Steenisia (Rubiaceae) newly recorded for mainland Asia with a new variety of *S. pleurocarpa* (Airy Shaw) Bakh.f.

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ABSTRACT. *Mussaendopsis malayana* T.Yamaz. (Rubiaceae), described based on material from the Malay Peninsula, is a distinct variety of *Steenisia pleurocarpa* (Airy Shaw) Bakh.f. It represents a new record for mainland Asia of *Steenisia* Bakh.f., a genus otherwise endemic to Borneo and the Natuna islands. The new combination *Steenisia pleurocarpa* var. *malayana* (T.Yamaz.) K.M.Wong is made.

Keywords. Asia, biogeography, Borneo, Malay Peninsula, *Mussaendopsis*, Rubiaceae, South China Sea, *Steenisia*, vicariance

Introduction

Mussaendopsis malayana T.Yamaz. (Rubiaceae) was described based on a collection from around 700 m elevation on the west side of Mount Tahan, between Sungai Luis and the summit, in Peninsular Malaysia (Yamazaki 2001). A good photograph of the holotype specimen (*Ohba & Miyamoto 90504*) and diagnostic drawings of a vegetative node with a stipule, the axillary inflorescences, flowers and fruits were provided with the description. Images of the holotype, an isotype sheet, and two sheets comprising a paratype collection (*Ohba & Miyamoto 90292*) were made available from the University of Tokyo herbarium (TI).

These collections from Mount Tahan are identifiable with *Steenisia pleurocarpa* (Airy Shaw) Bakh.f. from northwest Borneo, particularly in the very similar habit (low treelet); leaf form, venation and pubescence; interpetiolar stipules fringed with linear teeth; paired axillary compound-thyrsoid inflorescences; development of an enlarged calyx member (semaphyll) in some post-anthesis flowers and fruits; and septicidally dehiscent fruits with conspicuous ribbing on the outside (Bremer 1984). Yamazaki (2001) diagnosed the stipules in the Tahan material as intrapetiolar but this is clearly in error as revealed in his Fig. 2a and the material he cited.

Mussaendopsis and *Steenisia* compared

Although *Mussaendopsis* Baill. also has axillary inflorescences in which some flowers also develop an enlarged calyx member, that genus has many different attributes compared to *Steenisia* Bakh.f. Table 1 compares the characters of *Mussaendopsis* and *Steenisia*.

Mussaendopsis is a distinct genus of much taller trees, easily diagnosed by intrapetiolar stipules, glabrous leaves, right-contorted corolla lobes, free anthers in the open flower, and seeds that are winged all around (Bremekamp 1939, Puff & Igersheim 1994). The molecular evidence suggests a placement for *Mussaendopsis* within the tribe Condamineeae (Alejandro et al. 2005, Bremer 2009). *Steenisia*, on the other hand, is a genus of low treelets and subshrubs (Bremer 1984) with interpetiolar stipules, pubescent leaves, left-contorted (rarely valvate) corolla lobes, connate anthers in the open flower, and unwinged seeds that are or only slightly winged at two ends. There is as yet no indication of the systematic position of *Steenisia* from molecular studies (Bremer 2009), although Bremer (1984) had compared it with the Rondeletieae. It is interesting to note that two other genera with connate anthers in the open flower, *Argostemma* Wall. and *Neurocalyx* Hook.f., once accepted in the same tribe as *Steenisia* (Verdcourt 1958), are now placed by molecular inference in the Argostemmateae and Ophiorrhizeae, respectively (Bremer & Manen 2000, Robbrecht & Manen 2006, Rydin et al. 2009).

When describing his "*M. malayana*" Yamazaki (2001), however, had stated "this is the fourth species in the genus". He was apparently unaware that one of the "*Mussaendopsis*" species was transferred to *Greeniopsis* as early as 1909: *Mussaendopsis multiflora* Elmer, Leafl. Philipp. Bot. 1: 14 (1906) is now *Greeniopsis multiflora* (Elmer) Merr., Philipp. J. Sci., C 4: 325 (1909) (C.Puff, pers. comm.).

The studies of Puff & Igersheim (1994) reveal that *Mussaendopsis beccariana* stipules at inception are already fused up to near their apices, forming an appressed, resin-filled compartment around the young shoot apex, and the position of the apical cleft in the largely fused structure suggests an interpetiolar position at inception. Later ontogenetic development of the full stipular structure, however, is clearly intrapetiolar, with a thickened suture along the interpetiolar median, at which the stipular sheath splits into two clearly intrapetiolar members. In *Steenisia*, the apical buds are not protected in this way, and the stipules are only slightly connate basally and distinctly interpetiolar throughout.

The development of semaphylls is also different. In *Mussaendopsis*, these have already formed as enlarged petaloid structures even at the floral bud stage, although in those species of *Steenisia* where these are found, they form only in the post-anthesis stage. In both cases they persist into the fruit stage.

Professor Christian Puff (pers. comm.) points out that *Steenisia* (with its anther cones) is a typical buzz-pollinated taxon (where pollen is vibrated out of the anther cone by the close buzzing of bees and then collected) (Buchman, 1983), and thus no nectar is produced as reward. On the other hand, *Mussaendopsis* is fly-pollinated: the rotate corolla allows good landing space and a huge fleshy, disc-like nectar-producing structure surrounds the base of the style (the flowers resembling those of numerous Celastraceae taxa).

A new variety of *Steenisia pleurocarpa*

Bremer (1984) distinguished the various *Steenisia* species by characters such as crowded or well-spaced leaf arrangement along the stem, shape of the leaf base, calyx shape, presence / absence of semaphylls, semaphyll form and venation, style pubescence, ribbing of the fruit pericarp, and seed shape. The Malayan taxon is identifiable to

Table 1. Differentiating characteristics of *Mussaendopsis* and *Steenisia*.

	Mussaendopsis (2 spp. known)	***Steenisia*** (5 spp. known)
Leaf hairiness	glabrous	pubescent
Stipule insertion	intrapetiolar, connate for nearly whole length at first	interpetiolar, only basally connate
Stipule margin	following separation, margins entire except for tiny apical cleft	laciniate to fringed with linear teeth
Corolla lobe aestivation	right-contorted	left-contorted, rarely valvate
Anthers in the open flower	widely spaced out	connate into a central cone-like structure
Seeds	winged all around	not winged, or very slight wings at opposite ends only
Enlargement of one calyx lobe in a flower / fruit as a semaphyll	semaphyll present from flower bud stage	semaphyll developing at post-anthesis

Steenisia pleurocarpa, being identical in all these characteristics, overall habit (as low treelets), leaf form, and fruit form and size. Mature corollas were not available for the Malayan collections and so could not be directly compared, but flower bud material did not suggest any potential differences.

The only differences between the Malayan taxon and the Bornean material of *Steenisia pleurocarpa* are in peduncle length and degree of branching of the infructescence. Fourteen infructescences were measured for Bornean material, with peduncle length ranging 5.4–8.7 cm long, and the two infructescences in the Malayan material from Mount Tahan had peduncles that were 1.5 and 1.6 cm long. Also, the Bornean material had 3–4 (rarely 2) pairs of branches on the infructescence rachis, with the lowest branches ramifying to 3–5 orders (rarely 2 orders). In the Malayan material, the infructescences had only 1–2 pairs of branches on the infructescence rachis, with just 1–2 orders of ramification. Therefore, the Malayan material appears to have distinctly shorter, less branched infructescences compared to the Bornean material.

Here we propose to consider the Bornean and Malayan material as distinct varieties. The Malayan material is named as follows.

Steenisia pleurocarpa (Airy Shaw) Bakh.f. var. ***malayana*** (T.Yamaz.) K.M.Wong, ***comb. et stat. nov.***

Basionym: *Mussaendopsis malayana* T. Yamaz., J. Jap. Bot. 76 (2001) 28–30. TYPE: *Ohba & Miyamoto* 90504, Peninsular Malaysia, Pahang, Taman Negara, west side of Gunung Tahan, Sungai Luis – Summit, 700 m alt., 102°05'E 4°41'N to 102°15'E 4°39'N, 18 Mar 1990 (holotype TI, isotype TI).

Biogeographic implications

Steenisia was previously known only on Borneo (five species) and the Natuna islands (*S. borneensis* (Valeton) Bakh.f., one of the five mentioned). With the diagnosis of *Steenisia pleurocarpa* var. *malayana*, the genus is now newly recorded for the Malay Peninsula and mainland Asia. The genus thus has a distribution spanning both sides of the present South China Sea. The differences between both varieties of *Steenisia pleurocarpa* could be explained by vicariance of a formerly widespread ancestral taxon in this area, separating into two isolated populations that began to diverge evolutionarily.

This is plausible because there is palaeo-ecological, geomorphological and fossil evidence indicating periods of dryland contiguity between the Malay Peninsula and Borneo during the Quaternary from about 1.8 Ma to the Last Glacial Maximum (Flenley 1979, 1984; Morley & Flenley 1987; Stuijts et al. 1988; Morley 2000), when intervening sea levels could have fallen as much as 40–120 m below current level, allowing vegetation development and significant species range extensions (Heaney 1991, Voris 2000). These periods alternated with others during which sea-level rises would have segregated populations of organisms.

The occurrence of *Steenisia borneensis* in both Borneo and the Natuna islands in the South China Sea probably also bespeaks such former land connections that are now interrupted by present sea levels. Similarly, the gecko *Ptychozoon lionotum*, monitor lizard *Varanus nebulosus* and snake *Trimeresurus puniceus* are found in the Malay Peninsula with their eastern limit at the Natunas, and some Bornean herpetofauna also reach westward only as far as the Anambas and Natuna islands (Leong et al. 2003).

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