1.0 GENERAL INTRODUCTION

1.1 *Henckelia* sect. *Loxocarpus*

Loxocarpus R.Br., a taxon characterised by flowers with two stamens and plagiocarpic (held at an angle of 90–135° with pedicel) capsular fruit that splits dorsally has been treated as a section within *Henckelia* Spreng. (Weber & Burtt, 1998 [1997]). *Loxocarpus* as a genus was established based on *L. incanus* (Brown, 1839). It is principally recognised by its conical, short capsule with a broader base often with a hump-like swelling at the upper side (Banka & Kiew, 2009). It was reduced to sectional level within the genus *Didymocarpus* (Bentham, 1876; Clarke, 1883; Ridley, 1896) but again raised to generic level several times by different authors (Ridley, 1905; Burtt, 1958). In 1998, Weber & Burtt (1998 ['1997']) re-modelled *Didymocarpus*. *Didymocarpus s.s.* was redefined to a natural group, while most of the rest Malesian *Didymocarpus s.l.* and a few others morphologically close genera including *Loxocarpus* were transferred to *Henckelia* within which it was recognised as a section within. See **Section 4.1** for its full taxonomic history. Molecular data now suggests that *Henckelia* sect. *Loxocarpus* is nested within 'Twisted-fruited Asian and Malesian genera' group and distinct from other didymocarpoid genera (Möller *et al*. 2009; 2011).

1.2 State of knowledge and problem statements

Henckelia sect. *Loxocarpus* includes 10 species in Peninsular Malaysia (with one species extending into Peninsular Thailand), 12 in Borneo, two in Sumatra and one in Lingga (Banka & Kiew, 2009). The genus *Loxocarpus* has never been monographed. Peninsular Malaysian taxa are well studied (Ridley, 1923; Banka, 1996; Banka & Kiew, 2009) but the Bornean and Sumatran taxa are poorly known. The descriptions of the early species described from Borneo and Sumatra are very brief and do not allow

reliable comparison. Furthermore, there is no satisfactory key to all species. Recently, several new species have been collected from Peninsular Malaysia (Yao *et al*., *in press*) and Borneo (see **Section 4.5**) but are not yet published.

Distinctive characters used in circumscribing the Peninsular Malaysian taxa include: habit (rosette herb), lamina (upper surface densely silky hairy with hairs adpressed and aligned towards the leaf apex) and capsule (short, humped above, dehiscing to form a splash-cup). However, the above characters are only relevant to species from Peninsular Malaysia. The circumscription of *Loxocarpus* becomes unclear when the taxa described from Borneo (including two creeping species: *Henckelia procumbens* and *H. diffusa*) and Sumatra (two caulescent species, *H. caulescens* and *H. meijeri*) are considered (Weber & Burtt, 2001). Some Bornean taxa also lack the dense silky hairy upper surface lamina and have longer capsules (> 10 mm long).

Until this study, only one *Loxocarpus* species, *Henckelia ericii* (= *Loxocarpus holttumii*) had been included in molecular phylogenetic studies on Old World gesneriads (Möller *et al*., 2009; 2011). So, the circumscription and relationships of *Loxocarpus* species still remained unclear. The other *Henckelia* species from various regions were also included in those studies but the results showed them to be scattered in different clades but all of which were remote from the clades comprising the sect. *Loxocarpus* species.

Loxocarpus species display a high level of endemism throughout their distribution and therefore are extremely vulnerable to habitat disturbance. Hence, assessment of their conservation status is of great importance.

The three most important questions to answer in this study are:

(i) Is *Loxocarpus* a monophyletic group?

(ii) Does it warrant generic status or should it be kept as a section within *Henckelia*?

(iii) What are the characters circumscribing *Loxocarpus*?

1.3 Objectives of the study

I. To determine whether sect. *Loxocarpus* is a monophylectic group based on morphological and molecular phylogenetic studies

II. To determine whether *Loxocarpus* is a genus distinct from, or is a section of *Henckelia* based on morphological and molecular phylogenetic studies.

III. To provide detailed genus/sect. and species descriptions, nomenclature, distribution maps, and user-friendly key(s) to species.

IV. To assess conservation status of the *Loxocarpus* species.

2.0 MORPHOLOGY

2.1 Introduction and brief literature review

Morphological aspects of Peninsular Malaysian taxa are well studied. Banka (1996) carried out anatomical studies on trichome types, lamina, and vascular bundle arrangement in the petiole of Peninsular Malaysian *Loxocarpus* species. By using Scanning Electron Microscopy (SEM), he also studied the testa pattern. From these studies, Banka revealed the presence of multi-cellular long wavy trichomes, long-stalked glandular hairs and the absent of sclereids and tannins in Peninsular Malaysian *Loxocarpus*. These characters readily distinguished *Loxocarpus* from *Didymocarpus s.l.* (=*Henckelia s.l.*). Banka also pointed to the presence of reticulate fused crest and absence of papillae on the ellipsoid seed (as opposed to the rectangular or obovoid ones in *Henckelia*) were marked differences that complemented the decision to keep *Loxocarpus* separate at generic level. In contrast to the scenario of Peninsular Malaysian taxa, morphological aspects of Bornean taxa were poorly studied. Weber & Burtt (1998 ['1997']) amalgamated *Loxocarpus* and a couple of genera with plagiocarpic capsule that dehisced dorsally into *Henckelia*. This chapter is aimed to present the morphological diversity of *Loxocarpus* as a genus and the variations of structures within *Loxocarpus* species.

2.2 Materials and methods

All *Loxocarpus* species recognised in this study (see **Section 4.5**) were included in this macro-morphological study.

In general, the range of variation observed and measurements taken were based on herbarium specimens. Observations in the field on live plants were also included where possible. Measurement of seeds and flower parts was made using a digital calliper (Mitutoyo CD-6”CSX). Microscopic structures were observed through a 4×10

stereo-microscope (Olympus SZ61). Throughout this chapter, all species are name as *Loxocarpus* (see **Table 6.1** for full synonymy).

2.3 Indumentum

2.3.1 Hair types and position

Hairs are generally a mix of glandular and eglandular ones. Hairs of *Loxocarpus* are uniseriate. Glandular hairs are often stalked and the flat cells of multicellular colourless eglandular hairs are decussately arranged on top of one another.

Indumentum of vegetative parts is mainly eglandular and the glandular hairs when present are usually obscured. Glandular hairs on vegetative parts are often difficult to observe under 4×10 stereo-microscope especially on dried herbarium specimens. Banka's (1996) leaf anatomical study showed that the glandular hairs on leaf surfaces are minute. Erect hairs on *Loxocarpus repens* (**Plate 7e**) are a key character to the species.

Indumentum of inflorescences, bracts and flowers are usually a mix of glandular and eglandular hairs. Indumentum of the corolla inner surface, when present consists mainly of very short glandular hairs. This character is seen in the throat of *Loxocarpus caeruleus,* and on the lobes and is especially dense on the corolla mouth of *L. rufescens*, *L. holttumii*, and *L. sericiflavus*. It gives the flower a glistening appearance which may serves to attract the insect pollinator (see **Section 5.1.3**; **Plate 4c**). Indumentum of the ovary is usually glandular and persists until the fruiting stage. Indumentum of the capsule is usually glabrescence.

2.3.2 Hair colour

Most *Loxocarpus* species are covered in silvery hairs. The colourless hairs flat cells of *Loxocarpus* leaves upper surface are decussately arranged on top of one another. When the hairs are dense, adpressed and orientated in such a position where the tips are pointing towards the lamina apex (Banka & Kiew 2009), they reflect light and give whitish (**Plate 5a)** or silvery (**Plate 2c**) appearance. When wet, the leaves appeared green. However, there are exceptions. Hairs of *Loxocarpus caeruleus* (**Plate 3c**) and *L. holttumii* (**Plate 4b**) are ferruginous (conspicuous on petioles). *Loxocarpus sericiflavus* (**Plate 10b**) is characterised by greyish yellow hairs (especially in herbarium specimen), as its name suggests. Red glandular hairs on the peduncle and calyx of *Loxocarpus rufescens* are unique.

2.3.3 Hair density

Most *Loxocarpus* species are characterised by dense adpressed hairs on upper lamina surface, with some exceptions. In *Loxocarpus violoides,* the upper lamina is covered in a less dense layer of hairs (**Plate 12a**), while hairs of *L. coodei*, *L. conicapsularis* and *L. verbeniflos* (**Plate 11b**) are sparse, adpressed and spreading. *Loxocarpus repens* is characteristic in having sparse, erect hairs on the upper lamina surface and erect wavy hairs on the petiole. In *Loxocarpus rufescens,* field observation confirmed that the upper lamina surface of some mature leaves is glabrescent.

2.4 Habit and stem

All species of *Loxocarpus* are herbaceous. Most are rosette plants except for *Loxocarpus caulescens* and *L. meijeri* that are caulescence with erect stem up to 28 cm height while *L. repens, L. semitortus, L. stapfii*¸ *L. verbeniflos* and *L. violoides* are sometimes creeping.

Habit of *Loxocarpus* is correlated with habitat. Rootstocks tend to be longer when the plants grow in sandy heath forest or on mossy earthbanks. Some even develop a creeping stem with well-spaced leaves. For species which are only found on rock outcrops, *viz. Loxocarpus incanus*, the rootstock is sometimes lacking.

Rosette species have a woody rootstock (usually up to 15 cm) covered in long, wiry adventitious roots but the rootstock is lacking in some such as *Loxocarpus incanus*, *L. argenteus* and *L. angustifolius*. In creeping species, adventitious roots grow along the creeping stem in contact with soil.

2.5 Leaves

The leaves are alternate (or spirally) arranged. In the caulescent species, the leaves are well-spaced throughout compared with the leaves of rosette species that are crowded at the top but well-spaced below or are crowded at the top in creeping plants. However, the distance between leaves is not a consistent character in some species. For example, some specimens of *Loxocarpus repens* have a very long rootstock (to 26 cm) but all the leaves are crowded at the top.

All species are petiolate. The leaves of *Loxocarpus* are primarily plain green and are often paler beneath. Some populations of *Loxocarpus repens* have variegated leaves with a very pale green or silvery white patch in the middle of the leaf upper surface (**Plate 7d**). The lamina is generally small (less than 12 cm long and 4 cm wide) except *Loxocarpus caeruleus* (to 20 cm long and 15 cm wide) and *L. incanus* var. *incanus* (to 12 cm long and 11 cm wide).

The measurement of leaf petiole length is taken from the lowermost leaf because that is usually the longest in a plant. Petiole and lamina length ratio is a consistent character in separating the long-petioled species, such as *Loxocarpus caeruleus*, *L. holttumii*, *L. pauzii* and *L. semitortus*, from the rest. In cross section the petiole is terete

or grooved above. The petioles are mostly slender (less than 2.6 mm thick) but some are relatively thick, such as in *Loxocarpus caeruleus* and *L. holttumii* (to 3.5 mm thick) and *L. semitortus* (to 4 mm thick). Lamina of *Loxocarpus* is relatively thick, ranging from 70 μm to 700 μm in Peninsular Malaysian species (Banka & Kiew, 2009).

The shape of lamina varies from sub-obicular (lamina length as long as width) in *Loxocarpus holttumii* and *L. pauzii*, to narrowly oblong (*c.* 20 times longer than wide) in *L. taeniophyllus*, although the more common states are ovate, elliptic, oblanceolate, obovate or oblong. Sometimes a few of these variations in shape are observed in a single species. The lamina of *Loxocarpus incanus* and *L. sericiflavus* (**Plate 10b**) is sometimes slightly asymmetric at the base.

The lamina base is also very variable in shape across *Loxocarpus* species, ranging from attenuate, cuneate, truncate, rounded to cordate. Cuneate and rounded are the most common states. The base is usually equal, but unequal in asymmetric laminas. The lamina margin ranges from entire to serrulate, crenulate, crenate and serrate. The two caulescent species, *Loxocarpus caulescens* and *L. meijeri*, together with *L. caeruleus* are characteristic in having distinctly serrate leaf margins. Sometimes, the finely serrulate and crenulate margins are obscured by dense indumentum. The lamina apex ranges from acuminate, acute, blunt to rounded. Blunt or rounded apices are the common states.

The midrib and veins are generally obscure above, but are sometimes sunken especially in species with a thick lamina and they are conspicuous beneath *viz. Loxocarpus incanus*. Lateral vein pairs usually number up to seven pairs, but reach to 12 pairs in *L. sericiflavus* (**Plate 10b**). Sometimes, the 1–2 lowermost pair(s) arises from the lamina base, especially in species with a broad lamina base. Lateral veins are further branched in *Loxocarpus caeruleus* (**Plate 3c**), *L. holttumii* (partly), *L. incanus* var. *incanus*, *L. pauzii*, *L. repens* (partly), *L. rufescens* (distinct in populations of Bungo

Range, Sarawak), *L. semitortus* and *L. stapfii*. In the last two species, they are sometimes closely dendritic.

2.6 Inflorescences

The inflorescence is axillary. The degree of inflorescence branching for most species ranges from a reduced cyme with solitary flower (**Plate 3a**, **9c** & **12a**) to a simple pair-flowered cyme, to a 6-times branched dichasium (cymose panicle). The compact cyme *Loxocarpus repens* (**Plate 7b**) and *L. stapfii* appear umbel-like. The number of flower(s) on an inflorescence therefore ranges from 1, 4 or more. Generally, the more flowers an inflorescence bears, the smaller are the flowers. The arrangement of peduncle branching whether lax or compact is a good taxonomic character to distinguished species. Peduncles are usually green or sometimes purplish in *Loxocarpus holttumii*, *L. pauzii*, *L. semitortus*, *L. sericiflavus*, *L. verbeniflos* and *L. violoides*. Peduncles are usually long (to 30 cm) and slender. *Loxocarpus incanus* var. *incanus* and *L. tunkui* have relatively stout peduncles. Smaller plants usually produce one inflorescence at one time but in some species, such as *Loxocarpus* sp. B, a plant can have as many as 10 flowering inflorescences at one time.

2.7 Bracts and bracteoles

Bracts are arranged in an opposite pair, positioned slightly below the flower or the first branch. The shape ranges from linear, narrowly lanceolate, lanceolate, narrowly oblanceolate to deltoid. The measurements are usually to 5 mm long and to 1 mm wide but in *L. tunkui*, the bracts are up to 8 mm long. Long bracts (longer than 5 mm) are characteristic for *Loxocarpus argenteus*, *L. meijeri*, *L. sericeus*, *L. taeniophyllus* and *L. tunkui*. Bract apex shape ranges from acuminate to blunt. Bracteoles are usually tiny, reduced to a single one and are positioned at the branching point of pedicels.

2.8 Flowers

The flowers are 5-merous. Calyx colour ranges from pale green to white, sometimes with a darker green or violet tip. Generally, the calyx is indistinctly divided into upper and lower lips, with the upper lip with 3 lobes and often lower lip with 2 lobes is bigger. The calyx is scarcely tubular, with the length up to 1.8 mm long in *Loxocarpus incanus* var. *incanus* and 2.4 mm in *L. violoides*. The calyx lobes are almost split to the base and are usually deltoid or lanceolate in outline with a blunt or acute apex, but sometimes they are linear with an acuminate, and sometimes thickened, apex. Calyx lobe length is a good taxonomic character because it separates *Loxocarpus coodei* from *L. verbeniflos*, the two morphologically similar species.

The corolla is usually plain mauve-blue, sometimes very pale in *Loxocarpus angustifolius* to white in *Loxocarpus stapfii*. In some species the corolla has distinct colouration, such as a pale tube with darker violet lobes in *Loxocarpus sericiflavus* (**Plate 9d**) or 8 purple stripes along the corolla throat in *L. semitortus* (**Plate 9c**) or white with 2 purple spots at the sinuses of mid-lobe in *L. stapfii* or the violet corolla contrasts with dark purple stamens in *L. argenteus*.

The corolla is indistinctly divided into the upper and lower lip. Upper lip generally consists of the 2 upper lobes (except 1 fused upper lobe in the 4-merous *Loxocarpus pauzii* (**Plate 6h** & **i**) and the lower lip which is larger and consists of 2 lateral lobes and a mid-lobe.

Three major corolla shapes are observed in *Loxocarpus*: (i) Corolla tube shortly tubular (**Plate 9c**) to campanulate (2 to 6.1 mm long) (**Plate 4c** & **8c**), upper lobes recurved, lateral and lower lobes flared, lobes oblong in outline; (ii) lips deeply dissected, corolla scarcely tubular (1.1 to 3.3 mm long), corolla lobes recurved, lobes deltoid in outline, lobes number 5 in *L. argenteus* (**Plate 3b**) and *L. stapfii*, 4 in *L. pauzii* (**Plate 6h** & **i**); (iii) flat-faced (saintpaulioid) where the upper and lower lips are

deeply dissected, the corolla scarcely tubular (the constricted base) (0.9–5.6 mm long) (flowers of *L. violoides* (**Plate 12c**) are big and the corolla measures up to 3.2 cm long, thus having the long tube), upper lip with lobes dissected to the base, lobes oblong in outline, lower lip with 2 lateral lobes and a median lobe is larger.

Flat-faced flowers are held at about right angles to the pedicel but their orientation is often tilted (**Plate 7b**) while shortly tubular and broadly campanulate flowers are slightly nodding (**Plate 2b** & **4c**).

Among all *Loxocarpus* species, the fertile stamens number two. Staminodes usually number three or two (*Loxocarpus argenteus, L. conicapsularis, L. coodei, L. meijeri, L. repens, L. stapfii, L. taeniophyllus*) or rarely none (*L. pauzii*). Filaments are generally white or pale purple and are usually straight or slightly curved in campanulate flowered species, and honey-yellow and thickened in the distal half in flat-faced species (**Plate 7b**, **11d** & **12a**) and geniculate in *L. caeruleus* (**Plate 3c**). Filament length ranges from 2–4.5 mm long, except in *L. caeruleus* (8.6 mm long). Anthers are usually cream or yellow, but in *Loxocarpus argenteus* they are deep violet. Anthers are bilobed, with the pair coherent face-to-face or only at the ventral tip. Anthers are usually positioned at the mouth of corolla tube in campanulate flowers, or are entirely exposed in flat-faced flowers.

A nectary is usually absent in most species and when present, it is just a thin rim encircling the ovary base (*Loxocarpus semitortus* and *L. holttumii*) or is a bulge on the dorsal part of ovary (*L. angustifolius, L. caeruleus, L. rufescens, L. semitortus*). The ovary is usually green, conical or narrowly conical (0.8–3.7 mm long). The shorter ovaries are usually oblique. Ovules usually have a funiculus and the funicles are especially long in the short oblique ovary. The style is pale-coloured to almost white, is usually straight or is arched towards upper side of corolla. In *Loxocarpus incanus*, the style arches towards the upper side of corolla and fits into the corolla mouth cleft (**Plate**

5b). Stigma is usually white and ranges in the shape from punctiform to capitate. *Loxocarpus* pistil usually extends beyond the corolla tube during female stage (**Plate 4c**, **8d** & **9c**).

In *Loxocarpus* the anthers are always positioned lower than the stigma (**Plate 2a**, **3c**, **7b**, **8d**, **9d**, **11d** & **12c**). The stamens pair is connate to the corolla below the ovary base. *Loxocarpus* is protandrous and there are considerable differences between the female and male stages. In flat-faced flowers, as observed in *Loxocarpus repens*, in male stage the style is stubby, recurved upward with a punctiform stigma, and the two stamens are twisted with one another; in the female stage, the style has elongated and become straight, the stigma swollen and capitate and the stamens untwist.

Measurement of flowers, especially the ovary and style therefore depends on the flowering stage because the length of pistil differs considerably between male and female stage, for example, pistil length of *Loxocarpus argenteus* in male stage measures *c*. 1.85 mm and in in female stage *c*. 4.8 mm.

Based on the corolla shape and its partial (not every flat-faced flower species has a capsule more than 10 mm long) correspondence with capsule length, I informally categorise *Loxocarpus* species into 'Group A' (shortly tubular or campanulate corolla, corolla shape (i) and (ii)) (**Plate 4c** & **8c**) and 'Group B' (flat-faced corolla, corolla shape (iii)) (**Plate 11d** & **12c**). Capsule length of Group A species is less than 10 mm, while capsule length of Group B species ranges from 6–30 mm. However, the grouping is not an attempt to recognise infrageneric classification but it is used as a term for the convenient of discussion throughout the text.

The grouping is denoted in the general key to the species (**Section 4.4.1**) This grouping also corresponds with phylogenetic studies results (**Section 3.4**) and biogeographical perspectives (**Section 5.2.2.2**).

2.9 Fruits

The capsules are plagiocarpic, dehiscing along the upper suture into a splash cup or a trough (**Plate 2a**, **5c**, **7c** & **8e**). Young capsules are often a rich purple or pale green colour. The shape usually ranges from ovoid (3.3–8 mm long by 1.5–3 mm thick) in species such as *Loxocarpus repens* (**Plate 7c**), *L. stapfii*, *L. incanus* (**Plate 5c inset**) to obliquely conical (5–10 mm long by 0.9–3.1 mm thick) in most species. *Loxocarpus violoides*, *Loxocarpus* sp. B, and *L. verbeniflos* have long slender conical capsules (**Plate 12b**) (9–30 mm long by 1.1–2.5 mm thick) while the corniculate (horn-like) capsule (9–10 mm long by 2.8–3 mm thick) is characteristic of *L. caeruleus*. The style to 5 mm long sometimes persists in the capsule.

The capsule valves are usually straight or slightly curved upward in most species but are strongly curved in *Loxocarpus caeruleus* but they are never twisted. Capsules of *Loxocarpus caeruleus*, *L. incanus*, and *L. stapfii* are humped above.

2.10 Seeds

Seeds are narrowly to broadly ellipsoid and variation is observed for seeds within one capsule of most species. The dimensions range from 0.22–0.73 by 0.15–0.26 mm. Apices are acute or acuminate. The general cell pattern is reticulate for all Peninsular Malaysian species (Banka & Kiew, 2009).

2.11. Discussion and conclusion

The morphology of *Loxocarpus* is highly variable across the genus and within each species, especially the Bornean 'Group B' taxa.

Results from phylogenetic studies (**Section 3.6.2 iii**) showed that the habit, whether rosette or creeping is not a good character for showing relationships between species. They probably correspond with habitat. I observed intermediate between

creeping and rosette ‘species’. The rosette and creeping habit are ecological adaptations. Generally, populations that grow on moss beds and earth banks tend to have longer creeping stems while the populations that grow on vertical rock faces tend to have a rosette habit. Also, flower size is variable especially in 'Group B' species. In the species with both the creeping and rosette habits, the creeping populations tend to have smaller flower in relative to the rosette ones. The best example is *Loxocarpus violoides* with corolla length *c*. 1 cm in lowland creeping populations and to 3.2 cm in highland rosette populations. Pistil length and its relative position with other flower parts is also a bad taxonomic character because the pistil elongate after the male flowering phase.

Observations of populations in the field and of living plants in nursery found that style length in relation to corolla tube length is not a reliable taxonomic character. *Loxocarpus* species are protandrous. In the male stage, the style is contained within corolla tube but in the female stage it extends beyond the corolla mouth. Thus, the style and corolla tube length ratio is not a good character to distinguish species.

In contrast to the characters above, hair type, its position, colour, and density are good characters to distinguish species. Hair density on the lamina upper surface is the key character to differentiate a few Bornean taxa. *Loxocarpus coodei*, *L. repens, L. verbeniflos* and *L. violoides* are charaterised by relatively sparse hairs on upper lamina surface. The hair position is also an important key character. *Loxocarpus repens* is characterised by dense erect hairs on its petiole.

The single unifying character for *Loxocarpus* might be the testa surface pattern (Banka & Kiew, 2009). High similarity of reticulate testa surface is also observed across Sumatran (*Loxocarpus caulescens*), Bornean (*L. rufescens* and *L. verbeniflos*) and Peninsular Malaysian species (Beaufort-Murphy, 1983). At present, this is speculative as the seed surfaces of other species were only observed under stereomicroscope.

3.0 PHYLOGENETIC STUDIES

3.1 Brief Introduction and literature review

The molecular phylogenetic study of Möller *et al*. (2009) on didymocarpoid Gesneriaceae was based on three DNA molecular data sets, namely the *atpB-rbcL* spacer, the ITS region and *trnL-F* intron-spacer region and it showed that the genus *Henckelia* as defined by Weber & Burtt (1998 ['1997']) was not a monophyletic clade. However, this study included only five *Henckelia* species of which only one belonged to sect. *Loxocarpus*, *Henckelia ericii*. Unlike the other *Henckelia* species, it nested within the advanced Asian twisted-fruited dominated clade and is therefore only distantly related to the other *Henckelia* species with straight capsules. It was a surprising result because since its establishment *Loxocarpus* had been recognised as a close relative of *Didymocarpus*/*Henckelia* based on morphological characters (Weber & Burtt, 1998 ['1997']).

Now, the two imperative questions are: (i) does sect. *Loxocarpus* form a monophyletic clade and (ii) if so, is this monophyly group distinct from other *Henckelia* species. If answers to these questions are yes, should *Loxocarpus* be recognised as a genus instead of a section?

To this end, further molecular analyses on phylogenetic relations among *Henckelia* species and several other closely related Malesian didymocarpoid genera were carried out. A much larger sample, especially of taxa from sect. *Loxocarpus* and other *Henckelia* species were included.

Molecular phylogeny study including the laboratory work and phylogeny analysis on *Loxocarpus* was carried out at the Royal Botanic Garden Edinburgh (RBGE) in collaboration with the 'Gesneriaceae team', led by Michael Möller and David Middleton. RBGE is one of the leading world research institutes in the molecular

phylogenetic and taxonomic study of Old World Gesneriaceae. Thus, RBGE has a large DNA dataset of targeted gene regions of Gesneriaceae (*atpB-rbcL* spacer, ITS and *trnL-F*), with many of them not as yet published. These unpublished DNA data are crucial to determine the position of *Loxocarpus* within Old World Gesneriaceae with confidence, as well as to test the monophyly of *Loxocarpus*. Möller *et al.* (2009) have published several extensive molecular phylogenies, a preliminary phylogeny of the 'didymocarpoid Gesneriaceae', and a large scale molecular phylogenetic assessment of the advanced Asiatic and Malesian didymocarpoid Gesneriaceae with focus on non-monophyletic and monotypic genera (Möller *et al*., 2011) and a molecular systematic study and remodelling of the large genus *Chirita* and associated Gesneriaceae genera (Weber *et al.* 2011), the last including the largest sampling of Old World Gesneriaceae to date.

To produce comparable results with the large scale study on-going at RBGE, the present molecular phylogenetic study of *Loxocarpus* was based on sequences of the chloroplast DNA (cpDNA) *trnL-F* intron-spacer and nuclear ribosomal DNA (nrDNA) internal transcribed spacer (ITS) regions.

3.2 Materials

Total genomic DNA was extracted from silica-dried leaves of live collections. In this study, 35 sequences of *trnL-F* (18) and ITS (17) markers were newly acquired, the rest acquired from the RBGE dataset, including published and unpublished sequences. The newly acquired samples for this study are listed in **Table 3.1**.

Species selection

(i) Out-group selection: Taxa of basal Lamiales including representatives of Oleaceae, Tetrachondraceae, Scrophulariaceae, Plantaginaceae and Calceolariaceae were chosen as outgroup taxa. The trees were rooted at Oleaceae (Olmstead *et al*., 2000).

Table 3.1 List of newly acquired samples for this study. Taxa with more than one sample are numbered. (**Henckelia violoides* has never been included in *Loxocarpus*. It is regarded here as an 'in-group' based on its morphological character, *viz*. its flat-faced flower.)

Taxon**	**Voucher No.**	**Locality**
In-group		
Henckelia anthonysamyi (syn. of *Loxocarpus sericiflava*)	FRI 57986	Sungai Yong, Johor
Henckelia argentea (*Loxocarpus argenteus*)	FRI 57975	Bako NP, Sarawak
Henckelia browniana 291 (*Loxocarpus incanus*)	FRI 65450	G. Tebu, Terengganu
Henckelia browniana 294	KBG 2009-1300	Penang Hill, Penang
Henckelia browniana 296	FRI 65395	Lata Puteh, Perak
Henckelia browniana 297	FRI 65394	Lata Puteh, Perak
Loxocarpus pauzii	FRI 65371	Stong Waterfall, Kelantan
Henckelia ericii 186 (*Loxocarpus holttumii*)	FRI 65377	Gunung Panti, Johor
Henckelia gardneri (syn. of *Loxocarpus repens*)	FRI 65457	Crocker Range NP, Sabah
Henckelia minima 292 (syn. of *Loxocarpus incanus*)	FRI 65362	Ulu Bendul, Negeri Sembilan
Henckelia minima 489	FRI 65362	Ulu Bendul, Negeri Sembilan
Henckelia rufescens (*Loxocarpus rufescens*)	FRI 57968	G. Santubong, Sarawak
Henckelia sekayuensis (syn. of *Loxocarpus incanus* var. *sekayuensis*)	FRI 65445	Lata Sekayu, Terengganu
Henckelia semitorta (*Loxocarpus semitortus*)	FRI 67914	G. Ledang, Johor
Henckelia sericiflava (*Loxocarpus sericiflavus*)	FRI 57999	G. Belumut, Johor
Henckelia stenophylla 293 (*Loxocarpus angustifolius*)	FRI 65288	G. Tahan, Pahang
Henckelia verbeniflos (*Loxocarpus verbeniflos*)	FRI 65454	Tavui FR, Sabah
**Henckelia violoides* 289 (*Loxocarpus violoides*)	FRI 65458	Kinabalu NP, Sabah

Notes: Species name under both *Henckelia* and *Loxocarpus* are given to avoid confusion. For full listing of name change, see **Table 6.1.

(ii) In-group selection: Coronantheroid, gesnerioid and didymocarpoid Gesneriaceae samples across the Old World were included as ingroup. This was to locate the position of *Loxocarpus* within Gesneriaceae. To test the monophyly of *Loxocarpus*, other morphologically closely-related taxa, such as *Henckelia* species originating from Sothern India and Malesia regions, were included in the analysis. Samples of molecularly closely-related genera (Möller *et al*. 2009), such as *Emarhendia* Kiew, A.Weber & B.L.Burtt, *Spelaeanthus* Kiew, A.Weber & B.L.Burtt, and *Boea* Comm. *ex* Lam. were included. Two other monotypic genera in Peninsular Malaysia, *Senyumia* Kiew, A.Weber & B.L.Burtt and *Orchadocarpa* Ridl. were also included. These samples were mainly acquired from the dataset used in Möller *et al*. (2009, *partly unpublished*).

(iii) Study group: as many *Henckelia* sect. *Loxocarpus* species as were available (**Table 3.1**) were included.

3.3 Methodology

3.3.1 DNA extraction

Total genomic DNA from silica dried leaf material was extracted using CTAB procedure (Doyle & Doyle, 1987, 1990) or DNeasy®Plant Mini Kit (QIAgen Ltd.) according to the manufacturer's protocol.

3.3.2 Polymerase Chain Reaction (PCR)

PCR amplification was performed on a BioRad Tetrad® 2 cycler (BioRad, Hercules, CA, US). PCR amplification of the *trnL-F* intron spacer (*trnL-F*) was performed using primer 'c' and 'f' (Taberlet *et al*., 1991) (**Table 3.2**). Reaction contents (**Table 3.3**) and thermal cycle profile (**Table 3.4**) used are given below:

Table 3.2. List of primers used in this study.

Target DNA marker	Primer	Sequence
ITS1-5.8s-ITS2	Forward: 'AB 101'	ACG AAT TCA TGG TCC GGT GAA GTG TTC G
	Reverse: 'AB 102'	TAG AAT TCC CCG GTT CGC TCG CCG TTA C
trnL-F intron-spacer	Forward: 'c'	CGA AAT CGG TAG ACG CTA CG
	Reverse: 'f'	ATT TGA ACT GGT GAC ACG AG

Table 3.3. Reaction content of PCR for the amplification of *trnL-F* intron spacer sequences.

Reagent	volume (µl)
dNTPs (2mM)	2.5
10× NH4 reaction Buffer (Bioline, UK)	2.5
$MgCl_2$ (50mM)	1.25
Primer 'c'	0.75
Primer 'f'	0.75
BSA (Sigma, UK)	1
Biotaq polymerase (Bioline, UK)	0.2
DNA Template	1
H_2O	15.05
total	25.00

Table 3.4. Thermal cycle of PCR for the amplification of *trnL-F* intron spacer sequences.

Step	Temperature (˚C)	Time	Cycle(s)
1	94	4 min	1
2	94	45 sec	
3	55	45 sec	35
4	72	3 min	
5	72	10 min	1
6	4	Forever	

PCR amplification of the ITS was performed using "angiosperm-specific" primers AB101 and AB102 (Suh *et al*. 1993) (**Table 3.2**). Reaction contents (**Table 3.5**) and thermal cycle profile (**Table 3.6.**) used was as below:

Table 3.5. Reaction content of PCR for the amplification of ITS sequences.

Reagent	volume (µl)
dNTPs (2mM)	2.5
10× NH4 reaction Buffer	2.5
$MgCl_2$ (50mM)	1.25
primer AB 101	0.75
primer AB 102	0.75
BSA	1
DMSO (Sigma, UK)	1
Biotaq polymerase	0.2
DNA Template	1
H_2O	14.05
total	25.00

Table 3.6. Thermal cycle of PCR for the amplification of ITS sequences.

Step	Temperature (˚C)	Time	Cycle(s)
1	94	3min	1
2	94	1 min	
3	55	1min	30
4	72	90 sec	
5	72	5min	1
6	10	Forever	

PCR products were run on 1% agarose gels to check for amplification success and quality. Successfully amplified products were purified using ExoSAP-IT® (Amersham-Pharmacia Biotech. Inc., Piscataway, NJ, USA). Reaction contents (**Table 3.7.**) and the thermal cycle profile (**Table 3.8.**) of the purification reaction were as below:

Table 3.7. Reaction contents of PCR products purification.

Reagent	volume (µl)
PCR products	5
ExoSAP-IT	2

Table 3.8. Thermal cycle of PCR products purification.

Step	Temperature (˚C)	Time
1	37	15 min
2	80	15 min
3	10	Forever

The purified PCR products were used for cycle sequencing. Reactions contents (**Table 3.9.**) and thermal cycle (**Table 3.10.**) of the cycle sequencing of both *trnL-F* and ITS marker sequences are tabulated as below:

Table 3.9. Reaction contents of cycle sequencing for *trnL*-F and ITS.

ITS		trnL-F	
Reagent	Volume (µl)	Reagent	Volume (µl)
BigDye (ABI, Foster City, CA, USA)	0.5	BigDye (ABI, Foster City, CA, USA)	0.5
10× Buffer	2	10× Buffer	2
10uM Primer(Forward/reverse)	0.32	10uM Primer(Forward/reverse)	0.32
DMSO	0.4	DMSO	0
Purified PCR Product	1.78	Purified PCR Product	2.18
total	5.00	total	5.00

Table 3.10. Thermal cycle of cycle sequencing.

Step	Temperature (˚C)	Time	Cycle(s)
1	95	30 sec	
2	50	20 sec	24
3	60	4 min	
4	4	Forever	

3.3.3 Direct sequencing

The sequences were sent to the 'GenePool' sequencing service at the University of Edinburgh. The sequencing machine used was a 3730 DNA analyzer (Applied Biosystems Inc., Foster City, CA, USA). The PCR product of each sample was sequenced in both forward and reverse reactions with the two PCR primers for complete sequence confirmation.

3.3.4 Sequence alignment

Sequencher 4.5 (Gene Codes Corp, Ann Arbor, USA) was used to edit and assemble the forward and reverse sequences. Sequence matrices of both ITS and *trnL-F* were initially aligned using the computer programme BioEdit version 7.0.5.3 (Hall, 1999) and the alignments were then manually optimised in MacClade 4.08 (Madison & Madison, 2008).

3.3.5 Phylogenetic Analysis

Two datasets, namely Dataset I and II were analysed. The purpose of Dataset I was to confirm the position of *Loxocarpus* in relation to other Gesneriaceae genera. The analyses of Dataset II were carried out to test the monophyly of *Loxocarpus.*

For Dataset I only *trnL-F* data were used, for Dataset II *trnL-F* and ITS were used separately and as a combined matrix.

The two datasets were analysed by Maximum parsimony (MP) and Bayesian inference (BI) analyses.

MP was executed in PAUP 4.0b10 (Swofford, 2002), on unordered and unweighted characters. The 'out-group' rooting method was used, and 'parsimony' selected as optimality criterion. Gaps were treated as 'missing', and multistate taxa interpreted as 'uncertainty'. Character-state optimization used is 'Accelerated transformation' (ACCTRAN). The consistency index (CI), retention index (RI) and rescaled consistency index (RC) were calculated (**Table 3.11**). Parsimony ratchet (Nixon, 1999), was implemented with 1,000 replicates in PAUPRat (Sikes & Lewis, 2001) and PAUP*, to find starting trees. These were further optimised in PAUP*, with both TBR and Multrees on. Branch support in MP trees was provided by bootstrap analyses. Only values greater than 50% are shown. Bootstrap analyses were carried out

as 10000 random addition replicates with TBR on but Multrees off (Möller *et al*. 2009, 2011).

Table 3.11. Matrix characteristics of datasets used in MP analyses and statistical attributes of the trees generated.

Dataset	**I**	**II (a)**	**II (b)**	**II (c)**
Region	***trnL-F***	***trnL-F***	**ITS**	**Combined**
Number of taxa	156	49	51	51
Number of most parsimonious trees	816	148	48	12
Character-status summary:				
Total characters	1247	893	838	1731
Constant character	655	656	358	1014
Parsimony-uninformative variable character	189	124	130	254
Parsimony-informative characters	403 (32.3%)	113 (12.7%)	350 (42.8%)	463 (26.7%)
Statistical attributes:				
Tree length	1550	340	1790	2144
Consistency index (CI)	0.5903	0.8147	0.462	0.5149
Homoplasy index (HI)	0.4097	0.1853	0.538	0.4851
CI excluding uninformative characters	0.5178	0.6912	0.4088	0.4369
HI excluding uninformative characters	0.4822	0.3088	0.5912	0.5631
Retention index (RI)	0.8553	0.8302	0.6061	0.6307
Rescaled consistency index (RC)	0.5049	0.6764	0.28	0.3248
Average step(s) per character	1.24	0.3807	2.136	1.2386

Bayesian inference (BI) analysis was implemented in MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, 2007). Models and parameter priors were obtained independently for the *trnL-F* and ITS matrices using MrModeltest v2.3 (Nylander 2004). The model suggested by the Akaike Information Criterion (AIC; Akaike 1974) for *trnL-F* in Dataset I was GTR+I+G, in Dataset II GTR+G for *trnL-F* and GTR+I+G for ITS, in combined data GTR+G for *trnL-F* block and GTR+I+G for ITS block. Generations were run in two independent analyses each with four Markov Chain Monte Carlo (MCMC) chains (one cold and three heated). The number of generations run, sampling frequency, burn-in (empirically determined for each analysis by plotting the likelihood

against generations) and average standard deviation of split frequencies (ASDSF) is given in **Table 3.12**. From the remaining tree of both parallel runs majority rule consensus trees were generated in PAUP*, from which the posterior probabilities (PP) were obtained. Only values greater than 0.5 are shown and the branch with supporting value lower than that collapsed.

Table 3.12. Matrix characteristics of datasets used in BI analyses.

Dataset	**I**	**II(a)**	**II(b)**	**II(c)**
Region	***trnL-F***	***trnL-F***	**ITS**	**combined**
samples	156	51	51	51
model selected	GTR+I+G	GTR+G	GTR+I+G	
generations (g)	2000000	2000000	2000000	2000000
sampling frequency (g)	250	250	250	250
total trees saved	8000	8000	8000	8000
burn-in (trees/%)	600(7.5%)	80(1%)	80(1%)	80(1%)
ASDSF	0.015475	0.030653	0.008770	0.011030

The ITS sequences of *Loxocarpus pauzii* (=*Henckelia concinna*) showed a strong classical signal of being a hybrid (James Tosh, *pers. comm.*), or a case of incomplete lineage sorting or relaxed concerted evolution (Möller, *pers. comm*.). Fearing its inclusion would affect the phylogeny (for *trnL-F* is a maternal gene), it was not included in Dataset II. The sequences of *H. anthonysamyi* and *H. sericiflava* were excluded from analyses because their *trnL-F* sequence obtained were putative functional paralogues (Möller, *pers. comm.*), and the true *trnL-F* sequence could not be obtained. To confirm the unexpected position of the *trnL-F* sequences of these two taxa in the tree (close to basal Gesneriaceae, data not shown), DNA re-isolation and sequencing was carried out for the same accessions. In the second sequencing, only the *H. anthonysamyi* sample yield acceptable sequences. After its alignment, I found the second acquired sequence was not identical and, gappy compared to the first. Thus, both samples were excluded from the *trnL-F* analyses.

3.3.5.1 Dataset I

This dataset consisted of 156 samples which were acquired mainly from data used in Möller *et al*. (2009). The matrix consisted only of *trnL-F* sequences because sequences of marker ITS are too variable across the outgroup genera and very difficult if not impossible to align; the analysis of the *trnL-F* data matrix was sufficient to locate the *Loxocarpus* position amongst the Old World Gesneriaceae. The MP analysis results of this dataset are shown in **Fig. 3.1**. The BI analysis result of this dataset is shown in **Fig. 3.2**.

3.3.5.2 Dataset II

This dataset was analysed to test the monophyly of *Loxocarpus*. Fifty one samples were included in the analyses consisting of both *trnL-F* and ITS marker sequences. The *trnL-F* and ITS sequence matrices were analysed separately as Dataset II (a) and II (b) respectively, and combined as Dataset II (c). Summary of the matrix characteristics and statistical attributes of the trees generated is tabulated in **Table 3.11**.

Both MP and BI analyses of this dataset resulted in **Figures 3.3–3.14**. Results as shown in **Fig. 3.3–3.6** are based on *trnL-F* dataset, **Fig. 3.7–3.10** are based on ITS dataset and **Fig. 3.11–3.14** are based on combined dataset.

3.4 Results and discussion of phylogenetic analyses

The discussion presented below focuses on the phylogenetic position and relationships of *Loxocarpus*. Throughout the discussion, the species closely related and usually forming a clade are given a collective name, they are (a) 'Bornean *Loxocarpus*' (BORL) for all *Loxocarpus* species occurring in Borneo excluding *H. rufescens*; (b) 'Peninsular Malaysian *Loxocarpus*' (PMAL) for all *Loxocarpus* species occur in Peninsular Malaysia, excluding the *Henckelia browniana* species group but also

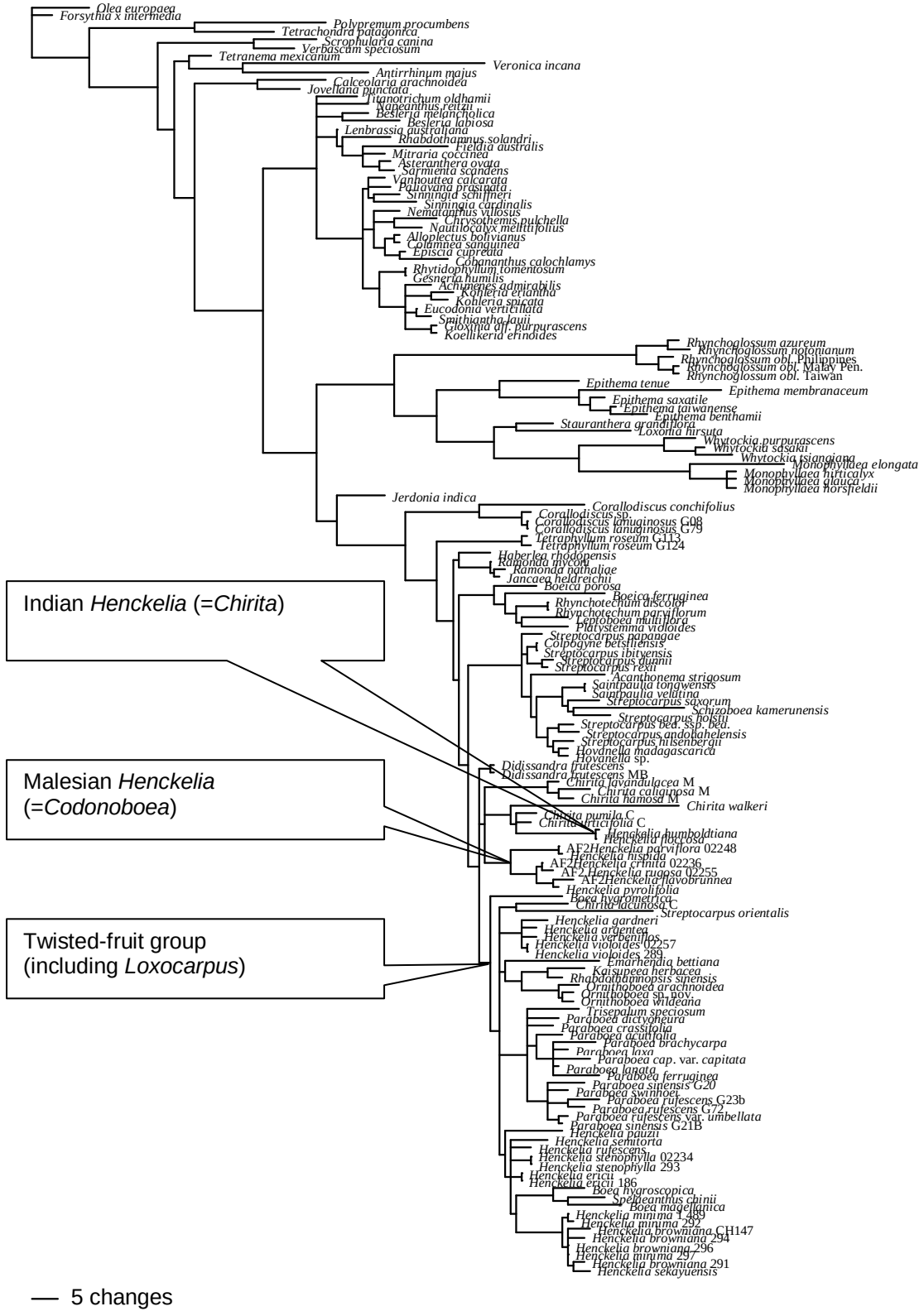


Fig. 3.1. A single representative phylogram of 816 most parsimonious (MP) trees of 1550 steps based on *trnL-F* sequences of 156 samples.

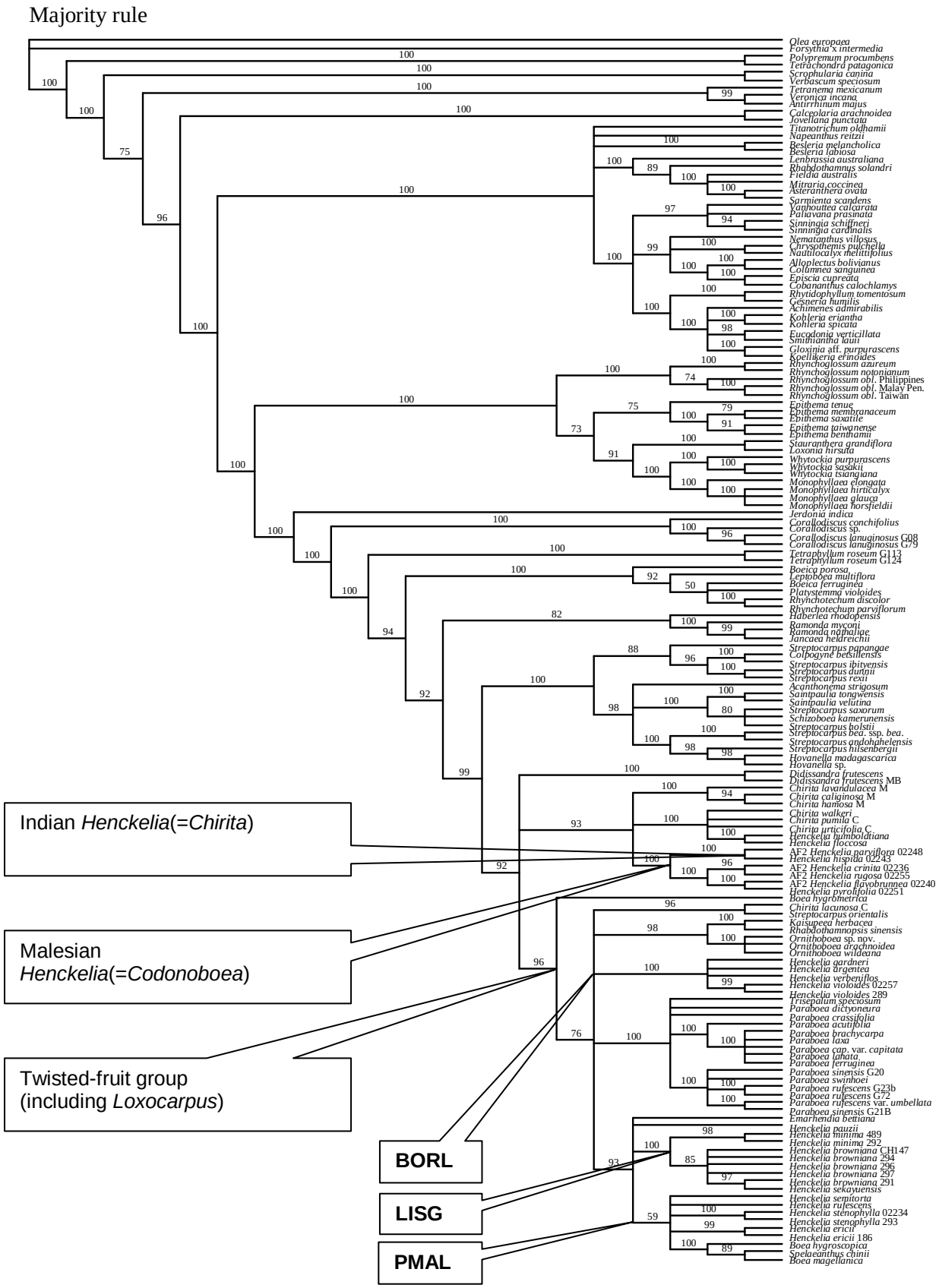


Fig. 3.2. Bayesian inference (BI) majority rule consensus tree based on *trnL-F* sequences of 156 samples. Posterior probability values are given above branches.

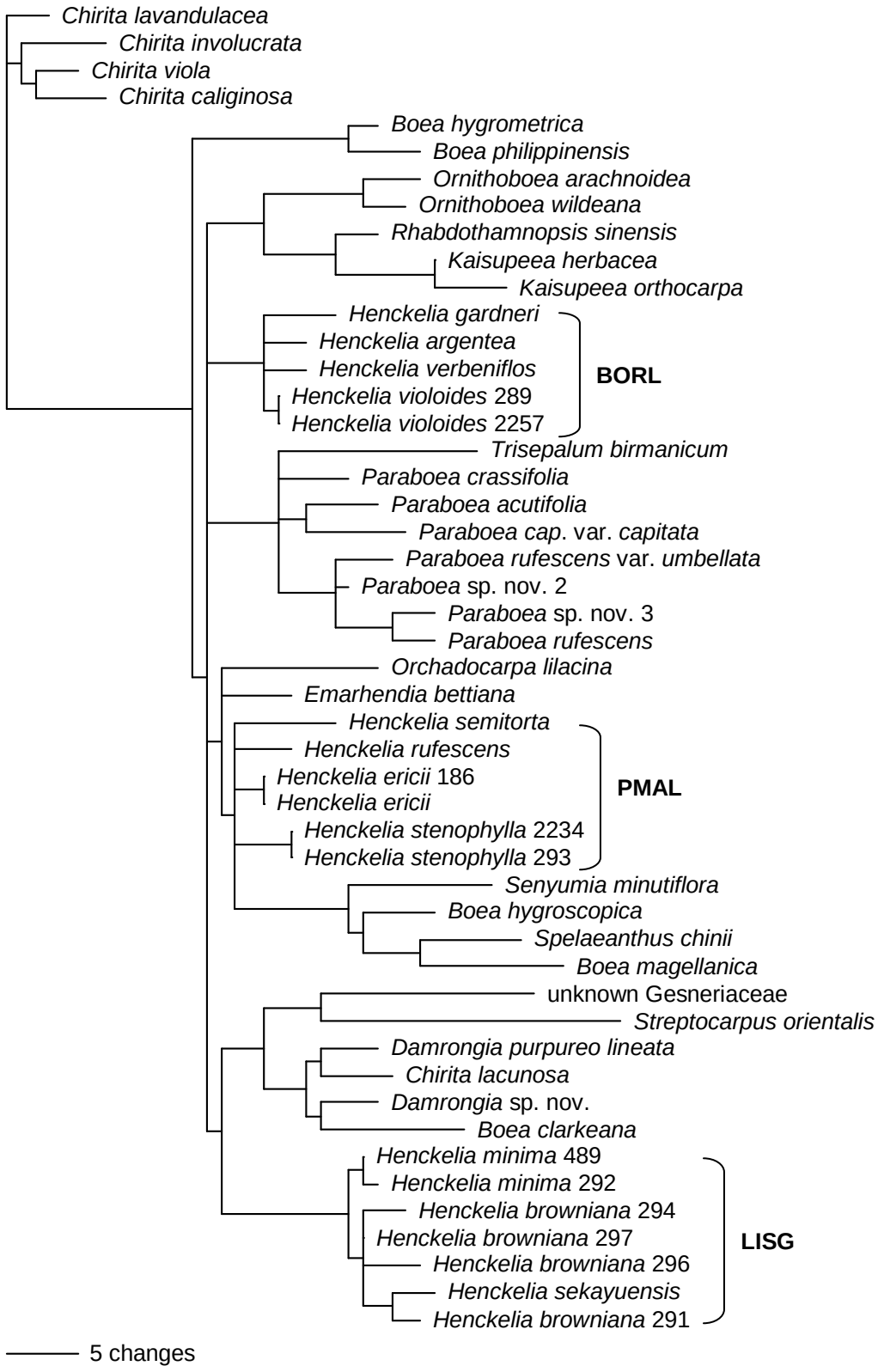


Fig. 3.3. A single representative phylogram of 148 MP trees of 340 steps, based on *trnL-F* sequences of 49 samples.

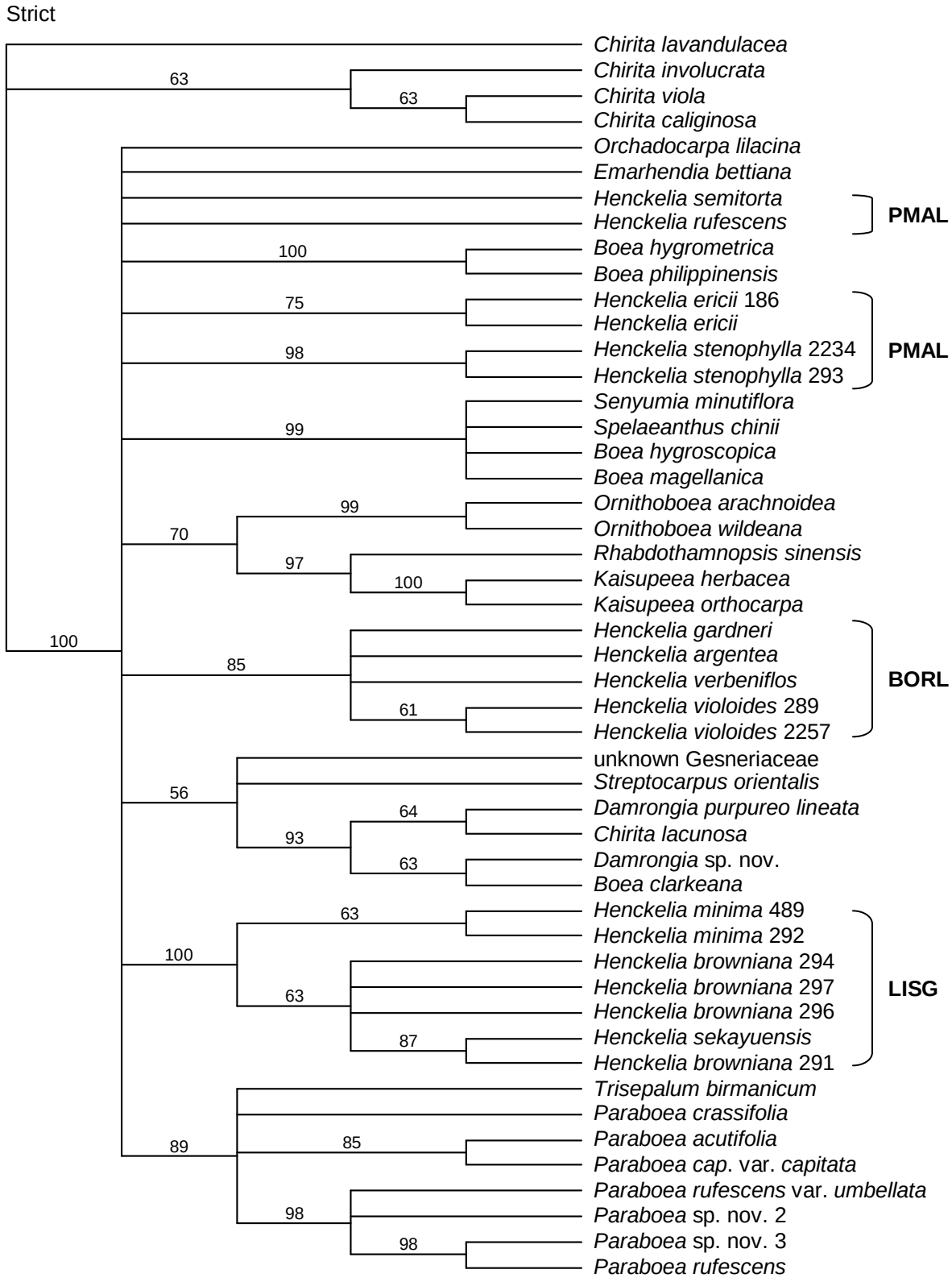


Fig. 3.4. Strict MP consensus tree of 148 most parsimonious trees of 340 steps based on *trnL-F* sequences of 49 samples (CI = 0.81; RI = 0.83; RC = 0.68). Bootstrap (BS) values are given above branches.

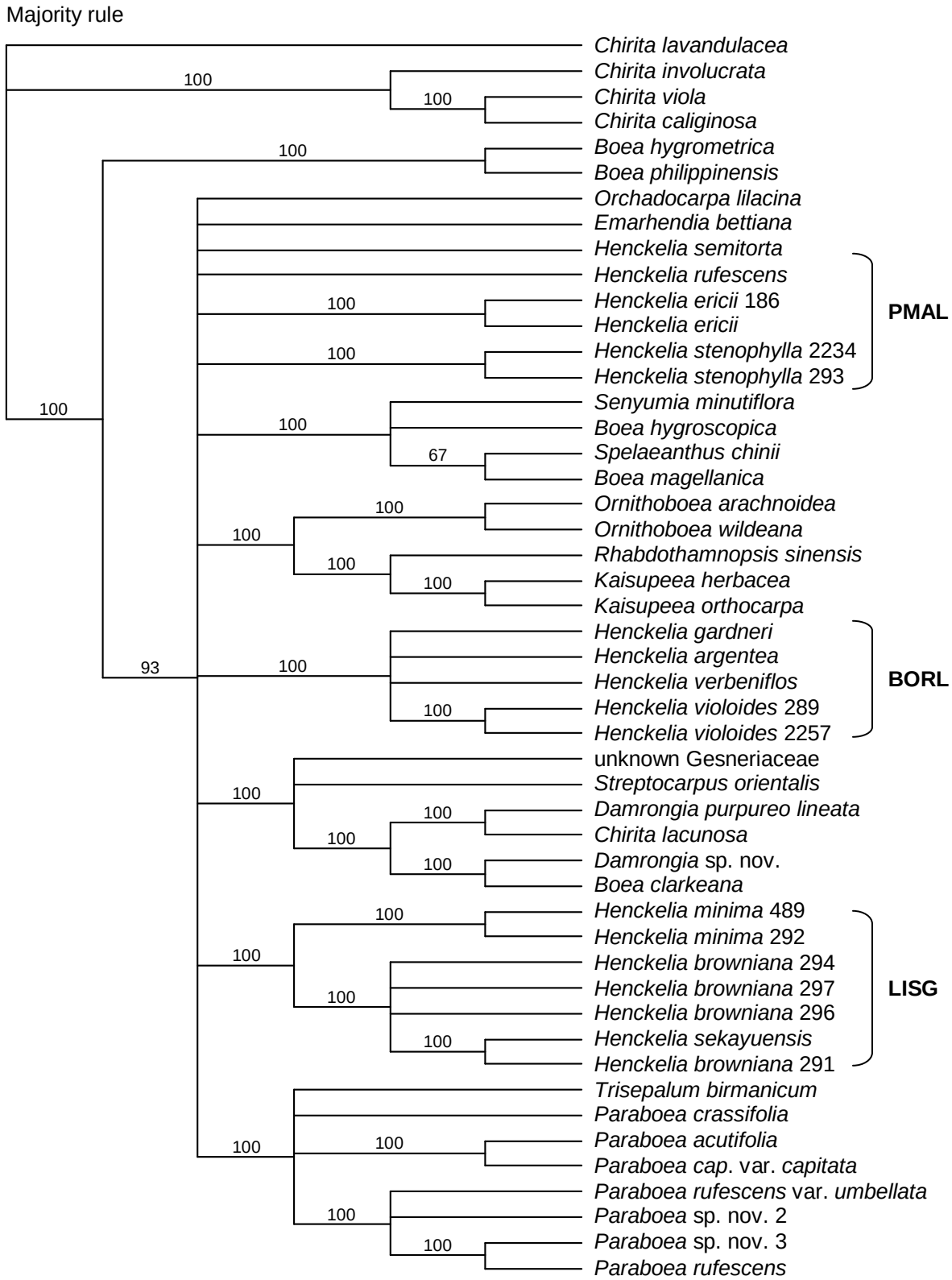


Fig. 3.5. MP 50% majority rule consensus tree of 148 most parsimonious trees based on *trnL-F* sequences of 49 samples.

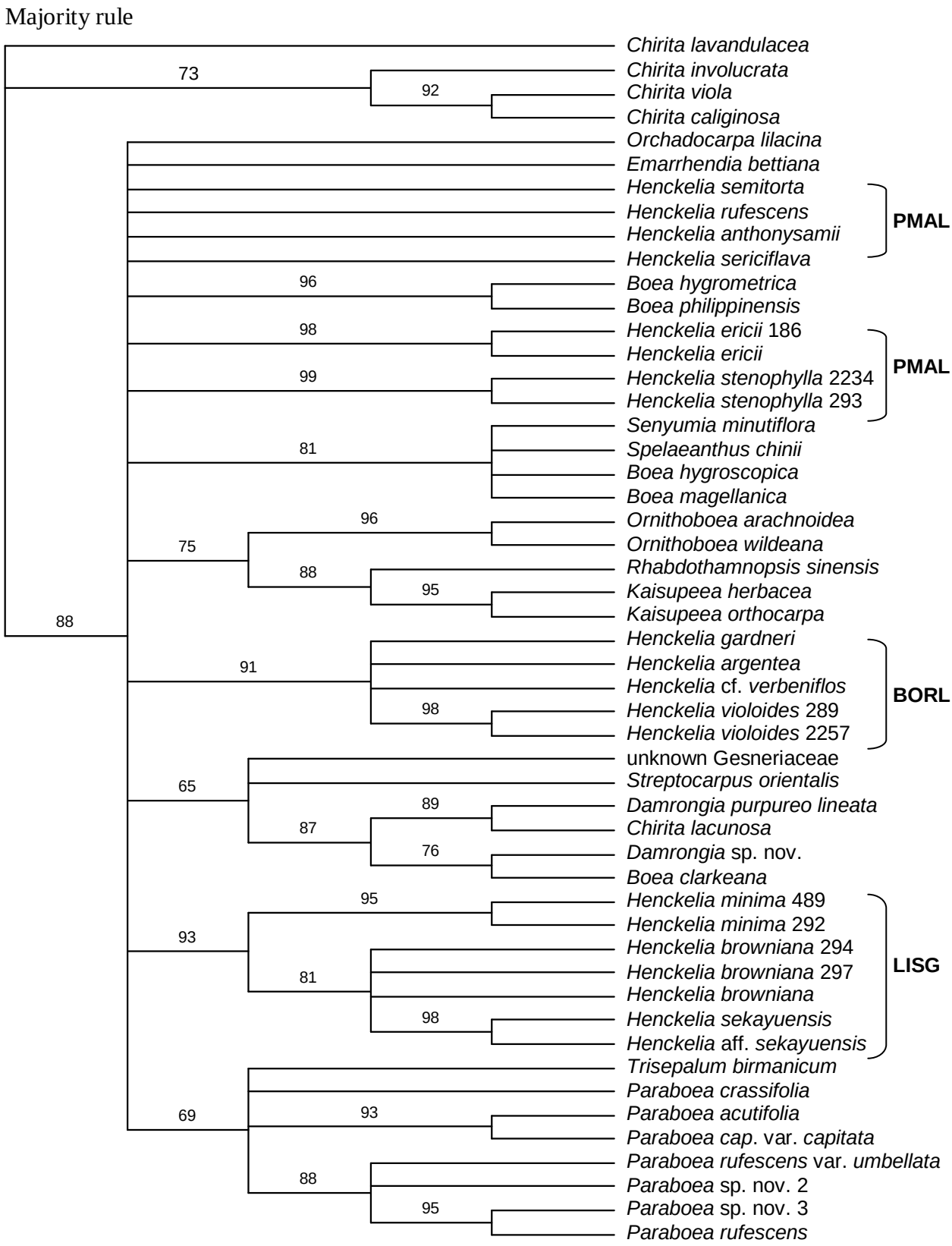


Fig. 3.6. BI majority rule consensus tree based on *trnL-F* sequences of 51 samples. Posterior probability (PP) values are given above branches.

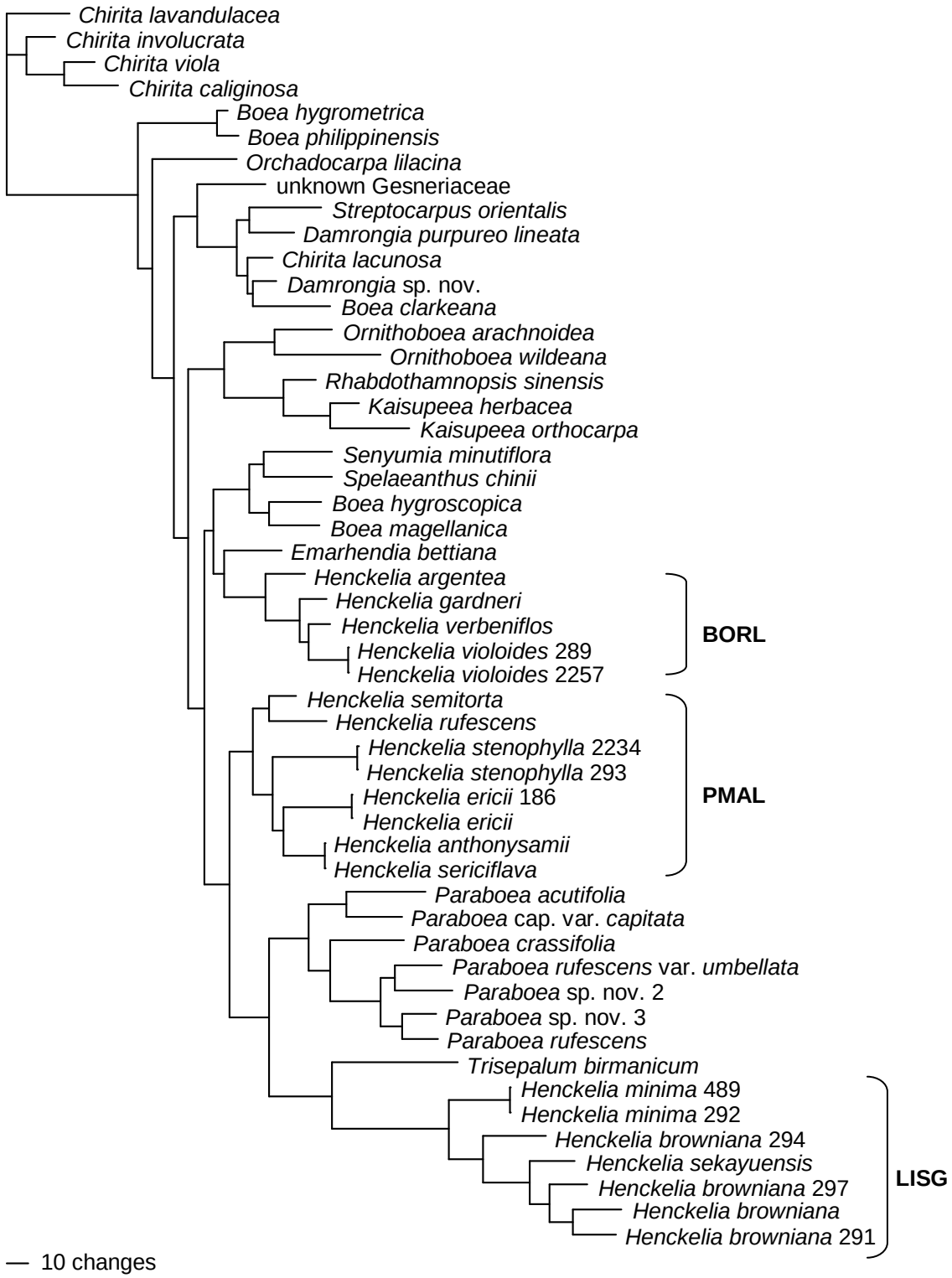


Fig. 3.7. A single representative phylogram of 48 MP trees of 1790 steps, based on ITS sequences of 51 samples.

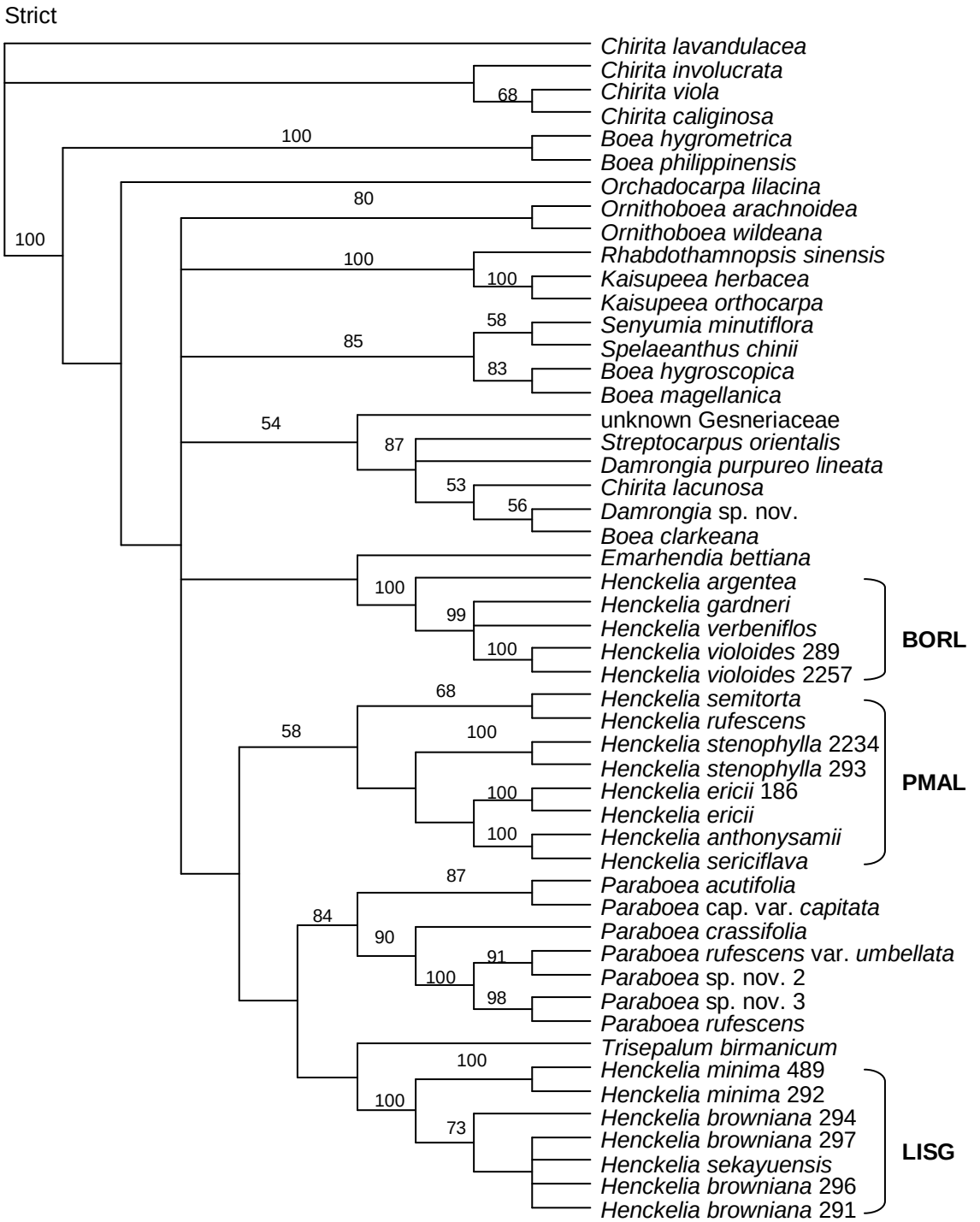


Fig. 3.8. Strict MP consensus tree of 48 most parsimonious trees of 1790 steps based on ITS sequences of 51 samples (CI = 0.46; RI = 0.61; RC = 0.28). Bootstrap (BS) values are given above branches.

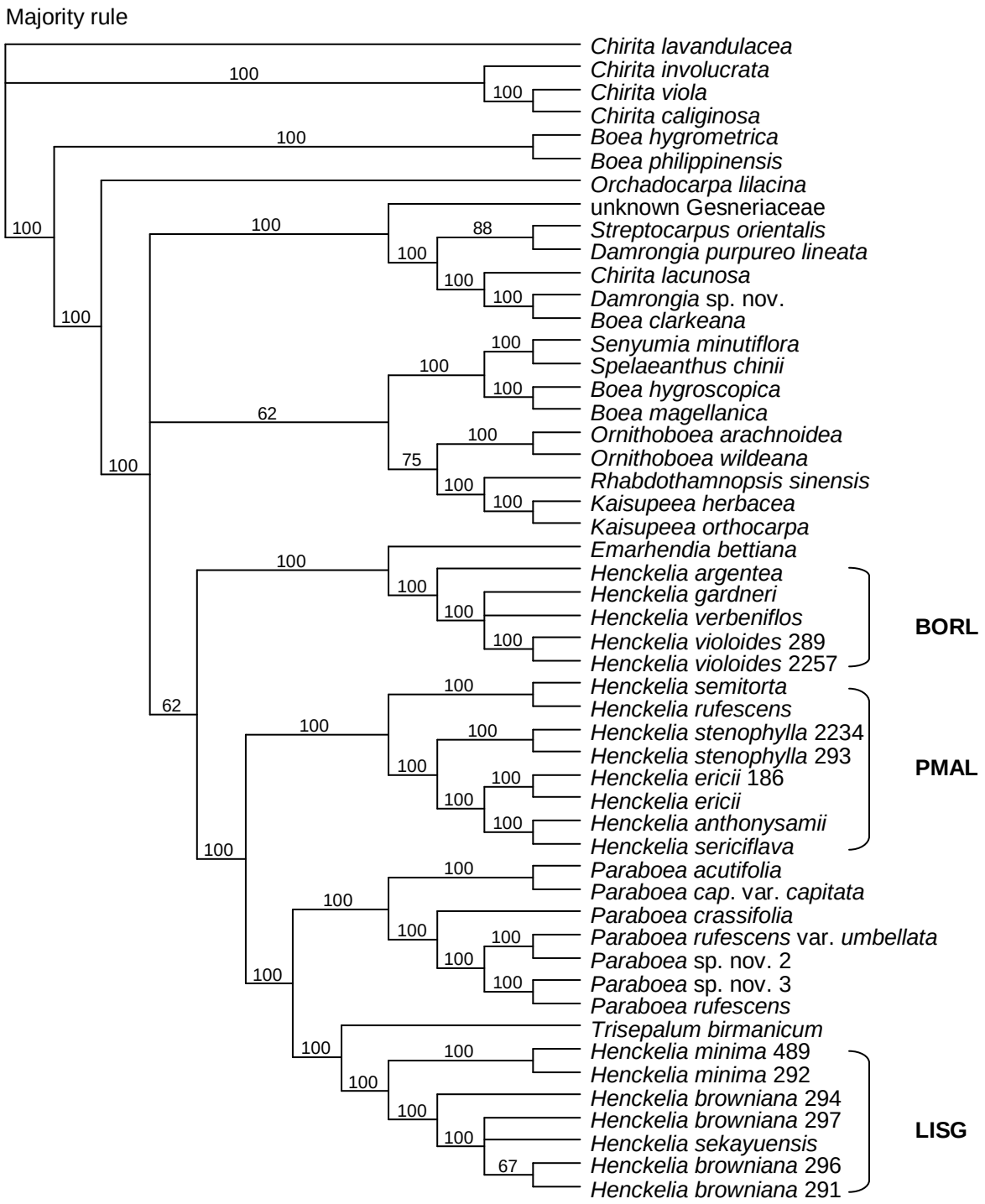


Fig. 3.9. MP 50% majority rule consensus tree of 1790 steps based on ITS sequences of 51 samples.

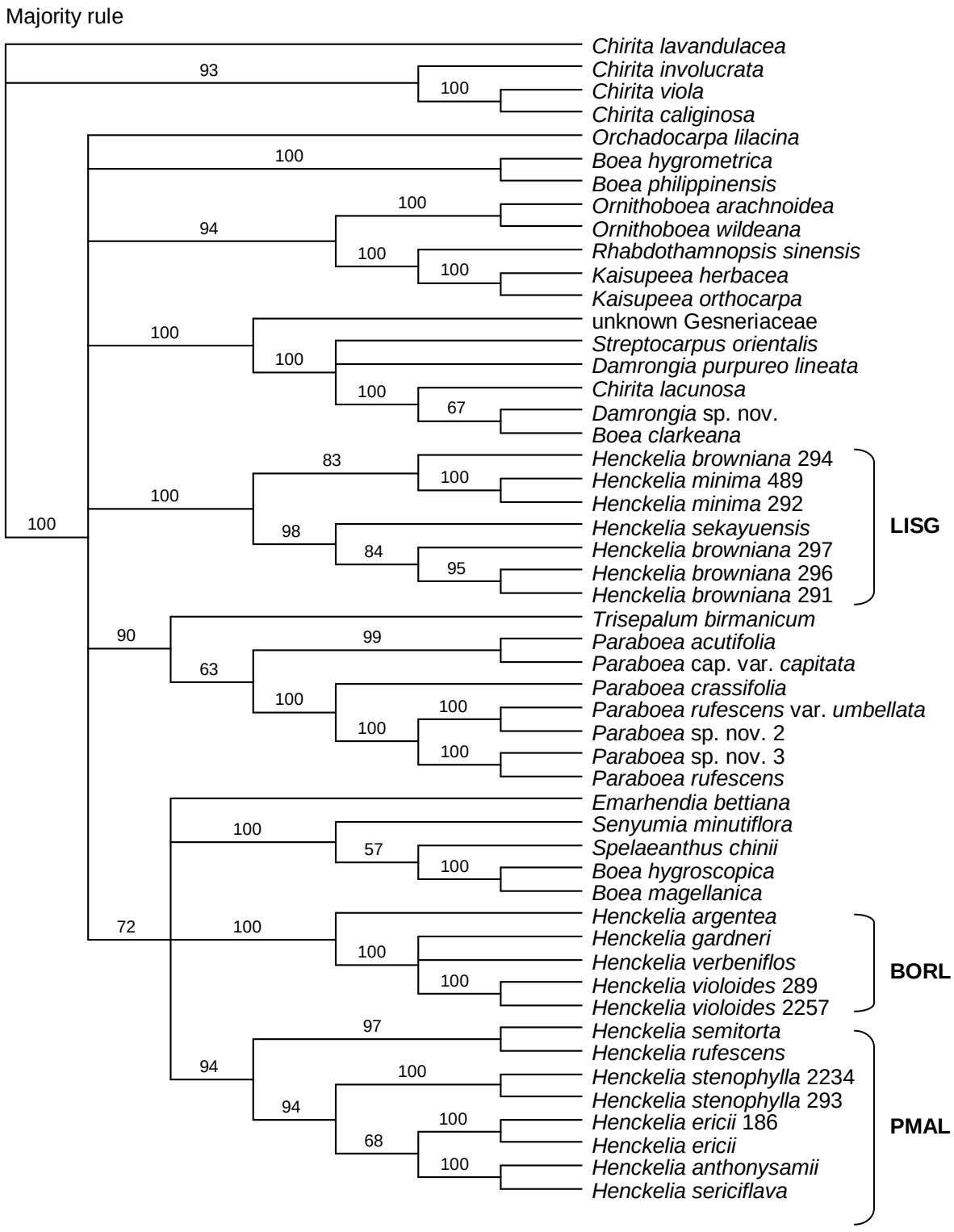


Fig. 3.10. BI majority rule consensus tree based on ITS sequences of 51 samples. Posterior probability (PP) values are given above branches.

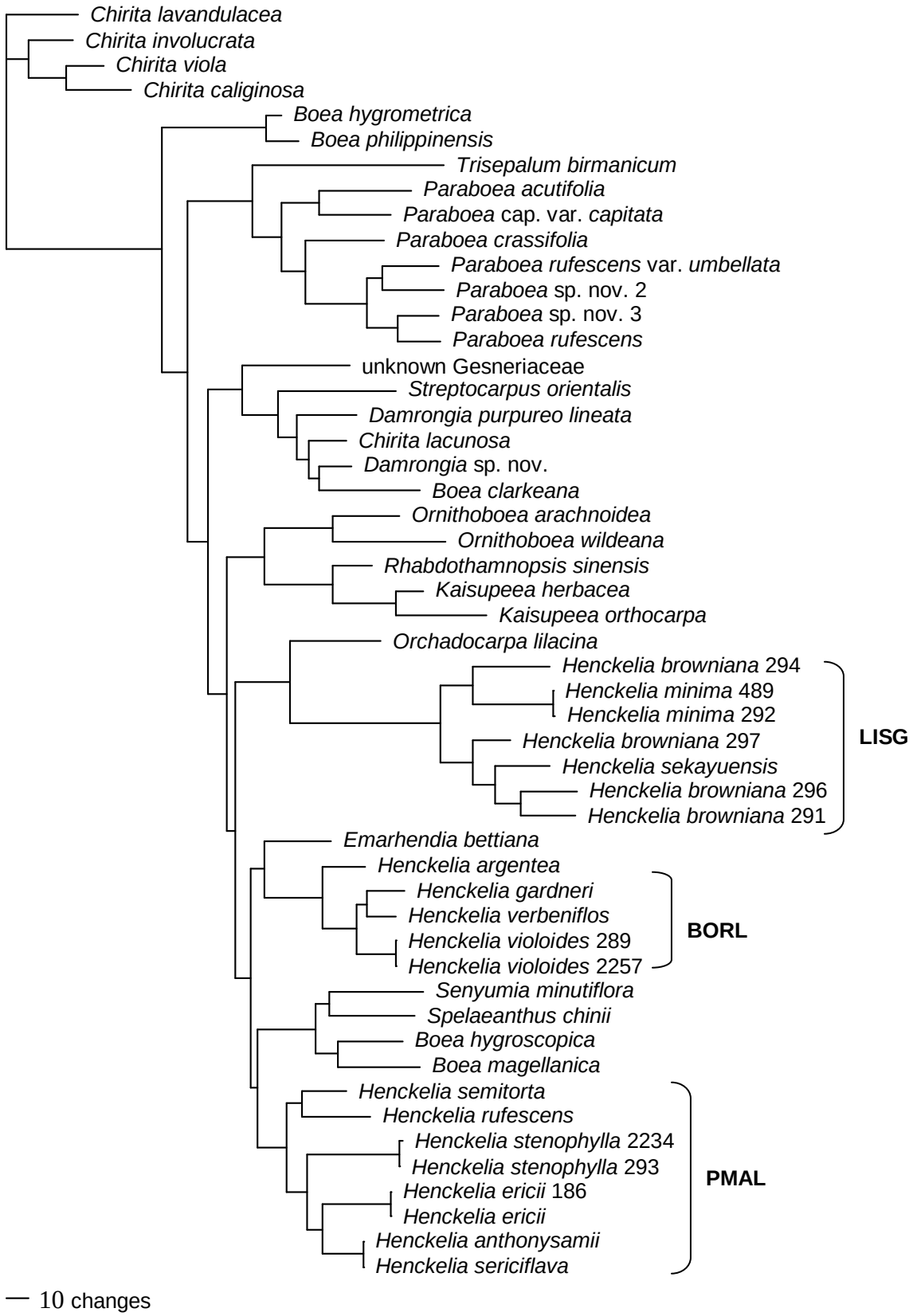


Fig. 3.11. A single representative phylogram of 12 MP trees of 2144 steps, based on ITS and *trnL-F* combined sequences of 51 samples.

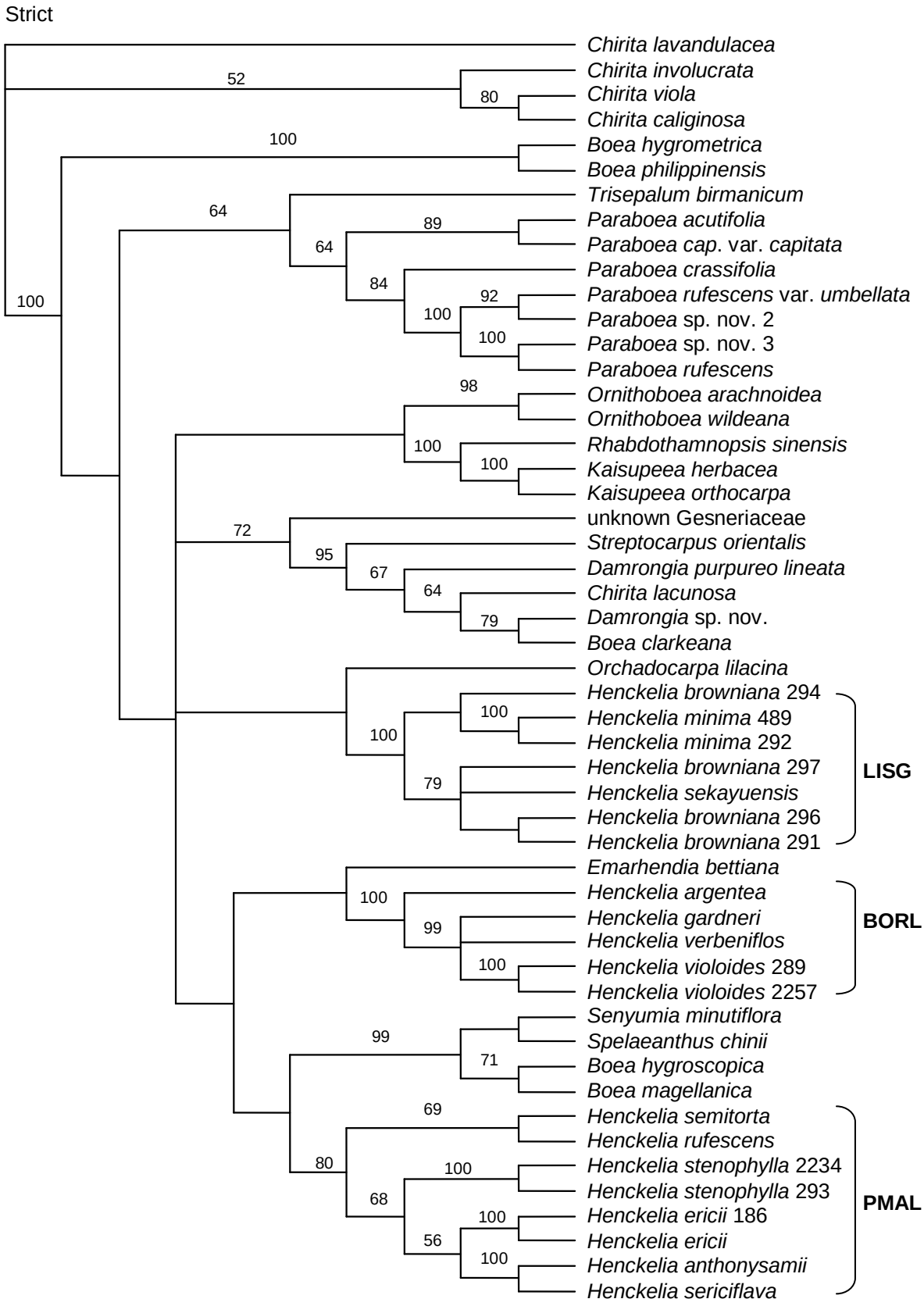


Fig. 3.12. Strict MP consensus tree of 12 most parsimonious trees of 2144 steps based on ITS and *trnL-F* combined sequences of 51 samples (CI = 0.51; RI = 0.63; RC = 0.32). Bootstrap (BS) values are given above branches.

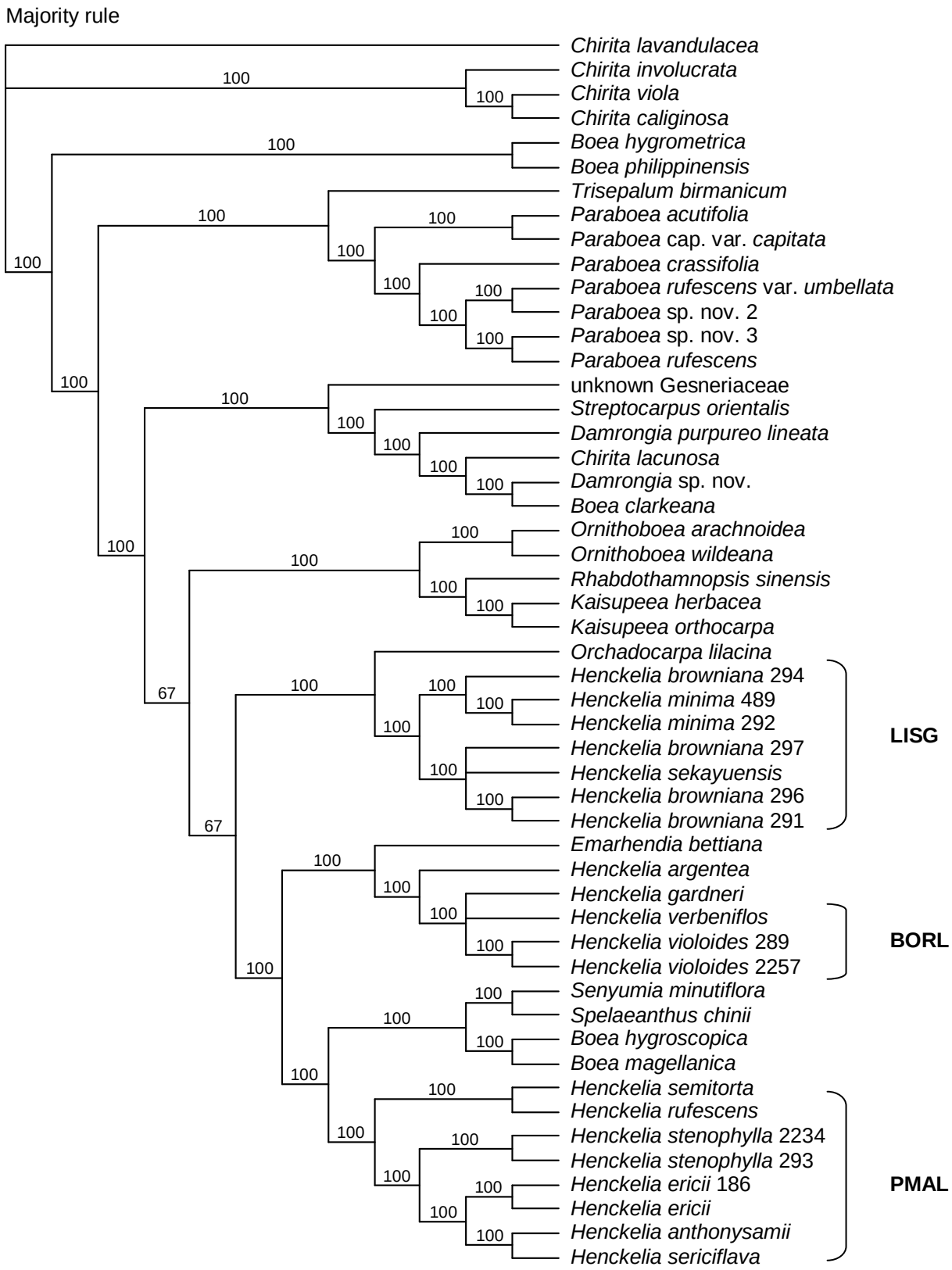


Fig. 3.13. MP 50% majority rule consensus tree of 2144 steps based on ITS and *trnL-F* combined sequences of 51 samples.

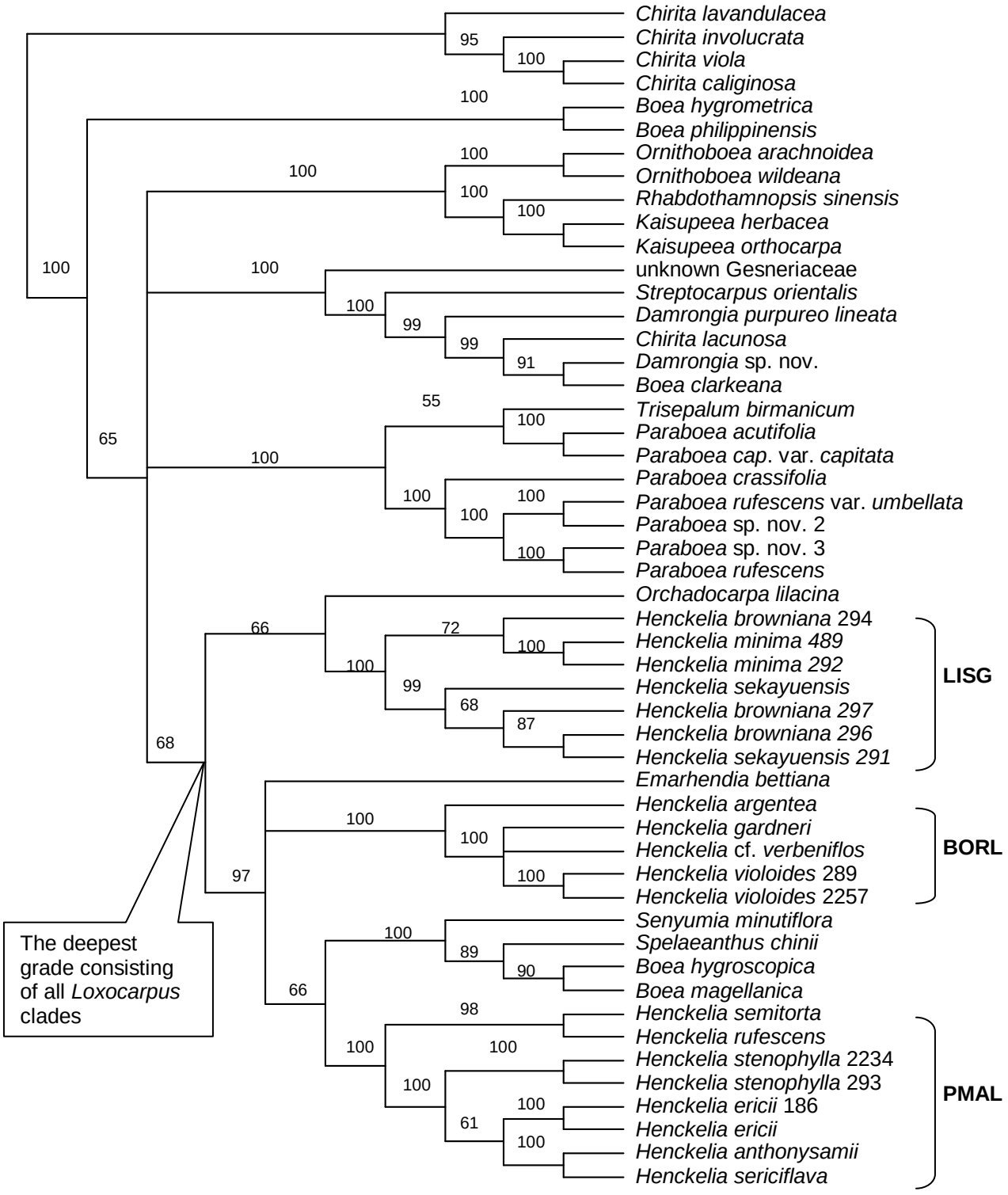


Fig. 3.14. BI majority rule consensus tree based on ITS and *trnL-F* combined sequences of 51 samples. Posterior probability (PP) values are given above branches.

including *H. rufescens* and; (c) '*Henckelia browniana* (*Loxocarpus incanus*) species group' (LISG) that included *Henckelia browniana*, *H. minima* and *H. sekayuensis*.

3.4.1 Dataset I

3.4.1.1 MP analysis of Dataset I

The phylogram (**Fig. 3.1**) indicates the position of *Henckelia s.l.* in Old World Gesneriaceae. *Henckelia s.l.* splits into the Indian *Henckelia* clade, the Malesian *Henckelia* clade excluding sect. *Loxocarpus*, and *Henckelia* sect. *Loxocarpus* clades which fell in a twisted-fruited advanced Asian and Malesian genera polytomic backbone. These results are in concordance with the findings of Möller *et al*. (2009) and Weber *et al*. (2011).

3.4.1.2 BI analysis of Dataset I

The Bayesian inference majority rule consensus tree (**Fig. 3.2**) showed a similar topology and confirmed that taxa in sect. *Loxocarpus* are distinct from highly supported (PP = 100) Malesian *Henckelia* (= *Codonoboea*).

The BORL formed a highly supported clade (PP = 100). The Peninsular Malaysian *Loxocarpus* species and a number of twisted-fruited advanced Asian and Malesian genera *viz*. *Emarhendia* and *Spelaeanthus*, and two *Boea* Comm. *ex* Lam. species from Australasia formed a clade (PP = 93) on polytomic backbone. Within this clade, the LISG formed a highly supported (PP = 100) sub-clade. Throughout the results of the analyses in this study, the inclusion of one Bornean species, namely *Henckelia rufescens*, in the clade which I call PMAL is remarkable. This placement has some morphological support since this species possesses a campanulate corolla ('Group A', see **Section 2.8**) which places it closer to most of Peninsular Malaysian species than to any species that occurs in Borneo. In this study, the LISG always formed a highly supported clade. These species are morphologically closely

similar in having the corolla mouth with a cleft between the 2 upper lobes (see **Section 4.3 ii**).

3.4.2 Dataset II

Having confirmed that *Loxocarpus* species are not phylogentically close to *Henckelia* species, Dataset II on a much reduced sample size, was analysed to test the monophyly of *Loxocarpus* species.

3.4.2.1 Dataset II (a), *trnL-F* analyses (49 samples)

The MP phylogram (**Fig. 3.3**) indicated that LISG was a fast changing (evolving) sub-clade. This might be due to the nature of its widespread distribution and limited gene flow due to isolated populations. The results showed that the closer the populations were located, the closer the phylogenetic relation was. MP strict consensus tree (**Fig. 3.4**), based on 148 trees of 340 steps, showed that twisted-fruited advanced Asian and Malesian genera formed a highly (BS = 100) supported polytomic backbone. The supported internal branching counted 25 and BS value of 11 branches (*c*. 44%) was greater than 90. LISG and BORL species formed clades in grade. The former is highly supported (BS = 100), while the latter has an intermediate support (BS = 85). The unresolved PMAL fell in a polytomic backbone with other genera. BI analysis majority rule tree (**Fig. 3.6**) showed a highly supported (PP = 88) twisted-fruited advanced Asian and Malesian genera polytomic backbone, similar to MP analysis results. LISG and BORL formed two highly supported subclades (PP = 93 and 91 respectively) in grade.

3.4.2.2 Dataset II (b), ITS analyses (51 samples)

Similar to *trnL-F* marker, ITS MP phylogram (**Fig. 3.7**) showed that LISG was the fastest evolving group. It was by far the clade with greatest changes in this analysis, *c*. 20 more changes comparing with the sister species, *Trisepalum birmanicum* (Craib) B.L.Burtt. Anyway, the sister relation showed in this phylogram might be due to long-branch attraction and does not illustrate the true relations between them. ITS sequences of *Henckelia anthonysamyi* and *Henckelia sericiflava* were identical (see **Section 4.3 iii**). ITS MP strict consensus tree (**Fig. 3.8**) based on 48 most parsimonious trees of 1790 steps yielded a better resolved topology compared with *trnL-F*. Again, twisted-fruited advanced Asian and Malesian genera formed a highly (BS = 100) supported clade. The supported internal branching counted 30 and BS value of 16 branches (*c*. 53%) was greater than 90. It had no major discrepancy in topology congruence with *trnL-F* MP strict consensus but was better resolved in grades. BORL formed a highly (BS = 100) supported clade sister to *Emarhendia*. Compared with *trnL-F* MP strict consensus tree, Peninsular Malaysian *Loxocarpus* (including *H. rufescens*) was better resolved in grade although the clade's branch is weakly supported (BS = 58). LISG formed a highly (BS = 100) supported clade sister to *Trisepalum birmanicum*. The sister relations are explained above.

BI analysis majority rule tree (**Fig. 3.10**) showed a highly supported (PP = 100) polytomic twisted-fruited advanced Asian and Malesian genera backbone. However, it displayed a different topology of the three *Loxocarpus* groups, which is an indication of high rate of ITS evolution and difficulty of MP analysis to retrieve the true relationships.

On the backbone, LISG formed a highly (PP = 100) supported clade that was distant from *Trisepalum birmanicum*, which was sister to *Paraboea*, a placement concurred to *trnL-F* MP and BI analyses topology. This suggests that BI analysis is able to overcome

long-branch attraction complication. A grade deeper, *Emarhendia*, *Senyumia*, *Spelaeanthus*, *Boea hygroscopica*, *B. magellanica*, PMAL and BORL formed a polytomic clade (PP = 72).

The results from the analysis above showed that *trnL-F* sequences matrix provides the topology backbone while the faster changing ITS matrix gives better resolutions on branching and grading. To retrieve a more convincing topology which can better represent the samples phylogeny, both markers are combined for analysis.

3.4.2.3 Dataset II (c), *trnL-F* and ITS combined analyses (51 samples)

The MP strict consensus tree (**Fig. 3.12**) based on the 12 most parsimonious trees of 2144 steps confirmed that twisted-fruited advanced Asian and Malesian genera form a highly (BS = 100) supported clade but the topology is not well resolved in the deeper grades. The supported internal branching counted 34 and BS value of 19 branches (*c*. 44%) is greater than 90. All sect. *Loxocarpus* spp. are nested in a not-supported backbone with a few twisted fruit genera. LISG forms a highly supported (BS = 100) clade sister to *Orchadocarpa*.

On the same backbone, BORL formed a highly supported clade (BS = 100) sister to *Emarhendia bettiana*. PMAL formed a moderately supported (BS = 80) clade, sister to a highly supported clade (BS = 99) consisting *Boea*, *Senyumia* and *Spelaeanthus*. The topology of the tree is more similar to ITS, relative to *trnL-F* strict consensus tree but is better resolved.

BI analysis majority rule tree (**Fig. 3.14**) is better resolved compared to strict consensus tree of MP analysis (**Fig. 3.11**). The different probably results because the latter could not precisely assess the fast-evolving ITS markers. All *Loxocarpus* spp., together with four monotypic Peninsular Malaysian genera (*Orchadocarpa*, *Emarhendia*, *Senyumia*, *Spelaeanthus*) and two Australasian *Boea* (*B. hygroscopica* and *B. magellanica*) formed a

weakly supported (PP = 68) clade. Within, LISG formed a highly supported clade (PP = 100) sister to *Orchadocarpa*, and the rest formed a highly supported clade (PP = 97) in a further grade. Within, BORL and PMAL formed a highly supported clade (both PP = 100). Unexpectedly, the two Peninsular Malaysian strictly limestone endemics, *viz. Senyumia minutiflora* and *Spelaeanthus chinii* formed a highly supported clade (PP = 100) together with two Australasian *Boea* species. Throughout the analyses, BI analyses results showed better resolution among the twisted-fruited genera and this finding concurs with Möller *et al*. (2009) results.

Both MP and BI analyses showed that *Loxocarpus* is paraphyletic and *Loxocarpus* species are principally divided into three highly supported clades.

3.5 Un-weighted Pair Group Method with Arithmetic Mean (UPGMA) analysis based on morphological data: A comparison

The purpose of this study is to compare the dendrogram generated using morphological data with phylogenetic trees generated using molecular data. This is not an attempt of numerical taxonomy.

3.5.1 Morphological data analysis

The dataset included 19 species (**Table 3.13**) that were the same as the last polytomic grade in **Fig. 3.14**. Twenty eight characters of habit, leaves, flowers and fruits were selected and the character states are scored numerically (**Appendix 3.1**). Missing data were scored as 0. Data matrix (**Appendix 3.2**) totalled 519 (532 minus 13) and the missing data is *c.* 2.5 % (13).

A statistical computer programme, Multi Variate Statistical Package (MVSP), Kovach Computing Services was used to execute UPGMA cluster analysis. The option for

‘Data transformation’ assigned was ‘None’ and the ‘Distance’ option was ‘Average Distance’.

Table 3.13. Species included in the morphological data analysis.

In-group taxa	**Sister taxa**
Henckelia anthonysamyi	*Boea hygroscopica*
Henckelia argentea	*Boea magellanica*
Henckelia browniana	*Emarhendia bettiana*
Henckelia ericii	*Orchadocarpa lilacina*
Henckelia gardneri	*Senyumia minutiflora*
Henckelia minima	*Spelaeanthus chinii*
Henckelia rufescens	
Henckelia sekayuensis	
Henckelia semitorta	
Henckelia sericiflava	
Henckelia stenophylla	
Henckelia verbeniflos	
Henckelia violoides	

Note: For listing of name change, see **Table 3.1**.

3.5.2 Results

The dendrogram (**Fig. 3.15)** resulted from the analysis showed that the grouping of the sect. *Loxocarpus* species included in this study reflects the floral morphological affinity. Species with saintpaulioid/flat-faced (see **Section 2.8**) flowers form group 'x', *'Henckelia brownina* species group' (see **Section 3.4**) branched out as group ‘y’ while all other species with campanulate or short tubular flowers forms group ‘z’. Morphological data analysis shows that *Loxocarpus* is monophyletic (**Fig. 3.15**), contrasting with the paraphyly *Loxocarpus* based on molecular data (**Fig. 3.11–3.14**). However, grouping within *Loxocarpus* is congruent and consistent with molecular data analyses results. Group ‘x’ is equivalent to BORL, ‘y’ to ‘LISG’ and ‘z’ to PMAL resulted from the molecular analyses.

3.6 Discussion and Conclusion: Inference from molecular and morphological phylogenetic studies results

Molecular data analyses indicated that *Loxocarpus* is paraphyletic, contrasting with morphological data analyses which indicated the monophyly of *Loxocarpus*.

The inclusion of *Loxocarpus* in 'twisted-fruited dominated Asian and Malesian' species (Möller, 2009; 2011) based on molecular data was unexpected. The four monotypic genera Peninsular Malaysian genera, *viz*. *Orchadocarpa*, *Emarhendia*, *Senyumia*, *Spelaeanthus*, and the two Australasian *Boea* species, *B. hygroscopica* and *B. magellanica* appeared as sister taxa *Loxcarpus* (**Figures 3.11–3.14**).

However, the monotypic spp. are distinct from *Loxocarpus* in their thin membranous, coarsely toothed leaves (Henderson, 1959; Kiew *et al*., 1997). Also, the *Orchadocarpa* capsule is orthocarpic. The close affinity of Australasian *Boea* to this group is at present inexplicable and might due to under-sampling of *Boea* species (Möller *et al*., 2011). Molecular phylogenetic study of other twisted fruited Malesian and Asian genera is still on going. Also, sampling of *Loxocarpus* spp. is not comprehensive. Both caulescent species from Sumatra are not included in the molecular DNA study. They are reinstated as *Loxocarpus* based on their morphological affinity.

Based on both molecular and morphological datasets, grouping within *Loxocarpus* spp. is congruent and consistent.

(i) LISG or group 'y' (**Fig. 3.15**) had a relatively long branch that the species were consistently bound together in grades might because of 'long branch attraction'. This shows that this widespread entity is a fast evolving clade. Probably, these closely related species were once widely distributed and evolved into several genotypically distinct populations due to geographical separation. The morphological character similarities of this group justify synonymising them under a species were given in **Section 4.3 ii**.

(ii) BORL or group ‘x’ (**Fig. 3.15**) mainly consists of flat-faced flowers species (Group B, see **Section 2.8**) except for *Henckelia argentea* (Group A, see **Section 2.8**). *Henckelia violoides* has never been included within *Loxocarpus* due to its long gutter-shaped capsule despite having a flat-faced corolla. The long-capsule species (capsule length greater than 10 mm, see **Section 2.7**) were related to the short capsule *Loxocarpus* species in having flat-faced flowers, and this affinity is supported by DNA molecular phylogenetic study. The inclusion of long-capsule species redefines the generic concept of the re-instated *Loxocarpus*.

(iii) PMAL or group ‘z’ (**Fig. 3.15**). Borneo and PM do not share any species, but based on both morphological and molecular data, a Bornean Riau Pocket species, *H. rufescens* has closer affinity to Malayan species rather than to other Bornean species. *Henckelia semitorta*, which sometimes possesses a creeping stem, settled right within the PMAL clade that consists of mainly tight-rosette species. It shows that habit is not important in phylogenetic grouping.

Henckelia sect. *Loxocarpus* is proven distinct from Malesian *Henckelia*(= *Codonoboea*) (Kiew & Lim, 2011) and Indian *Henckelia*(= *Chirita*) (Weber *et al*., 2011) (**Fig. 3.1–3.2**). This leaves *Loxocarpus* as the only available generic name for this entity.

Although grouping within *Loxocarpus* spp. is congruent and consistent based on both molecular and morphological datasets, molecular phylogenetic study of twisted fruited Malesian and Asian genera is still ongoing. Moreover, sampling of *Loxocarpus* taxa is not comprehensive. Thus, I refrain from splitting *Loxocarpus* into smaller monophyletic genera and instead recognising *Loxocarpus* as a paraphyletic genus for the time being.

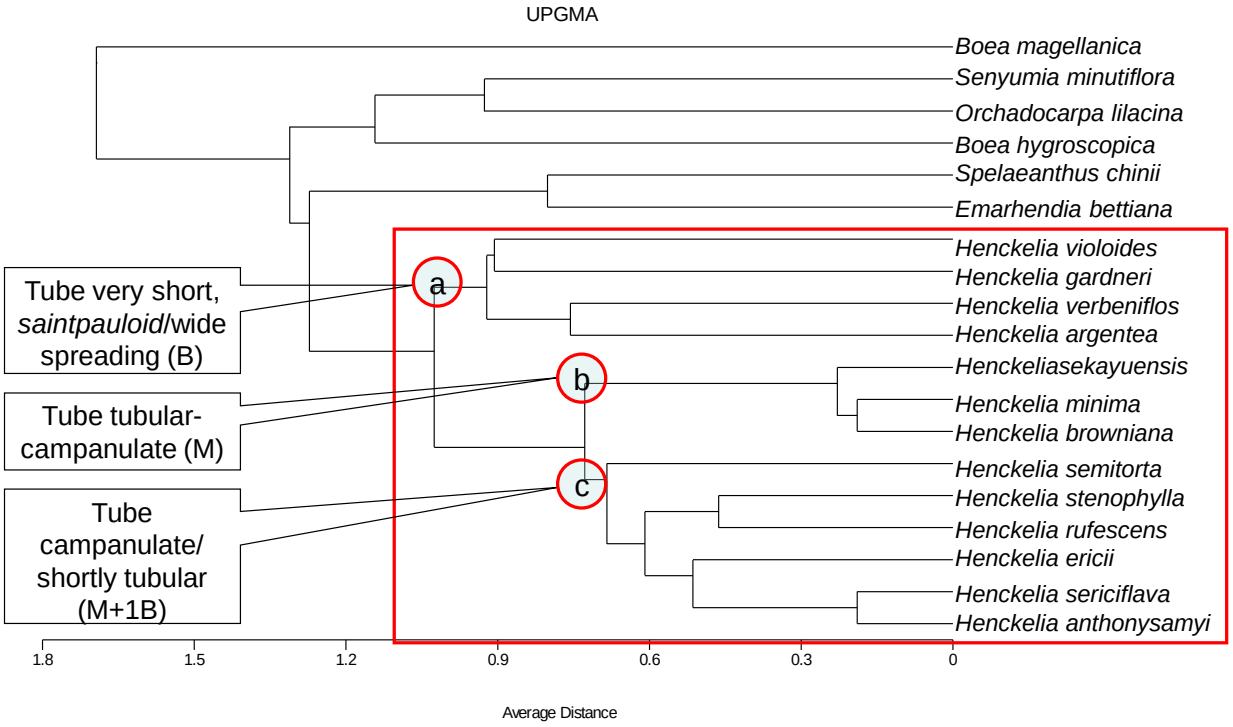


Fig. 3.15. Dendrogram based on morphological data. Within the rectangular box are *Loxocarpus* species and they split into ‘x’, ‘y’ and ‘z’ groups (B = Borneo; M = Peninsular Malaysia).

4.0 TAXONOMIC REVISION

4.1 Taxonomic history of *Loxocarpus*

Loxocarpus is primarily recognised by its conical short capsule with a broader base often with a hump-like swelling at the upper side (Banka & Kiew, 2009) which dehisces to form splash-cup and from which the seeds are bounced out by rain drops.

Originally, *Loxocarpus* was established by Brown in 1839 when he described *Loxocarpus incanus* R.Br. based on a Wallich collection from Penang [no. 809 (*Loxonia*? *alata*) in "Numerical List"]. The genus was aptly named (Greek, *loxos* – oblique; *carpos* – fruit), well describing the oblique capsule of the type species. Bentham (1876) included *Loxocarpus* as a section within *Didymocarpus* Wall. stating that the rosette habit and densely hairy leaves of *Loxocarpus incanus* resembled an Indian taxon, *Didymocarpus* sect. *Orthoboea*, thus did not warrant generic status.

However, this generic/sectional concept changed and expanded over time. Clarke (1883) followed Bentham in recognising *Loxocarpus* as a section within *Didymocarpus* and formally transferred *Loxocarpus incanus* as *Didymocarpus incanus* (R.Br.) C.B.Clarke. He described five new species: *Didymocarpus conicapsularis* C.B.Clarke, *D. petiolaris* C.B.Clarke, *D. rufescens* C.B.Clarke and *D. verbeniflos* C.B.Clarke from Borneo and *D. semitortus* C.B.Clarke from the Malay Peninsula.

Ridley (1896) at first followed Clarke's treatment and described *Didymocarpus caerulea* Ridl. from the Malay Peninsula and *D. sericea* Ridl. from Lingga. However, he later re-established *Loxocarpus* (Ridley, 1905) stating that the group ‘seems sufficiently distinct in its short tubed and short stamened flowers and horn-like capsule’ and made new combinations for *L. caruleus* (Ridl.) Ridl. and *L. semitortus* (C.B.Clarke) Ridl. Subsequently, he described *Loxocarpus angustifolia* Ridl. (Ridley, 1908) and *L. minimus*

Ridl. (Ridley, 1922). However, he never officially transferred species outside the Malay Peninsula to his re-instated *Loxocarpus*. Later, Henderson described *Loxocarpus papillosa* M.R.Hend. in 1927 and *L. holttumii* M.R.Hend. in 1929.

Burtt (1958) recognised *Loxocarpus* as a genus stating that 'the essential features of the short fruit swollen at base and beaked at the top and dehiscing by one side only' were the characters 'sufficient to distinguish *Didymocarpus* sect. *Orthoboea* Benth.' (=*Henckelia* Spreng. *s.s.*) and subsequently Burtt (1958, 1962, 1971 & 1982) described a number of species and made new combination for some. In 1958, he made three combinations for Bornean species: *Loxocarpus petiolaris* (C.B.Clarke) B.L.Burtt, *L. rufescens* (C.B.Clarke) B.L.Burtt, and *L. verbeniflos* (C.B.Clarke) B.L.Burtt and also transferred *Didymocarpus longipetiolatus* Merr. (1928) *nom. illegit., non* Gardner (1846) to *Loxocarpus* as *L. longipetiolatus* B.L.Burtt.

Burtt (1962) added two caulescent species from W Sumatra, namely *Loxocarpus caulescens* B.L.Burtt and *L. meijeri* B.L.Burtt and noted that their habits were different from most of the rosette congeneric species but the short corollas and capsules were good characters. He also made a new combination for *L. stapfii* (Kraenzl.) B.L.Burtt. In 1971, he described *Loxocarpus argenteus* B.L.Burtt and made a new combination for *Loxocarpus sericeus* (Ridl.) B.L.Burtt. In 1982, he added a creeping species, *Loxocarpus repens*. Kiew (1987) described *Loxocarpus tunkui* Kiew from Peninsular Malaysia.

In 1998, Weber & Burtt (1998 ['1997']) re-modelled *Didymocarpus*. *Didymocarpus s.s.* was redefined as a natural group, while most of the majority of Malesian *Didymocarpus s.l.* and a few others morphologically close genera including *Loxocarpus* were transferred to *Henckelia* and recognised as sect. In 1996, Burtt described four new species from Brunei: *Henckelia coodei* B.L.Burtt, *H. diffusa* B.L.Burtt, *H. gardneri* B.L.Burtt and *H.*

taeniophylla B.L.Burtt and made a new combination for *H. petiolaris* (C.B.Clarke) B.L.Burtt.

For some of the *Didymocarpus* species transferred to *Henckelia* that shared the same specific epithet with section *Loxocarpus* species, renaming was required: *L. angustifolia* as *H. stenophylla* A.Weber; *L. incanus* as *H. browniana* A.Weber; *L. holttumii* as *H. ericii*. Weber and *L. repens* as *H. procumbens* B.L.Burtt.

Banka & Kiew (2009) produced a monographic account on Peninsular Malaysian species. They included ten species including three new species, *viz. Henckelia anthonysamyi* Banka, *H. sekayuensis* Banka & Kiew and *H. sericiflava* Kiew & Banka with a species known only from two syntypes, *H. papillosa* (M.R.Hend.) A.Weber, excluded from the section. The exclusion was because *Henckelia papillosa* has a very short petiole and thin leaves and so appears to belong to *Henckelia* sect. *Boeopsis*.

The present study monographs all *Loxocarpus* species and reassesses the sectional status of *Loxocarpus*. Based on results from both molecular phylogenetic and morphological studies, *Loxocarpus* was reinstated as a paraphyletic genus. Yao *et al.* (*Blumea, in press*) added *Loxocarpus pauzii* T.L.Yao and proposed three new species and synonymised six species (see **Section 4.5**), bringing the total number of species to 23.

4.2 Generic description

Loxocarpus R.Br.

Cyrtandreae: 120 (1839); DC., Prod. 9: 277 (1845); Ridley, J. Straits Branch Roy. Asiat. Soc. 44: 61 (1905), J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 768 (1908), Fl. Malay. Penin. 2: 526 (1923); Burtt, Notes Roy. Bot. Gard. Edinburgh 22: 308 (1958); Henderson, Malay.

Wild Fls., Dicots.: 352 (1959). **Synonyms:** *Didymocarpus* Wall. sect. *Loxocarpus* (R.Br.) Benth. in Bentham & Hooker *f*., Gen. Pl. 2: 1022 (1876); Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 71, 98 (1883), Fl. Brit. India 4: 352 (1884). *Roettlera* Vahl sect. *Loxocarpus* (R.Br.) Fritsch, in Pflanzenfam. 4, 36: 147 (1894). *Henckelia* Spreng. sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burtt, Beitr. Biol. Pflanzen. 70: 334 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 9 (2009). **Type:** *Loxocarpus incanus* R.Br.

Rosette plants with or without rootstock, sometimes creeping, rarely caulescent. Indumentum usually of a layer of silky hairs, generally whitish, sometimes buff, usually dense, rarely sparse on lamina upper surface (*L. verbeniflos*). Leaves petiolate. Inflorescence a reduced cyme with a single flower or cymose, pedunculate. Flowers 5-merous. Calyx lobes free almost to base. Corolla usually campanulate or flat-faced, rarely shortly tubular (*L. semitortus*), mauve, purplish, bluish, rarely very pale to almost white; lobes more or less isomorphic but lower three lobes usually distinguishably larger than upper two lobes, upper lobes rarely fused (*L. pauzii*). Nectary usually absent, sometimes vestigial. Stamens connate to corolla base, usually short (in *L. caeruleus* geniculate); anthers kidney-shaped, coherent, usually included within corolla tube in campanulate and shortly tubular flowers or exposed in flat-faced flowers. Ovary conical, usually short and thick at base, sometimes slender; stigma punctiform, sometimes capitate and rarely peltate. Capsules plagiocarpic, often ovoid or conical, sometimes slender and gutter shaped, usually straight or slightly curved, rarely corniculate (*L. caeruleus*), dorsally split forming a splash cup or gutter. Seeds broadly to narrowly ellipsoid.

4.3 Species concept

Burtt (1982) mentioned "the small gesneriads of the Bornean montane (mossy) forests form a number of groups which are difficult taxonomically at both generic and specific level". This statement is true for *Loxocarpus*. The difficulty in delimiting generic circumscription is now overcome by molecular phylogenetic methods. However, *Loxocarpus* is still difficult taxonomically at the specific level, especially for morphologically variable and widespread species. For such taxa, I have adopted a broad species concept. The few paragraphs below explain my rationale with emphasis on synonymised taxa.

(i) *Loxocarpus repens* (Burtt, 1982) and *Henckelia diffusa* (Burtt, 1996) are two species distinguished by their distinctive creeping habit although Clarke (1883) had pointed out the creeping habit of *Loxocarpus* (*Didymocarpus petiolaris*).

In this treatment, materials better representing geographical distribution and morphological variation are now available. I observed intermediates between creeping and rosette 'species' and this enabled me to recognise two pairs of 'rosette-creeping' entities, *viz*. (a) *Henckelia violoides-Henckelia diffusa* and (b) *Henckelia gardneri-Henckelia procumbens*. Variation between the rosette and creeping habits was also observed within the following species: *Loxocarpus rufescens*, *L. semitortus*, *L. stapfii* and *L. verbeniflos*. In fact, the rosette and creeping habit are ecological adaptations. Generally, populations that grow on moss beds and earth banks tend to have longer creeping stems while the populations that grow on vertical rock faces tend to have a rosette habit. Therefore, I have synonymised the 'rosette–creeping' entities.

(ii) *Loxocarpus incanus-L. minimus-Henckelia sekayuensis* group is the most widespread entity in Peninsular Malaysia and Peninsular Thailand. The unifying character

of this entity is the cleft corolla mouth in between the two upper lobes. *Loxocarpus minima* is synonymised to *L. incanus*, while *Henckelia sekayuensis* is reduced to a varietal level.

Style length was used to distinguish *Henckelia sekayuensis*. However, observations of populations in the field and of living plants in the nursery found that style length in relation to corolla tube length is not a reliable taxonomic character. *Loxocarpus* species are protandrous. In the male stage, the style is contained within the corolla tube but in the female stage it extends beyond the corolla mouth. This elongation of the style is shared by *Emarhendia bettiana* (M.R.Hend.) R.Kiew, A.Weber & B.L.Burtt (Gesneriaceae) (Kiew *et al*., 1997).

(iii) Leaf size, flower number and indumentum colour were characters used to distinguish *Henckelia anthonysamyi* and *Henckelia sericiflava* (Banka & Kiew, 2009). With more specimens available for study, I found that these characters are not disjunctive. Furthermore, the molecular data (see **Chapter 3**) showed that these two species are identical. Thus, *Henckelia anthonysamyi* is synonymised with *Henckelia sericiflava* as *Loxocarpus sericiflavus comb. nov*.

4.4 Novelties, incompletely known species and excluded species

Materials available for *Loxocarpus* sp. 'A', 'B' and 'C' are sufficient to distinguish them as distinct species. They will be fully described and validly published in due course. They are included in the key to species and brief species descriptions are provided. Publication of *Loxocarpus pauzii* is currently in press.

There are about six incompletely known taxa, which I have named *Loxocarpus* sp. 1–6 (numbered as 24–29 in the identification list). Their species status is subject to reconsideration when more complete and better material becomes available. They are

neither included in the key to species nor are descriptions provided but the specimens are included in the identification list.

Henckelia papillosa (M.R.Hend.) A.Weber is excluded from this revision because it is morphologically closer to *Henckelia* (Banka & Kiew, 2009), of the group which is now known as *Codonoboea* Ridl.

4.5 Keys to the species

The general key to all species to some extent reflects the morphological affinity between species. A high level of endemism and restricted distributions of *Loxocarpus* species within a particular geographical region make the construction of regional keys practical. The regional keys are artificial and avoid flowers characters. Flowering material is often not available, and even if available the corolla is often not well preserved on herbarium specimens. Thus, to aid species identification, the regional keys emphasise vegetative and fruiting characters.

4.5.1 General key to the species

1a Habit rosette, or caulescent; stem erect, or creeping; corolla shortly tubular or campanulate with flared lobes or corolla tube short with deeply dissected lobes; capsule up to 10 mm long, generally ovoid or obliquely conical _____ 2 **(Group A)**

1b Habit rosette or stem creeping; corolla flat-faced; capsule 6–30 mm long, ovoid, obliquely conical, long slender conical or long slender cylindric _____ 15 **(Group B)**

(Group A)

2a Habit caulescent, stem erect, to 28 cm tall, rootstock lacking _____ 3

2b Habit rosette, stemless, rootstock present and to 11 cm long or sometimes lacking ____ 4

3a Lamina elliptic, 3 times longer than wide, margin crenulate, apex acute, lateral veins straight and ascending to margin (*c*. 20˚ to midrib); inflorescence lax _____ **9. L. meijeri**

3b Lamina ovate to elliptic, length less than 3 times width, margin serrate, apex acuminate to caudate, lateral veins gently curving to margin (*c*. 40˚ to midrib); inflorescence compact _____ **4. L. caulescens**

4a Corolla lobes deltoid, corolla tube short, between 1.1–3.3 mm long _____ 5

4b Corolla lobes oblong, corolla tube shortly tubular or campanulate, between 2–6.1 mm long _____ 8

5a Inflorescence a reduced cyme, flower solitary _____ 6

5b Inflorescence lax and much branched, or a compact cyme, flowers usually more than 1 _____ 7

6a Lamina above covered in dense spreading woolly hairs; capsule 17 mm long _____ _____ **23. Loxocarpus sp. C**

6b Lamina above covered in dense silky hairs; capsule 6–9 mm long _____ **2. L. argenteus**

7a Petioles much longer than lamina; lamina sub-orbicular to broadly ovate; inflorescence lax, much branched; corolla lobes 4 _____ **10. L. pauzii**

7b Petioles shorter than lamina or about the same length; lamina ovate-lanceolate to elliptic; inflorescence a compact cyme; corolla lobes 5 _____ **16. L. stapfii**

8a Longest petiole longer than lamina _____ 9

8b Longest petiole shorter or equal in length to the lamina _____ 11

9a Capsule strongly curved, corniculate (horn-like); lamina 6.5–20 by 4.5–15 cm _____ _____ **3. L. caeruleus**

9b Capsule straight, obliquely conical; lamina to 5.2 cm by 4 cm _____ 10

10a Indumentum ferruginous, rough; lamina sub-orbicular to broadly ovate, as long as wide; inflorescences with 2–15 flowers, corolla campanulate, plain mauve _____ **7. L. holttumii**

10b Indumentum buff, woolly; lamina ovate to elliptic, slightly longer than wide; inflorescence 1(–2) flower(s), corolla shortly tubular, pale mauve with 8 darker purple streaks in the throat _____ **13. L. semitortus**

11a Capsule straight, ovoid, humped above; corolla mouth with a cleft between the 2 upper lobes _____ **8. L. incanus**

11b Capsule straight or slightly curved upward, obliquely conical, not humped above; corolla mouth smoothly curved _____ 12

12a Lamina narrowly elliptic, 4 times longer than wide _____ 13

12b Lamina ovate, elliptic, oblong to oblanceolate, 2–3 times longer than wide _____ 14

13a Lateral veins 2–3 pairs, obscure beneath; inflorescence a reduced cyme with 1–2 flowers; capsule *c.* 8.5 mm long _____ **14. L. sericeus**

13b Lateral veins 4–6 pairs, prominent beneath; inflorescence a reduced cyme with 2–3 flowers or once branched with 4–9 flowers; capsule 5–6 mm long _____ **1. L. angustifolius**

14a Indumentum yellowish grey; lateral veins 8 pairs or more, lamina base unequal _____ **15. L. sericiflavus**

14b Indumentum silky or whitish; lateral veins less than 8 pairs, lamina base equal ____ 15

15a Petiole 3.5–7 cm; lateral veins to 4 pairs, lamina upper surface densely adpressed hairy; capsule 4–6 mm long _____ **18. L. tunkui**

15b Petiole 0.7–1.8(–3.5) cm; lateral veins 4–7 pairs, lamina upper surface densely adpressed hairy or sometimes glabrous; capsule 7–8 mm long _____ **12. L. rufescens**

(Group B)

16a Inflorescence a compact cyme, flowers 2 to 7 or, rarely a reduced cyme with a solitary flower (only in creeping plants with well-spaced leaves) _____ 17

16b Inflorescence a reduced cyme with a solitary flower or rarely with 2 _____ 18

17a Hairs on lamina upper surface adpressed, dense; lamina *c*. 7.4 by 2.9 cm, apex acute to acuminate; capsule long slender conical, more than 15 mm long ____ **22. Loxocarpus sp. B**

17b Hairs on lamina upper surface erect, sparse; lamina 2.5–5.5 by 1.5–3 cm, apex blunt; capsule obliquely conical, less than 10 mm long _____ **11. L. repens**

18a Hairs on upper lamina surface distinctly sparse (sometimes glabrous) relative to hairs on lower surface _____ 19

18b Hairs on both upper and lower lamina surfaces more-or-less equally dense _____ 21

19a Lamina 4 times longer than wide, width 0.4–0.7 cm; capsule obliquely conical, 6–8 mm long _____ **5. L. conicapsularis**

19b Lamina 2–3 times longer than wide, width 1.3–2.4 cm; capsule obliquely conical or long slender conical, 8.5–20 mm long _____ 20

20a Calyx lobes 0.9–1.2 mm _____ **19. L. verbeniflos**

20b Calyx lobes 5 mm or longer _____ **6. L. coodei**

21a Lamina narrowly oblong, more than 6 times longer than wide; capsule obliquely conical, 6–7 mm long _____ **17. L. taeniophyllus**

21b Lamina ovate to elliptic, as long as or twice as long as wide; capsule long slender conical or cylindric, more than 10 mm long _____ 22

22a Lamina margin entire, sometimes undulate; veins inconspicuous beneath _____ _____ **21. Loxocarpus sp. A**

22b Lamina margin shallowly serrate or finely serrulate; veins distinct or conspicuous beneath _____ **20. L. violoides**

4.5.2 Regional keys to the species

4.5.2.1 Key to species in Sumatra (including Lingga Archipelago)

1a Habit caulescent, stem erect _____ 2

1b Habit rosette, stemless or, stem when present creeping _____ 3

2a Lamina elliptic, 3 times longer than wide, margin indistinctly crenulate, apex acute, lateral veins straight and ascending to margin (*c.* 20˚ to midrib); inflorescence lax _____ _____ **9. L. meijeri**

2b Lamina ovate to elliptic, less than 3 times longer than wide, margin serrate, apex acuminate to caudate, lateral veins gently curving to margin (*c.* 40˚ to midrib); inflorescence compact **4. L. caulescens**

3a Lamina ovate, *c.* 2 times longer than wide **16. L. stapfii**

3b Lamina narrowly elliptic, at least 4 times longer than wide **14. L. sericeus**

4.5.2.2 Key to species in Borneo

1a Capsule more than 10 mm long 2

1b Capsule to 9 mm long 6

2a Flowering inflorescences at one time *c.* 10, a simple cyme to once branched, flowers 3 to 7 **22. Loxocarpus sp. B**

2b Flowering inflorescence(s) at one time 1–2(–4), a reduced cyme, flowers solitary, or rarely 2 3

3a Hairs on lamina upper surface distinctly sparse relative to hairs on lower surface **19. L. verbeniflos**

3b Hairs on both lamina upper and lower surfaces more or less equally dense 4

4a Lamina margin entire, sometimes undulate, veins not prominent beneath **21. Loxocarpus sp. A**

4b Lamina margin shallowly serrate or finely serrulate, veins distinct or conspicuous beneath 5

5a Lamina above covered in dense spreading woolly hairs; habit rosette; petiole grooved above; capsule conical, 17 mm long _____ **23. Loxocarpus sp. C**

5b Lamina above thinly spread with pubescent adpressed hairs; habit creeping or rosette, petiole terete; capsule cylindric, (15–)18–25(–30) mm long _____ **20. L. violoides**

6a Lamina at least 4 times longer than wide _____ 7

6b Lamina at most 3 times longer than wide _____ 8

7a Lamina elliptic, narrowly elliptic or oblong, 1.8–3.2 by 0.4–0.7 cm _____ _____ **5. L. conicapsularis**

7b Lamina narrowly oblong, 8–9 by 0.3–0.6 cm _____ **17. L. taeniophyllus**

8a Hairs on petiole shaggy _____ **11. L. repens**

8b Hairs on petiole adpressed _____ 9

9a Capsule ovoid; inflorescence a compact cyme, not branched or rarely branched _____ _____ **16. L. stapfii**

9b Capsule obliquely conical; inflorescence a reduced cyme, a simple cyme or up to once branched, never a compact cyme _____ 10

10a Hairs on upper surface sparse; calyx linear _____ **6. L. coodei**

10b Hairs on upper surface dense; calyx deltoid _____ 11

11a Lamina indumentum dull; bracts narrowly lanceolate; capsule straight _____ _____ **12. L. rufescens**

11b Lamina indumentum glossy; bracts lanceolate; capsule slightly curved _____ _____ **2. L. argenteus**

4.5.2.3 Key to species in Peninsular Malaysia and Peninsular Thailand

1a Longest petiole longer than the lamina _____ 2

1b Longest petiole shorter or equal in length to the lamina _____ 5

2a Capsule strongly curved, corniculate (horn-like); lamina 6.5–20 by 4.5–15 cm _____ _____ **3. L. caeruleus**

2b Capsule straight or slightly curved; lamina 2–5.2 by 1.4–4 cm _____ 3

3a Inflorescence 3–4 times branched; lamina margin serrulate _____ **10. L. pauzii**

3b Inflorescence at most twice branched; lamina margin shallowly crenate _____ 4

4a Indumentum ferruginous, rough; lamina sub-orbicular to broadly ovate, as long as wide; inflorescences with 2–15 flowers _____ **7. L. holttumii**

4b Indumentum buff, woolly; lamina ovate to elliptic, longer than wide; inflorescence 1(–2) flower(s) _____ **13. L. semitortus**

5a Lamina narrowly elliptic, 4 times longer than wide _____ **1. L. angustifolius**

5b Lamina broadly ovate, ovate, elliptic or oblanceolate, up to 3 times longer than wide _ _____ 6

6a Capsule humped above, straight, ovoid; corolla mouth with a cleft between the 2 upper lobes _____ **8. L. incanus**

6b Capsule not humped above, straight or slightly curved, obliquely conical; corolla mouth smoothly curved _____ 7

7a Indumentum dull; lateral veins 8 pairs or more, lamina base unequal _____ _____ **15. L. sericiflavus**

7b Indumentum glossy; lateral veins to 4 pairs, leaves lamina base equal ____ **18. L. tunkui**

4.6 Species description

1. *Loxocarpus angustifolius* Ridl. — **Fig. 4.1, Plate 1b, Plate 2a–b**

J. Linn. Soc., Bot. 38: 319 (1908), J. Fed. Malay States Mus. 6: 168 (1915), Fl. Malay. Penin. 2: 526 (1923). **Synonym:** *Henckelia stenophylla* A.Weber, Beitr. Biol. Pflanzen. 70: 357 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 19 (2009). **Type:** Peninsular Malaysia, Pahang, Kuala Teku, 9 VII 1905, *Wray & Robinson 5504* (holo BM; iso SING).

Habit rosette. Rootstock short, woody or lacking, 0–1 cm long, 0–0.8 mm thick; rootstock/stem indumentum: hairs buff, short, shaggy, dense; adventitious roots wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs greyish, silky, eglandular, on petiole, lamina above and veins beneath dense; on lamina beneath scattered with glandular hairs especially near margin. Petiole slender, 2–2.5 cm long, 1–1 mm thick, cross section slightly grooved above; longest petiole shorter than lamina. Lamina dirty green, beneath paler, moderately thick, narrowly elliptic, 3–5 × (0.4–)0.8–1(–1.3) cm, width:length ratio *c*. 1:4; base cuneate, equal, margin entire, apex acute or blunt; midrib and veins above prominent, beneath conspicuous, lateral veins 4–6 pairs. **Inflorescence** axillary, a simple cyme or once branched, flower(s) 2–9; indumentum of inflorescence: hairs mainly glandular with scattered straight eglandular hairs, on peducle, bracts and pedicel dense.

Peduncle green, slender, 5–8 cm long; bracts green, lanceolate, *c*. 2 × 1 mm, apex rounded; pedicel 3–5 mm long. **Flower** indumentum: hairs mainly glandular with scattered straight eglandular hairs; on outer surface of calyx dense; mainly of glandular hairs on corolla and dense; on ovary sparse. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 0.7 mm long, 1.1 mm wide, lobes lanceolate, apex blunt, *c*. 2.5 mm long, base 1 mm wide. Corolla white or pale mauve, plain, tube tubular-campanulate, 3.4–3.5 mm long, 3.4–3.5 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flared, oblong; upper lobes *c*. 2.2 × 2.5 mm, lateral lobes *c*. 2.8 × 2.8 mm, median lobe *c*. 2.8 × 3 mm. Fertile stamens 2; anthers included within corolla tube; filament white, straight or slightly curved, *c*. 2.3 mm long; anther cream, coherent face to face, kidney-shaped, *c*. 1.6 × 0.6 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary a bulge, at the dorsal part of ovary. Ovary conical, slightly oblique, *c*. 1.5 mm long, 0.9 mm wide; ovule with a funicle connecting to placenta ; style white, arched towards corolla ceiling, *c*. 2.5 mm long; stigma white, capitate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 5–6 mm long, 1 mm thick, sub-persistent style 2.5 mm long; valves straight, splitting into a wide trough; hairs glandular, short, erect, dense. **Seeds** ellipsoid, *c*. 0.5 × 0.2 mm, apices acute.

Distribution. Peninsular Malaysia; Pahang, known only from Taman Negara (National Park).

Habitat. Locally abundant in lowland, hill forest and lower montane forest to 1850 m asl. On sandstone boulders in fast flowing stream or on rock faces above stream.

Conservation status. Near Threatened [NT].

Plate 1

Loxocarpus angustifolius: **a.** natural habitat, below Lata Kor, trail to Gunung Tahan, **b.** habit.

Plate 2

Loxocarpus angustifolius: **a.** flowers, **b.** young capsule; *Loxocarpus argenteus*: **c.** habit.

Notes. A 'Group A' species. This species resembles *Loxocarpus sericeus* in its small habit and narrow leaves. See key 13 (**Sect. 4.4.1**) for differences.

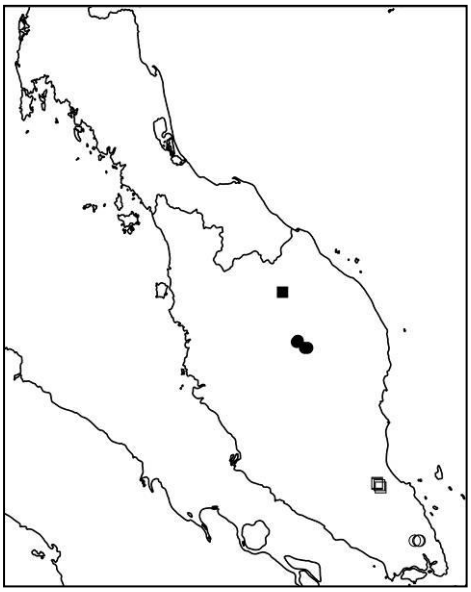


Fig. 4.1. Distribution of *Loxocarpus augustifolius* (●), *L. pauzii* (■), *L. holttumii* (○) and *L. tunkui* (□).

2. *Loxocarpus argenteus* B.L.Burtt — **Fig. 4.2, Plate 2c, Plate 3a–b**

Notes Roy. Bot. Gard. Edinburgh 31: 47 (1971). **Synonym:** *Henckelia argentea* (B.L.Burtt) B.L.Burtt, Beitr. Biol. Pflanzen. 70: 339 (1998). **Type:** Sarawak, Kuching [First] Division, Bako NP, Telok Assam, *c*. 45 m, on sandstone rocks in kerangas forest, 17 V 1962, *Burtt & Woods B1840* (holo E; iso SAR).

Habit rosette. Rootstock short, woody or lacking, 1.5–1.8 cm long, 5–7 mm thick; rootstock/stem indumentum: hairs silky, long, adpressed, dense; adventitious roots wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs silky, shiny, adpressed, on petiole, lamina above and beneath dense; young leaves covered in long shaggy hairs. Petiole slender, 1–2(–4.5) cm long, 1–1.5 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina green, beneath paler, moderately thick, ovate or elliptic, (4–)6–9 × 2–2.5–3.5 cm, width:length ratio *c*. 1:2; base cuneate or slightly rounded, equal, margin entire, apex acute; midrib and veins above obscure, beneath distinct, lateral veins 4–5 pairs. **Inflorescence** axillary, a reduced cyme, flower(s) 1; indumentum of

inflorescence: hairs long eglandular, adpressed on peduncle, bracts and pedicel, dense. Peduncle green, slender, 5–14 cm long; bracts green, lanceolate, *c*. 5–6 × 0.4 mm, apex acute; pedicel 3–10 mm long. **Flower** indumentum: hairs long eglandular, adpressed on calyx and corolla, dense; short, eglandular, erect on ovary; short, purple, glandular on filament, dense. Calyx green, 5 lobed, lobes somewhat equal, tube *c*. 0.8 mm long, 1.6 mm wide, lobes deltoid, apex thickened, blunt, *c*. 5.1 mm long, base 0.65 mm wide. Corolla violet, darker towards throat, tube short with deeply dissected lobes, 2.8–3.3 mm long, 3.1–3.7 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes recurved, deltoid; upper lobes *c*. 4 × 2.2 mm, lateral lobes *c*. 4.2 × 2 mm, median lobe *c*. 4.5 × 1.8 mm. Fertile stamens 2; anthers at the mouth of corolla tube; filament deep purple, straight, *c*. 2.5 mm long; anthers deep violet, coherent face to face, kidney-shaped, *c*. 1.75 × 0.92 mm; staminodes 2, deltoid. Nectary absent. Ovary narrowly conical, slightly oblique, *c*. 1.5 mm long, 0.7 mm wide; ovule with a funicle connecting to placenta ; style violet, straight, *c*. 1.8 mm long; stigma purple, stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, purplish when young, oblique conical, 6–9 mm long, 2.9–3.1 mm thick; valves slightly curved upward, splitting into a wide trough; hairs silky, eglandular, short, adpressed, dense. **Seeds** broadly ellipsoid, *c*. 0.55 × 0.25 mm, apices acute.

Distribution. Borneo; NW Sarawak, known only from a few localities in Bako NP.

Habitat. Locally abundant in coastal heath forest at 35–100 m asl. On sandstone boulders or rock faces under closed tree canopy.

Conservation status. Near Threatened [NT].

Plate 3

Lim, C.L.

Loxocarpus argenteus: flowers, **a.** side view, **b.** front view;
Loxocarpus caeruleus: **c.** habit, inset–the close-up of flower.

Notes. A 'Group A' species. Its recurved deltoid petals are remarkable. The filaments are covered with glistening dark purple glands, and the anthers are dark purple.

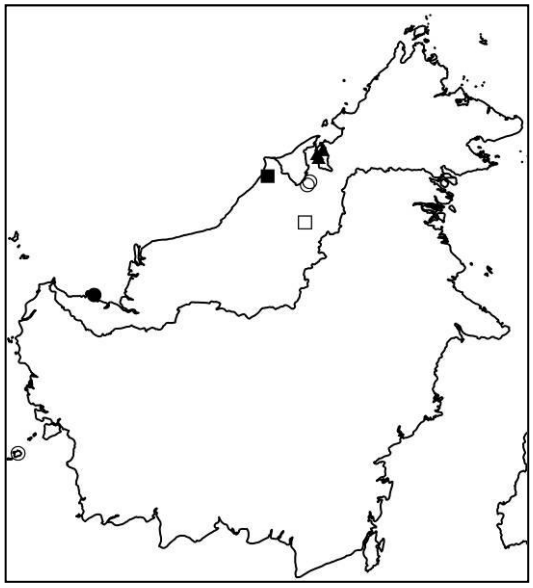


Fig. 4.2. Distribution of *Loxocarpus argenteus* (●), *L. conicapsularis* (○), *L. taeniophyllus* (▲), *Loxocarpus* sp. A (■) and *Loxocarpus* sp. B (□).

3. *Loxocarpus caeruleus* (Ridl.) Ridl. — **Fig. 4.3, Plate 3c**

J. Straits Branch Roy. Asiat. Soc. 44: 62 (1905), J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 769 (1908), Fl. Malay. Penin. 2: 527 (1923); Henderson, Malay. Wild Fls., Dicots.: 353, *fig.* 329D (1959); Weber & Kiew, Nat. Malaysiana 8(3): 24 (1983). **Basionym:** *Didymocarpus caerulea* Ridl., J. Linn. Soc., Bot. 32: 513 (1896). **Synonym:** *Henckelia caerulea* (Ridl.) A.Weber, Beitr. Biol. Pflanzen. 70: 341 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 13 (2009). **Type:** Peninsular Malaysia, Perak, Bkt. Larut, IX 1881, *Ridley 2476* (lecto K, designated by Banka & Kiew, 2009).

Habit rosette. Rootstock short, woody, 3–4 cm long, 5–7.5(–20) mm thick; habit in correlation with habitat: rootstock longer when growing in mossy earthbank; rootstock/stem indumentum: hairs brownish, shaggy, dense; adventitious roots wiry. Leaf bases persistent. **Stem** lacking or distinctive, 1–2 cm long. **Leaves** alternate, crowded at the top; hairs buff, shiny, shaggy on petiole, dense; greyish, adpressed on lamina above; buff, shaggy on lamina beneath, sparse; on veins beneath dense; lamina beneath when young

wooly. Petiole slender, 6–22 cm long, 1.5–3.5 mm thick, cross section grooved above; longest petiole longer than lamina. Lamina dirty green, beneath paler, thin, broadly ovate, 6.5–20 × 4.5–15 cm, width:length ratio *c*. 1:1; base rounded or cordate, slightly unequal, margin serrate, apex acute; midrib and veins above obscure, beneath prominent, lateral veins 6–7 pairs, lowermost 2–3 pair(s) arising from lamina base. **Inflorescence** axillary, twice branched, flower(s) 4–13; indumentum of inflorescence: hairs glandular sprinkled with a few longer eglandular hairs throughout peduncle, bracts and pedicel. Peduncle green, slender, (4–)7–15(–30) cm long; bracts green, narrowly lanceolate, *c*. 2.2 × 0.6 mm, apex acute; pedicel 1.5–3 mm long. **Flower** indumentum: hairs glandular sprinkled with a few longer eglandular hairs throughout calyx and ovary. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 1.5 mm long, 2.3 mm wide, lobes deltoid, apex acute, *c*. 2.6 mm long, base 1.2 mm wide. Corolla white or pale mauve, corolla violet-blue, tube darker, lobes pale, stamen white, honey yellow at proximal half (the knee) to the base; tube tubular-campanulate, 3.7–5.1 mm long, 2.6–3.1 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flared, oblong; upper lobes *c*. 4 × 4 mm, lateral lobes *c*. 4.2 × 4.2 mm, median lobe *c*. 4.2 × 4.2 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filament white, geniculate, *c*. 8.6 mm long; anthers brown or deep violet, coherent only at the ventral tip, kidney-shaped, *c*. 1.9 × 1 mm; staminodes 3, 3 club-shaped. Nectary a bulge, at the dorsal part of ovary. Ovary narrowly conical, *c*. 3 mm long, 0.8 mm wide; ovule with a funicle connecting to placenta ; style white, arched towards corolla ceiling, *c*. 3 mm long; stigma white, capitate, extended beyond corolla tube, exposed. **Capsule** brown, greenish when young, corniculate (horn-like), 9–10 mm long, 2.8–3 mm thick; valves curved upward, splitting into a splash cup;

hairs glandular, short, erect, dense. **Seeds** narrowly ellipsoid, *c*. 0.73 × 0.23 mm, apices acute.

Distribution. Peninsular Malaysia; known from a few mountains in Perak with disjunct distributions in Selangor (Bkt. Hitam [Etam]) and Pahang (G. Tahan).

Habitat. In lower montane forest at 900–1800 m asl. On wet mossy granite rock faces or steep moist banks.

Conservation status. Least Concern [LC]. Although habitat protection of some localities is provided for in various legislations related to Totally Protected Areas, quality of habitat in other localities is degrading. It was previously common in Bkt. Larut (Perak, Peninsular Malaysia) but was not found there in recent searching trips.

Notes. A 'Group A' species.

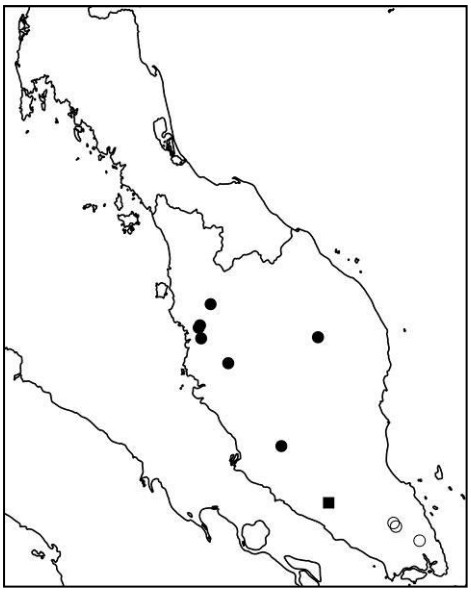


Fig. 4.3. Distribution of *Loxocarpus caeruleus* (●), *L. semitortus* (■) and *L. sericiflavus* (○).

4. *Loxocarpus caulescens* B.L.Burtt — **Fig. 4.4**

Notes Roy. Bot. Gard. Edinburgh 24: 44 (1962). **Synonym:** *Henckelia caulescens* (B.L.Burtt) A.Weber & B.L.Burtt, Beitr. Biol. Pflanzen. 70: 342 (1998). **Type:** Sumatra, Taram, E. of Pajakumbuh, 500–1000 m, sandstone region of River Tjampo, against steep

slope on rocks with bryophytes, 24 VIII 1957, *Meijer 6893* (holo L; iso E, K, L; photo of holo E).

Habit caulescent. Rootstock lacking; rootstock/stem indumentum: hairs silky, adpressed, dense; adventitious roots wiry. Leaf bases caducous. **Stem** distinctive, 8.5–28 cm long. **Leaves** alternate, well-spaced throughout; hairs silky, adpressed, on petiole, lamina above and beneath dense. Petiole slender, 3–4.2 cm long, 0.9 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina dark green, beneath paler, thin, ovate or elliptic, 5.8–7 × 2.5–3.4 cm, width:length ratio *c*. 1:2; base cuneate or rounded, equal, margin shallowly serrate, apex acuminate or caudate; midrib and veins above obscure, beneath conspicuous, lateral veins 5 pairs, lowermost 2 pair(s) arising from lamina base, lateral veins gently curving to margin (*c*. 40˚ to midrib). **Inflorescence** axillary, compact, once to twice branched, flower(s) 4–15; indumentum of inflorescence: hairs a mix of straight eglandular and glandular hairs, on peduncle and bracts, dense; glandular on the pedicel, dense. Peduncle slender, 5.5–9.2 cm long; bracts green, narrowly lanceolate, *c*. 3.8 × 0.4 mm, apex acuminate; pedicel 4 mm long. **Flower** indumentum: hairs glandular on the outer surface of calyx, corolla tube and ovary, dense. Calyx green, indistinctly 2-lipped; upper lip 3-lobed, lower lip 2-lobed; deeply dissected, lower lobes larger than upper lobes, tube *c*. 0.6 mm long, 0.8 mm wide, lobes deltoid, apex acute, *c*. 1.2 mm long, base 0.3 mm wide. Corolla purple, upper labella purple, lower 3 corolla lobes purple white, tube short, 2 mm long, 1.5 mm wide; upper lip with 2 upper lobes, lower lip with 3 lobes, lobes flared, oblong; upper lobes *c*. 2 × 1.5 mm. Fertile stamens 2; anthers at the mouth of corolla tube; filament curving upwards, *c*. 3 mm long; anther kidney-shaped, *c*. 1.25 × 1.75 mm. Ovary conical, *c*. 1.75 mm long; style *c*. 5 mm long; stigma punctiform.

Capsule brown, oblique conical, 8–10 mm long, 0.9 mm thick; valves curved downward, splitting into a trough; hairs glandular, shaggy, dense. **Seed** not known.

Distribution. Sumatra; known from N & W Sumatra and Riau.

Habitat. Primary forest of sandstone region at 500–1000 m asl.

Conservation status. Near Threatened [NT].

Notes. A 'Group A' species. It can be distinguished by its lateral veins gently curving to margin (c. 40˚ to midrib) and its compact inflorescence. Since no flowering material is available, descriptions on floral structure are adapted from the protologue. Field notes on type label record the upper labella as purple and the lower 3 lobes purple-white.

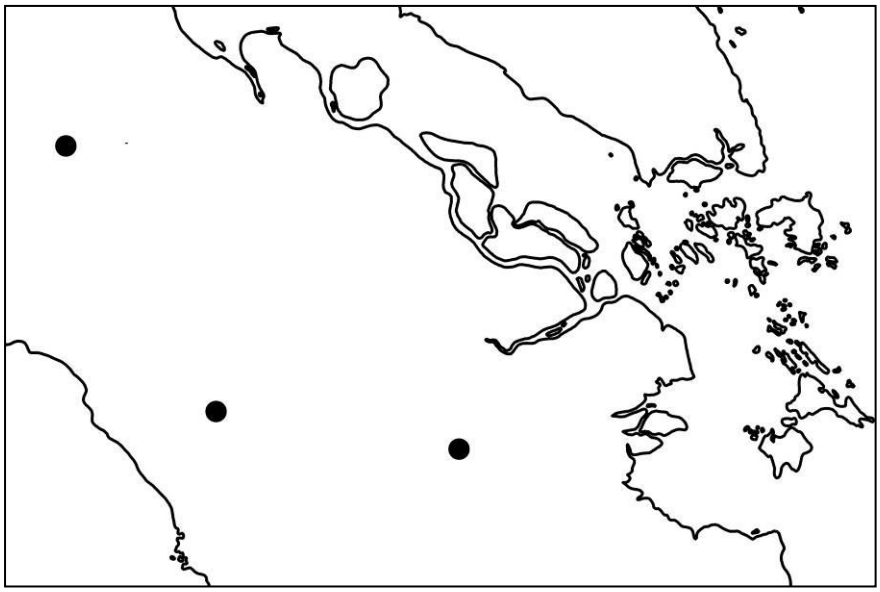


Fig. 4.4. Distribution of *Loxocarpus caulescens* (●).

5. *Loxocarpus conicapsularis* (C.B.Clarke) B.L.Burtt — **Fig. 4.2**

Notes Roy. Bot. Gard. Edinburgh 24: 45 (1962). **Basionym:** *Didymocarpus conicapsularis* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 100 (1883). **Synonym:** *Roettlera conicapsularis* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 476 (1891). *Henckelia conicapsularis* (C.B.Clarke) A.Weber & B.L.Burtt, Beitr. Biol. Pflanzen. 70: 342 (1998).

Type: Borneo, Karimata [Island], *Teijsmann 11215* (holo FI-BECC; iso BO; photo of holo E).

Habit rosette. Rootstock short, woody, 1–2 cm long, 1–3 mm thick; rootstock/stem indumentum: hairs short, adpressed, dense; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs silky, adpressed, on petiole and veins beneath dense; on lamina beneath sparse, on lamina above scarce or only a few scattered near margin. Petiole slender, (1–)1.5–2.3 cm long, 0.4–0.5 mm thick, cross section terete; longest petiole about equal in length to the lamina. Lamina green, beneath paler, thin, narrowly elliptic or elliptic or oblong, 1.8–3.2 × 0.4–0.7 cm, width:length ratio *c*. 1:4; base cuneate or slightly rounded, equal, margin crenulate, apex blunt or rounded; midrib and veins above obscure, beneath distinct, lateral veins 3–5 pairs, lowermost 0(–1) pair(s) arising from lamina base. **Inflorescence** axillary, a reduced cyme or a simple cyme, flower(s) 1; indumentum of inflorescence: hairs eglandular, adpressed on peduncle, bracts and pedicel, dense. Peduncle green, slender, 4–5.5 cm long; bracts green, linear, *c*. 1.5 × 0.3 mm, apex acuminate; pedicel (0.6–)1–1.5 mm long. **Flower** tilted, indumentum: hairs eglandular, adpressed on calyx, erect on ovary and pistil, dense; on corolla outer surface sparse, on inner surface scarce. Calyx green, 5-lobed, lobes somewhat equal, tube *c*. 0.5 mm long, 0.9 mm wide, lobes linear-lanceolate, apex acuminate, 2–3 mm long, base 0.5 mm wide. Corolla violet, pale violet (bluish-purple), centre white, tube very short, 2–3(–4) mm long, 3–5(–7) mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a mid lobe; upper lobes smaller, lateral and median lobes larger, lobes flat-faced (saintpaulioid), oblong; upper lobes *c*. 5 × 3–4 mm, lateral lobes *c*. 5–7 × 3–5 mm, median lobe *c*. 6 × 3 mm. Fertile stamens 2, pair-wise twisted; anthers projected beyond corolla tube, exposed; filament yellow, thicken at distal half, *c*. 3 mm long; kidney-shaped, *c*. 2 × 1

mm; staminode 2, deltoid. Nectary absent. Ovary conical, slightly oblique, *c*. 1.5 mm long, 0.6 mm wide; straight, *c*. 3 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 6–8 mm long, 1–2 mm thick, sub-persistent style 4 mm long; valves slightly curved upward, splitting into a trough; hairs eglandular, short, erect, dense. **Seed** not known.

Distribution. Borneo; NE Sarawak and Karimata Island, Kalimantan.

Habitat. Lowland forest at 30–100 m asl. On shale boulders in streams or on steep river banks of clay soil.

Conservation status. Near Threatened [NT].

Notes. A 'Group B' species. On a folder containing Mulu specimens in K, Burtt wrote: "this is distinct from the type (Teijsmann in FI-BECC) and will be described shortly". The specimens from Mulu NP with solitary-flowered reduced cymes do not match with Teijsmann's type that has a simple cyme. Since the branching of inflorescence varies considerably within one species, *viz. Loxocarpus incanus*, the Mulu populations are here treated as *Loxocarpus conicapsularis* until a specimen from Karimata with a corolla is available for examination.

6. *Loxocarpus coodei* (B.L.Burtt) T.L.Yao, *comb. nov*. — **Fig. 4.5**

Basionym: *Henckelia coodei* B.L.Burtt, in Kirkup *et al*.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996). **Type:** Brunei, Temburong, Temburong River at Wong Nguan rapids, 120 m, mixed lowland forest, shale[s], forest floor, terrestrial herb, 5 III 1990, *Coode 6617* (holo K; iso BRUN).

Habit rosette. Rootstock short, woody, 0.5 cm long, 2 mm thick; rootstock/stem indumentum: hairs buff, spreading, dense; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs buff, spreading, on petiole dense, adpressed; on lamina above scattered, along margin a fringe; shorter on lamina beneath, dense on veins, less dense on lamina. Petiole slender, 1 cm long, 1.2 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina dark green, beneath paler, thin or moderately thick, ovate or elliptic, 3.3–3.5 × 1.3–1.5 cm, width:length ratio *c*. 1:2; base cuneate or rounded, equal or slightly unequal, margin serrulate, apex acute or blunt; midrib and veins above obscure, beneath inconspicuous, lateral veins 3–4 pairs. **Inflorescence** axillary, a reduced cyme, flower 1; indumentum of inflorescence: hairs eglandular, long, shaggy on peduncle and bracts. Peduncle slender, 6 cm long; bracts green, linear, *c*. 3 × 0.2 mm, apex acuminate; pedicel 4 mm long. **Flower** indumentum: hairs eglandular, long, shaggy on calyx outer surface, dense, on corolla outer surface less dense, short on ovary, dense. Calyx green, 5-lobed, lobes somewhat equal, divided to the base, lobes linear, apex thickened, blunt, *c*. 5 mm long, base 0.25 mm wide. Corolla violet, tube very short; lobes flat-faced (saintpaulioid), oblong; upper lobes *c*. 4 × 3 mm, lateral lobes *c*. 5 × 2.5 mm, median lobe *c*. 4 × 3 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; thicken at distal half; anther yellow, kidney-shaped; staminode 2, deltoid. Nectary absent. Ovary conical or slightly oblique; straight; stigma peltate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 8.5 mm long, 2.3 mm thick; valves straight, splitting into a wide trough; hairs buff, eglandular, short, shaggy, dense. **Seed** not known.

Distribution. Borneo; NE Sarawak (Mulu NP) and E Brunei (Temburong).

Habitat. Mixed dipterocarp lowland forest at 10–350 m asl. On rocks along a ridge or on the forest floor.

Conservation status. Near Threatened [NT].

Notes. A 'Group B' species. Morphologically very close to *Loxocarpus verbeniflos* but distinguished by its longer calyx lobes.

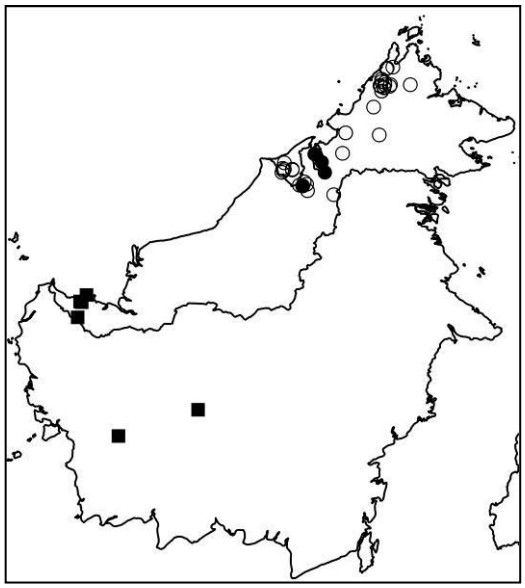


Fig. 4.5. Distribution of *Loxocarpus coodei* (●), *L. rufescens* (■) and *L. violoides* (○).

7. *Loxocarpus holttumii* M.R.Hend. — **Fig. 4.1, Plate 4a–c**

Gard. Bull. Straits Settlem. 4: 412 (1929), Malay. Wild Fls., Dicots. 354 (1959). **Synonym:** *Henckelia ericii* A.Weber, Beitr. Biol. Pflanzen. 70: 344 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 14 (2009). **Type:** Peninsular Malaysia, Johor, G. Panti, 14 II 1926, *Holttum 18097* (holo SING).

Habit rosette. Rootstock short, woody, 2.5–3 cm long, 5–7.5 mm thick; rootstock/stem indumentum: hairs brown, shiny, shaggy, dense; adventitious roots long, wiry. Leaf bases persistent. **Stem** lacking or distinctive, 2 cm long. **Leaves** alternate, crowded at the top; hairs ferruginous, rough, shiny, shaggy, on petiole dense; on lamina above and veins beneath dense; on lamina beneath sparse. Petiole relatively thick, 2.5–9 cm long, 2.5–3.5 mm thick, cross section slightly grooved above or terete; longest petiole longer than lamina.

Lamina dark green, beneath paler, thick, sub-orbicular or broadly ovate, 2–5 × 1.9–4 cm, width:length ratio *c*. 1:1; base truncate or cordate, equal, margin shallowly crenate, apex blunt or rounded; midrib and veins above sunken, beneath prominent, lateral veins 5–6 pairs, lowermost 2 pair(s) arising from lamina base. **Inflorescence** axillary, a simple cyme or once to twice branched, flower(s) 2–15; indumentum of inflorescence: hairs a mix of straight eglandular and glandular hairs on the peduncle, bracts and pedicel, dense. Peduncle purplish, slender, 7–20 cm long; bracts green, narrowly lanceolate, *c*. 1.25 × 0.45 mm, apex rounded; pedicel 2–3 mm long. **Flower** indumentum: hairs glandular on the outer surface of calyx and ovary, dense; on corolla outer surface sparse. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 0.6 mm long, 1.3 mm wide, lobes deltoid, apex acute, *c*. 1.7 mm long, base 0.7 mm wide. Corolla mauve, plain, tube campanulate, 3.6–3.8 mm long, 4.5–4.8 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller; lateral and median lobes larger, lateral lobes largest, lobes flared, oblong; upper lobes *c*. 1.7 × 3.3 mm, lateral lobes *c*. 2.7 × 3.5 mm, median lobe *c*. 3 × 4.2 mm. Fertile stamens 2; anthers included within corolla tube; filaments white, straight, *c*. 2.2 mm long; anther cream, coherent face to face, kidney-shaped, *c*. 1.5 × 0.85 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary a thin rim, encircling the ovary base. Ovary slightly oblique, *c*. 1.15 mm long, 0.7 mm wide; ovule with a funicle connecting to placenta ; style white, arched towards corolla ceiling, *c*. 3 mm long; stigma white, capitate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 7–8 mm long, 1.5–2 mm thick; valves straight, splitting into a trough; hairs glandular, short, erect, dense. **Seeds** broadly ellipsoid, *c*. 0.48 × 0.23 mm, apices acute.

Plate 4

Loxocarpus holttumii: **a.** habitat, **b.** habit, **c.** flower and capsule, the *Trigona* bee with filled pollen basket is probably a pollinator.

Distribution. Peninsular Malaysia; Johor, known only from Panti FR (G. Panti and Kota Tinggi Waterfall).

Habitat. Locally abundant on sandstone outcrops and cliff faces at 365–500 m asl.

Conservation status. Endangered [EN B2ab(iii)]. Habitat degradation is continuing.

Notes. A 'Group A' species.

8. *Loxocarpus incanus* R.Br. — **Fig. 4.6**

Notes. A 'Group A' species. The most widespread species in Peninsular Malaysia.

Key to varieties:

Lamina ovate to broadly ovate, to 2 times longer than wide; base truncate to rounded or cordate, rarely cuneate _____ **var. incanus**

Lamina narrowly elliptic or oblong, 3 times longer than wide; base cuneate _____

_____ **var. sekayuensis**

8a. var. *incanus* — Plate 5a–b

Cyrtandreae: 120 (1839); Ridley, J. Straits Branch Roy. Asiat. Soc. 44: 62 (1905), J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 769 (1908), J. Linn. Soc., Bot. 38: 319 (1908), Fl. Malay. Penin. 2: 527 (1923); Henderson, Malay. Wild Fls., Dicots.: 353, *fig*. 329A–C (1959); Kiew, Malay. Nat. J. 41: 223 (1987). **Homotypic synonyms:** *Loxonia*? *alata*, Wallich, Numer. List 809, *nom. nud*. *Loxocarpus alatus* A.DC. in DC., Prodr. 9: 277 (1845), *nom. illeg*. for *Loxocarpus incanus*. *Loxocarpus alata* R.Br. in Bennett (1840), wrongly in Index Kewensis 2: 221 (1895). *Didymocarpus incanus* (R.Br.) C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5: 98 (1883), Fl. Brit. India 4: 352 (1884); Ridley, J. Linn. Soc., Bot. 32: 512 (1896). *Roettlera alata* (A.DC.) O.Kuntze, Rev. Gen. Pl., 2: 476 (1891), *non Roettlera incana* Vahl. *Henckelia browniana* A.Weber, Beitr. Biol. Pflanzen. 70: 341 (1998); Banka

& Kiew, Edinburgh J. Bot. 66: 12 (2009). **Type:** Peninsular Malaysia, Penang, *Wallich 809* (lecto BM, designated by Banka & Kiew, 2009; isolecto K).

Heterotypic synonyms: *Loxocarpus minima* Ridl., J. Straits Branch Roy. Asiat. Soc. 86: 302 (1922), Fl. Malay. Penin. 2: 527 (1923). *Henckelia minima* (Ridl.) A.Weber, Beitr. Biol. Pflanzen. 70: 350 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 15 (2009), ***syn. nov.*** **Type:** Peninsular Malaysia, Negeri Sembilan, Bkt. Tangga, 22 XII 1920, *Ridley s.n.* (holo K [barcode K000450475]).

Habit rosette. Rootstock short, woody or lacking, 0–1.5 cm long, 0–6 mm thick; rootstock/stem indumentum: hairs white, adpressed, dense; adventitious roots wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs whitish, silky, spreading on petiole, dense; adpressed on lamina above, dense; on lamina and veins beneath less dense. Petiole relatively thick, (0.9–)2–9(–11) cm long, 0.5–2.6 mm thick, cross section slightly grooved above or terete; longest petiole shorter than lamina, or longest petiole about equal in length to the lamina. Lamina dark green, beneath paler, moderately thick or thick, ovate or broadly ovate or elliptic or sometimes slightly asymmetric, 2.2–6.5–12 × 1.7–5–11 cm, width:length ratio *c*. 1:1; base cuneate or truncate or rounded or cordate, slightly unequal or unequal, margin serrulate, apex acute or blunt; midrib and veins above sunken or inconspicuous, beneath conspicuous, lateral veins (3–)6–7 pairs, lowermost 1–2(–3) pair(s) arising from lamina base. **Inflorescence** axillary, a reduced cyme or a simple cyme or once to 4 times branched, flower(s) (1–)4–52; indumentum of inflorescence: a mix of eglandular and shorter glandular hairs on peduncle; eglandular hairs only on bracts; short glandular hairs sprinkled with a few long eglandular hairs on pedicel. Peduncle green, slender or relatively stout, (2.3–)10–16 cm long; bracts green, lanceolate, *c.* 1.8–3.6 × 0.3–0.5 mm, apex acute; pedicel 1.5–3 mm long. **Flower**

indumentum: a mix of eglandular and shorter glandular hairs; mainly of eglandular hairs on calyx, corolla, ovary (base with a few short glandular hairs) and pistil. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube 1.3–1.8 mm long, 2–2.5 mm wide, lobes deltoid, apex acute, 3–4.8 mm long, base 1.1–1.3 mm wide. Corolla pale mauve or blue, plain, tube tubular-campanulate, 3.4–5 mm long, 3.4–3.6 mm wide; upper lip with 2 lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, corolla mouth shallowly to deeply cleft in between the upper lobes, lobes flared, oblong; upper lobes *c*. 1–2.8 × 2.5–2.8 mm, lateral lobes *c*. 2.2–3.5 × 2.6–3.3 mm, median lobe *c*. 2.4–3.5 × 3–3.4 mm. Fertile stamens 2; anthers included within corolla tube; filaments white, straight, *c*. 2.8–3 mm long; anther cream, coherent face to face, kidney-shaped, 1.2–1.7 × 0.5–0.8 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary absent. Ovary conical, slightly oblique, 1.4–1.7 mm long, 1.1–1.3 mm wide; ovule with a funicle connecting to placenta ; style white, 2.3–3.5 mm long, arched towards corolla ceiling and fitting into a cleft; stigma white, capitate, extended beyond corolla tube, exposed. **Capsule** brown, greenish when young, ovoid, humped above, 4–6.5 mm long, 2–3 mm thick; valves straight, splitting into a splash cup; hairs glandular, short, dense. **Seeds** ellipsoid, 0.5–0.55 × 0.18–0.22 mm, apices acute.

Distribution. Peninsular Thailand and throughout Peninsular Malaysia.

Habitat. Evergreen forest in Peninsular Thailand, in Peninsular Malaysia from lowland to hill forest at 80–850 m asl. On granite boulders, often in streams or in forest.

Conservation status. Least concern [LC].

Note. The specimens recorded from G. Tahan (Ridley, 1908) actually belong to *Loxocarpus caeruleus* (Kiew, 1987).

Plate 5

Ong, P.T.

Loxocarpus incanus var. *incanus*: **a.** habitat, **b.** flower front view; *L. incanus* var. *sekayuensis*: **c.** habit, and fruit in inset.

8b. var. *sekayuensis* (Banka & Kiew) T.L.Yao, *comb*. & *stat*. *nov*. **— Plate 5c**

Basionym: *Henckelia sekayuensis* Banka & Kiew, Edinburgh J. Bot. 66: 16 (2009). **Type:** Peninsular Malaysia, Terengganu, Sekayu Recreational Forest, 29 VIII 1986, *Anthonysamy SA 638* (holo KEP).

Rootstock lacking, 0–0.8 cm long, 0–5 mm thick. **Leaves**: Petiole slender, 0.8–3 cm long, 7.5–14 mm thick, cross section slightly grooved above; longest petiole shorter than lamina. Lamina moderately thick, narrowly elliptic or oblong, 2.5–6 × 0.8–2.3 cm, width:length ratio *c*. 1:3; base cuneate, equal, margin serrulate; midrib and veins above obscure, beneath conspicuous, lateral veins 3–4 pairs, lowermost 1(–2) pair(s) arising from lamina base. **Inflorescence** a reduced cyme or a simple cyme or once branched, flower(s) 1–7; indumentum of inflorescence: hairs eglandular on bracts, dense. Peduncle green, slender, 2.6–8 cm long; bracts lanceolate, *c*. 1.1 × 0.35 mm, apex rounded; pedicel 2–2.6 mm long. **Flower** indumentum: hairs short, eglandular on calyx. Calyx tube *c*. 0.9 mm long, 1.8 mm wide, lobes deltoid, *c*. 2.3 long, base 1.2 mm wide. Corolla pale mauve, tube tubular-campanulate, 3.8–5.4 mm long, 3.1–3.2 mm wide; upper lobes *c*. 2.7 × 2.8 mm, lateral lobes *c*. 4 × 3.5 mm, median lobe *c*. 3 × 3.2 mm. Filaments *c*. 2.8 mm long; anthers *c*. 1.2 × 0.6 mm. Nectary absent. Ovary oblique, *c*. 1.6 mm long, 1.4 mm wide; ovule with a funicle connecting to placenta ; style white, *c*. 2.6 mm long, arched towards corolla ceiling and fitting into a cleft. **Capsule** brown, ovoid, 4–6 mm long, 2.5–3 mm thick; valves slightly curved upward. **Seeds** *c*. 0.22 × 0.15 mm.

Distribution. Peninsular Malaysia, known from S Kelantan and Terengganu.

Habitat. Lowland forest at 15–350 m asl. On granite rocks beside fast flowing streams.

Conservation status. Endangered [EN B1ab(iii)].

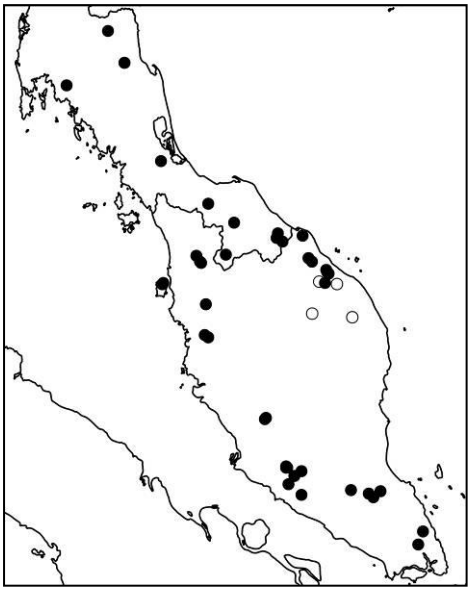


Fig. 4.6. Distribution of *Loxocarpus incanus* var. *incanus* (●) and var. *sekayuensis* (○).

9. *Loxocarpus meijeri* B.L.Burtt — **Fig. 4.7**

Notes Roy. Bot. Gard. Edinburgh 24: 45 (1962). **Synonym:** *Henckelia meijeri* (B.L.Burtt) A.Weber & B.L.Burtt, Beitr. Biol. Pflanzen. 70: 350 (1998). **Type:** Sumatra, Taram, east of Pajakumbuh, sandstone region of River Tjambo, 500-1000 m, 28 VIII 1957, *Meijer 7083* (holo L; photo of holo E)

Habit caulescent. Rootstock lacking; adventitious roots wiry. Leaf bases caducous. **Stem** distinctive, 20 cm long. **Leaves** alternate or sub-opposite below, well-spaced throughout; hairs silvery, on lamina above and beneath dense. Petiole slender, 4 cm long; longest petiole shorter than lamina, elliptic, (5–)8–11 × 2–3 cm, width:length ratio *c*. 1:3; base attenuate, equal, margin crenulate, apex acute; midrib and veins above obscure, beneath distinct, lateral veins 7 pairs, straight and ascending to margin (*c*. 20˚ to midrib)**.** **Inflorescence** axillary, lax, flower(s) 12; indumentum of inflorescence: hairs glandular-pilose on peduncle; silky sericeous on bracts. Peduncle slender, 10 cm long; bracts linear, *c*. 8 × 1 mm, apex acute. **Flower** indumentum: pubescence on corolla. Calyx 5-lobed, lobes

somewhat equal, deeply disected to the base, *c*. 3 mm long. Corolla violet or blue, tube funnel-shape, *c*. 2 mm long; 5-lobed, lobes flared, oblong; upper lobes *c*. 2 × 1 mm. Fertile stamens 2; anthers included within corolla tube; filament twisted; anthers coherent only at the ventral tip, *c*. 0.75 × 1.5 mm; staminodes 2, threadlike. Ovary conical, *c*. 1.5 mm long; style *c*. 3 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown. **Seed** not known.

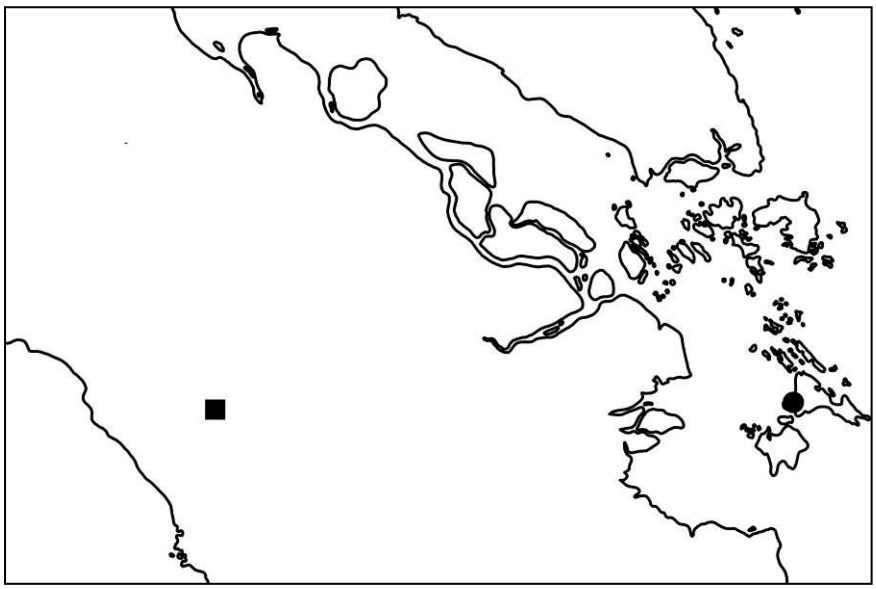


Fig. 4.7. *Loxocarpus meijeri* (■) and *L. sericeus* (●).

Distribution. Sumatra; known only from W Sumatra, Payakumbuh.

Habitat. Primary forest of sandstone region at 500–1000 m asl. Primary forest in a river valley.

Conservation status. Near Threatened [NT].

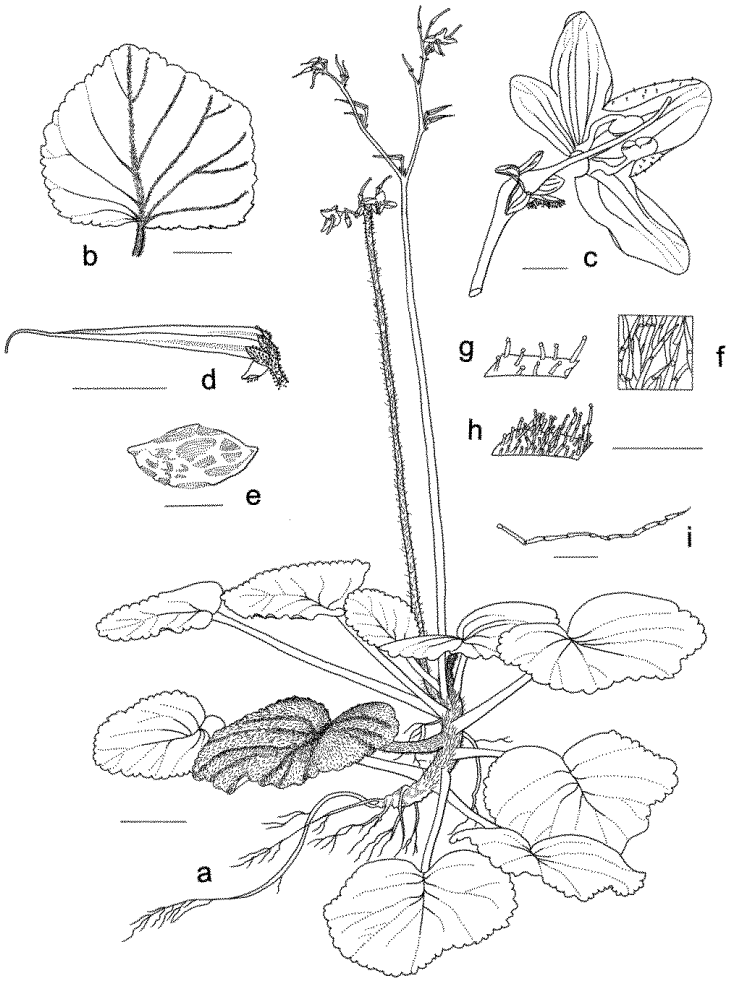
Notes. A 'Group A' species. It can be identified by its straight lateral veins that ascend to the margin (*c*. 20˚ to midrib); and its lax inflorescence. I was unable to locate the type or any specimen of this species. Parts of the description are adapted from the protologue. The fruit is unknown.

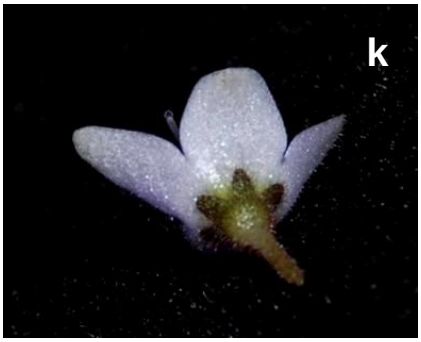
10. *Loxocarpus pauzii* T.L.Yao — **Fig. 4.1, Plate 6a–k**

in Yao, Kiew & Haron, Blumea (*in press*). **Type:** Peninsular Malaysia, Kelantan, G. Stong SP, Stong Waterfall, 26 VII 2008, *Yao et al. FRI 65371* (holo KEP; iso E).

Habit rosette. Rootstock short, woody, 1.5–3 cm long, 2.5 mm thick; rootstock/stem indumentum: hairs white, spreading, dense; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking or distinctive, 1 cm long. **Leaves** alternate, crowded at the top; hairs silky, adpressed, on petiole and lamina above dense, veins beneath less dense, lamina beneath scarce. Petiole slender, 5–11.5 cm long, 0.5 mm thick, cross section slightly grooved above; longest petiole longer than lamina. Lamina dark green, beneath paler, thin or moderately thick, sub-orbicular or broadly ovate, 2.3–3.3 × 2.5–3.5 cm, width:length ratio *c*. 1:1; base truncate or cordate, equal, margin serrulate, apex rounded; midrib and veins above obscure, beneath distinct, lateral veins 5 pairs, lowermost 2–3 pair(s) arising from lamina base. **Inflorescence** axillary, thrice to 4 times branched, flower(s) 11–42; indumentum of inflorescence: hairs a mix of straight eglandular and glandular, on peduncle dense; purple glandular on pedicel, dense. Peduncle purplish, slender, 14–18 cm long; bracts green, narrowly oblanceolate, *c*. 1.4 × 0.3 mm, apex rounded; pedicel 5–7 mm long. **Flower** indumentum: hairs purple glandular on outer surface of calyx, corolla and ovary, dense. Calyx green, 5-lobed, lobes somewhat equal, divided to the base, tube *c*. 0.75 mm long, 1.75 mm wide, lobes deltoid, apex acute, *c*. 2 mm long, base 1 mm wide. Corolla violet, plain, tube short with deeply dissected lobes, 1.8–1.9 mm long, 4.1–4.3 mm wide; 4-lobed, 1 upper lobe recurved, scarcely notched at the apex; 2 lateral lobes flared, median lobe laterally incurved, lobes recurved, deltoid; upper lobe *c*. 3.2 × 5 mm, lateral lobes *c*. 5.5 × 3.6 mm, median lobe *c*. 7 × 5 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filament white, curving upwards, *c*. 2 mm long; anther yellow, coherent only

Plate 6





Loxocarpus pauzii: **a.** habit, **b.** leaf lower surface, **c.** flower, **d.** capsule, **e.** seed, **f.** indumentum of leaf upper surface, **g.** indumentum of corolla outer surface, **h.** indumentum of ovary, **i.** trichome of petiole (all from *Yao* et al. *FRI 65371*) — Scale bars: a = 2 cm, b = 1 cm, c = 1 mm, d = 4 mm, e = 0.2 mm, f–i = 0.5, **j.** flower side-front view, **k.** flower back view.

at the ventral tip, kidney-shaped, *c*. 1.3 × 0.5 mm; staminode 0. Nectary a thin rim, partly encircling the ovary base. Ovary conical, *c*. 1.5 mm long, 0.7 mm wide; ovule not funiculus; style lilac, straight, *c*. 6 mm long; stigma purple, punctiform, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 7.5–8 mm long, 0.8–0.9 mm thick, sub-persistent style 2.5 mm long; valves straight, splitting into a wide trough; hairs glandular, short, erect, dense. **Seeds** ellipsoid, *c*. 0.4 × 0.2 mm, apices acute.

Distribution. Peninsular Malaysia; Kelantan, known only from Stong SP.

Habitat. Lowland to hill forest. On shaded to partially shaded wet granite cliff faces or on boulders *c*. 500 m asl or on soil with a thin humus layer under bamboo clumps at *c*. 315 m asl.

Conservation status. Near threatened [NT].

Notes. A 'Group A' species, remarkable for its four-lobed corollas.

11. *Loxocarpus repens* B.L.Burtt — **Fig. 4.8, Plate 7a–e**

Bot. J. Linn. Soc. 85: 24 (1982). **Homotypic synonym:** *Henckelia procumbens* B.L.Burtt, Beitr. Biol. Pflanzen. 70: 353 (1998). **Type:** Borneo, Sarawak, G. Mulu NP, G. Mulu, *c*. 1350 m, in upper montane forest, 14 VI 1962, *Burtt & Woods B 2097* (holo E; iso KEP, SAR, WU).

Heterotypic synonyms: *Henckelia gardneri* B.L.Burtt in Kirkup *et al*.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996), ***syn. nov.*** **Type:** Borneo, Sabah, Trus Madi, Kaintano ridge, 3500 ft., growing on well-drained stream-bank, very local; *Gardner 37*, cult. in Hort. Bot. Reg. Edinburgh sub 77 2460, fl. 8 VIII 1978 (holo E).

Habit rosette or creeping. Rootstock short, woody or lacking, (3–)5–12(–26) cm long, 3–6 mm thick; rootstock/stem indumentum: hairs a mix of buff tinged yellowish, long, shaggy eglandular and shorter glandular hairs; adventitious roots wiry, or along creeping stem, at intervals, wiry. Leaf bases caducous. **Stem** distinctive, 1.5–52 cm long. **Leaves** alternate, well-spaced throughout or crowded at the top or well-spaced below, crowded at the top; hairs silky, long, eglandular (sometimes mixed with shorter glandular hairs), shaggy on petiole and lamina beneath, dense; on lamina above erect. Petiole slender, 1–5.5 cm long, 0.7–2.5 mm thick, cross section slightly grooved above; longest petiole about equal in length to the lamina. Lamina dark green, sometimes with a pale green or silvery patch along the midrib, beneath paler, moderately thick or thick, ovate or oblong, 2.5–5.5 × 1.5–3 cm, width:length ratio *c*. 1:2; base rounded or broadly rounded or shallowly cordate, equal, margin serrulate or finely crenulate, apex blunt; midrib and veins above obscure, beneath inconspicuous or conspicuous, lateral veins 4–6 pairs, lowermost 1–2 pair(s) arising from lamina base. **Inflorescence** axillary, a compact cyme, flower(s) (1–)2–9; indumentum of inflorescence: hairs long glandular, sometimes scattered with eglandular hairs, shaggy on peduncle, bracts and pedicel, dense. Peduncle slender, 3–8(–12) cm long; bracts green, lanceolate or deltoid, *c*. 1.2–1.8 × 0.4–0.75 mm, apex acute or blunt; pedicel 2–5 mm long. **Flower** tilted, indumentum: hairs long glandular (sometimes scattered with eglandular hairs), shaggy on calyx outer surface, dense; a mix of short glandular and a few longer eglandular hairs, erect on corolla outer surface. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes slightly larger than upper lobes, sometimes lobes somewhat equal, tube *c*. 0.8 mm long, 1.3–2.5 mm wide, lobes deltoid, apex blunt or acute, 1.6–2.2 mm long, base 0.8–1.3 mm wide. Corolla violet or lilac or blue, tube very short, 1.1–1.5 mm long, 2–4.6 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a

median lobe; upper lobes smaller, lateral and median lobes larger, corolla flat-faced (saintpaulioid), oblong; upper lobes *c*. 1.2–7 × 1.2–8.6 mm, lateral lobes *c*. 1.5–9 × 1.8–6 mm, median lobe *c*. 2.2–5.4 × 1.5–4.5 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filaments white or yellow, straight, thickened at distal half, 0.9–3.4 mm long; anther white or cream, coherent only at the ventral tip, kidney-shaped, 1.2–2.1 × 0.6–1.1 mm; staminodes 2, threadlike. Nectary absent. Ovary conical or ovoid, oblique, 0.8–2.1 mm long, 0.8–1.9 mm wide; ovule with a funicle connecting to placenta ; style strongly curved upwards and straight, 3–8.5 mm long; stigma punctiform or peltate, extended beyond corolla tube, exposed. **Capsule** brown, purplish when young, ovoid, 6–8 mm long, 1.6–2.5 mm thick, sub-persistent style 3.5 mm long; valves slightly curved upward, splitting into a splash cup; hairs glandular, short, erect, dense. **Seeds** narrowly ellipsoid or ellipsoid, *c*. 0.52–0.65 × 0.19–0.26 mm, apices acute.

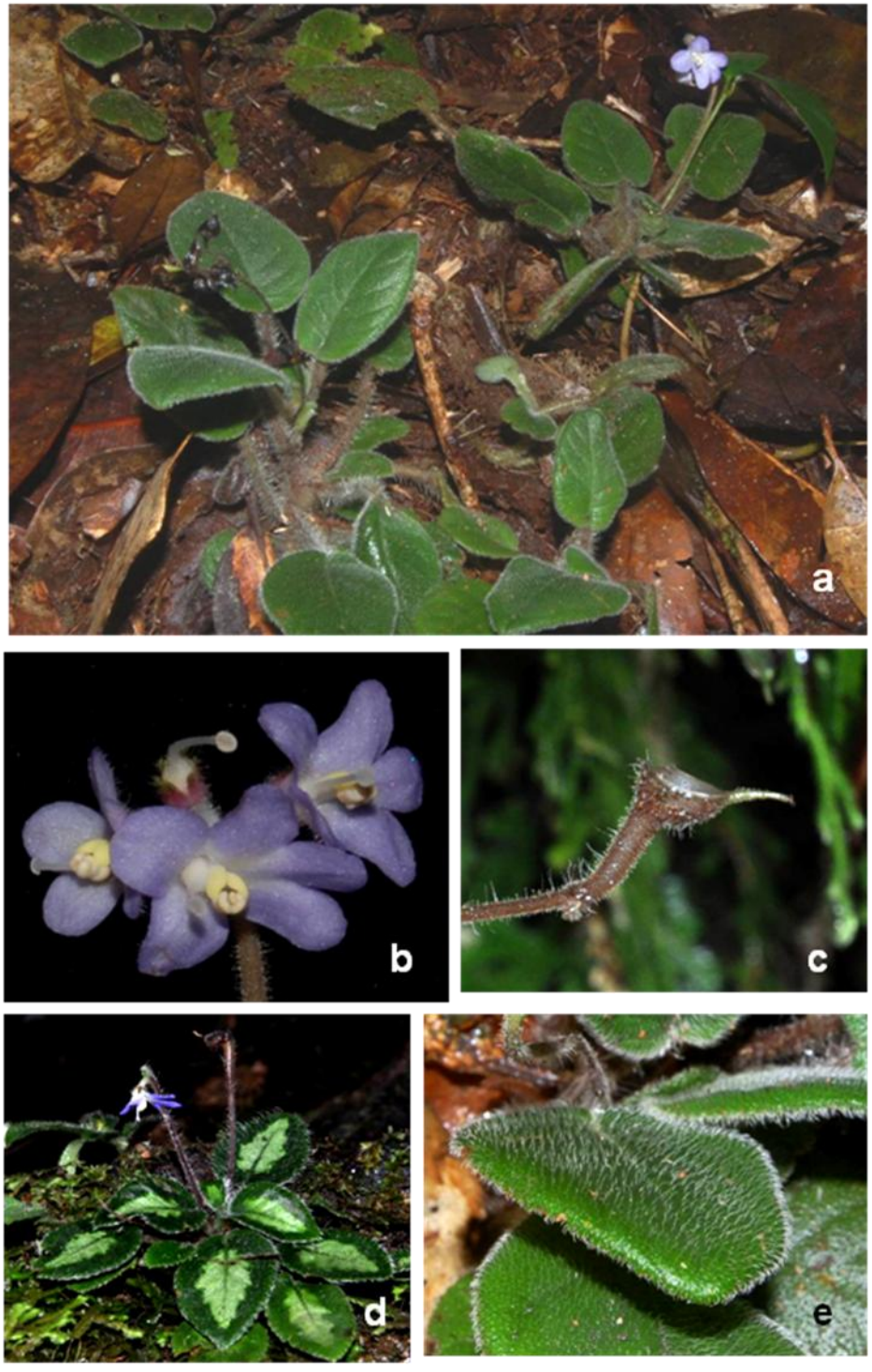
Distribution. Borneo; E Sarawak, E Brunei, Sabah and E Kalimantan.

Habitat. Lowland to lower montane forest at 90–1900 m asl. On mossy thin substrate over rock faces and tree bases along ridges or steep slopes.

Conservation status. Least Concern [LC].

Notes. A ‘Group B’ species. It is distinguished from other similar species (especially *Loxocarpus* sp. B, *L. verbeniflos* and *L. coodei* when not in flower) by its erect hairs on lamina surfaces and spreading hairs on the petiole.

Plate 7



Loxocarpus repens: **a.** habit, **b.** flowers, **c.** dehisced capsule, **d.** variegated leaves, **e.** erect hairs on lamina surface.

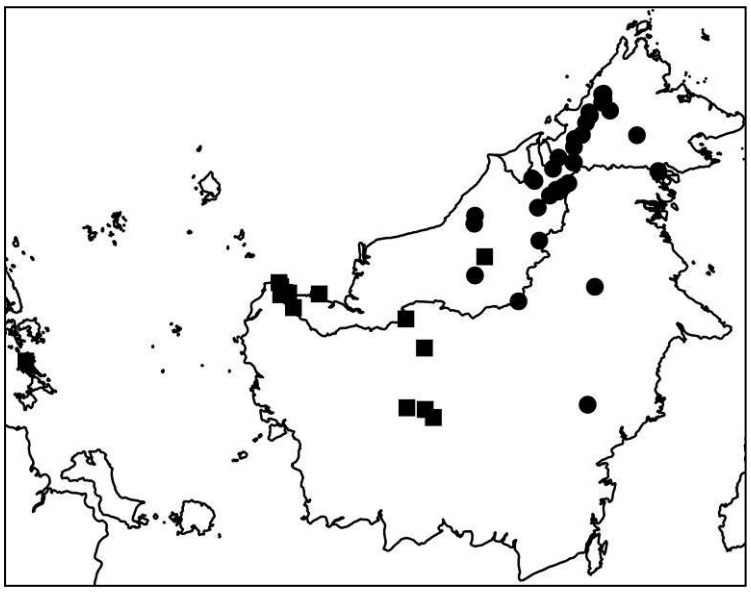


Fig. 4.8. Distribution of *Loxocarpus repens* (●) and *L. stapfii* (■).

12. *Loxocarpus rufescens* (C.B.Clarke) B.L.Burtt — **Fig. 4.5, Plate 8a–e**

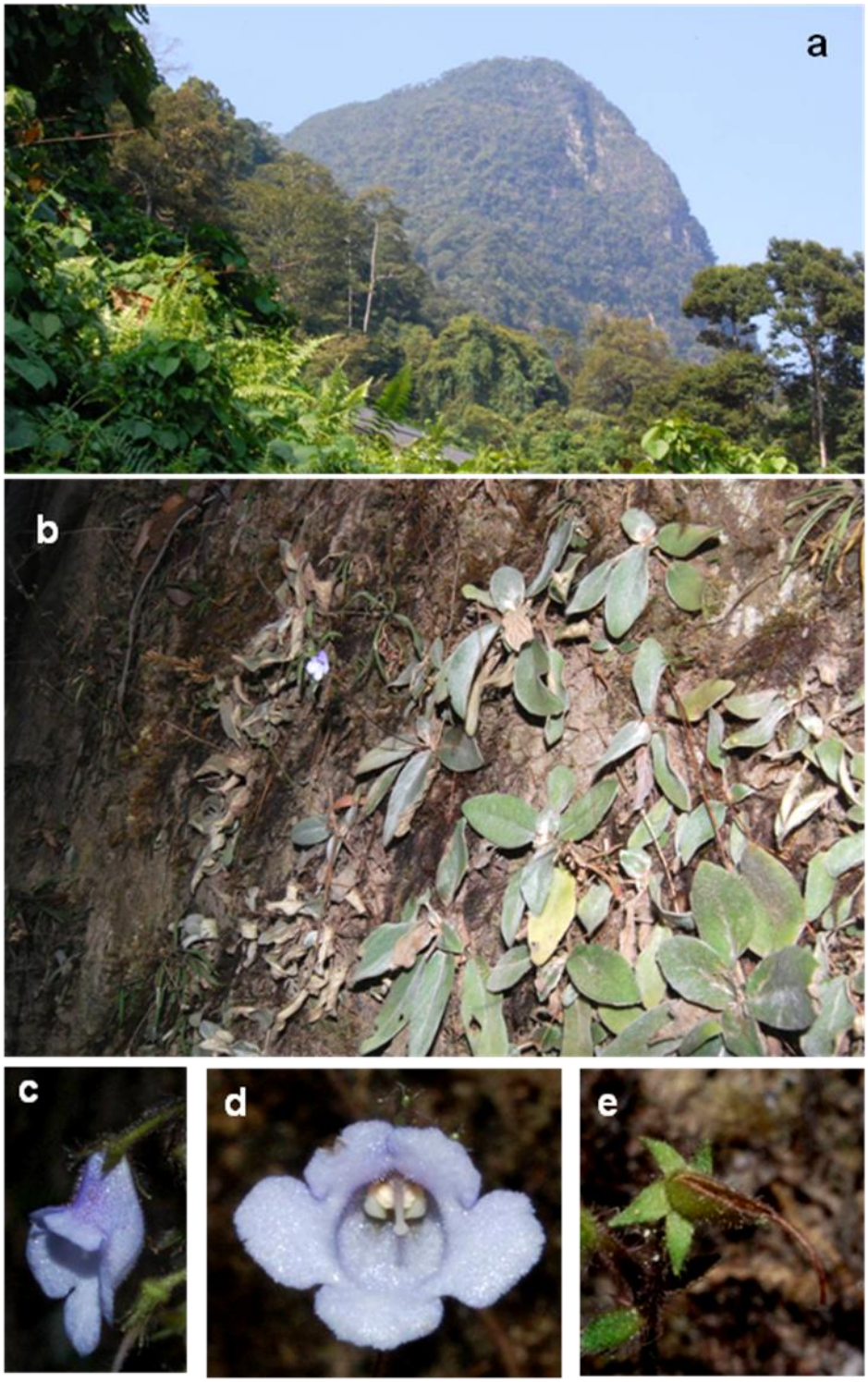
Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958), Notes Roy. Bot. Gard. Edinburgh 24: 46 (1962). **Basionym:** *Didymocarpus rufescens* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 99 (1883). **Homotypic synonym:** *Roettlera rufescens* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 477 (1891). *Henckelia rufescens* (C.B.Clarke) B.L.Burtt, Beitr. Biol. Pflanzen. 70: 355 (1998). **Type:** Borneo, altitude 1000 feet, 1853, *Lobb s.n.* (lecto K [barcode K000450486], designated here).

Heterotypic synonyms: *Didymocarpus johannis-winkleri* Kraenzl., Mitt. Inst. Allg. Bot. Hamburg 7: 89 (1927). **Type:** W Borneo, auf dem Bkt. Mehipit um 900 m, 19 XII 1924, *Winkler 1150* (holo HBG).

Habit rosette. Rootstock short, or long woody, 1–8(–10.5) cm long, 4–5 mm thick; habit in correlation with habitat: rootstock sometimes long even growing on rockface; rootstock/stem indumentum: hairs buff, shaggy, dense; adventitious roots only at the base of stem. Leaf bases persistent. **Stem** lacking or distinctive, 2–5 cm long. **Leaves** alternate, crowded at the top; hairs whitish, dull, wavy, shaggy, on petiole and young leaves lamina above dense, shedding off when mature, leaving shorter adpressed hairs; on lamina beneath

hairs sparse, sometimes glabrous, on veins beneath dense; young leaves covered with woolly hairs, sometimes persistent on the midrib of matures leaves. Petiole relatively thick, 0.7–1.8(–3.5) cm long, 0.5–1.5 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina dirty green, beneath paler, moderately thick, ovate or elliptic or oblong, 2–4.2(–7) × 0.9–1.9(–3.5) cm, width:length ratio *c*. 1:2; base cuneate or slightly rounded, equal, margin entire, apex acute or blunt; midrib and veins above obscure, beneath conspicuous, lateral veins 4–7 pairs. **Inflorescence** axillary, a reduced cyme or a simple cyme or once branched, flower(s) 1–4; indumentum of inflorescence: hairs reddish, eglandular with shorter glandular hairs on peduncle, bracts and pedicel. Peduncle green, slender, (2.3–)5.5–13.5 cm long; bracts green, lanceolate, *c*. 1.7 × 0.8 mm, apex acute; pedicel 0.3–0.5 mm long. **Flower** indumentum: hairs a mix of eglandular and glandular; reddish eglandular hairs and shorter glandular hairs on calyx outer surface; long stalked glandular hairs on corolla outer surface; short stalked glandular hairs on upper lip inner surface, dense; glandular hairs on ovary and pistil. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes slightly larger than upper lobes, tube *c*. 0.6 mm long, 1.6 mm wide, lobes deltoid, apex acute, *c*. 2.6 long, base 0.8 mm wide. Corolla blue, tube campanulate, *c*. 4.4 mm long, 4.6 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flared, oblong; upper lobes *c*. 1.7 × 3.8 mm, lateral lobes *c*. 3.2 × 4.6 mm, median lobe *c*. 3.2 × 4.4 mm. Fertile stamens 2; anthers included within corolla tube; filaments white, straight, *c*. 3 mm long; anther cream, coherent face to face, kidney-shaped, *c*. 1.4 × 0.7 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary a bulge, at the dorsal part of ovary. Ovary narrowly conical, *c*. 3 mm long, 1 mm wide; ovule with a funicle connecting to placenta ; style white, straight, *c*. 4 mm long; stigma white, stigma punctiform, extended beyond

Plate 8



Loxocarpus rufescens: **a.** habitat, Gunung Santubong, **b.** habit, **c.** flower side view, **d.** flower front view, **e.** dehisced capsule.

corolla tube, exposed. **Capsule** brown, purplish when young, oblique conical, 7–8 mm long, 1–1.2 mm thick, sub-persistent style 1.6–2.3 mm long; valves straight, splitting into a trough or splash-cup; hairs glandular, short, erect, dense. **Seeds** ellipsoid, *c*. 0.48 × 0.2 mm, apices acute.

Distribution. Borneo; Sarawak (Kuching and Kapit Divisions), mountains in W Kalimantan and Lingga Archipelago: P. Temiang.

Habitat. Lowland forest to lower montane forest; 150–1000 m asl. On sandstone outcrops or cliffs along ridges or steep slopes. In Sarawak mainly found in sandstone regions.

Conservation status. Least Concern [LC].

Notes. A 'Group A' species, and the only species with a campanulate corolla in Borneo. The lectotype is chosen for its fully open flower and mature capsule. It is a variable species; its capsule shape is generally obliquely conical but populations with a capsule opening to become a splash cup were observed in the field. Disjunct distribution in Sarawak, Kapit, Batu Laga (*Lai S72165*) and Lingga Archipelago, P. Temiang (*Bünnemeijer 7638*) are notable.

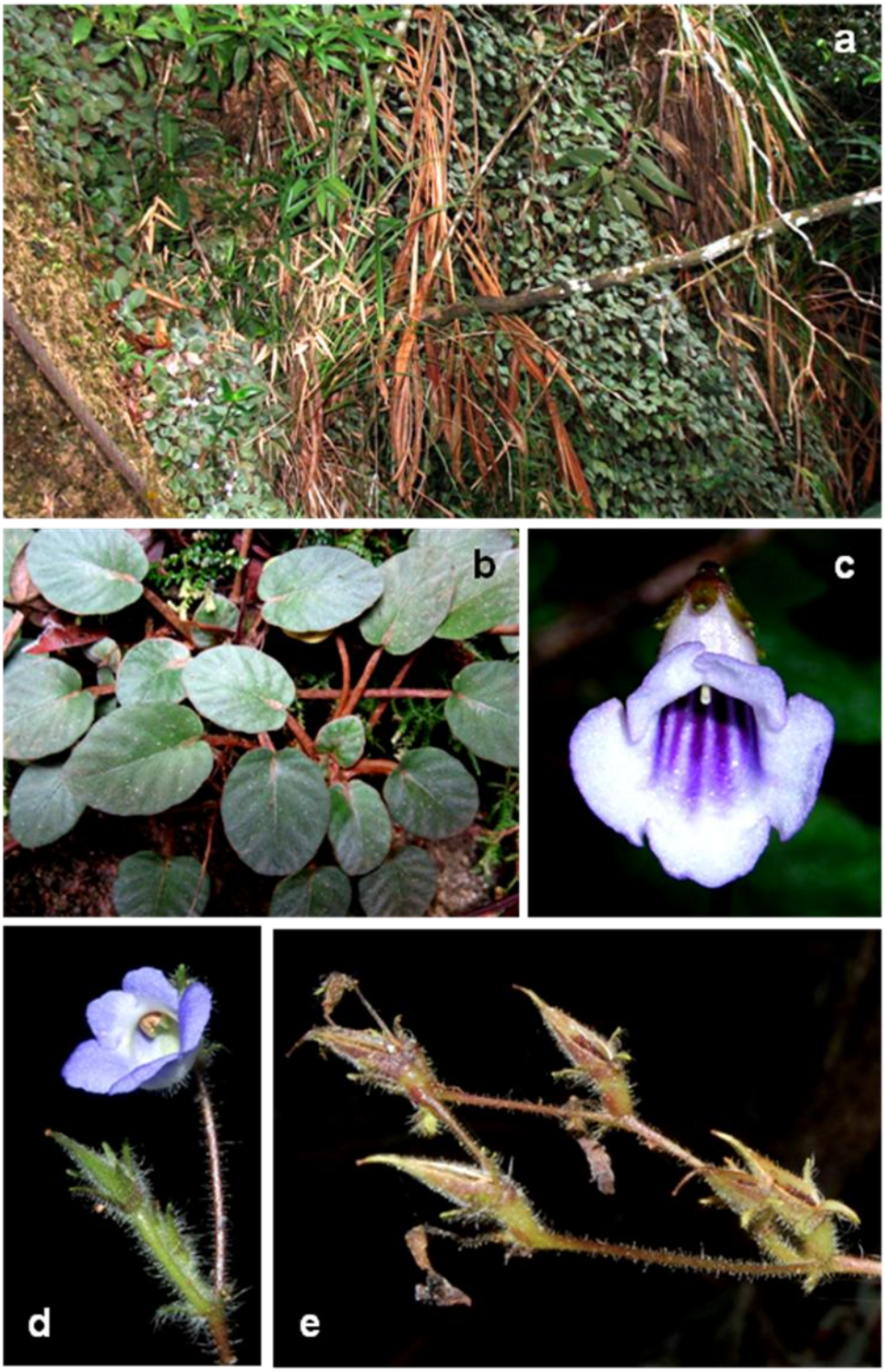
13. *Loxocarpus semitortus* (C.B.Clarke) Ridl. — **Fig. 4.3, Plate 9a–c**

J. Straits Branch Roy. Asiat. Soc. 44: 61 (1905), J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 768 (1908), Fl. Malay. Penin. 2: 526 (1923); Henderson, Malay. Wild Fls., Dicots.: 354 (1959). **Basionym:** *Didymocarpus semitortus* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 99 (1883), Fl. Brit. India 4: 352 (1884); Ridley, J. Linn. Soc., Bot. 32: 512 (1896). **Synonym:** *Roettlera semitorta* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 477 (1891). *Henckelia semitorta* (C.B.Clarke) A.Weber, Beitr. Biol. Pflanzen. 70: 356 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 17 (2009). **Type:** Peninsular Malaysia, Johor, G.

Ledang [Mt. Ophir, Malacca], *Griffith 3836* (lecto K, designated by Banka & Kiew, 2009; isolecto P).

Habit rosette. Rootstock short, woody, 2–5(–10) cm long, 3–5(–7) mm thick; habit in correlation with habitat: rootstock longer when growing in mossy earthbank; rootstock/stem indumentum: hairs buff, shiny, shaggy, dense; adventitious roots wiry. Leaf bases persistent. **Stem** distinctive, 2–8 cm long. **Leaves** alternate, crowded at the top or well-spaced below and crowded at the top; hairs buff, wooly, shiny, shaggy on petiole, dense; adpressed on lamina above and veins beneath, dense; lamina beneath glabrous. Petiole relatively thick, (2.5–)4–7(–11) cm long, 2–4 mm thick, cross section grooved above; longest petiole longer than lamina. Lamina dark green, beneath paler, thick, ovate or elliptic, 2–5.2 × 1.4–2.8 cm, width:length ratio *c*. 1:1; base truncate or rounded or cordate, equal, margin shallowly crenate, apex blunt or rounded; midrib and veins above sunken, beneath prominent, lateral veins 5–7 pairs, lowermost 1–2 pair(s) arising from lamina base. **Inflorescence** axillary, a reduced cyme or a simple cyme, rarely once branched, flower(s) 1–2(–4); indumentum of inflorescence: hairs pale brownish, straight, eglandular hairs on peduncle and pedicel, dense. Peduncle purple, slender, (3–)5–6(–10.5) cm long; bracts green, linear, *c*. 4 × 0.75 mm, apex rounded; pedicel 3–10(–15) mm long. **Flower** indumentum: hairs pale brownish, straight eglandular hairs; on outer surface of calyx and ovary dense; on outer surface of corolla tube moderately dense. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, lobes deltoid, apex acute, *c*. 3 mm long, base 1 mm wide. Corolla pale mauve, throat with 8 deep purple stripes, tube shortly tubular, 5.6 mm long, 5.2 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flared, oblong; upper lobes *c*. 3.2 × 3.6 mm, lateral lobes *c*. 4 × 5 mm, median lobe *c*. 3.5 ×

Plate 9



Chew, M.Y.

Nor Ezzawanis, A.T.

Imin, K.

Loxocarpus semitortus: **a.** habitat, **b.** habit, **c.** flower front view;
Loxocarpus sericiflavus: **d.** flower, **e.** capsules.

3.5 mm. Fertile stamens 2; anthers included within corolla tube; filaments straight or slightly curved, *c*. 2.8 mm long; anther deep violet, coherent face to face, kidney-shaped, *c*. 2 × 0.8 mm; staminodes absent or present, when present 2. Nectary a bulge, at the dorsal part of ovary. Ovary conical, *c*. 2.5 mm long, 2 mm wide; ovule with a funicle connecting to placenta ; style arched towards corolla ceiling, *c*. 5.5 mm long; stigma punctiform, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 7–8 mm long, 1.5–2 mm thick, sub-persistent style 3.5 mm long; valves slightly curved upward, splitting into a wide trough; hairs eglandular, short, shaggy. **Seeds** broadly ellipsoid, *c*. 0.6 × 0.3 mm, apices acute.

Distribution. Peninsular Malaysia; Johor, known only from G. Ledang SP.

Habitat. Lower montane forest at 900–1100 m asl. On moist granite rock faces, deeply shaded.

Conservation status. Near Threatened [NT].

Notes. A 'Group A' species. It is the only narrowly endemic species in the west coast of Peninsular Malaysia.

14. *Loxocarpus sericeus* (Ridl.) B.L.Burtt — **Fig. 4.7**

Notes Roy. Bot. Gard. Edinburgh 31: 49 (1971). **Basionym:** *Didymocarpus sericeus* Ridl., J. Linn. Soc., Bot. 32: 513 (1896); **Synonym:** *Henckelia sericea* (Ridl.) A.Weber, Beitr. Biol. Pflanzen. 70: 356 (1998). **Type:** Malay Island, Lingga [Island], *Nong-Chie s.n.* (lecto SING [barcode SING0106354], designated here).

Habit rosette. Rootstock short, woody, 1–1.5 cm long, 3–4 mm thick; rootstock/stem indumentum: hairs buff, adpressed, dense; adventitious roots long, or wiry. Leaf bases

caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs silky, adpressed, on lamina above and beneath dense. Petiole slender, (0.3–)1.5–2.5 cm long, 0.65–0.85 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina dirty green, beneath paler, thin, narrowly elliptic or sometimes slightly asymmetric, (2–)2.8–5 × (0.5–)0.8–1 cm, width:length ratio *c*. 1:4; base cuneate, equal, margin entire, apex acute; midrib and veins above obscure, beneath obscure, lateral veins 2–3 pairs. **Inflorescence** axillary, a reduced cyme or a simple cyme, flower(s) 1–2; indumentum of inflorescence: hairs eglandular, adpressed on peduncle, dense; eglandular hairs scattered with shorter glandular hairs on bracts and pedicel. Peduncle slender, (1–)6–8 cm long; bracts green, lanceolate, *c*. 5.2 × 1.5 mm, apex blunt; pedicel 3.7–5.2 mm long. **Flower** indumentum: hairs a mix of straight eglandular hairs and shorter glandular hairs; eglandular hairs scattered with shorter glandular hairs on outer surface of calyx, dense; short glandular hairs on ovary and pistil, dense. Calyx upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 0.4 mm long, 0.9 mm wide, lobes deltoid, apex acute, *c*. 1.5 mm long, base *c*. 0.4 mm wide. Corolla tube tubular-campanulate, 2.5 mm long, 1.2 mm wide; lobes flared, oblong. Fertile stamens 2; anthers at the mouth of corolla tube; filament straight; anthers kidney-shaped, *c*. 2.3 × 0.8 mm. Ovary conical, *c*. 1 mm long, 0.5 mm wide; style straight, *c*. 1.8 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, *c*. 8.5 mm long, 2–2.4 mm thick; valves straight, splitting into a splash cup; hairs glandular, short, erect, dense. **Seed** not known.

Distribution. Lingga Archipelago; known only from Pulau Lingga.

Habitat. About 250 m asl.

Conservation status. Critically Endangered [CR B2ab(iii)].

Notes. A 'Group A' species. Ridley (1915) mentioned that Hullett's specimen is identical to *L. angustifolius* and also Ridley (1923) listed Lingga within its distribution area. It seems that he thought *Loxocarpus sericeus* and *L. angustifolius* are conspecific but never synonymised one of them. In this treatment, they are recognised as two distinct species. The lectotype is chosen because the specimen has both flowers and fruits.

15. *Loxocarpus sericiflavus* (Kiew & Banka) T.L.Yao, *comb. nov*. — **Fig. 4.3, Plate 9d–e, Plate 10a–b**

Basionym: *Henckelia sericiflava* Kiew & Banka, Edinburgh J. Bot. 66: 18 (2009). **Type:** Peninsular Malaysia, Johor, G. Panti, 5 XII 1936, *Corner SFN 32538* (holo SING; iso SAR). **Heterotypic synonym:** *Henckelia anthonysamyi* Banka, in Banka & Kiew, Edinburgh J. Bot. 66: 11 (2009), ***syn. nov.*** **Type:** Peninsular Malaysia, Johor, Kahang Timor, Sg. Yong, 28 V 1987, *Anthonysamy SA 681* (holo KEP; iso E).

Habit rosette. Rootstock short, woody, 0.5–5(–9) cm long, 4–8 mm thick; habit in correlation with habitat: rootstock longer when growing in mossy earthbank; rootstock/stem indumentum: hairs buff yellowish, shiny, shaggy, dense; adventitious roots long, wiry. Leaf bases caducous, sometimes persistent. **Stem** lacking or distinctive, 0.5–7 cm long. **Leaves** alternate, crowded at the top or well-spaced below and crowded at the top; hairs yellowish grey, dull, eglandular (sometimes with shorter glandular hairs), on petiole dense; eglandular on lamina above and veins beneath, dense; lamina beneath scarce; young leaves covered with woolly hairs, sometimes persistent on the midrib of matures leaves. Petiole slender, 2.5–5 cm long, 1–1.5 mm thick, cross section grooved above; longest petiole shorter or longer than lamina. Lamina dirty green, beneath paler, moderately thick, ovate or elliptic or oblanceolate or oblong, sometimes slightly asymmetric, 4–12 × 1.6–4 cm, width:length ratio *c*. 1:3; base cuneate or slightly rounded, slightly unequal, margin

serrulate or shallowly crenate, apex acute or blunt; midrib and veins above sunken, beneath conspicuous, lateral veins 8–12 pairs, lowermost 1–2 pair(s) arising from lamina base. **Inflorescence** axillary, once to twice branched or thrice branched, flower(s) 3–15; indumentum of inflorescence: hairs a mixture of eglandular hairs and shorter glandular hairs on the peduncle, bracts and pedicel, dense. Peduncle purplish, slender, 8.5–12.5 cm long; bracts green, lanceolate, *c*. 1.8–2.5 × 0.4–1 mm, apex rounded; pedicel 3–7 mm long. **Flower** indumentum: hairs a mixture of eglandular hairs and shorter glandular hairs on outer surface of calyx and ovary, dense; sparse on corolla outer surface. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 0.6–1.1 mm long, 1.6–1.9 mm wide, lobes deltoid, apex acute, 2.5–3.5 mm long, base 0.7–1 mm wide. Corolla pale mauve or violet or blue, corolla tube sometimes very pale violet, close to white with violet or blue lobes; tube campanulate, 3–6.1 mm long, 3–7.6 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flared, oblong; upper lobes *c*. 1.5–2.7 × 3–3.2 mm, lateral lobes *c*. 2.8–4 × 4.1–5.4 mm, median lobe *c*. 2.7–3.8 × 4.5–5 mm. Fertile stamens 2; anthers included within corolla tube; filaments white, straight, *c*. 2.4–2.5 mm long; anthers cream or yellow, coherent face to face, kidney-shaped, *c*. 1.7–2.2 × 0.7–1.3 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary a thin rim or a bulge, at the dorsal part of ovary or encircling the ovary base. Ovary narrowly conical or slightly oblique, *c*. 1.1–3 mm long, 0.65–1 mm wide; ovule with a funicle connecting to placenta ; style white, straight, *c*. 0.9–3 mm long; stigma white, stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, purplish when young, oblique conical, 7–9 mm long, 1–2.5 mm thick, sub-persistent style 3.5 mm long; valves slightly curved upward, splitting into a

Plate 10

Loxocarpus sericiflavus: **a.** habitat, **b.** habit.

trough or into a wide trough; hairs glandular, short, erect, dense. **Seeds** narrowly ellipsoid or ellipsoid, *c*. 0.65–0.7 × 0.3 mm, apices acute.

Distribution. Peninsular Malaysia; Johor, known only from Kluang FR (G. Belumut and Sg. Yong) and Panti FR (G. Panti).

Habitat. Hill to lower montane forest at 200–1000 m asl. On sandstone cliff faces by streams, near waterfalls or in the forest just below summit, also found on steep earth banks.

Conservation status. Near Threatened [NT].

Notes. A 'Group A' species. Its leaves and stem are sticky in life. Populations in G. Belumut grow on both earth bank and rock face but populations in Sg. Yong only grow on sandstone rock faces.

16. *Loxocarpus stapfii* (Kraenzl.) B.L.Burtt — **Fig. 4.8**

Notes Roy. Bot. Gard. Edinburgh 24: 46 (1962). **Basionym:** *Didymocarpus stapfii* Kraenzl., Mitt. Inst. Allg. Bot. Hamburg 7: 89 (1927). **Synonym:** *Henckelia stapfii* (Kraenzl.) B.L.Burtt, Beitr. Biol. Pflanzen. 70: 356 (1998). **Type:** W Borneo [Kalimantan], auf dem Bkt. Mehipit, um 500 m, 8 XII 1924, *Winkler 661* (holo HBG; photo of holo E).

Heterotypic synonyms: *Didymocarpus longipetiolatus* Merrill, Sarawak Mus. Journal 3: 549 (1928) *non* Gardner (1846). *Loxocarpus longipetiolatus* B.L.Burtt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958). *Henckelia longipetiolata* (B.L.Burtt) B.L.Burtt, Beitr. Biol. Pflanzen. 70: 349 (1998), ***syn. nov.*** **Type:** Borneo, Sarawak, G. Pueh [Mt Poi], altitude above 1500 m, *Mjöberg 190* (holo UC; iso BM, K, US).

Habit rosette or creeping. Rootstock short, woody or lacking, 1–4 cm long, 3–7 mm thick; habit in correlation with habitat: rootstock sometimes long even growing on rockface; rootstock/stem indumentum: hairs silky, adpressed, dense; adventitious roots wiry, along

creeping stem, at intervals. Leaf bases caducous. **Stem** lacking or distinctive, 1–19 cm long. **Leaves** alternate, well-spaced throughout or crowded at the top; hairs silky, adpressed, on petiole, lamina above, lateral veins and further branched veinlets beneath dense; on lamina beneath sparse. Petiole slender, (2.5–)4.5–8 cm long, (0.7–)1–1.6 mm thick, cross section slightly grooved above or terete; longest petiole shorter than lamina, or longest petiole about equal in length to the lamina. Lamina green, beneath paler, thin or thick, ovate or broadly ovate or elliptic or obovate, (2.3–)4–6 × (1.1–)2.4–3.5 cm, width:length ratio *c*. 1:2; base cuneate or rounded or broadly rounded or cordate, equal, margin finely serrulate or entire, apex acute or blunt; midrib and veins above inconspicuous, beneath conspicuous or prominent, lateral veins 5–7 pairs, lowermost 2–3 pair(s) arising from lamina base. **Inflorescence** axillary, a compact cyme or once branched, flower(s) 3–11; indumentum of inflorescence: hairs eglandular, shaggy on the peduncle and bracts, dense; glandular on the pedicel, dense. Peduncle green or purple, slender, 5–15.5 cm long; bracts green, narrowly lanceolate, *c*. 3.4–4.5 × 0.7–0.8 mm, apex acute or blunt; pedicel 2.8–6 mm long. **Flower** indumentum: hairs a mix of straight eglandular and shorter glandular hairs; glandular on outer surface of calyx, filament and ovary, dense; glandular on corolla outer surface, dense, scattered with a few longer eglandular. Calyx green, 5-lobed, lobes somewhat equal, deeply dissected, tube *c*. 0.6–0.8 mm long, 1–1.2 mm wide, lobes deltoid, apex acute, *c*. 1.2–1.3 mm long, base 0.5–0.6 mm wide. Corolla white or pale mauve or blue, 2 purple patches at sinuses of mid-lobe; filaments, style and stigma purple at top; filament purple at swelling, tube short with deeply dissected lobes, 1.1–1.9 mm long, 1.6–2.6 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, median lobe largest, lobes flared, deltoid; upper lobes *c*. 0.5–2.9 × 0.5–1.6 mm, lateral lobes *c*. 1–3.4 × 1–2 mm, median lobe *c*. 1–3.2 × 1–2 mm. Fertile

stamens 2; anthers projected beyond corolla tube, exposed; filaments white, straight or slightly curved, *c*. 1.8–2 mm long; anthers cream, coherent face to face, kidney-shaped, *c*. 1.3 × 0.5–0.6 mm; staminodes 2, deltoid. Nectary absent. Ovary conical or slightly oblique, *c*. 1.2–1.5 mm long, 0.6–0.8 mm wide; ovule with a funicle connecting to placenta ; style white, straight, *c*. 3.6 mm long; stigma white, punctiform or capitate, extended beyond corolla tube, exposed. **Capsule** brown, ovoid, (3.3–)4–5.6 mm long, 1.5–2.5 mm thick; valves slightly curved upward, splitting into a splash cup; hairs glandular, short, erect to shaggy, dense. **Seeds** narrowly ellipsoid or ellipsoid, *c*. 0.5 × 0.2 mm, apices acute.

Distribution. Borneo: NW Sarawak (Kuching District), W & C Kalimantan and Lingga Archipelago: Pulau Temiang.

Habitat. Coastal forest to montane forest at 5–1500 m asl. On steep earth banks and cliff faces behind mangrove, granite or sandstone boulders along ridge to summit.

Conservation status. Least Concern [LC].

Notes. A 'Group A' species. Burtt (1962) mentioned that "this species (*L. stapfii*) is uncomfortably close to *L. longipetiolatus* and will take the priority over it if they prove conspecific." I concur with his view and synonymised the two. The populations from higher elevation of G. Berumput are quite distinctive in their numerous small and thick leaves, and sometimes bigger flower (*Burtt B 2786*). Lamina dimensions: 2.3–3.2 by 1.1–1.9 cm.

17. *Loxocarpus taeniophyllus* (B.L.Burtt) T.L.Yao, *comb. nov.* — **Fig. 4.2**

Basionym: *Henckelia taeniophylla* B.L.Burtt, in Kirkup *et al.*: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996). **Type:** Brunei, Temburong

distr., Bangar, northern slope of Bkt. Bangar, 10–100 m; rather dry rock in deep forest; flower blue; 18 I 1964, *Hotta 13263* (holo KYO; iso E).

Habit rosette. Rootstock short, woody or lacking, 0–1 cm long, 0.5 mm thick; rootstock/stem indumentum: hairs buff, adpressed, dense; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs buff, adpressed, on petiole, lamina above and beneath dense. Petiole slender, 1 cm long, 0.75 mm thick, cross section terete; longest petiole shorter than lamina. Lamina dirty green, moderately thick, narrowly oblong, 8–9 × 0.3–0.4(–0.6) cm, width:length ratio more than 1:6; base attenuate, equal, margin finely serrulate or entire, apex acute; midrib and veins above obscure, beneath inconspicuous or distinct, lateral veins 3–5 pairs. **Inflorescence** axillary, a reduced cyme, flower(s) 1; indumentum of inflorescence: hairs straight, long, eglandular, on peduncle, bracts and pedicel dense. Peduncle slender, 4–4.5 cm long; bracts linear, *c*. 5 × 0.4 mm, apex acuminate; pedicel (3–)7 mm long. **Flower** tilted, indumentum: hairs mainly straight, long, eglandular, on the outer surfaces of calyx, corolla and ovary dense throughout. Calyx green, 5-lobed, lobes somewhat equal, tube *c*. 0.9 mm long, 1.8 mm wide, lobes linear-lanceolate, apex thickened, blunt, *c*. 5 mm long, base 0.65 mm wide. Corolla violet, tube very short, 2 mm long, 3 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; lateral and median lobes larger, median lobe largest, lobes flat-faced (saintpaulioid), oblong; upper lobes *c*. 3 × 1.75 mm, lateral lobes *c*. 6 × 2 mm, median lobe *c*. 7 × 2 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filaments thickened at distal half, *c*. 3.2 mm long; anthers coherent only at the ventral tip, kidney-shaped, *c*. 2 × 1.45 mm; staminodes 2, threadlike. Nectary absent. Ovary narrowly conical, *c*. 1.7 mm long, 0.8 mm wide; style strongly curved upwards, *c*. 4.7 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown,

oblique conical, 6–7 mm long, 2 mm thick, sub-persistent style *c*. 3 mm long; valves slightly curved upward, splitting into a trough; hairs buff, eglandular, short, dense. **Seed** not known.

Distribution. Borneo; Brunei, known only from Temburong.

Habitat. Lowland to hill forest at 10–220 m asl. Sandstone cliff faces or boulders in forest.

Conservation status. Near Threatened [NT].

Note. A 'Group B' species. It is the only species with a very narrow ribbon-like lamina.

18. *Loxocarpus tunkui* Kiew — **Fig. 4.1**

Malay. Nat. J. 41: 221 (1987). **Synonym:** *Henckelia tunkui* (Kiew) A.Weber, Beitr. Biol. Pflanzen. 70: 357 (1998); Banka & Kiew, Edinburgh J. Bot. 66: 20 (2009). **Type:** Peninsular Malaysia, Pahang, Sg. Gerugal, 18 VI 1989, *Kiew KBH 86-10* (holo KEP; iso SING).

Habit rosette. Rootstock short, woody, 1.35–5 cm long, 0.5–1 mm thick; rootstock/stem indumentum: hairs buff, spreading, dense; adventitious roots long, or wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs silky, shiny, adpressed on petiole, lamina above and beneath, dense. Petiole slender, 3.5–4.5(–7 cm) long, 0.75–1 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina green, beneath paler, moderately thick, elliptic or oblanceolate, (3.5–)5.5–7.5 × (1.5–)2.5–3 cm, width:length ratio *c*. 1:2; base cuneate, equal, margin entire, apex acute; midrib and veins above obscure, beneath distinct, lateral veins 2–3(–4) pairs, lowermost 1 pair(s) arising from lamina base. **Inflorescence** axillary, once branched, flower(s) 4–6(–8); indumentum of inflorescence: hairs eglandular, adpressed on peduncle and bracts, dense; shorter glandular, erect on pedicel. Peduncle green, slender or relatively stout, 10–16 cm long;

bracts green, narrowly lanceolate, *c*. 8 × 1 mm, apex acute; pedicel 1–2 mm long. **Flower** indumentum: hairs glandular, erect on pedicel, outer surface of calyx, corolla, filament and ovary, dense. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, lobes deltoid, apex acute, *c*. 2 mm long, base 1 mm wide. Corolla purple, tube tubular-campanulate, 2 mm long, 2 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lateral lobes largest, lobes flared, oblong; upper lobes *c*. 2 × 1.5 mm, lateral lobes *c*. 4 × 2 mm, median lobe *c*. 2.5 × 2 mm. Fertile stamens 2; anthers included within corolla tube; filaments straight, *c*. 2.5 mm long; anthers yellow, kidney-shaped, *c*. 1.5 × 1 mm. Nectary a bulge. Ovary conical, slightly oblique, *c*. 1.5 mm long, 1 mm wide, style arched towards corolla ceiling, *c*. 3 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, oblique conical, 4–6 mm long, 1.5–2 mm thick; valves straight, splitting into a wide trough; hairs glandular, short, erect, dense. **Seeds** broadly ellipsoid, *c*. 0.45 × 0.2 mm, apices acute.

Distribution. Peninsular Malaysia; Pahang and Johor, known only from Endau-Rompin SP.

Habitat. Lowland to hill forest at 50–550 m asl. On sandstone cliffs in forest or boulders near waterfalls and streams.

Conservation status. Near threatened [NT].

Notes. A ‘Group A’ species. Its glossy laminas (due to silvery indumentum) resemble those of *Loxocarpus argenteus* ones.

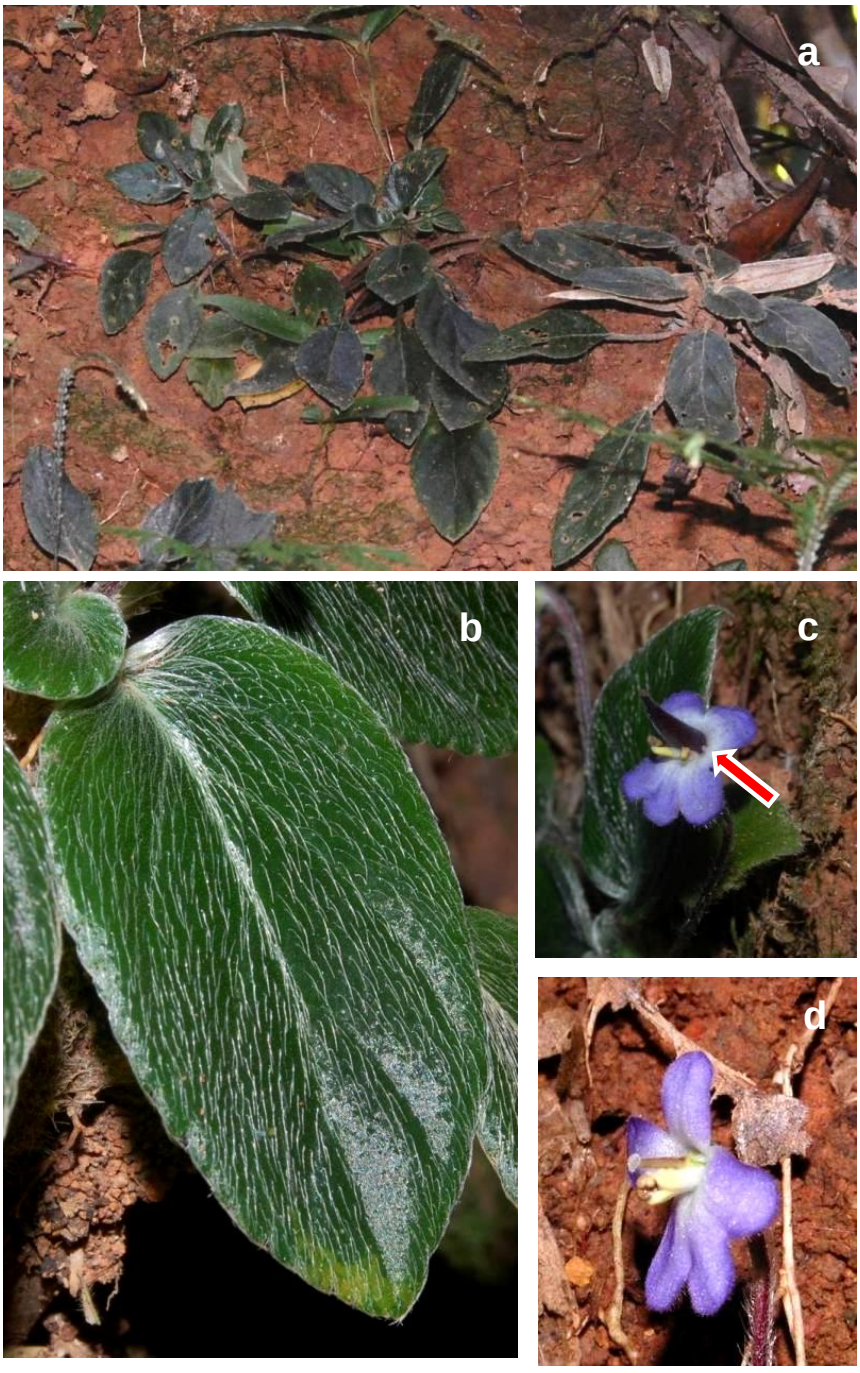
19. *Loxocarpus verbeniflos* (C.B.Clarke) B.L.Burtt — **Fig. 4.9, Plate 11a–d**

Notes Roy. Bot. Gard. Edinburgh 22: 308 (1958). **Basionym:** *Didymocarpus verbeniflos* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 99 (1883). **Synonym:** *Roettlera verbeniflos* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 477 (1891). *Henckelia verbeniflos* (C.B.Clarke) B.L.Burtt, Beitr. Biol. Pflanzen. 70: 358 (1998). **Type:** NE Borneo, Sandakan I., 1877–78, *Burbidge s.n.* (lecto BM; isolecto K [barcode K000450484], here designated). **Heterotypic synonyms:** *Didymocarpus petiolaris* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 100 (1883). *Roettlera petiolaris* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 476 (1891). *Loxocarpus petiolaris* (C.B.Clarke) B.L.Burtt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958). *Henckelia petiolaris* (C.B.Clarke) B.L.Burtt, in Kirkup *et al.*: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996), ***syn. nov.*** **Type:** Labuan, *Motley 374* (lecto K [barcode K000450483], designated here). *Henckelia sp*. 2 in Kirkup *et al*.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 136 (1996). **Specimens:** Belait, *Sands 5977*; Labu, *Ashton A122*.

Habit rosette. Rootstock short, woody or long, 1–6.5 cm long, 3–4 mm thick; rootstock/stem indumentum: hairs, buff tinged yellowish, spreading to shaggy, dense; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking or distinctive, 0.5–6 cm long. **Leaves** alternate, crowded at the top or well-spaced below, crowded at the top; hairs silky, spreading on petiole, dense; on lamina above and beneath adpressed, sparse or sometimes scarce; on veins beneath dense. Petiole slender, 1–3 cm long, 0.6–1 mm thick, cross section slightly grooved above or terete; longest petiole shorter than lamina. Lamina dark green, beneath paler, thin or moderately thick, ovate or narrowly elliptic or elliptic or oblong, 3.6–8 × 1.3–2.4 cm, width:length ratio *c*. 1:3; base attenuate or cuneate or slightly rounded or rounded, equal, margin shallowly serrate, apex acute or blunt or rounded; midrib and veins above obscure, beneath distinct or conspicuous, lateral veins 3–7 pairs,

lowermost 1 pair(s) arising from lamina base. **Inflorescence** axillary, a reduced cyme, flower(s) 1; indumentum of inflorescence: hairs eglandular throughout, adpressed, sprinkled with a few shaggy ones, on peduncle, bracts and pedicle dense. Peduncle purplish, slender, 2–6 cm long; bracts green, narrowly lanceolate or lanceolate, *c*. 1.4–2.4 × 0.3–0.4 mm, apex acute; pedicel 2–6 mm long. **Flower** tilted, indumentum: hairs eglandular throughout, adpressed, sprinkled with a few shaggy ones, on calyx outer surface dense; shorter on corolla outer surface, sparse; eglandular, short, erect on ovary. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes slightly larger than upper lobes, sometimes lobes somewhat equal, tube *c*. 0.45–1 mm long, 0.8–2 mm wide, lobes deltoid, apex acute, 0.9–1.2 mm long, base 0.5–0.8 mm wide. Corolla pale mauve or lilac or blue, tube very short, 0.9–2 mm long, 2–2.5 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes flat-faced (saintpaulioid), oblong; upper lobes 2.2–3.2 × 1.8–3.2 mm, lateral lobes 1.5–3.7 × 1.4–3 mm, median lobe 2.1–3 × 1.9–2.7 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filaments yellow, thickened at distal half, 2.9–3.1 mm long; anthers cream or yellow, coherent only at the ventral tip, kidney-shaped, 1.2–1.8 × 0.6–0.9 mm; staminodes 3, 2 threadlike, 1 a minute protrusion. Nectary absent. Ovary conical, slightly oblique, *c*. 1.6 mm long, 0.5–0.9 mm wide; style white, straight, *c*. 2.5–4 mm long; stigma white, capitate or peltate, extended beyond corolla tube, exposed. **Capsule** brown, purplish when young, oblique conical or long slender conical, 9–20 mm long, 1–2.5 mm thick, sub-persistent style 3–4 mm long; valves straight, splitting into a trough; hairs eglandular, short, spreading to erect. **Seeds** ellipsoid, *c*. 0.35–0.42 × 0.15–0.21 mm, apices acute.

Plate 11



Loxocarpus verbeniflos: **a.** habitat, **b.** adpressed hairs on lamina upper surface, **c.** young capsule with old corolla still attached at base, **d.** flower.

Distribution. Borneo; E Sarawak, Brunei, Labuan and Sabah.

Habitat. Lowland to lower montane forest at 10–1650 m asl. Generally on sandstone outcrops in forest or near streams, also on bare soil and sandy clay banks, less commonly on rotten stumps or tree base.

Conservation status. Least Concern [LC].

Notes. A 'Group B' species. The lectotype for *L. verbeniflos* is chosen for its mature capsule and precise locality. The specific epithet *verbeniflos* is preferred to *petiolaris* because it is more widely used in various publications and local herbaria. It is a morphologically variable species with widespread distribution.

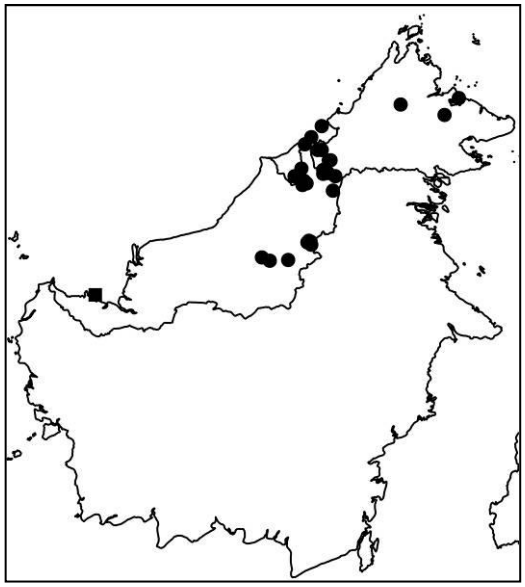


Fig. 4.9. Distribution of *Loxocarpus verbeniflos* (●) and *Loxocarpus* sp. C (■).

20. *Loxocarpus violoides* (C.B.Clarke) T.L.Yao, *comb. nov.* — **Fig. 4.5, Plate 12a–c**

Basionym: *Didymocarpus violoides* C.B.Clarke in A.DC. & C.DC., Monogr. Phan. 5(1): 97 (1883). **Homotypic synonym:** *Roettlera violo*[*i*]*des* (C.B.Clarke) O.Kuntze, Rev. Gen. Pl., 2: 477 (1891). *Henckelia violoides* (C.B.Clarke) B.L.Burtt, in Kirkup *et al.*: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996); Burtt in

Beaman *et al*.: The Plants of Mount Kinabalu 4: 376 & plate 41C (2001). **Type:** NE of Borneo, Lobong Peak, altitude 5000 ft, *Lobb s.n*. (holo K [barcode K000450488]).

Heterotypic synonym: *Henckelia diffusa* B.L.Burtt, in Kirkup *et al*.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996), ***syn. nov.*** **Type:** Brunei, Belait, subd. Labi, Mendaram valley below and close to waterfall, 4°20' N, 114°27' E, 100 m, Lambir formation, sandstone and shale, lowland dipterocarp forest, 18 III 1991, *Sands 5443* (holo K; iso BRUN, E, KEP).

Habit rosette or creeping. Rootstock short, woody, or long, or lacking, (2–)3–6(–15) cm long, 2–3(–4.5) mm thick; rootstock/stem indumentum: hairs silky, adpressed to spreading, dense; adventitious roots along creeping stem, at intervals, wiry, or only at the base of stem. Leaf bases caducous. **Stem** distinctive, 1–25 cm long. **Leaves** alternate, well-spaced throughout or crowded at the top; hairs silky, adpressed on petiole and veins beneath, dense; on lamina above and beneath less dense. Petiole slender, 1–4(–7.5) cm long, 0.5–1 mm thick, cross section terete; longest petiole about equal in length to the lamina. Lamina dark green, beneath paler, thin, ovate or broadly ovate or elliptic, 2.2–5.5 × 1.5–3 cm, width:length ratio *c*. 1:2; base cuneate or rounded or broadly rounded, equal, margin finely serrulate or shallowly serrate, apex acute or blunt; midrib and veins above obscure, beneath distinct or conspicuous, lateral veins 3–6 pairs, lowermost 1–2 pair(s) arising from lamina base. **Inflorescence** axillary, a reduced cyme or a simple cyme, flower(s) 1(–2); indumentum of inflorescence: hairs silky, eglandular, adpressed to shaggy, on peduncle, bracts and pedicel, dense. Peduncle purple, slender, 3.5–10 cm long; bracts green, linear, *c*. 2.8 × 0.25–0.4 mm, apex acute or acuminate; pedicel 5–15 mm long. **Flower** slightly tilted or tilted, indumentum: hairs silky, eglandular, on calyx outer surface, ovary and style, adpressed to shaggy, dense; on corolla outer surface sparse; minutely glandular on corolla

inner surface, erect, sparse. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes slightly larger than upper lobes, sometimes lobes somewhat equal, tube 0.9–2.4 mm long, 1.6–2.3 mm wide, lobes deltoid, apex acute, 1.4–4.4 mm long, base 0.6–1.7 mm wide. Corolla violet or lilac or blue, tube very short, 0.9–5.6 mm long, 2–5 mm wide; upper lip with 2 upper lobes, lobes divided to the base, lower lip with 2 lateral lobes and a median lobe; lateral and median lobes larger, median lobes largest, lobes flat-faced (saintpaulioid), oblong; upper lobes 4.3(–14) × 4(–17) mm, lateral lobes 5.8(–18) × 3.4(–13) mm, median lobe 5.2(–17) × 4.1(–14) mm. Fertile stamens 2, pair-wise twisted; anthers projected beyond corolla tube, exposed; filaments yellow, initially twisted and straighten later, thickened at distal half, *c*. 2.1–4.1 mm long; anthers yellow, coherent only at the ventral tip, kidney-shaped, *c*. 1.3–2.9 × 0.8–1.6 mm; staminodes (2–)3, 2 thread-like, 1 a minute protrusion or 2 thread-like. Nectary absent. Ovary conical, slightly oblique, *c*. 3.6–3.7 mm long, 1–2.3 mm wide; ovule with a funicle connecting to placenta ; style white, straight, *c*. 5.2–5.5 mm long; stigma white, capitate or peltate, extended beyond corolla tube, exposed. **Capsule** brown, purplish when young, slenderly cylindric, 15–25(–30) mm long, 1–2.2 mm thick, sub-persistent style 3.5–5 mm long; valves straight, splitting into a trough; hairs silky, eglandular, short, spreading, sparse. **Seeds** ellipsoid or broadly ellipsoid, 0.36–0.45 × 0.18–0.26 mm, apices acute.

Distribution. Borneo; W Brunei (Belait), E Sarawak, W & N Sabah.

Habitat. Lowland to montane forest at 25–2200 m asl.

On sandstone and shale outcrops or cliffs or slope and ridges; sandy slope in stream gully, steep earth banks prone to landslides by ridge crest or mossy tree base; also on ultramafic substrates.

Plate 12

Loxocarpus violoides: **a.** habit, **b.** slender capsule, **c.** flower side view.

Conservation status. Least Concern [LC].

Notes. A 'Group B' species. *Henckelia violoides* was never included within *Loxocarpus* because of its long (to 30 mm long) slender capsule even though its flat-faced flower strongly resembles those of *L. verbeniflos* and *L. repens*. However, molecular studies show that this species belongs with the other Bornean *Loxocarpus* and distant from Bornean *Henckelia*(=*Codonoboea*).

21. *Loxocarpus* sp. A — Fig. 4.2

Type: Borneo, Sarawak, Lambir NP, below Bkt. Lambir, sandstone cliff, *c*. 1500 feet, *Burtt B 11597* (holo KEP, iso SAR).

Habit rosette. Rootstock short, woody, or long, 2–4–9.5 cm long, 4–6 mm thick; rootstock/stem indumentum: hairs buff, adpressed, dense; adventitious roots long, wiry. Leaf bases persistent. **Stem** lacking or distinctive, 1–2 cm long. **Leaves** alternate, crowded at the top; hairs buff, adpressed on petiole, dense; on lamina above and beneath equally dense. Petiole relatively thick, (0.8–)2.8–3.8 cm long, 0.74–1.1 mm thick, cross section grooved above; longest petiole about equal in length to the lamina. Lamina dark green, beneath paler, moderately thick, ovate or elliptic or obovate, (2.5–)3.3–4.1 × (0.8–)1.3–1.5 cm, width:length ratio *c*. 1:2; base cuneate, equal, margin entire or undulate, apex acute or blunt; midrib and veins above obscure, beneath inconspicuous, lateral veins 3 pairs. **Inflorescence** axillary, a reduced cyme, flower(s) 1; indumentum of inflorescence: hairs buff, eglandular, shaggy, on peduncle and bracts dense; mix with shorter glandular hairs on pedicel. Peduncle slender, 4.5–6.5 cm long; bracts green, narrowly lanceolate, *c.* 1.5 × 0.3 mm, apex blunt; pedicel 0.5–0.9 mm long. **Flower** indumentum: hairs buff, eglandular, on calyx outer surface shaggy, dense; on corolla outer surface less dense, shorter, erect; on

ovary dense. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 0.6 mm long, 1 mm wide, lobes deltoid, apex acute, *c*. 1.4 mm long, base 0.5 mm wide. Corolla mauve, tube very short, 0.6 mm long, 1.1 mm wide; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; lateral and median lobes larger, lobes flat-faced (saintpaulioid), oblong; upper lobes *c*. 2.5 × 2.5 mm, lateral lobes *c*. 2.3 × 2 mm, median lobe *c*. 3 × 2.3 mm. Fertile stamens 2; anthers projected beyond corolla tube, exposed; filaments yellow, thickened at distal half, *c*. 2.2 mm long; coherent only at the ventral tip, kidney-shaped, *c*. 1.7 × 0.7 mm; staminodes 3, club-shaped. Nectary absent. Ovary narrowly conical or slightly oblique, *c*. 1.8 mm long, 1 mm wide; style curved upwards near stigma and straighten, *c*. 3 mm long; stigma capitate, extended beyond corolla tube, exposed. **Capsule** brown, long slender conical, 10–12 mm long, 1.1–1.4 mm thick, sub-persistent style 1.5 mm long; valves straight, splitting into a trough; hairs silky, a mix of eglandular and glandular, adpressed to erect. **Seed** not known.

Distribution. Borneo; Sarawak, known only from Lambir FR.

Habitat. Hill forest summit vegetation at *c*. 460 m asl. On sandstone cliffs or on kerangas soil.

Conservation status. Near Threatened [NT].

Notes. A 'Group B' species. This species is remarkable in its numerous crowded rosette leaves.

22. *Loxocarpus* sp. B — Fig. 4.2

Type: Borneo, Sarawak, Baram, Sg. Segelam, around Long Selatong Lepo Ga', *Chin 2797* (holo KLU).

Habit creeping, decumbent. Rootstock long, 6 cm long, 2 mm thick; rootstock/stem indumentum: hairs buff, shiny, adpressed, dense; adventitious roots wiry. Leaf bases persistent. **Stem** distinctive, 8 cm long. **Leaves** alternate, well-spaced below, crowded at the top; hairs buff, shiny, adpressed, on petiole dense, on lamina above and beneath dense. Petiole slender, 6 cm long, 0.9 mm thick, cross section terete; longest petiole about equal in length to the lamina. Lamina dark green, beneath paler, thin, ovate, *c*. 7.4 × 2.9 cm, width:length ratio *c*. 1:2 or *c*. 1:3; base cuneate, equal, margin finely serrulate, apex acuminate or acute; midrib and veins above obscure, beneath distinct, lateral veins 4(–5) pairs, lowermost 1 pair(s) arising from lamina base. **Inflorescence** axillary, compact cyme or once branched, flower 2–7; indumentum of inflorescence: hairs buff, shiny, eglandular, adpressed on peduncle, bracts and pedicel. Peduncle slender, 10.5–11.5 cm long; bracts linear, *c*. 4.4 × 0.4 mm, apex acuminate; pedicel 0.6–1.2 mm long. **Flower** indumentum: hairs buff, shinny, eglandular, adpressed on calyx, corolla outer surfaces and ovary, dense. Calyx green, upper lip 3-lobed, lower lip 2-lobed; lower lobes larger than upper lobes, tube *c*. 1 mm long, 1.9 mm wide, lobes linear-lanceolate, apex thickened, blunt, *c*. 3.9 long, base 1 mm wide. Corolla pale blue, tube very short, 1.8 mm long, 2.9 mm wide; upper lip with 2 upper lobes, divided to the base, lower lip with 2 lateral lobes and a median lobe, lobes deeply divided; lateral and median lobes larger, lobes flat-faced (saintpaulioid), oblong; upper lobes *c*. 7 × 3.8 mm, lateral lobes *c*. 5.6 × 3.5 mm, median lobe *c*. 4.8 × 3 mm. Fertile stamens 2, pair-wise twisted; anthers projected beyond corolla tube, exposed; filaments yellow, straight, thickened at distal half, *c*. 4.5 mm long; anthers coherent only at the ventral tip, kidney-shaped, *c*. 2.5 × 1.4 mm; staminodes 3, 2 club-shaped, 1 a minute protrusion. Nectary absent. Ovary conical, slightly oblique, *c*. 2.8 mm long, 1.8 mm wide; style straight, *c*. 2.3 mm long; stigma extended beyond corolla tube, exposed. **Capsule**

brown, slenderly cylindric, 17.5 mm long, 1.9 mm thick; valves straight, splitting into a trough; hairs silky, eglandular, adpressed, dense. **Seed** not known.

Distribution. Borneo; Sarawak, known only from Ulu Long Selatong.

Habitat. On rocky ridge.

Conservation status. Critically Endangered [CR B2ab(iii)].

Note. A 'Group B' species. This species is known only from the type.

23. *Loxocarpus* sp. C — Fig. 4.9

Type: Borneo, Sarawak, Tg. Po, in deep shade on dripping wet rocks near the sea, *Brooke 10614* (holo L).

Habit rosette. Rootstock short, woody or lacking, 0–1 cm long, 3 mm thick; rootstock/stem indumentum: hairs buff; adventitious roots long, wiry. Leaf bases caducous. **Stem** lacking. **Leaves** alternate, crowded at the top; hairs buff, woolly, shaggy, on lamina above dense; on lamina beneath less dense. Petiole slender, 2 cm long, 1 mm thick, cross section grooved above; longest petiole shorter than lamina. Lamina ovate or broadly ovate, *c*. 2.5 × 1.7 cm, width:length ratio *c*. 1:1; base cuneate or rounded, equal, margin shallowly serrate, apex blunt; midrib and veins above obscure, beneath distinct, lateral veins 3 pairs. **Inflorescence** axillary, a reduced cyme, flower(s) 1; indumentum of inflorescence: hairs buff, shiny. Peduncle slender, 5 cm long; bracts narrowly lanceolate, *c*. 3 × 0.5 mm, apex acute; pedicel 3 mm long. **Flower** normal. Corolla tube short with deeply dissected lobes; upper lip with 2 upper lobes, lower lip with 2 lateral lobes and a median lobe; upper lobes smaller, lateral and median lobes larger, lobes recurved, deltoid. **Capsule** brown, long

slender conical, 17 mm long, 2.5 mm thick; valves straight, splitting into a trough. **Seed** not known.

Distribution. Borneo; Sarawak, known only from Tg. Po (Bako NP).

Habitat. On dripping wet rocks near the sea in deep shade.

Conservation status. Critically Endangered [CR B2ab(iii)].

Notes. A 'Group B' species. This species is known only from the type.

4.7 Identification list

A total of 465 specimen numbers from AAU, BKF, BK, BM, BO, E, HBG, K, KEP, KINA, KLU, L, SAN, SAR, SING and UKMB were examined for this revision. The number in bold denotes the species number. Barcode number (with unspace herbarium acronym) or sheet number are used when collection number is not available or is unknown. Date is used when the specimen is not numbered. If only the year is known, it is bracketed. See anonymous for numbered specimens with unknown collector.

Table 4.1. List of taxa.

No.	Taxon
1	*Loxocarpus angustifolia*
2	*L. argenteus*
3	*L. caeruleus*
4	*L. caulescens*
5	*L. conicapsularis*
6	*L. coodei*
7	*L. holttumii*
8a	*L. incanus* var. *incanus*
8b	*L. incanus* var. *sekayuensis*
9	*L. meijeri*
10	*L. pauzii*
11	*L. repens*
12	*L. rufescens*
13	*L. semitortus*

14 *L. sericeus*
15 *L. sericiflavus*
16 *L. stapfii*
17 *L. taeniophyllus*
18 *L. tunkui*
19 *L. verbeniflos*
20 *L. violoides*
21 *Loxocarpus* sp. A
22 *Loxocarpus* sp. B
23 *Loxocarpus* sp. C

Aban SAN 67038: **20**; *Abang Mohtar & Othman* S 52678: **16**; *Abbe et al.* 9881: **2**; *Ali & Frankie, La* AI 191: **21**; AI 192: **21**; *Anderson* 3: **16**; 29: **12**; 203: **3**; JARA 82/1: **17**; S 22793: **5;** S 31832: **5;** S 4106: **19**; S 4583: **20**; S 8363: **12**; *Anderson & Keng* S 4249: **11**; *Anderson & Wright* S 25641: **12**; *Anonymous* 3170: **8a**; 6/1917: **8a**; 4-1102-94: **3**; C 3974: **16**; C 8271: **5;** SAN 128802: **20**; *Anthonysamy* SA 638: **8b**; SA 681: **8a**; SA 700: **8a**; SA 832: **3**; SA 861: **15**; *Argent* 26108512: **11**; C 13898: **20**; *Argent & Coppins* 1145: **11**; *Argent & Lamb* 1485: **11**; *Argent & Walpole* 1454: **20**; *Argent et al.* 689: **5;** 700: **20**; 836: **19**; 915: **20**; *Ariffin et al.* BRUN 16813: **19**; *Ashton* A 122: **19**; S 17963: **2**; *Atkins et al.* SA 596: **20**.

Bahiah BA 0049: **20**; *Balgooy, van* 7335: **2**; MMJ 7099A: **13**; *Balgooy, van & Setten, van* 5398: **12**; 5641: **12**; *Banka* RB 1: **13**; RB 10: **7;** RB 2: **8b**; RB 4: **3**; RB 7: **8a**; RB 8: **15**; *Barber* K000450482: **19**; *Beaman et al.* 6879: **12**; 8912: **11**; 9745: **11**; 11885: **20**; *Beccari* 2130: **12**; *Beusekom, van & Phengkhlai* 766: **8a**; *Bogner* 1411: **12**; 1449: **16**; *Bremer & Bremer* 1678: **2**; *Brooke* 8614: **19**; 10002: **19**; 10007: **23**; 10614: **16**; *Brunig* S 9526: **12**; *Bunnak* 264: **8a**; 741: **8a**; *Bünnemeijer* 6580: **14**; 7638: **16**; *Burbidge* (1877): **19**; *Burkill* 1241: **8a**; 2575: **8a**; 2593: **8a**; 2674: **8a**; *Burkill & Mohd Haniff* 12881: **3**; *Burtt* B 11390A: **19**; B 11597: **21**; B 12726: **11**; B 12798: **11**; B 2660: **28**; B 2666: **26**; B 2670: **27**; *Burtt & Martin* B 5003: **11**; B 5060: **11**; B 5171: **11**; B 5171A: **11**; B 5184: **19**; B 5217: **19**; B 5276: **11**; B 5313: **11**; B 5522: **19**; *Burtt & Woods* B 1840: **2**; B 1973: **12**; B 2075: **19**; B

2087: **20**; B 2097: **11**; B 2196: **19**; B 2252: **19**; B 2524: **12**; B 2681: **16**; B 2757: **16**; B 2786: **16**; *Buwalda* 6597: **4**.

Carrick & Enoch JC 472: **2**; *Chan* FRI 60540: **8a**; FRI 70273: **8a**; *Charoenphol et al.* 3890: **8a**; *Chew & Kamarul Hisham* FRI 60218: **3**; *Chew & Kiew* FRI 53770: **8a**; *Chew et al.* 1618: **20**; 1740: **20**; *Chin* 2797: **22**; *Chin et al.* 4575: **20**; *Chua et al.* FRI 26696: **8a**; FRI 39087: **3**; FRI 40553: **8b**; FRI 41754: **8b**; *Church et al.* 2574: **16**; NSF 281: **16**; *Cockburn* SAN 83028: **19**; *Collenette* 722: **11**; 822: **28**; 3/79: **20**; *Coode & Wong* MC 6617: **6;** *Coode et al.* MC 7288: **20**; MC 7553: **11**; *Corner* L0795054: **3**; L0795055: **3**; SFN 32538: **15**; SING0106320: **7;** SING0106321: **7;** SING0106360: **1**; *Cronk et al.* 24: **20**; *Curtis* 297: **8a**.

Daim 1104: **20**; DA 1014: **20**; *Davies et al.* SJD 99144: **11**; *Davison* GD 1 [18/6/1989]: **18**; GD 1 [28/1/1984]: **19**; *Dayang Awa & Lee* S 47598: **19**; S 47621: **19**; S 47625: **19**; S 47866: **11**; S 50734: **11**; *Dayang Awa & Othman* S 47076: **12**; *Derry* 599: **13**; *Dolois* KNP 12181: **20**; KNP 16320: **20**; *Dolois et al.* KNP 13950: **11**; KNP 18515: **20**; *Dransfield et al.* 1135: **20**.

Edwards 1936A: **8a**; *Endert* 4277: **11**; *Ernst* 1184: **3**.

Fidilis SAN 131406: **11**.

Gardner 37: **11**; *Gibot* SAN 55431: **20**; *Gordon et al.* BE 109: **13**; *Griffith* 3836: **13**; *Gwynne-Vaughan* 615: **8a**.

Hansen 35: **5;** 494: **8a**; 12048: **11**; *Harry & Pearce* ITTO/BB 0344: **16**; *Haviland* 118: **12**; 981: **12**; 351/269: **16**; Hav 583: **19**; SING0106338: **12**; SING0106367: **19**; *Haviland & Hose* Hav 3534: **20**; *Henderson* 11812: **3**; *Holttum* 9819: **15**; 10654: **7;** 18097: **7;** 19863: **3**; 20944: **20**; 25109: **8a**; SING0106324: **7;** *Hooker* (1831): **8a**; *Hotta* 12709: **20**; 13209: **19**; 13263: **17**; 13339: **6;** 14621: **11**; *Hullett* SING0106350: **13**; SING0106355: **14**.

Ilias S 13580: **16**; *Ilias & Mamit* S 29017: **12**; *Ilias & Yeo* S 38365: **21**; *Imaichi et al.* 37: **5;** *Iwatsuki* M 13113: **8a**; T 14513: **8a**.

Jamili SNP 05024: **11**; *Joffre et al.* BRUN 16939: **20**; *Johns et al.* 7043: **17**; *Julia et al.* S 91932: **19**; S 98083: **20**; S 99321: **19**.

Kamaruddin et al. 1338: **11**; *Kelsall* SING0106196: **3**; *Kerby* 260: **19**; *Kerr* 7166: **8a**; 7751: **8a**; 7872: **8a**; 13212: **8a**; 14912: **8a**; *Kiah* 31706: **1**; 35351: **8a**; *Kiew* KBH 2: **8b**; KBH 565: **19**; KBH 86-10: **18**; RK 1608: **8a**; RK 1687: **13**; RK 2111: **8a**; RK 2396: **7;** RK 2433: **3**; RK 2484: **1**; RK 2694: **8b**; RK 280: **19**; RK 388: **19**; RK 410: **19**; RK 4613: **20**; RK 4904: **8a**; RK 5096: **8a**; RK 5164: **8a**; RK 554: **20**; RK 555: **20**; RK 564: **19**; RK 576: **19**; RK 869: **16**; RK&KBH 563: **6;** SB 15: **8a**; UPM 3210: **8b**; UPM 5583: **24**; *Kiew & Ali* RK 4640: **11**; RK 4641: **11**; *Kiew & Anthonysamy* RK 4011: **1**; RK 4014: **1**; *Kiew & Kiew* RK 556: **20**; *Kiew et al.* RK 4946: **29**; S 93268: **25**; *King's collector* 1757: **8a**; 2426: **3**; 6990: **3**; 7192: **3**; *Kirkup & Coode* DW 489: **19**; *Kloss* 12169: **3**; 12188: **3**; *Kostermans* 12835: **11**; 12906A: **11**.

Lai & Yii S 72165: **16**; *Lai et al.* S 73502: **16**; S 73520: **16**; S 74773: **11**; S 80654: **19**; *Laman* TL 376: **12**; *Laman et al.* TL 159: **12**; TL 442: **12**; *Lamb* s.n., s.d.: **11**; *Larsen* 42206: **8a**; 42243: **8a**; *Larsen & Larsen* 32969: **8a**; *Larsen et al.* 45606: **8a**; 45888: **8a**; *Lau* LCT 079: **20**; *Lee* S 45532: **19**; S 51060: **11**; S 52341: **19**; S 52544: **11**; S 54122: **12**; *Lim* FRI 64836: **3**; *Lim & Kueh* FRI 64888: **1**; *Lim & Lee* S 90448: **19**; S 90470: **11**; *Lim et al.* FRI 56313: **1**; *Lobb* K000450473: **13**; K000450485: **12**; s.n., s.d.: **8a**; *Long (Forest Ranger)* 7: **8a**.

Maingay 1220: **13**; 1228: **8a**; 2725: **13**; *Martin* S 37931: **16**; S 38050: **20**; S 38912: **11**; *Maxwell* 81-176: **7;** 85-566: **8a**; *Meijer* 6893: **4**; 6955: **9;** 7083: **9;** SAN 19459: **11**; SAN 21930: **11**; SAN 22152: **20**; *Mendum & Lamb* 8: **11**; *Mendum et al.* MM 54: **11**; *Merton* 5002: **7;** *Middleton et al.* 4379: **8a**; *Mj"berg* 190: **16**; *Mogea & Wilde, de* MOGEA

405: **16**; *Mohd Hairul et al.* FRI 58993: **13**; FRI 60020: **8a**; FRI 70903: **8a**; *Mohd Haniff & Mohd Nur* 7957: **1**; 8136: **3**; *Mohd Nur* 11726: **8a**; SFN 20000: **8a**; *Mohd Shah & Ahmad* MS 2270: **8a**; *Mohd Shah & Samsuri* MS 3596: **13**; MS 3621: **13**; *Mohd Shah & Sidek* MS 1085: **3**; *Mohd Shah et al.* MS 3304: **8a**; *Motley* 374: **19**.

Nais et al. SNP 3672: **20**; *Native Collector* D 157: **12**; *Ng* FRI 1684: **7;** FRI 20965: **3**; *Ngadiman* SING0106185: **8a**; *Nielsen* 41: **20**; 273: **20**; 300: **5;** *Niyomdham* 3094: **8a**; *Nong Chie* SING0106354: **14**; *Nooteboom & Chai* 01829: **19**; *Nor Ezzawanis* FRI 54558: **15**.

Pauzi FRI 65258: **10;** FRI 65370: **10;** *Phillipps & Tan* SNP 0156: **20**; *Phillipps et al.* SNP 0148: **20**; SNP 2979: **11**; *Phillips* (1824): **8a**; *Phloenchit* 242: **8a**; 815: **8a**; *Phoon* FRI 60410: **8a**; *Pinmin* 174: **8a**; *Prayad* 439: **8a**; *Purseglove* P 4913: **2**; P 5530: **2**; *Purseglove & Mohd Shah* P 4760: **16**; P 4783: **16**.

Rafidah et al. FRI 52607: **8a**; *Rahim 2902*: **8a**; *Rahmat* 5913: **4**; *Rena et al.* S 43042: **6;** *Richards* R 5630: **20**; *Ridley* 2476: **12**; 3184: **12;** 1/1915: **1**; 9782: **3**; 12310: **3**; 16039: **13**; 16042: **3**; K000450475: **8a**; SING0106181: **8a**; SING0106182: **8a**; SING0106302: **3**; SING0106303: **3**; SING0106343: **12**; *Rimi et al.* KNP 09532: **20**; *Rosario* 3: **16**; *Runi & Yii* S 61143: **20**.

Said et al. BRUN 17623: **17**; *Sam* FRI 50144: **7;** S 91675: **19**; S 91886: **19**; *Sam & Basco* S 91693: **19**; *Sam & Jong* S 91706: **19**; *Sam et al.* FRI 44462: **18**; FRI 47110: **8a**; *Sands* 3974: **20**; *Sands & Johns* MS 5443: **20**; *Sands et al.* 5977: **19**; MS 6004: **20**; *Santisuk* 372: **8a**; *Saw* FRI 36335: **18**; FRI 37589: **18**; FRI 44393: **8b**; FRI 44950: **18**; *Scortechini* 1427: **3**; 466A: **3**; s.n., s.d.: **3**; *Seimund* 868: **1**; *Sinclair* 4769: **7;** SFN 38355: **12**; SFN 39109: **8a**; *Sinclair & Argent* 82-0823: **12**; *Sinclair & Kadim* 10308: **2**; S 10383: **16**; *Sinclair & Kiah* 38659: **3**; *Smitinand* 708: **8a**; BKF 46771: **8a**; *Spare* 1496: **3**; *Stevens et al.* 279: **12**; 346: **19**; *Stone* 7538: **2**; 13495: **3**; 14374: **7;** 14597: **7;** 14623: **8a**; 15220: **3**;

15505: **13**; *Strugnell* 14537: **3**; *Sumbing* SAN 127848: **11**; *Symington* FMS 35683: **20**; FMS 35770: **8**.

Tan S 28901: **12**; SING0106153: **18**; *Tay* 54: **20**; *Tay et al.* 89-0414: **20**; *Teruya* 880: **7;** *Teijsmann* 11215: **5;** *Thomas et al.* SNP 2482: **20**.

Ummul Nazrah et al. FRI 57110: **8a**.

Vogel, de et al. 8201: **11**.

Wallich 809B: **8a**; *Weber* 840723-2/1: **7;** 840803-1/2: **8a**; 840808-1/1: **8a**; UPM 3446: **13**; *Weber & Weber* UPM 04208: **8a**; UPM 4184: **3**; *Whitmore* FRI 12358: **13**; *Williams et al.* 1871: **8a**; *Winkler* 661: **12**; 1150: **16**; *Wong* WKM 1835: **11**; *Wong & Siow* WKM 316: **17**; *Wong et al.* WKM 2884: **11**; *Wray* 3809: **3**; *Wray & Robinson* 5430: **3**; 5504: **1**; *Wyatt-Smith* KEP 80147: **17**.

Yabainus KNP 14498: **18**; *Yahud et al.* S 87060: **19**; *Yalin* YS 43: **20**; *Yao* FRI 57996: **15**; FRI 65362: **8a**; FRI 65410: **8a**; *Yao & Chew* FRI 57999: **15**; FRI 65392: **8a**; FRI 65395: **8a**; *Yao & Lim* FRI 65288: **1**; *Yao et al.* FRI 55876: **10;** FRI 57940: **8a**; FRI 57948: **8a**; FRI 57953: **8a**; FRI 57968: **12**; FRI 57971: **12**; FRI 57975: **2**; FRI 57986: **15**; FRI 65371: **10;** FRI 65377: **7;** FRI 65445: **8b**; FRI 65450: **8a**; FRI 65454: **19**; FRI 65457: **11**; FRI 65458: **20**; FRI 74275: **11**; KNP A17116: **11**; *Yii* S 48458: **11**; *Yii & Abu Talip* S 58229: **11**; S 58230: **11**; *Yii & Banyeng* S 45998: **16**; *Yii & Runi* S 60575: **20**.

5.0 ECOLOGY, PHYTOGEOGRAPHIC PERSPECTIVES, AND CONSERVATION STATUS ASSESSMENT

5.1 Ecology

5.1.1 Altitudinal range

The altitudinal range of *Loxocarpus* species is wide, ranging from 5 m asl on sandy banks behind mangrove to 2200 m asl in montane forest (**Table 5.1**). However, most species occur in lowland forest (5–1000 m asl). The altitudinal range within a species is large in a few species, especially in the widespread species in Borneo such as *Loxocarpus stapfii*, *L. verbeniflos*, *L. violoides* and *L. repens*. They reach lower montane forest (1500–1900 m asl). Only *Loxocarpus violoides* reaches upper montane forest (2200 m asl). Interestingly, altitudinal range separates the only two widespread Peninsular Malaysian species, *Loxocarpus incanus* (below 850 m asl) and *L. caeruleus* (above 900 m asl).

5.1.2 Habit and habitat

Loxocarpus species generally grow in high humidity and shaded habitats. Many *Loxocarpus* are lithophytic and can be found on sandstone and granite, but are never found on limestone. Populations are often found on rock outcrops in streams or riverbanks and on wet dripping cliffs, less often on boulders in forest. Some species also occur on mossy earthbanks and in sandy heath forest. Populations growing on earthbanks tend to have longer rootstocks or a creeping habit. This might be because of more water and nutrients available for the plant to gain and sustain longer stem and more extensive root system. *Loxocarpus stapfii* populations growing on the summit and along the summit ridge of Gunung Pueh (Sarawak, Borneo) have a smaller and much thicker lamina compared with populations elsewhere, which might be due to increase in light intensity and lower humidity.

Table 5.1. The altitudinal range of *Loxocarpus* species. The list is arranged in incremental order of columns 'Min.' and 'Max.'. Bullet (●) indicates species confined to, 500 m asl or below in column A and 900 m asl or above in column B. *Loxocarpus* sp. B and C are excluded from the list due to lack of altitudinal data.

Species	**Altitude (m asl)**		**Altitudinal**	**A**	**B**
	Min.	**Max.**	**Difference (m)**		
Loxocarpus stapfii	5	1500	1495		
L. taeniophyllus	10	220	210	●	
L. coodei	10	350	340	●	
L. verbeniflos	10	1650	1640		
L. incanus var. *sekayuensis*	15	350	335	●	
L. violoides	25	2200	2175		
L. conicapsularis	30	100	70	●	
L. argenteus	35	100	65	●	
L. tunkui	50	550	500		
L. incanus var. *incanus*	80	850	720		
L. repens	90	1900	1810		
L. rufescens	150	1000	850		
L. sericiflavus	200	1000	800		
L. sericeus	250	250	0	●	
L. angustifolius	250	1850	1600		
L. pauzii	315	500	185	●	
L. holttumii	365	500	135	●	
Loxocarpus sp. A	460	460	0	●	
L. caulescens	500	1000	500		
L. meijeri	500	1000	500		
L. semitortus	900	1100	200		●
L. caeruleus	900	1800	900		●

Flower structure is plastic corresponding to their environment. *Loxocarpus violoides* and *L. semitortus* (both collected from above 1000 m asl) grown in the KEP nursery sometimes produced flowers with four stamens. The same has been observed in some *Streptocarpus* Lindl. (Gesneriaceae) in E (Möller, *pers. comm.*), a genus characterised by 2 stamens but nursery-grown plants produce flowers with two or four stamens. During a trip to Lata Puteh (Perak, Peninsular Malaysia), I observed that *Loxocarpus incanus* var. *incanus* populations persisting in a tree-fall gap across the rocky stream produced flowers with 6–7 corolla lobes.

5.1.3. Pollination

The colouration and structure of *Loxocarpus* flowers suggest that it is most probably insect pollinated. Attraction for pollinator observed in *Loxocarpus* includes (i) colour contrast; (ii) yellow exposed stamens (promise of reward) and (iii) glandular hairs.

The eight dark purple stripes down the corolla throat in *Loxocarpus semitorta*; the dark purple anthers and filament contrasting with paler corolla of *L. argenteus* and the purple 'eyes' of *L. stapfii* are the examples for colour contrast to guide the insect to the corolla mouth. Yellow exposed filaments and large yellow anthers as pollen-dummies are observed in *L. caeruleus* (Weber & Kiew, 1983) and flat-faced corolla species in Group B. Glandular hairs on corolla inner surface that give glistening appearance that might functions to attract insect are observed in *L. caerulea*, *L. holttumii*, *L. rufescens*, and *L. sericiflavus*. A morphological adaptation is the bulgy base of campanulate corolla that functions as a 'landing stage' is observed in *L. holttumii*, *L. sericiflavus*, and *L. rufescens*.

The nectary of *Loxocarpus* species, when present, is often vestigial, thus I believe pollen is the reward for the pollinator. The photographic record (**Plate 4 c**) of a *Trigona* bee with filled pollen baskets visiting *Loxocarpus holttumii* flowers in its natural habitat support this view. Self-pollination is very unlikely in *Loxocarpus* because plants of both Group A and B species kept in KEP nursery never set fruit. The style elongate after the flower fully opened. It shows that flowers of *Loxocarpus* species are protandrous and facilitate cross-pollination.

5.1.4 Dispersal

Dispersal by rain drops from canopy is the most logical postulation for a *Loxocarpus* seed dispersal mechanism, based on the capsule shape and habitat preference.

Loxocarpus capsules are held horizontally on an erect peduncle and the seeds contained within are tiny. Both splash cup and the gutter-shaped splitting capsule in *Loxocarpus* are suggested to disperse seeds by large water drops that drip through the canopy after rain (Kiew, 2009).

Raindrop-dispersed seeds may be bounced several meters away from the parent plant (Kiew, 2005). Short distance dispersal might contribute to high endemism as the speciation is driven by isolation (Blanc, 2002 quoted by Kiew, 2009) and this is true for *Loxocarpus.*

The seeds probably germinate immediately when they settle on a favourable site. When dispersal was prevented in a bagged plant of *Loxocarpus incanus* var. *incanus*, seedlings germinated within fruit capsule (Kiew, *pers. comm*.).

5.2 Phytogeographic perspectives

5.2.1 Geographic distribution and endemism

Loxocarpus is confined to Sundaland (**Fig. 5.1**), with species confined either to C Sumatra or Peninsular Thailand and Peninsular Malaysia or Lingga Archipelago or Borneo. Only *Loxocarpus rufescens* and *L. stapfii* are distributed in W Borneo, and with one record from Pulau Temiang (Lingga Archipelago). The W Coast of Peninsular Malaysia is notably poor in *Loxocarpus* species diversity, where *Loxocarpus semitortus* is the only narrowly endemic species, and the widespread *L. caeruleus* and *L. incanus* var. *incanus* are found. In contrast, species confined to E Borneo, namely *Loxocarpus repens*, *L. verbeniflos* and *L. violoides*, are widely distributed.

Endemism is high in *Loxocarpus* species. Out of 24 taxa treated in this revision, 17 taxa (*c.* 71 %) are narrowly endemic and are found in not more than 5 localities. Borneo

and Peninsular Malaysia have the highest number of narrowly endemic taxa (7 each), followed by Sumatra (2), Lingga Archipelago (1) and none in Peninsular Thailand.

Generally, species that occur on granite, such as *Loxocarpus incanus* and *L. caeruleus,* are more widespread, while species confined to sandstone, such as *L. argenteus, Loxocarpus holttumii,* and *L. sericiflavus,* are narrowly endemic.

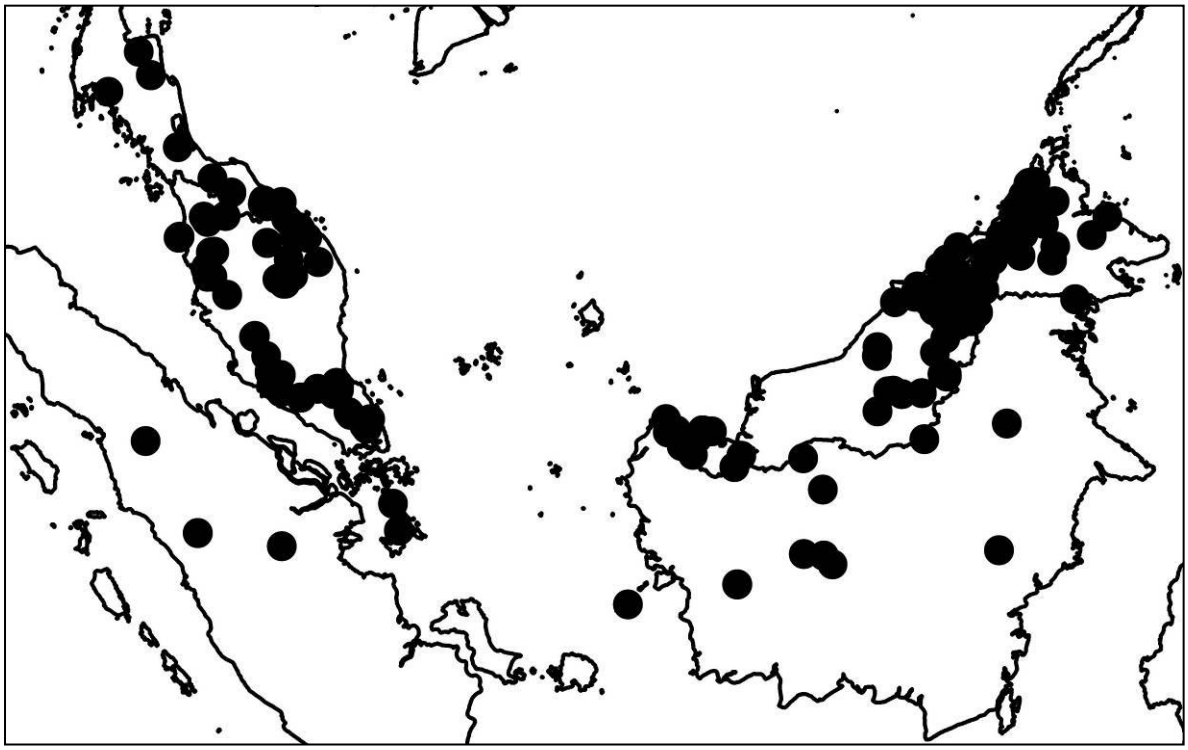


Fig. 5.1. The distribution of *Loxocarpus* species.

5.2.2 Phytogeographic perspectives of *Loxocarpus* species

The land connection between Sumatra, Peninsular Malaysia and Borneo existed during the Cenozoic (Holloway & Hall, 1998) and continuous forest cover across these regions at the last Glacial Maximum (Cannon *et al*., 2009) explains the continuous distribution range across Sumatra, Peninsular Malaysia and Borneo.

Table 5.2. Geographical distribution of *Loxocarpus*. [E] denotes narrowly endemic species.

Peninsular Malaysia (and P. Thailand) species	**Borneo (including Karimata Island) species**	**Sumatra species**	**Lingga Archipelago species**
Loxocarpus angustifolius [E]	*Loxocarpus argenteus* [E]	*Loxocarpus caulescens* [E]	*Loxocarpus sericeus* [E]
L. caeruleus	*L. conicapsularis* [E]	*L. meijeri* [E]	*L. stapfii*
L. holttumii [E]	*L. coodei* [E]		
L. incanus var. *incanus*	*L. repens*		
L. incanus var. s*ekayuensis* [E]	*L. rufescens*		
L. pauzii [E]	*L. stapfii*		
L. semitortus [E]	*L. taeniophyllus* [E]		
L. sericiflavus [E]	*L. verbeniflos*		
L. tunkui [E]	*L. violoides*		
	Loxocarpus A [E]		
	Loxocarpus B [E]		
	Loxocarpus C [E]		

5.2.2.1 The demarcations of phytogeographic areas

The demarcations of phytogeographic regions pertinent to *Loxocarpus* distribution are briefly discussed, and 'overlaid' on its distribution range.

All Peninsular Malaysian species are confined to the south of Kangar-Pattani Line (**Fig. 5.2**, line A–B) proposed by Whitmore (1984) except for *L. incanus* var. *incanus*, which extends northward to Surat Thani, Peninsular Thailand. Five Bornean species are confined to the north of Pontianak-Sipitang line (**Fig. 5.2**, line C–D) proposed by Ashton (1992) despite its proportionately small area. They are *Loxocarpus argenteus*, *L. coodei*, *L. taeniophyllus*, *Loxocarpus* sp. A and *Loxocarpus* sp. C.

Several Bornean species are rather widely distributed but none is distributed throughout Borneo. These species are limited to particular regions often marked by geographical barriers. *Loxocarpus repens* is distributed to the north of Batang Rajang and E Borneo; *L. rufescens* is distributed to the west of Batang Lupar and highlands in SW

Borneo; *L. stapfii* is common in NW Borneo and extends to Kapuas basin and the highlands of Central Borneo, with a stray distribution in the Lingga Archipelago.

5.2.2.2 Notable distribution patterns

(i) Group A and B — **Fig. 5.3**

Group A and B species find their limit at a N–S conceptual line (**Fig. 5.2**, line E–F) drawn across the middle of Borneo connecting Bintulu and Banjarmasin. This line to certain extend corresponds with geological feature of Borneo Island. W Sarawak is part

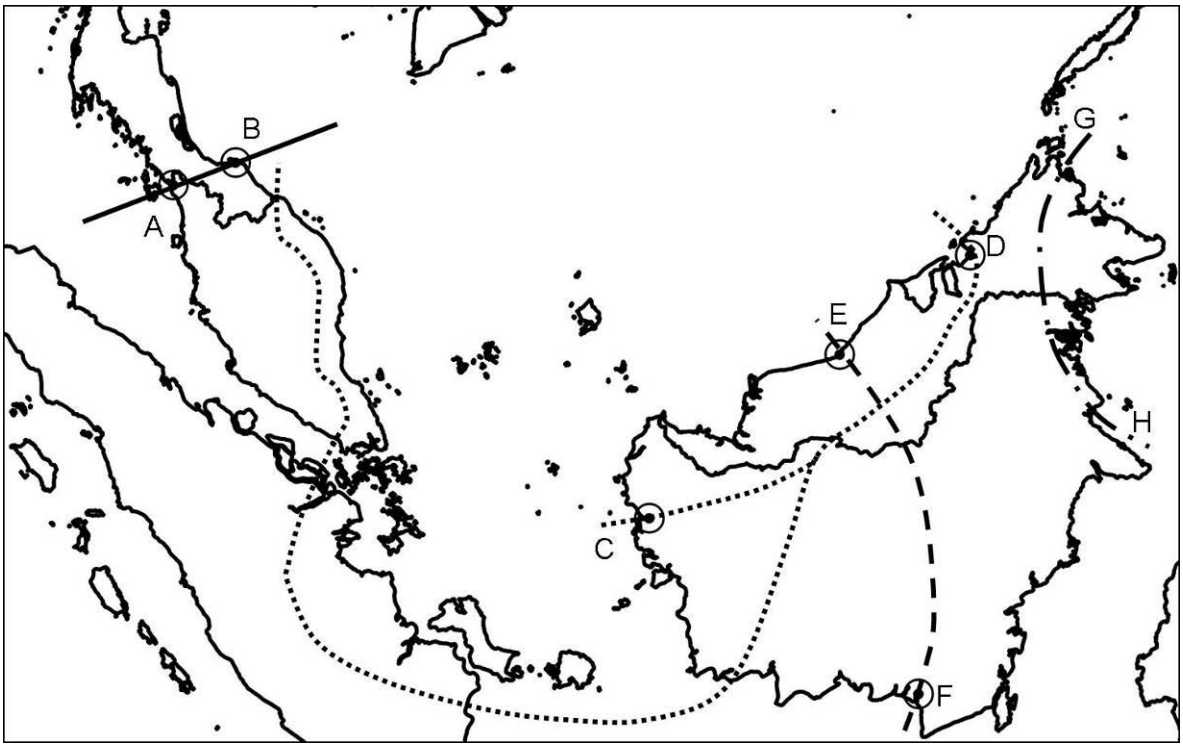


Fig. 5.2. The demarcations of phytogeographic regions pertinent to *Loxocarpus* distribution. Square dotted line marks 'Riau Pocket' defined by Ashton (1992); line G–H marks E Coast Sabah sub-province (Wong, 1998). (A=Kangar; B=Pattani; C=Pontianak; D=Sipitang; E=Bintulu; F=Banjarmasin).

of the ancient Sunda Shield dated to *c*. 80 million years old (Cretaceous and older) (Hazebroek & Abang Kashim, 2000). W & S Kalimantan also belong to this continental shelf area. In contrast, C and N Sarawak are dominated by rocks younger than *c*. 80 millions years (Late Cretaceous and Tertiary). Group B species distribution in Karimata Island is a dubious record (see **Section 4.5**, note under *Loxocarpus conicapsularis*).

(ii) Riau Pocket

Throughout the discussion below, I refer to the Riau Pocket as defined by Corner (1960), in which he included S Johor, Singapore, the Riau [Riouw] and Lingga Archipelagos, Bangka, Belitung [Biliton], W Borneo and SE Sumatra (the last with doubt) and Ashton's (1992, 1995) extension covering Peninsular Malaysia's E Coast and N Sarawak lowland and Brunei to Sipitang.

Loxocarpus confined in this area include *L. holttumii*, *L. sericiflavus* and *L. tunkui* in S Johor; *L. sericeus* in Lingga; *L. argenteus*, *L. rufescens*, *L. stapfii* and *Loxocarpus* sp. C in W Borneo; *L. conicapsularis*, *L. coodei*, *L. taeniophyllus* and *Loxocarpus* sp. A in N Sarawak lowland and Brunei to Sipitang. Widespread species such as *Loxocarpus incanus* (both varieties), *L. repens*, *L. verbeniflos* and *L. violoides* also occur in the Riau Pocket. The figures below illustrate the species richness of *Loxocarpus* in the Riau Pocket: 50 % are confined to it while 71 % can be found within it. No doubt, the Riau Pocket is the centre of speciation and morphological diversity for *Loxocarpus* (but if Ashton's extension is not taken into account, flat-faced corolla species, Group B, is not found within the Riau Pocket). Notably, the narrowly endemic species that grow on sedimentary rock outcrops in S Johor and NW Sarawak contribute to the species richness.

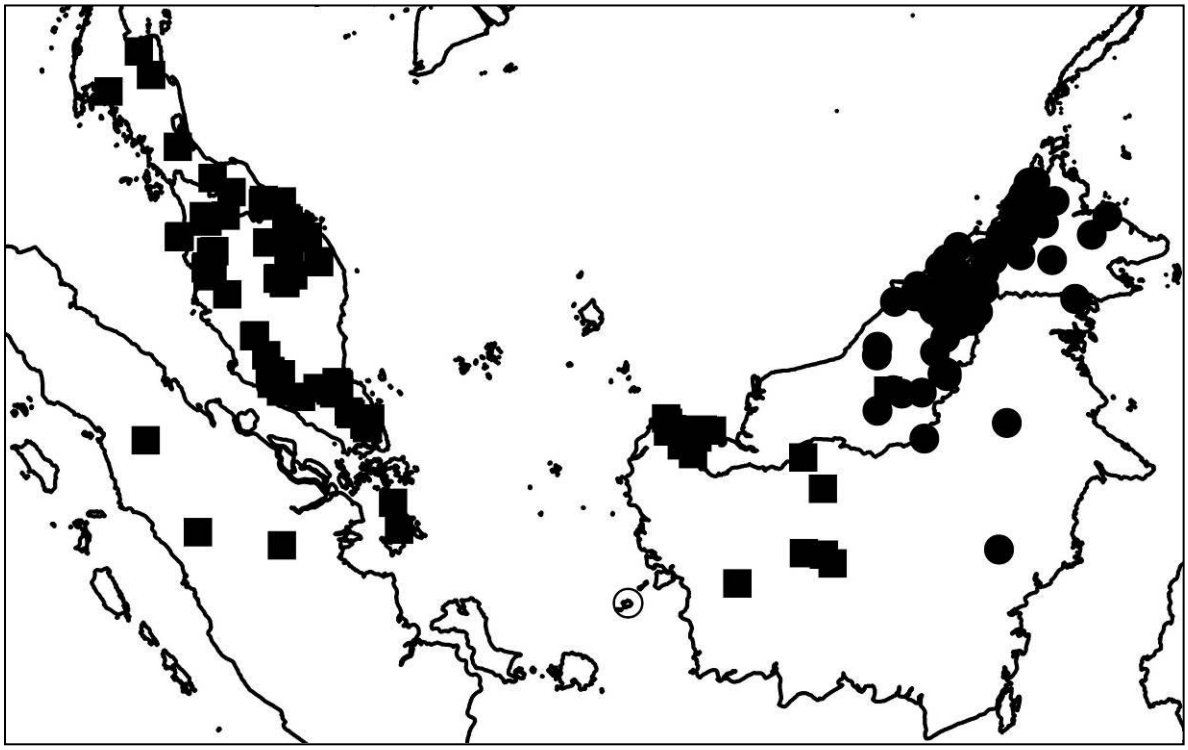


Fig. 5.3. Distribution of the two main flower morphological groups of *Loxocarpus*: Group A (■) and B (●).

Some notable morphological similarities are observed in some species confined within Corner's Riau Pocket, especially those occur in S Johor and NW Sarawak, *viz*. silky shiny hairs on upper lamina surface are shared by *Loxocarpus argenteus* and *L. tunkui* and the presence of short glandular hairs on the inner surface of corolla lips is shared by *Loxocarpus holttumii*, *L. rufescens* and *L. sericiflavus*.

Kaplan *et al*. (2002a, b) quoted by Bird *et al*.(2005) considered that throughout Sundaland during the last glacial maximum (with prolonged dry period), small tracts of S Malaya (Peninsular Malaysia), CE Sumatra and NW Borneo had the least possibility to have been covered in open vegetation. These areas coincide with the Riau Pocket, which might have played a role as refugia.

(iii) The absence of *Loxocarpus*

The distributions of *Loxocarpus* markedly absent from continuous tracts of land. This might due to the absence of suitable habitat, mainly because of large open water bodies, such as peat swamp in S Borneo; swampy delta of Lupar and Rajang Rivers; and Chini and Bera lakes in Pahang. Botanical undercollecting of these areas, notably C Sumatra may also be another reason.

At the specific level, *Loxocarpus incanus* var. *incanus* is not found in the high mountains along the Main Range. This species can be found at lower altitudes (850 m asl) in the foothills of Main Range, *viz.* Bukit Kutu (Selangor, Peninsular Malaysia). *Loxocarpus caeruleus*, a widespread highland species recorded from a few solitary mountains and ranges is absent in some botanically well-explored mountains along the Main Range. The reason for this is unknown.

5.2.2.3 'Stray' Record

Populations of *Loxocarpus incanus* var. *incanus* and *L. verbeniflos* 'stray' out of their typical geographical range into regions with marked seasonality.

Loxocarpus incanus var. *incanus* crosses the Kangar-Pattani Line into Peninsular Thailand and extends northward into Surat Thani (9°N) to the very northern boundary of Sundaland (Bird, 2005), where it is recorded in evergreen forest on rocks by streams which Whitmore (1984) called 'gallery forest' along water courses. This observation concurs with Iwatsuki (1973) records of Malesian element pteridophytes on Khao Luang (8˚30'N, 99˚40'E).

Loxocarpus verbeniflos extends to Sandakan, which falls in the E Coastal Sabah Sub-province (Ashton, 1992) influenced by marked seasonality (Wong, 1998). Field observation confirmed that *Loxocarpus verbeniflos* can only be found on shaded earth

banks or sandstone rock faces under canopy. In short, both species are confined to their typical ecological niche.

5.3 Conservation Status Assessment

5.3.1 The Rationale

There are no weedy species of Gesneriaceae in Malaysia and very few can survive long in disturbed habitats (Kiew, 2009) and this applies to *Loxocarpus* species. In fact, *Loxocarpus* species are confined to specific habitats and most species are narrowly endemic. Hence, disturbance of the locality and the habitat would bring about population or ultimately species extinction. Therefore, assessing the conservation status of these species and identifying the threats to their populations are of supreme importance.

To date, none of the *Loxocarpus* species had been evaluated for its conservation status based on the IUCN Red List Categories and Criteria Version 3.1 (2001). Moreover, the conservation status of *Loxocarpus* species outside Peninsular Malaysian has never been assessed.

5.3.2 Methodology

Conservation assessment based on IUCN Categories and Criteria (IUCN Version 3.1 (2001) was carried out using 'Conservation Assessment Tools' version 1.2 (Moat, 2007) executed in ArcView 3.2a (Environmental Research Institute Inc., US).

Distribution maps for each species assessed were plotted. The locality of occurrence includes both current and historic locations based on geo-referenced herbarium specimens examined in this study. Extent of Occurrence (EOO), Area of Occupancy (AOO) and number of locations were calculated. AOO was calculated using a 2 × 2 km grid (area of 4 sq. km) per location record. The occurrence of population(s) within Protected Areas is also

taken into account in the assessment. Information on the Protected Areas was obtained from protectedplanet.net (http://www.protectedplanet.net). The areas are recognised by World Commission on Protected Areas (WCPA). Also, areas under the protection of various legislations in Malaysia are also considered as Protected Areas. Conservation status was proposed for all species follows IUCN Version 3.1 (2001) Red List Categories.

5.3.3. Results and Conclusion

The results of conservation status assessment of *Loxocarpus* species are summarised in **Table 5.3** and the Red List Category in **Table 5.4**. Throughout the discussion below, the figures presented refer to the criteria's threshold value for Red List Category evaluation (IUCN, 2001).

Out of 24 taxa assessed, 5 (21 %) fall in threatened categories (CR, EN). *Loxocarpus sericeus*; *Loxocarpus* sp. B and *Loxocarpus* sp. C are confined to one locality and their AOO is less than 10 sq. km. The quality of their habitat is also continuously declining. Thus, these species meet the criteria B2ab(iii) and fall within 'Critically Endangered' category. The ambiguity of *Loxocarpus* sp. C occurrence within Protected Area is because Tanjong Po (Sarawak, Borneo), the only locality might fall within a light house area (Siali, *pers. comm*.), where Bako National Park has no authority on it. *Loxocarpus holttumii* is confined to three localities with AOO less than 500 sq. km while *L. incanus* var. *sekayuensis* is confined to 4 localities with EOO less than 5000 sq. km. The quality of their habitat is declining continuously. Thus, both fall within the 'Endangered' category, fulfilling B2ab(iii) and B1ab(iii) criteria respectively.

Twelve species fall within 'Near Threatened' category despite of all or part of their populations occur within Protected Areas. The reason for this is that the species are confined to, one locality and AOO is less than 10 sq. km for *Loxocarpus argenteus*, *L.*

meijeri, *L. pauzii*, *L. semitortus* and *Loxocarpus* sp. A; 2–5 localities and the EOO is less than 5000 sq. km for *L. angustifolius*, *L. conicapsularis*, *L. coodei*, *L. sericiflavus*, *L. taeniophyllus* and *L. tunkui* except for *L. caulescence* where EOO is less than 20000 sq. km.

Table 5.3. Area of Occupancy (AOO), Extent of Occupancy (EOO), number of collections, number of locations and the occurrence within Protected Areas for *Loxocarpus* species (n.a.=not available).

Taxon	No. Collection	No. Locality	EOO (sq. km)	AOO (sq. km) (2×2 km cell)	Within Protected Areas
Loxocrpus angustifolius	12	4	41	16	Yes
L. argenteus	11	1	n.a.	4	Yes
L. caeruleus	38	7	20672	28	Yes
L. caulescens	3	3	16140	12	Yes
L. conicapsularis	7	3	717	12	Yes
L. coodei	4	4	1613	16	Yes
L. holttumii	18	3	n.a.	12	No
L. incanus var. *incanus*	69	40	153744	160	Yes
L. incanus var. *sekayuensis*	9	4	2274	16	No
L. meijeri	2	1	n.a.	4	Yes
L. pauzii	4	1	n.a.	4	Yes
L. repens	53	32	167585	128	Yes
L. rufescens	30	6	38161	24	Yes
L. semitortus	17	1	n.a.	4	Yes
L. sericeus	3	1	n.a.	4	No
L. sericiflavus	8	3	62	12	Yes
L. stapfii	26	14	206251	56	Yes
L. taeniophyllus	6	3	77	12	Yes
L. tunkui	8	4	9	16	Yes
L. verbeniflos	46	30	65947	120	Yes
L. violoides	54	32	35697	128	Yes
Loxocarpus sp. A	4	1	n.a.	4	Yes
Loxocarpus sp. B	1	1	n.a.	4	No
Loxocarpus sp. C	1	1	n.a.	4	Yes (ambiguous)

Table 5.4. Summary for Red List Categories of *Loxocarpus* taxa.

Red list categories	**Species**	**Total**
Extinct (EX)	Nil	0
Extinct in the Wild (EW)	Nil	0
Critically endangered (CR)	*Loxocarpus sericeus*; *Loxocarpus* sp. B and *Loxocarpus* sp. C	3
Endangered (EN)	*Loxocarpus holttumii* and *L. incanus* var. *sekayuensis*	2
Vulnerable (VU)	Nil	0
Species threatened		**5**
Near Threatened (NT)	*Loxocarpus angustifolius*; *L. argenteus*; *L. caulescens*; *L. conicapsularis*; *L. coodei*; *L. meijeri*; *L. pauzii*; *L. semitortus*; *L. sericiflavus*; *L. taeniophyllus*; *L. tunkui* and *Loxocarpus* sp. A	12
Least Concern (LC)	*Loxocarpus caeruleus*; *L. incanus* var. *incanus*; *L. repens*; *L. rufescens*; *L. stapfii*; *L. verbeniflos* and *L. violoides*	7
Data Deficient (DD)	Nil	0
Not Evaluated (NE)	Nil	0
Taxa evaluated		**24**

All the species that fall within the ‘Least Concern’ category are widely distributed with EOO greater than 20000 sq. km. Notably, *Loxocarpus caeruleus* which previously was common on Taiping Hills (Perak, Peninsular Malaysia) are not found there on recent searching trips.

In a nutshell, habitat protection is the most important measure to safeguard plants.

6.0 GENERAL DISCUSSION AND CONCLUSIONS

6.1 General discussion

6.1.1 Expanded generic concept

Prior to the present study, *Loxocarpus* was defined solely based on morphological characters. However, the character (or combination of characters) used to circumscribe the genus (or sometimes as a section) was not well defined. The impression of *Loxocarpus* as a taxon defined by its short capsule less than 10 mm long is based only on Peninsular Malaysian species. In fact, a Bornean species which had long been included in *Loxocarpus*, *L. verbeniflos*, has a capsule 9–20 mm long. It is now clear that this problem arose because the genus had never been revised in its entirety. Strictly speaking, the inclusion of *Loxocarpus violoides* with capsules measuring up to 30 mm long does not change the generic definition of *Loxocarpus*. It just extends the range of capsule length.

It is difficult to define *Loxocarpus* using morphological characters due to its similarity to *Henckelia sensu* Weber & Burtt (1998 [‘1997’]). However, corolla shape is a useful character to define grouping (see **Section 2.8**) within *Loxocarpus*. Its flower characteristic support the inclusion of *Loxocarpus violoides* (=*Henckelia violoides*) into *Loxocarpus* despite its long capsule. This was predicted based on its flat-faced flower that links it with other Bornean *Loxocarpus* (Group B, flat-faced corolla) species.

Moreover, this finding is well supported by the molecular phylogenetic study. *Henckelia violoides* (*Loxocarpus violoides*) placed in BORL (**Section 3.4**) which is distant from Bornean *Henckelia* (*sensu* Weber & Burtt) (= *Codonoboea*) clade (Lim, C.L., *unpublished data*).

In the very last stages of this study, I found that *Henckelia alternifolia* (C.B.Clarke) B.L.Burtt might be better placed within *Loxocarpus* due to its leaves arrangement and indumentum. In fact, all Bornean *Henckelia* species with short-tubed or flat-faced corolla should be carefully re-examined and be included in future molecular phylogenetic studies in order to attain a natural classification for the Asian twisted-fruited genera.

6.1.2 Accepting paraphyletic *Loxocarpus*

Both Maximum parsimony (MP) (**Fig. 3.12**) and Bayesian inference (BI) (**Fig. 3.14**) analyses of molecular data showed that *Loxocarpus* is paraphyletic and that it nested in the Asian and Malesian twisted-fruited genera clades. This was a rather unexpected result because *Loxocarpus* species have straight capsules. An analogy is observed in African and Malagasy Gesneriad molecular phylogenetic studies: *Linnaeopsis* Engl. (= *Streptocarpus* Lindl.), *Saintpaulia* H. Wendl. and *Schizoboea* (Fritsch) B.L.Burtt are nested within *Streptocarpus* (Möller & Cronk, 2001b) but *Streptocarpus* species are readily distinguished by their twisted capsules as opposed to the other genera with straight capsules.

Phylogenetically, clades of *Loxocarpus* are still unstable. Sumatran *Loxocarpus* species with caulescent stem were not included into phylogenetic analyses and the Bornean species were also underrepresented. Close sister relation of two Australasian *Boea* species with *Senyumia minutiflora* and *Spelaeanthus chinii* forming a highly supported clade (PP = 100) is at present inexplicable. The latter two are endemic to Peninsular Malaysian and restricted to limestone hills. The position of this clade within *Loxocarpus* clades raises another perplexing question. Molecular phylogeny study of Asian twisted-fruited genera is on-going in Royal Botanic Garden Edinburgh. The inclusion of more Australasian species in molecular analyses might retrieve a different topology since Australasian *Boea* positioned close to *Loxocarpus* group (see **Fig. 3.14**).

However, *Loxocarpus* is clearly different from the sister taxa (see **Section 3.6** & **Fig. 3.15**) on morphological grounds. Recognition of paraphyletic genera is not exceptional and is sometimes inevitable and its theoretical and practical aspects rationales can be argued (Brummitt, 1997, 2002; Brummitt & Sosef, 1998; Sosef, 1997; Hörandl, 2006, 2007). However, others possess contrasting views (Ebach *et al*., 2006; Freudenstein, 1998; van Welzen, 1997, 1998; Wiley, 2009) and some have proposed other alternative classification methods (Hörandl, 2010; Stuessy & König, 2008).

Basic ideas behind Linnaean taxonomy are practicality and clear characters (Brummitt, 1997). Splitting the unstable *Loxocarpus* clades, which shared common characters into smaller monophyletic clades is not a wise choice. Great similarity of testa surface pattern is observed across Sumatran, Bornean and Peninsular Malaysian species (Beaufort-Murphy, 1983). Thus, for the time being, I retain *Loxocarpus* as a single paraphyletic genus.

For future study, I recommend a third marker complementing *trnL-F* and ITS to be acquired and analysed in order to confirm the topology of all Asian twisted fruited taxa. Inclusion of more Bornean, Sumatran and Australasian taxa is also much anticipated.

6.1.3 Dispersal and speciation–a projection of phylogenetic results and biogeographic perspectives

To correlate the biogeographic pattern of *Loxocarpus* species in the light of morphological and phylogenetical groupings, I used a phylogenetic tree to interpret the geographic distribution pattern. BI analyses trees showed better resolution among the twisted-fruited genera and this result is in concurrence with those of Möller *et al*. (2009)

findings. Thus, I used **Fig. 3.14** for the discussion below but I also refer to other trees where applicable.

Basal clades in tree **Fig. 3.14** consist mainly of Chinese and Indo-Chinese taxa, with a few widely distributed species reaching Malesia. All *Loxocarpus* species are placed in the derived end, which I call the 'deepest grade consisting of all *Loxocarpus* clades'. These clades are confined to West Sundaland.

LISG (**Section 3.4**) is a compact clade characterised by long-branch attraction grouping (**Fig. 3.11**). Also, it is morphologically diverse. I treated all the species within this clade as conspecific under *Loxocarpus incanus*. This is the most widespread species in, and as yet confined to Peninsular Malaysia (it reaches Peninsular Thailand south of 9˚N) even before the inclusion of *Henckelia sekayuensis* and *Loxocarpus minima*. Field observation on *Loxocarpus incanus* populations (Kiew, R., *pers. comm.*) in Endau Rompin State Park (Johor, Peninsular Malaysia) found that they are very localised and consisting of a small number of individuals each. I postulate that populations of *Loxocarpus incanus* are experiencing a process of rapid speciation. In other words, endemics with much confined distribution are in the making.

In BORL clade, all species except *Loxocarpus argenteus* possess flat-faced (saintpaulioid) corolla (Group B, see **Section 2.8**). Notably, Group B species are confined to the east of Bintulu–Banjarmasin line (**Fig. 5.2**). Species with Group A corolla also occur in Borneo but are confined to the west of Bintulu–Banjarmasin line. The flat-faced flower might be a derived character, probably as the outcome of allopatric speciation in Borneo and it is also an indicative of west-east dispersal.

PMAL clade consists of narrowly distributed species confined to Peninsular Malaysia and a relatively widely distributed Western Borneo species, *Loxocarpus rufescens*.

This species has a campanulate corolla, placing it close to other Peninsular Malaysian species. The disjunct distribution of this clade needs explanation.

Most *Loxocarpus* species occur in moist forested area sheltered from strong wind. Morphological attributes of capsules (**Plate 2b**, **5c inset**, **7c**, **8e**, **9e**, **12b**) and seeds (Banka & Kiew, 2009; Beaufort-Murphy, 1983) of *Loxocarpus* species suggest they are raindrop ballistic dispersed plants. Hence, long distance dispersal in recent times is very unlikely. The plausible explanation for PMAL disjunct distribution is that they are relicts (or descendants of relict species, which I call PMAL element below) of once widely distributed taxa.

Sundaland rainforest is currently in refugial stage and forest cover of lowland evergreen rainforest and upland evergreen rainforest areas were substantially greater during last glacial maximum (Cannon *et al*., 2009). Glacial cycles exposed and submerged the low-lying land mass of Sunda Shelf, which acted as a land bridge and on the other hand, a factor of geographic isolation. PMAL elements might once have been widely distributed on the Sunda Shelf during glacial maximums. In this context, glacial cycles also acted as pressure for PMAL taxa speciation.

Forest cover is more stable in the inland of East Borneo during the last glacial period (Wurster *et al*. 2010) compared with Ashton's Riau Pocket area due to land-sea area fluctuations and environmental changes. Compared to the widely distributed BORL species in E Borneo, extant PMAL species are relict of PMAL elements speciated due to geographical isolation and fragmented habitat pressures. This can explain the more derived position of PMAL relative to BORL.

By correlating the paleoenvironment findings of Sundaland and molecular phylogenetic study, I envisage that LISG, a widespread species group with a campanulate corolla speciated and acquired the flat-faced corolla when dispersed eastward via Sunda

Shelf to E Borneo. The flat-faced element persisted and further speciated sympatrically in E Borneo. PMAL element with a campanulate corolla was widely distributed on the Sunda Shelf during glacial maximums. The extant Riau Pocket PMAL taxa are the product of diverging speciation due to fragmented habitat pressure during this refugial period. This also explains the position of PMAL at the most derived end.

Möller & Cronk (2001a) postulated the dispersal direction and probable colonisation events of *Streptocarpus* based on clocked ITS sequence data. In this study, I am not able to map the phylogenetic tree with paleogeographical and paleoenvironmental changes such as the land bridge occurrence and forest cover continuity through time because I do not clock the molecular sequences.

6.2 Conclusions

This is the first monographic study of all *Loxocarpus* taxa since its establishment in 1839. Based on morphological and phylogenetic results, *Loxocarpus* is reinstated as a paraphyletic genus. The definition of *Loxocarpus* is now expanded to include species with flat-faced flowers and longer capsules (> 10 mm long). Materials better representing geographical distribution and morphological variation were available for the present study. Intermediate morphological forms were found between closely related species and the better field notes from recent collections led to a better understanding of habitat-induced characters. In the present taxonomic treatment, I have adopted a broad species concept, especially for morphologically variable and widespread species. My species concept was shaped mainly based on morphological characters with phylogenetic results used as supporting data.

Twenty three species are recognised in this taxonomic treatment, including 15 species reinstated, five new combinations, six species synonymised with one recognised as a variety, four species determined as novelties, and an enumeration of six incompletely known taxa. I concur with Banka & Kiew (2009) in excluding *Henckelia papillosa*. A summary of the name changes is provided in **Table 6.1**. Now, there are nine species represented in Peninsular Malaysia (one extending into Peninsular Thailand), 12 species in Borneo and 4 species in Sumatra and Lingga Archipelago. None except one is shared between these four regions.

Bornean and Peninsular Malaysian species were re-instated or transferred based on both morphological and molecular data. Unfortunately, two caulescent species from Sumatra were not included in the molecular phylogenetic study so are re-instated as *Loxocarpus* based solely on their leaf indumentum and capsule length.

Table 6.1. Summary of name change of *Loxocarpus* species as a result of this study.

Accepted names	**Basionyms**	**Synonyms**
Loxocarpus angustifolius Ridl.		*Henckelia stenophylla* A.Weber
Loxocarpus argenteus B.L.Burtt		*Henckelia argentea* (B.L.Burtt) B.L.Burtt
Loxocarpus caeruleus (Ridl.) Ridl.	*Didymocarpus caerulea* Ridl.	*Henckelia caerulea* (Ridl.) A.Weber
Loxocarpus caulescens B.L.Burtt		*Henckelia caulescens* (B.L.Burtt) A.Weber & B.L.Burtt
Loxocarpus conicapsularis (C.B.Clarke) B.L.Burtt	*Didymocarpus conicapsularis* C.B.Clarke	*Roettlera conicapsularis* (C.B.Clarke) O.Kuntze; *Henckelia conicapsularis* (B.L.Burtt) A.Weber & B.L.Burtt

Loxocarpus coodei (B.L.Burtt) T.L.Yao, *comb. nov.*	*Henckelia coodei* B.L.Burtt	
Loxocarpus holttumii M.R.Hend.		*Henckelia ericii* A.Weber
Loxocarpus incanus R.Br. var. *incanus*		Homotypic: *Loxonia*? *alata*, Wallich; *Loxocarpus alatus* A.DC.; *Loxocarpus alata* R.Br.; *Didymocarpus incanus* (R.Br.) C.B.Clarke; *Roettlera alata* (A.DC.) O.Kuntze; *Henckelia browniana* A.Weber; Heterotypic: *Loxocarpus minima* Ridl.; *Henckelia minima* (Ridl.) A.Weber, *syn. nov*.
Loxocarpus incanus R.Br. var. *sekayuensis* (Banka & Kiew) T.L.Yao, *comb*. & *stat. nov*.	*Henckelia sekayuensis* Banka & Kiew	
Loxocarpus meijeri B.L.Burtt		*Henckelia meijeri* (B.L.Burtt) A.Weber & B.L.Burtt
Loxocarpus pauzii T.L.Yao, *sp. nov*.		
Loxocarpus repens B.L.Burtt		Homotypic: *Henckelia procumbens* B.L.Burtt Heterotypic: *Henckelia gardneri* B.L.Burtt, *syn. nov.*
Loxocarpus rufescens (C.B.Clarke) B.L.Burtt	*Didymocarpus rufescens* C.B.Clarke	Homotypic: *Roettlera rufescens* (C.B.Clarke) O.Kuntze; *Henckelia rufescens* (C.B.Clarke) B.L.Burtt Heterotypic: *Didymocarpus johannis-winkleri* Kraenzl.
Loxocarpus semitortus (C.B.Clarke) Ridl.	*Didymocarpus semitortus* C.B.Clarke	*Roettlera semitorta* (C.B.Clarke) O.Kuntze

Loxocarpus sericeus (Ridl.) B.L.Burtt	*Didymocarpus sericeus* Ridl.	*Henckelia sericea* (Ridl.) A.Weber
Loxocarpus sericiflavus (Kiew & Banka) T.L.Yao, *comb. nov*.	*Henckelia sericiflava* Kiew & Banka	Heterotypic: *Henckelia anthonysamyi* Banka, *syn. nov*.
Loxocarpus stapfii (Kraenzl.) B.L.Burtt	*Didymocarpus stapfii* Kraenzl.	Homotypic: *Henckelia stapfii* (Kraenzl.) B.L.Burtt Heterotypic: *Didymocarpus longipetiolatus* Merrill; *Loxocarpus longipetiolatus* B.L.Burtt; *Henckelia longipetiolata* (B.L.Burtt) B.L.Burtt *syn. nov.*
Loxocarpus taeniophyllus (B.L.Burtt) T.L.Yao, *comb. nov*	*Henckelia taeniophylla* B.L.Burtt	
Loxocarpus tunkui Kiew		*Henckelia tunkui* (Kiew) A.Weber
Loxocarpus verbeniflos (C.B.Clarke) B.L.Burtt	*Didymocarpus verbeniflos* C.B.Clarke	*Roettlera verbeniflos* (C.B.Clarke) O.Kuntze; *Henckelia verbeniflos* (C.B.Clarke) B.L.Burtt Heterotypic: *Didymocarpus petiolaris* C.B.Clarke; *Roettlera petiolaris* (C.B.Clarke) O.Kuntze; *Loxocarpus petiolaris* (C.B.Clarke) B.L.Burtt; *Henckelia petiolaris* (C.B.Clarke) B.L.Burtt, *syn. nov*.
Loxocarpus violoides (C.B.Clarke) T.L.Yao, *comb. nov*.	*Didymocarpus violoides* C.B.Clarke	Homotypic: *Roettlera violo*[*i*]*des* (C.B.Clarke) O.Kuntze; *Henckelia violoides* (C.B.Clarke) B.L.Burtt Heterotypic: *Henckelia diffusa* B.L.Burtt, *syn. nov*.
Loxocarpus sp. A		
Loxocarpus sp. B		

Loxocarpus sp. C

With larger sampling included in this study, the molecular phylogenetic analyses results showed that *Loxocarpus* forms a paraphyletic entity together with a few Asian twisted-fruited genera. However, the groupings (see S**ections 3.5.2**) based on morphological data within *Loxocarpus* are congruent and consistent when compared with molecular data analyses results. Ecological data, such as habitat preference, altitudinal range, and distribution pattern studies are supporting the species circumscription in this treatment.

Ecological aspects of *Loxocarpus* species are presented and the study showed that habit is correlated with habitat. Pollination and dispersal as inferred from morphology and observation are discussed. The Ashton's Riau Pocket was determined as the centre of highest species diversity (16 taxa). Seventeen out of 24 taxa are narrowly endemic (*c*. 71 %). Lastly, the conservation status for all species was assessed. Five out of 24 taxa (*c*. 21 %) fall within threatened categories.

In a nutshell, all the objectives of this study have been achieved. Detailed species descriptions, nomenclature, distribution maps, and user-friendly key(s) to species are provided. *Loxocarpus* is confirmed as distinct from Indian *Henckelia* and Malesian *Henckelia*(= *Codonoboea*) based on molecular biology study. *Loxocarpus* is paraphyletic based on molecular datasets. *Loxocarpus* is reinstated as a paraphyletic genus with a revised circumscription characters (see **Section 4.2**) to include species with flat-faced flower and longer capsule (> 10 mm long). The reticulated epidermal cell pattern of the testa surface may prove to be a good unifying character for species in the genus *Loxocarpus*. However, this is at present speculative.

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Appendix 1

No.	Character	Character States	Score
	Habit and Leaves		
1	habit	rosette	1
		caulescence	2
2	leaves arrangement	alternate or spiral	1
		opposite	2
3	distance between leaves	crowded at the top	1
		well-spaced below, crowded at the top	2
4	petiole and lamina ratio, qualitative	petiole shorter than lamina	1
		petiole shorter or about the same length or longer than lamina	2
		petiole longer than lamina	3
		petiole longer than lamina or about the same length	4
5	lamina upper surface hairs, density and orientation	sparse, erect, spreading in all direction	1
		sparse, adpressed, spreading in all direction	2
		dense, somewhat neatly pointing towards lamina apex	3
6	lamina thickness, qualitative	thick	1
		moderately thick	2
		very thin	3
7	lamina margin	finely serrulate	1
		serrulate	2
		finely crenulate	3
		crenulate	4
		entire	5
		shallowly crenate	6
		serrate	7
		coarsely serrate	8
8	lateral veins extended from leaf base	present	1
		absent	2
	Inflorescence and Flower		
9	inflorescence branching	simple cyme	1
		simple cyme or branched	2
		branched and never a simple cyme	3
10	flower number in an inflorescence	not more than 2	1
		3 or more	2
11	flower type	shortly tubular	1
		tubular-campanulate	2
		campanulate	3
		tube very short	4
12	flower limbs	flared	1

		deeply dissected and wide spreading	2
		flat (saintpaulioid)	3
13	flower position	normal	1
		tilted	2
		resupinate	3
14	corolla colour	lilac-violet-bluish tone	1
		white	2
15	filaments thickness	slender	1
		thickened	2
16	filament colour	white	1
		yellow	2
		deep purple	3
17	anthers position	included within corolla tube	1
		projected beyond corolla tube, exposed	2
18	anther colour	white	1
		pale yellow, dull	2
		yellow	3
		deep violet	4
19	staminode number	numeric no.	
20	stigma position	exposed	1
		included within corolla tube	2
21	stigma shape	punctiform	1
		capitate	2
		peltate	3
		2-lobed	4
	Fruit		
22	capsule position	orthocarpic	1
		plagiocarpic	2
23	capsule shape	ovoid	1
		obliquely conical	2
		cylindric	3
24	capsule valves	straight	1
		slightly curved	2
		slightly twisted	3
		twisted	4
25	capsule dehiscence	both upper and lower sides	1
		upper side	2
		split into 4 valves	3
26	splitting of capsule, shape	in to a splash cup	1
		into a trough	2
		in between splash cup and trough shape	3
		to the base	4

27	capsule length	more than 20 mm	1
		10 mm or less	2
28	capsule thickness	at least 2 mm	1
		less than 2 mm	2

Appendix 2

Sp. no.		habit	leaves arrangement	distance between leaves	petiole and lamina ratio, qualitative	lamina upper surface hairs, density and orientation	lamina thickness, qualitative	lamina margin
1	*Henckelia anthonysamyi*	1	1	1	1	3	2	4
2	*Henckelia argentea*	1	1	1	3	3	2	5
3	*Henckelia browniana*	1	1	1	2	3	1	2
4	*Henckelia ericii*	1	1	1	3	3	1	3
5	*Henckelia gardneri*	1	1	2	2	1	1	3
6	*Henckelia minima*	1	1	1	2	3	2	2
7	*Henckelia rufescens*	1	1	1	1	3	2	5
8	*Henckelia sekayuensis*	1	1	1	2	3	2	2
9	*Henckelia semitorta*	1	1	1	3	3	1	4
10	*Henckelia sericiflava*	1	1	1	2	3	2	4
11	*Henckelia stenophylla*	1	1	1	1	3	2	5
12	*Henckelia verbeniflos*	1	1	2	2	2	2	5
13	*Henckelia violoides*	1	1	1	2	3	2	1
14	*Boea hygroscopica*	2	1	1	0	1	1	6
15	*Boea magellanica*	0	1	1	0	0	0	0
16	*Orchadocarpa lilacina*	1	2	1	2	1	3	6
17	*Emarhendia bettiana*	2	2	1	4	1	3	7
18	*Senyumia minutiflora*	2	2	1	1	1	3	7
19	*Spelaeanthus chinii*	2	2	2	4	1	3	7

Appendix 2

Sp. no.	lateral veins extended from leaf base	inflorescence branching	flower number in an inflorescence	flower type	flowers limbs	flower position	corolla colour	filaments shape	filament colour	anthers position	anther colour	staminode number
1	1	3	2	3	1	1	1	1	1	1	2	3
2	2	1	1	4	2	1	1	1	3	2	4	3
3	1	2	2	2	1	1	1	1	1	1	1	3
4	1	3	2	3	1	1	1	1	1	1	2	3
5	1	3	2	4	3	2	1	2	2	2	3	2
6	1	2	2	2	1	1	1	1	1	1	1	3
7	2	2	2	3	1	1	1	1	1	1	2	3
8	1	2	2	2	1	1	1	1	1	1	1	3
9	1	1	1	1	1	1	1	1	1	1	2	3
10	1	3	2	3	1	1	1	1	1	1	2	3
11	2	2	2	1	1	1	1	1	1	1	2	3
12	1	1	1	4	3	2	1	2	2	2	3	2
13	1	1	1	4	3	2	1	2	2	2	3	3
14	0	3	2	4	3	2	1	2	2	2	3	3
15	0	1	1	4	3	2	1	2	0	2	3	0
16	2	3	2	4	3	1	1	1	1	2	3	3
17	1	3	2	2	1	1	1	1	1	1	1	2
18	2	3	2	2	4	3	2	1	1	2	3	0
19	1	3	2	3	1	1	2	1	1	1	1	0

Appendix 2

Sp. no.	stigma position	stigma shape	capsule position	capsule shape	capsule valves	capsule dehiscence	splitting of capsule, shape	capsule length	capsule thickness
1	2	2	2	2	2	2	3	2	1
2	1	2	2	2	2	2	3	2	1
3	1	2	2	1	1	2	1	2	1
4	1	2	2	2	1	2	2	2	1
5	1	3	2	1	2	2	1	2	1
6	1	2	2	1	1	2	1	2	1
7	1	2	2	2	1	2	2	2	2
8	1	2	2	1	2	2	1	2	1
9	2	2	2	2	2	2	3	2	1
10	2	2	2	2	2	2	3	2	1
11	2	2	2	2	1	2	3	2	2
12	1	3	2	3	1	2	2	1	2
13	1	3	2	3	2	2	2	1	2
14	1	4	1	2	4	3	4	1	1
15	1	0	1	2	4	3	4	1	1
16	1	2	1	1	3	1	4	2	2
17	1	3	2	2	1	2	2	2	2
18	1	1	1	2	3	1	4	2	2
19	1	1	1	2	1	1	4	2	1