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

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**THE PHYLOGENY OF *MALLOTUS* S.S. (EUPHORBIACEAE S.S.)
INFERRED FROM DNA SEQUENCE AND MORPHOLOGICAL
DATA**

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manuscript

SUMMARY

Mallotus s.s. is a large ecologically important paleotropical genus in the family Euphorbiaceae. We investigated the phylogeny of the genus in order to 1) determine the evolutionary relationships within the *Mallotus* s.s. clade, 2) assess whether the six sections as circumscribed in the traditional classification reflect clades and evaluate the characters used in the classification, 3) determine what are the additional new clades and their supporting morphological characters. For this purpose we assembled different datasets: plastid (*matK*) and nuclear (*gpd*) DNA sequences, macromorphological features and leaf anatomical data, including quantitative characters. We found that sections *Mallotus*, *Polyadenii* and *Stylanthus* are monophyletic, *Axenfeldia* and *Rottleropsis* are polyphyletic, and *Philippinenses* is paraphyletic. Six additional clades with morphological synapomorphies were also identified. Many of the clades are widely distributed, implying extensive dispersal and/or migration during the evolution of *Mallotus* s.s. Adding quantitative morphological data to combined qualitative datasets, either treated with gap weighting or analyzed 'as such' with TNT, resulted in almost completely resolved phylogenies and increased support values. However, the higher-level relationships between the clades are not supported in our analyses and the position of many taxa is still ambiguous.

Key words: DNA sequence data, Euphorbiaceae, leaf anatomy, *Mallotus*, morphology, phylogenetics, quantitative characters, Rottlerinae.

INTRODUCTION

Mallotus Lour. is a large genus (c. 110 spp.) in the family Euphorbiaceae, consisting of shrubs, trees or seldom climbers. Typical features are the presence of fairly conspicuous, globose to disc-shaped glandular hairs (best seen on the lower leaf surface and inflorescences) and extrafloral nectaries on the upper leaf surface. The genus has a palaeotropical distribution, occurring mainly in (sub)tropical Asia and the West Pacific, with only two species in tropical Africa and Madagascar (Kulju et al., 2007, Chapter 3; Sierra et al., 2007).

Mallotus species are important components of the forest vegetation in Southeast Asia (Keßler, 2000; Slik et al., 2003a; Slik et al., 2003b; Eichhorn, 2006). The genus shows a large variety of life-history strategies, some species being early successional

¹This chapter appears both in this thesis and in the thesis of Soraya Sierra; both authors being equal main contributors.

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pioneers, while others are climax species. The species occur in different habitats, e.g., the understorey of primary forest, disturbed secondary forest, or open places like river banks, forest edges, and cleared areas. *Mallotus* species can be found on different types of soil, including limestone. They occur both in wet and periodically inundated areas but also on well-drained soil (Sierra et al., 2007).

The broad ecological variability within the genus led Slik et al. (2003a) to use *Mallotus* species, together with species of the related genus *Macaranga* Thouars., as indicators of different types of forest disturbance. Slik (2005) developed a methodology to assess the type of forest disturbance in lowland tropical forest in Borneo using *Macaranga* and *Mallotus* abundances, which is particularly useful when other ecological field data or historical records on disturbance are absent. This method is available online (<http://www.nationaalherbarium.nl/macmalborneo/index.htm>).

The large number of species in *Mallotus* together with their variable morphology has resulted in three main subgeneric classifications (Müller, 1865, 1866; Pax & Hoffmann, 1914; Airy Shaw, 1968). In the classification presently used (Airy Shaw, 1968), the genus was subdivided into eight sections, which were recently revised mainly for the Flora Malesiana area and Thailand (Bollendorff et al., 2000; Slik & Van Welzen, 2001b; Sierra & Van Welzen, 2005; Sierra et al., 2005; Sierra et al., 2006; Van Welzen & Sierra, 2006; Sierra et al., 2007; Van Welzen et al., in press).

In recent classifications of the Euphorbiaceae (Webster, 1994b; Radcliffe-Smith, 2001), the genus *Mallotus* was placed in the subtribe Rottlerininae together with seven or eight small genera. Because many of these genera closely resemble *Mallotus*, their delimitations have been challenged. Based solely on morphological similarities, two of the Rottlerininae genera, *Coccoceras* Miq. and *Deuteromallotus* Pax & K.Hoffm., have been suggested to be congeneric with *Mallotus* (Airy Shaw, 1963; McPherson, 1995; Bollendorff et al., 2000). Outside the Rottlerininae, *Mallotus* shares morphological and ecological similarities with another large Euphorbiaceae genus, *Macaranga*. This genus was classified in the separate, monogeneric subtribe Macaranginae by Webster (1994b) and Radcliffe-Smith (2001), but a molecular phylogenetic study of the uniovulate Euphorbiaceae indicated it being close to *Mallotus* (Wurdack et al., 2005).

Two phylogenetic studies have specifically investigated the relationship between *Mallotus* and related genera. An analysis based on morphological data suggested that *Mallotus* sections *Hancea* and *Oliganthae* are not part of the main *Mallotus* clade, and that *Mallotus* and *Macaranga* are closely related (Slik & Van Welzen, 2001a). A molecular phylogenetic study using nuclear and plastid markers and with more comprehensive taxon sampling (including all but one of the Rottlerininae genera, and c. 24% of *Mallotus* species) further clarified the boundaries of *Mallotus* and its relationships with other genera (Kulju et al., in press, Chapter 2). This study confirmed the exclusion of the sections *Hancea* and *Oliganthae*. These sections form a clade together with the Rottlerininae genera *Deuteromallotus* and *Cordemoya* Baill., and are separated with strong support from the main *Mallotus* clade. Additionally, this study showed that the *Mallotus* clade is sister to a monophyletic *Macaranga*. Furthermore, the phylogeny of Kulju et al. (in press, Chapter 2) confirmed the inclusion of *Coccoceras* in *Mallotus*, and demonstrated that *Neotrewia* Pax & K.Hoffm., *Octospermum* Airy Shaw and *Trewia* L., three mono- or ditypic Rottlerininae genera with atypically indehiscent fruits, are part of

the main *Mallotus* clade. The classification was subsequently changed to reflect these discoveries: a newly circumscribed *Mallotus* sensu stricto was formed by expanding *Cordemoya* to include the genus *Deuteromallotus* and *Mallotus* sections *Hancea* and *Oliganthes* (Sierra et al., 2006)² and by merging *Neotrewia*, *Octospermum* and *Trewia* with *Mallotus* (Kulju et al., 2007, Chapter 3).

The new *Mallotus* s.s. comprises the six remaining sections of Airy Shaw (1968), together with 5 species removed from section *Hancea* (Slik & Van Welzen, 2001b; Van Welzen et al., 2006). The sectional delimitations of Airy Shaw (1968) can be questioned, because they are based only on few characters (see Table 5.1). For instance, two species rich and morphologically diverse sections with truly opposite leaves, *Axenfeldia* and *Rottleropsis*, are distinguished only by a difference in leaf venation: pinnate in *Axenfeldia* and tripli- or palminerved in *Rottleropsis*. In the absence of suitable morphological characters to distinguish them, Sierra et al. (2007) merged the two sections into one large section, *Rottleropsis* s.l., indicating that sect. *Rottleropsis* s.l. needs further subdivision once a phylogeny could provide supported clades. The phylogenetic studies by Slik & Van Welzen (2001a) and Kulju et al. (in press, Chapter 2) tentatively suggest some of the sections not to be monophyletic. However, they suffer both from insufficient taxon sampling in the *Mallotus* s.s. clade, and from polytomies and low support in the resulting phylogenies. Thus, a study focusing on the phylogeny of *Mallotus* s.s. is clearly needed to evaluate the existing infrageneric classification

Table 5.1. Morphological characters used to distinguish sections according to the classification of *Mallotus* by Airy Shaw (Airy Shaw, 1968).

Section	Leaves	Upper surface of leaf blade with glandular hairs	Nerves	Fenugreek smell on dried plants	Spines on fruits	Fruits densely covered with glandular hairs
Philippinenses Pax & K.Hoffm	alternate	no	triplinerved	absent	absent	usually
Mallotus Lour.	alternate	no	tripli- or palminerved	absent	present	no
Stylanthus (Rechb.f. & Zoll.) Pax & K.Hoffm.	mostly alternate	usually	tripli- or palminerved	present	present	no
Polyadenii Pax & K.Hoffm.	mostly alternate	always	triplinerved, rarely pinnate	absent	absent	no
Axenfeldia Pax & K.Hoffm.	opposite	no	pinnate	absent	absent or present	no
Rottleropsis Müll.Arg.	opposite, rarely alternate	rarely	tripli- or palminerved	absent	absent or present	no

²Leaf anatomical differences between *Cordemoya integrifolia* (sub *Mallotus integrifolius*) and the genus *Mallotus* were already noticed by Rittershausen (1892).

(Airy Shaw, 1968) and the importance and evolution of the morphological characters involved. The new circumscription of *Mallotus* was taken as the basis for this article, and we are from this point onwards using ‘*Mallotus*’ in this sense without repeating ‘s.s.’.

The purpose of our study was to investigate the phylogeny of *Mallotus* and answer the following research questions: (1) what are the evolutionary relationships within the *Mallotus* clade, (2) do the sections as circumscribed in the classification by Airy Shaw (1968) reflect clades and what is the value of the characters used in this classification, (3) are there additional clades and if so, what are their supporting morphological characters. To answer these questions, three different datasets were gathered. A new macromorphological dataset was gathered for 94 *Mallotus* species. For a subset of this taxon sample, both leaf anatomical and DNA sequence data (and in addition, one palynological character) were collected. As four DNA regions previously used (Kulju et al., in press, Chapter 2) suffered from internal conflicts and did not provide well resolved and supported results, two new sequence regions, *matK* and *gpd*, were selected. The plastid gene *matK*, coding a maturase involved in splicing of type II introns, has proven to be phylogenetically informative in a wide range of taxonomic levels (see Soltis & Soltis, 1998 and references therein), and was recently suggested as a possible plant DNA barcode region (see <http://www.kew.org/barcoding/update.html>). However, as molecular evolution in plastid genome is rather conservative (Wolfe et al., 1987; Wolfe et al., 1989; Raubeson & Jansen, 2005), a fragment of the glyceraldehyde 3-phosphate dehydrogenase gene (*gpd*, also known as *GapC*), a low-copy number nuclear gene with introns, was sequenced as well. *Gpd* encodes an enzyme important in glycolysis (Figge et al., 1999). It has been shown to exhibit a high level of intraspecific variation in *Manihot esculenta* Crantz (Olsen & Schaal, 1999) and therefore has potential to resolve the relationships between closely-related *Mallotus* species.

MATERIAL AND METHODS

Outgroup choice and taxon sampling—*Blumeodendron* Kurz, *Cordemoya* (as circumscribed by Sierra et al., 2006) and *Macaranga* were used as outgroups, because they are closely related with *Mallotus* (Wurdack et al., 2005; Kulju et al., in press, Chapter 2). The taxon sampling for our three datasets, macromorphology, leaf anatomy and DNA sequences was different. For macromorphology 94 ingroup and 29 outgroup species were sampled. On the other hand, for DNA sequence data only a subset of this sample (47–49 ingroup and 8 or 9 outgroup species, depending on the DNA region) was included. The sampling for leaf anatomical data corresponds in most parts with the one for DNA sequences. For more details see Appendix 5.1 and paragraph ‘Sequence characteristics and indel characters’ in the Results section. When we refer to the ‘morphological dataset’, both macromorphological and leaf anatomical data are included.

Macromorphological data—Examination of specimens and the recent taxonomic revisions of *Mallotus* and *Cordemoya* in the Flora Malesiana area, Thailand and Africa (Bollendorff et al., 2000; Slik & Van Welzen, 2001b; Van Welzen et al., 2004; Sierra & Van Welzen, 2005; Sierra et al., 2005; Sierra et al., 2006; Sierra & Van Welzen, 2006; Van Welzen & Sierra, 2006; Van Welzen et al., 2006; Kulju et al., 2007, Chapter 3;

Sierra et al., 2007; Van Welzen et al., in press) were used as a source of information for constructing the morphological data matrix used in the phylogenetic analysis. For the taxa not included in the revisions mentioned above, observations were based on herbarium specimens selected to represent the distribution area of the taxa and their range of morphological variation. A list of specimens examined for non-Malesian, Thai or African species is available from the authors.

The characters used by Slik & Van Welzen (2001a) were taken into account while gathering a completely new morphological data matrix for our study. However, because our taxon sampling in *Cordemoya* and *Mallotus* was much more extensive, most characters were recoded. Additionally, because their data matrix included genera absent in our study (*Claoxylon* A.Juss., *Cleidion* Blume, *Sampantaea* Airy Shaw, *Wetria* Baill.), some of their characters were not applicable to our taxon sampling. The latter genera were omitted in this investigation, because studies by Wurdack et al. (2005) and Kulju et al. (in press, Chapter 2) indicate that they are not closely related to *Mallotus*.

In total 38 qualitative characters (15 vegetative and 23 reproductive) and 18 quantitative characters (2 vegetative and 16 reproductive) were recorded. Additional information, definitions of the characters and the data matrix are presented in Appendix 5.2.

Leaf anatomical and palynological data—The leaf anatomical characters used are based on a study by Fišer et al. (in prep.) on *Mallotus* and related genera. Transverse and paradermal sections, cuticular macerations and leaf clearings were observed with light microscopy. Critical point dried leaf samples were studied with scanning electronic microscopy (for details see Fišer et al., in prep.). In total 31 qualitative and 2 quantitative characters were recorded (Appendix 5.2). Palynological pilot studies revealed that little variation is present in the pollen of *Mallotus*, therefore only one character, exine ornamentation type, was used. Because of the large number of taxa only one or two collections per species could be studied for leaf anatomy and palynology.

Coding of the morphological data—Qualitative data were coded as unordered binary or multistate characters. The few missing data in the macromorphological matrix were mainly due to inapplicable characters or the lack of fertile material or literature information.

The use of quantitative characters in phylogenetic analysis is a controversial issue. Numerical data have been criticized by authors (Pimentel & Riggins, 1987; Crowe, 1994) who consider this type of data inappropriate and the methods for their conversion into discrete characters arbitrary. In contrast, quantitative data have been claimed to be suitable for phylogenetic analysis, because they fulfill the sole criterion for inclusion in phylogenetic analysis, which is the homology of character states (Rae, 1998). Furthermore, several authors have pointed out that regardless of whether morphological characters are coded qualitatively or quantitatively, the variation that they describe is fundamentally quantitative (Stevens, 1991; Thiele, 1993; Wiens, 2001).

Here we use both qualitative and quantitative data, and investigate the effect of adding quantitative data to conventional, qualitative datasets. When selecting quantitative characters for our analysis, characters based on field notes like habit or length of the plant were not taken into account, because it was uncertain if they had been properly

measured, and because they tend to be biased (e.g., short plants are more often collected because they are easier to reach). When features were highly dependent on each other, like length and width measures, only the measurement with the largest variation was taken into account. The length-width ratio was used only if this information was available from the descriptions.

Because discrete character states could not be defined, due to overlap, for most of the quantitative characters included in this study (except for the number of the thecae), we needed to use a coding method allowing overlap in the quantitative data. We evaluated two different methods. Several published methods are based on the transformation of the quantitative and often continuous information to a limited number of discrete characters states, which can be analyzed by ordinary phylogenetic algorithms. We used the gap-weighting method (Thiele, 1993), which was found to perform best among five different coding methods of quantitative data (Garcia-Cruz & Sosa, 2006). Additionally, we analyzed quantitative characters with the program TNT (Goloboff et al., 2003a), which allows using continuous ordered characters without discretization (Goloboff et al., 2006).

The gap weighting method (Thiele, 1993) divides the total interspecific range (the difference between maximum and minimum observed values) into N character states (generally the maximum number allowed in the analysis program), and assigns these states to taxa according to their mean values for the given character. The resulting characters are analyzed as ordered.

The coding of the gap weighting characters was done with MorphoCode v.1.0 (Schols et al., 2004). Before coding, the quantitative characters were log-transformed in order to equalize variances. In our study, true means could not be calculated, because actual measurements of specimens were not available from the revisional work of *Mallotus*. Therefore, the means of the maximum and minimum values given in the descriptions, excluding the extreme values in brackets, were used instead. This approach has also been used by Wieringa (1999, p. 65). When only one measurement was known and no range was available, this value was used as the mean. In the coding process 26 character states were used (the maximum allowed in the program MacClade; Maddison & Maddison, 2001). A weight of 25 was given to the unordered, qualitative morphological and DNA sequence characters. They thus attained the same maximum cost as the ordered, quantitative morphological characters.

One of the criticisms with the existing methods for discretization (including Thiele, 1993) is that they can attribute different characters states to terminals that do not differ significantly or vice versa (Farris, 1990). The phylogenetic analysis program TNT (Goloboff et al., 2003a) has an entirely different way to analyze continuous quantitative characters, avoiding this problem. In this method (Goloboff et al., 2006) the continuous quantitative data is analyzed ‘as such’, i.e., as ordered (additive) characters with the ranges expressed as polymorphisms. Continuous characters analyzed in this way seem to carry useful phylogenetic information, increasing resolution and/or support when added to traditional, qualitative datasets (Goloboff et al., 2006; Lehtonen, 2006).

For the TNT analysis, the quantitative characters in our study, measured in different scales, were range-standardized to have values from 0 to 65, using three decimal precision (the range of values allowed for continuous characters in TNT). Because

the recommended use of ± 1 SE (standard error of mean) as a range (Goloboff et al., 2006) could not be followed due to the way our data were recorded from morphological descriptions (see above), the actual range recorded was used instead. However, the extreme values reported in brackets were excluded. Reflecting the weighting used for the gap-weighting method, the qualitative characters analyzed together with ‘as such’ data were given the weight of 65.

DNA methods—The methods for DNA extraction, PCR amplification, sequencing and cloning generally follow Kulju et al. (in press, Chapter 2). For *matK* (including part of the flanking *trnK* intron), the primers published in Samuel et al. (2005) were used. This gene was amplified in either one or several fragments, depending on the quality of the template DNA. The primers GPDXF7 and GPDX9R (Strand et al., 1997) were initially used to amplify a fragment of *gpd* spanning three introns (Fig. 5.1). The amplifications in the outgroup taxa resulted in one *gpd* fragment only. However, in *Mallotus* this primer pair produced two fragments with lengths of c. 700 and c. 1200 bp. Cloning revealed both of them to be *gpd* paralogues, differing in intron content: the short fragment (as well as the fragment amplified in the outgroup taxa *Cordemoya* and *Macaranga*) misses one intron. This fourth intron, present in the long fragment, corresponds to the “intron d” of Olsen & Schaal (1999). Based on the cloned *gpd* sequences of *Mallotus polyadenos*, *M. philippensis*, *M. connatus*, *M. mollissimus*, and *M. nudiflorus*, new primers were designed to amplify only the short *gpd* paralog, which was used in the actual study:

GPDSLFL [5'-TTA TGA CCA CYG TCC AYT CC-3'
 GPDSR [5'-CAA AAA TRC TTG ATC TGC TAT CAC CA-3']

Additionally, four internal primers were designed for amplifying the short *gpd* paralog in three shorter fragments, to be used with degraded DNA samples extracted from herbarium specimens (Fig. 5.1):

GPDAR [5'-TWK ACC TTS GCA GCY CCA GT-3'
 GPDBF [5'-SCC RTC AAT GAA RGA CTG GA-3'
 GPDBR [5'-TMR TAK GAA GCC TCC TTT TCA-3'
 GPDCF [5'-CAC AGT YAG GCT TGA AAA RGA-3']

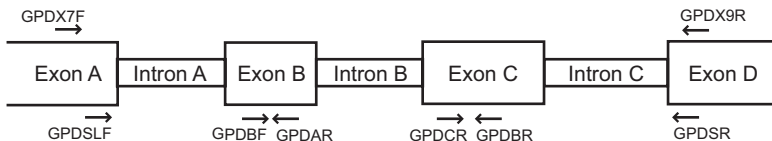


Fig. 5.1. Primers used in PCR and sequencing of *gpd*. Published primers (Strand et al., 1997) above, and the newly designed primers below.

PCR amplifications were carried out in 50 μ L reactions with 1 \times PCR Buffer (Qiagen, Hilden, Germany), 20 pmol of each primer, 5 nmol dNTPs, 0.5–4 μ g bovine serum albumin (BSA; Promega, Madison, Wisconsin, USA) and 2 U Taq DNA polymerase (Qiagen, Hilden, Germany). The concentration of $MgCl_2$ was 1.5 mM for *matK*, and 2.5–3 mM for *gpd*. The PCR program consisted of 4 min initial denaturation at 94°C, and 36–40 cycles of 30 s denaturation at 94°C, 30 s annealing at 49°C, 56°C or 60°C (for *matK*, *gpd* whole fragment, and *gpd* partial fragments, respectively), and 1.5 min extension at 72°C, followed by a final extension of 5 min at 72°C.

DNA sequence alignment and coding of indels—The sequences were aligned by eye using MacClade v.4.08 (Maddison & Maddison, 2001), following the guidelines of Kulju et al. (in press, Chapter 2). Indels were coded, after the exclusion of ambiguously alignable regions, as binary characters using simple indel coding (SIC; Simmons & Ochoterena, 2000) as implemented in the program SeqState (Müller, 2005a, 2006).

Phylogenetic analyses—The analyses were conducted with maximum parsimony (MP), and when appropriate, with Bayesian inference (BI). TNT v.1.1 (Goloboff et al., 2003a) was used for the MP analyses, treating polymorphic characters as uncertainties. Gaps in the alignment were treated as missing data, and the indel information was included as binary characters (see above). For searching the most parsimonious trees New Technology search strategies (Goloboff, 1999a; Nixon, 1999) were used, allowing the program to determine the search parameters with the initial level of 50 and continuing the search until the minimum length was found 7–30 times. The trees found with New Technology search were further swapped with TBR (tree bisection and reconnection) to potentially find more trees of the minimum length. Most of the analyses were replicated with PAUP* v.4.0b10 (Swofford, 2003), using Ratchet searches as implemented in PRAP v.1.21 (Müller, 2004), which resulted in strict consensus cladograms identical to those found with the TNT analyses (results not shown).

Because conventional resampling support values (i.e., bootstrap and jackknife) can be distorted by non-equal weights in the dataset, the support was measured with symmetric resampling (SR; Goloboff et al., 2003b). In this method the characters are allowed to have equal (symmetric) probability to be deleted or duplicated in resampled datasets. The SR support was calculated in TNT with 2000 pseudoreplicates, and in each pseudoreplicate conducting 10 RAS (random addition sequence) replicates, saving 100 trees per replicate. Instead of regular resampling frequencies commonly used with bootstrap or jackknife, the SR support was calculated as frequency differences ('CG' values; the difference in frequency between a group and the most frequent contradictory group). This approach gives more accurate measures for groups with low support (Goloboff et al., 2003b).

Bayesian inference (BI) of phylogeny with posterior probabilities (PP) was conducted with MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The models of molecular evolution were selected using the Akaike Information Criterion (AIC) as implemented in MrModelTest v.2.2 (Nylander, 2004). The chosen models were GTR+G for *matK* and HKY+G for *gpd* (also the hierarchical likelihood ratio tests resulted in the same models). The standard morphology model, allowing

gamma-distributed rates across characters, was used for the qualitative morphological data (with coding option 'informative'), and restriction site (binary) model for the indel data (with coding option 'variable'). The default MrBayes priors were used for all parameters, and two simultaneous runs were done, having 3–11 heated chains and 1 cold chain. The heating temperature was optimized to make the acceptance rates of chain swaps to be between 0.1 and 0.7; temperature values T used ranged from 0.01 to 0.02. Analyses were run until average standard deviation of split frequencies reached 0.01, indicating the convergence of two runs. The plot of generation vs. log probability was also inspected to ensure that stationarity was reached, and to determine the burn-in. The number of generations run ranged between 500,000–10,000,000 and c. 10–20% of the samples were discarded as burn-in.

Phylogenetic analyses were first conducted separately for three qualitative datasets (*matK*, *gpd* and morphology), and these results screened for hard incongruences (the cutoff limit for hard incongruences was here set to SR 60) before combined analyses of qualitative data. In the last phase, the quantitative morphological characters, either discretized with gap weighting method (Thiele, 1993), or coded 'as such' in TNT (Goloboff et al., 2006) were analyzed together with qualitative data.

Because the taxon sample for molecular data was much smaller than for morphological data (see above), two sets of analyses were run for combined datasets of molecular and morphological data: a first one with *reduced taxon sampling*, i.e., only including taxa with both molecular and morphological data, and a second one with *full taxon sampling*, i.e., including all possible taxa, but simultaneously introducing large amounts of missing data for the taxa sampled for morphology only.

The tracing of character evolution was performed with MacClade v.4.08 (Maddison & Maddison, 2001). For this purpose, all of the most parsimonious trees from the combined analyses including quantitative data (using both gap weighing and 'as such' methods) and with *full taxon sampling*, were examined. While examining the synapomorphies for the clades, only unambiguous character changes were taken into account.

RESULTS

DNA sequence characteristics and indel characters—Due to the difficulties in amplifying and sequencing *matK* and *gpd* from herbarium material, even when using internal primers for shorter fragments, only part of these sequences could be obtained for several taxa. For the 58 *matK* sequences acquired, 38 were sequenced completely, and the rest had c. 10–90% of missing data. Similarly, for the 55 *gpd* sequences, 38 were sequenced completely, and the rest had c. 25–60% of missing data (see Appendix 5.1 for details). Additionally, three species sequenced for *gpd* were completely missing from the *matK* dataset, and five species sequenced for *matK* were completely missing for *gpd*. The preliminary analyses of the separate *matK*, and *gpd* datasets, as well as of the *reduced taxon sampling* datasets of combined data, revealed that some of the taxa with incomplete sequences had unsure placements, causing reduced resolution and/or support values (result not shown). These taxa were excluded from the final analyses of the above-mentioned datasets.

MatK alignment provided in total 2229 nucleotide characters, from which eight were excluded as ambiguously alignable, and 238 as primer site characters (including the internal primer sites, which provided virtually no informative characters in *Mallotus*). *Gpd* alignment provided in total 724 nucleotide characters, from which eight were excluded as ambiguously alignable, and 92 as primer site characters (as in *matK*). The number of informative nucleotide characters was 144 (7.3%) for *matK*, and 137 (22.0%) for *gpd*.

The gaps in *matK* (1–25 bp in length) occurred mostly in the non-coding intron region flanking the *matK* gene, although six gaps of six bp in length were found in the *matK* coding sequence. All the gaps in *gpd* (1–29 bp in length) were located in introns. The SIC coding of indels resulted in 41 and 51 characters, of which 13 and 18 were informative (for *matK* and *gpd*, respectively). These indel characters were included in all the phylogenetic analyses. The analyses without indel characters (not shown) resulted in trees highly similar to the ones presented here. The sequence alignments are available from the authors.

Intraspecific and infra-individual polymorphisms—Two separate accessions were sequenced for four (*matK*) or five (*gpd*) *Mallotus* species. Because the acquired sequences were highly similar and were placed together in the preliminary analyses (not shown), only one of them was chosen to represent the species in the subsequent analyses. The sequence chromatograms were also screened for overlapping nucleotide peaks, which possibly indicate infra-individual polymorphisms. For *matK* no such polymorphisms were found, and for *gpd* their amount was relatively low (0–12 per sequence, on average 0.5 per sequence). The *gpd* clones sequenced for five species (3–4 clones per specimen) formed clades in the preliminary analyses (not shown), suggesting that the infra-individual variation in *gpd* will hardly, if at all, confound the phylogenetic results.

Separate analysis of matK and gpd datasets—Both *matK* and *gpd* analyses resulted in a supported *Mallotus* clade. Two outgroup clades, *Cordemoya* and *Macaranga*, also have strong support, the latter being sister to *Mallotus*.

MP analysis of *matK* data resulted in 120 most parsimonious trees (MPTs). MP and BI trees inferred from *matK* data are in most part congruent (Fig. 5.2), although BI resulted in a somewhat more resolved tree. The main difference is in the basal relationships in *Mallotus*: MP results show a large basal polytomy in *Mallotus*, whereas BI revealed the clade of sect. *Mallotus*, *M. philippensis* and *M. repandus* to be sister to the rest of the genus. The results of both analyses are relatively polytomous and show only few additional larger clades, which have no strong BS or PP support.

MP analysis of *gpd* data resulted in 3570 MPTs. Also the *gpd* data resulted in similar and mostly congruent trees when analyzed with MP and BI (Fig 5.3). In the results of both analyses *M. polyadenos* and *M. muticus* are sister to the rest of *Mallotus*.

Separate analysis of qualitative morphological dataset—The MP consensus (from 10,000 MPTs) resulting from qualitative morphological data and *full taxon sampling* (Fig. 5.4) shows a large polytomy with all *Macaranga* (restricted to one clade) and

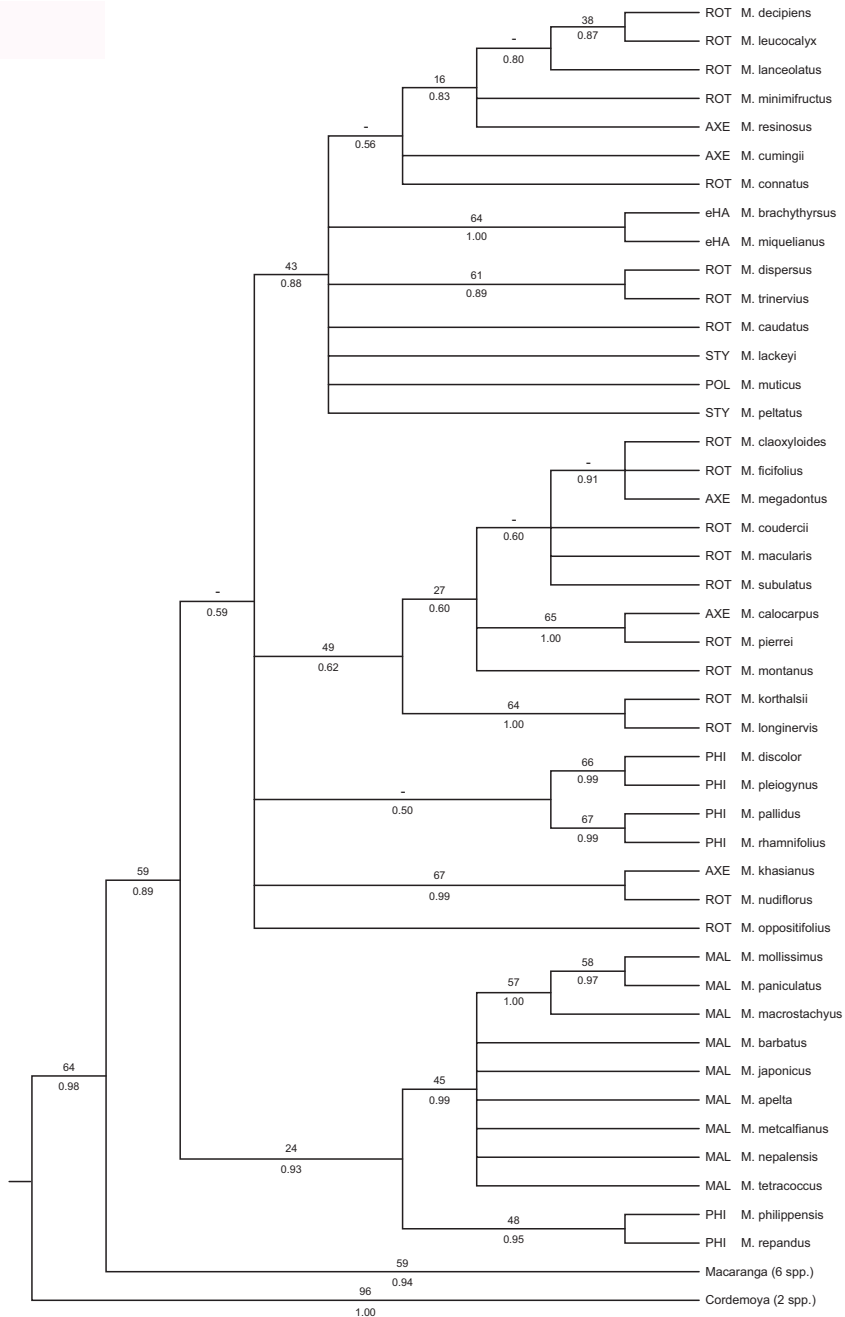


Fig. 5.2. Phylogenetic relationships of *Mallotus* inferred from *matK* data. A Bayesian majority consensus tree with posterior probabilities shown below the branches and parsimony symmetric resampling values above. Nodes that are not present in the parsimony strict consensus are indicated with the symbol '-'. *Mallotus* sections are indicated with three letter abbreviations.

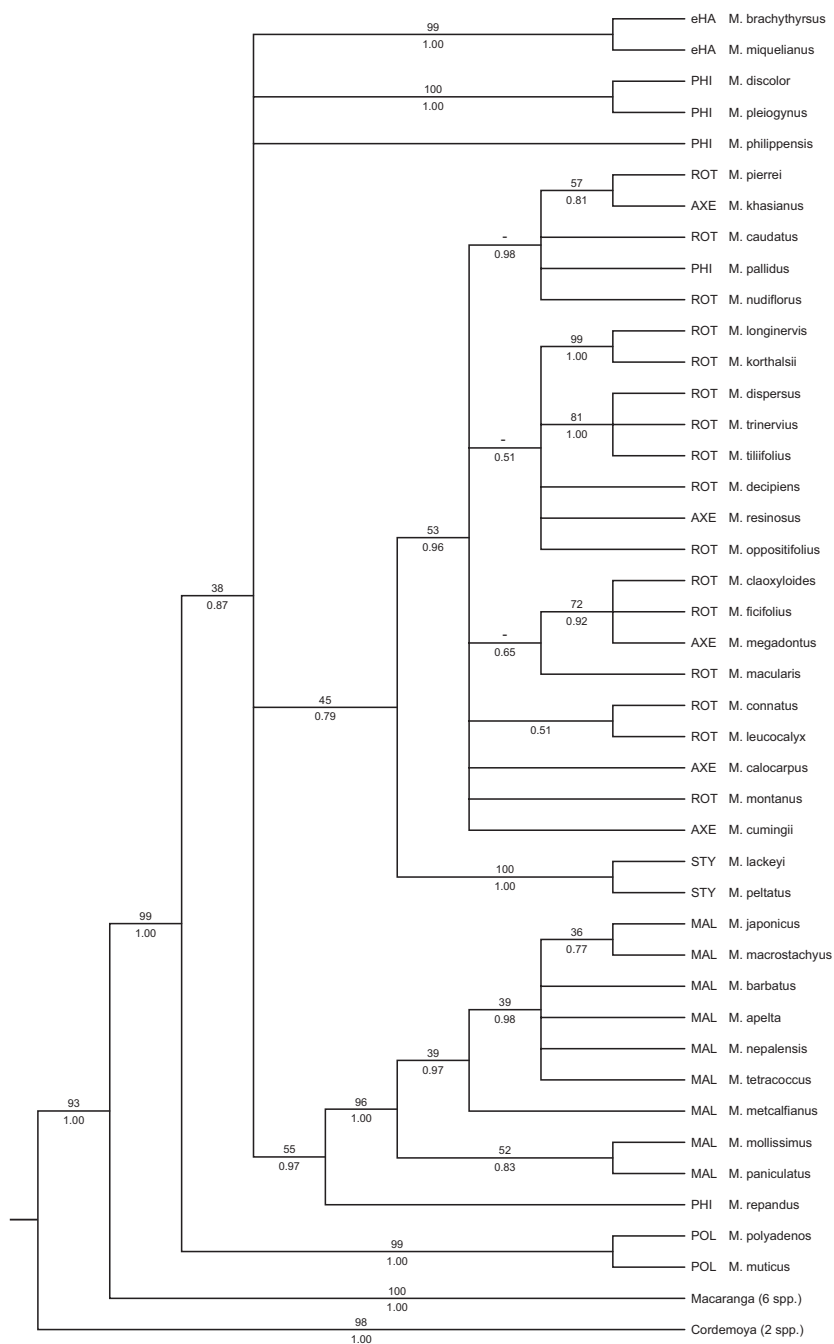


Fig. 5.3. Phylogenetic relationships of *Mallotus* inferred from *gpd* data. A Bayesian majority consensus tree with posterior probabilities shown below the branches and parsimony symmetric resampling values above. Nodes that are not present in the parsimony strict consensus are indicated with the symbol '-'. *Mallotus* sections are indicated with three letter abbreviations.

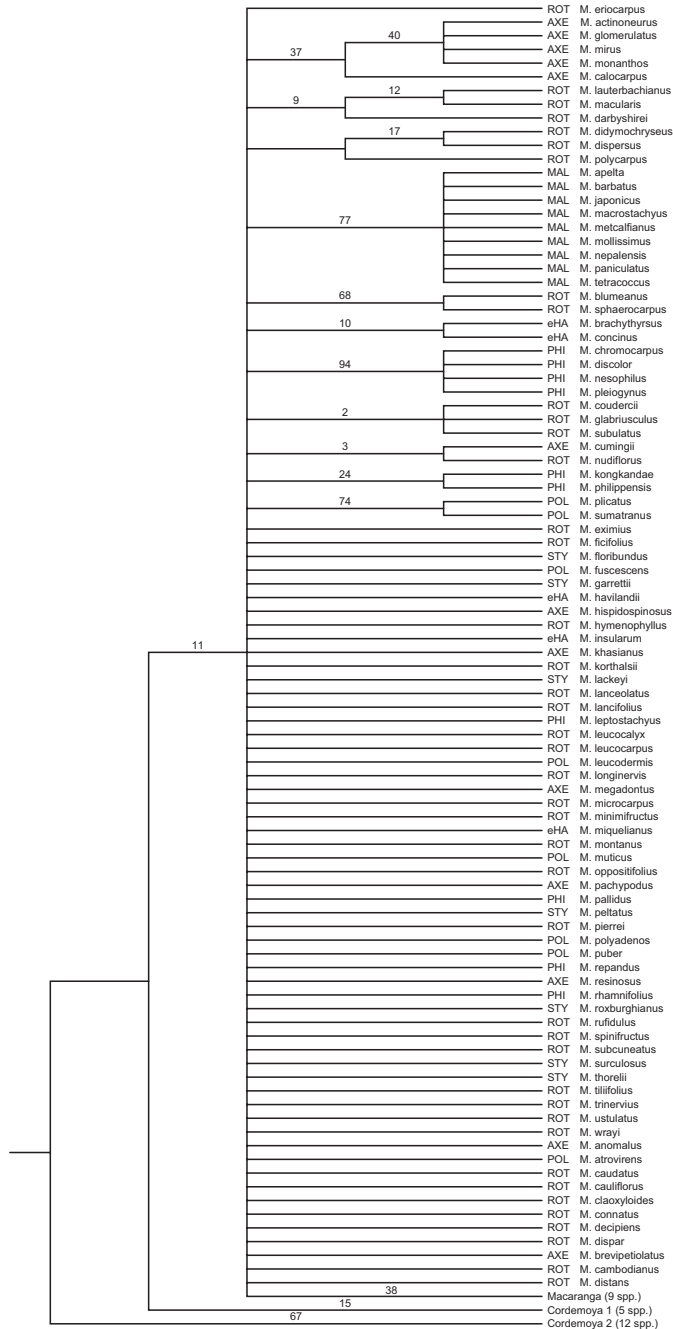


Fig. 5.4. Phylogenetic relationships of *Mallotus* inferred from qualitative morphological and leaf anatomical data. Parsimony strict consensus with symmetric resampling values above the branches. *Mallotus* sections are indicated with three letter abbreviations.

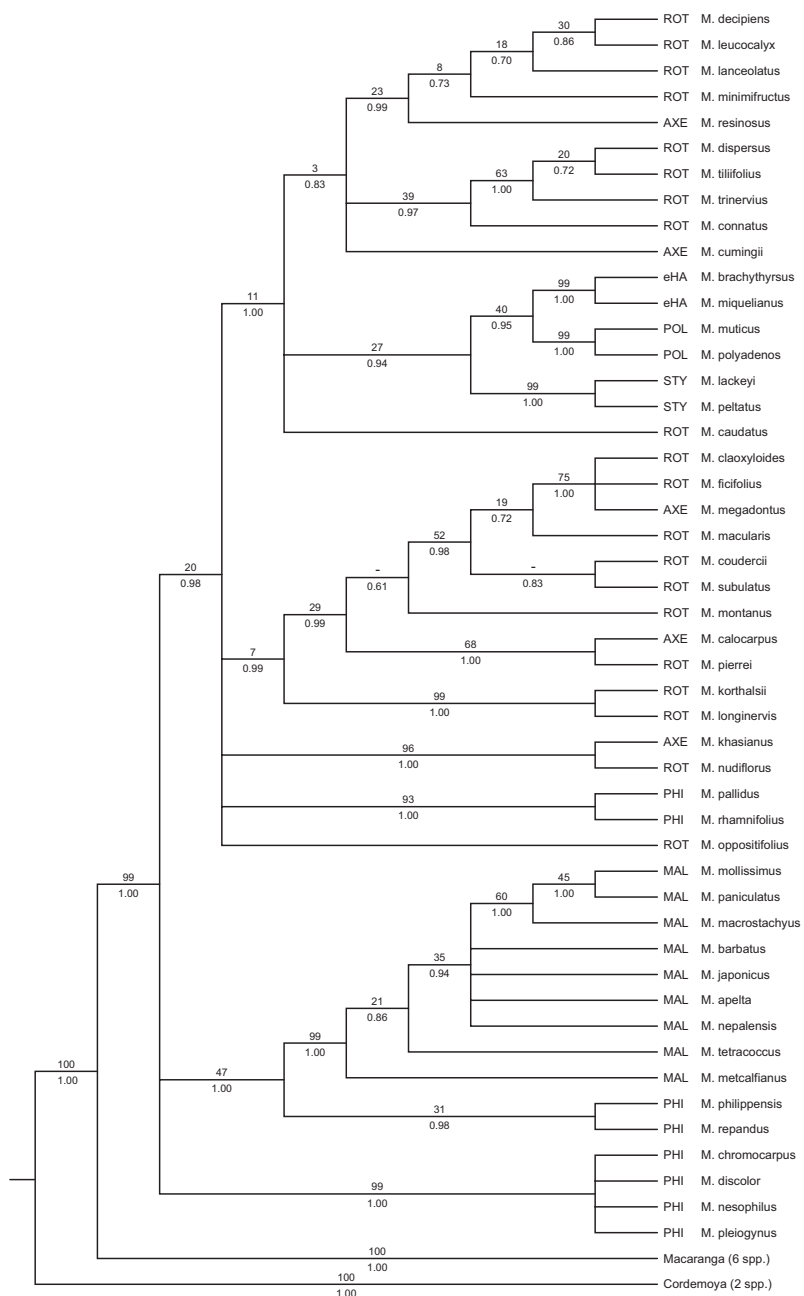


Fig. 5.5. Phylogenetic relationships of *Mallotus* inferred from the combined analysis of *matK*, *gpd*, and qualitative morphological and leaf anatomical data. Reduced taxon sampling. A Bayesian majority consensus tree with posterior probabilities shown below the branches and parsimony symmetric resampling values above. '-': node is not present parsimony strict consensus. *Mallotus* sections are indicated with three letter abbreviations.

Mallotus species. Only few clades in *Mallotus* are present. The analyses with *reduced taxon sampling*, either using MP or BI (trees not shown), did not result in more resolved or supported trees.

Combined analyses of qualitative data—As no hard incongruences were detected between *matK*, *gpd* and qualitative morphological datasets, combined analyses of *matK+gpd* and *matK+gpd+morphology* were conducted. Combining the two molecular datasets (not shown) resulted in a large basal polytomy, and no new supported clades. Combining molecular and qualitative morphological data resulted in increased resolution and support. In MP analysis with *full taxon sampling* (not shown) a large *Mallotus* polytomy is present, whereas with *reduced taxon sampling* (Fig. 5.5) more resolution and support are present. MP analysis of this dataset resulted in 747 MPTs. The BI analysis with *reduced taxon sampling* is mostly congruent with the MP analysis, but more resolved. The only notable clade present in the MP tree but not in the BI tree is the one with sect. *Mallotus*, *M. philippinenses*, *M. repandus*, and the four species similar to *M. pleiogynus* (SR 54).

Combined analyses including quantitative data—The results from the combined MP analyses with quantitative data and *full taxon sampling* are given in Figs. 5.6 (gap weighting; from 3 MPTs) and 7.7 ('as such' analysis; from 3 MPTs). These trees are highly resolved, but many clades are not or only poorly supported. The analyses of *reduced taxon sampling* are given in Figs. 5.8 and 5.9. The changes in the SR support in these trees, compared to the analyses of the same data without quantitative data are as follows (taking into account only the clades with were present in both trees of comparison): In the gap weighting analysis SR increased in 19 clades, remained the same in eight clades, and decreased in nine clades. In the 'as such' analysis SR increased in 20 clades, remained the same in seven clades, and decreased in five clades.

DISCUSSION

Measures of support—As our analyses included differential weighting of qualitative and quantitative data, the MP support was calculated using symmetric resampling (SR), a method avoiding the distortions in bootstrap and jackknife values caused by non-equal weights (Goloboff et al., 2003b). Moreover, our support values are not given as actual resampling frequencies, but as frequency differences ('GC') between the group and the most frequent contradictory group. This approach gives better measures for groups with low support (Goloboff et al., 2003b; but see also their example on p. 330 where frequency differences can be misleading).

When comparing the support levels in our results with studies employing the widely used PAUP* bootstrap implementation, two issues must be kept in mind. First, the results from each resampling replicate are assessed differently in PAUP* and TNT: in PAUP with 'frequency-within-replicates' (FWR) and in TNT with 'strict-consensus' (SC) approach (Soreng & Davis, 1998). The latter approach is also used in the program NONA (Goloboff, 1999b). FWR has been shown to yield, both in bootstrap and jackknife analyses, consistently higher support values than SC (Davis et al., 2004). Furthermore,

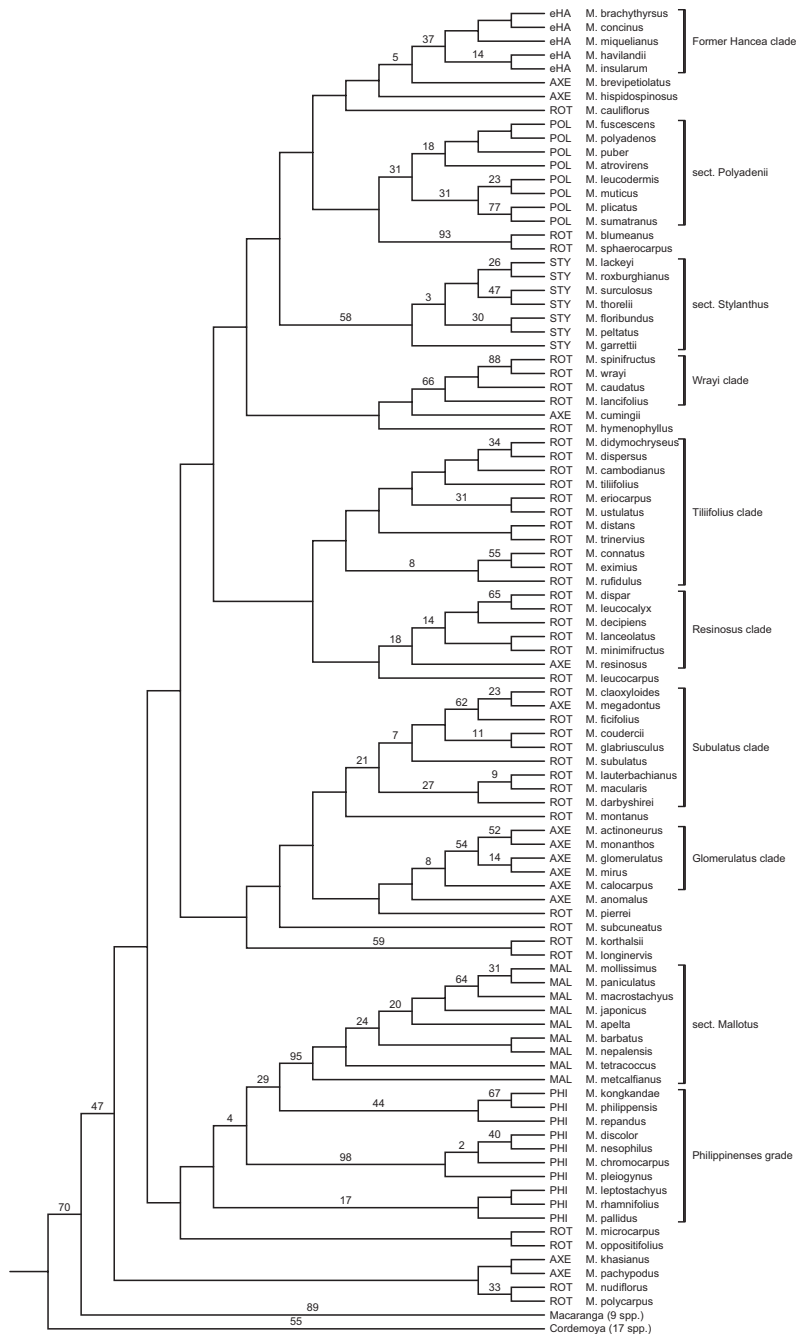


Fig. 5.6. Phylogenetic relationships of *Mallotus* inferred from the combined analysis of *matK*, *gpd*, qualitative and quantitative morphological and leaf anatomical data. Full taxon sampling, quantitative data analyzed with gap weighting method. A parsimony strict consensus with symmetric resampling values shown above the branches. *Mallotus* sections are indicated with three letter abbreviations.

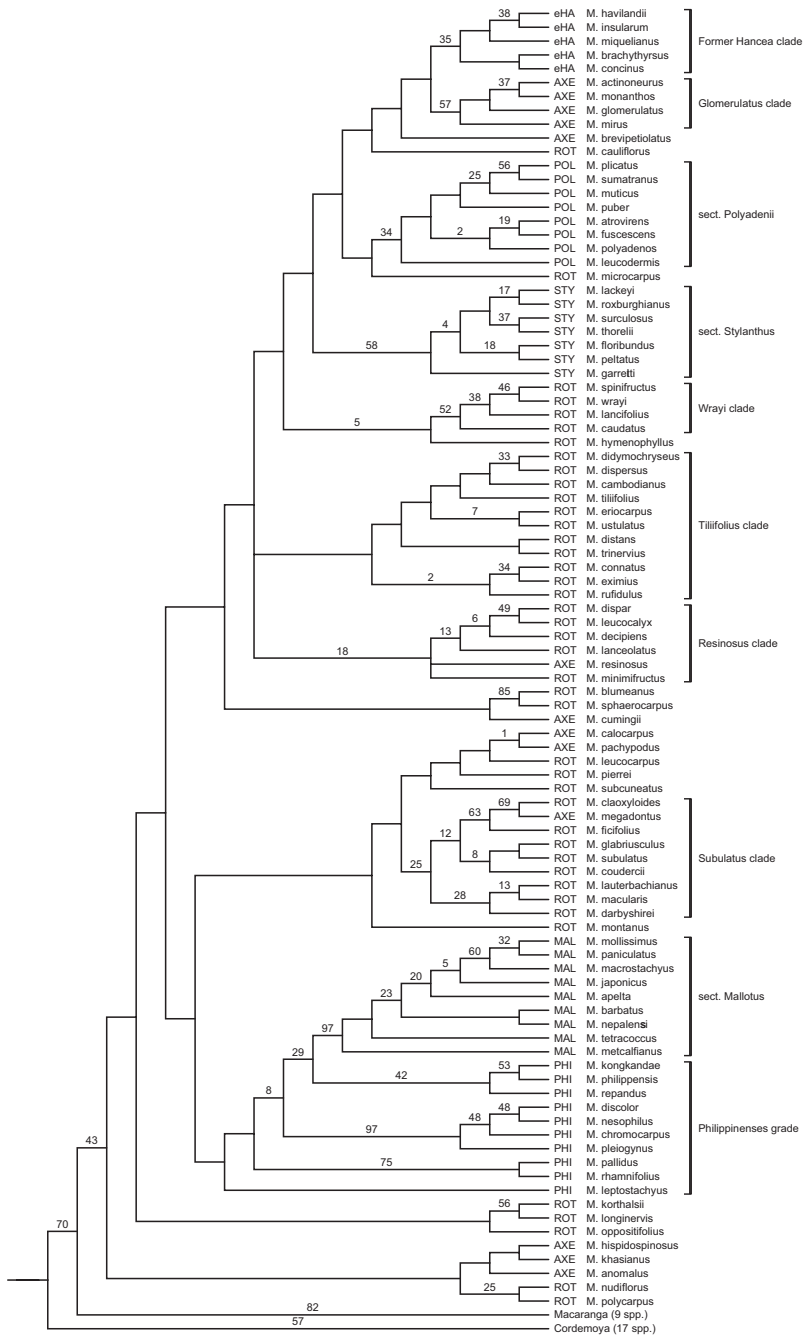


Fig. 5.7. Phylogenetic relationships of *Mallotus* inferred from the combined analysis of *matK*, *gpd*, qualitative and quantitative morphological and leaf anatomical data. Full taxon sampling, quantitative data analyzed with 'as such' method in TNT. A parsimony strict consensus with symmetric resampling values shown above the branches. *Mallotus* sections are indicated with three letter abbreviations.

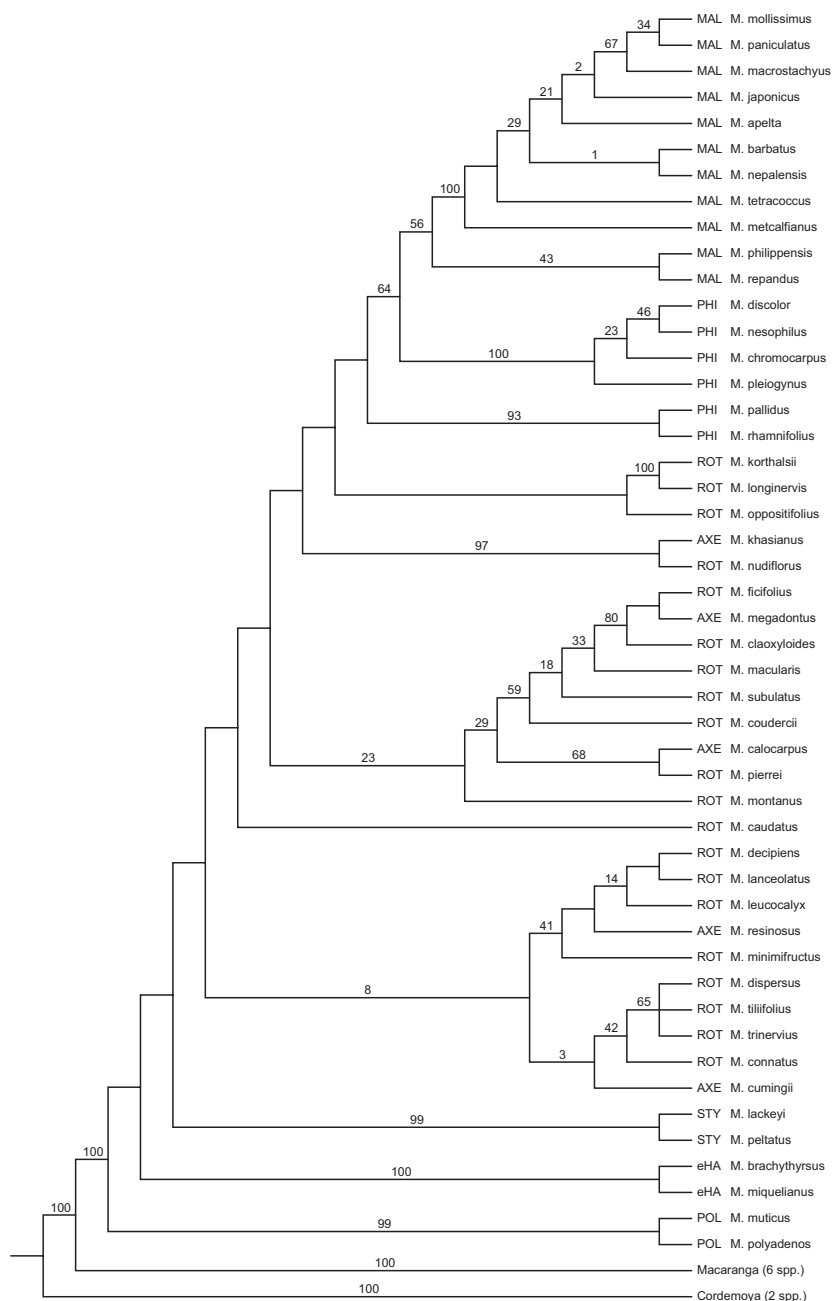


Fig. 5.8. Phylogenetic relationships of *Mallotus* inferred from the combined analysis of *matK*, *gpd*, qualitative and quantitative morphological and leaf anatomical data. Reduced taxon sampling, quantitative data analyzed with gap weighting method. A parsimony strict consensus with symmetric resampling values shown above the branches. *Mallotus* sections are indicated with three letter abbreviations.

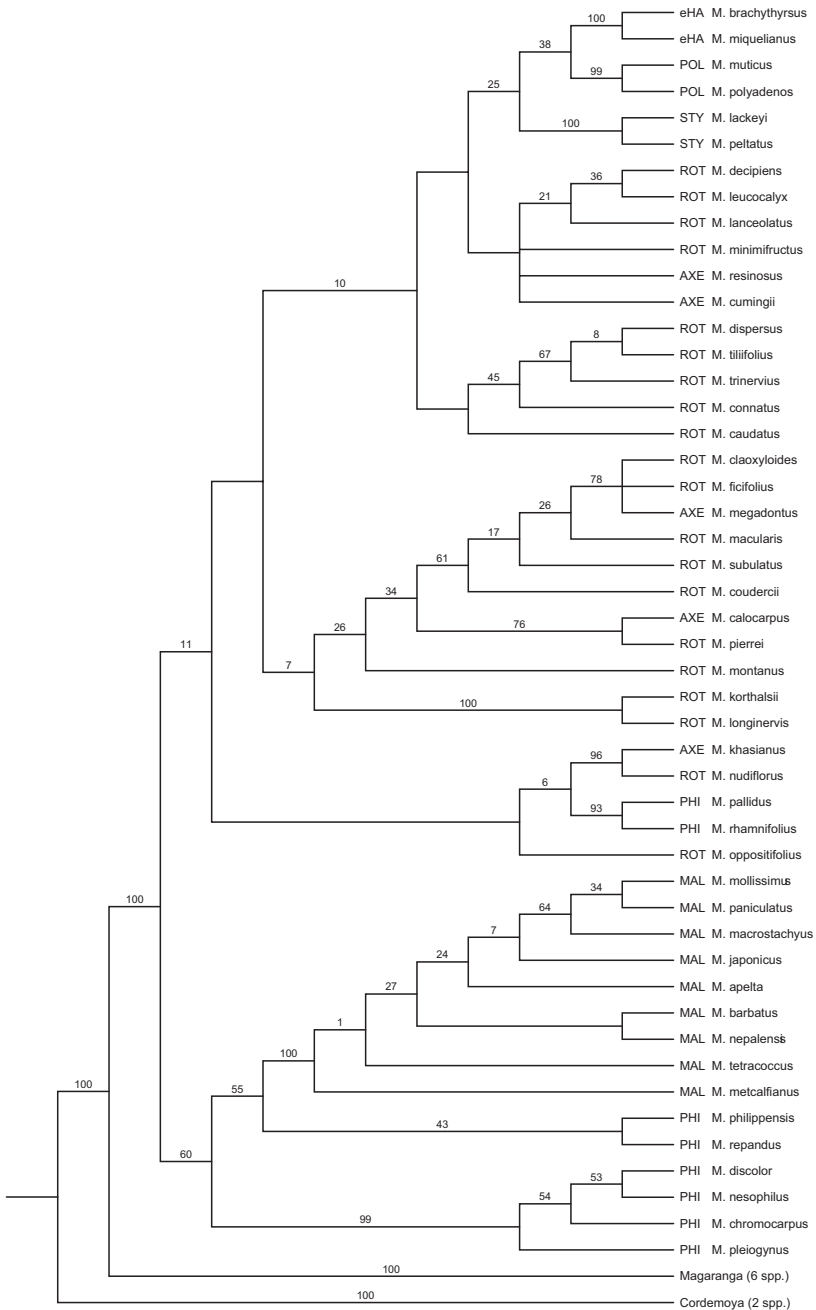


Fig. 5.9. Phylogenetic relationships of *Mallotus* inferred from the combined analysis of *matK*, *gpd*, qualitative and quantitative morphological and leaf anatomical data. Reduced taxon sampling, quantitative data analyzed with 'as such' method in TNT. A parsimony strict consensus with symmetric resampling values shown above the branches. *Mallotus* sections are indicated with three letter abbreviations.

FWR has been criticized, because it can give high support values for groups actually not supported by the data (De Laet et al., 2004; Goloboff & Pol, 2005). Bootstrap with FWR has so far remained, nevertheless, the most widely used measure of support, perhaps because of the popularity of the PAUP* software. Second, the frequency differences tend to be lower than the conventional resampling frequencies, because any contradicting group decreases the value. Therefore, the frequency differences cannot be directly compared to the frequencies.

The conventional cut-off limit has been 50% when showing bootstrap and jackknife frequencies on a phylogenetic tree. Because symmetric resampling values given as frequency differences can measure low support levels in a more meaningful way (Goloboff et al., 2003b), we chose to show also SR values lower than 50. As conventional bootstrap (and to some extent also jackknife) frequencies are currently the standard way to measure support in MP and ML frameworks, studies comparing them with the methods of Goloboff et al. (2003b) are highly needed.

In addition to MP SR, we measured the support with posterior probabilities (PP) in the Bayesian analysis context (BI). Although the topologies of MP and BI analyses were largely congruent, clear differences can be seen between SR and PP values. Many nodes highly supported by PP (i.e., ≥ 0.95) receive low SR values (ranging from 7 to 100). Posterior probabilities are generally higher than resampling (e.g., bootstrap) support values (Rannala & Yang, 1996) and they have been criticized on several grounds (Suzuki et al., 2002; Alfaro et al., 2003; Douady et al., 2003; Simmons et al., 2004). Moreover, the uniform topological priors used in Bayesian analysis can distort the posterior probabilities (Pickett & Randle, 2005), and analyses including taxa with unsure placement (e.g., due to missing data) can result in high posterior probabilities for unsupported nodes (Goloboff & Pol, 2005). The latter problem might be relevant in our study, because our datasets have a relatively high amount of missing data for some taxa. All these problems cast doubt on the validity of posterior probabilities as measures of support.

Dataset congruence, combined analyses and the missing data—The results of separate analyses based on *matK*, *gpd* and qualitative morphological data (Figs. 5.1–5.3) show no hard incongruences (as measured with MP SR); the datasets were thus combined. Combining the two molecular datasets (tree not shown) resulted in a big *Mallotus* polytomy and hardly any additional resolved clades. On the other hand, combined analyses of all three qualitative datasets (Fig. 5.5) show more resolution and in many cases also increased support, indicating the presence of a complementary phylogenetic signal in molecular and morphological datasets. For the clades having soft incongruences (SR < 60) between *matK* and *gpd*, however, combining the datasets resulted in decreased support.

The effects of missing data in phylogenetic analysis have been subject to considerable discussion. Wiens (2003) showed, contrary to popular belief, that large amounts of missing data are not by themselves necessarily a problem, but that the adverse effects (e.g., loss of resolution and support) arise when a taxon does not have characters to place it (confidently) in the tree (regardless of whether this taxon has a lot of missing data or not). We could see the behaviour observed in the simulations of Wiens (2003)

in our data as well: including some taxa with missing data decreased the resolution greatly, whereas others with a similar amount of missing data caused no adverse effects.

When combined analyses of all qualitative data were conducted with *full taxon sampling*, most of the support values in the resulting trees went drastically down (tree not shown), compared to the analyses of same data with *reduced taxon sampling* (the same can be seen when comparing *full* and *reduced taxon sampling* in the analyses including quantitative data; see below). A probable cause for this is the large amount of missing data introduced for the taxa lacking the molecular data completely (c. half of the complete taxon sample). The decrease in support is understandable, because our qualitative morphological data does not have a strong phylogenetic signal. There are thus very few characters supporting the placement of taxa without molecular data, and even some characters contradicting the signal present in the molecular data.

Effect of adding the quantitative data— Adding quantitative data to combined qualitative datasets, either treated with gap weighting (Thiele, 1993) or analyzed ‘as such’ with TNT (Goloboff et al., 2006), had a clear impact on the results. The MP trees from the analyses of combined qualitative data show several polytomies in *Mallotus* (Fig. 5.5), whereas the analyses including quantitative data resulted in almost completely resolved trees, both with *reduced taxon sampling* (Figs. 5.8 & 5.9) and *full taxon sampling* (Figs. 5.6 & 5.7). Furthermore, adding quantitative data to the *reduced taxon sampling* dataset increased the SR values more often than that it decreased them, indicating that in our case quantitative data contain phylogenetic information compatible with that of the qualitative data. This increase in the support values agrees with previous theoretical and empirical results stating that quantitative data are not fundamentally flawed but can be used to complement qualitative datasets (Thiele, 1993; Goloboff et al., 2006; Lehtonen, 2006).

However, although the results from gap weighting and ‘as such’ analyses share several clades with morphological synapomorphies (discussed in detail below), the (unsupported) higher-level relationships between these clades and the position of several taxa differ notably between these two coding methods (compare Figs. 5.6 & 5.7). This could be due to the different ways in which these methods treat the variability in quantitative data (i.e., the ranges in measurements): in gap weighting they are only used to calculate the means to be ranked, discarding the information about possible overlap, whereas in ‘as such’ analyses the ranges are directly taken into account as polymorphisms. Additionally, our quantitative data were recorded in a suboptimal way, i.e., only the ranges given in the descriptions were available. This can affect the methods in different ways, because in gap weighting only a crude estimate of the mean could be calculated, possibly affecting the ranking and transformation costs between the character states, whereas in ‘as such’ analyses no standard error of mean could be calculated (to be used as a way to assign costs only for statistically significant transformations). Further studies with properly sampled measurements are thus needed for comparisons of gap weighting and ‘as such’ analysis of quantitative data.

Evolutionary relationship in the *Mallotus* clade—Although our study revealed several relatively small clades, which are stable in different kinds of analyses and often also supported by SR, the constituents of bigger clades and the higher-level relationships in *Mallotus* s.s. are still ambiguous. This is manifested either by large basal polytomies or highly resolved, but unsupported backbones (especially in the analyses with quantitative data; e.g. Figs. 5.6 and 5.7) in *Mallotus*. The instability of these relationships is demonstrated by the fact that small changes in the matrix (e.g. deleting a few taxa or changing the coding of one or a few characters) could result in drastic changes in the phylogeny. Also, in the analyses including the quantitative data, the higher-level relationships inferred with *full taxon sampling* and *reduced taxon sampling* are clearly different as well (compare Figs. 5.6 & 5.7 with Figs. 5.8 & 5.9).

Similar results with an essentially unresolved *Mallotus* backbone were obtained earlier with four DNA markers and lower taxon sampling (only 31 *Mallotus* s.s. species; Kulju et al., in press, Chapter 2). Despite highly increased taxon sampling and analyzing two new DNA sequence markers together with morphology, the phylogeny of the *Mallotus* clade still remains largely unresolved.

In the phylogeny of Kulju et al. (in press, Chapter 2) *M. khasianus* and *M. nudiflorus* form a basal clade (i.e., sister to the rest of *Mallotus*), although this relationship is supported only by BI, and not by MP or ML (maximum likelihood). In our *full taxon sampling* analyses with quantitative data (Figs. 5.6 & 5.7) a similar result can be seen, although few other, previously unsampled, species also fall into the basal clade with *M. khasianus* and *M. nudiflorus* (in gap weighting *M. pachypodus* and *M. polycarpus*; in ‘as such’ analysis *M. anomalus*, *M. hispidospinosus* and *M. polycarpus*). On the other hand, this result is not congruent with the relationships shown by the combined analyses of qualitative data (both with *full* and *reduced taxon sampling*; Fig. 5.5), and neither with the results from *reduced taxon sampling* analyses with quantitative data (Figs. 5.8 & 5.9). Therefore, no consensus was thus reached in this matter.

Despite the partly non-supported and unstable phylogenies produced, several stable and sometimes also supported clades could be identified, and morphological synapomorphies for them could be found as well. Some of these clades correspond to certain *Mallotus* sections as defined by Airy Shaw (1968) or to informally recognized species groups, but part of them are novel groupings. These clades and the monophyly of *Mallotus* sections are discussed below; in these paragraphs we are mostly referring to the results of *full taxon sampling* analyses with quantitative data included (Figs. 5.6 & 5.7), because these trees were most resolved. Moreover, these clades are not contradicted by our other analyses (with the exception of the basal grade in the combined gap weighting analysis with *reduced taxon sampling*, see Fig 5.8). However, in our analyses the taxon sampling is incomplete in continental Asia, and adding these taxa might change the results obtained. The symmetric resampling support values in the text below are reported as ‘SR XX/XX’, where the first value is from analysis with the gap weighting method and the second one from analysis with the ‘as such’ method in TNT.

Monophyly of the *Mallotus* sections—According to our results, three of the six sections of Airy Shaw (1968) belonging to the *Mallotus* s.s., are monophyletic: *Mallotus*, *Polyadenii* and *Stylanthus*. On the other hand, sections *Axenfeldia* and *Rottleropsis* are polyphyletic (and *Rottleropsis* s.l. is paraphyletic), and section *Philippinenses* is paraphyletic.

Sections Mallotus and Philippinenses—Both morphological (Slik & Van Welzen, 2001a) and molecular (Kulju et al., in press, Chapter 2) phylogenies suggested that sect. *Mallotus* is monophyletic, although only few of its species were included in these studies. Our results confirm the monophyly of the section (SR 95/96). High support is given for sect. *Mallotus* in all of our other analyses as well. In the classification by Airy Shaw (1968) sect. *Mallotus* was recognized based on the presence of alternate leaves, tripli- or palminerved leaf venation and spiny fruits. Our results indicate that six morphological or anatomical synapomorphies support sect. *Mallotus* (9 spp. sampled out of c. 11), among them are the presence of paniculate inflorescences, pistillodes, spiny fruits, cork warts, stellate hairs, and the absence of tufted hairs. Section *Mallotus* has a wide distribution from India to Australia and New Guinea.

Previous studies suggested that section *Philippinenses* is paraphyletic (Slik & Van Welzen, 2001a) or polyphyletic (Kulju et al., in press, Chapter 2). Our results show that section *Philippinenses* (former sect. *Rottlera*, 10 spp. sampled out of 11) is indeed not monophyletic, and suggest that it is related to sect. *Mallotus*. Section *Philippinenses* was circumscribed by Airy Shaw (1968) based on the presence of alternate leaves with triplinerved venation, and unarmed fruits; it occurs from Pakistan to Southeast Asia and New Caledonia. However, the section, as circumscribed with these characters, is morphologically rather heterogeneous. Three species from New Guinea or Australia (*M. chromocarpus*, *M. nesophilus*, and *M. discolor*) differ from other species in sect. *Philippinenses* by characters shared with *M. pleiogynus* (formerly known as *Octospermum pleiogynum*): stipules absent, extrafloral nectaries prominent with raised margins, anther connectives conspicuously broadened (umbrella-like), and fruits indehiscent. Based on this evidence, and dealing with Malesian taxa only, Sierra et al. (2005) excluded the New Guinean species *M. chromocarpus* from sect. *Philippinenses*.

In the results (Figs. 5.6 & 5.7) of the combined analyses with quantitative data, sect. *Philippinenses* of Airy Shaw (1968), together with *M. pleiogynus*, is a paraphyletic group, because it forms a grade leading to sect. *Mallotus*. Moreover, *Mallotus pleiogynus* and the three *Philippinenses* species similar to it form a strongly supported clade (SR 98/97) with the above-mentioned synapomorphies, located in the middle of the *Philippinenses* grade. This clade is, therefore, innately part of Airy Shaw's sect. *Philippinenses*, and excluding it (as implied by Sierra et al., 2005) renders the section polyphyletic.

There was no SR support for the clade of both sections *Mallotus* and *Philippinenses*, and furthermore, in the analyses without quantitative data, the most basal taxa of the above-mentioned *Philippinenses* grade (*M. pallidus*, *M. rhamnifolius* and *M. leptostachyus*; the last one not present in the *reduced taxon sample*) are either placed away from the rest of sect. *Philippinenses* (Fig. 5.5) or are a part of a large basal polytomy. However, the clade of sect. *Mallotus* and three *Philippinenses* species (*M. philippensis*, *M. repandus* and *M. kongandae*; the latter not present in the *reduced taxon sample*; SR 29/29) is supported by morphological synapomorphies, i.e., stomata on adaxial leaf surface, absence of outer cuticular ledges, enlarged terminal vein tracheids) in all combined analyses. Also the grouping of this clade together with the *M. pleiogynus* and allies is supported (SR only 4/8 with *full taxon sampling*, but SR 60/64 with *reduced taxon sampling*) and has as synapomorphy the absence of simple hairs (polymorphic in some species). Additionally, most of the members of this clade have a local hypodermis.

In the clade of sect. *Mallotus* and (most of the) sect. *Philippenses* an interesting transformation in the character of fruit opening sequence can be noted. In most *Mallotus* species fruits open septicidally-loculicidally. This plesiomorphic condition is present also in the three *Philippinenses* species basal/unrelated to the rest of the section. In the clade of *M. pleiogynus* and allies fruits are indehiscent. In the clade of sect. *Mallotus* and three *Philippinenses* species, however, the opening sequence is reversed to be loculicidal-septicidal, a condition additionally present only in two species (*Cordemoya subpeltata* and *M. leucocarpus*) unrelated to this clade. As opposed to the septicidally-loculicidally opening fruits, in which the seeds generally fall down with dehiscing fruit wall fragments, in the loculicidally-septicidally opening fruits the seeds stay attached to the column after dehiscence. This might have an effect on the mode and efficiency of seed dispersal. The septicidally-loculicidally opening fruits facilitate mainly mechanical seed dispersal through explosive dehiscence (or perhaps epizoochory when fruits are spiny), whereas in the loculicidally-septicidally opening fruits the seeds stay attached in the infructescence and are readily available for bird dispersal. The thin aril-like fleshy layer surrounding the seeds of several species in sect. *Mallotus* and in *M. leucocarpus* (as well with loculicidal-septicidal fruits) support the bird dispersal hypothesis as well. The seed dispersal in *Mallotus* has not been studied extensively, but birds have been observed to disperse the seeds of *M. japonicus* in Japan (sect. *Mallotus*; Sato & Sakai, 2005), and of *M. paniculatus* (sect. *Mallotus*) and *M. philippensis* (sect. *Philippinenses*) in Thailand (Kitamura et al., 2005). All these species belong to the clade with loculicidal-septicidal fruits. The species of sect. *Mallotus* are wide-spread and abundant in secondary vegetation. The bird dispersal might facilitate the swift dispersal needed to colonize disturbed habitats efficiently, and therefore, could perhaps explain the success of sect. *Mallotus* in secondary vegetation.

Section Polyadenii—The phylogenies by Slik & Van Welzen (2001a) and by Kulju et al. (in press, Chapter 2) suggest that sect. *Polyadenii* is monophyletic. Our results confirm this, however with rather low SR (31/34). Sect. *Polyadenii* (all 8 spp. sampled; the section occurring from India to New Guinea and Australia) was circumscribed by Airy Shaw (1968) based on the presence of mostly alternate leaves, presence of glandular hairs on the upper surface of the leaf blade, triplinerved or rarely pinnate leaves and absence of spiny fruits. Two synapomorphies support sect. *Polyadenii*: domatia on the lower surface of the leaf blade and stomata concentrated under the glandular hairs. The latter is only present in two species outside sect. *Polyadenii*, *M. resinus* and *M. decipiens*. Two species in sect. *Polyadenii*, *M. plicatus* and *M. sumatranus*, are grouped together with high SR support. Their shared synapomorphy, the presence of wings in partly indehiscent fruits, might be a adaptation for wind dispersal.

Section Stylanthus—The phylogeny by Kulju et al. (in press, Chapter 2) suggested that sect. *Stylanthus* is monophyletic. Our results confirm this with SR 56/57. Section *Stylanthus* (all 7 spp. sampled; from India to New Guinea and the Solomon Islands) was circumscribed by Airy Shaw (1968) based on the presence of alternate to sometimes apically pseudo-opposite leaves, often presence of glandular hairs on the upper surface of leaf blade, tripli- or palminerved to rarely pinnate leaves, fenugreek smell of dried leaves, and the presence of spiny fruits. In our results sect. *Stylanthus* is supported by the presence of alternate leaves and the fenugreek smell in dried plants.

Sections Axenfeldia and Rottleropsis (= *Rottleropsis* s.l.)—The species (54 spp. sampled out of c. 68) of sect. *Axenfeldia* and *Rottleropsis* occur from India to Southeast Asia and the West Pacific. The circumscriptions of sections *Axenfeldia* and *Rottleropsis*, as proposed by Airy Shaw (1968; 1972), were based on the presence of opposite leaves. The main difference between the sections is in the leaf venation: pinnate in *Axenfeldia* and tripli- or palminerved in *Rottleropsis*. Airy Shaw (1968) mentioned that these sections are not ‘sharply demarcated’. Phylogenetic analyses based on morphological (Slik & Van Welzen, 2001a) and molecular data (Kulju et al., in press, Chapter 2), suggested that both sections are polyphyletic (with species from both sections intermixed), and that the venation character is homoplastic. However, both phylogenies suffer from insufficient taxon sampling for the *Mallotus* clade (including both sections dealt with here), and from low support for the resulting clades. In the absence of supported clades, during the revisional work of these sections, Sierra et al. (2007) could not use the phylogenetic results to propose a new classification of sections *Axenfeldia* and *Rottleropsis*. In the absence of suitable morphological characters to distinguish them, Sierra et al. (2007) merged the two sections into one large section, *Rottleropsis* s.l., indicating that sect. *Rottleropsis* s.l. needs further subdivision once a phylogeny could provide supported clades. The results of our analyses confirm the findings of previous phylogenetic analysis, however with low support, indicating that sects. *Axenfeldia* and *Rottleropsis* of Airy Shaw are polyphyletic, and that sect. *Rottleropsis* s.l. is paraphyletic.

Additional new clades in *Mallotus* s.s.—*The clade of former sect. Hancea species and sections Polyadenii and Stylanthus*—The morphological phylogeny by Slik & Van Welzen (2001a) suggested that four species (*M. brachythyrus*, *M. havilandii*, *M. insularum*, and *M. miquelianus*), previously assigned to *Mallotus* sect. *Hancea*, should be included in sect. *Axenfeldia* and *Rottleropsis*. These species share the presence of anisophyllous leaf pairs which differ in shape, one is generally elliptic, the other stipule-like or more or less obcordate (Slik & Van Welzen, 2001b). Later, Van Welzen et al. (2006) added one additional species, *M. concinnus*, to this group of morphologically similar species.

In our results these five species formerly assigned to sect. *Hancea* form a clade supported by the presence of opposite leaves with the smaller leaf different in shape than the bigger one (SR 37/35). This synapomorphy is almost unique for this clade, and outside the clade it is only present in the central Malesian species *M. minimifructus*. The species of the former sect. *Hancea* clade are restricted to Peninsular Malaysia and Borneo, with the exception of *M. miquelianus*, which occurs from Peninsular Thailand to the Philippines.

Furthermore, our results suggest that this group is not part of *Axenfeldia* and *Rottleropsis*. Instead it forms a clade together with sections *Stylanthus* and *Polyadenii*, among other taxa (e.g., *M. cauliflorus* and *M. brevipetiolatus*). In the analysis of qualitative data with *reduced taxon sampling*, these three clades are grouped together as well (SR 27, Fig. 5.5). This clade is characterized by the synapomorphy of glandular hairs on the upper leaf surface. However, this character is not present in all the species of the clade (e.g., not in *M. blumeanus*, *M. sphaerocarpus*, *M. hispidospinosus*, *M. miquelianus*), and it occurs also outside the clade, but then usually as a polymorphic character.

Glomerulatus clade—This clade contains species from Thailand and Peninsular Malaysia. In the gap weighing tree the clade (SR 8) is composed of five species characterized by the unique synapomorphy of pistillate inflorescences reduced to glomerules. However, in the ‘as such analysis’, the clade does not include *M. calocarpus*. Without this species, both trees have a clade (SR 54/57) supported by the absence of glandular hairs. *Mallotus* usually has glandular hairs spread all over the plant (Sierra et al., 2006). Their absence is rare, only typical of few species in the *Glomerulatus* and *Subulatus* clades.

Subulatus clade—This clade of ten species has a remarkably wide distribution, containing species from Africa (*M. subulatus*), Indo-China (*M. glabriusculus* and *M. coudercii*), New Guinea (*M. claoxyloides*, *M. darbyshirei*, *M. lauterbachianus* and *M. macularis*) and Australia (*M. claoxyloides*, *M. ficifolius* and *M. megadontus*). The clade (SR 21/25) is supported by a unique synapomorphy of umbel-like pistillate inflorescences (usually the inflorescences in *Mallotus* are racemes).

Resinosus clade—The six members of the clade (SR 18/18) occur from India, Sri Lanka, Indochina, Southeast Asia, New Guinea to Australia. Its species share general morphological similarities but can only be distinguished by the combination of a few characters. Our results suggest that it is supported by the synapomorphy of persistent stipules.

The type species of sections *Axenfeldia* (*Mallotus intermedius* (Baill.) N.P.Balak.) and *Rottleropsis* (*Mallotus lappaceus* Wall. ex Müll.Arg.) were not sampled in this study. However, based on morphological similarities (see Sierra et al., 2007) with the taxa of this clade, in particular *M. resinosus* for sect. *Axenfeldia*; *M. leucocalyx* and *M. dispar* for sect. *Rottleropsis*, it is likely that they might also belong here.

Wrayi clade—This clade comprises a species complex of four closely related species (treated by Van Welzen & Sierra, 2006). Previously, the species constituting this clade have often been misidentified (Reichenbach & Zollinger, 1856; Smith, 1910; Airy Shaw, 1963; Whitmore, 1973) or reduced to one species, *M. wrayi* (Airy Shaw, 1963; Meijer, 1967; Whitmore, 1973; Airy Shaw, 1975). Van Welzen & Sierra (2006) concluded that the *Mallotus wrayi* complex comprises four species instead of a single, very heterogeneous one, occurring in Peninsular Malaysia, Sumatra, Java and Borneo. Diagnostic characters for the four species are found in the density of the indument, length of inflorescences and bracts, bracts of the terminal bud, and stigma width and hairiness. The clade is supported by the synapomorphy of extrafloral nectaries on the nerves of the leaf upper surface (SR 66/52).

Tiliifolius clade—The eleven species of this clade (no SR support) occur from India, Sri Lanka, Indochina, Southeast Asia to Australia and the West Pacific. Most of the taxa have a restricted distribution, with the exception of *M. tiliifolius*, which is widespread. In the phylogeny by Slik & Van Welzen (2001a) it was suggested that *M. tiliifolius* is more related to the species in sect. *Philippinenses* (= sect. *Rottlera*), however, this is not confirmed by our results. The clade is supported by the synapomorphy of stellate

hairs, and in contrast to sect. *Mallotus* that solely has stellate hairs, the stellate hairs of the *tiliifolius* clade occur in combination with other hairs. In *Mallotus* s.s., the presence of simple and tufted hairs is more common than the presence of stellate hairs.

Furthermore, a subclade consisting of *M. tiliifolius*, *M. cambodianus*, *M. didymochryseus*, *M. dispersus*, *M. eriocarpus*, and *M. ustulatus* is characterized by having rough leaves on the leaf blade upper surface (usually smooth in *Mallotus*).

Three species in this subclade, *M. tiliifolius*, *M. didymochryseus* and *M. dispersus*, share a similar wetland and/or coastal ecology. *M. tiliifolius* is found on the edges of mangroves, swampy areas, sandy areas behind the beach, and *M. dispersus* is found on sand-dunes behind the foreshore. *M. didymochryseus* grows in the upper story of mixed primary or secondary alluvial lowland or swamp forest (periodically flooded to 1 m deep; Forster, 1999; Sierra et al., 2007).

Biogeography in *Mallotus* s.s.—Because our analyses did not result in completely stable phylogenies, no full biogeographical analysis was conducted. However, by observing the distributions in the clades discussed above, an interesting pattern emerges. Although some of the smaller clades have a rather restricted distribution, six out of the ten clades are widely distributed, typically ranging from India in the west, to New Guinea and/or Australia in the east. This pattern implies extensive dispersal and/or migration during the evolution of *Mallotus* and is in striking contrast with distribution patterns in the sister genus *Macaranga*, where the main clades are geographically rather uniform (Kulju et al., in press, Chapter 2). The most extreme distribution can be seen in the *Subulatus* clade, which comprises species from Africa, Indochina, New Guinea and Australia. Moreover, the two African species in *Mallotus* (*M. subulatus* and *M. oppositifolius*) are not closely related, belonging to different clades. This strengthens the hypothesis that Africa has been colonized by *Mallotus* two times from Asia (Kulju et al., in press, Chapter 2).

CONCLUSIONS

In this paper we used data from plastid and nuclear DNA sequences, macromorphology and leaf anatomy to infer the phylogenetic relationships in the genus *Mallotus* s.s. In addition to conventionally used qualitative morphological characters, we included number of quantitative characters in our analyses, and found that the signal in these characters was at least partly congruent with that in the qualitative data. The results allowed us to evaluate the infrageneric classification of Airy Shaw (1968) in a phylogenetic context, and three of the six sections (*Mallotus*, *Polyadenii* and *Stylanthus*) proved to be monophyletic, whereas three sections (*Philippinenses*, *Axenfeldia* and *Rottleropsis*) are para- or polyphyletic. Several additional, morphologically supported clades were also identified. However, because the overall structure and the backbone of the *Mallotus* s.s. phylogeny was not supported, nor stable across our different analyses, no new infrageneric classification can be proposed at the moment. In future studies the number of missing data should be reduced by sampling the DNA markers and leaf anatomy for additional species.

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APPENDICES

Appendix 5.1 — Voucher information for DNA sequence and leaf anatomical samples

Appendix 5.2. — List and datamatrix of macromorphological and leaf anatomical characters

Appendix 5.1. List with vouchers for the DNA sequences (including Genebank accession numbers) and leaf anatomy used in Chapter 7. Herbarium acronyms follow Holmgren et al. (1990). n.s. = DNA region not sequenced; * = partial sequence.

Species	Anatomy voucher	DNA voucher	Genebank Accession Number matK	Genebank Accession Number gpd
<i>Blumeodendron kurzii</i> J.J.Sm.	Bogor Botanical Garden IX.A.45 (L) Indonesia, Java, Bogor Botanical Garden	Gravendeel et al. 521 (L) Indonesia, Java, Bogor Botanical, Garden IX.C.144	EF582623	EF582685
<i>Cordemoya acuminata</i> (Baill.) Baill.	D'Alleizette 6522b (L) Madagascar, Famatave D'Alleizette s.n. (L)146441 (L) Madagascar, Famatave	—	n.s.	n.s.
<i>Cordemoya capuronii</i> (Léandri) S.E.C. Sierra, Kulju & Welzen	Rakotomalaza, Messmer & Rakotoavao 1502A (G) Madagascar, Ivohibe, Reserve Spéciale d'Ivohibe Messmer & Andriatsiferana NM698 (G) Madagascar, Antananarivo	—	n.s.	n.s.
<i>Cordemoya cordatifolia</i> (Slik) S.E.C. Sierra, Kulju & Welzen	Gutierrez et al. PNH 117545 (L) Philippines, Visayas, Samar, Sohoton	—	n.s.	n.s.
<i>Cordemoya eucausta</i> Airy Shaw	Wong 1191 (L) Brunei, Temburong, Kuala Belalong Coode MJE7930 (L) Brunei, Temburong, Batu Apoi	Slik MI085 (L) Indonesia, Kalimantan Timur, Labanan	EF582624	EF582686*
<i>Cordemoya grandistipularis</i> (Slik) S.E.C. Sierra, Kulju & Welzen	Maradio 286 (L) Indonesia, Sumatra, Taram Burley et al. 2021 (L) Indonesia, Sumatra, Riau, Bukit Karampal	—	n.s.	n.s.
<i>Cordemoya griffithiana</i> (Müll.Arg.) S.E.C. Sierra, Kulju & Welzen	Suppiah KEP 104951 (L) Malaysia, Johore, Labis FR	—	n.s.	n.s.
<i>Cordemoya hirsuta</i> (Elmer) S.E.C. Sierra, Kulju & Welzen	Ramos & Pascasio BS 34549 (L) Philippines, Mindanao, Surigao	—	n.s.	n.s.
<i>Cordemoya hookeriana</i> (Scem.) S.E.C. Sierra, Kulju & Welzen	Tsang 29561 (L) Vietnam, Tonkin, Ha-Coi, Taai Wong Mo Shan	—	n.s.	n.s.
<i>Cordemoya integrifolia</i> (Willd.) Baill.	Sieber Fl.mixa 199 (L)0293609 (L) Locality unknown Coode & Cadet 4958 (L) Reunion, Mare Longue	—	n.s.	n.s.
<i>Cordemoya kingii</i> (Hook.f.) S.E.C. Sierra, Kulju & Welzen	Smitinand 10945 (L) Thailand, Peninsular, Narathiwat, Waeng Shah 1558 (L) Malaysia, Pahang, Bukit Terom	—	n.s.	n.s.
<i>Cordemoya longistyla</i> (Merr.) S.E.C. Sierra, Kulju & Welzen	Gutierrez et al. PNH 117592 (L) Philippines, Visayas, Samar, Sohoton	—	n.s.	n.s.

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number
			matK gpd
<i>Cordemoya papuana</i> (J.J. Sm.) S.E.C. Sierra, Kulju & Welzen	Kostermans & Soegeng Reksodihardjo 387 (L) Indonesia, Irian Jaya, Sukarnapura	—	n.s.
<i>Cordemoya penangensis</i> (Müll.Arg.) S.E.C. Sierra, Kulju & Welzen	Kostermans 1318 (L) Indonesia, Maluku, Pate Pate, Gunung	—	n.s.
<i>Cordemoya spinulosa</i> (McPherson) S.E.C. Sierra, Kulju & Welzen	Rbevohitra 2052 (WAG) Madagascar, Toliara, St. Luce	—	n.s.
<i>Cordemoya stipularis</i> (Meijer ex Airy Shaw) S.E.C. Sierra, Kulju & Welzen	Arifin Berau 561 (L); Indonesia, Kalimantan Timur, Labanan	—	n.s.
<i>Cordemoya subpeltata</i> (Blume) M. Aparicio	Beusekom & Phengkhai 533 (L) Thailand, Peninsular, Ranong, Khao Nam Ron Middleton et al. 1735 (L) Thailand, Southwestern, Phetchaburi, Kaeng Kra Chian NP	Middleton et al. 494 (L) Thailand, Peninsular, Krabi, Khao Phanom Bencha NP	EF582625 EF582687*
<i>Macaranga albescens</i> L.M. Perry	Clemens 4829 (L) Papua New Guinea, Morobe, Ogerammang	—	n.s.
<i>Macaranga denticulata</i> (Blume) Müll.Arg.	Tanthana & Boonkongchart 29 (L) Thailand, Central, Nakhon Nayok, Khao Yai NP	—	n.s.
<i>Macaranga gigantea</i> (Reichb.f. & Zoll.) Müll.Arg.	Moog 00-55 (L) Malaysia, Sarawak, 1st Division, Kuching, Matang	Slik M866 (L) Indonesia, Kalimantan Timur, ITCI-concession	EF582626 EF582688
<i>Macaranga hypoleuca</i> (Reichb.f. & Zoll.) Müll.Arg.	Amin SAN 126634 (L) Malaysia, Sabah, Beaufort, Beaufort Hill	Slik M90 (L) Indonesia, Kalimantan Timur, Sungai Wain PF	EF582627 EF582689
<i>Macaranga inamoena</i> F.Muell. ex Benth.	Hyland 7735 (L) Australia, Queensland, Cook, State FR 310	Forster PIF29763 (BRI, L) Esser et al. 04-62 (L) Thailand, Northern, Chiang Mai, Doi Suthep	EF582628 EF582629 EF582691
<i>Macaranga karzii</i> Kuntze ex Pax & K.Hoffm.	Murata et al. T-42902 (L) Thailand, Northeastern, Loei, Phu Krading	—	n.s.
<i>Macaranga lowii</i> King ex Hook.f.	Shimizu & Nalampoon T-8189 (L) Thailand, Peninsular, Nakhon Si Thammarat, Thung Song	—	n.s.
<i>Macaranga subdentata</i> Benth.	Forster & Bean 13072 (L) Australia, Queensland, Cook, Little Mossman Logging Area	—	n.s.
<i>Macaranga tamaris</i> (L.) Müll.Arg.	Lantoh et al. SAN 111704 (L) Malaysia, Sabah, Tenom, Lagud	Slik M705 (L) Indonesia, Kalimantan Timur, Bukit Bangkirai	EF582630 EF582692
<i>Macaranga trichocarpa</i> (Reichb.f. & Zoll.) Müll.Arg.	Korthals s.n. (L) Indonesia, Kalimantan Selatan, Gunung Pamattan	Slik M398 (L) Indonesia, Kalimantan Timur, Bukit Bangkirai	n.s.
<i>Mallotus actinoneurus</i> Airy Shaw	Kochummen FRI 2499 (L) Malaysia, Malaya, Gunung Tebu	—	n.s.
<i>Mallotus apelta</i> Müll.Arg.	Tsang 293776 (L) Viet Nam, Tonkin, Ha-coi, Shui Mei	Soejarto et al. 10326 (L) Vietnam, Nghe An province	EF582632* EF582693*

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number matK	gpd
<i>Mallotus barbatus</i> Müll.Arg.	Maxwell 98-411 (L) Thailand, Northern, Chiang Rai, Kuhn Joe NP	Kuhn 90 (L) Leiden Botanical Garden, acc. 920695	EF582633	EF582694
<i>Mallotus blumeanus</i> Müll.Arg.	Rijksen 28773 (L) Indonesia, Sumatra, Aceh, Ketambe	—	n.s.	n.s.
<i>Mallotus brachyhyrsus</i> Merr.	Mamit S 35263 (L) Malaysia, Sarawak, 1st Division, Sungat Batu Purseglowe S 4665 (L) Malaysia, Sarawak, 1st Division, Pueh, Gunung Nicholson 1639 (L) Thailand, Southeastern, Chanthaburi, Prew Agricultural Station Kessler et al. Bernu 831 (L) Indonesia, Kalimantan Timur, Berau Inhutani I area	Slik M900 (L) Indonesia, Kalimantan Timur, ITCI-concession Vidal 5764 (L) Thailand, Southeastern, Chanthaburi, Phruoi Waterfall Slik M1243 (L) Indonesia, Kalimantan Timur, Labanan Brass 24245 (L) Papua New Guinea, Milne Bay, Opaigwari	EF582634	EF582695
<i>Mallotus calocarpus</i> Airy Shaw	—	—	EF582635*	EF582696*
<i>Mallotus caudatus</i> Merr.	—	—	EF582636	EF582697
<i>Mallotus chromocarpus</i> Airy Shaw	—	—	EF582638*	n.s.
<i>Mallotus cloaxyloides</i> (F.Muell.) Müll.Arg.	Forster & Machin 12257 (L) Australia, Queensland, Port Curtis, Moores Creek	Forster PIF29663 (BRL, L) Australia, Queensland, Port Curtis	EF582639	EF582699
<i>Mallotus concinnus</i> Airy Shaw	Chin 1552 (L) Malaysia, Kelantan, Gua Musang	—	n.s.	n.s.
<i>Mallotus comatus</i> M. Aparicio	Kostermans 21548 (L) Indonesia, Kalimantan Timur, Tanjung Reledeb	Gravendeel et al. 522 (L) Indonesia, Java, Bogor Botanic Gardens	EF582640	EF582700
<i>Mallotus coudercii</i> (Gagnep.) Airy Shaw	Kerr 19504 (L) Thailand, Southwestern, Ratchaburi, Ta Salao	Pooma & Phattarahirankanok 3856A (L) Thailand, Saraburi	EF582641*	EF582701*
<i>Mallotus cunningii</i> Müll.Arg.	Barbon et al. PPI 12719 (L) Philippines, Sito Kalumakan, Brgy. Matipuron, Milagros	Fernando 1735 (L) Philippines, Luzon, Los Baños, Mt. Makiling	EF582642	EF582702
<i>Mallotus decipiens</i> Müll.Arg.	Middleton et al. 1368 (L) Thailand, Southwestern, Prachuap Khiri Khan, Huay Yang NP	Middleton et al. 1104 (L) Thailand, Southwestern, Prachuap Khiri Khan, Kaeng Kra Chan NP Middleton et al. 1065 (L) Thailand, Southwestern, Prachuap Khiri Khan, Kaeng Kra Chan NP	EF582643*	EF582703
<i>Mallotus discolor</i> F.Muell. ex Benth.	Forster 14276 (L) Australia, Queensland, Port Curtis, Colosseum Creek	Forster PIF29659 (BRL, L) Australia, Queensland, Port Curtis	EF582645	EF582705
<i>Mallotus dispar</i> (Blume) Müll.Arg.	Reynoso PPI 4051 (L) Philippines, Luzon, Bataan, Mariveles	—	n.s.	n.s.
<i>Mallotus dispersus</i> P.L.Forst.	Russell-Smith & Lucas 4675 (L) Australia, Northern Territory, Arnhem Land, Port Bradshaw	Foster PFI15304 (L) Australia, Queensland, Cook, Muddy Bay	EF582646*	EF582706

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number mauK	gpd
<i>Mallotus ficifolius</i> (Baill.) Pax & K.Hoffm.	Forster & Machin 12257 (L) Australia, Queensland, Port Curtis, Moores Creek Forster et al. 27676 (L) Australia, Queensland, Cook, State FR 310	Forster PIF29782 (BRI, L) Australia, Queensland, Cook	EF582647	EF582707
<i>Mallotus floribundus</i> (Blume) Müll.Arg.	Sutrisno 43 (L) Indonesia, Java, Bogor	—	n.s.	n.s.
<i>Mallotus fuscescens</i> (Thwaites) Müll.Arg.	Kostermans 25651 (L) Sri Lanka, Southern, Galle, Beriliya	—	n.s.	n.s.
<i>Mallotus garrettii</i> Airy Shaw	Maxwell 97.474 (L) Thailand, Northern, Chiang Mai, Doi Luang NP	—	n.s.	n.s.
<i>Mallotus glomerulatus</i> Welzen	Poona et al. 2662 (L) Thailand, Central, Nakhon Pathom, Phu Langka NP	Koonkhanthod et al. 517 (L) Thailand, Northeastern, Nakhon Phanom, Phu Langka NP	EF582648*	n.s.
<i>Mallotus havilandii</i> Airy Shaw	Yit S 46226 (L) Malaysia, Sarawak, 1st Division, Gunung Berloban	Chai & Seng S22886 (L) Malaysia, Sarawak, 1st Division, Bukit Numpang	n.s.	n.s.
<i>Mallotus hispidospinosus</i> Welzen & Chayam.	Maxwell 98-321 (L) Myanmar, Tensasserim, Tawer, I-Tong village	—	n.s.	n.s.
<i>Mallotus japonicus</i> Müll.Arg.	Kuoh 12147 (L) Locality unknown	Kulju 100 (L) Leiden Botanical Garden	EF582649	EF582709
<i>Mallotus khasianus</i> Hook.f.	Nooteboom et al. 798 (L) Thailand, Northern, Chiang Mai, Doi Inthanon	Kessler PK3276 (L) Thailand, Northern, Nan province, Doi Phu Ka National Park	EF582650*	EF582710
<i>Mallotus korhalsii</i> Müll.Arg.	—	Peters 1032 (L) Indonesia, Kalimantan Barat, Raya Pasa NR	EF582651	EF582711*
<i>Mallotus laevis</i> Elmer	Kessler Berau 805 (L) Indonesia, Kalimantan Timur, Labanan	Slik M912 (L) Indonesia, Kalimantan Timur, ITCI-concession	EF582652	EF582712
<i>Mallotus lanceolatus</i> (Gagnep.) Airy Shaw	Kerr 5687 A (L) Thailand, Northeastern, Phetchabun, Phetchabun	Poona et al. 3817 (L) Thailand, Central, Lop Buri, Ban Sab Champa	EF582653*	EF582713*
<i>Mallotus leptostachyus</i> Hook.f.	Kerr 12098 (L) Thailand, Peninsular, Chumphon, Ban Krage Kerr 16442 (L) Thailand, Peninsular, Ranong, La-un	—	n.s.	n.s.
<i>Mallotus leucocalyx</i> Müll.Arg.	Reynoso et al. PPI 14754 (L) Philippines, Luzon, Camarines Sur, Barangay Guijalo	Chamchumroon VC2021 (L) Thailand, Peninsular, Tham Khao Yod	EF582654	EF582714*
<i>Mallotus leucodermis</i> Hook.f.	Argent et al. 96-31 (L) Indonesia, Borneo, Kalimantan Tengah	—	n.s.	n.s.
<i>Mallotus longinervis</i> M. Apaticio	Anderson S 25990 (L) Malaysia, Sarawak, 1st Division, Semengoh FR	Anderson S 25977 (L) Malaysia, Sarawak, 1st Division, Semengoh FR	EF582655*	EF582715

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number mauK	Number gpd
<i>Mallotus macrostachyus</i> (Miq.) Müll.Arg.	Cheng KEP FRI 27524 (L) Malaysia, Negeri Sembilan, Pasoh FR	Slik M262 (L) Indonesia, Kalimantan Timur, Bukit Bangkirai	EF582656	EF582716
<i>Mallotus macularis</i> Airy Shaw	Sidiyasa et al. 2815 (L) Indonesia, Irian Jaya, Mankwari, Gunung Meja	Sidiyasa et al. 2815 (L) Indonesia, Irian Jaya	EF582657*	EF582717*
<i>Mallotus megadontus</i> P.L.Forst.	Baitanoff 12193 (L) Australia, Queensland, Cook, Lizard Island	Hyland 7804 (L) Australia, Queensland, Cook, Claude River	EF582658*	EF582718*
<i>Mallotus met-alpinus</i> Croizat	Bunchuai 1826 (L) Thailand, Northeastern, Nong Khai, Ponepisai	Soejarto et al. 9725 (L) Vietnam, Bacflai Province, Quang Bath	EF582659*	EF582719*
<i>Mallotus microcarpus</i> Pax & K.Hoffm.	Cuong et al. 798 (L) Vietnam, Ninh Binh, Nho Quan, Cuc Phuong NP	—	n.s.	n.s.
<i>Mallotus minimifructus</i> S.E.C. Sierra	—	Raes NR578 (L)	EF582660*	EF582720*
<i>Mallotus miquelleanus</i> (Scheff.) Boerl.	Indonesia, Kalimantan Timur, Gunung Lumut	Slik M879 (L) Indonesia, Kalimantan Timur, ITCI-concession	EF582661	EF582721
<i>Mallotus mollissimus</i> (Geissel.) Airy Shaw	Teo & Pachiappan KL 3152 (L); Malaysia/Malaya, Unknown, Pahang, Taman negara	Gravendeel & Mudiana 701 (L) Indonesia, Bali, Bali Botanical Gardens, XII.CI.20	EF582662	EF582722
<i>Mallotus monanthos</i> Airy Shaw	Iwatsuki et al. P-917 (L) Philippines, Luzon, Ilocos Norte, Sauto Nino	—	n.s.	n.s.
<i>Mallotus montanus</i> (Müll.Arg.) Airy Shaw	Whitmore FRI 3544 (L) Malaya, Kuala Lompat Krau Game Reserve	Maxwell 85-457 (L) Thailand, Songkla	EF582663*	EF582723*
<i>Mallotus muticus</i> Müll.Arg.	Wood A 4675 (L) Malaysia, Sabah, Kinabatangan, Lamag	Slik M901 (L) Indonesia, Kalimantan Timur, ITCI-concession	EF582664	EF582724
<i>Mallotus nepalensis</i> Müll.Arg.	Koelz 25208 (L) India, Assam, Kohima	Slik M1234 (L) Indonesia, East Kalimantan, Labanan	EF582665	EF582725
<i>Mallotus nesophilus</i> Müll.Arg.	Balagooy & Bymes 1303 (L) Australia, Northern Territory, Arnhem Land, Alligator	Ohba et al. 8330555 (L) Nepal, Kali Gandaki	EF582666*	EF582726
<i>Mallotus nudiflorus</i> (L.) Kulju & Welzen	Kostermans 251 (L) Thailand, Southwestern, Kanchanaburi, Neekey	Cumming 10463 (L) Australia, Queensland, North Kennedy, Stuart Mountain	n.s.	EF582727*
<i>Mallotus oppositifolius</i> (Geissel.) Müll.Arg.	Warnecke 51 (L) Togo, Lome	Perianayagam RHT74579 (L, RHT) India, Tiruchi Dist., Srirangam	EF582667	EF582728
<i>Mallotus pallidus</i> (Airy Shaw) Airy Shaw	Chayamarit et al. 1845 (L) Thailand, Southwestern, Prachuap Khiri Khan, Khao Sam Roi Yot NP	Van Welzen 2003-5 (L) Thailand, Central, Phu Khae Botanical Garden	EF582668*	EF582729
		Wieringa et al. 4384 (WAG) Gabon, Ngounié, Sindira	EF582669	EF582730
		Middleton et al. 1136 (L) Thailand, Southwestern, Prachuap Khiri Khan, Khao Sam Roi Yot NP	EF582670	EF582731

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number matK gpd
<i>Mallotus paniculatus</i> (Lam.) Müll.Arg.	Forster et al. 28767 (L) Australia, Queensland, Cook, State FR 310	Slik M144 (L) Indonesia, Kalimantan Timur, Sungai Wain Forster PIF29762 (BRI, L) Australia, Queensland, Cook	EF582671 EF582733
<i>Mallotus peltatus</i> (Geisel.) Müll.Arg.	Geesink et al. 6813 (L) Thailand, Central, Saraburi, Sam Lahn	Slik M896 (L) Indonesia, Kalimantan Timur, ITCI-concession	EF582672 EF582734
<i>Mallotus philippensis</i> (Lam.) Müll.Arg.	Lantoh SAN 73452 (L) Malaysia, Sabah, Keningau, Sungai Pemalaaan Hiep 5370 (L) Vietnam, Ninh Binh, Nho Quan, Cúc Phuang NP	Gravendeel 504 (L) Indonesia, Java, Bogor Botanical Gardens, IX.C.23 Forster PIF29664 (BRI, L) Australia, Queensland, Port Curtis	EF582673* EF582735 EF582736
<i>Mallotus pterrei</i> (Gagnep.) Atry Shaw	Winit 446 (L) Thailand, Northern, Lamphun, Me Lee	Esser et al. 04-52 (L) Thailand, Northern, Lamphun, Bahn Hong, Doi Bah Bae	EF582675 EF582737
<i>Mallotus pleiogynus</i> Pax & K.Hoffm.	Schramm BW(Ind.) 2709 (L) Indonesia, Irian Jaya, Tami river	Polak NT11610 (L) Indonesia, Irian Jaya, Bird's Head Peninsula	EF582676 EF582738
<i>Mallotus polyadenos</i> F.Muell.	Forster et al. 27597 (L) Australia, Queensland, Cook, State FR 756	Forster PIF29780 (BRI, L) Australia, Queensland, Port Curtis	EF582677* EF582739
<i>Mallotus puber</i> Bollend.	Beer's collectors BSP17690 (L) Solomon Islands, Santa Isabel	—	n.s.
<i>Mallotus repandus</i> (Rottier) Müll.Arg.	Balgooy & Byrnes 1303 (L); Australia, Northern Territory, Arnhem Land, Alligator	Gravendeel et al. 515 (L) Indonesia, Java, Bogor Botanical Gardens XV.C.20-20a	EF582678 EF582740
<i>Mallotus resinosus</i> (Blanco) Merr.	Craven & Schodde 999 (L) Papua New Guinea, Gulf, Mountain Saw Vidal 5764 (L) Thailand, Southeastern, Chanthaburi, Phriou Waterfall	Kathriarachchi et al. HK67 (K, WU) Sri Lanka, Kurunegala, Weida	EF582679 EF582741
<i>Mallotus rhamnifolius</i> (Willd.) Müll.Arg.	Jayasuriya 1283 (L) Sri Lanka, Central, Amuradhapura, Rittigala Strict NR	Kathriarachchi et al. HK38 (K, WU) Sri Lanka, Ratnapura Distr., Putuwagahawala	EF582742* n.s.
<i>Mallotus roxburghianus</i> Müll.Arg.	Hooker & Thomson s.n. (L0293445) (L) India, Assam, Umran, Khasia	—	n.s.
<i>Mallotus rufidatus</i> (Miq.) Müll.Arg.	Colfs 164 (L) Indonesia, Lesser Sunda Islands, Nusa Tenggara Barat, Sumbawa	—	n.s.
<i>Mallotus sphaerocarпус</i> (Miq.) Müll.Arg.	—	Rijksen 28773 (L) Indonesia, Sumatra, Aceh, Ketambe	EF582681* n.s.
<i>Mallotus spinifracus</i> Welzen & S.E.C.Sierra	Mogea 4335 (L) Indonesia, Kalimantan Tengah, Upper Katingan River	—	n.s.
<i>Mallotus subulatus</i> Müll.Arg.	Breteler 5911 (L) Ivory Coast, Abidjan, Comoe bridge	Wheatley 16 (K) Cameroon, South West Prov., Fako, Buea	EF582682* n.s.

Appendix 5.1. Continued.

Species	Anatomy voucher	DNA voucher	Genbank Accession Number matK	gpd
<i>Mallotus subulatus</i> (continued)				
Müll.Arg.	Léonard 439 (L)	—	n.s.	n.s.
<i>Mallotus samatramis</i>	Zaire, Equateur, Mbandaka, Wendji	—	n.s.	n.s.
(Miq.) Airy Shaw	Posthumus 1077 (L)	—	n.s.	n.s.
<i>Mallotus tetraecoccus</i>	Indonesia, Sumatra, Jambi, Pahoe	—	n.s.	n.s.
Kurz	Cramer 3396 (L)	Kadriarachchi et al. HK2 (K, WU)	EF582683	EF582743
	Sri Lanka, Southern, Galle, Wanduramba	Sri Lanka, Matale, Knuckles	n.s.	n.s.
<i>Mallotus thorelii</i>	Put 3105 (L)	—	n.s.	n.s.
Gagnep.	Thailand, Peninsular, Prachin Buri, Aran Pratet	—	n.s.	n.s.
<i>Mallotus tilifolius</i>	Ava & Ismawi S 48717 (L)	Zippelius s.n. (L 0293185) (L)	n.s.	EF582744*
(Blume) Müll.Arg.	Malaysia, Sarawak, 1st Division, Gunung Santubong	Java	n.s.	n.s.
	Borssum Waalikes 157 (L)	—	n.s.	n.s.
	Indonesia, Java, Pulau Panaitan	—	n.s.	n.s.
	Htiq 10892 (L)	—	n.s.	n.s.
	Cambodia, Kampong Speu, Samrong Tong	—	n.s.	n.s.
<i>Mallotus trinervius</i>	Brass 14115 (L)	Brass 14115 (L)	EF582684*	EF582745*
(Schum. & Lauterb.) Pax & K.Hoffm.	Indonesia, Irian Jaya, Bernhard camp	Indonesia, Irian Jaya, Bernhard camp	n.s.	n.s.
<i>Mallotus wrayi</i>	Whitmore KEP FRI 8650 (L)	—	n.s.	n.s.
King ex Hook.f.	Malaysia, Johore, Lenggong FR	—	n.s.	n.s.

APPENDIX 5.2

List of macromorphological and leaf anatomical characters used in the phylogenetic analyses.

QUALITATIVE DATA

VEGETATIVE CHARACTERS

1. Stipules: (0) absent; (1) present.
2. Stipule type: (0) axillary; (1) interpetiolar.
3. Stipule persistence: (0) persistent at least in young shoots; (1) early caducous. The early caducous stipules can only be observed in the very youngest shoottips and/or the scars of them are present.
4. Phyllotaxis: (0) alternate; (1) opposite. We treat a verticillate leaf arrangement as a special case of alternate phyllotaxis. A subopposite arrangement (the leaves of a pair not precisely on the same level) is considered as essentially opposite. Plants with generally alternate leaves may have seemingly opposite leaves just beneath the inflorescences; these were not taken into consideration.
5. Fenugreek smell on leaves: (0) absent; (1) present. Fenugreek smell (Airy Shaw, 1972; Slik & Van Welzen, 2001b), also known as coumarine smell, can only be detected from dry material (including old collections).
6. Leaf base peltate: (0) no; (1) yes. Several species in *Mallotus* have somewhat subpeltate leaves. We define here peltate leaves as being peltate for more than 3 mm.
7. Leaf upper surface: (0) smooth; (1) rough. In some species the leaf upper surface feels rough to the touch because of stiff hairs on the lamina.
8. Extrafloral nectaries on upper leaf surface: (0) absent; (1) present.
9. Extrafloral nectaries: (0) between or below the nerves; (1) on the nerves. (Fig. A1)
10. Extrafloral nectary position: (0) basal group near petiole insertion; (1) at nerve axils; (2) along the whole midrib; (3) along the whole margin; (4) on the midrib. Extrafloral nectaries as a basal group is the most common type in *Mallotus*. Within this type the number and exact configuration of the nectaries varies considerably, but no clear boundaries between these potential subtypes could be found. The minute, orbicular, extrafloral nectaries which are sometimes present on the upper half were not taken into consideration.

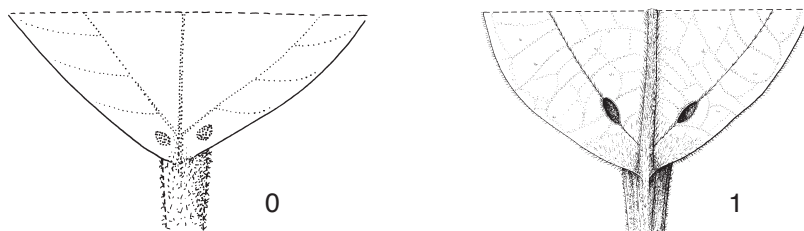


Fig. A1. Character 9. Extrafloral nectaries: 0 = between or below the nerves; 1 = on the nerves.

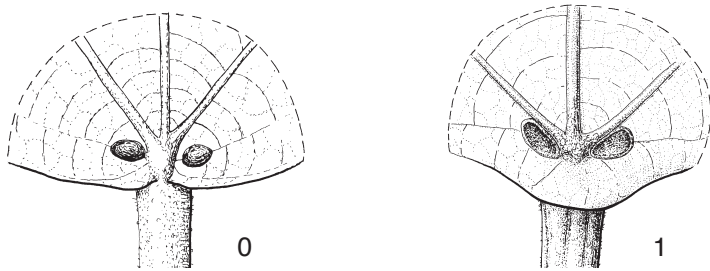


Fig. A2. Character 11. Extrafloral nectaries with raised margins: 0 = no; 1 = yes.

11. Extrafloral nectaries with raised margins: (0) no; (1) yes. (Fig. A2)
12. Leaf venation type: (0) triplinerved or palmate; (1) pinnate. Triplinerved leaves have two lateral veins originating from the petiole insertion, sometimes being faint and very close to the margin. The lateral nerves of pinnate leaves do not originate from the petiole insertion.
13. Domatia on lower leaf surface: (0) absent; (1) present. The domatia of *Mallotus* are usually composed of hair tufts, sometimes a shallow depression is also present.
14. Leaf lower surface with a dense layer of very short hairs: (0) no; (1) yes. This tomentose hair cover gives the leaf lower surface a greyish appearance, which should not be confused with a glaucous leaf surface.
15. The smaller leaf of an opposite leaf pair: (0) leaf-like, similar in shape as the larger leaf; (1) leaf-like, but different in shape than the larger leaf (obcordate); (2) stipuliform. (Fig. A3)

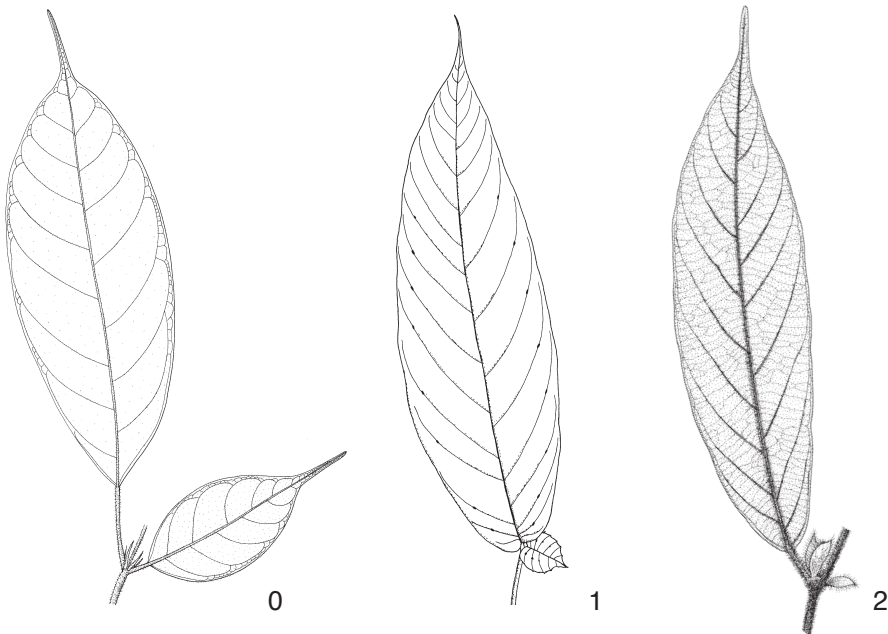


Fig. A3. Character 15. The smaller leaf of an opposite leaf pair: 0 = leaf-like, similar in shape as the larger leaf; 1 = leaf-like, but different in shape than the larger leaf (obcordate); 2 = stipuliform.

STAMINATE CHARACTERS

16. Staminate inflorescence type: (0) racemes; (1) panicles. Racemes are sometimes reduced in length due to the presence of very short internodes.
17. Filament fusion: (0) free; (1) connate. Connate filaments are fused into a tube at least in the lower half.
18. Filament hairiness: (0) glabrous; (1) hairy.
19. Thecae number: (0) two; (1) four.
20. Thecae hairiness: (0) glabrous; (1) hairy.
21. Connective shape: (0) narrow to somewhat widened; (1) umbrella-like. (Fig. A4)
22. Pollen ornamentation: (0) areolate; (1) perforate to microreticulate.
23. Pistillodes: (0) absent; (1) present.
24. Interstaminal disc-glands: (0) absent; (1) present.

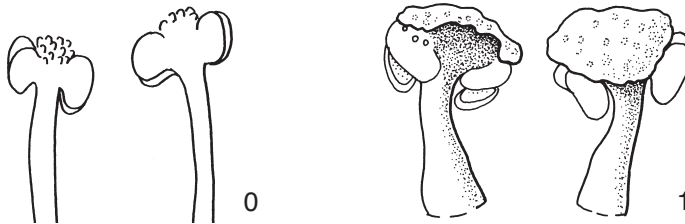


Fig. A4. Character 21. Connective shape: 0 = narrow to somewhat widened; 1 = umbrella-like.

PISTILLATE CHARACTERS

25. Pistillate inflorescence: (0) racemes or panicles; (1) umbel-like; (2) reduced to glomerules or one flower on a very short axis; (3) reduced to one terminal flower with a long axis. Almost all *Mallotus* species with panicles usually also have racemes (the most common inflorescence type), therefore both types are united in one character state. The umbel-like type often has few extra flowers below the terminal umbel (sometimes with clear internodes).
26. Pistillate bracts enclosing the flowers: (0) absent; (1) present.
27. Pistillate flower calyx aestivation: (0) valvate; (1) imbricate.
28. Pistillate flower calyx persistence: (0) persistent in fruit; (1) caducous.
29. Pistillate flower sepal fusion: (0) free to basally connate; (1) connate from base to apex. Free and basally connate sepals can be seen in a single collection in some species, therefore both are regarded as a single character state. This state is clearly different from the spatheous calyx connate from base to apex. (Fig. A5)

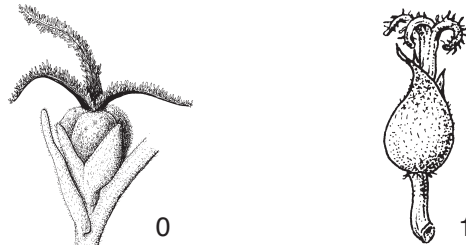


Fig. A5. Character 29. Pistillate flower sepal fusion: 0 = free to basally connate; 1 = connate from base to apex.

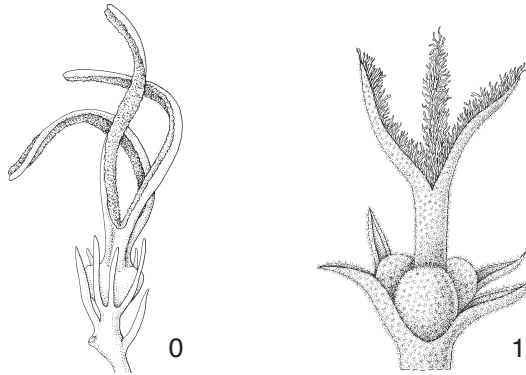


Fig. A6. Character 31. Stigmatic surface: 0 = papillose; 1 = plumose.

30. Pistillate sepal shape: (0) triangular; (1) narrowly triangular; (2) linear-triangular. These character states are defined by the following length/width ratios: 1–3 = triangular; 3–5 = narrowly triangular; >5 = linear-triangular.
31. Stigmatic surface: (0) papillose; (1) plumose. (Fig A6)
32. Annular disc: (0) absent; (1) present.
33. Fruit dehiscence: (0) early dehiscent; (1) tardily dehiscent; (2) indehiscent. Early dehiscent fruits will always open and in one collection usually all the fruits open at the same time when ripe. Tardily dehiscent fruits in one collection can open or not when ripe. Indehiscent fruits clearly do not open at all.
34. Fruit opening sequence: (0) loculicidally only; (1) septicidally only; (2) septicidally-loculicidally; (3) loculicidally-septicidally. In loculicidally-septicidally opening fruits the seeds stay attached to the column after dehiscence, whereas in septicidally-loculicidally opening fruits the seeds fall off together with the cocci. (Fig. A7)
35. Fruit wings: (0) absent; (1) present. The fruits of *M. sumatranus* and *M. plicatus* bear only one wing-like appendix per locule. Therefore, they were deemed non-homologous with spines (character 36), which occur in larger, non-fixed numbers. (Fig. A8)
36. Fruit spines: (0) absent; (1) present. The number and shape of the spines varies considerably. Here, we treat them as one character, but further research might prove them to be non-homologous.
37. Fruit surface non-glandular indument cover: (0) glabrous to sparse; (1) dense.
38. Fruit surface glandular indument cover: (0) glabrous to sparse; (1) dense. In the dense condition the glandular indument covers completely the fruit, which is distinct from glabrous or sparsely hairy fruits.

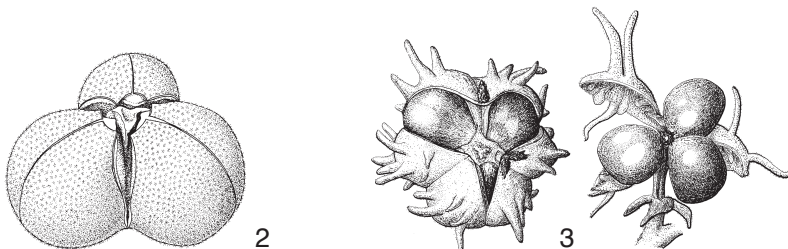


Fig. A7. Character 34. Fruit opening sequence: 2 = septicidally-loculicidally; 3 = loculicidally-septicidally.

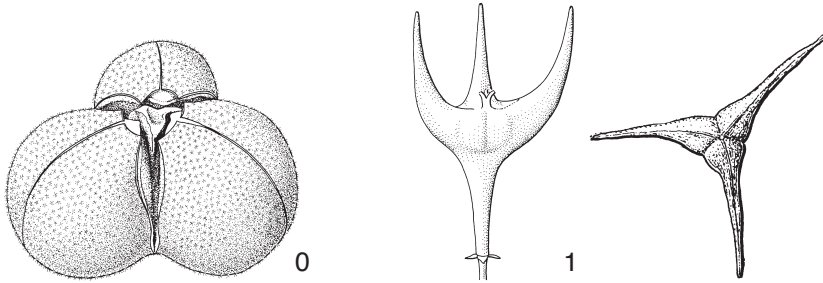


Fig. A8. Character 35. Fruit wings: 0 = absent; 1 = present.

39. Seed shape: (0) more or less globose; (1) lenticular; (2) subreniform.

LEAF ANATOMICAL CHARACTERS

40. Simple hairs: (0) absent; (1) present.

41. Simple hair type: (0) unicellular; (1) uniseriate.

42. Stalked stellate hairs: (0) absent; (1) present. (Fig. A9a)

43. Tufted hairs: (0) absent; (1) present. (Fig. A9b)

44. Capitate glandular hairs: (0) absent; (1) present. Capitate glandular hairs are composed of a unicellular head and a uniseriate stalk. (Fig. A10a)

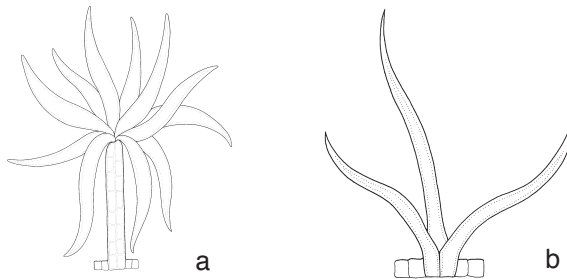


Fig. A9. Non-glandular hair types. a. Character 42: Stalked stellate hair; b. Character 43: Tufted hair

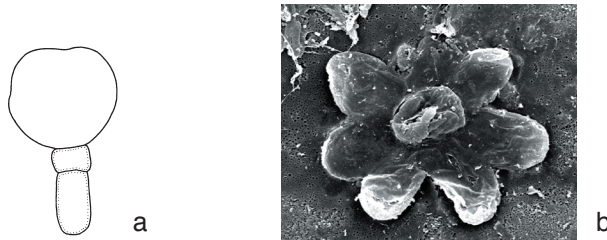


Fig. A10. Glandular hair types. a. Character 44: Capitate glandular hair; b. Character 45: Peltate-stellate glandular hair

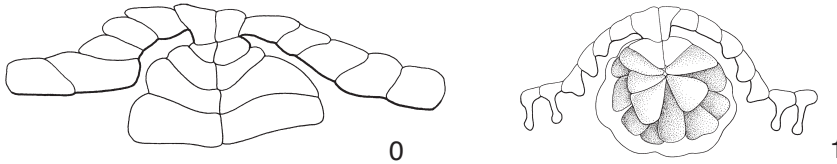


Fig. A11. Character 48. Organization of cells in globular to disc-shaped glandular hairs: 0 = type a; 1 = type b.

45. Peltate-stellate glandular hairs: (0) absent; (1) present. (Fig. A10b)
 46. Globular to disc-shaped glandular hairs: (0) absent; (1) present.
 47. Globular to disc-shaped glandular hairs on upper leaf surface: (0) absent; (1) present.
 48. Organization of cells in globular to disc-shaped glandular hairs: (0) type a; (1) type b. (Fig. A11)
 49. Margin of globular to disc-shaped glandular hairs: (0) conspicuously ridged; (1) (sub)entire. (Fig. A12)
 50. Papillae: (0) absent; (1) present.
 51. Papillae location: (0) lower surface; (1) upper surface.
 52. Papillae shape: (0) domes; (1) nipple-shaped; (2) conical; (3) elongated projections. (Fig. A13)
 53. Stomata on adaxial surface: (0) absent; (1) present. Stomata on adaxial surface occur over or near major veins, they are never distributed over the entire surface.

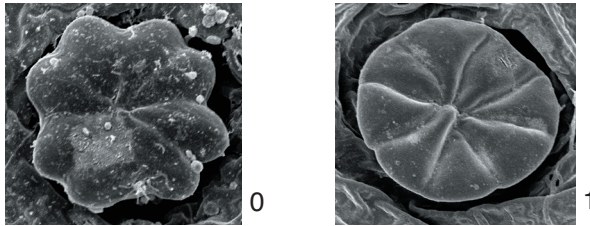


Fig. A12. Character 49. Margin of globular to disc-shaped glandular hairs: 0 = conspicuously ridged; 1 = (sub)entire.

54. Stomata concentrated under glandular hairs: (0) no; (1) yes. (Fig. A14a)
 55. Stomata with lobing of subsidiary cells beneath guard cells: (0) absent; (1) present. (Fig. A14b)
 56. Guard cell lumina in transverse section: (0) slit-like; (1) wider. (Fig. A15)
 57. Outer cuticular ledges: (0) absent; (1) present.
 58. Cork warts: (0) absent; (1) present. These cork warts are regularly circular and distributed over the entire lower and/or upper surface of the leaves. They should not be confused with the larger irregular cork warts of traumatic origin (e.g. resulting from insect damage).

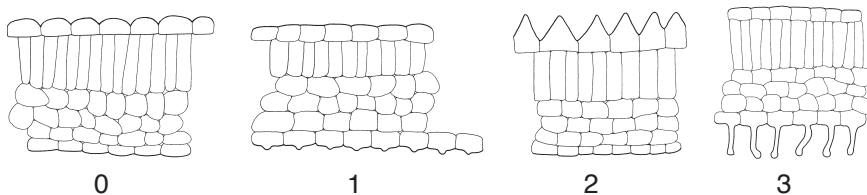


Fig. A13. Character 52. Papillae shape: 0 = domes; 1 = nipple-shaped; 2 = conical; 3 = elongated projections.

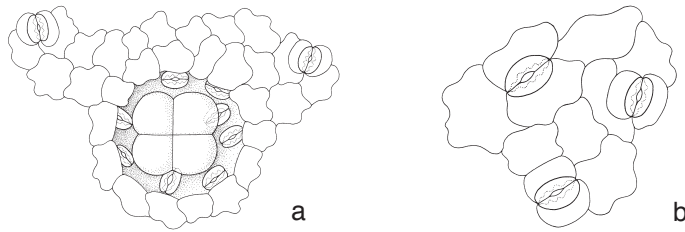


Fig. A14. Stomata. a. Character 54: Stomata concentrated under glandular hairs; b. Character 55: Stomata with lobing of subsidiary cells beneath guard cells.



Fig. A15. Character 56. Guard cell lumina in transverse section: 0 = slit-like; 1 = wider.

59. Epidermal striations: (0) absent; (1) present.
 60. Local hypodermis above some minor veins: (0) absent; (1) present.
 61. Bundle sheath extensions: (0) absent; (1) present. Bundle sheath extensions are composed of parenchymatous cells, extending towards the adaxial surface. Sometimes (especially in *Macaranga*) they are composed of parenchymatous and fibrous sclereids.
 62. Stomatal crypts: (0) absent; (1) present.
 63. Number of palisade tissue layers: (0) one; (1) more than one.
 64. Large crystal idioblasts (0) absent; (1) present. Most of the species have small crystals, which can be present in idioblasts or in regular mesophyll cells. In addition to that, several species also have large crystal idioblasts, which are considerably bigger than the minute crystals. Large crystals are usually in the size range of palisade cells or bigger.
 65. Fibrous sclereids: (0) absent; (1) present.
 66. Brachysclereids: (0) absent; (1) present. Brachysclereids are present in the ground tissue of midrib and petiole.
 67. Secretory cells: (0) absent; (1) present. Secretory cells are present in the ground tissue of midrib and petiole. (Fig. A16a)

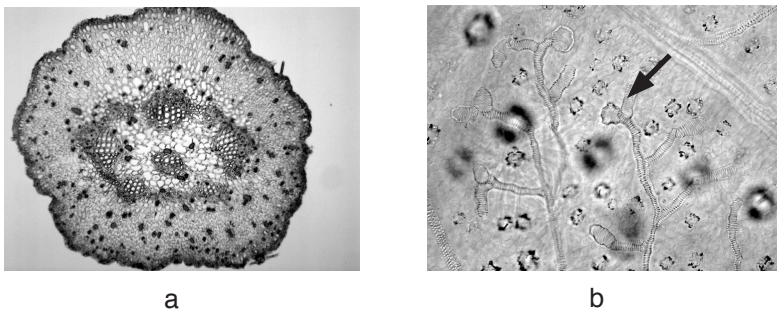


Fig. A16. a. Character 67: Secretory cells; b. Character 70: Terminal vein tracheids enlarged.

68. Petiole bundles: (0) separate; (1) fused.
 69. Pith bundles in petiole: (0) solitary or scattered; (1) in a cylinder. (Fig. A17)
 70. Terminal vein tracheids: (0) not enlarged; (1) enlarged. The ultimate vein endings may be composed of normal to thin tracheids, or they can end in conspicuously enlarged tracheids. (Fig. A16b)

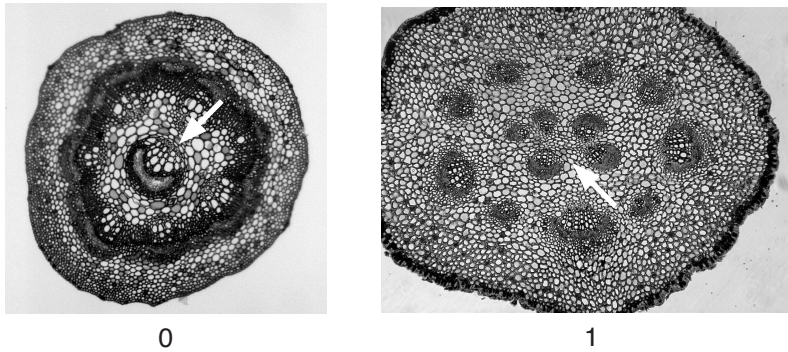


Fig. A17. Character 69. Pith bundles in petiole: 0 = solitary or scattered; 1 = in a cylinder

QUANTITATIVE DATA

VEGETATIVE CHARACTERS

71. Leaf length-width ratio
 72. Number of nerves per side on the leaf blade. The faint nerves at the apex (above sinus) were excluded when giving the total nerve count.

STAMINATE CHARACTERS

73. Staminate inflorescence length (cm)
 74. Staminate flower diameter (mm)
 75. Staminate pedicel length (mm)
 76. Stamen number
 77. Filament length (mm)
 78. Thecae length (mm)

PISTILLATE CHARACTERS

79. Pistillate inflorescence length (cm)
 80. Pistillate pedicel length (mm)
 81. Ovary length (mm)
 82. Number of locules in ovary
 83. Style length (mm)
 84. Stigma length (mm)
 85. Fruit length (mm). The spines (if present) were included in the length of the fruit, but the fruits wings (in *M. plicatus* and *M. sumatranus*) were excluded.
 86. Fruit spine length (mm)
 87. Fruit wall thickness (mm)
 88. Fruit column length (mm)

LEAF ANATOMICAL CHARACTERS

89. Stomata density (number/mm²). Generally, the frequency of stomata can vary in a species (depending on light intensity, amount of CO₂ in the air, etc.). However, we observed that some taxa, like *Cordemoya* subg. *Cordemoya*, have a high frequency of stomata, and therefore, we decided to include this character.
90. Stomata length (μm)

Morphological data matrix. Horizontal: character number, as listed in Appendix 5.2. Vertical: species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
<i>Blumeodendron kurzii</i>	0	?	?	0/1	0	0	0	0/1	0/1	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	1	1	0	0					
<i>Blumeodendron subrotundifolium</i>	0	?	?	0/1	0	0	0	0/1	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0				
<i>Blumeodendron tokbrei</i>	0	?	?	0/1	0	0	0	0/1	0	0/2	0	0/1	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0				
<i>Cordemoya acuminata</i>	1	0	0	1	0	0	0	0/1	?	?	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	2	0	0				
<i>Cordemoya capuronii</i>	1	0	1	0/1	0	0	0	0/1	?	?	0	1	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0				
<i>Cordemoya cordatifolia</i>	1	1	0	1	0	0	0	0	?	?	?	1	0	0	2	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	0			
<i>Cordemoya eucasta</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	0	0	?	?	?	?	?	?	0	0/3	0	0	1	0	0	0	0	0	0	2	0	0				
<i>Cordemoya grandistipularis</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	0	?	?	?	?	?	?	?	0	0	0	1	0	0	0	0	0	0	0	2	0	0				
<i>Cordemoya griffithiana</i>	1	1	1	0	0	0	0	?	?	?	?	1	0	0	2	0/1	0	?	?	?	?	?	?	0	0	0	0	0	1	0	0	0	0	0	2	0	0				
<i>Cordemoya hirsuta</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	0	0	2	0	0				
<i>Cordemoya hookeriana</i>	1	1	0	1	0	0	0	?	?	?	?	1	1	0	2	?	?	?	?	?	?	?	?	?	0/3	0	0	1	0	0	1	0	0	0	2	0	0				
<i>Cordemoya integrifolia</i>	1	0	0	0/1	0	0	0	0/1	?	?	?	0	1	0	0	2	0/1	0	0	0	0	0	0	0	0/3	0	0	0	2	0	0	0	0	0	2	0	0				
<i>Cordemoya kingii</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0			
<i>Cordemoya longistyla</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0				
<i>Cordemoya papuana</i>	1	1	1	0	0	0	0	?	?	?	?	1	1	0	2	0	0	0	0	0	0	0	0	0	0/3	0	0	1	0	0	1	0	0	0	2	0	0				
<i>Cordemoya penangensis</i>	1	1	0	1	0	0	0	?	?	?	?	1	0/1	0	2	0	0	0	0	0	0	0	0	0	0/3	0	0	1	0	0	1	0	0	0	2	0	0				
<i>Cordemoya spinulosa</i>	1	0	1	0/1	0	0	0	0/1	?	?	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0/3	0	0	0	2	0	0	0	0	0	2	0	0				
<i>Cordemoya stipularis</i>	1	1	0	1	0	0	0	?	?	?	?	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0					
<i>Cordemoya subpeltata</i>	1	1	0	0	0	0	0	?	?	?	?	1	0	0	2	?	?	?	?	?	?	?	?	0/3	0	0	0	1	0	0	1	0	0	0	3	0	0				
<i>Cordemoya wenzeliana</i>	1	1	0	1	0	0	0	?	?	?	?	1	0	0	2	?	?	?	?	?	?	?	?	0/3	0	0	0	1	0	0	1	0	0	0	2	0	0				
<i>Macaranga albescens</i>	1	0	1	0	0	1	0	0	?	?	?	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0				
<i>Macaranga denticulata</i>	1	0	1	0	0	1	0	1	0	0	0	0	0	0	?	1	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0				
<i>Macaranga gigantea</i>	1	0	0	0	1	0	?	?	?	?	?	0	0	0	?	1	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Macaranga hypoleuca</i>	1	0	0	0	1	0	?	?	?	?	?	0	0	0	?	1	0	0	1	0	0	?	?	0	0	0	0	0	0	1	?	0	0	?	?	?	0				
<i>Macaranga inamoena</i>	1	0	1	0	0	0	1	0	0	1	0	0	0	0	?	1	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0				
<i>Macaranga kurzii</i>	1	0	1	0	0	0	1	0	0	0	0	0	1	0	?	1	0	0	1	0	0	?	?	0	0	0	0	0	0	1	0	0	0	0	2	0	0				
<i>Macaranga repando dentata</i>	1	0	1	0	0	0	1	0	0	0	0	1	0	0	?	1	0	0	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0				
<i>Macaranga tanarius</i>	1	0	0	0	1	0	?	?	?	?	?	0	?	?	?	1	0	?	?	?	?	?	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0			
<i>Macaranga trichocarpa</i>	1	0	1	0	0	0	1	0	0	0	0	0	0	0	?	1	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0				
<i>Mallotus acinonervus</i>	1	0	0	0/1	0	0	0	1	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	2	0	0	0	0	0/1	1	0	0	0	2	0	0				
<i>Mallotus anomalis</i>	1	0	1	0	0	0	0	0/1	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0			
<i>Mallotus apelta</i>	1	0	1	0	0	0	1	0	0	0	0	1	?	0/1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0			
<i>Mallotus atrovirens</i>	1	0	1	0/1	0	0	1	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0		
<i>Mallotus barbatus</i>	1	0	0	0	1	0	0	1	0	0	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0			
<i>Mallotus blumeanus</i>	1	0	1	0	0	0	1	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	1	0	0	2	?	?	0				
<i>Mallotus brachythyrus</i>	1	1	1	0	0	0	1	0/1	0	0	0	1	0	0	2	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0			
<i>Mallotus brevipejalatus</i>	1	0	1	0	0	0	1	0	0/4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	2	0		
<i>Mallotus calocarpus</i>	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0		
<i>Mallotus cambodianus</i>	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0		
<i>Mallotus caudatus</i>	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	
<i>Mallotus caniflorus</i>	1	0	0	1	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0

Morphological data matrix. Continued.

	71	72	73	74	75	76	77	78	79	80
<i>Blumeodendron karzii</i>	1.42-3	6-11	1.2-5	3.5-4	6-11	25-30	?	0.7-0.8	15-20	?
<i>Blumeodendron subrotundifolium</i>	1.49-2.7	?	1.7-5.5	?	4-10	40-40	?	0.7-0.8	?	1.8-4
<i>Blumeodendron tokbrai</i>	1.71-2.66	?	4.5-17	?	?	15-33	?	0.7-0.8	4-6.8	?
<i>Cordemoya acuminata</i>	2.8-4	4-10	4.5-5	4.5-5	?	120-150	?	0.2-0.3	2.5-5	?
<i>Cordemoya capurani</i>	2.3-2.5	9-12	2.5-2	4.5-5	2.5-5	80-130	?	0.2-0.3	0.5-1.5	?
<i>Cordemoya cordatifolia</i>	2.2-5	11-17	3.5-5	3.5-3.5	3.5-4.5	50-60	?	0.3-0.3	?	?
<i>Cordemoya eucansta</i>	2.7-5	10-15	?	3.5-3.5	?	25-46	1.5-1.5	0.3-0.4	?	2.5-5
<i>Cordemoya grandistipularis</i>	?	11-17	?	?	?	?	?	?	?	?
<i>Cordemoya eriffithiana</i>	2.4-3	11-17	?	4.5-7	1.3-5	86-86	1.3-1.7	0.3-0.3	6-12	2-4.5
<i>Cordemoya hirsuta</i>	2.2-3.3	?	?	?	?	?	?	?	?	?
<i>Cordemoya hooseriana</i>	?	7-11	?	?	?	60-70	2-4.5	0.3-0.3	?	?
<i>Cordemoya integrifolia</i>	2.2-5	12-14	3-10	?	2.8-3.5	200-250	0.5-0.8	0.2-0.3	8-10	1-1.5
<i>Cordemoya kingii</i>	2.2-3	12-14	?	?	1-2.3	70-90	?	0.5-0.7	6-15	?
<i>Cordemoya longistyla</i>	2.3-3.3	8-11	6.5-9	?	?	50-100	1.3-2	0.4-0.5	7.7-10	?
<i>Cordemoya papuana</i>	2.3-4	9-15	?	4.4-5	?	32-40	1.8-3	0.2-0.3	?	?
<i>Cordemoya penangensis</i>	1.7-5.1	7-14	?	3.7-5.5	?	60-100	?	0.2-0.3	5-12	?
<i>Cordemoya spinulosa</i>	2.3-2.6	?	?	4.5-5	?	70-90	?	0.2-0.3	1.5-3	0.8-1
<i>Cordemoya stipularis</i>	2.5-4	11-15	?	4.5-4.5	?	56-56	?	0.4-0.5	?	2.4-5
<i>Cordemoya subpelata</i>	2.5-3	?	0.5-1.2	?	?	200-250	?	?	1.5-3	0.7-2
<i>Cordemoya wenzeliana</i>	2.6-3.7	9-12	?	?	?	?	?	?	?	1.5-6
<i>Macaranga albescens</i>	1.2-1.5	?	10-15	2.8-3	?	?	?	?	?	?
<i>Macaranga denticulata</i>	1.1-1.4	7-10	8-12	1.6-1.8	0.3-0.3	14-20	0.3-0.7	0.2-0.3	6.5-12.5	1.2-4.2
<i>Macaranga gigantea</i>	?	?	?	?	?	?	?	?	?	?
<i>Macaranga hypoleuca</i>	2.77-3.23	8-10	10-28	0.2-0.3	0.2-0.3	?	?	0.8-1	5-15	?
<i>Macaranga inamoena</i>	1.48-2.25	8-10	11-11	2.2-2.2	?	20-28	1.5-1.8	0.2-0.3	7-11	0.8-3
<i>Macaranga karzii</i>	?	?	7-13	?	1-1.5	14-17	1.5-1.8	0.2-0.3	?	0.5-0.5
<i>Macaranga repando dentata</i>	1.7-2.6	10-12	?	?	0.2-0.2	?	0.8-1	1.2-1.2	3.2-4.7	?
<i>Macaranga tanarius</i>	?	?	?	?	?	?	?	?	?	?
<i>Macaranga trichocarpa</i>	1.5-2.1	?	2.2-6.5	?	0.5-0.5	?	0.5-0.5	0.2-0.3	1.7-2	0.5-0.5
<i>Mallotus actinoneurus</i>	2.1-3.6	9-10	?	?	?	?	?	?	?	2.5-2.5
<i>Mallotus anomalus</i>	1.25-1.83	?	?	?	?	?	?	?	?	3.5-3.5
<i>Mallotus apelta</i>	1.59-2.05	?	11.5-17	?	?	100-120	?	0.2-0.3	18-22.5	?
<i>Mallotus atrovirens</i>	2-2.3	?	2.5-6	2.5-3	2.5-2.5	35-40	?	0.2-0.3	3.7-7.5	?
<i>Mallotus barbatus</i>	1-1.3	7-11	12-65	?	3.5-5	60-85	?	0.2-0.3	?	1-4.5
<i>Mallotus blumeanus</i>	2.1-2.8	?	7.5-20	3-3.3	1.5-7	28-40	0.25-1.5	0.1-0.2	8.5-16	1.3-2
<i>Mallotus brachylytrus</i>	2.2-3.4	9-13	2-2.6	?	?	60-60	?	0.2-0.3	?	?
<i>Mallotus brevipedatus</i>	2.5-3.8	8-16	?	3.5-5	1.5-7	20-35	?	0.3-0.4	4.7-10	?
<i>Mallotus calocarpus</i>	2.2-3.5	?	2-2.3	?	?	34-50	2.8-3	0.7-0.8	1-1.5	?
<i>Mallotus cambodanus</i>	1-1.3	?	8-10	3-3.5	1.2-1.5	35-45	1.5-2	0.2-0.3	2.2-3.5	2.5-2.5
<i>Mallotus caudatus</i>	2-2.6	?	6.5-19	2-4.5	2-3.4	24-60	1-2.6	0.2-0.3	1.3-26	2.2-3.4
<i>Mallotus caviflorus</i>	2.3-2.5	10-15	?	?	2.5-5	35-42	0.5-2.8	0.2-0.3	7.5-12.5	0.2-0.4

Morphological data matrix. Continued.

	71	72	73	74	75	76	77	78	79	80
<i>Mallotus chromocarpus</i>	1.3-1.8	?	?	2.8-3.8	1.5-2	30-36	0.6-1	0.2-0.3	?	?
<i>Mallotus clausyloides</i>	1.6-2.12	?	3.5-4	5-6.5	?	29-45	1.8-5.5	0.2-0.3	0.8-1.5	3-10
<i>Mallotus conatus</i>	2.5-2.7	?	?	?	?	?	?	?	?	1.7-1.7
<i>Mallotus connatus</i>	1.5-3	?	8-22	?	?	45-60	3.5-5	0.2-0.3	16-21	?
<i>Mallotus corderii</i>	1-1.9	?	1.5-3	?	0.5-1.3	25-29	?	0.2-0.3	6.3-12	0.9-7.4
<i>Mallotus cumingii</i>	1.5-3.5	6-11	7-21	3.2-6.9	1.8-6.8	30-60	0.9-4.2	0.2-0.3	3.7-12.5	?
<i>Mallotus darbyshirei</i>	1.9-2.4	?	?	?	?	?	?	?	3.8-4.5	6-10
<i>Mallotus decipiens</i>	1.9-2.4	?	7-16	2.5-4	1.8-2.2	22-32	1.3-3	0.2-0.3	6.8-16	0.3-1
<i>Mallotus didymochryseus</i>	1.1-1.4	?	20-22	?	3.5-4	60-90	?	0.2-0.3	5-12	?
<i>Mallotus discolor</i>	1.8-2.7	?	4.3-7	?	0.6-2	20-40	0.5-1.3	0.2-0.3	?	0.7-1.3
<i>Mallotus dispar</i>	2.1-2.5	?	6-12	3.5-4	?	28-50	1.5-2.5	0.2-0.3	5-12	?
<i>Mallotus dispersus</i>	1.3-1.63	?	?	?	1-3.5	62-78	0.6-2.5	0.3-0.3	?	?
<i>Mallotus distans</i>	1.37-2.2	?	2.9-3.7	?	1.8-2	35-35	1.7-2.3	0.1-0.2	3.8-9.7	0.5-0.8
<i>Mallotus eriocarpus</i>	2-2.5	?	2.4-3.4	?	2.5-3	35-50	?	0.2-0.3	2.8-5	?
<i>Mallotus eximius</i>	1.7-2.6	?	10-15	?	?	30-35	?	0.2-0.3	15-34	6-11
<i>Mallotus ficifolius</i>	1.17-1.6	?	2-6.5	?	?	20-33	?	0.2-0.3	1.5-4.5	3-3.5
<i>Mallotus floribundus</i>	0.7-1.9	7-11	7-23	?	1.3-5	25-55	?	0.5-0.7	3-11	?
<i>Mallotus fuscescens</i>	2.1-3.7	?	2.3-5.5	2-2.5	?	20-34	?	0.2-0.3	1.2-10	2.5-6
<i>Mallotus garretti</i>	1.3-2.3	?	10-13	3-4.5	2-3.3	30-45	?	0.2-0.3	?	?
<i>Mallotus glabrescens</i>	1.8-4	?	?	4.5-6	0.8-3	35-55	?	0.6-0.8	1.5-5.2	2-4.5
<i>Mallotus glomerulatus</i>	3-3.8	8-10	?	3.5-4	?	25-30	0.5-1	0.7-0.8	1.1-5	?
<i>Mallotus havilandii</i>	2.1-4.5	13-16	11-15	2.5	?	30-40	?	0.2-0.3	1.2-18	?
<i>Mallotus hispidospinosus</i>	2-3.4	?	2.5-5	3-3.3	5-11	60-70	0.5-1.2	0.2-0.3	3-3.5	?
<i>Mallotus hymenophyllus</i>	1.2-1.5	?	6-13.7	?	3-12	28-58	1-1.5	0.3-0.5	?	?
<i>Mallotus insularum</i>	2.1-3.2	8-12	6-9.5	3.5-5.5	1.5-3	30-55	2-3.2	0.2-0.3	?	?
<i>Mallotus japonicus</i>	1.05-2	?	9.5-25	3.5-6.5	?	60-90	?	0.2-0.3	4.9-5.8	0.5-2
<i>Mallotus khasianus</i>	1.8-4.3	7-12	7-53	?	5-15	40-86	1-4.5	0.5-0.7	20-45	?
<i>Mallotus kongkandae</i>	2.3-3.6	9-10	?	?	?	?	?	?	?	?
<i>Mallotus korhalsii</i>	1.2-1.7	?	3-22	?	0.5-3	23-33	2.3-3	0.1-0.2	4-24	1.5-3
<i>Mallotus lackeyi</i>	1.2-2.3	?	?	3-4.5	0.8-3	20-34	1-3.3	0.2-0.3	?	?
<i>Mallotus lanceolatus</i>	?	?	1.2-9	3-3.6	1.5-2.5	30-60	0.5-2	0.2-0.3	?	0.8-2.5
<i>Mallotus lanceifolius</i>	1.9-4.3	?	10-25	?	?	30-65	1.7-4	0.2-0.3	?	1.8-4.5
<i>Mallotus lauterbachianus</i>	1.6-2.1	?	5-14	?	6-10	30-65	1.8-5	0.3-0.4	2.7-4	?
<i>Mallotus leptostachyus</i>	?	?	?	?	1-1.5	40-60	0.7-2.5	0.2-0.3	?	0.5-0.8
<i>Mallotus leucocalyx</i>	1.5-1.9	?	3.5-12	3-4.2	?	20-40	?	0.2-0.3	9.4-16	?
<i>Mallotus leucocarpus</i>	1.06-1.09	?	?	?	?	?	?	?	?	?
<i>Mallotus leucodermis</i>	1.6-2.7	?	4-22	?	?	17-41	?	?	3-32.5	6-55
<i>Mallotus longervis</i>	?	?	8-12	1.8-2	0.5-0.8	18-25	0.5-1.5	0.2-0.3	6-17	2.5-3
<i>Mallotus macrostachyus</i>	1-1.3	?	?	4-4.5	3.2-4.2	60-90	?	0.2-0.3	?	?
<i>Mallotus macularis</i>	1.7-2.6	6-10	4.5-6	5-5.5	3-4.5	55-65	2.5-4	0.2-0.3	12-17	?
<i>Mallotus megalontus</i>	2.2-3.2	?	3.4-14	?	?	25-35	1.5-3	0.2-0.3	?	?
<i>Mallotus metcalfianus</i>	0.96-1.37	?	8-25	?	?	70-80	1-5.8	0.2-0.3	?	?

Morphological data matrix. Continued.

	71	72	73	74	75	76	77	78	79	80
<i>Mallotus microcarpus</i>	1.27-1.66	?	?	3-3.5	?	50-60	?	0.2-0.3	?	1.5-1.8
<i>Mallotus minimifractus</i>	1.8-3.3	?	6-10	3.3-4	1.7-3	40-90	1-2.5	0.2-0.3	3.4-12	?
<i>Mallotus nitqueletanus</i>	2.8-4.1	11-19	?	5-8.5	?	26-47	0.5-3.5	0.2-0.3	6.7-10	?
<i>Mallotus nitras</i>	2-2.9	?	?	?	?	?	?	?	1-1.7	?
<i>Mallotus mollissimus</i>	1.2-1.4	8-11	14-43	?	3-3.5	50-80	1.5-3	0.2-0.3	?	0.5-0.5
<i>Mallotus monanthos</i>	3.4-4	15-18	?	?	1-1.7	20-23	?	0.6-0.7	?	?
<i>Mallotus montanus</i>	1.6-2.5	?	2.5-4	3-3.5	1.2-1.5	20-30	?	0.2-0.3	?	0.8-1
<i>Mallotus muticus</i>	1.3-2.4	?	4-22	?	?	17-41	?	0.5-0.7	3.5-23.5	1-12
<i>Mallotus nepalensis</i>	1.2-1.8	?	9.5-10	7-7.5	?	60-70	1.5-3	0.2-0.3	7-7.5	0.5-1
<i>Mallotus nepohilus</i>	0.9-1.5	?	5.8-14.8	?	1-3.5	45-60	0.5-1	0.2-0.3	5.4-10.3	0.5-1
<i>Mallotus nudiflorus</i>	1-2.3	?	?	4.7-9	3.9-10	45-75	1.1-6	0.8-1.7	1.5-10.5	1-1.9
<i>Mallotus oppositifolius</i>	1.5-3.2	?	3-21	?	1.5-4	40-55	?	0.2-0.3	6.4-12.5	1.5-3.8
<i>Mallotus pachypodus</i>	2.1-2.7	6-10	?	?	?	?	?	?	?	?
<i>Mallotus pallidus</i>	2.4-4.1	8-10	?	?	2.3-5.2	50-70	0.6-3	0.2-0.3	?	?
<i>Mallotus paniculatus</i>	0.8-2	?	?	?	?	40-65	1.5-2	0.2-0.3	?	?
<i>Mallotus peltatus</i>	1.3-4	5-13	?	?	0.6-3	50-50	1-3.5	0.2-0.3	?	?
<i>Mallotus philippensis</i>	1.2-5.2	8-11	?	?	0.5-2	18-33	0.5-4	0.5-1	?	0.5-2
<i>Mallotus pierreii</i>	1-2.8	?	6-12	?	2.5-3.5	19-35	?	0.2-0.3	3-15	4-12
<i>Mallotus pleiogynus</i>	1.2-1.7	?	?	2.5-3.8	0.5-3	15-50	0.3-0.8	0.2-0.3	?	2-4.6
<i>Mallotus plicatus</i>	1.7-2.8	?	8-18	?	2.5-2.5	20-25	0.5-1.5	0.5-0.7	7-21	?
<i>Mallotus polyadenus</i>	1.5-4.3	?	2.8-20.7	?	0.8-4	20-100	1.5-3	0.2-0.3	3-21	2-3.5
<i>Mallotus polycarpus</i>	1-2-1.4	?	?	?	?	?	?	?	?	2-2.5
<i>Mallotus puber</i>	1.5-2.1	?	3-8.5	2-2.5	1.5-2	30-50	0.2-0.5	0.2-0.3	8-38.5	4-5-5
<i>Mallotus repandus</i>	1.1-2.2	?	15-15	?	1.8-5.2	30-75	?	0.5-0.8	?	?
<i>Mallotus resinosus</i>	1.7-4.3	8-12	1.7-17.3	2.5-4	?	29-40	1.5-2.5	0.2-0.3	2.1-7.2	0.5-1
<i>Mallotus rhannifolius</i>	1.9-4.8	?	10-13	3-4.5	?	40-45	0.8-2.5	0.2-0.3	2.6-5	1-1.5
<i>Mallotus roxburghianus</i>	1.04-1.38	?	18-22	4.3-4.5	2.5-4	50-50	1-1.3	0.2-0.3	7-21	5-13
<i>Mallotus rugifolius</i>	1.6-3	?	9-20	3-4.5	2.5-5	50-60	1.5-3.2	0.2-0.3	16-20	?
<i>Mallotus sphaerocarпус</i>	1.4-2	6-10	16-21	3-3.4	?	30-38	0.3-1.8	0.1-0.2	9-14	0.8-1.2
<i>Mallotus spinifractus</i>	2.6-2.9	?	?	?	?	?	?	?	?	0.5-0.5
<i>Mallotus subcuneatus</i>	1.5-2.5	?	2-3.5	?	?	30-40	2.5-4	0.1-0.2	?	?
<i>Mallotus subulatus</i>	1.6-2.4	4-11	2.7-13	?	?	42-50	?	0.5-0.7	2-7.5	4-12
<i>Mallotus sumatranus</i>	1.6-4.3	?	6-16.2	3.5-4	?	30-42	1.5-3	0.3-0.7	4.2-19.5	2-4.2
<i>Mallotus surculosus</i>	1.1-1.6	?	?	?	2.5-3	30-30	?	0.2-0.3	?	?
<i>Mallotus tetraococcus</i>	0.9-1.3	?	?	?	1.8-5	45-70	2-3.2	0.2-0.3	?	1-1.5
<i>Mallotus thorelii</i>	?	?	?	3.5-3.5	1.3-2.3	40-40	?	0.2-0.3	?	?
<i>Mallotus titifolius</i>	1-1.3	7-11	7-22	2.8-5.5	?	45-70	0.5-2.3	0.2-0.3	5-15	1.7-2.5
<i>Mallotus trinervius</i>	1.4-1.81	?	9-17	?	2-3.5	100-120	2.5-5	0.2-0.3	?	?
<i>Mallotus usulatus</i>	1-1.5	?	1.5-6	2.5-2.5	1.5-2	15-65	2-2.5	0.2-0.3	2.7-4	2-5-3
<i>Mallotus wrayi</i>	2.3-5	?	5-11	2.5-4.7	2-7.8	18-40	0.8-3	0.3-0.4	4-11	?

Morphological data matrix. Continued.

	81	82	83	84	85	86	87	88	89	90
<i>Blumeodendron kurzii</i>	1-1.5	?	?	?	27-40	?	1.5-1.5	17-23	45-55	23-27
<i>Blumeodendron subrotundifolium</i>	1-1.5	?	0.5-1.8	1.3-2	25-30	?	?	20-20	?	?
<i>Blumeodendron tokbrai</i>	1.8-2	?	0.7-0.8	?	19-40	?	?	22-22	?	?
<i>Cordemoya acuminata</i>	2.5-3	?	0.5-1	8-13	15-25	5-11	0.8-1.3	6-6.5	?	23-25
<i>Cordemoya capuroni</i>	1.8-2	?	0.5-1	8-15	11-13	14-17	0.3-0.5	?	?	23-25
<i>Cordemoya cordatifolia</i>	?	?	?	?	?	?	?	?	45-45	?
<i>Cordemoya eucanata</i>	?	?	0.5-0.5	4-10	8-15	0.5-1	0.5-1	?	24-24	17-21
<i>Cordemoya grandistipularis</i>	?	?	1.8-1.8	9.5-9.5	15-15	?	1-1.5	7-7.5	45-45	17-21
<i>Cordemoya griffithiana</i>	1.8-2	?	0.5-0.5	6-15	8-12	?	1-1.5	?	29-29	?
<i>Cordemoya hirsuta</i>	?	?	?	10-16	9-10	?	?	4.5-4.5	?	?
<i>Cordemoya hookeriana</i>	1.5-1.5	?	?	14-22	9-10	?	1-1.5	?	43-43	?
<i>Cordemoya integrifolia</i>	2-2.5	?	0.5-2	10-25	10-14	3-10	0.8-1	?	40-65	21-23
<i>Cordemoya kingii</i>	1.3-1.5	?	0.5-1	6-17	15-16	?	1-1.5	7-8.5	23-26	?
<i>Cordemoya longistyla</i>	3-3.2	?	1.5-2	15-15	7-10	?	1-1.5	?	?	22-25
<i>Cordemoya papuana</i>	1.5-1.8	?	0.5-1	8-12	9-15	4.5-6	0.5-1	?	?	19-22
<i>Cordemoya peanangensis</i>	2.8-3.2	?	0.7-1	5-10	5-6.5	?	0.5-1	3.5-7	?	20-21
<i>Cordemoya spinulosa</i>	1.5-1.7	?	0.5-1.5	6-11	8-10	1.7-2	0.3-0.5	3.8-4	55-55	?
<i>Cordemoya stipularis</i>	1.5-2	?	0.5-1	8-12	8-15	6-10	1-1.2	4.5-5	22-28	24-25
<i>Cordemoya subpeltata</i>	?	?	1-1.5	22-22	10-14	?	?	9.5-15	10-15	25-28
<i>Cordemoya wenzeliana</i>	1.5-2	?	0.5-1	?	10-14	?	1-1.2	?	?	?
<i>Macaranga albescens</i>	?	?	?	?	3.8-4	?	0.2-0.2	3-3.5	?	?
<i>Macaranga denticulata</i>	?	?	?	?	3-4.5	?	0.1-0.2	1.5-1.5	?	?
<i>Macaranga gigantea</i>	?	?	?	?	?	?	?	?	?	12-17
<i>Macaranga hypoleuca</i>	1-1.5	?	?	1-1.3	?	?	0.15-0.2	3.8-4	?	?
<i>Macaranga inamoena</i>	1.2-1.2	?	?	7-10	?	0.5-1	0.8-0.8	2.5-2.5	?	?
<i>Macaranga kurzii</i>	?	?	?	7-10.5	?	3.5-5	0.5-0.5	2.8-3	?	?
<i>Macaranga repando dentata</i>	?	?	0.5-0.5	12-40	?	0.5-1	?	3.8-4	?	?
<i>Macaranga tanarius</i>	?	?	?	?	?	?	?	?	?	22-24
<i>Macaranga trichocarpa</i>	1.2-1.2	?	?	?	7.5-8.5	?	0.8-0.8	3.5-3.5	?	?
<i>Mallotus actinoneurus</i>	2.3-2.5	?	2.2-2.2	?	15-18	?	1.8-2	11.5-11.5	?	19-27
<i>Mallotus anomalus</i>	2.5-2.5	?	1-1.2	1.5-2.5	?	?	?	?	?	?
<i>Mallotus apelta</i>	?	?	0.5-0.5	?	?	?	?	?	?	?
<i>Mallotus atrovirens</i>	?	?	?	?	?	5-10	?	?	?	?
<i>Mallotus barbatulus</i>	2.5-3.5	?	1.5-1.5	?	10-21	?	0.2-0.2	?	?	?
<i>Mallotus bumeanus</i>	1.8-2	?	0.2-0.5	?	10-12	?	0.1-0.1	?	60-60	21-25
<i>Mallotus brachylyrus</i>	?	?	?	?	?	?	0.2-0.2	?	23-38	16-27
<i>Mallotus brevipetiolatus</i>	1-1.4	?	0.5-0.7	1.3-3.5	?	0.2-0.4	0.2-0.2	?	21-24	?
<i>Mallotus calocarpus</i>	2.5-3.5	?	1.5-3	6-10	15-17	1.5-3	1-1.5	5.5-8	?	?
<i>Mallotus cambodianus</i>	1.5-1.5	?	0.5-0.5	?	?	?	0.3-0.3	4.3-5	25-31	25-31
<i>Mallotus caudatus</i>	1.2-2.5	?	1.3-3	?	10-17	?	0.5-1.3	?	30-30	?
<i>Mallotus cauliflorus</i>	2-2.5	?	0.3-0.5	?	9-11	0.5-1	0.8-1	4.5-5	?	23-24
								3.5-5		

Morphological data matrix. Continued.

	81	82	83	84	85	86	87	88	89	90
<i>Mallotus chromocarpus</i>	1.5-1.8	?	?	1-1.2	?	?	0.2-0.2	4-4.2	?	?
<i>Mallotus claxylloides</i>	1.8-2	?	0.5-1	3-3.5	6-8.5	1-1.3	0.8-1	?	?	26-30
<i>Mallotus conicus</i>	1.8-1.8	?	?	2-2.5	?	?	?	3.5-3.5	25-37	?
<i>Mallotus connatus</i>	2.5-3	?	?	?	10-15	1.5-3	0.8-1.2	?	26-38	21-23
<i>Mallotus condercii</i>	1.2-1.3	?	0.6-3	2-2.2	4.5-8	?	0.1-0.1	3-4.5	?	?
<i>Mallotus cunningii</i>	1.2-1.5	?	0.5-2.1	4.4-8.4	9-15	?	0.8-1.2	?	39-39	?
<i>Mallotus darbyshirei</i>	?	?	?	?	?	2.5-3	0.8-1	?	?	?
<i>Mallotus decipiens</i>	0.5-0.6	?	0.2-0.5	0.7-1	?	0.5-0.7	0.2-0.2	2.9-3.1	45-45	21-25
<i>Mallotus didymochrysenus</i>	1.6-1.8	?	0.2-0.4	2.3-2.7	10-12.5	?	0.5-0.5	?	?	?
<i>Mallotus discolor</i>	1.2-2	?	?	1-1.8	3.5-8	?	0.2-0.2	3.2-3.2	40-40	19-20
<i>Mallotus dispar</i>	1.5-1.8	?	0.7-1.3	3.5-6	8-12	?	0.7-1	26-28	17-23	17-23
<i>Mallotus dispersus</i>	2.5-3	?	0.5-1.2	3-3.5	8-12	?	0.5-0.5	8-10	26-32	?
<i>Mallotus dispansus</i>	2-2.3	?	?	3.5-4	8-8.5	?	?	4.5-5	?	?
<i>Mallotus eriocarpius</i>	1-1.2	?	0.2-0.2	?	5.5-7	0.5-1.5	0.3-0.3	?	?	?
<i>Mallotus erimius</i>	3.2-4	?	?	?	17-20	1.5-3	1.7-2	12-13	?	?
<i>Mallotus ficifolius</i>	1.8-2.2	?	0.5-1	3-3.5	?	?	0.8-1	?	12-26	?
<i>Mallotus floribundus</i>	1-1.5	?	?	4-11	10-20	?	?	?	?	?
<i>Mallotus fuscescens</i>	1.2-1.2	?	?	1.2-2	?	?	0.3-0.8	4.5-4.5	14-14	?
<i>Mallotus garretti</i>	1-1.5	?	1-2.5	?	10-10	2-2.5	?	?	?	?
<i>Mallotus glabrusculatus</i>	1.3-1.5	?	0.5-2	?	7-13	?	0.2-0.5	4.5-7	14-22	31-33
<i>Mallotus glomerulatus</i>	1.8-2	?	2-2.5	?	9-10	?	0.8-0.8	?	27-40	19-23
<i>Mallotus havilandii</i>	?	?	0.5-1	2.5-2.5	?	0.2-0.4	0.7-1.2	5.5-6	38-38	16-23
<i>Mallotus hispidospinosus</i>	?	?	?	?	?	2.5-3	?	4.5-5	11-17	19-23
<i>Mallotus hypenophyllus</i>	1.3-1.6	?	0.8-1.7	1.5-6	6-11	0.5-2	0.8-1	3-5.5	?	?
<i>Mallotus insularum</i>	1.8-1.8	?	0.5-1	2.5-2.5	?	?	?	?	24-24	19-25
<i>Mallotus japonicus</i>	2-2.3	?	0.5-1	2.2-7.8	?	?	0.2-0.2	5-5.5	60-60	27-34
<i>Mallotus khasianus</i>	1.2-2	?	0.5-2	5-14	9-18	1.2-2.3	1-1.4	5.5-10.8	45-45	21-32
<i>Mallotus kongkandae</i>	?	?	?	?	?	?	?	6-7.5	?	?
<i>Mallotus korhalsii</i>	1.5-2.1	?	0.2-0.5	?	5-11	1-1.7	1-1.5	?	?	?
<i>Mallotus lackeyi</i>	1-1.5	?	?	?	10-13	2-2.5	?	3.5-5	70-80	19-22
<i>Mallotus lanceolatus</i>	1.2-1.5	?	0.4-0.7	1.2-2.5	?	?	0.5-0.7	2.2-3.3	11-15	29-36
<i>Mallotus lancifolius</i>	1.7-2	?	0.5-1.5	2.7-8.3	8-16	1.5-3	0.5-0.8	?	?	?
<i>Mallotus lauterbachianus</i>	2.5-2.8	?	?	3-4.5	?	?	?	?	?	?
<i>Mallotus leptostachyus</i>	1-1.2	?	?	2-2.5	8-8.2	?	0.3-0.6	2.8-3	?	?
<i>Mallotus leucocarpus</i>	1.8-2	?	1.5-2	?	7-7.5	3-4.2	0.7-1	3-4.5	40-40	?
<i>Mallotus leucocaryx</i>	1.8-2	?	0.2-0.3	?	13.5-13.5	?	0.3-0.3	5.5-5.5	?	?
<i>Mallotus leucocarpus</i>	1.8-2	?	0.3-0.3	?	8-15	?	0.8-1	?	?	?
<i>Mallotus leucodermis</i>	1-1.3	?	0.5-1	1.8-2.3	5-5.5	?	0.1-0.2	2-2.2	12-12	17-25
<i>Mallotus longimervis</i>	3.2-4	?	1.2-1.2	?	11-16	?	0.2-0.2	?	?	?
<i>Mallotus macrostachyus</i>	2.8-3	?	0.6-0.8	?	7.5-9	1-1.2	?	5.5-7	30-33	28-30
<i>Mallotus macularis</i>	2-2.2	?	0.8-0.8	?	5.5-7	1-1.2	0.8-1	5.2-5.5	32-32	25-31
<i>Mallotus megalanthus</i>	?	?	?	?	15-17	?	0.2-0.2	5-5.5	100-100	17-19

Morphological data matrix. Continued.

	81	82	83	84	85	86	87	88	89	90
<i>Mallotus microcarpus</i>	?	?	?	?	?	0.2-0.2	0.2-0.2	1.8-2	40-40	19-21
<i>Mallotus minimifractus</i>	1.3-1.5	?	0.2-0.6	2.2-5.5	5-10	1.5-3.5	0.7-0.9	3.8-4	?	?
<i>Mallotus niqueletanus</i>	1.8-2.2	?	0.4-2	3.5-7	7-13	0.2-0.5	?	?	21-21	16-22
<i>Mallotus nitrus</i>	?	?	?	?	10-11	?	0.8-0.8	?	?	23-27
<i>Mallotus mollissimus</i>	2.2-3	?	0.5-1.2	2.2-3	10-16	8-10	0.2-0.2	?	80-80	?
<i>Mallotus monanthos</i>	?	?	?	?	17-17	?	?	?	35-40	23-25
<i>Mallotus montanus</i>	1-1.2	?	0.2-0.4	?	6-13	?	0.5-0.5	4-10	10-20	?
<i>Mallotus muticus</i>	2-2.5	?	1-1.2	2-2.5	12-25	?	?	15-15	?	?
<i>Mallotus nepalensis</i>	?	?	1-1.3	2.7-4	?	4.5-6	0.2-0.2	?	60-60	?
<i>Mallotus nesophilus</i>	1-1.5	?	?	?	3.5-5	?	0.2-0.2	2.8-3.2	?	?
<i>Mallotus nudiflorus</i>	3-3.5	?	1.7-5.9	12-24	18-29	?	?	?	60-70	23-27
<i>Mallotus oppositifolius</i>	1.2-1.4	?	0.2-0.6	1.3-1.7	?	2.5-2.5	0.2-0.2	2-2.8	28-30	17-25
<i>Mallotus pachyproctus</i>	?	?	?	?	15-15	?	1.5-1.8	?	?	?
<i>Mallotus pallidus</i>	1.4-1.7	?	?	?	7.3-7.8	?	0.6-0.8	?	90-90	10-12
<i>Mallotus paniculatus</i>	1.3-1.5	?	?	1.2-2	3-12	?	0.2-0.2	2.8-3.3	70-70	?
<i>Mallotus peltatus</i>	1.5-1.8	?	?	?	7-15	2-2.5	?	?	18-18	21-23
<i>Mallotus philippensis</i>	1-1.5	?	?	?	4-12	?	0.3-0.5	?	?	?
<i>Mallotus pierrei</i>	1.5-3	?	0.5-1	?	?	0.8-1.2	0.8-1	4.5-5.8	31-31	19-26
<i>Mallotus pleiogynus</i>	2.5-2.5	?	?	2.2-4.7	9-12	?	0.8-1	?	70-70	?
<i>Mallotus plicatus</i>	2-2.5	?	0.3-0.5	2-2.5	8-10	?	0.3-0.8	15-15	?	?
<i>Mallotus polyadenus</i>	1.1-1.3	?	0.1-0.2	2-2.5	12-12	?	0.8-1	?	?	?
<i>Mallotus polycarpus</i>	2-2.5	?	?	10-12	?	?	0.8-1	?	?	23-25
<i>Mallotus puber</i>	1-1.2	?	?	?	?	?	0.8-1	?	?	?
<i>Mallotus repandus</i>	1-1.2	?	1.5-1.5	1.5-2.5	5-11	?	0.5-1	3-7.5	60-70	17-28
<i>Mallotus resinosus</i>	1.3-1.7	?	0.2-0.5	2-3.5	?	1-2.2	0.7-1	?	31-31	19-23
<i>Mallotus rhamnifolius</i>	1.4-1.7	?	?	1.2-1.5	4.5-5.5	?	0.3-0.6	?	75-75	12-15
<i>Mallotus roxburghianus</i>	1-1.5	?	?	2-5.3	10-10	?	?	?	?	?
<i>Mallotus rugifolius</i>	2-5.3	?	0.2-1	?	8-20	2.8-4	0.8-1.1	?	30-50	19-22
<i>Mallotus sphaerocarpus</i>	2-2.2	?	0.4-0.7	1.8-3	15-19	0.5-1	0.1-0.1	?	?	?
<i>Mallotus spinifractus</i>	?	?	1.5-1.5	?	18-19	?	1-1.5	5.5-6.5	21-28	?
<i>Mallotus subincatus</i>	1.8-2.3	?	?	1.5-2	8-10	0.8-1	0.5-0.5	5-5.5	29-29	19-28
<i>Mallotus sumatranus</i>	3.5-3.5	?	0.8-2	2-3.5	?	?	0.5-0.5	?	?	?
<i>Mallotus succulotus</i>	1.8-2	?	0.5-1	2-5.3	8-10	2-2.5	?	2.5-3	34-34	?
<i>Mallotus tetraecoccus</i>	1.8-2	?	0.5-1	2-3.8	12-14	2-2.5	0.2-0.2	4.2-4.5	?	?
<i>Mallotus thorelii</i>	1.8-2	?	0.6-1.5	?	?	?	?	?	50-80	19-23
<i>Mallotus trifolius</i>	1.3-1.5	?	0.4-0.7	2.5-4.3	5-15	0.5-2	0.8-1	?	?	?
<i>Mallotus trinervius</i>	?	?	?	?	17-22.5	?	?	?	30-30	23-32
<i>Mallotus usulatus</i>	1.8-2.2	?	0.3-0.5	1.8-3	?	3-3.8	0.8-1	10-15	70-70	?
<i>Mallotus wrayi</i>	2-2.3	?	1-1.2	?	13-23	5-5.5	1-1.5	3.5-4	?	?