



Revision of the genus *Monotes* (Dipterocarpaceae) in D.R. Congo, with implications for Angola and its distinction from *Marquesia*

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Abstract

Within the framework of the preparation of the treatment of the family Dipterocarpaceae for the *Flore d'Afrique Centrale*, the revision of the genus *Monotes* in D.R. Congo is presented, including a discussion on its distinction from the closely related genus *Marquesia*. *Monotes* has suffered from taxonomic inflation. A much more synthetic treatment than earlier revisions is here proposed, with 15 new synonyms and seven species or subspecies downgraded to varietal rank. Twenty-seven taxa are accepted in D.R. Congo (13 species, 10 varieties and four forms), of which six are new to the flora of the country. One new species (*Monotes duvigneaudii*), one new subspecies (*Monotes rubriglans* subsp. *upembensis*) and three new varieties are described (*Monotes dasyanthus* var. *heterotrichus*, *M. duvigneaudii* var. *concolor*, *M. rubriglans* subsp. *upembensis* var. *griseocoriaceus*). Eleven new combinations are made. *Monotes hypoleucus* is extended, to include var. *angolensis*, var. *caloneurus*, var. *discolor*, var. *hypoleucus*, and var. *loandensis*. Lectotypes are designated for *M. adenophyllus* var. *homblei*, *M. dasyanthus* var. *dasyanthus* forma *sericea*, *M. dasyanthus* var. *mutetetwa*, *M. dawei*, *M. glaber*, *M. hirtii*, *M. hypoleucus*, *M. hypoleucus* var. *angolensis*, *M. hypoleucus* var. *caloneurus*, *M. kapiensis*, *M. katangensis*, *M. magnificus* var. *albidus*, *M. magnificus* var. *paucipilosus*, and *M. schmitzii*. Four supposed Angolan endemics (*M. carrisoanus*, *M. dawei*, *M. hutchinsonianus*, *M. noldeae*) and one supposed Congolian endemic (*M. schmitzii*) are refuted as forms without taxonomic standing. Another three are no longer endemic to Angola because of material collected in D.R. Congo (*M. hypoleucus* var. *loandensis*, *M. pearsonii*, *M. rubriglans*). In the current state of knowledge, eight taxa are endemic to D.R. Congo (*Monotes doryphorus*, *M. duvigneaudii* var. *duvigneaudii*, *M. duvigneaudii* var. *concolor*, *M. hirtii*, *M. hypoleucus* var. *angolensis* f. *oxyphyllinus*, *M. magnificus* var. *gigantophyllus*, *M. rubriglans* subsp. *upembensis* var. *upembensis* and *M. rubriglans* subsp. *upembensis* var. *griseocoriaceus*). The Upper Katanga region appears to represent the most prominent centre of diversity for the genus. Additional field work and collecting is necessary to complete the description of several taxa.

Key words: Africa, endemic, indumentum, Katanga, key, miombo, numerical taxonomy, taxonomic inflation, taxonomy, Zambezan Region

Introduction

“Les combinaisons de caractères sont quasi infinies et le genre Monotes nous apparaît comme un genre très jeune, tout plein de possibilités évolutives, dont les espèces, encore mal fixées, atténuent encore le peu de différence qui les sépare en s’hybridant” (Duvigneaud 1949: 41)

The family Dipterocarpaceae comprises some 500 species, predominantly Asian, which represent high commercial importance as timber-producing trees (meranti) (Ashton 1982, 2003; Soerianegara & Lemmens 1993). In Africa, their diversity is only modest. Within the framework of the preparation of a treatment of the Dipterocarpaceae for the *Flore d'Afrique Centrale* (D.R. Congo, Rwanda, Burundi), the revision of the central African representatives of the genus *Monotes* De Candolle (1868: 623) is presented. *Monotes* is one of the most characteristic tree genera of dry tropical forests of South-Central Africa (Wenger & Coetsee 1978). De Candolle (1868) established the genus *Monotes* to accommodate the first African representatives of the family Dipterocarpaceae. Gilg (1899, 1925) argued that *Monotes* was so distinct from Asian Dipterocarpaceae to merit recognition in a separate sub-family, the *Monotoideae*. Although

the correct affiliation of *Monotoideae* has long been debated (Kostermans 1989), molecular phylogenies support its position as the most basal lineage within Dipteroocarpaceae (Dayanandan *et al.* 1999).

The African Plant Database (version 3.4.0; <https://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an>) currently accepts 37 species of *Monotes*, all but two being endemic to the Zambezian regional centre of endemism (sensu White 1983); the Catalogue of Life (www.catalogueoflife.org) accepts 39 taxa (including infraspecific taxa) and the Plant List (www.theplantlist.org/) accepts 26 species and 27 species are unresolved. Gilg (1899, 1908, 1925) was the first monographer of the genus. De Wildeman (1927a) described new species from D.R. Congo and published the first key for that region. Bancroft (1937, 1939a) published the first critical revision of *Monotes*, in which, for the first time, the taxonomic value of the distribution and type of foliar indumentum was highlighted. Subsequently Duvigneaud (1949, 1959, 1961) gained an unrivalled knowledge of the genus, based on observations in the field and his copious material collected in southern D.R. Congo. Both Bancroft (1939a) and Duvigneaud (1949) provided penetrating discussions on the taxonomic value of characters and of species limits. They insisted on the presence of a complex pattern of variation, close affinities amongst many species, and the existence of a relatively large number of intermediate specimens. In this respect, Bancroft also made informative annotations on herbarium specimens.

Other workers have also characterized *Monotes* as a notoriously taxonomically difficult genus (White 1962; Verdcourt 1989; Catarino *et al.* 2013). In *Monotes* only a few morphological characters are considered taxonomically informative. While the indumentum of both leaf surfaces is taxonomically important, floral and fruit traits are generally considered to be of secondary importance. *Monotes* leaves exhibit an astounding diversity of hair types, first described by Duvigneaud (1949). However, the subtle variations in extent, thickness and density of indumentum and hair morphology are difficult to describe in standardised, unambiguous terms and thus to translate into effective identification keys. All earlier revisions of the genus suffer from a lack of illustrations of the indumentum and provide no precise characterizations of the hairs. In the present revision, for the first time, we provide illustrations of leaf surfaces in an effort to remove ambiguities in indumentum description.

For more than 60 years, the taxonomic treatment of *Monotes* in the Zambezian Region has relied on the work of Paul Duvigneaud (1949, 1961), which was followed, *ne varietur*, by subsequent authors (Verdcourt 1989; Catarino *et al.* 2013). Duvigneaud's taxonomic concepts have never been challenged. Verdcourt (1989: 10) insisted that “[Duvigneaud’s] knowledge of the genus was based on a long study of extensive material throughout the range of the genus; no one with much less experience can expect to do better.” An account of *Monotes* for Angola was recently published by Catarino *et al.* (2013), though without a critical taxonomic discussion.

The species limits in *Monotes* are often unclear, with few characters of diagnostic value and continuous variation in most traits. We found a comparatively large proportion of specimens to be intermediate between traditionally recognized species, and, moreover, that both Duvigneaud and Bancroft also left a comparatively high number of specimens unnamed because they considered them to represent intermediates.

A particularly difficult group is the complex of *M. caloneurus*-*M. elegans*, members of which are extremely widespread in the Zambezian Region. It comprises specimens with a puberulent upper surface of leaf and a more or less discoloured, greyish to whitish, tomentose lower surface of leaf. Leaf size, and density of the indumentum on the lower surface of the leaf are generally used to distinguish among taxa in this complex. Bancroft (1939a) insisted on the close relationships of *M. elegans* with both *M. caloneurus* and *M. hypoleucus* and on the polymorphism of *M. elegans* “[which] seems to include a number of variable forms, intermediate between *M. caloneurus* and *M. hypoleucus*”; she admitted that *M. elegans* is probably heterogeneous, recognizing “typical” and “atypical” forms. Duvigneaud (1949) tried to solve the problem by describing a new species, namely *M. schmitzii*, to accommodate the Congolese specimens that he could not unambiguously assign to either *M. elegans* or *M. caloneurus*.

As a result, the existing taxonomic framework has been used in a wide array of literature related to the Zambezian and adjacent regions. Now that doubt has arisen as to the merits of that framework, the validity of the conclusions of many previous studies will need to be checked. This emphasizes the need to act very carefully when proposing taxonomic changes.

To a large extent, the present taxonomic revision is based on a critical re-examination of the copious herbarium material collected by Paul Duvigneaud between 1948 and 1960. Our treatment is much more synthetic than all earlier treatments of the genus and departs significantly from Duvigneaud's and Bancroft's species concepts. The present revision has important implications for Angola, since previously overlooked specimens of several poorly known taxa thought to be endemic to Angola have been uncovered in the collections from D.R. Congo.

The subfamily Monotoideae contains two more genera, the recently discovered South-American *Pseudomonotes* Londoño *et al.* (1995: 230; Morton *et al.* 1999) and the African genus *Marquesia* Gilg (1908a: 485). The latter name was recently proposed for “conservation” against the older but obscurely published *Trillesanthus* Pierre (1901: 1)

(Sosef 2010a; Rijckevorsel 2011; Applequist 2012). In the literature, various characters (Table 1) have been used for the distinction between *Monotes* and *Marquesia*. Our investigations showed some of these do not hold, and it was deemed wise to conduct a more thorough morphological study to establish whether the two genera are sufficiently distinct. *Pseudomonotes*, although closely resembling *Monotes* because of its indumentum and appendaged stamens, seems sufficiently distinct, amongst others in having a glabrous ovary with minute styles.

Materials and Methods

Herbarium acronyms follow Thiers (continuously updated). All herbarium material from D.R. Congo present in BM, BR, BRLU, BRVU, K, LG, LSHI, P and POZG has been revised. The BRLU collection is one of the most important worldwide for the genus *Monotes*, comprising > 2500 sheets, ca. 75% of which collected by Paul Duvigneaud between 1948 and 1960. Importantly, a significant part of this material was collected by Duvigneaud after the completion of his account of *Monotes* for D.R. Congo (Duvigneaud 1949). Collections from Zambia and Angola in BR and BRLU have also been examined and additional material was obtained on loan from W and LISC. Additional specimens were investigated using the JSTOR Global Plants facility (<http://plants.jstor.org>).

To assess the claimed distinction between *Monotes* and *Marquesia*, 25 specimens were studied belonging to all three species of *Marquesia* and 20 taxa (18 species, one with three varieties) of *Monotes*. From relevant literature, we extracted the characters used to distinguish the two genera (see Table 1). To these we added flower bud shape, filament hairiness and pubescence of fruit wings.

To unravel the *M. caloneurus*-*M. elegans* complex, a numerical taxonomic approach has been followed. This used herbarium material identified by P. Duvigneaud as *M. elegans*, *M. caloneurus*, *M. schmitzii* and *M. hypoleucus*. Most Duvigneaud collections included several duplicate sheets; in which case two were used in the morphometric analysis. The type specimens of *M. schmitzii* and *M. hypoleucus* were included. For *M. elegans*, the type being destroyed, *Burt 1382*, a specimen used as a substitute of the type by Duvigneaud (1949) has been included. A few collections from neighbouring countries were also included. In all, this part of our study involved a total of 81 specimens (list of specimens in Appendix). The following characters, used by previous authors (Bancroft 1939a; Duvigneaud 1949, 1961) to discriminate taxa in this complex, were measured (only the largest, undamaged leaf was considered): Leaf length (“LL”), leaf width (“Lw”), L/w ratio, distance from base to largest width relative to leaf length (“shape”), petiole length (“Lpet”), number of lateral nerves on one side of the midrib (“nerves”), depth of apical sinus (“apsin”), depth of basal sinus (“basin”), fruit diameter (“Dfr”), length of longest calyx wing at fruiting stage (“Lwings”); density of hairs on upper surface (1 = sparse to absent; 2 = intermediate; 3 = dense) (“uphairs”); density of hairs on lower surface (same) (“lowhairs”). The color of the upper and lower surface of the leaf (“upcol” and “lowcol”) was assessed as follows. A digital picture was taken with a camera Nikon reflex D7000; the pictures were treated with image J (version 1.43), and the level of grey was encoded from 0 to 256; the modal level (the most frequent) was used.

To explore correlation patterns among variables, the data were analysed by Principal Component Analysis on the correlation matrix. Then, non metric multidimensional scaling (NMDS) was also performed as the data comprised two ordinal characters. Both analyses were performed using PAST 2.14 (Hammer 2012).

For the taxonomic revision, standard herbarium techniques were applied (Vogel 1987).

Note on Duvigneaud’s type specimens

Paul Duvigneaud used to gather copious material, especially from interesting taxa. For most of the new taxa described by him, the type collection has been mounted on several sheets with the same collection number. All sheets are kept in BRLU. Quite often, one of the sheets was marked with a red stamp “Holotype”. In such cases, that sheet is here accepted as the holotype, and all the other sheets with the same collection number are here considered as isotypes. When none of the sheets was marked as the holotype, one of them is here designated as the lectotype.

Duvigneaud’s type specimens were digitized at BR within the framework of the African Plant Initiative. They then received a barcode starting with the herbarium code “BR” while they are in fact deposited at BRLU. A BRLU barcode has been added recently.

Note on phytogeographic regions of D.R. Congo

We follow the phytogeographic system of Robyns (1948), endorsed by the Flore d’Afrique centrale. The genus *Monotes* is restricted to regions III (Bas-Congo), IV (Kasaï, including Kwango), V (Lower Katanga) and XI (Upper Katanga).

Results

On the distinction between Marquesia and Monotes

From the list of characters in Table 1, we already noted that the twig character does not hold. Various species of *Monotes* have furrowed twigs, while cylindrical ones are present in *Marquesia macroua*. The same goes for the leaf apex. While indeed all *Marquesia* species have acuminate leaf tips, those of *Monotes doryphorus*, *M. duvigneaudii*, *M. hirtii* and, sometimes, *M. dasyanthus* are also acuminate. Table 2 gives the results of our observations on the remainder of the characters. It shows that filament hairs are only characteristic for *Marquesia macroua* and thus diagnostic at species level. The same goes for the thickness of the fruit wall; only in *Marquesia excelsa* it is thin. The anther appendage is generally well developed in *Monotes* species, but in some it is truly minute (considered as absent by Duvigneaud 1949, 1961). We can conclude that there is indeed a tendency for the anther appendage to be well developed in *Monotes* but it can hardly serve as a diagnostic character at genus level. The same goes for the shape of the flower bud. Always cylindrical in *Marquesia* and generally conical in *Monotes*, but with some exceptions having an intermediate state. This leaves us with three characters which seem to be diagnostic at genus level. *Marquesia* has the outer petal surface glabrous or at most puberulent, a distinct androgynophore and incomplete locules. The latter character means the septae do not continue up to the tip of the ovarial cavity, but this character is sometimes very difficult to see in (rehydrated) herbarium material. *Monotes* has petals with a velvety outer surface, no androgynophore and completely separated locules. A new character came to our attention during this work, i.e. all *Monotes* species have fasciculate hairs on fruit wings (sometimes mixed with simple hairs), while *Marquesia* species have simple hairs only. Finally, all three *Marquesia* species have a fluted trunk (sometimes with buttresses) while this is never seen in *Monotes*, but this character is obviously of no use in the herbarium, except when supplied as part of the label information.

TABLE 1. Characters distinguishing *Monotes* and *Marquesia* according to the literature (Bancroft 1935, 1937; Duvigneaud 1961; Fries 1914a; Gilg 1925).

	<i>Marquesia</i>	<i>Monotes</i>
Twigs	furrowed	terete
Leaf blade	acuminate	rounded, emarginate or acute
Petals outside	± glabrous	silky or velvety hairy
Androgynophore	present	absent
Anther appendage	absent	present
Ovary locules	incomplete	complete
Fruit wall	thin	thick
Buttresses	present	absent

Morphometric analysis of the M. caloneurus-M. elegans complex

PC1 accounted for 27% of total variance and was positively correlated with leaf blade length, leaf blade width, petiole length and the density of hairs on lower surface of the leaf and negatively correlated with the density of hairs on the leaf upper surface and with the position of the largest leaf width. PC2 accounted for 13% of total variance and was positively correlated with the colour of the upper surface of the leaf, the length/width ratio of the leaf blade, fruit diameter and the length of the fruit wings. The projection of specimens on PC1-PC2 shows a more or less continuous pattern of variation (Fig. 1A), ranging from small-leaved specimens with denser indumentum on the upper surface of the leaf (left part of the scatter plot), to larger-leaved specimens with a more sparsely pubescent leaf upper surface and a thicker indumentum on the lower surface of the leaf (right part of the scatter plot). In conclusion, variation is essentially gradual, with considerable overlap between several *a priori* taxa. In particular, *M. elegans* and *M. schmitzii* form completely overlapping groups. *Monotes hypoleucus* tends to form a more distinct group, shifted towards positive values of PC1. *Monotes caloneurus* occupies a very large phenetic space, more or less intermediate between *M. schmitzii-M. elegans* on one hand and *M. hypoleucus* on the other hand. NMDS shows essentially the same pattern (Fig. 1B), confirming that *M. elegans*, *M. caloneurus* and *M. schmitzii* cannot be separated based upon the studied traits, and that *M. hypoleucus* forms a more distinct group. The two groups (i.e. *M. hypoleucus* vs. all other specimens) differ mostly in leaf size and the density of indumentum on lower and upper surface of leaf; the other traits are extremely variable within either group.

TABLE 2. *Marquesia-Monotes* character table.

Species	voucher	Herbarium	country/ region	petal indument outside	shape flowerbud	locules incomplete	androgynophore present	anther with appendage	filaments hairy	fruit pericarp
<i>Marquesia acuminata</i>	Fanshawe 3501	BR	Zambia	none	cylindrical	yes	yes	no	no	thick
<i>Marquesia excelsa</i>	McPherson 16289	BR	Gabon	none	cylindrical	yes	yes	no	no	thin
<i>Marquesia macroura</i>	Callens 4570	BR	DRC III	none	cylindrical	yes	yes	no	yes	thick
<i>Marquesia macroura</i>	Duvigneaud 797M	BRLU	DRC IV	puberulent	cylindrical	yes	yes	no	yes	thick
<i>Monotes adenophyllus</i>	Milne-Redhead 3923	BR	Zambia	velvety	conical	no	no	yes	no	thick
<i>Monotes africanus</i>	Schmitz 2181	BR	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes autenaei</i>	Lejoly 06/318bis	BRLU	DRC XI	velvety	conical	intermediate	no	nil/minute	no	thick
<i>Monotes dasyanthus</i>	Duvigneaud 3235M	BRLU	DRC XI	velvety	conical	no	no	nil/minute	no	thick
<i>Monotes doryphorus</i>	Duvigneaud 5269	BRLU	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes duvigneaudii</i>	Duvigneaud 5268	BRLU	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes engleri</i>	Fanshawe 4546	BR	Zambia	velvety	conical	no	no	minute	no	thick
<i>Monotes glaber</i>	Angus 966	BR	Zambia	velvety	intermediate	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>angolensis</i>	de Witte 3355	BR	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>caloneurus</i>	Reekmans 7671	BR	Burundi	velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>caloneurus</i>	Goldsmith 3/60	BRLU		velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>caloneurus</i>	BRLU0002856	BRLU	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>discolor</i>	BRLU0001993	BRLU	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>hypoleucus</i>	Duvigneaud 822	BRLU	DRC IV	velvety	conical	no	no	yes	no	thick
<i>Monotes katangensis</i>	De Giorgi s.n.	BR	DRC XI	velvety	conical	no	no	minute	no	thick
<i>Monotes kerstingii</i>	Jangoux 759	BR	Ivory Coast	velvety	intermediate	no	no	yes	no	thick
<i>Monotes madagascariensis</i>	Humbert 28621	BR	Madagascar	velvety	?	no	no	yes	no	thick
<i>Monotes magnificus</i>	FH 2255	BRLU	Tanzania	velvety	conical	no	no	yes	no	thick
<i>Monotes paivae</i>	Dechamps <i>et al.</i> 1389	BR	Angola	velvety	intermediate	no	no	yes	no	thick
<i>Monotes pearsonii</i>	Duvigneaud 5233BM	BRLU	DRC XI	velvety	conical	no	no	yes	no	thick
<i>Monotes hypoleucus</i> var. <i>discolor</i>	Schmitz 2132	BR	DRC XI	velvety	conical	no	no	yes	no	thick

From these analyses, it first appears that *M. schmitzii*, a putative endemic of Upper Katanga, cannot be maintained as a distinct taxon, even at a low rank. Secondly, *M. caloneurus* appears to represent a relatively heterogeneous, ill-defined assemblage, broadly overlapping with *M. schmitzii* + *M. elegans*. *Monotes caloneurus* and *M. elegans* are generally distinguished by leaf size (larger leaves in *M. caloneurus*), density of indumentum on lower surface (“curly” in *M. caloneurus* vs. “cottony” in *M. elegans*) and the indumentum on the upper surface (glabrescent in *M. caloneurus*, persistent in *M. elegans*). However, in the material from D.R. Congo, density of indumentum on both leaf surfaces shows a virtually continuous variation pattern and is combined in various ways. Moreover, we found indumentum density and leaf colour to be difficult to assess in a consistent way, as they vary considerably with leaf age. Duvigneaud himself was aware of these difficulties and left more than 20% of his collections in that complex without a name. Many of his collections also bear several names, a clear indication of Duvigneaud’s uncertainties and hesitations.

Finally, only the large-leaved forms with thick indumentum on the lower surface (“*M. hypoleucus*”) represent a relatively well defined group. Such variants are not evenly distributed across all of the Zambebian Region, being more widespread in Angola and D.R. Congo. They seem to deserve taxonomic recognition, even though intermediates with other forms also exist. In such a complex, we deem it biologically unjustified and practically unrealistic to discriminate taxa at the species level and because of the variation patterns described above, the varietal rank is thought to be the most appropriate. However, even at such a low rank, the limits of taxa are difficult to set on objective grounds. After checking the relevant type specimens, we now propose i) to merge *M. caloneurus*, *M. schmitzii* and *M. elegans* into a single taxon, and ii) to treat that taxon at varietal rank within *M. hypoleucus*. This corroborates earlier observations of Bancroft (1939a: 361), who emphasized the close relationships of *M. elegans* with both *M. caloneurus* and *M. hypoleucus*: “The Angolan forms of *M. elegans* are very similar to *M. hypoleucus*, and so, indeed, is the type specimen from Tanganyika; ...”, “...some of the more easterly forms of *M. elegans* are extremely difficult to separate from *M. caloneurus*, ...”, and “[*M. elegans*] thus seems to include a number of variable forms, intermediate between *M. caloneurus* and *M. hypoleucus*; ...”.

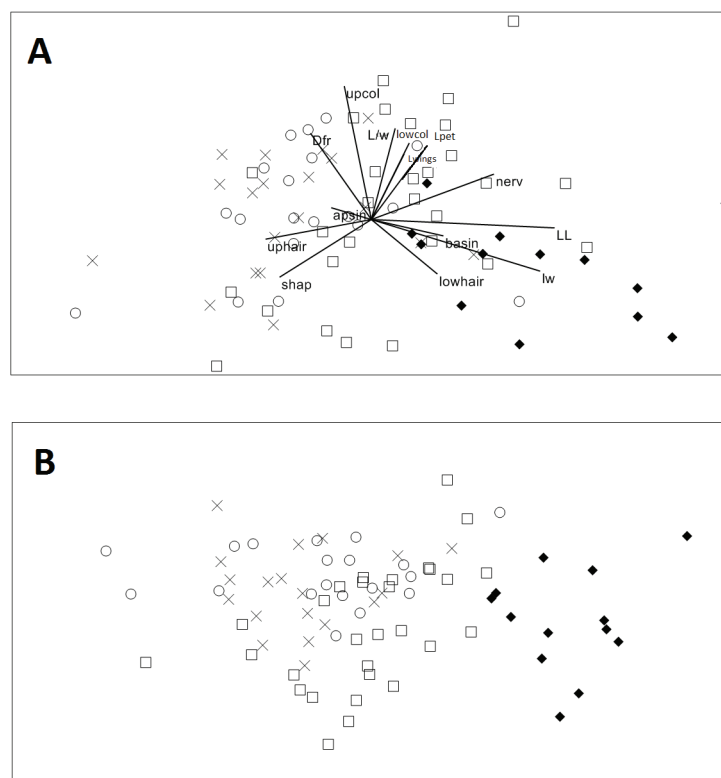


FIGURE 1. A. Principal Component Analysis of 14 variables. Projection of 81 samples on PC1 (27%) and PC2 (13%). Squares: *Monotes caloneurus*, circles: *M. elegans*, crosses: *M. schmitzii*, diamonds: *M. hypoleucus*. Apsin = depth of apical sinus, basin = depth of basal sinus, Dfr = fruit diameter, LL = Leaf length, Lw = leaf width, L/w = length/width ratio, lowcol = colour of lower surface of leaf, lowhair = density of hairs on lower surface, Lpet = petiole length, Lwings = length of calyx wings at fruiting stage, nerves = number of lateral nerves on one side of the midrib, shap = distance from base to largest width relative to leaf length, upcol = color of upper surface of leaf, uphair = density of hairs on upper leaf surface. **B.** Non metric multidimensional scaling, based on 14 variables. Projection of 81 samples on the first two axes. Squares: *Monotes caloneurus*, circles: *M. elegans*, crosses: *M. schmitzii*, diamonds: *M. hypoleucus*. See Appendix for the list of specimens included.

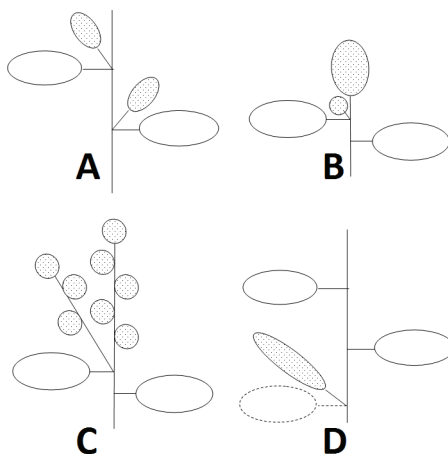


FIGURE 2. Inflorescence architecture in *Monotes*. **A.** Axillary cymes (*M. adenophyllus*, *M. africanus*, *M. doryphorus*, *M. hypoleucus*, *M. glaber*, *M. magnificus*, *M. pearsonii*). **B.** Short terminal congested panicle (often subtended by a variable number of axillary cymes) (*M. dasyanthus*, *M. duvigneaudii*, *M. hirtii*). **C.** Long terminal thyrses (*M. autennei*, *M. katangensis*). **D.** Axillary panicle or thyrses born below the leaves (*M. rubriglans* subsp. *upembensis*).

Taxonomic revision

A critical re-examination of Duvigneaud's rich collections proved to be most informative. Surprisingly, a comparatively high percentage of the specimens examined by Duvigneaud, amongst which many collected by himself, were left without a name. Many of these are intermediate and difficult to assign to a particular taxon. This corroborated our conclusion that Duvigneaud's taxonomic treatment showed important weaknesses. Even the few characters regarded by him as being taxonomically informative actually show a continuous pattern of variation. Virtually all character combinations are possible (which Duvigneaud himself acknowledged: "*Les combinaisons de caractères sont quasi infinies...*" (Duvigneaud 1949, p. 41). In this context, we feel that a too narrow species concept is both impractical and biologically unjustified. Our studies indicated that the limits of morphospecies are much less clear than generally assumed and that the genus has badly suffered from taxonomic inflation, with variants of minor importance being considered relevant at high taxonomic levels. Using a too narrow species concept would imply describing dozens of species to accommodate all the distinct character combinations within the reticulate variation pattern, which we deem not only useless, but also not complying with biological reality.

Accordingly, we here propose a much more synthetic treatment than earlier revisions. A justification of our decisions is provided below each taxon. The most significant changes include: i) merging *M. elegans* and *M. schmitzii* with *M. caloneurus*, and downgrading the latter to varietal rank within *M. hypoleucus*; ii) merging *M. carrissoanus*, *M. noldeae* and *M. oblongifolius* with *M. angolensis* and downgrading the latter to varietal rank within *M. hypoleucus*; iii) merging *M. adenophyllus* subsp. *delevoyi* with *M. adenophyllus* subsp. *adenophyllus* and *M. hutchinsonianus*, and downgrading this taxon and *M. adenophyllus* subsp. *homblei* to varietal rank; iv) downgrading *M. gigantophyllus* to varietal rank within *M. magnificus*; v) downgrading *M. mutetetwa* to varietal rank within *M. dasyanthus*; vi) downgrading *M. loandensis* to varietal rank within *M. hypoleucus*.

In total, 27 taxa are recognized for the study area, i.e. 13 species, 10 varieties and four forms. One species, one subspecies and three varieties are new to science and five are new to D.R. Congo. Some material may still represent additional new species, but is insufficient to draw a clear conclusion at this stage.

Contrary to all previous treatments which regarded reproductive characters as being taxonomically unimportant in the genus *Monotes*, we found inflorescence architecture to be informative and more constant within species than many vegetative characters, with four possible states (Fig. 2). The length of anther appendage is also of taxonomic value (inconspicuous in *M. autennei*, *M. dasyanthus* and *M. katangensis*, and clearly visible in all other species). We therefore propose two identification keys, one emphasizing leaf characters, and another one emphasizing reproductive characters.

Taxonomic treatment

Monotes De Candolle (1868: 623)

Type:—*Monotes africanus* (De Candolle 1868: 624).

Shrubs or medium-sized trees; bole without buttresses. Leaves rounded to emarginate or sometimes acuminate at the apex, with an extra-floral nectary at the base of the midrib above, indumentum of simple, fasciculate or stellate hairs that are straight, curved or coiled, and with additional spherical glandular hairs; venation generally densely reticulate beneath. Inflorescence of axillary cymes, sometimes grouped into axillary or terminal thyrses. Flower with sepals velvety or wholly tomentose outside and petals sericeous or velvety tomentose outside; flower bud generally ovoid; receptacle without androgynophore; stamens numerous, anthers short, connective generally with a short triangular to long ovate appendage or rarely only with a minute appendage; ovary hairy, completely (2)3- to 5-locular, with 2 ovules per locule; style 1, with 3 or 5 short stigmas. Fruit an achene, ± globose, with a thick and tough wall, surrounded by 5 subequal wings derived from the accrescent sepals, with fasciculate hairs.

A genus of about 20 species occurring throughout tropical Africa and in Madagascar, with its center of diversity in the Zambezi regional center of endemism (White 1983).

References:—Ashton (2003: 191); Bancroft (1935: 507; 1937: 132; 1939a: 330); Catarino *et al.* (2013: 264); De Wildeman (1927a: 163); Delevoy (1929: 325); Duvigneaud (1949: 39; 1961: 410); Gilg (1899: 127; 1908b: 287; 1925: 237); Verdcourt (1989: 4); White (1962: 258).

Keys to the species of *Monotes* in D.R. Congo

Important note:—The indumentum should be examined in mature, fully expanded, non-senescent, leaves; 20–40 times magnification is necessary. Leaves from coppice shoots should not be used.

Key 1, giving priority to vegetative characters

1. Leaf with basal gland reddish, with similar glands generally present in the axil of secondary nerves (sometimes concealed by hairs); bracts and stipules generally with a reddish tinge; leaf margin recurved and with an intra-marginal vein; flowers in thyrses, borne axillary on defoliated previous year's growth below the leaves 13a. *M. rubriglans* subsp. *upembensis*
- Leaf with basal gland brownish to blackish, with or without glands in the axil of nerves; bracts and stipules generally without reddish tinge; leaf margin recurved or not, with or without an intra-marginal vein; inflorescences terminal or flowers in pedunculate to subsessile cymes in the axils of leaves 2
2. Upper surface of the leaf pubescent, ± scaberulous; hairs straight, stiff or nearly so (somewhat curved and undulate in *M. pearsonii*), isolate or fasciculate, 0.15–1.5 mm long, discernible by touch (surface harsh to roughish), usually developing on cushion-like emergences of the leaf blade (Fig. 4A, B, D, E, F, G, J, P, Q; Fig. 5C, J, K); reticulation of the lower surface of leaf generally prominent and conspicuous, covered with more or less similar hairs 3
- Upper surface of the leaf glabrous (except on the nerves) (Fig. 4C, H, I, L, N, O), puberulent or tomentellous; hairs (if any) curled, undulate, vermiform, simple, fasciculate, or stellate, very short, mostly not exceeding 0.15 mm in length and not discernible by touch, not developing on cushion-like emergences (Fig. 4K, M; Fig. 5G, I); reticulation of the lower surface of leaf prominent or not, variously hairy or glabrous 9
3. Leaves broadly elliptic to suborbicular, nearly as broad as long ($l/w < 1.5$), rounded to distinctly emarginate at the apex; base truncate to distinctly cordate 4
- Leaves elliptic or oblong to oblong-obovate, at least 1.5 times longer than broad, with a tendency to become obtuse, acute or even acuminate at the apex; base cuneate to rounded or slightly cordate 6
4. Lower surface of the leaf with greyish to pale fulvous floccose-tomentose pubescence on the reticulum (Fig. 3R), areoles whitish, densely covered with stellate hairs; upper surface with simple hairs, mostly 0.5–1.5 mm long; leaf blade (12–)15–40 × (9–)13–30 cm, emarginate at the apex, distinctly cordate at the base (basal sinus > 1 cm), discolorous; glands in the axil of secondary nerves; petiole very thick (3–5 mm in diameter); fruit 13–30 mm in diameter (excluding wings) 11. *Monotes magnificus*
- Lower surface of the leaf tomentose, but not floccose, areoles pubescent or not; upper surface with hairs 0.15–0.8 mm long, all or some fasciculate; leaf blade 7–20 × 5–15 cm, emarginate to rounded at apex, truncate to cordate at base (basal sinus generally < 1 cm), discolorous or concolorous; glands present or absent in axils of secondary nerves; petiole more slender (≤ 3 mm in diameter); fruit 7–15 mm in diameter 5
5. Leaves bilobed or distinctly emarginate at the apex, with the apical sinus typically deeper than the basal one; indumentum of upper surface mostly of fascicles, each with 2–8 hairs, 0.15–0.30 mm long (Fig. 4D, 5C); leaf blade markedly coriaceous, below with

- distinctly prominent reticulation forming deep narrow cavities; inflorescences of subsessile cymes forming large terminal thyrses; anthers with inconspicuous appendage 3. *Monotes autennei*
- Leaves rounded or truncate to slightly emarginate at the apex, with the apical sinus not deeper than the basal one; upper surface of leaf with simple hairs mixed with fascicles of 2 or 3 hairs, 0.15–0.80 mm long (Fig. 4A,B); leaf blade not markedly coriaceous, reticulation of the lower surface not or moderately prominent, lax, not forming deep narrow cavities; inflorescences of axillary pedunculate to subsessile cymes; anthers produced into a conspicuous ovate or triangular appendage ... 1. *Monotes adenophyllus*
6. Leaf blade 3.4–9 × 1.2–4 cm, apex acute-acuminate; petiole 3–5(–10) mm long; reticulum of lower surface with stiff hairs only, areoles glabrous; leaf blade concolorous 8. *Monotes hirtii*
- Leaf blade larger, or, if < 9 × 4 cm, apex rounded; petiole 5–20 mm long; reticulum of lower surface with curly, flexuous or woolly hairs, areoles covered with stellate hairs or glabrous; leaf blade discolorous or concolorous 7
7. Upper surface harsh or roughish (at least when young) with stiff hairs (sometimes mixed with stellate hairs), 0.2–1 mm long, straight, solitary, usually not mixed with glands; lower surface of leaf beige to fulvous, with prominent reticulum forming cavities; nerves and reticulum hirsute, with straight or flexuous hairs; anther with inconspicuous appendage 8
- Upper surface soft to the touch, hairs just perceptible, short (0.15–0.4 mm long), curved to undulate, solitary or in pairs, mixed with many yellow sessile glands (Fig. 4R); lower surface of leaf whitish to greyish, reticulum not prominent, not forming cavities; nerves and reticulum sparsely pubescent, with curly, cottony or crispate hairs; anther produced into a conspicuous appendage 12. *Monotes pearsonii*
8. Leaf apex rounded to emarginate; upper surface of leaf with hairs 0.2–0.6 mm long, glabrescent; inflorescence of subsessile condensed cymes forming terminal showy thyrses up to 15 cm long, generally exceeding the uppermost leaf 10. *Monotes katangensis*
- At least some leaves with acute to acuminate apex; upper surface of leaf with hairs 0.4–1 mm long, persistent; inflorescence of remote subsessile clusters, more or less grouped at the end of twigs in a short congested panicle (< 6 cm long) much shorter than the uppermost leaf 4. *Monotes dasyanthus*
9. Leaf apex acute to narrowly acuminate 10
- Leaf apex obtuse to rounded or emarginate at tip, or rarely bluntly acuminate 11
10. Lower surface of leaf strongly discolorous, whitish (Fig. 3I), with a continuous layer of small stellate hairs (rarely concolorous and glabrous in var. *concolor* (Fig. 3J)); blade (6–)7.5–13 × (2–)3.5–5.5 cm; inflorescence of condensed cymes generally grouped in a small congested terminal panicle 6. *Monotes duvigneaudii*
- Lower surface of leaf concolorous and glabrous; blade (3–)4–10(–13) × (0.7–)1.5–3.6 cm; inflorescence of loose axillary cymes 5. *Monotes doryphorus*
11. Leaf blade glabrous and concolorous 7. *Monotes glaber*
- Leaf blade pubescent at least on lower surface, discolorous or concolorous 12
12. Interreticular areoles of lower surface of leaf hairy, blade more or less discolorous, with lower surface whitish, greyish, yellowish or beige; upper surface reticulate or smooth, glabrous or puberulent; leaf blade usually not bullate in the axil between primary and secondary nerves 13
- Interreticular areoles of lower surface of leaf glabrous, blade concolorous; upper surface reticulate, glabrous; leaf blade bullate in the axil between primary and secondary nerves 2. *Monotes africanus*
13. Upper surface of leaf markedly reticulate, with many yellow spherical glands, with indumentum slightly perceptible to the touch, comprising a mixture of short, simple and paired, more or less erect, curved or flexuous hairs (0.2–0.4 mm long) (Fig. 4R); inflorescence of narrow racemiform cymes 1–4 cm long, 1–1.5 cm wide 12. *Monotes pearsonii*
- Combination of traits different: upper surface of leaf not reticulate or, when reticulate, glabrous; hairs (when present) not perceptible to the touch, not exceeding 0.2 mm in length (Fig. 4K–O); inflorescence of larger and looser cymes .. 9. *Monotes hypoleucus* s.l.

Key 2, giving priority to reproductive characters

1. Inflorescences terminal, at the tips of vegetative twigs, above the leaves, often accompanied by a few axillary cymes (Fig. 2B,C) 2
- Inflorescences axillary (Fig. 2A,D) 6
2. Inflorescence a congested panicle 2–6(–8) cm long, not much longer than wide, not exceeding the leaves (Fig. 2B); some or all leaves acute to acuminate 3
- Inflorescence of one to several elongate thyrses 5–15 cm long, much longer than wide, exceeding the leaves (Fig. 2C); all leaves rounded to emarginate 5
3. Upper surface of leaf glabrous 6. *Monotes duvigneaudii*
- Upper surface of leaf pubescent, harsh to the touch 4

4. Anther with a conspicuous apical appendage; leaf blade 3.4–9 × 1.2–4 cm; petiole 3–5(–10) mm long 8. *Monotes hirtii*
 - Anther with inconspicuous appendage; leaf blade 6–14(–20) × 3–8(–12) cm; petiole 10–30 mm long 4. *Monotes dasyanthus*
5. Leaves bilobed or deeply emarginate at the apex, with the apical sinus typically deeper than the basal one; indumentum of upper surface mostly of fascicles, each with 2–8 hairs 3. *Monotes autennei*
 - Leaves rounded to slightly emarginate at the apex; indumentum of upper surface of simple hairs 10. *Monotes katangensis*
6. Inflorescence a thyrse up to 11 cm long borne axillary on defoliated previous year's growth below the leaves, with a few leaf-like bracts (Fig. 2D); bracts reddish; basal gland red 13a. *Monotes rubriglans* subsp. *upembensis*
 - Inflorescence of cymes at the axil of leaves, without leaf-like bracts (Fig. 2A); bracts generally brownish; basal gland brownish to blackish 7
7. Upper surface of leaf harsh or roughish to the touch, with stiff hairs, 0.15–1.5 mm long; leaf blade broadly elliptic to suborbicular, nearly as broad as long ($l/w < 1.5$), rounded to distinctly emarginate at the apex 8
 - Upper surface of leaf glabrous or with hairs not or slightly perceptible to the touch, 0.10–0.30 mm long; leaf blade elliptic to obovate ($l/w > 1.5$), acuminate, rounded to slightly emarginate at the apex Go to couplet 9 of Key 1
8. Fruit 13–30 mm in diameter (excluding wings); fruit wings 4.5–11 cm long; leaf lower surface with floccose-tomentose pubescence usually masking areoles (Fig. 3R); upper surface with simple hairs, mostly 0.5–1.5 mm long (Fig. 4Q); leaf blade (12–)15–40 × (9–)13–30 cm, emarginate at the apex, distinctly cordate at the base (basal sinus > 1 cm), discoloured; glands always present in the axil of secondary nerves; petiole very thick (3–5 mm in diameter) 11. *Monotes magnificus*
 - Fruit 7–15 mm in diameter (excluding wings); fruit wings 2.5–5 cm long; leaf lower surface more or less tomentose, but not floccose, not masking areoles (Fig. 3A,B); upper surface with hairs 0.15–0.8 mm long, all or some fasciculate (Fig. 4A,B); leaf blade 7–20 × 5–15 cm, emarginate to rounded at apex, truncate to cordate at base (basal sinus generally < 1 cm), discoloured or concolorous; glands present or absent in axils of secondary nerves; petiole more slender (≤ 3 mm in diameter) 1. *Monotes adenophyllus*

1. *Monotes adenophyllus* Gilg (1895: 275; 1899: 135); Engler (1921: 522)

Type:—TANZANIA. Ugogo, Pori, Pa-Kabombue, in trockener Steppe, *Böhm 31a* (holo-: B†; photo: BM!, BRLU!, K!).

Small tree up to 8 m (?); branchlets brownish, tomentellose. Leaf: petiole 10–30 mm long, 2–3 mm in diameter; blade rounded to shortly ovate, more rarely broadly ovate-elliptic, with length to width ratio typically < 1.5, truncate to slightly cordate at the base, rounded, truncate to slightly emarginate at the apex, 6–16(–19) × 4–13(–15.5) cm, concolorous or discoloured; secondary nerves 9–11(–13) pairs; upper surface ± scaberulous, reticulate, with hairs fasciculate and simple, (0.15–)0.2–0.7 mm long, clearly discernible by touch (surface harsh or roughish), developed on cushion-like emergences of the leaf blade, sometimes only sparsely pilose and glabrescent; secondary nerves above without glands at the axils, reticulum more or less impressed, often giving a quilted or bullose appearance; lower surface with reticulum prominent or not, glabrous to relatively densely hairy, with hairs 0.2–1.5 mm long, straight, flexuous, curly to crispate, sometimes almost woolly, shorter to longer than areole diameter; areoles 1–2 mm in diameter, glabrous or with stellate hairs, often with yellow glands. Inflorescences 2–12 cm long, axillary, brown-tomentellous, lax, on a 1–3(–6) cm long peduncle; pedicels 2–5 mm long. Flower: sepals 2.5–3.5 mm long, rufous-cottony-tomentose; petals densely sericeous-tomentose, 5–11 × 2.5–3.5 mm; stamens with anthers produced in a conspicuous apical appendage. Fruit subglobose, 12–15 mm in diameter, subsericeous-tomentellous, mucronate at the apex; wings generally broadly elliptic to obovate, sometimes oblong and narrower, (1.5–)2.5–5(–7) × 1–3 cm, yellow to brownish or, more rarely, purplish.

Discussion:—*Monotes adenophyllus* shows extensive variation in indumentum of the lower surface of the leaf, including forms that are almost completely glabrous. Duvigneaud (1949, 1961) recognized four infraspecific taxa (by order of decreasing pubescence: “*albidus*”, “*homblei*”, “*paucipilosus*”, “*glabrescens*”). However, the variation is essentially quantitative and extremely difficult to classify. A more synthetic treatment, with only two varieties is much more realistic. Due to the virtually continuous pattern of variation, and considering that those taxa are apparently sympatric over most of their fairly large distribution range, the rank of variety seems more appropriate than the rank of subspecies adopted by Duvigneaud (1961) and later authors (Verdcourt 1989; Catarino *et al.* 2013).

Key to the varieties:

1. Areoles glabrous; leaf blade concolorous 1a. var. *adenophyllus*
 - Areoles with stellate hairs; leaf blade more or less discoloured 1b. var. *homblei*

1a. *Monotes adenophyllus* Gilg var. *adenophyllus*

= *Monotes adenophyllus* Gilg subsp. *adenophyllus* (Verdcourt 1989: 7; Lebrun & Stork 1991: 144), *syn. nov.*

= *Monotes delevoiyi* De Wildeman (1927a: 171); Bancroft (1935: 512; 1939a: 344) ≡ *Monotes adenophyllus* Gilg subsp. *delevoiyi* (De Wild.) Duvigneaud (1959: 101; 1961: 413); Catarino *et al.* (2013: 266); Lebrun & Stork (1991: 144); White (1962: 263; fig. 46C). Type:—D.R. CONGO. Masolwa, 17 December 1921, *Delevoiy 524* (holo-: BR! [barcode BR0000008891600]), iso-: BRLU!), *syn. nov.*

= *Monotes verdicki* De Wildeman (1927a: 183, 1927b: 57); Bancroft (1935: 512; 1939a: 346). Type:—D.R. CONGO. Lukafu, February 1900, *Verdick 374* (holo-: BR! [barcode BR0000008899576]), *syn. nov.*

= *Monotes hutchinsonianus* Exell (1932: 219); Bancroft (1937: 138; 1939a: 353); Lebrun & Stork (1991: 144); Catarino *et al.* (2013: 269); Duvigneaud (1949: 57); Figueiredo & Smith (2008: 67). Type:—ANGOLA. Malange, 27 December 1930, *Gossweiler 9581* (BM! [barcode BM000603406], BRLU (fragm.!), COI!, K! [barcode K000240349], LISC! [barcode LISC019573]), *syn. nov.*

= “*Monotes pwetoensis* Robyns” in *schedis*, unpublished designation (Bancroft 1939a: 367), *syn. nov.*

= *Monotes magnificus* Gilg var. *glabrescens* Duvigneaud (1949: 54). Type as *Monotes delevoiyi*, *syn. nov.*

= *Monotes magnificus* Gilg var. *paucipilosus* Duvigneaud (1949: 55, Pl. 13: b,c). Lectotype (designated here):—D.R. CONGO. Katanga, Kinda, forêt claire à *Brachystegia* sur sable argileux blanc, 5 August 1948, *Duvigneaud 1131M* (lecto-: BRLU! [barcode BRLU0000090022302], isolecto-: BRLU! (4 sheets)), *syn. nov.*

= *Monotes adenophyllus* Gilg subsp. *subfloccosus* Duvigneaud (1959: 102); Duvigneaud (1961: 414). Type:—ZAMBIA. Northern Prov., Fort Rosebery-Luwingu road, 19 May 1931, *Stevenson 247/31* (holo-: FHO! [barcode 00006099], iso-: K!, NDO), *syn. nov.*

Diagnosis:—Leaf blade concolorous; areoles of lower surface of leaf glabrous or with a few stellate hairs; reticulum of lower leaf surface with hairs 0.2–1 mm long, shorter than or equalling areole diameter and not hiding areoles.

Illustrations:—Figs. 3A, 4A, 5A, 6B–D.

Distribution in D.R. Congo:—Widespread in Upper Katanga, though less common than var. *homblei*.

Distribution elsewhere:—Angola, Tanzania, Zambia.

Habitat and ecology:—Miombo woodland and bushy savannah, often on shallow lateritic or skeletal schistose substrate.

Vernacular names:—Ki(m)papa (Bemba).

Other representative specimens examined:—D.R. CONGO. Upper Katanga: Plaine de la Lufira, au N de Lukafu, forêt claire à *Julbernardia globiflora*, sur terre rose, 17 July 1948, *Duvigneaud 1259M* (BRLU!); Fungurume, forêt enrochée à *Brachystegia bussei*, 1956, *Duvigneaud & Timperman 2619* (BRLU!); territ. Lubudi, Kanoni, forêt à *Brachystegia bussei* sur macigno, 3 June 1957, *Duvigneaud 3378M* (BRLU!); Likasi, colline boisée de la série des mines à *Julbernardia paniculata* et *Brachystegia utilis*, 18 June 1957, *Duvigneaud 3586M* (BRLU!); Katofio (Kilwa), forêt sèche à *Julbernardia paniculata*, sol beige sur cuirasse latéritique, 1957, *Duvigneaud 3625M* (BRLU!); Mpwa, 10 km N Tinika, steppe arbustive suffrutescente à *Brachystegia nain* sur schistes psammitiques, 1957, *Duvigneaud 3639M* (BRLU!); Lukunki, savane à *Themeda* sur pente rocheuse calcaire, 11 January 1960, *Duvigneaud 4998M* (BRLU!); 20 km N de Bunkeya, haute savane arbustive sur dalle latéritique d’alluvions anciennes, 14 January 1960, *Duvigneaud 5044M* (BRLU!); Muvulu, verger à *Monotes* sur schiste à schistosité horizontale, 15 January 1960, *Duvigneaud 5059M* (BRLU!); 20 km S Kiubo, verger à *Monotes adenophyllus*, 17 January 1960, *Duvigneaud 5112M* (BRLU!); Kundelungu, under trees, 13 March 1908, *Kassner 2605* (BM!); 6 km NE Gombela, forêt claire, 26 May 1984, *Malaisse 13000* (BR!); Environs de Pweto, 1926, *Robyns 1954* (K!); 26 km de Jadotville vers Kolwezi, alluvions assez récentes, exondées, anciennement cultures, savane à hautes graminées, 17 April 1958, *Schmitz 5971* (BR!); Kampinda, km 24 route Balanga-Musosa, savane arborée, alt. 980 m, 17 June 1957, *Symoens 4058* (BRVU!); Upemba, *Vandenbrande K9* (BR!).

Discussion:—Forms with leaves showing a sparsely pilose lower reticulum have usually been recognized as *Monotes adenophyllus* subsp. *delevoiyi*, but Verdcourt (1989) already questioned the status of that taxon. However, variation in density and length of hairs on the reticulum is continuous and we have not been able to set the objective limits of “*delevoiyi*” and conclude that this taxon cannot be maintained.

Monotes hutchinsonianus, an enigmatic species said to be endemic of Angola, is a large-leaved form, with a deeply cordate leaf base and long inflorescences. Such forms are not rare in Upper Katanga (e.g. *Duvigneaud & Timperman 2123* (BRLU!); *Huart 11* (BR!); *Malaisse 11286* (BR!)); they are linked to smaller-leaved forms by many intermediates. Thus, *M. hutchinsonianus* is here merged with *M. adenophyllus* var. *adenophyllus*. Bancroft (1937) already suggested that *M. hutchinsonianus* and *M. delevoiyi* might be conspecific. Significantly, the type specimen of *M. hutchinsonianus* shows an extremely variable leaf shape, some of the leaves being very close to those of the type specimen of *M. glandulosus* (oblong-elliptic, obtuse at base and rounded at apex) and others to *M. adenophyllus*

(broadly ovate, cordate at base) (see e.g. the isotypes, barcode BM000603406 and barcode LISC019573). *Robyns 1954*, the specimen carrying the designation “*M. pwetoensis* Robyns” (*in schedis, unpubl.*) from Katanga was ascribed to *M. hutchinsonianus* by Bancroft and to *M. adenophyllus* by Duvigneaud, illustrating that species limits in the *M. glandulosus* group are very difficult to set.

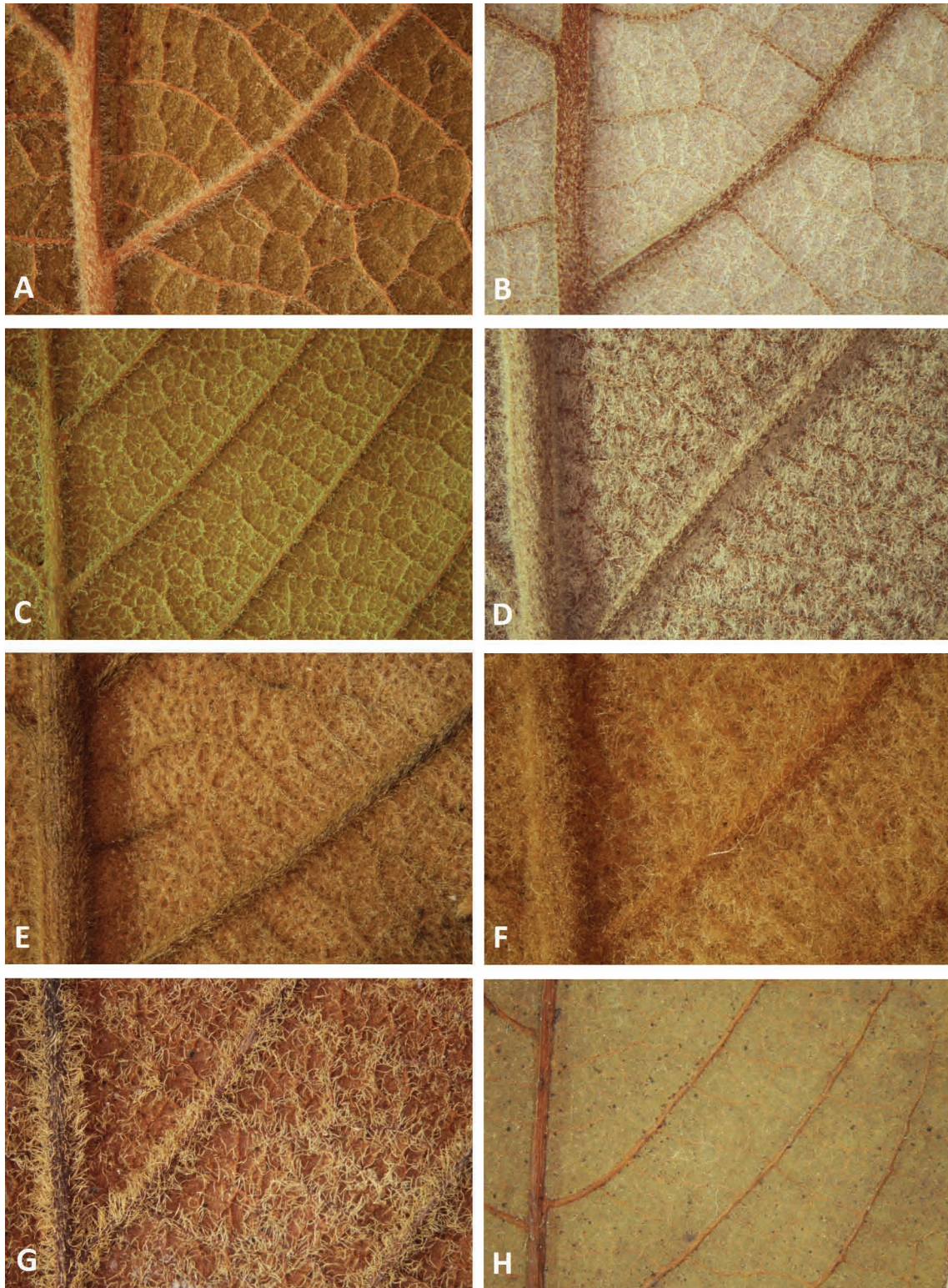


FIGURE 3 A–H. Details of lower surface of the leaf. **A.** *Monotes adenophyllus* var. *adenophyllus* (Duvigneaud 5112). **B.** *M. adenophyllus* var. *homblei* (Duvigneaud 4601). **C.** *M. africanus* (Duvigneaud 2006). **D.** *M. autennei* (Duvigneaud 5260). **E.** *M. dasyanthus* var. *dasyanthus* (Duvigneaud & Timperman 2341). **F.** *M. dasyanthus* var. *heterotrichus* (Duvigneaud 1141). **G.** *M. dasyanthus* var. *mutetetwa* (Duvigneaud 950). **H.** *M. doryphorus* (Duvigneaud 5267).

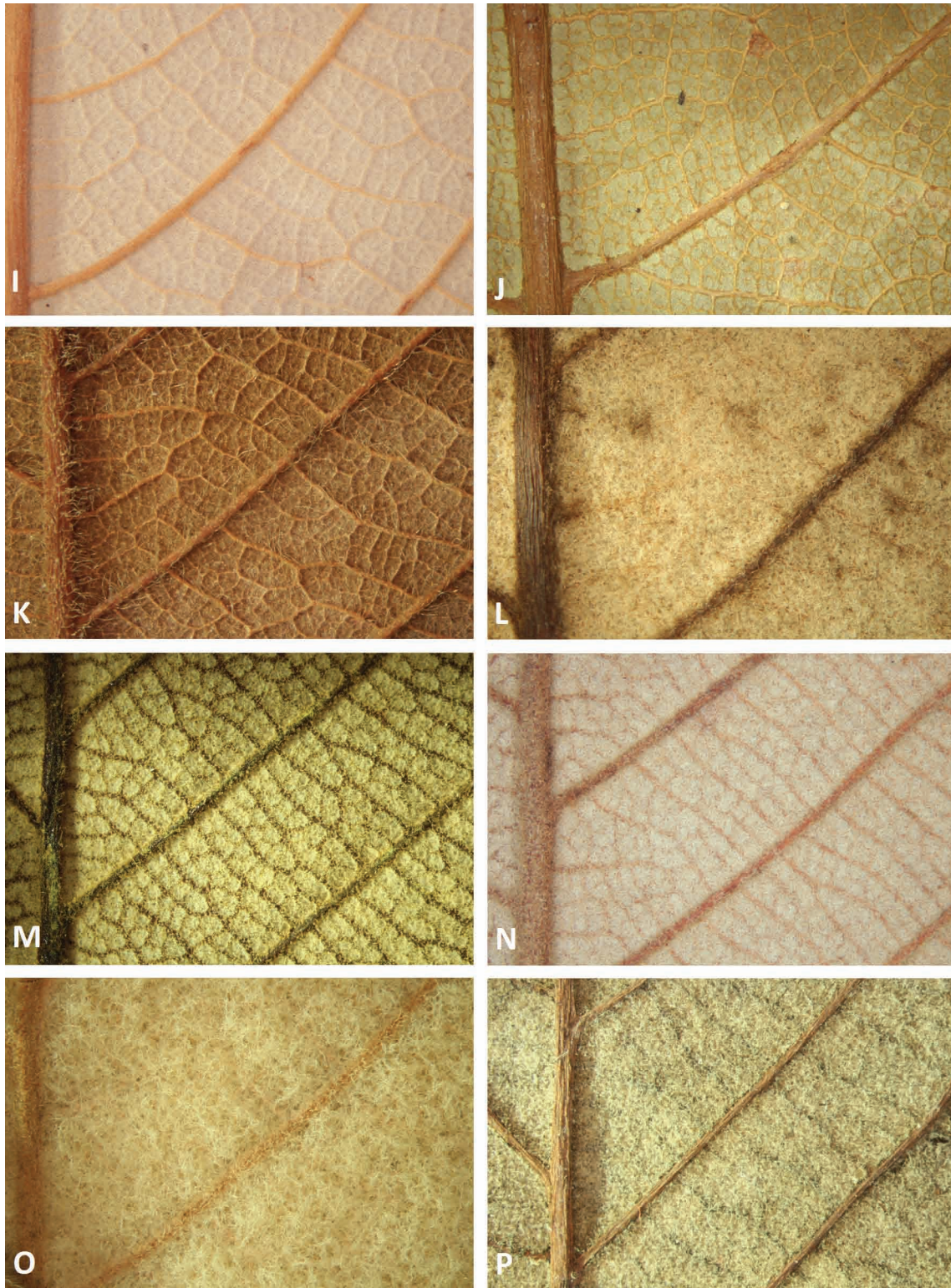


FIGURE 3 I–P. **I.** *M. duvigneaudii* var. *duvigneaudii* (Duvigneaud 4270M3). **J.** *M. duvigneaudii* var. *concolor* (Desenfans 3509). **K.** *M. hirtii* (Duvigneaud 3513). **L.** *M. hypoleucus* var. *hypoleucus* (Duvigneaud 822). **M.** *M. hypoleucus* var. *angolensis* (Duvigneaud 4518). **N.** *M. hypoleucus* var. *caloneurus* (Duvigneaud 5362). **O.** *M. hypoleucus* var. *discolor* (Schmitz 2132). **P.** *M. hypoleucus* var. *loandensis* (Duvigneaud 856M).

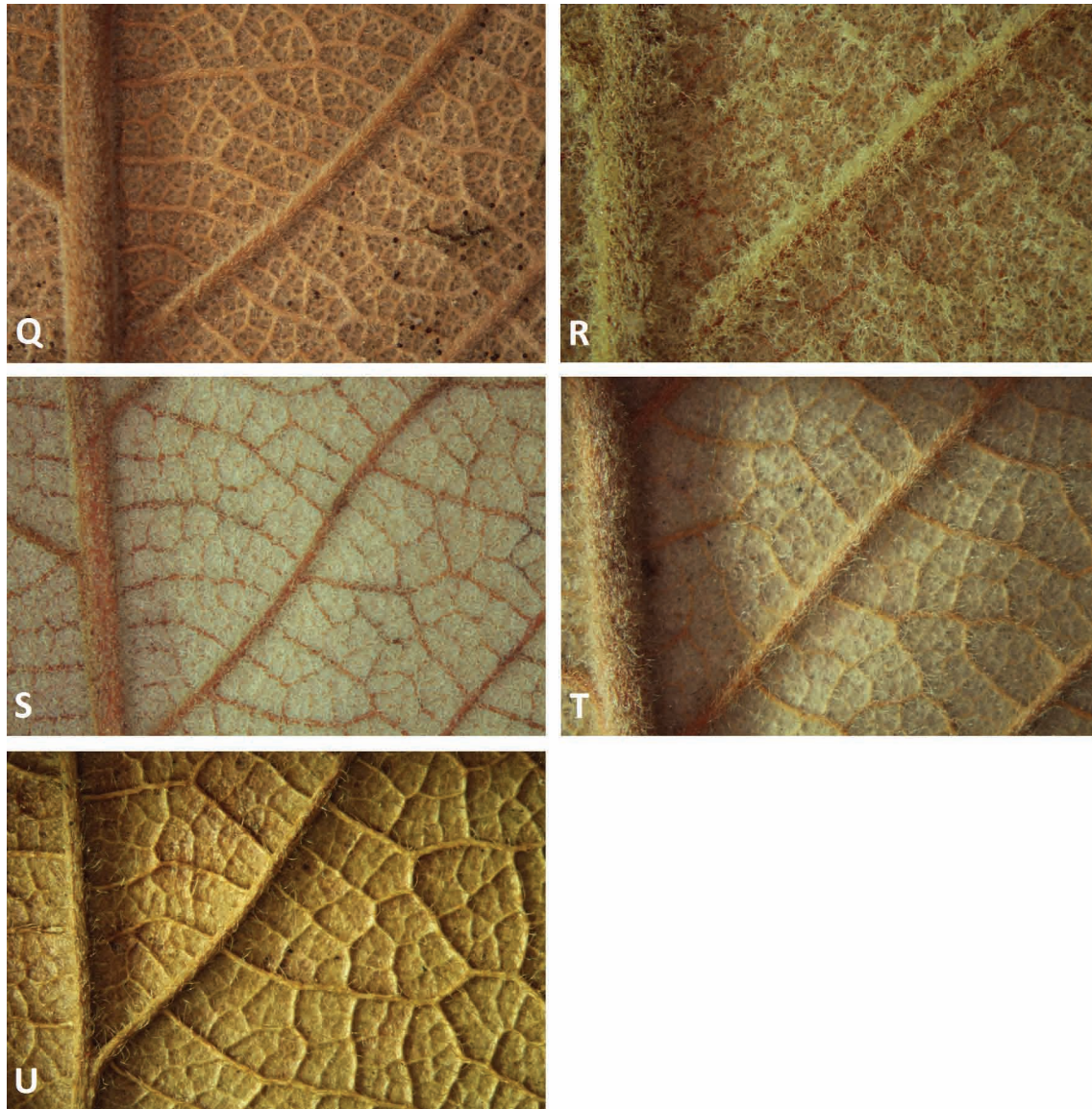


FIGURE 3 Q–U. **Q.** *M. katangensis* (Duvigneaud & Timperman 2641). **R.** *M. magnificus* var. *magnificus* (Duvigneaud 4826). **S.** *M. pearsonii* (Duvigneaud 5233). **T.** *M. rubriglans* subsp. *upembensis* var. *upembensis* (Desenfans 3703). **U.** *M. rubriglans* subsp. *upembensis* var. *griseocoriaceus* (Desenfans 3724). Each picture is 15 × 10 mm.

A morph of *Monotes adenophyllus* Gilg said to have a special type of hairs giving a subfloccose appearance to the lower surface of the leaf has been recognized as subsp. *subfloccosus* by Duvigneaud, but it is very difficult to define and is therefore not recognized here.

1b. *Monotes adenophyllus* Gilg var. *homblei* (De Wild.) Meerts, *comb. et stat. nov.*

Basionym: *Monotes homblei* De Wildeman (1915: 55); De Wildeman (1921: 133; 1927a: 175); Bancroft (1935: 512; 1937: 139; 1939a: 344). ≡ *Vatica homblei* De Wildeman (1915: 55). ≡ *Monotes magnificus* Gilg var. *homblei* (De Wild.) Duvigneaud (1949: 55, Pl. 13: a). ≡ *Monotes adenophyllus* Gilg subsp. *homblei* (De Wild.) Duvigneaud (1959: 102); Lebrun & Stork (1991: 144); Catarino *et al.* (2013: 266); Duvigneaud (1961: 414); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144); Meerts (2016: 222); Verdcourt (1989: 8); White (1962: 263).

Lectotype (designated here):—D.R. CONGO. Kapiri Valley, February 1913, *Homblé 1177* (lecto-: BR! [barcode BR000008891631]).

Diagnosis:—Differs from the type variety by the more or less discoloured leaf blade, with areoles of the lower surface of the leaf covered with stellate hairs; upper surface with indumentum often denser, more persistent and with a larger proportion of fasciculate hairs.

Leaf blade 6–16 × 4–13 cm, upper surface with reticulum markedly impressed, with hairs in fascicles of mostly

2 or 3, 0.15–0.4 mm long; lower surface discolorous, typically ash-grey, more rarely whitish, with short fasciculate hairs on the nerves mixed with long curled solitary hairs 1–1.5 mm long on the nerves and reticulation, those longer than areole diameter (areoles generally < 1 mm in diameter); interreticular areoles more or less densely covered with small stellate hairs; indumentum of reticulum and nerves often more or less fulvous, contrasting with the greyish indumentum of areoles.

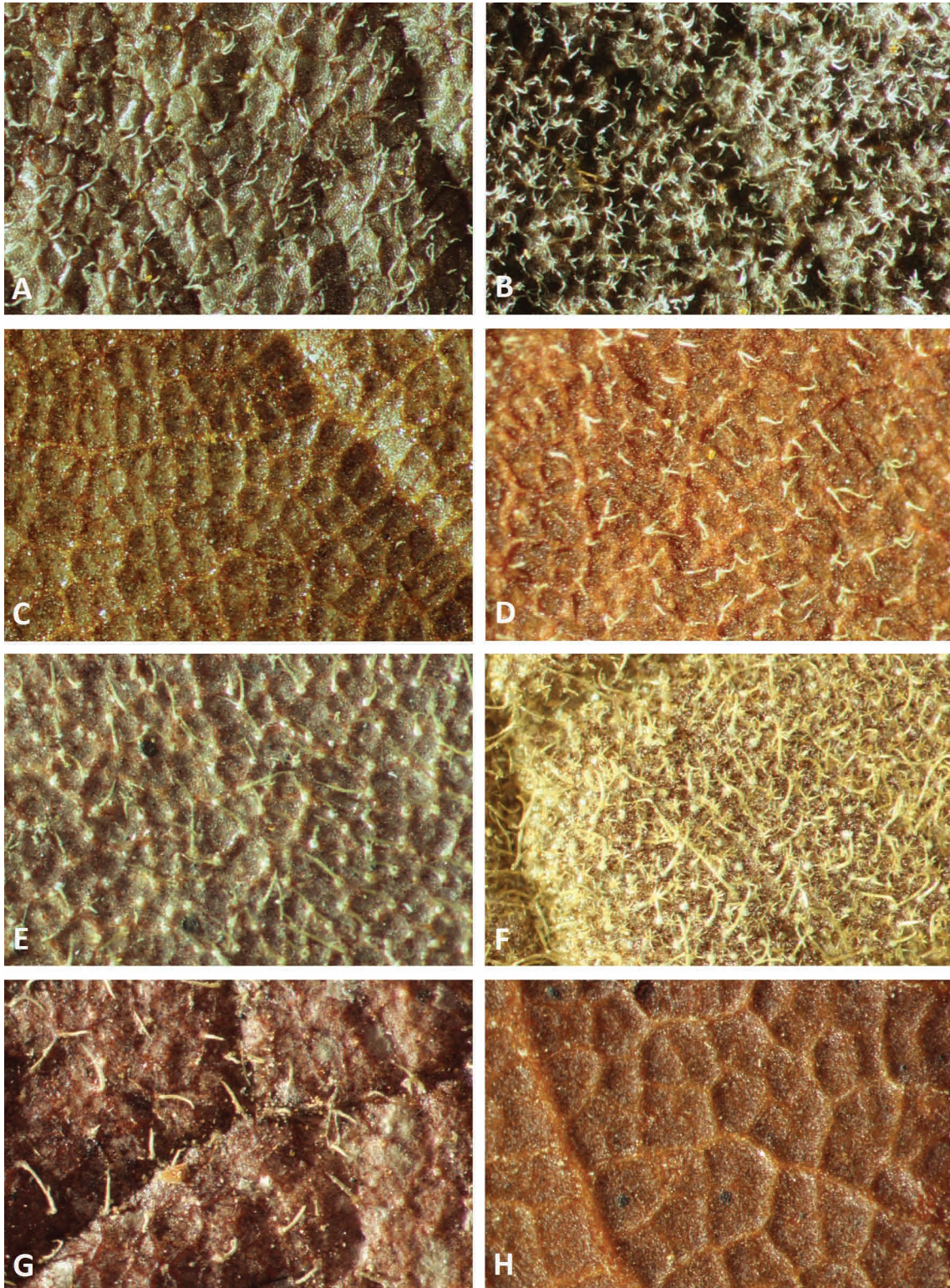


FIGURE 4 A–H. Details of upper surface of the leaf. **A.** *Monotes adenophyllus* var. *adenophyllus* (Duvigneaud 5044). **B.** *M. adenophyllus* var. *homblei* (Duvigneaud 4570). **C.** *M. africanus* (Duvigneaud 2006). **D.** *M. autennei* (Plancke 111/1532). **E.** *M. dasyanthus* var. *dasyanthus* (Duvigneaud & Timperman 2341). **F.** *M. dasyanthus* var. *heterotrichus* (Duvigneaud 4493). **G.** *M. dasyanthus* var. *mutetetwa* (Duvigneaud 950). **H.** *M. doryphorus* (Duvigneaud 5267).

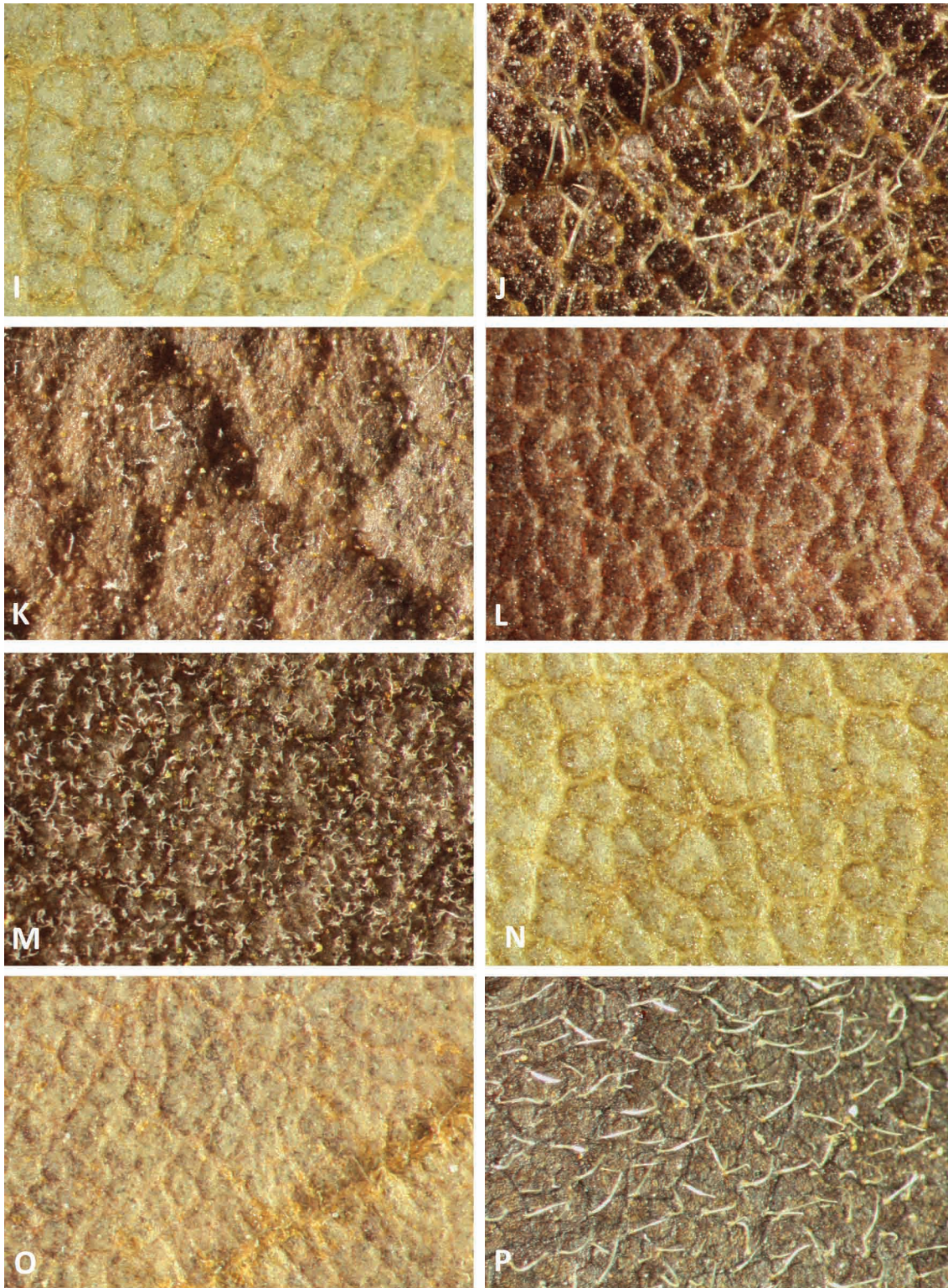


FIGURE 4 I–P. **I.** *M. duvigneaudii* var. *concolor*. **J.** *M. hirtii* (Duvigneaud 3513). **K.** *M. hypoleucus* var. *hypoleucus* (Duvigneaud 822). **L.** *M. hypoleucus* var. *angolensis* (Duvigneaud 5212). **M.** *M. hypoleucus* var. *caloneurus* (Duvigneaud 4850). **N.** *M. hypoleucus* var. *discolor* (Schmitz 2132). **O.** *M. hypoleucus* var. *loandensis* (Duvigneaud 856M). **P.** *M. katangensis* (Duvigneaud & Timperman 2641).

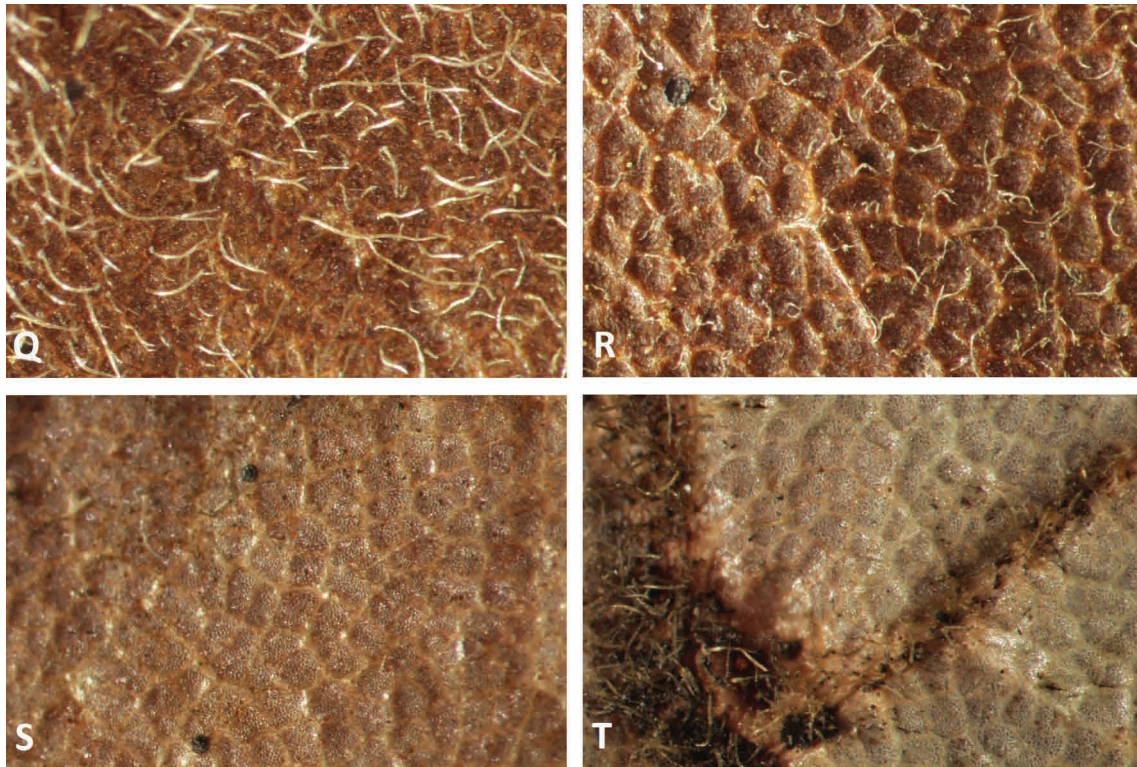


FIGURE 4 Q–T. **Q.** *M. magnificus* var. *magnificus* (Duvigneaud 4826). **R.** *M. pearsonii* (Duvigneaud 5233). **S.** *M. rubriglans* subsp. *upembensis* var. *upembensis* (Desenfans 3703). **T.** *M. rubriglans* subsp. *upembensis* var. *griseocoriaceus* (Desenfans 3724). Each picture is 3.3 × 2.2 mm.

Note:—*Homblé 1249* (BR!, K! (fragm.)), one of the two syntypes, has only sparse stellate hairs, and thus appears somewhat intermediate between var. *adenophyllus* and var. *homblei*. *Homblé 1177* is markedly discolorous and better represents the more usual state in specimens from Katanga. Therefore, *Homblé 1177* is here chosen as the lectotype of *Monotes homblei*.

Variation:—Var. *homblei* is very variable in colour of the lower surface of the leaf and density of the indumentum. Two forms can be recognized, with a range of intermediates.

Key to the forms:

1. Lower surface of leaf whitish; reticulum of lower surface with long woolly hairs 1ba. forma *albidus*
- Lower surface of leaf greyish; reticulum of lower surface with indumentum shorter, not woolly 1bβ. forma *homblei*

1ba. *Monotes adenophyllus* Gilg var. *homblei* (De Wild.) Meerts forma *homblei*

Diagnosis:—Lower surface of leaf greyish; indumentum of reticulum of lower surface shorter, not woolly.

Illustrations:—Figs 3B, 4B, 6A.

Distribution in D.R. Congo:—Widespread in Upper Katanga.

Distribution elsewhere:—Angola, Tanzania, Zambia.

Habitat and ecology:—Miombo woodland, wooded savannah, dambos, usually on shallow lateritic soil or rocky substrate.

Vernacular names:—Mupanga, mupanpa, mutalela (Lukafu).

Representative specimens examined:—**D.R. CONGO. Upper Katanga:** 15 km E de Menda, forêt-dembo à *Uapaca*, *Monotes*, sur latérite, 23 July 1956, *Duvigneaud & Timperman 2104* (BRLU!); Colline Kungarumembe, E de Kasompi, 30 July 1956, *Duvigneaud & Timperman 2182* (BRLU!); 25 km S Kolwezi, forêt claire à *Brachystegia* cf. *gossweileri* et *B. spiciformis*, 16 December 1959, *Duvigneaud, 4604M* (BRLU!); Nzilo, forêt-verger à *Monotes* sur pente faible, dans complexe rocheux des Kibara, 27 January 1960, *Duvigneaud 5260M* (BRLU!); Nzilo, forêt verger à *Monotes* sur pente faible dans le complexe rocheux des Kibara, 27 January 1960, *Duvigneaud 5620M* (BRLU!); Route

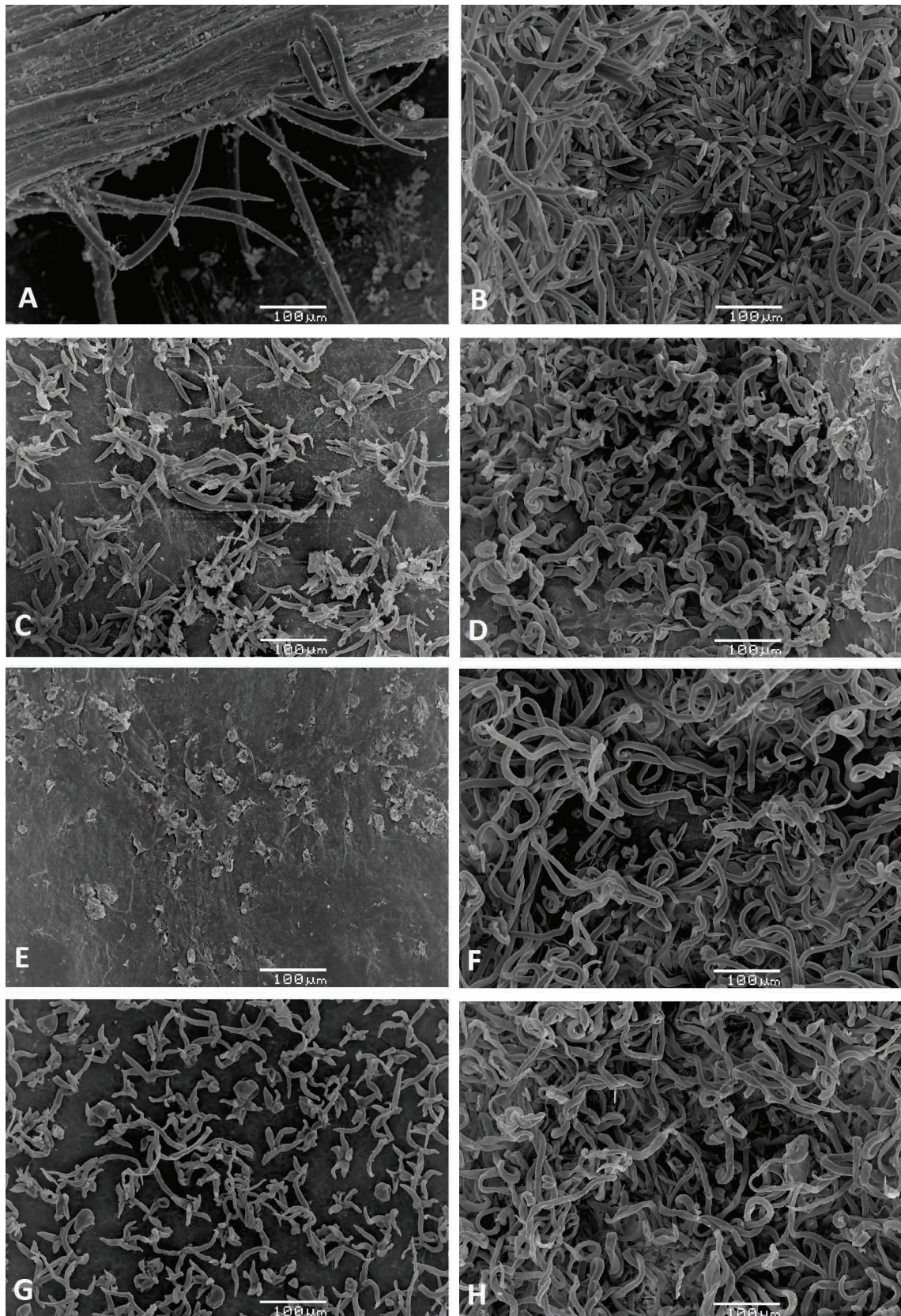


FIGURE 5 A–H. SEM photographs of leaf blade surfaces for 12 members of *Monotes*. **A.** *M. adenophyllus* var. *adenophyllus*, lower surface (*Delevoy* 524, type of *M. delevoyi*). **B.** *M. autennei*, lower surface (*Duvigneaud* 3267 (type of *M. autennei*)). **C.** *M. autennei*, upper surface (*Duvigneaud* 3267). **D.** *M. hypoleucus* var. *angolensis*, lower surface (*Duvigneaud* 950M2, type of *M. oxyphyllinus*). **E.** *M. hypoleucus* var. *angolensis*, upper surface (*Duvigneaud* 950M2). **F.** *M. hypoleucus* var. *caloneurus*, lower surface (*Schmitz* 1332 (type of *M. schmitzii*)). **G.** *M. hypoleucus* var. *caloneurus*, upper surface (*Schmitz* 1332 (type of *M. schmitzii*)). **H.** *M. hypoleucus* var. *hypoleucus*, lower surface (*Welwitsch* 1036 (type of *M. hypoleucus*)).

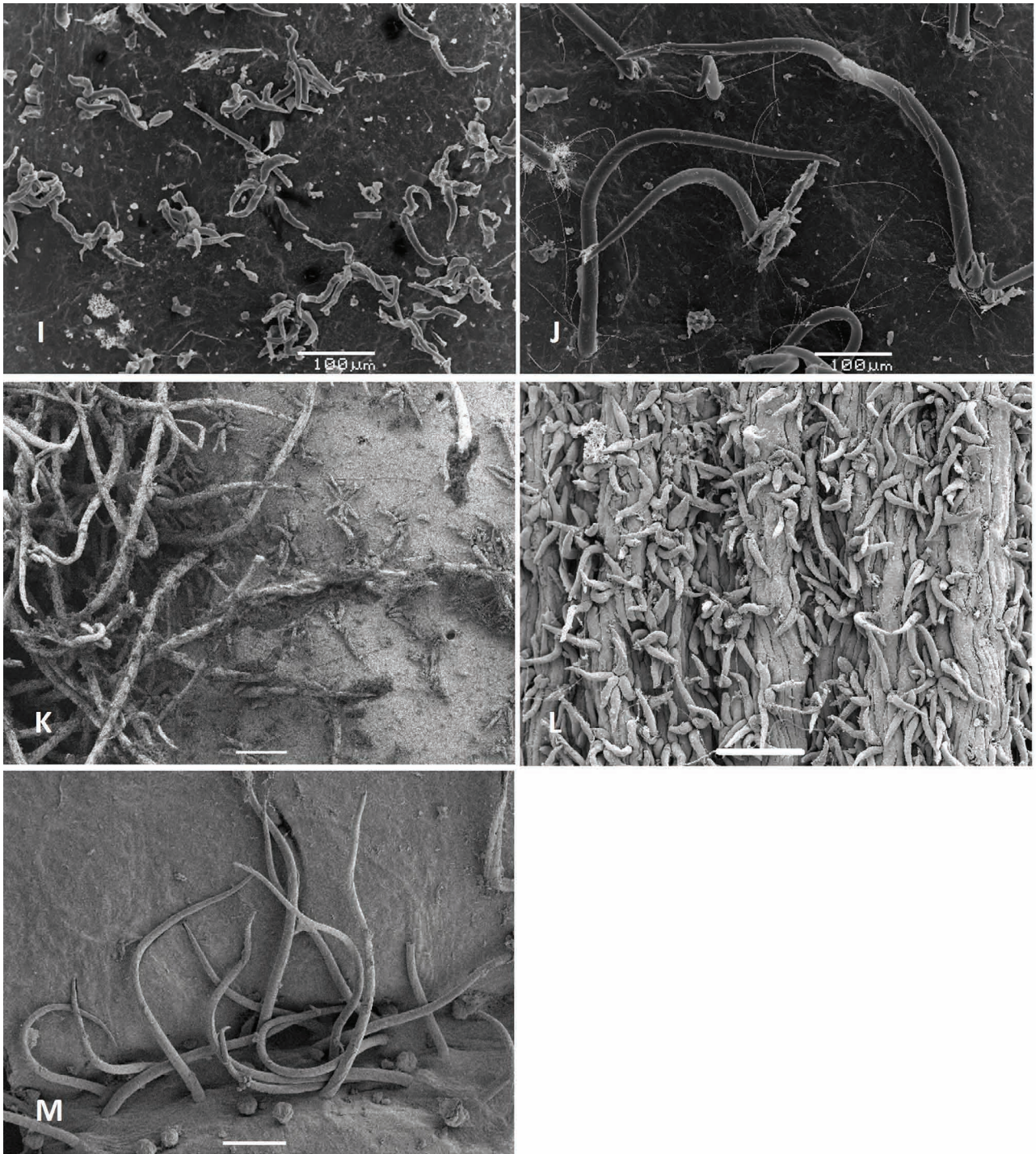


FIGURE 5 I–M. **I.** *M. hypoleucus* var. *hypoleucus*, upper surface (*Welwitsch 1036* (type of *M. hypoleucus*)). **J.** *M. magnificus* var. *gigantophyllus*, upper surface (*Duvigneaud 4597*). **K.** *M. dasyanthus* var. *heterotrichus*, upper surface (*Duvigneaud 4493Mo*). **L.** *M. duvigneaudii* var. *duvigneaudii*, lower surface (*Duvigneaud 5268M4*). **M.** *M. rubriglans* subsp. *upembensis* var. *upembensis*, upper surface (*de Witte 4232*). White bar = 100 μm .

Gombela-poste Luishi, 30 km NE Gombela, clairière dans la forêt claire sur pente rocheuse, *Xerophyta* dominant, 8 February 1982, *Malaisse & Robbrecht 1860* (BR!); Vallée de Luilu, 24 km NNW Kolwezi, forêt claire, 16 February 1982, *Malaisse & Robbrecht 2264* (BR!).

Note:—Intermediates are known between *M. adenophyllus* var. *homblei* and *M. dasyanthus* (e.g. Kasompi central, 4 August 1956, *Duvigneaud & Timperman 2203* (BRLU!); Route Kakanda-Fungurume, km 4, non mineralised soil in miombo forest, 6 April 1990, *Tropmetex 181* (BR!, K, MPN, WAG!)).

Duvigneaud & Timperman 2530 (BRLU!) is polymorphic for leaf pubescence on the same branch, with some

leaves discolorous with stellate hairs in areoles, and others concolorous with glabrous areoles; its leaves are mostly elliptic; it may represent a hybrid.

1bβ. *Monotes adenophyllus* Gilg var. *homblei* (De Wild.) Meerts forma *albidus* (P.A.Duvign.) Meerts, *comb. et stat. nov.*

Basionym: *Monotes magnificus* Gilg var. *albidus* Duvigneaud (1949: 54).

Lectotype (designated here):—D.R. CONGO. Upper Katanga, Lukafu, savane à *Brachystegia-Diplorhynchus* dans la plaine en contrebas des Kundelungu, 16 July 1948, *Duvigneaud 1217M* (lecto-: BRLU! [barcode BRLU0000090022036], isolecto-: BRLU! (3 sheets))

Diagnosis:—Lower surface of leaf whitish; reticulum of lower surface of leaf with long woolly hairs.

Distribution in D.R. Congo:—Upper Katanga.

Habitat and ecology:—Same as forma *homblei*.

Representative specimens examined:—D.R. CONGO. Upper Katanga: Mulungwishi, savane à *Acacia* au bord de la rivière Lukunki, 2 km E du village, 7 August 1956, *Duvigneaud & Timperman 2242* (BRLU!); Route Nzilo-Kibara, km 7.2 au départ de Delcommune sur route Delmar, verger à *Monotes*, 14 June 1957, *Duvigneaud 3514* (BRLU!).

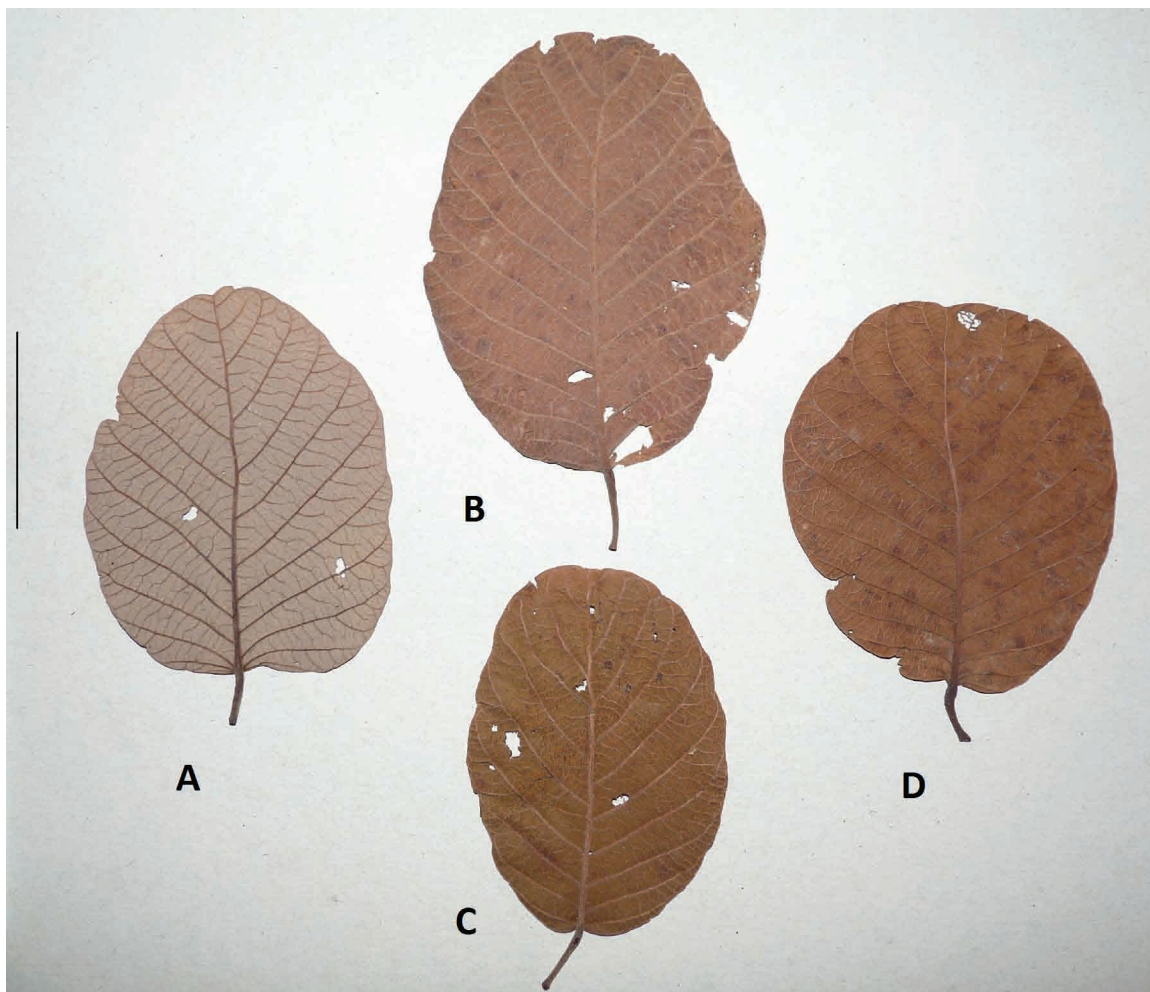


FIGURE 6. Colour photographs of leaves: *Monotes adenophyllus*. **A.** *M. adenophyllus* var. *homblei* (*Duvigneaud 4570M2*); **B–D.** *M. adenophyllus* var. *adenophyllus* (*Duvigneaud 5044*, *Duvigneaud 5112M*, *Duvigneaud 1393*). Scale bar = 5 cm.

2. *Monotes africanus* De Candolle (1868: 624 emend, excl. specim. *Kirk*)

≡ *Vatica africana* Welw. ex Oliver (1868: 173) pro parte excl. var. *hypoleuca*, var. *glomerata* & var. *glabra*. ≡ *Vatica africana* var. *denudans* Welwitsch (1869: 16; Tab. V, Fig. 1).

Type:—ANGOLA. Huila, Lopolo, 1860, *Welwitsch 1035* (BM! [barcode BM001209295, BM001209296], LISU! [barcode LISU234081, LISU234082, LISU234083], P! [barcode 00389101], COI!).

Shrub or small tree up to 8 m high; bark exfoliating in thin strips; branchlets greyish or brownish, glabrous to thinly pubescent. Leaf: petiole thinly pubescent, glabrescent, 5–15(–20) mm long, 1–2 mm in diameter; blade elliptic to oblong or obovate, (3.5–)5–10 × (1.5–)2–5.5 cm, rounded to slightly cordate at the base, obtuse to emarginate at the apex; lateral nerves in 8–14 pairs (with a tendency to the formation of short subsidiaries), nearly straight but incurved at the apex and vanishing without reaching the margin of the leaf; veins much more prominent than reticulation on lower surface; upper surface finely reticulate, with reticulum generally orange-lepidote, typically bullate in the axils of lateral nerves and midrib (with a corresponding depression on the lower surface), glabrous except sometimes for the midrib and lateral nerves, with numerous punctiform yellow glands; lower surface concolorous, puberulous with very minute curled or coiled hairs mixed with some straight ones on the nerves and reticulation, the interreticular areoles generally glabrous; midrib and lateral nerves slightly depressed above and prominent beneath. Inflorescences axillary, 1.5–3(–5) cm long, ± condensed or lax, few-flowered, fulvous-tomentellous; peduncle 1–3 cm long, slender. Flower: pedicel 3–8 mm long; sepals ca. 2 mm long, densely woolly-rufous-tomentose; petals ca. 8 mm long, densely greyish subsericeous-tomentose; stamens with anthers produced into a large, emarginate or triangular lobe. Fruit subglobose, 10–15 mm in diameter, rounded to conical at the apex, sericeous; wings elliptic to obovate, 2.5–3.5 × 1.2–1.6 cm, yellowish or brownish.

Illustrations:—Figs. 3C, 4C, 8A.

Distribution:—Widespread in Upper Katanga.

Distribution elsewhere:—Angola, Malawi, Mozambique, Tanzania, Zambia.

Habitat and ecology:—Miombo woodlands; transition between Uapaceto-Combretetum katangense and *Brachystegia boehmii* woodland; Xerobrachystegion (Schmitz 1971).

Uses:—Poles, tools; foodplant of the edible caterpillar of the cavorting emperor moth, *Usta terpsichore* (Saturniidae) (Malaisse 1997).

Other representative specimens examined:—D.R. CONGO. Upper Katanga: Parc d'Elisabethville (Lubumbashi), 10 June 1922, *Delevoy 929* (BR!); 12 km à l'ouest d'Elisabethville (Lubumbashi), forêt claire à *Brachystegia utilis* sur terre rougeâtre compacte et profonde, 14 July 1956, *Duvigneaud & Timperman 2006* (BRLU!); Entre Mindingi et Menda, 13 km de Menda, forêt claire à *Brachystegia floribunda* sur terre ocre, 17 July 1956, *Duvigneaud & Timperman 2079* (BRLU!); Menda, forêt claire à *Brachystegia longifolia* sur terre rouge légère, 22 July 1956, *Duvigneaud & Timperman 2092* (BRLU!); entre Mukumbi et Swambo, forêt claire sur terre ocre compacte, 1 June 1957, *Duvigneaud 3338* (BRLU!); Kasumbalesa, forêt claire de plateau à *Brachystegia utilis* sur sol brun à proximité des sources de la Luina, 3 December 1959, *Duvigneaud 4379M* (BRLU!); Sakania, forêt claire sur terre ocre caillouteuse à *Brachystegia boehmii* et *B. spiciformis*, 31 jan 1960, *Duvigneaud 5361BM* (BRLU!); Arboretum de l'Etoile, 5 km NE d'Elisabethville (Lubumbashi), forêt claire, January 1948, *Schmitz 1246* (BR!); Welgelegen, alt. 1300 m, lambeau de forêt claire en bordure d'un marais à *Rhynchospora candida*, 8 February 1962, *Symoens 9203* (BRVU!); Keyberg, forêt claire à Marquesia, près de la station expérimentale de l'INEAC, 3 February 1966, *Symoens 12158* (BM!).

Discussion:—Glabrescent specimens are superficially similar to *M. glaber*; the latter, however, differs in having yellow-green leaves often with an orange-tinged reticulum on the lower surface.

As already pointed out by Verdcourt (1989), the frequently used author combination “(Welw.) A.DC.” for *M. africanus* is not correct since De Candolle published his name in mid-July of 1868 while Welwitsch's name *Vatica africana* was validated by Oliver in October 1868. See further nomenclatural discussion under *Monotes hypoleucus*.

References:—Bancroft (1937: 136; 1939a: 372); Catarino *et al.* (2013: 266); De Wildeman (1927a: 168); Duvigneaud (1949: 42; 1961: 415); Engler (1910: 615, Fig. 532); Engler (1921: 522); Figueiredo & Smith (2008: 67); Gilg (1899: 137; 1903: 307; 1908b: 292); Lebrun & Stork (1991: 144); Meerts (2016: 222); Verdcourt (1989: 8); White (1962: 262).

3. *Monotes autennei* Duvigneaud (1958: 183)

Type:—D.R. CONGO. Kahundu, Dilolo, forêt claire à *Brachystegia boehmii*, 23 May 1957, *Duvigneaud 3267MI* (holo-: BRLU! [barcode BRLU0000090020735], iso-: BRLU! (3 sheets)).

Tree up to 17 m high; branchlets shortly puberulous to densely pubescent. Leaf: petiole 10–25 mm long, very thick (3–3.5 mm in diameter); blade broadly elliptic, obovate, sometimes suborbicular, (7–)12–18(–22) × (5–)9–12(–14) cm, leathery, broadly cordate to rounded at the base, obcordate-bilobate or deeply emarginate at the apex, typically with the apical sinus deeper than the basal one, often with extra leaf-glands in the axils of the lateral nerves; lateral nerves 12–15 pairs, slightly incurved, some of them bifurcate near the apex, nerves and bifurcations reaching the margin of the leaf; upper surface slightly scaberulous with short straight hairs 0.15–0.3 mm long in fascicles of 2–8 on small

white cushions, finally glabrous; lower surface greyish- or fulvous-pubescent (sometimes glabrescent when old), with relatively long curved hairs mixed with fasciculate ones, and with the interreticular areoles densely to sparsely covered with minute stellate hairs; midrib very thick and prominent beneath; veins and reticulation very prominent and forming deep cavities. Inflorescences, flowers and fruits as in *M. katangensis*.

Illustrations:—Figs. 3D, 4D, 5B,C, 7A,B, 13.

Distribution in D.R. Congo:—Widespread in Upper Katanga, apparently more frequent in the west.

Distribution elsewhere:—Zambia. Restricted distribution.

Habitat and ecology:—Miombo woodland; mixed high woodlands with *Marquesia acuminata* and *M. macroura* on grey compact soil; chipya on Kalahari sand.

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** 20 km E of Kasagi, territ. Kisenge, forêt à *Marquesia* sur terre grise compacte à petites termitières, *Duvigneaud & Timperman 2317Mo1* (BRLU!); 15 km N of Dilolo, forêt claire de plateau à *Marquesia* sur sol gris, 21 August 1956, *Duvigneaud & Timperman 2424* (BRLU!); Tshisenge, 17 km N of Dilolo, forêt claire à *Marquesia* sur sol gris compact, 1957, *Duvigneaud 2428M* (BRLU!); Dembo de la Lufupa, forêt claire de bordure à *Brachystegia longifolia* et *Cryptosepalum pseudotaxus*, *Duvigneaud & Timperman 2541* (BRLU!); Kalongwe, brousses denses avec *Monotes caloneurus*, 9 May 1957, *Duvigneaud 3090M* (BRLU!); Kolwezi, Colline D, forêt claire sur roches siliceuses cellulaires, 13 June 1957, *Duvigneaud 3494M*; Nzilo, forêt verger sur terre compacte, 14 June 1957, *Duvigneaud 3516M* (BRLU!); Kyamandjizi, forêt claire, 8 October 1981, *Malaisse 11939a* (BR!); route Nzilo-Le Marinelle, km 1.5, crête au dessus du barrage, formée de quartzite et de quartzophyllades, 21 September 1958, *Plancke 111/1532* (BRLU!).

Discussion:—*Monotes autennei* is generally easy to recognize by its large bilobed leaves with fasciculate hairs on the upper surface. Many specimens had been misidentified as *M. katangensis* or *M. magnificus*. Intermediates with *M. katangensis* are frequent (see note under that species). Some collections have a rounded leaf apex and ovate-elliptic leaves (*Desenfans 4012* (BRLU!)).

References:—Duvigneaud (1961: 414); Lebrun & Stork (1991: 144); Meerts (2016: 222).

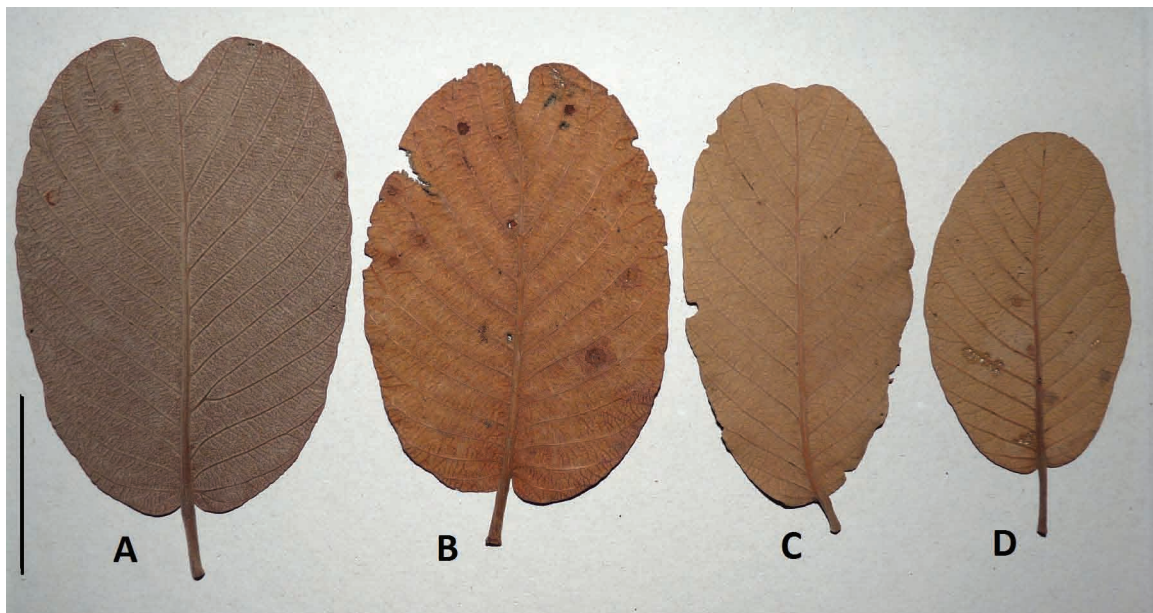


FIGURE 7. Colour photographs of leaves: *Monotes autennei*. **A.** *Duvigneaud 5260*, **B.** *Duvigneaud & Timperman 2545*. *M. katangensis*: **C.** *Duvigneaud & Timperman 2233*; **D.** *Duvigneaud & Timperman 2641*. Scale bar = 5 cm.

4. *Monotes dasyanthus* Gilg (1903: 307)

Type:—ANGOLA. [Cuando-Cubango], Kutsi [Cuchi River], unterhalb Kapulo, 2 May 1900, *Baum 888* (holo-: B†, iso-: BM! [barcode BM001209287], COI!, HBG! [barcode HBG507223], K! [barcode K000240364], M, W! [barcode W1901-0006479], Z! [barcode Z-000015505].).

Small tree 4–10(–15) m high; branchlets yellowish brown or blackish-velutinous. Leaf: petiole 10–30 mm long, ca. 3 mm in diameter; blade ovate to ovate-elliptic or oblong, 6–14(–20) × 3–8(–12) cm, rounded to slightly cordate at the base, more rarely cuneate, apex obtuse to acute or acuminate and mucronate, often bronze coloured in herbarium, generally discolorous; lateral nerves in 12–18 pairs, nearly straight, incurving at the apex, reaching the margin of the leaf; upper surface scaberulous, harsh to the touch, with straight or nearly straight stiff isolated hairs of 0.4–1 mm,

generally persistent, sometimes with a layer of short stellate hairs; lower surface fulvous- (more rarely grayish-) cottony-lanose-tomentose with long curled hairs on the nerves and reticulation and with the interreticular areoles generally covered with minute stellate hairs; midrib and lateral nerves slightly depressed above and very prominent and strong beneath. Inflorescences of subsessile dense clusters or racemiform cymes, the uppermost ones more or less grouped at the end of twigs in a congested panicle (< 6 cm) much shorter than the uppermost leaf, greyish- or brownish-velutinous-tomentose. Flower: pedicel 2–3 mm long; sepals ca. 3 mm long, densely sericeous-tomentose; petals ca. 9 mm long, densely sericeous-tomentose; stamens with connective produced into an inconspicuous appendage. Fruit subglobose, 8–10 mm in diam., densely sericeous-tomentose, conical at the apex; wings generally broadly obovate to spatulate, 3–4(–5) × 1.0–1.5(–2) cm, reddish purple.

Variation:—*M. dasyanthus* is very variable as to the thickness, colour and density of indumentum on the lower surface of the leaf, and presence/absence of stellate hairs on the upper surface. Three varieties can be recognized.

Key to the varieties:

- 1. Upper surface of leaf with a mixed indumentum of long simple straight hairs and a dense, persistent, layer of very short stellate hairs; lower surface always with a very dense woolly fulvous tomentum 4b. var. *heterotrichus*
- Upper surface of leaf with simple straight hairs, stellate hairs sparse or lacking; lower surface indumentum variable 2
- 2. Leaf discoloured; lower surface with areoles entirely covered by a continuous layer of stellate hairs; reticulum with long, more or less fulvous hairs, covering areoles or not 4a. var. *dasyanthus*
- Leaf concolorous to slightly discoloured; lower surface with stellate indumentum sparse or lacking; reticulum with flexuous hairs not hiding the areoles 4c. var. *mutetetwa*

4a. *Monotes dasyanthus* Gilg var. *dasyanthus*

Diagnosis:—Upper surface of leaf without stellate hairs; lower surface of leaf discoloured, with areoles covered with a dense layer of stellate hairs, more or less masked by long, woolly, fulvous hairs.

Variation:—*M. dasyanthus* var. *dasyanthus* is extremely variable for thickness, density and colour of the lower surface indumentum. We found very difficult to divide that variation. Two forms can be tentatively recognized.

Key to the forms:

- 1. Lower surface of leaf fulvous, with hairs on reticulum woolly, more or less hiding areoles 4aa. forma *dasyanthus*
- Lower surface of leaf greyish to beige, with hairs on reticulum silky, not hiding areoles 4aβ. forma *sericea*

4aa. *Monotes dasyanthus* Gilg var. *dasyanthus* forma *dasyanthus*

= *Monotes dasyanthus* sensu Bancroft (1937: 139; 1939a: 338, 372); De Wildeman (1927a: 170); Duvigneaud (1949: 60; 1961: 411); Engler (1921: 520); Exell & Mendonça (1951: 371); Figueiredo & Smith (2008: 67); Gilg (1908b: 288); Hutchinson (1931: 253); Lebrun & Stork (1991: 144); White (1962: 263).

Diagnosis:—Lower surface of leaf fulvous, with hairs on reticulum woolly, more or less hiding areoles.

Illustrations:—Figs. 3E, 4E, 9B.

Distribution in D.R. Congo:—Western Katanga, Haut-Kwango, Moyen-Kwango; characteristic of the “Lundian” (= Centro-Angolan) phytogeographic element in the flora of W Katanga (Duvigneaud 1958).

Distribution elsewhere:—Angola, Zambia.

Habitat and ecology:—Mixed dry forests with *Uapaca nitida* and *Berlinia giorgii* in the region of Kaniama (Mullenders 1954); wooded savannah at the periphery of clearings on mineralized soil; livunda (semi-evergreen mixed forest) (Duvigneaud 1958), mabwati.

Other representative specimens examined:—**D.R. CONGO. Lower Katanga:** Route Kamina-Bukama, à 65 km au sud de Kamina, forêt claire, 12 July 1952, *Galoux 129* (BRLU!). **Upper Katanga:** Mutshasha, brousse anthropique au contact du village indigène, 13 August 1956, *Duvigneaud & Timperman 2300M* (BRLU!); Malonga, 10 km W du village, forêt claire riche en *Monotes*, 14 August 1956, *Duvigneaud & Timperman 2319Mo* (BRLU!); Kapolo-Kisenge, ceinture à *Monotes* autour du dembo d’empoisonnement de la colline manganésifère, 21 May 1957, *Duvigneaud 2341* (BRLU!); Kisenge-Kamata, savane à *Monotes* en bordure du gisement de manganèse, 1956, *Duvigneaud & Timperman 2365* (BRLU!); Nasondoye, dilungu de la Lufupa, steppe arbustif au contact de la livunda, 11 February 1960, *Duvigneaud 5525Mo* (BRLU!); Kisenge-Kapolo, forêt de transition à la limite d’un gisement de manganèse, 25 September 1958, *Plancke 150/1913* (BRLU!).

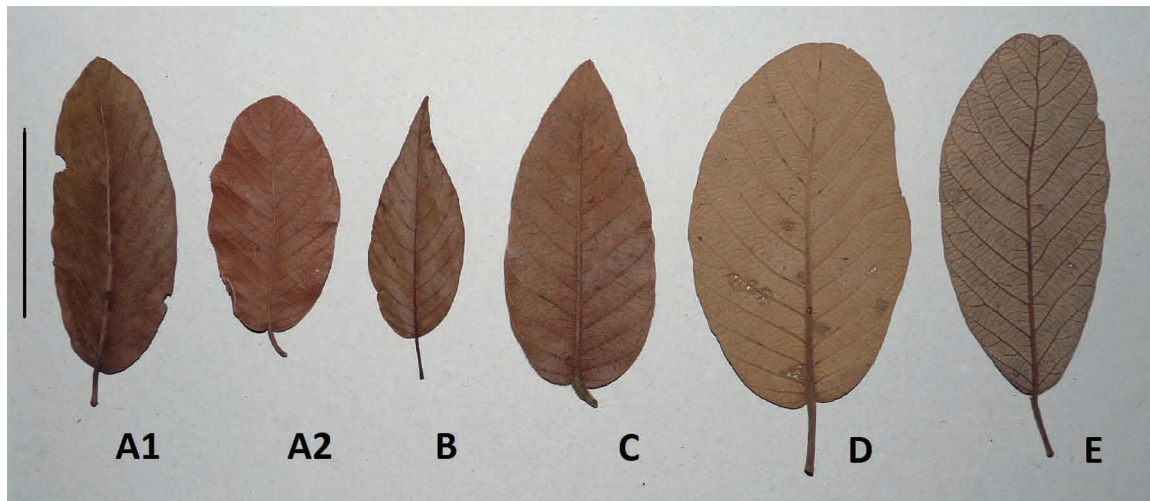


FIGURE 8. Colour photographs of leaves in members of *Monotes*. **A1-A2.** *M. africanus* (Duvigneaud 2006: 2 leaves). **B.** *M. doryphorus* (Duvigneaud 5267). **C.** *M. hirtii* (Duvigneaud 3513). **D.** *M. katangensis* (Duvigneaud & Timperman 2641). **E.** *M. pearsonii* (Duvigneaud 5233). Scale bar = 5 cm.

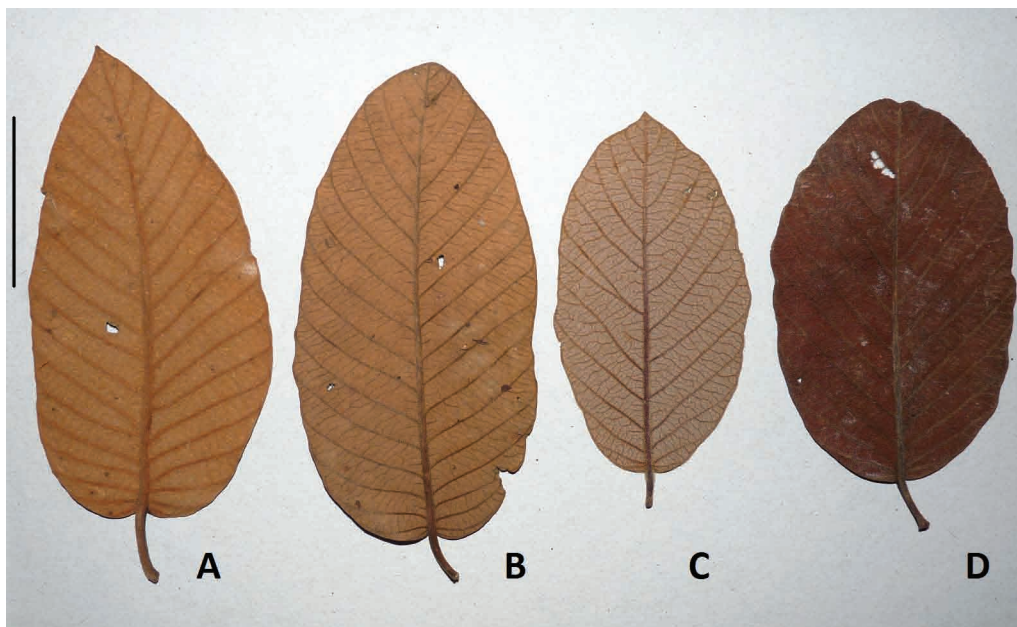


FIGURE 9. Colour photographs of leaves: *Monotes dasyanthus*. **A.** *M. dasyanthus* var. *heterotrichus* (Duvigneaud 1141M). **B.** *M. dasyanthus* var. *dasyanthus* (Duvigneaud & Timperman 2341). **C.** *M. dasyanthus* var. *dasyanthus* forma *sericea* (Desenfans 2185). **D.** *M. dasyanthus* var. *mutetetwa* (Duvigneaud 950M). Scale bar = 5 cm.

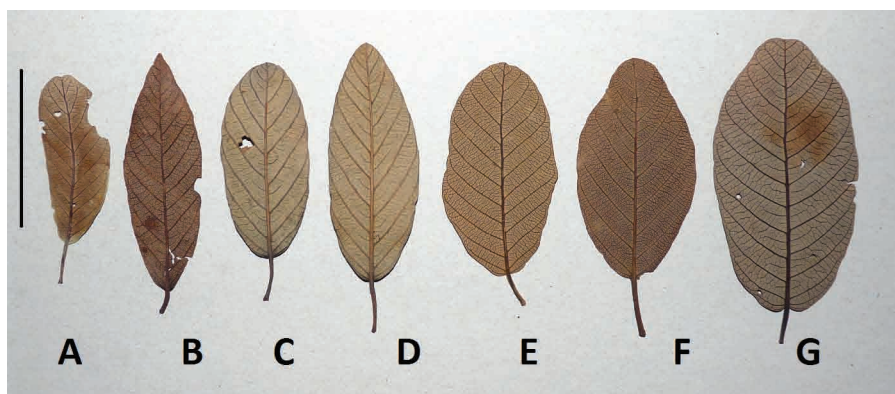


FIGURE 10. Colour photographs of leaves: *Monotes hypoleucus* var. *angolensis*. From left to right: **A.** Gossweiler 9150 (phenotype “*noideae*”). **B.** Duvigneaud 948 (forma *oxyphyllinus*). **C–D.** Duvigneaud 2242 (phenotype “*oblongifolius*”, two leaves from the same specimen). **E.** Desenfans 4518. **F.** Duvigneaud 5212BM. **G.** Duvigneaud 4541M1 (phenotype “*carrisoanus*”). Scale bar = 5 cm.

4aβ. *Monotes dasyanthus* Gilg var. *dasyanthus* forma *sericea* (P.A.Duvign.) Meerts, *comb. nov.*

Basionym: *Monotes mutetetwa* forma *sericea* Duvigneaud (1949: 59), excl. syntype *Herman 2335* (BR!).

Lectotype (designated here):—D.R. CONGO, Kaniama, *Lynes 66* (BR!).

Diagnosis:—Lower surface of leaf greyish to beige; reticulum with short, silky hairs, not masking areoles.

Illustration:—Fig. 9C.

Distribution in D.R. Congo:—Kwango, Lower Katanga.

Habitat and Ecology:—Data deficient, apparently the same as forma *dasyanthus*.

Representative specimens studied:—**D.R. CONGO. Kasai** (Kwango): Mwana Mutombo, forêt sèche, 24 April 1953, *Callens 3935* (BR!, KISA, WAG!). **Lower Katanga:** Lumba, 1100 m, October 1951, *Desenfans 2125* (BRLU!); Route Mato-Kamina, 15 km S de Mato, forêt à *Berlinia*, *Uapaca*, *Monotes*, 1000 m, October 1951, *Desenfans 2185* (BR!, BRLU!); Kamina, Haut-Lomami, forêt à *Berlinia-Uapaca*, 1120 m, 20 September 1947, *Mullenders 1375* (BR!).

Discussion:—This form appears more or less intermediate between var. *dasyanthus* and var. *mutetetwa*. It was treated by Duvigneaud (1949) under the latter variety, but, in our definition of var. *mutetetwa* (areoles glabrous), forma *sericea* is better placed under var. *dasyanthus*. The syntype *Herman 2335*, in our opinion, is better placed in forma *dasyanthus*.

4b. *Monotes dasyanthus* Gilg var. *heterotrichus* Meerts, *var. nov.*

Type:—D.R. CONGO. Upper Katanga, Dikuluwe, forêt claire à *Marquesia*, en bordure ouest du gisement de cuivre, 10 May 1957,

Duvigneaud 3127M (holo-: BRLU! [barcode BRLU0003155]; iso-: BRLU! [barcode BRLU0003156!]).

= *Monotes* sp. 1 (White 1962: 263).

Diagnosis:—Differs from the type variety by the following traits: indumentum of the leaf upper surface comprising long straight simple hairs and a dense, persistent, cover of much shorter, stellate hairs with 4–12 spreading branches ca. 100 µm long, arising from a bulbous base.

Shrub with flattish spreading crown. Leaf blade large, with at least a few exceeding 18 × 10 cm, lower surface always with a very thick fulvous tomentum of woolly hairs, completely hiding the areoles and reticulum. Fruit: wings often larger than in the type, 2.0–5.0 cm long, attenuate at base.

Illustrations:—Figs 3F, 4F, 5K, 9A.

Distribution in D.R. Congo:—D.R. Congo: Upper Katanga and Lower Katanga (Fig. 16F).

Distribution elsewhere:—NW Zambia (new record for that country); restricted distribution.

Habitat and ecology:—Miombo woodlands on sandy soil, transitional savannah at the periphery of copper and manganese clearings and dambos.

Other representative specimens examined:—**D.R. CONGO. Lower Katanga**, Haut Lomami, Songa, 17 August 1959, *Huart 130* (BR!). **Upper Katanga:** Kolwezi, forêt claire à *Brachystegia*, 6 July 1948, *Duvigneaud 1141M* (BRLU!); Nasondoye, fourche des routes de Sokele et de Dilolo, savane arbustive sur sable kalaharien à *Uapaca robynssii*, 10 August 1956, *Duvigneaud & Timperman 2297M* (BRLU!); Mutshasha, brousse anthropique au contact du village indigène, 13 August 1956, *Duvigneaud & Timperman 2300MIH* (BRLU!); Dikuluwe, forêt claire à *Marquesia* en bordure ouest du gisement de cuivre, 10 May 1957, *Duvigneaud 3127* (BRLU!); Dikuluwe, forêt de plaine sur sol brun vif, June 1957, *Duvigneaud 3521* (BRLU!); Dikuluwe, dembo d'empoisonnement au N de la colline cuprifère, steppe arbustif, 10 December 1959, *Duvigneaud 4480MI* (BRLU!); Dikuluwe, colline cuprifère, dembo d'empoisonnement vers la rivière, au S de la coline, steppe arbustif sur sable, 10 December 1959, *Duvigneaud 4493Mo* (BRLU!); Mpala, ceinture à *Uapaca robynssii* autour d'un bois noir sur sable du Kalahari, 26 January 1960, *Duvigneaud 5252M* (BRLU!).

ZAMBIA: Mwinilunga, margins of watershed sand plains, July 1955, *Edmonds E8/55* (BRLU!, FHO); A few miles N of Kalene Hill Mission, *Isoberlinia paniculata-Brachystegia longifolia* woodland on shallow Kalahari sands, 24 September 1952, *White 3361* (BRLU!, FHO).

4c. *Monotes dasyanthus* Gilg var. *mutetetwa* (P.A.Duvign.) Meerts, *comb. et stat. nov.*

Basionym: *Monotes mutetetwa* Duvigneaud (1949: 58, Pl. 14a, b, excl. forma *sericea*, excl. *Duvigneaud 971*); Mullenders (1954: 375, map).

Lectotype (designated here):—D.R. CONGO. Muniungu, forêt claire à *Uapaca-Daniellia*, sable noir en surface, 6 May 1948, *Duvigneaud 840M2* (lecto-: BRLU! barcode [BRLU0000090022043], isolecto-: BRLU! (5 sheets)).

Diagnosis:—Differs from the type variety essentially in having a concolorous leaf blade with areoles on the lower surface glabrous or very sparsely pubescent, and the hairs on the reticulum not masking the areoles.

Leaf blade ovate to elliptic or oblong, 8–18 × 4.5–14 cm, dark green to bronze, base slightly cordate or rounded, apex rounded to acute or acuminate, with up to 19 pairs of nerves; upper surface pubescent, scaberulous, harsh to the touch, hairs straight, stiff or nearly so, clearly separated from one another, 0.3–1 mm long, on cushion-like emergences; lower surface concolorous to slightly discolorous, areoles glabrous or with sparse stellate hairs, with yellow glands, nerves and reticulum hirsute, with pale fulvous to whitish, straight to flexuous, not woolly, 1–2 mm long hairs, areoles forming cavities. Flowers in dense axillary racemiform cymes ca. 4 cm long. Fruits apparently as in var. *dasyanthus*, occasionally with a pointed tip.

Illustrations:—Figs 3G, 4G, 9D.

Distribution in D.R. Congo:—Bas-Congo, Kwango.

Distribution elsewhere:—Angola? (many (all?) specimens assigned to “*M. mutetetwa*” in Angola (Catarino *et al.* 2013) probably belong in *M. dasyanthus* var. *dasyanthus*).

Habitat and ecology:—“Tumbi” and “Mabwati” (mixed, semi-evergreen dry forests) with *Uapaca nitida* and *Berlinia giorgii* (Mullenders 1954; Devred 1957); miombo woodland (ecology poorly known due to confusion with var. *dasyanthus*).

Other representative specimens examined:—**D.R. CONGO. Bas-Congo:** région de Kimvula-Pandi, s.d., *Duvigneaud s.n.* (BRLU!). **Kasaï** (Kwango): Kika Kiala, matumbi, 3 February 1952, *Callens 3034* (BM!, BR!); Région de Mawanga, savane boisée, 30 April 1953, *Callens 4061* (BR!, KISA); Route Feshi-Tono, forêt claire dégradée, 18 March 1956, *Devred 2978* (BR!); steppe entre Gungu et Kahemba (130 km S de Gungu), April 1948, *Duvigneaud 945M* (BRLU!); 5 km N de Kahemba, forêt claire à *Brachystegia-Julbernardia*, 30 May 1948, *Duvigneaud 950M* (BRLU!); Kahemba, route vers l’Angola, galerie forestière, 31 May 1948, *Duvigneaud 954M* (BRLU!, syntype); Entre Kwango-Wamba, village Monkondo, savane arbustive, 30 July 1944, *Germain 2522* (BR!, BRLU (fragm.!), KISA, L!).

Vernacular names:—Bokombolo tseke (Kiyaka), mukeletete (Kitchok); mutetetwa, ntetetwa (Kitchok).

Discussion:—Duvigneaud described *M. mutetetwa* to accommodate forms of *M. dasyanthus* with the reticulum and areoles not hidden by the fulvous indumentum and with leaves larger than the type. However, within *M. dasyanthus*, there is considerable variation in thickness and density of the lower surface indumentum, without a clear relation to leaf size. We here propose to divide *M. dasyanthus* following the same criterion as used to divide *M. adenophyllus*, i.e. presence/absence of stellate hairs in areoles. We thus restrict *M. mutetetwa* to the concolorous forms in which the stellate indumentum is sparse to lacking, downgrading it to varietal rank within *M. dasyanthus*.

Duvigneaud (1949) cites two syntypes, one in flower (*Duvigneaud 840M2*) and one in fruit (*Duvigneaud 954M*); the flowering specimen is here chosen as the lectotype.

Considering leaf shape and indumentum, *M. dasyanthus* var. *mutetetwa*, as already noted by Duvigneaud (1949), comes close to *M. glandulosus* Pierre, a poorly known taxon (see note at the end of this article). However, the latter has the anther with a conspicuous appendage, while the former has the anther with the appendage inconspicuous.

Intermediates with *M. caloneurus* exist (*Duvigneaud 2364* (BRLU!)).

5. *Monotes doryphorus* Duvigneaud (1958: 233)

Type:—D.R. CONGO. Haut-Katanga, Mutshatsha, forêt claire à *Pseudoberlinia paniculata* sur roches kibariennes dominant la rivière Lubudi, August 1956, *Duvigneaud & Timperman 2530M1* (holo-: BRLU! [barcode BRLU0000090020797], iso-: BRLU! (6 sheets, excl. BRLU0000090020773)).

≡ “*Monotes cuspidatus* P.A.Duvign.” *in schedis*, unpublished designation.

Tree up to 12 m high; branches glabrous to sparsely puberulent, glabrescent, longitudinally ridged, lenticellate; old twigs pale-coloured, more or less smooth; apical bud with ciliate appressed-pubescent scales. Leaf: petiole (7–)12–21(–25) mm long, slender (the most slender in the genus), less than 1 mm thick, often slightly dilated in upper part, glabrous or with scattered minute fasciculate hairs; blade narrowly ovate-lanceolate (3–)4–10(–13) × (0.7–)1.5–3.6(–4.0) cm, l/w ratio 3–5, base cuneate to rounded or rarely slightly cordate in the broadest leaves, apex acute to long acuminate, with 10–17 pairs of secondary nerves, generally markedly curved, anastomosing at short distance from the margin; upper surface reticulate and generally shiny (varnished), with reticulum often orange-lepidote, glabrous or, more rarely, with scattered small fasciculate hairs; nerves prominent on lower surface, glabrous or sparsely puberulous with fasciculate hairs; margin slightly recurved, with minute fasciculate hairs or, more rarely, glabrous; basal gland reddish, elongate, 1–2 × 0.7 mm. Inflorescence of small axillary cymes, rarely grouped to form a short panicle, lax,

few-flowered, peduncle 1–3 cm long, rachis minutely pubescent. Flower buds appressed pubescent, obconical, 2–3 mm long, pedicels ca. 1 mm long; bracts reddish, ciliate, 2–3 × 1.5 mm; stamens fused at base in a very short ring. Fruit: pedicel 3–4 mm long, minutely pubescent; achene globose, with conical beak, ca. 6–7 × 5–6 mm, with prominent veins in herbarium (or shrinking on drying?), more or less covered with fascicles of straight simple hairs; wings 1.0–3.0 × 0.6–0.9 cm, oblanceolate, oblong, lanceolate, rounded at apex, slightly unguiculate, minutely pubescent, with raised reticulum, yellowish brown.

Illustrations:—Figs. 3H, 4H, 8B, 14.

Distribution in D.R. Congo:—Western Upper Katanga, “sous-district de la Haute-Lubudi” and “district of the NW foothills of the Manika” (Duvigneaud 1958). Endemic of D.R. Congo (Fig. 16D).

Habitat and ecology:—Miombo forests, wooded savannahs, bushy savannahs, chypia, degraded forest, on various kinds of soil, often on rocky slopes on kibarrian shale. Flowering in February; fruiting in June.

Vernacular names:—Mudianshi, ngowa (Kiluba).

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** Relevé 168 au S du point Sunswe, pente N 40%, forêt claire, 30 January 1954, *Desenfans 5019* (BRLU!); Mukulakulu, forêt claire, 29 April 1953, *De Troyer 73* (BR!); Mutshasha, forêt à *Pseudoberlinia* sur colline schisteuse, September 1956, *Duvigneaud & Timperman 2530M* (BRLU!); 46 km E de Mutshasha, forêt claire à Mikondo sur sol ocre des plateaux avec nombreuses pierres, 24 August 1956, *Duvigneaud & Timperman 2533* (BRLU!); Saluseke (Kasaji), Brousse dégradée, *Duvigneaud 3290Di* (BRLU!); Entre Nzilo et Delcommune, verger à *Monotes doryphorus*, riche en *Protea hirtii*, sur pente de roches kibariennes, 14 December 1959, *Duvigneaud 4558Mi* (BRLU!); Delcommune, verger à *Monotes* div. sp. sur pente rocheuse de roches kibariennes, 14 December 1959, *Duvigneaud 4570Mi* (BRLU!); Mpala, forêt chypia à *Marquesia* et *Brachystegia floribunda*, 23 January 1960, *Duvigneaud 5221M* (BRLU!); Entre Lupusa et Kasekelesa, forêt claire de plaine à *Brachystegia spiciformis*, 23 January 1960, *Duvigneaud 5227* (BRLU!); Kasekelesa, chantier 1, forêt claire mélangée sur sol manganifère, 25 January 1960, *Duvigneaud 5239MI* (BRLU!); Nzilo, forêt verger à *Monotes* div. sp. enrochée, sur phyllades kibariennes, 27 January 1960, *Duvigneaud 5268Mi* (BRLU!); Nzilo, forêt de pente, 27 January 1960, *Duvigneaud 5269M* (BRLU!); Plateau des Kibara, ancienne piste Delmar, km 13, forêt claire à nombreux *Monotes*, 21 September 1958, *Plancke 113/1667* (BRLU!); Ancienne piste Delmar, km 31, Plaine de la Mabuya, 21 September 1958, *Plancke 118/1722* (BRLU!); 10 km de Kanzenze, sur la route de Busanga (40 km NW Kolwezi), forêt claire sur sol sablonneux, May 1952, *Schmitz 3984* (BR!); Upemba, 26 June 1956, *Vanden Brande K65* (BR!);

Discussion:—This species is strongly reminiscent of *Marquesia* in having ovate, long acuminate leaves and slender, furrowed twigs.

Some specimens are intermediate with *Monotes duvigneaudii* var. *concolor*; the relationship between the latter and *Monotes doryphorus* needs further investigation.

References:—Lebrun & Stork (1991: 144); Meerts (2016: 223).

6. *Monotes duvigneaudii* Meerts, sp. nov.

Type:—D.R. CONGO. Upper Katanga (administrative province of Lualaba), Nzilo, forêt verger à *Monotes* div. sp., enrochée, sur phyllades kibariennes, 27 January 1960, *Duvigneaud 5268M4* (holo-: BRLU! [barcode BRLU0004158]; iso-: BRLU!).

Diagnosis:—Differs from all other species of *Monotes* except *M. doryphorus* by the combination of ovate-lanceolate leaves with acute-acuminate apex and glabrous upper surface, and from *M. doryphorus* by the inflorescence in a terminal congested panicle (vs. small axillary cymes), the broader leaves (3.5–6.5 cm wide vs. 1.5–3.6) and the thicker petiole (ca. 2 mm thick vs. less than 1 mm).

Small tree (up to 5 m); leafy twigs channelled, ca. 3 mm in diameter, shortly and densely pubescent, glabrescent. Leaf: petiole 7–20(–25) mm long, 1.5–2 mm thick, densely and shortly pubescent, often canaliculated; blade ovate or ovate-elliptic to lanceolate, (6–)7.5–15 × (2–)3.5–6.5 cm, broadest at the lower third, l/w ratio (1.5–)2–3.5, rounded to slightly cordate or rarely cuneate at base, long acuminate or rarely acute at apex, rather coriaceous; basal gland generally narrowly elliptic (more rarely round), strongly depressed, reddish; upper surface glabrous except the margin which has a fringe of very short fasciculate hairs, markedly reticulate, reticulum orange-tinged; secondary nerves 13–18 pairs, slightly curved, anastomosing just before the margin or tangent to the margin, secondary nerves not depressed; margin slightly thickened and recurved; lower surface of leaf generally strongly discoloured, white or whitish to pale greyish, with a continuous layer of very short stellate hairs entirely covering areoles and reticulum, sparser on the secondary nerves, or, more rarely, concolorous (var. *concolor*); nerves slightly prominent, pale orange-tinged, with a sparser layer of stellate hairs and a few short straight appressed hairs on the costa. Inflorescence a more or less

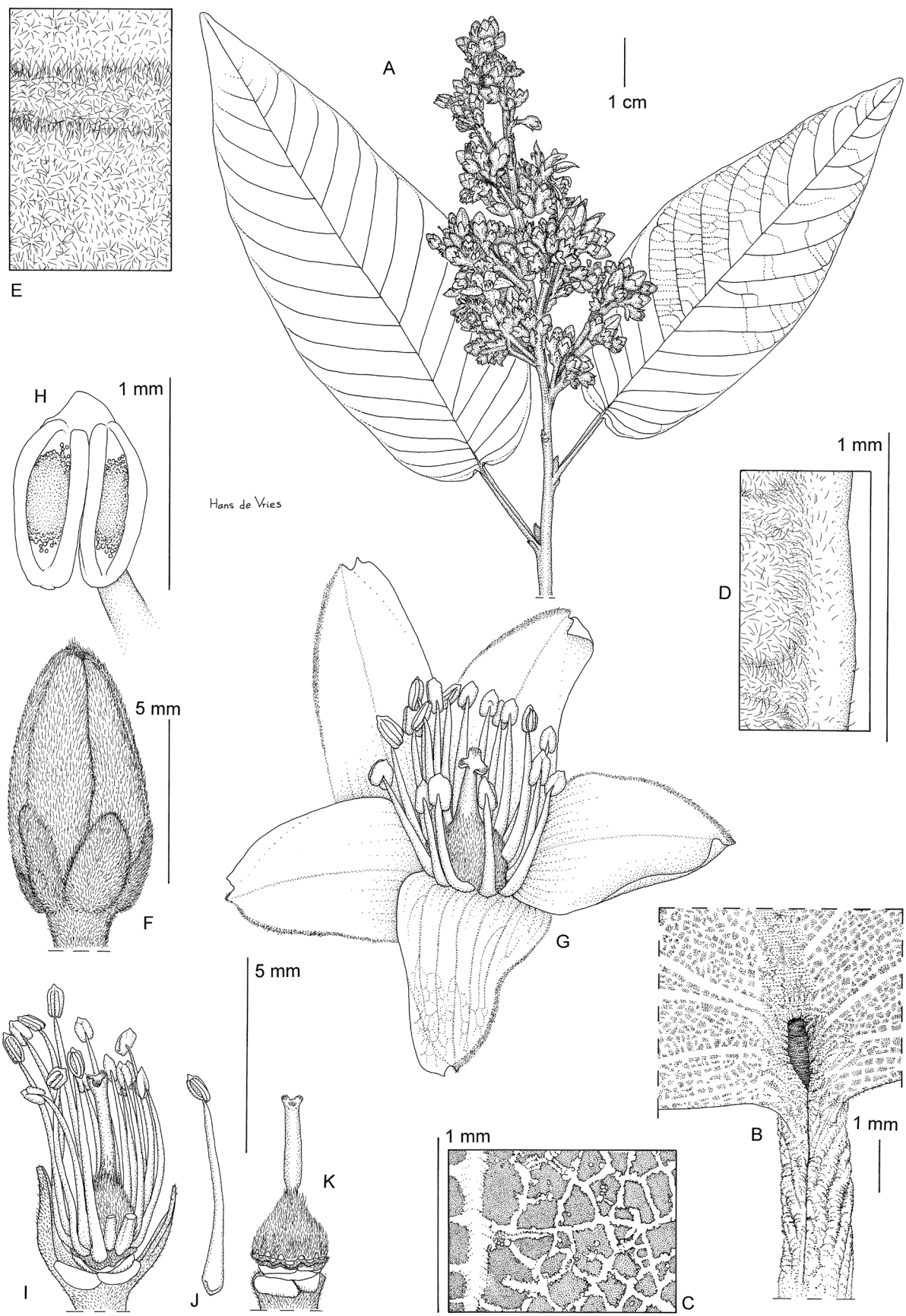


FIGURE 11. *Monotes duvigneaudii* var. *duvigneaudii*. **A.** Habit: flowering branch ($\times 1\frac{1}{2}$). **B.** Leaf base with gland ($\times 16$). **C.** Detail: upper surface of leaf ($\times 55$). **D.** Detail: leaf margin ($\times 95$). **E.** Detail: leaf lower surface with secondary vein ($\times 95$). **F.** Flower bud ($\times 10$). **G.** Flower ($\times 11$). **H.** Anther ($\times 65$). **I.** Flower, opened, two stamens removed ($\times 11$). **J.** Stamen ($\times 11$). **K.** Ovary ($\times 11$). (A–D, F–K: *Duvigneaud 5268M4*; E: *Duvigneaud 4570M3*). Drawing by Hans de Vries, Botanical Garden Meise (©).

condensed terminal panicle, 4–8 × 3–4 cm, consisting of subsessile narrow racemes or cymes 1–5 cm long, often with a few axillary racemes at the base, rarely consisting only of axillary racemes; axes densely pubescent. Flower: pedicel 1–2 mm long; floral bud ovoid-conical; sepals ovate, ca. 2 × 1.5 mm, apex obtuse, slightly carinate, densely sericeous tomentose; petals triangular-ovate, 7 × 2.5–3 mm, ca. 6-nerved, sericeous tomentose outside, almost glabrous inside; anther ca. 0.7 mm long, with short pointed apical appendage; ovary densely hirsute, apparently trilobular, thick-walled. Fruit unknown (but see var. *concolor*).

Eponymy:—The new species is dedicated to Paul Duvigneaud (1913–1991), professor at Brussels University, the unrivalled specialist on the taxonomy of *Monotes*, who collected several thousands *Monotes* specimens in southern D.R. Congo between 1948 and 1960.

Variation:—Density of stellate hairs on the lower surface of the leaf is very variable; two varieties can be recognized.

Key to the varieties:

1. Leaf blade strongly discoloured, with lower surface whitish, entirely covered with short appressed stellate hairs 6a. var. *duvigneaudii*
- Leaf blade concolorous, with indumentum of lower surface lacking or sparser, not covering the reticulum 6b. var. *concolor*

6a. *Monotes duvigneaudii* Meerts var. *duvigneaudii*

Diagnosis:—Lower surface of leaf strongly discoloured, white or whitish to pale greyish, with a continuous layer of very short stellate hairs entirely covering areoles and reticulum, sparser on the secondary nerves.

Illustrations:—Figs. 3I, 5L, 11.

Distribution in D.R. Congo:—Upper Katanga. Endemic of D.R. Congo (Fig. 16A).

Habitat and ecology:—Miombo woodland.

Additional specimens examined:—D.R. CONGO. Upper Katanga: Delcommune, verger à *Monotes* div. sp. sur pente rocheuse de phyllades kibariennes, 14 December 1959, *Duvigneaud 4570M3* (BRLU!); sine dato, sine loco, *Vanden Brande MitV221* (BRLU!).

Discussion:—A striking taxon strongly reminiscent of *Marquesia*, with ovate-acuminate leaves, slender twigs, and glabrous upper surface of the blade.

6b. *Monotes duvigneaudii* Meerts var. *concolor* Meerts, var. nov.

Type:—D.R. CONGO. Katanga: Upemba, Kibara, éboulis près de la rivière Manda, le long des chutes, alt. 1400 m, 13 April 1949, *de Witte 06092* (holo-: BR!; iso-: BR!).

Diagnosis:—Differs from the type variety by the concolorous leaves with a glabrous lower surface or with the indumentum not covering the reticulum.

Illustrations:—Figs. 3J, 4I.

Distribution in D.R. Congo:—Katanga, apparently rare (Fig. 16A). Endemic of D.R. Congo.

Habitat and ecology:—Shrub savannah or herbaceous savannah.

Additional specimens examined:—D.R. CONGO. Katanga: Kazia, savane herbacée, 25 June 1953, *Desenfans 3509* (BRLU!); Kazia, savane arbustive, 25 June 1953, *Desenfans 3584* (BRLU!).

Discussion:—This variety is superficially similar to *Marquesia acuminata* and *Monotes doryphorus*. Its relationship with the latter needs further investigation.

The type specimen of this variety is the sole collection of *M. duvigneaudii* with fruits. Its fruits are young, the wings are 1.5–2.0 × 0.8–1.0 cm with a reddish tinge, and the fruit is ovoid with a conical apex.

7. *Monotes glaber* Sprague (1909: 305)

Lectotype (designated here):—ZIMBABWE, valley of the Hanyani River, 17 May 1909; *Allen 734* (lecto-: K! [barcode K000240353]).

Tree 3–10(–20) m high; branchlets almost glabrous. Leaf: petiole 4–15 mm long, slightly pubescent; blade ovate-elliptic or elliptic to oblong or obovate-oblong, 4–9.5 × 1.5–5 cm, rounded to slightly cordate at the base, obtuse to truncate at the apex; lateral nerves in 7–11 pairs, progressively fading out well before reaching the margin; upper surface finely

reticulate, with reticulum generally orange-lepidote, shiny, glabrous, often yellowish green on drying; lower surface concolorous, smooth, glabrous; midrib and lateral nerves slightly depressed above and prominent beneath, reticulation scarcely prominent, orange-coloured. Inflorescences axillary, 2–4 cm long (shorter in the specimen from D.R. Congo), slender, lax (congested in the specimen from D.R. Congo), 4–10-flowered, brownish, glabrescent, on a slender peduncle 1–1.5 cm long (sessile in the specimen from D.R. Congo). Flower: pedicel ca. 5 mm long; sepals ca. 3 mm long, densely cottony-tomentose; petals ca. 7.5 mm long, brownish white, shortly greyish- or yellowish-sericeous-tomentose; stamens with anthers produced into a very short mucro. Fruit subglobose, 7–12 mm in diameter, sericeous, rounded or slightly conical at the apex; wings 2–3 × 1–1.5 cm, yellow or brownish, elliptic to obovate (description based on Duvigneaud (1961)).

Distribution in D.R. Congo:—A single collection in D.R. Congo, ca. 500 km N of the nearest localities in Zambia.

Distribution elsewhere:—Botswana, Zambia, Zimbabwe.

Habitat and ecology:—Miombo woodlands and wooded savannahs.

Additional specimen examined:—**D.R. CONGO. Upper Katanga:** Upemba, Munoi, bifurcation Lupiala, 890 m, savane arbustive, 3 June 1948, *de Witte 3902* (BR!).

Discussion:—The cited collection is the only one from D.R. Congo that can be tentatively ascribed to *M. glaber*. However, it is atypical in having flowers in dense subsessile cymes. It may represent a distinct taxon, but more material is necessary. See also note under *M. africanus*.

Allen 734 is here chosen as the lectotype, because the other syntype (*Baines s.n.* (K!)) is mounted on a sheet with a mixture of several gatherings.

References:—Bancroft (1939a: 372); Catarino *et al.* (2013: 269); Coates Palgrave (1957: 158, Pl. 160; 2005: 799, Fig. 198); De Wildeman (1927a: 173); Duvigneaud (1949: 43; 1961: 415); Eyles (1916: 421); Hutchinson (1931: 253); Kamumvuri *et al.* (2003: 2192); Lebrun & Stork (1991: 144); Meerts (2016: 223); Van Wyk & Van Wyk (1997: 176); White (1962: 261).

8. *Monotes hirtii* Duvigneaud (1958: 233)

Lectotype (designated here):—D.R. CONGO. Upper Katanga. Nzilo, verger à *Monotes*, 14 June 1957, *Duvigneaud & Hirt 3514M* (lecto-: BRLU! [barcode BRLU0000090022029]; isolecto-: BRLU! (6 sheets)).

Tree (height unknown); twigs densely hirsute, with simple spreading hairs ca. 1 mm long, glabrescent, purplish brown, with conspicuous pale lenticels. Leaves generally grouped at the end of branches; petiole 3–5(–10) mm long, ca. 1.5 mm in diameter, hirsute; blade ovate to ovate lanceolate, 3.4–9(–10.5) × 1.2–4 cm, l/w ratio 2–3, obtuse to rounded to slightly cordate at base, acute to shortly acuminate at apex, with acumen rounded to apiculate, concolorous, dark green to brownish green in herbarium; 10–13(–17) pairs of nerves, impressed on upper surface, prominent on lower surface; upper surface with orange reticulum, harsh to the touch, with simple straight hairs 1–2 mm long; lower surface with prominent reticulum, with similar hairs on the reticulum, areoles glabrous (rarely with a few stellate hairs), with sparse yellow glands; basal gland brown, with a fringe of long straight hairs; midnerve and lateral nerves deeply impressed above and prominent beneath, giving a quilted appearance. Inflorescence a short congested panicle at the end of branches, comprising 3–5 clusters 5–10 mm long, the lowermost ones shortly pedunculate, sometimes with a few axillary cymes. Flower: pedicel 1–3 mm long, slightly accrescent, pubescent; buds rounded, with silky hairs; sepals ovate-triangular, 2–3 mm long; petals oblong, ca. 10 mm long; anther with a short obtuse apical appendix. Fruit ca. 8 × 6 mm, markedly attenuate at tip, with persistent style, often sulcate, hirsute; wings 1.0–2.5 × 0.8–1.2 cm, ovate-elliptic, reddish, with sparse straight hairs and very short fasciculate hairs.

Illustrations:—Figs 3K, 4J, 8C, 15.

Distribution in D.R. Congo:—Upper Katanga. A rare species, with most specimens collected by Duvigneaud between 1956 and 1960 from a restricted area in the region of Nzilo (“district of the NW foothills of Manika”) (Fig. 16E). Endemic of D.R. Congo (Katanga).

Habitat and ecology:—Miombo open forests and wooded savannahs, mostly on rocky slopes and shallow stony soil, with *Brachystegia stipulata* and *B. microphylla*; sometimes forests on deep sandy soil with *B. longifolia*.

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** Keyberg, forêt claire à *Marquesia* sur pisolithes latéritiques, 12 July 1956, *Duvigneaud & Timperman 2003* (BRLU!); Territ. Kolwezi, Nzilo, forêt à *Brachystegia longifolia* sur terre sableuse, 14 June 1957, *Duvigneaud 3513M* (BRLU!); Entre Nzilo et Delcommune, forêt verger à *Brachystegia stipulata* et *Monotes hirtii* sur un replat dans un paysage de collines rocheuses à *Brachystegia microphylla*, 14 December 1959, *Duvigneaud 4554* (BRLU!); Nzilo, forêt enrochée sur crête

gréseuse à *Brachystegia microphylla*, 27 January 1960, *Duvigneaud 5259M* (BRLU!); Nzilo, forêt-verger enrochée de pente quartzitique, 27 January 1960, *Duvigneaud 5261M1* (BRLU!); Nzilo, forêt-verger à *Monotes* div. sp., enrochée, sur phyllades kibariennes, 27 January 1960, *Duvigneaud 5268* (BRLU!); Vallée de la Luilu, 24 km NNW Kolwezi, forêt claire, 16 February 1982, *Empain, Malaisse & Robbrecht 2227* (BR!).

Discussion:—A very distinct species on account of the small acuminate leaves with long straight hairs on both surfaces.

References:—Lebrun & Stork (1991: 144); Meerts (2016: 223).

9. *Monotes hypoleucus* (Oliver) Gilg (1899: 134)

≡ *Vatica africana* Welw. ex Oliver (1868: 173) var. *hypoleuca* Oliv. ≡ *Vatica africana* Welwitsch (1869: 15) var. *hypoleuca* Welwitsch (1869: 17; Tab. 5: Fig. 12).

Lectotype (designated here):—ANGOLA. Huila, Humpata, in schwach schattigen wäldern, December 1859, *Welwitsch 1036* (lecto: LISU! [barcode LISU234079]); paralectotypes: *Welwitsch 1036* (LISU! [barcode LISU234080]); BM! [barcode BM001046018], COI!, P! [barcode P00389099].

Shrub, small tree or tree up to 15(–20) m; branches grey-tomentose to tomentellous, quickly glabrescent. Leaf: petiole (3–)7–21(–40) mm long, 2(–3) mm thick; blade elliptic or ovate-elliptic to obovate-elliptic, (4–)6–16(–21) × (1.5–)2.5–9(–13.5) cm, ca. two times longer than wide, base rounded to slightly cordate, more rarely cuneate, apex rounded to emarginate, very rarely acute, markedly discolorous; secondary nerves in (8–)10–17(–20) pairs, nearly straight but incurved just before and generally without reaching the margin of the leaf, often with a tendency to form shorter subsidiary nerves; upper surface puberulent to almost glabrous, glabrescent, with dense to sparse indumentum not discernible by touch, only visible with a microscope, of more or less flexuous thin hairs 0.1–0.15(–0.25) mm long, most often stellate, in fascicles of 2–6, or, more rarely, simple, variable in shape, never straight, irregularly curled often mixed with yellow globulose glands; lower surface of leaf always discolorous, whitish, cream, beige, yellowish or grayish; secondary nerves and midrib prominent beneath, conspicuous, generally less pubescent and darker than the rest of the lamina, fulvous, brownish, reddish, glabrescent; areoles masked by hairs; reticulum masked or not by pubescence; indumentum of lower surface of leaf extremely variable in thickness and density, short to thick, comprising cottony, curly, crispate or woolly hairs (< 0.1–)0.1–1.5 mm long, often masking a layer of short stellate hairs concentrated in areoles. Inflorescence composed of pedunculated lax axillary cymes 2.5–8 cm long, peduncle densely beige-, grayish- to rufous-tomentose. Flower: pedicel 1–3 mm long, sepals ovate 2–3(–5) mm long, woolly-tomentellous; petals 6–9(–10) mm long, stamens with connective produced into a conspicuous, appendage. Fruit (6–)8–15(–20) mm in diameter, subglobose, sometimes conical and apiculate at the apex, woolly-tomentellous; wings elliptic to narrowly obovate, usually not unguiculate, (2–)2.5–5.5 × (0.4–)1–2 cm, variable in colour, pale brown, straw-coloured, red or purple, variable in shape, generally narrowly oblanceolate to narrowly elliptic, spatulate, markedly attenuate in the lower third, sometimes suborbicular, not hiding the fruit.

Discussion:—We here propose a much more synthetic treatment than earlier revisions, treating *M. angolensis* (incl. *M. carrissoanus*, *M. noldeae*, *M. oblongifolius*, *M. oxyphyllinus*), *M. caloneurus* (incl. *M. elegans*, *M. dawei*, *M. schmitzii*), *M. discolor*, *M. loandensis*, at varietal rank within a much extended species concept for *M. hypoleucus*. With this broader circumscription, *M. hypoleucus* is easily defined by its more or less discolorous leaves, with pubescent greyish, whitish or yellowish lower surface, and upper surface almost glabrous to puberulent with indumentum of very short fasciculate or stellate hairs. This redefined species shows extensive variation in leaf size, density and persistence of upper surface indumentum, and in thickness, extent and colour of the indumentum on the lower surface. That variation is extremely difficult to translate into a coherent taxonomic system. Most characters have a continuous variation within the complex. The five varieties retained here represent the most common nodes of a reticulate variation pattern. In our judgement, however, it is useful to distinguish these varieties and thus show the structure present in the pattern, which might be linked to ecology and/or geography. A fair number of intermediate specimens exist, which can conveniently be referred to as *M. hypoleucus* s.l.

Bancroft (1939a) already emphasized the close affinity between *M. angolensis* and *M. hypoleucus*. Duvigneaud (1949) was aware that the abovementioned “species” might represent varieties rather than true species and mentioned the existence of intermediates (p. 47, about *M. elegans*, *M. angolensis*, *M. schmitzii*: “Il est d’ailleurs fort probable qu’il ne s’agit là que de variétés d’une même espèce...”; p. 48, about *M. hypoleucus* and relatives: “...très apparentées aux espèces du groupe *caloneurus-angolensis*, avec lesquelles elles semblent former souvent des hybrides.”). Verdcourt also suspected that *M. caloneurus*, *M. elegans* and *M. angolensis* were not distinct at species rank, but “...did not want to tamper with the classification of Duvigneaud.” (Verdcourt 1989: 10). A critical reexamination of Duvigneaud’s

collections is particularly instructive, since a fair amount of material belonging to this complex was left by him without a name; quite often, Duvigneaud's hesitations are apparent in the form of several name changes *in schedis*. Obviously, Duvigneaud's treatment, as accepted by all subsequent authors, was an overly simplified representation of a much more complex biological reality.

Taxonomic difficulties are also aggravated by the ontogenic changes in hair density on both surfaces, with the upper surface of old leaves eventually becoming glabrous in all morphs, and the lower surface changing colour with ageing.

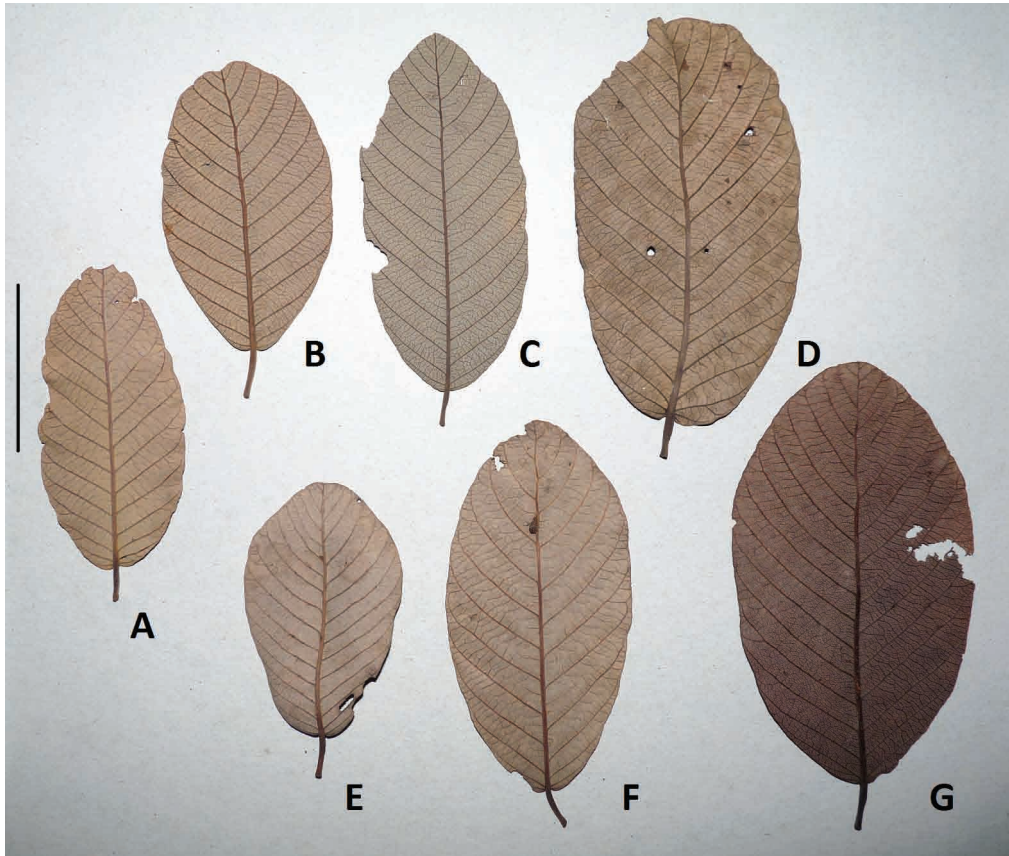


FIGURE 12. Colour photographs of leaves: *Monotes hypoleucus* var. *caloneurus*. **A.** Duvigneaud 4764, **B.** Duvigneaud 4850, **C.** Duvigneaud 3203, **D.** Duvigneaud 3338, **E.** Duvigneaud 2123, **F.** Duvigneaud 5095, **G.** Duvigneaud & Timpeman 2109. Scale bar = 5 cm.

Key to the varieties:

1. Petiole 18–35 mm long; fruit 15–20 mm in diameter; sepals 4–5 mm long; upper surface of leaf glabrous (except nerves), reticulate 9d. var. *discolor*
- Petiole (3–)7–21 mm long; fruit (6–)8–15 mm in diameter; sepals 2–3 mm long; upper surface of leaf glabrous or puberulent, reticulate or smooth 2

2. Indumentum on lower surface of leaf markedly thick and continuous, beige or cream (Fig. 3L), of tangled woolly or cottony hairs mostly > (0.5–)0.8 mm long; reticulum and areoles covered by hairs and generally not visible; leaf blade (10–)12–16(–20) × (5.5–)7–9(–13) cm 9a. var. *hypoleucus*
- Indumentum on lower surface of leaf generally thin and discontinuous, whitish, greyish or yellowish, with shorter crispate, curly or cottony hairs mostly < 0.8 mm long; reticulum often conspicuous; leaf blade often smaller (4–)7–14(–18) × 1.5–8.5 cm 3

3. Indumentum of lower surface of leaf generally yellowish, much more rarely greyish or whitish (Fig. 3M), of extremely short (< 0.1(–)0.2 mm), very crispate hairs with the lumen occupying a third of the diameter or less (≤ 5 μm); upper surface of leaf mostly without yellow glands; leaf blade 4–9(–10) × 1.5–4(–5) cm 9b. var. *angolensis*
- Indumentum of lower surface of leaf greyish to whitish, never yellowish, partly or entirely made of curly to cottony hairs (longest hairs: 0.3–0.8 mm), with the lumen occupying ca. half of the diameter (ca. 8 μm), mixed with short stellate hairs in areoles; upper surface of leaf with yellow glands; leaf blade variable in size 4

4. Leaf blade elliptic-spathulate, up to 9 × 4 cm; basal gland narrowly elliptic, 2–4 times longer than wide; lower surface of leaf with costa and secondary nerves almost glabrous, reddish-chestnut 9e. var. *loandensis*
 - Leaf blade elliptic, ovate-elliptic, obovate-elliptic, not spathulate, 6–14(–18) × 3–8.5 cm; basal gland rounded or shortly elliptic, 1 or 2 times longer than wide; lower surface of leaf with nerves more or less pubescent or, if almost glabrous, not reddish-chestnut 9c. var. *caloneurus*

9a. *Monotes hypoleucus* (Oliv.) Gilg var. *hypoleucus*

= *Monotes kapiensis* De Wildeman (1927a: 175; 1927b: 56); Bancroft (1937: 141; 1939a: 345). Lectotype (designated here):—D.R. CONGO. Vallée de Kapiri, versant plateau, February 1913, *Homblé 1228* (lecto-: BR! [barcode BR0000008891617], iso-: BR! [barcode BR0000008891334]).

Small tree or more often a stunted shrub; branches shortly grey-tomentose, glabrescent. Leaf: petiole 9–21 mm long, ca. 2 mm in diameter; blade broadly elliptic or ovate-elliptic to obovate-elliptic, (10–)12–16(–20) × (6–)7–9(–13) cm, base rounded to slightly cordate, apex rounded to emarginate, strongly discolorous; secondary nerves in (9–)13–17 pairs, fulvous-brownish below, contrasting with indumentum, of short crispate fulvous hairs, soon glabrescent, tertiary nerves slightly impressed above; upper surface generally brownish in herbarium, puberulent with more or less sparse persistent indumentum of more or less flexuous thin hairs 0.1–0.15 mm long in fascicles of 2–6, and yellow spherical glands; lower surface whitish to cream or beige, with thick dense indumentum of tangled woolly hairs, masking reticulum and areoles, with longest hairs > (0.5–)0.8 mm long, indumentum eventually becoming grayish and thinner in old leaves. Inflorescence composed of many-flowered long-pedunculated axillary cymes 5–8 cm long, peduncle densely tomentose, beige. Flower: pedicel 1–3 mm long, sepals ovate ca. 3 mm long, petals ca. 9 mm long. Fruit ca. 10–15 mm in diameter, spherical, subapiculate; wings elliptic to narrowly obovate, not unguiculate, 2.5–5 × 1–2 cm, pale brown.

Illustrations:—Figs. 3L, 4K, 5H,I.

Distribution in D.R. Congo:—Widespread in Kwango; rare in Katanga (Biano, Kundelungu).

Distribution elsewhere:—Angola, Zambia (first record for that country: *Mutumushi 1857* (K!)).

Habitat and ecology:—In Kwango in mixed dry semi-evergreen forests of the alliance Berlinio-Marquesion, especially the association with *Marquesia macrourea* and *Uapaca nitida*, subassociation with *Berlinia giorgii*; degraded forests (« Matumbi ») in contact with the steppic savannah (Devred 1957); miombo forests; in Upper Katanga in shrubby savannahs on Kalahari sand.

Vernacular names:—Kipapa (Kiluba), mupampa, mupemba (Kiyaka).

Other representative specimens examined:—D.R. CONGO. **Kasaï** (Kwango): Route Mawanga-Imbela, km 13, forêt claire, 19 July 1975, *Breyne 2611* (BR!); Vers Munene, savane boisée, 14 April 1953, *Callens 1158* (BR!); Haute-Muniungu, savane boisée, 14 April 1953, *Callens 1159* (BR!, KISA); Kiwangala, forêt sèche, 22 April 1953, *Callens 2952* (BR!); Bwana Mutombo, Matumbi, 7 July 1952, *Callens 3126* (BRLU!, KISA); région de Imbela, forêt sèche, 2 May 1953, *Callens 4121* (BR!); région de Imbela, savane boisée, 2 May 1953, *Callens 4122* (BR!, KISA); Mobanga, Mikondo, sous-bois, 19 March 1955, *Devred 1673* (BR!); Ingolobo (entre Popobakata et Munene), bosquet à *Monotes*, *Uapaca*, *Berlinia*, 27 April 1948, *Duvigneaud 774M* (BRLU!); Entre Ingolobo et Munene, steppe sableux reverdi après l'incendie, 27 April 1948, *Duvigneaud 779M* (BRLU!); Kenge, 30 km N de Munene, forêt claire à *Brachystegia wangermeeana-Uapaca*, 1 May 1948, *Duvigneaud 822* (BRLU!); Kahemba, forêt claire autour de la mission, 30 May 1948, *Duvigneaud 949M* (BRLU!); Kahemba, forêt de savane à *Brachystegia* sur sable du Kalahari, 5 October 1948, *Robyns 3727* (BR!, WAG!). **Upper Katanga:** Kyongwe (Relevé 142), 1300 m, forêt claire, 15 May 1953, *Desenfans 3226* (BRLU!); Steppe arbustive près de Lusinga (Kibara), 1650 m, *Lisowski, Malaisse & Symoens 4412* (POZG!).

Discussion:—*Monotes kapiensis* was synonymized with *M. discolor* by Bancroft (1939a) and with *M. hypoleucus* by Duvigneaud (1949). See note under var. *discolor*. Some collections from Kwango have very large leaves reminiscent of var. *discolor*, however they have fruits 12–15 mm in diameter and leaves with a puberulent upper surface (*Callens 4122*; *Devred 1673*).

Intermediates with var. *caloneurus* exist: *Duvigneaud 4667M* (BRLU!).

Hiern (1896: 62) correctly attributes this variety to Oliver by citing “*Vatica africana* Welw. ex Oliv. var. *hypoleuca* Oliv.”. Oliver, in the Flora of Tropical Africa (Oliver 1868: 173) wrote: “*Vatica africana*, Welw. in Linn. Trans. xxvii (ined.) t. 5”, clearly indicating that he did not want to publish the name. However, according to the rules of the International Code of Nomenclature (McNeill *et al.* 2012) the correct authority for *Vatica africana* is indeed Welw. ex Oliv., or just Oliv.

References:—Bancroft (1937: 140; 1939a: 379); Catarino *et al.* (2013: 269); De Wildeman (1913a: 42; 1921: 133; 1927a: 175); Durand & Durand (1909: 48); Duvigneaud (1949: 49); Engler (1921: 520); Figueiredo & Smith (2008: 67); Gilg (1908b: 288); Hiern (1896: 62); Lebrun & Stork (1991: 144).

9b. *Monotes hypoleucus* var. *angolensis* (De Wild.) Meerts, *comb. et stat. nov.*

Basionym: *Monotes angolensis* De Wildeman (1927a: 168); Bancroft (1937: 140; 1939a: 346, 379); Catarino *et al.* (2013: 267); Duvigneaud (1949: 46; 1961: 417); Exell & Mendonça (1951: 371); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144); White (1962: 262, fig. 46B).

Lectotype (designated here):—ANGOLA. Huila, Dongo, Forte Maria Pia, 8 February 1907, *Gossweiler 2910* (lecto-: BR! [barcode BR0000008891259], isolecto-: BM! [barcode BM001046015], COI!, K! [barcode K000240362], LISC).

= *Monotes oblongifolius* Hutchinson (1931: 248); Bancroft (1939a: 349). ≡ *Monotes angolensis* var. *oblongifolius* (Hutch.) Duvigneaud (1949: 47). Type:—ZAMBIA. Kaloswe, *Hutchinson & Gillet 3765* (holo-: K! [barcode K000240340]).

= *Monotes noldeae* Bancroft (1936b: 226); Bancroft (1937: 137); Bancroft (1939a: 355); Catarino *et al.* (2013: 270); Figueiredo & Smith (2008: 67). Type:—ANGOLA. Malange, Huila, April 1933, *Nolde 202* (holo-: BM! [barcode BM000603393]; iso-: BRLU! (fragm.), LISC!), *syn. nov.*

= *Monotes carrissoanus* Bancroft (1939a: 356, 1939b: 110); Catarino *et al.* (2013: 267); Exell & Mendonça (1951: 371); Figueiredo & Smith (2008: 67). Type:—ANGOLA. Moxico, between Caxipoque and Munhango, 7 May 1937, *Exell & Mendonça 1788* (holo-: BM! [barcode BM000603395]; iso-: BR!, BRLU! (fragm.), COI), *syn. nov.*

Diagnosis:—Differs from the type variety by the following traits: leaf blade smaller, 4–9(–10) × 1.5–4(–5) cm; lower surface with indumentum of extremely short (< 0.1(–0.2) mm), generally yellowish, crispate hairs, generally denser in areoles than on reticulum; upper surface reticulate, generally almost glabrous.

Tree up to 17 m high; branchlets tomentellous, soon becoming glabrous, often striated. Leaf: petiole (3–)7–20 mm long, relatively slender (1.5–2 mm in diameter); blade elliptic to ovate elliptic or obovate-elliptic, 4–9(–10) × 1.5–4.5(–5) cm, obtuse to rounded to slightly cordate at the base, more rarely cuneate, obtuse to truncate or slightly emarginate at the apex, sometimes acute (f. *oxyphyllinus*), discolorous; upper surface generally reticulate, at first with minute flexuous simple or fasciculate scattered hairs (< 0.2 mm), most often becoming almost glabrous except on nerves (more rarely persistently puberulent), sometimes viscid, rarely glandular-granulose; lower surface smoothly tomentellous, often more or less yellowish, much more rarely whitish, with extremely short coiled or crispate hairs covering the interreticular areoles most often < 0.2 mm long, with the lumen occupying a third of the diameter (ca. 5 µm) or less, yellowish to whitish; midrib prominent beneath; lateral nerves in (8–)10–13 pairs, with a very strong tendency to the formation of subsidiaries, nearly straight but incurved just before and generally without reaching the margin of the leaf, pubescent to almost glabrous; reticulum on undersurface often well visible, not hidden by hairs, glabrescent, more rarely tomentellous as the areoles and less visible. Inflorescences up to 2.5 cm long, axillary, relatively lax, few-flowered, greyish-tomentose, on a long slender peduncle. Flower: pedicel 3 mm long, sepals ovate 2–3 mm long, woolly-tomentellous; petals 6–8 mm long, densely sericeous-tomentellous; stamens with connective produced into a short triangular appendage. Fruit (6–)8–12 mm in diameter, subglobose, woolly-tomentellous, generally conical and apiculate at the apex; wings shiny, red or purple, sometimes pale brown or straw coloured, (2–)3–5 × 0.4–1(–2) cm, generally narrowly oblanceolate to narrowly elliptic, markedly attenuate in the lower third, not hiding the fruit.

Variation:—Our circumscription of var. *angolensis* is somewhat broader than *M. angolensis* De Wild. *sensu stricto*. In its typical form (leaf blade with yellow lower surface, conspicuous dark reticulum, base and apex rounded), *M. angolensis* is a striking and easily recognized taxon; however, typical forms are less frequent than intermediates with other forms in the complex. First, the taxonomic value of the yellow pigment in the indumentum of the lower surface of the leaf has been overestimated. Some collections with greyish indumentum do not differ from typical collections in other traits (e.g. *Liben 3816*; *Desenfans 2619*; *Duvigneaud 2545M1*, *4636M1* (BRLU!); *Lisowski, Malaisse & Symoens 11401* (POZG!). Secondly, in its typical form, var. *angolensis* has a very conspicuous reticulum not covered by hairs and darker than the areoles. However, in some forms the indumentum does cover the reticulum. *Monotes noldeae*, known from one or two collections from Angola, is one of such forms; specimens matching the type have been found in D.R. Congo (e.g. *Duvigneaud & Timperman 2402M* (BRLU!)). Such forms are closely related to *Monotes oblongifolius*, already synonymized with *M. angolensis* by Duvigneaud (1961) and because of a lack of any reliable discriminant character to maintain those taxa even at a low rank, we decided not to recognize them.

The four syntypes of *M. angolensis* differ in pubescence of the upper surface of the leaf; *Gossweiler 2893* and *Gossweiler 2910*, from Angola, are persistently puberulent, while *Delevoy 502* and *Delevoy 523*, from D.R. Congo, are almost glabrous (except on nerves); those four specimens are otherwise very similar. There is apparently geographic

variation in pubescence, since most of the copious material from D.R. Congo is glabrous, while material from Angola tends to be more pubescent. This once again illustrates extensive species polymorphism in *Monotes*, and the need of a broad species concept. It seems appropriate to choose a specimen from Angola as the lectotype; *Gossweiler 2910* [barcode BR0000008891259] is here chosen because it has flowers while the specimen *Gossweiler 2893* [barcode BR0000009860414] does not.

Monotes carrissoanus, another putative endemic of Angola known from only two collections, is very similar to typical var. *angolensis*, having a yellowish lower surface of the leaf and strikingly contrasting darker reticulum; phenotypes matching the type were collected in Upper Katanga (e.g. Plateau de la Manika, Uapacetum robynsii en bordure de steppe, 1957, *Duvigneaud 2545M2* (BRLU!); Nzilo, dépression avec *Monotes angolensis*, 14 June 1957, *Duvigneaud 3517* (BRLU!)); the new material from D.R. Congo shows that the supposed discriminant characters (particular pattern of tertiary venation, long petioles) represent individual variation occurring within the polymorphic var. *angolensis* and intermediates with other morphs occur in Katanga (e.g. *Duvigneaud & Timperman 2704*; *Duvigneaud 4541M1* (BRLU!); *Duvigneaud 4653* (BRLU!)). Thus, *M. carrissoanus* cannot be maintained even at low rank.

Dwarf forms are sometimes found (*Plancke 121/1590*, *121/1600* (BRLU!)), but it is unclear if such specimens represent suckers or a genuinely suffruticose variety.

The shape of leaf apex and the colour of lower surface of leaf are variable; two forms can be recognized, with a range of intermediates.

Key to the forms:

1. Leaf apex rounded to emarginate; lower surface of leaf yellowish 9ba. forma *angolensis*
- Leaf apex acute; lower surface of leaf greyish to whitish 9bβ. forma *oxyphyllinus*

9ba. *Monotes hypoleucus* var. *angolensis* (De Wild.) Meerts forma *angolensis*

Illustrations:—Figs. 3M, 4L, 5D,E, 10A–F.

Distribution in D.R. Congo:—Kwango, Lower Katanga, Upper Katanga.

Distribution elsewhere:—Angola, Zambia; mostly in the Centro-Angolan sector of the Zambebian region.

Habitat and ecology:—Miombo woodland, stunted miombo woodland with *Brachystegia spiciformis* and *Acrocephalus suberosus*; wooded savannah at the periphery of mineralised clearings; mixed dry semi-evergreen forests (“Mabwati”); wooded savannah; low, open miombo woodland, shrubby savannah, edge of dambos, often on Kalahari sand.

Vernacular names:—Kafuti (Kibemba), kipapa (Kibemba), mukala nsisi (Kitchok), mutembo (Kiluba), muyembe (Kitchok).

Other representative specimens examined:—ANGOLA. Huila, Ganguelas, February 1907, *Gossweiler 2893* (syntype: BM! [barcode BM001046016], BR!, COI, K! [barcode K000240361], LISC! [barcode LISC019508]).—

D.R. CONGO. Kasai (Kwango): Matambu, Kalenge, savane boisée dense, 14 April 1953, *Callens 1180* (BR!, KISA); près de Kitenda, savane boisée, *Callens 2169* (BM!, BR!); Kahemba, 29 April 1955, *Devred 1843* (BR!). Lower Katanga: Sazoza (route Kapanga-Sandoa, à la limite des deux territoires), forêt claire non dégradée, 5 October 1957, *Liben 3816* (BR!). Upper Katanga: 12 December 1921; *Delevoy 502* (syntype: BR!); 21 December 1921, *Delevoy 523* (syntype: BR!); Upemba [loc. illegible], 1140 m, 14 February 1948, *de Witte 03355* (BR!); Plateau des Bianco, bosquet à *Monotes* près d’une tête de source, 6 September 1956, *Duvigneaud & Timperman 2638* (BRLU!); Mitwaba, verger à Dipterocarpaceae sur sol de plateau, 17 January 1960, *Duvigneaud 5095M* (BRLU!); Plateau de la Manika, ferme Herman, forêt chypia sur sable au N de la ferme, 22 January 1960, *Duvigneaud 5212BM* (BRLU!); Kasekelesa, chantier 7, forêt claire mélangée sur terre brun-rouge sur sous-sol manganifère, 24 January 1960, *Duvigneaud 5228M* (BRLU!); Territoire de Sakania, env. Kipushia, Mont Kasamwa, savane, 1250 m, 29 April 1971, *Lisowski B-8946* (POZG!); à 6 km de Katentania, plateau des Bianco, savane à *Uapaca* et *Philippia*, près du Kraal de Maniungwe, alt. 1600 m, *Symoens 5829* (BRVU!); Près de Kiniamia, le long de la route Bianco-Lubudi, steppe arbustive à *Albizia antunesiana*, alt. 1600 m, 7 May 1966, *Symoens 12566* (BRVU!, K!); Katomia, Marungu, 10 June 1939, *Vanden Brande 182* (BR!).

9bβ. *Monotes hypoleucus* (Oliv.) Gilg var. *angolensis* (De Wild.) Meerts forma *oxyphyllinus* (P.A. Duvigneaud) Meerts, *comb. et stat. nov.*

Basionym: *Monotes oxyphyllinus* Duvigneaud (1949: 45 & Fig 12 a-d); Lebrun & Stork (1991: 144); Meerts (2016: 223).

Type:—D.R. CONGO. Haut-Kwango, Kahemba, 30 May 1948, *Duvigneaud 950M* (holo-: BRLU! [barcode BRLU0000090022548]; iso-: BRLU! (2 sheets), BM! (fragm.))

Diagnosis:—Leaf apex acute (at least in some leaves), petiole short, 3–10 mm long, lower surface of leaf whitish to greyish (not yellowish).

Illustration:—Fig. 5D, 10B.

Distribution in D.R. Congo:—Kwango, Upper Katanga.

Habitat and ecology:—Wooded savannahs.

Vernacular names:—Mutetetwa (Kitchok), mukala nsisi, mupemba nseke (Kitchok).

Other representative specimens examined:—**D.R. CONGO. Kasai** (Kwango): près Kitenda, savane boisée, 16 February 1950, *Callens 2169* (BM!, BR!, KISA); Bwana, 22 April 1953, forêt sèche, *Callens 3044* (BR!, KISA); Kidima, Nkwati, 4 February 1952, *Callens 3051* (BM!, KISA); Kambangu, forêt sèche, 23 April 1953, *Callens 3912* (BR!); 86 km N Kahemba, début de la forêt claire, brousse à *Pseudolachnostylis*, 29 May 1948, *Duvigneaud 948M* (BRLU!); Gunza, 10 km SE Kajiji, savane à *Monotes-Protea* sur sable, 1 June 1948, *Duvigneaud 975M* (BRLU!). **Upper Katanga:** Mubale, 1555 m, savane arbustive sèche, sur phyllades, 9 March 1953, *Desenfans 2618* (BRLU!); Vallée Munte, relevé 150, savane boisée, 22 August 1953, *Desenfans 4162* (BRLU!); Kolwezi, plateau de la Manika, Uapacatum *robynsii* en bordure de steppe, 29 August 1956, *Duvigneaud 2545M* (BRLU!); Mitwaba, plateau des Kibara au N du poste, verger à *Monotes* sur sol latérisé, 9 September 1956, *Duvigneaud & Timperman 2695* (BRLU!).

Discussion:—The diagnostic combination of traits often breaks down and forma *oxyphyllinus* is connected to other variants by many intermediates making a higher rank inappropriate (e.g. intermediates with forma *angolensis*: *Desenfans 384, 2618, 5945*; *Duvigneaud 3322, 3526*; *Duvigneaud & Timperman 2288, 2704*). Some collections have an almost glabrous lower leaf blade surface, with only a few stellate hairs in the areoles, and tend to be heterophyllous with markedly larger leaves on some twigs (regrowth?) (*Desenfans 3033, 3120*; *Duvigneaud 985M*); such forms may deserve taxonomic recognition but more material is needed.

9c. *Monotes hypoleucus* (Oliv.) Gilg var. *caloneurus* (Gilg) Meerts, *comb. et stat. nov.*

Basionym: *Monotes caloneurus* Gilg (1899: 136, excl. *Schweinfurth 2678* (B†, K!)); Bancroft (1937: 137; 1939a: 360); Catarino *et al.* (2013: 267); De Wildeman (1927: 170); Duvigneaud (1949: 44); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144).

Lectotype (designated here):—ANGOLA. Malange, March 1880, *Mechow 455* (lecto-: W! [barcode W1889-0054616]; isolecto-: B†, photo: BM!, K!).

= *Monotes elegans* Gilg (1908b: 291); Bancroft (1939a: 340, 376, 379); Catarino *et al.* (2013: 268); De Wildeman (1927: 172); Duvigneaud (1949: 47; 1961: 419); Engler (1921: 522); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144); Verdcourt (1989: 9); White (1962: 262). **Type:**—TANZANIA, bei Tabora, between Rubugwa and Mkigwa, miombowald, *Holtz 1474* (holo-: B†; BRLU! (photo of holotype)), *syn. nov.*

= *Monotes dawei* Bancroft (1936a: 43); Bancroft (1937: 141; 1939a: 354); Catarino *et al.* (2013: 268); Figueiredo & Smith (2008: 67). **Lectotype, designated here:**—ANGOLA, Bié, Libolo, Longa river, Dec. 1921, *Dawe 324* (lecto-: K!). ≡ *Monotes caloneurus* var. *dawei* (H.H. Bancr.) Duvigneaud (1949: 44); Lebrun & Stork (1991: 144), *syn. nov.*

= *Monotes schmitzii* Duvigneaud (1949: 51); Lebrun & Stork (1991: 144). **Lectotype (designated here):**—D.R. CONGO. Upper Katanga, Mukuen [incorrectly spelled “Metuen” in the protologue], 10 km SSW Elisabethville, sommet de la pente sud, sol superficiel, nombreux blocs rocheux, 15 April 1947, *Schmitz 469* (lecto-: BR! [barcode BR000005847105], isolecto-: BRLU!, YBI!), *syn. nov.*

Diagnosis:—Differs from the type variety by the following traits: indumentum of lower surface of the leaf thinner and/or sparser, with cottony or curly hairs, mostly < 0.8 mm, generally not completely hiding reticulum, or, when hiding reticulum, upper surface persistently tomentellous with stellate hairs.

Tree up to 15(–20) m high; branchlets tomentellous, becoming glabrous. Leaf: petiole 6–20 mm long, rather slender; leaf blade elliptic to ovate-elliptic or obovate-elliptic, (6–)7–14(–18) × 3–8.5 cm, obtuse, rounded to slightly cordate at the base, rounded to slightly emarginate at the apex; upper surface smooth, sparsely to densely puberulent or tomentellous, more or less glabrescent; hairs very short, not exceeding 0.15(–0.25) mm (often much shorter) and not discernible by touch, only visible with a microscope, simple, fasciculate, or stellate, variable in shape, never straight, irregularly curled, always mixed with yellow glands; lower surface discoloured, greyish, beige or whitish, with reticulum either conspicuous (hairs sparse) to inconspicuous (covered by indumentum); hairs variable in length

and density, with relatively short curled to cottony hairs on the nerves and reticulation, with the lumen occupying ca. half of the diameter (ca. 8 µm), and with the interreticular areoles densely covered with minute stellate hairs; at least some hairs > 0.3 mm long; midrib prominent beneath; lateral nerves in 12–16 pairs (with a strong tendency to the formation of short subsidiaries) curving towards the apex just before and without reaching the margin of the leaf; veins conspicuous; Inflorescences up to 8 cm long and 4 cm wide, axillary, pedunculate, relatively lax, many-flowered, greyish- or fulvous-tomentose; pedicels 2–3 mm long. Flower: sepals 3 mm long, with a dense cottony tomentum; petals 10 mm long, densely rufous-sericeous-tomentose; stamens with anthers produced into a rounded appendage. Fruit 10–15 mm in diameter, subglobose, rounded or slightly subconical at the apex; wings reddish or brownish, very variable in shape, suborbicular (2.5–2 cm in diameter) to linear (5.5 × 0.8 cm).

Illustrations:—Figs. 3N, 4M, 5F,G, 12A–G.

Distribution in D.R. Congo:—Lacs Edouard et Kivu, Upper Katanga, widespread.

Distribution elsewhere:—Angola, Burundi, Tanzania, Zambia; widely distributed in the north of the Zambezi Region.

Habitat and ecology:—Miombo woodlands on various types of soil, often on hill tops, on rocky soil; Brachystegieta-Monotetum katangense, sous-association à *Brachystegia utilis* (Schmitz 1971), degraded shrubby savannah on sandy soil.

Vernacular names:—Kansimba (Kiholoholo), kassumba (Kibemba), kimpampa (Kibemba), mumpunge (Kiholoholo), muyembe (Kiluba).

Uses:—Host of the edible caterpillar of the cavorting emperor moth, *Usta terpsichore* (Saturniidae) (Malaisse 1997); fire wood (N of Kalemie).

Other representative specimens examined:—ANGOLA. Malange, January 1880, *Mechow 434* (B†, M!, W!).—D.R. CONGO. Lacs Edouard et Kivu: Réserve forestière Colonie, Musingiro, April 1944, *Michelson 601* (BR!). Lower Katanga: Kaniama, savane claire, March 1938, *Herman 2222* (BR!). Upper Katanga: Route Baudouinville-Kapona, sol sablonneux, 17 July 1957, *Devred 3480* (BR!); Plateau des Bianco, 32 km N de Tenke, bosquet à *Uapaca-Philippia* sur sable, 3 August 1948, *Duvigneaud 1318M2* (BRLU!); S de Bianco-gare, vallon, pente sableuse, forêt claire à *Brachystegia-Monotes*, 6 August 1948, *Duvigneaud 1350M* (BRLU!); Entre Mukumbi et Swambo, 13 km E of Swambo, forêt claire à *Brachystegia spiciformis* sur plateau, terre rouge profonde, *Duvigneaud & Timperman 2109* (BRLU!); Mindingi, colline dominant la route, broussailles arbustives, 1 August 1956, *Duvigneaud & Timperman 2190M* (BRLU!); Mukumbi, brousse très arbustive de dégradation de la forêt claire sur sol sableux gris-rose, 3 August 1956, *Duvigneaud & Timperman 2195* (BRLU!); Kisenge, route de Divuma, forêt claire à *Marquesia*, et *Isobertia* sur terre grise compacte, 19 August 1956, *Duvigneaud & Timperman 2371* (BRLU!); Mitonte, forêt claire sur terre rouge, 3 May 1957, *Duvigneaud 3006 Mo* (BRLU!); Tantara, forêt à *Brachystegia microphylla* sur colline rocheuse, 14 May 1957, *Duvigneaud 3203* (BRLU!); entre Mukumbi et Swambo, forêt claire sur terre ocre compacte, 1 June 1957, *Duvigneaud 3338M1A* (BRLU!); Entre Swambo et Mukuni, forêt claire à *Brachystegia floribunda* sur terre rouge, 1957, *Duvigneaud 3345M4* (BRLU!); Musoshi, forêt claire à *Marquesia macroura*, 6 June 1957, *Duvigneaud 3424* (BRLU!); Entre Jadotville (Likasi) et Kambove, forêt claire sur terre rouge, June 1957, *Duvigneaud 3560Mo* (BRLU!); Mitwaba, verger à Dipterocarpaceae sur sol de plateau, 17 January 1960, *Duvigneaud 5095M* (BRLU!); 10 km S of Mitwaba, bosquet de pente à *Uapaca*, 17 January 1960, *Duvigneaud 5096M* (BRLU!) (“typical *M. caloneurus*” *fide* Duvigneaud *in schedis*); 12 km NW of Elisabethville (Lubumbashi), parcelle expérimentale de forêt claire sur sol ocre profond sur dolomie, *Gathy 93* (BRLU!); Mukuen, January 1948, *Schmitz 1332* (para-: BR!).

Discussion:—Var. *caloneurus* is the least well-defined entity within *M. hypoleucus*. It comprises a group of forms, extremely variable in density and persistence of the indumentum on the upper surface, distribution and thickness of the indumentum on the lower surface and leaf size. Variation of most of these traits is continuous. Even though some combinations of traits seem more frequent than others, we have not been able to find any reliable diagnostic trait to separate *M. elegans*, *M. caloneurus* and *M. schmitzii*.

The typification of *Monotes caloneurus* Gilg is problematic. Of the six specimens cited in the protologue, *Schweinfurth 2678*, originating from the Sudanian region belongs in *M. kerstingii* Gilg as already pointed out by Hutchinson & Dalziel (1927) and Bancroft (1939a). Both *Büchner 159* and *Büchner 524* have been lost in Berlin and no duplicates apparently exist. *Mechow 434* (W!, M!) and *Mechow 455* (W!) are the only syntype specimens remaining from Angola. *Mechow 434* deviates from the usual description of the taxon in having areoles mostly glabrous and indumentum restricted to the reticulum and hence, being very weakly discoloured. *Mechow 455* does show the pubescent areoles and is therefore here chosen as the lectotype.

The protologue of *M. schmitzii* cites two syntypes, collected from the same tree at two dates (*Schmitz 469*, with fruits; *Schmitz 1332*, with flowers). *Schmitz 469* is here chosen as the lectotype, because it has more extensive collecting information on the label.

Soon after its description, *Monotes dawei* was already recognized by Bancroft herself (1939a: 354) "...to be the least distinct member of the *caloneurus* group of forms..." and to represent "...a somewhat extreme, narrow-leaved form of *M. caloneurus* itself.". Such forms are certainly not endemic of Angola (Duvigneaud 1949: 45) (e.g. *Luxen 151* (BR!) and *Luxen 152* (BR!, P!)), both from Lower Katanga near Kalemie, and belong in the phenetic variation space of *M. hypoleucus* var. *caloneurus*.

The limits between var. *caloneurus* and var. *hypoleucus* are blurred by intermediate specimens (e.g. *Desenfans* s.n. (BRLU!), *Desenfans 5707* (BRLU!), *Duvigneaud 3676* (BRLU!), *Herman 2222* (BR!)). Although there is great overlap in leaf size between var. *angolensis* and var. *caloneurus*, the largest-leaved morphs of var. *angolensis* tend to have a glabrous upper surface of the leaf while the smallest-leaved forms of var. *caloneurus* generally have a densely tomentellose upper surface.

9d. *Monotes hypoleucus* var. *discolor* (R.E.Fr.) Meerts, *comb. et stat. nov.*

Basionym: *Monotes discolor* Fries (1914b: 153, t. 12 fig. 13–14); Bancroft (1937: 141; 1939a: 342, 378); De Wildeman (1927a: 172); Duvigneaud (1949: 50; 1961: 416); Engler (1921: 520); Exell & Mendonça (1951: 371); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144); Meerts (2016: 223); White (1962: 262; fig. 46A).

Type:—ZAMBIA. Mporokoso, 31 October 1911, *Fries 1175* (holo-: S!; iso-: UPS).

Diagnosis:—Differs from the type variety by the following traits: petiole longer, 18–40 mm (vs. 9–21 mm); fruit bigger, > 15 mm in diameter (vs. 10–15 mm), sepals longer (4–5 mm (vs. ca 3 mm)); upper surface of leaf glabrous, markedly reticulate, often more or less shiny.

Small tree up to 12 m high; branchlets pubescent, soon becoming glabrous. Leaf: petiole 20–40 mm long, ca. 3 mm in diameter; blade broadly elliptic to obovate or suborbicular, 13–21 × 8–13.5 cm, less than twice as long as wide, rounded or more often cordate at the base, rounded, truncate or emarginate at apex; upper surface green to yellowish-green, not turning brown in herbarium, finely reticulate, somewhat shiny, with numerous spherical yellow glands, glabrous except for the midrib; lower surface strikingly discolorous, whitish to cream, cottony-tomentose with curled or coiled hairs on the nerves and reticulation and completely hiding the reticulation and interreticular areoles, which are densely covered with minute stellate hairs, more rarely (f. *cordatus*) long hairs almost lacking and stellate hairs covering all the surface; midrib and lateral nerves slightly depressed above and very prominent beneath; lateral nerves in 16–21 pairs, curving towards the apex without reaching the margin of the leaf. Inflorescences axillary on young short leafy shoots; peduncles 3–8 cm long, relatively few-flowered and lax, densely rufous-tomentose. Flower: pedicel ca. 3 mm long, sepals 4–5 mm long, densely cottony-greyish-tomentose; petals ca. 10 mm long, densely fulvous-sericeous-tomentose; stamens with connective produced in a long triangular-oblong lobe ca. half as long as anther. Fruit 20 mm in diameter, subglobose, ± truncate and apiculate at the apex; wings 4.5–5.5 × 1–2 cm, brownish, spatulate, with sparse minute fasciculate hairs outside and inside.

Variation:—Var. *discolor* is variable in the indumentum on lower surface of the leaf and two forms can be distinguished.

Key to the forms:

1. Indumentum of lower surface of leaf with long woolly hairs masking the stellate hairs 9da. forma *discolor*
- Indumentum of lower surface of the leaf almost without woolly hairs, with stellate hairs well visible 9dβ. forma *cordatus*

9da. *Monotes hypoleucus* var. *discolor* (R.E.Fr.) Meerts forma *discolor*

= *Monotes discolor* var. *lanatus* Duvigneaud (1959: 102; 1961: 416); Lebrun & Stork (1991: 144).

Type:—ZAMBIA. Mwinilunga, 14 November 1955, *Holmes 1330* (holo-: K! [barcode K000815890]), *syn. nov.*

Diagnosis:—Lower surface of leaf with thick indumentum of woolly hairs more or less masking stellate hairs.

Illustrations:—Figs. 3O, 4N.

Distribution in D.R. Congo:—Upper Katanga; apparently uncommon.

Distribution elsewhere:—Angola, Zambia.

Habitat and ecology:—Miombo forests, wooded savannahs.

Other representative specimens examined:—D.R. CONGO. Upper Katanga: Kando, 2 km SO de la ferme CEPSE, forêt claire, 10 November 1977, *Darcis 262* (BR!); Keyberg, cultivé, 22 January 1958, *Delvaux 774* (BR!); Bianco, N de la vallée Kipiri (Bianco), 1580 m, steppe arbustive, 23 February 1969, *Lisowski, Malaisse & Symoens 3145*

(BR!, BRVU!, POZG!); Forêt claire sur les contreforts des Kundelungu, au-dessus de la Lufutizi, près de l'ancienne route, ca. 1540 m, 13 January 1971, *Lisowski, Malaisse & Symoens 12771, 12800* (POZG!); id. *Lisowski B-8950* (POZG!); 3 km N Luishi (?), Verger à *Uapaca-Monotes*, 12 June 1981, *Malaisse 12059* (BR!); Mukuen, 10 km SO Elisabethville (Lubumbashi), savane boisée non loin de la galerie de la Matuitui, 5 August 1948, *Schmitz 1958* (BR!).

Discussion:—Closely related to var. *hypoleucus*. *Monotes kapiensis* De Wild. is more or less intermediate between the two taxa; it was synonymised with *M. discolor* by Bancroft (1939a) and with *M. hypoleucus* by Duvigneaud (1949) and in the present work.

9dβ. *Monotes hypoleucus* var. *discolor* forma *cordatus* (Hutch.) Meerts, *comb. nov.*

Basionym: *Monotes cordatus* Hutchinson (1931: 246). ≡ *Monotes caloneurus* f. *cordatus* (Hutch.) Duvigneaud (1949: 44). ≡ *Monotes discolor* var. *cordatus* (Hutch.) Duvigneaud (1959: 102); Duvigneaud (1961: 416).

Type:—ZAMBIA. 20 miles south west of Serenje Corner, 15 July 1930, *Hutchinson & Gillett 3703* (holo-: K! [barcode K000240359]; iso-: BM!, BRLU! (fragm.))

Diagnosis:—Lower surface of leaf tomentellose, covered by white stellate hairs, almost lacking the usual lanose indumentum; reticulum not completely covered by indumentum.

Distribution in D.R. Congo:—Upper Katanga; rare.

Distribution elsewhere:—Angola (first records for the country: *Murta 115* (COI!), *Santos 896* (LISU!)), Zambia.

Habitat and ecology:—Miombo forests, wooded savannahs.

Other representative specimens examined:—D.R. CONGO. **Upper Katanga:** Dépression de la Kando, alt. 1200 m, forêt claire, 22 February 1978, *Malaisse 9511* (BR!, P!).

9e. *Monotes hypoleucus* var. *loandensis* (Exell) Meerts, *comb. et stat. nov.*

Basionym: *Monotes loandensis* Exell (1932: 220); Bancroft (1937: 137; 1939a: 353); Catarino *et al.* (2013: 270); Duvigneaud (1949: 50); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144).

Type:—ANGOLA. Malange, Quirima, 23 January 1931, *Gosswailer 9492* (holo-: BM! [barcode BM000603380]; iso-: COI!, K! [barcode K000240344], LISC! [barcode LISC019576]).

= *Monotes loandensis* var. *griseotomentosus* Duvigneaud (1949: 51 & Pl. 12 e–h). **Type:**—D.R. CONGO. Kwango, 42 km SW Kenge, forêt claire à *Uapaca*, 9 May 1948, *Duvigneaud 856M* (holo-: BRLU! [barcode BRLU0000090022319]; iso-: BRLU! (6 sheets)), *syn. nov.*

Diagnosis:—Differs from the type variety in the following traits: leaf blade smaller, more or less spatulate, lower surface of leaf with secondary nerves glabrous, reddish chestnut, basal gland narrowly elliptic.

Branchlets quickly glabrous, grey. Leaf: petiole 7–13 mm long, ca. 2 mm in diameter, blade obovate-spatulate to elliptic, 5–8 × 2–4 cm, generally at least 2.5 times longer than wide, base cuneate, apex rounded to emarginate, with 8–13 pairs of nerves; basal gland shiny, narrowly elliptic, 2–5 times longer than wide; upper surface of leaf generally reticulate, often granular (yellow sessile glands), generally glabrous, occasionally with minuscule hairs, glabrescent; lower surface discolorous, whitish to ash-greyish, with cottony indumentum covering areoles; secondary nerves and costa prominent, almost glabrous, red to chestnut coloured, contrasting with the grey-whitish indumentum; tertiary nerves generally forming a striking scalariform pattern. Flowers unknown. Fruit 8–10 mm, globose with an apicule, wings large, 3–5 × 1–2 cm.

Illustrations:—Figs. 3P, 4O.

Distribution in D.R. Congo:—Kwango; Upper Katanga.

Distribution elsewhere:—Angola; known only from a few collections.

Habitat and ecology:—Mixed dry semi-evergreen forests (“Mabwati”); wooded savannahs.

Other representative specimens examined:—D.R. CONGO. **Kasaï** (Kwango): 42 km SW Kenge, forêt claire à *Uapaca*, 9 May 1948, *Duvigneaud 856M*. **Upper Katanga:** Kambove-Kamoia, 1957, *Duvigneaud 3352–3353* (BRLU!).

Discussion:—We have maintained this taxon after much hesitation. All the supposed diagnostic traits can actually be found in var. *caloneurus* and in var. *angolensis* and their combination in some specimens is probably fortuitous. In agreement with this hypothesis, the single collection from Katanga perfectly matches the type in leaf size and shape, but departs from it in having a pubescent upper surface of the leaf. Catarino *et al.* (2013) indicate that “...the species

is known from three collections and three different localities. Two of these locations were surveyed several times after the species description, but no further collections are known". This, in our opinion, is another indication that this taxon represents individual variation of little taxonomic value. Intermediates with var. *angolensis* occur, e.g. *Duvigneaud & Timperman 2402* (BRLU!), *Desenfans 5919* (BRLU!), *Plancke 121/1584* (BRLU!).

10. *Monotes katangensis* (De Wild.) De Wildeman (1913b: 110)

≡ *Vatica katangensis* De Wildeman (1903: 92).

Lectotype (designated here):—D.R CONGO, Upper Katanga, Lukafu, July 1900, *Verdick 548* (BR! [barcode BR0000008891945]).

Tree up to 13–14 m high; branchlets tomentellous. Leaf: petiole 10–20 mm long, 2.5–3 mm in diameter; blade elliptic to oblong or obovate-oblong, 6–12(–14) × 2.7–7(–9) cm, rounded to slightly cordate at the base, obtuse to slightly emarginate and sometimes acute or apiculate at the apex; lateral nerves in 10–15 pairs, nearly straight, some of them furcate near the apex, nerves and bifurcations reaching the margin of the leaf; upper surface minutely tuberculate-subreticulate, scaberulous with straight or nearly straight simple hairs 0.2–0.5(–0.6) mm long, developed on minute, white tubercles, glabrescent, becoming yellowish brown to livid with age; lower surface beige to pale fulvous-pubescent with straight or curled hairs on the nerves, veins and reticulation, and with interreticular areoles covered with minute stellate hairs; midrib very thick and prominent beneath, with fasciculate hairs; reticulation very prominent below and forming deep cavities (depth ≥ 2 mm). Inflorescences of subsessile condensed multiflorous cymes forming large terminal thyrses up to 15 cm long, pale fulvous- or rufous-tomentose, often with a few reduced leaved; inflorescence leaves with upper surface indumentum comprising stellate hairs and simple straight hairs. Flower: pedicel 1–3 mm long; sepals 3–4 mm long, densely sericeous-tomentose, often with a few very reduced leaves; petals 8–10 mm × 2.7–4 mm, densely sericeous-tomentose; stamens with anthers not produced at the apex. Fruits densely crowded at the ends of the branches, subglobose, 7–9 mm in diameter, reticulate, tomentose, conical at the apex; wings 2.5–4.5 × 1–1.5(–2.3) cm, reddish purple, generally narrowly obovate-oblong to spatulate.

Illustrations:—Figs. 3Q, 4P, 7C,D, 8D.

Distribution in D.R. Congo:—Very common in Upper Katanga.

Distribution elsewhere:—Mozambique, Tanzania, Zambia, Zimbabwe.

Habitat and ecology:—Miombo woodlands often on compact, clayey or lateritic gravelly soil; characteristic of the *Brachystegia spiciformis*—*Monotetum katangense* vegetation on gravelly soil; scrub savannahs, dambos.

Vernacular names:—Kassolo, kazongo (Kitschokwe), kimpampa, kimpanya, kipapa (Kibemba), musanga, mutenta (Kiluba), saya.

Uses:—Timber. Wood hard and heavy, difficult to work; the species has ornamental value due to its bright red showy infrutescences.

Other representative specimens examined:—D.R. CONGO. Upper Katanga: Lubumbashi, 25 April 1912, *Bequaert 360* (BR!); Near Elisabethville [Lubumbashi], July–August 1919, *Burt-Davy 17984* (BM!); Mulumbi, June 1953, *Desenfans 3456* (BRLU!); Près de Kasongo Mwana, forêt claire, 14 July 1954, *Desenfans 5764* (BRLU!); Gare de Shilatembo, 31 July 1948, *Duvigneaud 1276M* (BRLU!); Grottes de Jadotville, crête rocheuse d'une colline schisteuse, forêt claire à *Brachystegia microphylla*, 1 August 1948, *Duvigneaud 1282M* (BRLU!); Dembo Atashyo, 10 km W de Mindingi, forêt dembo riche en *Uapaca*, 21 July 1956, *Duvigneaud & Timperman 2067* (BRLU!); 15 km E de Menda, forêt claire à *Uapaca*, *Monotes*, sur latérite, 23 July 1956, *Duvigneaud & Timperman 2104* (BRLU!); Kasompi, pente nue semi-désertique à petites termitières, sur grand conglomerat, à l'est de Kasompi Est, 2 September 1956, *Duvigneaud & Timperman 2600* (BRLU!); Sakania, forêt claire sur terre ocre caillouteuse à *Brachystegia boehmii* et *B. spiciformis*, 31 January 1960, *Duvigneaud 5361* (BRLU!); Kasompi, forêt sur terre rouge, 8 February 1960, *Duvigneaud 5474Mo* (BRLU!); Lubumbashi, brousse, 15 May 1912, *Homblé 325* (BR!); Près de la gare de Munama, forêt claire, 1220 m, 8 June 1959, *Lukuesa 649* (BRVU!); Montagne au N de Mitwaba, savane arbustive, 30 June 1988, *Pauwels 7138* (BR!); Lubumbashi, 2 November 1917, *Ringoet 58* (K!); Route Lubumbashi-Likasi, km 62, forêt claire, 30 June 1962, *Schaijes 1441* (BR!); Lubumbashi, 1937, *Salésiens 80* (WAG!); Bangu, poste de chemin de fer entre Dilolo et Malonga, forêt claire sur sol sablonneux, August 1956, *Schmitz 5351* (BR!); Lukafu, April 1900, *Verdick 486* (syntype: BR!).

Discussion:—The protologue cites two syntypes (*Verdick 486*, *Verdick 548*); the latter is here chosen as a lectotype because it clearly shows the typical inflorescence shape of the species.

M. katangensis is more variable in Katanga than in other parts of the Zambezi Region; leaves in particular are often larger than further south in the Zambezi Region. A number of collections have leaves up to 14 × 9 cm, with the apex emarginate, and a mixture of simple and fasciculate hairs on the upper surface. Such forms were designated as

"*M. katangensis* var. *mitwabaensis*" by Duvigneaud *in schedis* (unpublished name). These forms, which are not rare in Katanga, especially in the region of Mitwaba, are possibly introgressed by *M. autennei* (e.g. Mitwaba, savane à *Protea* et *Tephrosia manikensis* sur sable sur latérite, 9 September 1956, Duvigneaud & Timperman 2694 (BRLU!); Colline Bange, forêt claire, 6 June, 1954, Desenfans 6035 (BRLU!); Lubala près de Kibanda, 28 June 1954, Desenfans 6528 (BRLU!); Bifurcation route Elisabethville et Luba, 6 August 1954, Desenfans s.n. (BRLU!)).

Some forms have short hairs on the reticulum and almost no stellate hairs in the areoles (e.g. Duvigneaud & Timperman 2927M (BRLU!)). In some specimens, young leaves have a mixed indumentum of simple and stellate hairs on the upper surface of the leaf (e.g. Duvigneaud 3548 (BRLU!), Desenfans 5649 (BRLU!)); such indumentum is apparently always present on inflorescence leaves, which no previous author had noticed.

Glands are sometimes present in the axils of secondary nerves.

References:—Bancroft (1939a: 343, 372); Coates Palgrave (2005: 740); De Wildeman (1921: 134; 1926: 175; 1927a: 177, 1927b: 56); De Wildeman & Staner (1932: 66); Delevoy (1930: 17); Duvigneaud (1949: 60, t. 14 fig. C.; 1961: 411); Lebrun & Stork (1991: 144); Meerts (2016: 223); Meerts & Hasson (2016); Smith & Allen (2004: 64); Verdcourt (1989: 5); White (1962: 262; fig. 46F).

11. *Monotes magnificus* Gilg (1899: 135); Bancroft (1939a: 377); De Wildeman (1927a: 180); Duvigneaud (1949: 53; 1961: 412); Engler (1921: 520); Gilg (1908b: 290); Lebrun & Stork (1991: 144); Meerts (2016: 223); Verdcourt (1989: 7; 6: Fig. 2); White (1962: 263; fig. 46G)

Type:—TANZANIA. Makombe (Prov. Iringa), lande der Uhehe, an trockenen Bergabhängen auf rotem Laterit, February 1898, Götze 680 (B†).

Shrub to small tree up to 8 m. high; branchlets pubescent, becoming glabrous, thick (up to 1 cm). Leaf: petiole 20–35 mm long, 3–4 mm thick; blade suborbicular to broadly ovate, 12–45 × 9–30 cm, cordate at the base, emarginate at the apex; lateral nerves in (9–)10–11(–12) pairs (with a weak tendency to formation of short subsidiaries), slightly depressed above, slightly curving towards the apex, many of them producing 1–3 bifurcations on the side nearest the base of the leaf before reaching the margin, nerves and bifurcations anastomosing on the thickened margin; upper surface finely reticulate, substrigose, with straight single hairs 0.5–1.5 mm long; extra leaf-glands in the axils of the lateral nerves; lower surface discolorous, greyish- or brownish-floccose-tomentose, with relatively long dense curled hairs on the nerves and veins, and with the reticulations and interreticular areoles covered with minute stellate hairs, costa and veins very prominent and conspicuous, tertiary veins often forming a scalariform pattern, reticulation partially hidden by hairs, costa covered with dense straight simple hairs. Inflorescences axillary, few-flowered, sessile, often condensed in subterminal clusters, densely rufous-tomentose. Flower: pedicel 3–6 mm long; sepals ca. 7 mm long, rufous-sericeous-tomentose; petals 11–12 mm long, rufous-sericeous-tomentose; stamens with anthers produced into a short triangular apiculus. Fruit subspherical, 13–35 mm in diameter, slightly depressed at the apex, brownish, subsericeous-pubescent; wings 4.5–11 × 2.5–3 cm, yellow or reddish, broadly oblanceolate.

Variation:—This species is very variable as to size of leaf, fruit and fruit wings; the traits are correlated. Two varieties can be recognized.

Key to the varieties:

1. Leaf blade 25–45 × 17–30 cm; fruit 20–35 mm in diameter, with wings 8–11 cm long 11b. var. *gigantophyllus*
- Leaf blade 12–23 × 9–17 cm; fruit 13–20 mm in diameter, with wings 4.5–7 cm long 11a. var. *magnificus*

11a. *Monotes magnificus* Gilg var. *magnificus*

= *Monotes thomasii* De Wildeman (1927a: 182; 1927b: 56). Type:—D.R. CONGO. Msipashi (Kundelungu), 1 May 1923, Thomas 1250 (holo-: BR!).

= *Monotes magnificus* Gilg var. *eupilosus* Duvigneaud (1949: 54). Type as for *Monotes magnificus* Gilg.

Leaf blade 25–45 × 17–30 cm; fruit 20–35 mm in diameter, its wings 8–11 cm long.

Illustrations:—Figs. 3R, 4Q.

Distribution in D.R. Congo:—Upper Katanga.

Distribution elsewhere:—Malawi, Tanzania, Zambia.

Habitat and ecology:—Wooded savannah, scrub, steppic savannah, often at the periphery of mineralised clearings.

Vernacular names:—Kimpampa (Kibemba).

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** Mitwaba, route entre Mitwaba et Kiubo, 26 km au sud du poste, steppe sec très arbustive à *Uapaca robynsii* sur 70 cm de limon ocre sur grenaille latéritique, 11 September 1956, *Duvigneaud & Timperman 2731M2* (BRLU!); Mitwaba, steppe arbustif sur sol riche en étain, 1 July 1957, *Duvigneaud 3799M3* (BRLU!); Kakanda, signal I, bosquet de pente à *Uapaca robynsii* sur sol légèrement cuprifère, 29 November 1959, *Duvigneaud 4826M* (BRLU!); Shinkolobwe, dembo arbustif dans plaine latéritique, 23 December 1959, *Duvigneaud 4752M* (BRLU!); Kakanda, écotone entre gisements de pente et forêt claire, 29 December 1959, *Duvigneaud 4828M* (BRLU!); 50 km S Mitwaba, steppe arbustif à *Uapaca robynsii*, 17 January 1960, *Duvigneaud 5099* (BRLU!); Kisomona, in bush, 10 March 1908, *Kassner 2559* (K!); Kabambare-Kapuku, forêt claire, 27 September 1952, *Symoens 869* (BRLU!).

Discussion:—*Malaisse 16362* (BR!) is intermediate between *M. magnificus* and *M. adenophyllus*. *Duvigneaud 4828M* has deeply emarginated leaves (like *M. autennei*), but all the other traits are typical. *Duvigneaud 3206M* (BRLU!) is an example of intermediate specimen between var. *magnificus* and var. *gigantophyllus*.

11b. *Monotes magnificus* Gilg var. *gigantophyllus* (P.A.Duvign.) Meerts, comb. et stat. nov.

Basionym: *Monotes gigantophyllus* Duvigneaud (1949: 56); Lebrun & Stork (1991: 144); Meerts (2016: 223).

Type:—D.R. CONGO. Upper Katanga, in sylvis siccis prope Kasenga, 19 August 1948, *Duvigneaud 1395M* (holo-: BRLU! [barcode BRLU0000090020698], iso-: BRLU (3 sheets)).

Diagnosis:—Differs from the type variety in being a tortuose low shrub up to 3 m high, with much larger leaves 25–45 × 17–30 cm, bigger fruits 20–35 mm in diameter and fruit wings 8–11 cm long.

Illustration:—Fig. 5J.

Distribution in D.R. Congo:—Upper Katanga (Fig. 16E). Endemic of D.R. Congo.

Habitat and ecology:—Wooded savannah, open miombo woodland, dambos, grassy savannah, occasionally on slightly mineralised soil.

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** Kasenga, forêt claire, 20 August 1949, *Duvigneaud 1400* (BRLU!); Kakontwe, dembo à *Brachystegia stipulata* en contrebas des collines rocheuses, 15 July 1956, *Duvigneaud & Timperman 2031Mo* (BRLU!); Mukumbi, dembo incendié à *Cryptosepalum*, *Loudetia simplex*, 3 August 1956, *Duvigneaud & Timperman 2196* (BRLU!); Kisenge-Kamata, haute savane sur épaisse terre brune manganésifère, 16 August 1956, *Duvigneaud & Timperman 2324* (BRLU!); Kisenge-Kamata, forêt sur sol léger à *Brachystegia longifolia*, 18 August 1956, *Duvigneaud & Timperman 2364* (BRLU!); Mitwaba, 26 km au sud du poste, steppe sec arbustif à *Uapaca robynsii* sur 70 cm de limon ocre sur grenaille latéritique, *Duvigneaud & Timperman 2731* (BRLU!); Route Sogefor, steppe à *Vellozia* sur colline minéralisée, 19 June 1957, *Duvigneaud 3588* (BRLU!); Tilwizembe, verger de pente enrochée en contrebas du dembo d’empoisonnement, 15 December 1959, *Duvigneaud 4597* (BRLU!); Shinkolobwe, dembo arbustif dans une plaine latéritique, 23 December 1959, *Duvigneaud 4752M* (BRLU!); Village Kilembi, près de Katofio, bord de route, 1230 m, *Lukuesa 242* (LSHI!); Tilwizembe, forêt claire, 23 September 1956, *Plancke 133/1792* (BRLU!); Route Katofio-Msipashi, contreforts des Kundelungu, forêt claire à *Brachystegia*, 9 September 1954, *Schmitz 4653* (BR!); Kilembi, près de Katofio, bord de route près du village, 5 September 1957, *Symoens 242* (BRLU!).

Discussion:—*M. gigantophyllus* and *M. magnificus* differ in no qualitative trait, and the variation in leaf size is virtually continuous. Therefore, species rank does not seem justified and the varietal level was deemed the most appropriate.

12. *Monotes pearsonii* Bancroft (1936a: 44)

Type:—ANGOLA. In open forest in lower part of pass leading down to Lubango, 1785 m, May 8, 1909, *Pearson 2649* (holo-: K! [barcode K000240339]; iso-: BRLU! (fragm.), FHO).

Small tree up to 6 m high; young twigs more or less pubescent, glabrescent. Leaf: petiole 10–16(–21) mm long, 1.5 mm in diameter, shortly pubescent; blade very variable in shape even on the same branch, obovate to elliptic or ovate-elliptic, (4.5–)6–11.5 × (1.5–)2.5–6.5(–7) cm, base rounded, truncate or slightly cordate, apex rounded or emarginate, more rarely obtuse; secondary nerves in 10–14 pairs, distally curved and tangent to leaf margin, short intercalary nerves often present; upper surface markedly reticulate, with indumentum just perceptible, soft to the touch, persistent, with a mixture of short simple and geminate more less erect, curved or flexuous hairs (0.2–0.4 mm) and numerous yellow glands, becoming brownish when dry, secondary and tertiary nerves generally impressed; lower surface discolourous,

whitish to greyish, with reticulum well visible though not very prominent, often with a reddish tinge; areoles covered with small stellate hairs and reticulum with curled hairs (ca. 0.5 mm long), costa with fulvous indumentum of very short curled hairs. Inflorescence of narrow axillary racemose cymes of 1–4 cm long and 1–1.5 cm wide, with rachis densely tomentose. Flower: pedicel ca. 2 mm long, sepals broadly ovate-triangular, ca. 3 × 2.5 mm; petals ca. 9 × 3 mm, 8-nerved; anthers with conspicuous appendage. Fruit slightly depressed, ca. 18 mm in diameter; wings (materials from Angola) up to 8 × 2 cm, red, unguiculate at base, acute at apex.

Illustrations:—Figs. 3S, 4R, 8E.

Distribution in D.R. Congo:—Upper Katanga (first record for D.R. Congo).

Distribution elsewhere:—Angola; taxon known from few collections.

Habitat and ecology:—Wooded slopes on shallow rocky soil.

Other representative specimens examined:—**D.R. CONGO. Upper Katanga:** Kisenge-Kapolo, forêt sur sol léger à *Brachystegia longifolia*, 18 August 1956, *Duvigneaud & Timperman 2364* (BRLU!); Entre Mukumbi et Swambo, forêt sur terre ocre à *Brachystegia* “Sandwe” et *Monotes* sp., 28 December 1959, *Duvigneaud 4798M* (BRLU!); Kasekelesa, restes de la forêt primitive entre les carrières de Mn, 24 January 1960, *Duvigneaud 5233M* (BRLU!); Nzilo, forêt-verger à *Monotes* div. sp. enrochée, sur phyllades kibariennes, 27 January 1960, *Duvigneaud 5268M3* (BRLU!).

Discussion:—*M. pearsonii* was previously known from only three collections in southern Angola. ca. 1000 km south-west of the nearest Congolese localities. The new collections, though without fruits, have the characteristic pattern of pubescence of the type. They allow a more complete assessment of the variation in the species. The Katangan specimens are indeed much more variable in leaf shape than the Angolan ones; leaf shape sometimes varies on the same branch. In particular, some Katangan collections break down one of the supposedly diagnostic traits of the species, i.e. the possession of obovate leaves. However, we were not able to find any diagnostic trait to justify treating the Katangan material as a distinct taxon. Our circumscription of *M. pearsonii* is thus broader than previously defined based on just the scarce materials from Angola. The type specimen has very large unguiculate fruit wings, but *M. pearsonii* has not been collected in fruit in D.R. Congo.

At first sight, *M. pearsonii* is deceptively similar to some forms of *M. hypoleucus* var. *caloneurus*. However, *M. pearsonii* differs in the upper surface of the leaf being markedly reticulate and with hairs longer and stiffer, just perceptible to the touch. The hairs of *M. pearsonii* are ca. 12 µm in diameter, with a well-developed lumen of 4 µm; those of *M. caloneurus* are variable in thickness along their length (5–12 µm) and with the lumen almost obliterated at places.

References:—Bancroft (1936a: 44; 1937: 141; 1939a: 354, 378); Catarino *et al.* (2013: 272); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144).

13. *Monotes rubriglans* Bancroft (1937: 138); Bancroft (1939a: 358); Catarino *et al.* (2013: 272); Figueiredo & Smith (2008: 67); Lebrun & Stork (1991: 144); Meerts (2016: 223)

Type:—ANGOLA. Huila, 12 July 1928, *Bonnefoux & Villain 57* (holo-: P! [barcode P00389102]; iso-: BM! [barcode BM000603381], BRLU! (fragm.)).

Small tree (height unknown). Twigs pubescent to densely tomentose; stipules reddish, ciliate, more or less persistent. Leaf: petiole 11–40 mm long, pubescent; blade very variable in shape (even on the same twig), ovate, ovate-elliptic, elliptic, obovate, more rarely suborbicular, (4.5–)6–17.5 × 3–13 cm, rounded to slightly cordate at the base, generally emarginate or, more rarely, with a short broad acumen, often with the main nerve protruding in a short blunt mucro; secondary nerves 8–14 pairs; basal gland red, subsidiary red glands present along secondary nerves or at their axil; upper surface of leaf glabrous to pubescent, markedly reticulate and generally more or less shining, with the costa and secondary nerves somewhat impressed and with a fringe of simple hairs; lower surface of leaf with the costa, secondary nerves and reticulum very prominent, almost glabrous to hirsute; secondary nerves anastomosing in arches tangent to the margin, with a tendency of some nerves to be distally forked or ramified; leaf margin often more or less sinuose, recurved, generally thickened by an intra-marginal vein; lower surface of blade concolorous to discoloured, with the areoles glabrous to stellate-pubescent; yellow glands present on veins and areoles. Inflorescence: a thyrse, in the axil of current year leaves or on previous year’s growth; peduncle 1–8 cm, pubescent; bracts reddish, ciliate, generally persistent; flowers: pedicel 1–2 mm long, sepals broadly ovate-elliptic 3–5 × 2–4 mm, petals 8–12 × 4–5 mm, whitish with a reddish tinge within, stamens 5–8 mm long, anther with conspicuous appendage. Fruit ovoid, ca. 10 × 7 mm, with a conical apex; wings obovate, 2.0–4.0 × 0.8–1.5 cm, pale reddish.

Discussion:—In Katanga, the collections that can be referred to *Monotes rubriglans* carry the most diagnostic

traits of the species, i.e. the red basal gland, the tendency to form subsidiary glands, the reddish colours present in bracts, stipules and petals, and the markedly reticulate-areolate and more or less shiny upper surface of the leaf, with a fringe of cilia on the secondary nerves. The reticulation on the lower surface is also similar to the type, with the nerves anastomosing in arches tangent to the margin, and a tendency of some nerves to be distally forked or ramified. However, the Katangan collections depart from the type in having more pubescent twigs and leaves. They share a distinct, remarkable inflorescence architecture, having the flowers in long pedunculate thyrses on previous year's growth under the leaves. The inflorescence appears to consist of a specialised twig comprising a few reduced leaves. This particular inflorescence architecture is considered unique within *Monotes*, where flowers are born in terminal panicles and/or in cymes in the axils of leaves on current year's growth. We here propose to recognize the Katangan collections as a distinct subspecies.

Monotes rubriglans is a very poorly known taxon. For the type subspecies, in addition to the type specimen, Catarino *et al.* (2013) cite three collections from Angola. However, all of these depart from the type in many respects and probably do not belong here. More material is needed, especially from the type locality.

Key to the subspecies:

1. Inflorescence 4–11 cm long, much longer than wide, with a few reduced leaves; lower surface of leaf markedly pubescent, either in areoles or in reticulum or both; subsidiary glands present in the axils of secondary nerves 13a. subsp. *upembensis*
- Inflorescence shorter (2–3 cm long), ca. as long as wide, without reduced leaves; lower surface of leaf almost glabrous; subsidiary glands present, but located next to secondary nerves 13b. subsp. *rubriglans* (not present in D.R. Congo)

13a. *Monotes rubriglans* subsp. *upembensis* Meerts, *subsp. nov.*

Type:—D.R. CONGO. Katanga, Upemba, savane boisée entre Kilwesi et rivière Muye, 10 September 1948, *de Witte 04232* (holo-: BR!, iso-: BR!).

Diagnosis:—Differs from the typical subspecies by the inflorescence being composed of a long thyrses, or a narrow panicle, 4–11 cm long, much longer than wide, with a few reduced leaves, borne on defoliated twigs below the leaves, the more developed indumentum of the lower surface of the leaf, with either stellate hairs in areoles or simple hairs on veins and reticulum or both, the tomentose twigs and the subsidiary glands in the axils of secondary nerves (not next to the nerves).

Twigs densely tomentose; stipules reddish, ciliate, more or less persistent. Leaf: petiole 11–40 mm long, 2.5–3 mm in diameter, often distally dilated and geniculate, generally densely pubescent; subsidiary red glands present in the axil of secondary nerves, sometimes masked by hairs; upper surface of leaf blade often with reddish tinge on main nerve and/or with red flecks or completely reddish; upper surface with nerves densely pubescent; lower surface of leaf concolorous to discolorous, with the areoles glabrous to densely stellate-pubescent; costa, secondary nerves and reticulum generally with hyaline hairs. Inflorescence: a thyrses or a narrow panicle up to 11 cm long with 1–3 short branches, on previous year's growth, with one or a few reduced leaves; peduncle 3–8 cm, densely pubescent, striate, pale green; inflorescence leaves elliptic, ca. 25 × 10 mm, with a conspicuous mucro, greyish-green, with soon caducous minuscule lepidote-stellate hairs intermingled with long straight simple hairs; floral bracts reddish, ciliate, generally persistent. Flower: pedicel 1–2 mm long, sepals broadly ovate-elliptic 3–5 × 2–4 mm, petals 8–12 × 3.5–5 mm, whitish with a reddish tinge within, stamens 5–8 mm long. Fruit ovoid, ca. 10 × 7 mm, with a conical apex; wings obovate, 2.0–4.0 × 0.8–1.5 cm, pale reddish.

Variation:—The Katangan collections are extremely variable for many traits, including extent and density of indumentum, leaf colour and shape and petiole length. Leaf shape ranges from ovate to elliptic or obovate, with the leaf apex ranging from deeply emarginate to bluntly acuminate. Significantly, the type specimen of *Monotes rubriglans* shows similar variation in leaf shape within the same collection and even on the same twig. Although the Katangan material is obviously heterogeneous, variation is very difficult to translate into a coherent classification system. We propose to recognize two varieties.

Key to the varieties:

1. Upper surface of the leaf pale grey-green, generally with stiff hairs; lower surface brownish, generally without stellate hairs, with nerves and reticulum hirsute; leaf blade strongly coriaceous 13aβ. var. *griseocoriaceus*
- Upper surface of the leaf reddish green, generally glabrous (except nerves); lower surface whitish to beige, most often with a continuous indumentum of stellate hairs, with reticulum hirsute or not; leaf blade not particularly coriaceous 13aα. var. *upembensis*

13aa. *Monotes rubriglans* H.H.Bancr. subsp. *upembensis* Meerts var. *upembensis*

Young twigs densely tomentose; stipules linear to narrowly lanceolate, 20–30 × 2 mm, reddish. Leaf: petiole 12–40 mm long, 2–3 mm in diameter, tomentose; blade narrowly ovate to ovate-elliptic or elliptic, (6–)8.5–13 × (3–)5.5–8 cm, slightly cordate at base, rounded to retuse or emarginate at apex; upper surface often with a reddish tinge, often with reddish flecks in old leaves, generally glabrous except on main nerves with a fringe of hairs, sometimes with simple stiff hairs; lower surface generally beige to whitish, entirely covered by stellate hairs, often mixed with simple translucent hairs on nerves, rarely with areoles glabrous (but with yellow glands). Flowers: not observed. Fruits ovoid, ca. 10 × 7 mm, with a conical apex; wings obovate, 2.0–4.0 × 0.8–1.5 cm, pale reddish.

Illustrations:—Figs. 3T, 4S, 5M.

Distribution in D.R. Congo:—Katanga (Upemba region), apparently rare (Fig. 16C). Endemic of D.R. Congo.

Habitat and ecology:—miombo woodlands.

Other specimens examined:—**D.R. CONGO. Upper Katanga:** Upemba, savane boisée entre Kilwesi et rivière Muye, 10 September 1948, *de Witte 04231* (BR); Rivière Dona, au pied du Mulumbi, forêt claire sur schistes, 30 June 1953, *Desenfans 3703* (BRLU!); Upemba, 1.5 km NNO confluent Munte-Mufifie, alt. 950–1000 m, plaine xérique, 13 September 1953, *Desenfans 4446* (BRLU!).

Discussion:—The type has leaves with a glabrous upper surface (except a fringe of hairs on the nerves). However, some collections show stiff hairs on the upper surface (e.g. *Desenfans 3708* (BRLU!)). See note under following variety. *Desenfans 4446* lacks stellate hairs in the areoles and is very close to the type specimen of *M. rubriglans*. We have hesitated to assign it to the type subspecies but, given that the type locality is 1500 km to the SW of Upemba, we prefer to assign it to the same subspecies as the other Katangan collections.

13aβ. *Monotes rubriglans* H.H.Bancr. subsp. *upembensis* Meerts var. *griseocoriaceus* Meerts var. *nov.*

Type:—D.R. CONGO. Katanga, Rivière Dona, pied du Mulumbi, forêt claire sur schistes, 30 June 1953, *Desenfans 3724* (holo.: BRLU!).

≡ *Monotes* sp. (De Wildeman 1927a: 185).

Diagnosis:—Differs from the type variety by the very coriaceous leaves with the upper surface pale grey-green, often with stiff hairs, contrasting with the brownish lower surface.

Tree up to 9 m with trunk forked and tortuose (always?). Petiole distinctly dilated and geniculate distally and forming an angle with the leaf blade; blade very variable in shape, broadly elliptic, ovate, obovate, suborbicular, slightly cordate at base, rounded to emarginate at apex, 10–17.5 × 7.5–13 cm, 1.3–2 times as long as wide, very coriaceous; upper surface of blade pale grey-green, more or less harsh, with sparse to dense indumentum of stiff simple hairs 0.5–1(–1.5) mm long, much denser on the nerves, developing on cushion-like emergences of the leaf blade; nerves occasionally deeply impressed and leaf blade more or less quilted; main nerve with a reddish tinge on the upper surface; lower surface of leaf brownish, with tertiary nerves often forming a more or less clear ladder-pattern; nerves and reticulum hirsute, soft to the touch, with simple translucent hairs, 0.5–1.5 mm long, denser on costa and secondary nerves; areoles glabrous, with scattered yellow glands, or occasionally with minuscule lepidote-stellate hairs tending to disappear with age. Floral bracts ovate-elliptic, 5–10 × 3 mm, reddish, ciliate, often persistent; flowers: pedicel 1–2 mm long, sepals broadly ovate-elliptic 5 × 3–4 mm, petals ca. 12 × 5 mm, stamens ca. 8 mm long. Fruits not observed.

Illustrations:—Figs. 3U, 4T.

Distribution in D.R. Congo:—Upper Katanga, uncommon (Fig. 16B). Endemic of D.R. Congo.

Habitat and ecology:—Miombo woodland and wooded savannahs.

Vernacular names:—Kimpampa (Kibemba).

Other specimens examined:—**D.R. CONGO. Upper Katanga:** Masolwa, brousse, 20 December 1921, *Delevoy 514* (BR!); Riv. Dona, pied du Mulumbi, forêt claire sur schistes, 30 June 1953, *Desenfans 3711* (BRLU!); Mukulakulu, forêt claire sur sol sableux, 23 July 1953, *De Troyer 124* (BR!); Mitwaba, s.d., *Vanden Brande M237* (BRLU!).

Discussion:—This variety is quite noticeable because of its coriaceous leaves with pale grey-green upper surface and brownish lower surface. However, leaf shape and density of the indumentum are very variable. *De Troyer 124* and *Vanden Brande M237* have broadly ovate to suborbicular leaves which are hirsute and have deeply impressed nerves above, reminiscent of some forms of *Monotes adenophyllus*.

A number of other puzzling specimens from the same region are left unassigned. *Monotes rubriglans* appears as a very polymorphic complex in Katanga, possibly in active speciation in that area. More material and/or other sources of taxonomic evidence are needed to unravel this situation.

Insufficiently known species

14. *Monotes* sp. B “near *pearsonii*”

Diagnosis:—Differs from *Monotes pearsonii* in having broader leaves, uniformly maroon when dry, with completely glabrous areoles below; the pubescence pattern and reticulation of the upper surface is similar to that of *M. pearsonii*.

Distribution:—Upper Katanga. Endemic of D.R. Congo.

Habitat and ecology:—Miombo woodland.

Specimens examined:—**D.R. CONGO. Upper Katanga:** Kasompi ouest, forêt claire sur terre rouge profonde, S du gisement, 27 July 1956, *Duvigneaud & Timperman 2136* (BRLU!); entre Jadotville (Likasi) et Shinkolobwe, forêt de plateau à *Brachystegia utilis*, sur schiste, 28 December 1959, *Duvigneaud 4791M2* (BRLU!); Luishia, forêt claire de pente enrochée à *Brachystegia utilis*, 28 January 1960, *Duvigneaud 5292M* (BRLU!).

Discussion:—This taxon might be a variety of *Monotes pearsonii* with glabrous areoles on the lower surface of the leaf. It is also reminiscent of *M. africanus*, from which it differs mainly by the pubescent upper surface of the leaf and the broader leaves.

15. *Monotes* “near *redheadii*”

Young twigs densely tomentose. Leaf: petiole 7–10 mm long, 1–1.5 mm in diameter; blade narrowly elliptic, 4–8.5 × 1.5–3.6 cm, cuneate to rounded at base, acute to rounded at apex; secondary nerves in ca. 10–14 pairs, frequently with subsidiaries, straight, looping just before margin; upper surface reticulate, subglabrous; basal gland longer than wide; lower surface with reticulum araneose-tomentose, areoles glabrous, costa and nerves densely tomentose.

Distribution:—Upper Katanga.

Habitat and ecology:—Miombo woodland.

Specimens examined:—**D.R. CONGO. Upper Katanga:** Forêt claire, plateau des Kundelungu, 1550 m, 27 October 1969, *Lisowski, Malaisse & Symoens 7578* (LSHI!); 23 km WNW du poste de Lualaba (Kundelungu), bord d’un petit torrent au-dessus de l’escarpement rocheux, 1 km à droite de la chute de Kaloba, 7 January 1970, *Lisowski, Malaisse & Symoens 9242* (LSHI!, POZG!).

Discussion:—Both collections perfectly match the type of *Monotes redheadii* Duvigneaud (1959: 101), a species known from Zambia and Angola, except for the glabrous upper surface of leaf; *Lisowski, Malaisse & Symoens 8940* (POZG!) is glabrous on both surfaces.

16. *Monotes glandulosus* Pierre (1897: 1299)

Type:—ANGOLA (?). Sine loco, sine dato (holo-: P! [barcode P054013988]; iso-: BRLU! (fragm.); photo: BM!, K!).

Discussion:—*Monotes glandulosus* Pierre is an enigmatic taxon known from the type specimen only, probably from Angola. Bancroft (1939a) interpreted it as very closely related to *M. delevoyi*. Duvigneaud (1949) argued that it was almost similar to *M. mutetetwa*. The type specimen has oblong leaves with irregular margin, glabrous areoles, reticulum with curled hairs and upper surface with remains of short stiff hairs (ca. 0.25 mm long). Such a phenotype combines traits of *M. dasyanthus* var. *mutetetwa* and *M. adenophyllus* var. *adenophyllus* and a hybrid origin is possible. Some collections from D.R. Congo approach the type of *M. glandulosus*, especially *Callens 3034* (BM!, BR!), *Duvigneaud 2530M2* (BRLU!); *Duvigneaud 3071* (BRLU!).

References:—Bancroft (1937: 138; 1939a: 341); Catarino *et al.* (2013: 272); Duvigneaud (1949: 60); Figueiredo & Smith (2008: 67); Gilg (1908b: 291); Lebrun & Stork (1991: 144).

Other possible new taxa

A substantial number of specimens we studied are still difficult to assign to known taxa. Several of them probably represent new taxa, but more material is needed to establish this. Some of the most striking specimens include:

Plancke 154/2050bis (BRLU!) (Upper Katanga, Kisenge, petit gisement de Mn de Kapolo, forêt intermédiaire): a very striking suffrutescent form with narrowly elliptic subglabrous leaves ca. 5 times longer than wide. Most probably a new species.

Duvigneaud 5261M4 (BRLU!) (Upper Katanga, Nzilo, 27 January 1960, forêt-verger enrochée sur pente quartzitique): small ovate-lanceolate leaves, almost glabrous on the upper surface.

Species excluded

Monotes gilletii De Wildeman (1915: 56). Type:—D.R. CONGO. Région de Pese, *Van Naemen* sine numero in Gillet (syn-: BR! [barcode BR0000008889805 & BR0000008889416], isosyn-: K! [barcode K000240336] (fragm.)), = *Marquesia acuminata* (Gilg) R.E.Fr.

Conclusions

Diagnostic characters to distinguish the genus *Marquesia* from *Monotes* are fewer than assumed earlier, but still sufficient to maintain the two. While *Marquesia* has glabrous to puberulent outer petal surfaces, a distinct androgynophore, incomplete locules and fruit wings with simple hairs, *Monotes* has velvety petals, no androgynophore, complete locules and fruit wings with fasciculate hairs. The phylogenetic relationships between *Monotes* and *Marquesia* is in need of further investigation by means of molecular techniques. With this revision, we have provided the research hypothesis and laid the taxonomic foundation for such an approach.

In this revision, we propose a more synthetic treatment than previous accounts of the genus *Monotes*, broadening the taxonomic concept of several *Monotes* species. Accordingly, several species are here synonymized or downgraded to the rank of variety or forma.

The revision also discovered valuable new collections of species that had previously been only known from scanty material. New collections from D.R. Congo allow a better circumscription of the range of their variation, especially so for *M. rubriglans* and *M. pearsonii*. The circumscription of those taxa is hereredefined.

Our results have important implications for conservation. Several supposed endemics are here refuted. First, four supposed Angolan endemics are shown to be morphological variants without much taxonomic value (*M. carrissoanus*, *M. dawei*, *M. hutchinsonianus*, *M. noldeae*). Second, two species and a variety are shown to have a much broader distribution than previously thought (*M. hypoleucus* var. *loandensis*, *M. pearsonii*, *M. rubriglans*). Two Congolese endemics appear to have little taxonomic value (*M. oxyphyllinus*, *M. schmitzii*). Other endemics are confirmed or described, being well characterized (*M. doryphorus*, *M. duvigneaudii*, *M. hirtii*). In a genus where species delimitation is highly problematic and where, partly as a result of that, the species distribution ranges are poorly known, an assessment of the conservation status is premature, until the whole genus is revised based upon all available material.

We have not solved all taxonomic problems. The examined material still comprises a number of very puzzling specimens, some of which probably represent new species which we are not able to describe due to their incompleteness. A number of described species are still incompletely known due to a paucity of material. In D.R. Congo, future botanical explorations should be directed to regions which apparently harbour an exceptionally rich diversity of forms. For example, Duvigneaud collected copious materials in the region of Nzilo and the Kibara mountains, including endemic species and many variants difficult to assign to described taxa. The Upemba National Park also provided some puzzling collections. Such regions need further study using a population-based sampling strategy.

Finally, this revision indicates that with 27 taxa, the Katanga region undoubtedly qualifies as the most prominent hotspot for the genus *Monotes* (Angola: 15 taxa; Zambia: 12 taxa). The anthropogenic pressure on miombo woodland in Upper Katanga raises concerns as to the long term conservation of many members of *Monotes*.

Acknowledgements

The authors are most grateful to Iris Van der Beeten, Petra Ballings and Myriam De Haan (Agentschap Plantentuin Meise) for taking the SEM photographs and to Tariq Stevart (Missouri Botanical Garden) for preparing the maps. Hans de Vries prepared the illustration of *Monotes duvigneaudii*. Geoffrey Fadeur and Liliane Richil provided assistance in the curation of the *Monotes* collection at BRLU. The curators of BM, BR, BRVU, FHO, K, LG, LISC, LSHI, P, POZG and W are sincerely thanked for giving access to their collections or sending materials on loan. The constructive comments by the editor and three anonymous reviewers are gratefully acknowledged.

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FIGURE 13. Holotype of *Monotes autennei*.

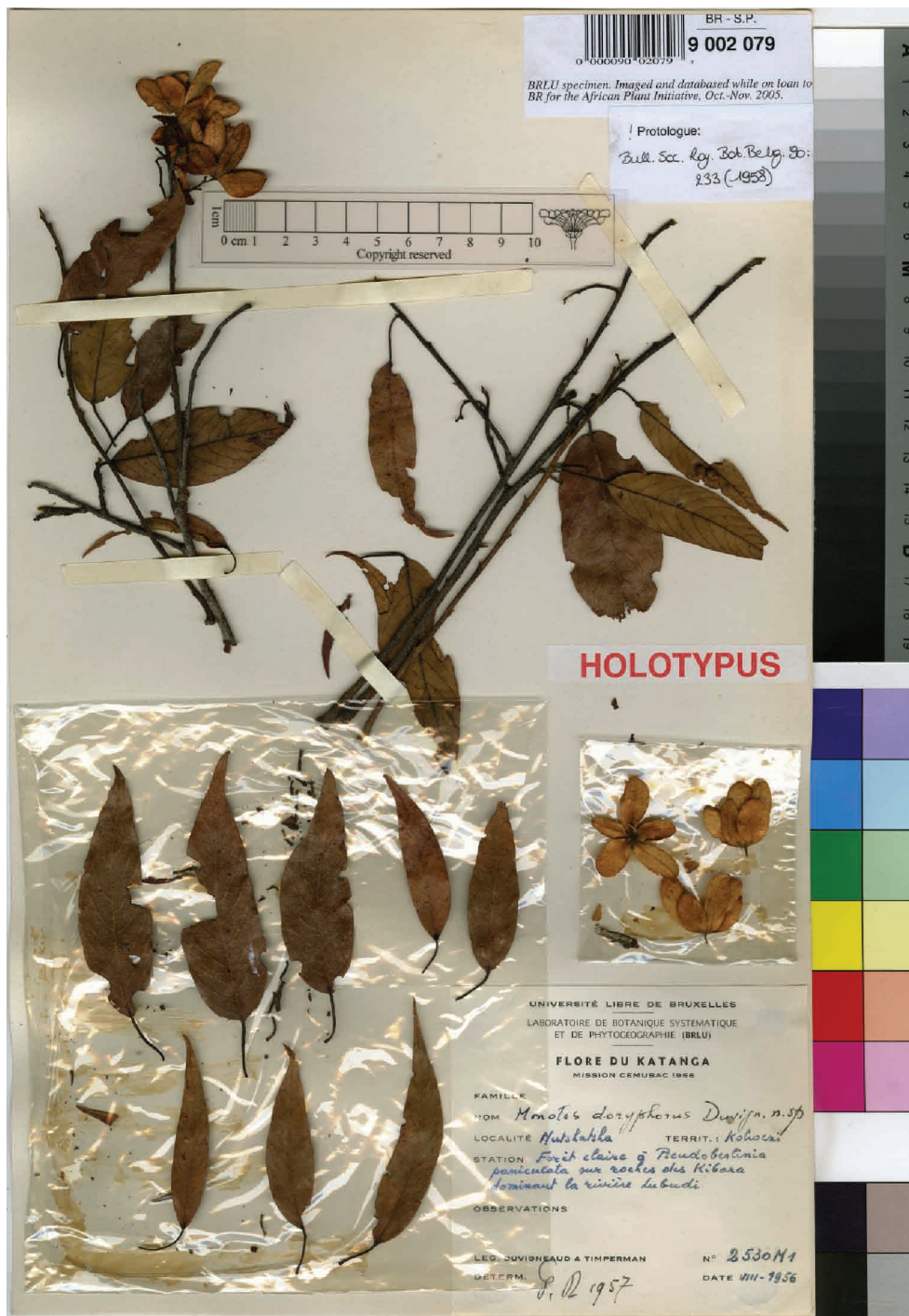


FIGURE 14. Holotype of *Monotes doryphorus*.



FIGURE 15. Lectotype of *Monotes hirtii*.

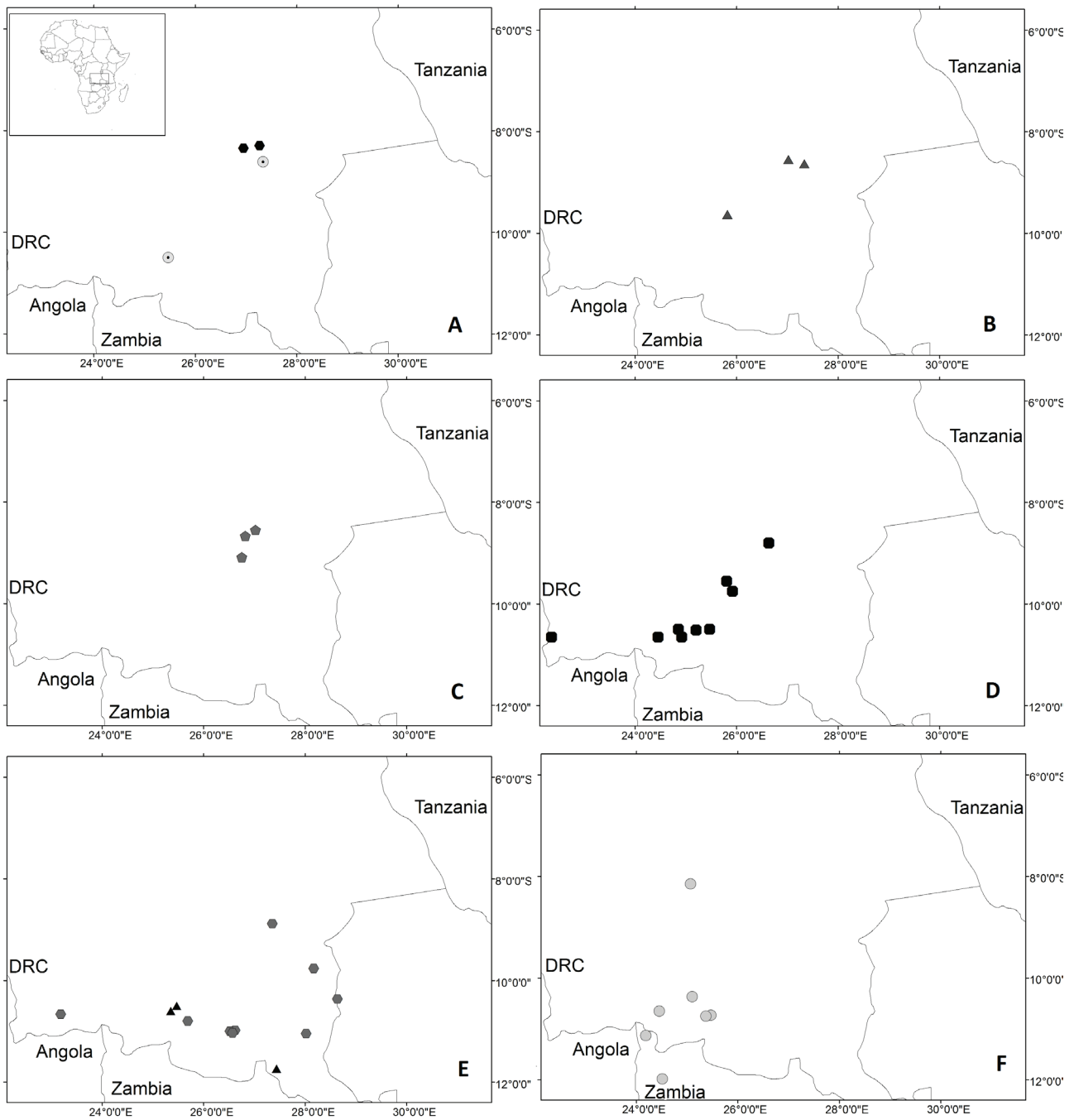


FIGURE 16. Distribution maps. **A.** *Monotes duvigneaudii* var. *duvigneaudii*: ⊙; var. *concolor*: ●; **B.** *M. rubriglans* subsp. *upembensis* var. *griseocoriaceus*: ▲; **C.** *M. rubriglans* subsp. *upembensis* var. *upembensis*: ◆; **D.** *M. doryphorus*: ■; **E.** *M. magnificus* var. *gigantophyllus*: ●; *M. hirtii*: ▲; **F.** *M. dasyanthus* var. *heterotrichus*: ●.

Appendix

Specimens used in the morphometric analysis (all in BRLU), with *a priori* identifications by Duvigneaud; all specimens are from D.R. Congo except otherwise stated.

M. caloneurus: *Desenfans s.n.*; *Desenfans 5707*; *Duvigneaud 1328M*; *Duvigneaud 1318M2*; *Duvigneaud 1322 1*; *Duvigneaud 1350M*; *Duvigneaud & Timperman 2630M*; *Duvigneaud & Timperman 2371*; *Duvigneaud 3267M2*; *Duvigneaud 3267M3*; *Duvigneaud 3804M1*; *Duvigneaud 4465M*; *Duvigneaud 4455M*; *Duvigneaud 1359AM*; *Exell & Mendonça 109* (Angola); *Herman 2222*.

M. elegans: *Adamson A51/34* (Tanzania); *Burt 1382* (Zambia); *Burt 6509* (Tanzania); *Burt 5920* (Zambia); *Burt 5483* (Tanzania); *Burt 5911* (Zambia); *Duvigneaud 3560M0*; *Duvigneaud 3203M*; *Duvigneaud 338M1A*.

M. hypoleucus: *Desenfans 3226*; *Duvigneaud 949M*; *Duvigneaud 822M*; *Duvigneaud 840M*; *Duvigneaud 779M*; *Duvigneaud 774M*; *Welwitsch 1036* (type) (Angola);

M. schmitzii: *Duvigneaud & Timperman 2190M*; *Duvigneaud & Timperman 2608M1*; *Duvigneaud 3617M*; *Schmitz 762*; *Schmitz 1332* (type); *White 2127*.