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Keys to the infrafamilial taxa and genera of Gesneriaceae

Weber A.[1*], Middleton D.J.[2], Clark J.L.[3] & M. Möller[4]

[1] Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria.
[2] Herbarium, Singapore Botanic Gardens, National Parks Board, 1 Cluny Road, 259569 Singapore.
[3] Science Department, Lawrenceville School, Lawrenceville, New Jersey – 08648, USA.
[4] Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, Scotland, UK.
[*]E-mail: anton.weber@univie.ac.at

Abstract: In recent years significant advances have been made in the taxonomy and classification of the Gesneriaceae, mostly based on molecular-phylogenetic research. This has led to major changes in the classification of the family and the establishment, reestablishment, recircumscription and synonymisation of many genera. Consequently, the treatment of the Gesneriaceae that was published in Kubitzki's *Families and Genera of Vascular Plants*, with brief descriptions and keys to all genera as well as the formal and informal groups of Gesneriaceae then recognised, has become rather out-of-date in a relatively short period of time. In 2013, a new formal classification of Gesneriaceae was published, with inclusion of *Sanango* in a third subfamily, reclassification of Gesnerioideae and *de-novo*-classification of Didymocarpoideae. In the present paper an effort is made to survey all of the taxonomic changes in the Gesneriaceae since the publication of these two treatments. This is done at all levels of the taxonomic hierarchy down to the genus level and new keys for the identification of the current infrafamilial taxa and genera are provided. As the taxonomic concepts of most genera are based on a combination of vegetative, floral and fruit characters, having fertile material is still a prerequisite for unambiguous identification. A glossary is provided to explain botanical terms largely specific to Gesneriaceae taxonomy.

Keywords: Classification, Gesneriaceae, Keys to subfamilies, tribes, subtribes and genera.

Introduction

The most recent treatment of the Gesneriaceae to include information on morphology, anatomy, phytochemistry, floral biology, seed dispersal *etc*., as well as brief descriptions of all genera then recognised, was in Kubitzki's *Families and Genera of Vascular Plants* (FGVP) (Weber, 2004). Since then, significant progress has been made on our understanding of relationships within the family, mainly due to the use of molecular data and phylogenetic analyses, which in turn has led to major changes in the delimitation of genera and the circumscription of infrafamilial taxa. The earliest deployment of molecular data in phylogenetic reconstruction in the Gesneriaceae was exploratory and did not result in changes in classification (*e.g*., Möller & Cronk, 1997, 2001; Smith & Carroll, 1997; Smith *et al*., 1997). The first major Old World group to be included in a molecular-phylogenetic analysis was the Epithemateae (Mayer *et al*., 2003) which is a group that has long been recognised (see Weber *et al*., 2013). From 2009 onwards, the focus of publications was on the much more speciose and complex group of Old World "Didymocarpoid Gesneriaceae" *sensu* Weber (2004) (*e.g*., Möller *et al*., 2009, 2011a; Weber *et al*., 2011a). These, and further studies on New World Gesneriaceae (*e.g*., Clark & Zimmer, 2003; Clark, 2005; Roalson *et al*., 2005a,b; Clark *et al*., 2006; Roalson & Clark, 2006; Smith & Clark, 2013), laid the foundation for a new formal classification of the family (Weber *et al*., 2013) and the establishment, reestablishment, redefinition and synonymisation of many genera. The classification published in Weber *et al.* (2013) forms the basis of the present paper and is graphically summarised in Fig. 1. Changes in the number and delimitation of genera that have taken place since 2004 are summarised in Table 1.

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In the FGVP treatment (Weber, 2004), keys to all formal and informal groups and all genera then recognised were provided. For the New World Gesneriaceae ("Gesnerioid Gesneriaceae") keys to the genera were given for each of the tribes then recognised. For the Old World "Didymocarpoid Gesneriaceae" (now subfamily Didymocarpoideae, tribes Epithemateae and Trichosporeae), the genera that are now in Trichosporeae were split into geographical keys. Due to insights from molecular data and the very many changes in generic delimitation, those keys are now largely outdated and in need of revision, particularly for the Old World Gesneriaceae.

The keys provided here are artificial, meaning that they are intended to enable identification of the infrafamilial taxa and genera, but do not reflect phylogenetic affinities. As the taxonomic concepts of most genera are based on a combination of vegetative, floral and fruit characters, having fertile material is still a prerequisite for unambiguous identification.

In many cases, an accurate identification of a taxon can only be done based on an understanding of characters described with specialist terminology. Therefore, we have compiled a short glossary for a better understanding of terms that are uncommon and/or specific to Gesneriaceae, such as "chiritoid stigma" or "plagiocarpic capsule." Users are encouraged to forward errors and/or inaccuracies in the keys to the authors. It is our intention to periodically update and improve this treatment in response to future changes in classification.

The keys cover all genera that were recognised and published by March 2020. However, we recognise that further research will continue to provide new data that will inevitably lead to a reconsideration of current delimitations. The high rate of species discovery in the family, particularly in Asia, with hitherto unknown morphological diversity, will continually test generic delimitations. The present paper is thus merely a snapshot of the Gesneriaceae at this moment in time.

Technical notes on the keys

(1) Bracketed keys are presented in a hierarchical manner. Firstly there is a key to the subfamilies, then the tribes are keyed out within their subfamilies, and then subtribes (when relevant) within their tribes. The genera are keyed out within their tribes or subtribes.

(2) In a number of places, infrafamilial taxa and genera, particularly heterogeneous ones, appear in a key or subkey in more than one place or in more than one subkey, and are then indicated as such with *p.p.* (*pro parte*), or *p.p.maj.* (*pro parte majore*). Where appropriate, the name(s) of the genus/genera is/are given for each lead, *e.g.*, subtribe Gesneriinae *p.p.* (*Gesneria*, *Rhytidophyllum*).

(3) If a genus is monospecific, the name of the only species is given in brackets, *e.g.*, *Fieldia* (only *F. australis*).

(4) In order to provide a bridge between current genus concepts and those of the FGVP treatment (Weber, 2004), reference is made to the synonymised genera both in Table 1 and in the keys, *e.g.*, *Gloxinia p.p.* (the former monospecific genus *Koellikeria*).

(5) The authorships of the infrafamilial taxa (subfamilies, tribes, subtribes) are given in the notes preceding each key. No authorships of the generic or specific names are given in the keys and in the text. These can be found in Weber *et al.* (2013) and/or in Table 1 for the genera that have been described as new or have undergone substantial changes or synonymisation since 2013.

(6) In the keys the distribution of a genus is given when the genus is narrowly endemic or when geographical information offers an additional contrast in the keys.

(7) Botanical terms explained in the Glossary are marked by a superscript G (*e.g.*, plagiocarpic^{G}). These terms are either more or less specific to Gesneriaceae taxonomy or seldom used in keys or plant descriptions outside the family. Explanations for widely used terms can be found, for instance,

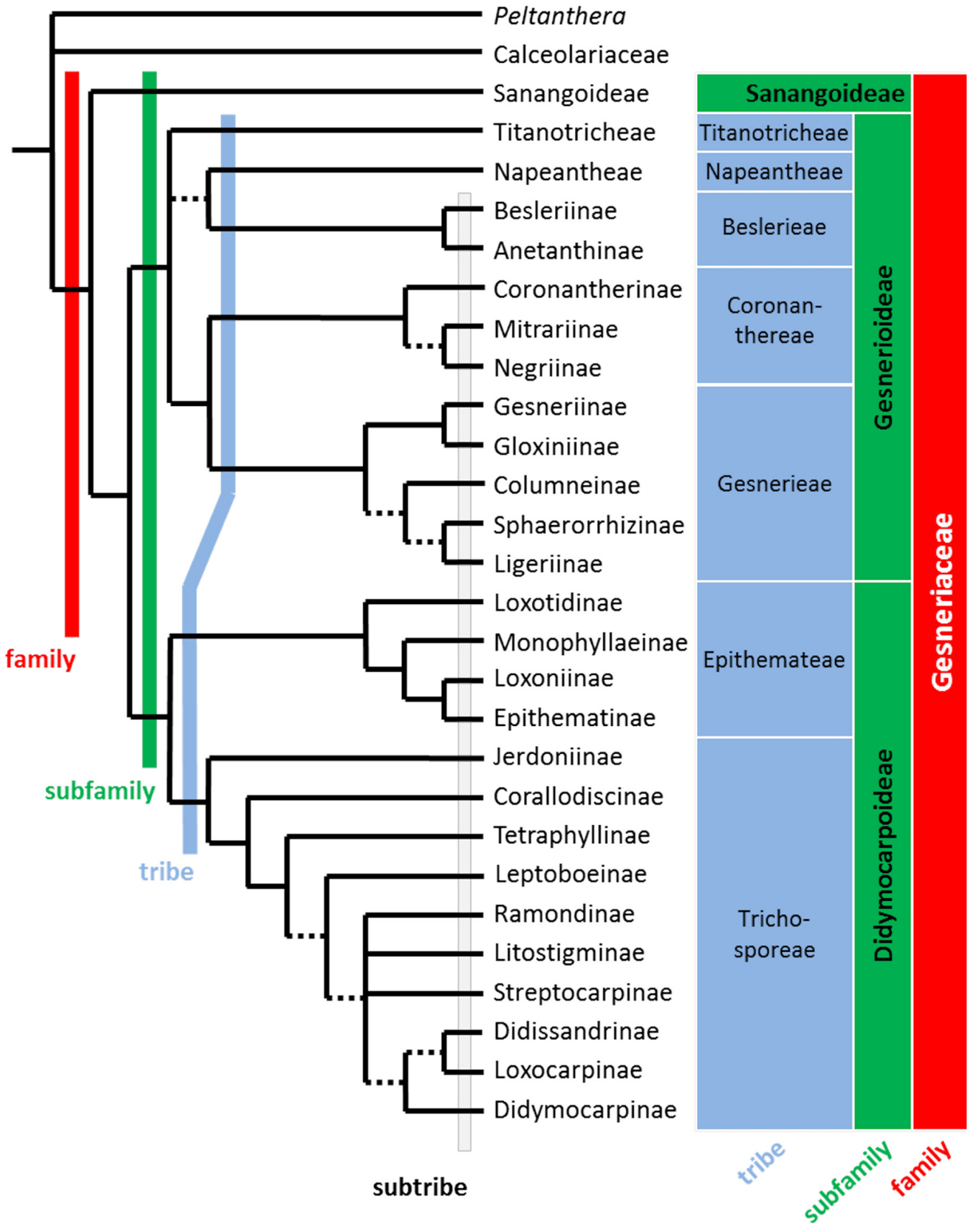

Fig. 1. Diagrammatic representation of the formal classification of Weber *et al.* (2013) [reproduced from *Selbyana* 31(2): 75, f.1. 2013; with permission].

Table 1. Survey of genera of Gesneriaceae that have been described as new, reestablished, redefined (bold), synonymised (in square brackets) or removed from the family (in square brackets and bold) since the treatment of Weber (2004).

Genus	Original publication	Systematic position (subfamily/tribe/ subtribe according to Weber *et al*., 2013)	Kind of change	References
[*Acanthonema* Hook.f.]	Curtis' Bot. Mag. 88: t. 5339 (1862)	Didymocarpeae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Nishii *et al*. (2015)
Alloplectus Mart.	Nov. Gen. Sp. Pl. 3: 53, t. 223 (1829)	Gesnerioideae Gesnerieae Columneinae	Redefined and species number reduced from >140 species to 5	Clark (2005); Clark *et al*. (2006)
Amalophyllon Brandegee	Univ. Calif. Publ. Bot. 6(4): 63 (1914)	Gesnerioideae Gesnerieae Gloxiniinae	Reestablished and segregated from *Phinaea,* most species of that genus now in *Amalophyllon*	Boggan *et al*. (2008)
[*Ancylostemon* Craib]	Notes Roy. Bot. Gard. Edinburgh 11: 233, 257 (1919)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al*. (2011b)
[*Anodiscus* Benth.]	in Benth. & Hook. f., Gen. Pl. 2: 998 (1876)	Gesnerioideae-Gesnerieae Gloxiniinae	Synonymised under redefined *Gloxinia*	Roalson *et al*. (2005a,b)
Billolivia D.J.Middleton	D.J.Middleton *et al*., Phytotaxa 161(4): 255 (2014)	Didymocarpoideae Trichosporeae Didymocarpinae	New genus, based on new collections	Middleton *et al*. (2014)
Boea Comm. *ex* Lam.	Encycl. Méth. 1: 401, fr. Béole (1783), ed. nouv. Padua 1: 396 (1785 ["1784"])	Didymocarpoideae Trichosporeae Loxocarpinae	Redefined; some species moved to *Damrongia* and *Dorcoceras*	Puglisi *et al*. (2016)
[*Bournea* Oliv.]	in Hook.f., Icon. Pl. 23 (Ser. 4): t. 2254 (1893)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al*. (2011b)
[*Briggsia* Craib]	Notes Roy. Bot. Gard. Edinburgh 11: 236 (1919)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis* (most species, including type), but some species placed in *Loxostigma*, and 2 spp. in the new genus *Glabrella,* see there	Möller *et al*. (2011b, 2014); Chen *et al*. (2014)
[**Brookea** Benth.]	in Benth. & Hook. f., Gen. Pl. 2: 939 (1876)	Plantaginaceae (?)	Listed under "Excluded genera" in Weber (2004); see discussion in Weber *et al*. (2013: p. 69): ending with "there is no specific evidence that it [*Brookea*] does belong to Gesneriaceae." No recent morphological or molecular-phylogenetic studies are available	See discussion under "Problematic and excluded genera" in this paper
[*Calcareoboea* C.Y.Wu ex H.W.Li]	Acta Bot. Yunnan. 4: 241 (1982)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Petrocodon*	Wang Y.Z. *et al*. (2011); Weber *et al*. (2011b)
[*Capanea* Decne. ex Planch.]	Fl. Serres Jard. Eur. 5: t. 499-500 (1849)	Gesnerioideae Gesnerieae Gloxiniinae	Synonymised under *Kohleria*	Roalson *et al*. (2005a)

Centrosolenia Benth.	London J. Bot. 5: 362 (1846)	Gesnerioideae Gesnerieae Columneinae	Reestablished after segregation from *Paradrymonia*	Mora & Clark (2016)
[**Charadrophila** Marloth]	Bot. Jahrb. Syst. 26: 358 (1899)	Stilbaceae	Listed under "Excluded Genera" in Weber (2004); now generally referred to Stilbaceae	Kornhall (2004); Oxelman *et al*. (2005); Tank *et al*. (2006)
Chautemsia A.O.Araujo & V.C.Souza	in A.O. Araujo *et al*., Taxon 59(1): 207 (2010)	Gesnerioideae Gesnerieae Gloxiniinae	New genus with unusual character combination; DNA data (from 5 loci) place the genus as sister to a clade comprising *Mandirola* and *Goyazia*, or, alternatively, in a clade with *Gloxiniopsis*.	Araujo *et al*. (2010)
Chayamaritia D.J.Middleton & Mich.Möller	in D.J.Middleton *et al*., Plant Syst. Evol. 301(7): 1961 (2015) [e-published]	Didymocarpoideae Trichosporeae Didymocarpinae	New genus, type species formerly in *Chirita* and *Henckelia*	Middleton *et al*. (2015)
[*Chirita* Buch.-Ham. ex D.Don]	Edinburgh Phil. J. 7: 83 (1822)	Didymocarpoideae Trichosporeae Didymocarpinae	Most species of *Chirita* sect. *Chirita* synonymised under *Henckelia*, most remaining species of the section moved to the resurrected genus *Damrongia*; *Chirita* sect. *Liebigia* and *Chirita* sect. *Microchirita* raised to generic rank; *Chirita* sect. *Gibbosaccus* synonymised under the hitherto monospecific genus *Primulina*. In consequence, *Chirita* is no longer recognised as a genus	Wang Y.Z. *et al*. (2011); Weber *et al*. (2011a)
[*Chiritopsis* W.T.Wang]	Bull. Bot. Res., Harbin, 1: 21 (21 July 1981), trans. & reimp. in Contr. New York Bot. Gard. 16: 5, 25 (1986)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Primulina*	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011a)
Christopheria J.F.Smith & J.L.Clark	Syst. Bot. 38(2): 453 (2013)	Gesnerioideae Gesnerieae Columneinae	New genus (the only species formerly in *Paradrymonia*)	Smith & Clark (2013)
Codonanthe (Mart.) Hanst.	Linnaea 26: 209 (1854 ["1853"])	Gesnerioideae Gesnerieae Columneinae	Redefined, no longer containing ant nest epiphytes	Chautems & Perret (2013)
Codonanthopsis Mansf.	Repert. Spec. Nov. Regni Veg. 36: 120 (1934)	Gesnerioideae Gesnerieae Columneinae	Redefined, containing ant nest epiphytes	Chautems & Perret (2013)
Codonoboea Ridl.	Fl. Malay Penins. 2: 533 (1923)	Didymocarpoideae Trichosporeae Didymocarpinae	Reestablished and greatly expanded. Formal transfer of the species of Peninsular Malaysia by Kiew & Lim (2011); formal transfer of species outside of Peninsular Malaysia by Middleton *et al*. (2013)	Weber *et al.* (2011a)
[*Colpogyne* B.L. Burtt]	in Humbert & Leroy, Fl. Madagascar et Comores 180: 150 (1971)	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Nishii *et al*. (2015)

Crantzia Scop.	Introd. 173 (1777)	Gesnerioideae Gesnerieae Columneinae	Reestablished and redefined after segregation from *Alloplectus*	Clark (2005); Clark *et al*. (2006)
[**Cubitanthus** Barringer]	J. Arnold Arbor. 65: 145 (1984)	Linderniaceae	Listed under "Genera of uncertain familial affiliation" in Weber (2004); now recognised as a member of Linderniaceae	Rahmanzadeh *et al*. (2005); Perret *et al.* (2012)
[**Cyrtandromoea** Zoll.]	Syst. Verz. Ind. Arch. 3: 55, 58 (1858)	Phrymaceae	Listed under "Excluded genera" in Weber (2004); now placed in Phrymaceae	Luna *et al*. (2019); Liu *et al.* (2020)
Damrongia Kerr ex Craib	Bull. Misc. Inform. Kew 1918: 364 (1918)	Didymocarpoideae Trichosporeae Loxocarpinae	Reestablished to include several species formerly placed in *Chirita* sect. *Chirita*; inclusion of the Asian species described under *Streptocarpus*	Triboun & Middleton (2010); Puglisi *et al.* (2016); Puglisi & Middleton (2017c)
[*Dayaoshania* W.T.Wang]	Acta Phytotax. Sin. 21: 319 (1983)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
[*Deinocheilos* W.T.Wang]	Guihaia 6: 1 (1986)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
Deinostigma W.T.Wang & Z.Y.Li	Acta Phytotax. Sin. 30(4): 356 (1992)	Didymocarpoideae Trichosporeae Didymocarpinae	Redefined and expanded (genus formerly monospecific); transfer of 5 species from *Primulina*	Möller *et al.* (2016, 2020)
Didymocarpus Wall.	Edinburgh Phil. J. 1: 378 (1819)	Didymocarpoideae Trichosporeae Didymocarpinae	Some species moved to *Petrocodon*	Weber *et al.* (2011b)
[*Dolicholoma* D.Fang & W.T.Wang]	Bull. Bot. Res., Harbin 1: 18 (1983)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Petrocodon*	Weber *et al.* (2011b)
Dorcoceras Bunge	Enum. Pl. China Bor.: 128 (1833 ["1832"])	Didymocarpoideae Trichosporeae Loxocarpinae	Reestablished after segregation from *Boea*; Thai species revised	Puglisi *et al.* (2016); Puglisi & Middleton (2017a)
Glabrella Mich.Möller & W.H.Chen	in Möller *et al*., Gard. Bull. Singapore 66(2): 198 (2014)	Didymocarpoideae Trichosporeae Didymocarpinae	New genus, established to accommodate 2 species of former *Briggsia*	Möller *et al*. (2014)
Glossoloma Hanst.	Linnaea 26: 191, 208, 209 (1854 ["1853"])	Gesnerioideae Gesnerieae Columneinae	Reestablished after segregation from *Alloplectus*	Clark (2005, 2009); Clark *et al*. (2006)
Gloxinella (H.E.Moore) Roalson & Boggan	Selbyana 25(2): 227 (2005)	Gesnerioideae Gesnerieae Gloxiniinae	New genus created by raising *Kohleria* sect. *Gloxinella* to generic rank; monospecific with *G. lindeniana*	Roalson *et al*. (2005a,b)
Gloxinia L'Hér.	in Aiton, Hort. Kew. 2: 331 (1789)	Gesnerioideae Gesnerieae Gloxiniinae	Redefined and reduced from 15 to 3 species: type species (*G. maculata*, *nom. illeg*. = *G. perennis*) + inclusion of the two monospecific genera *Koellikeria* and *Anodiscus*, see there	Roalson *et al.* (2005a,b)
Gloxiniopsis Roalson & Boggan	Selbyana 25(2): 228 (2005)	Gesnerioideae Gesnerieae Gloxiniinae	New genus, segregate of redefined *Gloxinia*; monospecific with *G. racemosa*	Roalson *et al.* (2005a,b)
Hemiboea C.B.Clarke	in Hooker's Icon. Pl. 18: t. 1798 (1888)	Didymocarpoideae Trichosporeae Didymocarpinae	Expanded to include *Metabriggsia*	Weber *et al.* (2011c)

[*Hemiboeopsis* W.T.Wang]	Acta Bot. Yunnan. 6: 397 (1984)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Henckelia*	Weber *et al.* (2011a)
Henckelia Spreng.	Anleit. 2: 402 (1817)	Didymocarpoideae Trichosporeae Didymocarpinae	Redefined to include *Chiritap.p.* and *Hemiboeopsis*, and to exclude the reestablished genera *Codonoboea* and *Loxocarpus*	Weber *et al.* (2011a); Middleton *et al.* (2013)
[*Hovanella* A.Weber & B.L.Burtt]	Beitr. Biol. Pflanzen 70 (1998 ["1997"])	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Nishii *et al.* (2015)
[*Isometrum* Craib]	Notes Roy. Bot. Gard. Edinburgh 11: 250 (1919)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
Jerdonia Wight	Icon. Pl. Ind. Orient. 4(2): 10, t. 1352 (1848)	Didymocarpoideae Trichosporeae Jerdoniinae	*Jerdonia* was placed under "Genera of uncertain familial affinities" in Weber (2004). See notes under Trichosporeae subtribe Jerdoniinae	Möller *et al.* (2009); Weber *et al.* (2013)
[*Koellikeria* Regel]	Index Sem. Hort. Bot. Turic. 4 (1847); Flora 31: 249 (1848)	Gesnerioideae–Gesnerieae Gloxiniinae	Synonymised under redefined *Gloxinia*	Roalson *et al.* (2005a,b)
Kohleria Regel	Index Sem. Hort. Bot. Turic. 4 (1847); Flora 31: 249 (1848)	Gesnerioideae–Gesnerieae Gloxiniinae	Slightly redefined by the inclusion of *Campanea* and the raising of *Kohleria* sect. *Gloxinella* to generic rank (see there)	Roalson *et al.* (2005a,b)
[*Lagarosolen* W.T.Wang]	Acta Bot. Yunnan. 6: 11, fig. 1 (1984)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Petrocodon*	Weber *et al.* (2011b)
Lesia J.L. Clark & J.F.Smith	Syst. Bot. 38(2): 456 (2013)	Gesnerioideae Gesnerieae Columneinae	New genus, established after segregation of *Alloplectus*; sister to a clade comprising *Codonanthe*, *Codonanthopsis* and *Nematanthus*	Smith & Clark (2013)
Liebigia Endl.	Gen. Pl. [Endlicher] 1407 (1841)	Didymocarpoideae Trichosporeae Didymocarpinae	Reestablished to include species formerly placed in *Chirita*	Weber *et al.* (2011a)
[*Linnaeopsis* Engl.]	Bot. Jahrb. Syst. 28: 482 (1900)	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus*, together with all other African and Madagascan genera of Trichosporeae	Nishii *et al.* (2015)
Litostigma Y.G.Wei, F.Wen & Mich.Möller	in Wei *et al.*, Edinburgh J. Bot. 67(1): 178 (2010)	Didymocarpoideae Trichosporeae Litostigminae	New genus, based on new collections	Wei *et al.* (2010)
Loxocarpus R.Br.	Cyrtandreae 120 (1839)	Didymocarpoideae Trichosporeae Loxocarpinae	Reestablished after segregation from *Henckelia sensu* Weber & Burtt (1998, "1997") and Weber (2004)	Middleton *et al.* (2013) based on the results published in Weber *et al.* (2011a)
Loxostigma C.B.Clarke	in A.DC. & C.DC., Monogr. Phan. 5(1): 59 (1883)	Didymocarpoideae Trichosporeae Didymocarpinae	Expanded to accommodate some species of the now defunct genus *Briggsia*	Möller *et al.* (2014)

Mandirola Decne.	Rev. Hort. 20, ser. 3, 2: 468 (1848)	Gesnerioideae Gesnerieae Gloxiniinae	Reestablished to accommodate three Brazilian species formerly placed in *Gloxinia*; the three species are very similar to *Achimenes*, and were once included in that genus. However, *Mandirola* is phylogenetically closer to *Goyazia* than to *Gloxinia* or *Achimenes*	Roalson *et al*. (2005a,b); Luna *et al*. (2020)
[*Metabriggsia* W.T.Wang]	Guihaia 3: 1 (1983)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Hemiboea*	Weber *et al.* (2011c)
[*Micraeschynanthus* Ridl.]	Fl. Malay Penins. 5, Suppl.: 324 (1925)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Aeschynanthus*	Middleton (2007)
Microchirita (C.B.Clarke) Yin Z.Wang	J. Syst. Evol. 49(1): 59 (2011)	Didymocarpoideae Trichosporeae Didymocarpinae	New genus after raising *Chirita* sect. *Microchirita* to generic rank	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011a); Puglisi & Middleton (2017d)
Middletonia C.Puglisi	in Puglisi *et al*., Taxon 65(2): 286 (2016)	Didymocarpoideae Trichosporeae Loxocarpinae	New genus (segregate of *Paraboea*)	Puglisi *et al.* (2016); Puglisi & Middleton (2017b)
Neomortonia Wiehler	Selbyana 1: 17 (1975)	Gesnerioideae-Gesnerieae Columneinae	Redefined by segregation of *Pachycaulos*	Smith & Clark (2013)
[*Nodonema* B.L.Burtt]	Bull. Mus. Natl. Hist. Natl. Paris, 4e sér., 3, sect B, Adansonia 4: 415 (1982 ["1981"])	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Nishii *et al.* (2015)
[*Opithandra* B.L.Burtt]	Baileya 4: 162 (1956)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
Oreocharis Benth.	in Benth. & Hook.f., Gen. Pl. 2: 1021 (1876)	Didymocarpoideae Trichosporeae Didymocarpinae	Redefined and considerably expanded through addition of species from 10 genera and through newly described species	Möller *et al.* (2011b, 2014); Middleton *et al*. (2013); Möller (2019); Wen *et al*. (2019)
Pachycaulos J.L.Clark & J.F.Smith	Syst. Bot. 38(2): 458 (2013)	Gesnerioideae Gesnerieae Columneinae	New monospecific genus, established for *P. nummularia*, a species formerly ascribed to various genera such as *Alloplectus*, *Columnea*, *Hypocyrta*, and *Neomortonia*	Smith & Clark (2013)
Pagothyra (Leeuwenb.) J.F.Smith & J.L.Clark	Syst. Bot. 38(2): 461 (2013)	Gesnerioideae Gesnerieae Columneinae	New monospecific genus created by the raising of *Episcia* sect. *Pagothyra* to generic rank	Smith & Clark (2013)

Paraboea (C.B.Clarke) Ridl.	J. Straits Branch Roy. Asiatic Soc. 44: 63 (1905)	Didymocarpoideae Trichosporeae Loxocarpinae	Redefined by inclusion of *Phylloboea* and *Trisepalum*; segregation of *Middletonia*, and description of more than 20 new species	Puglisi *et al.* (2011, 2016) Triboun & Middleton (2012)
Paradrymonia Hanst.	Linnaea 26: 180, 207 (1854 ["1853"])	Gesnerioideae Gesnerioideae Gesnerieae Columneinae	Redefined after segregation and reestablishment of *Trichodrymonia* and *Centrosolenia*	Mora & Clark (2016)
[*Paraisometrum* W.T.Wang]	in Weitzman *et al*., Novon 7: 431 (1998 ["1997"])	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
[*Paralagarosolen* Y.G.Wei]	Acta Phytotax. Sin. 42(6): 528 (2004)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Petrocodon*	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011b)
Petrocodon Hance	J. Bot. 21: 167 (1883)	Didymocarpoideae Trichosporeae Didymocarpinae	Redefined and expanded to include *Calcareoboea*, *Dolicholoma*, *Paralagarosolen*, *Tengia*, and some species of *Didymocarpus*	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011b)
Phinaea Benth.	in Benth. & Hook.f., Gen. Pl. 2: 997 (1876)	Gesnerioideae Gesnerieae Gloxiniinae	Reduced to 3 species, the large remainder transferred to the reestablished genus *Amalophyllon*	Boggan *et al.* (2008)
[*Phylloboea* Benth.]	in Benth. & Hook.f., Gen. Pl. 2: 102 (1876) ("*Phyllobaea*")	Didymocarpoideae Trichosporeae Loxocarpinae	Synonymised under *Paraboea*	Puglisi *et al*. (2011)
Primulina Hance	J. Bot. 21: 169 (1883)	Didymocarpoideae Trichosporeae Didymocarpinae	Redefined and enormously expanded by the inclusion of species hitherto placed in *Chirita* sect. *Gibbosaccus*, *Chiritopsis* and *Wentsaiboea p.p.* and many newly described species	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011a); Möller (2019); Wen *et al*. (2019)
Rachunia D.J.Middleton & C.Puglisi	Nordic J. Bot. 36(11)-e01992: 4 (2018)	Didymocarpoideae Trichosporeae Didymocarpinae	New genus, based on new collections	Middleton *et al.* (2018)
[**Rehmannia** Libosch. ex Fisch. & C.A.Mey.]	Index Sem. Hort. Petrop. 1: 36 (1835)	Orobanchaceae	Listed under "Excluded genera" in Weber (2014); early molecular-phylogenetic studies suggested a placement in Phrymaceae; Xia *et al*. (2009) found that *Rehmannia* + *Triaeophora* are sister to *Lindenbergia* + Orobanchaceae. Finally, APG IV enlarged Orobanchaceae to include *Rehmannia*, *Triaenophora* and *Lindenbergia* as the only non-parasitic members of the family.	Xia *et al.* (2009); APG IV (2016)
[*Saintpaulia* H.Wendl.]	Gartenflora, 42: 321, t. 1391 (1893)	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Christenhusz (2012); Nishii *et al.* (2015)
Sanango Bunting & Duke	Ann. Missouri Bot. Gard. 48: 270 (1961)	Sanangoideae	Included in Gesneriaceae and accommodated in a third subfamily, Sanangoideae	Weber *et al.* (2013)

[*Schizoboea* (Fritsch) B.L.Burtt]	Notes Roy. Bot. Gard. Edinburgh 33: 266 (1974)	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus*	Nishii *et al.* (2015)
Seemannia Regel	Gartenflora 4: 183 (1855)	Gesnerioideae Gesnerieae Gloxiniinae	Reestablished after segregation from the redefined genus *Gloxinia* (see there)	(2005a,b)
Shuaria D.A.Neill & J.L.Clark	in Clark *et al*., Syst. Bot. 35(3): 670 (2010)	Gesnerioideae Beslerieae Anetanthinae	New genus, based on new collections	Clark *et al.* (2010)
Somrania D.J. Middleton	in Middleton & Triboun, Thai Forest Bull., Bot. 40: 9–13 (2012)	Didymocarpoideae Trichosporeae Loxocarpinae	New genus, based on new collections	Middleton & Triboun (2012, 2013)
Sphaerorrhiza Roalson & Boggan	Selbyana 25(2): 236 (2005)	Gesnerioideae Gesnerieae Sphaerorrhizinae	New genus, segregate of redefined *Gloxinia*	Roalson *et al.* (2005a)
Streptocarpus Lindl.	Bot. Reg. 14, t. 1173 (1828)	Didymocarpoideae Trichosporeae Streptocarpinae	Redefined and expanded to include all (9) genera of Trichosporeae from Africa and Madagascar; Asian species moved to *Damrongia*	Nishii *et al.* (2015); Puglisi *et al.* (2016); revision of Thai *Damrongia* spp.: Puglisi & Middleton (2017c)
[*Tengia* Chun]	Sunyatsenia 6: 279 (1946)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Petrocodon*	Wang Y.Z. *et al.* (2011); Weber *et al.* (2011b)
[*Tetraphylloides* Doweld]	Phytotaxa 329(3): 293 (2017)	Didymocarpoideae Trichosporeae Tetraphyllinae	New name for *Tetraphyllum* (because thought to be an earlier homonym of a fossil angiosperm), but now considered superfluous	Doweld (2017); Bertling (2019)
[*Thamnocharis* W.T.Wang]	Acta Phytotax. Sin. 19: 485 (1981)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
Titanotrichum Soler.	Ber. Deutsch. Bot. Ges. 27: 393 (1909)	Gesnerioideae Titanotricheae	Included in Gesneriaceae-Gesnerioideae and accommodated in the monospecific tribe Titanotricheae	Wang C.N. *et al.* (2004b); Perret *et al*. (2012); Weber *et al.* (2013)
[*Trachystigma* C.B.Clarke]	in A.DC. & C.DC., Monogr. Phan. 5/1: 131 (1883)	Didymocarpoideae Trichosporeae Streptocarpinae	Synonymised under *Streptocarpus,* together with all other African and Madagascan genera of Trichosporeae	Nishii *et al.*(2015)
[*Tremacron* Craib]	Notes Roy. Bot. Gard. Edinburgh 10: 217 (1918)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Oreocharis*	Möller *et al.* (2011b)
Tribounia Middleton	in Middleton & Möller, Taxon 61(6): 1287–1288 (2012)	Didymocarpoideae Trichosporeae Didissandrinae	New genus, type species formerly in *Didymocarpus*	Middleton & Möller (2012)
Trichodrymonia Oerst.	Centralamer. Gesner. 38 (1858)	Gesnerioideae Gesnerieae Columneinae	Reestablished after segregation from *Paradrymonia*	Mora & Clark (2016)
[*Trisepalum* C.B.Clarke]	in A.DC. & C.DC., Monogr. Phan. 5: 138 (1883)	Didymocarpoideaee Trichosporeae Loxocarpinae	Synonymised under *Paraboea*	Puglisi *et al.* (2011)
[*Wentsaiboea* D.Fang & D.H.Qin]	Acta Phytotax. Sin. 42(6): 533 (2004)	Didymocarpoideae Trichosporeae Didymocarpinae	Synonymised under *Primulina*, although some species transferred to *Petrocodon*	Weber *et al.* (2011a,b)

in the online "Glossary of botanical terms" (https://en.wikipedia.org/wiki/Glossary_of_botanical_terms). As a first-class botanical dictionary William Stearn's classic *Botanical Latin* (last ed. 2004) is highly recommended.

Key to the subfamilies of Gesneriaceae

1. Hard-wood trees, to 15 m tall; inflorescences terminal bracteose[G] thyrses; corolla white, tubular, slightly curved and slightly gibbous near base, limb subactinomorphic, lobes triangular, pointed; nectary cup-shaped, large, ± as high as the globose ovary and enveloping it almost completely; fruit a bony capsule .... **1. Subfam. Sanangoideae** (only genus and species *Sanango racemosum*)

1. Predominantly perennial herbs, rarely trees, shrubs, subshrubs, lianas, climbers or annual herbs, if tree-like, wood soft to brittle; inflorescences emerging from the axils of the foliage leaves or bracts, rarely a terminal bracteose[G] thyrse or bracteose raceme; corolla of variable colour and shape, usually distinctly zygomorphic, rarely subactinomorphic or actinomorphic, lobes variable; nectary of various forms, if cup-shaped, surrounding the ovary base only; fruit not a bony capsule 2

2. Seedlings isocotylous[G]; fertile stamens 4, rarely 5 or 2 (only *Sarmienta*); nectary annular or divided into 1–5 separate glands, or nectary inconspicuous and adnate to the base of the ovary (tribe Coronanthereae), or lacking; ovary superior, semi-inferior or inferior; fruit a dry (never twisted) or fleshy capsule or an indehiscent (never sclerocarpous) or rupturing berry; Neotropics and southern hemisphere (temperate S America, SW Pacific, Australia), one monospecific tribe (Titanotricheae in E Asia) ..... **2. Subfam. Gesnerioideae**

2. Seedlings usually anisocotylous[G]; fertile stamens 2, less often 4, very rarely 1, rarely 5 (in taxa with actinomorphic flowers); nectary, if present, ring- or cup-shaped, occasionally lobed, rarely unilateral and tongue-like, never consisting of separate glands, sometimes lacking; ovary always superior; fruit usually a dry, cylindrical or less commonly ovoid-globose capsule, sometimes twisted (subtribes Loxocarpinae *p.p.* and Streptocarpinae *p.p.*), rarely indehiscent (a sclerocarpous or fleshy berry); Old World: Asia, Malesia, Pacific, Africa, a few genera/species in Europe and Australia, only one species of the SE Asian-Malesian genus *Rhynchoglossum* in the Neotropics (*R. azureum*) .... **3. Subfam. Didymocarpoideae**

1. Subfamily Sanangoideae

Subfam. Sanangoideae A.Weber, J.L.Clark & Mich.Möller was established in Weber *et al.* (2013). The subfamily is monospecific with only *Sanango racemosum* from Peru and SE Ecuador. The reasons for including *Sanango* in Gesneriaceae are given in Weber *et al.* (2013). Recent comprehensive molecular-phylogenetic work (Luna *et al.*, 2019) confirmed this treatment.

2. Subfamily Gesnerioideae

Subfam. Gesnerioideae Burnett corresponds largely to the traditionally delimited Gesnerioideae, but was restructured and expanded by Weber *et al.* (2013) to include the tribes Titanotricheae and Coronanthereae. The distribution thus includes Central America, tropical and temperate S America, SW Pacific and NE Australia, and E Asia (SE China, Taiwan and S Japan). The subfamily includes *c.* 77 genera with currently 1215 species (Clark *et al.*, this issue).

Key to the tribes of subfamily Gesnerioideae

1. Plants mostly reproducing asexually by means of tiny propagules ("bulbils") produced in masses above the flowering region; E Asia (SE China, Taiwan, S Japan) .... **Tribe Titanotricheae** (only genus and species *Titanotrichum oldhamii*) (see Table 1)

1. Plants mostly reproducing sexually, bulbils absent (not to be confused with the

subterranean scaly rhizomes[G] of Gesnerieae-Gloxiniinae); New World tropics and southern hemisphere 2

2. Nectary absent; corolla subactinomorphic and ephemeral; fruit a capsule, enclosed in a persistent calyx; plants terrestrial, leaves in a basal rosette; stomata clustered on mounds on leaf underside ..... **Tribe Napeantheae** (only *Napeanthus*)

2. Nectary present; corolla mostly zygomorphic and persistent; fruit variable, not enclosed in a persistent calyx; habit variable; stomata not clustered on mounds on leaf underside 3

3. Nectary adnate to the ovary (secreting tissue embedded in the basal part of the ovary), nectary thus never ring or cup-shaped or divided into separate glands or lacking; Southern hemisphere (temperate S America; SW Pacific, Australia) ..... **Tribe Coronanthereae**

3. Nectary not adnate to the ovary, distinctly ring or cup-shaped, or divided into separate glands, or lacking; Neotropics 4

4. Ovary superior; nectary annular (ring-shaped) or semi-annular; fruit an indehiscent or rupturing berry, with the pulp derived from placental tissue, or a fleshy or dry capsule; plants terrestrial; cymes usually without bracteoles[G] (except *Cremospermopsis*) ... **Tribe Beslerieae**

4. Ovary superior, semi-inferior or inferior; if ovary superior nectary often divided into 1–5 glands, otherwise annular; fruit a dry or fleshy capsule or an indehiscent berry, with the pulp derived from the fleshy funicles; plants terrestrial or epiphytic; cymes with bracteoles[G] ..... **Tribe Gesnerieae**

2.1. Tribe Titanotricheae

The monospecific tribe Titanotricheae T.Yamaz. ex W.T.Wang *et al.* was formerly assigned to subfam. Didymocarpoideae (synonym: Cyrtandroideae) when considered to belong to Gesneriaceae at all (see Weber, 2004). Following studies by Wang C.N. *et al.* (2004b), it is now assigned to subfam. Gesnerioideae. It contains only the genus *Titanotrichum*, with the single species *T. oldhamii*. This is the only genus/species of Gesnerioideae found in Asia (SE China, Taiwan, S Japan). It is unique in its prolific production of small propagules ("bulbils") in the inflorescence that serve for vegetative reproduction (Wang C.N. & Cronk, 2003; Wang C.N. *et al*., 2004a).

2.2. Tribe Napeantheae

Tribe Napeantheae Wiehler was established by Wiehler (1983) to accommodate the single genus *Napeanthus*, with *c*. 20 species distributed throughout the Neotropics. The plants are characterised by a rosette habit and nearly actinomorphic white, pale pink or pale blue flowers. Recent molecular data with increased taxon sampling strongly support Napeantheae and Beslerieae being basal lineages within the Gesnerioideae (Serrano-Serrano *et al*., 2017) or Napeantheae being the basal clade and sister to all other Gesnerioideae (Clark *et al*., 2010).

2.3. Tribe Beslerieae

Tribe Beslerieae Bartl. was first reestablished by Wiehler (1983) and this was adopted by Weber (2004) and Weber *et al*. (2013). In the latter paper the tribe was subdivided into two subtribes, following molecular-systematic work by Roalson & Clark (2006). Distribution is throughout the Neotropics. The tribe includes nine genera with more than 250 species.

Key to the subtribes of Beslerieae

1. Seed surface striate[G]; fruit an indehiscent or rupturing berry, or a dry 2-valved capsule dehiscing loculicidally, sometimes dehiscing tardily into 4 valves, or fruit dehiscing irregularly ..... **Subtr. Besleriinae**

1. Seed surface primarily reticulate[G], testa cells often with thin, sinuate side walls, outer walls flat or ± pouched to form a "papillate" or

"pustulate" seed surface; fruit a dry 2-valved capsule dehiscing septicidally, sometimes dehiscing tardily into 4 valves .... **Subtr. Anetanthinae**

2.3.1. Subtribe Besleriinae

Subtribe Besleriinae G.Don was reestablished in Weber *et al.* (2013). Of the four genera included (with a total of more than 240 species), the most speciose genus is *Besleria* with some 165 species. Distribution is throughout the Neotropics.

Key to the genera of subtribe Besleriinae

1. Fruit a globose, fleshy berry, with pulp of placental tissue, or a rupturing berry (with the carpel walls splitting regularly or irregularly, curving back and exposing a globose mass of placentae and seeds) ..... **Besleria**

1. Fruit a dehiscent semi-fleshy or dry capsule 2

2. Capsules semi-fleshy ..... **Gasteranthus**

2. Capsules dry, valves often membranous 3

3. Leaves opposite; nectary annular or semi-annular ..... **Cremosperma**

3. Leaves alternate; nectary a single dorsal bilobed gland ..... **Reldia**

2.3.2. Subtribe Anetanthinae

Subtribe Anetanthinae A.Weber & J.L.Clark was established in Weber *et al*. (2013). The five genera are each limited to fewer than five species, *Shuaria* and *Tylopsacas* are monospecific. Distribution is restricted to tropical South America.

Key to the genera of subtribe Anetanthinae

1. Leaves alternate, clustered on short shoots .. 2

1. Leaves opposite, arranged on elongate shoots 3

2. Leaves in a basal rosette; inflorescences with peduncules less than 5 cm; nectary ring-shaped, with 2 dorsal enlarged lobes; seed surface pustulate, side walls of testa cells straight; Guayana Highlands .... **Tylopsacas** (only *T. cuneata*)

2. Leaves in a basal rosette or clustered apically on short shoots; inflorescences with peduncle more than 5 cm; nectary ring-shaped, without enlarged lobes; seed surface smooth, side walls of testa cells sinuate; Colombia and Venezuela ..... **Resia**

3. Trees, 3–5(–8) m tall, with lepidote trichomes on vegetative and floral parts .... **Shuaria** (only *S. ecuadorica*) (see Table 1)

3. Perennial herbs or subshrubs, without lepidote trichomes 4

4. Bracteoles[G] absent; calyx ± actinomorphic; nectary a lobed sheath surrounding the ovary; capsules dehiscing septicidally, occasionally secondarily dehiscing loculicidally from the tips; seeds narrowly winged, surface smooth, side walls of testa cells sinuate ... **Anetanthus**

4. Bracteoles[G] present; calyx zygomorphic, becoming more so in fruit (3 to 4 lobes usually lanceolate and the remaining 1 or 2 much wider and ovate, often variable within the same inflorescence); nectary annular, often higher on both sides of ovary and low or absent between; capsules dehiscing loculicidally; seeds broadly winged, surface papillate .... **Cremospermopsis**

2.4. Tribe Coronanthereae

Tribe Coronanthereae Fritsch corresponds to subfam. Coronantheroideae of Wiehler (1983) and the "Coronantheroid Gesneriaceae" of Weber (2004). Burtt (1963) differentiated the following two tribes: Coronanthereae (Australia, SW Pacific) and Mitrarieae (temperate South America). The subdivision of a single tribe into three subtribes in Weber *et al*. (2013) followed Woo *et al*. (2011) who suggested that there had been multiple migrations from S America to the

SW Pacific and Australia. Nine genera with 28 species.

Key to the subtribes of Coronanthereae

1. Epiphytic creepers and subshrubs to 1 m tall, weak-stemmed and straggling; flowers solitary in leaf axils; fruit an indehiscent berry; temperate S America and E & SE Australia .... **Subtr. Mitrariinae**

1. Trees and shrubs, 2–15 m tall; inflorescences axillary cymes, comprising usually 3 to 8 (rarely one) flowers; fruit dehiscent or indehiscent; SW Pacific and Australia 2

2. Fruit a dry capsule, dehiscing by 2 or 4 valves (dehiscence septi- plus loculicidal), dehiscence starting from the capsule base, the valves remaining coherent at the apex; New Caledonia and New Zealand .... **Subtr. Coronantheriinae**

2. Fruit bivalved (dehiscing septicidally), dehiscence starting from the apex, or fruit fleshy and indehiscent (*Lenbrassia*); New Caledonia, Lord Howe Island and NE Australia ..... **Subtr. Negriinae**

2.4.1. Subtribe Coronantherinae

Subtribe Coronantheriinae Fritsch was revived by Woo *et al.* (2011) and adopted in Weber *et al.* (2013). The subtribe is restricted to the SW Pacific. It includes two genera, *Coronanthera*, with *c*. 20 species, and *Rhabdothamnus*, which is monospecific.

Key to the genera of subtribe Coronantherinae

1. Flowers in few to many-flowered axillary cymes; corolla greenish-yellowish; New Caledonia and the Solomon Islands .... **Coronanthera**

1. Flowers solitary in leaf axils; corolla red; New Zealand (North Island) .... **Rhabdothamnus** (only *R. solandri*)

2.4.2. Subtribe Mitrariinae

Subtribe Mitrariinae Hanst. was reestablished by Woo *et al.* (2011) and adopted by Weber *et al.* (2013). Apart from the three temperate S American genera *Asteranthera*, *Mitraria* and *Sarmienta*, formerly constituting the tribe Mitrarieae, it also includes *Fieldia* from SE Australia. All four genera are monospecific.

Key to the genera of subtribe Mitrariinae

1. Corolla pale yellow, tubular; Australia .... **Fieldia** (only *F. australis*)

1. Corolla bright red, if tubular, then with conspicuous constrictions at base and below the limb; temperate S America 2

2. Flowers erect; corolla strongly zygomorphic, with a prominent galeate upper lip and 3 lower lobes ..... **Asteranthera** (only *A. ovata*)

2. Flowers pendulous; corolla tubular, sharply constricted at base and (less prominently) below the limb, lobes (sub)equal 3

3. Flowers with inconspicuous bracteoles[G] below the calyx; fertile stamens 2; leaf margins entire or indistinctly crenate; S Chile and Chiloe Island ..... **Sarmienta** (only *S. repens*)

3. Flowers with conspicuous bracteoles[G] below the calyx, embracing the calyx and forming a broad deltoid sheath; fertile stamens 4; leaf margins coarsely crenate; Chile and adjacent Argentina ..... **Mitraria** (only *M. coccinea*)

2.4.3. Subtribe Negriinae

Subtribe Negriinae V.L.Woo, J.F.Smith & Garn.-Jones was established in Woo *et al.* (2011) and adopted by Weber *et al.* (2013). The subtribe includes plants of NE Australia and the SW Pacific. Two of the three genera are monospecific, one (*Depanthus*) includes two species.

Key to the genera of subtribe Negriinae

1. Fruit a fleshy berry; NE Australia .... **Lenbrassia** (only *L. australiana*)

1. Fruit a 2 or 4-valved capsule; SW Pacific 2
2. Corolla (sub)actinomorphic; stamens 5, anthers free; fruit a 2-valved capsule; New Caledonia ..... **Depanthus**
2. Corolla zygomorphic; stamens 4, anthers coherent; fruit a 4-valved capsule; Lord Howe Island (SW Pacific) ..... **Negria** (only *N. rhabdothamnoides*)

2.5. Tribe Gesnerieae

Tribe Gesnerieae Dumort. was considerably enlarged by Weber *et al.* (2013) due to the inclusion of the Episcieae, Gloxinieae, Sphaerorrhizinae, Sinningieae and Gesnerieae, each of which was instead recognised at the rank of subtribe. It is the largest tribe of Gesnerioideae, with some 57 genera and over 950 species. Distribution is throughout the Neotropics.

Key to the subtribes of tribe Gesnerieae

1. Ovary superior; plants terrestrial or epiphytic 2
1. Ovary semi-inferior or inferior; plants terrestrial 3
2. Woody, often spiny, terrestrial shrubs; corolla white, lobes spreading and truncate, actinomorphic; stamens 5, exserted; filaments very short; anthers exserted, forming a cone in the flower centre, thecae dehiscing by apical pores; nectary absent; fruit a dry, bivalved capsule; Caribbean .... **Subtr. Gesneriinae** *p.p.* (*Bellonia*)
2. Plants usually epiphytic herbs, less frequently terrestrial, with fibrous roots or rarely with a small tuber (*Lembocarpus*, *Rhoogeton*, some species of *Chrysothemis* and *Nautilocalyx*), or shrubs or vines, plants never spiny; corolla of various colours and shapes, usually oblique relative to the calyx, especially when spurred; stamens 4, usually included, filaments long, anthers never forming a central cone, thecae dehiscing longitudinally, rarely poricidally (*e.g.*, most spp. of *Drymonia*); nectary usually consisting of a single, bilobed gland, rarely of 5 separate glands or other configurations; fruit a fleshy bivalved capsule or indehiscent berry; widespread in the Neotropics .... **Subtr. Columneinae**
3. Ovary inferior; leaves alternate (except a few spp. of *Gesneria*); Caribbean, rarely in C & S America ..... **Subtr. Gesneriinae** *p.p.* (*Gesneria*, *Rhytidophyllum*)
3 Ovary usually semi-inferior, rarely superior or inferior; leaves opposite; Neotropics, Caribbean, N Argentina 4
4. Nectary annular; leaves of a pair with petiole bases joined across the nodes; the Caribbean ..... **Subtr. Gesneriinae** *p.p.* (*Pheidonocarpa*)
4. Nectary of 2–5 separate glands, rarely annular; leaves of a pair not joined across the nodes; Neotropics and the Caribbean 5
5. Tubers usually present, if absent, then basal part of stem swollen and succulent (*Sinningia p.p.*) or with perennial stems and then strictly confined to SE Brazil (*Paliavana*, *Vanhouttea*), never with scaly rhizomes[G]; C America to N Argentina, but mainly S & SE Brazil .... **Subtr. Ligeriinae**
5. Tubers absent; plants with or (rarely) without scaly[G] or stringy rhizomes[G]; Neotropics including Brazil 6
6. Subshrubs, shrubs, or small trees, without scaly[G] or stringy rhizomes[G]; Mexico and C America ..... **Subtr. Gloxiniinae** *p.p.* (*Moussonia*, *Solenophora*)
6. Herbs with scaly[G] or stringy rhizomes[G]; Neotropics including Brazil 7
7. Herbs with scaly rhizomes[G] (in *Seemannia* the scaly rhizomes produced at the tip of stringy rhizomes); widespread in the Neotropics .... **Subtr. Gloxiniinae** *p.p.maj.*
7. Herbs with stringy rhizomes[G], scaly rhizomes[G] lacking; Brazil (restricted to the Cerrado

domain) ..... **Subtr. Sphaerorrhizinae** (only *Sphaerorrhiza*) (see Table 1)

2.5.1. Subtribe Gesneriinae

Subtribe Gesneriinae Oerst. was reestablished by Weber *et al.* (2013) to include the genera previously included in tribe Gesnerieae. They are mostly found in the Caribbean and adjacent C and S America. Wiehler (1983) addressed the weak distinction of *Gesneria* and *Rhytidophyllum*, but to date the two genera are still recognised as distinct. Four genera with more than 100 species.

Key to the genera of subtribe Gesneriinae

1. Woody, often spiny shrubs; leaves opposite; corolla actinomorphic, lobes spreading, white, lobes almost free to base, rounded or truncate; fertile stamens 5, exserted; filaments short; anthers free, yellow, upright-connivent and forming a cone in the flower centre, thecae dehiscing by apical pores; nectary absent; ovary superior ..... **Bellonia**

1. Plants woody or herbaceous, never spiny; leaves opposite or alternate; corolla zygomorphic, tubular or campanulate, red, yellow or greenish; fertile stamens 4, included or exserted; filaments long; anthers coherent in pairs, never forming a central cone; colour variable; thecae dehiscing by longitudinal slits; nectary present, annular or lobed; ovary semi-inferior or inferior 2

2. Leaves opposite, petiole bases joined across the stem; ovary semi-inferior; capsules rostrate, rostrum long and curved ..... **Pheidonocarpa**

2. Leaves usually alternate, if opposite then petiole bases not joined across the stem; ovary inferior; capsules not rostrate 3

3. Capsules lacking ribs, usually villous; filaments adnate for 1–2 mm along base of corolla tube; base of filaments glabrous; leaves areolate, tomentose-hirsute, rarely glabrescent .... **Rhytidophyllum**

3. Capsules with or without prominent ribs, or warty, glabrous; filaments free and not fused to corolla tube; base of filaments densely pubescent; leaves smooth, rarely bullate, glabrous, scabrous or pilose ..... **Gesneria**

2.5.2. Subtribe Gloxiniinae

Subtribe Gloxiniinae G.Don includes the genera previously included in tribe Gloxinieae although the genera themselves have undergone substantial realignment (Roalson *et al*., 2005a,b, 2008). In addition to the genera treated in Weber (2004), seven genera have been reestablished or described as new (*Amalophyllon*, *Chautemsia*, *Gloxinella*, *Gloxiniopsis*, *Mandirola*, *Seemannia*, and *Sphaerorrhiza*), while three genera (*Anodiscus*, *Capanea* and *Koellikeria*) have been sunk into synonymy (see Table 1). *Gloxinia* has experienced a most drastic redefinition, with reduction of the *c.* 15 species to the type species and inclusion of the monospecific genera *Anodiscus* and *Koellikera*. Currently 21 genera with altogether more than 200 species are recognised. Distribution is throughout the Neotropics. A key with a different structure and more detailed information (*e.g.*, anatomical characters, chromosome numbers, distribution, given for all genera) was presented in Roalson *et al.* (2005a). Parallel use of their key and the following key is recommended.

Key to the genera of subtribe Gloxiniinae

1. Flowers in terminal racemes, arising singly from the axils of bracts; plants with scaly rhizomes[G] 2

1. Flowers in cymes or arising singly from the axils of foliage leaves, plants with or (rarely) without scaly rhizomes[G] 7

2. Bracts and their axillary flowers in an alternate or irregular arrangement; upper and lower bracts mostly equal is size, inflorescences thus sharply demarcated from the vegetative region 3

2. Bracts and their axillary flowers opposite; lower bracts usually larger than upper ones, inflorescences thus not sharply demarcated from the vegetative region 5

3. Plants small, less than 1 m tall, with leaves basally clustered; upper leaf surface white-dotted ..... **Gloxinia** *p.p.* (the former monospecific genus *Koellikeria*, see Table 1)

3. Plants large, to 1 m tall, with distinct stem and evenly spaced opposite leaves; upper leaf surface not white-dotted 4

4. Flowers with elongate narrow tube, broadening apically, slightly curved, colourful, often red-yellow, lobes often spotted, rarely white; nectary annular or shallowly 5-lobed; leaves green or red-marbled; Mexico .... **Smithiantha**

4. Flowers campanulate, white; nectary reduced; leaves green; Andes of Ecuador and Peru .... **Gloxinia** *p.p.* (the former monospecific genus *Anodiscus*, see Table 1)

5. Small, delicate herbs; indumentum hirsute or villous; corolla tubular or funnel-shaped, white, sometimes with purple markings on lobes; nectary of 5 glands, long, finger-like or sometimes connate with 2–3 glands .... **Diastema**

5. Robust, large and somewhat fleshy herbs; indumentum inconspicuous; corolla short- and broad-tubed, campanulate, blue or whitish; nectary much reduced or absent 6

6. Corolla with distinct gibbosity at base; bearing a dark violet osmophore on the inner side .... **Gloxinia** *p.p.* (*G. perennis* = *G. maculata*, *nom. illeg.*, type of *Gloxinia*)

6. Corolla without basal gibbosity; osmophore absent .... **Gloxiniopsis** (only *G. racemosa*) (see Table 1)

7. Corolla with short tube, flat-faced, rotate or subrotate, limb almost actinomorphic, white (rarely pinkish or yellowish); nectary reduced or absent 8

7. Corolla with elongate tube, tubular, funnel-shaped or campanulate, limb zygomorphic, coloured, if white, with purple lines, dots or similar markings inside; nectary present 10

8. Filaments as long as or shorter than the anthers, straight; fruit a dry rostrate capsule with a fringe of stiff trichomes on the inner margins of the valves; leaves sometimes with purplish (never white or silver) veins ..... **Niphaea**

8. Filaments longer than the anthers, those of the anterior[G] stamens curved inwards; fruit a fleshy or membranous capsule, not rostrate, valves without stiff trichomes; leaves sometimes with white or silvery veins 9

9. Fruit held erect above the foliage, fleshy at dehiscence, valves splitting broadly (to 180°), with sticky seeds adhering to valves .... **Phinaea** (see Table 1)

9. Fruit held on a slender curving pedicels, often placed below the leaves, valves membranous, opening only slightly, with the seeds falling freely (salt-shaker style) .... **Amalophyllon** (see Table 1)

10. Fruit a fleshy globose orange capsule, often rupturing when mature, crowned by the persistent calyx (with calyx lobes connate at least halfway), opening irregularly and exposing the placentae and seeds for animal-dispersal; nectary a large double-connate dorsal gland; branched shrubs to small trees with soft woody stems; scaly rhizomes[G] lacking; Mexico to northern Guatemala (*S. calycosa* extends into Panama) ..... **Solenophora**

10. Fruit a fleshy or dry capsule; not crowned by a persistent calyx, opening loculicidally; nectary annular, or divided into separate glands, or absent; unbranched terrestrial shrubs or herbs, rarely epiphytic; scaly rhizomes[G] usually present, rarely absent; Central & South America 11

11. Fruit a fleshy, green capsule, dehiscing dorsally, held horizontally with seeds exposed to rain 12

11. Fruit a dry or fleshy, often rostrate, capsule, dehiscing loculicidally into two valves 14

12. Capsules ovoid to elliptic; nectary annular to slightly 5-lobed; corolla bluish, lobes sometimes whitish, without a yellow blotch in the throat ..... **Gloxinella** (only *G. lindeniana*, the former *Kohleria lindeniana*) (see Table 1)

12. Capsules cylindrical; nectary much reduced or lacking; corolla white, lavender or bluish, with an orange-yellow blotch in the throat 13

13. Leaves strongly anisophyllous[G]; hooked trichomes usually present on calyx and hypanthium ..... **Monopyle**

13. Leaves (sub)isophyllous[G]; hooked trichomes on calyx and hypanthium absent ..... **Nomopyle**

14. Nectary annular, sometimes shallowly 5-lobed 15

14. Nectary composed of 2–5 individual glands, sometimes the two dorsal ones connate into a single bilobed gland 21

15. Herbs with wiry stems; leaves leathery, lateral veins reaching the margin and forming a marginal vein; ovary superior; C Brazil..... ..... **Goyazia**

15. Herbs with non-wiry erect stems; leaves membraneous, lateral veins not reaching the margin and forming a marginal vein; ovary semi- to completely inferior; C and S America, not restricted to C Brazil 16

16. Anthers free ..... **Heppiella**

16. Anthers coherent 17

17. Subshrubs or shrubs, without scaly rhizomes[G] ..... **Moussonia**

17. Herbs with scaly rhizomes[G] 18

18. Scaly rhizomes[G] usually produced at the tips of long stringy rhizomes[G]; corolla with barrel-shaped multicellular hairs at mouth; stigma pointed ..... **Seemannia** (see Table 1)

18. Long stringy rhizomes not present; corolla without barrel-shaped multicellular hairs at mouth; stigma bilobed[G], stomatomorphic[G] or cup-shaped, not pointed 19

19. Stems and leaves densely lanate-villous; corolla campanulate or broad-tubed; Mexico .... **Eucodonia**

19. Stems and leaves without woolly indumentum; corolla of various shapes; South and Central America 20

20. Flowers usually solitary in leaf axils, rarely in cymes; margins of corolla lobes usually entire; C America (mainly Mexico) and West Indies ..... **Achimenes**

20. Flowers usually in axillary cymes, rarely solitary; margins of corolla lobes toothed or fimbriate; Brazil ..... **Mandirola** (see Table 1)

21. Nectar glands finger-like; flowers solitary in leaf axils; fruit a fleshy plagiocarpic[G] capsule, dehiscing only on the dorsal side .... **Chautemsia** (see Table 1)

21. Nectar glands globose; flowers in axillary cymes; fruit a fleshy, membranous or dry orthocarpic[G] capsule, dehiscing by 2 valves 22

22. Capsules dehisce on both sides, fully reflexed and bivalved; corolla tubular or funnel-shaped, often distinctly to strongly pouched (hypocyrtoid[G]) or balloon-shaped with constricted mouth; stamens included; corolla never campanulate, greenish-yellowish and brown-spotted within and with exserted anthers and stigma; plants terrestrial, never epiphytic; with scaly rhizomes, occasionally with stolons ..... **Pearcea**

22. Capsules dehisce by a single longitudinal slit, never reflexed; corolla broad tubular or funnel-shaped, not pouched, never balloon-shaped and with constricted mouth; plants terrestrial or epiphyte (*Kohleria tigrina* and *K. grandiflora*); scaly rhizomes present; or corolla broadly campanulate, greenish-yellow, with brown

spots inside, anthers and stigma slightly exserted (in the former genus *Capanea*, see Table 1); plants epiphytic, scaly rhizomes absent ..... **Kohleria**

2.5.3. Subtribe Columneinae

Subtribe Columneinae Hanst. was reestablished by Weber *et al.* (2013) and corresponds to the tribe Episcieae in previous works. It is the largest group of Gesnerioideae, presently comprising 28 genera and more than 560 species (particularly due to the speciose genus *Columnea*). Eleven genera have been reestablished, newly described or redefined since the Gesneriaceae treatment of Weber (2004): *Alloplectus*, *Centrosolenia*, *Christopheria*, *Codonanthe*, *Codonanthopsis*, *Crantzia*, *Glossoloma*, *Neomortonia*, *Pachycaulos*, *Pagothyra*, *Trichodrymonia* (see Table 1). *Crantzia* and *Glossoloma* are well separated by molecular data and geography, but are difficult to define morphologically (Clark, 2005, 2009). Moreover, both have resupinate flowers, but in each genus there is one species with non-resupinate flowers. Their treatment in the below key (couplets 22 and 23) must remain unsatisfactory at present. When redefining *Codonanthe* and *Codonanthopsis*, only the latter proved to include ant epiphytes (Chautems & Perret, 2013). Distribution of the subtribe is throughout the Neotropics.

Key to the genera of subtribe Columneinae

1. Fruit an indehiscent, fleshy berry 2
1. Fruit a dry or fleshy capsule, dehiscing loculicidally by two valves 8
2. Plants terrestrial; axillary inflorescences pedunculate; flowers umbellate or congested into heads; calyx lobes cucullate, with reflexed margins ..... **Corytoplectus**
2. Plants epiphytic; inflorescences epedunculate, thus appearing as single axillary flowers; calyx lobes flat 3
3. Berry orange 4
3. Berry white, pink, red, purple, or lavender....6
4. Berry laterally compressed; corolla campanulate, lobes pink suffused with white, margins fimbriate .... **Neomortonia** (see Table 1)
4. Berry globose; corolla shape variable, lobes white or red, margins not fimbriate 5
5. Corolla campanulate to funnel-shaped, mostly white; stems not swollen; restricted to the Brazilian Atlantic forests ..... **Codonanthe** (*sensu* Chautems & Perret, 2013) (see Table 1)
5. Corolla strongly hypocyrtoid[G], bright red; stems swollen; Mexico to N Peru ..... **Pachycaulos** (only *P. nummularia*) (see Table 1)
6. Corolla tubular and elongate (> than 20 mm), if shorter, then with a narrow limb; from Mexico south to Ecuador and Bolivia, and east to Brazi ..... **Columnea** (in the traditional, wide sense; including the genera *Bucinellina*, *Dalbergaria*, *Pentadenia* and *Trichantha sensu* Wiehler, 1983; see Smith & Clark, 2013)
6. Corolla campanulate to subcampanulate, 8–20 mm long, widening to a broad limb; C America 7
7. Corolla with white lower lobes and reddish upper lobes; berry globose or depressed .... **Rufodorsia**
7. Corolla white throughout or reddish; berry ovoid, pointed ..... **Oerstedina**
8. Fruit a dry capsule 9
8. Fruit a fleshy capsule 10
9. Capsule wall robust; the valves opening to 180°; calyx not star-shaped, without a basal tube; lobes lanceolate, unequal, the lateral ones broader than the dorsal one (this is the one adjacent to the spur); corolla salverform; nectary annular, more prominent at the dorsal side; French Guiana ..... **Cremersia**

9. Capsule wall thin, papyraceous, valves opening to an angle of *c*. 90°; calyx star-shaped, with a short pentagonal-campanulate tube; lobes broadly triangular, spreading; corolla tubular, without a dorsal spur; nectary a single, slightly emarginate dorsal gland; endemic to the region of Cobán, Alta Verapaz, Guatemala .... **Cobananthus** (only *C. calochlamys*)

10. Plants with a subterranean tuber 11

10. Plants without a tuber 14

11. Calyx lobes connate for at least 3/4 of their length, forming a plicate cup or tube .... **Chrysothemis**

11. Calyx lobes free or nearly so 12

12. Stems elongate; tuber perennial; cymes short- or epedunculate, or reduced to single flowers; capsule valves opening by *c*. 90°; S America ... . **Nautilocalyx** *p.p.* (species with a tuber)

12. Leaves in a basal rosette (rarely only two or few leaves) arising from a small, annual underground tuber; cymes long-pedunculate, scapose; capsule valves opening to 180°; S America, restricted to Guiana shield 13

13. Corolla orange or red; nectary a single dorsal emarginate gland; Guyana ..... **Rhoogeton**

13. Corolla pale blue or white; nectary a thin, non-functional ring or completely reduced; Suriname and French Guiana .... **Lembocarpus** (only *L. amoenus*)

14. Plants with stolons arising from the leaf axils 15

14. Plants without stolons 17

15. Plants with one stolon per node ..... **Alsobia**

15. Plants with two stolons per node 16

16. Corolla white, blue, purple or red; Nicaragua to tropical S America ..... **Episcia**

16. Corolla pale yellow; Guiana shield (Guyana and French Guiana) ..... **Christopheria** (only *C. xantha*) (see Table 1)

17. Plants obligate epiphytes, often growing in ant gardens; anthers occasionally horned; base of corolla with spur; Central America, Caribbean, NW South America, Amazon basin .... **Codonanthopsis** (*sensu* Chautems & Perret, 2013) (see Table 1)

17. Plants terrestrial or facultative epiphytes; not associated with ant gardens; anthers not horned; base of corolla without spur; NW South America 18

18. Plants terrestrial, rosulate; inflorescences long-pedunculate, much longer than leaf tuft; flowers in a unilateral (scorpioid) cyme; nectary consisting of 2 large glands, a ventral and a dorsal one; Guyana .... **Lampadaria** (only *L. rupestris*)

18. Plants terrestrial or epiphytic, stem with distinct internodes between leaf pairs; inflorescences short-pedunculate or peduncle almost lacking (but pedicels sometimes much elongated, *e.g.*, in *Nematanthus* species with pendent flowers); nectary annular or of a single dorsal gland; plants not restricted to Guyana 19

19. Facultative epiphytic subshrubs to 4 m tall; calyx lobes ovate and auriculate at base, margin strongly and coarsely dentate in the lower part and entire at the apex (*Lesia savannarum*) or lacking serrations and entire (*L. tepuiensis*) .... **Lesia** (see Table 1)

19. Terrestrial subshrubs (not facultative) or epiphytic herbs; calyx lobes not as above, usually linear or lanceolate 20

20. Epiphytic climbing vines; inflorescences bracteate unilateral cymes (cincinnus, scorpioid cyme); mouth of corolla occluded throughout anthesis by the upfolded ventral corolla lobe .. .. **Pagothyra** (only *P. maculata*) (see Table 1)

20. Plants epiphytic or terrestrial, rarely vines or climbers; inflorescences not bracteate, unilateral cymes; mouth of corolla not occluded by the ventral corolla lobe 21

21. Leaf blade ± succulent, with a hypodermis; Atlantic coastal forests in Brazil ..... **Nematanthus**

21. Leaf blade not succulent and without a hypodermis; C and S America, except Atlantic coastal forest in Brazil 22

22. Flowers resupinate[G] (except *Crantzia tigrina* and *Glossoloma anomalum*, see species descriptions in Clark, 2009 and Clark, 2005, respectively) 23

22. Flowers not resupinate[G] 24

23. Plants epiphytic (only terrestrial in *Crantzia tigrina*); Lesser Antilles, coastal Venezuela, and the Guiana Shield ..... **Crantzia** (see Table 1)

23. Plants terrestrial (only epiphytic in 3 Andean species); southern Mexico to Panama, NW South America, and south to Bolivia ..... **Glossoloma** (see Table 1)

24. Obligate terrestrial herbs 25

24. Facultative epiphytic herbs, subshrubs or vines 26

25. Stems ± fleshy, erect or creeping and rooting at the nodes; corolla infundibuliform, trumpet shaped or salverform, usually with tube less than 4 times longer than broad ..... **Nautilocalyx** *p.p.*

25. Stems ± fleshy, decumbent and rooting at the nodes; corolla narrow-tubular and elongate, tube about 5 times longer than broad ..... **Centrosolenia** (see Table 1)

26. The four anthers coherent by their inwards-facing thecae, forming a column-like "salt-shaker", thecae elongate, sagittate, usually dehiscing by basal pores, with pores upside; pollen dry, powdery; or thecae rarely (by reversal) opening by longitudinal slits ..... **Drymonia**

26. The four anthers coherent into flat rectangles, squares, or into pairs; thecae not elongate and sagittate, dehiscing by longitudinal slits; pollen usually sticky 27

27. Anthers with an apical tuft of trichomes ("bearded") ..... **Paradrymonia**

27. Anthers glabrous 28

28. Terrestrial herbs or vines, with elongate shoots and evenly spaced leaves, or epiphytes, with reduced shoots and apically clustered leaves, plants often resembling tank bromeliads; fibrous roots absent; leaves with prominent secondary venation; calyx lobes linear to lanceolate; corolla funnelform or trumpet-shaped, spurred at the base, rarely pouched; throughout the Neotropics except SE Brazil, with a centre of diversity in Colombia ..... **Trichodrymonia** (see Table 1)

28. Epiphytic subshrubs with branched stems; fibrous roots present; leaves with inconspicuous secondary venation (at least when dry); calyx lobes ovate; corolla pouched below the mouth; Costa Rica to Peru, centre of diversity in the southern Andes of Colombia ..... **Alloplectus** (see Table 1)

2.5.4. Subtribe Sphaerorrhizinae

Subtribe Sphaerorrhizinae A.Weber & J.L.Clark was established in Weber *et al.* (2013). It corresponds to tribe Sphaerorrhizeae Roalson and Boggan, described in Roalson *et al.* (2005a). It comprises only one genus, *Sphaerorrhiza*, with four species, two of them only recently described (Araujo *et al.*, 2016). Distribution is restricted to Brazil (Cerrado domain). Morphologically, the most significant character is the presence of stringy rhizomes[G] with a succession of small tuber-like swellings.

2.5.5. Subtribe Ligeriinae

Subtribe Ligeriinae Hanst. was reestablished by Weber *et al.* (2013). It corresponds to the tribe Sinningieae of earlier works (*e.g.*, Wiehler, 1983; Burtt & Wiehler, 1995) and comprises three genera with more than 90 species. Its main distribution is in SE Brazil. In analyses based on six plastid DNA regions and nuclear *ncp*GS, Perret

et al. (2003) showed that *Vanhouttea* and *Paliavana* nest in *Sinningia* and those five lineages can be recognised in the genus. To date, however, this has not resulted in nomenclatural changes. The genera recognised here, consequently, do not reflect the phylogeny.

Key to the genera of subtribe Ligeriinae

1. Herbs, rarely shrubs, mostly with tubers, if without tubers, then stem fleshy and flowers white ..... **Sinningia**
1. Shrubs without tubers 2
2. Corolla tubular, cylindrical, red ....**Vanhouttea**
2. Corolla campanulate or funnel-shaped, variously coloured, but not red .....**Paliavana**

3. Subfamily Didymocarpoideae

Subfam. Didymocarpoideae Arn. (formerly subfam. Cyrtandroideae) has seen several, rather unsatisfactory, attempts to subdivide the group into natural entities. The morphological work of Weber (1975, 1976a,b,c, 1977a,b, 1978a,b, 1982) provided evidence that the genera now placed in tribe Epithemateae could be sister to the rest of the subfamily. This was confirmed in a molecular phylogenetic study by Mayer *et al.* (2003). Later studies by Möller *et al.* (2009, 2011a,b, 2016), Middleton and Möller (2012) and Middleton *et al.* (2014, 2015, 2018) clarified the relationships of the remaining genera which are here included in tribe Trichosporeae. Distribution of the subfamily is in the Old World (E and W Europe, tropical and subtropical Africa, warm-temperate, subtropical and tropical Asia, the Pacific), with one outlier occurring in tropical C and S America (*Rhynchoglossum azureum*). The subfamily currently includes 71 genera with around 2500 species.

Key to the tribes of subfamily Didymocarpoideae

1. Placentae triangular in cross section; ovary and fruit ± globose, fruit capsular, never indehiscent, capsule valves never twisted; style sharply demarcated from the ovary; seeds spirally striate[G]-reticulate[G], testa cells always without ornamentation; plants usually fleshy-succulent; leaves sometimes strongly asymmetrical ..... **Tribe Epithemateae**
1. Placentae lamelliform in cross section, recurved to revolute; ovary and fruit usually elongated, rarely ovoid or globose, fruit capsular or rarely indehiscent and berry-like, capsules opening by straight or twisted valves; style usually not well demarcated from the ovary; seeds straight-reticulate[G], testa cells often with ornamentations; plants rarely fleshy-succulent; leaves rarely asymmetrical .... **Tribe Trichosporeae**

3.1. Tribe Epithemateae

Tribe Epithemateae C.B.Clarke corresponds to the "Epithematoid Gesneriaceae" in Weber (2004). It is a small tribe comprising only seven genera with more than 85 species. Nevertheless, no fewer than four subtribes were (re)established in Weber *et al.* (2013) to reflect the wide range of divergent morphologies. Distribution is in tropical Asia, except one species of *Rhynchoglossum* (C and S America) and one species of *Epithema* (W and E Africa).

Key to the subtribes of tribe Epithemateae

1. Calyx lobes ovate to suborbicular, aestivation imbricate, inner surfaces with chalk-secreting glands; ovary/fruit bilocular[G], with axile placentae ..... **Subtr. Monophyllaeinae**
1. Calyx lobes triangular, pointed, aestivation valvate, inner surfaces without glands; ovary/fruit unilocular[G], with parietal placentae 2
2. Leaves alterniphyllous[G], arranged in two rows, blades strongly asymmetrical at base; inflorescences terminal, one-sided racemes with two rows of flowers; corolla with upper lip much smaller than the lower lip .... **Subtr. Loxotidinae** (only *Rhynchoglossum*)

2. Leaves iso-[G] to strongly anisophyllous[G] or only one leaf (enlarged macrocotyledon[G]) present; inflorescences branched (thyrses or cymes), flowers lax or congested; corolla with upper lip not much smaller than the lower lip 3

3. Lowermost cauline leaf (above large, transient macrocotyledon[G]) solitary, upper leaves in 1–2 (sub)isophyllous[G] pairs; inflorescences pedunculate, many-flowered, dense and (seemingly) terminal heads, flowers in 4 dense rows; sepals not plicate, spreading in fruit; fertile stamens 2 (but with two large staminodes); fruit a circumscissile capsule .... **Subtr. Epithematinae** (only *Epithema*)

3. Plant of different structure, without a solitary cauline leaf, leaves (sub)isophyllous[G] (*Gyrogyne*) or strongly anisophyllous[G]; inflorescences dense terminal heads (*Gyrogyne*) or branched thyrses, terminal or placed opposite to the large leaf; fertile stamens 4; fruit a 4-valved capsule or irregularly breaking into pieces, fruit unknown in *Gyrogyne* .... **Subtr. Loxoniinae**

3.1.1. Subtribe Loxotidinae

Subtribe Loxotidinae G.Don was revived by Weber *et al.* (2013) to accommodate the single genus *Rhynchoglossum* (incl. *Klugia*, Burtt, 1962). In Asia there are about 10 species. *Rhynchoglossum azureum* is the only species in the subfamily to be found in the New World. Recent regional revisions are available for Thailand (Pattharahirantricin, 2014) and Malesia (Kartonegoro, 2013). Distribution is in S and SE Asia, from India to New Guinea, one species (*R. azureum*) in central and tropical South America.

3.1.2. Subtribe Monophyllaeinae

Subtribe Monophyllaeinae A.Weber & Mich. Möller was established by Weber *et al.* (2013). Even though the two included genera, *Monophyllaea* and *Whytockia*, are rather dissimilar, a close relationship was predicted by Weber (1976b) based on a detailed morphological analysis. The relationship was confirmed in a molecular phylogenetic study by Mayer *et al.* (2003). Nomenclatural notes on *Whytockia* species were given by Wang Y.Z. (2003). At present, 6–8 species are recognised in *Whytockia* and almost 40 in *Monophyllaea*.

Key to the genera of subtribe Monophyllaeinae

1. Plants caulescent[G], with several strongly anisophyllous[G] leaf pairs; lamina of leaves strongly asymmetrical at base; inflorescences from the axils of the large leaves; S China, Taiwan ..... **Whytockia**

1. Plants usually with a single leaf (macrocotyledon[G]), rarely with several leaves of the same shape as the macrocotyledon[G]; lamina of leaf ± symmetrical; inflorescences from the axils of tiny bracts situated at the base of the leaf, or arising from the midrib or the stem (hypocotyl); SE Asia to New Guinea .... **Monophyllaea**

3.1.3. Subtribe Loxoniinae

Subtribe Loxoniinae A.DC. was resurrected by Weber *et al.* (2013) for three genera, two of them (*Loxonia*, 3 species; *Stauranthera*, *c.* 7 species) having a similar strongly anisophyllous[G] habit, a sympodial shoot organisation and an alternicladic[G]-thyrsic inflorescence structure (Weber, 1977b). Distribution is China, S and SE Asia. The position of the little known monospecific Chinese genus *Gyrogyne* is uncertain, both with respect to the tribal and subtribal position. Unfortunately, no molecular data for *Gyrogyne* are available and the only species in the genus may now be extinct.

Key to the genera of subtribe Loxoniinae

1. Leaves ± isophyllous[G]; inflorescences dense, few-flowered terminal heads; S China .... **Gyrogyne** (only *G. subaequifolia*; subtribal position uncertain)

1. Leaves strongly anisophyllous[G]; inflorescences anisocladic[G] thyrses, terminal, but (especially in *Loxonia*) seemingly arising from the axils of the small leaves; tropical SE Asia 2

2. Leaves ± densely studded with hooked hairs, grey-green; calyx not plicate; corolla greenish-white, with a distinctly bilabiate limb, not spurred ..... **Loxonia**

2. Leaves sparsely hairy, green, like the stems somewhat succulent; calyx plicate; corolla white-blue, with an orange-yellow hairy blotch on the palate, or white with a blue centre, broadly campanulate or (sub)rotate, with (*S. grandifolia*) or without (remaining species) a thick conical spur at the base .... **Stauranthera**

3.1.4. Subtribe Epithematinae

Subtribe Epithematinae DC. ex Meisn. was reestablished by Weber *et al.* (2013) to accommodate the single genus *Epithema*. A revision of this genus was recently published by Bransgrove and Middleton (2015), who recognised 20 species. Distribution is in Africa (*E. tenue*), S, E and SE Asia, Malesia and extending to the Solomon Islands.

3.2. Tribe Trichosporeae

Tribe Trichosporeae Nees was reestablished by Weber *et al.* (2013) and corresponds to the "Didymocarpoid Gesneriaceae" of Weber (2004), an informal name used in many papers on Old World Gesneriaceae published before 2013. Based on the molecular data of Möller *et al.* then available (2009, 2011a), a preliminary subdivision into 10 subtribes was suggested by Weber *et al.* (2013). This subdivision is unbalanced and difficult to handle. There are five subtribes that consist only of a single genus, so that the subtribal characters are *de facto* identical with those of the genera. The largest subtribe is Didymocarpinae, followed by the Loxocarpinae. Future molecular work might indicate where alliances lie and what characters can be found to define natural groups in this subtribe. Distribution of the tribe is from Europe through Africa and S and SE Asia to the Pacific. The tribe currently includes 71 genera with some 2400 species.

Key to the subtribes of tribe Trichosporeae

1. Fruit a septicidally dehiscent capsule, never twisted; E and W Europe .... **Subtr. Ramondinae**

1. Fruit dehiscing in various ways, very rarely septicidally (*Corallodiscus conchifolius*, a small, stolon-bearing and mat-forming plant from SW China), twisted or not, or fruit indehiscent (a hard or fleshy berry); Africa, Madagascar, Asia and the Pacific 2

2. Fruit dehiscent with straight or twisted capsule, when fruit straight then seeds always verruculose[G], when fruit twisted then seeds reticulate[G] or verruculose[G], indumentum variable, but very rarely of branched or glandular hairs or white-silvery matted[G] or arachnoid[G]; Africa, Madagascar and/or the Comoro Islands ..... **Subtr. Streptocarpinae** (only *Streptocarpus sensu* Nishii *et al.* 2015; including the former genera *Acanthonema*, *Colpogyne*, *Hovanella*, *Linnaeopsis*, *Nodonema*, *Saintpaulia*, *Schizoboea*, and *Trachystigma*)

2. Fruit indehiscent or dehiscent with straight or twisted capsule, when fruit straight, then seeds reticulate[G] or with various ornamentations, but very rarely verruculose[G], when fruit twisted, then plants usually with a glandular, white-silvery matted[G] or arachnoid[G] indumentum or with branched hairs; Asia, Malesia, Australasia and/or the Pacific 3

3. Corolla actinomorphic, 5 or 4-merous; fertile stamens equalling the number of corolla lobes 4

3. Corolla slightly to strongly zygomorphic, 5-merous; fertile stamens 4 or 2 5

4. Calyx 5-merous, corolla 4-merous; Sri Lanka ..... **Subtr. Leptoboeinae** *p.p.* (*Championia*)

4. Calyx and corolla 5 or 4-merous, calyx lobes equalling the number of corolla lobes; S and E China, Japan and Taiwan .....

..... **Subtr. Didymocarpinae** *p.p.* (*Conandron*, *Oreocharis p.p.*, *Petrocodon p.p.*, the species with radially symmetrical flowers)

5. Fertile stamens 4 6

5. Fertile stamens 2 13

6. Plants with stem bearing a tetramerous (pseudo)whorl of leaves at apex and pairs of cataphylls below; corolla broadly funnel-shaped, flowers almost sessile and crowded at stem apex; NE India, Bangladesh, Myanmar, Thailand ..... **Subtr. Tetraphyllinae** (only *Tetraphyllum*)

6. Plants acaulescent[G] or caulescent[G] with distinct internodes between leaf pairs or whorls; corolla of various shapes, flowers not sessile and crowded at stem apex 7

7. Corolla campanulate, shallowly campanulate or flat-faced 8

7. Corolla tubular or infundibuliform, straight or (rarely) arcuate 9

8. Plants with woody stem and tufted, long-hairy leaves at apex; capsules plagiocarpic[G], opening only dorsally; Borneo .... **Subtr. Didymocarpinae** *p.p.* (*Ridleyandra* sect. *Stilpnothrix*; the spp. of sect. *Ridleyandra* have broad-tubular flowers)

8. Plants of various habits: small, unifoliate[G] (*Platystemma*), acaulescent[G] or caulescent[G], with opposite (*Leptoboea*) or alternate leaves (*Boeica*); fruit indehiscent, berry-like (*Rhynchotechum*) or capsular, orthocarpic[G] or (*Beccarinda*) plagiocarpic[G]; mainland Asia and Sumatra ..... **Subtr. Leptoboeinae** *p.p.* (all genera excl. *Championia*)

9 Plants acaulescent[G] 10

9 Plants caulescent[G] 12

10. Corolla tubular, bearded on lower lip; bracteoles[G] in cymes lacking; leaves rhomboid to suborbicular, strongly wrinkled; lower elevation to alpine N, NE and S India, Bhutan, S China and Thailand ..... **Subtr. Corallodiscinae** (only *Corallodiscus*)

10. Corolla of various shapes; bracteoles[G] in cymes usually present; leaves of various shapes and textures; lower elevation to montane elevations 11

11. Upper side of corolla with a prominent dorsal boss[G], upper lip emarginate; filaments flattened, the upper pair hooded at the top, the lower pair with a broad appendage above the insertion, all four anthers coherent; SW India ..... **Subtr. Jerdoniinae** (only *Jerdonia indica*)

11. Corolla without a dorsal boss[G]; upper lip bilobed; filaments not flattened and/or appendaged; anthers free or cohering in pairs ..... **Subtr. Didymocarpinae** *p.p.* (acaulescent[G] genera with tetrandrous flowers)

12. Capsules longitudinally ribbed, tardily dehiscent; plants terrestrial; Borneo .... **Subtr. Didissandrinae** *p.p.* (all species except *Didissandra triflora* and *Tribounia*, with diandrous flowers)

12. Capsules not ribbed, not tardily dehiscent; plants of various habits, including epiphytes and climbers; widespread in Asia and Malesia ..... **Subtr. Didymocarpinae** *p.p.* (caulescent[G] genera with tetrandrous flowers)

13. Fruit indehiscent, a sclerocarpous or fleshy berry ..... **Subtr. Didymocarpinae** *p.p.* (*Cyrtandra*, *Billolivia*, *Sepikea*)

13. Fruit a capsule 14

14. Capsules twisted ... **Subtr. Loxocarpinae** *p.p.*

14. Capsules straight 15

15. Stigma disciform or crateriform; tiny rosette plants; flowers large in relation to the leaves, emerging singly from leaf axils; capsules 4-valved; S China .... **Subtr. Litostigminae** (only *Litostigma*)

15. Stigma capitate, bilobed[G] or chiritoid[G]; plant habit variable; flowers and leaves variable;

capsules variable; plants widespread in Asia 16

16. Capsules tardily dehiscent, longitudinally ribbed, finally disintegrating into several strands ..... **Subtr. Didissandrinae** *p.p.* (*Didissandra triflora*, the other species of the genus have tetrandrous flowers, see couplet 12)

16. Capsules not tardily dehiscent and longitudinally ribbed, not finally disintegrating into several strands 17

17. Corolla funnelform, with a prominent dorsal boss[G]; capsules pendulous and with a distinct stipe .. **Subtr. Didissandrinae** *p.p.* (*Tribounia*)

17. Corolla variable, dorsal boss[G] absent or not prominent; capsules variable 18

18. Plants terrestrial, lithophytic or epiphytic, usually lacking a silvery-white smooth, matted[G], arachnoid[G] or very sticky indumentum, never with branched hairs; corolla mostly tubular or campanulate, only rarely flat-faced; stigma capitate, 2-lipped (with upper and lower lobe), or chiritoid[G] .... **Subtr. Didymocarpinae** *p.p.*

18. Plants mostly lithophytic, more rarely terrestrial but not epiphytic, often with a silvery-white smooth, matted[G], arachnoid[G] or very sticky indumentum, hairs rarely branched; corolla tubular, campanulate, shallowly campanulate or flat-faced; stigma mostly capitate, rarely chiritoid[G] .... **Subtr. Loxocarpinae** *p.p.*

3.2.01. Subtribe Jerdoniinae

Subtribe Jerdoniinae A.Weber & Mich.Möller includes only the genus *Jerdonia*, with the single species *J. indica*, a rosette plant endemic to SW India (Nilgiri and Anamalai Hills) (Janeesha & Nampy, 2014). According to Möller *et al*. (2009), *Jerdonia* is the basalmost lineage and sister to all other members of tribe Trichosporeae.

3.2.02. Subtribe Corallodiscinae

Subtribe Corallodiscinae A.Weber & Mich.Möller comprises a single genus, *Corallodiscus*. The species number is unclear but is around five, of which three species are given in the *Flora of China* (Wang W.T. *et al*., 1998). The uncertainty in number of species is mainly explained by discontinuities in distribution and great variation in gross morphology due to the ancient history of the genus. This involved expansion/contraction cycles that allowed secondary contacts, hybridization and polyploidisation, and resulted in blurred species boundaries (Zhou *et al*., 2017). *Corallodiscus* includes rosette plants found in N and NE India, Bhutan, China, Nepal and Thailand and was recently recorded also from W India (Kamble *et al*., 2006), and most recently from S India (Padal *et al*., 2020).

3.2.03. Subtribe Tetraphyllinae

Subtribe Tetraphyllinae A.Weber & Mich.Möller is the third of the basalmost clades within Trichosporeae. It comprises a single genus, *Tetraphyllum* Griff. ex C.B.Clarke, with three species known from NE India, Bangladesh, Myanmar and Thailand. The long stems bear a tetramerous pseudowhorl at the apex, while the lower part bears pairs of small cataphylls.

In a recent paper, Doweld (2017) claimed that *Tetraphyllum* in the Gesneriaceae was a later homonym of the fossil genus *Tetraphyllum* Hosius & von der Marck and proposed a replacement of the genus and subtribe names with *Tetraphylloides* and Tetraphylloidinae, respectively. However, Bertling (2019) suggested that Dowell's names were superfluous because *Tetraphyllum* Hosius & von der Marck was not definitively a plant and was not, therefore, governed under the ICN (Turland *et al*., 2018).

3.2.04. Subtribe Leptoboeinae

Subtribe Leptoboeinae C.B.Clarke was reestablished by Weber *et al*. (2013) to accommodate a morphologically rather heterogeneous group of genera. The core genera are *Boeica* and *Leptoboea* (if they are generically distinct – the only difference seems to be the alternate *vs*. opposite leaf arrangement). *Boeica* is heterogeneous due to the

inclusion of *B. brachyandra*, *B. nutans* and *B. guileana*, differing in habit considerably from the species around the type, *B. fulva* (Burtt, 1977). *Rhynchotechum* (recently revised by Anderson & Middleton, 2013), and particularly *Beccarinda* and *Platystemma*, are morphologically somewhat out of place in this alliance, their position here rests entirely on molecular data. The inclusion of *Championia* needs molecular confirmation. Distribution of the most widespread genus, *Rhynchotechum*, is from India and China through SE Asia and Malesia to Papua Guinea. If *Championia* is included, subtr. Leptoboeinae comprises six genera with more than 40 species.

Key to the genera of subtribe Leptoboeinae

1. Fruit indehiscent, berry-like, white .... **Rhynchotechum**
1. Fruit a dry dehiscent capsule, usually brown 2
2. Plants acaulescent[G] or subacaulescent[G], leaves basal; fruit a plagiocarpic[G] capsule, dehiscing dorsally only; mainly N India to Vietnam .... **Beccarinda**
2. Plants with a distinct stem; fruit orthocarpic[G], dehiscing into 2 or 4 valves; widespread in S, E and SE Asia 3
3. Stem slender, bearing a single small and hairy leaf at its apex; flowers 1(–3) emerging from the axil of the leaf; corolla with short tube and wide limb, violet-like in form and colour; capsules ovoid, dehiscing loculicidally .... **Platystemma** (only *P. violoides*)
3. Plant without this habit; flowers variable; capsules variable 4
4. Leaves alternate ..... **Boeica**
4. Leaves opposite 5
5. Subshrubs calyx and corolla 5-merous, limb slightly zygomorphic, with rounded lobes; capsules 2(sometimes 4)-valved; mainland Asia ..... **Leptoboea**
5. Herbs; calyx 5-merous, corolla 4-merous, actinomorphic, with 4 equal triangular lobes; capsules 4-valved; Sri Lanka .... **Championia** (only *C. reticulata*)

3.2.05. Subtribe Ramondinae

Subtribe Ramondinae DC. ex Meisn. was reestablished in Weber *et al.* (2013) and includes all European representatives of Gesneriaceae. Molecular data place *Jancaea* in *Ramonda* (Petrova *et al.*, 2015), but no formal action has yet been taken. Altogether, the 2(–3) genera of the subtribe include 5 species.

Key to the genera of subtribe Ramondinae

1. Corolla tubular, limb zygomorphic, 5-lobed; stamens 4, didynamous, anthers cohering in pairs; disc present, annular ..... **Haberlea** (only *H. rhodopensis*, incl. *H. ferdinandi-coburgii*, Strid, 1991; Petrova *et al.*, 2014)
1. Corolla flat-rotate or campanulate, lobes and stamens matching in number 5 or 4; stamens of equal length, anthers free; disc reduced ... 2
2. Corolla flat-faced or very shallowly campanulate; stamens exserted; leaves green above, rusty brown below ..... **Ramonda**
2. Corolla campanulate, with short but distinct tube; stamens included; leaves white-woolly ..... **Jancaea** (only *J. heldreichii*)

3.2.06. Subtribe Litostigminae

Subtribe Litostigminae A.Weber & Mich.Möller was established in Weber *et al.* (2013). The subtribe comprises only the genus *Litostigma*, described in Wei *et al.* (2010), with two species from southern China.

3.2.07. Subtribe Streptocarpinae

Subtribe Streptocarpinae Ivanina was reestablished in Weber *et al.* (2013). It comprises only the genus *Streptocarpus* in the wide sense of Nishii *et al.* (2015)

with *c.* 180 species (Möller *et al*., 2019). It now includes all didymocarpoid genera formerly recognised in Africa, Madagascar and the Comoro Islands: *Acanthonema*, *Colpogyne*, *Hovanella*, *Linnaeopsis*, *Nodonema*, *Saintpaulia*, *Schizoboea*, *Streptocarpus* and *Trachystigma* (see Table 1). The four Asian species formerly referred to *Streptocarpus* are now in the genus *Damrongia* (subtribe Loxocarpinae) (Puglisi *et al*., 2016).

The large-scale study by Nishii *et al.* (2015) provided strong evidence that all African, Madagascan and Comoro Islands genera unequivocally form a monophyletic clade, with the genera mentioned above (with straight, untwisted fruits) nested in *Streptocarpus* (with twisted fruits) as formerly defined. Of the two options, (1) to divide *Streptocarpus* into several, newly (but some very weakly) defined genera, or (2) to greatly widen the concept of *Streptocarpus* and establish 12 well-defined sections within the two subgenera, the authors decided to adopt the second option.

3.2.08. Subtribe Didissandrinae

Subtribe Didissandrinae A.Weber & Mich.Möller was established in Weber *et al.* (2013). Morphologically, the two genera included in this subtribe look like they should belong in subtribe Didymocarpinae. However, the limited available molecular data places them as sister to subtribe Loxocarpinae (Möller *et al*., 2009, 2011a; Middleton & Möller, 2012). Whether this position is justified will need to be tested with additional molecular data. Distribution is in Thailand (*Tribounia*, 2 species) and the western part of Malesia (*Didissandra*, 8 species).

Key to the genera of subtribe Didissandrinae

1. Fruit a long slender cylindrical capsule, longitudinally ribbed when ripe, tardily loculicidally dehiscent, the valves finally disintegrating into strands along the sclerified vascular bundles, without a stipe, not pendulous; stamens 4, of equal or (*D. anisanthera*) unequal length, or stamens 2 (*D. triflora*); western Malesia ..... **Didissandra**

1. Fruit a loculicidally dehiscent capsule, not ribbed, with a long stipe at the base, pendulous; stamens 2; Thailand ..... **Tribounia**

3.2.09. Subtribe Loxocarpinae

Subtribe Loxocarpinae A.DC was reestablished in Weber *et al.* (2013). Presently, 14 genera are recognised. Since Weber (2004), five have been reestablished or described as new (*Damrongia*, *Dorcoceras*, *Loxocarpus*, *Middletonia*, *Somrania*), two were synonymised (*Phylloboea*, *Trisepalum*) and two greatly redefined (*Boea*, *Paraboea*) (see Table 1). The subtribe is morphologically somewhat heterogeneous. Important characters include the twisted fruits (otherwise only found in *Streptocarpus p.p.* in subtribe Streptocarpinae) and the glandular, silvery-white, matted[G] or arachnoid[G] indumentum (occasionally with branched hairs) of the vegetative plant parts in a number of genera (for indumentum details see Xu *et al*., 2008). In some genera, species with twisted and straight fruits can both be found (*e.g*., *Damrongia*, *Kaisupeea*, *Paraboea*). Important recent work on the group was done by Puglisi *et al.* (2011, 2016), recent revisions relate to the Thai species of *Damrongia* (Puglisi & Middleton, 2017c), *Dorcoceras* (Puglisi & Middleton, 2017a), *Middletonia* (Puglisi & Middleton, 2017b) and the genus *Ornithoboea* (Scott & Middleton, 2014). The distribution of the subtribe is from NE India, Indochina, southeastwards throughout SE Asia extending into Australia and the Solomon Islands, with a total of more than 210 species.

Key to the genera of subtribe Loxocarpinae

1. Fruit a twisted capsule 2

1. Fruit a straight capsule 12

2. Plants acaulescent[G]; leaves thin and delicate; indumentum of long, sticky hairs, not sericeous; plants often growing at the entrance

of limestone caves; plants restricted to Peninsular Malaysia 3

2. Plants caulescent[G] or acaulescent[G]; leaves robust; indumentum often sericeous, if composed of sticky hairs then plants caulescent[G]; plants at cave entrances or not; widespread 4

3. Capsules short-cylindrical, with several turns over its length; corolla flat-faced, usually resupinate[G], lobes reflexed; upper lip with hairs, lower lip glabrous ..... **Senyumia**

3. Capsules ovoid, thin-walled, slightly twisted, with one turn over its length, sometimes almost straight; corolla campanulate; margin of upper lip with glandular hairs, otherwise glabrous . ..... **Spelaeanthus** (only *S. chinii*)

4. Plants caulescent[G]; upper lip of corolla much smaller than lower lip, with a ring of tissue and often with hairs around the corolla throat, usually with a dense patch of hairs at base of lower lip ..... **Ornithoboea**

4. Plants acaulescent[G] or caulescent[G]; upper lip of corolla usually distinct even if smaller than lower lip, no well-demarcated ring of tissue and hairs around corolla throat, if lower lip hairy, not obviously with a clear and dense patch at base 5

5. Leaves with densely matted[G] hairs on the lower surface, often also with arachnoid[G] additional hairs 6

5. Leaves glabrous or pubescent, sometimes densely so, but not matted[G] and arachnoid[G] additional hairs absent 7

6. Anthers connate, filaments bent upwards; ovary without sessile glands .... **Paraboea** *p.p.*

6. Anthers coherent only at the beginning of anthesis, free later on, filaments straight, erect; ovary with sessile glands ..... **Middletonia** *p.p.*

7. Stigma lingulate[G]; Myanmar, Thailand .... **Paraboea** *p.p.* (the former monospecific genus *Phylloboea*)

7. Stigma capitate or chiritoid[G].....8

8. Corolla distinctly tubular; plants caulescent[G] 9

8. Corolla flat-faced or campanulate; plants caulescent[G] or acaulescent[G] 10

9. Plants of shrubby and twiggy habit, branching at the base and producing several, to 50 cm long stems; flowers emerging singly from the leaf axils; stigma capitate; S China .... **Rhabdothamnopsis** (only *R. sinensis*)

9. Plants erect or trailing herbs; flowers in axillary pair-flowered cymes[G]; stigma distinctly chiritoid[G]; S China, Myanmar, Thailand, Sumatra ..... **Damrongia** *p.p.*

10. Corolla flat-faced ..... **Boea**

10. Corolla campanulate 11

11. Plants caulescent[G] ..... **Kaisupeea** *p.p.*

11. Plants acaulescent[G] ..... **Dorcoceras**

12. Branched hairs present at least on lower leaf surface, often also elsewhere on the plant (use a lens) 13

12. Branched hairs absent 14

13. Corolla flat-faced ..... **Paraboea** *p.p.*

13. Corolla tubular ..... **Somrania**

14. Fruit globose-ovoid, not exceeding the calyx; endemic to Peninsular Malaysia .... **Orchadocarpa** (only *O. lilacina*)

14. Fruit ovoid to cylindrical, exceeding the calyx; widespread 15

15. Leaves with densely matted[G] hairs on the lower leaf surface, often also with arachnoid[G] additional hairs, if not densely matted[G] then stigma lingulate[G] ..... **Paraboea** *p.p.*

15. Leaves glabrous or pubescent, sometimes densely so but not matted[G] and arachnoid[G] additional hairs absent, stigma never lingulate[G]

..... 16

16. Plants caulescent[G]; upper lip of corolla much smaller than lower lip, with a ring of tissue and hairs around the corolla throat .... **Ornithoboea** *p.p.*

16. Plants acaulescent[G] or caulescent[G]; upper lip of corolla usually distinct even if smaller than lower lip, no well-demarcated ring of tissue and hairs around corolla throat 17

17. Upper lip of corolla tightly studded with oil-secreting glands consisting of a 1-celled stalk and a multicellular head; plants delicate, growing at entrance of limestone caves; Peninsular Malaysia .... **Emarhendia** (only *E. bettiana*)

17. Upper lip without these glands; plants delicate or not, growing in a wide range of habitats; widespread 18

18. Ovary with sessile glands; corolla almost flat-faced ..... **Middletonia** *p.p.*

18. Ovary without sessile glands; corolla flat-faced or campanulate 19

19. Fruit plagiocarpic[G], held horizontally and opening only along upper side .... **Loxocarpus**

19. Fruit orthocarpic[G], held straight and dehiscing into two valves 20

20. Corolla distinctly tubular ..... **Damrongia** *p.p.*

20. Corolla shallowly campanulate .... **Kaisupeea**

3.2.10. Subtribe Didymocarpinae

Subtribe Didymocarpinae G.Don was reestablished by Weber *et al.* (2013). It is by far the largest subtribe in subfam. Didymocarpoideae and in the Gesneriaceae, comprising 35 genera with well over 1900 species and with a distribution from India to the Pacific and from China to Java. It is morphologically very heterogeneous and the relationships between the genera are still little understood. Since the treatment by Weber (2004), eight genera have been reestablished or described as new (*Billolivia*, *Chayamaritia*, *Codonoboea, Glabrella*, *Liebigia*, *Microchirita*, *Primulina*, *Rachunia*, see Table 1), and 21 genera have been synonymised (including large genera such as *Briggsia* and *Chirita*) (see Table 1). Recircumscriptions have led to quite radical redefinitions and/or expansions of some genera (*e.g.*, *Deinostigma*, *Oreocharis*, *Petrocodon*, and *Primulina*). In *Petrocodon*, which until recently was known only to include one penta- and more than 20 diandrous species, now also includes three tetrandrous species (Yu *et al.*, 2015; Li *et al.*, 2019; Zhang *et al.*, 2019). Evidently, much work is still necessary before we have a satisfactory understanding of all genera to then be reflected in a satisfactory classification. As the subtribe is so large, we present here the genera in four subkeys based on two easily observable characters: the stamen number and habit. Many genera are extremely heterogeneous, occurring more than once in a subkey, or in more than one subkey.

Key to the subkeys of subtribe Didymocarpine

1. Flowers with 5 fertile stamens ..... Subkey 1

1. Flowers with 4 fertile stamens ..... Subkey 2

1. Flowers with 2 fertile stamens 2

2. Plants acaulescent[G] ..... Subkey 3

2. Plants caulescent[G] ..... Subkey 4

Subkey 1: Genera of subtribe Didymocarpinae with 5 fertile stamens and actinomorphic flowers

1. Stamens combined into a tube surrounding the style; connectives with long apical projections; corolla blue .... **Conandron** (only *C. ramondioides*)

1. Stamens not forming a central tube; connectives without projections; corolla of various colours, including blue 2

2. Corolla urceolate, lobes triangular, pointed, white or tinged pink; stamens included;

capsules 4-valved .... **Petrocodon** *p.p.* (*P. scopulorum*, the only species of the former genus *Tengia*, see Table 1; the species with 4 and 2 stamens are covered in Subkeys 2 and 3, respectively)

2. Corolla flat-faced or campanulate, lobes rounded, white or purple to blue; stamens exserted; capsules 2-valved .... **Oreocharis** *p.p.* (*O. leiophylla*, the former *Bournea leiophylla*, and *O. esquirolei*, the only species of the former genus *Thamnocharis*: in the latter the flowers are variable and include 5 and 4-merous forms; see Table 1; the *Oreocharis* species with 4 and 2 stamens are covered in Subkeys 2 and 3, respectively)

Subkey 2: Genera of subtribe Didymocarpinae with 4 fertile stamens

1. Flowers actinomorphic, calyx and corolla 4-merous ..... **Oreocharis** *p.p.* (*O. sinensis*, the former *Bournea sinensis*, and *O. esquirolei*, the only species of the former genus *Thamnocharis*; in the latter the flowers are variable and include 5- and 4-merous forms; see Table 1; the *Oreocharis* species with 5 and 2 stamens are covered in Subkeys 1 and 3, respectively)

1. Flowers slightly to strongly zygomorphic, calyx and corolla 5-merous 2

2. Calyx zygomorphic, 2-lipped, upper (adaxial) lip consisting of a single lobe (fused halfway with the remaining lobes), lower (abaxial) lip 4-lobed (fused to ¾ to upper lip); disc tubular; capsules narrowly ellipsoid; Hainan Island (China) ..... **Cathayanthe** (only *C. biflora*)

2. Calyx usually actinomorphic, if zygomorphic then with 3 upper lobes and 2 lower lobes, lobes free to base or connate; disc ring-like or (rarely) cup-shaped or rudimentary; capsules elongate, rarely conical or ovoid 3

3. Ovary bilocular[G], only adaxial locule fertile; placenta 1, axile; capsules plagiocarpic[G]; cymes 1–3-flowered .... **Briggsiopsis** (only *B. delavayi*)

3. Ovary unilocular[G]; placentae 2, parietal; capsules orthocarpic[G]; cymes 1 to many-flowered 4

4. Anthers of the two lower stamens dithecous, those of the upper pair monothecous; fruit cylindrical, subcarnose, breaking irregularly into pieces; Borneo ..... **Hexatheca**

4. Anthers all dithecous; fruit dehiscing loculicidally (rarely septicidally or both); widespread 5

5. Plants climbing or epiphytic, rarely epilithic; corolla long- or short-tubular, usually arcuate; frequently red, also yellow or other colours 6

5. Plants terrestrial; corolla broadly tubular, narrowing abruptly towards the base or infundibuliform; usually light-coloured, not red 7

6. Plants climbing (one of the *c.* 100 species terrestrial), rooting in the soil and clinging to the bark of trees by means of short adhesive roots generated along the nodes and internodes; leaves herbaceous, lateral veins clearly visible ..... **Agalmyla** *p.p.*

6. Plants usually epiphytic, rarely epilithic, rooting at nodes only; leaves leathery-fleshy, with a several-layered hypodermis on lower leaf side, lateral veins ± invisible .... **Aeschynanthus**

7. Plants with a single, strongly anisophyllous[G] leaf pair on stem apex..... ..... **Raphiocarpus** *p.p.* (*R. sesquifolius*)

7. Plants caulescent[G] or of acaulescent rosette or tufted habit; all or several leaves capable of producing axillary flowers or inflorescences 8

8. Plants caulescent[G], with long stem and distinct internodes 9

8. Acaulescent[G] rosette plants or plants with short stem and tuft of alternate leaves at stem apex 11

9. Corolla long- and broad-tubed, somewhat ventricose on abaxial side, spotted inside, with two ridges in the throat; seeds with or without a hair-like appendage on each end .... **Loxostigma**

9. Corolla infundibuliform, rarely campanulate or flat-faced, with two or several longitudinal streaks; seeds without hair-like appendages, but sometimes with a long tapering brown apex at each end 10

10. Seeds with a long tapering brown apex at each end ..... **Anna**

10. Seeds ellipsoid, without appendages .... **Raphiocarpus** *p.p.* (species other than *R. sesquifolius*)

11. Capsules dehiscing on upper side only; stigma lingulate[G], formed by the lower carpel only; corolla broad-tubular (*Ridleyandra* sect. *Ridleyandra*) or campanulate to flat-faced (*R.* sect. *Stilpnothrix*); S Thailand, Malay Peninsula, Borneo ..... **Ridleyandra**

11. Capsules 2 or 4-valved; stigma capitate or bilobed[G] (with upper and lower lobe); corolla variable; N Thailand, Vietnam, Myanmar, NE India, Bhutan, S China, and Japan 12

12. Capsules 4-valved; stigma capitate; corolla infundibuliform ..... **Petrocodon** *p.p.* (*P. hunanensis*, *P. longitubus*, and *P. tongziensis* (recently discovered species with 4 stamens instead of 5 or 2; for the latter two conditions see Subkeys 1 and 3, respectively)

12. Capsules 2-valved, valves often remaining joined along ventral suture; stigma usually bilobed; corolla of various shapes, rarely infundibuliform 13

13. Rosette or tufted plants with indistinct stem, petioles and leaves usually hairy; corolla morphology very variable .... **Oreocharis** *p.p.maj.* (*sensu* Möller *et al.* 2011b; the species with 4 stamens, including those of the former genera *Ancylostemon*, *Briggsia p.p.* (incl. type), *Isometrum*, *Paraisometrum* and *Tremacron*; see Table 1; the *Oreocharis* species with 5 and 2 stamens are covered in Subkeys 1 and 3, respectively)

13. Plants with short (5-6 cm long) stem, petioles and leaves glabrous; corolla broadly tubular, gibbous abaxially ..... **Glabrella** (see Table 1)

Subkey 3: Genera of subtribe Didymocarpinae with 2 fertile stamens, plants of acaulescent[G] habit

1. Fertile stamens the posterior[G] pair .... **Oreocharis** *p.p.* (the species of the former genus *Opithandra*, see Table 1; the *Oreocharis* species with 2 stamens in anterior[G] position are covered in the present Subkey, the species with 5 and 4 stamens are covered in Subkeys 1 and 2, respectively)

1. Fertile stamens the anterior[G] pair 2

2. Upper lip of corolla 4-lobed, lower lip undivided 3

2. Upper lip of corolla 2-lobed or entire, lower lip 3-lobed, lobes rounded or triangular-acute 4

3. Corolla lobes triangular-acute; corolla bowl-shaped or campanulate, white .... **Allocheilos**

3. Adaxial corolla lobes deltoid, abaxial lobes broadly triangular; corolla narrowly funnelform-tubular, red ..... **Petrocodon** *p.p.* (*P. coccineus*, the former *Calcareoboea coccinea*, see Table 1; species with 5 and 4 stamens are covered in Subkeys 1 and 2)

4. Upper lip of corolla entire, triangular-obtuse or semi-orbicular 5

4. Upper corolla lip shortly incised or distinctly 2-lobed 6

5. Corolla tubular to tubular-funnelform, much longer than limb; calyx lobes free to base, oblong or linear; stamens exserted; leaf blade elliptical, base truncate ..... **Oreocharis** *p.p.* (the former genus *Deinocheilos*, see Table 1; the species with 5 and 4 stamens are covered in Subkeys 1 and 2, respectively)

5. Corolla tube broadly tubular-campanulate, nearly equalling limb; calyx campanulate, lobes connate, blunt; stamens included; leaf blade cordate or kidney-shaped ..... **Gyrocheilos**

6. Upper corolla lip shortly incised at apex .... **Petrocosmea** *p.p.* (*P.* sect. *Anisocheilos*; see also couplet 12)

6. Upper corolla lip distinctly 2-lobed 7

7. Upper corolla lobes fused ± to half..... .....**Petrocosmea** *p.p.* (see also couplet 12)

7. Upper corolla lobes free or almost free to mouth..... 8

8. Lobes of upper lip usually larger than those of lower lip, lower lip with 3 or (by reduction of the middle lobe) 2 lobes; all corolla lobes broadly triangular-acute; corolla with short narrow tube and large, ± flat limb, pink, darker in the centre; stamens sometimes reduced to 1; stigma bilobed[G], with equal upper and lower lobe ..... **Oreocharis** *p.p.* (the former monospecific genus *Dayaoshania*) (see Table 1; the *Oreocharis* species with 5 and 4 stamens are covered in Subkeys 1 and 2, respectively)

8. Lobes of upper lip equal to or smaller than those of lower lip; lobes rounded or triangular; corolla variable, rarely pink; stamens always 2; stigma capitate or chiritoid[G] 9

9. Capsules orthocarpic[G] 10

9. Capsules plagiocarpic[G] 14

10. Stigma capitate, globose or punctiform 11

10. Stigma chiritoid[G] 13

11. Corolla with ± long tube, limb often small in relation to tube, exhibiting a wide spectrum of forms (including urceolate, tubular, infundibuliform, salverform, lobes triangular-pointed, rarely rounded) .... **Petrocodon** *p.p.maj.* (see Table 1; the species with 2 stamens; species with 5 and 4 stamens are covered in Subkeys 1 and 2)

11. Corolla flat-faced or campanulate, with short- and broad-tube, limb large in relation to tube, lobes rounded 12

12. Corolla flat-faced, tube broad and shorter than limb, blue, purple or white; anthers not villous, thecae parallel; capsules narrowly ellipsoid to ovoid ....**Petrocosmea** *p.p.* (see also couplet 7)

12. Corolla campanulate to short- and broad-tubed, tube longer than limb, white or bluish, with londitudinal streaks on lower side; anthers villous, thecae widely divaricate; capsules globose .... **Metapetrocosmea** (only *M. peltata*)

13. Leaves opposite (at least in young plants); calyx divided to base or sometimes basally connate to form a short tube, valvate, lobes ± equal; S China, Vietnam ....**Primulina** *p.p.maj.* (see Table 1)

13. Leaves alternate; calyx with 5 lobes divided to base, strongly imbricate, upper lobe distinctly larger; Thailand, Laos .... **Chayamaritia** (see Table 1)

14. Stigma capitate .....**Codonoboea** *p.p.* (most species caulescent[G] and with spaced leaf pairs, but some, particularly the former *Didymocarpus*/*Henckelia* sect. *Heteroboea* producing tufts of alternate leaves near ground) (see Table 1)

14. Stigma chiritoid[G].....15

15. Many plant parts, particularly the pedicels, with hooked hairs; S China and Vietnam .... **Deinostigma** *p.p.*

(see Table 1) (usually caulescent[G], but some species with very short stem and leaves crowded near ground; see Subkey 4)

15. Plants without hooked hairs 16

16. Ovary bilocular[G], with only the upper carpel fertile; leaves in a rosette; S China, Vietnam ..... **Primulina** *p.p.* (some species around *P. dryas*; otherwise in the genus fruit orthocarpic[G] and both carpels fertile) (see Table 1)

16. Ovary unilocular[G], with both carpels fertile; leaves in a basal rosette or arising singly from a small tuber; S & SW India, Nepal, Sri Lanka ..... **Henckelia** *p.p.* ("core *Henckelia*", *Henckelia* sect. *Henckelia sensu* Weber & Burtt, 1998 ["1997"]) (see Table 1)

Subkey 4: Genera of subtribe Didymocarpinae with 2 fertile stamens, plants of caulescent[G] habit (stems erect, ascending or creeping)

1. Plants climbing or epiphytic, more rarely lithophytic but then distinctly climbing or scrambling 2

1. Plants terrestrial or epilithic, stem elongated with distinct internodes, or short, with leaves crowded near the ground (but with distinct internodes), erect, ascending or creeping 3

2. Plants climbing (usually on trees, occasionally on rocks); corolla bright red, yellow, green or combination of these colours . **Agalmyla** *p.p.* (the few species with 2 stamens; the species with 4 stamens are covered by Subkey 2)

2. Plants epiphytic, if terrestrial or epilithic then scrambling, not climbing; corolla white or light-coloured ..... **Lysionotus**

3. Plants creeping 4

3. Plants erect or ascending 5

4. Stigma lingulate[G] or chiritoid[G]; leaves strongly anisophyllous[G]; flowers small campanulate or large infundibuliform; creeping stem with long or short internodes; India, Sri Lanka and mainland Asia to S China ..... **Henckelia** *p.p.* (the non-creeping *Henckelia* species are covered below and the acaulescent[G] species in Subkey 3)

4. Stigma capitate; leaves ± isophyllous; flowers usually large and infundibuliform; creeping stem with distinct internodes; Malesia, particularly Malay peninsula ..... **Codonoboea** *p.p.* (*C. reptans* and similar species; the erect species are covered below and the acaulescent[G] species in Subkey 3)

5. Plants small and delicate; comprising a single internode and a single leaf (rarely 2 or more leaves) 6

5. Plants large and robust; with several to many leaves or leaf pairs 7

6. (Sub)unifoliate[G] habit inherent; plants annual or perennial-rhizomatous; leaves solitary (macrocotyledon?), rarely 2 or more; N & NW India, Thailand and Myanmar ..... **Henckelia** *p.p.* (caulescent[G] unifoliate species, *cf*. Sirimongkol *et al*., 2019; the caulescent[G] and acaulescent[G] species of *Henckelia* are covered below and by Subkeys 3 respectively)

6. Unifoliate[G] habit facultative; plants annual and principally caulescent[G]; with a solitary leaf (macrocotyledon[G]) below and spaced leaf pairs above, but starting to flower in an early stage of development, with the flower(s) arising from the axil of the macrocotyledon[G]; under special conditions the plants persist in this stage until they fruit and die; from S China to Java ..... **Microchirita** *p.p.* (see also couplet 19)

7. Fruit indehiscent, a hard (sclerocarpous) or fleshy berry; large terrestrial herbs or subshrubs 8

7. Fruit a dehiscent, dry capsule; habit variable..... 10

8. Posterior[G] stamen pair fertile; leaves opposite; New Guinea (Sepik area) ..... **Sepikea**

(only *S. cylindrocarpa*; genus doubtful, description of stamen position perhaps erroneous and genus probably congeneric with *Cyrtandra*; Burtt, 2001)

8. Anterior[G] stamen pair fertile; leaves opposite or alternate 9

9. Leaves opposite; isophyllous[G] to strongly anisophyllous[G] (small leaves reduced to stipule-like scales); Nicobar Islands, Thailand and Taiwan through Malesia and the S Pacific to the Hawaiian Islands, S Japan, but not occurring in mainland China, Vietnam and Cambodia ..... **Cyrtandra**

9. Leaves alternate, without stipule-like scales opposing the leaves; S Vietnam (southern Annamite range) and possibly neighbouring Cambodia ..... **Billolivia** (see Table 1)

10. Stigma undivided, capitate, truncate or clavate 11

10. Stigma bilobed[G] or chiritoid[G] 14

11. Capsules orthocarpic[G] 12

11. Capsules plagiocarpic[G] 13

12. Lowermost pair of bracteoles[G] large, boat shaped; stem wiry; calyx lobes free, imbricate; corolla campanulate; stigma clavate; Thailand ..... **Rachunia** (only *R. cymbiformis*) (see Table 1)

12. Lowermost pair of bracteoles[G] small, unremarkable; stem not wiry; calyx lobes free or connate, valvate; corolla usually tubular or infundibuliform, stigma capitate; S China and N & NE India to the N of Peninsular Malaysia and N Sumatra) ..... **Didymocarpus**

13. Ovary/fruit unilocular[G], placentae 2, parietal-lateral; capsules usually straight; stigma capitate; leaves opposite or alternate; (mainly western) Malesia: Sumatra, S Thailand, Peninsular Malaysia, Borneo, few spp. further east ..... **Codonoboea** (see Table 1)

13. Ovary/fruit bilocular[G], placenta 1, axile-median; capsules usually curved; stigma capitate or truncate; leaves opposite; China, Vietnam, Taiwan, and S Japan ..... **Hemiboea** (including the former monospecific genus *Metabriggsia*; see Table 1)

14. Stigma bilobed[G] 15

14. Stigma chiritoid[G] 17

15. Stigma lobes of equal size, oblate or semiorbicular; plants annual; stems square-angled; stamens adnate to corolla tube near mouth ..... **Didymostigma**

15. Stigma lobes of unequal size, the upper one distinctly smaller; plants perennial; stems square-angled or terete; stamens adnate to the corolla in the middle of the tube 16

16. Stems square-angled; indumentum pubescent; calyx narrow, with linear-lanceolate lobes; corolla white to lavender; anthers apically coherent; S China ..... **Allostigma** (only *A. guangxiense*)

16. Stems terete, indumentum sericeous; calyx campanulate, with rounded lobes; corolla white; anthers coherent face to face; S China, N Vietnam ..... **Pseudochirita** (only *P. guangxiensis*)

17. Capsules plagiocarpic[G]; ovary/fruit bilocular[G] throughout or in the lower part; plants, especially the inflorescence axes and pedicels, with hooked hairs; S China and Vietnam ..... **Deinostigma** (see Table 1)

17. Capsules orthocarpic[G]; ovary/fruit unilocular[G] throughout; plants without hooked hairs; widely distributed 18

18. Plants large, coarse perennial herbs or subshrubs, stems to 2 m tall; leaves asperous on upper side; ovary and fruit with a short stipe; Sumatra, Java and Bali ..... **Liebigia** (the former *Chirita* sect. *Liebigia*) (see Table 1)

18. Plants much smaller, herbaceous, not subshrubby; leaves not asperous; ovary and fruit without a stipe; ranging from S China to Java 19

19. Plants usually annual-monocarpic, stem and leaves fleshy-juicy; inflorescences (one to) several in leaf axils, sometimes forming a conspicuous series of flower pairs ("crested inflorescence"); India, Myanmar, S China, Thailand, Vietnam, Laos, Cambodia, Sumatra, Java and Borneo ..... **Microchirita** (the former *Chirita* sect. *Microchirita*) (see Table 1)

19. Plants perennial, stem and leaves usually not fleshy-juicy; inflorescences never crested; Sri Lanka, NE India, Nepal, S China, N Thailand, Myanmar, and Vietnam ..... **Henckelia** *p.p.* (most species of the former *Chirita* sect. *Chirita* and including the former monospecific genus *Hemiboeopsis*, for the species of the acaulescent[G] "core *Henckelia*" see Subkey 3)

Problematic and excluded genera

Weber (2004) included two annexes to the treatment of the genera of Gesneriaceae, entitled 'Genera of uncertain affiliation' and 'Excluded genera'. The former included the genera *Sanango*, *Cubitanthus*, and *Jerdonia*, the latter *Brookea*, *Charadrophila*, *Cyrtandromoea*, *Rehmannia*, and *Titanotrichum* (see Table 1). Three of them, *Sanango*, *Jerdonia* and *Titanotrichum*, each comprising only a single species, are now definitely included in the Gesneriaceae: *Sanango* is placed in a subfamily of its own (Sanangoideae), *Jerdonia* is on the first branching lineage within Didymocarpodeae-Trichosporeae and is formally recognised as subtribe Jerdoniinae, and *Titanotrichum* is placed in subfamily Gesnerioideae, tribe Titanotricheae and is the only Asian taxon in the subfamily (see also notes under the respective subtribes).

Due to the radical reorganisation of the Scrophulariaceae and the restructuring of the order Lamiales (now containing 26 families), a much more precise placement of the excluded genera is now possible compared to 2004. *Cubitanthus* is now placed in Linderniaceae, *Charadrophila* in Stilbaceae, *Cyrtandromoea* in Phrymaceae, and *Rehmannia* in Orobanchaceae (for further details and references see Table 1) (summarised and discussed in Luna *et al*., 2019).

The only genus for which no progress can be reported is *Brookea*. This was assigned to the Gesneriaceae by Hallier (1903), while other authors (including Burtt, 1963) considered it to belong to Scrophulariaceae. Fischer (2004) placed *Brookea* in Scrophulariaceae-Bowkerieae/ Stilbaceae, where it is both morphologically and geographically isolated. To the best of the authors' knowledge, the genus has not yet been included in any molecular-phylogenetic study. Nevertheless, the chance that this Bornean genus of four tree species belongs in the Gesneriaceae is remote.

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Glossary

Acaulescent: Stem absent or indistinct, plants of rosette habit or leaves forming a tuft at ground level; contrasting to → caulescent.

Alterniclady (adj. alternicladic): Alternate position of axillary shoots (particularly inflorescences) in → anisophyllous or alterniphyllous shoots.

Alterniphylly (adj. alterniphyllous): Extreme form of → anisophylly, with the small leaf of a leaf pair being completely reduced. The remaining large leaves form two rows recalling a distichous leaf arrangement (pseudo-distichy, *e.g*. *Rhynchoglossum*).

Anisoclady (adj. anisocladic): Axillary shoots of an → anisophyllous leaf pair of different size. The extreme form of anisoclady is → alterniclady.

Anisocotyly (adj. anisocotylous): In contrast to à isocotyly of Sanangoideae and Gesnerioideae, the two cotyledons behave differently in the Didymocarpoideae. One, the "microcotyledon", stops growth at a very early point of time and later withers away, while the other, the

"macrocotyledon", does not stop growing and reaches a much larger size than the microcotyledon. It may grow to the size and form of a normal foliage leaf (*e.g. Microchirita*) or may grow to a huge leaf that remains the only leaf of the plant (*Monophyllaea*, *Streptocarpus p.p.*). Anisocotyly is not known outside of Gesneriaceae (see also Jong, 1970, 1978; Jong & Burtt, 1975; Nishii *et al*., 2010, 2017). For functional aspects of anisocotyly see Burtt (1970).

Anisophylly (adj. anisophyllous): In plants with opposite leaf arrangement, the two leaves of a pair being unequal in size. In the case of slight or moderate anisophylly the smaller leaves are only reduced in size, in the case of strong anisophylly the smaller leaves may also take on a different leaf form (scale-like, stipule-like; *e.g. Cyrtandra p.p.*, *Henckelia p.p.*). Complete reduction of the small leaves results in à alterniphylly.

Anterior stamens: The two lateral stamens in abaxial (lower or front) position within the flower; contrast:→ posterior stamens.

Arachnoid indumentum: Spiderweb-like hair-cover. It never forms a dense layer (like in the → matted indumentum) and the hairs are very thin and loosely interwoven with each other (see Xu *et al*., 2008).

Bilobed stigma: Stigma consisting of 2 lobes. In the case of Gesneriaceae a more specific definition is necessary, as the lobes may either represent the lobes of the upper and lower carpel (common in Didymocarpoideae) or fused carpel halves (left- and right position of stigma lobes; found in many Gesnerioideae). In the former type, reduction of the upper lobe may result in a → lingulate or → chiritoid stigma.

Bilocular ovary: Ovary completely divided into two locules by the presence of a septum. In Gesneriaceae bilocular ovaries are rare. Examples include *Deinostigma poilanei*, *Monophyllaea*, *Whytockia* and a few other species in Didymocarpinae; here both carpels are fertile and produce a central, axile placenta. Moreover, bilocular ovaries are characteristic of genera in which the abaxial carpel is reduced and infertile. Here only the upper carpel produces a placenta in axile-adaxial position (*Hemiboea*, spp. of *Primulina*). Contrast: → unilocular ovary.

Boss: A prominent swelling or inflation of the dorsal region of a corolla, typical for a few genera in Gesneriaceae, such as species in *Hemiboea* and *Tribounia*, and *Jerdonia indica* (see Middleton & Möller, 2012).

Bracteole(s): Bract(s) within the cyme, subtending consecutive cyme units, or if cyme reduced to a solitary flower, bract(s) placed at base of pedicel.

Bracteose thyrse/raceme: Thyrse/raceme with the lateral cymes/solitary flowers emerging from the axils of bracts.

Caulescent habit: Plant with distinct stem and distinct internodes, leaves or leaf pairs/whorls thus distinctly spaced. The stem can be erect, ascending or creeping: Contrast: → acaulescent.

Chiritoid stigma: Typical stigma form of the former genus *Chirita*: upper stigma lobe absent, lower lobe enlarged and usually emarginate to bifid. Now known to occur in many genera of Didymocarpoideae-Trichosporeae.

Hypocyrtoid: Referring to the corolla form of some Neotropical Gesneriaceae (based on the former genus *Hypocyrta*): corolla strongly pouched on the dorsal or the ventral side and mouth much constricted: (*e.g. Drymonia p.p., Gasteranthus p.p., Nematanthus p.p.*, *Pachycaulos*, *Pearcea*). The large pouch is the most prominent and conspicuous part of the corolla, while the mouth is reduced to a small opening. An extreme form of the hypocyrtoid corolla is the balloon-shaped flower of some *Pearcea* species.

Isocotyly (adj. isocotylous): Equal size and very limited growth of the two cotyledons after germination. Compare to → anisocotyly.

Isophylly (adj. isophyllous): Equal size of the two leaves of a pair in shoots with opposite leaf arrangement.

Lingulate stigma: Stigma form with upper stigma lobe absent and lower lip tongue-like (not emarginated or bifid).

Macrocotyledon, microcotyledon: → Anisocotyly.

Matted indumentum: Dense white silvery hair-cover found particularly in genera of Loxocarpinae, looking like a layer of matted cashmere wool-like hair; → arachnoid indumentum.

Orthocarpy (adj. orthocarpic): Term relating to the ovary and fruit position in the flower: in orthocarpic fruits, the fruit is positioned in straight continuation of the pedicel, in → plagiocarpic fruits the fruit is held at a distinct angle to the pedicel.

Pair-flowered cyme: Special type of cyme found in Gesneriaceae, Calceolariaceae and Plantaginaceae. Each cyme unit appears to end in a flower pair instead of a single flower (for details and interpretation see Weber, 2013).

Phyllomorph (adj. phyllomorphic): A leaf-stem construct to describe the anomalous development of species in *Streptocarpus* and other genera of Old World Gesneriaceae. It is a leaf-stem construct that consists of a lamina and petiolode (a petiole transitional to and functioning as a stem). A trinity of meristems (petiolode, basal and groove meristem) located at the junction between lamina and petiolode governs the growth of the phyllomorph and the plant, respectively (see also Jong 1970, 1978; Jong & Burtt, 1975; Nishii *et al*., 2015, 2017; this issue).

Plagiocarpy (adj. plagiocarpic): Term relating to the ovary and fruit position. In contrast to → orthocarpic fruits, in plagiocarpic fruits the fruit forms a distinct angle (135° to 90°) with the pedicel (see Weber, 2004).

Posterior stamens: The two stamens in adaxial (upper or rear) position within the flower; contrast: → anterior stamens.

Resupination (adj. resupinate): Upside-down orientation of zygomorphic flowers. The reverse position can be reached in two ways: (1) twisting of the pedicel by 180° (*e.g.*, many species of *Alloplectus*, *Crantzia*, *Glossoloma* and *Nematanthus*, all belonging to Gesnerioideae; resupination is rare in the Didymocarpoideae: *Senyumia*), (2) back-flipping of the flowers (species of *Oreocharis*).

Reticulate seed surface: Testa cells polygonal, with the thickened lateral cell walls forming a raised reticulum. Reticulate seeds are common in Didymocarpoideae (see Beaufort-Murphy, 1983).

Scaly rhizome: Subterranean, usually several cm long stolons consisting of a thin central axis and densely packed pairs or whorls of small fleshy leaf scales. They survive in the ground when the above-ground plant parts die back in the dry period and sprout when favourable conditions return. This special type of rhizome is found in most genera of Gloxiniinae.

Stipe: Thin, stalk-like and sterile basal part of the ovary and fruit, respectively (*e.g. Liebigia*, *Tribounia*, some spp. of *Didymocarpus*).

Stomatomorphic stigma: A mouth-shaped stigma, with stigma lobes arranged like lips.

Striate seed surface: Seeds with thickened walls of testa cells, cells narrow and elongated, forming straight or more frequently spiral rows around the seed body; compare with → reticulate and → verruculose seeds.

Stringy rhizome: Rhizome type characteristic of the genus *Sphaerorrhiza*: subterranean stolons with a succession of tuber-like swellings, often breaking apart and each propagule giving rise to a new plant. Stringy rhizomes are also found in *Seemannia*, here in combination with scaly rhizomes. The latter are produced at the tips of long stringy rhizomes.

Unifoliate: Plant producing a single leaf only. This may represent a → macrocotyledon in short-lived (monocarpic) plants (*e.g.*, *Monophyllaea*, → phyllomorphic spp. of *Streptocarpus*) or a solitary foliage leaf in the successive seasonal shoot units of perennial plants (*e.g.*, *Platystemma*, *Raphiocarpus sesquifolius*).

Unilocular ovary: Interior of ovary not divided by a septum. In most Gesneriaceae, the ovary is unilocular for most of its length with parietal intrusive bifid recurving placentae (with a short bilocular part often being found at the base), but there are genera in which the ovary is à bilocular.

Verruculose seed surface: Seed surface reticulate, with a special type of ornamentation: the outer surface of each testa cell has a large central ± hemispherical protrusion or papilla (see Beaufort-Murphy, 1983). This seed type is found in many species of *Streptocarpus* (*sensu* Nishii *et al*., 2015), particularly of subg. *Streptocarpella*.

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