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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher number</th>
<th>Deposited in</th>
<th>Origin</th>
<th>trnL-F</th>
<th>ITS or ITS1 / ITS2</th>
</tr>
</thead>
</table>
| Calcareoboea coccinea | M. Möller MMO 01-141 | E, WU | China, Guangxi, 
ex H.W.Li (1982: 243) | FJ501516 | FJ501365 |
| Chirita gemella        | L. Averyanov 1987 [Cult. RBGE 19941913] | E | Vietnam, Hong 
D.Wood (1972: 370) | FJ501523 | FJ501345 |
| Chirita longgangensis  | A. Takhtajan & N. Aruzyto 1975 [Cult. RBGE 19941915] | E | Vietnam, 
| Chirita minutinaculata | J. M. Li 067134 | PE | China, Guangxi, 
| Chirita pinnata        | Expedition Beijing 896526 (US 294374) | US | China, Guangxi, 
| Chirita pinnatifida    | Q. J. Xie J-037 (US 422838) | US | China, Guangxi, 
(Hand.-Mazz.) B. L. Burtt (1960: 99) | FJ501527 | FJ501350 |
| Chirita spinulosa      | Y. Z. Wang 067133 | PE | China, Guangxi, 
| Chiritopsis glandulosa | J. M. Li 054291 | PE | China, Guangxi, 
D. Fang & W.T. Wang in Wang & 
L. Zeng & D. H. Qin in Fang et al. (1993: 470) | DQ872804 | DQ872841 |
| Chiritopsis repanda    | ex Smithsonian Institute 94-083 [Cult. RBGE 19951206] | E | China, Guangxi, 
| Didymocarpus hancei    | M. Möller MMO 08-1342 | E | China, Guangxi, 
Hemsley (1890: 229) | HQ632944 | HQ633041 |
| Didymocarpus niveolanosus | M. Möller MMO 06-861 | E | China, Guangxi, 
D. Fang & W.T. Wang in Wang & 
Pan (1982: 133) | JF697588 | JF697576 |
| Dolicholoma jasminiflorum | M. Möller MMO 06-851 | E | China, Guangxi, 
D. Fang & W.T. Wang in Wang & 
Pan (1983b: 19) | Wei et al., 2010a | Wei et al., 2010a |
| Lagarosolen ainslifolius | Y. M. Shui et al. 44071 | KUN | China, Yunnan, 
W. H. Chen & Y. M. Shui nomen 
Maguan county | HQ632941 | HQ633038 |
| Lagarosolen coriacefolius | Y. G. Wei (2006: 273) | E | China, Guangxi, 
Yanqshuo county | HQ632943 | HQ633040 |
### Table 1 (continued)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher number</th>
<th>Deposited in</th>
<th>Origin</th>
<th>(\text{trnL-F} )</th>
<th>(\text{ITS or ITS1/ITS2} )</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lagarosolen hispidus</em> W.T.Wang (1984b: 12)</td>
<td>Y.M.Shai et al. 82661</td>
<td>E</td>
<td>China, Yunnan, Maguan county</td>
<td>HQ632939</td>
<td>HQ633036</td>
</tr>
<tr>
<td><em>Lagarosolen integrifolius</em> D.Fang &amp; L.Zeng in Fang et al. (1993: 463)</td>
<td>M.Möller MMO 06-865</td>
<td>E</td>
<td>China, Guangxi, Longzhou county</td>
<td>HQ632940</td>
<td>HQ633037</td>
</tr>
<tr>
<td><em>Lagarosolen luo</em> Yan Liu &amp; W.B.Xu in Xu et al. (2010: 7)</td>
<td>Y.G.Wei 8012</td>
<td>IBK</td>
<td>China, Guangxi, Jingxi county</td>
<td>HQ632938</td>
<td>HQ633035</td>
</tr>
<tr>
<td><em>Lagarosolen sp.nov.</em> Y.G.Wei 0903</td>
<td>IBK</td>
<td></td>
<td>China, Guangxi, Hechi city</td>
<td>JF697589</td>
<td>JF697577</td>
</tr>
<tr>
<td><em>Loxostigma fimbrisepalum</em> K.Y.Pan in Wang &amp; Pan (1982: 143)</td>
<td>Y.Z.Wang 991005</td>
<td>PE</td>
<td>China, Yunnan, Jining county</td>
<td>FJ501507</td>
<td>Wei et al., 2010a</td>
</tr>
<tr>
<td><em>Lysionotus pauciflorus</em> Maximowicz (1874: 534)</td>
<td>M.Möller MMO 01-101</td>
<td>E, WU</td>
<td>China, Yunnan, Xichou county</td>
<td>FJ501497</td>
<td>FJ501331</td>
</tr>
<tr>
<td><em>Lysionotus petelotii</em> Pellegrin (1930: 503)</td>
<td>M.Möller MMO 01-100/4</td>
<td>E</td>
<td>China, Yunnan, road to Xichou</td>
<td>FJ501496</td>
<td>HQ632974</td>
</tr>
<tr>
<td><em>Paralagarosolen fangianus</em> (Y.G.Wei) J.M.Li &amp; Y.Z.Wang in Wang et al. (2011: 60)</td>
<td>M.Möller MMO 07-1168</td>
<td>E</td>
<td>China, Guangxi, Napo county</td>
<td>Wei et al., 2010a</td>
<td>Wei et al., 2010a</td>
</tr>
<tr>
<td><em>Petrocodon dealbatus</em> Hance (1883: 167)</td>
<td>Q.J.Xie J-042 (US 422841)</td>
<td>US</td>
<td>China, Guangdong, Lianxian county</td>
<td>FJ501537</td>
<td>FJ501358</td>
</tr>
<tr>
<td><em>Petrocodon ferrugineus</em> Y.G.Wei (2007: 135)</td>
<td>M.Möller MMO 06-784</td>
<td>E</td>
<td>China, Guangxi, Xincheng county</td>
<td>HQ632946</td>
<td>HQ633043</td>
</tr>
<tr>
<td><em>Tengia scopalorum</em> Chun (1946: 281, pl. 46)</td>
<td>F.Wen 2010-02</td>
<td>IBK</td>
<td>China, Guizhou, Xiwen county</td>
<td>HQ632947</td>
<td>HQ633044</td>
</tr>
<tr>
<td><em>Wentsaiboea renifolia</em> D.Fang &amp; D.H.Qin (2004: 534)</td>
<td>M.Möller MMO 06-791</td>
<td>E</td>
<td>China, Guangxi, Duan county</td>
<td>Wei et al., 2010a</td>
<td>Wei et al., 2010a</td>
</tr>
<tr>
<td><em>Wentsaiboea tiandengensis</em> Yan Liu &amp; B.Pan in Liu et al. (2010: 739, fig. 2-3E)</td>
<td>M.Möller MMO 07-1164</td>
<td>E</td>
<td>China, Guangxi, Tiandeng county</td>
<td>HQ632945</td>
<td>HQ633042</td>
</tr>
</tbody>
</table>

**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. nivolanus) and Wentsaiboea tiandengensis (Liu et al. 2010). Other species of Didymocarpus form an independent clade and D. cortusifolius Léveillé (1906: 427) is more closely related to Allocheilos Wang (1983a: 321) and Gyrocheilos Wang (1981a: 28) (Möller 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 Möller 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 Möller 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 Möller 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. Möller), 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 Wentsiaiboea 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).

The remaining 11 samples formed a strongly supported clade (BS=94%; PP=1.00) but with few well supported internal branches. Lagarosolen ainslifolius 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 [Calcereoboëa 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 pentameric, 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), Burtt (1970) much earlier had predicted a very close relationship of Tengia with Petrocodon (tribe Didymocarpeae). Burtt 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, Burtt 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 descendence 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).

**Calcereoboëa** and **Didymocarpus** (Fig. 3A, G & J). Burtt (2001) took a taxonomic decision which is difficult for the outsider to understand: he transferred Didymocarpus bonii to the hitherto monotypic Calcereoboëa and he also announced inclusion of Didymocarpus hancei in that genus. Calcereoboëa and the two species of Didymocarpus have extremely different flowers: Calcereoboëa 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. Burtt (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 Burtt’s prediction. Currently, there are no molecular data pertaining to the placement of Didymocarpus bonii, but we are confident that Burtt (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. Cyrtandra 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-obluse (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. corticefolius 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).
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 Tenga 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.


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 polyphylectic and heterogeneous, 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 Wentsaiioea.

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 Burtt (2001) has transferred D. bonii to Calcareaoboea, 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* no*men nudum*) and two under *Lagarosolen* (*L. ainsliifolius* no*men 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.
*Calcareoboea* C.Y.Wu ex Li (1982: 241). Type: *Calcareoboea coccinea* C.Y.Wu ex H.W.Li.

Basionym:—*Didymocarpus bonii* Pellegrin (1926: 416).
Notes:—Molecular data are lacking for this species, the transfer is *fide* Burtt (2001), who included *Didymocarpus bonii* in *Calcereoboea* as a second species and predicted (correctly) that also *D. hancei* is closely allied to *Calcereoboea*. Nevertheless, confirmation is needed.

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

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

*Petrocodon dealbatus* Hance (1883: 167).
Heterotypic synonym:—*Petrocodon longistylus* Kraenzlin (1928: 216).


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

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

Basionym:—*Didymocarpus hancei* Hemsley (1890: 229).
Basionym:—*Lagarosolen hechiensis* Wei, Liu & Wen (2008: 299, fig. 1).


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

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

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 & Burtt 1998) with oblong or oblanceolate leaves with pinnate venation.

Notes:—No molecular data available.


**Petrocodon scopulorum** (Chun) Y.Z.Wang in Wang *et al.* (2011: 60, as: ‘*P. scopulorum*’).
Basionym:—*Tengia scopulorum* Chun (1946: 281, pl. 46).
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 "*scopulorum*" is corrected here into "*scopulorum*", as this is the genetivus pluralis of *scopulus*, Lat. (meaning cliff or rock).

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.
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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.

Acknowledgements

The work was carried out in cooperation between the University of Vienna (supported by the Austrian Science Fonds, FWF-Proj. No. P-13107-Bio), the Guangxi Institute of Botany and the Royal Botanic Garden Edinburgh (RBGE). We are grateful to Robert Mill for a critical reading of the manuscript. RBGE is supported by the Scottish Government Rural and Environment Research and Analysis Directorate (RERAD). Fieldwork of MM was supported by the RBGE Expedition Fund and of FW by the Guangxi Natural Science Foundation (2011GNNSB018050). YGW benefitted from support through the Science & Technology Innovation Program of the Guangxi Academy of Sciences Fund.

References

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:

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Upper diagonal: Proportion of successful state exchanges between chains
Lower diagonal: Number of attempted state exchanges between chains
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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.
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Run 1

Plot of splits 1 to 20 from tmp6cc6B/Cumulative/outVqbfJm sorted by widest range

Run 2

Plot of splits 1 to 20 from tmp6cc6B/Cumulative/outIk0deI sorted by widest range