

Uncorrelated variation in widespread species: species delimitation in *Strobilanthes echinata* Nees (Acanthaceae)

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Species that show high levels of infraspecific variation in several quantitative characters are often difficult to accommodate adequately in taxonomies. The recognition of a large number of formal taxa, at either specific or infraspecific rank, may suggest incorrectly that the variation is discrete and discontinuous. However, the alternative of recognizing a smaller number of variable taxa is resisted by some because this may conceal localized patterns of variation. The problem is particularly acute for taxa that occur over a large geographical area, because specimens taken from widely separated localities may appear very distinct when considered without reference to the full range of variation. The difficulty in delimiting *Strobilanthes echinata* Nees (Acanthaceae) highlights the problems taxonomists face in dealing with such widespread and variable taxa. This species has the characteristics of an ochlospecies, with multiple characters varying in an uncorrelated fashion across a wide geographical area. We recognize a single, widespread, and morphologically variable species, and reduce a large number of names to synonymy. We explain why we do not recognize formal infraspecific taxa and provide a detailed description of the variation seen in both vegetative and reproductive characters. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 156, 131–141.

ADDITIONAL KEYWORDS: infraspecific variation – ochlospecies – species concepts – traits.

INTRODUCTION

It is frequently observed that levels of infraspecific variation are not uniform within genera (Darwin, 1859; Hawkes, 1986; McDade, 1995; Cronk, 1998). Determining the limits of variable and often geographically widespread taxa is problematic and may lead to taxonomies that prove to be unstable, unworkable, and sometimes controversial. An extreme example is *Allophylus cobbe* (L.) Raeusch., widespread in the neo- and palaeotropics, which has been treated as either a single polymorphic species (Adema, Leenhouts & Van Welzen, 1994), or split into more than 169 separate species (Radlkofer, 1895; Leenhouts, 1967).

Recent taxonomic studies of *Strobilanthes* (Acanthaceae), a species-rich genus from South and South-

East Asia, have demonstrated that infraspecific variation is not homogeneous across the genus. Some species, such as *S. bibracteata* Blume, are relatively uniform morphologically, occupy a geographically restricted area, and pose few problems to delimit (Bennett & Scotland, 2003). Others, such as *S. cernua* Blume, *S. atropurpurea* Nees (= *S. wallichii* Nees), and *S. auriculata* Nees, exhibit a wide range of morphological variation across a broad geographical area that makes the determination of species boundaries less straightforward (Wood, 1994; Bennett & Scotland, 2003; Wood & Scotland, 2003). In *Strobilanthes*, one of the most problematic species to delimit has been *S. echinata* Nees, a species first described from Meghalaya in north-east India. As circumscribed here, it extends from the Himalayas through Burma, Thailand, Cambodia, Vietnam, and China to Malaysia and Indonesia. *Strobilanthes echinata* is one of several species of *Strobilanthes* that are readily recognizable by the short, condensed heads of flowers

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and prominent bracts that are often leaf-like, with the outer ones fully enclosing the innermost flowers. Working with herbarium specimens of *S. echinata* is particularly difficult because only one flower per inflorescence matures at a time, and specimens usually have only a single flower, from which it is often difficult or impossible to observe characters of the androecium and gynoecium. Accurate and detailed field notes of the floral structure are invaluable in understanding the species of this group, but, regrettably, are often inadequate or missing entirely.

In this taxonomic revision of *S. echinata*, we reduce a large number of names to synonymy. We have adopted the pattern-based phylogenetic species concept of Nelson & Platnick (1981: 12) – ‘the smallest detected samples of self-perpetuating organisms that have unique sets of characters’ – using observations of morphological characters from a large sample of herbarium specimens from across its geographical range. *Strobilanthes echinata* exhibits a wide range of continuous morphological variation that has no clear geographical pattern, a feature that is characteristic of ochlopecies. We discuss how taxonomists have accounted for morphological variation within other ochlopecies, and explain why we have avoided the use of formal infraspecific taxa in *S. echinata*.

RESOLVING COMPLEX MORPHOLOGICAL VARIATION IN A TAXONOMIC FRAMEWORK

All species show some degree of morphological variation when analysed finely enough, but very often this variation is too trivial or continuous to warrant formal recognition in a classification (Hawkes, 1986). When the pattern of morphological variation within a species becomes complex and extensive, traditional taxonomic treatments are often unable to accommodate it adequately (Whitmore, 1976). Although the use of infraspecific categories continues to be adopted by taxonomists (Hamilton & Reichard, 1992), there is often a lack of consistency in the way in which different categories are used (Stace, 1986; Hamilton & Reichard, 1992). One solution to this problem, as demonstrated by the last major treatment of *Strobilanthes* (Bremekamp, 1944), is the formal description of many narrowly defined species that differ from each other in only small degrees. Bremekamp’s approach to species delimitation was strongly criticized by Van Steenis (1957) for splitting populations into their smallest possible units. Although Bremekamp maintained that his species concept did not differ significantly from that of previous botanists of the Malesian region, such as Blume and Merrill (Bremekamp, 1959: 94), many of the species he rec-

ognized were local forms that could only be separated by insignificant differences by others (Van Steenis, 1957: 176). Alternatively, variation may be formally represented by a proliferation of infraspecific taxa. For example, more than 100 infraspecific taxa have been formally described in *Solanum nigrum* L. (Solanaceae), ranging in rank from subspecies to subforma and using a combination of up to four infraspecific ranks (PBI *Solanum* Project, 2007). If the morphological variation within these species is truly quantitative and continuous, the number of such finely divided taxa that could potentially be described is limited only by the density of specimen sampling.

The term ‘ochlopecies’, introduced by White (1962) for species that cannot be satisfactorily subdivided, is useful here. Although the term may be merely an excuse for excessive lumping (Mabberley, 1979), it may also represent a distinct form of infraspecific variation well suited for studies of evolutionary processes (Cronk, 1998). An ochlopecies may be maintained as a highly polymorphic species, but with a detailed account of the infraspecific variation, such as that given by White (1962) for *Diospyros mespiliformis* A.DC. (Ebenaceae). This was also the method adopted by Pennington (1969) for *Vavaea amicornum* Benth. (Meliaceae), where formal infraspecific taxa were not recognized because: (1) none of the variants were sufficiently correlated with geography; (2) different variants frequently occupied the same habitats and localities; (3) most variants were based on slight, often single, vegetative differences; and (4) it was believed that some variants had arisen polytopically. A similar situation is seen in *Alyxia reinwardtii* Blume (Apocynaceae), where many previously described species and infraspecific taxa were reduced to synonymy because of the continuous nature of the variation (Middleton, 2000). An alternative approach is to describe a series of infraspecific groups, but not give them formal taxonomic recognition, an approach adopted by Wasshausen & Wood (2004) for *Dicliptera squarrosa* Nees (Acanthaceae), by Clark (1994) for *Walsura pinnata* Hassk. (Meliaceae), and by Mabberley (1979) for *Chisocheton lasiocarpus* (Miq.) Valetton (Meliaceae). Although Mabberley (1979) recognized that many intermediates may be found between the ‘discrete’ morphological entities described, the recognition of formal taxonomic groups may suggest discrete taxa where none exist.

Recent treatments of *Strobilanthes* and related genera (Carine & Scotland, 2000; Moylan, Pennington & Scotland, 2002; Bennett & Scotland, 2003; Wood, Bennett & Scotland, 2003) have used the pattern-based phylogenetic species concept of Nelson & Platnick (1981), and have reduced many species described by Bremekamp (1944, 1957) to synonymy. In adopting the phylogenetic species concept, greater importance

was placed on the ability to readily diagnose species using morphological means than on species acting as descriptors of variation, gene flow, reproductive isolation, or other characteristics that alternative species concepts aim to capture. The status of infraspecific taxa under this phylogenetic species concept was clarified by Cracraft (1983). Non-diagnostic characters, which are often used as evidence for infraspecific ranks (Hamilton & Reichard, 1992), are not interpreted from a formal taxonomic standpoint, because such variation exists within the smallest taxonomic unit (Cracraft, 1983). Under this species concept, to continue with the use of subspecies and varieties renders these categories subjectively chosen descriptors of non-diagnostic variation that do not represent real entities (Cracraft, 1983). In not using infraspecific categories, the study of infraspecific variation is now shifted into the realm of population biology – investigating the dynamics of character change within and between populations. The recognition of fewer, widespread and variable species may be objected to by some (for example, Whitmore, 1976) for diminishing the utility of the classification for ecologists and foresters who wish to have finer degrees of variation formally accounted for. Greater insight into the patterns of variation that exist within ochlopecies, such as *S. echinata*, may be obtained using molecular data, such as amplified fragment length polymorphism (AFLP) and inter-simple sequence repeat (ISSR) analysis (for example, Patton & Smith, 1994; Brunell & Whitkus, 1997; Miller & Spooner, 1999; Broadhurst *et al.*, 2004; Kamada, Yamashiro & Maki, 2007).

TAXONOMIC TREATMENT

Strobilanthes echinata Nees in Wall., Pl. Asiat. Rar. 3: 85. 1832. *Strobilanthes pectinata* T. Anderson in J. Linn. Soc., Bot. 9: 474. 1867, *nom. superfl.* *Goldfussia echinata* (Nees) N.P. Balakr., Fl. Jowai, 2: 355. 1983. *Type*: INDIA. Meghalaya, *F. da Silva* in *Wallich 2356* (lectotype: K-W, designated here).

Dicliptera crenata Miq., Fl. Batavia 2: 844 (1858). *Type*: INDONESIA. Sumatra, *T. Horsfield s.n.* (isotype: BM).

Strobilanthes pectinata var. *daltonii* C.B. Clarke in Hook. f., Fl. Brit. Ind. 4: 447. 1884. *Strobilanthes echinata* var. *daltonii* (C.B. Clarke) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 274. 1944. *Goldfussia echinata* (Nees) N.P. Balakr. var. *daltonii* (Clarke) V. Singh & P. Singh in J. Econ. Taxon. Bot. 15(3): 705. 1991, publ. 1992. *Type*: INDIA. ‘Sikkim’, probably Darjeeling, *J.D. Hooker s.n.* (lectotype: K, sheet annotated by Anderson and Clarke, designated here).

Strobilanthes maingayi Clarke in Hook. f., Fl. Brit. Ind. 4: 448. 1884. *Tetraglochidium maingayi* Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 221. 1944. *Type*: MALAYSIA. *Maingay Kew Dist. 1182* (holotype: K; isotype: A).

Strobilanthes hirtisepala C.B. Clarke in J. Asiat. Soc. Bengal 74: 655. 1908. *Tetraglochidium hirtisepalum* (C.B. Clarke) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 221. 1944. *Type*: MALAYSIA. *King’s collector 2215* (lectotype: K, designated here).

Strobilanthes poilanei Benoist in Bull. Mus. Hist. Nat. (Paris) 27: 545. 1921. *Type*: CAMBODIA. *E. Poilane 208* (holotype: P).

Strobilanthes thunbergiiiflora S. Moore in J. Bot. 63, Suppl. 78. 1925. *Tetraglochidium thunbergiiiflorum* Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 218. 1944. *Type*: INDONESIA. Sumatra, *H.O. Forbes 2564a* (holotype: BM).

Strobilanthes jugorum Benoist in Bull. Soc. Bot. France 81: 601. 1934. *Tetraglochidium jugorum* (Benoist) Bremek. in Proc. Kon. Ned. Akad. Wetensch., Ser. C, Biol. Med. Sci., 60: 2. 1957. *Type*: VIETNAM. North Vietnam. *P.A. Pételot s.n.* (holotype: P).

Strobilanthes pectinata var. *glandulosa* Imlay in Kew Bull. 1939: 119. 1939. *Strobilanthes echinata* var. *glandulosa* (Imlay) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 274. 1944. *Type*: THAILAND. Mt. Pu Huat, *A.F.G. Kerr 14512* (holotype: K; isotype: BM).

Strobilanthes pectinata var. *punctata* Imlay in Kew Bull. 1939: 119. 1939. *Strobilanthes echinata* var. *punctata* (Imlay) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 274. 1944. *Type*: THAILAND. Kao Keo Range, *A.F.G. Kerr 4993* (holotype: K; isotype: BM).

Strobilanthes pectinata var. *acuminata* Imlay in Kew Bull. 1939: 119. 1939. *Strobilanthes echinata* var. *acuminata* (Imlay) Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 274. 1944. *Type*: THAILAND. Kao Luang, *A.F.G. Kerr 15464* (holotype: K (2 sheets); isotype: BM).

Strobilanthes maingayi var. *glabra* Imlay in Kew Bull. 1939: 119. 1939. *Type*: THAILAND. Kao Luang, *A.F.G. Kerr 10835* (holotype: K).

Strobilanthes latebracteata Imlay in Kew Bull. 1939: 119. 1939. *Type*: THAILAND. Kao Soi Dao, *A.F.G. Kerr 19190* (holotype: K; isotype: BM).

Tetraglochidium menangkabwense Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede

Sect. 41(1): 216. 1944. *Type*: INDONESIA. Sumatra, Tanang Talu, *H.A.B. Bünnemeyer 1034* (holotype: L).

Tetraglochidium deliense Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 217. 1944. *Type*: INDONESIA. Sumatra, Sibolangit, *J.A. Lörzing 5330* (holotype: L; isotype: U).

Tetraglochidium benculense Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 219. 1944. *Type*: INDONESIA. Sumatra, Kota Donak, *C.N.A. de Voogd 1083* (holotype: L).

Tetraglochidium hallierii Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 41(1): 220. 1944. *Type*: INDONESIA. Kalimantan, Gunang Damoos, *J.G. Hallier 611* (holotype: L).

Tetraglochidium maingayi var. *paucinervium* Bremek. in Dansk Bot. Ark. 23: 206. 1965. *Type*: THAILAND. Prachinburi, Khao Khieo, *K. Larsen 10159* (holotype: U; isotypes: C, K).

Tetraglochidium hirsutum Bremek. in Proc. Kon. Ned. Akad. Wetensch., Ser. C, Biol. Med. Sci., 60: 2. 1957. *Type*: LAOS. *Vidal 1637* (holotype: U).

Strobilanthes calvata J.R.I. Wood in Edinburgh J. Bot. 51(2): 233. 1994. *Type*: MYANMAR. Chawngmaw, *F. Kingdon Ward 3482* (holotype: E).

Description: Plietesimal undershrubs up to 2 m in height; stems sulcate, glabrous to densely hispid with brownish hairs, somewhat glabrescent below. Leaves moderately to strongly anisophyllous, both surfaces glabrous to hispid-hirsute with brownish hairs, more commonly pubescent along the veins of the lower surface only, subglabrous above, the lower surface often whitish and paler than the upper, cystoliths very prominent above, less so below; laminae 1.5–2.3 × 1–8 cm, ovate, ovate-elliptic, or (mostly Borneo) oblong-elliptic; base acuminate; margins undulate to crenate, less commonly serrate, sparsely ciliate; apex acuminate, commonly falcate; petioles 0.5–4.5 cm long, glabrous to hispid. Inflorescences usually solitary, bracteate heads borne on short axillary branchlets which are equal to or, commonly, shorter than the subtending leaves; heads 2.5–5 cm long; bracts persistent, usually of two kinds, the indumentum and cystolith coverage similar to the leaves but sparser; outer bracts sometimes appressed to the head, sometimes appearing as a reduced leaf pair below the head, or sometimes absent, 2.1–4.3 × 1.1–2.6 cm, elliptic, ovate, obovate, or oblong-ovate, apex acute, obtuse, rounded or ± fimbriate, margin usually crenate but sometimes entire, undulate or serrate, base acuminate; inner bracts similar to outer bracts but smaller, 2–3 × 0.7–0.8 cm, obovate, oblong-obovate or spatulate with teeth on distal margins

only; bracteoles 11–23 × 1.5 mm, linear-oblong or linear-oblongate, apex obtuse, undulate or ± fimbriate (India and Bhutan only). Calyx subequally five-lobed, divided to the base, the lower surface glabrous or pubescent, sparsely pubescent above, lobes 12–19 × 1–1.8 mm, linear-oblong, apex acute. Corolla (4–)5–5.5 cm long, white or pale pink or pale mauve, outer surface glabrous, curved to almost straight, resupinate, basal cylindrical tube 13–18 × 2–3 mm, widened asymmetrically at point of curvature, the expanded portion of tube 23–32 mm long and 12–16 mm wide at mouth, lobes ovate, rounded 6–9 mm long. Stamens 4, didynamous, the shorter pair of filaments c. 3 mm long, usually glabrous, the longer pair of filaments c. 5 mm long, usually pilose in the lower half, occasionally glabrous or entirely pilose; anthers 2–3.5 × 1.5–2.5 mm, glabrous, apiculate with the connective extended to a ± conspicuous point; pollen ellipsoidal, tricolporate, bireticate, usually scalariform. Ovary c. 3 mm long, oblong, glabrous; ovules 4. Style c. 2.5 cm long, glabrous. Capsule 1.2–1.8 cm long, glabrous, four-seeded. Seeds 3–5 × 2.3–4 mm, broadly ovoid, pilose with appressed mucilaginous hairs, basal areole minute.

Distribution: Bhutan, Burma (north only), Cambodia, China (Yunnan, Guangxi, Guangdong), India (Darjeeling district, Arunachal Pradesh, Meghalaya, Nagaland), Indonesia (Kalimantan, Sumatra), Laos, Malaysia (Malaya, Sarawak), Singapore, Thailand, Vietnam (north, south) (Fig. 1).

Altitude: 100–2700 m.

Variation

Strobilanthes echinata is a highly variable plant throughout its range and has been described under many different specific names from Burma, Cambodia, India, Laos, Malaysia, Sumatra, Thailand, and Vietnam. For the most part, Bremekamp (1944, 1957) attempted to account for the variation by recognizing a large number of species, whereas other authors, notably Imlay (1939), attempted to account for the variation by the recognition of varieties. There is clearly an unusual degree of variation in this species, and several of the more extreme forms appear at first sight to be distinct enough to be described as species. However, these forms have no clear geographical pattern: the dense heads subtended by glabrous, oblong bracts of the type of *S. calvata* (*Kingdon Ward 3482*) from the Himalayas in upper Burma are almost perfectly matched by *Shimizu et al. 26595* from the Isthmus of Kra in southern Thailand, although curiously the former has glabrous filaments, whereas the latter is one of the few examples of a plant with all

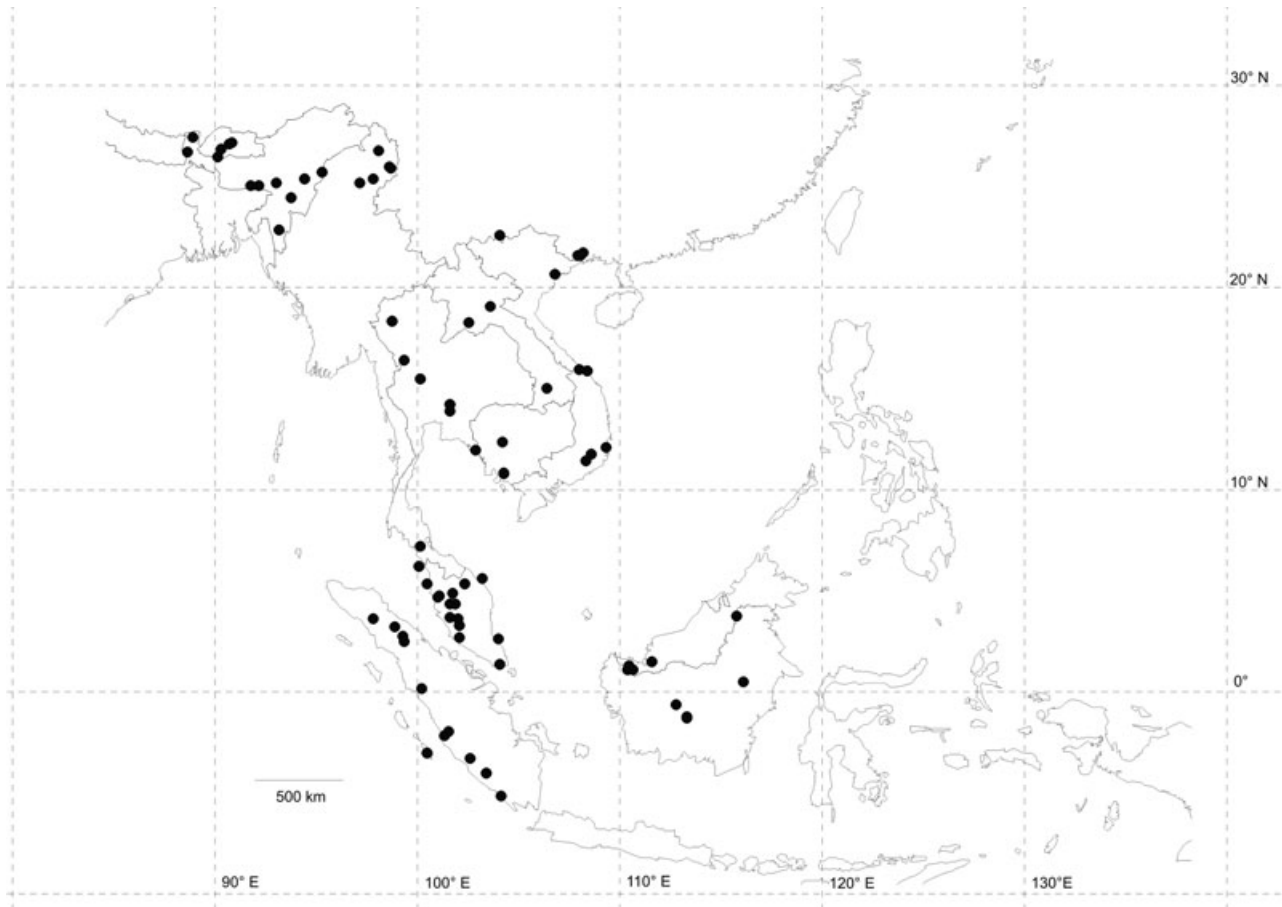


Figure 1. Distribution map of *Strobilanthes echinata* Nees.

filaments entirely pilose. Variation is present in many characters, as described in the following sections.

Anisophylly: Plants are usually clearly anisophyllous, but there is considerable variation, sometimes even on the same plant.

Indumentum: Plants vary from glabrous to hispid hairy. In most countries, both forms occur at nearly equal frequency, although we cannot say whether or not populations are mixed. However, populations along the border of China with its southern neighbours are uniformly glabrous, whereas those from India and Bhutan are almost always hairy (*Bor* 6246 is an exception). Plants with the rough brownish hairs described as var. *daltonii* by Clarke occur in the east Himalayas from Darjeeling to Burma, but are also found in Borneo, Malaya, and Sumatra.

Leaf shape and dimensions: Leaves are ovate-elliptic and the apex acuminate or falcate. In most populations, leaves are about 5–10 cm in length and larger leaves are rare. Collections from upper Burma

(*Kingdon Ward* 12842, *Kaulbach* 332), Laos (*Vidal* 998B) and Vietnam (*Poilane* 30308), in which the leaves are unusually small, are associated with bracts which are entire or at most undulate on the margins. The range of variation is shown in Figures 2 and 3.

Flower heads: There is considerable variation in size, but this is related essentially to bract dimensions. Some specimens appear to have very compact swollen heads, but this seems to be related mainly to the development of the capsule within the head. However, specimens from Borneo and, to some extent, Indo-China are laxer than elsewhere, and the individual flowers within the head are easily distinguished from one another.

Bract shape and dimensions: Leaves and bracts are not always clearly differentiated, and variation in the shape and size of both is to a considerable extent correlated (Figs 2, 3). Thus, the specimens noted above for their unusual sized leaves are also remarkable for the size of their bracts. Bracts vary within individual flower heads; the outer bracts sometimes

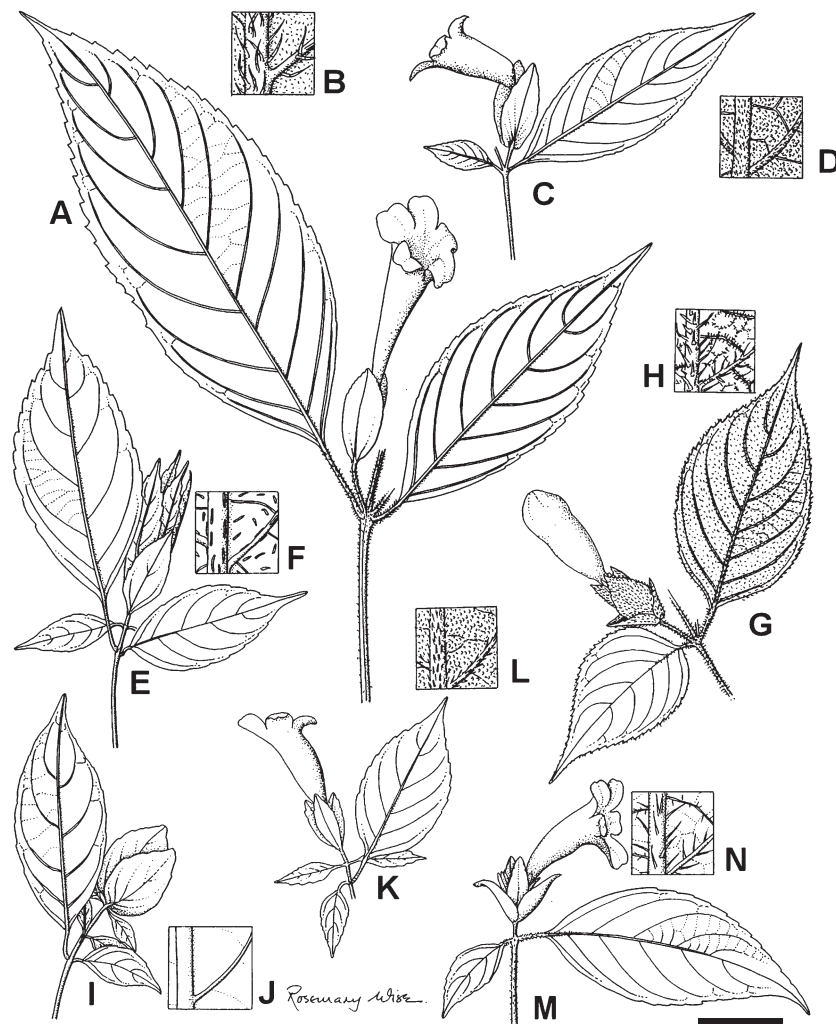


Figure 2. Variation in vegetative and floral characters in *Strobilanthes echinata* Nees, illustrating leaf and inflorescence morphology and detail of the abaxial leaf surface. A, B, Drawn from *Forbes 254a* from Sumatra (type of *S. thunbergiiiflora*). C, D, Drawn from *Kaulback 332* from Burma. E, F, Drawn from *Tsang 27034* from Vietnam. G, H, Drawn from *Lace 2237* from India. I, J, Drawn from *Poilane 3638* from Vietnam. K, L, Drawn from *Ridley 7167* from Malaysia. M, N, Drawn from *Smitinand 8329* from Thailand. Scale bar: A, C, E, G, I, K, M, 25 mm; B, D, F, H, J, L, N, 2.5 mm.

separate from the flower head and are commonly shorter, broader, and more ovate than the inner bracts, which are longer and more oblong in outline. The most common shape is ovate and this is found throughout the range of the species, but they may be narrow or broad. Elliptic and oblong-elliptic bracts are also quite frequent, particularly amongst populations from Malaya and Borneo, and rounded bracts are sometimes seen, particularly in specimens from south Vietnam (*Poilane 3638*, *23906*, *Evrard 927*). The apex varies from acute (*Poilane 8004*) to obtuse (*Mohamed Shah 1089*, *Ridley 5516*) or, on the inner bracts, to fimbriate, especially on plants from India, Thailand, and Sumatra (*Robinson & Kloss s.n.* ex Siolak Daras, *Clarke 4763*, *Phengklai 4066*). One very striking collection is *Tsang 27034* from Vietnam near

the border with China, which has bracts 4 cm long with caudate apices.

Bract dentation: Bracts are usually serrate or crenate, but the dentations are quite frequently reduced so that the margin is merely undulate, or the dentations are restricted to the area near the apex or even suppressed altogether (*Kingdon Ward 12842*, *Maxwell 99–156*). In most collections from western Borneo, the dentation is often noticeably stronger (*Church et al. 2552*, *Haviland s.n.*, *Yii 51368*).

Calyx: The calyx is always subequally five-lobed, with narrow linear lobes which vary from acute to obtuse to obscurely dentate or fimbriate at the tip. This is an unusually wide range of variation within a species,

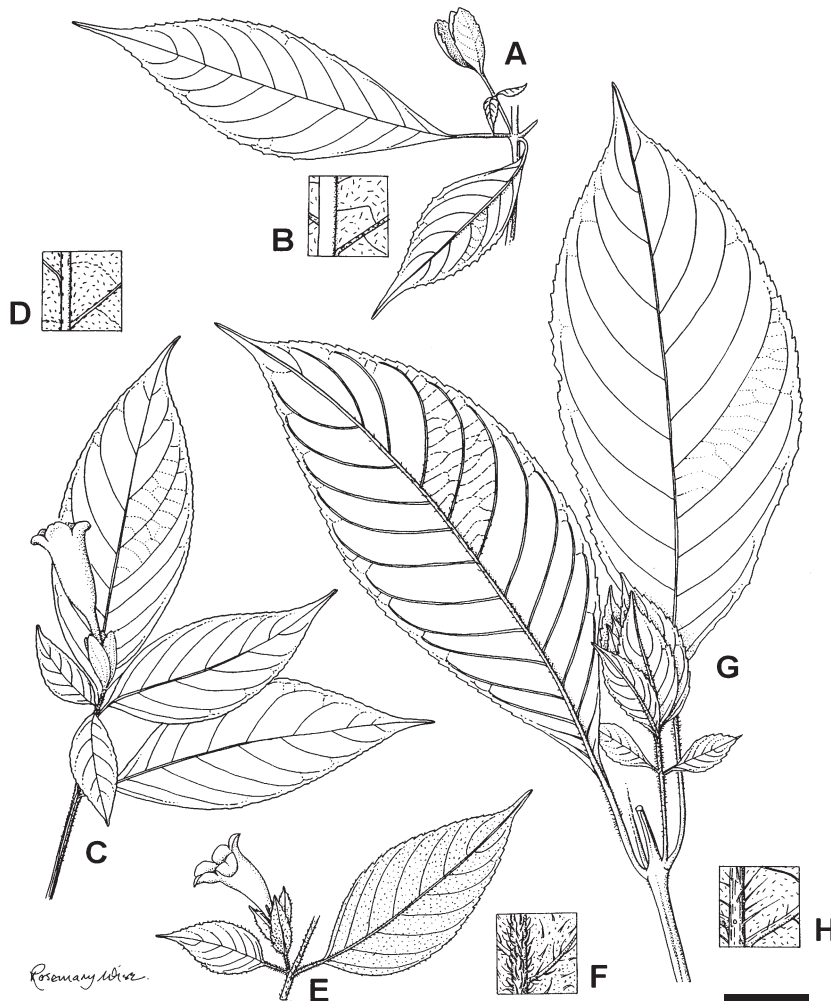


Figure 3. Variation in vegetative and floral characters in *Strobilanthes echinata* Nees, illustrating leaf and inflorescence morphology and detail of the abaxial leaf surface. A, B, Drawn from *Kingdon Ward 3482* from Burma (type specimen of *S. calvata*). C, D, Drawn from *Bartlett 7914* from Sumatra. E, F, Drawn from *Kings's collector 2215* from Malaysia (type specimen of *S. hirtisepala*). G, H, Drawn from *Church, Ismail & Ruskandi 2552* from Kalimantan. Scale bar: A, C, E, G, 25 mm; B, D, F, H, 6 mm.

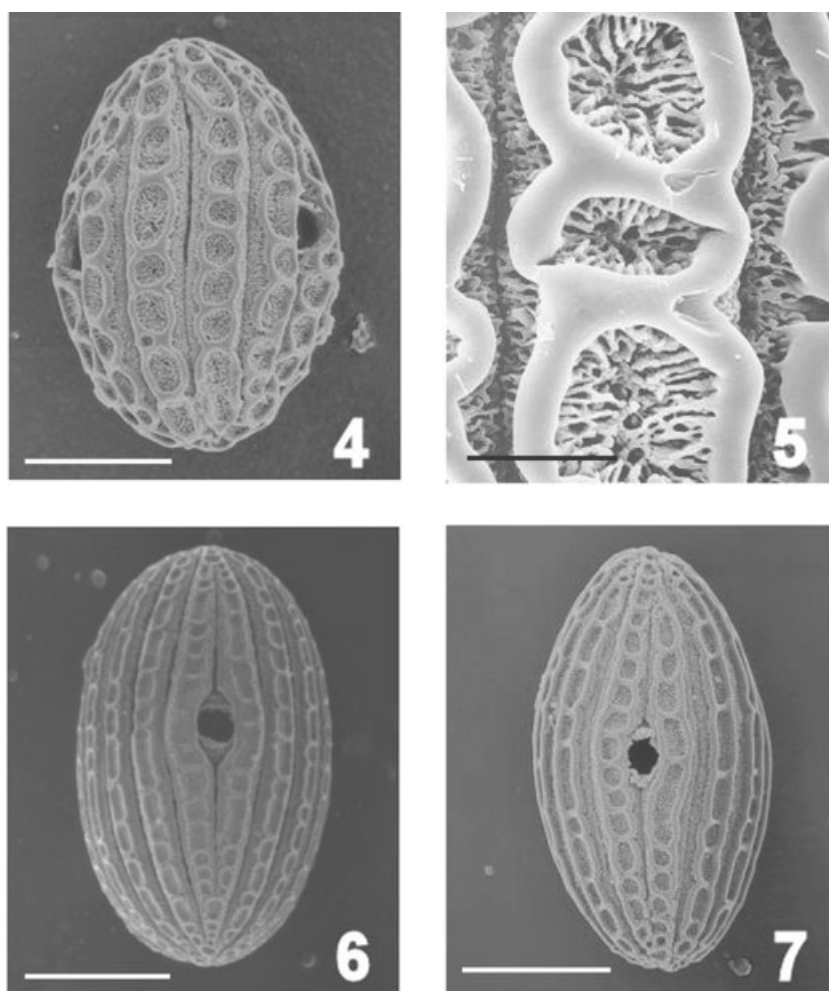
and the only available explanation is that of Wood (1994: 195): it is related to whether or not the collection was made in a year of mass flowering.

Corolla: So few collections have well-preserved flowers or field notes that it is difficult to observe variation in corolla morphology. A constant feature of all specimens is the glabrous exterior of the corolla, but flower colour seems to vary. It is predominantly white or pale lilac, but field notes also mention yellow, cream, and glossy purple. Glossy purple flowers are mainly recorded from Burma.

Androecium: A characteristic of this species is the apiculate anthers, but the amount by which the connective is extended varies considerably. In some specimens, notably two from north Vietnam (*Tsang 26669*

and *Schmidt s.n.*) and one from Sumatra (*Forbes 2564a*), the connective is much extended, whereas in a few specimens (*Lace 2237*) it is essentially muticous. The indumentum of the filaments is also variable. The two shorter filaments are usually glabrous, whereas the two longer filaments are normally pilose in the lower half. However, in a few specimens, the filaments are completely glabrous (for example, *Kaulbach 332* from Burma and *Ridley 7167* from Penang), whereas in a few other specimens they are complexly pilose (for example, *Shimizu et al. 16595* from southern Thailand and *Schmidt s.n.* from Vietnam).

Pollen: Pollen is always ellipsoid, ribbed, tricolporate, and constant in size, but the detailed scalariform patterning varies. Figures 4–7 show how the patterning varies from great prominence with the exine



Figures 4–7. Pollen of *Strobilanthes echinata* Nees. Figs 4, 5. *Kerr 10835* from Kao Luang, Thailand. Fig. 6. *Mohammed Hariff 5173* from Kedah Peak, Malaysia. Fig. 7. *Garrett 564* from Chiang Mai, Thailand. Scale bars: Figs 4, 6, 7, 30 μm ; Fig. 5, 6 μm .

forming circles (*Kerr 10835*; Figs 4, 5) to the typical scalariform patterning of many species of *Strobilanthes* (*M. Hariff 5173*; Fig. 6). In other forms, the scalariform patterning is much less prominent (*Garrett 564*; Fig. 7).

Life form: Remarkably little is known about life form. Wood (1994: 196) summarized the information from Darjeeling, indicating that it probably flowered in 12-year cycles. Elsewhere, over its entire range, there is no information, except for the field label of *Kerr 5308*, which suggests that it flowers in 7-year cycles in Thailand, and that of *Brockleman 29*, which suggests a 13-year flowering cycle. However, the following more detailed information was received in 2004 from J. F. Maxwell of Chiangmai:

I have some more notes about *Strobilanthes echinata* from Kow Yai. I collected flowers of this species in April 2003 and fruits in July 2003. From that time the plants, all of them in the entire forest, slowly died and by early 2004 there was no trace of them . . . a very common species there. This week (28 July 2004) I was quite pleased to find seedlings of *S. echinata* all over the place. The interesting point of this *S. echinata* is that it was known to flower profusely in April 1995 and nothing else was noticed or collected until May 2002 when only a few individuals flowered. . . . It is apparent that there is a *c.* 10 years interval from the time of flowering/fruitleting until the next flower show.

Whether *S. echinata* is plietesimal throughout its entire range is unrecorded. The need for accurate field observations similar to those quoted above cannot be too strongly emphasized.

REPRESENTATIVE SPECIMENS

BHUTAN. Marichoma Gompa, 1300–1600 m, 3.vii.1914, *R. E. Cooper 1168* (BM, E); Tongsa, 27°29'N, 90°28'E, 2300 m, 28.vi.1938, *B. J. Gould 627* (K); Phuntscholing Dist., Ganglakha to Sorchen, 1 km above Sintilalakha, 26°55'N, 89°30'E, 1800 m, 9.vi.1991, *J. R. I. Wood 7380* (E); Chukha Dist., summit above Gedu, 27°04'N, 89°35'E, 2100 m, 23.vi.1990, *J. R. I. Wood 7271* (E).

CAMBODIA. Phnom San-Kas, Pursat, 12°30'N, 104°00'E, 15.xi.1938, *R. Muller 470* (P).

CHINA. Guangdong: Kung P'ing Shan, T'aan Faan, Fan, Ch'eng district, 21°50'N, 107°55'E 15–24.viii.1936, *W. T. Tsang 26669* (C, E, K, P); Guangxi: Me Kon, Seh-Feng, Dar Shan, Nanning, 800 m, 3.xi.1928, *R. C. Ching 8383* (GXMI).

INDIA. Meghalaya: Jarain, Jaintea Hills, 25°20'N, 92°8'E, 20.xi.1872, *C. B. Clarke 18312* (K); Rungtong, Khasi Hills, 25°20'N, 91°24'E, 1300 m, 15.xi.1871, *C. B. Clarke 14763* (BM). Manipur/Nagaland: Kohima, 25°45'N, 94°10'E, 21.x.1885, *C. B. Clarke 40970* (K); 1300 m, 31.xiii.1935, *Bor 6246* (K); Pulinabadza, Naga Hills, xi.1886, *D. Prain s.n.* (CAL, K); Pedi, Naga Hills, 11.ix.1935, *N. L. Bor 6488* (K). Manipur, Nungpa, 24°45'N, 93°26'E, 1600 m, xi.1907, *Anonymous* (K). Mizoram: Lushai Hills, 23°10'N, 92°50'E, 29.xii.1924, *N. E. Parry 9* (K). West Bengal, Darjeeling, 27.02'N, 88°16'E, 2200 m, 8.xii.1862, *T. Anderson 1059* (BM); Gumpahar, 27.02'N, 88°16'E, 1800–2100 m, 27.v.1902, *J. H. Lace 2237* (E). Sikkim. Rungbee, 13.viii.1869, *C. B. Clarke 8572* (BM, K).

INDONESIA. Kalimantan: Landah, 0°06'N, 110°55'E, iii.1878, *J. E. Teysman 111/78* (K); Bukit Mehijist, 500 m, 29.xii.1924 *H. Winkler 1152* (E); Km 96, Katingan River, 1°10'S, 113°10'E, 100 m, 20.i.1983, *H. Wiradinata 3353* (A, K); *ibid.*, 3.ii.1983, *H. Wiradinata 3521* (A); 1 km W of Uut Labang, along Sungai Uut Labang, Serawai, 0°36'N, 112°38'E, 750 m, 15.x.1995, *A. H. Church, Ismail & Ruskandi 2552* (A); between Long Bawan and Panado, 3°52'N, 115°42'E, 1000 m, 11.vii.1981, *R. Geesink 9009* (A, BO (*n.v.*), KYO, L.). Sumatra, *sin. loc.*, 1880, *H. O. Forbes 1906* (BM); SW of Paoe, 1300 m, 1880, *H. O. Forbes 2514b* (BM); Barong Baru, Tapan, 3.vi.1914, *H. C. Robinson & C. B. Kloss s.n.* (BM, K); Siolah Daras, Kerenji, 1°92'N, 101°30'E, 900 m, 16.iii.1914, *H. C. Robinson & C. B. Kloss s.n.* (BM, K, US); Karo Highlands, above Berastagi, 2°50'N, 99°00'E, 1500–1600 m, 27.i.1929, *J. A. Loerzing 15080a* (L.); Hoeta Bagasan, Asahan, 7.ix.1934–4.ii.1935, *Rahmat Si Boeea 6985* (A, MICH, US); Loemban Ria, Asahan, 2°58'N, 99°07'E, 8.ii.1934–12.iv.1934, *Rahmat Si Boeea 7914*

(A, MICH); Adian Rindang, Asahan near Tomoean Dolok, 17.xi.1935–10.xii.1935, *Rahmat Si Boeea 8665* (A, MICH); *ibid.*, *Rahmat Si Boeea 8685* (A, MICH); *ibid.*, *Rahmat Si Boeea 8786* (A, MICH); Aek Moette, Asahan, 3°01'N, 100°15'E, 500 m, 15.vi.1936–9.vii.1936, *Rahmat Si Boeea 9234* (A, L, MICH, NY, US); Aek Moente, Asahan, 3°01'N, 100°15'E, 500 m, 15.vi.1936–9.vii.1936, *Rahmat Si Boeea 9404* (A, MICH, NY, US); Tomoean Dolok, Asahan, 1000 m, 1–20.viii.1936, *Rahmat Si Boeea 9838* (A, MICH); Gunong Setan along Lau Alas, 3°45'N, 97°50'E, 1200 m, 24.iii.1937, *C. G. G. J. Van Steenis 10084* (A); Gunong Kemeru, 3°44'N, 97°30'E, 600–900 m, 21.viii.1971, *K. Iwaksuki et al. 752* (K, KYO).

LAOS. Paksong near Houei Champi, Pak Se, 15°11'N, 106°14'E, *J. E. Vidal 998B* (P); Vientiane, 5 km W of Khon Phouk village, Hin Heup, 18°30'N, 102°20'E, 225 m, 22.viii.1999, *J. F. Maxwell 99–156* (CMU).

MALAYSIA. Peninsular Malaysia: *sin. loc.*, *B. Scortechini 337* (UC). Kedah, Langkawi Island, West Hill, 5°26'N, 100°15'E, 750 m, x.1889, *C. Curtis s.n.* (BM, W); Mt. Raya, 6°22'N, 99°49'E, 10.xi.1921, *M. Harriff 7199* (BM); *ibid.*, 2.v.1938, *C. F. Symington 34739* (FRIM); Jerai State Park, 1°32'N, 111°25'E, *B. C. Stone & F. Hallé 12726* (PH); Kedah Peak, 5°48'N, 102°10'E, 23.ii.1920, *M. Harriff 5173* (K); *ibid.*, 6.vi.1971, *H. Keng 200* (SINU). Pahang, Telom, 3°80'N, 101°35'E, xi.1908, *H. N. Ridley 13620* (BM, K); Labok Tamang, 4°26'N, 101°23'E, 1150 m, 8.vi.1923, *M. R. Henderson 10961* (UC); Gunong Rokam, Pulau Tioman, 2°68'N, 103°78'E, 800 m, 2.v.1927, *M. Nur 18806* (K); Sungai Lemoi, 4°28'N, 101°36'E, 19.ix.1931, *Ja'amat 28192* (FRIM, K); Frasers Hill, 3°72'N, 101°75'E, 1000 m, 14.xi.1963, *M. E. D. Poore 1345* (K); Penang, 1886, *C. Curtis 298* (K); Pulau Pinang, 1898, *H. N. Ridley 7167* (BM); Richmond Pool, 5°73'N, 103°00'E, 22.vii.1907, *I. H. Burkill 2577* (BM); *ibid.*, 22.vii.1917, *I. H. Burkill 2592* (BM). Perak, Birch's Hill, Maxwell's Hill, 1250 m, 9.ix.1949, *J. Sinclair 3036* (E); Maxwell Hill, 5°00'N, 100°88'E, 1200–1400 m, *J. Sinclair 38646* (BM, E); path to Gunong Hijau, Maxwell's Hill, 4°52'N, 100°49'E, 1450 m, 4.xii.1965, *M. Shah & Sidek 1089* (A); Selangor, Genting Bidai, 3°18'N, 101°49'E, 1.ix.1914, *C. B. Kloss s.n.* (BM, K); Menang Gasing, Ulu Langat, 3°07'N, 101°49'E, ii.1917, *C. B. Kloss s.n.* (BM). Negri Sembilan: Bukit Tanga, 4°36'N, 101°32'E, 19.xii.1920, *H. N. Ridley s.n.* (K). East Malaysia: Sarawak, 1st Division, Pengulu Ambat, Sarawak River, 1°20'N, 110°20'E, vi.1890, *G. D. Haviland s.n.* (K); Gunong Penrissen, Serian, 1°10'N, 110°30'E, 2.v.1962, *I. Paie 16338* (K, SING); Gunong Merubong, Ulu Sungai Sluba, Padawan, 1°10'N, 110°16'E, 200 m, 18.ix.1987, *P. C. Yui 51368* (K).

MYANMAR. Laktang, 26°13'N, 98°25'E, 2700 m, 3.viii.1919, *F. Kingdon Ward 3458* (E); valley of Nam Tisang, 27°05'N, 97°49'E, 650 m, 7.ix.1926, *F. Kingdon Ward 7374* (K); hills west of Mali Hba, 25°42'N, 97°30'E, 1000 m, 29.vii.1937, *F. Kingdon Ward 12842* (BM); Mahtum, 25°28'N, 96°52'E, 1600 m, 11.viii.1939, *R. Kaulback 332* (BM).

SINGAPORE. Salatar Forest, 1°25'N, 103°50'E, 18.ix.1948, *J. Sinclair 24742 & 5123* (E).

THAILAND. Chiang Mai: Doi Angka, 18°35'N, 98°29'E, 2140 m, 4.vi.1930, *H. B. G. Garrett 564* (K); higher elevations of Doi Inthanon, 18°35'N, 98°29'E, 1900–2595 m, 19.xii.1965, *M. Tagawa et al. 2860* (KYO); Doi Inthanon, 18°35'N, 98°29'E, 1200–2580 m, 24.vi.1978, *C. Phengklai et al. 4066* (A); *ibid.*, 2.v.1921, *A. F. G. Kerr 5308* (BM); summit of Doi Inthanon, 18°35'N, 98°29'E, 2565 m, 31.xii.1989, *J. F. Maxwell 89–1629* (A, MO). Chiang Rai: Doi Pa Hom Pok, NW of Phan, 1300–2000 m, *K. Iwatsuki et al. 9572* (K). Nathon Nayok: Khao Khieo, Khao Yai National Park, 14°26'N, 101°22'E, 1300 m, 29.viii.1963, *T. Smitinand & H. O. Sleumer 8329* (K); *ibid.*, 780 m, 21.iv.1995, *W. Y. Brockleman 29* (CMU); *ibid.*, 783 m, 23.v.2002, *Petrmitr 522* (CMU); *ibid.*, 750 m, 4.iv.2003, *J. F. Maxwell 03–66* (CMU); *ibid.*, 6.vii.2003, *J. F. Maxwell 03–150* (CMU). Ranong: Khao Pawta Luangkaeo, Kaper District, 940–980 m, 9.xii.1979, *T. Shimizu et al. 26595* (KYO). Saraburi: Khao Khieo, 16°65'N, 99°05'E, 2565 m, 1000 m, 8.vi.1979, *E. Vidal et al. 6360* (P). Trang: Kao Kalikiri, 800–900 m, 1.iv.1928, *A. F. G. Kerr 14954* (BM); Kao Keo Range, 12.iii.1928, *A. F. G. Kerr 14528* (BM). Krat: Kao Kuap, 22.v.1930, *N. Put 2940* (BM).

VIETNAM. North: Taai Wong Mo Shan, Chukphai, Ha-Coi, 21°50'N, 107°45'E, 16–22.x.1936, *W. T. Tsang 27034* (C, E, P); Pon Bieng, Xam Dong, 20°54'N, 106°38'E, 1200 m, 5.v.1954, *Schmidt s.n.* (P). South: West of Nha Trang, 12°15'N, 109°11'E, 1800 m, 23.v.1922, *E. Poilane 3638* (P); Col des Ibuages near Taurane, 16°07'N, 108°22'E, 1050 m, 14.ix.1923, *E. Poilane 8004* (P); Dalat, 11°56'N, 108°25'E, 20.vi.1924, *F. Evrard 927* (P); Massif du Brian near Djising, Haut Douai, 11°34'N, 108°10'E, 1600–1800 m, 16.i.1935, *E. Poilane 23906* (P); North of Dalat, 11°56'N, 108°25'E, 1500 m, 3.ix.1940, *E. Poilane 30308* (K, P); Massif de Bidoup, Haut Douai, 12°05'N, 102°40'E, 2000 m, 15.x.1940, *E. Poilane 30941* (P); Maison du Lac, Bach Ma, 16°10'N, 107°50'E, 27.vii.1943, *J. E. Vidal 176 A* (P); Bach ma National Park, Thua Thien-Hue Province, 16°12'N, 107°52'E, 400 m, 29.i.1990, *M. F. Newman 172* (E).

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