Cover images: Canthiumera robusta K.M.Wong & X.Y.Ng, spec. nov. Top left: leafy branch with inflorescences; note also keeled stipules. Top right: flower with tufts of pale moniliform hairs visible opposite corolla lobes. Below left: fruits. Below right: pyrenes. Photos: Ang Wee Foong (top left) and X.Y. Ng (remaining images).
The Editors would like to thank all reviewers of volume 17(2):

Andrew Powling, School of Biological Sciences, University of Portsmouth, Portsmouth, United Kingdom
George Argent, Royal Botanic Garden Edinburgh, Edinburgh, United Kingdom
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FLORA OF SINGAPORE PRECURSORS, 8. SYSTEMATY OF THE NEW SOUTHEAST ASIAN GENERA CANTHIUMERA AND DIBRIDSONIA
(RUBIACEAE: VANGUERIEAE), WITH NOTES ON PLANT ARCHITECTURE AND REPRODUCTIVE ECOLOGY

Received June 28, 2018; accepted September 20, 2018

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ABSTRACT

Key words: Borneo, Canthium complex, corolla hairs, dispersal ecology, India, Indochina, Java, Malay Peninsula, Malesia, moniliform hairs, Philippines, pyrene, Sumatra, Thailand, tree architecture.

ABSTRAK

Kata kunci: Arsitektur pohon, Borneo, ekologi pemencaran, Filipina, India, Indochina, Jawa, komplek Canthium, Malesia, piren, rambut moniliform, rambut pada mahkota, Semenanjung Malaysia, Sumatra, Thailand.
INTRODUCTION

TAXONOMIC HISTORY OF THE CANTHIUM COMPLEX AND SCOPE OF THE PRESENT WORK

_Canthium s.l._ has been, and still is, an heterogeneous assemblage of genera (Bridson, 1985; 1992; Wong, 1988; 1989; Lantz & Bremer, 2004; Razafimandimbison _et al._, 2009). Following the narrowing of the type alliance of _Canthium_ Lam. to spiny trees or shrubs, scramblers and climbing taxa found in India and Sri Lanka (type provenances) as well as Africa (including Madagascar) and Southeast Asia by Bridson (1985; 1992) and Wong (1988; 1989), various non-spiny, mainly arborescent taxa previously identified with _Canthium s.l._ and allies have been allocated to or confirmed as other genera. For example, _Psydrax_ Gaertn. has been reinstated as a genus distributed from Africa (Bridson, 1985) to South and Southeast Asia (Bridson, 1985; Wong 1988; 1989; Ridsdale, 1998; Arriola & Alejandro, 2013; Mahyuni _et al._, 2018; Wong & Mahyuni, 2018) as well as East Asia (Chen _et al._, 2011). Also, _Keetia_ E Phillips was again recognized for tropical and southern Africa (Bridson, 1986); _Psyrostria_ Comm. ex Juss. was recircumscribed (Bridson, 1987) and augmented (Davis _et al._, 2007; Razafimandimbison _et al._, 2007; Alejandro _et al._, 2014; Arriola _et al._, 2015; 2016a); _Afrocanthium_ (Bridson) Lantz & B.Bremer was elevated to generic status (Lantz & Bremer, 2004); still other species first named as _Canthium_ were transferred to the related _Cyclophyllum_ Hook.f. (Davis & Ruhsam, 2005; and _Bullockia_ (Bridson) Razafim., Lantz & B. Bremer were more precisely delimited as a distinct genus (Razafimandimbison _et al._, 2009). More recently, Arriola _et al._ (2016b) described _Kanapia_ Arriola & Alejandro, a genus in this taxonomic complex restricted to the Philippines.

Genera such as _Psydrax_, _Cyclophyllum_ and others in the _Canthium_ alliance were clearly distinguished from a 'spiny group' including _Canthium s.s._ in the combined analysis using molecular (ITS and _trnT-F_ sequences) and 30 morphological characters by Lantz & Bremer (2004). Furthermore, Razafimandimbison _et al._ (2009), analysing sequence data from two nuclear (ETS and ITS) regions, were able to confirm that _Peponidium_ (Baill.) Arènes was indeed a distinct genus accommodating all Comorean, Malagasy, and Seychellenian 'Canthium' species (Razafimandimbison _et al._, 2007), and that _Pyrostria_ included _Leroya_ Cavaco, _Neoleroya_ Cavaco, _Pseudopeponidium_ Homolos ex Arènes, and _Scyphochlamys_ Balf.f. For the first time also, the analyses of Razafimandimbison _et al._ (2009) indicated that the Southeast Asian _Canthium confertum_ Korth. (placed by Bridson (1987) in her Group IV of _Pyrostria_ s.l. and allies) was closely allied to _Cyclophyllum_. Thus the dismemberment and realignment of the _Canthium_ complex has continued to this day.

What has emerged is that there are good morphological distinctions among the genera or clusters of genera. The _Canthium s.s._ group (including the type, _Canthium parviflorum_ Lam. = _C. coromandelicum_ (Burm.f.) Alston) can be distinguished by its mostly scrambling and climbing habit, axillary spines developing from supernumerary axillary buds, and flowers that are solitary, fasciculate or in cymes (Bridson 1985; 1992). The flowers or inflorescences are characteristically borne in the axils of leaves on normal shoots (developing elongate internodes), as well as in the axils of both normal leaves and scale- or bract-like reduced leaves found on axillary short-shoots ('brachyblasts', with internodes condensed into a very short axis) (Wong, 1988; 1989). Compared against this, all the other mostly arborescent members of the _Canthium_ complex are unarmed, do not have supernumerary axillary buds or produce brachyblasts, and have flowers in clearly branched to sub-umbellate cymes. In this paper, we address the key morphological distinction of two groups of arborescent Southeast Asian taxa aberrant within _Canthium_ that have been commonly identified with _C. glabrum_ Blume and _C. confertum_ Korth., and propose them as new genera after comparison with other superficially similar generic elements identified so far.

MATERIALS AND METHODS

This study was carried out using conventional approaches for herbarium taxonomic studies. Specimens at the BKF, BO, BRUN, K, KEP, L, P, SAN, SAR, SING and VNM herbaria (acronyms follow Thiers continuously updated) were examined. In addition, JSTOR images of type specimens and specimen catalogues at BM, K, L, P and SING were also checked. We acknowledge that this contribution is a continuing, morphologically based, taxonomic resolution to be considered in light of the situation that molecular phylogenetic analyses will only provide finer resolution of the _Canthium_ complex in Southeast Asia, against the challenges of comprehensive taxon sampling and gaining additional insights from additional gene regions, in due time.

Several characters discussed in past works—such as stipule form, flower sexuality, presence of a tubular part of the calyx limb, the form of the anther connective on its dorsal side, and fruit shape—have been excluded either because they are basically uninformative or have not been sufficiently well-documented or represented in specimen material. The characters in this survey...
(Table 1) thus include plant habit, presence of supernumerary axillary buds and spines, inflorescence form, corolla form, presence of a deflexed hair-ring and other hair types in the corolla throat, anther orientation, style length, base of stigma (or styril head complex), and pyrene form including development of an apical-dorsal crest and lateral shoulders. These are characters that have received better documentation or are accessible through the available specimen material, and which could potentially illuminate our comparative studies.

In some cases, we have had to resort to better corroboration of the data. For example, both species of Kanapia were described as "scrambling shrubs", but this is not consistent with documentation on the associated specimen material available in the BO and K herbaria. Also, the stipules of Kanapia were noted as being without keels, but in fact there are keels developed; instances such as this have been considered in the decision to exclude stipule characteristics from the present survey, after verification that there were no significant variations for the character.

Nomenclatural considerations follow the International Code of Nomenclature (McNeill et al., 2012). Plant architectural analysis followed the approach of Hallé et al. (1978).

DISTINCTIVE MORPHOLOGY OF TWO ODD 'CANTHIUMS'

Canthium glabrum was described by Blume (1823) and Canthium confertum by Korthals (1851), and both have remained in that genus unconformably all this time. They are different (1851), and both have remained in that genus Canthium confertum (1851), and both have remained in that genus Canthium glabrum.

A feature within Vanguerieae flowers that requires better understanding is the presence and significance of a band of long, stiff deflexed hairs, inserted at or below the corolla throat and found in some taxa but not others (Table 1, Fig. 1B); when such hairs are inserted on a band of thickened tissue, this coincides with a noticeable constriction of the corolla at or below the throat, which often makes the corolla tube or its lower part somewhat bulbous or urceolate. This band of stiff deflexed hairs inserted at or below the throat, and the constriction of the corolla tube below the lobes are characteristics found in a number of genera in the complex, such as Bullockia, Canthium s.s., Canthium glabrum, Kanapia, Keetia, Perakanthus, and Psydrax, for example, but are significantly lacking in C. confertum (Wong, 1988; 1989) (Fig. 8B), Cyclophyllum (Mouly & Jeanson, 2015) and Pyrostria (Bridson, 1987). Instead, in Canthium confertum, Cyclophyllum and Pyrostria, only fine, moniliform hairs (which under low magnification have been described as fine, pale crisped hairs: Bridson (1987), Wong (1988; 1989)) congest the upper part of the inner corolla tube and the throat (Fig. 8B, C).

Fine moniliform hairs are also present in addition to the deflexed hair ring at the throat in Canthium glabrum (Koorders 29055f (BO), Fig. 1) and Kanapia (Elmer 17714 (BO)); however, in Perakanthus only stiff unicellular hairs congest the throat in addition to the deflexed hair-ring found (Puff & Wong, 2005). Perakanthus also has other unique features, such as spiky long erect hairs all over the outer surface of the corolla (compared to glabrous or largely glabrous outer corolla surfaces in Canthium glabrum and Kanapia), and filaments as long as the erect throat hairs and which carry the anthers above the hairs (compared to short filaments that, together with the anthers are in the same level as the throat hairs) (Puff & Wong, 2005). Canthium glabrum has the throat's moniliform hairs gathered in five distinct dense tufts (each tuft with hairs longest in the middle) in between stamens and opposite to the corolla lobe bases (Fig. 1, 4B), whereas Kanapia has subequally long moniliform hairs distributed densely and evenly as a ring around the throat (Table 1).

Cyclophyllum and Pyrostria are easily distinguished from Canthium confertum by their stigmatic form, which has been described as capitate with a convex base (Mouly & Jeanson, 2015) or solid with the style attached at the base (Bridson, 1987). The stigma in Canthium confertum has a small basal recess which accommodates the insertion of the style apex (Wong, 1988; 1989) (Fig. 8B) and is therefore more reminiscent of the mirtiform stigma or
Table 1. Key distinctions among *Canthium* s.s., *Canthium confertum*, *C. glabrum*, *Bullockia*, *Cyclophyllum*, *Kanapia*, *Keetia*, *Perakanthus*, *Psydrax*, and *Pyrostria*. *Canthium confertum* and *C. glabrum* columns are coloured for easy comparison.

<table>
<thead>
<tr>
<th>Plant habit</th>
<th>'Canthium' confertum</th>
<th>Cyclophyllum</th>
<th>Pyrostria</th>
<th>'Canthium' glabrum</th>
<th>Perakanthus</th>
<th>Kanapia</th>
<th>Bullockia</th>
<th>Keetia</th>
<th>Psydrax</th>
</tr>
</thead>
<tbody>
<tr>
<td>climbers, scramblers, small trees with scrambling branches</td>
<td>small trees</td>
<td>shrubs, treetlets, small trees</td>
<td>climbers, shrubs, small trees</td>
<td>small trees</td>
<td>treelets</td>
<td>treelets, small trees</td>
<td>scramblers, shrubs, small trees</td>
<td>climbers, scramblers</td>
<td>small trees</td>
</tr>
<tr>
<td>Axillary supernumerary buds &amp; spines</td>
<td>present</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
<td>(absent)</td>
</tr>
<tr>
<td>Flowers / Inflorescences</td>
<td>solitary flowers / fascicles / short cymes, in leaf axils on normal shoots, or in leaf &amp; bract axils on short shoots</td>
<td>short sub-umbellate cymes; in leaf axils on normal shoots only</td>
<td>fascicles / short dichasial cymes; in leaf axils on normal shoots only</td>
<td>short sub-umbellate cymes; in leaf axils on normal shoots only</td>
<td>fascicles / short cymes; in leaf axils on normal shoots only</td>
<td>clearly branched cymes; in leaf axils on normal shoots only</td>
<td>fascicles / short cymes; in leaf axils on normal shoots only</td>
<td>clearly branched cymes; in leaf axils on normal shoots only</td>
<td>fascicles of 1–few flowers, sub-umbellate cymes; in leaf axils on normal shoots only</td>
</tr>
<tr>
<td>Corolla form</td>
<td>subrotate-urceolate (constricted just below lobes); lobes spreading</td>
<td>salverform; lobes spreading</td>
<td>subrotate-cylindric; lobes spreading</td>
<td>subrotate-urceolate (constricted just below lobes); lobes spreading</td>
<td>urceolate to short-tubular bulbous base (constricted just below lobes); lobes spreading</td>
<td>subrotate-urceolate (constricted just below lobes); lobes spreading</td>
<td>tubular; lobes sub-erect</td>
<td>tubular - campanulate-late (constricted below lobes); lobes reflexed</td>
<td>tubular to infundibular; lobes reflexed</td>
</tr>
<tr>
<td>Deflexed hair-ring at corolla throat</td>
<td>present at / just below throat</td>
<td>nil</td>
<td>nil</td>
<td>present at / just below throat</td>
<td>present at / just below throat</td>
<td>present at / just below throat</td>
<td>present at / just below throat</td>
<td>present at / just below throat</td>
<td>present at / just below throat</td>
</tr>
<tr>
<td>Other hairs at corolla throat</td>
<td>nil or sparse short hairs</td>
<td>continuous band of exert dense moniliform hairs</td>
<td>continuous band of exert dense moniliform hairs</td>
<td>discrete tufts of exert dense moniliform hairs between anthers</td>
<td>discrete tufts of exert dense moniliform hairs between anthers</td>
<td>continuous band of exert dense moniliform hairs</td>
<td>nil or sparse short hairs</td>
<td>nil or sparse short hairs</td>
<td>nil or sparse short hairs</td>
</tr>
<tr>
<td></td>
<td>Canthium s.s.</td>
<td>'Canthium' confertum</td>
<td>Cyclophyllum</td>
<td>Pyrostria</td>
<td>'Canthium' glabrum</td>
<td>Perakanthus</td>
<td>Kanapia</td>
<td>Bullockia</td>
<td>Koezia</td>
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<td>------------------</td>
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<td>-------------------</td>
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<td>---------</td>
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<td>---------</td>
</tr>
<tr>
<td>Anther orientation</td>
<td>erect to spreading or reflexed</td>
<td>erect to spreading</td>
<td>erect</td>
<td>erect to spreading</td>
<td>erect to spreading</td>
<td>erect</td>
<td>erect</td>
<td>strongly reflexed</td>
<td></td>
</tr>
<tr>
<td>Style length</td>
<td>almost = corolla tube</td>
<td>almost = corolla tube</td>
<td>only slightly &gt; than corolla tube</td>
<td>only slightly &gt; than corolla tube</td>
<td>almost = corolla tube</td>
<td>slightly &gt; to 2 × corolla tube</td>
<td>almost = corolla tube</td>
<td>2-3 × corolla tube</td>
<td></td>
</tr>
<tr>
<td>Base of stigma/ stylar head complex</td>
<td>mitriform</td>
<td>very slightly recessed</td>
<td>solid</td>
<td>solid</td>
<td>very slightly recessed</td>
<td>mitriform</td>
<td>mitriform</td>
<td>mitriform</td>
<td>mitriform</td>
</tr>
<tr>
<td>Pyrene form</td>
<td>plano-ovoid, no shoulders</td>
<td>plano-ovoid, no shoulders</td>
<td>plano-ovoid to ellipsoid, no shoulders</td>
<td>plano-ovoid with sub-level to upcurved shoulders forming lateral keels</td>
<td>plano-ovoid with sub-level to rounded shoulders forming lateral keels</td>
<td>plano-ovoid with sub-level to rounded shoulders not forming sharp keels</td>
<td>sub-ellipsoid to plano-ovoid, no shoulders</td>
<td>plano-ovoid, no shoulders + lid-like area on ventral or apical part</td>
<td></td>
</tr>
<tr>
<td>Pyrene apical- dorsal crest</td>
<td>slight, at apex only &amp; rounded, ridge-like; to ± half-way down dorsal side</td>
<td>slight, at apex only &amp; rounded, ridge-like; to ± half-way down dorsal side</td>
<td>keel-like; apex to entire length of dorsal side</td>
<td>keel-like; apex to entire length of dorsal side</td>
<td>rounded, ridge-like; to ± half-way down dorsal side</td>
<td>slight, at apex only &amp; rounded, ridge-like; to ± half-way down dorsal side</td>
<td>slight, at apex only &amp; rounded, ridge-like; to ± half-way down dorsal side</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyrene surface</td>
<td>verrucose</td>
<td>verrucose</td>
<td>verrucose</td>
<td>verrucose</td>
<td>± smooth</td>
<td>± smooth</td>
<td>verrucose</td>
<td>verrucose to ± smooth</td>
<td></td>
</tr>
<tr>
<td>Distribution</td>
<td>Africa, Madagascar, India, Malesia</td>
<td>Malay Peninsula, Borneo, Philippines</td>
<td>N Guinea, SW Pacific, Australia</td>
<td>trop Africa/ Madagascar, SE Asia</td>
<td>India, Indochina, W Malesia</td>
<td>Malay Peninsula</td>
<td>Philippines</td>
<td>E trop &amp; S Africa</td>
<td>trop &amp; S Africa</td>
</tr>
</tbody>
</table>

Table 1. (continued)
Fig. 1. Flowers of Canthiumera species (formerly placed as *Canthium glabrum*). A. *Canthiumera glabra* flower (note short calyx limb). B. *C. glabra*, longitudinal section through corolla showing ring of stiff deflexed hairs inside the tube and bundles of sub-erect moniliform hairs at the throat. C. *Canthiumera robusta* flower (note calyx limb as long as, and hiding, corolla tube). [A & B from Himnah Rustiami HR 2001 (BO); C from M. Nur s.n. 16 Aug 1917 (BO)]. Scale bar is 1 mm. Drawn by K.M. Wong.

Stylar head complex (Igersheim, 1993) of a number of genera in the *Vanguerieae*. Also, *Cyclophyllum* typically has salverform corollas in which the lobes are much shorter than the tube (Mouly & Jeanson, 2015); the other two taxa typically have subrotate to cylindric corollas where the lobes are subequal to (i.e., at most only slightly longer or shorter than) the tube (Table 1).

Pyrene form has been found to be distinctive in various genera among the *Canthium* complex and allies (Bridson, 1985; 1986; 1987), and several taxa from Southeast Asia, including *Kanapia*, *Perakanthus* and those identified with *Canthium confertum* (Figs. 7C, 8E) and *C. glabrum* (Figs. 2, 4D, 5C & D6), which have pyrenes that develop a prominent apical-dorsal crest and two lateral 'shoulders', stand out in this regard (Wong, 1988; 1989). All the other Southeast Asian taxa, including *Psydrax*, have pyrenes that are generally plano-convex and rounded, ovoid, ellipsoid, or obovoid in outline, without distinct keels or shoulders (Table 1).

Whereas the apical-dorsal pyrene crest in *Canthium confertum* and *Kanapia* is only slightly developed and at most reaches to about halfway down the pyrene, that in *Canthium glabrum* and *Perakanthus* continues as a prominent keel that reaches to the pyrene base (Fig. 2). Accompanying the development of the apical-dorsal crest is a broadening out of the upper lateral parts of the pyrene into 'shoulders'. In *Canthium confertum* and *Kanapia* (Fig. 2), the pyrene shoulders are the least prominent among these taxa and slope downwards ca. 45°, whereas in *Canthium glabrum* and *Perakanthus*, the shoulders are more level sideways and only slope very slightly or are even slightly upcurved. The pyrene surface in *Canthium confertum* and *Kanapia* is verrucose (knobbly or with scattered protuberances) as in many other *Vanguerieae* genera, but smooth in *Canthium glabrum* and *Perakanthus* (Table 1).

Molecular work has indicated some improved taxonomic clarity in this complex (Lantz & Bremer, 2004; Razafimandimbison et al., 2009) but lack of sampling in Southeast Asian taxa continues to limit resolution of some key areas. While *Canthium glabrum* has apparently not been included in published molecular phylogenetic analyses, the phylogenetic position of *Canthium confertum* demonstrated by Razafimandimbison et
al. (2009) is of much significance. The latter was recovered in a sister position to the Cyclophyllum clade, and both were in turn well-distinguished from the other Pyrostria s.l. The shared morphological characteristics among Cyclophyllum, Pyrostria and Canthium confertum discussed above (viz. corolla throat congested by moniliform hairs and without a deflexed hair-ring) probably reflect their close phylogenetic relationship parallel to that shown by Razafimandimbison et al. (2009).

Here we describe two new genera in the Vanguerieae, one to accommodate Canthium glabrum and three other species, and another for Canthium confertum and two congeners.

THE NEW GENERA


Type species: Canthiumera glabra (Blume) K.M.Wong & Mahyuni.

Diagnosis. This new genus was previously placed with Canthium Lam. but differs from Canthium s.s. in being arborescent (not scrambling or climbing) in habit and not developing supernumerary axillary buds, axillary spines or axillary short-shoots ('brachyblasts') as in Canthium s.s. It resembles Perakanthus Robyns ex Ridl. in having pyrenes that develop a prominent keel-like apical-dorsal crest that extends down to the pyrene base, with two lateral shoulder-like extensions. However, Canthiumera has a glabrous or largely glabrous outer corolla surface, flexuous-suberect moniliform hairs above a ring of deflexed hairs at the corolla throat, and short filaments that, together with the anthers, are at the same level as the throat hairs, whereas Perakanthus has spiky erect long hairs all over the corolla outer surface, stiff erect unicellular hairs above the ring of deflexed hairs at the corolla throat, and its filaments are as long as the throat hairs and carry the anthers above the hairs.

Trees. Stipules triangular-ovate, with a slight to pronounced median keel prolonged into an apical
Key to Canthiumera species

1. Corolla tube in open flower mostly to entirely hidden by the calyx limb. Pyrenes with sub-horizantal to slightly uparched shoulders ................................................................. 3. C. robusta
   Corolla tube in open flower conspicuous with only the base hidden by the calyx limb. Pyrenes with shoulders sloping downward ................................................................. 2

2. Corolla broadly cylindric and slightly flared outwards. Leaf margin and veins on lower surface with long spreading hairs .................................................................................. 2. C. neilgherrensis
   Corolla urceolate and inflated. Leaf margin glabrous, veins on lower surface glabrous to sub-puberulent ................................................................. 3

3. Calyx 1–1.5 mm long; corolla lobes about the same length as the tube; style puberulent … 1. C. glabra
   Calyx 2–2.5 mm long; corolla lobes longer than the tube; style glabrous ........................................ 4. C. siamensis

cusp or lobe. Leaves opposite and decussate on vertical stem axes but distichous on lateral (horizontal) branches; frequently with pit-domatia in the axils of secondary or higher-order veins. Inflorescences axillary on lateral branches, pedunculate, cyme-like or sub-umbellate, bracts small and inconspicuous. Flowers bisexual; corolla subrotate-cyme urceolate to broadly cylindric, constricted just below corolla lobes, glabrous or short-pubescent outside, throat with dense tufts of erect-spreading (becoming flexuous-crised) moniliform hairs longest at the base of corolla lobes, the tube around the same length as the lobes or shorter, inside with a ring of stiff deflexed hairs just below the throat, corolla lobes spreading in the open flower; stamens alternate with the corolla lobes and not longer than the corolla throat hairs, anthers ovate with broad connective, suberect to spreading, inserted on short filaments at the throat; style glabrous or pubescent, stigma globose to club-shaped, with a slight basal recess; ovary with 2 locules, each locule with a solitary ovule inserted near the upper part. Fruits ellipsoid, obovoid or obcordate-compressed; pyrenes obovoid-compressed, ventrally plane, dorsally with a prominent keel-like crest reaching to the base, laterally with two sub-apical extensions ('shoulders') flattening out as keels and reaching to the base, smooth. Seeds one in each pyrene.

Distribution. India, Myanmar, Thailand, Indochina, West Malasia (Sumatra, Malay Peninsula, Java, Borneo); four species.

Etymology. The genus name is composed of Canthium, the genus with which it was confused, and the Latin umera which means shoulder, referring to the prominent lateral extensions in the pyrene.

1. Canthiumera glabra (Blume) K.M.Wong & Mahyuni, comb. nov. (Fig. 1A, B; 2)

(BO); 1913, S.H. Koorders Kds 38216β (BO); Ponorogo, Madin, 1901, S.H. Koorders Kds 38781β (BO). West Java. Banten, Cikandi, 1 May 1933, Shieldt s.n. (BO); Bogor Botanic Garden, IV-E.146, 28 Jan 1927, Anonymous s.n. (BO); Bogor, Laladon, Ciomas, 19 Apr 1920, R.C. Bakhuisen v.d. Brink 3437 (BO), 23 Jan 1921, R.C. Bakhuisen v.d. Brink 5106 (BO); Cibodas, Ciampea, 13 Jan 1929, C.G.G.J. van Steenis 2695 (BO); Cibular, 22 Feb 1951, Nedi & Idjam 464 (BO); Depok, no date, 1901, Sugandiradjja 237 (BO); Garut, 19 Aug 1893, S.H. Koorders Kds 13972β (BO); Jampong Kulon, 28 Aug 1891, S.H. Koorders Kds 6497β (BO); Lewiliang, 9 Dec 1928, van Leeuwen-Reijnvaan 11985 (BO); Kalapanunggal, 24 Dec 1920, V. G.e 590 (BO), 24 Dec 1920, C.A. Backer 31112 (BO); Pelabuhan Ratu, 1900, S.H. Koorders Kds 12296β (BO); Sukabumi, Preanger, Pangentjongan, Aug 1899, S.H. Koorders Kds 11803β (BO), Apr 1898, S.H. Koorders Kds 26702β (BO), 5 Apr 1899, S.H. Koorders Kds 34302β (BO); Tasik Malaya, 25 Jul 1917, S.H. Koorders Kds 47943β (BO); 5 Aug 1917, S.H. Koorders Kds 47928β (BO); Tegal Sapi, 5 Jan 1924, 240 m, R.C. Bakhuisen v.d. Brink 3180 (BO). Sumbawa. West Sumbawa, Sumbawa Besar, Semongkat Atas, Kuswata 122 (BO).

2. Canthiumera neilgherrensis (Wight) K.M.Wong, comb. nov. (Fig. 3)


Canthiumera neilgherrensis var. chartacea (Gamble) K.M.Wong, comb. nov.


Other specimens examined. India. Pulneys, no date Wight 1422 (K [K000031506, K000031507]).

Note. Miquel (1857) was the first to point out that Canthium glabrum was not distantly related from ("Haud longe distare videtur") C. neilgherrensis (sic!) Wight.

Canthiumera neilgherrensis var. chartacea has chartaceous leaves with 5–6 pairs of secondary veins, compared with the typical variety which has coriaceous leaves with 6–8 pairs of secondary veins. There is too scant material on which to consider if these differences are truly consistent; furthermore, flowers are known only for the typical variety.


Diagnosis. The new species Canthiumera robusta is superficially similar to Canthiumera glabra (Blume) K.M.Wong & Mahyuni, but differs in having mature flowers with the corolla tube mostly to completely hidden by the calyx limb and pyrenes with slightly uparched lateral extensions. In contrast, Canthiumera glabra has mature flowers with only the corolla tube base hidden by the calyx limb and pyrenes with rounded to downwardly sloping lateral extensions. (Fig. 1C, 2, 4, 9, 10)


Tree to 25 m tall. Stipules with a basal triangular-ovate portion 2–3 mm long and a pronounced median keel prolonged into an apical cusp or lobe to 5 mm long. Leaves ovate to elliptic, 7–18 × 3–9 cm, apex acute to slightly cuspidate, base obtuse-rounded to cuneate, typically subcoriaceous when fresh but often drying with a chartaceous texture, secondary veins (5–)6–8–(10) pairs, frequently with pit-domatia in the axes of secondary or higher-order veins, often with intermediate veins in between secondaries; petioles 7–14 mm long. Inflorescences with short peduncles 1–3 mm long and branches 3–6 mm long, the axes mostly glabrescent, rarely scantily hispid. Flowers on short pedicels 2.3 mm long; calyx obconical, hypanthium 1.5–2 mm long, limb ca. 1.5–2 mm long with 5 minute triangular teeth; corolla subrotate-urceolate, constricted just below corolla lobes, glabrous, tube ca. 1.5–2 mm long and nearly to completely hidden by the calyx limb in the open flower, throat with dense tufts of pale erect-spreading (becoming flexuous-crisped) moniliform hairs longest at the base of corolla lobes, inside with a ring of stiff deflexed hairs just below the throat; corolla lobes around the same length as the tube or slightly longer, spreading to slightly recurved in the open flower; stamens with...
Fig. 3. *Canthiumera neilgherrensis*, reproduced from Wight, Icon. Pl. Ind. Orient. 3(4) (1846) tab. 1064bis. The main drawing depicts a flowering leafy branch. The numbered parts are: 1. Inflorescence; 2. Inside of split corolla; 3. Dorsal (L) and ventral views of anther; 4. Flower with corolla and part of calyx removed, showing disk and gynoecium; 5. Longitudinal section through ovary, disk and calyx; 6. Transverse section through ovary; 7. Cluster of fruits; 8. Single fruit; 9. Transverse section through fruit; 10. Longitudinal section through fruit showing attachment of pyrenes in the locules; 11. Lateral view of young pyrene; 12. Longitudinal section through seed showing embryo within; 13. Embryo with cotyledonary primordia at bottom. Scales omitted for simplicity.
anthers 2–2.5 mm long on short filaments ca. 0.5 mm long, suberect to spreading in the open flower; style 2.5–3 mm long, glabrous, stigma 1–1.5 mm long, globose to club-shaped, with a slight basal recess; ovary with 2 locules, each locule with a solitary ovule. *Fruits* ellipsoid to obovoid, 4-ridged when dry, to 50 × 36 mm when fresh, 40 × 28 mm when dried, ripening dark bluish green to purplish black, drying black; pyrenes to 44 × 26 mm, ventrally plane, the dorsal crest keel-like, to 5–7 mm wide, continuous and narrowing from apex to base, the shoulders sub-horizontal to slightly upcurved, extending as keels 2–4 mm wide down to the base, smooth. *Seeds* one in each pyrene.

**Notes.** Both Korthals (1851) and Miquel (1857) adopted the name *Canthium glabrum* for Bornean and Sumatran material, respectively. Hooker (1880) listed *Canthium glabrum* Blume as being distributed "from Tenasserim, Pegu, and the Andaman Islands, to Singapore and Penang", besides Java. Thus began a misassumption that was perpetuated in the absence of revisionary studies across the region, an effort long delayed by the morphologically very mixed nature, and formidable species richness, of the entire *Canthium* complex. In the ensuing floristic treatments for the Malay Peninsula by King & Gamble (1904), Ridley (1923), Craib (1932), and Gamble (1904), Ridley (1923), Craib (1932), and Merrill (1921) adopted *Plectronia glabra*.

*Canthiumera robusta* has pyrenes that reach 26 × 16 mm have also been found in the wild, as well as in nursery generated material (through uniparental or biparental selfing) raised from the same mother tree. The degree of sensitivity to inbreeding depression has not been investigated.

**Other specimens examined.** (All glabrous inflorescences.) **Anambas Island.** *(Indonesia.)* Pulau Siantan, 30 Mar 1928, C.G.G.J. van Steenis 749 (BO), east coast, 30 Mar 1928, M.R. Henderson *SFN* 20144 (BO, SING [SING0190655]).


Fig. 4. *Canthiumera robusta* K.M.Wong & X.Y.Ng, *spec. nov*. A. Leafy branch with inflorescences; note also keeled stipules. B. Flower with tufts of pale moniliform hairs visible opposite corolla lobes. C. Fruits. D. Pyrenes. Photos by Ang Wee Foong (A) and X.Y. Ng (B–D).


**Canthiumera robusta** material with slightly hispid inflorescence branches include the following: **Malay Peninsula.** **Malaysia.** Kedah: Langkawi Island, Bt. Sawar FR, 11 Dec 1969, T.C. Whitemore s.n. (KEP [KEP208464]). Perak: no date, L. Wray Jr. 1369 (SING [SING0189388]). **Thailand.** Tongkah, Aug 1892, Hamid s.n. (SING [SING0189546, SING0192940]). Borneo. **Malaysia.** North Borneo, Dec 1912, Amdjah 981 (BO).

4. **Canthiumera siamensis** (K.Schum.) K.M.Wong. comb. nov. (Fig. 5, 6) Basionym: **Plectronia siamensis** K.Schum., Bot. Tidsskr. 24 (1902) 335. **Canthium siamense** (K.Schum.) Pitard, Flore générale de l’Indochine 3 (1924) 300. — Type: J. Schmidt 622, Siam, Chantaburi, Koh Chang, near Lem Dan, 25 Feb 1900 (holotype C [C10018081], isotype K [K000763638]).

**Canthium glabrum** var. pedunculatum Pitard, Flore générale de l’Indochine 3 (1924) 292. — Type: M. Poilane 1609, Laos, Sam nuea, 29 Sep 1920 (lectotype P [P03937320], here designated; isolectotype P [P03937322]).


**Other specimens examined.** **Andamans.** No specific locality, no date, King's Coll. 201 (P [P03937352]), 8 Mar 1901, Prain's Coll. 16 (P [P03937304]); S Andaman, N Corbyn’s Cove, 27 Jan 1894, King's Coll. s.n. (P [P03937351]). **Cambodia.** Koh Kong province, Phnom Phloun Sam, 300 m asl, 4 Mar 1966, M. Martin 296 (P [P03937323]), Timor Sor Village, 98 m asl, 18 Nov 2009, S.K. Cheng et al. CL 1210 (SING [SING0174972]); Siem Reap & Angkor, 21-22 Dec 1917, A. Chevalier 36323 (P [P03937164]).

**India.** **Assam.** Sibsagar, Pedal 169 (P [P03937305]). **Laos.** Prov. Bassac, entry to B. Phinh & B. Nong keo, 200 m asl, 18 Oct 1928, M. Poilane 16016 (VNM [VNM00011999]); Sanavakhet to Quangtri, km 130, 9 Jan 1925, M. Poilane 11553 (VNM [VNM00011998]). **Myanmar.** Coast of Tenasserim, no date, W. Gomez in N. Wallich 8412 (K [K000031514]), N. Wallich 8412B (K [K000031515]). **Thailand.** No locality, no date, A.F.G. Kerr 7938 (TCD [TCD0017737]), Kerr 17608 (TCD [TCD0017738]). **E Thailand.** Chaiyaphum province; Khan Shan district, Kamang, Trung, Phu Khiao Wildlife Sanctuary, 22 Jan 2004, T. Wongprasert & S. Khaoiam 14-1 (BFK [SN144326, SN144327]). Nakorn Ratchasima province; Balik Chong district, Khao Yai National Park, Wang Jumpee area, 14°27’N, 101°23’E, 725 m, 17 Aug 2002, S. Somchin 3 (1924) 291, Kerr 17608 (TCD [TCD0017738]). **N Thailand.** Chiang Mai province: Muang district, Doi Sutep, 139 m, 17 Aug 2002, S. Somchin 3 (1924) 291, Kerr 17608 (TCD [TCD0017738]). **South China.** Hong Kong; Kwangtung, 139 m, 17 Aug 2002, S. Somchin 3 (1924) 291, Kerr 17608 (TCD [TCD0017738]). **Indonesia.** **Java.** Java: Semarang, 200 m asl, 12 Mar 1877, P. van Beusekom & C. Charoenpol 194 (BO, SING [SING0019990]). **Sumatra.** (Indonesia.) Simaloer, 12 Nov 1917, Achmad 77 (BO), 15 Jan 1918, Achmad 184 (BO), 25 Nov 1918, Achmad 759; Gayo Alaslanden Lami Sagoe, 21 Jun 1904, Pringgar Atmodjo 447 (BO). Riau; Pulau Karimun, 26 May 1980, H.N. Ridley 1620 (SING); Tiga Puluh Mountains, Bukit Karampal area, 0°46’S, 102°32’E, ca. 100 m, 13 Nov 1988, J.S. Burley, Tikurin et al. 1435 (SING [SING0192610]); Batoe Paulajeh, 600 ft, H.O. Forbes 2678 (BO); Sibual-bual, Sipirok, 27 May 1993, J.J. Afriastini 2516 A (BO).
Fig. 5. Canthiumera siamensis. A. Flower. B. Longitudinal section through flower with corolla removed, showing ovule attachment in ovary locules and style with 2-lobed stigma. C. Pyrene, oblique-dorsal view. D. Pyrene, ventral view showing transverse scar of placental attachment. Scale bars are 2 mm. Reproduced from J. Pitard (1924) in F. Gagnepain, H. Lecomte & H. Humbert (eds), *La Flore générale de l’Indochine* Vol. 3.

Fig. 6. Canthiumera siamensis: pyrenes in dorsal view, with the vertical preformed germination slit along the dorsal crest visible. The pyrenes are 17 mm long. From Thorel 1234, ‘Cochinchine’ (BO).
2004, T. Wongprasert & S. Khaoiam 41-58 (BFK [SN144267, SN144268]). **Peninsular Thailand.**

Hatien province: Phuquoc, 30 Dec 1983, J. Harmand 932 (BFK [SN196475, SN196476]). Patthalung province: see Khanom Tung Song district, Kao Yeh National Park, Riang Tong falls, 150 m, 25 Sep 1986, J.F. Maxwell 86-73 (BFK [SN095484]).

Trang province: Na Yong district, Kao Chong, 7° 33'N, 101° 50'E, 200 m, 28 Feb 1974, C. Thorel 32754 (BKF [SN144267, SN144268]).

Khao Kho district, Hala, Klong Ai Kading, 50 m, 21 Feb 2003, C. Niyondham & P. Puudja 7079 (BFK [SN196475, SN196476]). Patthalung province: see Bahn Poto district, Kao Boo-Kao Yeh National Park, Riang Tong falls, 150 m, 25 Sep 1986, J.F. Maxwell 86-73 (BFK [SN095484]).

Chonburi province: Khaokhieo open zoo, 9 Dec 2000, C. Phengklai et al. 15466 (BKF [SN192167]).

Kanchanaburi province: Sangklaburi district, Toong Yai Naresuan Wildlife Reserve, 450 m, 11 Oct 1993, J.F. Maxwell 93-1210 (BFK [SN186798, SN187666]).


Vietnam. **Cochinchine (S Vietnam).**
No locality, 1862–1866, C. Thorel 853 (P [P03937356]). Bienhoa province: Mt. Nui Chua Chan, 300 m asl, 10 Jan 1928, M. Poilane 14446 (VMN [VMN00011997]), 200–300 m asl, 24 Aug 1931, M. Poilane 19395 (VMN [VMN00012000, VMN00013579]), 200–800 m asl, 10 Jan 1914, F. Fleury in A. Chevalier 29912 (P [P03937347, P03937348, P03937354, P04605437]).

Gia Dinh province: Thu dau mot, no date, E. Lefèvre 289 (P [P03937355]), 1862–1866, C. Thorel 1234 (BO [BO-1323143], P [P03937357, P03937358]), Thu dau mot, R. Bung, Sep 1874, L. Pierre 3240 (P [P03937303, P03937306, P04951059]).

Hatien province: Phu quo, 30 Dec 1919, M. Poilane 897 (VMN [VMN00011994]), Iles de Poulo Condor, Sep 1876, J. Harmand 932 (P [P03937308], VMN [VMN00011995]), Condor, Oct 1876, J. Harmand 1918 (P [P03937307]).

**Tonkin (N Vietnam).**

Yen Khe Trung: Do-thong, 12 Nov 1882, H. Bon 1831 (P [P03937343, P03937344]).

**Notes.** Pitard (1924) maintained both names, but *C. siamense* as a poorly known taxon. Under his enumeration of *Canthium glabrum*, Craib (1932) stated: "*C. siamense*, Pitard... which is still represented by the type collection only... is, so far as the material goes, too near *C. glabrum* as interpreted here".

**Dibridsonia** K.M.Wong. **genus novum.**
Type species: *Dibridsonia conferta* (Korth.) K.M.Wong

**Diagnosis.** This new genus was previously placed with *Canthium Lam.* but differs from *Canthium s.s.* in being arborescent (not scrambling or climbing) in habit and not developing supernumerary axillary buds, axillary spines or axillary short-shoots ('brachylasts') as in *Canthium s.s.* It resembles *Cyclophyllum Hook.f.* and *Pyrostria Comm.* ex Juss. in lacking a ring of deflexed hairs at the corolla throat, and instead has dense flexuous-suberect moniliform hairs. It differs from both *Cyclophyllum* and *Pyrostria* in its stigma base that is slightly recessed, and in its pyrene form which has a rounded ridge-like apical-dorsal crest reaching halfway down to the base with two lateral sloping shoulder-like protrusions (both *Cyclophyllum* and *Pyrostria* have solid stigmas, and their pyrenes are plano-obovoid without conspicuous apical-dorsal crests or shoulder-like protrusions).

Trees. **Stipules** triangular-ovate, with a slight to pronounced median keel prolonged into an apical cusp or lobe. **Leaves** opposite and decussate on vertical stem axes but distichous on lateral (horizontal) branches; frequently with pith-domatia in the axils of secondary veins. **Inflorescences** axillary on lateral branches, pedunculate, subumbellate, bracts small and inconspicuous. **Flowers** functionally unisexual; corolla subtrose or broadly funnel-shaped, glabrous outside, throat with a continuous dense band of erect spreading (becoming flexuous-crisped) moniliform hairs, the tube around the same length as the lobes, inside without a ring of stiff deflexed hairs just below the throat, corolla lobes spreading in the open flower; stamens alternate with the corolla lobes and not longer than the corolla throat hairs, anthers ovate, with a slight to conspicuous apical-cuspidate, sometimes rounded, often prominently beaked, the two parts of the anther base with two lateral sloping shoulder-like protrusions (both *Cyclophyllum* and *Pyrostria* have solid stigmas, and their pyrenes are plano-obovoid without conspicuous apical-dorsal crests or shoulder-like protrusions).

Trees. **Stipules** triangular-ovate, with a slight to pronounced median keel prolonged into an apical cusp or lobe. **Leaves** opposite and decussate on vertical stem axes but distichous on lateral (horizontal) branches; frequently with pith-domatia in the axils of secondary veins. **Inflorescences** axillary on lateral branches, pedunculate, subumbellate, bracts small and inconspicuous. **Flowers** functionally unisexual; corolla subtrose or broadly funnel-shaped, glabrous outside, throat with a continuous dense band of erect-spreading (becoming flexuous-crisped) moniliform hairs, the tube around the same length as the lobes, inside without a ring of stiff deflexed hairs just below the throat, corolla lobes spreading in the open flower; stamens alternate with the corolla lobes and not longer than the corolla throat hairs, anthers ovate with broad connective, suberect to spreading, inserted on short filaments at the throat; style glabrous or pubescent, stigma globose to club-shaped, with a slight basal recess; ovary with 2 (rarely 5) locules, each locule with a solitary ovule inserted near the upper part. **Fruits** obovate to obcordate-compressed (rarely subglobose and
Key to species of *Dibridsonia*

1. Leaves drying dark brown, with 5–7 pairs of secondary veins that loop conspicuously near the leaf margin. Fruits 13–20 mm long, on pedicels 10–18 mm long ........................................ 3. *D. oblongifolia*

Leaves drying pale greenish brown, with 3–4 pairs of secondary veins that fade near the leaf margin. Fruits not exceeding ca. 10 mm long, on short pedicels not exceeding 5 mm long ...................... 2

2. Leaves with 3–4 pairs of secondary veins impressed on the upper leaf surface and conspicuous pit-domatia in their axils with the midrib on the lower surface. Fruits obovoid, 2-locular, with 1–2 pyrenes ........................................................................ 1. *D. conferta*

Leaves with 3 pairs of secondary veins flat to raised on the upper leaf surface and without conspicuous domatia in vein axils on the lower surface. Fruits subglobose and 5-lobed, 5-locular, with 5 pyrenes ...................................................... 2. *D. culionensis*

5-lobed; pyrenes obovoid-compressed, ventrally plane, dorsally with a rounded ridge-like crest reaching to only halfway to the base, laterally with two rounded sub-apical extensions (‘shoulders’) sloping downwards, verrucose or minutely tuberculate. Seeds one in each pyrene.

**Distribution.** West Malesia and the Philippines; three species.

**Etymology.** The genus honours Diane M. Bridson, whose research on the taxonomy of the *Canthium* complex at the Royal Botanic Gardens, Kew, was both illuminating and inspiring.

1. **Dibridsonia conferta** (Korth.) K.M.Wong, comb. nov. (Fig. 7, 8)

With leaves drying dark brown, with 5–7 pairs of secondary veins that loop conspicuously near the leaf margin. Fruits 13–20 mm long, on pedicels 10–18 mm long. Seed one in each pyrene. Leaves drying pale greenish brown, with 3–4 pairs of secondary veins that fade near the leaf margin. Fruits not exceeding ca. 10 mm long, on short pedicels not exceeding 5 mm long.


**Malay Peninsula. Malaysia.** Johor: Gunong Le-
Fig. 7. *Dibridsonia conferta*. A. Female flowers showing spreading anthers (empty) and broadly 2-lobed stigmas, with a continuous ring of pale moniliform hairs at the corolla throat. B. Fruiting branch. C. Pyrenes with characteristic verrucose surface. Photos by X.Y. Ng.
Fig. 8. *Dibridsonia conferta*. A. Inflorescence with one flower removed (stippled surface). B. Longitudinal section through female flower, showing band of moniliform hairs at the corolla throat. C. Corolla fragment bearing moniliform hairs. D. Fruit. E. Pyrene, dorsal (left) and ventral views. a, empty anther; p, peduncle; s, stigma. Scale bars represent 2 mm, except C (1 mm). [A & B from Wong s.n., MacRitchie Reservoir forest; C & D from Samsuri SA 1363 (SING)]. Drawn by K.M. Wong.
Canthium (Elm.) Merr., Enum. Philipp. Fl. Pl. 3 (1923) 535.

35 (1928) 8.


isotypes A [A00092466], K [K000763620], NY


Excluded taxon. The name Plectronia glandulosa Merr. (Merrill 1918: 365) has been associated with the Canthium confertum alliance. This was supposedly derived from Ixora glandulosa Blanco Fl. Filip. (1837) 61; ed. 2 (1845) 42; ed. 3, 1 (1877) 78 and Merrill (1918) states: "Ixora glandulosa was erroneously reduced by Fernandez-Villar to Canthium confertum Korth., a species unknown from the Philippines. It is certainly identical with the form described by me in 1906 as Plectronia viridis, but Blanco's specific name being the older is here accepted." Merrill (1918) then nominated as an "Illustrative specimen" the collection Merrill: Species Blancoanae No. 897, Luzon, Bataan Province, Mount Mariveles, Mar 1915 (P [P00836623]). But note that Blanco (1837) described a 4-dentate calyx and 4-lobed corolla, so that interpretation of that entity as a member of the Canthium complex becomes difficult and ambiguous. On the other hand, at the MA Herbarium, the specimen Llanos 198 [MA757232] is annotated by E. Quisumbing in Sep 1958 as lectotype of "Canthium glandulosum" (Blanco) Merr. (Ixora glandulosa Blanco)"; however, this is a spiny taxon and is correctly Fagerlindia microcarpa (Barl. ex DC.) Rids. Considering all this, combinations putatively based on Ixora glandulosa Blanco are best ignored.

TREE ARCHITECTURE

We were able to observe tree form in Canthiumera glabra in the Bogor Botanical Gardens and C. robusta and Dibridsonia conferta in Brunei, Peninsular Malaysia and Singapore. Basically, the lateral (axillary) inflorescences have no influence on shoot growth and plant architecture. The form is a relatively simple one with a monopodial orthotropic stem axis bearing opposite and decussate leaves, and producing branches continuously at most nodes at somewhat even spacing.

The branches are monopodial plagiotropic axes bearing opposite leaves dichotomously (Fig. 9). Primary branches seldom bear flowers directly but, instead, flowering (and fruiting) occurs mostly along secondary and higher-order branch axes (Fig. 9). Branch growth is also continuous. The primary branches survive for a relatively short period and do not attain very large size even at their base, and in older trees the lower branches senesce and fall off in a "self-pruning" manner, eventually and typically forming an erect trunk with pairs of horizontal to distally pendulous, relatively slender branches forming its crown.

This combination of axis behaviour in tree architectural analysis is characteristic of what is
known as Cook's model (Hallé et al., 1978). Additionally, the second-order branches along a main (primary) branch are usually in pairs, where alternate pairs have one branch horizontal on one side and the other branch deflexed. The remaining branch pairs each have one branch horizontal on the opposite side and the other deflexed. Deflexed branch members are sometimes abortive or deciduous at an early stage (Fig. 9) (Wong, 1988; 1989). In the Canthium alliance, observed species of Canthiumera, Dibridsonia and Psydrax share this distinctive architecture.

DISPERAL ECOLOGY

The fruits of Canthiumera and Dibridsonia are fleshy drupes which contain substantial mesocarp surrounding the pyrenes, and are characteristic of animal-dispersed fruits.

In Canthiumera fruits, the two pyrenes are orientated such that their ventral surfaces face each other, and the angles thus formed by their sharp keel-like crests and lateral shoulders within the endocarp mass (Fig. 10A) probably serve as a deterrent against their mastication by frugivores. Instead, frugivores are likely to either eat only the pulp around the pyrenes and discard the intact pyrenes, or swallow the fruits whole and get rid of the pyrenes later. The keeled, apical-dorsal pyrene crest is likely also a defense against gnawing by seed predators which might gain access secondarily to the discarded bare pyrenes. The elongate embryo within the seed is surrounded by a small amount of endosperm which seems to not be a sufficient reward for seed predators that must first get past the hard, keeled endocarp (pyrene shell) (Fig. 10B). The Canthiumera pyrene structure therefore seems effective for maximizing mesocarp volume and minimizing seed and endosperm volume, in a trade-off between providing a substantial amount of pulp to attract and reward herbivore dispersers, and discouraging
Canthiumera robusta fruits ripen from green to bluish grey and are relatively large in size. Fruits which ripen to grey are rare, and, in comparison to those which ripen to more common colors such as red or black, they may be a less-preferred resource that is only opportunistically utilized by birds (Duan et al., 2014). Dull-colored fruits are usually known to be primarily mammal-dispersed (Knight & Siegfried, 1983; Corlett, 1996). In Singapore, Canthiumera robusta fruits are known to be eaten by frugivorous birds with larger gape sizes, such as the red-crowned barbet (Megalaima rafflesii) and common hill myna (Gracula religiosa), which have been observed to peck at the pulp of ripening fruits and then swallow and regurgitate the pyrenes, or swallow the fruits whole and later regurgitate the pyrenes (Bird Ecology Study Group 2016a; 2016b). Canthiumera robusta fruit consumption by primates has not been documented in Singapore, but in Sumatra, it is known to be eaten by the Mentawai langur (Presbytis potenziani) (Hadi, 2012 as ‘Canthium glabrum’). Primates are known to deal with seeds in several ways (Corlett & Lucas, 1990), and it seems possible that they may simply discard the pyrenes of Canthiumera robusta on site. Other arboreal and nocturnal mammals for which fruit color is a less important signal, such as civets, may also have a role in dispersing Canthiumera robusta fruits. The common palm civet (Paradoxurus hermaphroditus) is known to swallow fruits that are large relative to its gape size, and because it can travel hundreds of meters over the duration of its gut-passage time, and passes out intact seeds, often on bare or open sites such as forest gaps (Ridley, 1930; Nakashima et al., 2010), it could potentially be an important longer-distance disperser of Canthiumera robusta seeds. Furthermore, we have observed that ripe and uneaten Canthiumera robusta fruits which have fallen to the ground will ferment readily in the warm tropical climate.
(suggesting their high sugar content), and we speculate that they could attract yet other dispersal agents such as ground-dwelling mammals to feed on the fermenting pulp, and in doing so move the pyrenes some distance away from the tree.

There is little documentation about Canthiumera glabra dispersal, but it is probably similar to that of C. robusta. Canthiumera siamensis (as ‘Canthium glabrum’) is reportedly eaten by civets in the Andaman Islands (Akshaya & Manchi, 2018), and by hornbills and gibbons in Thailand (Kitamura et al., 2002). The latter study reports the fruit colour of Canthiumera siamensis as yellow, which suggests a different dispersal ecology for this species which occurs in seasonal tropical forests. Canthiumera neilgherrensis is very rare, and little is known about its ecology.

In comparison to Canthiumera, Dibridsonia pyrenes are distinctly verrucose and less angular, with sloping lateral shoulders, and a much less prominent crest that is ridge-like rather than keeled, and reaches only halfway to the pyrene base. Despite the lack of a sharp keeled crest, the knobby, tough endocard may nevertheless defend well against gnawing by seed predators. The fruits of Dibridsonia do not exceed 2 cm in length and would fit the gape sizes of many frugivores. The fruits and the pyrenes are presumably easy to swallow whole.

The fruits of Dibridsonia conferta ripen from green to bright orange, which immediately suggests their attractiveness to both birds and arboreal mammals. Dibridsonia conferta (as ‘Canthium confertum’) has been reported in the diet of long-tailed macaques (Macaca fascicularis) in Singapore (Lucas & Corlett 1991). The dispersal ecologies of Dibridsonia culionensis and D. oblongifolia are not known.

GERMINATION

We have observed Canthiumera robusta seed germination in our own trials. Germination of Canthiumera robusta begins with the emergence and downward elongation of the radicle from the preformed germination slit along the apex of the pyrene dorsal crest (Fig. 10C). In our own trials, the time to first germination was 31 days, with a germination period of 60 days, and with 50–60% germination (based on two trials). Ng (1992) documented the germination period of Canthiumera robusta (as ‘Canthium glabrum’) as 80 days. The germination of Dibridsonia is not known.

ACKNOWLEDGEMENTS

We are grateful to the National Parks Board, Singapore, the Herbarium Bogoriense, Research Center for Biology-LIPI and the Bogor Botanic Garden for support that made this work possible. The Keepers and Curators of the BKF, BO, BRUN, KEP, K. L, SAN, SAR, SING and VNM herbaria are specially thanked for hosting our study visits. We especially thank Dr Joan Pereira (Sandakan) and Dr Kongkanda Chayamarit (Bangkok) for helpful corrections and remarks on the manuscript. Ang Wee Foong and Lim Wei Hao (National Parks Board, Singapore) kindly gave permission for using their images of Canthiumera robusta. Wei Wei Seah (SING Herbarium) and Ian Turner (Flora of Singapore Liaison Officer at the K Herbarium) helped with literature and specimen matters. Pak Harto of the Bogor Botanic Garden kindly helped collect material of Canthiumera glabra. RM acknowledges Prof. Mien A. Rifai, Prof. Tukirin Partomihardjo, Dr. Tatik Chikmawati and Dr. Nunik Sri Ariyanti.

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