Systematics and Biogeography of the *Dissochaeta* alliance (Melastomataceae)

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CHAPTER 1

General Introduction

General Introduction

The family Melastomataceae Juss. (order Myrtales) is the seventh largest family of the angiosperms with approximately 5100 species and 170 genera (Wurdack 1986; Renner 1993; Veranso-Libalah et al. 2018). Melastomataceae display an immense diversity in habit, including herbs, shrubs, small trees, lianas and rarely epiphytes. The family is recognized by its acrodromal leaf venation, well-developed hypanthia, bisexual and diplostemonous flowers and poricidal anthers (Clausing & Renner 2001b). They are found in a wide range of habitats, from lowland to montane tropical forests, in savannas as well as in disturbed secondary vegetation (Renner 1993; Clausing & Renner 2001b). The family has a pantropical distribution with most species concentrated in the Neotropics (Renner 1993; Clausing & Renner 2001b). No genera are shared between the Palaeotropics and the Neotropics, though a few Neotropical species have naturalized as weeds in the Old World like *Bellucia pentamera* Naudin, *Miconia crenata* (Vahl) Michelang. and *Tibouchina urvilleana* Cogn. (Cellinese 1999).

One of the interesting groups in the classification of Melastomataceae is the *Dissochaeta* alliance. This group belongs to the palaeotropical tribe Dissochaeteae (Triana 1872; Cogniaux 1891; Maxwell 1984). The circumscription of this taxon is still problematic due to an inconsistent generic concept within the group. The purpose of this thesis is to tackle the problems at various levels and from different viewpoints. The species will be defined first, after which their phylogeny based on molecular data will be inferred. The resulting molecular phylogeny will be the basis for a new classification of the group. Finally, the biogeographic history of the group will be analysed. This introduction provides general information on the *Dissochaeta* alliance.

General morphology and ecology of *Dissochaeta* alliance

The *Dissochaeta* alliance comprises members of subtribe Dissochaetinae tribe Dissochaeteae, which are characterized by their woody habit with cymose thyrsoid inflorescences, tetramerous flowers, eight stamens in two whorls and berry fruits (Maxwell 1984; Clausing & Renner 2001a). Based on wood anatomy, the *Dissochaeta* alliance has alternate inter-vessel pits, vessel elements with a wide diameter and rays up to 7 cells wide (Van Vliet 1981). According to the last generic circumscription, the alliance consists of the genera *Creochiton* Blume, *Diplectria* (Blume) Rchb., *Dissochaeta* Blume, *Macrolenes* Naudin and *Pseudodissochaeta* M.P.Nayar (Maxwell 1984; Clausing & Renner 2001a). Some genera in the *Dissochaeta* alliance are sometimes similar because of their overlapping morphological features. Some species also show a high variation in morphological characters and a wide distribution. This makes species identification sometimes difficult. Most species in the *Dissochaeta* alliance are lianas or scrambling shrubs that may climb over other trees or bushes (Fig. 1-1C). However, erect or spreading shrubs (Fig. 1-1A) and epiphytic shrubs (Fig. 1-1B) can also be found. Many species grow in the fully exposed edges of tropical or evergreen rain forests, newly open logged forests, along the roads or in (seasonally dry) river beds (Maxwell 1984; Clausing & Renner 2001a). Few of them grow inside dense forests (Nayar 1969a; Maxwell 1984).

As most of Melastomataceae, the *Dissochaeta* alliance has a simple acrodromous leaf venation (Fig. 1-1D,E), with opposite phyllotaxy and pairs of leaves of equal size and shape (Maxwell 1984; Fig. 1-1F). Among the species, the leaves vary in size and shape, ranging from ovate to oblong-lanceolate. The apex of the leaf blades is usually acuminate and the

margin mostly entire (rarely serrulate) and the base of the leaf blade varies from cordate to cuneate (Fig. 1-1D,E), but a few species have an oblique (asymmetric) base (Nayar 1969a). All species are exstipulate and petiolate, but a few are subsessile. The nodes commonly have interpetiolar outgrowths between the leaves, which vary between lines or ridges to conspicuous lobes or crests (Fig. 1-1F,G).

The inflorescences of the *Dissochaeta* alliance are cymose, growing in terminal (Fig. 1-2A) or axillary (Fig. 1-2B) panicles with at the end of every ramification three terminal flowers (Maxwell 1984). *Creochiton* is the only genus with pseudoumbellate inflorescences in the alliance (Fig. 1-2C; Kartonegoro & Veldkamp 2013). The bracts in the inflorescences are homologous with leaf pairs and they support every node with ramifications. The pairs of bracteoles only subtend single flowers in the terminal part of the inflorescences. The bracts and bracteoles vary in shape and some of them are used for identification. The calyx tube or

Fig. 1-1. Morphological vegetative characters of the *Dissochaeta* alliance. **A–C.** Habit of shrubs (**A.** erect (*Pseudodissochaeta spirei*); **B.** epiphyte (*Creochiton bibracteatus*); **C.** Scrambling (*Dissochaeta vacillans*); **D–E.** Leaf venation (**D.** sub basal lateral nerves; **E.** basal lateral nerves); **F–G.** Leaf nodes (**F.** lined interpetiolar growth; **G.** lobed interpetiolar growth). Photographs by: **A.** Y. Liu; **B–C, F.** A. Kartonegoro; **D.** P.B. Pielser **E.** nifty.com; **G.** D.S. Penneys.

campanulate or tubular, though a few species have a cyathiform tube. The calyx lobes can be fully united and are then truncate or they can be free or half-truncate with apically triangular, small undulations or teeth-like lobes. All members of the alliance basically have 4-merous flowers with 4 calyx lobes and 4 corollas. The corolla of most of the species is white or pink, rarely purple (Maxwell 1984; Fig. 1-3).

The combination of eight stamens divided over two equal whorls (outer and inner) of four is the most common one (Maxwell 1984; Clausing & Renner 2001a; Fig. 1-3). These two whorls of stamens can be equal or unequal, isomorphic or dimorphic, all fertile or semi-fertile. The semi-fertile stamens refer to flowers that have one fertile whorl, while the other one is infertile (staminodes). The staminodes are reduced stamens that became infertile and either became small or they have fully disappeared (Fig. 1-3E–F,H). Typical for Melastomataceae is that the stamens usually possess a connective with dorsally and ventrally

Fig. 1-2. Inflorescences and infructescences of the *Dissochaeta* alliance. **A–C.** Inflorescences (**A.** terminal panicle, *Pseudodissochaeta spirei*; **B.** axillary panicles, *Dissochaeta annulata*; and **C.** axillary pseudoumbels, *Creochiton roseus*). **D–F.** Infructescences (**D.** cauliflory, *Pseudodissochaeta lanceata*; **E.** terminal panicle, *Dissochaeta celebica*; **F.** terminal pseudoumbels, *Creochiton* sp.). Photographs by: **A.** L. Yezi, **B.** D.S. Penneys, **C.** P.B. Pelser, **D.** Y. Liu, **E.** Supriyatna, **F.** D.L. Nickrent.

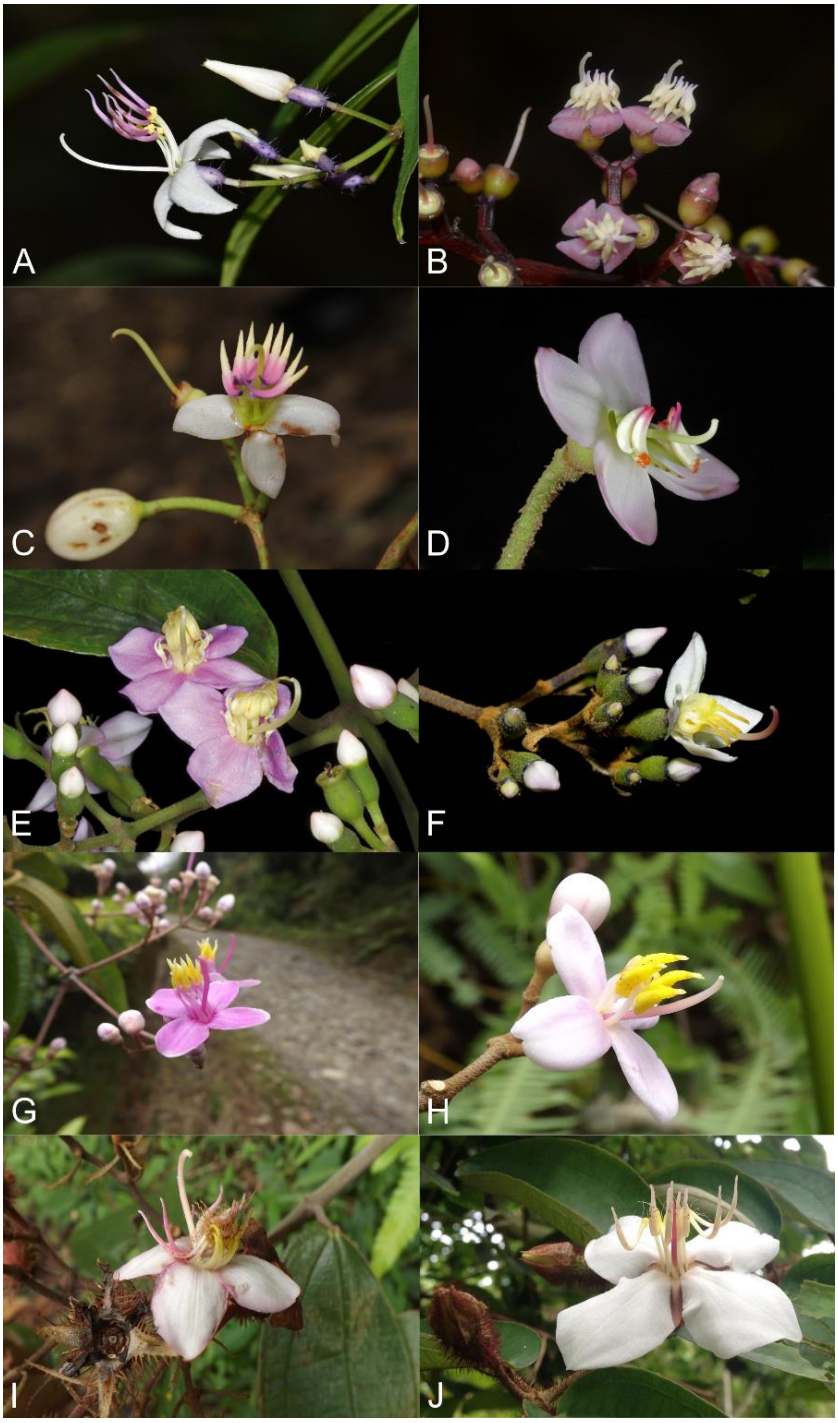

Fig. 1-3. Flowers of *Dissochaeta* alliance, **A.** *Pseudodissochaeta septentrionalis*; **B.** *Pseudodissochaeta spirei*; **C.** *Creochiton roseus*; **D.** *Creochiton* sp.; **E.** *Diplectria barbata*; **F.** *Diplectria divaricata*; **G.** *Dissochaeta bakhuizenii*; **H.** *Dissochaeta fallax*; **I.** *Macrolenes muscosa*; and **J.** *Macrolenes echinulata*. Photographs by: **A.** Y. Liu, **B.** L. Yezi, **C, G–I.** A. Kartonegoro, **D.** D.L. Nickrent, **E.** H. Le, **F.** L. Co, **J.** C. Ng.

appendages of varying shape and size. The ovary is superior, concrescent with the hypanthium by four or eight septae, which create the so-called extra-ovarian chambers between ovary and hypanthium. The stamens develop from these chambers. The placentation is usually axillary except for some *Creochiton* species that have a basal placentation (Kartonegoro & Veldkamp 2013). The style grows in opposite direction from the stamens, usually with a curved apex and a capitate stigma. The *Dissochaeta* alliance has berry fruits with many cuneate seeds inside (Fig. 1-2D–F; Maxwell 1984).

Most of species in the *Dissochaeta* alliance are found in disturbed and therefore relatively open vegetations such as tree fall gaps, forest margins, river margins, and roadsides (Fig. 1-1C; Maxwell 1982, 1984; Clausing & Renner 2001a). A few species of the alliance also can be found in close vegetation, shaded places within primary or secondary forests. Most of them grow abundantly in the lower tropical Dipterocarp and evergreen forests, while some can grow in montane forest to 2500 m altitude (Maxwell 1984). The species do not have a particular flowering and fruiting season, but are found flowering or fruiting throughout the year as long as they live in a suitable habitat with proper light (Maxwell 1984). Pollination of the flowers is still not observed, but is seemingly by small flying insects or ants (person. Obs.). The plants have attractive fleshy, small fruits, that are likely attractive to birds that can act as dispersal agents. No real uses are recorded for any morphological parts of the species in the *Dissochaeta* alliance.

Taxonomic History of *Dissochaeta* alliance

The history of the *Dissochaeta* alliance is like a swing going back and forth, between either many small genera (like this thesis) or a few large ones. Most of the genera were proposed by Blume (1831a, 1831b), like three scrambling shrub genera (*Aplectrum* Blume, *Dissochaeta*, *Marumia* Blume) and one genus of epiphytic shrubs (*Creochiton*). *Dissochaeta* comprised 15 species with eight of them split off from *Melastoma* L. (in its wide sense: Jack 1823; Blume 1826; De Candolle 1828). Blume (1831a, 1831b) proposed to divide the genus into two sections, section *Dissochaeta* and section *Diplectria* Blume, which differ in the shape of the calyx tube, the appendages at the base of the anthers and the indumentum of the ovary apex. Later, Reichenbach (1841) raised section *Diplectria* to genus level. Blume (1831a) described three species in the genus *Aplectrum*, which have an ovate-globose calyx tube and four stamens alternating with four staminodes. Blume did not indicate the similarity/difference between *Aplectrum* and *Dissochaeta* sect. *Diplectria*; the latter also has four staminodes alternating with four stamens. He also did not mention the position of the fertile and sterile stamens in relation to the position of the petals, a character later used to separate genera (Maxwell 1980a, 1984). The genus *Creochiton* was established with two species previously also included in *Melastoma* (Blume 1831a, 1831b).

Korthals (1842–1844) accepted Blume's *Aplectrum*, *Dissochaeta* and *Marumia* as distinct genera of scrambling shrubs. He proposed another new scrambling genus, *Dalenia* Korth., which has similarities with *Dissochaeta*, but deviates by a caducous calyptra that encloses the petals before anthesis. Naudin (1851) placed *Diplectria* back in *Dissochaeta* and made a new division of the genus into two groups without any nomenclatural status, *Inermes* Naudin and *Bisetosae* Naudin, which differ from each other in lacking or having bristle appendages at the base of the anthers, respectively. Furthermore, Naudin (1851) maintained the genera *Aplectrum*, *Creochiton*, *Dalenia* and *Marumia*. He also proposed other new scrambling genera, *Omphalopus* Naudin and *Macrolenes* (Naudin 1851). The genus *Macrolenes* was established to accommodate a palaeotropical scrambling shrub described as *Maieta annulata*

Vent. (Ventenat 1803). He regarded *Maieta* Aubl. As neotropical only, and referred the palaeotropical species to the new genus. Naudin (1851) was unaware of the relationship between *Macrolenes* and *Marumia* when he accepted both names, thinking that *Marumia* could be distinguished by pentamerous instead of tetramerous flowers.

The name *Aplectrum* is a later homonym of *Aplectrum* (Nutt.) Torr., already proposed by Torrey (1826) for a subgenus of *Corallorrhiza* (Orchidaceae) established by Nuttal (1818). Therefore, Gray (1854) introduced the new name *Anplectrum* A.Gray as a valid genus name for Blume's *Aplectrum*, which was followed by Triana (1872) in his World Melastomataceae account by uniting all species of *Diplectria* and *Aplectrum* within *Anplectrum*. Subsequently, Triana (1872) synonymized *Macrolenes* under the older genus *Marumia*.

Baillon (1877) divided *Dissochaeta* into nine sections: sect. *Anoplodissochaeta* Baill., sect. *Anplectrum* (A.Gray) Baill., sect. *Creochiton* (Blume) Baill., sect. *Dalenia* (Korth.) Baill., sect. *Dicellandra* (Hook.f.) Baill., sect. *Eudissochaeta* Blume ex Endl. (invalid name, = sect. *Dissochaeta*), sect. *Omphalopus* (Naudin) Baill., sect. *Oxyotandra* Baill. and sect. *Sakersia* (Hook.f.) Baill. His broad circumscription of the genus also included the African genera *Dicellandra* Hook.f. and *Sakersia* Hook.f. (= *Dichaetanthera* Endl.). Nevertheless, he still maintained *Marumia* as a distinct genus separate from *Dissochaeta* (Baillon 1877).

Cogniaux (1891), in his monograph of the family, accepted Triana's concept and rejected Baillon's generic classification of *Dissochaeta*, but maintained *Marumia*. He reinstated several genera from *Dissochaeta* such as *Creochiton*, *Dalenia* and *Omphalopus* (Cogniaux 1891). He also divided *Dissochaeta* into three sections, sect. *Diplostemones* Cogn., sect. *Isostemones* Cogn., and sect. *Dissochaetopsis* Cogn. Cogniaux's classification of *Dissochaeta* and allied genera was adopted by Krasser (1893) except that he synonymized *Anplectrum* with the older genus *Diplectria*. The number of infrageneric taxa in *Dissochaeta* increased when Merrill (1917) proposed the new species *Dissochaeta glabra* Merr. and placed it in a new section *Disparistemones* Merr.

Enchosanthera Guillaumin was established for *E. anomala* (King & Stapf ex King) Guillaumin based on *Anplectrum anomalum* King & Stapf ex King (Guillaumin 1913). The new genus was proposed because it differed from *Anplectrum* by the shape and structures of the eight heteromorphous anthers. Later on, *Eisocreochiton* Quisumb. & Merr. was described, similar to *Creochiton* in its vegetative and inflorescence characters (Quisumbing & Merrill 1928). Nayar (1970) revised the genus *Eisocreochiton* and assigned it to tribe *Dissochaeteae*, close to *Creochiton*.

Bakhuizen van den Brink (1943), in his comprehensive work on the Melastomataceae of the Malay Archipelago (Malesian Region), established two new scrambling genera, *Backeria* Bakh.f. and *Neodissochaeta* Bakh.f., based on the small size of the calyx tube and the presence of narrow extra-ovarian chambers, respectively. He also still maintained the genera *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta* and *Omphalopus* as distinct genera. He discussed the possible illegitimacy of the name *Anplectrum*, which he considered to be a superfluous orthographic variant of *Aplectrum* (both bad Greek) and he preferred to regard *Diplectria* and *Backeria* as accepted names instead (Bakhuizen van den Brink 1943, 1964; Veldkamp et al. 1979). On the other hand, Bakhuizen van den Brink (1943) recognized that *Marumia* Blume is an illegitimate name because it is a later homonym of *Marumia* Reinw. in the Actinidiaceae (Reinwardt 1828). Later, he then reestablished the genus *Macrolenes* as a valid generic name to replace *Marumia* (Bakhuizen van den Brink 1943; Veldkamp 1979). Erronously, he excluded *Creochiton* from the Dissochaeteae and classified it in the

Astronieae based on the basal placentation and he did not mention the status of *Enchosanthera*. Furtado (1963) was apparently not aware of *Enchosanthera* Guillaumin and described new genus *Anplectrella* Furtado for the same species, *Anplectrum anomalum*.

The genus *Backeria* was maintained by Raizada (1968), but he synonymized all species of *Diplectria* with it. However, since *Diplectria* is an older name than *Backeria*, *Diplectria* is the correct generic name (Veldkamp et al. 1979) in this circumscription.

Pseudodissochaeta was established for a homogenous group that resembled *Dissochaeta* but differing in being erect shrubs or small trees, instead of scrambling shrubs or woody climbers (Nayar 1969a). The genus can be distinguished from resembling genera not only by its habit of erect shrub, but also by its leaves with a serrulate margin, flowers with 8 equal and isomorphic stamens, a connective with dorsally spurred and ventrally bilobed or biauriculate appendages (Nayar 1969a; Maxwell 1984).

Maxwell (1980a, 1984) recognized five genera within the *Dissochaeta* alliance: *Creochiton*, *Diplectria*, *Dissochaeta*, *Macrolenes* and *Pseudodissochaeta*. In agreement with Bakhuizen van den Brink (1943) and Veldkamp et al. (1979), he also maintained *Diplectria* as a distinct genus allied to *Dissochaeta* with *Backeria* synonymized under it. He also synonymized *Dalenia*, *Neodissochaeta* and *Omphalopus* with *Dissochaeta* and subsumed *Marumia* under *Macrolenes*. He divided *Dissochaeta* into three sections: sect. *Dissochaeta*, sect. *Anoplodissochaeta* and sect. *Omphalopus*, mostly based on floral characters, especially the stamens. The other four genera remained without an infrageneric classification (Maxwell 1984). Veldkamp (1979) and Maxwell (1980a, 1984) also noted that the characters supposedly differentiating among *Anplectrella*, *Creochiton*, *Eisocreochiton* and *Enchosanthera* were insufficient to separate them at the generic level and that they had to be united into a single genus under the oldest name, *Creochiton*.

Lately, *Pseudodissochaeta* has been treated under *Medinilla* Gaudich. ex DC. (subtribe Medinillinae tribe Dissochaeteae) based on its morphological similarity (Chen 1983, 1984; Chen & Renner 2007) as the habit and floral characters showed a closer resemblance with *Medinilla* than with *Dissochaeta* (Chen & Renner 2007). However, the wood anatomy of the genus already questioned the validity of this classification as it confirms similarity with *Dissochaeta* rather than with *Medinilla* (Van Vliet 1981).

It will now be obvious that morphology alone cannot solve the generic delimitations. Likely, phylogenetic analyses may do so.

Molecular phylogeny of the *Dissochaeta* alliance

Several molecular phylogeny studies of particular taxa or groups were performed within the Melastomataceae (Veranso-Libalah et al. 2017; Bacci et al. 2019; Zhou et al. 2019b). However, there are only few studies related to the *Dissochaeta* alliance. Generally, only a few species from the alliance were included in the phylogenetic studies (Fig. 4), also when tribe Dissochaeteae was specifically analysed as done by Clausing & Renner (2001a, 2001b), Zeng et al. (2016), Zhou et al. (2019b) and Penneys et al. (2020). The molecular phylogenetic studies of Dissochaeteae by Clausing & Renner (2001a) showed Dissochaeteae to be non-monophyletic, as it was divided over two distinct lineages, the *Dissochaeta* and *Medinilla* alliances. However, only a few species of the *Dissochaeta* alliance were included and two allied genera (*Creochiton* and *Pseudodissochaeta*) were unsampled. Within the *Dissochaeta* alliance, *Dissochaeta* was resolved as sister to *Diplectria* + *Macrolenes* (Clausing & Renner 2001a). Later molecular phylogenetic studies strongly support *Pseudodissochaeta*, the non-

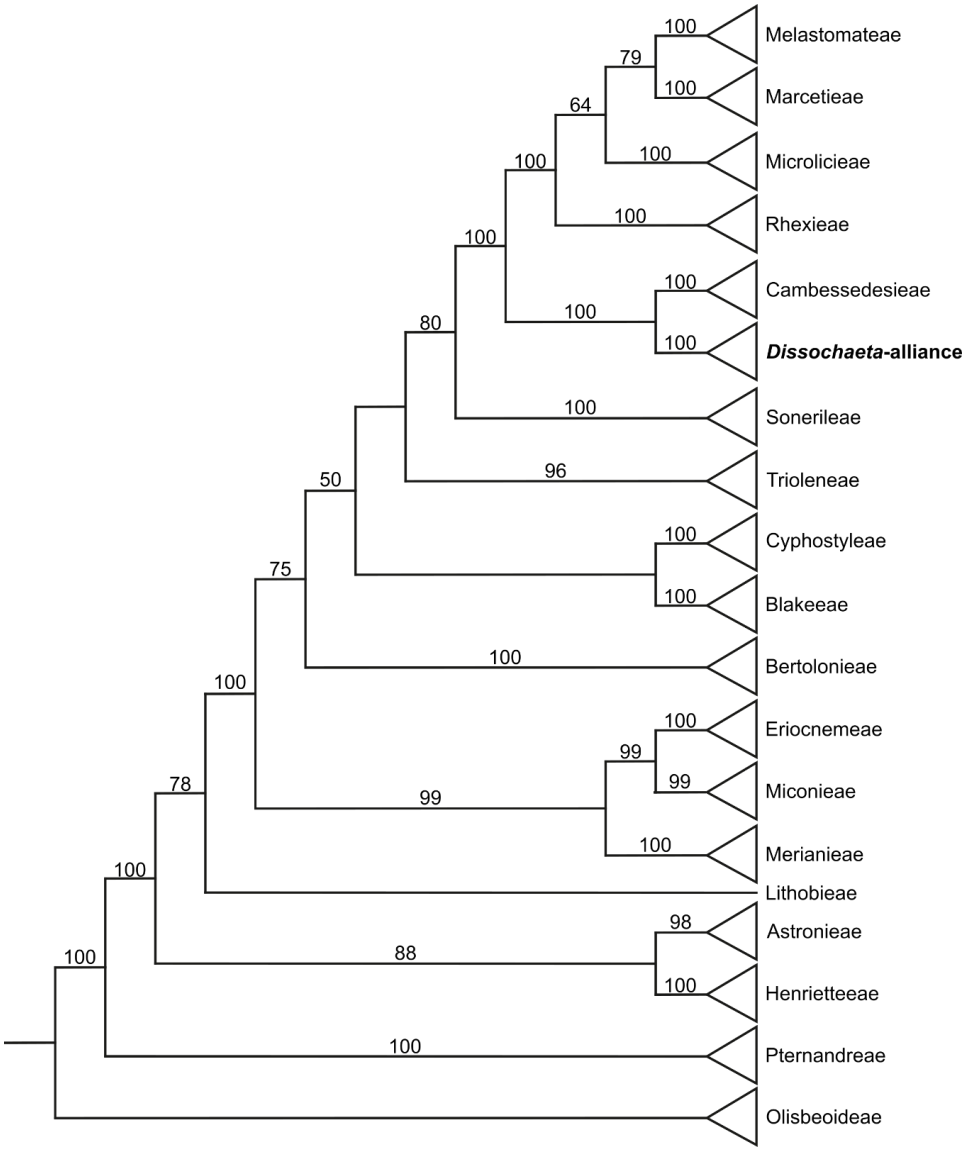

Fig. 1-4. Maximum-likelihood (ML) phylogenetic tree of Melastomataceae modified from Penneys et al. (2020). The *Dissochaeta* alliance is shown in bold. Numbers along branches indicated ML bootstrap support percentages above 50%.

scrambling genus, as part of the *Dissochaeta* alliance but unrelated to *Medinilla* (Zeng et al. 2016; Zhou et al. 2019a, 2019b). The most recent molecular phylogenetic study of the family, which included *Dissochaeta* alliance, was by Penneys et al. (2020). The *Dissochaeta* alliance was recovered as monophyletic and sister to the Neotropical tribe Cambessedesieae, but the analysis only included *Diplectria*, *Dissochaeta* and *Macrolenes* and did not include other genera such as *Creochiton* and *Pseudodissochaeta* (Fig. 1-4; Penneys et al. 2020). These preliminary studies suggest that the *Dissochaeta* alliance is monophyletic, nevertheless, *Creochiton* is still not included and the number of sampled species per genus needs to

increase, especially for *Dissochaeta*, before one can ascertain the monophyly of all the genera and sections. Up to now, all phylogenies did not unequivocally solve the generic circumscriptions within the *Dissochaeta* alliance because of insufficient sampling. Thus, the problem of the generic delimitation within the alliance still needs an improved phylogenetic analysis to reflect the real phylogeny of the group.

Problems

In conclusion, the generic circumscription within the *Dissochaeta* alliance is still unstable. The generic boundaries among some genera in the alliance are problematic due to morphologically intermediate species and doubtful homology assessments (Clausing & Renner 2001a). Also, all scrambling shrubs or woody climbers are considered as the single genus *Dissochaeta*. This circumscription was supported by preliminary molecular phylogenies of the group, which suggested that the scrambling habit evolved only once (Clausing & Renner 2001a; Renner et al. 2001b; Zhou et al. 2019b). However, the variability in the floral characters was not and could not be used (too few samples) to separate the genus into several genera that provide a better reflection of the phylogeny of the group (Maxwell 1984; Renner 1993). The differentiation in the development and fertility of the stamens is clear and can be used to distinguish several genera within the scrambling shrubs group, e.g. *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*. In addition, the position and relationship of *Creochiton* is still questionable since no species samples were represented in any molecular phylogenetic study. *Creochiton* was sometimes recognized as part of *Dissochaeta* alliance based on the similarity of its floral and fruit morphological appearance (Veldkamp 1979; Maxwell 1984; Kartonegoro & Veldkamp 2013), however, it was also considered to be part of the Astronieae due to its basal placentation (Mansfeld 1925; Bakhuizen van den Brink 1943). *Pseudodissochaeta* was proposed to be closely related to *Dissochaeta* and, therefore, to be part of the *Dissochaeta* alliance (Nayar 1969a; Maxwell 1984). Nevertheless, the genus is known to have floral morphological similarities with *Medinilla* and was sometimes classified as part of it (Chen 1983, 1984; Chen & Renner 2007). A recent molecular phylogeny (Zhou et al. 2019b) showed that *Pseudodissochaeta* is grouped within the *Dissochaeta* alliance, not with *Medinilla*, but the relationship with *Dissochaeta* was still not clearly solved. Only an improved sampling of the *Dissochaeta* alliance can provide a phylogeny that will satisfactorily circumscribe the various lineages and the taxa they represent.

Research questions, aim and outline

Based on the taxonomic problems encountered, the following research questions are addressed in this thesis, whereby the *Dissochaeta* alliance is considered to comprise the genera *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes* and *Pseudodissochaeta*:

- Which species should be assigned to the *Dissochaeta* alliance? How do they differ morphologically and ecologically? What are their diagnostic morphological characters?

- Is the *Dissochaeta* alliance monophyletic? Which taxa are closely related with the alliance? Which evolutionary traits can be used to recognize the clade(s)/groups?

- If the *Dissochaeta* alliance is monophyletic, then how can the phylogenetic results be translated into a new classification of monophyletic and recognizable genera? Which morphological apomorphies (newly evolved characters) support the classification?

- Does the molecular phylogeny corroborate any of the formerly proposed infrageneric taxa? How do they relate to each other?

- Where and when did the major diversification events occur in the *Dissochaeta* alliance? Which scenario results from the historical biogeography of the genera and species? How can we explain the migration routes?

The aim of this PhD research is to focus on the systematics, the phylogenetic relationships, an improved classification and the historical biogeography of *Dissochaeta* alliance.

In **Chapter 2–5**, taxonomic revisions of all genera in the *Dissochaeta* alliance are carried out. Vegetative and reproductive morphological characters are examined and used in the descriptions. Geographical, ecological and other secondary information are obtained from herbarium specimens. All literature related to the genus is reviewed. All currently known species are enumerated. Keys to the species are provided, together with descriptions and notes for all taxa. Chapter 2 contains a revision of the epiphytic shrubs of the genus *Creochiton* (published before PhD study). In this revision, *Anplectrella*, *Eisocreochiton* and *Enchosanthera* are recognized as synonyms. Twelve species are recognized within the genus, whereby one is raised from variety level. Chapter 3 contains a revision of scrambling shrubs of *Dissochaeta*. In this chapter, genera *Dalenia* and *Diplectria* are treated under synonym of *Dissochaeta*. Some other genera, such as *Aplectrum*, *Anplectrum*, *Backeria*, *Neodissochaeta* and *Omphalopus*, are also considered as a part of *Dissochaeta* and are therefore synonymized. Fifty-four species and two varieties are recognized in the genus with one species and one variety newly described and illustrated. Chapter 4 contains the revision of another scrambling shrubs of *Macrolenes* with *Marumia* treated as a synonym. Seventeen species are now known in this genus of which three species are newly described and illustrated. Chapter 5 contains the revision of the erect and spreading shrubs of *Pseudodissochaeta*, whereby its distinctiveness from *Dissochaeta* and *Medinilla* is reviewed. Five species are recognized.

In **Chapter 6**, the phylogeny of the *Dissochaeta* alliance and its relationships with other taxa in the Dissochaeteae s.l. is reconstructed. The monophyly of the *Dissochaeta* alliance is tested using a molecular phylogenetic approach. Two nuclear markers (ETS, ITS) and four chloroplast markers (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) were sequenced for all genera within the *Dissochaeta* alliance. Sequenced data of other taxa in the tribe Dissochaeteae s.l. obtained from GenBank were also included in the analyses in order to understand the phylogenetic relationship among all taxa. Molecular phylogenetic trees were constructed based on Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI). The monophyly of the *Dissochaeta* alliance is established, together with the polyphyly of the Dissochaeteae s.l. The monophyly of the *Dissochaeta* alliance is here used to redefine tribe Dissochaeteae, which will now only include the *Dissochaeta* alliance. A new generic circumscription and classification within the *Dissochaeta* alliance is proposed. *Pseudodissochaeta*, *Creochiton*, *Dissochaeta* and *Macrolenes* are maintained, while *Dalenia* and *Diplectria* are reinstated. Characters supporting each clade are briefly discussed and presented in a taxonomic treatment and nomenclatural changes are made where necessary.

In **Chapter 7**, the historical biogeography of the *Dissochaeta* alliance is analyzed. Molecular dating is performed in a Bayesian framework with the program BEAST v.2.4.8 (Bouckaert et al. 2014), and ancestral area reconstructions are hypothesized with the both Bayesian-based Statistical Dispersal-Vicariance Analysis (S-DIVA) and the Statistical Dispersal-Extinction-Cladogenesis (S-DEC) model, implemented in the RASP (Reconstruct Ancestral

State in Phylogenies) program (Yu et al. 2015). The dispersal/vicariance events are discussed in the light of the tectonic history of Southeast Asia, especially Malesian region, and a likely historical biogeography is reconstructed.

CHAPTER 2

Revision of *Creochiton* (Melastomataceae)

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Revision of *Creochiton* (Melastomataceae)

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Abstract

A taxonomic revision of the Malesian genus *Creochiton* (Melastomataceae) is presented. Twelve species are recognized, although one is based on the original description only. *Creochiton turbinatus* (comb. nov.) is raised to specific rank from a variety of *C. ledermannii*. A key to the species, descriptions, ecological habitats, distributions (with maps), synonymy, taxonomic notes, vernacular names and an index to collections are provided.

Keywords

Creochiton, Malesia, Melastomataceae, new combination, revision.

Introduction

The genus *Creochiton* (Melastomataceae) was established by Blume (1831a, 1831b) for two species from Java previously included in *Melastoma* L.: *C. bibracteatus* (Blume) Blume (Blume 1826; *Melastoma bibracteatum* Blume) and *C. pudibundus* (Blume) Blume (Blume 1823; *Melastoma pudibundum* Blume). The latter is here designated as the lectotype. The name is derived from the Greek, kreas chitoon (κρεας χιτων), fleshy garment, which refers to the usually large and thickened bracteoles that cover the flowerbud before anthesis. Note that the gender of chiton is male and all epithets have here been corrected where necessary. The genus is easily recognized as woody climbers (scrambling shrubs), creepers, or epiphytic shrubs with distinct fleshy bracteoles enveloping the flower buds. It has been regarded by most authors as allied to *Dissochaeta* Blume. The circumscription employed here is after Veldkamp (1979) followed by Maxwell (1980a, 1980b, 1984).

There is a remark by Kadereit (née Clausing; 2006) that *Creochiton* would partially belong to *Dissochaeta* but (in litt.) she then thought that *Creochiton anomalus* (King & Stapf ex King) Veldkamp, *C. furfuraceus* (M.P.Nayar) Veldkamp and *C. monticola* (Ridl.) Veldkamp would belong there because of the axillary placentation, anthers with ventral appendages and extraovarial chambers.

Naudin (1852) pointed out similarities to the American subtribe Pyxidanthinae ('Pyxidantheae') Naudin, but noted that perhaps it was better placed with the subtribe Dissochaetinae ('Dissochaeteae') Naudin (Naudin 1851). Triana (1866, 1872) elevated this to the tribe Dissochaeteae (Naudin) Triana in which he was followed by later authors, e.g. Cogniaux (1891), Krasser (1893), Maxwell (1984). Baillon (1877) even regarded *Creochiton* in a heterogeneous assembly of genera ranked as sections of *Dissochaeta* but did not make the necessary combinations for the two *Creochiton* species. Because of the close relationships between the two genera both are included in the Dissochaeteae, e.g. because of their habit and the shape of their inflorescences (Triana 1872; Cogniaux 1891; Krasser 1893; Maxwell 1984).

Mansfeld (1925) put *Creochiton* into the capsular-fruited tribe Astronieae Triana on the basis of the basal placentation. Bakhuizen van den Brink (1943) agreed with this and although he knew that the fruits are berry-like, he created the subtribe Creochitoninae (Miq.) Bakh.f. because of the leaf-like bracteoles that clasp the flower buds, and the cuneate seeds. This division is not supported by wood anatomy (Van Vliet 1981) and macromorphology (Veldkamp 1979) and *Creochiton* should be included in the Dissochaetinae.

Enchosanthera was established by Guillaumin (1913) for *E. anomala* (King & Stapf ex King) Guillaumin based on *Anplectrum anomalum* King & Stapf ex King. He decided to create a separate new genus because it differed from *Anplectrum* A.Gray by the shape and structures of the eight heteromorphous anthers. He distinguished *Creochiton* by the homomorphous stamens. Veldkamp (1979) reduced *Enchosanthera* to *Creochiton* because the differences seemed only of specific value. The structure and nervation of the leaves (plinerved) and rather thick bracteoles were more similar to *Creochiton* than to *Dissochaeta*.

Eisocreochiton was described by Quisumbing & Merrill (1928) on the basis of *E. bracteatus* Quisumb. & Merr. They said that it was similar to *Creochiton* in its vegetative and inflorescences characters. The differences were in the number of stamens and the presence of extra-ovarial chambers. Although no fruits were available, they placed their new genus in the capsular-fruited Oxysporeae Triana near *Blastus* Lour. Judging from labels in BO Ohwi in 1945 already equated it with *Creochiton*. Nayar (1970) revised the genus and correctly assigned it to the baccate Dissochaeteae. He distinguished three species, *E. bracteatus* (Quisumb. & Merr.) M.P.Nayar, *E. furfuraceus* M.P.Nayar, and *E. monticola* (Ridl.) M.P.Nayar. Veldkamp (1979) and Maxwell (1980a, 1980b, 1984) noted that the characters supposedly differentiating between *Creochiton* and *Eisocreochiton* cannot separate them at the generic level and that they must be united into a single genus. Similar to the situation in *Dissochaeta*, the number of stamens and the presence and depth of the extra-ovarial chambers are of specific value only, not generic. With this in mind, the three species of *Eisocreochiton* were transferred to *Creochiton* (Veldkamp 1979). Furtado (1963) was apparently not aware of *Enchosanthera* and described *Anplectrella* for the same species, *Anplectrum anomalum*. Being homotypic, the name *Anplectrella* is superfluous.

General morphology

Habit

The species of *Creochiton* are creepers (scrambling shrubs) or epiphytic shrubs, 2–40 m in height or sometimes woody climbers, e.g. the Philippine species (*C. bracteatus* (Quisumb. & Merr.) Veldkamp, *C. dipterus* Elmer and *C. roseus* Merr.). Inflorescences are only seen on thin twigs, which suggest that the growth mode is sympodial as seems usual for the Dissochaeteae. This is most obvious in *C. anomalus* where the inflorescences are terminal. Because of these older stems are rarely collected it cannot be ascertained how exactly the plants climb. For *C. brevibracteatus* Mansf. Mansfeld reported that the stem is as thick as an arm. A specimen of *C. roseus* (*PNH 9924, Sulit*) is described as 5–6 m tall and 1 cm diameter. Usually, they have terete branchlets except for *C. furfuraceus* and *C. monticola* where they are obscurely triangular and become terete when mature. They are never flattened. The nodes are usually thickened with or without a distinct interpetiolary ridge. The indument is variable from absent to densely stellate furfuraceous or floccose (*C. bibracteatus* and *C. ledermannii* Mansf.).

Leaves

The leaves of *Creochiton* are more or less coriaceous when dry. The shape is quite variable, usually they are ovate-elliptic oblong and only rarely suborbicular. They are largest in *C. bibracteatus* (6–12.5 × 3.2–7.5 cm) and smallest in *C. monticola* (2–3 × 1.4–1.5 cm). The apex usually is acute or rounded while in three species it is retuse (*C. anomalus*, *C. ledermannii* and *C. monticola*). The base is mostly rounded or cuneate, or sometimes subcordate in *C. bibracteatus*, and the margin always entire. Similar to nearly all Melastomataceae genera, *Creochiton* has acrodromal venation with one or two pairs of lateral nerves which arise at or above the base. This subbasal or plinerved nervation is a character that usually distinguishes *Creochiton* from *Dissochaeta*. It is also found in *Boerlagea* Cogn., *Medinilla* Gaudich. ex DC., *Pachycentria* Blume and *Plethiandra* Hook.f., but these are different in habit. The secondary venation is scalariform. Generally, the upper side of the leaves is glabrous with sunken main nerves, while the pubescence of the lower sides is similar to that of the branchlets.

Inflorescence

The inflorescence of *Creochiton* is either a cymose pseudoumbel with 3–5 flowers or a thyrse with up to 35 flowers. It is mostly axillary except for *C. anomalus* where it is terminal. The main axis is usually terete and sparsely to densely furfuraceous. Bracts are present at each node and there is a pair of bracteoles at the base of each pedicel which usually more or less covers the flower bud. In general, they are coriaceous, caducous, concave and usually glabrous, more rarely furfuraceous in- or outside. In *C. bracteatus*, *C. brevibracteatus* and *C. dipterus* they are thin and do not fully enclose the flower bud and are still present at the time of anthesis.

Flowers

The flowers are tetramerous, similar to those of *Dissochaeta*. The calyx tube or hypanthium is usually campanulate or urceolate with a truncate rim or with 4 wave-like teeth. It has the same indument as the main axis and branchlets.

The petals are ovate to elliptic. The colours vary between white, pink or purplish, but cannot be used to distinguish species. Their length has here been measured as much as possible from buds about to open. Similar to *Dissochaeta*, the characters of the stamens are also considered to have specific taxonomic value. When there are only 4 stamens the anthers are usually equal and homomorphic. When there are 8 stamens, they may be either homomorphic or heteromorphic, in which case the oppositipetalous ones are smaller.

The anthers are elongate and glabrous and open distally with a single pore. The connective usually has a dorsal appendage (a triangular, hastate or sagittate crest in alternipetalous anthers and spur-like or ligular in oppositipetalous ones) and in *C. anomalus* and *C. monticola* there are two lateral appendages (ligular or filiform).

The ovary is from half to nearly 2/3 times as long as the hypanthium. The apex is usually glabrous, but sometimes densely pubescent. Similar to other genera in Dissochaeteae it is concrescent with the hypanthium with or without septs forming extra-ovarial chambers in which the anthers are inserted before anthesis (Kartonegoro & Veldkamp 2010). The chambers vary from absent to shallow to reaching to halfway or to the base of the ovary.

Fruits

The fruits of *Creochiton* as in all other Dissochaeteae are berry-like, globose or subglobose, colourful when mature, sometimes with four small calyx remnants. They are variously described as berries, leathery berries, or even indehiscent capsules. True berries by definition have a well-developed usually juicy or fleshy mesocarp, with the seeds immersed in it and without cavities or septs. Capsules are by definition dehiscent. An ancient term for fruits with a dry indehiscent pericarp with several hollow cells without contents except for the many seeds was carcerule. They are usually glabrous, but sometimes they are sparsely furfuraceous. In *C. turbinatus* (J.F.Maxwell) Karton. there are distinct vertical ridges by which they look turbinate-shaped. The seeds are numerous, smooth and curved.

Distribution and Ecology

Creochiton is an endemic genus of the Malesian region ranging from the Malay Peninsula and E Sumatra (*C. anomalus*: Johor, Perak; Indragiri, Bangka) to the Central and New Britain Provinces of Papua New Guinea (*C. novoguineensis* (Baker f.) Veldkamp). There is no indication for a centre of diversity due to a more or less equal number of species in every region. *Creochiton monticola* and *C. furfuraceus* are endemic to Borneo; *C. ledermannii*, *C. novoguineensis* and *C. turbinatus* to New Guinea; while *C. bracteatus*, *C. dipterus* and *C. roseus* to the Philippines. *Creochiton pudibundus* and *C. bibracteatus* were previously known only from Java but now the first has been found in Sulawesi and the second in Ceram.

Creochiton mainly grow as epiphytic shrubs or woody climbers with adventitious roots in rainforests that are not affected by seasonal climate. Perhaps this explains its absence in the Lesser Sunda Islands. Some species are found in mountain forests up to 2000 m altitude like *C. bibracteatus*, *C. monticola*, *C. novoguineensis* and *C. pudibundus*.

Several species such as *C. anomalus*, *C. furfuraceus*, *C. ledermannii* and *C. turbinatus* are known from lowland primary forest or swampy forest between 50–500 m. The plants usually grow at the edge of primary or secondary forest, near river banks or in disturbed forest with gaps in the canopy. The scarce number of specimens in the herbarium is probably due to the fact that the plants grow high in the trees. According to Furtado (1963) all specimens of *C. anomalus* in the Malay Peninsula were collected from logged or fallen trees.

Taxonomic treatment

Creochiton Blume

Creochiton Blume, Flora 14: 506. 1831; Naudin, Ann. Sci. Nat., Bot. sér. 3, 18: 153. 1852; Miq., Fl. Ned. Ind. 1(1): 559. 1855; Triana, Trans. Linn. Soc. London 28: 85. 1872; Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 604. 1891; Krasser in Engl. & Prantl., Nat. Pflanzenfam. 3, 7: 179. 1893; Merr., Publ. Bur. Sci. Gov. Lab. 29: 32. 1905; Enum. Philipp. Pl. 3: 191. 1923; Koord., Exkurs.-Fl. Java 2: 693. 1912; Fl. Tjibodas 3: 212. 1923; Bakh.f., Contr. Melastom.: 307. 1943; Fl. Java 1: 362. 1964. — *Dissochaeta* Blume sect. *Creochiton* (Blume) Baill., Hist. Pl. 7: 15, 51. 1877. — Lectotype (designated here): *Creochiton pudibundus* (Blume) Blume.

Enchosanthera Guillaumin, Bull. Soc. Bot. France 60: 341. 1913. — *Anplectrella* Furtado, Gard. Bul. Singapore 20: 106. 1963, *nom. superfl.* — Type: *Enchosanthera anomala* (King & Stapf ex King) Guillaumin [*Anplectrella anomala* (King & Stapf ex King) Furtado = *Creochiton anomalus* (King & Stapf ex King) Veldkamp].

Eisocreochiton Quisumb. & Merr., Philipp J. Sci. 37:177. 1928; M.P. Nayar, J. Bombay. Nat. Hist. Soc. 67: 87. 1970. — Type: *Eisocreochiton bracteatus* Quisumb. & Merr. [= *Creochiton bracteatus* (Quisumb. & Merr.) Veldkamp].
Dissochaeta Blume fide Kadereit, Edinburgh J. Bot. 63: 3. 2006. *p.p.*
Diplectria auct. Non (Blume) Rchb.: Kuntze, Revis. Gen. Pl. 1: 246. 1891. *p.p.*
Melastoma auct. Non Burm. Ex L.: Blume, Cat. Gew. Buitenzorg 71. 1823; Bijdr. Fl. Ned. Ind. 17: 1071. 1826; DC., Prodr. 3: 148. 1828.

Woody creepers, climbers, scrambling or epiphytic shrubs; branchlets commonly terete or sometimes obscurely triangular, glabrous to densely covered with brown furfuraceous or floccose hairs, sometimes with adventitious roots; nodes thickened or rarely flattened, with or without an interpetiolary ridge. Leaves with acrodromal venation, thin, subcoriaceous or coriaceous, ovate to oblong rarely suborbicular, apex acute or rounded to retuse, base cuneate to subcordate, margin entire; leaves glabrous above, midrib immersed, glabrous to densely furfuraceous, glabrous to densely tomentose below; nervation plinerved with one or two main lateral nerves arising at or above the base, midrib raised below; secondary nervation pinnate, commonly reticulate; petiole terete, dorsally grooved, glabrous to densely furfuraceous. Inflorescences commonly axillary, either umbellate, 3–5-flowered or paniculate with up to 35 flowers, rarely terminal (*C. anomalus*); main axis terete, sparsely to densely furfuraceous; bracts minute to conspicuous, thin or coriaceous; bracteoles distinct, paired, commonly coriaceous, concave, obovate or orbicular, caducous, glabrous or densely furfuraceous, enclosing the flower bud, rarely thin or minute; pedicel terete, glabrous to densely furfuraceous; flower tetramerous; hypanthium campanulate or nearly urceolate, glabrous to densely furfuraceous, hairs simple or stellate; calyx rim truncate or wavy with 4 short lobes; petals ovate or elliptic, glabrous, acute tip, white, pink to purplish. Stamens 4 or 8, equal or unequal, if 8, 4 alternipetalous larger, 4 oppositipetalous smaller; filaments flat, straight; anthers basifix, cylindric, elongate, straight or slightly curved at anthesis, opening with a single terminal pore; connective with a triangular, hastate or sagittate crest in alternipetalous ones, triangular, spur-like or ligular in oppositipetalous ones, lateral appendages commonly absent, rarely paired; ovary globose, 0.5–0.75 times as long as the hypanthium, glabrous, 4-locular, placentation axillary or basal; stigma capitate; style straight or curved, glabrous, slender; extra-ovarial chambers rarely developed or narrowed at the top of the ovary, or extending to about half the length of the ovary. Fruits berry-like, globose to subglobose, green or purplish when mature, glabrous; stalk glabrous or sparsely furfuraceous, seeds numerous, cuneate, curved, flat-topped.
Distribution — The genus with twelve species is endemic to the Malesian region (Peninsular Malaysia, Sumatra, Borneo, Java, Sulawesi, Moluccas, Philippines and New Guinea), but is not yet found in the Lesser Sunda Islands.

Key to species of *Creochiton*

1 Hypanthium densely furfuraceous 2
1 Hypanthium glabrous, glabrescent or sparsely furfuraceous 4
2 Leaf underneath glabrescent (but for midrib) [Philippines] 3
2 Leaf underneath densely furfuraceous or densely tomentose [Java, Moluccas] .... **2. *C. bibracteatus***
3 Bracteoles partially covering the flower bud, thin, outside densely furfuraceous..... ..... **5. *C. dipterus***
3 Bracteoles completely covering the flower bud, fleshy, outside glabrous .... **11. *C. roseus***
4 Petiole glabrous to sparsely furfuraceous..... 5

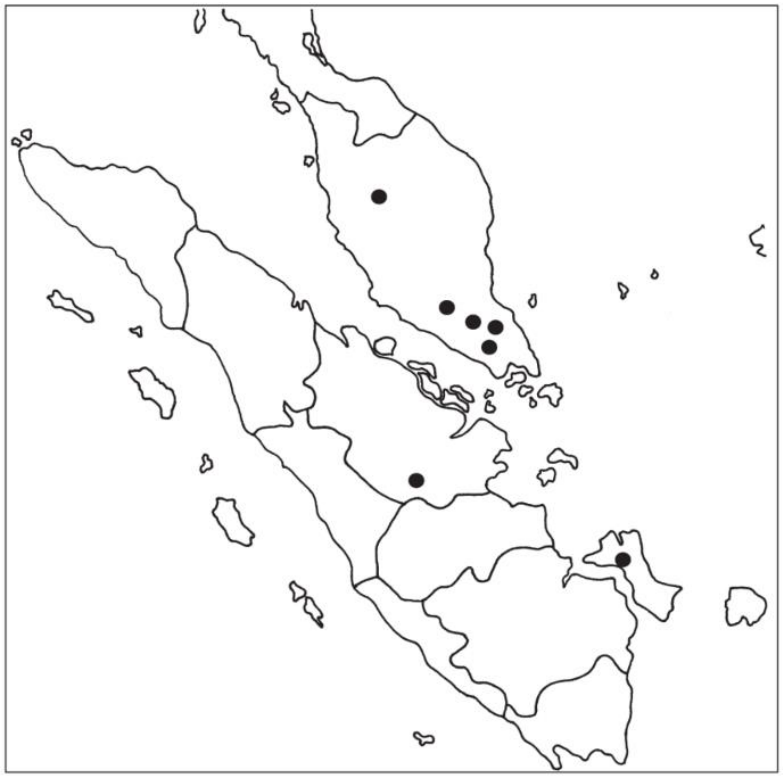
4 Petiole densely furfuraceous or floccose 8
5 Petiole 8–15 mm long; leaf blades 4.5–13 cm long, base cuneate to rounded, apex acuminate to acute. Inflorescences axillary; bracteoles ovate to obovate, completely covering bud, fleshy, glabrous or densely furfuraceous; stamens equal [Borneo, Sulawesi, Java, New Guinea] 6
5 Petiole 2–6 mm long; leaf blades 1.5–4 cm long, base acute, apex rounded or retuse. Inflorescences terminal; bracteoles linear, partially covering bud, thin, scaly; stamens unequal [Peninsular Malaysia, Sumatra] ..... **1. *C. anomalus***
6 Leaf apex acute; bracteoles obovate; stamens 8, lateral appendages and extra-ovarial chambers absent [Java, Sulawesi, New Guinea] 7
6 Leaf apex acuminate; bracteoles ovate; stamens 4, lateral appendages and extra-ovarial chambers present [Borneo] ..... **6. *C. furfuraceus***
7 Petiole sparsely furfuraceous; leaf underneath glabrous (but for midrib); inflorescences paniculate, many-flowered; bracteoles densely furfuraceous; hypanthium sparsely stellate furfuraceous; fruits subglobose [New Guinea] ..... **9. *C. novoguineensis***
7 Petiole glabrous or with some hairs; leaf underneath pubescent; inflorescences umbellate, few-flowered; bracteoles and hypanthium glabrous; fruits globose [Java, Sulawesi] ..... **10. *C. pudibundus***
8 Petiole 8–20 mm long; leaf 3.5–7 by 1.8–4 cm, underneath glabrous to glabrescent (but for midrib); leaf apex acute 9
8 Petiole 2–6 mm long; leaf 2–6 by 2.2–3.1 cm, underneath glabrous to densely tomentose; leaf apex retuse 10
9 Leaf base cuneate; inflorescences umbellate; bracteoles completely covering the flower bud, 6–7 mm long; hypanthium sparsely stellate furfuraceous; stamens 4, lateral appendages present [Philippines] ..... **3. *C. bracteatus***
9 Leaf base rounded; inflorescences paniculate; bracteoles partially covering the flower bud, 1 mm long; hypanthium glabrous; stamens 8, lateral appendages absent [New Guinea] ..... **4. *C. brevibracteatus***
10 Leaf 3.4–6 by 2.2–3.1 cm, underneath glabrescent to densely tomentose; inflorescences umbellate, few-flowered; bracteoles orbicular or ovate; stamens equal, lateral appendages absent [New Guinea] 11
10 Leaf 2–3 by 1.4–1.5 cm, underneath glabrous (but for midrib); inflorescences paniculate, many-flowered; bracteoles obovate; stamens unequal, lateral appendages present [Borneo] ..... **8. *C. monticola***
11 Leaves obovate, apex retuse, underneath densely tomentose; bracteoles inside stellate furfuraceous; hypanthium sparsely stellate furfuraceous; fruits subglobose, smooth ..... **7. *C. ledermannii***
11 Leaves ovate, apex acute or retuse, underneath glabrescent (but for midrib); bracteoles inside glabrous; hypanthium glabrescent; fruits globose, ridged ..... **12. *C. turbinatus***

1. *Creochiton anomalus* (King & Stapf ex King) Veldkamp — Map 2-1

Creochiton anomalus (King & Stapf ex King) Veldkamp, Blumea 24: 431, 438. 1979. — *Anplectrum anomalum* King & Stapf ex King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 58. 1900; Ridl., Fl. Malay Penins. 1: 800. 1922. — *Enchosanthera anomala* (King & Stapf ex King) Guillaumin, Bull. Soc. Bot. France 60: 341, f. 1, 2. 1913. — *Anplectrella anomala* (King & Stapf ex King) Furtado, Gard. Bull. Singapore 20: 106. 1963. — Lectotype (designated by Veldkamp in Blumea 24: 431. 1979): *King's Collector 5779* (lecto CAL

n.v.; isolecto K [K000859588!, K000859589!, K000859590!] L [L0008838!], P [P02274804!, P02274805!], SING!), Malaysia, Perak, Gopeng.

Epiphytes or woody climbers, 10–40 m in height; branchlets terete, covered by stellate brown scales, glabrescent; nodes thickened with an interpetiolary ridge. Leaves coriaceous, obovate to elliptic, apex rounded to retuse, base acute; above glabrous, light green, sparsely stellate scaly on the midrib, below densely covered with stellate tomentose hairs, yellowish green, dark brown when dry; 1.5–4 × 1–3 cm; nervation with 1–2 pairs of lateral nerves from above the base; petiole 3–8 cm long, covered with stellate scales, 2–6 mm long. Inflorescences terminal, paniculate, few- to many-flowered; main axis angular, covered with stellate scales, furfuraceous; secondary axes, 1–6 mm long; bracts minute or linear; bracteoles linear, not enveloping the flower buds, covered with brown scales, 2–3 mm; pedicel covered with stellately furfuraceous hairs, 8–11 mm long. Hypanthium campanulate to nearly urceolate, 4–5 × 2–3 mm, stellate furfuraceous, green, becoming brown when dry; calyx rim truncate, furfuraceous with 4 small undulations ca. 0.5 mm long; petals elliptic, white or pink, 4–5 × 2–2.5 mm. Stamens 8, unequal, the alternipetalous ones: filament flat, ca. 3 mm long; anther elongate, yellow, glabrous, ca. 7 mm long; connective with a triangular to sagittate, crest ca. 2 mm long, purple; lateral appendages paired, ligular, 1–1.5 mm long; the oppositipetalous ones: filament flat, ca. 3 mm long; anther elongate, ca. 5 mm long; connective with a ligular crest, ca. 1 mm long; lateral appendages absent; ovary globose, glabrous, ca. 3 mm long; style glabrous, slender, straight, 5–7 mm long; extra-ovarial chambers 8, half as long as the ovary. Fruits subglobose, glabrous to sparsely furfuraceous, green to yellowish green, 4–6 × 3–4 mm; seeds ca. 0.6 mm long.



Map 2-1. Distribution of *C. anomalus* (●).

Distribution — Peninsular Malaysia (Johor, Perak) and Sumatra (Riau, Bangka).
Ecology & Habitat — Lowland or swampy primary rainforest between 100–550 m elevation.
Note — *Creochiton anomalus* differs from all species by the terminal paniculate inflorescences. It has linear bracteoles which partially cover the flower bud. The species has 8 heteromorphous stamens that are similar to those of *C. monticola* from Borneo, but the oppositipetalous stamens are smaller and have no lateral appendages. Similar to *C. brevibracteatus* but differs by its shorter petiole and leaves.
Specimen examined — **MALAYSIA.** Johor: Mersing, Lengor FR., *Whitmore 400* (BO, L, SING); Mawai, *Corner SFN30876* (BO, SING); Layang-Layang, Bukit Badak, *Hassan & Kadim H.13* (L, SING); Rongam FR., *Burkill 1792* (L, SING). Perak: Gopeng, *King's Collector 5779* (L, SING). **INDONESIA.** Bangka-Belitung: Bangka, Sungei Slan, *Teijsmann s.n.* (BO). Jambi: Indragiri uplands, Muara Pajanki, *Buwalda 6431* (BO, L, SING).

2. *Creochiton bibracteatus* (Blume) Blume — Fig. 2-1, Map 2-2

Creochiton bibracteatus (Blume) Blume, Flora 14: 507. 1831; Naudin, Ann. Sci. Nat., Bot. sér. 3, 18: 154. 1852; Miq., Fl. Ned. Ind. 1(1): 560. 1855; Triana, Trans. Linn. Soc. London 28: 85, t. 7, f. 91. 1872; Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 605. 1891; Krasser in Engl. & Prantl, Nat. Pflanzenfam. 3, 7: 178, f. 77a. 1893; Koord., Exkurs.-Fl. Java 2: 693. 1912; Fl. Tjibodas 3: 212. 1923; Bakh.f., Contr. Melastom.: 308. 1943; Fl. Java 1: 362. 1964. — *Melastoma bibracteatum* Blume, Bijdr. Fl. Ned. Ind. 17: 1071. 1826; DC., Prodr. 3: 148. 1828. — *Diplectria bibracteata* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891, *nom. inval. prov.* — Lectotype (designated here): *C.L. Blume s.n.* (lecto L [L0008839!]; isolecto L [L0931127!]), Indonesia, Java.
Creochiton superbus Naudin, Ann. Sci. Nat., Bot. sér. 3, 18: 153. 1852; Miq., Fl. Ned. Ind. 1(1): 560. 1855. — Type: *H. Zollinger 3009* (holo G [G00316259!]; iso L!, P [P02274801!, P02274802!], U [U0004001!]), Indonesia, Java, Mt Salak.

Epiphyte or climber, up to 10–26 m in height; branchlets terete, densely brown furfuraceous; nodes thickened by the interpetiolary ridge. Leaves thin, ovate to suborbicular, apex acute to rounded, base rounded to subcordate, glabrous above but puberulous near base, midrib sunken, densely stellate furfuraceous to floccose below, 6–12.5 × 3.2–7.5 cm; nervation plinerved with 2 pairs of main nerves arising above the base; petiole densely furfuraceous, 10–27 mm long. Inflorescences axillary 4–6 cm long, umbellate with 3–5 flowers; main axis terete, up to 4.5 cm long, densely furfuraceous; bracts oblong, glabrous, ca. 4 mm long; bracteoles obovate, coriaceous, concave, enveloping the flower buds, densely furfuraceous outside, glabrous inside, violet, 6–15 × 4–6 mm; pedicel densely furfuraceous, 10–15 mm long; flower bud ca. 10 mm long. Hypanthium campanulate, densely stellate furfuraceous, 3–5 × 2–3 mm; calyx rim truncate with 4 small undulations, 0.5–1 mm long; petals oblong, white, 7–9 × 4 mm. Stamens 8, equal; filament flat, ca. 4 mm long; anther elongate, 4–6 mm long; connective with a sagittate crest 1–1.5 mm long; lateral appendages absent; ovary ellipsoid, glabrous, ca. 3 mm long; style glabrous, curved when mature, 6–10 mm long; extra-ovarial chambers shallow about 1/5 as long as the ovary or absent. Fruits globose or subglobose, vertically depressed, glabrous, dark green to black, 8–10 × 7 mm; stalk densely furfuraceous; seeds ca. 1 mm long.
Distribution — Java (west) and Moluccas (Ceram).
Ecology & Habitat — Slope of secondary forest, edge of forest or mossy mountain forest between 1100–1600 m elevation.

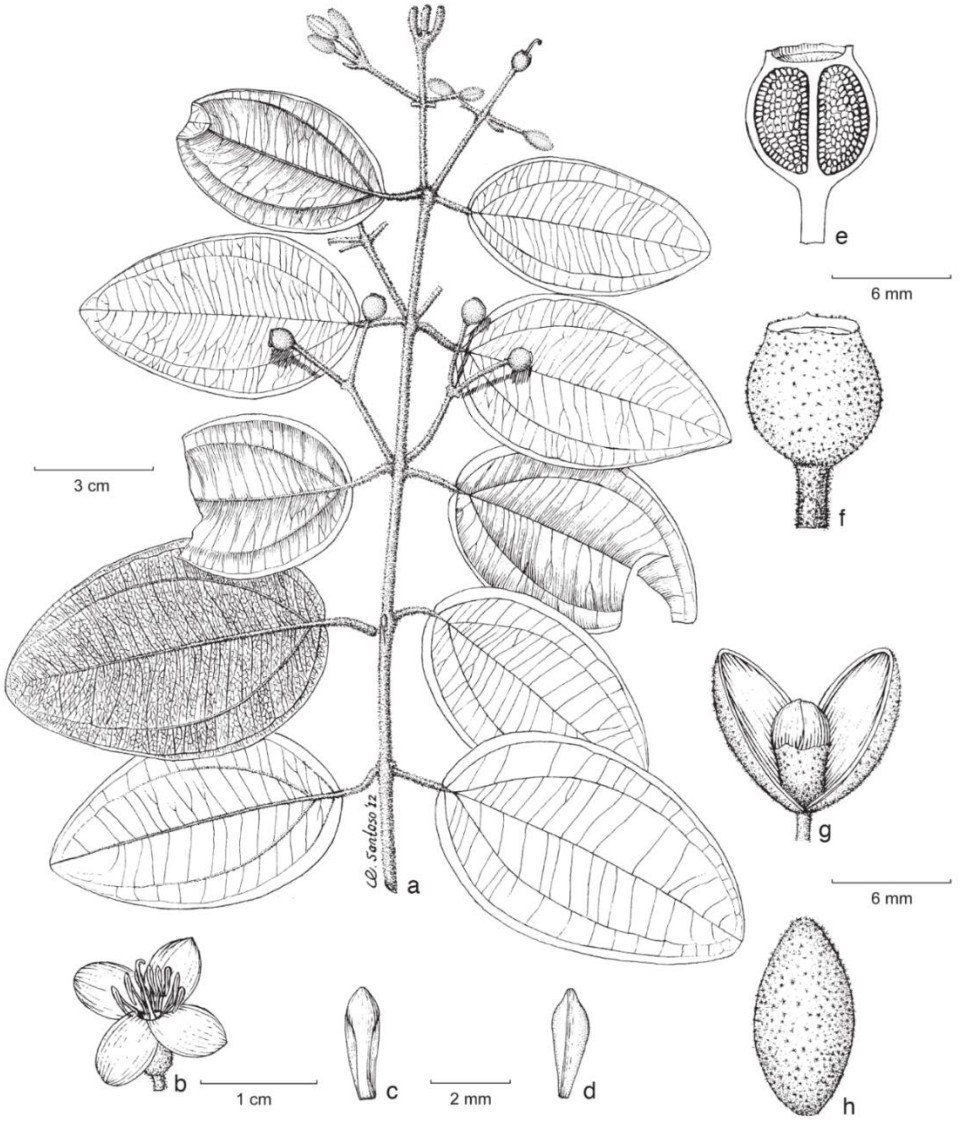


Fig. 2-1. *Creochiton bibracteatus*. **a.** Habit; **b.** flower; **c, d.** stamen in flower bud (c = abaxial; d = adaxial); **e.** cross section fruit; **f.** mature fruit; **g.** flower bud with a pair of bracteoles; **h.** bracteole (all: *Backer 10623*, BO).

Vernacular name — *Harendong areuy* (Sundanese: used for about every climbing Melastomataceae).

Note — *Creochiton bibracteatus* can easily be distinguished from the other species by the densely furfuraceous petioles, rounded to subcordate leave base, large, ovate to suborbicular leaves up to 12.5 cm long, below furfuraceous to floccose, and the densely stellate furfuraceous hypanthium. The axillary umbellate inflorescences and 8 equal stamens in this species are similar to *C. pudibundus* but it differs from the latter by being glabrous or with sparsely stellate hairs in most parts and by the coriaceous leaves. Previously the species was known only as epiphytic shrubs or climbers in the western part of Java, but in 1917 one

collection was made in Mautipass, Ceram, that is indistinguishable from the Java specimens (*Rutten 1970*, BO).

Specimen examined — **INDONESIA.** West Java: Bogor, Mt. Salak, *Zollinger 3009* (L); Cianjur, Mt. Gede-Pangrango, Cibodas, *Koorders 25873β* (BO); *Ibid.*, *Koorders 25907β* (BO); *Ibid.*, *Bruggeman 272* (BO); *Ibid.*, *Sapei 91* (BO); between Puncakpass and Rarahan, *van Steenis 11541* (BO, L); Sukabumi, Cicurug, Ciherang, *Bakhuizen van den Brink 7304* (BO); Mt. Halimun, Nirmala, *Backer 10623* (BO); *Ibid.*, *Uchida 73* (BO); Bandung, Mt. Papandayan, Sumadra near Talun, *Backer 5617* (BO). No specific location: *Blume s.n.* (L); *de Vriese 91* (L); *de Vriese 40* (L); *de Vriese 51* (L): *Teijsmann s.n.* (L); *Hasskarl s.n.* (L); *Argorris s.n.*(L). Moluccas: Ceram, Mautipass, *Rutten 1970* (BO).

Map 2-2. Distribution of *C. bibracteatus* (●) and *C. pudibundus* (■).

3. *Creochiton bracteatus* (Quisumb. & Merr.) Veldkamp — Map 2-3

Creochiton bracteatus (Quisumb. & Merr.) Veldkamp, Blumea 24: 438. 1979. — *Eisocreochiton bracteatus* Quisumb. & Merr., Philipp. J. Sci. 37: 177, pl. 4. 1828; M.P.Nayar, J. Bombay Nat. Hist. Soc. 67: 88. 1970 ('*bracteata*'). — Type: *M. Ramos & G.E. Edaño BS 45610* (holo PNH, probably lost; iso BM [BM000944491!], BO!, K [K000859580!], NY, P [P05259309!], SING, US [US00120440!]), Philippines, Luzon, Nueva Vizcaya Province, Mt Alzapan.

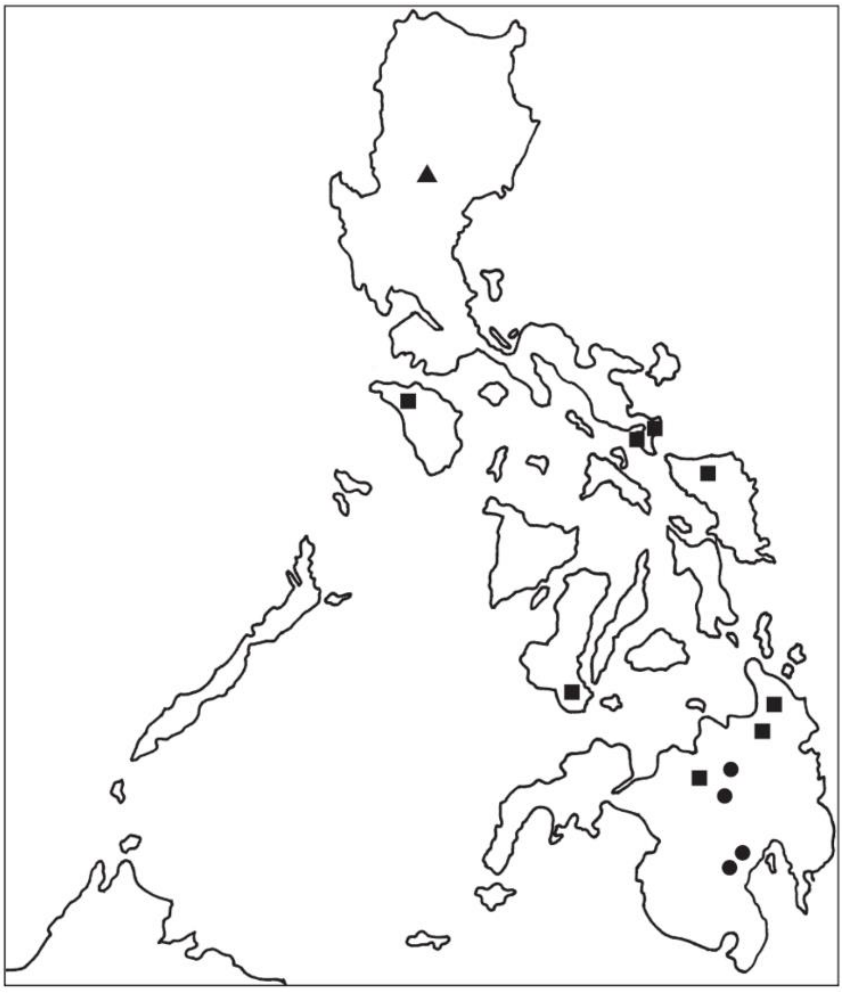
Climbers; branchlets terete, sparsely puberulous, 2 mm in diameter; nodes with an interpetiolary ridge. Leaves thin, ovate, apex acute or acuminate, base cuneate, glabrous above, glabrescent below midrib densely furfuraceous, 3.5–6 × 1.8–3.6 cm; nervation plinerved with two pairs of main nerves arising above the base; petiole densely stellate furfuraceous to floccose, 10–20 mm long. Inflorescences axillary, thyrsoid up to 4 cm long, 5-flowered; main axis angular, densely furfuraceous, 2–4 cm long; bracts elliptic, sparsely furfuraceous, 8–11 × 5–7 mm; bracteoles ovate to suborbicular, glabrous to sparsely furfuraceous, thin, 6–7 × 3–4 mm, enveloping the flower buds; pedicel densely stellate furfuraceous, 7–8 mm long. Hypanthium campanulate, sparsely stellate furfuraceous, 3–4 × 2–3 mm; calyx rim truncate with 4 shallow undulations, ca. 0.3 mm long; petals ovate, apex acute, base rounded, 3–4 × 3 mm. Stamens 4, equal; filament flat, ca. 3 mm long; anthers

ellipsoid, 4–5 mm long; connective with a triangular crest, 0.75–1 mm long; lateral appendage paired, 0.8–1.5 mm long; ovary globose, glabrous, 2–3 mm long; style glabrous, ca. 6 mm long; extra-ovarial chambers deep, half as long as the ovary. Fruits and seeds not seen.

Distribution — Philippines (Luzon), only known from the type.

Ecology & Habitat — Climbing on trees on forested slopes at 1700 m elevation.

Note — *Creochiton bracteatus* differs from all congeners by its densely furfuraceous to densely floccose petioles, 10–20 mm long, leaf base cuneate, underneath glabrescent (except midrib) and extra-ovarial chambers half as long as the ovary. Similar to *C. furfuraceus* by its 4 equal alternipetalous stamens, but differs by having glabrescent branchlets and underside of the leaves while the latter has densely furfuraceous branchlets and underside of the leaves. Its bracts and bracteoles are very distinct being large, thin, membranous, and veined. The bracteoles are also not concave and do not fully enclose the flower buds as in the other species.



Map 2-3. Distribution of *C. bracteatus* (▲), *C. dipterus* (■) and *C. roseus* (●).

4. *Creochiton brevibracteatus* Mansf.

Creochiton brevibracteatus Mansf., Bot. Jahrb. Syst. 60: 135. 1925. — Type: *C.L. Ledermann 8660* (holo B†), Papua New Guinea, E Sepik, Aprilfluβ (April River), Standlager (Main Camp).

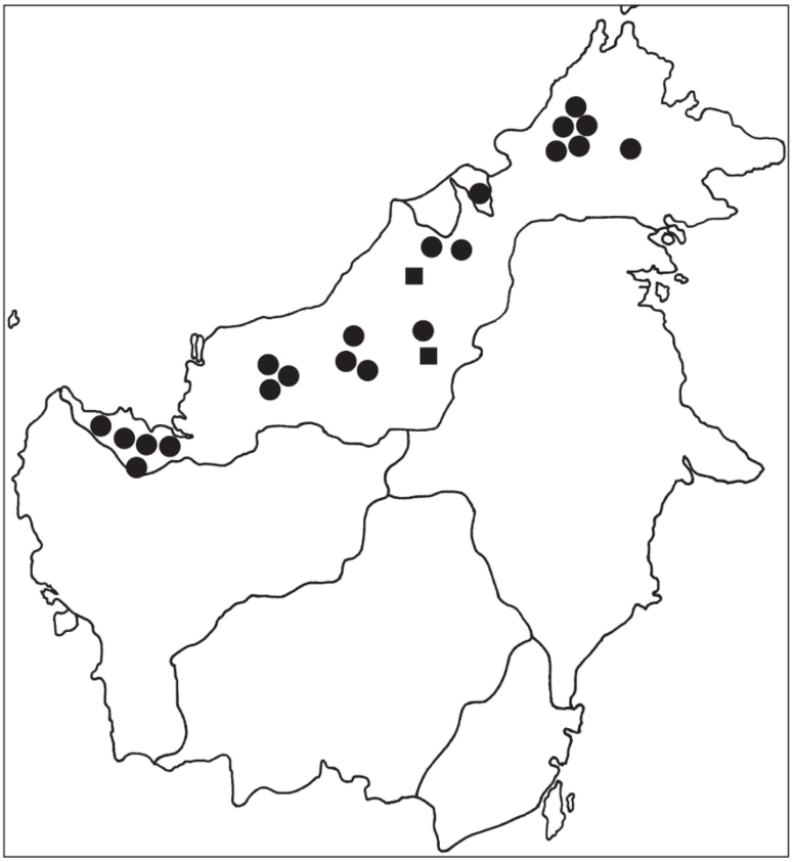
Liana; stem as thick as an arm, innovations terete, furfuraceous. Leaves ovate, rarely broadly elliptic, 5–7 × 3–4 cm, 5-nerved (excl. marginal nerves), base rounded, apex acute, dark green, above glabrous, below glabrous except for the prominent nerves, petiole 8–15 mm long, furfuraceous. Inflorescences paniculate, axillary, up to 5 cm long, incl. the 2 cm long peduncle, axes somewhat furfuraceous; pedicels 7 mm long, about glabrous; bracteoles hardly 1 mm long. Hypanthium glabrous, 4 mm long, hardly 4-dentate; petals 4, ovate, shortly before anthesis 5 mm long, white. Stamens 8, subequal, filaments 3 mm long, anthers 4 mm long, dorsal appendix 1.5 mm long. Fruits and seeds not seen.
Distribution — New Guinea (E Sepik).
Ecology & Habitat — Primary forest with many tree ferns, bamboos, small palms and *Selaginella* up to 1 m, at c. 100 m elevation.
Note — No specimens have been seen, and the description is after Mansfeld (1925). From this the species seem to differ from all congeners by: Petioles 8–15 mm long, densely furfuraceous. Leaves 5–7 × 3–4 cm, underneath glabrous (but for midrib). Inflorescence paniculate. Bracteoles partially covering the flower bud, ca. 1 mm long. Hypanthium glabrous. The type was lost during the Second World War. The description agrees quite well with the Philippine *C. dipterus* which differs mainly by the possibly more pubescent leaves, 3-flowered cymes, bracteoles 5–7 mm long, hypanthium densely stellate furfuraceous, rim truncate with four 0.3–0.5 mm long lobes.

5. *Creochiton dipterus* Elmer — Map 2-3

Creochiton dipterus Elmer, Leafl. Philipp. Bot. 4: 1192. 1911; Leafl. Philipp. Bot. 10: 3659. 1939; Merr., Enum. Philipp. Pl. 3: 190. 1923. — Type: *A.D.E. Elmer 9813* (holo PNH *n.v.*; iso E, MO), Philippines, Negros, Negros Oriental Province, Dumaguete (Cuernos Mts).

Climbers, up to 25 m high; branchlets terete, glabrescent to sparsely brown furfuraceous; nodes thickened with interpetiolary ridge. Leaves coriaceous, ovate, apex acute to obtuse, base rounded or subcordate; glabrous above, yellowish green, glabrescent below, midrib densely furfuraceous, 4–7.5 × 2–4.5 cm; nervation plinerved with 1 pair of main nerves arising above the base; petiole densely furfuraceous, 5–17 mm long. Inflorescences axillary, a 3-flowered cyme, 1.5–2.5 cm long; main axis terete, densely furfuraceous, 2 cm long; bracts ovate, densely furfuraceous, veined, c. 3 mm long; bracteoles ovate, orbicular to oblong, thin, densely furfuraceous on both sides, veined, yellowish, half enveloping the flower buds, 5–7 × 2–5 mm; pedicel densely furfuraceous, 8–9 mm long. Hypanthium campanulate, densely stellate furfuraceous, yellowish green, 3–4 × 2 mm; calyx rim truncate with 4 small distinct lobes, 0.3–0.5 mm long; petals elliptic, apex rounded, 4–5 × 4 mm, white. Stamens 8, equal; filament flat, cream, 3–4 mm long; anther elongate, pinkish or purple, 4–5 mm long; connective with a sagittate crest, light cream, ca. 1 mm long; lateral appendages absent; ovary 2–3 mm long, glabrous; style glabrous, pink, 9–11 mm long; extra-ovarial chambers not developed. Fruits globose, glabrous, ca. 5 × 5 mm, green and turning red when ripe; seeds 0.5–0.7 mm long.
Distribution — Philippines (Luzon, Mindanao, Mindoro, Negros).
Ecology & Habitat — Primary or disturbed forest on ridge slope, between 450–1800 m elevation.

Vernacular name — *Buyon-Buyon* (Visayan).
Note — *Creochiton dipterus* is distinguished by its coriaceous leaves, underneath glabrescent (but for midrib), the umbellate 3-flowered inflorescence, thin, ovate, orbicular to oblong bracteoles which partially cover the flower bud, and the absence of extra-ovarial chambers. It resembles *C. ledermannii* by the shape of the leaves and fruits but differs by its glabrescent leaves, the single cyme and thin bracteoles, while the latter has densely tomentose leaves, umbellate inflorescences and coriaceous bracteoles. The shape of stamens is similar to *C. novoguineensis* but it differs by the shape and indument of the leaves.
Specimen examined — **PHILIPPINES.** Luzon: Sorsogon Province, Irosin (Mt. Bulusan), *Elmer 16671* (BO, L). Mindanao: Agusan Province, Butuan, San Mateo Bo., Tungao So, *Mendoza PNH 41952* (BO, L); *Ibid.*, Cabadbaran (Mt. Urdaneta), *Elmer 14119* (BO, L). Mindoro: San Teodoro, Subaan River, *Ridsdale SMHI 1162* (BO, L).



Map 2-4. Distribution of *C. furfuraceus* (■) and *C. monticola* (●).

6. *Creochiton furfuraceus* (M.P.Nayar) Veldkamp — Map 2-4

Creochiton furfuraceus (M.P.Nayar) Veldkamp, Blumea 24: 438. 1979. — *Eisocreochiton furfuraceus* M.P.Nayar, J. Bombay Nat. Hist. Soc. 67: 88, pl. 1. 1970 ('*furfuracea*'). — Type: *M. Jacobs 5293* (holo K [K000859586!]; isotypes B, CANB, G, L [L0008840!], S, SAR, US), Malaysia, Borneo, Sarawak, 3rd Div., Kapit District, Belaga Subdistrict, Rejang River.

Woody climbers; branchlets angular, becoming terete, densely puberulous with brown hairs; nodes thickened with an interpetiolary ridge. Leaves coriaceous, ovate to elliptic, apex acuminate, base rounded; glabrous above with stellate hairs on the midrib, below densely stellate furfuraceous, 4.5–7 × 2.5–3 cm; nervation plinerved with 1 pair of main nerves arising above the base; petiole densely covered with brown puberulous hairs, 8–11 mm long. Inflorescences axillary, thyrsoid, 3–10 cm long, with 10–35 flowers; main axis terete, densely stellate puberulous, 2–6 cm long; pedicel densely furfuraceous, 4–5 mm long; bracteoles coriaceous, ovate, concave, apex rounded, 5–6 × 3–4 mm, stellate furfuraceous on both sides, enveloping the flower buds. Hypanthium campanulate, ca. 2.5 × 2 mm, stellate furfuraceous, pale brownish; calyx rim truncate; petals ovate, apex acute, base truncate, ca. 2.5 × 2 mm, sordidly pink margined, centre white. Stamens 4, equal; filament flat, white, ca. 1.5 mm long; anthers elongate, curved, ca. 2 mm long, pale green; connective with a triangular crest, ca. 0.75 mm long, lateral appendages paired, ca. 0.7 mm long; ovary ca. 2 mm long, glabrous, 4-ridged at the top; style glabrous, pinkish, 2–2.5 mm long; extra-ovarial chambers shallow, 1/5 as long as the ovary. Fruits globose, stellate furfuraceous, ca. 5 × 5 mm; seeds 0.7–0.8 mm long.

Distribution — Borneo (Sarawak).

Ecology & Habitat — Primary forest on sandstone substratum hills at below 500 m elevation.

Note — *Creochiton furfuraceus* can be distinguished by its dense furfuraceous indument in most parts, axillary thyrsoid inflorescences with 10–35 flowers, coriaceous bracteoles and 4 equal stamens. It is similar to *C. bracteatus* by having 4 equal stamens and the shape of the anthers but differs by a less dense indument on most parts, smaller inflorescences with only ca. 5 flowers, large and thin bracteoles and deep extra-ovarial chambers.

Specimen examined — **MALAYSIA.** Sarawak: 3rd Division, Kapit District, Belaga Subdistrict, leaf bank of Rejang River, *Jacobs 5293* (L); Baram District, Apo Dari, *Chai S.35814* (L).

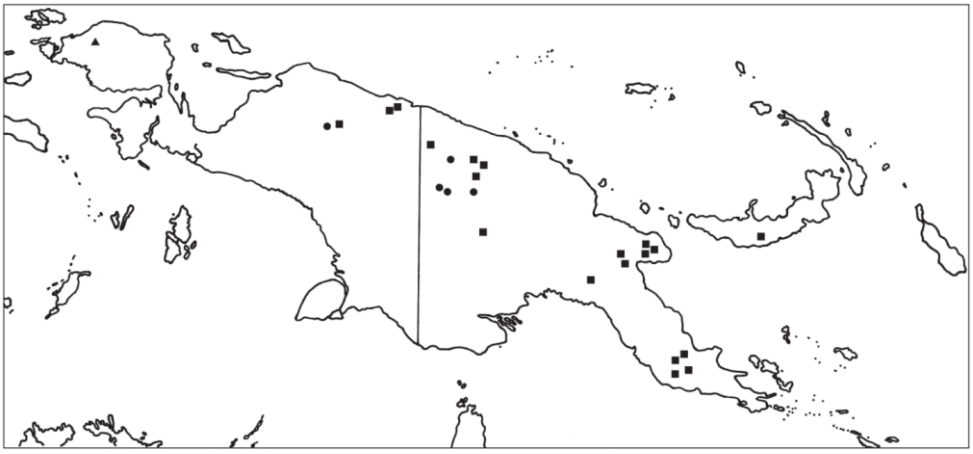
7. *Creochiton ledermannii* Mansf. **—** Map 2-5

Creochiton ledermannii Mansf., Bot. Jahrb. Syst. 60: 135. 1925. **—** Lectotype (designated here): *C.L. Ledermann 12943* (lecto B†; isolecto L), Papua New Guinea, Sepikgebiet, Felsspitze.

Creochiton ledermannii Mansf. var. *turbinatus* auct. non J.F.Maxwell: J.F. Maxwell, Gard. Bull. Singapore 33: 323. 1980, quoad paratypi.

Epiphytes or climbers, 2–3 m in height; branchlets terete, densely furfuraceous to floccose; nodes thickened with an interpetiolary ridge. Leaves coriaceous, obovate, apex retuse, base rounded to cuneate; glabrous above, dark green, densely tomentose below, midrib densely furfuraceous, glossy and paler green, 3.4–4 × 2.4–3 cm; nervation plinerved with 1 pair of main nerves arising from above the base; petiole densely furfuraceous, 2–6 mm long. Inflorescences axillary, up to 6 cm long, umbellate with 3 flowers; main axis terete, densely furfuraceous, 2–7 cm long; bracts elliptic, glabrous, ca. 12 × 3 mm; bracteoles coriaceous, orbicular or ovate, concave, glabrous outside, densely furfuraceous inside, enveloping the flower buds, whitish, 4–8 × 6 mm, whitish; pedicel glabrescent to sparsely furfuraceous, 7–18 mm long. Hypanthium urceolate, sparsely to densely stellate furfuraceous, ca. 3 × 2 mm, teeth triangular, ca. 0.5 mm long; petals elliptic, 3–4.2 × 2 mm, red-purplish. Stamens 8, equal; filament flat, 2–2.5 mm long; anthers elongate, 2–3 mm long; connective with a triangular crest, ca. 1.5 mm long; lateral appendages absent; ovary globose, 1.5–1.8 mm long, glabrous; style glabrous, ca. 5 mm long; extra-ovarial chambers shallow, 1/5 as long as the

ovary. Fruits subglobose, glabrous to puberulous, greenish white, 4–7 × 4 mm; seeds ca. 0.5 mm long.
Distribution — New Guinea.
Ecology & Habitat — Rainforest on river bank at 200–250 m elevation.
Vernacular name — *Apunengapok* (Waskuk).
Note — Characteristics of *C. ledermannii* are the retuse apex leaf, axillary umbellate 3-flowered inflorescences, bracteoles coriaceous and concave, hypanthium urceolate, calyx rim distinctly truncate, and 8 equal stamens. It differs from *C. turbinatus* by its dense indument and retuse leaf apex, while the latter is less pubescent with an acute leaf apex. The shape of the stamens is similar to *C. pudibundus*, but this differs by the sparsely puberulous leaves, glabrous petioles and bracteoles, absence of extra-ovarial chambers, and the subglobose fruits. The paratypes of *C. turbinatus* (*Hoogland & Craven 10735*, *Docters van Leeuwen 10382*) were regarded to belong here.
Specimen examined — **INDONESIA.** Papua: Mamberamo River, Syrina, *Docters van Leeuwen 10382* (BO, L). **PAPUA NEW GUINEA**. Sepik: Ambunti Subdistrict, Along Yapa (Hunstein River), *Hoogland & Craven 10735* (BO, L); *Ledermann 12943* (L).



Map 2-5. Distribution of *C. ledermannii* (●), *C. novoguineensis* (■) and *C. turbinatus* (▲).

8. *Creochiton monticola* (Ridl.) Veldkamp — Map 2-4

Creochiton monticola (Ridl.) Veldkamp, Blumea 24: 433, 438. 1979. — *Anplectrum monticola* Ridl., Kew Bul. 1: 31. 1946. — *Eisocreochiton monticola* (Ridl.) M.P.Nayar, J. Bombay Nat. Hist. Soc. 60: 89, pl. 2. 1970. — Type: *C.J. Brooks 50* (holo K [K000859585!]; iso BO!), Malaysia, Borneo, Sarawak, Mt Ben Kajan.
Creochiton kinabaluensis Heine, Mitt. Bot. Staatssamml. München 6: 214. 1953. — Lectotype (designated here): *J. Clemens & M.S. Clemens 32646 = 33951* (holo M; iso A., BM!, BO!, K [K000859583!], L [L0008843!]), Malaysia, Borneo, Mt Kinabalu, Mt Nungkok.

Climbers, often epiphytic, up to 30 m tall; branchlets angular becoming terete, furfuraceous. Leaves coriaceous, elliptic, apex acute to retuse, base cuneate; glabrous on both sides, 2–4.5 × 1.4–2.6 cm; with 1–2 pairs of main nerves arising from above the base; petiole glabrous to furfuraceous, 3–5 mm long. Inflorescences axillary, up to 3.5 cm long, paniculate, 4–10-flowered; main axis angular, stellate furfuraceous, 1.5–2.5 cm long; bracts ovate, glabrous, veined, 5–7 × 4 mm; bracteoles thin, pale, obovate, glabrous to sparsely furfuraceous on both

sides, veined, 3–7 × 3.4 mm, enveloping the flower buds; pedicel furfuraceous, ca. 2 mm long. Hypanthium campanulate, glabrous to sparsely furfuraceous, green, pink, 2–2.5 × 2 mm; calyx rim truncate with 4 shallow undulations; petals oblong to lanceolate, apex acute, ca. 4 × 2.5 mm, cream to pink or reddish. Stamens 8, unequal, the alternipetalous ones: filaments flat, 2–2.5 mm long; anther elongate, red, ca. 2.5 mm long; connective with a triangular crest, 1–1.5 mm long; lateral appendages paired, ca. 0.5 mm long; the oppositipetalous ones: filament flat, ca. 1.5 mm long; anthers ca. 1.5 mm long, bent; connective with spur-like crest, ca. 0.5 mm long; lateral appendages ligulate, ca. 0.75 mm long or absent; ovary globose, glabrous, 1–1.5 mm long; style glabrous, ca. 5 mm long; extra-ovarial chambers shallow, about 1/5 as long as the ovary. Fruits subglobose, glabrous, whitish, yellowish green, or purple when mature, 2–5 × 1–5 mm; seeds ca. 0.75 mm long.
Distribution — Borneo (Sabah, Sarawak).
Ecology & Habitat — Montane forest at 820–2000 m elevation.
Note — *Creochiton monticola* is easily recognized by its small leaves (< 4.5 cm long), glabrous underneath, axillary paniculate inflorescences and obovate bracteoles. Morphologically it cannot be mistaken for *C. anomalus* which has densely tomentose leaves, acute base, terminal inflorescences with thin bracteoles which partially cover the flower bud, and long extra-ovarial chambers (about half as long as the ovary). The stamens differ by the oppositipetalous ones having lateral appendages 1–1.5 mm long while they are 0.5–0.75 mm long or absent in the latter.
Specimen examined — **MALAYSIA.** Sabah: Mt. Kinabalu, Tenompok, *Clemens 28616* (BO); *Ibid.*, *Clemens 28616A* (BO); *Ibid.*, Colombon Basin, Below Kebambang Lobang, *Clemens 34455* (BO, L); *Ibid.*, Mt. Nunkok, *Clemens 32646* (BO, L). Sarawak: Mt. Ben Kajan, *Brooks 50* (BO, K).

9. *Creochiton novoguineensis* (Baker f.) Veldkamp & M.P.Nayar — Map 2-5

Creochiton novoguineensis (Baker f.) Veldkamp & M.P.Nayar, Blumea 24: 438. 1979. — *Dissochaeta novoguineensis* Baker f., J. Bot. 61(Suppl.): 21. 1923; Mansf., Bot. Jahrb. Syst. 60: 114. 1925. — Lectotype (designated by Veldkamp in Blumea 24: 438. 1979): *H.O. Forbes 708* (lecto BM [BM000944490!]; isolecto BM [BM001190923!], E [E00288097!], K [K000859576!], L [L0008844!, L0008845!, L0008847!, L0008848!], P [P02274803!]), Papua New Guinea, Central District, Sogeri Region, Mt Wori-Wori.
Creochiton divitiflorus Mansf., Bot. Jahrb. Syst. 60: 135. 1925. — Type: *C.L. Ledermann 9576* (holo B; iso L [L0008846!]), Papua New Guinea, East Sepik District, Etappenberg.
Creochiton schlechteri Mansf., Bot. Jahrb. Syst. 60: 134. 1925. — Type: *F.R.R. Schlechter 19234* (holo B; iso K [K000859577!, K000859578!], S!), Papua New Guinea, Kaiser Wilhelmsland, Jaduna.

Epiphytes or woody climbers, up to 20 m in height; branchlets terete, glabrous to furfuraceous, young ones more or less densely furfuraceous, up to 5 mm in diameter; nodes thickened. Leaves coriaceous, elliptic to oblong, apex acute, base cuneate; glabrous, dark green above, pale green below, midrib below brown furfuraceous, 7.2–13 × 2.4–6 cm; nervation with 1–2 pairs of main nerves arising above the base close to the margin; petiole sparsely furfuraceous, 10–13 mm long. Inflorescences axillary, umbellate to paniculate, up to 14 cm long, up to 35 flowers; main axis terete, furfuraceous; bracteoles coriaceous, obovate, glabrous outside, sparsely stellate furfuraceous inside, white or yellowish, 3–7 × 2–3 mm, enveloping the flower buds. Hypanthium campanulate, light green, sparsely stellate furfuraceous, 3–5 × 2–3 mm; calyx rim truncate, with distinct undulations, ca. 1 mm long; petals elliptic, apex acuminate, creamy, white or pinkish, ca. 9 × 6 mm. Stamens 8, equal;

filament flat, 3–4 mm long; anthers elongate, purplish, 4–5 mm long; connective with a sagittate crest, 0.5–1 mm long; lateral appendages absent; ovary glabrous, top concave, 2–3 mm long; style glabrous, ca. 6 mm long; extra-ovarial chambers not developed. Fruits subglobose, glabrous, 5–6 mm long, dark red turning bluish purple or black; seeds ca. 0.7 mm long.
Distribution — New Guinea.
Ecology & Habitat — Ridge forest at 175–2000 m elevation.
Vernacular name — *Marendekan* (Wagau).
Note — *Creochiton novoguineensis* differs from all congeners by: petioles 10–13 mm long, sparsely furfuraceous, leaves 7.2–13 cm long, base cuneate, underneath glabrous (but for midrib). Inflorescence paniculate, many-flowered, bracteoles completely covering the flower bud, 3–7 mm long, fleshy, and hypanthium sparsely stellate furfuraceous. Similar to *C. ledermannii* in the shape of 8 equal stamens, but differs in the shape of leaves and inflorescences. *Creochiton novoguineensis* has oblong glabrous leaves and paniculate inflorescences, while *C. ledermannii* has obovate leaves underneath densely tomentose and umbellate inflorescences. Contrary to the other species in New Guinea, *C. novoguineensis* has no developed extra-ovarial chambers. The leaves of this species sometimes have basal lateral main nerves close to the margin of the leaf (*Aet & Idjan 296*).
Specimen examined — **INDONESIA.** Papua: Yapen, Serui near Wamiami, *Aet & Idjan 296* (BO, L); Cycloop Mts., path Dozai-Dafonsoro, Baimungun, *van Royen & Sleumer 6365* (BO, L); Mamberamo River, *Docters van Leeuwen 9915* (BO, L). **PAPUA NEW GUINEA.** Morobe: Lae Subdistrict, Markham Point, *Stevens & Martin LAE 54749* (BO, L); Sogeri Region, Mt. Wori-Wori, *Forbes 708* (L, E).

10. *Creochiton pudibundus* (Blume) Blume — Fig. 2-2, Map 2-2

Creochiton pudibundus (Blume) Blume, Flora 14: 506. 1831; Naudin, Ann. Sci. Nat., Bot. sér. 3, 18: 154. 1852; Miq., Fl. Ned. Ind. 1(1): 560. 1855; Triana, Trans. Linn. Soc. London 28: 85. 1872; Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 604. 1891; Krasser in Engl. & Prantl, Nat. Pflanzenfam. 3, 7: 178, f. 77b, 1893; Koord., Exkurs.-Fl. Java 2: 693. 1912; Fl. Tjibodas 3: 212. 1923; Bakh.f., Contr. Melastom. 309. 1943; Fl. Java 1: 363. 1964. — *Melastoma pudibundum* Blume, Cat. Gew. Buitenzorg 71. 1823; Bijdr. Fl. Ned. Ind. 17: 1071. 1826; DC., Prodr. 3: 148. 1828. — *Diplectria pudibunda* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated here): *C.L. Blume s.n.* (lecto L [L0008850!]; isolecto BO!, K [K000859582!], L [L0537327!, L0008849!]), Indonesia, Java, G. Salak, Cicalobak.
Creochiton pudibundus (Blume) Blume var. *coriaceus* Naudin, Ann. Sci. Nat., Bot. sér. 3, 18: 154. 1852; Miq., Fl. Ned. Ind. 1(1): 560. 1855. — Type: *H. Zollinger 3196* (holo G-DC [G00316258!]; iso L!), Indonesia, Java.
Creochiton emarginatus Miq., Fl. Ned. Ind. 1(1): 561. 1855. — Type: *F.W. Junghuhn s.n.* (holo U [U0004002!]; iso L!), Indonesia, Java, Pengalengan.

Epiphytes, up to 1 m high, or climbers, ca. 30 m high; branchlets terete, glabrous to sparsely furfuraceous, 4.5–6.5 mm in diameter; nodes thickened with an interpetiolary ridge. Leaves coriaceous, ovate to elliptic, apex acute, base rounded or cuneate, glabrous above, midrib sunken above, sparsely puberulous to furfuraceous below, 7–10 × 3.7–5.8 cm; nervation plinerved with 2 pairs of main nerves arising from above the base; petiole glabrous to puberulous, terete, 8–15 mm long. Inflorescences axillary, umbellate with 4–7 flowers, 3–5 cm long; main axis terete, puberulous, 1.5–3 cm long; bracts ovate, densely stellate hairy, 2–3 mm long; bracteoles glabrous, obovate, cream, concave, enveloping the flower bud, 7–10

× 4–5 mm; pedicel sparsely stellate furfuraceous, ca. 5 mm long. Flower bud ca. 11 × 10 mm. Hypanthium campanulate, glabrous, rather angular, 2–4 × 2–3 mm; calyx rim truncate with 4 undulations, ca. 0.5 mm long; petals ovate, violet or red, glabrous, 6–13 × 6–7 mm. Stamens 8, equal; filament flat, ca. 7 mm long; anther elongate, 5–7 mm long; connective with a triangular crest, 0.5–1 mm long; lateral appendages absent; ovary globose, glabrous, ca. 3 × 2 mm; style glabrous, curved when mature, ca. 10 mm long; extra-ovarial chambers not developed. Fruits globose, glabrous, white, 3–5 × 4–6 mm; stalk glabrous 1.5–1.7 cm long; seeds 0.7–0.75 mm long.

Distribution — Java (west) and Sulawesi (southwest, southeast).

Ecology & Habitat — Edge of primary or secondary forest, edge of river or on a mountain slope at 1000–1400 m elevation.

Vernacular name — *Caluncung*, *Harendong areuy* (Sundanese for about any climbing Melastomataceae), *Harendong areuy putih*, *Harendong areuy merah*.

Note — *Creochiton pudibundus* is easily recognized by its coriaceous ovate to elliptic glabrous leaves, underneath sparsely puberulous to densely furfuraceous, axillary umbellate inflorescences, coriaceous, concave bracteoles. Similar to C. bibracteatus in the axillary umbellate inflorescence, number and shape of the stamens, but differs in the shape and indument of the leaves which in *C. bibracteatus* are thin, ovate and densely tomentose. *Creochiton ledermannii* differs by the small leaves with a retuse apex and a denser indument. Apparently not collected in Java after *Bakhuizen 5524* (13 June 1922).

Specimen examined — **INDONESIA.** West Java: Bogor, Mt. Salak in Kampong Babojong, *Koorders 24251β* (BO); *Ibid.,* above Gunung Bunder, *Backer 35201* (BO); *Ibid.*, Cianten, S of Leuwiliang, *Backer 25976* (BO); *Ibid.*, Pasir Pogor, SW of Masing, Pasir Dalem, *Bakhuizen van den Brink 5524* (BO, L); Jasinga, Pasir Cangkuwang, Cirarak, *de Voogd s.n.* (BO). Cianjur, NW of Sindanglaya, *Backer 21533* (BO). Bandung, Cigua Plantation, S of Cireungkas, *Backer 15169* (BO); Pengalengan, *Junghuhn s.n.* (L). South-East Sulawesi: Bukit Porema, *Kjellberg 2637* (BO). South Sulawesi: Pasui – Rante Lemo, *Kjellberg 1619* (BO). no specific location: *de Vriese s.n.* (BO, L). *Blume s.n.* (BO, L).

11. *Creochiton roseus* Merr. — Map 2-3

Creochiton roseus Merr., Publ. Bur. Sci. Gov. Lab. 29: 32. 1905; Enum. Philipp. Pl. 3: 191. 1923. — Type: *E.B. Copeland 1297* (holo PNH, probably lost; iso K [K000859579!], NY [NY00221643!], US!), Philippines, Mindanao, Davao District, Todaya.

Woody climbers, up to 6 m high; branchlets terete, sparsely furfuraceous, distally floccose, 2–3 mm in diameter; nodes thickened with an interpetiolary ridge. Leaves thin to subcoriaceous, ovate to elliptic, apex acute, base rounded to cuneate; above glabrous, below glabrescent, midrib densely furfuraceous, 6.2–9 × 3.2–4.5 cm; nervation plinerved with 1–2 pairs of main nerves arising from above the base; petiole densely furfuraceous, 1.5–2 cm long. Inflorescences axillary, 2–3 cm long, umbellate to paniculate, 3–5-flowered; main axis densely furfuraceous, 1–2.5 cm long; bracts not seen; bracteoles subcoriaceous, obovate to elliptic, veined, apex rounded, glabrous outside, densely stellate furfuraceous inside, enveloping the flower buds, 6–12 × 4–6 mm; pedicel 0.5–1 cm long. Hypanthium campanulate or urceolate, densely stellate furfuraceous, 3–5 × 2–3 mm; calyx rim truncate; petals elliptic, apex obtuse ca. 7 × 3–4 mm, bluish pink. Stamens 8, equal; filament flat, greenish, 4–4.5 mm long; anthers elongate, yellow, 4.5–5 mm long; connective with a triangular crest, purple, ca. 1 mm long; lateral appendages absent; ovary 3–4 mm long, glabrous, apex concave; style glabrous, greenish, 8–9 mm long; extra-ovarialchambers not developed. Fruits globose, depressed, 6–7 × 8–10 mm, green, glabrous; seeds 0.8–1 mm long.

Distribution — Philippines (Mindanao).
Ecology & Habitat — Primary forest at 800–1200 m elevation.
Vernacular name — *Isag* (Baguio).

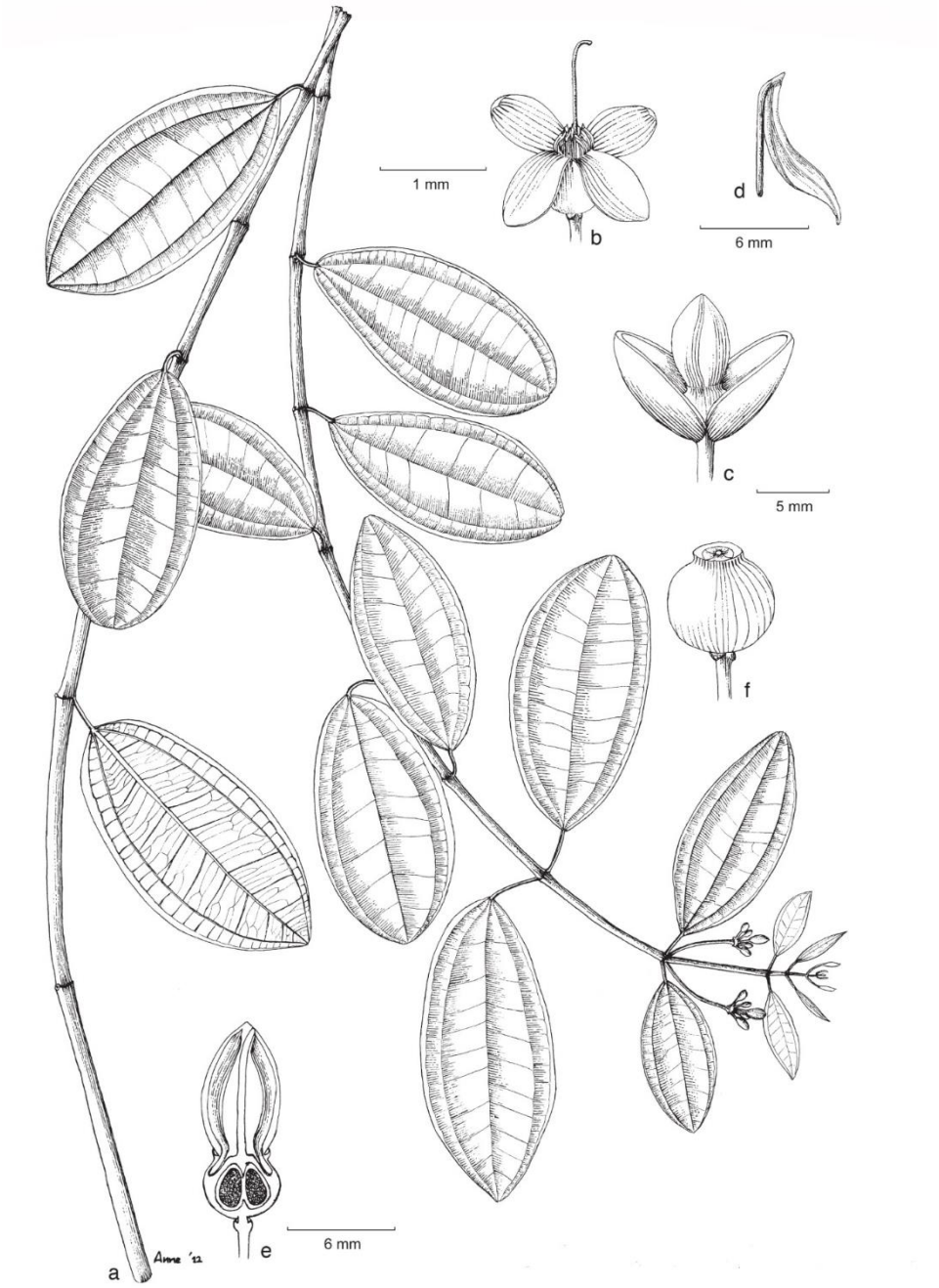


Fig. 2-2. *Creochiton pudibundus*. **a.** Habit; **b.** flower; **c.** flower bud with a pair bracteole; **d.** mature stamen; **e.** cross section of flower bud; **f.** fruit (**a**: *Backer 35201*; **b–e**: *Bakhuizen van den Brink 5524*; **f**: *Backer 15169*, all BO).

Note — *Creochiton roseus* is distinguished by its floccose branchlets, 3–5-flowered inflorescences, densely stellate furfuraceous hypanthium with a completely truncate calyx rim. *Creochiton dipterus* differs by the coriaceous leaves, and 4 small distinct teeth on the rim of the calyx. Another Philippine species, *C. bracteatus*, has thin bracteoles and only 4 stamens.
Specimen examined — **PHILIPPINES.** Mindanao: District of Davao, Todaya (Mt. Apo), *Elmer 10563* (BO, L); *Ibid.*, *Copeland 1297* (NY, US); Bukidnon, Mt. Candoon, *Ramos & Edaño BS38878* (BO, L); Mt. Katanglad, *Sulit PNH9924* (L); Zamboanga, *Merrill 8104* (L).

12. *Creochiton turbinatus* (J.F.Maxwell) Karton., **comb. & stat. nov.** — Map 2-5

Creochiton ledermannii Mansf. var. *turbinatus* J.F.Maxwell, Gard. Bull. Singapore 33: 323, t. 7. 1980, quoad typus. — Type: *BW 12260 (F.A.W. Schram)* (holo L [L0008841!]; iso A, BO!, BRI [BRI-AQ0060033!], CANB, K!, LAE, MAN), Indonesia, New Guinea, E of Sorong, Warsamson Valley, Asbakin.

Epiphytes; branchlets terete, glabrescent, innovations densely furfuraceous; nodes thickened with an interpetiolary ridge. Leaves coriaceous, ovate, apex acute, base rounded, above glabrous, light green, below glabrescent midrib densely furfuraceous, 4–6 × 2.2–3.1 cm; nervation plinerved with 1 pair of main nerves arising from above the base; petiole densely furfuraceous, 3–5 mm long. Inflorescences axillary, up to 5 cm long, umbellate, 2–5-flowered; main axis terete, densely furfuraceous; bracts ovate, glabrescent, ca. 2 × 1 mm; bracteoles coriaceous, orbicular, concave, glabrous, enveloping the flower buds, yellowish green, 5–7 × 3–4 mm; pedicel densely furfuraceous, 5–10 mm long. Hypanthium campanulate, glabrescent, 2–3 × 2 mm, calyx rim truncate; petals elliptic, 2–3 × 2 mm. Stamens 8, equal; filament flat, ca. 2 mm long; anthers elongate, 2–3 mm long; connective with a triangular crest, ca. 1 mm long; lateral appendages absent; ovary globose, 1–1.4 mm long, glabrous; style glabrous, ca. 4 mm long; extra-ovarial chambers shallow, 1/5 as long as the ovary. Fruits globose, glabrous, green, 4–6 × 3–4 mm, turbinate with 8 distinct lines; seeds ca. 0.5 mm long.
Distribution — New Guinea (West Papua).
Ecology & Habitat — Primary forest on humid sandy clay inundated in the wet season, riverbank, at 50–150 m altitude.
Vernacular name — *Apunengapok* (Waskuk).
Note — *Creochiton turbinatus* differs from all congeners by: petioles 3–5 mm long, leaves ovate, 2.2–3.1 cm wide, base rounded, apex acute, underneath glabrescent (but for midrib). The inflorescences are umbellate with orbicular bracteoles which completely cover the flower bud, 5–7 mm long, fleshy, glabrous. It differs from *C. ledermannii* by having glabrescent leaves with an acute apex, and the turbinate fruits. The umbellate inflorescences of *C. turbinatus* are not 3-, but 5-flowered. This species is only known from the type collected near Sorong in Indonesian New Guinea. The paratypes (*Hoogland & Craven 10735, Docters van Leeuwen 10382*) belong to *C. ledermannii*, because the leaves are densely tomentose and have a retuse apex.
Specimen examined — **INDONESIA.** West Papua: Sorong, Asbakin, Warsamson Valley, *Schram BW12260* (BO, L).

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CHAPTER 3

A revision of *Dissochaeta* (Melastomataceae, Dissochaeteae)

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A revision of *Dissochaeta* (Melastomataceae, Dissochaeteae)

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Abstract

Dissochaeta is a plant genus of woody climbers, classified in the tribe Dissochaeteae (Melastomataceae). The taxonomic history of the genus is complicated and includes some allied genera like *Dalenia*, *Diplectria*, *Macrolenes* and *Omphalopus*. Most of them are already regarded as synonyms of *Dissochaeta* except for *Macrolenes* which is considered a separate genus here as well. *Dissochaeta* is recognized by its scrambling habit, interpetiolar outgrowths, 4-merous flowers, dimorphic stamens and berry-like fruits. A taxonomic revision of *Dissochaeta* is presented, which includes references, a complete list of synonyms, detailed morphological descriptions of the species and an identification key, as well as information on the distribution, habitat and ecology, vernacular names, notes and lists of examined specimens. Fifty-four species and two varieties of *Dissochaeta* are recognized. We designate several lectotypes, propose eleven new combinations and we describe one new species and one new variety.

Keywords

Dissochaeta, *Macrolenes*, Melastomataceae, revision, Southeast Asia, taxonomy.

Introduction

Dissochaeta Blume is a genus of woody climbers found in Southeast Asia. The plants typically grow in open or secondary habitats, where they climb in small trees or shrubs. The genus is characterised by its scrambling growth habit, opposite phyllotaxy with interpetiolar outgrowths, terminal or rarely axillary inflorescences, 4-merous flowers, 2-whorls of dimorphic stamens and berry-like fruits. Some species are restricted both geographically and elevationally, while others are widespread. The genus *Macrolenes* Naudin closely resembles *Dissochaeta* and also consists of woody climbers with a scrambling habit, but differs in some vegetative and flowering aspects. Together with *Macrolenes*, *Dissochaeta* is included within Tribe Dissochaeteae (Naudin) Triana (Triana 1872; Cogniaux 1891; Bakhuizen van den Brink 1943; Maxwell 1984; Clausing & Renner 2001a). On the other hand, the genus is also considered as part of tribe Miconieae (Blume 1831a, 1831b; Don 1832; Endlicher 1840; Naudin 1851; Miquel 1855; Renner 1993). Taxonomic revisions for parts of the genus and its allies can be found in Bakhuizen van den Brink (1943), Veldkamp et al. (1979), Nayar (1980) and Renner et al. (2001b).

Taxonomic history

Dissochaeta was first proposed by Blume (1831a) and consisted of 15 species with eight of them split off from *Melastoma* L. (in its wide sense: Jack 1823; Blume 1826; De Candolle 1828). The word *Dissochaeta* is derived from the Greek word's "dissos", meaning double and "chaitè", meaning hair or bristle and alludes to the two filiform appendages at the base of the anthers (Backer 1936; Maxwell 1980a; Kartonegoro & Veldkamp 2010). This feature is present in most of the species, but absent in a few. Blume (1831a) proposed two sections in the genus, section *Dissochaeta* and section *Diplectria* Blume, which differ in the shape of the calyx tube, the appendages at the base of the anthers and the indumentum of the ovary apex. Section *Dissochaeta* has a cyathiform calyx tube, 4-dentate calyx lobes and an apically pubescent ovary, while section *Diplectria* has a cylindric calyx tube, truncate lobes and an ovary with a glabrous apex (Blume 1831a, 1831b). Section *Dissochaeta* was subdivided by Blume (1831a) into three informal groups, a) Tetrandrae, flowers with 4 stamens, without any staminodes; b) Octandrae flowers with 4 stamens, alternating with 4 staminodes; and c) Octandrae flowers with 8 fertile stamens (Maxwell 1980a; Kartonegoro & Veldkamp 2010).

Blume (1831a) also described the new genus *Aplectrum* Blume, comprising three species, which have an ovate-globose calyx tube and four stamens alternating with four staminodes. The anthers of *Aplectrum* were said to be inappendiculate, unlike the appendiculate anthers of *Dissochaeta* (Blume 1831a). Blume did not indicate the similarity/ difference between *Aplectrum* and *Dissochaeta* sect. *Diplectria*, which also has four staminodes alternating with four stamens. He also did not mention the position of the fertile and sterile stamens in relation to the position of the petals, a character later used to separate genera (Maxwell 1980a). Later, Reichenbach (1841) raised section *Diplectria* to genus level as *Diplectria*. Simultaneously with the establishment of *Dissochaeta* and *Aplectrum*, Blume (1831a) established *Marumia* Blume (=*Macrolenes*), also a woody climber, but different in having axillary inflorescences, persistent and long calyx lobes, eight fertile stamens and several filiform appendages at the base of the anthers.

Korthals (1844) accepted Blume's *Dissochaeta* and *Aplectrum* as distinct groups of woody climbing genera in Melastomataceae in his Netherland Indies (Indonesia) Melastomataceae account. He proposed a new woody climber genus, *Dalenia* Korth., which has similarities with *Dissochaeta*, but instead has a deciduous calyptra which encloses the petals before anthesis. Naudin (1851) included *Diplectria* in *Dissochaeta* and made a new division of the genus into two groups without any nomenclatural status, *Inermes* Naudin and *Bisetosae* Naudin, which differ from each other in lacking or having bristle appendages at the base of the anthers, respectively. The *Inermes* group has similarities with Blume's *Diplectria* and *Bisetosae* with Blume's *Dissochaeta*. Furthermore, Naudin (1851) maintained the genera *Aplectrum* and *Dalenia* and he also proposed a new genus, *Omphalopus* Naudin, with 3 species defined by having filaments attaching to the anthers in the middle (medifixed) and a tessellate surface of the locules (Naudin 1851).

The name *Aplectrum* is a later homonym of *Aplectrum* (Nutt.) Torr., already proposed by Torrey (1826) for a subgenus of *Corallorrhiza* (Orchidaceae) by Nuttal (1818). Therefore, Gray (1854) introduced the new name *Anplectrum* A.Gray as a valid genus name for Blume's *Aplectrum*, which was followed by Triana (1872) in his World Melastomataceae account by uniting all species of *Diplectria* and *Aplectrum* within *Anplectrum*.

Baillon (1877) divided *Dissochaeta* into nine sections: *Anoplodissochaeta* Baill., *Anplectrum* (A.Gray) Baill., *Creochiton* (Blume) Baill., *Dalenia* (Korth.) Baill., *Dicellandra* (Hook.f.)

Baill., *Eudissochaeta* Blume ex Endl. (invalid name for section *Dissochaeta*), *Omphalopus* (Naudin) Baill., *Oxyotandra* Baill. and *Sakersia* (Hook.f.) Baill. His broad circumscription of the genus also included the non-woody climbing genera *Creochiton* Blume (woody epiphyte), *Dicellandra* Hook.f. (herb to woody) and *Sakersia* Hook.f. (woody = *Dichaetanthera* Endl.) with *Dissochaeta*. The distribution of the genus also became wider, because *Dicellandra* and *Dichaetanthera* are African genera.

Cogniaux (1890, 1891), in his monograph of the family, accepted Triana's (1872) concept and rejected Baillon's generic classification (1877). He reinstated several genera and divided *Dissochaeta* into three sections, sect. *Diplostemones* Cogn. (invalid name, should have been section *Dissochaeta*; Kartonegoro & Veldkamp 2010), with a truncate or obscurely lobed calyx and eight stamens with elongate appendages; sect. *Isostemones* Cogn., with a similar calyx but with four stamens with elongate appendages; and sect. *Dissochaetopsis* Cogn., with long, linear to lanceolate, caducous calyx lobes and four straight stamens with short appendages. Cogniaux's classification of *Dissochaeta* and allied genera were adopted by Krasser (1893) except that he synonymized *Anplectrum* with the older genus *Diplectria*. The number of infrageneric taxa increased when Merrill (1917) proposed the new species *Dissochaeta glabra* Merr. and placed it in a new section *Disparistemones* Merr.

Bakhuizen van den Brink (1943), in his comprehensive work on the Melastomataceae of the Malay Archipelago (Malesian Region), did not adopt an infrageneric classification for *Dissochaeta*, quite unlike previous authors. Thus, he described some new species in *Dissochaeta* and established two new woody-climbing genera, *Backeria* Bakh.f. and *Neodissochaeta* Bakh.f., based on the small size of the calyx tube and the presence of narrow extra-ovarian chambers, respectively. Like Cogniaux (1890, 1891), he also maintained the genera *Dalenia* and *Omphalopus* as distinct genera. He discussed the possible illegitimate character of the name *Anplectrum*, which he considered to be a superfluous orthographic variant of *Aplectrum* (both bad Greek) and he preferred to regard *Diplectria* and *Backeria* as accepted names instead (Bakhuizen van den Brink 1943, 1964; Veldkamp et al. 1979).

Nayar (1966, 1969c) considered *Neodissochaeta* as a distinct genus and added some new species to it. The genus *Backeria* was also maintained by Raizada (1968), but he synonymised all species of *Diplectria* with it. However, since *Diplectria* is an older name than *Backeria*, *Diplectria* is the correct generic name (Veldkamp et al. 1979) in this circumscription.

Maxwell (1980a, 1980b) divided *Dissochaeta* into only three sections: sect. *Dissochaeta*, sect. *Anoplodissochaeta* and sect. *Omphalopus*. This separation is mostly based on floral characters, especially the stamens. Section *Dissochaeta* has well-developed calyx lobes (>2 mm long) and curved stamens, while sections *Anoplodissochaeta* and *Omphalopus* have undeveloped calyx lobes (<2 mm long) and straight stamens. Section *Omphalopus* differs from sect. *Anoplodissochaeta* by having tessellate-reticulate locules (vs. smooth ones) and medifixed anthers (vs. basifixed). In agreement with Bakhuizen van den Brink (1943) and Veldkamp et al. (1979), he also maintained *Diplectria* as a distinct genus allied to *Dissochaeta* with *Backeria* synonymised under it and he included *Dalenia*, *Neodissochaeta* and *Omphalopus* in *Dissochaeta*.

Results of molecular phylogenetic studies by Clausing & Renner (2001a) showed that a woody climbing or scrambling growth habit evolved only once in the Asian Melastomataceae. Based on that result, Renner et al. (2001b) recognised only the single genus *Dissochaeta*, with two other genera, *Diplectria* and *Macrolenes*, as synonyms. Renner et al. (2001b) ignored the differences in floral characters. *Macrolenes*, sister to *Dissochaeta*

(Clausing & Renner 2001a), differs from *Dissochaeta* in a unique combination of vegetative and floral characters (presence of a pair of hair cushions at the base of the lower leaf surface, axillary inflorescences, long and persistent calyx lobes and the anthers with several basal filiform appendages) and is, therefore, considered to be a distinct genus, separate from *Dissochaeta* (Bakhuizen van den Brink 1943; Nayar 1980; Maxwell 1984).

Circumscription of Dissochaeta proposed in this study

Diplectria is here considered to be a synonym of *Dissochaeta* since both genera have correlating floral characters with intermediates between the extreme forms. This concept of *Dissochaeta*, including *Diplectria*, was already pointed out by Backer (Bakhuizen van den Brink 1943), following Naudin's concept (Naudin 1851). *Dissochaeta* and *Diplectria* show a strong morphological similarity (Bakhuizen van den Brink 1943; Veldkamp et al. 1979; Maxwell 1984) in their scrambling habit and terminal inflorescences with 2–5 ramifications, but were distinguished based on floral characters like the position of the stamens and staminodes on the hypanthium (Veldkamp et al. 1979; Maxwell 1980b). According to Maxwell (1984), *Diplectria* differs from *Dissochaeta* in having four fertile stamens opposite the petals (oppositipetalous) and four staminodes alternate to the petals (alternipetalous). In contrast, in *Dissochaeta* the alternipetalous stamens are always fertile, while the oppositipetalous stamens are either fertile, staminodes or absent. Based on these differences, these two genera were even classified in two different subtribes, Diplectrinae J.F.Maxwell and Dissochaetinae Naudin (Maxwell 1980b, 1984). However, there are strong similarities between *Dissochaeta* and *Diplectria* in the structure of the stamens: their position in bud, connective appendages and the direction and shape of the alternipetalous stamens. The oppositipetalous stamens of *Diplectria* also similar to those of *Dissochaeta*. The shape and orientation of the oppositipetalous stamens in *Dissochaeta beccariana* Cogn., *Dissochaeta glandulosa* Merr., *Dissochaeta laevis* Ohwi ex J.F.Maxwell and *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell are similar to those of *Diplectria*. These four *Dissochaeta* species also have a pair of glandular patches abaxially on the base of the leaf blades, which is also found in several species of *Diplectria* and, therefore, they are considered as intermediate between the two genera and which are here regarded congeneric because of the resulting continuous morphological variation.

Dalenia was distinguished from *Dissochaeta* based on the presence of a calyptra enclosing the petals in bud (Korthals 1844; Naudin 1851; Miquel 1855; Triana 1872; Cogniaux 1890, 1891; Krasser 1893; Bakhuizen van den Brink 1943; Nayar 1966). The calyptra is in fact the hypanthium/calyx and it falls off when flowers are mature. Despite this calptriform hypanthium, the habit, position of the inflorescences, stamen characters and the baccate fruits are highly similar to those of *Dissochaeta* and *Diplectria* within the tribe Dissochaeteae (Nayar 1966). As the inflorescence position and the stamen characters are considered to be more important characters for the recognition of genera, the presence of the calyptra is regarded as a variation within the genus and *Dalenia* is considered as congeneric with *Dissochaeta* in this revision following Maxwell (1980b, 1984) and Renner et al. (2001b).

Omphalopus was also distinguished from *Dissochaeta* by its tessellate reticulate anthers with medifixed filament attachments (Naudin 1851; Miquel 1855; Triana 1872; Cogniaux 1890, 1891; Krasser 1893; Bakhuizen van den Brink 1943). This unusual insertion seems to be insufficient for separating the genus and since the habit, leaves arrangement, inflorecences, calyx tube and fruits resemble those of *Dissochaeta*, it may by considered as a synonym (Maxwell 1980b; Renner et al. 2001b; Kartonegoro & Veldkamp 2010).

Macrolenes was also known to have similar habit and ecological aspects with *Dissochaeta*. The genus also grows as woody climbers with a scrambling habit, but differs in some vegetative and flowering aspects with *Dissochaeta*. *Macrolenes* can be distinguished from *Dissochaeta* by a combination of some characters, e.g. axillary inflorescences (vs. mainly terminal in *Dissochaeta*), a pair hair cushion domatia on the base of abaxial leaves (vs. cushion domatia absent), longer and distinct calyx lobes (vs. mainly shorter and often indistinct calyx lobes) and several fimbriate, filiform appendages on the alternipetalous anthers (vs. only a pair of filiform, non-fimbriate appendages on the alternipetalous anthers). Some species of *Dissochaeta* have long calyx lobes, similar to those of *Macrolenes*, but they are usually erect, not reflexed and mostly fall off when fruiting. Based on those constant differences in morphological characters between two genera, here we agree to keep *Macrolenes* as a separate genus from *Dissochaeta*.

Fifty-four species and two varieties are recognised in this revision. Species delimitations are based on clear morphological discontinuities in more than a single character. Specific characters used for recognition are shown in the descriptions, notes and the key. We have not recognised subspecies, because no allopatric forms were found, but instead either described the infraspecific variation without any taxonomic categories or we recognised varieties when a character shows a discontinuity. An infrageneric classification is not (yet) included in this revision, a future better resolved phylogeny should form the basis for that.

Materials and methods

This revision is based on the analysis of gross morphological characters of *Dissochaeta* for which more than 2000 herbarium specimens were studied and for which the following herbaria are thanked for loans/facilities: ANDA, BM, BO, E, K, L, SING and U (abbreviations follow Thiers 2018). Additionally, the *Dissochaeta* collections in the databases and specimen images from A (http://kiki.huh.harvard.edu/databases/specimen_index.html), AAU, BISH (http://nsdb.bishopmuseum.org), BK, BR, BRI, C, CAS, CM, F, FI, G, GH, HBG (http://www.herbariumhamburgense.de/Data_Spermatophyta/index.php), KEP, MCU, MICH, MO, MPU, NY (http://sweetgum.nybg.org/science/vh), P, PH, PNH, S, TCD, US (http://collections.nmnh.si.edu/search/botany) and JSTOR Global Plants (http://plants.jstor.org) were also used. Investigation of morphological characters including indumentum, flowers and fruits was performed with binocular stereomicroscopes. The types of almost all names were examined either as actual specimens or as images. Morphological descriptions and measurements were made from dried specimens and fresh material with terminology following Bakhuizen van den Brink (1943), Nayar (1966, 1980), Veldkamp et al. (1979), Maxwell (1980a, 1984) and Renner et al. (2001b). Distribution maps were prepared using DIVA-GIS (http://www.diva-gis.org/). A list of selected examined specimens was prepared and listed under each species per country and, secondarily, per province or island. All examined specimens are also alphabetically listed together in a separate index.

Results

Morphology

Habit

All species of *Dissochaeta* are essentially woody climbers with a scrambling growth habit. This scrambling growth is also known for *Macrolenes* and some species of *Creochiton*

(Kartonegoro & Veldkamp 2013), but otherwise unknown within Old World Melastomataceae (Clausing & Renner 2001a). Most of the known species are reported to climb on to the branches of mainly small trees or shrubs, though sometimes they reach up to 30 m high (Fig. 3-1). The species do not scramble into big canopy trees, because they need open space to germinate and grow rather than dense shade. Due to their scrambling growth, individuals usually have thin branches with non-self-supporting, long internodes and pendent flowering and fruiting branches (Maxwell 1984; Clausing & Renner 2001a; Kartonegoro & Veldkamp 2010). In some species, adventitious roots are also common, which lignify and become hook-shaped structures after desiccation (Clausing & Renner 2001a).

Fig. 3-1. Habit of *Dissochaeta*. Photos by A. Kartonegoro (left) and D.S. Penneys (right).

Branchlets

The branchlets are usually terete and rarely angular, though, in some taxa angular branchlets become terete when older. The indumentum of the branchlets is variable, ranging from subglabrous, glabrescent or covered with sparse or dense stellate hairs with a punctate, furfuraceous, tomentose, or floccose appearance. In addition, some species also have short or long, dense, simple, glandular or eglandular bristle hairs. Mature branches are usually glabrescent.

Nodes

Nodes of all species bear some kind of large and swollen interpetiolar outgrowths (stipules are unknown in the family), which vary from just lines and ridges to crest-like and often annular outgrowths (Fig. 3-2). In some species, such a *D. glabra*, *D. glandiformis* J.F.Maxwell, *D. pulchra* (Korth.) J.F.Maxwell, *D. sarawakensis* and *D. stipularis* (Blume) Clausing, the interpetiolar outgrowth is conspicuous and wide, which may help climbing and stabilisation in the same way thorns or hooks do in other scramblers (Clausing & Renner 2001a). The indumentum of the nodes is similar to that of the branchlets, but denser.

Fig. 3-2. Nodes of *Dissochaeta*. **a.** *D. glabra* **b.** *D. macrosepala* **c.** *D. pulchra* **d.** *D. viminalis*. Photos by D.S. Penneys (**a, b**), J. Henrot (**c**), A. Kartonegoro (**d**).

Leaves

Like in most Melastomataceae, the phyllotaxis in *Dissochaeta* is opposite in one row (distichous, never decussate) with equal-sized (isophyllous) leaves. The shape is quite variable from ovate, elliptic to oblong or combinations of these within species. The apex usually is acuminate with a varying tip length. The margin is generally entire and becomes wavy when dry except for *D. pulchra* and *D. rectandra* Karton., which have a slightly serrulate margin. The leaf base varies between rounded, subcordate to shallowly cordate with distinct sinuses. The venation of the leaves is acrodromal with a midrib at the base and one or two pairs of major secondary (lateral) veins. Another pair of lateral veins also arises from the base and runs along or merges with the leaf margin and forms an intramarginal vein. In general, there are numerous secondary veins and a reticulate pattern of finer, higher order veins (Maxwell 1984). The main veins are usually sunken adaxial and raised on abaxial. Most species have a dark glossy, glabrous adaxial leaf surface except in some species, e.g. *D. hirsutoidea* Furtado, *D. porphyrocarpa* Ridl. and *D. rostrata* Korth., which are hispid and covered by sparse or dense bristle hairs. On the abaxial surface, the indumentum varies amongst the species from glabrous to stellate puberulous to furfuraceous, tomentose, floccose or setose with glandular or eglandular bristle hairs. Unfortunately, the leaves are usually not sufficient for definitive determinations and many species of *Dissochaeta* require flowers or fruits for identification because many vegetative characters are generally shared by two or more taxa.

A pair of peculiar thin-walled corky cushions at the base of the leaf blades on the abaxial surface, called “glandular patches”, are found in species like *D. beccariana*, *D. glabra*, *D. glandulosa* and *D. laevis*. This feature resembles a pair of hair cushions at the base of the leaf

blades on the lower surface in *Macrolenes*. Their function, if any and homology with domatia, are unknown (Maxwell 1984).

Petiole

The petioles are well developed in all species and are terete with a dorsal groove, which may give the impression of a flattened petiole. The indumentum is similar to that found on the branchlets except for being setose in *D. sarawakensis* and *D. stipularis*.

Inflorescences

The inflorescences are cymose and, in most species, they are terminal, multi-flowered raceme-like thyrses or panicles. Axillary inflorescences with few flowers are found in a few species: *D. acmura* Stapf & M.L.Green, *D. axillaris* Cogn. and *D. laevis*. *Dissochaeta annulata* Hook.f. ex Triana, *D. conica* (Bakh.f.) Clausing, *D. atrobrunnea* G.Kadereit and *D. viminalis* (Jack) Clausing sometimes have terminal and axillary inflorescences. Terminal inflorescences are usually panicles with reduced leaves on the proximal nodes of the axis (Maxwell 1984). The length of the terminal inflorescences varies from 10–16 cm (*D. biligulata* Korth.) to up to 90 cm (*D. glabra*). The rachis is usually angular or 4-angled instead of being terete and the nodes and indumentum are similar to those on the branchlets except in *D. sarawakensis* and *D. stipularis*. Ramifications of the panicles can be up to 5 orders and the branching within it is decussate with 3-flowered cymules terminating each terminal ramification (Maxwell 1984). The central flower of the terminal cymules usually has a longer pedicel than the two lateral ones, which are, in fact, the last order of ramification. In most species, the central flower of the cymules will mature and open first, followed by the two lateral ones, which bloom simultaneously. Likewise, for most members of the family, the flowers are actinomorph and epigynous. Here, they are also 4-merous with similar size of the petals.

Bracts and bracteoles

Bracts and bracteoles are present in all species even though some of them fall off before anthesis (Maxwell 1984). In this revision, bracts are pairs of leaf-like organs opposite at each node at every ramification level of the inflorescences, whereby the bracts on the primary axes nodes are the largest and the size gradually diminishes with each higher node. Bracteoles are recognised as an appendage or leaf-like structure subtending the base of each pedicel and are found only basal to the lateral flowers of the terminal 3-flowered cymules. The shape of bracts and bracteoles is also of taxonomic value, because it varies between minute, subulate, linear, lanceolate, ovate and suborbicular. Distinct bracteoles are found in *D. beccariana*, *D. bracteata* (Jack) Blume and *D. glandulosa*, which sometimes enclose flowers buds.

Hypanthium and calyx

Like in most Melastomataceae, the receptacle forms a tube, the hypanthium, with calyx lobes at the apex, alternating with whorls of petals and stamens (Hansen 1984). The shape of the hypanthium varies from campanulate, urceolate, tubular to cyathiform or funnelform and can be terete or angular. The size of the hypanthium also varies from small (2–4 mm long) in *D. biligulata*, *D. glabra* var. *glabra* and *D. gracilis* (Jack) Blume to large (8–10 mm long) in *D. axillaris*. The indumentum of the hypanthium ranges from glabrous to stellate-furfuraceous to tomentose to floccose with or without scattered to dense bristle hairs. This indumentum is important to identify certain species (Maxwell 1984). The presence of eight vertical ridges on the hypanthium is typical for species like *D. leprosa* (Blume) Blume, *D. pallida* (Jack) Blume and *D. spectabilis* J.F.Maxwell.

There are four calyx lobes, but these are not always visible as the calyx of most species may be truncate, undulate or have four small points. Calyx lobes can be rounded or triangular as in *D. annulata*, *D. atrobrunnea* and *D. leprosa* or can be linear to long, lanceolate as in *D. johorensis* Furtado, *D. macrosepala* Stapf and *D. porphyrocarpa*. The lobes are important for identification. The indumentum of the calyx lobes is similar to that of the hypanthium.

Petals

As the flowers are 4-merous, four free petals are commonly present. The petals are usually contorted in bud and overlap. The petal bud is always conical with an acute or acuminate tip, but some are rounded in *D. fallax* (Jack) Blume. The petals are thin, conspicuous, symmetric and colourful. Even though the colour of the petals generally has very little taxonomic value, in some cases the constant colour of the petals is useful to distinguish the species. The most frequent shapes are ovate, obovate and suborbicular with rounded or obtuse to acute tips and a clawed base. In a few species, the margin and tip of the petals are somewhat bristly, e.g. *D. hirsutoidea*, *D. johorensis*, *D. malayana* Furtado and *D. porphyrocarpa*. The petals are reflexed or erect.

Stamens

The stamens provide the best taxonomic characters for identification (Kartonegoro & Veldkamp 2010). In most species, 8 heterantherous stamens are usually present in two, dimorphic staminal whorls, an outer, alternipetalous and an inner, oppositipetalous one (Maxwell 1984; Kartonegoro & Veldkamp 2010). The alternipetalous stamens are known as the pollinating stamens and the oppositipetalous (alternisepalous) ones are the feeding stamens (Kadereit 2006; Kartonegoro & Veldkamp 2010). Most species have 8 fully developed and complete fertile stamens; in some species only 4 fertile stamens developed with the other 4 stamens being staminodial or absent.

The filaments are well-developed, flattened, glabrous and uniform in shape. Their length and orientation vary with the stage of maturity of the stamens. The filaments originate at the same level below the inner margin of the hypanthium. In both anther types (alternipetalous and oppositipetalous) before anthesis, the filaments are abaxial (facing outside) and the anthers adaxial (facing towards the inside) (Fig. 3-3I,II). The filaments alternating with the petals are straight and the point of attachment with the anthers distinct, while those opposite the petals are sharply bent and incurved before reaching the rather indistinct point of attachment with the anthers. Distally there is a sharp bend shortly below the attachment to the anther, the stipopodium (Fig. 3-3; Veldkamp et al. 1979). When dissecting the filament, it disarticulates and breaks here easily, although the “natural” point of breakage is apparently between the stipopodium and the connectival area of the basal crest and lateral appendages (Veldkamp et al. 1979). The attachment of the filament to the anther is usually near the base (basifixed) except in *D. fallax* where the filament is inserted in the middle part of the anther (medifixed). In bud, the stamens are inserted at the inner margin of the hypanthium, either in the extra-ovarial chambers or not.

The anthers are elongate, subulate and glabrous and open distally with a single pore. In mature flowers, they reverse their orientation by bending upwards and become less apical to the filaments. Filaments become longer and curve sideways or straight upwards. The stipopodium of mature oppositipetalous stamens becomes flexed to sinuate and leaves a scar-line, thus the filament and anther are not in parallel alignment (Maxwell 1984). The anthers here are more or less hook- to S-shaped, while the alternipetalous anthers are usually curved, sickle-shaped (Fig. 3-4a). In a few species, the orientation of all anthers is straight, e.g. *D.*

bakhuizenii Veldkamp, *D. inappendiculata* Blume and *D. vacillans* (Blume) Blume (Fig. 3-4b). The oppositipetalous anthers are usually thicker and shorter than the alternipetalous ones. Their thecae are smooth and glabrous except in *D. fallax* where they are tessellate-reticulate.

Fig. 3-3. Stamens of *Dissochaeta* in bud. **I.** facing outside; **II.** facing inside; **III.** separated stamens, alternipetalous (left); oppositipetalous (right). **a.** filaments; **b.** thecae; **c.** point of attachment oppositipetalous stamens with filaments; **d.** stipopodium; **e.** point of attachment alternipetalous stamens with filaments; **f.** basal crest. Photos by A. Kartonegoro (**I**) and D.S. Penneys (**II, III**).

Fig. 3-4. Mature flowers with mature stamens. **a.** curved anthers (*D. bracteata*); **b.** straight anthers (*D. inappendiculata*). Photos by D.S. Penneys (**a**) and A. Kartonegoro (**b**).

The connective of the alternipetalous anthers can be sterile, without thecae, in the basal part. This sterile zone is the pedoconnective and is found in some Melastomataceae and varies in size relative to the size of the stamens (Kadereit 2006; Wong 2016). In the oppositipetalous anthers, a pedoconnective is rare or not developed. The base of the pedoconnective usually has basal appendages (basal crest), which are membranous and triangular, hastate, oblong or ligular in shape. Lateral appendages are solitary or paired, filiform to ribbon-like and sometimes divided at the tip (Kartonegoro & Veldkamp 2010). The two appendages in oppositipetalous anthers extend from the lower part of the thecae and are adaxially bifid, ligular, or have spuriform appendages and, laterally or basally, there may or may not be a pair of filiform appendages.

Pollen

Although the stamens of *Dissochaeta* are diverse and display many different shapes and orientations, the pollen is uniform and is not of much taxonomic use. It has been described as 3-colpate with the colpi alternating with three pseudocolpi, prolate, 14–20 × ca. 11 µm, with a psilate or smooth exine (Maxwell 1984).

Staminodes

Staminodes are found in several species of *Dissochaeta*. Species included in *Diplectria* by Bakhuizen van den Brink (1943), Veldkamp et al. (1979) and Maxwell (1984) have staminodes in alternipetalous stamen whorl. They have anthers with undeveloped thecae, which are terete, ligular or triangular and infertile and lack the pedoconnective. However, the filaments, basal crest and lateral appendages are well developed, similar to the fertile alternipetalous stamens that are present in many species. These staminodes are functional in order to increase the attraction of the flowers by their colourful appendages and they might signal a large amount of available pollen (Kadereit, person. comm.). Oppositipetalous staminodes are different and have small thecae, ± ⅓ of the length of the alternipetalous ones

with minute or well-developed connective appendages and with or without lateral appendages. Differing from those previously, it seems that these staminodes are just stamen rudiments without function (Kadereit, person. comm.).

Gynoecium

The height of the ovary ranges from about ⅓ to nearly the length of the hypanthium. The ovary is glabrous, villous or has several bristly hairs at the tip where it joins with the style. The ovary apex is usually rounded or conical to mammiform in a few species, like *D. bakhuizenii* and *D. nodosa* Korth. The placentation in *Dissochaeta* is similar to that of the other genera in the tribe (except for a few *Creochiton* species, Kartonegoro and Veldkamp 2013), with a single placenta in each of the four locules, axillary attached to the middle of the central column. The style in bud is straight, but slightly curved at maturity, especially at the apex. The curved orientation of the mature style is usually opposite to that of the filaments. In the heterantherous species like *D. divaricata* (Willd.) G.Don, *D. glabra* and *D. viminalis*, the filaments of the two whorls are bent differently (Kadereit, person. comm.). The style is glabrous except in a few species where it is pubescent. The stigma of all species is capitate, but minute and inconspicuous.

Extra-ovarial chambers

Between the hypanthium and the ovary, there are usually septa which form between the chambers. These chambers are known as extra-ovarial chambers and the stamens develop from here (Bakhuizen van den Brink 1943; Hansen 1984; Maxwell 1984; Kartonegoro & Veldkamp 2010). The number and depth of these extra-ovarial chambers depend on the number and size of the fertile stamens. Usually, there are 4 or 8 chambers, which vary from shallow to reaching the base of the ovary (Kartonegoro & Veldkamp 2010). The depth of the chambers was used by Bakhuizen van den Brink (1943) to separate *Backeria* and *Neodissochaeta* from *Dissochaeta*.

Fruits

The fruit in Tribe Dissochaeteae, including *Dissochaeta*, is baccate (berry) with mainly a subglobose, ovoid to urceolate shape. The indumentum resembles that of the hypanthium. The colour is green at first, then becomes dark blue to purple when ripe. Some species like *D. biligulata* and *D. gracilis* have 8 distinct lines on the surface of the fruits, while in *D. leprosa* and *D. spectabilis*, 8 ridges are also common. When fruiting, the remnants of the calyx lobes are sometimes persistent in an erect or downward reflexed position or they fall off. Seeds have a cuneate shape, are smooth and flat-topped.

Distribution and ecology

Dissochaeta is distributed in South China to Southeast Asia, mainly the Malesian region, including the Nicobar Islands (India) (Map 3-1). It is found north and south of the equator along the Southeast Asian tropical rainforest belt but is absent in the eastern part of the Lesser Sunda Islands (Flores, Sumba and Timor). Borneo is the centre of diversity of the genus with 26 species of which 17 are endemic. From the Philippine Islands to New Guinea, the number of taxa and their abundance declines. The occurrence of the genus in mainland India is questionable (see note under *D. divaricata*).

Dissochaeta is found mostly in tropical evergreen and perpetually wet forest with little or no seasonal variation in temperature and rainfall (Maxwell 1984). The species are found predominantly in secondary vegetation or more open places within the primary vegetation,

such as tree fall gaps, river margins and roadsides. They climb several metres high and produce their flowering and fruiting branches over the tops of trees and larger shrubs. The genus has nodes which bear large interpetiolar outgrowths, which may help climbing and stabilisation in the same way thorns or hooks do in other scramblers (Clausing & Renner 2001a). According to Clausing & Renner (2001a), *Dissochaeta* has a faster growth rate than other scramblers and often outcompetes them. The climbing habit is reflected in the very wide wood vessels for hydraulic conductivity and thin-walled fibres for limited mechanical support (Van Vliet 1981). These woody climbers apparently only flower when mature and only on the branchlets which are in an exposed, open position. Branchlets that are not exposed to direct sunlight, regardless of their maturity or height in the forest, do not produce flowers (Maxwell 1984). The majority of species and varieties revised here are confined to lowland and hilly areas up to 1500 m elevation; however, some taxa are restricted to lowland or montane forest. Some species from the lowland forest are usually found in mixed dipterocarp forest, heath forest or swampy forest. Species occuring in montane forest are *D. alstonii* M.P.Nayar, *D. celebica* Blume, *D. intermedia* Blume, *D. leprosa*, *D. marumioides* Cogn., *D. nodosa*, *D. rectandra* and *D. spectabilis*, which can reach from 1200 to 2500 m elevation. There is no specific flowering and fruiting season, the species flower and fruit throughout the year. Some taxa, like *D. biligulata* and *D. gracilis*, sometimes have flowers and fruits together in the same inflorescence. Individual mature plants that reach the canopy or another suitable open area, regularly flower and fruit, but concurrently with many other individuals of the same species. This suggests that flowering and fruiting may be random, but is perhaps cyclic and may, therefore, be regulated by various environmental factors (Maxwell 1984).

Taxonomic treatment

Dissochaeta Blume

Dissochaeta Blume, Flora 14: 492. 1831. — *Dissochaeta* sect. *Dissochaeta* Blume, Flora 14: 493. 1831. — *Dissochaeta* sect. *Eudissochaeta* Blume ex Endl., Gen. Pl. 1219. 1840, *nom. inval.* — *Dissochaeta* sect. *Diplostemones* Cogn. in Boerl., Handl. Fl. Ned. Ind. 2: 533. 1890, *nom. superfl.* — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 128. 2010): *Dissochaeta vacillans* (Blume) Blume.

Dissochaeta Blume sect. *Diplectria* Blume, Flora 14: 501. 1831. — *Diplectria* (Blume) Rchb., Deut. Bot. Herb.-Buch. 174. 1841. — Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Diplectria cyanocarpa* (Blume) Kuntze [= *Dissochaeta divaricata* (Willd.) G.Don].

Aplectrum Blume, Flora 14: 502. 1831 [non Torr. 1826], *nom. inval.* — Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Aplectrum viminale* (Jack) Blume [= *Dissochaeta viminalis* (Jack) Clausing].

Dalenia Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 243. 1844. — *Dissochaeta* sect. *Dalenia* (Korth.) Baill., Hist. Pl. 7: 51. 1877. — Type: *Dalenia pulchra* Korth. [= *Dissochaeta pulchra* (Korth.) J.F.Maxwell].

Omphalopus Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851. — *Dissochaeta* sect. *Omphalopus* (Naudin) Baill., Hist. Pl. 7: 51. 1877. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 118. 1943): *Omphalopus fallax* (Jack) Naudin [= *Dissochaeta fallax* (Jack) Blume].

Anplectrum A.Gray, U. S. Expl. Exped., Phan. 1: 597. 1854, *nom. nov.* for *Aplectrum* Blume, [non. Torr. 1826]. — *Dissochaeta* sect. *Anplectrum* (A.Gray) Baill., Hist. Pl. 7: 51. 1877. — Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Anplectrum viminale* (Jack) Triana [= *Dissochaeta viminalis* (Jack) Clausing].

Backeria Bakh.f., Contr. Melastom.: 130. 1943, *nom. superfl.* — Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Backeria viminalis* (Jack) Bakh.f. [= *Dissochaeta viminalis* (Jack) Clausing].

Neodissochaeta Bakh.f., Contr. Melastom.: 134. 1943, *nom. superfl.* — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 128. 2010): *Neodissochaeta gracilis* (Jack) Bakh.f. [= *Dissochaeta gracilis* (Jack) Blume].

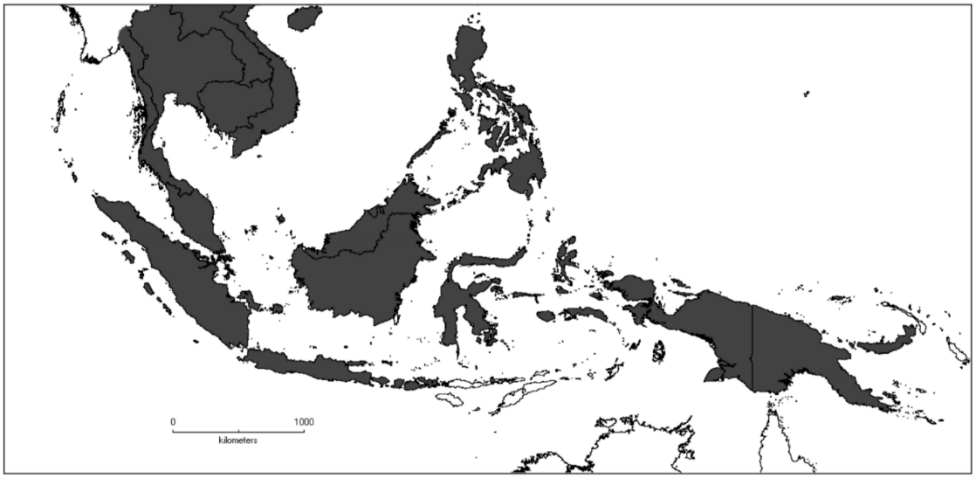
Melastoma auct. non Burm. ex L.: Jack, Trans. Linn. Soc. London 14: 3. 1823; Blume, Bijdr. Fl. Ned. Ind. 17: 1067. 1826. *p.p.*, excl.type.

Woody climbers, scrambling; bark greyish, tan to light brown, finely fissured. Branchlets terete or subangular; glabrous to tomentose or floccose with minute stellate or simple glandular or eglandular bristly hairs; sometimes with adventitious roots; nodes swollen with an interpetiolar annular line, ridge or crest, annular or pectinate. Leaves opposite; petioles terete, rarely flattened with a dorsal groove, glabrous to tomentose or with bristly hairs; blades membranous, subcoriaceous or rarely chartaceous with acrodromal venation, ovate to lanceolate, rarely suborbicular, base rounded to cordate, margins entire, rarely serrulate, apex acute to acuminate, midnerve with 1 or 2 pairs of lateral veins and 1 pair of intramarginal veins, secondary venation reticulate; nerves typically sunken adaxially, raised abaxially; adaxial side glabrous, rarely with scattered simple bristle hairs, abaxial side glabrous to densely brown tomentose or with dense bristle hairs. Inflorescences terminal, or rarely axillary, many-flowered, thyrses with 2 to 5 ramifications, decussate, ending with 3-flowered cymules; main axis quadrangular, indumentum similar to that of the branchlets; bracts and bracteoles distinct or minute, linear to ovate, glabrous to densely tomentose, mostly inconspicuous and early caducous; pedicels glabrous to tomentose, sometimes with bristle hairs, longer in central flower, shorter in lateral ones. Flowers 4–merous. Hypanthium campanulate, urceolate, tubular or cyathiform, glabrous to densely tomentose, with or without bristle hairs, often with 4 or 8 vertical ridges; calyx lobes truncate or with distinct rounded, triangular or lanceolate lobes, glabrous or with scattered bristle hairs to nearly densely tomentose; petals in bud conical or rounded, tubular or angular, tip rounded to acute or acuminate, contorted; mature petals ovate, obovate or suborbicular, reflexed or not, apex acute or obtuse, base thin, truncate to clawed, symmetric, glabrous, sometimes with appressed hairs at base and apex or margins puberulous. Stamens 4 or 8, heterantherous when 8, alternipetalous and oppositipetalous or 4 alternipetalous only, smooth or tessellate-reticulate, beaked or not, with terminal pore; filaments flattened, straight or curved sideways; anthers basifixed, sometimes medifixed; the alternipetalous ones thinner, when mature straight or curved and sickle-shaped, at base forming a pedoconnective, sometimes locule not developed and of being staminodal, basal crest membranous, triangular, sagittate, hastate or ligular, with or without paired filiform lateral appendages; the oppositipetalous ones thicker, when mature straight or curved with hooked or S-shaped, connective ridge with erose, bifid or spur-like appendages, basally with or without filiform appendages, sometimes reduced and staminodial less than ⅓ as long as the alternipetalous or absent. Ovary ⅓ to nearly as long as the hypanthium, apex glabrous to densely villous, sometimes with scattered bristle hairs, 4-locular; style straight or curved and hooked at the tip when mature; stigma minute, capitate; ovary concrescent with the hypanthium, with or without 4 or 8 longitudinal septa forming extra-ovarial chambers for the anthers, shallow to reaching to the base of the ovary. Fruits baccate, globose, ovoid to urceolate, dark blue or purple when mature, sometimes with four prominent erect or reflexed calyx remnants, glabrous to floccose; some with distinct vertical ridges. Seeds numerous, cuneate, smooth, flat-topped.

Distribution — The genus has 54 species and two varieties which are distributed in South China to South–East Asia, mainly in the Malesian Region (Map 3-1). It is present in South China (Hainan; Chen & Renner 2007), Myanmar, Indochina (Cambodia, Laos and Vietnam), the Nicobar Islands, Thailand and throughout Malesia except for the eastern part of the Lesser Sunda Islands (Flores, Sumba and Timor). Borneo is the centre of its distribution with almost 50% of the species. Some species also have a restricted distribution.

Ecology — The genus is found predominantly in secondary vegetation or more open places within the primary vegetation, such as tree fall gaps, river margins and roadsides (Kadereit 2006) in evergreen forest, mixed dipterocarp forest, heath forest, hilly forest, swamp forest and montane forest. The plants climb several metres high and produce their flowering and fruiting branches over the tops of small trees and larger shrubs at the end of branches that are in the open.

Notes — From its inception in 1831, several authors created infrageneric classifications (Blume 1831a, 1831b; Endlicher 1840; Naudin 1851; Miquel 1855; Baillon 1877; Cogniaux 1890, 1891; Krasser 1893; Merrill 1917; Maxwell 1980b), which were based on floral characters that are highly variable. Therefore, we here refrain from using an infrageneric classification until a phylogenetic analysis shows the various clades that can be recognized morphologically.



Map 3-1. Distribution of *Dissochaeta* (grey).

Key to species of *Dissochaeta*

1 Nodes of branchlet swollen with a raised prominent annular crest-like, collarshaped, pulvinate or pectinate interpetiolar ridge, more than 2 mm in length from base 2
1 Nodes of branchlet swollen with a line or raised interpetiolar ridge, less than 2 mm in length from base 16
2 Interpetiolar ridge with pectinate appendages, apex acute, up to 10 mm long from base and ca. 1 mm wide, pointing upwards and downwards from base [Borneo] ..... **31. *D. latifolia***
2 Interpetiolar ridge with annular crest-like, collar-shaped or pulvinate appendages, pointing horizontally, 3–6 mm long from base and as wide as nodes 3
3 Branchlets and leaf blades abaxially glabrous to stellate-puberulous or – punctate 4
3 Branchlets and leaf blades abaxially densely stellate-furfuraceous to tomentose 15

4 Leaf blades underneath glabrous, with a pair of glandular patches at base in the axil of the lateral nerve 5
4 Leaf blades underneath glabrous or stellate-puberulous or -punctate, without a pair of glandular patches at base in the axil of the lateral nerve 11
5 Inflorescences 30–90 cm long; anthers of alternipetalous stamens with undeveloped thecae, staminodes flattened 6
5 Inflorescences 10–25 cm long; anthers of alternipetalous stamens with developed thecae, fertile, rostrate [Borneo] 7
6 Inflorescences up to 90 cm long with 4 or 5 ramifications; hypanthium cyathiform-tubular; staminodes with a triangular basal crest, base emarginate or hastate, up to 2 mm long [Borneo] ..... **20. *D. glabra***
6 Inflorescences 30–35 cm long with 3 or 4 ramifications; hypanthium suburceolate; staminodes with a triangular basal crest, base emarginate or hastate, ca. 1 mm long [New Guinea] ..... **40. *D. papuana***
7 Leaf blades membranous, ovate or suborbicular, margin slightly serrulate; petal bud enclosed within a calyptra showing constriction with hypanthium ..... **43. *D. pulchra***
7 Leaf blades subcoriaceous, ovate to elliptic, margin entire; petal bud not enclosed within a calyptra 8
8 Bracts linear; bracteoles subulate, stellate-furfuraceous, 0.5–1 mm long 9
8 Bracts elliptic to oblong; bracteoles ovate to oblong, glabrous, whitish, 6–14 mm long 10
9 Branchlets and interpetiolar crest densely covered with simple 1–2 mm long bristle hairs; leaf base subcordate; inflorescences terminal; hypanthium campanulate, 2–3 mm long ..... **49. *D. sarawakensis***
9 Branchlets and interpetiolar crest glabrous; leaf base rounded; inflorescences terminal and axillary; hypanthium cyathiform, cup-shaped, 3–4 mm long ..... **30. *D. laevis***
10 Bracteoles ovate, 6–8 mm long; hypanthium tubular 4–7 × 2–3 mm, calyx lobes truncate with undulate tip; fruits subglobose to ovoid, 5–8 × 3–6 mm ..... **9. *D. beccariana***
10 Bracteoles oblong to lanceolate, ca. 14 × 3–4 mm; hypanthium campanulate 5–6 × 4–5 mm, calyx lobes truncate, level; fruits urceolate, ca. 10 × 6 mm ..... **22. *D. glandulosa***
11 Leaf blades abaxially stellate puberulous or punctate; calyx lobes truncate with widened undulate tip; alternipetalous stamens fertile, anther thecae lanceolate, pedoconnective developed 12
11 Leaf blades abaxially glabrous; calyx lobes truncate with erect apiculate tip, 0.3–0.5 mm long; alternipetalous stamens staminodial, thecae undeveloped, flattened, 0.5–4 mm long, pedoconnective not developed 13
12 Leaf blades underneath stellate-puberulous, 3–5.25 cm wide; calyx lobes ca. 1 mm long; alternipetalous stamens with thecae 4–5 mm long, pedoconnective ca. 0.5 mm long, lateral appendages absent; ovary with puberulous apex ..... **7. *D. bakhuizenii***
12 Leaf blades underneath stellate-punctate, 5–9.2 cm wide; calyx lobes 1–1.5 mm long; alternipetalous stamens with thecae 7–8 mm long, pedoconnective 1.5–2 mm long, lateral appendages paired, filiform, 2–2.5 mm long; ovary with pubescent and bristly apex [Peninsular Malaysia] ..... **45. *D. rectandra***
13 Leaf blades ovate; petiole glabrous and dorsally with bristle hairs; hypanthium urceolate, glabrous [Borneo] ..... **37. *D. micrantha***
13 Leaf blades elliptic to elliptic-oblong; petiole densely brown stellate-furfuraceous and covered with scattered or dense bristle hairs; hypanthium cyathiform, tubular or campanulate, densely furfuraceous or pubescent 14

14 Interpetiolar ridge and petioles densely covered with erect, thick, 4–6 mm long bristle hairs; leaf blades membranous; bracts oblong-lanceolate, margin ciliate; hypanthium tubular-campanulate [Borneo] ..... **36. *D. maxwellii***
14 Interpetiolar ridge and petioles sparsely covered with slender, ca. 2 mm long bristle hairs; leaf blades subcoriaceous; bracts linear, margin not ciliate; hypanthium tubular-cyathiform [Peninsular Malaysia, Sumatra, Java, Borneo, Palawan] ..... **52. *D. stipularis***
15 Leaf blades subcoriaceous, ovate to suborbicular, nervation with 1–2 pairs of lateral nerves; calyx lobes truncate with indistinct apex; petal bud enclosed with calyptra showing constriction with hypanthium [Borneo] ..... **42. *D. pubescens***
15 Leaf blades membranous, ovate-elliptic, nervation with 1 pair of lateral nerves; calyx lobes distinct with 2–2.5 mm long triangular or rounded apex; petal bud not enclosed with calyptra [Sumatra] ..... **21. *D. glandiformis***
16 Branchlets, petioles, inflorescence axes, hypanthium and fruits covered with dense or scattered simple erect or curved bristle hairs 17
16 Branchlets, petioles, hypanthium and fruits not covered with dense or scattered simple erect or curved bristle hairs 27
17 Calyx lobes triangular or truncate with a slightly triangular apex, 1–3 mm long 18
17 Calyx lobes linear-lanceolate, 3–11 mm long 25
18 Leaf blades densely covered with bristle hairs on both sides 19
18 Leaf blades devoid of bristle hairs on both sides or covered only on midnerve underneath 23
19 Bracts and bracteoles oblong, sparsely stellate-puberulous, densely bristly only along the margin [Borneo] ..... **46. *D. rostrata***
19 Bracts and bracteoles linear, densely stellate-furfuraceous and densely bristly on both surfaces 20
20 Hypanthium campanulate or tubular, 4–5.5 mm long; fruits subglobose, 4–6 mm long 21
20 Hypanthium suburceolate, 6–10 mm long; fruits subglobose, 8–10 mm long 22
21 Bristles on branchlets capitate (apex glandular); leaf blades coriaceous; calyx lobes 2.5–3 mm long; petal buds glabrous at tip; calyx remnant in fruits reflexed [Sumatra] .... **2. *D. alstonii***
21 Bristles on branchlets not capitate (apex eglandular); leaf blades membranous; calyx lobes ca. 1 mm long; petal buds bristly at tip; calyx remnant in fruits erect [Borneo] .... **25. *D. hirsutoidea***
22 Hypanthium 5–6 × 2–2.5 mm, calyx lobes with acute apex, up to 2 mm long; petal buds glabrous at tip [Peninsular Malaysia & Riau Archipelago] ..... **29. *D. johorensis***
22 Hypanthium 8–10 × 3–4 mm, calyx lobes with undulate apex, up to 1.5 mm long; petal buds bristly at tip [Peninsular Malaysia] ..... **34. *D. malayana***
23 Branchlets covered with minute stellate hairs and dense dark red-brown bristle hairs; nodes thickly covered with stellate hairs and thick brown bristle hairs; bracteoles subulate, densely bristly; stamens with minute basal crest, less than 1 mm long (Borneo) – Inflorescences terminal and axillary [Borneo] ..... **5. *D. atrobrunnea***
23 Branchlets covered with minute stellate hairs and scattered bristle hairs; nodes without bristle hairs; bracteoles oblong or lanceolate, lacking bristle hairs; stamens with triangular or ligular basal crest, 1–4 mm long – Inflorescences terminal 24
24 Leaf blades subcoriaceous, with prominent nervation; bracteoles 10–15 × ca. 2 mm; hypanthium campanulate, 8–10 × 5–7 mm, calyx lobes with acute apex, ca. 3 mm long; petal buds without bristle hairs at apex; fruits urceolate, 13–15 × 5–10 mm [Peninsular Malaysia] ..... **24. *D. griffithii***

24 Leaf blades membranous, without prominent nervation; bracteoles ca. 3.5 × 1 mm; hypanthium tubular, ca. 4 × 2 mm, calyx lobes with obtuse apex, ca. 1 mm long; petal buds bristly at apex; fruits ovoid, 5–6 × 3–3.5 mm [Borneo] ..... **16. *D. densiflora***
25 Bristle hairs on branchlets, petioles and hypanthium curved; leaf blades membranous, hirsute, covered with curved bristle hairs on both surfaces, 9.7–12 cm long; hypanthium campanulate, 5–6 mm long, calyx lobes 3–4 mm long; petal buds with bristly apex [Borneo] ..... **41. *D. porphyrocarpa***
25 Bristle hairs on branchlets, petioles and hypanthium straight; leaf blades subcoriaceous, above glabrous, below densely pubescent or floccose, 13–20 cm long; hypanthium tubular or suburceolate, 7–9 mm long, calyx lobes 6–11 mm long; petal buds with glabrous apex [Sumatra] 26
26 Branchlets, petioles and hypanthium axes pubescent and with 4–5 mm long bristle hairs; bracteoles subulate, ca. 2 mm long ..... **26. *D. horrida***
26 Branchlets, petioles and hypanthium axes floccose and with 1–2 mm long bristle hairs; bracteoles subulate, 5–10 mm long ..... **19. *D. floccosa***
27 Inflorescences axillary, up to 10 cm long, thyrse with 1–20 flowers 28
27 Inflorescences terminal, 12–57 cm long; thyrse with more than 20 flowers 31
28 Branchlets, leaf underneath and hypanthium glabrous; alternipetalous stamens staminodal, anther locules undeveloped, flattened, pedoconnective not developed 29
28 Branchlets, leaf blades underneath and hypanthium stellate-furfuraceous to tomentose; alternipetalous stamens fertile, thecae developed, C-shaped, pedoconnective developed 30
29 Leaf blades subcoriaceous, petioles glabrous; hypanthium 7–8 × ca. 5 mm, calyx lobes with irregularly cracked or rounded tip, 1–2 mm long; extraovarial chambers extending almost to base of ovary; fruits 7–8 × 5–6 mm..... **14. *D. conica***
29 Leaf blades membranous, petioles densely covered with red-brown bristles at lateral groove at attachment with blade; hypanthium 3–4 × 2–2.5 mm, calyx lobes truncate, ca. 0.5 mm long; extra-ovarial chambers extending only to ⅓ of upper part of ovary; fruits 4–5 × 3–4 mm ..... **54. *D. viminalis***
30 Branchlets glabrescent; leaf blades membranous, base subcordate; inflorescences with 3–10 flowers; hypanthium tubular or funnelform; alternipetalous stamens with 3–4 mm long pedoconnective [Philippines] ..... **1. *D. acmura***
30 Branchlets densely stellate-tomentose; leaf blades subcoriaceous, base rounded; inflorescences with 15–20 flowers; hypanthium campanulate; alternipetalous stamens with ca. 5 mm long pedoconnective [Borneo & Sulu Arch.] ..... **6. *D. axillaris***
31 Flowers with 4 alternipetalous stamens; oppositipetalous stamens absent or not developed 32
31 Flowers with 8 stamens, both alternipetalous and oppositipetalous well developed or staminodial 42
32 Calyx lobes truncate with acute or triangular tip 33
32 Calyx lobes slightly triangular or lanceolate with acute tip 40
33 Leaf base subcordate; anthers medifixed, with tessellate-reticulate thecae, basal crest triangular, orbicular or ligular, 2–3 mm long, lateral appendages absent or not developed; pedoconnective not developed ..... **18. *D. fallax***
33 Leaf base rounded; anthers basifixed, with smooth thecae, basal crest triangular or hastate, 0.5–1 mm long, lateral appendages paired, filiform or ribbonlike; pedoconnective developed 34
34 Hypanthium suburceolate or urceolate; stamens with straight or curved anthers when mature 35

34 Hypanthium campanulate; stamens with curved anthers when mature 38
35 Hypanthium robust, 5–8 × 3–4 mm; stamens with curved anthers .....**32. *D. leprosa***
35 Hypanthium small, 3–5 × 2–2.5 mm; stamens with straight anthers 36
36 Petiole 6–8 mm long; inflorescences short, 10–15 cm long; pedicels those of central flowers 1–2 mm long, those of lateral flowers ca. 0.5 mm long; fruits subglobose with 8 lines .....**10. *D. biligulata***
36 Petiole 10–17 mm long; inflorescences long, 15–57 cm long; pedicels those of central flowers 2–4 mm long, those of lateral flowers 1–3 mm long; fruits ovoid-urceolate without lines 37
37 Bracteoles minute, less than 1 mm long; calyx lobes distinctly triangular, erect persistent when fruiting, 1–2 mm long [Borneo] .....**47. *D. rubiginosa***
37 Bracteoles linear, 1–2 mm long; calyx lobes truncate with triangular point, widened or reflexed persistent when fruiting, less than 1 mm long [Moluccas & New Guinea] ....**3. *D. angiensis***
38 Leaf blades abaxially, petioles and inflorescence axes glabrous or sparsely puberulous [Java & Lesser Sunda] .....**53. *D. vacillans***
38 Leaf blades abaxially, petioles and inflorescence axes stellate-furfuraceous or tomentose 39
39 Leaf blades underneath densely tomentose; hypanthium campanulate-angular with 4 ridges; petal buds 3–7 mm long; mature petals ovate to oblong, 6–10 × 3–5 mm, pink; extraovarial chambers deep, extending to base of ovary [Java] .....**28. *D. intermedia***
39 Leaf blades underneath stellate-furfuraceous; hypanthium campanulateterete without ridges; petal buds 2–2.5 mm long; mature petals obovate, 3–4 × ca. 2 mm, dark purple; extraovarial chambers shallow, extending to upper ⅓ of ovary [Sulawesi & Philippines] ..... **31.1. *D. celebica* var. *celebica***
40 Bracteoles minute, subulate, 1–2 mm long; hypanthium tubular or funnelform; stamens with straight filaments and anthers when mature, basal crest ligular, ca. 2 mm long [New Guinea].....**12. *D. brassii***
40 Bracteoles linear, 2–5 mm long; hypanthium campanulate; stamens with curved filaments and anthers when mature, basal crest triangular or rounded, ca. 0.5 mm long..... 41
41 Leaf blades underneath stellate-furfuraceous; central flowers with 1–2 mm long pedicels, in lateral flowers ca. 0.5 mm long; calyx lobes persistent when fruiting [Sulawesi] ....**13.2. *D. celebica* var. *longilobata***
41 Leaf blades underneath stellate-tomentose; central flowers with 3–4 mm long pedicels, in lateral flowers 1–2 mm long; calyx lobes caducous when fruiting [New Guinea]..... .....**50. *D. schumannii***
42 Alternipetalous stamens fertile, well developed; oppositipetalous fertile or staminodal 43
42 Alternipetalous stamens staminodal, not well developed; oppositipetalous ones fertile, well developed 56
43 Alternipetalous and oppositipetalous stamens distinctly unequal; oppositipetalous ones less than half the length of alternipetalous ones 44
43 Alternipetalous and oppositipetalous stamens subequal or equal in length; oppositipetalous ones more than half the length of the alternipetalous ones..... 45
44 Leaf blades underneath glabrous; hypanthium glabrous; filaments curved sideways, alternipetalous and oppositipetalous anthers curved, whitish, with a pair of wavy filiform lateral appendages .....**23. *D. gracilis***
44 Leaf blades underneath stellate-furfuraceous; hypanthium glabrescent to stellate-furfuraceous; filaments straight, alternipetalous and oppositipetalous anthers straight, yellow, without lateral appendages .....**27. *D. inappendiculata***

45 Leaf blades subcoriaceous, coriaceous or chartaceous, underneath stellate punctate 46
45 Leaf blades membranous, underneath glabrous, stellate-furfuraceous or tomentose 50
46 Hypanthium densely stellate-tomentose; calyx lobes slightly 4-triangular with acute apex 47
46 Hypanthium glabrous to stellate-furfuraceous; calyx lobes truncate with acute apex.... 49
47 Hypanthium tubular to suburceolate, calyx lobes lanceolate, 4–4.5 mm long, reflexed when mature [Borneo]..... **33. *D. macrosepala***
47 Hypanthium campanulate, calyx lobes triangular, 1–3 mm long, erect when mature.... 48
48 Bracteoles linear, 2–3 mm long; hypanthium at early buds urceolate or subglobose, enclosing the petal bud; petal buds 2–4 mm long; mature petals ca. 10 × 5–7 mm; stamens with a fimbriate basal crest; fruits subglobose to urceolate, 8–10 × 4–7 mm [Malay Peninsula & Riau Arch.] ..... **44. *D. punctulata***
48 Bracteoles lanceolate or oblong, up to 10 mm long; hypanthium at early buds campanulate, not enclosing the petal bud; petal buds 7–8 mm long; mature petals 12–20 × 10–14 mm; stamens with triangular or erose basal crest; fruits ovoid to urceolate, 13–15 × 5–10 mm ..... **4. *D. annulata***
49 Hypanthium stellate-furfuraceous; bracteoles conspicous, ovate to oblong, 5–9 mm long, enclosing the hypanthium ..... **11. *D. bracteata***
49 Hypanthium glabrous; bracteoles inconspicous, linear or lanceolate, 2–4 mm long, caducous [Malay Peninsula, Sumatra, Borneo]..... **39. *D. pallida***
50 Calyx lobes triangular or rounded with obtuse or acute tip, 2–4 mm long 51
50 Calyx lobes truncate with 4 acute or triangular points, 0.5–1 mm long..... 52
51 Hypanthium densely stellate-furfuraceous and with scattered, thickened, 1–2 mm long bristles; calyx lobes rounded, apex obtuse, margin ciliate, ca. 2 mm long; petal buds 3–5 mm long [Sumatra] ..... **35. *D. marumioides***
51 Hypanthium densely brown stellate-tomentose, slightly 8-ridged and without bristles; calyx lobes triangular, apex acute, margin not ciliate, 3–4 mm long; petal buds 8–10 mm long [Peninsular Malaysia & Sumatra] ..... **51. *D. spectabilis***
52 Branchlets, leaf blades underneath, inflorescence axes and hypanthium glabrous, glabrescent to sparsely puberulous..... 53
52 Branchlets, leaf blades underneath, inflorescence axes and hypanthium densely furfuraceous to tomentose 54
53 Hypanthium narrowly campanulate to suburceolate, 1–3 mm in width, calyx lobes with undulate or rounded apex, 0.5–1 mm long; stamens with a pair of filiform lateral appendages [Java & Lesser Sunda Islands]..... **53. *D. vacillans***
53 Hypanthium broadly campanulate, ca. 3 mm in width, calyx lobes with acute, triangular apex, ca. 1 mm long; stamens lacking lateral appendages [Sumatra] ..... **38. *D. nodosa***
54 Bracteoles linear, ca. 1.5 mm long; hypanthium suburceolate; thecae tesselate-reticulate, oppositipetalous stamens with ligular basal appendages and lacking lateral appendages.. ..... **18. *D. fallax***
54 Bracteoles linear-lanceolate, 3–6 mm long; hypanthium campanulate; thecae smooth, oppositipetalous stamens with spuriform basal appendages and a pair of filiform lateral appendages..... 55
55 Leaf blade base emarginate or subcordate; petioles 8–10 mm long; bracteoles linear, 3–4 mm long; hypanthium campanulate-angular, ca. 2 mm wide [Philippines] .... **15. *D. cumingii***
55 Leaf blade base rounded; petioles 10–15 mm long; bracteoles lanceolate, 5–6 mm long; hypanthium campanulate-terete, 3–5 mm wide [Java]..... **48. *D. sagittata***

56 Leaf blades membranous or subcoriaceous; hypanthium cyathiform-tubular or cup-shaped; fruits subglobose 57
56 Leaf blades chartaceous; hypanthium campanulate-angular to suburceolate, slightly 4- or 8-lined; fruits urceolate 58
57 Leaf blades subcoriaceous, petioles glabrous; hypanthium 7–8 × ca. 5 mm, calyx lobes with irregularly cracked tip or rounded apex, 1–2 mm long; extra-ovarial chambers extending almost to base of ovary ..... **14. *D. conica***
57 Leaf blades membranous, petioles densely covered with red-brown bristles at lateral groove near the attachment with base of leaf blade; hypanthium 3–4 × 2–2.5 mm, calyx lobes indistinct, ca. 0.5 mm long; extra-ovarial chambers extending only to upper ⅓ of ovary ..... **54. *D. viminalis***
58 Leaf blades underneath glabrous but with sparsely stellate hairs along the nerves, with a pair of glandular patches at base; petiole glabrous to stellate-puberulous, covered with bristle hairs at dorsal line, 5–8 mm long; calyx lobes with minutely pointed tips, ca. 0.5 mm long ..... **8. *D. barbata***
58 Leaf blades underneath glabrous or stellate-furfuraceous, without a pair of glandular patches at base; petiole sparsely to densely covered with stellate hairs and often with dense bristle hairs, 10–15 mm long; calyx lobes without distinct tip, ca. 1 mm long ..... **17. *D. divaricata***

1. *Dissochaeta acmura* Stapf & M.L.Green — Map 3-2

Dissochaeta acmura Stapf & M.L.Green, Bull. Misc. Inform. Kew 1913: 42. 1913. — Lectotype (designated here): *H. Cuming 2838* (lecto K [K000859613!]): Philippines, Luzon, Province of Albay.

Climbing up to 8 m in height. Branchlets terete, 2.5–4 mm in diameter, covered with stellate hairs, dense on young branches and nodes, glabrescent; nodes swollen, with interpetiolar ridge; internodes 5–10 cm long. Leaves: petioles flattened, 10–23 mm long, densely stellate-furfuraceous; blades ovate to elliptic, 8.3–17.2 × 3.7–6.8 cm, membranous, rarely subcoriaceous, base rounded or subcordate, margin entire, apex acute or acuminate, tip 0.5–2 cm long; nervation prominent above, with 1 pair of lateral nerves, 1 pair of intramarginal nerves; adaxially glabrous, abaxially brown stellate-tomentose, dense on midrib. Inflorescences axillary, 5.5–10 cm long, 3–10 flowers; main axis terete, densely stellate-furfuraceous and with simple glandular hairs; primary axes 11–13 cm long, with 3 or 4 nodes; secondary axes 1–1.4 cm long, with 1 or 2 nodes; tertiary axes 0.8–1 cm long, with 1 node or undeveloped; bracts linear, ca. 5 mm long, densely stellate-furfuraceous, caducous; bracteoles linear, 1–2 mm long, densely stellate-furfuraceous, caducous; pedicel densely stellate-furfuraceous, 5–7 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium tubular or slightly funnelshaped, 7–11 × 3–5.5 mm, densely stellate-tomentose, sparsely covered with scattered simple glandular bristle hairs; calyx lobes truncate with 4 minute tips, 1–3 mm long; petal buds conical, 8–13 × 3–9 mm; mature petals obovate to suborbicular, 18–20 × 13–15 mm, reflexed or not, base clawed, apex obtuse, glabrous, white or white with pinkish hue, hairy at edge. Stamens 8, unequal, glabrous, filaments curved sideways; alternipetalous stamens with white-creamy filaments, 10–12 mm long, apex yellow, anthers slightly curved, sickle-shaped, slender, thecae 10–12 mm long, pink, pedoconnective 3–4 mm long, basal crest bifid up to 2 mm long, lateral appendages paired, filiform, white, 3–3.5 mm long; oppositipetalous stamens with white filaments, ca. 10 mm long, anthers S-shaped, thecae 10–12 mm long, pink, basal crest minute or ligular, ca. 0.5 mm long, margin erose, lateral appendages paired, filiform, 5–6 mm long, bright white.

Ovary ¾ of hypanthium in length, apex glabrous, 8-ridged; style 17–22 mm long, glabrous, curved sideways, opposite to the filaments, slightly curved at the end when mature, whitish; stigma minute; extra-ovarial chambers 8, the 4 alternipetalous ones extending to near the base of the ovary, the 4 oppositipetalous ones extending to about the middle of the ovary. Fruits urceolate, ellipsoid, 8–15 × 5–10 mm, stellatefurfuraceous, brownish green when unripe; calyx remnants persistent, erect, widened. Seeds ca. 0.5 mm long.

Distribution — Philippines.

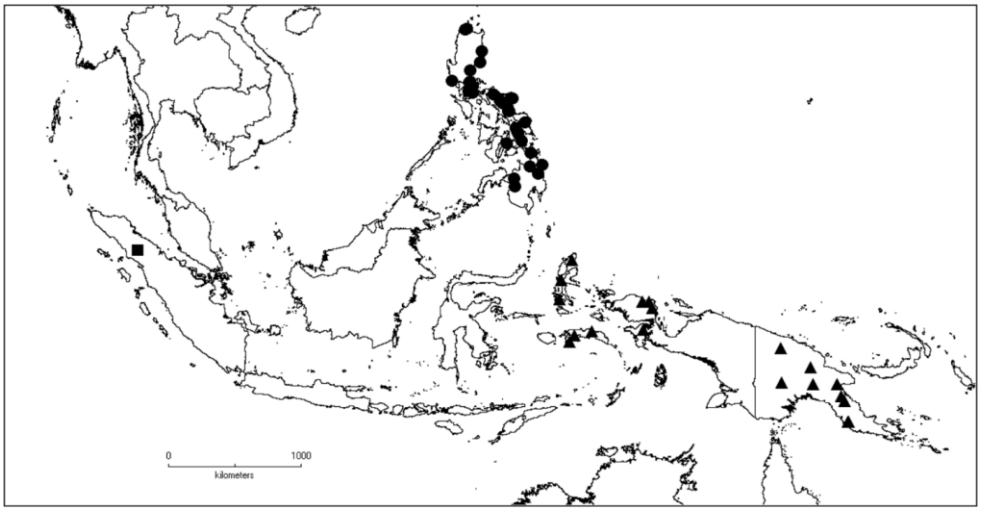
Ecology and habitat — Open shade, along ridges, on wet or less sandy ground in forest or secondary forest at 220–300 m elevation.

Note — *Dissochaeta acmura* resembles *D. axillaris* in having axillary inflorescences, but differs in its membranous leaf blades and triangular mature calyx lobes, while *D. axillaris* has coriaceous leaf blades and truncate calyx lobes.

Specimens examined — **PHILIPPINES.** Biliran: Mt. Suiro, 30 Apr 1954, *Sulit PNH 21567* (K, L, PNH). Catanduanes: *Ramos BS 30366* (BM, P); San Miguel, 21 Nov 1991, *Barbon, Garcia & Alvarez PPI 2425* (L). Cebu: Cebu Central, 800 m, May 1998, *Bicknell 1490* (L). Leyte: 1 May 1914, *Wenzel 414* (BM); 14 May 1914, *Wenzel 662* (BM); Baybay, Villa Solidaridad, 150 m, *Gutierrez PNH 119985* (PNH). Luzon: Aurora, Diteki, 550 m, 9 May 1996, *Fuentes & Fernando PPI 37255* (L); *Ibid.*, 450 m, 19 May 1996, *Fuentes & Fernando PPI 37459* (L); *Ibid.*, Casiguran, Bianoan, 19 Mar 1993, *Barbon, Garcia & Fernando PPI 9293* (L); Cagayan, Claveria, 467 m, 3 Aug 1995, *Garcia et al. PPI 18314* (L); *Ibid.*, Santa Praxedes, 520 m, 11 Aug 1995, *Garcia, Fuentes & Romero PPI 18494* (L); Camarines Norte, Basud, Mount Nilisan, 9 Sep 1991, *Reynoso, Romero & Fuentes PPI 1317* (L); Camarines Sur, Iriga, Mt. Asog, 14 Jun 1992, *Barbon, Romero & Fuentes PPI 8440* (L); Laguna, Jun-Aug 1915, *MacGregor BS 22859* (BM, P); Zambales, San Antonio, Aug 1910, *Ramos BS 437* (U); *Ibid.*, Sep–Oct 1912, *Ramos BS 16612* (BM, L); San Mariano, SO. Agal, 200 m, 2 Jul 1994, *Barbon, Romero & Fuentes PPI 13023* (L); Sorsogon, Irosin, Mt. Bulusan, 300 m, Dec 1915, *Elmer 15257* (BM, BO, K, L, P, PNH, U), *Ibid.*, 300 m, Aug 1916, *Elmer 16844* (BM, BO, K, L, P, PNH, U); *Ibid.*, Lake Polog, Aug 1915, *Ramos BS 23644* (BM, BO, K, P, PNH); Albay Province, *Cuming 2838* (K); Quezon Province, Lalawinan, Tipuan, 2 Sep 1991, *Barbon, Alvarez & Garcia PPI 2212* (K, L); *Ibid.*, Burdeos, Kinabuawan, 24 Aug 1991, *Barbon, Alvarez & Garcia PPI 2037* (K, L); *Ibid.*, Tayabas, *Cuming 815* (BM, K); *Ibid.*, *Cuming 2840* (K); *Ibid.*, Lucban, May 1907, *Elmer 8236* (BM, BO, K, L, P, PNH, U); *Ibid.*, Mt. Tulaog, May 1917, *Ramos & Edano BS 29114* (BO). Mindanao: Agusan Del Norte, Butuan, San Mateo, Tungao, 250 m, 31 May 1961, *Mendoza PNH 41847* (BO, K, L, PNH); *Ibid.*, 8 Jun 1961, *Mendoza PNH 42217* (L, PNH); *Ibid.*, 85 m, 25 Aug 1966, *Jurane PNH 98404* (PNH); Agusan del Sur, Dinagat, Binahanan, 80 m, 9 Oct 1991, *Gaerlan, Sagcal & Fernando PPI 4855* (L); Lanao del Sur, Lake Lanao, Camp Keithley, 1907, *Clemens 1155* (BO); Surigao, 3 Jul 1927, *Wenzel 3043* (BO, K); Surigao del Sur, Aras-Asan, 250 m, 17 May 1975, *University of San Carlos 819* (L); Cotabato, Mabuhay Mining Camp, 25 May 1950, *Aňonuevo PNH 13453* (BM, PNH). Samar: Oquendo, Mt. Mahagna, 220 m, 17 Apr 1951, *Sulit PNH 14463* (K, L, PNH); *Ibid.*, 30 Apr 1951, *Sulit PNH 14514* (BM, K, L, PNH); Paranas, 17 Oct 1992, *Reynoso, Sagcal & Garcia PPI 7448* (L); *Ibid.*, 400 m, 1 May 1996, *Reynoso & Majaducon PPI 21956* (L).

2. *Dissochaeta alstonii* M.P.Nayar — Map 3-2

Dissochaeta alstonii M.P.Nayar, Bull. Bot. Surv. India 11: 188. 1969. — *Dissochaeta rostrata* Korth. var. *alstonii* (M.P.Nayar) J.F.Maxwell, Gard. Bull. Singapore 33: 318. 1980. — Type: *A.H.G. Alston 14813* (holo BM [BM000944479!]), Indonesia, North Sumatra, Tapanuli, between Sidikalang and Pongkolan, 1200 m elev., 27 Mar 1954.



Map 3-2. Distribution of *D. acmura* (●), *D. alstonii* (■) and *D. angiensis* (▲).

Branchlets terete, 3–4 mm in diameter, covered with stellate hairs and glandular bristles; nodes swollen, with an interpetiolar ridge; internodes 4–7 cm long. Leaves: petioles terete, 5–8 mm long, densely stellate-furfuraceous; blades ovate, 6–8.5 × 3–4 cm, subcoriaceous, base subcordate, margin entire, ciliate, apex acuminate, tip ca. 1 cm long; nervation prominent above, with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous and with scattered bristle hairs on midrib, abaxially punctate, midrib with dense stellate hairs, brown furfuraceous and bristle hairs. Inflorescences terminal, many-flowered, 20–30 cm long; main axis angular, densely setose with glandular bristles and stellate-furfuraceous hairs; primary axes up to 28 cm long with 6–8 nodes, secondary axes 1.5–4 cm long with 1–3 nodes, tertiary axes up to 1 cm long with 1 node; bracts linear, 3–6 mm long, densely setose with glandular bristles; bracteoles linear, 3–4 mm long, densely setose with glandular bristles; pedicels densely setose with glandular bristles, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, tubular, 4.5–5.5 × 2–3 mm, densely setose and covered with glandular bristles and stellate-furfuraceous hairs; calyx lobes triangular, 2.5–3 mm long, densely setose; petal buds conical, 3–4 mm long; mature petals obovate to ovate-oblong, ca. 4.5 × 2.5 mm, base clawed, apex acuminate, glabrous but glandulose-setose at margin, pink. Stamens 8, unequal, glabrous, filaments curved sideways; alternipetalous stamens with 4–4.5 mm long filaments, anthers rostrate, sickle-shaped, thecae 4.5–5 mm long, pedoconnective ca. 0.5 mm long, basal crest erose, up to 0.4 mm long, lateral appendages subulate, paired, ca. 2 mm long; oppositipetalous stamens with ca. 3.5 mm long filaments, anthers hook-shaped, thecae 3.5–4 mm long, basal crest minute, erose, ca. 0.2 mm long, lateral appendages minute, ca. 0.2 mm long. Ovary half as long as hypanthium, apex stellate-furfuraceous; style 9–11 mm long, glabrous, apex curved; stigma punctiform; extra-ovarial chambers 8, extending to near the base of ovary. Fruits subglobose, 4.5–5.5 × ca. 4 mm, covered with dense glandular bristles and stellate-furfuraceous hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Sumatra (North).

Ecology and habitat — Montane forest at ca. 1200 m elevation.

Note — *Dissochaeta alstonii* is known only from the type from Northern Sumatra. The species resembles *D. rostrata*, by having a setose and bristly appearance on branchlets and

hypanthium. It differs by having glandular bristles in most parts, like branches, leaves and hypanthium while, in *D. rostrata*, the bristles are simple, not glandular.

3. *Dissochaeta angiensis* Kaneh. & Hatus. ex Ohwi — Map 3-2

Dissochaeta angiensis Kaneh. & Hatus. ex Ohwi, Bot. Mag. (Tokyo) 57: 5. 1943. — Lectotype (designated here): *R. Kanehira & S. Hatusima 13374* (lecto FU; isolecto L [L0537256!]), Indonesia, West Papua, Arfak Mts., track to Lake Gita from Momi, 1300 m elev., 4 Apr 1940.

Climbing up to 7 m in height. Branchlets terete, 3–6 mm in diameter, covered with densely stellate-furfuraceous hairs, rarely pubescent; nodes swollen, interpetiolar ridge slightly raised; internodes 5–12.3 cm long. Leaves: petioles terete, 10–17 mm long, densely stellate-furfuraceous; blades ovate, elliptic to oblong, 8.2–18 × 4–7 cm, membranous to nearly subcoriaceous, base rounded or emarginate, margin entire, rarely subserrulate, apex acuminate, tip 1–1.5 cm long; nervation with 1 (rarely 2) pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark glossy green, abaxially brown stellate-furfuraceous, dense on midrib. Inflorescences terminal and in the upper leaf axils, many-flowered, up to 57 cm long; main axis angular, densely stellate-furfuraceous; primary axes up to 54 cm long with 6–8 nodes, secondary axes up to 18.5 cm long with 1–3 nodes, tertiary axes 1–4 cm long with 1 or 2 nodes or sometimes undeveloped; bracts linear, ovate or elliptic, 1.7–3.5 × ca. 1.2 cm long, densely brown stellate-furfuraceous, caducous; bracteoles linear, 1–2 mm long, densely stellate-furfuraceous, caducous; pedicels densely stellate-furfuraceous, 3–4 mm long for central flowers, 2–3 mm long for lateral flowers. Hypanthium urceolate, 4–5 × 2–2.5 mm, densely stellate-furfuraceous; calyx lobes truncate with 4 triangular tips, ca. 1 mm long; petal buds conical, 3–4 mm long, blades ovate, base clawed, apex acute; mature petals oblong, 7–9 × 4–6 mm, base clawed, margin ciliate, apex obtuse, glabrous, white to pinkish. Stamens 4, equal, alternipetalous, filaments straight; alternipetalous stamens with 5–7 mm long filaments, anthers oblong or lanceolate, thecae slightly straight, 5–6 mm long, yellow, pedoconnective short or slightly undeveloped, basal crest hastate or triangular, 0.75–1 mm long, lateral appendages ligular, ribbon-like or paired and filiform with irregular margins, 0.75–2 mm long. Ovary ¾ of hypanthium in length, apex villous; style 10–12 mm long, glabrous; stigma capitate, minute; extraovarial chambers 4, shallow, extending ca. ⅓ of ovary. Fruits ovoid-urceolate, 5–8 × 2.5–7 mm, glabrous to glabrescent, green when young, calyx remnants persistent, widened. Seeds ca. 0.5 mm long.
Distribution — Moluccas and New Guinea.
Ecology and habitat — Lowland hill forest to lower montane forest at 50–1300 m elevation.
Vernacular names — Moluccas: *siri utan* (Ambon); *arendong* (Bacan). New Guinea: *tsoin* (Kutubu); *johnihoeveke* (middle Waria).
Note — *Dissochaeta angiensis* resembles *D. celebica* Blume but differs by having a much larger urceolate hypanthium and short lateral appendages (0.75–2 mm) on the alternipetalous stamens. The mature anthers are straight rather than curved.
Specimens examined — **INDONESIA.** Moluccas: Bacan, Mt. Damar, Masurung, 200 m, 12 Aug 1937, *Nedi 28* (BO); Ceram, Honitetu–Wae Tuba, 4 Feb 1938, *Eyma 2771* (BO, L); *Ibid.*, Between Raniki and Manusela, 1000 m, 24 Jun 1918, *Kornassi 1403* (BO). North Moluccas: Halmahera, Mt. Sembilan, 600 m, 28 Sep 1951, *Pleyte 299* (BO, K, L, PNH); Morotai, Mt. Pare-Pare, Rawa Panjang, 1000 m, 28 May 1949, *Kostermans 1322* (BO, K, L, PNH). West Papua: Vogelkop Peninsula, Ije River Valley, Bamfot Village, 850 m, 2 Nov 1961, *van Royen & Sleumer 7646* (BO, K, L); *Ibid.*, Isjon River Valley, Son Village, 650 m, 28 Oct 1961, *van Royen & Sleumer 7574* (BO, K, L); Arfak Mountains, Angi, 1300 m, 4 Apr

1940, *Kanehira & Hatusima 13374* (L); Bomberai Peninsula, Tangguh, 50 m, 21 Feb 2002, *Takeuchi, Sambas & Maturbongs 16004* (BO). **PAPUA NEW GUINEA.** Central Division: Sogeri, Subitana, 22 Jun 1954, *Womersley & van Royen NGF 5815* (BO, K), *Ibid.*, 1885, *Forbes 459* (BM). Chimbu: Haia, 640 m, 16 Sep 1996, *Takeuchi 11200* (K). East Sepik: Waskuk Hills, between Garuka and Waskuk, 60 m, 28 Jun 1995, *Takeuchi & Regalado 10198* (L). Madang: Bismarck Range, Gulno Village, 1050 m, 15 Oct 1995, *Takeuchi 10790* (L). Morobe: Kipu, Tiaura, 800 m, 7 Jan 1966, *Streimann NGF 26113* (BO, K, L); Wampit, Bupu Village, 760 m, 3 Mar 1964, *Millar NGF 23243* (L); *Ibid.*, 1310 m, 13 Jul 1967, *Millar NGF 22928* (L); Wareo, 600 m, 25 Dec 1935, *Clemens 1395* (L). Southern Highlands: Tari, Bosavi Mission-Mulimia Govt. Stn., 700 m, 2 Sep 1986, *Gideon LAE 57470* (K, L).

4. *Dissochaeta annulata* Hook.f. ex Triana — Fig. 3-5, Map 3-3

Dissochaeta annulata Hook.f. ex Triana, Trans. Linn. Soc. London 28: 83, tab. 7, fig. 89a. 1872. — *Diplectria annulata* (Hook.f. ex Triana) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated here): *W. Griffith KD 2268* (lecto K [K000859545!]; isolecto K [K000859544!]), Malaysia, Penang, Penang Hill.

Dissochaeta robinsonii Merr., Philipp. J. Sci., C 11: 298. 1916. — *Dissochaeta annulata* Hook.f. ex Triana var. *robinsonii* (Merr.) Bakh.f., Contr. Melastom. 231. 1943. — Lectotype (designated here): *C.B. Robinson 2024* (lecto BO [BO1747982!]; isolecto BM [BM000944486!], GH [GH00072242!], K [K000859510!], L [L0537257!], NY [NY00228565!], P [P02274818!], US [US00120532!]), Indonesia, Moluccas, Ambon, Hitoemesen, 100 m elev., 5 Nov 1913.

Dissochaeta johannis-winkleri O.Schwartz, Mitt. Inst. Allg. Bot. Hamburg 7: 251. 1931. — *Dissochaeta annulata* Hook.f. ex Triana var. *johannis-winkleri* (O.Schwartz) J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980. — Lectotype (designated here): *J. Winkler 590* (lecto HBG [HBG522821!]; isolecto BO [BO1865970!], HBG [HBG522822!]), Indonesia, West Kalimantan, Lebang Hara 160 m elev., 5 Dec 1924.

Dissochaeta deusta Ohwi, Bot. Mag. (Tokyo) 57: 6. 1943. — Lectotype (designated here): *R. Kanehira & S. Hatusima 11999* (lecto FU; isolecto BO [BO1747983!], L [L0537258!]), Indonesia, West Papua, Nabire, Dallman, 400 m elev., 1 Mar 1940.

Dissochaeta simalurensis Bakh.f., Contr. Melastom.; 228. 1943. — Type: *Achmad 1197* (holo L [L0537260!]; iso BO!) Indonesia, Aceh, Simaloer Eiland, 24 Jun 1919.

Dissochaeta annulata Hook.f. ex Triana var. *setosa* Bakh.f., Contr. Melastom.; 231. 1943. — Type: *Iboet 12* (holo L [L0537259!]; iso BO [BO1865981!, BO1865982!]), Indonesia, West Sumatra, Mentawai Eilanden, Siberoet Eiland, 8 Sep 1924.

Dissochaeta ramosii auct. non Merr.: Furtado, Gard. Bull. Singapore 20: 112 (1963). *p.p.*, excl. type.

Climbing up to 30 m in height. Branchlets terete, 3–6 mm in diameter, densely to sparsely brown stellate-furfuraceous to glabrescent, often with dense or scattered bristles; nodes swollen with interpetiolar ridges, internodes 5.5–8 cm long. Leaves: petioles terete, 7–28 mm long, densely stellate-tomentose; blades ovate, 6–15 × 3.5–8 cm, subcoriaceous to coriaceous, rarely membranous, base broadly cordate, rarely rounded, margin entire, apex acuminate, tip 1–1.5 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, bright green with prominent nervation, abaxial greyish-brown, stellate-punctate to tomentose. Inflorescences terminal or in the upper leaf axils, up to 25 cm long, many-flowered; main axis terete to subangular, brown stellate-furfuraceous; primary axis 16–20 cm long with 4–5 nodes, secondary axis 2.5–3 cm long with 1–2 nodes, tertiary axis 0.8–1 cm long with 1 node; bracts lanceolate to oblong, rarely

linear, 1–3 × 0.5–1 cm, densely brown stellate-tomentose, caducous; bracteoles lanceolate to oblong, rarely linear, ca. 10 × 5 mm, densely tomentose; pedicels densely tomentose, 3–5 mm long in central flowers, 1–3 mm long in lateral flowers. Hypanthium campanulate, (6–)10–15 × (3–)7–8 mm, densely stellate-tomentose, sometimes with few scattered gland-tipped bristles up to 1mm long; calyx lobes truncate with rounded, triangular or acute tips, erect, 1–3 mm long; petal buds conical, 7–8 mm long, bright pink; mature petals ovate to obovate, 12–20 × 10–14 mm, reflexed, base clawed, apex rounded, glabrous with ciliate margin, white or white pinkish. Stamens 8, unequal, filaments curved sideways, light yellow; alternipetalous stamens with (10–)12–14 mm long filaments, anthers slender, sickle shaped, curved, thecae (12–)16–18 mm long, maroon, pedoconnective 4–7 mm long, basal crest entire, erose or bifid, up to 2 mm long, lateral appendages paired, filiform, 6–8 mm long, yellow; oppositipetalous stamens with (8–)10–12 mm long filaments, anthers S-shaped, thecae (10–)12–14 mm long, light yellow, basal crest ligular, obtuse or erose, 1–4 mm long, lateral appendages paired, filiform, 10–12 mm long, yellow. Ovary half as long as hypanthium, apex villous; style (12–)18–22 mm long, curved sideways in direction opposite to the filaments, curved at the tip, glabrous, white; stigma minute; extra-ovarial chambers 8, extending to near the base of the ovary. Fruits ovoid to urceolate, sometimes subglobose, (10–)13–15 × 5–10 mm, densely stellate tomentose, green brownish; calyx lobes persistent. Seeds ca.0.75 mm long.

Distribution — Malay Peninsula, Sumatra (Simeuleu, Bangka, Mentawai & Riau Archipelago), Borneo, Sulawesi (South-East), Moluccas and New Guinea.

Ecology and habitat — Lower montane, evergreen forest on granite, old secondary forest, Kerangas forest, open places at 50–1550 m elevation.

Vernacular names — Peninsular Malaysia: *akar sendudok* (Malay). Sumatra: *olor sigepu bala* (Simeuleu). Borneo: *akar kemunting* (Iban); *gelagan akar* (Dayak); *kelawit* (Ti); *ulur-ulur bukit* (Brunei); *apeh talah* (Apokayan).

Notes — 1. One of the most widespread species in the Malesian Region. Surprisingly never found in mainland Sumatra, only on Simeuleu Island, Mentawai Islands, Riau Archipelago and Bangka Island. The species also does not occur in the Philippines and the southern part of Malesia (Java to the Lesser Sunda Islands); in Sulawesi, it was only found in the South-Eastern Peninsula.

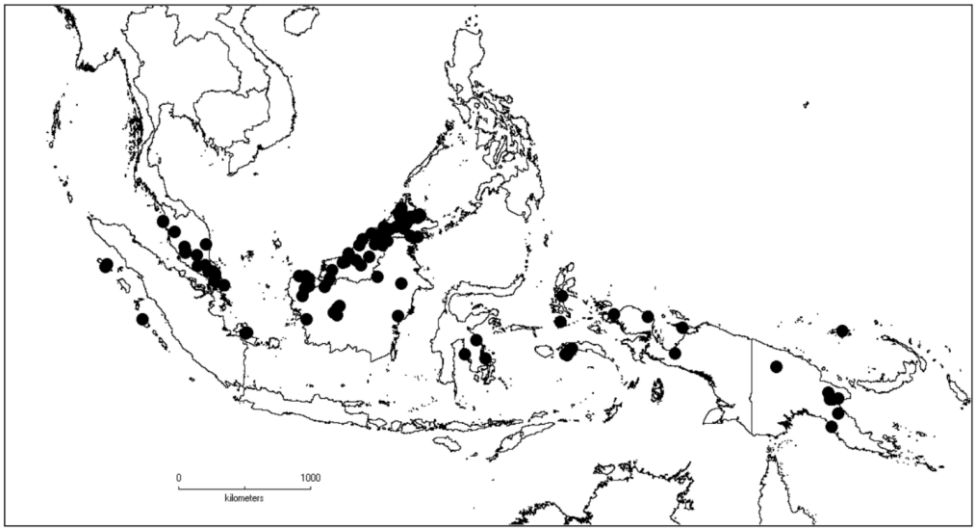
2. The appearance of *D. annulata* resembles that of *D. axillaris* and *D. bracteata* in the shape of the leaf blades and the stamens. It differs from *D. axillaris* by its terminal inflorescence (instead of axillary) and slightly triangular calyx lobes (instead of truncate). It is distinct from *D. bracteata* by its densely brown stellate-tomentose indumentum in most parts and the campanulate hypanthium, while *D. bracteata* is mostly glabrous with a more tubular hypanthium.

3. The establishment of varieties was initiated by Bakhuizen van den Brink (1943) and Maxwell (1980b) and it was mostly based on inconstant characters. The variety *robinsonii* was based on the rather small size of the inflorescences, including the size of hypanthium and bracts compared to typical *D. annulata*; we consider size too variable to support the separation of taxa, especially when all the other characters are similar, e.g. indument, hypanthium shape, stamen shape. Moreover, other varieties, *johannis-winkleri* and *setosa*, are only based on a simple character such as a more setose indumentum with additional bristles on the part of flowers and fruits. Since the variation in these characters is continuous, it is better to merge these varieties into the synonymy of *D. annulata*.

Selected specimens examined — **MALAYSIA.** Johor: Gunung Blumut, 900 m, 24 Mar 1923, *Holttum SFN 10657* (BM, BO, K); Gunung Ledang, 900 m, 17 Jul 1969, *Whitmore FRI 12371* (K, L); Kota Tinggi, 50 m, 22 Apr 1978, *Maxwell 78-207* (L); Labis forest

Reserve, Endau River, 24 Jul 1977, *Maxwell 77-359* (L). Pahang: Fraser's Hill, 4 Aug 1967, *Carrick 1613* (K, L); Kuantan, Panching, 130 m, 8 Jun 1968, *Ogata 10513* (L); Tasek Bera, 16 Oct 1930, *Henderson SFN 24057* (K). Penang: Penang Hill, *Griffith KD 2268* (K); Government Hill, *Maingay KD 788* (K, L). Perak: *Scortechini 235* (L, P). Selangor: Genting Highlands, Gunong Ulu Kali, 1500 m, 9 Apr 1978, *Maxwell 78-81a* (L); Ulu Gombak, 26 May 1966, *Carrick 1474* (K, L). Terengganu: Jerteh, Ulu Besut, Bukit Tangga, 900 m, 19 Jul 1984, *Shah & Mahmud 4944* (L). Sabah: Keningau, Nabawan, 21 Aug 1976, *Dewol SAN 83879* (K, L); Lamag, Gunong Lotong, Inarat, 400 m, 22 May 1976, *Cockburn SAN 83349* (K, L); Ranau, Lohan to Mamut Copper Mine, 1000 m, 9 Jul 1984, *Beaman et al. 10647* (K, L); *Ibid.*, Mount Kinabalu, Eastern Shoulder, 1066 m, 14 Jun 1961, *Chew, Corner & Stainton RSNB 69* (BO, K, L); Tenom, Kemabong-Katubu, 29 Apr 1972, *Cockburn & Saikeh SAN 70032* (K, L); Sandakan, Sep–Dec 1920, *Ramos BS 1207* (BO, PNH); Tawau, Tawau Hill, 300 m, 15 Jul 1974, *Aban & George SAN 79761* (K, L). Sarawak: *Beccari PB 3282* (K, P); Kuching, Matang, 760 m, *Haviland 546* (K); Baram, Kelabit Highland 1066 m, 6 Nov 1974, *Chai S.35320* (K, L); Bintulu, Nyabau, 90 m, 15 Jun 1966, *Sibat S.24556* (BO, K, L); Marudi, Tinjar, Ulu Dapoi, 14 Apr 1965, *Wright S.23062* (K, L); Balingian, Ulu Sg. Arip, Bukit Iju, 24 Jul 1965, *Sibat S.23617* (BO, K, L); Niah, Gunung Subis, Jan 1961, *Mohidin S.21636* (K, L); Betong, Bukit Sadok, 15 Oct 1982. *Banyeng & Ilias Paie S.45094* (K, L). **SINGAPORE.** Bukit Timah, 1893, *Ridley 5087* (BM). **BRUNEI.** Temburong: Bukit Belalong, 21 Jul 1989, *Wong 1434* (K). **INDONESIA.** Aceh: Simeuleu Island, 24 Jun 1919, *Achmad 1197* (BO, L). Bangka Belitung: Bangka, Lobok Besar, G. Mangkol, 50 m, 12 Sep 1949, *Kostermans & Anta 632* (BO, K, L). Riau Archipelago: Bintan Island, Gunung Bintan, 350 m, 13 Jun 1919, *Bünnemeijer 6158* (BO). West Sumatra: Mentawai Islands, Siberut Island, 8 Sep 1924, *Iboet 12* (BO, L). Central Kalimantan: Katingan-Seruyan Logging Area, 212 m, 27 Jul 2011, *Susanti et al. 276* (BO). East Kalimantan: G. Beratus, 700 m, 18 Jul 1952, *Kostermans 7595* (BO, K, L); Long Sungai Barang, 750 m, 6 May 1993, *van Valkenburg 1252* (BO, L, P); Muan Region, Sungai Riko, 20 m, Dec 1950, *Kostermans 4386* (BO, L). North Kalimantan: Long Bawan, Krayan, 1150 m, 17 Jul 1981, *Kato, Okamoto & Walujo B-9017* (BO, L). West Kalimantan: Pontianak, Bentiang, Gunung Mayung, 800 m, 28 Oct 1980, *Shea 26643* (BO, L); Sintang, Bukit Baka National Park, 310 m, 9 Nov 1993, *Church et al. 637* (L); Lebang Hara, 160 m, 5 Dec 1924, *Winkler 590* (BO, HBG); Ketapang, Gunung Palung National Park, Cabang Panti, 930 m, 20 Oct 1997, *Laman et al. 1357* (BO, L). South East Sulawesi: North Kolaka, Mt. Mekongga, 931 m, 30 Jun 2011, *Widjaja et al. 9718* (BO). Moluccas: Ambon, Hitumesen, 100 m, 5 Nov 1913, *Robinson 2024* (BM, BO, GH, K, L, NY, P, US); Waai, Bukit Pompule, 450 m, 28 Dec 1984, *Ramlanto 461* (BO, L); Ceram, Honitetu-Wae Tuba, 4 Feb 1938, *Eyma 2770* (BO); Obi, Anggai, Gunung Batu Putih, 300 m, 20 Nov 1974, *de Vogel 4181* (BO, L). North Moluccas: Halmahera, Weda Bay, Tolu Blewen Camp, 475 m, 3 Feb 2013, *Gushilman, Haris & Lasut 382* (BO, L). Papua: Yapen Island, Nyora Uta, 750 m, 14 Aug 1997, *Widjaja, Partomihardjo & Ruskandi 6894* (BO, K, L). West Papua: Nabire, Dallman, 400 m, 1 Mar 1940, *Kanehira & Hatusima 11999* (BO, L); Sorong, Remu River, 8 May 1954, *van Royen 4081* (L). **PAPUA NEW GUINEA.** Central Province: Bereina, between Kubuna and Bakoiudu, 14 Jan 1981, *Vinas & Nagari UPNG 4849* (L). East Sepik: Hunstein Range 440 m, 18 Jul 1990, *Takeuchi 6192* (BO, K, L). Manus: Lorengau, Buyang, 530 m, 7 Mar 1981, *Kerenga & Croft LAE 77282* (K, L). Morobe: Buko Creek, Gurakor, 487 m, 11 Jan 1962, *Millar NGF 14452* (K, L); Wampit River, Bupu River, 762 m, 3 Mar 1964, *Millar NGF 23241* (BO, K, L); Lae, 200 m, 21 Nov 1973, *Jacobs 9676* (BO, L).

Fig. 3-5. *Dissochaeta annulata*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruit. Photos by D.S. Penneys, vouchers: *Penneys 2506* (WNC).



Map 3-3. Distribution of *D. annulata* (●).

5. *Dissochaeta atrobrunnea* G.Kadereit — Map 3-4

Dissochaeta atrobrunnea G.Kadereit, Edinburgh J. Bot. 63(1): 4, fig. 1. 2006. — Type: *K. Sidiyasa PBU 229* (holo E [E00225106!]; iso BO [BO0009659!], K [K001089634!], L [L2542233!]), Indonesia, Central Kalimantan, Barito Ulu, Project Barito Ulu Base Camp, 1 Jun 1990.

Climbing up to 20 m in height. Branchlets terete, 4–6 mm in diameter, densely covered with stellate hairs and dark red-brown bristle hairs; nodes swollen, with interpetiolar ridge, thickly covered with stellate hairs and dark-red bristle hairs thickened at base; internodes 3.5–6 cm long. Leaves: petioles terete, 5–9 mm long, densely covered with stellate hairs and bristles; blades ovate, 8–11 × 4–7 cm, subcoriaceous, base cordate, margin entire, apex acuminate, densely bristly, tip 0.5–1 cm long; nervation with 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous with prominent nerves, abaxially with sparsely brown stellate hairs, more dense on midrib and with bristle hairs. Inflorescences terminal (many-flowered) and axillary (9–15 flowers), up to 20 cm long, up to 7 cm long when axillary; main axis angular, flattened at upper side, densely covered with stellate hairs and bristles; when terminal with primary axes up to 16 cm long with 6 or 7 nodes, secondary axes 5–6 cm long with 2 or 3 nodes, tertiary axes 0.8–1 cm long with 1 node; when axillary with primary axes, up to 5 cm long with 2 or 3 nodes, secondary axes up to 1 cm long with 1 node, tertiary axes not developed; bracts elliptic, 10–15 × 3–5 mm, densely covered with bristle hairs; bracteoles subulate, 7–9 × 1–2 mm, densely covered with bristle hairs; pedicels densely covered with stellate hairs and bristles, 2–3 mm long in central flowers, ca. 1 mm long or subsessile in lateral flowers. Hypanthium campanulate, 6–8 × 3–4 mm, densely covered with stellate hairs and bristle hairs; calyx lobes triangular, 1–2 mm long, densely covered with bristle hairs; petal bud conical, 5–6 mm long, apex bristly; mature petals ovate, 10–12 × 5–6 mm, glabrous, reflexed, base clawed, apex obtuse, white with purple flush or pinkish. Stamens 8, subequal, filaments curved sideways; alternipetalous stamens with ca. 9 mm long filaments, anthers slightly curved, sickle-shaped, thecae 8–9 mm long, pedoconnective 3–4 mm long, basal crest minute, lateral appendages paired, filiform, up to 6 mm long; oppositipetalous stamens with ca. 7 mm long filaments, anthers S-shaped, thecae 8–9 mm

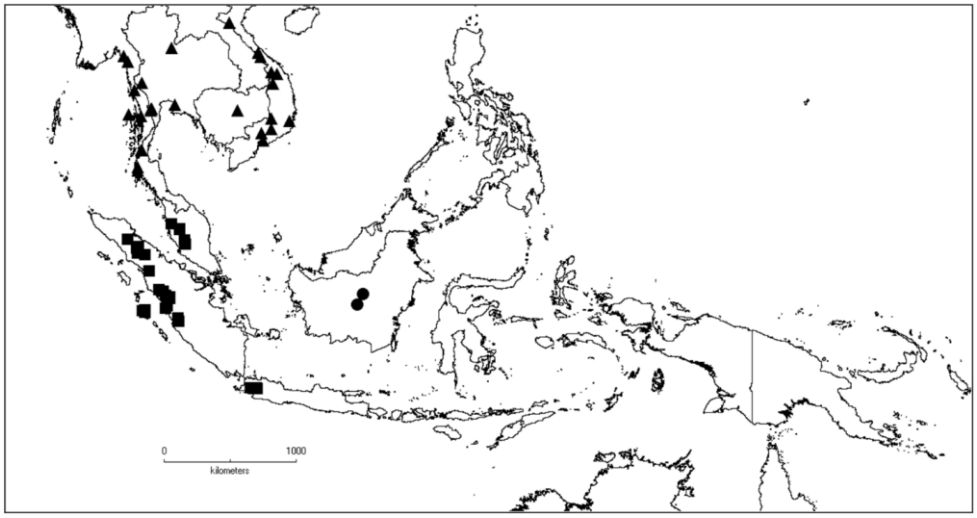
long, basal crest absent, lateral appendages paired, filiform, 5–6 mm long. Ovary ⅔ of hypanthium in length, apex thickened, bristly; style slightly curved when mature, 7–8 mm long; stigma minute; extra-ovarial chambers 8, the 4 alternipetalous ones extending to the base of the ovary, the 4 oppositipetalous ones extending to about the lower third of the ovary. Fruits urceolate, ca. 12 × 5–6 mm, covered with stellate hairs and dark red-brown bristles; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Borneo (Central Kalimantan).

Ecology and habitat — Primary and secondary lowland dipterocarp forest on swampy soil and in open areas at ca. 150 m elevation.

Note — *Dissochaeta atrobrunnea* is known only from three collections from lowland dipterocarp forest in Central Kalimantan, Indonesia. The species resembles *D. alstonii* from North Sumatra by its dense bristles found all over the branchlets, petioles and hypanthium, but differs by having longer bristles and a larger hypanthium and fruits. The appearance of the vegetative organs sometimes resembles *Macrolenes hirsuta* (Cogn.) J.F.Maxwell, which is different in its flowering organs (Kadereit 2006).

Specimens examined — **INDONESIA.** Central Kalimantan: Barito Ulu, 1 Jun 1990, *Sidiyasa PBU 229* (BO, E, K, L); *Ibid.*, Trail Jalang Babang, 18 Jun 1990, *Ridsdale PBU 81* (L); Kahayan River, South of Tumbang Sian, 150 m, 1 May 1988, *Burley & Tukirin 852* (BO, K, L).



Map 3-4. Distribution of *D. atrobrunnea* (●), *D. bakhuizenii* (■) and *D. barbata* (▲).

6. *Dissochaeta axillaris* Cogn. — Map 3-5

Dissochaeta axillaris Cogn. in H.J.P.Winkl., Bot. Jahrb. Syst. 48: 108. 1913. — Lectotype (designated here): *H.J.P. Winkler 3033* (lecto L [L0652534!]; isolecto BM [BM00094485!], BO!, BR [BR-518825!], K [K000859508!], WRSL), Indonesia, Central Kalimantan, Semurung, Sungei Tarik, 18 Jul 1908.

Dissochaeta ramosii Merr., J. Straits Branch Roy. Asiat. Soc. 86: 340. 1922. — Lectotype (designated here): *M. Ramos BS 1758* (lecto PNH [PNH32282!]; isolecto A [A00072206!], K [K000859509!], US [US00120531!]), Malaysia. Borneo, Sabah, Sebuga near Sandakan, Dec 1920.

Dissocaheta acmura auct. non. Stapf & M.L.Green: Bakh.f., Contr. Melastom.; 227. 1943. *p.p.*, excl. type.

Climbing up to 15 m in height. Branchlets terete, 4–5 mm in diameter, covered with brown stellate-tomentose hairs; nodes swollen, with interpetiolar ridges; internodes 6–9 cm long. Leaves: petioles terete, 9–18 mm long, densely stellate-tomentose; blades ovate or ovate-elliptic, 9–20 × 4–8.7 cm, subcoriaceous, base rounded, margin entire, apex acuminate, tip up to 1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely stellate-tomentose. Inflorescences axillary, up to 9 cm long, 15–20 flowers; main axes densely stellate-tomentose; primary axes 4–11 cm long with 2 or 3 nodes, secondary axes 1–4.5 cm long with 1 or 2 nodes, tertiary axes ca. 1.5 cm long with 1 node or not developed; bracts linear, ca. 5 mm long, stellate-tomentose, caducous; bracteoles linear, 3–4 mm long, stellate-tomentose, caducous; pedicels densely stellate-tomentose, 4–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 8–10 mm × ca. 6 mm, densely covered with stellate-tomentose hairs, sometimes with capitate bristles; calyx lobes truncate, without distinct tip, ca. 1.5 mm long, sometimes with 4 minute acute tips; petal bud conical, 5–10 mm long mature petals ovate to suborbicular, 15–20 × 10–20 mm, base clawed, apex rounded, glabrous, white or pinkish white. Stamens 8, unequal, filaments curved sideways; alternipetalous stamens with 10–11 mm long filaments, anthers curved, sickle-shaped, thecae ca. 10 mm long, apex rostrate, pedoconnective ca. 5 mm long, basal crest erose, ca. 1 mm long, lateral appendages paired, filiform, 5–10 mm long; oppositipetalous stamens with ca. 10 mm long filaments, anthers S-shaped, thecae 10–12 mm long, basal crest ligular, ca. 0.5 mm long, sometimes with a pair of capillary appendages, ca. 1 mm long, lateral appendages paired, filiform, 7–8 mm long. Ovary ¾ of hypanthium in length, apex villous; style glabrous, curved at tip, 10–12 mm long; stigma minute; extra-ovarial chambers 8, extending almost to the base of the ovary. Fruits urceolate, ca. 15 × 12 mm, sparsely covered with stellate hairs or glabrous; calyx remnant truncate, persistent. Seeds ca. 0.75 mm long.

Distribution — Borneo and Philippines (Southwestern Islands).

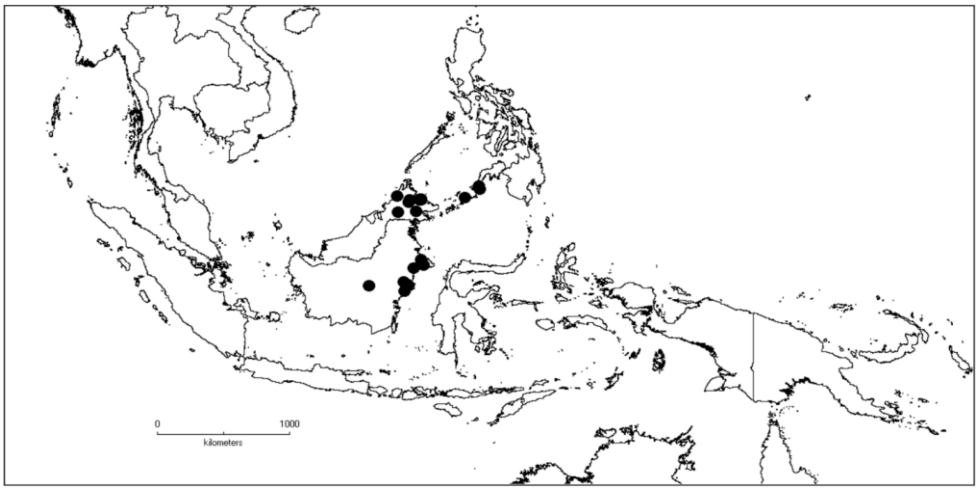
Ecology and habitat — Primary open lowland forest or on limestone at 10–930 m elevation.

Vernacular name — Borneo: *rinsim* (Kinabatangan).

Note — *Dissochaeta axillaris* is easy to distinguish from all other species by its tomentose indumentum and axillary inflorescences. Differences with *D. acmura*, another species with axillary inflorescences species, are the more subcoriaceous leaf blades and the small petal buds which are sunken inside the calyx lobes. The distribution of those two species does not overlap. Sometimes this species is misidentified as *D. annulata*, which has leaf blades with a subcordate base and terminal inflorescences.

Selected specimens examined — **MALAYSIA.** Sabah: Beluran, Bidu-Bidu Forest Reserve, 1 Mar 1991, *Maikin & Lideh SAN 131046* (L); Bongol, 365 m, *Haviland 1385* (K); Sandakan, Long Manis, 9 Aug 1962, *Mikil SAN 31570* (BO, K, L); *Ibid.*, Myburgh, Oct-Dec 1921, *Elmer 20106* (BM, BO, K, L, P, U); *Ibid.*, Kabili-Sepilok FR., 26 Jun 1937, *Enggoh BNB 7270* (K, L); *Ibid.*, Sebuga, *Ramos BS 1758* (K, PNH); Beluran, Bongaya FR, 45 m, 17 Jul 1975, *Aban & Kodoh SAN 81978* (K, L); Lahad Datu, Danum Valley, 22 Jul 1986, *Leopold et al. SAN 114565* (K, L). **INDONESIA.** Central Kalimantan: Semurung, Sungai Tarik, 18 Jul 1908, *Winkler 3033* (BM, BO, BR, K, L). East Kalimantan: Samarinda, Loa Haur, 60 m, 12 May 1952, *Kostermans 6846* (BO, K, L, PNH); East Kutai, Sungai Susuk Region, 26 Jun 1951, *Kostermans 5452* (BO, K, L); West Bengalon, Sebongkok Utara, 102 m, 6 Apr 1996, *Ambriansyah & Arbainsyah AA 1667* (BO, K, L, P); Samboja, 50 m, 6 Jul 1995, *Ambriansyah et al. AA 1280* (K, L, P); Sangkulirang, Mangapu, 10 m, 19 Jun 1937, *Aet 739* (BO, L);

Sebulu, 50 m, 1 Dec 1980, *Kato & Wiriadinata B-6995* (BO, L). West Kalimantan: Ketapang, Gunung Palung National Park, Cabang Panti, 930 m, 20 Oct 1997, *Laman et al. 1357* (BO, K). **PHILIPPINES.** Basilan: Nov 1912, *Miranda FB 17872* (BM, K, L, P). Mindanao: St. Cruz Island, Sapamoro, 20 Dec 1961, *Olsen 989* (L). Sulu: Jolo, Mt. Daho, Sep 1924, *Ramos & Edaño BS 43902* (L, P).



Map 3-5. Distribution of *D. axillaris* (●).

7. *Dissochaeta bakhuizenii* Veldkamp — Fig. 3-6, Map 3-4

Dissochaeta bakhuizenii Veldkamp, Blumea 24: 443. 1979. — Type: *H.A.B. Bünnemeijer 1053* (holo L [L0537231!]; iso BO [BO1744599!, BO1747935!], PNH), Indonesia, West Sumatra, Ophir District, Tanang Taloe, 1100 m elev., 15 Jun 1917.

Dissochaeta microplectrosa J.F.Maxwell, Gard. Bull. Singapore 33: 313, fig. 3. 1980. — Type: *J.A. Lörzing 13673* (holo L [L0537283!]; iso BO!), Indonesia, North Sumatra, Karoland, Mount Sinabung, 1400 m elev., 19 Aug 1928.

Neodissochaeta reticulata auct. non. Bakh.f.: Bakh.f., Contr. Melastom.: 143. 1943. *p.p.*, excl. type.

Dissochaeta sagittata auct. non. Blume: Bakh.f., Contr. Melastom.: 233. 1943. *p.p.*, excl. type.

Climbing up to 30 m in height. Branchlets terete, 3–5 mm in diameter, greyish or brown stellate-puberulous with small bristle enations; nodes swollen, interpetiolar ridge distinct with collar-shaped ridge or crest-like; internodes 5–10 cm long. Leaves: petioles flattened, 10–15 mm long, stellate-furfuraceous; blades elliptic or ovate-elliptic, 7.5–13.5 × 3–5.25 cm, membranous, base rounded, margin entire, apex acuminate, tip ca. 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, glossy green, abaxially densely, brown, short stellate-puberulous. Inflorescences terminal, up to 25 cm long, manyflowered; main axis glabrous to sparsely stellate-puberulous, rarely bristly; primary axes up to 14 cm long with 4 or 5 nodes, secondary axes up to 5 cm long with 2 or 3 nodes, tertiary axes up to 2 cm long with 1 or 2 nodes; bracts and bracteoles minute, inconspicuous, caducous; pedicels sparsely stellate-furfuraceous, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate tubular, 2–5 × 1–3 mm, sparsely stellate-puberulous or nearly glabrous, somewhat 8-ridged; calyx truncate with 4 undulate lobes, widened, ca. 1 mm long, glabrous; petal bud conical, 3–5 × 2–3 mm; mature

petals ovate, 4–5 × ca. 4 mm, base clawed, apex rounded, glabrous with ciliate margin, pale pink to violet. Stamens 8, equal or subequal, filaments straight; alternipetalous stamens with 4–6 mm long filaments, anthers oblong or lanceolate, straight, thecae 4–5 mm long, yellow, pedoconnective ca. 0.5 mm long, basal crests triangular with a small pair of acute auricles, 1.5–2 mm long, lateral appendages absent or prolonged from basal crest, 1–2 mm long; oppositipetalous stamens with 2.5–3 mm long filaments; anther oblong-lanceolate, straight, thecae 3–4 mm long, yellow, basal crest ligular, 1–1.5 mm long, lateral appendages a minute pair of auricles or absent. Ovary half as long as hypanthium, apex puberulous; style glabrous, curved at top, 10–12 mm long; stigma minute; extraovarial chambers 8, extending to the middle of the ovary. Fruits ovoid or subglobose, 4–5 × 3–4 mm, glabrous, often with 8 lines, apex mammiform; calyx lobe remnants persistent. Seeds ca. 0.4 mm long.

Fig. 3-6. *Dissochaeta bakhuizenii*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1103* (BO, L).

Distribution — Peninsular Malaysia, Sumatra and Java (West).
Ecology and habitat — Secondary forest, montane forest or near a crater in open forest, at 700–1550 m elevation.
Vernacular names — Sumatra: *sanduduk* (Batak); *pulutu* (Mentawai). Java: *harendong areuy* (Sundanese).
Note — This species can easily be distinguished by the presence of only fertile stamens without any lateral appendages and fruits with a mammiform apex. The mammiform apex on the fruits resembles that of *D. nodosa* from Sumatra and *D. rectandra* from Peninsular Malaysia. In the indumentum of the lower leaf surface, it resembles *D. inappendiculata* Blume and it is sometimes misidentified when vegetative only.
Selected specimens examined — **MALAYSIA.** Pahang: Cameron Highlands, Robinson's Falls, 1600 m, 16 Apr 1978, *Maxwell 78-197* (L); *Ibid.*, 1400 m, 20 Mar 1992, *Klackenberg & Lundin 673* (L); Fraser's Hill, 1550 m, 27 Sep 1978, *Maxwell 78-368* (L). Perak: Bukit Larut, Dec 1883, *King's collector 5284* (L); *Ibid.*, Gunung Hijau, 1320 m, 13 Jul 2006, *Kamarul Hisham et al. FRI 52047* (BO, L). Selangor: Genting Highlands, Gunong Ulu Kali, 1200 m, 9 Apr 1978, *Maxwell 78-83* (L). **INDONESIA.** Aceh: Mt. Leuser, Gunung Bandahara, 800–1000 m, 20 Mar 1975, *de Wilde & de Wilde-Duyfjes 15596* (BO, K). Jambi: Kerinci, Kayu Aro, 850 m, 21 Oct 1954, *Meijer 3007* (BO); *Ibid.*, Sungai Kumbang, 1400 m, 4 Apr 1914, *Robinson & Boden-Kloss s.n.* (BM). Mentawai Islands: Siberut, 10 Sep 1924, *Boden-Kloss SFN 12282* (BO, K). North Sumatra: Karo, Mount Sinabung, 1400 m, 19 Aug 1928, *Lörzing 13673* (BO, L); *Ibid.*, Road from Siantar to Berastagi, 1000 m, 21 Feb 1932, *Bangham & Bangham 951* (K); Tapanuli, Between Sidikalang and Pongkolan, 1200 m, 27 Mar 1954, *Alston 14790* (BM, BO, PNH); Prapat, Gunung Batu Lopang, 1400 m, 8 Jul 1972, *de Wilde & de Wilde-Duyfjes 13528* (BO, K); Sibolangit, Bandar Baru, 800 m, 17 Jun 1916, *Lörzing 4349* (BO); Sipirok, Dolok Sibual-Buali, 1200 m, 8 Mar 1983, *Zahro 69* (BO). West Sumatra: Ophir, Tanang Talu, 1100 m, 15 Jun 1917, *Bünnemeijer 1053* (BO, L) Lubuk Sikaping, Mt. Gadang, 700 m, 15 Jun 1953, *van Borssum-Waalkes 1893* (BO, K); Batu Sangkar, Mount Sago, Puncak Pato, 1200 m, 10 Mar 1989, *Nagamasu 3782* (ANDA). Banten: Between Citorek & Muncang, 800 m, 22 Jun 1911, *Backer 1839* (BO). West Java: Mt. Salak, Gunung Bunder to Kawah Ratu, 1300 m, 8 Jan 1941, *de Voogd & Bloembergen s.n.* (BO, L); *Ibid.*, Cangkuang, 1000 m, 16 Sep 1985, *van Balgooy 5161* (BO, L, P); Mt. Halimun, Malasari, 1055 m, 10 Oct 2017, *Kartonegoro 1103* (BO, L); Mt. Sembung, *Backer 12256* (BO).

8. *Dissochaeta barbata* (Triana ex C.B.Clarke) Karton.**, comb. nov. —** Map 3-4

Anplectrum barbatum Triana ex C.B.Clarke in Hook.f., Fl. Brit. India 2: 546. 1879. — *Backeria barbata* (Triana ex C.B.Clarke) Raizada, Indian Forester 94: 435. 1968. — *Diplectria barbata* (Triana ex C.B.Clarke) Franken & M.C.Roos in Veldkamp et al., Blumea 24: 415, fig. 3A. 1979. — Type: *N. Wallich 4082* (holo K-W [K000859568!]), Myanmar, Martaban, Chappedong.
Anplectrum stellulatum Geddes, Bull. Misc. Inform. Kew 1928: 236. 1928. — Lectotype (designated here): *A.F.G. Kerr 5870* (lecto K [K000859555!]; isolecto BK [BK-257160!], BM!), Thailand, Phitsanulok, Nakhon Thai, 200 m elev., 17 Apr 1922.
Anplectrum cyanocarpum auct. non. Triana: Kurz, Forest Fl. Burma 1: 508. 1877. *p.p.*, excl. type.
Anplectrum glaucum auct. non. Triana: C.B.Clarke in Hook.f., Fl. Brit. India 2: 545. 1879. *p.p.*, excl. type.

Dissochaeta divaricata auct. non. G.Don: Clausing in Renner et al., Fl. Thailand 7(3): 423. 2001. *p.p.*, excl. type.

Climbing up to 10 m in height. Branchlets terete, 3–5 mm in diameter, glabrous or with scattered minute stellate hairs; nodes swollen, with interpetiolar ridge; internodes 4–6.5 cm long. Leaves: petioles terete, 10–15 mm long, glabrous to stellate-puberulous, covered with bristle hairs at dorsal side; blades ellipticoblong to oblong, 6.5–13 × 2.5–5 cm, chartaceous, base rounded, margin entire, apex acuminate, tip ca. 1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially with sparsely stellate hairs at nerves, with a pair of basal glandular patches. Inflorescences terminal, up to 30 cm long, many-flowered; main axis terete, glabrous or stellate-puberulous; primary axes up to 28 cm long with 8 or 9 nodes, secondary axes up to 10 cm long with 4 or 5 nodes, tertiary axes up to 2 cm long with 1 or 2 nodes, quarternary axes up to 1 cm long with 1 node; bracts linear, 2–4 mm long, stellate puberulous; bracteoles linear, 3–4 mm long, stellate puberulous; pedicels stellate-puberulous, 4–6 mm long in central flowers, 2–4 mm long in lateral flowers. Hypanthium campanulate-angular to suburceolate, 5–6 × 2–3 mm, slightly 4-ridged, glabrous or stellately puberulous; calyx lobes truncate, without 4 distinct tips, ca. 1 mm long; petal bud conical, 4–5 mm long; mature petals ovate-elliptic, ca. 7 × 4–4.5 mm, not reflexed, base clawed, apex acute, pink to purplish. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with 3–4 mm long filaments, thecae rudimentary, slender, terete, ca. 4 mm long, pedoconnective undeveloped, basal crest triangular, ca. 2 mm long, acute or erose at tip, thin, lateral appendages in a pair, linear to filiform, ca. 2 mm long; oppositipetalous stamens with 5–6 mm long filaments, anthers thick, curved, S-shaped, thecae 8–9 mm long, yellow, apex rostrate, basal crest triangular, ca. 1 mm long, basal appendages bifid, 1–2 mm long. Ovary ⅔ of hypanthium in length, apex glabrous; style glabrous, 13–15 mm long, curved at the end, slender, pink; stigma minute; extra-ovarial chambers 4, oppositipetalous, extending almost to the base of the ovary. Fruits urceolate, 7–8 × 4–5 mm, glabrous; calyx lobe remnants persistent. Seeds numerous, ca. 0.75 mm long, cuneate.

Distribution — Myanmar, Indochina, South China (Hainan; fide Chen & Renner 2007) and Thailand.

Ecology and habitat — Mixed deciduous and disturbed evergreen forest to mountainous forest at 90–1500 m elevation.

Vernacular name — *kyar ma naing* (Myanmar), 藤牡丹, *teng mu dan* (China).

Note — *Dissochaeta barbata* resembles *D. divaricata* in the hypanthium and fertile stamens, with the alternipetalous stamens staminodal and the oppositipetalous ones fertile. *Dissochaeta barbata* differs in having a subglabrous indumentum in most parts and in possessing a pair of glandular patches on the base of leaf blades underneath. This is the only known species that is completely distributed outside the Malesian region.

Selected specimens examined — **MYANMAR.** Ban Han: *Bon s.n.* (P). Martaban: Chappedong, *Wallich 4082* (K). Tanintharyi: Yaphyu, Alel Taung, Kyaukshut Village, 297 m, 24 Mar 2015, *Armstrong et al. 627* (NY). Tenasserim: 31 May 1869, *Helfer 2290* (K), Kallin Kwan Chaung, 60 m, 10 Feb 1926, *Parkinson 1691* (K); Mergui, *Griffith KD 2289* (K). **CAMBODIA.** Chuo Chan, *Pierre s.n.* (BM, K, L). **VIETNAM.** Bien Hoa: Chiao Pang, Mar 1877, *Pierre s.n.* (P). Bum Mo: 18 May 1921, *Hayata 337* (P). Haut Donnai: Blao, 1000 m, 21 Feb 1933, *Poilane 22026* (L, P). Khanh Hoa: Dien Khanh, Hon Ba, 900 m, 24 Jun 2004, *Soejarto & Ninh 13310* (L, P). Kontum: Dakto, Ngok Guga, 1000 m, 27 Nov 1946, *Poilane 35651* (L, P). Lang Go Rum: Cu Bi, 600 m, 28 Jul 1925, *Poilane 12234* (P). Nghe An: Con Cuong, Ye Khe, 16 Oct 2008, *Du et al. 3009* (K). Quang Duc: Dak Song, 800 m,

19 Mar 1953, *Schmid s.n.* (P). Quang Nam: Moi Se Go, 1500 m, 25 Feb 1941, *Poilane 31700* (P). Quang Tri: Lang Vieng Ap, 400 m, 13 Jun 1924, *Poilane 10854* (L, P). **THAILAND.** Chonburi: Kao Re Chan, 600 m, 21 Apr 1931, *Lakshnakara 739* (K). Kanchanburi: Thong Paphum, 19 Apr 1967, *Nimanong 89* (L). Petchaburi: Khao Cong, 8 Jan 1929, *Kerr 16573* (BM, K, L); Kaeng Krachan, Panoen Thung, 100 m, 27 Jan 2005, *Williams et al. 1148* (L). Phang Nga: Kapong, 100 m, 17 Feb 1929, *Kerr 17113* (BM, K); Kao Paw Ta Luang Keo, 29 Apr 1974, *Larsen 33470* (K, L, P). Phitsanulok: Nakhon Thai, 200 m, 17 Apr 1922, *Kerr 5870* (BK, BM, K). Ranong: Khlong Kam Puan, 100 m, 1 May 1973, *Geesink & Santisuk 5098* (L); Muang, 400 m, 25 Apr 2005, *Pooma et al. 5259* (L).

9. *Dissochaeta beccariana* Cogn. — Map 3-6

Dissochaeta beccariana Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 559. 1891. — *Neodissochaeta beccariana* (Cogn.) M.P.Nayar, Kew Bull. 20: 159. 1966. — Lectotype (designated here): *O. Beccari PB 2190* (lecto FI [FI007928!]; isolecto K [K000859504!]), Malaysia, Sarawak, Santubong.

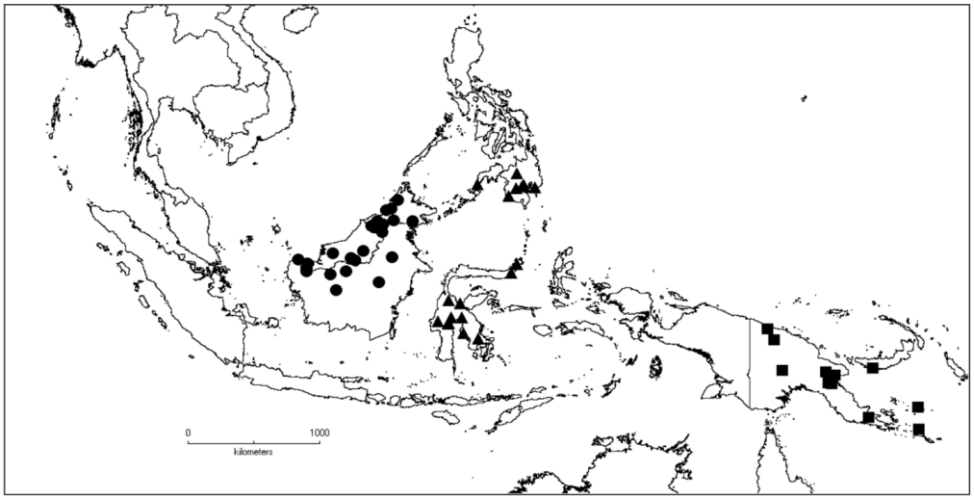
Neodissochaeta magnibracteata Bakh.f., Contr. Melastom.: 142. 1943. — Type: *J.G. Hallier 2013* (holo L [L0537263!]; iso BO [BO1865993!, BO1865994!, BO1865995!], K [K000859505!], SING), Indonesia, West Kalimantan, Soengei Kenepai, 1893.

Climbing up to 30 m in height. Branchlets terete, 3–5 mm in diameter, glabrous, sometimes with scattered bristles; nodes swollen, with a raised interpetiolar, crest-like ridge, sparsely covered with stellate hairs; internodes 8–9 cm long. Leaves: petioles terete, 1.3–1.5 cm long, glabrous except small bristles abaxiallyly; blades broadly ovate, 11–16 × 6.2–7.5 cm, subcoriaceous, base rounded, margin entire, apex acuminate, tip up to 2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous with sparsely stellate hairs on the midrib, with a basal pair of glandular patches. Inflorescences terminal, up to 22 cm long, many-flowered; main axis glabrous to sparsely stellatepuberulous; primary axes up to 18 cm long with 4 or 5 nodes, secondary axes up to 4 cm long with 1 or 2 nodes, tertiary axes ca. 1 cm with 1 node; bracts elliptic, ca. 3 × 1.2 cm, conspicuous, glabrous, white; bracteoles ovate, conspicuous, 6–8 × 6–7 mm, glabrous, white; pedicels glabrous or sparsely stellate-puberulous, 5–6 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium tubular, 4–7 × 2–3 mm, glabrous or stellately-puberulous; calyx lobes truncate, with or without 4 small undulate tips, ca. 0.5 mm long; petal bud conical, up to 4 mm long, apex with narrow acute tip; mature petals broadly ovate, 6–7 × 5–6 mm, reflexed, purple, base clawed to slightly cordate, apex acute. Stamens 8, subequal, filaments straight, light yellow; alternipetalous stamens with 4–5 mm long filaments, anthers curved, sickle-shaped, thecae 4–5 mm long, apex acute, purple, pedoconnective ca. 1 mm long, basal crest triangular, thin, erose, irregular margin 1–2 mm long, lateral appendages paired, filiform, 3–5 mm long; oppositipetalous stamens with 5–6 mm long filaments, bent at the attachment to anthers, anthers thick, slightly curved, hook-shaped, thecae 5–7 mm long, yellow, apex obtuse, basal crest thin, ligular, 1–2 m long, lateral appendages paired, filiform, 1–2 mm long. Ovary half as long as hypanthium, apex glabrous; style glabrous, 16–18 mm long, curved at the end, slender, pale yellow; stigma minute, pinkish; extra-ovarial chambers 8, shallow to nearly undeveloped. Fruits subglobose to ovoid, 5–8 × 3–6 mm, glabrous, with 8 slight lines along the surface; calyx lobe remnants persistent. Seeds ca. 0.75 mm long.

Distribution — Borneo.

Ecology and habitat — Lowland to montane dipterocarp forest in open shade at 30–1400 m elevation.

Vernacular name — *Akar* (Iban).
Note — The species is easily recognised because all parts are usually glabrous, the leaf blades abaxially have a pair of glandular patches at the base and the bracts and bracteoles are white. The most similar species is *D. glandulosa*, also with glabrous parts and glandular patches, but it has a larger, campanulate hypanthium.
Selected specimens examined — **MALAYSIA.** Sabah: Beaufort, Beaufort Rail-Line, 10 m, 22 Mar 1962, *Mikil SAN 34540* (K, L); Keningau, Pensiangan Kayu, 17 Oct 1985, *Sumbing SAN 110362* (L); *Ibid.*, Crocker Range, 1400 m, 17 Oct 1999, *Davies et al. 99128* (L); Tawau, Road Kalabakan, 26 Jul 1962, *Aban Gibot SAN 30555* (K, L); Ranau, Mt. Kinabalu, Dallas, 900 m, 5 Aug 1931, *Clemens 30342* (BM, K, L). Sarawak: *Beccari PB 2190* (FI, K); Sibu, Rejang, Jul 1893, *Haviland 3628* (BM, K); Bario, Bukit Lawi, 1500 m, 2 Aug 1985, *Awa & Lee S.50537* (L); Kuching, Gunung Penrissen, 2 May 1962, *Ilias Paie S.16326* (K); *Ibid.*, Semenggoh FR., 19 Oct 1966, *Banyeng S.26207* (BO, K, L); Belaga, Linau Balui, Sg. Nawai, 800 m, 5 Sep 1978, *Lee S.40000* (K, L); Kapit, Balleh, Menyiong, Sungai Sebatu, 500 m, 12 Nov 1979, *Othman et al. S.41368* (K, L); *Ibid.*, Wong Kijang, 25 Oct 1988, *Othman et al. S.56049* (L); Limbang, Sungai Ensungei, Tg. Long Amok, 11 Sep 1980, *George et al. S.42845* (K, L); Miri, Gunung Mulu National Park, 1400 m, 9 Mar 1990, *Yii & Abu Talib S.58277* (K, L). **BRUNEI.** Belait: Melilas, Ulu Ingei, 30 m, 5 Mar 1996, *Said BRUN 17315* (K). Temburong: Ulu Belalong, 500 m, 21 Jan 1994, *Dransfield et al. 7392* (K, L). **INDONESIA.** East Kalimantan: West Kutai, Long Ibut, 130 m, 16 Aug 1925, *Endert 2552* (BO, L); *Ibid.*, Mount Kemul, 1200 m, 26 Sep 1925, *Endert 3572* (BO, L). West Kalimantan: Pontianak, Gunung Bentuang, 200 m, 24 Jun 1989, *Burley & Tukirin 2857* (BO, L); Sungai Kenepai, 1893, *Hallier 2013* (BO, K, L); Sintang, 120 m, 18 Apr 1994, *Church et al. 1000* (BO, L); Kapuas Hulu, Mendalam Rivers, 170 m, 15 Mar 2000, *Albertus 45* (L).



Map 3-6. Distribution of *D. beccariana* (●), *D. brassii* (■) and *D. celebica* var. *celebica* (▲).

10. *Dissochaeta biligulata* Korth. — Fig. 3-7, Map 3-7

Dissochaeta biligulata Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 240. 1844. — *Anplectrum biligulatum* (Korth.) Triana, Trans. Linn. Soc. London 28: 85. 1872. — *Diplectria biligulata* (Korth.) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Neodissochaeta biligulata* (Korth.) Bakh.f., Contr. Melastom.: 140. 1943. — Lectotype (designated here):

P.W. Korthals s.n. (lecto L [L0537285!]; isolecto L [L0537284!]), Indonesia, West Sumatra, Gunung Paauw.

Dissochaeta microcarpa Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 72. 1851. — Type: *C. Gaudichaud-Beaupré 80* (holo P [P02274814!]), Singapore, Singapore Island, Feb 1837.

Dissochaeta bancana Miq., Fl. Ned. Ind. 1(1): 529. 1855. — Lectotype (designated here): *T. Horsfield 19* (lecto K [K000859500!]; isolecto K [K000859501!]), Indonesia, Bangka.

Dissochaeta celebica Blume var. *contracta* King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 54. 1900. — Lectotype (designated here): *King's collector 2911* (lecto K [K000859535!]; isolecto BM!, CAL), Malaysia, Perak, Larut, Apr 1882.

Dissochaeta scortechinii King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 55. 1900. — Lectotype (designated here): *B. Scortechini 23* (lecto K [K000859536!]; isolecto SING), Malaysia, Perak.

Dissochaeta celebica auct. non. Blume: Triana, Trans. Linn. Soc. London 28: 83. 1872; C.B.Clarke in Hook.f., Fl. Brit. India 2: 544. 1879; Cogn. in Boerl., Handl. Fl. Ned. Ind. 2: 533. 1890; Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 561. 1891; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 54. 1900; Cogn. in H.J.P.Winkl., Bot. Jahrb. Syst. 48: 108. 1913; Ridl., Fl. Malay Penins. 1: 798. 1922; Merr., Univ. Calif. Publ. Bot. 15: 224. 1929; Craib, Fl. Siam. Enum. 1, 4: 697. 1931; Bygrave & A.P.Davis, Checkl. Fl. Pl. Gymnosperms Brunei Darussalam 186. 1996; Cellin. in J.H.Beaman & C.E.Anderson, Pl. Mt. Kinabalu 5: 99. 2004. *p.p.*, excl. type.

Dissochaeta intermedia auct. non. Blume: C.B.Clarke in Hook.f., Fl. Brit. India 2: 544. 1879. *p.p.*, excl. type.

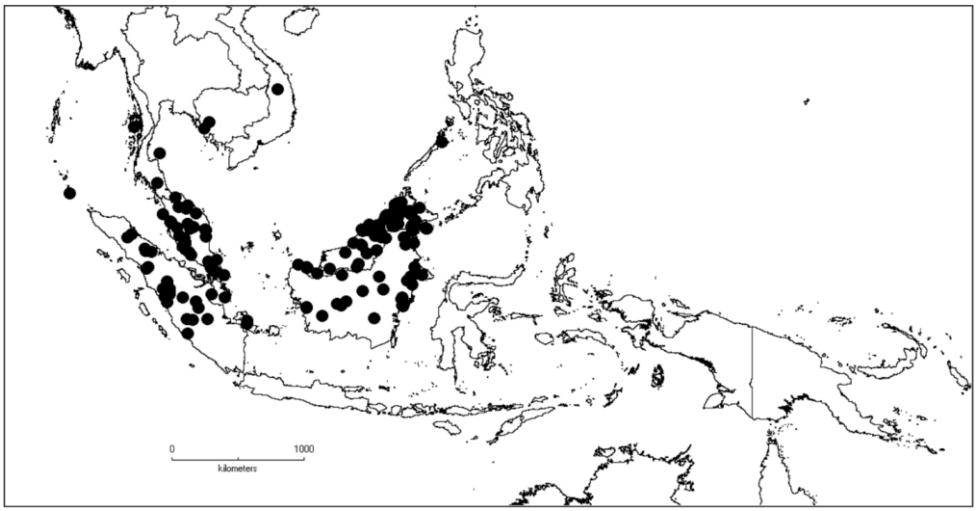
Neodissochaeta celebica auct. Non. Bakh.f.: Bakh.f., Contr. Melastom. 141. 1943. *p.p.*, excl. type.

Dissochaeta monticola auct. non. Blume: Clausing in S.S.Renner et al., Fl. Thailand 7(3): 428. 2001. *p.p.*, excl. type.

Dissochaeta intermedia Blume var. *sagittata* auct. non. J.F.Maxwell: Cellin. In J.H.Beaman & C.E. Anderson, Pl. Mt. Kinabalu 5: 99. 2004. *p.p.*, excl. type.

Climbing up to 5 m height. Branchlets terete, 3–4 mm in diameter, densely brown stellate-furfuraceous; nodes swollen, with interpetiolar line; internodes 4–6.5 cm long. Leaves: petioles terete, 6–8 mm long, brown stellate-furfuraceous; blades ovate-oblong or elliptic-oblong, 7–15 × 2.5–5.4 cm, membranous, base rounded, margin entire, apex acuminate, tip ca. 1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, yellowish-green, abaxially densely covered with minute brown stellate-furfuraceous hairs. Inflorescences terminal, 10–16 cm long, many-flowered; main axis angular, brown stellate-furfuraceous; primary axes up to 15 cm long with 6–8 nodes, secondary axes 2–4 cm long with 2 or 3 nodes, tertiary axes 0.5–1 cm long with 1 node; bracts linear, ca. 3 mm long, brown stellate-furfuraceous; bracteoles linear, 2–2.5 mm long, brown stellate-furfuraceous; pedicel densely stellate-furfuraceous, 1–2 mm long in central flowers, ca. 0.5 mm long or absent in lateral flowers. Hypanthium suburceolate, 3–4 × 2–2.5 mm, brown stellate-furfuraceous; calyx lobes truncate with 4 undulate tips, ca. 1 mm long; petal buds conical, 2–3 mm long, glabrous; mature petals ovate to elliptic, 5–6 × 3–3.5 mm, reflexed, base clawed, apex obtuse, glabrous, white or pinkish-white, sometimes transparent. Stamens 4, equal, alternipetalous, filaments curved sideways, ca. 5 mm long, white, pinkish at base, anthers oblong-lanceolate, thecae 3.5–5 mm long, straight, pink, pedoconnective ca. 1 mm long, basal crest triangular or erose with irregular margin, yellow, ca. 0.5 mm long, lateral appendages paired, filiform, 2–3 mm long. Ovary ¾ of hypanthium in length, apex villous; style glabrous, ca. 9 mm long, pointing in direction opposite to filaments, curved at

tip; stigma minute; extra-ovarial chambers 4, shallow, reaching to upper third of ovary. Fruits globose, ca. 6 × 4–5 mm, glabrous, bright green, slightly 8 vertical lines present; calyx lobes remnant persistent. Seeds ca. 0.5 mm long.
Distribution — India (Nicobar Islands), Myanmar, Indochina (Cambodia and Vietnam), southwards through Thailand to western Malesia (Malay Peninsula, Sumatra and Borneo) and Philippines (Palawan).
Ecology and habitat — Secondary lowland forest, opened primary forest or disturbed forest, dipterocarp forest or montane forest from sea level to 1500 m elevation.
Vernacular names — Sumatra: *akar kemunting* (Bintan). Borneo: *kemanti Omang* (Iban); *luka kalapat* (Penan).
Note — Generally, recognised as *D. celebica* by most authors because of the similarity in the small flowers with only four fertile stamens. *Dissochaeta biligulata* differs from *D. celebica* by its dark brown furfuraceous indumentum on the leaves below, a truncate calyx with lobes with undulate tips, a white or pinkish-white corolla and globose fruits with distinct lines. In *D. celebica*, the indumentum underneath the leaf blades is less dense, the calyx lobes are glabrous, purple and have a triangular apex, the corolla is dark purple and the fruit ovoid without distinct lines. This species is very common in the open dipterocarp forest in western Malesia.



Map 3-7. Distribution of *D. biligulata* (●).

Selected specimens examined — **INDIA.** Nicobar Islands: East West Road, 20 Jul 1976, *Balakrishnan 3899* (L). **MYANMAR.** Tenasserim: Domel Island, 14 Jan 1829, *Helfer 2286* (K). **CAMBODIA.** Kah Kong: Lhuom Rovaal, 600 m, 27 Feb 1966, *Anon 758* (P); Mount Rodam Meong Daeum, 650 m, 23 Feb 1966, *Martin 348* (P). **VIETNAM.** Ha Tay: Mount Bavi, Tonkin River, Jun 1908, *dÁlleizette 2420* (L). **THAILAND.** Narathiwat: Sungei Kolok, 4 Mar 1974. *Larsen 32923* (K, L). Pattalung: Tamote Falls, 225 m, 9 Aug 1986, *Maxwell 86-552* (L). Pattani: Bukit, 25 Jan 1931, *Put 3635* (K). Surat Thani: Ko Panghan, 3 Jun 1927, *Put 778* (BM, K). Trang: Khao Pap Pa, 13 Mar 1974, *Larsen 33279* (P). Yala: Nikhom Kulong, 500 m, 31 Dec 1972, *Santisuk & Nimanong BKF 54194* (K, L). **MALAYSIA.** Johor: Kluang, 24 Nov 1967, *Alphonso, Sanusi & Sidek S.200* (K, L); Gunung Pulai, 550 m, 29 Jan 1978, *Maxwell 78-24* (L). Malacca: *Griffith KD 2288* (BO, K). Negri Sembilan: Gunung Angsi, 730 m, 25 Nov 1923, *Nur SFN 11708* (BO, K); Nilai, near Seremban, Jinderam Estate,

90 m, 22 Sep 1957, *Shah 129* (BO, K, L). Pahang: Sungai Tahan, 27 Jul 1936, *Kiah SFN 31912* (BO, K, PNH); Fraser's Hill, Girdle Road, 1200 m, 26 Aug 1959, *Shah & Kadim 680A* (BO, K, L). Penang: *Wallich 4050* (K, P); Government Hill, 20 Jan 1903, *Curtis 3806* (BM, BO). Perak: *Scortechini 23* (K); Larut, *King's collector 2911* (BM, K); Trolak, 22 Mar 1967, *Chelliah KEP 104685* (K, L); Ulu Bubong, 120–180 m, Jun 1886, *King's collector 10290* (BM, K). Selangor: Ulu Gombak, 21 Aug 1968, *Teo & Purseglove 165* (K, L); Kuala Lumpur, 5 Mar 1915, *Ridley s.n.* (BM, K, L). Terengganu: Kemaman, Sungai Nipah, 24 Jun 1932, *Corner SFN 25848* (K). Sabah: Beaufort, Klas FR, 23 Jul 1973, *Dewol & Abdul Karim SAN 77821* (K, L); Keningau, Kitau, 8 Sep 1982, *Amin SAN 95456* (K, L); Kalabakan, Seranum, 21 Sep 1983, *Fidilis & Suali SAN 101240* (K, L); Lahad Datu, Danum Valley, 238 m, 6 Jul 2006, *Rosalia et al. SAN 145986* (K); Lamag, Sungai Tangkulap, 30 Jun 1983, *Amin SAN 97451* (L); Nabawan, Jalan Nabawan-Pandewan, 12 Feb 1990, *Sumbing SAN 128120* (K); Pensiangan, Pensiangan Kayu FR., 28 Jan 1994, *Fidilis SAN 136931* (K); Tawau, Oct 1922–Mar 1923, *Elmer 21840* (BM, BO, K, L, P, PNH, U); Ranau, Kampung Kiau, 30 Nov 1915, *Clemens 10122* (PNH); *Ibid.*, Kampung Merungin, 300 m, 18 Nov 1975, *Leopold & Saikeh SAN 82620* (K, L); Mt. Kinabalu, 1060 m, 14 Jun 1961, *Chew, Corner & Stainton RSNB 68* (K, L); *Ibid.*, Kelawat, near Tamparuli, 900 m, 2 Mar 1954, *Darnton 230* (BM, L); Sipitang, Mesapol FR, 30 m, 25 Nov 1968, *Ogata 11671* (L). Sarawak: Baram, Kelabit Highland, 1066 m, 6 Nov 1974, *Chai S.35335* (K, L); Belaga, Sungai Murum, 600 m, 13 May 1994, *Lai et al. S.68539* (K); Kuching, Oct 1892, *Haviland 1901* (BM, K); *Ibid.*, Selang FR., 30 m, 25 Jul 1957, *Ilias Paie S.8460* (BO, K, L); Limbang, Bukit Pagon, Sungai Sipayan, 540 m, 3 Aug 1984, *Awa & Lee S.47645* (L); Marudi, Bario, 1100 m, 12 Apr 1995, *Beaman & Repin 164* (K); Miri, Lambir National Park, 5 Apr 1966, *Sibat S.25075* (BO, K, L); *Ibid.*, Riam Road, 30 m, 3 Dec 1962, *Au S.17254* (BO, K, L); Betong, Bukit Sadok, 15 Oct 1982, *Banyeng & Ilias Paie S.45085* (K, L); Dataran Tinggi Merurong, Sungai Jelalong, 330 m, 9 Oct 1984, *Othman & Yii S.48814* (K, L); Baram, Ulu Koyan, Mount Dulit, 900 m, 15 Sep 1932, *Richards 1818* (K, L). **SINGAPORE.** Feb 1837, *Gaudichaud-Beaupré 80* (P); Oct 1861, *Anderson 67* (BM, K, P); Seletar, 27 Mar 1889, *Ridley 2025* (BM); MacRitchie Reservoir 10 m, 15 Jul 1982, *Maxwell 82-194* (L); Pierce Reservoir, 60 m, 20 Oct 1957, *Burkill HMB 1227* (K, L, PNH). **BRUNEI.** Belait: Jalan Merangking-Buau, 10 Aug 1991, *Nangkat 265* (K, L); Bukit Teraja, 160 m, 27 Sep 1957, *Ashton BRUN 671* (BO, K, L). Seria: Andulau FR, 25 m, 31 Jul 1963, *Fuchs & Muller 21150* (K, L). Temburong: Batu Apoi, 350 m, 29 Oct 1991, *Simpson & Marsh 2502* (BO, K, L). **INDONESIA.** Aceh: Mt. Leuser, Gunung Bandahara, 1350 m, 20 Feb 1980, *Prawiroatmodjo 2386* (BO, K); *Ibid.*, Klut Nature Reserve, Pucuk Lembang, 40 m, 8 Jul 1985, *de Wilde & de Wilde-Duyfjes 19788* (BO). Bangka-Belitung: Bangka, *Horsfield 19* (K); *Ibid.*, Menumbing, *Teijsmann s.n.* (BM, BO, K, U). Bengkulu: Lebong Tandai, Apr 1922, *Brooks 6675* (K). Jambi: Bangko, 160 m, 10 Aug 1925, *Posthumus 687* (BO, L); Harapan Rain forest, 31 Mar 2013, *Wardi et al. BOHK 390* (BO, K). North Sumatra: Asahan, Dolok Tomuan, 1000 m, 20 Aug 1936, *Rahmat Si Boeea 9964* (L); Padang Sidempuan, Padang Lawas, Huta Imbaru, 20-21 Jun 1933, *Rahmat Si Toroes 4634* (K, L); South Tapanuli, Batang Toru, 640 m, 6 Jun 2003, *Takeuchi & Sambas 18228* (BO); Pematang Siantar, 6 Apr 1954, *Alston 15233* (BM, L); Besitang, Sikundur, 100 m, 15 Aug 1971, *Iwatsuki et al. S-401* (BO, L). Riau: Indragiri Hulu, Berapit, 13 Apr 1939, *Buwalda 6535* (BO, K, L, PNH); Rengat, Bukit Tigapuluh, 100 m, 14 Nov 1988, *Burley & Tukirin 1472* (BO, K, L). Riau Archipelago: Bintan Island, Gunung Bintan, 40 m, 12 Jun 1919, *Bünnemeijer 6114* (BO, L). West Sumatra: Tanah Datar, Lembah Anai, 600 m, 24 Dec 1983, *Rahayu & Maskuri 473* (BO, K); Batu Sangkar, Mt. Sago, 1200 m, 10 Mar 1989, *Nagamasu 3773* (BO, L); Lima Puluh Kota, Gunung Malintang, 1100 m, 18 Jul 1918, *Bünnemeijer 3587* (BO, K, L, P); *Ibid.*, Harau Valley, Sarasah Bonta, 700 m, 12 Sep 2017,

Kartonegoro 1088 (BO, L); Lubuk Sikaping, Mt. Gadang, 700 m, 15 Jun 1953, *van Borssum-Waalkes 1888* (BO); Paauw, *Korthals s.n.* (L). Central Kalimantan: Barito Ulu, 25 Jun 1990, *Ridsdale PBU 692* (BO, L); Bukit Raya, Tumbang Tapi, 100 m, 18 Jan 1983, *Veldkamp 8297* (BO, L). East Kalimantan: West Kutai, Besilau Tuwa, 20 m, 22 Jun 1925, *Endert 1593* (BO, L); Sangkulirang, Sampayau, 25 m, 9 Jun 1937, *Aet 669* (BO, K, L); East Kutai, Sungai Menubar Region, 5 m, 5 Jun 1951, *Kostermans 4960* (BO, K, L); Wanariset Research Area, Semoi Road, 20 m, 10 Mar 1992, *Ambriansyah & Arifin AA 468* (K, L); Between Papadi & Pamilau, 700–800 m, 9 Aug 1981, *Geesink 9295* (L, P); Long Iram, Maruwai, Lampunut, 310 m, 19 Mar 1999, *Kessler et al. 2657* (L); Wain River, 24 Jun 1910, *Rutten 170* (U). North Kalimantan: Tarakan, 25 Oct 1953, *Meijer 1866* (BO, K, L). South Kalimantan: Hayup, 28 Jun 1908, *Winkler 2627* (BM, BO, K, L, P). West Kalimantan: Sungai Blu'u, 1896, *Jaheri 704* (BO); Ketapang, Gunung Palung National Park, Cabang Panti, 20 m, 24 Oct 1996, *Laman et al. 110* (BO, K, L). **PHILIPPINES.** Palawan: Taytay, Ibangley, Pagdanan Range, 50–70 m, 31 Jan 1991, *Soejarto & Fernando 7458* (L); *Ibid.*, *Stone et al. PPI 368* (L).

Fig. 3-7. *Dissochaeta biligulata*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by D.S. Penneys; vouchers: *Penneys 2488* (WNC) & *Penneys 2509* (WNC).

11. *Dissochaeta bracteata* (Jack) Blume — Figure 3-8, Map 3-8

Dissochaeta bracteata (Jack) Blume, Flora 14: 495. 1831. — *Melastoma bracteatum* Jack, Trans. Linn. Soc. London 14: 9. 1823, "bracteata". — Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 129. 2010): *N. Wallich 4044* (neo K-W [K000859538!]; isoneo BM!, K-W [K000859537!]), Malaysia, Penang.

Dissochaeta bracteata Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot., tab. 55. 1842, nom. illeg., non Blume (1831). — *Dissochaeta korthalsii* Miq., Fl. Ned. Ind. 1(1): 528. 1855. — Lectotype (designated here): *P.W. Korthals s.n.* (lecto L [L0822680!]; isolecto L [L0822679!]), Indonesia, West Sumatra, Doekoe.

Dissochaeta bracteosa Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 76. 1851. — Lectotype (designated here): *C. Gaudichaud-Beaupré 97* (lecto P [P02274815!]; isolecto P [P02274816!]), Malaysia, Pulo Pinang, Mar 1837.

Climbing up to 15 m in height. Branchlets terete, 3–5 mm in diameter, stellate-puberulous; nodes swollen, interpetiolar ridge undulate, densely brown pubescent; internodes 8–11 cm long. Leaves: petioles terete, 5–10 mm long, densely brown stellate-furfuraceous; blades ovate, 6–13 × 3–7 cm, chartaceous, base cordate to subcordate, margin entire, apex acuminate, tip 0.3–0.5 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, glossy, with prominent nervation, abaxially glabrous to sparsely stellatepunctate, young leaves densely stellate-furfuraceous. Inflorescences terminal, up to 20 cm long, many-flowered; main axis stellate-puberulous; primary axes up to 15 cm long with 5 or 6 nodes, secondary axes 2.5–3.5 cm long with 1 or 2 nodes, teriary axes 0.8–1 cm long with 1 node; bracts ovate, 10–12 × 5–6 mm, densely brown stellate-furfuraceous; bracteoles ovate or ovate-oblong, 5–9 × 2–4 mm, reflexed inside, enclosing the flower bud, densely stellate-furfuraceous; pedicels brown stellate-furfuraceous, 4–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium tubular, 3–8 × 2–4 mm, densely brown stellate-furfuraceous, ridge conspicuous; calyx lobes truncate with rounded or triangular tip, 1–2 mm long, stellate-furfuraceous; petal bud conical, 1–4 mm long; mature petals ovate, ca. 10 × 5–7 mm, reflexed, base clawed, apex rounded, glabrous or with appressed hairs at base inside, bright purple with white lines. Stamens 8, unequal, filaments curved sideways, whitish; alternipetalous stamens with 6–8 mm long filaments, anthers linear or lanceolate, curved, sickle-shaped, thecae 13–15 mm long, pink, pedoconnective 3–4 mm, basal crests erose or triangular, irregular, ca. 1 mm long, yellow, lateral appendages paired, filiform, 3–5 mm long, sometimes divided at the apex; oppositipetalous stamens with 5–6 mm long filaments, slightly bent at apex, stipopodium ca. 1 mm long, anthers lanceolate, S-shaped, locule 8–10 mm long, thick, bright white or yellow with pink apex, basal crest hastate, 1–2 mm long, yellow, lateral appendages paired, filiform, 4–5 mm long. Ovary half as long as the hypanthium, apex pubescent; style glabrous or subglabrescent, 6–10 mm long, curved at top; stigma minute; extra-ovarial chambers 8, extending to the middle and the base of the ovary. Fruits urceolate, elongate, 6–10 × 3–5 mm, stellate-puberulous to nearly glabrous, yellowish-green when unripe; calyx lobes caducous. Seeds ca. 0.5 mm long.

Distribution — Thailand (Chanthaburi), Peninsular Malaysia (Kedah, Malacca and Penang), Sumatra (North, West and Belitung), Java (West), Borneo (Sabah and Sarawak), Philippines (Panay) and Moluccas (Ceram).

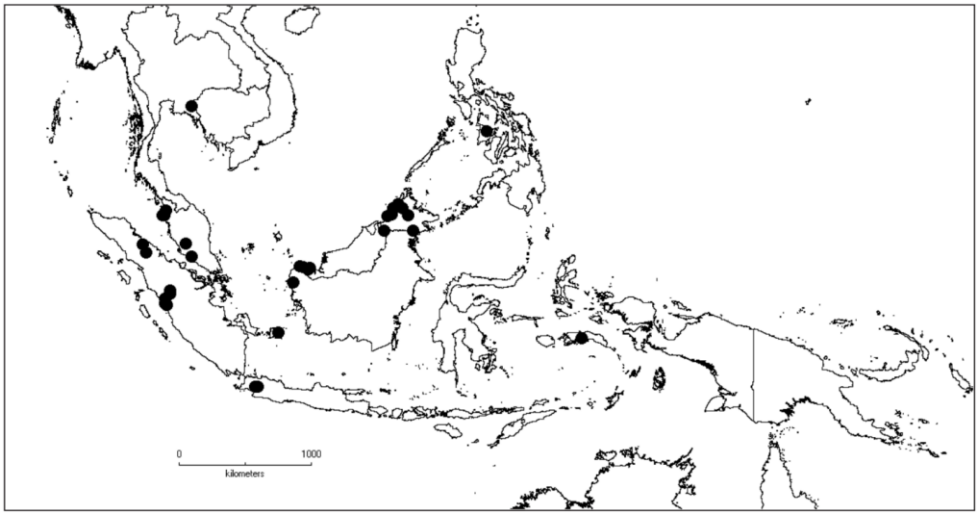
Ecology and habitat — Secondary montane forest or on the edge of the forest and open area at 600–900 m elevation.

Vernacular names — Peninsular Malaysia: *oosa* (Malay). Sumatra: *andor si ramu dalik* (Batak).

Fig. 3-8. *Dissochaeta bracteata*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by A. Kartonegoro; vouchers *Kartonegoro 1074* (BO, L).

Note — *Dissochaeta bracteata* has distinct ovate bracteoles, which cover the hypanthium when in bud. It is sometimes confused with *D. annulata*, which has similar robust chartaceous leaves and inflorescences, but differs in having a much more glabrous or puberulous abaxially leaf surface. The hypanthium of *D. bracteata* is urceolate, more campanulate in *D. annulata*. Even though the species has a wider distribution than any other species, its occurrence is rather scattered in each region with low numbers of samples.

Specimens examined — **THAILAND.** Chanthaburi: Khao Soi Dao, 1800 m, 28 Apr 1930, *Kerr 19192* (BM, K). **MALAYSIA.** Kedah: Gurun, Gunung Jerai, 16 Jul 1994, *Zainudin et al. 5131* (K, L). Malacca: *Maingay KD 791 (1217)* (K). Penang: *Wallich 4044* (BM, K); *Ibid.*, Mar 1837, *Gaudichaud-Béaupre 97* (P); Government Hill, Apr 1890, *Curtis 2298* (K); Penang Hill, 730 m, 14 Sep 1966, *Ding Hou 839* (K, L); Batu Pulau, 1905, *Fox s.n.* (BM). Selangor: Genting Highlands, Gunong Ulu Kali, 1600 m, 3 Jun 1978, *Maxwell 78-308* (L). Sabah: Beaufort, Quary, 12 Sep 1970, *Aban Gibot SAN 66948* (K); Beluran, Ulu Tungud Forest Reserve, 600 m, 24 Jul 2005, *Joanes et al. SAN 146905* (K); Papar, Keningau Road, 20 Feb 1975, *Abdul Karim SAN 78421* (K, L); Penampang, Inobong, 22 Jul 2010, *Aloysius et al. SAN 152101* (L); Ranau, Mount Kinabalu, Kota Belud to Kibayo, 28 Oct 1915, *Clemens 9816* (BO, PNH); *Ibid.*, Dallas, 900 m, Sep 1931, *Clemens 30339* (BO, K, L); *Ibid.*, Between Kota Belud and Kaliau, 450 m, 11 Mar 1954, *Darnton 505* (BM); *Ibid.*, Nosurong, 19 May 1986, *Amin & Jarius SAN 114333* (L); Tawau, Silimpopon, St. Lucia, 22 m, 5 Jun 1940, *Orolfo 22* (K, L). Sarawak: Kuching, 19 Apr 1893, *Haviland 151* (BM, K, L); *Ibid.*, Mount Santubong, May 1961, *Bujang S.13494* (K); *Ibid.*, Belvedere 15 m, 12 Sep 1955, *Purseglove P.4353* (K, L); Lundu, Sematan, Gunung Pueh, 820 m, 23 Jun 1974, *James et al. S.34495* (K, L); *Ibid.*, Pandan, 25 May 1986, *Abang Mohtar et al. S.53018* (AAU, L). **INDONESIA.** Bangka-Belitung: Belitung Island, Manggar, *Teijsmann s.n.* (BO). North Sumatra: Deli Serdang, Bangun Purba, 175 m, 14 Mar 1925, *Lörzing 11439* (BO); Asahan, Dolok Tomouan, 1000 m, 10–15 Jun 1936, *Rahmat Si Boeea 9075* (L). West Sumatra: Padang, Limau Manis, 400 m, 5 Sep 2017, *Kartonegoro 1056* (BO, L); Lima Puluh Kota, Pangkalan Koto Baharu, 100 m, Apr 1915, *Jacobson 2412* (BO); *Ibid.*, Harau Valley, Sarasah Bonta, 500 m, 11 Sep 2017, *Kartonegoro 1074* (BO, L); Padang Panjang, 550 m, 1 Aug 1957, *Meijer 7180* (L); Pariaman, Duku, *Korthals s.n.* (L). West Java: Bogor, Bolang, Cirangsad, 600 m, 19 Jul 1912, *Backer 4139* (BO). Moluccas: Ceram, Masohi, Wae Ruwata, 150-200 m, 2 Dec 1990, *Burley & Tukirin 4325* (BO, K, L). **PHILIPPINES.** Panay: Capiz, Oct-Nov 1925, *Edaño BS 46108* (BO, P).



Map 3-8. Distribution of *D. bracteata* (●).

12. *Dissochaeta brassii* (M.P.Nayar) Karton., **comb. nov. —** Map 3-6

Neodissochaeta brassii M.P.Nayar, Kew Bull. 20: 160. 1966. — Type: *L.J. Brass 28743* (holo K [K000859607!]; iso L [L0537255!]), Papua New Guinea, Milne Bay, Woodlark Island, Kulumadau, 100 m elev., 14 Nov 1956.

Dissochaeta angiensis auct. non. Ohwi: Veldkamp, Blumea 24: 441. 1979. *p.p.*, excl. type.

Climbing up to 10 m in height. Branchlets terete, 3–4 mm in diameter, glabrescent to densely covered with brown stellate-furfuraceous hairs; nodes swollen, with interpetiolar line; internodes 4–6.5 cm long. Leaves: petioles flattened, 1.2–1.6 cm long, densely stellate-furfuraceous; blades elliptic, 9–13.4 × 3.4–6.4 cm, membranous, base rounded or emarginate, margin entire, apex acuminate, tip 1.5–1.8 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark glossy green, abaxially densely brown stellate-furfuraceous, rarely rugose. Inflorescences terminal, 15–22 cm long, many-flowered; main axis densely brown stellate-furfuraceous; primary axes up to 15.5 cm long with 3 or 4 nodes, secondary axes 3–6 cm long with 2 or 3 nodes, tertiary axes 0.6–1.8 cm long with 1 node; bracts linear, 1.5–2 cm long, densely tomentose; bracteoles minute, 1–2 mm long, caducous, densely brown stellate-furfuraceous; pedicels stellatefurfuraceous, 2–3 mm long in central flowers, 1–2 mm in lateral flowers. Hypanthium tubular or funnelform, 4–6 × 2–3 mm, densely brown stellate-tomentose; calyx lobes slightly triangular, 2–2.5 mm long; petal bud conical, 5–7 × 2–3 mm, glabrous; mature petals obovate, 7–8 × ca. 4 mm, base clawed, apex rounded, glabrous, white or pale pink. Stamens 4, equal, alternipetalous, filaments straight, 5–6 mm long; anthers oblong-lanceolate, thecae 5–6 mm long, straight, yellow, pedoconnective bent, ca. 1 mm long, basal crest ligular, up to 2 mm long, lateral appendages erose or paired, filiform with irregular margin, 1.5–2.5 mm long. Ovary ⅔ of hypanthium in length, apex pubescent; style 8–9 mm long, glabrous; stigma minute; extra-ovarial chambers 4, extending to the middle of the ovary. Fruits urceolate, obpyriform, 6–8 × 5–6 mm, glabrescent; calyx remnants caducous. Seeds ca. 0.5 mm long.

Distribution — New Guinea (Papua New Guinea).

Ecology and habitat — On the edge of forests, secondary forest or road banks at 100–700 m elevation.

Note — Veldkamp (1979) regards this species as a synonym of *D. angiensis*, which is also distributed in New Guinea and also has only 4 stamens. *Dissochaeta brassii* differs in having slightly triangular, 2–2.5 mm long calyx lobes, while *D. angiensis* has truncate, ca. 1 mm long calyx lobes. The lobes of this species will fall off when fruiting and the shape of the fruits is then sometimes similar to resembling species.

Specimens examined — **PAPUA NEW GUINEA.** East Sepik: Ambunti, Waskuk Hills, 100 m, 28 Jun 1995, *Regalado & Takeuchi 1426* (K, L). Gulf: Lakekamu, Avi Avi River, 105 m, 25 Oct 1996, *Takeuchi & Kulang 11438* (K, L, P). Milne Bay: Maneau Range, Mt. Dayman, 700 m, 17 Jul 1953, *Brass 23485* (L); Woodlark Island, Kulumadau, 100 m, 14 Nov 1956, *Brass 28743* (K, L); Misima Island, Mt. Sisa, 21 Jul 1956, *Brass 27443* (L). Morobe: Herzog Mts., above Gabensis, 680 m, 12 Jun 1991, *Takeuchi 7040* (L); *Ibid.*, *Takeuchi 7040A* (L); Lae, Markham Point, 240 m, 9 Jan 1963, *Henty NGF 14886* (BO, K, L); Along Tymne-Wago track, 600 m, 14 Mar 1963, *Hartley 11395* (K); Labu Swamp, 7 May 1990, *Takeuchi 5668* (BO, K, L). New Britain: Kandrian, Piri Longi, 400 m, 13 Mar 1965, *Sayers NGF 21952* (BO, K, L). Sepik: Lumi, Mt. Torricelli, 884 m, 22 Aug 1961, *Darbyshire 247* (K, L). Southern Highlands: Lake Kutubu, near Tage, 823 m, 21 Sep 1961, *Schodde 2189* (K, L).

13. *Dissochaeta celebica* Blume

Dissochaeta celebica Blume, Mus. Bot. 1(3): 36. 1849. — *Neodissochaeta celebica* (Blume) Bakh.f., Contr. Melastom. 141. 1943. — Lectotype (designated here): *E.A. Forsten 305* (lecto L [L0537287!]; isolecto L [L0625953!]), Indonesia, North Sulawesi, Res. Menado, Tomohon, G. Mahawoe, Feb 1841.

Dissochaeta subviridis Elmer, Leafl. Philipp. Bot. 4: 1193. 1911. — Lectotype (designated here): *A.D.E. Elmer 10577* (lecto GH [GH00072246!]; isolecto BISH [BISH1003278!], BM [BM000944483!], BO [BO1751865!], CAS [CAS0033376!], E [E00680851!], HBG [HBG514874!], K [K000859610!], L [L0537286!], MO [MO-313697!], NY [NY00228566!], P [P02274813!], U [U0004006!], US [US00120533!]), Philippines, Mindanao, Davao Del Sur, District of Davao, Todaya (Mt. Apo), 3500 ft., May 1909.

Climbing up to 8 m in height. Branchlets terete, ca. 3 mm in diameter, glabrescent to sparsely covered with brown stellate hairs, more densely so in young parts; nodes swollen, with an interpetiolar line; internodes 5.7–6 cm long. Leaves: petioles terete, 1–1.2 cm long, densely stellate-furfuraceous; blades ovate-elliptic, 8.4–10 × 3.3–4.5 cm, membranous, base rounded to nearly emarginate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely covered with brown stellatefurfuraceous hairs. Inflorescences terminal or in the upper leaf axils, up to 30 cm long, many-flowered; main axis densely covered with brown stellate-furfuraceous hairs; primary axes up to 28 cm long with 5 or 6 nodes, secondary axes up to 6 cm long with 2 or 3 nodes, tertiary axes 1.2–2 cm long with 1 or 2 nodes; bracts lanceolate, 8–11 mm long, densely stellate-furfuraceous, caducous; bracteoles linear, 3–5 mm long, densely stellate-furfuraceous, caducous; pedicels covered with brown stellate hairs, 1–2 mm long in central flowers, ca. 0.5 mm long in lateral flowers or latter subsessile. Hypanthium campanulate funneliform, 3–4 × 1–1.5 mm, densely covered with brown stellate-furfuraceous hairs; calyx lobes truncate with small triangular tips, 1–3 mm long, glabrous, purple inside; petal bud conical, 2–3.5 mm long; mature petals obovate, 3–4 × ca. 2 mm long, reflexed, base clawed, apex rounded, dark purple, glabrous. Stamens 4, equal, alternipetalous; filaments glabrous, curved sideways, 4–5 mm long, bent at the end, white pinkish; anthers oblong, curved, thecae 3–4 mm long, yellowish-white, pedoconnective ca. 1 mm long, basal crest triangular or rounded, ca. 0.5 mm long, lateral appendages filiform, 2–3 mm long, paired, with irregular margin, brownish. Ovary ¾ of hypanthium in length, apex pubescent; style glabrous, 5–6 mm long, curved at the end, purple; stigma minute; extra-ovarial chambers 4, shallow. Fruits subglobose or ovoid, 5–8 × 3–5 mm long, densely covered with stellate hairs and becoming glabrous when mature, calyx lobes persistent, 1–3 mm long. Seeds numerous, ca. 0.5 mm long.

Distribution — Sulawesi and Philippines (Mindanao).

Note — See under *D. biligulata*.

Key to varieties of *D. celebica*

1 Calyx lobes truncate with small triangular tips, ca. 1 mm long, glabrous, purple inside; petal bud 2–2.5 mm long; fruits ovoid, 5–8 × 3–5 mm long, without longitudinal lines ... . **var. *celebica***

1 Calyx lobes slightly triangular, 2–3 mm long, densely brown stellate-furfuraceous; petal bud 3–3.5 mm long; fruits subglobose, 6–8 × 4–5 mm long, slightly 8-lined .... **var. *longilobata***

13.1. *Dissochaeta celebica* Blume var. ***celebica*** — Fig. 3-9, Map 3-6

Hypanthium campanulate-funneliform, 3–4 × ca. 1 mm long, densely covered with brown stellate-furfuraceous hairs; calyx lobes truncate with small triangular tips, ca. 1 mm long, glabrous, purple inside; petal bud conical, 2–2.5 mm long. Fruits ovoid, 5–8 × 3–5 mm long, densely covered with stellate hairs and becoming glabrous when mature, calyx lobes persistent, erect, ca. 1 mm long.
Distribution — Sulawesi and Philippines (Mindanao).

Fig. 3-9. *Dissochaeta celebica* var. *celebica*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by Supriatna; voucher: *Widjaja et al. 9846a* (BO).

Ecology and habitat — Open montane forest at 600–1900 m elevation.
Vernacular names — Philippines: *getungu ulangan* (Zamboanga); *lebong* (Cebuano); *tolasola* (Bagobo).
Specimens examined — **INDONESIA.** Central Sulawesi: Poso, Between Boro and Sungai Malei, 1700 m, 11 Aug 1937, *Eyma 1656* (BO); Lore Lindu Area, Sopu Valley, 1000 m, 22 May 1979, *de Vogel 5517* (BO, K, L). North Sulawesi: Tomohon, Mt. Mahawu, Feb 1841, *Forsten 305* (L); *Ibid.*, 800 m, 13 Feb 2009, *Girmansyah 1187* (BO); Bolaang Mongondow, Mt. Ambang, Lake Moat Area, 1000 m, 14 Apr 1985, *de Vogel & Vermeulen 7177* (BO, L). South Sulawesi: Malili, between Takolekaju and Tawi Baru, 30 Oct 1938, *Eyma 4168* (BO); Masamba, between Mabusa and Sae, 1700 m, 21 Jul 1937, *Eyma 1167* (BO, L); Rantepao, on the way to Palopo, 14 Feb 1993, *Afriastini 2125A* (BO, K, L); Tojambu, 1000 m, 28 Jun 1929, *Kjellberg 1820a* (BO). South East Sulawesi: Mt. Mekongga, Tinukari Village, 1900 m, 11 Jul 2011, *Widjaja et al. 9846a* (BO); *Ibid.*, Hura-Hura, 1426 m, 28 Nov 2010, *Widjaja & Sujadi 9400* (BO); Rawa Aopa, 26 Dec 1978, *Prawiroatmodjo & Soewoko 1984* (L). West Sulawesi: Mt. Papandangan, 1913, *Rachmat 397* (BO, L). **PHILIPPINES.** Mindanao: Bukidnon Subprovince, Mt. Candoon, Jun-Jul 1920, *Ramos & Edaño BS 38870* (BO); Cotabato, Kidapawan, Mt. Apo, Mar-Apr 1991, *Gaerlan, Alvarez & Garcia PPI 2635* (L); *Ibid.*, Koronadakal, Mt. Magulo, 1455 m, 10 Apr 1992, *Gaerlan, Fuentes & Romero PPI 5245* (L); Davao del Sur, Todaya, Mt. Apo, May 1909, *Elmer 10577* (BISH, BM, BO, CAS, E, GH, K, L, MO, NY, P, U, US); *Ibid.*, 914 m, 4 Apr 1905, *Williams 2571* (K); *Ibid.*, Gumate District, 1000 m, Mar 1964, *Anon. ANU 1541* (L); *Ibid.*, Mt. McKinley, 1066 m, 29 Aug 1946, *Edaño PNH 1042* (L, PNH); Davao Oriental, Mount Galintan, Jun 1927, *Ramos & Edaño BS 48858* (P); Zamboanga del Norte, 600 m, 1 Feb 1958, *Frake PNH 38277* (L).

13.2. *Dissochaeta celebica* Blume var. ***longilobata*** Karton., **var. nov. —** Fig. 3-10, Map 3-9

Type: *M.M.J. van Balgooy 3205* (holo BO!; iso K, L [L0652533!]), Indonesia, Central Sulawesi, Mount Roreka Timbu, 2000 m elev., 8 May 1979.

Hypanthium campanulate, 3–4 × 1–1.5 mm long, densely covered with brown stellate-furfuraceous hairs; calyx lobes slightly triangular, 2–3 mm long, densely brown stellate-furfuraceous; petal bud conical, 3–3.5 mm long. Fruits subglobose, 6–8 × 4–5 mm, densely covered with stellate hairs and becoming glabrous when mature, slightly 8-lined; calyx lobes persistent, 2–3 mm long.
Distribution — Sulawesi (Central Sulawesi).
Ecology and habitat — Montane forest dominated by Agathis at ca. 2000 m elevation.
Note — This variety is known only from the type and differs from the var. *celebica* by its long triangular calyx lobes (2–3 mm long), persistent in fruit. The length of the calyx lobes is often similar to that of *D. schumannii* from New Guinea, though they are usually caducous in that species.

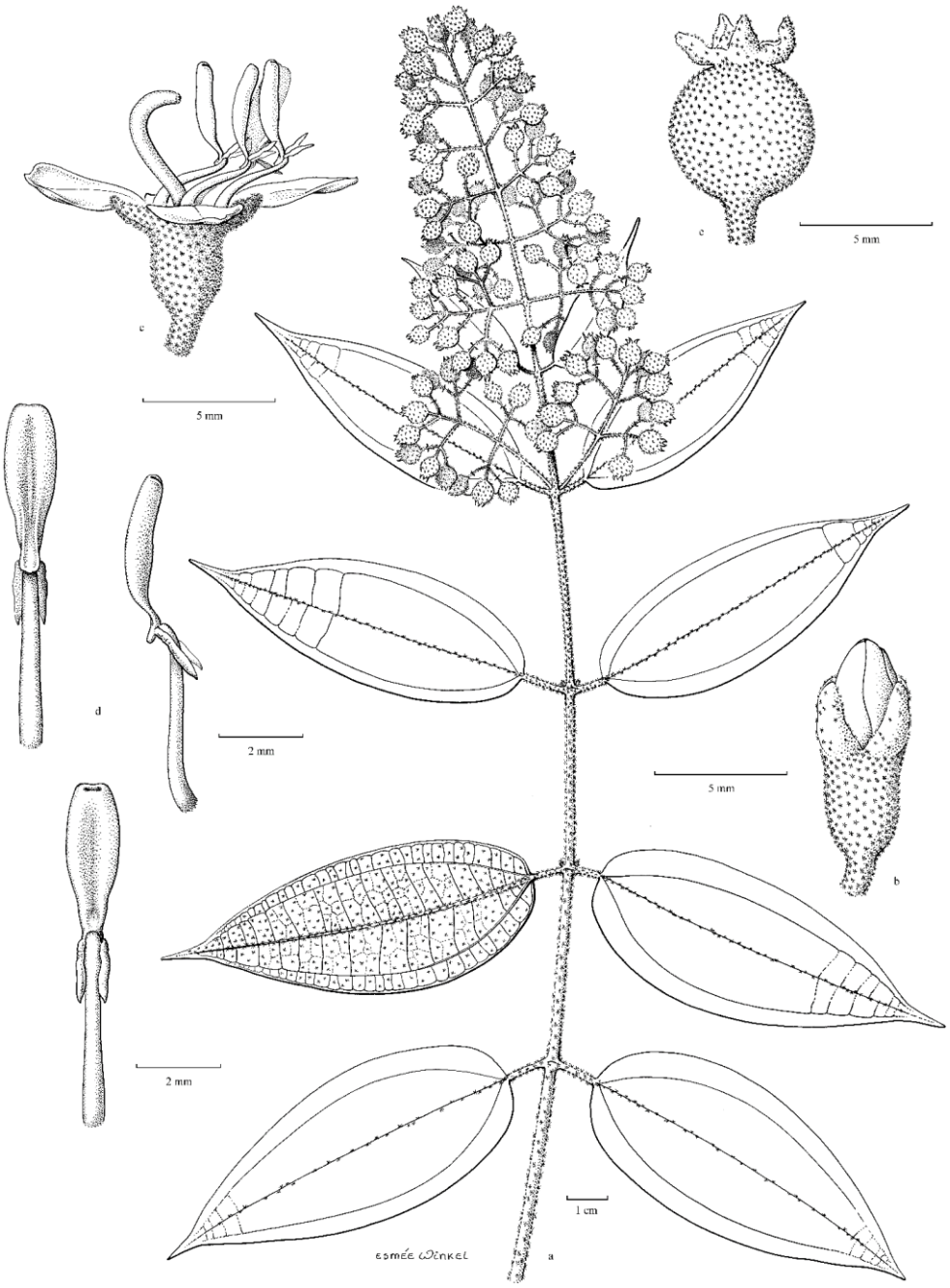
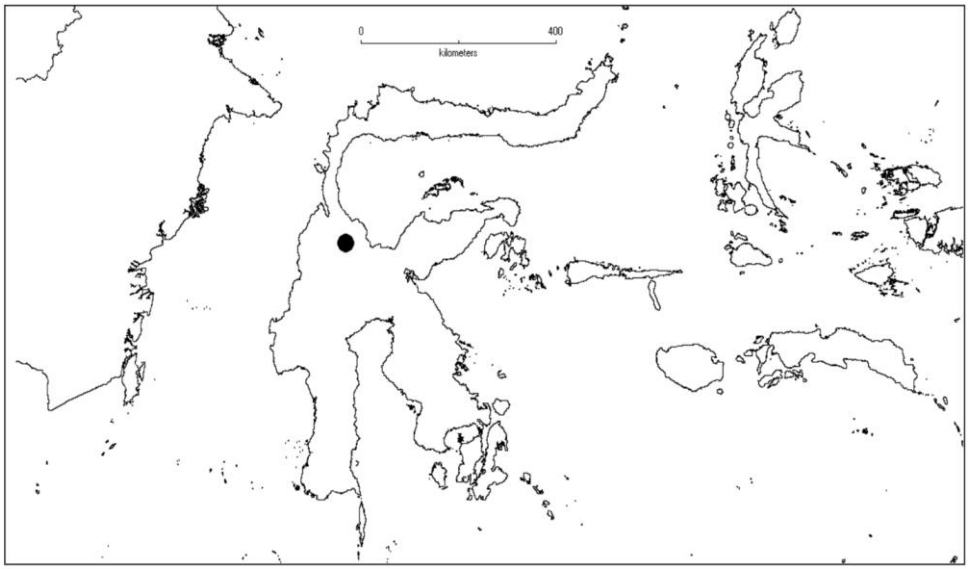


Fig. 3-10. *Dissochaeta celebica* var. *longilobata*. **a.** habit; **b.** hypanthium; **c.** open flower; **d.** stamens; **e.** fruit. [drawn from *van Balgooy 3205* (L)].



Map 3-9. Distribution of *D. celebica* var. *longilobata* (●).

14. *Dissochaeta conica* (Bakh.f.) Clausing — Fig. 3-11, Map 3-10

Dissochaeta conica (Bakh.f.) Clausing in S.S.Renner et al., Fl. Thailand 7(3): 423. 2001. — *Diplectria conica* Bakh.f., Contr. Melastom. 202. 1943. — Type: *H.A.B. Bünnemeijer 3094* (holo L [L0537295!]; iso BO [BO1865987!, BO1865988!], L [L0537294!]), Indonesia, West Sumatra, Agam, Brani, 950 m elev., 19 Jun 1918.

Anplectrum crassinodum Merr., Pap. Michigan Acad. Sci. 24: 85. 1939, *nom. illeg.*, non Merr. (1929). — Lectotype (designated by Veldkamp et al. in Blumea 24: 414. 1979): *Rahmat si Boeea 7781* (lecto MICH [MICH-1111809!]; isolecto L [L0008856!], S [SG-439!]), Indonesia, North Sumatra, Asahan, Near Loemban Ria, 5–12 Apr 1934.

Climbing up to 4 m in height. Branchlets terete, 4–5 mm in diameter, glabrous; nodes swollen, with raised interpetiolar ridge; internodes 4–6.5 cm long. Leaves: petioles terete, 5–10 mm long, glabrous; blades ovate to ovate-elliptic, 10–16 × 4.5–6.5 cm, subcoriaceous, base rounded, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous. Inflorescences terminal and axillary, when terminal, up to 20 cm long and many-flowered, when axillary, up to 10 cm long and with 3–10 flowers; main axis angular, glabrous; primary axes up to 16 cm long with 4 or 5 nodes, secondary axes 1.5–4 cm long with 1–3 nodes, tertiary axes up to 1.5 cm long with 1 node; bracts linear, 2–4 mm long, glabrous, caducous; bracteoles linear, 1–2 mm long, glabrous; pedicels glabrous, 5–8 mm long in central flowers, 4–5 mm long in lateral flowers. Hypanthium cyathiform-tubular, cup-shaped, 7–8 × ca. 5 mm, glabrous; calyx lobes truncate, 1–2 mm long, without distinct tips or with irregularly cracked or rounded tips; petal bud conical, 5–6 mm long; mature petals ovate, 7–8 × ca. 6 mm, reflexed, white or pale purple, base clawed, apex acute. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with ca. 4 mm long filaments, thecae rudimentary, slender, terete, sinuate, ca. 6 mm long, basal crest oblong to triangular, ca. 1 mm long, acute at tip, thin, lateral appendages paired, ligular, ca. 1 mm long; oppositipetalous stamens with 6–7 mm long filaments, anthers thick, curved, S-shaped, thecae 9–10 mm long, connective crest bifid, erose, ca. 0.75 mm long, basal appendages paired, spur-like, ca. 1 mm long, erect. Ovary half

as long as hypanthium, apex glabrous; style curved at the end, slender, ca. 15 mm long, glabrous; stigma minute, papillose; extra-ovarial chambers 4, oppositipetalous, extending almost to the base of the ovary. Fruits subglobose to urceolate, 7–8 × 5–6 mm, glabrous; calyx lobes remnant persistent, erect. Seeds ca. 0.5 mm long.
Distribution — Peninsular Malaysia, Sumatra and Java (West).
Ecology and habitat — Low montane forest in open places at 600–950 m elevation.

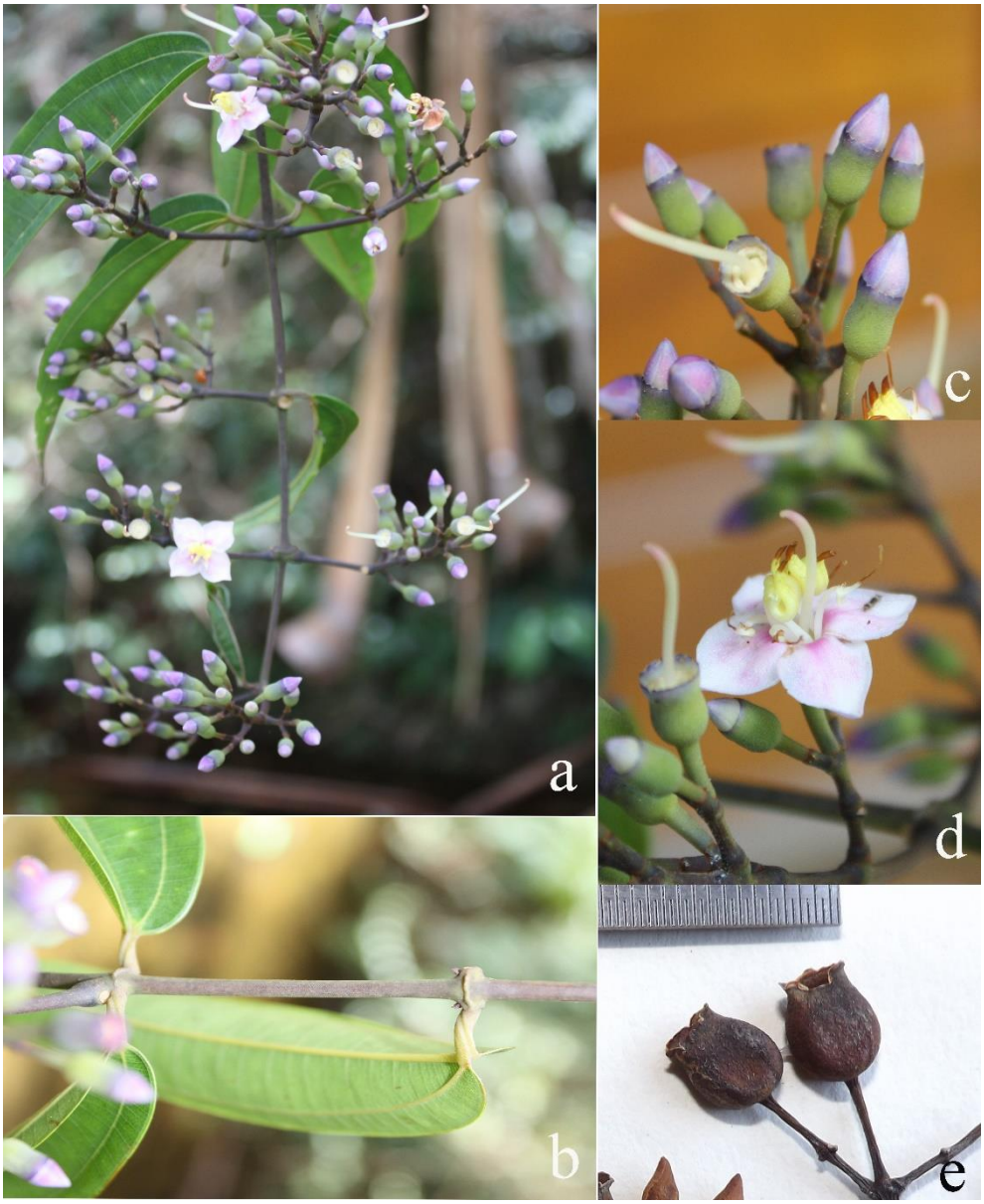
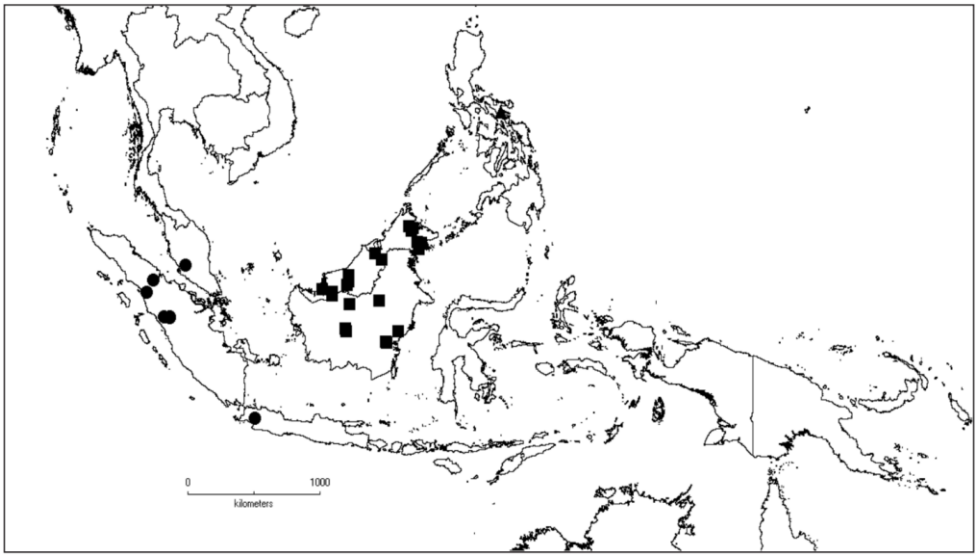


Fig. 3-11. *Dissochaeta conica*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1078* (BO, L) & *Kartonegoro 1101* (BO, L).

Specimens examined — **MALAYSIA.** Selangor: Ulu Gombak, 15 Jun 1967, *Carrick 1569* (K, L). **INDONESIA.** North Sumatra: Asahan, Lumban Ria, *Rahmat Si Boeea 7781* (L, MICH, S); Tapanuli Selatan, Batang Toru, Telek Nauli, 885 m, 25 Mar 2004, *Takeuchi et al. 18794* (L). West Sumatra: Agam, Brani, 950 m, 19 Jun 1918, *Bünnemeijer 3094* (BO, L); Lima Puluh Kota, Harau Valley, Sarasah Bonta, 500 m, 11 Sep 2017, *Kartonegoro 1078* (BO, L); *Ibid.*, Kelok Sembilan, 800 m, 13 Sep 2017, *Kartonegoro 1101* (BO, L). West Java: Bogor, Nanggung, Mt. Menapa, 600 m, 18 Dec 1940, *van Steenis 17412* (BO, K, L).



Map 3-10. Distribution of *D. conica* (●), *D. cumingii* (▲) and *D. densiflora* (■).

15. *Dissochaeta cumingii* Naudin — Map 3-10

Dissochaeta cumingii Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 75. 1851. — Lectotype (designated here): *H. Cuming 1344* (lecto P [P02274812!]; isolecto BM!, K [K000859608!, K000859609!], L [L0537227!]), Philippines, Luzon, Province of Albay.

Branchlets terete, 3–4 mm in diameter, densely brown stellate-furfuraceous; nodes swollen, with interpetiolar line; internodes 7–8 cm long. Leaves: petioles flattened, 8–10 mm long, densely brown stellate-furfuraceous; blades ovate-oblong, 7.8–12 × 2.4–4.3 cm, membranous, base emarginate, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely covered with brown stellate-furfuraceous hairs. Inflorescences terminal or in the upper leaf axils, up to 28 cm long, many-flowered; main axis angular, densely covered with brown stellate-furfuraceous hairs; primary axes up to 25 cm long with 5 nodes, secondary axes up to 6 cm long with 2 or 3 nodes, tertiary axes 0.7–1 cm long with 1 node; bracts linear, 5–6 mm long, densely stellate-furfuraceous, caducous; bracteoles linear, 3–4 mm long, densely stellate-furfuraceous, caducous; pedicels covered with brown stellate hairs, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, angular, 3–5 × ca. 2 mm, densely covered with brown stellate-furfuraceous hairs; calyx lobes truncate with triangular tip, ca. 1 mm long, densely stellate-furfuraceous; petal bud conical, 2–3 mm long, blades elliptic, 5–5.5 × ca. 2 mm; mature petals not seen. Stamens 8, subequal, filaments glabrous, curved sideways; alternipetalous stamens with 6–7 mm long filaments, anthers

lanceolate, curved, sickle-shaped, thecae 6–7 mm long, pedoconnective 1–2 mm long, basal crest triangular, ca. 1 mm long, lateral appendages paired, filiform, with irregular margin, 3–4 mm long; oppositipetalous stamens with 5–6 mm long filaments, anthers lanceolate, hook-shaped, thecae 4–5 mm long, basal crest minute, bifid or spuriform, ca. 0.5 mm long, lateral appendages paired, filiform, 3–4 mm long. Ovary of hypanthium in length, apex pubescent; style slightly curved at apex, 6–8 mm long, glabrous; stigma minute; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits ovoid, 6–7 × 4–5 mm, densely covered with brown stellate-furfuraceous, slightly 8-lined; calyx remnants persistent, erect. Seeds ca. 0.5 mm long.

Distribution — Philippines (Luzon).

Note — This species is known only from the type and lacks any collection notes. The description of the flowers is based on immature flowers which, in some characters, such indumentum and the number and shape of the stamens, resemble *D. sagittata* Blume from Java.

16. *Dissochaeta densiflora* Ridl. — Map 3-10

Dissochaeta densiflora Ridl., Kew Bull. 1: 32. 1946. — *Dissochaeta rostrata* Korth. var. *densiflora* (Ridl.) J.F.Maxwell, Gard. Bull. Singapore 33: 319. 1980. — Lectotype (designated here): *G.D. Haviland 1550* (lecto K [K000859631!]; isolecto SAR), Malaysia, Sarawak, Saribas, Sungai Plandok, 19 Jul 1892.

Dissochaeta rostrata Korth. var. *esetosa* J.F.Maxwell, Gard. Bull. Singapore 33: 319, fig. 4. 1980. — Type: *F.H. Endert 2304* (holo L [L0537223!]; iso BO [BO1850828!], K [K000859632!]), Indonesia, East Kalimantan, W. Koetai, Hikam Batoe Beng, 25 m elev., 29 Jul 1925.

Climbing up to 10 m in height. Branchlets terete but angular at top part, 2–3 mm in diameter, densely covered with brown stellate-tomentose hairs and scattered short bristle hairs; nodes swollen, with interpetiolar line; internodes 7.3–14 cm long. Leaves: petioles terete, 4–10 mm long, densely stellate-tomentose and with scattered short bristle hairs; blades ovate-elliptic to elliptic, 8.3–11.5 × 3.8–6.5 cm, membranous, base emarginate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous except stellate hairs at midrib, abaxially densely covered with brown stellate-tomentose hairs. Inflorescences terminal, up to 25 cm long, many-flowered; main axis densely covered with brown stellate-tomentose and bristle hairs; primary axes up to 20 cm long with 6 or 7 nodes, secondary axes 2.5–5 cm long with 2 or 3 nodes, tertiary axes 6–8 mm long with 1 node; bracts lanceolate or linear, ca. 7 × 1 mm, densely stellate-tomentose and with bristle hairs, caducous; bracteoles lanceolate, ca. 3.5 × 1 mm, densely stellate-tomentose outside, glabrous inside, margin with bristle hairs, caducous; pedicels brown stellate-tomentose, 2–3 mm long in central flowers, 1–1.5 mm long in lateral flowers. Hypanthium tubular, ca. 4 × 2 mm, densely brown stellate-tomentose and with scattered short bristle hairs; calyx lobes triangular, ca. 1 mm long, margin with bristle hairs, apex acute, tomentose; petal bud conical, ca. 2.5 mm long, apex bristly; mature petals ovate, 5–6 × 3–4 mm long, reflexed, base clawed, apex obtuse and bristly, rest glabrous, pale purple or purple. Stamens 8, unequal, filaments glabrous, white, curved sideways; alternipetalous stamens with 5–7 mm long filaments, anthers slender with narrow tip, curved, sickle-shaped, thecae 7–10 mm long, yellow, pedoconnective 1–1.5 mm long, basal crest triangular or ligular, 1–1.5 mm long, lateral appendages paired, filiform, 2–3 mm long; oppositipetalous stamens with 5-6 mm long filaments, anthers S-shaped, thecae 6–8 mm long, basal crest ligular, ca. 1 mm long, lateral appendages paired, filiform, ca. 2 mm long. Ovary ⅔ of

hypanthium in length, apex pubescent; style curved at the end, 10–12 mm long, glabrous, white; stigma minute, light purple; extra-ovarial chambers 8, shallow or nearly to the middle of the ovary. Fruits ovoid, 5–6 × 3–3.5 mm, densely covered with stellate-tomentose hairs, sometimes becoming caducous when mature, calyx lobes persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Borneo.

Ecology and habitat — Secondary forest along logging road and river banks or submontane forest at 400–1320 m elevation.

Vernacular names — *akar kemunting* (Iban); *lamoy puruk bawi* (Dayak).

Specimens examined — **MALAYSIA.** Sabah: Beluran, Bidu-Bidu Forest Reserve, 21 Jul 1970, *Leopold SAN 128874* (K, L); Lahad Datu, Danum Valley, Ulu Segama, 170 m, 25 Feb 1986, *Edwards 2110* (K, L, P); Lamag, Ulu Sungai Lokan, 12 Nov 1979, *Aban & Petrus SAN 90697* (K, L); Sandakan, Telupid Road, 15 Aug 1979, *Aban Gibot SAN 91256* (K); Mostyn, Kalumpang Forest Reserve, 17 Feb 1966, *Nordin & Ali SAN 54413* (K); *Ibid.*, Tingkayu Camp, 180 m, 14 Sep 1966, *Sinanggul SAN 57228* (K, L). Sarawak: Kapit, Bukit Raya, 14 Jan 1965, *Jugah S.23863* (K); *Ibid.*, Pelagus, 7 Jul 1979, *Lee S.40214* (L); *Ibid.*, Upper Rejang River, 1929, *Clemens 21139* (BO, K); *Ibid.*, *Clemens 21569* (K); Kakus, Ulu Mayeng, 150 m, 13 Jul 1964. *Sibat S.21720* (K, L); *Ibid.*, Tau Range, 152 m, 7 Jun 1956, *Purseglove 5401* (K); Lubok Antu, Lanjak Entimau, Bukit Sengkajang, 600 m, 18 Mar 1974, *Chai S.33998* (K, L); *Ibid.*, Ulu Sg. Bengkari, 21 Mar 1974, *Chai S.34082* (K, L); Miri, Gunung Mulu, 1320 m, 8 Mar 1990, *Yii & Abu Talib S.58220* (L); Saribas, Sungai Plandok, 19 Jul 1892, *Haviland 1550* (K). **INDONESIA.** Central Kalimantan: Bukit Raya, Upper Katingan River, Tumbang Samba, 150 m, 22 Dec 1982, *Mogea & de Wilde 4339* (BO, K, L); *Ibid.*, Tumbang Tubus, 150 m, 6 Jan 1983, *Veldkamp 8077* (BO, L). East Kalimantan: West Kutai, Hikam Batu Beng, 25 m, 29 Jul 1925, *Endert 2304* (BO, K, L); Balikpapan, Gunung Meratus, 25 Jun 2003, *Arbainsyah et al. AA 3115* (BO, K, L); *Ibid.*, Road Kenangan to Mount Meratus, 400 m, 27 Mar 1995, *Kessler et al. 913* (K, L, P).

17. *Dissochaeta divaricata* (Willd.) G.Don — Fig. 3-12, Map 3-11

Dissochaeta divaricata (Willd.) G.Don, Gen. Hist. 2: 783. 1832. — *Melastoma divaricatum* Willd., Sp. Pl., ed. 4, 2(1): 596. 1799, "divaricata". — *Anplectrum divaricatum* (Willd.) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria divaricata* (Willd.) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria divaricata* (Willd.) Raizada, Indian Forester 94: 435. 1968. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *Klein 2 "8218" in Herb. Rottler* (lecto B-W [81218-010!]; isolecto C [C10014562!, C10014563!], K [K000859557!], L [L0008867!, fragm.]), India Orientali.

Melastoma glaucum Jack, Trans. Linn. Soc. London 14: 15. 1823, "glauca". — *Dissochaeta glauca* (Jack) Blume, Flora 14: 501. 1831. — *Anplectrum glaucum* (Jack) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Backeria glauca* (Jack) Raizada, Indian Forester 94: 435. 1968. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *W. Jack 49* (lecto E [E00288100!]; isolecto BM [BM000944473!], G [G00353714!], L [L0008857!]), Malaysia, Peninsular Malaysia, Penang, 1819.

Melastoma cyanocarpum Blume, Bijdr. Fl. Ned. Ind. 17: 1073. 1826. — *Dissochaeta cyanocarpa* (Blume) Blume, Flora 14: 501. 1831. — *Anplectrum cyanocarpum* (Blume) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria cyanocarpa* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *C.L. Blume 616* (lecto L [L0008862!]; isolecto K [K000859552!], L [L0008861!, L0008863!, L0008864!, L0008865!]), Indonesia, West Java, G. Salak.

Osbeckia tetrandra Roxb., Fl. Ind. 2: 224. 1832. — *Diplectria tetrandra* (Roxb.) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated here): *W. Roxburgh s.n.* (lecto G [G00353906!]), Malaysia, Pulo Pinang.

Dissochaeta anceps Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 69. 1851. — *Anplectrum divaricatum* (Willd.) Triana var. *anceps* (Naudin) Cogn. in Boerl., Handl. Fl. Ned. Ind. 2: 534. 1890. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *H. Zollinger 3044* (lecto P [P05259330!]; isolecto BM [BM000944474!], BO [BO1752509!], BR [BR5188239!], G [G00353563!, G00353564!], MPU [MPU-013527!], P [P05283594!]), Indonesia, Lampung, Gunung Batin, 20 Sep 1845.

Dissochaeta spoliata Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 69. 1851. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *C. Gaudichaud-Beaupré 95* (lecto P [P05259341!]; isolecto G [G00353567!], P [P05259342!]) Malaysia, Pulo Pinang, Mar 1837.

Dissochaeta pepericarpa Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 71. 1851. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *H. Cuming 2259* (lecto P [P05259335!]; isolecto BR [BR5187911!, BR5188567!], G [G00353565!, G00353566!], K [K000859566!], L [L2537846!, L0008858!, L0008859!, L0008860!]), Malaysia, Malacca, 1821.

Dissochaeta palembanica Miq., Fl. Ned. Ind., Eerste Bijv. 2: 317. 1861. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 202. 1943): *J.E. Teijsmann HB 3634* (lecto U [U0004003!]; isolecto BO [BO1752507!, BO1426869!]), Indonesia, South Sumatra, Res. Palembang, Enim, Pandan Oeloe.

Dissochaeta furfurascens Elmer, Leafl. Philipp. Bot. 8: 2754. 1915. — *Diplectria furfurascens* (Elmer) M.P.Nayar in Veldkamp et al., Blumea 24: 413, fig. 2A. 1979. — Lectotype (designated here): *A.D.E. Elmer 13352* (lecto BO [BO1752508!]; isolecto BISH [BISH-1003259!], BM [BM000944475!], E [E00288099!], GH [GH00072244!, GH00072245!], HBG [HBG514872!], K [K000859549!], L [L0008868!], MO [MO313698!], NY [NY00228563!], P [P05259310!], PNH [PNH198551!], U [U0004004!]), Philippines, Mindanao, Agusan Province, Cabadbaran (Mt. Urdaneta), Jul 1912.

Anplectrum suluense Merr., Philipp. J. Sci. 30: 417. 1926. — Lectotype (designated here): *M. Ramos & G.E. Edaño BS 44461* (lecto K [K000859548!]; isolecto L [L0008866!], NY [NY00221310!]), Philippines, Sulu Archipelago, Jolo, Sep 1924.

Anplectrum patens Geddes, Bull. Misc. Inform. Kew 1928: 72. 1928. — Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): *A.F.G. Kerr 7215* (lecto K [K000859554!]; isolecto BK [BK216091!], BM!, TCD [TCD-0016998!]), Thailand, Pattani, Bachaw, 50 m, 16 Jul 1923.

Climbing up to 20 m in height. Branchlets terete, 3–5 mm in diameter, glabrous or sparsely to densely covered with brown minute stellate hairs, rarely with dense 2–4 mm long bristle hairs; nodes swollen, with interpetiolar ridge; internodes 3–6 cm long. Leaves: petioles terete, 5–8 mm long, sparsely to densely covered with stellate hairs and often with dense bristle hairs; blades ovate-elliptic, elliptic-oblong to oblong, 6–11 × 2.5–4 cm, chartaceous, base rounded to shallowly cordate, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous or with sparse, stellate hairs, more dense at the midrib. Inflorescences terminal, 9–20 cm long, many-flowered; main axis angular, glabrous or sparsely to densely covered with stellate hairs, often with bristle hairs; primary axes up to 18 cm long with 3–5 nodes, secondary axes up to 4 cm long with 2 or 3 nodes, tertiary axes up to 0.5 cm long with 1

node; bracts ovate or lanceolate, leaf-like, 4–10 × 1–4 mm, covered with stellate hairs, margin ciliate; bracteoles lanceolate or subulate, 2–4 mm long, densely covered with stellate hairs, apex bristly; pedicels glabrous or dorsally covered with stellate hairs, 4–5 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium campanulate-angular to suburceolate, 6–7 × 2–3 mm, slightly 8-ridged, sparsely to densely covered with stellate hairs, often with scattered capitate bristles; calyx lobes truncate, ca. 0.5 mm long, apex with 4 minute points, purplish; petal bud conical, 5–9 mm long, acuminate at tip; mature petals ovate, 5–9 × 3–4 mm, reflexed, base clawed, apex acuminate, white or white purplish to purple. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with 3–4 mm long filaments, thecae rudimentary, slender, curved, flat, 3–4 mm long, basal crest triangular or hastate, ca. 1 mm long, thin, lateral appendages absent or prolonged from the basal crest, up 2 mm long; oppositipetalous stamens with 4–5 mm long filaments, anthers thick, curved, hook-shaped or S-shaped, thecae 6–10 mm long, yellow, basal appendages bifid, 0.5–1 mm long, connective crest spur-like, triangular, erose, ca. 0.5 mm long. Ovary half as long as hypanthium, apex glabrous; style glabrous, 13–15 mm long, curved at the end, slender, purplish; stigma minute, pappilose; extra-ovarial chambers 4, oppositipetalous, extending almost to the base of the ovary. Fruits urceolate, 4–8 × 2–4 mm, glabrous to puberulous, slightly 8-lined; calyx lobes remnant persistent. Seeds ca. 0.75 mm long.

Distribution — Myanmar, Indochina, Thailand, throughout Malesia (Peninsular Malaysia, Sumatra, Java, Borneo, Philippines, Sulawesi, Moluccas and New Guinea, absent in Lesser Sunda Islands).

Ecology and habitat — Primary and secondary forests, along rivers, roads, on waste lands; usually in the lowlands, rarely up to 1460 m elevation (Veldkamp et al. 1979).

Vernacular names — Peninsular Malaysia: *tuniong utan* (Penang); *sesendok* (Perak). Sumatra: *kedudu akar* (Riau); *kadudu* (Jambi); *sidodo akar* (Palembang). Java: *caluncung areuy* (Sunda). Borneo: *buah apetaah* (Kutai, Kenyah); *akar kemunting* (Iban); *uduk-uduk hutan* (Brunei); *kauelan* (Bagobo).

Notes — 1. *Dissochaeta divaricata* is one of the species with the most widespread distribution in the region and it has a wide variation in the indumentum. The specimens vary from glabrous to densely pubescent on the branchlets, abaxially surfaces of the leaf blades, inflorescences axes and the hypanthium. Sometimes they also have scattered bristle hairs on these parts. The variation in bracts and bracteoles ranges from linear to lanceolate, leaf-like. The acuminate tip of the petal bud is a good character for recognizing the species and for distinguishing it from other species, e.g. *D. barbata* and *D. conica*.

2. *Melastoma divaricatum* Willd. was reported by Willdenow (1799) from “India Orientali”, although the type is labelled only “Ind.”. At that time, “India Orientali” did not refer to what is now India, but to the entire region now known as South and Southeast Asia, the former British East Indies. Veldkamp et al. (1979) and Maxwell (1980a) presumed that the actual source of the type specimen might have been from southern Thailand or further south on the Malay Peninsula.

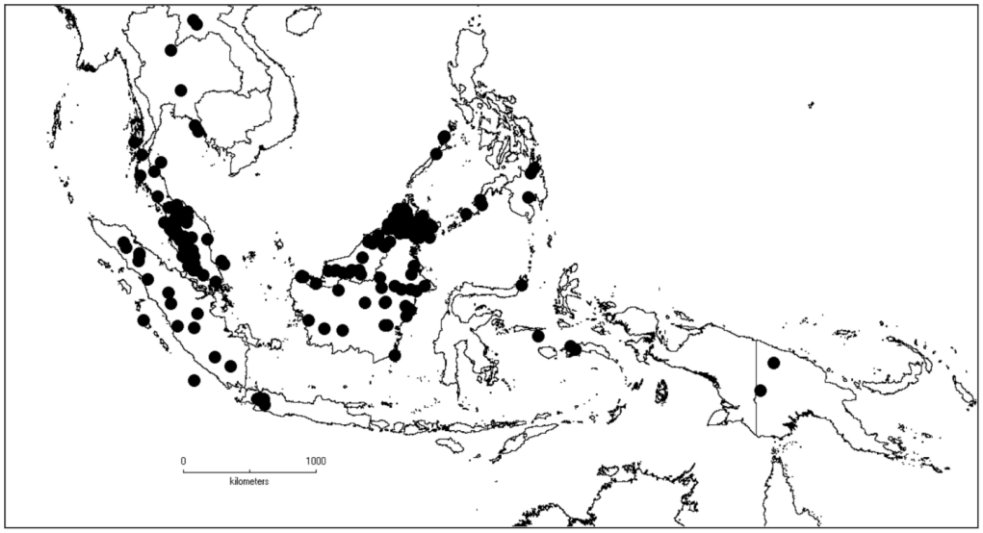
Selected specimens examined — **MYANMAR.** Lamby Kyum, Jun 1909, *dÁlleizette 2445* (L). **LAOS.** Vientiane: Vang Vieng, Pu Yang, 250 m, 20 May 2011, *Maxwell 11-25* (L). **THAILAND.** Nakhon Nayok: Khao Yai, 800 m, 24 May 1970, *Smitinand BKF 46194* (L). Nakhon Si Thammarat: Wat Kiri Wang, 100 m, 2 May 1918, *Kerr 15580* (BM, K). Narathiwat: Khao Tae Saton, 20 Nov 1961, *Sangkhachand BKF 36947* (K, L, P). Phang Ngha: Nai Chong, 100 m, 11 May 1973, *Geesink & Santisuk 5336* (K, L, P). Pattani: Bachaw, 50 m, 16 Jul 1923, *Kerr 7215* (BK, BM, K, TCD); Betong, 500 m, 11 Mar 1925, *Kerr 10075* (BM, K). Ranong: 4 Jan 1929, *Kerr 16529* (BM, K). Surat Thani: Kao Samui, 50 m, 1 Jan 1930, *Kerr 17904* (BM, K). Trang: Khao Libong, 300 m, 23 Apr 1930, *Kerr 19087* (BM, K).

Trat: Koh Kut Island, 5 Apr 1959, *Sorensen, Larsen & Hansen 7175* (L); Koh Chang Island, 3 Aug 1973, *Geesink & Phengkhlai 6262* (L). Uttaradit: Ban Phra, 400 m, 18 Apr 1970, *Smitinand & Cheke BKF 46605* (K, L). Yala: Ban Rang, 100 m, 24 Apr 1974, *Geesink & Hattink 6394* (K, L); Bannang Sata, Bahng Lahng, 150 m, 12 Nov 1986, *Maxwell 86-905* (L).

Fig. 3-12. *Dissochaeta divaricata*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by D.S. Penneys; voucher: *Penneys 2472* (WNC).

MALAYSIA. Johor: Bukit Bonang, 1900, *Ridley 11103* (K); Pulau Pemanggil, Bukit Durian, 8 Jul 1966, *Noor & Samsuri 66* (K, L). Kedah: Baling, G. Inas, Bukit Iboi, 2 Nov 2007, *Imin, Kueh & Phoon FRI 58596* (K, L). Malacca: *Griffith KD 2288* (BM, K, L, P); 1821, *Cuming 2259* (BR, G, K, L, P); Tampin, 21 Nov 1916, *Burkill SFN 2297* (K). Negri Sembilan: Bukit Tangga, 19 Dec 1920, *Ridley s.n.* (BM, K); Jinderam Estate, 90 m, 22 Sep 1957, *Shah 133* (K, L). Pahang: Cameron Highlands, 1210 m, 10 Apr 1937, *Nur SFN 32600* (L, P); Fraser's Hill, 19 Jun 1967, *Carrick 1575* (K, L), Richmond, 1280 m, 16 Apr 1955, *Purseglove 4114* (K, L). Penang: 1819, *Jack 49* (BM, L); Mar 1837, *Gaudichaud-Beaupré 95* (G, P); Government Hill, *Maingay KD 793* (K, L). Perak: Goping, Aug 1880, *King's collector 369* (BM, L, P); Maxwell's Hill, 42 m, 19 Sep 1949, *Sinclair & Kiah SFN 38817* (BM, K, L); Sungai Siput, 180 m, 5 Oct 1967, *Ng FRI 5739* (K). Selangor: Genting-Simpah road, 5 Feb 1965, *Ng KEP 99079* (K, L); Kepong, 31 Jan 1968, *Ogata 10040a* (L); Ulu Gombak, 2 Dec 1965, *Carrick 1428* (K, L). Terengganu: Kemaman, Bukit Kajang, 152 m, 4 Nov 1935, *Corner SFN 30207* (K, L). Sabah: Beaufort, Halogilat, Saliwangan, 8 May 1973, *Dewol & Karim SAN 77566* (K, L); Keningau, Sepulut, Labang, 18 Oct 1988, *Fidilis SAN 125669* (K, L); *Ibid.*, Witti Range, 600 m, 22 Sep 1983, *Beaman 7030* (K, L); Kalabakan, 15 Apr 1982, *Fidilis SAN 94758* (K, L); Ranau, Kota Belud, Kelawat, 10 Apr 1950, *Kiah SFN 38984* (K, L, P); Lahad Datu, Danum Valley, 7 May 1989, *Ridsdale 1981* (K); Sosopodon, 1066 m, 25 Jun 1963, *Sinanggul SAN 38278* (K, L); Sandakan, Dec 1921, *Elmer 20333* (BM, BO, K, L, P, U); *Ibid.*, *Ramos BS 1292* (P); *Ibid.*, Kalatuan, 6 Jul 1948, *Abdul Rahim A 418* (K, L); Tawau, *Elmer 21187* (BM, BO, K, L, P, U). Sarawak: *Beccari PB 2186* (K); Bakelalan, *Brooke 10391* (BM, L); Balleh, Ulu Mujong, 250 m, 20 Mar 1964, *Ashton S.13984* (K, L); Baram, *Hose 181* (BM, K, L, P); Kapit, Bukit Raya, 457 m, 16 Oct 1965, *Jugah S.23880* (K, L); Miri, Kelabit Highlands, 950 m, 1 Mar 1995, *Christensen & Apu 717* (K); Gat, Upper Rejang River, 2 Jul 1929, *Clemens 21568* (BM, K, L, P); Sibu, Rejang, Aug 1893, *Haviland 3143* (BM, K); Sarikei, 6 Jul 1954, *Brooke 8757* (BM, L). **SINGAPORE.** *Jack s.n.* (L). **INDONESIA.** Aceh: Gayoland, Gajah-Blangkajeren, 1400 m, 27 Feb 1937, *van Steenis 9411* (BO, K, L); Leuser Mts., Lau Ketambe, 400 m, 4 Jun 1972, *de Wilde & de Wilde-Duyfjes 12568* (BO, K, L). Bengkulu: Enggano Island, Malakoni, Kuala Besar, 50 m, 22 Apr 2015, *Ardiyani et al. E167* (BO). Jambi: Batang Sungai, 200 m, Sep 1925, *Posthumus 937* (BO, L). Lampung: Gunung Batin, 20 Sep 1845, *Zollinger 3044* (BM, BO, BR, G, MPU, P). Mentawai Islands: Siberut, 11 Sep 1924, *Boden-Kloss SFN 13082* (BO, K). North Sumatra: Brastagi, 1250 m, 21 Feb 1932, *Bangham 1140* (K); Sibolangit, 500 m, 18 Dec 1927, *Lörzing 12317* (BO, K, L); Tapanuli, Between Sidikalang and Pongkolan, 1200 m, 27 Mar 1954, *Alston 14816* (BM, L). Riau: Tigapuluh Mts., Talanglakat, 100 m, 4 Nov 1988, *Burley & Tukirin 1084* (BO, K, L). South Sumatra: Enim, Pandan Ulu, *Teijsmann HB 3634* (BO). West Sumatra: Lima Puluh Kota, Harau Valley, Sarasah Bonta, 500 m, 11 Sep 2017, *Kartonegoro 1069* (BO, L). West Java: Bogor, Mount Paniisan, 700 m, 9 Dec 1923, *Bakhuizen van den Brink 6165* (BM, BO, K, L); Mount Salak, *Blume s.n.* (K, L). Central Kalimantan: Sampit River, Kuala Kwayan, Permantang, 50 m, 25 Jan 1954, *Alston 13234* (BM, BO); Barito Ulu, 8 Jun 1990, *Ridsdale PBU 456* (BO, L); Nanga Buli, Sungai Buluh, 250 m, 26 Feb 1984, *Hansen 1212* (L). East Kalimantan: East Kutai, Sg. Menubar, 5 Jun 1951, *Kostermans 4961* (BO, K, L); *Ibid.*, Muara Ancalong, Long Lees, 100 m, 6 Mar 1978, *Wiriadinata 1151* (BO, K, L); West Kutai, Hikam Batu Beng, 80 m, 28 Jul 1925, *Endert 2270* (BO, K, L); Tanjung Redeb, Birang River, 23 Oct 1963, *Kostermans 21644* (BO, K, L); Berau, Mt. Menyapa, Kelai River, 19 Oct 1963, *Kostermans 21364* (BO, K, L); Gunung Gadut, 31 Mar 1908, *Winkler 1752* (BM, K); Samarinda, Loa Haur, 40 m, 16 May 1952, *Kostermans 6965* (BO, K, L). North Kalimantan: Krayan, Long Bawan, 1000 m, 16 Jul 1981, *Ueda & Darnaedy B-8515* (BO, L). South Kalimantan: Salimohi, Simpokok, 15 Jul 1908,

Winkler 2970 (BM); Pulau Laut, 100 m, 6 Nov 1928, *van Slooten 2282* (BO, K, L). West Kalimantan: Danau Sentarum, Semujan Hill, 4 Jul 1986, *Giesen 69* (K, L). North Sulawesi: Gurupahi, 600 m, 19 Mar 1917, *Kaudern 6* (L). Moluccas: Ceram, Piru, 400 m, 16 Nov 1918, *Rutten 1904* (BO, L, U); Sula, Mount Berberi, *Atje 318* (BO, L). **PHILIPPINES.** Mindanao: Agusan, Cabadbaran (Mt. Urdaneta), Jul 1912, *Elmer 13352* (BISH, BM, BO, E, GH, K, L, MO, NY, P, PNH, U); Davao, Mt. McKinley, 640 m, 1 Oct 1946, *Edaño PNH 1008* (PNH). Palawan: Pagdanan, Ibangley, 40 m, 21 Apr 1984, *Podzorski SMHI 906* (K, L). Sulu: Jolo, Sep 1924, *Ramos & Edaño BS 44461* (K, L). **PAPUA NEW GUINEA.** Sepik: *Ledermann 6654* (L). Western District: Kiunga, 30 m, 6 Aug 1971, *Streimann LAE 51727* (L).



Map 3-11. Distribution of *D. divaricata* (●).

18. *Dissochaeta fallax* (Jack) Blume — Fig. 3-13, Map 3-12

Dissochaeta fallax (Jack) Blume, Flora 14: 493. 1831. — *Melastoma fallax* Jack, Trans. Linn. Soc. London 14: 13. 1823. — *Omphalopus fallax* (Jack) Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 277, pl. 4, fig. 5. 1851. — Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 132. 2010): *H.O. Forbes 2882a* (neo L [L0822678!]; isoneo BM!), Indonesia, Bengkulu, Ajer Angat, G. Kaba.

Melastoma reinwardtianum Blume, Bijdr. Fl. Ned. Ind. 17: 1069. 1826. — *Dissochaeta reinwardtiana* (Blume) Hochr., Candollea 2: 472. 1925. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 119. 1943): *H. Kuhl & J.C. van Hasselt s.n.* (lecto L [L0537272!]; isolecto L [L0537269!, L0537270!]), Indonesia, West Java.

Dissochaeta reticulata Blume, Flora 14: 499. 1831. — *Omphalopus reticulatus* (Blume) Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 278. 1851. — *Neodissochaeta reticulata* (Blume) Bakh.f., Contr. Melastom. 143. 1943. — *Dissochaeta velutina* Blume var. *reticulata* (Blume) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 144. 1943): *C.L. Blume s.n.* (lecto L [L0008896!]; isolecto L [L0008897!], P [P05283565!]), Indonesia, Java.

Dissochaeta ligulata Blume, Mus. Bot. 1(3): 35. 1849. — *Anplectrum ligulatum* (Blume) Triana, Trans. Linn. Soc. London 28: 85. 1872. — *Diplectria ligulata* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 144. 1943): *F.W. Junghuhn s.n.* (lecto L [L0008898!]), Indonesia, Java.

Dissochaeta diepenhorstii Miq., Fl. Ned. Ind., Eerste Bijv. 2: 317. 1861. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 119. 1943): *H. Diepenhorst HB 1323* (lecto U [U0004007!]; isolecto BO [BO1865969!]), Indonesia, West Sumatra, Priaman.

Omphalopus fallax (Jack) Naudin var. *novoguineensis* Mansf., Bot. Jahrb. Syst. 60: 113. 1925. — Lectotype (designated here): *F.R.R. Schlechter 15159* (lecto NY [NY00229576!]), Papua New Guinea, Kaiser Wilhelmsland, Kani-Gebirges, 1000 m, 7 Jan 1908.

Melastoma leprosum auct. Non. Blume: Blume, Bijdr. Fl. Ned. Ind 17: 1068. 1826. *p.p.*, excl. type

Dissochaeta inappendiculata auct. Non. Blume: Triana, Trans. Linn. Soc. London 28: 84. 1872. *p.p.*, excl. type.

Dissochaeta celebica auct. Non. Blume: Baker f., J. Bot. 62(Suppl.): 40. 1924. *p.p.*, excl. type.

Dissochaeta leprosa auct. Non. Blume: Baker f., J. Bot. 62(Suppl.): 40. 1924. *p.p.*, excl. type.

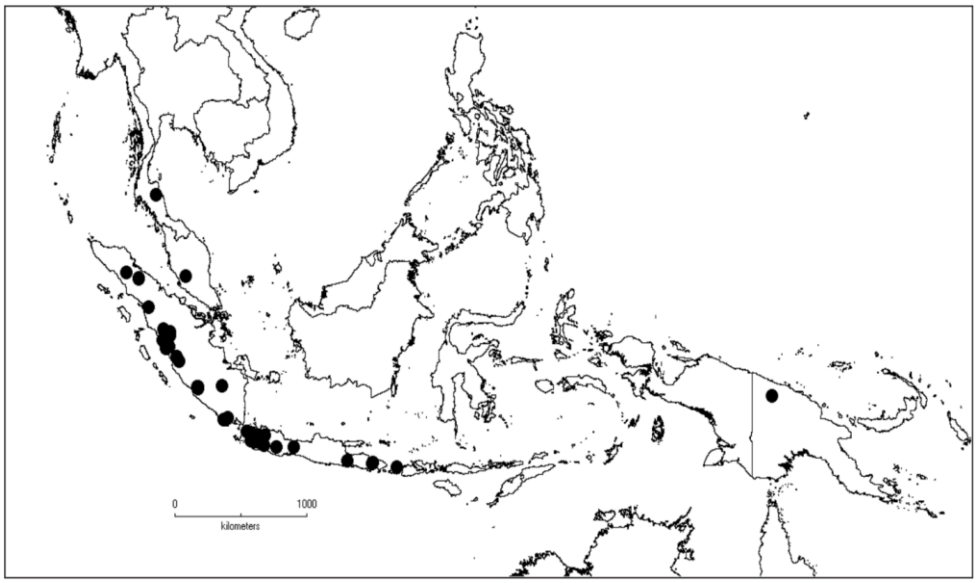
Climbing up to 25 m in height. Branchlets terete or subquadrangular, 3–6 mm in diameter, puberulous to brown stellate-furfuraceous; nodes swollen, with raised interpetiolar ridge; internodes 3.5–7 cm long. Leaves: petioles terete, 8–20 mm long, puberulous to densely stellate-furfuraceous; blades ovate to ovate-oblong, 6–15.5 × 3–7 cm, membranous, base cordate or subcordate, rarely rounded, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, light green, glossy, abaxially densely brown stellate-furfuraceous. Inflorescences terminal and in the upper leaf axils, up to 35 cm long, many-flowered; main axis densely stellate-furfuraceous; peduncle up to 8 cm long; primary axes up to 15 cm long with 4 or 5 nodes, secondary axes 3–3.5 cm long with 1–3 nodes, tertiary axes up to 5 mm long with 1 node or undeveloped; bracts linear, 2–3 mm long, densely brown furfuraceous, caducous; bracteoles linear, minute, ca. 1.5 mm long, brown furfuraceous, caducous; pedicels densely stellate-furfuraceous, 3–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium urceolate, 3–6 × 2–3 mm, green, densely stellate-furfuraceous; calyx lobes truncate with triangular tips, 0.5–1(–2.5) mm long, widened, glabrous or with stellate hairs; petals bud rounded or rarely subconical, 4–10 mm long, with a rounded tip; mature petals obovate, 7–8 × 2–4 mm, not reflexed, base clawed, apex rounded, glabrous or inside with appressed hairs at the base, white pinkish or pink. Stamens 4 or 8, equal or subequal when 8, all fertile, filaments bright white, straight, curved at the end; alternipetalous stamens with 4–5 mm long filaments, anthers ovate or lanceolate, when mature falcate, straight, medifixed, thecae 3–6.5 mm long, bright yellow, beaked, pedoconnective not developed, basal crests triangular, orbicular or ligular, 1–3 mm long, attached to the attachment of the filament, white, lateral appendages absent; the oppositipetalous stamens smaller, with 2–3 mm long filaments, anthers oblong, oblong-lanceolate, medifixed, thecae 2–4 mm long, tessellate-reticulate, yellow, basal crests ligular, erect or sometimes tapering horizontally inward to the anther, 1–1.5 mm long, lateral appendages absent. Ovary half or ⅔ of hypanthium in length, apex pubescent; style 7–15 mm long, curved at the end, glabrous, white with pinkish base; stigma minute; extra-ovarial chambers absent or shallow. Fruits urceolate or subglobose, 4–8(–12) × 4–5(–7) mm, stellatepuberulous, calyx lobe remnants persistent, 1–2 mm long. Seeds ca. 0.5 mm long.

Distribution — Thailand (Southern Peninsula), Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands (Bali, Lombok) and New Guinea (Papua New Guinea).

Ecology and habitat — Primary or secondary submontane forest, rarely near a crater or at the edge of a forest, 400–1600 m elevation.
Vernacular names — Sumatra: *air wangian* (Minang); *akar gameh* (Pariaman); *gedang serian* (Lampung). Java: *harendong areuy*, *harendong beureum*, *harendong oyot* (Sunda). Lesser Sunda: *priyato* (Bali).
Notes — 1. *Dissochaeta fallax* is easily distinguished by its 4 or 8 stamens with tessellate-reticulate thecae and medifixed anthers. The hypanthium is suburceolate, slender and smaller than the petals in bud, which are usually rounded. This species is common in West Malesia (Sumatra and Java), but so far not found in Borneo and further east except for one collection from New Guinea. The stamens make *Dissochaeta fallax* so different from the other species that it has long been regarded as a distinct genus, *Omphalopus* (Naudin 1851, Miquel 1855, Triana 1872, Cogniaux 1891, Bakhuizen van den Brink 1943). We regard these differences only as infrageneric variation and we follow previous authors (Blume 1831a, Maxwell 1980b, Clausing & Renner 2001a, Kartonegoro & Veldkamp 2010) to include it in *Dissochaeta*. Future phylogenetic analyses may point out the true relationship of this species.
2. The correct identification of *D. reticulata* is problematic. Naudin (1851) and Miquel (1855) correctly considered this species to be part of former *Omphalopus*, together with *O. fallax* based on its stamen characters. Blume (1831a), Veldkamp (1979), Kartonegoro & Veldkamp (2010) regarded it as a distinct species in *Dissochaeta* based on 8 subequal fertile stamens, in which it is similar to *D. inappendiculata*. Bakhuizen van den Brink (1943, 1964) placed this species under *Neodissochaeta*. On the other hand, Maxwell (1980b) erroneously considered the species to be a variety of *D. velutina* (a synonym of *D. vacillans*). Like *D. fallax*, the type of *D. reticulata* also shows the stamens to have tessellate-reticulate thecae, medifixed stamens and an inappendiculate crest. Therefore, the name is here synonymized with *D. fallax*, whereby the variation in the number of stamens became 4 or 8.
Selected specimens examined — **THAILAND.** Nakhon Si Thammarat: Khao Luang, 750 m, 19 May 1968, *van Beusekom & Phengkhlai 880* (K, L, P). **MALAYSIA.** Selangor: Genting Highlands, Gunong Ulu Kali, 1500 m, 9 Apr 1978, *Maxwell 78-81* (L). **INDONESIA.** Aceh: Gayoland, between Kampong Kapi and Kampong Aunan, 1100 m, 21 Mar 1937, *van Steenis 9972* (BO). Bengkulu: Air Hangat, Bukit Kaba, *Forbes 2882a* (BM, L); Suban Ayam, 1200 m, 12 Jul 1916, *Ajoeb 350* (BO); Balai, 500 m, 13 Jan 1931, *de Voogd 581* (BO, L). Jambi: Kerinci, Siolak Deras, 915 m, 18 Mar 1914, *Robinson & Boden-Kloss s.n.* (BM, K). Lampung: Sukaraja, 28 Aug 1915, *Cramer 107* (BO); Mt. Tanggamus, 1600 m, 2 May 1968, *Jacobs 8213* (L). North Sumatra: Bandar Baru, Mt. Sibayak, 900 m, 9 Oct 1928, *Lörzing 14075* (BO, L); Sibolangit, 12 Sep 1920, *Lörzing 7351a* (BO); Padang Sidempuan, Mt. Lubuk Raya, 1000 m, 13 Apr 1978, *Maskuri 282* (BO, L). South Sumatra: Muara Dua, Tenang, 700 m, 10 Jan 1930, *de Voogd 556* (BO). West Sumatra: Pariaman, *Diepenhorst HB 1323* (BO, U); Mt. Malintang, 1 Aug 1918, *Bünnemeijer 4225* (BO, K, L, U); Mt. Merapi, 1250 m, 13 Sep 1918, *Bünnemeijer 4514* (BO, K, L, U); Lubuk Sikaping, Mt. Gadang, 700 m, 15 Jun 1953, *van Borssum-Waalkes 1893* (BO, L); Lima Puluh Kota, Kelok Sembilan, 700 m, 20 Dec 1987, *Hotta & Okada 1637* (BO); *Ibid.*, Mt. Sago, Ladang Laweh, 900 m, 28 Jul 1957, *Meijer 7245* (L); Solok, Mount Talang, 1250 m, 2 Oct 1988, *Hotta & Nagamasu 12* (BO, L). Banten: Between Bayah & Sangkop, 600 m, 20 Jun 1911, *Backer 1722* (BO); Pasir Orai, *Forbes 460* (BM, BO); Mt. Karang, Galusur, 700 m, 31 Jun 1912, *Koorders 40738β* (BO). Central Java: Purbalingga, Mt. Slamet, 1300 m, 13 Mar 2004, *Hoover et al. Deden-36* (BO). East Java: Lumajang, Sumber Mujur, Mar 1928, *Adm. Ondern. Soember Moedjoer s.n.* (BO, L, U). West Java: Mt. Paniisan, 600 m, 28 Oct 1928, *van Steenis 2300* (BO, L); Leuwiliang, Cianten, 900 m, 30 Aug 1918, *Backer 25698* (BO); Mt. Menapa, 600 m, 18 Dec 1940, *van Steenis 17373* (BO, K, L); Mt. Salak, Kampong Babojong, 700 m,

18 Sep 1896, *Koorders 24270β* (BO, K, L); Mt. Halimun, Malasari, 1055 m, 10 Oct 2017, *Kartonegoro 1106* (BO, L); Cianjur, Cibeber, Cidadap, 1000 m, *Bakhuizen van den Brink 2769* (BO); *Ibid.*, Takokak, *Koorders 33358β* (BO); Tasikmalaya, Singaparna, Mt. Galunggung, 900 m, 13 Aug 1913, *Backer 8619* (BO). Bali: Jembrana, Mt. Mesehe, 500 m, 18 May 2013, *Kartonegoro et al. 737* (BO); Mt. Pala 495 m, 5 Sep 1918, *Sarip 219* (BO, L). West Nusa Tenggara: Lombok, Mt. Rinjani, Jeruk Manis waterfall, 904 m, 16 Feb 2005, *Azuma et al. A259* (BO). **PAPUA NEW GUINEA.** Sepik: Kaiser Wilhelmsland, Kani Mountains, 1000 m, 7 Jan 1908, *Schlechter 15159* (NY).

Fig. 3-13. *Dissochaeta fallax*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** immature fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1106* (BO, L).



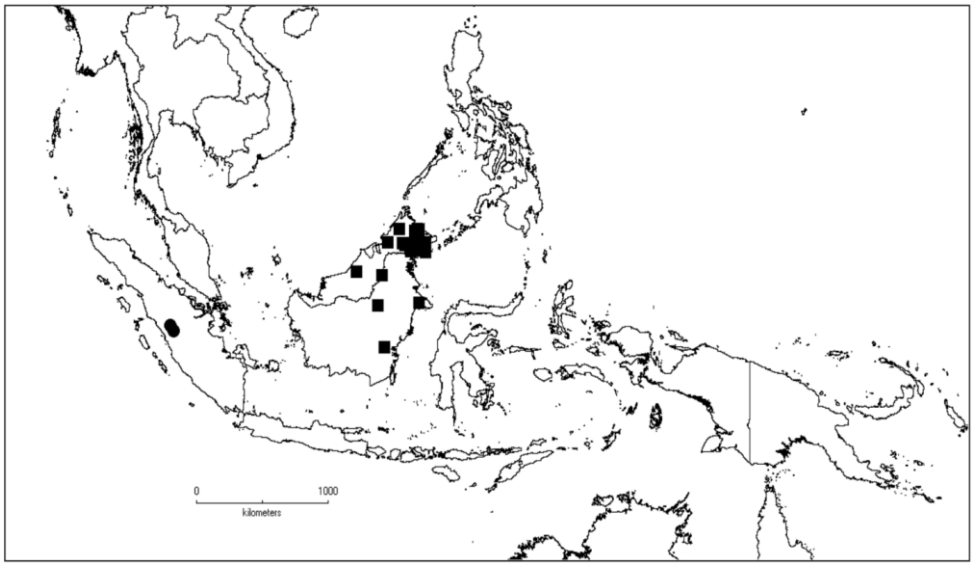
Map 3-12. Distribution of *D. fallax* (●).

19. *Dissochaeta floccosa* (J.F.Maxwell) Karton., **comb. nov.** — Map 3-13

Dissochaeta rostrata Korth. var. *floccosa* J.F.Maxwell, Gard. Bull. Singapore 33: 319, fig. 5. 1980. — Type: *S. Maradjo 350* (holo L [L0537273!]; iso L [L0537271!], PNH [PNH59964!], SING), Indonesia, West Sumatra, Pajakumbuh, Pakan Raba, Aer nan Dingin, 600 m elev., 1 Sep 1957.

Branchlets terete, 5–6 mm in diameter, floccose, covered with dense stellate pubescent hairs and with 1–2 mm long capitate bristle hairs; nodes swollen, with interpetiolar ridge; internodes 12–14 cm long. Leaves: petioles terete, ca. 10 mm long, floccose, densely covered with pubescent hairs and with 1–2 mm long brown bristle hairs; blades ovate or ovate-elliptic, 17–20 × 7–9.5 cm, subcoriaceous, base emarginate to slightly cordate, margin entire, apex acuminate, tip 2–3 cm long; nervation with 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely floccose, covered with pubescent hairs. Inflorescences terminal, up to 40 cm long, many-flowered; main axis angular, floccose, densely covered with pubescent hairs and 1–2 mm long capitate bristle hairs; primary axes up to 36 cm long with 5 or 6 nodes, secondary axes up to 6 cm long with 2 or 3 nodes, tertiary axes up to 2 cm long with 1 or 2 nodes, quarternary axes when developed up to 1 cm long with 1 node; bracts linear, 10–13 mm long, floccose, densely covered with pubescent hairs and with 1–2 mm long capitate bristle hairs; bracteoles subulate, 5–10 mm long, floccose, densely covered with pubescent hairs and with 1–2 mm long capitate bristle hairs; pedicels floccose, densely covered with pubescent hairs and with capitate bristle hairs, 6–7 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium tubular, 7–9 × 3–4 mm, floccose, densely covered with pubescent hairs and with capitate bristle hairs; calyx lobes linear-lanceolate or triangular, 7–11 mm long, floccose, densely covered with pubescent hairs and capitate bristle hairs, base truncate, apex acute; petal bud conical, 3–5 mm long; mature petals not seen. Stamens 8, subequal, filaments curved sideways; alternipetalous stamens with 8–9 mm long filaments, anthers slender, curved, sickle-shaped, thecae 14–15 mm long, pedoconnective 2–3 mm long, basal crest minute, triangular, ca. 1 mm long, lateral

appendages paired, filiform, 2–4 mm long; oppositipetalous stamens with ca. 8 mm long filaments, anthers S-shaped, thecae 12–14 mm long, basal crest with minute auricles, ca. 0.5 mm long, lateral appendages paired auricles, 1–1.5 mm long. Ovary ¾ of hypanthium in length, apex floccose; style glabrous, in bud ca. 15 mm long; stigma minute; extra-ovarial chambers 8, extending to the base of the ovary. Fruits urceolate, ca. 10 × 5–6 mm, floccose, densely covered with pubescent hairs and capitate bristle hairs; calyx lobes remnant persistent, 8–11 mm long, reflexed. Seeds ca. 0.5 mm long.



Map 3-13. Distribution of *D. floccosa* (●) and *D. glabra* var. *glabra* (■).

Distribution — Sumatra (West).
Ecology and habitat — Lowland forest at 300–600 m elevation.
Note — *Dissochaeta floccosa* is known only from 2 collections. This species closely resembles *D. horrida* in having long, linear-lanceolate calyx lobes of up to 11 mm long and similar number and shape of the stamens, but differs in having a floccose indumentum all over with shorter bristle hairs.
Specimen examined — **INDONESIA.** West Sumatra: Payakumbuh, Pakan Raba, 600 m elev., 1 Sep 1957, *Maradjo 350* (L, PNH); Sawahlunto Sijunjung, Kulampi, 300 m, 21 Apr 2000, *Erlo 32* (ANDA).

20. *Dissochaeta glabra* Merr.

Dissochaeta glabra Merr., J. Straits Branch Roy. Asiat. Soc. 76: 101. 1917. — *Diplectria glabra* (Merr.) M.P.Nayar in Veldkamp et al., Blumea 24: 421, fig. 4B. 1979. — Lectotype (designated here): *A. Villamil 242* (lecto PNH [PNH32349!]; isolecto US [US00120530!]), Malaysia, Sabah, Kalabakan, Pinajas River, 20 m elev., 8 Oct 1916.

Climbing up to 15 m in height. Branchlets terete, 4–5 mm in diameter, glabrous; nodes swollen, with prominent annular crest-like interpetiolar ridge, often with bristle hairs; internodes 6–8.5 cm long. Leaves: petioles terete, 7–10 mm long, furfuraceous and dorsally with bristle hairs; blades ovate to ovate-oblong, 9–16 × 4.5–8 cm, subcoriaceous, base rounded to shallowly subcordate, margin entire, apex acuminate, tip 0.5–0.8 cm long;

nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous, basally with a pair of glandular patches. Inflorescences terminal, up to 90 cm long, many-flowered; main axis angular, glabrous or sparsely covered with stellate hairs; primary axes up to 80 cm long with 7–10 nodes, secondary axes 8–20 cm long with 5–7 nodes, tertiary axes up to 6 cm long with 1–3 nodes, quarternary axes if developed 1–3 cm long with 1 or 2 nodes, quinternary axes when developed up to 0.5 cm with 1 node; bracts linear, 4–5 mm long, caducous, stellate puberulous; bracteoles subulate, ca. 1 mm long, densely covered with stellate hairs; pedicels stellate puberulous, 3–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium cyathiform-tubular, 4–6 × 2–3.5 mm, glabrous or sparsely covered with stellate hairs; calyx lobes truncate, ca. 0.5 mm long, apex with 4 minute points, purplish; petal bud conical, 1–5 mm long; mature petals suborbicular, 3–6 × 3–4.5 mm, reflexed, base clawed, apex acute, white purplish or purple. Stamens 8, unequal, filaments flattened, straight; alternipetalous stamens staminodial, with 3–5 mm long filaments, anthers rudimentary, slender, terete, thecae 0.5–2 mm long, basal crest triangular, 0.75–2 mm long, thin, apex acute, base emarginate or hastate, lateral appendages prolonged from the theca vestige, paired, filiform, 3–6 mm long; oppositipetalous stamens with 4–6 mm long filaments, anthers thick, curved, hook-shaped or S-shaped, thecae 5–6 mm long, yellow, basal crest triangular, 0.3–2 mm long, erose to bifid, lateral appendages ligular with bifid apex, 0.5–1 mm long. Ovary half to ¾ of hypanthium in length, apex glabrous; style 8–12 mm long, curved at the end, slender, glabrous; stigma minute, capitate; extra-ovarial chambers 4, oppositipetalous, extending from ⅓ to the middle of the ovary. Fruits subglobose to urceolate, 4–7 × 4–5 mm, glabrous, slightly 8-lined; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Borneo.

Note — Within the genus, *D. glabra* has the longest and most robust inflorescences (up to 90 cm long) with up to 5 degrees of ramifications, but it has smaller flowers. Due to the flowers and stamens, this species closely resembles *D. conica* and *D. papuana*. The glabrous appearance and the glandular patches at the leaf base below are similar to *D. beccariana*, which is also endemic to Borneo, but differs in the shape of the alternipetalous stamens.

Key to varieties of *D. glabra*

1 Hypanthium ca. 4 × 2 mm, glabrous or sparsely covered with stellate hairs; petal bud 1–1.5 mm long; mature petals 3–4 × 3–3.5 mm, white; fruits subglobose to urceolate, 4–5 × ca. 4 mm ..... **var. *glabra***

1 Hypanthium 5–6 × ca. 3.5 mm, glabrous; petal bud 4–5 mm long; mature petals 5–6 × ca. 4.5 mm, violet or pink; fruits urceolate, 6–7 × ca. 5 mm ..... **var. *kinabaluensis***

20.1. *Dissochaeta glabra* Merr. var. ***glabra*** — Fig. 3-14, Map 3-13

Diplectria glabra (Merr.) M.P.Nayar ssp. *glabra*: Veldkamp et al., Blumea 24: 421, fig. 4B. 1979.

Diplectria glabra (Merr.) M.P.Nayar var. *glabra*: J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980.

Hypanthium ca. 4 × 2 mm, glabrous or sparsely covered with stellate hairs, dark green; petal bud conical, 1–1.5 mm long; mature petals suborbicular, 3–4 × 3–3.5 mm, reflexed, white purplish or purple, base clawed, apex acute. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with ca. 3 mm long filaments, thecae ca. 0.5 mm long, basal crest triangular, ca. 0.75 mm long, thin, base emarginate or hastate, apex acute, lateral

appendages prolonged from the locule vestige, paired, filiform, 3–4 mm long; oppositipetalous stamens with 4–5 mm long filaments, thecae 5–6 mm long, yellow or creamy, basal crest triangular, ca. 0.3 mm long, erose to bifid, lateral appendages ligular with bifid apex, ca. 0.5 mm long. Ovary half to ¾ of hypanthium in length, apex glabrous; style glabrous, 8–10 mm long, curved at the end, slender; stigma minute, capitate; extra-ovarial chambers extending to half of the ovary. Fruits subglobose to urceolate, 4–5 × ca. 4 mm, glabrous.

Distribution — Borneo.

Ecology and habitat — Lowland mixed dipterocarp forest to lower montane forest, in open places at 20–1200 m elevation.

Specimens examined — **MALAYSIA.** Sabah: Kalabakan, Pinajas River, 20 m, 8 Oct 1916, *Villamil 242* (K, PNH, US); *Ibid.*, Ulu Sungai Kalabakan, 19 May 1984, *Fidilis & Martin SAN 103669* (K, L); *Ibid.*, Gunong Rara, 21 Apr 1972, *Shea SAN 75633* (K, L); Lahad Datu, Danum Valley, 12 Jun 1986, *Campbell et al. SAN 112059* (L); *Ibid.*, 7 May 1989, *Ridsdale 1961* (K, L); *Ibid.*, 238 m, 6 Jul 2006, *Suzana et al. SAN 147687* (K, L); *Ibid.*, Silabukan, 183 m, 21 Apr 1967, *Sinanggul SAN 58046* (K, L); *Ibid.*, Ulu Segama, 170 m, 25 Feb 1986, *Edwards 2111* (K); *Ibid.*, 200 m, 28 Feb 1985, *Argent et al. 108277* (K, L); Lamag, Inarat, Gunong Lotong, 1000 m, 16 Aug 1976, *Saikeh SAN 83210* (K); Nabawan, Gunung Lotong, Meliah Basin, 19 Apr 1988, *Madani SAN 124418* (K); Ranau, Sungai Nabutan, 23 Mar 1982, *Joseph SAN 94559* (K, L); Sandakan, Segaliud Lokan, 106 m, 30 May 1963, *Banang SAN 36928* (K, L); *Ibid.*, Gadong Camp, 58 m, 4 Apr 1963, *James SAN 35395* (K, L); *Ibid.*, Gomantong, 17 Apr 1970, *Rusonkhan SAN 66574* (K); *Ibid.*, Kabili-Sepilok, 4 Jun 1937, *Enggoh 7246* (K); *Ibid.*, Sepilok, 7 Apr 1954, *Wood A 2987* (K, L); Tenom, Mandalom, 27 Aug 1987, *Asik SAN 120365* (K, L); Tawau, *Elmer 20794* (BM, L, P, PNH, U), St. Lucia, Pinayas, 60 m, 8 May 1940, *Orolfo 8* (K, L). Sarawak: Bintulu, Tubau, Ulu Jejalong, Bukit Sekiwa, 300 m, 2 Sep 1986, *Mochtar S.53947* (AAU, L). **INDONESIA.** East Kalimantan: West Kutai, Hikam Batu Beng, 80 m, 28 Jul 1925, *Endert 2275* (BO, L); Sangkulirang, Babi Jolong, 40 m, 3 Jun 1937, *Aet 599* (BO). North Kalimantan: Malinau, 20 m, 2 Jul 1981, *Geesink 8926* (L). South Kalimantan: Muara Uya, Jaro Dam, 80 m, 17 Nov 1971, *de Vogel 881* (K, L).

20.2. *Dissochaeta glabra* Merr. var. ***kinabaluensis*** (Veldkamp) Karton., **comb. nov.** — Fig. 3-15, Map 3-14

Diplectria glabra (Merr.) M.P.Nayar ssp. *kinabaluensis* Veldkamp, Blumea 24: 422, fig. 1A, 4C. 1979. — *Diplectria glabra* (Merr.) M.P.Nayar var. *kinabaluensis* (Veldkamp) J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980. — Type: *G. Mikil SAN 46742* (holo L [L0008869!]; iso K [K000859551!], L [L0008870!], SAN), Malaysia, Sabah, Sosopodon, near Kundasang, 4500 ft. elev., 15 Jul 1964.

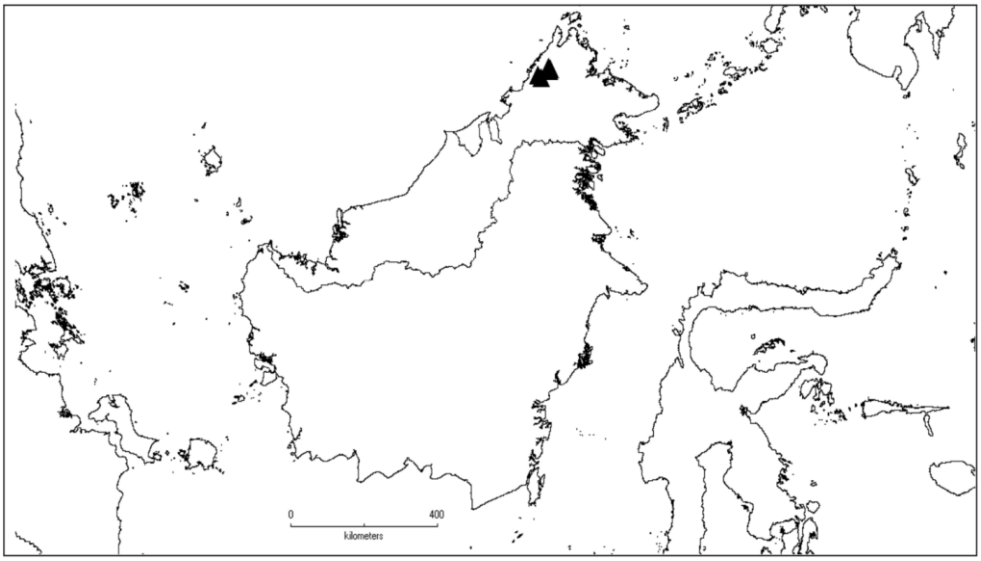
Hypanthium 5–6 × ca. 3.5 mm, glabrous, reddish; petal bud conical, 4–5 mm long; mature petals suborbicular, 5–6 × ca. 4.5 mm, not reflexed, violet or pink, base clawed, apex acute. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with ca. 5 mm long filaments, thecae 1–2 mm long, basal crest triangular, ca. 2 mm long, thin, apex acute, base emarginate or hastate, lateral appendages prolonged from the locule vestige, paired, filiform, 5–6 mm long; oppositipetalous stamens with ca. 6 mm long filaments, thecae 5–6 mm long, yellow, basal crest bifid, ca. 2 mm long, lateral appendages ligular with bifid apex, ca. 1 mm long. Ovary half as long as hypanthium, apex glabrous; style glabrous, 11–12 mm long, curved at the end, slender; stigma minute, capitate; extra-ovarial chambers 8, extending to ⅓ of the ovary. Fruits urceolate, 6–7 × ca. 5 mm, glabrous.

Distribution — Borneo (Sabah).
Ecology and habitat — Montane forest at 1300–1500 m elevation.
Note — This variety differs from var. *glabra* in having larger inflorescences, flowers and fruits. The fruits of var. *kinabaluensis* are rather urceolate instead of subglobose. The distribution of the variety is restricted to the montane forest of the Mount Kinabalu Complex and Crocker Range in Sabah, Borneo.

Fig. 3-14. *Dissochaeta glabra* var. *glabra*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by D.S. Penneys; vouchers: *Penneys 2446* (WNC), *Penneys 2474* (WNC) & *Penneys 2487* (WNC).

Specimens examined — **MALAYSIA.** Sabah: Ranau, Mt. Kinabalu, Ulu Liwagu-Ulu Mesilau, 1220 m, 2 Sep 1961, *Chew, Corner & Stainton RSNB 2647* (K, L); *Ibid.*, Tenompok, 1500 m, 29 Apr 1932, *Clemens 29442* (BM, K, L, NY); *Ibid.*, Penibukan, 1500 m, 10 Jan 1933, *Clemens 30865* (BM, K, L); *Ibid.*, 7 Feb 1933, *Clemens 31520* (BM); *Ibid.*, 2000 m, 26 Oct 1933, *Clemens 40940* (BM, K, L); *Ibid.*, 1670 m, 13 Nov 1933, *Clemens 50337* (BM, K); *Ibid.*, Gurulau, 1500 m, 25 Nov 1933, *Clemens 50476* (BM, K, L); *Ibid.*, 29 Nov 1933, *Clemens 50555A* (BM); *Ibid.*, Sosopodon, Kundasang, 1370 m, 15 .Jul 1964, *Mikil SAN 46742* (K, L); Tambunan, Mount Alab, 1500 m, 2 Mar 1995, *Pereira et al. 111* (L).

Fig. 3-15. *Dissochaeta glabra* var. *kinabaluensis*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower. Photos by D.S. Penneys; voucher: *Penneys 2542* (WNC).



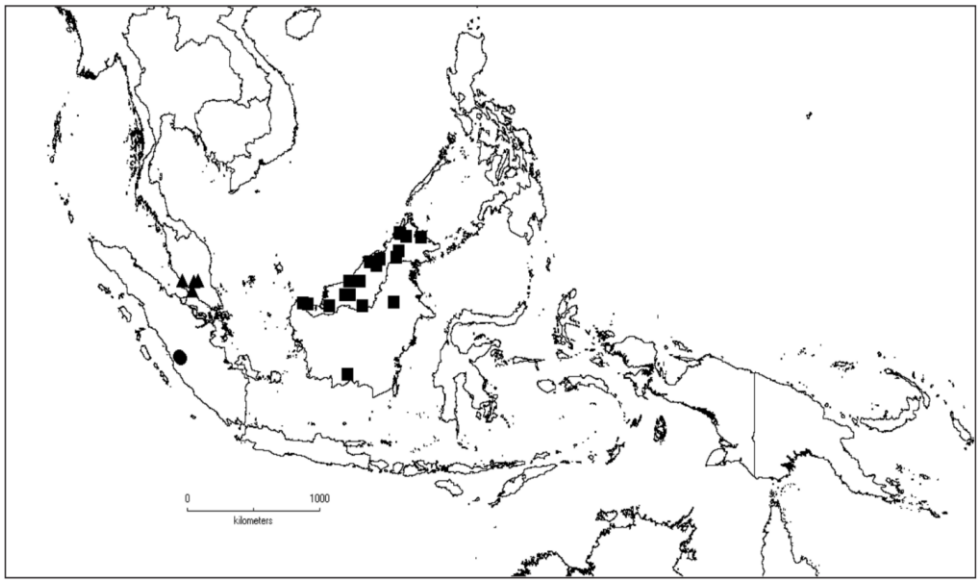
Map 3-14. Distribution of *D. glabra* var. *kinabaluensis* (▲).

21. *Dissochaeta glandiformis* J.F.Maxwell — Map 3-15

Dissochaeta glandiformis J.F.Maxwell, Gard. Bull. Singapore 33: 313, fig. 1. 1980. — Type: *W. Meijer 7282* (holo L [L0537274!]), Indonesia, Jambi, Kerintji Region, Gunung Tudjuh, 1800 m elev., Jul 1956.

Climbing up to 10 m in height. Branchlets terete, 4–5 mm diameter, densely stellate-furfuraceous; nodes swollen, with annular ridge crest-like, angular or ligular interpetiolar ridges up to 5 mm wide; internodes 6–8 cm long. Leaves: petioles flattened, 10–16 mm long, densely stellate-furfuraceous; blades ovate to ovate-elliptic, 7–16 × 5–8.5 cm, membranous, base rounded, margin entire, apex acuminate, tip 0.5–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely brown stellate-tomentose. Inflorescences terminal and in the upper leaf axils, up to 22 cm long, many-flowered; main axis angular, densely stellate-furfuraceous; primary axes up to 18–20 cm long with 4–5 nodes, secondary axes 2–5 cm long with 2 or 3 nodes, tertiary axes 1–2.5 cm long with 1 or 2 nodes, quartenary axis up to 0.5 cm long when developed with 1 node; bracts minute, inconspicous; bracteoles linear, 1–2 mm long, densely stellatefurfuraceous; pedicels densely stellate-furfuraceous, 4–5 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium campanulate, slightly angular, 3–5 × 1–3 mm, with four distinct ridges, densely stellate-tomentose, somewhat pointing sideways from pedicels; calyx lobes triangular with rounded tips, 2–2.5 mm long, widened, stellate-furfuraceous; lobes in bud distinctly united in thin acorn-like shape with sutures and opening when mature; petal bud conical, 3–6 mm long; mature petals ovate or oblong, 6–9 × 3–5 mm, base clawed, apex obtuse, glabrous or inside at base with appressed hairs, pink. Stamens 4, equal, alternipetalous, filaments flat, 4–6 mm long, straight, apex bent, anthers linear-lanceolate, sickle-shaped or falcate, thecae 5–6 mm long, yellow, pedoconnective ca. 1 mm long, basal crests minute, triangular, ca. 1 mm long, narrow with acute apex, lateral appendages paired, filiform, 3–5 mm long, tan. Ovary half or ⅔ of hypanthium in length, apex pubescent; style erect, 8–13 mm long, curved at apex, glabrous, purple; stigma minute; extra-ovarial chambers 4, alternipetalous, extending to the base of the ovary. Fruits ovoid, 5–6 × 3–5 mm, glabrous

to sparsely stellate-furfuraceous, rarely with distinct vertical ridges, green, often pointing sideways from the pedicels; calyx lobe remnants persistent or sometimes caducous. Seeds ca. 0.5 mm long.
Distribution — Sumatra (West).
Ecology and habitat — Montane forest at 900–2500 m elevation.
Note — *Dissochaeta glandiformis* resembles to *D. intermedia* with brown stellate-tomentose hairs in leaf blades abaxiallyly and having only 4 alternipetalous stamens with two filiform lateral appendages. This species differs from the latter by having a conspicous interpetiolar ridge (annular and crest-like or ligular) at the nodes and longer calyx lobes (2–2.5 mm long). The calyx lobes are distinctly united and have an acornlike appearance when in bud, splitting into four lobes at maturity (Maxwell 1980b). This species is restricted to the montane forest of the Mount Kerinci complex, Sumatra.
Specimens examined — **INDONESIA.** Jambi: Mt. Tujuh, 1800 m, Jul 1956, *Meijer 7282* (L); *Ibid.*, 6 Aug 1956, *Jacobs 4517* (BO). West Sumatra: Mt. Kerinci, 900 m, 8 Feb 1920, *Bünnemeijer 8074* (BO, L); *Ibid.*, 2500 m, 7 Apr 1920, *Bünnemeijer 9230* (BO, K, L); *Ibid.*, 2000 m, 13 Apr 1920, *Bünnemeijer 9379* (BO, L, U); *Ibid.*, 1800 m, 12 May 1920, *Bünnemeijer 10477* (BO, L).



Map 3-15. Distribution of *D. glandiformis* (●), *D. glandulosa* (■) and *D. griffithii* (▲).

22. *Dissochaeta glandulosa* Merr. — Map 3-15

Dissochaeta glandulosa Merr., Univ. Calif. Publ. Bot. 15: 224. 1929. — Lectotype (designated here): *A.D.E. Elmer 20259* (lecto BO [BO1421691!]; isolecto BISH [BISH-1003260!], BM [BM001190924!, BM001190925!], BR [BR00000522241!], BRI [BRI-AQ0023052!], C [C10014564!], CAS [CAS0033425!], CM [CM-1527!], F [F65407!], GH [GH00072204!, GH00072205!], HBG [HBG514873!], K [K000859503!], L [L0537261!], MICH [MICH-1111782!], NY [NY00228564!], PH [PH00009602!, PH00009603!], S [SG-2104!], U [U0124130!]), Malaysia, Sabah, Myburgh Province, Sandakan, Oct–Dec 1921.

Climbing up to 15 m in height. Branchlets terete, 3–4 mm in diameter, glabrous; nodes swollen, with crest-like interpetiolar ridge; internodes 7–11 cm long. Leaves: petioles terete, 1.3–1.8 cm long, glabrous; blades broadly ovate, 8.5–11.5 × 5.6–6.7 cm, subcoriaceous, base rounded to emarginate, margin entire, apex acuminate, tip up to 1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous, basally with a pair of glandular patches on abaxially. Inflorescences terminal, up to 25 cm long, many-flowered; main axis glabrous; primary axes up to 11 cm long with 3 nodes, secondary axes 4–4.5 cm long with 1 or 2 nodes, tertiary axes ca. 2 cm long with 1 node; bracts elliptic-oblong, 20–27 × 8–10 mm, glabrous, whitish; bracteoles oblong to lanceolate, ca. 14 × 3–4 mm, glabrous, whitish; pedicels glabrous, purplish, 4–5 mm long in central flowers, 3–4 mm long in lateral flowers. Hypanthium campanulate, 5–6 × 4–5 mm, glabrous, at early stages subglobose to urceolate and enclosing petal bud; calyx lobes truncate, level, 1–2 mm long; petal bud conical, 6–7 mm long; mature petals broadly ovate, 5–6 × ca. 5 mm, base clawed, apex acute, purple above, whitish below. Stamens 8, subequal, filaments curved sideways, light yellow; alternipetalous stamens with ca. 6 mm long filaments, anthers slender, curved, sickle-shaped, thecae ca. 4 mm long, pedoconnective ca. 1 mm long, apex acute, basal crest thin, 1–1.5 mm long, margin erose to fimbriate, lateral appendages paired, filiform, 2–4 mm long, fimbriate; oppositipetalous stamens with 5–6 mm long filaments, bent at the attachment to anthers, anthers thick, slightly curved, hook-shaped, thecae 5–6 mm long, apex obtuse, yellow, basal crest thin, ligular, 2–2.5 mm long, bifid, lateral appendages paired, filiform, up to 2 mm long. Ovary half as long as hypanthium, apex villous; style ca. 14 mm long, glabrous, curved at the end, slender, light green-yellow; stigma minute, purplish; extra-ovarial chambers shallow to nearly undeveloped. Fruits urceolate, ca. 10 × 6 mm, glabrous; calyx lobe remnants persistent. Seeds ca. 0.75 mm long.

Distribution — Borneo.

Ecology and habitat — Lowland Mixed Dipterocarp forests on ridge at 50–400 m elevation.

Note — *Dissochaeta glandulosa* resembles *D. beccariana* because of the similar glabrous indumentum and conspicuous white bracts. However, this species has a much larger campanulate hypanthium (5–6 × 4–5 mm in *D. glandulosa*, 4–7 × 2–3 mm in *D. beccariana*) and urceolate fruits (subglobose in *D. beccariana*).

Specimens examined — **BRUNEI.** Belait: Labi, Bukit Teraja, 350 m, 18 Oct 1991, *Simpson & Marsh 2115* (K, L). Temburong: Amo, Ulu Belalong, 480 m, 20 Jan 1994, *Coode et al. 7864* (L). **MALAYSIA.** Sabah: Nabawan, Ulu Sungai Nabawan, 22 Feb 1990, *Fidilis SAN 128385* (L); Penampang, Crocker Range, Kota Kinabalu–Tambunan Road, 900 m, 1 Oct 1983, *Beaman & Beaman 7110* (K, L); Pensiangan, Pensiangan Kayu FR, 23 Jul 1992, *Fidilis SAN 136035* (K, L); Sandakan, Myburgh, Oct-Dec 1921, *Elmer 20259* (BISH, BM, BO, BR, BRI, C, CAS, CM, F, GH, K, L, MICH, NY, PH, S, U); Ranau, Ulu Tungud, 343 m, 27 Jul 2005, *Saw et al. SAN 146062* (L); *Ibid.*, Mount Kinabalu, Penibukan, 1200 m, 14 Mar 1931, *Clemens 32150* (BM). Sarawak: Betong, Batang Layar, 1 Jul 1980, *Lee S.41990* (L); Bintulu, Bukit Pesu, Ulu Kuala Semut, 160 m, 20 Aug 1963, *Fuchs 21352* (K, L); *Ibid.*, Ulu Segan, 274 m, 25 Aug 1968, *Ilias Paie S.27219* (K, L); Kapit, Belaga, Rejang River, 500 m, 31 Aug 1958, *Jacobs 5361* (K, L), Pelagus Protected Forest, 100 m, 16 Sep 1973, *Chai et al. S.33173* (BO, K, L); *Ibid.*, Ulu Baleh, 400 m, 6 May 1991, *Runi et al. S.63213* (K, L); Kuching, Selang FR., 91 m, 25 Jul 1957, *Ilias Paie S.8462* (K, L); Lundu, *Haviland 1508* (BM, K); Miri, Mulu, Gunung Mulu National Park, 400 m, 14 Oct 1977, *Chai S.39492* (K, L). **INDONESIA.** Central Kalimantan: Kotawaringin Timur, Mentaya River, 50 m, 11 Feb 1994, *Argent & Wilkie 9441* (L). East Kalimantan: West Kutai, Long Petah, 600 m, 10 Sep 1925, *Endert 3126* (BO, K).

23. *Dissochaeta gracilis* (Jack) Blume — Fig. 3-16, Map 3-16

Dissochaeta gracilis (Jack) Blume, Flora 14: 498. 1831. — *Melastoma gracile* Jack, Trans. Linn. Soc. London 14: 14. 1823, "gracilis". — *Neodissochaeta gracilis* (Jack) Bakh.f., Contr. Melastom. 137. 1943. — Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 134. 2010): *C.N.A. de Voogd 591* (neo L [L0822677!]; isoneo BO!), Indonesia, Bengkulu, Boekit Daoen, Balai, 1000 m elev., 13 Jul 1931.

Melastoma vacillans Blume var. *pallens* Blume, Bijdr. Fl. Ned. Ind. 17: 1074. 1826. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 134. 2010): *C.L. Blume s.n.* (lecto L [L0008889!]; isolecto BO!, L [L0008885!, L0008886!, L0008887!, L0008888!]), Indonesia, Java.

Dissochaeta brachyanthera Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 74. 1851. — Lectotype (designated here): *H. Zollinger 3511* (lecto P [P05283573!]; isolecto A [A00072203!], BM!, L [L0537238!], P [P05283585!, P05283587!]), Indonesia, West Java, Mount Perbakti, 2 Jun 1848.

Neodissochaeta puberula Bakh.f., Contr. Melastom. 139. 1943. — Type: *L.M.R. Rutten 86* (holo U [U0004008!]), Indonesia, East Kalimantan, Samarinda, Sungai Wain.

Neodissochaeta compressa Bakh.f., Contr. Melastom. 146. 1943. — Type: *H.J.P. Winkler 2809* (holo L [L0537275!]; iso BM [BM001190927!], BO [BO1765008!], K [K000859495!], WRSL), Indonesia, South Kalimantan, Limowia, Batoe Babi, 10 Jul 1908.

Climbing up to 20 m in height. Branchlets terete or nearly quadrangular, 3–4 mm in diameter, glabrous or sparsely puberulous; nodes swollen, with interpetiolar line; internodes 4–6.5 cm long. Leaves: petiole terete, 7–15 mm long, glabrous or sparsely puberulous; blade ovate to elliptic, 8–17 × 3–8 cm, membranous, base rounded, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous. Inflorescences terminal and in the upper leaf axils, 8–20 cm long, cymous, with many flowers; main axis angular, glabrous to sparsely furfuraceous; primary axes 5–17 cm long with 4–6 nodes, secondary axes 1–2 cm long with 2 or 3 nodes, tertiary axes 0.5–0.6 cm long with 1 or 2 nodes; bracts linear or elliptic, 3–6 mm long, thin, sparsely or densely stellate-pubescent; bracteoles linear or rarely oblong, 6–8 mm long, glabrous to stellate-pubescent; pedicels glabrescent, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate or suburceolate, 2–3 × ca. 2 mm, glabrous or sparsely puberulous; calyx lobes truncate with undulate tips, 0.5–0.7 mm long, rarely with minutely triangular tip, glabrous; petal bud conical, 2–3 mm long; mature petals ovate, oblong or suborbicular, 2–3 × 2–3 mm, reflexed, base clawed, apex obtuse, glabrous, veined, white or pale pink. Stamens 8, unequal, filaments curved sideways; alternipetalous stamens with 3–5 mm long filaments, curved, bent at end point, anthers clavate, sickle-shaped, thecae 4–6 mm long, white or pink, pedoconnective white, 1–2 mm long, basal crests membranous, 0.25–0.5 mm long, thin, lateral appendages paired, flat, wavy, filiform, ca. 2 mm long, yellow; oppositipetalous stamens with ca. 2 mm long filaments, anthers smaller, slender, somehow staminodial, curved, thecae 1–1.5 mm long, white or pinkish, basal crests minute or spuriform, erect or ligular, ca. 0.3 mm long, lateral appendages paired, filiform, 1.5–2 mm long, yellow. Ovary half as long as hypanthium, apex villous or glabrous; style 4–6 mm long, curved at end. glabrous, white; stigma minute; extra-ovarial chambers 4, alternipetalous, extending to the middle of the ovary. Fruits globose, 5–6 × 2–4 mm, glabrous, bright green with distinct, 8-lined, purple when ripe; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Thailand, Peninsular Malaysia, Sumatra, Java and Borneo.

Fig. 3-16. *Dissochaeta gracilis*. **a.** habit; **b.** hypanthium; **c.** flower; **d.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1113* (BO, L).

Ecology and habitat — Primary or secondary disturbed forest, regrowth forest or riparian, lowland to mountain forest at 10–1500 m elevation.

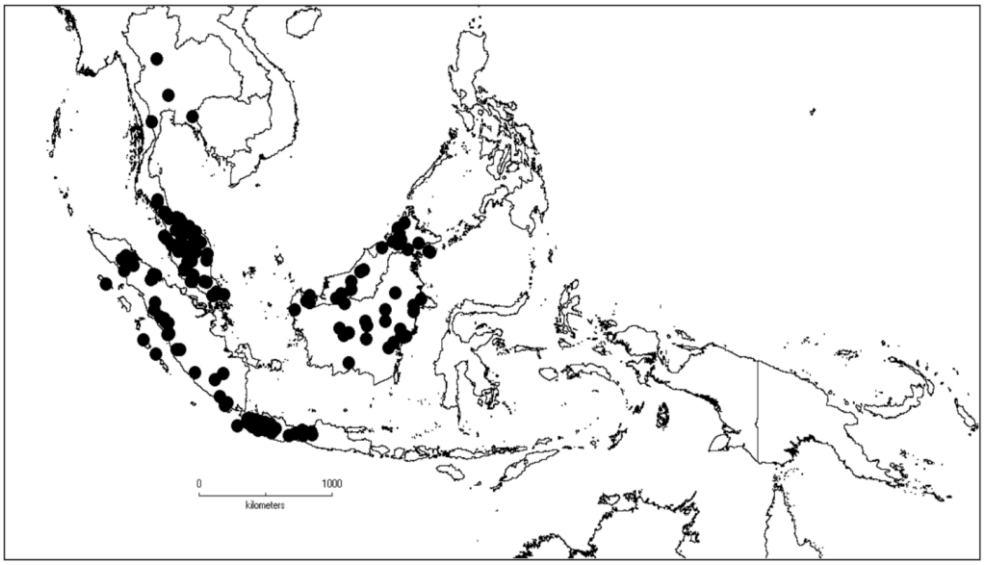
Vernacular names — Peninsular Malaysia: *sedudu akar* (Malay). Sumatra: *alor sitabong detay* (Simeuleu). Java: *kecambang areuy*, *harendong areuy*, *kingkilaban* (Sunda), *kalikadep*, *walak* (Java).

Note — This species can easily be distinguished by its thin leaf blades, glabrous on both surfaces and with four fertile alternipetalous stamens and four oppositipetalous staminodes. It has the smallest hypanthium of all species. The extra-ovarial chambers are shallow when compared to the size of the hypanthium and fertile stamens. Amongst all the species, *D. gracilis* is the most common species found in a wide elevation range, between 10–1500 m elevations. This species is also widespread west, but never east of Wallace's line.

Selected specimens examined — **THAILAND.** Ayutthaya: Sukirin Poo Kao Tong, 200 m, 28 Mar 1987, *Maxwell 87-254* (L, P). Chanthaburi: Khao Soi Dao, 100 m, 29 Apr 1930, *Kerr 19233* (BM, K). Narathiwat: Waeng, 15 Nov 1962, *Sangkhachand BKF 46913* (K); *Ibid.*, Hala Bala 380 m, 20 Apr 2004, *Chongko 315* (L); Sungei Kolok, 28 Feb 1974, *Larsen & Larsen 32731* (L). Pattani: Kao Kalakiri, 600 m, 11 Sep 1923, *Kerr 7812* (BM, K).

Petchaburi: Khao Daen, 200 m, 19 Apr 1928, *Kerr 15310* (BM, K). Songkhla: Khao Nam Kang, Na Thawee, 100-150 m, 13 Jun 1992, *Larsen et al. 42845* (P); Ton Nga Chang, 250 m, 17 Aug 1995, *Larsen et al. 45732* (L). Sukhothai: Klaung Tan, 400 m, 11 Mar 1928, *Kerr 14470* (BM, K). Trang: Trang Ridge, 800 m, 28 Aug 1915, *Vanpruk 697* (K); Khao Pap Pa, 13 Mar 1974, *Larsen & Larsen 33279* (L). Yala: 8 Feb 1973, *Sangkhachand & Phusomsaeng 1539* (P); Betong, 300 m, 31 Jul 1923, *Kerr 7433* (BM, K); Bannang Sata, 21 Dec 1966, *Sangkhachand BKF 40970* (K, L, P). **MALAYSIA.** Johor: Panti, 19 Nov 1966, *Suppiah KEP 98980* (K, L); Labis, 150 m, 14 Apr 1967, *Suppiah KEP 104968* (K, L); Kota Tinggi, 50 m, 22 Apr 1978, *Maxwell 78-211* (L). Kelantan: Channing, 2 Feb 1917, *Ridley s.n.* (K); Ulu Sungai Lebir Kecil, 17 Sep 1967, *Cockburn FRI 7132* (K, L). Malacca: *Griffith s.n.* (BM). Negeri Sembilan: Jelebu, Serting Forest Reserve, 200 m, 1 Oct 1996, *Gardette 2280* (L). Pahang: Kuala Lipis, Ulu Chimeras, 21 Nov 1924, *Burkill & Haniff SFN 15726* (BO); Kuala Tahan, 60 m, 16 Feb 1968, *Shah 1308* (K, L); Ulu Sungai Kuantan, 183 m, 11 Jun 1934, *Symington & Kiah SFN 28776* (BO, K). Penang: *Wallich 4050* (P); Batu Kawau, Aug 1885, *Curtis 398* (K). Perak: Goping, *King's collector 657* (BM, K, P); Gunong Bubu, 610 m, 18 Aug 1966, *Chew 1236* (K, L); Larut & Matang, Bukit Larut, 645 m, 21 Mar 2007, *Phoon & Kueh FRI 53289* (K, L). Selangor: Rawang, May 1896, *Ridley 7332* (K); Genting Highlands, Ulu Gombak 325 m, 2 Jun 1978, *Maxwell 78-297* (L). Terengganu: Kemaman, Bukit Kajang, 183 m, 4 Nov 1935, *Corner SFN 30223* (K); Ulu Terengganu, Sekayu, Bt. Lanjut, 20 Sep 1969, *Loh FRI 13499* (K, L). Sabah: Keningau, Tulid Area, Ulu Sg. Sembuan, 20 Sep 1988, *Asik Mantor SAN 125639* (K, L); Lahad Datu, Danum Valley, 14 May 1989, *Ridsdale 2017* (L); Ranau, Kampong Poring, 30 Mar 1995, *Sambuling 596* (K); Tawau, Mar 1923, *Elmer 21427* (BM, BO, K, L, U); Semporna, Sg. Montoritip, 13 m, 24 Feb 1964, *Aban Gibot SAN 40929* (L). Sarawak: Bukit Mersing, Anap, 200 m, 24 Aug 1964, *Sibat S.21910* (BO, K, L); Kuching, 17 Oct 1894, *Haviland & Hose 3387* (BM, K, L); *Ibid.*, Mount Penrissen, 1100 m, 4 Dec 1994, *Beaman & Gregory-Smith 11090* (K); Limbang, Bukit Pagon, Sg. Sipayan, 540 m, 3 Aug 1984, *Awa & Lee S.47645* (K); Dataran Tinggi Merurong, Sungei Jelalong, Sungei Ebau, 350 m, 11 Oct 1984, *Othman et al. S.48867* (K, L). **SINGAPORE.** Bukit Timah, 1894, *Langlasse 83* (P). **BRUNEI.** Temburong: Batu Apoi, 350 m, 29 Oct 1991, *Simpson & Marsh 2503* (K, L). **INDONESIA.** Aceh: Gayoland, Palo to Kongke, 1000 m, 4 Mar 1937, *van Steenis 9478* (BO, K, L); Kutacane, Gunung Gurah, 22 Mar 1954, *Alston 14627* (BM, BO); Mt. Leuser, Bengkong River, 200 m, 16 Jul 1979, *de Wilde & de Wilde-Duyfjes 18739* (BO, K, L); Simeuleu Island, Tapah, 26 Mar 1920, *Achmad 1757* (BO, K, L). Bengkulu: Rimbo Pengadang, 1000 m, 9 Jun 1916, *Ajoeb 115* (BO); Bukit Daun, Balai, 1000 m, 13 Jul 1931, *de Voogd 591* (BO, L). Jambi: Kerinci, Siolak Deras, 915 m, 18 Mar 1914, *Robinson & Boden-Kloss s.n.* (BM, K). Lampung: Semaka, Sukaraja, 530 m, 28 Aug 2008, *Arifiani et al. 922* (BO); Kota Agung, Ulu Belu, 22 Aug 1915, *Cramer 90* (BO, L). Mentawai Islands: Siberut, 8 Jul 1953, *van Borssum-Waalkes 2659* (BO, K, L); Sipora, 9 Oct 1924, *Boden-Kloss SFN 14661* (BO, K). North Sumatra: Bukit Lawang, 100–150 m, 30 Jan 1980, *Wiriadinata & Maskuri 538* (BO, K, L); Asahan, Bandar Puluh, H.S. Yates 1599 (BO, P); *Ibid.*, *Yates 1271* (BM, BO, L). South Sumatra: Muara Dua, Tenang, 700 m, 10 Jan 1930, *de Voogd 555* (BO); Lake Ranau, G. Raya, 1300 m, 2 Nov 1929, *van Steenis 3538* (BO, L). West Sumatra: Bukit Tinggi, Mangani, 1100 m, 15 Jun 1918, *Bünnemeijer 3015* (BO, L); Agam, Brani, 900 m, 22 Jun 1918, *Bünnemeijer 3199* (BO, L, U). Banten: Pandeglang, Menes, 100 m, Mar 1913, *Backer 7032* (BO); Mt. Pulosari, 900 m, Mar 1913, *Backer 7054* (BO); Ujung Kulon, Mt. Payung, 300–400 m, 8 Jan 1964, *Wirawan 265* (BO, K, L). Central Java: Banyumas, Mt. Slamet, upper Baturraden, 800 m, 12 Apr 1911, *Backer 186* (BO); Pekalongan, Between Doro and Petung Kriono, 600 m, 8 Sep 1914, *Backer 15750* (BO); Semarang, Mt. Ungaran 1200 m, 22 Mar 1913, *Docters van Leeuwen 1264* (BO); *Ibid.*, Mt. Telomoyo, *Koorders*

35839β (BO). West Java: Bogor, Mt. Salak, Gunung Bunder, 1000 m, 8 Aug 1909, *Backer 31628* (BO); Leuwiliang, Cianten, 1000 m, 1 Sep 1918, *Backer 25894* (BO); Puraseda, 450 m, 20 Dec 1930, *Bakhuizen van den Brink 7641* (BO, K, L, U); Mt.Pangrango, Bodogol, 600 m, 4 Apr 2009, *Kartonegoro 314* (BO); Mt. Halimun, Nirmala, 1100 m, 27 Dec 1913, *Backer 11160* (BO); *Ibid.*, 1300 m, 10 Jun 1980, *van Balgooy & Wiriadinata 2921* (BO, K, L); *Ibid.*, 12 Oct 2017, *Kartonegoro 1113* (BO, L); Sukabumi, Jampang Tengah, 650 m, 27 Sep 1970, *Kostermans 23846* (BO, K, L); Cianjur, Cibeber, Cidadap, 1000 m, 12 Jun 1917, *Backer 22493* (BO); *Ibid.*, 12 Jun 1916, *Bakhuizen van den Brink 3839* (BO, K, L). Central Kalimantan: Bukit Raya, Tumbang Riang, 150 m, 25 Nov 1982, *Mogea & de Wilde 3669* (BO, L); *Ibid.*, Tumbang Tapi, 100 m, 20 Jan 1983, *Veldkamp 8326* (BO, L, PNH); Barito Ulu, 25 May 1990, *Ridsdale PBU 187* (BO, K, L). East Kalimantan: West Kutai, Long Liang Beng, 250 m, 31 Aug 1925, *Endert 3015* (BO, K, L); *Ibid.*, Kombeng, 30 m, 23 Nov 1925, *Endert 5174* (BO, K, L, PNH). South Kalimantan: Limowia, Batu Babi, 10 Jul 1908, *Winkler 2809* (BM, BO, K, L). West Kalimantan: Long Blu'u, 1896, *Jaheri 1297* (BO); Sintang, HPH Km. 87, 100 m, 24 Apr 1994, *Church et al. 1078* (BO, K, L).



Map 3-16. Distribution of *D. gracilis* (●).

24. *Dissochaeta griffithii* (M.P.Nayar) Karton, **comb. nov.** — Map 3-15

Macrolenes griffithii M.P.Nayar, J. Jap. Bot. 55: 47. 1980. — *Dissochaeta annulata* Hook.f. ex Triana var. *griffithii* (M.P.Nayar) J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980. — Type: *W. Griffith KD 2269* (holo K [K001096571!]), Malaysia, Malacca.

Branchlets terete, 3–4 mm in diameter, densely covered with brown stellate-furfuraceous hairs and simple dark, 2–3 mm long bristle hairs; nodes swollen, with distinct interpetiolar ridge; internodes 4–5.5 cm long. Leaves: petioles terete, 3–6 mm long, densely covered with brown stellate-furfuraceous hairs and simple dark, 2–3 mm long bristle hairs; blades ovate or ovate-oblong, 6–10 × 2.5–3.5 cm, subcoriaceous, base cordate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark green, abaxially densely covered with brown stellate-furfuraceous hairs. Inflorescences terminal or in upper leaf axils, up to 12 cm long

when terminal, many-flowered, 3–4 cm long when axillary, with 1–3 flowers; main axis angular, densely covered with brown stellate-furfuraceous hairs and simple dark bristle hairs; primary axes 8–9 cm long with 3 or 4 nodes, secondary axes 1–2 cm long with 1 or 2 nodes, tertiary axes when developed ca. 0.5 cm long with 1 node; bracts oblong to lanceolate, 15–20 × 6–8 mm, densely brown stellate-furfuraceous; bracteoles lanceolate, 10–15 × ca. 2 mm, densely brown stellate-furfuraceous; pedicels densely covered with bristle hairs, ca. 1 mm long in central flowers, ca. 0.5 mm long or nearly sessile in lateral flowers. Hypanthium campanulate, 8–10 × 5–7 mm, densely covered with stellate-tomentose hairs and simple 3–5 mm long eglandular bristle hairs; calyx lobes triangular with acute tips, 2.5–3 × 2–3 mm; petal buds conical, 6-8 mm long, apex acute; mature petals ovate to oblong, 11–14 × 6–7.5 mm, reflexed, base clawed, apex obtuse, glabrous with ciliate margin, pink. Stamens 8, unequal, filaments curved sideways, light yellow; alternipetalous stamens with 12–14 mm long filaments, anthers lanceolate, slender, sickle-shaped, thecae 16–18 mm long, apex rostrate, pedoconnective 4–5 mm long, basal crest entire, erose or bifid, 1–2 mm long, lateral appendages paired, filiform, 6–7 mm long; oppositipetalous stamens with 11–12 mm long filaments, anthers hook- or S-shaped, thecae 10–12 mm long, basal crest ligular, obtuse or erose, ca. 1 mm long, lateral appendages paired, filiform, 4–5 mm long, yellow. Ovary ¾ of hypanthium in length, apex villous; style 22–24 mm long, curved sideways in direction opposite to the filaments, curved at the tip, glabrous; stigma minute; extra-ovarial chambers 8, extending to near the base of the ovary. Fruits ovoid to nearly subglobose, 13–15 × 5–8 mm, densely covered with stellate-tomentose hairs and simple 3–5 mm long eglandular bristle hairs; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Peninsular Malaysia.

Ecology and habitat — Lowland primary forest in open places at 27–120 m elevation.

Note — 1. The appearance of the hypanthium with distinct calyx lobes was recognized by Nayar (1980) as typical for *Macrolenes*, but the character of the stamens and its appendages closely resemble *Dissochaeta*, with a pair of filiform appendages on the alternipetalous stamens and not fimbriate appendages as is common in *Macrolenes*. This species resembles *Macrolenes echinulata* (Naudin) Bakh.f. which is also distributed in Peninsular Malaysia but differs in lacking paired hair cushions at the base of the leaves abaxiallyly (present in *M. echinulata*) and only has one pair of lateral appendages at alternipetalous stamens (which are fimbriate in *M. echinulata*).

2. Maxwell (1980b) reduces this species to a variety of *D. annulata* based on the similarity in the number and shape of the stamens. *Dissochaeta griffithii* differs from *D. annulata* by its distinct triangular calyx lobes (truncate in *D. annulata*) and hypanthium with dense simple eglandular bristle hairs (lacking or with scattered glandular bristle hairs in *D. annulata*).

Specimens examined — **MALAYSIA.** Malacca: *Griffith KD 2269* (K); *Maingay KD 784* (K). Negeri Sembilan: Jelebu, Pasoh Forest Reserve, 80–120 m, 9 Jun 1996, *Gardette 1989* (K, L). Pahang: Tasek Bera, 76 m, 28 Oct 1961, *Chew & Noor 270* (K, L). Selangor: Rantau Panjang, 27 m. 29 Sep 1927, *Strugnell 13965* (K).

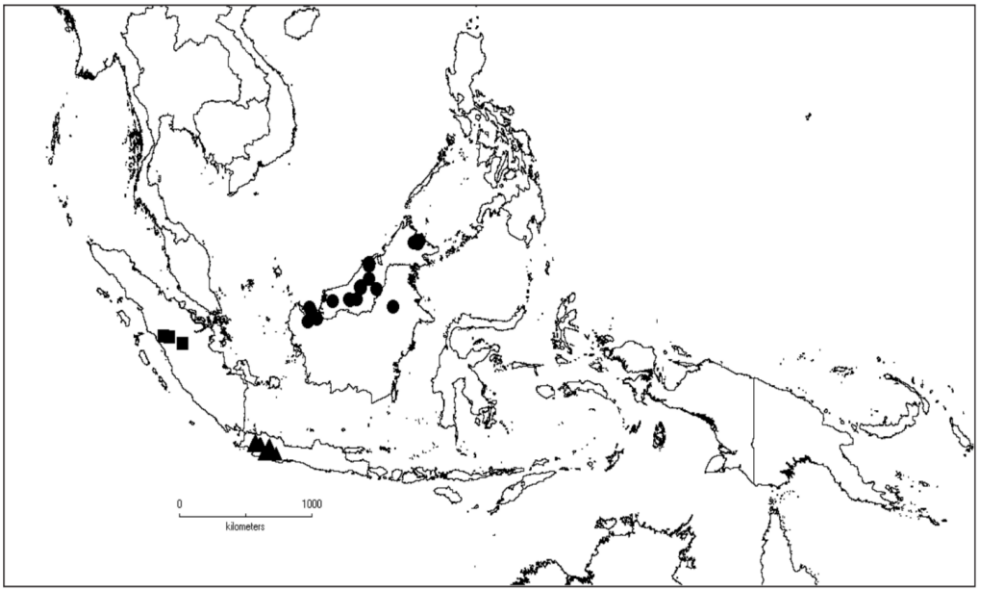
25. *Dissochaeta hirsutoidea* Furtado — Fig. 3-17, Map 3-17

Dissochaeta hirsutoidea Furtado, Gard. Bull. Singapore 20: 109, fig. 2C. 1963. — Type: *C. Boden-Kloss SFN 19156* (holo SING; iso BO!, K [K000859628!]), Malaysia, Sabah, Sandakan, Bettotan, 19 Aug 1927.

Dissochaeta stellulata Furtado, Gard. Bull. Singapore 20: 113, fig. 2F. 1963. — Type: *G.D. Haviland 862* (holo SAR; iso K [K000859626!]), Malaysia, Sarawak, Lodong.

Climbing up to 9 m in height. Branchlets terete, 3–5 mm in diameter, densely covered with dark thin bristle hairs; nodes swollen, with interpetiolar ridge; internodes 6–9 cm long. Leaves: petioles terete, 5–15 mm long, densely covered with bristle hairs; blades ovate or ovate-elliptic, 6–15.5 × 2–8.7 cm, membranous, base cordate, margin entire, ciliate, apex acuminate, tip 0.5–1 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially hirsute, scabrid, glabrous or with scattered stellate and bristle hairs, abaxially densely covered with bristle hairs in most part, more dense at midrib and margin. Inflorescences terminal, up to 30 cm long, many-flowered; main axis angular, covered with sparsely minute stellate hairs and dense bristle hairs; primary axes up to 26 cm long with 4–6 nodes, secondary axes 1.5–9 cm long with 1–4 nodes, tertiary axes 0.8–2 cm long with 1 or 2 nodes, quarternary axes when developed up to 1 cm long with 1 node; bracts linear, 6–7 mm, covered with dense bristle hairs; bracteoles linear, 2–3 mm long, covered with dense bristle hairs; pedicels densely stellate-furfuraceous and with glandular bristle hairs, 3–4 mm long in central flowers, ca. 1 mm long in lateral flowers. Hypanthium campanulate, 4–5 × ca. 2 mm, densely covered with glandular capitate bristle hairs; calyx lobes truncate, ca. 1 mm long, apex triangular; petal bud conical, 2–3 mm long, apex bristly; mature petals oblong, 6–7 × 2–3 mm, reflexed, base clawed, apex obtuse, bristly, rest glabrous, white or purplish. Stamens 8, subequal, filaments curved sideways; alternipetalous stamens with ca. 5 mm long filaments, anthers lanceolate, sickle-shaped, thecae 8–9 mm long, purple, apex rostrate, pedoconnective 0.5–1 mm long, basal crest minute, triangular, 0.3–0.5 mm long, lateral appendages paired, auricles or filiform, 0.5–2 mm long; oppositipetalous stamens with 3–4 mm long filaments, anther thick, S-shaped, thecae 7–8 mm long, purple, basal crest minute, spur-like, erect, ca. 0.2 mm long, lateral appendages absent or a minute pair of erect auricles. Ovary half as long as the hypanthium, apex villous; style 6–7 mm long, curved at end, glabrous; stigma minute, capitate; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits subglobose, 4–6 × 3–4 mm, densely covered with glandular bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.
Distribution — Borneo.
Ecology and habitat — Lowland mixed dipterocarp forest, open places or along road sides at 20–250 m elevation.
Specimens examined — **MALAYSIA.** Sabah: Sandakan, Lamag Road, 13 Sep 1971, *Imbungan & Patrick SAN 74187* (K); *Ibid.*, Segaliud Lokan, 17 Mar 1975, *Madani SAN 81490* (K, L); *Ibid.*, Bettotan, 19 Aug 1927, *Boden-Kloss SFN 19156* (BO, K); *Ibid.*, Sepilok Forest Reserve, 21 Sep 1963, *Meijer SAN 34332* (K, L); *Ibid.*, Telupid Road, 20 Aug 1978, *Aban Gibot SAN 91283* (K, L); *Ibid.*, Sungai Lantoh, 15 m, 23 Aug 1977, *Saikeh SAN 87884* (K, L). Sarawak: Belaga, Ulu Belaga, Sungai Semawat, 250 m, 15 Oct 1981, *Hansen 645* (L); *Ibid.*, Batang Belaga, 250 m, 29 Oct 1981, *Hansen 878* (L); *Ibid.*, Sepakau, 250 m, 5 Nov 1981, *Hansen 954* (L); Kapit, Bukit Raya, 14 Jan 1965, *Jugah S.23863* (L); Lodong, *Haviland 862* (K); Baleh, Mujong, Amau, 14 Apr 1964, *Ilias Paie S.19868* (K, L); Kapit, Pelagus, Bukit Wong, 150 m, 20 Apr 1963, *Ashton S.17786* (BO, K, L); Marudi, Sungai Silat Basin, Sungai Palutan, 24 Mar 2003, *Normaya et al. S.91083* (L); Serian, Sabal Tapang, 237 m, 12 May 1974, *Tong S.34270* (K, L); Santubong, 60 m, 20 Mar 1967, *Chew 1428* (K, L); Samarahan, 1 Feb 1955, *Brooke 9669* (BM, L); Long Bah, 14 Aug 1954, *Brooke 9010* (L). **BRUNEI.** Belait: Labi, Between Mendaram and Teraja, 1 May 1988, *Wong s.n.* (K); *Ibid.*, Bukit Teraja, 22 May 1993, *Nangkat et al. BRUN 15203* (K); *Ibid.*, Bukit Telingan, 170 m, 7 Jun 1995, *Kalat, et al. BRUN 16512* (L). **INDONESIA.** East Kalimantan: West Kutai, Long Petah, 400 m, 16 Sep 1925, *Endert 3360* (BO, L). West Kalimantan: Pontianak, Gunung Bentuang, 200 m, 19 Jun 1989, *Burley & Tukirin 2692* (BO, L); Ibid., 250 m, 23 Jun 1989, *Burley & Tukirin 2827* (BO, L).

Fig. 3-17. *Dissochaeta hirsutoidea*. **a.** habit; **b.** branchlet; **c.** abaxial midrib; **d.** hypanthium and flower. Photos by J. Henrot.



Map 3-17. Distribution of *D. hirsutoidea* (●), *D. horrida* (■) and *D. intermedia* (▲).

26. *Dissochaeta horrida* (Bakh.f.) Karton., **comb. nov.** — Fig. 3-18, Map 3-17

Macrolenes horrida Bakh.f., Contr. Melastom. 208. 1943. — *Dissochaeta rostrata* Korth. var. *horrida* (Bakh.f.) J.F.Maxwell, Gard. Bull. Sing. 33: 320. 1980. — Type: *H.A.B. Bünnemeijer 3200* (holo L [L0537276!]; iso BO [BO1751324!, BO1751325!]), Indonesia, West Sumatra, Agam, Brani, 850 m elev., 22 Jun 1918.

Climbing up to 2 m in height. Branchlets terete, 4–5 mm in diameter, densely covered with brown-reddish pubescent hairs and with 4–5 mm long brown-reddish bristle hairs, young parts densely covered with red pubescent hairs and bristle hairs; nodes swollen, with interpetiolar ridge; internodes 7–8 cm long. Leaves: petioles terete, 10–15 mm long, densely covered with brown-reddish pubescent hairs and with 4–5 mm long brown-reddish bristle hairs; blades broadly ovate to suborbicular, 13–18 × 6–10 cm, subcoriaceous, base emarginate, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark green, abaxially densely brown-reddish pubescent. Inflorescences terminal, up to 60 cm long, many-flowered; main axis angular, densely covered with brown-reddish pubescent hairs and with 4–5 mm long brown bristle hairs; primary axes up to 34 cm long with 6 or 7 nodes, secondary axes up to 6 cm long with 2 or 3 nodes, tertiary axes up to 2 cm long with 1 or 2 nodes, quarternary axes when developed up to 1 cm long with 1 node; bracts linear, 7–9 mm long, densely covered with brown-reddish pubescent hairs and with 4–5 mm long brown-reddish bristle hairs; bracteoles subulate, ca. 2 mm long, densely covered with brown-reddish pubescent hairs and with 4–5 mm long brown-reddish bristle hairs; pedicels densely covered with brown pubescent hairs and with glandular tip bristle hairs, 6–7 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium tubular, 7–8 × ca. 3 mm, densely covered with brown-reddish pubescent hairs and with brown-reddish glandular-tipped bristle hairs; calyx lobes linear-lanceolate, 6–10 mm long, base truncate, apex acute, densely covered with brown-reddish pubescent hairs and with glandular-tipped bristle hairs; petal bud conical, 3–4 mm long, glabrous; mature petals oblong to suborbicular, 6–8 × 5–6 mm, purple. Stamens 8, subequal, filaments curved sideways; alternipetalous stamens with 6–8 mm long filaments, anthers slender, curved, sickle-shaped, thecae 12–13 mm long, pedoconnective with 1–3 mm long, basal crest minute, triangular, ca. 0.5 mm long, lateral appendages paired, filiform, 1.5–2 mm long; oppositipetalous stamens with 5 mm long filaments, bent at the end, anthers curved, S-shaped, thecae 9–10 mm long, basal crest consisting of minute auricles, ca. 0.3 mm long, lateral appendages paired, auricles, 0.5–1 mm long. Ovary ¾ of hypanthium in length, apex villous; style 15–20 mm long, glabrous; stigma minute; extra-ovarial chambers 8, extending to the base of the ovary. Fruits urceolate, ca. 10 × 5–6 mm, densely covered with brownreddish pubescent hairs and with glandular-tipped bristle hairs; calyx lobe remnants persistent, lanceolate, 6–8 mm long, reflexed. Seeds ca. 0.7 mm long.

Distribution — Sumatra (West).

Ecology and habitat — Lowland dipterocarp forest or open cliff area at 500–850 m elevation.

Note — *Dissochaeta horrida* is easy to recognized with most parts have reddish brown pubescent hairs and dense bristle hairs except the green, glabrous adaxially surface of the leaf blades. The shape of the calyx lobes (linear-lanceolate, 6–10 mm long) resembles *D. floccosa*, also from Sumatra, but the indumentum of the latter is floccose rather than pubescent.

Specimens examined — **INDONESIA.** Riau: Indragiri, Taluk, 11 Jan 1956, *Meijer 4271* (L). West Sumatra: Agam, Brani, 850 m, 22 Jun 1918, *Bünnemeijer 3200* (BO, L); Lima

Puluh Kota, Harau Valley, Sarasah Bonta, 500 m, 2 May 2001, *Uce et al. 106* (ANDA); *Ibid.*, 11 Sep 2017, *Kartonegoro 1073* (BO, L).

Fig. 3-18. *Dissochaeta horrida*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1073* (BO, L).

27. *Dissochaeta inappendiculata* Blume — Fig. 3-19, Map 3-18

Dissochaeta inappendiculata Blume, Flora 14: 499. 1831. — Lectotype (designated here): *C.L. Blume s.n.* (lecto L [L0537236!]; isolecto K [K000859623!], L [L0537235!], P [P05283569!]), Indonesia, Java.

Dissochaeta inappendiculata Blume var. *purpurascens* Blume, Flora 14: 499. 1831. — Type: *H. Kuhl & J.C. van Hasselt s.n.* (holo L [L0537245!]), Indonesia, West Java, Preanger Regentsch., Mount Megamendoeng.

Dissochaeta inappendiculata Blume var. *tomentosa* Blume, Flora 14: 499. 1831. — Type: *F.W. Junghuhn s.n.* (holo L [L0537237!]), Indonesia, West Java, Rendang.

Dissochaeta cinnamomea Blume, Mus. Bot. 1(3): 36. 1849. — Lectotype (designated here): *C.L. Blume s.n.* (lecto L [L0537241!]; isolecto L [L0537240!]), Indonesia, Java.

Dissochaeta vacillans auct. non. Blume: Veldkamp, Blumea 24: 440. 1979. *p.p.*, excl. type.

Fig. 3-19. *Dissochaeta inappendiculata*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1104* (BO, L).

Climbing up to 20 m in height. Branchlets terete, 3–5 mm diameter, glabrous or glabrescent or sometimes with stellate-hairs; nodes swollen, with interpetiolar ridge; internodes 6–9 cm long. Leaves: petioles terete or flattened, 5–18 mm long, glabrous, rarely furfuraceous; blades elliptic to oblong, (5–)7–14 × (1–)3–6 cm, membranous, base rounded, margin entire, apex acute or acuminate, tip 0.5–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely brown stellate-furfuraceous. Inflorescences terminal, up to 34 cm long, many-flowered; main axis angular, stellate-puberulous or stellatefurfuraceous; primary axes 22.5–32 cm long with 8–10 nodes, secondary axes 2–8 cm long with 2–5 nodes, tertiary axes 1–2.5 cm long with 1 or 2 nodes,

quarternary axes when developed 0.4–0.8 cm long with 1 node; bracts linear to lanceolate, (0.7–)2–3.5 × 1–1.5 mm, caducous, glabrescent; bracteoles linear, 1–2 mm long, glabrescent or stellate-furfuraceous, sometimes with bristly hairs along the margin; pedicels brown stellate-puberulous, 4–6 mm long in central flowers, 2–4 mm long in lateral flowers. Hypanthium campanulate to suburceolate, 1–4 × 1–3 mm, glabrescent to densely furfuraceous or stellate-furfuraceous; calyx lobes truncate with 4 undulate, 0.5–1 mm long, rounded, or subtriangular apices, glabrous, purplish; petal bud conical to subrounded, 1–5 mm long; mature petals obovate, 4–6 × 2–3 mm, not reflexed, apex acute, base clawed, glabrous or inside with appressed hairs at base, purple to purplish-white. Stamens 8, unequal, filaments straight, pink; alternipetalous stamens with 2–3.5 mm long filaments, anthers oblong or lanceolate, thecae 3–4 mm long, straight, yellow, pedoconnective not formed or absent, basal crests triangular or ovate, ca. 1 mm long, with acute narrow apex, bright white, lateral appendages absent; oppositipetalous stamens staminodal, with 1.5–2 mm long filaments, thecae 1–1.5 mm long, clavate, straight, yellow, basal crests spuriform, ca. 0.5–0.8 mm long, erect, lateral appendages absent. Ovary ⅔ of hypanthium in length, apex puberulous; style 5–8 mm long, curved at apex, glabrous, purple; stigma minute; extra-ovarial chambers 4, reaching to the middle of the ovary. Fruits subglobose to urceolate, 2–5(–7) × 2–5 mm, glabrous to sparsely stellate-furfuraceous; calyx lobes persistent, erect. Seeds ca. 0.5 mm long.

Distribution — Peninsular Malaysia, Sumatra and Java.

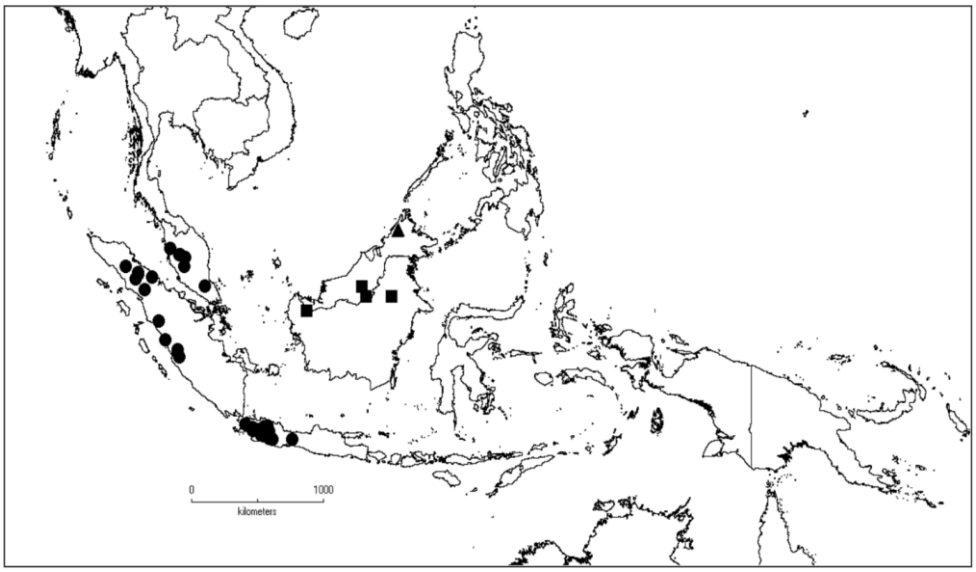
Ecology and habitat — Primary montane forest or secondary forest, edge of forest with open shaded area at 400–1800 m elevation.

Vernacular names — Java: *harendong*, *harendong cai* (Sunda).

Note — *Dissochaeta inappendiculata* is easily recognised by its purple corolla, eight straight stamens of which the alternipetalous ones are fertile and the oppositipetalous ones are staminodal. The alternipetalous stamens are always inappendiculate and usually without lateral appendages and with a triangular or orbicular crest. The oppositipetalous (less than ⅓ of the alternipetalous ones) have a distinct spuriform crest (Kartonegoro & Veldkamp 2010).

Selected specimens examined — **MALAYSIA.** Pahang: Cameron Highlands, 1600 m, 14 Apr 1978, *Maxwell 78-139* (L); *Ibid.*, Tanah Rata, Robinson's Fall, 11 Sep 1985, *Latiff, Zainudin & Miran 859* (L); Fraser's Hill, 19 Jun 1967, *Carrick 1574* (K, L); *Ibid.*, 1000 m, 1 Apr 2000, *Vermeulen & Duistermaat 2023* (L); Telom, Nov 1890, *Ridley 13686* (BM). Perak: Maxwell's Hill, 4 Mar 1965, *Hardial & Samsuri 278* (K, L). **INDONESIA.** Aceh: Kutacane, Gunung Gurah, 22 Mar 1954, *Alston 14628* (BM). Jambi: Mt. Kerinci, Kayu Aro, 1400 m, 9 Aug 1956, *Jacobs 4550* (BO, K); *Ibid.*, Sungai Penuh, 3 Jun 1914, *Robinson & Boden-Kloss s.n.* (BM, K). North Sumatra: *Yates 1424* (BM); Toba, Siburong-Burong, 1200 m, 23 Jun 1896, *Ouwehand s.n.* (BO); Berastagi, 1300 m, 29 Aug 1971, *Iwatsuki et al. S-405* (BO); Dairi, 1400 m, 1939, *Dames 72* (BO); Karo, Sikulikap Waterfall, 1200 m, 6 Mar 1973, *Soedarsono 432* (BO); Sibolangit, 600 m, 12 Sep 1920, *Lörzing 7351* (BO). West Sumatra: Mt. Kerinci, 1700 m, 16 Mar 1920, *Bünnemeijer 8937* (BO); Ophir, Talu, 950 m, 10 Apr 1917, *Bünnemeijer 124* (BO); Padang, Air Sirah, 1000 m, 2 May 1985, *de Vogel & Vermeulen 7312* (BO). Banten: Pandeglang, Mt. Pulosari, 1050 m, 11 Feb 1954, *Adelbert 476* (BO, K, L); *Ibid.*, 762 m, 11 May 1843, *Zollinger 1288* (P). Central Java: Banyumas, Mt. Slamet, Baturaden, 1200 m, 14 Apr 1911, *Backer 296* (BO). West Java: Bogor, Pasir Madang, 13 Aug 1843, *Zollinger 1489* (BM, P); Nanggung, 600 m, 23 Dec 1913, *Backer 10522* (BO); Mt.Salak, Gunung Bunder, 8 Aug 1909, *Backer s.n.* (BO); Mt.Halimun, Nirmala, 1400 m, 19 Dec 1913, *Backer 10794* (BO); *Ibid.*, Malasari, 1055 m, 10 Oct 2017, *Kartonegoro 1104* (BO, L); Mount Gede, Situ Gunung, 1000 m, 19 Nov 1933, *van Steenis 5685* (BO); Cianjur, Mt. Gede, 1200 m, Oct 1877, *Pierre 3032* (P); Cibeber, Cidadap, 1100

m, 11 Sep 1917, *Backer 23703* (BO); Bandung, Mt. Jayagiri, 1460 m, 26 Mar 1920, *Lam 141* (BO, L); Mt. Malabar, 2130 m, 19 Oct 1861, *Anderson 92* (K); *Ibid.*, 26 Mar 1880, *Forbes 1047* (P); Mt. Sembung, 1300 m, 18 Mar 1914, *Backer 12256* (BO); Garut, Mt. Cikuray, Pasir Klotok, 1000 m, 15 Aug 1913, *Backer 8687* (BO).



Map 3-18. Distribution of *D. inappendiculata* (●), *D. laevis* (■) and *D. macrosepala* (▲).

28. *Dissochaeta intermedia* Blume — Map 3-17

Dissochaeta intermedia Blume, Flora 14: 493. 1831. — Lectotype (designated here): *C.L. Blume 539* (lecto L [L0537299!]; isolecto K [K000859493!, K000859494!], L [L0537296!, L0537297!, L0537298!], P [P05283548!]), Indonesia, West Java, Preanger Regentsch., Mount Pangrango, Gegerbentang.

Dissochaeta monticola Blume, Flora 14: 494. 1831. — Lectotype (designated here): *C.L. Blume s.n.* (lecto L [L0537300!]; isolecto L [L0537301!, L0537302!]), Indonesia, West Java, Kuripan.

Climbing up to 20 m in height. Branchlets terete, 4–7 mm diameter, glabrescent to densely stellate-furfuraceous; nodes swollen, with interpetiolar ridge or line; internodes 8–9 cm long. Leaves: petioles flattened, 10–20 mm long, glabrescent to densely stellate-furfuraceous; blades ovate to ovate-elliptic, 7–16 × 5–8.5 cm, membranous, base rounded, margin entire, apex acuminate, tip 0.5–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely brown stellate-tomentose. Inflorescences terminal and in the upper leaf axils, up to 32 cm long, many-flowered; main axis angular, densely stellate-furfuraceous; primary axes up to 25–30 cm long with 4–6 nodes, secondary axes 2–7 cm long with 2 or 3 nodes, tertiary axes 1–3 cm long with 1 or 2 nodes, quartenary axis up to 0.8 cm long when developed with 1 node; bracts minute, inconspicuous; bracteoles linear to ovate-oblong, 1–2 mm long, densely stellate-furfuraceous; pedicels densely stellate-furfuraceous, 4–7 mm long in central flowers, 2–4 mm long in lateral flowers. Hypanthium campanulate, slightly angular, 2–5 × 1–3 mm, with four distinct ridges, stellate-puberulous to densely stellate-tomentose, somewhat pointing sideways from pedicels; calyx lobes truncate with undulate tips, 0.5–1 mm long, widened,

stellatefurfuraceous; petal bud conical 3–7 mm long; mature petals ovate or oblong, 6–10 × 3–5 mm, base clawed, apex obtuse, glabrous or inside at base with appressed hairs, pink or violet. Stamens 4, equal, alternipetalous, filaments flat, 4–6 mm long, straight, apex bent, anthers linear-lanceolate, sickle- or S-shaped or falcate, thecae 5–6 mm long, yellow, pedoconnective ca. 1 mm long, basal crests minute, triangular, ca. 1 mm long, narrow with acute apex, lateral appendages paired, filiform, 3–4 mm long, tan. Ovary half or ⅔ of hypanthium in length, apex pubescent; style erect, 8–12 mm long, curved at apex, glabrous, purple; stigma minute; extra-ovarial chambers 4, alternipetalous, extending to the base of the ovary. Fruits ovoid, 5–6 × 3–5 mm, glabrous to sparsely stellate-furfuraceous, rarely with distinct vertical ridges, green, often pointing sideways from the pedicels; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Java (West).

Ecology and habitat — Primary montane forest or in edge of forest in open, 1200–2000 m elevation.

Vernacular names — harendong cai, harendong areuy, harendong kowe (Sunda).

Note — *Dissochaeta intermedia* resembles *D. leprosa* in the number and shape of the stamens, but is different in having a smaller hypanthium and truncate calyx lobes with undulate tips. Together with *D. leprosa*, this species is common at high elevations up to 2000 m in Java.

Specimens examined — **INDONESIA.** West Java: Bogor, Puncak Pass, 1300 m, 3 Mar 1927, *Beumée A390* (BO); *Ibid.*, Cisarua, 1200 m, 19 Feb 1950, *van Steenis 12735* (L); Mt. Salak, 1200 m, *Raap 158* (L); Kuripan, *Blume s.n.* (L); Megamendung, *Kuhl & van Hasselt s.n.* (L); *Ibid.*, *Junghuhn s.n.* (U); Mt.Halimun, Nirmala, 1250 m, 9 Jun 1980, *van Balgooy & Wiriadinata 2889* (BO, L); *Ibid.*, Mt. Bintang Gading, 19 May 2002, *Hoover et al. 5502* (BO); Cianjur, Mt.Gede, Cibodas, *Boerlage s.n.* (L); *Ibid.*, 1400 m, 22 Aug 1879, *Arsin 19556* (BO); *Ibid.*, 9 Jun 1906, *Pulle 4073* (U); *Ibid.*, 19 Jul 1913, *Koorders 42153β* (BO); *Ibid.*, 6 May 1914, *Lörzing 1493* (BO); *Ibid.*, 14 Feb 1915, *Ridley s.n.* (K); *Ibid.*, Gunung Putri, 6 Nov 1896, *Koorders 25927β* (BO); *Ibid.*, Sindanglaya, 1400 m, 6 Jun 1917, *Backer 22286* (BO); *Ibid.*, *Hallier 626* (BO); *Ibid.*, 25 Aug 1893, *Hallier 432* (BO); *Ibid.*, 1915, *Sapiin 57* (BO); *Ibid.*, 15 Jul 1908, *Valeton s.n.* (BO); *Ibid.*, Mt. Pangrango, *de Monchy s.n.* (BO); *Ibid.*, Geger Bentang, *Blume 539* (K, L, P); Bandung, Mt. Tangkuban Perahu, 1700 m, 4 Apr 1912, *Backer 2387* (BO); *Ibid.*, 1600 m, 5 Mar 1912, *Backer 2415* (BO); *Ibid.*, Jul 1915, *Docters van Leeuwen 2301a* (BO); *Ibid.*, 24 Jul 1927, *Docters van Leeuwen 11423* (BO); *Ibid.*, 2000 m, 21 Nov 1952, *Meijer 1363* (BO); *Ibid.*, 28 May 1908, *Zeijlstra 19* (BO); *Ibid.*, 6 Feb 1927, *Wisse 1188* (BO); Mt. Patuha, Telaga Patengan, 1700 m, 28 Mar 1914, *Backer 12787* (BO); Mt. Burangrang, Situ Lembang, 1600 m, 24 Jul 1920, *Bakhuizen van den Brink 4557* (BO, K, L); *Ibid.*, 30 Dec 1956, *Reksodihardjo 6* (BO); Mt. Malabar, 27 Jun 1871, *Scheffer s.n.* (BO); Mt. Mandalagiri, 1570 m, 29 Mar 1920, *Lam 230* (BO).

29. *Dissochaeta johorensis* Furtado — Map 3-19

Dissochaeta johorensis Furtado, Gard. Bull. Singapore 20: 110, f. 2B. 1963. — Type: *H.N. Ridley 4185* (holo SING; iso BM [BM000944478)!, K [K000859526!]), Malaysia, Johor, Gunong Panti, 1892.

Dissochaeta hirsuta auct. non. Hook.f. ex Triana; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 51. 1900; Ridl., Fl. Malay Penins. 1: 797. 1922. *p.p.*, excl. type.

Climbing up to 4.5 m in height. Branchlets terete, 2–4 mm in diameter, densely covered with brown stellate-furfuraceous hairs and 1–2 mm long bristle hairs; nodes swollen, with interpetiolar ridge; internodes 3.5–7.5 cm long. Leaves: petioles terete, 6–10 mm long,

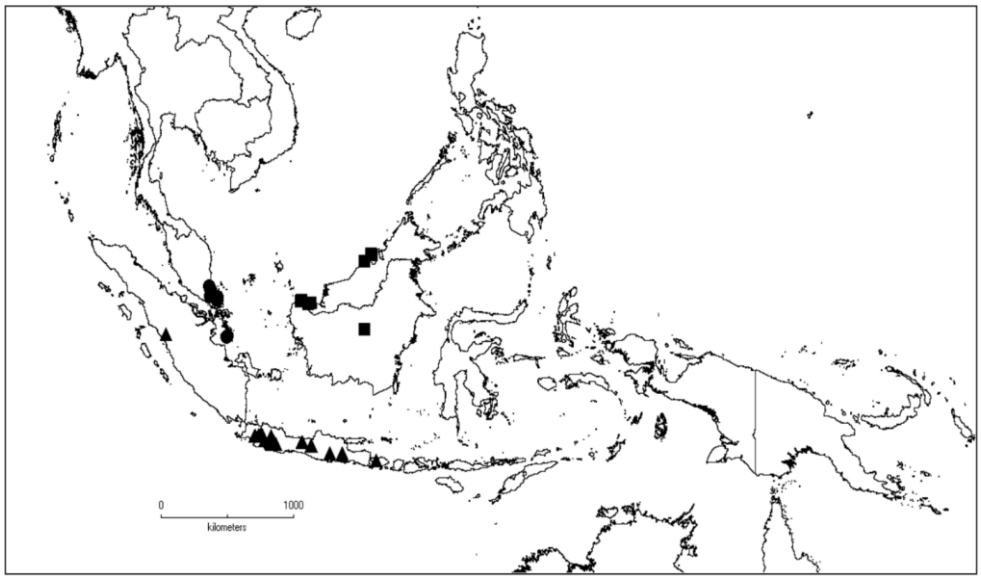
densely covered with stellate-furfuraceous and bristle hairs; blades ovate or elliptic, 7–10 × 2.8–6 cm, membranous, base emarginate, margin entire, ciliate, apex acuminate, tip 1–1.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially hirsute to scabrid with scattered bristle hairs, abaxially densely covered with bristle hairs in most part, more densely so at midrib and margin. Inflorescences terminal, up to 25 cm long, many-flowered; main axis angular, densely covered with brown stellate-furfuraceous and bristle hairs; primary axes up to 21 cm long with 5 or 6 nodes, secondary axes 2–6 cm long with 1–3 nodes, tertiary axes up to 1 cm long with 1 node; bracts linear, ca. 4 mm long, densely covered with stellate-furfuraceous and bristle hairs; bracteoles linear, ca. 2 mm long, densely covered with stellate-furfuraceous and bristle hairs; pedicels densely covered with stellatefurfuraceous and bristle hairs, ca. 4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium suburceolate, 5–6 × 2–2.5 mm, densely covered with stellatefurfuraceous hairs and glandular bristle hairs, dark green; calyx lobes slightly triangular, 1–2 mm long, tips acute, densely bristly, pinkish; petal bud conical, 3–4.5 mm long, apex glabrous; mature petals obovate to oblong, 7–8 × ca. 3 mm, not-reflexed, base clawed, apex acute, glabrous, pink or violet. Stamens 8, subequal, filaments curved sideways, pale yellow; alternipetalous stamens with 6–7 mm long filaments, anthers lanceolate, sickle-shaped, thecae 10–11 mm long, apex rostrate, white-cream, pedoconnective 1–1.5 mm long, basal crests minute, triangular, ca. 0.5 mm long, lateral appendages paired, filiform, up to 3 mm long, cream; oppositipetalous stamens with 6–7 mm filaments, anther thick, S-shaped, thecae 9–10 mm long, white-cream, basal crests minute, laminar or spur-like, ca. 0.5 mm long, lateral appendages small, bifid, ca. 0.3 mm long or paired and filiform, 2–2.5 mm long. Ovary ⅔ of hypanthium in length, apex villous; style curved at end, 9–12 mm long, glabrous, white; stigma minute, capitate; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits urceolate, 8–10 × 4.5–5 mm, sparsely stellate-furfuraceous and densely covered with glandular bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Peninsular Malaysia (Johor) and Sumatra (Riau Archipelago).

Ecology and habitat — Edge of evergreen forest in open thickets and lowland forest at 10–200 m elevation.

Note — *Dissochaeta johorensis* resembles *D. rostrata* in its indumentum of dense bristle hairs on most parts, but differs by its acute, triangular calyx lobes (vs. obtuse, ovate lobes) and urceolate fruits (vs. subglobose to ovoid fruits). The shape of the stamens and the appendages in both species are also different.

Specimens examined — **MALAYSIA.** Johor: Kota Tinggi, Gunong Panti, 1892, *Ridley 4185* (BM, K); *Ibid.*, 1880, *Kunstler 197* (K, P); *Ibid.*, 200 m, 8 Apr 1977, *Maxwell 77-181* (L); *Ibid.*, 7 Feb 1978, *Maxwell 78-31* (L); *Ibid.*, 50 m, 8 Dec 1979, *Maxwell 79-48* (L); *Ibid.*, 4 Jan 1980, *Bremer 1840* (K); Kluang FR., 60 m, 31 Jan 1966, *Ng KEP 97965* (K); *Ibid.*, 24 Nov 1967, *Alphonso, Sanusi & Sidek S.197* (K, L); Endau Rompin, Kuala Jasin, 100 m, 1 Mar 1996, *van Balgooy 7114* (L); Lombong FR, 30 m, 22 May 1959, *Burkill HMB 1822* (K, L); Sungai Kayu, 9 Mar 1937, *Kiah SFN 32357* (BM, K, PNH); Gunong Muntahak, 183 m, 3 Mar 1928, *Nur SFN 19975* (BM, BO, K); Labis, Sungei Kinchin, 30 m, 25 Aug 1988, *Saw FRI 36361* (L). **INDONESIA.** Riau Archipelago: Lingga Islands, Singkep Island, Kampung Raya, 10 m, 1 Aug 1919, *Bünnemeijer 7096* (BO); *Ibid.*, Manggu, 40 m, 2 Aug 1919, *Bünnemeijer 7175* (BO); *Ibid.*, Dabo, 40 m, 4 Aug 1919, *Bünnemeijer 7276* (BO).



Map 3-19. Distribution of *D. johorensis* (●), *D. latifolia* (■) and *D. leprosa* (▲).

30. *Dissochaeta laevis* Ohwi ex J.F.Maxwell — Map 3-18

Dissochaeta laevis Ohwi ex J.F.Maxwell, Gard. Bull. Singapore 33: 315, fig. 2. 1980, "laeve". — Type: *F.H. Endert 3127* (holo L [L0537281!]; iso BO [BO1760872!], K [K000859490!]), Indonesia, East Kalimantan, W. Koetai, Long Petah, 600 m elev., 10 Sep 1925.

Climbing up to 6 m in height. Branchlets terete, 3–4 mm in diameter, glabrescent; nodes swollen, with short flat crest-like interpetiolar ridge, margin often with minute bristles; internodes 5–6 cm long. Leaves: petioles terete, 8–10 mm long, glabrous, tessellate; blades ovate to ovate-elliptic, 6–12 × 2.3–5.5 cm, membranous, base rounded, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous, basally with a pair of glandular patches abaxially. Inflorescences terminal and axillary, up to 11 cm long when terminal, up to 9 cm long when axillary, many-flowered; main axis glabrescent; primary axes up to 8 cm long with 3 or 4 nodes, secondary axes 2–4.5 cm long with 2 or 3 nodes, tertiary axes 0.6–1 cm long with 1 node; bracts linear, 1–2 mm long, stellate-furfuraceous; bracteoles subulate, 0.5–1 mm long, stellate-furfuraceous; pedicels stellate-furfuraceous, ca. 4 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium cyathiform, cup-shaped, 3–4 × ca. 2 mm, glabrous; calyx lobes truncate, ca. 0.3 mm long, with 4 distinct undulations; petal bud conical, 2–3 mm long, apex narrowly acuminate, glabrous; mature petals ovate, ca. 5 × 2.5 mm, reflexed, base clawed, apex acuminate, glabrous. Stamens 8, subequal, filaments straight; alternipetalous stamens with 2.5–3 mm long filaments, anthers oblong or ovate, curved, sickle-shaped, thecae ca. 3 mm long, pedoconnective short, ca. 0.3 mm long, basal crest triangular or ligular with hastate base, ca. 1.5 mm long, lateral appendages absent or paired, filiform, up to 1.5 mm long; oppositipetalous stamens with 2–2.5 mm long filaments, anthers sickle- or S-shaped, thecae ca. 2.5 mm long, basal crest ligular, ca. 2 mm long, lateral appendages absent. Ovary half as long as hypanthium, apex glabrous; style straight, 7–8 mm long, glabrous;

stigma minute; extra-ovarial chambers shallow. Fruits globose, 3–5 × 3–4 mm, glabrous; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.
Distribution — Borneo.
Ecology and habitat — Mixed dipterocarp forest or heath forest at 600–800 m elevation.
Note — A glabrous species with a pair of glandular patches near the base of the leaf blade on the abaxially surface, resembling *D. beccariana*, *D. glabra*, *D. glandulosa* and *D. papuana*. It differs from these taxa by the axillary inflorescences.
Specimens examined — **MALAYSIA.** Sarawak: Belaga, Linau-Balui, Sungei Jelini, 800 m, 1 Sep 1978, *Lee S. 39326* (K, L); Kapit, Batang Balui, Bukit Kumbong, 700 m, 27 Feb 1992, *Runi et al. S.62014* (K, L). **INDONESIA.** East Kalimantan: West Kutai, Long Petah, 600 m, 10 Sep 1925, *Endert 3127* (BO, K, L). West Kalimantan: Pontianak, Bentiang, Gunung Dawuh, 800 m, 29 Oct 1980, *Shea 26846* (BO, L).

31. *Dissochaeta latifolia* (Triana) Karton., **comb. nov.** — Map 3-19

Anplectrum latifolium Triana, Trans. Linn. Soc. London 28: 85. 1872. — *Diplectria latifolia* (Triana) Kuntze, Revis. Gen. Plant 1: 246. 1891. — Lectotype (designated by Veldkamp et al. in Blumea 24: 412. 1979): *T. Lobb s.n.* (lecto K [K000859553!]), Malaysia, Borneo, 1853.

Climbing up to 9 m in height. Branchlets terete, 5–6 mm in diameter, glabrous to covered with brown stellate-furfuraceous hairs; nodes swollen, with pectinate or subulate interpetiolar appendages, apex acute, up to 10 mm long and 1 mm wide, pointing upwards and downwards; internodes 10–16 cm long. Leaves: petioles terete, 15–25 mm long, densely covered with brown stellate-furfuraceous hairs; blades suborbicular to ovate, 17–19 × 8.5–10 cm, subcoriaceous, base slightly subcordate, margin entire, apex acute; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, glossy green, abaxially sparsely brown stellate-furfuraceous to glabrescent. Inflorescences terminal, up to 20 cm long, manyflowered; main axis angular, densely stellate-furfuraceous; primary axes up to 18 cm long with 4 or 5 nodes, secondary axes up to 4 cm long with 2 or 3 nodes, tertiary axes up to 0.8 cm long with 1 or 2 nodes; bracts linear, 4–6 mm long, densely stellate-furfuraceous; bracteoles subulate, 1–3 mm long, densely stellate-furfuraceous; pedicels densely stellate-furfuraceous, often with a few scattered capitate bristles, 5–6 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium tubular, ca. 6 × 2 mm, glabrous to glabrescent; calyx lobes truncate, level, ca. 0.5 mm long; petal bud conical, 3–4 mm long, apex acuminate and bristly; mature petals suborbicular, 6–7 × ca. 6 mm, base clawed, apex acuminate, pink. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial with 2–3 mm long filaments, anthers rudimentary, terete, thecae 2–3 mm long, basal crest triangular or ovate, 1–2 mm long, apex acuminate, lateral appendages paired, ligular, ca. 2 mm long; oppositipetalous stamens with 4–5 mm long filaments, anthers thick, curved, hook- or S-shaped, thecae 10–11 mm long, apex rostrate, yellow, basal crest ligular, ca. 1 mm long, lateral appendages absent or minute, bifid, ca. 0.5 mm long. Ovary ⅔ of hypanthium in length, apex glabrous; style curved at the end, 8–10 mm long, glabrous, slender; stigma minute; extra-ovarial chambers 4, oppositipetalous, extending to the base of the ovary. Fruits urceolate, 8–9 × ca. 6 mm, glabrous; calyx lobe remnants persistent, erect. Seeds ca. 0.75 mm long.
Distribution — Borneo.
Ecology and habitat — Lowland mixed dipterocarp forest or heath forest at 45–150 m elevation.

Note — *Dissochaeta latifolia* resembles *D. pubescens* in the tomentose indumentum of the branchlets, abaxially leaf surfaces and inflorescences. The size and shape of the leaves of both species are also similar, sometimes resulting in a misidentification. *Dissochaeta latifolia* is different in not having a membranous calyptra that encloses the petal bud before anthesis. The pectinate and subulate appendages in the interpetiolar nodal ring are also distinct in *D. latifolia*, making it easy to recognise amongst all species of *Dissochaeta*.
Specimens examined — **MALAYSIA.** Sarawak: *Beccari PB 800* (K, P); *Beccari PB 1089* (K); *Lobb s.n.* (K); Miri, Lambir Hills, 152 m, 10 Jun 1961, *Bakar S.4367* (K, L); *Ibid.*, 5 Dec 1962, *Joseph Au S.17256* (L); Kuching, Semariang Batu, 25 Jun 1976, *Bagong et al. S.37642* (K, L); Lundu, Sematan, Pueh, Sungai Kopak, 200 m, 20 Aug 1996, *Jawa & Lai S.74524* (L). **BRUNEI.** Belait: Sungai Liang, 1 Feb 1989, *Nangkat 89* (K, L); Andulau, 45 m, 24 Apr 1957, *Ashton S.5922* (K, L). **INDONESIA.** Central Kalimantan: Barito Ulu, 24 Jun 1990, *Ridsdale PBU 647* (BO, K, L).

32. *Dissochaeta leprosa* (Blume) Blume — Fig. 3-20, Map 3-19

Dissochaeta leprosa (Blume) Blume, Flora 14: 494. 1831. — *Melastoma leprosum* Blume, Bijdr. Fl. Ned. Ind 17: 1068. 1826. — *Omphalopus leprosus* (Blume) Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 278. 1851. — *Dissochaeta intermedia* Blume var. *leprosa* (Blume) J.F.Maxwell, Gard. Bull. Singapore 33: 315. 1980. — Lectotype (designated here): *H. Kuhl & J.C. van Hasselt s.n.* (lecto L [L0008890!]; isolecto K [K000859492!], L [L0822675!, L0822676!]), Indonesia, West Java, Mount Gede.
Dissochaeta calothyrsa Miq., Fl. Ned. Ind. 1(1): 523. 1855. — Lectotype (designated here): *F.W. Junghuhn 13* (lecto U [U0004009!]; iso L [L0822682!, L0822683!, L0822684!]), Indonesia, West Java, Pengalengan.

Climbing up to 25 m in height. Branchlets terete, 4–6 mm in diameter, densely stellate-furfuraceous to stellate-tomentose; nodes swollen, with interpetiolar ridge; internodes 11–13 cm long. Leaves: petioles flattened, 12–18 mm long, densely stellate-furfuraceous; blades ovate-elliptic or elliptic, 8–17 × 4.8–8 cm, membranous, base rounded or subcordate, margin entire, apex acuminate, tip 0.5–1.5 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely stellate-tomentose. Inflorescences terminal, up to 27 cm long, many-flowered; main axis angular, densely stellate-tomentose; primary axes up to 22 cm long with 3 or 4 nodes, secondary axes 4–5 cm long with 2 nodes, tertiary axes 1.2–1.5 cm long with 1 node; bracts lanceolate, ca. 10 × 2 mm, densely stellate-tomentose, caducous; bracteoles linear or lanceolate, 1–6 mm long, densely stellate-pubescent; pedicels densely stellate-tomentose, 7–8 mm in central flowers, 3–5 mm long in lateral flowers. Hypanthium campanulate or suburceolate, 5–8 × 3–4 mm, slightly angular, covered with densely stellate-tomentose hairs; calyx lobes truncate with distinctly triangular tips, 3–4 mm long, erect, densely stellate-tomentose; petal buds conical, 7–10 mm long, apex acute; mature petals obovate or ovate, 6–10 × 3–8 mm, base clawed, apex obtuse, glabrous or hairy at base inside, pink or white purplish. Stamens 4, equal, alternipetalous, filaments flat, 4–8 mm long, straight, apex bent, anthers glabrous, linear or lanceolate, falcate or S-shaped, thecae 8–12 mm long, pedoconnective 1–2 mm long, basal crests distinctly triangular, 1–1.5 mm long, narrow with acute apex, lateral appendages paired, flat, filiform, 4–7 mm long, sometimes divided at the apex. Ovary half or ⅔ of hypanthium in length, apex pubescent; style 8–15 mm long, apex curved, glabrous; stigma capitate; extra-ovarial chambers 4, alternipetalous, extending to the base of the ovary. Fruits ovoid or urceolate, 7–12 × 5–6 mm, stellate-puberulous or nearly stellate-tomentose, greenish

when unripe, with 4 distinct vertical ridges; calyx lobe remnants persistent, 2–3 mm long; stalks densely stellate-furfuraceous, 4–11 mm long. Seeds ca. 0.75 mm long.
Distribution — Sumatra, Java and Lesser Sunda Islands (Bali).
Ecology and habitat — Primary or secondary montane forest, rarely near crater, at 1000–1700 m elevation.
Vernacular names — Java: *harendong cai* (Sunda); *kramas madu* (Java).
Note — *Dissochaeta leprosa* resembles *D. intermedia*, but differs in the larger hypanthium and distinctly triangular calyx lobe tips. Otherwise, *D. leprosa* has a more tomentose indumentum than *D. intermedia*. The similarity in shape of the alternipetalous stamens between both species made Maxwell (1980b) regard *D. leprosa* as a variety of *D. intermedia*, but because of the differences in size and shape of the hypanthium, the calyx lobe tips and the alternipetalous stamens, it is considered to be a distinct species (Kartonegoro & Veldkamp 2010).

Fig. 3-20. *Dissochaeta leprosa*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower. Photos by C. Bravard.

Specimens examined — **INDONESIA.** West Sumatra: Mt. Singgalang, *Beccari PS 369* (BM, L). Central Java: Pekalongan, Mt. Praboto, 1350 m, 12 Sep 1914, *Backer 15983* (BO); *Ibid.*, Petung Kriono, 1400 m, 9 Sep 1914, *Backer 15787* (BO); Semarang, Mt. Telomoyo, 1500 m, 14 Jun 1892, *Koorders 27844β* (BO); *Ibid.*, 12 May 1899, *Koorders 35840β* (BO); *Ibid.*, *Koorders 35841β* (BO); Magelang, Mt. Andong, 19 Jun 1897, *Koorders 27846β* (BO). East Java: Ponorogo, Mt. Wilis, Sikandang, 15 Aug 1897, *Koorders 29308β* (BO); Malang, Punten, 1200 m, 25 Dec 1928, *van Steenis 2486* (BO); Mt. Kawi, 1160 m, 13 May 1982, *Anon. FS 48* (L). West Java: Bogor, Puncak Pass, 1 Sep 1896, *Sapiin 1115* (BO); *Ibid.*, Mt. Pancar, 20 Dec 1893, *Schiffner 2291* (BO, L); *Ibid.*, Gunung Melati, *Went s.n.* (L); Mt.Halimun, *Uchida 20* (BO); *Ibid.*, Mt. Botol, 4 Mar 2000, *Hoover et al. 32663* (BO); *Ibid.*, Nirmala Estate, 1300 m, 10 Jun 1980, *van Balgooy & Wiriadinata 2922* (BO, L); Cianjur, Mt. Gede, *Kuhl & van Hasselt s.n.* (L); *Ibid.*, Cibodas, 1400 m, 10 Dec 1925, *Danser 5955* (L); *Ibid.*, 24 Oct 1898, *Koorders 31506β* (BO); *Ibid.*, 16 Oct 1898, *Koorders 31523β* (BO); *Ibid.*, 18 Oct 1896, *Koorders 25949β* (BO); *Ibid.*, Geger Bentang, 1600 m, 2 Jun 1948, *Kakah 92* (BO, L); *Ibid.*, 20 Jul 1914, *Backer 14714* (BO); *Ibid.*, 27 Mar 1924, *Bruggeman 48* (BO); *Ibid.*, 4 Aug 1924, *Bruggeman 211* (BO); *Ibid.*, 11 Sep 1927, *Bruggeman 839* (BO); *Ibid.*, *Scheffer s.n.* (BO); *Ibid.*, 1 May 1950, *van Ooststroom 13840* (L, PNH); *Ibid.*, 3 Jul 1896, *Raap 667* (L); *Ibid.*, *Boerlage s.n.* (L); *Ibid.*, 10 Feb 1895, *Hallier 626a* (BO); Cibeber, Mt. Beser, 1000 m, 27 Jun 1917, *Smith 719* (BO, L, U); Bandung, Mt. Tangkuban Perahu, 1600 m, 26 Dec 1919, *Horst 2* (BO); *Ibid.*, 26 Jul 1927, *Docters van Leeuwen 11487* (BO); *Ibid.*, 18 Jul 1916, *Docters van Leeuwen 2301* (BO); *Ibid.*, *Boerlage s.n.* (L); *Ibid.*, *de Vriese 149* (L); *Ibid.*, Oct 1903, *Backer s.n.* (BO); *Ibid.*, 4 Mar 1912, *Backer 2386* (BO); *Ibid.*, 28 May 1908, *Zeijlstra 19* (L); Cibeureum, 1550 m, 3 Apr 1911, *Smith & Rant 125* (BO, U); Mt. Malabar, *Scheffer s.n.*(BO); Pengalengan, *Junghuhn 13* (L, U); Mt.Rendang, *Junghuhn s.n.* (L); Garut, Mt.Guntur, 1500 m, 1937, *Karsten 66* (L); Pagencongan, Jan 1909, *Backer s.n.* (BO); Cianjur, Cireungas, Gunung Malang, 14 Mar 1909, *Backer s.n.* (BO). Bali: Mt. Patas, 1015 m, 20 Nov 1918, *Sarip 465* (BO).

33. *Dissochaeta macrosepala* Stapf — Fig. 3-21, Map 3-18

Dissochaeta macrosepala Stapf, J. Linn. Soc., Bot. 42: 80. 1914. — *Dissochaeta rostrata* Korth. var. *macrosepala* (Stapf) J.F.Maxwell, Gard. Bull. Singapore 33: 320. 1980. — Type: *L.S. Gibbs 3951* (holo K [K000859636!]), Malaysia, Sabah, Ranau, Mt. Kinabalu, Ridge above Bundu Tuhan, 3000 ft. elev., Feb 1910.

Climbing up to 3 m in height. Branchlets terete, 3–4 mm in diameter, densely covered with brown stellate-tomentose hairs, glabrescent; nodes swollen, with interpetiolar ridge; internodes 4.4–5.5 cm long. Leaves: petioles terete, 5–8 mm long, densely brown stellate-tomentose; blades ovate, 6–6.2 × 4–4.3 cm, subcoriaceous, base cordate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, with prominent reticulate sunken venation, abaxially densely covered with brown stellate-tomentose hairs. Inflorescences terminal, up to 15 cm long, manyflowered; main axis densely covered with brown stellate-tomentose hairs; primary axes up to 12 cm long with 3 or 4 nodes, secondary axes 2–2.5 cm long with 1–3 nodes, tertiary axes up to 1 cm long with 1 node; bracts linear or leaf-like, 4–15 mm long, stellate-tomentose, caducous; bracteoles subulate, 2–6 mm long, stellatetomentose, caducous; pedicels brown stellate-tomentose, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium tubular to suburceolate, 5–6 × 2–3 mm, densely brown stellate-tomentose; calyx lobes lanceolate, 4–4.5 mm long, apex acute, tomentose; petal buds conical, 4–5 mm long, glabrous; mature petals ovate, 6–8 × 4–5 mm, base clawed, apex acute,

bright pink. Stamens 8, subequal, filaments curved sideways, yellowish; alternipetalous stamens with 6–7 mm long filaments, anthers slender, lanceolate, sickle-shaped, thecae 8–9 mm long, purplish, pedoconnective 2–3 mm long, basal crest triangular 1–2 mm long, whitish, lateral appendages prolonged from base of crest, paired, filiform, 4–5 mm long, whitish; oppositipetalous stamens with 5–6 mm long filaments, anthers thicker, S-shaped, thecae 6–7 mm long, purplish, basal crest minute or spur-like, whitish, lateral appendages from base with a paired, ligulate appendages, ca. 1 mm long, whitish. Ovary ⅔ of hypanthium in length, apex pubescent; style 10–12 mm long, curved at the apex, glabrous, white with purplish apex; stigma minute, capitate, yellowish; extra-ovarial chambers 8, extending nearly to the middle of the ovary. Fruits ovoid or urceolate, 8–9 × 5–6 mm long, densely covered with stellate-tomentose hairs; calyx lobes persistent, reflexed. Seeds ca. 0.5 mm long.
Distribution — Borneo (Mount Kinabalu).
Ecology and habitat — Lower montane forest, in open places, at ca. 914 m elevation.
Note — The indumentum of *D. macrosepala* resembles *D. densiflora*, but the former species is different in the long, lanceolate calyx lobes. Maxwell (1980b) considered both species as varieties of *D. rostrata*. Stapf & Green (1914) incorrectly noted that the species has four stamens, but it has 8 stamens like the other similar species.
Specimens examined — **MALAYSIA.** Sabah: Ranau, Mt. Kinabalu, Bundu Tuhan, 914 m, Feb 1910, *Gibbs 3951* (K); *Ibid.*, Dallas, 914 m, 1 Dec 1931, *Clemens 30340* (L).

34. *Dissochaeta malayana* Furtado — Map 3-20

Dissochaeta malayana Furtado, Gard. Bull. Singapore 20: 110. 1963. — *Dissochaeta rostrata* Korth. var. *malayana* (Furtado) J.F.Maxwell, Gard. Bull. Singapore 33: 320. 1980. — Type: *E.J.H. Corner SFN 30381* (holo SING [SING0051682!]), Malaysia, Terengganu, Kemaman, Bukit Kajang 350 m.

Branchlets terete, 2–3 mm in diameter, covered with scattered, ca. 1 mm long, dark purple bristle hairs; nodes swollen, with interpetiolar ridge, densely covered with brown stellate-furfuraceous hairs and scattered bristles; internodes 4.5–7 cm long. Leaves: petioles terete, 5–8 mm long, densely covered with stellate-furfuraceous and bristle hairs; blades ovate, 7.5–10 × 3.5–4.8 cm, membranous, base emarginate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces hirsute, with sparse stellate hairs and scattered dark bristle hairs, more densely so at midrib and margin. Inflorescences terminal, up to 15 cm long, many-flowered; main axis angular, covered with scattered, dark purple bristle hairs; primary axes up to 12 cm long with 3–5 nodes, secondary axes 2–5 cm long with 1 or 2 nodes, tertiary axes up to 1.5 cm long with 1 node; bracts linear, 3–4 mm long, with stellate-furfuraceous and dark purple bristle hairs; bracteoles linear or subulate, 1–2 mm long, with stellate-furfuraceous and dark bristle hairs; pedicels with densely stellate-furfuraceous and dark purple capitate bristle hairs, 5–6 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium suburceolate, 8–10 × 3–4 mm, densely covered with stellate-furfuraceous and dark capitate purple bristle hairs; calyx lobes truncate with undulate tip, 1–1.5 mm long; petal buds conical or rounded, 4–5 mm long, apex bristly; mature petals obovate, ca. 7 × 4 mm, notreflexed, base clawed, apex rouded, bristly, otherwise glabrous, pink-purple. Stamens 8, subequal, filaments curved sideways, yellow; alternipetalous stamens with 7–8 mm long filaments, anthers lanceolate, sickle-shaped, thecae ca. 10 mm long, apex rostrate, yellow, pedoconnective 1–1.5 mm long, basal crests minute, triangular, ca. 0.5 mm long, lateral appendages paired, filiform, 3–4 mm long; oppositipetalous stamens with 7–8 mm filaments, anthers thick, slightly S-shaped, thecae 9–10 mm long, pink, basal crests minute, ligular or spur-like, ca. 0.5 mm long, lateral

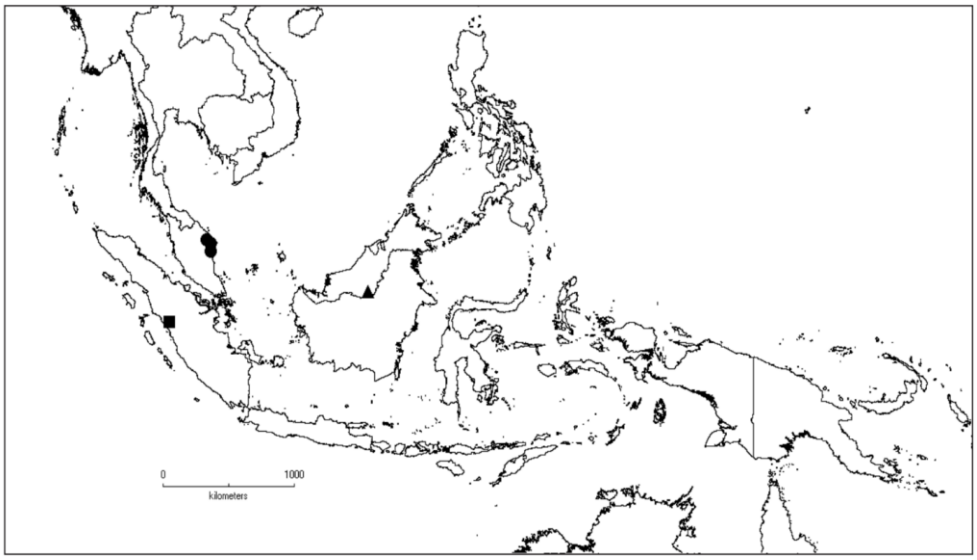
appendages paired, filiform, 1–1.5 mm. Ovary ⅔ of hypanthium in length, apex villous and bristly; style 13–15 mm long, curved at end, glabrous, pink; stigma minute, capitate; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits urceolate, 8–10 × 4.5–5 mm, sparsely stellate-furfuraceous and densely covered with dark capitate bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Peninsular Malaysia (Terengganu).

Ecology and habitat — Lowland forest at 150–400 m elevation.

Note — This species resembles *D. johorensis*; both species have most parts covered by bristle hairs. *Dissochaeta malayana* is different in having more distinct dark purple bristle hairs and truncate calyx lobes and geographically it is disjunct, only present in the northern part of the peninsula.

Fig. 3-21. *Dissochaeta macrosepala*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower Photos by D.S. Penneys; voucher: *Penneys 2512* (WNC)].



Map 3-20. Distribution of *D. malayana* (●), *D. marumioides* (■) and *D. maxwellii* (▲).

Specimens examined — **MALAYSIA.** Terengganu: Ulu Brang, 365 m, Jul 1937, *Moysey & Kiah SFN 33858* (BO, K); Kemaman, Bukit Kajang, *Corner SFN 30381* (SING); Dungun, Jerangau Road, 16 Nov 1954, *Sinclair & Kiah SFN 40492* (BM, BO, K, L).

35. *Dissochaeta marumioides* Cogn. — Map 3-20

Dissochaeta marumioides Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 556. 1891, non. *D. marumioides* Furtado (1963) [see under *D. spectabilis*]. — Type: *O. Beccari s.n.* (holo FI [FI007931!]), Indonesia, West Sumatra, Mt. Singgalang, 1600 m elev.

Branchlets terete, 3–5 mm in diameter, brown stellate-furfuraceous; nodes swollen, with annular interpetiolar ridge; internodes 3–5 cm long. Leaves: petioles flattened, 10–15 mm long, densely stellate-furfuraceous; blades ovate-elliptic, 8.3–14 × 3.5–5 cm, membranous, base cordate, margin entire, apex acuminate, tip 1–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark green, abaxially brown stellate-furfuraceous. Inflorescences terminal, up to 20 cm long, up to 20 flowers; main axis quadrangular, densely stellate-furfuraceous; primary axes up to 17 cm long with 5 nodes, secondary axes up to 3 cm long with 1 or 2 nodes, tertiary axes when developed 0.6–0.7 cm long with 1 node; bracts leaf-like, oblong-lanceolate, 15–22 × 4–6 mm, densely brown stellate-furfuraceous; bracteoles linear, 2–3 mm long, densely brown stellate-furfuraceous; pedicels densely brown stellate-furfuraceous, ca. 3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 7–9 × 3–5 mm, densely with stellate-furfuraceous and scattered, thickened, 1–2 mm long bristles; calyx lobes rounded, ca. 2 mm long, margin ciliate, apex obtuse, stellate-furfuraceous; petal buds conical, 3–5 mm long, acute; mature petals elliptic to suborbicular, ca. 12 × 9 mm, base clawed, apex acute, glabrous. Stamens 8, unequal, filaments curved sideways, glabrous; alternipetalous stamens with 6–7 mm long filaments, anthers slightly curved, lanceolate, thecae ca. 8 mm long, pedoconnective ca. 2 mm long, basal crest triangular, ca. 1.5 mm long, thin, entire or bifid, lateral appendages 4, filiform, 2–3 mm long; oppositipetalous stamens with ca. 6 mm long filaments, anthers sinuate, curved, thecae ca. 8 mm long, basal crest minute, ca. 0.3 mm long,

lateral appendages paired, filiform appendages 2–3 mm long. Ovary ⅔ of hypanthium in length, apex villous; style ca. 15 mm long, curved at top, glabrous; stigma minute; extra-ovarial chambers 8, extending nearly to the base of the ovary. Fruits not seen.
Distribution — Sumatra (West).
Ecology and habitat — Montane forest at ca. 1600 m elevation.
Note — *Dissochaeta marumioides* is only known from the type from Mount Singgalang, West Sumatra. This species has a non-bristly indumentum on branchlets and leaves; though sparse bristles are present on the hypanthium and calyx lobes. The 4 lateral appendages of the alternipetalous stamens are exceptional, all other species in the genus having 2. The calyx lobes with rounded apex are similar to those of *D. rostrata* from Borneo, but the species differs in the shape of the bracts.

36. *Dissochaeta maxwellii* (Karton.) Karton., **comb. nov.** — Map 3-20

Diplectria maxwellii Karton., Kew Bull. 73-23: 1, fig. 1. 2018. — Type: *Runi et al. S.63137* (holo K [K000566618!]; isotypes: KEP [KEP43526!], L [L3908632!], SAN!, SAR), Malaysia, Sarawak, Kapit Division, Batang Baleh, Nanga Serani, 500 m elev., 4 May 1991.

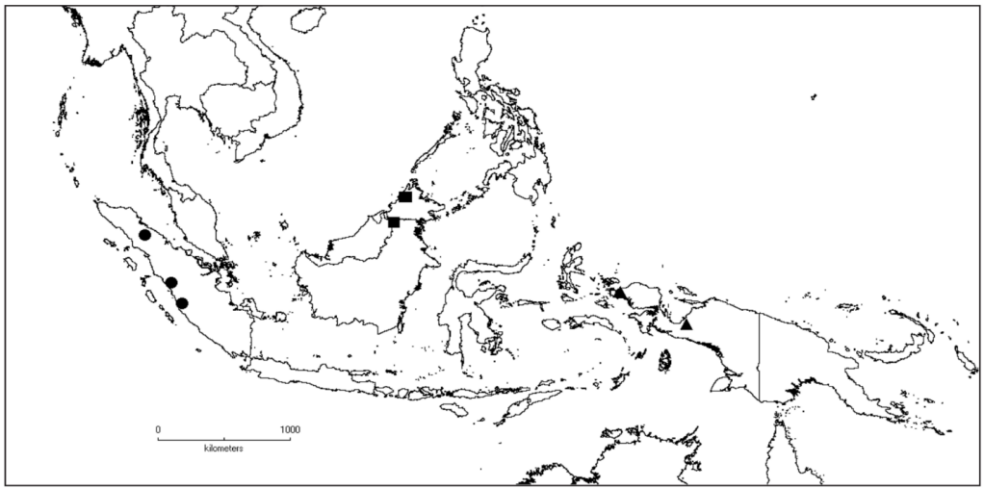
Climbing up to 6 m in height. Branchlets terete, angular in the upper branches, ca. 3 mm in diameter, glabrous to sparsely stellate-puberulous; nodes swollen, with distinct interpetiolar ridge, annulum, densely covered with stellate-pubescent hairs and 4–6 mm long, brown, bristle hairs, prominent, ca. 0.1 mm thick at base, narrowing towards the acute tip; annulus 1–2 mm high, brownish; internodes ca. 5–6 cm long. Leaves: petioles terete, 10–12 mm long, densely stellate-pubescent and covered with dense, 4–7 mm long, brown bristle hairs; blades elliptic-oblong, 10.3–12.9 × 3.8–5 cm, membranous, base rounded, margin entire, apex acuminate, tip 1.2–1.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark green, abaxially glabrous or stellate-puberulous on midrib and sparsely hairy on lateral veins, light brown. Inflorescences terminal, up to 14.8 cm long, many-flowered; main axis quadrangular, densely stellate-pubescent and sparsely covered with bristle hairs, purplish-green, nodes densely stellate-pubescent and densely covered with 3–5 mm long brown bristle hairs; primary axes ca. 12 cm long with 3 or 4 nodes, secondary axes 1.5–6 cm long with 1 or 2 nodes, tertiary axes 6–8 mm long with 1 node; bracts oblong-lanceolate, 5–7 mm long, densely stellatepubescent, covered with 3–4 mm brown bristle hairs at the margin; bracteoles oblong, 2–3 mm long, densely stellate-pubescent; pedicels densely stellate-pubescent, purplish, 4–7 mm long in central flowers, 3–3.5 mm long in lateral flowers. Hypanthium tubular, campanulate, 3.5–4 × ca. 2.5 mm, densely pubescent and sparsely covered with glandular bristle hairs in middle and base; calyx lobes truncate, ca. 0.5 mm long, minutely apiculate; petal buds conical, 1–2 mm long, acute; mature petals obovate, 3–4.5 × 2.5–3 mm, apex acute, base clawed, glabrous. Stamens 8, unequal, filaments straight, glabrous; alternipetalous stamens staminodial with 3–4 mm long filaments, anthers reduced, thecae rudimentary, lanceolate, 2–4 mm long, terete, thin, basal crest triangular with erose tip, ca. 1 mm long, lateral appendages absent; oppositipetalous stamens with ca. 3 mm long filaments, anthers clavate, sickle-shaped, curved, thecae 4–5 mm long, glabrous, smooth, basal crest minute, ca. 0.3 mm long, lateral appendages paired, small, ligular, ca. 0.5 mm long. Ovary ⅔ of hypanthium in length, densely pubescent at top; style curved at top, 6–10 mm long, glabrous; stigma minute, inconspicuous; extra-ovarial chambers 4, extending to the middle of the ovary. Fruits globose, 5–8 × 3–6 mm, glabrous, red when ripe; calyx lobe remnants persistent, erect. Seeds ca. 0.5 mm long.
Distribution — Borneo (Sarawak).
Ecology and habitat — Sub-montane forest at ca. 500 m elevation.

Vernacular name — *akar kemunting* (Kapit).
Note — A distinct species that resembles *D. viminalis* in the number and shape of the stamens, but differs in having dense prominent bristle hairs on the nodes, petioles, bracts and bracteoles. Known only from the type from Kapit Division, Sarawak.

37. *Dissochaeta micrantha* (Veldkamp) Karton., **comb. nov.** — Map 3-21

Diplectria micrantha Veldkamp, Blumea 24: 422, fig. 5B. 1979. — *Diplectria glabra* (Merr.) M.P.Nayar var. *micrantha* (Veldkamp) J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980. — Type: *I.H. Sario SAN 28959* (holo L [L0008871!]; iso K [K000859550!], SAN), Malaysia, Sabah, Ranau District, Mount Kinabalu, Sosopodon, 4720 ft. elev., 30 Jan 1962.

Branchlets terete, 3–4 mm in diameter, glabrous; nodes swollen, with prominent annular, 2–3 mm wide, crest-like interpetiolar ridge, margin with 3–5 mm long simple bristles; internodes 6–12 cm long. Leaves: petioles terete, 5–10 mm long, glabrous to nearly furfuraceous and dorsally with bristle hairs; blades ovate, 6.5–9 × 3.5–5 cm, subcoriaceous, base cordate, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous except scattered stellate hairs on the nerves. Inflorescences terminal, up to 25 cm long, many-flowered; main axis angular, glabrous; primary axes up to 23 cm long with 7–9 nodes, secondary axes 8–10 cm long with 5–7 nodes, tertiary axes up to 1.5 cm long with 1 or 2 nodes, quarternary axes when developed up to 0.5 cm long with 1 node; bracts linear or ligular, 3–4 mm long, glabrous, caducous; bracteoles subulate, 1–2 mm long, glabrous; pedicels stellate-furfuraceous, 2–3 mm long in central flowers, ca. 1 mm long in lateral flowers. Hypanthium urceolate, ca. 3 × 1–1.5 mm, glabrous; calyx lobes truncate, ca. 0.3 mm long, apex with 4 minute points; petal buds conical, 1–1.5 mm long; mature petals suborbicular, 2–2.5 × ca. 2 mm, reflexed, base clawed, apex acute, pink. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with ca. 1 mm long filaments, thecae rudimentary, ca. 0.5 mm long, slender, terete, basal crest triangular, thin, ca. 1 mm long, apex erose, base with a small auricle, lateral appendages absent; oppositipetalous stamens with 1–2 mm long filaments, anthers thick, oblong, thecae 2–2.5 mm long, white, basal crest keels bifid, ca. 0.2 mm long, lateral appendages bifid, ca. 0.3 mm long. Ovary ⅔ of hypanthium in length, apex glabrous; style 3–4 mm long, glabrous; stigma minute, capitate; extra-ovarial chambers 4, oppositipetalous, extending to ⅓ of the ovary. Fruits subglobose, 4–5 × ca. 4 mm, glabrous; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.
Distribution — Borneo (Sabah and North Kalimantan).
Ecology and habitat — Montane forest on river banks or in open places at 1100–1400 m elevation.
Note — The description of the flowers is based on a bud only since mature flowers are still unknown. This species is restricted to the montane forests of Mount Kinabalu, Sabah and Kayan Mentarang, North Kalimantan.
Specimens examined — **MALAYSIA.** Sabah: Ranau, Mt. Kinabalu, Sosopodon, 1440 m, 30 Jan 1962, *Sario SAN 28959* (K, L); *Ibid.*, Tenompok, 1500 m, 29 Feb 1932, *Clemens 28588* (BM, K); *Ibid.*, May 1932, *Clemens 30341* (K); *Ibid.*, between Tenompok and Kundasan, 1400 m, 15 Jul 1957, *Sinclair et al. 9235* (L); *Ibid.*, Sungai Mamut, 1200–1400 m, 15 Feb 1969, *Kokawa & Hotta 5798* (L). **INDONESIA.** North Kalimantan: Krayan, Kayan Mentarang, Long Bawan, 1100 m, 29 Jul 1981, *Kato et al. B-10105* (BO, L).



Map 3-21. Distribution of *D. micrantha* (■), *D. nodosa* (●) and *D. papuana* (▲).

38. *Dissochaeta nodosa* Korth. — Map 3-21

Dissochaeta nodosa Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844. — *Aplectrum nodosum* (Korth.) Blume, Mus. Bot. 1(3): 37. 1849. — *Anplectrum nodosum* (Korth.) Triana, Trans. Linn. Soc. London 28: 84. 1872. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *P.W. Korthals s.n.* (lecto L [L0537233!]; isolecto L [L0537232!]), Indonesia, West Sumatra, Indrapoera.

Dissochaeta montana Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 558. 1891. — Type: *O. Beccari PS 4124* (holo FI [FI007930!]), Indonesia, West Sumatra, Mt. Singgalang, 1700 m elev.

Anplectrum yatesii Merr., Pap. Michigan Acad. Sci. 19: 175. 1934. — *Dissochaeta yatesii* (Merr.) Veldkamp, Blumea 24: 435, 443. 1979. — Lectotype (designated here): *H.S. Yates 2012* (lecto BO [BO1429407!]; isolecto L [L0537225!], MICH [MICH-1111808!], NY [NY00221311!]), Indonesia, North Sumatra, Karoland, Berastagi, 12 Mar 1926.

Branchlets terete, 4–5 mm in diameter, stellate-furfuraceous; nodes swollen, interpetiolar ridge present; internodes 5.5–7.3 cm long. Leaves: petioles flattened, 8–10 mm long, stellate-furfuraceous; blades ovate to elliptic, 8.3–12.5 × 3.5–6 cm, membranous, base subcordate, margin entire, apex acuminate, tip ca. 8–15 mm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous to sparsely stellate-furfuraceous. Inflorescences terminal, up to 17 cm long, many-flowered; main axis angular, glabrescent to sparsely stellate-puberulous; primary axes up to 15 cm long with 5 or 6 nodes, secondary axes up to 4 cm long with 1 or 2 nodes, tertiary axes up to 1.5 cm long with 1 node; bracts and bracteoles inconspicuous, caducous; pedicels sparsely stellate-furfuraceous, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium broadly campanulate, ca. 4 × 3 mm, stellate-furfuraceous; calyx lobes truncate with 4 triangular tips, ca. 1 mm long, glabrous; petal buds conical, 2–3 mm long; mature petals obovate, 3–4 × ca. 3 mm, base clawed, apex rounded, glabrous. Stamens 8, equal or subequal, straight, filaments straight; alternipetalous stamens with filaments 4–6 mm long, anthers oblong or lanceolate, thecae ca. 5 mm long, pedoconnective ca. 0.5 mm long, basal crest triangular, ca. 1.5 mm long, acute, lateral appendages absent; oppositipetalous stamens with filaments ca. 3 mm long, anthers lanceolate, thecae 3–4 mm long, thick, basal crest ligular, 1–1.5 mm long,

lateral appendages absent. Ovary ¾ of hypanthium in length, apex puberulous; style 8–10 mm long, curved at top, glabrous; stigma minute; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits subglobose, 6–7 × 3–4 mm, glabrescent, apex mammiform; calyx lobes persistent, erect. Seeds ca. 0.5 mm long.
Distribution — Sumatra.
Ecology and habitat — Montane forest, in open places at 1300–1700 m elevation.
Specimens examined — **INDONESIA.** North Sumatra: Karo, Brastagi, *Yates 2012* (BO, L, MICH, NY). West Sumatra: Mount Singgalang, *Beccari PS 4124* (FI); Indrapura, *Korthals s.n.* (L).

39. *Dissochaeta pallida* (Jack) Blume — Fig. 3-22, Map 3-22

Dissochaeta pallida (Jack) Blume, Flora 14: 500. 1831. — *Melastoma pallidum* Jack, Trans. Linn. Soc. London 14: 12. 1823, "pallida". — Lectotype (designated here): *W. Jack 55* (lecto BM [BM000944482!]) Malaysia, Penang.

Dissochaeta ovalifolia Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 76. 1851. — Lectotype (designated here): *C. Gaudichaud-Beaupré 94* (lecto P [P02274807!]; isolecto P [P02274808!]), Malaysia, Pulo Pinang, Mar 1837.

Dissochaeta superba Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 77. 1851. — Lectotype (designated here): *C. Gaudichaud-Beaupré 93* (lecto P [P02274809!]; isolecto P [P02274810!, P02274811!]), Malaysia, Peninsular Malaysia, Pulo Pinang, Mar 1837.

Dissochaeta astrosticta Miq., Fl. Ned. Ind., Eerste Bijv. 2: 318. 1861. — Lectotype (designated here): *J.E. Teijsmann HB 3424* (lecto BO [BO1865965!]; isolecto BM [BM000944481!], BO [BO1865966!], K [K000859484!], U [U0004010!, U0124122!]), Indonesia, Sumatra, Bangka bij Djeboes.

Dissochaeta sumatrana Boerl. & Koord. in Koord.-Schum., Syst. Verz. 2: 46. 1911. — Type: *S.H. Koorders 22330β* (holo BO [BO1294108!]), Indonesia, Riau, Sangkamiang, 40 m elev., 29 Mar 1891.

Dissochaeta borneensis Bakh.f., Contr. Melastom. 231. 1943. — Type: *Mondi 252* (holo L [L0126153!]; iso BO [BO1779331!, BO1779332!, BO1779333!], K [K000859487!, K000859488!]), Indonesia, West Kalimantan, Pontianak, Kp. Andjongan, 5 Apr 1931.

Climbing up to 25 m in height. Branchlets terete, 2–4 mm in diameter, smooth, sparsely covered with minute stellate hairs, glabrescent; nodes swollen, with interpetiolar ridge; internodes 7–11.5 cm long. Leaves: petioles flattened, 10–20 mm long, sparsely furfuraceous; blades ovate to elliptic, 6–14 × 4–8 cm, subcoriaceous, base broadly rounded to cordate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous or punctate. Inflorescences terminal and axillary; up to 25 cm long when terminal, up to 11 cm long when axillary; many-flowered; main axis sparsely furfuraceous or glabrous; primary axes 8–15 cm long with 5 or 6 nodes, secondary axes 4.5–5 cm long with 1 or 2 nodes, tertiary axes 0.8–1.2 cm long with 1 node; bracts linear or lanceolate, 5–7 mm long, glabrous or furfuraceous; bracteoles linear or lanceolate, 2–4 mm long; pedicels glabrous, 4–5 mm long in central flowers, ca. 2 mm long in lateral flowers. Hypanthium campanulate-tubular, 6–8 × 4–5 mm, obscurely 8-lined or 8-ridged, glabrous or punctate; calyx lobes truncate, 1–2 mm long, with 4 undulate or acute tips; petal buds slightly conical, 9–15 mm long; mature petals obovate to oblong, 7–8 × ca. 5 mm, reflexed, base clawed, apex acute to subrounded, glabrous, bright white or white pinkish. Stamens 8, unequal, filaments curved sideways, yellow; alternipetalous stamens with 10–12 mm long filaments, anthers narrow, curved, sickle-shaped, thecae 12–15 mm long, pedoconnective 3–4 mm, basal crest triangular, ca. 1 mm

long, lateral appendages paired, filiform, 5–6 mm long; oppositipetalous stamens with 9–10 mm long filaments, anthers S-shaped, thecae 4–7 mm long, thick, basal crest ligular, ca. 1 mm long, lateral appendages paired, filiform, 5–6 mm long. Ovary half as long as hypanthium, apex pubescent; style slender, 20–24 mm long, glabrous; stigma minute; extra-ovarial chambers 8, extending nearly to the base of the ovary. Fruits ovoid-urceolate, 8–10 × 6–7 mm, glabrous, punctate; calyx lobe, remnants persistent, widened. Seeds ca. 0.5 mm long.

Distribution — Malay Peninsula, Sumatra and Borneo (Western part).

Ecology and habitat — Primary lowland dipterocarp forest, in open places from 60–700 m elevation.

Vernacular names — Peninsular Malaysia: *akar sunudo*, *akar duman bukit*, *akar sial munahon* (Malacca). Sumatra: *kedudu akar* (Riau). Borneo: *lingkodo kliko* (Pontianak).

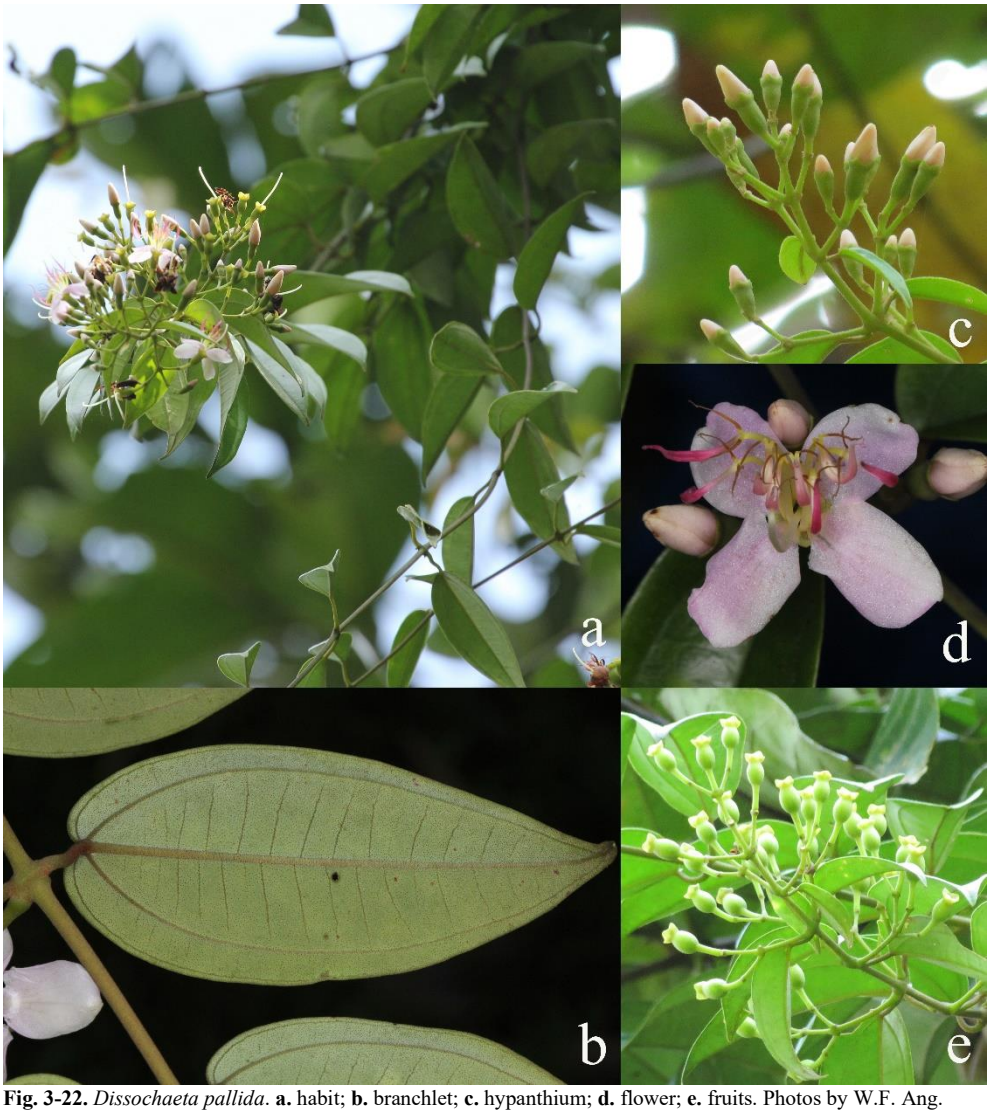
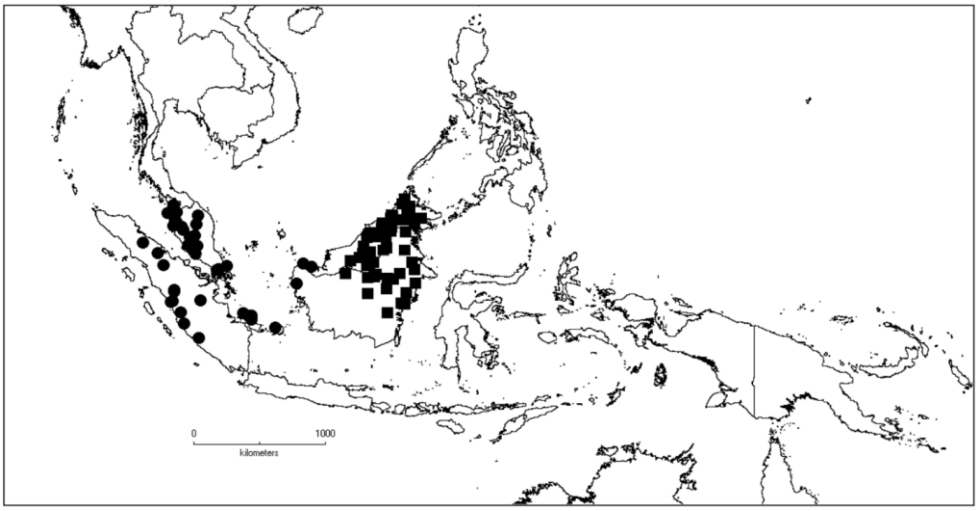


Fig. 3-22. *Dissochaeta pallida*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. Photos by W.F. Ang.



Map 3-22. Distribution of *D. pallida* (●) and *D. pulchra* (■).

Note — *Dissochaeta pallida* is distinguished by its campanulate-tubular 8-lined or 8-ridged hypanthium and truncate calyx lobes with undulate acute tip. The minute punctation on the abaxially leaf surface is a reliable field character to recognise this species. The indumentum on the leaves is similar to that of *D. punctulata* Hook.f. ex Triana, from which it differs in the indumentum of the hypanthium and the number of appendages of the stamens.

Specimens examined — **MALAYSIA.** Kedah: Gunong Bintang, 300 m, 8 Apr 1968, *Sidek 276* (K, L); Bukit Perak, 26 Nov 1969, *Chan FRI 13138* (K). Kelantan: Bukit Baka, 2 Jun 1982, *Stone & Chin 15244* (L). Malacca: *Griffith KD 2292* (K). Negri Sembilan: Jelebu, Pasoh Forest, 80-120 m, 19 Jun 1996, *Gardette 2046* (K, L); Gunong Angsi, 457 m, 20 Nov 1923, *Nur SFN 11529* (BO). Pahang: Gunong Tahan, 21 Jun 1922, *Haniff & Nur SFN 8077* (K); Ulu Krau, Gunung Benom, 580 m, 20 Apr 1967, *Yusoff KEP 99109* (K, L). Penang: *Jack 55* (BM); *Wallich 4049* (BM, K, L, NY, P); *Walker 28* (BM, K); *Hullet 179* (BM, P); Mar 1837, *Gaudichaud-Beaupré 93* (P); *Gaudichaud-Beaupré 94* (P); *Gaudichaud-Beaupré 96* (P); Government Hill, 152 m, Oct 1884, *Curtis 80* (K); *Ibid.*, Apr 1890, *Curtis 2297* (K, P); *Ibid.*, *Maingay KD 792* (BM, K, L); *Ibid.*, *Maingay KD 793 (2227)* (K, L); Western Hill, 700 m, 1 Mar 1965, *Hardial & Samsuri 181* (K, L); *Ibid.*, 720 m, 7 Feb 1991, *Saw FRI 37342* (L); Penang Hill, 22 Aug 1879, *King's collector s.n.* (P). Perak: *Scortechini 22* (P); *Scortechini 371* (L); *Scortechini 1650* (L, P); *Scortechini s.n.* (P); Larut, Nov 1881, *King's collector 2570* (K); *Ibid.*, Mar 1883, *King's collector 3965* (BO); Maxwell's Hill, 4 Mar 1965, *Hardial & Samsuri 295* (K, L); Dending, 13 Mar 1896, *Anon s.n.* (BM); Tapah, *Wray 1370* (U); *Ibid.*, Nov 1888, *Ridley s.n.* (BM); Thaiping Hill, 300–450 m, Feb 1886, *King's collector 8499* (P). Selangor: Klang Watercatchment, 12 Mar 1922, *Burkill SFN 6841* (BO, K); Kuala Lumpur, *Ridley 2015* (BM); Semangkok, 700 m, 6 May 1970, *Chan FRI 13278* (K). Sarawak: Kuching, 22 Mar 1893, *Haviland 3144* (K); Lundu, Gunung Pueh, 60 m, 19 Mar 1996, *Julaihi & Runi S.73359* (L). **SINGAPORE.** *Maingay KD 793 (2685)* (BM, K); Bukit Timah, Mar 1890, *Ridley 2017a* (BM); Choa Chu Kang, 9 Dec 1890, *Ridley 2017* (BM); Jurong River, 13 Mar 1919, *Burkill SFN 4081* (BO); Seletar, 29 Mar 1889, *Ridley s.n.* (BM). **INDONESIA.** Bangka-Belitung: Bangka, *Kobus s.n.* (BO); *Ibid.*, *Horsfield 15* (K); *Ibid.*, Jibus, *Teijsmann HB 3424* (BM, BO, K); *Ibid.*, *Teijsmann s.n.* (BO); *Ibid.*, Plangas, *Teijsmann HB 3197* (BO); *Ibid.*, Sungai Liat, Bukit Tampang, 70 m, 23 Oct 1917, *Bünnemeijer 1675* (BO); Belitung, Tanjung Pandan, *Teijsmann s.n.* (BO). Bengkulu: *Brooks*

s.n. (K). North Sumatra: Labuhan Batu, Aek Kanopan, Lundut Concession, Kualu, 14 Mar 1927, *Bartlett 6900* (K, L); *Ibid.*, 1 Apr 1927, *Bartlett 7315* (L); *Ibid.*, Kota Pinang, Langga Payung, 7-30 Mar 1933, *Rahmat Si Toroes 3294* (L); *Ibid.*, 7–14 Apr 1933, *Rahmat Si Toroes 3837* (L). Riau: Indragiri Hulu, Kuala Belilas, 22 Apr 1939, *Buwalda 6666* (BO, K, L, PNH); Sangkamiang, 40 m, 29 Mar 1891, *Koorders 22330β* (BO). West Sumatra: Padang, Limau Manis, 400 m, 5 Sep 2017, *Kartonegoro 1058* (BO, L); Lima Puluh Kota, Taram, River Campo, 500-1000 m, 26 Aug 1957, *Meijer 7024* (L); *Ibid.*, *Meijer 7026a* (L); *Ibid.*, Kelok Sembilan, 800 m, 20 May 2001, *Putri et al. 63* (ANDA). West Kalimantan: Pontianak, Kp. Anjongan, 5 Apr 1931, *Mondi 252* (BO, K, L).

40. *Dissochaeta papuana* (Mansf.) Karton., **comb. nov.** — Map 3-21

Anplectrum papuanum Mansf., Nova Guinea 14: 202. 1924. — *Diplectria papuana* (Mansf.) Bakh.f., Contr. Melastom. 202. 1943. — *Diplectria glabra* (Merr.) M.P.Nayar var. *papuana* (Mansf.) J.F.Maxwell, Gard. Bull. Singapore 33: 313. 1980. — Lectotype (designated here): *R.F. Janowsky 132* (lecto L [L0008872!]; isolecto BO [BO1865947!]), Indonesia, Papua, Siriworivier, Jul 1912.

Branchlets terete, 3–4 mm in diameter, glabrous; nodes swollen, with raised annular crest-like interpetiolar ridge, often with bristle hairs; internodes 6–8.7 cm long. Leaves: petioles terete, ca. 10 mm long, furfuraceous and dorsally with bristle hairs; blades ovate, 8–16 × 4.5–9 cm, membranous to subcoriaceous, base cordate, margin entire, apex acuminate, tip 1–1.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous, abaxially with a pair of glandular patches at the base. Inflorescences terminal, up to 30 cm long, many flowered; main axis angular, covered with stellate hairs; primary axes up to 28 cm long with 6 or 7 nodes, secondary axes up to 13 cm long with 4 or 5 nodes, tertiary axes up to 5 cm long with 3 or 4 nodes, quarternary axes when developed 1–1.5 cm long with 1 or 2 nodes; bracts linear, ca. 3 mm long, stellate-furfuraceous, caducous; bracteoles subulate, ca. 1 mm long, densely stellate-furfuraceous; pedicels stellate-furfuraceous, ca. 3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium suburceolate, 3–4 × ca. 2 mm, glabrous; calyx lobes truncate, ca. 0.5 mm long, apex triangular; petal buds conical, 1.5–2 mm long, apex acuminate; mature petals ovate, 3–3.5 × ca. 2 mm, reflexed, base clawed, apex acute, glabrous. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial, with ca. 2 mm long filaments, anthers rudimentary, thecae ca. 2 mm long, slender, terete, basal crest triangular, ca. 1 mm long, thin, base emarginate or hastate, apex acute, lateral appendages absent; oppositipetalous stamens with ca. 3 mm long filaments, anthers thick, curved, S-shaped, thecae 3–3.5 mm long, yellow, basal crest bilobed, ca. 0.3 mm long, lateral appendages absent. Ovary half as long as hypanthium, apex glabrous; style 7–8 mm long, curved at the end, slender, glabrous; stigma minute, capitate; extra-ovarial chambers 4, oppositipetalous, extending to the middle of the ovary. Fruits subglobose, 3–4 × ca. 3 mm, glabrous; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — New Guinea (Indonesian Papua).

Ecology and habitat — Lowland forest at river banks at ca. 50 m elevation.

Note — *Dissochaeta papuana* resembles *D. glabra* in its glabrous appearance and pair of glandular patches at the abaxially base of the leaves, but differs in the ovate shape of the leaf blade and the more urceolate hypanthium.

Specimens examined — **INDONESIA.** Papua: Geelvink Bay, Siriwo River, Jul 1912, *Janowsky 132* (BO, L). West Papua: Sorong, 50 m, 28 Aug 1948, *Pleyte 705* (BO, K, L).

41. *Dissochaeta porphyrocarpa* Ridl. — Fig. 3-23, Map 3-23

Dissochaeta porphyrocarpa Ridl., Kew Bull. 1: 32. 1946. — *Dissochaeta rostrata* Korth. var. *porphyrocarpa* (Ridl.) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — Lectotype (designated here): *G.D. Haviland 1287* (lecto K [K000859633!]), Malaysia, Sarawak, Ulu Tawaran, 2000 ft.

Dissochaeta tawaensis Furtado, Gard. Bull. Singapore 20: 114. 1963. — Type: *A.D.E. Elmer 21426* (holo SING [SING0051874!]; iso BM [BM000944477!, BM001190928!], BO [BO1429430!], C [C10014565!], K [K000859635!], L [L0537282!], P [P05283550!], U [U0004011!]), Malaysia, Sabah, Elphinstone Province, Tawao.

Dissochaeta punctulata auct. Non. Hook.f. ex Triana: Merr., Univ. Calif. Publ. Bot. 15: 224. 1929. *p.p.*, excl. type.

Climbing up to 6 m in height. Branchlets terete, ca. 3 mm in diameter, sparsely brown stellate-puberulous and densely covered with 1–2 mm long curved purplish-tip bristle hairs; nodes swollen, with an interpetiolar ridge; internodes 6.5–8 cm long. Leaves: petioles terete, 8–15 mm long, densely covered with stellate hairs and curved bristle hairs; blades ovate or elliptic, 9.7–12 × 4.7–7.8 cm, membranous, base subcordate, margin entire, apex acute; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially scabrid, with hairs and scattered curved bristle hairs, abaxially densely covered with curved bristle hairs in most parts, more densely so on midrib and margin. Inflorescences terminal, up to 24 cm long, many-flowered; main axis angular, densely covered with minute stellate hairs and curved purplish-tip bristle hairs; primary axes up to 12 cm long with 3 or 4 nodes, secondary axes 1.5–5 cm long with 1 or 2 nodes nodes, tertiary axes up to 1 cm long when developed with 1 node; bracts linear, 7–8 mm, covered with dense bristle hairs; bracteoles linear, ca. 4 mm long, covered with dense bristle hairs; pedicels densely stellate-furfuraceous and with curved purplish-tipped bristle hairs, 3–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 5–6 × 3–4 mm, densely covered with brown stellate and curved purplish-tipped bristle hairs; calyx lobes truncate at base, slightly lanceolate, 3–4 mm long, densely bristly, glabrous inside; petal buds conical, 4–8 mm long, apex bristly; mature petals ovate-oblong, 5–6 × 3–5 mm, reflexed, apex obtuse, base clawed, glabrous, purple. Stamens 8, unequal, filaments curved sideways, light green; alternipetalous stamens with ca. 7 mm long filaments, anthers lanceolate, sickle-shaped, thecae 9–10 mm long, apex rostrate, purple, pedoconnective ca. 2 mm long, basal crests minute, triangular or ligular, 1–2 mm long, lateral appendages paired, filiform, 4–5 mm long, white; oppositipetalous stamens with ca. 6 mm long filament, anthers thick, S-shaped, thecae 8–9 mm long, purple, basal crests minute, spur-like, erect, ca. 0.5 mm long, lateral appendages paired, filiform, 1–2 mm long, white. Ovary ⅔ of hypanthium in length, apex villous; style 8–10 mm long, curved at end, glabrous, light green; stigma minute, capitate; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits urceolate, 8–10 × 6–8 mm, densely covered with curved purplish-tip bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Borneo.

Ecology and habitat — Primary mixed Dipterocarp forest or low montane forest on river banks or in open places at 180–900 m elevation.

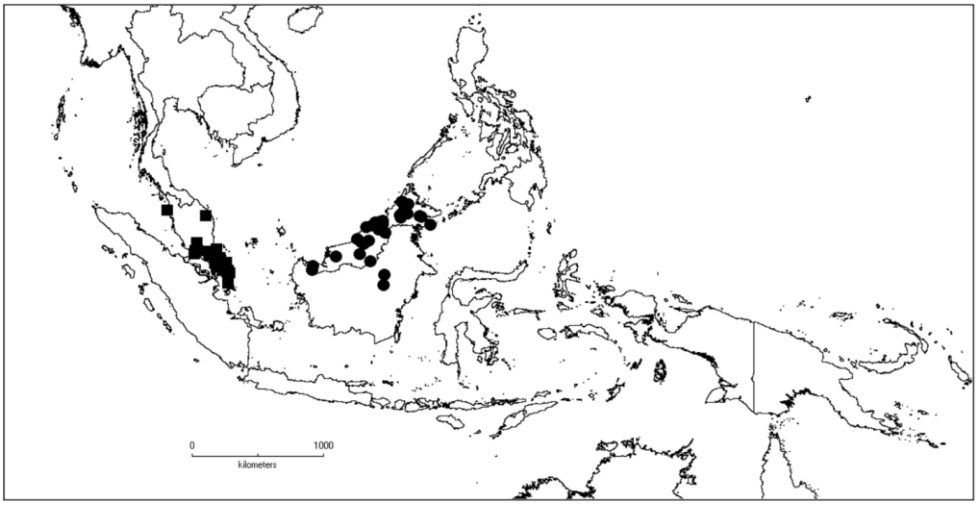
Vernacular name — *Bang derd* (Kenyah).

Note — The bristles in *D. porphyrocarpa* are distinct as they are eglandular, short and curved; they resemble those of *D. rostrata*. However, bracteoles in *D. porphyrocarpa* are caducous while persistent and conspicuous in *D. rostrata*.

Fig. 3-23. *Dissochaeta porphyrocarpa*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** alternipetalous stamen; **e.** oppositipetalous stamen; **f.** fruit. Photos by D.S. Penneys; voucher: *Penneys 2486* (WNC).

Specimens examined — **MALAYSIA.** Sabah: Keningau, Crocker Range, 15 Aug 1978, *Abas SAN 85957* (K, L); *Ibid.*, Witti Range Area, Ulu Sg. Mantuluk, 17 Jan 1986, *Asik SAN 113279* (K); Nabawan, 12 Nov 1973, *Dewol & Abdul Karim SAN 77955* (K, L); Kalabakan, Ulu Segama, 16 Dec 1982, *Fidilis SAN 95585* (L); Lahad Datu, Danum Valley, 238 m, 6 Jul 2006, *Rosalia et al. SAN 145988* (K, L); *Ibid.*, Ulu Segama, 16 Jul 1970, *Cockburn SAN 70925* (K, L); Nabawan, Ulu Sungai Nabawan, 21 Feb 1990, *Asik SAN 128382* (L); Pandewan, Mesopo River, 10 Mar 1986, *Sumbing & Asik SAN 114076* (K, L); Pinangah, Imbak River, 200 m, 1 Jul 2000, *de Wilde, Tajudin & Postar SAN 143959* (K); Ranau, Ulu Sg. Bidon, 19 Jul 1985, *Amin & Ismail SAN 110449* (K, L); *Ibid.*, Mt. Kinabalu, Gurulau Spur, 8 Nov 1915, *Clemens 10789* (PNH); *Ibid.*, Mt. Kinabalu, Gurulau Spur, 27 Nov 1915,

Clemens 10824 (PNH); *Ibid.*, Mt. Kinabalu, Dallas, 914 m, 7 Aug 1931, *Clemens 30359* (K, L); *Ibid.*, 11 Aug 1931, *Clemens 26058A* (BO); *Ibid.*, 31 Oct 1931, *Clemens 26028* (BM, BO, K, L); *Ibid.*, Nov 1931, *Clemens 30357* (BO, K, L); *Ibid.*, Ulu Tungud, 343 m, 27 Jul 2005, *Saw et al. SAN 146068* (L); Tawau, Oct 1922–Mar 1923, *Elmer 21426* (BM, BO, C, K, L, P, SING, U). Sarawak: Ulu Tawaran, 600 m, *Haviland 1287* (K); Tampassuk, near Kiau, 1066 m, *Haviland 1288* (K); Baram, Ulu Tinjar, Dulit Range, 365 m, 11 Aug 1974, *Chai S.34771* (K, L); Balleh, Mujong, N Semperaja, 200 m, 17 Apr 1964, *Othman S.19873* (K, L); Belaga, Sungai Semawat, 250 m, 19 Oct 1981, *Hansen 705* (L); Bintulu, Lumut Range, Ulu Sg. Gelang Bata, 250 m, 19 Sep 1992, *Mochtar & Yii S.65799* (K, L); *Ibid.*, Tubau, Bukit Sekiwa, 180 m, 4 Sep 1986, *Mochtar S.53996* (L); Kapit, Batang Balui, Sungai Jitang, 300 m, 28 Feb 1992, *Othman et al. S.62032* (L); Marudi, Pulong Tau National Park, Ulu Sungai Baong, 9 May 2007, *Sang et al. S.98016* (K); Miri, Lambir National Park, 27 Sep 1978, *George S.40438* (K); *Ibid.*, Gunung Mulu, Melinau Crossing, 200 m, 5 May 1978, *Argent & Coppins 1160* (BM); Padawan, Kampung Braang Wah, 300 m, 8 May 1975, *James et al. S.37410* (K, L); *Ibid.*, Bukit Woen, 350 m, 2 Oct 1987, *Yii S.61445* (K, L). **BRUNEI.** Belait: Labi, Mendaram Valley, 20 m, 23 Oct 1989, *Forman & Blewett 1034* (K, L); *Ibid.*, 18 Mar 1991, *Sands & Johns 5445* (K, L); *Ibid.*, Wong Kadir, 150 m, 19 Mar 1993, *Coode et al. 7227* (K, L). Temburong: Kuala Belalong, Batu Apoi, 17 Nov 1991, *Hansen 1579* (K, L); Temburong River Valley, 50 m, 27 Apr 1992, *Johns et al. 7389* (K, L). **INDONESIA.** East Kalimantan: West Kutai, River Kiauw, 700 m, 27 Oct 1925, *Endert 4660* (BO, L); *Ibid.*, Long Ibut, 150 m, 10 Nov 1925, *Endert 4754* (BO).



Map 3-23. Distribution of *D. porphyrocarpa* (●) and *D. punctulata* (■).

42. *Dissochaeta pubescens* (Merr.) Karton., **comb. nov.** — Map 3-24

Dalenia pubescens Merr., J. Straits Branch Roy. Asiat. Soc. 86: 338 (1922). — Lectotype (designated here): *M.S. Clemens 10301* (lecto A [A00072194!]), Malaysia, Sabah, Kiau, Mount Kinabalu, 4 Des 1915.

Anplectrum beccarianum Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 568. 1891. — *Diplectria beccariana* (Cogn.) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Dalenia beccariana* (Cogn.) M.P.Nayar, Kew Bull. 20: 157. 1966. — Lectotype (designated here): *O. Beccari PB 809* (lecto FI [FI008755!]; isolecto BR [BR5188895!], K [K000859574!, K000859575!]), Malaysia, Sarawak.

Dalenia furfuracea Ridl., Kew Bull. 1: 33. 1946. — Lectotype (designated by Nayar in Kew Bull. 20: 159. 1966): *G.D. Haviland & C. Hose 144* (lecto K [K000859506!]; isolecto BM [BM001190921!, BM001190922!], SING), Malaysia, Sarawak, Pengkulu Ampat.

Dalenia beccariana (Cogn.) M.P.Nayar var. *matangensis* M.P.Nayar, Kew Bull. 20: 158. 1966. — Type: *H.N. Ridley 12259* (holo K [K000859571!]; iso SING), Malaysia, Sarawak, Matang, Aug 1905.

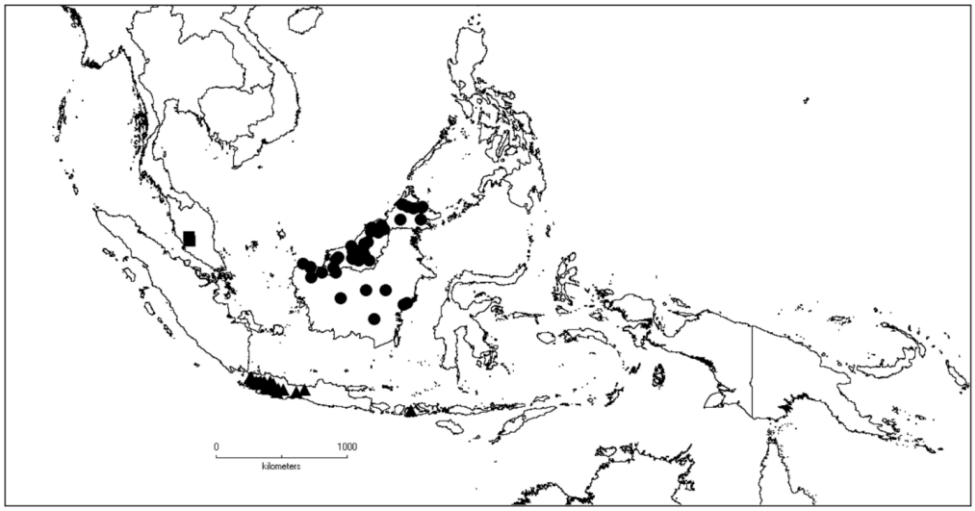
Climbing up to 20 m in height. Branchlets terete, 4–5 mm in diameter, covered with brown stellate-furfuraceous hairs; nodes swollen, with raised annular crest-like interpetiolar ridge, apex rounded, up to 6 mm high, densely covered with stellate hairs; internodes 8–21 cm long. Leaves: petioles terete, 15–35 mm long, densely brown stellate-furfuraceous; blades suborbicular, ovate to elliptic, (8–)15–30 × (4–)10–20 cm, subcoriaceous, base rounded to cordate, margin entire, apex acute or acuminate, tip 0.5–1 cm long; nervation with 1 or 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, glossy green, abaxially densely covered with brown pubescent hairs. Inflorescences terminal, up to 80 cm long, many-flowered; main axis angular, densely covered with brown stellate hairs; primary axes 35–76 cm long with 6–10 nodes, secondary axes up to 18 cm long with 2–4 nodes, tertiary axes up to 4 cm long with 1 or 2 nodes, quarternary axes when developed up to 8 mm long with 1 node; bracts either crest-like, erect, as wide as the rachis, 2–3 mm high or somewhat ligulate, 1.5–2 mm long, both types caducous, oftenly seen only on the terminal cymules; bracteoles linear or ligulate, 1–2 mm long, caducous; pedicels densely stellate-furfuraceous, brown, 9–10 mm long in central flowers, 5–8 mm long in lateral flowers. Hypanthium campanulate to suburceolate, 6–10 × 4–6 mm, covered with stellate pubescent hairs; calyx lobes truncate, without 4 distinct tips, ca. 0.5 mm long, forming calyptra enveloping petal buds, calyptra conical, up to 9 mm long, with acute tip, densely brown pubescent; petal buds conical, 7–8 mm long, apex acute; mature petals ovate, 7–8 × ca. 4 mm, base clawed, apex acute to obtuse, white to pink or purple. Stamens 8, unequal, filaments straight, white; alternipetalous stamens staminodial with 4–5 mm long filaments, anthers rudimentary, thecae ca. 2 mm long, slender, basal crest triangular 1–1.5 mm long, lateral appendages paired, thin, flat, filiform, 4–5 mm long; oppositipetalous stamens with 4–5 mm long filaments, anthers thick, curved, hooked- or S-shaped, thecae 8–9 mm long, apex rostrate, yellow, basal crest shortly triangular, ca. 0.5 mm long, lateral appendages absent or minute points. Ovary ⅔ of hypanthium in length, apex glabrous; style 13–15 mm long, curved at the end, slender, glabrous, white; stigma minute; extra-ovarial chambers 4, oppositipetalous, reaching to the base of the ovary. Fruits ovoid-urceolate, rarely subglobose, 10–12 × 6–8 mm, brown stellate-pubescent; calyx lobes remnant persistent, erect. Seeds ca. 0.5 mm long.

Distribution — Borneo.

Ecology and habitat — Lowland dipterocarp forest or low montane forest, roadside along the forest edges, river banks or logged forests at 25–900 m elevation.

Vernacular name — *Akar lagan* (Sintang).

Note — *Dissochaeta pubescens* is recognised by its robust leaf blades (up to 30 × 20 cm) and inflorescences (up to 80 cm long). The typical indumentum of most parts resembles that of *D. axillaris* and *D. latifolia*. In bud, the petals of *D. pubescens* are enclosed by a thin calyptra, which will fall off during anthesis. The calyptra is similar to that of *D. pulchra*. The epithet pubescens, the first available heterotypic synonym, is used here for the new combination name because an older *Dissochaeta beccariana* already exists.



Map 3-24. Distribution of *D. pubescens* (●), *D. rectandra* (■) and *D. vacillans* (▲).

Specimens examined — **MALAYSIA.** Sabah: Labuk Sugut, Bukit Timimbang, 21 Sep 1984, *Sigin et al. SAN 67567* (K); Lahad Datu, Ulu Segama, 14 Aug 1986, *Joseph SAN 116983* (K); Nabawan, Nabawan–Pandewan Road, 12 Mar 1990, *Sumbing SAN 128066* (K); Sandakan, Batu Lima, Sep-Dec 1920, *Ramos BS 1585* (BM, BO, K, L, P); Labuk Road, 137 m, 8 Dec 1971, *Dewol, Leopold & Shea SAN 74565* (K, L); Ranau, Mount Kinabalu, Kiau, 4 Dec 1915, *Clemens 10301* (A); *Ibid.*, Dallas, 914 m, 1 Oct 1931, *Clemens 26667* (BM, K, L); *Ibid.*, *Clemens 30389* (K, L); *Ibid.*, Ulu Tungud, Gunung Monkobo, 296 m, *Saw et al. SAN 146684* (L). Sarawak: 26 Oct 1894, *Haviland & Hose 144E* (L); 1871, *Beccari PB 809* (K); Kuching, Matang, Aug 1905, *Ridley 12259* (K); *Ibid.*, 17 Mar 1955, *Brooke 9714* (L); Pengkulu Ampat, *Haviland 144* (BM, K); Kapit, Balleh, Ulu Mujong, 26 Mar 1964, *Asah S.21200* (K); *Ibid.*, 17 Apr 1964, *Othman S.19946* (BO, K, L); Baram, Batang Tinjar, Ulu Sg. Sekiwa, 152 m, 1 Sep 1974, *Tong S.35025* (K, L); *Ibid.*, Mount Dulit, 300 m, 16 Aug 1932, *Richards 1301* (K, L); *Ibid.*, Ulu Sungai Melinau, 122 m, 24 Jun 1961, *Anderson S.4071* (K, L); Bintulu, Ulu Segan, 244 m, 24 Aug 1968, *Ilias Paie S.27216* (BO, K, L); Kapit, Bukit Raya, 518 m, 4 May 1969, *Soepadmo & Chai S.28175* (K, L); *Ibid.*, Pelagus, 7 Jul 1979, *Lee S.40230* (K, L); Limbang, Ulu Mendamit, Sg. Ensungei, 14 Sep 1980, *George et al. S.42897* (K, L); Lundu, Mount Poi, 1929, *Clemens 20270* (K); Miri, Gunong Mulu, Melinau Gorge, 375 m, 2 Feb 1978, *Hansen 244* (K); Marudi, Pulong Tau, 15 May 2007, *de Kok et al. S.97859* (K); Tatau, Batang Anap, 240 m, 12 Jun 1982, *Mochtar S.41775* (K, L); Betong, Bukit Sadok, 15 Oct 1982, *Banyeng & Ilias Paie S.45092* (K, L); Sibu, Ulu Sungai Pasai, Bukit Tanggi, 50 m, 29 Mar 1992, *Yii & Jegong S.64404* (K, L); Sri Aman, Batang Ai, 350 m, 12 Dec 1994, *Yii et al. S.69527* (L); Batang Balui, Ulu Sungai Elyak, 950 m, 12 Mar 1989, *Yii S.56745* (K); *Ibid.*, *Yii S.56746* (K); Tubau, Merurong, 16 Oct 1984, *Othman et al. S.48949* (K); *Ibid.*, Batu Laga, 960 m, 19 Mar 1989, *Yii S.56899* (AAU, L); Ulu Simunjan, G. Angkong, 23 Sep 1975, *Martin & Othman S.36955* (K, L). **BRUNEI.** Belait: Labi, Mendaram, 30 m, 20 Jun 1995, *Kalat et al. BRUN 16786* (K, L). Temburong: Pagon, 150 m, 22 Jul 1990, *Wong 1869* (K); Kuala Belalong, 25 m, 22 Jun 1989, *Boyce et al. 392* (K, L). Tutong: Ulu Tutong, Bukit Bahak, 210 m, 17 Dec 1991, *Kirkup et al. 578* (K). **INDONESIA.** Central Kalimantan: Barito Ulu, 25 May 1990, *Ridsdale PBU 185* (BO, L). East Kalimantan: West Kutai, Long Liang Beng, 250 m, 1 Sep 1925, *Endert 3060* (BO, K, L); Samarinda, ITCI concession area, 250 m, 7 Jun 1989, *van Balgooy 5840* (L); Wanariset, Samboja-Semoi road,

50 m, 7 May 1991, *Ambriansyah & Arifin W728* (K, L). West Kalimantan: Pontianak, Bentiang, Gunung Bayuh, 750 m, 31 Oct 1980, *Shea 27146* (BO, K, L); Sintang, Bukit Baka, Sungai Ella, 320 m, 21 Oct 1993, *Church et al. 273* (BO, L).

43. ***Dissochaeta pulchra*** (Korth.) J.F.Maxwell — Fig. 3-24, Map 3-22

Dissochaeta pulchra (Korth.) J.F.Maxwell, Gard. Bull. Singapore 33: 318. 1980. — *Dalenia pulchra* Korth. In Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. Tab. 58. 1842. — *Dalenia speciosa* Korth. In Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 244. 1844. — *Dalenia korthalsii* Blume, Mus. Bot. 1(3): 39. 1849. — Lectotype (designated here): *P.W. Korthals s.n.* (lecto L [L0537210!]; isolecto L [L0537211!, L0729471!, L0729472!, L0729473!], P [P02274827!]), Indonesia, Central Kalimantan, Kapoeas-Barito, Tewe Rivier.

Anplectrum macrophyllum Ridl., Kew Bull. 1: 31. 1946. — Lectotype (designated here): *C. Hose 478* (lecto K [K000859569!]; isolecto BM!, E [E00288103!, E00288104!], K [K000859570!], L [L0537213!], P [P02274828!], PNH [PNH24835!], SING), Malaysia, Sarawak, Baram, Pata River, Nov 1894.

Climbing up to 13 m in height. Branchlets terete, 2–3 mm in diameter, glabrous, smooth; nodes swollen, with pulvinate interpetiolar ridge, crest-like or laminar up to 5 mm wide, dark purple; internodes 11.5–15 cm long. Leaves: petioles flattened, 15–25 mm long, glabrous; blades ovate to suborbicular, 14–20 × 8.5–13 cm, membranous, base broadly cordate, margin slightly serrulate, apex acuminate, tip 1.5–2 cm long; nervation with 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous and partially scabrid, with a pair of glandular patches at base. Inflorescences terminal, up to 25 cm long, many-flowered; main axis angular, glabrous, purplish-blue; primary axes up to 13 cm long with 4 or 5 nodes, secondary axes 1–3 cm long with 1 or 2 nodes, tertiary axes 0.5–1 cm long with 1 node; bracts lanceolate, 6–10 mm long, furfuraceous, caducous; bracteoles subulate, 1–2 mm long; pedicels glabrous, 5–7 mm long in central flowers, 2–5 mm long in lateral flowers. Hypanthium campanulate-tubular, 8–9 × 3–4 mm, glabrous, purplish; calyx lobes truncate with undulate tips, 1–2 mm long, forming thin calyptra enveloping petal buds, calyptra conical, up to 8 mm long, with acute tip, glabrous, purple; petal buds conical, 4–6 mm long; mature petals ovate, 8–12 × 7–8 mm, reflexed, apex acute, base clawed, glabrous, white or white pinkish. Stamens 8, subequal, filaments curved sideways, white; alternipetalous stamens with 6–7 mm long filaments, anthers narrow, curved, sickle-shaped, thecae 8–10 mm long, bright yellow, pedoconnective ca. 0.5 mm long or undeveloped, basal crest thin, triangular or ligular, 0.8–1 mm long, lateral appendages paired, filiform, 1–2 mm long; oppositipetalous stamens with 6–7 mm long filaments, anthers S-shaped, thecae 7–8 mm long, thick, yellow, basal crest ligular or spur-like, ca. 0.5 mm long, lateral appendages paired, small auricles or bifid, ca. 1 mm long. Ovary half as long as hypanthium, apex glabrous; style slender, 12–14 mm long, reddish, turning white apically, glabrous; stigma minute, purple; extra-ovarial chambers 8, the 4 alternipetalous ones extending nearly to the base of the ovary, the 4 oppositipetalous ones extending to the middle of the ovary. Fruits ovoid-urceolate, 9–10 × ca. 7 mm, glabrous, blue-violet; calyx lobe remnants persistent, widened. Seeds ca. 0.75 mm long.

Distribution — Borneo.

Ecology and habitat — Primary or secondary forest, low montane forest, river banks in riparian forest at 80–1000 m elevation.

Vernacular names — *dangkong* (kadazan putatan); *buak penan* (Kenyah); *kunceng badak gaka* (Tunjung Benua).

Fig. 3-24. *Dissochaeta pulchra*. **a.** habit; **b.** branchlet; **c.** leaf node; **d.** infrutescence/inflorescence; **e.** flower. Photos by J. Henrot.

Notes — 1. *Dissochaeta pulchra* is easily 142ecognized by its thin, glabrous, ovate-suborbicular leaf blade with minutely serrulate margin; all other species have entire margins. The crest-like interpetiolar ridge is similar to *D. stipularis* and *D. pubescens*, but there are differences in shape and number of the fertile stamens. This species also has abaxially glandular patches at the base of the leaves similar to *D. beccariana*, *D. glabra*, *D. glandulosa* and *D. laevis*.

2. The epithet *pulchra* is considered as a valid name for the species as it is based on Korthals' plate 58, published in 1842, two years earlier than the description in which the epithet *speciosa* was used (Korthals 1844, Nayar 1966). Blume (1849) tried to settle the matter by

giving a new name, *D. korthalsii* to the species. It follows that *D. speciosa* and *D. korthalsii* are both superfluous names under the Code and are therefore illegitimate. Both *D. pulchra* and *D. speciosa* have been used by various authors, but *D. speciosa* appears to have been the most widely used (Nayar 1966).

Specimens examined — **MALAYSIA.** Sabah: Beaufort, Gunung Lumaku, 300 m. 5 Mar 1969, *Nooteboom 1138* (L); *Ibid.*, 6 Mar 1969, *Nooteboom 1198* (L); *Ibid.*, Halogilat, 10 May 1973, *Dewol & Karim SAN 77594* (L); *Ibid.*, Rayoh, 15 Aug 1972, *Saikeh SAN 72234* (L); Beluran, Bukit Luminitong, 11 Mar 1982, *Aban Gibot SAN 94467* (L); Kalabakan, Gunong Rara, 488 m, 15 Apr 1972, *Chow SAN 75687* (L); Keningau, Pinangah FR, 24 Sep 1985, *Asik SAN 110269* (K); *Ibid.*, Imbak River, 200 m, 6 Jul 2000, *de Wilde, Tajudin & Good SAN 143924* (K); Lahad Datu, Ulu Sungai Bole, 1 Mar 1988, *Dewol et al. SAN 123756* (L); Nabawan, Sungai Pingas-Pingas, 27 May 1986, *Fidilis & Asik SAN 115864* (L); Pensiangan, Ponontomon, 19 Aug 1994, *Asik SAN 139507* (L); Ranau, Kampung Monggis, 23 Feb 1998, *Rumutom 473* (K); *Ibid.*, Telupid, Tampias, 14 Dec 1974, *Aban & Kodoh SAN 81101* (L); Sandakan, Telupid-Ranau Road, 91 m, 15 Aug 1978, *Madani SAN 89206* (L); Sipitang, Muruk Miau, 175 m, 27 Apr 1997, *Kulip et al. SAN 133876* (L); Tenom, near Pangi, 150 m, 23 Dec 1968, *Kokawa & Hotta 2603* (L); *Ibid.*, Gunong Lumaku, 12 Sep 1991, *Maikin et al. SAN 132681* (L); *Ibid.*, Crocker Range, Rayoh, 26 Sep 1974, *Dewol & Karim SAN 78319* (L); Tongod, Maliau Valley, 250 m, 16 Jul 2001, *Postar, et al. SAN 144145* (L). Sarawak: Balleh, Ulu Mujong, Sungai Sebatang, 18 Apr 1964, *Othman S.21105* (BO, L); Baram, Pata River, Nov 1894, *Hose 478* (BM, L, P, PNH); *Ibid.*, Selungo, 25 Nov 1914, *Native Collector 2819* (PNH); *Ibid.*, Tinjar River, Sg. Bok, Long Teru, 50–100 m, 10 Mar 1969, *Hotta 6113* (L); Belaga, Linau, Sg. Bunut, 3 Nov 1982, *Lee S.45415* (L); *Ibid.*, Ulu Belaga, Sungai Semawat, 250 m, 17 Oct 1981, *Hansen 670* (L); *Ibid.*, Bukit Kuang, 900 m, 8 Mar 1989, *Yii S.56571* (L); *Ibid.*, Sungai Berangan, 600 m, 18 Aug 1995, *Pereira et al 246* (L); *Ibid.*, Batu Laga, 600 m, 24 Jun 1995, *Lai et al. S.72466* (K); *Ibid.*, Sungai Murum, 14 Aug 2001, *Yahud S.84494* (L); Kapit, Upper Rejang River, 1929, *Clemens 21140* (BO); *Ibid.*, *Clemens 21579* (BO); *Ibid.*, Batang Baleh, Sungai Serani, 200 m, 5 May 1991, *Runi, et al. S.63183* (K, L); *Ibid.*, Ulu Balui, 100-500 m, 17 Aug 1995, *Sugau 165B* (L); Maputi, 21 Jun 1955, *Brooke 10091* (BM, L); Marudi, Bok-Tisam, Bukit Mentagai, 122 m, 10 May 1965, *Sibat S.23280* (L); *Ibid.*, Pulong Tau National Park, Long Lobang River, *de Kok et al. S.97859* (K). **BRUNEI.** Temburong: Kuala Belalong, Batu Apoi Forest Reserve, 20 Nov 1991, *Hansen 1593* (L); *Ibid.*, Bukit Gelagas, 350 m, 20 Oct 1991, *Simpson & Marsh 2510* (L). **INDONESIA.** Central Kalimantan: Tewe River, *Korthals s.n.* (L, P). East Kalimantan: Sungai Bocleng, 1898, *Amdjah 115* (BO); Pamaluan, *Rutten 103* (U); West Kutai, Long Gemelei, 200 m, 28 Aug 1925, *Endert 2933* (BO, L); *Ibid.*, Long Puhus, 80 m, 9 Aug 1925, *Endert 2425* (BO, L); *Ibid.*, Mahakam Ulu, Hulu Riam Halo, 100 m, 28 Jun 1975, *Wiriadinata 691* (BO); *Ibid.*, Tabang, 160 m, 20 Dec 1980, *Kato & Wiriadinata B-7131* (BO, L); *Ibid.*, Gunung Kongkat–Gunung Kongbotak, 29 Jan 1981, *Kato & Wiriadinata B-5202* (L); Kutai National Park, Kayu Mas, 130 m, 25 Jul 1986, *Tagawa, Suzuki & Miyagi 077* (BO); *Ibid.*, 200 m, 19 Aug 1986, *Tagawa, Suzuki & Miyagi 587* (BO); Balikpapan, Kenangan, 700 m, 13 Aug 1974, *Dransfield 4414* (BO, L); Sangkulirang, Karangan River, Batu Pondong, 100 m, 3 Sep 1957, *Kostermans 13690* (BO, L); Sebulu, 28 Dec 1978, *Murata et al. B-587* (BO); *Ibid.*, *Murata et al. B-600* (BO, L); Kenangan, PT ITCI Area, 100 m, 1 Mar 1991, *Sidiyasa 719* (K, L); Berau, Inhutani I area, 175 m, 6 Oct 1996, *Kessler et al. Berau 128A* (L); Sungai Nakan, 13 Jun 1986, *Arbainsyah AA1921* (BO). North Kalimantan: Long Bawan, Krayan, 1100 m, 28 Jul 1981, *Kato, Okamoto & Walujo B-10052* (BO, L); Bulungan, Seturan River, 200 m, 5 Oct 1999, *Ismail & Arifin BRF 1714* (BO); Malinau, Pujungan, Kayan Mentarang National Park, 1000 m, 24 Jul 1992, *McDonald & Ismail 3600*

(BO, L); *Ibid.*, 200-500 m, 5 Apr 2002, *Koizumi & Lalo 317* (BO, L); Ulu Sebuku, Aug 1912, *Amdjah 404* (BO, L). South Kalimantan: Tabalong, 750 m, 6 Jul 2000, *Sidiyasa & Arifin 2010* (L). West Kalimantan: Sungai Blu'u, 1896, *Jaheri 1104* (BO); Penigin, 1896, *Jaheri 330* (BO).

44. *Dissochaeta punctulata* Hook.f. ex Triana — Map 3-23

Dissochaeta punctulata Hook.f. ex Triana, Trans. Linn. Soc. London 28: 83. 1872. — Lectotype (designated here): *W. Griffith KD 2291* (lecto K [K000859531!]; isolecto BM!), Malaysia, Peninsular Malaysia, Malacca.

Climbing up to 27 m in height. Branchlets terete, 3–5 mm in diameter, sparsely furfuraceous with minute red-brown hairs; nodes swollen, with interpetiolar line; internodes 2–7 cm long. Leaves: petioles terete, 5–15 mm long, striate, glabrescent; blades ovate or ovate-elliptic, 4.2–11 × 2.5–5.5 cm, subcoriaceous, base rounded to cuneate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially sparsely stellate punctate. Inflorescences terminal and in the upper leaf axils, up to 15 cm long, many-flowered; main axis densely stellate-furfuraceous; primary axes 15–20 cm long with 4–6 nodes, secondary axes 3–10 cm long with 2–4 nodes, tertiary axes 1–2 cm long with 1 or 2 nodes; bracts linear, ca. 4 mm long, densely furfuraceous, caducous; bracteoles linear, 2–3 mm long, densely furfuraceous, caducous; pedicels densely furfuraceous, 2–3 mm long in central flowers, 1–2 mm long or subsessile in lateral flowers. Hypanthium campanulate, but urceolate to subglobose at first stage, enclosing the petal bud, 6–10 × 5–6 mm, densely red-brown tomentose; calyx lobes triangular with acute tips, 1–2 mm long, densely stellate-furfuraceous, densely pubescent inside; petal buds conical, 2–4 mm long; mature petals obovate, ca. 10 × 5–7 mm, reflexed, base clawed, apex rounded, glabrous with ciliate margin, white. Stamens 8, unequal to subequal, filaments curved sideways, white yellowish; alternipetalous stamens with (5–)9–10 mm long filaments, anthers curved, sickle-shaped, slender, thecae 9–12 mm long, flexed, maroon, pedoconnective 3–4 mm long, basal crest fimbriate, somewhat branched, 4–5 mm long, lateral appendages paired, filiform or fimbriate, 7–8 mm long; oppositipetalous stamens with 5–8 mm long filaments, anthers S-shaped, thick, thecae 7–8 mm long, yellow, basally erose or bifid or with a fimbriate crest, somewhat branched, 3–5 mm long, lateral appendages paired, irregularly filiform, 6–8 mm long. Ovary ¾ of hypanthium in length, apex villous; style slender, 5–8 mm long, curved at top, white; stigma minute, villous; extra-ovarial chambers absent or not developed. Fruits urceolate or subglobose, 8–10 × 4–7 mm, sparsely to densely furfuraceous; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Malay Peninsula and Sumatra (Riau Archipelago).

Ecology and habitat — Disturbed lowland primary forest or secondary forest at 300–600 m elevation.

Vernacular name — Peninsular Malaysia: *akar muroyan busuh* (Malacca).

Specimens examined — **MALAYSIA.** Johor: Feb 1890, H.N. Ridley 2016 (BM); Puiron, Nov 1891, *Cantley 62* (K); Gunung Pulai, 24 Apr 1922, *Nur & Kiah SFN 7799* (BO, K); *Ibid.*, 18 Dec 1922, *Best SFN 7849* (BO); *Ibid.*, 4 Sep 1971, *Chan FRI 17660* (K, L); *Ibid.*, 550 m, 29 Jan 1978, *Maxwell 78-23* (L); *Ibid.*, 500 m, 18 Jan 1981, *Maxwell 81-15* (L); Bukit Paloh, 30-60 m, 9 Apr 1958, *Shah & Kadim 431* (K, L); Endau, Kampong Hubong, 18 Jul 1959, *Kadim & Noor 357* (BO, K); Mawai-Jemaluang Road, 5 May 1935, *Corner SFN 29377* (BO, K); Labis, 27 Apr 1986, *Saw FRI 34336* (K, L). Malacca: *Griffith s.n.* (BO, K, L, P); *Griffith KD 2291* (BM, K); *Hervey s.n.* (BM); 16 May 1886, *Maingay KD 789 (1220A)* (K, L); Sungai Hudang, 1892, *Ridley 548* (BM, K). Negri Sembilan: Tebong, 19 Jan 1917, *Ridley*

s.n. (K); Jelebu, Pasoh Forest, 80-120 m, 10 May 1996, *Gardette 1850* (K, L); *Ibid.*, *Gardette 1850B* (K, L). Penang: *Walker 30* (BM, K). Terengganu: Gunong Padang, Ulu Brang, 600 m, 23 Sep 1969, *Whitmore FRI 12786* (K, L); *Ibid.*, *Whitmore FRI 12794* (K, L). **SINGAPORE.** *Cantley s.n.* (BM); Bukit Timah, 21 Sep 1890, *Ridley 3858* (BM, L); *Ibid.*, 24 Feb 1977, *Maxwell 77-88* (L); Changi, 26 May 1891, *Ridley s.n.* (BM); Punggol, Mar 1878, *Hullett 505* (K); Pierce Reservoir, 25 Jun 1955, *Sinclair SFN 40649* (BO, K, L, P); *Ibid.*, 13 May 1981, *Maxwell 81-91* (L); Tanjong Gul, 5 Feb 1950, *Sinclair s.n.* (L, P); Bukit Mandai, 1893, *Anon 4803* (BM); Seletar, 22 Jul 1892, *Ridley 3918* (BM). **INDONESIA.** Riau Archipelago: Lingga Islands, Rejai Island, 20 m, 19 Aug 1919, *Bünnemeijer 7633* (BO, K, PNH); Senggarang Island, *Teijsmann s.n.* (BO, L); Bintan Island, Tanjung Pinang, *Teijsmann s.n.* (BO); *Ibid.*, Gunung Bintan, 300 m, 19 Jun 1919, *Bünnemeijer 6162* (BO); *Ibid.*, Mount Kijang, 25 m, 30 Jun 2013, *Girmansyah 1847* (BO).

45. *Dissochaeta rectandra* Karton., **sp. nov.** — Fig. 3-25, Map 3-24

Type: *J.C. Carrick 1606* (holo L [L2533494!]; isotypes: K!, KLU, L [L2533495!], SING), Malaysia, Pahang, Fraser's Hill, 3 Aug 1967.

Diagnosis. Resembles *D. bakhuizenii* Veldkamp. Leaf blade margin entire or thinly serrate with glabrous to sparsely stellate punctation below. Hypanthium campanulate-angular, 6–8 × 3–3.5 mm, glabrescent to sparsely stellate-puberulous, calyx lobes truncate with 4 small undulate points, 1–1.5 mm long, glabrous outside, stellate-furfuraceous inside. Stamens 8, subequal, filaments and anthers straight upwards, alternipetalous stamens with triangular basal crest and paired, filiform, lateral appendages, oppositipetalous stamens with ligular basal crest and paired filiform appendages. Fruits with mammiform apex.

Climbing up to 7.5 m. Branchlets terete, 3–5 mm in diameter, glabrescent; nodes swollen, interpetiolar ridge distinct with annular crest-like ridge; internodes 5–12 cm long. Leaves: petioles flattened, 10–23 mm long, stellate-punctate; blades elliptic or ovate-elliptic, 9.5–18 × 5–9.2 cm, membranous, base rounded to slightly cuneate, margin entire or thinly serrate, apex acuminate, tip 1–2 cm long; nervation with 1–2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark green, abaxially glabrous to brownish stellate-punctate, maroonish and glabrous when young. Inflorescences terminal, up to 40 cm long, many-flowered; main axis terete, glabrescent to sparsely stellate-puberulous; primary axes up to 33 cm long with 5 or 6 nodes, secondary axes up to 10 cm long with 3 or 4 nodes, tertiary axes 1–2.5 cm long with 1 or 2 nodes, quarternary axes when developed up to 0.8 cm long with 1 node; bracts linear, 2–2.5 mm long, stellate-furfuraceous, caducous; bracteoles subulate, 1–1.5 mm long, stellate-furfuraceous; pedicels stellate-furfuraceous, 4–6 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium campanulate-angular, 6–8 × 3–3.5 mm, glabrescent to sparsely stellate-puberulous; calyx lobes truncate with 4 small undulate points, 1–1.5 mm long, glabrous outside, stellate-furfuraceous inside; petal buds conical, 4–9 × 2–3 mm, glabrous; mature petals obovate to suborbicular, 10–11 × 8–9 mm, base clawed, margin ciliate, apex rounded, glabrous, pink to dark purple. Stamens 8, subequal, filaments straight, white pinkish; alternipetalous stamens with 8–9 mm long filaments, anthers lanceolate, thecae 7–8 mm long, straight, yellow, pedoconnective 1.5–2 mm long, basal crests triangular, 1–1.5 mm long, acute, lateral appendages prolonged from basal crest, paired, filiform, 2–2.5 mm long; oppositipetalous stamens with filaments 7–8 mm long, bent at top, anthers oblong-lanceolate, thecae 6–7 mm long, straight, yellow, basal crest ligular, 1–1.5 mm long, apex narrow, lateral appendages paired, filiform, 2–3 mm long.

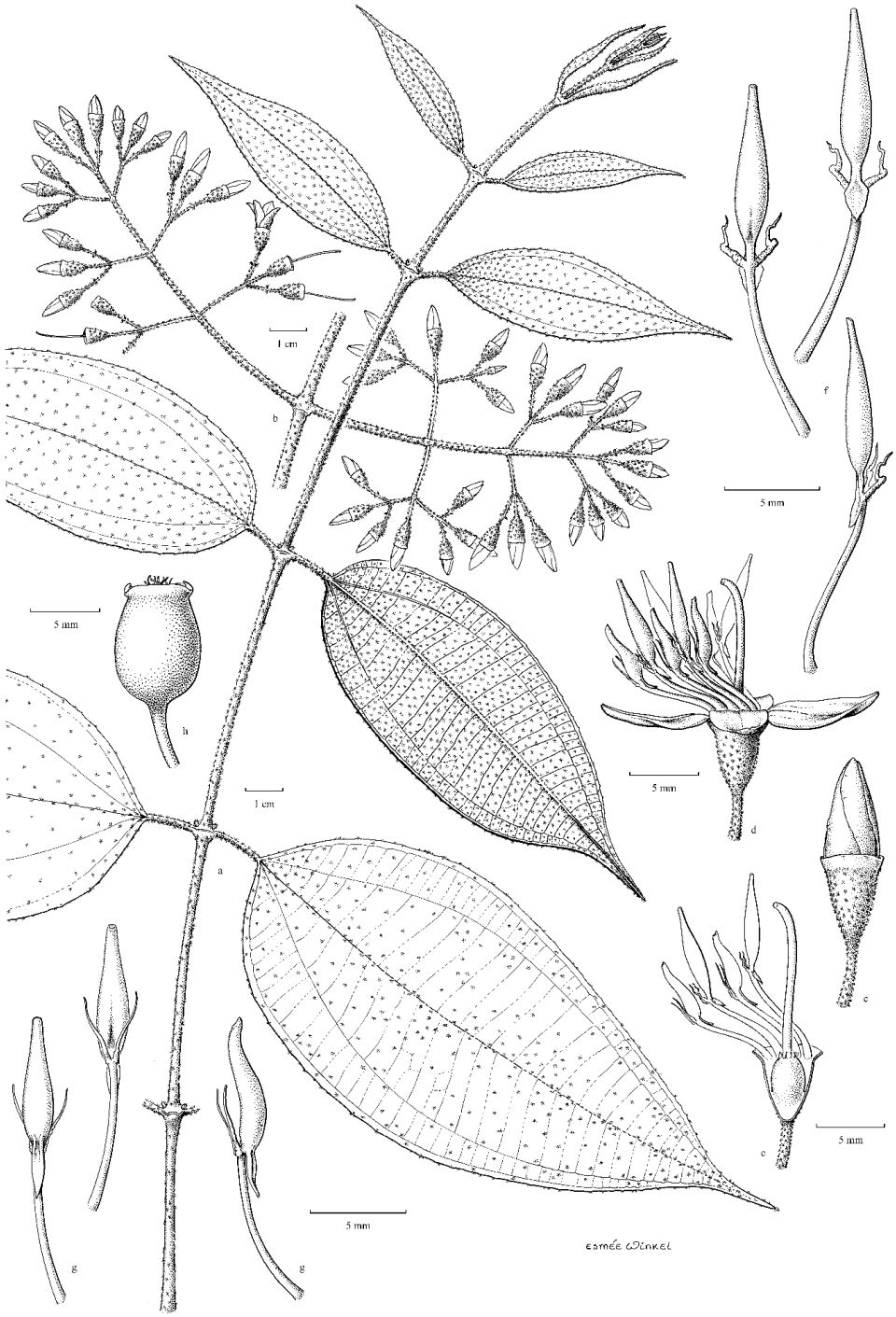


Fig. 3-25. *Dissochaeta rectandra*. **a.** habit; **b.** inflorescence; **c.** hypanthium; **d.** open flower; **e.** ovary; **f.** alternipetalous stamens; **g.** oppositipetalous stamens; **h.** fruit. [drawn from *Carrick 1606* (L)].

Ovary half as long as hypanthium, apex pubescent, bristly; style 12–13 mm long, straight, curved at top, glabrous; stigma minute, capitate; extra-ovarial chambers 8, extending from the middle to the base of the ovary. Fruits urceolate, 8–10 × 6–9 mm, apex mammiform, bristly, rest glabrous; calyx lobes persistent, erect. Seeds ca. 0.5 mm long.
Distribution — Peninsular Malaysia (Selangor and Pahang).
Ecology and habitat — Montane forest, open areas along road sides at 1280–1800 m elevation.
Etymology — The species is named after the orientation and shape of its stamens, erect, straight upwards when mature.
Note — *Dissochaeta rectandra* resembles *D. bakhuizenii* in having 8 fertile stamens, a triangular basal crest (alternipetalous) and ligular basal crest (oppositipetalous). *Dissochaeta rectandra* has thinly serrate leaf margins, large flowers and longer lateral appendages on the stamens (vs. entire margins of leaf blades, smaller flowers and short to absent lateral appendages in *D. bakhuizenii*). This species is restricted to the montane forest of Fraser's Hill (Pahang) and the Genting Highlands (Selangor).
Specimens examined — **MALAYSIA.** Pahang: Fraser's Hill, 3 Aug 1967, *Carrick 1606* (K, L); *Ibid.*, Richmond, 1280 m, 16 Apr 1955, *Purseglove 4112* (L). Selangor: Genting Highlands, Gunong Ulu Kali, 1800 m, 3 Jun 1978, *Maxwell 78-307* (L); *Ibid.*, 1500 m, 3 Jun 1978, *Maxwell 78-312* (L).

46. *Dissochaeta rostrata* Korth. — Map 3-25

Dissochaeta rostrata Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844) — *Anplectrum korthalsii* Triana, Trans. Linn. Soc. London 28: 85. 1872. — *Diplectria korthalsii* (Triana) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated here): *P.W. Korthals s.n.* (lecto L [L0729470!]; isolecto L [L0729469!]), Indonesia, South Kalimantan, G. Prarawin.

Dissochaeta hirsuta Hook.f. ex Triana, Trans. Linn. Soc. London 28: 83. 1872. — *Dissochaeta rostrata* Korth. var. *hirsuta* (Hook.f. ex Triana) J.F.Maxwell, Gard. Bull. Singapore 33: 319. 1980. — Type: *J. Motley s.n.* (holo K [K000859629!]), Malaysia, Sarawak, Labuan.

Dissochaeta setosa O.Schwartz, Mitt. Inst. Allg. Bot. Hamburg 7: 250. 1931. — *Dissochaeta rostrata* Korth. var. *setosa* (O.Schwartz) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — Lectotype (designated here): *J. Winkler 1167* (lecto HBG [HBG522818!]; isolecto BO [BO1747972!], HBG [HBG522819!, HBG522820!], L [L0008893!]), Indonesia, West Kalimantan, Lebang Hara 150 m elev., 1 Jan 1925.

Macrolenes ruttenii Bakh.f., Contr. Melastom. 210. 1943. — Type: *L.M.R. Rutten 535* (holo U [U0004012!]), Indonesia, East Kalimantan, Samarinda, Soengei Boengaloen, 12 Nov 1911.

Climbing up to 8 m in height. Branchlets terete, 2–4 mm in diameter, sparsely brown puberulous and densely covered with 1–2 mm long bristle hairs; nodes swollen, with interpetiolar ridge, thickly covered with bristle hairs; internodes 7–7.5 cm long. Leaves: petioles terete, 8–18 mm long, densely covered with bristle hairs; blades ovate, ovate-elliptic to elliptic, 7.5–14 × 3.8–9 cm, membranous, base emarginate, margin entire, apex acuminate, tip ca. 1 cm long; nervation with 2 pairs of lateral nerves and 1 pair of intramarginal nerves; adaxially hirsute, covered with scattered bristle hairs, abaxially densely covered with bristle hairs in most part, more densely so at midrib and margins. Inflorescences terminal, up to 25 cm long, manyflowered; main axis terete, densely covered with bristle hairs; primary axes up to 15 cm long with 4 nodes, secondary axes 2–4 cm long with 2 or 3 nodes, tertiary axes up

to 1 cm long with 1 node; bracts oblong-lanceolate, 15–17 × ca. 5 mm, sparsely stellate puberulous and with dense bristle hairs, thin; bracteoles oblong, 4–7 × 2–3 mm, sparsely stellate puberulous and margin with dense bristle hairs; pedicels densely stellate-furfuraceous and with bristle hairs, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate or suburceolate, ca. 4 × 2.5–3 mm, densely covered with brown stellate hairs and bristle hairs; calyx lobes subtriangular or oblong, 2–2.5 mm long, apex obtuse, densely bristly at margin, pinkish to purplish; petal bud conical, 2–3.5 mm long, apex bristly; mature petals obovate or suborbicular, 5–6 × 4–5 mm, not-reflexed, base clawed, apex rounded, glabrous, veined, purple, light purple or pink. Stamens 8, subequal, filaments curved sideways, pale yellow; alternipetalous stamens with 4–5 mm long filaments, anthers lanceolate, sickle-shaped, thecae 5–6 mm long, apex rostrate, purple, pedoconnective ca. 2 mm long, basal crests minute, thin, ca. 0.5 mm long, lateral appendages paired, wavy, filiform, 1–2 mm long, white; oppositipetalous stamens with 4–5 mm long filaments, anthers thick, S-shaped, thecae 4–5 mm long, basal crest minute, ca. 0.5 mm long, lateral appendages paired, filiform, ca.1 mm long, white. Ovary ⅔ of hypanthium in length, apex villous; style curved at end, 10–11 mm long, glabrous, white; stigma minute, capitate; extra-ovarial chambers 8, extending to the middle of the ovary. Fruits subglobose or ovoid, 5–6 × 3–5 mm, densely covered with bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Borneo.

Ecology and habitat — In mixed lowland dipterocarp forest, open areas at margin of forest and in riverine forest at 50–200 m elevation.

Vernacular name — *akar kemunting* (Iban).

Notes — 1. *Dissochaeta rostrata* can easily be distinguished from other species with a bristly indumentum by its oblong-lanceolate bracts and bracteoles and subtriangular-oblong calyx tube.

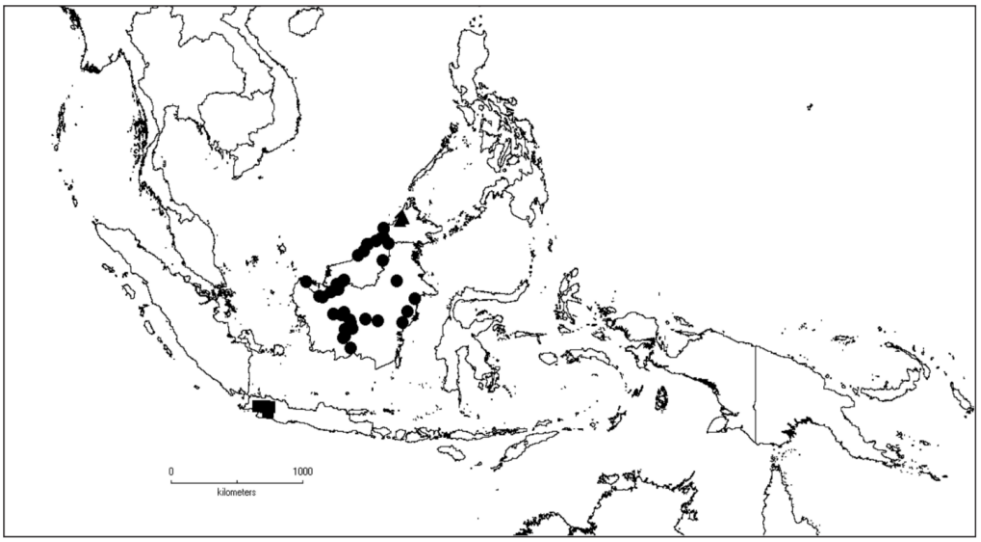
2. The type collection (*Korthals s.n.*) from Leiden is only vegetative with mature leaves. The type of *D. hirsuta* (*Motley s.n.*) from Kew consists of a fruiting branch with mature leaves. The appearance of both is similar (shape and indumentum on the leaf blades), therefore we consider them to indicate the same species and we synonymise *D. hirsuta* with *D. rostrata*, an action following Veldkamp & Nayar (1979).

3. *Dissochaeta setosa* (type *Winkler 1167*), which is also limited to Borneo, has fruits that are similar to *D. hirsuta* with the distinct subtriangular-oblong calyx lobe remnants, hence we also included *D. setosa* in the species concept of *D. rostrata*.

4. Maxwell (1980b) recognised several species with a bristly indumentum as varieties of *D. rostrata* and made the species concept of the latter much wider. Here we consider them to represent distinct species: *D. alstonii*, *D. densiflora*, *D. floccosa*, *D. horrida*, *D. macrosepala*, *D. malayana* and *D. porphyrocarpa*.

Specimens examined — **MALAYSIA.** Sarawak: Parai, 11 Dec 1892, *Haviland 2036* (BM, K); Bintulu, Bukit Urang, 30 m, 7 Dec 1959, *Brunig S.11981* (K); Kuching, *Bartlett s.n.* (BM); Lubok Antu, River Delok, Nanga Sumpa, 150 m, 27 Feb 1993, *Christensen 1244* (K), Lubok Antu, Lanjak Entimau, 14 Mar 1974, *Chai S.33819* (K); Kapit, Ulu Katibas, Sg. Joh, 110 m, 27 Jun 1993, *Zainudin 4535* (L); *Ibid.*, 150 m, 15 Nov 1997, *Pearce et al. ITTO/BB 0431* (BO); Lawas, 22 May 1955, *Brooke 10034* (BM, L); Lundu, Mt. Gading, 100 m, 19 Jul 1963, *Chew 597* (K, L); Marudi, Long Tukan, 13 Mar 1972, *Othman, Jugah & Anyie S.31862* (K, L); Miri, Lambir National Park, 8 May 1966, *Banyeng S.25084* (BO, K, L); *Ibid.*, Ulu Sungei Lepoh, 18 Sep 1978, *George S.40264* (L); Labuan, *Motley s.n.* (K); Niah, Niah River, 4 Apr 1979, *Yii S.40124* (L). **BRUNEI.** Belait: Jalan Merangking-Buau, 10 Aug 1991, *Nangkat 251* (K, L). Temburong: Batu Apoi, Selapon, 30 m, 27 Jan 1994, *Coode et al. 7912*

(L). **INDONESIA.** Central Kalimantan: Sungai Mentaya, 50 m, 1 Aug 1993, *Wilkie 93374* (BO, E, K, L); *Ibid.*, *Tuke P1 1000* (L); *Ibid.*, *Tuke P5 1010* (L); Kapuas, Kayu Mas, 130 m, 24 Apr 1979, *Kessler et al. 1461* (BO, L); Sampit River, Kuala Kuayan, 20 m, 1 Aug 1953, *Kostermans 8045* (BO, L); *Ibid.*, 27 Nov 1982, *Afriastini 427* (BO); *Ibid.*, Permantang, 50 m, 27 Jan 1954, *Alston 13375* (BM); *Ibid.*, 4 Apr 1984, *Hansen 1366* (L); Bukit Raya, Tumbang Samba, 200 m, 27 Nov 1982, *Mogea & de Wilde 3716* (BO, L); *Ibid.*, 19 Dec 1982, *Nooteboom 4370* (BO, L); *Ibid.*, Batu Badinding, 23 Dec 1982, *Mogea & de Wilde 4376* (BO, L); *Ibid.*, Tumbang Tubus, 150 m, 6 Jan 1983, *Veldkamp 8076* (BO, L). East Kalimantan: Sangata, Mentoko River, 300 m, 24 Jan 1979, *Leighton 433* (L); Sebulu, 10 Aug 1973, *Kartawinata 1185* (BO, L); *Ibid.*, 27 Dec 1978, *Murata et al. B-459* (BO, L); Road Kenangan to Gunung Meratus, 400 m, 27 Mar 1995, *Kessler et al. 913* (P); Samarinda, Bengalon, 12 Nov 1911, *Rutten 535* (U); West Kutai, Long Petah, 450 m, 16 Sep 1925, *Endert 3360* (BO). South Kalimantan: Mount Prarawin, *Korthals s.n.* (L). West Kalimantan: Sintang, 150 m, 11 Apr 1994, *Mahyar et al. 832* (BO, L); *Ibid.*, Sungai Posang, 110 m, 30 Apr 1994, *Mahyar et al. 1229* (BO, L); *Ibid.*, Tegua Tibun, 75 m, 16 Oct 2000, *Albertus & Sidiyasa 2236* (L); Lebang Hara, 150 m, 1 Jan 1925, *Winkler 1167* (BO, L); Sanggau, Noyan, Ngira, 20 Feb 1994, *de Jong 749* (BO, L); Katingan-Seruyan, 213 m, 26 Jul 2011, *Susanti et al. 264* (BO).



Map 3-25. Distribution of *D. rostrata* (●), *D. rubiginosa* (▲) and *D. sagittata* (■).

47. *Dissochaeta rubiginosa* Stapf — Map 3-25

Dissochaeta rubiginosa Stapf, J. Linn. Soc., Bot. 42: 79. 1914. — Type: *L.S. Gibbs 3977* (holo K [K000859491!]), Malaysia, Sabah, Ranau, Mount Kinabalu, Gurulau Spur, 5500 ft elev., Feb 1910.

Branchlets terete, 3–5 mm in diameter, covered with densely stellate-furfuraceous hairs; nodes swollen, interpetiolar ridge raised; internodes 3.5–10 cm long. Leaves: petiole terete, 10–15 mm long, densely stellate-furfuraceous; blade elliptic-oblong or oblong, 7–11 × 2–4.8 cm, membranous, base rounded or cuneate, margin entire, apex acuminate, tip 0.5–1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, dark glossy green, abaxially brown, stellate-furfuraceous. Inflorescences terminal and in the

upper leaf axils, cymous, with many flowers, 17–25 cm long; main axis angular densely stellatefurfuraceous; primary axes up to 23 cm long with 5–7 nodes, secondary axes 2–9 cm long with 2–5 nodes, tertiary axes 0.7–1.8 cm long with 1 or 2 nodes; bracts and bracteoles minute, less than 2 mm long, densely stellate-furfuraceous, caducous; pedicel densely stellate-furfuraceous, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium urceolate, 3–4 × 1–1.5 mm, densely stellate-furfuraceous; calyx lobes truncate with 4 triangular tips or occasionally slightly free triangular lobes, ca. 1 mm long; petal bud conical, 3–5 mm long, glabrous; mature petals oblong, 5–6 × ca. 2 mm, glabrous, red, base clawed, apex acute. Stamens 4, equal, filaments straight; alternipetalous stamens with 4–5 mm long filaments, anthers oblong or lanceolate, thecae ± straight, 4–5 mm long, pedoconnective short or slightly undeveloped, ca. 0.5 mm long, basal crest triangular, up to 1 mm long, lateral appendages paired, filiform, of unequal length, ca. 2 mm long at one side, 1–1.5 mm long on the other side. Ovary ¾ of hypanthium in length, apex villous; style glabrous, 7–10 mm long, straight but slightly curved apically; stigma capitate; extra-ovarial chambers 4, alternipetalous, shallow, reaching to ca. ⅓ of ovary. Fruits ovoid-urceolate, 5–6 × 3–3.5 mm, glabrescent, calyx remnant persistent up to 2 mm long. Seeds ca. 0.5 mm long.
Distribution — Borneo (Sabah).
Ecology and habitat — Montane forest at 900–1670 m elevation.
Note — *Dissochaeta rubiginosa* resembles *D. angiensis* in indumentum and number of stamens, but differs by having more distinct triangular calyx lobes. The erect persistent calyx on the fruits is also different from *D. angiensis*. Stapf & Green (1914) mention the collections *Wallich 4052* from Penang and *Helfer 2286* from Myanmar and refer them to this species. However, both specimens have a shorter (<3 mm long) campanulate hypanthium rather than the urceolate and long hypanthium (3–4 mm long) of *D. rubiginosa* and both are identified as *D. biligulata* in this revision. The flower petals were recorded as red, a colour uncommon in the genus (Stapf & Green 1914).
Specimen examined — **MALAYSIA.** Sabah: Ranau, Mount Kinabalu, Gurulau Spur, 1670 m, *Gibbs 3977* (K); *Ibid.*, Marai Parai spur, 22 Nov 1915, *Clemens 10941* (PNH); *Ibid.*, Dallas, 900 m, *Clemens 26058A* (K, L); *Ibid.*, Sosopodon, 1500 m, *Gintus SAN 56381* (K, L); *Ibid.*, *Kokawa & Hotta 5190* (L); Tambunan, Mt. Alab, *Kokawa & Hotta 2089* (L).

48. *Dissochaeta sagittata* Blume — Map 3-25

Dissochaeta sagittata Blume, Flora 14: 500. 1831. — *Dissochaeta intermedia* Blume var. *sagittata* (Blume) J.F.Maxwell, Gard. Bull. Singapore 33: 315. 1980. — Lectotype (designated here): *C.L. Blume 11* (lecto L [L0537226!]; isolecto L [L0537228!]), Indonesia, Java, Bantam.

Climbing up to 7 m in height. Branchlets terete, 3–4 mm in diameter, densely stellate-furfuraceous; nodes swollen, with interpetiolar ridge, covered by stellate-furfuraceous hairs; internodes 6–7 cm long. Leaves: petioles flattened, 10–15 mm long, densely stellate-furfuraceous; blades oblong, 8.5–13 × 3–4.5 cm, membranous, base rounded, margin entire, apex acuminate, tip ca. 1 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely brown stellate-furfuraceous. Inflorescences terminal and in the upper leaf axils, up to 30 cm long, many-flowered; main axis quadrangular, densely stellate-furfuraceous; primary axes up to 26 cm long with 5 or 6 nodes, secondary axes 3–6 cm long with 2 or 3 nodes, tertiary axes up to 0.8–2 cm long with 1 or 2 nodes; bracts oblong to lanceolate, 9–10 × 2–3 mm, stellate-furfuraceous; bracteoles lanceolate, 4–6 mm long, stellate-furfuraceous, distinctly nerved; pedicels densely stellate-furfuraceous, 4–7 mm long in central flowers, 2–5 mm long in lateral flowers. Hypanthium

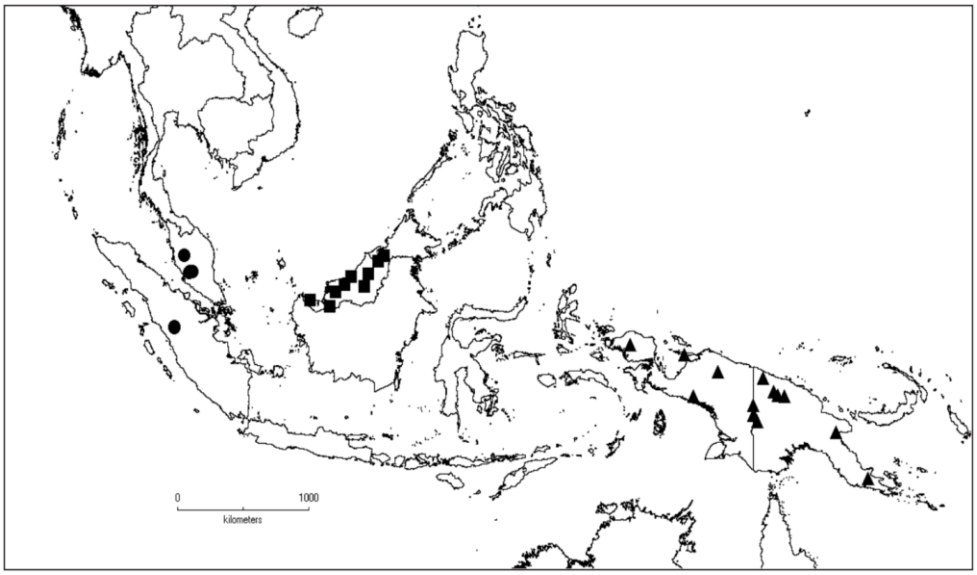
campanulate, 4–7 × 3–5 mm, densely stellate-furfuraceous; calyx lobes truncate with 4 more or less triangular tips, ca. 1 mm long, stellate-furfuraceous; petal buds conical, 2–8 mm long; mature petals oblong, 9–11 × ca. 4 mm, base clawed, apex obtuse, glabrous, red to pinkish-red. Stamens 8, unequal, filaments straight; alternipetalous stamens with ca. 6 mm long filaments, anthers lanceolate, thecae 6–7 mm long, straight, pedoconnective 1–1.5 mm long, basal crest triangular, hastate to sagittate, ca. 1.5 mm long, lateral appendages paired, filiform, 3–4 mm long, sometimes unequal in length; oppositipetalous stamens with 4–6 mm long filaments, anthers ovate, thecae 3–5 mm, straight or falcate, basal crest spuriform or ligulate, 0.5–1 mm long, lateral appendages absent. Ovary ⅔ of hypanthium in length, apex pubescent; style 13–15 mm long, curved at apex, glabrous; stigma minute, capitate; extra-ovarial chambers 8, extending to below the middle of the ovary. Fruits urceolate, 8–10 × 5–6 mm, sparsely hairy to glabrescent; calyx lobes persistent, erect. Seeds ca. 0.5 mm long.
Distribution — Java (West).
Ecology and habitat — Secondary forest at 700–1400 m elevation.
Specimens examined — **INDONESIA.** Banten: *Blume 11* (L). West Java: Bogor, Mt. Karang Gantungan, *Backer 6272* (BO); *Ibid.*, Cisangku, *Backer 10549* (BO); Cianjur, Sukanegara, *Hellendoorn 8* (BO); Mt. Gede, *Raap 695A* (L); Bandung, Nanggerang, *Backer 9097* (BO).

49. *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell — Map 3-26

Dissochaeta sarawakensis (M.P.Nayar) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — *Neodissochaeta sarawakensis* M.P.Nayar, Bull. Bot. Surv. India 11: 195. 1969. — Type: *G.D. Haviland 69* (holo K [K000859625!]), Malaysia, Sarawak, Pengkulu Ampat.

Climbing up to 9 m in height. Branchlets terete, 3–4 mm in diameter, covered with thin, 1–2 mm long bristle hairs; nodes swollen, with distinct crestlike interpetiolar ridges, margin bristly, up to 4 mm wide; internodes 2–5 cm long. Leaves: petioles terete, 4–7 mm long, sparsely stellate-puberulous and with scattered bristles at dorsal groove; blades ovate to elliptic, 5–6 × 2.3–3.8 cm, subcoriaceous, base rounded to subcordate, margin entire, apex acuminate, tip ca. 0.5 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; surfaces glabrous, sometimes abaxially with pair of glandular patches at base. Inflorescences terminal, up to 10 cm long, many-flowered; main axis stellate-furfuraceous; primary axes up to 4 cm long with 2 or 3 nodes, secondary axes 1–2 cm long with 1 or 2 nodes, tertiary axes up to 0.8 cm long with 1 node; bracts linear, 2–3 mm long, glabrous; bracteoles subulate, ca. 1 mm long, stellate-furfuraceous; pedicels furfuraceous, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 2–3 × ca. 2 mm, glabrous; calyx lobes truncate, ca. 0.5 mm long, with 4 small minute points; petal buds conical, 2–3 mm long, apex narrowly acuminate, glabrous; mature petals ovate, ca. 5 × 3.5 mm, glabrous, reflexed, base clawed, apex acute, white or pale pink. Stamens 8, equal, filaments curved sideways; alternipetalous stamens with 3–4 mm long filaments, anthers oblong, curved, sickle-shaped, thecae 3–4 mm long, yellow, pedoconnective short, ca. 0.5 mm long, basal crest ligular, bi- or trifid, ca. 2 mm long, lateral appendages paired, filiform, 4–5 mm long; oppositipetalous stamens with 3–4 mm long filaments, anthers S-shaped, thecae 3–3.5 mm long, yellow, basal crest ligular, ca. 1.5 mm long, lateral appendages paired, filiform, ca. 2 mm long. Ovary ⅔ of hypanthium in length, apex glabrous; style glabrous, ca. 9 mm long, reddish; stigma minute; extra-ovarial chambers absent or not developed. Fruits globose, 2–3 × ca. 2 mm, glabrous; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.
Distribution — Borneo (Brunei and Sarawak).

Ecology and habitat — Heath forest or mixed dipterocarp forest at 240–1000 m elevation.
Vernacular names — *akar kemunting* (Iban); *akar kitum* (Kenyah).
Note — Vegetatively similar to *D. stipularis* in its distinct wide, crest-like interpetiolar ridges and glabrous leaf blades. The difference is that *D. sarawakensis* has fertile alternipetalous stamens, which are equal to the oppositipetalous ones, while in *D. stipularis* the alternipetalous stamens are staminodes, reduced and smaller than the oppositipetalous ones.
Specimens examined — **MALAYSIA.** Sarawak: Pengkulu Ampat, *Haviland 69* (K); Baram, Gunung Mulu, 365 m, 4 Jul 1961, *Anderson & Keng K7* (BO, K, L); *Ibid.*, Ulu Tinjar, Dulit Range, 300 m, 9 Aug 1974, *Chai S.34713* (K, L); Balingian, Bawan, Begrih, 10 m, 20 Oct 1963, *Chai S.19481* (K); Bintulu, Segan FR., 244 m, 18 Aug 1968, *Ilias Paie S.27040* (BO, K, L); Kuching, Mount Matang, 396 m, 27 Mar 1929, *Clemens 20929* (BO, K); Kapit, Batang Rejang, Batu Laga, 1000 m, 12 Sep 1984, *Mochtar S.48265* (K, L); Sri Aman, Gunong Silantek, 530 m, 27 Aug 1980, *Ilias Paie S.42599* (K, L). **BRUNEI.** Temburong: Amo, Bukit Tudal, 840-1160 m, 6 Oct 1994, *Bygrave et al. 29* (K, L).



Map 3-26. Distribution of *D. sarawakensis* (■), *D. schumannii* (▲) and *D. spectabilis* (●).

50. *Dissochaeta schumannii* Cogn. — Map 3-26

Dissochaeta schumannii Cogn. in K.Schum. & Hollrung, Fl. Kais. Wilh.-Land: 88. 1889. — *Neodissochaeta schumannii* (Cogn.) M.P.Nayar, Kew Bull. 20: 160. 1966. — Lectotype (designated here): *U.M. Hollrung 656* (lecto BO [BO1747958!]; isolecto BR [BR5187904!], K [K000859604!], L [L0537229!]), Papua New Guinea, Kaiser Wilhelmsland, Augusta Fluss, 1887.

Neodissochaeta lamiana Bakh.f., Contr. Melastom. 142. 1943. — Type: *H.J. Lam 935* (holo L [L0537230!]; iso BO [BO1747956!], K [K000859605!, K000859606!], U [U0004013!]), Indonesia, Papua, Prauwenbivak, Mamberamo River, 140 m elev., 29 Aug 1920.

Climbing up to 4.5 m in height. Branchlets terete, 3–4 mm in diameter, sparsely to densely covered with stellate hairs; nodes swollen, with interpetiolar line; internodes 7.5–8.5 cm long. Leaves: petioles terete, 8–10 mm long, stellate-furfuraceous; blades ovate to elliptic, 8–16 × 4–6.5 cm, membranous, base emarginate, margin entire, apex acuminate, tip up to 1 cm long;

nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially with dense, stellate, brown or grey tomentose hairs. Inflorescences terminal, up to 25 cm long, manyflowered; main axis densely stellate-furfuraceous; primary axes 12–20 cm long with 4 or 5 nodes, secondary axes 3–6 cm long with 2 or 3 nodes, tertiary axes 1–2 cm long with 1 node; bracts lanceolate, 3–4 × ca. 2 mm, stellate-furfuraceous; bracteoles linear, 2–4 mm long, stellate-furfuraceous, caducous; pedicels stellate-tomentose, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 3–4 × ca. 2 mm, densely stellate-tomentose, sometimes with a few scattered, ca. 0.5 mm long glandular bristles; calyx lobes slightly triangular, ca. 4 × 2.5 mm, apex acute, densely stellatefurfuraceous, sometimes with a few glandular bristles, caducous; petal buds conical, ca. 4 mm long, glabrous; mature petals obovate, 4–5 × ca. 3 mm, base clawed, apex obtuse, glabrous, pink. Stamens 4, equal, alternipetalous, filaments curved sideways, 3–4 mm long, anthers oblong, curved, sickle-shaped, thecae 3–4 mm long, yellow, pedoconnective ca. 1 mm long, basal crest triangular with irregular edge, ca. 0.5 mm long, lateral appendages paired, filiform, 1–1.5 mm long. Ovary ¾ of hypanthium in length, apex villous; style slender ca. 5 mm long; stigma minute; extra-ovarial chambers 4, alternipetalous, shallow, ca. ¼ of ovary. Fruits globose or ovoid, 5–6 × 3–4 mm, glabrous or stellate puberulous, slightly 8-lined; calyx lobe remnants, caducous. Seeds ca. 0.5 mm long.

Distribution — New Guinea.

Ecology and habitat — Lowland primary forest, in open places at 90–600 m elevation.

Vernacular names — *nangumush* (Waskuk); *soiya* (Wagu).

Note — Different from other tetrandrous species by its distinct triangular calyx lobes which are caducous in fruit. The leaf blade underneath is also typical by the greyish tomentose indumentum, which differs from other New Guinean species (e.g. *D. angiensis* and *D. brassii*).

Specimens examined — **INDONESIA.** Papua: Camp Prauwen, Mamberamo River, 140 m, 29 Aug 1920, *Lam 935* (BO, K, L); Mimika, Kuala Kencana, 65 m, 25 Jan 1998, *Johns, et al. 8887* (BO, K, L); *Ibid.*, 10 m, 10 Apr 2000, *Utteridge et al. 312* (BO, K, L); *Ibid.*, 20 Nov 2000, *Lucas et al. 24* (BO, K, L); Ingembit to Konomptan, 12 Jun 1967, *Reksodihardjo 481* (BO, K, L). West Papua: Ayawasi, 450 m, 18 Mar 1996, *Ridsdale 2327* (L). **PAPUA NEW GUINEA.** East Sepik: Ambunti, Near Wagu, 90 m, 1 Jun 1966, *Hoogland & Craven 10180* (BO, K, L); *Ibid.*, 8 Jul 1966, *Hoogland & Craven 10514* (BO, K, L); *Ibid.*, Mount Garamambu, 21 Aug 1949, *Womersley NGF 3751* (BO, K, L). Milne Bay: Biniguni Airstrip, Mt. Suckling, 365 m, 5 Jul 1972, *Pullen 8424* (BO, K, L). Morobe: Lae, Gabensis, 600 m, 25 Apr 1990, *Simaga 1836* (L). Sepik: Kaiser Wilhelmsland, Augusta River, 1887, *Hollrung 656* (BO, K, L). Western District: Kiunga, 21 m, 5 Aug 1971, *Streimann & Katik NGF 46798* (BO, K, L); *Ibid.*, Ingembit, 146 m, 13 Jun 1967, *Henty, Ridsdale & Galore NGF 33015* (L); Bigel, 24 May 2002, *Piskaut UPNG 20172* (K, L). West Sepik: Carpentaria, Ekwaii River, 500 m, Dec 1977, *Hoover 473* (L).

51. *Dissochaeta spectabilis* J.F.Maxwell — Fig. 3-26, Map 3-26

Dissochaeta spectabilis J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — *Dissochaeta marumioides* Furtado, Gard. Bull. Singapore 20: 111, fig. 1. 1963, non Cogn. (1891). — Type: *A. Johnston & M. Johnston 86* (holo SING [SING0051582!]), Malaysia, Pahang, Cameron Highlands, Tanah Rata, 1300–1500 m elev.

Climbing up to 5 m in height. Branchlets terete, 3–5 mm in diameter, densely stellate-furfuraceous; nodes swollen, with interpetiolar ridge; internodes 4–5.5 cm long. Leaves: petioles flattened, 10–15 mm long, densely stellate-furfuraceous; blades ovate, ovate-elliptic

or elliptic, 9–13.5 × 4.3–6 cm, membranous, base rounded to subcordate, margin entire, apex acuminate, tip 1.5–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially densely brown stellatetomentose. Inflorescences terminal, up to 42 cm long, many-flowered; main axis angular, densely stellate-tomentose; primary axes up to 38 cm long with 4–7 nodes, secondary axes 1.2–7.5 cm long with 1–4 nodes, tertiary axes 0.7–2.5 cm long with 1 or 2 nodes, quarternary axes when developed 0.3–0.8 cm long with 1 node; bracts linear, 8–10 mm long, densely stellate-tomentose, caducous; bracteoles linear, 5–6 mm long, densely stellate-tomentose; pedicels densely stellate-tomentose, 2–4 mm in central flowers, 1-2 mm long or subsessile in lateral flowers. Hypanthium campanulate, 7–8 × 3–4 mm, slightly 8-ridged, densely stellate-tomentose; calyx lobes triangular, 3–4 mm long, erect, apex acute, densely stellate-tomentose; petal buds conical, 8–10 × 3–4 mm, glabrous; mature petals obovate or ovate, ca. 10 × 8 mm, glabrous, reflexed, base clawed, apex obtuse, pink. Stamens 8, unequal, filaments flattened, white, base pinkish, apex yellowish, curved sideways; alternipetalous stamens with 8–10 mm long filaments, anthers lanceolate, sickle-shaped, thecae 12–14 mm long, pink, pedoconnective 3–5 mm long, basal crests distinctly triangular, ca. 1 mm long, yellow, narrow with acute apex, lateral appendages paired, filiform, 2–3 mm long, yellow; oppositipetalous stamens with 8–10 mm long filaments, anthers S-shaped, thecae 7–10 mm long, thick, cream to bright pink, basal crest spur-like, ca. 1 mm long, bifid, erect, lateral appendages paired, filiform, 2–3 mm long, brownish. Ovary ¾ of hypanthium in length, apex pubescent; style glabrous, 10–12 mm long, white, apex curved; stigma capitate, minute; extra-ovarial chambers 8, extending almost to the base of the ovary. Fruits ovoid or urceolate, 13–15 × 8–20 mm, stellate-puberulous or nearly stellate-tomentose, with calyx lobes remnant persistent to sometimes caducous. Seeds ca. 0.75 mm long.

Distribution — Peninsular Malaysia (Pahang and Selangor) and Sumatra (West).

Ecology and habitat — Lower to upper montane forest, in open places at 520–1740 m elevation.

Note — *Dissochaeta spectabilis* can be distinguished from other species by its dense tomentose indumentum and erect, triangular, calyx lobes, which are subpersistent in fruit. The calyx lobes are remniscent of the genus *Macrolenes*, therefore Furtado (1963) used this as an epithet (*marumioides*, like *Marumia*, a synonym of *Macrolenes*). Since this epithet was already used by Cogniaux (1891) for a species from Sumatra, *D. marumioides* Furtado became a later illegitimate homonym. Therefore, Maxwell (1980b) proposed the new name of *D. spectabilis*.

Specimens examined — **MALAYSIA.** Pahang: Bentong, 1500 m, 17 May 1987, *Worthington 12804* (L); Gunung Bunga Buah, 1432 m, 4 Dec 2006, *Kamarul Hisham et al. FRI 52081* (K, L); Cameron Highlands, Robinson Falls, 1430 m, 30 Aug 1956, *Burkill HMB 750* (K, L); *Ibid.*, Tanah Rata, 1300-1500 m, *Johnston & Johnston 86* (SING); *Ibid.*, 1550 m, 14 Apr 1978, *Maxwell 78-133* (L). Selangor: Genting Highlands, Gunong Ulu Kali, 1670 m, 17 Dec 1977, *Stone 13535* (K); *Ibid.*, 1700 m, 3 Jun 1978, *Maxwell 78-323* (L, P); *Ibid.*, 5 Aug 1979, *Stone 14131* (L); *Ibid.*, 1700 m, 11 Jun 1977, *Siew 95* (L); *Ibid.*, 1520 m, 2 Jul 1977, *Siew 210* (L). **INDONESIA.** West Sumatra: Lima Puluh Kota, Aer Putih, 520 m, 22 Feb 1954, *Alston 13816* (BM, BO); *Ibid.*, Harau Valley, Sarasah Bonta, 500-580 m, 17 Apr 1999, *Seren 65* (ANDA); *Ibid.*, Kelok Sembilan, 800 m, 20 May 2001, *Zul et al. 43* (ANDA); *Ibid.*, 13 Sep 2017, *Kartonegoro 1100* (BO, L).

Fig. 3-26. *Dissochaeta spectabilis*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flowers; **e.** fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1100* (BO, L).

52. *Dissochaeta stipularis* (Blume) Backer ex Clausing — Map 3-27

Dissochaeta stipularis (Blume) Backer ex Clausing in S.S.Renner et al., Fl. Thailand 7, 3: 431. 2001. — *Melastoma stipulare* Blume, Bijdr. Fl. Ned. Ind 17: 1073. 1826. — *Aplectrum stipulare* (Blume) Blume, Flora 14: 503. 1831. — *Anplectrum stipulare* (Blume) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria stipularis* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria stipularis* (Blume) Bakh.f., Contr.

Melastom. 132. 1943. — Lectotype (designated by Veldkamp et al. in Blumea 24: 424. 1979): *C.L. Blume 857* (lecto L [L0537306!]; isolecto L [L0537304!, L0537305!], P [P02274923!]), Indonesia, West Java, G. Seribu.

Anplectrum annulatum Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria annulata* (Triana) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria annulata* (Triana) Raizada, Indian Forester 94: 435. 1968. — Type: *N. Wallich 4056* (holo K), Malaysia, Peninsular Malaysia, Penang.

Anplectrum lepidoto-setosum King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 56. 1900. — Lectotype (designated here): *B. Scortechini 2106* (lecto K [K000859525!]; isolecto CAL, SING), Malaysia, Peninsular Malaysia, Perak.

Anplectrum crassinodum Merr., Univ. Calif. Publ. Bot. 15: 223. 1929, non. Merr. (1939). — Lectotype (designated here): *A.D.E. Elmer 21291* (lecto BO [BO1865944!]; isolecto K [K000859624!], L [L0537307!], SING), Malaysia, Sabah, Elphinstone Province, Tawao.

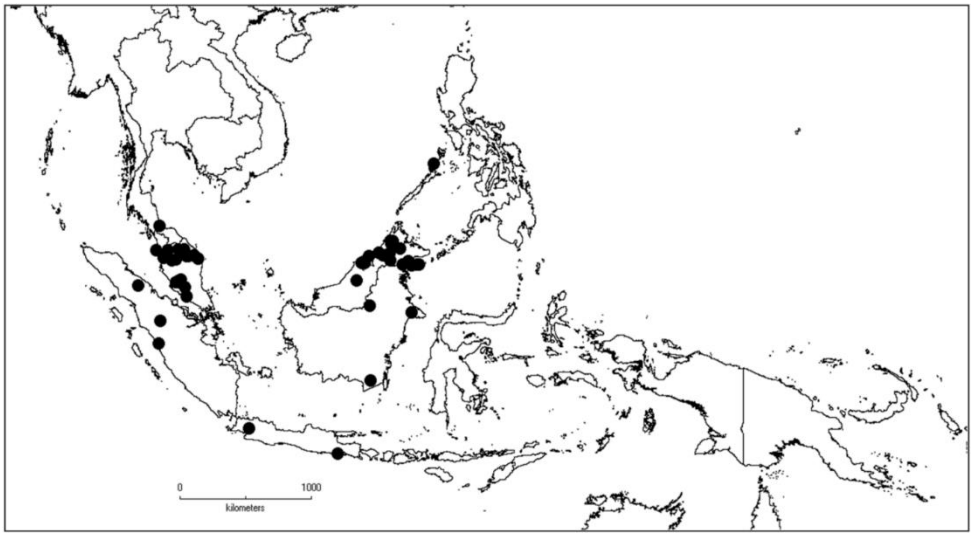
Diplectria annulata (Triana) Kuntze var. *seticarpa* Furtado, Gard. Bull. Singapore 20: 107. 1963. — Type: *M. Shah 176* (holo SING!; iso BO [BO1760865!], K [K000859524!], L [L0537303!]), Malaysia, Pahang, Bentong, Sabai Estate, 400 ft. elev., 27 Jan 1958.

Climbing up to 8 m in height. Branchlets terete, 3–4 mm in diameter, with minute stellate hairs and scattered, ca. 2 mm long, reddish-brown bristles; nodes swollen, with raised annular crest-like interpetiolar ridge, up to 5 mm wide, densely covered with stellate hairs and scattered bristles; internodes 4.7–10 cm long. Leaves: petioles terete, 5–8 mm long, densely with stellate hairs and bristles; blades elliptic to elliptic oblong, 11–13.5 × 3.7–4.8 cm, membranous or subcoriaceous, base rounded to subcordate, margin entire, apex acute or acuminate, tip 1–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous, except sparse stellate hairs and bristles at base of midrib. Inflorescences terminal, up to 12 cm long, many-flowered; main axis densely covered with stellate hairs and bristles, bright red; primary axes 3–5 cm long with 2–4 nodes, secondary axes up to 4 cm long with 1 or 2 nodes, tertiary axes up to 1.5 cm long with 1 node; bracts linear, 5–8 mm long, densely stellate-furfuraceous and bristly; bracteoles linear, 3–4 mm long, densely stellate-furfuraceous and bristly; pedicels densely stellate-furfuraceous and with bristle hairs, 3–5 mm long in central flowers, 1–3 mm long in lateral flowers, bright red. Hypanthium cyathiform-tubular, 3–3.5 × 2–2.5 mm, glabrous or stellately furfuraceous and covered with bristle hairs; calyx lobes truncate with 4 small points, ca. 0.5 mm long, densely bristly; petal buds conical, 1–2 mm long; mature petals ovate, 2–3 × ca. 2 mm, base clawed, apex acute, white or white purplish. Stamens 8, unequal, filaments straight; alternipetalous stamens staminodial with 2–2.5 mm long filaments, anthers rudimentary, thecae 2–3 mm long, slender, terete, white, basal crest triangular or ligular, thin, ca. 1 mm long, lateral appendages paired, linear, flat, filiform, ca. 1 mm long; oppositipetalous stamens with 2–3 mm long filaments, anthers thick, curved, hooked, thecae 2–3 mm long, apex obtuse, yellow, basal crest shortly triangular, ca. 0.3 mm long, lateral appendages absent. Ovary ⅔ of hypanthium in length, apex glabrous; style 4–6 mm long, curved at the end, slender, glabrous, pink; stigma minute; extra-ovarial chambers 4, oppositipetalous, shallow reaching only upper ⅓ of the ovary. Fruits subglobose, 4–5 × 3–4 mm, glabrous or bristly; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Thailand (Southern Peninsula), Peninsular Malaysia, Sumatra, Java, Borneo and Philippines (Palawan).

Ecology and habitat — Secondary forest or along riverbanks at 75–250 m elevation.

Vernacular names — Peninsular Malaysia: *kayu matahari* (Pahang); *akar lekumbang* (Selangor); *sesendok* (Perak). Borneo: *kudok-kudok* (Brunei).



Map 3-27. Distribution of *D. stipularis* (●).

Specimens examined — **THAILAND.** Songkhla: Hat Yai, Ko Hong, 75 m, 23 Jan 1986, *Maxwell 86-45* (L). **MALAYSIA.** Kelantan: Chaning, 2 Feb 1917, *Ridley s.n.* (K); Gunong Stong, 244 m, 15 Aug 1969, *Whitmore FRI 12509* (K, L); Sungai Terang, S. Lebir, 8 Jul 1935, *Henderson SFN 29646* (K); *Ibid.*, Ulu Lebir, *Anon. FRI 17707* (K, L); Kuala Mersing, Sungai Brok, 183 m, 13 Jun 1967, *Ng FRI 5423* (L). Malacca: Ayer Panas, Nov 1894, *Ridley 1574* (BM). Negeri Sembilan: Jelebu, Serting Forest Reserve, 200 m, 1 Oct 1996, *Gardette 2279* (L). Pahang: Bentong, Sabai Estate, 122 m, 27 Jan 1958, *Shah 176* (BO, K, L). Penang: Government Hill, Oct 1886, *Curtis 1078* (K). Perak: *Scortechini 2106* (K); Grik, 16 Nov 1966, *Ismail KEP 95044* (K, L); Gunong Bubu, 19 Jun 1969, *Selvaraj FRI 11163* (L). Selangor: Kepong, 1 Sep 1927, *Pawanche & Awang Lela 13652* (K); Klang Gates, 1 Jan 1921, *Ridley s.n.* (K); Ulu Gombak, 180 m, 26 Aug 1928, *Strugnell 13618* (K). Terengganu: Dungun, Jerangau Road, 16 Nov 1954, *Sinclair & Kiah SFN 40491* (BM, K, L); Ulu Brang, 106 m, Jul 1937, *Moysey & Kiah SFN 33853* (K); Tasik Kenyir, Simpan Tembat, 217 m, 19 Nov 2008, *Kamarul Hisham FRI 59338* (L). Sabah: Beaufort, Beaufort Hill, 29 m, 12 Mar 1962, *Mikil SAN 28134* (L); Kalabakan, Benaword, 24 Apr 1980, *Fidilis & Sumbing SAN 91826* (L); Keningau, Sepulut, 10 Jul 1974, *Fidilis & Sumbing SAN 103629* (K, L); Nabawan, Rashna Road, 21 Aug 1976, *Dewol SAN 83878* (L); Witti Range, Shang Lian, 23 Aug 1985, *Sumbing SAN 110178* (L); Ulu Sungai Tinagalan, 15 Nov 1985, *Asik SAN 113060* (L); Ranau, Trus Madi, Mamut Copper Mine, 1000 m, 9 Jul 1984, *Beaman et al. 10653* (L); *Ibid.*, Mount Kinabalu, 550 m, 8 Jun 1961, *Chew, Corner & Stainton RSNB 528* (L); *Ibid.*, Hot Spring, 762 m, 23 Sep 1964, *Mikil SAN 41905* (L); Sandakan, Telupid, Tangkulap, 28 May 1988, *Dewol & Maidil SAN 124683* (L); Semporna, Mount Pock, 91 m, 24 Nov 1965, *Gansau SAN 54477* (L); Tawau, 1923, *Elmer 21291* (BO, K, L); *Ibid.*, Apas Road, 30 m, 24 Jun 1959, *Meijer SAN 19243* (L, PNH); *Ibid.*, Tawau River, 300 m, 11 Nov 1968, *Kokawa & Hotta 892* (L); *Ibid.*, Brumas, 8 Feb 1977, *Fidilis & Awang SAN 85351* (L); Tenom, Tomani, Kambaliangan Hill, 122 m, 10 Oct 1966, *Talip SAN 50522* (L). Sarawak: Baram, Mount Dulit, Ulu Tinjar, 300 m, 23 Aug 1932, *Richards* 1401 (L). **BRUNEI.** Belait: Merangking, 17 Nov 1994, *Nangkat et al. BRUN 15570* (K); *Ibid.*, 40 m, 12 Apr 1995, *Ismail et al. BRUN 16601* (L); Muara, Bukit Tempayan, 19 May 1994, *Joffre et al. BRUN 15465* (K). Tutong: Ulu Tutong, Kampong Litad, 29 Jun 1993, *Nangkat et al. BRUN 15229* (K, L); Tasik

Merimbun, 27 Feb 1996, *Ogata et al. Og-B94* (L); *Ibid.*, 20 m, 15 Sep 2000, *Suzuki K.13181* (L); Sungei Tutong, 20 m, 5 Nov 1991, *Simpson & Marsh 2600* (L). **INDONESIA.** North Sumatra: Pematang Siantar, 450 m, 22 Jul 1937, *Lörzing 17296* (BO, L). Riau: Kampar, Tambun, Bukit Suligi, 400-550 m, 29 Apr 1999, *Arbain & Tamin 12 AS* (ANDA). West Sumatra: Padang, Limau Manis, 400 m, 14 Dec 1991, *Nurainas 071* (ANDA). Banten: Gunung Seribu, *Blume s.n.* (L, P). East Java: Malang, Tirtoyudo, Pujiharjo, Tumpak Kembang, Oct 2002, *Riswan, Afriastini & Nurdin ML051* (BO, L). East Kalimantan: Sangkulirang, Pelawan Besar, Gunung Toda, 25 m, 11 May 1937, *Aet 294* (BO, L); Long Sungai Barang, 750 m, 16 Oct 1991, *van Valkenburg 1041* (L). South Kalimantan: Tanah Laut, Kintap, 200 m, 17 Apr 1985, *Leeuwenberg & Rudjiman 13432* (L). **PHILIPPINES.** Palawan: Pagdanan Range, San Vicente, 100 m, 23 Apr 1984, *Podzorski SMHI 944* (K, L).

53. ***Dissochaeta vacillans*** (Blume) Blume — Fig. 3-27, Map 3-24

Dissochaeta vacillans (Blume) Blume, Flora 14: 495. 1831. — *Melastoma vacillans* Blume, Bijdr. Fl. Ned. Ind. 17: 1074. 1826. — *Neodissochaeta vacillans* (Blume) Bakh.f., Contr. Melastom. 144. 1943. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *C.G.C. Reinwardt s.n.* (lecto L [L0008894!]; isolecto L [L0008895!]), Indonesia, West Java, Buitenzorg, Tjiawi.

Dissochaeta fusca Blume, Flora 14: 497. 1831. — *Dissochaeta inappendiculata* Blume var. *fusca* (Blume) Miq., Fl. Ned. Ind. 1(1): 525. 1855. — *Neodissochaeta fusca* (Blume) Bakh.f., Contr. Melastom. 136. 1943. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *C.L. Blume 1791* (lecto L [L0729468!]; isolecto K [K000859621!], L [L0537244!], P [P05283572!]), Indonesia, Java.

Dissochaeta fusca Blume var. *ferruginea* Blume, Flora 14: 497. 1831. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *J.C. van Hasselt s.n.* (lecto L [L0537248!]; isolecto L [L0537239!, L0537247!]), Indonesia, Java, Bantam.

Dissochaeta fusca Blume var. *obtuso-acuminata* Blume, Flora 14: 497. 1831. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *C.L. Blume s.n.* (lecto L [L0537242!]; isolecto L [L0537246!]), Indonesia, West Java, Buitenzorg, Tjiampea.

Dissochaeta velutina Blume, Flora 14: 497. 1831. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 143. 2010): *H. Kuhl & J.C. van Hasselt s.n.* (lecto L [L0537234!]; isolecto K [K000859622!], L [L0537249!, L0537250!]), Indonesia, Java, Bantam, Leuwi Boengoer.

Dissochaeta decipiens Blume, Mus. Bot. 1(3): 36. 1849. — Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 10: 131. 2010): *H. Kuhl & J.C. van Hasselt s.n.* (lecto L [L0008892!]; isolecto K [K000859489!], L [L0008891!]), Indonesia, Java.

Dissochaeta monticola auct. non. Blume: Triana, Trans. Linn. Soc. London 28: 83. 1872. *p.p.*, excl. type.

Climbing up to 3 m height. Branchlets terete or subquadrangular, 2–6 mm diameter, glabrescent to stellate-furfuraceous; nodes swollen, with interpetiolar ridge; internodes 4.5–10 cm long. Leaves: petioles terete, 5–24 mm long, puberulous to furfuraceous; blades ovate, ovate-oblong or elliptic-oblong, 6.5–15 × 2.5–7 cm, membranous, base rounded, margin entire, apex acuminate, tip 0.5–2 cm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially glabrous to nearly brown sparsely stellate-furfuraceous. Inflorescences terminal and in the upper leaf axils, up to 30 cm long, many-flowered; main axis angular, sparsely stellate-furfuraceous; peduncle up to 7 cm long; primary axes up to 25 cm long with 4–6 nodes, secondary axes up to 4 cm long with 1–3

nodes, tertiary axes up to 1.5 cm long with 1 node; bracts minute or linear, ca. 3 mm long, furfuraceous, caducous; bracteoles minute or linear to oblong, 1.5–4 mm long, stellate-furfuraceous; pedicels sparsely stellate-furfuraceous, 4–6 mm long in central flowers, 1–3 in lateral flowers. Hypanthium campanulate or suburceolate, 2–5 × 1–3 mm, glabrescent or sparsely to densely stellate-furfuraceous; calyx lobes truncate, 0.5–1 mm long, with 4 undulating apices, rounded, or subtriangular, glabrous; petal buds conical, 2–4 mm long; mature petals ovate or oblong, 5–6 × ca. 3 mm, base clawed, apex obtuse, glabrous or with

Fig. 3-27. *Dissochaeta vacillans*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flowers; **e.** immature fruit. Photos by A. Kartonegoro; voucher: *Kartonegoro 1105* (BO).

minute hairs at margin, white-pinkish or pink. Stamens 8, sometimes 4 with the oppositipetalous ones undeveloped, unequal when 8, filaments straight; alternipetalous stamens with 2–4 mm long filaments, anthers oblong or lanceolate, thecae 3–5 mm long, yellow, pedoconnective ca. 0.5 mm long, basal crests triangular, 1–2 mm long, margin irregular, lateral appendages paired, filiform, 1.5–3 mm long; oppositipetalous stamens when developed with 2–3 mm long filaments, anthers ovate-oblong or lanceolate, thecae 2.5–4 mm long, basal crests triangular or ligular, 0.5–1 mm long, erect, lateral appendages paired or reduced to a single lateral one, filiform, 1–2 mm long. Ovary half or ⅔ of hypanthium in length, apex puberulous or pubescent; style 5–8 mm long, apex curved, glabrous; stigma minute; extra-ovarial chambers 8, the 4 alternipetalous ones extending between the apex and the middle of the ovary, the 4 oppositipetalous ones shallow. Fruits subglobose to urceolate, 3–6(–10) × 2–6 mm, glabrous; stalks 2–5(–7) mm long, calyx lobe persistent, erect. Seeds ca. 0.5 mm long.

Distribution — Java and Lesser Sunda Islands (Sumbawa).

Ecology and habitat — Forest, secondary or depleted forest or edge of river at 500–1400 m elevation.

Vernacular names — Java: *harendong areuy*, *harendong bokor areuy*, *harendong gede* (Sunda).

Note — *Dissochaeta decipiens*, with only four fertile, alternipetalous stamens, is synonymized with *D. vacillans*, because it has a similar appearance due to the indumentum on the branchlets, leaves and inflorescences; moreover, the shape of the stamens and the appendages are also similar.

Specimens examined — **INDONESIA.** Banten: Pandeglang, Mt. Karang, *Backer 7470* (BO); *Ibid.*, Galusur, 500 m, 28 May 1912, *Koorders 40659β* (BO); *Ibid.*, 700 m, 1 Jun 1912, *Koorders 40727β* (BO); *Ibid.*, Menes, Mt. Pulasari, 1000 m, Mar 1913, *Backer 7055* (BO); Lebak, *van Hasselt s.n.* (L); *Ibid.*, Leuwi Bungur, *Kuhl & van Hasselt s.n.* (L); *Ibid.*, Citorek & Muncang, *Backer 1835* (BO). Central Java: Mt. Slamet, Baturaden, 1000 m, 30 Mar 1970, *Bernardius D43051* (BO); Pekalongan, Josorejo, *Backer 16219* (BO). West Java: Bogor, Mt. Salak, Gunung Bunder to Kawah Ratu, 1300 m, 8 Jan 1941, *de Voogd & Bloembergen s.n.* (BO); *Ibid.*, C.A. Backer 4198 (BO); *Ibid.*, Upper Lido, 1200 m, 22 Feb 2000, *Wiriadinata & Hoover 31188* (BO); *Ibid.*, *Hoover & Hendra 32564* (BO); Leuwiliang, Puraseda, 500 m, 2 Feb 1929, *van Steenis 2712* (BO); *Ibid.*, Mt. Butik Buligir, *Backer 6150* (BO); *Ibid.*, Mt. Sunarari, 1000 m, 1 Jan 1913, *Backer 6380* (BO); Ciampea, *Blume s.n.*(L); Ciawi, *Reinwardt s.n.* (L); Puncak Pass, Tugu, Above Gunung Mas, 1300-1500 m, 18 Mar 1952, *Meijer 105* (BO, K, L); *Ibid.*, Gunung Luhur, Tugu, 1700 m, 8 Aug 1982, *van Balgooy & Mogea 4284* (BO); Mount Pangrango, Bodogol, *Kartonegoro 318* (BO); Mt. Halimun, *Backer 10914* (BO); *Ibid.*, *Bakhuizen van den Brink 3336* (BO, L, U); *Ibid.*, Cikaniki, 1000 m, 11 Jan 2001, *Arifiani et al. 142* (BO); *Ibid.*, 9 Mar 2000, *Hoover, Girmansyah & Hunter 32172* (BO); *Ibid.*, Nirmala, 1300 m, 10 Jun 1980, *van Balgooy & Wiriadinata 2922* (BO, L); *Ibid.*, Malasari, 1055 m, 10 Oct 2017, *Kartonegoro 1105* (BO); Cianjur, Mt. Gede, Cibodas, 1450 m, *Boerlage s.n.* (BO); *Ibid.*, *Scheffer s.n.* (BO); *Ibid.*, 3 Nov 1987, *Widjaja 3220* (BO); *Ibid.*, Sindanglaya, 1000 m, Dec 1916, *Backer 21507* (BO); *Ibid.*, Pasir Pangsalatan, 1500 m, 2 Jun 1948, *Enoh 181* (BO, L); *Ibid.*, *Koorders 31670β* (BO); Sukanegara, *Hellendoorn 5* (BO); Cibeber, Campaka, 1000 m, 16 Jun 1923, *Smith 822* (BO, L); *Ibid.*, Cidadap, Cadas Malang, 1000 m, 19 Apr 1916, *Bakhuizen van den Brink 1469* (BO); *Ibid.*, 20 Mar 1923, *Winckel 1176β* (BO,K, L); Takokak, 1200 m, 9 Jun 1900, *Koorders 33314β* (BO); *Ibid.*, *Koorders 33315β* (BO); Bandung, Cigenteng, 1400 m, 26 Jan 1897, *Koorders 26306β* (BO); Mt. Tangkuban Prahu, 1600 m, 26 Jul 1927, *Docters van Leeuwen 11487a* (BO); Mt. Sembung, Margalangu, 1200 m, 19 Mar 1914, *Backer 12298* (BO); Garut, Rawa Cangkuang, *Scheffer*

s.n. (BO); *Ibid.*, Pasawahan, 400 m, 31 Dec 1911, *Backer 2261* (BO); *Ibid.*, Mt. Ciparay, 1100 m, 27 Jul 1914, *Backer 15041* (BO); Mt.Cikuray, Pasir Kolotok, 1000 m, 15 Aug 1913, *Backer 8685* (BO); Tasikmalaya, Panjalu, 720 m, 4 Aug 1917, *Koorders 47851β* (BO). West Nusa Tenggara: Sumbawa, Sumbawa Barat, Mt. Batulante, 700 m, 3 Nov 1961, *Kostermans 19164* (BO, K, P).

54. *Dissochaeta viminalis* (Jack) Clausing — Fig. 3-28, Map 3-28

Dissochaeta viminalis (Jack) Clausing in S.S.Renner et al., Fl. Thailand 7(3): 433. 2001. — *Melastoma viminale* Jack, Trans. Linn. Soc. London 14: 16. 1823, "viminalis". — *Aplectrum viminale* (Jack) Blume, Flora 14: 502. 1831. — *Anplectrum viminale* (Jack) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria viminalis* (Jack) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria viminalis* (Jack) Bakh.f., Contr. Melastom. 133. 1943. — Neotype (designated by Veldkamp et al. in Blumea 24: 427. 1979): *C.L. Blume 856* (neo L [L0008883!]; isoneo L [L0008882!]), Indonesia, West Java, G. Seribu.

Melastoma rostratum Blume, Bijdr. Fl. Ned. Ind 17: 1074. 1826. — *Aplectrum rostratum* (Blume) Blume, Flora 14: 502. 1831. — *Anplectrum rostratum* (Blume) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria rostrata* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria viminalis* (Jack) Bakh.f. var. *rostrata* (Blume) Bakh.f., Contr. Melastom. 134. 1943. — Lectotype (designated by Veldkamp et al. in Blumea 24: 427. 1979): *C.L. Blume 856* (lecto L [L0008883!]; isolecto L [L0008882!]), Indonesia, West Java, G. Seribu.

Aplectrum pallens Blume, Mus. Bot. 1(3): 38. 1849. — *Anplectrum pallens* (Blume) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Backeria pallens* (Blume) Raizada, Indian Forester 96: 435. 1968. — Lectotype (designated by Veldkamp et al. in Blumea 24: 428. 1979): *P.W. Korthals s.n.* (lecto L [L0008877!]; isolecto K [K000859618!], L [L0008875!, L0008876!], P [P02274926!, P02274927!]), Indonesia, West Sumatra.

Aplectrum confine Blume, Mus. Bot. 1(3): 38. 1849. — *Aplectrum pallens* Blume var. *confinis* (Blume) Miq., Fl. Ned. Ind. 1(1): 554. 1855. — *Anplectrum confine* (Blume) Triana, Trans. Linn. Soc. London 28: 84. 1872. — *Diplectria confinis* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria viminalis* (Jack) Bakh.f. var. *confinis* (Blume) Bakh.f., Blumea 12: 61. 1963. — Lectotype (designated by Veldkamp et al. in Blumea 24: 427. 1979): *P.W. Korthals s.n.* (lecto L [L0008878!]; iso K [K000859620!], L [L0008879!, L0008880!], P [P02274925!]), Indonesia, West Sumatra.

Aplectrum pallens Blume var. *latum* Miq., Fl. Ned. Ind. 1, 1: 554. 1855. — Lectotype (designated by Veldkamp et al. in Blumea 24: 427. 1979): *P.W. Korthals s.n.* (lecto L [L0008873!]; isolecto K [K000859619!], L [L0008874!], P [P02274928!, P02274929!]), Indonesia, West Sumatra, Mount Malintang.

Dissochaeta anomala King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 55. 190). — *Diplectria anomala* (King) Veldkamp, Blumea 24: 426, fig. 5C. 1979. — Lectotype (designated here): *King's collector (Kunstler) 2258* (lecto K [K000859556!]; isolecto BM!, CAL, SING), Malaysia, Perak, Larut, Aug 1881.

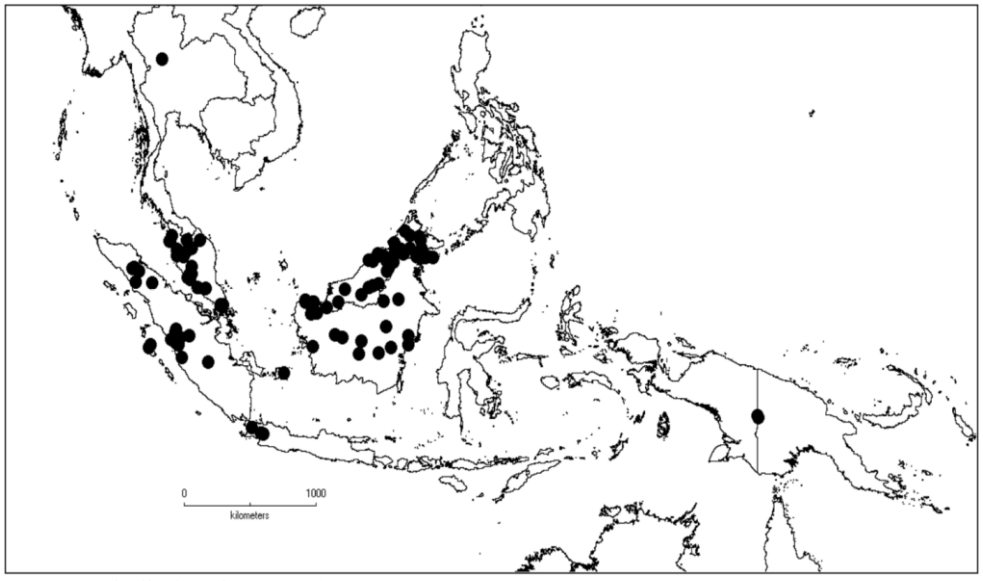
Climbing up to 5 m in height. Branchlets terete, 3–5 mm in diameter, glabrous; nodes swollen, with raised interpetiolar ridge, covered with stellate hairs; internodes 3–4 cm long. Leaves: petioles terete, 3–8 mm long, glabrous to minutely stellate puberulous, densely covered with red-brown bristles lateral of the groove and near the attachment with the blade; blades ovate, elliptic-oblong to oblong, (2.5–)5–14 × (1–)2–6 cm, membranous, base rounded to cordate when large, margin entire, apex acute or acuminate, tip 8–15 mm long; nervation with 1 pair of lateral nerves and 1 pair of intramarginal nerves; adaxially glabrous, abaxially

glabrous with sparsely stellate hairs at the midrib and nerves. Inflorescences terminal and axillary, when terminal up to 12 cm long, many-flowered, when axillary ones up to 5.5 cm long, 3–9-flowered; main axis stellate-puberulous; primary axes up to 5 cm long with 2–4 nodes, secondary axes up to 2 cm long with 1–3 nodes, tertiary axes when developed up to 0.5 cm long with 1 node; bracts linear or elliptic, 3–6 × 3–4 mm, stellate-puberulous, caducous; bracteoles ovate to oblong, 3–4 mm long, stellate-puberulous, margin ciliate; pedicels glabrescent to stellate-puberulous, 3–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium cyathiform-tubular, 3–4 × 2–2.5 mm, glabrous or stellately-puberulous; calyx lobes truncate, ca. 0.5 mm long, without any distinct tips; petal buds conical, 1–2 mm long, apex acuminate; mature petals ovate, 4–5 × ca. 3 mm, reflexed, base clawed, apex acute, white. Stamens 8, unequal, filaments flattened, straight; alternipetalous stamens staminodial with 1–2 mm long filaments, anthers rudimentary, thecae 2–3 mm long, slender, terete, curved, white, basal crest ovate, thin, ca. 1 mm long, lateral appendages paired, flat, filiform, 1–1.5 mm long; oppositipetalous stamens with 1.5–2 mm long filaments, anthers thick, curved, hook-shaped, thecae 2–2.5 mm long, apex obtuse, white, basal crest consisting of a short pair of keels, ca. 0.2 mm long, lateral appendages absent. Ovary half as long as hypanthium, apex glabrous; style 5–6 mm long, curved at the end, slender, glabrous, pink; stigma minute; extra-ovarial chambers 4, oppositipetalous, shallow, extending only upper ⅓ of the ovary. Fruits subglobose, 4–5 × 3–4 mm, glabrous or stellate-puberulous; calyx lobe remnants persistent. Seeds ca. 0.5 mm long.

Distribution — Thailand, Malay Peninsula, Sumatra, Java, Borneo and New Guinea.

Ecology and habitat — Lowland and mixed dipterocarp forest, open areas, road sides or river banks at 45–1150 m elevation.

Vernacular names — Peninsular Malaysia: *akar sindodo* (Kelantan); *laka tulang* (Penang). Sumatra: *kadudu besar* (Jambi); *karamunting akar* (Belitung). Borneo: *akar kemunting* (Iban); *wa perawi* (Kelabit).



Map 3-28. Distribution of *D. viminalis* (●).

Note — This species is easily recognised by the glabrous branchlets and the dense, parallel, brown bristle hairs at the apex of the petioles. The shape and number of stamens resemble

those of *D. stipularis* and *D. maxwellii*. The neotype of *Melastoma viminale* Jack that was chosen by Veldkamp et al. (1979) in Leiden was said to be collected by Kuhl & Van Hasselt from Mount Seribu in West Java. It is seemingly the specimen collected by Blume, who visited the mountain in 1824 while Kuhl & Van Hasselt never visited that locality. He mostly did collect in Banten (Bantam) Province (Van Steenis-Kruseman 1950).

Selected specimens examined — **THAILAND.** Sukhotai: Kalung Tan, 400 m, 11 Mar 1928, *Kerr 14461* (BM, K). Narathiwat: Phu Khao Thong, Lamthan Thong Reservoir, 120 m, 21 Jul 2004, *Pooma et al. 4520* (L). **MALAYSIA.** Johor: Tebing Tinggi, Nov 1900, *Ridley 11105* (K). Kedah: Gunong Jerai, Sungai Terol, 762 m, 12 Sep 1979, *Keng et al. 122* (L). Kelantan: Kuala Tapah, Ulu Sungai Aring, 21 Sep 1967, *Cockburn FRI 7154* (K, L). Malacca: *Maingay KD 795 (2663)* (K, L). Pahang: Raub, Sungai Sempan, 16 Apr 1970, *Soepadmo 653* (K). Penang: *Wallich 4053* (BM, K); West Hill, Mar 1915, *Ridley s.n.* (BM, K); Penang Hill, 22 Aug 1879, *King's collector s.n.* (P). Perak: Larut Hill, *King's collector 2258* (BM, K); Ulu Bubong, *King's collector 10468* (BM, K); Gunong Bubu, 600 m, 18 Aug 1966, *Chew 1230* (K, L); Taiping Hill, Batu Hampar, 8 Dec 1965, *Shah & Sidek 1163* (K, L); Maxwell Hill, May 1886, *Wray 641* (K). Selangor: Rantau Panjang, Jul 1914, *Boden-Kloss s.n.* (BM, K); Ayer Hitam, Puchong, 17 Jan 1968, *Teo & Purseglove 23* (K, L). Sabah: Kalabakan, Hap Seng, 20 May 1982, *Fidilis SAN 94808* (K); Keningau, Sepulut, 20 Oct 1983, *Sigin & Francis SAN 69084* (K, L); Kinabatangan, Nurod-Urod, 680 m, 20 Nov 2006, *Sugau et al. SAN 149046* (K); Lahad, Datu, Danum Valley, 3 May 1989, *Ridsdale 1935* (L); Lamag, Inarat, Gunong Lotung 381 m, 7 May 1976, *Cockburn SAN 83025* (L); Ranau, Mount Kinabalu, Dallas, 914 m, 27 Oct 1931, *Clemens 26872* (BM); Sandakan, Telupid Road, 152 m, 23 Sep 1969, *Talip & Termiji SAN 67969* (L); Tawau, 1923, *Elmer 21305* (BM, L, P, U); *Ibid.*, *Elmer 21649* (BM, L, P, U). Sarawak: *Beccari PB 372* (P); *Native collector 86* (L, P, PNH); *Native collector 580* (BM, L, P, PNH); Bario, Kelabit Highlands, 1000 m, 25 Mar 1970, *Nooteboom & Chai 1664* (L); Kapit, Balleh, Ulu Sungai Melinau, 24 Apr 1976, *Chai et al. S.37213* (L); Kuching, Sep 1892, *Haviland & Hose 159* (L); *Ibid.*, 26 Jan 1894, *Haviland & Hose 971* (BM, L); Lubok Antu, Ulu Sungai Kaup, Bukit Ubah-Ribu 600 m, 12 Mar 1974, *Chai S.33794* (L); Lundu, Gunung Undan 200 m, 30 Apr 1983, *Yii & Jegong S.45974* (L); Miri, Lambir Hill, 21 May 1966, *Sibat S.24301* (BO, L); Serian, Gunung Rawan 830 m, 5 Apr 1983, *Awa & Ilias Paie S.45555* (L). **SINGAPORE.** *Maingay KD 2492* (BM); Mandai Road, 16 Feb 1936, *Corner SFN 30666* (K); Pulau Ubin, 1890, *Ridley 2014* (BM); Nee Soon 10 m, 28 Nov 1980, *Maxwell 80-210* (L); MacRitchie Resevoir, Thompson Ridge 5 m, 2 Jul 1981, *Maxwell 81-158* (L); Pierce Reservoir 5 m, 18 Nov 1981, *Maxwell 81-222* (L). **BRUNEI.** Tutong: Tasik Merimbun, 7 Apr 1988, *Wong 347* (L). **INDONESIA.** Aceh: Mount Leuser, Lau Ketambe, Gunung Mamas 800-1000 m, 9 Feb 1975, *de Wilde & de Wilde-Duyfjes 14660* (L). Bangka-Belitung: Belitung Island, Manggar, *Teijsmann s.n.* (BO, L). Jambi: Sungai Lesing, 30 m, Oct 1925, *Posthumus 987* (BO, L). North Sumatra: Asahan, Dolok Tomuan, Jun 1936, *Rahmat Si Boeea 9041* (L); Bohorok, Bukit Lawang, 30 Aug 1983, *Whitmore & Kalima 3245* (K, L). Riau: Indragiri, Taluk, 13 Jan 1956, *Meijer 4329* (L). West Sumatra: Lima Puluh Kota, Mount Malintang, *Korthals s.n.* (L); Harau Ravine, 500 m, 15 Aug 1956, *Jacobs 4596* (L); *Ibid.*, 11 Sep 2017, *Kartonegoro 1075* (BO, L); Sungei Bulu, Sep 1878, *Beccari PS 913* (L); *Ibid.*, *Beccari PS 934* (BM, L); Indrapura, *Korthals s.n.* (L, P); Sijunjung, Muaro Kalumpi, Sungai Kwantan, 170 m, 28 Feb 1974, *de Vogel 2748* (BO, L); Solok, Talang Babungo, 1100 m, 26-27 May 2001, *Chan et al. 85* (ANDA); Mentawai Islands, Siberut Island, 25 Sep 1924, *Iboet 276* (BO, L). Banten: Gunung Seribu, *Kuhl & van Hasselt 856* (L). West Java: Bogor, Leuwiliang, Pasir Sijahe 600 m, *Bakhuizen van den Brink 6401* (BO, U); *Ibid.*, Gunung Ciputi 550 m, 17 Jun 1921, *Bakhuizen van den Brink 853* (BO, U). Central Kalimantan: Buntok, Sarbaballo Lake, 21 Aug 1908, *Winkler 3272* (L); Kapuas,

Fig. 3-28. *Dissochaeta viminalis*. **a.** habit; **b.** branchlet; **c.** leaf node; **d.** hypanthium; **e.** flower; **f**. fruits. Photos by A. Kartonegoro; vouchers: *Kartonegoro 1075* (BO, L)]

Kutai, Long Ibut, 130 m, 10 Aug 1925, *Endert 2559* (BO, L); Long Sei Barang, 750 m, 13 May 1993, *Ambriansyah AA 763* (L). North Kalimantan: Krayan, Long Bawan, Gunung Leputung, 900 m, 9 Jul 1981, *Kato et al. B-7957* (BO, L). West Kalimantan: Pontianak, Bentiang, Gunung Mikei 750 m, 30 Oct 1980, *Shea 27039* (BO, L); Sintang, Sungai Posang 110 m, 22 Apr 1994, *Church et al. 1041* (BO, K, L). **PAPUA NEW GUINEA.** Western

District: Kiunga, Ingembit, 91 m, 8 Jun 1967, *Henty, Ridsdale & Galore NGF 31814* (L); *Ibid.*, 10 Jun 1967, *Ridsdale, Henty & Galore NGF 31912* (K, L); *Ibid.*, 125 m, 29 May 1969, *Reksodihardjo 295* (BO, L).

Excluded taxa

Anplectrum anomalum King & Stapf ex King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69(1): 58. 1900 = ***Creochiton anomalus*** (King & Stapf ex King) Veldkamp, Blumea 24: 438. 1979.

Anplectrum assamicum C.B.Clarke in Hook.f., Fl. Brit. India 2: 546. 1879 = ***Pseudodissochaeta assamica*** (C.B.Clarke) M.P.Nayar, J. Bombay Nat. Hist. Soc. 65: 559. 1969.

Anplectrum homoeandrum Stapf, Trans. Linn. Soc. London, Bot. 4: 161. 189 = ***Medinilla homoeandra*** (Stapf) M.P.Nayar, Kew Bull. 20: 240. 1966.

Anplectrum monticola Ridl., Kew Bull. 1: 31. 1946 = ***Creochiton monticola*** (Ridl.) Veldkamp, Blumea 24: 438. 1979.

Aplectrum myrtifolium Miq., Fl. Ned. Ind. 1(1): 555. 1855 = ***Medinilla myrtiformis*** (Naudin) Triana, Trans. Linn. Soc. London 28: 86. 1872.

Aplectrum myrtiforme Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 305. 1851 = ***Medinilla myrtiformis*** (Naudin) Triana, Trans. Linn. Soc. London 28: 86. 1872.

Anplectrum ovalifolium A.Gray, U. S. Expl. Exped., Phan. 15: 597. 1854 = ***Medinilla ovalifolia*** (A.Gray) A.C.Sm., Contr. U. S . Nat. Herb. 37: 85. 1967.

Anplectrum parviflorum Benth., Fl. Hongk. 116. 1861 = ***Blastus cochinchinensis*** Lour., Fl. Cochinch. 2: 527. 1790.

Anplectrum rubifructus (Ohwi) Ohwi, Bull. Natl. Sci. Mus., Tokyo 26: 12. 1949 = ***Medinilla rubifructus*** Ohwi, Bot. Mag. (Tokyo) 57: 7. 1943.

Anplectrum yunnanense Kraenzl., Vierteljahrsschr. Naturf. Ges. Zürich 76: 153. 1931 = ***Pseudodissochaeta septentrionalis*** (W.W.Sm.) M.P.Nayar, J. Bombay Nat. Hist. Soc. 65: 565. 1969.

Dissochaeta barthei Hance ex Benth., Fl. Hongk. 115. 1861 = ***Barthea barthei*** (Hance ex Benth.) Krasser in Engl. & Prantl, Nat. Pflanzenfam. 3, 7: 175. 1893.

Dissochaeta bibracteata (Blume) Baill., Hist. Pl. 7: 25. 1877 = ***Creochiton bibracteatus*** (Blume) Blume, Flora 14: 507. 1831.

Dissochaeta heteromorpha Naudin, Ann. Sci. Nat. Bot. sér. 3, 15: 78. 1851 = ***Dichaetanthera heteromorpha*** (Naudin) Triana, Trans. Linn. Soc. London 28: 61. 1872.

Dissochaeta novoguineensis Baker f., J. Bot. 61(Suppl.): 21. 1923 = ***Creochiton novoguineensis*** (Baker f.) Veldkamp & M.P.Nayar, Blumea 24: 438. 1979.

Dissochaeta pentamera Burkill, Bull. Misc. Inform. Kew 1906: 5. 1906 = ***Poikilogyne pentamera*** (Burkill) Baker f. in Gibbs, Phytogeogr. & Fl. Arfak Mts. 157. 1917.

Dissochaeta quintuplinervis Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 556. 1891 = ***Catanthera quintuplinervis*** (Cogn.) M.P.Nayar, Gard. Bull. Singapore 24: 353. 1969.

Dissochaeta sarcorhiza Baill., Adansonia 12: 88. 1877 = ***Medinilla sarcorhiza*** (Baill.) Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 587. 1891.

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CHAPTER 4

A taxonomic revision of *Macrolenes* (Melastomataceae)

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A taxonomic revision of *Macrolenes* (Melastomataceae)

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Abstract

Macrolenes (Melastomataceae: Dissochaeteae), a genus of woody climbers in Malesia, is taxonomically revised. Seventeen species are recognised, of which three are new to science. The genus is characterized by its scrambling habit, axillary inflorescences, 4-merous flowers and dimorphic stamens. An identification key, nomenclature, descriptions, typification, geographic distributions and taxonomic notes are provided. The affinities with *Dissochaeta*, also climbers, are discussed.

Keywords

Dissochaeta, Dissochaeteae, *Macrolenes*, Malesia, Melastomataceae, revision, taxonomy

Introduction

Macrolenes Naudin is a genus of woody climbers distributed strictly in the Malesian region. The genus is allied to *Dissochaeta* Blume; both are characterized by a scrambling growth habit, opposite phyllotaxy sometimes with interpetiolar outgrowths, flowers 4-merous, 2 whorls of dimorphic stamens and berry-like fruits. *Macrolenes* and *Dissochaeta* are classified in tribe Dissochaeteae (Naudin) Triana (Bakhuizen van den Brink 1943; Maxwell 1984; Clausing & Renner 2001a), but are sometimes also considered to be part of tribe Miconieae (Naudin 1851; Miquel 1855; Renner 1993). The last complete revision of *Macrolenes* was by Bakhuizen van den Brink (1943) and some notes were published by Nayar (1980). The species occurring in Thailand were revised by Renner et al. (2001b), who regarded *Macrolenes* as a synonym of *Dissochaeta*.

A molecular phylogenetic study (Clausing & Renner 2001a) showed that a woody climbing or scrambling growth habit evolved only once in the Southeast Asian Melastomataceae, and that the two species of *Macrolenes* analysed form a clade with two species of *Dissochaeta* and two of *Diplectria*. So far, however, only these six species were sampled for phylogenetic analysis and a denser sampling is required for a more confident differentiation between these three genera.

Macrolenes can be distinguished from *Dissochaeta* by a combination of morphological characters (Table 4-1), e.g., axillary inflorescences (versus mainly, but not always, terminal in Dissochaeta), a pair of abaxial hair cushion domatia on the base of the leaf blades (versus cushion domatia absent), longer and distinct calyx lobes, e.g. half or more of hypanthium length (versus mainly shorter and often indistinct calyx lobes, e.g. less than half of hypanthium length) and several fimbriate, filiform appendages on the connective of the alternipetalous stamens (versus only a pair of filiform, non-fimbriate appendages on the

connective of the alternipetalous stamens) (Kartonegoro et al. 2018). Some species of *Dissochaeta* have long calyx lobes, similar to those of *Macrolenes*, but they are usually erect, not reflexed, and mostly fall off when fruiting (Kartonegoro et al. 2018). Based on those constant morphological differences between *Macrolenes* and *Dissochaeta*, we here keep the genera separate, following a number of earlier authors (Bakhuizen van den Brink 1943; Maxwell 1980a, 1984; Nayar 1980; Kartonegoro et al. 2018).

Table 4-1. Differences in morphological characters between *Macrolenes* and *Dissochaeta*.

Structure/Character	***Macrolenes***	***Dissochaeta***
Base of leaf blade	Abaxially with a pair of hair cushion domatia	Abaxially without a pair of hair cushion domatia
Inflorescence	Axillary	Terminal or rarely axillary
Hypanthium Indumentum	Distinct, sometimes with branched tips	Indistinct, without branched tips
Calyx lobes	Distinct, well-developed, half to as long as the length of the hypanthium	Indistinct, not welldeveloped, less than half the length of the hypanthium
Connective appendages	Fimbriate filiform on the alternipetalous stamens	A filiform pair or absent on the alternipetalous stamens

Taxonomic history

The genus *Macrolenes* was established by Naudin (1851) to accomodate a Javanese woody climber described as *Maieta annulata* by Ventenat (1803). Naudin regarded *Maieta* as Neotropical only, and considered the Palaeotropical species to belong to a new genus. The name *Macrolenes* is based on the Greek words 'makros', large, and 'lenos', wool, referring to the long and large, fimbriate, filiform appendages on the stamens (Backer 1936; Maxwell 1980a). Naudin regarded the genus to be morphologically very similar to *Dissochaeta* based on the climbing habit and characters of the flowers, but different in having larger calyx lobes and different connective appendages (Naudin 1851; Bakhuizen van den Brink 1943; Maxwell 1980a, 1984; Kartonegoro et al. 2018).

For many years, the name *Marumia* Blume was used for species of *Macrolenes* (Triana 1872; Clarke 1879; Cogniaux 1890, 1891; King 1900; Ridley 1922) until Bakhuizen van den Brink (1943) recognised that *Marumia* Blume (1831a, 1831b) is an illegitimate name under the Code (Turland et al. 2018) because it is a later homonym of *Marumia* Reinw. He then reestablished *Macrolenes* and also pointed out that the first legitimate name in the genus was published by Naudin (1851), and not by Miquel (1855) as had been assumed, as the short generic description by Naudin is sufficient for valid publication (Bakhuizen van den Brink 1943; Veldkamp 1979). This nomenclatural problem began when Blume (1823) took up Reinwardt's genus name of *Marumia* when he transferred four species of *Saurauia* Willd. into it. At that time, however, *Marumia* had itself still not been validly published as it lacked a description (Turland et al. 2018 – Art. 38.1). Unfortunately, Nees von Esenbeck (1825) did not rectify this, when he reviewed Blume's work. In 1828, Reinwardt validated the name *Marumia* and regarded the genus as close to *Vanalphenia* Lesch. and *Scapha* Noronha, two genera now included in *Saurauia* in the Actinidiaceae. Blume (1831a, 1831b), however, considered *Marumia* Reinw. to be a synonym of *Reinwardtia* Blume ex Nees (also Actinidiaceae), which is a later homonym of *Reinwardtia* Dumort. Blume (1831a, 1831b) decided to adopt the generic name as a distinct genus within the Melastomataceae based on

a newly described species (*Marumia zeylanica* Blume) and three species transferred from *Melastoma* L. (*M. muscosa* (Blume) Blume, *M. nemorosa* (Jack) Blume and *M. stellulata* (Jack) Blume). Under today's Code, Blume's use of the name for another genus is illegitimate under article 53.1 (Turland et al. 2018).

Naudin (1851) was unaware of the relationship between *Macrolenes* and *Marumia* when he accepted both names and proposed the new species *Marumia echinulata* Naudin, thinking that *Marumia* could be distinguished by pentamerous instead of tetramerous flowers. Miquel (1855) considered *Macrolenes* as doubtfully distinct from *Dissochaeta*, an opinion shared by Bentham & Hooker (1867) and other botanists (Triana 1872; Clarke 1879; Cogniaux 1890, 1891; Krasser 1893; King 1900; Ridley 1922).

In this revision, seventeen species are recognised. Thirteen were already known, one new combination is made and three species are described as new. All species are endemic to the Malesian region, especially to the western part including the southern part of the Peninsular Thailand. *Macrolenes nemorosa* (Jack) Bakh.f., *M. pachygyna* (Korth.) M.P.Nayar and *M. stellulata* (Jack) Bakh.f. are widespread but absent from Java. This revision is solely based on morphological features from herbarium specimens.

Materials and methods

Material for the study, including online specimen images (https://plants.jstor.org/collection), was provided by the following herbaria: AAU, ANDA, BK, BM, BO, BR, E, G, K, KEP, L, M, P, PE, PNH, SING, and U (herbarium acronyms follow Thiers 2018). Measurements were made on representative herbarium specimens. Surface indumentum of the leaves, flowers and fruits were examined from dried specimens, flower and fruit colour in vivo were obtained from data on the labels; the latter were also the source for the ecological notes, vernacular names and local uses of a species. Species delimitation in this revision is based mostly on the shape, size and indumentum of the calyx tube or the hypanthium. Some species have different types of hairs on branchlets, leaves and the hypanthium, e.g., *Macrolenes dimorpha* (Craib) J.F.Maxwell, *M. hirsuta* (Cogn.) J.F.Maxwell, and *M. stellulata*. Unlike *Dissochaeta*, the stamens and the depth of the extra-ovarial chambers are uniform among the species and, therefore, not useful as specific characters.

General morphology

Habit

The species of *Macrolenes* are, like those of *Dissochaeta*, woody climbers with a scrambling growth habit. Usually, the plants climb in small trees or shrubs and very rarely climb into high trees. In some species, adventitious roots are common, which lignify and soon desiccate and become a hook-shaped structure (Clausing & Renner 2001a). The branchlets may be terete and glabrous, or covered by a stellatefurfuraceous, tomentose to slightly setose indumentum. The nodes are usually swollen with a distinct interpetiolar ridge, sometimes with only an annular ridge or sometimes a crest-like appearance (e.g., *Macrolenes annulata* (Vent.) Naudin and *M. stellulata*).

Leaves

The phyllotaxis of all species of *Macrolenes* is opposite and, as in *Dissochaeta*, the leaves are arranged in two rows (Kartonegoro et al. 2018). The leaves of several species are

coriaceous when dry. The shape of the blades varies from broadly ovate to elliptic to oblong. The apex of the blades is usually acuminate, the margin entire and the base subcordate to cordate. An acrodromal venation is common in *Macrolenes* with one pair of lateral veins arising from the base, just beside the midrib, and an additional pair of intramarginal veins also present. In general, the leaf blades have numerous secondary veins and the finer veins form a reticulate pattern; the midrib is sunken above and raised below (Maxwell 1984). The upper surface is usually glabrous with a glossy green colour, while the lower part varies from glabrous, to puberulous to furfuraceous to tomentose with a brownish colour. On the lower surface of the leaf blade a pair of hair cushions (domatia) at the base is common (Fig. 4-1a), which are patches of simple or stellate hairs that are persistent when dry (Maxwell 1984). This domatia feature is found in all species in the genus and can be used to distinguish it from *Dissochaeta*. This feature resembles a pair of glandular patches at the base of the leaf blades in some species of *Dissochaeta*, the function of which is also still unknown (Maxwell 1984; Kartonegoro et al. 2018). Similar to *Dissochaeta*, the petiole in *Macrolenes* is terete or cylindrical with a dorsal groove that may give the petiole a flat appearance. The indumentum of the petiole is commonly similar to that of the branchlets (Kartonegoro et al. 2018).

Inflorescences

The inflorescences of *Macrolenes* are axillary and consist of few-flowered cymes with 1–15 flowers. The main axes of the cymes are usually terete, angular or 4-angled with distinctly swollen nodes. The indumentum is similar to that of the branchlets. *Dissochaeta* can have high order ramifications, up to 5 orders (Maxwell 1984; Kartonegoro et al. 2018), but the ramifications in *Macrolenes* usually have 1–3 orders of opposite branches that end with 3-flowered cymules in the last ramification. Sometimes the inflorescence only consists of a single flower in the leaf axil. The central flower of the terminating cymules has one less order of ramification and has a pedicel longer than that of the two lateral ones (Maxwell 1984). The central flower will mature and bloom first and is followed later by the two lateral ones simultaneously. Bracts and bracteoles are paired and vary from linear to ovate, but are usually caducous. The bracts are present on the nodes of each ramification, while the bracteoles are found on each pedicel, where they subtend a single flower.

Hypanthium and calyx

The shape of the hypanthium varies from tubular to campanulate to suburceolate. The indumentum of the hypanthium is an important character for distinguishing the species in *Macrolenes*. There is a range from glabrous to tomentose to floccose or setose with or without dense bristle hairs, sometimes the surfaces are tuberculate. The bristle hairs vary from simple to branched, with or without a barbed tip. Several species, such as *Macrolenes hirsuta*, *M. pachygyna* and *M. stellulata*, are found with branched or barbed-tip bristle hairs. The size of the hypanthium can be used to distinguish *Macrolenes* from *Dissochaeta* as *Macrolenes* always has a larger hypanthium than *Dissochaeta*. Another important character is in the calyx lobes, which are usually welldeveloped, distinctly triangular or rounded and mostly have a length similar to the hypanthium (Fig. 4-1b).

Petals

The petals are thin, conspicuous, symmetric, colourful and have a visible venation. They are usually obovate or suborbicular with an obtuse apex and clawed base. The colour of the petals varies from white to pink to bright purple, but cannot be used to distinguish the species. The petals are not reflexed when mature.

Fig. 4-1. Morphology of *Macrolenes*. **a.** Leaves with a pair of hair cushions at the base in *Macrolenes stellulata*; **b.** Hypanthium with well-developed and reflexed calyx lobes in *Macrolenes nemorosa*; **c.** Flower with fimbriate appendages on the connectives of the alternipetalous stamens in *Macrolenes muscosa*. **a** from *Forbes 3008* (K); **b** from *Kartonegoro 1070* (BO); **c** from *Kartonegoro 1108* (BO). (Photos: A. Kartonegoro)

Stamens

Unlike the similar genera *Creochiton* Blume and *Dissochaeta*, the characters of the stamens in *Macrolenes* are not considered to be of great taxonomic importance to distinguish the species. This is because in all species the stamens are uniform in shape and number (Maxwell 1984; Kartonegoro & Veldkamp 2010, 2013; Kartonegoro et al. 2018). All species have 8 heterantherous, fertile stamens in usually two, dimorphic staminal whorls, an outer, alternipetalous one, and an inner, oppositipetalous one (Maxwell 1980a; Nayar 1980). The alternipetalous stamens are known as pollinating stamens and the oppositipetalous ones are the feeding stamens (Kadereit 2006; Kartonegoro & Veldkamp 2010). Staminodes are unknown in *Macrolenes* as all stamens are well-developed in the flowers.

All stamens have filaments that are equal in shape, they are flattened and curved sideways when mature. The length and direction of the filaments are uniform and they curve in the opposite direction to that of the style (Fig. 4-1c). The stamens are inserted within the hypanthium in the extra-ovarial chambers. Before anthesis, the filaments face towards the outside while the anthers face towards the inside, similar to *Dissochaeta* (Maxwell 1984; Kartonegoro et al. 2018). The filaments that alternate with the petals are straight and the point

of attachment with the anthers is clearly on the top, while those opposite to the petals are sharply bent and incurved before reaching the point of attachment with the anthers and the attachment to the anther is called the stipopodium (Veldkamp et al. 1979; Maxwell 1984; Kartonegoro et al. 2018). Both types of anthers are basifixed.

The anthers are elongated and glabrous and open distally with a single pore. In mature flowers the anthers reverse their orientation from being folded next to the filaments to bending upwards away from the filaments (Maxwell 1984; Kartonegoro et al. 2018).

When the flowers are mature, the anthers of the alternipetalous stamens are curved in a sickle-shape, while the anthers of the oppositipetlaous stamens are hooked or 'S'-shaped. The oppositipetalous anthers are usually thicker and shorter than the alternipetalous ones. The connective of the alternipetalous anthers is usually sterile in the basal part and lacks a theca. This sterile zone is known as the pedoconnective and is found in some taxa of the Melastomataceae and varies in size correlating with the size of the stamens (Kadereit 2006; Wong 2016; Kartonegoro et al. 2018). A pedoconnective in the oppositipetalous stamens is uncommon or not developed. The base of the pedoconnective usually has basal appendages or a crest that is prolonged into several fimbriate or capillary appendages (Fig. 4-1c). The connective in the oppositipetalous stamens extends from the lower part of the thecae and is adaxially bifid, or has ligular, erose or spuriform appendages and laterally or basally a pair of filiform appendages.

Ovary

The relative length of the ovaries varies from about ⅓ the length of the hypanthium to nearly as long as the hypanthium. The ovary has a villous indumentum. The ovary tip is usually rounded or conical. The placentation of the ovules in *Macrolenes* is similar to the other genera in the tribe Dissochaeteae (except for a few *Creochiton* species), axillary with one placenta in each of the four locules; the placenta is attached to the middle of the central column (Maxwell 1984). The style in bud is straight and at maturity slightly curved, especially at the tip. The direction of curve of the style is usually opposite to that of the curve of the filaments. The stigma of all species is minute and capitate to inconspicuous. There are 8 extra-ovarial chambers, which mostly extend from the top of the ovary to the middle or base. The anthers included to these chambers when immature and still in bud.

Fruit

Like in all other genera in tribe Dissochaeteae, the fruits of *Macrolenes* are berries, ovoid to urceolate and colourful when mature, with four persistent remnants of the calyx lobes. The indumentum of the fruits resembles that of the hypanthium and the colour is green at first, later ripening to dark blue to purple. Clausing et al. (2000) suggest that, unlike in *Dissochaeta*, in *Macrolenes* the hard berries are characterized by a persistent endocarp in which the ground tissues of the mesocarp and hypanthium are not fused and in both the ground tissue contains a dense ring of sclereids. Based on our observations, we cannot confirm this as a constant differentiating character. The seeds are cuneate, flat-topped and smooth.

Distribution and ecology

Macrolenes is mainly distributed in West Malesia: Malay Peninsula, Sumatra, Java and Borneo. Some species are also found in the southern part of Peninsular Thailand. The genus has never been recorded in Cambodia, Laos or Vietnam or further to the west. It is also absent in eastern Malesia (Philippines, Sulawesi, Lesser Sunda Islands, Moluccas and New Guinea).

Ecologically, *Macrolenes* resembles *Dissochaeta*, as the species are woody climbers in tropical evergreen and perpetually wet forest types with little or no seasonal variation in temperature and rainfall (Maxwell 1984; Clausing & Renner 2001a; Kartonegoro et al. 2018). The genus is predominantly found in secondary vegetation or in more open places within primary vegetation, such as tree fall gaps, river margins and roadsides. The plants climb several metres high and produce their flowering and fruiting branches over the tops of trees and larger shrubs. These woody climbers apparently only flower when the branchlets are in an exposed location. Branchlets that are not exposed to direct sunlight, regardless of their height in the forest or maturity, do not produce flowers (Maxwell 1984).

Most species are confined to lowland and hilly areas up to 1500 m elevation and occur in a variety of lowland forest types, such as mixed dipterocarp forest, heath forest or swampy forest. Some taxa are found in montane forest, e.g. *Macrolenes glabrata* M.P.Nayar, *M. muscosa* (Blume) Bakh.f. and *M. neglecta* M.P.Nayar. There is no specific flowering and fruiting season and the plants flower and fruit throughout the year.

Taxonomic treatment

Macrolenes Naudin

Macrolenes Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851. — Type: *Macrolenes annulata* (Vent.) Naudin.

Marumia Blume, Flora 14: 503. 1831, nom. Illeg., non Reinw. (1828). — Lectotype (designated here): *Marumia muscosa* (Blume) Blume [=*Macrolenes muscosa* (Blume) Bakh.f.].

Maieta auct. non Aubl.: Vent., Choix Pl. 32. 1803. *p.p.*, excl. type.

Melastoma auct. non Burm. ex L.: Jack, Trans. Linn. Soc. London 14: 3. 1823; Blume, Bijdr. Fl. Ned. Ind. 17: 1067. 1826; DC., Prodr. 3: 144. 1828. *p.p.*, excl. type.

Huberia auct. non DC.: DC., Prodr. 3: 167. 1828; G.Don, Gen. Hist. 2: 779. 1832. *p.p.*, excl. type.

Dissochaeta auct. non Blume: Clausing in S.S.Renner et al., Fl. Thailand 7(3): 418. 2001. *p.p.*, excl. type.

Woody climbers, scrambling; bark tan to light brown, finely fissured. Branchlets terete; glabrescent to tomentose or floccose with minute stellate or simple glandular or eglandular bristle hairs; adventitious roots common; nodes swollen, with an interpetiolar annular line, ridge or crest. Stipules not present. Leaves opposite, simple; petioles terete, with a dorsal groove, glabrescent to tomentose; blades ovate to oblong, membranous to subcoriaceous, base shallowly cordate, margins entire, apex acute to acuminate, midvein with 1 pair of lateral veins and 1 pair of intramarginal veins, secondary venation reticulate; adaxially glabrous, greenish glossy, abaxially glabrous to densely brown tomentose, basally with a pair of hair cushion domatia of simple or stellate hairs. Inflorescences axillary, cymose, with 1–15 flowers, often paniculate thyrses with 1–3 ramifications, generally ending in 3-flowered cymules; main axis terete or quadrangular, indument similar to that of the branchlets; bracts and bracteoles distinct or minute, linear to ovate or suborbicular, densely stellate-tomentose, often ciliate or serrate, rarely inconspicuous and early caducous; pedicels longer in the central flower, shorter in the lateral ones, furfuraceous to tomentose, sometimes with bristle hairs. Flowers 4-merous. Hypanthium campanulate, urceolate or tubular, glabrous to densely tomentose or rarely floccose with minute brown stellate hairs, with or without simple or branched- or barbed-tip bristle hairs, usually covered by minute brown stellate hairs,

sometimes tuberculate; calyx lobes distinct, triangular, ovate or lanceolate, generally at least half as long as the hypanthium, glabrous or densely tomentose, with or without bristle hairs, margin often ciliate, apex acute or rounded. Petals in bud conical, tip acute, blades half overlapping along one side, glabrous or tomentose; mature petals ovate, obovate or spathulate, symmetric, clawed, base thin, apex obtuse, glabrous or tomentose along the margin of the half overlapping dorsal margin, white, pink or violet. Stamens 8, heterantherous, dimorphic, in two rows, 4 alternipetalous and 4 oppositipetalous, all fertile, smooth, thecae with terminal pore; filaments flattened, straight in bud, curved sideways when mature, glabrous, white or yellowish; the alternipetalous ones longer and thinner than the oppositipetalous ones, when mature sickle-shaped, at base forming a pedoconnective, connective basal crest membranous, annular, prolonged into several fimbriate, filiform appendages, laterally sometimes an additional pair of filiform appendages, longer than the fimbriate appendages; the oppositipetalous stamens hooked or S-shaped when mature, connective ridge with erose, bifid or keeled appendages, basally extended with a pair of filiform appendages. Ovary half to ¾ as long as the hypanthium, 4-locular, apex generally villous and bristly; style curved at the tip when mature, curved in the opposite direction to the curve of the filaments; stigma minute, capitate; ovary concrescent with the hypanthium, with 8 longitudinal septa forming extra-ovarial chambers for the anthers, reaching to (nearly) the base of the ovary. Fruits baccate, ovoid to urceolate, glabrous to floccose, hairs similar to those on hypanthium; with four prominent reflexed calyx remnants. Seeds numerous, cuneate, smooth, flat-topped.

Distribution — Seventeen species found in the southern part of Peninsular Thailand, Malay Peninsula, Sumatra, Java and Borneo (Map 4-1).

Map 4-1. Distribution of *Macrolenes* (dark grey).

Habitat & ecology — Predominantly found in secondary vegetation or more open places within primary vegetation, such as tree fall gaps, river margins and roadsides (Maxwell 1984; Kadereit 2006) in several types of everwet forest, of which the preferred habitats are evergreen forest, mixed dipterocarp forest, and submontane forest. They climb several metres high and produce their flowering and fruiting branches only in open space over the tops of small trees and larger shrubs or bushes.

Notes — Even though *Macrolenes* is similar in habit, flower merosity, stamen type and habitat preference to *Dissochaeta*, the genus can easily be distinguished by its combination of axillary inflorescences, leaf blades with an abaxial pair of hair cushion domatia at the base, large flowers, distinct calyx lobes, fimbriate filiform appendages on the connective of the alternipetalous stamens and a distinct bristle indumentum on the hypanthium. The number and type of stamens and their connective appendages are important for species recognition in *Dissochaeta*, but these characters are uniform in *Macrolenes*.

Key to species of *Macrolenes*

1 Branchlets covered with minute stellate hairs and dense simple bristle hairs 2
1 Branchlets glabrescent, stellate-furfuraceous or -tomentose, floccose, with or without scattered bristle hairs 3
2 Branchlets covered with c. 0.75 mm long thick, brown and prominent bristle hairs [Borneo] ..... **8. *M. hirsuta***
2 Branchlets covered with 2–3 mm long simple slender, dark-maroon bristle hairs [Malay Peninsula, Sumatra] ..... **5. *M. echinulata***
3 Petioles with scattered slender black bristle hairs, 3–5 mm long [Borneo] .... **2. *M. bipulvinata***
3 Petioles without any bristle hairs 4
4 Hypanthium and fruits without bristle hairs [Southern Thailand, Peninsular Malaysia, Sumatra & Borneo] ..... **11. *M. nemorosa***
4 Hypanthium and fruits (unknown for *M. neglecta*) covered with scattered or dense bristle hairs/tubercles 5
5 Bristle hairs on hypanthium glabrous, not covered with minute stellate hairs 6
5 Bristle hairs/tubercles on hypanthium covered with minute stellate hairs 8
6 Leaf blades abaxial sparsely stellate-puberulous to glabrous; calyx lobes lanceolate [Sumatra & Java] ..... **1. *M. annulata***
6 Leaf blades abaxial stellate-tomentose to pubescent; calyx lobes ovate or triangular 7
7 Bracteoles ovate, margin serrate, glabrous, persistent [Sumatra] ..... **10. *M. neglecta***
7 Bracteoles subulate, margin entire, pubescent, caducous [Thailand] ..... **6. *M. esetosa***
8 Bristle hairs on hypanthium strongly and prominently branched or barbed at tip 9
8 Bristle hairs/tubercles on hypanthium simple, not branched or barbed at tip, capitate to some slightly branched 11
9 Nodes with annular crest-like interpetiolar ridge; leaf blades abaxially stellate-puberulous; bracts ovate, 10–12 mm long, margin ciliate, persistent; hypanthium tubular, greyish when dry [Peninsular Malaysia, Sumatra, Borneo] ..... **14. *M. stellulata***
9 Nodes with simple interpetiolar ridge; leaf blades abaxially stellate-tomentose; bracts linear or lanceolate, 5–8 mm long, margin not ciliate, caducous; hypanthium campanulate to suburceolate, brownish when dry 10
10 Pedicels stellate-furfuraceous and without bristle hairs; hypanthium with branched- or barbed-tip bristle hairs which are covered with minute stellate hairs from apex to base [Sumatra, Borneo] ..... **12. *M. pachygyna***

10 Pedicels stellate-furfuraceous and covered with bristle hairs; bristle hairs of hypanthium with minute stellate hairs at apex only, base glabrous [Borneo] ..... **17. *M. veldkampii***
11 Leaf blades abaxial glabrous; petioles 15–25 mm long; hypanthium with simple unbranched-tip or weakly branched at tip, 5–6 mm long bristle hairs [Peninsular Malaysia] ..... **7. *M. glabrata***
11 Leaf blades abaxial stellate furfuraceous, tomentose or floccose; petioles 5–12 mm long; hypanthium with simple capitate or non branched-tip 0.5–5 mm long bristle hairs/tubercles 12
12 Margin of calyx lobes with dense bristle hairs, ciliate 13
12 Margin of calyx lobes without dense bristle hairs, not ciliate 14
13 Leaf blades subcoriaceous; petioles c. 10 mm long; bristles in hypanthium fully covered by minute stellate hairs; calyx lobes triangular, 5–6 × 2–3 mm; petals in bud brown tomentose or pubescent [Sumatra & Java] ..... **9. *M. muscosa***
13 Leaf blades membranous; petioles 6–8 mm long; bristles in hypanthium covered by minute stellate hairs only at tip; calyx lobes slightly triangular, 9–11 × 4–6 mm; petals in bud glabrous [Sumatra] ..... **15. *M. subulata***
14 Hypanthium campanulate-cyathiform, calyx lobes triangular 3.5–5 mm long; petals in bud stellate-furfuraceous; ovary ¾ as long as hypanthium 15
14 Hypanthium campanulate or campanulate-tubular, calyx lobes triangular 5–15 mm long; petals in bud glabrous (unknown for M. rufolanata); ovary ⅔ as long as hypanthium .. 16
15 Branchlet, petiole and inflorescence axes floccose; bracts and bracteoles oblong or lanceolate, persistent; hypanthium floccose and with scattered 1–2 mm long capitate bristle hairs [Borneo] ..... **3. *M. bruneiensis***
15 Branchlet, petiole and inflorescence axes tomentose; bracts and bracteoles minute, less then 1 mm long, caducous; hypanthium tomentose and with c. 0.5 mm long tubercles [Sumatra] ..... **16. *M. tuberculata***
16 Nodes with interpetiolar crest-like ridge; leaf blade membranous; bracteoles elliptic or elliptic-oblong, 10–12 mm long, persistent; hypanthium with up to 4 mm long bristle hairs; calyx lobes 9–15 × 6–8 mm [Thailand, Peninsular Malaysia, Sumatra] .... **4. *M. dimorpha***
16 Nodes with interpetiolar simple ridge; leaf blade subcoriaceous; bracteoles ovate, 2–3 mm long, caducous; hypanthium with up to 1.5 mm long bristle hairs; calyx lobes 5–7 × c. 3 mm [Peninsular Malaysia] ..... **13. *M. rufolanata***

1. *Macrolenes annulata* (Vent.) Naudin — Map 4-2

Macrolenes annulata (Vent.) Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851. — *Maieta annulata* Vent., Choix Pl. 32. 1803. — *Huberia annulata* (Vent.) DC., Prodr. 3: 167. 1828. — *Marumia annulata* (Vent.) Triana, Trans. Linn. Soc. London 28: 82. 1872. — Type: *F. de Lahaye s.n. "2860"* (holo G-DC [G00341515!]), Indonesia, Java.

Marumia zeylanica Blume, Flora 14: 505. 1831. — *Macrolenes zeylanica* (Blume) Bakh.f., Contr. Melastom. 212. 1943. — Type: *Leg. Ign. (Herb. Van Royen)* (holo L [L0537198!]), Zeylania??.

Marumia horsfieldii Miq., Fl. Ned. Ind. 1(1): 536. 1855. — Lectotype (designated here): *T. Horsfield 19* (lecto L [L0537199!]; isolecto K [K000867116!]), Indonesia, Java, G. Praoe.

Climbing up to 30 m high. Branchlets terete, 3–5 mm in diameter, glabrous or glabrescent; nodes swollen, with a 1–3 mm wide annular crest-like interpetiolar ridge; internodes 3.8–5 cm long. Leaves: petioles terete, 5–8 mm long, stellate-furfuraceous; blades elliptic to oblong, 8–14 × 2.5–5 cm, membranous, base shallowly cordate, margin entire, apex

acuminate, acumen 1–1.5 cm long, adaxially glabrous, dark green, abaxially sparsely stellate-puberulous to glabrous. Inflorescences 5–13 cm long, 1–3-flowered cymes to 10–20-flowered panicles; main axis angular, stellatefurfuraceous; primary axis 2–4 cm long with 1 node or in panicles up to 5 cm long with 2 nodes, secondary axis when developed 1–1.3 cm long or when in long panicles up to 2 cm long with 1 or 2 nodes, tertiary axis in panicles up to 1.5 cm long with 1 node; bracts linear, 5–6 mm long, stellate-furfuraceous, margin entire, caducous; bracteoles subulate to linear, ca. 5 mm long, stellate-furfuraceous; pedicels stellate-furfuraceous and with scattered simple bristle hairs, 4–5 mm long in central flowers, 1–3 mm long in lateral flowers. Hypanthium campanulate-tubular, 7–8 × 3–4 mm, covered with stellate-furfuraceous hairs and 1.5–2 mm long simple glabrous bristle hairs; calyx lobes lanceolate with truncate base, 4–5 × ca. 2 mm, sparsely stellate-furfuraceous, apex obtuse, margin entire, with short bristle hairs. Petals in bud conical, 8–10 mm long, glabrous; mature petals obovate, 10–14 × 9–10 mm, base clawed, apex obtuse, glabrous, pink. Stamens alternipetalous stamens with 10–11 mm long filaments, anther slender, sickle-shaped, thecae 15–17 mm long, pink to purplish, pedoconnective ca. 5 mm long, connective basal crest small, annular, prolonged into several fimbriate, filiform appendages, 4–5 mm long, lateraly with paired, filiform appendages, 5–6 mm long; oppositipetalous stamens with 8–9 mm long filaments, anthers S-shaped, thick, thecae 14–15 mm long, connective with a pair of ridges or keels, ca. 1 mm long, basally with paired, filiform lateral appendages, 4–6 mm long. Ovary half as long as hypanthium, apex villous; style 18–21 mm long, curved at apex, glabrous; stigma minute; extra-ovarial chambers extending from middle to base of the ovary. Fruits urceolate, 10–12 × 7–8 mm, sparsely covered with stellate-furfuraceous hairs and simple glabrous bristle hairs; calyx lobes persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Sumatra, Java.

Habitat & Ecology — Edge of primary lowland forest, disturbed forest or montane forest; at 350–1500 m elevation.

Note — 1. *Macrolenes annulata* can easily be recognised by its simple, 1.5–2 mm long bristle hairs on the hypanthium, but the branchlets, leaves and petioles are rather glabrous to glabrescent and lack bristle hairs. The species resembles *Macrolenes echinulata*, which also has dark maroon bristles on all parts except the leaves. *Macrolenes neglecta* is also similar due to its bristle hairs on the hypanthium, but differs in having subcoriaceous leaf blades that are tomentose underneath.

2. *Macrolenes annulata* does not occur in Sri Lanka or South Coast India, therefore it is doubtful that the holotype of *Marumia zeylanica* with the annotation "*herb. Van Royen*", Zeylania, was really collected on Sri Lanka (formerly Ceylon) or South India. It more likely came from Sumatra or Java where all other collections came from. Perhaps the specimen was transferred via Sri Lanka/S India to the Netherlands as the Dutch had trading posts in those areas.

Specimens examined — **INDONESIA.** Aceh: Mount Leuser Nat. Park., Gunung Bandahara, 800 m, 20 Mar 1975, *de Wilde & de Wilde-Duyfjes 15597* (K, L). Lampung: Kota Agung, 350 m, 19 May 1968, *Jacobs 8499* (K, L). North Sumatra: Serdang, Penampang road, 10 Jul 1929, *Coert 734* (L). South Sumatra: *Forbes 1832* (BM); *Forbes 2852* (BM, K, L). West Sumatra: Lima Puluh Kota, Atas Halaban, Bukit Ngalau Kasemeh, 580 m, 26 May 1994, *Hendra 9* (ANDA); *Ibid.*, *Nofril 69* (ANDA). Java: *Horsfield s.n.* (L); *de Lahaye s.n. "2860"* (G-DC). Central Java: Mount Prahu, *Horsfield 19* (K, L).

2. *Macrolenes bipulvinata* (Korth.) Bakh.f. — Map 4-2

Macrolenes bipulvinata (Korth.) Bakh.f., Contr. Melastom. 218. 1943. — *Dissochaeta bipulvinata* Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844. —

Marumia bipulvinata (Korth.) Triana, Trans. Linn. Soc. London 28: 82. 1872. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 218. 1943): *P.W. Korthals s.n.* (lecto L [L06346514!]; isolecto BR [BR519595!], P [P05283656!, P05283657!]), Indonesia, Borneo, SE Borneo, G. Rantau.

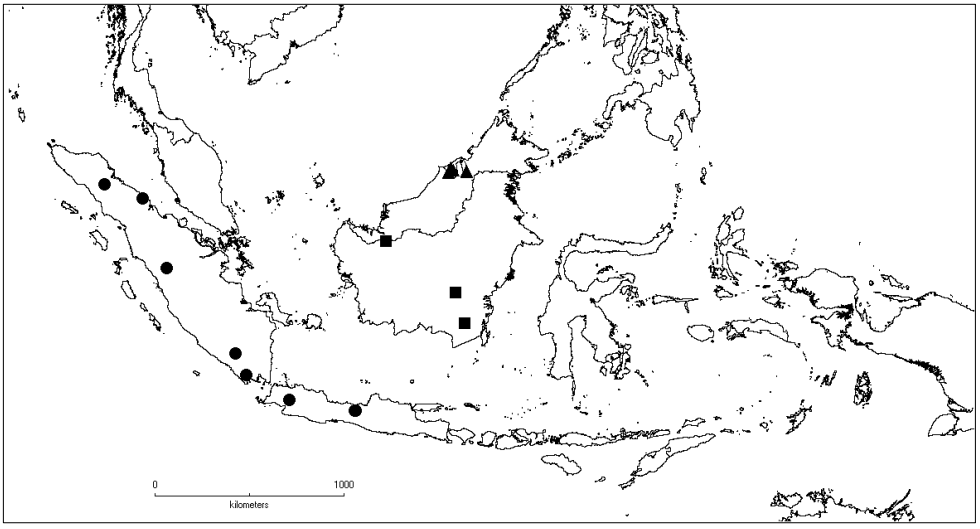
Climbing up to 2 m high. Branchlets terete, 3–6 mm in diameter, densely covered with brown stellate-furfuraceous to tomentose hairs and scattered, 3–5 mm long, simple, black bristle hairs; nodes swollen, with an annular crest on the interpetiolar ridges, densely brown tomentose; internodes 5–12 cm long. Leaves: petioles terete, c. 5 mm long, densely stellate-furfuraceous and with scattered, simple, black bristle hairs of 3–5 mm long; blades ovate-elliptic, 8.5–14 × 3–6.5 cm, subcoriaceous, base shallowly cordate, margin entire, apex acuminate, acumen ca. 5 mm long, adaxially glabrous or with scattered stellate hairs, abaxially brown tomentose. Inflorescences, flowers and fruits unknown.

Distribution — Borneo (Kalimantan).

Habitat & Ecology — Lowland Dipterocarp forest in open areas at ca. 150 m elevation.

Note — This species was described by Korthals in 1844 (Korthals, 1842–1844) based on only two collections with only vegetative branches and lacking any generative parts. The presence of a pair of hair cushions on the base of the leaves is typical for *Macrolenes*, and not *Dissochaeta*. The appearance of its branchlets and leaves resembles *Macrolenes pachygyna*, but the latter usually lacks bristle hairs. The bristle hairs in *Macrolenes hirsuta* are more prominent, thicker and erect and different from those of *M. bipulvinata*. *Macrolenes echinulata* has denser bristle hairs on branchlets and petioles, which are rather scatttered in *M. bipulvinata*.

Specimens examined — **INDONESIA.** South Kalimantan: Dusun, *Korthals s.n.* (L); Mount Rantau, *Korthals s.n.* (BR, L, P). West Kalimantan: Sintang, Ketungau Tengah, Nanga Kelapan, 150 m, 15 Apr 2014, *Kartonegoro & Pratama 781* (BO).



Map 4-2. Distribution of *M. annulata* (●); *M. bipulvinata* (■); and *M. bruneiensis* (▲).

3. *Macrolenes bruneiensis* Karton., **sp. nov.** — Fig. 4-2, Map 4-2

Type: *N. Nangkat 246* (holo BO!; iso BRUN!, K!, L!, SING), Brunei Darussalam, Belait District, Merangking-Buau Road, 10 August 1991.

Macrolenes stellulata auct. non. Bakh.f.: Bygrave & A.P.Davis, Checkl. Fl. Pl. Gymnosperms Brunei Darussalam 187. 1996. *p.p.* excl. type.

Diagnostic. Climber with dense floccose indumentum and also cyathiform hypanthium with rather short triangular calyx lobes, ca. 5 × 3.5 mm. Shape and size of the hypanthium closely resembles *Macrolenes tuberculata* Karton. but differs in indumentum type as *M. tuberculata* has a tuberculate indumentum.

Climbing up to 3 m high. Branchlets terete, 3–4 mm in diameter, floccose, densely covered with brown stellate-tomentose hairs; nodes swollen, with interpetiolar ridges, densely covered with brown stellate-tomentose hairs; internodes 4–4.5 cm long. Leaves : petioles terete, ca. 5 mm long, floccose, with densely brown stellate-tomentose hairs; blades ovate to ovate-elliptic, 8–10 × 3–4.5 cm, subcoriaceous, base subcordate, margin entire, apex acuminate, acumen 0.7–1 cm long, adaxially sparsely stellatefurfuraceous, dark green with prominent nervation, abaxially floccose, with dense brown stellate-tomentose hairs. Inflorescences 6–8 cm long, with 3–9 flowers; main axis terete, floccose, densely brown tomentose; primary axis 2.5–3.5 cm long with 1 or 2 nodes, secondary axis 1.3–1.5 cm long with 1 node, tertiary axis not developed; bracts oblong or lanceolate, 6–7 × 2–3 mm, stellate-tomentose; bracteoles lanceolate, 5–6 × ca. 2 mm, stellate-tomentose; pedicels floccose, densely stellatetomentose, 4–5 mm long in all flowers. Hypanthium campanulate-cyathiform, 9–12 × 6–7 mm, floccose, woolly, densely covered with dense brown stellate-tomentose hairs and scattered, 1–2 mm long capitate bristles; calyx lobes triangular with subacute tip, ca. 5 × 3.5 mm, densely stellate-tomentose, margin entire. Petals in bud conical, tip subacute, covered with stellate-furfuraceous hairs, 4–6 mm long; mature petals suborbicular, 7–9 × 7–8 mm, base clawed, apex obtuse, glabrous adaxially, half stellate-furfuraceous and half glabrous abaxially, white. Stamens : alternipetalous stamens with 4–5 mm long filaments, anthers curved, sickle-shaped, thecae 5–8 mm long, pedoconnective 3–4 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform, 4–5 mm long appendages, laterally with paired, filiform appendages, 5–6 mm long; oppositipetalous stamens with 4–5 mm long filaments, anthers hooked- or S-shaped, 5–6 mm long, connective with a minute thin keel or with ligular crest, ca. 0.3 mm long, basally with paired, filiform lateral appendages, 4–5 mm long. Ovary ¾ as long as hypanthium, apex pubescent; style 10–12 mm long, curved at tip, above glabrous, below stellate-tomentose; stigma minute, capitate; extra-ovarial chambers extending to the middle of the ovary. Fruits ovoid, 8–10 × 6–7 mm, brown, floccose, densely covered with ca. 1 mm long erect bristle hairs covered with densely crowded, minute, brown stellate hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

Distribution — Borneo (Brunei Darussalam).

Habitat & Ecology — Heath forest or secondary lowland dipterocarp forest at 30–300 m elevation.

Etymology — Species epithet name is after the country of occurrence.

Note — This species was initially believed to be *Macrolenes pachygyna*, but it differs in the bristle hairs on the hypanthium not being branched or barbed at the tip; the indumentum on the branchlets, leaves, petioles and hypanthium being rather floccose and very distinct when compared to other species; the shape of the hypanthium being rather cyathiform instead of tubular with short calyx lobes, ca. 5 mm long, and thereby resembling *M. tuberculata* but which has a different indumentum. *Macrolenes bruneiensis* is known only from Brunei Darussalam, Borneo.

Specimens examined — **BRUNEI.** Belait: Bukit Sawat, 30 m, 11 Jul 1995, *Hussain et al. BRUN 16866* (K, L); Labi, Bukit Teraja, 7 Dec 1991, *Kirkup et al. 456* (K); Merangking-

Buau Road, 10 Aug 1991, *Nangkat 246* (BO, K, L). Temburong: Amo, Bukit Tudal, 4 Oct 1994, *Davis et al. 469* (K); Gunung Retak, 250 m, 26 Apr 1992, *Johns et al. 7349* (K, L).

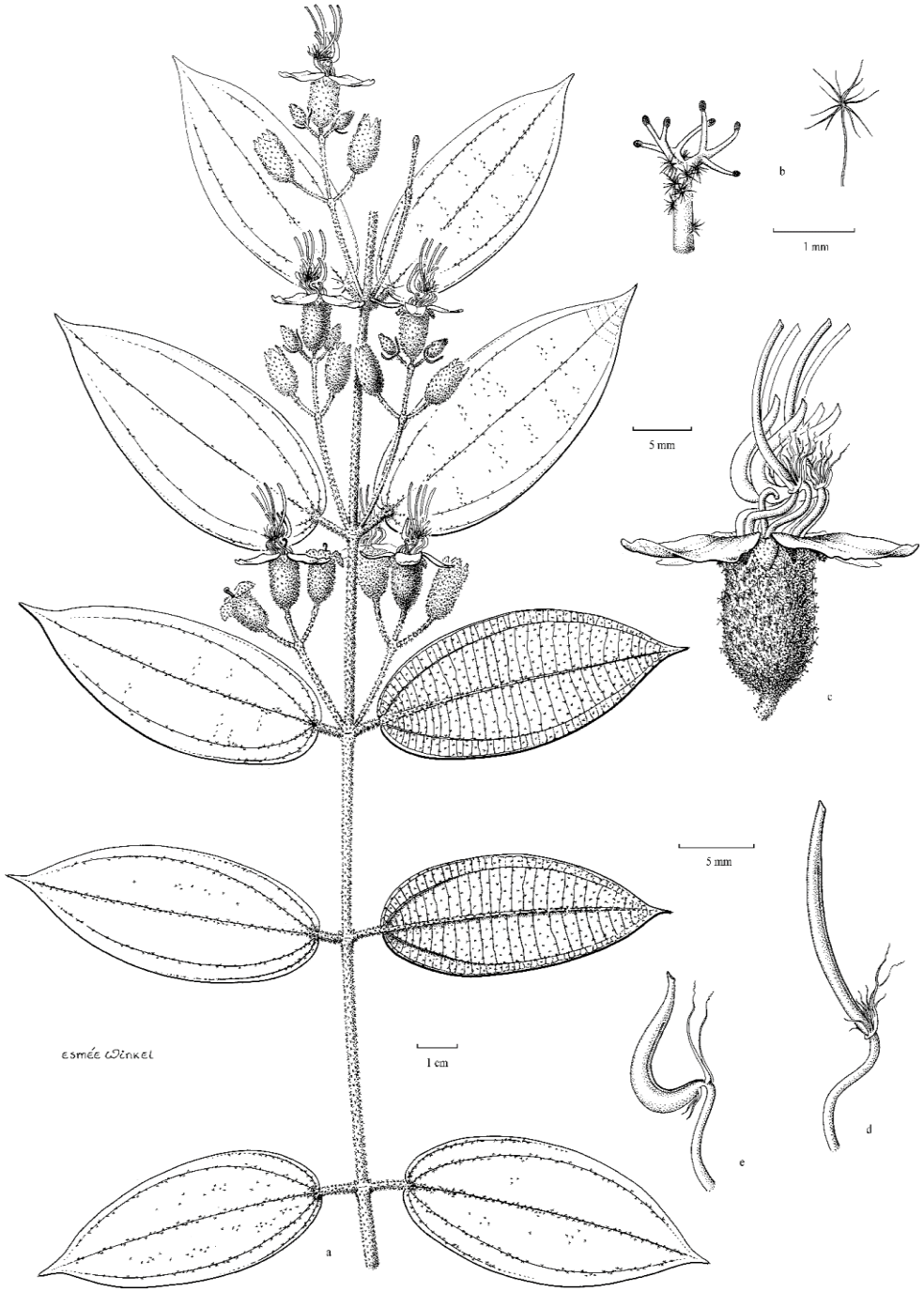


Fig. 4-2. *Macrolenes bruneiensis*. **a.** habit; **b.** indumentum; **c.** flower; **d.** alternipetalous stamen; **e.** oppositipetalous stamen. All from *Nangkat 246* (L). Drawn by Esmée Winkel.

4. *Macrolenes dimorpha* (Craib) J.F.Maxwell — Map 4-3

Macrolenes dimorpha (Craib) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — *Marumia dimorpha* Craib, Bull. Misc. Inform. Kew 1930: 320. 1930. — Lectotype (designated here): *A.F.G. Kerr 7283* (lecto K [K000859521!]; isolecto AAU!, BK [BK257159!], BM [BM000944449!], E [E00285930!]), Thailand, Yala, Bannang Sata, 50 m alt., 22 July 1923.

Dissochaeta affinis auct. non. Clausing: Clausing in S.S.Renner et al., Fl. Thailand 7, 3: 421. 2001. *p.p.*, excl. type.

Climbing up to 6 m high. Branchlets terete, 3–5 mm in diameter, densely covered with brown stellate-tomentose hairs and scattered, ca. 1 mm long, small, simple bristle hairs; nodes swollen, with an annular, crest-like, interpetiolar ridge; internodes 9.5–11 cm long. Leaves : petioles terete, ca. 10 mm long, densely stellate-tomentose; blades ovate-elliptic to elliptic, 11–17 × 5.2–8.4 cm, membranous, base cordate, margin entire, apex acuminate, acumen 1–1.5 cm long, adaxially glabrous, dark green, abaxially densely brown stellate-tomentose. Inflorescences up to 8 cm long, with 3–9 flowers; main axis angular, densely covered with stellate-tomentose hairs and scattered bristles; primary axis 4–8 cm long with 1–3 nodes, secondary axis 0.7–1.5 cm long with 1 node, tertiary axis not developed; bracts ovate-elliptic, 12–17 by 6–7 mm, stellate-tomentose; bracteoles elliptic or elliptic-oblong, 10–12 × 4–5 mm, densely stellate-tomentose, persistent; pedicels densely brown stellate-tomentose, also with scattered bristle hairs covered with small brown stellate hairs, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate-tubular, 12–14 × 7–8 mm, covered with brown stellate-tomentose hairs and sparsely with 1–4 mm long simple bristle hairs completely covered with dense stellate hairs; calyx lobes slightly triangular, 9–15 × 6–8 mm, densely brown stellate-tomentose, apex acute. Petals in bud conical, 5–6 mm long, glabrous; mature petals obovate or suborbicular, 22–28 × 21–26 mm, reflexed, base clawed, apex obtuse, glabrous, white to pinkish. Stamens : alternipetalous stamens with 14–15 mm long filaments, anthers slender, sickle-shaped, thecae 22–25 mm long, white, pedoconnective 8–10 mm long, basal crest enlarged into an annular crest, prolonged into several fimbriate, filiform appendages, 9–10 mm long, laterally with paired, filiform appendages, 9–11 mm long, rarely branching at end; oppositipetalous stamens with 14–15 mm long filaments, anthers S-shaped, thick, thecae 18–20 mm long, connective with a pair of ridges or keels, ca. 1 mm long, basally with paired, filiform lateral appendages, up to 10 mm long. Ovary half to ⅔ as long as hypanthium, apex villous; style 20–22 mm long, curved at apex, glabrous, pink; stigma minute; extra-ovarial chambers extending from middle to base of the ovary. Fruits urceolate, ca. 15 × 10–12 mm, densely covered with brown stellate-tomentose and simple bristle hairs covered with stellate hairs; calyx lobes persistent, reflexed. Seeds ca. 0.75 mm long.

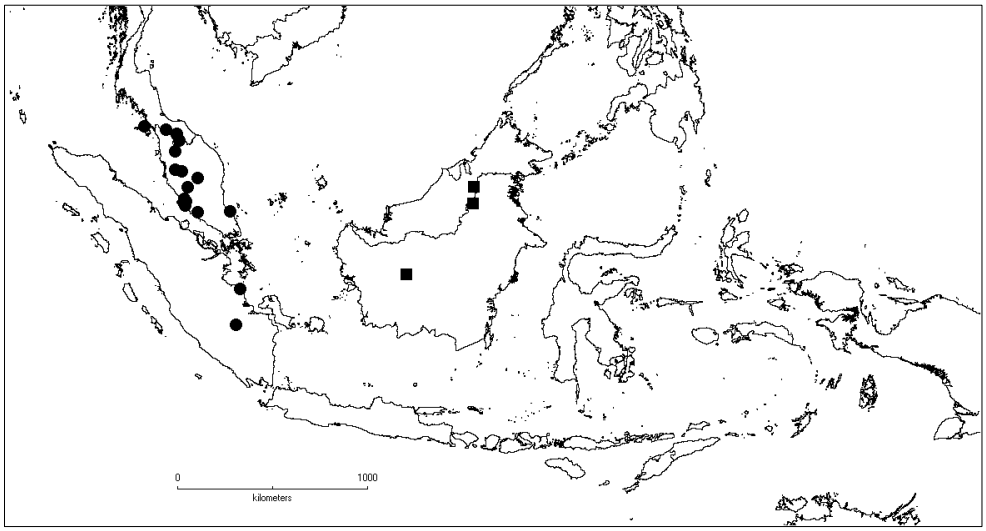
Distribution — Thailand (South), Peninsular Malaysia and Sumatra.

Habitat & Ecology— Disturbed lowland, swamp forest to low montane forest at road sides; 5–1550 m elevation.

Note — *Macrolenes dimorpha* can be distinguished by its short and unbranched bristle hairs on the hypanthium. The species resembles *Macrolenes rufolanata*, which also has short bristle hairs, but differs in also having dense bristle hairs on the calyx lobes, while *M. dimorpha* lacks bristles on the calyx lobes. Some specimens of *Macrolenes dimorpha*, collected in the montane forests of Peninsular Malaysia, have denser and longer bristle hairs on the surface of the hypanthium than the collections from the lowland.

Specimens examined — **THAILAND.** Satun: Teratao, 5 m, 18 Jan 1928, *Kerr 14163* (BM, K). Songkhla: Ban Prakawp, 50 m, 20 Jul 1928, *Kerr 15859* (BM, K, L). Yala: Bannang Sata,

50 m, 22 Jul 1923, *Kerr 7283* (AAU, BK, BM, E, K); *Ibid.*, Khao Pok Yok, 950 m, 16 Jun 1992, *Larsen et al. 42919* (P); Nikhom Kua Long, 100 m, 18 Dec 1972, *Santisuk & Nimanong 425* (K, L, P). **MALAYSIA.** Johor: Mersing-Endau Road, 13 Sep 1969, *Kochummen FRI 2797* (K, L). Kedah: Kroh, 120 m, 6 Aug 1941, *Nauen SFN 38047* (K). Malacca: *Hervey s.n.* (BM). Pahang: Fraser's Hill, 1250 m, 25 Aug 1959, *Burkill 2001* (K); *Ibid.*, 1550 m, 27 Sep 1978, *Maxwell 78-369* (L); Cameron Highlands, 1100 m, 21 Oct 1967, *Iwatsuki et al. M-13702* (L); *Ibid.*, 1550 m, 14 Apr 1978, *Maxwell 78-140* (L); *Ibid.*, *Maxwell 78-141* (L); Rompin, Lesong FR., 200 m, *Maxwell 80-77* (L). Perak: Grik, 20 Nov 1966, *Ismail KEP 98508* (K, L). Selangor: Fraser's Hill, 19 Jun 1967, *Carrick 1573* (K, L); *Ibid.*, 9 Jul 1966, *Stone* 6402 (K, L); RRI Station, 60 m, 17 Jan 1966, *Ng KEP 100016* (K, L); Klang, Bukit Changgang, 5 Oct 1937, *Nur SFN 34017* (K, L, P); Puchong, 8 Feb 1968, *Teo & Purseglove 26* (K, L). **INDONESIA.** Jambi: Sungai Pamusiran Dalam, 24 Feb 1975, *Apandi & Undang 11* (L). South Sumatra: Petaling, Sungai Lalang, 11 Dec 1979, *Laumonier TFB 361* (L).



Map 4-3. Distribution of *M. dimorpha* (●); and *M. hirsuta* (■).

5. *Macrolenes echinulata* (Naudin) Bakh.f. — Fig. 4-3, Map 4-4

Macrolenes echinulata (Naudin) Bakh.f., Contr. Melastom. 209. 1943. — *Marumia echinulata* Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 280. 1851. — *Dissochaeta echinulata* (Naudin) Clausing in S.S.Renner et al., Fl. Thailand 7(3): 425. 2001. — Lectotype (designated here): *C. Gaudichaud-Beaupré 79* (lecto P [P02274823!]; isolecto G [G00319903!], P [P02274821!, P02274822!, P02274825!, P02274826!]), Singapore, February 1837.

Marumia rhodocarpa Wall. ex Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 550. 1891. — Lectotype (designated here): *N. Wallich 4045* (lecto K [K000859533!]; isolecto K [K000859532!]), Singapore.

Marumia sumatrana Boerl. & Koord. In Koord.-Schum., Syst. Verz. 2: 46. 1911. — Type: *S.H. Koorders 22331β* (holo BO [BO1294109!]), Indonesia, Sumatra, Soengei Djati, 30 m alt., 10 March 1891.

Marumia zeylanica Blume var. *subglabrata* C.B.Clarke in Hook.f., Fl. Brit. India 2: 542. 1879. — *Marumia rhodocarpa* Wall. ex Cogn. var. *subglabrata* (C.B.Clarke) Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 551. 1891. — Lectotype (designated here): *T. Anderson*

64 (lecto K [K000859534!]; isolecto BM [BM000944446!], P [P05283589!]), Singapore, October 1861.

Marumia zeylanica auct. Non. Blume: Triana, Trans. Linn. Soc. London 28: 82 (1872); Clarke in Hooker, Fl. Brit. India 2: 542. 1879. *p.p.*, excl. type.

Climbing up to 3 m high. Branchlets terete, 3–4 mm in diameter, densely covered with stellate hairs and simple, dark maroon, 2–3 mm long bristle hairs; nodes swollen, with an interpetiolar ridge; internodes ca. 4 cm long. Leaves: petioles flattened, 5–10 mm long, densely covered with stellate-tomentose hairs and simple bristle hairs; blades ovate to elliptic, 7.5–14 × 3.8–5.8 cm, subcoriaceous, base subcordate to cordate, margin entire, apex acuminate, acumen ca. 1 cm long, adaxially glabrous, abaxially densely covered with brown stellate-tomentose hairs. Inflorescences 4–7 cm long, with 1–7 flowers; main axis angular, densely covered with stellate-tomentose hairs and bristles; primary axis 2.5–3 cm long with 1 or 2 nodes, secondary axis 1.5–2 cm long with 1 node, tertiary axis not developed; bracts leaf-like, elliptic-oblong, or linear, 4–5 × 1.2–1.6 cm when leaf-like, 5–7 mm long when linear, above glabrous, underneath stellate-tomentose; bracteoles linear or subulate, 2–4 mm long, densely stellate-tomentose, caducous; pedicels densely brown stellate-tomentose, 3–4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 10–12 × 5–6 mm, densely covered with brown stellate-tomentose hairs and 2–3 mm long, simple, glabrous bristle hairs; calyx lobes triangular-ovate, 7–10 × ca. 5 mm, apex acute, densely brown stellate-tomentose and bristly. Petals in bud conical, ca. 8 mm long; mature petals ovate to suborbicular, 15–18 × 12–13 mm, not reflexed, base clawed, apex obtuse, glabrous, white, pinkish. Stamens: alternipetalous stamens with 10–12 mm long creamy filaments, anthers slender, sickle-shaped, thecae ca. 20 mm long, white, pedoconnective ca. 5 mm long, connective basal crest enlarged into an annular crest with 5–7 fimbriate filiform appendages, 6–7 mm long, laterally with paired, filiform appendages, 6–8 mm long; oppositipetalous stamens with 10–12 mm long creamy filaments, anthers S-shaped, thick, thecae 10–11 mm long, connective with a pair of ridge or keels, ca. 1 mm long, basally with paired, filiform lateral appendages, 4–6 mm long. Ovary half as long as hypanthium, apex villous; style 15–18 mm long, curved at apex, glabrous; stigma minute; extra-ovarial chambers extending from middle to base of the ovary. Fruits urceolate, 13–15 × 9–10 mm, densely covered with brown stellate-tomentose and simple glabrous bristle hairs; calyx lobes persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Malay Peninsula & Sumatra.

Habitat & Ecology — Lowland or swampy forest, in open places at 30–40 m elevation.

Vernacular Name — Sumatra: *Kemunting akar* (Lingga).

Note — *Macrolenes echinulata* is easily echinulate by its dense simple, unbranched, dark maroon bristle hairs on the branchlets, petioles, inflorescence axes and hypanthium. The leaves are abaxially rather tomentose and lack bristles. The distribution of the species is restricted to the lowland forest of the southern part of the Malay Peninsula (Malacca, Johor and Singapore) and Sumatra (Riau and Riau Archipelago). Triana (1872) and Clarke (1879) considered this species to be a synonym of *Macrolenes zeylanica* (= *M. annulata*) because of the simple, glabrous, bristle hairs but they overlooked the difference in density and the fact that the bristle hairs in *M. annulata* only occur on the hypanthium, and not on the branchlets, where they are present in *M. echinulata*.

Fig. 4-3. *Macrolenes echinulata*. **a.** habit; **b**. branchlet; **c.** hypanthium; **d.** flower; **e.** mature fruits (Photos: C. Ng).

Specimens examined — **MALAYSIA.** Johor: Sungai Tukong, 30 m, 28 Jul 1930, *Spare F 828* (K). Malacca: *Cuming 2383* (K); *Gaudichaud-Beaupré s.n.* (P); *Griffith KD 2270* (K); *Maingay KD 785* (K, L). **SINGAPORE:** *d'Alleizette 2444* (L); *Gaudichaud-Beaupré 79* (G, P); *Seeman 2367* (K); *Anderson 64* (BM, K); *Anderson 68* (BM, K, P); *Lobb 42* (K); *Ridley 15470* (BM, K); *Ridley s.n.* (BM); *Schomburgh 68* (BM, P); *Walker 33* (BM, K); *Wallich 4045* (K); *King's Collector 278* (P); 7 Sep 1879, *King's Collector s.n.* (K); 11 Aug 1894, *Langlasse 178* (P); Jurong Road, 19 Oct 1932, *Corner SFN 26035* (K); Nee Soon, 25 Jun 1978, *Maxwell 78-334* (L); Seletar Reservoir, 11 Mar 1971, *Noor SRMN 13* (L); Ang Mo Kio, 8 Mar 1889, *Ridley 258* (BM); Mandai Road, 10 Dec 1949, *Sinclair s.n.* (L, P).

INDONESIA. Riau: Sunagi Jati, 30 m, 10 Mar 1891, *Koorders 22331β* (BO). Riau Archipelago: Lingga Island, Tanjung Buton, Kampung Daik, 30 m, 28 Jul 1919, *Bünnemeijer 7065* (BO, K, L).

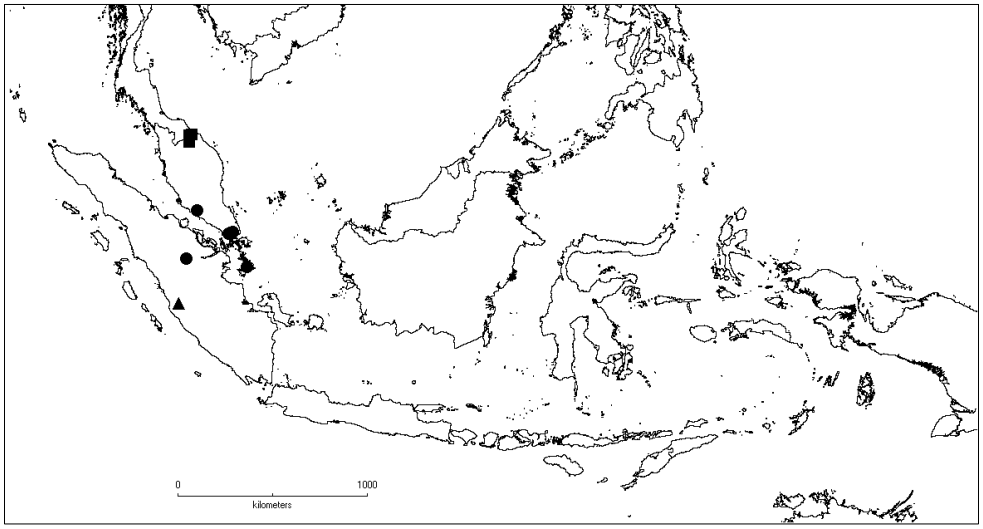


Fig. 4-4. Distribution of *M. echinulata* (●); *M. esetosa* (■); and *M. neglecta* (▲).

6. *Macrolenes esetosa* (Craib) Karton., **comb. & stat. nov.** — Map 4-4

Marumia rhodocarpa Wall. ex Cogn. var. *esetosa* Craib, Fl. Siam. Enum. 10: 697. 1931. — *Macrolenes echinulata* (Naudin) Bakh.f. var. *esetosa* (Craib) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — Lectotype (designated here): *D. Bourke s.n.* (lecto K [K000859518!]; isolecto BK [BK257157!]), Thailand, Narathiwat, Sungai Padi, August 1924.

Branchlets terete, 3–5 mm in diameter, glabrescent; nodes swollen, with interpetiolar ridge; internodes 5–9.5 cm long. Leaves: petioles terete or subangular, 6–12 mm long, pubescent with minute appressed greyish stellate hairs; blades ovate to elliptic-oblong, 6–14 × 3.2–5.5 cm, membranous, base subcordate, margin entire, apex acuminate, acumen 0.5–0.7 cm long, adaxially glabrous, dark green, abaxially pubescent, covered with minute greyish stellate hairs. Inflorescences 3.5–4.5 cm long, with 3–5 flowers; main axis angular, covered with greyish stellate-tomentose hairs; primary axis 2–2.5 cm long with 1–2 nodes, secondary axis ca. 0.5 cm long with 1 node, tertiary axis not developed; bracts lanceolate, 9–10 × 1.7–2 mm, stellate-tomentose, greyish; bracteoles subulate, ca. 2 mm long, stellate-tomentose, caducous; pedicels stellatefurfuraceous, bristly at apex, 3–5 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate-tubular, 8–11 × 5–6 mm, densely covered with greyish stellate-tomentose hairs and 1.5–2.5 m long, brown, thick, glabrous bristle hairs; calyx lobes triangular, 4–5 × 2–3 mm, reflexed, apex acute, rarely obtuse, sparsely bristly. Petals in bud conical, 5–6 mm long, glabrous; mature petals not seen, pink to violet (*Williams 17219*). Stamens (in bud): alternipetalous stamens with 5–7 mm long filaments, anthers slender, straight, thecae 10–14 mm long, pedoconnective 2–3 mm long, connective basal crest enlarged into an annular crest with several fimbriate, filiform appendages, 2–4 mm long, laterally with paired, filiform appendages, ca. 4 mm long; oppositipetalous stamens with 5–6 mm long filaments, anthers straight, thick, thecae 8–12

mm long, connective with a pair of ridges or keels, ca. 1 mm long, basally with paired, filiform lateral appendages, 4–5 mm long. Ovary half as long as hypanthium, apex pubescent; style 13–15 mm long, curved at apex, glabrous; stigma minute; extra-ovarial chambers extending from middle to base of ovary. Fruits urceolate to ovoid, 10–13 × 6–8 mm, sparsely covered with greyish stellate-tomentose hairs and dense 1.5–2.5 mm long brown, thick, glabrous bristle hairs; calyx lobes persistent, reflexed. Seeds ca. 0.5 mm long.
Distribution — Southern Peninsular Thailand (Narathiwat).
Habitat & ecology — Evergreen forest on roadside.
Note — *Macrolenes esetosa* was previously considered to be a variety of *M. echinulata* due to its hypanthium of minute stellate hairs and bristles that are simple without a branching tip (Craib 1931; Maxwell 1980b). Unlike *Macrolenes echinulata*, this species lacks bristle hairs on branchlets, petioles and inflorescence axes. The bristle hairs of *Macrolenes esetosa* are found only on the hypanthium and the upper part of the pedicels. The bristle hairs are erect and thicker than in *Macrolenes echinulata*, and have a golden-brown colouration, while in *M. echinulata* the bristle hairs are found on branchlets, petioles, inflorescence axes and hypanthium, and they are rather slender and dark maroon. The species also resembles *Macrolenes annulata* that also has a setose hypanthium, but *M. esetosa* differs in having a pubescent lower leaf surface and triangular calyx lobes (lower leaf surface sparsely stellate-puberulous to glabrous and calyx lobes lanceolate in *M. annulata*).
Specimens examined — **THAILAND.** Narathiwat: Sungai Padi, 14 May 1950, *Williams 17219* (K); *Ibid.*, Aug 1924, *Bourke s.n.* (BK, K); Waeng, 27 Nov 1962, *Sangkhachand 883* (L).

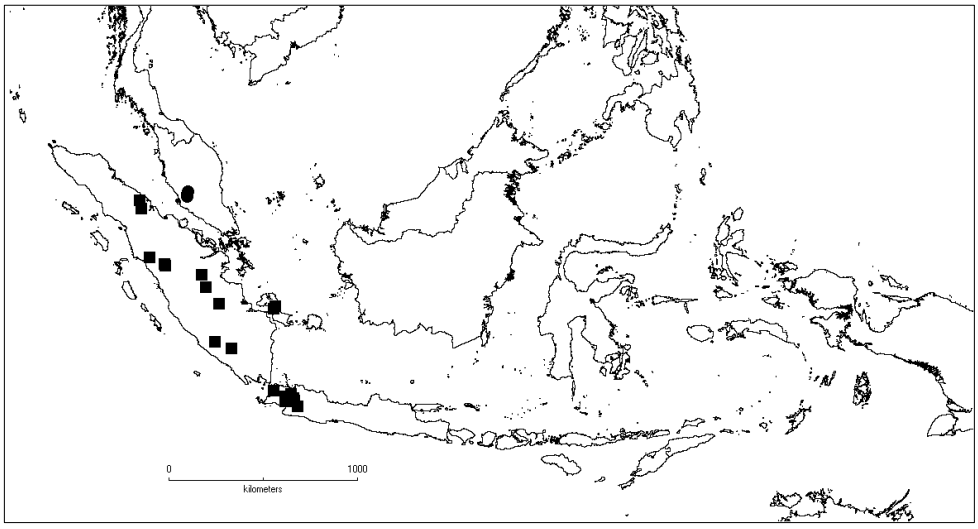
7. *Macrolenes glabrata* M.P.Nayar — Map 4-5

Macrolenes glabrata M.P.Nayar, J. Jap. Bot. 55: 48. 1980. — Type: *A.H. Millard 1756* (holo K!; iso KLU), Malaysia, Peninsular Malaysia, Selangor, Ulu Klang Ampang, 1 September 1959.

Branchlets terete, 3–6 mm in diameter, covered with minute brown stellatefurfuraceous hairs; nodes swollen, with an annular interpetiolar ridge; internodes 5–13 cm long. Leaves: petioles terete, 15–25 mm long, stellate-furfuraceous; blades ovate, 10–16 × 5–7 cm, subcoriaceous, base slightly cordate, margin entire, apex acuminate, acumen 1.5–2 cm long, adaxially glabrous, dark glossy green, abaxially glabrous, sparsely stellate-puberulous on midrib and veins. Inflorescences 7–10 cm long, with 3–9 flowers; main axis stellate-furfuraceous; primary axis 6–9 cm long with 1 or 2 nodes, secondary axis 1–2 cm long with 1 node or not developed, tertiary axis not developed; bracts linear, 8–10 mm long, stellate-furfuraceous, esetose, caducous; bracteoles linear, 4–6 mm long, stellate-furfuraceous, esetose, caducous; pedicels densely brown stellate-tomentose, 3–5 mm long in central flowers, 1–3 mm long in lateral flowers. Hypanthium urceolate, 10–12 × 6–8 mm, densely covered with brown stellate-tomentose hairs and 5–6 mm long bristles covered with minute stellate hairs, simple or weakly barbed and branched at tips; calyx lobes triangular-ovate with acute tips, 6–8 × 4–5 mm, densely covered with minute stellate hairs and bristle hairs at margin, inside glabrous. Petals in bud conical, 9–10 mm long, stellate-furfuraceous, apex rounded; mature petals suborbicular, 18–20 × ca. 18 mm, reflexed, base clawed, apex obtuse, glabrous inside, white with pinkish hue. Stamens: filaments white in lower half, yellow in upper half; alternipetalous stamens with ca. 15 mm long filaments, anthers curved, sickle-shaped, thecae 20–22 mm long, pedoconnective ca. 7 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform appendages, 6–7 mm long, lateral appendages, not or poorly developed; oppositipetalous stamens with ca. 12 mm long filaments, anthers S-

shaped, thecae 14–15 mm long, connective with a thin keel crest, extended with a pair of filiform 4–5 mm long appendages, lateral appendages paired, filiform, ca. 6 mm long. Ovary half as long as hypanthium, apex villous; style 23–25 mm long, curved at tip, glabrous, reddish; stigma minute; extra-ovarial chambers extending almost to base of ovary. Fruits urceolate, ca. 15 × 10 mm, glabrescent and covered with simple or barbed bristle hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.
Distribution — Peninsular Malaysia (Selangor).
Habitat & Ecology — Montane forest, in open area or road side at ca. 1500 m elevation.
Vernacular name — *Akar kelompang* (Selangor).

Note — This species resembles *Macrolenes stellulata* in the bristle hairs on the hypanthium, which are simple or weakly branched or barbed at the tip, but the leaves are rather glabrous on both surfaces, not tomentose. The species is known only from the mountain area of Genting Highlands at the border of Selangor with Pahang State.
Specimens examined — **MALAYSIA.** Selangor: Ulu Gombak, 31 May 1967, *Carrick 1563* (K, L); Genting Highlands, Gunung Ulu Kali, 1500 m, 3 Jun 1978, *Maxwell 78-311* (L); Ulu Klang Ampang, 1 Sep 1959, *Millard 1756* (K).



Map 4-5. Distribution of *M. glabrata* (●); and *M. muscosa* (■).

8. *Macrolenes hirsuta* (Cogn.) J.F.Maxwell — Map 4-3

Macrolenes hirsuta (Cogn.) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — *Marumia hirsuta* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 553. 1891. — Lectotype (designated here): *J.E. Teijsmann HB 8658* (lecto BO [BO1859504!]; isolecto BO [BO1859502!, BO1859503!], FI [FI007927!], U), Indonesia, Borneo, West Kalimantan, Sintang.

Branchlets terete, 3–4 mm in diameter, covered with minute brown stellate-tomentose hairs and dense, prominent, thick, simple, c. 0.75 mm long bristle hairs; nodes swollen, with a raised annular interpetiolar ridge; internodes 4.5–6 cm long. Leaves: petioles terete, 5–7 mm long, densely stellate-tomentose and with scattered simple bristle hairs; blades ovate to ovate-elliptic, 11–12.5 × 5–5.5 cm, coriaceous, base cordate with ca. 5.7 mm long sinuses, margin entire, apex acuminate, acumen 1–1.5 cm long, adaxially glabrous, shiny green with prominent midvein and secondary veins, abaxially brown tomentose and with a pair of hair

cushions at base. Inflorescences up to 7 cm long, with 1–3 flowers; main axis angular, with stellate-tomentose hairs and scattered simple bristle hairs covered with minute stellate hairs, more dense at tip that then appears to be capitate; primary axis up to 3.5 cm long with 1 or 2 nodes, secondary axis 1–1.5 cm long with 1 node, tertiary axis not developed; bracts not seen; bracteoles thin, suborbicular, 13–15 × 12–14 mm, concave, enclosing flower buds, margin serrulate, stellate-puberulous, caducous; pedicels stellate-tomentose and with scattered simple bristle hairs covered with minute stellate hairs, more dense at tip that then appears to be capitate, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate, 9–10 × 7–8 mm, densely covered with minute stellate hairs and 3–4 mm long bristle hairs, branched or barbed at tip, latter densely covered with minute stellate hairs at tip only; calyx lobes triangular with rounded tips, 7–8 × 4–5 mm, densely stellate-tomentose and with bristle hairs with branched or barbed tip, densely covered with minute brown stellate hairs. Petals in bud conical, 8–10 mm long, covered with stellate-furfuraceous hairs; mature petals not seen. Stamens: alternipetalous stamens (in bud) with 3–4 mm long filaments, anthers slender, thecae 7–8 mm long, pedoconnective 3–4 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform appendages, 3–4 mm long, lateral appendages not developed; oppositipetalous stamens with 3–4 mm long filaments, anthers thick, thecae ca. 7 mm long, connective with minute fimbriate hairs, basally with paired, filiform lateral appendages, 4–5 mm long. Ovary half to ¾ as long as hypanthium, apex villous; style 7–8 mm long, glabrous; stigma minute, capitate; extra-ovarial chambers extending almost to base of ovary. Fruits urceolate, 12–14 × 9–10 mm, densely covered with minute stellate hairs and 3–4 mm long simple bristle hairs with branched or barbed tip, densely covered with minute stellate hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Borneo.

Habitat & Ecology — Lower montane dipterocarp forest, in open areas or edges at ca. 950 m elevation.

Note — *Macrolenes hirsuta* is distinct by the dense, erect and thick, prominent bristle hairs on the branchlets, petioles and inflorescence axes. The bristles are thicker than those of *Macrolenes bipulvinata* and *M. echinulata*. The shape and the indumentum of the hypanthium are similar to those in *Macrolenes veldkampii* but the latter lacks bristles on the branchlets and petioles.

Specimens examined — **MALAYSIA.** Sarawak: Bario, Kelabit Highlands, Trail to Pa Ukat, 12 Apr 1995, *Latiff et al. 4237* (K). **INDONESIA.** North Kalimantan: Malinau, Kayan Mentarang, 950 m, 26 Nov 1991, *Van Valkenburg & Stockdale 1081* (K, L). West Kalimantan: Sintang, *J.E. Teijsmann HB 8658* (BO, FI).

9. *Macrolenes muscosa* (Blume) Bakh.f. — Fig. 4-4, Map 4-5

Macrolenes muscosa (Blume) Bakh.f., Contr. Melastom. 211. 1943. — *Melastoma muscosum* Blume, Bijdr. Fl. Ned. Ind. 17: 1070. 1826. — *Marumia muscosa* (Blume) Blume, Flora 14: 504. 1831. — *Dissochaeta muscosa* (Blume) G.Kadereit in Mabberley, Pl.-Book ed. 4: 1101. 2017. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 212. 1943): *C.L. Blume s.n.* (lecto L [L0008927!]; isolecto K [K000867117!, K000867118!], MPU [MPU-013522!, MPU-013523!], P [P05283626!, P05283627!, P05283629!]), Indonesia, Java.

Macrolenes magnibracteata Bakh.f., Contr. Melastom. 209. 1943. — Type: *H.A.B. Bünnemeijer 96* (holo L [L0537195!]; iso BO [BO1849059!, BO1849060!]), Indonesia, Sumatra, Ophir District, N of Taloe, 950 m alt., 10 April 1917.

Fig. 4-4. *Macrolenes muscosa*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** immature fruits. (Photos A, E from Z. Al Anshori; B, C & D, A. Kartonegoro).

Climbing up to 10 m high. Branchlets terete, 3–6 mm in diameter, densely covered with brown minute stellate-furfuraceous hairs; nodes swollen, with interpetiolar ridge; internodes 3–7.5 cm long. Leaves: petioles terete, ca. 10 mm long, densely brown stellate-tomentose; blades ovate to oblong, 8–15 × 3.5–6 cm, subcoriaceous, base rounded to shallowly subcordate, margin entire, apex acuminate, acumen ca. 1 cm long, adaxially mostly glabrous or with stellate hairs on veins, abaxially densely brown stellate-tomentose. Inflorescences 5–7 cm long, with 1–9 flowers; main axis angular, densely brown stellate-tomentose; primary axis 2–3 cm long with 1 node, secondary axis up to 1 cm long with 1 node or not developed, tertiary axis not developed; bracts lanceolate or oblong, 10–20 × 3–7 mm, brown stellate-tomentose, caducous; bracteoles linear or oblong, 6–8 mm long, stellate-tomentose; pedicels densely stellate-tomentose, 4–6 mm long in central flowers, 2–4 mm long in lateral flowers.

Hypanthium campanulate-tubular, 10–12 × 5–6 mm, densely covered with brown stellate-tomentum hairs and simple, 4–5 mm long bristles covered with brown stellate hairs; calyx lobes triangular with acute tips, 5–6 × 2–3 mm, densely covered with brown minute stellate hairs, margin laciniate. Petals in bud conical, 4–6 mm long, brown tomentose or pubescent; mature petals ovate to elliptic, 13–15 × 8–11 mm, base clawed, apex obtuse, glabrous adaxially, half glabrous and half pubescent abaxially, white or bright pink. Stamens: alternipetalous stamens with 10–11 mm long filaments, anthers curved, sickle-shaped, thecae 18–20 mm long, apex rostrate, pedoconnective 4–5 mm long, connective basal crest thin, enlarged, annular, rounded, with several fimbriate, filiform appendages, up to 9 mm long, lateral appendages paired, filiform, 8–9 mm long; oppositipetalous stamens with 9–10 mm long filaments, anthers hookor S-shaped, 11–13 mm long, connective with a thin keel crest, ca. 1 mm long, lateral appendages paired, filiform, ca. 5 mm long. Ovary half as long as hypanthium, apex villous; style 18–22 mm long, curved at tip, glabrous; stigma minute; extra-ovarial chambers extending from middle to base of ovary. Fruits urceolate, 14–15 × 7–8 mm, brown, densely covered with stellate-tomentose hairs and simple, 4–5 mm long bristles covered with brown stellate hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Sumatra and West Java.

Habitat & Ecology — Lowland forest to lower montane forest, in open places; 50–1000 m elevation.

Vernacular names — Java: *Areuy caluncung*, *caluncung beureum*, *harendong badak*, *harendong bulu* (Sunda).

Note — *Macrolenes muscosa* resembles *M. dimorpha* in its simple bristle hairs on the hypanthium, which are covered by minute stellate hairs. However, the bristles on *Macrolenes muscosa* are longer (4–5 mm long) than those of *M. dimorpha* (1–4 mm long). The calyx lobes and bracteoles of *M. muscosa* are usually covered with bristle hairs and are ciliate at the margin. The bracts and bracteoles of the specimens from Sumatra are larger and are more oblong-shaped than the Javan specimens that are smaller and rather linear or lanceolate.

Specimens examined — **INDONESIA.** Bangka-Belitung: Bangka Island, Gunung Mangkol, 50 m, 12 Sep 1949, *Kostermans & Anta 620* (BO, K, L, P); *Ibid.*, 15 Sep 1949, *Kostermans & Anta 734* (BO, K, L). Jambi: 100 m, 18 Aug 1925, *Posthumus 715* (BO, L); Harapan Rain Forest, 6 Apr 2013, *Wardi BOHK 471* (BO, K). North Sumatra: Labuhan Batu, Aek Kanopan, Lundut, 23 Mar 1927, *Bartlett 7050a* (K, L); *Ibid.*, *Bartlett 7296* (K, L); Asahan, Kuala Masihi, *Yates 2278* (BM). Riau: Indragiri Hulu, Muara Pajanki, 9 Apr 1939, *Buwalda 6450* (BO, K, L). South Sumatra: Ogan Ulu, *Teijsmann HB 3958* (BO, K, U); Tanjung Enim, Seleman, 150 m, 10 Mar 1972, *De Vogel 1224* (BO, K, L). West Sumatra: Ophir, N of Talu, 950 m, 10 Apr 1917, *Bünnemeijer 96* (BO, L); Taram, Kapalo Banda, 1 Apr 1988, *Delita et al. 7* (ANDA); Lima Puluh Kota, Harau Valley, 500 m, 12 Dec 1956, *Meijer 5391a* (L). Banten: Gunung Seribu, *Blume s.n.* (L). West Java: Bogor, Bolang, 600 m, 11 May 1924, *Docters van Leeuwen 7907* (BO, K, L); Bogor, Cianten, Gunung Batu, 31 Aug 1918, *Backer 25794* (BO, L); Bogor, Gunung Kembang, 22 Jun 1924, *Bakhuizen van den Brink Jr. 3410* (BO, U); Bogor, Puraseda, Ranca Badak, 450 m, 2 Feb 1929, *Bakhuizen van den Brink 7033* (BO, K, L); Bogor, Parungpung, 750 m, 22 Dec 1930, *Bakhuizen van den Brink 7696* (BO, L); Bogor, Mount Halimun, Nirmala Plantation, 1000 m, 10 Jun 1980, *Van Balgooy & Wiriadinata 2944* (BO, L); *Ibid.*, 1100 m, 1 Nov 2014, *Arief 302* (BO, PE); *Ibid.*, 1100 m, Nov 1997, *Suzuki K11066* (L); *Ibid.*, Malasari, 1055 m, 10 Oct 2017, *Kartonegoro 1108* (BO, L); Bogor, Mount Salak, 950 m, 10 Apr 1904, *Hochreutiner 771* (L); Bogor, Tapos, *Junghuhn s.n.* (L, U); Cianjur, Cidadap, Cadas Malang, 1000 m, 20 Oct 1916, *Bakhuizen van den Brink 1858* (BO, L); *Ibid.*, 1 May 1923, *Winckel 1302* (BO, K, L,

U); *Ibid.*, 18 May 1917, *Winckel s.n.* (L); Depok, Pancoran Mas Nature Reserve, 93 m, 31 May 1924, *Beumée 6729* (BO, L); Sukabumi, Cibadak, Kelapa Nunggal, 800 m, 18 Apr 1974, *Wiriadinata 89* (BO, K, L). Unknown location (Java): *Boerlage s.n.* (L); *Blume s.n.* (K, L, MPU, P); *Junghuhn 742* (K); *Kuhl & Van Hasselt 56* (L); *Spanoghe s.n.* (K); *De Vriese 72* (L); *De Vriese 96* (L); *De Vriese 110* (L); *Zollinger 1409* (BM, P).

10. *Macrolenes neglecta* M.P.Nayar — Map 4-4

Macrolenes neglecta M.P.Nayar, J. Jap. Bot. 55: 46. 1980. — Type: *H.C. Robinson & C. Boden-Kloss s.n.* (holo BM [BM000944488!]; iso K [K000867115!]), Indonesia, Sumatra, Korinchi, Sungei Kumbang, 4500 ft alt., 10 April 1914.

Branchlets terete, 3–5 mm in diameter, brown stellate-furfuraceous; nodes swollen, with an annular crest-like interpetiolar ridge; internodes 8–11 cm long. Leaves: petioles terete, 8–10 mm long, brown stellate-tomentose; blades ovate, 6–9 × 3–4.7 cm, coriaceous, base shallowly cordate, margin entire, apex acuminate, acumen ca. 0.5 cm long, adaxially glabrous, dark green, abaxially densely stellate-tomentose. Inflorescences up to 9 cm long, with 1–3 flowers; main axis angular, terete, brown stellate-furfuraceous; primary axis up to 7.5 cm long with 1 or 2 nodes, secondary axis when developed 1–1.5 cm long with 1 node; bracts and bracteoles ovate, 8–9 × 6–7 mm, glabrous, thin, margin serrate, apex acute, persistent; pedicels stellatefurfuraceous, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium tubular, 8–9 × 4–5 mm, covered with stellate-furfuraceous hairs and dark simple, glabrous, 1.5–2 mm long bristle hairs; calyx lobes ovate or triangular, 7–8 × 4–5 mm, margin serrate, apex acute, glabrous. Petals in bud conical, 5–7 mm long; mature petals suborbicular, 14–15 × ca. 14 mm, base clawed, apex obtuse, glabrous, pink. Stamens: alternipetalous stamens with ca. 12 mm long filaments, anthers slender, sickle-shaped, thecae 16–17 mm long, pedoconnective ca. 5 mm long, connective basal crest small with several fimbriate, filiform appendages, 4–5 mm long, lateral appendages paired, filiform, ca. 5 mm long; oppositipetalous stamens with ca. 10 mm long filaments, anthers S-shaped, thick, thecae 11–13 mm long, connective with a pair of ridges or keels, ca. 0.5 mm long, lateral appendages paired, filiform, 4–5 mm long. Ovary half as long as hypanthium, apex villous; style 15–17 mm long, curved at apex, glabrous; stigma minute; extra-ovarial chambers extending from middle to base of ovary. Fruits and seeds not seen.
Distribution — Sumatra (Kerinci Range).
Habitat & Ecology — Montane forest at ca. 1300 m elevation.
Note — Known only from the type from the Kerinci Range in Western Sumatra. The species typically resembles *Macrolenes annulata* with its simple, glabrous bristle hairs and triangular-ovate calyx lobes. However, the leaves of *Macrolenes neglecta* are subcoriaceous and densely covered with stellate-tomentose hairs on the blade beneath, while *M. annulata* has membranous, glabrous leaves.

11. ***Macrolenes nemorosa*** (Jack) Bakh.f. — Fig. 4-5, Map 4-6

Macrolenes nemorosa (Jack) Bakh.f., Contr. Melastom. 206. 1943. — *Melastoma nemorosum* Jack, Trans. Linn. Soc. London 14: 8. 1823, '*nemorosa*'. — *Marumia nemorosa* (Jack) Blume, Flora 14: 505. 1831. — Lectotype (designated by Nayar in J. Jap. Bot. 55: 50. 1980): *W. Jack 51* (lecto BM [BM000944447!]), Malaysia, Penang.
Marumia affinis Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. t. 60. 1842. — *Dissochaeta affinis* (Korth.) Clausing in Renner et al., Fl. Thailand 7(3): 421. 2001. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 207. 1943): *P.W.*

Korthals s.n. (lecto L [L0537251!]; isolecto K [K000859511!, K000859513!, K 000859516!, K000859517!], L [L0537252!], P [P05283673!, P05283676!]), Indonesia, Borneo, Bandjermasin, G. Sakoembang.

Marumia leprosa Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 241. 1844. — *Macrolenes nemorosa* (Jack) Bakh.f. var. *leprosa* (Korth.) Bakh.f., Contr. Melastom. 208. 1943. — Lectotype (Bakhuizen van den Brink in Contr. Melastom. 208. 1943): *P.W. Korthals s.n.* (lecto L [L0537253!]; isolecto BO [BO1769284!], K [K000859511!, K000859513!, K000859514!], L [L0008931!, L053725!], MPU [MPU-013526!], P [P05283622!, P05283623!], S [SG-3964!]), Indonesia, Borneo, Bandjermasin, G. Sakoembang.

Marumia bancana Scheff., Natuurk. Tijdschr. Ned.-Indië 31: 355. 1870. — *Macrolenes nemorosa* (Jack) Bakh.f. var. *bancana* (Scheff.) Bakh.f., Contr. Melastom. 207. 1943. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 208. 1943): *J.E. Teijsmann s.n.* (lecto L; isolecto BO [BO1769279!, BO1769280!], K [K000859515!]), Indonesia, Sumatra, Bangka, Djeboes.

Marumia verrucosa Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 549. 1891. — *Marumia nemorosa* (Jack) Blume var. *verrucosa* (Cogn.) Ridl., Fl. Malay Penins. 1: 795. 1922. — Lectotype (designated here): *F. Kehding 091* (lecto FI [FI008754!]; isolecto BR [BR519628!]), Malaysia, Peninsular Malaysia, Malacca, Klang.

Marumia impressa Craib, Bull. Misc. Inform. Kew 1930: 321. 1930. — Lectotype (designated here): *A.F.G. Kerr 17110* (lecto K [K000859519!]; isolecto BK [BK257158!], BM [BM000944448!], K [K000859520!]), Thailand, Phang Nga, Kapong, Takuapa, 100 m alt., 17 February 1929.

Climbing up to 12 m high. Branchlets terete, 3–4 mm in diameter, covered with brown stellate-furfuraceous hairs; nodes swollen, with interpetiolar ridges; internodes 7.5–10 cm long. Leaves: petioles flattened, 8–10 mm long, densely stellate-tomentose; blades ovate-elliptic to elliptic, 8–16 × 3.8–9 cm, membranous or subcoriaceous, base rounded to shallowly subcordate, margin entire, apex acuminate, acumen up to 0.5 cm long, adaxially mostly glabrous or with stellate hairs on veins, abaxially densely stellate-tomentose. Inflorescences 5–8 cm long, with 1–3 flowers; main axis densely stellate-tomentose; primary axis 3–3.5 cm long with 1 node, secondary axis 1–1.8 cm long with 1 node or not developed, tertiary axis not developed; bracts lanceolate, 12–15 × c. 4 mm long, stellate-tomentose, caducous; bracteoles subulate or oblong, 3–4 mm long, stellate-tomentose, caducous; pedicels densely stellate-tomentose, 2–4 mm long in central flowers, c. 1 mm long or subsessile in lateral flowers. Hypanthium campanulate-tubular or suburceolate, 8–15 × 5–7 mm, villous, densely covered with stellate-tomentum only; calyx lobes triangular with acute or acuminate tips, 7–15 × 3–6 mm, densely covered with minute stellate hairs. Petals in bud conical, 7–9 mm long; mature petals suborbicular, 20–25 × 18–20 mm, reflexed, base clawed, apex obtuse, glabrous, white-pinkish to pink. Stamens: alternipetalous stamens with 10–11 mm long yellow filaments, anthers curved, sickle-shaped, thecae 18–20 mm long, yellow, apex rostrate, pedoconnective 7–8 mm long, connective basal crest thin, enlarged, annular, rounded, with fimbriate, filiform, up to 5 mm long appendages, lateral appendages paired, filiform, 6–7 mm long; oppositipetalous stamens with ca. 10 mm long yellow filaments, anthers S-shaped, 13–15 mm long, connective with a thin keel crest, up to 2 mm long, lateral appendages paired, filiform, 5–6 mm long. Ovary ⅓ to half as long as hypanthium, apex pubescent; style 20–22 mm long, curved at tip, glabrous; stigma minute; extra-ovarial chambers extending almost to base of ovary. Fruits urceolate, 10–15 × 7–10 mm, brown,

densely covered with stellate-tomentose hairs only; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Thailand (Southern Peninsula), Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Disturbed evergreen lowland forest to lower montane forest, heath forest, peat swamps, riverine forest, roadsides; 10–1250 m elevation.

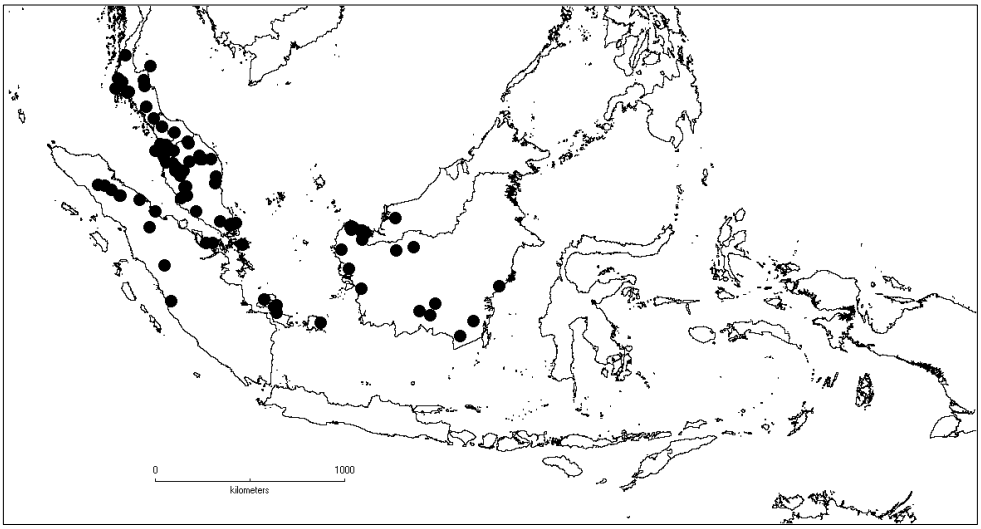
Vernacular names — Peninsular Malaysia: *Banga utan*. Sumatra: *pancung pelangit* (Bengkalis), *akar penangil* (Bangka). Borneo: *kemasulan* (Katingan), *mangkodok* (Sarawak).

Fig. 4-5. *Macrolenes nemorosa*. **a.** habit; **b.** branchlet; **c.** hypanthium; **d.** flower; **e.** fruits. e from *Hardial & Sidek 383* (K). (Photos: A. Kartonegoro).

Note — *Macrolenes nemorosa* is the only species that can easily be recognised by its villous or tomentose indumentum on most parts and by the lack of any bristle hairs. It has a wide distribution, similar to that of *Macrolenes pachygyna* and *M. stellulata*, and ranges from Thailand, and Peninsular Malaysia to Sumatra and Borneo; not recorded for Java.

Specimens examined — **THAILAND.** Krabi: Tambon Khao Panom, 100 m, 30 Mar 1930, *Kerr 18780* (BM, K); Nong Khon, 15 Aug 1964, *Sangkhachand BKF 46354* (K, L). Nakhon Si Thammarat: Kao Den, 200 m, 14 Apr 1928, *Kerr 15308* (BM, K); Kao Soi Dao, 100 m, 29 Apr 1930, *Kerr 19235* (BM, K, L). Narathiwat: Nikhom Waeng, 6 Mar 1974, *Larsen & Larsen 33025* (K, P); Sungei Kolok, 7 Sep 1966, *Sangkhachand & Nimanong 1325* (K, L); Ban Bala-Pookaotong, 420 m, 4 Oct 2003, *Promchua 64* (L). Phang Nga: Kapong, Takuapa, 100 m, 17 Feb 1929, *Kerr 17110* (BK, BM, K); *Ibid.*, 75 m, 17 Jul 1972, *Larsen et al. 31095* (K, L); Thai Muang, Khao Lumpee Hat Thai Muang, 30 m, 22 Jun 2006, *Williams 2045* (K, L). Ranong: Khlong Kam Puan, 100 m, 26 Apr 1973, *Geesink & Santisuk 4955* (K, L, P); *Ibid.*, 1 May 1973, *Geesink & Santisuk 5097* (L, P); *Ibid.*, 26 Apr 1974, *Larsen & Larsen 33404* (K, L, P); Muang Leng, 11 Jan 1966, *Hansen & Smitinand BKF 40175* (L). Songkhla: Rattapoom, Boripat Falls, 50 m, 30 Aug 1986, *Maxwell 86-644* (L); Khao Luke Lome, 450 m, 16 Sep 1986, *Maxwell 86-683* (L). Surat Thani: Panom, 50 m, 25 Mar 1927, *Kerr 12420* (BM, K); *Ibid.*, 20 Aug 1976, *Praphat 65* (K, L, P); Kaw Samui, 31 May 1927, *Put 742* (BM, K, L). Trang: Khao Chong, 150 m, 13 Aug 1975, *Maxwell 75-810* (L). Yala: Chaung, 24 Jun 1930, *Kiah SFN 24378* (K). **MALAYSIA.** Johor: Alor Bukit, 22 Nov 1966, *Hardial 529* (L); Kluang, 5 Mar 1973, *Hardial 1095* (L); Kota Tinggi, 21 May 1978, *Maxwell 78-242* (L); *Ibid.*, *Maxwell 78-246* (L); *Ibid.*, *Ridley 15381* (BM); *Ibid.*, Kuala Sedili, 23 Jun 1959, *Kadim & Noor 128* (L); *Ibid.*, Mersing Road, 31 Aug 1977, *Maxwell 77-397* (L); *Ibid.*, Mawai Baharu, 22 May 1978, *Maxwell 78-276* (L). Kedah: Semeling, Mar 1911, *Bell & Haniff s.n.* (K); Sungai Patani, 2 Sep 1938, *Wolfe & Abdul Kadir SFN 21460* (BM, K). Kelantan: Gua Musang, road from Kuala Betis to kampong How, 12 Oct 1985, *Latiff & Zainudin 1070* (L); Sungei Lebir, Kuala Rantong, 5 Sep 1967, *Cockburn KEP 116000* (K); Kampung Parit, 18 Feb 1933, *Haniff SFN 10234* (BO); Kuala Aring, 1 Sep 1899, *Yapp 126* (K). Malacca: *Griffith KD 2271* (K); *Maingay KD 786* (L): Klang, *Kehding 091* (BR, FI). Pahang: Fraser's Hill, 16 Sep 1922, *Burkill & Holttum SFN 8647* (BO); *Ibid.*, 1500 m, 29 Sep 1978, *Maxwell 78-371* (L); Lubok Temang, 12 Jun 1923, *Henderson FMS 11024* (L); Sungai Telom, 1036 m, 23 Oct 1930, *Kiah & Strugnell SFN 23926* (BM); Cameron Highlands, 1200 m, 12 Apr 1937, *Nur SFN 32639* (K); Ulu Sungai Kuantan, 213 m, 11 Jun 1934, *Symington & Kiah SFN 28781* (K). Penang: *Jack 51* (BM); *Phillips s.n.* (K); *Schomburgh s.n.* (K); *Wallich 4043A* (BM, K, P); Bukit Penang, 165 m, *Curtis 1008* (K); Penara Bukit, 350 m, 3 Jun 1938, *Yahya SFN 21444* (K). Perak: *King's Collector 10366* (P); *Scortechini 64* (P); *Scortechini s.n.* (L); Maxwell's Hill, *Bodden-Kloss s.n.* (BM); *Ibid.*, 1250 m, 16 Sep 1949, *Sinclair & Kiah SFN 38738* (BM, K); *Ibid.*, 22 Nov 1980, *Keng et al. 28* (L); Sungei Siput, 11 Sep 1920, *Burkill SFN 6327* (BO); Grik, 18 Jun 1924, *Burkill SFN 12429* (BO); Sungai Krian, 27 Oct 1938, *Spare SFN 36039* (K, P); Gunung Batu Putih, *Wray 1221* (BM, K). Selangor: Rantau Panjang, 31 Jul 1914, *Boden-Kloss 82* (K); *Ibid.*, 3 Aug 1914, *Boden-Kloss s.n.* (K); Sungei Buloh, 17 Jan 1966, *Hardial & Sidek 383* (K, L); Gading, 500 m, 20 Jul 1969, *Loh FRI 13386* (K, L); Klang Gates, Jan 1921, *Ridley s.n.* (K). Terengganu: Gunong Padang, 1200 m, Jun 1937, *Moysey & Kiah SFN 31048* (K); Bundi, 1904, *Rostados s.n.* (BM, K); Tasik Kenyir, Simpan Tembat, 221 m, 19 Nov 2008, *Kamarul Hisham et al. FRI 59335* (L). Sarawak: *Bartlett s.n.* (BM); *Beccari PB 554* (K, P); *Beccari PB 776* (K, P); *Beccari PB 2024* (P); *Native Collector 89* (BM, L, P); *Native Collector 549* (BM, L); *Native Collector 1459* (K, P); *Native Collector 1793* (BM); Kuching, 11 Apr 1954, *Brooke 8329* (BM, L); *Ibid.*, *Haviland 145* (BM, L); *Ibid.*, *Sakib s.n.* (K); *Ibid.*, Mount Penrissen, *Haviland 69* (K); Lundu,

Biawak, Ulu Sungai Pasir, 9 Apr 1997, *Jamree et al. S.76759* (K); *Ibid.*, Samunsan, Sungei Belinsa, 10 Mar 1989, *Othman et al. S.62272* (K, L); *Ibid.*, Pueh, Sungai Kopak, 200 m, 19 Aug 1996, *Rantai Jawa & Lai S.74519* (L); *Ibid.*, Salampit, 19 Jul 1989, *Yahud et al. S.56690* (K, L); Sibu, Naman, 26 Feb 1958, *Sanusi S.9765* (K, L). **INDONESIA.** Aceh: Mount Leuser National Park, Gunung Kemiri, 10 Mar 2008, *Sumadijaya 342* (BO); *Ibid.*, Gunung Bandahara, 1000 m, 27 Jun 1972, *De Wilde & De Wilde-Duyfjes 13414* (K, L). Bangka-Belitung: Bangka, Batu Rusak, *Berkhout s.n.* (BO); *Ibid.*, Melabun, 80 m, 15 Nov 1917, *Bünnemeijer 1989* (BO, L); *Ibid.*, Sungai Selan, *Teijsmann s.n.* (BO, L); *Ibid.*, Jibus, *Teijsmann s.n.* (BO, K, L); Belitung Island, Manggar, *Teijsmann s.n.* (BO). North Sumatra: *Yates 1207* (BM, K, L); Sibolangit, 900 m, 13 Oct 1917, *Lörzing 5333* (BO, L); Mount Sibayak, Bandar Baru, 900 m, 10 Oct 1928, *Lörzing 14128* (BO, K, L); Labuan Bilik, Bila, 8 Oct 1928, *Lörzing 14308* (BO, K, L); Labuhan Batu, Kota Pinang, Langga Payung, March 1933, *Rahmat Si Toroes 3287* (L); *Ibid.*, *Rahmat Si Toroes 3403* (L); Bohorok, Bukit Lawang, 17 Feb 1973, *Soedarsono 245* (BO, L). Riau: Rangsang Island, 24 Jul 1918, *Bruinier 39* (BO); *Ibid.*, *Bruinier 92* (BO). Riau Archipelago: Bengkalis, Selat Panjang, 15 Nov 1919, *Beguin 473* (BO); Dompak Island, 10 m, 24 Jun 1919, *Bünnemeijer 6416* (BO, L). West Sumatra: *Korthals s.n.* (P); Lima Puluh Kota, Harau Valley, Sarasah Bonta, 500 m, 27 Apr 2002, *Silvia et al. 35* (ANDA); *Ibid.*, 11 Sep 2017, *Kartonegoro 1070* (BO, L); *Ibid.*, 12 Sep 2017, *Kartonegoro 1097* (BO, L). Central Kalimantan: Sampit, Cempaka Mulia, 20 Jan 1954, *Alston 13135* (BM, L, PNH); Sei Gohong, Rungun River, 50 m, 14 Jan 2001, *Sidiyasa et al. 2418A* (L); Sebangau Nat. Park, Katingan River, Sungai Landabung, 15 Mar 2007, *Wardani & Amir 554* (BO). East Kalimantan: Balikpapan, Sungai Wain, 200 m, 16 Jan 2005, *Bernard et al. RC#4* (L). South Kalimantan: Mount Sakumbang, *Korthals s.n.* (K, L, P); *Ibid.*, *Korthals s.n.* (K, L, MPU, P, S); Mount Pamatton, *Korthals s.n.* (L); Mount Sakumbang, *Korthals s.n.* (L). West Kalimantan: Ulu Kenepai, *Hallier 1442* (BO, L); Rasau Jaya, Sungai Punggur Besar, 8 Nov 1976, *Kartawinata 1421* (BO, K, L); Kapuas Hulu, Pentulak Lake, 7 Oct 1949, *Main 1951* (BO, K, L); Ketapang, Gunung Palung National Park, Cabang Panti, 20 m, 23 Mar 1997, *Laman et al. 994* (BO, L). Unknown location (Kalimantan): *De Vriese 141* (L); *De Vriese 167* (L).



Map 4-6. Distribution of *M. nemorosa* (●).

12. ***Macrolenes pachygyna*** (Korth.) M.P.Nayar — Map 4-7

Macrolenes pachygyna (Korth.) M.P.Nayar, J. Jap. Bot 55: 49. 1980. — *Marumia pachygyna* Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. t. 59. 1842. — *Dissochaeta pachygyna* (Korth.) I.M.Turner, Taxon 67: 628. 2018. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 217. 1943): *P.W. Korthals s.n.* (lecto L [L0008936!]; isolecto K [K000867112!], L [L0537218!, L0537219!], P [P05283680!, P05283682!], S [SG-3965!]), Indonesia, Borneo, Kapoeas-Barito, Tewe River.

Marumia jackii Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 243. 1844. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 217. 1943): *P.W. Korthals s.n.* (lecto L [L0537214!]; isolecto K [K000867113!], L [L0008935!], P [P05283635!, P05283636!]), Indonesia, West Sumatra, G. Malintang.

Marumia vulcanica Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 243. 1844. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 217. 1943): *P.W. Korthals s.n.* (lecto L [L0537216!]; isolecto L [L0008934!, L0537215!], P [P05283633!]), Indonesia, West Sumatra, G. Merapi.

Marumia stellulata Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 243. 1844, *nom. Illeg.*, non Blume (1831). — *Marumia reticulata* Blume, Mus. Bot. 1, 3: 34. 1849. — *Macrolenes reticulata* (Blume) Bakh.f., Contr. Melastom. 215. 1943. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 216. 1943): *P.W. Korthals s.n.* (lecto L [L0537217!]; isolecto P [P02274819!]), Indonesia, Sumatra, Indrapoera.

Dissochaeta reformata Blume, Mus. Bot. 1, 3: 36. 1849. — *Anplectrum reformatum* (Blume) Triana, Trans. Linn. Soc. London 28: 85. 1872. — *Diplectria reformata* (Blume) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — Lectotype (designated by Veldkamp & Nayar in Blumea 24: 434. 1979): *P.W. Korthals s.n.* (lecto L [L0537220!]; isolecto L [L0537221!]), Indonesia, Borneo, Barito, Doesoen.

Marumia oligantha Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 281. 1851. — Lectotype (designated here): *H. Zollinger 3070* (lecto P [P02274820!]; isolecto BM!, BO [BO1751361!], G-DC [G00319905!]), Indonesia, Sumatra, Lampong, Gunung Logie, 30 September 1845.

Marumia korthalsiana Miq., Fl. Ned. Ind., Eerst. Bijv. 2: 318. 1861. — Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 217. 1943): *J.E. Teijsmann HB 820* (lecto U [U0004055!]; isolecto BO [BO1764891!]), Indonesia, West Sumatra, Loeboek Sikaping.

Marumia stellulata auct. non. Blume: Naudin, Ann. Sci. Nat., Bot. sér. 3, 15: 282. 1851; Miq., Fl. Ned. Ind. 1(1): 535. 1855; Triana, Trans. Linn. Soc. London 28: 82. 1872; Cogn. in Boerl., Handl. Fl. Ned. Ind. 2: 532. 1890; Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 552. 1891. *p.p.* excl. type.

Macrolenes stellulata auct. non. Bakh.f.: Bakh.f., Contr. Melastom. 216. 1943. *p.p.* excl. type.

Climbing up to 15 m high. Branchlets terete, 3–4.5 mm in diameter, densely covered with minute brown stellate-furfuraceous hairs, glabrescent at the end; nodes swollen, with a simple interpetiolar ridge, densely stellate-furfuraceous; internodes 5.5–10.5 cm long. Leaves: petioles terete, 8–15 mm long, densely brown stellate-furfuraceous; blades elliptic, elliptic-oblong to oblong, 8.8–18 × 3.3–8.7 cm, subcoriaceous, base subcordate, margin entire, apex acuminate, acumen 0.3–1 cm long, adaxially glabrous, dark glossy green, abaxially densely brown stellate-furfuraceous to tomentose. Inflorescences 5–10 cm long, with 1–12 flowers; main axis angular, densely brown stellate-furfuraceous; primary axis 4–8 cm long with 1 or 2 nodes, secondary axis 1–2 mm long with 1 node or not developed; bracts linear, 5–6 mm

long, not ciliate, stellate-tomentose, caducous; bracteoles lanceolate, linear or subulate, 4–10 × 1–2 mm long, not ciliate, stellate-tomentose, caducous; pedicels terete, densely stellatefurfuraceous, thickened to 2–3 mm in diameter, 2–3 mm long in central and lateral flowers. Hypanthium campanulate to suburceolate, 10–16 × 5–9 mm, brownish when dry, densely covered with brown stellate-furfuraceous hairs and 2–3 mm long bristles barbed or branched at tip, completely covered with minute brown stellate hairs; calyx lobes triangular, 4–7 × 3–5 mm, tips acute, densely covered with minute stellatefurfuraceous hairs, margin ciliate, bristles with simple or branched tip and covered with minute brown stellate hairs. Petals in bud conical, 5–13 mm long, apex acute, stellate-furfuraceous; mature petals obovate to suborbicular, 10–25 × 7–15 mm, reflexed, base clawed, apex obtuse, above glabrous, underneath half stellatefurfuraceous and half glabrous, white. Stamens: alternipetalous stamens with 13–15 mm long filaments, anthers curved, sickle-shaped, thecae 15–17 mm long, apex rostrate, pedoconnective ca. 9 mm long, connective basal crest lamellar and annular, prolonged into several fimbriate, filiform appendages, 9–10 mm long, laterally with paired, filiform appendages, 9–10 mm long; oppositipetalous stamens with 8–12 mm long filaments, anthers S-shaped, 13–15 mm long, connective with a thin keel crest, up to 3 mm long, basally with paired, filiform lateral appendages, 7–11 mm long. Ovary ⅔ as long as hypanthium, apex densely covered with capitate bristle hairs and smooth brown hairs; style 20–30 mm long, curved at tip, white, upper part glabrous, base densely covered with brown hairs; stigma minute, capitate; extra-ovarial chambers extending to near base of ovary. Fruits ovoid or urceolate, 10–15 × 6–12 mm, sparsely covered with stellate hairs and densely covered with branched- or barbed-tip bristle hairs, apex densely covered with capitate bristle hairs and smooth brown hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Sumatra and Borneo.

Habitat & Ecology — Primary or secondary lowland Dipterocarp forest, lower montane forest, swamp forest, riverine or heath forest, in open or logged places; 10–1180 m elevation.

Vernacular names — Sumatra: *kangon sipuan* (Sungei), *sikaduduk rimbo* (Minang). Borneo: *letah letah* (Murut), *radi akar* (Sanggau).

Notes — 1. The species has conspicuous bristle hairs with a branched or barbed tip and it is covered with minute stellate hairs from base to apex. Bristle hairs on *Macrolenes hirsuta* and *M. veldkampii* are also barbed at the tip, but only covered by minute stellate hairs in the upper part, while the base is glabrous. The other species with barbed-tip bristle hairs is *Macrolenes stellulata* that differs in rather puberulous leaves and distinct, ovate-lanceolate bracts and bracteoles.

2. Naudin (1851) erroneously wrote that the type of *Macrolenes oligantha* (*Zollinger 3070*) was collected on Java, but the label indicates that it was collected on Gunung Logie ('Gunung Sugih'), Lampung, Sumatra. The latter is more likely as no other specimens from Java are known. Only *Macrolenes annulata* and *M. muscosa* are known from Java.

3. Nayar (1980) correctly took this species out of the synonymy of *Macrolenes stellulata* (Jack) Bakh.f. *Macrolenes pachygyna* has elliptic-oblong leaves and linear bracts and bracteoles, while *M. stellulata* has oblong-ovate leaves and laciniate leaf-like bracts and bracteoles. The basionym of the species (*Marumia pachygyna*) was validly published by Korthals with illustration plate earlier in 1842 and followed by the full description in 1844 (Turner 2018).

Specimens examined — **MALAYSIA.** Sabah: Kalabakan, Luasong, 22 Sep 1980, *Fidilis & Sumbing SAN 91872* (K, L); *Ibid.*, 26 Apr 1982, *Fidilis SAN 94793* (K, L); *Ibid.*, 23 Feb 1982, *Fidilis & Sumbing SAN 95684* (L); *Ibid.*, 190 m, 20 Jul 2001, *Postar et al. SAN 144073* (K, L); Kalabakan, Sapulut, Labang, 25 Oct 1988, *Fidilis & Sawan SAN 125276* (K, L);

Kalabakan, Brantian, 6 Apr 1972, *Kumin SAN 75321* (K, L); Kinabatangan, Bukit Garam, 20 Feb 1987, *George et al. SAN 117562* (K); Kinabatangan, Sungai Mananggul, 28 Jan 1988, *Joseph et al. SAN 123830* (K, L); Lamag, Ulu Sungai Pin, 8 Sep 1979, *Leopold & Petrus SAN 90978* (K, L); Keningau, Mandalom, 21 Feb 1989, *Sawan SAN 125399* (K, L); Lahad Datu, Silam, 11 Jan 1966, *Ahmad Talip SAN 52942* (K, L); Lahad Datu, Danum Valley, Ulu Segama, 200 m, 28 Feb 1985, *Argent et al. 108275* (K); *Ibid.*, 16 Mar 1988, *George et al. SAN 123927* (K); *Ibid.*, 30 Jun 2006, *Karolus 66* (K); *Ibid.*, 14 May 1989, *Ridsdale 2022* (K, L); *Ibid.*, 16 Mar 2008, *Ridsdale SAN 148778* (K); Lahad Datu, Silabukan, 230 m, 18 Feb 1963, *Sitiol SAN 33427* (K, L); Lahad Datu, Ulu Tabin, 750 m, 15 Jan 1990, *Dewol SAN 129537* (K, L); Kaboy River, 15 m, 17 Nov 1932, *Burot 2690* (BO, K, L); Nabawan, Witti Range, Tiulon, 800 m, 11 Mar 1982, *Dewol SAN 94956* (L); *Ibid.*, Nabawan-Pandawan Road, 17 Mar 1990, *Sumbing SAN 128479* (L); Ranau, Mount Kinabalu, Mount Nunkok, 900 m, 31 May 1933, *Clemens 32765* (BM, BO, K, L); *Ibid.*, Penibukan, 1200 m, 2 Nov 1933, *Clemens 50066* (K, L); *Ibid.*, Penokok, 1200 m, *Haviland 1345* (K); Sandakan, Kabili-Sepilok, 100 m, 1 May 1935, *Castro 4502* (K); Ibid., 9 Apr 1954, *Wood A1963* (K, L); Sandakan, *Elmer 20241* (BM, BO, K, L, P, PNH, U); *Ibid.*, *Ramos BS 1211* (BO, K); Sandakan, Segaliud Lokan, 15 Jan 1975, *Aban SAN 81124* (L); *Ibid.*, 7 Mar 1975, *Leopold & Kodoh SAN 81380* (K, L); *Ibid.*, 11 Mar 1975, *Leopold & Kodoh SAN 81430* (K, L); *Ibid.*, 8 Oct 1988, *Majawat et al. SAN 102411* (K); *Ibid.*, Elopura, 18 Nov 1947, *Cuadra A1118* (BO, K); Sandakan, Telupid, 60 m, 19 May 1978, *Dewol SAN 79466* (K, L); Sandakan, Tanjung Batu, 10 m, 25 Mar 1948, *Anthony A774* (K); Sandakan, Sungai Menuil, 17 m, 15 Mar 1963, *Sayu Elleh SAN 35426* (K, L); Tawau, *Elmer 20548* (BM, BO, K, L, P, U); *Ibid.*, *Elmer 21540* (BM, BO, K, L, P, U); Tawau, Merotai Kecil, 45 m, 28 Dec 1963, *Aban SAN 18610* (K); *Ibid.*, Balung River, 170 m, 17 Jul 1963, *Aban SAN 36998* (K, L). Sarawak: *Barber 313* (K); *Brooks 1024* (BM); Balingian, Bawan, 10 m, 20 Oct 1963, *Chai S.19479* (BO, K, L); Baram, Dec 1894, *Hose 228* (BM, K); *Ibid.*, Anap, 700 m, 8 Sep 1964, *Sibat S.21991* (K, L); *Ibid.*, Bukit Mersing, 1300 m, 1 Jun 1956, *Purseglove 5260* (K, L); *Ibid.*, Sungai Tau, 60 m, 28 May 1956, *Purseglove 5112* (K, L); *Ibid.*, Ulu Tinjar, Mount Dulit, 1000 m, 29 Aug 1932, *Richards 1520* (K); Belaga, Ulu Belaga, Sepakau Logging Camp, 250 m, 13 Oct 1981, *Hansen 601* (L); *Ibid.*, Batang Balui, Batu Laga, 600 m, 6 Mar 1989, *Yii S.56517* (K, L); *Ibid.*, 30 Mar 1989, *Yii S.62379* (K, L); Bintulu, Nanga Sapulow, 50 m, 5 Jul 1966, *Ding Hou 465* (BO, K, L); Bintulu, Similaujan FR., 100 m, 3 Sep 1991, *Frodin 2180* (L); Bintulu, Tatau, Bukit Kana, 500 m, 24 Mar 1995, 24 Mar 1995, *Yii & Jugah S.71623* (L); Kapit, Bukit Tibang, 1300 m, 9 Jul 1969, *Anderson & Paie S.28604* (K, L); Kapit, Rejang, Pelagus, 18 Apr 1963, *Ashton S.18298* (BO, K, L); Kapit, Balleh, Menyiong, 500 m, 12 Nov 1979, *Othman et al. S.41366* (K, L); Kuching, *Beccari PB 1022* (BM, K, P); *Ibid.*, *Beccari PB 2311* (K); *Ibid.*, *Beccari PB 2355* (P); Kuching, Bau, 60 m, 15 Dec 1965, *Chai & Seng S.16198* (K, L); Kuching, Kubah, 85 m, 17 Sep 1994, *Rantai Jawa et al. S.68453* (K, L); Kuching, Matang, 21 Jan 1894, *Haviland 146* (BM, BO, K); *Ibid.*, 300 m, 25 Oct 1929, *Clemens 20933* (K); *Ibid.*, *Gibbs 4424* (BM); *Ibid.*, 20 m, 7 Jan 1964, *Chai S.19757* (BO, K, L); Kuching, Gunung Gading, 988 m, 4 May 2007, *Sabran et al. S.83747* (K); Lubok Antu, Sungai Engkari, 21 Mar 1974, *Chai S.34081* (K, L); Miri, Bakam Road, 3 Apr 1966, *Sibat S.24739* (BO, K, L); *Ibid.*, 7 Apr 1966, *Benang S.24838* (BO, K, L); Lundu, Ulu Sungai Samunsam, 27 Mar 1989, *Othman et al. S.56634* (AAU, L); Miri, Gunung Mulu, 29 Jul 1977, *Chai S.39573* (K, L); Miri, Lambir Hill, 50 m, 6 Jul 1962, *Paie S.16609* (BO, K, L); *Ibid.*, 22 Oct 1983, *Mochtar S.47117* (K, L); *Ibid.*, 4 Mar 1966, *Awang S.24114* (BO, K, L); Miri, Sungai Bakong, 80 m, 26 Feb 1966, *Sibat S.24453* (BO, K, L); Miri, Ulu Luak, 50 m, *Othman S.21311* (K, L); Mukah, Mukah Hill, 13 Jul 1997, *Stephen et al. S.77357* (AAU, K, L); Sarikei, Lanjak Entimau, Sungai Merinum, 280 m, 1 Nov 1998, *Julaihi & Jamree*

S.79209 (K, L); Serian, Tebedu, 26 Jun 1996, *Jamree et al. S.73760* (K); Sibu, Gat, Mount Majau, 25 Jul 1929, *Clemens 21594* (BO, K); Simunjan, Sabal, 400 m, 25 Feb 1995, *Runi et al. S.71293* (L); Mount Sengghai, 370 m, 30 Dec 1927, *Native Collector 5153* (BO); Marudi, 300 m, Feb 1932, *Richards 2661* (K, L); Kampong Liam, 5 Nov 1976, *Yeo & Jugah S.38400* (K, L). **BRUNEI.** Belait: Kuala Ingei, 30 m, 7 Jul 1957, *Ashton BRUN 152* (BO, K, L); Sungei Belait, 3 Nov 1989, *Forman & Blewett 1194* (K, L); Labi, 17 Feb 1969, *van Niel 4585* (L); *Ibid.*, Malayan Ulu, 2 Aug 1997, *Ogata et al. 527* (L); Sungai Rampayoh, 9 Jan 1994, *Kirkup & Coode 795* (L); Bukit Puan, 29 Aug 1960, *Sinclair & Kadim 10484* (K, L); Melilas, 100 m, 24 Nov 1992, *Thomas et al. 109* (K, L); Bukit Sawat, 10 Apr 1997, *Ogata et al. 464* (L). Temburong: Sungai Belalong, 50 m, 17 Feb 1991, *Argent et al. 916* (K, L); Batu Apoi, Selapon, Bukit Belitun, 100 m, 29 Jan 1994, *Coode et al. 7940* (L). Tutong: Panchong-Benutang, 10 m, 21 Oct 1989, *Forman & Blewett 994* (K, L); Ulu Tutong, Ramba, 150 m, 11 May 1992, *Johns et al. 7625* (K). **INDONESIA.** Aceh: Mount Leuser National Park, Klut Nature Reserve, Pucuk Lembang, 40 m, 8 Jul 1985, *De Wilde & De Wilde-Duyfjes 19809* (BO, L). Bengkulu: Lebong Tandai, Jul 1922, *Brooks 7922* (K); Bukit Kaba, 800 m, 29 Mar 1922, *de Voogd 1372* (BO). Lampung: Sep 1845, *Zollinger 778* (P); Gunung Sugih, 30 Sep 1845, *Zollinger 3070* (BO, BM, G, P); Krui, Sukau, 28 Jan 1924, *Bouman-Houtman 11* (BO). North Sumatra: Sidikalang, road Sidikalang-Pongkolan, 1200 m, 27 Mar 1954, *Alston 14794* (BM, L); Lau Lintang, Gunung Rinte, 280 m, *Lörzing 16323* (BO, L). South Sumatra: *Forbes 2783* (BM, L, P); Ranau Lake, 700 m, 7 Nov 1929, *de Voogd 426* (BO). West Sumatra: Mount Singgalang, Jul 1878, *Beccari PS 109* (BM, K, L); Mount Merapi, *Korthals s.n.* (L, P); Mount Talang, 1550 m, 20 Oct 1918, *Bünnemeijer 5180* (BO); Pariaman, Bukit Tambun Tulang, 450 m, 28 Mar 1987, *Den 9* (ANDA); Lubuk Sikaping, *Teijsmann HB 820* (BO, U); Payakumbuh, Mount Sago, 900 m, 9 Jun 1955, *Meijer 3421* (BO); Lubuk Paraku, 500 m, 17 Sep 1988, *Nagamasu 3311* (ANDA); Mount Malintang, *Korthals s.n.* (K, L, P); Indrapura, *Korthals s.n.* (L, P). Central Kalimantan: Nanga Bulik, Sungai Buluh, 300 m, 29 Feb 1984, *Hansen 1233* (BO, L); *Ibid.*, Sungai Lamandau, 50 m, 12 Mar 1984, *Hansen 1270* (BO); *Ibid.*, *Hansen 1283* (BO, L); Katingan River, Tumbang Samba, 235 m, 19 Jan 1995, *Jarvie & Ruskandi 5014* (BO, L); *Ibid.*, 200 m, 22 Dec 1982, *Mogea & De Wilde 4337* (BO, K, L); *Ibid.*, 100 m, 5 Feb 1983, *Wiriadinata 3548* (BO, L); Tewe River, *Korthals s.n.* (K, L, P, S); Ulu Barito, Dusun, *Korthals s.n.* (L). East Kalimantan: West Kutai, Hikam Batu Beng, 50 m, 26 Jul 1925, *Endert 2248* (BO, K, L); *Ibid.*, 29 Jul 1925, *Endert 2293* (BO, K, L); *Ibid.*, 15 Oct 1925, *Endert 4173* (BO, L); Sungei Doho, *Jaheri 1591* (BO); Tanjung Redeb, Birang River, 10 m, *Kessler Berau-317* (L); Berau, Mount Ilas Bungaan, 300 m, 9 Sep 1957, *Kostermans 13747* (BO, K, L); Mului, 414 m, 1 Dec 2005, *Raes et al 717* (K, L). North Kalimantan: Krayan, Long Bawan, Gunung Batu Linanit, 1100 m, 31 Jul 1981, *Kato et al. B-10295* (BO, L); Sebatik Island, 28 Dec 1954, *Kostermans 10711* (BO, L); Nunukan, Sungai Semboyong, Nov 1953, *Meijer 2193* (BO, K, L); *Ibid.*, Sungai Simengkadu, Dec 1953, *Meijer 2361* (BO, K, L). West Kalimantan: Sintang, 150 m, 10 Apr 1994, *Church 816* (BO, K, L); Ibid., Ketungau Tengah, Nanga Kelapan, 150 m, 15 Apr 2014, *Kartonegoro & Pratama 777* (BO); Smitauw, *Hallier 1361* (BO, K, L, P); Sungai Kenepai, *Hallier 1971* (BO); Gunung Melawi, *Teijsmann HB 8659* (BO); Sungai Landak, *Teijsmann s.n.* (BO); Sanggau, Noyan, Ngira, 14 Oct 1993, *de Jong 552* (L).

13. *Macrolenes rufolanata* (Ridl.) J.F.Maxwell — Map 4-7

Macrolenes rufolanata (Ridl.) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — *Marumia rufolanata* Ridl., Fl. Malay Penins. 5: 310. 1925. — Lectotype (designated here): *I.H. Burkill & M. Haniff SFN 15661* (lecto K [K000867119!]; isolecto SING

[SING0052046!, SING0052047!]), Malaysia, Peninsular Malaysia, Pahang, Kuala Lipis, Ulu Chimeras, 200 ft alt., 18 November 1924.

Branchlets terete, 4–6 mm in diameter, densely tomentose, covered with minute brown stellate-furfuraceous hairs; nodes swollen, with interpetiolar ridge; internodes 6–10 cm long. Leaves: petioles terete, 10–12 mm long, densely brown stellatefurfuraceous; blades elliptic to elliptic-oblong, 7.5–12 × 3–6 cm, subcoriaceous, base subcordate, margin entire, apex acuminate, acumen ca. 5 mm long, adaxially glabrous, dark glossy green, abaxially densely brown stellate-tomentose. Inflorescences 8–15 cm long, with 3–10 flowers; main axis terete, densely brown stellate-furfuraceous; primary axis 5–10 cm long with 2 or 3 nodes, secondary axis 1.5–2 cm long with 1 node, tertiary axis not developed or up to 5 mm long; bracts ovate, 6–7 × 4–5 mm, densely stellate-tomentose with simple bristle hairs on margin, caducous; bracteoles ovate, 2–3 × ca. 2 mm, densely brown stellate-tomentose with simple bristle hairs on margin, caducous; pedicels densely brown stellate-tomentose, 2–3 mm long in central flowers, ca. 1 mm long or almost absent in lateral flowers. Hypanthium campanulate, 10–12 × 6–7 mm, densely covered with minute brown stellate-furfuraceous hairs and 1–1.5 mm long simple, thick, bristles, densely covered with brown minute stellate hairs, appearing to be capitate; calyx lobes triangular with acute tips, 5–7 × ca. 3 mm, densely covered with minute brown stellate hairs, outer surface also covered with ca. 1 mm long bristle hairs densely covered with brown stellate hairs, inner surface lacking bristle hairs, margin without bristle hairs, not ciliate. Petals in bud and when mature not seen, ovate, apparently white, centre of abaxial surface scurfy (see Ridley 1925). Stamens: alternipetalous stamens (in bud) with 10–12 mm long white filaments, anthers straight, thecae 10–11 mm long, apex rostrate, pedoconnective ca. 4 mm long, connective basal crest thin, annular, with several fimbriate, filiform appendages, 4–6 mm long, lateral appendages paired, filiform, 4–5 mm long; oppositipetalous stamens with ca. 10 mm long white filaments, anthers straight, thecae 8–10 mm long, connective with a thin keel crest, up to 2 mm long, lateral appendages paired, filiform, 5–6 mm long. Ovary ⅔ as long as hypanthium, apex villous; style 10–12 mm long, glabrous, villous near base; stigma minute; extra-ovarial chambers extending almost to base of ovary. Fruits ovoid to suburceolate, 10–15 × 7–9 mm, brown, densely covered with minute brown stellate-furfuraceous hairs and 1–1.5 mm long simple, thick bristles densely covered with brown minute stellate hairs; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Peninsular Malaysia.

Habitat & Ecology — Lowland forest, in open places at 60–90 m elevation.

Vernacular Name — *Akar sendudo* (Kelantan).

Note — Furtado (1963) reduced *Macrolenes rufolanata* to a synonym of *M. stelullata*, because he supposed that the flowers in their young stage of development, with unbranched bristle hairs, would ultimately produce bristle hairs that branch at the apex when mature. However, the holotype (*SFN 15661*) in Kew has mature flowers and all bristles are neither branched nor barbed at the apex.

Specimens examined — **MALAYSIA.** Kelantan: Ulu Sungai Kelantan, Sungai Jenal, 25 Oct 1967, *Cockburn FRI 7417* (L); Sungei Lebir, Bukit Batu Papan, 120 m, 4 Jul 1936, *Henderson SFN 29504* (K). Pahang: Kuala Lipis, Ulu Chimeras, 70 m, 18 Nov 1924, *Burkill & Haniff SFN 15661* (K, SING); Gunong Tahan, 22 Jul 1936, *Kiah SFN 31760* (K). Selangor: Fraser's Hill, 1160 m, 25 Apr 1966, *Stone 6283* (L).

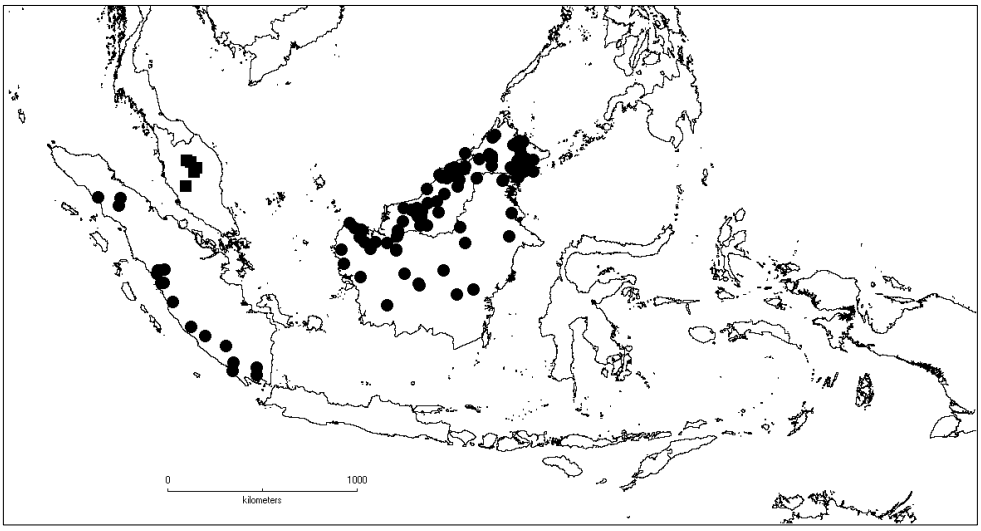


Fig. 4-7. Distribution of *M. pachygyna* (●) and *M. rufolanata* (■).

14. ***Macrolenes stellulata*** (Jack) Bakh.f. — Map 4-8

Macrolenes stellulata (Jack), Contr. Melastom. 216. 1943. — *Melastoma stellulatum* Jack, Trans. Linn. Soc. London 14: 6. 1823, '*stellulata*'. — *Marumia stellulata* (Jack) Blume, Flora 14: 505. 1831. — Neotype (designated here): *Deden et al. BOHK 239* (neo BO!; isoneo K [K000812315!], KEP), Indonesia, Sumatra, Jambi Province, Harapan Rain Forest, Nawai River, Kapas River branch, 70 m alt., 8 April 2013.

Marumia ciliatiloba Baker f., J. Bot. 62(Suppl.): 40. 1924. — *Macrolenes ciliatiloba* (Baker f.) Bakh.f., Contr. Melastom. 215. 1943. — *Macrolenes stellulata* (Jack) Bakh.f. var. *ciliatiloba* (Baker f.) J.F.Maxwell, Gard. Bull. Singapore 33: 321. 1980. — Lectotype (designated here): *H.O. Forbes 3008* (lecto BM [BM000944489!]; isolecto K [K000867111!], L [L0008933!, L0537222!]), Indonesia, Sumatra, Res. Palembang, Soekaradja, Roepit River, 600 ft alt.

Macrolenes submembranacea Bakh.f., Contr. Melastom. 214. 1943. — Type: *C.G.G.J. van Steenis 3522* (holo L [L0537196!]; iso BO [BO1751371!, BO1751372!], SING) Indonesia, Sumatra, Res. Bencoelen, G. Raja, Lake Ranau, 1300 m elev., 2 November 1929.

Climbing up to 15 m high. Branchlets terete, 3–4 mm in diameter, covered with minute brown stellate-furfuraceous hairs; nodes swollen, with an annular, crest-like interpetiolar ridge; internodes 5–7 cm long. Leaves: petioles terete or flattened, 10–15 mm long, densely stellate-tomentose; blades ovate-elliptic to elliptic, 9–14 × 4.7–6 cm, subcoriaceous, base subcordate to cordate with 5–7 mm long sinuses, margin entire, apex acuminate, acumen 0.5–1 cm long, adaxially glabrous, abaxially brown stellate-puberulous. Inflorescences 10–15 cm long, with 3–15 flowers; main axis angular, stellate-tomentose; primary axis 5–9 cm long with 1 or 2 nodes, secondary axis 1.5–3 cm long with 1 node, tertiary axis not developed; bracts ovate, 10–12 × ca. 8 mm, stellate-tomentose, margin ciliate, purplish, persistent; bracteoles ovate or suborbicular, 6–7 × 5–6 mm, stellate-tomentose, margin ciliate, purplish; pedicels stellate-tomentose and covered with scattered simple bristle hairs, 2–3 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium tubular, 12–21 × 5–9 mm, greyish when dry, densely covered with minute stellate-tomentum and 3–4 mm long bristles with barbed or branched tip, completely covered with dense minute greyish-brown stellate-tomentose hairs;

calyx lobes triangular or oblong with truncate base with acute tip, 6–9 × 3–4 mm, margin ciliate with simple or barbed-tip bristle hairs and densely covered with minute greyish-brown stellate hairs, densely stellatetomentose, purplish. Petals in bud conical, 9–14 mm long, covered with stellatefurfuraceous hairs; mature petals obovate to suborbicular, 20–22 × 15–18 mm, reflexed, base clawed, apex obtuse, above glabrous, underneath half stellatefurfuraceous, half glabrous, white or purple. Stamens: alternipetalous stamens with 15–16 mm long yellow filaments, anthers slender, curved, sickle-shaped, thecae 24–26 mm long, yellow, apex rostrate, pedoconnective 7–8 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform appendages, 8–10 mm long, pointing sidewards, lateral appendages not developed; oppositipetalous stamens with 13–14 mm long yellow filaments, anthers S-shaped, thecae 18–20 mm long, yellow, connective with a minute thin keel crest or short hairs, basally with ligular appendages prolonged into a single or a pair of filiform, 9–10 mm long appendages. Ovary ⅔ as long as hypanthium, apex villous and with several 2–3 mm long capitate bristle hairs; style 24–26 mm long, curved at tip, glabrous, stellate-furfuraceous at base; stigma minute, capitate; extra-ovarial chambers extending almost to base of ovary. Fruits urceolate, ca. 20 × 10–12 mm, densely covered with minute stellate-tomentose hairs and 3–4 mm long bristles with barbed or branched tips, covered by dense minute greyish-brown stellate hairs, apex densely with several capitate bristle hairs; calyx lobe remnants persistent, not reflexed. Seeds ca. 0.75 mm long.

Distribution — Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Lowland secondary forest and dipterocarp forest, in open places or along roadsides; 30–310 m elevation.

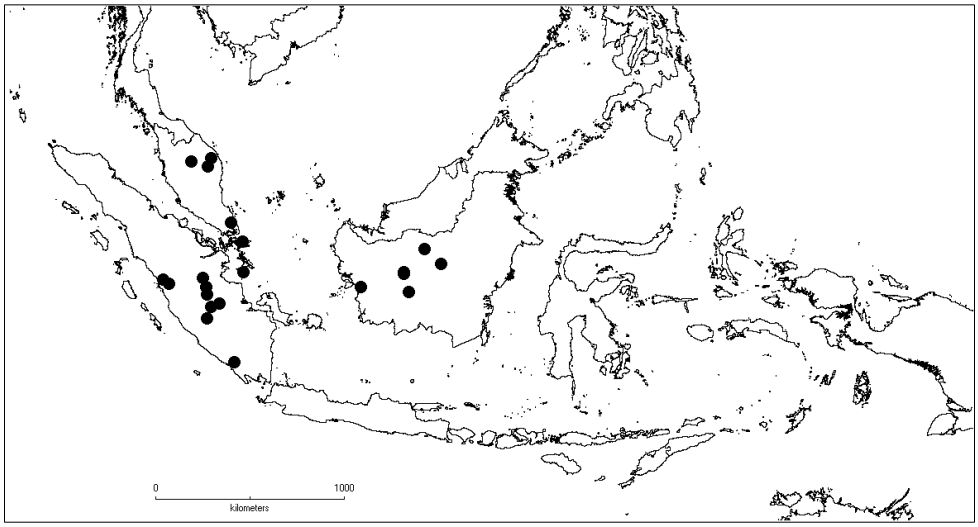
Vernacular name — Peninsular Malaysia: *Akar sundok* (Malay); Sumatra: *daduruh akar* (Bengkulu); *kedudu akar* (Jambi).

Notes — 1. *Macrolenes pachygyna* was considered to be a synonym of *M. stellulata* by Bakhuizen van den Brink (1943) based on the barbed tip of the bristle hairs on the hypanthium but is considered to be a distinct taxon in this revision. In the description of this species, Jack (1823) wrote that the leaves are oblong-ovate with a cordate base and the bracts are leaf-like, while in *Macrolenes pachygyna* the leaves are rather elliptic-oblong with a rounded base and the bracts are linear, not-leaf-like.

2. The type specimens of *Melastoma stellulatum* were collected from Sumatra but were lost during shipment to Europe. Therefore, a neotype is choosen in this revision. Maxwell (1980b) considered *Macrolenes ciliatiloba* to be a variety of *M. stelullata* sensu Bakh.f., which is actually *M. pachygyna* with its branched or barbed-tip of the bristle hairs on the hypanthium. The bristles in *Macrolenes stellulata* are rather densely covered with minute greyish-brown stellate hairs and the leaf underneath is puberulous, not tomentose. Bracts and bracteoles on both species are also different, ovate or suborbicular or leaf-like with a laciniate margin in *Macrolenes stellulata*, linear or lanceolate and lacking a laciniate margin in *M. pachygyna*.

Specimens examined — **MALAYSIA.** Johor: Mersing Road, 30 m, 4 Jan 1966, *Burkill 3900* (L). Kelantan: Relai, 22 Oct 1967, *Cockburn FRI 7298* (K, L). Pahang: Kuala Aur, Ulu Sungai Sepia, 40 m, 16 Jul 1970, *Shah & Noor 1922* (L). Terengganu: Ulu Brang, 120 m, Jul 1937, *Moysey & Kiah SFN 33835* (L). **INDONESIA.** Bengkulu: Lake Ranau, Mount Raya, 1300 m, 2 Nov 1929, *van Steenis 3522* (BO, L). Jambi: 200 m, Sep 1925, *Posthumus 927* (BO, L); Sungai Lesing, Oct 1925, *Posthumus 989* (BO); Teluk Rendah, 250 m, 20 Aug 1983, *Rahayu 324* (BO, L); Harapan rain Forest, 70 m, 3 Apr 2008, *Siahaan 3* (K); *Ibid.*, *Deden et al. BOHK 239* (BO, K). Riau: Rengat, Bukit Tiga Puluh Nat. Park, Bukit Karampal, 100 m, 14 Nov 1988, *Burley & Tukirin 1449* (BO, K, L). Riau Archipelago: Singkep Island, Manggu, 40 m, 2 Aug 1919, *Bünnemeijer 7170* (BO, K, L); *Ibid.*, *Bünnemeijer 7187* (BO, L); Bintan Island, Bukit Sipinjang, *Teijsmann s.n.* (BO, L). South Sumatra: Sukaraja, Rupit

River, 200 m, *Forbes 3008* (BM, K, L). West Sumatra: Solok, Tabek, Talang Babungo, 1100 m, 26 May 2001, *Coco et al. 27* (ANDA); *Ibid.*, *Ivon et al. 18* (ANDA). Central Kalimantan: Barito Ulu, Joloi River, 15 Jun 1990, *Ridsdale PBU 554* (K, L); Kotawaringin Timur, Sangai, 100 m, 27 Sep 1996, *Argent et al. 9635* (L). West Kalimantan: Ketapang, Gunung Palung, 30 m, 22 Jun 1986, *van Balgooy & van Setten 5561* (BO, L); *Ibid.*, Cabang Panti, 20 m, 21 Oct 1996, *Laman et al. 56* (BO, K, L); Sintang, Bukit Baka, 310 m, 9 Nov 1993, *Church et al. 633* (BO, K, L); Liang Gagang, *Hallier 3022* (BO, L); Sintang, 25 Jun 1894, *Langlasse 95* (P).



Map 4-8. Distribution of *M. stellulata* (●).

15. *Macrolenes subulata* J.F.Maxwell — Fig. 4-6, Map 4-9

Macrolenes subulata J.F.Maxwell, Gard. Bull Singapore 33: 321, fig. 6. 1980. — Type: *M. Jacobs 8028* (holo L [L0537194!]; iso BO [BO1865976!], K [K000867110!], KEP [KEP110313!], SING [SING0052049!]), Indonesia, Sumatra, Lampung Province, Mt. Tanggamus, 1100–1200 m alt., 25 April 1968.

Climbing up to 2 m high. Branchlets terete, 3–4 mm in diameter, densely covered with brown stellate-furfuraceous hairs and often with scattered bristle hairs covered by stellate hairs at the tip; nodes swollen, with interpetiolar ridge; internodes 4–5.5 cm long. Leaves: petioles terete, 6–8 mm long, densely brown stellate-furfuraceous and with scattered bristle hairs covered by stellate hairs at the tip; blades ovate to ovate-elliptic, 7.7–9.5 × 3.2–5 cm, membranous, base shallowly cordate, margin entire, apex acuminate, acumen 0.5–1 cm long, adaxially glabrous, dark green, abaxially sparsely covered with brown stellate hairs, densely so on veins. Inflorescences 5–7 cm long, with 1–3 flowers; main axis angular, densely brown stellate-furfuraceous and with scattered bristle hairs covered by stellate hairs at the tip; primary axis 2.5–4 cm long with 1 node, secondary axis not developed; bracts lanceolate, 10–12 × 3–5 mm, brown stellate-furfuraceous; bracteoles lanceolate, 6–10 × 3–5 mm, densely stellate-furfuraceous; pedicels densely covered with minute brown stellate-furfuraceous hairs and bristle hairs covered by stellate hairs at the tip, ca. 4 mm long in central flowers, 1–2 mm long in lateral flowers. Hypanthium campanulate-tubular, 10–12 × 6–7 mm, densely covered with minute brown stellate-furfuraceous hairs and with 1–3 mm long, thick,

Fig. 4-6. *Macrolenes subulata*. **a.** habit; **b.** hypanthium with mature flower; **c.** hyanthium; **d.** flower; **e.** fruit. (Photos: A. Kartonegoro).

simple bristle hairs covered by stellate hairs at the tip; calyx lobes slightly triangular, 9–11 × 4–6 mm, densely brown stellate-tomentose, apex acute, margin with short thick bristle hairs. Petals in bud conical, 5–6 mm long, glabrous; mature petals obovate or suborbicular, 25–30 × 20–25 mm, not reflexed, base clawed, apex obtuse, glabrous, white with purple tinge. Stamens: alternipetalous stamens with 14–15 mm long bright yellow filaments, anthers slender, sickle-shaped, thecae 23–25 mm long, pink, pedoconnective 6–7 mm long, whitish, connective basal crest small with several fimbriate, filiform appendages, 5–6 mm long,

lateral appendages paired, filiform, 7–8 mm long; oppositipetalous stamens with 12–14 mm long bright yellow filaments, anthers S-shaped, thick, thecae 16–18 mm long, connective with a pair of ridges or keels, ca. 1 mm long, basally with paired, filiform lateral appendages, 6–8 mm long. Ovary ⅔ as long as hypanthium, apex villous; style 20–22 mm long, curved at apex, glabrous, dark pink, white at apex; stigma minute, capitate; extra-ovarial chambers extending from the middle to base of ovary. Fruits seen immature, ca. 12 × 6–7 mm, densely covered with brown minute stellatefurfuraceous hairs and 1–3 mm long, thick, bristle hairs covered by stellate hairs at the tip; calyx lobes persistent, reflexed. Seeds seen immature, ca. 0.4 mm long.

Distribution — Sumatra (Lampung).

Habitat & Ecology — Montane forest in open places at 800–1200 m elevation.

Note — This species resembles *Macrolenes dimorpha* from Peninsular Malaysia and Thailand in its indumentum of most parts, but differs in having bristle hairs that are covered with brown stellate hairs on the upper part with the base glabrous. The species is so far known only from Mount Tanggamus in Lampung Province, Sumatra.

Specimens examined — **INDONESIA.** Lampung: Mount Tanggamus, 1100 m, 25 Apr 1968, *Jacobs 8028* (BO, K, L, KEP, SING); *Ibid.*, Gisting, 800 m, *Hughes et al. SUBOE 71* (BO, E).

16. *Macrolenes tuberculata* Karton. **sp. nov.** — Fig. 4-7, Map 4-9

Type: *W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 19573* (holo BO!; iso K!, L!), Indonesia, North Sumatra, Mount Leuser National Park, Besitang, Sikundur, 50–100 m alt., 8 August 1979.

Diagnostic. Hypanthium tuberculate, cyathiform, rather short, slightly triangular to subrounded, calyx lobes ca. 3.5 × 3 mm, with acute to obtuse tips; similar in the size of the hypanthium and the length of the calyx lobes to *Macrolenes bruneiensis,* but differing in the type of the indumentum where *M. tuberculata* has tuberculate bristles and *M. bruneiensis* has floccose bristles.

Climbing up to 25 m high. Branchlets terete, 3–4 mm in diameter, covered with minute brown stellate-furfuraceous hairs; nodes swollen, with interpetiolar ridges; internodes 3.5–7 cm long. Leaves: petioles terete, 8–10 mm long, stellate-furfuraceous; blades elliptic-oblong to oblong, 5.5–13 × 2–4.3 cm, subcoriaceous, base slightly to broadly subcordate, margin entire, apex acuminate, acumen 0.5–1 cm long, adaxially glabrous, dark glossy green, abaxially densely stellate-tomentose. Inflorescences 3–5 cm long, with 1–3 flowers; main axis terete, densely brown stellate-furfuraceous; primary axis 1.5–2.5 cm long with 1 node, secondary axis when developed ca. 0.7 cm long; bracts and bracteoles minute, caducous; pedicels densely brown stellate-furfuraceous, ca. 5 mm long in central flowers, 2–3 mm long in lateral flowers. Hypanthium campanulate-cyathiform, ca. 10 × 6–8 mm, densely covered with minute brown stellate-furfuraceous hairs and ca. 0.5 mm long tubercles covered with minute brown stellate hairs; calyx lobes slightly triangular to subrounded with acute to obtuse tips, ca. 3.5 × 3 mm, densely covered with minute stellate hairs, reflexed. Petals in bud conical, ca. 5 mm long, brown stellate-tomentose; mature petals obovate to suborbicular, 8–12 × 6–10 mm, reflexed, base clawed, apex acute, above glabrous, underneath half glabrous, half densely brown stellate-tomentose, white to pinkish white. Stamens: alternipetalous stamens with ca. 7 mm long yellowish filaments, anthers curved, sickle-shaped, thecae 10–11 mm long, pink, pedoconnective ca. 4 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform appendages, up to 3 mm long, lateral appendages not

developed; oppositipetalous stamens with ca. 6 mm long filaments, anthers S-shaped, thecae 8–9 mm long, pink, connective with a thin keel crest, ca. 0.5 mm long, basally with paired, filiform lateral appendages, 5–6 mm long. Ovary ¾ as long as hypanthium, apex pubescent; style 12–13 mm long, densely stellate-pubescent, glabrous and curved at tip; stigma minute, capitate; extra-ovarial chambers extending to the middle of the ovary. Fruits ovoid, 10–12 × ca. 9 mm, densely covered with brown stellate hairs and small tubercles; calyx lobe remnants persistent, reflexed. Seeds ca. 0.5 mm long.

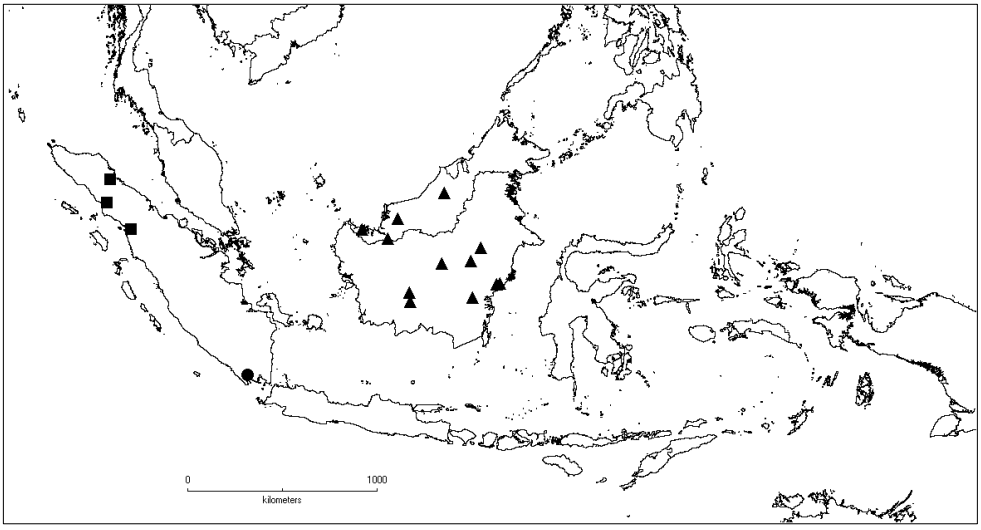
Distribution — Sumatra (North).

Habitat & Ecology — Lowland tropical forest in open area or secondary logged forest at 50–250 m elevation.

Etymology — The species epithet refers to the tuberculate appearance of the hypanthium surface.

Note — *Macrolenes tuberculata* is recognized by its campanulate-cyathiform and tuberculate hypanthium. The tubercles (ca. 0.5 mm long) on the hypanthium are covered by minute stellate hairs. Like *M. bruneiensis*, this species has a small hypanthium and short calyx lobes of only ca. 3.5 mm long.

Specimens examined — **INDONESIA.** Aceh: Mount Leuser Nat. Park, Subulussalam, Alas River, Lae Batu-Batu, 50 m, 5 Aug 1985, *De Wilde & De Wilde-Duyfjes 20667* (L). North Sumatra: Mount Leuser Nat. Park, Besitang, Sikundur, 100-250 m, 15 Aug 1971, *Iwatsuki et al. S-407* (BO, K, L); *Ibid.*, 50 m, 29 Jan 1983, *Maskuri 1103* (BO, K, L); *Ibid.*, 50–100 m, 8 Aug 1979, *de Wilde & de Wilde-Duyfjes 19573* (BO, K, L); *Ibid.*, 20 Jul 1991, *De Wilde & De Wilde-Duyfjes 21086* (L, U).



Map 4-9. Distribution of *M. subulata* (●); *M. tuberculata* (■); and *M. Veldkampii* (▲).

17. *Macrolenes veldkampii* Karton., **sp. nov.** — Fig. 4-8, Map 4-9

Type: *P.J.A. Kessler et al. 2656* (holo BO!; iso K!, L [L0370302!], WAN) Indonesia, Borneo, East Kalimantan, Long Iram subdistrict, Maruwai, block Lampunut, 310 m, 0˚04’S 114˚52’E, 19 March 1999.

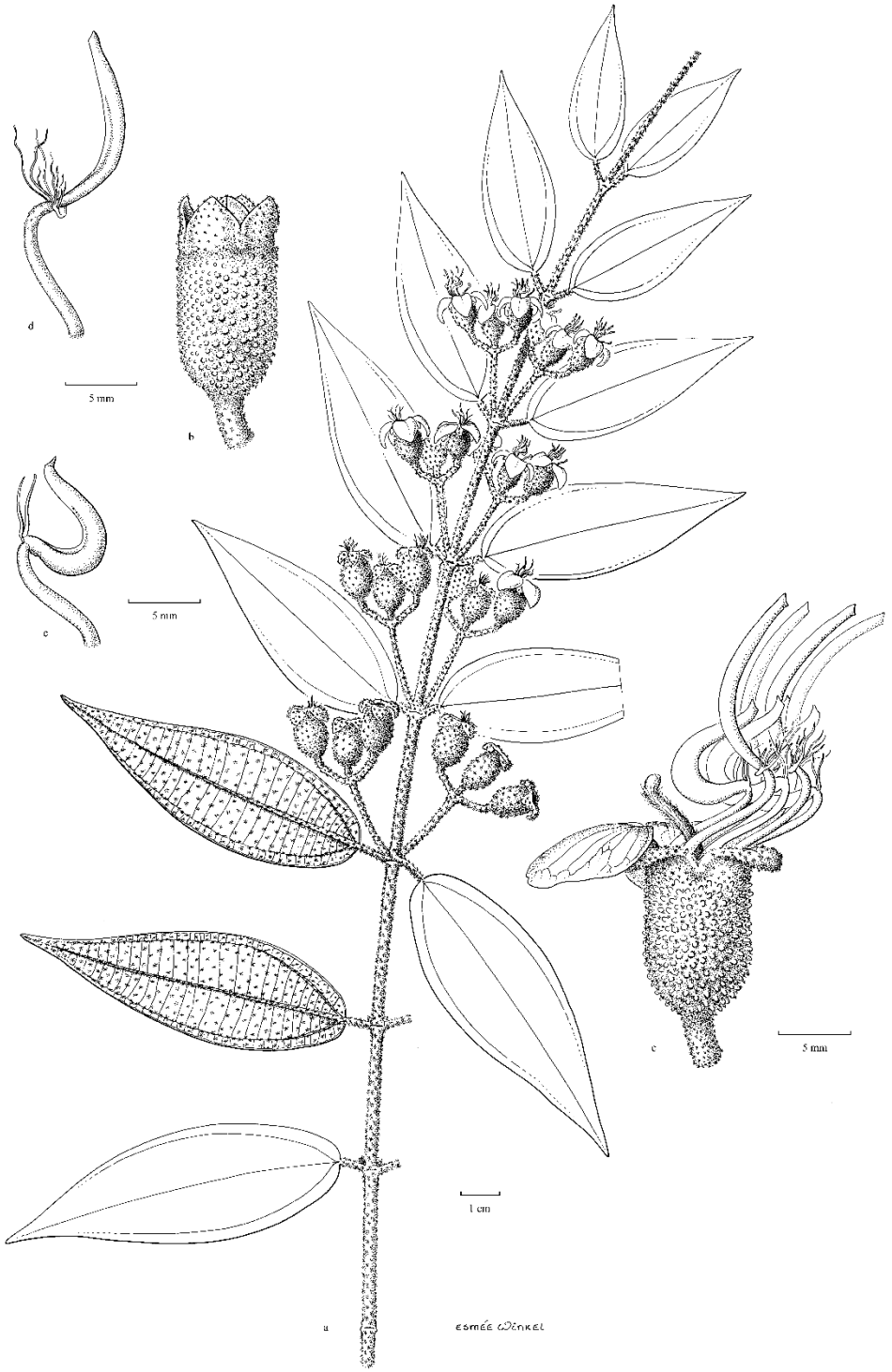


Fig. 4-7. *Macrolenes tuberculata*. **a.** habit; **b.** hypanthium; **c.** flower; **d.** alternipetalous stamen; **e.** oppositipetalous stamen. **a, c–e** from de *Wilde & de Wilde-Duyfjes 20667* (L); **b** from *Maskuri 1103* (L). Drawn by Esmée Winkel

Diagnostic. Resembles *Macrolenes pachygyna* in indumentum around the hypanthium of erect bristle hairs with barbed or branched tips, only the apex covered with dense, minute brown stellate hairs (the bristle hairs of *M. pachygyna* are completely covered with small brown stellate hairs).

Climbing up to 8 m high. Branchlets terete, 3–5 mm in diameter, densely covered with minute brown stellate-furfuraceous hairs; nodes swollen, with simple interpetiolar ridge; internodes 3.3–7 cm long. Leaves: petioles terete, 5–7 mm long, densely stellate-tomentose; blades ovate-elliptic, 6.5–8.4 × 3–3.8 cm, subcoriaceous, base cordate, margin entire, apex acuminate, acumen ca. 0.5 cm long, adaxially glabrous, dark green, abaxially densely brown stellate-tomentose. Inflorescences 5.5–11 cm long, with 1–12 flowers; main axis terete or subangular, densely brown tomentose, often with scattered capitate bristle hairs; primary axis 2.5–7 cm long with 1 or 2 nodes, secondary axis 0.8–2.4 cm long with 1 node or not developed, tertiary axis if developed up to 1.7 cm long; bracts linear or lanceolate, 7–8 × ca. 2 mm, entire, stellate-tomentose outside, glabrous inside, caducous; bracteoles linear or lanceolate, 4–5 mm long, stellate-tomentose outside, glabrous inside; pedicels densely covered with minute stellate-furfuraceous hairs and bristle hairs covered with dense minute stellate hairs at tip, tip appearing to be capitate, 2–3 mm long in central and lateral flowers. Hypanthium campanulate, 9–12 × 7–9 mm, brownish when dry, densely covered (surface of hypanthium not visible) with ca. 2 mm long erect bristle hairs with barbed or branched tips, latter covered with dense minute brown stellate hairs, base of bristles glabrous or subglabrous; calyx lobes triangular with acute tips, 5–6 × 3–4 mm, densely covered with bristle hairs as on hypanthium, margin ciliate and covered with minute brown stellate hairs. Petals in bud conical, 5–6 mm long, covered with stellate-furfuraceous hairs; mature petals obovate to suborbicular, 15–18 × 8–10 mm, not reflexed, base clawed, apex obtuse, above glabrous, underneath half stellate furfuraceous, half glabrous. Stamens: alternipetalous stamens with ca. 6 mm long filaments, anthers curved, sickle-shaped, thecae 15–16 mm long, pedoconnective 4–5 mm long, connective basal crest thin, annular, prolonged into several fimbriate, filiform appendages, 5–6 mm long, lateral appendages not developed; oppositipetalous stamens with ca. 6 mm long filaments, anthers S-shaped, thecae 9–11 mm long, connective with a minute thin keel crest, ca. 0.3 mm long, basally with paired, filiform lateral appendages, 5–6 mm long. Ovary ¾ as long as hypanthium, apex pubescent; style 15–16 mm long, stellate-furfuraceous and with scattered capitate bristle hairs, above glabrous, curved at tip; stigma minute, capitate; extra-ovarial chambers extending almost to base of ovary. Fruits urceolate, 10–12 × 8–9 mm, brown, densely covered with ca. 2 mm long erect bristle hairs with barbed or branched tips, latter covered with dense minute brown stellate hairs, base of bristles glabrous or subglabrous; calyx lobe remnants persistent, reflexed. Seeds ca. 0.75 mm long.

Distribution — Borneo.

Habitat & Ecology — Secondary lowland or mixed Dipterocarp forest, sometimes water-logged at 50–600 m elevation.

Etymology — The species epithet acknowledges the late Jan Frederik "Jan Frits" Veldkamp, a Dutch agrostologist, who also worked on Southeast Asian Melastomataceae (for obituary see Baas & Hovenkamp 2018a, 2018b).

Note — The bristles on the hypanthium have a branched and barbed apex, in which *Macrolenes veldkampii* resembles *M. pachygyna*, but the bristles are only covered by minute stellate hairs in the upper part, while the base is glabrous. The bristle hairs are also present on the pedicels and the calyx lobes, whereas *Macrolenes pachygyna* has no bristle hairs here.

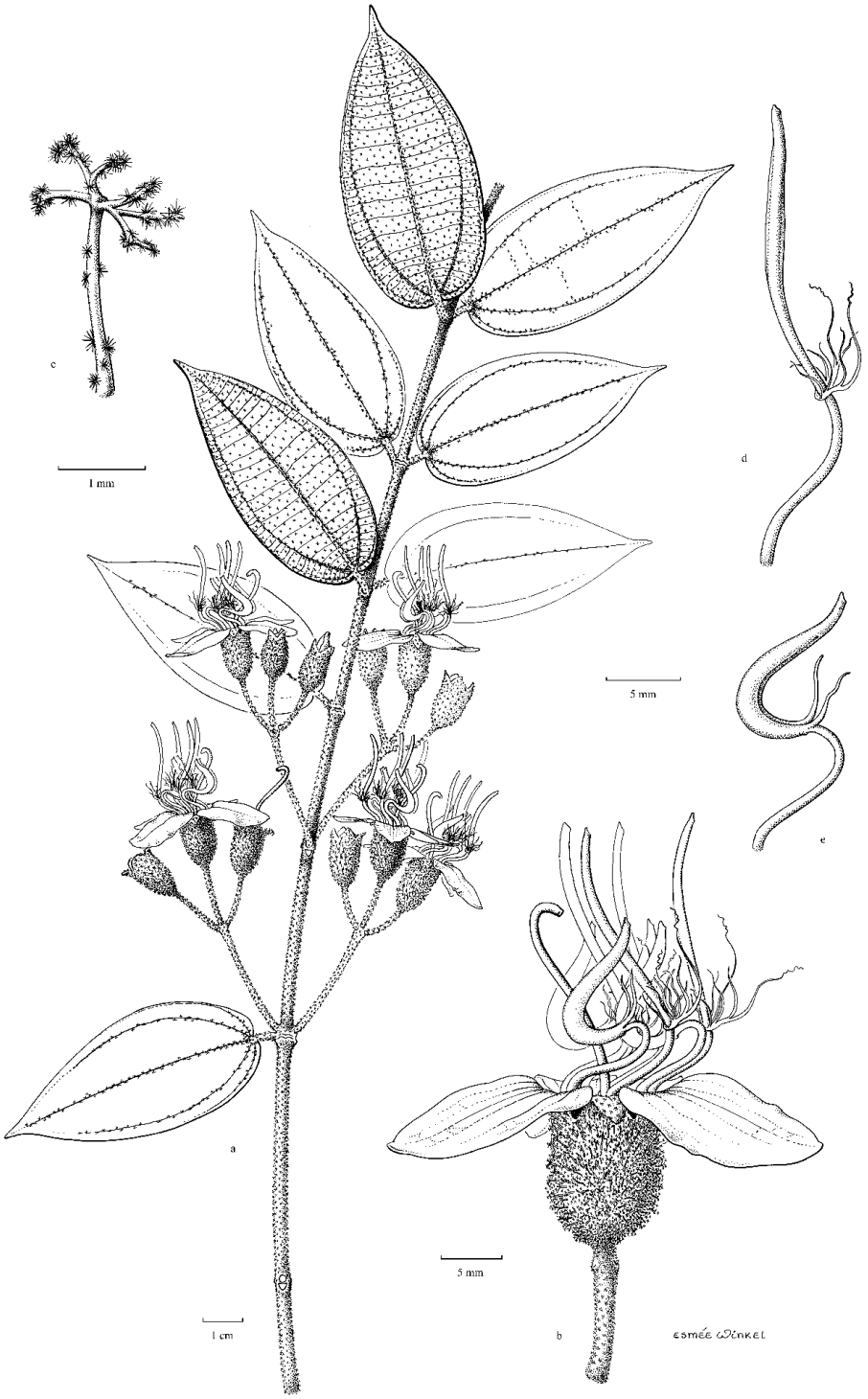


Fig. 4-8. *Macrolenes veldkampii*. **a.** habit; **b.** flower; **c.** indumentum; **d.** alternipetalous stamen; **e.** oppositipetalous stamen. All from *Kostermans 13041* (L). Drawn by Esmée Winkel.

Specimens examined — **MALAYSIA.** Sarawak: Baram, Ulu Tinjar, Mount Dulit, 13 Sep 1932, *Richards 1770* (K); Kuching, *Bartlett s.n.* (BM); *Ibid.*, *Beccari PB 125* (K, P); *Ibid.*, *Beccari PB 379* (K, P); *Ibid.*, *Beccari PB 632* (K, P); Pengkulu Ampat, 31 Oct 1890, *Haviland 147* (BM, K); Sri Aman, Kampong Pungur Tapang, 5 Nov 1980, *Paie S.42719* (K, L). **INDONESIA.** Central Kalimantan: Kuala Kuayan, Permantang, 50 m, 30 Mar 1984, *Hansen 1318* (BO); Barito Ulu, 2 Jun 1990, *Ridsdale PBU 275* (BO, K, L); *Ibid.*, 26 May 1990, *Sidiyasa PBU 132* (BO, L); Kotawaringin Timur, Sangai, 50 m, 21 Sep 1996, *Argent & Wilkie 963* (L). East Kalimantan: *Ambriansyah & Arifin W 217* (L); Long Iram, Maruwai, Lampunut, 310 m, 19 Mar 1999, *Kessler et al. 2656* (BO, K, L); *Ibid.*, *Kessler et al. 2676* (BO, K, L); Mount Palimasan, 600 m, 14 Sep 1956, *Kostermans 13041* (BO, K, L); Bukit Bangkirai, 17 Feb 2001, *Ruskandi & Rugayah 400* (BO). South Kalimantan: Tabalong, 190 m, 5 Jul 2000, *Sidiyasa & Arifin 2007* (BO, L).

Excluded Taxa

Macrolenes griffithii M.P.Nayar, J. Jap. Bot. 55: 47. 1980. — Type: *W. Griffith KD 2269* (holo K [K001096571!]), Malaysia, Peninsular Malaysia, Malacca. = ***Dissochaeta griffithii*** (M.P.Nayar) Karton., PhytoKeys 107: 91. 2018.

Macrolenes horrida Bakh.f., Contr. Melastom. 208. 1943. — Type: *H.A.B. Bünnemeijer 3200* (holo L [L0537276!]; iso BO [BO1751324!, BO1751325!]), Indonesia, West Sumatra, Agam, Brani. = ***Dissochaeta horrida*** (Bakh.f.) Karton., PhytoKeys 107: 95. 2018.

Macrolenes ruttenii Bakh.f., Contr. Melastom. 210. 1943. — Type: *L.M.R. Rutten 535* (holo U [U0004012!]), Indonesia, East Kalimantan, Samarinda, Bengalon. = ***Dissochaeta rostrata*** Korth. in Temminck, Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844.

Marumia warburgii Cogn. in Warburg, Bot. Jahrb. Syst. 13: 393. 1891. — Lectotype (designated here): *O. Warburg 30* (lecto BR [BR528055!]; isolecto B), Papua New Guinea, Sattelberg. = ***Rhodomyrtus trineura*** (F.Muell.) F.Muell. ex Benth. var. ***novoguineensis*** (Diels) A.J.Scott, Kew Bull. 33: 324. 1978 (Myrtaceae).

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CHAPTER 5

A taxonomic revision of *Pseudodissochaeta* (Melastomataceae, Dissochaeteae)

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A taxonomic revision of *Pseudodissochaeta* (Melastomataceae, Dissochaeteae)

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Abstract

The mainly Southeast Asian genus *Pseudodissochaeta* (Melastomataceae, Dissochaeteae) is revised based on a study of herbarium collections. The relationships of *Pseudodissochaeta* to *Dissochaeta* and *Medinilla* are discussed and some important characters distinguishing it from its relatives, including habit, leaf base and margin and floral characters, are provided. Five species are recognized without any infraspecific taxa. A key to the species, descriptions of each species, distribution (maps), ecology, habitat, images and a list of the specimens examined are given.

Keywords

Melastomataceae, *Pseudodissochaeta*, revision, shrub, Southeast Asia.

Introduction

Pseudodissochaeta M.P.Nayar (1969a) was established for a small homogenous group of species that resembles *Dissochaeta* Blume (1831a) in inflorescence/infructescence types, but it comprises erect shrubs or small trees instead of scrambling shrubs or woody climbers. The genus can be distinguished from allied genera by the erect woody habit and the leaves with generally serrulate margins, flowers with 8 equal or subequal and isomorphic stamens, connectives with dorsally spurred and ventrally bilobed or biauriculate appendages (Nayar 1969a, Maxwell 1984, Renner et al. 2001b). *Pseudodissochaeta* is derived from the Greek word “pseudo” meaning false or fake, in reference to *Dissochaeta*, which it resembles (Maxwell 1984).

Before the establishment of the genus by Nayar (1969a), some of the species of *Pseudodissochaeta* were placed under seven different genera, i.e. *Allomorphia* Blume, *Anerincleistus* Korth., *Anplectrum* A.Gray, *Backeria* Bakh.f., *Diplectria* (Blume) Rchb., *Medinilla* Gaudich. ex D.C., *Oritrephes* Ridl. (Clarke 1879, Kuntze 1891, Smith 1911, Craib 1913, Guillaumin 1921, Li 1944, Raizada 1968). Morphologically, *Pseudodissochaeta* shares some general (superficial) similarities with these genera. Some authors have even considered the genus to have capsular fruits, which is typical for the Oxysporeae Triana

(Smith 1911, Guillaumin 1921a). In fact, the fruits of *Pseudodissochaeta* are berries, just like other genera of Dissochaeteae (Naudin) Triana (Li 1944).

Pseudodissochaeta has been treated under *Medinilla* during the past few decades based on their morphological similarity (Chen 1983, 1984, Chen & Renner 2007, Cho et al. 2016). Its habit and floral characters better resemble *Medinilla* than *Dissochaeta* (Chen & Renner 2007). Nevertheless, recent molecular phylogenetic studies indicate that *Medinilla* is nested in Asian Sonerileae Triana, while *Pseudodissochaeta* consistently formed a strongly supported clade with *Dissochaeta* and alliances (Zhou et al. 2019, Kartonegoro et al. 2021). The wood anatomy of the genus also supports a close relationship with *Dissochaeta* rather than the *Medinilla*-alliance (Van Vliet 1981, Van Vliet et al. 1981, Kartonegoro et al. 2021). Morphologically, *Pseudodissochaeta* can be distinguished from *Dissochaeta* and *Medinilla* by its sometimes serrulate leaf margin (vs. entire) or oblique leaf base (vs. equal) or a combination of the two characters. Inflorescences in *Pseudodissochaeta* are thyrses with tetramerous flowers which are more similar to *Dissochaeta* than to *Medinilla*. However, the shape of stamens with dorsally spurred and biauriculate appendages is found in *Medinilla*. Based on the above molecular, anatomical and morphological evidences, *Pseudodissochaeta* is excluded from *Medinilla* and recognized as a distinctive genus. The morphological differences among *Dissochaeta*, *Medinilla* and *Pseudodissochaeta* are shown in Table 5-1.

Table 5-1. Differences in morphological characters among *Dissochaeta*, *Medinilla* and *Pseudodissochaeta*

Character	*Dissochaeta*	*Medinilla*	*Pseudodissochaeta*
Habit	Scrambling shrubs	Erect, climbing, spreading or epiphytic shrubs or rarely small trees	Erect or spreading shrubs
Leaf base	Regular	Regular	Oblique or regular
Leaf margin	Entire	Entire	Serrulate (except *P. spirei*)
Floral merosity	4-merous	4-, 5-, or 6-merous	4-merous
Calyx lobes	Semi truncate with triangular tip	Truncate with teeth-like or triangular tip	Truncate with teeth-like tip
Stamen shape	Dimorphic	Iso- or dimorphic	Isomorphic
Connective appendages	Dorsally triangular, ventrally biligulate or inappendiculate	Dorsally spurred, ventrally bilobed or biauriculate	Dorsally spurred, ventrally bilobed or biauriculate

Materials and methods

This revision is based on the analysis of morphological characters from specimens in the following herbaria: AAU, BM, E, K, L, P, PE, S (herbarium acronyms follow Thiers 2018, continuously updated), including online specimen images (https://plants.jstor.org/collection; https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US; https://www.aubot.dk/search_form.php; http://pe.ibcas.ac.cn/en/; http://herbarium.nrm.se/search/specimens/). Examination of morphological characters including indumentum, flowers and fruits was performed with binocular stereomicroscopes. The types of almost all names were examined either as actual specimens or as images. Morphological descriptions and measurements were made from dried specimens and fresh material with terminology following Bakhuizen van den Brink (1943), Nayar (1969a), Maxwell (1984), Renner et al. (2001b) and Kartonegoro et al. (2018, 2019). Distribution maps were prepared using DIVA-GIS (http://www.diva-gis.org/). A list of selected examined specimens is included under each species by country and, secondarily, by province.

General Morphology, Habitat and Distribution

Pseudodissochaeta has been described as erect or spreading shrubs up to 5 m tall, but some specimens are small trees up to 6 m. Herbarium labels indicate that *P. spirei* (Guillaumin) Veldkamp & Maxwell is a woody climber, but in fact the species is actually a spreading shrub in habit, not scrambling. The branchlets may be terete or quadrangular and 4-grooved, or slightly flattened. *Pseudodissochaeta subsessilis* (Craib) M.P.Nayar has angular branchlets that are often striate and clearly winged. Some species have young parts that possess a furfuraceous indumentum of stellate hairs, but become glabrescent. Mature branches are usually terete (except *P. subsessilis*) and have a thinner indumentum or are entirely glabrous (Maxwell 1984). The nodes of the branchlets and sometimes those of the branches are swollen and have the same type of indumentum as the internodes. Interpetiolar growth is uncommon and often inconspicuous.

Like most Melastomataceae, the leaf arrangement is opposite with equally sized leaves. Leaf blades are ovate to lanceolate with acute or acuminate tips. The leaf margin is serrulate, or exceptionally slightly serrulate to entire in *P. spirei*. The base of the blades varies from rounded, cuneate to oblique cordate in *P. assamica* (C.B.Clarke) M.P.Nayar, *P. spirei*, and *P. subsessilis*. Those three species have clasping and subsessile blades, a feature not found elsewhere in the tribe. In general, the leaf blades in all species have 1–2 pairs of lateral nerves, a pair of intramarginal nerves, numerous secondary nerves and a reticulate pattern of higher order nerves. The main nerves are usually sunken adaxially and raised on the abaxial surface. The leaf surface is mostly glabrous at maturity but sparsely puberulous on the veins, usually denser on the midrib and lateral nerves.

Pseudodissochaeta has a terminal, rarely axillary, cymose, paniculate or thyrsoid inflorescence, that is usually subtended by reduced leaves at the lower nodes of the primary axis. This form is common in all Dissochaeteae except *Creochiton* Blume, which has an umbellate inflorescence in most species (Kartonegoro & Veldkamp 2013). *Pseudodissochaeta lanceata* M.P.Nayar differs from its congeners in having inflorescences that grow from leafless stems (cauliflory) or from the root stock. This inflorescences type is similar to some species of *Heteroblemma* (Blume) Cámara-Leret, Ridd.-Num. & Veldkamp or *Medinilla* (Regalado 1990, Chen & Renner 2007, Camara-Leret et al. 2013). The branching within the inflorescences is opposite with 3-flowered cymules terminating each ultimate ramification. The axillary inflorescences have, beside the primary axis, well developed secondary axes, and distinct pedicels. The axes of the inflorescences are generally terete or quadrangular, with indumentum and nodes similar to those of the branchlets. A pair of bracts is present at each node of the inflorescence with a pair of bracteoles at the base of each pedicel, however, in most instances they fall off before anthesis.

The flowers are 4-merous. The shape of the hypanthium is mostly campanulate, cyathiform or tubular, either glabrous or with a few scattered minute stellate hairs. The calyx lobes are truncate or united but still with four teeth-like or submarginally thickened tips (recalling the situation in *Medinilla*), or patches of bristles (*P. lanceata*) that represent reduced or modified calyx lobes. The four petals are usually thin, conspicuous, symmetric, and usually colourful, but of very little taxonomic importance. The most frequent shapes are ovate, obovate, and suborbicular with a rounded or acute tip and a truncate or clawed base. All species have glabrous petals with visible venation or they are sometimes thicker with invisible veins near the middle and with thinner margins. The petals are imbricate in bud.

Pseudodissochaeta generally has eight fertile stamens in two whorls (inner and outer) borne in a ring at the summit of the hypanthium. As in other genera in the Dissochaeteae (Kartonegoro & Veldkamp 2013, Kartonegoro et al. 2018, 2019), the inner whorl is opposite the petals (oppositipetalous) and the outer whorl is alternate with the petals (alternipetalous). All stamens have well developed filaments, which are remarkably uniform in most species. Filaments vary in length according to the stage of maturity and in most cases they are glabrous. All species have eight isomorphic, equal or subequal stamens, which differ from those in the other genera of the Dissochaeteae. The anthers are terete, slightly curved to sinuate, and narrowed to a single, oblique pore at the tip. The connectives develop small appendages, which may be triangular, spur-like or bulbous-lobed dorsally and ventrally bilobed or biauriculate. *Pseudodissochaeta subsessilis* and *P. spirei* differ slightly in having shorter and thicker anthers whereby the alternipetalous ones in the former and both whorls in the latter have a thickened connective ridge dorsally. The appendages of the anthers in *Pseudodissochaeta* recall those of *Medinilla* rather than those of *Dissochaeta*.

The ovaries in the genus range from about half to ¾ as long as the hypanthium. Entirely glabrous ovaries are typical for *Pseudodissochaeta*. The placentation in *Pseudodissochaeta* is axillary with one placenta in each of the four locules, being attached to the middle of the central column. This type of placentation is commonly shared in Dissochaeteae except for some *Creochiton* species with basal placentation (Kartonegoro & Veldkamp 2013). The stigma in all species is very inconspicuous, capitate or punctiform and not useful for species recognition. The style in bud is straight and at maturity it is frequently curved at the tip. *Pseudodissochaeta*, which has relatively small flowers, have extra-ovarial chambers extending almost or completely to the base of the ovary. *Pseudodissoehaeta spirei* has shorter chambers, which are about half as long as the ovary.

A baccate fruit is found in all species of *Pseudodissochaeta*. The fruit colour changes from green to a dark blue-blackish or purple at full ripeness and has intermediate colours ranging from pink or red to dark blue. In addition to various vegetative features, the size of the fruit, shape and width of the areolus, and the thickness of the pericarp are among the most reliable characters that can be used for identification. The seeds of *Pseudodissochaeta* are numerous, cuneate, with a prominent hilum and papillose testa (Maxwell 1984), which also resemble those of *Medinilla*. Unlike most *Pseudodissochaeta*, other genera of Dissochaeteae commonly have cuneate, flat-topped seeds (Maxwell 1984, Kartonegoro et al. 2018, 2019).

Pseudodissochaeta is mostly found in tropical evergreen forests, with little seasonal variation in temperature and rainfall. They are present in primary shaded forest, but sometimes also in rather degraded forest, open forest margins, riverbanks or road sides, ranging in elevation from 80 up to 2000 m. The genus is distributed from E Bhutan and NE India, eastward to S China (including Hainan), N Myanmar, Indochina (Cambodia, Laos, Vietnam), and N Thailand.

Taxonomic Treatment

Pseudodissochaeta M.P.Nayar

Pseudodissochaeta M.P.Nayar, J. Bombay Nat. Hist. Soc. 65(3): 557. 1969; S.S.Renner, Nordic J. Bot. 13: 524. 1993; S.S.Renner et al., Fl. Thailand 7(3): 475. 2001. — Type: *Pseudodissochaeta assamica* (C.B.Clarke) M.P.Nayar

Erect or spreading shrubs or small trees up to 6 m in height; branchlets terete or angular, glabrous or softly hairy; nodes swollen with interpetiolar lines or crests, somewhat bristly. Leaves petiolate or subsessile; blades membranaceous or subcoriaceous, ovate to oblong-lanceolate, base equal or oblique, cuneate, rounded or cordate, margin serrulate or rarely entire, apex acute to acuminate; lateral nerves 2–6, intramarginal nerves 2; veins sunken adaxially, raised abaxially; surfaces glabrous but sparsely pilose on the abaxial nerves. Inflorescences terminal paniculate cymes, rarely axillary; thyrses up to 3 ramifications (rarely up to 4 or 5) with 3 to many flowers; bracts and bracteoles subulate, caducous. Flowers 4-merous. Hypanthium cyathiform, tubular or campanulate, calyx lobes truncate with shallowly 4 teeth-like lobes. Petals obovate to suborbicular, glabrous. Stamens 8, in two whorls, equal to subequal; anthers curved or sickle-shaped, apex rostrate; pedoconnective inconspicuous; connective basally with appendages, dorsally spurred or triangular, ventrally bilobed or biauriculate. Ovary 4-loculed, half to ¾ as long as the hypanthium, adnate to hypanthium with 8-septae forming extra-ovarial chambers; placentas axillary; extra-ovarial chambers extending to the middle or base of the ovary; style glabrous, filiform, apex slightly curved; stigma capitate or punctiform. Fruits berries, subglobose, ovoid or urceolate, glabrous or rarely with sparse capitate bristles, light to dark green becoming dark purple when ripe; seeds numerous, cuneate.

Distribution — Five species distributed mainly in Southeast Asia, ranging from east Bhutan, northeastern India, northern Myanmar, southern China, Hainan, northern Thailand and Indochina (Cambodia, Laos, Vietnam).

Key to species of *Pseudodissochaeta*

1 Leaves subsessile or shortly petiolate, up to 5 mm long, leaf length 42 times of petiole length or more; leaf base oblique, cordate (or auriculate); hypanthium campanulate or cyathiform-campanulate; fruits subglobose to globose 2
1 Leaves with well-developed petioles, 3–10 mm long, leaf length 24 times of petiole length or less; leaf base regular, obtuse, cuneate or rounded; hypanthium tubular or urceolate; fruits ovoid or urceolate 4
2 Branchlets quadrangular, winged; hypanthium with 8 faint ridges ..... **5. *P. subsessilis***
2 Branchlets terete, not winged; hypanthium without ridge 3
3 Nodes and petioles covered with bristles; leaf base shallowly cordate, leaf margin serrulate ..... **1. *P. assamica***
3 Nodes and petioles glabrous; leaf base deeply cordate, leaf margin subserrulate or entire ..... **4. *P. spirei***
4 Petioles 7–10 mm long; leaves 12–24 cm long, ovate-oblong to oblong; inflorescences inserted on leafless stems or on root stocks; calyx lobes and petals bristly at tip ..... **2. *P. lanceata***
4 Petioles 3–10 mm long; leaves 4.3–10 cm long, ovate, rarely ovate-oblong; inflorescences terminal and axillary; calyx lobes and petals not bristly at tip ..... **3. *P. septentrionalis***

1. *Pseudodissochaeta assamica* (C.B.Clarke) M.P.Nayar — Fig. 5-1, Map 5-1

Pseudodissochaeta assamica (C.B.Clarke) M.P.Nayar, J. Bombay Nat. Hist. Soc. 65(3): 559, fig. 1. 1969; Veldkamp & M.P.Nayar, Blumea 24: 432. 1979. — *Anplectrum assamicum* C.B.Clarke in Hook.f., Fl. Brit. Ind. 2: 546. 1879; J. Linn. Soc., London, Bot. 25: 23, t. 10. 1890 (emend. descr.); Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 569. 1891; P.C.Kanjilal & Das, Fl. Assam 2: 303. 1938. — *Diplectria assamica* (C.B.Clarke) Kuntze, Revis. Gen. Pl. 1: 246. 1891. — *Backeria assamica* (C.B.Clarke) Raizada, Indian Forester 94: 435.

1968. — *Medinilla assamica* (C.B.Clarke) C.Chen, Acta Phytotax. Sin. 21: 419. 1983; C.Chen & S.S.Renner, Fl. China 13: 393. 2007. — Lectotype (designated here): India, Assam, Naga Hills, *Griffith 1445 [KD 2285]* (lecto K [K000867403!]; isolecto K [K000867404!], L [L0009218!], M [M-0137604!]).

Shrubs, 2.5–4 m tall; branchlets terete, slightly quadrangular distally, glabrous, sparsely covered with simple bristles near the nodes; nodes swollen, with distinct interpetiolar ridges, densely covered with simple, glabrous bristles 0.5–2 mm long; internodes 6–7 cm long. Leaves: subsessile or shortly petiolate, petiole terete, 3–5 mm long, furfuraceus or pubescent and densely covered with bristles 2–3 mm long; blades subcoriaceous, elliptic-oblong or oblong-lanceolate, 10–21 × 3.5–8 cm; base oblique, unequally shallowly cordate, margin serrulate, apex acuminate (tip up to 1.5 cm long); lateral nerves 2 or 4, intramarginal veins 2, very thin; secondary venation with at least 30 pairs of sub-opposite nerves, finer veins reticulate; mature blades glabrous and drying brown to olive green to light green; abaxially sparsely furfuraceous and bristly on the midrib and lateral nerves. Inflorescences terminal paniculate cymes, 10–37 cm long, multiflowered; main axis quadrangular, glabrous, sparsely bristly near the nodes; primary axis 9–27 cm long with 6–8 nodes; secondary axes 1–12 cm long with 1–4 nodes; tertiary axes up to 3 cm long with 2–3 nodes; quarternarly axes, when developed, up to 9 mm long with 1–2 nodes; bracts lanceolate, 2–2.5 × ca. 1 mm, glabrous, caducous; bracteoles subulate, 1–1.5 mm long; pedicels glabrous, 2–3 mm long in central flower, 1–2 mm long in lateral flowers. Hypanthium cyathiform or campanulate, glabrous or with scattered minute scales near the base, 3–5 × 2–3 mm; calyx lobes truncate with 4 teeth-like tips, acute, up to 0.5 mm long; petal buds conical, obtuse, 2.5–5 mm long; petals thin, ovate to oblong, 3–5.5 × 3.5–4 mm, acute at the tip, glabrous, pink. Stamens glabrous, equal, filaments flattened, 4–5 mm long; anthers slightly curved and rostrate, 4–5 mm long, pedoconnective when present ca. 0.25 mm long, connective appendaged at base, dorsally with a ca. 1 mm long, obtuse, thickened, triangular crest, ventrally extended, then bilobed or biauriculate, ca. 0.5 mm long. Ovary ¾ as long as hypanthium, apex glabrous; extra-ovarial chambers extending to the middle of ovary; style glabrous, straight, 9–11 mm long; stigma minute. Fruits subglobose to globose, 4.5–7 × 3–5 mm, apex mammiform, green turning black when ripe, calyx remnant somewhat flattened; seeds minutely papillose, ca. 0.75 mm long.

Distribution — E Bhutan, NE India, N Myanmar.

Ecology — Evergreen forest gulley at 255–1000 m elevation.

Vernacular name — *Dai dafla* (Assam); *Sagaing* (Kachin).

Notes — 1. The species is easily distinguished from the others by its dense bristles on nodes and petioles (Fig. 5-1). Some of the Chinese collections with glabrous nodes and petioles were identified as this species, but they are actually *P. spirei* based on the glabrous leaf nodes and petioles.

2. Clarke (1879) described this species in *Anplectrum* (now *Diplectria*), however species of *Diplectria* are scrambling woody climbing shrubs with dimorphic stamens whereby the outer whorl consists of staminodes.

3. Nayar (1969a) erroneously selected *Clarke 42323* as a lectotype for the species because Clarke's emended description was based on it but this is not the actual type material (Clarke 1879, 1890). The actual type material was *Griffith KD 2285* (Clarke 1879) as indicated later by Veldkamp & Nayar (1979). Clarke (1879) did not indicate in which herbarium the holotype was placed, therefore the duplicates are syntypes and the K specimen, bearing Clarke's label, is here designated as lectotype.

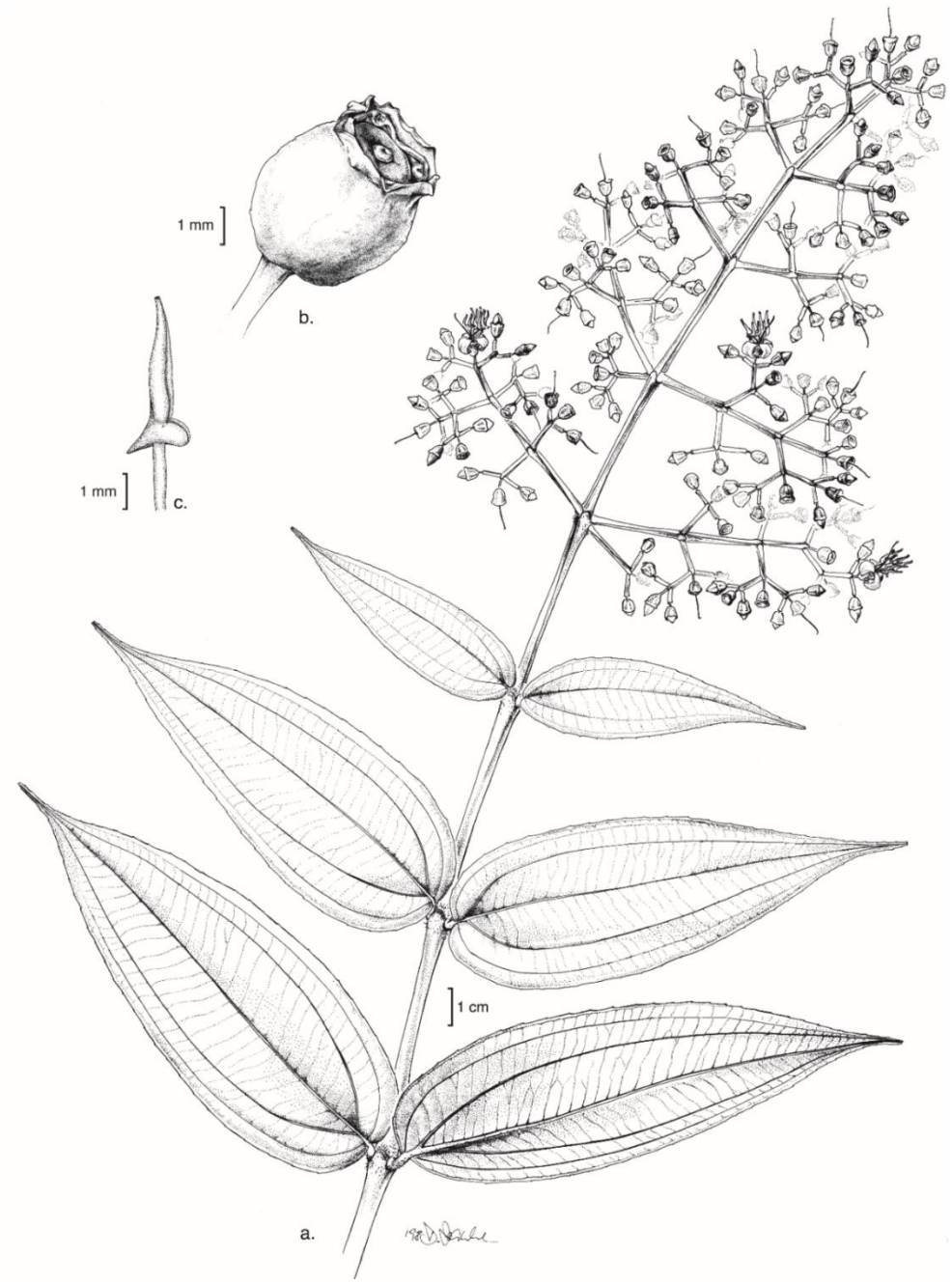
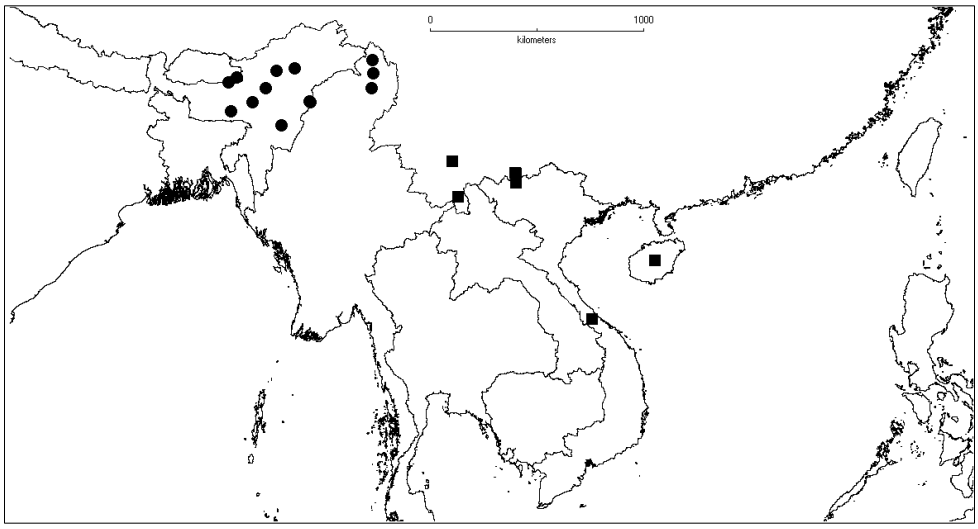


Fig. 5-1. *Pseudodissochaeta assamica*. **a.** Habit; **b.** fruit; **c.** stamen [Taken from Calusing 1999; Drawn by Doris Franke].

Specimens examined — **BHUTAN.** No specific location: *Griffith KD 2018* (K). **INDIA.** Assam: *Masters 173* (L); Menoka, *Chand 5254* (L); North Lakhimpur, 300 m, 25 Jan 1971, *Stainton 6726* (L); Subansiri, Pabin to Sayala, 19 Nov 1964, *Sastry 40751* (L). Meghalaya: Khasi Hills, *Anon. s.n.* (L). Nagaland: Naga Hills. *Griffith 1445 [KD 2285]* (K, L, M); *ibid.*,

Masters 1330 (P). Manipur: Mokoo, 750 m, 30 Nov 1885, *Clarke 42323* (BM, K). Arunachal Pradesh: Daffla Hills, *Badul Khan 71* (P). No specific location: *Jenkins s.n* (P). **MYANMAR.** Kachin: Nam Tamai Valley, 1000 m, 27 Aug 1948, *Kaulback 95* (BM); Mali Hka River, 17 Aug 1937, *Kingdon-Ward 12818* (BM); Suprabum, Hpuginhku River, 1000 m, 31 Dec 1961, *Keenan, Tan Aung & Tha Hla 3110* (K).



Map 5-1. Distribution map of *P. assamica* (●) & *P. lanceata* (■).

2. *Pseudodissochaeta lanceata* M.P.Nayar — Fig. 5-2, Map 5-1

Pseudodissochaeta lanceata M.P.Nayar, J. Bombay Nat. Hist. Soc. 65(3): 563, f. 3. 1969; P.H.Hô, Ill. Fl. Vietnam 2(1): 114, t. 3938. 1992 ("lanceolata"). — *Medinilla lanceata* (M.P.Nayar) C.Chen, Acta Phytotax. Sin. 21: 421. 1983; C.Chen & S.S.Renner, Fl. China 13: 394. 2007. — Type: China, Hainan, Hong Ta, July 1893, *Chinese Coll.* 406 (holo K [K000867414!]; iso K [K000867415!]).

Medinilla radiciflora C.Y.Wu, Fl. Yunnan. 2: 133, t. 32, f. 1-5. 1979. non Quisumb. & Merr. (1928). — Type: China, Yunnan, Pingbian, Mawei, Yakou Village 533 m, 16 Aug 1953, *PY Mao 2926* (holo PE, image!; iso IBSC).

Erect shrubs, 2–5 m tall; branchlets terete, striate and with scattered, glabrous or with glandular bristles 0.5–0.75 mm long; nodes swollen with interpetiolar lines with minute bristles; internodes 4.5–5.5 cm long. Leaves: petiole terete, 7–10 mm long, glabrous; blades subcoriaceous, ovate-oblong or oblong, 12–24 × 3.5–6.5 cm, base regular, cuneate to obtuse, margin serrulate, apex acuminate-rostrate, tip up to 2.5 cm long; lateral nerves 2, intramarginal nerves 2, thinner; secondary venation obscure; drying olive-greenish on both surfaces, glabrous. Inflorescences inserted on leafless stems or on root stocks, multiflowered, 15–40 cm long; main axis quadrangular, striate, minutely puberulous; primary axis up to 38 cm long with 5–7 nodes, secondary axes up to 12 cm with 2–4 nodes, tertiary axes up to 2.5 cm long with one node, quarternary axes when developed, up to 6 mm long, 5th axes when developed, 1–2 mm long; bracts subulate, 2–4 mm long; bracteoles subulate, up to 0.5 mm long; pedicels terete, glabrous, 3–4 mm long in central flower, 2.5–3 mm long in lateral flowers. Hypanthium tubular, 5–6 × ca. 2.5 mm, minutely papillose-puberulous and becoming glabrous; calyx lobes truncate with 4 teeth-like lobes with several glandular

bristles 0.5–0.75 mm long; petal buds conical, 2–3 mm long; petals thin, broadly elliptic, 6–8 × 4–5 mm, acute and with few glandular bristles at the tip, clawed at the base, bright white to pink. Stamens equal, glabrous, filaments flattened, 4–4.5 mm long, anthers slightly curved, narrowed at the tip, 5.5–6 mm long, connective dorsally with a triangular appendage of ca. 1 mm long, ventrally extending into a bilobed or biauriculate appendage, of ca. 0.5 mm long. Ovary half as long as hypanthium, glabrous, tip with slightly 4-lobed cup enclosing the base of the style; style straight, 10–12 mm long, glabrous; stigma minute, punctiform; extraovarial-chambers extending (nearly) to the base of the ovary. Fruits urceolate, ca. 8 × 7 mm, puberulous, minutely tuberculate; seeds ca. 0.5 mm long.

Distribution — Southern China (Hainan, Yunnan), Vietnam.

Ecology — Sparse to dense forests, shaded damp places, valleys, hillsides at 400–1000 m elevation (Chen & Renner 2007).

Vernacular Name — 酸脚杆 *suan jiao gan* (China).

Notes — This species is readily distinguished from the others by the combination of well-developed petioles and ovate-oblong to oblong leaves 12–24 cm long (Fig. 5-2). The tubular hypanthium is distinct for this species and *P. septentrionalis*, but they differ in leaf size and the inflorescences inserted on leafless stems or on root stocks in the former and both terminal and axillary in the latter. *Pseudodissochaeta lanceata* resembles *P. subsessilis* in the appearance of the leaf blades, but differs from the latter in the well-developed petioles and a regular leaf base (subsessile with an oblique leaf base).

Specimens examined — **CHINA.** Hainan: Hong Ta, Jul 1893, *Chinese Collector 406* (K). Yunnan: Pingbian Miao, District 1, 22 Aug 1953, *Mao 2983* (PE); Pingbian Miao, Mawei, 16 Aug 1953, *Mao 2926* (PE); *ibid.*, 21 Aug 1954, *Feng 5098* (PE); *ibid.*, Baiyan, Youmaji Paper mill, 900 m, 19 Oct 1954, *Feng 4563* (PE); Mengla, Xiaola Highway KM63, 580 m, 15 Mar 1983, *236-46 team 4431* (PE). **VIETNAM.** Quang Tri: 400 m, 1 Aug 1935, *Poilane 24896* (P); Tonkin: Phong Tho, Lao Cay, 14 Dec 1937, *Poilane PM40* (P).

3. *Pseudodissochaeta septentrionalis* (W.W.Sm.) M.P.Nayar — Fig. 5-3, Map 5-2

Pseudodissochaeta septentrionalis (W.W.Sm.) M.P.Nayar, J. Bombay Nat. Hist. Soc. 65(3): 565, fig. 4. 1969; Veldkamp & M.P.Nayar, Blumea 24: 435. 1979; S.S.Renner et al., Fl. Thailand 7(3): 475. 2001. — *Oritrephes septentrionalis* W.W.Sm., J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 7: 69. 1911. — *Medinilla septentrionalis* (W.W.Sm.) H.L.Li, J. Arn. Arbor. 25: 38. 1944; C.Chen & S.S. Renner, Fl. China 13: 393. 2007. — Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65(3): 565 .1969): Myanmar, S. Shan, Kung Lung, 3000 ft elev., July 1909, *R.W. MacGregor 751* (lecto E [E00288102!])

Medinilla caerulescens Guillaumin, Bull. Soc. Bot. France 68: 5. 1921; in Lecomte, Fl. Gén. Indo-China 2: 921. 1921; Craib, Fl. Siam. Enum. 1(4): 699. 1931. — Lectotype (designated by Veldkamp & Nayar in Blumea 24: 435. 1979): Laos, Attapeu, Mar. 1877, *F.J. Harmand 1243* (lecto P [P02274898!]; isolecto P [P02274899!, P02274900!]).

Medinilla caerulescens Guillaum. var. *nuda* Craib, Fl. Siam. Enum. 1(4): 699. 1931. — Lectotype (designated here): Thailand, Phetchaburi, Dan Sai, Phu Lom Lo, 1200 m elev., 9 Apr. 1922, *A.F.G. Kerr 5787* (holo K [K000867400!]; isotype BK, BM [BM000546419!]).

Anplectrum yunnanense Kraenzl., Vierteljahrsschr. Naturf. Ges. Zürich 76: 153. 1931; Veldkamp & M.P.Nayar, Blumea 24: 435. 1979. — Lectotype (designated here): China, Yunnan, Szemoo, 4000 ft elev., *A. Henry 11705D* (lecto K [K000867409!]; isolecto E [E00285927!]).

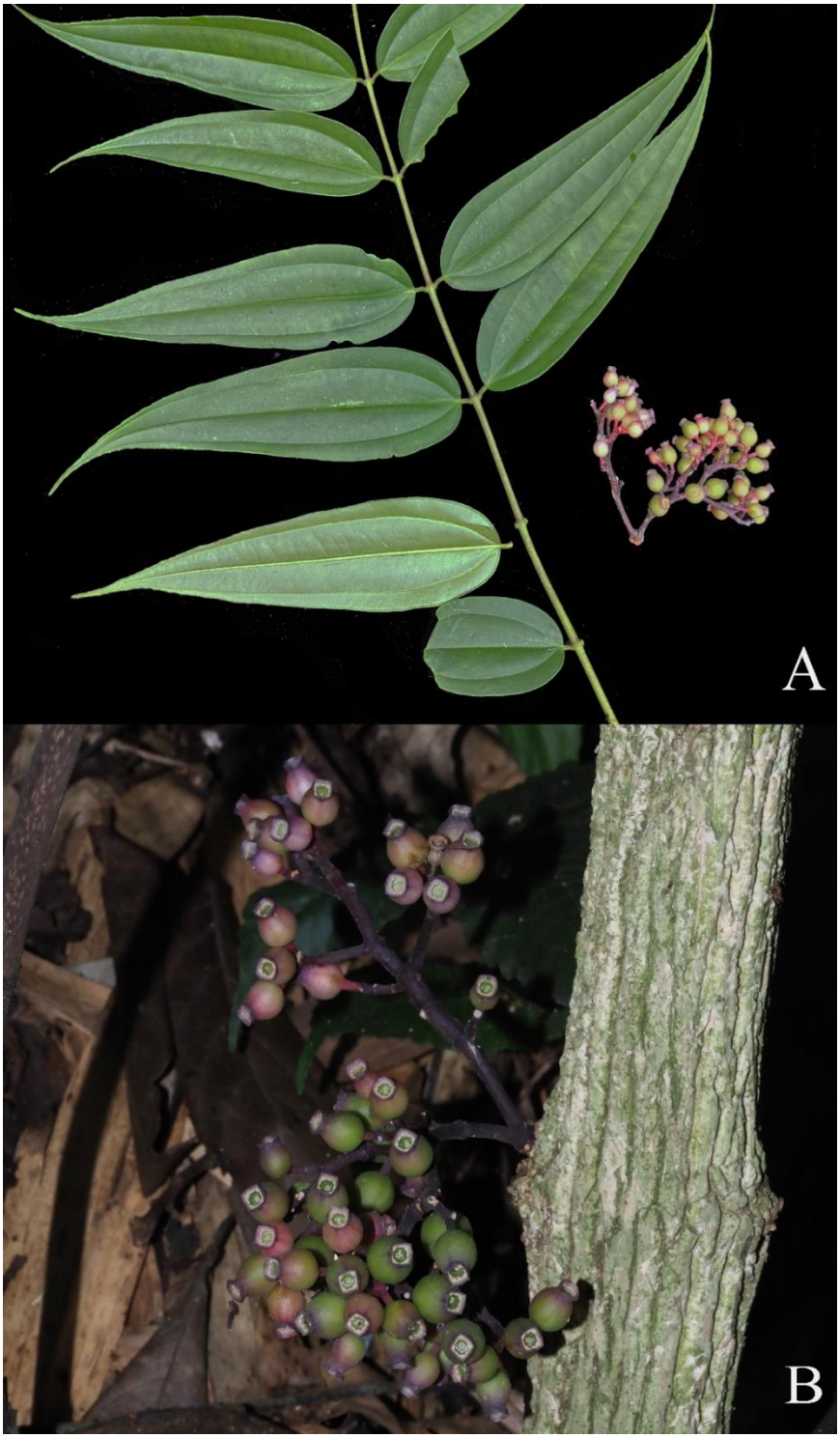


Fig. 5-2. *Pseudodissochaeta lanceata*. **A.** Branchlet; **B.** Infructescence. Photograph by Y.-S. Chen.

Erect shrubs, 1–5 m tall or small trees, up to 6 m tall; branchlets terete, smooth and glabrous; nodes swollen with minute bristles giving a puberulous-fimbriate appearance, interpetiolar lines distinct; internodes 2–4(–5) cm long. Leaves: petiole terete, 3–10 mm long, glabrous except puberulous near the tip; blades papery, ovate, rarely ovateoblong, 4.3–6(–10) × 1.5-3.6 cm, base oblique, obtuse, cuneate or rounded, margin serrulate, apex acuminate-rostrate, tip 10–15 mm long; lateral nerves 2, intramarginal nerves 2, thinner; secondary venation thin and inconspicuous; glabrous on both surfaces, drying dull greenish to brownish. Inflorescences terminal and axillary cymes of 1-, 3-, 5- or 7- flowers, 2–5 cm long; main axis slightly angular, compressed, slender, smooth and glabrous; primary axis 1.2–4 cm long with 2–3 nodes, secondary axes (when developed) 9–11 mm long with one node; bracts subulate, 1–1.5 mm long, glabrous, caducous; bracteoles minute, subulate, up to 0.5 mm long; pedicels glabrous, 1–2 mm long in central flower, 0.5–1 mm long in lateral flowers. Hypanthium tubular and becoming slightly urceolate after flowering, 3–6 × 2–3 mm, glabrous or sometimes with scattered, glandular bristles of ca. 1 mm long; calyx lobes truncate, apex appear with 4 undulations or 4 yellowish teeth-like lobes of ca. 0.5 mm long, glabrous; petal buds conical, 3–5 mm long, without bristles; petals elliptic or oblong, 5–6 × 3.5–4 mm, acute at the tip, broadly clawed at the base, glabrous, purplish or pink or white, reflexed at maturity. Stamens glabrous, equal, filaments 5–6.5 mm long, creamy white, anthers curved, slender, C-shaped, purplish pink, rostrate at the tip, 8–13 mm long, pedoconnective when present ca. 0.5 mm long, connective dorsally yellow spurred with a rounded lobe of 0.5–0.6 mm long, ventrally extending into yellow biauriculate appendages of 0.4–0.5 mm long. Ovary 2/3 as long as hypanthium, tip cup-like with an undulate margin enclosing the base of the style; style slender, 9–11 mm long glabrous, pale pink or white; stigma minute, punctate; extra-ovarial chambers extending to the base of the ovary. Fruits ovoid to urceolate, 7–8 × 4–6 mm, glabrous; seeds minutely papillose, ca. 0.6 mm long.

Distribution — Southern China, Laos, Cambodia (Cho et al. 2016), NE Myanmar, N Thailand, Vietnam.

Ecology — Dense primary or degraded evergreen forests, forest margins, near a ravine, moist clayey soil, damp shady areas at 200–1800 m elevation (Chen & Renner 2007; Cho et al. 2016).

Vernacular name — 北酸角杆 *bei suan jiao gan* (China).

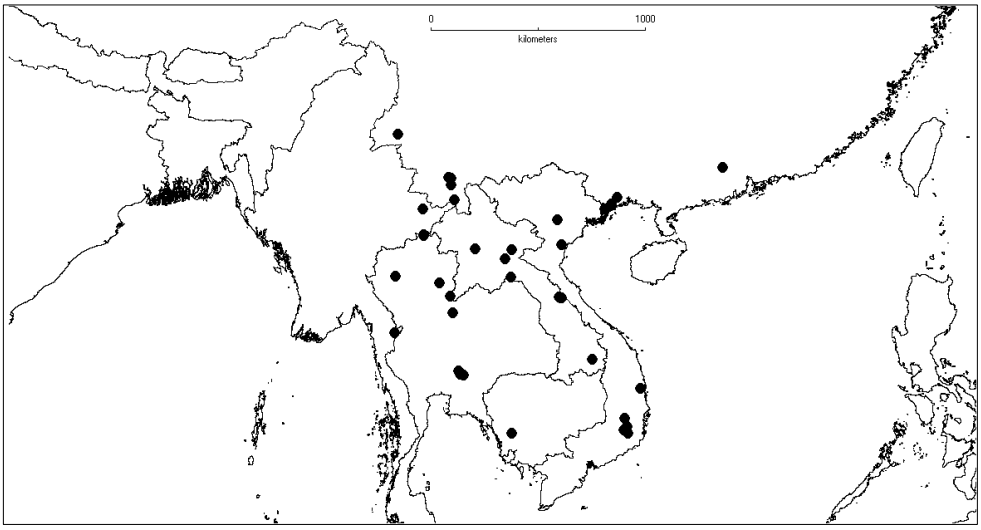
Note — *Pseudodissochaeta septentrionalis* is easily recognized by its small ovate leaf blade (less than 10 cm long) and terminal-axillary inflorescences with scattered bristles on its campanulate hypanthia (Fig. 5-3). It resembles *P. assamica* in its slender curved stamens. The species is variable in habit and petal colour; the height of the plants diminishes with increasing elevation.

Specimens examined — **CHINA.** Guangdong: Dinghu, Dinghu-Shan, 120 m, 29 Jul 1963, *Ting & Shih 797* (L); *ibid.,* 6 Nov. 1963, *Ting & Shih 1109* (L); *ibid.,* 3 Sep 1985, *Liao 15246* (L); Fang Cheng District, Taan Faan, Kung Ping Shan and vicinity, 1-9 Sep 1936, *Tsang 26788* (P). Yunnan: Lung-ling Hsien, 5 Apr 1934, *Tsai 55666* (P); Simao, *Henry 110705C* (E, L), *Henry 11705D* (E, K), Da Whei Shan 1400 m, 20 Oct 2001, *Zhou 215* (PE); Xishuangbanna, Puwen - Kun Luo Highway KM619, 21 Apr 1957, *China-Soviet Team 8053* (PE); *ibid.,* Jinhong, Meng Song, 1400 m, 30 Mar 2003, *Zhou 838* (PE). No specific location: *Forrest 27163* (E, P), *Forrest 26642* (E, P). **LAOS.** Attapeu: *Harmand 1243* (P). Khammouane: Kaeng Doer, Houay Wang Jang, 590 m, 22 Oct 2005, *Newman et al. LAO434* (E, L, P); *ibid.*,25 Oct 2005, *Newman et al. LAO517* (E, L, P); *ibid.,* Nakai Nam Theun 856 m, 23 May 2006, *Newman et al. LAO1244* (E, L). Kung Kruang: *Spire 536* (P). Paksan: Bassac, 1200 m, 19 Sep 1928, *Poilane 15622* (P). Xieng: Khou Hang, 28 Sep 1926, *Delacour s.n.* (P); Kham District, Tha Village, 25 Oct. 2006, *Souliya LAOS-851* (L). No specific

location: *Harmand 118* (P); *Spire 336* (P). **MYANMAR.** Shan: Kung Lung, 1200 m, Jul 1909, *MacGregor 751* (E). **THAILAND.** Chiang Mai: Chom Thong, Doi Inthanon National Park, North of KM 38 Huai Hoi area, 1700 m, 31 Jan 1993, *Maxwell 93-126* (L). Chiang Rai: Doi Tung, Wat Noi Temple, 1150 m, 2 Dec 2004, *Maxwell 04-761* (L); *ibid.,* Along the Wat Noi – Wat Huai Nam Khun Trail, 1130 m, 21 Sep 2010, *Van de Bult 1071* (L). Nakhon Nayok: Khao Yai National Park, 950–1050 m, 9 Oct 1979, *Shimizu et al. T-19708* (L). Nakhon Ratchasima: Khao Yai National Park, Phao Laem, 1100-1200 m, 19 Oct 1969, *Van Beusekom & Charoenpol 1761* (L, P); *ibid.*, 700 m, Jan 1964, *Phengkhlai 432 (BKF38004)* (K, L, P); *ibid.* 30 Oct 1970, *Charoenpol, Larsen & Warncke 4286* (L); *Ibid.,* 2 Sep 1967, *Hardial 593* (L); *ibid.,* Khao Rom, 650 m, 3 Dec 1983, *Fukuoka & Ito T-34628* (L). Na Noi:

Fig. 5-3. *Pseudodissochaeta septentrionalis*. **A.** Habit; **B.** Branchlet with inflorescences; **C.** Flower; and **D.** Fruits. Photographs by: Y. Liu (A–C), nifty.com (D)

Doi Khun Ssathan, 10 km SW of Ban San Tha, 1000–1300 m, 19 Nov 1993, *Larsen et al. 44616* (AAU, L). Phetchaburi: Dan Sai, Phu Lom Lo, 1200 m, 9 Apr. 1922, *Kerr 5787* (BM, K). Phitsanulok: PHu Mieng Mountain, 1300 m, 28 Jul 1966, *Larsen, Smitinand & Warncke 953* (AAU, P). Prachinburi: Khao Yai National Park, 800 m, 12 Aug 1966, *Larsen, Smitinand & Warncke 310* (AAU, L). Saraburi: Khao Yai, 800 m, 5 Dec 1965, *Vidal 4613* (P); *Ibid.*, 1000 m, 5 Dec 1965, *Vidal 4577* (L, P). Tak: Mae Sot- Umphang Road KM. 117–118, 1100 m, 24 Apr 2004, *Pooma et al. 4652* (L). No specific location: *Put 3569* (L), *Put 3761* (L). **VIETNAM.** Dac Kiet: Thanh Hoa, 13 Sep 1920, *Poilane 1835* (P). Haut Donnaï: Dalat, 1500 m, 12 Sep 1940, *Poilane 30361* (P); *ibid.*, *Hayata 221* (P); *ibid.*, *Hayata 164* (P); *ibid.*, *Chevalier 40331* (P). Kray Am & Gia Deun, 1500 m, 1 May 1941, *Poilane 32656* (P); Dangkia & Dang Le, 1000 m, 29 Jan 1934, *Poilane 23500* (P); *ibid.*, *Poilane 18610* (P). Lam Dong: Lac Duong, Da Chay, 1700 m, 17 Mar 1997, *Averyanov, Binh & Lôc VH2748* (P); *ibid.*, 27 Mar 1997, *Averyanov, Binh & Lôc VH3261* (P); *ibid.*,1600-1650 m, 4 Apr 1997, *Averyanov, Binh & Lôc VH3679* (P); *ibid.*, 4 May 1997, *Averyanov et al. VH4551* (P). Binh Dinh: Qui Nhon, Mang Giang, 1600 m, 22 Aug 1930, *Poilane 18075* (P). Lang Bi Ninh, 700 m, 27 Jul 1925, *Poilane 12229* (P). Tonkin: Dam-ha, Lomg Ngong Village, Sai Wong Mo Shan, *Tsang 30024* (L, P); *ibid.*, *Tsang 30462* (L, P); Ha-coi, Chuk Pai, Taai Wong Mo Shan, *Tsang 27021* (P); *ibid.*, *Tsang 29118* (L, P); *ibid.*, *Tsang 29162* (L, P); *ibid.*, *Tsang 29430* (L); Mon Cay, Pac-si and vicinity, *Tsang 26929* (P); Liang Lian, Jul 1908, *d'Alleizette s.n.* (L).



Map 5-2. Distribution of *Pseudodissochaeta septentrionalis* (●).

4. *Pseudodissochaeta spirei* (Guillaumin) Veldkamp & J.F.Maxwell — Fig. 5-4, Map 5-3

Pseudodissochaeta spirei (Guillaumin) Veldkamp & J.F.Maxwell, Gard. Bull. Singapore 33: 324. 1980. — *Medinilla spirei* Guillaumin, Bull. Soc. Bot. France 68: 4. 1921; in Lecomte, Fl. Gén. Indo-China 2: 921. 1921: H.L.Li, J. Arn. Arbor. 25: 38. 1944; C.Y.Wu & C.Chen, Fl. Yunn. 2: 130, t.31, f. 6–8. — Lectotype (designated by Maxwell & Veldkamp in Gard. Bull. Singapore 33: 324. 1980): Vietnam, Nghé An, Co Ba, 7 Aug 1914, *J, Chevalier [coll. F. Fleury] 32408* (lectotype P [P00700366!]; isolecto P [P00700367!, P00700368!]).

Shrubs, 1–4 m tall, somewhat spreading; branchlets terete, smooth, glabrous; nodes with distinct interpetiolar lines; internode 6–9(–11) cm long. Leaves: subsessile or shortly petiolate, petiole terete, up to 1 mm long, glabrous; blades subcoriaceous, ovate-oblong or elliptic-oblong, 10–21 × 3–11 cm, base oblique, deeply cordate, margin subserrullate or entire, apex acuminate, tip up to 1.5 mm long; lateral nerves 2, intramarginal nerves 2, thinner; secondary veins 15–20, finer veins inconspicuous; glabrous on both surfaces. Inflorescences terminal, multiflowered, 8–23 cm long; main axis terete to quadrangular, glabrous except for the nodes, the latter with patches of puberulous hairs; primary axis 6–20 cm long with 2–5 nodes; secondary axes 3–8 cm long with 1–3 nodes; tertiary axes up to 3 cm long with 1–2 nodes; quarternarly axes, when developed, up to 1 cm long with 1–2 nodes; bracts subulate, 0.5–1 cm long, caducous; bracteoles subulate, 0.2–0.4 mm long; pedicels quadrangular, glabrous, 1–2 mm long. Hypanthium cyathiform-campanulate, smooth, glabrous, 4–4.5 × ca. 4 mm, light green to pale brown; calyx lobes truncate with 4 minute submarginal teeth-like lobes; petal buds conical, glabrous, 2–3 mm long; petals suborbicular, 3–4 × 3–3.5 mm, obtuse at the tip, broadly clawed at the base, glabrous, pink, reflexed. Stamens subequal, glabrous, filaments 2–3 mm long, white; anthers slightly curved, rostrate at the tip, 2–3 mm long, pale yellow or whitish, connective extending dorsally with a spur or triangular appendage of 1.5–2 mm long, and ventrally with two minute lobes less than 0.5 mm long. Ovary half as long as hypanthium, 4-ridged at the top, glabrous; style glabrous, 6–7 mm long; stigma minute, capitate; extra-ovarial chambers half as long as the ovary. Fruits subglobose, 5–7 × 5–6 mm, smooth, glabrous; seeds ca. 0.5 mm long.

Distribution — Southern China, Laos, Vietnam.

Ecology — Evergreen sparse to dense forest, forest edges, valleys, hillsides, streamsides, damp places, trail sides at 200–1300 m elevation (Chen & Renner 2007).

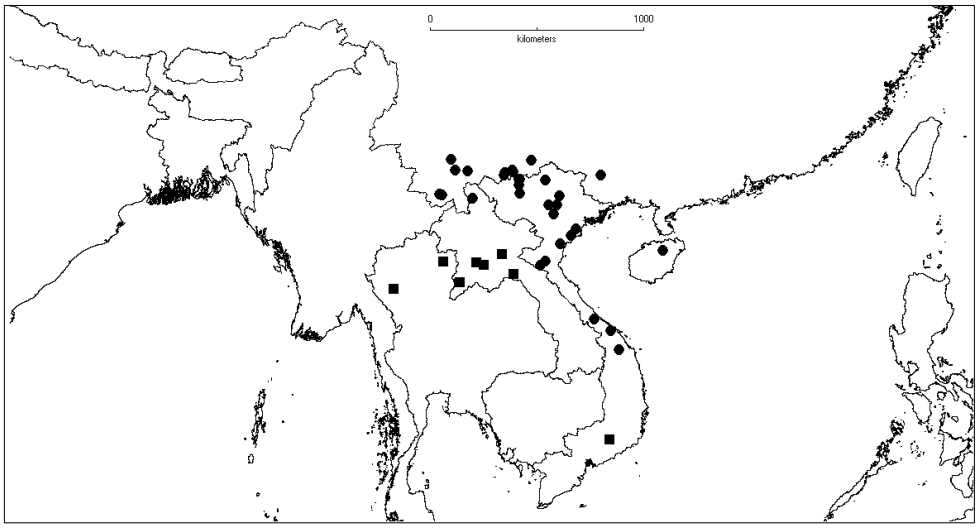
Vernacular name — 顶花酸角杆 *ding hua suan jiao gan* (China).

Note — *Pseudodissochaeta spirei* (Fig. 6) is the only species in the genus that has almost entire or subserrulate leaf margins. Because of the subsessile leaf blade with oblique clasping base it closely resembles *P. assamica* and *P. subsessilis*. However, *P. spirei* does not have bristly nodes like *P. assamica*. It also differs from the latter two in the ovate-oblong leaf blades (vs. oblong-lanceolate). Some authors have described this species as a climber. Nevertheless, most collections of this species have recorded it as an erect or spreading shrub. Therefore, the former interpretation can be regarded as incorrect. Woody climbing or scrambling shrubs are only known in the other genera of *Dissochaeta* allies, i.e. *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes* (Kartonegoro et al. 2018, 2019).

Specimens examined — **CHINA.** Guangxi: *Ching 7536 (FM23435)* (PE); *Chow s.n.* (PE). Hainan: Kan-en District, Sam Mo Watt, Chim Fung Ling, 16 Apr 1934, *Lau 3793* (P). Yunnan: *Chow 130* (PE); *Gao 43* (PE); Ping-pien Hsien, 1300 m, 14 Jul 1934, *Tsai 60888* (PE); Nansha River, 20 Aug 1953, *Xiao 31* (PE); Locust Castle, 23 Apr 1953, *Fan 50* (PE); Nanxi District, *Han 28* (PE); Jinping, 28 Apr 1953, *Jiang 45* (PE); *ibid.*, 26 May 1953, *Wu & Hu 29* (PE); Man Ba, May 1953, *Dong 160* (PE); Dam, 8 May 1953, *Cai 956* (PE); Manlai, 9 Apr 1953, *Cai 200* (PE); *ibid.*, 15 Dec 1953, *Mao 3318* (PE); Si-chour-hsien, Ting-mann, 1000 m, 13 Oct 1947, *Feng 12399* (PE); *ibid.*, 23 Dec 1939, *Wang 85910* (PE); Saga Village, Jun 1953, *Anon 130* (PE); Pingbian Miao, Yaoshan, Dudian, Bai Quanchong, 850 m, 28 Oct 1954, *Feng 5220* (PE); *ibid.*, Liangzhi, Gewu, 760 m, 21 Apr 1954, *Wan 3940* (PE); Areca Village, 220 m, 24 Mar 1958, *Feng 21698* (PE); Hekou Yao, Wayao Roadside, 180 m, 26 Jun 1953, *Liu 92* (PE). LAOS. Cach Trap: *Spire 1541* (P). **VIETNAM.** Chai Nguyen: Cho-Cho, *Eberhardt 3990* (P). Dong Tri: Quang Tri, 700 m, 16 Jun 1924, *Poilane 10955* (L, P). Dac Kiet: Thanh Hoa, 9 Sep 1920, *Poilane 1803* (P). Huei: Nui Bach Ma, 18 Apr 1939, *Poilane 29815* (P); *ibid.*, 300–400 m, 26 Apr 1959, *Poilane 30021* (L, P); *ibid.*, 24 Apr

1943m, *Vidal 840A* (P). Lao Cai: Van Ban Nature Reserve, 20 Apr 2013, *Swenson et al. 1279* (S); *Ibid.*, *Swenson et al. 1280* (S). Nghe An: Nghia Hung, 17 May 1914, *Fleury 32564* (P); Co Ba, 7 Aug 1914, *Fleury 32408* (P); Con Cuông, Pu Mat National Park, Khe Kem waterfall, 28 Apr 2013, *Swenson et al. 1481* (S); *Ibid.*, *Swenson et al. 1496* (S). Nguyen Guang: Bach Ngoc, *Eberhardt 4817* (P). Tramy: Quang Nam, 500 m, 22 Feb 1941, *Poilane 31477* (P); *ibid.*, *Poilane 31479* (P); *ibid.*, 20 Feb 1941, *Poilane 31381* (P). Tam Dao, 1000 m, 7 Oct 1963, *Pocs & Dang Khoi 723* (P). Tonkin: Phu Tho, Chan Mong, 18-19 Apr 1914, *Fleury 32178* (P); *ibid.*, 19-20 Apr 1914, *Fleury 32190* (P); *ibid.*, 20-21 Apr 1914, *Fleury 32223* (P); Pho Lu, Lao Cai, 6 Feb 1936, *Poilane 25169* (P); Chobo, 400 m, 14 Apr 1926, *Colani 3006* (P); *ibid.*, 17 Nov 1887, *Balansa 3507* (P); *ibid.,* May 1909, *d'Alleizette s.n.* (L); Dong Dong, Feb 1886, *Balansa 1139* (P); Tschantaio, Mount Ba-ni, 24 Jul 1886, *Balansa 2873* (P).

Fig. 5-4. *Pseudodissochaeta spirei*. **A.** Habit; **B.** Inflorescence; **C.** Flowers; and **D.** Fruits. Photographs by Y. Liu (A), J. Lundberg (B, D), Lijiang Yezi (C).



Map 5-3. Distribution of *P. spirei* (●) & *P. subsessilis* (■).

5. *Pseudodissochaeta subsessilis* (Craib) M.P.Nayar — Fig. 5-5, Map 5-3

Pseudodissochaeta subsessilis (Craib) M.P.Nayar, J. Bombay Nat. Hist. Soc. 65(3): 561, fig. 2. 1969; S.S.Renner et al., Fl. Thailand 7(3): 476. 2001. — *Allomorphia subsessilis* Craib, Bull. Misc. Inform. Kew 1913: 69. 1913; Guillaumin in Lecomte, Fl. Gén. Indo-China 2: 902. 1921; Craib, Fl. Siam. Enum. 1(4): 686. 1931. — *Medinilla subsesilis* (Craib) M.P.Nayar ex P.H.Hô, Ill. Fl. Vietnam 2,1: 114, . 3937. 1992, non Merr. (1912). — Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65(3): 561. 1969): Thailand, Chiang Mai, Maharat, Doi Wao, 300–900 m elev., 23 Feb. 1912, *A.F.G. Kerr 2427* (lectotype K [K000867401!]; isolectotypes BM [BM000944536!, BM000944537!], E [E00288101!], K [K000867402!]).

Anerincleistus sessilifolius Guillaumin, Bull. Soc. Bot. France 68: 4. 1921; in Lecomte, Fl. Gén. Indo-China 2: 905. 1921. — Lectotype (designated here): Laos, Exp. Me-Kong, Paklai, *C. Thorel s.n.* (lectotype P [P00700369!]).

Shrubs or small trees, 2–5 m tall; branchlets quadrangular, winged, greenish to brownish, nodes with distinct interpetiolar lines or small crests, stellate furfuraceous, glabrescent; internodes 4–6 cm long. Leaves: subsessile or shortly petiolate, petiole densely stellate-furfuraceous or stellate-pubescent, 1–2.5(–5) mm long; blades chartaceous, oblong-lanceolate or lanceolate, 10–18.5(–27) × 2.8–4.2(–6.8) cm, base oblique, unequally auriculate or cordate, margin minutely serrulate, apex acute or acuminate; lateral nerves 2 or 4, intramarginal veins 2; upper surface minutely brownish puberulous when young, glabrous with age, dark green, abaxial surface mainly light green, glabrous but nerves softly brownish pubescent with dense stellate hairs, cross-venules distinct. Inflorescence terminal, 13–28 cm long, main axis quadrangular, glabrous or sparsely brownish pubescent, dark purple; primary axis, 13–25 cm long with 7–10 nodes; secondary axes 4–6 cm long with 3–4 nodes; tertiary axes up to 10 mm long with 1–2 nodes; quarternarly axes (when developed) up to 2 mm long with 1 node; bracts subulate, ca. 1.5 mm long, inconspicuous, caducous; bracteoles subulate, 1–2 mm long; pedicel subangular, softly brownish pubescent with stellate hairs, 0.8–1 mm long on central flower, 0.5–0.8 mm long on lateral flowers. Hypanthium campanulate, 2–3.5

Fig. 5-5. *Pseudodissochaeta subsessilis* (*Kerr 2427*, Isolectotype E).

× 1–2 mm, glabrous, faintly 8-ridged, light green; calyx lobes truncate with four small teeth-like tips of ca. 0.5 mm long; petal buds conical, ca. 1 mm long; petals obovate to suborbicular, 2.5–3 × ca. 3 mm, apex rounded, base narrow, reflexed at maturity, white, pink, or violet. Stamens subequal, filament 1.5–2 mm long, whitish; anther curved, 2.5–3 mm long, creamy, connective dorsally ending in a thick short spurred yellow appendage 0.4–0.5 mm long, ventrally ending in two auricles ca. 0.3 mm long. Ovary ca. 2/3 as long as hypanthium, glabrous, ridged at the top; style 5–7 mm long, filiform, glabrous, creamy; stigma minute, capitate, light red or pink; extra-ovarial chambers extending to the middle of the ovary. Fruits subglobose, ca. 6 × 5 mm, glabrous. Seeds ca. 0.5 mm long.
Distribution — Laos, Thailand, Vietnam.
Ecology — Evergreen forest or degradated 231eciduous forest at 200–1030 m elevation.
Note — In many respects *P. spirei* (Fig. 5-4) resembles *P. subsessilis* (Fig. 5-5), however the former is easily distinguished by its terete branchlets (vs. angular branchlets) and wider blades with entire margin (vs. narrow blades with serrulate margin). *Pseudodissochaeta assamica* also resembles *P. subsessilis* but the latter does not have bristly nodes and petioles. In addition, *P. assamica* has larger flowers and stamens than *P. subsessilis*. Chen & Renner (2007) recognized these differences as intraspecific variations and regarded *P. spirei* and *P. subsessilis* as synonyms of *P. assamica*.
Specimens examined — **LAOS.** Borikhane: King Cham, 200 m, 28 Mar 1932, *Kerr 20779* (BM, K, L, P). Xieng Khuoang: Pahia & Na Di, 1000 m, Apr 1949, *Vidal 904B* (P). Pak Lai: *Thorel s.n.* (P). Vientiane: Kasi, Muang Kheung Village, Namon Village Road, near Nam Lik River, 325 m, 25 Aug 1999, *Maxwell 99-208* (L), Vang Vieng, Pu Yang Hill, above Pohn Sooung Village, 325 m, 20 May 2011, *Maxwell 11-28* (L, P); *ibid.*, *Maxwell 11-29* (L, P). **THAILAND.** Chiang Mai: Maharat, Doi Wao, 1000 m, 23 Feb 1912, *Kerr 2427* (BM, E, K); Doi Tiu, 300 m, *Kerr 5042* (BM, K, P). VIETNAM. Lam Dong: Blao, 800 m, 25 Apr 1933. *Poilane 22376* (P); *ibid.*, 4 Feb 1933, *Poilane 21834* (P). Ban Au Kun, 3 Oct 1957, *Tixier s.n.* (P).

Excluded species

Pseudodissochaeta raphioides C.Hansen, Bull. Mus. Natl. Hist. Nat., B, Adansonia Sér. 4, 11(3): 280. 1990. = **Oxysporeae**.

Pseudodissochaeta rosea (Guillaumin) J.F.Maxwell, Gard. Bull. Singapore 35(2): 216. 1983. = ***Sporoxeia rosea*** (Guillaumin) C.Hansen, Bull. Mus. Natl. Hist. Nat., B, Adansonia Sér. 4, 12(1): 41. 1990.

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CHAPTER 6

Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe Dissochaeteae

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Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe Dissochaeteae

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Abstract

The *Dissochaeta* alliance (= subtribe Dissochaetinae) is a group of woody climbing taxa within tribe Dissochaeteae (Melastomataceae) and comprises 90 species mainly distributed in Southeast Asia. The circumscription of the alliance and its genera has been problematic when based on only morphological characters. With a broad sampling of relevant taxa, this study aims at a natural circumscription of and revised generic delimitation within this alliance. A molecular phylogeny based on two nuclear (nrETS, nrITS) and four chloroplast (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) markers confirmed the non-monophyly of Dissochaeteae s.l. Taxa traditionally placed in Dissochaeteae are found in three lineages in distant positions within Melastomataceae. The *Medinilla* alliance is resolved within Sonerileae + Oxysporeae, while the monophyletic *Dinophora*/*Ochthocharis* lineage forms a polytomy with Marcetieae, Melastomateae, Microlicieae, and Rhexieae; and the well-supported *Dissochaeta* alliance is sister to the Cambessedesieae. Based on the molecular results, Dissochaeteae is redefined to exclude the *Medinilla* alliance and *Dinophora*/*Ochthocharis*. It consists of six successively branching major clades, which we treat as six genera, *Pseudodissochaeta*, *Creochiton*, *Dalenia* (*Dissochaeta* sect. *Dalenia*), *Diplectria* (*Dissochaeta* sect. *Diplectria*), *Macrolenes* and *Dissochaeta* s.str. To avoid a paraphyletic *Dissochaeta*, *Dalenia* and *Diplectria* are resurrected, *Macrolenes* is expanded to include the *Dissochaeta rostrata* complex, and a narrowly circumscribed *Dissochaeta* s.str. is adopted. A re-investigation of morphological characters based on herbarium material provides support of newly defined taxa. Two sections for *Macrolenes* are newly proposed and two sections of *Dissochaeta* s.str. are maintained. Important morphological traits, such as habit and floral characters are discussed to show the morphological support for each delimited genus and the establishment of a new classification of the tribe.

Keywords

Classification; *Dissochaeta* alliance; Dissochaeteae; Melastomataceae; molecular phylogenetics; Southeast Asia; taxonomy.

Introduction

The species-rich pantropically distributed angiosperm family Melastomataceae Juss. s.l. (incl. Memecylaceae DC., cf. APG III, 2009) is particularly diverse in growth forms. Among the over 5700 species in ca. 177 genera (Renner 1993; Christenhusz & Byng 2016; Michelangeli et al. 2020) are trees, shrubs, subshrubs, geophytes, true epiphytes, perennial and annual herbs, and various forms of woody climbers, such as root climbers and scrambling shrubs. While the former climbing growth forms evolved in various melastome genera, the last is rare and seems to be restricted to the paleotropical subtribe Dissochaetinae (Clausing & Renner 2001a). The majority of melastome species is easily assigned to the family by their acrodromal leaf venation, well-developed hypanthia, bisexual, diplostemonous flowers and poricidal anthers (Clausing & Renner 2001b; Rocha et al. 2016). Although the family ranges among the most diverse tropical angiosperm families and is ubiquitous in lowland to montane tropical forests, it also occurs in savannas as well as in disturbed secondary vegetation of tropical regions (Renner 1993; Clausing & Renner 2001b), Melastomataceae are still understudied especially in the Palaeotropics where ca. one-third of the species are found (Renner 1993; Veranso-Libalah et al. 2018).

Throughout the taxonomic history of Melastomataceae, androecium morphology provided useful characters especially for the delimitation of genera and species (e.g., Triana 1872; Renner 1993; Clausing & Renner 2001b; Goldenberg et al. 2003; Michelangeli et al. 2011; Veranso-Libalah et al. 2020). Naturally, the morphological variability of the androecium in melastomes, especially the elaborate anther appendages and staminodes, is closely linked to the diversity of pollinators. Melastome flowers are predominantly bee pollinated with pollen collected by buzz pollination being the most prevalent pollination syndrome (Renner 1989; Kriebel & Zumbado 2014). The subtribe Dissochaetinae is particularly diverse in androecial morphology ranging from minute flowers with isomorphic unappendaged stamens to large flowers with colorful dimorphic stamen whorls (Fig. 6-1).

Dissochaeteae. — The tribe Dissochaeteae was first proposed by Triana (1866) to accommodate palaeotropical genera previously included in the subtribe Dissochaetinae Naudin of tribe Miconieae DC. (Naudin 1851; Miquel 1855). Traditionally, Dissochaeteae were morphologically defined by stamens with well-developed appendages, an epigynous ovary that develops into a berry, axillary placentation, and cochleate seeds (Triana 1866, 1872; Cogniaux 1891; Krasser 1893; Maxwell 1984; Jacques-Félix 1995). They may be terrestrial or epiphytic, whereby growth forms include erect shrubs, and woody climbers or scrambling shrubs (Triana 1872; Cogniaux 1891; Maxwell 1984; Clausing & Renner 2001a). Dissochaeteae as currently circumscribed (Clausing 1999) are distributed from tropical Africa through Madagascar to tropical Asia and the Western Pacific Islands with the Malesian region as its center of diversity (Triana 1872; Cogniaux 1891; Krasser 1893; Maxwell 1984; Jacques-Félix 1995). The name Dissochaeteae was changed to Medinilleae Hook.f. by Hooker (Bentham & Hooker 1867; Baillon 1877), because the genus name *Medinilla* Gaudich. ex DC. has priority over *Dissochaeta* Blume; however, at the tribal level Dissochaeteae is older and therefore the accepted name. Dissochaeteae was again included inside Miconieae (Renner 1993) because both tribes have berries as fruits but were separated

into two groups based on geographical distribution, the Neotropical and Palaeotropical Miconieae.

In the original circumscription of Dissochaeteae, 12 genera were treated in this tribe by Triana (1872), 2 from Africa (*Dicellandra* Hook.f. and *Sakersia* Hook.f.), 9 from Tropical Asia (*Anplectrum* A.Gray [=*Diplectria* (Blume) Rchb.], *Carionia* Naudin, *Creochiton* Blume, *Dalenia* Korth., *Dissochaeta*, *Marumia* Blume [=*Macrolenes* Naudin], *Omphalopus* Naudin, *Pachycentria* Blume, *Pogonanthera* Blume) and 1 widespread palaeotropical genus (*Medinilla*; Table 1). The generic circumscription within Dissochaeteae have changed over the years, with several genera resurrected, synonymized as well as new additions; *Backeria* Bakh.f., *Boerlagea* Cogn., *Catanthera* F.Muell., *Heteroblemma* Camara-Léret et al., *Hypenanthe* Blume, *Medinillopsis* Cogn., *Myrianthemum* Gilg, *Neodissochaeta* Bakh.f., *Orthogoneuron* Gilg, *Phaeoneuron* Gilg, *Preussiella* Gilg, *Pseudodissochaeta* M.P.Nayar and *Tetraphyllaster* Gilg (Cogniaux 1891; Gilg 1898; Bakhuizen van den Brink 1943; Nayar 1969a, 1982; Camara-Léret et al. 2013). The circumscription of the tribe changed several times, sometimes by moving some genera (*Dicellandra*, *Sakersia*) into another tribe, or by adding some other genera such as *Dinophora* Benth., *Kendrickia* Hook.f., *Ochthocharis* Blume and *Plethiandra* Hook.f. (Renner 1993; Jacques-Félix 1995; Clausing & Renner 2001a). Table 6-1 provides an overview and summary of generic classification schemes within Dissochaeteae.

An infratribal classification of Dissochaeteae was first proposed by Maxwell (1980b), who recognized two subtribes, Dissochaetinae and Diplectrinae J.F.Maxwell, based on floral morphology. A new subtribe, Medinillinae J.F.Maxwell was later added on the basis of flower merosity and wood anatomical characters (Van Vliet et al. 1981; Maxwell 1984). Subtribe Dissochaetinae included *Creochiton*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*; while subtribe Diplectrinae included only *Diplectria*, and subtribe Medinillinae included *Boerlagea*, *Carionia*, *Catanthera*, *Dicellandra*, *Dichaetanthera*, *Medinilla*, *Pachycentria*, *Plethiandra*, and *Pogonanthera* (Maxwell 1984). Jacques-Félix (1995) treated *Dinophora* and *Ochthocharis* in Dissochaeteae due to their indehiscent, berry-like fruits (Table 6-1).

The placement of most genera of Dissochaeteae in their respective subtribes has generally been unequivocal, but the circumscription of some genera is problematic. For example, *Catanthera* is morphologically, especially the floral characters, similar to Medinilla and placed in Medinillinae, but wood anatomy suggests that the genus is part of Dissochaetinae because of the presence of a scandent/lianous habit that seems to resemble *Dissochaeta* (Van Vliet 1981; Van Vliet et al., 1981). Diplectrinae was considered monogeneric and only included *Diplectria* species because of the reduction of the alternipetalous stamens to staminodia, even though all the other characters are similar (or identical) to those of *Dissochaeta*, therefore, *Diplectria* can be classified again in Dissochaetinae (Van Vliet et al. 1981; Clausing & Renner 2001a; Kartonegoro et al. 2018). Most species of *Pseudodissochaeta* are true shrubs, but they have been classified close to the lianas/scramblers inside Dissochaetinae (Nayar 1969a; Maxwell 1984; Clausing & Renner 2001a; Renner et al. 2001b). Morphologically, *Pseudodissochaeta* closely resembles *Medinilla*, and the classification becomes a problem when *Pseudodissochaeta* is considered to be a synonym of *Medinilla*, which is part of the Medinillinae (Chen 1983, 1984; Chen & Renner 2007).

Fig. 6-1. Flowers of representative genera of *Dissochaeta* alliance. **A.** *Pseudodissochaeta septentrionalis*; **B.** *Pseudodissochaeta spirei*; **C.** *Creochiton roseus*; **D.** *Dalenia magnibracteata*; **E.** *Dalenia pulchra*; **F.** *Dalenia glabra*; **G.** *Diplectria conica*; **H.** *Diplectria viminalis*; **I.** *Macrolenes hirsutoidea* (sect. *Terminaliflores*); **J.** *Macrolenes macrosepala* (sect. *Terminaliflores*); **K.** *Macrolenes echinulata* (sect. *Macrolenes*); **L.** *Macrolenes nemorosa* (sect. *Macrolenes*); **M.** *Macrolenes subulata* (sect. *Macrolenes*); **N.** *Dissochaeta bracteata* (sect. *Diplostemones*); **O.** *Dissochaeta pallida* (sect. *Diplostemones*); **P.** *Dissochaeta vacillans* (sect. *Dissochaeta*); **Q.** *Dissochaeta biligulata* (sect. *Dissochaeta*); **R.** *Dissochaeta fallax* (sect. *Dissochaeta*); **S.** *Dissochaeta inappendiculata* (sect. *Dissochaeta*); **T.** *Dissochaeta bakhuizenii* (sect. *Dissochaeta*). — Photos by Y. Liu (A, D, P), L.J. Yezi (B), A. Kartonegoro (C, G, H, L–N, R–T), J. Henrot (E), D.S. Penneys (F, J, Q), Supriyatna (I), C. Ng (K), W.F. Ang (O).

Table 6-1. Classification history of the genera in tribe Dissochaeteae s.l.

Bentham & Hooker 1867	Triana 1872	Cogniaux 1891	Gilg 1898	Bakhuizen van den Brink 1943	Maxwell 1984	Jacques-Félix 1995	Current Treatment[1]
Medinilleae	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**	**Dissochaeteae**
Anplectrum	***Anplectrum***	***Anplectrum***		Treated in ***Diplectria***	Treated in ***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
				Backeria	Treated in ***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
		Boerlagea		***Boerlagea***	***Boerlagea***		***Boerlagea***[4] (*Medinilla* alliance)
Carionia	***Carionia***	***Carionia***		Treated in ***Medinilla***	***Carionia***		Treated in ***Medinilla***[3,4] (*Medinilla* alliance)
				Treated in ***Medinilla***	***Catanthera***		***Catanthera***[4] (*Medinilla* alliance)
Creochiton	***Creochiton***	***Creochiton***		***Creochiton*** *(*Astronieae)	***Creochiton***		***Creochiton***[9] (*Dissochaeta* alliance)
Dalenia	***Dalenia***	***Dalenia***		***Dalenia***	Treated in ***Dissochaeta***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Dicellandra	***Dicellandra***	***Dicellandra***	***Dicellandra***		***Dicellandra***	***Dicellandra*** (Sonerileae)	***Dicellandra***[5] (Sonerileae)
Dinophora (Osbeckieae)	***Dinophora*** **(**Osbeckieae**)**	***Dinophora*** **(**Osbeckieae**)**	***Dinophora*** **(**Osbeckieae**)**			***Dinophora***	***Dinophora***[5] (*Dinophora* alliance)
Treated in ***Anplectrum***	Treated in ***Anplectrum***	Treated in ***Anplectrum***		***Diplectria***	***Diplectria***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Dissochaeta	***Dissochaeta***	***Dissochaeta***		***Dissochaeta***	***Dissochaeta***		***Dissochaeta***[10] (*Dissochaeta* alliance)
Treated in *Medinilla*	Treated in ***Medinilla***	Treated in ***Medinilla***		Treated in ***Medinilla***	***Medinilla* sect. *Heteroblemma***		***Heteroblemma***[8] (*Medinilla* alliance)
Treated in ***Medinilla***	Treated in ***Medinilla***	Treated in ***Medinilla***		***Hypenanthe***	***Hypenanthe***		Treated in ***Medinilla***[3,4] (*Medinilla* alliance)
Kendrickia (Oxysporeae)	***Kendrickia*** (Oxysporeae)	***Kendrickia*** (Oxysporeae)			***Kendrickia*** (Oxysporeae)		***Kendrickia***[4] (*Medinilla* alliance)
Treated in ***Marumia***	Treated in ***Marumia***	Treated in ***Marumia***		***Macrolenes***	***Macrolenes***		***Macrolenes***[11] (*Dissochaeta* alliance)
Marumia	***Marumia***	***Marumia***		Treated in ***Macrolenes***	Treated in ***Macrolenes***		Treated in ***Macrolenes***[11] (*Dissochaeta* alliance)
Medinilla	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***	***Medinilla***[3,4] (*Medinilla* alliance)

Bentham & Hooker 1867	Triana 1872	Cogniaux 1891	Gilg 1898	Bakhuizen van den Brink 1943	Maxwell 1984	Jacques-Félix 1995	Current Treatment[1]
		Medinillopsis		Treated in ***Plethiandra***	Treated in ***Plethiandra***		Treated in ***Plethiandra***[7] (*Medinilla* alliance)
			Myrianthemum			Treated in ***Medinilla***	Treated in ***Medinilla***[2] (*Medinilla* alliance)
				Neodissochaeta	Treated in ***Dissochaeta***		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
Ochthocharis (Oxysporeae)	***Ochthocharis*** (Oxysporeae)	***Ochthocharis*** (Oxysporeae)		***Ochthocharis*** (Oxysporeae)		***Ochthocharis***	***Ochthocharis***[5] (*Dinophora* alliance)
Omphalopus	***Omphalopus***	***Omphalopus***		***Omphalopus***	***Dissochaeta*** sect. *Omphalopus*		Treated in ***Dissochaeta***[10] (*Dissochaeta* alliance)
			Orthogoneuron			Treated in ***Gravesia*** (Sonerileae)	Treated in ***Gravesia***[4] (Sonerileae)
Pachycentria	***Pachycentria***	***Pachycentria***		***Pachycentria***	***Pachycentria***		***Pachycentria***[6] (*Medinilla* alliance)
			Phaeoneuron			Treated in ***Ochthocharis***	Treated in ***Ochthocharis***[5] (*Dinophora* alliance)
Plethiandra (Astronieae)	***Plethiandra*** (Astronieae)	***Plethiandra*** (Astronieae)		***Plethiandra***	***Plethiandra***		***Plethiandra***[7] (*Medinilla* alliance)
Pogonanthera	***Pogonanthera***	***Pogonanthera***		***Pogonanthera***	***Pogonanthera***		Treated in ***Pachycentria***[6] (*Medinilla* alliance)
			Preussiella			***Preussiella*** (Sonerileae)	***Preussiella***[5] (Sonerileae)
					Pseudodissochaeta		***Pseudodissochaeta***[12] (*Dissochaeta* alliance)
Sakersia	***Sakersia***	***Sakersia***	***Sakersia***		Treated in ***Dichaetanthera***		Treated in ***Dichaetanthera***[4] (Melastomateae)
			Tetraphyllaster			Treated in ***Tristemma*** (Melastomateae)	Treated in ***Tristemma*** [4] (Melastomateae)

[1]Based on the last account of the generic revision; [2]Jacques-Félix 1977; [3]Regalado 1995; [4]Renner 1993; [5]Jacques-Félix 1995; [6]Clausing 2000; [7]Kadereit 2005; [8]Camara-Léret et al. 2013; [9]Kartonegoro & Veldkamp 2013; [10]Kartonegoro et al. 2018; [11]Kartonegoro et al. 2019; [12]Kartonegoro et al., 2020.

Earlier molecular phylogenetic analyses, based on the combined chloroplast markers *ndhF* and *rpl16*, showed that Dissochaeteae is not monophyletic (Clausing & Renner 2001a, 2001b). This result was later confirmed by other phylogenetic studies of the family that included representatives of the group (Goldenberg et al. 2012; Zeng et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019a, 2019b). The phylogenetic trees from these studies, showed three major lineages within Dissochaeteae, 1) Medinillinae; 2) *Dinophora* + *Ochthocharis*; and 3) Dissochaetinae (Clausing & Renner 2001a, 2001b; Zeng et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019a, 2001b). The Medinillinae is closely related to the Sonerileae DC. complex (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b), while *Dinophora* + *Ochthocharis* are related to the Rhexieae DC. (Veranso-Libalah et al. 2018). Dissochaetinae forms a monophyletic group but its sister group remained unclear. Depending on the study it is sister to either the Sonerileae complex + Medinillinae or to Blakeeae Benth. & Hook.f. (Clausing & Renner 2001a), Cyphostyleae Gleason + Blakeeae (Bacci et al. 2019), or the Cambessedesieae (Penneys et al. 2020). The phylogenetic analyses by Zhou et al. (2019b) also showed that Dissochaetinae is sister to a large clade consisting of Sonerileae-Oxysporeae + Medinillinae. Eventhough the non-herbaceous plants in all genera of Dissochaeteae share berry fruits and cochleate seeds, these characters seem to be rather homoplasious. In general, fruit morphology does not reflect a shared history but is homoplasious and an adaptation to different modes of dispersal (Clausing et al. 2000; Clausing & Renner 2001a; Bacci et al. 2019).

***Dissochaeta* alliance. —** The *Dissochaeta* alliance was first proposed to recognize an informal group of woody climbing or scrambling shrub taxa of Dissochaeteae (Maxwell 1982). It comprises c. 71 species of scrambling shrubs distributed from southern China southward into Indochina, Thailand, and the Malesian region, with Sumatra-Peninsular Malaysia-Borneo as its center of distribution (Kartonegoro et al. 2018, 2019). The *Dissochaeta* alliance is characterized as shrubs having a lianous scrambling habit, growing in open areas or forest edges in Southeast Asia (Maxwell 1984; Kartonegoro et al. 2018, 2019). This scrambling growth form probably evolved only once from a shrubby growth form in Old World Melastomataceae (Clausing & Renner 2001a). Thin branches with long internodes have been suggested as morphological adaptations promoting scrambling growth (Clausing & Renner 2001a). Some species develop interpetiolar outgrowths on the nodes to support the scrambling activity (Clausing & Renner 2001a; Kartonegoro et al. 2018). A lianous growth form is also known for a few New World taxa of Blakeeae, but these usually grow as true epiphytes (Penneys & Judd 2013). Along with the scrambling shrub habit, another apparent synapomorphy for this group is their pattern of flower development (Kartonegoro et al. 2018, 2019). Flowers of the *Dissochaeta* alliance have 4 (haplostemon) equal, or 8 (diplostemon) dimorphic stamens in two whorls with various well-developed appendages (Maxwell 1984; Renner et al. 2001b; Kartonegoro et al. 2018, 2019, 2020). Like all Melastomataceae taxa, stamens are folded in bud. The folding point of the stamens is at the attachment between anthers and filaments for the alternipetalous stamens, while the oppositipetalous ones have a fold in the filaments below the attachment point with the anthers (Maxwell 1984; Kartonegoro et al. 2018). When mature, the stamens will reverse their orientation into curved or straight anthers with varying shape. The number of fertile stamens can be 8 or 4 because either the inner or the outer staminal whorl can be reduced (Kartonegoro et al. 2018).

Previous taxonomic work of the *Dissochaeta* alliance resulted in different generic concepts and was mainly based on morphology and overlooked other important approaches, such as anatomy, cytology and molecular phylogenetics. Genera included by different authors are

Backeria, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, *Neodissochaeta* and *Omphalopus* (Bakhuizen van den Brink 1943; Nayar 1966, 1980; Raizada 1968; Veldkamp et al. 1979; Maxwell 1984; Renner et al. 2001b; Kartonegoro et al. 2018, 2019; see also Table 6-1). In addition, the genera, *Creochiton* and *Pseudodissochaeta* were also treated as part of the alliance (Maxwell 1984; Kartonegoro et al. 2020). The decision whether to include the non-scrambling genera into the alliance was based on similarity of floral characters, such as merosity and stamen dimorphism with distinct connective appendages (Maxwell 1980, 1984). Therefore, the *Dissochaeta* alliance can be generalized as Dissochaetinae and consisting of all genera of the subtribe.

Within the *Dissochaeta* alliance, an infrageneric classification has only been proposed for *Dissochaeta*, the largest genus of the group. In the protologue of *Dissochaeta*, Blume (1831a, 1831b) proposed two sections, *Dissochaeta* sect. *Dissochaeta* and sect. *Diplectria* Blume, based on hypanthium shape and connective appendages. Baillon (1877) further divided the genus into nine sections: *Dissochaeta* sect. *Anoplodissochaeta* Baill., sect. *Anplectrum* (A.Gray) Baill. (≡ sect. *Diplectria*), sect. *Creochiton* (Blume) Baill., sect. *Dalenia* (Korth.) Baill., sect. *Dicellandra* (Hook.f.) Baill., sect. *Eudissochaeta* Blume ex Endl. (invalid name, ≡ sect. *Dissochaeta*), sect. *Omphalopus* (Naudin) Baill., sect. *Oxyotandra* Baill., and sect. *Sakersia* (Hook.f.) Baill. Cogniaux (1891) rejected Baillon's generic concept of *Dissochaeta* and resurrected some genera such as; *Anplectrum*, *Creochiton*, *Dalenia*, *Dicellandra*, *Omphalopus* and *Sakersia*. He also rearranged the infrageneric classification of *Dissochaeta* and proposed three new sections; *Dissochaeta* sect. *Diplostemones* Cogn., sect. *Dissochaetopsis* Cogn. and sect. *Isostemones* Cogn. An additional section of *Dissochaeta*, *D*. sect. *Disparistemones* Merr. was proposed by Merrill (1917).

An initial molecular phylogenetic study of Dissochaeteae by Clausing & Renner (2001a) showed that the *Dissochaeta* alliance is monophyletic. However, their analyses included only a few species of the *Dissochaeta* alliance and two allied genera (*Creochiton*, *Pseudodissochaeta*) were not sampled. Within the *Dissochaeta* alliance, *Dissochaeta* was resolved as sister to *Diplectria* + *Macrolenes* (Clausing & Renner 2001a). More recent molecular phylogenetic studies strongly support *Pseudodissochaeta*, a non-scrambling taxon, as part of the *Dissochaeta* alliance but unrelated to *Medinilla* (Zeng et al. 2016; Zhou et al. 2019a, 2019b). However, *Creochiton* remains unsampled, and the number of species sampled per genus needs to be improved especially for *Dissochaeta* to ascertain that all the genera and sections are natural lineages.

Aims. — Using sequence data extended to six loci (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) with a much more comprehensive sampling than any previous investigation, this study seeks (1) to confirm the polyphyly of Dissochaeteae as currently circumscribed (Table 1) and identify the position of the lineages within the Melastomataceae; (2) to test the monophyly of the *Dissochaeta* alliance; (3) to resolve phylogenetic relationships among genera and sections within the *Dissochaeta* alliance; and (4) to investigate selected morphological characters as potential synapomorphies for delimiting clades or genera in the alliance.

Material and Methods

Taxon sampling. — For a broad taxon sampling of Dissochaeteae and relevant outgroups we compiled a total of 121 accessions of which 78 represent 63 species and 1 variety of Dissochaeteae (see Appendix 6-1). Within the *Dissochaeta* alliance, 44 of 90 species (50%) were sampled from the following genera: *Creochiton* (4 species sampled/12 species in

genus); *Dissochaeta* (28/56); *Macrolenes* (9/17); *Pseudodissochaeta* (3/5). From the *Medinilla* alliance, 16 species belonging to *Heteroblemma* (1/13), *Medinilla* (13/±400) and *Pachycentria* (2/8) were sampled. We also included the African endemic monospecific *Dinophora* (*D. spenneroides* Benth.) and two species of the only disjunct African / Southeast Asian genus *Ochthocharis*, two genera with an unclear phylogenetic placement. As outgroups to test the monophyly of the traditional Dissochaeteae, we selected 44 taxa from Melastomateae (8 species), Miconieae (4), Oxysporeae (5), Kibessieae (4), Merianieae (4), Sonerileae (4), Cambessedesieae (2), Henrietteeae (2), Marcetieae (2), Olisbeoideae (2), and one each from Astronieae, Bertolonieae, Blakeeae, Eriocnemeae, Microlicieae, Rhexieae, and Trioleneae. A complete list of the taxa sampled in this study, their collection localities, voucher information, and Genbank accession numbers are provided in the Appendix 6-1.

Morphological data used for generic delimitations of Dissochaeteae including data on floral morphology that substantiated our floral diagrams were obtained from the literature (Bakhuizen van den Brink 1943; Nayar 1969a, 1982; Veldkamp et al. 1979; Hansen & Wickens 1981; Maxwell 1984; Regalado 1995; Jacques-Félix 1995; Clausing 2000; Kadereit 2005; Cámara-Leret et al. 2013; Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019, 2020) and supplemented by the first author during studies of herbarium material and visits to the herbaria BM, BO, E, K, L, SING and U, and through online repositories of AAU (https://www.aubot.dk/search_form.php), HBG (http://www.herbariumhamburgense.de/Data_Spermatophyta/index.php), P (https://science.mnhn.fr/all/search), and PE (http://pe.ibcas.ac.cn/en/#).

DNA extraction, polymerase chain reaction amplification, and sequencing. — Total genomic DNA was extracted, either from silica-gel dried leaves or herbarium specimens, using either the modified CTAB procedure (Doyle & Doyle 1987) using a 96-well Thermo ScientificKingFisher Flex extraction (Thermo Fisher Scientific, Waltham, MA, U.S.A.), following the manufacturer's instructions, or using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), with modification to the manufacturer's protocol following Goldenberg et al. (2008). During the lysis stage, 30 µl Proteinase-K was added to all samples, which were incubated at 42°C for 20–22 hours. Two nuclear ribosomal loci, the internal transcribed spacer (nrITS) and the external transcribed spacer (nrETS) regions, and four plastid loci (*ndhF*, *psbK-psbL*, *rbcL*, and *rpl16*) were amplified and sequenced following the protocols outlined by Clausing & Renner (2001a, 2001b), Fritsch et al. (2004), Rocha et al. (2016), Zeng et al. (2016), Veranso-Libalah et al. (2017, 2018) and Bacci et al. (2019). The nuclear markers have been widely used in phylogenetic studies due to their relatively high rate of nucleotide substitutions providing resolution even at lower taxonomic levels in Melastomataceae (Rocha et al. 2016). Also, the selected plastid loci have proven to be variable at both the tribal and generic levels in the family (Clausing & Renner 2001a, 2001b; Michelangeli et al. 2004, 2013; Goldenberg et al. 2008; Penneys & Judd 2013; Zeng et al. 2016; Veranso-Libalah et al. 2017; Bacci et al. 2019). Amplification and sequencing of ITS and *ndhF* markers were done via two segment regions using overlapping primers. All primers used in this study are shown in Table 6-2.

Polymerase chain reactions (PCR) were performed with a total volume of 25 µl containing the following: template DNA (1-1.5 µL), 10 pMol/µL primers (0.5 µL each), 2.5 nM dNTPs (1.5 µL), 10x Buffer (Qiagen) (2.5 µL), 25 nM MgCl2 (1 µL), DNA Taq polymerase (Qiagen) (0.25 µL) and miliQ water (16-18 µL). Specifically, for ITS 0.25 µL Bovine Serum Albumin (BSA) was added. PCR programs for all markers are shown in Table 6-3. PCR products were run on 1% agarose gels to check the quality of the amplified DNA. Cycle sequencing was

carried out either at Baseclear (Leiden, The Netherlands) or StarSEQ (Mainz, Germany) with the same forward and reverse primers used in the amplifications. In addition to the 368 newly generated sequences, 272 were downloaded from GenBank (Appendix 6-1).

Table 6-2. Primers of the six markers used in this study and the sources of primer sequences.

Marker	Primer name	Primer sequence 5' → 3'	Source
nrETS	ETS NY320 F	AGA CAA GCA TAT GAC TAC TGG CA	Veranso-Libalah & al. (2018)
nrETS	ETS 1428 Mel Spec R	ACG TGT CGC GTC TAG CAG GCT	Veranso-Libalah & al. (2018)
nrITS	ITS1-MEL F	GGA GAA GTC GTA ACA AGG TTT C	Veranso-Libalah & al. (2017)
nrITS	ITS1-MEL R	CTT GCG TTC AAA GAA TTG ATG G	Veranso-Libalah & al. (2017)
nrITS	ITS2-MEL F	CGG CTC TTG CAT CGA TGA AG	Veranso-Libalah & al. (2017)
nrITS	ITS2-MEL R	CCA CCT TCC AGT GAA CTT GG	Veranso-Libalah & al. (2017)
ndhF	*ndhF*-972 F	GTCTCAATTGGGTTATATGATG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1603 R	GCATAGTATTGTCCGATTCATRAGG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1318 F	GGATTAACYGCATTTTATATGTTTCG	Olmstead & Sweere (1994)
ndhF	*ndhF*-1955 R	CGATTATATGACCAATCATATA	Olmstead & Sweere (1994)
psbK	*psbK* F	TTA GCC TTT GTT TGG CAA G	Reginato & al. (2010)
psbL	*psbL* R	AGA GTT TGA GAG TAA GCA T	Reginato & al. (2010)
rbcL	*rbcL*-1 F	ATGTCACCACAAACRGAGACTAAAGC	De Groot & al. (2011)
rbcL	*rbcL*-1361 R	TCAGGACTCCACTTACTAGCTTCACG	De Groot & al. (2011)
rpl16	*rpl16*-71 F	GCTATGCTTAGTGTGTGACTCGTTG	Jordan & al. (1996)
rpl16	*rpl16*-1516 R	CCCTTCATTCTTCCTCTATGTTG	Kelchner & Clark (1997)

Phylogenetic analyses. — Contigs of forward and reverse sequences were assembled and manually edited using either Geneious Prime Sequence Analysis Tools version 2019.2.1 (Biomatters, Auckland, NZ) or Sequencher 4.1.4 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequence alignment was done using MAFFT v.7 (Katoh & Standley 2013) implemented in Geneious via plugins with default settings and the results manually checked. Phylogenetic analyses were performed under maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. We separately analysed each of the six individual datasets (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Later we combined the two nuclear (nrETS, nrITS) and four plastid datasets (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) and ran each analysis to check for conflicts between the two matrices. Since no supported conflict was detected a concatenated matrix of all six individual datasets was again analysed. The

best-fitting model for each marker was determined using the Akaike information criterion corrected (AICc) in jModelTest v.2.1.6 (Darriba et al. 2012) through the CIPRES portal (www.phylo.org; Miller et al. 2010). The best fit substitution models selected for the datasets are shown in Table 6-4.

Table 6-3. Thermocycler programs for the PCR amplification of all markers.

Marker		**nrETS**	**nrITS**	***ndhF***	***psbK-psbL***	***rbcL***	***rpl16***
Initial denaturation	Temperature (°C)	94	94	94	94	93	94
	Time (m)	4	1	4	2	3	3
Cycle		40	40	40	40	35	35
Denaturation	Temperature (°C)	94	94	94	94	94	94
	Time (s)	30	20	30	30	45	45
Annealing	Temperature (°C)	58	63	54	55	62	58
	Time (s)	30	30	30	30	45	45
Extension	Temperature (°C)	72	72	72	72	72	72
	Time (s)	45	60	60	30	105	75
Final extension	Temperature (°C)	72	72	72	72	72	72
	Time (s)	7	8	7	7	6	7

The MP analyses were carried out in PAUP* v.4.a165 (Swofford 2002). A heuristic search was conducted of 1000 replicates with random sequence addition, TBR branch swapping and MulTrees on. Swapping was performed on a maximum of 100 trees. All characters were unordered and equally weighted, while gaps were treated as missing data. Bootstrap values (Felsenstein 1985) were calculated from 1000 random replicates using a heuristic search with TBR branch swapping and one random addition-sequence per replicate. The ML trees were generated using RAxML v.8.2.12 using the GTR+I+Γ model and inferred under default settings (Stamatakis 2014). Node support was calculated in RAxML with 1000 bootstrap replicates using a fast bootstrapping algorithm (Stamatakis et al. 2008). Bayesian inference (BI) analyses were carried out using MrBayes v.3.2.7a (Ronquist et al. 2012). The Markov Chain Monte Carlo (MCMC) analyses were carried out with four simultaneous chains of 10 million generations sampling one tree every 1000 generations in two independent runs. The individual output log files were examined using Tracer v.1.7.1 (Rambaut et al. 2018) to assess convergence of both runs. The resultant tree files were combined using LogCombiner v.1.8.4 (Drummond & Rambaut 2007). The first 2500 trees (25%) were discarded as burn-in, and a maximum clade credibility (MCC) tree was constructed using TreeAnnotator v.1.8.4 (Drummond et al. 2012). All analyses (MP, ML and BI) were run through the CIPRES portal (http://www.phylo.org/; Miller et al. 2010).

Results

Out of the total of 640 sequences used in the analyses, 368 were newly generated (Appendix 6-1). The combined data matrix consisted of 77 nrETS sequences, 106 for nrITS, 120 for *ndhF*, 118 for *psbK-psbL*, 112 for *rbcL* and 112 for *rpl16* (Table 4). Gene trees from combined plastid (121 terminals) and nuclear datasets (114 terminals), revealed congruencies in all three analyses without any significant conflicts (Suppl. 6-1 & 6-2). Most of the resolved clades are present in both gene trees (Dissochaeteae; incl. *Dissochaeta* alliance, *Medinilla* alliance and *Dinophora* + *Ochthocharis*), although some clades are poorly supported. The combined dataset contained 121 terminals and 5641 characters from all six loci (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) and showed a similar topology as the individual gene trees but with higher branch support values (Fig. 6-2).

In the parsimony analysis the aligned matrix with all combined regions had 1893 (36%) parsimony informative characters. The Consistency Index (CI) and Retention Index (RI) were 0.47 and 0.76, respectively. Other relevant information of the parsimony analyses is shown in Table 6-4. In general, the nuclear markers produced better resolved trees, probably because of the greater number of informative characters. However, lower CI and RI values for the nuclear markers indicate a greater proportion of homoplasy and less synapomorphies, respectively.

Table 6-4. Summary statistics of genomic regions sequenced for phylogenetic analyses of *Dissochaeta* alliance.

	ETS	**ITS**	***ndhF***	***psbK-psbL***	***rbcL***	***rpl16***	**Nuclear**	**Plastid**	**Combined**
Accession terminals	77	106	120	118	112	112	114	121	121
Aligned characters	693	1057	1001	528	1244	1118	1750	3891	5641
% missing data	36	12	1	2	7	7	6	0	0
Parsimony informative sites	433 (62%)	602 (57%)	298 (30%)	157 (30%)	142 (11%)	256 (23%)	1039 (59%)	854 (22%)	1893 (36%)
Conserved sites	149	340	552	256	1007	665	481	2477	2958
Length of most parsimonius trees	2259	3449	1064	536	472	983	5918	3154	9167
Consistency Index (CI)	0.46	0.38	0.59	0.68	0.59	0.63	0.4	0.6	0.47
Retention Index (RI)	0.76	0.69	0.87	0.88	0.84	0.83	0.71	0.85	0.76
Best substitution model (AICc)	TVM +I+Γ	GTR+ I+Γ	TVM+I +Γ	TVM +Γ	TPM1 uf+I+ Γ	TVM +Γ	GTR+ I+Γ	TVM +I+Γ	TVM+I +Γ

Tree topologies from the ML, MP and BI analyses of the complete dataset were overall congruent with a well-resolved backbone. We considered the clades as statistically supported when the bootstrap values from the ML (BS) and MP (PBS) analyses were ≥ 70% and the posterior probabilities (PP) were ≥ 0.95 for the BI analysis. In our analyses, Dissochaeteae s.l. (including *Medinilla* alliance, *Dissochaeta* alliance, *Dinophora* + *Ochthocharis* lineages) was recovered as polyphyletic (Figs. 6-2, 6-3). The *Medinilla* alliance (clade A) is grouped with the Sonerileae + Oxysporeae lineage (PP=1/BS=100/PBS=100). Although a well-supported *Dinophora* + *Ochthocharis* lineage (clade B; PP=1/BS=100/PBS=96) is recovered, it is in a polytomy with Melastomateae, Microlicieae, Marcetieae and Rhexieae

(Fig. 6-2). The species of the *Dissochaeta* alliance form a well-supported monophyletic lineage (clade C; PP=1/BS=100/PBS=100), that is sister to Cambessedesieae (Fig. 6-2).

Three Dissochaeteae genera, *Heteroblemma*, *Medinilla* and *Pachycentria* are recovered within the unresolved *Medinilla* alliance lineage (clade A; Fig. 6-3A). *Medinilla* is recovered as paraphyletic with *Pachycentria* nested within it. Except for the Madagascan *Medinilla* (*M. lophoclada* Baker, *M. chermezonii* H.Perrier and *M. micrantha* Jum. & H.Perrier) which formed a well-supported monophyletic clade (PP=1/BS=92/PBS=92), the remaining *Medinilla* species sampled are unresolved (Fig. 6-3A).

The *Dissochaeta* alliance is composed of six well-supported lineages (clade C; Fig. 6-3B). The well-supported *Pseudodissochaeta* lineage (clade E; PP=1/BS=100/PBS=100) is sister to all other lineages within the *Dissochaeta* alliance. There is little or no resolution between the three *Pseudodissochaeta* species sampled (Fig. 6-3B). *Creochiton* forms the second strongly supported monophyletic lineage (clade F; Fig. 6-3B; PP=1/BS=100/PBS=100) and is sister to the scrambling shrub taxa (clade D). Within *Creochiton*, *C. ledermannii* Mansf. is closely related to *Creochiton* sp. (PP=1/BS=100/PBS=99) but these two are in a polytomy with *C. roseus* Merr. and *C. bibracteatus* (Blume) Blume (Fig. 6-3B).

The scrambling shrubs lineage (clade D; including *Dissochaeta* s.l. and *Macrolenes*), is recovered as well-supported and monophyletic (PP=1/BS=100/PBS=100; Fig. 6-3B), with four well-supported sub-lineages within it (clades G, H, I and J in Fig. 6-3B). Clade G consists of all the species sampled from *Dissochaeta* sect. *Dalenia* and *Dissochaeta* sect. *Disparistemones* (PP=1/BS=97=PBS=77; Fig. 6-3B) and is sister to the well supported clade consisting of clades H, I and J. *Dissochaeta* sect. *Dalenia* consists of *Dissochaeta pubescens* Karton. (*Dalenia beccariana* (Cogn.) M.P.Nayar) and *Dissochaeta beccariana* Cogn. (*Dalenia magnibracteata* Karton.) and it is resolved as sister to *Dissochaeta* sect. *Disparistemones* (*Dalenia glabra* (Merr.) Karton.). Clade H is sister to clade I/J and represents a well-supported lineage comprising the species sampled from *Dissochaeta* sect. *Diplectria* (PP=1/BS=100/PBS=100). Clade I comprises *Macrolenes* (PP=1/BS=100/PBS=100; Fig. 6-3B) and splits into the *Macrolenes* s.str. lineage (Clade L; PP=1/BS=95/PBS=87) and the *Dissochaeta rostrata* complex (clade K; PP=0.99/BS=71/PBS=64). Within *Macrolenes* s.str. (clade L), 9 of the 17 *Macrolenes* species sampled are recovered in this lineage, with the interspecific relationships mostly resolved (Fig. 6-3B). The last lineage recovered within the scrambling shrubs lineage is the well-supported *Dissochaeta* s.str. (clade J; PP=1/BS=99/PBS=92). This lineage comprises two well supported sub-lineages; *Dissochaeta* sect. *Diplostemones* is supported (clade M; PP=1/BS=98/PBS=93) as sister to the other four lineages in clade N (PP=1/BS=99/PBS=100). Clade N consists of *Dissochaeta* sect. *Dissochaeta* + *Dissochaeta* sect. *Isostemones* + *Dissochaeta* sect. *Omphalopus* + *Dissochaeta* sect. *Anoplodissochaeta*. Apart from sect. *Dissochaeta*, which is recovered as paraphyletic, the remaining sections are monophyletic.

Discussion

Redefining Dissochaeteae. — This study represents (1) an expanded molecular phylogenetic study of the tribe Dissochaeteae s.l. with a broad outgroup sampling, and (2) a comprehensive molecular phylogenetic study of the *Dissochaeta* alliance (= subtribe Dissochaetinae). Of the 13 genera currently treated within Dissochaeteae (Table 6-1; one but last column), eight were sampled (*Creochiton*, *Dinophora*, *Dissochaeta*, *Heteroblemma*,

Macrolenes, *Ochthocharis, Pachycentria* and *Pseudodissochaeta*. We were not able to include *Boerlagea* (only known from the type collection), *Catanthera* (PCR failure and incomplete sequences), *Kendrickia* (no material available to us), and *Plethiandra* (incomplete sequences). According to our results, previous classifications of Dissochaeteae s.l. (i.e., Triana 1866, 1872; Cogniaux 1891; Krasser 1893; Gilg 1898; Bakhuizen van den Brink 1943; Van Vliet et al. 1981; Maxwell 1984; Jacques-Félix 1995; Clausing 1999) do not represent a natural, evolutionary unit because the tribe is polyphyletic (Figs. 6-2, 6-3). Our molecular phylogenetic results are similar to those of earlier studies (Clausing & Renner 2001a; Goldenberg et al. 2012; Zeng et al. 2016; Veranso-Libalah et al. 2108; Zhou et al. 2019a, 2019b; Penneys et al. 2020). The berry fruits and the cochleate seeds, used as diagnostic characters for the tribe, are homoplasious and have multiple parallel origins (Clausing et al. 2000). Clausing et al. (2000), suggested that berry fruits may have evolved at least three times within the family. Thus, the berries are a synapomorphy for tribe Dissochaeteae, but not all taxa with berries are Dissochaeteae. Berries are also present in other Melastomataceae lineages: Blakeeae, Henrietteeae, Miconieae, Olisbeoideae and some Old World Melastomateae (Clausing & Renner 2001a; Michelangeli et al. 2004; Penneys et al. 2010; Penneys & Judd 2013; Stone 2014).

The monophyly of the *Dissochaeta* alliance is supported by the following shared morphological characters: thyrsoid inflorescences, tetramerous diplostemonous flowers with unequal/subequal stamens produced in two whorls (alternipetalous and oppositipetalous) and berry fruits (Maxwell 1984). Based on wood anatomy, the *Dissochaeta* alliance have alternate inter-vessel pits, vessel elements with a wide diameter, and rays up to 7 cells wide (Van Vliet 1981). Together with morphology and wood anatomy, our molecular phylogenetic results clearly support a recircumscription of a narrower Dissochaeteae (excluding *Medinilla* alliance, *Dinophora* and *Ochthocharis*) (clades A and B in Figs. 6-2, 6-3). The *Dissochaeta* alliance or subtribe Dissochaetinae clade is thus the only member of Dissochaeteae. With this redefinition, Dissochaeteae (clade C in Fig. 6-2, 6-3B) is only distributed from East Bhutan, Northeast India, Southern China throughout Southeast Asia to New Guinea with no entities in Africa, Madagascar, West and Central India, or Sri Lanka.

Placement of *Medinilla* alliance. — The monophyly of the *Medinilla* alliance (sensu Maxwell 1984; including *Pachycentria* and *Heteroblemma*) is not strongly supported in this study. Its closest relatives are still unknown since it is nested in the still sparsely sampled Sonerileae+Oxysporeae complex (see also Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019a, 2019b). Except for the Madagascan endemic *Medinilla* species (*M. lophoclada*, *M. chermezonii*, *M. micrantha*; PP=1/BS=92/PBS=92) and *Pachycentria* (PP=1/BS=100/PBS=100), which formed monophyletic lineages and are nested among Southeast Asian *Medinilla*. The genera *Catanthera*, *Kendrickia* and *Plethiandra*, all treated in the *Medinilla* alliance, are unsampled in this study, but were earlier found to be nested inside Sonerileae+Oxysporeae (Clausing & Renner 2001a). *Catanthera* and *Kendrickia* are closely related to *Heteroblemma*, while *Plethiandra* is closely related to *Medinilla* (Clausing & Renner 2001a). The monospecific genus, *Boerlagea* is still unsampled in a phylogenetic context. So far, less than 10% of the species in *Medinilla* alliance have been included in phylogenetic studies. Such confirmation awaits a very broadly sampled study of the putative members of that group, along with a diverse array of Sonerileae+Oxysporeae taxa, as well as genera from across the family. With a comprehensive sampling of the *Medinilla* alliance, intergeneric relationships will be better understood in the future.

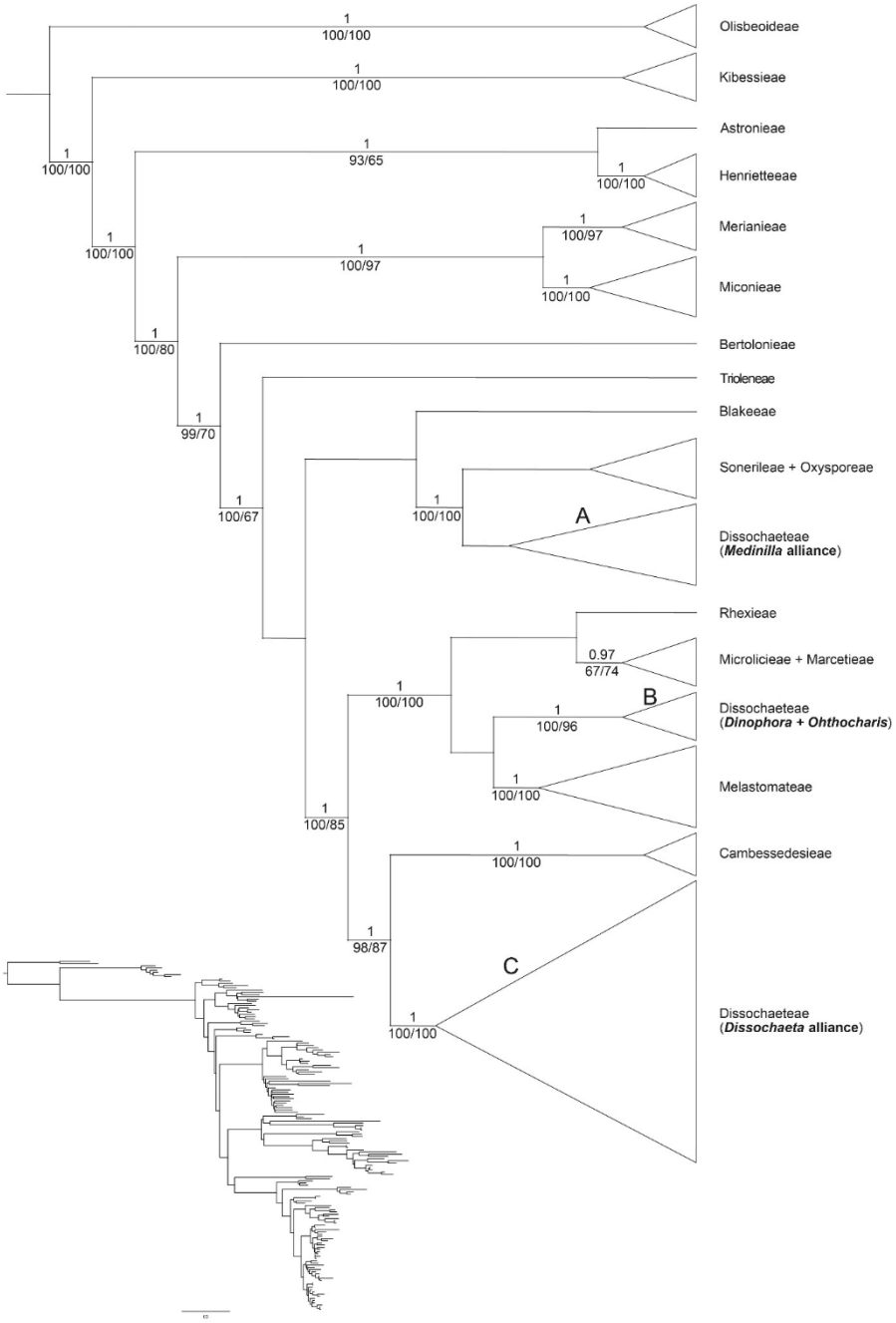


Fig. 6-2. The phylogenetic analyses of Dissochaeteae s.l. plus a broad outgroup sampling reveal the polyphyly of Dissochaeteae with three lineages (A-C) recovered in distinct positions within Melastomataceae. Analyses are based on combined nuclear (nrETS, nrITS) and plastid (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) data. Tree resulting from the maximum likelihood (ML) analysis with posterior probabilities above branches, ML bootstrap support values (left) and bootstrap support values resulting from the parsimony analysis (right) below branches. Posterior probabilities below 0.80 and bootstrap values below 50 are not shown. The major clades recognised in Dissochaeteae s.l. in this study are given in bold.

Placement of *Dinophora* and *Ochthocharis*. — Jacques-Félix (1983, 1995) included *Dinophora* and *Ochthocharis* in Dissochaeteae based on the presence of berry fruits. Previously, *Dinophora* was treated in Rhexieae (Bentham 1849), Bertolonieae (Van Tieghem 1891), and Melastomateae (=Osbeckieae) (Triana 1872; Baillon 1877; Cogniaux 1891; Gilg 1898; Renner 1993), and *Ochthocharis* was placed in Oxysporeae (Triana 1872; Cogniaux 1891; Krasser 1893; Bakhuizen van den Brink 1943; Hansen & Wickens 1981; Renner 1993). A previous molecular study suggested that *Dinophora* is not part of Melastomateae (Veranso-Libalah et al. 2017), but instead closely related to *Ochthocharis* and both were found in a polytomy together with Rhexieae, Marcetieae, Microlicieae and Melastomateae (Veranso-Libalah et al. 2018; Zhou et al. 2019b).

Like previous studies, our phylogenetic results support the monospecific *Dinophora* and the two species of *Ochthocharis* sampled as sister genera (Fig. 6-3A; Clade B), but in a polytomy with several other Melastomataceae tribes. A detailed morphological assessment with better phylogenetic resolution is necessary for the tribal placement of these genera. The type of *Ochthocharis*, *O. javanica* Blume, is still unsampled. Nevertheless, these genera are excluded from the redefined Dissochaeteae.

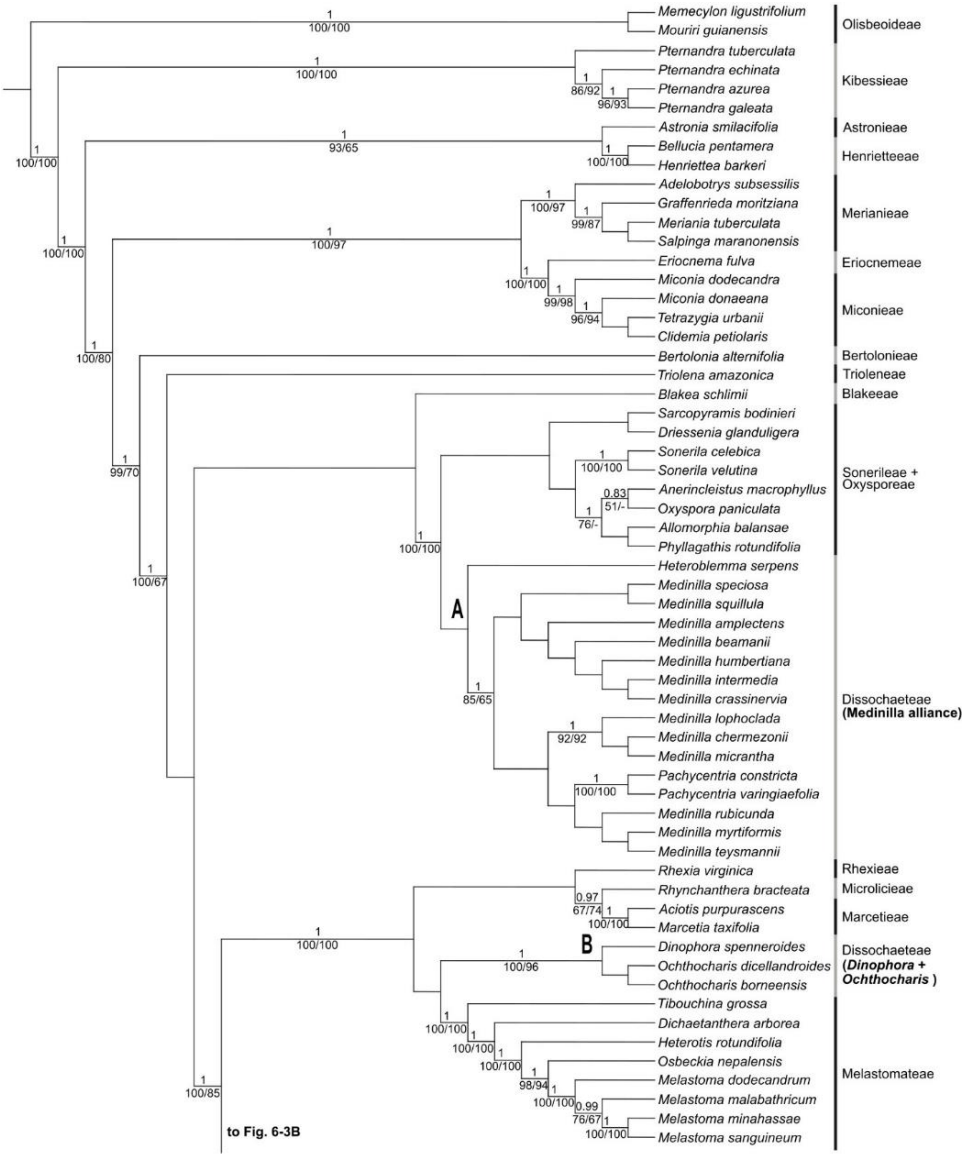
Phylogenetic relationships within Dissochaeteae. — The newly defined Dissochaeteae (*Dissochaeta* alliance) is strongly supported as monophyletic in our BI, ML, and MP analyses (Fig. 6-2, 6-3B; PP=1/BS=100/PBS=100). This confirms earlier phylogenetic studies by Clausing & Renner (2001a), Zeng et al. (2016), Zhou et al. (2019b). The Dissochaeteae are resolved as sister to neotropical tribe Cambessedesieae with strong support values (PP=1/BS=98/PBS=87; Figs. 6-2, 6-3B). *Cambessedesia* and related genera were placed in a new tribe, Cambessedesieae by Bochorny et al. (2019). With a comprehensive sampling including all genera ever treated in the *Dissochaeta* alliance and 44 of putatively 90 species, our results strongly support the monophyly of this lineage (Fig. 6-3B). Six lineages were resolved in the *Dissochaeta* alliance; *Pseudodissochaeta* (clade E), *Creochiton* (clade F), *Dalenia* (clade G), *Diplectria* (clade H). *Macrolenes* (clade I) and *Dissochaeta* s.str. (clade J). Below we discuss in detail each of these lineages.

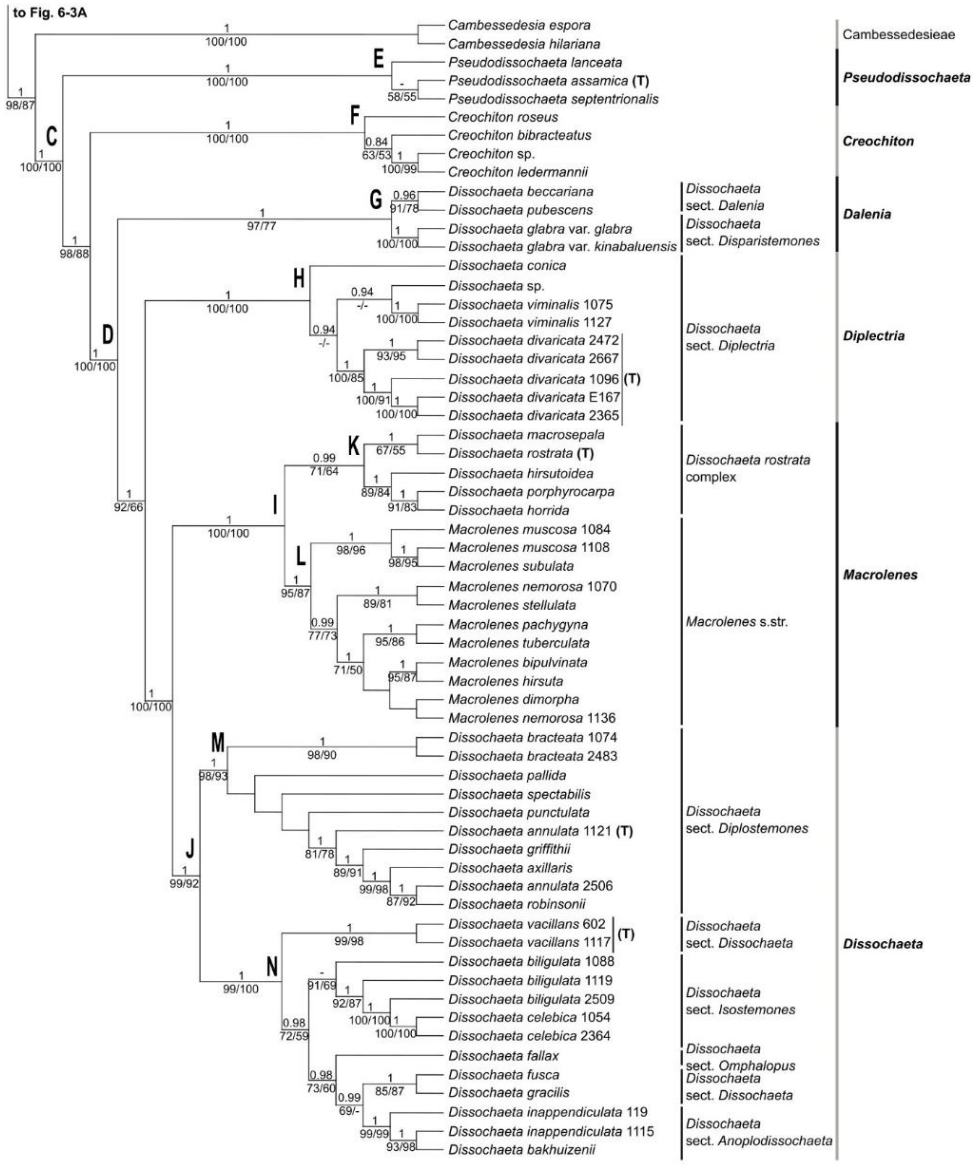
***Pseudodissochaeta*. —** *Pseudodissochaeta* consists of five species found in east Bhutan, northeast India, upper Myanmar, Indochina, southern China, Hainan, North Thailand (Nayar 1969a; Maxwell 1984; Clausing 1999; Renner et al. 2001b; Kartonegoro et al. 2020). These species are shrubs or small trees with 8 equal stamens, dorsally spurred and ventrally biauriculate (Nayar 1969a; Maxwell 1984; Clausing 1999; Renner et al. 2001b; Zhou et al. 2019b; Kartonegoro et al. 2020; see Figs. 6-1A–B). Morphologically, *Pseudodissochaeta* closely resembles *Medinilla*, which explains why some authors formerly regarded the genus as a synonym of *Medinilla* (Chen 1983, 1984; Chen & Renner 2007). However, in agreement with molecular results (see below), wood anatomy suggests it to be a member of the *Dissochaeta* alliance and not part of the *Medinilla* alliance (Van Vliet 1981; Van Vliet et al. 1981).

Our phylogenetic analyses included three of the five currently recognized *Pseudodissochaeta* species (including the type *P. assamica*; Clade E; Fig. 6-3B). Our results show that *Pseudodissochaeta* is a monophyletic lineage and a member of the *Dissochaeta* alliance and not part of the Medinilla alliance, and thereby confirm previous molecular studies even with more restricted sampling of the *Dissochaeta* alliance (Zeng et al. 2016; Zhou et al. 2019b). *Pseudodissochaeta* is recovered as the sister clade to all remainig Dissochaeteae. The genus is distinguished by its unique leaf features (serrulate margins with oblique base) and terminal

(axillary in *P. septentrionalis*) thyrsoid inflorescences. Like the other Dissochaeteae species, *Pseudodissochaeta* has curved stamens arranged in two whorls (Figs. 6-1A–B, 6-4). However, considering the huge variability of stamen morphology in lineage E, this is a rather weak trait.

Fig. 6-3A & 6-3B. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae s.l. and *Dissochaeta* alliance with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined data matrix (nrETS, nrITS, *ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values (only values ≥50) resulting from the ML analysis (left) and parsimony analysis (right). **A.** *Medinilla* alliance; **B.** *Dinophora* + *Ochthocharis*; **C.** *Dissochaeta* alliance; **D.** Scrambling shrub genera; **E.** *Pseudodissochaeta*; **F.** *Creochiton*; **G.** *Dalenia*; **H.** *Diplectria*; **I.** *Macrolenes*; **J.** *Dissochaeta*; **K.** *Macrolenes* sect. *Terminaliflores*; **L.** *Macrolenes* sect. *Macrolenes*; **M.** *Dissochaeta* sect. *Diplostemones*; **N.** *Dissochaeta* sect. *Dissochaeta*.





***Creochiton*. —** *Creochiton* has about 12 species, scattered throughout the Malesian region, and mostly in mountainous areas (Kartonegoro & Veldkamp 2013). They are epiphytic shrubs or lianas with haplostemonous or diplostemonous flowers, 4 alternipetalous or 8 alternipetalous-oppositipetalous equal stamens (Blume 1831a; Veldkamp 1979; Clausing 1999; Kartonegoro & Veldkamp 2013). The dorsally spurred or triangular and ventrally inappendiculate or biligulate appendaged stamens of *Creochiton* are similar to those of *Dissochaeta* (Fig. 6-1C). Some authors treated *Creochiton* in Astronieae based only on the basal placentation present in some species (Mansfeld 1925; Bakhuizen van den Brink 1943), but its habit, wood anatomy, floral morphology, and berry fruits corresponded with other Dissochaeteae genera (Triana 1866, 1872; Cogniaux 1891; Van Vliet 1981; Maxwell 1984;

Renner 1993; Kartonegoro & Veldkamp 2013). Basal placentation evolved in parallel in *Creochiton* and in the tribe Astronieae (Maxwell 1984). *Creochiton* flowers can either have 4 alternipetalous or 8 alternipetalous-oppositipetalous well developed fertile stamens (Kartonegoro & Veldkamp 2013; Fig. 6-4). The variability in stamen number and ventral appendages compelled some authors (Quisumbing & Merrill 1928; Nayar 1970) to recognize two genera, *Eisocreochiton* Quisumb. & Merr. and *Creochiton*. *Eisocreochiton* differed from *Creochiton* by having 4 alternipetalous stamens with ventrally biligulate appendages, and *Creochiton* has 4 alternipetalous and 4 oppositipetalous stamens and is ventrally inappendiculate (Nayar 1970). However, *E. monticola* (Ridl.) M.P.Nayar is morphologically intermediate between the two genera having 8 stamens with the inner whorl stamens distinctly smaller and ventrally inappendiculate (Kartonegoro & Veldkamp 2013). Therefore, *Eisocreochiton* has been treated as a synonym of *Creochiton* (Veldkamp 1979; Kartonegoro & Veldkamp 2013).

Nevertheless, the status of *Eisocreochiton* is still debatable because none of its three species (*E. bracteatus* Quisumb. & Merr., *E. furfuraceus* M.P.Nayar, *E. monticola*) were included in this study. We included only three of the twelve currently recognized species, plus one undescribed species thought to belong in *Creochiton*. Our phylogenetic results support the monophyly of *Creochiton* (clade F) and it is resolved as sister to the scrambling shrubs of Dissochaeteae. Morphologically, this group is also very distinct from the other genera of the Dissochaeteae by having an epiphytic habit, plinerved leaf venation, with fleshy, caducous and concave bracteoles that envelop the flower buds and umbellate inflorescences (Blume 1831; Kartonegoro & Veldkamp 2013).

Scrambling shrubs lineage — We included 37 species of the two previous recognized genera (*Dissochaeta* and *Macrolenes*) of the scrambling shrubs in the molecular phylogenetic analyses (Table 6-1; Kartonegoro et al. 2018, 2019). Our results strongly support monophyly of these scrambling shrubs lineage in all three analyses (clade D; Fig. 6-3B). Within this lineage, *Macrolenes* is monophyletic while *Dissochaeta* s.l. (sensu Kartonegoro et al. 2018) is paraphyletic. Two alternative taxonomic solutions are possible for the scrambling shrubs lineage. The first option would be to recognize a widely circumscribed and large *Dissochaeta* s.l. (including *Dalenia*, *Diplectria* and *Macrolenes*), which would be highly supported by molecular data but defined by only a single morphological character, the scrambling habit. The second option would be to recognize four genera (*Dalenia*, *Diplectria*, *Macrolenes* and *Dissochaeta*) which would each be supported by molecular data and by several diagnostic and good morphological characters. After careful consideration we chose the second option as the more stable and feasible one, and recognize four genera within the scrambling shrub lineage. Below, we discuss these four genera.

***Dalenia* (*Dissochaeta* sect. *Dalenia*). —** The genus *Dalenia* was proposed by Korthals (1844) and accepted by some authors (Cogniaux 1891; Bakhuizen van den Brink 1943; Nayar 1966). Baillon (1877) regarded it as a synonym of *Dissochaeta* because of the distinct calyptriform hypanthium, but treated it as a section, *Dissochaeta* sect. *Dalenia*. In the previous account by Nayar (1966), three species are recognized in this genus; *Dalenia pulchra* Korth. (=*Dissochaeta pulchra* (Korth.) J.F.Maxwell), *Dalenia beccariana* and *Dalenia furfuracea* Ridl. (both =*Dissochaeta pubescens*). *Dalenia beccariana* was sampled in our molecular phylogeny. This species are sister to *Dalenia glabra* (= *Dissochaeta glabra* Merr., type of *Dissochaeta* sect. *Disparistemones*) with which they formed a monophyletic clade (Clade G; PP=1/BS=97/PBS=77; Fig. 6-3B).

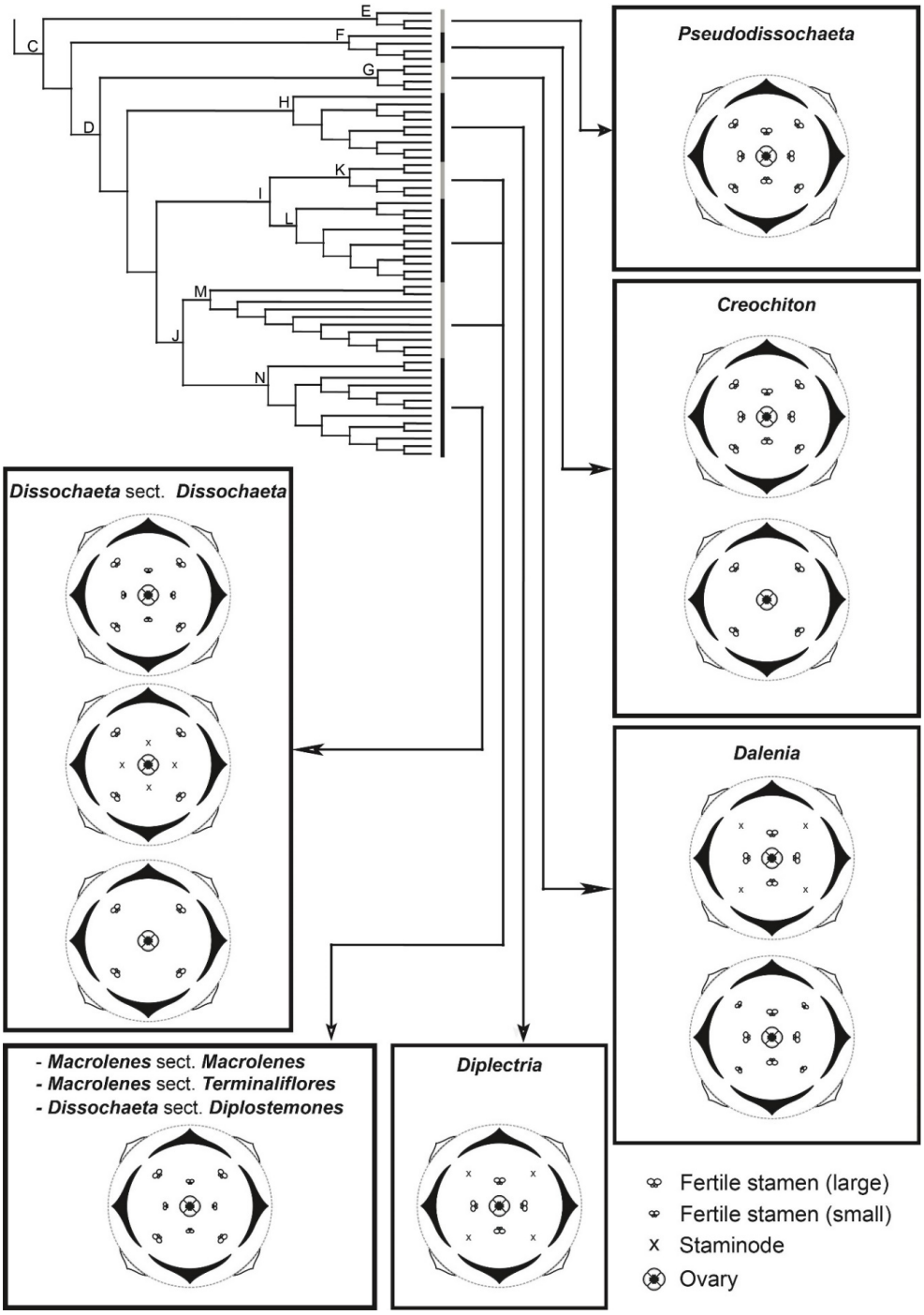


Fig. 6-4. Maximum likelihood (ML) phylogenetic cladogram of *Dissochaeta* alliance with an overview of floral characters including stamen dimorphism and anther fertility. Floral diagram drawn by A. Frenger.

Dalenia (clade G in Fig. 6-3B) can be morphologically distinguished by its interpetiolar growths (lobes, laminar, or pectinate crests) and leaf blade bases with a pair of glandular patches abaxially (Fig 6-5B-E). These interpetiolar growths are suggested to be helpful for climbing and stabilizing onto other plants (Clausing & Renner 2001a; Kartonegoro et al. 2018). The function of the foliar glandular patches in this group is still unknown (Maxwell 1984; Kartonegoro et al. 2018). Several field observations (AK, pers. obs.) indicate that the glands may attract insects like ants, which probably protect against herbivory. Staminal characteristics such as number and shapes of the fertile stamens seem to be variable in this lineage. All species have a fully truncate calyx and 4 well-developed oppositipetalous stamens (Figs. 6-1D–F, 6-4). Alternipetalous stamens vary considerably from forms with reduced and smaller thecae (⅓ of the oppositipetalous ones) to fully undeveloped thecae (staminodes) (Fig. 6-1F). Together with morphology, our molecular phylogenetic results support the reinstatement and expansion of the genus *Dalenia*.

Dissochaeta beccariana (=*Dalenia magnibracteata*) is included in this clade (Fig. 6-1D), even though it is morphologically intermediate between two genera, *Diplectria* and *Dissochaeta* s.str. (Kartonegoro et al. 2018). Although several species (including the type *Dalenia pulchra*; Fig. 6-1E) remain unsampled in a phylogenetic context, their morphology supports the placement in this expanded *Dalenia*. *Dissochaeta glandulosa* Merr., *Dissochaeta laevis* J.F.Maxwell, *Dissochaeta latifolia* (Triana) Karton., *Dissochaeta papuana* (Mansf.) Karton. and *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell will now be treated in *Dalenia*. *Dissochaeta* sect. *Disparistemones* (Merrill 1917) will be treated as a synonym of *Dalenia*. *Dalenia* will include nine species (see Taxonomic treatment) mainly distributed in Borneo, and one species in New Guinea.

***Diplectria* (*Dissochaeta* sect. *Diplectria*). —** *Diplectria* was first proposed as a section of *Dissochaeta* (Blume 1831a), a view adopted by several authors (Naudin 1851; Miquel 1855). Reichenbach (1841) raised it to the generic rank. The genus was also formerly known as *Anplectrum* (Triana 1872; Cogniaux 1891; Ridley 1922; Merrill 1923), and later considered a synonym of *Diplectria* (Bakhuizen van den Brink 1943; Veldkamp et al. 1979; Maxwell 1980, 1984; Renner 1993). *Diplectria* consists of ca. 11 species distributed in Southeast Asia from Myanmar to New Guinea (Veldkamp et al. 1979). Morphologically, all the species in this genus can be recognized by having tubular or cyathiform hypanthia and (as in *Dalenia*) truncate sepals without any tips (Figs. 6-1G–H, 6-5G). The genus can also be recognized by having a well-developed oppositipetalous stamens with rostrate, thick and oblong anthers, while the alternipetalous whorl is not developed or reduced to staminodes (Figs. 6-1G–H & 6-4; Veldkamp et al. 1979; Maxwell 1984).

Our molecular phylogenetic analyses included three species (with the type *Diplectria divaricata* (Willd.) G.Don) and one undescribed species. The results support monophyly of *Dissochaeta* sect. *Diplectria* (clade H; Fig. 6-3B; PP=1/BS=100/PBS=100). Both morphological and molecular phylogenetic evidence support the reinstatement of the genus *Diplectria* as was earlier suggested (Bakhuizen van den Brink 1943; Veldkamp et al. 1979; Maxwell 1980, 1984; Renner 1993), and it now consists of seven species (see Taxonomic Treatment). The subtribe Diplectrinae (Maxwell 1980, 1984) is not supported in this study, and the undeveloped outer whorl of stamens used to diagnose this subtribe is shared with some species of *Dalenia*.

***Macrolenes*. —** The genus *Macrolenes* comprises ca. 17 species, restricted to west Malesia and Southern Thailand (Kartonegoro et al. 2019). *Macrolenes* has the following diagnostic characters: axillary inflorescences consisting of few-flowered cymes, diplostemonous

flowers, robust hypanthia (more than 8 mm long; Kartonegoro et al. 2019), well-developed free calyx lobes, 8 subequal stamens in two whorls (alternipetalous and oppositipetalous) and all fertile (Figs. 6-1K–M, 6-4, 6-5I). Like some *Dissochaeta* species, the stamens of *Macrolenes* also have triangular or hastate dorsal and fimbriate ventral appendages (Bakhuizen van den Brink 1943; Nayar 1980; Kartonegoro et al. 2019). Unlike other allied genera, some species of *Macrolenes*, have hard berries, that are characterized by a persistent endocarp in which the ground tissue of the mesocarp and hypanthium is not fused and parts have a dense ring of sclereids in the ground tissue (Clausing et al. 2000; Kartonegoro et al. 2019). *Macrolenes* species also have a pair of hair cushion domatia near the abaxial leaf base (Fig. 6-5F).

Fig. 6-5. Some morphological characters of *Dissochaeta* alliance: **A-D.** Interpetiolar growth; **A,** ridges (*Dissochaeta annulata*); **B & C,** lobes (**B,** *Dalenia glabra*; **C,** *Dalenia pulchra*); **D,** pectinate (*Dalenia latifolia*); **E & F,** leaf domatia; **E,** glandular patches (*Dalenia glabra*); **F,** hair cushions (*Macrolenes pachygyna*); **G-I,** sepals; **G,** truncate (*Diplectria divaricata*); **H,** semi truncate (*Dissochaeta annulata*); **I,** free lobes (*Macrolenes nemorosa*). — Photographs by D.S. Penneys (A, B, E, G), J. Henrot (C), J.S. Wai (H), A. Kartonegoro (I). D taken from *Lobb s.n.*, F from *Carrick 1563* (both from Kew Herbarium)

We sampled 9 species of *Macrolenes* in our molecular phylogenetic analyses. The results (Fig. 6-3B) showed that *Macrolenes* is a well-supported monophyletic lineage (Clade L; Fig. 6-3B; PP=1/BS=95/PBS=87) and recovered as sister to the *Dissochaeta rostrata* complex

(Clade K; PP=0.99/BS=71/PBS=64). A recognition of *Macrolenes* at genus level would leave *Dissochaeta* paraphyletic. However, extending *Marcolenes* to include the *Dissochaeta rostrata* complex would create monophyletic, well-defined entities. Morphologically, the species of the *Dissochaeta rostrata* complex have terminal inflorescences (not axillary like the remaining *Macrolenes*), but share well-developed sepals, and the size of the hypanthia varies from small (less than 5 mm long) to robust (more than 9 mm long; Fig. 6-1I–J) of which the latter again resembles *Macrolenes*. Apart from these diagnostic features species of these two clades are morphologically similar. Based on our molecular phylogenetic results and morphology, we therefore suggest a broader circumscription of *Macrolenes* to include all the species in the *Dissochaeta rostrata* complex rather than recognize another distinct genus (Clade I; Fig. 6-3B). *Macrolenes*, as defined here, will include the five species of the *Dissochaeta rostrata* complex (clade L), and also another five species which are not included in the molecular analyses, that presumably are part of it based on morphological similarity of free sepals and 8 fertile stamens (*Dissochaeta alstonii* M.P.Nayar, *Dissochaeta atrobrunnea* G.Kadereit, *Dissochaeta floccosa* (J.F.Maxwell) Karton., *Dissochaeta johorensis* Furtado, and *Dissochaeta marumioides* Cogn.). The genus will include 27 species in total (see Taxonomic Treatment). Morphologically, *Macrolenes* has the following diagnostic characters: flowers with well developed free sepals and well developed curved 8 fertile stamens in 2 whorls (Figs. 6-4, 6-5I).

The *Dissochaeta rostrata* complex (clade K) and the *Macrolenes* s.str. clade (clade L) are also individually supported (Fig. 6-3B) and morphologically distinct. *Macrolenes* s.str. (clade L) has a pair of abaxial hair cushion domatia near the leaf base, axillary inflorescences and fimbriate filiform appendages on the connectives of the alternipetalous stamens. On the other hand, the *Dissochaeta rostrata* complex has terminal inflorescences, lacks the hair cushion domatia, and the alternipetalous stamens connectives usually have only biligulate or 4-ligulate appendages (Fig. 6-1I–J). We considered that the character differences between two groups are variability within the genus and not separation on the generic level. With additional evidence from the phylogenetic tree, we propose that *Macrolenes* s.str. and *Dissochaeta rostrata* complex be recognized as *Macrolenes* sect. *Macrolenes* and sect. *Terminaliflores*, respectively (see Taxonomic Treatment).

***Dissochaeta* s.str. —** *Dissochaeta* comprises ca. 40 species distributed from the Nicobar Islands, Myanmar, Indochina, Thailand, and throughout the Malesian Region (Maxwell 1984; Kartonegoro & Veldkamp 2010). The species can be identified by having conspicuous interpetiolar lines or crests (Fig. 6-5A), diplostemonous flowers, semi-truncate sepals with 4 small triangular tips (Fig. 6-5H), terminal inflorescences (except *Dissochaeta acmura* Stapf & M.L.Green and *Dissochaeta axillaris* Cogn., which have axillary inflorescences), and 8 unequal (dimorphic) stamens (Figs. 6-1N–T; Maxwell 1984; Kartonegoro & Veldkamp 2010; Kartonegoro et al. 2018). Similar to *Macrolenes*, the 4 alternipetalous stamens are larger and longer, they are known as the pollinating stamens, and the 4 oppositipetalous ones are smaller and shorter and known as the feeding stamens (Kadereit 2006, Kartonegoro & Veldkamp 2010; see Fig. 6-4). In a few species of *Dissochaeta* sect. *Dissochaeta* the oppositipetalous stamens are reduced to staminodes (<1/3 the size of the alternipetalous ones) or absent, with the flowers appearing to have only the 4 outer whorl stamens (Figs. 6-1Q–S, 6-4). Like in the other Dissochaeteae genera, the base of the stamens and the connective comes with an appendage. The appendages vary in shape and size, the dorsal appendage may be spur-like, triangular, hastate, or ligular, and the ventral one can be bisetose, bifid, or sometimes inappendiculate (Kartonegoro et al. 2018).

Our molecular analyses included 16 species of *Dissochaeta* s.str. (clade J), and some internal relationships were recovered (Fig. 6-3B). The clade contains all species of *Dissochaeta* sect. *Dissochaeta* and four other sections (*Diplostemones*, *Isostemones*, *Omphalopus*, *Anoplodissochaeta*) as well as the type of the genus, *Dissochaeta vacillans* (Blume) Blume (Cogniaux 1891; Maxwell 1980; Kartonegoro & Veldkamp 2010). To avoid the recognition of paraphyletic taxa (see under *Macrolenes*) and to classify into medium sized, well recognizable genera, the circumscription of *Dissochaeta* is narrower here than in previous treatments (see Taxonomic Treatment).

Within *Dissochaeta* s.str. lineage, two well-supported sublineages are evident in the phylogenetic analyses: *Dissochaeta* sect. *Diplostemones* (clade M; PP=1/BS=98/PBS=93) and *Dissochaeta* sect. *Dissochaeta* including three other sections (*Isostemones*, *Omphalopus*, and *Anoplodissochaeta*) (clade N; PP=1/BS=99/PBS=100). Although some other sections were recovered, they were poorly supported and nested within sect. *Dissochaeta*. As a result, we suggest the recognition of the two well-supported lineages as sections (sect. *Diplostemones* and sect. *Dissochaeta*) within *Dissochaeta* s.str.

Morphologically, *Dissochaeta* sect. *Diplostemones* can be distinguished by the robust hypanthia (6–15 mm long). The flowers have 8 slender (lanceolate-ligulate) dimorphic stamens of which the larger, alternipetalous ones are arcuate (Fig. 6-1N–O). The stamens of *Dissochaeta* sect. *Diplostemones* are similar to those of the *Dissochaeta rostrata* complex, which is now considered as part of *Macrolenes* but differ from the latter by having semi-truncate (not fully free) calyx lobes. *Dissochaeta* sect. *Dissochaeta* usually has much smaller hypanthia (2–5 mm long) and the stamens are ovate-oblong and erect (Fig. 6-1P–T). These erect stamens are unique to *Dissochaeta* within the Dissochaeteae. When there are 8 fertile stamens, they are usually subequal and dimorphic. Some species (e.g., *Dissochaeta gracilis* (Jack) Blume and *Dissochaeta inappendiculata* Blume) have the oppositipetalous stamens reduced to staminodes smaller in size (⅓ the size of the alternipetalous ones) (Fig. 6-1S). A few other species (e.g., *Dissochaeta biligulata* Korth., *Dissochaeta celebica* Blume, and *Dissochaeta fallax* (Jack) Blume) have the oppositipetalous stamens completely reduced and only 4 fertile alternipetalous stamens remain (Fig. 6-1Q–R). Most *Dissochaeta* species have ventrally biligulate or bisetose connective appendages, however, a few species (e.g., *Dissochaeta bakhuizenii* Veldkamp, *Dissochaeta fallax*, and *Dissochaeta inappendiculata*) are inappendiculate (Fig. 6-1S–T).

Conclusion

This study clarifies the circumscription of the tribe Dissochaeteae and the six monophyletic genera that it contains, namely; *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes*, and *Pseudodissochaeta*. The phylogenetic analyses presented here employed two nuclear ribosomal regions (ETS and ITS), and four chloroplast regions (*ndhF*, *psbK-psbL*, *rbcL*, and *rpl16*). Our results confirm earlier studies (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b) that the Dissochaeteae s.l. is polyphyletic and that more distantly related genera such as the *Medinilla* alliance, *Dinophora*, and *Ochthocharis* should be excluded. As defined here, *Dalenia* and *Diplectria* are resurrected, *Macrolenes* is broadened to include species formerly placed in the *Dissochaeta rostrata* complex, and the core genus of the tribe, *Dissochaeta*, is somewhat narrowed.

Taxonomic Treatment

Tribe **Dissochaeteae** Triana in Bull. Congr. Int. Bot. Hort. Amsterdam 1865: 459. 1866 ≡ [Tribe Miconieae subtribe] Dissochaetinae Naudin, Ann. Sci. Nat., Bot. sér. 3, 14: 67. 1850. – Type: *Dissochaeta* Blume

Shrubs, erect, terrestrial, epiphytic, scramblers, or woody climbers; adventitious roots common; branches terete, glabrous or with stellate hairs and sometimes with simple, soft bristles. Wood vessel elements wide, with alternate inter-vessel pit, rays up to 7 cells wide. Branchlets terete to quadrangular, glabrous or sparsely to densely covered with stellate hairs and sometimes with soft, simple bristles; nodes swollen, with or without a pair of interpetiolar growth lines, ridges, crests, lobes, these laminar or pectinate. Leaves opposite; petioles well-developed or subsessile, terete with a dorsal groove, glabrous or with stellate hairs or bristly; blade thin, chartaceous to coriaceous, ovate to lanceolate or rarely suborbiculate, base cuneate, rounded to slightly cordate, rarely oblique, margin entire, rarely serrulate, apex acuminate; midnerves with 1–3 pairs of basal nerves and a pair of intramarginal nerves; secondary venation pinnate, nerves typically sunken above, slightly raised below; surfaces glabrous to stellately furfuraceous or bristly, indumentum mainly dense on the main nerves, abaxially sometimes with a pair of glandular patches or hair cushion domatia at base. Inflorescences terminal or axillary panicle of cymes, thyrses, rarely umbels, multi- or few-flowered; main axis terete or quadrangular, indumentum similar to branchlets, branching with 2–5 ramifications, cymules 3-flowered at end of branches; bracts and bracteoles paired at each node of the ramifications, thin to subcoriaceous, caducous or persistent, sometimes bracteoles fleshy, enveloping the flower buds. Flowers 4-merous, haplotemonous or diplostemonous; pedicels terete or sometimes not developed. Hypanthium campanulate, tubular, cyathiform, or urceolate, glabrous or with stellate hairs, often with simple glandular or barbed bristles, infrequently tuberculate. sepals completely truncate, with 4 small undulations or teeth, sometimes semi-truncate with 4 triangular tips, or free with well-developed rounded, triangular, or linear lobes; persistent at maturity. Petals elliptic to suborbicular, tip acute to rounded, base clawed, glabrous, generally thin, colourful, reflexed or flat at maturity, caducous after fertilisation. Stamens 8, iso- or dimorphic, equal to unequal, inserted in 2 whorls, outer alternate with the petals, inner opposite with the petals, all fertile or 1 whorl staminodal, sometimes only with 4 stamens; filaments flattened, glabrous; anthers 2-thecate, basifixed, rarely medifixed, smooth, rarely tesselate-reticulate, opening by single terminal pore, straight in bud, inserted in extra-ovarial chambers, slightly curved (sickle- or S-shaped) or straight when mature, ovoid or narrow lanceolate; connective with appendages, dorsally with a spuriform, hastate, or triangular crest, ventrally with a pair of auriculate, ligular to filiform appendages or fimbriate, rarely inappendiculate. Ovary inferior, ¼ to ¾ as long as hypanthium, apex glabrous to pubescent or bristly; locules 4, placenta axillar, rarely basal; style glabrous, curved distally, usually herkogamous; stigma minute, capitate; ovary concrescent with hypanthium with 4 or 8 septae, forming 4 or 8, shallow to deep, extra-ovarial chambers. Fruit a berry, globose to urceolate, exocarp thin, rarely woody, glabrous or with stellate hairs, frequently with barbed bristle hairs, dark purple to blackish when ripe, fleshy; sepals persistent. Seeds numerous, usually cuneate or cochleate, flat-topped, slightly curved, with smooth or papillose testa, hilum black.

Distribution — East Bhutan, northeast India, Southern China (incl. Hainan), Southeast Asia to Papua New Guinea (except eastern part of the Lesser Sunda Islands). Mostly found in the Malesian Region, especially in the everwet triangle of Sumatra, Malay Peninsula and Borneo. Occurring from sea level to ca. 2,000 m elevation.

Key to genera

1 Erect or epiphytic shrubs; interpetiolar ridge indistinct; stamens 8, rarely 4; isomorphic, equal to subequal 2
1 Scrambling shrubs with climbing habit; interpetiolar ridge distinct; stamens 8 or 4; when 8 dimorphic, unequal 3
2 Erect terrestrial shrubs; leaf margin serrulate, lateral nerves basally triplinerved; inflorescences paniculate cymes, thyrsoid; flowers with inconspicuous bracteoles; connective appendages ventrally bi-auriculate or bilobed ..... **5. *Pseudodissochaeta***
2 Epiphytic shrubs; leaf margin entire, lateral nerves plinerved (side nerves starting above the base); inflorescences umbels; flowers with a pair of fleshy bracteoles; connective appendages ventrally biligulate or inappendiculate ..... **1. *Creochiton***
3 Interpetiolar growth with lobes, laminar, or pectinate; leaves abaxially with a pair of glandular patches at base ..... **2. *Dalenia***
3 Interpetiolar growth with lines or ridges; leaves abaxially without glandular patches at base 4
4 Calyx lobes free, distinct rounded, triangular or lanceolate in shape; apex acute or obtuse ..... **5. *Macrolenes***
4 Calyx lobes truncate or partly truncate; apex acute or absent 5
5 Calyx lobes fully truncate; alternipetalous stamens staminodal, oppositipetalous fertile .. .. **3. *Diplectria***
5 Calyx lobes partly truncate; alternipetalous stamens fertile, oppositipetalous fertile or staminodal or absent ..... **4. *Dissochaeta***

1. *Creochiton* Blume in Flora 14: 506. 1831 ≡ *Dissochaeta* sect. *Creochiton* (Blume) Baill., Hist. Pl. 7: 15. 1877 – Lectotype: (designated by Kartonegoro & Veldkamp in Blumea 58: 219. 2013): *Creochiton pudibundus* (Blume) Blume.

= *Enchosanthera* Guillaumin in Bull. Soc. Bot. France 60: 341. 1913 ≡ *Anplectrella* Furtado in Gard. Bull. Singapore 20: 106. 1963 – Type: E*nchosanthera anomala* (King & Stapf ex King) Guillaumin [≡ *Creochiton anomalus* (King & Stapf ex King) Veldkamp].

= *Eisocreochiton* Quisumb. & Merr. in Philipp. J. Sci. 37: 177. 1928 – Type: *Eisocreochiton bracteatus* Quisumb. & Merr. [≡ *Creochiton bracteatus* (Quisumb. & Merr.) Veldkamp].

Morphological diagnosis. – Epiphytic shrubs or woody climbers. Leaves subcoriaceous or chartaceous, nervation plinerved. Inflorescences axillary, umbellate, 3-5 flowers, haplo- or diplostemonous, rarely paniculate; bracteoles distinct, coriaceous, concave, enclosing the flower buds; flower with 4 or 8 fertile stamens, equal or unequal, connective dorsally spurred, ventrally biligulate or inappendiculate.

Creochiton anomalus (King & Stapf ex King) Veldkamp in Blumea 24: 438. 1979 ≡ *Anplectrum anomalum* King & Stapf ex King in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 69: 58. 1900 ≡ *Enchosanthera anomala* (King & Stapf ex King) Guillaumin in Bull. Soc. Bot. France 60: 341. 1913 ≡ *Anplectrella anomala* (King & Stapf ex King) Furtado in Gard. Bull. Singapore 20: 106. 1963 – Lectotype (designated by Veldkamp in Blumea 24: 438. 1979): Peninsular Malaysia, Perak, Goping, *King's collector 5779* (CAL; isolectotypes: K barcode K000859588!, K000859589!, K000859590!, L barcode L 0008838!, P barcode P02274804!, P02274805!).

Distribution. – Peninsular Malaysia & Sumatra.

Creochiton bibracteatus (Blume) Blume in Flora 14: 507. 1831 ≡ *Melastoma bibracteatum* Blume in Bijdr. Fl. Ned.-Ind 17: 1071. 1826 ≡ *Dissochaeta bibracteata* (Blume) Baill. in Hist. Pl. 7: 25. 1877 ≡ *Diplectria bibracteata* (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro & Veldkamp in Blumea 58: 221. 2013): Java, *Blume s.n.* (L barcode L0008839!; isolectotype: L barcode L0931127!).
Distribution. – Java (West).

Creochiton bracteatus (Quisumb. & Merr.) Veldkamp in Blumea 24: 438. 1979 ≡ *Eisocreochiton bracteatus* Quisumb. & Merr. in Philipp. J. Sci. 37: 177. 1928 – **Lectotype (designated here):** Philippines, Luzon, Nueva Vizcaya, Mt. Alzapan, *Ramos & Edaño BS 45610* (US barcode 00120440 [image!]; isolectotypes: BM barcode BM000944491!, BO!, K barcode K000859580!]).
Distribution. – Philippines (Luzon).
Note. – Kartonegoro & Veldkamp (2013) refered to the holotype of the species in PNH but said that the original collection was lost. Therefore, we selected the lectotype of the extant collection from other herbaria.

Creochiton brevibracteatus Mansf. in Bot. Jahrb. Syst. 60: 135. 1925 – Holotype: New Guinea, East Sepik, April River, main camp, *Ledermann 8660* (B†).
Distribution. – Papua New Guinea.
Note. –No other specimens could be assigned to this taxon and, therefore, no neotype could be selected (Kartonegoro & Veldkamp, 2013).

Creochiton dipterus Elmer in Leafl. Philipp. Bot. 4: 1192. 1911 – **Neotype (designated here):** Philippines, Mindanao, Agusan, Mount Urdaneta, *Elmer 14119* (K barcode K000859581!; isoneotypes: E barcode E00504432!, MO barcode MO-2196137 [No. 748099; image!], US barcode US02927693 [image!]).
Distribution. – Philippines.
Note. – Neither the original type collection of the species (*Elmer 9813*), nor any other associated specimens could be found in any herbaria, because they were probably destroyed during the Second World War when PNH burned down. We hereby designate another specimen (*Elmer 14119*), housed at K and cited by Elmer, as the neotype.

Creochiton furfuraceus (M.P.Nayar) Veldkamp in Blumea 24: 438. 1979 ≡ *Eisocreochiton furfuraceus* M.P.Nayar in J. Bombay. Nat. Hist. Soc. 67: 88. 1970 – Holotype: Borneo, Sarawak, 3rd Division, Kapit District, Belaga Subdistrict, Rejang River, *Jacobs 5293* (K barcode K000859586!; isotypes: CANB, G , L barcode L0008840!, S, SAR, US).
Distribution. – Borneo.

Creochiton ledermannii Mansf. in Bot. Jahrb. Syst. 60: 135. 1925 – Lectotype (designated by Kartonegoro & Veldkamp in Blume 58: 223. 2013): New Guinea, Sepik, Felsspitze, *Ledermann 12943* (B; isolectotype: L barcode L0931128!).
Distribution. – New Guinea.

Creochiton monticola (Ridl.) Veldkamp in Blumea 24: 433. 1979 ≡ *Anplectrum monticola* Ridl. in Kew Bull. 1: 31. 1946 ≡ *Eisocreochiton monticola* (Ridl.) M.P.Nayar in J. Bombay Nat. Hist. Soc. 67: 89. 1970 – Lectotype (designated here): Borneo, Sarawak, Mt. Benkayang, *Brooks 50* (K barcode K000859585!; isolectotype BO!).
Distribution. – Borneo.

Note. – Kartonegoro & Veldkamp (2013) did not select the lectotype of the species from the extant collections. Therefore, we selected one of the lectotypes of the extant collection from K ew herbarium (K).

Creochiton novoguineensis (Baker f.) Veldkamp & M.P.Nayar in Blumea 24: 438. 1979 ≡ *Dissochaeta novoguineensis* Baker f. in J. Bot. 61(Suppl.): 21. 1923 – Lectotype (designated by Veldkamp in Blumea 24: 438. 1979): New Guinea, Central District, Sogeri Region, Mt. Wori-Wori, *Forbes 708* (BM barcode BM000944490!; isolectotypes: BM barcode BM001190923!, E barcode E00288097!, K barcode K000859576!, L barcode L0008844!, L0008845!, L0008847!, P barcode P02274803 [image!]).
Distribution. – New Guinea.

Creochiton pudibundus (Blume) Blume in Flora 14: 506. 1831 ≡ *Melastoma pudibundum* Blume, Catalogus: 71. 1823 ≡ *Diplectria pudibunda* (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro & Veldkamp in Blumea 58: 225. 2013): Java, Mt. Salak, Cicalobak, *Blume s.n.* (L barcode L0008850!; isolectotypes: BO!, L barcodes L0537327!, L0008849!).
Distribution. – Java (West).

Creochiton roseus Merr. in Publ. Bur. Sci. Gov. Lab. 29: 32. 1905 – **Lectotype (designated here):** Philippines, Mindanao, Davao District, Todaya, *Copeland 1297* (US barcode US00120527 [image!]; isolectotypes K barcode K000859579!, NY barcode 00221643 [image!]).
Distribution. – N Sulawesi and Philippines (Mindanao).
Note. – Merill (1905) did not specify the holotype of this species, therefore, from among all extant syntype collections, we selected US specimen as the lectotype.

Creochiton turbinatus (J.F.Maxwell) Karton. in Blumea 58: 226. 2013 ≡ *Creochiton ledermannii* var. *turbinata* J.F.Maxwell in Gard. Bull. Singapore 33: 323. 1980 – Holotype: New Guinea, West Papua Province, E of Sorong, Warsamson Valley, Asbakin, *Schram BW 12260* (L barcode L0008841!; isotypes: A, BO!, BRI barcode BRI-AQ0060033 [image!], CANB, K, LAE, MAN).
Distribution. – New Guinea (West Papua).

2. *Dalenia* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 243. 1844 ≡ *Dissochaeta* sect. *Dalenia* (Korth.) Baill., Hist. Pl. 7: 51. 1877 – Type: *Dalenia pulchra* Korth.
= *Dissochaeta* sect. *Disparistemones* Merr. in J. Straits Branch Roy. Asiat. Soc. 76: 101. 1917 – Type: *Dissochaeta glabra* Merr. [≡ *Dalenia glabra* (Merr.) Karton.].

Morphological diagnosis. – Woody climbers with scrambling growth; nodes swollen with distinct interpetiolar growth, lobes, laminate or pectinate. Leaves at base with pair of glandular patches adaxially. Flowers diplostemonous, with cyathiform or tubular hypanthium, calyx lobes truncate with 4 shallow undulations. Stamens 8, unequal, alternipetalous smaller, fertile or reduced into staminodes, oppositipetalous larger, fertile.

Dalenia beccariana (Cogn.) M.P.Nayar in Kew Bull. 20: 157. 1966 ≡ *Anplectrum beccarianum* Cogn. In Candolle & Candolle, Monogr. Phan. 7: 568. 1891 ≡ *Diplectria beccariana* (Cogn.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 126. 2018): Borneo, Sarawak, *Beccari PB 809* (FI

barcode FI008755 [image!]; isolectoypes: BR barcode 000005188895 [image!], K barcode 000859574!, K000859575!).
Distribution. – Borneo.

Dalenia glabra (Merr.) Karton., **comb. nov.** ≡ *Dissochaeta glabra* Merr. in J. Straits Branch Roy. Asiat. Soc. 76: 101. 1917 ≡ *Diplectria glabra* (Merr.) M.P.Nayar in Blumea 24: 421. 1979 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 78. 2018): Borneo, Sabah, Kalabakan, Pinayas River, *Villamil 242* (PNH no. 32349 [image!]; isolectotypes: K!, US barcode US00120530 [image!]).
Distribution. – Borneo.

Dalenia glabra var. ***kinabaluensis*** (Veldkamp) Karton., **comb. nov.** ≡ *Diplectria glabra* ssp. *kinabaluensis* Veldkamp in Blumea 24: 422. 1979 ≡ *Diplectria glabra* var. *kinabaluensis* (Veldkamp) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 ≡ *Dissochaeta glabra* var. *kinabaluensis* (Veldkamp) Karton. in PhytoKeys 107: 81. 2018 – Holotype: Borneo, Sabah, Mount Kinabalu, Sosopodon near Kundasang, *Mikil SAN 46742* (L barcode L 0008869!; isotypes: K barcode K000859551!, L barcode L0008870!, SAN).
Distribution. – Borneo (Sabah).

Dalenia glandulosa (Merr.) Karton., **comb. nov.** ≡ *Dissochaeta glandulosa* Merr. in Univ. Calif. Publ. Bot. 15: 224. 1929 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 85. 2018): Borneo, Sabah, Sandakan, *Elmer 20259* (BO No. BO-1421691!; isolectotypes: BISH barcode BISH1003260 [image!], BM barcodes BM001190924!, BM001190925!, BR barcode 00000522241 [image!], BRI barcode BRI-AQ0023052 [image!], C barcode C10014564 [image!], CAS barcode 0033425 [image!], CM barcode 1527 [image!], F barcode V0063526F [No. 530617, image!], GH barcode 00072204, 00072205 [images!], HBG barcode HB-G514873 [image!], K barcode K000859503!, L barcode L0537261!, MICH barcode 1111782 [image!], NY barcode 00228564 [image!], PH barcode 00009602, 00009603 [images!], S No. S-G-2104 [image!], U barcode U0124130!).
Distribution. – Borneo.

Dalenia laevis (Ohwi ex J.F.Maxwell) Karton., **comb. nov.** ≡ *Dissochaeta laevis* Ohwi ex J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Holotype: Borneo, East Kalimantan, West Kutai, Long Petah, *Endert 3127* (L barcode L0537281!; isotypes: BO No. BO-1760872!, K barcode K000859490!).
Distribution. – Borneo.

Dalenia latifolia (Triana) Karton., **comb. nov.** ≡ *Anplectrum latifolium* Triana in Trans. Linn. Soc. London 28: 85, t. 7, f. 90d. 1872 ≡ *Diplectria latifolia* (Triana) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Dissochaeta latifolia* (Triana) Karton. in PhytoKeys 107 (2018) 105 – Lectotype (designated by Veldkamp et al. in Blumea 24: 412. 1979): Borneo, *Lobb s.n.* (K barcode K000859553!).
Distribution. – Borneo.

Dalenia magnibracteata (Bakh.f.) Karton., **comb. nov.** ≡ *Neodissochaeta magnibracteata* Bakh.f. in Contr. Melastom. 142. 1943 – Holotype: Borneo, West Kalimantan, Sungei Kenepai, *Hallier 2013* (L barcode L0537263!; isotypes BO Nos. BO-1865993!, BO-1865994!, BO-1865995!, K barcode K000859505!).

= *Dissochaeta beccariana* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 559. 1891 ≡ *Neodissochaeta beccariana* (Cogn.) M.P.Nayar in Kew Bull. 20: 159. 1966 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 45. 2018): Borneo, Sarawak, Santubong, *Beccari PB 2190* (FI barcode FI007928 [image!]; isolectotype: K barcode K000859504!).

Distribution. – Borneo.

Note. – The specific epithet *magnibracteata*, the first available heterotypic synonym, is used here for the new combination because the species name *Dalenia beccariana* already exists.

Dalenia papuana (Mansf.) Karton., **comb. nov.** ≡ *Anplectrum papuanum* Mansf. in Bot. Jahrb. Syst. 60: 115. 1925 ≡ *Diplectria papuana* (Mansf.) Bakh.f. in Contr. Melastom. 202. 1943 ≡ *Diplectria glabra* var. *papuana* (Mansf.) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 121. 2018): New Guinea, Papua Province, Siriwo River, *Janowsky 132* (L barcode L0008872!; isolectotype: BO No. BO-1865947!).

Distribution. – New Guinea (Indonesian Papua).

Dalenia pulchra Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: t. 58. 1842 ≡ *Dalenia speciosa* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 244. 1844 ≡ *Dalenia korthalsii* Blume, Mus. Bot. 1: 39. 1849 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 129. 2018): Borneo, Central Kalimantan, Tewe River, *Korthals s.n.* (L barcode L0537210!; isolectotypes: L barcodes L0537211!, L0729471!, L0729472!, L0729473!, P barcode P02274827 [image!]).

Distribution. – Borneo.

Dalenia sarawakensis (M.P.Nayar) Karton., **comb. nov.** ≡ *Neodissochaeta sarawakensis* M.P.Nayar in Bull. Bot. Surv. India 11: 195, pl. 1. 1969 ≡ *Dissochaeta sarawakensis* (M.P.Nayar) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Holotype: Borneo, Sarawak, Pengkulu Ampat, *Haviland 69* (K barcode K000859625!).

Distribution. – Borneo (Brunei & Sarawak).

3. *Diplectria* (Blume) Rchb., Deut. Bot. Herb.-Buch. 174. 1841 ≡ *Dissochaeta* Blume sect. *Diplectria* Blume in Flora 14: 501. 1831 – Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Diplectria cyanocarpa* (Blume) Kuntze [≡ *Diplectria divaricata* (Willd.) Kuntze].

= *Aplectrum* Blume in Flora 14: 502. 1831 ≡ *Anplectrum* A.Gray in U.S. Expl. Exped., Phan. 1: 597. 1854. ≡ *Backeria* Bakh.f., Contr. Melastom.: 130. 1943 – Lectotype (designated by Veldkamp et al. in Blumea 24: 410. 1979): *Aplectrum viminale* (Jack) Blume [≡ *Diplectria viminalis* (Jack) Kuntze].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with curved petiole, sometimes pubescent or bristly. Flowers diplostemonous, with cyathiform or tubular hypanthium, calyx lobes truncate with 4 small undulation tips. Stamens 8, unequal, alternipetalous reduced to staminodes, oppositipetalous larger, fertile.

Diplectria barbata (Triana ex C.B.Clarke) Franken & M.C.Roos in Blumea 24: 415, f. 3A. 1979 ≡ *Anplectrum barbatum* Triana ex C.B.Clarke in Hooker, Fl. Brit. India 2: 546. 1879 ≡ *Backeria barbata* (Triana ex C.B.Clarke) Raizada in Indian Forester 94: 435. 1968 ≡ *Dissochaeta barbata* (Triana ex C.B.Clarke) Karton. in PhytoKeys 107: 43. 2018 – Holotype: Burma, Martaban, Chappedong, *Wallich 4082* (K-W barcode K000859568!).
Distribution. – Myanmar, S China, Indochina, N Thailand.

Diplectria conica Bakh. f., Contr. Melastom. 202. 1943 ≡ *Dissochaeta conica* (Bakh.f.) Clausing in Santisuk & Larsen, Fl. Thailand 7: 423. 2001 – Holotype: Sumatra, West Sumatra Province, Agam, Brani, *Bünnemeijer 3094* (L barcode L0537295!; isotypes: BO Nos. BO-1865987!, BO-1865988!, L barcode L0537294!).
Distribution. – Peninsular Malaysia, Sumatra & Java.

Diplectria divaricata (Willd.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma divaricatum* Willd. in Sp. Pl. 2: 596. 1799 ≡ *Dissochaeta divaricata* (Willd.) G.Don in Gen. Hist. 2: 783. 1832 ≡ *Anplectrum divaricatum* (Willd.) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria divaricata* (Willd.) Raizada in Indian Forester 94: 435. 1968 – Lectotype (designated by Veldkamp et al. in Blumea 24: 417. 1979): India Orientali, *Klein 2 "8218" in Herb. Rottler* (B-W barcode B -W 08218-01 0 [image!]; isolectotypes C barcodes C10014562, C10014563 [images!], K barcode K000859557!, L barcode L0008867!).
Distribution. – From Myanmar to Papua New Guinea.

Diplectria maxwellii Karton. in Kew Bull. 73, 23: 1. 2018 ≡ *Dissochaeta maxwellii* (Karton.) Karton. in PhytoKeys 107: 114. 2018 – Holotype: Borneo, Sarawak, Kapit, batang Balleh, Nanga Serani, *Runi et al. S.63137* (K barcode K000566618!; isotypes: KEP barcode 43526 [image!], L 2D-code L.3908632!, SAN [images!], SAR).
Distribution. – Borneo (Sarawak).

Diplectria micrantha Veldkamp in Blumea 24: 422, f. 5B. 1979 ≡ *Diplectria glabra* var. *micrantha* (Veldkamp) J.F.Maxwell in Gard. Bull. Singapore 33: 313. 1980 ≡ *Dissochaeta micrantha* (Veldkamp) Karton. in PhytoKeys 107: 115. 2018 – Holotype: Borneo, Sabah, Mount Kinabalu, Sosopodon, *Sario SAN 28959* (L barcode L0008871!; isotypes: K barcode K000859550!, SAN).
Distribution. – Borneo.

Diplectria stipularis (Blume) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma stipulare* Blume in Bijdr. Fl. Ned.-Ind. 17: 1073. 1826 ≡ *Aplectrum stipulare* (Blume) Blume in Flora 14: 503. 1831 ≡ *Anplectrum stipulare* (Blume) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria stipularis* (Blume) Bakh.f. in Contr. Melastom. 132. 1943 ≡ *Dissochaeta stipularis* (Blume) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 431. 2001 – Lectotype (designated by Veldkamp & al. in Blumea 24: 424. 1979): Java, Gunung Seribu, *Blume 857* (L barcode L0537306!; isolectotypes L barcodes L0537304!, L0537305!, P barcode P02274923 [image!]).
Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Borneo and Philippines (Palawan).

Diplectria viminalis (Jack) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Melastoma viminale* Jack in Trans. Linn. Soc. London 14: 16. 1823 ≡ *Aplectrum viminale* (Jack) Blume in Flora

14: 502. 1831 ≡ *Anplectrum viminale* (Jack) Triana in Trans. Linn. Soc. London 28: 84. 1872 ≡ *Backeria viminale* (Jack) Bakh.f., Contr. Melastom. 133. 1943 ≡ *Dissochaeta viminalis* (Jack) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 433. 2001 – Neotype (designated by Veldkamp & al. in Blumea 24: 427. 1979): Java, West Java, Gunung Seribu, *Blume 856* (L barcode L0008883!; isoneotype L barcode L0008882!).
Distribution. – Thailand, Malay Peninsula, Sumatra, Java, Borneo and New Guinea.

4. *Dissochaeta* Blume in Flora 14: 492. 1831 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Dissochaeta vacillans* (Blume) Blume.
= *Omphalopus* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851 – Type (designated by Bakhuizen van den Brink in Contr. Melastom. 118. 1943): *Omphalopus fallax* (Jack) Naudin [≡*Dissochaeta fallax* (Jack) Blume].
= *Neodissochaeta* Bakh.f., Contr. Melastom.: 134. 1943 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Neodissochaeta gracilis* (Jack) Bakh.f. [≡*Dissochaeta gracilis* (Jack) Blume].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with straight petiole, glabrous, sometimes pubescent or bristly. Flowers haplo- or diplostemonous, with campanulate hypanthia, calyx lobes semi-truncate, united at base with 4 triangular tips. Stamens 4 or 8, unequal, alternipetalous larger, fertile, oppositipetalous smaller, reduced to staminodes or absent.

Dissochaeta sect. ***Diplostemones*** Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 555. 1891 – **Type (designated here):** *Dissochaeta annulata* Hook.f. ex Triana.

Morphological diagnosis. – Inflorescences terminal. Flowers diplostemonous. Hypanthium campanulate or urceolate, densely covered with stellate hairs, infrequently with sparse bristle hairs. Sepals truncate at base, tip triangular. Stamens 8, dimorphic, unequal or subequal; alternipetalous longer, sickle-shaped; oppositipetalous shorter, S-shaped; anthers curved; connective appendages dorsally triangular, ventrally biligulate.

Dissochaeta acmura Stapf & M.L.Green in Bull. Misc. Inform., Kew 1913: 42. 1913 – Lectotype (designated by Kartonegoro & al. in PhytoKeys 107: 27. 2018): Philippines, Luzon, Albay, *Cuming 2838* (K barcode K000859613!).
Distribution. – Philippines.

Dissochaeta annulata Hook.f. ex Triana in Trans. Linn. Soc. London 28: 83, t. 7, f. 89a. 1872 ≡ *Diplectria annulata* (Hook.f. ex Triana) Kuntze in Revis., Gen. Pl. 1: 246. 1891 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 32. 2018): Peninsular Malaysia, Penang, Penang Hill, *Griffith KD 2268* (K barcode K000859545!; isolectotype: K barcode K000859544!).
Distribution. – Sumatra, Malay Peninsula, Borneo.

Dissochaeta axillaris Cogn. in Bot. Jahrb. Syst. 48: 108. 1912 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 38. 2018): Borneo, Central Kalimantan, Semurung, Sungei Tarik, *Winkler 3033* (L barcode L0652534!; isolectotypes: BM barcode BM000944485!, BO!, BR barcode 000005188253 [image!], K barcode K000859508!, WRSL).
Distribution. – Borneo and Philippines (Sulu).

Dissochaeta bracteata (Jack) Blume in Flora 14: 495. 1831 ≡ *Melastoma bracteatum* Jack in Trans. Linn. Soc. London 14: 9. 1823 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 130. 2010): Peninsular Malaysia, Penang, *Wallich 4044* (K-W barcode K000859538!; isoneotypes: BM!, K-W barcode K000859537!).
Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines and Moluccas.

Dissochaeta griffithii (M.P.Nayar) Karton. in PhytoKeys 107: 91. 2018 ≡ *Macrolenes griffithii* M.P.Nayar in J. Jap. Bot. 55: 47. 1980 ≡ *Dissochaeta annulata* var. *griffithii* (M.P.Nayar) J.F.Maxwell in Gard. Bull. Singpore 33: 313. 1980 – Holotype: Peninsular Malaysia, Malacca, *Griffith KD 2269* (K barcode K001096571!).
Distribution. – Peninsular Malaysia.

Dissochaeta leprosa (Blume) Blume in Flora 14: 494. 1831 ≡ *Melastoma leprosum* Blume in Bijdr. Fl. Ned.-Ind. 17: 1068. 1826 ≡ *Omphalopus leprosus* (Blume) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 278. 1851 ≡ *Dissochaeta intermedia* var. *leprosa* (Blume) J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 107. 2018): Java, West Java, Mount Gede, *Kuhl & Van Hasselt s.n.* (L barcode L0008890!; isolectotypes: K barcode K000859492!, L barcodes L0822675!, L0822676!).
Distribution. – Sumatra (West), Java, Lesser Sunda Islands (Bali).

Dissochaeta malayana Furtado in Gard. Bull. Singapore 20: 110. 1963 ≡ *Dissochaeta rostrata* var. *malayana* (Furtado) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 – Holotype: Peninsular Malaysia, Terengganu, Kemaman, Bukit Kajang, *Corner SFN 30381* (SING barcode SING0051682!).
Distribution. – Peninsular Malaysia (Terengganu).

Dissochaeta nodosa Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 239. 1844 ≡ *Aplectrum nodosum* (Korth.) Blume in Mus. Bot. 1, 3: 37. 1849 ≡ *Anplectrum nodosum* (Korth.) Triana in Trans. Linn. Soc. London 28: 84. 1872 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Sumatra, West Sumatra, Indrapura, *Korthals s.n.* (L barcode L0537233!; isolectotype L barcode L0537232!).
Distribution. – Sumatra.

Dissochaeta pallida (Jack) Blume in Flora 14: 500. 1831 ≡ *Melastoma pallidum* Jack in Trans. Linn. Soc. London 14: 12. 1823 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 118. 2018): Peninsular Malaysia, Penang, *Jack 55* (BM barcode BM000944482!).
Distribution. – Malay Peninsula, Sumatra and Borneo.

Dissochaeta punctulata Hook. f. ex Triana in Trans. Linn. Soc. London 28: 83. 1872 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 132. 2018): Peninsular Malaysia, Malacca, *Griffith KD 2291* (K barcode K000859531!; isolectotype: BM!).
Distribution. – Malay Peninsula, Sumatra (Riau Archipelago).

Dissochaeta robinsonii Merr. in Philipp. J. Sci., C 11: 198. 1916 ≡ *Dissochaeta annulata* var. *robinsonii* (Merr.) Bakh. f., Contr. Melastom. 231. 1943 – Lectotype (designated by

Kartonegoro et al. in PhytoKeys 107: 32. 2018): Moluccas, Ambon, Hitumessen, *Robinson 2024* (BO No. BO-1747982!; isolectotypes: BM barcode BM000944486!, GH barcode GH00072242 [image!], K barcode K000859510!, L barcode L0537257!, NY barcode 00228565 [image!], P barcode P02274818 [image!], US barcode US00120532 [image!]).
Distribution. – SE Sulawesi, Moluccas, New Guinea.

Dissochaeta spectabilis J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Dissochaeta marumioides* Furtado in Gard. Bull. Singapore 20: 111. 1963, non Cogn. 1891 – Holotype: Peninsular Malaysia, Pahang, Cameron Highlands, Tanah Rata, *Johnston 86* (SING barcode SING0051582!).
Distribution. – Peninsular Malaysia (Pahang, Selangor), Sumatra (West).

Dissochaeta sect. ***Dissochaeta*** – Type: *Dissochaeta vacillans* (Blume) Blume.
= *Omphalopus* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851. ≡ *Dissochaeta* sect. *Omphalopus* (Naudin) Baill. in Hist. Pl. 7: 51. 1877 – Type: *Dissochaeta fallax* (Jack) Blume.
= *Dissochaeta* sect. *Anoplodissochaeta* Baill. in Hist. Pl. 7: 51. 1877 – Type: *Dissochaeta inappendiculata* Blume.
= *Dissochaeta* sect. *Isostemones* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 561. 1891 – Type (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 128. 2010): *Dissochaeta monticola* Blume [≡ *Dissochaeta intermedia* Blume].
= *Dissochaeta* sect. *Dissochaetopsis* Cogn. in A.DC. & C.DC, Monogr. Phan. 7: 563. 1891. – Type: *Dissochaeta schumannii* Cogn.

Morphological diagnosis. – Inflorescences terminal. Flowers haplo- or diplostemonous. Hypanthium campanulate, glabrous or densely covered with stellate hairs. Sepals truncate with 4 small triangular tips. Stamens 4 or 8, dimorphic, unequal; alternipetalous fertile; oppositipetalous, shorter, staminodal or absent; anthers straight; connective appendages dorsally triangular, ventrally biligulate or inappendiculate.

Dissochaeta angiensis Kaneh. & Hatus. ex Ohwi in Bot. Mag. (Tokyo) 57: 5. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 30. 2018): New Guinea, West Papua Province, Arfak Mts., Angi, track Lake Gita from Momi, *Kanehira & Hatusima 13374* (FU; isolectoype: L barcode L0537256!).
Distribution. – Moluccas, New Guinea.

Dissochaeta bakhuizenii Veldkamp in Blumea 24: 443. 1979 – Holotype: Sumatra, West Sumatra Province, Ophir District, Tanang Talu, *Bünnemeijer 1053* (L barcode L0537231!; isotype: BO No. BO-1744599!, BO-1747935!, PNH).
Distribution. – Peninsular Malaysia, Sumatra & Java.

Dissochaeta biligulata Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot.: 240. 1844 ≡ *Anplectrum biligulatum* (Korth.) Triana in Trans. Linn. Soc. London 28: 85. 1872 ≡ *Diplectria biligulata* (Korth.) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Neodissochaeta biligulata* (Korth.) Bakh.f., Contr. Melastom. 141. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 47. 2018): Sumatra, West Sumatra Province, Gunung Paauw, *Korthals s.n.* (L barcode L0537285!; isolectotype: L barcode L0537284!).
Distribution. – Myanmar, Nicobar Islands, Thailand, Indochina, Malay Peninsula, Sumatra, Borneo, and Philippines (Palawan).

Dissochaeta brassii (M.P.Nayar) Karton. in PhytoKeys 107: 55. 2018 ≡ *Neodissochaeta brassii* M.P.Nayar in Kew Bull. 20: 160. 1966 – Holotype: Papua New Guinea, Woodlark Island, Kulumadau, *Brass 28743* (K barcode K000859607!; isotype: L barcode L0537255!).
Distribution. – Papua New Guinea.

Dissochaeta celebica Blume in Mus. Bot. 1, 3: 36. 1849 ≡ *Neodissochaeta celebica* (Blume) Bakh.f. in Contr. Melastom. 141. 1943 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 57. 2018): Sulawesi, North Sulawesi, Tomohon, Mount Mahawu, *Forsten 305* (L barcode L0537287!; isolectotype: L barcode L0625953!).
Distribution. – Philippines (Mindanao), Sulawesi.

Dissochaeta celebica var. ***longilobata*** Karton. in PhytoKeys 107: 59. 2018 –Holotype: Sulawesi, Central Sulawesi, Mount Roreka Timbu, *van Balgooy 3205* (BO; isotypes: K, L barcode L0652533!).
Distribution. – Sulawesi (Central).

Dissochaeta cumingii Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 75. 1851 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 64. 2018): Philippines, Luzon, Albay Province, *Cuming 1344* (P barcode P02274812 [photo!]; isolectotypes: BM barcode BM001190926!, K barcodes K000859608!, K000859609!, L barcode L0537227!).
Distribution. – Philippines (Luzon).

Dissochaeta densiflora Ridl. in Kew Bull 1: 32. 1946 ≡ *Dissochaeta rostrata* var. *densiflora* (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 319. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 65. 2018): Borneo, Sarawak, Saribas, Sungei Plandok, *Haviland 1550* (K barcode K000859631!; isolectotype: SAR).
Distribution. – Borneo.

Dissochaeta fallax (Jack) Blume in Flora 14: 493. 1831 ≡ *Melastoma fallax* Jack in Trans. Linn. Soc. London 14: 13. 1823 ≡ *Omphalopus fallax* (Jack) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 277. 1851 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 132. 2010): Sumatra, Bengkulu, Ayer Angat, Gunung Kaba, *Forbes 2882a* (L barcode 0822678!; isoneotype: BM!).
Distribution. – Thailand, Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands (Bali & Lombok) and Papua New Guinea.

Dissochaeta fusca Blume in Flora 14: 497. 1831 ≡ *Neodissochaeta fusca* (Blume) Bakh. f., Contr. Melastom. 136. 1943 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Java, *Blume 1791* (L barcode L0729468!; isolectotypes: K barcode K000859621!, L barcode L0537244!, P barcode P05283572!).
Distribution. – Java, Lesser Sunda Islands (Sumbawa).

Dissochaeta glandiformis J.F.Maxwell in Gard. Bull. Singapore 33: 313, f. 1. 1980 – Holotype: Sumatra, Kerinci Region, Gunung Tujuh, *Meijer 7282* (L barcode L0537274!).
Distribution. – Sumatra (Kerinci Range).

Dissochaeta gracilis (Jack) Blume in Flora 14: 498. 1831 ≡ *Melastoma gracile* Jack in Trans. Linn. Soc. London 14: 14. 1823 ≡ *Neodissochaeta gracilis* (Jack) Bakh.f. in Contr. Melastom. 137. 1943 – Neotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 134. 2010): Sumatra, Bengkulu, Bukit Daun, Balai, *de Voogd 591* (L barcode L0822677!; isoneotype: BO!),
Distribution. – S Thailand, Malay Peninsula, Sumatra, Java, Borneo.

Dissochaeta inappendiculata Blume in Flora 14: 499. 1831 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 98. 2018): Java, *Blume s.n.* (L barcode L0537236!; isolectotypes: K barcode K000859623!, L barcode L0537235!, P barcode P05283569!).
Distribution. – Peninsular Malaysia, Sumatra, Java.

Dissochaeta intermedia Blume in Flora 14: 439. 1831 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 101. 2018): Java, West Java, Mount Pangrango, Gegerbentang, *Blume 539* (L barcode L0537299!; isolectotypes: K barcodes K000859493!, K000859494!, L barcodes L0537296!, L0537297!, L0537298!, P barcode P05283548!).
Distribution. – Java.

Dissocchaeta rectandra Karton. in PhytoKeys 107: 134. 2018 – Holotype: Peninsular Malaysia, Pahang, Fraser's Hill, *Carrick 1606* (L 2D-code L.2533494!; isotypes: K!, KLU, L 2D-code L.2533495!, SING).
Distribution. – Peninsular Malaysia.

Dissochaeta rubiginosa Stapf in J. Linn. Soc., Bot. 42: 79. 1914 – Holotype: Borneo, Sabah, Mount Kinabalu, Gurulau Spur, *Gibbs 3977* (K barcode K000859491!).
Distribution. – Borneo.

Dissochaeta sagittata Blume in Flora 14: 500. 1831 ≡ *Dissochaeta intermedia* var. *sagittata* (Blume) J.F.Maxwell in Gard. Bull. Singapore 33: 315. 1980 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 140. 2018): Java, Bantam, *Blume 11* (L barcode 0537226!; isolectotype: L barcode L0537228!).
Distribution. – Java.

Dissochaeta schumannii Cogn. in Schumann & Hollrung, Fl. Kais. Wilh. Land: 88. 1889 ≡ *Neodissochaeta schumannii* (Cogn.) M.P.Nayar in Kew Bull. 20: 160. 1966 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 143. 2018): New Guinea, East Sepik, Augusta River, *Hollrung 656* (BO No. BO-1747958!; isolectotypes: BR barcode 000005187904 [image!], K barcode K000859604!, L barcode L0537229!).
Distribution. – New Guinea.

Dissochaeta vacillans (Blume) Blume in Flora 14: 495. 1831 ≡ *Melastoma vacillans* Blume in Bijdr. Fl. Ned.-Ind. 17: 1074. 1826 ≡ *Neodissochaeta vacillans* (Blume) Bakh.f., Contr. Melastom. 144. 1943 – Lectotype (designated by Kartonegoro & Veldkamp in Reinwardtia 13: 143. 2010): Java, West Java, Bogor, Ciawi, *Reinwardt s.n.* (L barcode L0008894!; isolectotype: L barcode L0008895!).
Distribution. – Java.

5. *Macrolenes* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851 – Type: *Macrolenes annulata* (Vent.) Naudin.
= *Marumia* Blume in Flora 14: 503. 1831, non Reinw. (1828). – Type (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 192. 2019): *Marumia muscosa* (Blume) Blume [≡ *Macrolenes muscosa* (Blume) Bakh.f.].

Morphological diagnosis. – Woody climbers with scrambler growth; nodes swollen with indistinct interpetiolar growth, lines or ridges. Leaves with straight petiole, pubescent or bristly. Flowers diplostemonous, with campanulate or urceolate hypanthium, calyx lobes free with rounded, triangular or lanceolate shape, tips obtuse or acute. Stamens 8, unequal, alternipetalous larger, fertile, oppositipetalous smaller, fertile.

Macrolenes Naudin sect. ***Macrolenes*** – Type: *Macrolenes annulata* (Vent.) Naudin.

Morphological diagnosis. – Inflorescences axillary. Hypanthium campanulate or urceolate, densely covered with stellate hairs or simple bristle hairs or apically stellate bristle hairs, infrequently floccose. Calyx lobes rounded, triangular, apex acute, half as long as hypanthium length. Stamens dimorphic, unequal; anthers curved; alternipetalous longer, sickle-shaped, connective appendages dorsally triangular, ventrally fimbriate; oppositipetalous, shorter, S-shaped, connective appendages dorsally triangular, ventrally biligulate.

Macrolenes annulata (Vent.) Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 311. 1851 ≡ *Maieta annulata* Vent., Choix Pl. 32. 1803 ≡ *Huberia annulata* (Vent.) DC., Prodr. 3: 167. 1828 ≡ *Marumia annulata* (Vent.) Triana in Trans. Linn. Soc. London 28: 82. 1872 – Holotype: Java, *de Lahaye s.n. "2860"* (G-DC barcode G00341515 [image!]).
Distribution. – Sumatra and Java.

Macrolenes bipulvinata (Korth.) Bakh.f., Contr. Melastom. 218. 1943 ≡ *Dissochaeta bipulvinata* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844 ≡ *Marumia bipulvinata* (Korth.) Triana in Trans. Linn. Soc. London 28: 82. 1872 – Lectotype (designated by Bakhuizen van den Brink in Contr. Melastom. 218. 1943): Borneo, SE Borneo, G. Rantau, *Korthals s.n.* (L 2D-code L.2541989!; isolectotypes: BR barcode 00000519595!, P barcodes P05283656!, P05283657!).
Distribution. – Borneo (Kalimantan).

Macrolenes bruneiensis Karton. in Gard. Bull. Singapore 71: 200. 2019 – Holotype: Borneo, Brunei Darussalam, Belait District, Merangking-Buau Road, *Nangkat 246* (BO!; isotypes: BRUN!, K!, L!, SING barcode SING 0157809!).
Distribution. – Borneo (Brunei).

Macrolenes dimorpha (Craib) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia dimorpha* Craib in Bull. Misc. Inform. Kew 1930(7): 320. 1930 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 202. 2019): Thailand, Yala, Bannang Sata, *Kerr 7283* (K barcode K000859521!; isolectotypes: AAU [image!], BK barcode 257159 [image!], BM barcode BM000944449!, E barcode E00285930!).
Distribution. – S Thailand, Peninsular Malaysia, Sumatra.

Macrolenes echinulata (Naudin) Bakh.f., Contr. Melastom.: 209. 1943 ≡ *Marumia echinulata* Naudin in Ann. Sci. Nat., Bot. sér. 3, 15: 280. 1851 ≡ *Dissochaeta echinulata*

(Naudin) Clausing in Santisuk & Larsen, Fl. Thailand 7(3): 425. 2001 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 204. 2019): Singapore, *Gaudichaud-Beaupré 79* (P barcode P02274823 [image!]; isolectotypes: G barcode G00319903 [image!], P barcodes P P02274821, P02274822, P02274825, P02274826 [images!]).
Distribution. – Malay Peninsula, Sumatra.

Macrolenes esetosa (Craib) Karton. in Gard. Bull. Singapore 71: 208. 2019 ≡ *Marumia rhodocarpa* var. *esetosa* Craib, Fl. Siam. 10: 697. 1931 ≡ *Macrolenes echinulata* var. *esetosa* (Craib.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 208. 2019): Thailand, Narathiwat, Sungai Padi, *Bourke s.n.* (K barcode K000859518!; isolectotypes: BK barcode 257157 [image!].
Distribution. – Southern Thailand.

Macrolenes glabrata M.P.Nayar in J. Jap. Bot. 55: 48. 1980 – Holotype: Peninsular Malaysia, Selangor, Ulu Klang Ampang, *Millard 1756* (K!; isotype KLU).
Distribution. – Peninsular Malaysia (Selangor).

Macrolenes hirsuta (Cogn.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia hirsuta* Cogn. in A.DC. & C.DC., Monogr. Phan. 7: 553. 1891 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 210. 2019): Borneo, Kalimantan, Sintang, *Teijsmann HB 8658* (BO No. BO-1859504!; isolectotypes: BO Nos. BO-1859502!, BO-1859503!, FI barcode FI007927 [image!], U).
Distribution. – Borneo.

Macrolenes muscosa (Blume) Bakh.f., Contr. Melastom.: 211. 1943 ≡ *Melastoma muscosum* Blume in Bijdr. Fl. Ned.-Ind. 17: 1070. 1826 ≡ *Marumia muscosa* (Blume) Blume in Flora 14: 504. 1831 ≡ *Dissochaeta muscosa* (Blume) G.Kadereit in Mabb., Pl.-Book, ed. 4: 1101. 2017 – Lectotype (designated by Bakhuizen van den Brink in Contr, Melastom. 212. 1943): Java, *Blume s.n.* (L barcode L0008927!; isolectotypes: K barcodes K000867117!, K000867118!, M , MPU barcodes MPU-013522!, MPU-013523! P barcodes P05283626!, P05283627!, P05283629!).
Distribution. – Sumatra, Java.

Macrolenes neglecta M.P.Nayar in J. Jap. Bot. 55: 46. 1980 – Holotype: Sumatra, Kerinci, Sungei Kumbang, *Robinson & Kloss s.n.* (BM barcode BM000944488; isotype: K barcode K000867115!).
Distribution. – Sumatra (Kerinci Range).

Macrolenes nemorosa (Jack) Bakh.f., Contr. Melastom. 206. 1943 ≡ *Melastoma nemorosum* Jack in Trans. Linn. Soc. London 14: 8. 1823 ≡ *Marumia nemorosa* (Jack) Blume in Flora 14: 505. 1831 – Lectotype (designated by Nayar in J. Jap. Bot. 55: 50. 1980): Peninsular Malaysia, Penang, *Jack 51* (BM barcode BM000944447!).
Distribution. – S Thailand, Peninsular Malaysia, Sumatra and Borneo.

Macrolenes pachygyna (Korth.) M.P.Nayar in J. Jap. Bot. 55: 49. 1980 ≡ *Marumia pachygyna* Korth., Ver. Nat. Gesch. Bed. Bezitt., Bot. t. 59. 1842 ≡ *Dissochaeta pachygyna* (Korth.) I.M.Turner in Taxon 67(3): 628. 2018 – Lectotype (designated by Bakhuizen van

den Brink in Contr. Melastom. 217. 1943 & Turner in Taxon 67: 628. 2018): Borneo, Kalimantan, Kapuas-Barito, Tewe River, *Korthals s.n.* (L barcode L0008936!; isolectotypes K barcode K000867112!, L barcodes L0537218!, L0537219!, P barcodes P05283680! P05283682!, S No. S-G-3965!).
Distribution. – Sumatra, Borneo.

Macrolenes rufolanata (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 ≡ *Marumia rufolanata* Ridl. in Fl. Malay Penins. 5: 310. 1925 – Lectotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 227. 2019): Peninsular Malaysia, Pahang, Kuala Lipis, Ulu Chimeras, *Burkill & Haniff SFN 15661* (K barcode K000867119!; isolectotypes SING barcodes SING0052046!, SING0052047!).
Distribution. – Peninsular Malaysia.

Macrolenes stellulata (Jack) Bakh.f., Contr. Melastom.: 216. 1943 ≡ *Melastoma stellulatum* Jack in Trans. Linn. Soc. London 14: 6. 1823 ≡ *Marumia stellulata* (Jack) Blume in Flora 14: 503. 1831 – Neotype (designated by Kartonegoro et al. in Gard. Bull. Singapore 71: 228. 2019): Sumatra, Jambi, Harapan Rain Forest, Nawai River, *Deden et al. BOHK 239* (BO!; isoneotypes: K barcode K000812315!, KEP).
Distribution. – Peninsular Malaysia, Sumatra, Borneo.

Macrolenes subulata J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Holotype: Sumatra, Lampung, Mt. Tanggamus, *Jacobs 8028* (L barcode L0537194!; isotypes: BO No. BO-1865976!, K barcode K000867110!, KEP barcode 110313 [image!], SING barcode SING 0052049!).
Distribution. – Sumatra (Lampung).

Macrolenes tuberculata Karton. in Gard. Bull. Singapore 71: 232. 2019 Distribution. – Holotype: Sumatra, North Sumatra, Besitang, Sikundur, *de Wilde & de Wilde-Duyfjes 19573* (BO!; isotypes K barcode K001045168!, L!).
Distribution. – Sumatra (North).

Macrolenes veldkampii Karton. in Gard. Bull. Singapore 71: 236. 2019 – Holotype: Borneo, East Kalimantan, Long Iram, Maruwai, Block Lampunut, *Kessler et al. 2656* (BO!; isotypes: K barcode K000276099! , L barcode L0370302!, WAN).
Distribution. – Borneo.

Macrolenes sect. ***Terminaliflores*** Karton., **sect. nov.** – Type: *Macrolenes rostrata* (Korth.) Karton.

Morphological diagnosis. – Inflorescences terminal. Hypanthium campanulate or urceolate, densely covered with stellate hairs and simple bristle hairs, infrequently floccose. Calyx lobes rounded, triangular or linear lanceolate, apex acute, half to as long as hypanthium length. Stamens dimorphic, unequal or subequal; alternipetalous, longer, oppositipetalous, shorter; anthers curved, sickle-shaped; connective appendages dorsally triangular, ventrally biligulate.

Macrolenes alstonii (M.P.Nayar) Karton., **comb. nov.** ≡ *Dissochaeta alstonii* M.P.Nayar in Bull. Bot. Surv. India 11: 188. 1969 ≡ *Dissochaeta rostrata* var. *alstonii* (M.P.Nayar)

J.F.Maxwell in Gard. Bull. Singapore 33: 318. 1980 – Holotype: Sumatra, Tapanuli, between Sidikalang and Pongkolan, *Alston 14813* (BM barcode BM000944479!).
Distribution. – Sumatra (North).

Macrolenes atrobrunnea (G.Kadereit) Karton., **comb. nov.** ≡ *Dissochaeta atrobrunnea* G.Kadereit in Edinburgh J. Bot. 63: 4, f. 1. 2006 – Holotype: Borneo, Central Kalimantan, Barito Ulu, *Sidiyasa PBU 229* (E barcode E00225106!; isotypes: BO No. BO-0009659!, K barcode K001089634!, L 2D-code L.2542233!, WAN).
Distribution. – Borneo (Central Kalimantan).

Macrolenes floccosa (J.F.Maxwell), Karton., **comb. nov.** ≡ *Dissochaeta rostrata* var. *floccosa* J.F.Maxwell in Gard. Bull. Singapore 33: 319, f. 5. 1980 ≡ *Dissochaeta floccosa* (J.F.Maxwell) Karton. in PhytoKeys 107: 77. 2018 – Holotype: Sumatra, West Coast, Payakumbuh, Pakan Raba, *Maradjo 350* (L barcode L0537273!; isotypes: L barcode L0537271!, PNH No. 59964 [image!], SING barcode SING0051679!).
Distribution. – Sumatra (West).

Macrolenes hirsutoidea (Furtado) Karton., **comb. nov.** ≡ *Dissochaeta hirsutoidea* Furtado in Gard. Bull. Singapore 20: 109, f. 2C. 1963 — Holotype: Borneo, Sabah, Sandakan, Bettotan, *Boden-Kloss SFN 19156* (SING; isotypes: BO!, K barcode K000859626!).
Distribution. – Borneo.

Macrolenes horrida Bakh.f., Contr. Melastom. 208. 1943 ≡ *Dissochaeta rostrata* var. *horrida* (Bakh.f.) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 ≡ *Dissochaeta horrida* (Bakh.f.) Karton. in PhytoKeys 107: 95. 2018 – Holotype: Sumatra, West Coast, Agam, Brani, *Bünnemeijer 3200* (L barcode L0537276!; isotypes: BO Nos. BO-1751324!, BO-1751325!).
Distribution. – Sumatra (West).

Macrolenes johorensis (Furtado) Karton., **comb. nov.** ≡ *Dissochaeta johorensis* Furtado in Gard. Bull. Singapore 20: 110. 1963 – Holotype: Peninsular Malaysia, Johor, Gunong Panti, *Ridley 4185* (SING; isotypes: BM barcode BM000944478!, K barcode K000859526!).
Distribution. – Peninsular Malaysia (Johor), Sumatra (Riau Archipelago).

Macrolenes macrosepala (Stapf) Karton., **comb. nov.** ≡ *Dissochaeta macrosepala* Stapf in J. Linn. Soc., Bot. 42: 80. 1914 ≡ *Dissochaeta rostrata* var. *macrosepala* (Stapf) J.F.Maxwell in Gard. Bull. Singapore 33: 320. 1980 – Holotype: Borneo, Sabah, Mount Kinabalu, ridge above Bundu Tuhan, *Gibbs 3951* (K barcode K000859636!).
Distribution. – Borneo (Sabah).

Macrolenes marumioides (Cogn.) Karton., **comb. nov.** ≡ *Dissochaeta marumioides* Cogn. in Candolle & Candolle, Monogr. Phan. 7: 556. 1891 – Holotype: Sumatra, West Coast, Mount Singgalang, *Beccari s.n.* (FI barcode FI007931 [image!]).
Distribution. – Sumatra (West).

Macrolenes porphyrocarpa (Ridl.) Karton., **comb. nov.** ≡ *Dissochaeta porphyrocarpa* Ridl. in Kew Bull. 1: 32. 1946 ≡ *Dissochaeta rostrata* var. *porphyrocarpa* (Ridl.) J.F.Maxwell in Gard. Bull. Singapore 33: 321. 1980 – Lectotype (designated by Kartonegoro et al. in

PhytoKeys 107: 122. 2018): Borneo, Sarawak, Ulu Tawaran, *Haviland 1287* (K barcode K000859633!).
Distribution. – Borneo.

Macrolenes rostrata (Korth.) Karton., **comb. nov.** ≡ *Dissochaeta rostrata* Korth., Verh. Nat. Gesch. Ned. Bezitt., Bot. 239. 1844 ≡ *Anplectrum korthalsii* Triana in Trans. Linn. Soc. London 28: 85. 1872 – Lectotype (designated by Kartonegoro et al. in PhytoKeys 107: 136. 2018): Borneo, South Kalimantan, Mount Prarawin, *Korthals s.n.* (L barcode L0729470!; isolectotype: L barcode L0729469!).
Distribution. – Borneo.

6. *Pseudodissochaeta* M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 557. 1969 – Type: *Pseudodissochaeta assamica* (C.B.Clarke) M.P.Nayar.

Morphological diagnosis. – Erect or rarely spreading shrubs; nodes swollen with indistinct interpetiolar growth or lines. Leaves with straight petiole or subsessile, glabrous or rarely bristly; base oblique or asymmetric, few symmetric; margin serrulate. Flowers with campanulate or urceolate hypanthium, calyx lobes truncate with four tooth-like tips. Stamens 8, equal to subequal, fertile; connective appendages dorsally spurred, ventrally biauriculate or bilobed.

Pseudodissochaeta assamica (C.B.Clarke) M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 559. 1969 ≡ *Anplectrum assamicum* C.B.Clarke in Hook.f., Fl. Brit. India 2: 546. 1879 ≡ *Diplectria assamica* (C.B.Clarke) Kuntze in Revis. Gen. Pl. 1: 246. 1891 ≡ *Backeria assamica* (C.B.Clarke) Raizada in Indian Forester 94: 435. 1968 ≡ *Medinilla assamica* (C.B.Clarke) C.Chen in Acta Phytotax. Sin. 21: 419. 1983 – Lectotype (designated by Kartonegoro et al. in Phytotaxa 468: 165. 2020): India, Assam, Naga Hills, *Griffith 1445 (KD 2285)* (K barcode K000867403!; isotypes: K barcode K000867404!, L barcode L0009218!, M barcode M0137604 [image!]).
Distribution. – E Bhutan, NE India, N Myanmar.

Pseudodissochaeta lanceata M.P.Nayar in J. Bombay Nat. Hist. Soc. 65(3): 563. 1969 ≡ *Medinilla lanceata* (M.P.Nayar) C.Chen in Acta Phytotax. Sin. 21: 421. 1983 – Holotype: China, Hainan, Hong Ta, *Chinese collector 406* (K barcode K000867414!; isotype: K barcode K000867415!).
Distribution. – S China (Hainan, Yunnan), N Vietnam (Tonkin).

Pseudodissochaeta septentrionalis (W.W.Sm.) M.P. Nayar in J. Bombay Nat. Hist. Soc. 65(3): 565. 1969 ≡ *Oritrephes septentrionalis* W.W.Sm. in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 7: 69. 1911 ≡ *Medinilla septentrionalis* (W.W.Sm.) H.L.Li in J. Arnold Arbor. 25: 38. 1944 – Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65: 565. 1969): Burma, S. Shan, Kung Lung, *MacGregor 751* (E barcode E00288102 [image!]).
Distribution. – N Mynamar, S China, N Thailand, Indochina.

Pseudodissochaeta spirei (Guillaumin) Veldkamp & J.F.Maxwell in Gard. Bull. Singapore 33: 324. 1980 ≡ *Medinilla spirei* Guillaumin in Bull. Soc. Bot. France 68: 4. 1921 – Lectotype (designated by Veldkamp & Maxwell in Gard. Bull. Singapore 33: 324. 1980): Vietnam, Nghe An, Co Ba, *Chevalier 32408* (P barcode P00700366 [image!]; isolectotypes P barcodes P00700367, P00700368 [images!]).

Distribution. – S China, Vietnam.

Pseudodissochaeta subsessilis (Craib) M.P.Nayar in J. Bombay Nat. Hist. Soc. 65: 561. 1969 ≡ *Allomorphia subsessilis* Craib in Bull. Misc. Inform. Kew 1913: 69. 1913 ≡ *Medinilla subsessilis* M.P.Nayar ex P.H.Hô in Ill. Fl. Vietnam 2, 1: 114. 1992, non Merr., 1912 – Lectotype (designated by Nayar in J. Bombay Nat. Hist. Soc. 65: 561. 1969): Thailand, Chiang Mai, Doi Wao, *Kerr 2427* (K barcode K000867401!; isolectotypes: BM barcodes BM0009444536!, BM000944537!, E barcode E00288101 [image!], K barcode K000867402!).
Distribution. – N Thailand.

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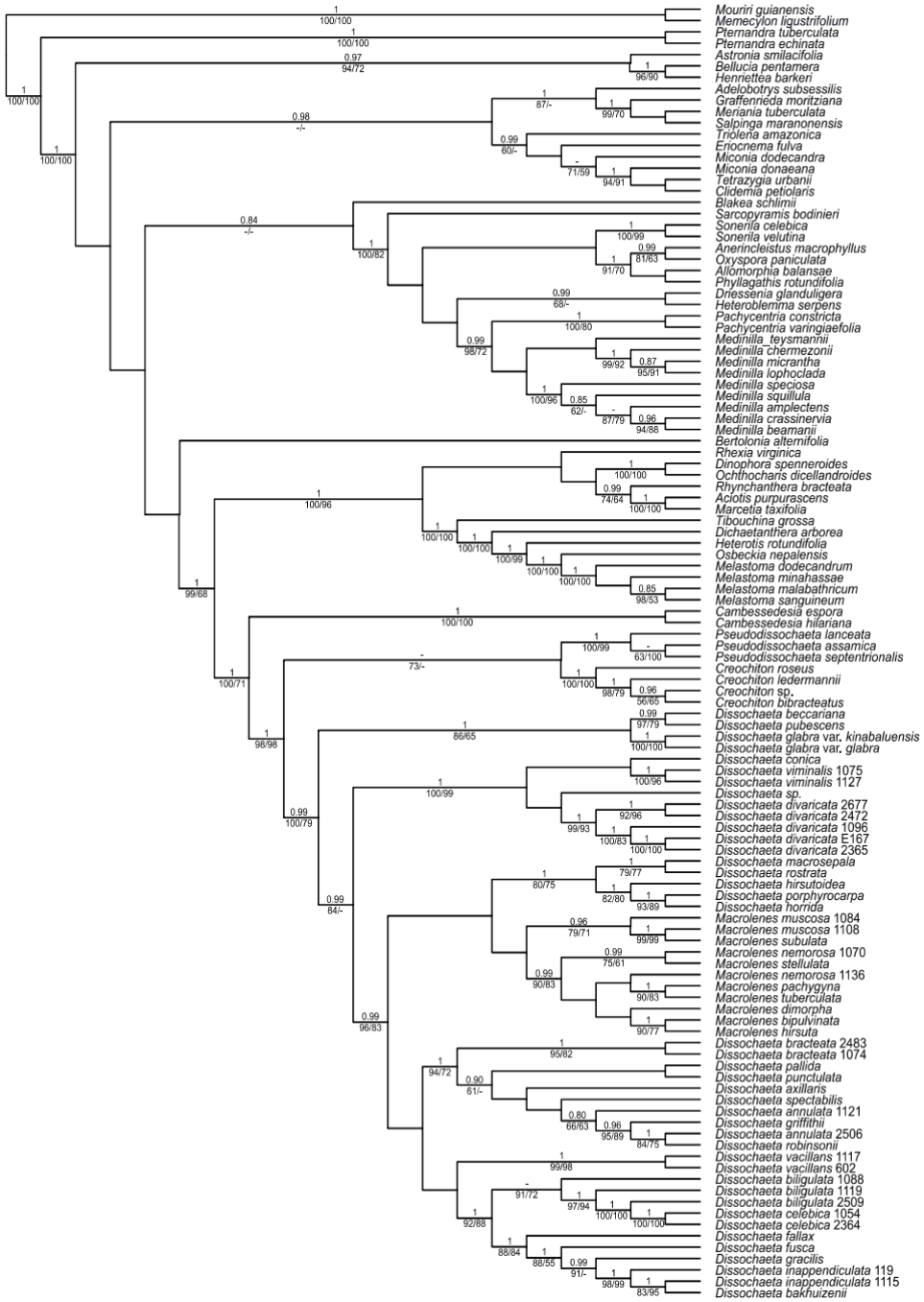
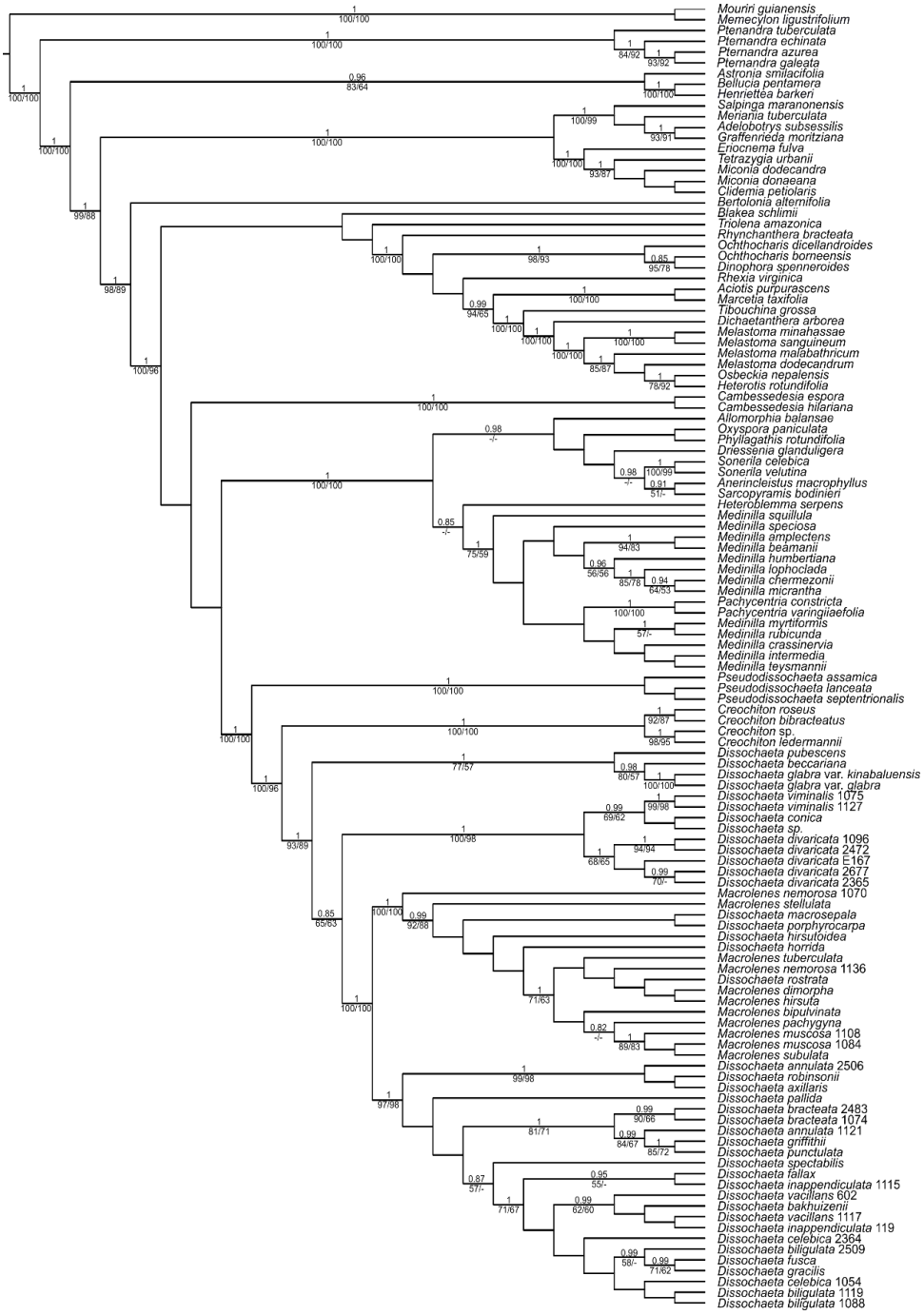
Suppl. 6-1. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae *s.l.* with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined nuclear data matrix (nrETS, nrITS). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values resulting from the ML analysis (only values ≥50) and bootstrap values resulting from the parsimony analysis (only values ≥50).



Suppl. 6-2. Maximum likelihood (ML) phylogenetic cladogram of Dissochaeteae *s.l.* with representatives of Asian, African and Madagascan Dissochaeteae, and outgroups derived from the combined chloroplast data matrix (*ndhF*, *psbk-psbL*, *rbcL*, *rpl16*). Values above branches refer to posterior probabilities resulting from Bayesian inference (only values ≥0.80), values below branches refer to bootstrap values resulting from the ML analysis (only values ≥50) and bootstrap values resulting from the parsimony analysis (only values ≥50).



Appendix 6-1. *Voucher information. Species name (following a new taxonomic treatment), synonym, country, region, collector and collector number, herbarium code if available. GenBank accessions numbers are given for all nrETS, nrITS, ndhF,* psbK-psbL, rbcL, rpl16 *sequences included in this study. Missing sequence data is indicated by a dash (–). DNA sequences newly generated for this study are marked with an asterisk (*).*

OUTGROUP: ***Aciotis purpurascens*** (Aubl.) Triana, Guyana, *F. Michelangeli 2454* (NY), KU500992, KU501055, AF215561, JQ730461, –, AF322231; ***Adelobotrys subsessilis*** Gleason, Peru, *F. Michelangeli 493* (BH), MH781591, AY966407, MH760283, MH781651, MH747567, AY966419; ***Allomorphia balansae*** Cogn., China, *Y. Liu 451* (SYS), –, MG644470, MK994792, MK994792, MK994792, MK994792; ***Anerincleistus macrophyllus*** Bakh.f., Malaysia, Borneo, *Y. Liu 673* (SYS), –, MN031184, MK994887, MK994887, MK994887, MK994887; ***Astronia smilacifolia*** Triana, Malaysia, Borneo, *Y. Liu 664* (SYS), –, EF683153, MK994883, MK994883, MK994883, MK994883; ***Bellucia pentamera*** Naudin, *D.S. Penneys 1868* (CAS), –, GU968788, AF215578, –, KF781624, AF215615; ***Bertolonia alternifolia*** Baumgratz, Amorim & A.B.Jardim, Brazil, *L.F. Bacci 375* (UEC), MH722270, MH708155, MH729204, MK296663, MH729221, MH722278; ***Blakea schlimii*** (Naudin) Triana, *F. Michelangeli 1227* (NY), –, AY460441, KX826821, KX826821, KX826821, KX826821; ***Cambessedesia espora*** Naudin, *P.J.F. Guimarães 397* (RB), MK165019, JQ730062, JQ899114, JQ730481, JQ899088, JQ899064; ***Cambessedesia hilariana*** DC., *P.J.F. Guimarães 405* (RB), MK165024, JQ730063, JQ899115, JQ730482, JQ899089, JQ899065; ***Clidemia petiolaris*** Triana, *M. Chase 2534* (K), KM893562, KF821452, AM235410, KF821882, AM235643, AM235446; ***Dichaetanthera arborea*** Baker, Madagascar, *A. Razanatsima 823* (MO), –, KX889222, AF272800, KY284742, –, AF294470; ***Driessenia glanduligera*** Stapf, Malaysia, Borneo, *Y. Liu 657* (SYS), –, MN031197, MK994879, MK994879, MK994879, MK994879 ; ***Eriocnema fulva*** Naudin, *F. Almeda 8416* (CAS), KF820735, MH743831, AY553781, MK296694, AY553777, AY553772; ***Graffenrieda moritziana*** Triana, *F. Michelangeli 832* (NY), KF820749, AY460451, EU055944, JQ730504, EU711390, JF832031; ***Henriettea barkeri*** (Urb. & Ekman) Alain, *G. Ionta 2029* (FLAS), –, KJ933957, KX826824, KX826824, KX826824, KX826824; ***Heterotis rotundifolia*** (Sm.) Jacq.-Fél., Dominica, *D.S. Penneys 1304* (FLAS), –, JQ730089, AF215565, –, U26323, AF270745; ***Marcetia taxifolia*** Triana, Venezuela, *F. Michelangeli 680* (BH), KU501041, JQ730102, GU968825**,** JQ730521, **–**, **–**; ***Melastoma dodecandrum*** Lour., China, –, MK292847, MH748092, MH748092, MH748092, MH748092; ***Melastoma malabathricum*** L., *D.S. Penneys 1998* (CAS), –, JQ730105, AF272810, JQ730524, AF270748, AB436376; ***Melastoma minahassae*** Karst.-Mey., Indonesia, Sulawesi, *A. Kartonegoro 1052* (BO), MW462395*, –, MW462472*, MW462324*, MW462634*, MW414599*; ***Melastoma sanguineum*** Sims, Indonesia, Sumatra, *A. Kartonegoro 1099* (BO), MW462396*, JQ730106, MW462473*, MW462325*, MW462635*, MW414600*; ***Memecylon ligustrifolium*** Champ. ex Benth., China, *Y. Liu 726* (SYS), –, KP093034, MK994913, MK994913, MK994913, MK994913; ***Meriania tuberculata*** Triana, Colombia, *P.P. Pedraza 2142* (NY), MH781647, MH819925, MH760361, MH781715, MH747639, –; ***Miconia dodecandra*** Cogn., *F. Michelangeli 758* (NY), KF821020, KF821600, KX826826, KX826826, KX826826, KX826826; ***Miconia donaeana*** Naudin, *F. Michelangeli 727* (NY), KF821024, KY782466, EU056028, KF822206, AM235648, AM235451; ***Mouriri guianensis*** Aubl., FJ792921, FJ792969, AF215575, –, AF215529, AF215610; ***Osbeckia nepalensis*** Hook., *D.S. Penneys 1986* (CAS), –, JQ730118, MH729215, JQ730539, KX527055, MH722991; ***Oxyspora paniculata*** DC., Vietnam, *Y. Liu 523* (SYS), –, MN031212, MK994819, MK994819, MK994819, MK994819; ***Phyllagathis rotundifolia*** (Jack) Blume, Malaysia, *Y. Liu M50* (SYS), –, MG644436, MK994912, MK994912, MK994912, MK994912; ***Pternandra azurea*** (Blume) Burkill, Indonesia, Sumatra, *A. Kartonegoro 1077* (BO), –, –, MW462477*, MW462329*, MW462639*, MW414604*; ***Pternandra echinata*** Jack, Malaysia, *I.J. Chen 542*, –, KF781604, AF215559, –, AF215520, AF270744; ***Pternandra galeata*** Ridl., Indonesia, Sumatra, *A. Kartonegoro 1057* (BO), –, –, MW462478*, MW462330*, MW462640*, MW414605*; ***Pternandra tuberculata*** (Korth.) M.P.Nayar (*Pternandra korthalsiana*), Malaysia, Borneo, *Y. Liu 651* (SYS), –, MW462551*, MK994877, MK994877, MK994877, MK994877; ***Rhexia virginica*** L., *F. Michelangeli 1448* (NY), KF462879, DQ985643, KX826830, KX826830, KX826830, KX826830; ***Rhynchanthera bracteata*** Triana, *F. Zenteno 8801* (NY), KF462880, JQ730137, KX826831, KX826831, KX826831, KX826831; ***Salpinga maranonensis*** Wurdack, *J.L. Clark 6979* (US), MF029372, KY991873, JF831982, MF104983, JF832008, JF832048; ***Sarcopyramis bodinieri*** H.Lév., China, *Y. Liu 502* (SYS), –, MN031206, MK994810, MK994810, MK994810, MK994810; ***Sonerila celebica*** Bakh.f. Indonesia, Sulawesi, *A. Kartonegoro 1027*, MW462398*, MW462552*, MW462479*, MW462331*, MW462641*, MW414606*; ***Sonerila velutina*** Cogn., Malaysia, Borneo, *Y. Liu 683* (SYS), –, MN031224, MK994892, MK994892, MK994892, MK994892; ***Tetrazygia urbanii*** Cogn., *L. Struwe 1166* (NY), KF821374, KF821772, AF270753, KF822547, AF215538, AF215619; ***Tibouchina grossa*** Cogn., *J.C. Zabala 1* (UPTC), KF462935, JQ730192, JF831983, JQ730612, JF832009, JF832050; ***Triolena amazonica*** (Pilg.) Wurdack, *R. Goldenberg 965* (NY), MK165055, –, JF831984, MK296700, NC_031890, JF832051. **— INGROUP:** ***Creochiton bibracteatus*** (Blume) Blume, Indonesia, Java, *A. Kartonegoro 1111* (BO), –, MW462480*, MW462399*, MW462242*, MW462553*, MW290997*; ***Creochiton ledermannii*** Mansf., Indonesia, Papua, *M. Mambrasar 81* (BO), –, MW462481*, MW462400*, MW462243*, MW462554*, MW290998*; ***Creochiton roseus*** Merr., Indonesia, Sulawesi, *A. Kartonegoro* 1051 (BO), MW462332*, MW462482*, MW462401*, MW462244*, MW462555*, MW290999*; ***Creochiton* sp.**, Indonesia, Sulawesi, *A. Kartonegoro 927* (BO), –, MW462483*,

MW462402*, MW462245*, MW462556*, MW291000*; ***Dalenia beccariana*** (Cogn.) M.P.Nayar (*Dissochaeta pubescens*), Brunei Darussalam, Temburong, *A. Kartonegoro 1118* (BO), –, MW462519*, MW462442*, MW462297*, MW462600*, MW295981*; ***Dalenia glabra*** Merr. var. ***glabra*** (*Dissochaeta glabra* var. *glabra*), Malaysia, Borneo, *D.S. Penneys 2446* (WNC), MW462354*, MW462506*, MW462429*, MW462273*, MW462586*, MW295982*; ***Dalenia glabra*** Merr. var. ***kinabaluensis*** (Veldkamp) Karton. (*Dissochaeta glabra* var. *kinabaluensis*), Malaysia, Borneo, *D.S. Penneys 2542* (WNC), MW462357*, MW462508*, MW462431*, MW462276*, MW462589*, MW295985*; ***Dalenia magnibracteata*** (Bakh.f.) Karton. (*Dissochaeta beccariana*), Malaysia, Borneo, *Y. Liu 676* (SYS), –, MG644477, MK994889, MK994889, MK994889, MK994889; ***Dinophora spenneroides*** Benth., Cameroon, *M.C. Veranso 107* (MJG), MF397951, KX889227, MF398047, KY284746, –, –; ***Diplectria conica*** Bakh.f. (*Dissochaeta conica*), Indonesia, Sumatra, *A. Kartonegoro 1101* (BO), MW462347*, MW462498*, MW462419*, MW462263*, MW462576*, MW414548*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Indonesia, Enggano, *Ardiyani et al. E167* (BO), MW462350*, MW462503*, MW462425*, MW462269*, MW462582*, MW414554*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Indonesia, Sumatra, *A. Kartonegoro 1096* (BO), MW462348*, MW462499*, MW462421*, MW462264*, MW462578*, MW414550*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Philippines, Mindanao, *D.S. Penneys 2365* (WNC), –, MW462500*, MW462422*, MW462266*, MW462579*, MW414551*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Malaysia, Borneo, *D.S. Penneys 2472* (WNC), MW462349*, MW462501*, MW462423*, MW462267*, MW462580*, MW414552*; ***Diplectria divaricata*** (Willd.) Kuntze (*Dissochaeta divaricata*), Thailand, Songkhla, *J.S. Wai 2677* (PSU), –, MW462502*, MW462424*, MW462268*, MW462581*, MW414553*; ***Diplectria* sp.**, Indonesia, Borneo, *A. Kartonegoro 1135* (BO), –, MW462524*, MW462447*, MW462295*, MW462606*, MW414573*; ***Diplectria viminalis*** (Jack) Kuntze (*Dissochaeta viminalis*), Indonesia, Sumatra, *A. Kartonegoro 1075* (BO), MW462377*, MW462528*, MW462451*, MW462299*, MW462610*, MW414577*; ***Diplectria viminalis*** (Jack) Kuntze (*Dissochaeta viminalis*), Indonesia, Borneo, *A. Kartonegoro 1127* (BO), MW462380*, MW462530*, MW462452*, MW462302*, MW462612*, MW414579*; ***Dissochaeta annulata*** Hook.f. ex Triana, Indonesia, Bintan, *A. Kartonegoro 1121* (BO), MW462333*, MW462485*, MW462404*, MW462247*, MW462559*, MW414532*; ***Dissochaeta annulata*** Hook.f. ex Triana, Malaysia, Borneo, *D.S. Penneys 2506* (WNC), MW462335*, MW462486*, MW462405*, MW462249*, MW462560*, MW414533*; ***Dissochaeta axillaris*** Cogn., Indonesia, Borneo, *A. Kartonegoro 1126* (BO), MW462336*, –, –, MW462250*, MW462561*, –; ***Dissochaeta bakhuizenii*** Veldkamp, Indonesia, Java, *A. Kartonegoro 1116* (BO), MW462339*, MW462488*, MW462408*, MW462253*, MW462564*, MW414536*; ***Dissochaeta biligulata*** Korth., Indonesia, Sumatra, *A. Kartonegoro 1088* (BO), MW462340*, MW462489*, MW462409*, MW462254*, MW462565*, MW414537*; ***Dissochaeta biligulata*** Korth., Indonesia, Bintan, *A. Kartonegoro 1119* (BO), MW462341*, MW462490*, MW462410*, MW462255*, MW462566*, MW414538*; ***Dissochaeta biligulata*** Korth., Malaysia, Borneo, *D.S. Penneys 2509* (WNC), MW462343*, MW462492*, MW462411*, MW462257*, MW462568*, MW414540*; ***Dissochaeta bracteata*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1074* (BO), MW462344*, MW462494*, MW462413*, MW462258*, MW462570*, MW414542*; ***Dissochaeta bracteata*** (Jack) Blume, Malaysia, Borneo, *D.S. Penneys 2483* (WNC), MW462345*, MW462495*, MW462414*, MW462259*, MW462571*, MW414543*; ***Dissochaeta celebica*** Blume, Indonesia, Sulawesi, *A. Kartoengoro 1054* (BO), –, MW462496*, MW462415*, MW462260*, MW462572*, MW414544*; ***Dissochaeta celebica*** Blume, Philippines, Mindanao, *D.S. Penneys 2364* (WNC), –, MW462497*, MW462417*, MW462261*, MW462574*, MW414546*; ***Dissochaeta fallax*** (Jack) Blume, Indonesia, Java, *A. Kartonegoro 1106* (BO), MW462351*, MW462504*, MW462426*, MW462270*, MW462583*, MW414555*; ***Dissochaeta fusca*** Blume, Indonesia, Java, *A. Kartonegoro 1105* (BO), MW462353*, MW462505*, MW462428*, MW462272*, MW462585*, MW414557*; ***Dissochaeta gracilis*** (Jack) Blume, Indonesia, Java, *A. Kartonegoro 1113* (BO), MW462358*, MW462509*, MW462432*, MW462277*, MW462590*, MW414558*; ***Dissochaeta griffithii*** (M.P.Nayar) Karton., Indonesia, Bintan, *A. Kartonegoro 1122* (BO), MW462359*, MW462510*, MW462433*, MW462278*, MW462591*, MW414559*; ***Dissochaeta inappendiculata*** Blume, Indonesia, Java, *A. Kartonegoro 1115* (BO), MW462364*, MW462515*, MW462438*, MW462283*, MW462596*, MW414564*; ***Dissochaeta inappendiculata*** Blume, Indonesia, Sumatra, *W. Santoso 119* (BO), MW462362*, MW462513*, MW462436*, MW462281*, MW462594*, MW414562*; ***Dissochaeta pallida*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1058* (BO), MW462366*, MW462517*, MW462440*, MW462285*, MW462598*, MW414566*; ***Dissochaeta punctulata*** Hook.f. ex Triana, Indonesia, Bintan, *A. Kartonegoro 1123* (BO), MW462369*, MW462520*, MW462443*, MW462289*, MW462601*, MW414568*; ***Dissochaeta robinsonii*** Merr., Indonesia, Moluccas, *Gushilman 382* (BO), MW462372*, MW462522*, MW462444*, MW462292*, MW462603*, MW414569*; ***Dissochaeta spectabilis*** J.F.Maxwell, Indonesia, Sumatra, *A. Kartonegoro 1100* (BO), MW462374*, MW462525*, MW462448*, MW462296*, MW462607*, MW414574*; ***Dissochaeta vacillans*** (Blume) Blume, Indonesia, Java, *Y. Liu 602* (SYS), –, MG644478, MK994856, MK994856, MK994856, MK994856; ***Dissochaeta vacillans*** (Blume) Blume, Indonesia, Java, *A. Kartonegoro 1117* (BO), MW462376*, MW462527*, MW462450*, MW462298*, MW462609*, MW414576*; ***Heteroblemma serpens*** (Stapf) Cámara-Leret, Ridd.-Num. & Veldkamp, Malaysia, Borneo, *Y. Liu 671* (SYS), –, MN031200, MK994886, MK994886, MK994886, MK994886; ***Macrolenes bipulvinata*** (Korth.) Bakh.f., Indonesia, Borneo, *A.*

Kartonegoro 781 (BO), –, MW462532*, MW462453*, MW462304*, MW462614*, MW414580*; ***Macrolenes dimorpha*** (Craib) J.F.Maxwell, Indonesia, Borneo, *A. Kartonegoro 1134* (BO), MW462382*, MW462533*, MW462454*, MW462305*, MW462615*, MW414581*; ***Macrolenes hirsuta*** (Cogn.) J.F.Maxwell, Indonesia, Borneo, *A. Kartonegoro 1139* (BO), MW462383*, MW462534*, MW462455*, MW462306*, MW462616*, MW414582*; ***Macrolenes hirsutoidea*** (Furtado) Karton. (*Dissochaeta hirsutoidea*), Indonesia, Borneo, *A. Kartonegoro 1141* (BO), MW462360*, MW462511*, MW462434*, MW462279*, MW462592*, MW414560*; ***Macrolenes horrida*** Bakh.f. (*Dissochaeta horrida*), Indonesia, Sumatra, *A. Kartonegoro 1073* (BO), MW462361*, MW462512*, MW462435*, MW462280*, MW462593*, MW414561*; ***Macrolenes macrosepala*** (Stapf) Karton. (*Dissochaeta macrosepala*), Malaysia, Borneo, *D.S. Penneys 2512* (WNC), MW462365*, MW462516*, MW462439*, MW462284*, MW462597*, MW414565*; ***Macrolenes muscosa*** (Blume) Bakh.f., Indonesia, Sumatra, *A. Kartonegoro 1084* (BO), MW462384*, MW462535*, MW462456*, MW462307*, MW462617*, MW414583*; ***Macrolenes muscosa*** (Blume) Bakh.f., Indonesia, Java, *A. Kartonegoro 1108* (BO), MW462386*, MW462537*, MW462458*, MW462308*, MW462619*, MW414585*; ***Macrolenes nemorosa*** (Jack) Bakh.f., Indonesia, Sumatra, *A. Kartonegoro 1070* (BO), –, MW462538*, MW462459*, MW462309*, MW462620*, MW414586*; ***Macrolenes nemorosa*** (Jack) Bakh.f., Indonesia, Borneo, *A. Kartonegoro 1136* (BO), MW462387*, MW462541*, MW462462*, MW462310*, MW462623*, MW414589*; ***Macrolenes pachygyna*** (Korth.) M.P.Nayar, Indonesia, Borneo, *A. Kartonegoro 777* (BO), MW462389*, MW462543*, MW462463*, MW462311*, MW462625*, MW414590*; ***Macrolenes porphyrocarpa*** (Ridl.) Karton. (*Dissochaeta porphyrocarpa*), Malaysia, Borneo, *D.S. Penneys 2486* (WNC), MW462367*, MW462518*, MW462441*, MW462286*, MW462599*, MW414567*; ***Macrolenes rostrata*** (Korth.) Karton. (*Dissochaeta rostrata*), Indonesia, Borneo, *R. Susanti 264* (BO), MW462373*, MW462523*, MW462445*, MW462293*, MW462604*, MW414570*; ***Macrolenes stellulata*** (Jack) Bakh.f., Indonesia, Borneo, *R. Susanti 297* (BO), MW462390*, MW462544*, MW462464*, MW462313*, MW462626*, MW414591*; ***Macrolenes subulata*** J.F.Maxwell, Indonesia, Sumatra, *Hughes et al. SUBOE71* (BO), MW462391*, MW462545*, MW462465*, MW462314*, MW462627*, MW414592*; ***Macrolenes tuberculata*** Karton., Indonesia, Borneo, *A. Kartonegoro 1128* (BO), MW462392*, MW462546*, MW462466*, MW462315*, MW462628*, MW414593*; ***Medinilla amplectens*** Regalado, Malaysia, Borneo, *Y. Liu 663* (SYS), –, MN031219, MK994882, MK994882, MK994882, MK994882; ***Medinilla beamanii*** Regalado, Malaysia, Borneo, *Y. Liu 658* (SYS), –, MN031220, MK994880, MK994880, MK994880, MK994880; ***Medinilla chermezonii*** H.Perrier, Madagascar, *Patrice 8570* (MO), MG518536, MG518548, MG702557, MG518563, –, –; ***Medinilla crassinervia*** Blume, Indonesia, Sulawesi, *A. Kartonegoro 1055* (BO), MW462393*, MW462547*, MW462467*, MW462316*, MW462629*, MW414594*; ***Medinilla humbertiana*** H.Perrier, –, –, AF215557, –, AF215517, AF215602; ***Medinilla intermedia*** Blume, Indonesia, Java, *A. Kartonegoro 1109* (BO), –, –, MW462468*, MW462318*, MW462630*, MW414595*; ***Medinilla lophoclada*** Baker, Madagascar, *J.A. Ramahenina 327* (MO), MG518537, –, MG702558, MG518564, –, –; ***Medinilla micrantha*** Jum. & H.Perrier, Madagascar, *J.A. Ramahenina 271* (MO), MG518538, –, MG702559, MG518565, –, –; ***Medinilla myrtiformis*** Triana, Indonesia, Sulawesi, *A. Kartonegoro 924* (BO), –, –, MW462469*, MW462319*, MW462631*, MW414596*; ***Medinilla rubicunda*** (Jack) Blume, Indonesia, Sumatra, *A. Kartonegoro 1072* (BO), –, –, MW462470*, MW462320*, MW462632*, MW414597*; ***Medinilla speciosa*** (Reinw. ex Blume) Blume, Malaysia, Borneo, *Y. Liu 669* (SYS), –, MN031221, MK994885, MK994885, MK994885, MK994885; ***Medinilla squillula*** Veldkamp, Indonesia, Moluccas, *P.P. Lowry II 7287* (MO), MG518539, MG518547, MG702560, MG518566, –, –; ***Medinilla teysmannii*** Miq., Indonesia, Sulawesi, *A. Kartonegoro 934* (BO), MW462394*, –, MW462471*, MW462322*, MW462633*, MW414598*; ***Ochthocharis borneensis*** Blume, Malaysia, Borneo, *Y. Liu 689* (SYS), –, –, MK994895, MK994895, MK994895, MK994895; ***Ochthocharis dicellandroides*** (Gilg) C.Hansen & Wickens, Gabon, *E. Bidault et al. 2116* (BRLU), MG518526, –, MG702562, MG518550, –, –; ***Pachycentria constricta*** (Blume) Blume, Indonesia, Sumatra, *A. Kartonegoro 1076* (BO), MW462397*, MW462548*, MW462474*, MW462326*, MW462636*, MW414601*; ***Pachycentria varingiaefolia*** (Blume) Blume, Indonesia, Sumatra, *S. Barber 76* (E), –, MW462549*, MW462475*, MW462327*, MW462637*, MW414602*; ***Pseudodissochaeta assamica*** (C.B.Clarke) M.P.Nayar (*Medinilla assamica*), China, *Y. Liu 590* (SYS), –, MG644480, MK994848, MK994848, MK994848, MK994848; ***Pseudodissochaeta lanceata*** M.P.Nayar (*Medinilla lanceata*), China, *Y. Liu 593* (SYS), –, MN031232, MK994850, MK994850, MK994850, MK994850; ***Pseudodissochaeta spetentrionalis*** (W.W.Sm.) M.P.Nayar (*Medinilla septentrionalis*), China, *Y. Liu 618* (SYS), –, MN031231, MK994778, MK994778, MK994778, MK994778.

CHAPTER 7

Historical Biogeography of the Southeast Asian and Malesian tribe Dissochaeteae (Melastomataceae)

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Historical Biogeography of the Southeast Asian and Malesian tribe Dissochaeteae (Melastomataceae)

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Abstract

The region of Tropical Southeast Asia and the Malay Archipelago is a very appealing area for research because of its outstanding biodiversity, being one of the most species-rich areas in the world with high levels of endemism, and because of its complex geological history. The high number of species in tribe Dissochaeteae (Melastomataceae) and their tendency to narrow endemism makes the tribe an ideal group for examining biogeographic patterns. We sampled 58 accessions spread over 42 accepted and two undescribed species of the Dissochaeteae. Two nuclear (ETS, ITS) and four chloroplast regions (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*) were used for divergence time estimation and ancestral area reconstruction. Results from the molecular dating analysis suggest that the diversity of Dissochaeteae in the Southeast Asian region resulted from a South American ancestor in the late Eocene. The ancestor of the Dissochaeteae might have migrated from South America to Southeast Asia via North America and then entered Eurasia over the North Atlantic land bridge during the Eocene. The origin and early diversification of the Dissochaeteae in Southeast Asia dates back to the middle Oligocene, and most of the genera originated during the Miocene. Indochina and Borneo are most likely the area of origin for the most recent common ancestor of the Dissochaeteae and for many of the early diverging clades of some genera within Southeast Asia.

Keywords

Ancestral area reconstruction, Dissochaeteae, divergence time estimation, historical biogeography, Malesia, Melastomataceae, shrubs, Southeast Asia, tropical rain forests.

Introduction

The region of Tropical Southeast Asia and the Malay Archipelago (Malesia) is a very appealing area for research because of its outstanding biodiversity, being one of the most species-rich areas in the world (Lohman et al. 2011; Grudinski et al. 2014; Atkins et al. 2020), with high levels of endemism, and a complex geological history (Hall 2002, 2009; Grudinski et al. 2014). The area harbours 20–25% of the world's vascular plants and is the meeting point of many biotas from various origins (Woodruff, 2010; van Welzen et al. 2011; Richardson et al. 2012; Zhou et al. 2019b). The vegetation of Southeast Asia has been influenced by the, still continuing, Asian–Australian collision, although the extensive forests of the western part were not substantially invaded by Australian elements (Richardson et al.

2012; De Bruyn et al. 2104). It contains the biodiversity hotspots of Indo-Burma, Sundaland, Wallacea, and Papuasia (Myers et al. 2000; Mittermeier et al. 2003; Brooks et al. 2006; Cannon et al. 2009). The Malesian region, as part of Southeast Asia, extends from the Malay Peninsula eastwards to Papua New Guinea (van Steenis 1950; Raes & van Welzen 2009) and contains an estimated 42,000 plant species of which 70% are endemic (Roos 1993; van Welzen et al. 2005). The high biodiversity is to a high extent the result of the very complex plate tectonic movements and resulting islands and orogenesis during the last 50 million years (Hall 2009; Woodruff 2010; De Bruyn et al. 2014; Atkins et al. 2020). Plant dispersals in Malesia have facilitated the floristic exchange between the continents of Asia and Australia (Crayn et al. 2015; Buerki et al. 2016; Thomas et al. 2017). However, the origins of the region's flora and its biogeographic patterns in this region are still incompletely understood and remain a focus for many botanists (Baker & Couvreur 2012; Richardson et al. 2012). The importance of linking biogeographical patterns to the phylogeny of different taxa lays in the fact that the current flora is the result of evolutionary events that are spread over geological time, and therefore differ among taxa, hampering any generalization.

Phytogeographically, Malesia can be separated into three main subregions, coinciding with three of the biodiversity hotspots: West Malesia or the Sunda Shelf, Wallacea, and east Malesia or the Sahul Shelf (New Guinea) (Raes & van Welzen 2009; van Welzen et al. 2011; Atkins et al. 2020). All areas (except Palawan and a few neighboring islands that rafted from China) originated at some time from the Australian part of Gondwana, whereby west Malesia and parts of Southeast Asia mainland, split off as various terranes, and arrived much earlier at their more or less present position than the Wallacean Islands and the Sahul Shelf. For the distribution patterns of recent groups, the Sunda Shelf is a part of Asia. The Philippines in Wallacea are an amalgamation of island arcs at the edge of the Philippine plate and areas colliding from the east (part of the outer Melanesian Arc) and west (Palawan and Culion) (Hall 2009). Borneo in the west and New Guinea in the east represent the two most important centres of plant species richness and endemism within Malesia (van Welzen et al. 2005; Su & Saunders 2009; De Bruyn et al. 2014; Atkins et al. 2020). The quarternary cycles of glacial and interglacial events together with related changes in the climate affected the sea levels, island connectivity, species occurrences and contractions and expansions in vegetation ranges (Woodruff 2010; van Welzen et al. 2011; Cannon 2012; Morley 2012). Several phylogenetic and biogeographical studies of Malesian plant taxa assumed the three main biogeographic origins of Malesian lineages: (1) Eurasia, with colonization via continental Southeast Asia, e.g. numerous taxa of boreotropical origin (Morley 2003; Li et al. 2017; Zhou et al. 2019; Atkins et al. 2020; Yu & van Welzen 2020) or via the mountain ranges of Taiwan Island and the Philippines (van Steenis 1964); (2) Gondwanan origin via the rafting Indian fragment into continental Southeast Asia (Thomas et al. 2012; Nauheimer et al. 2012) or via migration along the Arabian and south Asian coasts (Sirichamorn et al. 2014; Chen et al. 2019); (3) Australia, with colonization from the Australian continent (Barker et al. 2007; Morley 2003).

The tribe Dissochaeteae (Melastomataceae) comprises six genera and c. 90 species of shrubs, that inhabit the tropical lowland and lower to mid-montane rainforests in Southeast Asia, ranging from Bhutan, NE India, Myanmar, South China, Indochina, Thailand and throughout the Malesian Region (Kartonegoro et al. 2021). The centre of diversity of the group in Southeast Asia is in west Malesia (Malay Peninsula, Sumatra, Borneo) with more than 75% of all species (Maxwell 1984; Kartonegoro et al. 2018, 2019, 2020). Morphologically, the tribe contains shrubs with an erect habit (*Pseudodissochaeta* M.P.Nayar, 5 species), epiphytes or climbers (*Creochiton* Blume, 12 species) and woody scramblers or climbers

(*Dalenia* Korth., 9 species; *Diplectria* (Blume) Rchb., 7 species; *Dissochaeta* Blume, 30 species; *Macrolenes* Naudin, 17 species) (Kartonegoro et al. 2021). Other typical characters of this group are the swollen nodes with distinct interpetiolar lines or growth, thyrsoid inflorescences, 4-merous diplostemonous flowers with iso- or dimorphic stamens, and fleshy berries as fruits (Kartonegoro et al. 2021). The fruits of the species in the Dissochaeteae are likely dispersed by birds or small mammals, like in other Melastomataceae taxa with berries (Renner 2004b), but observations are lacking. Recent molecular phylogenetic studies revealed the monophyly of the tribe Dissochaeteae, from which some genera are excluded as they are part of the *Medinilla* alliance, closely related to the Sonerileae (Zeng et al. 2016; Zhou et al. 2019b; Kartonegoro et al. 2021).

Previous phylogenetic and biogeographical studies have focused on the diversification of the polyphyletic Dissochaeteae s.l., including the *Medinilla* alliance, which are not closely related to the *Dissochaeta* alliance (Renner et al. 2001a; Berger et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019b). The stem age of Dissochaeteae s.l. (including Sonerileae) was estimated to be 38 Ma (Berger et al. 2016), 39.63 Ma (Veranso-Libalah et al. 2018), or 34.78 Ma (Morley & Dick 2003), all in the same range with an expected origin in South America. Two alternative routes of dispersal of (the ancestors of) this large group from South America were hypothesized: (1) Long distance oceanic dispersal of the lineages to the Old World is possible via trans-Atlantic stepping stones during the late Oligocene (Veranso-Libalah et al. 2018); or (2) migration from South America to North America and then to Eurasia via the North Atlantic land bridge and a subsequential spread to SE Asia during the Eocene when the global temperature was still high (Zhou et al. 2019b). The basal clade of Dissochaeteae s.l./Sonerileae is estimated to have originated c. 17.31 Ma and diversified in Southeast Asia following the second scenario (Zhou et al. 2019b). However, the limited samples used in the previous studies are not suitable to accurately describe the biogeographical patterns, diversification rates and dispersal routes within the Dissochaeteae in Southeast Asia, particularly in the Malesian region. Here, we present a broad sampling of the Dissochaeteae from various localities across Southeast Asia that has been used to construct a well-resolved phylogenetic tree based on a combination of nuclear and chloroplast markers. We use these data to estimate divergence times, ancestral ranges, and biogeographical patterns in order to gain insights in the evolutionary history of Dissochaeteae.

Material and Methods

Taxon sampling, DNA sequencing and sequence alignment

A total of 58 accessions from 42 accepted and two undescribed species in the tribe Dissochaeteae were sampled, which is the same set as used for the phylogeny analysis of the group by Kartonegoro et al. (2021). Forty-four species (out of c. 90) and one variety of the tribe represent: *Creochiton* (12 spp. in total/3 species + 1 undescribed species sampled), *Dalenia* (9/3 species + 1 variety), *Diplectria* (7/3 species + 1 undescribed species sampled), *Dissochaeta* (30/16), *Macrolenes* (27/14), and *Pseudodissochaeta* (5/3). As outgroup, 99 species were selected from Astronieae (2), Bertolonieae (3), Blakeeae (3), Cambessedesieae (2), *Dinophora* alliance (3), Eriocnemeae (1), Henrietteeae (3), Kibessieae (6), Marcetieae (4), *Medinilla* alliance (16), Melastomateae (17), Merianieae (6), Miconieae (7), Microlicieae (1), Olisbeoideae (2), Oxysporeae (10), Rhexieae (3), Sonerileae (7) and Trioleneae (3). A complete list of the taxa sampled in this study, voucher information, and Genbank accession numbers are provided in Appendix 7-1.

Total genomic DNA was extracted and selected markers were sequenced and aligned as described in Kartonegoro et al. (2021). The selected markers consisted of two nuclear (ribosomal internal transcribed spacers [nrITS] and ribosomal external transcribed spacer [nrETS]) and four plastid loci (*ndhF*, *psbK-psbL*, *rbcL*, *rpl16*). Some of the sequences were downloaded from the nucleotide database of the National Centre for Biotechnology Information (http://www.ncbi.nlm.nih.gov).

Divergence time estimation

Four dating priors were utilized to estimate the divergence times, two secondary calibrations from a recent study of Myrtales (Berger et al. 2016) and Asian Sonerileae (Zhou et al. 2019b), and two fossils of Melastomataceae that were widely used in previous biogeographical studies of the family (Renner et al. 2001a; Morley & Dick 2003; Renner 2004a, 2004b; Veranso-Libalah et al. 2018; Zhou et al. 2019b). The Melastomataceae crown node (Fig. 7-1, point a) was calibrated using a secondary calibration to constrain the age estimate for the most recent common ancestor (MRCA) of Melastomataceae at 64.5 Ma (74.8–56.1 Ma; 95% HPD). The age of the Asian Sonerileae (Fig. 7-1, point c) was constrained at 20.25 Ma (15.71-25.24; 95% HPD). The Melastomatoideae (excluding Olisbeoideae and Kibessieae) crown node (Fig. 7-1, point b) was calibrated using the age of *Acrovenia laevis* Hickey, a fossilized leaf from the Eocene (c. 53 Ma) of northwestern North America (Hickey 1977). Another fossil calibration is from the Miocene, Rhexieae seed from Eurasia to constrain the crown node of Rhexieae (Fig. 7-1, point d) (26–23 Ma; Collinson & Pingen 1992). We selected a normal distribution prior for the secondary calibration with a standard deviation of 6.5 for the Melastomataceae and 3.5 for the Asian Sonerileae crown node, equivalent to the 95% estimated HPD (Berger et al. 2016; Zhou et al. 2109b). For fossil calibrations, we selected a lognormal distribution prior with a mean of 1.5 and standard deviation of 1, with the off-sets (minimum bounds) 53 for Melastomatoideae (point b) and 23 for Rhexieae (point d), allowing the possibility that these nodes are older than the fossils themselves (Sauquet 2013; Berger et al. 2016; Veranso-Libalah et al. 2018; Zhou et al. 2019b).

Bayesian divergence time estimation was performed using BEAST v.2.4.8 (Bouckaert et al. 2014) on the CIPRES Science Gateway 3.3 (https://www.phylo.org: Miller et al. 2010), with data partitioned per marker. The best-fitting models for each partition dataset were determined using the Akaike information criterion (AIC) model as incorporated in jModelTest v.2.1.6 (Darriba et al. 2012). Nucleotide substitution models of sequence evolution for each partition were GTR+I+Γ for ETS, ITS, *ndhF*, *rbcL* and GTR+Γ for *psbK-psbL*, *rpl16*. The input file was created by BEAUti v.2.6.2 (part of the BEAST package; Bouckaert et al. 2019). We used an uncorrelated lognormal relaxed molecular clock model (Drummond et al. 2006) and the Yule tree prior (Yule 1925; Gernhard 2008), although the birth–death model resulted in a similar topology and divergence times (not shown). Four independent Markov Chain Monte Carlo (MCMC) analyses were run, each of 200 million generations and sampling every 20,000 generations. Output log files were analysed using Tracer v.1.7.1 (Rambaut et al. 2018) to assess the degree of convergence and adequate effective sample sizes (ESS) for each parameter (> 200). As “burn-in”, 10% of the samples of each run were removed prior to combining the independent runs using LogCombiner v.2.6.2 (Bouckaert et al. 2019). The Maximum Clade Credibility (MCC) tree was generated using TreeAnnotator v.2.6.2 (Bouckaert et al. 2019), which was visualized with FigTree v.1.4 (Rambaut 2009).

Ancestral area reconstruction

Bayesian-based statistical dispersal–vicariance analysis (S-DIVA) for ancestral area reconstructions (Yu et al. 2010; based on DIVA by Ronquist 1996a, 1996b, 1997) and likelihood-based analyses under the statistical dispersal-extinction-cladogenesis (S-DEC) model (based on the method by Ree & Smith 2008), implemented in RASP v.3.02 (Reconstruct ancestral State in Phylogenies; Yu et al. 2015), were used to reconstruct ancestral areas at internal nodes. Prior dispersal constraints between the areas in four timeframes (S-DEC) were defined based on the geographical distances at the relevant time of Southeast Asia (Hall 2002, 2009) and is equal to the constraints used by Yu & van Welzen (2020, their table 2, see there). All analyses were based on the output trees and the MCC tree from the BEAST divergence time analyses. For both S-DIVA and S-DEC, the maximum number of ancestral areas at each node was constrained to two as ancestral ranges were assumed to be similar to the ranges of extant species. The MCC tree was pruned from the outgroups to include only the ingroup (Dissochaeteae) to avoid potential bias at the root. For species represented by multiple accessions all but one accession was pruned. The only exceptions are when multiple accessions, representing different morphological forms and different distribution area or islands, were included.

Each taxon was assigned presence in one or more biogeographical area(s) based on its extant distribution in nine geographic regions, based on a combination of geological information of Southeast Asia (Hall 2002, 2012; van Welzen et al. 2011), previous biogeographical studies (Nauheimer et al. 2012; Yu & van Welzen 2020; Atkins et al. 2020; Yu & van Welzen 2020), and current knowledge of species distributions and relationships in the Dissochaeteae (Maxwell 1984; Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019). The nine biogeographical areas are: A = East Bhutan, Northeast India and Northwest Myanmar; B = Indo-China (incl. Cambodia, Laos, Central to East Myanmar, South China, Hainan, Thailand and Vietnam); C = Southern Thailand and Malay Peninsula (incl. Riau Archipelago); D = Sumatra and its adjacent islands; E = Java and Lesser Sunda Islands; F = Borneo; G = Sulawesi; H = the Philippine Islands; I = Moluccas and New Guinea (incl. the Bismarck Archipelago). The distribution of sampled taxa based on biogeographical regions assigned above are shown in Table 7-1.

Table 7-1. Distribution of the sampled taxa. The abbreviations in the column 'distributions' refer to the biogeographical areas assigned in the ancestral area analyses.

Taxon	Distribution
***Creochiton bibracteatus* (Blume) Blume**	E
***Creochiton ledermannii* Mansf.**	I
***Creochiton roseus* Merr.**	GH
***Creochiton* sp. "Sulawesi"**	G
***Dalenia beccariana* (Cogn.) M.P.Nayar**	F
Dalenia glabra* (Merr.) Karton. var. *glabra	F
***Dalenia glabra* (Merr.) Karton. var. *kinabaluensis* (Veldkamp) Karton.**	F
***Dalenia magnibracteata* Karton.**	F
***Diplectria conica* Bakh.f.**	CD
***Diplectria divaricata* (Willd.) Kuntze "Borneo"**	F
***Diplectria divaricata* (Willd.) Kuntze "Enggano"**	D
***Diplectria divaricata* (Willd.) Kuntze "Mindanao"**	H
***Diplectria divaricata* (Willd.) Kuntze "Sumatra"**	D
***Diplectria divaricata* (Willd.) Kuntze "Thailand"**	C
***Diplectria viminalis* (Jack) Kuntze "Borneo"**	F
***Diplectria viminalis* (Jack) Kuntze "Sumatra"**	D
***Diplectria* sp. "Borneo"**	F
***Dissochaeta annulata* Hook.f. ex Triana "Bintan"**	C

***Dissochaeta annulata* Hook.f. ex Triana "Borneo"**	F
***Dissochaeta axillaris* Cogn.**	F
***Dissochaeta bakhuizenii* Veldkamp**	CDE
***Dissochaeta biligulata* Korth. "Bintan"**	C
***Dissochaeta biligulata* Korth. "Borneo"**	F
***Dissochaeta biligulata* Korth. "Sumatra"**	D
***Dissochaeta bracteata* (Jack) Blume "Borneo"**	F
***Dissochaeta bracteata* (Jack) Blume "Sumatra"**	D
***Dissochaeta celebica* Blume "Mindanao"**	H
***Dissochaeta celebica* Blume "Sulawesi"**	G
***Dissochaeta fallax* (Jack) Blume**	CDE
***Dissochaeta fusca* Blume**	E
***Dissochaeta gracilis* (Jack) Blume**	CDEF
***Dissochaeta griffithii* (M.P.Nayar) Karton.**	C
***Dissochaeta inappendiculata* Blume "Java"**	E
***Dissochaeta inappendiculata* Blume "Simeuleu"**	D
***Dissochaeta pallida* (Jack) Blume**	CD
***Dissochaeta punctulata* Hook.f. ex Triana**	C
***Dissochaeta robinsonii* Merr.**	GI
***Dissochaeta spectabilis* J.F.Maxwell**	CD
***Dissochaeta vacillans* (Blume) Blume**	E
***Macrolenes bipulvinata* (Korth.) Bakh.f.**	F
***Macrolenes dimorpha* (Craib) J.F.Maxwell**	C
***Macrolenes hirsuta* (Cogn.) J.F.Maxwell**	F
***Macrolenes hirsutoidea* (Furtado) Karton.**	F
***Macrolenes horrida* Bakhf.**	D
***Macrolenes macrosepala* (Stapf) Karton.**	F
***Macrolenes muscosa* (Blume) Blume "Java"**	E
***Macrolenes muscosa* (Blume) Blume "Sumatra"**	D
***Macrolenes nemorosa* (Jack) Bakh.f. "Borneo"**	F
***Macrolenes nemorosa* (Jack) Bakh.f. "Sumatra"**	D
***Macrolenes pachygyna* (Korth.) Bakh.f.**	F
***Macrolenes porphyrocarpa* (Ridl.) Karton.**	F
***Macrolenes rostrata* (Korth.) Karton.**	F
***Macrolenes stellulata* (Jack) Bakh.f.**	CDF
***Macrolenes subulata* J.F.Maxwell**	D
***Macrolenes tuberculata* Karton.**	D
***Pseudodissochaeta assamica* (C.B.Clarke) M.P.Nayar**	A
***Pseudodissochaeta lanceata* M.P.Nayar**	B
***Pseudodissochaeta septentrionalis* (W.W.Sm.) M.P.Nayar**	B

Results

Divergence time estimation

The Dissochaeteae was estimated to have diverged from its closest South American relative, the Cambessedesieae, in the late Eocene (Fig. 7-1, node A; stem age: 39.32 Ma; 95% HPD: 47.03–31.69 Ma). The origin and early diversification of the Dissochaeteae in Southeast Asia dates back to the middle Oligocene (crown age 25.58 [31.93–19.51] Ma), and most of the genera originated during the Miocene. The Beast MCC tree of the Dissochaeteae including the outgroup, as generated here (Fig. 7-1), has a similar topology as the MrBayes one resulting from phylogenetic analyses by Kartonegoro et al. (2021). The MCC chronogram for the Dissochaeteae crown group is shown as Fig. 7-2 (this figure also contains all node numbers referred to below). The Indo-Burmese *Pseudodissochaeta* (node 116) branched off first from the remaining Dissochaeteae (node 114) (Fig. 7-2). The crown node of *Pseudodissochaeta* is in the late Miocene (node 116; 7.76: 13.66–2.86 Ma). The age of this crown group as found by Zhou et al. (2019b: 6.38: 10.49–2.79 Ma) is within our HPD range. A short internode with unsatisfactory resolution was observed within *Pseudodissochaeta*

(node 113), indicating the onset of speciation in the early Pleistocene (5.78: 10.82–1.74 Ma) (Fig. 7-3; Table 7-2). Next, *Creochiton* (node 111) splits off (Fig. 7-3) and this genus diverges from the scrambling shrubs genera (node 108) around the late Oligocene at stem age 25.71 (32.52–19.45) Ma and a crown age of 10.72 (16.53–5.29) Ma. The group of the scrambling shrubs (*Dalenia*, *Diplectria*, *Dissochaeta* and *Macrolenes*) has a crown age of 21.37 (27.16–16.03) Ma (node 108). The *Dalenia* clade was the first of this group to diversify (node 107) at 14.32 (21.53–6.84) Ma, with subsequent speciation during the late Miocene until Pleistocene (Fig. 7-2). The ancestor of *Diplectria* (node 103) splits off next at 15.04 (19.93–10.59) Ma, followed by the core of of *Dissochaeta* and *Macrolenes* (node 95), which originated during the transition between the middle tot the late Miocene (14.37 [18.77–10.36] Ma), and diversified further in the late Miocene. *Macrolenes* (node 94) has as crown age 9.69 (13.12–5.59) Ma. The crown group of *Dissochaeta* (node 79) is from the late Miocene (11.75 [15.70–8.29] Ma). Summaries of divergence time estimates (mean ages and 95% HPD) and PP values of the Dissochaeteae stem node and all nodes within the Dissochaeteae crown group are presented in Table 7-2.

Table 7-2. Summary of the dated phylogeny and ancestral areas. Shown from left to right are node numbers of figure 2, posterior probabilities, mean ages of the stem age and 95% height of the posterior density intervals (HPD), mean ages of the crown age and 95% height of the posterior density intervals (HPD), most likely S-DEC reconstructions area and relative probability (RP), most parsimonious S-DIVA reconstructions area and marginal probability (MP) and remarks about the corresponding taxonomy. The abbreviations (A–H) indicate the areas.

Node	Posterior	Stem Age	95% HPD	Crown Age	95%HPD	S-DEC	RP	S-DIVA	MP
115	1	39.32	47.03–31.69	28.96	36.28–22.09	BF	0.22	BF	0.73
114	1	28.96	36.28–22.09	7.76	13.66–2.86	AB	0.61	B	0.65
113	0.77	7.76	13.66–2.86	5.78	10.82–1.74	AB	0.69	AB	1
112	1	28.96	36.28–22.09	25.71	32.52–19.45	F	0.31	FG	0.88
111	1	25.71	32.52–19.45	10.72	16.53–5.29	G	0.43	G	0.94
110	0.77	10.72	16.53–5.29	8.44	13.70–3.92	G	0.47	EG	1
109	1	8.44	13.70–3.92	3.66	6.97–1.00	GI	0.85	GI	1
108	1	25.71	32.52–19.45	21.37	27.16–16.03	F	0.58	F	0.91
107	1	21.37	27.16–16.03	14.32	21.53–6.84	F	0.95	F	1
106	0.98	14.32	21.53–6.84	10.07	17.48–3.44	F	1	F	1
105	1	14.32	21.53–6.84	1.72	3.65–0.31	F	1	F	1
104	1	21.37	27.16–16.03	19.3	24.59–14.29	F	0.41	F	0.94
103	1	19.30	24.59–14.29	15.04	19.93–10.59	D=DF	0.37	DF=CF	0.5
102	0.94	15.04	19.93–10.59	12.80	17.34–8.81	DF	0.43	F	0.94
101	0.94	12.80	17.34–8.81	9.21	13.55–5.05	F	0.5	F	0.91
100	1	9.21	13.55–5.05	3.57	6.53–1.15	DF	0.96	DF	1
99	1	12.80	17.34–8.81	9.15	13.09–5.57	DF	0.59	DF	0.91
98	1	9.15	13.09–5.57	5.57	9.26–2.08	CF	0.54	CF	1
97	1	9.15	13.09–5.57	5.71	9.20–2.62	D	0.82	D	1
96	1	5.71	9.20–2.62	1.21	2.55–0.21	DH	0.99	DH	1
95	1	19.30	24.59–14.29	14.37	18.77–10.36	DF	0.43	F	0.87
94	1	14.37	18.77–10.36	9.69	13.12–5.59	DF	0.76	DF	0.5
93	0.99	9.69	13.12–5.59	8.07	11.43–5.06	F	0.75	F	1
92	1	8.07	11.43–5.06	4.15	7.64–1.12	F	1	F	1
91	1	8.07	11.43–5.06	6.19	9.43–3.38	F	0.68	F	1
90	1	6.19	9.43–3.38	3.95	6.76–1.45	DF	0.75	DF	1
89	1	9.69	13.12–5.59	7.72	10.78–5.04	DF	0.63	D=DF	0.5
88	1	7.72	10.78–5.04	5.29	8.11–2.92	D	0.88	D	1
87	1	5.29	8.11–2.92	3.29	5.52–1.32	DE	0.72	DE	1
86	1	7.72	10.78–5.04	5.64	8.24–3.28	DF	0.79	DF	0.46
85	1	5.64	8.24–3.28	3.59	6.04–1.35	D	0.93	D	0.5
84	1	5.64	8.24–3.28	4.18	6.37–2.27	DF	0.51	F	0.65
83	1	4.18	6.37–2.27	2.36	4.10–0.82	F	1	F	1
82	0.29	4.18	6.37–2.27	3.65	5.67–1.78	F	0.49	F	1

81	0.27	3.65	5.67–1.78	3.24	5.44–1.19	F	0.63	F	1
80	1	3.65	5.67–1.78	1.77	3.40–0.41	DF	0.95	DF	1
79	1	14.37	18.77–10.36	11.75	15.70–8.29	D	0.64	EF=F	0.45
78	1	11.75	15.70–8.29	9.49	12.88–6.46	D	0.4	CF	0.96
77	1	9.49	12.88–6.46	4.72	8.25–1.51	DF	0.77	DF	1
76	0.87	9.49	12.88–6.46	8.42	11.53–5.50	CD	0.49	C	1
75	0.77	8.42	11.53–5.50	6.58	9.84–3.24	C	0.64	C	1
74	0.74	8.42	11.53–5.50	7.09	9.90–4.29	C	0.6	C	1
73	1	7.09	9.90–4.29	5.38	7.95–3.02	C	0.78	C	1
72	1	5.38	7.95–3.02	3.64	5.62–1.87	CF	0.84	CF	0.99
71	1	3.64	5.62–1.87	2.29	3.78–0.99	F	0.62	F	0.98
70	1	2.29	3.78–0.99	1.67	2.91–0.70	FG=FI	0.46	FG=FI	0.5
69	1	11.75	15.70–8.29	7.88	11.03–4.98	DE	0.53	E=EF	0.45
68	0.99	7.88	11.03–4.98	6.57	9.17–4.21	DE	0.37	DE	0.19
67	0.63	6.57	9.17–4.21	5.96	8.55–3.62	D	0.48	DG=DH =CD=DF	0.25
66	1	5.96	8.55–3.62	4.61	6.87–2.44	CF	0.16	CH=CF= CG	0.33
65	1	4.61	6.87–2.44	3.21	5.11–1.49	FG=FH	0.31	FH=FG	0.5
64	1	3.21	5.11–1.49	1.64	2.96–0.51	GH	0.9	GH	1
63	0.99	6.57	9.17–4.21	5.07	7.38–2.95	DE	0.36	E	0.82
62	0.99	5.07	7.38–2.95	3.72	5.70–2.01	DE	0.67	E	0.86
61	1	3.72	5.70–2.01	2.13	3.98–0.53	E	1	E	0.82
60	1	3.72	5.70–2.01	1.99	3.36–0.82	DE	0.98	DE	1
59	1	1.99	3.36–0.82	0.63	1.34–0.10	E	0.84	E	0.82

Ancestral area reconstruction

The most probable ancestral area of the Dissochaeteae (Fig. 7-3A, Table 2, node 115) was inferred to be Indo-China and Borneo (area BF) in both the S-DEC and S-DIVA analyses (Relative Probability, RP = 0.22, Marginal Probability, MP = 0.73, respectively). This was followed by ongoing dispersal and vicariance events within the crown Dissochaeteae (clade of node 115; areas BF) into Indo-Burma (the *Pseudodissochaeta* clade, areas AB; node 114) and Borneo (area F; node 112, ancestral node for the other four genera). *Pseudodissochaeta* (crown node 114, Fig. 7-3A) diverged first on mainland Southeast Asia (area AB; RP = 0.61, MP = 0.65) and speciated within Southeast Asia mainland. The other genera of the alliance then speciated on Borneo (F) or dispersed to other Malesian areas with subsequent speciation. *Creochiton* (node 111) diverged and originated on Sulawesi (area G; RP = 0.43, MP = 0.94) and dispersed and speciated within or northwards to the Philippines, westwards to Java and eastwards to New Guinea. Borneo (area F) was estimated to be the most probable ancestral area of the scrambling taxa (node 108, Fig. 7-3A, RP= 0.58, S-DIVA MP= 0.91), from there, via dispersal and speciation and/or vicariance events the group spread over the adjacent islands of Malay Peninsula, Sumatra, Java or eastwards into Sulawesi, the Philippines, the Moluccas and New Guinea. *Dalenia* diverged and originated in Borneo (area F; RP = 0.95, MP = 1.0), followed by *Diplectria* with two possibilities as ancestral areas, Sumatra (D) or Sumatra-Borneo (DF) based on S-DEC (RP= 0.37) and Sumatra-Borneo (DF) or Malay Peninsula-Borneo (CF) based on S-DIVA (MP= 0.50). *Macrolenes* has as ancestral area Sumatra-Borneo (Fig. 7-3B, area DF; RP= 0.76, MP= 0.5) and *Dissochaeta* Sumatra (D) based on S-DEC (RP= 0.64) and Java-Borneo (EF) or Borneo (F) based on S-DIVA (P= 0.45) (Fig. 7-3B). Summaries of ancestral ranges and their relative probabilities of clades within the Dissochaeteae are given in Table 7-2 and Fig. 7-3A & 7-3B.

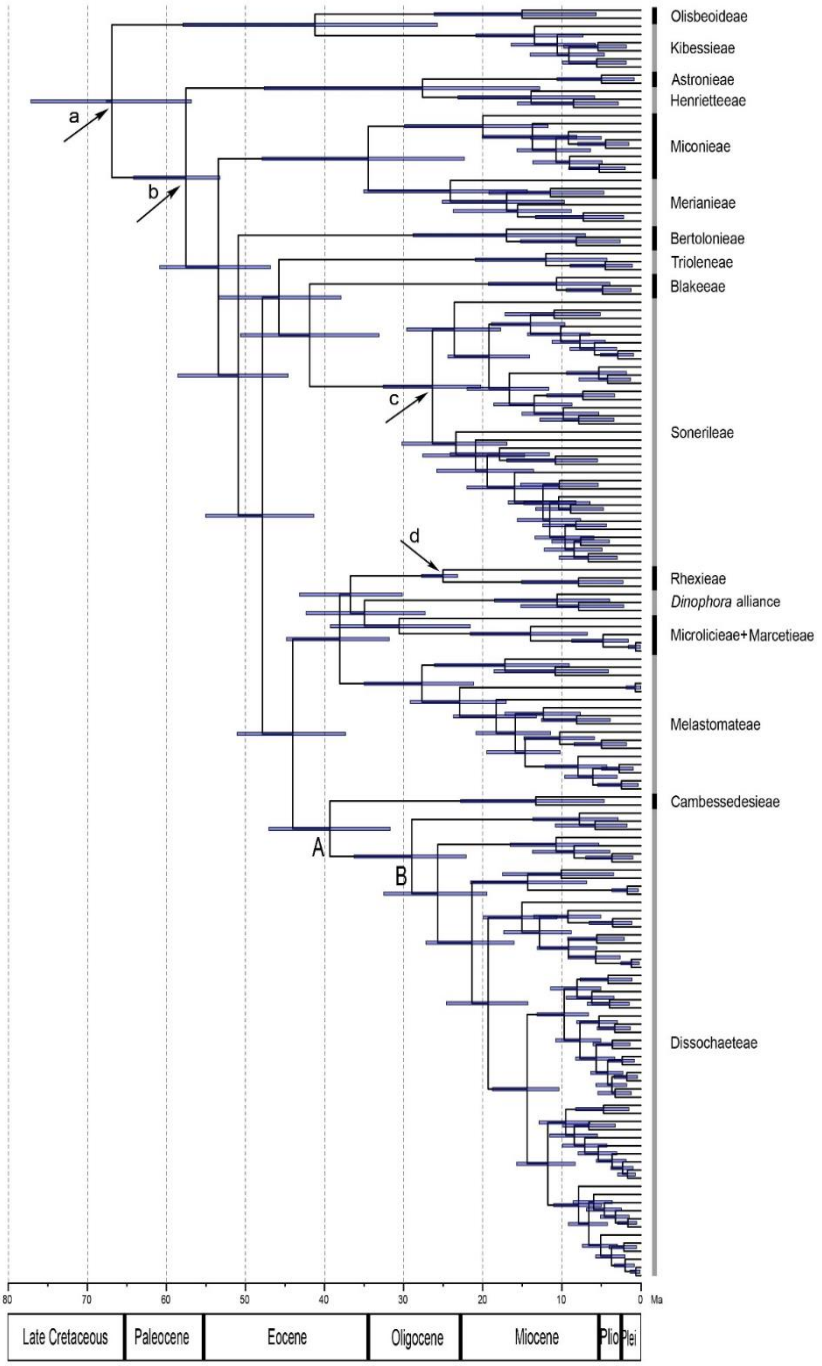

Fig. 7-1. Maximum clade credibility chronogram of the Dissochaeteae and outgroups. The blue node bars represent the 95% Highest Posterior Density intervals (HPD). **A.** Stem age of the Dissochaeteae; **B.** crown age the Dissochaeteae. Arrows refer to the calibration points: **a.** MRCA Melastomataceae; **b.** crown Melastomatoideae (excl. Olisbeoideae + Kibessieae); **c.** crown Asian Sonerileae; **d.** crown Rhexieae. (a & c secondary calibration; b & d fossil calibration). Ma = million years ago; Plei = Pleistocene; Plio = Pliocene.

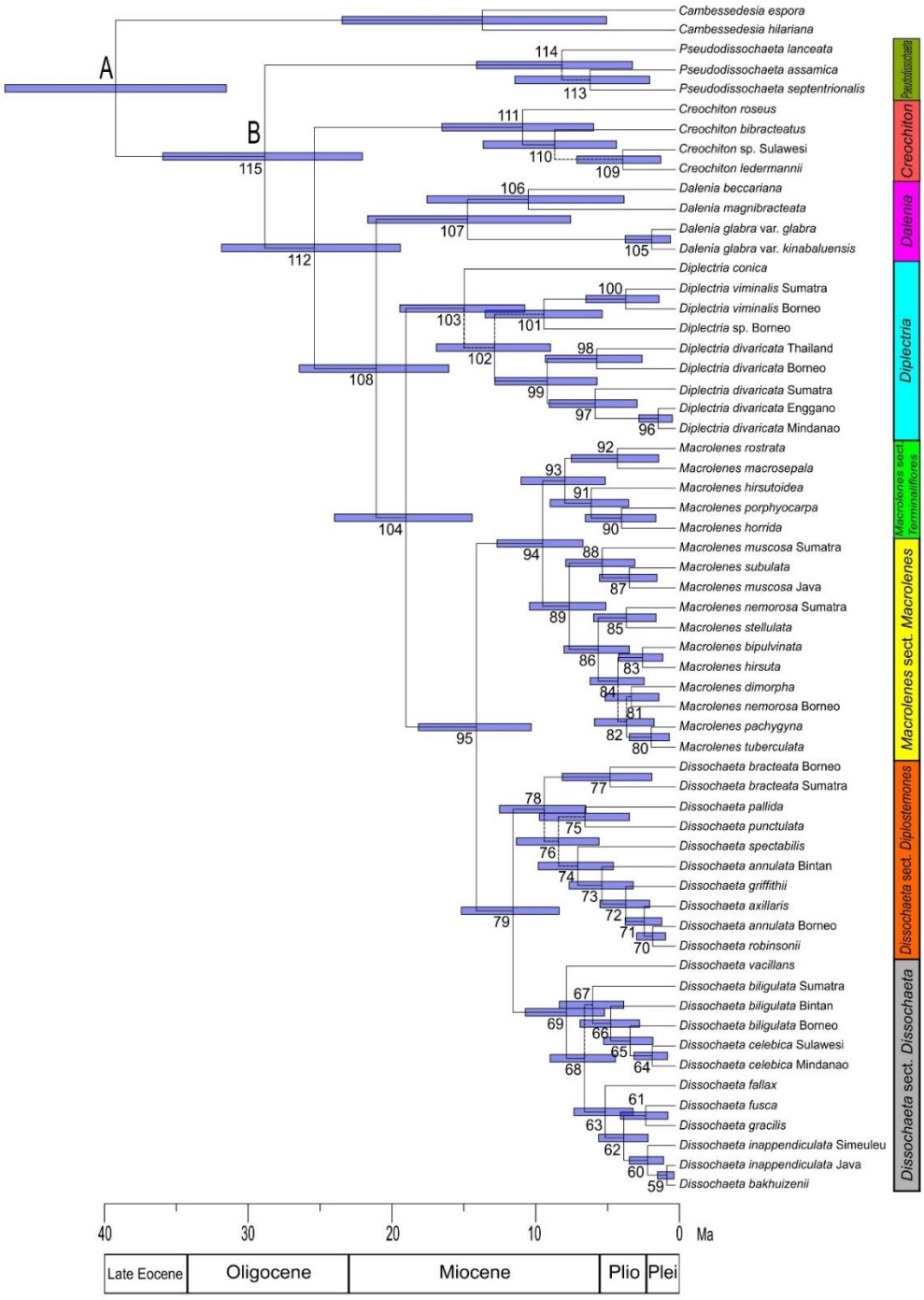

Fig. 7-2. Maximum clade credibility chronogram of the Dissochaeteae **(B)** including the Cambessedesieae as outgroup **(A)**; the blue node bars representing the 95% HPD (highest posterior density intervals). Dashed branches lead to nodes with posterior clade probabilities of <0.95. Node numbers correspond to Table 1. Ma = million years ago; Plei = Pleistocene; Plio = Pliocene.

Discussion

Phylogeny

Our Dissochaeteae and outgroup MCC tree (Fig. 7-1) is in general similar to the Melastomataceae MCC tree of Renner et al. (2001a), Berger et al. (2016), Veranso-Libalah et al. (2018) and Zhou et al. (2019b), which describe the same topologies. Most of the previous studies suggested that the origin of Melastomataceae was in the late Cretaceous and the crown age is early Paleocene, which is confirmed here. The crown age of the Melastomataceae here is estimated to be 66.91 (77.14–56.83) Ma. Olisbeoideae and Kibessieae are recognized as the basal clades that diversified within the Melastomataceae, followed by the remaining groups in the family (Fig. 7-1). The MCC tree topology of the Dissochaeteae (clade B) is similar in topology with the other phylogenetic trees of the group (Kartonegoro et al. 2021). The Dissochaeteae s.l., which include the *Medinilla* alliance and *Dinophora-Ochthocharis*, appeared to be not monophyletic. The newly defined Dissochaeteae (s.str.) now only includes the monophyletic *Dissochaeta* alliance with convincing and strong support values (Kartonegoro et al. 2021). The sister group of the newly defined Dissochaeteae is the South American Cambessedesieae (Fig. 7-1). Within the tribe, six distinct and strongly supported clades (genera) are recognized (Fig. 7-2). They are *Creochiton*, *Dalenia*, *Diplectria*, *Dissochaeta*, *Macrolenes* and *Pseudodissochaeta*.

Diversification of Dissochaeteae

The biogeographical reconstructions (Fig. 7-1, 7-2) showed that the Dissochaeteae originated from a South American ancestor in the late Eocene (Fig. 7-1, node A; stem age 39.32 Ma; 95% HPD 47.03–31.69). Two scenarios may likely explain the migration to Southeast Asia. The ancestor of the Dissochaeteae might have migrated from South America to Southeast Asia via North America and then entered Eurasia over the North Atlantic land bridge during the Eocene, when the global temperatures were warmer and tropical forests had expanded northwards and occupied regions from the equator to mid-latitudes across all northern continents (Li et al. 2017; Zhou et al. 2019b). The existence of the boreotropical forests and the North American land bridges connecting the Old and the New Worlds enabled intercontinental biotic exchange of tropical forest taxa in both directions (Brikiatis 2014; Li et al. 2017). This hypothesis is also supported by Eocene Melastomataceae fossils discovered from North America (Hickey 1977). The alternative migration scenario from South America is a direct trans-Atlantic (long distance) dispersal of the lineages to Africa via oceanic stepping stones and dispersal from Africa to Southeast Asia as proposed for tribe Melastomateae by Veranso-Libalah et al. (2018). Our study, in combination with the evidence given by the North American fossils, suggests that the first scenario is more plausible. Also, migration from North America to Asia during middle to late Eocene has been identified in the phylogeny of different plant taxa, such as Annonaceae clade of *Asimina* Adans. / *Disepalum* Hook.f. (Li et al. 2017) and the legume clade Cladrastis Raf. (Duan et al. 2020).

The divergence time between the sister groups Cambessedesieae and the Dissochaeteae is estimated at 39.32 Ma (Figs. 7-1, 7-2, Node A; 95% HPD 47.03–31.69) during the late Eocene, with vicariance resulting in two groups, one restricted to the Neotropics (Cambessedesieae) and the other to Southeast Asia (Dissochaeteae), respectively. The decline of global temperatures around the Eocene-Oligocene boundary constricted and fragmented boreotropical forests, resulting in the extinction/disappearance of the northern

mid-latitudinal tropical vegetations and their migration southwards to tropical regions like in Southeast Asia (Morley 2003; Li et al. 2017).

Our result agrees with Zhou et al. (2019b), who also postulated the splitting of the Dissochaeteae from the South American lineage, though based on different phylogenetic data. Therefore, there are also differences with Zhou et al. (2019b). Based on a limited sampling, Zhou et al. (2019b) estimated the crown age of the Dissochaeteae (*Dissochaeta-Pseudodissochaeta*) clade at 17.31 Ma (95% HPD: 24.22–10.72), which is younger than what we found. The slightly older stem age recovered in the present analysis is likely due to the inclusion of a broader ingroup sampling and the inclusion of a more closely related outgroup taxon, Cambessedesieae. This differs from Zhou et al. (2019b), who found the Sonerileae-Oxysporeae to be the sister group.

The pattern of diversification in the late Miocene, mostly the result of speciation in the last 10–5 Ma, is reported in other Southeast Asian genera such as *Artabotrys* R.Br. (Annonaceae; Chen et al. 2019), *Begonia* L. (Begoniaceae; Thomas et al. 2012) and *Cyrtandra* J.R.Forst. & G.Forst (Gesneriaceae; Atkins et al. 2020). There are a number of geological factors, which are likely to have been drivers of diversification during this period. During the late Oligocene to early Miocene, the Sunda and Sahul shelves moved closer together, creating land in the centre of the region for the first time (Hall 2002, 2009). The climate and sea level fluctuations of the Pleistocene glacial periods resulted in cyclic vicariance with frequent habitat fragmentations and amalgamations (Voris 2000; Woodruff 2010; Cannon 2012; Morley 2012). During glacial periods, when due to sea level drops many islands were connected, species may have become widespread, while during interglacials rises in sea level broke up the distributions, which likely resulted in speciations.

Table 7-3. Summary of the crown age and ancestral areas reconstruction from S-DEC and S-DIVA analyses of genera and sections in Dissochaeteae.

Genera/sections	Crown Age (Ma)	95% HPD	Ancestral Area	
			S-DEC	S-DIVA
Pseudodissochaeta	7.76	13.66–2.86	NE India & Indochina	Indochina
Creochiton	10.72	16.53–5.29	Sulawesi	Sulawesi
Dalenia	14.32	21.53–6.84	Borneo	Borneo
Diplectria	15.04	19.93–10.59	Sumatra= Sumatra-Borneo	Sumatra-Borneo =Malay Peninsula-Borneo
Macrolenes	9.69	13.12–5.59	Sumatra-Borneo	Sumatra-Borneo
Macrolenes sect. ***Terminaliflores***	8.07	11.43–5.06	Borneo	Borneo
Macrolenes sect. ***Macrolenes***	7.72	10.78–5.04	Sumatra-Borneo	Sumatra=Sumatra-Borneo
Dissochaeta	11.75	15.70–8.29	Sumatra	Java-Borneo=Borneo
Dissochaeta sect. ***Diplostemones***	9.49	12.88–6.46	Sumatra	Malay Peninsula-Borneo
Dissochaeta sect. ***Dissochaeta***	7.88	11.03–4.98	Sumatra-Java	Java=Java-Borneo

Ancestral range reconstruction

Indochina and Borneo (BF) are most likely the area of origin for the most recent common ancestor of the Dissochaeteae (Fig. 7-3A; node 115) and for many of the early diverging clades of some genera within Southeast Asia based on DEC and S-DIVA analyses. They are also the species richest areas (c. 70% of the species) and show the most abundant

morphological diversity. The combination of Indochina and Borneo represents a large area, long ago emerged (Indochina and south Borneo), and since then with a stable geological history and covered by extensive rainforests, also during glacial maxima; this offers a compelling explanation for the in-situ diversification of the Dissochaeteae (Hall 2012; De Bruyn et al. 2014).

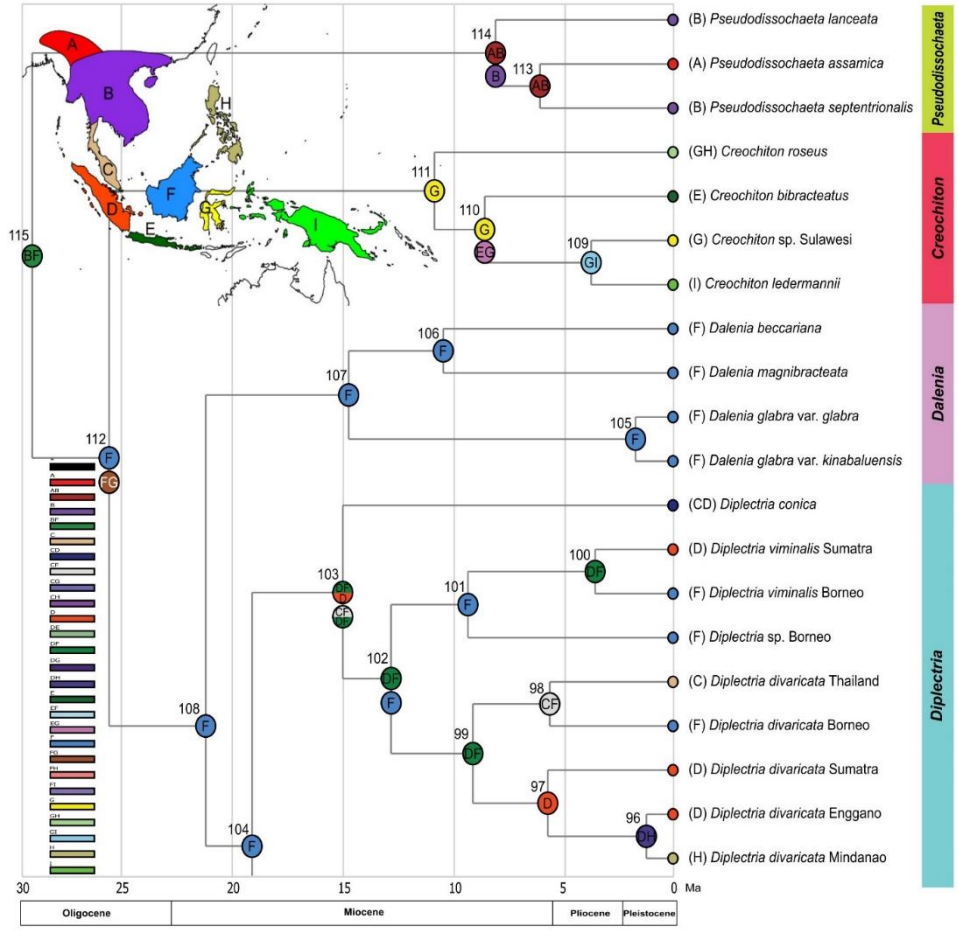

Fig. 7-3A. Ancestral range optimization for the Dissochaeteae. Pie charts at nodes represent optimization under maximum-likelihood S-DEC. When S-DIVA analyses yield a different optimization, then the results are shown below to the relevant nodes. Node numbers indicated next to pie charts correspond to Table 7-2. Colours in the pie charts correspond with geographical areas (see inset map); Ma, million years ago. **A** = E Bhutan, NE India and NW Myanmar; **B** = Indochina, incl. C & E Myanmar, S China, Hainan and Thailand; **C** = S Thailand, Malay Peninsula and Riau Archipelago; **D** = Sumatra and surrounding islands; **E** = Java and Lesser Sunda Islands excl. Sumba, Flores and Timor; **F** = Borneo; **G** = Sulawesi; **H** = Philippines incl. Palawan; and **I** = Moluccas and New Guinea. Map source using DIVA-GIS (http://www.diva-gis.org/) with modification.

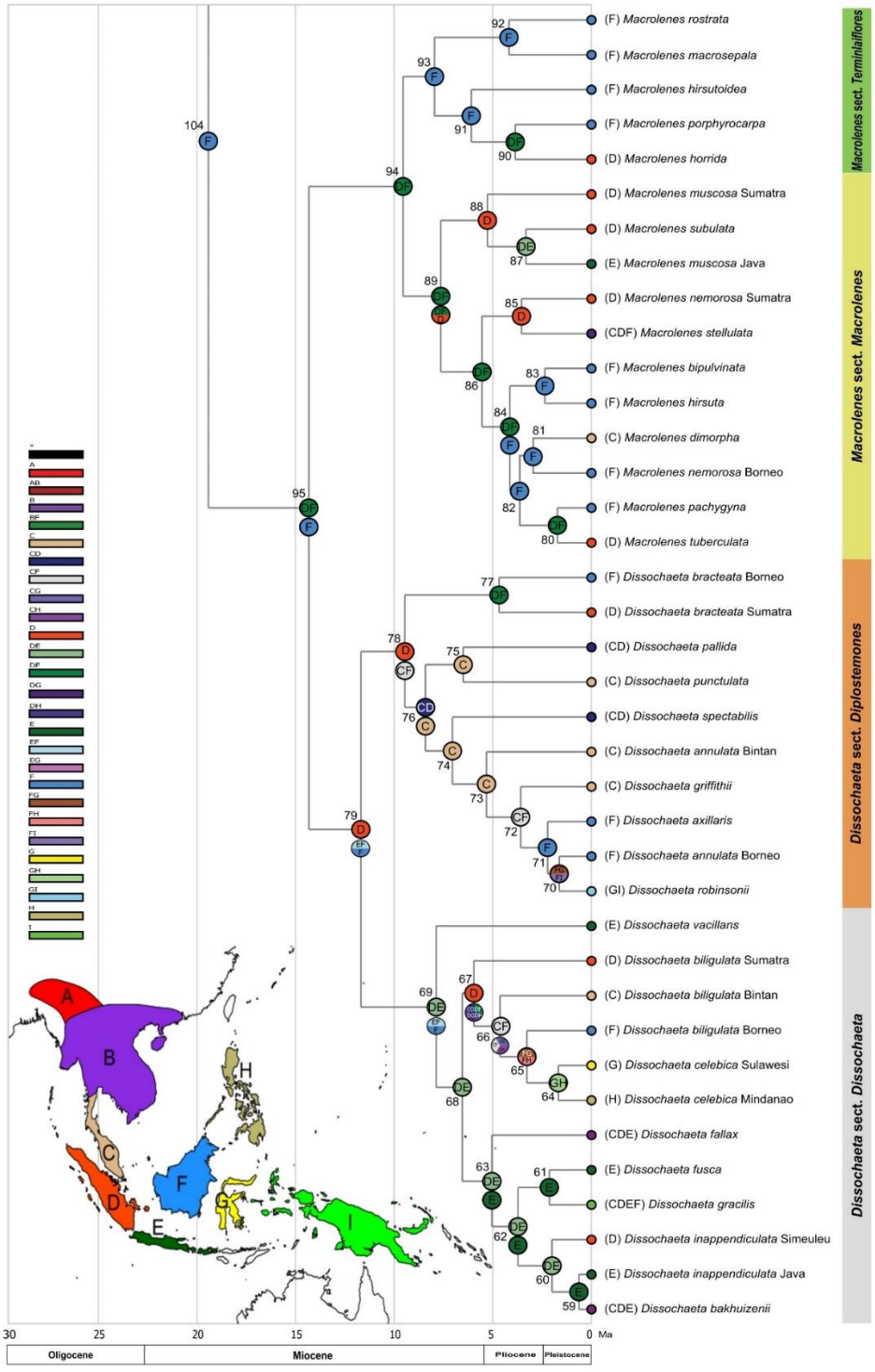

Fig. 7-3B. Continuation of Fig. 7-3A

A split between the basal Indo-Burmese and a predominantly Malesian clade occurred in the Middle Oligocene (clade 115; Figure 7-3A). Dispersal from Indo-China (B) westward into Bhutan, NE India and W Myanmar occurred at the time of at least node 114 (origin of the genus *Pseudodissochaeta*; Fig. 7-3A, Table 7-3: area AB). Colonization of west Malesia and western Wallacea (the Philippines, Sulawesi) by the Dissochaeteae started at the time of the ancestral nodes 115 and 112 (Fig. 7-3A) during the middle Oligocene and early Miocene. The S-DEC analysis indicated Borneo (F) as the origin of Malesian diversification of this group, while the S-DIVA analysis included Sulawesi (FG) as ancestral area (Fig. 7-3A; node 112). Part of west Sulawesi was already close to Borneo, before the east Malesian microplates came close and especially volcanoes could have been colonized early (Hall 2002, 2009). Hall often implied that most east Malesian microplates were submerged when they moved, but dispersal patterns show that it is very likely that more areas were above water than described by Hall (2009), and thus already offered stepping stones for dispersal (van Welzen et al. 2005). After the origin in Borneo, the Malesian taxa started to disperse mainly within west Malesia, but also eastwards, but few crossed Wallace's Line, mainly from Borneo to Sulawesi, passing the narrow, but deep and fast flowing Makassar Strait (*Dissochaeta celebica* Blume, *D. robinsonii* Merr.). Dispersal within the west Malesia region can potentially be explained by overland dispersal when most of extant islands were perhaps still connected (Hall 2009).

Dispersal of some lineages within west Malesia or Wallacea eastwards to the Sahul Shelf (New Guinea) occurred in the late Pliocene and early Pleistocene (nodes 109 and 70; Fig. 7-3A, 7-3B). Initial diversification in Southeast Asia mainland to western Malesia and subsequent dispersal events from western Malesia to eastern Malesia from the early Miocene onwards have been inferred for lineages of several angiosperm genera such as *Aglaia* Lour. (Meliaceae; Grudinski et al. 2014), *Artabotrys* (Annonaceae; Chen et al. 2019), *Begonia* (Begoniaceae; Thomas et al. 2012a), *Cyrtandra* (Gesneriaceae; Atkins et al. 2020), *Goniothalamus* (Blume) Hook.f. & Thomson (Annonaceae; Thomas et al. 2017), *Meiogyne* Miq. - *Fitzalania* F.Muell. (Annonaceae; Thomas et al. 2012b), *Pseuduvaria* Miq. (Annonaceae; Su & Saunders 2009), *Mallotus* Lour. and *Macaranga* Thouars (Euphorbiaceae; van Welzen et al. 2014) and *Trigonostemon* Blume (Euphorbiaceae; Yu & van Welzen 2020). The west to east dispersal appears to have been particularly prevalent from the mid Miocene onwards as warmer and wetter conditions prevailed, rainforest expanded and extant land emerged east of Wallace's Line (Richardson et al. 2012; Grudinski et al. 2014; Crayn et al. 2015). Still, there are examples of dispersal in the opposite direction, such as in Proteaceae (Barker et al. 2007), *Macaranga* (Euphorbiaceae, van Welzen et al. 2014) and Myrtaceae (Sytsma et al. 2004).

Creochiton (Fig. 7-3A; node 111) is the first genus that split off within the Malesian taxa of the Dissochaeteae. Sulawesi is apparently the ancestral area of the genus (Table 7-3), but this may be a sampling artifact as samples of four west Malesian species failed in the molecular analysis. Most likely is that the ancestor might have been on Borneo (before node 112, Fig. 7-2), with dispersal to Sulawesi, perhaps by birds eating the berries. The data used show three dispersal events from Sulawesi to other areas during the late Miocene and Pliocene. Dispersal northward to the southern Philippines (node 111) and eastwards to the Moluccas and New Guinea (node 109) with inter-island dispersal when the Australian plate collided and microplates emerged in Wallacea (Hall 2009). East to west dispersal back from Wallacea into Western Malesia mainly occurred in the late Miocene (8.44; 13.70–3.92 Ma; node 110) when most of the islands within Wallacea started to rise (or sea floors sank) (Hall 2002, 2009).

All species of the scrambling shrubs group, originated on Borneo, (Fig. 7-3A; node 108), have a similar habit and habitat preference. This was followed by dispersal within Borneo (nodes 108, 107, 104) and westward to Sumatra (nodes 103, 95). Within this group, *Dalenia* (node 107) originated first and mainly diversified on Borneo during the late Miocene to Pleistocene (Fig. 7-3A, Table 3). The only species outside Borneo, *Dalenia papuana* (Mansf.) Karton. from New Guinea, was not sampled in this study, so we cannot comment on this dispersal over Wallace's line. *Diplectria* (Fig. 7-3A, Table 7-3; node 103) most likely originated on Borneo and Sumatra (DF) or Sumatra (D) after dispersal from Borneo (S-DEC optimisation). Alternatively, the S-DIVA analysis showed an origin of the genus on Borneo and Sumatra (DF) or Sumatra and the Malay Peninsula (CF) (Tables 7-2, 7-3). The Philippine *Diplectria divaricata* (Willd.) Kuntze seemingly arrived from Sumatra (nodes 97 and 96) based on both analyses. Three possible dispersal routes might qualify to explain the diversification in the Philippines; whereby all migration routes pass Borneo first and then either via Palawan, the Sulu Archipelago or Sulawesi reaching the Philippines during the Pliocene and Pleistocene. It is also possible that all routes were used as the species occur in all these areas. The migration route through Palawan or the Sulu Archipelago to the main Philippine Islands is also known for the genus *Trigonostemon* (Euphorbiaceae; Yu & van Welzen 2020).

The ancestral area of *Dissochaeta* and *Macrolenes* (splitting at node 95) is estimated to be Sumatra-Borneo (DF) based on S-DEC analysis, while S-DIVA gives Borneo (F) as estimate (Fig. 3B). *Macrolenes* (node 94), which has west Malesia as present distribution, originated on Sumatra-Borneo (DF) (Table 7-3). With several dispersals/vicariance events, *Macrolenes* diversified during the late Miocene to Pleistocene in the Sundaland, favoured by a larger extension of evergreen forest during this period especially between Borneo and Sumatra or within Borneo. Several dispersal events enlarged the distribution to the Malay Peninsula (node 82 from Borneo; node 85 from Sumatra) and to Java (node 88 and 87 from Sumatra) (Fig. 7-3B). The origin of *Dissochaeta* (node 79) is either on Sumatra (D), based on the S-DEC analysis, while S-DIVA gives two possibilities, Java and Borneo (EF) or Borneo (F) (Table 7-2, 7-3; Fig. 7-3B). *Dissochaeta* sect. *Diplostemones* Cogn. (node 78) has its crown group at 8.17 (10.97–5.58) Ma. The S-DEC analysis estimated the origin of the section to be on Sumatra (D), followed by several dispersal events to the Malay Peninsula and Borneo during the late Miocene to Pliocene (these latter two areas were optimised as the area of origin by S-DIVA) (Table 7-3). Dispersals to Borneo from Sumatra are shown at node 78 and 77, or passed via the Malay Peninsula first at node 73 and 72 (Fig. 7-3B). Long distance dispersal to east Malesia (Moluccas and New Guinea) might have been the case on nodes 71 and 70, directed from Borneo via Sulawesi. The age of the crown group of *Dissochaeta* sect. *Dissochaeta* (node 69) is c. 6.79 (9.35–4.41) Ma with an origin either on Sumatra and Java (DE), based on the S-DEC analysis, or Java and Borneo or Borneo according to the S-DIVA analysis (Table 7-3). Diversification within the section occurred during the late Miocene to Pleistocene with dispersal within Sumatra and Java (nodes 69, 68, 63, 62, 61, 60 and 59), dispersal from Sumatra to Malay Peninsula (node 67), followed by dispersal east to Borneo (node 66) and to Sulawesi-Philippines (nodes 65 and 64). Dispersal into the Philippines from Borneo occurred more likely via Palawan rather than via Sulawesi because Palawan forms almost a "bridge" (was connected to Borneo during glacial periods), while Sulawesi was a little more isolated at by the deep Makassar Strait (Fig. 7-3B).

The MCC phylogenetic tree is based on only 44 species out of the 90 species in the Dissochaeteae. Some species are sampled more than once, especially the species with wider distributions, to assess how they originally dispersed. If more species are added to the

analyses, changes in the patterns, dispersal routes, areas of origin may occur. The undersampling showed in the case of *Creochiton* a divergent area of origin, Sulawesi, east of Wallace's line, while all other origins were in West Malesia, which necessitates an unlikely explanation like long-distance dispersal from the western part of Southeast Asia to Sulawesi. The splitting of the clade from its ancestor happened in the Late Oligocene (25.71 Ma) with dispersal from Borneo into Sulawesi (Hall 2009, 2012). Some Sumatran and Bornean species were missing in the analyses and possibly, this can change the date and place of origin of the genus and its dispersal/diversification. A comparable problem appears in *Dissochaeta*, where some eastern Malesian and western Southeast Asian Continental species were not included. The dispersal of the genus into East Malesia or Continental Southeast Asia is, therefore, not resolved.

Biogeographic patterns

Indo-China and Borneo

Indo-China–Borneo was estimated as the most likely ancestral area for the Dissochaeteae. Indochina and Borneo are areas with the longest emergence histories, and they have been major diversification hotspots through time and key sources for lineage dispersal across the region (De Bruyn et al. 2014). Indochina and Borneo have long been recognized as two of the most diverse biodiversity hotspots in Southeast Asia across several taxonomic groups through all time periods (Myers et al. 2000; Lohman et al. 2011; De Bruyn et al. 2014). Of the two areas is it most likely that Indochina was the first area in which the ancestor of the Dissochaeteae settled in Asia, as from here the basal *Pseudodissochaeta* clade developed and dispersed westwards into NE India and Bhutan (Fig. 7-3A). Borneo is the cradle of dispersal events in the remaining part of the Dissochaeteae in Malesia, with many dispersal events to the Philippines, Sulawesi, Sumatra, Malay Peninsula, Java, Moluccas and New Guinea (Fig. 7-3A & 7-3B). The island is not only an important evolutionary hotspot in terms of high species numbers and in situ diversification, but also an important source for subsequent emigration (De Bruyn et al. 2014; Atkins et al. 2020). Borneo represents the original 'heartland' of the group, the area with the highest species numbers and greatest abundance in morphological diversity. High dispersal levels between the islands on the Sunda Shelf, especially between Borneo and nearby islands reflect the shared geological history of these continental islands, which formed continuous land masses during at least some of the glacial maxima (Voris 2000; Hall 2012). At these times there would also have been more extensive areas of rainforest (Cannon et al. 2009, 2012; Raes et al. 2014), facilitating exchange and dispersal in a wet forest group, like the Dissochaeteae.

Wallace Line

Wallace's line divides the floristic region of the Malay Archipelago or Malesia into a western and eastern part (Wallace 1860; van Welzen et al. 2011; Chen et al. 2019; Yu & van Welzen 2020). The tectonic and climatic history of Malesia has resulted in different floras in both areas (van Welzen et al. 2005, 2011; Grudinski et al. 2014). The line runs east of the Philippine islands, between Borneo and Sulawesi, and between Bali and Lombok, which were never connected during the Pleistocene glacial maxima (Voris 2000), possibly hindering dispersal between West Malesia (Sunda shelf) and East Malesia (Sahul shelf). The position of the line was later revised with alternative lines proposed, mostly by zoologists reflecting their taxonomic groups of interest (van Welzen et al. 2011; Crayn et al. 2015). The Merrill-Dickerson or Huxley line in the west and Lydekker's line in the east delimit a zone called Wallacea (the Philippines, Sulawesi, Lesser Sunda Islands and Moluccas). Wallacea

is a good phytogeographic region with many endemic species, especially in the Philippines, but it is also a transition zone between west and east Malesia and plays an important role in the floristic exchanges between the Sunda and Sahul Shelves (van Welzen et al. 2005, 2011). Java has been added to the region because of comparable climatic conditions (yearly dry monsoon on most of the island), resulting in similar floral elements (van Welzen et al. 2005, 2011; van Welzen & Raes 2011). Geologically, Wallacea represents the area of collision between Sundaland and the present-day Indian-Australian plate, whereby west Wallacea is separated from the Sunda Shelf by the deep Makassar Strait, and also during glacial periods the islands (some united) remained at most stepping stones for dispersal, but never formed a continuous land corridor between the Sunda and Sahul Shelves (e.g. Voris 2000; van Welzen et al. 2005; Hall 2009; Lohman et al. 2011). At present, the region generally has a long or brief dry monsoon compared to the everwet Sunda and Sahul Shelves and if this climatic difference was also in place in the Pliocene/Pleistocene, it could have acted as an environmental filter to everwet plant taxa, including Dissochaeteae, causing the number of species to decrease eastwards (Sahul) (van Welzen et al. 2005, 2011). Lianas/woody climbers are mostly restricted to the everwet areas, which is demonstrated here too, only the two non-climbing genera occur in monsonal areas (*Pseudodissochaeta* in Southeast Asia mainland, and *Creochiton* in east Malesia, extending even to the everwet New Guinea). There are few climbing species that also reach Sulawesi and New Guinea/Moluccas. As such one might also state that Weber's line (between Sulawesi and the Moluccas, east of the Lesser Sunda Islands) and Lydekker's line (between the Moluccas and New Guinea, east of the Lesser Sunda Islands) indicate major limits (likely due to monsonal influences) in the dispersal of the Dissochaeteae.

The most probably common migration route from Sundaland across Wallace's line is through Sulawesi or the Philippines to eastern Wallacea/New Guinea (Su & Saunders 2009; Thomas et al. 2012a; Nauheimer et al. 2012; Buerki et al. 2016; Chen et al. 2019; Atkins et al. 2020; Yu & van Welzen 2020). Our biogeographical reconstructions of Dissochaeteae (Fig. 7-3) identified four dispersal events across Wallace's line from West Malesia to Wallacea and East Malesia. Three of them show dispersal from Borneo (node 112 and 111; 71 and 70; 65 and 64) to Sulawesi and Philippines and one, rather oddly, from Sumatra (node 97 and 96) to the Philippines (but more samples may change this view). All dispersal events occurred in the Late Miocene and/or Pliocene and Pleistocene, when marine gaps diminished following convergence of the Sunda and Sahul shelves (Hall 2009). The west to east Malesian dispersal occurring near node 71 likely occurred with Sulawesi as a stepping stone. Most of the west-east dispersal or vice-versa via Wallacea took place during the last 10 Ma (van Welzen et al. 2005). There is one indication of a reverse dispersal from Wallacea to West Malesia on node 110, going from Sulawesi to Java. However, in some analyses, Java is also thought to be part of Wallacea just as Sulawesi (van Welzen et al. 2011). However, the phylogeny is not complete and various east Malesian species are still lacking, thus reversed, east-west dispersals via Wallacea are perhaps still undetected.

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Appendix 7-1. – List of sequences used in this study. Taxa, voucher information, location and GenBank accession numbers for the nuclear and plastid DNA regions.

Taxon	Tribe/ Group	Voucher	Location	ETS	ITS	*ndhF*	*psbK-psbL*	*rbcL*	*rpl16*
Aciotis paludosa	Marcetieae	*Guimarães 317*, RB	S America	KF462814	JQ730040	–	JQ730460	–	–
Aciotis purpurascens	Marcetieae	*Michelangeli 2454*, NY	S America	KU500992	KU501055	AF215561	JQ730461	–	AF322231
Aciotis rubricaulis	Marcetieae	*Michelangeli 2542*, NY	S America	KU500993	KU501057	–	JQ730462	JQ592644	–
Adelobotrys subsessilis	Merianieae	*Michelangeli 493*, BH	S America	MH781591	AY966407	MH760283	MH781651	MH747567	AY966419
Allomorphia balansae	Sonerileae	*Liu 451*, SYS	China	–	MG644470	MK994792	MK994792	MK994792	MK994792
Anerincleistus macrophyllus	Sonerileae	*Liu 673*, SYS	Malaysia (Borneo)	–	MN031184	MK994887	MK994887	MK994887	MK994887
Astronia meyeri	Astronieae	*Fernando 2551*	Philippines	–	KF78158	–	–	KF781611	–
Astronia smilacifolia	Astronieae	*Liu 664*, SYS	Malaysia (Borneo)	–	EF683153	MK994883	MK994883	MK994883	MK994883
Barthea barthei	Sonerileae	*Liu 575*, SYS	China	–	MG644388	KY873324	KY873324	KY873324	KY873324
Bellucia pentamera	Henrietteae	*Penneys 1868*, CAS	S America	–	GU968788	AF215578	–	KF781624	AF215615
Bertolonia acuminata	Bertolonieae	*Bacci 171*, UEC	S America	MK296603	MK258150	KX826820	KX826820	KX826820	KX826820
Bertolonia alternifolia	Bertolonieae	*Bacci 375*, UEC	S America	MH722270	MH708155	MH729204	MK296663	MH729221	MH722278
Bertolonia mosenii	Bertolonieae	*Goldenberg 804*, NY	S America	MK296614	MH708156	JF831973	MK296678	JF831998	JF832024
Blakea gracilis	Blakeeae	*Michelangeli 845*, NY	S America	–	AY460445	JF831974	–	JF831999	JF832025
Blakea schlimii	Blakeeae	*Michelangeli 1227*, NY	S America	–	AY460441	KX826821	KX826821	KX826821	KX826821
Blakea trinervia	Blakeeae	*Penneys 1629*, FLAS	S America	–	KY782453	AF215555	–	AF215516	AF215600
Blastus cochinchinensis	Sonerileae	*Liu 446*, SYS	China	–	MG644467	MK994909	MK994909	MK994909	MK994909
Bredia hirsuta	Sonerileae	*Liu 634*, SYS	China	–	MN031213	MK994872	MK994872	MK994872	MK994872
Cambessedesia espora	Cambessedesieae	*Guimarães 397*, RB	S America	MK165019	JQ730062	JQ899114	JQ730481	JQ899088	JQ899064
Cambessedesia hilariana	Cambessedesieae	*Guimarães 405*, RB	S America	MK165024	JQ730063	JQ899115	JQ730482	JQ899089	JQ899065
Clidemia capillaris	Miconieae	*Penneys 1607*, FLAS	S America	KF821285	EU055861	EU056121	KF822471	–	–
Clidemia petiolaris	Miconieae	*Chase 2534*, K	S America	KM893562	KF821452	AM235410	KF821882	AM235643	AM235446
Clidemia umbellata	Miconieae	*Judd 8084*, FLAS	S America	KF820711	EU055674	EU055929	KF821911	–	–
Creochiton bibracteatus	Dissochaeteae	*Kartonegoro 1111*, BO	Indonesia (Java)	–	MW462480	MW462399	MW462242	MW462553	MW290997
Creochiton ledermannii	Dissochaeteae	*Mambrasar 81*, BO	Indonesia (Papua)	–	MW462481	MW462400	MW462243	MW462554	MW290998
Creochiton roseus	Dissochaeteae	*Kartonegoro 1051*, BO	Indonesia (Sulawesi)	MW462332	MW462482	MW462401	MW462244	MW462555	MW290999
***Creochiton* sp.**	Dissochaeteae	*Kartonegoro 927*, BO	Indonesia (sulawesi)	–	MW462483	MW462402	MW462245	MW462556	MW291000
Cyphotheca montana	Sonerileae	*Liu 596*, SYS	China	–	MG644447	MK994852	MK994852	MK994852	MK994852

Dalenia beccariana	Dissochaeteae	*Kartonegoro 1118,* BO	Brunei Darussalam	–	MW462519	MW462442	MW462287	MW462600	MW295981
Dalenia glabra* var.*glabra	Dissochaeteae	*Penneys 2446,* WNC	Malaysia (Borneo)	MW462354	MW462506	MW462429	MW462273	MW462586	MW295982
Dalenia glabra var. kinabaluensis	Dissochaeteae	*Penneys 2542,* WNC	Malaysia (Borneo)	MW462357	MW462508	MW462431	MW462276	MW462589	MW295985
Dalenia magnibracteata	Dissochaeteae	*Liu 676,* SYS	Malaysia (Borneo)	–	MG644477	MK994889	MK994889	MK994889	MK994889
Dichaetanthera arborea	Melastomateae	*Razanatsima 823,* MO	Madagascar	–	KX889222	AF272800	KY284742	–	AF294470
Dichaetanthera articulata	Melastomateae	*Ravelonarivo 4320,* MO	Madagascar	MF397949	KX889224	MF398044	KY284743	–	–
Dinophora spenneroides	*Diophora*-alliance	*Veranso 107,* MJG	Africa (Cameroon)	MF397951	KX889227	MF398047	KY284746	–	–
Diplectria conica	Dissochaeteae	*Kartonegoro 1101,* BO	Indonesia (Sumatra)	MW462347	MW462498	MW462419	MW462263	MW462576	MW414548
Diplectria divaricata	Dissochaeteae	*Ardiyani et al. E167,* BO	Indonesia (Sumatra)	MW462350	MW462503	MW462425	MW462269	MW462582	MW414554
Diplectria divaricata	Dissochaeteae	*Kartonegoro 1096,* BO	Indonesia (Sumatra)	MW462348	MW462499	MW462421	MW462264	MW462578	MW414550
Diplectria divaricata	Dissochaeteae	*Penneys 2472,* WNC	Malaysia (Borneo)	MW462349	MW462501	MW462423	MW462267	MW462580	MW414552
Diplectria divaricata	Dissochaeteae	*Penneys 2365,* WNC	Philippines (Mindanao)	–	MW462500	MW462422	MW462266	MW462579	MW414551
Diplectria divaricata	Dissochaeteae	*Wai 2677,* PSU	Thailand	–	MW462502	MW462424	MW462268	MW462581	MW414553
***Diplectria* sp.**	Dissochaeteae	*Kartonegoro 1135,* BO	Indonesia (Borneo)	–	MW462524	MW462447	MW462295	MW462606	MW414573
Diplectria viminalis	Dissochaeteae	*Kartonegoro 1075,* BO	Indonesia (Sumatra)	MW462377	MW462528	MW462451	MW462299	MW462610	MW414577
Diplectria viminalis	Dissochaeteae	*Kartonegoro 1127,* BO	Indonesia (Borneo)	MW462380	MW462530	MW462452	MW462302	MW462612	MW414579
Dissochaeta annulata	Dissochaeteae	*Kartonegoro 1121,* BO	Indonesia (Bintan)	MW462333	MW462485	MW462404	MW462247	MW462559	MW414532
Dissochaeta annulata	Dissochaeteae	*Penneys 2506,* WNC	Malaysia (Borneo)	MW462335	MW462486	MW462405	MW462249	MW462560	MW414533
Dissochaeta axillaris	Dissochaeteae	*Kartonegoro 1126,* BO	Indonesia (Borneo)	MW462336	–	–	MW462250	MW462561	–
Dissochaeta bakhuizenii	Dissochaeteae	*Kartonegoro 1116,* BO	Indonesia (Java)	MW462339	MW462488	MW462408	MW462253	MW462564	MW414536
Dissochaeta biligulata	Dissochaeteae	*Kartonegoro 1088,* BO	Indonesia (Sumatra)	MW462340	MW462489	MW462409	MW462254	MW462565	MW414537
Dissochaeta biligulata	Dissochaeteae	*Kartonegoro 1119,* BO	Indonesia (Bintan)	MW462341	MW462490	MW462410	MW462255	MW462566	MW414538
Dissochaeta biligulata	Dissochaeteae	*Penneys 2509,* WNC	Malaysia (Borneo)	MW462343	MW462492	MW462411	MW462257	MW462568	MW414540
Dissochaeta bracteata	Dissochaeteae	*Kartonegoro 1074,* BO	Indonesia (Sumatra)	MW462344	MW462494	MW462413	MW462258	MW462569	MW414541
Dissochaeta bracteata	Dissochaeteae	*Penneys 2483,* WNC	Malaysia (Borneo)	MW462345	MW462495	MW462414	MW462259	MW462571	MW414543

Dissochaeta celebica	Dissochaeteae	*Kartonegoro 1054,* BO	Indonesia (Sulawesi)	–	MW462496	MW462415	MW462260	MW462572	MW414544
Dissochaeta celebica	Dissochaeteae	*Penneys 2364,* WNC	Philippines (Mindanao)	–	MW462497	MW462417	MW462261	MW462574	MW414546
Dissochaeta fallax	Dissochaeteae	*Kartonegoro 1106,* BO	Indonesia (Java)	MW462351	MW462504	MW462426	MW462270	MW462583	MW414555
Dissochaeta fusca	Dissochaeteae	*Kartonegoro 1105,* BO	Indonesia (Java)	MW462353	MW462505	MW462428	MW462272	MW462585	MW414557
Dissochaeta gracilis	Dissochaeteae	*Kartonegoro 1113,* BO	Indonesia (Java)	MW462358	MW462509	MW462432	MW462277	MW462590	MW414558
Dissochaeta griffithii	Dissochaeteae	*Kartonegoro 1122,* BO	Indonesia (Bintan)	MW462359	MW462510	MW462433	MW462278	MW462591	MW414559
Dissochaeta inappendiculata	Dissochaeteae	*Kartonegoro 1115,* BO	Indonesia (Java)	MW462364	MW462515	MW462438	MW462283	MW462596	MW414564
Dissochaeta inappendiculata	Dissochaeteae	*Santoso 119,* BO	Indonesia (Sumatra)	MW462362	MW462513	MW462436	MW462281	MW462594	MW414562
Dissochaeta pallida	Dissochaeteae	*Kartonegoro 1058*	Indonesia (Sumatra)	MW462366	MW462517	MW462440	MW462285	MW462598	MW414566
Dissochaeta punctulata	Dissochaeteae	*Kartonegoro 1123,* BO	Indonesia (Bintan)	MW462369	MW462520	MW462443	MW462289	MW462601	MW414568
Dissochaeta robinsonii	Dissochaeteae	*Gushilman 382,* BO	Indonesia (Moluccas)	MW462372	MW462522	MW462444	MW462292	MW462603	MW414569
Dissochaeta spectabilis	Dissochaeteae	*Kartonegoro 1100*	Indonesia (Sumatra)	MW462374	MW462525	MW462448	MW462296	MW462607	MW414574
Dissochaeta vacillans	Dissochaeteae	*Kartonegoro 1117,* BO	Indonesia (Java)	MW462376	MW462527	MW462450	MW462298	MW462609	MW414576
Dissotis crenulata	Melastomateae	*Goyder 7476,* GRA	Africa	MF397959	KX889236	MF398056	KY284756	–	–
Dissotis tubulosa	Melastomateae	*Veranso 221,* MJG	Africa (Cameroon)	MF397997	KX889271	MF398093	KY284795	–	–
Driessenia glanduligera	Sonerileae	*Liu 657,* SYS	Malaysia (Borneo)	–	MN031197	MK994879	MK994879	MK994879	MK994879
Eriocnema fulva	Eriocnemeae	*Almeda 8416,* CAS	S America	KF820735	MH743831	AY553781	MK296694	AY553777	AY553772
Fordiophyton longipes	Sonerileae	*Liu 610,* SYS	China	–	MK775301	MK994858	MK994858	MK994858	MK994858
Graffenrieda latifolia	Merianieae	*Penneys 1303,* FLAS	S America	KF820744	AY460450	EU055943	MF105119	MF069928	AM235447
Graffenrieda moritziana	Merianieae	*Michelangeli 832,* NY	S America	KF820749	AY460451	EU055944	JQ730504	EU711390	JF832031
Henriettea barkeri	Henrietteeae	*Ionta 2029,* FLAS	S America	–	KJ933957	KX826824	KX826824	KX826824	KX826824
Heteroblemma serpens	Sonerileae	*Liu 671,* SYS	Malaysia (Borneo)	–	MN031200	MK994886	MK994886	MK994886	MK994886
Heterotis rotundifolia	Melastomateae	*Penneys 1304,* FLAS	Dominica	–	JQ730089	AF215565	–	U26323	AF270745
Macrolenes bipulvinata	Dissochaeteae	*Kartonegoro 781,* BO	Indonesia (Borneo)	–	MW462532	MW462453	MW462304	MW462614	MW414580
Macrolenes dimorpha	Dissochaeteae	*Kartonegoro 1134,* BO	Indonesia (Borneo)	MW462382	MW462533	MW462454	MW462305	MW462615	MW414581
Macrolenes hirsuta	Dissochaeteae	*Kartonegoro 1139,* BO	Indonesia (Borneo)	MW462383	MW462534	MW462455	MW462306	MW462616	MW414582
Macrolenes hirsutoidea	Dissochaeteae	*Kartonegoro 1141,* BO	Indonesia (Borneo)	MW462360	MW462511	MW462434	MW462279	MW462592	MW414560

Macrolenes horrida	Dissochaeteae	*Kartonegoro 1073,* BO	Indonesia (Sumatra)	MW462361	MW462512	MW462435	MW462280	MW462593	MW414561
Macrolenes macrosepala	Dissochaeteae	*Penneys 2512,* WNC	Malaysia (Borneo)	MW462365	MW462516	MW462439	MW462284	MW462597	MW414565
Macrolenes muscosa	Dissochaeteae	*Kartonegoro 1084,* BO	Indonesia (Sumatra)	MW462384	MW462535	MW462456	MW462307	MW462617	MW414583
Macrolenes muscosa	Dissochaeteae	*Kartonegoro 1108,* BO	Indonesia (Java)	MW462386	MW462537	MW462458	MW462308	MW462619	MW414585
Macrolenes nemorosa	Dissochaeteae	*Kartonegoro 1070,* BO	Indonesia (Sumatra)	–	MW462538	MW462459	MW462309	MW462620	MW414586
Macrolenes nemorosa	Dissochaeteae	*Kartonegoro 1136,* BO	Indonesia (Borneo)	MW462387	MW462541	MW462462	MW462310	MW462623	MW414589
Macrolenes pachygyna	Dissochaeteae	*Kartonegoro 777,* BO	Indonesia (Borneo)	MW462389	MW462543	MW462463	MW462311	MW462625	MW414590
Macrolenes porphyrocarpa	Dissochaeteae	*Penneys 2486,* WNC	Malaysia (Borneo)	MW462367	MW462518	MW462441	MW462286	MW462599	MW414567
Macrolenes rostrata	Dissochaeteae	*Susanti 264,* BO	Indonesia (Borneo)	MW462373	MW462523	MW462445	MW462293	MW462604	MW414570
Macrolenes stellulata	Dissochaeteae	*Susanti 297,* BO	Indonesia (Borneo)	MW462390	MW462544	MW462464	MW462313	MW462626	MW414591
Macrolenes subulata	Dissochaeteae	*Hughes SUBOE71*, BO	Indonesia (Sumatra)	MW462391	MW462545	MW462465	MW462314	MW462627	MW414592
Macrolenes tuberculata	Dissochaeteae	*Kartonegoro 1128,* BO	Indonesia (Borneo)	MW462392	MW462546	MW462466	MW462315	MW462628	MW414593
Marcetia taxifolia	Marcetieae	*Michelangeli 680,* BH	S America	KU501041	JQ730102	GU968825	JQ730521	–	–
Medinilla amplectens	Sonerileae	*Liu 663,* SYS	Malaysia (Borneo)	–	MN031219	MK994882	MK994882	MK994882	MK994882
Medinilla beamanii	Sonerileae	*Liu 658,* SYS	Malaysia (Borneo)	–	MN031220	MK994880	MK994880	MK994880	MK994880
Medinilla chermezonii	Sonerileae	*Patrice 8570,* MO	Madagascar	MG518536	MG518548	MG702557	MG518563	–	–
Medinilla crassinervia	Sonerileae	*Kartonegoro 1055,* BO	Indonesia (Sulawesi)	MW462393	MW462547	MW462467	MW462316	MW462629	MW414594
Medinilla humbertiana	Sonerileae		Madagascar	–	–	AF215557	–	AF215517	AF215602
Medinilla intermedia	Sonerileae	*Kartonegoro 1109,* BO	Indonesia (Java)	–	–	MW462468	MW462318	MW462630	MW414595
Medinilla lophoclada	Sonerileae	*Ramaheniana 327,* MO	Madagascar	MG518537	–	MG702558	MG518564	–	–
Medinilla micrantha	Sonerileae	*Ramaheniana 271,* MO	Madagascar	MG518538	–	MG702559	MG518565	–	–
Medinilla myrtiformis	Sonerileae	*Kartonegoro 924,* BO	Indonesia (Sulawesi)	–	–	MW462469	MW462319	MW462631	MW414596
Medinilla rubicunda	Sonerileae	*Kartonegoro 1072,* BO	Indonesia (Sumatra)	–	–	MW462470	MW462320	MW462632	MW414597
Medinilla speciosa	Sonerileae	*Liu 669, SYS*	Malaysia, Borneo	–	MN031221	MK994885	MK994885	MK994885	MK994885
Medinilla squillula	Sonerileae	*Lowry II 7287,* MO	Indonesia (Moluccas)	MG518539	MG518547	MG702560	MG518566	–	–
Medinilla teysmannii	Sonerileae	*Kartonegoro 934,* BO	Indonesia (Sulawesi)	MW462394	–	MW462471	MW462322	MW462633	MW414598
Melastoma candidum	Melastomateae	–	China	KR822664	MK292851	KY745894	KY745894	KY745894	KY745894
Melastoma dodecandrum	Melastomateae	–	China	–	MK292847	MH748092	MH748092	MH748092	MH748092
Melastoma malabathricum	Melastomateae	*Penneys 1998,* CAS	–	–	JQ730105	AF272810	JQ730524	AF270748	AB436376

Melastoma minahassae	Melastomateae	*Kartonegoro 1052,* BO	Indonesia (Sulawesi)	MW462395	–	MW462472	MW462324	MW462634	MW414599
Melastoma sanguineum	Melastomateae	*Kartonegoro 1099,* BO	Indonesia (Sumatra)	MW462396	JQ730106	MW462473	MW462325	MW462635	MW414600
Memecylon ligustrifolium	Olisbeoideae	*Lui 726,* SYS	China	–	KP090334	MK994913	MK994913	MK994913	MK994913
Meriania sanguinea	Merianieae	*Fernandez 2215,* QCN	S America	–	KY991534	MH760349	MH781703	MH747628	–
Meriania tuberculata	Merianieae	*Pedraza 2142,* NY	S America	MH781647	MH819925	MH760361	MH781715	MH747639	–
Miconia dodecandra	Miconieae	*Michelangeli 758,* NY	S America	KF821020	KF821600	KX826826	KX826826	KX826826	KX826826
Miconia donaeana	Miconieae	*Michelangeli 727,* NY	S America	KF821024	KY782466	EU056028	KF822206	AM235648	AM235451
Miconia hookeriana	Miconieae	*Cultivated*, M	S America	KF821059	EU055781	EU056040	KF822244	–	–
Mouriri guianensis	Olisbeoideae		S America	FJ792921	FJ792969	AF215575	–	AF215529	AF215610
Ochthocharis borneensis	*Dinophora*-alliance	*Liu 689,* SYS	Malaysia (Borneo)	–	–	MK994895	MK994895	MK994895	MK994895
Ochthocharis dicellandroides	*Dinophora*-alliance	*Bidault 2116,* BRLU	Africa (Gabon)	MG518526	–	MG702562	MG518550	–	–
Osbeckia australiana	Melastomateae	*Brenan 7008,* NY	Australia	KF462868	JQ730116	–	JQ730538	–	–
Osbeckia chinensis	Melastomateae	–	–	–	–	AF215570	–	AF215525	AF210378
Osbeckia nepalensis	Melastomateae	*Penneys 1986,* CAS	Asia	–	JQ730118	MH729215	JQ730539	KX527055	MH722991
Osbeckia stellata	Melastomateae	*Penneys 1969,* CAS	Asia	–	JQ730119	MK331713	MK331713	MK331713	MK331713
Oxyspora paniculata	Sonerileae	*Liu 523,* SYS	Vietnam	–	MN031212	MK994819	MK994819	MK994819	MK994819
Pachycentria constricta	Sonerileae	*Kartonegoro 1076,* BO	Indonesia (Sumatra)	MW462397	MW462548	MW462474	MW462326	MW462636	MW414601
Pachycentria varingiaefolia	Sonerileae	*Barber 76,* E	Indonesia (Sumatra)	–	MW462549	MW462475	MW462327	MW462637	MW414602
Phyllagathis dispar	Sonerileae	*Liu M20,* SYS	Malaysia (Borneo)	–	MG644429	MK994910	MK994910	MK994910	MK994910
Phyllagathis rotundifolia	Sonerileae	*Liu M50,* SYS	Malaysia	–	MG644436	MK994912	MK994912	MK994912	MK994912
Plagiopetalum serratum	Sonerileae	*Liu 717,* SYS	China	–	MN031170	MK994902	MK994902	MK994902	MK994902
Pseudodissochaeta assamica	Dissochaeteae	*Liu 590,* SYS	China	–	MG644480	MK994848	MK994848	MK994848	MK994848
Pseudodissochaeta lanceata	Dissochaeteae	*Liu 593,* SYS	China	–	MN031232	MK994850	MK994850	MK994850	MK994850
Pseudodissochaeta septentrionalis	Dissochaeteae	*Liu 618,* SYS	China	–	MN031231	MK994778	MK994778	MK994778	MK994778
Pternandra azurea	Kibessieae	*Kartonegoro 1077,* BO	Indonesia (Sumatra)	–	–	MW462477	MW462329	MW462639	MW414604
Pternandra coerulescens	Kibessieae	*Chen 543*	Malaysia	–	KF781602	–	–	KF781630	–
Pternandra echinata	Kibessieae	*Chen 542,* SYS	Malaysia	–	KF781604	AF215559	–	AF215520	AF270744
Pternandra galeata	Kibessieae	*Kartonegoro 1057*	Indonesia (Sumatra)	–	–	MW462478	MW462330	MW462640	MW414605
Pternandra multiflora	Kibessieae	*Clausing 142,* MJG	Malaysia	–	GU968801	AF215560	–	–	AF215603
Pternandra tuberculata	Kibessieae	*Liu 651,* SYS	Malaysia (Borneo)	–	MW462551	MK994877	MK994877	MK994877	MK994877
Rhexia aristosa	Rhexieae	*Naczi 12065,* NY	N America	KF462878	JQ730134	–	JQ730555	–	–

Rhexia mariana	Rhexieae	*Ionta 397,* FLAS	N America	–	DQ985631	AF272819	JQ730556	KJ773817	AF323723
Rhexia virginica	Rhexieae	*Michelangeli 1448,* NY	N America	KF462879	DQ985643	KX826830	KX826830	KX826830	KX826830
Rhynchanthera bracteata	Microlicieae	*Zenteno 8801, NY*	S America	KF462880	JQ730137	KX826831	KX826831	KX826831	KX826831
Salpinga maranonesis	Merianieae	*Clark 6979,* US	S America	MF029372	KY991873	JF831982	MF104983	JF832008	JF832048
Sarcopyramis bodinieri	Sonerileae	*Liu 502,* SYS	China	–	MN031206	MK994810	MK994810	MK994810	MK994810
Sonerila celebica	Sonerileae	*Kartonegoro 1027,* BO	Indonesia (Sulawesi)	MW462398	MW462552	MW462479	MW462331	MW462641	MW414606
Sonerila velutina	Sonerileae	*Liu 683,* SYS	Malaysia (Borneo)	–	MN031224	MK994892	MK994892	MK994892	MK994892
Sporoxeia calvicalcarata	Sonerileae	*Liu 716,* SYS	China	–	MN031176	MK994901	MK994901	MK994901	MK994901
Tetrazygia urbanii	Miconieae	*Struwe 116,* NY	S America	KF821374	KF821772	AF270753	KF822547	AF215538	AF215619
Tibouchina grossa	Melastomateae	*Zabala 1,* UPTC	S America	KF462935	JQ730192	JF831983	JQ730612	JF832009	JF832050
Tibouchina longifolia	Melastomateae	*Majure 4277*	S America	–	KY782469	KX826833	KX826833	KX826833	KX826833
Tibouchina urvilleana	Melastomateae	–	–	KR822670	AY460439	MK726030	MK726030	MK726030	MK726030
Tigridiopalma magnifica	Sonerileae	*Zeng G001,* SYS	China	–	KM521848	MF663760	MF663760	MF663760	MF663760
Triolena amazonica	Trioleneae	*Goldenberg 965,* NY	S America	MK165055	–	JF831984	MK296700	NC031890	JF832051
Triolena piloides	Trioleneae	*Penneys 1626,* FLAS	S America	–	KY782507	MH729219	–	MH729238	MH722300
Triolena spicata	Trioleneae	*Penneys 1726,* FLAS	S America	MK296627	KY782508	–	MK296701	MH729240	–

SUMMARY AND CONCLUSIONS

Summary and Conclusions

Dissochaeta Blume (Melastomataceae, tribe Dissochaeteae) is well-known as a scrambling plant genus found in Southeast Asia, where it is an inhabitant of the tropical rainforests or evergreen forests. The genus is characterized by its lianous climbing habit, colourful inflorescences in the shape of a crown and fleshy fruits. This genus is also part of a larger group of genera distributed in Southeast Asia with similar morphological appearances, and together they are called the *Dissochaeta* alliance. Since the first botanical studies of these genera in the 19th century, up to now, botanists proposed many different ways of separating and recognizing genera in the *Dissochaeta* alliance based on morphological characters (Fig. 8-1). Baillon (1877) united most of the related genera into a large genus *Dissochaeta* sensu lato (s.l. = in the wider sense) and divided this large genus in several sections based on morphological similarities. Later on, Cogniaux (1891) and Bakhuizen van den Brink (1943) accepted *Dissochaeta* in a stricter sense (sensu stricto = s.str.) by changing most of Baillon's sections back to generic level again. Maxwell (1984) had a slightly different view then Cogniaux (1891) and Bakhuizen van den Brink (1943), he simplified the generic concept within the *Dissochaeta* alliance by accepting only five genera, *Creochiton*, *Diplectria*, *Dissochaeta*, *Macrolenes* and *Pseudodissochaeta*. This generic concept was followed by Renner (1993), but Renner et al. (2001b) united all scrambling shrub genera into the single genus *Dissochaeta*. Molecular phylogenetic studies of the tribe Dissochaeteae (Clausing & Renner 2001a; Zhou et al. 2019b) indicated that *Dissochaeta* is monophyletic (one ancestor and all its descending species in one group) with *Diplectria* and *Macrolenes* nested in it. Apart from that, *Pseudodissochaeta* was recognized as a distinct genus, sister to *Dissochaeta*. These results suggested that a wide generic taxonomic concept of *Dissochaeta* (s.l.) better reflects the evolution of the genus. However, these studies are generally not comprehensive enough to draw final conclusions about the circumscription of the genera because of insufficient sampling. *Dissochaeta* and its allies are morphologically variable, which often hinders species or generic level identifications because they look similar. The main objectives of this thesis are to clarify the relationships among species and genera within the *Dissochaeta* alliance and to provide a new classification, which reflects the evolutionary and biogeographic traits of this plant group. The study focuses on three aspects of the *Dissochaeta* alliance: the taxonomy, molecular phylogeny and historical biogeography.

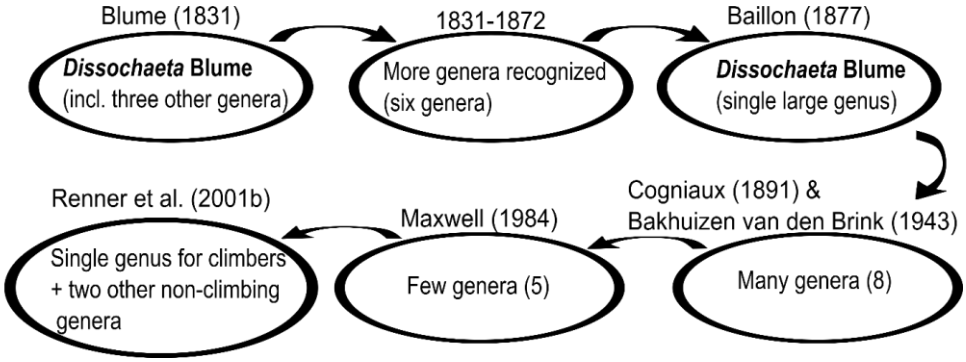


Fig. 8-1. Summary and time line of the various generic circumscription (= the delimitation of which subordinate taxa are part of the studied genus) within the *Dissochaeta* alliance.

- *Which species should be assigned to the* Dissochaeta *alliance? How do they differ morphologically and ecologically? What are their diagnostic morphological characters?*

The revision of the *Dissochaeta* alliance (Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019, 2020; see chapters 2–5) showed that *Creochiton* contains 12 species, *Dissochaeta* (incl. the former genera *Dalenia* and *Diplectria*) contains 54 species and two varieties, *Macrolenes* contains 17 species and *Pseudodissochaeta* contains 5 species. Morphologically, these genera share similarities like woodiness (shrubs or lianas), cymose thyrsoid inflorescences with tetramerous diplostemonous flowers, eight stamens in two whorls (outer=alternipetalous and inner=oppositipetalous), with various connective appendages, and fleshy berries as fruits. All species recognized in these taxonomic revisions are distributed in Southeast Asia, ranging from east Bhutan, northeast India, Andaman-Nicobar Islands eastwards to Myanmar, South China, Indochina, Thailand, southwards throughout the Malesian region but absent in the eastern part of the Lesser Sunda Islands (Figs. 8-2 & 8-3).

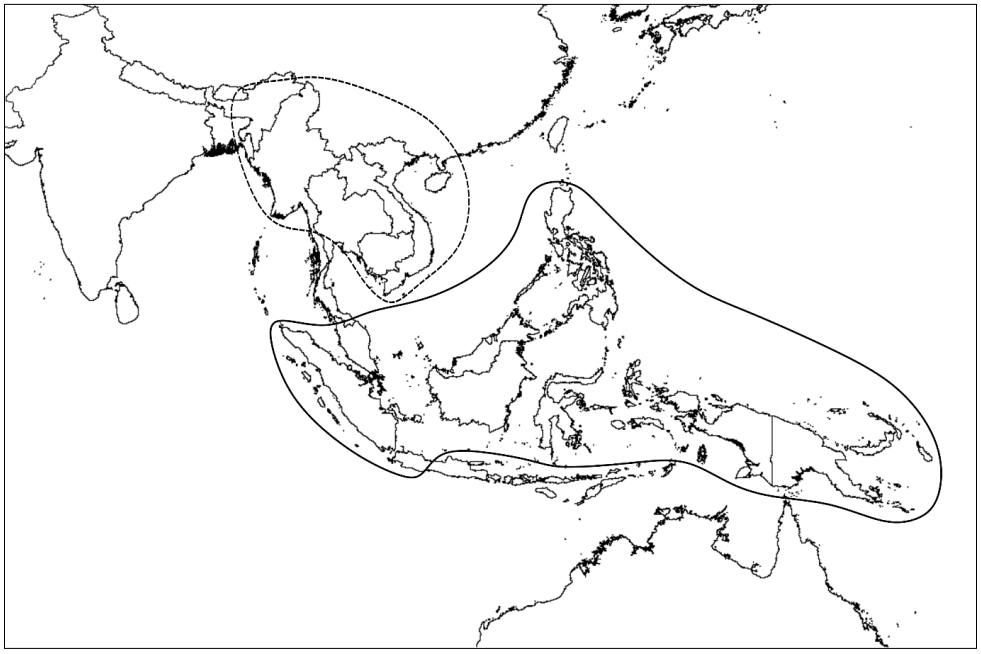


Fig. 8-2. Distribution map of *Creochiton* (continuous line) & *Pseudodissochaeta* (dashed line).

Creochiton consists of epiphytic shrubs or rarely climbers (Chapter 2). The genus is easily spotted by its distinct pair of bracteoles, which envelop the flower buds. Some species have fleshy and concave bracteoles and when these enclose the flower buds, they have a globose appearance (Fig. 8-4A&B). Unlike the other genera in the *Dissochaeta* alliance, *Creochiton* has axillary pseudoumbellate inflorescences except for the West Malesian *C. anomalus* (King) Veldkamp. *Creochiton* is mostly found at high, up to 2000 m elevation, in montane forests. The species prefer a humid but exposed habitat.

Dissochaeta (incl. *Dalenia* and *Diplectria*) is the largest genus in the alliance and also widely distributed throughout Southeast Asia. The genus has a scrambling habit, terminal or rarely axillary cymose panicles, flowers with usually eight dimorphic stamens in two whorls (Fig. 8-4C&D). Some species only have four fertile stamens, because the other four are undeveloped and became staminodes (infertile, partly reduced stamens) or they completely disappeared (Fig. 8-4E&F).

The undeveloped stamens form the outer whorl or the inner whorl. The stamens have distinct connective appendages, they are dorsally triangular or spurred and ventrally biligulate or even inappendiculate.

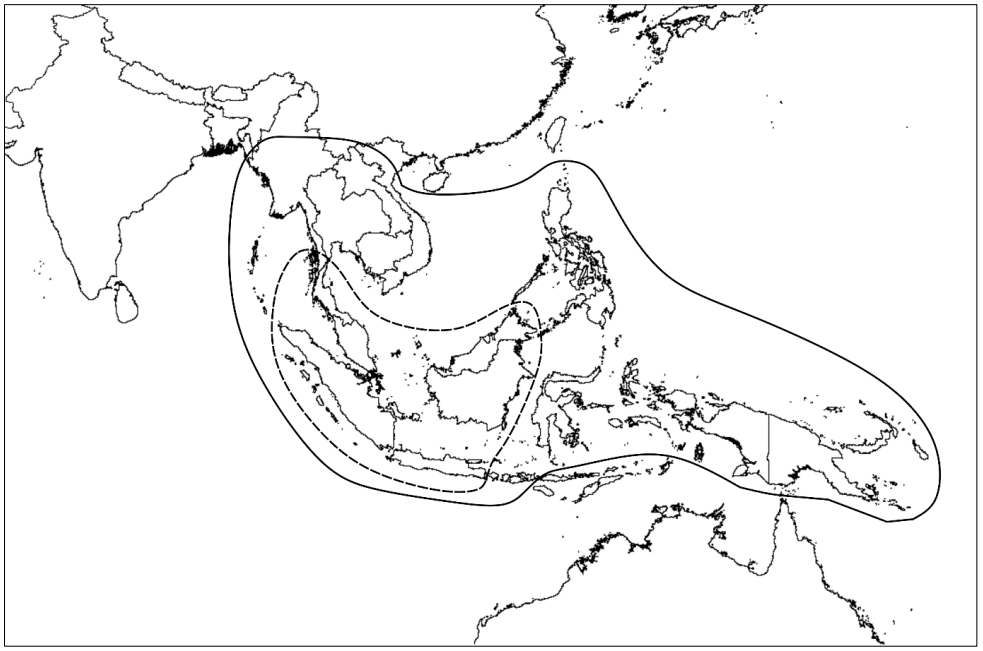


Fig. 8-3. Distribution map of *Dissochaeta* (continuous line) & *Macrolenes* (dashed line).

Macrolenes also has a scrambling habit and cymose panicles as inflorescences, similar to *Dissochaeta*. The genus can be distinguished from the latter by its pair of hair cushions at the leaf base on the lower surface, axillary inflorescences and ventrally fimbriate filiform appendages on the outer whorl stamens (Fig. 8-4I&J). *Dissochaeta* and *Macrolenes* predominantly inhabit secondary vegetations or small open places such as tree fall gaps or they appear along the roadsides. Few species are present in montane forests up to 2500 m elevation.

Pseudodissochaeta are erect and spreading shrubs, a habit unlike all the other genera in the *Dissochaeta* alliance. They are distributed only in mainland Southeast Asia, outside the Malesian region. The flowers have eight isomorphic, equal to subequal stamens (Fig.8- 4K&L). Some of the species can also be recognized by their distinct oblique leaf base and serrulate leaf margin. *Pseudodissochaeta* usually grows in tropical evergreen forests with rather open vegetation.

All genera revised here grow in a nonseasonal climate, thus without seasonal variation in temperature and rainfall. This allows them to grow and flower throughout the year. The pollination of the flowers has never been observed. Likely small flying insects or bees are pollinators and thus take care of the biological reproduction in the alliance. Ants were seen visiting the flowers of some species, but visitors are not necessarily pollinators and it is still highly questionable whether or not the ants are pollinators. Dispersal of the fruits is likely zoochorous (by animals). The fleshy and colourful ripe fruits are eaten by birds or small mammals. The small and numerous seeds per fruit likely easily disperse to other, hopefully also suitable habitats, after defecation.

- *Is the* Dissochaeta *alliance monophyletic? Which taxa are closely related with the alliance? Which evolutionary traits can be used to recognize the clade(s)/groups?*

The tribe Dissochaeteae, in its previous circumscription (sensu lato), appeared to be polyphyletic (more than one origin) in some molecular phylogenetic studies (Clausing & Renner 2001a; Zhou et al. 2019b). Their phylogenetic trees showed three major lineages within the Dissochaeteae: 1) the *Medinilla* alliance; 2) *Dinophora* + *Ochthocharis*; and 3) the *Dissochaeta* alliance (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b). In this thesis, the molecular phylogenetic study based on chloroplast (*ndhF*, *psbK-psbL*, *rbcL* and *rpl16*) and nuclear (nrETS and nrITS) markers using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI) analyses, confirmed the polyphyly of Dissochaeteae s.l. The analyses indicate that the berry fruits and the cochleate seeds, used as diagnostic characters for the tribe, are homoplasious and have multiple parallel origins; the berries may have evolved at least three times within the family.

In agreement with the previous studies, the *Dissochaeta* alliance is a strongly supported monophyletic group, which includes the genera *Creochiton*, *Dissochaeta* (incl. *Dalenia* and *Diplectria*), *Macrolenes* and *Pseudodissochaeta*. The *Dissochaeta* alliance forms a sister group with the South American tribe Cambessedesieae. The monophyly of the *Dissochaeta* alliance is also supported by the following shared morphological characters: thyrsoid inflorescences, tetramerous flowers with eight unequal/subequal stamens in two whorls and berry fruits (Maxwell 1984). Concerning the wood anatomy, the *Dissochaeta* alliance has alternate inter-vessel pits, vessel elements with a wide diameter and rays up to 7 cells wide (Van Vliet 1981).

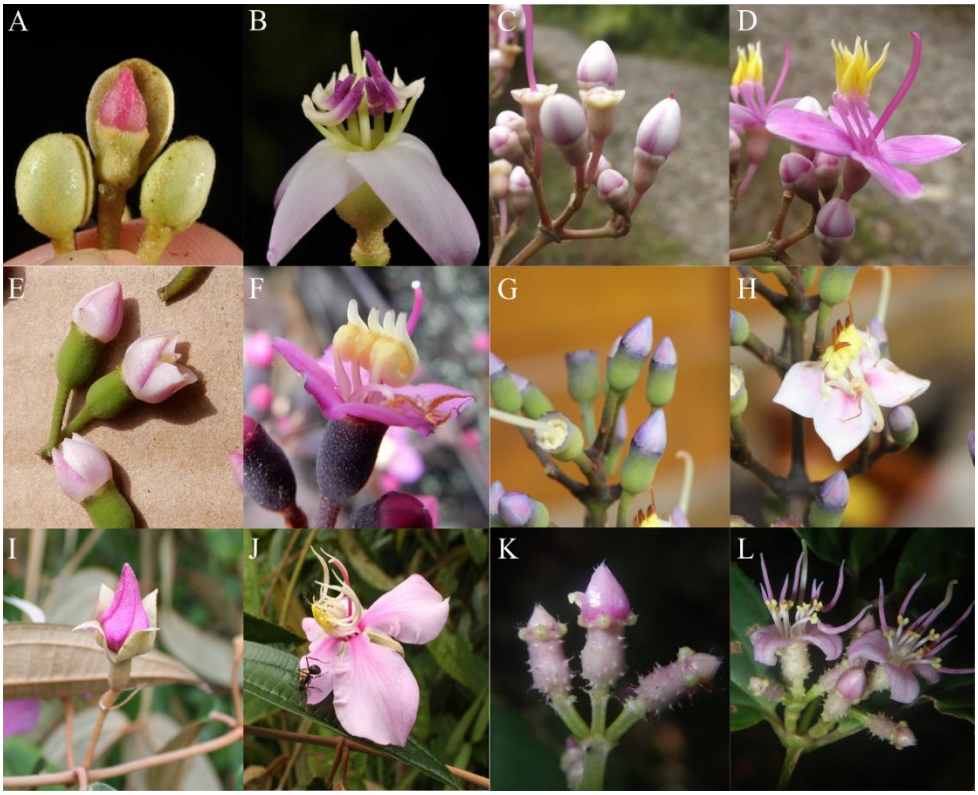


Fig. 8-4. Flower bud and mature flowers of *Dissochaeta* alliance. **A&B.** *Creochiton roseus*; **C&D.** *Dissochaeta bakhuizenii*; **E&F.** *Dalenia glabra*; **G&H.** *Diplectria conica*; **I&J.** *Macrolenes nemorosa*; **K&L.** *Pseudodissochaeta* sp. Photographs by P. Pielser (A&B), A. Kartonegoro (C,D,G,H,I,J), D. Penneys (E&F), M. Nuraliev (K&L).

- *If the* Dissochaeta *alliance is monophyletic, then how can the phylogenetic results be translated into a new classification of monophyletic and recognizable genera? Which morphological apomorphies (newly evolved characters) support the classification?*

The phylogenetic results, together with morphology and wood anatomy, support a recircumscription to a narrower tribe Dissochaeteae (excluding the *Medinilla* alliance, and the genera *Dinophora* and *Ochthocharis*). The clade (= monophyletic group) of the *Dissochaeta* alliance or subtribe Dissochaetinae is hereby raised to the tribal rank as Dissochaeteae. With this redefinition, Dissochaeteae is only distributed from east Bhutan, northeast India, and South China throughout Southeast Asia to New Guinea with no entities in Tropical Africa, Madagascar, Sri Lanka and mainland India (Figs. 8-2 & 8-3). Within the *Dissochaeta* alliance, six lineages/clades are recovered with strong statistical support from all analyses. The phylogeny of tribe Dissochaeteae shows that three clades coincide with three (monophyletic) genera, *Creochiton*, *Macrolenes* and *Pseudodissochaeta* (Fig. 8-5). *Dissochaeta* (sensu Kartonegoro et al. 2018) is paraphyletic (one ancestor but not all descending species included) and includes five lineages, each with strong or moderate supported values (Fig. 8-5). The first lineage (A) consists of what was known as the *Dissochaeta* sect. *Dalenia* clade. The second is *Dissochaeta* sect. *Disparistemones* (B). The third lineage (C) is *Dissochaeta* sect. *Diplectria*. The fourth lineage (D) is the *Dissochaeta rostrata* complex (informal group), which is grouped and sister to the *Macrolenes* clade. The last lineage (E) is the clade that consists of the remaining *Dissochaeta* species (*Dissochaeta* s.str.) including *Dissochaeta* sect. *Anoplodissochaeta*, sect. *Diplostemones*, sect. *Dissochaeta*, sect. *Dissochaetopsis*, sect. *Isostemones*, sect. *Omphalopus* inside it. Based on these molecular phylogenetic results, *Dalenia* and *Diplectria* are reinstated again to generic rank, which makes the generic concept of *Dissochaeta* narrower (*Dissochaeta* s.str.). The *Dissochaeta* sect. *Disparistemones* is included under *Dalenia*. The *Dissochaeta rostrata* complex, which is closely related to *Macrolenes*, is included in the latter, thus broadening the circumscription of *Macrolenes*.

Pseudodissochaeta forms the most basal clade within the *Dissochaeta* alliance, sister to all other taxa in the alliance. Next, *Creochiton* branches off and is sister to all scrambling shrub genera (*Dalenia*, *Diplectria*, *Dissochaeta* and *Macrolenes*). Within the scrambling shrub clade, *Dalenia* is basal, followed by *Diplectria* and the final split is between *Dissochaeta* and *Macrolenes*. Several morphological traits support the various clades. Some character states are individually typical for a genus/clade, but other clades have to be characterized by a combination of character states. The habit of shrubs is shared by all taxa in the *Dissochaeta* alliance in three different states. Erect, terrestrial shrubs is the plesiomorphic (original or primitive) state, present in *Pseudodissochaeta*, but as such typical for this genus within the alliance. This is followed by epiphytic shrubs that are typical for *Creochiton*. The most common state is scrambling shrubs, the most derived (last evolved) character state, shared by *Dalenia*, *Diplectria*, *Dissochaeta* and *Macrolenes*. The scrambling habit evolved only once in the old world Melastomataceae (Clausing & Renner 2001a). Interpetiolar growth is usually shown between the attachments of the petioles of the opposite leaves and it likely facilitates the climbing habit by providing a hold. Genera with scrambling shrubs have different forms of interpetiolar growth. The interpetiolar growth of *Diplectria*, *Dissochaeta* and *Macrolenes* consists only of a simple raised line or small ridges. *Dalenia* is the only genus with a more developed interpetiolar growth, which forms lobes or produces a pectinate structure.

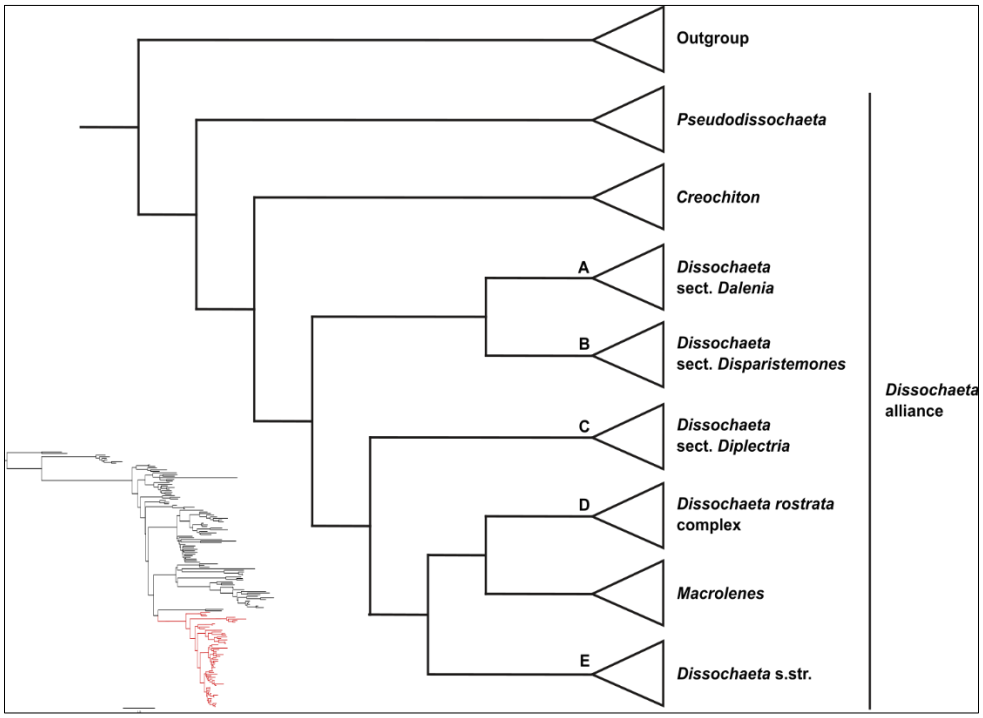


Fig. 8-5. Simplified phylogenetic tree of the *Dissochaeta* alliance, whereby the triangles represent the species. **A.** *Dissochaeta* sect. *Dalenia* (now *Dalenia)*; **B.** *Dissochaeta* sect. *Disparistemones* (now *Dalenia)*; **C.** *Dissochaeta* sect. *Diplectria* (now *Diplectria*); **D.** *Dissochaeta rostrata* complex (now *Macrolenes*); **E.** *Dissochaeta* s.str. (now *Dissochaeta*). Bottom left: cladogram from complete Melastomataceae samples whereby the red group forms the *Dissochaeta* alliance.

Truncate or united calyx lobes is plesiomorphic in the alliance. They are usually visible as only four small teeth or undulations or sometimes triangular shapes are present as the tips on the hypanthium (outgrown flower receptacle). *Pseudodissochaeta* usually has four small thickened teeth-like enations as calyx lobes. *Creochiton*, *Dalenia* and *Diplectria* also have truncate calyx lobes, but visible as small undulations at the apex of the hypanthium. Sometimes these undulations do not even develop and the hypanthium has no calyx extensions and shows a flat edge. In *Dissochaeta* the partially truncate calyx tube has four triangular tips. The length of these tips varies within the genus from short (half as long as the truncate part) to long (twice as long as the truncate part). The calyx lobes of *Macrolenes* differ from all other genera in the alliance. The genus has as synapomorphy four, free, well-developed calyx lobes with a rounded, triangular or linear shape. The length of the lobes varies, up to as long as the hypanthium.

Isomorphic (equal) stamens are considered as the plesiomorphic state and they are found in the basal clades, like *Pseudodissochaeta*. *Creochiton* generally has species with isomorphic stamens except *C. anomalus* and *C. monticola* (Ridl.) Veldkamp. All woody climbing genera have dimorphic stamens (2 shapes) as synapomorphy. Dimorphic stamens usually differ in the size and shape of the anthers. Having only fertile stamens in both whorls is the plesiomorphic state in the *Dissochaeta* alliance and present in most genera: *Pseudodissochaeta*, *Creochiton*, *Dissochaeta* and *Macrolenes*. An infertile outer whorl is shared by *Dalenia* and *Diplectria*, of which the outer stamens develop to 1/3 of the fertile stamens or they are fully reduced. An infertile inner whorl of stamens is found in a few species of *Creochiton* and *Dissochaeta*.

- Does the molecular phylogeny corroborate any of the formerly proposed infrageneric taxa? How do they relate to each other?

Only within *Dissochaeta* (in various circumscriptions) infrageneric taxa were described (Blume 1831a, 1831b; Baillon 1877; Cogniaux 1891; Merrill 1917). In this thesis, based on the results of the phylogenetic analyses, some sections are now recognized as distinct genera. They are sections *Creochiton*, *Dalenia* and *Diplectria*. The remaining sections are now still

part of genus *Dissochaeta*. The molecular phylogeny of *Dissochaeta* shows that there are only two supported clades within *Dissochaeta*, that can be considered as infrageneric taxa (section level; Fig. 8-6). The first clade is classified as section *Diplostemones* (C) and the other is section *Dissochaeta* (D). Infrageneric taxa were never proposed for *Macrolenes*. However, the inclusion of the well-supported *Dissochaeta rostrata* complex in the genus has to be acknowledged, and two sections are now recognized (Fig. 8-6); Section *Terminaliflores* (A) is established to acknowledge the *Dissochaeta rostrata* group, while the remaining species (formerly *Macrolenes* in the strict sense) are now included in section *Macrolenes* (B).

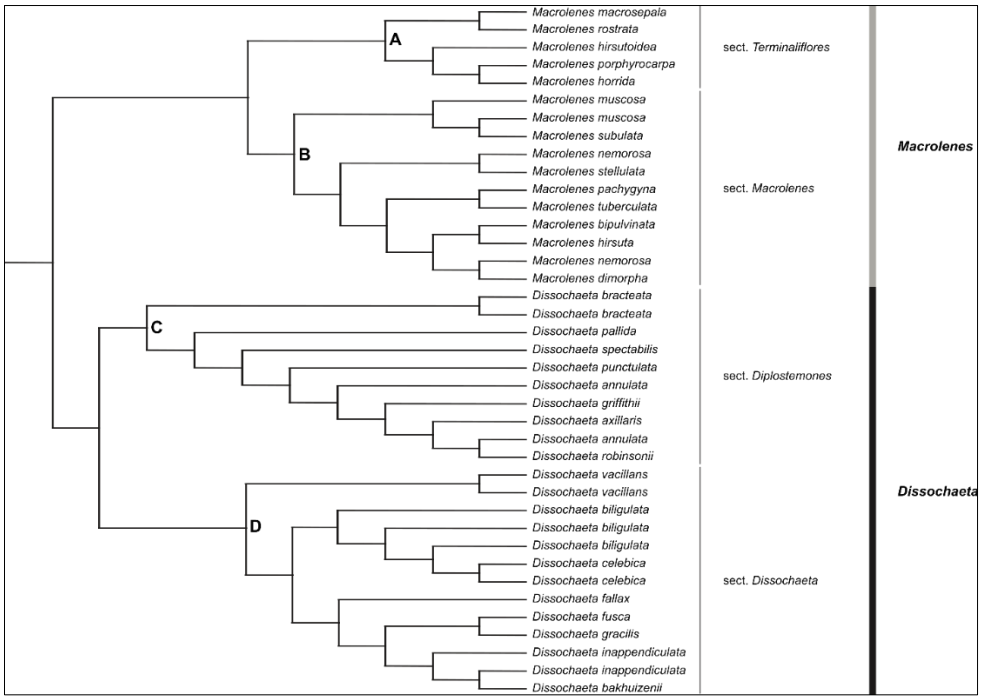


Fig. 8-6. Phylogenetic tree of the *Macrolenes* and *Dissochaeta* clades showing the new infrageneric classification in sections.

- *Where and when did the major diversification events occur in the* Dissochaeta *alliance? Which scenario results from the historical biogeography analysis of the genera and species? How can we explain the migration routes?*

Molecular dating analyses suggest an origin of the *Dissochaeta* alliance in South America. The alliance was split from the South American Cambessedesieae in the late Eocene (39.32 Ma) and dispersed to and radiated within Southeast Asia in the middle Oligocene (28.96 Ma). The ancestor of the *Dissochaeta* alliance might have migrated from South America to Southeast Asia. A wide ancestral distribution in Southeast Asia (Indochina and Borneo) was inferred as the area of origin of the *Dissochaeta* alliance, where much of the speciation occurred (Fig. 8-7). Mainland Southeast Asia (areas AB; Fig. 8-7) is proved as the area of origin of the genus *Pseudodissochaeta* (I). *Creochiton* (II) likely originated on Sulawesi (area G; Fig. 8-7) and dispersed several times northward to the Philippines, westward to Java and eastward to Moluccas-New Guinea. The scrambling shrub genera (*Dalenia*, *Diplectria*, *Dissochaeta* and *Macrolenes*) likely originated on Borneo (area F; Fig. 8-7). *Dalenia* (III)

originated on Borneo, followed by various speciation events on the island (area F; Fig. 8-7). *Diplectria* (IV) and *Macrolenes* (V) might have a Borneo-Sumatra origin (areas DF; Fig. 8-7) while *Dissochaeta* (VI)'s origin might be Sumatra (area D; Fig. 8-7). Numerous dispersal events are inferred within Borneo, westward to Sumatra, Malay Peninsula and Java or eastward across Wallace's line to Sulawesi, the Philippines and the Moluccas-New Guinea, the extension to the latter two areas occurred with Sulawesi as stepping stone (Fig. 8-7). The recent dispersal patterns of the *Dissochaeta* alliance are similar to patterns identified in several other Southeast Asian plant groups, and highly congruent with geological events in Southeast Asia.

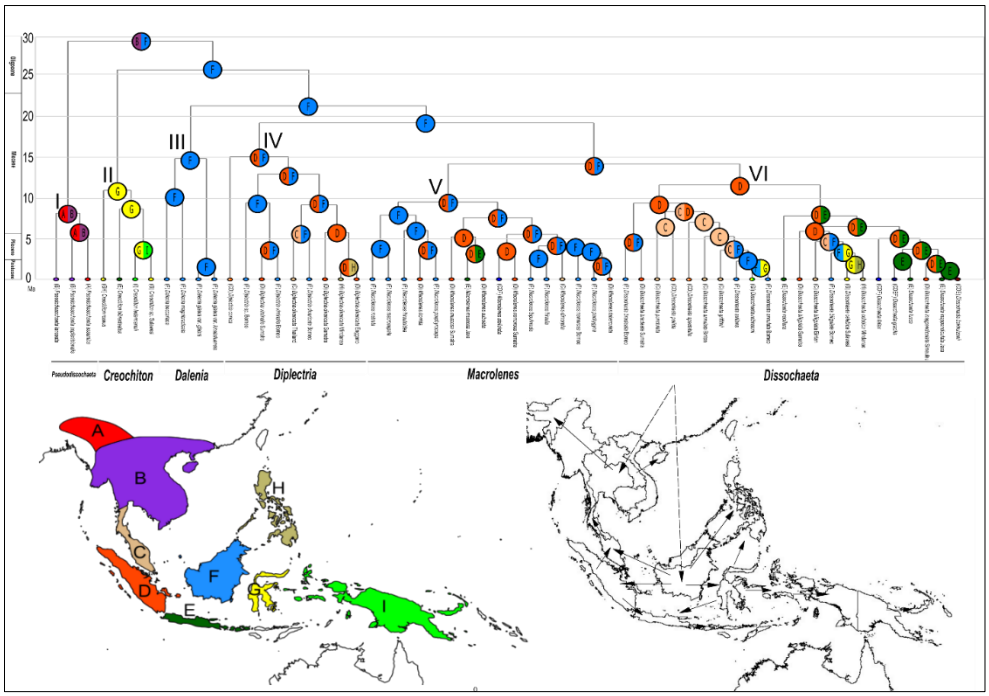


Fig. 8-7. Possible ancestral areas and dispersal routes for the *Dissochaeta* alliance. Colours in the pie charts and map correspond with geographical areas; Ma, million years ago. **A:** E Bhutan, NE India and NW Myanmar; **B:** Indochina, incl. C & E Myanmar, S China, Hainan and Thailand; **C:** S Thailand, Malay Peninsula and Riau Archipelago; **D:** Sumatra and surrounding islands; **E:** Java and Lesser Sunda Islands excl. Sumba, Flores and Timor; **F:** Borneo; **G:** Sulawesi; **H:** Philippines incl. Palawan; and **I:** Moluccas and New Guinea. Clade: **I.** *Pseudodissochaeta*; **II.** *Creochiton*; **III.** *Dalenia*; **IV.** *Diplectria*; **V.** *Macrolenes*; VI. *Dissochaeta*.

SAMENVATTING EN CONCLUSIES

Samenvatting en Conclusies

Dissochaeta Blume (Melastomataceae, tribus Dissochaeteae) staat bekend als een klimmend plantengeslacht dat voorkomt in Zuidoost-Azië in de tropische regenwouden of groenblijvende bossen. Het geslacht wordt gekenmerkt door zijn liaan-achtige klimgewoonte, kleurrijke bloeiwijzen in de vorm van een kroon en vlezige vruchten. Dit geslacht maakt ook deel uit van een grotere groep geslachten verspreid in Zuidoost-Azië met vergelijkbare morfologische kenmerken, en samen worden ze de *Dissochaeta*-alliantie genoemd. Sinds de eerste botanische studies van deze geslachten in de 19e eeuw lopend tot nu toe, hebben botanici veel verschillende classificaties voorgesteld om de geslachten in de *Dissochaeta*-alliantie te scheiden en te herkennen op basis van morfologische kenmerken (Fig. 8-1). Baillon (1877) verenigde de meeste verwante geslachten in een groot geslacht *Dissochaeta* sensu lato (s.l. = in de ruimere zin) en verdeelde dit grote geslacht in verschillende secties op basis van morfologische overeenkomsten. Later accepteerden Cogniaux (1891) en Bakhuizen van den Brink (1943) *Dissochaeta* in striktere zin (sensu stricto = s.str.) door de meeste secties van Baillon weer terug te brengen naar het geslachts niveau. Maxwell (1984) had een iets andere mening dan Cogniaux (1891) en Bakhuizen van den Brink (1943), hij vereenvoudigde het geslachtsconcept binnen de *Dissochaeta*-alliantie door slechts vijf geslachten te accepteren, *Creochiton*, *Diplectria*, *Dissochaeta*, *Macrolenes* en *Pseudodissochaeta*. Dit generieke concept werd gevolgd door Renner (1993), maar Renner et al. (2001b) verenigde alle klimmende struik geslachten tot het enkele geslacht *Dissochaeta*. Moleculaire fylogenetische studies van de stam Dissochaeteae (Clausing & Renner 2001a; Zhou et al. 2019b) gaven aan dat *Dissochaeta* monofyletisch is (één voorouder en al zijn nageslacht in één groep) met *Diplectria* en *Macrolenes* erin genesteld. Afgezien daarvan werd *Pseudodissochaeta* erkend als een apart geslacht, het zuster geslacht van *Dissochaeta*. Deze resultaten suggereerden dat een breed generiek taxonomisch concept van *Dissochaeta* (s.l.) de evolutie van het geslacht beter weerspiegelt. Deze onderzoeken zijn echter over het algemeen niet alomvattend genoeg om definitieve conclusies te trekken over de omschrijving van de geslachten omdat de steekproeven te beperkt waren. *Dissochaeta* en zijn bondgenoten zijn morfologisch variabel, wat vaak de identificatie van soorten of geslachten belemmert omdat ze op elkaar lijken. De belangrijkste doelstellingen van dit proefschrift zijn om de relaties tussen soorten en geslachten binnen de *Dissochaeta*-alliantie te verduidelijken en om een nieuwe classificatie te bieden, die de evolutionaire en biogeografische eigenschappen van deze plantengroep weerspiegelt. De studie concentreert zich op drie aspecten van de *Dissochaeta*-alliantie: de taxonomie, moleculaire fylogenie en historische biogeografie.

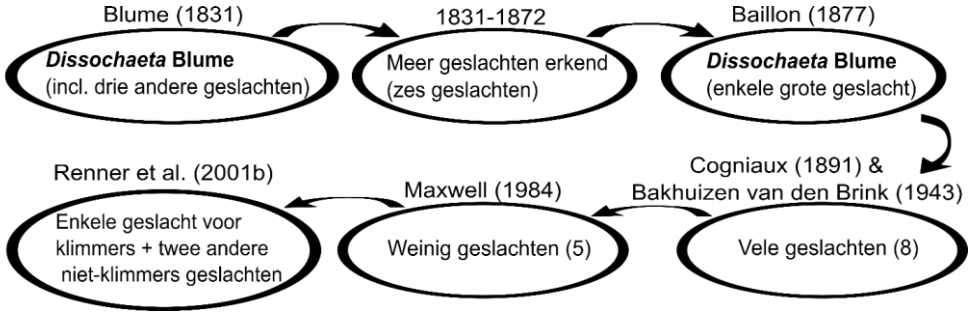


Fig. 8-1. Samenvatting en tijdlijn van de verschillende geslachts omschrijvingen (= de afbakening waarvan ondergeschikte taxa deel uitmaken van het bestudeerde geslacht) binnen de *Dissochaeta*-alliantie

- *Welke soort moet worden toegewezen aan de* Dissochaeta-*alliantie? Hoe verschillen ze morfologisch en ecologisch? Wat zijn hun diagnostische morfologische kenmerken?*

De herziening van de *Dissochaeta*-alliantie (Kartonegoro & Veldkamp 2013; Kartonegoro et al. 2018, 2019, 2020; zie hoofdstukken 2–5) toonde aan dat *Creochiton* 12 soorten bevat, *Dissochaeta* (incl. de voormalige geslachten *Dalenia* en *Diplectria*) 54 soorten en twee variëteiten, *Macrolenes* bevat 17 soorten en *Pseudodissochaeta* bevat 5 soorten. Morfologisch vertonen deze geslachten overeenkomsten zoals houtigheid (struiken of lianen), cymose thyrsoïde bloeiwijzen met tetramere tweevoudige bloemen, acht meeldraden in twee kransen (buitenste = afwisselend met kroonbladen en binnenste = tegenover kroonbladen), met verschillende aanhangsels aan de connectieven en vlezige bessen als vruchten. Alle soorten die in deze taxonomische herzieningen worden erkend, zijn verspreid in Zuidoost-Azië, variërend van Oost-Bhutan, Noordoost-India, Andaman-Nicobaren in oostelijke richting tot Myanmar, Zuid-China, Indochina, Thailand, zuidwaarts door de hele Maleise regio maar afwezig in het oostelijke deel van de Kleine Soenda-eilanden (Fig. 8-2 & 8-3).

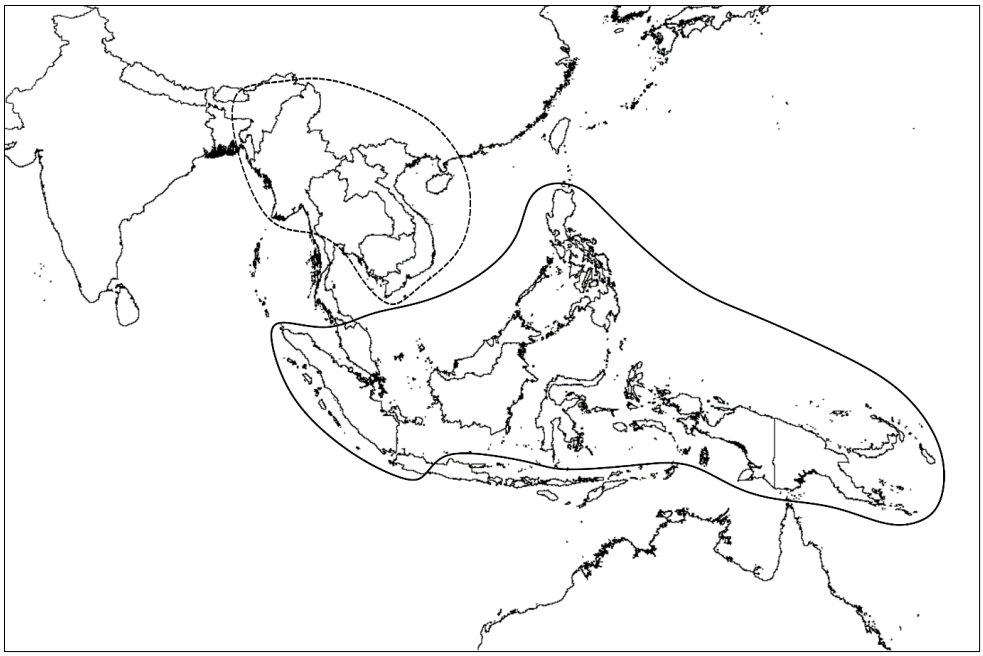


Fig. 8-2. Verspreidingskaart van *Creochiton* (doorlopende lijn) & *Pseudodissochaeta* (stippellijn).

Creochiton bestaat uit epifytische struiken of zelden klimmers (hoofdstuk 2). Het geslacht is gemakkelijk te herkennen aan zijn aparte paar schutbladen, die de bloemknoppen omhullen. Sommige soorten hebben vlezige en concave schutbladen en wanneer deze de bloemknoppen omsluiten, zien ze er bolvormig uit (Fig. 8-4A&B). In tegenstelling tot de andere geslachten in de *Dissochaeta*-alliantie, heeft *Creochiton* axillaire pseudoumbellate bloeiwijzen behalve de West-Maleisische *C. anomalus* (King) Veldkamp. *Creochiton* wordt meestal gevonden op grote hoogte, tot 2000 m hoogte, in bergbossen. De soort geeft de voorkeur aan een vochtig maar open habitat.

Dissochaeta (incl. *Dalenia* en *Diplectria*) is het grootste geslacht in de alliantie en ook wijd verspreid in Zuidoost-Azië. Het geslacht heeft een klimmende gewoonte, terminale of zelden axillaire cymose-pluimen, bloemen met gewoonlijk acht dimorfe meeldraden in twee kransen (Fig. 8-4C&D). Sommige

soorten hebben maar vier vruchtbare meeldraden, omdat de andere vier onontwikkeld zijn en staminodia zijn geworden (onvruchtbare, gedeeltelijk verkleinde meeldraden) of volledig verdwenen zijn (Fig. 8-4E&F). De onontwikkelde meeldraden vormen de buitenste krans of de binnenste krans. De meeldraden hebben verschillende verbindende aanhangsels, ze zijn dorsaal driehoekig of gespoord en ventraal biligulaat of zelfs zonder aanhangsel.

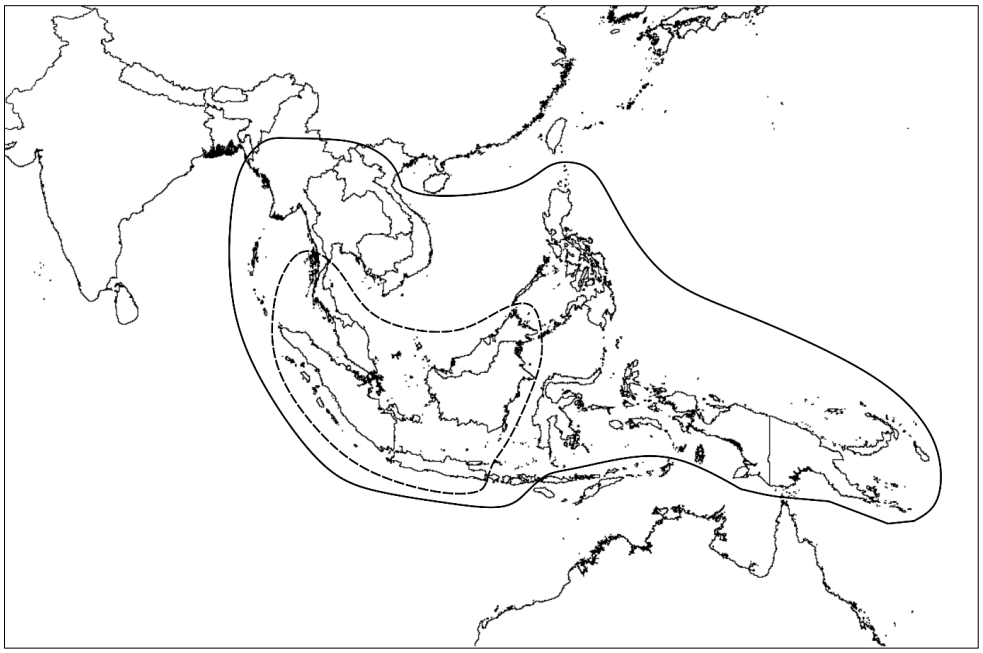


Fig. 8-3. Verspreidingskaart van *Dissochaeta* (doorlopende lijn) & *Macrolenes* (stippellijn).

Macrolenes heeft ook een klimmende gewoonte en cymose-pluimen als bloeiwijzen, vergelijkbaar met *Dissochaeta*. Het geslacht kan van de laatste worden onderscheiden door zijn paar haarkussens op de bladbasis aan de onderzijde, axillaire bloeiwijzen en ventraal fimbriate draadvormige aanhangsels op de buitenste krans meeldraden (Fig. 8-4I&J). *Dissochaeta* en *Macrolenes* leven voornamelijk in secundaire vegetaties of kleine open plekken zoals openingen ontstaan door vallende bomen of ze zijn aanwezig langs de bermen. Er zijn maar weinig soorten in de bergbossen tot een hoogte van 2500 m.

Pseudodissochaeta zijn rechtopstaande en spreidende struiken, een habitus die anders is dan alle andere geslachten in de *Dissochaeta*-alliantie. Ze komen alleen voor op het vasteland van Zuidoost-Azië, buiten de Maleise regio. De bloemen hebben acht isomorfe meeldraden, gelijk of bijna gelijke meeldraden (Fig. 8-4K&L). Sommige soorten zijn ook te herkennen aan hun aparte schuine bladbasis en gekartelde bladrand. *Pseudodissochaeta* groeit meestal in tropische groenblijvende bossen met vrij open vegetatie.

Alle hier herziene geslachten groeien in een niet-seizoensgebonden klimaat, dus zonder seizoensvariaties in temperatuur en regenval. Hierdoor kunnen ze het hele jaar door groeien en bloeien. De bestuiving van de bloemen is nooit waargenomen. Waarschijnlijk zijn kleine vliegende insecten of bijen bestuivers en zorgen zo voor de biologische voortplanting in de alliantie. Er zijn mieren gezien die de bloemen van sommige soorten bezochten, maar bezoekers zijn niet noodzakelijk bestuivers en het is nog steeds zeer de vraag of de mieren bestuivers zijn. Verspreiding van de vruchten is waarschijnlijk zoöchoor (door dieren). De

vlezige en kleurrijke rijpe vruchten worden gegeten door vogels of kleine zoogdieren. De kleine en talrijke zaden per vrucht verspreiden zich via ontlasting waarschijnlijk gemakkelijk naar andere, hopelijk ook geschikte habitats.

- *Is de* Dissochaeta-*alliantie monofyletisch? Welke taxa zijn nauw verwant met de alliantie? Welke evolutionaire kenmerken kunnen worden gebruikt om de clade(s) / groepen te herkennen?*

Het tribus Dissochaeteae, in zijn vorige omschrijving (sensu lato), bleek polyfyletisch te zijn (meer dan één oorsprong) in sommige moleculair fylogenetische studies (Clausing & Renner 2001a; Zhou et al. 2019b). Hun fylogenetische bomen vertoonden drie belangrijke afstammingslijnen binnen de Dissochaeteae: 1) de *Medinilla*-alliantie; 2) *Dinophora* + *Ochthocharis*; en 3) de *Dissochaeta*-alliantie (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b). In dit proefschrift werd bij de moleculaire fylogenetische studie gebruik gemaakt van chloroplast (*ndhF*, *psbK-psbL*, *rbcL* en *rpl16*) en nucleaire (nrETS en nrITS) markers en werden de data statistisch geanalyseerd met behulp van Maximum Parsimony (MP), Maximum Likelihood (ML) en Bayesian Inference (BI) analyses, wat de polyfyly van Dissochaeteae s.l. bevestigde. De analyses geven aan dat de bessenvruchten en de cochleate zaden, die als diagnostische kenmerken voor het tribus worden gebruikt, homoplaas zijn en meerdere parallelle oorsprongen hebben; de bessen zijn binnen de familie minstens drie keer zijn geëvolueerd.

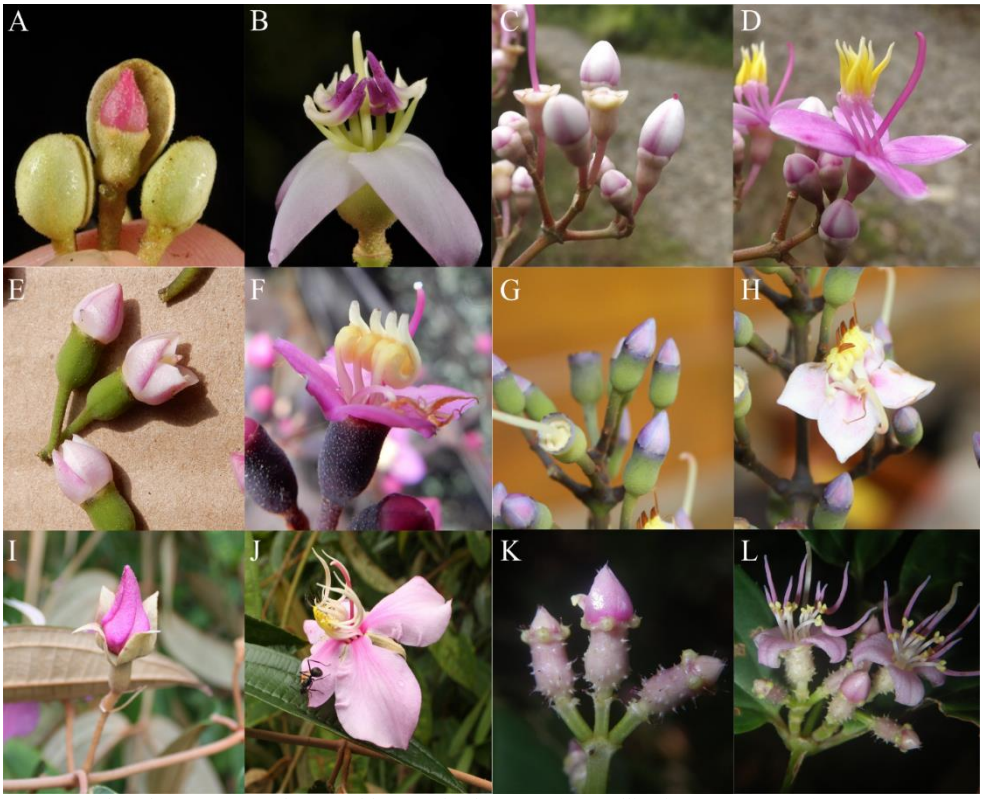


Fig. 8-4. Bloemknoppen en volwassen bloemen in de *Dissochaeta*-alliantie. **A&B.** *Creochiton roseus*; **C&D.** *Dissochaeta bakhuizenii*; **E&F.** *Dalenia glabra*; **G&H.** *Diplectria conica*; **I&J.** *Macrolenes nemorosa*; **K&L.** *Pseudodissochaeta* sp. Foto's door P. Pielser (A&B), A. Kartonegoro (C, D, G, H, I, J), D. Penneys (E&F), M. Nuraliev (K&L).

In overeenstemming met de eerdere studies is de *Dissochaeta*-alliantie een sterk ondersteunde monofyletische groep, die de geslachten *Creochiton*, *Dissochaeta* (inclusief *Dalenia* en *Diplectria*), *Macrolenes* en *Pseudodissochaeta* omvat. De *Dissochaeta*-alliantie vormt een zustergroep met het Zuid-Amerikaanse tribus Cambessedesieae. De monofylie van de *Dissochaeta*-alliantie wordt ook ondersteund door de volgende gemeenschappelijke morfologische kenmerken: thyrsoïde bloeiwijzen, tetramere bloemen met acht ongelijke / subgelijke meeldraden in twee kransen en bessen (Maxwell 1984). Wat de houtanatomie betreft, heeft de *Dissochaeta*-alliantie afwisselende stippels tussen vaten, vat elementen met een wijde diameter en stralen tot 7 cellen breed (Van Vliet 1981).

- *Als de* Dissochaeta-*alliantie monofyletisch is, hoe kunnen de fylogenetische resultaten dan worden vertaald in een nieuwe classificatie van monofyletische en herkenbare geslachten? Welke morfologische apomorfieën (nieuw ontwikkelde kenmerken) ondersteunen de classificatie?*

De fylogenetische resultaten, samen met de morfologie en de houtanatomie, ondersteunen een terugkeer naar een smallere stam Dissochaeteae (met de *Medinilla*-alliantie en de geslachten *Dinophora* en *Ochthocharis* uitgesloten). De tak (= monofyletische groep in een fylogenetische boom) met de *Dissochaeta*-alliantie of subtribus Dissochaetinae wordt hierbij verheven tot de rang van tribus en heet Dissochaeteae. Door deze herdefiniëring is Dissochaeteae alleen aanwezig in Oost-Bhutan, Noordoost-India tot Zuid-China, door heel Zuidoost-Azië naar Nieuw-Guinea zonder vertegenwoordigers in Tropisch Afrika, Madagaskar, Sri Lanka en het vasteland van India (Fig. 8-2 & 8-3). Binnen de *Dissochaeta*-alliantie worden zes takken teruggevonden met sterke statistische ondersteuning in alle analyses. De fylogenie van het tribus Dissochaeteae laat zien dat drie takken samenvallen met drie (monofyletische) geslachten, *Creochiton*, *Macrolenes* en *Pseudodissochaeta* (Fig. 8-5). *Dissochaeta* (sensu Kartonegoro et al. 2018) is parafyletisch (één voorouder maar niet alle afstammende soorten inbegrepen) en omvat vijf geslachten, elk met sterke of matige statistische ondersteuning (Fig. 8-5). De eerste tak (A) bestaat uit wat bekend stond als de *Dissochaeta* sectie *Dalenia* tak. De tweede is *Dissochaeta* sectie *Disparistemones* (B). De derde tak (C) is *Dissochaeta* sectie *Diplectria*. De vierde tak (D) is het *Dissochaeta rostrata*-complex (informele groep), die de zustergroep is van de *Macrolenes* tak. De laatste tak (E) bestaat uit de overgebleven *Dissochaeta* soorten (*Dissochaeta* s.str.) inclusief *Dissochaeta* sectie *Anoplodissochaeta*, sectie *Diplostemones*, sectie *Dissochaeta*, sectie *Dissochaetopsis*, sectie *Isostemones*, sectie *Omphalopus*. Op basis van deze moleculaire fylogenetische resultaten worden *Dalenia* en *Diplectria* weer teruggebracht tot geslachts niveau, wat het geslachts concept van *Dissochaeta* smaller maakt (*Dissochaeta* s.str.). *Dissochaeta* sectie *Disparistemones* is nu een deel van *Dalenia*. Het *Dissochaeta rostrata*-complex, dat nauw verwant is aan *Macrolenes*, maakt deel uit van de laatste, waardoor de omschrijving van *Macrolenes* wordt verbreed.

Pseudodissochaeta vormt de meest basale tak binnen de *Dissochaeta*-alliantie, de zus van alle andere taxa in de alliantie. Vervolgens vertakt *Creochiton* af en is het zustergeslacht van alle geslachten met klimmende struiken (*Dalenia*, *Diplectria*, *Dissochaeta* en *Macrolenes*). Binnen de klauterende struiktak splitst *Dalenia* basaal af, gevolgd door *Diplectria* en de laatste splitsing is tussen *Dissochaeta* en *Macrolenes*. Verschillende morfologische kenmerken ondersteunen de verschillende takken. Sommige kenmerktoestanden zijn individueel typerend voor een geslacht / tak, maar andere takken worden gekenmerkt door een combinatie van kenmerktoestanden. De struik habitus wordt gedeeld door alle taxa in de *Dissochaeta*-alliantie in drie verschillende toestanden. Rechtopstaande, terrestrische struiken

is de plesiomorfe (oorspronkelijke of primitieve) toestand, aanwezig in *Pseudodissochaeta*, maar als zodanig typerend voor dit geslacht binnen de alliantie. Dit wordt gevolgd door epifytische struiken die typisch zijn voor *Creochiton*. De meest voorkomende toestand is klimmende struik, de meest afgeleide (laatst ontwikkelde) kenmerktoestand, aanwezig bij *Dalenia*, *Diplectria*, *Dissochaeta* en *Macrolenes*. Het klimmen is slechts één keer geëvolueerd in de oude wereld Melastomataceae (Clausing & Renner 2001a). Interpetiolaire groei wordt meestal getoond tussen de aanhechtingen van de bladstelen van de tegenovergestelde bladeren en het vergemakkelijkt waarschijnlijk het klimmen door een houvast te bieden. Geslachten met klimmende struiken hebben verschillende vormen van interpetiolaire groei. De interpetiolaire groei van *Diplectria*, *Dissochaeta* en *Macrolenes* bestaat alleen uit een eenvoudige verhoogde lijn of kleine ribbels. *Dalenia* is het enige geslacht met een meer ontwikkelde interpetiolaire groei, die lobben vormt of een pectinate structuur produceert.

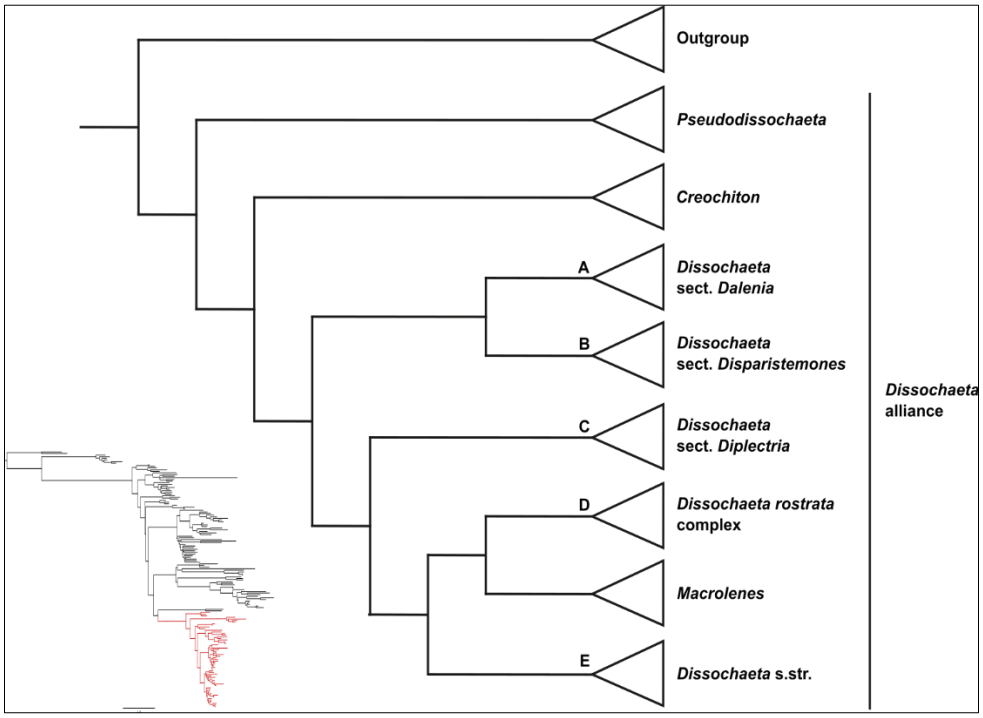


Fig. 8-5. Vereenvoudigde fylogenetische boom van de *Dissochaeta*-alliantie, waarbij de driehoeken de soorten voorstellen. **A.** *Dissochaeta* sectie *Dalenia* (nu *Dalenia*); **B.** *Dissochaeta* sectie *Disparistemones* (nu *Dalenia*); **C.** *Dissochaeta* sectie *Diplectria* (nu *Diplectria*); **D.** *Dissochaeta rostrata*-complex (nu *Macrolenes*); **E.** *Dissochaeta* s.str. (nu *Dissochaeta*). Linksonder: het cladogram van de complete set Melastomataceae-monsters waarbij de rode groep de *Dissochaeta*-alliantie vormt.

Afgeknotte of verenigde kelklobben zijn plesiomorf in de alliantie. Ze zijn meestal zichtbaar omdat er slechts vier kleine tanden of golvingen of soms driehoekige vormen aanwezig zijn als de uiteinden van het hypanthium (= uitgegroeide bloembasis). *Pseudodissochaeta* heeft gewoonlijk vier kleine verdikte tandenachtige enaties als kelklobben. *Creochiton*, *Dalenia* en *Diplectria* hebben ook afgeknotte kelklobben, maar die zijn zichtbaar als kleine golvingen aan de top van het hypanthium. Soms ontwikkelen deze golvingen zich niet eens en heeft het hypanthium alleen een platte rand. In *Dissochaeta* heeft de gedeeltelijk afgeknotte kelkbuis vier driehoekige uiteinden. De lengte van deze tips varieert binnen het geslacht van kort (half zo lang als het afgeknotte deel) tot lang (twee keer zo lang als het afgeknotte deel). De kelklobben van *Macrolenes* verschillen van alle andere geslachten in de alliantie. Het

geslacht heeft als afgeleid kenmerk vier, vrije, goed ontwikkelde kelklobben met een ronde, driehoekige of lineaire vorm. De lengte van de lobben varieert, tot zo lang als het hypanthium.

Isomorfe (gelijke) meeldraden worden beschouwd als de plesiomorfe toestand en ze worden gevonden in de basale takken, zoals *Pseudodissochaeta*. *Creochiton* heeft over het algemeen soorten met isomorfe meeldraden behalve *C. anomalus* en *C. monticola* (Ridl.) Veldkamp. Alle houtachtige klimmende geslachten hebben dimorfe meeldraden (2 vormen) als synapomorfie. Dimorfe meeldraden verschillen meestal in de grootte en vorm van de helmknoppen. Het hebben van alleen vruchtbare meeldraden in beide kransen is de plesiomorfe toestand in de *Dissochaeta*-alliantie en aanwezig in de meeste geslachten: *Pseudodissochaeta*, *Creochiton*, *Dissochaeta* en *Macrolenes*. Een onvruchtbare buitenste krans wordt gedeeld door *Dalenia* en *Diplectria*, waarvan de buitenste meeldraden zich ontwikkelen tot 1/3 van de vruchtbare meeldraden of ze zijn volledig verkleind. Een onvruchtbare binnenste krans van meeldraden wordt gevonden in een paar soorten *Creochiton* en *Dissochaeta*.

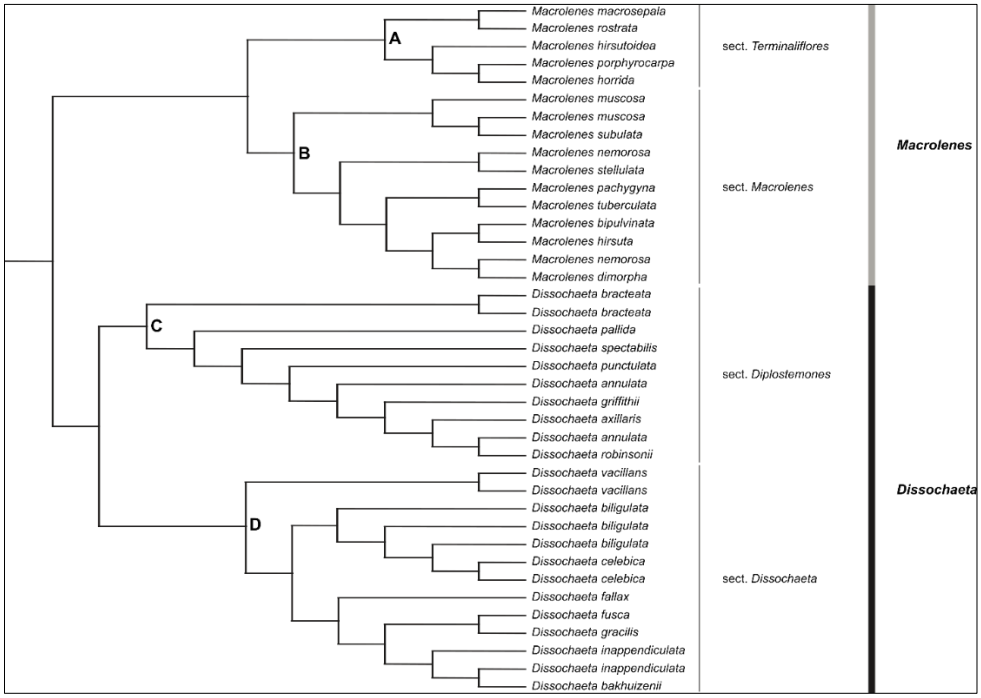


Fig. 8-6. Fylogenetische boom van de *Macrolenes* en *Dissochaeta* takken met de nieuwe infragenerische classificatie in secties.

- Bevestigt de moleculaire fylogenie één van de eerder voorgestelde infragenerische taxa? Hoe verhouden ze zich tot elkaar?

Alleen binnen *Dissochaeta* (in verschillende omschrijvingen) werden infragenerische taxa beschreven (Blume 1831a, 1831b; Baillon 1877; Cogniaux 1891; Merrill 1917). In dit proefschrift, gebaseerd op de resultaten van de fylogenetische analyses, worden sommige secties nu erkend als verschillende geslachten. Het zijn secties *Creochiton*, *Dalenia* en *Diplectria*. De overige secties maken nu nog deel uit van het geslacht *Dissochaeta*. De moleculaire fylogenie van *Dissochaeta* laat zien dat er binnen *Dissochaeta* slechts twee statistisch ondersteunde takken zijn, die kunnen worden beschouwd als infragenerische taxa op sectie niveau (Fig. 8-6). De eerste tak is geclassificeerd als sectie *Diplostemones* (C) en de andere is sectie *Dissochaeta* (D). Infragenerische taxa waren nooit voorgesteld voor *Macrolenes*. De opname van het statistisch goed ondersteunde *Dissochaeta rostrata*-complex in het geslacht moet echter worden erkend en twee secties zijn nu duidelijk (Fig. 8-6); sectie *Terminaliflores* (A) is opgericht om de *rostrata* groep te erkennen, terwijl de

overige soorten (voorheen *Macrolenes* in strikte zin) nu zijn opgenomen in sectie *Macrolenes* (B).

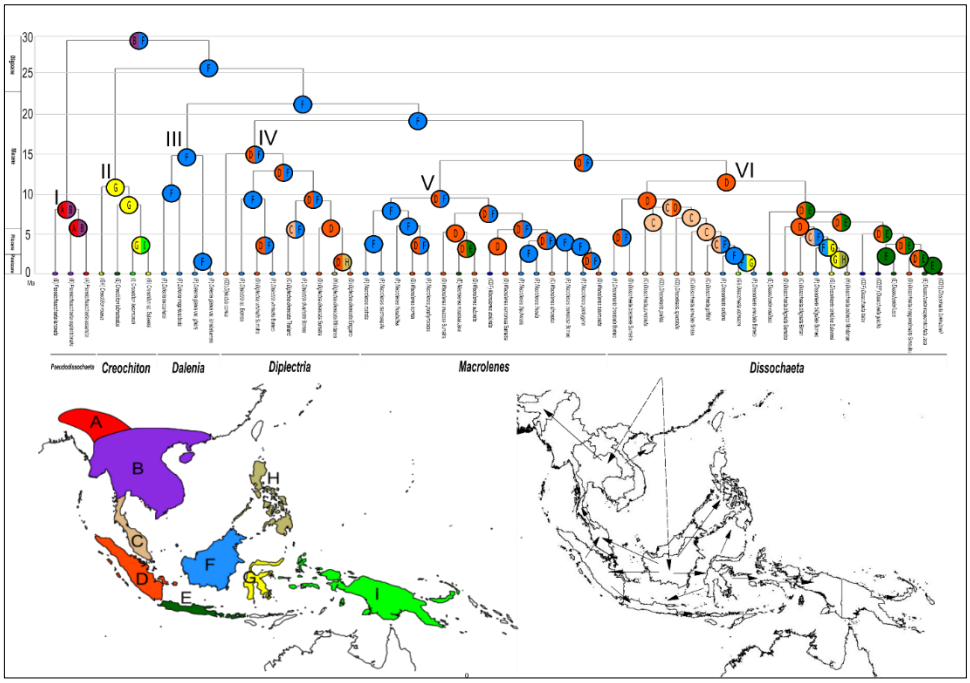


Fig. 8-7. Mogelijke voorouderlijke gebieden en verspreidingsroutes voor de *Dissochaeta*-alliantie. Kleuren in de cirkeldiagrammen en kaart komen overeen met geografische gebieden; Ma, miljoen jaar geleden. **A:** E Bhutan, NO India en NW Myanmar; **B:** Indochina, incl. C & E Myanmar, S China, Hainan en Thailand; **C:** S Thailand, Maleis schiereiland en Riau-archipel; **D:** Sumatra en omliggende eilanden; **E:** Java en Kleine Soenda-eilanden excl. Sumba, Flores en Timor; **F:** Borneo; **G:** Sulawesi; **H:** Filippijnen incl. Palawan; en **I:** Molukken en Nieuw-Guinea. Takken: **I.** *Pseudodissochaeta*; **II.** *Creochiton*; **III.** *Dalenia*; **IV.** *Diplectria*; **V.** *Macrolenes*; **VI.** *Dissochaeta*.

- Waar en wanneer vond de belangrijkste diversificatie plaats in de Dissochaeta*-alliantie? Welk scenario is het resultaat van de historische biogeografische analyse van de geslachten en soorten? Hoe kunnen we de migratieroutes verklaren?*

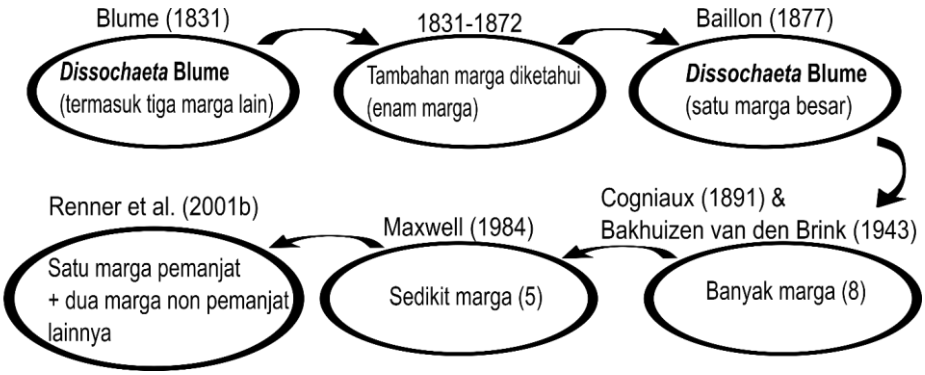
Moleculaire dateringsanalyses suggereren een oorsprong van de *Dissochaeta*-alliantie in Zuid-Amerika. De alliantie werd afgesplitst van de Zuid-Amerikaanse Cambessedesieae in het late Eoceen (39,32 Ma) en verspreidde zich naar Zuidoost-Azië waar het uitwaaierde in in het middelste Oligoceen (28,96 Ma). De voorouder van de *Dissochaeta*-alliantie is mogelijk gemigreerd van Zuid-Amerika naar Zuidoost Azië. Een brede voorouderlijke verspreiding in Zuidoost-Azië (Indochina en Borneo) is waarschijnlijk het gebied van oorsprong van de *Dissochaeta*-alliantie, waar veel van de soortvorming plaats vond (Fig. 8-7). Het vasteland van Zuidoost-Azië (gebieden AB; Fig. 8-7) is het oorsprongsgebied van het geslacht *Pseudodissochaeta* (I). *Creochiton* (II) is waarschijnlijk ontstaan op Sulawesi (gebied G; Fig. 8-7) en verspreidde zich verschillende keren noordwaarts naar de Filippijnen, westwaarts naar Java en oostwaarts naar Molukken-Nieuw Guinea. De geslachten met klimmende struiken (*Dalenia*, *Diplectria*, *Dissochaeta* en *Macrolenes*) zijn waarschijnlijk ontstaan op Borneo (gebied F; Fig. 8-7). *Dalenia* (III) is ontstaan op Borneo, gevolgd door

een radiatie van soorten op het eiland (gebied F; Fig. 8-7). *Diplectria* (IV) en *Macrolenes* (V) zouden een oorsprong in Borneo-Sumatra hebben (gebieden DF; Fig. 8-7), terwijl de oorsprong van *Dissochaeta* (VI) Sumatra zou kunnen zijn (gebied D; Fig. 8-7). Er zijn talrijke verspreidings gebeurtenissen binnen Borneo, westwaarts naar Sumatra, het Maleis schiereiland en Java of oostwaarts over de Wallace lijn naar Sulawesi, de Filippijnen en de Molukken-Nieuw-Guinea; de uitbreiding naar de laatste twee gebieden vond plaats met Sulawesi als springplank (Fig. 8-7). De recente verspreidingspatronen van de *Dissochaeta*-alliantie zijn ook gevonden voor verschillende andere Zuidoost-Aziatische plantengroepen, en ze zijn in hoge mate congruent met de geologische gebeurtenissen in Zuidoost-Azië.

RINGKASAN DAN SIMPULAN

Ringkasan dan Simpulan

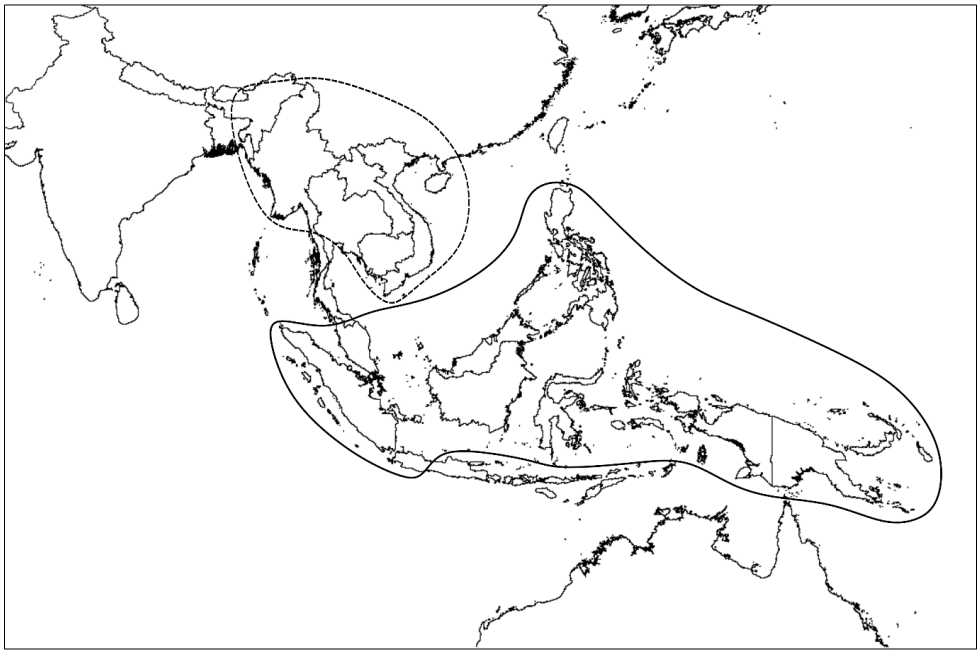
Dissochaeta Blume (Melastomataceae, puak Dissochaeteae) dikenal sebagai marga tumbuhan pemanjat yang tersebar di Asia Tenggara, dimana merupakan penghuni hutan hujan tropis atau hutan hijau sepanjang tahun. Marga ini dicirikan oleh perawakan memanjat dan merambat, perbungaan warna-warni membentuk tajuk, dan buah berdaging. Marga ini bersama bagian dari kelompok marga-marga lain yang tersebar di Asia Tenggara dengan penampakan morfologi yang serupa, dan bersama-sama mereka disebut kerabat *Dissochaeta*. Sejak studi botani pertama dari marga ini pada abad ke-19 hingga sekarang, ahli botani mengusulkan banyak cara berbeda untuk memisahkan dan mengenali marga-marga dalam kerabat *Dissochaeta* berdasarkan karakter morfologi (Gbr. 8-1). Baillon (1877) menyatukan sebagian besar marga terkait ke dalam marga besar *Dissochaeta* sensu lato (s.l. = dalam arti yang lebih luas) dan membagi marga besar ini dalam beberapa seksi berdasarkan kemiripan morfologi. Kemudian, Cogniaux (1891) dan Bakhuizen van den Brink (1943) menerima *Dissochaeta* dalam pengertian yang lebih sempit (sensu stricto = s.str.) dengan mengubah sebagian besar seksi Baillon kembali ke tingkat marga kembali. Maxwell (1984) memiliki pandangan yang sedikit berbeda dengan Cogniaux (1891) dan Bakhuizen van den Brink (1943), ia menyederhanakan konsep marga dalam kerabat *Dissochaeta* dengan hanya menerima lima marga, *Creochiton*, *Diplectria*, *Dissochaeta*, *Macrolenes* dan *Pseudodissochaeta*. Konsep umum ini diikuti oleh Renner (1993), tetapi Renner et al. (2001b) menyatukan semua marga semak pemanjat menjadi satu marga *Dissochaeta*. Studi filogenetik molekuler puak Dissochaeteae (Clausing & Renner 2001a; Zhou et al. 2019b) menunjukkan bahwa *Dissochaeta* bersifat monofiletik (satu nenek moyang dan semua spesies keturunannya dalam satu kelompok) dengan *Diplectria* dan *Macrolenes* bersarang di dalamnya. Selain itu, *Pseudodissochaeta* diakui sebagai marga yang berbeda, berkerabat dengan *Dissochaeta*. Hasil ini menunjukkan bahwa konsep taksonomi umum yang luas dari *Dissochaeta* (s.l.) lebih mencerminkan evolusi marga. Namun, studi ini umumnya tidak cukup komprehensif untuk menarik kesimpulan akhir tentang batasan marga karena pengambilan sampel yang kurang memadai. *Dissochaeta* dan kerabatnya secara morfologis bervariasi, yang sering menyulitkan identifikasi jenis atau tingkat marga karena mereka terlihat serupa. Tujuan utama dari disertasi ini adalah untuk memperjelas hubungan antar jenis dan marga dalam kerabat *Dissochaeta* dan untuk menyajikan klasifikasi baru, yang mencerminkan ciri-ciri evolusi dan biogeografi dari kelompok tumbuhan ini. Studi ini berfokus pada tiga aspek kerabat *Dissochaeta*: taksonomi, filogeni molekuler, dan sejarah biogeografi.



Gbr. 8-1. Ringkasan dan garis waktu dari berbagai batasan marga (= batasan di mana taksa bawahan merupakan bagian dari marga yang dipelajari) dalam kerabat *Dissochaeta*

- *Jenis-jenis mana yang harus dimasukkan ke dalam kerabat* Dissochaeta*? Bagaimana mereka berbeda secara morfologi dan ekologi? Apa karakter morfologi diagnostik mereka?*

Revisi taksonomi kerabat *Dissochaeta* (Kartonegoro & Veldkamp 2013; Kartonegoro *et al.* 2018, 2019, 2020; lihat Bab 2-5) menunjukkan bahwa *Creochiton* terdiri dari 12 jenis, *Dissochaeta* (termasuk marga *Dalenia* dan *Diplectria*) terdiri dari 54 jenis dan dua varietas, *Macrolenes* terdiri dari 17 jenis dan *Pseudodissochaeta* terdiri dari 5 jenis. Secara morfologis, marga-marga ini memiliki kemiripan seperti tumbuhan berkayu (semak atau liana), perbungaan tajuk berbatas dengan bunga berbilangan empat, delapan benang sari dalam dua lingkaran (luar = berseling daun mahkota dan dalam = berlawanan daun mahkota), dengan berbagai pelengkap ikat, dan buah berdaging. Semua jenis yang diketahui dalam revisi taksonomi ini tersebar di Asia Tenggara, mulai dari Bhutan timur, India timur laut, Kepulauan Andaman-Nicobar ke arah timur hingga Myanmar, Tiongkok bagian selatan, Indochina, Thailand, ke arah selatan di seluruh wilayah Malesia tetapi tidak ada di bagian timur dari Kepulauan Sunda Kecil (Gbr. 8-2 & 8-3).

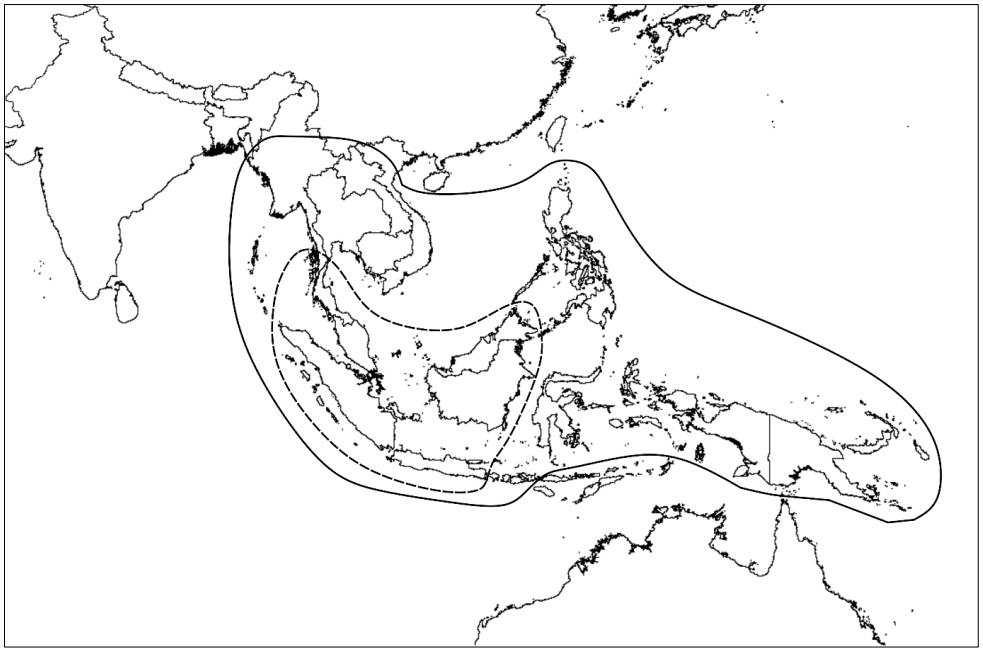


Gbr. 8-2. Peta Distribusi *Creochiton* (garis bersambung) & *Pseudodissochaeta* (garis putus-putus).

Creochiton terdiri dari semak epifit atau jarang memanjat (Bab 2). Marga ini mudah dikenal oleh sepasang daun penumpu bunganya yang unik, yang menyelimuti kuncup bunga. Beberapa jenis memiliki daun penumbu bunga berdaging dan cekung dan ketika masih menutupi kuncup bunga, mereka memiliki penampakan membulat (Gbr. 8-4A&B). Berbeda dengan marga-marga lain dalam kerabat *Dissochaeta*, *Creochiton* memiliki perbungaan memayung palsu di ketiak kecuali untuk *C. anomalus* dari Malesian Barat (King) Veldkamp. Jenis-jenis *Creochiton* sebagian besar ditemukan di dataran tinggi, hingga ketinggian 2000 m, di hutan pegunungan. Jenis-Jenis ini lebih menyukai habitat yang lembab tetapi terbuka.

Dissochaeta (termasuk *Dalenia* dan *Diplectria*) adalah marga terbesar dalam kerabat dan juga tersebar luas di seluruh Asia Tenggara. Marga ini memiliki kebiasaan memanjat, perbungaan malai berbatas di ujung atau jarang di ketiak, bunga dengan delapan benang sari dua bentuk dalam dua lingkaran (Gbr. 8-4C&D). Beberapa jenis hanya memiliki empat

benang sari subur, karena empat lainnya tidak berkembang dan menjadi staminodia (benang sari tidak subur, tereduksi sebagian) atau hilang sama sekali (Gbr. 8-4E&F). Benang sari yang belum berkembang membentuk lingkaran luar atau lingkaran dalam. Benang sari memiliki pelengkap ikat yang berbeda, mereka berbentuk segitiga atau memacu di bagian punggung dan berlipat ganda atau bahkan tidak beraturan di bagian perut.



Gbr. 8-3. Peta distribusi *Dissochaeta* (garis bersambung) & *Macrolenes* (garis putus-putus).

Macrolenes juga memiliki kebiasaan memanjat dan perbungaan malai berbatas, mirip dengan *Dissochaeta*. Marga ini dapat dibedakan dari yang sebelumnya dengan sepasang bantal rambut di pangkal daun di permukaan bawah, perbungaan di ketiak dan pelengkap ikat benang-benang di bagian perut pada benang sari lingkaran luar (Gbr. 8-4I&J). *Dissochaeta* dan *Macrolenes* sebagian besar menempati vegetasi sekunder atau tempat terbuka kecil seperti celah pohon tumbang atau muncul di sepanjang tepi jalan. Beberapa jenis ada di hutan pegunungan hingga ketinggian 2500 m.

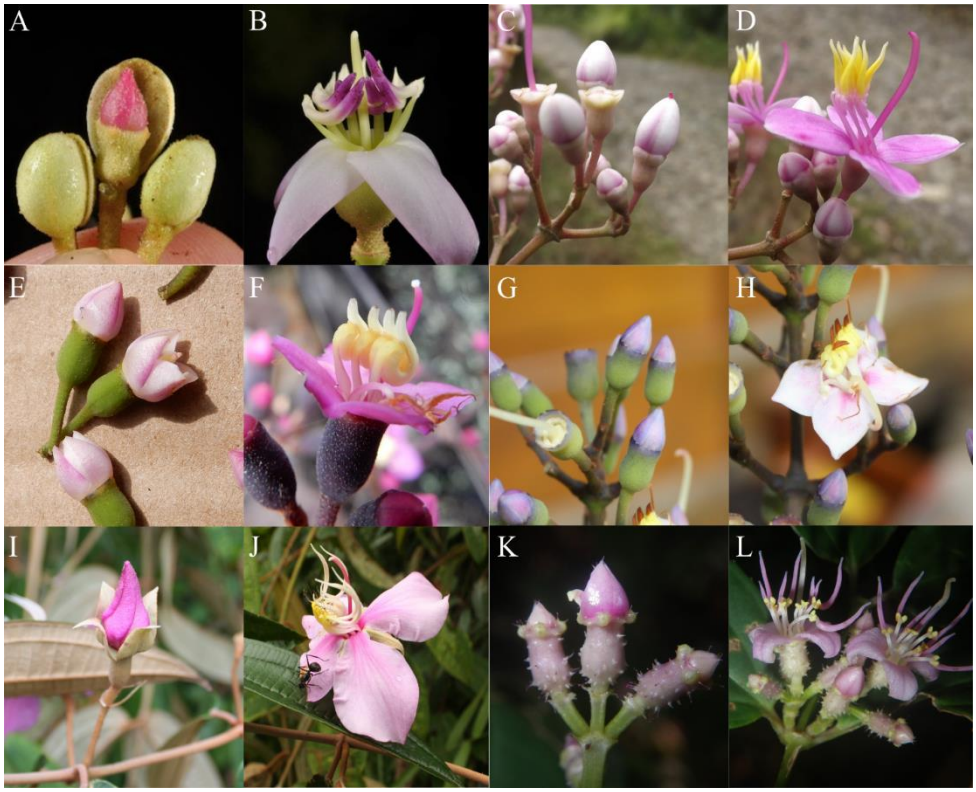
Pseudodissochaeta meupakan perdu tegak dan menyebar, sebuah perawakan tidak seperti semua marga lain dalam kerabat *Dissochaeta*. Marga ini hanya tersebar di daratan Asia Tenggara, di luar wilayah Malesia. Bunga marga ini memiliki delapan benang sari sama bentuk dan sama besar (Gbr. 8-4K&L). Beberapa jenis juga dapat dikenali dari pangkal daun asimetris yang berbeda dan tepi daun yang bergerigi. *Pseudodissochaeta* umumnya tumbuh di hutan hijau sepanjang tahun dengan vegetasi agak terbuka.

Semua marga yang direvisi di sini tumbuh dalam iklim non-musiman, sehingga tanpa variasi suhu dan curah hujan musiman. Hal ini memungkinkan mereka dapat tumbuh dan berbunga sepanjang tahun. Penyerbukan bunga belum pernah diamati sebelumnya. Serangga terbang atau lebah kecil kemungkinan sebagai penyerbuk dan membantu menjaga reproduksi biologis dalam kerabat. Semut sering terlihat mengunjungi bunga beberapa jenis, tetapi kunjungan ini belum tentu berhubungan dengan penyerbukan dan masih dipertanyakan apakah semut adalah penyerbuk atau bukan. Penyebaran buah kemungkinan besar bersifat

zoochorous (oleh hewan). Buah matang yang berdaging dan berwarna-warni dimakan oleh burung atau mamalia kecil. Benih yang kecil dan banyak per buahnya cenderung mudah menyebar ke habitat lain, juga cocok bersemai setelah hewan tersebut buang air besar.

- *Apakah kerabat* Dissochaeta *monofiletik? Taksa mana yang berkerabat erat dengan kerabat* Dissochaeta*? Sifat evolusi mana yang dapat digunakan untuk mengenali klade / kelompok?*

Puak Dissochaeteae, dalam batasan sebelumnya (sensu lato), tampak polifiletik (lebih dari satu garis nenek moyang) dalam beberapa studi filogenetik molekuler (Clausing & Renner 2001a; Zhou et al. 2019b). Pohon filogenetik yang dihasilkan menunjukkan tiga garis keturunan utama dalam Dissochaeteae: 1) kerabat *Medinilla*; 2) *Dinophora* + *Ochthocharis*; dan 3) kerabat *Dissochaeta* (Clausing & Renner 2001a; Zeng et al. 2016; Zhou et al. 2019b). Dalam disertasi ini, studi filogenetik molekuler berdasarkan penanda kloroplas (*ndhF*, *psbK-psbL*, *rbcL* dan *rpl16*) dan inti (nrETS dan nrITS) menggunakan analisis *Maximum Parsimony* (MP), *Maximum Likelihood* (ML) dan *Bayesian Inference* (BI) mengkonfirmasi polifili puak Dissochaeteae s.l. Analisis menunjukkan bahwa buah berdaging dan biji kokleat, yang digunakan sebagai karakter diagnostik puak tersebut, bersifat homoplasi dan memiliki beberapa asal yang paralel; buah beri berdaging mungkin telah berevolusi setidaknya tiga kali dalam Suku Melastomataceae.



Gbr. 8-4. Kuncup bunga dan bunga masak dari kerabat *Dissochaeta*. **A&B.** *Creochiton roseus*; **C&D.** *Dissochaeta bakhuizenii*; **E&F.** *Dalenia glabra*; **G&H.** *Diplectria conica*; **I&J.** *Macrolenes nemorosa*; **K&L.** *Pseudodissochaeta* sp. Foto oleh P. Pielser (A&B), A. Kartonegoro (C, D, G, H, I, J), D. Penneys (E&F), M. Nuraliev (K&L).

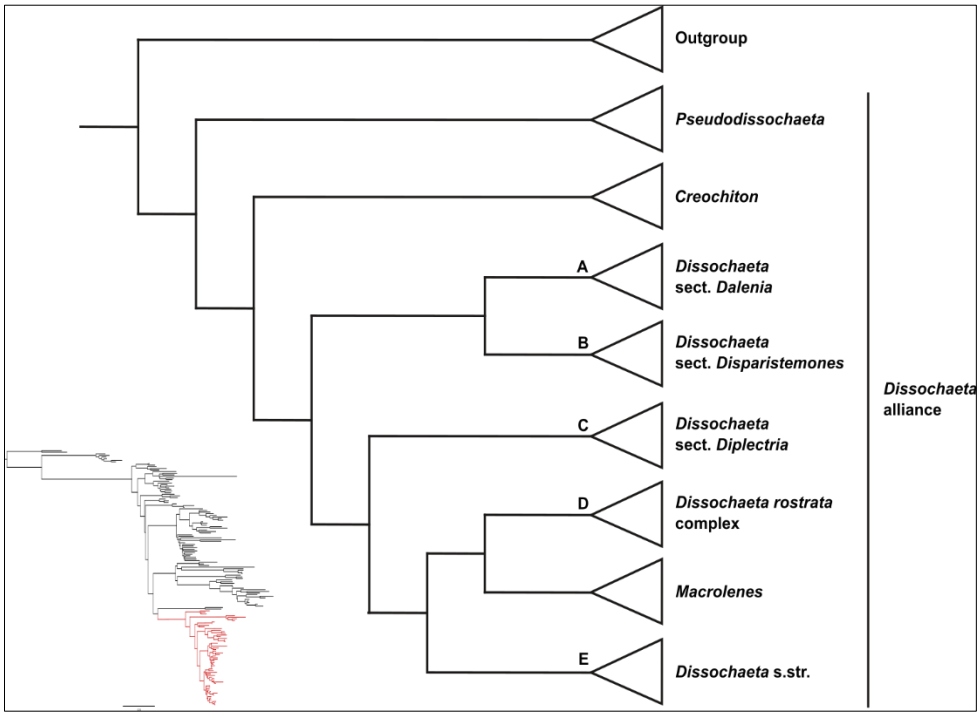
Sejalan dengan studi sebelumnya, kerabat *Dissochaeta* merupakan kelompok monofiletik yang sangat didukung oleh nilai statistik yang tinggi, yang meliputi marga *Creochiton*, *Dissochaeta* (termasuk *Dalenia* dan *Diplectria*), *Macrolenes* dan *Pseudodissochaeta*. Kerabat *Dissochaeta* membentuk kedekatan erat dengan puak Cambessedesieae dari Amerika Selatan. Monofili kerabat *Dissochaeta* juga didukung oleh karakter morfologi berikut: perbungaan tajuk, bunga berkelipatan empat dengan delapan benang sari tidak sama / agak sama dalam dua lingkaran dan buah beri berdaging (Maxwell 1984). Mengenai anatomi kayu, kerabat *Dissochaeta* memiliki lubang antar pembuluh yang berseling, elemen pembuluh dengan diameter lebar dan lebar jari-jari kayu hingga 7 sel (Van Vliet 1981).

- *Jika kerabat* Dissochaeta *monofiletik, lalu bagaimana hasil filogenetik dapat diterjemahkan ke dalam klasifikasi baru marga yang monofiletik dan dapat dikenali? Apomorfis morfologi manakah (karakter yang berevolusi) yang mendukung klasifikasi?*

Hasil filogenetik, bersama dengan morfologi dan anatomi kayu, mendukung pengaturan ulang konsep puak Dissochaeteae yang lebih sempit dari sebelumnya (tidak termasuk kerabat *Medinilla*, dan marga *Dinophora* dan *Ochthocharis*). Kelompok monofiletik dari kerabat *Dissochaeta* atau anak puak Dissochaetinae dengan ini dinaikkan ke peringkat puak sebagai Dissochaeteae. Dengan definisi ulang ini, Dissochaeteae hanya tersebar dari Bhutan timur, India timur laut, dan Cina Selatan di seluruh Asia Tenggara hingga New Guinea tanpa entitas di Afrika Tropis, Madagaskar, Sri Lanka, dan daratan India (Gbr. 8-2 & 8-3). Di dalam kerabat *Dissochaeta*, enam garis keturunan / kelompok diketahui dengan dukungan nilai statistik yang kuat dari semua analisis. Filogeni puak Dissochaeteae menunjukkan bahwa tiga kelompok bertepatan dengan tiga marga (monofiletik), *Creochiton*, *Macrolenes* dan *Pseudodissochaeta* (Gbr. 8-5). *Dissochaeta* (sensu Kartonegoro et al. 2018) ditemukan parafiletik (satu nenek moyang tetapi tidak semua jenis keturunan termasuk) dan mencakup lima garis keturunan, masing-masing dengan nilai statistic yang didukung kuat atau sedang (Gbr. 8-5). Silsilah pertama (A) terdiri dari apa yang dikenal sebagai kelompok *Dissochaeta* seksi *Dalenia*. Yang kedua adalah *Dissochaeta* seksi *Disparistemones* (B). Silsilah ketiga (C) adalah *Dissochaeta* seksi *Diplectria*. Silsilah keempat (D) adalah kompleks *Dissochaeta rostrata* (kelompok informal), yang dikelompokkan dan bersaudara dekat dengan kelompok *Macrolenes*. Silsilah terakhir (E) adalah kelompok yang terdiri dari jenis-jensi *Dissochaeta* yang tersisa (*Dissochaeta* s.str.) termasuk *Dissochaeta* seksi *Anoplodissochaeta*, seksi *Diplostemones*, seksi *Dissochaeta*, seksi *Dissochaetopsis*, seksi *Isostemones*, seksi *Omphalopus* di dalamnya. Berdasarkan hasil filogenetik molekuler ini, *Dalenia* dan *Diplectria* dikembalikan ke peringkat marga, yang membuat konsep marga *Dissochaeta* lebih sempit (*Dissochaeta* s.str.). *Dissochaeta* seksi *Disparistemones* termasuk dalam *Dalenia*. Kompleks *Dissochaeta rostrata*, yang berkerabat erat dengan *Macrolenes*, termasuk dalam marga tersebut, sehingga memperluas konsep batasan marga *Macrolenes*.

Pseudodissochaeta membentuk kelompok paling dasar dalam kerabat *Dissochaeta*, kerabat dari semua taksa lain dalam grup. Selanjutnya, *Creochiton* bercabang dan merupakan kerabat dari semua marga semak pemanjat (*Dalenia*, *Diplectria*, *Dissochaeta* dan *Macrolenes*). Dalam kelompok semak pemanjat, *Dalenia* berposisi di basal, diikuti oleh *Diplectria* dan percabangan terakhir adalah antara *Dissochaeta* dan *Macrolenes*. Beberapa ciri morfologi mendukung identitas kelompok. Beberapa status karakter secara individual khas untuk marga / kelompok, tetapi kelompok lain harus dicirikan oleh kombinasi status karakter. Perawakan semak atau perdu terbagi dalam semua taksa dalam kerabat *Dissochaeta* di tiga bagian yang berbeda. Perdu tegak, terestrial merupakan kondisi plesiomorfik (asli atau primitif), terdapat di *Pseudodissochaeta*, khas untuk marga ini dalam kerabat. Selanjutnya diikuti oleh semak epifit yang khas untuk *Creochiton*. Keadaan yang paling umum adalah semak pemanjat,

kondisi karakter yang paling umum diturunkan (terakhir berevolusi), terdapat pada *Dalenia*, *Diplectria*, *Dissochaeta*, dan *Macrolenes*. Perawakan memanjat berevolusi hanya sekali di suku Melastomataceae di palaeotropik (Clausing & Renner 2001a). Pertumbuhan interpetiolar biasanya ditunjukkan di antara pelekatan tangkai daun dari daun yang berlawanan dan kemungkinan memfasilitasi kebiasaan memanjat untuk memberikan sokongan. Marga dengan semak pemanjat memiliki bentuk pertumbuhan interpetiolar yang berbeda. Pertumbuhan interpetiolar *Diplectria*, *Dissochaeta*, dan *Macrolenes* hanya tampak dari pertumbuhan interpetiolar garis sederhana atau undukan kecil. *Dalenia* adalah satu-satunya marga dengan pertumbuhan interpetiolar yang lebih berkembang, yang tampak membentuk lobus atau menghasilkan struktur pektinat.

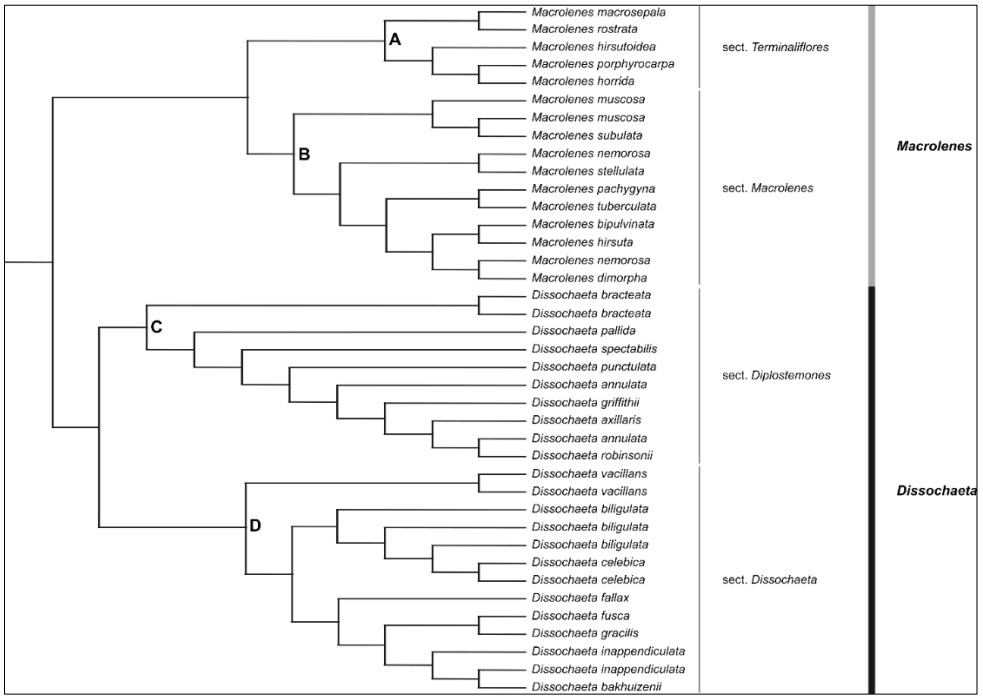


Gbr. 8-5. Pohon filogenetik yang disederhanakan dari kerabat *Dissochaeta*, di mana segitiga mewakili jenis-jenis. **A.** *Dissochaeta* seksi *Dalenia* (sekarang *Dalenia*); **B.** *Dissochaeta* seksi *Disparistemones* (sekarang *Dalenia*); **C.** *Dissochaeta* seksi *Diplectria* (sekarang *Diplectria*); **D.** Kompleks *Dissochaeta rostrata* (sekarang *Macrolenes*); **E.** *Dissochaeta* s.str. (sekarang *Dissochaeta*). Kiri bawah: kladogram dari sampel Melastomataceae lengkap dimana kelompok merah membentuk kerabat *Dissochaeta.*

Lobus kelopak yang menyatu bersifat plesiomorfik dalam kerabat. Mereka biasanya terlihat karena hanya dengan empat gigi kecil atau undulasi atau terkadang bentuk segitiga di ujung tabung kelopak (wadah bunga yang tumbuh besar). *Pseudodissochaeta* biasanya memiliki empat enasi mirip gigi kecil yang menebal sebagai lobus kelopak. *Creochiton*, *Dalenia* dan *Diplectria* juga memiliki lobus kelopak bunga yang menyatu, tetapi terlihat seperti gelombang kecil di puncak tabung kelopak. Kadang-kadang gelombang ini bahkan tidak berkembang dan tabung kelopak tidak memiliki ekstensi kelopak dan menunjukkan tepi yang rata. Pada *Dissochaeta*, lobus kelopak yang terpotong sebagian memiliki empat ujung berbentuk segitiga. Panjang bagian yang menyatu ini bervariasi dalam marga dari pendek (setengah panjang bagian yang terpotong) hingga panjang (dua kali lebih panjang dari bagian yang terpotong). Lobus kelopak *Macrolenes* berbeda dari semua marga lain dalam kerabat. Marga ini memiliki karakter yang diturunkan berupa empat lobus kelopak bebas, yang berkembang dengan baik dengan bentuk bulat, segitiga atau linier. Panjang lobus bervariasi, sampai sepanjang panjang tabung kelopak.

Benang sari isomorfik (sama bentuk) dianggap sebagai keadaan plesiomorfik dan ditemukan di kelompok basal, seperti *Pseudodissochaeta*. *Creochiton* umumnya memiliki jenis-jenis dengan benang sari isomorfik kecuali *C.*

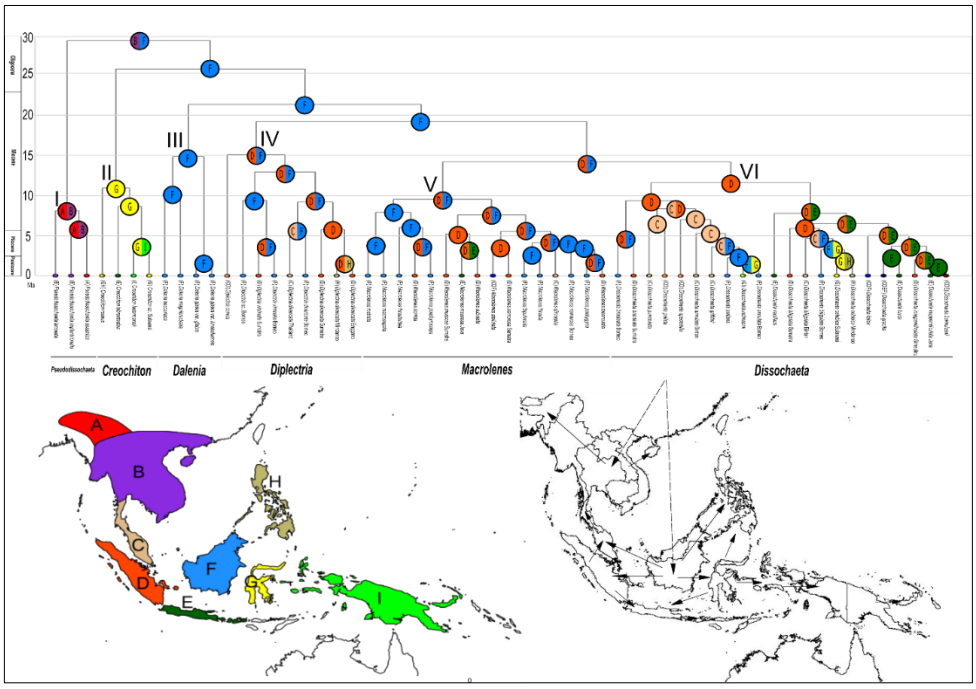
anomalus dan *C. monticola* (Ridl.) Veldkamp. Semua marga pemanjat berkayu memiliki benang sari dimorfik (dua bentuk) sebagai sinapomorfis. Benang sari dimorfik biasanya berbeda dalam ukuran dan bentuk kepala sari. Memiliki benang sari subur di kedua lingkaran benang sari adalah keadaan plesiomorfik dalam kerabat *Dissochaeta* dan hadir di sebagian besar marga: *Pseudodissochaeta*, *Creochiton*, *Dissochaeta* dan *Macrolenes*. Lingkaran luar benang sari yang tidak subur (infertil) terdapat pada *Dalenia* dan *Diplectria*, di mana benang sari luarnya berkembang hanya 1/3 dari benang sari subur atau sepenuhnya berkurang. Lingkaran benang sari yang tidak subur ditemukan pada beberapa spesies *Creochiton* dan *Dissochaeta* pada lingkaran dalam.



Gbr. 8-6. Pohon filogenetik dari kelompok *Macrolenes* dan *Dissochaeta* menunjukkan klasifikasi anak marga baru dalam beberapa seksi.

- Apakah filogeni molekuler mendukung taksa anak marga yang pernah diusulkan sebelumnya? Bagaimana mereka berkerabat satu sama lain?

Hanya dalam *Dissochaeta* (dalam berbagai batasan konsep) taksa anak marga diusulkan (Blume 1831a, 1831b; Baillon 1877; Cogniaux 1891; Merrill 1917). Dalam disertasi ini, berdasarkan hasil analisis filogenetik, beberapa seksi dalam *Dissochaeta* kini dikenali sebagai marga yang berbeda. Mereka adalah seksi *Creochiton*, *Dalenia* dan *Diplectria*. Seksi yang tersisa sekarang masih menjadi bagian dari marga *Dissochaeta*. Filogeni molekuler *Dissochaeta* menunjukkan bahwa hanya ada dua kelompok yang didukung dalam *Dissochaeta*, yang dapat dianggap sebagai taksa anak marga (tingkat seksi; Gbr. 8-6). Kelompok pertama diklasifikasikan sebagai seksi *Diplostemones* (C) dan yang lainnya adalah seksi *Dissochaeta* (D). Taksa anak marga tidak pernah diusulkan untuk *Macrolenes* sebelumnya. Namun, masuknya kompleks *Dissochaeta rostrata* yang didukung dengan baik dalam marga tersebut harus diakui, dan dua seksi sekarang dikenali (Gbr. 8-6); Seksi Terminaliflores (A) diusulkan untuk mengakomodasi kompleks *Dissochaeta rostrata*, sedangkan jenis-jenis yang tersisa (sebelumnya *Macrolenes* dalam arti sempit) sekarang dimasukkan dalam seksi *Macrolenes* (B).



Gbr. 8-7. Kemungkinan area leluhur dan rute penyebaran kerabat *Dissochaeta*. Warna pada diagram lingkaran dan peta sesuai dengan wilayah geografis; Ma = jutaan tahun yang lalu. **A:** Bhutan timur, India Timur Laut dan Myanmar Barat Laut; **B:** Indochina, termasuk. Myanmar Tengah dan Timur, Tiongkok bagian Selatan, Hainan dan Thailand; **C:** Thailand bagian selatan, Semenanjung Malaya dan Kepulauan Riau; **D:** Sumatera dan pulau-pulau sekitarnya; **E:** Jawa dan Kepulauan Sunda Kecil kecuali. Sumba, Flores dan Timor; **F:** Borneo; **G:** Sulawesi; **H:** Filipina termasuk Palawan; dan **I:** Maluku dan New Guinea. Kelompok: **I.** *Pseudodissochaeta*; **II.** *Creochiton*; **III.** *Dalenia*; **IV.** *Diplectria*; **V.** *Macrolenes*; **VI.** *Dissochaeta*.

- *Di mana dan kapan peristiwa diversifikasi besar terjadi di kerabat* Dissochaeta*? Skenario mana yang dihasilkan dari analisis sejarah biogeografi dari marga dan jenis dalam kerabat* Dissochaeta*? Bagaimana hal ini dapat menjelaskan rute migrasi / persebaran?*

Analisis penanggalan molekuler menunjukkan asal usul kerabat *Dissochaeta* di Amerika Selatan. kerabat ini terpecah dari puak Cambessedesieae di Amerika Selatan pada akhir masa Eocene (39,32 Ma) dan menyebar ke dan di Asia Tenggara pada masa pertengahan Oligocene (28,96 Ma). Leluhur kerabat *Dissochaeta* mungkin telah bermigrasi dari Amerika Selatan ke Asia Tenggara. Sebaran leluhur yang luas di Asia Tenggara (Indochina dan Borneo) disimpulkan sebagai area asal kerabat *Dissochaeta*, tempat banyak spesiasi terjadi (Gbr. 8-7). Asia Tenggara Daratan (area AB; Gbr. 8-7) dibuktikan sebagai area asal marga *Pseudodissochaeta* (I). *Creochiton* (II) kemungkinan besar berasal dari Sulawesi (area G; Gbr. 8-7) dan tersebar beberapa kali ke utara ke Filipina, ke barat ke Jawa dan ke timur ke Maluku-New Guinea. Marga semak pemanjat (*Dalenia*, *Diplectria*, *Dissochaeta* dan *Macrolenes*) kemungkinan besar berasal dari Borneo (area F; Gbr. 8-7). *Dalenia* (III) berasal dari Borneo, diikuti oleh berbagai peristiwa spesiasi di dalam pulau tersebut (area F; Gbr. 8-7). *Diplectria* (IV) dan *Macrolenes* (V) kemungkinan berasal dari Borneo-Sumatera (area DF; Gbr. 8-7) sedangkan *Dissochaeta* (VI) mungkin berasal dari Sumatera (area D; Gbr. 8-7). Banyak kejadian penyebaran disimpulkan di Borneo, ke barat ke Sumatera, Semenanjung Malaya dan Jawa atau ke timur melintasi garis *Wallace* ke Sulawesi, Filipina dan Maluku-New Guinea, perluasan ke dua wilayah terakhir terjadi dengan Sulawesi sebagai batu

loncatan (Gbr. 8-7). Pola penyebaran baru-baru ini dari kerabat *Dissochaeta* mirip dengan pola yang diidentifikasi di beberapa kelompok tumbuhan Asia Tenggara lainnya, dan sangat sesuai dengan kejadian geologi di Asia Tenggara.

REFERENCES

References

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105–121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

Atkins H.J., Bramley G.L.C., Johnson M.A., Kartonegoro A., Nishii K., Kokubugata G., Möller M. & Hughes M. 2020. A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography. *Frontiers of Biogeography* 12: e44814. https://doi.org/10.21425/F5FBG44814

Baas P. & Hovenkamp P.H. 2018a. In memoriam Jan-Frits Veldkamp (31 March 1941 – 12 November 2017). *Blumea* 63: 1–10.

Baas P. & Hovenkamp P.H. 2018b. Obituary: Jan Frits Veldkamp (1941–2017). *Sibbaldia* 16: 5–6.

Bacci L.F., Michelangeli F.A. & Goldenberg R. 2019. Revisiting the classification of Melastomataceae: implications for habit and fruit evolution. *Botanical Journal of the Linnean Society* 190(1): 1–24. https://doi.org/10.1093/botlinnean/boz006

Backer C.A. 1936. *Verklarend woordenboek van wetenschappelijke plantennamen*. Noordhoff NV., Groningen.

Baillon H. 1877. *Histoire de plantes*. Vol. 7. Librairie Hachette & C., Paris.

Baker E.G. 1923. Polypetalae. In: Rendle A.B., *et al.*, Dr H.O. Forbes's New Guinea plants. *Journal of Botany, London* 61 (Suppl.): 1–64.

Baker E.G. 1924. Melastomataceae. In: Rendle A.B., Forbes's Malayan plants. *Journal of Botany, London* 62 (Suppl.): 39–42.

Baker W.J. & Couvreur T.L. 2012. Biogeography and distribution patterns of Southeast Asian palms. In: Gower D., Johnson K., Richardson J., Rosen B., Ruber L. & Williams S. (Eds.) *Biotic evolution and environmental change in Southeast Asia. Systematics Association Special Volume Series*. Cambridge University Press, New York. pp. 164–190.

Bakhuizen van den Brink Jr. R.C. 1943. *A contribution to the knowledge of the Melastomataceae occurring in the Malay Archipelago, especially in the Netherlands East Indies*. PhD Thesis, Universiteit Utrecht, pp. 1–391. [Reprinted in: *Recueil des Travaux Botaniques Néerlandais* 40: 1–391. 1946; *Mededeelingen van het Botanisch Museum en Herbarium van de Rijks Universiteit te Utrecht* 91: 1–391. 1947].

Bakhuizen van den Brink Jr. R.C. 1964. Melastomataceae. In: Backer C.A. & Bakhuizen van den Brink Jr R.C. (Eds.), *Flora of Java*. Vol. 1. NV.P. Noordhoff, Groningen, pp. 354–374.

Bakhuizen van den Brink Jr R.C. & Koster J.T. 1963. Notes on the Flora of Java VIII. *Blumea* 12: 61–69.

Barker N.P., Weston P.H., Rutschmann F. & Sauquet H. 2007. Molecular dating of the "Gondwanan" plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. *Journal of Biogeography* 34: 2012–2027. https://doi.org/10.1111/j.1365-2699.2007.01749.x

Bentham G. 1849. Melastomaceae. in: Hooker W.J. (Ed.), *Niger flora.* Hippolyte Baillière, London, pp. 344–358. https://doi.org/10.5962/bhl.title.594

Bentham G. & Hooker J.D. 1867. *Genera Plantarum*. Vol. 1. L. Reeve & Co., London.

Berger B.A., Kriebel R., Spalink D. & Sytsma K.J. 2016. Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. *Molecular Phylogenetics and Evolution* 95: 116–136. https://doi.org/10.1016/j.ympev.2015.10.001

Blume C.L. 1823. *Catalogus van eenige der merkwaardigste zoo in- als uit-heemsche gewassen te vinden in 's Lands Plantentuin te Buitenzorg*. Lands Drukkerij, Batavia.

Blume C.L. 1826. Melastomeae. *Bijdragen tot de flora van Nederlandsch Indië*. Vol. 17. Lands Drukkerij, Batavia, pp. 1067–1080.

Blume C.L. 1831a. Ueber einige Ostindische und besonders Javanische Melastomaceen. *Flora* 14: 465–528.

Blume C.L. 1831b. Over eenige Oostindische, bijzonder Javaansche Melastomaceen. *Bijdragen tot de Natuurkundige Wetenschappen* 6: 211–268 (234–242).

Blume C.L. 1849. *Museum botanicum Lugduno-Batavum*. Vol. 1. E.J. Brill, Leiden.

Bochorny T., Michelangeli F.A., Almeda F. & Goldenberg R. 2019. Phylogenetics, morphology and circumscription of Cambessedesieae: a new Neotropical tribe of Melastomataceae. *Botanical Journal of the Linnean Society* 190: 281–302. https://doi.org/10.1093/botlinnean/boz018

Bouckaert R., Heled J., Kühnert D., Vaughan T., Wu C.H., Xie D., Suchard M.A., Rambaut A. & Drummond A.J. 2014. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Computational Biology* 10: e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Bouckaert R., Vaughan T.G., Barido-Sottani J., Duchêne S., Fourment M., Gavryushkina A., Heled J., Jones G., Kühnert D., De Maio N., Matschiner M., Mendes F.K., Müller N.F., Ogilvie H.A., du Plessis L., Popinga A., Rambaut A., Rasmussen D., Siveroni I., Suchard M.A., Wu C.H., Xie D., Zhang C., Stadler T. & Drummond A.J. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15: e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Brikiatis L. 2014. The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. *Journal of Biogeography* 41: 1036–1054. https://doi.org/10.1111/jbi.12310

Brooks A.T.M., Mittermeier R.A., da Fonseca G.A.B., Gerlach J., Hoffmann M., Lamoreux J.F., Mittermeier C.G., Pilgrim J.D. & Rodrigues A.S.L. 2006. Global biodiversity conservation priorities. *Science* 313: 58–61. https://doi.org/ doi: 10.1126/science.1127609

Buerki S., Gallaher T., Booth T., Brewer G., Forest F., Pereira J.T. & Callmander M.W. 2016. Biogeography and evolution of the screw-pine genus *Benstonea* Callm. & Buerki (Pandanaceae). *Candollea* 71: 217–229. http://dx.doi.org/10.15553/c2016v712a8

Bygrave P.C. & Davis A.P. 1996. Melastomataceae. In: Coode M.J.E., Dransfield J., Forman L.L., Kirkup D.W. & Said I.M. (Eds), *A checklist of the flowering plants & gymnosperms of Brunei Darussalam*. Darusima Trading & Printing Co., Bandar Sri Begawan, pp. 184–199.

Cámara-Leret R., Ridder-Numan J.W.A. & Veldkamp J.F. 2013. Revision of *Heteroblemma* gen. nov. (*Dissochaeteae – Melastomataceae*) from Malesia and Vietnam. *Blumea* 58: 229–240. https://doi.org/10.3767/000651913X674945

Cannon C.H. 2012. Quarternary dynamics of Sundaland forests. In: Gower D., Johnson K., Richardson J., Rosen B., Ruber L. & Williams S. (Eds.) *Biotic evolution and environmental change in Southeast Asia. Systematics Association Special Volume Series*. Cambridge University Press, New York. pp. 115-137.

Cannon C.H., Morley R.J. & Bush A.B.G. 2009. The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 106: 11188–11193. https://doi.org/10.1073/pnas.0809865106

Cellinese N. 1999. *Systematics of the Asian Sonerileae (Melastomataceae)*. PhD Thesis, University Reading, United Kingdom. Pp 1–323.

Cellinese N. 2004. Melastomataceae. In: Beaman J.H. & Anderson C. (Eds), *The plants of Mount Kinabalu. Vol. 5, Dicotyledon families Magnoliaceae to Winteraceae*. Natural History Publications, Kota Kinabalu, pp. 92–118.

Chen C. 1983. On *Medinilla* Gaud. of China in relation to the drift of the Indian Plate. *Acta Phytotaxonomy Sinica* 21(4): 416–422.

Chen C. 1984. *Medinilla*. In: Chen C. (Ed.) *The Flora Reipublicae Popularis Sinicae.* Vol. 1. Science Press, Beijing, pp. 268–280.

Chen C. & Renner S.S. 2007. Melastomataceae. In: Wu Z.Y., Raven P.H. & Hong D.Y. (Eds.), *Flora of China*. Vol. 13. Science Press, Beijing, pp. 360–399.

Chen J.H., Thomas D.C. & Saunders R.M.K. 2019. Geographic range and habitat reconstruction shed light on palaeotropical intercontinental disjunction and regional diversification patterns in *Artabotrys* (Annonaceae). *Journal of Biogeography* 46: 2690–2705. https://doi.org/10.1111/jbi.13703

Cho S.H., Kim B.Y., Lee J.H. & Phourin, C. 2016. Two newly recorded species of the genus *Medinilla* from Cambodia. *Korean Journal of Plant Taxonomy* 46(3): 301–305

Christenhusz M.J.M. & Byng J.W. 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* 261: 201–217. https://doi.org/10.11646/phytotaxa.261.3.1

Clarke C.B. 1879. Melastomaceae. In: Hooker J.D. (Ed.), *Flora British India*. Vol. 2. L. Reeve & Co., London, pp. 512–565.

Clarke C.B. 1890. On the plants of Kohima and Muneypore. *Journal of the Linnean Society, London, Botany* 25: 1–106.

Clausing G. 1999. *Die Systematik der Dissochaeteae und ihre Stellung innerhalb der Melastomataceae*. PhD Dissertation. Johannes-Gutenberg Universität, Mainz, pp. 1–218.

Clausing G. 2000. Revision of *Pachycentria* (Melastomataceae). *Blumea* 45: 341–375.

Clausing G. & Renner S.S. 2001a. Evolution of growth form in epiphytic Dissochaeteae (Melastomataceae). *Organisms, Diversity & Evolution* 1(1): 45–60. https://doi.org/10.1078/1439-6092-00004

Clausing G. & Renner S.S. 2001b. Molecular phylogenetics of Melastomataceae and Memecylaceae: implications for character evolution. *American Journal of Botany* 88(3): 486–498. https://doi.org/ 10.2307/2657114

Clausing G., Meyer K. & Renner S.S. 2000. Correlations among fruit traits and evolution of different fruits within Melastomataceae. *Botanical Journal of the Linnaean Society* 133: 303–326.

Cogniaux C.A. 1889. Melastomaceae. In: Schumann K. & Hollrung U.M. (Eds), *Die flora von Kaiser Wilhelms Land*. Asher & Co., Berlin, pp. 86–88.

Cogniaux C.A. 1890. Melastomaceae. In: Boerlage J.G. (Ed.), *Handleiding tot de kennis der flora van Nederlandsch Indië*. Vol. 2. EJ Brill, Leiden, pp. 500–538.

Cogniaux C.A. 1891. Melastomaceae. In: de Candolle A. & de Candolle C. (Eds), *Monographiae Phanerogamarum*. Vol. 7. Massson, Paris, pp. 1–1256.

Collinson M.E. & Pingen M. 1992. Seeds of the Melastomataceae from the Miocene of Central Europe. In: Kovar-Eder J. (Ed.) *Palaeovegetational development in Europe*. Museum of Natural History, Vienna. pp. 129–139.

Craib W.G. 1913. Contributions to the flora of Siam. Additamentum III. *Bulletin of Miscellaneous Information Kew* 1913: 65–72.

Craib W.G. 1930. Contributions to the flora of Siam. Additamentum XXIX. *Bulletin of Miscellaneous Information Kew* 1930: 320.

Craib W.G. 1931. Melastomaceae. *Florae Siamensis enumeration; A list of the plants known from Siam*. Vol. 10. Bangkok Times Press Ltd., Bangkok, pp. 674–715.

Crayn D.M., Costion C. & Harrington M.G. 2015. The Sahul-Sunda floristic exchange: Dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography* 42: 11–24. https://doi.org/10.1111/jbi.12405

Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. https://doi.org/10.1038/nmeth.2109

De Bruyn M., Stelbrink B., Morley R.J., Hall R., Carvalho G.R., Cannon C.H. & von Rintelen T. 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology* 63: 879–901

De Candolle A.P. 1828. *Prodromus systematis naturalis regni vegetabilis*. Vol. 3. Sumtibus Sociorum Treuttel & Würtz, Paris.

De Groot G.A., During H.J., Maas J.W., Schneider H., Vogel J.C. & Erkens R.H. 2011. Use of *rbcL* and *trnL-F* as a two-locus DNA barcode for identification of NW-European ferns: an ecological perspective. *PLos One* 6(1): e 16371. https://doi.org/10.1371/journal.pone.0016371

Dickerson R.E. 1928. Distribution of life in the Philippines. Bureau of Printing, Manila.

Don G. 1832. *General history of the dichlamydeous plants*. Vol. 2. JG & F Rivington, London, pp. 728–806.

Doyle J.J. & Doyle J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemistry Bulletin* 19: 11–15.

Drummond A.J. & Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214. https://doi.org/10.1186/1471-2148-7-214

Drummond A.J., Ho S.Y.W., Phillips M.J. & Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PloS Biology* 4: 699–710. https://doi.org/10.1371/journal.pbio.0040088

Drummond A.J., Suchard M.A., Xie D. & Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973. https://doi.org/10.1093/molbev/mss075

Duan L., Harris A.J., Su C., Ye W., Deng S.W., Fu L., Wen J. & Chen H.F. 2020. A fossil-calibrated phylogeny reveals the biogeographic history of the *Cladrastis* clade, an amphi-Pacific early-branching group in papilionoid legumes. *Molecular Phylogenetics and Evolution* 143: 106673. https://doi.org/10.1016/j.ympev.2019.106673

Elmer A.D.E. 1911. New Melastomataceae. *Leaflets of Philippine Botany* 4: 1191–1230.

Elmer A.D.E. 1915. Two hundred twenty-six new species – II. *Leaflets of Philippine Botany* 8: 2719–2883.

Elmer A.D.E. 1939. Irosin Melastomataceae. *Leaflets of Philippine Botany* 10: 3649–3672.

Endlicher S. 1836–1840. *Genera plantarum secundum ordines naturales*. Fr. Beck Universitatis, Vindobonae, pp. 1205–1223.

Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791. https://doi.org/10.2307/2408678

Fritsch P.W., Almeda F., Renner S.S., Martins A.B. & Cruz B.C. 2004. Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). *American Journal of Botany* 91(7): 1105–1114. https://doi.org/10.3732/ajb.91.7.1105

Furtado C.X. 1963. Notes on some Malaysian Melastomaceae. *Gardens' Bulletin Singapore* 20: 105–122.

Geddes E. 1928. *Anplectrum patens* Geddes. Contribution to the Flora of Siam. Additamentum XXIV. *Bulletin of Miscellaneous Information Kew* 1928: 62–72. https://doi.org/10.2307/4107648

Geddes E. 1928. *Anplectrum stellulatum* Geddes. Contribution to the Flora of Siam. Additamentum XXV. *Bulletin of Miscellaneous Information Kew* 1928: 234–247. https://doi.org/10.2307/4107694

Gernhard T. 2008. The conditioned reconstructed process. *Journal of Theoritical Biology* 253: 769–778. https://doi.org/10.1016/j.jtbi.2008.04.005

Gilg E. 1898. *Monographieen afrikanischer Pflanzen-Familien und -Gattungen*, *Vol. 2, Melastomataceae*. Engelmann, Leipzig. https://doi.org/10.5962/bhl.title.53505

Goldenberg R., Teixeira S.P. & Martins A.B. 2003. Anther dehiscence and circumscription of *Miconia* sect. *Hypoxanthus* (Melastomataceae). *Kew Bulletin* 58: 195–203. https://doi.org/10.2307/4119362

Goldenberg R., Penneys D.S., Almeda F., Judd W.S. & Michelangeli F.A. 2008. Phylogeny of *Miconia* (Melastomataceae): Patterns of stamen diversification in a megadiverse neotropical genus. *International Journal of Plant Sciences* 169: 963–979. https://doi.org/10.1086/589697

Goldenberg R., de Fraga C.N., Fontana A.P., Nicolas A.N. & Michelangeli F.A. 2012. Taxonomy and phylogeny of *Merianthera* (Melastomataceae). *Taxon* 61(5): 1040–1056. https://doi.org/10.1002/tax.615010

Gray A. 1854. Botany phanerogamia. Part 1. In: Wilkes C. (Ed.) *United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842*. C. Sherman, Philadelphia.

Grudinski M., Wanntorp L., Panell C.M., Muellner-Riehl A.N. 2014. West to east dispersal in a widespread animal-dispersed woody angiosperm genus (*Aglaia*, Meliaceae) across the Indo-Australian Archipelago. *Journal of Biogeography* 41: 1149–1159. https://doi.org/10.1111/jbi.12280

Guillaumin M.A. 1913. Contribution à l'étude des Mélastomacées d'Extrême-Orient, IV–V. *Bulletin de la Société Botanique de France* 60: 341–342.

Guillaumin M.A. 1921a. Contribution à l'étude des Mélastomacées d'Extrême-Orient, Supplément. *Bulletin de la Société Botanique de France* 68: 2–11.

Guillaumin M.A. 1921b. Mélastomacées. In: Lecomte, P.H. (Ed.) *Flore Générale de l'Indo-Chine*. Volume 2. Masson & Cie, Paris, pp. 864–938.

Hall R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20: 353–431. https://doi.org/10.1016/S1367-9120(01)00069-4

Hall R. 2009. Southeast Asia's changing palaeogeography. *Blumea* 54: 148–161. https://doi.org/10.3767/000651909X475941

Hall R. 2012. Sundaland and Wallacea: geology, plate tectonics and palaeogeography. In: Gower D., Johnson K., Richardson J., Rosen B., Ruber L. & Williams S. (Eds.) *Biotic evolution and environmental change in Southeast Asia. Systematics Association Special Volume Series*. Cambridge University Press, New York. pp. 32–78.

Hansen C. 1984. Melastomataceae of Gunung Mulu National Park. In: Jermy A.C. (Ed.), *Studies on the flora of Gunung Mulu National Park Sarawak*. Sarawak Forest Department, Kuching, pp. 105–135.

Hansen C. 1990a. New species of *Pseudodissochaeta* Nayar and *Sonerila* Roxb. (Melastomataceae) from Indo-China. *Bulletin du Muséum National d'Histoire Naturelle. Section B, Adansonia: Botanique Phytochemie, Sér. 4*, 11: 279–286.

Hansen C. 1990b. New species and combinations in *Allomporphia*, *Phyllagathis*, and *Sporoxeia* (Melastomataceae) in Indo-China. *Bulletin du Muséum National d'Histoire Naturelle. Section B, Adansonia: Botanique Phytochemie, Sér. 4*, 12(1): 37–41.

Hansen C. & Wickens G.E. 1981. A revision of *Ochthocharis* (Melastomataceae), including *Phaeoneuron* of Africa. *Kew Bulletin* 36(1): 13–29.

Heine H. 1953. Diagnoses novae plantarum in Borneo septentrionali a J. et M.S. Clemens lectarum. *Mitteilungen (aus) der Botanischen Staatssammlung München* 1: 214–215.

Hickey J.L. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of Western North Dakota. Geological Society of America, Colorado.

Hochreutiner B.P.G. 1925. Plantae Hochreutineranae. *Candollea* 2: 317–513.

Hô P.H. 1992. *An illustrated Flora of Vietnam*. Vol. 2. Mekong Printing, Hanoi.

IUCN. 2010. *Guidelines for using the IUCN Red List Categories and Criteria. Version 8.1*. Prepared by the Standards and Petitions Subcommitee in March 2010. Downloadable from http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf.

Jack W. 1823. On the Malayan species of *Melastoma*. *Transaction of the Linnean Society London* 14(1): 1–22. https://doi.org/10.1111/j.1095-8339.1823.tb00077.x

Jacques-Félix H. 1977. Synonymes nouveaux de Mélastomatacées d'Afrique et de Madagascar. *Adansonia* sér. 2, 17: 77–78.

Jacques-Félix H. 1983. Mélastomatacées. In: Satabié B. & Leroy J.-F. (Eds.), *Flore du Cameroun*, Vol. 24. Délégation Générale à la Recherche Scientifique et Technique, Yaounde.

Jacques-Félix H. 1995. Histoire des Melastomataceae d'Afrique. *Bulletin du Muséum National d'Histoire Naturelle. Section B, Adansonia: Botanique Phytochemie, Sér. 4*, 16: 235–311.

Jordan W.C., Courtney M.W. & Neigel J.E. 1996. Low levels of intraspecific genetic variation at a rapidly evolving chloroplast DNA locus in North American duckweeds (Lemnaceae). *American Journal of Botany* 83(4): 430–439. https://doi.org/ 10.2307/2446212

Kadereit G. 2005. Revision of *Plethiandra* Hook.f.: a polystaminate, East Asian genus of Melastomataceae. *Edinburgh Journal of Botany* 62(3): 127–144. https://doi.org/10.1017/S0960428606000175

Kadereit G. 2006. A new species of *Dissochaeta* Blume (Melastomataceae) from Kalimantan (Borneo, Indonesia). *Edinburgh Journal of Botany* 63(1): 3–8. https://doi.org/10.1017/S0960428606000382

Kanjilal U.N., Kanjilal P.C. & Das A. 1938. *Flora of Assam*. *Volume 2, Connaraceae to Cornaceae*. Prabasi Press, Calcutta.

Kartonegoro A. 2018. *Diplectria maxwellii* (Melastomataceae), a new species from Sarawak, Borneo. *Kew Bulletin* 73-23: 1–3. https://doi.org/10.1007/s12225-018-9741-x

Kartonegoro A. & Veldkamp J.F. 2010. Revision of *Dissochaeta* (Melastomataceae) in Java, Indonesia. *Reinwardtia* 13(2): 125–145. https://doi.org/10.14203/reinwardtia.v13i2.2133

Kartonegoro A. & Veldkamp J.F. 2013. Revision of *Creochiton* (Melastomataceae). *Blumea* 58(3): 217–227. https://doi.org/10.3767/000651913X674134

Kartonegoro A., Veldkamp J.F., Hovenkamp P. & Van Welzen P.C. 2018. A Revision of *Dissochaeta* (Melastomataceae, Dissochaeteae). *PhytoKeys* 107: 1–178.

Kartonegoro A., Hovenkamp P. & van Welzen P. 2019. A taxonomic revision of *Macrolenes* (Melastomataceae). *Gardens' Bulletin Singapore* 71(1): 185–241. doi: 10.26492/gbs71(1).2019-12

Kartonegoro A., Liu Y., Mota de Oliveira S. & Van Welzen P. 2020. A taxonomic revision of *Pseudodissochaeta* (Melastomataceae, Dissochaeteae). *Phytotaxa* 468(2): 159–174. https://doi.org/10.11646/phytotaxa.468.2.1

Kartonegoro A., Veranso-Libalah M.C., Kadereit G., Frenger A., Penneys D.S., Mota de Oliveira S. & Van Welzen P.C. 2021. Molecular phylogenetics of the *Dissochaeta* alliance (Melastomataceae): Redefining tribe Dissochaeteae. *Taxon* 70(4): 793–825. https://doi.org/10/1002/tax.12508

Katoh K. & Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kelchner S.A. & Clark L.G. 1997. Molecular evolution and phylogenetic utility of the chloroplast *rpl16* intron in *Chusquea* and the Bambusoideae (Poaceae). *Molecular Phylogenetics and Evolution* 8(3): 385–397. https://doi.org/10.1006/mpev.1997.0432

King G. 1900. Materials for a flora of the Malayan Peninsula 1. *Journal of the Asiatic Society of Bengal*. Part 2. Natural History 69: 1–87.

Koorders S.H. 1912. *Exkursionsflora von Java*. Vol. 2. Fischer, Jena.

Koorders S.H. 1923. *Flora von Tjibodas*. Vol. 2. Visser & Co., Batavia.

Korthals P.W. 1842–1844. Bijdrage tot de kennis der Indische Melastomaceae. In: Temminck C.J. (Ed.), *Verhandelingen over De natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, Botanie*. Natuurkundige Commissie, Leiden, pp. 236–243.

Kränzlin F.W.L. 1931. Beiträge zur Kenntnis der Melastomataceae. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 76(3): 147–159.

Krasser F. 1893. Melastomataceae. In: Engler A. & Prantl K. (Eds.), *Die natürlichen Pflanzenfamilien*. Teil 3, Abt. 7. Engelmann, Leipzig, pp. 130–199.

Kriebel R. & Zumbado M.A. 2014. New reports of generalist insect visitation to flowers of species of *Miconia* (Miconieae: Melastomataceae) and their evolutionary implications. Brittonia 66: 396–404. https://doi.org/10.1007/s12228-014-9337-1

Kuntze O. 1891. *Revisio genera plantarum*. Vol. 1. Arthur Felix, Leipzig.

Kurz S. 1877. *Forest flora of British Burma. Vol. 1. (Ranunculaceae to Cornaceae)*. Governement Printing, Calcutta.

Li H.L. 1944. Studies in the Melastomataceae of China. *Journal of the Arnold Arboretum* 25: 1–42.

Li P.S., Thomas D.C. & Saunders R.M.K. 2017. Historical biogeography and ecological niche modelling of the *Asimina-Disepalum* clade (Annonaceae): Role of ecological differentiation in Neotropical-Asian disjunctions and diversification in Asia. *BMC Evolutionary Biology* 17: 188. https://doi.org/10.1186/s12862-017-1038-4

Lohman D.J., De Bruyn M., Page T., von Rintelen K., Hal R., Ng P.K.L., Shih H.T., Carvalho G.R. & von Rintelen T. 2011. Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics* 42: 205–226

Mansfeld R. 1924. Melastomataceae. *Nova Guinea* 14: 199–207.

Mansfeld R. 1925. Die Melastomaceen von Papuasien. In: Lauterbach C. (Ed.), Beiträge zur Flora von Papuasien. XIII. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 60: 105–143.

Maxwell J.F. 1980a. *Taxonomic revision of Diplectrinae Maxw. and Dissochaetinae Naud. (Dissochaeteae) Melastomataceae*. PhD Thesis, University of Singapore, pp. 1–568.

Maxwell J.F. 1980b. Taxonomic notes on the tribe Dissochaeteae (Naudin) Triana (Melastomataceae). *Gardens' Bulletin Singapore* 33: 312–327.

Maxwell J.F. 1982. Woody climbing melastomes in the Malay Peninsula. *Malayan Nature Journal* 35: 149–163.

Maxwell J.F. 1983. Taxonomic and nomenclatural notes on *Oxyspora* DC., *Anerincleistus* Korth., *Poikilogyne* Baker f., and *Allomorphia* Bl. (Melastomataceae, tribe Oxysporeae). *Gardens' Bulletin Singapore* 35(2): 209–226.

Maxwell J.F. 1984. Taxonomic studies of the Melastomataceae (Part 1). A revision of subtribes Dissochaetinae Maxw. and Dissochaetinae Naudin (genera *Diplectria* (Bl.) Reichb., *Dissochaeta* Bl., *Macrolenes* Naudin, *Creochiton* Bl., and *Pseudodissochaeta* Nayar). *Federation Museums Journal* 29: 45–117.

Merrill E.D. 1905. New or noteworthy Philippine plants III. *Publications of the Bureau of Science Government Laboratories* 29: 5–50.

Merrill E.D. 1916. Reliquiae Robinsonianae. *The Philippine Journal of Science, C. Botany* 11(5): 243–319.

Merrill E.D. 1917. Contribution to our knowledge of the Flora of Borneo. *Journal of the Straits Branch of the Royal Asiatic Society* 76: 74–117.

Merrill E.D. 1922. New or noteworthy Bornean plants II. *Journal of the Straits Branch of the Royal Asiatic Society* 86: 312–342.

Merrill E.D. 1923. *An enumeration of Philippine flowering plants*. Vol. 3. Bureau of Printing, Manila.

Merrill E.D. 1926. Additions to our knowledge of the Philippine Flora, III. *The Philippine Journal of Science, C. Botany* 30(4): 389–430.

Merrill E.D. 1929. Plantae Elmerianae Borneenses. *University of California Publications in Botany* 15: 1–316.

Merrill E.D. 1934. New Sumatran Plants. *Papers of the Michigan Academy of Science, Arts and Letters* 19: 149–203.

Merrill E.D. 1939. New Sumatran Plants IV. *Papers of the Michigan Academy of Science, Arts and Letters* 24: 63–92.

Michelangeli F.A., Penneys D.S., Giza J., Soltis D., Hils M.H. & Skean J.D. 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. *Taxon* 53(2): 279–290. https://doi.org/10.2307/4135608

Michelangeli F.A., Nicolas A.N., Morales-Puentes M.E. & David H. 2011. Phylogenetic relationships of *Allomaieta*, *Alloneuron*, *Cyphostyla*, and *Wurdastom* (Melastomataceae) and the resurrection of the tribe Cyphostyleae. Int. J. Plant Sci. 172: 1165–1178. https://doi.org/10.1086/662032.

Michelangeli F.A., Guimaraes P.J.F., Penneys D.S., Almeda F. & Kriebel R. 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Botanical Journal of the Linnean Society* 171: 38–60. https://doi.org/10.1111/j.1095-8339.2012.01295.x

Michelangeli F.A., Almeda F., Goldenberg R. & Penneys D.S. 2020. A guide to curating New World Melastomataceae collections with a linear generic sequence to world-wide Melastomataceae. *Preprints* 2020, 2020100203. https://doi.org/ 10.20944/preprints202010.0203.v1

Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: 2010 gateway computing environments workshop (GCE) 1–8.

Miquel F.A.W. 1855. *Flora van Nederlandsch Indië*. Vol. 1. C.G. van der Post, Amsterdam.

Miquel F.A.W. 1860-1861. *Flora van Nederlandsch Indië. Eerste Bijvoegsel. Sumatra, zijne plantenwereld en hare voortbrengselen. Prodromus florae Sumatranae*. C.G. van der Post, Utrecht.

Mittermeier R.A., Mittermeier C.G., Brooks T.M., Pilgrim J.D., Konstant W.R., da Fonseca G.A.B. & Kormos C. 2003. Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America* 100: 10309–10313. www.pnas.org/cgi/doi/10.1073/pnas.1732458100

Morley R.J. 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology Evolution and Systematics* 6: 5–20. https://doi.org/10.1078/1433-8319-00039

Morley R.J. 2012. A review of the Cenozoic palaeoclimate history of Southeast Asia. In: Gower D., Johnson K., Richardson J., Rosen B., Ruber L. & Williams S. (Eds.) *Biotic evolution and environmental change in Southeast Asia. Systematics Association Special Volume Series*. Cambridge University Press, New York. pp. 79-114.

Morley R.J. & Dick C.W. 2003. Missing fossils, molecular clocks, and the origin of the Melastomataceae. *American Journal of Botany* 90: 1638–1644. https://doi.org/10.3732/ajb.90.11.1638

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Naudin C. 1851. Melastomacearum quae in Museo parisiensi continentur monographicae descriptiones et secundum affinitates distributionis tentamen. *Annales des Sciences Naturelles; Botanique,* sér. 3, 15: 67–79, 277–283.

Naudin C. 1852. Melastomacearum quae in Museo parisiensi continentur monographicae descriptiones et secundum affinitates distributionis tentamen. *Annales des Sciences Naturelles, Botanique*, sér. 3, 18: 141, 153–154.

Nauheimer L., Boyce P.C. & Renner S.S. 2012. Giant taro and its relatives: A phylogeny of the large genus *Alocasia* (Araceae) sheds light on Miocene floristic exchange in the Malesian region. *Molecular Phylogenetics and Evolution* 63: 43–51.

Nayar M.P. 1966. Contributions to the knowledge of Indo-Malaysian and other Asiatic Melastomataceae. *Kew Bulletin* 20(1): 155–161. https://doi.org/10.2307/4107906

Nayar M.P. 1969a. *Pseudodissochaeta*: A new genus of Melastomataceae. *Journal of the Bombay Natural History Society* 65(3): 557–568.

Nayar M.P. 1969b. *Dissochaeta alstonii* sp. nov. (Melastomataceae). *Bulletin of the Botanical Survey of India* 11: 188–189.

Nayar M.P. 1969c. A new species of *Neodissochaeta* Bakh.*f.* (Melastomataceae). *Bulletin of the Botanical Survey of India* 11: 195–196.

Nayar M.P. 1970. A synopsis of the genus *Eisocreochiton* Quisumb. & Merr. (Melastomataceae). *Journal of the Bombay Natural History Society* 67: 87–90.

Nayar M.P. 1980. Notes on Asian Melastomataceae (3): New species and notes on the genus *Macrolenes* Naud. *The Journal of Japanese Botany* 55(2): 45–52.

Nayar M.P. 1982. Revision of the genus *Catanthera* F.v.Muell. (Melastomataceae). *Reinwardtia* 10(1): 35–61.

Nees von Esenbeck T.F.L. 1825. Catalogus van eenige der merkwaardigste zoo in- als uitheemse gewassen te vinden in ‘s Lands Plantentuin te Buitenzorg opgemaakt door C.L. Blume. *Flora* 8: 97–160.

Nuttal T. 1818. *The genera of the North American plants and a catalogue of the species to the year 1817*. D. Heartt, Philadelphia.

Ohwi J. 1943. The Kanehira-Hatusima 1940 collection of New Guinea plants. XVI. *Botanical Magazine Tokyo* 57: 1–19. https://doi.org/10.15281/jplantres1887.57.1

Olmstead R.G. & Sweere J.A. 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Systematic Biology* 43: 467–481. https://doi.org/10.1093/sysbio/43.4.467

Penneys D.S. & Judd W.S. 2013. Combined molecular and morphological phylogenetic analyses of the Blakeeae (Melastomataceae). *International Journal of Plant Sciences* 174(5): 802–817. https://doi.org/10.1086/670011

Penneys D.S., Michelangeli F.A., Judd W.S. & Almeda F. 2010. Henrietteeae (Melastomataceae): A new Neotropical berry-fruited tribe. *Systematic Botany* 35(4): 783–800. https://doi.org/10.1600/036364410X539862

Penneys D.S., Almeda F., Michelangeli F.A., Goldenberg R., Martins A.B. & Fritsch P.W. 2020. Lithobieae and Eriocnemeae: two new Neotropical tribes of Melastomataceae. *Phytotaxa* 453(3): 157–178. https://doi.org/10.11646/phytotaxa.453.3.1

Quisumbing E. & Merrill E.D. 1928. New Philippine plants. *The Philippine Journal of Science* 37: 177–178.

Raes N. & van Welzen P.C. 2009. The demarcation and internal division of Flora Malesiana: 1857–present. *Blumea* 54: 6–8. https://doi.org/ 10.3767/000651909X475888

Raes N., Cannon C.H., Hijmans R.J., Peissens T., Saw L.G., van Welzen P.C. & Slik J.W.F. 2014. Historical distribution of Sundaland's Dipterocarp rainforests at Quaternary glacial maxima. *Proceedings of the National Academy of Sciences of the United States of America* 111: 16790–16795. https://doi.org/ 10.1073/pnas.1403053111

Raizada M.B. 1968. Some name changes in the Flora of India. *Indian Forester* 94(6): 432–462.

Rambaut A. 2009. *FigTree*. Online. Available: http://tree.bio.ed.ac.uk/software/figtree

Rambaut A., Drummond A.J., Xie D., Baele G. & Suchard M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Ree R.H. & Smith S.A. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4–14. https://doi.org/10.1080/10635

Regalado J.C. 1990. Revision of *Medinilla* (Melastomataceae) of Borneo. *Blumea* 35: 5–70.

Regalado J.C. 1995. Revision of Philippine *Medinilla* (Melastomataceae). *Blumea* 40: 113–193.

Reginato M., Michelangeli F.A. & Goldenberg R. 2010. Phylogeny of *Pleiochiton* (Melastomataceae, Miconieae): total evidence. *Botanical Journal of the Linnean Society* 162(3): 423–434. https://doi.org/10.1111/j.1095-8339.2009.01022.x

Reichenbach H.G.L. 1841. *Der deutsche Botaniker, Erster Band: Das Herbarienbuch, Erklärung des natürlichen Pflanzensystems, systematische Aufzählung, Synonymik und Register der bis jetzt bekannten Pflanzengattungen*. Arnoldisschen Buchandlung, Dresden.

Reinwardt C.G.C. 1828. Nova plantarum indicarum genera. In: Hornschuch C.F. (ed.), *Sylloge Plantarum Novarum Itemque Minus Cognitarum a Praestantissimis Botanicis adhuc Viventibus Collecta et a Societate Regia Botanica Ratisbonensi*, edita 2. C.E. Brenck, Regensburg.

Renner S.S. 1989. A survey of reproductive biology in Neotropical Melastomataceae and Memecylaceae. Ann. Mo. Bot. Gard. 76: 496–518. https://doi.org/10.2307/2399497

Renner S.S. 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic Journal of Botany* 13(5): 519–540. https://doi.org/10.1111/j.1756-1051.1993. tb00096.x

Renner S.S. 2004a. Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *Philosophical Transaction of the Royal Society of London B: Biological Sciences* 359: 1485–1494. https://doi.org/10.1098/rstb.2004.1530

Renner S.S. 2004b. Bayesian analysis of combined chloroplast loci, using multiple calibrations, supports the recent arrival of Melastomataceae in Africa and Madagascar. *American Journal of Botany* 91: 1427–1435. https://doi.org/10.3732/ajb.91.9.1427

Renner S.S., Clausing G. & Meyer K. 2001a. Historical biogeography of Melastomataceae: The roles of Tertiary migration and longdistance dispersal. *American Journal of Botany* 88: 1290–1300. https://doi.org/10.2307/3558340

Renner S.S., Clausing G., Cellinese N. & Meyer K. 2001b. Melastomataceae. In: Santisuk T. & Larsen K. (Eds.), *Flora of Thailand*. Vol. 7, Ser. 3. Prachachon Co. Ltd., Bangkok, pp. 412–497.

Richardson J.E., Costion C.M. & Muellner A.N. 2012. The Malesian floristic interchange: Plant migration patterns across Wallace's Line. In: Gower D., Johnson K., Richardson J.E., Rosen B., Rüber L. & Williams S. (Eds.) *Biotic evolution and environmental change in Southeast Asia*. Cambridge University Press, New York. pp. 138–163.

Ridley H.N. 1922. *The flora of the Malay Peninsula*. Vol. 1. L. Reeve & Co., London.

Ridley H.N. 1925. *The flora of the Malay Peninsula*. Vol. 5. L. Reeve & Co., London.

Ridley H.N. 1946. Additions to the flora of Borneo and other Malay Islands: XIX. *Kew Bulletin* 1: 31–40. https://doi.org/10.2307/4109088

Rocha M.J.R., Batista J.A.N., Guimarães P.J.F. & Michelangeli F.A. 2016. Phylogenetic relationships in the *Marcetia* alliance (Melastomataceae, Melastomateae) and implications for generic circumscription. *Botanical Journal of the Linnean Society* 181: 585–609. https://doi.org/10.1111/boj.12429

Ronquist F. 1996a. *"DIVA, version 1.1"*. Computer program and manual available from ftp.systbot.uu.se and www.systbot.uu.se/staff/f_ronquist.html. Uppsala University, Uppsala.

Ronquist F. 1996b. Reconstructing the history of host-parasite associations using generalised parsimony. *Cladistics* 11: 73–89.

Ronquist F. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology* 46: 193–201.

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Roos M.C. 1993. State of affairs regarding Flora Malesiana: progress in revision work and publication schedule. *Flora Malesiana Bulletin* 11: 133–142.

Roxburgh W. 1832. *Flora Indica: Descriptions of Indian plants*. Vol. 2. W. Thacker & Co, Calcutta.

Sauquet H. 2013. A practical guide to molecular dating. *Comptes Rendus Palevol* 12: 355–367. https://doi.org/10.1016/j.crpv.2013.07.003

Schwartz O. 1931. Melastomataceae. In: Irmscher E. (Ed.), Beiträge zur Kenntnis der Flora von Borneo. *Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg* 7: 237–257.

Sirichamorn Y., Thomas D.C., Adema F.A.C.B. & van Welzen P.C. 2014. Historical biogeography of *Aganope*, *Brachypterum* and *Derris* (Fabaceae, tribe Millettieae): insight into the origins of Palaeotropical intercontinental disjunctions and general biogeographical patterns in Southeast Asia. *Journal of Biogeography* 41: 882–893. https://doi.org/ 10.1111/jbi.12262

Smith W.W. 1911. Plantarum novarum in Herbario Horti Regii Calcuttensis cognitarum decas. *Journal and Proceedings of the Asiatic Society of Bengal* 7: 69–75.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. https://doi.org/10.1093/ bioinformatics/btu033

Stamatakis A., Hoover P. & Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57(5): 758–771. https://doi.org/10.1080/10635150802429642

Stapf O. & Green M.L. 1913. *Dissochaeta acmura* Stapf & M.L.Green. Decades Kewenses. Plantarum novarum in Herbario Horti Regii Conservatarum; decades LXX-LXXI. *Bulletin of Miscellaneous Information Kew 1913*: 39–42. https://doi.org/10.2307/4118407

Stapf O. & Green M.L. 1914. Melastomaceae. In: Gibbs L.S. (ed.), A contribution to the flora and plant formations of Mount Kinabalu and the Highlands of British North Borneo. *Journal of the Linnean Society, Botany* 42: 78–81.

Stone R.D. 2014. The species rich, paleotropical genus *Memecylon* (Melastomataceae): Molecular phylogenetics and revised infrageneric classification of the African species. *Taxon* 63(3): 539–561. https://doi.org/10.12705/633-7788

Su Y.C.F. & Saunders R.M.K. 2009. Evolutionary divergence times in the Annonaceae: Evidence of a late Miocene origin of *Pseuduvaria* in Sundaland with subsequent diversification in New Guinea. *BMC Evolutionary Biology* 9: 153. doi:10.1186/1471-2148-9-153.

Swofford D.L. 2002. PAUP*: *Phylogenetic analysis using parsimony (*and other methods), version 4.0 Beta*. Sinauer, Sunderland.

Sytsma K.J., Litt A., Zjhra M.L., Pires J.C., Nepokroeff M. & Conti E. 2004. Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences* 165: 85–105. https://doi.org/10.1086/421066

Thiers B. 2018, continuously updated. *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. http://sweetgum. nybg.org/science/ih/ [accessed on 13 February 2018]

Thomas D.C., Hughes M., Phutthai T., Ardi W.H., Rajbhandary S., Rubite R., Twyford A.D. & Richardson J.E. 2012a. West to east dispersal and subsequent rapid diversification of the megadiverse genus *Begonia* (Begoniaceae) in the Malesian archipelago. *Journal of Biogeography* 39: 98–113. https://doi.org/10.1111/j.1365-2699.2011.02596.x

Thomas D.C., Surveswaran S., Xue B., Sankowsky B., Mols J.B., Kessler P.J.A. & Saunders R.M.K. 2012b. Molecular phylogenetics and historical biogeography of the *Meiogyne-Fitzalania* clade (Annonaceae): Generic paraphyly and late Miocene-Pliocene diversification in Australasia and the Pacific. *Taxon* 61: 559–575. https://doi.org/10.1002/tax.613006

Thomas D.C., Tang C.C. & Saunders R.M.K. 2017. Historical biogeography of *Goniothalamus* and Annonaceae tribe Annoneae: dispersal-vicariance patterns in tropical Asia and intercontinental tropical disjunctions revisited. *Journal of Biogeography* 44: 2862–2876. https://doi.org/ 10.1111/jbi.13086

Torrey J. 1826. *A compendium of the flora of the Northern and Middle States*. J. & J. Harper, New York.

Triana J.J. 1866. Dispositio Melastomacearum. *Bulletin of the International Botanical & Horticultural Congress Amsterdam 1865*: 457–461.

Triana J.J. 1872 ["1871"]. Les Mélastomacées. *Transactions of the Linnean Society, London* 28(1): 1–188. https://doi.org/10.1111/j.1096-3642.1871.tb00222.x

Turland N.J., Wiersema J.H., Barrie F.R., Greuter W., Hawksworth D.L., Herendeen P.S., Knapp S., Kusber W.H., Li D.Z., Marhold K., May T.W., McNeill J., Monro A.M., Prado J., Price M.J. & Smith G.F. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Regnum Vegetabile 159*. Koeltz Botanical Books, Glashütten.

Turner I.M. 2018. The importance of the plates in the *Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen*, *Botanie* for the nomenclature of South-East Asian plants. *Taxon* 67(3): 621–631.

Van Steenis C.G.G.J. 1950. The delimitation of Malaysia and its main plant geographical divisions. *Flora Malesiana*, Ser. I, 1: 70–85.

Van Steenis C.G.G.J. 1964. Plant geography of the mountain flora of Mt Kinabalu. *Proceedings of the Royal Society of London Series B, Biological Sciences* 161: 7–38. https://doi.org/10.1098/rspb.1964.0072

Van Steenis-Kruseman M.J. 1950. Malaysian plant collectors and collections being a cyclopaedia of botanical exploration in Malaysia and a guide to the concerned literature up to the year 1950. In: van Steenis C.G.G.J. (ed.), *Flora Malesiana, Ser. 1, Spermatophyta*. Vol. 1. Noordhoff-Kolff N.V., Jakarta.

Van Tieghem P. 1891. Classification anatomique des Mélastomacées. *Bulletin de la Société Botanique de France* 38: 114–124. https://doi.org/10.1080/00378941.1891.10828542

Van Vliet G.J.C.M. 1981. Wood anatomy of the palaeotropical Melastomataceae. *Blumea* 27: 395–462.

Van Vliet G.J.C.M., Koek-Noorman J. & Ter Welle B.J.H. 1981. Wood anatomy, classification and phylogeny of the Melastomataceae. *Blumea* 27: 463–473.

Van Welzen P.C. & Raes N. 2011. The floristic position of Java. *Gardens' Bulletin Singapore* 63: 329–339.

Van Welzen P.C., Slik J.W.F. & Alahuhta J. 2005. Plant distribution patterns and plate tectonics in Malesia. *Biologiske Skrifter* 55: 199–217.

Van Welzen P.C., Parnell J.A.N. & Slik J.W.F. 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? *Biological Journal of the Linnean Society* 103: 531–545. https://doi.org/10.1111/j.1095-8312.2011.01647.x

Van Welzen P.C., Strijk J.S., van Konijnenburg-Van Cittert J.H.A., Nucete M. & Merckx V.S.F.T. 2014. Dated phylogenies of the sister genera *Macaranga* and *Mallotus* (Euphorbiaceae): Congruence in historical biogeographic patterns? *PLoS ONE* 9: e85713

Veldkamp J.F. 1979 ["1978"]. Notes on *Creochiton*, *Dissochaeta*, and *Macrolenes* (Melastomataceae). *Blumea* 24: 437–446.

Veldkamp J.F. & Nayar M.P. 1979 ["1978"]. The synonymy of the species of *Anplectrum* (Melastomataceae). *Blumea* 24: 431–435.

Veldkamp J.F., Franken N.A.P., Roos M.C. & Nayar M.P. 1979 ["1978"]. A revision of *Diplectria* (Melastomataceae). *Blumea* 24: 405–430.

Ventenat E.P. 1803. *Choix de plantes*. Láuteur, Paris.

Veranso-Libalah M.C., Stone R.D., Fongod A.G., Couvreur T.L. & Kadereit G. 2017. Phylogeny and systematics of African Melastomateae (Melastomataceae). *Taxon* 66(3): 584–614. https://doi.org/10.12705/663.5

Veranso-Libalah M.C., Kadereit G., Stone R.D. & Couvreur T.L. 2018. Multiple shifts to open habitats in Melastomateae (Melastomataceae) congruent with the increase of African Neogene climatic aridity. *Journal of Biogeography* 45(6): 1420–1431. https://doi.org/10.1111/jbi.13210

Veranso-Libalah M.C., Stone R.D & Kadereit G. 2020. Towards a complete phylogeny of African Melastomateae: Systematics of *Dissotis* and allies (Melastomataceae). Taxon 69: 946–991. https://doi.org/10.1002/tax.12317

Voris H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153–1167. https://doi.org/10.1046/j.1365-2699.2000.00489.x

Wallace A.R. 1860. On the zoological geography of the Malay Archipelago. *Journal of the Proceedings of the Linnean Society: Zoology* 4: 172-184.

Willdenow C.L. 1799. *Caroli Linne Species Plantarum*. Tomus II, Pars I. GC Nauk, Berolini.

Winkler H.J.P. 1913. Beiträge zur kenntnis der flora und pflanzengeographie von Borneo II. *Botanische Jahrbücher fur Systematik* 48: 87–118.

Wong K.M. 2016. *The genus Melastoma in Borneo including 31 new species*. Natural History Publication, Kota Kinabalu.

Woodruff D.S. 2010. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity and Conservation* 19: 919–941. https://doi.org/ 10.1007/s10531-010-9783-3

Wu C.Y. 1979. *Flora Yunnanica*. Vol. 2. Science Press, Beijing.

Wurdack J.J. 1986. Atlas of hairs for Neotropical Melastomataceae. *Smithsonian Contributions to Botany* 63: 1–80.

Yu R.Y. & van Welzen P.C. 2020. Historical biogeography of *Trigonostemon* and *Dimorphocalyx* (Euphorbiaceae). *Botanical Journal of the Linnean Society* 192: 333–349. https://doi.org/10.1093/botlinnean/boz075

Yu Y., Harris A.J. & He X.J. 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution* 56: 848–850. https://doi.org/ 10.1016/j.ympev.2010.04.011

Yu Y., Harris A.J., Blair C. & He X. 2015. RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87: 46–49. https://doi.org/10.1016/j.ympev.2015.03.008

Yule G.U. 1925. A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S. *Philosophical Transactions of the Royal Society London, Series B* 213: 21–87

Zeng S.J., Zou L.H., Wang P., Hong W.J., Zhang G.Q., Chen L.J. & Zhuang X.Y. 2016. Preliminary phylogeny of *Fordiophyton* (Melastomataceae), with the description of two new species. *Phytotaxa* 247(1): 45–61. https://doi.org/10.11646/ phytotaxa.247.1.3

Zhou Q.J., Lin C.W., Dai J.H., Zhou R.C. & Liu Y. 2019a. Exploring the generic delimitation of *Phyllagathis* and *Bredia* (Melastomataceae): Acombined nuclear and chloroplast DNA analysis. *Journal of Systematics and Evolution* 57(3): 256–267. https://doi.org/10.1111/jse.12451

Zhou Q.J., Lin C.W., Ng W.L., Dai J.H., Denda T., Zhou R.C. & Liu Y. 2019b. Analyses of plastome sequences improve phylogenetic resolution and provide new insight into the evolutionary history of Asian Sonerileae/Dissochaeteae. *Frontiers in Plant Science* 10: 1477, 1–16.

Curriculum Vitae

Abdulrokhman Kartonegoro was born on 4 January 1980 in Jakarta, Indonesia. He started to study for his Bachelor degree in Biology in 1999 at the University of Indonesia and graduated in 2005. In 2006 he was appointed as research staff in the Research Center for Biology, Indonesian Institute of Sciences (LIPI). His major task was research on plant diversity, especially the taxonomic and systematic aspects. Logically, he was based in Herbarium Bogoriense (BO) in Bogor, West Java. Once he started his engagement with plants, Melastomataceae was one of his specialities with Malesia as his region of focus. During the early years in Herbarium Bogoriense, he received a scholarship to carry on a study for his Master Degree with the New England Tropical Conservatory (NETC) within the Indonesian Biodiversity Exploration and Taxonomy Project (IBETP) in 2008. The research topic for his Master Degree was the taxonomy of the genus *Rhynchoglossum* Blume (Gesneriaceae) in Malesia under supervision of Prof. Dr. Elizabeth A. Widjaja and Dr. Sri S. Tjitrosoedirdjo. He graduated in 2011. After finishing his Master Degree, Abdulrokhman mostly worked in Herbarium Bogoriense on the families Melastomataceae and Gesneriaceae. In 2016, Abdulrokhman was granted a scholarship from the Indonesian Ministry of Research and Technology within its Research and Innovation in Science and Technology Project (RISET-PRO). He started his PhD study in 2017 at the University of Leiden and he was stationed in Naturalis Biodiversity Center, The Netherlands, under the supervision of Prof.dr. Peter C. van Welzen and the late Dr. Peter Hovenkamp, who was in 2019 replaced by Dr. Sylvia Mota de Oliveira. During his study in Leiden, he assisted several times in the course Tropical Plant Families for MSc and PhD students and gave lectures on the families Piperaceae and Araceae. Besides teaching, Abdulrokhman also undertook field works, during which he collected the Melastomataceae needed for his study. The field work was conducted in various regions of Indonesia (West Sumatra, West Java, West Kalimantan and Riau Archipelago) in 2017 and 2019. Most of the field work activities were funded by the Indonesian Ministry of Research and Technology (Kemenristek-BRIN), Leids Universiteits Fonds of Leiden University (Leiden Univeristy Fund, LUF) and the Alberta Mennega Stichting (Alberta Mennga Foundation) of the Netherlands. He also followed some scientific events, courses and symposia held by the Graduate School for Production Ecology & Resource Conservation (PE&RC) chaired from Wageningen University, The Netherlands. After his graduation he will continue his career as a botanical researcher at his original institution, the Research Center for Biology, Indonesian Institute of Sciences (LIPI), Bogor, Indonesia, of which the Herbarium Bogoriense is a part.

List of publications

Kartonegoro A. 2018. *Diplectria maxwellii* (Melastomataceae), a new species from Sarawak, Borneo. *Kew Bulletin* 73-23: 1–3. https://doi.org/10.1007/s12225-018-9741-x

Kartonegoro A. & Veldkamp J.F. 2010. Revision of *Dissochaeta* (Melastomataceae) in Java, Indonesia. *Reinwardtia* 13(2): 125–145. https://doi.org/10.14203/reinwardtia.v13i2.2133

Kartonegoro A. & Veldkamp J.F. 2013. Revision of *Creochiton* (Melastomataceae). *Blumea* 58(3): 217–227. https://doi.org/10.3767/000651913X674134

Kartonegoro A., Veldkamp J.F., Hovenkamp P. & van Welzen P.C. 2018. A Revision of *Dissochaeta* (Melastomataceae, Dissochaeteae). *PhytoKeys* 107: 1–178. https://doi.org/10.3897/phytokeys.107.26548

Kartonegoro A., Hovenkamp P. & van Welzen P. 2019. A taxonomic revision of *Macrolenes* (Melastomataceae). *Gardens' Bulletin Singapore* 71(1): 185–241. https://doi.org/10.26492/gbs71(1).2019-12

Kartonegoro A., Liu Y., Mota de Oliveira S. & van Welzen P. 2020. A taxonomic revision of *Pseudodissochaeta* (Melastomataceae, Dissochaeteae). *Phytotaxa* 468(2): 154–179. https://doi.org/10.11646/phytotaxa.468.2.1

Kartonegoro A., Veranso-Libalah M.C., Kadereit G., Frenger A., Mota de Oliveira S. & van Welzen P.C. 2021. Molecular phylogenetics of *Dissochaeta* alliance (Melastomataceae): Redefinig of tribe Dissochaeteae. *Taxon* 70(4): 793–825. https://doi.org/10/1002/tax.12508

Kartonegoro A., Mota de Oliveira S. & van Welzen P.C. 2021. Historical biogeography of the Southeast Asian *Dissochaeta* alliance (Melastomataceae). *Journal of Systematics and Evolution* (Early online Version). https://doi.org/10.1111/jse.12752

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