

Evolution of growth form in epiphytic Dissochaeteae (Melastomataceae)

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Abstract

We trace the evolution of root climbing and scrambling in Dissochaeteae and Sonerileae, two closely related groups that comprise the majority of Old World climbing Melastomataceae. The morphological and anatomical adaptations of the different climbers are interpreted in the context of a phylogeny based on chloroplast (cp) DNA sequences of the *ndhF* gene, generated for 31 representatives of Dissochaeteae and Sonerileae/Oxysporeae plus nine outgroups. For 20 of these taxa, the *ndhF* sequences were combined with cpDNA *rpl16* intron sequences to obtain higher statistical support. Parsimony, minimum evolution, and maximum likelihood approaches yield congruent topologies that imply that scrambling growth evolved once in the common ancestor of Dissochaetinae, a group of ~40 species centered around *Dissochaeta* and its close relatives *Macrolenes* and *Diplectria*. Root climbing, on the other hand, likely evolved in the common ancestor of *Catanthera*, *Kendrickia*, and *Medinilla* section *Heteroblemma* (together 26 species). In Melastomataceae overall, scrambling is restricted to Dissochaetinae, while root climbing has evolved several times. The scramblers are diverse in open disturbed habitats and show adaptations such as sarmentose branches, hook-shaped adventitious roots, and interpetiolar outgrowths that enhance their ability to lean on and clamber over other plants. Root climbers in the *Catanthera-Kendrickia-Heteroblemma* clade are restricted to humid habitats and show adaptations such as anomalous growth of the secondary xylem (a rare feature in the family), living climbing roots, and pseudoalternate phyllotaxy, which allows optimal arrangement of the normally opposite melastome leaves against the host's trunk.

Key words: adaptive radiation, anomalous secondary xylem, Dissochaeteae, epiphytism, root climbers, scrambling shrubs, Sonerileae

Introduction

The evolution of climbing growth, a form of epiphytism, allows the efficient allocation of resources and the acquisition of new resources, such as higher light levels or crown-foraging pollinators and fruit dispersers. Conceivably, it could have led to a diversification of ecological roles and attendant morphological and physiological adaptations in different species of a lineage, the hallmark of adaptive radiation (Schluter, 1996; Givnish, 1997). To date, few phylogenies are available for groups with different types of epiphytism that would allow one to trace the evolution of epiphytic growth forms on a phylogenetic tree and to investigate possible adaptive radiation in epiphytic lineages by comparing species numbers in clades with different attributes. Here we use a clade of paleotropical Melas-

tomataceae that possesses a wide range of epiphytic and terrestrial growth forms as a system in which to study morphological and ecological divergence among closely related species.

As with many ecologically determined categories, epiphytism covers a range of biological life forms and morphological growth forms that have been grouped in different ways (Schimper, 1888; Kress, 1986; Benzing, 1987; Gentry & Dodson, 1987; Gentry, 1991). Most climbers are rooted in the ground but rely on other plants for support. Different from true epiphytes that germinate atop other plants and never become ground-connected, they can allocate resources that others allocate for support for extension growth and reproduction (Darwin, 1867). Hemiepiphytes and stranglers, a third type of epiphytes, germinate on branches or trunks of trees and with age send roots to the ground, thus allocat-

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ing resources to self-support as well as to terrestrial foraging as their demand increases with size. A rarely considered fourth group of epiphytes, sometimes called casual or facultative epiphytes, consists of species in which some individuals function as true epiphytes while others are free-standing terrestrials or scramblers. Casual epiphytism is common in Melastomataceae, but has received little attention due to a paucity of morphological evidence.

Most Melastomataceae, a family of ~4500 species in 150–166 genera, are shrubs, trees, or herbs. The ability to grow epiphytically has evolved in 22 genera that together comprise several hundred species, making Melastomataceae a significant contributor to the world's epiphytes and climbers (Kress, 1986; Renner, 1986; Gentry & Dodson, 1987; Gentry, 1991). True and facultative epiphytism is common in *Blakea* and *Topobea* in the neotropics, with together 160 species, and in *Medinilla*, *Plethiandra*, and *Pachycentria* in the paleotropics with, respectively, ~200, six, and seven species of epiphytic shrubs (Renner, 1986, 1997; Clausing, 2000). Root climbing has evolved in nine genera in the neotropics and in nine or ten in the paleotropics, which together contain ~110 scandent species, about half in the New World genera, half in the Old World genera. Scrambling is restricted to the paleotropics where it is found in ~40 species that make up the subtribe Dissochaetinae of the tribe Dissochaeteae (Maxwell, 1980a,b, 1983). The circumscription of the latter has been problematic, and several genera have been added to, or removed from Dissochaeteae since their last complete treatment (Cogniaux, 1891). Their core, however, has always consisted of the Southeast Asian genera *Boerlagea*, *Creochiton*, *Dissochaeta* (including *Diplectria* and *Macrolenes*), *Medinilla*, and *Pachycentria* (including *Pogonanthera*) (Cogniaux, 1891; Bakhuizen, 1943; Maxwell, 1980b). Two genera from Africa have been removed on the basis of seed morphology (Renner, 1993), while four others from Southeast Asia were added for a variety of reasons (*Catanthera*, *Kendrickia*, *Plethiandra*, *Pseudodissochaeta*; Bakhuizen, 1943; Nayar, 1969, 1982; Renner, 1993).

Similar uncertainties of circumscription exist in and around Sonerileae, the only other paleotropical tribe containing epiphytes, in addition to numerous terrestrial herbs and shrubs. Analyses of nuclear internal transcribed spacer sequences and chloroplast (cp) *ndhF* gene sequences have shown that Sonerileae (including Oxysporeae; Renner, 1993) and Dissochaeteae are closely related (Clausing, 1999). A subsequent survey of the family that relied on three cpDNA regions furthermore showed that Sonerileae are embedded within Dissochaeteae (Clausing & Renner, in press). However, in these studies, Dissochaeteae and Sonerileae were represented by only five and two species, respectively.

Dissochaeteae contain ~380 species in nine genera; Sonerileae ~500 species in 25 genera.

The tribal and generic circumscription problems in Dissochaeteae/Sonerileae are daunting because of the great number of species and genera involved; phylogenetic reconstruction will require sequencing many representatives, including several aberrant small genera from Borneo, China, and Africa. Fully aware of these problems, we here analyze morphological and molecular data that address the evolution of growth form in and around *Dissochaeta* and *Medinilla*. We are particularly interested in whether there is evidence for adaptive radiation triggered through the evolution of specialized growth forms. Clearly, such evidence cannot be provided solely by phylogenetic techniques, which by their nature do not address the adaptive value and heritability of traits. Rather, phylogenies let us infer how many times a trait evolved and whether clades possessing that trait are species-poor or species-rich. The latter, in turn, may suggest that presence of the trait was repeatedly, and perhaps predictably, associated with bursts of speciation.

Material and methods

Taxon sampling

Representatives of Dissochaeteae, Sonerileae (including Oxysporeae), and their outgroups were selected based on earlier morphological and molecular analyses of the family's lineages (Cogniaux, 1891; Renner, 1993; Clausing & Renner, in press). Twenty-eight *ndhF* sequences and five *rpl16* sequences were newly generated for this study and combined with 16 *ndhF* and 15 *rpl16* sequences in hand from the family-level analysis (Clausing & Renner, in press). The 40 exemplars (listed in Table 1 with authors of taxonomic names, tribal assignment, voucher material, geographical ranges, and GenBank accession numbers) represent nine of the 12 genera of Dissochaeteae including the recently added *Catanthera*, *Kendrickia*, and *Plethiandra*. We lack *Boerlagea* (1 species), *Creochiton* (9 species), and *Pseudodissochaeta* (6 or 7 species). Exemplars further include 11 of the 25 genera of Sonerileae, both genera of Blakeeae, the closest outgroup, and seven genera representing more distant outgroups. Within *Medinilla*, our sample represents eight of 11 to 18 taxonomic subgroups recognized by different workers (Regalado, 1990, 1995; Clausing, 1999). *Medinilla alternifolia* and *M. serpens* were sampled as representatives of *Medinilla* section *Heteroblemma* Blume, *M. rubrifrons* as representative of section *Medinilla*; *M. sessiliflora* and *M. stephanostegia* as representatives of the two alliances named after them; *M. suberosa* as representative of the *M. succulenta* alliance; and finally three Madagascan species that represent different subgroups.

The data matrix consisted of 40 complete *ndhF* sequences with the following three exceptions (Table 1). Sequences of *Diplectria viminalis*, *Dissochaeta annulata*, and *Medinilla humblotii* each lacked between 300 and 360 base pairs (bp) because of amplification difficulties. These missing sections

Table 1. Species sequenced for this study. Vouchers are deposited in the herbaria of the University of Mainz (MJG), the National University of Colombia (COL), the Missouri Botanical Garden (MO), the California Academy of Sciences (CAS), and Stockholm (S). Tribal assignments follow Cogniaux (1891) except that *Kendrickia* and *Plethiandra* are included in Dissochaeteae (see text). AS = Astronieae; BE = Bertolonieae; BL = Blakeae; DI = Dissochaeteae; ME = Melastomeae; MI = Miconieae; MR = Merianieae; OX = Oxysporeae; RH = Rhe-xieae; SO = Sonerileae.

| Tribe | Species | DNA Source | Taxon range | GenBank accession # <i>ndhF</i> | GenBank accession # <i>rpl16</i> |
|-------|--|--------------------------------------|--|---------------------------------|----------------------------------|
| AS | <i>Astronia smilacifolia</i> Triana ex C. B. Clarke | Clausing 189, MJG | Malay Peninsula | AF215552 | AF215596 |
| BE | <i>Monolena primuliflora</i> J. D. Hook. | Cultv. BG Mainz | Central and South America | AF215553 | AF270743 |
| BL | <i>Blakea trinervia</i> L. | Cultv. BG Mainz | Jamaica | AF215555 | AF215600 |
| BL | <i>Topobea brenesii</i> Standley | Almeda & Daniels 7185, CAS | Central America | AF271665 | |
| DI | <i>Catanthera pilosa</i> M. P. Nayar | Clausing 258, MJG | Borneo | AF289367 | |
| DI | <i>Catanthera quintuplinervis</i> (Cogn.) M. P. Nayar | Clausing 196, MJG | Borneo, Sumatra | AF289368 | |
| DI | <i>Catanthera tetrandra</i> Stapf | Clausing 214, MJG | Borneo | | AF289365 |
| DI | <i>Diplectria divaricata</i> (Willd.) O. Ktze. = <i>Dissochaeta divaricata</i> (Willd.) G. Don | Clausing 236, MJG | Throughout tropical SE Asia | AF215556 | AF215601 |
| DI | <i>Diplectria viminalis</i> (Jack) O. Ktze. = <i>Dissochaeta viminalis</i> (Jack) Clausing | Clausing 233, MJG | Malay Peninsula, Sumatra, Java, Borneo, New Guinea | AF322236 | |
| DI | <i>Dissochaeta annulata</i> Hook.f. ex Triana | Clausing 243, MJG | Malay Peninsula and Borneo | AF322237 | |
| DI | <i>Dissochaeta bracteata</i> (Jack) Blume | Clausing 183, MJG | Malay Peninsula, Borneo, Sumatra, Java, Panay (Philippines) | AF289369 | AF294471 |
| DI | <i>Kendrickia walkeri</i> (Wight) Triana | Cultv. BG Stockholm | Ceylon, S India | AF289371 | |
| DI | <i>Macrolenes nemorosa</i> (Jack) Bakh.f. = <i>Dissochaeta affinis</i> (Korth.) Clausing | Clausing 174, MJG | Malay Peninsula, Sumatra, and Borneo | AF289372 | AF289364 |
| DI | <i>Macrolenes stellulata</i> (Jack) Bakh.f. = <i>Dissochaeta reformata</i> Blume | Clausing 182, MJG | Malay Peninsula, Sumatra, Java, and Borneo | AF289373 | |
| DI | <i>Medinilla alternifolia</i> Blume | Clausing 184, MJG | Malay Peninsula, Sumatra, Borneo | AF289374 | AF322229 |
| DI | <i>Medinilla ericarum</i> Jum. & Perrier | Cultv. BG Mainz | Madagascar | Partially sequenced (see text) | |
| DI | <i>Medinilla humbertiana</i> Perrier | Cultv. BG Mainz Clausing 289, MJG | Madagascar | AF215557 | AF215602 |
| DI | <i>Medinilla humblotii</i> Cogn. | Cultv. BG Mainz Clausing 296, MJG | Madagascar | AF322235 | |
| DI | <i>Medinilla rubrifrons</i> Regalado | Clausing 211, MJG | East Kalimantan, Sabah | AF289375 | AF294838 |
| DI | <i>Medinilla serpens</i> Stapf | Clausing 268, MJG | Sarawak | AF289376 | |
| DI | <i>Medinilla sessiliflora</i> Regalado | Clausing 154, MJG | Borneo | AF289377 | |
| DI | <i>Medinilla stephanostegia</i> Stapf | Clausing 257, MJG | Mount Kinabalu (Borneo) | AF289378 | |
| DI | <i>Medinilla suberosa</i> Regalado | Cultv. BG Mainz Clausing 220, MJG | Borneo | AF289379 | |
| DI | <i>Pachycentria constricta</i> (Blume) Blume | Clausing 263, MJG | Throughout tropical SE Asia | AF289381 | |
| DI | <i>Pachycentria pulverulenta</i> (Jack) Clausing = <i>Pogonanthera pulverulenta</i> (Jack) Blume | Clausing 230, MJG | Malay Peninsula, Sumatra, Java, Philippines, Celebes, Moluccas, New Guinea | AF289383 | |
| DI | <i>Plethiandra cuneata</i> Stapf | Clausing 129, MJG | Borneo | AF289384 | |
| DI | <i>Plethiandra hookeri</i> Stapf | Clausing 219, MJG | Borneo | AF289385 | |

Table 1. (Continued).

| Tribe | Species | DNA Source | Taxon range | GenBank accession # <i>ndhF</i> | GenBank accession # <i>rpl16</i> |
|-------|---|--|-------------------------|------------------------------------|-------------------------------------|
| ME | <i>Dichaetanthera asperrima</i> Cogn. | Clausing 280, MJG | Madagascar | AF215564 | AF215607 |
| MI | <i>Clidemia rubra</i> (Aubl.) Mart. | Cultv. BG Bonn | S America | AF215579 | AF215616 |
| MI | <i>Leandra mexicana</i> (Naudin) Cogn. | Cultv. BG Bonn | Central America | AF215580 | AF215617 |
| MR | <i>Meriania nobilis</i> Triana | Barriga 21192, COL | Colombia | AF215577 | AF215614 |
| OX | <i>Anerinckleistus macrophyllus</i> Bakh.f. | Clausing 248, MJG | Borneo | AF289366 | |
| OX | <i>Blastus borneensis</i> Cogn. | Clausing 163, MJG | Indochina and Malaysia | AF215585 | AF215621 |
| OX | <i>Driessenia glanduligera</i> Stapf | Clausing 254, MJG | Borneo | AF215586 | AF215622 |
| OX | <i>Oxyspora beccarii</i> (Cogn.) Maxw. = <i>Anerinckleistus beccarii</i> Cogn. | Clausing 186, MJG | Borneo | AF289380 | |
| RH | <i>Rhexia virginica</i> L. | Cultv. BG Mainz | E North America | AF215587 | AF215623 |
| SO | <i>Amphiblemma cymosum</i> (Schr. & Wendl.) Naudin | Cultv. BG Mainz | Tropical W Africa | AF215588 | AF215624 |
| SO | <i>Calvoa orientalis</i> Taub. | Cultv. Amani BG, Tanzania; C. Orava 1, MJG | East Africa | AF215589 | |
| SO | <i>Gravesia guttata</i> (Hook.) Triana | Cultv. BG Mainz | Madagascar | AF270755 | |
| SO | <i>Gravesia rutenbergiana</i> Cogn. | Clausing 287, MJG | Madagascar | AF289370 | |
| SO | <i>Gravesia viscosa</i> H. Perrier | Clausing 304, MJG | Madagascar | | AF215625 |
| SO | <i>Phyllagathis gymnantha</i> Korth. | Clausing 209, MJG | Borneo | AF215590 | AF215626 |
| SO | <i>Sonerila beccariana</i> Cogn. | Clausing 270, MJG | Throughout Malaysia | AF289389 | |
| SO | <i>Sonerila brunonis</i> Wight & Arn. | Klackenberg & Lundin 506, S | India | AF289386 | |
| SO | <i>Sonerila nervulosa</i> Ridley | Clausing 261, MJG | Throughout Malaysia | AF289387 | |
| SO | <i>Sonerila obliqua</i> Korth. | Clausing 170, MJG | Malaysia to Philippines | AF289388 | |

were complemented with the respective sections from close relatives that, when compared to all other species in the matrix, introduced no synapomorphic intrageneric characters that would have influenced parsimony analyses. Specifically, *Diplectria viminalis* was complemented with a section of 300 bp from *Diplectria divaricata*; *Dissochaeta annulata* with a section of 360 bp from *Dissochaeta bracteata*; and *Medinilla humblotii* with a section of 360 bp from *M. ericarum*. The remainder of the *M. ericarum* sequence was not used in the analysis. Including thus complemented, rather than partial, sequences facilitated maximum likelihood, distance, and bootstrap analyses, procedures that are severely affected by missing data. Three additional species, *Pachycentria pulverulenta*, *Sonerila nervulosa*, and *Sonerila beccariana*, were scored as ambiguous ("nnnn") for missing sections and only included in exploratory analyses in an attempt to break up long branches leading to their congeners, *Pachycentria constricta* and *Sonerila brunonis*.

DNA extraction, amplification, and sequencing

Fresh leaves for extraction of total DNA were obtained directly from the field or from cultivated greenhouse plants; silica

gel-dried leaf material was used in a few cases. Total DNA was isolated using genomic DNA extraction kits (QIAGEN, Valencia, California), DNeasy plant mini kits (QIAGEN), or NucleoSpin plant DNA extraction kits (Macherey-Nagel, Dören) according to manufacturers' instructions. PCR amplification followed standard protocols. The *ndhF* gene was amplified with primers developed by Olmstead and Sweere (1994). We amplified the exon between positions 972 and 1955 (i.e., codon 305 of solanaceous sequences; Olmstead & Sweere, 1994), using forward primer *ndhF*-972F, reverse primer *ndhF*-1955R, and one or two pairs of internal primers (*ndhF*-1318F, *ndhF*-1318R, *ndhF*-1603F, and *ndhF*-1603R). PCR products were purified by running the entire product on an agarose gel and recovering the amplified DNA with the help of QIAquick gel extraction kits (QIAGEN) or via NucleoSpin extraction kits (Macherey-Nagel GmbH & CoKG). Cycle sequencing of the amplified double-stranded products was conducted with the ABI Prism Dye Terminator cycle sequencing kit (Perkin Elmer, Norwalk, CT). The dye was removed by ethanol precipitation and samples were then run on an ABI 373 automated sequencer at the University of Mainz. Consensus sequences were constructed using Sequencher software (version 3.1; GeneCodes Corp., Ann Arbor, MI).

For a subset of taxa, we combined *ndhF* sequences with *rpl16* cpDNA intron sequences available from our earlier family-wide survey (Clausing & Renner, in press) or newly generated for this study (Table 1). To amplify this ~800 bp-long intron we used primers 1067F and 18R designed by Asmussen (1999).

Phylogenetic analyses

Alignment was done manually. Phylogenetic analyses of aligned sequences were conducted with PAUP* version 4.0b.4a (Swofford, 2000). The search strategy adopted consisted of heuristic searches with 10 random taxon addition replicates and tree bisection-reconnection (TBR) swapping. The MulTrees, Collapse, and Steepest Descent options of PAUP were in effect during all searches, and character changes were interpreted under ACCTRAN optimization. Characters were unweighted and unordered, gaps were treated as missing data, and ambiguous characters as unknowns. Tree length (L), consistency index (CI), and retention index (RI) were taken from PAUP. Nonparametric bootstrap support was estimated based on 100 to 1000 replications with the same search options as used before, except that closest taxon addition was used.

Minimum evolution trees (Rzhetsky & Nei, 1992a, b; implemented in PAUP*) were generated using log-determinant (LogDet) genetic distances (Lockhart et al., 1994), heuristic searches, and TBR swapping. LogDet transformation of the data may be particularly useful when taxa have irregular base compositions (Lockhart et al., 1994), which may lead to erroneous phylogenetic reconstruction.

Maximum likelihood analyses were performed using the general time-reversible model (Yang 1994), which estimates independent probabilities for the six possible nucleotide substitutions (the Q matrix), and also allows unequal base frequencies. Among-site rate heterogeneity was accommodated in two ways. Some proportion of nucleotide sites was assumed invariable (P_{inv}), while the distribution of substitution rates over the remaining sites was assumed to follow a gamma distribution whose shape parameter α determines rate heterogeneity. The Q matrix, P_{inv} , and α were estimated simultaneously, using the discrete approximation of Yang (1994; implemented in PAUP*) with four rate categories to approximate the continuous gamma distribution. Base frequencies were the empirically observed ones. Because the dependence of model parameters on tree topology is minor as long as strongly supported groups are maintained (Yang & Kumar, 1996; Sullivan et al., 1999), these parameters were estimated from the data

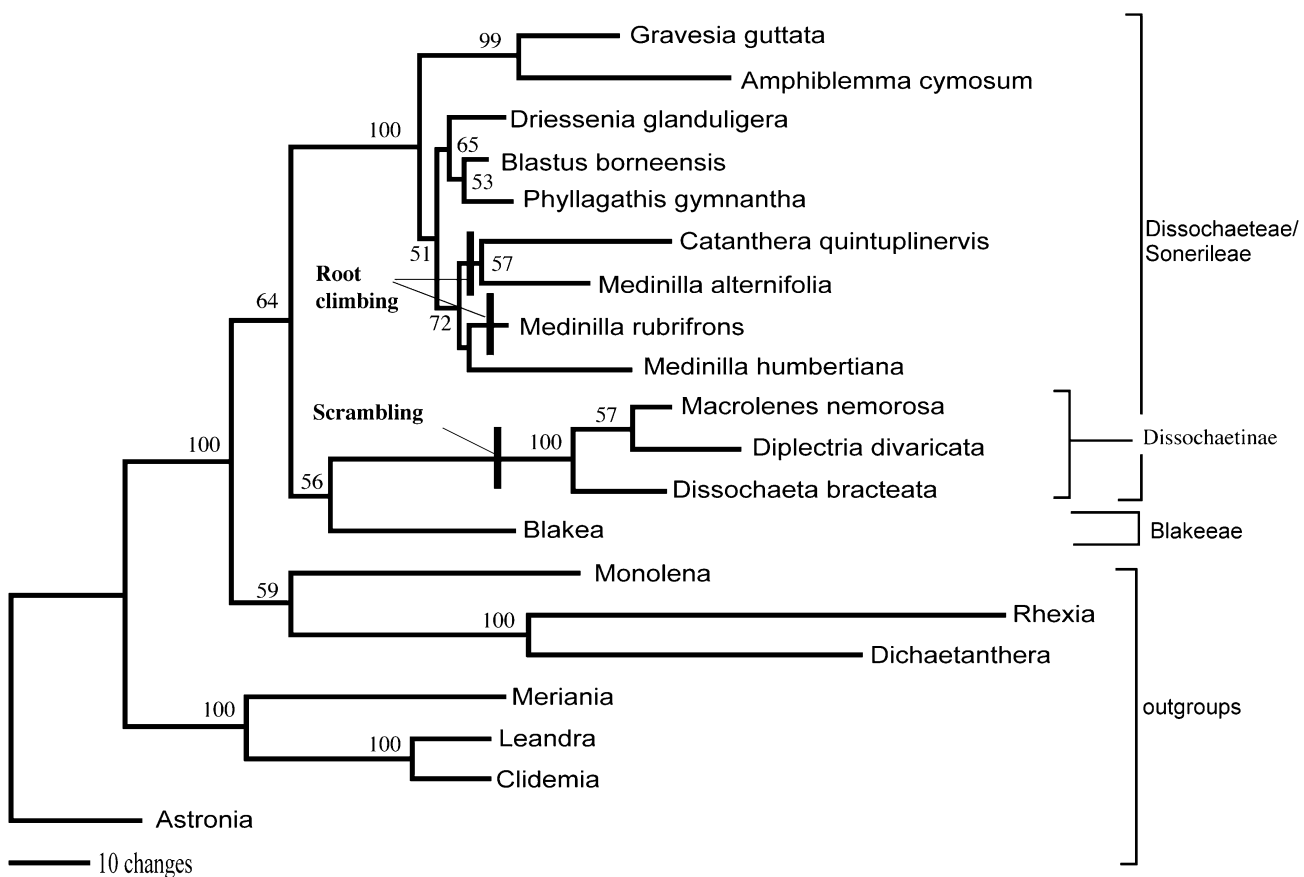


Fig. 1. One of six equally parsimonious trees found using 20 combined *ndhF* gene and *rpl16* intron sequences from Dissochaeteae, Sonerileae, and relevant outgroups (L = 594, CI = 0.82, RI = 0.76). Bootstrap support values >50% at nodes are based on 1000 replications. For outgroup species names see Table 1.

without complete branch swapping and with the starting tree obtained via neighbor-joining. The estimated parameters were then used in a heuristic ML search with TBR swapping, again using a neighbor-joining tree as starting tree. The resulting highest likelihood tree was used to re-estimate P_{inv} and α , and another TBR swapping heuristic search was then conducted with the improved model parameters.

In the electronic supplement of *Organisms, Diversity & Evolution* at <http://senckenberg.uni-frankfurt.de/odes/2001-1-1.htm> Figures 4 and 6 are shown in colour.

Results

The aligned *ndhF* and *rpl16* data matrices contained 1968 nucleotide positions of which 250 varied autapomorphically and 171 were parsimony-informative. There were 16 insertions or deletions (indels) in the 20 *rpl16* intron sequences, of which a single nucleotide insertion uniquely shared by *Blastus* and *Driessenia* was informative in the ingroup. Of four indels in the 20 *ndhF* sequences used in the combined matrix, none were informative in the ingroup. Most-parsimonious trees were generated independently from the two matrices, followed by bootstrap analyses, to assess whether there was strong conflict among data partitions (i.e., >80% bootstrap support). In the absence of such conflict, the data were combined in a global analysis.

Parsimony analysis of the combined gene and intron sequences resulted in six equally parsimonious trees ($L = 594$, $CI = 0.82$, $RI = 0.76$) of which one is shown in Figure 1. The six trees differed in the precise relationships among the three species of *Medinilla* and the single species *Catanthera*, with none of the relationships having strong statistical support. The phylogeny shows neotropical Blakeeae and paleotropical Dissochaetaeae/Sonerileae as a weakly supported clade (64% bootstrap support). Within this clade, Blakeeae appear as sister to *Dissochaeta*, *Diplectria*, and *Macrolenes*, that is, the Dissochaetinae, but again with low support. The remaining Dissochaetaeae/Sonerileae form a strongly supported clade (100%). The African Sonerileae in the analysis, *Amphiblemma* (Africa) and *Gravesia* (Africa and Madagascar), also form a strongly supported clade (99%).

The aligned *ndhF* sequences of nine outgroups and 31 representatives of Dissochaetaeae comprised 1006 positions of which 120 varied autapomorphically and 134 potentially synapomorphically. Of seven indels, four were informative in the ingroup, namely a 6 bp insertion shared by the species of *Macrolenes* and *Diplectria*, partially overlapping 6 bp and 12 bp insertions shared by *Catanthera*, *Medinilla sessiliflora*, and *M. suberosa*; a 6 bp deletion shared by all species of Blakeeae, *Macrolenes*, and *Diplectria*; and partially overlapping insertions of 3, 6, or 9 bp shared by many Dissochaetaeae.

Parsimony analysis resulted in 84 equally parsimonious trees ($L = 456$, $CI = 0.69$, $RI = 0.75$), the strict consensus of which is shown in Figure 2. As in the tree resulting from the combined gene and intron data, Blakeeae and Dissochaetaeae/Sonerileae form a poorly supported clade (67% bootstrap support), and Blakeeae appear as sister group to Dissochaetinae (60% bootstrap support). Dissochaetinae are solidly monophyletic (93% bootstrap support) and, together with the dubiously placed Blakeeae, sister to a strongly supported (91%) large clade comprising the remainder of the ingroup (Fig. 2). Four species groups are discernable within this large clade; an African/Madagascan Sonerileae clade; a Madagascan *Medinilla* clade; a *Plethiandra* clade; and a barely supported clade that we here refer to as the *Heteroblemma* alliance. It is comprised of *Catanthera*, a genus of ivy-like climbers, *Kendrickia*, a woody climber, and *Medinilla alternifolia*, and *M. serpens*. The last are members of *Medinilla* section *Heteroblemma*, which contains nine doubtfully distinct species of herbaceous climbers or creepers (Regalado, 1990).

The minimum evolution (ME) tree obtained from the same data is shown as a phylogram in Figure 3. As expected from the lack of resolution in the parsimony tree, branch lengths at the base of the *Medinilla/Heteroblemma/Sonerileae* polytomy are extremely short. A difference compared to the parsimony tree is that ME shows the paleotropical Dissochaetaeae/Sonerileae as monophyletic and sister to the neotropical Blakeeae, albeit with only 58% bootstrap support.

Maximum likelihood analysis of the data yielded a single most likely topology (not shown) that differed from the ME tree in minor rearrangements within the *Medinilla-Sonerileae* polytomy and in the placement of Blakeeae as sister to Dissochaetinae. The estimated proportion of invariable sites was 0.43 and the gamma shape parameter was 0.98, indicating that a few sites in the matrix change at high rates while most have low substitution rates or are invariable (Yang & Kumar, 1996).

The addition of three species with incomplete *ndhF* sequences (Materials and methods), *Sonerila nervulosa*, *Sonerila beccariana*, and *Pachycentria pulverulenta*, did not change the composition or relative positions of any of the well-supported clades. However, it resulted in ME trees in which the SE Asian *Sonerila brunonis*, *S. nervulosa*, and *Sonerila beccariana* were sister to the two Madagascan species of *Medinilla*. This was due to a uniquely shared substitution at alignment position 263. Judging from *ndhF* substitutions outside those of Dissochaetaeae (Clausing & Renner, in press), this base pair is homoplastic in melastomes and the substitution could thus have arisen independently in Madagascan *Medinilla* and the three species of *Sonerila*. *Pachycentria pulverulenta* appears a sister to *P. constricta* in the same position as shown in Figure 3.

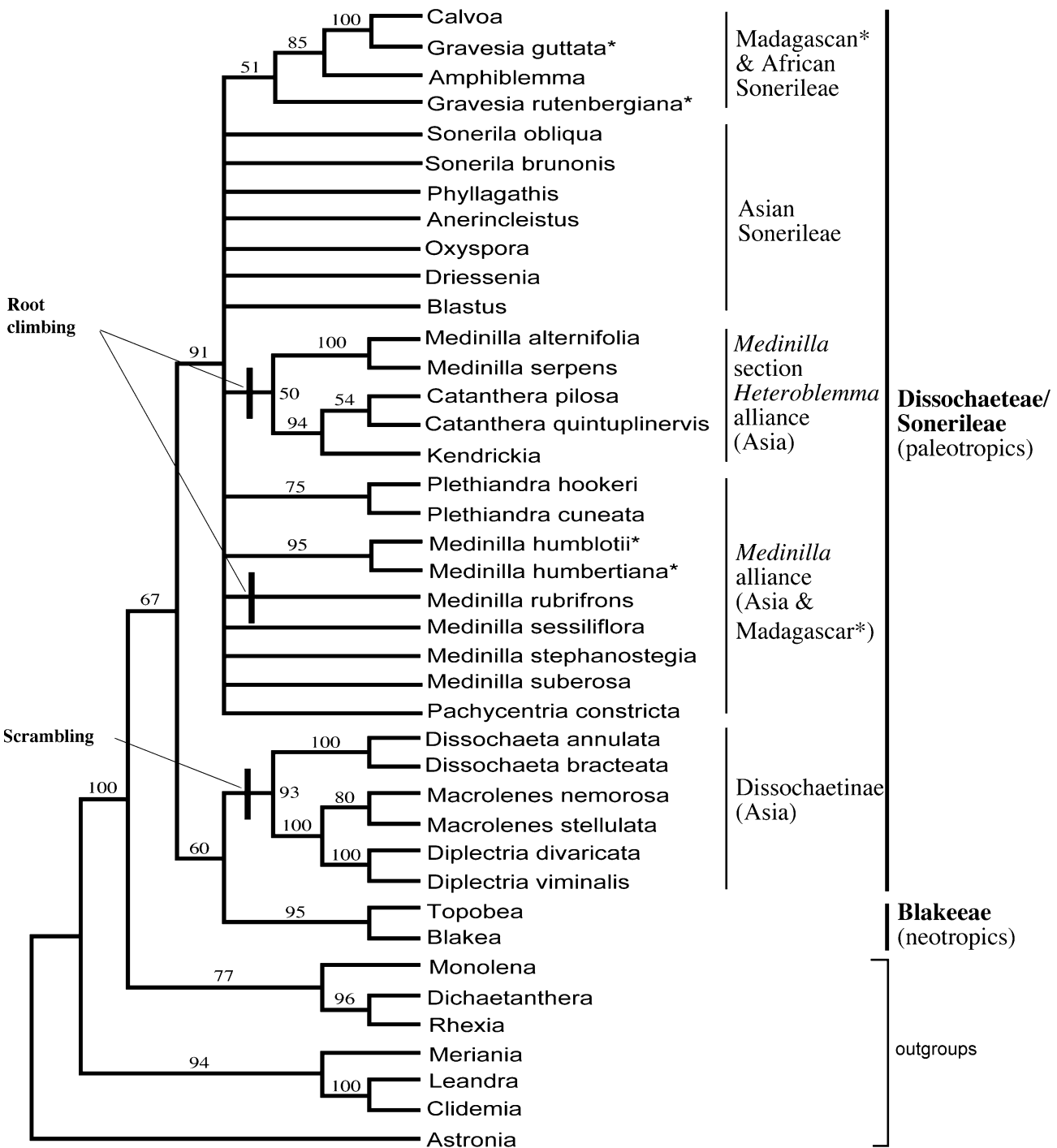


Fig. 2. Strict consensus of 84 equally parsimonious trees ($L = 456$, $CI = 0.69$, $RI = 0.75$) found using *ndhF* gene sequences for 40 Dissochaeteae/Sonerileae and outgroups. Bootstrap support values above branches are based on 100 replications. Species names are given for genera with more than one species in the analysis, and species from Madagascar are marked with an asterisk.

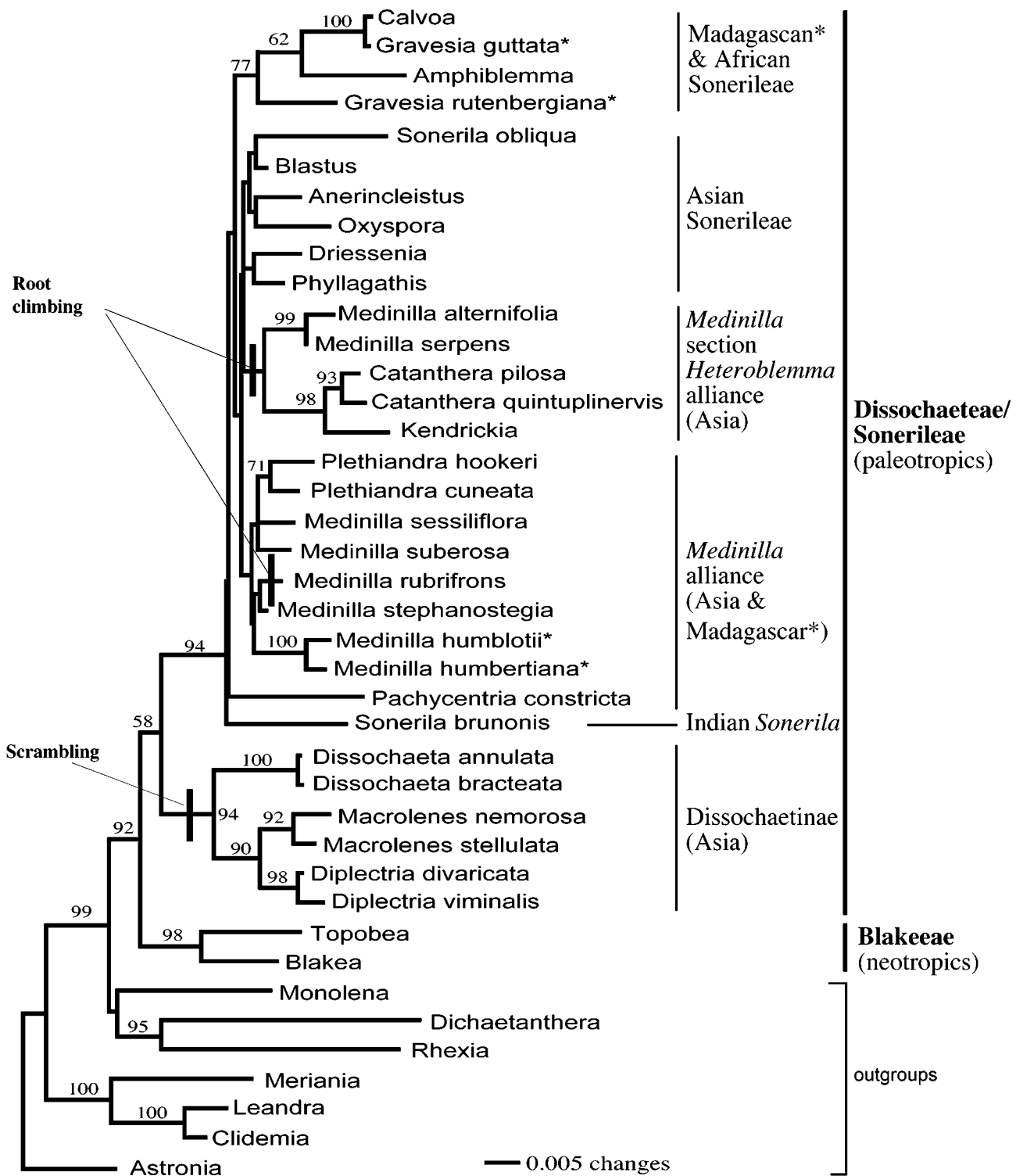


Fig. 3. Minimum evolution tree using log-determinant genetic distances for *ndhF* gene sequences from Dissochaeteae/Sonerileae and outgroups. Bootstrap values (>50%) above branches are based on 500 replications. Species names are given for genera with more than one species in the analysis, and Madagascan species are marked with an asterisk.

Discussion

Phylogenetics of Dissochaeteae and Sonerileae

The unexpectedly close relationships of Dissochaeteae and Sonerileae discovered by Clausing (1999; Clausing & Renner, in press) is confirmed in the present study, which includes all but three genera of Dissochaeteae and nine of 25 genera of Sonerileae. While the relatively few substitutions in the *ndhF* gene are insufficient to resolve the monophyly and relationships of the Dissochaeteae/Sonerileae complex as a whole, they reveal two major clades within the complex. One consists of Dissochaetinae (*Dissochaeta* and its segregates *Diplectria* and *Macrolenes*), the other of *Medinilla* and relatives plus Sonerileae. The grouping of *Medinilla* and Sonerileae, which has between 91 and 94% bootstrap support, contradicts all traditional classifications that used fruit type, whether capsular or baccate, as the primary character to group tribes of Melastomataceae (Cogniaux, 1891: p. 9, key to the family; Renner, 1993). This resulted in the placement of most capsular-fruited genera in an unnatural Sonerileae and all berry-fruited genera in Dissochaeteae. Recent molecular and morphological studies indicate that, in general, fruit morphology in Melastomataceae does not reflect shared history as much as adaptation to different modes of dispersal (Clausing et al., 2000).

The conflicting placement of Blakeeae as either sister to Dissochaetinae (under parsimony and ML optimization criteria) or sister to a monophyletic Dissochaeteae/Sonerileae complex (under ME criteria) and the low bootstrap values in this part of the tree (also when *rpl16* and *ndhF* sequences were combined) indicate the need for more data. The *ndhF* sequences of Blakeeae and Dissochaetinae share several unique substitutions and indels, but this is not true of their *rpl16* intron sequences. Blakeeae consist of the closely related genera *Blakea* and *Topobea*, which contain ~160 species distributed from Mexico to Amazonia and the West Indies. They are characterized by axillary flowers that each are subtended by two pairs of decussate persistent bracts, and are morphologically isolated within the family. Most Blakeeae are massive epiphytic shrubs; a few are terrestrial shrubs or treelets (Renner, 1986). Whether epiphytism in Blakeeae is ancestral or secondarily derived is unknown.

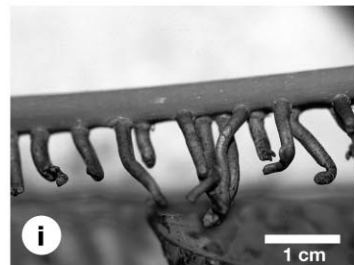
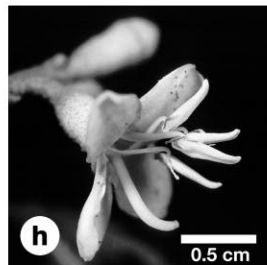
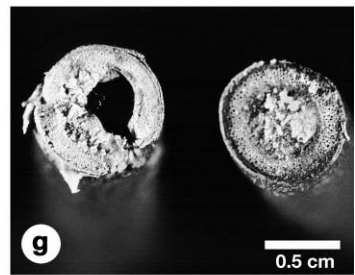
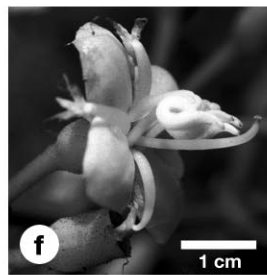
Another clade newly discovered in this analysis (but see Clausing, 1999) is the *Heteroblemma* alliance, comprising *Medinilla* sect. *Heteroblemma*, *Catanthera*, and *Kendrickia* (Figs. 2, 3). Although it is barely apparent in the *ndhF* data, this grouping is supported by wood anatomical and morphological data discussed in the next section. From the parsimony and minimum evolution *ndhF* topologies (Figs. 2, 3) it appears that Madag-

ascan and African Sonerileae form a clade (although with only 51 and 77% bootstrap support) that is nested among Asian Dissochaeteae/Sonerileae. This could imply that the Madagascan and African Sonerileae came from Asia. The two Madagascan species of *Medinilla* also form a clade (that has 95–100% support), which the minimum evolution topology (Fig. 3) shows nested among Asian *medinillas*, albeit without statistical support. Combined gene and intron data (Clausing & Renner, in press and unpublished) strongly support the Asian derivation of both the Madagascan/African Sonerileae and the Madagascan/African *medinillas*. Molecular clock dating of genetic distances among the Asian and Madagascan species in both groups suggests that Asian Sonerileae reached Madagascar via long-distance-dispersal during the Miocene, while the Madagascan *medinillas* arrived only a few million years ago (Renner et al., in press b).

Plethiandra, a small genus characterized by a pleiostemonous androecium with straight unappendaged stamens, also may be nested within *Medinilla* (Fig. 3). Clearly, however, more sequence data are needed for a representative sample of *medinillas* before relationships in this genus will become clear. Especially important will be to include morphologically distinct species, such as *Medinilla microcephala* Regalado (*Cephalomedinilla* Merr.), *Medinilla setigera* (Blume) Miq. (*Hypenanthe* (Blume) Blume), and *Medinilla coronata* Regalado (*Carionia* Naudin).

The evolution of growth form

Scrambling growth (Fig. 4): Our results show that scrambling growth among Old World Melastomataceae evolved only once. This is evident from the strongly supported monophyly of Dissochaetinae (comprised of *Macrolenes*, *Dissochaeta*, and *Diplectria*) seen in the *ndhF* and *ndhF* + *rpl16* topologies (Figs. 1–3). Growth forms for all species in this subtribe are given in Maxwell's (1980a,b, 1983) monograph, which was based on first-hand knowledge of many of the species in the field. Besides *Dissochaeta*, *Macrolenes*, and *Diplectria*, Maxwell's Dissochaetinae include *Creochiton*, with nine species of woody climbers, creepers, or epiphytic shrubs in New Guinea, Java, and the Philippines, and *Pseudodissochaeta*, with five or six species of trees and shrubs, and one climbing species in Indochina and China, which are not included here. The monophyly and definite placement of both genera are problematic and must await DNA sequence data. Maxwell's views on the circumscription of *Diplectria*, *Macrolenes*, and *Dissochaeta* also are not universally shared (Renner et al., in press a); generic boundaries among the three are problematic due to intermediate species and doubtful homology assessments (Clausing, in preparation).



Excluding *Pseudodissochaeta* and *Creochiton*, Dissochaetinae comprise ~40 species of scramblers. Scrambling growth in Melastomataceae is unknown outside Dissochaetinae, which have a series of morphological adaptations that relate to this growth form. The thin branches are non-self-supporting and have long internodes. As in most climbers (Hegarty, 1989), there is a sharp differentiation between pendent flowering and fruiting branches (Fig. 4b, e) and long-internodal “extension” branches. The nodes of many species furthermore bear large interpetiolar outgrowths (Fig. 4d), which may help climbing and stabilization in the same way thorns or hooks do in other scramblers. Adventitious roots, which are ubiquitous in Dissochaetinae, are lignified and soon dry out to become hook-shaped structures that adhere to the carrier plant (Fig. 4i). Cross sections of the wood show a wide pith with scattered vascular bundles and a narrow ring of xylem (Fig. 4g), and older branches may become hollow and occupied by ants once the pith degenerates (cf. Clausen, 1998).

Dissochaetinae are abundant in disturbed and therefore relatively open vegetation such as tree fall gaps, forest margins, river margins, and roadsides (e.g., Fig. 4a). Their fast growth, a key feature of scramblers, which “borrow” structural support from other plants, relates to the low proportion of stiffening tissues in the secondary wood and allows them to compete in early successional vegetation. Most species climb less than five meters high, but some, such as *Diplectria beccariana*, can grow up to 15 meters into the canopy. Nothing is known about water conductivity and vulnerability to drought in Dissochaetinae, but the geographic range of the clade indicates that it may be limited by dry or cold conditions. Most species of the Dissochaetinae are restricted to tropical regions of the Malay Archipelago between 10°N and 8°S.

Dissochaetinae are uniform in habit but show pronounced variation in flower and fruit morphology. Flowers measure between 0.5–3 cm in diameter. The two stamen whorls are strongly dimorphic, and both may be fertile, or the outer or inner whorl may be smaller, staminodial (Fig. 4f), or absent (Fig. 4h). Heteranthery is common in species of *Macrolenes* and *Dissochaeta* sect. *Dissochaeta* (Fig. 4c). Fruits are indehiscent, and vary in size, degree of fleshiness, and sclerification. The evolutionary sequence of these changes and their adaptive role, if any, is unclear and must await molecular and experimental data. However, much mor-

phological diversification in flower and fruit characters is apparent, which may reflect adaptation to different ecological roles within the new habitat opened up by the scrambling growth form.

Root climbing (Fig. 5; Table 2): Among the taxa we sequenced, root climbing is present in *Medinilla* sect. *Heteroblemma* (9 species), *Catanthera* (16 species), *Kendrickia* (1 species), and *Medinilla rubrifrons*. The first three form a weakly supported clade (Figs. 2, 3), while the position of *M. rubrifrons* is unresolved. *Medinilla rubrifrons* is a member of sect. *Medinilla*, which includes ~15 species of epiphytic shrubs (Regalado, 1990; Fig. 6d). Root climbing in the Old World is also found in *Medinilla sedifolia* Jum. & Perr. (Madagascar) and the Sonerileae *Dicellandra* (Africa), *Gravesia* (Madagascar), *Fordiophyton*, and *Oxyspora* (both from Southeast Asia). The two root climbers in the analysis, *Catanthera* and *Kendrickia*, turn out to be sister groups in spite of having quite different flowers and fruits (Table 2). *Kendrickia* has dehiscent fruits that open along four longitudinal cracks, while *Catanthera* has soft berries (Table 2; Fig. 5Ae, Cd), a fruit morphological difference that resulted in their separate traditional tribal placements. Thus, Cogniaux (1891) treated *Kendrickia* in the Oxysporeae (= Sonerileae), while placing the single species of *Catanthera* of which he had material in *Dissochaeta*, as *D. quintuplinervis*. This “*Dissochaeta*” *quintuplinervis* differed from all other Dissochaetinae in its ivy-like habit and flexuose stem. After various attempts to place it, including in a section of *Medinilla* (Bakhuizen, 1943), the species was placed in *Catanthera* (Nayar, 1982).

Kendrickia, *Catanthera*, and *Medinilla* sect. *Heteroblemma* are united by a complex wood anatomical synapomorphy that relates to their growth form. After a closed cylinder of secondary xylem has been formed in young stems, the cambium starts to produce parenchymatous tissue at usually four equidistant positions. Continuing production of xylem between these meristematic patches results in a cloverleaf-shaped xylem (Fig. 5Aa). In older stems, the xylem pattern can be more complex due to additional centers of reduced xylem, and the variation of cambial growth finally yields butterfly- or star-shaped secondary xylem bundles embedded in phloem tissue (Clarke 1907; Vliet 1981; our Fig. 5Ba, Ca). Vliet interpreted the anomalous growth in the three genera as resulting from parallel evolution, a view almost certainly

Fig. 4. Morphology of scrambling shrubs: a. *Dissochaeta annulata* growing in secondary vegetation, b. flowering branches of *Diplectria glabra* subsp. *kinabaluensis*, c. heteranthery in *Dissochaeta annulata*, d. interpetiolar outgrowth of *Diplectria stipularis*, e. flowering and fruiting branches of *Diplectria divaricata*, f. staminodial outer stamen whorl in *Diplectria glabra* subsp. *kinabaluensis*, g. cross section of wood showing the wide pith that may become hollow in older branches, h. haplostemonous flower of *Dissochaeta monticola*, i. lignified adventitious roots in *Dissochaeta gracilis*. This Figure is shown in colour in the electronic supplement of *Organisms, Diversity & Evolution* at <http://senckenberg.uni-frankfurt.de/odes/2001-1-1.htm>.



Table 2. Morphology of *Catanthera*, *Kendrickia*, and *Medinilla* section *Heteroblemma*.

| | <i>Catanthera</i> | <i>Kendrickia</i> | <i>Medinilla</i> sect. <i>Heteroblemma</i> |
|----------------|--|--|---|
| Branches | Up to 4 cm in diam., all branches clinging to substrate or pendent | Up to 3 cm in diam., fertile branches self-subtending and spreading, others clinging to substrate | Up to 1 cm in diam., all branches clinging to substrate |
| Leaves | Isophyll or anisophyll; petioles long; secondary venation obscure | Heterophyll (leaves of fertile and sterile branches slightly different in shape); petioles short; secondary venation obscure | Anisophyll, pseudoalternate; petioles long (5–17 cm); secondary venation prominent |
| Inflorescences | Axillary; bracts minute | Axillary or terminal; bracts absent | Axillary; bracts absent |
| Flowers | 4-merous; hypanthium campanulate, wall thin | 4-merous; hypanthium angular-campanulate, wall thick | 4-merous; hypanthium campanulate, wall thin |
| Androeceum | Diplostemonous or haplostemonous, stamen whorls isomorph or dimorph; stamens with a dorsal spur and two ventral appendages | Diplostemonous, stamen whorls isomorph; stamens with a dorsal spur, ventral appendages lacking | Diplostemonous, stamen whorls isomorph; stamen with a dorsal spur, ventral appendages very small or lacking |
| Gynoeceum | Ovary 2/3 to 1/1 as long as hypanthium, extraovarian chambers reaching the base of the ovary | Ovary 2/3 as long as hypanthium, totally adnate, extraovarian chambers lacking | Ovary 2/3 to 1/1 as long as hypanthium, extraovarian chambers reaching the base of the ovary |
| Fruits | Soft berries, pericarp not or weakly sclerified, placenta persistent | Fleshy capsule that opens by 4 longitudinal cracks, placenta persistent | Hard berries, pericarp sclerified, placenta persistent |
| Seeds | Ovate, testa smooth | Prismatic, testa smooth | Comma-shaped, testa papillate |

influenced by their distant positions in previous classifications based on stamens and fruits (Table 2).

Compared to the uniformity of the scramblers, root-climbing Melastomataceae are diverse in habit (Table 2; Fig. 5). *Kendrickia* has erect or spreading fertile branches and vegetative branches that cling to the substrate (Fig. 5A). The leaves of sterile and fertile branches differ slightly in shape (Fig. 5Ab, c). *Catanthera* grows ivy-like, and its leaves are isophyllous or anisophyllous (Fig. 5Cb), with one member of each pair much smaller and usually early caducous, which results in a pseudoalternate phyllotaxy (Fig. 5Cb). Species of *Heteroblemma* have thin branches that cling to the substrate and large, long-petiolate leaves (Fig. 5Bb) that are always pseudoalternate. Pseudoalternate phyllotaxy in Melastomataceae is restricted to climbing species (Renner, 1993), which in some cases replace all leaves on one side of the stem by climbing roots.

The root climbers' androeceum morphology is relatively uniform (Table 2; Fig. 5Ad, Bc). The androeceum of *Catanthera*, however, has dimorphic stamens whorls

as already described for *Dissochaeta* (Fig. 5Cc), with the inner stamen whorl smaller, staminodial, or absent. The fleshy capsule, which opens by four longitudinal cracks (Fig. 5Ae), and the prismatic seeds (Fig. 5Af) of *Kendrickia* are unique, while the fruits of *Catanthera* and *Medinilla* sect. *Heteroblemma* are simple berries common in the tribe (Fig. 5Cd).

Root-climbing taxa are restricted to more shady (less disturbed) habitats than the scramblers. This may be because their exposed living climbing roots, different from the dead adventitious roots that serve as hooks in Dissochaetinae, are draught-sensitive (Fig. 6g). Thus, species of *Catanthera* occur in rainforest on Sumatra, Borneo, Sulawesi, and New Guinea; *Kendrickia* is restricted to humid montane forests in South India and Ceylon; and most species of *Medinilla* sect. *Heteroblemma* are only known from a few locations in lowland forests in Borneo (Regalado, 1990). Only *M. alternifolia* is more widespread, occurring in Borneo, Sumatra, and the Malayan Peninsula. Root climbers also have not undergone extensive specia-

Fig. 5. Morphology of root climbers: A. *Kendrickia walkeri*, a. anomalous growth of the secondary xylem, b. and c. heterophyllous leaves, d. cross section of flower, e. capsule, f. seed with prismatic shape; B. *Medinilla serpens* (*Medinilla* sect. *Heteroblemma*), a. anomalous growth of the secondary xylem, b. pseudoalternate, large, long-petiolate leaves, c. isomorphic stamens; C. *Catanthera* spec., a. anomalous growth of the secondary xylem, b. strongly anisophyllous leaves, c. cross section of flower with dimorphic stamens, d. berry.

tion. Of all root-climbing Melastomataceae, *Catanthera* with 16 species and *Adelobotrys* with 25, are the only sizeable genera; all other root-climbing lineages contain between one and ten species. *Adelobotrys* is a member of the neotropical Merianieae and thus phylogenetically distant from Dissochaeteae (Clausing & Renner, in press).

True and facultative epiphytism (Fig. 6): Within the family, facultative and obligate epiphytism (with plants never connected to the ground) evolved a few times, mostly in New World Blakeeae and in Old World *Medinilla* and *Pachycentria*. The former two taxa are species-rich, perhaps due to restricted gene flow among epiphytically growing individuals as has been suggest-

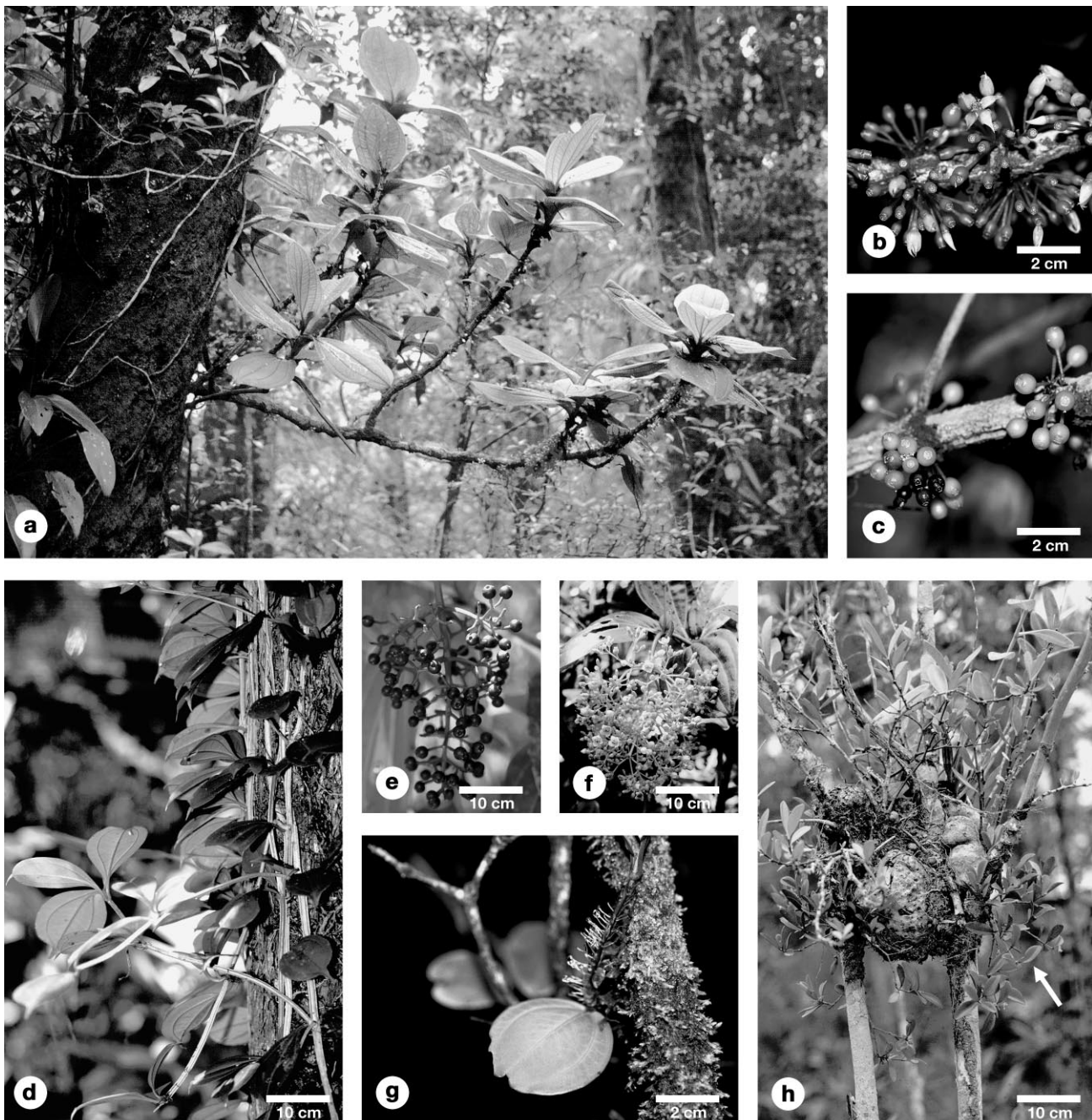


Fig. 6. Morphology of facultative and true epiphytes: a.–c. *Medinilla amplexens* Regalado, growth form, flowers and fruits, d. climbing branches of *Medinilla rubrifrons*, e. +f. flowers and fruits of *Medinilla speciosa* (Reinw. ex Blume) Blume, g. living adventitious roots of *Medinilla clarkei* King, h. *Pachycentria glauca* Triana growing on *Hydrophytum*. This Figure is shown in colour in the electronic supplement of *Organisms, Diversity & Evolution* at <http://senckenberg.uni-frankfurt.de/odes/2001-1-1.htm>.

ed for orchids (Pijl & Dodson, 1966). In the Dissochaeteae/Sonerileae complex, facultative or obligate epiphytism is almost restricted to *Medinilla*, *Pachycentria* (including *Pogonanthera*; Clausen, 2000), and *Plethiandra*, lineages whose phylogenetic relationships are not resolved by our data (Figs. 2, 3). These genera are diverse in species, but not morphology. Thus, there may be over 200 facultatively epiphytic species of *Medinilla*, many of which can be distinguished from each other only by minute characters (Regalado, 1990, 1995). Also, phenotypical plasticity can be seen in individuals growing under different conditions, for example, terrestrially vs. epiphytically. Among the few morphological adaptations seen in obligately epiphytic members of the *Medinilla* alliance are seeds that are attractive to ants and pearl bodies that are harvested by ants (e.g., in *Pachycentria constricta* and *P. glauca*; Clausen, 1998). Both features result in the seeds regularly being planted in ant gardens (Fig. 6h). As far as known, the other epiphytes all rely on birds for seed dispersal, and these species accordingly have purple, blue, or black juicy berries, often on reddish or pink infructescence stalks (Fig. 6c, e).

Our results show that scrambling growth in Melastomataceae is likely to have evolved once in the ancestor of Dissochaetinae, a group of ~40 species that are especially successful in secondary vegetation due to their innovative mode of scrambling. Once this niche had been opened up, Dissochaetinae may have undergone diversification in vegetative and reproductive morphology and phenology to avoid competition among closely related and often sympatric species. For example, six species of scrambling Dissochaetinae that co-occurred along a stretch of road in Sabah (*Diplectria beccariana*, *D. divaricata*, *D. stipularis*, *Dissochaeta annulata*, *D. beccariana*, and *D. intermedia*; Clausen, personal observation) differed from each other mainly in flower and fruit morphology and phenology.

Compared to the scramblers and true or facultative epiphytes, the root climbers studied here show more diversification in habit, although they all share anomalous secondary growth. In the family, root climbing has evolved in 18 of 150 genera, but there is no notable diversification in species numbers since most of these genera have 1-10 species (the largest has 25 species). Within angiosperms, too, scrambling and root climbing have evolved many more times than true epiphytism, but the subsequent evolutionary radiation of scandent taxa has not been pronounced. Thus, climbers are found in some 130 families of flowering plants, about twice as many as contain true epiphytes, but a large proportion of climbing taxa have only one to three scandent species (Gentry & Dodson, 1987; Gentry, 1991).

If diversification into different ecological roles via morphological adaptation is the criterion of adaptive ra-

diation within a lineage, the scramblers and root climbers fulfill it to a greater extent than do the facultative or obligate epiphytic shrubs. Scrambling growth and root climbing each have opened up new habitat in different lineages of Melastomataceae. In the Dissochaetinae, scrambling growth atop secondary vegetation provides access to light and – a corollary of high light levels – more abundant pollinators and dispersers than available in forest interiors. In the *Heteroblemma* alliance and other climbing medinillas, adventitious roots provide a firm hold on supporting trunks and branches, while simultaneously allowing up-take of the stem run-off, which contains many nutrients leached from the canopy (Nadkarni, 1981). The latter may be particularly important in melastomes that grow on heavily leached soils of low nutrient content.

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