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Leaf anatomy of *Mallotus* and the related genera *Blumeodendron* and *Hancea* (Euphorbiaceae *sensu stricto*)

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The leaf anatomy of *Mallotus* and *Hancea* (both subtribe Rottlerinae, tribe Acalypheae) and *Blumeodendron* (tribe Pycnocomeae) from Euphorbiaceae *sensu stricto* (subfamily Acalyphoideae) was studied in detail on the basis of 84 specimens belonging to 71 species. Some leaf anatomical features do not show much variation; almost all species have a relatively constant dorsiventral mesophyll, paracytic stomata and collateral bundles in the mesophyll. However, the diversity of other characters is great, especially the hair types, and useful in characterizing infrageneric groups. Capitate glandular hairs are characteristic for *Hancea*, whereas globular to disc-shaped glandular hairs occur in most *Mallotus* spp. Glandular hairs are absent in the two other genera. Morphological diversity in globular to disc-shaped hairs in *Mallotus* also provides taxonomically important information. *Hancea* is characterized by the presence of brachysclereids and cristarque cells and by an abundance of columnar and fibriform mesophyll sclereids. *Blumeodendron* shares with *Hancea* the presence of brachysclereids and fibriform sclereids, but is further characterized by the presence of giant stomata. In this study, leaf anatomy is used to discuss the infrageneric delimitation of *Mallotus* and *Hancea* and to compare these genera with the more distantly related *Blumeodendron*. *Botanical Journal of the Linnean Society*, 2012, **169**, 645–676.

ADDITIONAL KEYWORDS: Acalypheae – Acalyphoideae giant stomata – cristarque cells – glandular hairs – sclereids.

INTRODUCTION

Mallotus Lour. is a large genus of Euphorbiaceae, comprising about 110 species. It occurs mainly in Southeast Asia and the West Pacific, with two species in Africa and Madagascar (Kulju, Sierra & van Welzen, 2007a). Until recently, it was placed in subtribe Rottlerinae with seven or eight small genera, including *Cordemoya* Baill., *Trewia* L., *Neotrewia* Pax & K.Hoffm. and *Octospermum* Airy Shaw (Webster, 1994; Radcliffe-Smith, 2001). The large genus *Macaranga* Thou., although sharing morphological and ecological similarities with *Mallotus*, was until recently classified in the monogeneric subtribe Macaranginae (Webster, 1994; Radcliffe-Smith, 2001). Wurdack, Hoffmann & Chase (2005) conducted a molecular phylogenetic study of Euphorbiaceae *sensu stricto* (*s.s.*) and demonstrated that *Macaranga*, *Mallotus* and *Trewia* form a well-supported clade, which is sister to *Blumeodendron* Kurz (tribe Pycnocomeae).

Due to its high morphological variability, *Mallotus* has been subdivided into a number of sections (Müller Argoviensis, 1865, 1866; Pax & Hoffmann, 1914; Airy Shaw, 1968). Airy Shaw (1968), for example, proposed eight sections, based on morphological characters. However, recent morphological and molecular studies by Sierra *et al*. (2010) indicated that *Mallotus* was polyphyletic. To obtain monophyly, Airy Shaw's sections *Hancea* and *Oliganthae* had to be excluded from the genus (and now form the genus *Hancea* Seem.)

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and some small, closely related genera, namely *Trewia*, *Neotrewia* and *Octospermum*, were included in *Mallotus* (Kulju *et al*., 2007a). Van Welzen *et al*. (2006) proposed the exclusion of five species from Airy Shaw's section *Hancea*, as these were true *Mallotus* spp. (see phylogenetic analysis in Sierra *et al*., 2010). Subsequently, section *Hancea* (without those five species) was excluded from *Mallotus* and placed with *Mallotus* section *Oliganthae* in the genus *Cordemoya*, which afterwards had to be renamed *Hancea*; at the time writing, *Hancea* comprises 17 species (Sierra *et al*., 2006, 2007; see Fig. 2). Besides the changes at the generic level, phylogenetic studies by Slik & van Welzen (2001b) also suggested on the basis of morphology that some *Mallotus* sections, namely *Axenfeldia* Baill. and *Rottleropsis* Müll.Arg. are polyphyletic.

To resolve these problems of conflicting classifications, a phylogenetic study using molecular (plastid and nuclear DNA sequences), morphological, leaf anatomical and palynological characters was conducted on *Mallotus* and related genera (Kulju *et al*., 2007b; Sierra *et al*., 2010). Leaf anatomical characters, which are discussed in detail in this article, were used in the combined phylogenetic analyses, and several leaf anatomical synapomorphies were found for some sections of *Mallotus*. In this new phylogenetic analysis, *M*. sections *Mallotus*, *Polyadenii* and *Stylanthus* Rchb. & Zoll. were found to be monophyletic. *Mallotus* sections *Axenfeldia* and *Rottleropsis* were polyphyletic and *M*. section *Philippinenses* Pax & K.Hoffm. is a grade, forming a monophyletic group with section *Mallotus* (Sierra *et al*., 2010). Additionally, six other clades were identified: a clade of the five species of former section *Hancea* (which we will now call the *Miquelianus* clade), the *Glomerulatus* clade, the *Subulatus* clade, the *Resinosus* clade, the *Wrayi* clade and the *Tiliifolius* clade (Sierra *et al*., 2010). These clades are mainly monophyletic groups in the polyphyletic sections *Axenfeldia* and *Rottleropsis*.

A detailed leaf anatomical study of some *Mallotus* and *Hancea* spp. had already been conducted by Rittershausen (1892) and Hussin, Wahab & Teh (1996). Based on some leaf anatomical characters, Rittershausen (1892) suggested that *Mallotus integrifolius* Müll.Arg. (now *Hancea integrifolia*; the authorities for all recent names of the sampled species are given in the Appendix) does not share similarities with other *Mallotus* spp. and should be excluded from *Mallotus* on the basis of the presence of intraxylary phloem in the stem. More than a century later, Hussin *et al*. (1996) published a leaf anatomical article on 15 species of *Mallotus* from the Malayan region and one from Thailand. Their study also included four species which now belong in *Hancea* (*H. kingii*, *H. penangensis*, *H. subpeltata* and *H. griffithiana*). *Hussin et al*. (1996) questioned the subgeneric classification of Airy Shaw, e.g. the placement of *Mallotus leucodermis* Hook.f and *M. muticus* (Müll.Arg.) Airy Shaw in section *Polyadenii*, or *M. kingii* Hook.f and *M. griffithianus* Hook.f. in *M*. section *Hancea*. Some of their doubts have been recently refuted by the results of the combined molecular and morphological phylogenetic study of Kulju *et al*. (2007b) and Sierra *et al*. 2007, 2010), which confirms the placement of *M. leucodermis* Hook.f and *M. muticus* Müll.Arg. in *M*. section *Polyadenii*, and *M. kingii* Hook.f and *M. griffithianus* Müll.Arg. in the genus *Hancea*.

Several studies concentrated also on some specific leaf anatomical characters in a limited number of species within the genera. Metcalfe & Chalk (1979) briefly mentioned the presence of a papillate epidermis, bundle sheath extensions (BSEs) and elongated sacks in *Mallotus* and laticiferous cells in *Macaranga*. Some attention was also drawn to the 'subglandular hairs' of *M. philippensis*. Kirkby (1884) also discussed the structure of the glandular hairs of *M. philippensis*, the main component of kamala powder, which is still used as a natural dye in Southeast Asia. Inamdar & Gangadhara (1977a, b) focused on the structure and ontogeny of stomata and trichome types in some Euphorbiaceae. Their studies included *M. polycarpus* (previously *Trewia polycarpa* Benth.) and *M. philippensis*. O'Dowd (1982), Fiala *et al*. (1994) and Guhling *et al*. (2005) focused on ant–plant interactions and studied extrafloral nectaries, pearl bodies, glandular trichomes and cuticular waxes mostly in *Macaranga*. Blüthgen & Reifenrath (2003) conducted a study on extrafloral nectaries in Australian rainforest plants, including *M. paniculatus*, *M. mollissimus* and some *Macaranga* spp.

Sister to *Mallotus* is the genus *Macaranga* (Wurdack *et al*., 2005; Kulju *et al*., 2007b), a genus of > 200 species (Whitmore, 2008). Based on leaf anatomy, this genus is comparable with *Mallotus*, although groups within *Macaranga* have their own apomorphic character states. We will not treat *Macaranga* here (too big), but we will briefly describe *Macaranga* in the Discussion.

In this paper we present the results of extensive research on the comparative leaf anatomy of selected species of the closely related genera *Mallotus* and *Hancea* and the more distantly related *Blumeodendron*. The sections and groups of *Mallotus* used to describe leaf anatomy are based on the results of the phylogenetic analysis of Sierra *et al*. (2010). Species that were not part of any group or section in that analysis are here described separately. The previous and new subdivisions of *Mallotus* are also compared and discussed.

MATERIAL AND METHODS

Material examined

All material was taken from herbarium specimens. Most specimens are stored in the Netherlands Centre for Biodiversity Naturalis (National Herbarium of the Netherlands branch = L). The specimens studied and authors of plant names are given in the Appendix. As a rule mature leaves were selected, but in cases where hairs were early caducous, young leaves were sampled in addition to mature ones, and examined with a scanning electron microscope. In most cases, only one leaf per species was sectioned.

Methods

Transverse and paradermal sections

Leaves were rehydrated by boiling in water for a few minutes and were then stored in 50% alcohol. Cross sections of different thicknesses were made from the middle of the lamina and petiole with a Reichert sledge microtome. Half of the sections were bleached with diluted household bleach (1:1) and stained with a safranin/haematoxylin mixture, and the other half were left unbleached and unstained. Freehand paradermal sections were taken from adaxial and abaxial leaf surfaces, and treated in the same way as the transverse sections. All sections were mounted in euparal.

Cuticular macerations

Cuticular macerations were made by placing leaf samples in a mixture of 30% hydrogen peroxide and glacial acetic acid (99–100%) (1:1) at 60 °C overnight. The following day the maceration mix was rinsed with water and the air in leaves was removed using an exsiccator. After that, the cuticle was carefully cleaned and placed in a preheated (40 °C) mixture of 0.5% Sudan IV in 70% alcohol for 2–3 h and mounted in glycerine gelatine preheated to 40 °C.

Leaf clearings

Two small squares of leaf tissue of each specimen were placed in 10% KOH and autoclaved for 20 min at 115 °C. The cleared specimens were washed several times in water, placed for a few minutes in diluted household bleach (1:1) to make them transparent, washed several times in water and mounted in glycerine gelatine preheated to 40 °C.

Photographs of transverse sections, cuticular macerations and leaf clearings were taken with an SIS Colorview 1 digital camera using the AnalySIS software.

Many of the leaves were studied with a scanning electron microscope. For this, two small squares of alcohol-stored leaves were taken from midrib and margin regions and dehydrated with acetone. After dehydration, the acetone-infiltrated specimens were critical-point dried using liquid CO_2. Dried samples were mounted on aluminium stubs and sputter-coated with gold using a Bal-Tec SCD 005 sputter coater. Leaf surfaces were then examined with a JEOL JSM-5300 SEM and photographed via the computer program SEMaFORE.

RESULTS

The results of this study agree largely with the short descriptions provided for several species by Rittershausen (1892) and Hussin *et al*. (1996) and with the general description in Metcalfe & Chalk (1979). The results are presented in two parts. The first part gives a general survey of leaf anatomical characters. The second part includes the descriptions of the species clades in *Mallotus* (Fig. 1; Sierra *et al*., 2010: fig. 3) and *Hancea* (Fig. 2; Sierra *et al*., 2007). The *Philippinenses* grade was subdivided into three groups, which are also found in the phylogenetic tree of Sierra *et al*. (2010), namely the *Rhamnifolius*, *Philippinenses* and *Pleiogynus* groups. *Mallotus nudiflorus*, *M. khasianus* and *M. polycarpus* are here treated together as the *Nudiflorus* group, although the clade does not have any support in the phylogenetic tree of Sierra *et al*. (2010). Species that are not included in any clade or section are described separately. Selected leaf anatomical characters are listed in Table 2.

Survey of leaf anatomical characters

Indumentum (Figs 3–10, 25–30, 31–33)

The indumentum of the examined genera consists of several types of hairs: short and long simple unicellular hairs (Figs 25, 27), simple uniseriate hairs (composed of two to four cells), stellately tufted hairs (Figs 26, 27–29, 31B), stellate hairs with a multicellular stalk (Fig. 31A), peltate non-glandular hairs, capitate glandular hairs (Figs 4, 32A), peltate-stellate hairs with a central glandular cell (Fig. 3) and globular to disc-shaped glandular hairs (Figs 5–10, 32B, C). The last-named are further subdivided into peltate-like (Fig. 32C) and bladder-like (Fig. 32B) glandular hairs.

Stellately tufted hairs are common in *Mallotus* (mainly absent in *Macaranga*). They can appear star-shaped (stellately tufted) or non-stellate, with thin or thick cell walls, with arms in one plane or radiating outwards in all directions. Stellate hairs with a multicellular stalk have a multiseriate, short to long, in some species sclerified stalk. Tufts are composed of six to > 30 arms.

Glandular hairs prove to be among the most informative characters in the three studied genera. Capi-

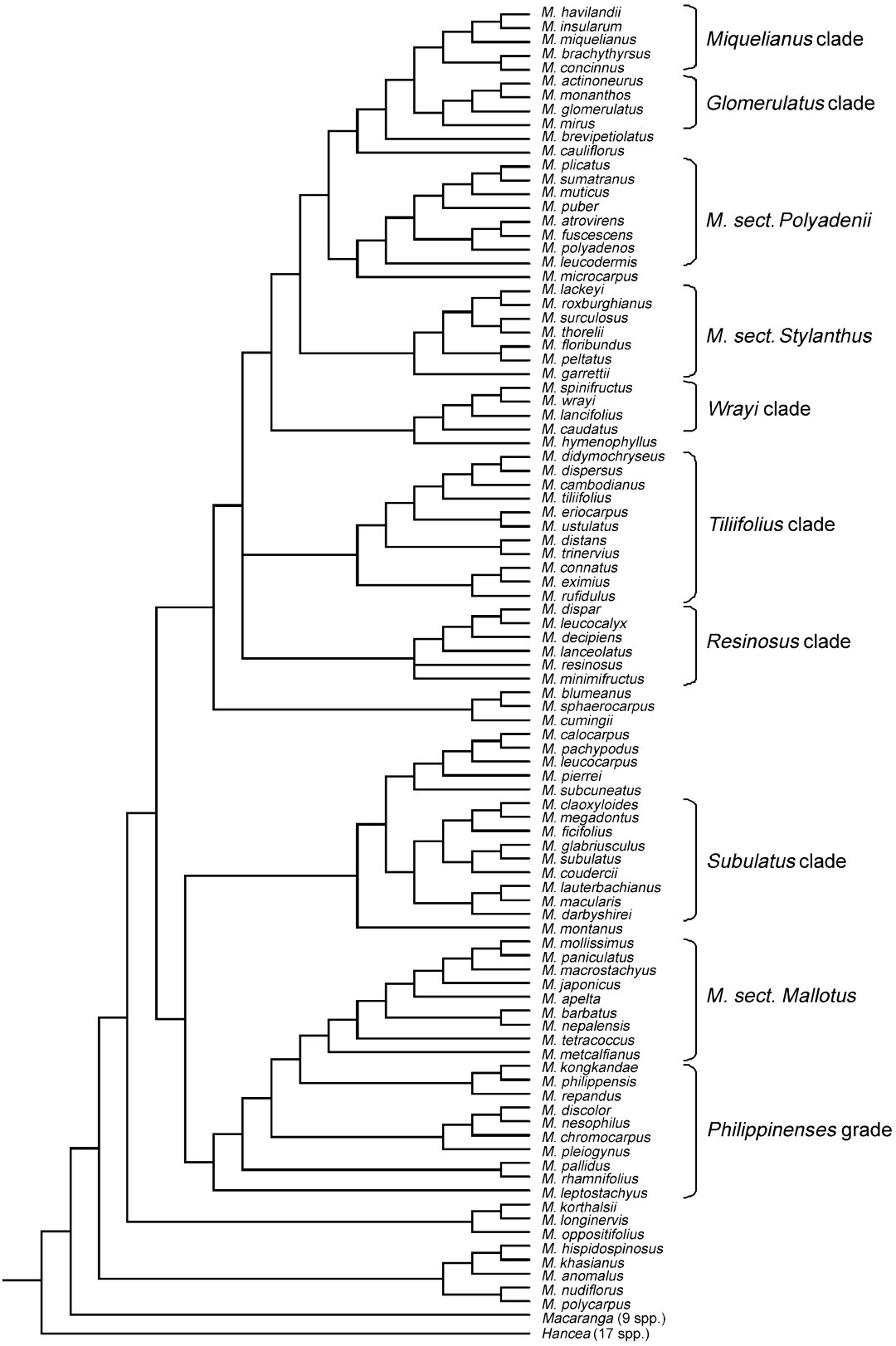


Figure 1. A strict consensus, parsimony-based cladogram summarizing the phylogenetic relationships of *Macaranga*, *Mallotus* and *Hancea* (based on molecular and morphological markers) adapted from Sierra *et al*. (2010: fig. 3).

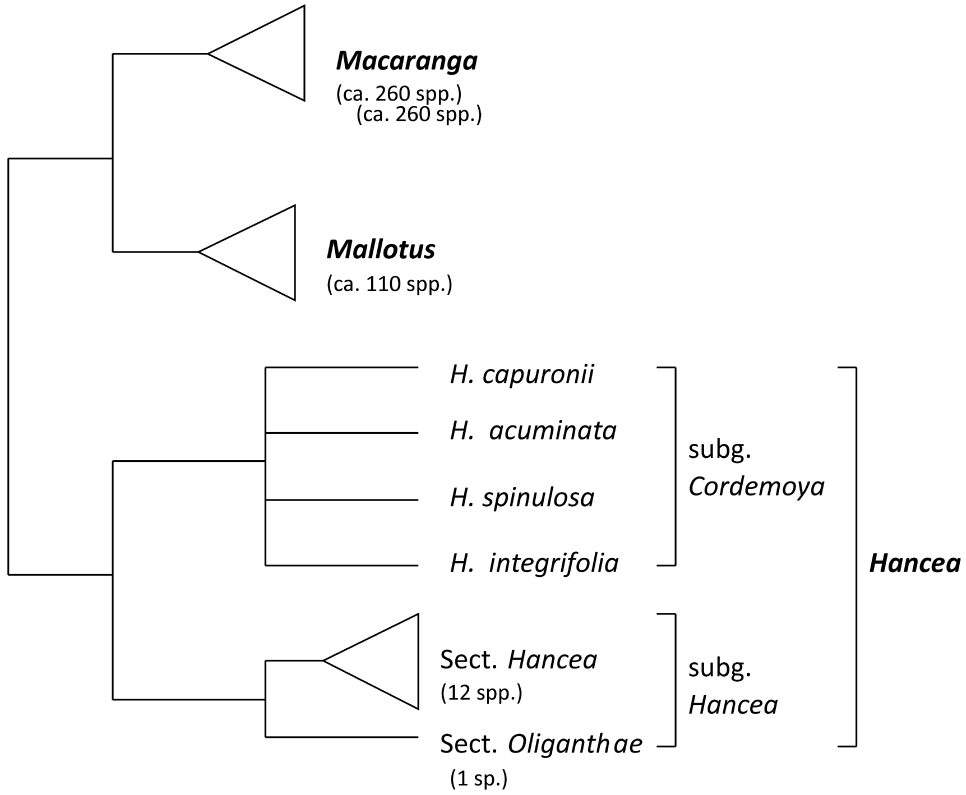
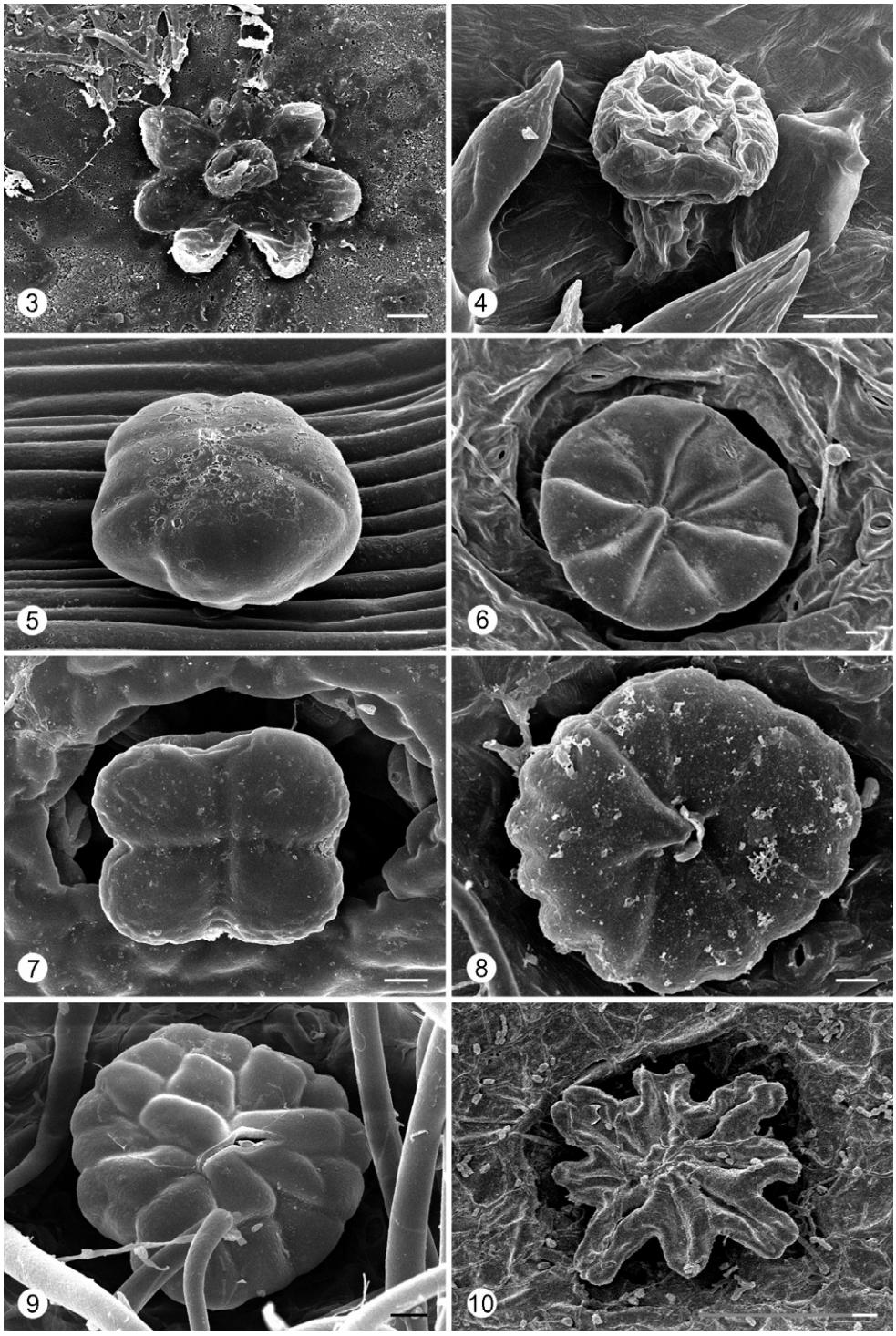
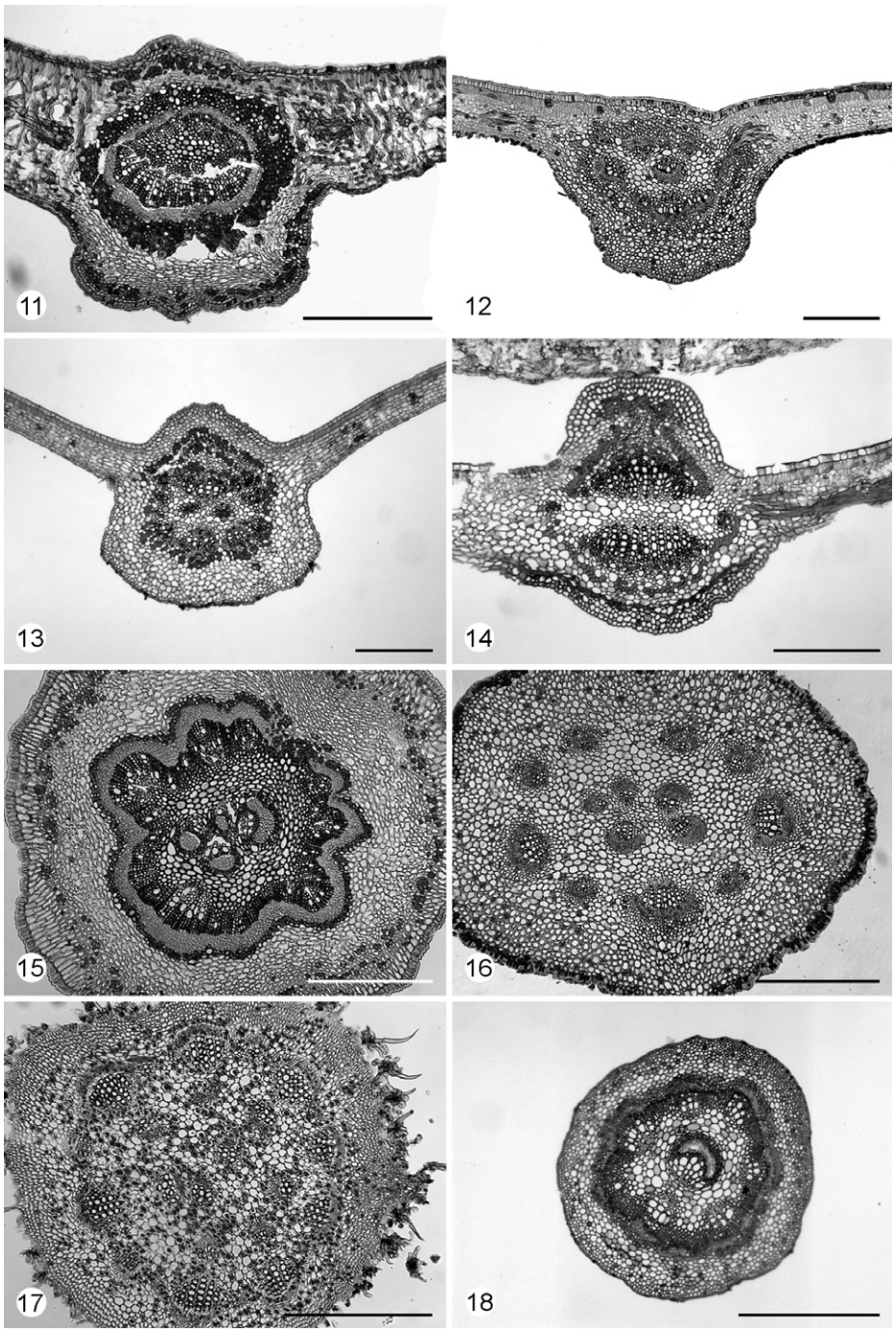


Figure 2. Simplified cladogram summarizing the phylogenetic relationships between *Macaranga*, *Mallotus* and *Hancea* (adapted from Sierra *et al*., 2006: fig. 1). Especially the new circumscription and classification of the genus *Hancea* is shown.

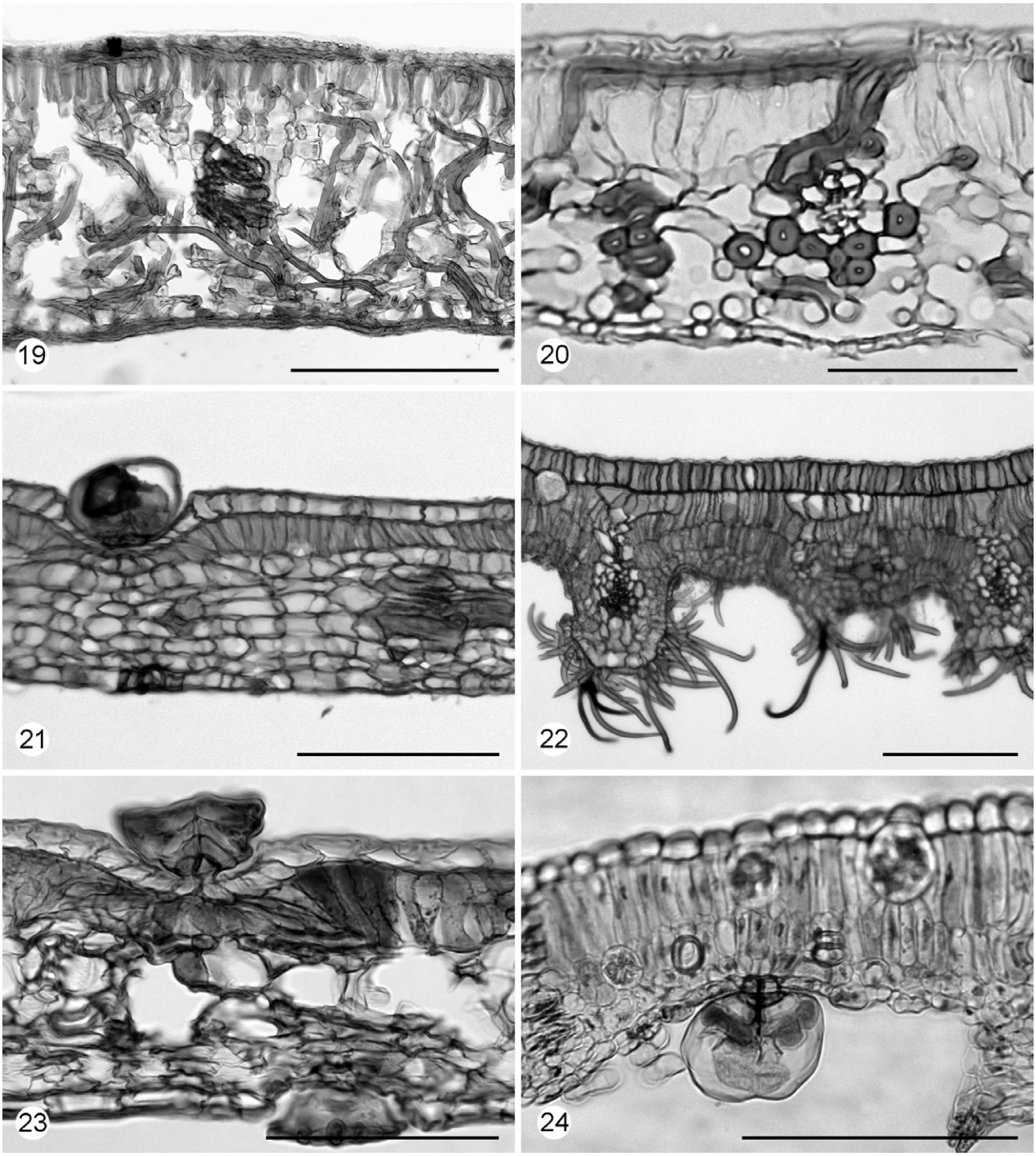
tate glandular hairs are composed of a bi- to tricellular, approx. 20-µm-long stalk and a unicellular, approx. 30-µm-wide globular head. The shape and thin cell walls of these hairs together suggests a glandular nature, although their content and physiology have never been studied. The abundance of the capitate hairs varies between the species from very rare to abundant (usually around the midrib). In some species they can be easily overlooked because of their rarity and minute size. In addition, the relatively small capitate hairs can be camouflaged by the bigger tufted hairs. Probably for this reason they have not been mentioned in previous publications (Hussin *et al*., 1996). Capitate glandular hairs are restricted to *Hancea*, with a few exceptions in *Mallotus*. Peltate-stellate hairs with a central glandular cell (Fig. 3) consist of six to ten oval to elongated, flattened, thin-walled arms and a central globular cell. Peltate-stellate hairs with a central glandular cell are restricted to *Hancea* subgenus *Cordemoya*. Globular to disc-shaped glandular hairs are the most common and variable type of glandular hairs in *Mallotus*. The glandular hairs range between 60 and 100 µm in diameter. Several different subdivisions of globular to disc-shaped glandular hairs can be made according to their morphology: peltate-like glandular hairs (Fig. 32C) are always inserted in a depression in the lamina, which is usually rather deep, so that the flattened head of the glandular hair is at the same level as the leaf blade. The head is composed of a few layers of radially arranged cells, whereas the short and wide stalk comprises two cells. Bladder-like glandular hairs (Fig. 32B) are round to oval in transverse view. The organization of cells is different from the peltate-like glandular hairs; the cells in bladder-like hairs radiate three-dimensionally from the base of the hair; the head probably contains a secretion product. Sometimes the glandular hairs are flattened, in which case they can have either an entire circumference or they can have ridges. In most cases they are characterized by a segmental arrangement of eight, 16 or 32 cells. However, this subdivision is probably artificial, as some types of glandular hairs intergrade with others. A distinct type of glandular hairs was also noted in some species: the globular hairs consist of numerous three-dimensionally arranged cells, giving the hairs their unique glomerulous appearance (Figs 9, 32B).



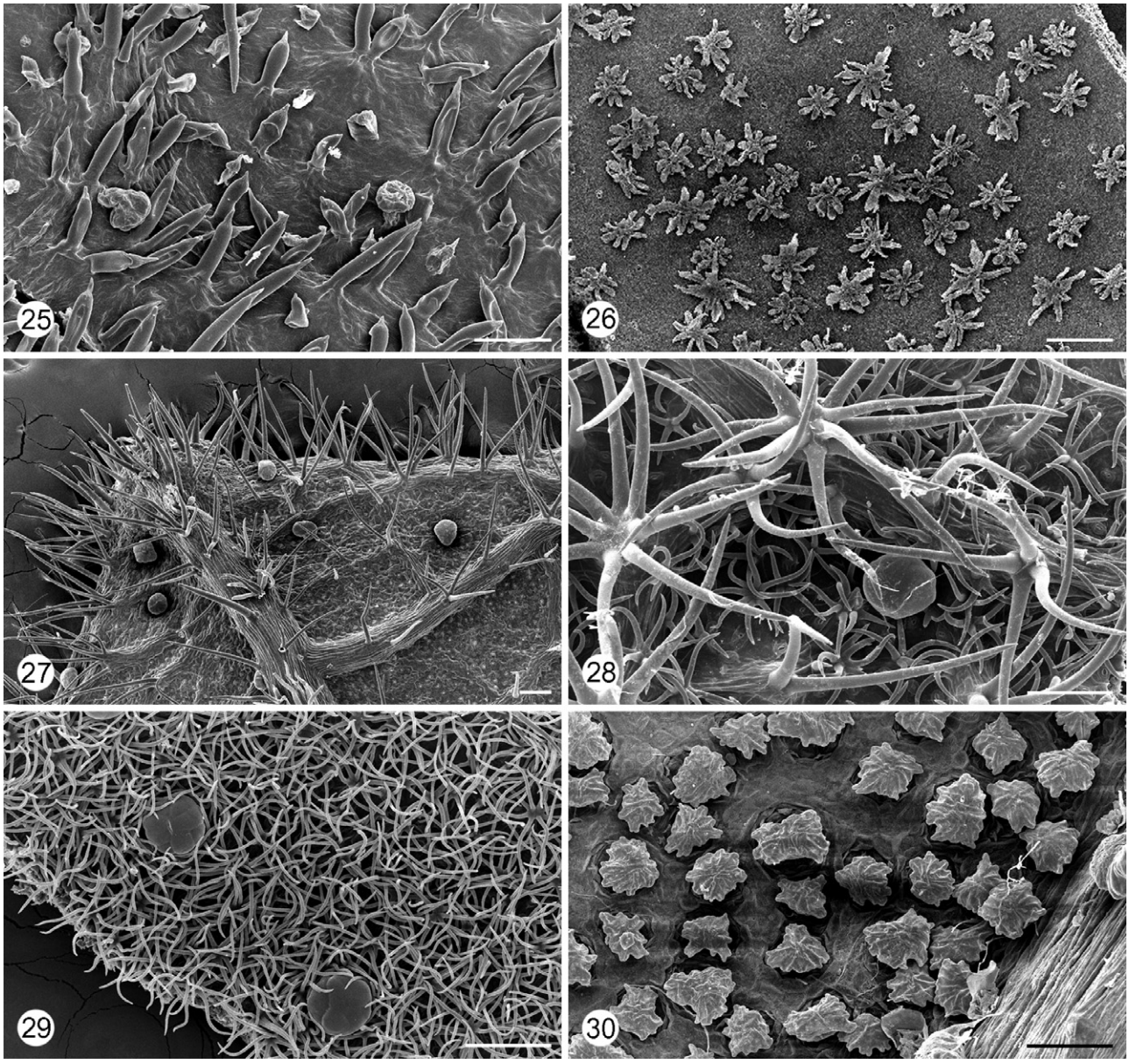
Figures 3–10. Glandular hairs. Fig. 3. Peltate-stellate hair with a central glandular cell of *Hancea spinulosa*. Fig. 4. Capitate glandular hair of *H. spinulosa*. Figs 5–10: globular to disc-shaped glandular hairs. Fig. 5. Globular glandular hair of *Mallotus lackeyi*. Fig. 6. Disc-shaped glandular hair with an entire circumference and an upper layer of eight cells of *M. decipiens*. Fig. 7. Glandular hair of *M. resinosus* lying in a deep depression of the lamina. Fig. 8. Glandular hair of *M. oppositifolius* showing a ridged circumference. Fig. 9. Glandular hair of *M. repandus* composed of numerous three-dimensionally radiating cells. Fig. 10. Conspicuously ridged peltate-like glandular hair of *M. polyadenos*. Scale bars = 100 μm. Figures 3 and 6 reproduced from *Taxon* 59(1): 101–116, with permission.



Figures 11–18. Transverse sections of midrib and petiole. Fig. 11. *Blumeodendron kurzii*, closed vascular cylinder surrounded by a thick fibrous sheath. Fig. 12. Vascular system of *Hancea integrifolia* composed of partially merged vascular bundles with one pith bundle. Fig. 13. *Mallotus cauliflorus*, vascular system composed of separate bundles, surrounded by fibres. Fig. 14. Two vascular arcs in *Mallotus megadontus*, each supported by fibrous sheaths with additional fibres in the upper ridge. Fig. 15. *Blumeodendron kurzii*, petiole vascular system composed of merged vascular bundles with a few internal pith bundles. Fig. 16. Petiole vascular system of *Hancea integrifolia*, composed of separate bundles with an internal ring of pith bundles. Fig. 17. Vascular system of *Mallotus macrostachyus*, composed of separate bundles with many internal pith bundles. Fig. 18. *Mallotus caudatus*, vascular system composed of merged vascular bundles with one internal pith bundle and a fibrous sheath. Scale bars Figs 11–14: 200 μm; Figs 15–18: 500 μm. Figures 16 and 18 reproduced from *Taxon* 59(1): 101–116, with permission.



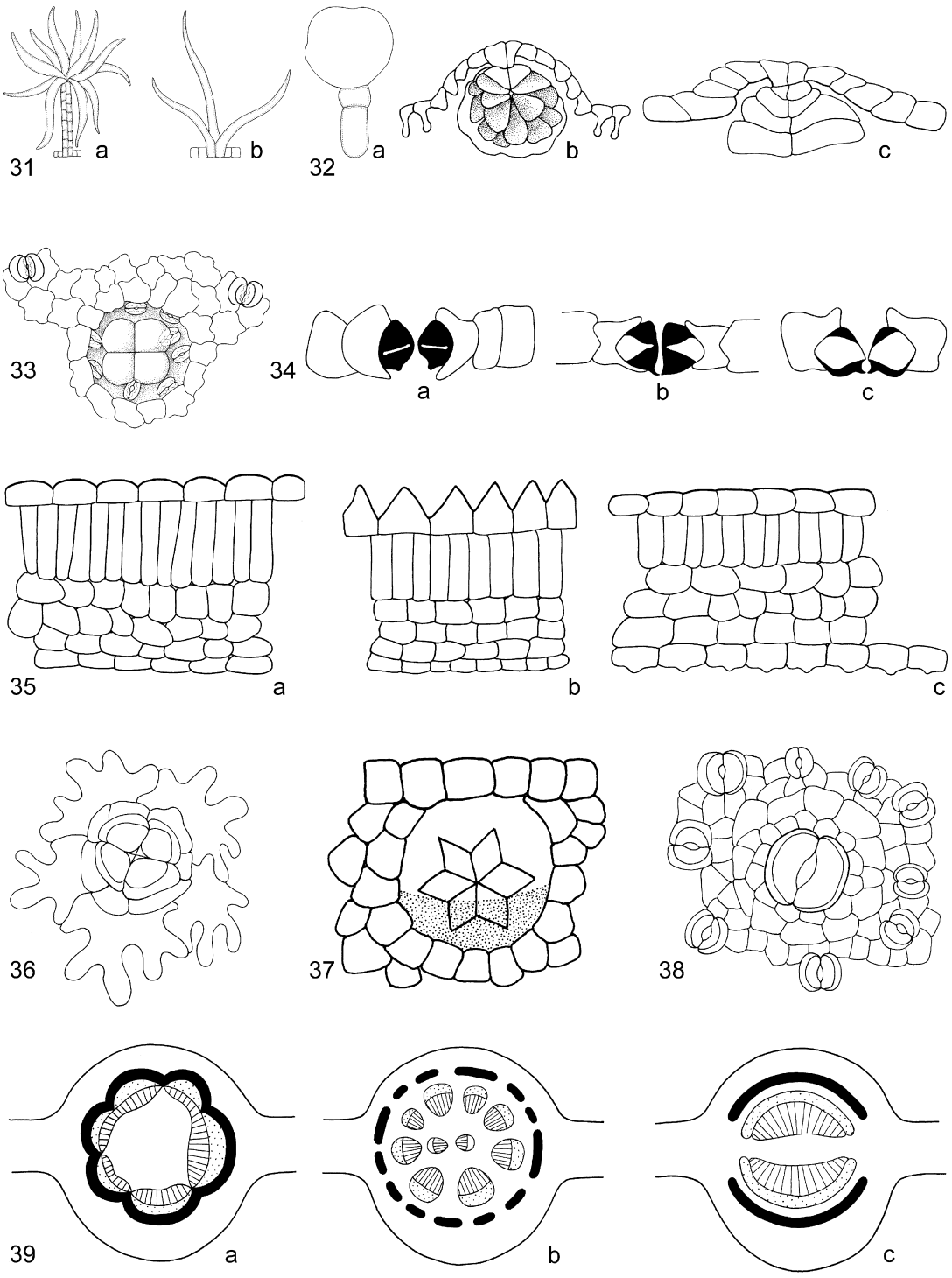
Figures 19–24. Transverse sections of the leaf lamina. Fig. 19. *Blumeodendron kurzii* with an abundance of fibres in the lamina. Fig. 20. *Hancea cordatifolia* with fibrous sclereids. Fig. 21. *Mallotus cauliflorus* with a globular glandular hair inserted on the adaxial epidermis. Fig. 22. *Mallotus tiliifolius* showing crypts and a homogeneous mesophyll; note the presence of a hypodermis above some veins. Fig. 23. *Mallotus polyadenos* with a peltate-like glandular hair inserted on each side of the lamina. Fig. 24. *Mallotus paniculatus* showing a two-layered palisade mesophyll and a thin spongy mesophyll; note the presence of large idioblasts with druses and a globular glandular hair on the abaxial epidermis. Scale bars = 100 μm.



Figures 25–30. SEM leaf surfaces. Fig. 25. Abaxial surface of *Hancea subpeltata* with small simple hairs with a sharp tip and capitate glandular hairs. Fig. 26. Lamina of *Blumeodendron kurzii* with minute stellate-peltate non-glandular hairs. Fig. 27. Abaxial surface of *Mallotus lackeyi* with stellately tufted hairs and globular glandular hairs in depressions. Fig. 28. Abaxial suface of *Mallotus dispersus* with small and large stellately tufted hairs and a globular glandular hair. Fig. 29. Abaxial surface of *M. rhamnifolius* with simple and stellately tufted hairs. Fig. 30. *Mallotus polyadenos*, peltate-like glandular hairs. Scale bars = 10 μm.

Persistent hair bases and mini-cork warts (Fig. 36)
Some species have persistent, heavily cutinized hair bases on the adaxial surface that may develop into small cork warts after concentric cell divisions in or around the basal cells of the caducous stellate hairs. They vary in distinctness from just cutinized hair bases (several *Mallotus* spp.) to small but distinct cork warts (*Hancea p.p.*, *Blumeodendron*). These evenly distributed small cork warts should be distinguished from the irregular cork warts of traumatic origin (e.g. insect bites), which can occur in most plant species.

Epidermal cells
The epidermis of the studied species is always single-layered and generally thicker at the adaxial side of



Figures 31–39. Fig. 31. Stellate hairs: A, stalked; B, tufted. Fig. 32. Glandular hairs: A, capitate, on various parts of the plant; B, bladder-like, drawn abaxially but also present adaxially; C, peltate-like, drawn abaxially but also present adaxially. Fig. 33. Stomata in 'glandular crypts', in a depression under glandular hairs. Fig. 34. Lumina of guard cells: A, slit-like; B and C, wider. Fig. 35. Papillae: A, domed adaxially (also occurring abaxially); B, conical adaxially; C, nipple-shaped abaxially (also occurring adaxially). Fig. 36. Cork wart of basal cells of caducous stellate hair. Fig. 37. Cristarque cell. Fig. 38. Giant stoma among normal sized ones. Fig. 39. Midrib vascularization: A, closed ring of vascular tissue; B, cylinder of separate bundles with two pith bundles; C, opposed adaxial and abaxial arcs; black: sclerenchyma; dots: phloem; lines: xylem. Figures 31–35 reproduced from *Taxon* 59(1): 101–116, with permission.

the leaf. Epidermal cells are sometimes enlarged around the insertions of hairs. Anticlinal walls of unspecialized epidermal cells vary from straight to strongly undulating, depending on the species or the habitat. The abaxial and adaxial surfaces do not necessarily consist of the same cell-wall type. The epidermal pattern in *Mallotus* and *Hancea* is usually modified over the midrib, but unchanged in *Blumeodendron*. The epidermis is covered with a thin to thick cuticle. The cuticle is rather thin in most *Mallotus* spp., but thicker in *Hancea* and especially thick in *Blumeodendron*. When the cuticle is < 1 μm thick, we note it as a thin cuticle, but when the cuticle is thicker, we report its thickness.

Mesophyll (Figs 19–24)

The majority of the studied species have a dorsiventral mesophyll with predominantly one layer of adaxial palisade cells and a few layers of spongy cells (Figs 19–21, 23). Hussin *et al*. (1996) mentioned this as a uniting character for all *Mallotus* and *Hancea* spp. they investigated. Only a few non-related species have a multilayered palisade mesophyll (Figs 22, 24). Weakly dorsiventral to homogeneous leaves without a distinct spongy layer are found in a few *Mallotus* spp. and *Hancea* subgenus *Cordemoya*. Compact isobilateral mesophyll is found in *H. capuronii* (Leandri) S.E.C.Sierra, Kulju & Welzen, *H. integrifolia* and *M. nudiflorus*. *Blumeodendron* is recognized by a one- to two-layered palisade mesophyll and an extensive, more than ten-layered spongy mesophyll (Fig. 19).

Papillae (Fig. 35)

Papillae may be confined to the adaxial (Fig. 35A, B) or abaxial leaf surface (Fig. 35C), or are present only in the vicinity of glandular hairs. Three distinct types of papillae may be recognized in the studied genera. Conical papillae are usually found on the adaxial surface (Fig. 35B); in several species, they are combined with cuticular striations. Dome-shaped papillae (Fig. 35A) are less obvious, they sometimes occur only on the circumference of glandular cavities and can be present either adaxially or abaxially. Nipple-shaped papillae (Fig. 35C) are the least obvious type, intergrading with normal epidermal cells and conical papillae and can be present on both surfaces.

The stomatal complex (Figs 33, 34)

According to Metcalfe & Chalk (1979), mature stomata of Euphorbiaceae belong to the paracytic, anisocytic and anomocytic types. Stomata of the genera studied here are all paracytic. They are mostly confined to the abaxial surface of the lamina, but some species bear a low number of stomata on the adaxial surface, especially overlying the major veins; only a few species studied here have a considerable number of stomata on the adaxial side in between veins.

The guard cell pairs range between 12 and 36 μm in length and 8 and 21 μm in width. The lumina of guard cells may be slit-like (as in *Blumeodendron* and *Hancea*; Fig. 34A) or wider in cross section (most *Mallotus* spp.; Fig. 34B, C). Outer cuticular ledges are either present or absent, varying with the species. Inner cuticular ledges are inconspicuous or absent in most species.

'Giant' stomata (Fig. 38) are raised above the leaf surface and are much larger and less frequent than the normal stomata. The giant stomata have well-developed outer rims, and are restricted to *Blumeodendron*.

Another peculiarity regarding stomata is a low frequency of stomata on the abaxial surface in section *Polyadenii*. A closer look at the macerations and transverse sections reveals the presence of stomata in 'glandular crypts' (Fig. 33); glandular hairs in this particular section lie in a depression in the leaf surface and most of the stomata are concentrated under the glandular hairs. A few species show lobing of subsidiary cells just under the guard cell pairs (once also reported for a group of Linaceae; Van Welzen & Baas, 1984).

Crystals

Crystals of calcium oxalate are frequent among the studied species. They occur either in specialized cells of globular or ovoid shape (idioblasts), or in unspecialized cells in the mesophyll, midrib and petiole. They can be prismatic or star-like (druses). Both kinds of crystals can occur in the same species.

Prismatic crystals are usually located in the parenchymatous bundle sheaths of the veins, although they also occur in non-specialized mesophyll cells. Druses (Fig. 24) can be present in palisade and/or spongy mesophyll, ground tissue of the petiole and midrib or, although rarely, in epidermal cells. Very small druses occur also in the phloem. Certain species have druses of one size only, whereas others have crystals of two distinct sizes. Large crystal idioblasts can measure up to 60% of the thickness of the lamina in vertical diameter.

A systematically rather important feature is the presence of cristarque cells, which are restricted to only a few dicotyledonous families (Dickison, 2000: 228). These cells have a U-shaped lignified wall thickening with a druse crystal in the lumen (Fig. 37). They are found mainly in the ground tissue of the petiole and midrib, but can be present also in the palisade mesophyll. In this study they were found in six *Hancea* spp.

Bundle sheath extensions
BSEs are columns of colourless, parenchymatous or sclerenchymatous cells, usually developed on opposite sides of minor veins in leaves of many dicotyledons (Wylie, 1952). They are connected to the bundle sheath and can extend upwards and downwards to both epidermal layers.

Hypodermis
In *Mallotus* and *Hancea*, a continuous hypodermis is absent, whereas a local hypodermis above midrib and veins is quite frequent and occurs in many species. A local hypodermis often represents a continuation of the BSEs; sometimes the hypodermis is composed only of a two- to three-cell-wide strip and it is thus difficult to state whether it should be termed hypodermis or a BSE. For the purpose of the present study, we use the term 'local hypodermis' when the outer layer of the BSE is considerably wider than the part of the BSE adjacent to the vascular bundle. If the outermost layer of the BSE is as wide as the inner part, we recorded it as an absence of a hypodermis.

Petiole and midrib vascularization (Figs 11–18, 39)
The vascular system of the petiole consists of a cylinder of either separate (Figs 16, 17) or (partly) fused vascular bundles (Figs 15, 18). Central (pith) bundles are present or absent.

Not much variation can be observed in the vascular types of the midrib. The first type to be observed is the system with an opposed adaxial and abaxial arc (Figs 14, 39C), sometimes with a few additional vascular bundles on the sides. The other type noted is a cylinder of separate bundles (Figs 12, 13, 39B), which can sometimes merge to form a closed ring of vascular tissue (Figs 11, 39A). Central bundles can be present, although they are quite rare in the first type.

Mechanical tissue of the vascular system
Fibres supporting the vascular tissue are either present or absent in different species of the examined genera. Sclerenchymatous fibres can form a thin to thick sheath or cap supporting the vascular tissue of petiole and midrib (and other veins; Figs 40, 42, 43). Fibres supporting the vascular tissue of petiole and midrib are abundant in *Blumeodendron* and *Hancea*. The vascular system in the midrib of *Blumeodendron* has an extremely thick (seven or eight layers) fibre sheath. Fibres are either present (e.g. Fig. 14) or absent (e.g. Fig. 17) in different *Mallotus* spp. Some sections or groups can be recognized by thick fibre sheaths (e.g. in the *Glomerulatus* clade).

Vein endings
Veins can terminate either freely in the mesophyll or they can develop a closed network, enclosing islands of chlorenchyma (Metcalfe & Chalk, 1979). In the first type, terminal cells of the veins can be observed. Terminal tracheids can be long and thin, not supported by fibres, or the veins may end in clusters of several enlarged tracheids. Intermediates between both extreme types are common.

Foliar sclereids (Figs 19, 20, 40, 43)
Different types of sclereids are found in the examined genera. Brachysclereids, more or less isodiametric cells, occurring mainly in the peripheral and/or central ground tissue of the petiole and midrib, are present in *Hancea*. Sometimes they occur in clusters. Idioblastic mesophyll sclereids (Fig. 20) varying from columnar to fibriform, and unbranched to branched, are also found in *Hancea*.

Sclereids associated with bundle sheath fibres occur frequently in *Mallotus* (Figs 40, 43). They are discussed in the section about the mechanical tissue of the vascular system. Fibriform sclereids are abundant in the leaves of *Blumeodendron*, where they run in all directions and give strong support to the leaf mesophyll (Fig. 19).

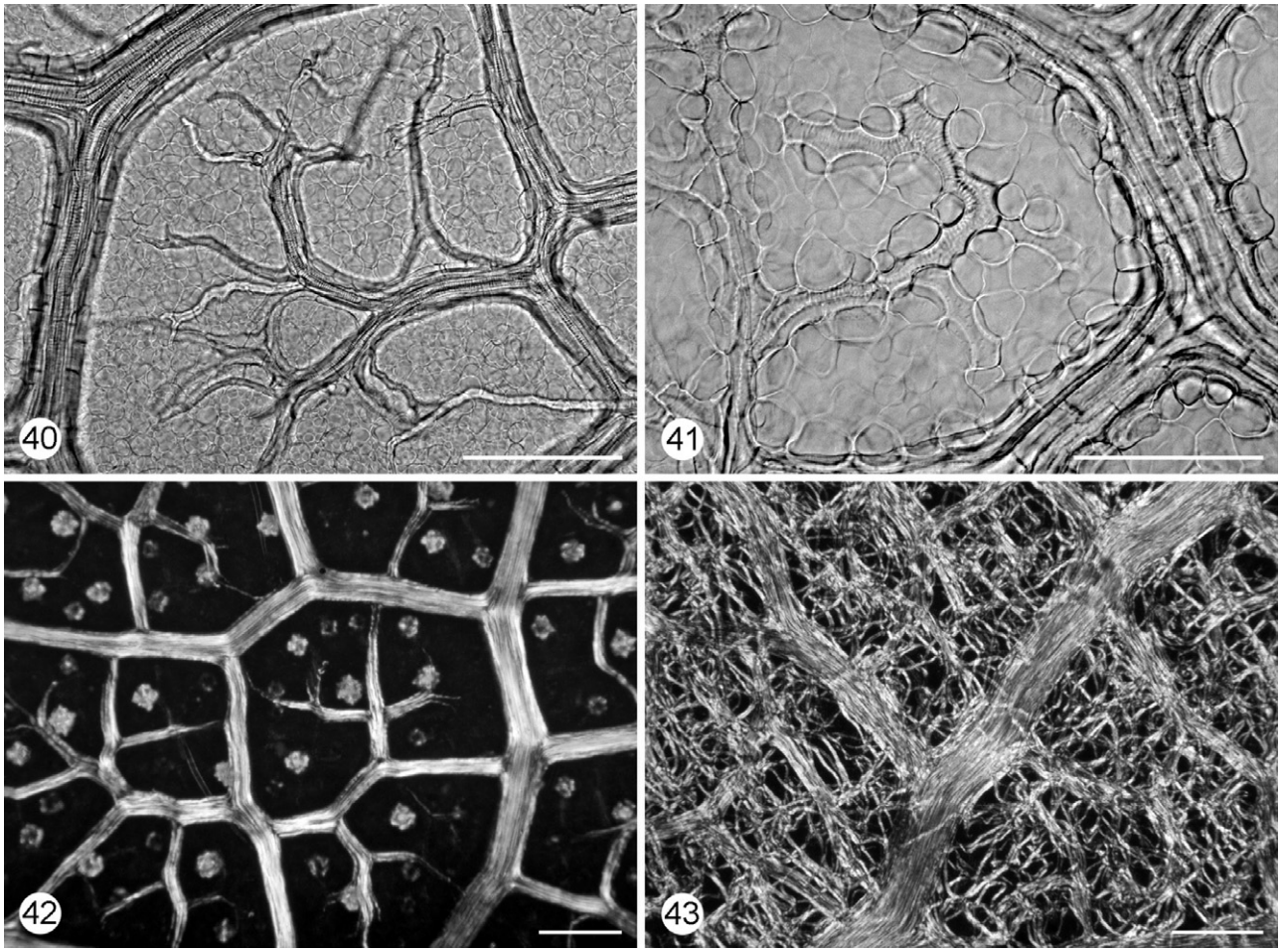
Secretory cells
Secretory cells are present in some *Mallotus* spp. They are restricted to the ground tissue of the petiole and midrib and sometimes to larger veins. Their content has not been studied, but is likely to be tannin. Tannin idioblasts are found in many families; their content oxidizes to brown and reddish brown phlobaphenes (Evert, 2006: 477), which are easily observed in unbleached sections.

Anatomical descriptions

In the descriptions below salient leaf anatomical features of the genera are summarized. In the descriptions of infrageneric taxa (sections, species groups and individual species) only positive features are included; absence of characters can be inferred from Table 1.

1. Blumeodendron (Figs 11, 15, 19, 26)
Species examined: *Blumeodendron kurzii*.

In surface view: Indumentum consisting of small, thin-walled, peltate-stellate, probably non-glandular hairs. Hairs early caducous, leaving a scar on the leaf surface after shedding. Persistent hair bases merging with minute cork warts present on both surfaces. Stomata in two types: the more frequent, almost round stomata, on average 23 μm long and 21 μm wide, and the more rare 'giant' stomata, 35 μm long and 40 μm wide, raised above the surface, with con-



Figures 40–43. Leaf clearings. Fig. 40. *Mallotus khasianus* with fibres detaching from veins and ending in mesophyll. Fig. 41. Large bundle sheath cells of *Mallotus muticus*. Fig. 42. Leaf clearing under polarized light of *Mallotus nudiflorus* showing veins sheathed by fibres. Fig. 43. Leaf clearing under polarized light of *Hancea capuronii*.

Table 1. Selected leaf anatomical characters which can be used to distinguish between the genera

Character	*Blumeodendron*	*Hancea*	*Mallotus*
Peltate-stellate glandular hairs	–	–/+	–
Capitate glandular hairs	–	+/–	–*
Globular to disc-shaped glandular hairs	–	–	+/–
Stalked stellate hairs	–	–	–/+
Simple hairs	–	+	+/–
Tufted hairs	–	–*	+/–
Bundle sheath extensions	–	–	–/+
Pith bundles in the vascular tissue of the midrib	–	–/+	–/+
Secretory cells	–	–	–/+
Brachysclereids	+	–/+	+*
Giant stomata	+	–	–
Cristarque cells	–	–/+	–
Fibriform sclereids	++	+/++	–/+/++

Key: –, absent in all species; –* absent only in one species; –/+, absent in most species; +*, present only in one species; +/–, present in most species; +, present in all species; +/++, present to abundant in species; ++, abundant in all species; –/+/++, absent to present to abundant in species.

spicuous cuticular ledges; giant stomata scattered on the abaxial surface, most frequent near the veins.

In transverse section: Cuticle 8–10 μm thick. Spongy cells seemingly with large intracellular spaces. Midrib slightly raised adaxially, with a continuous vascular cylinder. Petiole with a cylinder of partially merged bundles. Veins embedded in mesophyll, abaxially and adaxially supported with thick strands of fibres. Fibriform sclereids abundant, running vertically and horizontally in the mesophyll, forming a dense network as seen in leaf clearings. Crystals frequent, present as minute druses inside non-modified mesophyll cells and in small idioblasts in the mesophyll. Prismatic crystals present, associated with the veins. Brachysclereids present in the ground tissue of the petiole and midrib.

Note: Leaf clearings difficult to study because of the abundance of mesophyll sclereids.

2. Hancea

2.1 Subgenus Cordemoya (Figs 3, 4, 12, 16, 43)
Species examined: *Hancea acuminata*, *H. capuronii*, *H. integrifolia*, *H. spinulosa*. Revision: Sierra *et al*. (2006, 2007).

In surface view: Indumentum consisting of short simple hairs, usually adpressed to flattened on the surface. Longer hairs present on midrib, nerves and petiole of *H. acuminata*. Few tufted hairs present on petiole of *H. capuronii*. Glandular hairs of two types present: thin-walled sessile peltate-stellate hairs with a globular central cell, and capitate glandular hairs (found in *H. capuronii* and *H. acuminata*). Stomata 21–25 μm long and 9–17 μm wide.

In transverse section: Cuticle 6–8 μm thick. Mesophyll compact, weakly dorsiventral to isobilateral (*H. capuronii*). Midrib adaxially flat in *H. integrifolia* but raised in other species. Stomata with thickened walls and narrow, slit-like lumina as seen in transverse section. Outer stomatal ledges present. Local hypodermis present or absent. Vascular system in midrib composed of a cylinder of separate vascular bundles (merged in *H. acuminata*), sheathed by a more or less continuous thick sheath of thick-walled fibres. Veins embedded in mesophyll, surrounded by thick-walled fibre sheaths. Vascular system in petiole composed of a circle of separate vascular bundles with no central bundles (*H. capuronii*), one central bundle (*H. acuminata*, *H. spinulosa*) or a concentric medullary vascular system (*H. integrifolia*). Vascular bundles surrounded by a continuous fibre cap in *H. capuronii* or an interrupted cap in *H. spinulosa* and *H. integrifolia*. Foliar sclereids present, especially abundant in *H. capuronii* and *H. spinulosa*. Large idioblasts with druses present in all species except in *H. capuronii*. Cristarque cells present in *H. acuminata*, *H. capuronii* and *H. spinulosa*. Prismatic crystals associated with bundle sheaths.

2.2 Subgenus Hancea, section Hancea (Fig. 20)
Species examined: *Hancea cordatifolia*, *H. eucausta*, *H. griffithiana*, *H. hirsuta*, *H. hookeriana*, *H. kingii*, *H. longistyla*, *H. papuana*, *H. penangensis*, *H. stipularis*. Revision: Slik & van Welzen (2001a); Sierra *et al*. (2006, 2007).

In surface view: Leaves glabrous or indumentum consisting of simple unicellular hairs, mostly on midrib and major veins. Stomata 14–25 μm long and 8–24 μm wide. Cork warts present.

In transverse section: Cuticle thin. Mesophyll dorsiventral. Midrib with two opposing vascular arcs, supported by thick caps of fibres. Central bundles usually absent. Smaller veins sheathed by fibres. Petiole with a (partially) merged cylinder of bundles in *H. eucausta*, *H. griffithiana*, *H. kingii*, *H. longistyla* and *H. penangensis*. Medullary bundles usually present. Fibriform sclereids abundant in all species, running horizontally and vertically in mesophyll. Brachysclereids present in some species, occurring mainly in the peripheral and/or central ground tissue of petiole and midrib. Crystals infrequent to abundant, present as small druses in palisade or spongy cells (*H. griffithiana*, *H. papuana*), in small idioblasts and in large infrequent idioblasts in the palisade layer. Cristarque cells present in some species (see Table 2).

2.3 Subgenus Hancea section Oliganthae (Fig. 25)
Species examined: *H. subpeltata*. Revision: Sierra *et al*. (2006, 2007).

In surface view: Indumentum consisting of simple short erect unicellular hairs with a pointed tip and longer simple hairs, occurring on veins. Glandular hairs capitate, present on the abaxial surface near veins. A few persistent hair bases merging with mini-cork warts present on the adaxial surface. Stomata 25–28 μm long and 9–12 μm wide.

In transverse section: Cuticle adaxially 2 μm thick, abaxially thinner. Mesophyll dorsiventral. Midrib with two opposing arcs surrounded by fibres. One medullary bundle present. Smaller veins sheathed by fibres. Petiole with a cylinder of separate to partially merged bundles with additional central bundles, each with a thin cap of fibres. Fibriform sclereids abun-

dant, forming a dense network as observed in leaf clearings. Idioblasts with druses present in the mesophyll.

3. Mallotus

3.1 Nudiflorus group (Fig. 40)
Species examined: *M. hispidospinosus*, *M. khasianus*, *M. nudiflorus*, *M. polycarpus*. Revision: Kulju *et al*. (2007a); Sierra *et al*. (2007).

In surface view: Indumentum scattered (glabrous in *M. khasianus*), composed of tufted and simple hairs, present mostly on veins. Globular glandular hairs present predominantly abaxially. Adaxial glandular hairs in *M. polycarpus* lying in a deep depression in the lamina. Outline of glandular hairs usually subentire, sometimes irregular, with indistinct ridges. Nipple-shaped papillae present on the adaxial side of *M. nudiflorus*. Anticlinal division cell walls sometimes thickened in *M. khasianus*. Stomata confined to the abaxial surface, but rather frequent also above nerves on the adaxial surface in *M. nudiflorus*. Guard cell pairs 21–27 μm long and 12–20 μm wide.

In transverse section: Cuticle thin. Stomata with thickened inner and outer walls with medium-sized lumina, outer ledges present at least in *M. khasianus*. Local hypodermis usually present. Fibriform sclereids absent except in *M. khasianus*. Midrib adaxially raised or grooved, with two large arcs, surrounded by scattered fibres extending into the adaxial groove. Vascular system in midrib of *M. khasianus* with a predominantly continuous cylinder. Smaller veins in lamina embedded in mesophyll, abaxially or on both sides with fibre caps. BSEs present in *M. polycarpus* and above larger veins in *M. khasianus*. Petiole with a cylinder of vascular bundles with one to three central bundles. Phloem merged in *M. nudiflorus*. Sclerenchyma in petiole absent. Crystals present as large druses in *M. nudiflorus* and *M. polycarpus*, and as minute druses in *M. khasianus* (especially frequent in palisade cells). Prismatic crystals present in *M. hispidospinosus* and *M. khasianus*, mostly associated with veins.

Note: Petiole, leaf clearing and cuticular maceration not examined in *M. polycarpus*. Cuticular maceration not examined in *M. nudiflorus*. Petiole not examined in *M. hispidospinosus*.

3.2 Mallotus oppositifolius (Fig. 8)
In surface view: Indumentum consisting of tufted and simple hairs, and of globular glandular hairs. Glandular hairs slightly flattened, sunken in depressions in the lamina, entire to ridged; their uppermost layer consisting of 16 cells. Adaxial and abaxial surface slightly papillate, papillae dome-shaped, some epidermal cells larger than others. Stomata on average 21 μm long and 10 μm wide. A few stomata present adaxially on midrib.

In transverse section: Cuticle thin. Inner and outer stomatal walls equally thickened, outer stomatal ledges present. Local hypodermis present above (some) veins. Midrib grooved, with an adaxial and abaxial arc, both with fibrous caps. Veins embedded in lamina, usually with strands of fibres on the adaxial and abaxial side, or surrounded by fibres. Parenchymatous bundle sheaths elongating into BSEs. Veins ending in thin and long tracheids. Petiole with a dissected vascular cylinder with one central bundle. Bundles accompanied by thin-walled fibre caps on the outer side. Solitary fibres in lamina absent. Large druses present, reaching 60 μm in size. Smaller crystal idioblasts also scattered in mesophyll, druses scattered also in ground tissue and phloem in petiole. Prismatic crystals associated with veins.

3.3 Rhamnifolius group (Fig. 29)
Species examined: *M. pallidus*, *M. rhamnifolius*. Revision: Sierra *et al*. (2007).

In surface view: Indumentum composed of stellately tufted, two- to eight-armed, mostly thin-walled hairs, densely covering the abaxial epidermis. Adaxial epidermis with simple and thin-walled tufted hairs on veins. Some thick-walled stellately tufted hairs with many arms (> 20) present on midrib. Simple unicellular hairs scattered on midrib. Glandular hairs present on the abaxial side, sometimes ridged. Stomata confined to the abaxial surface, guard cell pairs 12–15 μm long and 9–10 μm wide.

In transverse section: Cuticle thin. Adaxial epidermis in *M. pallidus* papillate, papillae dome-shaped. Guard cells of stomata with thickened walls, inner walls slightly thicker than outer ones, lumina slit-like to medium wide, outer stomatal ledges present in *M. rhamnifolius*. Local hypodermis present above major veins. Mesophyll dorsiventral in *M. rhamnifolius* and isobilateral in *M. pallidus*, composed of only three layers in the latter: the uppermost and lowermost layer composed of normal palisade cells, the middle layer composed of shorter cells with abundant crystals. Midrib adaxially flat or slightly concave, with two opposing vascular arcs in *M. rhamnifolius*, and a cylinder of few large vascular bundles in *M. pallidus*. Vascular bundles in midrib of *M. pallidus* surrounded by scattered thick-walled fibres on the phloem side; fibres absent in *M. rhamnifolius*.

Table 2. Selected leaf-anatomical characters per infrageneric group and per species

			Mesophyll			Hairs					Globular to disc-shaped glandular hairs		Stomata	
Section/group	Species	Lamina thickness (μm)	Type of mesophyll	No. of palisade layers	No. of spongy layers	Simple	Tufted	Stalked stellate	Peltate-stellate with a central cell	Capitate glandular	AB	AD	Length	Width
Blumeodendron	*Blumeodendron kurzii*	145	D	1	9	–	*+	–	–	–	–	–	23	21
Hancea subgenus	*Hancea acuminata*	110	D	1	4	+	–	–	+	+	–	–	24	15
Cordemoya	*Hancea capuronii*	265	I	–	–	+	–	–	+	+	–	–	24	14
	Hancea integrifolia	210	± I	1	8	+	–	–	+	?–	–	–	22	11.5
	Hancea spinulosa	210	D	2	9	+	–	–	+	?–	–	–	21	14
Hancea subgenus	*Hancea cordatifolia*	125	D	1	4	+	–	–	–	? +	–	–	19	10.5
Hancea	*Hancea eucausta*	120	D	1	6	+	–	–	–	+	–	–	19.5	12.5
	Hancea griffithiana	110	D	1	3	? +	–	–	–	+	–	–	15	11.5
	Hancea hirsuta	145	D	1	4	+	–	–	–	?	–	–	19	16.5
	Hancea hookeriana	135	D	1	4	–	–	–	–	? +	–	–	17	7.5
	Hancea kingii	65	D	1	3	+	–	–	–	+	–	–	17	11.5
	Hancea longistyla	130	D	1	5	+	–	–	–	+	–	–	24	12.6
	Hancea papuana	140	D	1	4	+	–	–	–	?	–	–	20.5	14
	Hancea penangensis	215	D	1	6	+	–	–	–	?	–	–	20	11
	Hancea stipularis	260	D	1	4	+	–	–	–	?	–	–	23.5	15
	Hancea subpeltata	80	D	1	4	+	+	–	–	+	–	–	24.5	13
Calocarpus group	*Mallotus calocarpus*	55	D	1	2–3	+	+	–	–	–	+	–	27.5	17
	Mallotus pierrei	70	D	1	4	+	+	–	–	–	+	–	23	19
Miquelianus	*Mallotus brachythyrsus*	195	D	1	6–7	+	–	–	–	–	+	+	25	11.5
clade	*Mallotus concinnus*	145	D	1	5	+	+	–	–	–	+	–	31	15
	Mallotus havilandii	?	D	?	?	+	+	–	–	–	+	–	19	13.5
	Mallotus insularum	80	D	1	4	–	–	–	–	–	+	? +	21	11.5
	Mallotus miquelianus	100	D	1	5	+	+	–	–	–	+	–	19	10
Glomerulatus	*Mallotus actinoneurus*	55	D	1	4	+	+	–	–	–	–	–	26.5	17
clade	*Mallotus glomerulatus*	150	D	1	6–9	+	+	–	–	–	–	–	28.5	22
	Mallotus mirus	90	D	1	4	–	+	–	–	–	–	–	24.5	15
Section *Mallotus*	*Mallotus barbatus*	35	D	1	2	+	+	+	–	–	+	–	19	13.5
	Mallotus japonicus	135	D	1	3–4	+	+	+	–	–	+	–	30	18
	Mallotus macrostachyus	55	D	1	2	+	–	+	–	–	+	–	18	17
	Mallotus metcalfianus	85	D	2	1	–	–	+	–	–	+	–	18	17
	Mallotus paniculatus	75	D	2	2	–	–	+	–	–	+	–	17	13
Nudiflorus group	*Mallotus hispidospinosus*	75	D	1	4	+	+	–	–	–	+	–	21	12.5
	Mallotus khasianus	145	D	1	6–8	+	+	–	–	–	+	–	26	17
	Mallotus nudiflorus	150	I	3 AD, 2 AB	2	–	+	–	–	–	+	–	26.5	19
	Mallotus polycarpus	135	D	2	6	+	+	–	–	–	+	+	27	20
Philippinenses	*Mallotus philippensis*	110	I			+ (multicellular)	+	–	–	–	+	–	?	?
grade	*Mallotus repandus*	110	D	1	6	+ (multicellular)	+	–	–	–	+	–	21	17

Pleiogynus group	*Mallotus discolor*	130	D–compact	2–3	3–4	–	+	–	–	–	+	–	20	12.5
	Mallotus nesophilos	120	D–compact	2	2	–	+	–	–	–	+	–	21	21
	Mallotus pleiogynus	95	D–compact	2–3	2–3	+	+	–	–	–	+	–	18.5	15.5
Section *Polyadeni*	*Mallotus leucodermis*	290	D	1	14	–	–	–	–	–	+	+	22	18.5
	Mallotus muticus	135	D	1	4	–	–	–	–	–	+	+	19	16
	Mallotus polyadenos	130	D	1	5	–	–	–	–	–	+	+	25	13.5
Resinosus clade	*Mallotus decipiens*	215	D	1	6	+	–	–	–	–	+	–	23	14.5
	Mallotus dispar	85	D	1	2	+	+	–	–	–	+	+	20	12.5
	Mallotus lanceolatus	110	D	1	4	+	+	–	–	–	+	–	32	17
	Mallotus leucocalyx	95	D	1	3–4	+	+	–	–	–	+	–	21	15
	Mallotus resinosus	125	D	1	5	+	–	–	–	–	+	–	21	14
Rhamnifolius group	*Mallotus pallidus*	80	I			+	+	–	–	–	+	–	12.5	10.5
	Mallotus rhamnifolius	50	D	1	4	+	+	–	–	–	+	–	15	9.5
Section *Stylanthus*	*Mallotus lackeyi*	65	D	1	3	+	+	–	–	–	+	+	19	9.5
	Mallotus peltatus	85	D	1	4	+	+	–	–	–	+	–	22	11.5
Subulatus clade	*Mallotus ficifolius*	120	D	1	4–5	+	+	–	–	–	+	–	25	19
	Mallotus claoxyloides	95	D	1	4	+	+	–	–	–	–	–	28.5	18
	Mallotus coudercii	85	D	1	3	+	–	–	–	–	–	–	28.5	19
	Mallotus glabriusculus	115	D	1	4	–	–	–	–	–	+	–	31.5	21.5
	Mallotus macularis	155	D	1	6	+	+	–	–	–	–	–	29	14
	Mallotus megadontus	210	D	1	7	–	+	–	–	–	+	–	27	19
	Mallotus subulatus	105	D	1	4	+	+	–	–	–	+	–	21	13.5
Tiliifolius clade	*Mallotus connatus*	80	D	1–2	6	+	+	–	–	–	+	–	22	14.5
	Mallotus dispersus	95	D	2	1	+	+	–	–	–	+	+	?	?
	Mallotus rufidulus	75	D	1	5	+	+	–	–	–	+	–	19	14.5
	Mallotus tiliifolius	100–210	I/H			+	+	+	–	+	+	–	?	?
	Mallotus trinervius	120	D	1	4	+	+	–	–	–	–	–	27.5	18
	Mallotus ustulatus	76–130	D	1–2	4–7	+	+	–	–	–	+	+	15	13.5
Wrayi clade	*Mallotus caudatus*	90	D	1	4	+	+	–	–	–	+	–	17	9.5
	Mallotus spinifructus	55	D	1	3	+	+	–	–	–	+	–	15	9
	Mallotus wrayi	105	D	1	4	–	+	–	–	–	+	–	16	8.5
	Mallotus blumeanus	100	D	1	7–8	–	+	–	–	–	+	+	22.5	15
	Mallotus cauliflorus	100	D	1	6	+	–	–	–	–	+	+	17	10
	Mallotus oppositifolius	110	D	1	6	+	–	–	–	–	+	–	21	10.5

Table 2. Continued

Section/group	Species	Cork warts & persistent hair bases	Epidermal cell wall		Other structures							Midrib vascularization	
			AD	AB	Mesophyll sclereids	BSEs	Crystals	Cristarque cells	Secetory cells	Brachy-sclereid	Enlarged tracheid endings	Vascular system	Central pith bundles
Blumeodendron	*Blumeodendron kurzii*	+	U	C/U	+	–	P	–	–	+	?	± CC	–
Hancea subgenus	*Hancea acuminata*	–	C	C	+	–	P	+	–	–	?	CC	–
Cordemoya	*Hancea capuronii*	–	S	S	+	–	R	+	–	+	?	CSB	–
	Hancea integrifolia	–	S	S	+	–	P	–	–	–	–	CSB	+
	Hancea spinulosa	–	S	U	+	–	P	+	–	–		CPMB	+
Hancea subgenus *Hancea*	*Hancea cordatifolia*	+ –	U	U	+	–	R	–	–	–	–	2 OA	–
	Hancea eucausta	++	SU	SU	+	–	R	+	–	+	–	2 OA	–
	Hancea griffithiana	+ –	SU	SU	+	–	R	–	–	–	–	2 OA	–
	Hancea hirsuta	+	?	?	+	–	F	–	–	–	–	2 OA	+
	Hancea hookeriana	– +	U	U	+	–	F	–	–	–	–	2 OA	–
	Hancea kingii	+ –	SU	SU	+	–	P	–	–	+	–	$	+
	Hancea longistyla	+ –	SU	SU	+	–	R	–	–	+	–	2 OA	+
	Hancea papuana	+	U	U	+	–	P	–	–	+	–	3 OA	–
	Hancea penangensis	– +	U	U	+	–	F	+	–	–	–	2 OA	–
	Hancea stipularis	++	U	U	+	–	P	+	–	+	–	2 OA	–
	Hancea subpeltata	– +	C	SU	+	–	P	–	–	–	–	2 OA	+
Calocarpus group	*Mallotus calocarpus*	–	U	U	+	– +	F	–	–	–	– +	2 OA	–
	Mallotus pierrei	–	S	S/C	–	–	P	–	–	–	–	2 OA	–
Miquelianus clade	*Mallotus brachythyrsus*	–	C	C/U	+	–	R	–	–	–	–	2 OA	–
	Mallotus concinnus	–	C	C	+	–	F	–	?	–	–	?	?
	Mallotus havilandii	?	U	C	–	?	?	–	–	–	–	?	?
	Mallotus insularum	–	U	U	+	–	P	–	–	–	–	?	?
	Mallotus miquelianus	–	U	U	+	–	P	–	–	–	–	2 OA	–
Glomerulatus clade	*Mallotus actinoneurus*	–	C	C/U	+	–	P	–	–	–	–	2 OA	–
	Mallotus glomerulatus	–	C	U	+	–	F	–	–	–	–	2 OA	–
	Mallotus mirus	–	C	U	+	–	F	–	–	–	–	2 OA	–
Section *Mallotus*	*Mallotus barbatus*	+	C/U	S	–	+	P	–	–	–	±	CSB	+ (phloem)
	Mallotus japonicus	+	U	S/C	–	+	F	–	–	–	+	2 OA	–
	Mallotus macrostachyus	+	S	?	–	+	F	–	–	–	+	2 OA	+ (phloem)
	Mallotus metcalfianus	+	C	?	–	+	F	–	–	–	+	2 OA	–
	Mallotus paniculatus	+	S	?	–	+	F	–	–	–	+	CSB	–
Nudiflorus group	*Mallotus hispidospinosus*	–	SU	SU	–	–	R	–	–	–	?	2 OA	–
	Mallotus khasianus	–	U	U	+	–	F	–	–	–	–	?	?
	Mallotus nudiflorus	–	S	S	–	–	R	–	–	–	–	2 OA	–
	Mallotus polycarpus	–	S/C/U	S/C	–	–	R	–	–	–	?	2 OA	–
Philippinenses grade	*Mallotus philippensis*	–	S/C	S/C	–	+	P	–	–	–	– +	CSB	–
	Mallotus repandus	+	S	S	+	+	P	–	–	–	+	2 OA	–
Pleiogynus group	*Mallotus discolor*	–	S	S	–	–	P	–	–	–	±	CSB	+
	Mallotus nesophilos	–	S	S	–	+	F	–	–	–	–	CSB	–
	Mallotus pleiogynus	–	S	S	–	+	P	–	–	–	±	CPMB	+

Section *Polyadeni*	*Mallotus leucodermis*	–	C	C	–	–	R	–	–	–	–	2 OA	–
	Mallotus muticus	–	S	S	–	–	P	–	–	–	–	2 OA	–
	Mallotus polyadenos	–	C/U	S	+	–	R	–	–	–	–	2 OA	–
Resinosus clade	*Mallotus decipiens*	–	C	C	+	–	P	–	–	–	?	2 OA	–
	Mallotus dispar	–	U	U	–	–	R	–	–	–	–	2 OA	–
	Mallotus lanceolatus	–	C/U	S/U	+	–	F	–	–	–	?	2 OA	–
	Mallotus leucocalyx	–	C	S	–	–	F	–	–	–	–	2 OA	–
	Mallotus resinosus	–	S	S	+	–	P	–	–	–	–	CPMB	–
Rhamnifolius group	*Mallotus pallidus*	–	C	C	–	+	F	–	–	–	–	CSB	–
	Mallotus rhamnifolius	–	U	S/C	–	+	P	–	–	–	– +	2 OA	–
Section *Stylanthus*	*Mallotus lackeyi*	–	SU	C/U	+	+	R	–	–	–	–	2 OA	–
	Mallotus peltatus	–	S	C	+	–	R	–	–	–	–	2 OA	–
Subulatus clade	*Mallotus ficifolius*	–	C/U	C/U	+	+	F	–	–	–	–	2 OA	–
	Mallotus claoxyloides	–	U	S/C	+	Sometimes	P	–	–	–	–	2 OA	–
	Mallotus coudercii	–	U	U	+	–	F	–	–	–	–	2 OA	–
	Mallotus glabriusculus	–	U	U	+	Sometimes	R	–	–	–	–	2 OA	–
	Mallotus macularis	–	U	U	+	–	F	–	–	–	–	2 OA	–
	Mallotus megadontus	–	C	C	+	+	R	–	–	–	+	2 OA	–
	Mallotus subulatus	–	C	C	+	–	F	–	–	–	–	2 OA	–
Tiliifolius clade	*Mallotus connatus*	–	U	C/U	+	–	P	–	–	–	–	2 OA	–
	Mallotus dispersus	–	?	?	+	–	P	–	–	–	–	CSB	–
	Mallotus rufidulus	–	U	C	–	–	F	–	–	–	–	2 OA	–
	Mallotus tiliifolius	–	S	S	–	On nerves	F	–	–	–	+	CPMB	–
	Mallotus trinervius	–	S	S	+	–	P	–	+	–	–	2 OA	–
	Mallotus ustulatus	–	S	?	+	–	F	–	–	–	–	CSB	–
Wrayi clade	*Mallotus caudatus*	–	U	U	+	–	P	–	–	–	?	2 OA	–
	Mallotus spinifructus	+ on nerves	U	U	+	+	P	–	–	–	–	CC	–
	Mallotus wrayi	–	U	U	+	–	R	–	+	–	–	2 OA	–
	Mallotus blumeanus	–	S	C/U	+	–	R	–	–	–	– +	2 OA	–
	Mallotus cauliflorus	–	S	S	+	–	P	–	–	–	?	CSB	+
	Mallotus oppositifolius	–	S	S/C	–	+	P	–	–	–	–	2 OA	–

Table 2. Continued

Section / group	Species	Petiole vascularization	
		Vascular system	Central pith bundles
Blumeodendron	*Blumeodendron kurzii*	CPMB	+
Hancea subgenus	*Hancea acuminata*	CSB	+
Cordemoya	*Hancea capuronii*	CSB	–
	Hancea integrifolia	CSB	+
	Hancea spinulosa	CSB	+
Hancea subgenus *Hancea*	*Hancea cordatifolia*	?	?
	Hancea eucausta	CC	–
	Hancea griffithiana	CSB	+
	Hancea hirsuta	?	?
	Hancea hookeriana	?	?
	Hancea kingii	CPMB	+
	Hancea longistyla	?	?
	Hancea papuana	?	?
	Hancea penangensis	CPMB	+
	Hancea stipularis	?	?
	Hancea subpeltata	CSB	+
Calocarpus group	*Mallotus calocarpus*	?	?
	Mallotus pierrei	CPMB	+
Miquelianus clade	*Mallotus brachythyrsus*	CSB	+
	Mallotus concinnus	?	?
	Mallotus havilandii	?	?
	Mallotus insularum	?	?
	Mallotus miquelianus	CSB	+
Glomerulatus clade	*Mallotus actinoneurus*	?	?
	Mallotus glomerulatus	?	?
	Mallotus mirus	?	?
Section *Mallotus*	*Mallotus barbatus*	CSB	–
	Mallotus japonicus	CSB	+
	Mallotus macrostachyus	CSB	+
	Mallotus metcalfianus	CPMB	+
	Mallotus paniculatus	CSB	+
Nudiflorus group	*Mallotus hispidospinosus*	?	?
	Mallotus khasianus	CSB	+
	Mallotus nudiflorus	CPMB	+
	Mallotus polycarpus	?	?
Philippinenses grade	*Mallotus philippensis*	CC	+
	Mallotus repandus	CSB	+
Pleiogynus group	*Mallotus discolor*	CSB	+
	Mallotus nesophilos	CSB	+
	Mallotus pleiogynus	CPMB	+
Section *Polyadeni*	*Mallotus leucodermis*	?	?
	Mallotus muticus	CC	+
	Mallotus polyadenos	CC	–

Resinosus clade	*Mallotus decipiens*	CSB	+
	Mallotus dispar	CC	–
	Mallotus lanceolatus	?	?
	Mallotus leucocalyx	CSB	+
	Mallotus resinosus	CSB	+
Rhamnifolius group	*Mallotus pallidus*	CSB	+
	Mallotus rhamnifolius	CPMB	+
Section *Stylanthus*	*Mallotus lackeyi*	CPMB	+
	Mallotus peltatus	CSB	+
Subulatus clade	*Mallotus ficifolius*	CSB	+
	Mallotus claoxyloides	CSB	+
	Mallotus coudercii	?	?
	Mallotus glabriusculus	?	?
	Mallotus macularis	?	?
	Mallotus megadontus	?	?
	Mallotus subulatus	CSB	+
Tiliifolius clade	*Mallotus connatus*	CSB	+
	Mallotus dispersus	CSB	+
	Mallotus rufidulus	?	?
	Mallotus tiliifolius	CPMB	+
	Mallotus trinervius	CSB	+
	Mallotus ustulatus	CSB	+
Wrayi clade	*Mallotus caudatus*	CC	+
	Mallotus spinifructus	CPMB	+
	Mallotus wrayi	CC	+
	Mallotus blumeanus	CSB	+
	Mallotus cauliflorus	CPMB	+
	Mallotus oppositifolius	CSB	+

Abbreviations: AB, abaxially; AD, adaxially; BSEs, bundle sheath extensions; C, curved; CC, continuous cylinder; CPMB, cylinder of partially merged bundles; CSB, cylinder of separate bundles; D, dorsiventral; F, frequent (abundant); H, homogeneous; I, isobilateral; 2 OA, two opposing arcs; P, present; R, rare; S, straight; SU, strongly undulating; U, undulating; $, adaxially merged bundles, abaxially arc; +, present; –, absent; ?, unknown; /, separator between variable character states.

Veins surrounded by conspicuous parenchymatous bundle sheaths, with extensions towards the adaxial epidermis (also towards abaxial epidermis in *M. pallidus*). Smaller veins supported by few fibres adaxially. Tracheid endings sometimes enlarged in *M. rhamnifolius*. Petiole with a continuous or partially fused vascular system, surrounded by a thin, continuous sheath of fibres, with one central bundle. Crystal idioblasts with small and large druses present; small druses also very frequent in normal mesophyll cells in *M. pallidus*, especially in the middle layer. Prismatic crystals associated with bundle sheaths of veins.

3.4 Philippinenses group (Fig. 9)
Species examined: *M. philippinensis*, *M. repandus*. Revision: Sierra, van Welzen & Slik (2005).

In surface view: Indumentum on the abaxial side dense, while glabrous to sparse on the adaxial surface. Indumentum consisting of simple thick-walled uniseriate hairs, large stellately-tufted hairs with multicellular arms and minute stellately-tufted hairs with unicellular arms. Glandular hairs abundant, consisting of numerous radially arranged cells, giving a glomerulous appearance. Stomata in *M. repandus* confined to the abaxial surface, guard cell pairs 21 μm long and 17 μm wide. Stomata not observed in *M. philippensis* because of the dense indumentum.

In transverse section: Cuticle thin. Guard cells in transverse section with thickened walls (inner walls thicker), lumina wide (*M. philippensis*) or slit-like (*M. repandus*). Outer cuticular ledges present. Local hypodermis present above veins, composed of large parenchymatous cells; hypodermis locally present outside the vein region. Lamina dorsiventral (*M. repandus*) or isobilateral with stomatal crypts (*M. philippensis*). Midrib slightly to considerably raised adaxially, with a cylinder of large separate bundles in *M. philippensis* or two opposing arcs in *M. repandus*. Veins slightly to strongly raised, in *M. repandus* surrounded by large bundle sheath cells. Smaller veins with or without abaxial fibre strands, larger veins supported by fibres on both sides. Parenchymatous BSEs present. Veins sometimes ending in enlarged tracheids. Petiole with a continuous cylinder surrounded by a fibre sheath in *M. philippensis*, and with a cylinder of separate bundles in *M. repandus*, in both species with one central bundle. Crystals present in large idioblasts with druses (up to 60 μm in *M. repandus*), in *M. repandus* present also as minute druses in idioblasts or regular spongy cells.

3.5 Pleiogynus group
Species examined: *M. discolor*, *M. nesophilus*, *M. pleiogynus*. Revision: Kulju *et al*. (2007a); Sierra *et al*. (2007).

In surface view: Abaxial epidermis densely covered with stellately tufted hairs with up to 11 arms. Indumentum of *M. pleiogynus* composed of minute and large tufted hairs and simple hairs present on petiole. Globular glandular hairs frequent to scarce. Outline of glandular hairs ridged, clavate cells inside the glandular hairs radiating three-dimensionally. Epidermis slightly papillate (dome-shaped papillae occurring on the abaxial side of *M. discolor* and *M. nesophilus* and on the adaxial side of *M. pleiogynus*). Stomata confined to the abaxial side, 18–21 μm long and 12–21 μm wide.

In transverse section: Cuticle up to 2 μm thick. Guard cell walls thickened, lumina medium wide. Local hypodermis present above veins or absent. Midrib adaxially flat to slightly raised, with a cylinder of few partially fused bundles with small central bundles in *M. discolor* and *M. pleiogynus* (one in *M. nesophilus*). Fibre sheath around the vascular system in midrib and petiole interrupted, composed of thin- to thick-walled fibres, fibres present also in association with central bundles in midrib of *M. discolor*. Smaller bundles with or without adaxial and abaxial fibre strands. BSEs present or absent. Vein endings not or slightly enlarged in *M. nesophilus*; in *M. discolor* and *M. pleiogynus* tracheids clustered, composed of short, thick, usually enlarged cells. Vascular tissue in petiole composed of a discontinuous cylinder of vascular bundles with one or more central bundles. Crystals scattered in petiole of *M. nesophilus* and *M. pleiogynus*. Foliar sclereids absent, sclerenchyma always associated with vascular bundles. Crystals present as large druses, representing up to 50% of the height of the lamina, and as smaller crystalliferous cells in spongy tissue.

3.6 Section Mallotus (Figs 18, 24)
Species examined: *M. barbatus*, *M. japonicus*, *M. macrostachyus*, *M. metcalfianus*, *M. paniculatus*. Revision: Sierra & van Welzen (2005).

In surface view: Abaxial epidermis usually densely covered with stellate hairs with short to long multiseriate stalks (30–125 μm long); hairs confined to veins in *M. barbatus* only. Bladder-like glandular hairs present abaxially. Dome-shaped or conical papillae present in most species. Cuticular striations present or absent. Adaxial surface with persistent, heavily cutinized hair bases of the caducous stellate hairs that may develop into small cork warts.

Stomata confined to the abaxial surface, adaxially present on midrib of *M. japonicus*. Guard cell pairs 18–30 μm long and 13–18 μm wide.

In transverse section: Cuticle thin. Hypodermis present above veins. Midrib usually slightly raised, vascular system in midrib composed of a cylinder of separate bundles or two opposing arcs. Central bundles absent in all species except in *M. barbatus* and *M. macrostachyus*. Vascular system with or without fibre support. Veins embedded in mesophyll in *M. japonicus*, while raised above abaxial surface in other species (extremely so in *M. barbatus*). BSEs reaching the adaxial epidermis present in all species. Fibrous BSEs present in *M. tetracoccus*, continuing into a parenchymatous hypodermis. Parenchymatous BSEs in *M. japonicus* and *M. paniculatus* composed of large round cells. BSEs in *M. macrostachyus* composed of thin-walled fibres, cells near adaxial epidermis flattened, as in *M. metcalfianus*. Veins ending in usually enlarged tracheids. Vascular system in petiole with a ring of separate or partially fused vascular bundles with several central bundles or an internal ring of bundles. Crystals in petiole abundant to scattered. Sclerenchyma in petiole absent. Solitary fibres detaching from bundles and ending in parenchyma rare, irregular sclereids present in *M. barbatus*. Crystals in lamina present as large druses (usually > 50% of height of lamina in transverse section). Smaller crystalliferous cells with druses also frequent in mesophyll.

3.7 Calocarpus group
Species examined: *M. calocarpus*, *M. pierrei*. Revision: Sierra *et al*. (2007).

In surface view: Indumentum consisting of simple short and tufted hairs with two to five arms, mostly present on nerves. Hairs pointed and stiff, usually with a wide base, arms in one tuft sometimes of different lengths. Glandular hairs entire to subentire. Stomata present abaxially and adaxially near veins, guard cell pairs 23–27 μm long and 17–19 μm wide; stomata of *M. calocarpus* with cuticular striations extending as lateral wings.

In transverse section: Lamina and cuticle thin. Abaxial epidermal cells of *M. pierrei* in transverse section of different sizes, some cells (especially those surrounding hairs) large, representing more than one-third of the lamina thickness. Midrib adaxially raised, with an adaxial and abaxial vascular arc, in *M. calocarpus* accompanied by thick fibre caps. Veins slightly raised above abaxial leaf surface (*M. pierrei*) or embedded in mesophyll (*M. calocarpus*). Vascular bundles in *M. calocarpus* with abaxial and adaxial caps of fibres or entirely surrounded by fibres. BSEs rarely present in *M. pierrei*. Minor veins terminating in unmodified tracheids, sometimes branching at the end. Bundle sheath fibres abundant in *M. calocarpus*, often terminating in branched structures, while entirely absent in *M. pierrei*. Small crystal idioblasts abundant in the palisade layer and in the lowermost layer of spongy tissue in *M. calocarpus*. Prismatic crystals associated with veins.

3.8 Glomerulatus clade
Species examined: *M. actinoneurus*, *M. glomerulatus*, *M. mirus*. Revision: van Welzen, van der Ham & Kulju (2004); Sierra *et al*. (2007).

In surface view: Indumentum consisting of simple short and short stellately tufted hairs with two to five arms, present mostly on nerves. Hairs stiff and pointed, usually with a wide basal part, arms in one tuft sometimes of different lengths. Glandular hairs absent. Stomata present abaxially and adaxially near veins, guard cell pairs 19–28 μm long and 15–22 μm wide.

In transverse section: Cuticle thin. Mesophyll dorsiventral. Midrib adaxially raised (extremely so in *M. glomerulatus*), with an adaxial and abaxial arc, each accompanied by bundle caps. Veins embedded in mesophyll, with adaxial and abaxial fibre caps or entirely sheathed by fibres. *Mallotus glomerulatus* with abundant strands of fibres in mesophyll, not associated with veins. BSEs usually absent. Minor veins terminating in unmodified tracheids, sometimes branching at the ends. Fibres abundant in *M. glomerulatus*, forming a dense network. Crystals absent in *M. actinoneurus* but abundant in *M. glomerulatus* and *M. mirus*, where present as large and minute crystal idioblasts and as small druses in the palisade and spongy cells. Prismatic crystals associated with veins.

3.9 Subulatus clade (Fig. 14)
Species examined: *M. claoxyloides*, *M. coudercii*, *M. ficifolius*, *M. glabriusculus*, *M. macularis*, *M. megadontus*, *M. subulatus*. Revision: Sierra *et al*. (2007).

In surface view: Leaves glabrous or indumentum sparse, hairs usually confined to nerves. Nonglandular hairs simple and tufted, present in most species. Tufted hairs in some species composed of thick-walled, stiff arms with conspicuous cell-wall pits at the base and surrounded by enlarged epidermal cells. Glandular hairs observed on the adaxial surface of most species, usually (sub)entire in surface view, except in *M. claoxyloides*, where the margin is ridged; uppermost layer composed of 16 cells, radiat-

ing horizontally. Cuticular striations usually present, confined to the adaxial epidermis (abaxially in *M. claoxyloides*). Stomata confined to the abaxial surface, but scattered also on the adaxial side of *M. coudercii* and *M. megadontus* and over midrib and major veins of *M. claoxyloides* and *M. subulatus*. Guard cell pairs 21–31 μm long and 13–21 μm wide. Stomata with cuticular striae extending as lateral wings in some species.

In transverse section: Cuticle thin. Some epidermal cells in *M. claoxyloides* and *M. ficifolius* slightly enlarged on the abaxial side (strongly enlarged on the abaxial side of veins and at hair bases). Guard cells with thickened inner and outer walls, cuticular ledges present. Palisade cells wide and low in *M. coudercii* and *M. macularis*. Midrib adaxially raised, with two opposing arcs and some lateral bundles on each side. Vascular cylinder in midrib supported by a continuous fibre sheath or an interrupted cap. *M. macularis* with an adaxial cap of fibres and with clustered fibres on the abaxial and lateral sides. Veins embedded in mesophyll or slightly raised. Vein endings composed of thin and elongated tracheids with thin endings in *M. coudercii* and *M. subulatus*; wide tracheids with enlarged endings found in *M. megadontus*. Tracheids in other species normal or slightly enlarged. Large parenchymatous bundle sheath cells present in *M. claoxyloides* and *M. ficifolius*; in the latter elongating into BSEs, composed both of parenchyma cells and fibres. BSEs sometimes present in *M. glabriusculus*, absent in other species. Petiole with a vascular cylinder composed of separate bundles with one or two central bundles. Fibres present on the outer side of bundles in *M. coudercii* and *M. subulatus*. Fibres detaching from veins, forming a dense network of mesophyll fibres in all species. Crystals present as large and minute idioblasts containing druses in spongy and palisade tissue. Prismatic crystals associated with veins.

Note: Petiole examined only for *M. claoxyloides*, *M. coudercii* and *M. subulatus*.

3.10 Resinosus clade (Fig. 7)
Species examined: *M. decipiens*, *M. dispar*, *M. lanceolatus*, *M. leucocalyx*, *M. resinosus*. Revision: Sierra *et al*. (2007).

In surface view: Indumentum sparse, consisting of short to long simple hairs, and sometimes of tufted hairs; both types present mostly on nerves. Glandular hairs on the abaxial surface lying in shallow to deep depressions; in transverse view flattened, resembling those of *M*. section *Polyadenii*. An outline of eight cells usually observed on the adaxial surface (only in *M. resinosus* the uppermost layer of glandular hairs composed of four or eight clearly visible cells). Globular glandular hairs of *M. leucocalyx* round to flattened in transverse view, entire in surface view. *M. decipiens* and *M. leucocalyx* showing nipple-shaped papillae in the vicinity of glandular hairs. Epidermis of *M. resinosus* with dome-shaped papillae. Guard cell pairs 20–32 μm long and 12–17 μm wide. Stomata of *M. decipiens* and *M. resinosus* concentrated in crypts under glandular hairs, elsewhere scattered on the abaxial surface (in *M. lanceolatus* a few stomata present also adaxially). Some species show lobing of subsidiary cells just under the guard cells.

In transverse section: Cuticle 2–4 μm thick. Guard cells in transverse section with thickened outer and inner walls (inner wall thicker than the outer one) and with outer stomatal ledges. Lumina of stomata of medium size, slit-like in *M. leucocalyx*. Local hypodermis present above midrib. Midrib flat or raised, with an adaxial and abaxial arc or a partially merged cylinder in *M. resinosus* (phloem merged). Vascular system supported by fibre sheaths or caps. Veins embedded in mesophyll, with adaxial and abaxial strands of fibres or completely sheathed by fibres. Veins ending in long, single tracheids. Petiole with a cylinder of separate vascular bundles or merged into a continuous cylinder. Fibrous sheath surrounding the vascular system in all species except in *M. decipiens*. One central vascular bundle present in some species. Irregular terminal fibriform sclereids present in *M. resinosus* and to some extent in *M. decipiens* and *M. lanceolatus*. Crystals present as large idioblasts with druses in palisade or spongy parenchyma. Minute druses also present in palisade cells of *M. decipiens* and *M. leucocalyx*, and in spongy cells of *M. leucocalyx* and *M. resinosus*. Prismatic crystals abundant and associated with veins.

Note: Petiole not examined in *M. lanceolatus*. Cuticular maceration not examined in *M. resinosus*.

3.11 Tiliifolius clade (Figs 22, 28)
Species examined: *M. connatus*, *M. dispersus*, *M. rufidulus*, *M. tiliifolius*, *M. trinervius*, *M. ustulatus*. Revision: Sierra *et al*. (2007).

In surface view: Indumentum composed of simple, tufted and rarely stalked stellate hairs, the latter usually present on midrib and petiole, sometimes also on minor veins of *M. tiliifolius*. Simple and tufted hairs in *M. connatus*, *M. dispersus* and *M. ustulatus* usually with a wide, pitted base; simple hairs quite short (40–95 μm). Tufted hairs in *M. dispersus* and *M. trinervius* of two types: smaller, thin-walled stellately-tufted hairs, and larger, more rigid hair

tufts with fewer arms. Tufted hairs in *M. tiliifolius* with many arms, stalked stellate hairs present on midrib and petiole. Adaxial surface of *M. tiliifolius* covered with evenly distributed large hair tufts, possibly bearing multicellular stalks. Tufted hairs in *M. rufidulus* larger on midrib and major veins and smaller on lamina. Globular to disc-shaped glandular hairs observed in all species except in *M. trinervius*. Glandular hairs of *M. dispersus*, *M. tiliifolius* and *M. ustulatus* globular, with a (sub)entire margin in surface view; in *M. connatus* usually flattened (possibly an artefact of drying), entire or subentire; in *M. rufidulus* flattened, entire, but with a clear pattern of 16 cells radiating from the centre. Capitate glandular hairs observed in *M. tiliifolius*. Cuticular striations present in *M. dispersus*. Stomata confined to the abaxial side, adaxially present near veins in *M. trinervius*. Guard cell pairs 15–28 μm long and 13–18 μm wide.

In transverse section: Cuticle thin. Adaxial epidermal cells much larger than the abaxial ones. Some epidermal cells enlarged in *M. rufidulus* and at hair bases of *M. connatus*, *M. dispersus* and *M. ustulatus*, especially adaxially. Adaxial epidermal cells of *M. tiliifolius* extremely tall. Stomata prominent in *M. rufidulus* and *M. trinervius. Mallotus tiliifolius* and *M. trinervius* showing thickened walls, inner walls thicker than outer ones, lumina medium wide. In *M. rufidulus* both walls equally thick. Local hypodermis present above veins in *M. connatus*, *M. tiliifolius* and *M. ustulatus*. Palisade tissue in *M. trinervius* composed of unusually elongated cells, representing over 50% of the lamina thickness. Lamina of *M. tiliifolius* with stomatal crypts; mesophyll isobilateral with several layers of palisade cells without a distinct spongy tissue. Stomatal crypts also locally present in *M. dispersus* and *M. trinervius*. Midrib adaxially flat to slightly raised, grooved only in *M. trinervius*. Vascular system composed of two opposing arcs or an adaxial arc and a few merged abaxial bundles, organized in a half-cylinder. *Mallotus ustulatus* with an interrupted sheath of fibres around the vascular system. Vascular arcs supported by fibre caps in all species except *M. ustulatus*. Veins sheathed by fibres and with additional parenchymatous bundle sheaths extending towards the adaxial epidermis. Vein endings enlarged in *M. tiliifolius* (not observed for other species). Vascular system in petiole composed of a cylinder of separate or partially merged bundles with one or a few central bundles. Fibrous sheaths in petiole absent in all sampled species. Foliar sclereids present in some species as fibres detaching from veins. Crystals present as large and small druse idioblasts in the mesophyll (extremely large in *M. trinervius*, ranging in size between 50 and 70 μm). Secretory cells present in ground tissue of petiole and midrib of *M. trinervius*.

Note: No petiole and cuticular maceration available for *M. rufidulus*. No cuticular maceration and no leaf clearing available for *M. trinervius*. No cuticular maceration available for *M. tiliifolius*. Petiole not studied for *M. glabriusculus*.

3.12 Wrayi clade (Fig. 18)
Species examined: *M. caudatus*, *M. spinifructus*, *M. wrayi*. Revision: van Welzen & Sierra (2006)

In surface view: Indumentum composed of flat (two-dimensional) in *M. wrayi* to three-dimensionally, stellately-tufted thin-walled hairs in all other species (see photos in van Welzen & Sierra, 2006), and of simple hairs in *M. caudatus* and *M. spinifructus*. Glandular hairs flattened, without conspicuous ridges; uppermost glandular cell layer probably composed of 16 cells. Stomata confined to the abaxial side, but present also adaxially on veins. Guard cell pairs 15–17 μm long and 8–9 μm wide.

In transverse section: Cuticle thin. A unique feature is the presence of one mesophyll layer (two in *M. wrayi*) of larger, thin-walled, rounded isodiametric cells between the palisade layer and the spongy tissue. Midrib with two opposing arcs or a merged cylinder, with interrupted fibre sheaths; sometimes fibres rather scattered on the adaxial side. In *M. caudatus* and *M. spinifructus* additional adaxial strands of phloem and fibres present above the adaxial arc. Veins embedded in mesophyll, smaller veins with abaxial fibre caps, larger ones usually with fibre caps on both sides or even fully sheathed by fibres. BSEs sometimes present in *M. spinifructus*. Vascular system in petiole composed of a fused or partly fused cylinder with one to three central bundles, surrounded by a continuous fibre sheath. Foliar sclereids present as fibres detaching from vascular bundles. Crystals present as large druses in palisade parenchyma. Prismatic crystals rare, associated with veins. Secretory cells present in ground tissue of petiole and midrib in *M. wrayi*.

Note: Cuticular macerations not examined.

3.13 Section Stylanthus (Figs 5, 33)
Species examined: *M. lackeyi*, *M. peltatus*. Revision: Slik & van Welzen (2001a).

In surface view: Indumentum consisting of simple and tufted hairs. Tufted hairs mostly pointed and stiff, composed of two to more than ten arms, arms some-

times of different lengths. A few tufted hairs on midrib with obtuse tips. Glandular hairs globular to flattened in transverse section, in *M. lackeyi* lying in a depression of lamina, predominantly entire in surface view. Adaxial and abaxial epidermis in *M. lackeyi* with dome-shaped papillae, some epidermal cells enlarged. Stomata confined to the abaxial side, 19–22 μm long and 9–11 μm wide. Few stomata in *M. lackeyi* present also adaxially on major veins.

In transverse section: Cuticle thin. Guard cells with thickened inner and outer walls and medium wide lumina. Outer stomatal ledges present (in *M. lackeyi* also inner ones). Midrib adaxially slightly raised in *M. lackeyi*, grooved in *M. peltatus*, with an adaxial and abaxial vascular arc, surrounded by an interrupted fibre sheath. Minor veins embedded in mesophyll. Vascular bundles in *M. lackeyi* surrounded by large bundle sheath cells, extending towards the adaxial epidermis. BSEs present in *M. lackeyi*. Veins ending in thin and long tracheids, sometimes slightly enlarged in *M. peltatus*. Petiolar vascular system in *M. lackeyi* composed of an outer and inner cylinder of vascular bundles and an additional central bundle. *M. peltatus* with a vascular cylinder composed of separate bundles and two central bundles. Fibres detaching from vascular bundles to form fibriform mesophyll sclereids. Crystals present as large druses in palisade tissue, representing 50–75% of thickness of lamina. Minute druses present in palisade cells of *M. peltatus*.

3.14 Section Polyadenii (Figs 10, 23, 30)
Species examined. *M. leucodermis*, *M. muticus*, *M. polyadenos*. Revision: Bollendorff, van Welzen & Slik (2000).

In surface view: Non-glandular hairs absent. Glandular hairs frequent on both surfaces. Glandular hairs peltate-like on the abaxial side, each one lying in a deep depression of the lamina. The uppermost layer of glandular hairs composed of eight, 16 or 32 cells. Adaxial glandular hairs slightly different in shape, without conspicuous ridges but still with a clear pattern of cells radiating from the centre. Stomata confined to the abaxial surface, present mostly in depressions under glandular hairs, elsewhere scattered. Guard cell pairs 19–25 μm long and 14–19 μm wide.

In transverse section: Cuticle thin. Guard cells with thickened walls and medium lumina, outer stomatal ledges present. Spongy parenchyma in *M. leucodermis* extremely thick, organized in columns, surrounded by large intracellular spaces. Midrib adaxially concave in *M. muticus* and slightly raised in *M. polyadenos*, with a groove in *M. leucodermis*. Vascular system of midrib with two large opposing arcs and surrounded by a sheath of thin- to thick-walled fibres. Minor veins embedded in mesophyll, surrounded by thin-walled fibrous sheaths (or sclerified parenchyma cells). Vein endings sometimes enlarged in *M. muticus*. Vascular system in petiole composed of an almost continuous cylinder. Foliar sclereids present as thin-walled fibres in mesophyll of *M. polyadenos*, detaching from bundle sheaths and veins. Crystals in lamina infrequent, present as druses inside small (*M. muticus*, *M. polyadenos*) or large (*M. leucodermis*) idioblasts. Prismatic crystals associated with veins.

Note: Petiole and midrib not examined in *M. leucodermis*.

3.15 Miquelianus clade
Species examined: *M. brachythyrsus*, *M. concinnus*, *M. havilandii*, *M. insularum*, *M. miquelianus*. Revision: van Welzen *et al*. (2006).

In surface view: Indumentum consisting mostly of simple and sometimes stellately tufted hairs; the latter present in *M. concinnus*, *M. havilandii* and *M. miquelianus* (in the last-named according to van Welzen *et al*., 2006, but not observed in the present study). Glandular hairs in transverse section either flattened with a conspicuously ridged margin (*M. havilandii*, *M. insularum*) or round in transverse section with a (sub)entire margin (*M. brachythyrsus*, *M. cauliflorus*). Glandular hairs often lying in depressions in lamina. Stomata confined to the abaxial surface, with few stomata adaxially on veins in *M. brachythyrsus* and *M. miquelianus*. Guard cell pairs 19–31 μm long and 10–15 μm wide. Stomata of *M. insularum* with striae extending as lateral wings.

In transverse section: Cuticle up to 5 μm thick. Inner and outer guard cell walls equally thickened, lumina relatively wide and in central position. Local hypodermis present above major veins in *M. brachythyrsus*. Midrib (available only for *M. brachythyrsus* and *M. miquelianus*) adaxially raised, with two opposing arcs. Vascular system surrounded by a fibre sheath. Additional strands of fibres occurring adaxially in the groove above the midrib; scattered fibres present between the adaxial arc and adaxial fibre cap. Petiole (available only for *M. brachythyrsus* and *M. miquelianus*) with separate bundles forming a cylinder, with one or two additional central bundles. Veins with an adaxial and abaxial strand of fibres or completely surrounded by a thick fibrous sheath. Foliar sclereids present as fibres detaching from bundles. Crystals present as minute druses, scattered in palisade and

spongy cells, and as larger idioblasts in palisade and spongy tissue. In *M. cauliflorus* large druses present also in the adaxial epidermis.

Note: Leaf clearing and maceration not available for *M. insularum*. Midrib and petiole not examined in *M. concinnus*, *M. havilandii* or *M. insularum*.

3.16 Mallotus blumeanus
Revision: Sierra *et al*. (2007).

In surface view: Indumentum consisting of stellately tufted hairs with many arms (> 30), present mostly on veins. Some tufts distinctive, with mostly pointed and stiff arms but also a few thin-walled, elongated arms, easily breaking off. Globular glandular hairs composed of three-dimensionally radiating cells. Stomata confined to abaxial surface, on average 22 μm long and 15 μm wide.

In transverse section: Cuticle thin. Midrib adaxially flat, with an adaxial and abaxial arc and few additional lateral bundles, surrounded by a thin, interrupted fibre sheath. Veins embedded in mesophyll, fibres present on the abaxial side of veins. Veins surrounded by conspicuous parenchymatous bundle sheath cells. Minor veins terminating in long tracheids, sometimes with slightly enlarged endings. Petiole with a cylinder of separate bundles with two central bundles. Petiole bundles with few thin-walled fibre caps. Foliar sclereids present as fibres detaching from vascular bundles. Crystals present as large and minute druses in the mesophyll.

3.17 Mallotus cauliflorus (Fig. 21)
Revision: Sierra *et al*. (2007).

In surface view: Non-glandular hairs absent except for a few simple hairs present on petiole. Glandular hairs scattered on both surfaces, inserted in lamina, round in transverse section. Stomata on average 17 μm long and 10 μm wide, with cuticular striae extending as lateral wings. Cuticle thin. Guard cells with thickened inner and outer cell walls, relatively wide lumina and conspicuous outer stomatal ledges. Midrib adaxially grooved, with a cylinder of separate bundles, supported by a continuous sheath of fibres. Central bundles present. Veins embedded in mesophyll, sheathed by fibres. Vascular system in petiole composed of a cylinder of bundles with two central bundles and without any supporting sclerenchyma. Crystals infrequent, present as relatively large druses in palisade layer. Druses present also in enlarged epidermal cells.

Note: Petiole, leaf clearing and maceration not examined.

DISCUSSION

The leaf anatomical diversity in *Blumeodendron*, *Hancea* and *Mallotus* reported above shows an ambiguous pattern that in some instances supports clades reconstructed by Sierra *et al*. (2010) from molecular and morphological (including leaf anatomical) datasets; in many other instances clades appear to be quite heterogeneous with regard to leaf anatomy. Whether this is due to rampant homoplasy among most leaf anatomical characters or to doubtful monophyly of the proposed clades cannot be answered here. This is because, as indicated by Sierra *et al*. (2010), at least the phylogenetic reconstruction of *Mallotus s.s*. is far from robust, and many clades recognized by them have little or hardly any support [although the support for the genera *Hancea* (still referred to as *Cordemoya*), *Macaranga* and *Mallotus* is high; Kulju *et al*., 2007b]. It would therefore be too speculative to attempt scenarios for the evolution of leaf anatomical diversification in *Mallotus* and its relatives, and we therefore confine ourselves to a general discussion of the leaf anatomy of the various taxonomic groups and putative clades sampled for this study.

MALLOTUS AND *MACARANGA*

The genus *Macaranga*, which is sister to *Mallotus* (Wurdack *et al*., 2005; Kulju *et al*., 2007b) and shares with it morphological and ecological similarities, is at least as diverse as the genus *Mallotus* with regard to leaf anatomy (Fišer Pečnikar, pers. observ.). Globular to disc-shaped hairs, similar to those in *Mallotus*, are common in *Macaranga* and are a shared synapomorphy by both genera. However, several non-glandular types of hair can also be found: besides the common simple unicellular and tufted hairs we observed also small curved unicellular hairs, branched multicellular hairs or long curly hairs; these types have not been reported for *Mallotus*. On the other hand, *Macaranga* lacks stellate or stellately bundled hairs (with exceptions for a few individual species). Several *Macaranga* spp. show unusually elongated palisade cells and a distinct type of papillae on the abaxial surface. Most species have conspicuous BSEs, both parenchymatous and fibrous (or mixed). Different from *Mallotus* is the vascularization of the midrib. Although some species have two opposing arcs, some also have an open vascular cylinder composed of vascular bundles, similar to those in *Hancea* subgenus *Cordemoya*. Pith bundles, which are usually absent in *Mallotus* midribs but present in, for

example, *H. integrifolia*, *H. spinulosa* and *H. subpeltata*, are often present in *Macaranga*. The presence of secretory cavities in the petiole and midrib is also mostly restricted to *Macaranga*. Although Hussin *et al*. (1996) reported the occurrence of secretory cells in inner ground tissue of midrib in *Mallotus macrostachyus*, we were not able to confirm their finding. Secretory cells are extremely rare in *Mallotus*; they were found in two species only.

Generic distinctness of *Blumeodendron*, *Hancea* and *Mallotus*

Hussin *et al*. (1996) could not clearly correlate leaf anatomy with any classification. This may be due to their limited sampling (only 16 species, and *Hancea* was mixed with *Mallotus*). Table 1 indicates that each genus has its own, more or less unique combination of characters. However, the sampling of *Blumeodendron* consisted of one species only and it is therefore impossible to discuss the leaf anatomical distinctiveness of the genus. Nevertheless, at least two species of *Blumeodendron* (the sampled *B. kurzii* and also *B. calophyllum* Airy Shaw; Fišer Pečnikar, pers. observ.) have giant stomata and a thick cuticular layer. *Hancea* as a whole is characterized by capitate glandular hairs, and most species also share the presence of brachysclereids, cristarque cells and the abundance of mesophyll sclereids. The last character is probably the reason why it was extremely difficult to make sections and cuticular macerations in subgenus *Hancea*. The two subgenera are distinct: subgenus *Cordemoya* differs from subgenus *Hancea* by the presence of peltate-stellate hairs with a central globular cell. *Mallotus* shows the greatest variability within its numerous species and species groups, but can be separated from *Hancea* by the presence of globular to disc-shaped glandular hairs (although they are absent in one *Mallotus* group, but this seems to be a reversal). Pith bundles in the vascular tissue of the midrib are (mostly) absent in *Mallotus*, but present in some *Hancea* spp., as observed also by Hussin *et al*. (1996).

Sections or monophyletic groups in *Mallotus*

Several infrageneric groups within *Mallotus* can be recognized by anatomical synapomorphies. Here we elaborate on the analysis by Sierra *et al*. (2010) and show (partly more clearly) which anatomical states are apomorphies. Most groups can be found in Figure 2. Only two clades lack anatomical synapomorphies: the *Subulatus* and *Resinosus* clades. All other clades have (possibly apomorphic) anatomical characteristics.

Mallotus section Mallotus: typical characters for this group are the presence of persistent hair bases, stalked stellate hairs and the absence of stellately tufted hairs. Stellate hairs also occur in the *Mallotus tiliifolius* clade, but then always in combination with tufted hairs.

Mallotus section Mallotus plus part of the Philippinenses grade (M. kongkandae, M. philippensis, M. repandus): This is the section Mallotus clade extended with three species of the Philippinenses grade. Typical characters are the presence of stomata on the adaxial leaf surface and the absence of outer cuticular ledges and enlarged terminal vein tracheids.

Mallotus section Mallotus plus Philippinenses grade: A typical character for the complete clade is the absence of simple hairs (although some species are polymorphic, see Table 1). Most species in this group have a local hypodermis.

Mallotus section Polyadenii: The anatomical synapomorphy for this section is the presence of stomata concentrated under the glandular hairs. However, this is a homoplasious character and it is also found as two parallel developments in *M. resinosus* and *M. decipiens* of the *Mallotus resinosus* clade.

Mallotus miquelianus clade plus section Polyadenii and Stylanthus: Typical are the glandular hairs on the upper leaf surface. However, there are reversals for *M. blumeanus*, *M. hispidospinosus*, *M. miquelianus* and *M. sphaerocarpus*. Thus, it is not a strong character for this clade, and it is occasionally present outside the clade.

Mallotus glomerulatus clade: This clade lacks glandular hairs, a character found in parallel in the *subulatus* clade.

Mallotus tiliifolius clade: As already was mentioned for section *Mallotus*, for both groups the presence of stellate hairs is typical, but in the *tiliifolius* clade the stellate hairs occur in combination with bundled hairs. In the clade, *M. cambodianus*, *M. didymochryseus*, *M. dispersus*, *M. eriocarpus*, *M. tiliifolius* and *M. ustulatus* have a rough upper leaf surface.

Mallotus wrayi clade: A layer of thin-walled round cells is present under the palisade layer.

Blumeodendron

Blumeodendron leaves show some sclerophyllous characteristics: a rather thick lamina with a thick cuticular layer and abundant fibro-sclereids detach-

ing from the veins and running in all directions in the mesophyll. Brachysclereids are present in the ground tissue of the petiole. Brachysclereids are also present in *Hancea*, which also shares some sclerophyllous characteristics (e.g. sclereids, thicker cuticle).

Large (giant) stomata with conspicuous stomatal ledges are found scattered between the normal stomata on the lower surface of *B. kurzii*. Sampling of more *Blumeodendron* spp. is needed to assess the diagnostic value of this character for the genus.

Hancea

The subdivision of *Hancea* into two subgenera is supported by leaf anatomical characters. All species of subgenus *Hancea* have a similar mesophyll organization, composed of one palisade and a few spongy layers. Fibres associated with vascular bundles are an important character shared by all *Hancea* spp. The presence of thick-walled fibres and sclereids in subgenus *Hancea* might contribute to the extremely difficult sectioning of the leaves. Also, cuticular macerations are difficult to obtain, probably because of the same reason.

Brachysclereids have been found in *Blumeodendron* and *Hancea*. Brachysclereids were already mentioned in the study conducted by Hussin *et al*. (1996), who found them only in *H. griffithiana*, and not in the two other *Hancea* spp., which were included in their research (*H. penangensis* and *H. kingii*). In our study, brachysclereids were found in all sampled species in *H*. section *Hancea*, but in *H*. section *Cordemoya* they were found in one species only. However, wider sampling is needed to see whether the absence in other species is a result of incomplete sampling or that the character is really polymorphic in that group. Outside the early branching clades, brachysclereids were found only in one *Mallotus* spp. (*M. rufidulus*).

Similarly to brachysclereids, cristarque cells have been found in almost all species of *Hancea* studied. Although this character is regarded as highly diagnostic (Dickison, 2000), the presence of cristarque cells is more common than apparent from the literature (Baas, 1972; van Welzen & Baas, 1984).

Small cork warts in *H*. section *Hancea* are more typical than the minute ones in *Blumeodendron* and in *M*. section *Mallotus*, which we mention in the previous chapters as persistent hair bases. Their origin in *H*. section *Hancea* is not clear. However, their occurrence is not homologous to the occurrence in *Blumeodendron* and *Mallotus*. According to Stace (1965) and Joffily & Cardoso Vieira (2005) the presence of cork warts can be an important taxonomic character, but they should not be confused with irregular cork warts of traumatic origin (e.g. insect bites) which occur in most of the species.

Hussin *et al*. (1996) mentioned that non-glandular hairs are absent in *H. griffithiana*, *H. kingii* and *H. penangensis*. Our study revealed that simple hairs are present in these species; they are, however, restricted to midrib and larger veins. Hussin *et al*. (1996) also found glandular cells in the ground tissue in the petiole of *H. penangensis*; we were unable to find these in our studied specimen.

Ecologically important characters

Leaf anatomical characters can show a large intraspecific variation in response to environmental factors (Rocas, Barros & Scarano, 1997). Abaxial stomatal density, thickness of palisade and spongy layers, and compactness of parenchyma are, for example, characters which can be affected by environmental factors. We examined these characters, and as expected did not find them to be phylogenetically informative. Also, the number of specimens studied per species was too low to conclude anything about any anatomical response to environmental conditions. It is striking that *Blumeodendron*, *Hancea* and the related *Ptychopyxis* Miq. (not included) all have thick and stiff coriaceous leaves. This is counterintuitive as they are typical lowland rainforest species, whereas the leaf structure seems more indicative for a dry mediterranean type of climate. In contrast, the species in *Mallotus* section *Mallotus* are pioneer species (Slik, Kessler & van Welzen, 2003) and they are generally found in exposed conditions. However, all species have a thin lamina instead of the expected thickly coriaceous leaves. However, sclerophyllic, xeromorphic and mesomorphic leaf attributes often co-occur in the same tropical ecosystem and are related in a complex way to alternative life strategies involving individual leaf longevity and herbivory (Baas, 1975; Onoda *et al*., 2011).

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APPENDIX

List of vouchers used for leaf anatomical study

Species	Voucher	Herbarium
Blumeodendron kurzii (Hook.f.) J.J.Sm.	Bogor Botanical Garden 45	L
Hancea acuminata (Baill.) S.E.C.Sierra, Kulju & Welzen.	D'Alleizette 6522b	G
	D'Alleizette s.n. (L O146441)	L
Hancea capuronii (Leandri) S.E.C.Sierra, Kulju & Welzen	Rakotomalaza, Messmer & Rakotovao 1502A	G
	Messmer & Andriatsiferana NM698	L
Hancea cordatifolia (Slik) S.E.C.Sierra, Kulju & Welzen	Gutierrez *et al*. PNH 117545	L
Hancea eucausta (Airy Shaw) S.E.C.Sierra, Kulju & Welzen	Wong 1191	L
	Coode 7930	L
Hancea griffithiana (Müll.Arg.) S.E.C.Sierra, Kulju & Welzen	Suppiah KEP 104951	L
Hancea hirsuta (Elmer) S.E.C.Sierra, Kulju & Welzen	Ramos & Pascasio BS 34549	L
Hancea hookeriana (Seem.) S.E.C.Sierra, Kulju & Welzen	Tsang 29561	L
Hancea integrifolia (Willd.) S.E.C.Sierra, Kulju & Welzen.	Sieber Flora mixta 199 (L0293609)	L
	Coode & Cadet 4958	L
Hancea kingii (Hook.f.) S.E.C.Sierra, Kulju & Welzen	Smitinand 10945	L
	Shah 1558	L
Hancea longistyla (Merr.) S.E.C.Sierra, Kulju & Welzen	Gutierrez *et al*. PNH 117592	L
Hancea papuana (J.J. Sm.) S.E.C.Sierra, Kulju & Welzen	Kostermans & Soegeng- Reksodihardjo 387	L
Hancea penangensis (Müll.Arg.) S.E.C Sierra, Kulju & Welzen	Kostermans 1318	L
Hancea spinulosa (McPherson) S.E.C.Sierra, Kulju & Welzen	Rbevohitra 2052	WAG
Hancea stipularis (Meijer ex Airy Shaw) S.E.C.Sierra, Kulju & Welzen	Arifin Berau 56	L
Hancea subpeltata (Blume) M.Aparicio	Beusekom & Phengkhlai 533	L
	Middleton *et al*. 1735	L
Mallotus actinoneurus Airy Shaw	Kochummen FRI 2499	L
Mallotus barbatus Müll.Arg.	Maxwell 98–411	L
Mallotus blumeanus Müll.Arg.	Rijksen 28773	L
Mallotus brachythyrsus Merr.	Mamit S 35263	L
	Purseglove S 4665	L
Mallotus calocarpus Airy Shaw	Nicholson 1639	L
Mallotus caudatus Merr.	Kessler *et al*. Berau 831	L
Mallotus cauliflorus Merr.	Ramos & Edaño BS 33460	L
Mallotus claoxyloides (F.Muell.) Müll.Arg.	Forster & Machin 12257	L
Mallotus concinnus Airy Shaw	Chin 1552	L
Mallotus connatus M.Aparicio	Kostermans 21548	L
Mallotus coudercii (Gagnep.) Airy Shaw	Kerr 19504	L
Mallotus decipiens Müll.Arg.	Middleton *et al*. 1368	L
Mallotus discolor F.Muell. ex Benth.	Forster 14276	L
Mallotus dispar (Blume) Müll.Arg.:	Reynoso *et al*. PPI 4051	L
Mallotus dispersus P.I.Forst.	Russel-Sith & Lucas 4675	L
Mallotus ficifolius (Baill.) Pax & K.Hoffm.	Forster & Machin 12257	L
	Forster *et al*. 27676	L
Mallotus glabriusculus (Kurz) Pax & K.Hoffm.	Winit 689	L
Mallotus glomerulatus Welzen	Pooma *et al*. 2662	L

APPENDIX *Continued*

List of vouchers used for leaf anatomical study

Species	Voucher	Herbarium
Mallotus havilandii Airy Shaw	Yii S 46226	L
Mallotus hispidospinosus Welzen & Chayam.	Maxwell 98–321	L
Mallotus insularum (Airy Shaw) Slik	Bloembergen 4482	L
Mallotus japonicus Müll.Arg.	Kuoh 12147	L
Mallotus khasianus Hook.f.	Nooteboom *et al*. 798	L
Mallotus lackeyi Elmer	Kessler Berau 805	L
Mallotus lanceolatus (Gagnep.) Airy Shaw	Kerr 5687	L
Mallotus leucocalyx Müll.Arg.	Reynoso *et al*. PPI 14754	L
Mallotus leucodermis Hook.f.	Argent *et al*. 96-31	L
Mallotus macrostachyus (Miq.) Müll.Arg.	Cheng KEP FRI 27524	L
Mallotus macularis Airy Shaw	Sidiyasa *et al*. 2815	L
Mallotus megadontus P.I.Forst.	Batianoff 12193	L
Mallotus metcalfianus Croizat	Bunchuai 1826	L
Mallotus miquelianus (Scheff.) Boerl.	Teo & Pachiappan KL 3152	L
Mallotus mirus S.E.C.Sierra	Kerr 19835	L
Mallotus muticus Müll.Arg.	Wood A 4675	L
Mallotus nesophilus Müll.Arg.	Balgooy & Byrnes 1303	L
Mallotus nudiflorus (L.) Kulju & Welzen	Kostermans 251	L
Mallotus oppositifolius (Geiseler) Müll.Arg.	Warnecke 51	L
Mallotus pallidus (Airy Shaw) Airy Shaw	Chayamarit *et al*. 1845	L
Mallotus paniculatus (Lam.) Müll.Arg.	Forster *et al*. 28767	L
Mallotus peltatus (Geiseler) Müll.Arg.	Geesink *et al*. 6813	L
Mallotus philippensis (Lam.) Müll.Arg.	Lantoh SAN 73452	L
	Hiep 5370	L
Mallotus pierrei (Gagnep.) Airy Shaw	Winit 446	L
Mallotus pleiogynus Pax & K.Hoffm.	Schram BW(Ind.) 2709	L
Mallotus polyadenos F.Muell.	Forster *et al*. 27597	L
Mallotus polycarpus (Benth.) Kulju & Welzen	Stocks & Law s.n. (GH)	L
Mallotus repandus (Rottler) Müll.Arg.	Stocks s.n. (L0436500)	L
Mallotus resinosus (Blanco) Merr.	Craven & Schodde 999	L
	Vidal 5746	L
Mallotus rhamnifolius (Willd.) Müll.Arg.	Jayasuriya 1283	L
Mallotus rufidulus (Miq.) Müll.Arg.	Coifs 164	L
Mallotus spinifructus Welzen & S.E.C.Sierra	Mogea 4335	L
Mallotus subulatus Müll.Arg.	Breteler 5911	L
Mallotus tiliifolius (Blume) Müll.Arg.	Awa & Ismawi S 48717	L
	Borssum Waalkens 157	L
	Huq 10892	L
Mallotus trinervius (K.Schum. & Lauterb.) Pax & K.Hoffm.	Brass 14115	L
Mallotus ustulatus (Gagnep.) Airy Shaw	Huq & Phurin 10892	L
Mallotus wrayi King ex Hook.f.	Whitmore KEP FRI 8650	L