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A new species of *Paraboea* (Gesneriaceae) from a karst cave in Guangxi, China, and observations on variations in flower and inflorescence architecture

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A new species of Gesneriaceae, *Paraboea trisejala* W.H.Chen & Y.M.Shui, from a karst cave in Guangxi, China is described and illustrated. The new species differs from other species of *Paraboea* by its three-lobed calyx. Variation in flower and inflorescence architecture was observed under cultivation. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 681–688.

ADDITIONAL KEYWORDS: actinomorphy – floral morphology – pair-flowered cyme – *Paraboea trisejala* **sp. nov.** – spatiotemporal flower development – zygomorphy.

INTRODUCTION

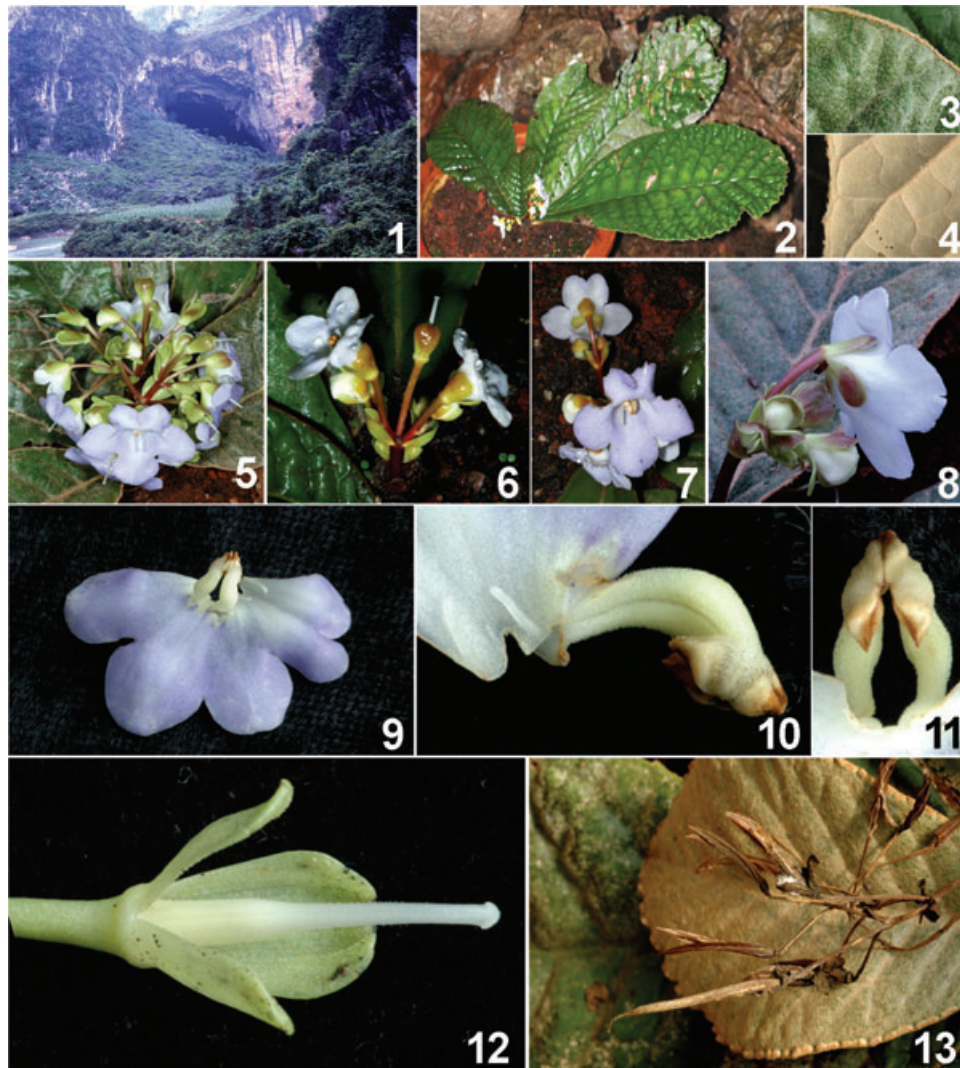
China has the most extensive area of karst topography, with an abundance of endemic and relictual seed plants (Xu, 1993; Fang *et al.*, 1994). The largest karst areas occur in the provinces of Guangxi, Guizhou and south-east Yunnan, totalling about 280 000 km². Here, the types of karst landscapes are rich, including typical karst peak forests, basins, hills, funnels, pan-like lowland and deep V-shaped gorges, harbouring numerous caves (Fig. 1). The environment in these caves is characterized by a steady temperature and humidity, together with diffuse light levels, creating the opportunity for the establishment of a unique flora with numerous narrow endemic species. This area of China was hardly affected by Quaternary glaciations (Fang *et al.*, 1994; Shui & Chen, 2006). Thus, this large area and the diversity of the unique karst habitats have provided excellent environments for the evolution and development of biological diversity.

Gesneriaceae show an extreme abundance and diversity in this region in China, with, so far, 41

genera and 169 species reported, 15 of which are endemic genera (36.6%) and 126 are endemic species (74.6%) (Wang *et al.*, 1998; Li & Wang, 2004; Chen & Shui, 2006; Liu, Wei & Tang, 2006). Furthermore, Gesneriaceae appear to maintain a phylogenetically diverse range of taxa here (Burt, 1963; Burt & Wiehler, 1995; Fang *et al.*, 1995; Wei, Zhong & Wen, 2004). Thus, further studies on Gesneriaceae will be significant for understanding the evolution and conservation of plants in the karst region of China.

In May 2005, some of the authors (WHC, YMS and MDZ) encountered a species of Gesneriaceae when collecting companion plants of *Begonia* during a field survey in Guangxi, China (Fig. 1). Because the species of Gesneriaceae had no flowers, several plants were introduced to the glasshouse at Kunming Botanic Garden. Two months later, one individual flowered. It had only one inflorescence with five flowers in 2005. The following year, the plant produced several inflorescences with many flowers. Early inflorescences produced a greater number of and larger flowers than subsequent inflorescences. After comparisons with similar taxa (Wang, 1990; Li & Wang, 2004), it became clear that the plants represented a new species of *Paraboea*. The observed variations in the flowers

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Figures 1–13. Photographic images of habitat and morphology of *Paraboea trisejala* sp. nov. Fig. 1. Habitat. Figs 2–12. Habit of a flowering individual under glasshouse conditions. Fig. 2. Gross morphology. Fig. 3. Upper surface of leaves. Fig. 4. Lower surface of leaves. Fig. 5. Overview of several inflorescences. Fig. 6. Face view of an individual inflorescence. Fig. 7. Face and back view of individual flowers. Fig. 8. Lateral view of an individual flower. Fig. 9. View of a flower cut laterally. Fig. 10. Lateral view of anthers. Fig. 11. Face view of a pair of anthers. Fig. 12. Ovary and persistent trilobed calyx. Fig. 13. Inflorescences with mature, dry, dehisced fruits.

and inflorescence architecture provided us with an opportunity to discuss the evolution of these characters in Gesneriaceae (Ivanina, 1965; Palee *et al.*, 2006).

MATERIAL AND METHODS

PLANT MATERIALS

The plants were collected from the karst region in Guangxi, China. The type specimen was collected from living plants cultivated in the glasshouse at Kunming Botanic Garden, and deposited at the herbarium of Kunming Institute of Botany (KUN), Chinese Academy of Sciences. Through comparisons

of diagnostic characters with material of Gesneriaceae from China, Vietnam and Thailand (Burt, 2001), it was confirmed that the species had not been recorded before. With no mature fruits from the glasshouse, the description of these is based on the paratype specimen collected in the field.

OBSERVATIONS ON INFLORESCENCES AND FLOWERS

From July 2005 to August 2006, three individuals were observed at Kunming Botanic Garden. During the flowering period, every inflorescence and every flower ordination of each individual were recorded.

The size of all flowers was examined and measured, and the changing sequence of flowers and inflorescences was described and illustrated according to Weber (1973).

SPECIES DESCRIPTION

Paraboea trisepala W.H.Chen & Y.M.Shui, *sp. nov.* (Figs 2–13, 14A–L)

Type: CHINA. Guangxi: Jingxi County, 23°01'N, 106°36'E, at the entrance of a limestone cave on a hillside, at 300 m altitude, introduced to Kunming Botanic Garden (22.v.2005), 10.vii.2006 (fl), Y. M. Shui *et al.* B2005-468 (*holotype:* KUN; *isotype:* PE).

Diagnosis: Species nova quae calicis lobis plerumque tribus inaequalibus, lobo superiore obovato, 4–8 × 4–7 mm, ad apicem emarginato, lateralibus duobus

obovatis, 4–8 × 2–3 mm, ad apicem obtusis vel rotundatis, a speciebus *Paraboeae* ceteris valde differt.

Description: Herb perennial, stemless. Rhizomes thick, c. 8 mm in diameter. Leaves rosulate, basal, clustered at the top of rhizomes; petiole short and thick, 0.5–0.7 cm long, 0.6–0.7 cm in diameter, densely covered with appressed grey woolly hairs. Leaf blade obovate, 11–26 × 5.6–11 cm, thin leathery, adaxially thinly arachnoid when young, glabrescent when mature, abaxially densely appressed woolly hairs, base attenuate to broadly cuneate, apex rounded to obtuse, margin remotely crenate to subentire with a densely woolly strip, principal vein concave adaxially, convex abaxially, lateral veins 11–14 on each side of principal vein, concave and glabrescent adaxially, convex and densely woolly abaxially, veinlet obscure and slightly concave adaxially and convex abaxially. Dichotomous cymes axillary or subterminal, one- to five-branched, 1–19-flowered. Peduncles 3.5–6.6 cm long, glabrous; bracts 2, cochlear, opposite, 8–10 × 5–7 mm, apex obtuse, glabrous. First flowers larger than consecutive ones. Pedicels 0.9–2.1 cm long. Calyx zygomorphic, greenish and glabrous, usually three-lobed from base; lobes unequal, upper lobe obovate, 4–8 × 4–7 mm, or c. 5.6 × 2.5 mm when three-divided, apex emarginate, margin entire; lower lobes 2, obovate, 4–8 × 2–3 mm, apex obtuse or rounded. Corolla zygomorphic, glabrous, bluish or purplish inside, whitish outside, 1.5–3.1 cm long, 1.5–2.6 cm across; tube obliquely campanulate, swollen, longer than to occasionally nearly equalling limb, 0.7–1.0 cm long, 0.9–1.2 cm in diameter, limb two-lipped, upper lip shorter than lower lip; upper lip 0.8–1.2 × 0.9–1.3 cm, two-lobed, lobes semi-orbicular 3–6 × 4–7 mm, apex obtuse or emarginate; lower lip 1.1–1.9 × 2.1–2.6 cm, three-lobed, central lobe broadly ovate, 5–7 × 6–9 mm, lateral two obliquely ovate 4–6 × 5–8 mm, apex obtuse. Stamens 2, included, adnate to abaxial side of corolla tube near base; anthers dorsifixed, yellow, transversely spindle-shaped, 2.7–3.2 × 1.4–1.9 mm, coherent at the lateral sides, thecae divaricate at base, confluent at apex, dehiscing longitudinally; connective not projecting, puberulent; filaments baculiform, puberulent, 4–5 mm long, inflated and curved on the upper part; staminodes 2, linear, c. 3 mm long, adnate to adaxial side of corolla tube near base. Disc inconspicuous. Pistil puberulent, 6–10 mm long; ovary narrowly ovoid to conical, 2–3 mm long, one-loculed in the upper part and four-loculed in the middle and lower part; in the upper part of ovary, placentas 2, parietal, projecting inward, two-cleft; in the middle and lower part, placentas 4, axile, projecting inward, undivided; stigma 1, terminal, capitate,

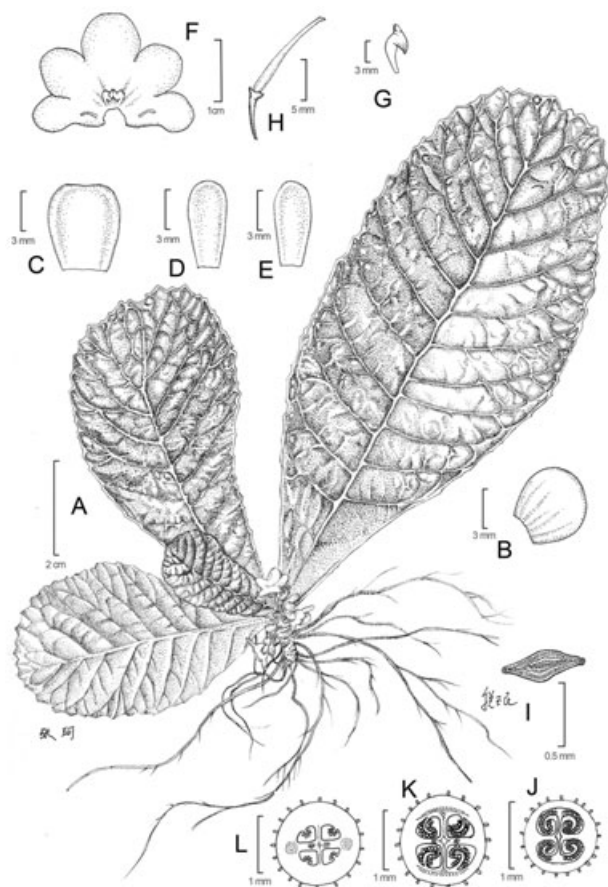


Figure 14. Line drawings of *Paraboea trisepala* *sp. nov.*: A, plant; B, bract; C, upper lobe of the calyx; D, E, lateral lobes of the calyx; F, cut face of a corolla, showing two stamens and two staminodes; G, lateral view of anther; H, ovary; I, seed; J–L, transverse section through upper (J), middle (K) and lower (L) part of the ovary. All drawings based on the holotype. A–H drawn by Ke Zhang and I–L drawn by Yu M. Shui.

KEY TO CHINESE SPECIES WITH STRAIGHT FRUITS IN *PARABOEAE*

1. Stem ramose; peduncle 2–2.7 cm long; bracts *c.* 0.3 mm long; calyx lobes 5, 1–1.2 mm long; corolla 4–5 mm long, outside sparsely glandular puberulent; leaf blade 0.9–2.5 × 0.4–1 cm.....*Paraboea velutina*
Stemless; peduncle 2.5–21 cm long; bracts 2–25 mm long; calyx lobes 5, rarely 3, 2–6.5 mm long; corolla 9–31 mm long, outside glabrous; leaf blade 1–33.5 × 0.3–11 cm.....2
2. Leaf blade base attenuate to broadly cuneate; bracts 5–25 mm long.....3
Leaf blade base peltate-auriculate or peltate and rounded to cuneate; bracts 1–3(–4) mm long.....4
3. Calyx lobes 3, extremely rarely 5, obovate, unequal, upper 4–6.5 × 4–6.5 mm, or *c.* 5.6 × 2.5 mm when three-divided, apex emarginate, lower 2, 4–5 × 2 mm, apex obtuse or rounded; filaments 5–6 mm long; staminodes 2, *c.* 3 mm long; pistil puberulent; capsule pubescent.....*Paraboea trisekala*
Calyx lobes 5, lanceolate-oblong or oblong, 5–8 × 1–2 mm, equal, apex obtuse or rounded; filaments *c.* 2 mm long; staminodes 3, 1–1.5 mm long; pistil and capsule glabrous.....*Paraboea nutans*
4. Leaf blade 6–33.5 × 3–14.3 cm; lateral veins 11–18 on each side of midrib; petiole 1–9 cm long; calyx two-lipped, woolly outside, adaxial lip two-toothed, teeth *c.* 0.7 mm long, abaxial lip three-lobed from base, lobes *c.* 2 × 1.5 mm; staminodes 2, *c.* 2 mm long; ovary woolly, *c.* 5 mm long.....*Paraboea peltifolia*
Leaf blade 1–5 × 0.3–2.2 cm; lateral veins 4–6 on each side of midrib; petiole 0.3–0.9 cm long; calyx five-lobed from base, glabrous outside, lobes lanceolate, 2–3.5 × *c.* 0.6 mm; staminode 1, *c.* 0.2 mm long; ovary glabrous, *c.* 1.5 mm long.....*Paraboea filipes*

with numerous papillae. Capsule straight in relation to pedicel, linear or narrowly oblong, pubescent, 2.1–2.2 cm long, dehiscent loculicidally to base; valves 4, 1.9–2.0 cm long, straight. Seeds 0.5–0.6 × 0.2 mm, unappendaged.

Distribution and habitat: Only known from the type locality: China, Guangxi, Jingxi County. The new species grows on the surface of rocks near the entrance of a dry limestone cave on the upper part of a karst hill. The main companion species are calcicolous and xerophilous plants, such as the ferns *Adiantum caudatum* L. (Adiantaceae), *Ctenitopsis devexa* (Kunze) Ching & Wang (Dryopteridaceae), *Hypodematium crenatum* Kuhn & Decken (Woodsiaceae) and *Pteris deltodon* Baker (Pteridiaceae) and the seed plants *Debregesia longifolia* Wedd. (Urticaceae), *Elatostema rupestre* Wedd. (Urticaceae), *Ficus obscura* Blum (Moraceae), *Ficus sarmentosa* Buch.-Ham. ex Sm. (Moraceae), *Periploca forrestii* Schltr. (Asclepiadaceae), *Rauwolfia verticillata* Baill. (Apocynaceae) and *Spiradiclis baishaiensis* X.X.Chen & W.L.Sha (Rubiaceae).

Phenology: Flowering from June to September in the glasshouse at Kunming (2000 m altitude, mean temperature in the glasshouse similar to the field in Jingxi); fruiting from October to November.

Paratype: China. Guangxi, Jingxi County, 23°01'N, 106°36'E, at the entrance of a limestone cave on the upper part of a hillside, at 300 m altitude, with dry fruits, 22.v.2005, *Y. M. Shui et al.* B2005-150 (KUN).

Relationships: The genus *Paraboea* includes about 88 species, distributed in Bhutan, China, Indonesia, Malaysia, Myanmar, Philippines, Thailand and Vietnam. In China, there are about 18 species and one variety, most limited to karst regions (Li & Wang, 2004). Four of the Chinese taxa have straight fruits, like the new species here. The new species is easily distinguishable from the other species of *Paraboea* by its three-lobed calyces. In this respect, it is similar to several other Gesneriaceae species, including *Gyrocheilos retrotrichum* W.T.Wang var. *oligolobum* W.T.Wang.

RESULTS AND DISCUSSION

VARIATION IN INFLORESCENCE ARCHITECTURE

Gesneriaceae inflorescences are composed of units of pair-flowered cymes, possessing a terminal flower and a front flower (Troll, 1969; Weber, 1973, 1982a, b.). They can branch monochasially (left or right), dichasially or both to varying degrees. Although species-specific branching patterns exist with some *Streptocarpus* species, for example *S. rexii* possesses mostly only a single pair-flowered cyme per inflorescence (Hilliard & Burt, 1971), the branching order is not fixed within species and even individuals can show variations (Weber, 1973; Wang & Li, 2002; Haston & Ronse De Craene, 2007; M. Möller, pers. observ.).

The inflorescences of *P. trisekala* are composed of pair-flowered cymes and single-flowered cymes (Fig. 15). The first inflorescences are more complex, branching laterally left and right, when they occur earlier. In the individual of *P. trisekala* observed here, the first inflorescence has 19 flowers, including eight

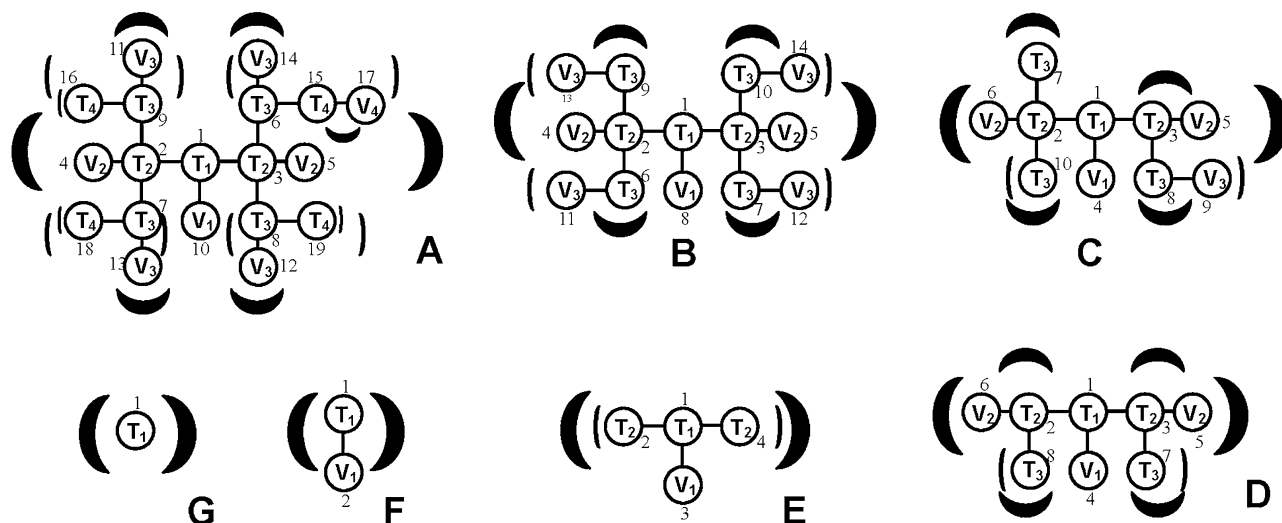


Figure 15. Schematic diagram of the inflorescence architecture of consecutive inflorescences observed in an individual of *Paraboea triseipala* sp. nov.: A–G, first to seventh inflorescence, showing a progressive decrease in the number of flowers from 19 to 14 to ten to eight to four to two and a single flower. T, terminal flower; V, front flower. The number outside the circle shows the sequence of flowering (starting from 1); the number inside the circle shows the hierarchical levels of the hypopodium for a peduncle.

pair-flowered cymes in four hierarchical levels (Fig. 15A, T₁–T₄) and three single-flowered cymes, occurring in terminal T₄ positions 16, 18 and 19 (Fig. 15A); the second inflorescence has seven pair-flowered cymes, in three hypopodium levels (T₁–T₃), with no single-flowered cyme, i.e. each terminal flower (T) has a front flower (V), for example T₃ → V₃; the third has ten flowers, including four pair-flowered and two single-flowered cymes, including flowers 7 and 10 (Fig. 15C); the fourth has eight flowers, including three pair-flowered and two single-flowered cymes, including flowers 7 and 8 in terminal positions (Fig. 15D); the fifth has four flowers, including one pair-flowered cyme and two single-flowered cymes at positions 2 and 4 (Fig. 15E); the sixth has two flowers in one pair-flowered cyme (Fig. 15F); the final inflorescence has only one single-flowered cyme (Fig. 15G).

Thus, although the development of the pair-flowered cymes is the standard unit of a Gesneriaceae inflorescence, as found in *P. triseipala*, the single-flowered cymes are not randomly distributed. They always develop last in an inflorescence, terminating the inflorescence branching. This is not unique in Gesneriaceae, and has also been noticed by Weber (1973) in *Chirita*. Whether the observed decrease in number of flowers per inflorescence over the flowering period shows an evolutionary flexibility or is related to the increasing age of the individual, the nutritional state of the plant or the reproductive success (i.e. a resource allocation away from new developing inflorescences to developing seeds of older inflorescences) is at present unclear. However, an increase in branch-

ing is often observed in plants under cultivation (M. Möller, pers. observ.), where water and nutrient levels are usually not limiting. The observation here for *P. triseipala* in cultivation, however, indicates the opposite effect, which suggests that resource allocation may well be involved.

VARIATION IN SIZE OF FLOWERS

In *P. triseipala*, the size of the flowers usually decreases with the development of an inflorescence (Fig. 5). In the first, larger flowers, the upper lobe of the calyx was *c.* 6.5 × 6.5 mm, the lateral two *c.* 6.5 × 2.6 mm, the corolla *c.* 3.1 cm in diameter, the lower lip of the corolla *c.* 2.9 cm, three-lobed, the middle lobe *c.* 9 × 11 mm, the lateral two *c.* 7.5 × 10 mm, the upper lip of the corolla *c.* 1.4 cm, two-lobed, the lobes *c.* 7.3 × 8.5 mm. In the medium-sized flower, the upper lobes of the calyx were *c.* 5 × 5 mm, the lateral *c.* 5 × 2 mm, the lower lip of the corolla *c.* 1.9 cm long, three-lobed, the middle lobe *c.* 7 × 9 mm, the lateral two *c.* 6 × 8 mm, the corolla *c.* 2.6 cm in diameter, the upper lip of the corolla *c.* 1.2 cm long, two-lobed, the lobes *c.* 6 × 7 mm, the apex obtuse. In small flowers, the upper lobes of the calyx were *c.* 4 × 4 mm, the lateral *c.* 4 × 2 mm, the upper lip of the corolla *c.* 0.8 cm long, two-lobed, the lobes *c.* 3 × 4 mm, the corolla *c.* 1.5 cm in diameter, the lower lip of the corolla *c.* 1.1 cm long, three-lobed, the lobes *c.* 5 × 6 mm.

This change in flower size has not been reported previously for Gesneriaceae, and, by contrast, mirror flowers of identical sizes have been observed in

P. rufescens (Gao *et al.*, 2006). It is possible that, towards the end of flowering, the resource allocation into the production of flowers results in smaller flowers. At present, it is unknown whether the size variation in flowers in the same inflorescence is significant in the pollination of *Paraboea* species with straight styles and fruits.

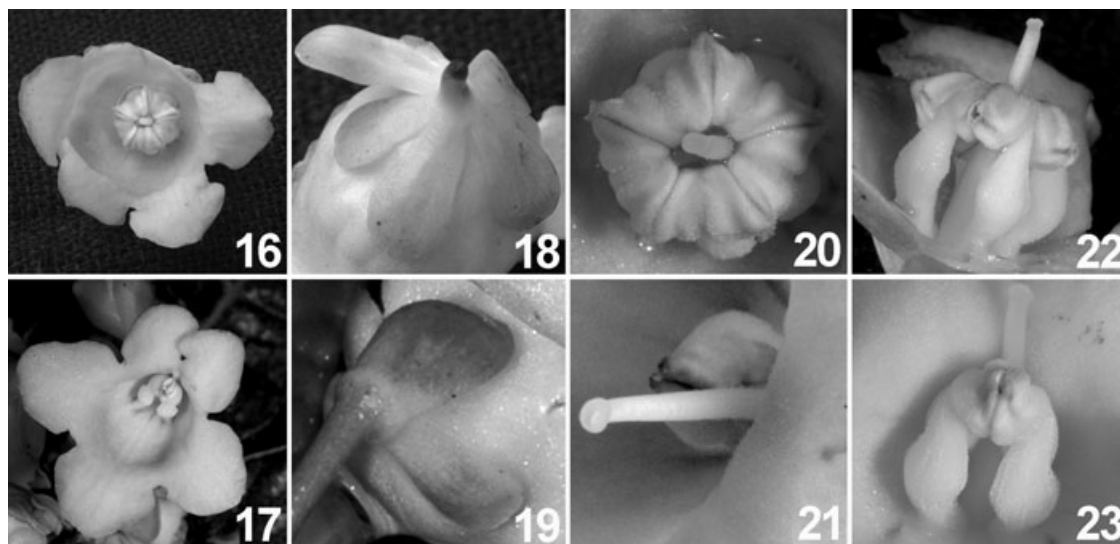
SPATIOTEMPORAL PATTERN OF FLOWER DEVELOPMENT IN INFLORESCENCES

Figure 15 shows the flowering order of the flowers in the inflorescences of an individual. To illustrate the variation and dynamics of inflorescence development, a detailed description for the first inflorescence is given here. In this first inflorescence, flowers 1 and 10 are included in the first hypopodium (peduncle) (terminology from Haston & Ronse De Craene, 2007), 2 and 4 and 3 and 5 in the second axis hypopodia, 7 and 13, 9 and 11, 6 and 14 and 8–12 in the third axis hypopodia, and 15–19 in the fourth level hypopodia. Thus, the flowering sequence progresses from the first to the third axis and is not sequential within the cyme unit, but overlapping across cymes. In particular, the front flower of the first hypopodium was found to be greatly delayed, not developing before the flowers in the third hypopodia started to flower. The consecutive inflorescences show a similar pattern of temporal and spatial development, but possess progressively fewer cyme units (Fig. 15).

This spatiotemporal offset development, combined with the flower size variation, may partly reduce geitonogamy between the flowers in the same cymes, and thus self-pollination overall. With only a few flowers open at any time, differences in flower sizes may attract different pollinators, thus increasing the chances of allogamy. In fact, *P. rufescens* (Franch.) Burt also discourages geitonogamy by providing mirror-image flowers (Gao *et al.*, 2006). In *Paraboea*, these mirror-image flowers only occur in species of *Paraboea* with twisted fruits (Y. M. Shui, unpubl. data).

ACTINOMORPHIC FLOWER IN *P. TRISEPALA*

An actinomorphic flower was encountered in the new species (Figs 16–23). In this flower, the lobes of the calyx and corolla were pentamerous (Figs 18, 19), with the units showing the morphology of the ventral (lower) lobes of zygomorphic flowers (Figs 16, 17). Five fertile anthers were produced (Figs 20, 21), each between two corolla lobes. The style was erect, in a central position and enclosed by the five anthers (Figs 20–23). This flower probably arose from a mis-expression of *CYCLOIDEA*, *DICHOTOMA* or *DIVARICATA*, genes involved in the expression of flower asymmetry (Almeida, Rocheta & Galego, 1997). Actinomorphic flowers occur quite frequently under cultivation and have been observed in different genera of Gesneriaceae (e.g. *Streptocarpus* and *Rhyn-*



Figures 16–23. Developmental novelties in flower morphology in *Paraboea trisepala* sp. nov. Figs 16, 17. Change in flower symmetry. Fig. 16. Ventralized flower with five equal-sized ‘ventral’ lobes of the corollas and five fertile stamens. Fig. 17. Normal type. Figs 18, 19. Change in calyx lobe numbers. Fig. 18. Five equal-sized lobes. Fig. 19. Normal type with unequal lobes, the dorsal three lobes fused into one large lobe. Figs 20, 21. Change in the number of fertile anthers, face view. Figs 22, 23. Change in the number of fertile anthers, lateral view. Figs 20, 22. Five fertile anthers. Figs 21, 23. Normal type with two fertile anthers.

choglossum), and are usually not heritable. Stable genetic mutants, however, have great potential for horticulture, such as seen for the genus *Sinningia* (Citerne & Cronk, 1999), for which a single mutation was found in the gene *CYCLOIDEA* (Citerne, Möller & Cronk, 2000). It is interesting that changes in the expression pattern of a single gene have such a pleiotropic effect and can affect several key taxonomic characters, such as the shape of the corolla lobes, the number of calyx lobes and the number and morphology of the filament and anthers, as in *P. trisepala*.

The actinomorphic flower in *P. trisepala* was the terminal flower in a pair-flowered cyme. These isolated ventralized flowers are often the result of developmental abnormalities, when the front flower is aborted early or does not form at all, and thus forces the terminal flower to develop symmetrically, usually ventralized in Lamiales, in the absence of polarizing developmental cues (Luo *et al.*, 1995).

The symmetric flower in *P. trisepala* shows striking similarities with actinomorphic flowers of certain genera in Gesneriaceae (e.g. *Conandron* and *Ramonda*). The actinomorphic structure of flowers is ancestral in Lamiales and zygomorphy derived (Tank *et al.*, 2006), with at least two independent unrelated reversions to actinomorphy in Generaceae (Möller *et al.*, 1999; Citerne, Möller & Cronk, 2000). This indicates that the morphologies of developmental simplifications derived from complex zygomorphic forms are evolutionarily viable (Cronk & Möller, 1997). Whether these 'simplified' ventralized flowers in *P. trisepala* are functional is yet to be demonstrated. The occurrence of the actinomorphic flower in *Paraboea* does not indicate the need for a novel evolutionary trajectory, but its developmental potential.

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