



How to tackle revisions of large genera: lessons from *Macaranga* and *Mallotus* (*Euphorbiaceae*)

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Key words

Euphorbiaceae
Macaranga
Mallotus
phylogeny
revision
species rich genera

Abstract Two approaches to revise large genera are discussed. The first approach can be done by a single person, who revises the genus area after area. The other approach is by a team that revises per infrageneric taxon (preferably a single person per infrageneric group). The two approaches have their positive and negative sides, but both give good results. One problem with both approaches is to keep an overview of a possible infrageneric classification. The latter problem can be tackled by performing phylogenetic analyses based on molecular markers (providing core phylogeny) in combination with morphological, palynological, and anatomical data (providing apomorphies for infrageneric taxa).

Published on 30 October 2009

INTRODUCTION

Revisions of large genera (more than a hundred species) are usually problematical. The major difficulty is to keep an overview, not only to remember all species and their differences (analytical phase), but also to see groupings in the species based on typical characters that may represent possible infrageneric taxa (synthetic phase). The genera *Macaranga* Thouars (c. 240 spp.) and *Mallotus* Lour. (c. 110 spp.) are two such large groups. Here an additional difficulty is that the two genera are morphologically quite indistinct. Moreover, they both occur in similar habitats and they responded in the same morphological way to changes in ecological niche (smaller and narrow leaves in primary forest surroundings changing to large and broad leaves in pioneer habitats; Slik et al. 2003). The two genera also show a similar distribution, ranging from Africa to Madagascar and the Mascarenes and from India throughout southeast Asia to the West Pacific and Australia. Typical for both genera is the presence of glandular hairs with a globose to disc-shaped head (here referred to as glandular scales; see Sierra et al. 2006: f. 3d–f) and generally extrafloral nectaries on the upper leaf surface. Furthermore, dioecy is common and the generally dehiscent fruits often carry soft spines. There is only one 'official' difference between the two genera, *Macaranga* has anthers with 3–4 thecae, and *Mallotus* only has 2-thecate anthers. All other characters are typical for only part of the genera (e.g., stellate hairs and opposite leaves are present in *Mallotus* only, but not all species show them; idem for *Macaranga* where groups of species live in association with ants, and many species have panicles instead of racemes, but the panicles also occur in *Mallotus* section *Mallotus*).

The classification of the two genera is also a problem, at the suprageneric level, generic level, as well as the infrageneric classification. The fact that the difference between the two genera is defined by two character states of the same character already indicates that one state is probably plesiomorphic and, therefore, one of the two genera is likely to be a paraphyletic group. This makes it even stranger that the most recent classifications (Webster 1994, Radcliffe-Smith 2001) place the

two genera in different subtribes (*Macaranga* in the monothetic *Macaranginae* and *Mallotus* with several other genera in the *Rottlerinae*). Moreover, there are four small genera (*Cordemoya* Baill., *Neotrewia* Pax & K. Hoffm., *Octospermum* Airy Shaw, and *Trewia* L.) that are also indistinguishable from *Mallotus* and their relation to *Macaranga* and *Mallotus* had to be re-evaluated too. The infrageneric classifications also posed problems, but we will only touch upon these in this paper.

The purpose of this paper is to discuss three items:

- the pros and cons of two different revisional approaches;
- the benefits of including macromorphological, anatomical, and palynological studies;
- the usefulness of phylogenetic analyses.

REVISIONS

The ways in which *Macaranga* and *Mallotus* were revised are more or less opposite, but both worked well. The two approaches are summarised in Table 1.

Macaranga was mainly revised by a single person, the late Tim Whitmore, with assistance by Stuart Davies. A one-person approach has the advantages that the species concept will be more or less similar for all species, and probably it is easier to keep an overview of all species and possible infrageneric groups. The major disadvantage is that the revision will take a long time with the possibility of an untimely end to the project, because the revisor has to stop prematurely. One of the major problems with revising large genera is the enormous amount of research material. Whitmore handled this problem via an area approach. The whole distribution range was subdivided in more or less natural areas (e.g., the island groups in Malesia) and the species of each area were revised separately. This approach should typically be done by a single person, several persons revising different areas will cause problems with species concepts. There are a few obvious disadvantages to the area approach. Widespread species have to be linked after every area revision. Additional problematic issues may be widespread species that show geographical variation or clines, especially if some of the extremes received different names, then nomenclatorial problems also arise. Related to this is the problem of interpreting widespread species, because the type

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Table 1 Differences between the two approaches of large revisions. In **bold** benefits, in *italics* drawbacks

team size	one person	several to many
sequence of revision	area after area	section after section
species concept	similar	<i>may differ</i>
overview species	relatively simple	<i>more difficult</i>
duration of revision	<i>long</i>	relatively short
widespread species	<i>linking of island formst difficult</i>	studied as a whole
names	<i>types later interpreted</i>	types included directly
infrageneric overview	difficult	easy (when sections correct) otherwise difficult

is often not included in the first revisions. This caused problems in a former revision of *Mallotus* by Airy Shaw, who also used an area approach. Compare the results for Thailand, the same species names in Airy Shaw (1972) and Van Welzen et al. (2000) cover partly different *Mallotus* species as in Van Welzen et al. (2007). The species concepts are more or less the same, but after studying types from especially Java, it appeared that several entities received wrong names in the 1972 and 2000 revisions. A domino effect occurred because the species only differ in small details: giving one wrong name to a pile automatically resulted in wrong names for other piles. Finally, the area approach may be problematic for keeping an overview of the infrageneric groups. After each area revision the species classification should be rechecked. The problem can be overcome by a separate phylogenetic study (see next chapter).

Mallotus was revised by a team (seven persons). Airy Shaw presented the last infrageneric classification of *Mallotus* in 1968. He recognised eight sections, which were generally easy to identify. The revisions were made per section, and this has resulted in quite a few publications: Section *Polyadenii* Pax & K.Hoffm. (Bollendorff et al. 2000), sections *Hancea* Pax & K.Hoffm. and *Stylanthus* (Rchb.f. & Zoll.) Pax & K.Hoffm. (Sliik & Van Welzen 2001), section *Philippinenses* Pax & K.Hoffm. (Sierra et al. 2005; formerly section *Rottlera* (Willd.) Rchb.f. & Zoll.), section *Mallotus* (Sierra & Van Welzen 2005), genus *Cordemoya* (incl. *Mallotus* section *Oliganthae* Airy Shaw: Sierra et al. 2006; presently changed to *Hancea*, Sierra et al. 2007), section *Rottleropsis* (incl. section *Axenfeldia* (Baill.) Pax & K.Hoffm.: Sierra et al. 2007); and the small genera *Trewia*, *Neotrewia*, and *Octospermum* (Kulju et al. 2007b).

Revisions by teams are best done per section, whereby each section is revised by a single person or, in case of more persons, then with one person in charge. This will best guarantee a constant species concept (e.g., *Mallotus kongkandae* Welzen & Phattar. was originally described as a variety *mengliangensis* C.Y.Wu ex S.M.Hwang of *Mallotus philippensis* (Lam.) Müll. Arg., but the differences with *M. philippensis* are such that recognition on the species level was warranted; Sierra & Van Welzen 2006). With widespread species it is easier to obtain an overview of the variation and to interpret type specimens. Another benefit is the much shorter duration of the complete revision. A big drawback is the lack of a complete overview of all species by at least a single person. This makes the construction of identification keys more difficult (though computer programs may help out). Related to this problem is the re-classification of species that were incorrectly placed in, for instance, a section (e.g., five species were incorrectly placed in section *Hancea*, but were otherwise difficult to place in another section; Van Welzen et al. 2006). Similarly, a lack of an overview on the species level also complicates an infrageneric classification unless the classification on which the revisions were based was correct (see also next chapter). Here too, a phylogenetic study may help to pinpoint the infrageneric taxa.

PHYLOGENY

One of the problems to be solved was the generic distinction between *Macaranga* and *Mallotus* and their relationship with small genera like *Cordemoya*, *Neotrewia*, *Octospermum*, and *Trewia*. A phylogenetic analysis based on four molecular markers (*trnL-F*, ITS, *ncpGS*, *phyC*) showed that *Macaranga* is a monophyletic group (Kulju et al. 2007a), while *Mallotus* appeared to be paraphyletic. The largest part of *Mallotus* is a sister group of *Macaranga*. This *Mallotus* group (*Mallotus* s.s.) is monophyletic when the genera *Neotrewia*, *Octospermum*, and *Trewia* are included. The (re)transfer of these small genera to *Mallotus* is published by Kulju et al. (2007b). A problem is that *Trewia* is an older name than *Mallotus*, therefore, Kulju & Van Welzen (2008) wrote a proposal to conserve the name *Mallotus* against *Trewia*. A basal group of *Mallotus* species (sections *Oliganthae* and *Hancea* excluding five species: Sliik & Van Welzen 2001, Van Welzen et al. 2006) grouped together with the Madagascar genus *Cordemoya* and all other *Mallotus* species of Madagascar and the Mascarene islands, also formerly known as the genus *Deuteromallotus*. An elegant solution was to transfer the basal *Mallotus* species to *Hancea* (Sierra et al. 2006, 2007). This resulted in a monophyletic genus *Hancea*, sister to the also monophyletic sister groups *Mallotus* s.s. and *Macaranga*. The recognisability of the three genera was also increased (see next chapter).

The phylogenetic analysis (Kulju et al. 2007a) and subsequent transfer of species to *Hancea* (Sierra et al. 2006, 2007) resulted in a well-corroborated infrageneric classification for *Hancea*, in accordance with the sections already recognised under *Mallotus* (Fig. 1). Each of these groups have their own typical characters. Two subgenera are recognised (Sierra et al. 2006): *Cordemoya* (Baill.) S.E.C.Sierra, Kulju & Welzen (all Indian Ocean taxa) and *Hancea* (all Asian taxa). The latter subgenus is divided into the sections *Hancea* Seem. (former *Mallotus* section *Hancea* excluding the five deviating species) and monotypic section *Oliganthae* (Airy Shaw) S.E.C.Sierra, Kulju & Welzen (former *Mallotus* section *Oliganthae*).

The phylogenetic analyses (Kulju et al. 2007a: core phylogeny of the genera based on molecular data; Sierra et al. submitted: detailed phylogeny of *Mallotus* including morphology and anatomy, f. 1) did not provide sufficient data for infrageneric classifications of *Macaranga* and *Mallotus*. The first analysis did not comprise enough species (Kulju et al. 2007a), but the *Macaranga* part was well resolved and relatively well supported, but this was hardly the case with *Mallotus*. Also, the second analysis (Sierra et al. submitted), that included many more species and almost for all species morphological data, did not result in a better cladogram for *Mallotus*, especially the basal branches were badly resolved and certainly not statistically supported. It was remarkable that the inclusion of quantitative morphological and anatomical characters did improve the resolution (though not the support). Still, several sections appeared to be monophyletic. We only mention those of *Mallotus*, because

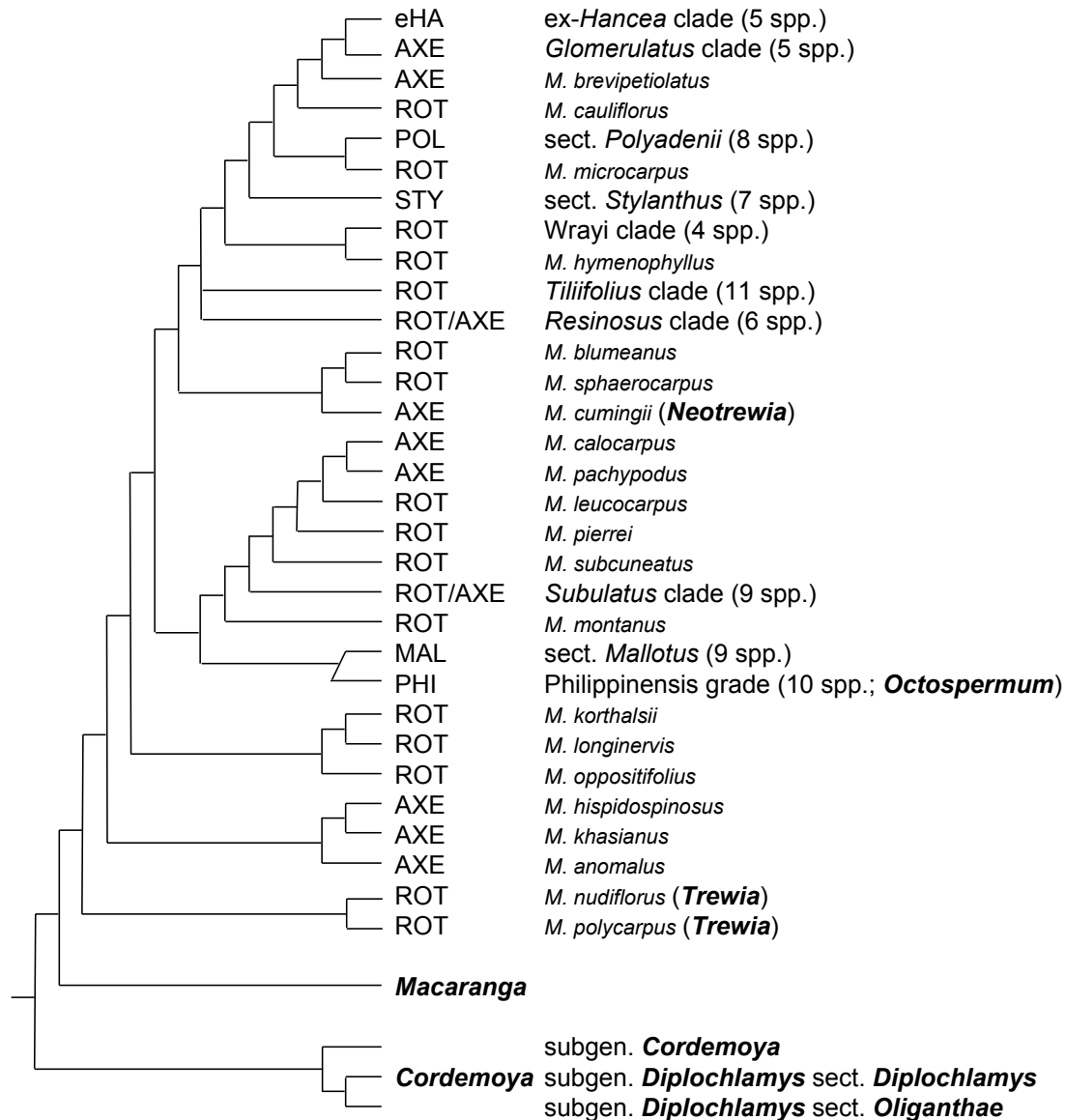


Fig. 1 On of the cladogram of *Mallotus* (Sierra et al. submitted) based on molecular markers and qualitative and quantitative macromorphological and anatomical characters (quantitative characters used 'as is' with program TNT). Abbreviations indicate the former sections in *Mallotus*: AXE = *Axenfeldia*; eHa = *ex-Hancea*; MAL = *Mallotus*; PHI = *Phillipinensis*; POL = *Polyadenii*; ROT = *Rottleropsis*; STY = *Stylanthus*). Added are the infrageneric groups of *Hancea* (subgen. *Cordemoya* = *Cordemoya* s.s. + *Deuteromallotus*; sect. *Hancea* = former *Mallotus* sect. *Hancea*; sect. *Oliganthae* = former *Mallotus* sect. *Oliganthae*). The monophyletic groups within *Mallotus* are indicated, just as the *Phillipinensis* grade (diagonal line at base of Hennigian comb); sections *Axenfeldia* and *Rottleropsis* s.s. are polyphyletic, when united into *Rottleropsis* s.l. (Sierra et al. 2007) then the group is paraphyletic.

they were introduced already. Sections *Mallotus*, *Polyadenii*, and *Stylanthus* are monophyletic, while section *Phillipinensis* (= section *Rottlera*) is paraphyletic and forms a monophyletic grade with section *Mallotus*. Unfortunately, the largest sections, *Axenfeldia* and *Rottleropsis* are polyphyletic (and paraphyletic when united under *Rottleropsis* s.l.; Sierra et al. 2007), though several small monophyletic groups can be distinguished (see also next chapter).

CHARACTERS

The phylogenetic analysis of *Mallotus* was not only based on molecular markers, a palynological (Sierra et al. 2006), and extensive morphological (section revisions) and anatomical data (Fišer et al. in prep.) were included. Especially, the anatomical study proved to be valuable in terms of apomorphies (characteristics) for generic and infrageneric groups, e.g., the glandular scales proved to have many different types.

Cordemoya and *Mallotus* differ in the ornamentation of the pollen, *Cordemoya* has an areolate ornamentation with scabrae,

and *Mallotus* a perforate or micro-reticulate ornamentation (also with scabrae), and capitate glandular hairs with multicellular stalks and sessile peltate-stellate hairs with a central cell (see Sierra et al. 2006: f. 3a–c). The opposite, glandular scales (f. 1a), are typical for *Macaranga* and *Mallotus* s.s. (few reversals exist). Besides the number of thecae in the anthers, the presence of stellate hairs or stellately bundled hairs is typical for *Mallotus* s.s.

Several of the sections in *Mallotus* now have more apomorphies than before (Sierra et al. submitted). Section *Mallotus* has as apomorphies the presence of paniculate inflorescences, pistillodes, spiny fruits, cork warts, stellate hairs, and no stellately tufted hairs. In the polyphyletic *Axenfeldia/Rottleropsis* sections several groups are distinct, e.g., the *Glomerulatus* group with the pistillate inflorescences reduced to glomerules, the *Subulatus* group with umbel-like pistillate inflorescences, the *ex-Hancea* clade with the opposite leaves differing in shape, the *Wrayi* clade (Van Welzen & Sierra 2006) with extrafloral nectaries on the nerves of the upper leaf surface, etc.

CONCLUSIONS

The two scenarios for tackling revisions of large genera have their pros and cons (Table 1), but both give good results. If a rather speedy revision is essential, then a section revision by a team is the way to proceed.

We also indicated the necessity of phylogenetic research (which solved generic boundaries, and indicated the problems with former infrageneric classifications) and good macromorphological, palynological and anatomical research (provided many characters and synapomorphies). These researches will or may slow down the revision work, but the end result is a well-supported classification and good revisions.

Therefore, we do not opt for the quick and dirty approach (which resulted in many wrongly applied names in *Mallotus* in past revisions), but more for the slow and thorough approach via a team of collaborators.

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