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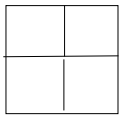

Cover images: *Canthiumera robusta* K.M.Wong & X.Y.Ng, *spec. nov*. Top left: leafy branch with inflorescences; note also keeled stipules. Top right: flower with tufts of pale moniliform hairs visible opposite corolla lobes. Below left: fruits. Below right: pyrenes. Photos: Ang Wee Foong (top left) and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

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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

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ABSTRACT
WONG, K. M., MAHYUNI, R., NG, X. Y. & NEO, L. 2018. 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. *Reinwardtia* 17(2): 101–124. — The recognition of a number of distinct genera by morphological and molecular phylogenetic attributes from the *Canthium s.l.* complex still leaves a core group of morphologically disparate taxa. The distinguishing features of the spiny *Canthium s.s.* and two groups of non-spinescent Southeast Asian tree taxa still commonly identified with *C. glabrum* Blume and *C. confertum* Korth. are assessed against those of *Cyclophyllum* Hook.f., *Bullockia* (Bridson) Razafim., Lantz & B.Bremer, *Kanapia* Arriola & Alejandro, *Keetia* E.Phillips, *Perakanthus* Robyns ex Ridl., *Psydrax* Gaertn., and *Pyrostria* Comm. ex Juss., similarly arborescent genera that have been so distinguished through recent studies. *Canthium glabrum* and *C. confertum* are, respectively, the bases of the genera *Canthiumera* K.M.Wong & Mahyuni and *Dibridsonia* K.M.Wong newly described here. The new species *Canthiumera robusta* K.M.Wong & X.Y.Ng is described; new nomenclatural combinations include *C. glabra* (Blume) K.M.Wong & Mahyuni, *C. neilgherrensis* (Wight) K.M.Wong, *C. neilgherrensis* var. *chartacea* (Gamble) K.M.Wong, *C. siamensis* (K.Schum.) K.M.Wong, *Dibridsonia conferta* (Korth.) K.M.Wong, *D. culionensis* (Elm.) K.M.Wong, and *D. oblongifolia* (Quisumb. & Merr.) K.M.Wong. *Canthium glabrum* var. *pedunculatum* Pitard, *Plectronia neilgherrensis* var. *chartacea* Gamble and *Canthium confertum* Korth. are lectotypified. *Plectronia viridis* Merr. and *P. leytensis* Merr. are reduced to synonymy under *Dibridsonia conferta*. Notes on the tree architecture, dispersal ecology and germination of *Canthiumera* and *Dibridsonia* are provided.

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

ABSTRAK
WONG, K.M., MAHYUNI, R., NG, X.Y. & NEO, L. 2018. Prekursor Flora Singapura, 8. Sistematika marga baru dari Asia Tenggara *Canthiumera* dan *Dibridsonia* (Rubiaceae: *Vanguerieae*), dengan catatan arsitektur pohon dan ekologi reproduktif. *Reinwardtia* 17(2): 101–124. — Pengenalan sejumlah marga secara morfologi dan filogenetik molekuler dari komplek *Canthium s.l.* masih menyisakan kelompok taksa dengan morfologi berbeda. Perbedaan ciri-ciri khas *Canthium s.s.* yang berduri dan juga dua kelompok pohon tanpa duri yang tersebar di Asia Tenggara umumnya masih diidentifikasi dengan nama *C. glabrum* Blume and *C. confertum* Korth. kini dibandingkan dengan marga *Cyclophyllum* Hook.f., *Bullockia* (Bridson) Razafim., Lantz & B.Bremer, *Kanapia* Arriola & Alejandro, *Keetia* E.Phillips, *Perakanthus* Robyns ex Ridl., *Psydrax* Gaertn., and *Pyrostria* Comm. ex Juss., yang merupakan marga yang sama-sama berperawakan pohon dibedakan melalui studi terbaru. *Canthium glabrum* dan *C. confertum* masing-masing merupakan dasar dari marga baru *Canthiumera* K.M.Wong & Mahyuni dan *Dibridsonia* K.M.Wong disajikan disini. Jenis baru *Canthiumera robusta* K.M.Wong & X.Y.Ng dipaparkan; kombinasi nomeklatur baru termasuk *C. glabra* (Blume) K.M.Wong & Mahyuni, *C. neilgherrensis* (Wight) K.M.Wong, *C. neilgherrensis* var. *chartacea* (Gamble) K.M.Wong, *C. siamensis* (K.Schum.) K.M.Wong, *Dibridsonia conferta* (Korth.) K.M.Wong, *D. culionensis* (Elm.) K.M.Wong, and *D. oblongifolia* (Quisumb. & Merr.) K.M.Wong. Lektotipe dipilih untuk *Canthium glabrum* var. *pedunculatum* Pitard, *Plectronia neilgherrensis* var. *chartacea* Gamble dan *Canthium confertum* Korth. *Plectronia viridis* Merr. dan *P. leytensis* Merr. dijadikan sinonim *Dibridsonia conferta.* Catatan tentang arsitektur pohon, ekologi penyebaran dan perkecambahan *Canthiumera* dan *Dibridsonia* disajikan.

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); *Pyrostria* 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 was 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 Seychellean '*Canthium*' species (Razafimandimbison *et al.,* 2007), and that *Pyrostria* included *Leroya* Cavaco, *Neoleroya* Cavaco, *Pseudopeponidium* Homolles 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 stylar 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 from a few allied *Vanguerieae* genera that have been more consistently recognized as genera, such as *Perakanthus* Robyns ex Ridl. and *Psydrax* (Wong, 1988; 1989; Puff & Wong, 2005), and there are apparently no alternative generic or infra-generic names applicable to them.

In Table 1, we present a comparison of these taxa with the allied *Bullockia*, *Cyclophyllum*, *Kanapia*, *Keetia*, and *Pyrostria*. It is clear that several characters such as habit, supernumerary buds and spininess are very useful to distinguish between *Canthium s.s.* (the group containing the type alliance of *Canthium* Lam.) and the rest of the complex. Some other characters, such as the reflexed anthers and long-exserted styles of *Psydrax*, or the salverform corollas of *Cyclophyllum*, seem also distinctive of individual genera. But the genera are, generally, distinguished well only by combinations of characteristics. Importantly, features such as corolla hair types, and pyrene form and their attendant characteristics, appear to group either *Canthium confertum* or *C. glabrum* with certain other taxa, or be useful distinctions.

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.*, *C. 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 29055β* (BO), Fig. 1) and *Kanapia* (*Elmer 17714* (BO)); however, in *Perakanthus* only stiff erect 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 mitriform 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.

	Canthium s.s.	*'Canthium' confertum*	*Cyclophyllum*	*Pyrostria*	*'Canthium' glabrum*	*Perakanthus*	*Kanapia*	*Bullockia*	*Keetia*	*Psydrax*
Plant habit	climbers, scramblers, small trees with scrambling branches	small trees	shrubs, treelets, small trees	climbers, shrubs, small trees	small trees	treelets	treelets, small trees	scramblers, shrubs, small trees	climbers, scramblers	small trees
Axillary supernumerary buds & spines	present	(absent)	(absent)	(absent)	(absent)	(absent)	(absent)	(absent)	(absent)	(absent)
Flowers / Inflorescences	solitary flowers / fascicles / short cymes, in leaf axils on normal shoots, or in leaf & bract axils on short shoots	short sub-umbellate cymes; in leaf axils on normal shoots only	fascicles / short dichasial cymes; in leaf axils on normal shoots only	short sub-umbellate cymes; in leaf axils on normal shoots only	short sub-umbellate to clearly branched cymes; in leaf axils on normal shoots only	fascicles / short cymes; in leaf axils on normal shoots only	clearly branched cymes; in leaf axils on normal shoots only	fascicles / short umbellate cymes; in leaf axils on normal shoots only	clearly branched cymes; in leaf axils on normal shoots only	fascicles of 1–few flowers, sub-umbellate cymes; in leaf axils on normal shoots only
Corolla form	subrotate-urceolate (constricted just below lobes); lobes spreading	subrotate-cylindric; lobes spreading to re-curved	salverform; lobes spreading	subrotate to cylindric; lobes spreading	subrotate-urceolate (constricted just below lobes); lobes spreading	urceolate to short-tubular bulbous base (constricted just below lobes); lobes spreading	subrotate-urceolate (constricted just below lobes); lobes spreading	tubular; lobes sub-erect	tubular- campanu-late (constricted below lobes); lobes reflexed	tubular to infundibular; lobes reflexed
Deflexed hair-ring at corolla throat	present at /just below throat	nil	nil	nil	present at /just below throat	present at /just below throat	present at /just below throat	present at /just below throat	present at /just below throat	present at /just below throat
Other hairs at corolla throat	nil or sparse short hairs	continuous band of exsert dense *moniliform* hairs	continuous band of exsert dense *moniliform* hairs	continuous band of exsert dense *moniliform* hairs	discrete tufts of exsert dense *moniliform* hairs between anthers	discrete tufts of exsert dense *unicellular* hairs between anthers	continuous band of exsert dense *moniliform* hairs	nil or sparse short hairs	nil or sparse short hairs	nil or sparse short hairs

Table 1. (continued).

	Canthium s.s.	*'Canthium' confertum*	*Cyclophyllum*	*Pyrostria*	*'Canthium' glabrum*	*Perakanthus*	*Kanapia*	*Bullockia*	*Keetia*	*Psydrax*
Anther orientation	erect to spreading or reflexed	erect to spreading	erect to spreading	erect	erect to spreading	erect to spreading	erect to spreading	erect	erect	strongly reflexed
Style length	almost = corolla tube	almost = corolla tube	only slightly > than corolla tube	only slightly > than corolla tube	almost = corolla tube	slightly > to 2 × corolla tube	almost = corolla tube	only slightly > than corolla tube	2–3 × corolla tube	2–3 × corolla tube
Base of stigma/ stylar head complex	mitriform	very slightly recessed	solid	solid	very slightly recessed	mitriform	mitriform	mitriform	mitriform	mitriform
Pyrene form	plano-obovoid, no shoulders	plano-obovoid with sloping shoulders not forming sharp keels	plano-obovoid, no shoulders	plano-obovoid to ellipsoid, no shoulders	plano-obovoid with sub-level to upcurved shoulders forming lateral keels	plano-obovoid with sub-level to rounded shoulders forming lateral keels	plano-obovoid with sloping shoulders not forming sharp keels	sub-ellipsoid to plano-obovoid, no shoulders	plano-obovoid, no shoulders + lid-like area on ventral or apical part	plano-ellipsoid to ovoid to sub -globose, no shoulders
Pyrene apical-dorsal crest	slight, at apex only	rounded, ridge-like; to ± half-way down dorsal side	slight, at apex only	apex only or nil	keel-like; apex to entire length of dorsal side	keel-like; apex to entire length of dorsal side	rounded, ridge-like; to ± half-way down dorsal side	slight, at apex only	apex only or nil	apex only or nil
Pyrene surface	verrucose	verrucose	verrucose	verrucose	± smooth	± smooth	verrucose	verrucose	verrucose to ± smooth	verrucose
Distribution	Africa, Madagascar, India, Malesia	Malay Peninsula, Borneo, Philippines	N Guinea, SW Pacific, Australia	trop Africa/ Madagascar, SE Asia	India, Indochina, W Malesia	Malay Peninsula	Philippines	E trop & S Africa	trop & S Africa	Africa to Malesia, Australia, Pacific

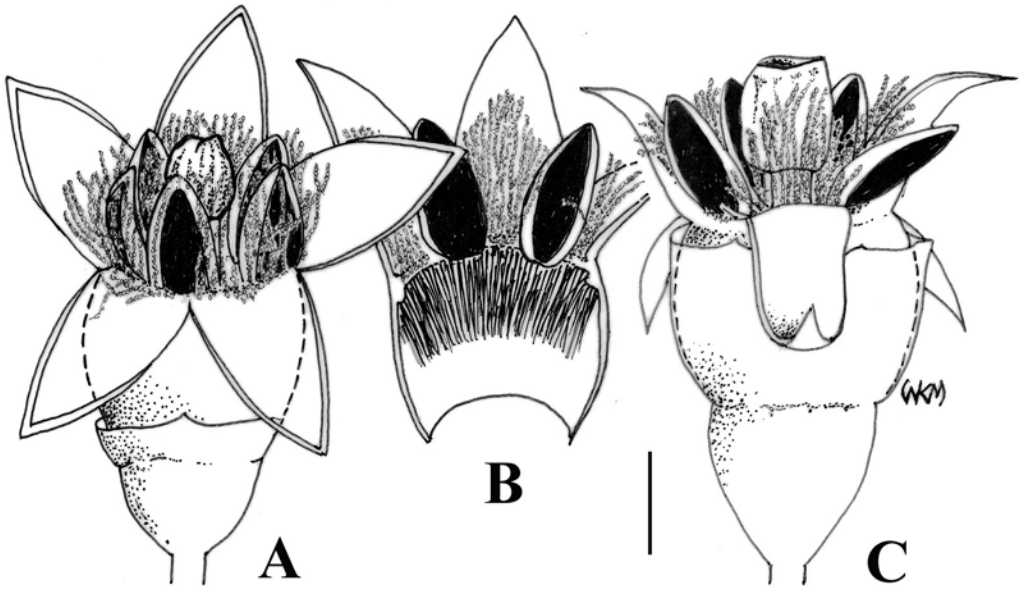

Fig. 1. Flowers of *Canthiumera* species (formerly placed as *'Canthium glabrum'*). A. *Canthiumera glabra* flower (note short calyx limb). B. *C. glabra*, longitudinal section through corolla showing ring of stiff deflexed hairs inside the tube and bundles of sub-erect moniliform hairs at the throat. C. *Canthiumera robusta* flower (note calyx limb as long as, and hiding, corolla tube). [A & B from *Himmah 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*

Fig. 2. Pyrenes of *Kanapia monstrosa* (upper row: dorsal (left) and ventral views) compared with those of species formerly placed as *'Canthium glabrum'*, presently distinguished as *Canthiumera robusta* (lower left) and *C. glabra* (lower centre and right). Scale bar is 5 mm long. *Kanapia* from *Reynoso et al. PPI 14841*, Philippines (BO); *C. robusta* from *Wong WKM 196*, Brunei (SING); *C. glabra* from *Ridha s.n.*, Bogor Botanical Garden (centre) and *Nedi & Idjan 464*, W Java (BO). Photo by K.M. Wong.

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

Canthiumera K.M.Wong & Mahyuni, ***genus novum.***

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-horizontal 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-urceolate to broadly cylindric, constricted just below corolla lobes, glabrous or short-pubescent outside, throat with dense tufts of erect-spreading (becoming flexuous-crisped) 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 Malesia (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 *umerus* 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)
Basionym: *Canthium glabrum* Blume, Cat. Gew. Buitenzorg (Blume) (1823) 45; Bijdr. Fl. Nederl. Ind. 16 (1827) 967; Candolle, Prodr. 4 (1830) 474; Backer & Bakhuizen, Fl. Java 2 (1965) 320. *Plectronia glabra* (Blume) Koorders & Valeton in Koorders, Exkursionsfl. Java 3 (1912) 260 (*in clavi*), Bijdr. Booms. Java 8 (1912) 137. *Psydrax glabra* (Blume) Deb & M.Gangop., Nelumbo 54 (2012) 267. — Type: *C.L. Blume s.n.*, Java, Salak, "ki-tja rolok" (holotype L [L0062935]).

Other specimens examined. Bali. Jembrana, Dewasana, 23 Apr 2014, *Himmah Rustiami HR 2001* (BO); Ubud, Monkey Forest, 5 Apr 1975, *W. Meijer & Noerta 8087* (BO). **Java.** No specific locality, no date, *C. L. Blume s.n.*, Java "var. puberula" (L [L0057512, L0057513, L0057514]), *C.L. Blume s.n.*, Java (L [L0058032, L0058033, L0062934], P [P03937196, P03937201]), *H. Forbes 373* (BO), 22 Mar 1899, *S.H. Koorders Kds 33131β* (BO). ***Central Java.*** Banjarnegara, 19 Nov 1891, *S.H. Koorders Kds 6484β* (BO); Banjumas, no date, *S.H. Koorders 20095β* (P [P03937200]), 13 Apr 1923, *P. Tunner 6246* (BO); Banyuwangi ('Besoeki, Rogodjampi'), 7 Sep 1897, *S.H. Koorders Kds 29055β* (BO), 1900, *S.H. Koorders Kds 29058β* (BO); Jepara, 20 Apr 1936, *Wagiman 30* (BO); north of Kudus, Gunung Muria, Tjollo, 25 Nov 1951, *A. Kostermans 6271* (BO); Nusakambangan, 16 Sep 1896, *S.H. Koorders Kds 24602β* (BO); Pekalongan, 12 Apr 1928, *Hoffmann 6240* (BO), 11 Apr 1897, *S.H. Koorders Kds 27526β* (BO); Prov. Semarang, no date, *S.H. Koorders 6485β* (P [P03937199]); Semarang, Telawa, 21 Aug 1923, *Vincent 4696* (BO), Semarang, Ambarawa, Telomojo, *S.H. Koorders Kds 27914β* (BO); Prov. Tegal, *S.H. Koorders 6522β* (P [P03937198]). ***East Java.*** Jember, 1930, *C.A. Backer 17746* (BO); Kediri, Soekaradja, 1896, *S.H. Koorders Kds 22646β* (BO), 30 May 1896, *S.H. Koorders Kds 22789β* (BO); Malang, Jul 1930, *Ag. Ulteê 1* (BO), 13 May 1896, *S.H. Koorders Kds 23514β* (BO); Pasuruan, Gunung Arjuno, 1900, *S.H. Koorders Kds 23957β*

(BO); 1913, *S.H. Koorders Kds 38216β* (BO); Ponorogo, Madiun, 1901, *S.H. Koorders Kds 38781β* (BO). ***West Java.*** Banten, Cikandi, 1 May 1933, *Sheildi s.n*. (BO); Bogor Botanic Garden, IV-E.146, 28 Jan 1927, *Anonymous s.n*. (BO); Bogor, Laladon, Ciomas, 19 Apr 1920, *R.C. Bakhuizen v.d. Brink 3437* (BO), 23 Jan 1921, *R.C. Bakhuizen v.d. Brink 5106* (BO); Cibodas, Ciampea, 13 Jan 1929, *C.G.G.J. van Steenis 2695* (BO); Ciburial, 22 Feb 1951, *Nedi & Idjan 464* (BO); Depok, no date, 1901, *Sugandiradja 237* (BO); Garut, 19 Aug 1893, *S.H. Koorders Kds 13972β* (BO); Jampang 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. Bakhuizen 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)
Basionym: *Canthium neilgherrense* Wight, Icon. Pl. Ind. Orient. 3(4) (1846) 4, tab. 1064*bis*. *Canthium neilgherrense* var. 1, Hooker f., Fl. Brit. India 3 (1880) 133. *Plectronia neilgherrensis* (Wight) Bedd., Fl. Sylv. S. India Forester's Man. Bot. (1872) cxxxiv/6. — Type: *Wight s.n.*, India, Sisparah on the Neilgherries, no date ("presented 1871") (holotype K [K000763659]).

Canthiumera neilgherrensis var. chartacea (Gamble) K.M.Wong, *comb. nov*.
Basionym: *Plectronia neilgherrensis* var. *chartacea* Gamble, Fl. Madras (1921) 441. *Canthium neilgherrense* var. *chartacea* (Gamble) Swamin., Biol. Mem. 2(1–2) (1977) 67. *Canthium neilgherrense* var. 2, Hooker f., Fl. Brit. India 3 (1880) 133. — Type: *Wight s.n.*, India, Pulney Mountains, Sep 1836 (lectotype K [K000031505], here designated).

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. neilgheirense* (*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.

3. **Canthiumera robusta** K.M.Wong & X.Y.Ng, *spec. nov.* — Type: *X.Y. Ng et al. SING 2018-409*, Singapore, Mandai Road Track 7, 11 Jun 2018 (holotype SING; isotypes K, BO, A, KEP, L, BRUN, SGN, SAN, BKF).

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)

Canthium glabrum auct. non Blume (1823): Korthals, Nederl. Kruidk. Arch. 2(2) (1851) 234, *p.p.*; Miquel, Fl. Nederl. Ind. 2 (1857) 254, *p.p.*; Hooker f., Fl. Brit. India 3 (1880) 133, *p.p.*; King & Gamble, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 73(3) (1904) 61, *p.p.*; Ridley, Fl. Malay Penins. 2 (1923) 124, *p.p.*; Craib, Fl. Siam. Enum. 2(1) (1932) 139, *p.p.*

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 axils 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. 1064*bis*. 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 Wong (1988; 1989), and for Borneo by Coode *et al.* (1996), the identity *Canthium glabrum* was used; Merrill (1921) adopted *Plectronia glabra.*

Canthiumera robusta has pyrenes that reach 40 × 24 mm in wild, presumably crossed, material, but batches of smaller pyrenes up to only 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]). **Borneo. *Brunei Darussalam*.** Belait district: Labi, Kampong Tenajor area, 27 Nov 1988, *Mohd Haslani Abdullah HA 47* (BRUN, SING [SING0189228]). Brunei Muara district: Jerudong, Bukit Shahbandar, 10 Mar 1988, *K.M. Wong WKM 196* (SING [SING0189307]). Tutong district: Layong-Gadong pipeline track, 1 Mar 1992, *J. Dransfield et al. JD 7234* (BRUN, KEP). ***Indonesia.*** West Kalimantan: Sungei Landak, no date, *Teysmann 19297* (BO). ***Malaysia.*** Sabah: Kinabatangan, Bukit Garam, 25 Feb 1987, *George et al. SAN 117635* (SAN); Ranau, Kampung Kituntul, 21 Jan 1986, *Amin et al. SAN 106843* (SAN), Solong, 20 Jun 1987, *Amin et al. SAN 118136* (SAN). Sarawak: Bukit Rawan Tebakang Area, 1 Apr 1983, *D. Awa & I. Paie S. 45248* (SAN); Kapit, Bena Sut, Sungei Marting, 9 Nov 1988, *Othman et al. S. 62157* (K, KEP [KEP137583], L, MO, SAN, SAR). **Malay Peninsula. *Malaysia*.** Johor: Mawai, 17 Jan 1938, *Ngadiman SFN 34763* (BO); Ulu Sebol FR, 7 Feb 1980, *P. Vethevelu FRI 25321* (KEP [KEP208482]); Sungei Sebong, Jason Bay, 15 Jun 1934, *E.J.H. Corner SFN 28532* (SING [SING0189319]). Kedah: Gunong Jerai, 3 Mar 1957, *K.M. Kochummen KEP 85076* (KEP [KEP208426]); Langkawi Island, Bt. Sawar FR, 11 Dec 1969, *T.C. Whitmore FRI 15001* (SING [SING0189503]). Kelantan: Stong, Tengah FR, Sungei Semuliang, 5°18.92'N, 101°56.77'E, 500 m, *M.Y. Chew & A. Angan FRI 53479* (SING [SING0110032]); Ulu Kelantan, Gunung Rabong, 2000 ft, 11 Mar 1972, *T.C. Whitmore FRI 20606* (KEP, SING [SING0189342]), 2500–3300 ft, 12 Mar 1972, *Mohd. Shah. MS 2512* (KEP [KEP181919], SING [SING0189441]). Melaka: 2 Aug 1885, *V.M. Alvins 2060* (SING [SING0189317]); Bt. Bruang, Jul 1890, *R. Derry 398* (SING [SING01893210]). Pahang: Bentong, Sabai Estate, 27 Jan 1958, *Mohd. Sah, 173* (BO, SING [SING0189311]); Cheraga, Sg. Telom, 1000 ft, 26 May 1971, *Zainudin b. Sohadi FRI 14734* (KEP [KEP181909]), 1200 ft, 26 May 1971, *T.C. Whitmore FRI 20030* (SING [SING0189334]); Jerantut, 8 Mar 1996, *L.E. Theo & Olivier Tarelli KL 4568* (KEP); Kuala Lompat, Lata Tujuh, 2500 ft, 24 Apr 1978, *Y.C. Chan FRI 25125* (KEP [KEP181911], SIN [SING0189344]); Kuantan, 2 Mar 1931, *M. Soh 15117* (SING [SING0189310]). Penang: Sep 1886, *C. Curtis 988* (SING [SING0189313]); Balik Pulau, Jun 1898, *H.N. Ridley 9421* (SING [SING0189443]); Penara Bukit, Apr 1901, *C. Curtis s.n.* (SING [SING0189246]). Perak: Bubu FR, 5 Apr 1933, *D.B. Arnot, 30665* (KEP [KEP181912]); Kledang Saiong, 4 Mar 1931, *Symington KEP 25637* (KEP [KEP181918]); Kledang Saiong FR, 3 Apr 1934, *D.B. Arnot KEP 33690* (KEP [KEP181915]); Sungei Guar valley, *T.C. Whitmore, FRI 0675* (SING [SING0189459]); Ulu Bubong, 1886, *King's Coll. 10199* (SING [SING0189320]); Ulu Sepetang, 25 Feb 1909, *M. Ashin 235* (KEP [KEP208471]). Selangor: 24 Sep 1916, *G.E.S. Cubitt 847* (SING [SING0189314]); Kuala Lumpur, Weld Hill Reserve, 24 Sep 1916, *F.G. Hamid 847* (KEP [KEP208453]); Kuala Kubu, 8 Apr 1980, *K.M. Kochummen KEP 29084* (SING [SING0189389]); Kepong, Bt. Lagong FR, 10 Jan 1967, *Gerus KEP 99458* (SING [SING0189502]); Templer Park, 11 Feb 1971, *T.C. Whitmore FRI 15844* (KEP [KEP208488], SING [SING0189337]). Terengganu: Bukit Kajang, 500 ft, 17 Nov 1935, *E.J.H. Corner SFN 30504* (SING

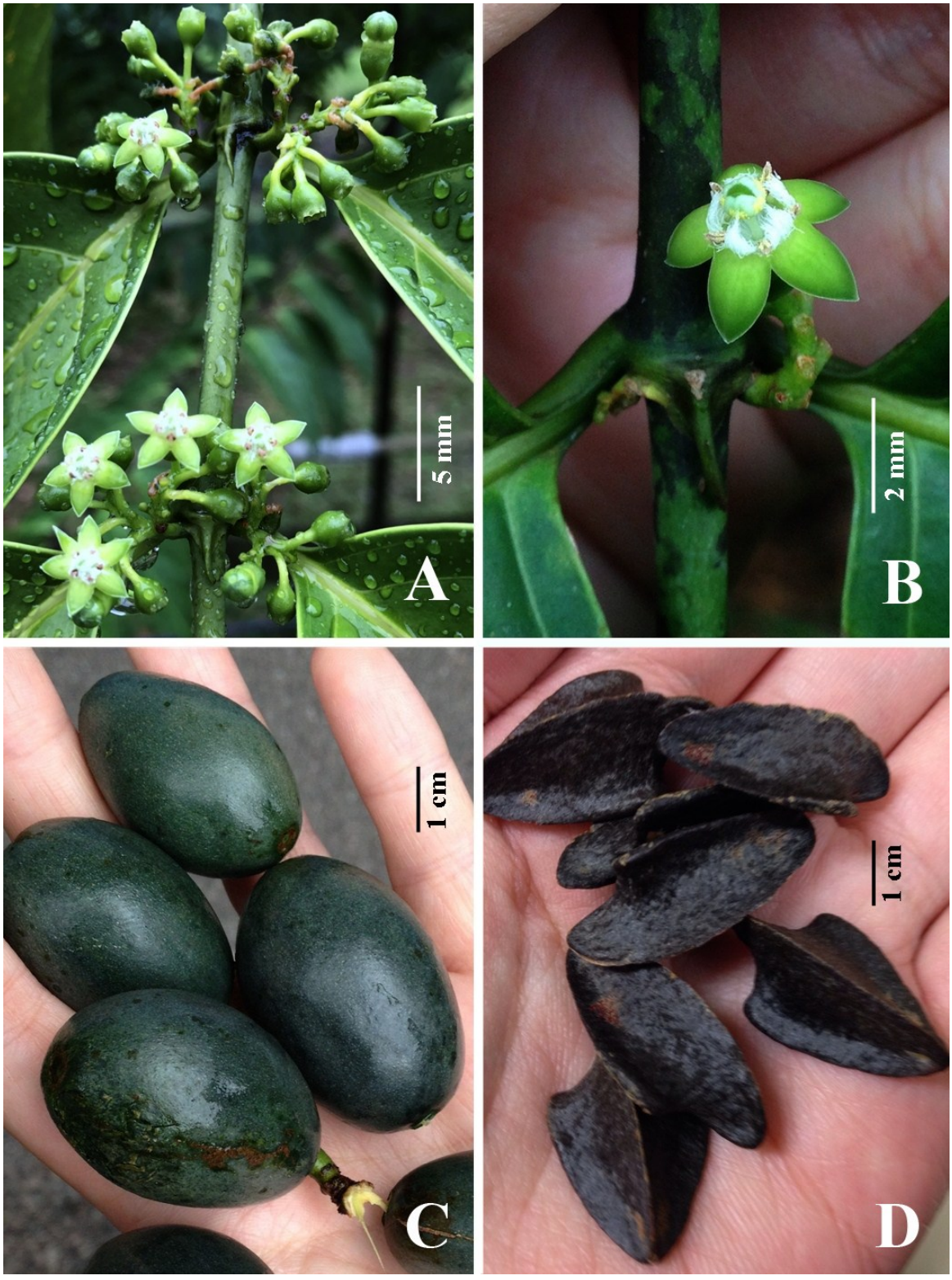

Fig. 4. *Canthiumera robusta* K.M.Wong & X.Y.Ng, *spec. nov*. A. Leafy branch with inflorescences; note also keeled stipules. B. Flower with tufts of pale moniliform hairs visible opposite corolla lobes. C. Fruits. D. Pyrenes. Photos by Ang Wee Foong (A) and X.Y. Ng (B–D).

[SING0189312]); Dungun, Bt. Bauk FR, 15 May 1976, *Y.C. Chan FRI 25068* (KEP, SING [SING0189393]); Kemaman, 500 ft, 10 Nov 1935, *E.J.H. Corner SFN 30362* (BO), Kemaman, Ulu Bendong, 1 Nov 1936, *E.J.H. Corner SFN 30119* (BKF [SN125134], SING [SING0189316]); Gunung Padang, 400 ft, 16 Sep 1969, *T.C. Whitmore FRI 12621* (SING [SING0189315]). ***Singapore.*** Botanic Gardens, Lower Garden, 16 Aug 1917, *Md. Nur s.n.* (BO), 17 Sep 1931, *Md. Nur s.n.* (BO); near Bukit Kallang, 16 Sep 1982, *J.F. Maxwell 82-255* (BKF [SN124973]); Bukit Mandai, 9 Apr 1892, *H.N. Ridley 4434* (SING [SING0019983]); Mandai Road Track 7, 11 Jun 2018, *X.Y. Ng et al. SING 2018-631* (SING, K); Bukit Timah NR, 15 Apr 1970, *R.D. Hill H.314* (SING); MacRitchie Reservoir, 10 Mar 1977, *Samsuri Ahmad SA 1456* (SING [SING0019988]); Nee Soon Swamp Forest, 12 Jun 2007, *D. Liew 2007-331* (SING [SING0093484]); Seletar, no date, 1891, *H.N. Ridley 6718* (SING [SING0019989]); Sungei Hantu opposite Pulau Serimbun, 28 Mar 1953, *J. Sinclair SFN 39530* (SING [SING0239956]); Tuas, no date, 1892, *J.S. Goodenough 3984* (SING [SING0019984]). ***Peninsular Thailand.*** Kasoom, Nov 1896, *C. Curtis 3249* (SING [SING0189545, SING0192941]). Khaw Pak Hill, 1 Dec 1918, *M. Haniff & M. Nur 3647* (BO, SING [SING0192939]). Yala, way to Be Tong, 150 m, 19 Dec 1972, *T. Santisuk & B. Nimanony 444* (BKF [SN105492]). **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 1890, *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, Tukirin et al. 1435* (BO, SING [SING0192610]); Batoe Paulajeh, 600 ft, *H.O. Forbes 2678* (BO); Sibual-bual, Sipirok, 27 May 1993, *J.J. Afriastini 2516 A* (BO).

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. Whitmore 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 1969*, Laos, Sam nuea, 29 Sep 1920 (lectotype P [P03937320], here designated; isolectotype P [P03937322]).

Canthium glabrum auct. non Blume (1823): Pitard, Flore générale de l'Indochine 3 (1924) 291, *p.p.*; Craib, Fl. Siam. Enum. 2(1) (1932) 139, *p.p.*

Plectronia glabra auct. non (Blume) Koorders & Valeton (1912): Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46(2) (1877) 153, Forest Fl. Burma 2 (1877) 35, *p.p.*

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 Phlong Saom, 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 36232* (P [P03937164]). **India.** ***Assam.*** Sibsagar, *Peal 169* (P [P03937305]). **Laos.** Prov. Bassac, entry to B. Phinh & B. Niong 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: Khon Shan district, Kamang, Trung, Phu Khiao Wildlife Sanctuary, 22 Jan 2004, *T. Wongprasert & S. Khaoiam 41-14* (BKF [SN144326, SN144327]). Nakhon Ratchasima province: Bahk Chong district, Khao Yai National Park, Wang Jumpee area, 14°27'N, 101°23'E, 725 m, 17 Aug 2002, *S. Somchin 4* (BKF [SN155704]), Khao Yai National Park, Haew Suwat waterfall, 14°45'N, 102°E, 800 m, 20 Oct 1969, *C.F. van Beusekom & C. Charoenpol* 1975 (BKF [SN050566], L). ***N Thailand.*** Chiang Mai province: Muang district, Doi Sutep-Pui National Park, Chang Kian Valley, 975 m, 24 Feb 1995, *J.F. Maxwell 95-159* (BKF [SN091345], CMU). Lampang province: Muang Bahn district, Jae Sown National Park, Bah Miang village, 1 Dec 1995, *J.F. Maxwell 95-1217* (BKF [SN108748], CMU). Nan province: Pua district, Doi Phu Ka National Park, 900 m, 24 Nov 1999, *T. Wongprasert s.n.* (BKF [SN112175, SN112176]). ***NE Thailand.*** Nong Khai province: Buong Karn district, Wat Chotinos Mammakorn, *ca.* 100 m, 25 Jan

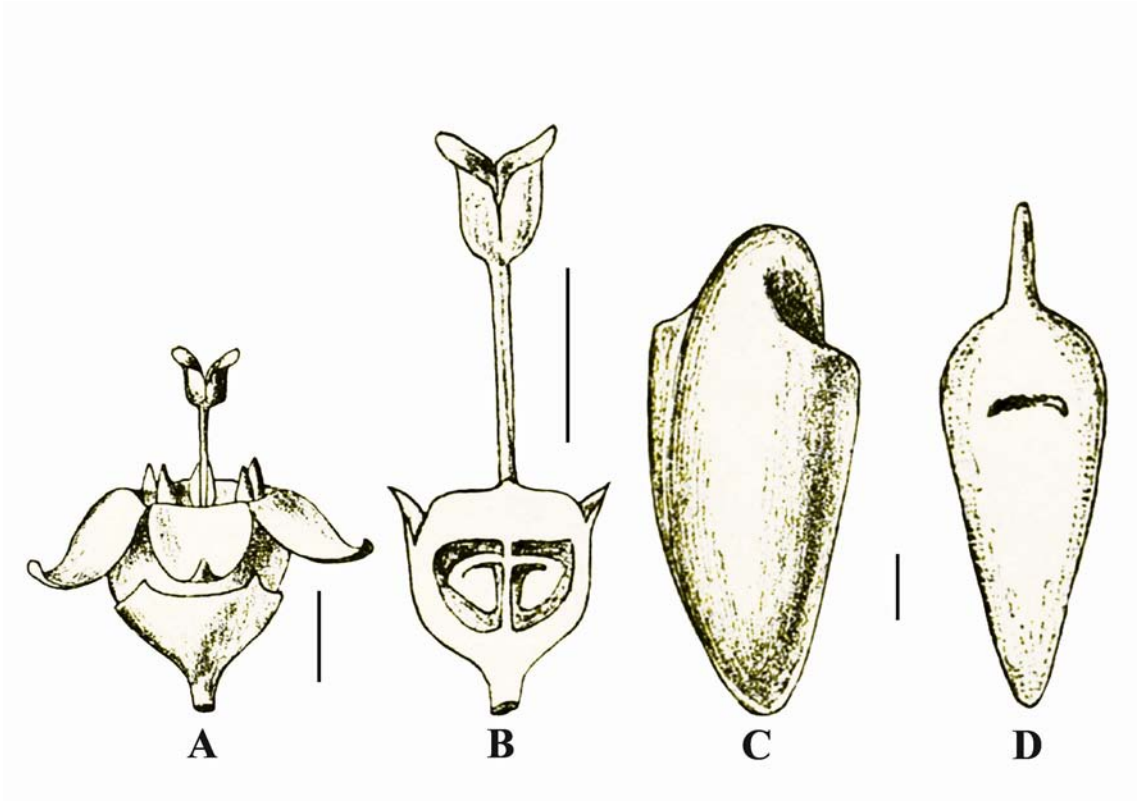

Fig. 5. *Canthiumera siamensis*. A. Flower. B. Longitudinal section through flower with corolla removed, showing ovule attachment in ovary locules and style with 2-lobed stigma. C. Pyrene, oblique-dorsal view. D. Pyrene, ventral view showing transverse scar of placental attachment. Scale bars are 2 mm. 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* (BKF [SN144267, SN144268]). ***Peninsular Thailand.*** Nakhon Si Thammarat province: Tung Song district, Yong waterfall, 17 Mar 1972, *T. Santisuk & B. Nimanony 285* (BKF [SN120409, SN120410]). Narathiwat province: Sungei Kolok district, Nikom Waenge, 5°50'N, 101°50'E, 200 m, 28 Feb 1974, *K. Larsen & S.S. Larsen 32754* (AAU, BKF [SN050596], K]); Waeng district, Bala-Hala, 28 Sep 1997, *C. Niyondham 5182* (BKF [SN120831, SN120832]), Bala-Hala, Klong Ai Kading, 50 m, 21 Feb 2003, *C. Niyondham & P. Puudjaa 7079* (BKF [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 86-743* (BKF [SN095484]). Ranong province: Kapur, Klong Naka, 13 Nov 1973, *T. Santisuk 574* (BKF [SN050595, SN 207019]). Surat Thani province: Ban Na San, 13 Oct 1955, *S. Phengnaren 504* (BKF [SN050592]). Trang province: Na Yong district, Kao Chong, 7° 33'N, 99°48'E, 125 m, Jan 2001, *S. Davies & A. Sinbumroong 2001-016* (A, BKF [SN157036]). ***SE Thailand.*** Chonburi province: Khaokhieo open zoo, 9 Dec 2000, *C. Phengklai 12900* (BKF [SN129167]). Trat province: Ko Kut district, 2 Dec 2006, *C. Phengklai et al. 15466* (BKF [SN163846, SN163847]). ***SW Thailand.*** Kanchanaburi province: Sangklaburi district, Toong Yai Naresuan Wildlife Reserve, 450 m, 11 Oct 1993, *J.F. Maxwell 93-1210* (BKF [SN186798, SN187666]). Uthaithani province: no specific locality, 450 m, 13 Feb 1991, *T. Santisuk et al. 249* (BKF [SN197931, SN197932]). **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 14496* (VNM [VNM00011997]), 200–300 m asl, 24 Aug 1931, *M. Poilane 19395* (VNM [VNM00012000, VNM00013579]), 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: Phuquoc, 30 Dec 1919, *M. Poilane 897* (VNM [VNM00011994]); Iles de Poulo Condor, Sep 1876, *J. Harmand 932* (P [P03937308], VNM [VNM00011995]), Condor, Oct 1876, *J. Harmand 1918* (P [P03937307]). ***Tonkin (N Vietnam).*** No locality, no date, *H. Bon s.n.* (BO (BO-1323144]), *H. Bon 6188* (P [P03937341, P03937342]), *H. Bon 6201* (P [P03937345, P03937346]). Backan province: Sep 1919, *P. Eberhardt 4618* (P [P03937309], VNM [VNM00011996]). Ha-coi: Taai Wong Mo Shan, near Chuk-phai, 3 May–22 Jun 1939, *W.T. Tsang 29044* (A, SING [SING0192948]). 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 ('brachyblasts') 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 pit-domatia in the axils of secondary veins. *Inflorescences* axillary on lateral branches, pedunculate, subumbellate, bracts small and inconspicuous. *Flowers* functionally unisexual; corolla subrotate 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)
Basionym: *Canthium confertum* Korth., Nederl. Kruidk. Arch. 2(2) (1851) 235. — Type: *P.W. Korthals s.n.*, Borneo, G. Pamatton (lectotype A [A00092452], here designated; possible isolectotypes K [K000763635, K000763636], L [L0000158, L0000159, L0000160, L0000161, L0000162, L0000163, L0000164]).

Plectronia viridis Merr., Philipp. J. Sci. 1, Suppl. (1906) 131. — Type: *E.D. Merrill 3945*, Luzon, Bataan Province, Mt Mariveleo (holotype PNH, probably destroyed; isotypes K [K000763616], US [US00138321]).
Plectronia leytensis Merr., Philipp. J. Sci., C 8 (1913) 49. *Canthium leytense* (Merr.) Merr., Philipp. J. Sci., C 35 (1928) 8. —Type: *M. Ramos Bur. Sci. 15383*, Leyte, Dagami, Aug 1912 (holotype PNH, probably destroyed; isotypes K [K000763621], P [P00836750]).

Note. In his protologue, Korthals records "*Crescit ad montem Pamatton, Poeloe-Lampei: Borneo.*" A series of Korthals' collections of this species is available, mostly at L, but the A sheet is the only one with the locality written in Korthals' hand; this is taken as lectotype here.

Other specimens examined. Borneo. *Brunei Darussalam.* Belait: Andulau F.R., 2 May 1957, *P.S. Ashton S 5944* (BO, S); Bukit Puan, 17 May 1957, *P.S. Ashton S 7887* (SING [SING0189271]). Temburong: Bangar-Batu Apas road, 30 Mar 1957, *G.H.S. Wood SAN 17094* (BO). ***Indonesia.*** East Kalimantan: Sungei Bloeoe, 1896–97, *Jaheri 1566* (BO). ***Malaysia.*** Sabah: Balambangan Island, 13 Sep 1927, *C.B. Kloss SFN 19288* (BO, SING); Danum Valley, 14 May 1989, *C.E. Ridsdale 2014* (SAN), 31 May 1989, *C.E. Ridsdale 2063* (SAN); Gunong Silam, 14 Apr 1992, *C. Puff & R. Buchner 920414-1/5* (SAN); Kota Kinabalu, Pulau Gaya, 15 Apr 1977, *B.C. Stone et al. SAN 86835* (KEP [KEP208624], L, SAN, SAR, SING); Mount Kinabalu, Mesilau River, 5000 ft asl, 9 Apr 1964, *W.L. Chew & E.J.H. Corner RSNB 4883* (SAN, SING); Lahad Datu, Sapong Ayer, 5 Mar 1963, *Muin Chai SAN 33356* (KEP [KEP208394], SAN); Ranau, Tinompok, 4500 ft asl, 17 Nov 1962, *P. Badak SAN 32380* (KEP [KEP208438]); Sandakan, Sepilok F.R., 19 Feb 1955, *G.H.S. Wood A 2875* (A, BRI, K, KEP, L, SING [SING0189367]), Sepilok Laut F.R., 4 Mar 1978, *Termiji & Paul SAN 85491* (SAN); Semporna, Selangan F.R., 22 Sep 1968, *B. Sindin SAN 63821* (SAN, SING [SING018923]); Tambunan, Gunong Trus Madi, 12 Aug 1988, *Fidilis SAN 25468* (SAN); Tawau, Tawau Hills F.R., 6 Jul 1974, *G. Aban & P. Minjulu SAN 79667* (SAN, SING [SING0189224]); Telupid, Pinangah, Ulu Sungei Melikop, 30 May 1985, *Dewol & Langkap SAN 109190* (SAN, SING [SING0189818]). Sarawak: Marudi, Tinjar, Ulu Dapoi, 7 Apr 1965, *Sibat anak Luang S 22982* (A, K, L, SAN, SING [SING0189243]); Miri, Bukit Lambir, 8 Jul 1962, *Ilias Paie S 16623* (K, L, SAN, SAR, SING [SING0189244]); Serian, Sabal F.R., 17 Jun 1960, *F.G. Nahar S 12694* (A, K, L, SAN, SAR, SING [SING0189297]); Similajau N.P., Sungei Likau, 7 May 1990, *Othman et al. S 59027* (K, KEP [KEP68941], L, MO, SAN, SAR). **Malay Peninsula. *Malaysia.*** Johor: Gunong Le-

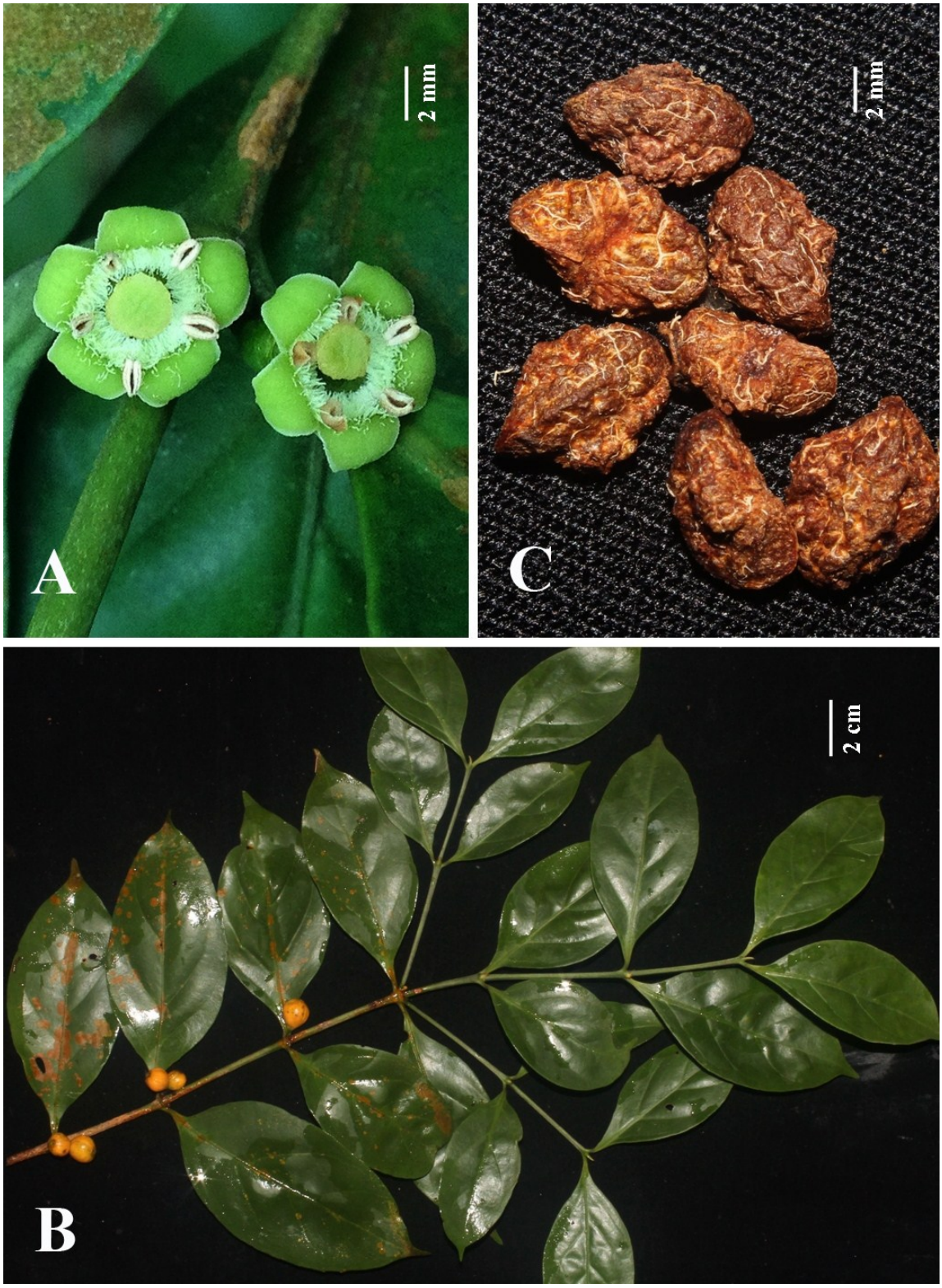

Fig. 7. *Dibridsonia conferta*.. A. Female flowers showing spreading anthers (empty) and broadly 2-lobed stigmas, with a continuous ring of pale moniliform hairs at the corolla throat. B. Fruiting branch. C. Pyrenes with characteristic verrucose surface. Photos by X.Y. Ng.

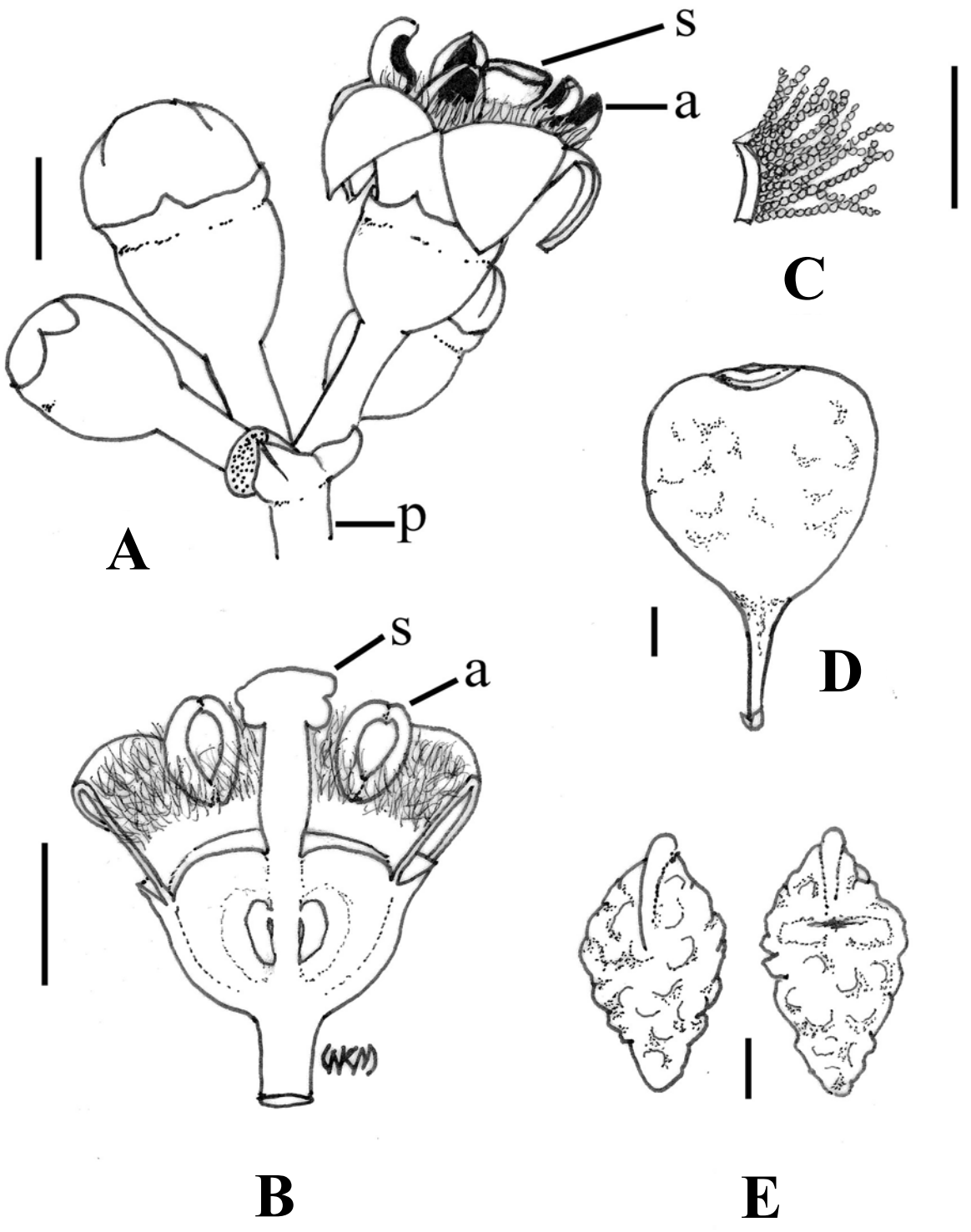

Fig. 8. *Dibridsonia conferta.* A. Inflorescence with one flower removed (stippled surface). B. Longitudinal section through female flower, showing band of moniliform hairs at the corolla throat. C. Corolla fragment bearing moniliform hairs. D. Fruit. E. Pyrene, dorsal (left) and ventral views. a, empty 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.

dang, 26 Nov 1971, *H.S. Loh FRI 19217* (KEP, SING [SING0189413]); Jason Bay, Sungei Tuanseh, 13 Mar 1966, *J. Sinclair SFN 10867* (E, FI, G, K, L, SING [SING0189418]); Mersing, Pulau Setindan, 15 Aug 1935, *Corner SFN 29770* (SING [SING0189414]); Sungai Kayu, 18 Mar 1937, *Henderson & Kiah SFN 32426* (BKF [SN125132], KEP, SING [SING0189419]); Ulu Sebol F.R., 6 Feb 1980, *Vethevelu FRI 25295* (KEP, SING [SING0189499]). Kelantan: Gunong Stong, 1000 ft asl, 13 Oct 1935, *Symington KEP 37830* (SING [SING0189410]); Ulu Sat F.R., 2 Feb 1970, *Kochummen FRI 2542* (KEP [KEP208355]). Melaka: Merlimau, 19 Apr 1886, *V.M. Alvins s.n.* (SING [SING0189411]). Pahang: Bentong, Raka Hill F.R., 20 Feb 1972, *Kochummen FRI 16654* (KEP [KEP208352]); Bukit Taun, 22 Oct 1897, *H.W. Lake & H.J. Kelsall s.n.* (SING [SING0189417]); Genting Highlands road, 13 Dec 1974, *K.M. Kochummen FRI 23049* (KEP, SING [SING0189478]); Tahan River, 1891, *Ridley 2245* (SING [SING0189255]). Penang: Penang Hill, 10 Jan 1918, *Haniff & Nur SFN 3021* (BO, KEP, SING), Moniot's Road, 1500 ft asl, Sep 1901, *Curtis 3672* (SING [SING0189412, SING0189421]). Selangor: Kuala Lumpur, Weld Hill Res., date unclear, *Ahmad KEP 4577* (SING [SING0189420]). ***Singapore.*** Changi, Feb 1894, *H.N. Ridley 5910* (SING [SING0019991]); Labrador Nature Reserve, open cliffs, 15 Feb 1982, *J.F. Maxwell 82-41* (BKF [SN124968, SN124969], SING [SING0019957]); MacRitchie Reservoir, 9 Dec 1976, *M. Shah & J.F. Maxwell 3962* (SING [SING0019968]), Lornie Trail, 9 Dec 2003, *S. Lee et al. MRR 9* (SING [SING0050008]); Pulau Tekong, 1890, *H.N. Ridley 489X* (last digit missing) (SING [SING0019958]); Pulau Ubin, Sep 2008, *I. Ali SING 2008-370* (SING [SING0146646]); Woodland, Kranji, 7 Jan 1890, *H.N. Ridley 1895* (SING [SING0019970, SING0019977]), Kranji, 1897, *H.N. Ridley 11263* (SING [SING0019954]).

2. **Dibridsonia culionensis** (Elm.) K.M.Wong, *comb. nov.*
Basionym: *Lasianthus culionensis* Elm., Leafl. Philipp. Bot. 1 (1906) 11. *Plectronia culionensis* (Elm.) Merr., Enum. Philipp. Fl. Pl. 3 (1923) 535. *Canthium culionense* (Elm.) Merr., Philipp. J. Sci. 35 (1928) 8. — Type: *E.D. Merrill 615*, Culion, Halsey, Dec 1902 (holotype PNH, probably destroyed; isotype SING [SING0058335]).

3. **Dibridsonia oblongifolia** (Quisumb. & Merr.) K.M.Wong, *comb. nov.*
Basionym: *Canthium oblongifolium* Quisumb. & Merr., Philipp. J. Sci. 37 (1928) 200. — Type: *G.E.Edaño Bur. Sci. 46109*, Panay, Capiz, Oct & Nov 1925 (holotype PNH, probably destroyed; isotypes A [A00092466], K [K000763620], NY [NY00130996], US [US00138301]).

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* (Bartl. ex DC.) Ridsd. 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 distichously (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

Fig. 9. A fruiting branch of *Canthiumera robusta.* Note the unequal branch pair at the second node from bottom. Photo by Lim Wei Hao.

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.

DISPERSAL 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

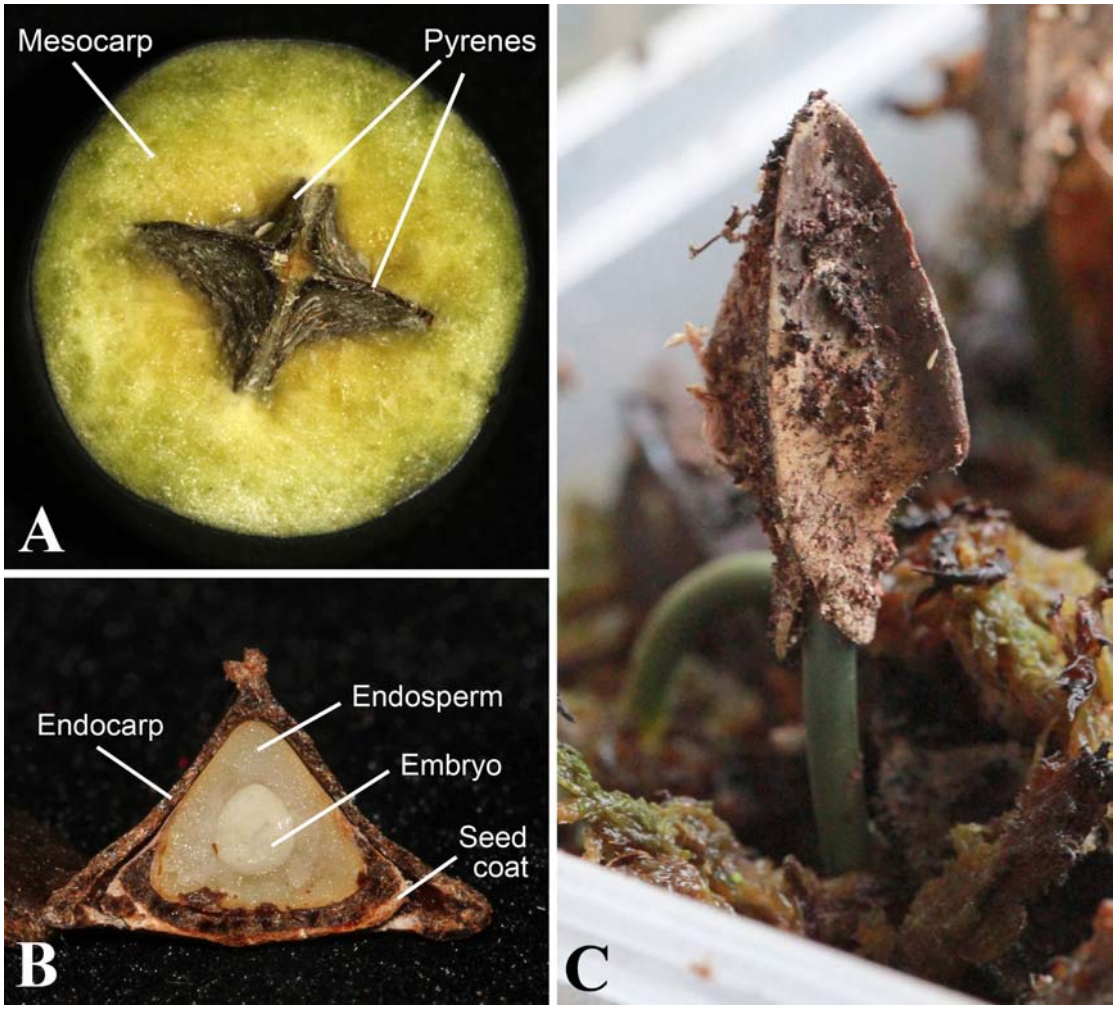

Fig. 10. *Canthiumera robusta.* A. Transverse section of fresh fruit showing the bases of two ventrally facing pyrenes in a substantial mesocarp matrix. B. Transverse section of pyrene. C. Newly germinated seedling with the radicle having penetrated the preformed germination slit at the pyrene apex and grown downwards, and the green hypocotyl elongating and raising the seed case. Photos by X. Y. Ng.

seed predation and damage.

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 knobbly, tough endocarp 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.

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