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# You win some you lose some: updated generic delineations and classification of Gesneriaceae-implications for the family in China

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**Abstract:** Over the last two decades molecular phylogenetic research on Gesneriaceae has greatly advanced our understanding of species relationships and generic delimitations. It has allowed the proposal of a new classification of the family that is thought to reflect the natural relationships of the taxa better than traditional morphological classifications. Dramatic taxonomic changes were implemented affecting the classification of Gesneriaceae in China. Many traditional genera have been split, merged or newly defined. Additionally, new genera have been established based on recently collected material, illustrating on the one hand gaps in fieldwork in China, and on the other hand the biological richness of the Gesneriaceae in China. Here, we summarize and present an overview of our work and the taxonomic consequences.

**Key words:** China, classification, Gesneriaceae, molecular phylogenies, systematics

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## 得与失: 苦苣苔科新的属级界定与分类系统 ——中国该科植物之变迁

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**摘要:** 过去 20 年对苦苣苔科植物的分子系统学研究已经极大地拓展了对这个科的种间关系与属一级之界定的理解。该文提供了一个苦苣苔科植物新分类系统, 与传统的经典形态学分类系统比较, 这一新系统被认为能更好地反映科下分类单元彼此之间的自然关系。众多传统意义上的属被分割、合并或者重新定义, 这些巨大的分类变动正在影响着中国的苦苣苔科植物系统分类。此外, 基于最近采集的材料, 一些新属得以建立, 一方面说

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明在中国还有相当多的野外工作需要做;而另一方面则再次证明了中国的苦苣苔科植物多样性是如此之丰富。在此,针对目前已经完成的工作和分类结论,对中国苦苣苔科植物的新分类系统进行了总结与概述,并深入地讨论了部分传统分类学上存在困惑的疑难属。

**关键词:** 中国, 分类, 苦苣苔科, 分子系统学, 系统分类

Gesneriaceae are a medium-sized family in the order Lamiales, with main distribution in the tropics and subtropics of both the Old and the New World. Particularly rich in Gesneriaceae is China. In the original (Chinese) version of the “*Flora of China*”, Wang et al (1990) listed 413 species in 56 genera, in the later English version (Wang et al, 1998) the number increased to 442 species, while the number of genera remained the same: 354 species and 25 genera (many of them monotypic), respectively, were considered to be endemic. Without a doubt, China is a significant centre of diversity of the family, with the majority of taxa found in China’s South and Southwest, in the provinces of Yunnan, Guizhou, Guangdong and Guangxi Autonomous Region (Wang et al, 1992). The species density decreases northwards and the furthest locality North are the Yenshan Mts at 41°N.

In the last two decades, the implementation of molecular methods has resulted in worldwide dramatic changes in the definition and infrafamilial classification of angiosperm families and in the delineation of genera attributed to them. This is particularly true for the Chinese Gesneriaceae, in which an unproportionally high number of taxonomic changes has been made. In the following, the partly dramatic changes of traditional generic concepts of Chinese Gesneriaceae are surveyed, and the position of the Chinese Gesneriaceae in recent classifications are shown and discussed.

## 1 Classifications of Gesneriaceae and amendments at generic level

Traditionally, the family Gesneriaceae was subdivided into two subfamilies, Gesnerioideae and Cyrtandroideae (e. g., Bentham, 1876; Fritsch, 1893–1894; Burt, 1963). The last formal classification based on morphology (and partly cytogenetic data) was that of Burt and Wiehler (1995), who recognized three subfamilies: (1) Gesnerioideae (56 genera; predominantly

Neotropical); (2) Coronantheroideae (9 genera, southern hemisphere; temperate South America to Australia); (3) Cyrtandroideae (= now Didymocarpoideae; 82 genera, chiefly paleotropical, including three genera in Europe). The distribution of the c. 3 400 species is roughly equal between the Neotropics and Palaeotropics.

Traditional classifications were based on a few key morphological features such as seed anatomy, post-germination characteristics of the seedlings, nectary structure and ovary position. Thus, the Neotropical Gesneriaceae were characterized by the presence of seed endosperm, isocotily (both cotyledons showing equal and limited growth after germination), a nectary often consisting of separate glands, and often partly or fully inferior ovary position, while the Palaeotropical Gesneriaceae were characterized by the lack of endosperm, by continued growth of one cotyledon after germination (anisocotily; Fritsch, 1904; Burt, 1963, 1970; Jong, 1970; Nishii et al, 2004; Mantegazza et al, 2007), a basically ring-shaped nectary and superior ovary position. Subfam. Coronantheroideae was characterized by isocotylous seedlings, a nectary ‘adnate’ to the ovary base, and superior ovary position.

Burt & Wiehler (1995) subdivided the three subfamilies into the following tribes (number of genera in brackets): [1] Gesnerioideae: Gloxinieae (23), Episcieae (21), Beslerieae (8), Napeantheae (1) and Gesnerieae (2); [2] Coronantheroideae: only Coronanthereae (9), [3] Cyrtandroideae: Klugieae (7), Didymocarpeae (64), Trichosporeae (6), Cyrtandreae (3), Titanotricheae (1).

The first classification taking to some extent molecular data into account, was that of Weber (2004). However, particularly for the Palaeotropical Gesneriaceae the molecular data situation was insufficient and no formal classification was presented. Weber (2004), therefore, proposed a provisional classification, recognising four informal groups: (1) Coronantheroid Gesneriaceae;

(2) Gesnerioid Gesneriaceae; (3) Epithematooid Gesneriaceae; (4) Didymocarpooid Gesneriaceae. The latter and the largest group was subdivided into morphogeographical assemblages: ‘Basal Asiatic genera’, ‘European genera’, ‘African and Madagascan genera’ and ‘Advanced Asiatic and Malesian genera’.

Especially by the work of the first author (MMO) and associates, in the last 10 years a comprehensive data basis was established for the palaeotropical Gesneriaceae that enabled a better understanding of the phylogenetic diversification of that large and enormously diversified group. In parallel, also considerable progress was made with regard to Neotropical Gesneriaceae, including the work of one of the authors (JLC). In 2013, a new formal classification was published that was entirely based on molecular data (Weber et al, 2013).

By the inclusion of *Sanango*, which was repeatedly shown to be sister to Gesneriaceae in previous molecular studies, three subfamilies were recognised: Sanangoideae (only *Sanango*), Gesnerioideae and Didymocarpoideae. Wiehler’s subfam. Coronantheroideae was included as a tribe (Coronanthereae) in Gesnerioideae. Apart from the traditional Gesnerioideae (subdivided into the tribes Beslerieae, Napenatheae and Gesnerieae) a fifth, and rather aberrant, tribe was included in Gesnerioideae: the monospecific Titanotricheae from E Asia. This is the only tribe that does not occur in the Neotropics or the southern hemisphere, but with a single species (*Titanotrichum oldhamii*) in East Asia (E China, Taiwan region of China, S Japan). The former Cyrtandoideae, now referred to as Didymocarpoideae, were subdivided into two tribes: Epithemateae and Trichosporeae. The former is apparently an ancient assemblage of few and rather isolated genera that fall into four subtribes, while the latter includes a large number of genera and is obviously still in a stage of active evolution. In this tribe provisionally 10 subtribes have been recognised, the by far largest being subtribe Didymocarpinae.

Apart from a new infrafamilial classification of the family, another important aspect of the molecular work is the improvement in the understanding of generic delimitations. In fact, a wealth of taxonomic changes resulted from the molecular studies, both with respect to

Neotropical and Palaeotropical taxa. On the one hand, many genera have been reduced to synonymy (e. g. Möller et al, 2011b; Weber et al, 2011b,c; Nishii et al, 2015; Puglisi et al, in press), on the other hand, some genera have been revived (e. g. *Centrosolenia*: Mora & Clark, 2016; *Crantzia*: Clark, 2005; Clark et al, 2006; *Damrongia*: Weber et al, 2011a; *Glossoloma*: Clark et al, 2006; Clark, 2009; *Liebigia*: Weber et al, 2011a; *Mandirola*: Roalson et al, 2005a,b; Boggan 2006; *Seemannia*: Roalson et al, 2005a,b; Boggan 2006; *Trichodrymonia*: Mora & Clark 2016) or newly described (e. g. *Billolivia*, Middleton et al, 2014; *Chatuemsia*: Araujo et al, 2010; *Christopheria*: Smith & Clark 2013; *Chayamaritia*: Middleton et al, 2015; *Glabrella*: Möller et al, 2014; *Gloxinella*: Roalson et al, 2005a,b, Boggan, 2006; *Gloxiniopsis*: Roalson et al, 2005a,b; Boggan, 2006; *Lesia*: Smith & Clark, 2013; *Litostigma*: Wei et al, 2010; *Pachycaulos*: Smith & Clark, 2013; *Pagothyra*: Smith & Clark, 2013; *Somrania*: Middleton & Triboun, 2012; *Sphaerorrhiza*: Roalson et al, 2005a,b; *Tribounia*: Middleton & Möller, 2012). In many cases the species content changed dramatically (e. g., *Primulina*: increment from 1 to >150 species; *Alloplectus*: reduction from c. 140 to 5 species: Clark et al, 2006).

## 2 Position of Chinese Generiaceae in the classification of Weber et al (2013)

In Table 1 the classification of Weber et al (2013) is given, with indication of the position of genera presently recognised for China. Distribution is either endemic or includes adjacent countries (some genera with main distribution further South and reaching China with a few or a single species only).

A most striking discrepancy with former classifications is the position of *Titanotrichum*. This monotypic genus was established (based on *Rehmannia oldhamii* Hemsl.) by Solereder in 1909 and placed in Scrophulariaceae. It is characterised by a terminal racemose inflorescence and the presence of masses of seedling-like propagules in the upper part of the inflorescence (Wang et al, 2004b). Burt (1963, 1977) earmarked *Titanotrichum* as a ‘genus anomalum’ within Gesneriaceae-

Table 1 Classification of Gesneriaceae according to Weber et al (2013) and taxa represented in China

Rank	No. of genera/species no./genera represented in China	
<b>Gesneriaceae</b> Rich. & Juss. in DC.		
1. Subfam. Sanangoideae A. Weber, J. L. Clark & Mich. Möller	1/	1
2. Subfam. <b>Gesnerioideae</b> Burnett		
2.1. Tribe <b>Titanotricheae</b> Yamaz. ex W. T. Wang	1/	1 <i>Titanotrichum</i> Soler.
2.2. Tribe Napeantheae Wiehler	1/	20+
2.3. Tribe Beslerieae Bartl.		
2.3.1. Subtribe Besleriinae G. Don	4/	239+
2.3.2. Subtribe Anetanthinae A. Weber & J. L. Clark	5/	12+
2.4. Tribe Coronanthereae Fritsch		
2.4.1. Subtribe Coronantherinae Fritsch	2/	14–21
2.4.2. Subtribe Mitrariinae Hanst.	4/	4
2.4.3. Subtribe Negriinae V. L. Woo, J. F. Smith & Garn.–Jones	3/	3
2.5. Tribe Gesnerieae Dumort. (1829)		
2.5.1. Subtribe Gesneriinae Link	4/	100
2.5.2. Subtribe Gloxiniinae G. Don	21/	200+
2.5.3. Subtribe Columneinae Hanst.	26/	525+
2.5.4. Subtribe Sphaerorrhizinae A. Weber & J. L. Clark	1/	2
2.5.5. Subtribe Ligeriinae Hanst.	3/	91
3. Subfam. <b>Didymocarpoideae</b> Arn.		
3.1. Tribe <b>Epithemateae</b> C. B. Clarke		
3.1.1. Subtribe <b>Loxotidinae</b> G. Don	1/	≈15 <i>Rhynchoglossum</i> Blume
3.1.2. Subtribe <b>Monophyllacinae</b> A. Weber & Mich. Möller	2/	38+ <i>Whytockia</i> W. W. Sm.
3.1.3. Subtribe <b>Loxoninae</b> A. DC.	2(3)/	9+ ? <i>Gyogyne</i> W. T. Wang, <i>Stauranthera</i> Benth.
3.1.4. Subtribe <b>Epithematinae</b> DC. ex Meisn.	1/	20+ <i>Epithema</i> Blume
3.2. Tribe <b>Trichosporeae</b> Nees		
3.2.01. Subtribe Jerdoniinae A. Weber & Mich. Möller	1/1	1
3.2.02. Subtribe <b>Corallo-discinae</b> A. Weber & Mich. Möller	1/	3–5 <i>Corallo-discus</i> Batalin
3.2.03. Subtribe Tetraphyllinae A. Weber & Mich. Möller	1/	3
3.2.04. Subtribe <b>Leptoboecinae</b> C. B. Clarke	6/	43 <i>Beccarinda</i> Kuntze, <i>Boeica</i> C.B.Clarke, <i>Leptoboeca</i> Benth., <i>Platystemma</i> Wall., <i>Rhynchotechum</i> Blume
3.2.05. Subtribe Ramondinae DC. ex Meisn.	3(2)/	5
3.2.06. Subtribe <b>Litostigminae</b> A. Weber & Mich. Möller	1/	2 <i>Litostigma</i> G. Wei, F. Wen & Mich. Möller
3.2.07. Subtribe Streptocarpinae Ivanina	1/	177
3.2.08. Subtribe Didissandrinae A. Weber & Mich. Möller	2/	10
3.2.09. Subtribe <b>Loxocarpinae</b> A. DC.	14/	202+ <i>Damrongia</i> Kerr, <i>Dorcoceras</i> Bunge, <i>Middletonia</i> C. Puglisi, <i>Ornithoboeca</i> Parish ex C. B. Clarke, <i>Paraboeca</i> (C. B. Clarke) Ridl., <i>Rhabdothamnopsis</i> Hemsl.
3.2.10. Subtribe <b>Didymocarpinae</b> G. Don	32	1660–1830 <i>Aeschynanthus</i> Jack, <i>Allocheilos</i> W. T. Wang, <i>Allostigma</i> W. T. Wang, <i>Anna</i> Pellegr., <i>Briggsiopsis</i> K. Y. Pan, <i>Cathayanthe</i> Chun, <i>Conandron</i> Sieb. & Zucc., <i>Cyrtandra</i> J. R. Forst. & G. Forst., <i>Didymocarpus</i> Wall., <i>Didymostigma</i> W. T. Wang, <i>Glabrella</i> Mich. Möller & W. H. Chen, <i>Gyrocheilos</i> W. T. Wang, <i>Hemiboea</i> C. B. Clarke, <i>Henckelia</i> Spreng., <i>Loxostigma</i> C. B. Clarke, <i>Lysionotus</i> D. Don, <i>Metapetrocosmea</i> W. T. Wang, <i>Microchirita</i> (C. B. Clarke) Yin Z. Wang, <i>Oreocharis</i> Benth., <i>Petrocodon</i> Hance, <i>Petrocosmea</i> Oliv., <i>Primulina</i> Hance, <i>Pseudochirita</i> W. T. Wang, <i>Raphiocarpus</i> Chun

Bold face: Taxon represented in China; Underlined: Endemic to China; Spaced print: New genus for China; ?: Genus maybe extinct.

ae. Based on the aberrant morphology, Wang et al (1990) established a separate tribe in subfam. Cyrtandroideae (now Didymocarpoideae) for its accommodation, while Weber (2004) proposed to exclude it from Gesneriaceae. The molecular study of Wang et al (2004a) confirmed its position within Gesneriaceae, but yielded the surprising result that it is more closely allied to the New World than to the Old World Gesneriaceae. Weber et al (2013), therefore, included *Titanotrichum* in subfam. Gesnerioideae as a monospecific tribe. Apart from the geographical distribution (SE mainland China, Tai-

wan region of China, S Japan) which is difficult to explain for a member of subfam. Gesnerioideae, this taxonomic placement is in line with the isocotylous seedlings (the interpretation of Wang et al, 2002 as anisocotylous is erroneous). Whether the distribution of *Titanotrichum* is to be regarded as a northern outlier of the southern hemisphere Gesneriaceae or an early immigrant from the Neotropics remains unexplained. In the isocotylous seedlings it is similar to both groups, but other characters, including the curious propagules, indicate an isolated position.

Table 2 List of present and past genera of Chinese Gesneriaceae.

Genus (alphabet.) (Chinese name)	Intrafamilial position: Subfamily Tribe Subtribe	Distribution	Species number	Species no. in China (endemic)	Tax. status	Reference	Remarks
<i>Aeschynanthus</i> Jack 毛茛苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	From S China, N & S India throughout Malesia to New Guinea and the Solomon Islands	≈185	≈34 (≈13)	Emended by inclusion of <i>Micraeschynanthus</i>	Middleton, 2007	The inclusion of the monotypic genus <i>Micraeschy- nanthus</i> (Malay peninsula) has little bearing on the definition of <i>Aeschynanthus</i>
<i>Allocheilos</i> W.T.Wang 异唇苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China (Guizhou, E Yunnan)	2	2 (2)	No change		
<i>Allostigma</i> W.T. Wang 异片苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China	1	1 (1)	No change		See text under <i>Oreocharis</i>
<i>Ancylostemon</i> Craib 直瓣苣苔属			–	–	Sunk into <i>Oreocharis</i>	Müller et al, 2011b; Chen et al, 2014b	See text under <i>Oreocharis</i>
<i>Anna</i> Pellegr. 大苞苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	China, N Vietnam	4	4 (3)	No change		
<i>Beccarinda</i> Kuntze 横蒴苣苔属	Didymocarpoideae Trichosporeae <i>Leptoboehniae</i>	NE India, Burma, S China, Vietnam, Su- matra	≈8	5 (4)	No change		
<i>Boea</i> Comm. ex Lam. 旋蒴苣苔属			10	–	Redefined; Chinese spp. now in <i>Dorcoceras</i> and <i>Damrongia</i>	Puglisi et al, in press	See text under <i>Boea</i>
<i>Boeica</i> C.B. Clarke 短筒苣苔属	Didymocarpoideae Trichosporeae <i>Leptoboehniae</i>	Bhutan, S China, N & NE India, Myan- mar, N Vietnam, NW Malaya	≈12	7 (3)	No change		
<i>Bournea</i> Oliv. 四数苣苔属			–	–	Sunk into <i>Oreocharis</i>	Müller et al, 2011b	See text under <i>Oreocharis</i>
<i>Briggsia</i> Craib 粗筒苣苔属			–	–	Partly sunk into <i>Oreo- charis</i> , partly transferred to <i>Loxostigma</i> , and two spp. forming the new genus <i>Glabrella</i>	Müller et al, 2011b; Chen et al, 2014b; Müller et al, 2014	See text under <i>Briggsia</i> and <i>Oreocharis</i>
<i>Briggsiopsis</i> K.Y.Pan 筒花苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China (C & S Si- chuan, NE Yunnan, Guizhou)	1	1 (1)	No change		
<i>Calcareoboaea</i> C.Y. Wu ex H.W.Li 朱红苣苔属			–	–	Sunk into <i>Petrocodon</i>	Wang et al, 2011; Weber et al, 2011b	See text under <i>Petrocodon</i>
<i>Chirita</i> Buch. –Ham. ex D.Don 唇柱苣苔属			–	–	Split into 5 genera and synonymisation with <i>Henckelia</i>	Wang et al, 2011; Weber et al, 2011a	See text under <i>Chirita</i>
<i>Chiritopsis</i> W.T. Wang 小花苣苔属			–	–	Sunk into <i>Primulina</i>	Wang et al, 2011; Weber et al, 2011a	See text under <i>Chirita</i>
<i>Cathyanthe</i> Chun 扁蒴苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China (Hainan)	1	1 (1)	No change		
<i>Conandron</i> Sieb. & Zucc. 苦苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	E China, Taiwan re- gion of China, S Ja- pan	1	1	No change		
<i>Corallodiscus</i> Batalin 珊瑚苣苔属	Didymocarpoideae Trichosporeae Corallodisceae	Bhutan, China, N & NE India, Nepal, Thailand	3–5	3	No change		
<i>Cyrtandra</i> J.R. Forst. & G.Forst. 浆果苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	Nicobar Islands and S Thailand through Malesia incl. Taiwan region of China and the S Pacific to the Hawaiian Islands	652–818	1 (1)	No change		

## 续表2

Genus (alphabet.) (Chinese name)	Intrafamilial position; Subfamily Tribe Subtribe	Distribution	Species number	Species no. in China (endemic)	Tax. status	Reference	Remarks
<b>Damrongia</b> Kerr 丹氏苣苔属(新拟)	Didymocarpoideae Trichosporeae Loxocarpinae	China to Sumatra	10	1 (1)	Re-established for particular species of erstwhile <i>Chirita</i> ; inclusion of <i>Boea clarkeana</i> Hemsl. and the Asian species described in <i>Streptocarpus</i>	Weber et al, 2011a; Puglisi et al, in press	See text under <i>Chirita</i> and <i>Damrongia</i>
<i>Dayaoshania</i> W.T. Wang 瑶山苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<i>Deinocheilos</i> W.T. Wang 全唇苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<b>Didymocarpus</b> Wall. 长蒴苣苔属	Didymocarpoideae Trichosporeae Didymocarpinae	from N and NE India, Nepal and S China southwards to the Malay Peninsula and N Sumatra	>70	≈30 (≈24)	Some spp. transferred to <i>Petrocodon</i>	Weber et al, 2011b	See text under <i>Petrocodon</i>
<b>Didymostigma</b> W.T.Wang 双片苣苔属	Didymocarpoideae Trichosporeae Didymocarpinae	SE China (Guangdong, Fujian, Guangxi)	3	3 (3)	No change		
<i>Dolicholoma</i> D.Fang & W.T. Wang 长檐苣苔属			-	-	Sunk into <i>Petrocodon</i>	Weber et al, 2011b	See text under <i>Petrocodon</i>
<b>Dorcoceras</b> Bunge 羚角苣苔属(新拟)	Didymocarpoideae Trichosporeae Loxocarpinae	China, Thailand, Cambodia, Vietnam, Philippines and Indonesia	4	2 (1 or 2?)	Re-established for particular (non-Australasian) species of <i>Boea</i>	Puglisi et al, in press	See text under <i>Boea</i> and <i>Dorcoceras</i>
<b>Epithema</b> Blume 盾座苣苔属	Didymocarpoideae Epithemateae Epitheminae	S China, Taiwan region of China	20	2	No change at genus level	revised by Bransgrove & Middleton, 2015	
<b>Glabrella</b> Mich. Möller & W.H. Chen 光叶苣苔属	Didymocarpoideae Trichosporeae Didymocarpinae	S China, Taiwan region of China	3	3 (3)	New genus established for 3 spp. of <i>Briggsia</i> not to be included in <i>Oreocharis</i> or <i>Loxostigma</i>	Weber et al, 2014; Wen et al, 2015a,b	See text under <i>Briggsia</i> and <i>Oreocharis</i>
<b>Gyrocheilos</b> W.T.Wang 圆唇苣苔属	Didymocarpoideae Trichosporeae Didymocarpinae	S China (Guangxi, Guangdong, SE Guizhou), Vietnam	5	4 (3)	No change		
<b>Gyrogyne</b> W.T.Wang 圆果苣苔属	Didymocarpoideae Epithemateae Loxoniinae (?)	S China (W Guangxi)	1	1 (1)	Position in Epithemateae-Loxoniinae uncertain		Probably extinct
<b>Hemiboea</b> C.B.Clarke 半蒴苣苔属	Didymocarpoideae Trichosporeae Didymocarpinae	C & S China, Taiwan region of China, N Vietnam, S Japan	31	31 (30)	Inclusion of <i>Metabriggsia</i> (2 spp.)	Weber et al, 2011c	Inclusion does not affect the traditional concept of <i>Hemiboea</i>
<i>Hemiboeopsis</i> W. T. Wang			-	-	Sunk into <i>Henckelia</i>	Weber et al, 2011a	
<b>Henckelia</b> Spreng. 南洋苣苔属/ 汉克丽亚花属	Didymocarpoideae Trichosporeae Didymocarpinae	From S China to Sri Lanka	c. 55	23 (12)	Redefined to include <i>Chirita</i> p.p. (excl. <i>Microchirita</i> and <i>Primulina</i> ) and <i>Hemiboeopsis</i> , and to exclude <i>Codonoboaea</i>	Weber et al, 2011a; Middleton et al, 2013	See text under <i>Chirita</i> and <i>Henckelia</i>
<i>Isometrum</i> Craib 金盏苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<i>Lagarosolen</i> W.T. Wang 细筒苣苔属			-	-	Sunk into <i>Petrocodon</i>	Weber et al, 2011b	See text under <i>Petrocodon</i>
<b>Leptoboea</b> Benth. 细蒴苣苔属	Didymocarpoideae Trichosporeae Leptoboeinae	Bhutan, N and NE India, S China (Yunnan), Myanmar, Thailand	2-3	1	No change		



续表2

Genus (alphabet.) (Chinese name)	Infrafamilial position; Subfamily Tribe Subtribe	Distribution	Species number	Species no. in China (endemic)	Tax. status	Reference	Remarks
<i>Litostigma</i> Y.G. Wei, F.Wen & Mich. Möller 凹柱苣苔属	Didymocarpoideae Trichosporeae Litostigminae	China (Guizhou, Yunnan)	2	2 (2)	Genus recently established	Wei et al, 2010	See text under <i>Litostigma</i>
<i>Loxostigma</i> C.B.Clarke 斜片苣苔属(新 拟)/紫花苣苔属	Didymocarpoideae Trichosporeae Didymocarpiniae	S China (Sichuan, Yunnan, Guizhou, Guangxi), N Vietnam	11	11 (8)	Recently inclusion of caulescent <i>Briggsia</i> species	Möller et al, 2014	See text under <i>Briggsia</i>
<i>Lysionotus</i> D.Don 吊石苣苔属	Didymocarpoideae Trichosporeae Didymocarpiniae	From N India and Nepal eastwards through N Thailand, N Vietnam and S China to S Japan	28	26 (18)	No change		
<i>Metabriggsia</i> W. T. Wang 单座苣苔属			-	-	Included in <i>Hemiboea</i>	Weber et al, 2011c	
<i>Metapetrocosmea</i> W.T.Wang 盾叶苣苔属	Didymocarpoideae Trichosporeae Didymocarpiniae	S China (Hainan)	1	1	No change		
<i>Microchirita</i> (C.B. Clarke) Y.Z.Wang 钩序苣苔属	Didymocarpoideae Trichosporeae Didymocarpiniae	From the Western Ghats of India to the foothills of the Hima- layas, through conti- nental SE Asia to Sumatra, Borneo and Java	≈18	2 (1)	Raised from <i>Chirita</i> sect. <i>Microchirita</i> to generic rank	Wang et al, 2011; Weber et al, 2011a	See text under <i>Chirita</i>
<i>Middletonia</i> C. Puglisi 米氏苣苔属	Didymocarpoideae Trichosporeae Loxocarpiniae	India, Bangladesh, Bhutan, China, Burma, Thailand, Laos, Cambodia, Vietnam, Malaysia	4	1	Genus recently estab- lished for four species of <i>Paraboea</i>	Puglisi et al, in press	See text under <i>Middletonia</i> and <i>Paraboea</i>
<i>Opithandra</i> B.L. Burt 后蕊苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<i>Oreocharis</i> Benth. 马铃薯苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpiniae</i>	China, Thailand, Vietnam, Myanmar, Bhutan, NE India, Japan	>106	>102 (>98)	Expanded to include <i>Ancylostemon</i> Craib, <i>Bournea</i> Oliv., <i>Briggsia</i> <i>Craib p. p.</i> -incl. type, <i>Dayaoshania</i> W. T. Wang, <i>Deinocheilos</i> W. T. Wang, <i>Isometrum</i> Craib, <i>Opithandra</i> B. L. Burt, <i>Paraisometrum</i> W. T. Wang, <i>Thamnocharis</i> W. T. Wang, and <i>Tremacron</i> Craib; Inclusion of further ten spp.of <i>Briggsia</i>	Möller et al, 2011b; Möller et al, 2014; Chen et al, 2014b	See text under <i>Briggsia</i> and <i>Oreocharis</i>
<i>Ornithoboea</i> Parish ex C.B.Clarke 喜鹊苣苔属	Didymocarpoideae Trichosporeae Loxocarpiniae	From S China and Vietnam southwards to N Penins. Malaysia	16	5 (1)	No change	Revised by Scott & Mid- dleton, 2014	
<i>Paraboea</i> (C.B. Clarke) Ridl. 蛛毛苣苔属	Didymocarpoideae Trichosporeae Loxocarpiniae	Bhutan, China, Indonesia, Malaysia, Myanmar, Philippines, Thailand, Vietnam	132	26 (14)	Expanded by inclusion of <i>Phylloboea</i> and <i>Trisepalum</i> ; removal of four species and place- ment in the new genus <i>Middletonia</i>	Puglisi et al, 2011  Puglisi et al, in press	See text under <i>Paraboea</i> and <i>Middletonia</i>
<i>Paraisometrum</i> W. T.Wang 弥勒苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<i>Paralagarosolen</i> Y. G. Wei 方鼎苣苔属			-	-	Sunk into <i>Petrocodon</i>	Wang et al, 2011; Weber et al, 2011b	See text under <i>Petrocodon</i>

续表2

Genus (alphabet.) (Chinese name)	Infrafamilial position: Subfamily Tribe Subtribe	Distribution	Species number	Species no. in China (endemic)	Tax. status	Reference	Remarks
<b>Petrocodon</b> 石山苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	China, N Vietnam, NE Thailand	29	28 (27)	Expanded to include <i>Calcareoboea</i> C. Y. Wu ex H. W. Li, <i>Didymo-</i> <i>carpus</i> Wall. <i>p.p.</i> (ex- cl. type), <i>Dolicholoma</i> D. Fang & W. T. Wang, <i>Lagarosolen</i> W. T. Wang, <i>Paralaga-</i> <i>rosolen</i> Y. G. Wei, <i>Tengia</i> Chun and <i>Wentsaiboea</i> D. Fang & D. H. Qin, <i>p.p.</i> (excl. type)	Wang et al, 2011; Weber et al, 2011b	See text under <i>Petrocodon</i>
<b>Petrocosmea</b> 石蝴蝶属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	NE India, S China, Myanmar, Thailand, S Vietnam.	42	34 (34)	No change		
<b>Platystemma</b> 堇叶苣苔属	Didymocarpoideae Trichosporeae <i>Leptoboeinae</i>	Nepal, Bhutan, N India, SW China	1	1	No change		
<b>Primulina</b> 报春苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	Essentially southern half of China and Vi- etnam	>169	>154 (>151)	Enormous expansion of the previously mono- typic genus by inclu- sion of <i>Chirita</i> sect. <i>Gibbosaccus</i> , <i>Chiritop-</i> <i>sis</i> , <i>Deltocheilos</i> , and <i>Wentsaiboea p.p.</i> (incl. type)	Wang et al, 2011; Weber et al, 2011a	See text under <i>Chirita</i>
<b>Pseudochirita</b> 异裂苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China (C & W Guangxi), Vietnam	1	1 (1)	No change		
<b>Raphiocarpus</b> 漏斗苣苔属	Didymocarpoideae Trichosporeae <i>Didymocarpinae</i>	S China and N & C Vietnam	13	8 (7)	No change since We- ber 2004, but changes to be expected		
<b>Rhabdothamnopsis</b> 长冠苣苔属	Didymocarpoideae Trichosporeae <i>Loxocarpinae</i>	S China	1	1 (1)	No change		
<b>Rhynchoglossum</b> 尖舌苣苔属	Didymocarpoideae Epithemateae <i>Loxotidinae</i>	From India and S China to New Guinea, one (to 3?) spp. in C America	≈ 15	2 (1)	No change		Recent descrip- tion of 2 new and morphologically odd spp. from Thailand ( Pat- tharahratricin 2014)
<b>Rhynchotechum</b> 线柱苣苔属	Didymocarpoideae Trichosporeae <i>Leptoboeinae</i>	NE India, Nepal, Bhutan, SW & S China, SE Asia and Malesia to New Guinea	21	6 (2)	No change		
<b>Stauranthera</b> 十字苣苔属	Didymocarpoideae Epithemateae <i>Loxoninae</i>	Malesia, S China	≈ 5	1	No change		Revision in prep. (Weber, in prep.)
<i>Streptocarpus</i> , Asiatic species 扭果花属/海角苣 苔属	-	-	-	-	Sunk into <i>Damrongia</i>	Puglisi et al, in press	See text under <i>Damrongia</i>
<i>Tengia</i> Chun 世纬苣苔属	-	-	-	-	Sunk into <i>Petrocodon</i>	Wang et al, 2011; Weber et al, 2011b	See text under <i>Petrocodon</i>
<i>Thamnocharis</i> W. T. Wang 辐花苣苔属	-	-	-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<b>Titanotrichum</b> 台闽苣苔属/俄氏 草属	Gesnerioideae <i>Titanotricheae</i>	SE China, Taiwan region of China, S Japan	1	1	Placed in subfam. Gesnerioideae	Wang et al, 2004a; Perret et al, 2013; Weber et al, 2013	



续表2

Genus (alphabet.) (Chinese name)	Infrafamilial position; Subfamily Tribe Subtribe	Distribution	Species number	Species no. in China (endemic)	Tax. status	Reference	Remarks
<i>Tremacron</i> Craib 短檐苣苔属			-	-	Sunk into <i>Oreocharis</i>	Möller et al, 2011b	See text under <i>Oreocharis</i>
<i>Trisepalum</i> C. B. Clarke 唇萼苣苔属			-	-	Sunk into <i>Paraboea</i>	Puglisi et al, 2011	See text under <i>Paraboea</i>
<i>Wentsaiboea</i> D.Fang & D.H.Qin 文采苣苔属			-	-	Partly (incl. type) sunk into <i>Primulina</i> , partly into <i>Petrocodon</i>	Weber et al, 2011a,b	See text under <i>Chirita</i> and <i>Pet- rocodon</i>
<b><i>Whytockia</i></b> W. W. Sm. 异叶苣苔属	Didymocarpoideae Epithemateae Monophyllaeinae	S China, Taiwan re- gion of China	8	8 (8)	No change		

Note: Presently accepted genera in bold face. Genera that have been synonymised since the publication of the "Flora of China" (Wang 1990, Wang et al, 1998) are given in square brackets and not bold. Infrafamilial position according to Weber et al (2013).

With regard to subfam. **Didymocarpoideae**, both tribes, Epithemateae and Trichosporeae, are represented in China.

In tribe **Epithemateae**, which is apparently a relict tribe with morphologically rather odd and isolated genera, all four subtribes are represented in China. From the seven genera two are missing in China: *Monophyllaea* in subtribe Monophyllaeinae (this thus contains only *Whytockia*, with some six species in South China and Taiwan region of China), and *Loxonia* in Loxoniinae (containing in China *Stauranthera* and, with some uncertainty, the ill-known and possibly extinct *Gyrogyne*). In both cases the genera are distributed in the SE Asian tropics: *Monophyllaea* includes more than 40 species, with distribution throughout Malesia (Sumatra to New Guinea and S Thailand to Java), *Loxonia* comprises three species restricted to western Malesia (Sumatra, Malay Peninsula and Borneo). *Whytockia* is particularly remarkable as morphological studies (Weber, 1976, 1982) indicate that the genus has retained primitive characters in relation to *Monophyllaea*, suggesting that subtribe Monophyllaeinae has originated in the extratropics and, after reaching the South East Asian tropics, radiated into the many species of *Monophyllaea*. *Stauranthera* and *Gyrogyne* are represented with a single species each in China, *Rhynchoglossum* and *Epithema* with two species each.

Tribe **Trichosporeae**, with 10 subtribes tentatively recognised by Weber et al (2013), is represented by five subtribes in China.

Among the more primitive alliances, subtribe **Corallodiscinae**, with the single genus *Corallodiscus*, is remarkable. Its few species are rosette plants with scapose inflorescences and tetrastaminate flowers.

Morphologically heterogeneous is subtribe **Leptoboeinae**, which is represented by almost all of its genera in China (the only lacking genus is the South Indian *Championia*, the inclusion of which in Leptoboeinae still requires confirmation). Leptoboeinae includes rosette plants (*Beccarinda*), sub-shrubby caulescent plants (*Leptoboea*, *Boeica*, *Rhynchotechum*) and unifoliate plants (*Platystemma*). *Leptoboea*, *Boeica* and *Rhynchotechum* have (correctly!) thought to be closely related in older classifications, but Burt (1963) assumed a close relationship of *Rhynchotechum* with *Cyrtandra*, placing both in subfam. Cyrtandroideae tribe Cyrtandreae, because the two genera have indehiscent, berry-like fruits in common. Apart from the changes in taxonomic position as compared to former classifications, no changes in the definition of the genera have been prompted by molecular systematic studies.

Another monogeneric subtribe is **Litostigminae**. The genus *Litostigma* was recently established in 2010, based on newly collected material from Guizhou and Yunnan. The genus represents an important morphological link between the basal lineages of tribe Trichosporeae with seeds without elaborate testa cell ornamentation, straight fruit and septicidal and loculicidal dehiscence and derived lineages with predominantly loculicidal dehiscence and two stamens (Wei et al, 2010).

Subtribe **Loxocarpinae** is the second largest subtribe of Trichosporeae. In total it includes about a dozen genera. Two of them, *Dorcoceras* and *Middletonia*, have been (re-)established very recently (Puglisi et al, in press), and both are represented in China, together with *Damrongia*, *Ornithoboea*, *Paraboea* and *Rhabdothamnopsis*. The latter is with a single species endemic to China, while the remaining genera have their main distribution mostly further south. A characteristic feature of the subtribe (but not present in all taxa) is the twisted capsule. Both in this and the following subtribe many changes in generic delimitations have been induced by the recent molecular-systematic investigations. These are listed in Table 2 and discussed in the following chapter.

Subtribe **Didymocarpinae** is by far the largest subtribe of tribe Trichosporeae. It includes over 30 genera, with 24 represented in China. Six genera with one or very few species (i.e. *Allocheilos*, *Allostigma*, *Briggsiopsis*, *Cathayanthe*, *Didymostigma*, *Metapetrocosmea*) are endemic to this country, others have their main distribution elsewhere and reach with one or few species the southernmost part of China (e. g., *Cyrtandra*, with >800 species is the largest genus of Gesneriaceae, reaches with a single species to South Taiwan, China). *Microrchirita* with a wide distribution from the Western Ghats of India, the foothills of the Himalayas, through continental SE Asia into Sumatra, Borneo and Java, has two species in China (out of c. 18).

The subtribes of Trichosporeae not represented in China are Jerdoniinae (only *Jerdonia indica*, S India), Tetrphyllinae (only *Tetrphyllum*, 3 spp., NE India, Bangladesh, Burma, Thailand), Ramondinae (*Haberlea*, *Ramonda*, *Jancaea*; 5 spp., SW and SE Europe), Streptocarpinae (traditionally 9 genera, recently all amalgamated in *Streptocarpus*, Nishii et al, 2015; 176 spp.; Africa, Comoro Islands and Madagascar), and Didissandrinae (*Didissandra*, *Tribounia*; c. 10 spp., W Malesia, Thailand). Altogether, these subtribes include only one or few genera; as to species number, Streptocarpinae is clearly the largest subtribe. The link from the African to the Asiatic (including Chinese) species via the “Asiatic species of *Streptocarpus*” proved untenable; the Asiatic species described in *Streptocarpus* be-

long to the purely Asian genus *Damrongia* (Puglisi et al, in press).

### 3 Taxonomic fate of the Chinese genera of Gesneriaceae

In Table 2 all genera that have been used to accommodate Chinese (including Taiwan) species are listed and briefly commented on. In some genera (that is, for instance, all genera of tribe Epithemateae) no changes in the taxonomic delineation have occurred, in others the inclusion of formerly distinct genera has little bearing on their new definition (e. g. the inclusion of *Metabriggsia* into *Hemiboea*, in which differences in the ovary structure simply proved erroneous, Weber et al, 2011c). However, others have a rather complex taxonomic history which require a more detailed explanation. In the following the fate of the latter genera, plus new or newly established genera is briefly outlined, as far as changes since the treatment of Wang et al (1990) and Wang et al (1998) are concerned. *De facto*, all changes occurred from 2010 onwards, with the new genus *Litostigma* (Wei et al, 2010) as the first.

**Boea.** This was previously a widespread Asiatic-Malesian genus, with three species (*B. clarkeana*, *B. hygrometrica*, and *B. philippensis*) represented in southern China. From the recent molecular-systematic studies of Puglisi et al (in press), *Boea* emerged as an essentially Australasian genus, with distribution in Eastern Indonesia, Papua New Guinea, the Solomon Islands and Queensland (Australia). The genus *Dorcoceras* was re-established to accommodate the remaining species distributed in Burma (1 sp.), Cambodia (1 sp.) and China (2 spp.). In addition, *Boea hygrometrica* (endemic to China) and *B. philippensis* (Philippines and Vietnam) were included in *Dorcoceras* (the former representing the type species of *Dorcoceras*). *Boea clarkeana* (= *Streptocarpus clarkeanus*), however, was attributed to the genus *Damrongia* (see there).

**Briggsia.** The genus is no longer relevant, as the alliance around the type species (*B. longifolia*) has been synonymised with *Oreocharis* (Möller et al, 2011b, 2014). In its traditional concept, *Briggsia* in-

cluded acaulescent rosette plants as well as caulescent plants, both with characteristic large and ventrally pouched (“briggsoid”) flowers. Its three acaulescent and strikingly glabrous species are now in the new genus *Glabrella* and the three caulescent species are in *Loxostigma* (Möller et al, 2014; Wen et al, 2015a, b). The “briggsoid” flowers arose apparently independently in different alliances (Möller et al, 2011b). See also notes for *Oreocharis*.

**Chirita.** Dramatic changes occurred in this traditional and large genus (with up to 140 species described herein, placed in four sections: sect. *Chirita*, sect. *Liebigia*, sect. *Microchirita*, and sect. *Gibbosaccus*; Wood, 1974; Hilliard, 2003), ending in a synonymisation of the genus with *Henckelia* (Weber et al, 2011a). The character defining *Chirita* was traditionally seen in the “chiritoid” stigma: a stigma with upper and lower lobe, but the upper largely or completely reduced, and the lower one expandend and often bipartite. The molecular studies clearly revealed that this character is homoplastic, having evolved independently in several alliances of tribe Trichosporeae. As a consequence, *Chirita* was split into five genera, with the majority of *Chirita* sect. *Chirita* (and the monotypic *Hemiboeopsis*, China and Laos) amalgamated with *Henckelia* sect. *Henckelia* (from South India). The remaining species of *Chirita* sect. *Chirita* were included in the revived genus *Damrongia* (see below). *Chirita* sect. *Liebigia* was raised to generic level (*Liebigia* Endl., not represented in China). *Chirita* sect. *Microchirita* was also raised to genus level (*Microchirita*, with two species in China), and *Chirita* sect. *Gibbosaccus* was, together with *Chiritopsis* and *Wentsaiboea* (including its type species and a later published species, *W. luochengensis*, Liu et al, 2010; Xu et al, 2012), included in the originally monotypic genus *Primulina* (Wang et al, 2011; Weber et al, 2011a; Li & Xia, 2012). The latter genus is essentially geographically restricted to China, with some species extending or endemic to Vietnam.

*Primulina* has been expanded from a monotypic genus to one with 100 species at the time of its redefinition (Weber et al, 2011a) and over the last few years has become a genus with over 160 species. The morphological

variation is relatively limited compared to other genera, and is based on diandrous zygomorphic flowers usually infundibuliform but variable in size and coloration, and a vegetative habit with rhizomatous compact stems with leaves in a basal rosette, with decussate phyllotaxy or in whorls of three (rarely alternate). This character distinguishes this genus to a great length from *Petrocodon*, where the leaves are always alternate. Another possibly distinguishing feature are the chromosome numbers which are almost uniformly  $2n = 36$  in *Primulina* (>100 species counted, with one exception of a tetraploid number, Christie et al, 2012), whereas it is  $2n = 20$  in the only member of *Petrocodon* so far counted (*P. hancei*, Cao et al, 2003; Möller & Pullan, 2015 onwards).

**Damrongia.** This is a genus re-established by Weber et al (2011a) for the accomodation of a couple of species previously placed in *Chirita*. The species represent rosette plants with scapose inflorescences, infundibuliform corollas with 2 stamens, and a pistil with a “chiritoid” stigma (see *Chirita*). It was thought to be restricted to Thailand and the NW of Peninsular Malaysia, but the Chinese *Boea clarkeana* also proved to belong to that genus (Puglisi et al, in press). The same applies for the Asian species described in *Streptocarpus* on grounds of the twisted fruits (Puglisi et al, in press).

**Dorcoceras.** Re-established genus segregated from *Boea* by Puglisi et al (in press). See *Boea* above.

**Glabrella.** New genus established by Möller et al (2014) for two species of *Briggsia*, which do not fit into *Oreocharis* or *Loxostigma*. A third species was added by Wen et al (2015a,b). See *Briggsia* and *Oreocharis*.

**Henckelia.** The genus *Henckelia* Spreng. was re-established when the unwieldy and broadly circumscribed *Didymocarpus* was changed and split into 3 smaller entities: *Didymocarpus* s. str., *Henckelia* (with five sections: sect. *Henckelia*, S India and Sri Lanka, sect. *Loxocarpus*, sect. *Heteroboea*, sect. *Loxocarpus*, sect. *Didymanthus* and sect. *Glossadenia*) and *Hovanella* (Weber & Burt, 1998). The molecular data of Möller et al (2009) indicated that the split was not sufficient and that *Henckelia* had to be redefined. This was done by Weber et al (2011a). The type section (*Henckelia*.

sect. *Henckelia*, S India and Sri Lanka) was amalgamated with most of *Chirita* sect. *Chirita* and the monotypic *Hemiboopsis* (see under *Chirita* above), sect. *Loxocarpus* has returned to generic level (Weber et al, 2011a; Middleton et al, 2013; Yao, 2012), and the last three sections have been included in the re-established and largely expanded genus *Codonoboea* (Kiew & Lim, 2011; Middleton et al, 2013). Neither *Loxocarpus* nor *Codonoboea* have species in China.

**Litostigma.** This new genus established by Wei et al (2010) for two Chinese species form a separate subtribe (Litostigminae) (see there).

**Microchirita.** This genus has been established by raising *Chirita* sect. *Microchirita* to generic level (Wang et al, 2011; Weber et al, 2011a). It can be characterized by inflorescences that usually appear in two or several in a leaf axil, often displaced onto the petiole, often consisting of a short-stalked serial flower pair only, but this repeated several times. From the c. 25 species 2 occur in China; *M. hamosa* and *M. prostrata* (recently described by Li & Xia, 2012).

**Middletonia.** A new genus established by Puglisi et al (in press) for the accommodation of four species separated from *Paraboea*, with one species distributed in China (*M. multiflora*).

**Oreocharis.** While *Oreocharis* included some 27 species in its traditional delineation (Wang et al, 1998), the number increased enormously through the inclusion of *Ancylostemon*, *Bournea*, *Briggsia* p. p. (incl. type), *Dayaoshania*, *Deinocheilos*, *Isometrum*, *Opithandra*, *Paraisometrum*, *Thamnocharis*, and *Tremacron* (Möller et al, 2011b; Middleton et al, 2013). As the species of *Briggsia* transferred to *Oreocharis* included the type species (*B. longifolia*), the remaining species were left without generic placement. In recent studies (Chen et al, 2014b; Möller et al, 2014; Wen et al, 2015a, b), the rest were attributed to the following three genera: the caulescent species were referred or returned to *Loxostigma*, three acaulescent species with glabrous leaves and stems were moved into a new genus *Glabrella*, and 11 acaulescent species were transferred to *Oreocharis*. New species were recently described (Liu et al, 2012; Chen et al 2013, 2015; Tan et al 2013, 2015;

Rossini & Freitas 2014; Li & Li 2015, Yang et al, 2015), and *Oreocharis* comprises 106 species, all representing acaulescent rosette plants with scapose inflorescences, but with considerable variability in the symmetry, shape and coloration of the flowers. *Oreocharis leiophylla* and *O. sinensis* (making up the former genus *Bournea*) have actinomorphic flowers. The corolla shape in *Oreocharis* varies from tubular, through funnel-shaped, campanulate to “briggsioid”, the stamen number is (1), 2, 4 or (in actinomorphic flowers) 4 or 5 in line with the number of petals, in some diandrous species (previously constituting the genus *Opithandra*) the posterior stamens are the fertile ones (while it is the reverse in most other diandrous Gesneriaceae), and the anthers may be fused or free and coherent at the tips or at the faces. These floral characters have been formerly used to define genera, but, as the molecular data show, the species relationships run across genera and these are thus untenable. Like in *Petrocodon*, the flowers combine a range of corolla shapes and colours suggesting different pollinator adaptations, sometimes in parallel.

**Paraboea.** This widespread and species-rich genus was revised by Xu et al (2008), who recognised 89 species, c. 20 of them found in China. Changes since then relate to the inclusion of the monotypic *Phylloboea* (Myanmar) and *Trisepalum* (c. 13 spp., 1 in China) (Puglisi et al, 2011). More recently, Puglisi et al (in press) removed four species from *Paraboea* and placed them in the new genus *Middletonia*. In the new delineation the genus contains 132 species of which 26 occur in China, of these 14 exclusively there (i.e. endemic).

**Petrocodon.** In its traditional concept, *Petrocodon* was a genus with two Chinese species, both with small, white flowers and two fertile stamens. Based on molecular data, Wang et al (2011) added *Tengia* (with small white, pentamerous actinomorphic flowers and five stamens), *Calcareaoboea* (with large, red and tubular flowers), and *Paralagarosolen* (with long-tubed hypocrateriform flowers). Shortly afterwards, Weber et al (2011b) added the monotypic *Dolicholoma* (with flowers with narrow tube and subactinomorphic limb with long, acute lobes), all species of *Lagarosolen* (with flowers similar to those of *Dolicholoma* and *Paralagarosolen*), one spe-

cies of *Wentsaiboea* (excl. type) and three species of *Didymocarpus* (*D. hancei*, *D. mollifolius*, *D. niveolanosus*). This resulted in a genus size of around 20 species. The recent description of new species by Wen et al (2012), Chen et al (2014a), Hong et al (2014), Xu et al (2014) and Li & Wang (2015) increased the species number to almost 30. The different flower shapes and colours now assembled in *Petrocodon* suggest different pollinator adaptations, including bee, butterfly and bird pollination. Until recently, *Petrocodon* could be defined by possessing 2 stamens or 5 (in the former genus *Tengia* with actinomorphic flower). Using both morphological and molecular data, a species possessing 4 stamens was described: *P. hunanensis* (Yu et al, 2015). This indicates (a) the great diversity that is still unexplored in China, and (b) that the use of molecular data has apparently given the right signal to place the species in the right genus.

## 4 Discussion and Outlook

### 4.1 You win some, you lose some

The recent taxonomic changes have changed the generic picture of Gesneriaceae in China considerably. From the 56 genera listed in Wang et al (1998), and two genera established a few years later (*Paralagarosolen*; Wei, 2004; *Wentsaiboea*; Fang & Qin, 2004), the number has dropped to 45 (Table 1). Since 2010, and essentially based on molecular data, seven new genera have been added to China, either based on newly collected material (*Litostigma*), or from segregation of existing genera in China (*Glabrella*, *Damrongia*, *Dorcoceras*, *Middletonia*, *Microchirita*, and *Primulina*; see previous chapter), or by a new circumscription of genera (*Henckelia*).

On the other hand, a considerable number of genera (22) are lost by synonymisation with other genera (*Ancylostemon*, *Boea*, *Bournea*, *Briggsia*, *Calcareo-boea*, *Chirita*, *Chiritopsis*, *Dayaoshania*, *Deinocheilos*, *Dolicholoma*, *Hemiboeopsis*, *Isometrum*, *Lagarosolen*, *Metabriggsia*, *Opithandra*, *Paraisometrum*, *Paralagarosolen*, *Tengia*, *Thamnocharis*, *Tremacron*, *Trisepalum*, *Wentsaiboea*). Also, the four Asiatic species of *Strepto-*

*carpus* (Hilliard & Burt, 1971), one of them, *S. clarkeanus* (Hemsl.) Hilliard and B.L. Burt (≡ *Boea clarkeana* Hemsl., as such in the Flora of China of Wang et al, 1990; Wang et al, 1998), from China, have found a proper generic place (*Damrongia*). *Streptocarpus*, therefore, can be definitely removed from the list of genera extending into China.

By tribe, there is no change in generic state in Epithemateae, as to Trichosporeae-Litostigminae there is the addition of one genus (*Litostigma*), in Trichosporeae-Loxocarpinae there are two fewer genera in China (*Boea*, *Trisepalum*), but three additional ones (*Damrongia*, *Dorcoceras*, *Middletonia*), an overall net gain of one. The greatest changes occurred in Trichosporeae-Didymocarpinae, with a loss of 20 genera, and a gain of three (*Glabrella*, *Henckelia*, *Microchirita*), thus an overall loss of 17 genera. This tribe is still not fully understood and further work is necessary to understand its evolution, and further changes may be in the waiting, though these may be less drastic, but fine-tuning.

The number of Gesneriaceae genera endemic to China has decreased from 27 (Wang et al, 1998; Wei 2004; Fang & Qin, 2004) to 11. Ten of them included only one to three species (*Allocheilos* [2], *Allostigma* [1], *Briggsiopsis* [1], *Cathayanthe* [1], *Didymostigma* [3], *Glabrella* [3], *Gyrogynae* [1], *Litostigma* [2], *Metapetrocosmea* [1], *Rhabdothamnopsis* [1]), a drop from 22 previously. Of the remaining endemic genera, almost a dozen have unusual morphologies combined with isolated evolutionary positions (Möller et al, 2011a).

Over the decades, there seems to be an overall tendency to include small or monotypic genera (and the large *Dichrotrichum*) that had been raised on the basis of the presence of an unusual characteristic, into larger ones on grounds of more shared than distinguishing characteristics. This is important, since single character taxonomy is fraught with problems when picking the ‘wrong’ character a genus was not established for.

### 4.2 Morphological parallelisms and reversals

Burt (e. g. Burt, 1963) pointed out that in Gesneriaceae there are many exceptions and apparent parallelisms in form, and that the homology of similar



characters on which a genus is based, is sometimes difficult to ascertain (e. g. Burt, 1968). The erstwhile genus *Chirita* is a prime example, in which strong emphasis was given to the special type of stigma (“chiritoid stigma”). The molecular data have unambiguously shown that the chiritoid stigma has evolved several times independently, and *Chirita* thus had to be split into five genera (Weber et al, 2011a) (see also below).

At the generic level, the number of fertile stamens (4 or 2) played a significant role, especially in Chinese Gesneriaceae. For example, *Deinocheilos* (with 2 stamens) has been kept separate from *Tremacron* (4 stamens), though the two genera are otherwise indistinguishable.

Floral symmetry is another problematic character of importance both at the generic and at the tribal level. Fritsch (1893/1894, 1908) established tribe Ramondeae to include *Corallodiscus*, *Haberlea*, *Petrocosmea*, *Ramonda* and *Saintpaulia*. His intention was to recognise a group with similar vegetative habit (flat rosette plants) with septicidal capsule dehiscence, rather than floral shape. Thus, this tribe included four genera with zygomorphic flowers (two of which have long floral tubes and four stamens: *Haberlea* and *Corallodiscus*, and two with flat-faced corollas with 2 stamens: *Petrocosmea* and *Saintpaulia*), and one with actinomorphic flowers (“*Ramondia*” = *Ramonda*). He placed another genus with actinomorphic flowers, *Conandron*, in a separate tribe. Burt (1970) accepted this view and suggested that actinomorphic genera were not related, that zygomorphy was ancestral in the family and actinomorphic genera the result of separate independent losses of flower asymmetry. Wang et al (1990) and Wang et al (1992) held the opposite view and considered actinomorphy as ancestral. They redefined tribe Ramondeae to include only genera with actinomorphic flowers: *Bournea*, *Conandron*, *Ramonda*, *Tengia* and *Thamnocharis*. Molecular phylogenetic work has proven Burt’s view to be correct since they showed that all actinomorphic genera have independent origins (Möller et al, 1999, 2009, 2011a; Wang et al, 2010).

Hidden homoplasies destabilize a classification system that wants to reflect phylogeny, and single character

taxonomy may lead to an inflation of small or monotypic genera. With the rise of molecular phylogenetic methods during the last 20 years or so, we have become more aware of the presence and levels of homoplasies among morphological characters and how small and monotypic genera are related or part of larger entities (Möller et al, 2011a). This has been shown for the Neotropical Gesneriaceae as well as for the Afro-Malagasy Gesneriaceae of tribe Streptocarpaceae, which have been reduced from nine often small genera (7 with <3 species) to one genus *Streptocarpus* (Nishii et al, 2015). There are numerous examples of morphological homoplasies that have resulted in dramatic changes in classification for the New World Gesneriaceae. The convergence of resupinate flowers was recently discovered to be independently derived in three lineages that resulted in a new generic classification for members of the Columneinae (Clark & Zimmer, 2003; Clark et al, 2006). The convergence of hypocyrtoid or “pouched” flowers within *Drymonia* and across several lineages of closely related genera has resulted in a revised circumscription of genera in the Columneinae (Clark et al, 2012; Smith & Clark 2013; Clark et al, 2015). Recent phylogenetic results have elucidated the convergence of radially symmetrical flowers and that has resulted in the circumscription of more narrowly defined genera in the Gloxiniinae (Smith et al, 2004; Roalson et al, 2005b; Clark et al, 2011).

### 4.3 Holistic approach to the taxonomy

Uncertainties in the correct genus assignment abound. Photographs of *Litostigma crystallina* were published under *Petrocosmea crystallina* (Shui & Chen 2006) before its accommodation in a new genus (Wei et al, 2010). The recently described species, *Primulina guangxiensis* was initially placed with a superficially similar species (Liu et al, 2011), but after molecular studies, partly by the same authors, it was discovered that it belonged in *Petrocodon* (assuming the integrity of the molecular data) and was transferred to this genus (Xu et al, 2014).

In some cases incomplete knowledge of generic concepts might be at issue, in others perhaps the discovery of species with new character combinations, such as *Petrocodon hunanensis* with four stamens, cause un-



certainty. However, with the availability of molecular data and an extensive data set of molecular sequences on public databases, such as GenBank, these uncertainties can be addressed by molecular approaches.

However, where traditional taxonomic approaches are concerned, the utilisation and balancing of all characters, not just one or a few, has to be considered in taxonomic decisions. This might have become more complex with the new delineations of some genera, and the 'traditional' characters of corolla shape, stigma or androecium may be largely inadequate. Additional or hitherto undervalued characters may be required.

#### 4.4 Open issues

At the suprageneric taxonomic level we present classification on the basis of what is currently known. The classification of tribe Trichosporeae, particularly subtribe Didymocarpaceae, is still to be completed. Because of the large number of representatives in this subtribe residing in China, it can play a pivotal role in this endeavour.

At the generic level, *Raphiocarpus* is still an unsatisfactorily known entity. The data so far indicate intricate links to several genera including *Loxostigma*. The inclusion of the caulescent '*Briggsia*' into *Loxostigma* (Möller et al, 2014) has expanded its definition to include seeds without appendages, narrowing its gap to *Raphiocarpus*, but its link to this genus is unexplored.

The relationship between *Didymocarpus* and *Gyrocheilos* is still unresolved. Some Chinese species of *Didymocarpus* were transferred to *Petrocodon* (Weber et al, 2011b). In the phylogeny of Möller et al (2011a), *D. cortusifolius* fell as sister to *Gyrocheilos*, apart from *Didymocarpus* proper, and may belong in this genus. Li et al (2015) published a molecular phylogeny on Chinese species and found similar results to Möller et al (2011a). Perhaps other basal rosette-forming ones from sect. *Heteroboaea* may follow as suggested by Weber & Burt (1998).

The new circumscriptions of *Henckelia* and *Damrongia* are quite wide. They include acaulescent and caulescent species, and the latter species with straight and twisted fruits. Such an assemblage seems at first dissatisfying, but it has precedence in other genera. The

genus *Streptocarpus* was characterised for species possessing twisted fruits. Though it includes a wide range of morphological forms, from unifoliate, plurifoliate, rosettes, herbaceous and woody caulescent forms (Hilliard & Burt, 1971). It has now also been extended to include species with non-twisted fruits (Nishii et al, 2015).

#### 4.5 Outlook

The work summarised here is very much a work in progress and far from complete. The finding of new genera based on new collections (e. g. *Litostigma*), and morphotypes that expand the new circumscriptions (e. g. *Petrocodon hunanensis* with four stamens), are examples which demonstrate that the full diversity in Gesneriaceae in China is not yet known and is an exciting prospect for finding further 'links' through intensified and systematic fieldwork. Also, the great number of new species described in some genera, especially *Primulina*, which ballooned from around 100 when it was redefined in 2011, to currently >160 with many more species to be described, illustrates the need for continued floristic surveys and detailed fieldwork to fully document the diversity of Gesneriaceae in China. Systematic fieldwork efforts combined with detailed herbarium studies and molecular work has unearthed several genera over the last few years from Thailand and Vietnam (e. g. *Somrania*, Middleton & Triboun 2012; *Tribounia*, Middleton et al, 2012; *Billolivia*, Middleton et al, 2014; *Chayamaritia* Middleton et al, 2015). Recent discoveries outlined here clearly demonstrate the recent progress in Gesneriaceae diversity of China, but more importantly the future need to continue phylogenetic and taxonomic studies for a long-term stable classification. Without a doubt, there is still much to be done.

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