Asiatic genera is in need of further studies. The subtribe Loxocarpinae is supported, but needs further morphology-based studies. It comprises all Asiatic genera and species with *Streptocarpus*-like, twisted fruits. However, it includes also genera and species (e.g., *Paraboea* p.p.) with straight fruits, including the type genus, *Loxocarpus*, which in itself is perhaps not monophyletic (e.g., Weber et al. 2011a). It is still not entirely clear that the twisted-fruited taxa are plesiomorphic within the subtribe. The Loxocarpinae are separated from the African and Madagascan genera only by the straight-fruited Didissandrinae. This suggests that twisted fruits have originated twice or twisted fruits originated once in the Loxocarpinae + Streptocarpinae (including the Didissandrinae), and have been lost in the Didissandrinae (and certain genera and species in both subtribes). Further sample and data-expanded cladistic-based studies are needed to better understand the evolution and diversification of fruit morphology in these groups. The least understood group of the Trichosporeae is subtribe Didymocarpinae. This is the largest and most recently diversified group. All members are straight-fruited, but the divergent morphological variation is remarakable because it includes genera defined by appendaged seeds (traditional tribe Trichosporeae), indehiscent fruits (previous tribe Cyrtandreae), and capsular fruits with unappendaged seeds (Didymocarpeae).

The available molecular data and the new classification also challenge a new interpretation of the historical phytogeography of the Gesneriaceae. In brief, it can be taken for granted that the family is of New World (rather than, as the ''Cathaysian hypothesis'' suggests, of Asiatic) origin (Perret et al. 2013). Invasion from there was apparently in several waves, the last (of at least two) concerned the Coronanthereae. This clearly involved the Antarctic region (''Austral-Antarctic track''), perhaps 35 My ago. There are arguments that the first dispersal of Gesneriaceae from the New World to the Paleotropics, giving rise to the split Gesnerioideae/Didymocarpoideae, was during the late Paleocene/Early Eocene (ca. 45 mya; Perret et al. 2013). During this period the climate was sufficiently warm to allow floristic exchanges between South America, the Antarctica and Australasia (Morley 2003). From there, the plants reached South and South East Asia by means and at times that are currently not fully understood. However, invasion was apparently in all directions, including Africa and Madagascar, the European subcontinent, and the continents and islands of the Pacific. Migration to the north (present-day northern China and Japan) was limited by climatic restrictions. Invasion of the European subcontinet was early, simply by migration on land. Africa was reached secondarily as well, either from Europe or from Asia via Madagascar (as suggested by the considerable morphological diversity found here, see Hilliard & Burtt 1971). The position of *Titanotrichum* in the Gesnerioideae suggests a further invasion event from the New World. Without having relatives further south, it is difficult to explain its present distribution in S Japan, SE China and Taiwan. A different migration route than via Antarctica and the Indian plate (e.g., via Beringia) is a possibility, but migration must have occurred much earlier (and under much warmer climatic conditions) than in the Pleistocene during the presence of the Beringia landbridge. Another hypothesis was proposed by Perret et al. (2013: 12), namely, ''that *Titanotrichum* arose in Taiwan and China following long-distance dispersal from South America during the Miocene. This long-distance dispersal scenario may be supported by the evolution of a dispersal mechanism based on the production of tiny and numerous bulbils in the inflorescence.'' Future work will show which scenario is the more likely one.

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LITERATURE CITED

Albach, D.C., H.M. Meudt, and B. Oxelman. 2005. Piecing together the ''new'' Plantaginaceae. Amer. J. Bot. 92: 297–315.

APG III (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161: 105–121.

Arnott, G.A.W. 1832. Botany. Pp. 30–145 *in* M. Napier, ed. Encyclopedia Britannica, ed. 7, 5. Edinburgh.

Barringer, K. 1984. *Cubitanthus*, a new genus of Gesneriaceae from Brazil. J. Arnold Arbor. 65: 145–147.

———. 1986. Reinstatement of the genus *Sanango* Bunting & Duke (Buddlejaceae). Phytologia 59: 363–364.

Beaufort-Murphy, H.T. 1983. The seed-surface morphology of the Gesneriaceae, utilizing the scanning electric microscope and a new system for diagnosing seed morphology. Selbyana 6: 220–422.

Bentham, G. 1876. Gesneriaceae. Pp. 990–1025 *in* G. Bentham and J.D. Hooker, eds. Genera plantarum 2(2). Reeve & Co., Williams & Norgate, London.

Brown, R. 1839. On Cyrtandreae. [Part reprint from J.J. Bennett and R.R. Brown eds. Plantae Javanicae Rariores, part 1, incl. t. 24, mostly preprint from part 2: 105–122 and t. 25].

Bunting, G.S. and J.A. Duke. 1961. *Sanango*: new Amazonian genus of Loganiaceae. Ann. Missouri Bot. Gard. 48: 269–274.

Burnett, G.T. 1835. Outlines of Botany. J. Churchill, London.

Burtt, B.L. 1954. Studies in the Gesneriaceae of the Old World. I. General introduction. Notes Roy. Bot. Gard. Edinburgh 21: 185–192.

———. 1963. 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.

———. 1970. Studies in the Gesneriaceae of the Old World. XXXI. Some aspects of functional evolution. Notes Roy. Bot. Gard. Edinburgh 30: 1–10.

———. 1977. Classification above the genus, as exemplified by Gesneriaceae, with parallels from other groups. Plant Syst. Evol., Suppl. I: 97–109.

———. 1997. Old World Gesneriaceae. V. Suprageneric names. Edinburgh J. Bot. 54: 85–90.

———. 2001. A survey of the genus *Cyrtandra* (Gesneriaceae). Phytomorphology 51(3/4) (Golden Jubilee Issue 2001): 393–404.

Burtt, B.L., and H. Wiehler. 1995. Classification of the family Gesneriaceae. Gesneriana 1: 1–4.

Candolle, A.P. 1816. Essai sur les propriétés médicales des plantes, comparées avec leurs formes extérieures et leur classification naturelle. Crochard, Paris.

———. 1839. Gesneriaceae. In A.P. de Candolle, ed. Prodromus regni vegetabilis. VII. Treuttel & Wrtz, Paris.

———. 1845. Cyrtandraceae. In A. de Candolle, ed. Prodromus regni vegetabilis. IX. Fortin, Masson & Soc., Paris.

Chamisso, A., and D. Schlechtendal. 1828. De plantis expeditione speculatoria Romanzoffiana observatis. Linnaea 3: 1–367.

Christenhusz, M.J.M. 2012. On African violets and Cape primroses – towards a monophyletic *Streptocarpus* (Gesneriaceae). Phytotaxa 46: 3–9.

Clark, J.L., D.A. Neill, J.A. Gruhn, A. Weber, and T. Katan. 2010. *Shuaria* (Gesneriaceae), an arborescent new genus from the Cordillera del Cóndor and Amazonian Ecuador. Syst. Bot. 35: 662–674.

Clarke, C.B. 1883. Cyrtandreae. *In* A. and C. de Candolle, eds. Monographiae phanerogamarum 5/1. Masson, Paris.

Crocker, C.W. 1860. Notes on the germination of certain species of Cyrtandreae. J. Proc. Linn. Soc. Bot. 5: 65–66.

Cronquist, A. 1968. The evolution and classification of flowering plants. Ed. 1. New York Botanical Press, New York.

———. 1988. The evolution and classification of flowering plants. Ed. 2. New York Botanical Press, New York.

Darbyshire, I. 2006. Gesneriaceae. Pp. 1–75 *in* H.J. Beentje and S.A. Ghazanfar, eds. Flora of tropical East Africa. Roy. Bot. Garden Kew, London.

Dickison, W.C. 1994. A re-examination of *Sanango racemosum*. 2. Vegetative and floral anatomy. Taxon 43: 601–618.

Don, D. 1822. Descriptions of two new genera of Nepaul plants. Edinburgh Phil. J. 7: 82–87.

Don, G. 1838. A general system of gardening and botany: containing a complete enumeration and description of all plants hitherto known. (A general history of the dichlamydeous plants). Vol. IV. Rivington & Co., London.

Endlicher, S. 1839. Genera plantarum secundum ordines naturales disposita. Part 9. F. Beck, Wien.

Fischer, E. 2004. Scrophulariaceae. Pp. 333–432 *in* K. Kubitzki and J.W. Kadereit, eds. The families and genera of vascular plants. Vol. 7. Flowering plants. Dicotyledons. Lamiales (except Acanthaceae, including Avicenniaceae). Springer, Berlin/Heidelberg.

Fritsch, K. 1893–1894. Gesneriaceae. Pp. 133–144 (1893) and 145–185 (1894) *in* A. Engler and K. Prantl, eds. Die Natürlichen Pflanzenfamilien IV/3B. W. Engelmann, Leipzig.

———. 1904. Die Keimpflanzen der Gesneriaceen mit besonderer Berücksichtigung von *Streptocarpus*, nebst vergleichender Studien über die Morphologie dieser Familie. G. Fischer, Jena.

———. 1908. Gesneriaceae. Pp. 317–319 *in* A. Engler and K. Prantl, eds. Die Natürlichen Pflanzenfamilien, Ergänzungshefte II, Nachträge III zu den Teilen II–IV für die Jahre 1899 bis 1904. W. Engelmann, Leipzig.

Greuter, W., J. McNeill, R. Barrie, H.-M. Burdet, V. Demoulin, T.S. Filguerias, D.H. Nicolson, P.C. Silva, J.E. Skog, P. Trehane, N.J. Turland, and D.L. Hawksworth (eds & compilers). 2000. International Code of Botanical Nomenclature (''Saint Louis Code'') adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July–August 1999. Regnum vegetabile 138. Koeltz Scientific Books, Königstein, Germany.

Hallier, H. 1903. Vorläufiger Entwurf des natürlichen (phylogenetischen) Systems der Blütenpflanzen. Bull. Herb. Boiss. 11, ser. 2, vol. 3.

Hanstein, J. 1854. Die Gesneraceen des Königlichen Herbariums und die Gärten zu Berlin nebst Beobachtungen über die Familie im Ganzen. I. Abschnitt: Allgemeine Übersicht. Linnaea 26: 145–216.

Hill, A. 1938. The monocotylous seedlings of certain dicotyledons. With special reference to the Gesneriaceae. Ann. Bot. 2(1): 127–143.

Hilliard, O.M., and B.L. Burtt. 1971. *Streptocarpus*. An African plant study. Univ. of Natal Press, Pietermaritzburg.

Ivanina, L.I. 1965a. Primencenie karpologisheskogo metoda sistematke semeistva Gesneriaceae. [Application of the carpological method to the taxonomy of the family Gesneriaceae]. Botanicheski Zhurnal 50: 29–43 (in Russian).

———. 1965b. Application of the carpological method to the taxonomy of Gesneriaceae. Notes Roy. Bot. Gard. Edinburgh 26: 383–402.

———. 1967. Semeijstvo gesnerievykh: karpologicheskij obzor. The family Gesneriaceae (The Carpological Review). Komarov Botanical Institute, Leningrad (in Russian).

Jack, W. 1823. On Cyrtandraceae, a new natural order of plants. Trans. Linn. Soc. 14: 23–44.

Jensen, S.R. 1994. A re-examination of *Sanango racemosum*. 3. Chemotaxonomy. Taxon 43: 619–623.

Jong, K. 1970. Developmental aspects of vegetative morphology of *Streptocarpus*. PhD Thesis, University of Edinburgh, Edinburgh.

Jussieu, A.-L. 1804. Troisième mémoire. Sur les caractères généraux des familles, tirés des graines, et confirmés ou rectifiés par les observations de Gaertner. Ann. Mus. Natl. d''Hist. Nat. 5: 417–429.

Kiew, R. and R. Lim. 2011. Names and new combinations for Peninsular Malaysian species of *Codonoboea* (Gesneriaceae). Garden's Bull. Singapore 62: 253–275.

Leeuwenberg, A.J.M. 1958. The Gesneriaceae of Guiana. Acta Bot. Neerl. 7: 291–444.

———. 1960. *Tylopsacas* nom. nov. Taxon 9: 220–221.

Leeuwenberg, A.J.M, and P.W. Leenhouts. 1980. *Peltanthera*, *Sanango*. Pp. 61–64 *in* P. Hiepko and H. Melchior, eds. Die natürlichen Pflanzenfamilien. Ed. 2, Vol. 28b I Angiospermae: Ordnung Gentianales Fam. Loganiceae. Chapter 2. Taxonomy. Duncker & Humblot, Berlin.

Maldonado, S., M. Otegui, and J.P. Bozini. 1998. Embryological studies in *Sanango racemosum* (Loganiaceae s.l.). Nord. J. Bot. 18: 599–609.

Mantegazza, R., M. Möller, C.J. Harrison, S. Fior, C. De Luca, and A. Spada. 2007. Anisocotyly and meristem initiation in an unorthodox plant, *Streptocarpus rexii* (Gesneriaceae). Planta 225: 653–663.

Marloth, R. 1899. *Charadrophila* Marloth nov. gen. Bot. Jahrb. Syst. 26: 358–359.

Martén-Rodríguez, S., C.B. Fenster, I. Agnarsson, L.E. Skog, and E.A. Zimmer. 2010. Evolutionary breakdown of pollination specialization in a Caribbean plant radiation. New Phytol. 188: 403–417.

Martius, C.F.P. 1829. Nova Genera species plantarum. Vol. 3: 72. Lindauer: Munich.

Mayer, V., M. Möller, M. Perret, and A. Weber. 2003. Phylogenetic position and generic differentiation of Epithemateae (Gesneriaceae) inferred from plastid DNA sequence data. Amer. J. Bot. 90: 319–327.

McNeill, J., F.R. Barrie, W.R. Buck, V. Demoulin, W. Greuter, D.L. Hawksworth, P.S. Herendeen, S. Knapp, K. Marhold, J. Prado, W.F. Prud'Homme Van Reine, G.F. Smith, J.H. Wiersema, and N.J. Turland. 2012. International Code of Nomenclature for algae, fungi, and plants (''Melbourne Code''), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011 (electronic ed.), Bratislava: International Association for Plant Taxonomy, http://www.iapt-taxon.org/nomen/main.php, retrieved 2012-12-20.

Middleton, D.J. 2007. A revision of *Aeschynanthus* (Gesneriaceae) in Thailand. Edinburgh J. Bot. 64: 363–429.

Middleton, D.J., and M. Möller. 2012. *Tribounia*, a new genus of Gesneriaceae from Thailand. Taxon 61(6): 1286–1295.

Middleton, D.J., and P. Triboun. 2012. *Somrania*, a new genus of Gesneriaceae from Thailand. Thai Forest Bull. (Bot.) 40: 9–13.

Middleton, D.J., A. Weber, A., T.L. Yao, S. Sontag, and M. Möller. 2013. The current status of the species hitherto assigned to *Henckelia* (Gesneriaceae). Edinburgh J. Bot. 70: 1–20.

Möller, M., and Q.C.B. Cronk. 1997a. Origin and relationships of *Saintpaulia* H.Wendl. (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. Amer. J. Bot. 84: 956–965.

———. 1997b. Phylogeny and disjunct distribution: evolution of *Saintpaulia* (Gesneriaceae). Proc. Roy. Soc. London, ser. B, 264: 1827–1836.

Möller, M., M. Clokie, P. Cubas, and Q.C.B. Cronk. 1999. Integrating molecular phylogenies and developmental genetics: a Gesneriaceae case study. Pp. 375–402 *in* P.M. Hollingsworth, R.M. Bateman, and R.J. Gornall, eds. Molecular Systematics and Plant Evolution. Taylor & Francis, London.

Möller, M., and Q.C.B. Cronk. 2001a. Evolution of morphological novelty: a phylogenetic analysis of growth patterns in *Streptocarpus* (Gesneriaceae). Evolution 55: 918–929.

———. 2001b. Phylogenetic studies in *Streptocarpus* (Gesneriaceae): reconstruction of biogeographic history and distribution patterns. Syst. Geogr. Plants 71: 545–555.

Möller, M. and J.L. Clark. 2013. The state of molecular studies in the family Gesneriaceae: a review. Pp. 95–125 *in* J.R. Clark, ed. Proceedings of the World Gesneriad Research Conference 2010. Selbyana 31: 65–253.

Möller, M., M. Pullan, M. Kiehn, and L.E. Skog. 2002 onw. RBGE WebCyte – Gesneriaceae cytology database. http://elmer.rbge.org.uk/webcyte/webcyte.php.

Möller, M., M. Pfosser, C.G. Jang, V. Mayer, A. Clark, M.L. Hollingsworth, Z.J.M. Barfuß, M. Kiehn, and A. Weber. 2009. A preliminary phylogeny of the didymocarpoid Gesneriaceae based on three molecular data sets: incongruence with available tribal classifications. Amer. J. Bot. 96: 989–1010.

Möller, M., A. Forrest, Y.-G. Wei, and A. Weber. 2011a. A molecular phylogenetic assessment of the advanced Asiatic and Malesian didymocarpoid Gesneriaceae with focus on non-monophyletic and monotypic genera. Plant Syst. Evol. 292: 223–248.

Möller, M., D. Middleton, K. Nishii, Y.-G. Wei, S. Sontag, and A. Weber. 2011b. A new delineation for *Oreocharis* incorporating an additional ten genera of Chinese Gesneriaceae. Phytotaxa 23: 1–36.

Morley, R.J. 2003. Interplate dispersal paths for megathermal angiosperms. Persp. Plant Ecol. Evol. Syst. 6: 5–20.

Nishii, K., A. Kuwabara, and T. Nagata. 2004. Characterization of anisocotylous leaf formation in *Streptocarpus wendlandii* (Gesneriaceae): significance of plant growth regulators. Ann. Bot. 94: 457–467.

Norman, E.M. 1994. A re-examination of *Sanango racemosum*. 1. Morphology and distribution. Taxon 43: 591–600.

———. 2000. Buddlejaceae. Flora Neotropica. Monogr. 81: 1–225. New York Bot. Garden, New York.

Olmstead, R.G., C.W. de Pamphilis, A.D. Wolfe, N.D. Young, W.J. Elisons, and P.A. Reeves. 2001. Disintegration of the Scrophlariaceae. Amer. J. Bot. 88: 348–361.

Oxelman, B., P. Kornhall, R.G. Olmstead, and B. Bremer. 2005. Further disintegration of Scrophulariaceae. Taxon 54: 411–425.

Perret, M., A. Chautems, R. Spichiger, G. Kite, and V. Savolainen. 2003. Systematics and evolution of tribe Sinningieae (Gesneriaceae): evidence from phylogenetic analyses of six plastid DNA regions and nuclear *ncpGS*. Amer. J. Bot. 90: 445–460.

Perret, M., A. Chautems, A.O. de Araujo, and N. Salamin. 2013. Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. Bot. J. Linn. Soc. 171: 61–79.

Puglisi, C., D.J. Middleton, P. Triboun, and M. Möller. 2011. New insights into the relationships between *Paraboea*, *Trisepalum* and *Phylloboea* (Gesneriaceae) and their taxonomic consequences. Taxon 60: 1693–1702.

Rauschert, S. 1982. Nomina nova generica et combinationes novae spermatophytorum et pteridophytorum. Taxon 31: 554–563.

Reveal, J.L. 1995. Subfamily names in an 1832 preprint of an article on botany for the seventh edition of the Encyclopaedia Britannica. Taxon 44: 589–596.

———. 1995 onw. (edition 2011). Indices Nominum supragenericorum plantarum vascularium. Alphabetical listing by genera of validly published suprageneric names. Entries as of 17 February 2011 or later. http://www.plantsystematics.org/reveal/pbio/fam/allspgnames.html

———. 2010. A checklist of familial and suprafamilial names for extant vascular plants. Phytotaxa 6: 1–402.

———. 2012. An outline of a classificatin scheme for extant flowering plants. Phytoneuron 37: 1–221.

Ridley, H.N. 1923. Flora of the Malay Peninsula. Crown Agents for the Colonies, London.

Roalson, E.H., J.K. Boggan, L.E. Skog, and E.A. Zimmer. 2005a. Untangling Gloxinieae (Gesneriaceae). I. Phylogenetic patterns and generic boundaries inferred from nuclear, chloroplast, and morphological cladistic data sets. Taxon 54: 389–410.

Roalson, E.H., J.K. Boggan, and L.E. Skog. 2005b. Reorganization of tribal and generic boundaries in the Gloxinieae (Gesneriaceae: Gesnerioideae) and the description of a new tribe in the Gesnerioideae, Sphaerorrhizeae. Selbyana 25: 225–238.

Ruiz, R. and J. Pav6n. 1794. Florae Peruvianae et Chilensis prodromus. De 6rden del Rey, Madrid.

Ruiz, R. and J. Pavon. 1798. Systema vegetabilium florae Peruvianae et Chilensis. Gabrielis de Sancha, Madrid.

Schäferhoff, B., A. Fleischmann, E. Fischer, D.C. Albach, T. Borsch, G. Heubl, and K.F. Müller. 2010. Towards resolving Lamiales relationships: insights from rapidly evolving chloroplast sequences. BMC Evol. Biol. 10: 352.

Singh, V., and D.K. Jain. 1978. Floral anatomy and systematic position of *Cyrtandromoea*. Proc. Indian Acad. Sci. 87: 71–74.

Skog, L.E. 1976. A study of the tribe Gesnerieae, with a revision of *Gesneria* (Gesneriaceae: Gesnerioideae). Smithson. Contr. Bot. 29: 1–182.

Skog, L.E., and L.P. Kvist. 2002. Novae Gesneriaceae Neotropicarum IX: *Cremospermopsis*, a new genus from Colombia. Novon 12: 262–269.

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

Smith, J.F., and J.L. Clark. 2013. Molecular phylogenetic analyses reveal undiscovered monospecific genera in Episcieae (Gesneriaceae). Syst. Bot. 38: 451–463.

Solereder, H. 1909. Über die Gattung *Rehmannia*. Ber. Deutsch. Bot. Ges. 27: 390–404.

Soltis, D.E., S.A. Smith, N. Cellinese, K.J. Wurdack, D.C. Tank, S.F. Brockington, N.F. Refulio-Rodriguez, J.B. Walker, M.J. Moore, B.S. Carlsward, C.D. Bell, M. Latvis, S. Crawley, C. Black, D. Diouf, Z.X. Xi, C.A. Rushworth, M.A. Gitzendanner, K.J. Sytsma, Y.Q. Qiu, K.W. Hilu, C.C. Davis, M.J. Sanderson, R.G. Olmstead, W.S. Judd, M.J. Donoghue, and P.S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. Amer. J. Bot. 98: 704–730.

Stearn, W.T. 1967. Meisner's Plantarum Vascularium Genera. J. Soc. Bibliogr. Nat. Hist. 4: 291–297.

Tank, D.C., P. Beardsley, S. Kelchner, and R.G. Olmstead. 2006. Review of the systematics of Scrophulariaceae s.l. and their current disposition. L.A.S. Johnson Review no. 7. Australian Syst. Bot. 19: 289–307.

Wang, C.N., M. Möller, and Q.C.B. Cronk. 2004a. Phylogenetic position of *Titanotrichum oldhamii* (Gesneriaceae) inferred from four different gene regions. Syst. Bot. 29: 407–418.

———. 2004b. Altered expression of *GFLO*, the Gesneriaceae homologue of *FLORICAULA/LEAFY*, is associated with the transition to bulbil formation in *Titanotrichum oldhamii*. Dev. Genes Evol. 214: 122–127.

———. 2004c. Aspects of sexual failure in the reproductive processes of a rare bulbiliferous plant, *Titanotrichum oldhamii* (Gesneriaceae), in subtropical Asia. Sex. Plant Reprod. 17: 23–31.

———. 2004d. Population genetic structure of *Titanotrichum oldhamii* (Gesneriaceae), a subtropical bulbiliferous plant with mixed sexual and asexual reproduction. Ann. Bot. 93: 201–209.

Wang, W.T., K.Y. Pan, Z.Y. Zhanh, and Z.Y. Li. 1990. Flora reipublicae popularis sinicae. Vol. 69. Science Press, Beijing.

Wang,Y.Z. 2003. Ovary structure of the genus *Gyrogyne* (Gesneriaceae, Epithemateae). Austral. Syst. Bot. 16: 629–632.

Wang, Y.Z., Z.Y. Li, K.Y. Pan, and X.H. Zou. 2002. Pattern and significance of seedling development in *Titanotrichum oldhamii* (Gesneriaceae). Acta Bot. Sinica 44: 903–907.

Wang, Y.Z., R.B. Mao, Y. Liu, J.M. Li, Y. Dong, Z.Y. Li, and J.F. Smith. 2011. Phylogenetic reconstruction of *Chirita* and allies (Gesneriaceae) with taxonomic treatments. J. Syst. Evol. 49: 50–64.

Weber, A. 1971. Zur Morphologie des Gynoeceums der Gesneriaceen. Österr. Bot. Zeitschr. 119: 234–305.

———. 1973. Die Struktur der paarblütigen Partialfloreszenzen der Gesneriaceen und bestimmter Scrophulariaceen. Beitr. Biol. Pflanzen 49: 429–460.

———. 1975a. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). I. Die Sproß- und Infloreszenzorganisation von *Monophyllaea* R.Br. Bot. Jahrb. Syst. 95: 174–207.

———. 1975b. The cristate inflorescence of *Chirita* sect. *Microchirita* (Gesneriaceae). Notes Roy. Bot. Gard. Edinburgh 34: 221–230.

———. 1976a. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). II. Morphologie, Anatomie und Ontogenese der Blüte von *Monophyllaea* R.Br. Bot. Jahrb. Syst. 95: 435–454.

———. 1976b. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). III. *Whytockia* als morphologische und phylogenetische Ausgangsform von *Monophyllaea*. Beitr. Biol. Pflanzen 52: 183–205.

———. 1976c. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). IV. Wuchsform, Infloreszenz- und Blütenmorphologie von *Epithema*. Plant Syst. Evol. 126: 287–322.

———. 1977a. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). V. Revision der Gattung *Loxonia* (Gesneriaceae). Plant Syst. Evol. 127: 201–216.

———. 1977b. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). VI. Morphologie und Verwandtschaftsbeziehungen von *Loxonia* und *Stauranthera*. Flora 166: 153–175.

———. 1978a. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). VII. Sproß-, Infloreszenz- und Blütenbau von *Rhynchoglossum*. Bot. Jahrb. Syst. 99: 1–47.

———. 1978b. Beiträge zur Morphologie und Systematik der Klugieae und Loxonieae (Gesneriaceae). VIII. Ein typologischer Vergleich zwischen *Rhynchoglossum klugioides* und *Loxonia*. Linzer Biol. Beitr. 10: 217–228.

———. 1982a. Contributions to the morphology and systematics of Klugieae and Loxonieae (Gesneriaceae). IX. The genus *Whytockia*. Notes Roy. Bot. Gard. Edinburgh 40: 113–121.

———. 1982b. Evolution and radiation of the pair-flowered cyme in Gesneriaceae. Australian Syst. Bot. Soc. Newsl. 30: 23–41.

———. 1988. Contributions to the morphology and systematics of Klugieae - Loxonieae (Gesneriaceae), X. Development, interpretation, and phylogeny of the inflorescence of *Epithema*. Beitr. Biol. Pflanzen 63: 431–451.

———. 1989. Family position and conjectural affinities of *Charadrophila capensis* Marloth. Bot. Jahrb. Syst. 111: 87–119.

———. 1995. Developmental aspects of the pair-flowered cyme of Gesneriaceae. Gesneriana 1: 18–28.

———. 2004a. Gesneriaceae. Pp. 63–158 *in* K. Kubitzki and J.W. Kadereit, eds. The families and genera of vascular plants. Vol. 7. Flowering plants. Dicotyledons. Lamiales (except Acanthaceae, including Avicenniaceae). Springer, Berlin/Heidelberg.

———. 2004b. Gesneriaceae and Scrophulariaceae: Robert Brown and now. Telopea 10: 543–571.

———. 2013. Pair-flowered cymes in the Lamiales: structure, distribution, and origin. Ann. Bot. 112: 1577–1595.

Weber, A. and B.L. Burtt. 1997a [publ. 1998]. *Didissandra*: redefinition and partition of an artificial genus of Gesneriaceae. Beitr. Biol. Pflanzen 70: 153–177.

———. 1997b [publ. 1998]. Revision of the genus *Didissandra*. Beitr. Biol. Pflanzen 70: 191–223.

———. 1997c [publ. 1998]. Remodelling of *Didymocarpus* and associated genera (Gesneriaceae). Beitr. Biol. Pflanzen 70: 293–363.

Weber, A., D.J. Middleton, A.L. Forrest, R. Kiew, C.L. Lim, A. Rafidah, T.L. Yao, S. Sontag, P. Triboun, Y.-G. Wei, T.-L. Yao, and M. Möller. 2011a. Molecular systematics and remodelling of *Chirita* and associated genera (Gesneriaceae). Taxon 60: 767–790.

Weber, A., Y.-G. Wei, S. Sontag, and M. Möller. 2011b. Inclusion of *Metabriggsia* into *Hemiboea* (Gesneriaceae). Phytotaxa 23: 37–48.

Weber, A., Y.-G. Wei, C. Puglisi, F. Wen, V. Mayer, and M. Möller. 2011c. A new definition of the genus *Petrocodon* (Gesneriaceae). Phytotaxa 23: 49–67.

Wei, Y.-G., F. Wen, W.-H. Chen, Y.-M. Shui, and M. Möller. 2010. *Litostigma*, a new genus from China: a morphological link between basal and derived Didymocarpoid Gesneriaceae. Edinburgh J. Bot. 67: 161–184.

Wiehler, H. 1976. A report on the classification of *Achimenes*, *Eucodonia*, *Gloxinia*, *Goyazia*, and *Anetanthus* (Gesneriaceae). Selbyana 1: 374–403.

———. 1983. A synopsis of Neotropical Gesneriaceae. Selbyana 6: 1–219.

———. 1994. A re-examination of *Sanango racemosum*. 4. Its new systematic position in Gesneriaceae. Taxon 43: 625–632.

Wight, R. 1848. Icones plantarum Indiae orientalis. Vol. 4, part 2. J.R.I. Wood, Madras, India.

———. 1850. Gesneraceae. Pp. 180–182, pl. 159–159b *in* R. Wight, ed. Illustrations of Indian botany. Vol. 2. P.R. Hunt, Madras, India.

Wilson, C.L. 1974a. Floral anatomy in Gesneriaceae. I. Cyrtandroideae. Bot. Gaz. (Crawfordsville) 135: 247–256.

———. 1974b. Floral anatomy in Gesneriaceae. II. Gesnerioideae. Bot. Gaz. (Crawfordsville) 135: 256–268.

Wolfe, A.D., C.P. Randle, S.L. Datwyler, J.J. Morawetz, N. Arguedas, and J. Diaz. 2006. Phylogeny, taxonomic affinities, and biogeography of *Penstemon* (Plantaginaceae) based on ITS and cpDNA sequence data. Amer. J. Bot. 93: 1699–1713.

Woo, V.L., M.M. Funke, J.F. Smith, P.J. Lockhart, and J.P. Garnock-Jones. 2011. New World origins of Southwest Pacific Gesneriaceae: multipe movements across and within the South Pacific. J. Plant Sci. 172: 434–457.

Xia, Z., Y.-Z. Wang, and J.F. Smith. 2009. Familial placement and relations of *Rehmannia* and *Triaenophora* (Scrophulariaceae s.l.) inferred from five gene regions. Amer. J. Bot. 96: 519–530.

Zollinger, H. 1854–1855. Systematisches Verzeichnis der im Indischen Archipel in den Jahren 1842 bis 1848 gesammelten, sowie der aus Japan empfangenen Pflanzen. E. Kiesling, Zürich.