



A new definition of the genus *Petrocodon* (Gesneriaceae)

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Abstract

Based on molecular studies, the small Chinese genus *Petrocodon* (two species and one variety) has been recently enlarged to include the monotypic genera *Calcareoboea*, *Paralagarosolen* and *Tengia*. It is shown here that the (6–7) species of *Lagarosolen*, the monotypic *Dolicholoma*, a few species of *Didymocarpus*, and a number of new species that have recently been published (but not formally described) under *Petrocodon* and *Lagarosolen* should be included in this genus. This raises the size of the genus from five to around 20 species. With respect to the floral diversity (corolla form, size, and coloration; with the exception of *Tengia*, the androecium is always diandrous) and inferred pollination syndromes (different forms of melittophily, ornithophily, psycho- and/or sphingophily), *Petrocodon* represents one of the most varied genera of Old World Gesneriaceae, comparable to some New World genera.

Key words: *Calcareoboea*, *Didymocarpus*, *Dolicholoma*, Lamiales, *Lagarosolen*, molecular systematics, *Paralagarosolen*, pollination syndromes, *Tengia*

Introduction

A recent molecular phylogenetic study (Möller *et al.* 2009) revealed that the Chinese genera *Petrocodon* (three species with small, white, urceolate flowers, with buzz-pollination syndrome) and *Calcareoboea* (monotypic in its original concept, with large, long-tubular, bright red, apparently ornithophilous flowers) form a strongly supported clade. This was confirmed in the study of Wang *et al.* (2011) who also added *Paralagarosolen* (with long-tubed hypocrateriform flowers) and *Tengia* (with flowers similar to *Petrocodon*, but with five fertile stamens) to the clade and expanded the definition of *Petrocodon* to include these four genera, with five species in total. The present paper provides molecular evidence that this definition is still too narrow and that some more genera have to be included in *Petrocodon*. In addition, the new definition demonstrates strikingly, and exemplarily for the Old World Gesneriaceae, how unreliable traditional generic definitions, often based exclusively on floral characters, are. *Petrocodon* emerges as one of the florally most diverse clades of Old World Gesneriaceae.

Material and Methods

Plant material

Leaf material for newly acquired sequences came from silica gel dried field collections. Most molecular data came from previous work (Möller *et al.* 2009, 2011a, Weber *et al.* 2011), sequences for three taxa were

additionally acquired and for another three they came from GenBank (Table 1). A total of 31 samples was included in the analyses, comprising 30 species (including 2 undescribed species) and 1 variety. Based on previous work (Möller *et al.* 2009, 2011a, Weber *et al.* 2011) and an extended analysis on 259 didymocarpoid Gesneriaceae (data not shown), it was demonstrated that the *Petrocodon* clade was monophyletic. Suitable outgroup samples for this clade were *Lysionotus* Don (1822: 85) (*L. pauciflorus*, *L. petelotti*) and *Loxostigma* Clarke (1883: 59) (*L. fimbrisepalum*, *L. griffithii*) and the newly defined genus *Primulina* Hance (1883: 169) (10 species, Wang *et al.* 2011, Weber *et al.* 2011). The trees were rooted on the *Lysionotus* and *Loxostigma* samples (based on the data presented in Möller *et al.* 2009, 2011a, Weber *et al.* 2011).

TABLE 1: List of the 31 didymocarpoid Gesneriaceae samples included in the phylogenetic analysis, including voucher number and deposition, origin information and respective GenBank accession numbers.

Taxon	Voucher number	Deposited in	Origin	<i>trnL-F</i>	ITS or ITS1 / ITS2
<i>Calcareaoboea coccinea</i> C.Y.Wu ex H.W.Li (1982: 243)	<i>M.Möller MMO 01-141</i>	E, WU	China, Guangxi, Napo county	FJ501516	FJ501365
<i>Chirita gemella</i> D.Wood (1972: 370)	<i>L.Averyanov 1987 [Cult. RBGE 19941913]</i>	E	Vietnam, Hong Quang Special Region, Cat Hai	FJ501523	FJ501345
<i>Chirita longgangensis</i> W.T.Wang in Wang & Huang (1982: 171)	<i>A.Takhtajan & N.Aruzytov 1975 [Cult. RBGE 19941915]</i>	E	Vietnam, unknown locality	AJ492290	FJ501347
<i>Chirita minutimaculata</i> D.Fang & W.T.Wang in Wang (1981b: 55)	<i>J.M.Li 067134</i>	PE	China, Guangxi, Longzhou county	DQ872815	DQ872828
<i>Chirita pinnata</i> W.T.Wang (1984a: 25)	<i>Expedition Beijing 896526 (US 294374)</i>	US	China, Guangxi, Rongshui county	FJ501526	FJ501349
<i>Chirita pinnatifida</i> (Hand.-Mazz.) B.L.Burtt (1960: 99)	<i>Q.J.Xie J-037 (US 422838)</i>	US	China, Guangdong, Lianxian county	FJ501527	FJ501350
<i>Chirita spinulosa</i> D.Fang, & W.T.Wang in Wang (1981b: 67)	<i>Y.Z.Wang 067133</i>	PE	China, Guangxi, Fusui county	DQ872813	DQ872830
<i>Chiritopsis glandulosa</i> D.Fang, L.Zeng & D.H.Qin in Fang <i>et al.</i> (1993: 470)	<i>J.M.Li 054291</i>	PE	China, Guangxi, Pingle county	DQ872804	DQ872841
<i>Chiritopsis repanda</i> W.T.Wang var. <i>guilinensis</i> W.T.Wang (1992: 299)	<i>ex Smithsonian Institute 94-083 [Cult. RBGE 19951206]</i>	E	China, Guangxi, Guilin city	AJ492292	FJ501351
<i>Didymocarpus hancei</i> Hemsley (1890: 229)	<i>M.Möller MMO 08-1342</i>	E	China, Guangxi, Hezhou city	HQ632944	HQ633041
<i>Didymocarpus niveolanosus</i> D.Fang & W.T.Wang in Wang & Pan (1982: 133)	<i>M.Möller MMO 06-861</i>	E	China, Guangxi, Jingxi county	JF697588	JF697576
<i>Dolicholoma jasminiflorum</i> D.Fang & W.T.Wang in Wang (1983b: 19)	<i>M.Möller MMO 06-851</i>	E	China, Guangxi, Napo county	Wei <i>et al.</i> , 2010a	Wei <i>et al.</i> , 2010a
<i>Lagarosolen ainsliifolius</i> W.H.Chen & Y.M.Shui <i>nomen nudum</i>	<i>Y.M.Shui et al. 44071</i>	KUN	China, Yunnan, Maguan county	HQ632941	HQ633038
<i>Lagarosolen coriaceifolius</i> Y.G.Wei (2006: 273)	<i>M.Möller MMO 06-913</i>	E	China, Guangxi, Yangshuo county	HQ632943	HQ633040

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TABLE 1 (continued)

Taxon	Voucher number	Deposited in	Origin	<i>trnL-F</i>	ITS or ITS1 / ITS2
<i>Lagarosolen hechiensis</i> Y.G.We, Yan Liu & F.Wen (2008: 299)	<i>M.Möller MMO 07-1077</i>	E	China, Guangxi, Hechi city	HQ632942	HQ633039
<i>Lagarosolen hispidus</i> W.T.Wang (1984b: 12)	<i>Y.M.Shui et al. 82661</i>	E	China, Yunnan, Maguan county	HQ632939	HQ633036
<i>Lagarosolen integrifolius</i> D.Fang & L.Zeng in Fang <i>et al.</i> (1993: 463)	<i>M.Möller MMO 06-865</i>	E	China, Guangxi, Longzhou county	HQ632940	HQ633037
<i>Lagarosolen lui</i> Yan Liu & W.B.Xu in Xu <i>et al.</i> (2010: 7)	<i>Y.G.We 8012</i>	IBK	China, Guangxi, Jingxi county	HQ632938	HQ633035
<i>Lagarosolen</i> sp.nov.	<i>Y.G.We 0903</i>	IBK	China, Guangxi, Hechi city	JF697589	JF697577
<i>Loxostigma fimbrispalum</i> K.Y.Pan in Wang & Pan (1982: 143)	<i>Y.Z.Wang 991005</i>	PE	China, Yunnan, Jinping county	FJ501507	Wei <i>et al.</i> , 2010a
<i>Loxostigma griffithii</i> (Wight) C.B.Clarke (1883: 60)	<i>Kew/Edinburgh Kanchenjunga Expedition (1989) 940 [Cult. RBGE 19892473A]</i>	E	Nepal, Yamphudin	FJ501508	FJ501338
<i>Lysionotus pauciflorus</i> Maximowicz (1874: 534)	<i>M.Möller MMO 01-101</i>	E, WU	China, Yunnan, Xichou county	FJ501497	FJ501331
<i>Lysionotus petelotii</i> Pellegrin (1930: 503)	<i>M.Möller MMO 01-100/4</i>	E	China, Yunnan, road to Xichou	FJ501496	HQ632974
<i>Paralagarosolen fangianus</i> (Y.G.We) J.M.Li & Y.Z.Wang in Wang <i>et al.</i> (2011: 60)	<i>M.Möller MMO 07-1168</i>	E	China, Guangxi, Napo county	Wei <i>et al.</i> , 2010a	Wei <i>et al.</i> , 2010a
<i>Petrocodon dealbatus</i> Hance (1883: 167)	<i>Q.J.Xie J-042 (US 422841)</i>	US	China, Guangdong, Lianxian county	FJ501537	FJ501358
<i>Petrocodon dealbatus</i> Hance var. <i>denticulatus</i> (W.T.Wang) W.T.Wang in Wang <i>et al.</i> (1990: 420)	<i>Y.G.We 2010-03</i>	IBK	China, Guizhou, Liping county	JF697590	JF697578
<i>Petrocodon ferrugineus</i> Y.G.We (2007: 135)	<i>M.Möller MMO 06-784</i>	E	China, Guangxi, Xincheng county	HQ632946	HQ633043
<i>Primulina tabacum</i> Hance (1883: 169)	<i>Q.J.Xie & C.X. Ye s.n. [Cult. RBGE 19951540]</i>	E	China, Guangdong, Lian River	AJ492300	FJ501352
<i>Tengia scopulorum</i> Chun (1946: 281, pl. 46)	<i>F.Wen 2010-02</i>	IBK	China, Guizhou, Xiuwen county	HQ632947	HQ633044
<i>Wentsaiboea renifolia</i> D.Fang & D.H.Qin (2004: 534)	<i>M.Möller MMO 06-791</i>	E	China, Guangxi, Duan county	Wei <i>et al.</i> , 2010a	Wei <i>et al.</i> , 2010a
<i>Wentsaiboea tiandengensis</i> Yan Liu & B.Pan in Liu <i>et al.</i> (2010: 739, fig. 2-3E)	<i>M.Möller MMO 07-1164</i>	E	China, Guangxi, Tiandeng county,	HQ632945	HQ633042

Plant names

For convenience and for avoiding confusion, the traditional names of the genera/species, as they appear in the “Flora of China” (Wang *et al.* 1998), plus *Wentsaiboea tiandengensis* described recently in Liu *et al.* (2010), are used in the text and in the phylogenetic trees. The current and new names of the *Petrocodon* alliance are given in the formal treatment below.

Samples used in the analysis

The ingroup comprises 17 samples, including seven species of *Lagarosolen* (*L. coriaceifolius*, *L. hechiensis*, *L. ainsliifolius*, *L. lui*, *L. integrifolius*, *L. hispidus*, *L. sp. nov.*), the two species, plus a variety, of *Petrocodon* (*P. dealbatus*, *P. dealbatus* var. *denticulatus*, *P. ferrugineus*), one species of *Calcareoboea* (*C. coccinea*), the three monotypic genera *Dolicholoma* (*D. jasminiflorum*), *Paralagarosolen* (*P. fangianus*) and *Tengia* (*T. scopulorum*), two samples of *Didymocarpus* (*D. hancei*, *D. niveolanosus*) and *Wentsaiboea tiandengensis* (Liu *et al.* 2010). Other species of *Didymocarpus* form an independent clade and *D. cortusifolius* L veill  (1906: 427) is more closely related to *Allocheilos* Wang (1983a: 321) and *Gyrocheilos* Wang (1981a: 28) (M ller *et al.* 2009, 2011a). The other two species of *Wentsaiboea*, including the type, *W. renifolia*, have been included in *Primulina* (Wang *et al.* 2011).

DNA extraction, PCR, and sequencing

The molecular methods and protocols followed M ller *et al.* (2009, 2011a). For all samples sequences of both the *trnL-F* intron-spacer (*trnL-F*) and the ITS regions were acquired. Newly acquired sequences were deposited in GenBank.

Molecular-phylogenetic analysis

Maximum parsimony and Bayesian inference analyses were carried out as described in M ller *et al.* (2009, 2011a, b) and Weber *et al.* (2011), using PAUP* v4.0b10 (Swofford, 2002), and MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, 2007). Combined *trnL-F* and ITS sequences were analysed after their combinability was checked using the incongruence length difference (ILD; $P=0.22$) test implemented as partition homogeneity test (PHT) in PAUP*. Alignment gaps with consistent boundaries were coded as additional characters according to the simple method of Simmons & Ochoterena (2000), 4 in *trnL-F*, 13 in ITS. Parsimony branch support was obtained through bootstrap analyses as performed in M ller *et al.* (2009, 2011a) with 10000 replicates, TBR on, MulTrees off.

MrBayes settings for the best-fit models were selected separately for *trnL-F*, the ITS spacers and the 5.8S gene by AIC in MrModeltest 2.3 (Nylander 2004), and were GTR+I, GTR+I+G and SYM+I, respectively, gaps were treated as standard characters. For the 31 samples here 1.5 million generations were run. The burn-in level was determined as 4% of the generations, after plotting likelihood values against generations (Appendix 1). The posterior probabilities (PP) were obtained from MrBayes using the 'sumt' command. The PP branch support values showed a high correlation between the two parallel Bayesian runs (Appendix 1).

Morphological analysis

Personal collections (by M. M ller), photographs and published descriptions of all species of the *Petrocodon* clade were evaluated to assess the floral morphology of the species included in the analysis. Functional conclusions were drawn from the floral characters established. Unfortunately, to date few field observations on the pollination are available of the species concerned.

Results

Matrix characteristics

The *Petrocodon* matrix with 31 samples included 1566 characters (*trnL-F*: 847 characters, ITS: 719), of which 241 (15.4%) were phylogenetically informative.

Phylogenetic analyses

The MP analysis of the combined data resulted in one most parsimonious tree (Fig. 1) of 816 steps (CI=0.7145; RI=0.7658). The topology of the BI tree was identical (Fig. 2). Samples of the outgroup genera *Lysionotus*, *Loxostigma* and *Primulina* each formed highly supported sister relationships (BS=100%;

PP=1.00) and a monophyletic clade (BS=100%; PP=1.00) of *Primulina* (BS=100%; PP=1.00) sister to the *Petrocodon* clade (BS=100%; PP=1.00) was retrieved. Our focus was on the latter clade, which was well supported (BS=90%; PP=1.00). *Didymocarpus niveolanosus* and *Lagarosolen hispidus* (the type species of that genus) formed a highly supported sister clade to the remaining samples, although this relationship received low support (BS=57%; PP=0.84). The next clade to split off included four species (BS=72%; PP=1.00), two *Lagarosolen*, *Paralagarosolen fangianus* and *Wentsaiboea tiandengensis*, but with low to modest branch support. The last was sister to *Lagarosolen lui* (BS=77%; PP=0.82), and these were linked in grades to *Paralagarosolen* (BS=59%; PP=0.91) and *Lagarosolen integrifolius* (BS=72%; PP=1.00).

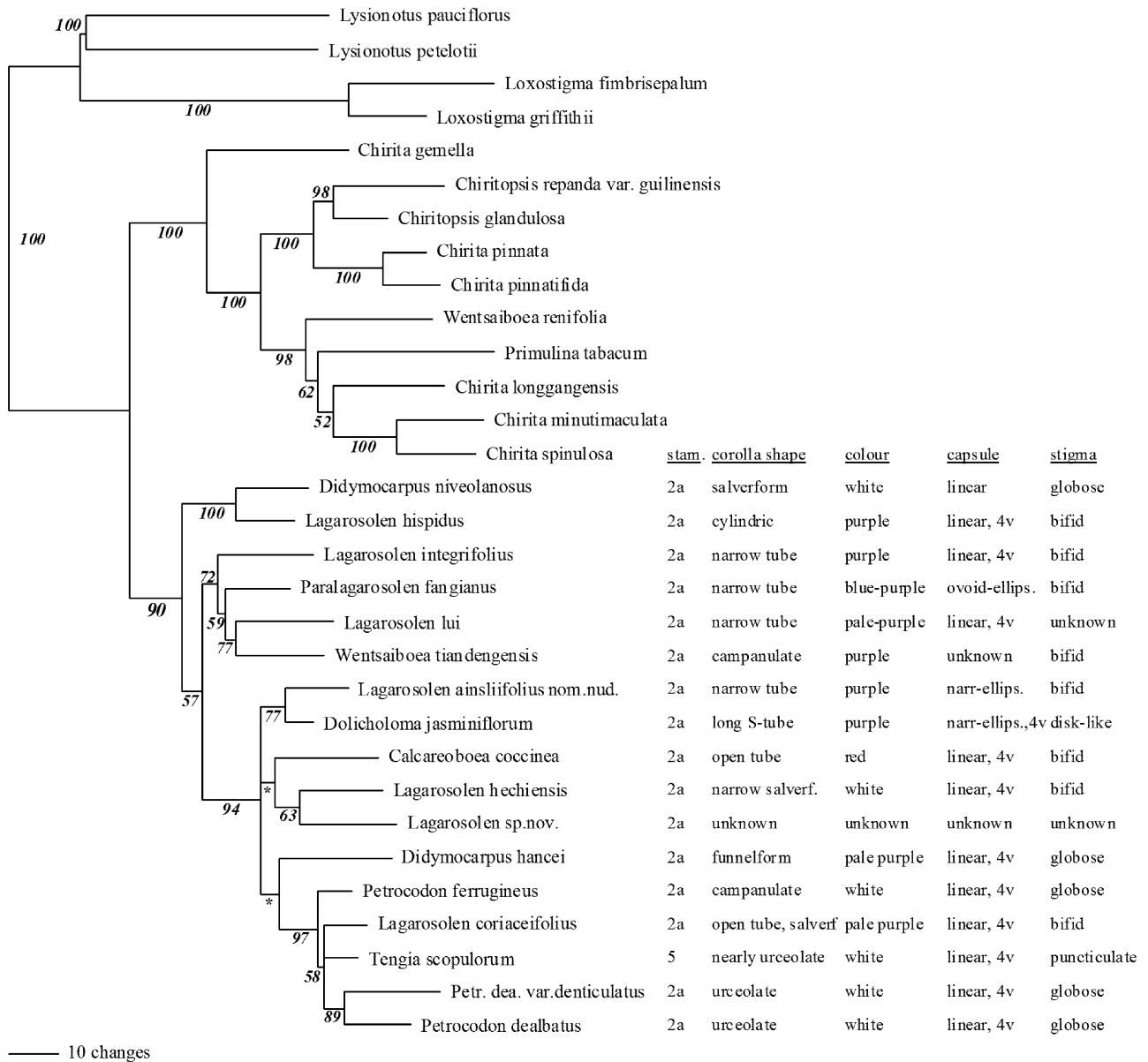


FIGURE 1: Single most parsimonious tree based on combined *trnL-F* and ITS data plus gap characters. PHT: 0.22, 816 steps length, CI= 0.7145; RI=0.7658 ; RC=0.5472. Numbers below branches are bootstrap values. * denote branches receiving <50% branch support. Number of fertile stamens (stam.: a, anterior pair), corolla shape, colour, capsule shape and dehiscence (4v, dehiscent into 4 valves), and stigma characters indicated in box.

The remaining 11 samples formed a strongly supported clade (BS=94%; PP=1.00) but with few well supported internal branches. *Lagarosolen ainsliifolius nomen nudum* and *Dolicholoma jasminiflorum* formed a clade with medium MP branch support (BS =77%), but high BI support (PP=1.00). The relationship of the

two *Lagarosolen* samples, *L. hechiensis* and *L. sp. nov.*, received some support (BS=63%; PP=0.82). Within this clade, the three *Petrocodon* samples (*P. ferrugineus*, *P. dealbatus*, *P. dealbatus* var. *denticulatus*), *Tengia scopulorum* and *Lagarosolen coriaceifolius* formed a very strongly supported clade (BS=97%; PP=1.00). Among these, the two *Petrocodon dealbatus* varieties were closely related (BS=89%; PP=1.00).

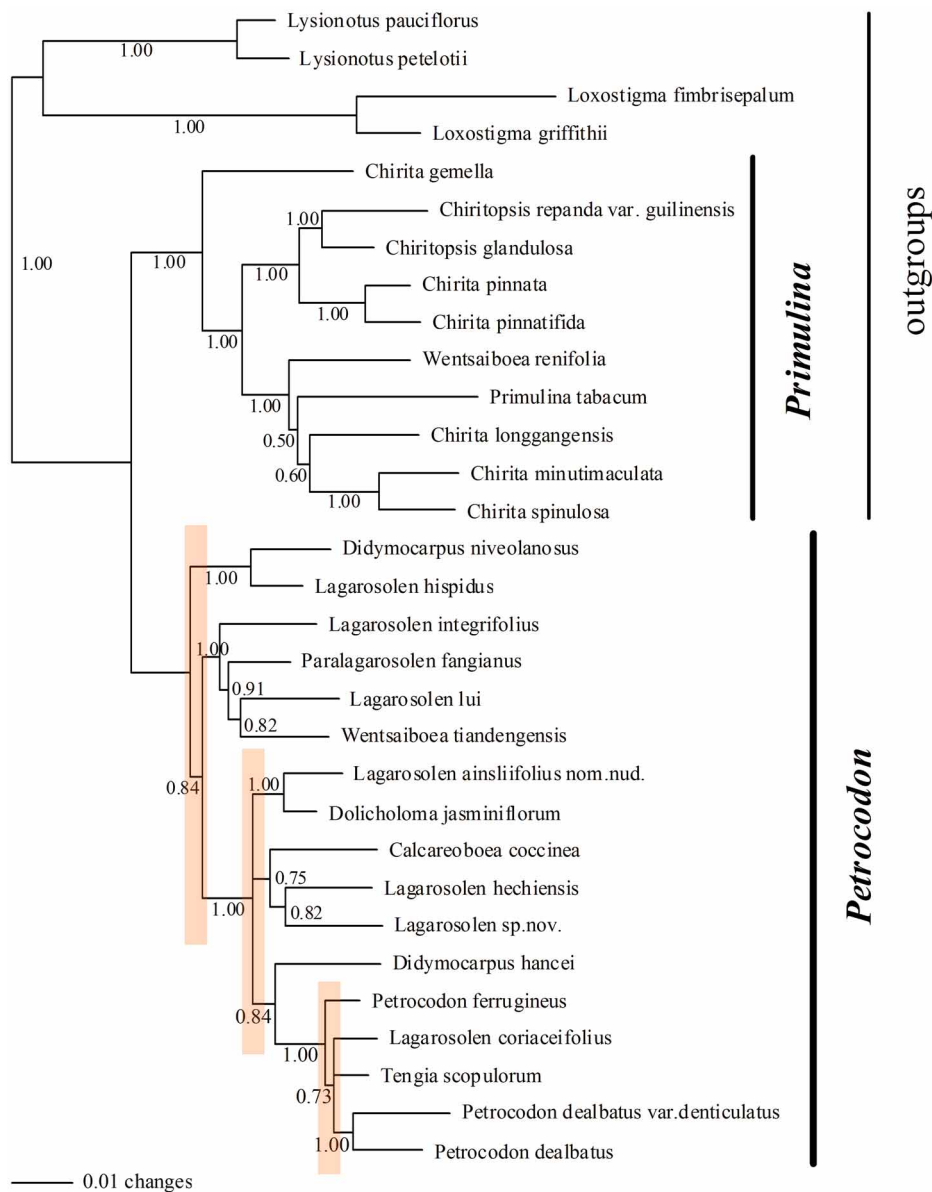


FIGURE 2: Bayesian inference tree with average branch lengths, based on combined *trnL-F*, ITS and alignment gap characters. Numbers below branches are posterior probabilities. Bars indicate radiation events.

Discussion

Phylogenetic considerations

For morphologically complex groups of plants, the reconstruction of phylogenetic relationships based on independent data, such as neutrally evolving molecular DNA sequences, is an important tool to understand the morphological diversification within these groups.

Following Möller *et al.* (2011a), we reconstructed the phylogenetic relationships for the *Petrocodon* clade, a highly supported clade of advanced didymocarpoid Gesneriaceae, dominated by species of the genus *Lagarosolen*. This clade contains species of eight genera, with *Didymocarpus*, *Lagarosolen* and *Petrocodon* represented by more than one species each. None of these genera formed monophyletic subclades, neither in

the MP nor the BI analyses of the combined data set (Figs. 1, 2), nor in individual *trnL-F* and ITS analyses (data not shown). This demonstrates that the current classification does not reflect relationships by descent correctly. We consider our analysis as highly representative since we included all but three species [*Calcareoboea bonii* = *Didymocarpus bonii*; *Petrocodon angustifolius nomen nudum*, described and illustrated in Wei *et al.* (2010b), but not yet validly published; and *P. multiflorus*, recently described by Jiang *et al.* 2010] of the genera retrieved exclusively in the *Petrocodon* clade. It is unlikely that their addition will significantly change our present results.

The phylogenetic trees of the didymocarpoid Gesneriaceae, particularly in the BI analysis, were characterised by short internal and long terminal branches (Möller *et al.* 2009, 2011a). This was found particularly in the *Petrocodon* clade but also, to a lesser degree, in the *Primulina* clade retrieved in the present study (Fig. 2). This suggests rapid evolutionary radiations. The *Petrocodon* clade has apparently experienced several such radiation events, once at the beginning of its diversification, once later in the middle of its evolution, and once more recently for a group of five species hitherto placed in three different genera (Fig. 2). This burst of speciation, leading to a high diversity in floral characteristics, may well be linked to the repeated diversification of pollination syndromes, since similar ones are scattered throughout the phylogenetic tree (Figs. 2, 3).

Morphological-taxonomical considerations

The alliance under consideration can be distinctively characterised as to the vegetative habit and the inflorescences: all taxa are rhizomatous rosette plants (with apparently alternate leaf arrangement, Fig. 4) and scapose, axillary inflorescences. Leaves are usually elliptic or ovate (Fig. 4). The flowers in the *Petrocodon* clade are arranged in few- to several-flowered aggregates (pair-flowered cymes), rarely are the cymes reduced to single flowers. There are also strong agreements in the flower characters, especially in those that have been used to delineate genera, such as the number of fertile stamens, and stigma shape: with the exception of *Tengia* (with five stamens in the pentamerous, actinomorphic flowers), the flowers of all taxa are diandrous and zygomorphic. The stigma is capitate or slightly bilobed, with an upper and lower lobe, corresponding to “two stigmas” in Wang’s terminology (e.g., Wang *et al.* 1998). The greatest variation is in the corolla form and coloration (Fig. 3), and this was the basis on which the originally circumscribed six genera were differentiated.

In the following discussion, the genera of the *Petrocodon* clade are addressed in some closer detail. We argue that the floral dissimilarities can be interpreted as reflecting different pollination syndromes.

Petrocodon* and *Tengia (Fig. 3L & M). The close (or at least possible) relationship of *Petrocodon* and *Tengia* has been addressed in the literature long before the advent of molecular systematics: while Wang *et al.* (1990, 1998) considered *Tengia* to be related to other genera with actinomorphic flowers and placed *Tengia* in tribe Ramondieae (sensu Wang *et al.* 1990), Burt (1970) much earlier had predicted a very close relationship of *Tengia* with *Petrocodon* (tribe Didymocarpeae). Burt argued that both have a similar, white, urceolate corolla, and differ only in the number of stamens: *Petrocodon* has only two stamens, while *Tengia* has five. Moreover, Burt concluded that the corolla actinomorphy and pentandry of *Tengia* is an evolutionarily secondary condition, derived from corolla zygomorphy and tetrandry or diandry (here we confirm its descent from diandry). Indeed, it has been recently confirmed by molecular studies that genera with actinomorphic flowers do not represent a monophyletic group and that floral actinomorphy has secondarily and independently evolved in several alliances of the didymocarpoid Gesneriaceae (Möller *et al.* 1999, 2009, Wang *et al.* 2010).

Calcareoboea* and *Didymocarpus (Fig. 3A, G & J). Burt (2001) took a taxonomic decision which is difficult for the outsider to understand: he transferred *Didymocarpus bonii* to the hitherto monotypic *Calcareoboea* and he also announced inclusion of *Didymocarpus hancei* in that genus. *Calcareoboea* and the two species of *Didymocarpus* have extremely different flowers: *Calcareoboea* has long-tubular, bright red flowers with a four-toothed upper lip and a single-toothed lower lip, while the other two *Didymocarpus* species have shortly campanulate, light-coloured flowers with a two-lobed upper lip and a three-lobed lower

lip. Burt (2001: 86) recognised that “the floral differences were associated with the pollination mechanisms of the plants, and such features are known to be unreliable as sole generic criteria”.

Our data show that *Didymocarpus hancei* indeed falls into the *Petrocodon* clade (Figs. 1, 2). Within that clade, it is not particularly close to *Calcareoboea*, but the general affinity is in agreement with Burt’s prediction. Currently, there are no molecular data pertaining to the placement of *Didymocarpus bonii*, but we are confident that Burt (2001) was correct and, moreover, that (at least) one more species of *Didymocarpus* (*D. mollifolius*) belongs to this alliance. *Calcareoboea coccinea* was already included in *Petrocodon* by Wang *et al.* (2011) and needs no further discussion.

Lagarosolen and **Paralagarosolen** (Fig. 3B, C, E, H & K). The name of the latter already suggests its close affinity with *Lagarosolen*. The two genera share a rather narrow-cylindrical, not pouched corolla tube and a bilobed stigma, but *Paralagarosolen* was said to differ from *Lagarosolen* in “having leaves sometimes peltate at base, cyme with only one flower, corolla lobes rounded-obtuse at apex, and capsule ovoid-ellipsoid” (Wei 2004: 528). These characters, however, hardly warrant generic separation. Peltate leaves occur in species of several genera [e.g. *Cyrandra peltata* Jack (1823: 30), *Briggsia longipes* Craib (1920: 262), *Drymonia peltata* (Oliv.) Moore (1955: 112), *Metapetrocosmea peltata* (Merr. & Chun) Wang (1981b: 39), *Petrocosmea peltata* Merrill & Chun (1935: 320), *Paraboea peltifolia* D.Fang & L.Zeng in Fang *et al.* (1995: 606), *Sinningia tuberosa* (Mart.) Moore (1973: 40)], the reduction of the cymes to single flowers is a common phenomenon, rounded-obtuse (vs. acute) corolla lobes occur also in *Lagarosolen jingxiensis* and *L. lui* (Wei *et al.* 2010b: 263, 264). Although a slender (“linear”) fruit seems to be characteristic of *Lagarosolen* (but the fruit is unknown in some species), *L. lui* has an “elliptic” fruit (Wei *et al.* 2010b: 265). Consequently, the generic separation appears rather weak and *Lagarosolen* itself is heterogeneous in floral characters. The corolla morphology of the type species (*L. hispidus*: narrow tube tapering toward the base, corolla lobes narrowly triangular, acute at tip and projecting forward) is only found in a few species. *L. coriaceifolius* has a distinctly broader tube and broadly triangular lobes, *L. hechiensis* has an infundibuliform flower with patent, acute lobes, and *L. jingxiensis* and *L. lui* have a patent limb with rounded corolla lobes. The genus, based essentially on corolla characters, is thus not very well characterised. This is likely the reason why the species of *Lagarosolen* appear scattered over the whole clade - they do not form a coherent group, neither in their molecular characteristics nor in floral morphology.

Dolicholoma (Fig. 3F). The narrow tube and the subactinomorphic limb with long, acute lobes are shared between *Dolicholoma* and *Lagarosolen*. It is difficult to understand why Wang (1984b), when establishing *Lagarosolen*, did not address the floral similarity of the two genera. When establishing *Dolicholoma* D.Fang & W.T.Wang in Wang (1983b), the authors placed that genus in the proximity of *Didymocarpus*, while they referred *Lagarosolen* in the proximity of *Chirita* Buch.-Ham. ex Don (1825: 89). The reason was probably the difference in the stigma (“disciform” in *Dolicholoma*, and “shortly bilobed” in *Lagarosolen*).

Pollination syndromes

It is conceivable that the considerable diversity in floral forms and coloration have a functional background. In the absence of flower visitor data, likely pollination syndromes have to be inferred from floral morphology. In fact, the eye-catching flowers of some taxa, in particular the red, tubular flowers of *Calcareoboea*, the white, bell-shaped flowers of *Petrocodon* and *Tengia*, the narrow-tubed, light-coloured flowers of *Paralagarosolen* and some *Lagarosolen* species, and the oblique-campanulate flowers of the species of *Didymocarpus* included here, can be related to pollination syndromes. The flowers of *Calcareoboea* can be classified as bird pollinated flowers. The corolla colour (bright red), corolla form (tubular, widening toward the limb), position of stamens (beneath the corolla roof), limb structure (upper lip of four small tooth-like and downcurved corolla lobes forming a helmet, lower lip of a single recurved lobe), the presence of a well-developed, cup-shaped nectary, the horizontal or downward-inclined position of the flowers, their number and arrangement into a wreath radiating in all directions (thus eye-catching and visible from far away), and the long, stout peduncle suggests that the bird perches on the peduncle and enters the flower with the beak from below, the pollen being deposited on the beak or forehead (nototribic pollen deposition).



FIGURE 3: Examples of flower morphology of various taxa belonging to the *Petrocodon* clade arranged by phylogenetic relationships as suggested by the molecular data: A, *Didymocarpus niveolanosus*; B, *Lagarosolen integrifolius*; C, *Paralagarosolen fangianus*; D, *Wentsaiboea tiandengensis*; E, *Lagarosolen ainsliifolius*; F, *Dolicholoma jasminiflorum*; G, *Calcareoboea coccinea*; H, *Lagarosolen hechiensis*; J, *Didymocarpus hancei*; K, *Lagarosolen coriaceifolius*; L, *Tengia scopulorum*; M, *Petrocodon dealbatus*.

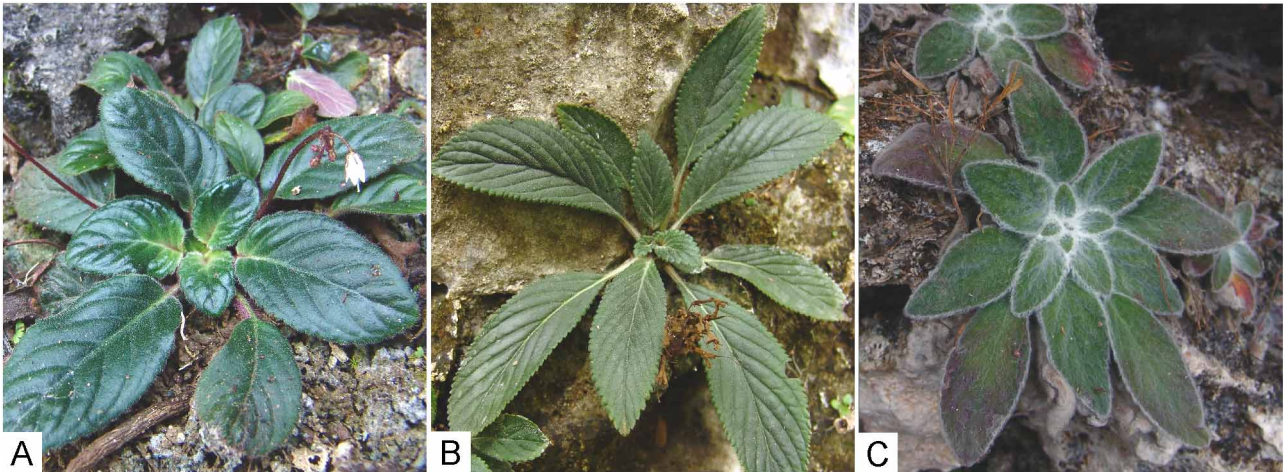


FIGURE 4: Examples of vegetative habit of various taxa belonging to the *Petrocodon* clade: A, *Petrocodon ferrugineus*; B, *Didymocarpus hancei*; C, *Didymocarpus niveolanosus*.

The corolla form (bell-shape or urceolate), the apically confluent locules of the anthers, the small (non-functional?) ring-like nectary, and the nodding position of the flowers of *Petrocodon* and *Tengia* suggest buzz-pollination by bees (see also Wang *et al.* 2010). The long, narrow-tubed, hypocrateriform flowers of *Dolicholoma*, *Paralagarosolen* and some species of *Lagarosolen* suggest pollination by butterflies. Other species of *Lagarosolen* are possibly bee-pollinated and the same certainly applies for the obliquely campanulate flower of the relevant *Didymocarpus* species.

The floral diversity thus approaches to some extent that of some neotropical genera such as *Achimenes* Persoon (1807: 164), *Gasteranthus* Bentham (1846: 233) or *Sinningia* Nees von Esenbeck (1825: 297) (e.g., Wiehler 1983, Perret *et al.* 2001, 2003, Skog & Kvist 2000, Roalson *et al.* 2002, 2003).

Taxonomic consequences

The distribution of genetic diversity (branch lengths) of the highly supported *Petrocodon* clade (Möller *et al.* 2011a, and present results), the erratic distribution of the *Lagarosolen* species, and the divergent corolla morphology on which the genera have been based (likely reflecting different pollination syndromes) lead us to the conclusion that this clade is an alliance of species which has experienced radiations during its evolution involving often parallel adaptations to different pollinators. The largest genus in the alliance, *Lagarosolen*, with seven species, is apparently polyphyletic and heterogeneous, as indicated by the molecular data and supported by the heterogeneity of the corolla characters. In view of the fact that the genera were based solely on corolla characters, that the corolla characters can be associated with pollination syndromes, and that *Lagarosolen* is apparently polyphyletic, it seems best to dispense with the traditional genera and to include the genera and species discussed into *Petrocodon* (the oldest generic name). Wiehler's credo "pollination syndromes do not constitute genera" (Wiehler 1983), has seemingly not found much echo in the taxonomy of Old World Gesneriaceae so far, but the present work represents an important step in this direction. Principally, our taxonomic decision is in agreement with the conclusions of Wang *et al.* (2011), but the present circumscription of *Petrocodon* is much wider, including *Lagarosolen*, *Dolicholoma*, particular species of *Didymocarpus*, and a species described recently under *Wentsaiboea*.

With regard to *Didymocarpus*, molecular data were available for *D. hancei* and *D. niveolanosus*. These species are apparently related to *D. mollifolius*, which we also transfer to *Petrocodon*. As Burt (2001) has transferred *D. bonii* to *Calcareoboea*, we retain it in *Petrocodon* as well. In all of these cases, molecular data are needed to confirm their positions.

There are also a number of species, which have been described (but not formally established) and are illustrated in Y.G. Wei *et al.*'s splendid book "Gesneriaceae of South China" (Wei *et al.* 2010b). One species

has been described under *Petrocodon* (*P. angustifolius nomen nudum*) and two under *Lagarosolen* (*L. ainsliifolius nomen nudum*, *L. sp. nov.*) (see also below). Available molecular data show, that they all fall into the *Petrocodon* clade and should be validly described under this genus. In total, including the unpublished species, *Petrocodon* encompasses more than 20 species, which is four times as many as in the concept of Wang *et al.* (2011).

Formal treatment

***Petrocodon* Hance (1883: 167).**

Type: *Petrocodon dealbatus* Hance.

Heterotypic synonyms:

Didymocarpus Wallich (1819: 378), pro parte excl. type. Type: *D. primulifolius* D. Don.

Tengia Chun (1946: 279). Type: *Tengia scopulorum* Chun.

Calcareoboea C.Y. Wu ex Li (1982: 241). Type: *Calcareoboea coccinea* C.Y. Wu ex H.W. Li.

Dolicholoma D. Fang & W.T. Wang in Wang (1983b: 18). Type: *Dolicholoma jasminiflorum* D. Fang & W.T. Wang.

Lagarosolen Wang (1984b: 11). Type: *Lagarosolen hispidus* W.T. Wang.

Paralagarosolen Wei (2004: 528). Type: *Paralagarosolen fangianus* Y.G. Wei.

Wentsaiboea Fang & Qin (2004: 533), pro parte excl. type. Type: *W. renifolia* D. Fang & D.H. Qin = *Primulina renifolia* (D. Fang & D.H. Qin) Y.Z. Wang in Wang *et al.* (2011: 62).

***Petrocodon bonii* (Pellegr.) A. Weber & Mich. Möller, comb. nov.**

Basionym:—*Didymocarpus bonii* Pellegrin (1926: 416).

Homotypic synonym:—*Calcareoboea bonii* (Pellegr.) Burt (2001: 86).

Notes:—Molecular data are lacking for this species, the transfer is *fide* Burt (2001), who included *Didymocarpus bonii* in *Calcareoboea* as a second species and predicted (correctly) that also *D. hancei* is closely allied to *Calcareoboea*. Nevertheless, confirmation is needed.

***Petrocodon coccineus* (C.Y. Wu ex H.W. Li) Y.Z. Wang in Wang *et al.* (2011: 60).**

Basionym:—*Calcareoboea coccinea* C.Y. Wu ex Li (1982: 243, fig. 1).

***Petrocodon coriaceifolius* (Y.G. Wei) Y.G. Wei & Mich. Möller, comb. nov.**

Basionym:—*Lagarosolen coriaceifolius* Wei (2006: 273, fig. 1; “*L. coriaceifolium*”).

***Petrocodon dealbatus* Hance (1883: 167).**

Heterotypic synonym:—*Petrocodon longistylus* Kraenzlin (1928: 216).

***Petrocodon dealbatus* var. *denticulatus* (W.T. Wang) W.T. Wang in Wang *et al.* (1990: 420).**

Basionym:—*Petrocodon denticulatus* Wang (1975: 101).

***Petrocodon fangianus* (Y.G. Wei) J.M. Li & Y.Z. Wang in Wang *et al.* (2011: 60).**

Basionym:—*Paralagarosolen fangianus* Wei (2004: 529, fig. 1).

***Petrocodon ferrugineus* Y.G. Wei (2007: 135, fig. 1).**

***Petrocodon hancei* (Hemsl.) A. Weber & Mich. Möller, comb. nov.**

Basionym:—*Didymocarpus hancei* Hemsley (1890: 229).

Petrocodon hechiensis* (Y.G.We, Yan Liu & F.Wen) Y.G.We & Mich.Möller, *comb. nov.

Basionym:—*Lagarosolen hechiensis* Wei, Liu & Wen (2008: 299, fig. 1).

Petrocodon hispidus* (W.T.Wang) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Lagarosolen hispidus* Wang (1984b: 12).

Petrocodon integrifolius* (D.Fang & L.Zeng) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Lagarosolen integrifolius* D.Fang & L.Zeng in Fang *et al.* (1993: 463).

Petrocodon jasminiflorus* (D.Fang & W.T.Wang) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Dolicholoma jasminiflorum* D.Fang & W.T.Wang in Wang (1983b: 19).

Petrocodon jingxiensis* (Yan Liu, H.S.Gao & W.B.Xu) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Lagarosolen jingxiensis* Liu, Gao & Xu (2008: 274, fig. 1).

Petrocodon lui* (Yan Liu & W.B.Xu) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Lagarosolen lui* Yan Liu & W.B.Xu in Xu *et al.* (2010: 7, fig. 1).

Petrocodon mollifolius* (W.T.Wang) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Didymocarpus mollifolius* Wang (1984b: 21).

Notes:—No molecular data available, but the species is similar to *P. hancei* and *P. niveolanosus*. The three species form a group of rosette plants (very unlike true *Didymocarpus*, for the morphology of which see Weber & Burt 1998) with oblong or oblanceolate leaves with pinnate venation.

Petrocodon multiflorus F.Wen & Y.S.Jiang in Jiang *et al.* (2011: 57).

Notes:—No molecular data available.

Petrocodons niveolanosus* (D.Fang & W.T.Wang) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Didymocarpus niveolanosus* D.Fang & W.T.Wang in Wang & Pan (1982: 133).

Petrocodon scopulorum (Chun) Y.Z.Wang in Wang *et al.* (2011: 60, as: '*P. scopulorus*').

Basionym:—*Tengia scopulorum* Chun (1946: 281, pl. 46).

Heterotypic synonym:—*Tengia scopulorum* Chun var. *potiflora* (S.Z.He) W.T.Wang, A.L.Weitzman & L.E.Skog in Weitzmann *et al.* (1998: 434).

Basionym:—*Tengia potiflora* S.Z.He in He & Cong (1992: 269).

Notes:—Following Wei *et al.* (2010b) and Wang *et al.* (2011), *Tengia scopulorum* var. *potifolia* is included here in typical *P. scopulorum*. Wang's spelling "*scopulorus*" is corrected here into "*scopulorum*", as this is the *genetivus pluralis* of *scopulus*, Lat. (meaning cliff or rock).

Petrocodon tiandengensis* (Yan Liu & B.Pan) A.Weber & Mich.Möller, *comb. nov.

Basionym:—*Wentsaiboea tiandengensis* Yan Liu & B.Pan in Liu *et al.* (2010: 739, fig. 2–3E).

The following species are also relevant:

Lagarosolen ainsliifolius W.H.Chen & Y.M.Shui, *nom. nud.* (Shui & Chen 2006: 169, Wei *et al.* 2010b: 266, in both as: '*L. ainsliifolia*').

Notes:—Described and illustrated, but not validly published in Shui & Chen (2006) and Wei *et al.* (2010b). Included in the present molecular analysis.

Lagarosolen sp. nov., voucher: Y.G. Wei 0903.

Notes:—Included in the present molecular analysis.

Petrocodon angustifolius Y.G. Wei, F. Wen & H.Z. Lü, nom. nud. (Wei *et al.* 2010b: 538, as: '*L. angustifolia*').

Notes:—Described and illustrated, but not validly published in Wei *et al.* (2010b). No molecular data available.

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Appendix 1: Diagnostics of the Bayesian inference analysis of the *Petrocodon* dataset of combined *trnL-F* and ITS sequence data plus alignment gap matrix.

Number of taxa = 31
 Number of characters = 1566
 Number of generations = 1500000

Average standard deviation of split frequencies: 0.002526

Analysis completed in 13383 seconds
 Analysis used 13382.17 seconds of CPU time
 Likelihood of best state for "cold" chain of run 1 was -6919.19
 Likelihood of best state for "cold" chain of run 2 was -6924.13
 Acceptance rates for the moves in the "cold" chain of run 1:
 With prob. Chain accepted changes to
 59.19 % param. 1 (revmat) with Dirichlet proposal
 27.56 % param. 2 (revmat) with Dirichlet proposal
 67.94 % param. 3 (revmat) with Dirichlet proposal
 19.72 % param. 4 (state frequencies) with Dirichlet proposal
 19.96 % param. 6 (state frequencies) with Dirichlet proposal
 91.82 % param. 9 (gamma shape) with multiplier
 47.26 % param. 10 (prop. invar. sites) with sliding window
 13.38 % param. 11 (topology and branch lengths) with extending TBR
 20.35 % param. 11 (topology and branch lengths) with LOCAL

Acceptance rates for the moves in the "cold" chain of run 2:
 With prob. Chain accepted changes to
 59.53 % param. 1 (revmat) with Dirichlet proposal
 27.31 % param. 2 (revmat) with Dirichlet proposal
 67.48 % param. 3 (revmat) with Dirichlet proposal
 19.73 % param. 4 (state frequencies) with Dirichlet proposal
 19.71 % param. 6 (state frequencies) with Dirichlet proposal
 91.67 % param. 9 (gamma shape) with multiplier
 47.43 % param. 10 (prop. invar. sites) with sliding window
 13.37 % param. 11 (topology and branch lengths) with extending TBR
 20.57 % param. 11 (topology and branch lengths) with LOCAL

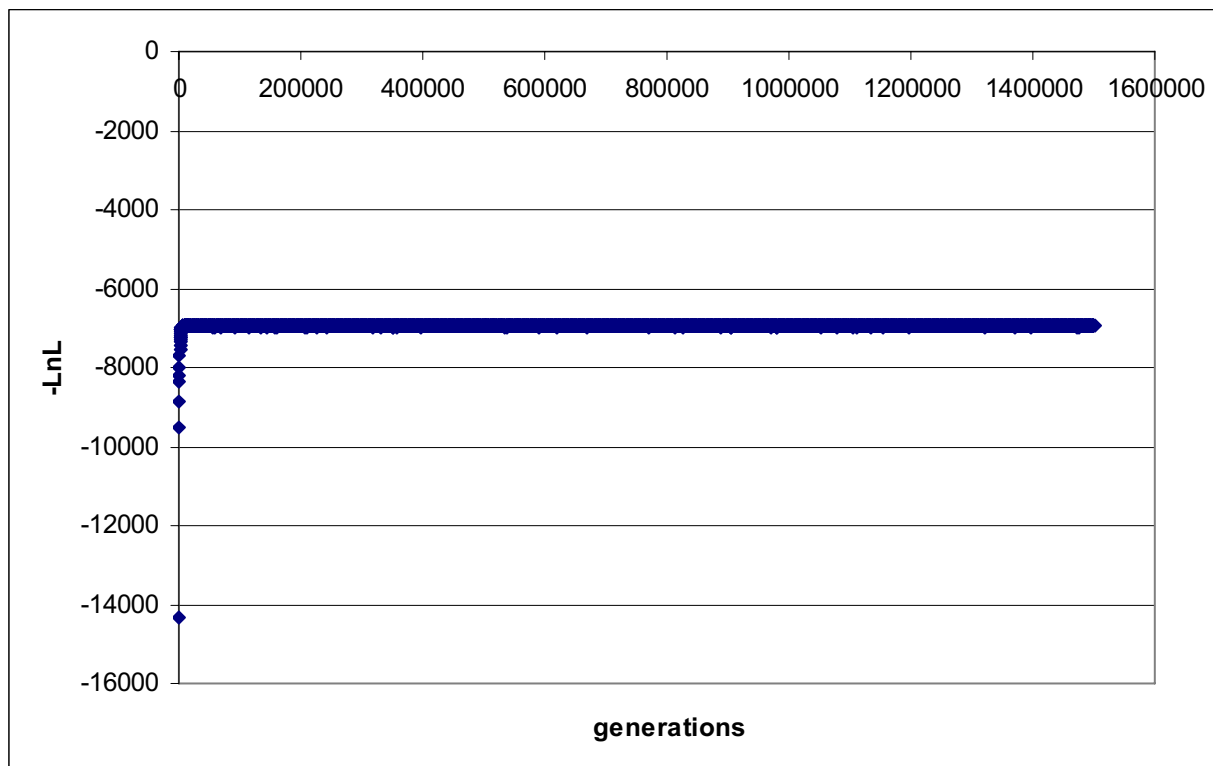
Chain swap information for run 1:

	1	2	3	4
1		0.34	0.08	0.02
2	249733		0.43	0.13
3	249575	249342		0.48
4	250971	249797	250582	

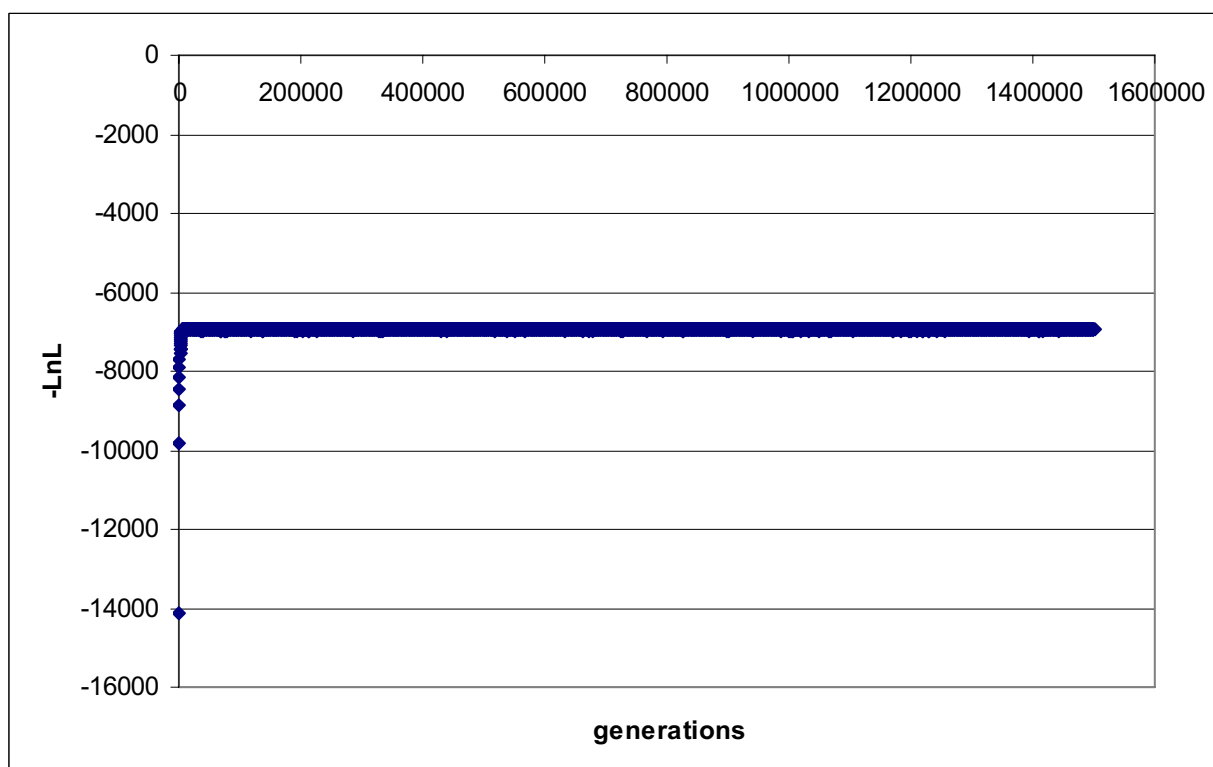
Chain swap information for run 2:

	1	2	3	4
1		0.34	0.08	0.02
2	250320		0.42	0.13
3	249876	250915		0.47
4	250135	249156	249598	

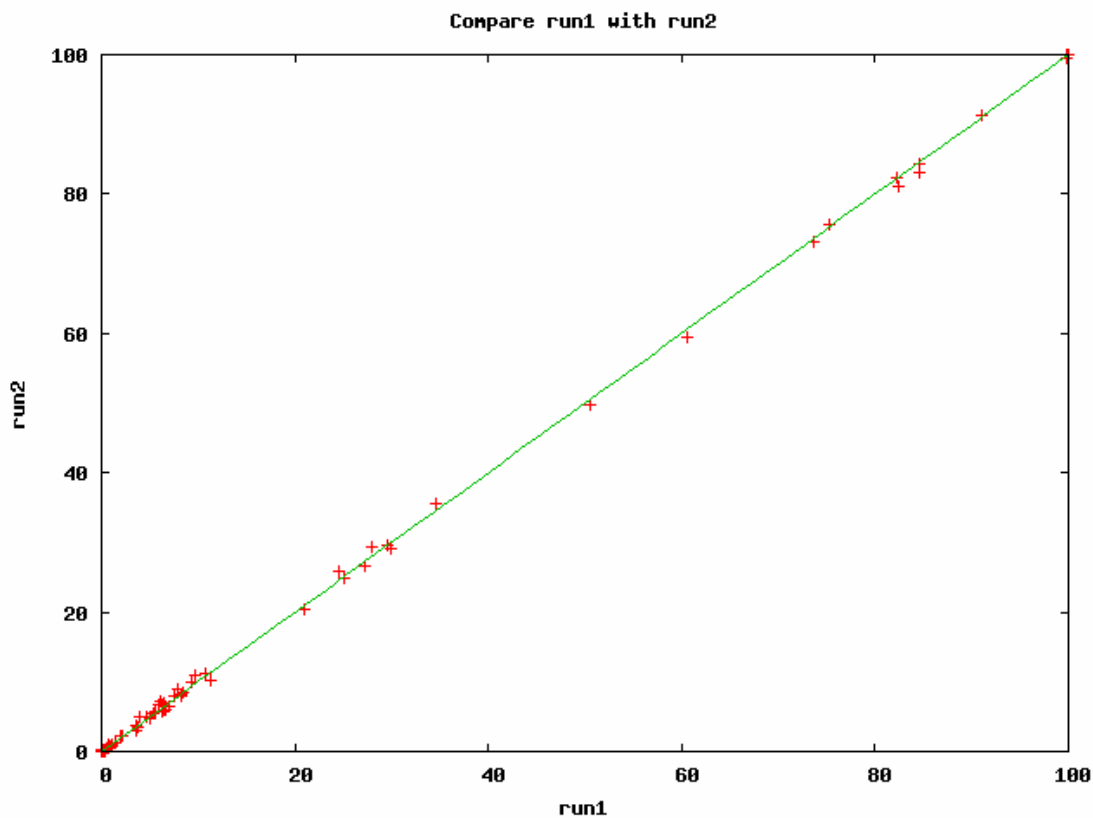
Upper diagonal: Proportion of successful state exchanges between chains
 Lower diagonal: Number of attempted state exchanges between chains



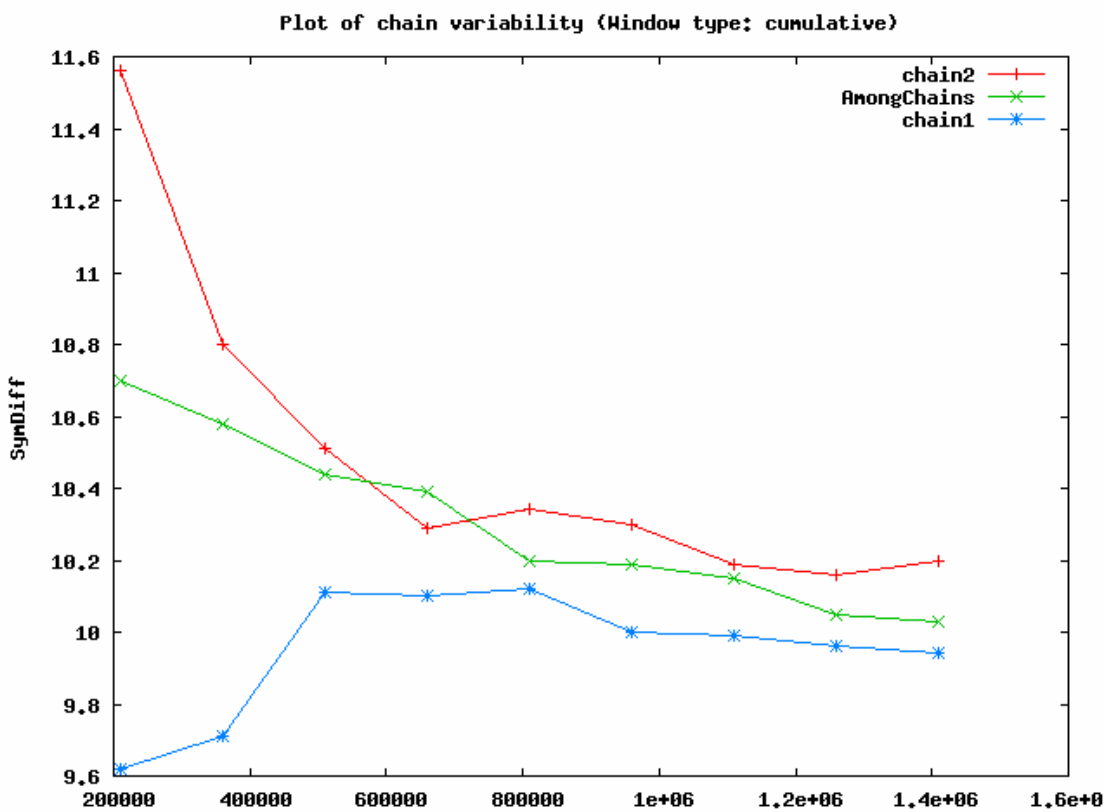
generations vs -lnL values, run 1
burn-in 4%



generations vs -lnL values, run 2
burn-in 4%



Petrocodon combined data. Posterior probabilities run 1 versus run 2.



Petrocodon combined data: Symmetric tree differences within and between run 1 vs run 2.

