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Leaf anatomy of various groups in *Macaranga* (*Bicolor*, *Denticulata*, *Gracilis*, *Javanica*, *Pachystemon*, *Pruinosae*, *Tanarius* and *Winklerianae*) and *Ptychopyxis* (*Euphorbiaceae*)

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Keywords

Acalyphoideae
Fibriform sclereids
Hair types
Palaeotropics
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Abstract The leaf anatomy of eight (generally informal) groups of *Macaranga* and *Ptychopyxis* (*Euphorbiaceae*, *Acalyphoideae*) was studied based on 79 species (plus various infraspecific taxa) represented by 123 collections. All species showed abaxial, paracytic stomata (perhaps an exception for *M. javanica*), a dorsiventral mesophyll, extra-floral nectaries on the leaf surfaces, collateral bundles and druse-like crystals. All *Macaranga* species showed disc-shaped glandular hairs, a character shared with its sister genus *Mallotus*, bundle sheet extensions, a generally local hypodermis and quite often papillae, present in various sizes and often concentrated around the disc-shaped glandular hairs that are sunken in cavities shielding the stomata. Some *Macaranga* species show fibriform sclereids, which are much more abundant in *Ptychopyxis*. *Ptychopyxis* has a much higher number of (unhidden) stomata than *Macaranga* and the bundle sheet extensions and hypodermis were not observed. Cuticular macerations were difficult to make in all specimens as the cuticles were very thin. Transverse sections sometimes failed, especially in *Ptychopyxis*, due to abaxially extending nerves and thin in between mesophyll.

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INTRODUCTION

Macaranga Thouars, with about 300 species, is one of the largest genera within the *Euphorbiaceae*. It is present in the wetter areas of Sub-Saharan Africa and Madagascar, and ranges from India to southern and central China, through Southeast Asia and the Malay Archipelago to the West Pacific and northern and eastern Australia (Davies 2001; Whitmore 2008). *Macaranga* is classified in the subfamily *Acalyphoideae*, tribe *Acalypheae*, subtribe *Rottlerinae*, comprising taxa with stipules, like most *Euphorbiaceae* (Webster 2014). The sister genus *Mallotus* Lour. is classified in the same subtribe (Wurdack et al. 2005, Kulju et al. 2007, Sierra et al. 2010). The two genera show a similar morphological variation in relation to their ecology, narrow and relatively elongated leaves in species from primary rainforest, species with large and broad leaves that are often lobed in pioneer habitats (Slik et al. 2003). Both genera are often confused, not only because of this resembling morphology, but also by characters like the presence of extrafloral nectaries (EFNs) on the adaxial leaf surface and (with few exceptions) the abaxial glandular disc-shaped hairs on the leaves, which in *Macaranga* are often neatly ordered in rows and more random in *Mallotus*. *Mallotus* usually has stellately bundled hairs abaxially on the leaves and in the inflorescences, these are (few exceptions) absent in *Macaranga*. The number of stamens in *Macaranga* (1–30) is generally (much) lower than in *Mallotus* (15–130), while the staminate flowers in *Macaranga* are smaller and usually with bigger bracts; moreover, the inflorescences in *Macaranga* are usually paniculate and more racemose thyrsoid in *Mallotus* (except some of the pioneer species, e.g., *Mallotus paniculatus* (Lam.) Müll.Arg.). The fruits in both genera often have spiny appendages, but in *Macaranga* a number of species have fruits with glandular areas (extrafloral nectaries) instead of appendages.

Whitmore (2008) distinguished many informal groups within *Macaranga*. Of the groups treated in this study, the *Bicolor*, *Denticulata*, *Pachystemon*, *Pruinosae*, *Tanarius* and *Winklerianae* groups, comprise mainly pioneer species, while those of *Gracilis* are small forest trees of high mountains and the *Javanica* group occurs mainly in secondary forests. *Tanarius* is often present on soil that is heavily disturbed, usually multiple times (Slik et al. 2003). Three of the pioneer groups are obligate myrmecophytes (*Pachystemon*, *Pruinosae* and *Winklerianae*), whereby the ants nest in the hollow twigs or can easily hollow out twigs (Bronstein et al. 2006) and either eat from the various

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EFNs (Fiala & Maschwitz 1992a) or food bodies (solid droplets of exudate) (Fiala & Maschwitz 1992b) and/or farm their aphids inside the nests. The ants protect the leaves against herbivory and overgrowing plants and fungi (Fiala et al. 1989, Agrawal & Rutter 1998, Davies et al. 2001 and references therein). Also the non-myrmecophytic species of *Macaranga* and *Mallotus* possess the EFNs or produce, especially when young and more herbaceous, food bodies (e.g., *Macaranga tanarius* (L.) Müll.Arg., pers. obs. PCvW), always with the purpose to attract the protecting ants. The pioneer species germinate fast in open unshaded spaces and with their very large to enormous leaves (largest in *M. gigantea* (Rchb.f. & Zoll.) Müll.Arg. and *M. siamensis* S.J.Davies) shading out the soil, allowing other, more primary forest plants to germinate.

The groups, as circumscribed by Whitmore (2008), were compared to three phylogenies to determine their possible monophyly; two studies (Davies et al. 2001, Bänfer et al. 2004) concentrated on the myrmecophytes, while van Welzen et al. (2014, based on Kulju et al. 2007) used a subsampling from the complete genus. Davies et al. (2001) used a mix of morphological and ITS molecular data and gave a parsimony analysis; Bänfer et al. (2004) used AFLP data together with a phenetic analysis (neighbour joining), and van Welzen et al. (2014) based their phylogeny on various molecular sequences and a Bayesian analysis. The *Pachystemon* and *Pruinosae* groups were monophyletic in Davies et al. (2001) and Bänfer et al. (2004), but as indicated, with a strong bias in taxon sampling. The *Bicolor* group is a grade in Davies et al. (2001, called *Pachystemon 4*) and monophyletic in Bänfer et al. (2004, called *Puncticulata* group). *Winklerianae* was monophyletic in Bänfer et al. (2004), but only represented by a single sample in the two other studies. In van Welzen et al. (2014) none of the groups were monophyletic, but here the sampling of most groups was inadequate. Therefore, all groups used in this study are considered to be informal.

Ptychopyxis Miq., a small genus with 11 species, can be found in the Malay Archipelago and SE Asia mainland (Stoops & van Welzen 2013). It is classified in the same subfamily and tribe, but then in the related subtribe *Blumeodendrinae*, comprising taxa that lack stipules (Webster 2014). Morphologically, it resembles *Macaranga*, but the thick leaves and its rarity (no fresh samples) defied any successful sampling for phylogenetic analyses. The leaves also show extrafloral nectaries and most species often have densely hairy parts with simple hairs. Typical and distinctive for the genus are the stamens with free filaments and dorsi-basifixed anthers attached to a broad triangular connective. It is included in this study because of its likely relationship with *Macaranga* and the lack of knowledge surrounding this taxon.

The leaf anatomy of other related genera, *Blumeodendron* Kurz, *Hancea* Seem. and *Mallotus*, was described by Fišer Pečnikar et al. (2012). *Hancea* is in the same subtribe as *Macaranga*, *Blumeodendron* in the same subtribe as *Ptychopyxis*. All of them, also the genera included in this study, show a dorsiventral mesophyll, paracytic stomata and collateral bundles in the mesophyll (Norfaizal et al. (2012) report staurocytic stomata for *M. javanica* (Blume) Müll.Arg., which we could not confirm). Typical for *Hancea* are the capitate glandular hairs and cristarque cells, and together with *Blumeodendron* the leaves contain brachysclereids and columnar and fibriform mesophyll sclereids. *Blumeodendron* shows giant stomata, not found in the other genera. Typical for *Mallotus* are the globular to disc-shaped hairs, which come in different types.

Fišer Pečnikar et al. (2012) already indicated that *Macaranga* is leaf anatomically even more variable than *Mallotus*. Here we present the leaf anatomy of various groups in *Macaranga* with different ecology, ranging from primary forest trees to pioneers living together with ants.

MATERIAL AND METHODS

This chapter follows Fišer Pečnikar et al. (2012) for the sake of comparison.

MATERIAL

The material was supplied by the herbarium of Naturalis Biodiversity Center, The Netherlands (L). The samples are listed in Appendix 1 including a reference to the species, name of the collector and number, QR code (referring to the Naturalis database, visible via https://bioportal.naturalis.nl/), provenance and sometimes a remark is provided. Except for a few species not present in L, all *Macaranga* species of the selected groups and all except one *Ptychopyxis* species were sampled once per species, but several samples were taken when the species were widespread, covering their distribution and variability. The samples are kept in Naturalis Biodiversity Center. The species concept in *Macaranga* follows Davies (2001) and Whitmore (2008) and in *Ptychopyxis* follows Stoops & van Welzen (2013). Authors of species names can be found in Appendix 1.

METHODS

Handling of samples

Dried herbarium leaves were rehydrated by boiling them briefly, at most up to 15 minutes, in water and then stored in 50% alcohol, enabling handling of multiple specimens at the same time and re-use if some analytical method failed.

Transverse and paradermal sections

Transverse sections were made of each leaf of the middle of the lamina (midrib), the margin and the petiole with a sledge microtome (Reichert MT-09 or MT-10). The cuttings were 15–30 μm thick. Paradermal sections were made by hand of upper and lower surface. Half of the sections were bleached with diluted (1:1) household bleach (3%, VWR chemicals) and stained in a safranine/alcian blue solution for 20 seconds (one part 1% safranine in 50% ethanol and two parts 0.25% alcian blue in water), followed by three times rinsing in demiwater. All sections, coloured and uncoloured, were dehydrated by an ethanol/xylene series (two times ethanol 50%, two times ethanol 70%, two times ethanol 96%, two times ethanol 100% (Biosolve) and two times xylene or Euparal essence, each step with a duration of one minute). All sections were mounted in Euparal green, with half of the cuttings of all parts coloured and the other half uncoloured; two slides were made per sample; the slides were dried under pressure in a stove at 60°C. Normally the sections were cut by placing the leaf between parts of the pith of elderberries (*Sambucus nigra* L., Viburnaceae), but the transverse sections of *Ptychopyxis* broke in small pieces due to a thin parenchyma between thick, hard veins. Embedding in paraplast instead of using the elderberry pith did not give much improvement. Unfortunately, the sections of *M. trachyphylla* got lost.

Cuticular macerations

For cuticular leaf macerations, two strips of leaf were used per sample, each containing both/either part of the midrib and part of the margin. The strips were placed overnight at 60°C in a mixture (1:1) of acetic acid (96%) and hydrogen peroxide (30%), rinsed with water and air bubbles removed by placing the strips in an exsiccator for 20–30 minutes. The cuticles were then carefully cleaned from adhering tissue with a soft brush when possible and coloured in a mixture of 0.5% Sudan IV in 70% alcohol for 2–3 hours at 40°C. After colouring, they were mounted in glycerin gelatin preheated to 55°C. Each slide (two per sample) shows the upper and lower cuticle of the leaf.

Leaf clearings

This technique was applied if not all characters were visible with the macerations and cuttings. Two strips of a leaf were placed in 10% KOH and autoclaved at 115°C for 20 minutes. They were then rinsed with water and bleached in diluted household bleach (1:1) till transparent and rinsed again with water. The strips were mounted in glycerin gelatin preheated to 55°C.

Analysis of the slides

With the help of a compound microscope (Olympus BX-51 or Nikon Eclipse E600Pol) the object slides were analysed. Descriptions of the leaf anatomy were made per species and all characters were represented in a table. Photos were made through a Zeiss Axio Imager.M2 with an Axiocam 305 colour camera and ZEN 3.8 software, and were edited with Adobe PhotoShop 2025.

RESULTS

Microscopic slides

The production of the slides went usually well for *Macaranga* specimens, but was highly troublesome with *Ptychopyxis*. In *Ptychopyxis* the veins are high and with much sclerenchyma, while the intermediate parenchyma is rather thin; this resulted in tearing the sections apart, even when embedded in paraplast. Therefore, the results for *Ptychopyxis* are incomplete.

Characters

The characters are summarized in Table 1 and will be discussed in the same sequence following the headers of Table 1 (in bold). The legend of all abbreviations follows the same sequence.

Thickness of lamina

The thickness of the laminas, measured between the nerves, varies between 50 and 250 μm (Table 1) and overlaps among all groups. However, the pioneer groups (myrmecophytes and the *Tanarius* group) tend to have the thinnest leaves, but also with the most protruding nerves. The latter also applies to *Ptychopyxis*.

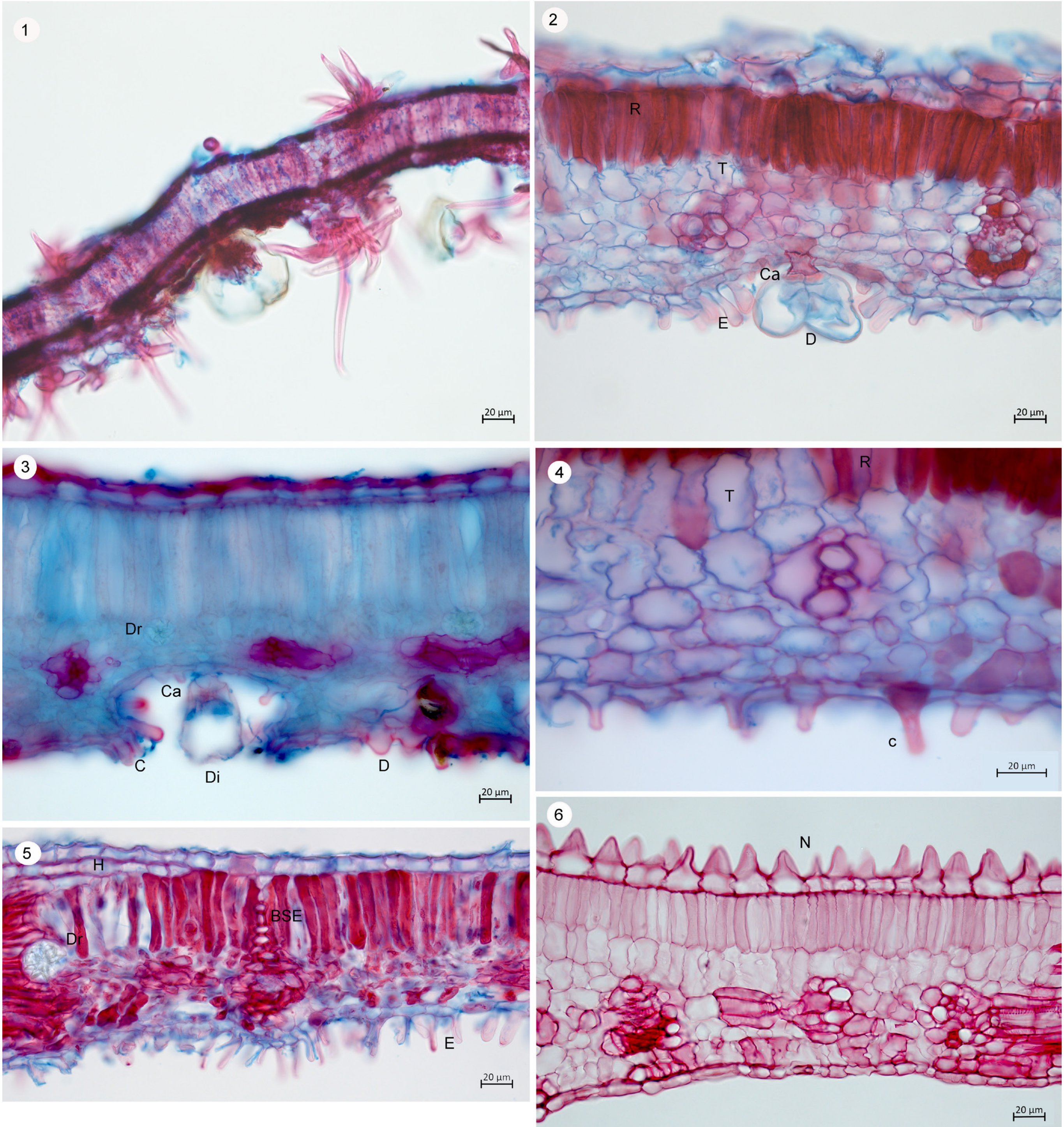
Epidermal cells

The epidermal layers are on both sides single-layered and thicker at the adaxial side. The cuticle is never thick, the abaxial one is even thinner than the adaxial one; the cuticles of the myrmecophytic and the Tanarius groups are the thinnest. Due to these thin cuticles and the presence of especially abaxial papillae (see below) it was often impossible to view the anticlinal walls in surface view. The anticlinal walls vary from almost straight to undulating (Table 1), quite often the walls are somewhat undulating. The majority of *Macaranga* samples show more straight anticlinal walls, especially adaxially, but mainly undulating in *Gracilis* and *Winkleriae*. *Ptychopyxis* has mainly undulating walls. The curvature of the cells can vary within species, e.g., *M. indica* (*Denticulata*), *M. tanarius* (*Tanarius*). Adaxially, the epidermal cells usually radiate from sub-epidermal druse idioblasts when present. Epidermal cells above major veins have straight anticlinal walls, are longer than wide and parallel to the veins.

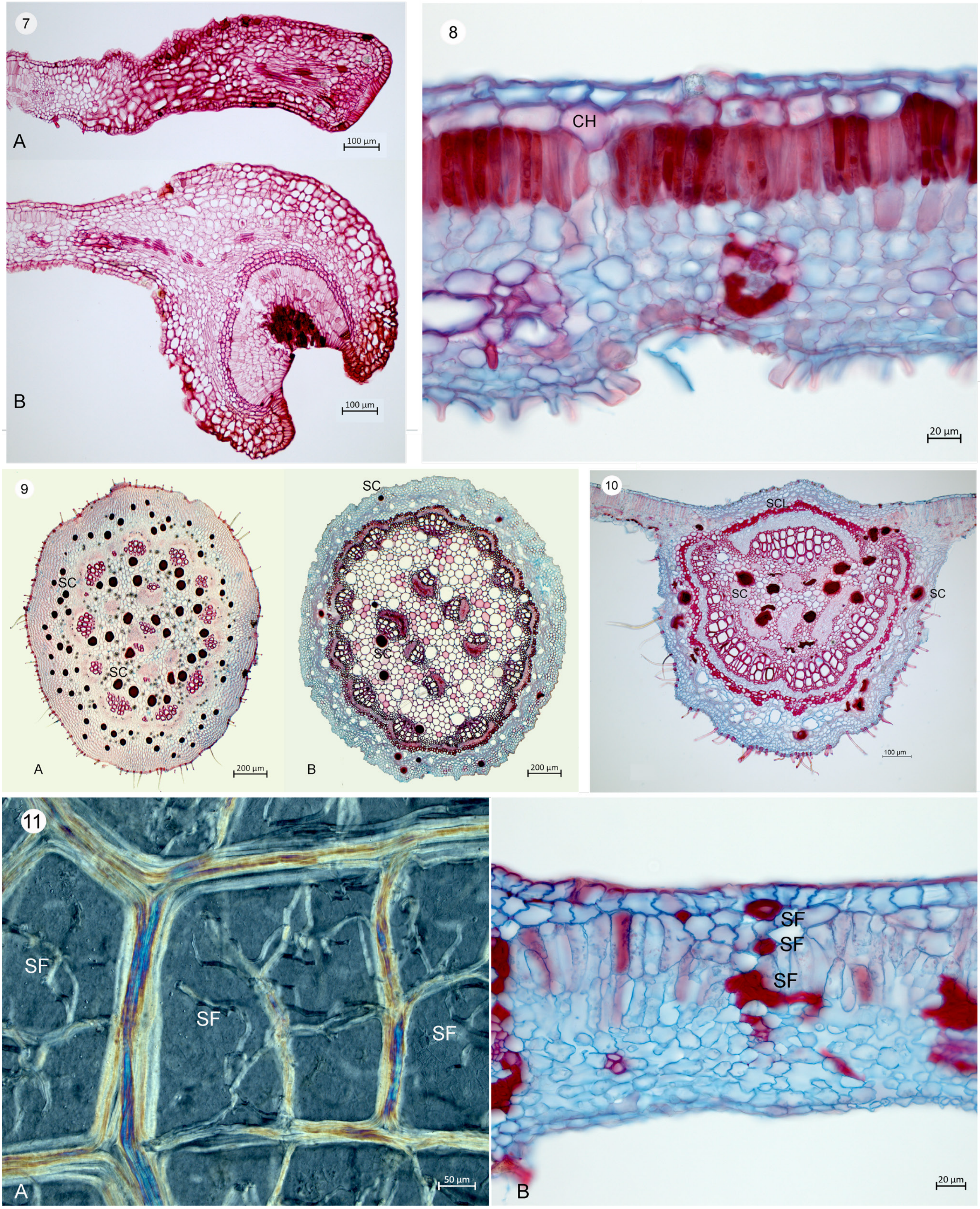
In the *Pachystemon* group some species show a waxy layer abaxially (Table 1), visible as a blueish grey layer in the dried material (*M. glandibraceteolata*, *M. havilandii*, *M. hullettii* and *M. hypoleuca*).

Indumentum

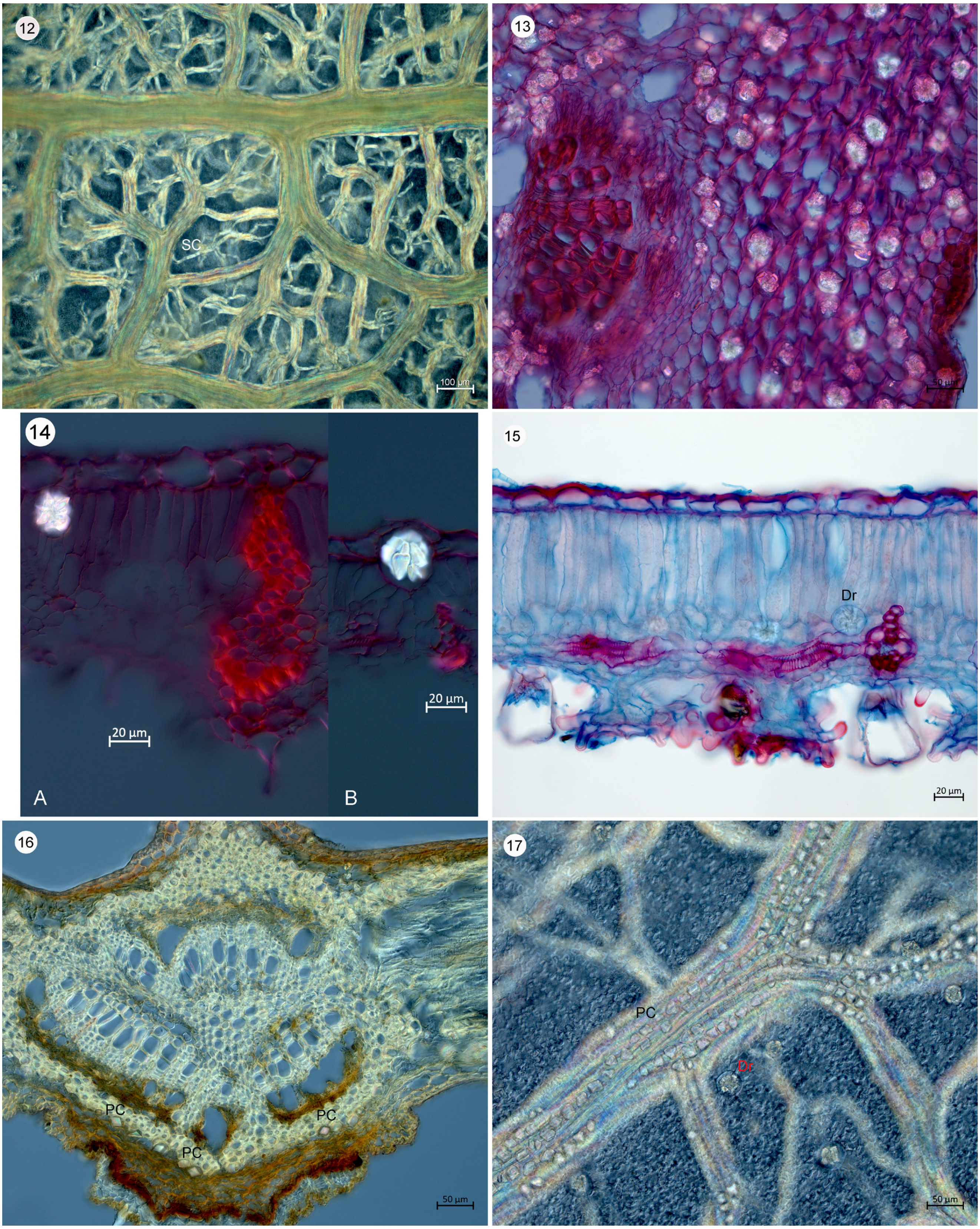
Most trichomes are found at the abaxial leaf surface, especially the disc-shaped hairs (Table 1). Adaxially the hairs are often only found on the basal parts of the midrib and major nerves; if hairy then the leaves are generally glabrescent adaxially. Simple, one-celled, lignified hairs can be short or long, narrow or wide, straight, bent or sinuous. Quite often short(er) and long(er) hairs are present, with the shorter then generally being curly. Fišer Pečnikar et al. (2012: 671) also mention branched multicellular hairs for *Macaranga*, but these were not observed. It is seldom that the simple hairs are stellately tufted, e.g., most species of *Pruinosae*, and one sample of *M. harveyana* (*Smith 9671*, *Tanarius*; Fig. 1). In *Pruinosae* and *Smith 9671* it are especially the shortest hairs that sometimes group, the long hairs only group if no small hairs are present. The disc-shaped glandular hairs (DGH) are of the bladder-like type (Fišer Pečnikar et al. 2012: fig. 32b; Figs 1, 2) and generally occur abaxially, often in cavities (Table 1; Figs 2, 3), only in the *Gracilis* group *M. kostermansii* (once), *M. misimae* and *M. suleensis* also had DGHs adaxially. The heads of DGHs have basally cells radiating in all directions, the rest of the head is likely filled with a secretion product (there are generally veins endings near the hairs) and the heads can be globular or flattened (perhaps a drying artefact). The cavities can be quite deep with the head of the hair on leaf surface level, often sealing off stomata underneath. The cavity is often filled and surrounded by longer papillae (Figs 2, 3; Table 1). In *Bicolor* and *Denticulata* the DGHs are partly sunken, in *Gracilis* level with the leaf surface or sunken, level to sunken in *Javanica* and *Tanarius*, mainly sunken in *Pachystemon* and *Pruinosae*, and sunken in *Winklerianae*.



Figures 1–6. Fig. 1 Stellately tufted hairs adaxially and especially abaxially in *Macaranga harveyana* (Müll.Arg.) Müll.Arg. (*Tanarius* group), also visible an abaxial disc-shaped glandular hair. also visible a bladder-like disc-shaped hair (coloured transverse section of Smith 9671). **Fig. 2.** Bladder-like disc-shaped hair (D) in *Macaranga pachyphylla* Müll.Arg. var. *pachyphylla* (*Bicolor* group). The T indicates the transition layer, spongy tissue resembling palisade cells, (coloured transverse section of *Maskari 19*). **Fig. 3.** Dome-shaped papillae (D) in *Macaranga costulata* Pax & K.Hoffm.(Javanica group; coloured transverse section of SAN 131278). **Fig. 4.** Conical papillae (C) in *Macaranga bicolor* Müll.Arg. (Bicolor group; coloured transverse section of BS 15000). **Fig. 5.** Elongated papillae (E) in Macaranga rhizinoides (Blume) Müll.Arg. (Bicolor group) with a druse (Dr) in the sponge tissue (coloured transverse section of BS 15000). **Fig. 6.** Adaxial nipple-shaped papillae (N) in *Macaranga angulata* S.J.Davies (Pachystemon group; coloured transverse section of Nooteboom 1404).. Abbreviations: BSE = Bundle Sheath Extension; Ca = Cavity; C = Conical papilla; Di = bladder-like disc-shaped hair; Dr = Druse; E = Elongated papilla; H = Local hypodermis R = Red coloured palisade cells.



Figures 7–11. Fig. 7. Extrafloral nectaries (EFN). **A**. Dome-shaped EFN in *Macaranga indistincta* Whitmore (*Pachystemon* group; coloured transverse section of *Fiala 19*). **B**. Crater-like EFN in *Macaranga caladiifolia* Becc. (*Pachystemon* group; coloured transverse section of *Haviland & Hose 464E*). **Fig. 8.** Contiuous hypodermis (CH) in *Macaranga pachyphylla* Müll.Arg. var. *pachyphylla* (*Bicolor* group; coloured transverse section of *Maskari 19*). **Fig. 9. A**. Cylinder of separate vascular bundles in petiole in *Macaranga tanarius* (L.) Müll.Arg. (*Tanarius* group); coloured transverse section of *Middleton* et al. *2182*). **B**. more or less joined vascular bundles in petiole in *Macaranga bicolor* Müll.Arg. (*Bicolor* group; coloured transverse section of *BS 15000*), with a few separate bundles in the pith; sclerenchyma around cylinder lacking. SC all dark red. **Fig. 10.** Midrib with a small adaxial arc and a larger abaxaial of partly fused vascular bundles, separate ones in the pith; the midrib is surrounded by a narrow layer of sclerenchyma (SCL) in *Macaranga pilosula* Airy Shaw (*Tanarius* group; SC coloured transverse section of *Brass 28752*). **Fig. 11.** Sclerenchyma fibres (SF) detaching from vascular bundles in *Macaranga bicolor* Müll.Arg. (*Bicolor* group; sections of *BS 15000*). **A**. Leaf clearing with polarized light. **B**. coloured transverse section. Abbreviations SC = Secretory cells.



Figures 12–17. Fig. 12. High density of sclerenchyma fibres (SC) in *Ptychopyxis costata* Miq. var. *oblanceolata* Airy Shaw (leaf clearing with polarized light of *KEP FRI 29103*). **Fig. 13.** Druses in petiole of *Macaranga sinensis* (Baill.) Müll.Arg. (*Javanica* group; coloured transverse section under polarize light of *Elmer 14231*). **Fig. 14. A.** and **B.** Druse idioblasts in the palisade of *Macaranga glandibracteolata* S.J.Davies (*Pachystemon* group; coloured transverse section with polarized light of *Fiala 34*). **Fig. 15.** Druse idioblast (Dr) in sponge parenchyma in the transitional layer; also two sunken bladder-like disc-shaped hairs visible in *Macaranga costulata* Pax & K.Hoffm. (coloured transverse section of *SAN 131278*). **Fig. 16**. Prismatic crystals (PC) on outside of sclerenchyma layer in midrib of *Ptychopyxis costata* Miq. var. *oblanceolata* Airy Shaw (coloured transverse section with polarized light of *KEP FRI 29103*). **Fig. 17.** Prismatic chrystals (PC) along the sclerenchyma layers of the major nerves, also visible druse idioblasts (Dr) in palisade of *Ptychopyxis javanica* (J.J.Sm.) Croizat (leaf clearing with polarized light of *Koorders 2741*).

Papillae

Papillae are usually present, generally abaxially, but may also occur adaxially (Table 1). Four, not well-separated types of papillae are recognized in the studied species, varying in the length of the papillae. *Dome-shaped* (D in Fig. 3) are slightly convex epidermal cells, and can be present on both surfaces; *conical* (C; Fig. 4) papillae are higher and, together with the even longer *elongated* (E; Fig. 5) papillae, they are mainly present abaxially, especially around the bladder-like hairs where they are longest. The *elongated* papillae may apically be broadened and appear clavate. *Nipple-shaped* (N; Fig. 6) papillae are the least obvious type, randomly intergrading with flat epidermal cells and elongated papillae, here the outer cell wall is not convex, but narrowed into a point. Above nerves the epidermal cells may form papillae on both sides of the lamina.

Extrafloral nectaries at leaf margin

Next to EFNs near the adaxial base of the leaves, with some species the nerves may also end in an EFN at the margin. RL checked these anatomically for *Pachystemon*, *Pruinosae* and *Winklerianae* (Table 1). They can vary from dome-shaped (Fig. 7a) to even crater-like (Fig. 7b). In *M. indistincta* (Fig. 7a) the epidermal cells in the centre of the dome are long and secreting, a vein ends in the mesophyll that changes from palisade and spongy tissue to more square/rounded hypodermis-like cells. In *M. caladiifolia* (Fig. 7b) the situation is more complex, here in the middle of the crater-like EFN a half-circular layer of small cells is present, a vein going underneath and ending outside the small cells; around the layer of small cells the same hypodermis-like cells as in *M. indistincta*, of which the sub-epidermal cells are often idioblastic and filled with content, in colour similar to the red-coloured cells sometimes encountered in the palisade (see Mesophyll); inside the small cells elongated secreting cells, that especially in the centre appear to be full of content.

Stomatal complex

The stomata are paracytic in all groups, as also reported by Fišer Pečnikar et al. (2012) for the related genera *Blumeodendron*, *Hancea* and *Mallotus*. An exception might be staurocytic stomata in *M. javanica* as reported by Norfaizal et al. (2012). The stomata were difficult to study in the cuticular macerations due to the thinness of most cuticles. Also, in the transverse sections the ledges of the guard cells, three types mentioned in Fišer Pečnikar et al. (2012), were difficult to observe and are not mentioned in Table 1. When the disc-shaped glandular hair are in cavities, then the stomata are concentrated under them in the cavities. In *Ptychopyxis* the stomata are very dense abaxially.

Mesophyll

The leaves are dorsiventral, with a single adaxial palisade layer. The cells can be quite long in the thicker-leaved species. Often there are idioblasts, wider, translucent cells, with druses, which, when close to the epidermis, appear to be in the epidermis (epidermal cells thin above them). The palisade layer in most species appears to contain very long cells, often up to half of the leaf thickness. This may be typical for *Macaranga* as they are shorter in *Ptychopyxis* and in the genera treated by Fišer Pečnikar et al. (2012). In some species, spread over all groups, but most common in the *Bicolor* group, there are (in the coloured slides) palisade cells with a very dark red solid content (Figs 2, 4, Table 1). The content is not analysed. The spongy tissue can have up to 10 cells (Table 1) and is often quite compact. In the spongy tissue there are often also idioblasts with druses, most often in the subpalisade layer. In many samples the subpalisade layer resembles the palisade cells, but the cells are shorter and they resemble other cells in the spongy tissue and also lack the dark red content, therefore they are considered to be part of the spongy tissue and in Table 1 they referred to as intermediate layer present or absent (Figs 2, 4).

Bundle Sheath Extensions

In *Macaranga* the bundle sheath extensions (BSEs) consist of generally parenchymatous cells, colourless and in transverse section usually rather round to more square, as high as wide, and thus deviating from the palisade and spongy tissue cells (Fig. 5). In all *Macaranga* species the BSEs are around the larger vascular bundles and reach both epidermal layers, but are absent with the smallest vascular bundles. No BSEs were found in the *Ptychopyxis* species (this could not be studied in *P. caput-medusae*). The large BSE cells can be seen around the vascular bundles in leaf clearings, called ‘large bundle sheath cells’ in Fišer Pečnikar et al. (2012: fig. 41).

Hypodermis

A hypodermis is locally adaxially present as sub-epidermis above the midrib and larger veins, those with a BSE. The hypodermis is generally a (slight) widening of the BSE (Fig. 5). In some species a much wider hypodermis is present near the midrib, continuing over some of the larger veins next to the midrib. In several species, especially in *Pruinosae*, an (almost) continuous hypodermis is present (Table 1; Fig. 8).

Petiole and midrib vascularisation

The vascular system of the petiole consists generally out of a cylinder of separate (Fig. 9) to partly fused bundles, only in *Gracilis* there is a higher fusion of bundles in half of the species (Table 1). Separate vascular bundles are usually present in the central pith except in half of the species of *Gracilis* (the ones with fused bundles). The sclerenchyma fibres are generally absent and if present, often local (for instance per bundle) and in thin layers. Sometimes, instead of sclerenchyma, the tissue looks more collenchymatous (walls not woody, thickened).

In the midrib there is generally a small adaxial arc and a larger abaxial arc of fused or partly fused bundles, often with two additional bundles to the side between both arcs (Fig. 10, Table 1). Separate bundles in the pith are usually present (Table 1). The sclerenchyma fibres are usually present, but never forming a thick layer. In *Gracilis* the midribs were small and contained none or very few vascular bundles in the pith.

Secretory cells

Macaranga, like *Mallotus* (Fišer Pečnikar et al. 2012), is known to have secretory cells with reddish secretion (Webster 2014). They are present in the pith and ground tissue of the major veins, petiole and midrib (Table 1). In transverse section they are visible as slightly larger cells with often a brown-reddish content in the non-coloured cuttings, red in the coloured ones (Figs 9, 10). The secretory cells are absent in *Ptychopyxis*.

Sclereid fibres / Fibriform sclereids

The sclerenchyma fibres around the veins and midrib can detach and run in all directions, horizontally and vertically between both palisade layers (Fig. 11; Table 1). They provide extra support for the often large leaves in the pioneer species of *Macaranga*. They are present in the Bicolor, Pachystemon, and Pruinosae groups, absent in the Denticulata, Gracilis, Javanica, and Winklerianae groups, and a few present in the Tanarius group. The fibres can best be seen with polarized light in cleared leaf fragments, but the clearings were not present for the groups *Pachystemon*, *Pruinosae* and *Winklerianae*; for these latter three groups transverse sections were interpreted. In transverse sections they appear as brachysclereids or branching and unbranched sclereids (Fig. 11b). The fibres are especially abundant in *Ptychopyxis* (Fig. 12; Table 1), where they often connect.

Vein endings

The leaf clearings were used to study the vein endings, these were not available for the *Pachystemon*, *Pruinosae* and *Winkleriae* groups. In most *Macaranga* species the bigger veins like to form closed networks, the splitting off smaller veins end usually free, seemingly often near the DGHs (there the last xylem elements were usually seen) (Table 1). In *Ptychopyxis* the veins either formed closed networks or, especially the smaller ones, often ended in fibriform sclereids (see above) (Table 1).

Crystals

Crystals of calcium oxalate are most frequent in the non-pioneer species of *Macaranga* and in *Ptychopyxis*. In *Macaranga* only druses were found, in *Ptychopyxis* also prismatic crystals (Table 1). The petioles showed the highest amounts of crystals, especially in *Javanica* (Fig. 13). In the petiole they were generally present in the ground tissue, in the phloem and the pith; the largest crystals in the ground tissue and pith, very small ones in the phloem. In the midrib there are less crystals in the same tissue types, and this reduces further in the larger nerves. In the latter druses are most general in the ground tissue. In the mesenchyma the druses occur in special, larger cells, idioblasts. In the palisade these idioblasts (Fig. 14) hold the larges druses and these can be very close against the adaxial epidermis. In the spongy tissue the druse idioblasts are generally present in the subpalisade layer (Fig. 15) and these are much smaller than in the palisade idioblasts. The prismatic cells in *Ptychopyxis* are present in the ground tissue of petiole, midrib and bigger nerves, in the cells outside the layer of sclerenchyma cells (Figs 16, 17, Table 1). In a few species (Table 1) druses were seen in the local hypodermises (*Pruinosae* group) and perhaps in the adaxial epidermis in a few specimens of the *Tanarius* group (Table 1).

DISCUSSION

For *Macaranga* the species concept of Whitmore (2008) was used, when compared to Plants of the World Online (POWO continuously updated), only few changes occurred. The varieties of *M. pachyphylla* (*Bicolor*), *M. quadriglandulosa* and *M. tanarius* (both *Tanarius*) are now synonymized with the species, and *M. pustulata* is considered a synonym of *M. denticulata* (*Denticulata*). Generally, Whitmore (2008) distinguished between hairy and (more) glabrous forms, but the variation between the extremes is usually gradual, not warranting any taxonomic distinction. Leaf anatomically the various samples of the different varieties and the two synonym species did not differ much from each other, mainly in characters where variation can be expected, like hair density, vascularization, sclerenchyma sheets, crystal content. The same applies to the more widespread species of which several specimens were sampled, not too much variation in characters, also not in *M. tanarius* of which 17 samples were present. The same variation as with the synonyms was found, only two exceptions, one specimen of *M. harveyana* (*Smith 9671*) showed stellate hairs, absent in the other specimen (*Sykes 139c*). A re-identification of *Smith 9671* ended in the same identification. In *M. gracilis* there is some variation in petiole and midrib vascularization, more developed in *Schodde 1478* than *Hartley 12715*, more fused bundles, presence of pith bundles and more sclerenchyma. Likely, this is a difference between more mature and juvenile leaves. Most of these group have large leaves with not too many leaves per herbarium sheet. In order to be less invasive, the young leaves were often sampled. These often appeared to be too poorly developed for scoring characters, therefore, these were, when possible, resampled for (more) mature leaves (Appendix 1).

The stomatal complex could not be studied in much detail due to the very thin cuticles, especially abaxially where the stomata are found. Where visible the stomata appeared to be paracytic as reported by Fišer Pečnikar et al. (2012) for *Mallotus* and related genera. Kadiri et al. (2019) found different types of paracytic stomata in two African *Mallotus* species, *M. oppositifolius* (Geiseler) Müll.Arg. (paracytic in var. *pubescens* Pax and paracytic and brachyparacytic in var. *glabratus* Müll.Arg.; varieties not recognized any longer in POWO continuously updated) and *M. subulatus* Müll.Arg. (paracytic, brachyparacytic and hemiparacytic). These variations were not visible in our material. So far, only Thakur & Patil (2014) reported one exception for *Mallotus*, seemingly in *M. stenanthes* Müll.Arg. anisocytic stomata are present. Norfaizal et al. (2012) report staurocytic stomata for *Macaranga javanica*, but we could not confirm this as the cuticular macerations were too thin and the stomata were hidden in cavaties under the DGHs.

The density in stomata is much higher in *Ptychopyxis*, where almost no epidermal cells are present between the stomata, than in *Macaranga*, where epidermal cells were well visible between the stomata, especially when the stomata were present under the sunken DGHs. Cuticular striations were reported for *Mallotus subulatus* by Kadiri et al. (2019), but these were not seen in any of our samples.

In *Macaranga* the presence of only abaxial stomata, hidden under the sunken DGHs in combination with long papillae surrounding the DGHs, are typically adjustments to controlling and diminishing evaporation (e.g., Zahedi et al. 2025, and references therein). They are typical for the pioneer species, which germinate and grow in full sun in the tropics. Contrary to what Zahedi et al. (2025) report, small thick leaves when transpiration has to be diminished, the leaves are generally large and thin. However, these species are tropical rain forest species, with high amounts of rain per year, pioneers in gaps, and then a large, thin leaf is beneficial to receive more light, grow fast and shade out competition.

The petioles generally contain less sclerenchyma than the midribs. One might expect higher amounts of sclerenchyma in the petioles as they have to upheld the entire, often big, leaves. However, the sections were generally made just below the base of the leaf blade, the area where there is usually a pulvinus, a part that has to be flexible as the blade, by varying the osmotic pressure in cells, follows the sun during daytime. The petioles show far more crystals than the midrib, which may be correlated with still some support for the leaf blades.

Fišer Pečnikar et al. (2012) recorded secretory cells in the ground tissue of the petiole, midrib and some larger veins for only some species in *Mallotus*. They discussed that the (non studied) content may be oxidized tannins called phlobaphenes (Evert 2006: 477), seemingly found in many families and typically coloured reddish brown. These cells are also present and common in all *Macaranga* samples, but not only in the ground tissue, also in the pith. Therefore, it is not surprising that *Macaranga* is reported to secrete red exudate (e.g., Webster 2014: 128), unlike *Mallotus*. The exudate originates from the secretory cells. Rudall (1987: 146) indicates that Solereder (1908: 746) reported non-articulated laticifers for *Macaranga*, but Solereder (1908: 746) only reported laticiferous cells for *Macaranga*. We did not observe any laticifers, which can of course be hidden by sclerenchyma and wood vessels in leaf clearings, but in the sections only straight-cut cells were found, no diagonally cut tubes, like is often the case with sideveins. Therefore, we consider laticifers to be absent in *Macaranga*. Moreover, laticifers are rare in subfamily Acalyphoideae (Webster 1994: 8), in which *Macaranga* is classified; Webster (1994) even stated that the rare observations have to be confirmed and Vitarelli et al. (2015) indicate that the erroneous listing by Rudall (1987) is the only mentioning of laticifers in *Macaranga*. Laticifers are typical for the two other subfamilies (for a review see Rudall 1987). Red exudate is rare in the Acalyphoideae and more typical for the subfamily Crotonoideae. However, recently Mouzella et al. (2025) reported laticifers for various Acalyphoideae, among them for the African *Macaranga heudelotti* Baill. (laticiers branching) and the (New Guinean-)Australian *Mallotus claoxyloides* (F.Muell.) Müll.Arg. and *M. nesophilus* Müll.Arg., all associated to phloem. No secretory cells were found in *Ptychopyxis*.

Fibriform sclereids are abundant in *Ptychopyxis*, just as Fišer Pečnikar et al. (2012) found for *Blumeodendron*. This is an indication that their joined classification in subtribe Blumeodendrinae (Webster 2014: 125) is likely correct. Fibriform sclereids are more rare in *Macaranga* and found in the *Bicolor*, *Pachystemon* and *Pruinosae* groups. Especially, in the latter two groups they may add to the support of the large leaves. Fišer Pečnikar et al. (2012) reported brachysclereids for *Mallotus* and *Blumeodendron*, but it is unclear from the sections whether these are real separate cells, or just fibriform sclereids cut transversely and thus resembling brachysclereids. We think it is more prudent to support the latter conclusion.

CONCLUSIONS

Table 2 shows the main differences between the different groups and taxa. *Ptychopyxis* is clearly different from *Macaranga*, as it has no DGHs, abaxially many more stomata, no hypodermal cells, no bundle sheet extensions, no red exudate secreting cells, many fibriform sclereids and the presence of prismatic crystals.

Mallotus (see Fišer Pečnikar et al. 2012), the sister genus of *Macaranga*, shares the DGHs with *Macaranga*, but differs in the generally stellately bundled hairs (rare in *Macaranga*, the group *Pruinosae* excepted in this study) and the rarity of the red exudate secreting cells. The vascular system of the midrib in *Macaranga* shows more often two arcs (upper smaller) with in between an additional vascular bundle on each side than *Mallotus* and generally shows vascular bundles in the pith.

The researched groups in *Macaranga* do not show unique anatomical characters by which they can be recognized. Often a majority of the samples shows a typical character or a combination of characters is typical for the groups (bold in Table 2). *Denticulata* and *Winklerianae* are anatomically the least typical groups. *Winklerianae* has extrafloral nectaries along the leaf margin and no abaxial papillae, while *Denticulata* has no typical characters (druses in ground tissue of major veins is a bit of an exception), making all characters a typical combination for this group. *Bicolor* has a combination of the intermediate, subpalisade spongy tissue layer, fibriform sclereids and druses in the ground tissue of the major nerves. *Gracilis* has as typical character, the small midribs that mainly lack pith bundles, while the abundance of druses in especially the petiole is typical for *Javanica*. *Pachystemon* usually shows adaxial papillae and also the intermediate spongy tissue layer. Most typical is the *Pruinosae* group with like *Tanarius* usually two types of hairs abaxially and unlike *Tanarius* it has generally stellately bundled hairs and a more continuous hypodermis. *Pachystemon* and *Pruinosae* show often fibriform sclereids, more so than *Bicolor*.

So far, only a minority of the *Macaranga* species has been analysed, 79 species out of 308 accepted species (POWO continuously updated), eight groups out of the 19 recognized (next to many unplaced species) by Whitmore (2008). Different characters or characters states may of course occur, but the results of this study already show a quite homogenous picture for most groups.

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Table 1. Anatomical characters of *Macaranga* and *Ptychopyxis* specimens. Sequence of characters as in Results. *General abbreviations*: Adax = Adaxial, Abax = Abaxial, NA= not applicable; ± = sometimes or somewhat, + = present, ++ = abundant, – = absent, ? = unknown. *Anticlinal epidermal cells*: S = straight, ±SU = somewhat undulating, U = undulating, ? = not well visible. *Indumentum*: first consonant: l = long, s = short; second(–third) consonant: c = curly, s = straight/basally bent, s–c = straight to curly (if four or six consonants then two types of hairs), stel = stellately tufted; dom = in some domatia; ven = hairs on basal part main veins or basal part midrib; l = level, ps = partly sunken, su = sunken. *Papillae*: C = conical, D = dome-shaped, DGHs = near disc-shaped glandular hairs, E = elongated, F = flat, N = nipple. *Extrafloral nectaries*: Cl = club-shaped, Cr = crescent shaped (club-shaped with crater), E = elongated, m = continuation margin (not raised), R = round, U = unspecialized. *Hypodermis*: C = continuous, L = Local. *Petiole vascularization*: CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, coll = collenchymatous tissue present, CSB = cylinder of separate bundles, T = thin layer of sclerenchyma. *Midrib vascularization*: 2AFB = two arcs of fused bundles, 2APFB = two arcs of partly fused bundles, CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, T = thin. *Vein endings*: C = connected, F = free, FScl = fibriform sclereids. *Crystals*: EP = Epidermis, G = ground tissue, Hy = hypodermis, P = palisade, Pl = phloem, Pi = pith, S = spongy tissue, Scl = sclerenchyma, subP = subpalisade layer in spongy tissue.

Group	Species	Collector	Lamina thickness	Anticlinal epidermal walls		Abaxial wax layer	Indumentum					Papillae	
						Simple (unicellular)		Bladder-like glandular					
			(µm)	Adax	Abax		Adax	Abax	Adax	Abax	Position Abax	Adax	Abax
Bicolor	*M. bicolor*	*BS 15000*	145	S	S	–	–	+(ls–±c)	–	+	ps	F	F–D
		PPI 6744	120	S	S?	–	±(ls: ven)	+(ls–±c)	–	+	ps	F	F–C
	M. congestiflora	*PPI 73*	160	S	S?	–	–	+(ls)	–	+	ps	F	F
	M. pachyphylla var. *pachyphylla*	*Maskari 19*	165	?	?	–	±(ls: ven)	+(ls)	–	+	ps	F	F; E (DGHs)
		Okada et al. 1037	190	S	S	–	±(sc: ven)	+(ls + sc)	–	+	ps	F	F; E (DGHs)
	M. pachyphylla var. *glabra*	*KEP FRI 12114*	165	S	S	–	–	±(ls)	–	+	ps	F	E
		SAN 56312	210	S	S	–	–	–	–	+	ps	F	C, D (continuous), E, F, N (random)
	M. puncticulata	*Ambriansgah AA 1527*	100	S	S?	–	–	±(ss: ven)	–	+	ps	F	F, N; E (DGHs)
		SFN 34041	235	S	NA	–	–	++(ss: ven)	–	+	ps	F	F, N, C; E (very long, DGHs)
	M. sarcocarpa	*Moog 00-43*	155	S	S	–	+(ls: ven)	++	–	+	ps	F	F to C; E (DGHs)
Denticulata	*M. denticulata*	*Anonymous s.n.*	125	S	±SU	–	±(lc)	++(lc)	–	+	ps	F	N, E
		Soejarto et al. 11215	140	S	S?	–	–	±(lc)	–	+	ps	F	D, N, E
	M. indica	*Chand 2856*	160	S	S	–	–	±(ls)	–	+	ps	F	E
		Worthington 13162	110	U	?	–	–	±(ls)	–	+	ps	F	C, E
	M. peltata	*Hohenacker 511*	140	S	S	–	–	+(ls)	–	+	ps	F	D, E
	M. pustulata	*Dickason 8572*	150	S	S	–	–	+(sc)	–	+	ps	F	E
	M. rhizinoides	*Junghuhn s.n.*	150	S	?	–	–	++(lc)	–	+	ps	F	E

Gracilis	*M. domatiosa*	*Craven & Schodde 1300*	140	U	U?	–	–	– (sc: dom)	+	+	l	F	F
		van Valkenburg 158	240	U	U	–	–	–	+	+	l	F	F
	M. gracilis	*Hartley 12715*	175	U	U	–	–	–	+	+	l	F	F
		Schodde 1478	135	U	U	–	–	–	+	+	su	F	F
	M. kostermansii	*BW 14149*	250	S	U	–	–	–	–	+	su	F	F
		van Royen & Sleumer 7384	175	±SU	U	–	–	±(ls: ven)	+ (once)	+	su	F	F(–D)
	M. misimae	*Brass 27540*	100	U	U	–	+(ls)	++(ls)	+ (ven)	+	su	F	F(–D)
		Brass 32404	175	U	U	–	+(ls)	++(ls)	+ (ven)	+	su	F	F
	M. suleensis	*LAE 59703*	120	±SU	±SU	–	–	±(ls: ven)	+ (ven)	+	l	F	F
Javanica	*M. costulata*	*SAN 131278*	137,5	U	U	–	–	+(sc)	–	++	su	D	D; E (DGHs)
	M. cumingii	*PPI 6794*	140	S	?	–	–	±(ls)	–	++	ps	F	C
	M. endertii	*Kostermans 6026*	190	±SU	S	–	–	+(ls+sc)	–	++	ps	F	D–C; E (DGHs)
	M. heynei	*Argent & Iqbar 9961*	192,5	S	S	–	–	+(sc)	–	++	su	F	D–N-C; E (DGHs)
		KEP FRI 14050	170	S	S	–	–	+(sc)	–	++	su	F	F–D; E (DGHs)
	M. javanica	*Koorders 2381*	117,5	S	U	–	±(ven)	+(sc)	–	++	su	F–D	F–D–C; E (DGHs)
		Mk. Ar. 585	190	±SU	S	–	±(ven)	+(sc)	–	++	su	F	F–D–C; E (DGHs)
	M. laciniata	*KEP FRI 12874*	155	U	U	–	–	+(ls)	–	++	su	F–D	D; E (DGHs)
	M. loheri	*Vanoverbergh 2752*	142,5	S	S	–	–	–	–	++	ps	F	F–D; N (DGHs)
	M. sinensis	*Elmer 14231*	140	S	S	–	–	–	–	++	ps	F	F–D; C (DGHs)
	M. spathicalyx	*Aiba 1615*	150	±SU	±SU	–	–	–	–	++	ps	F	F–D; E (DGHs)
	M. sumatrana	*Korthals s.n.*	112,5	S	?	–	+(ss)	++(ls)	–	++	su	F	E
	M. sylvatica	*Elmer 10109*	140	±SU	U	–	–	±(ls)	–	+	l–ps	F	F
	M. waturandangii	*Van Balgooy 3384*	160	±SU	±SU	–	–	±(ls)	–	+	l–ps	F	F
Pachystemon	*M. aetheadenia*	*Kessler el al. 1333*	160	S	?	–	–	few(ls)	–	++	l	D	C, D; E (nerves, clavate)
	M. angulata	*Nooteboom 1404*	145	S	U	–	–	few(ls)	–	few	l?	C, N	F, C; N (nerves)
	M. bancana	*Forbes 2980*	110	±SU	U	–	–	few(ss)	–	+	su	C, N	F
		Singh 163	185	S	U	–	–	few(ls)	–	+	su	N	F; C (nerves)
	M. beccariana	*S 51400*	165	±SU	S?	–	–	few(ls)	–	few	su	N–C	F
	M. caladiifolia	*Haviland & Hose 464 E*	165	S	S	–	few(ss–c)	few(ss–c)	–	++	su	F; D (nerves)	N, E
	M. calcicola	*S 15288*	140	U	U	–	–	+(ss–c)	–	few	su	F	F
	M. constricta	*KEP FRI 3431*	110	S	S	–	–	+(sc)	–	++	ps	C,N	E
	M. depressa	*SAN 95431*	130	±SU	?	–	+(ls,ss: ven)	+(ls,ss)	–	few	su	F	F
	M. depressa f. *glabra*	*SAN 97352*	210	S	S	–	+(ls,ss: ven)	+(ls,ss)	–	few	su	F; C (nerves)	F; D (nerves)

Pachystemon	*M. depressa* f. *strigosa*	*van Balgooy 6124*	115	S	S	–	+(ls,sc: ven)	+(ls,ss)	–	few	su	F; D (nerves)	F; D (nerves)
	M. glandibracteolata	*Fiala 34*	105	S	?	+	–	+(sc)	–	few	ps	F, N	E
	M. havilandii	*van Welzen 907*	70	±SU	?	+	–	+(sc)	–	few	l	C, N	E; N (nerves)
	M. hullettii	*Albertus 54*	160	±SU	U	–	–	+(sc)	–	few	su	F	F
		Singh & bin Samsuri 302	145	U	U	+	–	–	–	+	su	F	F
	M. hypoleuca	*Gardner & Sidisun-thorn ST 428*	155	S	S	+	–	+(sc)	–	+	su	F	C
		S 56696	210	S	S	+	–	+(sc)	–	+	su	F	C
	M. indistincta	*Fiala 19*	110	S	S?	–	few(ls)	++(ls,sc)	–	+	su	C	F
	M. kingii	*KEP FRI 5220*	115	S	?	–	–	+(sc)	–	few	su	F	F
	M. lamellata	*Slik et al. M-1075*	65	U	?	–	–	+(sc)	–	+	su	F	F; C (nerves)
	M. motleyana	*Chin & Mustafa 3289*	175	S	S?	–	–	few(ls,ss)	–	+	l	N	E
		S 68897	150	S	S?	–	–	+(sc)	–	+	ps	N, C	E (clavate)
	M. petanostyla	*Nooteboom 1370*	145	±SU	U	–	–	+(ss)	–	few	su	F	F
	M. rostrata	*SAN 46770*	175	±SU	U	–	+(ss: nerves)	+(ls,ss)	–	+	su	F	F
	M. trachyphylla	*Fuchs & Muller 21159*	NA	S	S	–	+(ls,sc: nerves)	+(ls,sc)	NA	NA	NA	NA	NA
	M. triloba	*van Steenis 3652*	150	S	S?	–	few(ss)	+(ls, ss)	–	+	su	C	F
	M. umbrosa	*Laman et al. 630*	110	S	?	–	–	–	–	+	su	C	F
	M. velutina	*Church 17*	110	S	?	–	–	+(ls,sc)	–	+	su	C; N (nerves)	E
	M. velutiniflora	*Davies et al. 981204*	190	S	S	–	–	–	–	+	su	C, N	F
Pruinosae	*M. gigantea*	*Gentry & LaFrankie 66907*	95	S	S?	–	+(sc, stel)	+(l±s; sc, stel)	–	++	su	F	E
		S 42644	130	S	S?	–	+(sc, stel)	+(l±s; sc, stel)	–	++	su	F	E
	M. hosei	*bb 2162*	115	S	?	–	–	+(ls, stel)	–	+	su	F	E (clavate)
		KEP 98511	65	S	?	C	–	+(ls, stel)	–	+	ps	F	F, D, N
	M. pearsonii	*Keith 1617*	130	S	S?	–	+(sc: ven)	+(ls,sc, stel)	–	++	su	F	E (clavate)
		Korthals s.n.	60	?	S?	–	+(sc: ven)	+(few ls; sc, stel)	–	++	ps	F	F, C; E (nerves)
	M. pruinosa	*KEP FRI 1187*	125	S	±S?	–	+(sc: ven)	+(ls,sc)	–	++	su	F	E
	M. puberula	*Dransfield 7212*	155	S	±S?	–	+(ls: ven)	+(ls,ss, stel)	–	++	su	F	E
	M. siamensis	*Murata et al. T-16482*	125	S	?	–	+(ls,sc: ven)	+(ls,ss, stel)	–	++	su	F	F
Tanarius	*M. brachytricha*	*Weiblen 1713*	100	S	S	–	±(ls,ss–c)	++(ls,ss–c)	–	++	ps	F–N	F, E
	M. clavata	*Brass 23921*	100	U	?	–	±(ls)	+(ls)	–	+	ps	F	F; E (continuous)
	M. darbyshirei	*BW 7092*	110	S	S	–	±(ls)	++(ls,ss)	–	++	ps	F, D	F, E
		Takeuchi et al. 17894	185	S	S	–	±(ls)	±(ls)	–	++	ps	F, N	F, E

Tanarius	*M. harveyana*	*Smith 9671*	100	S	S	–	(ls,ss, stell.)	+(ls;ss:stell.)	–	++	ps	F	F, E
		Sykes 139C	65	?	?	–	+(ls,ss)	+(ls,ss)	–	++	ps	F	F
	M. minahassae	*Whitmore & Sidiyasa 3521*	55	U	U	–	+(ls,ss)	+(ls,ss)	–	++	ps	F	F; C (DGHs)
	M. nusatenggarensis	*Schmutz 4184*	125	S	S	–	+(ss)	++(ss)	–	+	ps	F	F, C
	M. pilosula	*Brass 28752*	140	S	S	–	–	±(ls,ss)	–	++	ps	F	F, C–E
	M. quadriglandulosa var. *quadriglandulosa*	*Craven (& Schodde) 414*	100	S	?	–	±(ls)	++(ls,ss)	–	++	ps	F	F, E
		Takeuchi & Wiakabu 9760	145	S	S	–	–	–	–	++	ps	F	F
	M. quadriglandulosa var. *variabilis*	*NGF 4170*	155	S	S	–	–	–	–	+	l	F	F
	M. salomonensis	*Hoogland 3463*	90	S	S	–	–	–	–	+	ps	F	F
	M. tanarius	*Brass 24052*	95	S	?	–	±(ls,ss)	+(ls,ss)	–	++	ps	F	F; E (± clavate)
		BSIP 19482	85	S	S	–	±(ls,sc)	±(ls,sc)	–	++	ps	F	F
		BW 13543	110	S	?	–	+(ls–c,ss–c)	+(ls–c,ss–c)	–	++	ps	F	F, E
		Coveny & Haegi 9921	145	S	?	–	±(ls–c,ss–c)	±(ls–c,ss–c)	–	++	su	F	C
		Hotta 13168	95	?	?	–	+(ls,ss)	++(ls,ss)	–	+	su	F, D	F, C
		Jaag 154	115	S	?	–	+(ls,ss)	++(ls,ss)	–	+	su	F, D	F, C
		Jensen 90	50	S	S	–	+(ss)	+(ss)	–	+	ps	F	F, E
		Middleton et al. 2182	95	S	?	–	+(ls,ss)	++(ls,ss)	–	+	su	F	F, C–E
		Rachmat 329	105	±SU	±SU	–	+(ls,ss)	+(ls,ss)	–	+	su	C, F	F; C–E (DGHs)
		Rahim 14	85	S	S	–	+(ls,ss)	++(ls,ss)	–	++	su	F	F, C; E (DGHs)
		Rutten 1665	75	S?	S	–	+(ss–sc: few)	+(ls: few)	–	++	su	F	F; C (DGHs)
		Santos 4654	100	±SU	±SU	–	+(ls,ss)	+(ls,ss)	–	++	su	F	F; C (longest DGHs)
		van Schaik & van Noordwijk 118	90	S	?	–	+(ls,ss–sc)	+(ls,ss–sc)	–	++	su	F	C; E (DGHs)
	M. tanarius var. *tanarius*	*Johansson et al. 343*	110	±SU	±SU	–	+(ls: juvenile)	–	–	+	ps?	F	F
		Mahroji et al. SA 165	125	S	?	–	–	+(ls: few)	–	++	su	F	D
		Phusomsaeng & Pinnin 346	70	U	U	–	+(ls,ss)	+(ls,ss)	–	+	su	F	F; C (DGHs)
	M. tanarius var. *tomentosa*	*Forbes 1274*	90	±SU	S?	–	+(ls,ss)	++(ls,ss)	–	++	su	F	F, C
	M. tentaculata	*Schodde (& Craven) 4666*	60	U	U?	–	+(ls)	+(ls)	–	+	ps	D	F, E
	M. tsonane	*Polak 853*	195	S	?	–	–	–	–	++	su	C, F	F; E (DGHs)
Winkle-rianae	*M. winkleri*	*Church et al. 2706*	150	U	±SU	–	–	–	–	+	su	F	F
		Kessler et al. 973	75	±SU	±SU	–	–	–	–	+	su	F	F
	M. winkleriella	*S 39521*	120	U	±SU	–	–	–	–	+	su	F	F

Ptychopyxis	*P. arborea*	*Kostermans 5816*	77,5	U	?	–	–	++(ls)	–	–	NA	F	F
	P. bacciformis	*SAN 65441*	87,5	U	S	–	–	±(ss)	–	–	NA	F	F
	P. caput-medusae	*SFN 34800*	125	U	?	–	+(ls: ven)	++(ls)	–	–	NA	F	F
	P. chrysantha	*Takeuchi 6000*	155	U	U	–	–	±(ss)	–	–	NA	F	F
	P. costata var. *costata*	*Amiroeddin et al. 62*	75	U	S	–	+(ls: ven	++(ls)	–	–	NA	F	F
	P. costata var. *oblance-olata*	*KEP FRI 29103*	82,5	U	S	–	+(ls: ven)	++(ls)	–	–	NA	F	F
	P. glochidiifolia	*Kostermans 4552*	107,5	U	S	–	–	–	–	–	NA	F	F
	P. grandis	*Webb 3355*	n/a	U	U	–	–	–	–	–	NA	F	F
	P. javanica	*Koorders 2741*	147,5	U	U	–	–	±(ls)	–	–	NA	F	F
	P. kingii	*Haviland 3673*	125	U	±SU	–	±(ls)	±(ls)	–	–	NA	F	F

Table 1 (Continued). Anatomical characters of *Macaranga* and *Ptychopyxis* specimens. Sequence of characters as in Results. *General abbreviations*: Adax = Adaxial, Abax = Abaxial, NA= not applicable; ± = sometimes or somewhat, + = present, ++ = abundant, – = absent, ? = unknown. *Anticlinal epidermal cells*: S = straight, ±SU = somewhat undulating, U = undulating, ? = not well visible. *Indumentum*: first consonant: l = long, s = short; second(–third) consonant: c = curly, s = straight/basally bent, s–c = straight to curly (if four or six consonants then two types of hairs), stel = stellately tufted; dom = in some domatia; ven = hairs on basal part main veins or basal part midrib; l = level, ps = partly sunken, su = sunken. *Papillae*: C = conical, D = dome-shaped, DGHs = near disc-shaped glandular hairs, E = elongated, F = flat, N = nipple. *Extrafloral nectaries*: Cl = club-shaped, Cr = crescent shaped (club-shaped with crater), E = elongated, m = continuation margin (not raised), R = round, U = unspecialized. *Hypodermis*: C = continuous, L = Local. *Petiole vascularization*: CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, coll = collenchymatous tissue present, CSB = cylinder of separate bundles, T = thin layer of sclerenchyma. *Midrib vascularization*: 2AFB = two arcs of fused bundles, 2APFB = two arcs of partly fused bundles, CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, T = thin. *Vein endings*: C = connected, F = free, FScl = fibriform sclereids. *Crystals*: EP = Epidermis, G = ground tissue, Hy = hypodermis, P = palisade, Pl = phloem, Pi = pith, S = spongy tissue, Scl = sclerenchyma, subP = subpalisade layer in spongy tissue.

Group	**Species**	**Extrafloral Nectaries at leaf margin**			**Hypodermis**	**Mesenchym**				**Bundle Sheet Extensions**	**Petiole vascularization**			**Midrib vascularization**			**Secreting cells**	**Secreting cells**
		Shape	Shape secretory cells	Veins		No. palisade layers	Red palisade cells	Intermediate layer	No. spongy layers		Vascular system	Central pith bundles	Sclerenchyma	Vascular system	Central pith bundles	Sclerenchyma	in pith and ground tissue of midrib and large veins	in ground tissue petiole
Bicolor	*M. bicolor*				L	1	+	+	5–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	+	–	5-7	Ad+Ab	CSB	+	coll one side	2AFB	+	+	+	+
	M. congestiflora				L	1	–	+	5	Ad+Ab	CSB	+	coll	2APFB	+	–	+	+
	M. pachyphylla var. *pachyphylla*				L	1	+	+	5–6	Ad+Ab	CPFB	+	+	2APFB	+	+	+	+
					L	1	+	+	5–6	Ad+Ab	CSB	+	–	2APFB	+	–	+	+
	M. pachyphylla var. *glabra*				L	1(2)	+	+	6–9	Ad+Ab	CPFB	+	T	2AFB	+	+	+	+
					L	1(2)	–	+	5	Ad+Ab	CSB	+	–	2APFB	+	–	+	+
	M. puncticulata				–?	1	+	±	3–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L (to C)	1	+	–	5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. sarcocarpa				L	1	–	±	3–5	Ad+Ab	CSB	+	coll	2APFB	+	±	+	+

Denticulata	*M. denticulata*				L	1	–	–	7	Ad+Ab	CSB	+	coll	2AFB	+	+	+	+
					L	1	–	–	5	Ad+Ab	CSB	+	T (local)	2AFB	+	+	+	+
	M. indica				L	1	–	–	8	Ad+Ab	CSB	+	few elements	2APFB	+	+	+	+
					L	1	–	–	6–8	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. peltata				L	1	–	–	3–6	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
	M. pustulata				L	1	–	±	8	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. rhizinoides				L	1	+	–	7–9	Ad+Ab	CSB	+	coll	2APFB	+	+	+	+
Gracilis	*M. domatiosa*				L	1	–	–	5–9	Ad+Ab	CSB	–	T per bundle	2AFB?	–	+	+	+
					L	1	–	–	5–9	Ad+Ab	CSB	–	T	2APFB	–	+	+	+
	M. gracilis				L	1	–	–	7–9	Ad+Ab	CSB	–	–	2APFB	–	+	+	+
					L	1	–	–	5–9	Ad+Ab	CPFB	+	+	2AFB	+	+	+	+
	M. kostermansii				L (large veins)	1	–	+	5–9	Ad+Ab	CSB	–	–	CPFB	–	+	+	+
					L	1	–	+	5–10	Ad+Ab	CSB	–	–	2AFB	–	+	+	+
	M. misimae				L	1	–	–	3–5	Ad+Ab	CFB	+	+	CFB	+	+	+	+
					L	1	–	–	3–5	Ad+Ab	CFB	+	+	2AFB	+	T	+	+
	M. suleensis				L (to C)	1	–	–	5–9	Ad+Ab	CSB	+	T	2AFB	+	+	+	+
Javanica	*M. costulata*				L	1–2	–	±	4–8	Ad+Ab	CSB	+	coll	2APFB	+	+	+	+
	M. cumingii				L	1	–	–	4–7	Ad+Ab	CSB	+	T Adax arc	2AFB	+	+	+	+
	M. endertii				L	2	–	+	6	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. heynei				L	1–2	–	–	9	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	7	Ad+Ab	CPFB	+	T (esp. Adax arc)	2AFB	+	+	+	+
Javanica	*M. javanica*				L	1	–	–	2–6	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	2–7	Ad+Ab	CSB	+	T Adax arc	2APFB	+	+	+	+
	M. laciniata				L	1–2	–	–	7	Ad+Ab	CSB	+	T (more Adax)	2AFB	+	+	+	+
	M. loheri				L	1	–	+	5	Ad+Ab	CPFB	+	Adax arc	2AFB	+	+	+	+
	M. sinensis				L	1–2	–	–	8	Ad+Ab	CSB	+	– (to Adax T)	2APFB	+	+	+	+
	M. spathicalyx				L	1	–	+	6–8	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. sumatrana				L	1	–	–	3–6	Ad+Ab	CSB	+	Adax T	2APFB	–	T	+	+
	M. sylvatica				L	1–2	–	+	8	Ad+Ab	CSB	+	Adax T	2AFB	+	+	+	+
	M. waturan-dangii				L	1	+	±	7–9	Ad+Ab	CSB	+	–	2APFB	–	+	+	+

Pachystemon	*M. aetheadenia*	Cr	E	+	L	1(–2)	–	–	4–6	Ad+Ab	CSB	+	–	2APFB	+	–	+	+
	M. angulata	Cl	–	+	L	1	–	+	4–6	Ad+Ab	CPFB	+	–	2APFB	+	+	+	+
	M. bancana	Cl	–	–	L	1	–	+	4–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
		Cl	–	+	L	1	–	+	4–5?	Ad+Ab	CPFB	+	T	2APFB	+	+	+	+
	M. beccariana	?	?	?	L/C	1	–	+	4–6	Ad+Ab	CSB	+	–	2AFB	+	–	+	+
	M. caladiifolia	Cr	E	+	L	1	+	–	c. 5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. calcicola	Cr	E	+	L	1	–	+	4–6	Ad+Ab	CPFB	+	–	2AFB	+	+	+	+
	M. constricta	–	–	+	L	1	+	–	4–6	Ad+Ab	CPFB	+	–	2APFB	+	+	+	+
	M. depressa	Cr	E	+	L	1	–	–	5–7	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
	M. depressa f. *glabra*	Cr	E	+	L	1	–	+	c. 6	Ad+Ab	?	?	?	2APFB	+	+	+	?
	M. depressa f. *strigosa*	Cr	E	+	L	1	–	+	c. 4	Ad+Ab	CSB	+	–	2AFB	+	T	+	+
	M. glandibrac-teolata	Cl	E	+	L	1	–	+	c. 4	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. havilandii	Cr	E	+	L	1	few	–	3–4	Ad+Ab	?	?	?	2AFB	+	T	+	?
	M. hullettii	Cl	E	+	L	1	–	+	6–7	Ad+Ab	CPFB	+	T	2APFB	+	+	+	+
		Cl	R	+	L	1	–	+	4–6	Ad+Ab	CPFB	+	T	CPFB	+	+	+	+
	M. hypoleuca	Cl	R	+	L	1	few	–	c. 4	Ad+Ab	?	?	?	2APFB	+	+	+	?
		Cl	R	+	L (almost C)	1	few	+	5–6	Ad+Ab	CPFB	+	T	2AFB	+	+	+	+
	M. indistincta	Cl	E	+	L	1	few	+	c. 5	Ad+Ab	CSB	+	–	2APFB	+	–	+	+
Pachystemon	*M. kingii*	–	–	–	L (midrib adax)	1	few	–	4–6	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. lamellata	M	U	+	L	1	+	–	c. 3	Ad+Ab	CSB	+	T	2AFB	+	+	+	+
	M. motleyana	Cl	E	+	L	1	±	+	c. 6	Ad+Ab	CSB	+	–	2AFB	+	Adax T	+	+
		Cl–Cr	U	+	L	1	+	–	5–6	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. petanostyla	M	R	–	L	1	+	+	5–6	Ad+Ab	?	?	?	2APFB	+	+	+	?
	M. rostrata	Cl	?	+	L	1	+	+	5–6	Ad+Ab	CSB	+	T	2APFB	+	+	+	+
	M. trachyphylla	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	M. triloba	Cr	E	+	L	1	few	+	5–6	Ad+Ab	CPFB	+	–	2APFB	+	+	+	+
	M. umbrosa	Cl	?	+	L	1	+	+	5–6	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. velutina	M–Cl	E	+	L	1	+	+	3–4	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. velutiniflora	Cl	R	+	L	1	+	+	6–7	Ad+Ab	?	?	?	2APFB	+	+	+	?

Pruinosae	*M. gigantea*	Cr	E	+	L	1(–2)	+	–	4–5	Ad+Ab	?	?	?	2APFB	+	+	+	?
		Cr	E	+	L	1	+	–	2–4	Ad+Ab	?	?	?	2APFB	+	+	+	?
	M. hosei	Cl	E	+	C	1	+	–	3–4	Ad+Ab	CSB	+	T	2APFB	+	+	+	+
		Cl	E	+	C	1	?	–	3–4	Ad+Ab	?	?	?	2APFB	+	–	+	?
	M. pearsonii	Cl	–	+	C	1	+	–	2–3	Ad+Ab	?	?	?	CPFB	+	+	+	?
		M–Cl	–	+	C	1	–	–	c. 3	Ad+Ab	?	?	?	2AFB	+	–	+	?
	M. pruinosa	Cl	E	+	C	1	+	–	c. 4	Ad+Ab	?	?	?	2APFB	+	+	+	?
	M. puberula	Cl	–	+	C	1	–	–	3–5	Ad+Ab	?	?	?	2AFB	+	+	+	?
	M. siamensis	Cl	R	+	L	1	+	–	c. 2	Ad+Ab	?	?	?	2APFB	+	T & few	+	?
Tanarius	*M. brachytricha*				L	1	+	–	2–3	Ad+Ab	CSB	+	–	2AFB	+	weak Adax	+	+
	M. clavata				L	1	+	–	2–4	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. darbyshirei				L	1	+	–	5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	+	–	2–5	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
	M. harveyana				L	1	+	–	c. 4	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	?	–	2–3	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. minahassae				L	1	–	–	2–3	Ad+Ab	CSB	+	–	2AFB	+	+	+	+

Tanarius	*M. nusateng-garensis*				L	1	–	–	3–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. pilosula				L	1	–	–	3–5	Ad+Ab	CPFB	+	–	2AFB	+	+	+	+
	M. quadriglan-dulosa var. *quadriglandu-losa*				L	1	–	–	3–5	Ad+Ab	CSB	+	–	2APFB	+	T	+	+
					L	1	–	–	4–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. quadriglan-dulosa var. *variabilis*				L	1	–	–	5–9	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
	M. salomon-ensis				L	1	–	–	4–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. tanarius				L	1	–	–	1–5	Ad+Ab	CSB	+	–	2APFB	+	T	+	+
					L	1	–	–	3–7	Ad+Ab	CSB	+	–	2APFB	– (young)	–	+	+
					L	1	–	–	3–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	–	–	3–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	–	–	1–5	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	3–5	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	3–5	Ad+Ab	CSB	+	–	2APFB	–	– (young)	+	+
					L	1	–	–	3–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	–	–	2–5	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	2–7	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
					L	1	–	–	3–7	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	2–7	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	2–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
Tanarius	*M. tanarius* var. *tanarius*				L	1	–	–	3?	Ad+Ab	CSB	+	–	2AFB	–	+	+	+
					L	1	+	–	2–5	Ad+Ab	CSB	+	–	2AFB	+	+	+	+
					L	1	–	–	1–3	Ad+Ab	CSB	+	–	2AFB	+	T	+	+
	M. tanarius var. *tomentosa*				L	1	–	–	3–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+
	M. tentaculata				L	1	–	–	c. 3	Ad+Ab	CSB	+	–	2APFB	+	T	+	+
	M. tsonane				L	1	–	–	5–9	Ad+Ab	CSB	+	–	2APFB	?	?	+	+
Winkle-rianae	*M. winkleri*	Cr	E	+	L	1	+	±	4–6	Ad+Ab	?	?	?	2APFB	+	+	+	?
		Cr	E	+	L	1	+	±	c. 4	Ad+Ab	CPFB	+	–	2APFB	+	–	+	+
	M. winkleriella	Cr	E	+	L	1	–	±	4–5	Ad+Ab	CSB	+	–	2APFB	+	+	+	+

Ptychopyxis	*P. arborea*				N	1	–	–	n/a	Not	CPFB	+	+	2AFB	+	+	–	–
	P. bacciformis				N	1	–	–	5–7	Not	CSB	+	–	2AFB	+	+	–	–
	P. caput-me-dusae				n/a	NA	NA	NA	NA	NA	CSB	+	–	2AFB	+	+	–	–
	P. chrysantha				N	1	–	–	c. 7	Not	CPFB	+	few	2APFB	+	Few cells	–	–
	P. costata var. *costata*				N	1	–	+	4–5	Not	CSB	+	Adax	2APFB	+	+	–	–
	P. costata var. *oblanceolata*				N	1	–	+	5–7	Not	CSB	+	Adax	2APFB	–	+	–	–
	P. glochidiifolia				N	1	–	+	c. 8	Not	?	?	?	2APFB	+	+	–	–
	P. grandis				N	1	–	–	c. 8	Not	CSB	+	+	2APFB	+	+	–	–
	P. javanica				N	1	–	–	5–7	Not	CSB	+	few, most Adax	2AFB	–	+	–	–
	P. kingii				N	1	–	–	6	Not	CSB	+	–	2AFB	+	+	–	–

Table 1 (Continued). Anatomical characters of *Macaranga* and *Ptychopyxis* specimens. Sequence of characters as in Results. *General abbreviations*: Adax = Adaxial, Abax = Abaxial, NA= not applicable; ± = sometimes or somewhat, + = present, ++ = abundant, – = absent, ? = unknown. *Anticlinal epidermal cells*: S = straight, ±SU = somewhat undulating, U = undulating, ? = not well visible. *Indumentum*: first consonant: l = long, s = short; second(–third) consonant: c = curly, s = straight/basally bent, s–c = straight to curly (if four or six consonants then two types of hairs), stel = stellately tufted; dom = in some domatia; ven = hairs on basal part main veins or basal part midrib; l = level, ps = partly sunken, su = sunken. *Papillae*: C = conical, D = dome-shaped, DGHs = near disc-shaped glandular hairs, E = elongated, F = flat, N = nipple. *Extrafloral nectaries*: Cl = club-shaped, Cr = crescent shaped (club-shaped with crater), E = elongated, m = continuation margin (not raised), R = round, U = unspecialized. *Hypodermis*: C = continuous, L = Local. *Petiole vascularization*: CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, coll = collenchymatous tissue present, CSB = cylinder of separate bundles, T = thin layer of sclerenchyma. *Midrib vascularization*: 2AFB = two arcs of fused bundles, 2APFB = two arcs of partly fused bundles, CFB = cylinder of fused bundles, CPFB = cylinder of partly fused bundles, T = thin. *Vein endings*: C = connected, F = free, FScl = fibriform sclereids. *Crystals*: EP = Epidermis, G = ground tissue, Hy = hypodermis, P = palisade, Pl = phloem, Pi = pith, S = spongy tissue, Scl = sclerenchyma, subP = subpalisade layer in spongy tissue.

Group	**Species**	**Fibriform sclereids**	**Vein end-ings**	**Crystals**								
		above and below palisade, originat-ing from bundle sheeths		Druses petiole	Druses midrib	Druses nerves	Druses mesenchym	Prismatic petiole	Prismatic midrib	Prismat-ic bigger nerves	Prismatic mesen-chym	Special
Bicolor	*M. bicolor*	+	C & F	G, Pl, Pi	G, Pl, Pi	G Abax	S (few)	–	–	–	–	
		+	C & F	G, Pl, Pl	G, Pl, Pi	G Abax	P, S (subP)	–	–	–	–	
	M. congesti-flora	+	C	G	G	G	S (subP)	–	–	–	–	
	M. pachyphylla var. *pachyphylla*	±	?	–	–	–	S (subP) few	–	–	–	–	
		±	C	G, Pl, Pi	G, Pl	–	P few, S few	–	–	–	–	
	M. pachyphylla var. *glabra*	±	C	Pl, Pi	Pl, Pi	–	P few, S few	–	–	–	–	
		±	C & F	G, Pl, Pi	Pl, Pi few	–	P few, S few	–	–	–	–	
	M. puncticulata	–	C & F	G, Pl, Pi	G few, Pl, Pi	–	P few, S few	–	–	–	–	
		–	NA	G, Pl, Pi	G, Pl, Pi	G, Pi few	P few, S few	–	–	–	–	
	M. sarcocarpa	±	C?	G, Pl, Pi	G, Pl, Pi	G	P, S	–	–	–	–	
Denticulata	*M. denticulata*	–	F	G, Pl, Pi	G, Pl, Pi	G	P	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G, Pi big nerves	S	–	–	–	–	
	M. indica	–	F	G, Pl, Pi	G, Pl, Pi	G	P few, S ++	–	–	–	–	
		–	F	G, Pl, Pi	G, Pl, Pi	G	S ++	–	–	–	–	
	M. peltata	–	C & F	G, Pl, Pi	G, Pl, Pi	G	P, S	–	–	–	–	
	M. pustulata	–	C & F	G, Pl, Pi	G, Pl, Pi	G big nerves	S	–	–	–	–	
	M. rhizinoides	–	C & F	G, Pl, Pi	G, Pl, Pi	G big nerves	P (against Ep), S	–	–	–	–	

Gracilis	*M. domatiosa*	–	C & F	G, Pl, Pi	G, Pl, Pi	G, Pi few	P, S	–	–	–	–	
		–	?	G, Pl	G, Pl, Pi few	G	S	–	–	–	–	
	M. gracilis	–	C & F	G, Pl	G few, Pl few, Pi few	–	S few	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi few	–	S near midrib	–	–	–	–	
	M. kostermansii	–	C & F	G, Pl, Pi	G few, Pl, Pi	–	P, S few	–	–	–	–	
		–	C & F	G, Pl, Pi	G few, Pl, Pi	–	P, S few					
	M. misimae	–	C & F	G, Pi few	G, Pl few	G few	P few, S few	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	–	P (against Ep), S (subP)	–	–	–	–	
	M. suleensis	–	C & F	G, Pl, Pi	G, Pl, Pi few	–	S	–	–	–	–	Druses Hy
Javanica	*M. costulata*	–	C & F	G ++, Pl few, Pi ++	G, Pl, Pi	G few	S (subP)	–	–	–	–	
	M. cumingii	–	C & F	G ++, Pl few, Pi ++	G, Pl, Pi	G few	P	–	–	–	–	
	M. endertii	–	C & F	G ++, Pl few, Pi ++	G	–	–	–	–	–	–	
	M. heynei	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G few, Pl	S (subP)	–	–	–	–	
		–	C & F	++: G, Pl, Pi	G, Pl, Pi	G few	–	–	–	–	–	
	M. javanica	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G	–	–	–	–	–	
		–	C & F	++: G, Pl, Pi	G, Pl, Pi	G, Pi big nerves	S (subP)	–	–	–	–	
	M. laciniata	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G few	P few, S (subP)	–	–	–	–	
	M. loheri	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G	P, S	–	–	–	–	Druses in Adax Ep?
	M. sinensis	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G	P few, S (subP)	–	–	–	–	
	M. spathicalyx	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G	P (small veins), S (subP)	–	–	–	–	
	M. sumatrana	–	C & F	++: G, Pl, Pi	G, Pl, Pi	G	P, S (subP)	–	–	–	–	
	M. sylvatica	–	C & F	++: G, Pl, Pi	Pl few, Pi few	G few	P few, S few (near nerves)	–	–	–	–	
	M. waturandangii	–	C & F	++: G, Pl, Pi	G	G	P, S	–	–	–	–	

Pachystemon	*M. aetheadenia*	–	NA	G few, Pi	G few, Pi	–	–	–	–	–	–	
	M. angulata	+	NA	G, Pl, Pi	–	–	–	–	–	–	–	
	M. bancana	+	NA	–	–	–	P few, S few	–	–	–	–	
		+	NA	G few, Pl, Pi	G few, Pi	–	–	–	–	–	–	
	M. beccariana	+?	NA	G few, Pl few	G few	–	–	–	–	–	–	
	M. caladiifolia	?	NA	G few, Pi few	–	–	P few, S few	–	–	–	–	
	M. calcicola	+	NA	G, Pi	G	–	P few, S few	–	–	–	–	
	M. constricta	+	NA	–	G few, Pl, Pi	–	P, few S	–	–	–	–	
	M. depressa	+	NA	G, Pl, Pi	G rare	–	P, S	–	–	–	–	
	M. depressa f. *glabra*	+	NA	?	G few	–	few P, S regularly	–	–	–	–	
	M. depressa f. *strigosa*	+	NA	G, Pl, Pi	G, Pi	–	P, few S	–	–	–	–	
	M. glandibrac-teolata	+	NA	?	G, Pl, Pi	–	P, S	–	–	–	–	
	M. havilandii	+?	NA	?	G few, Pl, Pi	–	S	–	–	–	–	
	M. hullettii	+	NA	G few, Pi	–	–	–	–	–	–	–	
		+	NA	G, Pl, Pi	G few, Pl, Pi	–	P	–	–	–	–	
	M. hypoleuca	+	NA	?	G, Pl, Pi	–	S	–	–	–	–	
		+	NA	G, Pl, Pi	G, Pl, Pi	G few	S	–	–	–	–	
	M. indistincta	+	NA	G, Pl, Pi	G, Pl, Pi	–	P few, S few	–	–	–	–	
	M. kingii	–	NA	?	G, Pl, Pi	G	P	–	–	–	–	
	M. lamellata	–	NA	G, Pl, Pi	G, Pl, Pi	–	P	–	–	–	–	
	M. motleyana	+?	NA	G, Pl, Pi	G, Pl, Pi	–	P, S	–	–	–	–	
		+	NA	?	G, Pl	–	P, S	–	–	–	–	
	M. petanostyla	+	NA	?	G, Pl, Pi	–	P, S few	–	–	–	–	
	M. rostrata	+	NA	G, Pl, Pi	G, Pl, Pi	G	P, S	–	–	–	–	
	M. trachyphylla	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
	M. triloba	+	NA	G, Pl, Pi	G, Pl, Pi	G big nerves	P, S	–	–	–	–	
	M. umbrosa	+?	NA	?	G, Pl, Pi	G big nerves	–	–	–	–	–	
	M. velutina	+	NA	?	G, Pl, Pi few	G big nerves	P, S	–	–	–	–	
	M. velutiniflora	+	NA	?	G, Pl, Pi	G big nerves	P, S	–	–	–	–	

Pruinosae	*M. gigantea*	+?	NA	?	G, Pl, Pi	G Abax big nerves	P, S	–	–	–	–	
		+?	NA	?	G few, Pl, Pi	G Abax big nerves	P few, S (subP)	–	–	–	–	
	M. hosei	?	NA	G few, Pl, Pi	G few, Pl, Pi		P, S	–	–	–	–	
		?	NA	?	G, Pl, Pi	–	–	–	–	–	–	
	M. pearsonii	?	NA	?	Pl few	G Abax big nerves	S (subP)	–	–	–	–	Druses in Hy
		–	NA	?	–	G few?	S few?	–	–	–	–	
	M. pruinosa	+	NA	?	G, Pl	G few	P, S	–	–	–	–	Druses in Hy
	M. puberula	+	NA	?	–	–	–	–	–	–	–	
	M. siamensis	+	NA	?	–	–	–	–	–	–	–	
Tanarius	*M. brachytricha*	–	mainly C	G, Pl, Pi	–	G few	S (subP)	–	–	–	–	
	M. clavata	–	mainly C	G, Pl, Pi	G, Pl, Pi	G	P, S (mainly subP)	–	–	–	–	
	M. darbyshirei	–	mainly C	G, Pl, Pi	G, Pl, Pi	G	P, S (mainly subP)	–	–	–	–	
		–	mainly C	G, Pl, Pi	G, Pl, Pi	–	S (subP)	–	–	–	–	
	M. harveyana	–	mainly C	G, Pl, Pi	G, Pl, Pi	–	P few, S (subP)	–	–	–	–	
		–	?	G, Pl, Pi	– (immature leaf)	G few big nerves	S (mainly subP)	–	–	–	–	
	M. minahassae	–	mainly C	G, Pl, Pi	G, Pl, Pi	G few, Pl	S (mainly subP)	–	–	–	–	
	M. nusatengga-rensis	–	mainly C	G, Pl, Pi	Pl few, Pi	–	–	–	–	–	–	
	M. pilosula	–	mainly C	G, Pl, Pi	G, Pl, Pi	G big nerves	P, S (subP)	–	–	–	–	
	M. quadriglan-dulosa var. *quadriglandu-losa*	±	mainly C	G, Pl, Pi	G, Pl, Pi	G big nerves	P, S (subP)	–	–	–	–	
		±	mainly C	G, Pl, Pi	G, Pl, Pi	G big nerves	P few, S few	–	–	–	–	
	M. quadriglan-dulosa var. *variabilis*	±	mainly C	G, Pl, Pi	G, Pl, Pi	G, Pi big nerves	P few, S (mainly subP)	–	–	–	–	
	M. salomon-ensis	–?	C & F	G, Pl, Pi	G, Pl, Pi	G	P few, S few (subP)	–	–	–	–	

Tanarius	*M. tanarius*	–	C & F	G, Pl, Pi	G, Pl, Pi	G	P, S	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	P few, S few	–	–	–	–	
		–	mainly C	G, Pl, Pi	G, Pl, Pi	G few big nerves	P, S (subP)	–	–	–	–	
		–?	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	S (subP)	–	–	–	–	
		–	mainly C	G, Pl, Pi	G, Pl, Pi	G few big nerves	P, S (subP)	–	–	–	–	Druses Adax Ep?
		–	mainly C	G, Pl, Pi	G, Pl, Pi	–	P, S (subP)	–	–	–	–	
		–	mainly C	G, Pl, Pi	G, Pl, Pi	–	S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	–	P few, S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	S (subP)	–	–	–	–	Druses Adax Ep?
		–	C & F	G, Pl, Pi	–	–	–	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	P, S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	P, S (subP)	–	–	–	–	Druses Adax Ep?
	M. tanarius var. *tanarius*	–	C & F	G, Pl, Pi	G, Pl, Pi	–	S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	S (subP)	–	–	–	–	
		–	C & F	G, Pl, Pi	–	–	P few, S (subP)	–	–	–	–	
	M. tanarius var. *tomentosa*	–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	P few, S (subP)	–	–	–	–	
	M. tentaculata	–	C & F	G, Pl, Pi	G, Pl, Pi	–	P few, S (subP)	–	–	–	–	
	M. tsonane	–	C & F	G, Pl, Pi	G, Pl, Pi	G few big nerves	P few, S (subP)	–	–	–	–	
Winkle-rianae	*M. winkleri*	+?	NA	?	Pl few, Pi few	–	–	–	–	–	–	
		–	NA	G, Pl, Pi	Pi	G	–	–	–	–	–	
	M. winkleriella	–	NA	G, Pl, Pi	–	–	–	–	–	–	–	

Ptychopyxis	*P. arborea*	++	C or ending in FScl	Pl	G	–	P, S (mainly subP)	G	G (outside Scl)	Around Scl	_	
	P. bacciformis	++	C or ending in FScl	Pl, Pi	G, Pl	–	P, S few	G	G (outside Scl)	Around Scl	_	
	P. caput-medu-sae	++	C or ending in FScl	G, Pl, Pi	Pi	–	P?	G	G (outside Scl)	Around Scl	_	
	P. chrysantha	++	C or ending in FScl	G, Pi	G Adax above scl, Pi	–	S	G (outside Scl)	G (outside Scl)	Around Scl	_	
	P. costata var. *costata*	++	C or ending in FScl	G, Pl, Pi	G few, Pl, Pi few	–	P (against Ep)	G	G (outside Scl)	Around Scl	_	
	P. costata var. *oblanceolata*	++	C or ending in FScl	G, Pl, Pi	G, Pl, Pi	–	P (against Ep)	G (outside Scl)	G (outside Scl)	Around Scl	_	
	P. glochidiifolia	++	C or ending in FScl	?	Pl	–	P (against Ep)	+	G (outside Scl)	Around Scl	_	
	P. grandis	+++	C or ending in FScl	Pl	Pl	–	P (against Ep)	G (outside Scl), Pi	G (outside Scl), Pi	Around Scl	_	
	P. javanica	++	C or ending in FScl	G, Pl, Pi	Pl	–	P, S (mainly subP)	G (outside Scl)	G (outside Scl), Pi	Around Scl	_	
	P. kingii	++	C or ending in FScl	G, Pl, Pi	G, Pl, Pi	–	P (against Ep), S (mainly subP)	+	G (outside Scl), Pi	Around Scl	_	

Table 2. The major anatomical differences between *Macaranga* and *Ptychopyxis* and between the various groups in *Macaranga*. In bold the more typical character states. – = absent, + = present, ++ or +++ = abundant, E = elongated papillae.

Character	Macaranga								Ptychopyxis
	Bicolor	**Denticulata**	**Gracilis**	**Javanica**	**Pachystemon**	**Pruinosae**	**Tanarius**	**Winklerianae**	
Extrafloral nectaries margin	mainly +	mainly –	mainly –	mainly –	mainly +	+	mainly –	+	–
Disc-shaped glandular hairs	+	+	+	+	+	+	+	+	–
Abaxial simple hairs	mostly 1 type	1 type	1 type	mostly 1 type	often 2 types	**mostly 2 types**	**mostly 2 types**	–	mostly 1 type
Abaxial stellate hairs	–	–	–	–	–	**mainly +**	– (1 specimen +)	–	–
Adaxial papillae	–	–	–	few dome shaped	**most +**	–	some	–	–
Abaxial papillae	mainly +	mainly E	mainly – (flat)	– to +	– to +	mainly E	mainly E	– (flat)	– (flat)
Stomatal density	low	low	low	low	low	low	low	low	**high**
Hypodermis	local	local	local	local	local	**mainly continuous**	local	local	**absent**
Intermediate layer adax spongy tissue	**mainly +**	mainly –	mainly –	mainly –	**mainly +**	–	–	±	mainly –
Bundle sheet extensions	+	+	+	+	+	+	+	+	–
Petiole & mirib pith vascular bundles	+	+	**half –**	+	+	+	+	+	+
Exudate secreting cells	+	+	+	+	+	+	+	+	–
Fibriform sclereids	**±**	–	–	–	mainly +	mainly +	some +	–	**++/+++**
Druses ground tissue petiole	+	+	+	**++**	+	+	+	+	+
Druses ground tissue (major) nerves	**half +**	**+**	few +	**+**	few +	few +	most +	mainly –	–
Druses in palisade	in palisade	in palisade	in palisade	in palisade	in palisade	in palisade	in palisade	–	subepidermal
Prismatic crystals	–	–	–	–	–	–	–	–	**+**

APPENDIX 1

An overview of the groups/taxa, sampled species, and per species collector(s) or institutes and their numbers, L herbarium QR-codes, locations and the maturity of all species (mature unless stated differently, then Ju = juvenile, Ma = Mature).

	Species	Collector	QR-code	Location	Maturity
Bicolor	*M. bicolor* Müll.Arg.	*BS 15000*	L.2237032	Philippines	
		PPI 6744	L.2237025	Philippines	Ju + Ma
	M. congestiflora Merr.	PPI 73	L.2230721	Philippines	
	M. pachyphylla Müll.Arg. var. *pachyphylla*	*Maskari 19*	L.2238598	Java	
		Okada et al. *1037*	L.2238305	Malay Peninsula	Ju + Ma
	M. pachyphylla Müll.Arg. var. *glabra* (Whitmore) Whitmore	*KEP FRI 12114*	L.2238610	Malay Peninsula	
		SAN 56312	L.2238624	Borneo	Ju + Ma
	M. puncticulata Gage	*Ambriansiah AA 1527*	L.2231174	Borneo	Ju + Ma
		SFN 34041	L.2231253	Malay Peninsula	
	M. sarcocarpa Airy Shaw	*Moog 00-43*	L.2231752	Borneo	Ju + Ma
Denticulata	*M. denticulata* (Blume) Müll.Arg.	*Anonymous s.n.*	L.2241843	Java	
		Soejarto et al. *11215*	L.2241392	Vietnam	
	M. indica Wight	*Chand 2856*	L.2242089	India	
		Worthington 13162	L.2242093	Malay Peninsula	
	M. peltata (Roxb.) Müll.Arg.	*Hohenacker 511*	L.2238485	India	
	M. pustulata King ex Hook.f.	*Dickason 8572*	L.2231190	Myanmar	
	M. rhizinoides (Blume) Müll.Arg.	*Junghuhn s.n.*	L.2231866	Java	
Gracilis	*M. domatiosa* Airy Shaw	*Craven & Schodde 1300*	L.2241644	New Guinea	
		van Valkenburg 158	L.2241634	New Guinea	
	M. gracilis Pax & K.Hoffm.	*Hartley 12715*	L.2230882	New Guinea	
		Schodde 1478	L.2230883	New Guinea	
	M. kostermansii L.M.Perry	*BW 14149*	L.2237754	New Guinea	
		van Royen & Sleumer 7384	L.2237755	New Guinea	
	M. misimae Airy Shaw	*Brass 27540*	L.2238216	New Guinea	Ju + Ma
		Brass 32404	L.2238218	New Guinea	
	M. suleensis Whitmore	*LAE 59703*	L.2242480	New Guinea	
Javanica	*M. costulata* Pax & K.Hoffm.	*SAN 131278*	L.2230525	Borneo	
	M. cumingii (Baill.) Müll.Arg.	*PPI 6794*	L.2241587	Philippines	
	M. endertii Whitmore	*Kostermans 6026*	L.2241617	Borneo	
	M. heynei I.M.Johnst.	*Argent & Iqbar 9961*	L.2230754	Malay Peninsula	
		KEP FRI 14050		Sumatra	
	M. javanica (Blume) Müll.Arg.	*Koorders 2381*	L.2237863	Malay Peninsula	
		Mk. Ar. 585	L.2237453	Java	
	M. laciniata Whitmore & Airy Shaw	*KEP FRI 12874*	L.2237781	Malay Peninsula	
	M. loheri Elmer	*Vanoverbergh 2752*	L.2238093	Philippines	
	M. sinensis (Baill.) Müll.Arg.	*Elmer 14231*	L.2231635	Philippines	
	M. spathicalyx Whitmore & S.J.Davies	*Aiba 1615*	L.2231653	Borneo	
	M. sumatrana Müll.Arg.	*Korthals s.n.*	L.2242483	Sumatra	
	M. sylvatica Elmer	*Elmer 10109*	L.2242440	Philippines	
	M. waturandangii Whitmore	*Van Balgooy 3384*	L.2232852	Sulawesi	
Pachystemon	*M. aetheadenia* Airy Shaw	*Kessler el al. 1333*	L.2224935	Borneo	
	M. angulalata SJ.Davies	*Nooteboom 1404*	L.2236657	Borneo	
	M. bancana (Miq.) Müll.Arg.	*Forbes 2980*	L.2236850	Malay Peninsula	
		Singh 163	L.2236917	Sumatra	
	M. beccariana Merr.	*S 51400*	L.2237147	Borneo	

Pachystemon	*M. caladiifolia* Becc.	*Haviland & Hose 464 E*	L.2230336	Borneo	
	M. calcicola Airy Shaw	*S 15288*	L.2230313	Borneo	
	M. constricta Whitmore & Airy Shaw	*KEP FRI 3431*	L.2230586	Malay Peninsula	
	M. depressa (Müll.Arg.) Müll.Arg.	*SAN 95431*	L.2241815	Borneo	
	M. depressa (Müll.Arg.) Müll.Arg. f. *glabra* Whitmore	*SAN 97352*	L.2241767	Borneo	
	M. depressa (Müll.Arg.) Müll.Arg. f. *strigosa* Whitmore	*van Balgooy 6124*	L.2241749	Borneo	
	M. glandibracteolata S.J.Davies	*Fiala 34*	L.2230879	Borneo	
		Native Collector 168	L.2230917	Borneo	
	M. hullettii King ex Hook.f.	*Albertus 54*	L.2241912	Borneo	
		Singh & bin Samsuri 302	L.2242064	Malay Peninsula	
	M. hypoleuca (Rchb.f. & Zoll.) Müll. Arg.	*Gardner & Sidisunthorn ST 428*	L.2241851	Thailand	
		S 56696	L.2242173	Borneo	
	M. indistincta Whitmore	*Fiala 19*	L.2237740	Borneo	
	M. kingii Hook.f	KEP FRI 5220	L.2237789	Malay Peninsula	
	M. lamellata Whitmore	*Slik* et al. *M-1075*	L.2237744	Borneo	
	M. motleyana (Müll.Arg.) Müll.Arg.	*Chin & Mustafa 3289*	L.2238188	Malay Peninsula	
		S 68897	L.4310071	Borneo	
	M. petanostyla Airy Shaw	*Nooteboom 1370*	L.2238488	Borneo	
	M. rostrata Heine	*SAN 46770*	L.2231787	Borneo	
	M. trachyphylla Airy Shaw	*Fuchs & Muller 21159*	L.2232274	Borneo	
	M. triloba (Thunb.) Müll.Arg.	*van Steenis 3652*	L.2232522	Sumatra	
	M. umbrosa S.J.Davies	*Laman* et al. *630*	L.2232480	Borneo	
	M. velutina (Rchb.f. & Zoll.) Müll.Arg.	*Church 17*	L.2232917	Borneo	
	M. velutiniflora S.J.Davies	*Davies* et al. *981204*	L.2232879	Borneo	
Pruinosae	*M. gigantea* (Rchb.f. & Zoll.) Müll. Arg.	*Gentry & LaFrankie 66907*	L.2237183	Malay Peninsula	
		S 42644	L.2237393	Borneo	
	M. hosei King ex Hook.f.	*bb 2162*	L.2230920	Borneo	
		KEP 98511	L.2231016	Malay Peninsula	
	M. pearsonii Merr.	*Keith 1617*	L.2238561	Borneo	
		Korthals s.n.	L.2238552	Borneo	
	M. pruinosa (Miq.) Müll.Arg.	*KEP FRI 1187*	L.2231337	Malay Peninsula	
	M. puberula Heine	*Dransfield 7212*	L.2231272	Borneo	
	M. siamensis S.J.Davies	*Murata* et al. *T-16482*	L.2231718	Thailand	
Tanarius	*M. brachytricha* Airy Shaw	*Weiblen 1713*	L.2230399	New Guinea	Ju + Ma
	M. clavata Warb.	*Brass 23921*	L.2230193	New Guinea	
	M. darbyshirei Airy Shaw	*BW 7092*	L.2241570	New Guinea	Juvenile
		Takeuchi et al. *17894*	L.2241571	New Guinea	Ju + Ma
	M. harveyana (Müll.Arg.) Müll.Arg.	Smith 9671	L.2230836	Cook islands	Ju + Ma
		Sykes 139C	L.2230832	Fiji	Ju + Ma
	M. minahassae Whitmore	*Whitmore & Sidiyasa 3521*	L.2238212	Sulawesi	Juvenile
	M. nusatenggarensis Whitmore	*Schmutz 4184*	L.2238288	Lesser Sunda Islands	Ju + Ma
	M. pilosula Airy Shaw	*Brass 28752*	L.2238460	New Guinea	Ju + Ma
	M. quadriglandulosa Warb. var. *quadriglandulosa*	*Craven & (Schodde) 414*	L.2232016	New Guinea	
		Takeuchi & Wiakabu 9760	L.2232017	Bougainville	

Tanarius	*M. quadriglandulosa* Warb. var. *variabilis* L.M.Perry	*NGF 4170*	L.2232021	New Guinea	
	M. salomonensis L.M.Perry	*Hoogland 3463*	L.2231745	New Guinea	
	M. tanarius (L.) Müll.Arg.	*Brass 24052*	L.2232193	New Guinea	
		BSIP 19482	L.2232155	Solomon Islands	
		BW 13543	L.2232230	New Guinea	
		Coveny & Haegi 9921	L.2232144	Australia	Ju + Ma
		Hotta 13168	L.2242608	Borneo	
		Jaag 154	L.2242489	Lesser Sunda Islands	
		Jensen 90	L.2232254	Kei Islands	Juvenile
		Middleton et al. *2182*	L.2242398	Thailand	
		Rachmat 329	L.2242549	Celebes	
		Rahim 14	L.2242414	Malay Peninsula	
		Rutten 1665	L.2232250	Moluccas	
		Santos 4654	L.2242633	Philippines	
		van Schaik & van Noordwijk 118	L.2242388	Sumatra	Ju + Ma
	M. tanarius (L.) Müll.Arg. var. *tanarius*	*Johansson* et al. *343*	L.2232462	Sulawesi	Ju + Ma
		Mahroji et al. *SA 165*	L.3968932	Moluccas	
		Phusomsaeng & Pinnin 346	L.2232460	Thailand	
	M. tanarius (L.) Müll.Arg. var. *tomentosa* (Blume) Müll.Arg.	*Forbes 1274*	L.2242379	Java	
	M. tentaculata Airy Shaw	*Schodde (& Craven) 4666*	L.2232293	New Guinea	Ju + Ma
	M. tsonane Whitmore	*Polak 853*	L.2232475	New Guinea	Ju + Ma
Winklerianae	*M. winkleri* Pax & K.Hoffm.	*Church* et al. *2706*	L.2238732	Borneo	
		Kessler et al. 973	L.2232784	Borneo	
	M. winkleriella Whitmore	*S 39521*	L 2238735	Borneo	
Ptychopyxis	*P. arborea* (Merr.) Airy Shaw	*Kostermans 5816*	L.2253169	Borneo	
	P. bacciformis Croizat	*SAN 65441*	L.2253129	Borneo	
	P. caput-medusae (Hook.f.) Ridl.	*SFN 34800*	L.2253121	Malay Peninsula	
	P. chrysantha (K.Schum.) Airy Shaw	*Takeuchi 6000*	L.2253446	New Guinea	
	*P. cosata M*iq. var. *costata*	*Amiroeddin* et al. *62*	L.2253466	Sumatra	
	P. costata Miq. var. *oblanceolata* Airy Shaw	*KEP FRI 29103*	L.2253477	Malay Peninsula	
	P. glochidiifolia Airy Shaw	*Kostermans 4552*	L.2253436	Borneo	
	P. grandis Airy Shaw	*Webb 3355*	L.2253412	Borneo	
	P. javanica (J.J.Sm.) Croizat	*Koorders 2741*	L.2253403	Java	
	P. kingii Ridl.	*Haviland 3673*	L.2253382	Borneo	