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REASSESSMENT OF THE GENERIC STATUS OF CODONOBOEA (GESNERIACEAE) AND ITS SPECIES

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SUMMARY

The genus *Codonoboea* Ridley is reduced to sectional level within *Didymocarpus*. Section *Codonoboea* is distinguished by its epiphyllous flowers. It includes four species: *Didymocarpus corneri* Kiew (a new species), *D. ericiflorus* Ridley, *D. lilacinus* Ridley, and *D. niveus* (Kiew) Kiew. *Didymocarpus caelestis* (Ridley) Kiew and *D. leucocodon* (Ridley) Kiew, both of which Ridley placed in *Codonoboea*, are excluded from sect. *Codonoboea*.

INTRODUCTION

Ridley (1893) described *Didymocarpus lilacinus* from the lowlands of the Tahan valley and noted that he did not know any species closely allied to it. He drew attention to its inflorescence, which he wrote "seems to arise from the middle of the petiole, but in reality what appears to be the base of the petiole is a short branch from which the leaf also springs." In 1905, Ridley refrained from placing *D. lilacinus* in any section of *Didymocarpus* regarding it as of doubtful affinity. He again drew attention to the inflorescence which is adnate to the petiole and noted this species might perhaps be generically distinguished.

In 1915, Ridley described two montane species from Gunung Tahan, *Didymocarpus ericiflorus* and *Paraboea leucocodon*. *Didymocarpus ericiflorus*, which he noted was allied to *D. lilacinus* in its "connature of the axillary peduncle of the inflorescence to the petiole in the groove of which it seems to be imbedded." In the campanulate corolla and short stamens, Ridley noted that *D. lilacinus* and *D. ericiflorus* differed from *Paraboea* species, which have anthers that are free and ovate (not reniform or connivent), nor are there rudiments of a second pair of stamens. He considered that *D. lilacinus* and *D. ericiflorus* "may well form a distinct section, if not a genus."

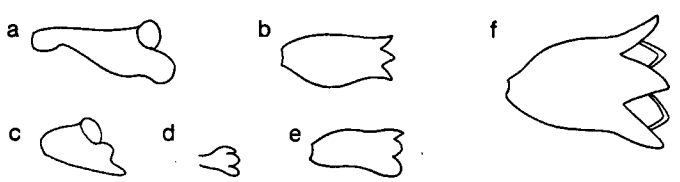

Fig. 1. Corolla shapes in *Didymocarpus*. — a. *D. niveus*; b. *D. ericiflorus*; c. *D. corneri*; d. *D. lilacinus*; e. *D. caelestis*; f. *D. leucocodon*; all × 1.70.

Ridley (1915) noted that *Paraboea leucocodon* was not clearly allied to any other species known to him. It has large (2.5 cm long) campanulate corollas and connivent stamens. However, the peduncle is not adnate to the petiole but is an axillary cyme bearing 1–4 flowers.

In 1923 Ridley transferred these three species to a new genus, *Codonoboea,* which in his key to the genera he distinguished from species of *Didymocarpus* by their campanulate corolla with a short tube and short, thick, sinuate filaments, and from species of *Paraboea* by their gibbous corolla with tooth-like lobes. However, the corolla lobes of *Codonoboea lilacina* are broad and rounded. It is also not clear what Ridley meant by a gibbous corolla as in fact there is no difference in shape between the campanulate corollas of species of *Codonoboea* and *Paraboea* sect. *Campanulati.*

It is difficult to understand why *Paraboea leucocodon* was grouped with *Didymocarpus lilacinus* and *D. ericiflorus.* It differs in habit (it is a robust plant) and its opposite leaves that grow at the top of a long bare stem with a thick corky bark, the peduncle which arises from the leaf axil and is free from the petiole, the inflorescence which is cymose with 1–4 flowers, the corolla which is broadly campanulate with acute lobes and the capsule which is thick. With the inclusion of *Paraboea leucocodon,* it is not surprising that the genus *Codonoboea* is poorly defined and that it is difficult to distinguish from *Didymocarpus* and *Paraboea* sect. *Campanulati.* This is compounded by none of its species having a pronounced gibbose corolla.

In 1929, Ridley described a further species, *Codonoboea caelestis* from Kelantan, which, however, produces solitary flowers on long pedicels from the leaf axils. It differs from the other three species in being densely silky, and in its leaves being arranged in a compact tuft at the top of the stem.

Recently, another *Codonoboea* species, *C. nivea,* was described (Kiew, 1987). This species is closely similar to *C. lilacina* in habit, in its soft, narrowly lanceolate, distant leaves with a toothed margin, its epiphyllous flowers and its extremely slender pedicels. It differs in its larger flowers, which are distinctly gibbose. It also shares the same habitat: both species grow in the lowlands on steep earthbanks devoid of other vegetation.

In 1935, Corner collected in Trengganu another species, which is closely similar to *Codonoboea lilacina* and *C. nivea* in habit, habitat and in possessing epiphyllous flowers. This is described as a new species, *Didymocarpus corneri,* below.

THE EPIPHYLLOUS CONDITION IN CODONOBOEA

The flowers of these species arise on the petiole either in a series in a groove (*Didymocarpus lilacinus, D. ericiflorus* and *D. niveus*) or on a raised crest (*D. corneri*). They are displaced between 5 to 25 mm from the leaf axil and in *D. corneri* onto the midrib. New flowers arise acropetally with between one flower (*D. corneri*) and five to eight flowers (*D. niveus*) open at a time. The pedicels of the young buds are recurved, but straighten and elongate as they develop. A series of flowers and fruits are produced which are orientated in the same direction. The pedicels persist long after the capsule has disintegrated.

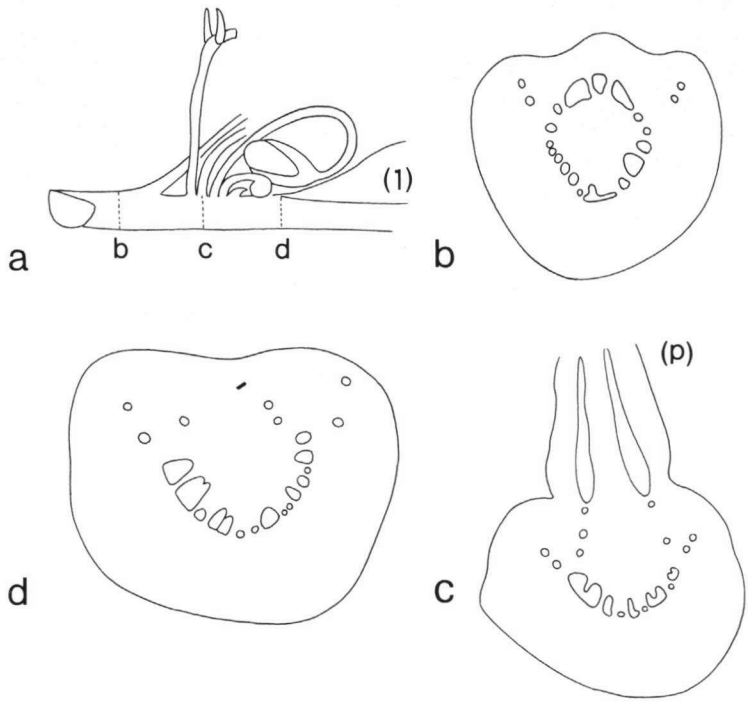

Fig. 2. Epiphyllous flowers on the petiole of *Didymocarpus corneri* Kiew. a. Transverse sections showing the arrangement of vascular bundles in the petiole; b. behind the flowers; c. beneath the flowers; d. above the flowers. — (l) = lamina; (p) = pedicel.

The condition of epiphylly in these species is comparable with that of *Streptocarpus gardenii* (Jong, 1978), which produces inflorescences from the petiole. In this species the vasculature of the petiole below the inflorescences is cylindrical, the adaxial portion of which separates and enters the peduncle. Above the flowers the vasculature of the petiole is crescentic in TS with a narrow gap adaxially. In *Didymocarpus corneri*, the xylem does not form a complete cylinder in the proximal part of the petiole (fig. 2b), in TS the vascular bundles are arranged in a circle and the large adaxial bundles enter the pedicels (fig. 2c). Above the flowers the vasculature of the petiole is crescentic (fig. 2d).

Dickenson & Sattler (1975) have discussed the morphological implications of epiphylly in *Helwingia japonica* (Helwingiaceae), which exhibits the same pattern of vasculature as the above two species. They conclude that epiphylly in *H. japonica* results from the activity of a basal intercalary meristem positioned proximally to the inflorescence primordium, which was initially more or less axillary, so that as the petiole elongates the inflorescence primordium is carried up the leaf. They point out there is a continuum between the epiphyllous and axillary condition depending on the degree of activity of this meristem.

The series of flowers of both these four epiphyllous *Codonoboea* species and those in sect. *Heteroboea*, where the flowers are basically axillary, are produced in the manner described and figured by Weber (1975) for *Chirita elphinstonia*, where the first bud does not use up the whole inflorescence meristem and from the remaining portion another bud develops and so on to produce acropetally a series of accessory buds. This process gradually shifts the youngest bud up the petiole or midrib to what Weber calls a "somewhat epiphyllous" position. This process is also seen in *Didymocarpus albomarginatus* (sect. *Didymanthus*), where a series of cymose inflorescences is produced on a crest until the youngest is shifted 6–7 mm from the axil.

Wood (1974) suggested that in *Chirita* epiphylly is beneficial in enhancing the attractiveness of the flowers to the pollinator as the flowers, which are white in the epiphyllous species, are positioned to contrast with the green leaf. (The non-epiphyllous species of *Chirita* have purple flowers.) However, in *Didymocarpus* there is no correlation between flower colour and the epiphyllous condition and indeed the sessile leaf as seen in species of sect. *Heteroboea* creates the same condition of bringing the flower close to the contrasting background of the green lamina. Flower colour in sect. *Heteroboea* ranges from white, to pink or pale purple, to deep purple or red. The pollination biology of these species remains unknown.

THE GENERIC STATUS OF CODONOBOEA

Is it possible to define the genus *Codonoboea* precisely? And if so, how is it distinguished from *Didymocarpus*, which now includes the species previously grouped under *Paraboea* sect. *Campanulati* (Burtt, 1971)?

First the anomalous *Codonoboea leucocodon* and *C. caelestis* should be excluded from *Codonoboea* for the reasons given above. The salient feature that then distinguishes *C. lilacina*, *C. ericiflora* and *C. nivea*, from all other species of *Didymocarpus* in Peninsular Malaysia is the epiphyllous inflorescence. These species in addition have erect, wiry stems with distant, lanceolate leaves. The lowland species are also conspicuous by their particularly slender pedicels.

Unlike *Loxocarpus* and *Chirita* (both genera with two stamens which are closely related to *Didymocarpus*), species of *Codonoboea* do not have a 'Gestalt' that makes them immediately recognisable in the field. *Loxocarpus* and *Chirita* are distinguished by additional characters too: *Loxocarpus* by its habit, indumentum, inflorescence, small purple flowers and short, squat fruits and *Chirita* by its limestone habitat and spathulate stigma. *Codonoboea* s.str. can be distinguished from *Didymocarpus* by the single character of the epiphyllous inflorescence.

But is the epiphyllous inflorescence a good character by which to distinguish a genus in the Gesneriaceae? Some species of *Chirita*, which Wood (1974) placed in sect. *Microchirita*, have epiphyllous inflorescences. However, this section is distinguished from the other two by additional characters of habit, leaf arrangement and division of the calyx. In any case while the majority of species in sect. *Microchirita* have epiphyllous inflorescences, a few have axillary inflorescences.

In view of the fact that species of *Codonoboea* differ from species of *Didymocarpus* in just a single character, the epiphyllous inflorescence, and not in characters of the corolla, stamens, stigma and fruit, this genus is reduced to sectional level within *Didymocarpus*.

While the definition of sections of *Didymocarpus* in Peninsular Malaysia and the species they comprise need re-examination, it is preferable to keep these four species separate for, as Ridley noted in 1893, they do not show close affinity with any other section.

In habit and in their erect, wiry stems and distant lanceolate leaves they come closest to species such as *D. hispidus* Ridley and *D. robinsonii* Ridley of sect. *Didymanthus*. However, their leaves are thinner, they do not have cymose inflorescences and their flowers are smaller.

Didymocarpus section Codonoboea

Didymocarpus sect. *Codonoboea* (Ridley) Kiew, *stat. nov.* — *Codonoboea* Ridley, Fl. Mal. Pen. 2 (1923) 533. — Lectotype: *Didymocarpus lilacinus* Ridley, Trans. Linn. Soc. II, 3 (1893) 330.

Inter sectione *Didymocarpo* floribus epiphyllo recedit.

Shrubby herbs with erect, wiry stems. *Leaves* lanceolate, alternate or opposite, spirally arranged, distant. *Flowers* epiphyllous, that is, flowers arise from a series of accessory shoots displaced at least 5 mm from the leaf axil, the youngest flower being produced distally. *Capsule* medium-sized and slender.

Distribution. There are four species in Peninsular Malaysia, in Johore, Pahang, and Trengganu.

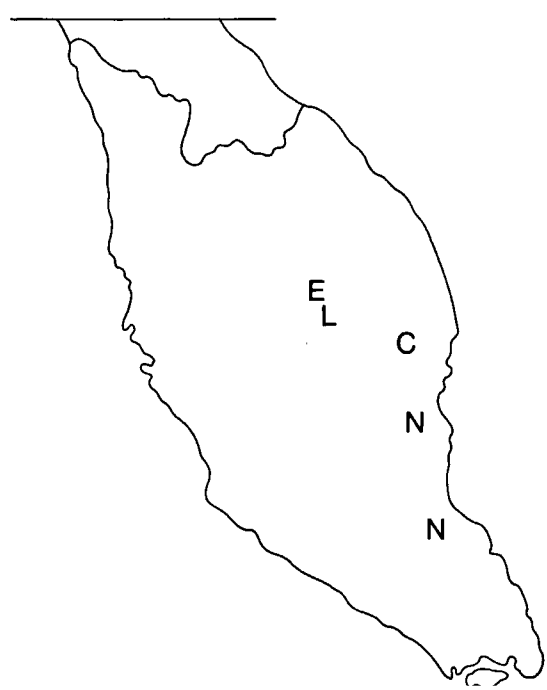

Fig. 3. Distribution of species of *Didymocarpus* sect. *Codonoboea* in Peninsular Malaysia. C = *D. corneri*; E = *D. ericiflorus*; L = *D. lilacinus*; N = *D. niveus*.

KEY TO THE SPECIES

1a. Leaves subcoriaceous, glabrous, opposite, margin entire, pedicels thick **2. D. ericiflorus**
b. Leaves chartaceous, softly hairy, alternate, margin toothed, pedicels extremely slender 2
2a. Corolla 20 mm long, gibbose with a narrow base; lamina of leaves viscid; capsule 3–3.5 cm long . . . . . **4. D. niveus**
b. Corolla 5–7 mm long, not gibbose; lamina of leaves not viscid; capsule to 2 cm long 3
3a. Leaf base rounded, margin finely dentate, petiole 15–33 mm long **1. D. corneri**
b. Leaf base decurrent, margin crenate, petiole 5 mm long . . . . **3. D. lilacinus**

1. Didymocarpus corneri Kiew, *spec. nov.* – Figs. 2, 4.

A *Didymocarpus lilacini* petiolatis longioribus, foliis basi rotundatis et margine minutus dentatis differt. — T y p u s: *Kiew RK 2655* (holo L; iso K, SING, UPM), Sg. Nipa, Trengganu.

Shrubby herb to 1.5 m tall, flowering at 15 cm tall, stem woody branching with 2–3 erect shoots. Indumentum of young stem, petiole, lower surface of midrib and veins, bracts, pedicel and calyx a densely matted layer of short appressed hairs. *Leaves* spirally arranged. *Lamina* narrowly lanceolate, sometimes slightly falcate, to 15.5 by 4 cm, apex narrowly attenuate to cuspidate, base rounded sometimes almost cordate, sometimes unequal, membraneous, young leaves whitish at base, soft, in dried state punctate above and below, upper surface softly hairy, densely covered by short hairs particularly on tertiary veins and by occasional long hairs, lower lamina

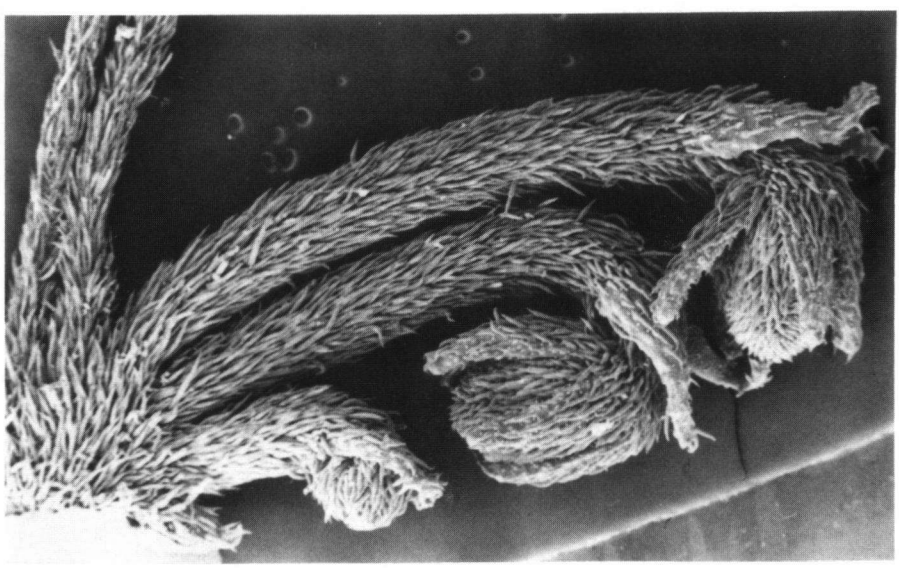

Fig. 4. A series of epiphyllous flowers of *Didymocarpus corneri* Kiew.

with scattered long hairs. Margin minutely dentate, sometimes bidentate. Midrib and veins plane above, prominent below, veins (14–)20(–28) pairs. Petiole slender, 1.5–3.3 cm long, upper surface plane proximally, grooved distally above flowers. *Flowers* produced distally from a series of accessory shoots on the petiole or rarely on midrib c. 10–25 mm from leaf axil, sometimes forming a crest 2 mm tall. First flower c. 1 mm distant from the rest, which are crowded together. One flower opens at a time. Pedicel very slender, curled in bud, elongating and becoming erect and 17–22 mm long in flower; then curving so that the fruit is positioned below leaf, persistent. Bracts 2, ligulate, 2 mm long. *Calyx* 2 mm long, almost divided to base; lobes 5, green, narrowly acute. *Corolla* broadly campanulate, 7 by 4 mm, minutely pubescent outside, white tinged pale mauve (*Kiew RK 2655*) or yellowish white (*Corner s.n.*), tube 3 mm long, lobes rounded 2.5 mm wide, upper 2 recurved, lower 3 straight and projecting 3 mm beyond the upper. *Stamens* 2, enclosed in corolla tube; filament thick, c. 3 mm long, geniculate at apex; anthers large, 1.7 by 1 mm, oblong, constricted in centre, connivent. *Ovary* oblong 2 by 1.5 mm, style 3 mm long, projecting beyond corolla tube, pale fawn, thick, columnar, ovary and style minutely pubescent; stigma minute, rounded. *Capsule* straight, narrowly cylindric, 20 by c. 1 mm, apex acuminate, minutely pubescent.

Distribution. Endemic to Peninsular Malaysia: Trengganu, Kemaman. Fig. 3.

Ecology. Very common on earthbanks and by streams in lowland forest, c. 100 m above sea level.

PENINSULAR MALAYSIA. Trengganu, Kemaman, Sg. Nipa, *Corner s.n.* (SING), 20 Nov. 1935, fl.; *R. Kiew RK 2655* (K, L, SING, UPM), 5 May 1988, fl.

Notes. Like *Didymocarpus lilacinus* and *D. niveus*, this species grows on steep earth banks in lowland forest. Compared with the other two species, it is common where it grows. However, its distribution appears local as it has not been found elsewhere in Trengganu.

In vegetative characters, it resembles *D. niveus* in its finely dentate leaf margin but in floral characters it is similar to *D. lilacinus* in the shape, size and colour of the corolla. However, it differs from both in its longer petiole and rounded leaf base. It is unusual among *Didymocarpus* species in that the pedicels curve after flowering so that the fruit is hidden under the leaf.

The species is named for E.J.H. Corner, who made two collecting trips to the area in June 1932 and October 1935, which yielded several novelties, including *Didymocarpus floribundus* (Henderson) Burtt.

2. Didymocarpus ericiflorus Ridley

Didymocarpus ericiflorus Ridley, J. Fed. Mal. States Mus. 6 (1915) 166. — *Codonoboea ericiflora* (Ridley) Ridley, Fl. Mal. Pen. 2 (1923) 533. — Type: *Ridley 16283* (holo K; iso SING), Gunung Tahan, Pahang.

Distribution. Endemic to Peninsular Malaysia: Pahang, Gunung Tahan. Fig. 3.

Ecology. Hill forest, c. 1000 m above sea level.

PENINSULAR MALAYSIA. G. Tahan, Wray's Camp, *Ridley 16283* (K; SING), July 1911, fl.; *Holttum 20709* (SING), 29 Aug. 1928, fl.

Notes. This species is rare and has only been collected twice. I was not able to refind it at the type locality.

Apart from the epiphyllous flowers and narrowly lanceolate distantly spaced leaves, this is the most disparate of the four species having opposite leaves with an entire margin and a subcoriaceous texture, and thick fruit stalks. In addition, unlike the other species it is montane.

3. Didymocarpus lilacinus Ridley

Didymocarpus lilacinus Ridley, Trans. Linn. Soc. II, 3 (1893) 330; J. Roy. Asiatic Soc. Str. Br. 43 (1905) 56. — *Codonoboea lilacina* (Ridley) Ridley, Fl. Mal. Pen. 2 (1923) 534. — Type: *Ridley 2165* (holo, K; iso SING), Tahan Valley, Pahang.

Distribution. Endemic to Peninsular Malaysia: Pahang, Tahan Valley. Fig. 3.

Ecology. Earthbanks devoid of other vegetation in lowland forest, c. 100 m above sea level.

PENINSULAR MALAYSIA. Pahang: Tahan Valley, 1893, *Native Coll. s.n.* (K); *Ridley 2165* (K, SING), July 1911, fl.; *Md. Nur s.n.* (SING), Sept. 1929; *Henderson SFN 24847* (K, SING), 7 June 1931; *Mohd Shah MS 2717* (SING); *R. Kiew RK 1216* (UPM), 5 Sept. 1982; *R. Kiew RK 2407* (UPM), 20 March 1987.

Notes. This species is known from one or two clumps along the Tahan Valley where it grows on steep earthbanks. Its very soft leaves wilt in dry spells when other undergrowth plants with more fleshy leaves, like *D. platypus* or sonerilas do not.

4. Didymocarpus niveus (Kiew) Kiew, *comb. nov.*

Codonoboea nivea Kiew, Mal. Nat. J. 41 (1987) 210. — Type: *Kiew B.H. KBH 86-33* (holo UPM; iso K, L, SING), Johore, Sg. Kinchin.

Distribution. Endemic to Peninsular Malaysia: Johore, Ulu Endau (G. Janing, Sg. Kinchin); Pahang, Sg. Lembing.

Ecology. Earthbanks devoid of other vegetation in lowland forests c. 100 m above sea level.

PENINSULAR MALAYSIA. Johore: G. Janing, *R. Kiew RK 2139* (UPM); Ulu Kinchin, *Kiew B. H. KBH 86-33* (K, L, SING, UPM), 26 May 1986, fl. — Pahang: Sg. Lembing, *Anthonysamy SA 569* (UPM), 25 Aug. 1986.

Notes. Although in vegetative characters it resembles *D. corneri* and *D. lilacinus*, it differs from these two species in its much larger corolla, which in size and shape of the lobes resembles the larger flowered species in sect. *Didymanthus* and *Heteroboea*. It differs from these, however, in its narrowly tubular base (fig. 1a) which gives it a gibbose shape not seen in these other species. It is also unique among Malayan *Didymocarpus* species in having a viscid leaf surface.

Compared with the other three species, it has a wider distribution and is known from three localities in the southeastern part of the Peninsula (fig. 3).

EXCLUDED SPECIES

Didymocarpus caelestis (Ridley) Kiew, *comb. nov.*

Codonoboea caelestis Ridley, Kew Bull. (1929) 259. — T y p e: *Henderson SFN 19683* (holo K; iso SING), Kelantan, Gua Musang.

D i s t r i b u t i o n. Endemic to Peninsular Malaysia: Kelantan, Gua Musang (Sg. Kerteh at Gua Ninik).

E c o l o g y. Streambanks in lowland forest.

PENINSULAR MALAYSIA. Kelantan-Gua Musang, Sg. Kerteh, *Md. Nur SFN 11964* (K, SING), 6 Feb. 1924; *Henderson SFN 19683* (CGE, K, SING), 26 Oct. 1927.

N o t e s. Although Md. Nur and Henderson recorded this species as common along the banks of the Sg. Kerteh near Gua Ninik, a recent visit (1987) shows that this area is now covered by oil palm to the very banks of the Sg. Kerteh, which now no longer support any wild or nonweedy species, except for *Homalomena humilis*. Unless populations of this species grow in the remote headwaters of the Sg. Kerteh, there is strong reason for believing this species is now extinct.

As mentioned above, this species does not have epiphyllous flowers and in its dense silky indumentum and dense tuft of sessile leaves, it does not resemble the four species now assigned to sect. *Codonoboea*. In habit, it most resembles species in sect. *Heteroboea*, but differs from them in its narrowly lanceolate leaves with entire margin and its smaller flowers. At present it is probably wisest not to assign it to a specific section.

Didymocarpus leucocodon (Ridley) Kiew, *comb. nov.*

Paraboea leucocodon Ridley, J. Fed. Mal. States Mus. 6 (1915) 167. — *Codonoboea leucocodon* (Ridley) Ridley, Fl. Mal. Pen. 2 (1923) 533. — T y p e: *Ridley 16041* (holo K; iso SING), Gunung Tahan, Pahang.

D i s t r i b u t i o n. Endemic to Peninsular Malaysia: Pahang, G. Tahan.

E c o l o g y. Common in shaded mossy montane forest, especially on ridges and in gullies from 1200–1700 m.

PENINSULAR MALAYSIA. G. Tahan, *Ridley 16041* (annotated by Ridley as *D. campanula*) (K, SING), July 1911, fl.; *Md. Nur SFN 20951* (SING), 30 Aug. 1929, buds; *R. Kiew RK 2448* (UPM), 25 March 1987, buds.

N o t e s. This species does not belong in sect. *Codonoboea* as it produces 1–4-flowered cymes from the leaf axils. Nor is it closely allied to any other species in Peninsular Malaysia. It has several unusual features not seen in other Malayan species, such as a thick, corky bark; turgid rather brittle leaves; the matted indumentum on the outside of the corolla, and acute corolla lobes.

It is a common species above Wray's Camp and below the stunted vegetation of the *padang* (Kiew, 1989). Apparently flowering gregariously, Ridley (1915) described it as "remarkable for its beautiful white bells."

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