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

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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 than 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.

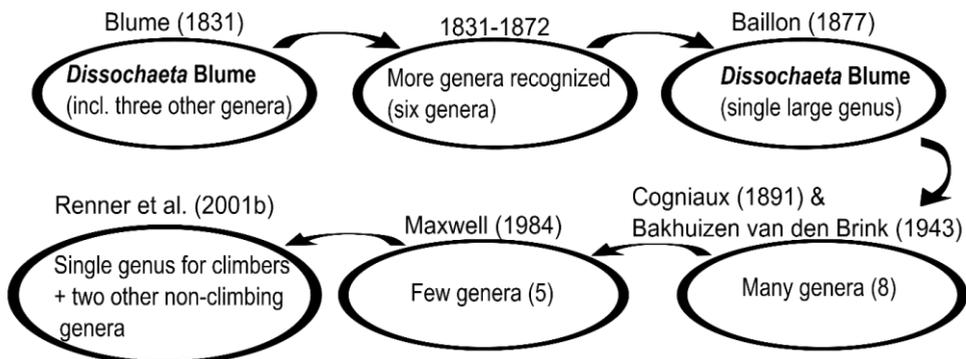


Fig. 8-1. Summary and time line of the various generic circumscription (= the delimitation of which subordinate taxa are part of the studied genus) within the *Dissochaeta* alliance.

- 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).

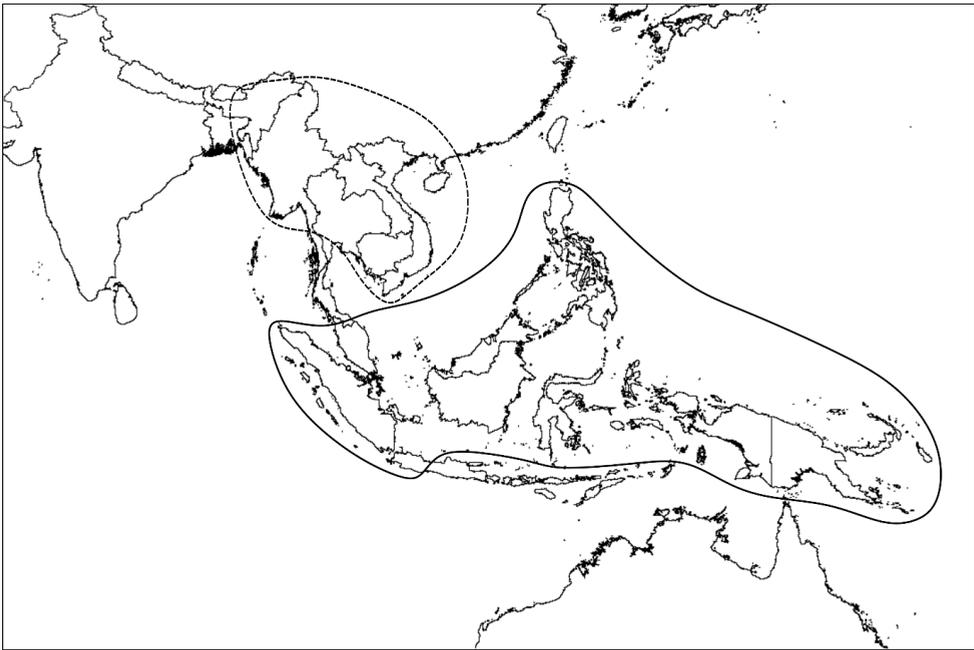


Fig. 8-2. Distribution map of *Creochiton* (continuous line) & *Pseudodissochaeta* (dashed line).

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.

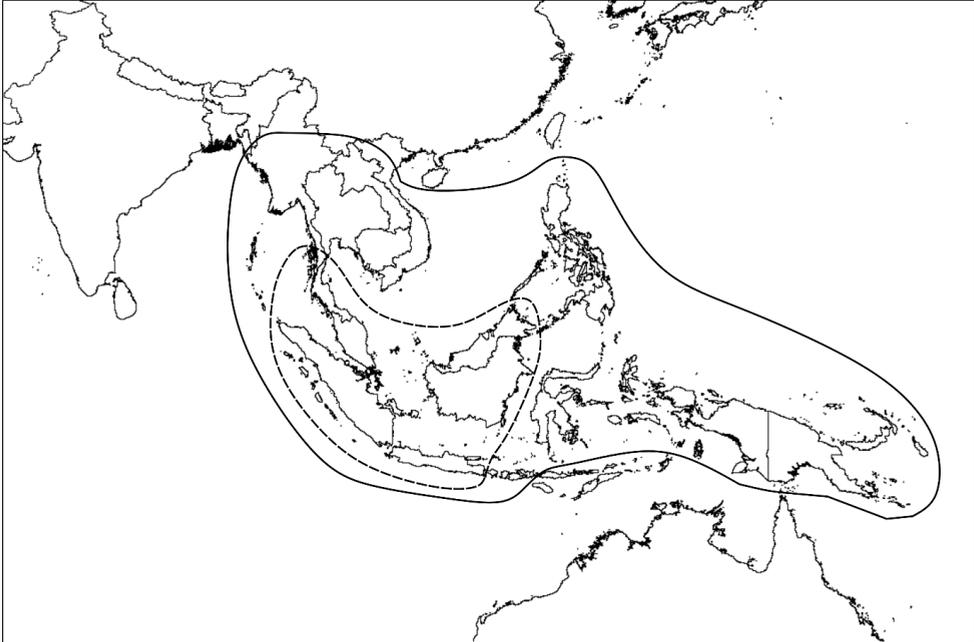


Fig. 8-3. Distribution map of *Dissochaeta* (continuous line) & *Macrolenes* (dashed line).

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 *Dipletria*), *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.** *Dipletria 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.

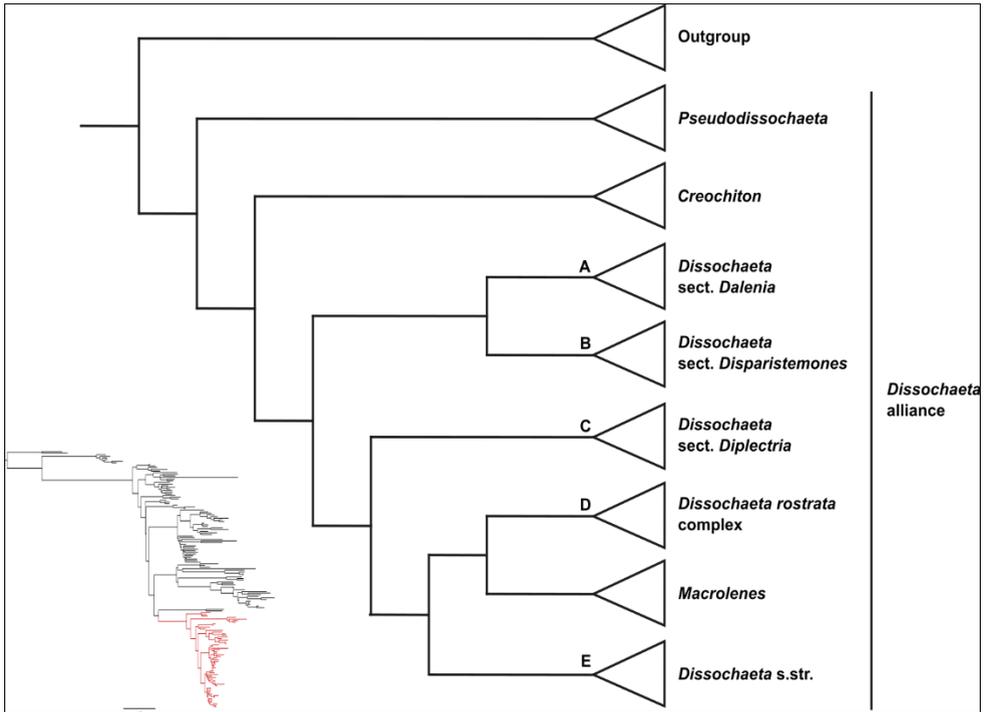


Fig. 8-5. Simplified phylogenetic tree of the *Dissochaeta* alliance, whereby the triangles represent the species. **A.** *Dissochaeta* sect. *Dalenia* (now *Dalenia*); **B.** *Dissochaeta* sect. *Disparistemones* (now *Dalenia*); **C.** *Dissochaeta* sect. *Diplectria* (now *Diplectria*); **D.** *Dissochaeta 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).

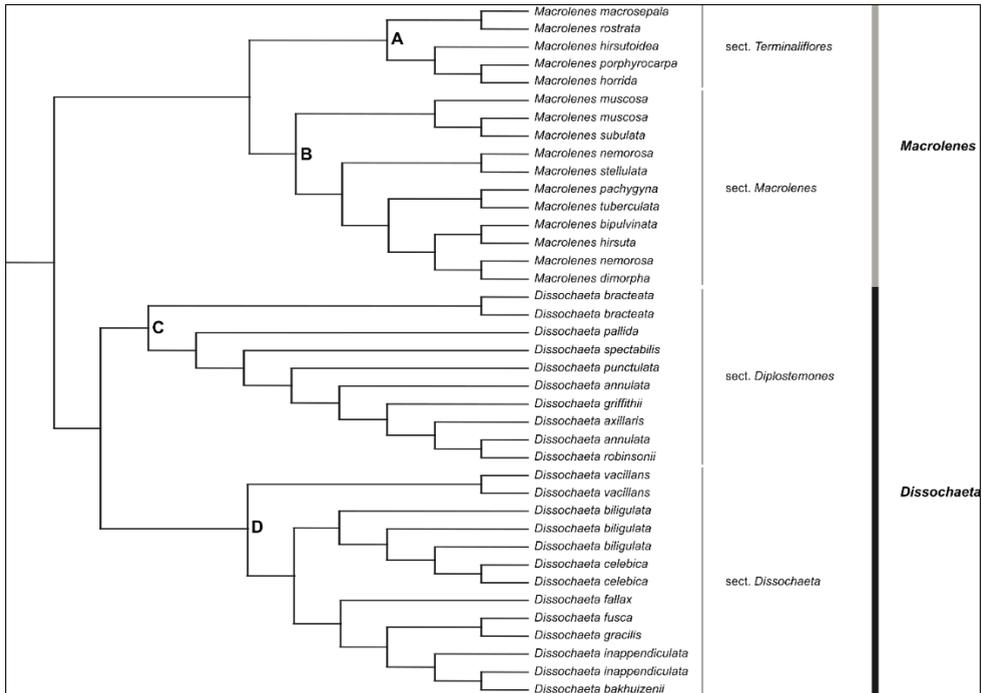


Fig. 8-6. Phylogenetic tree of the *Macrolenes* and *Dissochaeta* clades showing the new infrageneric classification in sections.

- 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.

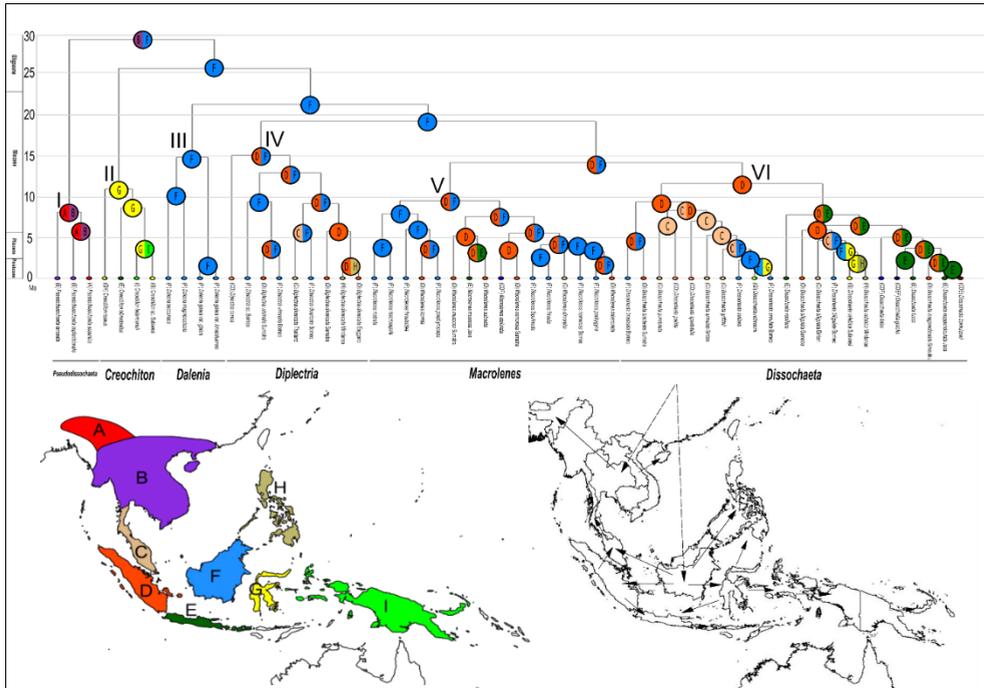


Fig. 8-7. Possible ancestral areas and dispersal routes for the *Dissochaeta* alliance. Colours in the pie charts and map correspond with geographical areas; Ma, million years ago. **A:** E Bhutan, NE India and NW Myanmar; **B:** Indochina, incl. C & E Myanmar, S China, Hainan and Thailand; **C:** S 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*.

