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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 sessile. 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; Clausen & 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 pseudumbels, *Creochiton roseus*). **D–F.** Infructescences (**D.** cauliflory, *Pseudodissochaeta lanceata*; **E.** terminal panicle, *Dissochaeta celebica*; **F.** terminal pseudumbels, *Creochiton* sp.). Photographs by: **A.** L. Yezi, **B.** D.S. Penneys, **C.** P.B. Pelsner, **D.** Y. Liu, **E.** Supriyatna, **F.** D.L. Nickrent.

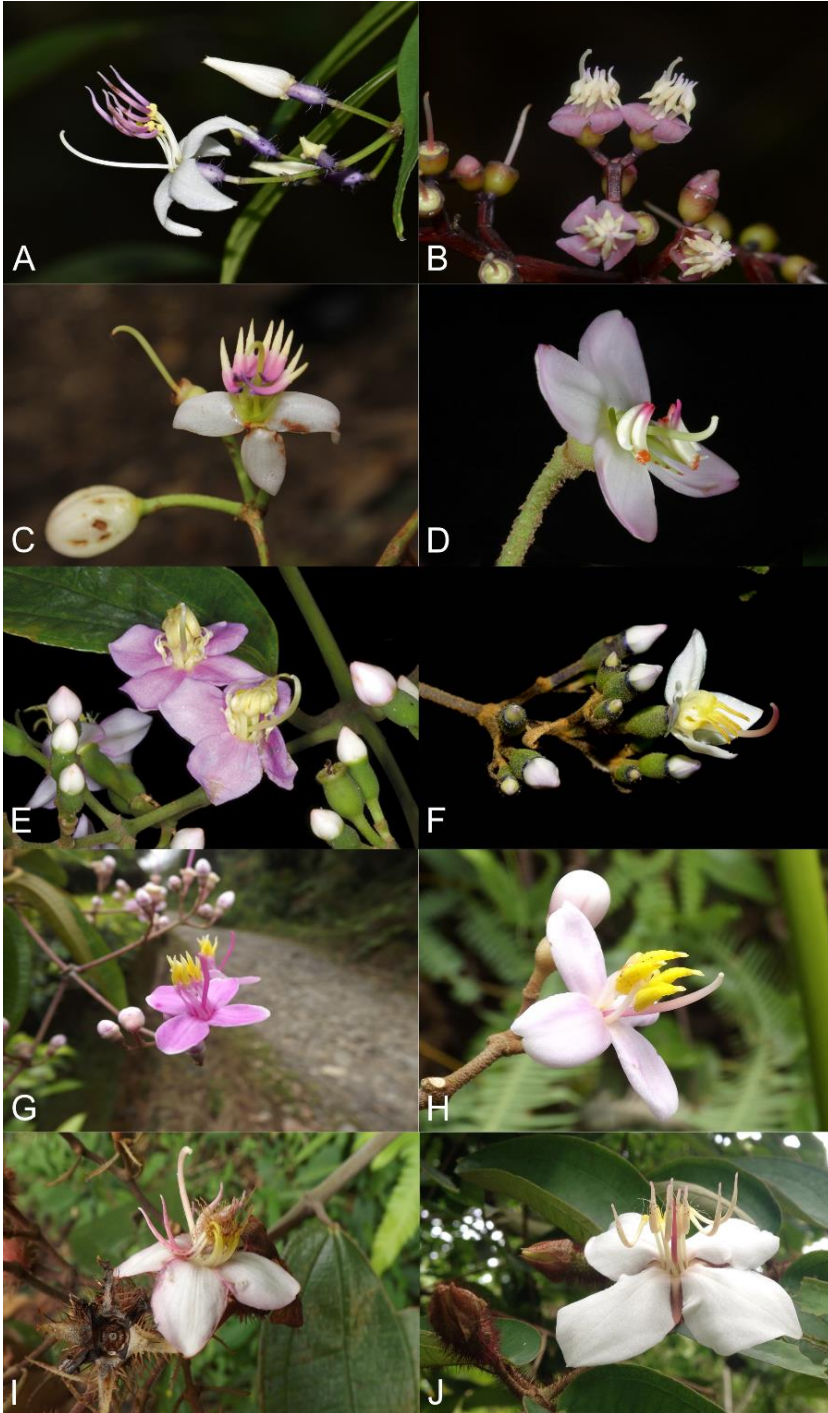


Fig. 1-3. Flowers of *Dissochaeta* alliance, **A.** *Pseudodissochaeta septentrionalis*; **B.** *Pseudodissochaeta spirei*; **C.** *Creochiton roseus*; **D.** *Creochiton* sp.; **E.** *Diplectria barbata*; **F.** *Diplectria divaricata*; **G.** *Dissochaeta bakhuizenii*; **H.** *Dissochaeta fallax*; **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; Clausen & 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 Nuttall (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 Clausen & Renner (2001a, 2001b), Zeng et al. (2016), Zhou et al. (2019b) and Penneys et al. (2020). The molecular phylogenetic studies of *Dissochaeteae* by Clausen & 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* (Clausen & Renner 2001a). Later molecular phylogenetic studies strongly support *Pseudodissochaeta*, the non-

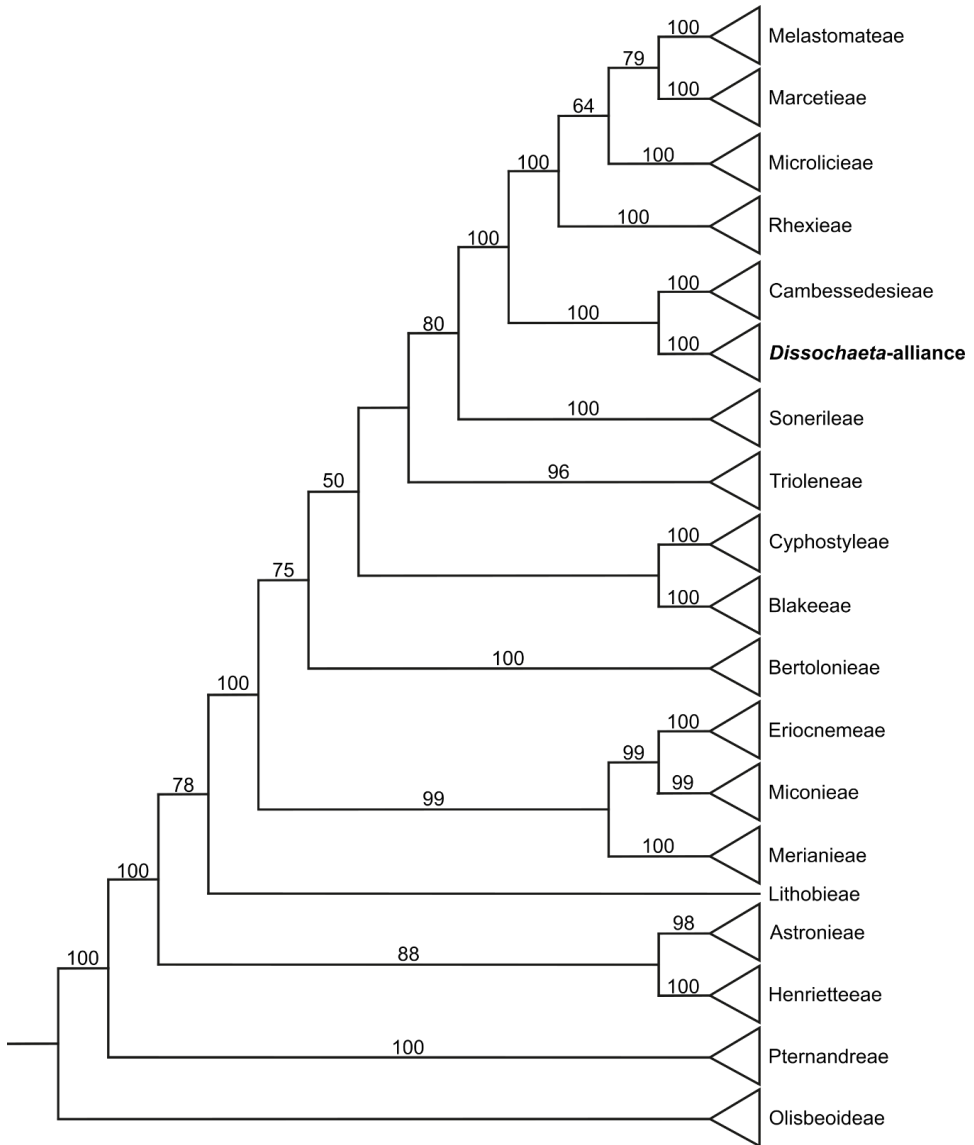


Fig. 1-4. Maximum-likelihood (ML) phylogenetic tree of Melastomataceae modified from Penneys et al. (2020). The *Dissochaeta* alliance is shown in bold. Numbers along branches indicated ML bootstrap support percentages above 50%.

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.