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**Phylogenetic and taxonomic studies in *Macaranga*,
Mallotus and other acalyphoid genera (Euphorbiaceae s.s.)**

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SUMMARY & CONCLUSIONS

This study concerns the phylogeny and systematics of selected genera in the subfamily Acalyphoideae s.s. of the angiosperm family Euphorbiaceae s.s. The main focus is on *Macaranga*, *Mallotus* and related small genera in the subtribe Rottlerinae with the following principal research questions: 1) Are *Macaranga* and *Mallotus* monophyletic, or is *Macaranga* nested within *Mallotus* as recently suggested? 2) What is the phylogenetic position of the small genera in the subtribe Rottlerinae in relation to *Macaranga* and *Mallotus*? 3) What are the evolutionary relationships within *Macaranga* and *Mallotus*, and are the infrageneric groups in these genera monophyletic? 4) How are the *Macaranga* and *Mallotus* species occurring in Africa and Madagascar related to those in Asia and what kind of biogeographical scenario could explain the Afro-Asian distribution pattern? Furthermore, the genus *Cleidion* in Malesia was revised, and the morphology, pollen structure and phylogenetic position of *Afrotrewia*, a previously insufficiently known African genus, was studied.

In Chapter 2 the phylogeny of *Macaranga*, *Mallotus* and related genera in subtribe Rottlerinae is presented. For this purpose one plastid (*trnL-F*) and three nuclear (*ITS*, *ncpGS*, *phyC*) sequence markers were sequenced for a taxon sample of more than 90 species, including all the Rottlerinae genera except New World *Avellanita* and all the infrageneric groups of *Macaranga* and *Mallotus*. The results demonstrated the monophyly of *Macaranga* and the paraphyly of *Mallotus* and revealed three highly supported main clades: 1) the *Cordemoya* s.l. clade, comprising the genera *Cordemoya* and *Deuteromallotus* and the *Mallotus* sections *Hancea* and *Oliganthae*; 2) the *Macaranga* clade with all sampled *Macaranga* species; and 3) the *Mallotus* s.s. clade with the remaining *Mallotus* species together with the genera *Coccoceras*, *Neotrewia*, *Octospermum* and *Trewia*. Furthermore, the *Macaranga* and *Mallotus* s.s. clades are sister groups, and the *Cordemoya* s.l. clade is basal to the two other main clades.

In the *Macaranga* clade two basal lineages (comprising mostly species from the section *Pseudorottlera*) and a crown group with three biogeographically homogeneous main clades were identified. Half of the infrageneric *Macaranga* groups were found to be non-monophyletic. On the other hand, in the *Mallotus* s.s. clade the data did not result in a well resolved and well supported phylogenetic tree. In both the *Macaranga* and *Mallotus* s.s. clades the African and/or Madagascan taxa are nested in Asian clades, suggesting colonizations (probably one in *Macaranga* and two in *Mallotus* s.s.) from Asia to Africa and Madagascar.

Chapter 3 reflects the phylogenetic findings of Chapter 2 to the classification, reshaping the genus *Mallotus* to become monophyletic. The three small Asiatic genera, *Neotrewia*, *Octospermum* and *Trewia*, were merged with *Mallotus*. In addition, a full taxonomic treatment of the species transferred was given, and their morphology in

comparison to *Mallotus* was discussed. The monotypic *Neotrewia* and *Octospermum* had originally been described within *Mallotus* and were here transferred back to it. *Trewia*, on the other hand, was confirmed to have two distinct species, for which new combinations in *Mallotus* are made. These taxonomic changes, together with a paper by Sierra et al. (2006) in which the genus *Cordemoya* was expanded to cover the taxa falling into the *Cordemoya* s.l. clade, define a newly circumscribed *Mallotus* sensu stricto. Chapter 3 is accompanied by Chapter 4, where a proposal was made to conserve the name *Mallotus* against the older name *Trewia*, which would otherwise be the correct name for the newly circumscribed genus.

In Chapter 5 the phylogeny of the newly circumscribed *Mallotus* (*Mallotus* s.s.) was studied in more detail. For this purpose the taxon sampling was increased significantly, and data were gathered from plastid and nuclear DNA sequences (*matK* and *gpd*), macromorphology and leaf anatomy, employing also quantitative characters. Quantitative data was treated in two distinct ways, by coding them as discrete characters with the gap weighting method and by analyzing the ranges ‘as such’, i.e., as polymorphic ordered characters in the program TNT. In both cases the support for most clades (measured with the symmetric resampling method) increased when qualitative data were accompanied by quantitative data, indicating that the latter contains phylogenetic information. The results from the combined analyses of all data show that *Mallotus* sections *Mallotus*, *Polyadenii* and *Stylanthus* are monophyletic. On the other hand, sections *Axenfeldia* and *Rottleropsis* are polyphyletic, and section *Philippinenses* is paraphyletic. Six additional clades with morphological synapomorphies were also identified. Many of the sectional and other clades have a wide distribution, indicating extensive dispersal and/or migration during the evolution of *Mallotus*. However, the higher-level relationships between the clades were poorly supported and the position of many taxa is still ambiguous.

In Chapter 6 the taxonomic revision of the genus *Cleidion* in *Malesia* is presented. This pantropical genus of c. 33 species belongs to the same core acalyphoid subclade, A1, as *Cordemoya*, *Macaranga* and *Mallotus*. The species in *Cleidion* share an anther type that is unique within Euphorbiaceae. The structure of the flower clusters in staminate inflorescences was found to be taxonomically important. One new species, *C. luziae* from the Moluccas, New Guinea and the Solomon Islands, was described. After synonymizing *C. salomonis* with *C. papuanum*, and treating *C. lanceolatum* as a variety of *C. ramosii*, in total seven Malesian *Cleidion* species are recognized. In addition, *C. megistophyllum* from the Philippines is treated as a species doubtfully belonging to the genus *Cleidion*.

Chapter 7 concentrates on *Afrotrewia*, a previously insufficiently known monotypic Euphorbiaceae genus from Africa. Newly found material made it possible to provide a neotypification, an amended description and illustrations for this genus. In addition to Cameroon, the distribution of *Afrotrewia* was extended to Gabon. The phylogenetic position of the genus was determined by sequencing two plastid regions, *trnL-F* and *rbcL*, and analyzing the acquired sequences together with a previously published Euphorbiaceae s.s. dataset. The results show that *Afrotrewia* is part of the core acalyphoid clade, and not related to the genus *Necepsia*, as was suggested earlier. The precise position of *Afrotrewia* remains, however, ambiguous. Additionally, the pollen of *Afrotrewia* was studied with light microscopy and scanning electron microscopy. The genus resembles several other acalyphoid genera in pollen structure. These genera

are, however, scattered throughout the tree obtained from DNA sequence data, and not closely related to *Afrotrewia*.

CONCLUSIONS AND FUTURE RESEARCH

This study clarified the relationships between *Macaranga*, *Mallotus* and the small Rottlerinae genera. Because the three main clades were strongly supported, the formal taxonomic changes necessary to make *Mallotus* monophyletic could be confidently conducted. Although insights were also gained into the evolutionary relationships inside *Macaranga* and *Mallotus*, there is still much scope for additional research on these genera.

The sequence markers used in Chapter 2 provided a relatively well resolved and supported phylogeny of the genus *Macaranga*. However, the *Macaranga* taxon sample in this study, although covering all the infrageneric groups and most of the morphological variation, included only about 20% of the species in this genus. Therefore, in future phylogenetic studies in *Macaranga*, perhaps focusing on each of the main clades separately, taxon sampling should primarily be improved. Additional fast-evolving generic markers could also be added to resolve the relationships between closely related species. Furthermore, the knowledge on the macromorphology and anatomy of *Macaranga* should be deepened.

In contrast with *Macaranga*, the phylogenetic relationships within the genus *Mallotus* proved to be very difficult to resolve. Increasing the taxon sampling and employing new data sources for Chapter 5 made it possible to some extent to assess the traditional infrageneric classification and to identify several new clades with morphological synapomorphies, but the general lack of support did not warrant a new classification to be proposed and a detailed biogeographical analysis to be conducted. These difficulties in achieving a robust phylogeny, especially concerning the basal relationships, could be due to events in the early evolutionary history of the genus, e.g., rapid radiation. Improving the dataset used in Chapter 5 (e.g., acquiring molecular data for a wider taxon sample) and using yet additional genetic markers might still result in a better supported phylogenetic tree. On the other hand, detecting confounding events like interspecific hybridization with phylogeographical methods might further shed light on the evolutionary history of the genus *Mallotus*.

The studies on *Cleidion* and *Afrotrewia* conducted in Chapters 6 and 7 also call for additional research. As a relatively small pantropical genus, *Cleidion* would make an interesting subject for a phylogenetic study, with an emphasis on its biogeographical history. The monophyly of the genus, suggested by a unique anther type, should also be tested. The sequence markers already tested on the related genera *Macaranga* and *Mallotus* could be used for *Cleidion* as well. In the study of *Afrotrewia* the precise phylogenetic position of this genus could not be determined. This demonstrates that the currently available phylogenetic datasets for the subfamily Acalyphoideae s.s. need to be expanded with additional taxon sampling and new sequence markers. Furthermore, the *Afrotrewia* study suggested that the value and role of pollen characters in the Euphorbiaceae s.s. classification needs to be re-evaluated in the light of the molecular phylogenetic findings.

