REVISION OF MELIOSMA (SABIACEAE), SECTION LORENZANEA EXCEPTED, LIVING AND FOSSIL, GEOGRAPHY AND PHYLOGENY

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SUMMARY

Up to the present *Meliosma* was subdivided into two sections, *Simplices* and *Pinnatae*. These taxa are shown to be artificial, and a new, less simple but more natural infrageneric subdivision is made, viz. into the subgenera *Kingsboroughia* and *Meliosma*, subdivided into the sections *Hendersonia* and *Kingsboroughia*, and *Meliosma* and *Lorenzanea* respectively. The old sections *Simplices* and *Pinnatae* have been reduced to subsections of sect. *Meliosma*. This new system is primarily based upon endocarp characters which were as yet unknown; it has appeared that the morphology of the endocarp shows very important features. In subg. *Kingsboroughia* the vascular bundle connecting pedicel and seed is situated outside the endocarp wall, which is considered the most primitive situation, whereas in subg. *Meliosma* it is enclosed within the endocarp. The endocarp types of the four sections, in the sequence mentioned above, show an increasing degree of specialization, i.e. an increasing degree of enclosure of the vascular bundle by the endocarp wall; the most primitive type is found in the Malesian sect. *Hendersonia*, and the most specialized one in the American sect. *Lorenzanea*. The latter does not occur outside the New World, whereas the other three sections are SE. Asian, sect. *Kingsboroughia* and sect. *Meliosma* subsect. *Simplices* centering in SW. Central China, N. Upper Burma and Tonkin, and sect. *Hendersonia* and sect. *Meliosma* subsect. *Pinnatae* centering in N. Sumatra, Malaya, and N. Borneo; these areas are shown to be probable, primary centres of origin of the species of these groups. Subg. *Kingsboroughia* and sect. *Meliosma* have thus bicentric areas, which are considered homologous, hence suggesting a similar distributional history of the taxa involved. Similar bicentric areas are also found in some other, unrelated genera, and may be not uncommon.

Subg. *Meliosma* is a common, widespread, diversified taxon, in contrast to subg. *Kingsboroughia* which has only three uniform species covering small and disjunct areas. It is demonstrated that subg. *Kingsboroughia* is a relict group, which was much more widespread in former geologic periods than it is at present. This is supported among other things by the transpacific disjunct distribution of *M. alba* which at present only occurs in SW. Central China and in S. Mexico (formerly known as two separate species which were never compared).

The history of the distribution of *Meliosma* during the Tertiary period can be partly reconstructed with the help of fossil records of this genus, more than 40 of which have been evaluated, mostly on the basis of paleobotanical literature. It appears that most of these records, including endocarps and leaf-imprints, are reliable, especially those of endocarps. With the help of these it can be established that the four sections and the two subsections of *Meliosma* were already recognizable as early as the Lower Eocene. From that time on their distributional history can be more or less traced up to the present. It is very probable that during the warm Eocene sect. *Meliosma* entered America via Beringia (the reverse possibly holds for sect. *Lorenzanea*), whereas it is certain that sect. *Kingsboroughia* did so at a later phase of the Tertiary, when the climate was cooler and a forest of warm-temperate ecology covered a wide zone in the northern hemisphere. The Pleistocene glaciations destroyed most of this vegetation and consequently the area of sect. *Kingsboroughia* was reduced to a few small relict stations, of which the localities of the above-mentioned disjunct *M. alba* are the most remarkable ones.

The taxonomic revision proper deals only with the SE. Asian sections of *Meliosma;* the American sect. *Lorenzanea* has been excluded. Up to the present the number of Asian species of *Meliosma* was estimated to be nearly 100, the number of names even being twice as much. Of these species only 15 are recognized here, and no new species have been described. A number of these are widely distributed, complex species, which can be subdivided into several subspecies. It appears that in all species these subspecies are isolated from each other, either geographically, or ecologically (by altitude or habitat). One special case of ecological isolation has been found, viz. between two different-sized subspecies flowering respectively in the undergrowth and in the upper tree storey of lowland tropical rain forest.

Finally, evidence has been found that *Meliosma* is a self-pollinator, which would favour the origin and perpetuation of local races, and hence would account for the richness of forms in *Meliosma* species.

INTRODUCTION

Originally it was my intention to revise *Sabiaceae* for the Flora of Thailand and I started with the genus *Meliosma*.

The genus has never been monographed and I had only some regional revisions of adjacent countries at my disposition, viz. on the species of China by Cufodontis¹) and by How²) and on those of Indo-China by Gagnepain & Vidal³).

As happens frequently, especially in genera containing species which are widely distributed in the Indo-Malesian region, the integration of the Thailand material with these regional revisions appeared to be unsatisfactory and this finally showed the necessity of

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¹) G. Cufodontis (1939). Revision der chinesischen Meliosma-Arten. Oesterr. Bot. Z. 88: 246—268.

²) F. C. How (1955). Revision of the Chinese Meliosma. Acta Phytotax. Sinica 3: 421—452, pl. 55—58 (in Chinese, with English summary; a French translation provided by the courtesy of Dr. J. Vidal).

³) F. Gagnepain & J. Vidal (1960). Sabiacées. Fl. Camb., Laos & Vietnam, fasc. 1: 11—59, 9 fig.

revising the genus as a whole for the Old World and to the scrutiny of its representation in the New World tropics.

The present revision is based on the examination of over 3000 collecting numbers of the Old World, including almost all type specimens. In addition a close study of certain New World species appeared of vital importance.

This study would not have been possible without the generous cooperation of the directors of several herbaria from which I could borrow sheets to make the revision as complete as possible. Apart from the Rijksherbarium, Leiden, these herbaria are from the following institutions: Arnold Arboretum, Cambridge, Mass.; Royal Forest Herbarium, Bangkok; British Museum (Nat. Hist.) Botany Department; Herbarium Bogoriense, Bogor; Royal Botanic Gardens, Edinburgh; Gray Herbarium, Harvard University, Cambridge, Mass.; Istituto Botanico, Firenze; Royal Botanic Gardens, Kew; Forestry Institute, Kepong, Malaysia; Laboratoire de Phanérogamie, Paris; Forest Department, Sandakan, Sabah, Malaysia; Botanic Gardens, Singapore; Botanisch Museum & Herbarium, Utrecht, and the Naturhistorisches Hofmuseum, Vienna.

The documentation of fossil evidence of *Meliosma* is as good as complete, thanks to the cooperation of Dr. L. Rüffle, Berlin, Dr. J. A. Wolfe, Menlo Park, Cal., Dr. W. H. Zagwijn, Geologische Dienst, Haarlem, Netherlands, and the curator of the paleobotanical collections of the British Museum (Nat. Hist.), Department of Palaeontology, who kindly provided me with material, photographs, or literature references.

The present work has gained considerably in value by the excellent drawings made by Miss R. van Crevel, which are as much artistic as exact and instructive; for this achievement I am very thankful to her. Many thanks are also due to Miss E. van Nieuwkoop, who did the typing, and part of the correcting of the manuscript, in a virtually perfect way. I also thank Mrs. Irene den Hartog who kindly assisted with the English language in the introduction.

Professor C. G. G. J. van Steenis who supervised my work, has greatly stimulated my enthousiasm by his continuous, critical interest. I shall not easily forget the vivid discussions we had, and the pushing way in which he coached me during the writing of the manuscript. I am very grateful to him for his positive attitude and the various kinds of support I received.

PART I. GENERAL OBSERVATIONS

A. SYSTEMATICAL POSITION OF MELIOSMA

For a full historical survey of the systematical position of *Meliosma*, the reader is referred to Chen (1943).

Meliosma is generally placed in the family *Sabiaceae* Bl., together with *Sabia* and *Ophiocaryon* (syn. *Phoxanthus*), a classification which was introduced by Bentham and Hooker *f.* (1862). Within this family the genera *Meliosma* and *Ophiocaryon* on the one hand, and *Sabia* on the other, certainly form natural groups, being Warburg's (1895) tribes *Meliosmeae* and *Sabieae*. Recently, Airy Shaw (1966) has expressed doubt about the naturalness of the *Sabiaceae* in the sense of Bentham and Hooker *f.*, and returned to the earlier concept of a monogeneric family *Sabiaceae*, introducing a separate family *Meliosmaceae* which includes *Meliosma* and *Ophiocaryon*. The relationship between these families, he says, requires confirmation. I do not wish to go into this matter until having revised *Sabia*, and for the present prefer to classify *Meliosma* in *Sabiaceae* in the sense of Bentham and Hooker, who gave a good description of the family.

Regarding the possible relationships of the *Sabiaceae* with other families there is no consensus of opinion. Most authors have related them (especially *Meliosma*) to the *Sapindaceae*, *Hippocastanaceae*, or *Anacardiaceae*; others assume a relationship (especially of *Sabia*) with amongst others the *Menispermaceae*, *Lardizabalaceae*, *Icacinaceae*, and *Schisandraceae* (see Chen, 1943).

B. INFRAGENERIC SUBDIVISION

Up till now, within *Meliosma* two sections were distinguished, viz. the simple-leaved sect. *Simplices* Warb. and the pinnate-leaved sect. *Pinnatae* Warb. New morphological evidence, discussed in the next chapter, has proved this subdivision to be artificial and has provided the criteria for a new subdivision which is based upon more characters and, hence, probably better reflects natural affinities.

The distinction of the two subgenera is here based upon three criteria, viz. the structure of the endocarp, that of the flower, and a marked character of the leaf. The distinction of the sections in subg. *Meliosma* is based only on the structure of the endocarp, while a further subdivision of sect. *Meliosma* in subsections and series is found in leaf characters.

For practical reasons this hierarchic sequence is not strictly followed in the key to the species.

The following system of the genus is here adopted:

- Subg. *Meliosma* p. 430
  - Sect. *Lorenzanea* (Liebm.) Beus. p. 431
  - Sect. *Meliosma* p. 431
    - Subsect. *Simplices* (Warb.) Beus. p. 434
      - Ser. *Rectinervia* Beus. p. 435
      - Ser. *Curvinervia* Beus. p. 447
    - Subsect. *Pinnatae* (Warb.) Beus. p. 484
- Subg. *Kingsboroughia* (Liebm.) Beus. p. 516
  - Sect. *Hendersonia* Beus. p. 517
  - Sect. *Kingsboroughia* p. 518

C. NOTES ON THE MORPHOLOGY

a. Inflorescence

In all species of *Meliosma* the inflorescence is a panicle, mostly three or four times branched, the side-axes repeating the mode of branching of the main axis; the flowers do not open in a definite succession.

In most species the panicle is terminal, usually without a distinct demarcation between twig and rachis, the latter being the mere extension of the twig (only in the species of subg. *Kingsboroughia* and in *M. lanceolata* and *hirsuta* is there a distinct demarcation). Mostly the panicle is leafy, the lower primary side-axes being subtended by normal to small or reduced leaves gradually decrescent upwards into bracts. Such a terminal, leafy panicle (fig. 1, type A) may be considered the primary, possibly also the most primitive type of inflorescence in *Meliosma*, from which basic type all other types can be derived by a contraction and reduction process, with the ramiflorous panicle as the most extremely derived form. Such derived panicle types are rare in comparison to the basic type; they are realized in only a few species, but in these species usually several possibilities are found. In these species the panicle type is usually an important discriminative character on the infraspecific level.

A few variants of the basic type A occur, of which the most important one is represented in fig. 1, type C; here the decrescent leaves are wanting, a situation which is now and then found in most species, but which may also be a constant specific (e.g. in *M. lanceolata* and *M. hirsuta*) or subspecific character.

The first step in the series towards axillary panicles is characterized by a contraction of the basal part of the main axis causing the lower primary side-axes to be somewhat crowded together; these lower primary side-axes are usually longer than normal, and may be particularly profusely branched, adopting the habit of separate panicles (fig. 1, type D). This type of inflorescence has been found in *M. lepidota* ssp. *squamulata*, *kinabaluensis*, and *dumicola*, and in *M. simplicifolia* ssp. *yunnanensis*, *rigida*, and *fordii*.

If in the panicle of type D the main axis above the contracted lower primary side-axes does not develop, the situation of fig. 1, type E, arises; the main axis ends in a terminal vegetative bud, which is usually well visible, sometimes small and reduced. Type E occurs in all subspecies of *M. lepidota* except ssp. *vulcanica*, and in *M. simplicifolia* ssp. *yunnanensis*, *laui*, *rigida*, and *fordii*. It is, moreover, the normal situation in *M. alba*. A variant of type E is represented in fig. 1, type F; here only one lower primary side-axis has developed. This type is very similar to the leafless variant of the basic type (type C), but can be recognized by the presence of a small bud at the base of the peduncle, usually somewhat pushed aside, which is the terminal bud of the main axis. It has been observed in *M. lepidota* ssp. *squamulata*, *kinabaluensis*, and *lepidota*, and rarely in *M. simplicifolia* ssp. *yunnanensis* and *rigida*.

The next stage is characterized by the development of the terminal bud of type E, not into an inflorescence, however, but into a small leafy twig (fig. 1, type G), which might be compared with virescence of the top part of the panicle. This may go along with a somewhat less crowded position of the lower primary side-axes, which now assume the habit of single axillary panicles. Type G has been found in all subspecies of *M. lepidota*, except ssp. *vulcanica*.

If the number of panicles in type G is reduced to only one — then being the parallel of type F — the situation of fig. 1, type H, arises, occurring in all subspecies of *M. lepidota*, except ssp. *dumicola*, and very rarely as an anomaly in various other species.

The final stage is reached when the main axis has assumed the complete habit of a twig, bearing one or more ramiflorous panicles (fig. 1, type I). This type is only found in *M. lepidota* ssp. *longipes*, *lepidota*, and *dolichomischa*.

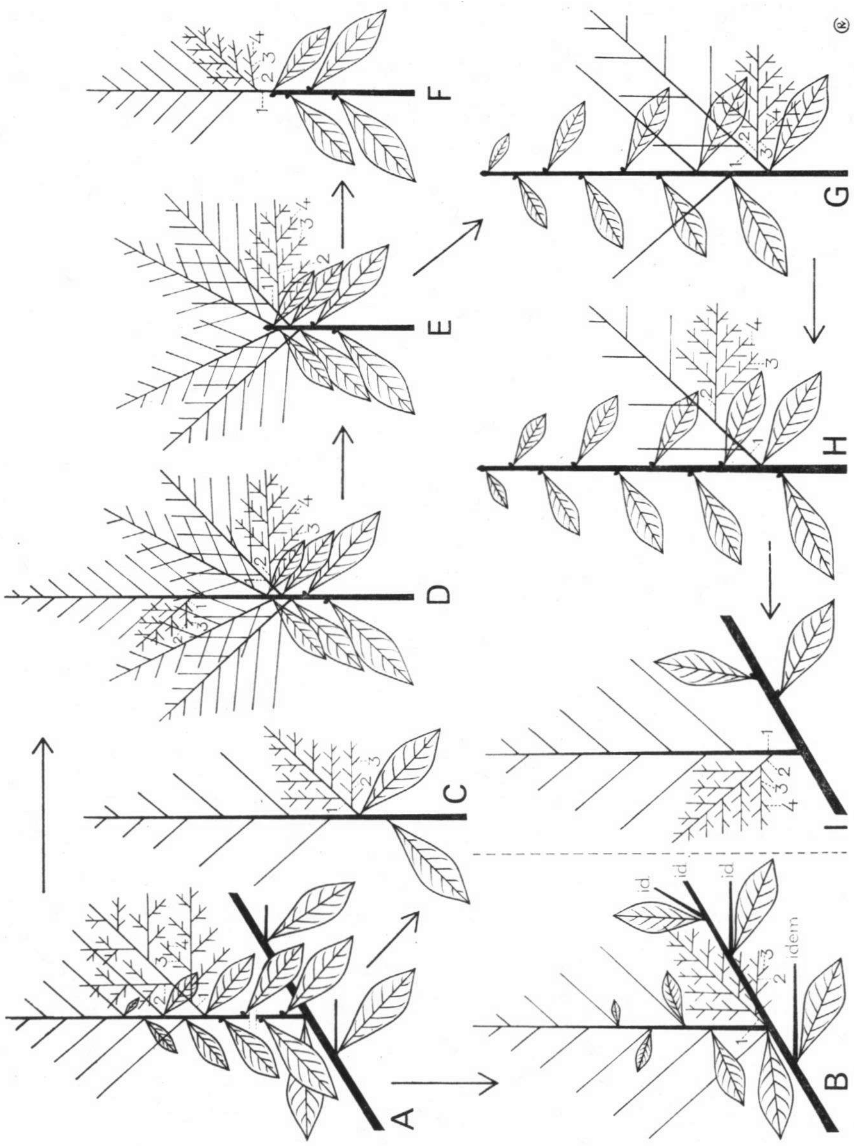

Fig. 1. Hypothetical derivation of various types of inflorescences in *Meliosma* from the basal type A. See the text.

The latter panicle-types, G, H, and I, should not be confused with a rare variant of the basic type A, which is represented in fig. 1, type B. In this case, which sometimes occurs in *M. henryi* ssp. *thorelii*, and rarely in *M. simplicifolia* ssp. *yunnanensis*, the flowering twigs as a whole are reduced to such an extent that the panicles become pseudo-axillary.

The normal panicle in *Meliosma* is not longer than *c.* 60 cm, and has nearly always a more or less erect position. In *M. lanceolata* and *M. hirsuta*, however, they are as a rule much bigger and pendulous, attaining a length of up to about 1½ m (see photogr. 1). A virtually extreme situation is found in a rare form of *M. lepidota* ssp. *longipes* in which the axillary or ramiflorous panicles can grow out to a length of 2 m, the axes being thin and flaccid.

The flowers in *Meliosma* may be distinctly pedicelled but are usually sessile or almost so, and very crowded, often in glomerules. If such glomerules are very crowded along the outermost axes, the flowers may be seemingly arranged in dense spikes. This spike-like type is in more or less recognizable form found in several species, but is often especially distinct in *M. lanceolata* and several subspecies of *M. simplicifolia.*

b. Bracts

The bracts are small and very uniform in all species, and generally do not provide useful characters for identification. The only exceptions to this occur in *M. parviflora*, in *M. simplicifolia* ssp. *pungens* and *thomsonii*, and rarely in *M. lepidota* ssp. *vulcanica*. Here at the base of each flower a varying number of empty bracts are found; these are more or less crowded, spirally arranged, and link up with the sepals, thus forming a kind of involucre. The presence and the number of such empty bracts are useful for identification.

c. Flower

The morphology of the flower of *Meliosma* is very remarkable; it has repeatedly been described and discussed, lastly by Vidal (1960), who also gave a concise summary of the opinions of previous authors. In short, the flower consists of the following elements: 3 imbricate sepals, subtended by 1 or more sepal- or bracteole-like elements; 3 imbricate petals; 3 scale-like elements opposite the 3 petals and at the base adherent to these; 2 stamens, with at the base of each an adherent scale-like, entire or lobed appendage; a disk, usually with 5 teeth, 4 of which are usually paired and situated opposite the stamens; 1 ovary with 2 locules, each with 2 ovules (see fig. 2 A, B).

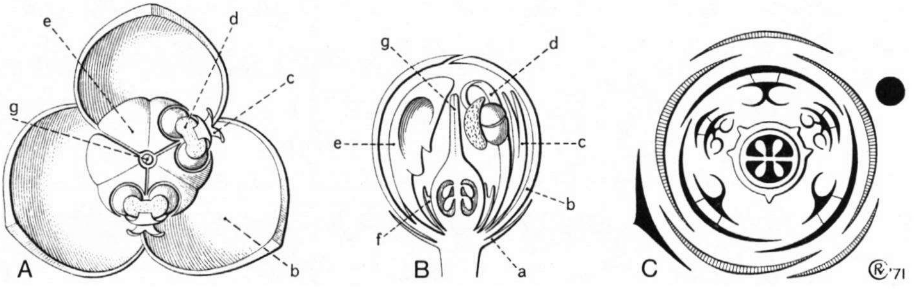

Fig. 2. Flower of *Meliosma*. A. Semi-diagrammatical sketch of flower (subg. *Meliosma*) with opened outer petals, but stamens still in bud position. B. Semi-diagrammatical length section of bud (subg. *Meliosma*). C. Diagram (subg. *Kingsboroughia* and subg. *Meliosma*).

Names of the flower parts: a. sepals, b. outer petals, c. inner petals, d. fertile stamens, e. staminodes, f. disk, g. style.

The presence of some unusual elements and the irregular structure of this flower have been the subject of attempts towards interpretation. With regard to this the authors can be divided up into two schools. The first of these, mainly comprising English and German authors, considers the *Meliosma* flower essentially 5-merous, with epipetalous stamens. In this conception the number of sepals is 5, whether or not with 1 or 2 bracteoles. The number of petals is also 5, of which the 3 outer ones are normal and the 2 inner ones are more or less reduced, being the appendages to which the 2 stamens are adhering. The stamens are also considered to be 5 in number, with 3 of them staminodial, somewhat enlarged and deformed, adherent to the base of the 3 outer petals. The most important supporters of this view were Wight & Arnott (1834), Blume (1849), Bentham & Hooker (1862), Urban (1895), and Warburg (1895), most later authors following them.

The second conception which was proposed by what might be called the French school, starts from the presumption that the flower of *Meliosma* is essentially 3-merous, with only 2 alternipetalous stamens. Following this idea, the number of sepals is 3, whereas the 1 or more sepal- or bracteole-like elements represent bracteoles. The 3 scale-like organs adherent to the petals are interpreted as a coronule, and the appendages at the base of each of the 2 stamens are considered an outgrowth of the filaments. This conception was initially adhered to by Blume (1823), judging from his description of the genus to which he gave the name *Meliosma*, but he later changed his view (see above). However, Baillon (1874) adopted it again and was followed in this by Lecomte (1908), and Gagnepain (1950).

If the arguments leading to each of these points of view are compared, it is at once clear that all evidence pleads in favour of the first of them. In fact, the conception of the French school is not much more than a mere registration of the flower parts just as they at first sight seem to be, without much interpretation, but it is partly also based on false observation. It is claimed, for instance, that the scales adherent to the petals are a coronule, and that the appendages to the stamens are part of the filaments. This is either misjudgement or it has been overlooked that these are visibly separate organs and not part of the petals and filaments respectively, but only more or less adherent to these and easily removed. Such arguments being invalid, it is clear that the French conception does not provide any positive elements towards an understanding of the *Meliosma* flower, and should be abandoned, as was consequently done by Vidal (1960).

The following arguments can be advanced in support of the assumption that *Meliosma* has essentially 5-merous flowers with epipetalous stamens.

1. Many species, especially in South America, have 5 about equal sepals, but in other species the outer 1 or 2 may be more or less reduced, 1 being sometimes even wanting. Furthermore, the outermost sepal may sometimes occur lowered on the pedicel, being seemingly a bracteole. In fact, I have never observed a real bracteole in *Meliosma*, and I propose, therefore, that this term should not be used in this genus.
2. The appendages adhering to the filaments can be differently shaped, being sometimes minute, lobed scales, but in some species being relatively large organs, not much smaller than the smallest petal, and of the same shape and texture as the petals. Moreover, they take exactly those positions in the flower that would be expected to be occupied by the 2 inner petals when the flower were 5-merous.
3. The 3 scale-like elements opposite and adhering to the 3 petals are still vaguely recognizable as transformed stamens, as their cavities can reasonably be assumed to be homologous with anther-cells; they serve to house the anthers of the fertile stamens when the flower is in bud.

4. The 5 teeth on the disk, which surrounds the ovary, usually show the same tendency towards asymmetry as do most other parts of the flower, 4 of them being paired, one solitary. Moreover, the 2 teeth pairs are situated exactly opposite the fertile stamens.

If the *Meliosma* flower is accepted to be essentially 5-merous, with a series of reductions and adaptations towards being seemingly 3-merous, all peculiarities displayed by it come to fit in a coherent framework (fig. 2 C). There cannot be the slightest doubt about the validity of this conception, which is logical in every respect. As has been shown by Urban (1895), it also provides a good basis for studying the affinities of *Meliosma* with other genera; the closely related South American genus *Ophiocaryon* shows the same reduction tendencies, but is less advanced in this respect, taking an intermediate position between *Meliosma* and *Sabia*, the flowers of the latter being unalterably 5-merous.

As a specialized functional unit the *Meliosma* flower is very remarkable. The three outer petals are imbricate, but only very slightly, along a narrow, flimsy margin, whereas they are rather firm and somewhat fleshy for the main part; in fact, the buds have the character of three-subvalvate[1]) globules. In bud the anther-cells are sharply bent down- and inwards by a fold near the top of the filament; the laterally protruding anther-cells fit in the cavities of the staminodes (the staminode between the two fertile stamens has two cavities, the other two staminodes only one, the second being reduced. Compare fig. 2 A, C). This complex of fertile stamens and staminodes envelops the pistil, the staminodes often being somewhat connate at the top, leaving a pore through which the top of the style protrudes. The pollen ripens and the anther-cells burst while the flower is still in bud, but the pollen is still unable to escape from the anther-cells as these are locked in the cavities of the staminodes. When the bud is fully mature, it explodes at the slightest touch, the stamens snapping backwards and flinging a puff of pollen into the air (cf. *Berberis*). When the flower is open, petals and stamens, having done their duty, very soon drop off; hence in a *Meliosma* panicle almost only buds and passed flowers are found, but very few intact open flowers. It is still not known how this exploding mechanism works.

It should be noted that the above described mechanism occurs in subg. *Meliosma*, but not in subg. *Kingsboroughia*. In the latter the flower structure is essentially the same as in subg. *Meliosma*, but the outer petals are much more imbricate and differently shaped. They open in the usual way; in view of the similar specialized structure of the flowers in subg. *Kingsboroughia*, one could assume that this group has lost the exploding mechanism secondarily, but one could as well imagine that it has never developed here.

Though the complex *Meliosma* flower is rather uniform in all species, it possesses some features, which provide characters useful for specific and infraspecific delimitation, which I shall now briefly evaluate:

1) *Buds*. In general *Meliosma* flowers are very uniform in shape and size, and measurements of the size of the buds only rarely provide useful characters for delimitation. It has appeared practical to express flower size in *Meliosma* (except in subg. *Kingsboroughia*) by the diameter (ø) of the mature buds[2]).

2) *Sepals*. The shape of the sepals is very uniform, and cannot be used as a good character for discrimination, but the presence or absence of pubescence on the outside of the sepals usually has taxonomic significance. However, one should be aware that also in

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[1]) In several descriptions they have been described erroneously as valvate!

[2]) See remark 3 b on p. 428 for recognizing the mature state of flower buds.

glabrous sepals the margin is usually ciliolate; this is a common condition throughout the genus without value for identification.

3) *Outer petals.* The outer petals of species of subg. *Meliosma* are differently shaped compared with those of subg. *Kingsboroughia*, providing a good character to separate these groups. Within these subgenera, however, they are extremely uniform; only in sect. *Meliosma* is there one subspecies (*M. pinnata* ssp. *ferruginea*) which stands out by having pubescent outer petals. Because the outer petals are always unequal in one and the same flower, it is better not to use their size as a character; to characterize the size of a flower I have used that of mature buds (see above).

4) *Inner petals.* The shape and the size of the inner petals provide important characters for specific as well as for infraspecific delimitation. In general they can be divided into two types, viz. the entire, about lanceolate type, and the bifid type. They may be ciliolate or fimbriate or not, and especially in the bifid type various subtypes can be distinguished (compare fig. 3).

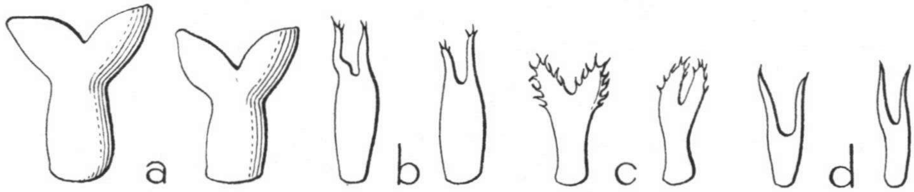

Fig. 3. Various types of inner petals in *M. simplicifolia*. a. ssp. *pungens* (*Wight 1542*, in L), b. ssp. *rigida* (*Faber 985*), c. ssp. *fruticosa* (*Rahmat 8132*), d. ssp. *simplicifolia* (*Lörzing 14715*). All × 18.

5) *Stamens.* Fertile stamens as well as staminodes are generally uniform, and when some variation occurs (e.g. in the connective), this is inconstant and not apt to serve taxonomic purposes. The variation in size is correlated with that of the whole flower and thus not of interest as a useful character.

6) *Disk.* The disk shows a high degree of variation. It is usually a well-developed 5-toothed annulus, of which the teeth may also be reduced to a varying extent, the margin being irregularly toothed, lobed, or waved, but even the disk as a whole may be almost or completely reduced. In SE. Asian *Meliosmas* at least the disk does not provide useful characters or hardly so.

7) *Ovary.* The ovary provides good characters, viz. in being pubescent or glabrous, which is usually a constant specific character[1]); its measurements are of minor importance. In one or two cases the length ratio of ovary and style can be used as an additional subspecific character.

d. Endocarp and seed

The ovary of *Meliosma* usually contains four ovules and only one[2]) of these develops into a seed. The fruit is a drupe with a rather thin pulpy mesocarp and a stony to crustaceous endocarp. The endocarp of *Meliosma* has a very characteristic structure, shared only by the allied genus *Ophiocaryon*. Its shape is usually subglobose to sometimes semiglobose, ellipsoid or pyriform, its surface is sometimes smooth but usually provided with a more

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[1]) Even in fruiting specimens it can as a rule be established whether the ovary was glabrous or pubescent; see remark 3 f on p. 428.

[2]) Exceptionally, two ovules develop, resulting in an anomalous, didymous fruit.

or less prominent reticulum. When dehiscent it splits into two valves; the plane of dehiscence is marked by a more or less prominent keel which runs all around the endocarp. At the ventral side there is a usually narrow pore through which the seed is connected with the vascular bundle towards the pedicel. For a correct understanding of the topography of the endocarp, I shall give the following technical terminology describing the situation:

The pore is located on the ventral side of the endocarp (more or less directed towards the pedicel). The distance between dorsal and ventral side is defined as the *height* of the endocarp, the length measurement of the endocarp in the plane of the median keel, perpendicular to the height, is defined as the *length* of the endocarp, and the length measurement of the dorso-ventral section perpendicular to the plane of the median keel is defined as the *width* of the endocarp.

Up till now the endocarps of *Meliosma* had only been superficially studied. I made a close comparative examination which has revealed a number of interesting phenomena. It appears that shape and structure of the endocarps provide very important characters for the infrageneric subdivision. Basically, two groups can be distinguished:

1) Endocarps which only enclose the seed, whereas the vascular bundle connecting pedicel and seed is running outside the endocarp wall. The position of the endocarp in the fruit is oblique, the ventral pore facing laterally downward. This situation is characteristic for subg. *Kingsboroughia* (fig. 4 A, B).

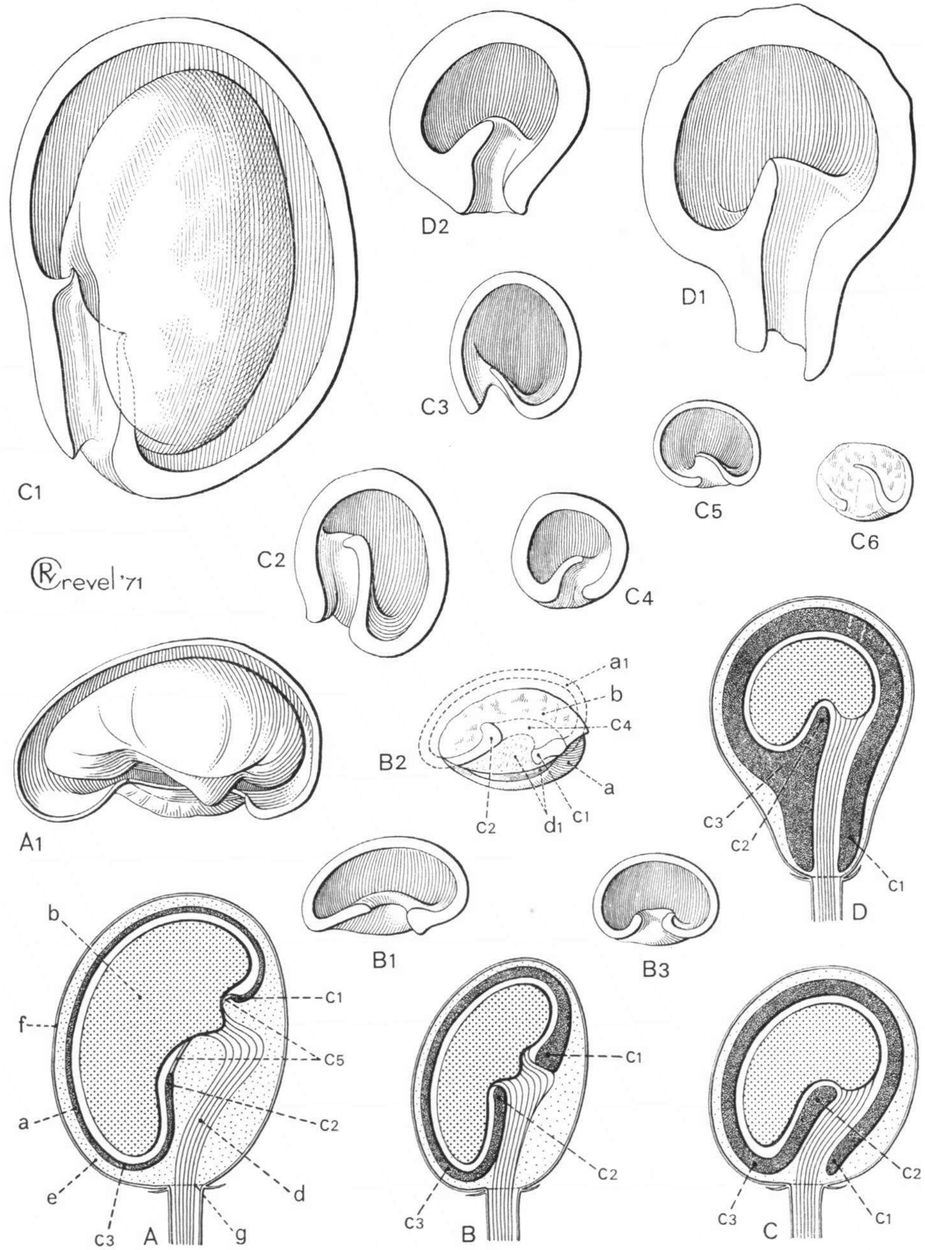
2) Endocarps which enclose both seed and vascular bundle, the latter being situated in a marginal canal inside. The position of the endocarp in the fruit is not oblique, the ventral pore facing downward (but the position of the seed is still oblique!). This situation is characteristic for subg. *Meliosma* (fig. 4 C, D).

Both groups can be subdivided into two types:

The first type of the first group (fig. 4, type A) is characterized by a vascular bundle running freely in the pulpy mesocarp of the fruit. The endocarp wall is thin, and conforms to the shape of the concave seed. In the centre of its concave ventral side the endocarp possesses a rather wide, especially thin-walled, flat, and smooth piece of tissue, through which protrudes the indurated tip of the conical ventral part of the seed, which is connected with the vascular bundle (see fig. 12 G 1). This type A is unique in *Meliosma* and is only found in *M. rufo-pilosa* (sect. *Hendersonia*) (a dorso-ventral length section is pictured in fig. 4 A 1).

The second type of the first group (fig. 4, type B) shows a vascular bundle running in a groove in the ventral surface of the endocarp, entering the wall through the ventral pore, and linking up with the seed inside the endocarp. The endocarp wall is distinctly thicker than in type A, and also the outward shape of it is a much less precise copy of the shape of the seed than is the case in type A. Furthermore, the seed is entirely enclosed by the endocarp wall, without a part of the seed protruding from it as in type A. Moreover, the central, flat, smooth piece of tissue of the ventral wall, which is found in type A, does not occur in type B. Type B occurs in *M. alba* and *M. veitchiorum* (sect. *Kingsboroughia*) (dorso-ventral length sections of endocarps of both species are illustrated in fig. 4 B 1, 3).

The first type of the second group (fig. 4, type C) is characterized by a downward extension of point c 1, which part of the wall makes the impression of being folded over the vascular bundle, thus forming a narrow, short to long marginal canal through which this bundle runs towards the cavity proper of the endocarp in which it is connected with the seed. The shape of the seed is still essentially the same as in type B and A, but the shape of the endocarp has changed considerably as a consequence of a relative thickening of the wall; it no longer reflects the shape of the seed. Type C is found in all species of sect.


C1
D2
D1
C3
C5
C6
C2
C4
RvCrevel '71
A1
a1
b
c4
B2
a
c2
d1
c1
c3
c2
c1
D
B1
B3
b
c1
f
c5
a
c2
e
d
c3
A
g
c1
c2
c3
B
c2
c1
c3
C

Meliosma (dorso-ventral length sections of endocarps of various species are pictured in fig. 4 C 1—5).

The second type of the second group (fig. 4, type D) is in principle the same as the foregoing one, but with an additional feature. The points c 1 and c 3 have extended ventrally, causing a lengthening of the marginal canal. Moreover, the endocarp wall is considerably thicker than in type C, but the seed still has essentially the same shape as in the foregoing types. Type D is characteristic for sect. *Lorenzanea*, the ventral extension being short to long, causing the endocarp to vary from almost globose to more or less pyriform (dorso-ventral length sections of endocarps of a few species are illustrated in fig. 4 D 1, 2).

From this survey it will be clear that the types A, B, C, and D represent a series. When analyzing this series from A to D the following phenomena are obvious:

a) The shape of the seed and the course of the vascular bundle are conservative characters, not varying essentially in the different types.
b) The endocarp, on the other hand, is rather liable to modification, in which two tendencies are obvious, viz. a tendency towards greater thickness of the wall, and a tendency to enclose the vascular bundle to an increasing degree.

Of course this series can also be read from D towards A, but there is good reason to prefer the above sequence, as may become evident from the following.

From the fact that the endocarps have been divided into two groups it might already be supposed that I consider the morphological gap between the types A, B and C, D larger than that between A and B, and C and D mutually. The close relationship between C and D is obvious enough, but it is more obscure in A and B. The following arguments are advanced to support it. When examining fossil endocarps of subg. *Kingsboroughia*, which, as far as I have seen them, all belong to type B, I was struck by the fact that locule-casts of these endocarps (which in fact represent rather exact casts of the seed) are so very much similar to the endocarp of type A (compare fig. 12 F and G 1, 2). It is as if type B was composed out of type A just by putting a wall around the latter. Such a similarity can hardly be considered accidental, and may point to a close affinity[1]). This similarity I explain as follows. Type A represents a very primitive stage of the development of an endocarp wall. This wall is still thin and incomplete, not enclosing the whole seed, but leaving a ventral piece free. In this connection the thin and smooth central piece of tissue (c5) at the ventral side of the endocarp is interesting, since it differs so

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[1]) From other characters of the species of subg. *Kingsboroughia* — to which endocarp types A and B belong — it appears that they indeed form a very homogeneous, certainly natural group.

Fig. 4. Length sections of the four types of endocarps in *Meliosma:* A—D diagrammatical sections of the fruit, A1—D2 sections of only the endocarps, all, except C6, from nature. All × 3.

A. subg. *Kingsboroughia* sect. *Hendersonia.* — A1. *M. rufo-pilosa* (*Pennington 7942*). — B. subg. *Kingsboroughia* sect. *Kingsboroughia.* — B1. *M. veitchiorum* (*Tsai 57833*). — B2. † *M. cantiensis* (*London Clay fossil nr. V 22781* in Brit. Mus. Nat. Hist.; see Reid & Chandler, 1933, t. 18 f. 30). — B3. *M. alba* (*Wilson 154*). — C. subg. *Meliosma* sect. *Meliosma.* — C1. *M. sumatrana* (*Meijer SAN 28853*). — C2. *M. simplicifolia* ssp. *fruticosa* (*Sinclair SF 39501*). — C3. *M. pinnata* ssp. *macrophylla* (*bb. 19556*). — C4. *M. henryi* ssp. *thorelii* (*Tsang 7299*). — C5. *M. lepidota* ssp. *squamulata* (*Tsang 25933*). — C6. † *M. sheppeyensis* (copied from Reid & Chandler, 1933, t. 18 f. 33). — D. subg. *Meliosma* sect. *Lorenzanea.* — D1. *M. herbertii* (*Sintenis 6177*). — D2. *M. dentata* (*Hinton 8431*).

Names of various parts: a. endocarp wall, a1. reconstruction of endocarp wall, b. seed, c1—c3. different loci of ventral endocarp wall (see text), c4. reconstruction of endocarp wall surrounding ventral pore, c5. scar tissue (see text), d. vascular bundle, d1. vascular bundle tissue ('plug'), e. mesocarp, f. exocarp, g. attachment pedicel—fruit.

remarkably from the rest of the endocarp wall. In my opinion this ventral piece is not part of the normal endocarp wall, but represents a kind of scar tissue formed to cover that part of the seed which is left uncovered by the authentic endocarp wall (comparable to a fontanel). A good argument for this also is that the median keel along which the endocarp splits into two valves does not or hardly extend to this aberrant piece of wall tissue. I have split one or two mature endocarps as a further check, and indeed, in contrast to the normal endocarp wall, the scar tissue did not split evenly, but broke irregularly or along the suture with the normal wall. If the above interpretation is correct, then the parts c 1 and c 2 in fig. 4, type A, are homologous with the parts c 1 and c 2 in fig. 4, type B. Type B can now easily be derived from type A, by just letting c 1 and c 2 encroach upon the ventral centre of the seed, until they reach the point of attachment of the vascular bundle, which, of course, must be left free. The process of vaulting, which then starts, wil produce the stage represented by type B.

The question now to be posed is which extreme of the series A to D is to be considered the most primitive, type A or type D. I think the most obvious, but admittedly subjective answer to this question is that the evolutionary line from an incomplete towards a complete endocarp, and from a free-running towards an enclosed vascular bundle, hence from simple to complex, is the most logical sequence; thus the type A should be considered most primitive and type D most advanced. However, one could also imagine that a reduction process is responsible for the variation series in *Meliosma* endocarps. Other arguments have to be produced to settle this dilemma, for which I refer to part II chapter C, where arguments are given in favour of the hypothesis that subg. *Kingsboroughia* (to which types A and B belong) represents an ancient relict group; hence, the series of endocarp types from A to D can safely be assumed to be arranged according to an increasing specialization.

For the many interesting relationships between fossil and recent *Meliosma* endocarps, I refer to part II chapter B, C, where they have been analyzed and amply discussed.

The endocarps of *Meliosma* provide many characters, not only useful, as has been demonstrated, for infrageneric delimitation, but also for the identification of species and subspecies, as appears from the following observations:

1) The *size of the endocarp* is usually rather constant, especially within one subspecies, but may also vary considerably (cf. fig. 29 A 1—4).

2) The *shape of the endocarp* may vary from ellipsoid or pyriform to usually globose or sometimes semiglobose. Furthermore, in sect. *Meliosma* the endocarps may be more or less oblique, as the median keel often has a strong outward curve on one side (cf. fig. 22, K, L, and fig. 29 B 1); the presence or absence of this character may be useful for subspecific identification.

3) The *median keel* may be hardly developed to strongly prominent. The median keel may also provide the following characters: as has been shown, in sect. *Meliosma* the endocarp wall in the plane of the median keel curves ventrally inwards on one side and runs straight downwards on the other; at the latter the median keel is often somewhat extended, thus forming a usually small to minute ventral processus or tubercle (cf. fig. 22 H 2, 3, K, L, and fig. 29 B 2, 4, 6, 7). The presence or absence of such a processus may be an additional subspecific character.

4) The *surface reticulation* is rarely absent (cf. fig. 22 F 1, 2) or faint (cf. fig. 22 H 2, 3), moderately prominent (cf. fig. 22, most specimens) and sometimes strongly prominent (cf. fig. 22 Q 1, 2); it may be fine (cf. fig. 22 J 2) to coarse (cf. fig. 22 E 2).

5) The *ventral pore* may be more or less sunken (cf. fig. 29 B 1, 2), somewhat spouted (cf. fig. 22 P, Q 2), or neither sunken nor spouted (cf. fig. 22, many specimens). In *M.*

alba and *M. veitchiorum* (subg. *Kingsboroughia*) the ventral pore is usually not visible but filled with hard tissue of the vascular bundle as is also the ventral groove; this tissue is indicated by the term 'plug', following the practice in paleobotanical literature (cf. fig. 34 e).

N.B. It may seem difficult to distinguish between endocarps of subglobose shape belonging to sect. *Meliosma* and those of sect. *Lorenzanea* (cf. fig. 22 Q 1, 2, and R). However, the profile of the splitted endocarp (cf. fig. 4 C 2—5 and D 1, 2) is always decisive.

The *embryo* in the seed of *Meliosma* shows remarkable features; it is described at some length by Urban (1895) and Warburg (1895). As I cannot add anything new, it is sufficient to refer to these authors.

e. Seedling

Seedlings have only rarely been collected. The specimens seen by me (not very young and all belonging to sect. *Meliosma* subsect. *Pinnatae*) all have dentate leaflets, also those of (sub)species which in adult stage are characterized by entire leaflets. Dentation of leaves and leaflets of seedlings (also of water-shoots!) may be a general rule. For a better understanding of the relationships between the infrageneric taxa, especially the closely related subsections *Pinnatae* and *Simplices* (sect. *Meliosma*), it is advisable to cultivate specimens from seed, and to study the development of the embryo, cotyledons, and first leaves.

f. Leaves

The leaves in *Meliosma* provide several good characters. Subgenera, subsections, and series are characterized by special leaf-types and also most species and subspecies can be recognized by their leaves. However, since leaves in particular are subject to phenotypic variation, and leaves in *Meliosma* may indeed vary very much, it is not always easy to distinguish essential from non-essential characters. An additional difficulty of which one should be aware, is that characters constant in one species or subspecies are sometimes variable in others. A critical evaluation of the diagnostic value of leaf characters has resulted on the one hand in the discovery of good characters not used before, and on the other in the devaluation of characters on wich often species had been based. The most important leaf characters will be discussed below.

1. *Leaf composition.* Up till now the subdivision into sections was based on whether the leaves are simple or pinnate. Though this is indeed an important character, the consequent application of it results in artificial taxa. More fundamental value should be attached to the following character, viz. whether the leaves (when pinnate) have one or three top leaflets[1]; the former type can be distinguisged from the latter by the petiolule of its top leaflet having an articulation. These conditions are correlated with fundamental fruit and flower characters upon which the subdivision into two subgenera has been based. A subdivision into groups with simple and with pinnate leaves, however, is only appropriate at subsectional level (see chapter B).

In pinnate-leaved *Meliosma* the number of leaflet-pairs is sometimes rather characteristic for species (e.g. in *M. lanceolata* and *M. hirsuta* with many, in *M. sarawakensis* with very few leaflet-pairs), as well as for subspecies (e.g. those of *M. pinnata*). Generally, however, this character is rather much subject to variation, with consequently much overlap between different taxa.

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[1] Rarely, leaves of intermediate character occur, but only as an occasional anomaly on twigs with otherwise normal leaves.

2. *Shape and size of leaves and leaflets.* These characters are even more variable than the number of leaflet-pairs, and thus mostly useless for specific delimitation; they are only occasionally useful as additional characters in subspecific delimitation, for instance the length/width ratio (leaf index).

3. *Dentation.* The absence or presence of teeth is sometimes a more or less constant specific or subspecific character, but usually in the same taxon leaves or leaflets may be dentate or not.

4. *Pubescence.* The presence or absence of pubescence is usually an important subspecific character, especially the pubescence on the midrib on the upper surface of leaf or leaflet. Types of pubescence, however, have not proved to be very constant and moreover are difficult to describe satisfactorily; I have, therefore, not payed much attention to them in this revision. The same holds for the presence or absence of glands or glandular hairs, which proved to be a rather erratic feature. The only exception to this is the *domatia* which often occur as small to minute tufts of hair in the axils of the nerves, sometimes also of the veins, on the lower surface of leaves or leaflets. The absence or presence of domatia is sometimes a constant (sub)specific character.

5. *Midrib.* On the upper surface of leaves or leaflets the midrib may be prominent to usually impressed. Such a prominent midrib is a specific character of *M. sumatrana.* It is, moreover, a more or less constant character in a few subspecies of *M. simplicifolia* and in one subspecies of *M. pinnata.* However, it is not always easy to distinguish between prominent and impressed midribs (see remark 1 e on p. 428).

6. *Nerves.* The nerves may be ascending or (almost) straight, and mainly on these characters the series *Curvinervia* and *Rectinervia* have been distinguished within subsect. *Simplices.* Moreover, the number of nerves is rather important for the delimitation of subspecies in most species of subsect. *Simplices.*

7. *Relative length of the petiole.* This is only rarely a constant feature, for example in *M. hirsuta* which has subsessile leaflets. It may also be useful for the distinction of subspecies, for example in the pair *M. lepidota* and *M. simplicifolia* which possess overlapping ranges of this ratio.

g. Anatomy

For this survey no original observations have been made on the anatomy of *Meliosma.* The following account is based completely on data from literature. For a concise survey of the anatomical characters of leaf, petiole, twig, and wood of *Meliosma*, the reader is referred to Metcalfe and Chalk (1950), who also give an almost complete bibliography.

Special studies on the anatomy of leaf-blade and petiole have been carried out by Dihm (1907) and Le Renard (1908). It appears amongst other things that the vascular system in the petiole is always cylindrical. The indumentum consists of simple hairs; capitate-glandular hairs occur also in most species, not only on leaves, but also in the inflorescences. I found that the occurrence of these hair types is often not constant for the species.

Some interesting contributions on the wood structure are those of Moll and Janssonius (1911), Kanehira (1921), den Berger (1926), Record and Hess (1943), and Desch (1954). One should be aware, however, that identifications of voucher specimens on which the descriptions are based, are often erroneous and that the variability of the species investigated is usually not taken into account.

As the most important general wood characters of *Meliosma* can be mentioned: Growth rings present or absent. Vessels solitary and in radial groups, medium-sized; perforations mixed, simple, scalariform. Parenchyma scanty, paratracheal. Rays usually conspicuous, of two distinct sizes, uniseriates and multiseriates. Fibres with simple or small bordered pits, occasionally septate. The bark is characterized by dilatating rays. According to Heimsch (1942), who gives a comparative study of the secondary xylem in the *Gruinales* and the *Terebinthales* in the sense of Wettstein, *Meliosma* has a relatively primitive level of xylem organisation.

For additional data on wood and bark structure, I refer to the summarized field notes under the species and subspecies in the special part of this revision. Economic uses of *Meliosma* are similarly dealt with; the wood is generally light, soft, and not very durable, hence not very useful for timber.

Summarizing, it can be stated that the anatomical knowledge is still unsatisfactory, at least from a taxonomic point of view. For instance, it is not yet clear whether the anatomical characters of *Meliosma* and *Sabia* support their generally assumed relationship. Moreover, as anatomical analyses up till now have been made in a rather haphazard way, and names of voucher specimens are usually not reliable, their taxonomic value on the specific level is very low. I suggest that future research should be more focussed on the infrageneric subdivision of the genus as given in this revision. With regard to this it would be interesting to know whether the important macromorphological differences between the subgenera *Kingsboroughia* and *Meliosma* have a parallel in anatomical characters.

h. Pollen, chromosomes, and chemical characters

Up to the present, only Erdtman (1952) has given diagnoses of the pollen types of *Meliosma* and of the other genera of the *Sabiaceae*, which are based, however, on very few samples. It appears that these pollen types much resemble each other, and it is observed that similar types also occur in several other families. Mr. J. Muller of the Rijksherbarium has preliminary investigated about 25 pollen samples of various species of *Meliosma*, and could find only minute differences. To obtain more detailed information, it will be necessary, however, to use the more advanced magnifying technique of the scanning electron microscope. It is intended, therefore, to make a further analysis of the pollen, not only of *Meliosma*, but also of *Ophiocaryon* and *Sabia*. The results of this work will be published at a later stage.

Few chromosome counts have been published. Darlington & Wylie (1955) give only one, viz. 2n = 32, for *M. wightii* (= *M. simplicifolia* ssp. *pungens*), the basic chromosome number being x = 16. Fedorov (1969) enumerates counts for three more species, viz. *M. myriantha*: 2n = 32?, *M. simplicifolia* (= *M. simplicifolia* ssp. *simplicifolia*): 2n = 32, and *M. tenuis* (= *M. dilleniifolia* ssp. *tenuis*): 2n = 32?. These counts thus all refer to species of subsect. *Simplices*. Therefore, it would be interesting to have some counts of species belonging to other infrageneric taxa; the assumedly primitive subg. *Kingsboroughia* in particular is promising in this respect.

For a few species of sect. *Meliosma* subsect. *Pinnatae* it is repeatedly reported in collector's notes that the inner bark soon discolours into deep orange or red on exposure. This is probably an oxidizing process, but it is not known what chemical compound is involved. Prof. R. Hegnauer informs me that up to the present hardly any chemical research has been done on *Meliosma*, hence nothing of importance can be communicated.

D. GENECOLOGY AND SUBSPECIFIC DIFFERENTIATION

Most species of *Meliosma* display a considerable regional, discontinuous variation, on the basis of which the numerous subspecies recognized in this revision have been distinguished. These subspecies are mostly demonstrably isolated from each other, either geographically and/or ecologically; often there are relatively narrow zones of overlap in between in which intermediate forms are not unusually found. The geographical pattern of subspecies arrangement can be either serial (*M. dilleniifolia, M. myriantha*), or radial (*M. simplicifolia, M. lepidota, M. henryi, M. pinnata*). A centre of dispersal and highest morphological differentiation is more or less apparent in each of the above species (see chapter E).

In *M. simplicifolia, M. lepidota*, and *M. pinnata* I have distinguished between primary and secondary subspecies; primary subspecies radiate from a common centre and are mainly isolated geographically (often partly ecologically), whereas secondary subspecies occur more or less at the periphery of the specific area and may be isolated either geographically (whether or not disjunct) or ecologically. Secondary subspecies, moreover, are considered derivatives of primary subspecies; their variability is low, and their characters link up distinctly with those of the primary subspecies to which they are allied. In most of the primary subspecies, which mostly cover a much larger area than do the secondary ones, a more or less decreasing variability towards the margin of the area can be observed. This tendency is also found in some species in which no subspecies could be distinguished, e.g. in *M. sumatrana*. Between subspecies, geographical isolation may pass into ecological isolation (altitudinal and habitat) in areas where they overlap. There is one case of assumed ecological isolation which deserves special mention, viz. that between *M. pinnata* ssp. *macrophylla* and its derivative ssp. *sylvatica*. Both are constituents of lowland tropical rain forest and are found in the same localities, but the former is in the field notes always described as a huge canopy tree, whereas the latter ia always recorded to be a small treelet of the undergrowth. I assume that ssp. *macrophylla* does not flower until it has reached the upper storey of the forest, but that ssp. *sylvatica* soon becomes reproductive and always remains a dwarf treelet. I think that it is well possible that reproductive isolation between interfertile taxa is effectuated by their occurring in different strata of the complex lowland rain forest biocoenosis which then represent different 'niches'. However, this mode of ecological isolation seems to be exceptional in *Meliosma*; geographical and altitudinal isolation is the rule, isolation by preference for different habitats being somewhat less common.

Recently Ashton (1969: 169) described a comparable case of sympatric occurrence in tropical trees of two subspecies in an overlapping part of their areas, viz. of *Shorea macroptera* ssp. *baillonii* and ssp. *macropterifolia* in North Borneo, of which the first is a lower-storey tree and the latter a canopy tree, as could be derived from their girth histiograms (l.c. fig. 7). Such stratified sympatric subspecies keep distinct by isolation through different pollination systems, either vertical stratification of insect pollen vectors, or different flowering times, or other barriers to outcrossing pre- and post-fertilisation such as is here the case in *Meliosma* through its selfing.

From the foregoing it can be concluded that race forming in *Meliosma* has been caused mainly by processes of geographical isolation and by differential selective altitude and habitat factors, and combinations between these.

Between local populations within species or subspecies of *Meliosma*, there is sometimes considerable variation. I presume that inbreeding may play a part in the differentiation of such populations, for which I can produce the following arguments.

It is true that the structure of the *Meliosma* flower seems to be well adapted to avoid self-pollination; in bud the introrse-transversal slit of the walls of the anther-cells is already open, and the pollen is ripe, but it cannot be liberated because the actual bursting of the anther-cells is inhibited by their being enclosed in the staminodes, so that no contact is possible between pollen and stigma of the same flower (see chapter C sub c). However, as soon as the flower-bud has exploded, the pollen disperses into the air, and much of it will certainly land on stigmas of adjacent, already open flowers in the same panicle, or of flowers in other panicles of the same tree or shrub. Hence it is very probable that self-pollination, not so much of individual flowers but especially between different flowers of the same plant, is a common feature in *Meliosma*, unless there is a physiological barrier. The presence of such a barrier, however, is not very likely, as is apparent from the following observation. In the early spring of 1971 I observed some hardy *Meliosma* species, cultivated in the open in Kew Botanic Gardens. I noticed that the only specimen of *M. dilleniifolia* (ssp. *flexuosa*), which had apparently flowered the previous summer and occurred at a considerable distance from other *Meliosma* specimens — which had no flowers or fruit — was bearing some well-developed fruits. This clearly points to successful self-pollination. Of course only experimental research can be conclusive in this respect, for instance, to check whether the seeds of such fruits would indeed germinate.

However, the evidence available nevertheless suggests that self-pollination may be a common feature in *Meliosma*. Hence inbreeding may favour the reproduction of isolated plants, in which the chance of cross-pollination with other specimens is very small. Such isolated, inbreeding plants may thus give rise to the establishment and perpetuation of local populations which consist of single biotypes; such self-pollination 'acts as an insurance against the failure of cross-pollination' (Heslop-Harrison, 1963). Actually, the often very scattered occurrence of many species in tropical forests is an established fact, and it is well imaginable that the above 'insurance' saves them from local extinction. The variation between local populations of *Meliosma* may possibly be explained in the above way.

E. DISTRIBUTION PATTERNS

For a proper understanding of the distribution pattern of *Meliosma*, the distribution of subgenera, sections, and subsections has been analyzed separately. In fig. 5 the areas of subg. *Meliosma* and *Kingsboroughia* have been mapped; moreover, in fig. 6 also the areas of sect. *Meliosma* subsect. *Simplices* and *Pinnatae* have been represented separately. With regard to the latter, it is clear that sect. *Meliosma* has a bicentric area, its two subsections each having their own centre of highest species frequency, viz. subsect. *Simplices* (7 spp.) in SW. and Central China, with only 2 species entering W. Malesia, and subsect. *Pinnatae* (5 spp.) in W. Malesia (N. Borneo, N. and Central Sumatra), with only 1 species extending far into continental Asia and E. Malesia.

Looking now at the Asian area of subg. *Kingsboroughia* (3 spp.) in fig. 5, it appears that this is characterized by essentially the same bicentricity[1]) as is sect. *Meliosma*, falling apart into a SE. and Central Chinese part (sect. *Kingsboroughia*, with 2 spp.), and a W. Malesian part (sect. *Hendersonia*, with 1 species). The difference between these two sectional areas lies in the fact that the area of subg. *Kingsboroughia* (which is poor in species) is small and disjunct and that of subg. *Meliosma* sect. *Meliosma* (which is much richer in species) is large and continuous.

In part II chapter C sub 1 arguments will be given in support of the conception that subg. *Kingsboroughia* is a relict group which in former periods was richer in species and covered a much larger area than it does to-day. If one assumes that the Old World relict areas of the two sections of subg. *Kingsboroughia* still represent their primary centres of dispersal, it is probable that the bicentric area of subg. *Meliosma* sect. *Meliosma* on the one hand, and that of the now depauperated subg. *Kingsboroughia* on the other, are

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[1]) The S. Mexican area (1 species) for the moment remaining out of consideration.

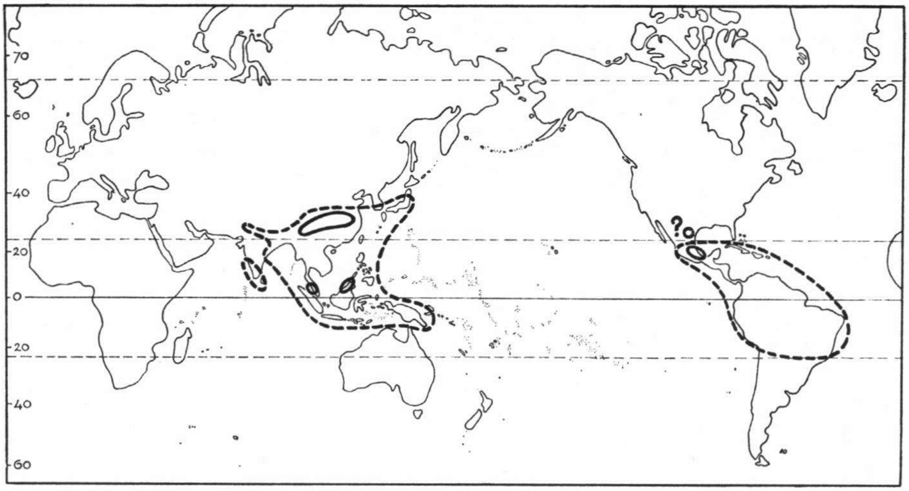

Fig. 5. Generalized area of *Meliosma* subg. *Kingsboroughia* (solid line) and subg. *Meliosma* (broken line). The locality indicated by a question mark is taken from literature but could not be checked.

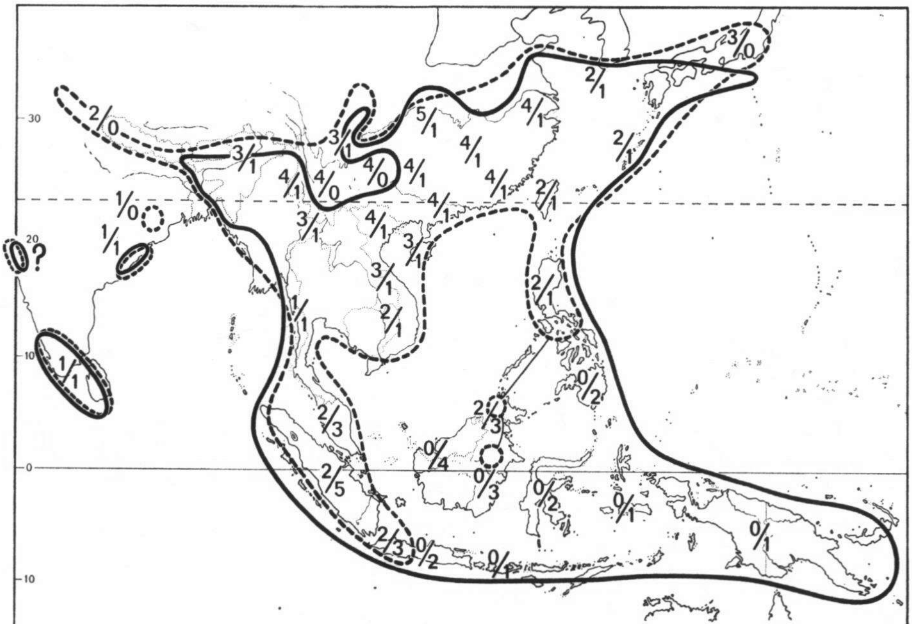

Fig. 6. Generalized area of subg. *Meliosma* sect. *Meliosma* subsect. *Simplices* (broken line) and subsect. *Pinnatae* (solid line). Species density is given for various parts of the area; the figure above the hyphen indicates the number of species belonging to subsect. *Simplices*, that below the hyphen the number of species belonging to subsect. *Pinnatae*.

homologous (cf. Diels, 1928), which means that their conformity is due to a similar history of distribution (see also Van Steenis, 1971). The tenability of this assumption will now be examined with the help of an analysis of the distribution patterns of the species of both groups.

a. Species distribution and centres of origin in subg. Meliosma sect. Meliosma

1) Subsect. *Simplices*

Within subsect. *Simplices* two series are distinguished, ser. *Rectinervia* and ser. *Curvinervia.* The species of these series show different distribution patterns, which will be treated successively.

Ser. *Rectinervia* consists of three species, of which the areas have been depicted in fig. 20 and 21. *M. dilleniifolia* covers an elongated wide zone from the western Himalaya via Central China to Japan, while *M. myriantha* and *M. parviflora* only occur in the eastern part of this zone, from West Central China to Japan and East China respectively. The distribution of *M. dilleniifolia,* which is the most widespread one of the three, is especially interesting. Four subspecies can be distinguished within it, each covering a separate segment of the total area. In the remarks on *M. dilleniifolia* (p. 440) and on ssp. *cuneifolia* (p. 443) it has been noted that ssp. *cuneifolia* takes a central position, since it has the greatest morphological differentiation, and that the other three, less polymorphous subspecies can be considered as being derived from it; in this connection the remarkable var. *multinervia* of ssp. *cuneifolia* seems to take a crucial position (See p. 444). Hence, for a probable centre of subspecies radiation of *M. dilleniifolia* the most obvious location would be the centre of the area of ssp. *cuneifolia,* and more particularly the area of its var. *multinervia.*

Much less obvious is the situation in *M. parviflora* and *M. myriantha* which do not show such a rich morphological and geographical differentiation. *M. parviflora* shows remarkably constant characters in which only a tendency of slightly increasing impoverishment can be observed towards the eastern end of its area. It is probably rather closely related to *M. dilleniifolia,* distinctly shows the closest resemblance to ssp. *cuneifolia* of the latter. *M. myriantha,* on the other hand, is broken up into two subspecies, of which the western ssp. *pilosa* shows a somewhat greater morphological variation than does the eastern ssp. *myriantha.* Furthermore, the closest morphological affinity of *M. myriantha* is again with *M. dilleniifolia* ssp. *cuneifolia.*

Though the above evidence is meagre, it is nevertheless obvious that — if one wishes to utilize the criterion of the occurrence of greatest morphological differentiation and of morphologically most closely related forms to trace the centre of origin and dispersal — the most probable area from where the species of ser. *Rectinervia* may have radiated, is situated in West Central China (NE. Yunnan, E. Szechuan, N. Kweichow, W. Hupeh). From this centre *M. dilleniifolia* is then considered to have expanded west- and eastwards, *M. parviflora* and *M. myriantha* only eastwards. Thus the areas of the species of ser. *Rectinervia* form a coherent, logically explainable pattern (see also p. 377).

Ser. *Curvinervia,* the second group of subsect. *Simplices,* consists of four species, two of which are very widespread, their areas extending into W. Malesia. Among the latter *M. simplicifolia* has the widest distribution and will be discussed first. It consists of eight subspecies, five of which are considered primary and three secondary; their areas have been pictured in fig. 27. It appears from this map that there is considerable overlap between several subspecific areas, though in general they are more or less replacing. In the remarks on *M. simplicifolia* (see p. 463) and its subspecies, however, it has been shown that in cases of overlapping of areas ecological isolation (mostly by preference for different altitudinal zones) takes the place of geographical isolation. If allowance be made for this ecological dimension, the overlapping is fictitious. Keeping this in mind, a careful consideration of fig. 27 will reveal them to be an outstanding example of subspecific areas diverging from a common centre. The focus of these areas is the western and southern part of Yunnan, where all five primary subspecies are found almost side by side. The three secondary subspecies, however, are situated at the margin of the area of *M. simplicifolia*; they are considered offsplits from primary subspecies, with which they form subspecies pairs, viz. *pungens—thomsonii*, *fruticosa—fordii*, and *laui—rigida* (see the remarks relating to this under the subspecies). The irregular pattern of some of the areas as well as the sometimes wide disjunctions can generally easily be accounted for on the base of regional topographical and climatological conditions. The disrupted areas of ssp. *fruticosa* and ssp. *simplicifolia* in Malesia may be due to both scarceness and undercollecting of these taxa. In principle, however, the distribution pattern is clear enough. In this connection the area of *M. paupera*, plotted on the same map in fig. 27, should be mentioned. This species is considered a derivative of *M. simplicifolia* ssp. *fordii*, having about the same ecological requirements, its area falling within that of ssp. *fordii*.

The next species of ser. *Curvinervia*, *M. lepidota*, consists of seven subspecies, of which the collecting localities have been plotted in fig. 24. At first sight the distribution pattern of this species seems to be very different from that of *M. simplicifolia*. Its total area only covers the central and southeastern part of that of *M. simplicifolia*, and it is broken up into no less than seven, mostly rather small, subspecific areas, whereas in *M. simplicifolia* the same area is mainly occupied by only four subspecies, *fordii*, *fruticosa*, *rigida*, and *laui*, most of which have a much wider distribution. These differences, however, are less fundamental than they seem to be. In the first place it should be noted that in S. China and the Indo-Chinese Peninsula the subspecies arrangement of *M. lepidota* is in fact similar to that of *M. simplicifolia*. It is the Malesian part of the area which shows a great difference in subspecies formation. It should be pointed out, however, that the subspecies of *M. lepidota* in Malesia are exclusively mountain plants, as contrasted to *M. simplicifolia* ssp. *fruticosa* which covers about the same area, but may be found in lowlands as well as in mountains. Since racial differentiation is known to be often more active in mountain than in lowland species, that *M. lepidota* has produced no less than four subspecies in Malesia can easily be understood. In this respect it is important to note that the Malesian subspecies *kinabaluensis*, *dolichomischa*, and *lepidota* form a morphologically closely knit group (see the remarks under those subspecies). When considering in which part of its area *M. lepidota* shows the greatest morphological differentiation, all evidence points to the Tonkin region, where three subspecies, ssp. *dumicola*, ssp. *longipes*, and ssp. *squamulata*, are found close together.

Referring to the remarks under *M. lepidota* and its subspecies, the general distribution pattern of this species can now be characterized as follows: The three subspecies *dumicola*, *longipes*, and *squamulata*, the first two of which are markedly polymorphous, have areas diverging from a common centre in Tonkin; the other four subspecies, which are morphologically uniform and of a derived character, are grouped along the southern and eastern margin of the area. Thus, following the same criteria as applied to the other species, the Tonkin region can be indicated as the most probable centre from where subspecific radiation may have started. Hence, there is an essential similarity of this distribution pattern with that of *M. simplicifolia*. In both species the subspecies can be divided on morphological grounds into a group of a primary and a group of a more secondary character; the areas of the primary subspecies diverge from a common centre, whereas towards the periphery the areas of the derived subspecies are situated. The only remarkable difference is that, in contrast with *M. simplicifolia, M. lepidota* has not expanded far to the west and the north.

The remaining species of ser. *Curvinervia, M. henryi*, is much rarer and less widespread than the foregoing ones. Its collecting localities have been mapped in fig. 23. After what has been said before, the interpretation of the distribution pattern of its subspecies does not present difficulties, though the localities are sparse. It is clear that the three subspecies of *M. henryi* must be considered, also on morphological grounds, primary ones, which radiated from a common centre in Yunnan. Though the exact position of this centre cannot be established from the scant evidence available, it is distinctly situated close to that of *M. simplicifolia.*

Summarizing now the evidence found in the distribution of the species of ser. *Curvinervia*, it will be clear that three of the four species of this series should be regarded as being of primary nature, *M. paupera* being a derivative of *M. simplicifolia.* Of these three species the centres of subspecific radiation are interesting, since they are all located in a relatively small area which comprises SW. & Central Yunnan and Tonkin. Within this central area the individual centres of the three species show a distinct tendency to be replacing, that of *M. simplicifolia* being situated in the western-southwestern part, that of *M. lepidota* in the southeastern part, and that of *M. henryi* being less well defined, possibly situated more towards the northeast than the other centres. In fig. 7a I have roughly indicated the position of these centres.

I have also tried to locate the centres of the three species of ser. *Rectinervia*; this gave more difficulty, for reasons explained before (p. 375). The position of the centre of *M. dilleniifolia* can be established with reasonable certainty, but this is hardly possible for *M. parviflora* and *M. myriantha.* For them, however, I have provisionally, and admittedly somewhat arbitrarily, chosen the region in which they show greatest morphological differentiation, which in both coincides with the westernmost part of their areas (see fig. 7a, and compare with fig. 20 and 21). Again, as in the species of ser. *Curvinervia*, but on still weaker grounds, it can be observed that the possible centres of the species of ser. *Rectinervia* are more or less replacing.

Concluding on the taxonomic-geographic pattern in subsect. *Simplices*, it appears that the centres of ser. *Rectinervia* and ser. *Curvinervia* can safely be assumed to be represented by the combined centres of their species. In fig. 7a it can be seen that the centres of the series are replacing, together composing the centre of subsect. *Simplices.*

In view of the harmonious composition of the taxonomy and distribution pattern of subsect. *Simplices* which shows no essential gaps or inexplainable features, I think it justified to identify the taxonomic centre of this subsection with the centre of its origin. I assume, moreover, that speciation in this subsection started by a cleavage, of which the series *Rectinervia* and *Curvinervia* and their replacing centres still bear evidence. This cleavage was followed by the origin of the present species, of which the still traceable, more or less replacing centres of dispersal can probably also be considered as their centres of origin. From these centres the species started a process of expansion and diversification into subspecies, which followed homologous patterns in both the *Rectinervia* and the *Curvinervia*, resulting in progressive equiformal areas of different size (cf. Hultén, 1937). Naturally, there were individual differences in genetical structure and ecological success between the species, leading to various patterns which are not exact replicas.

2) Subsect. *Pinnatae*

Subsect. *Pinnatae* consists of five species, four of which are mainly restricted to W. Malesia, whereas the fifth, *M. pinnata*, not only extends far into E. Malesia, but also

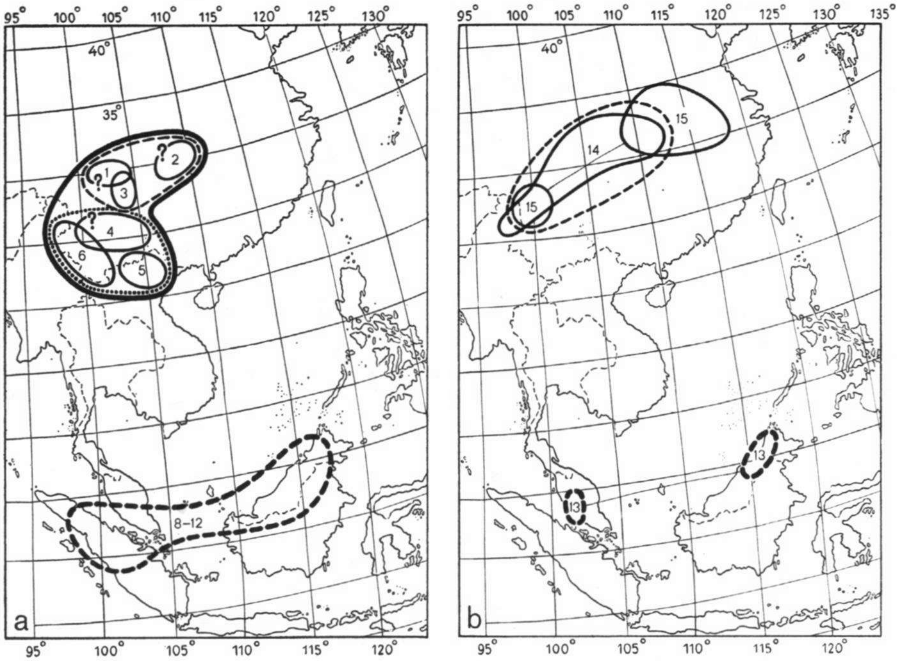

Fig. 7. a. Hypothetical centres of origin of species (———), series (— — — ser. *Rectinervia*, ... ser. *Curvinervia*), and subsections (——— subsect. *Simplices*, — — — subsect. *Pinnatae*) of subg. *Meliosma* sect. *Meliosma*.

Fig. 7. b. Areas of the species (——— *M. alba* and *M. veitchiorum*, — — — *M. rufo-pilosa*) of subg. *Kingsboroughia*.

The hypothetical centre of origin of subg. *Kingsboroughia* sect. *Kingsboroughia* species group *M. alba* and *M. veitchiorum* is indicated by a thin broken line (— — —).

The figures in the areas represent the serial numbers of the species as adopted in this revision.

occurs in continental Asia, where it covers about the same area as does *M. simplicifolia* (subsect. *Simplices*). Thus *M. pinnata* is by far the most widespread species of subsect. *Pinnatae*, and as its infraspecific structure is also very complex, it is in these aspects the counterpart of *M. simplicifolia*.

The area of *M. pinnata* (see fig. 32) is composed of nine subspecific areas, which are — as in most species of subsect. *Simplices* — geographically and/or ecologically replacing (see the remarks under *M. pinnata*, p. 495, and its subspecies). As in *M. simplicifolia* and *M. lepidota* the subspecies fall apart into two groups, one group of primary subspecies, the areas of which are large and take a central position, and one of secondary derived subspecies which are situated at the periphery of the specific range. Ssp. *macrophylla*, *ridleyi*, *ferruginea*, and *arnottiana* are regarded as primary subspecies, with a central distribution; the subspecies *humilis*, *pendula*, *sylvatica*, *angustifolia*, and *pinnata* are considered of secondary nature. Here a difference with *M. simplicifolia* and *M. lepidota* should be noticed, viz. that the areas of the primary subspecies of *M. pinnata* do not all diverge from a common, relatively small centre. Actually, the areas of ssp. *macrophylla*, *ferruginea*, and *arnottiana* are grouped around that of ssp. *ridleyi*, which thus represents a kind of nucleus, not only geographically, but also because of the fact that it has a high degree of polymorphism as compared with the other subspecies. This central position of ssp. *ridleyi* is supported by the fact that its endocarps sometimes show peculiarities which I consider primitive and by the fact that a good species, *M. sarawakensis*, is a probable derivative of it (see p. 516); the fragmented area of the latter falls for an essential part within the area of ssp. *ridleyi* (see fig. 32). Given this evidence, the most probable location of the centre of origin of *M. pinnata* should then be sought within the area of ssp. *ridleyi*, hence in W. Central Malesia (North & Central Sumatra, S. Malay Peninsula, N. & NW. Borneo).

I will now proceed to examine the relation of the distribution patterns of the three remaining species of subsect. *Pinnatae* to that of *M. pinnata* and *M. sarawakensis*.

The area of *M. sumatrana* covers Java, Sumatra, the Malay Peninsula, Borneo, Celebes, and Mindanao (fig. 30).

Within this species, no subspecies could be recognized, but nevertheless there is considerable regional variation. It has been shown (see the remarks on p. 489) that the greatest morphological differentiation is found in Borneo (especially N. and NW. Borneo) and to a less degree in Sumatra. Hence the morphological core of *M. sumatrana* populations coincides with that of *M. pinnata* and *M. sarawakensis*.

The area of the next species, *M. lanceolata* (mapped in fig. 30, as that of *M. sumatrana*), appears to show some similarity to that of *M. sumatrana*. However, judging from the one-sided western development of its area, *M. lanceolata* — being well represented in W. Java, Sumatra, and the Malay Peninsula, but rare in Borneo, and absent elsewhere — either became very rare or extinct more eastwards, or has never occupied more eastern outposts. Within *M. lanceolata* no subspecies have been recognized, but it is nevertheless a rather variable species, which has developed greatest diversity in Sumatra (see the remarks to this species on p. 492). The distribution of its var. *polyptera* (also plotted in fig. 30), for instance, is significant in this connection and corresponds to the picture which has been found in the foregoing species of subsect. *Pinnatae*.

Finally, *M. hirsuta* should be mentioned. It is a rare species certainly closely related to *M. lanceolata* (see remark on p. 494) and is known only from the type locality in the Res. Sumatra's West Coast, marked in fig. 30. This locality also fits very well into the framework of the areas of the other species.

Summarizing, it is clear that the area in which subsect. *Pinnatae* has developed its greatest morphological differentiation, and from where some of its species safely can be assumed to have expanded into adjacent regions, is composed of N. Central Sumatra, W. & NW. Borneo, and, less distinctly, South Malaya. Applying the same criteria as for subsect. *Simplices* the centre of origin of subsect. *Pinnatae* must be located within this large area (see fig. 7a).

The centres of origin of the two subsections of subg. *Meliosma* sect. *Meliosma* have now been defined as precisely as possible, and are mapped approximately in fig. 7a.

In the next paragraph a similar attempt will be made to locate the centres of origin of the two sections of subg. *Kingsboroughia*.

b. Species distribution and centres of origin in subg. Kingsboroughia

1) Sect. *Kingsboroughia*

The areas of the two species of this section (*M. alba* and *M. veitchiorum*) have been mapped in fig. 7b; it is obvious that they coincide essentially in the Old World, leaving the Mexican occurrence of *M. alba* out of consideration. They cover an elongated range from Southwest to East Central China, in this respect being similar to that of the species of sect. *Meliosma* subsect. *Simplices* ser. *Rectinervia* (see fig. 20 and 21). However, as both *M. alba* and *M. veitchiorum* are very uniform species, no centres can be indicated within their areas, in contrast to most species of subg. *Meliosma* sect. *Meliosma.*

For a proper understanding of these areas, it should be remembered that they are of relict nature, which is particularly apparent from the rich fossil evidence from other parts of the world (see part II, chapter C 1). On the basis of the locations of fossil finds which I classified under *M. alba* and *M. veitchiorum* (see fig. 16 and 17), I have made an approximative reconstruction of the areas they may have had in the Upper Tertiary (see fig. 7b). Considering the very large Tertiary distribution of *M. veitchiorum* and *M. alba* in Eurasia, the present occurrence of *M. alba* in a transpacific disjunction comes to stand in a new light, as its relict range falls into shape with the category of the Arcto-Tertiary type (see part II, chapter C sub 1).

From the living and fossil evidence available, I am unable to indicate the location of the centre of these two species; nevertheless it is beyond doubt that the present distribution patterns represent relict areas, but little can be concluded from these, as a once widespread species does not necessarily retreat to the centre from where the primary expansion took place in an earlier period. A weak argument in favour of the view that the section was originally Asian is the fact that there are in Indo-Australia two living species and in America only one.

2) Sect. *Hendersonia*

The area of the only species of this section, *M. rufo-pilosa,* mapped in fig. 7b, consists of only a few isolated localities in the lower montane zone of the Central Malay Peninsula and North Borneo. As in *M. alba* and *M. veitchiorum* no centre can be indicated within the small and disrupted area of this morphologically uniform species.

I assume that *M. rufo-pilosa* is also a relict species; the arguments for this assumption are given in part II chapter C sub 1. Unfortunately, there is no fossil evidence to sustain this view.

It is thus clear that no direct evidence concerning the possible location of the centres of origin of the two sections of subg. *Kingsboroughia* can be found, neither in the distributional patterns, nor in the morphological differentiation of its species; in sect. *Meliosma,* as we have seen, these centres are fairly obvious, However, the equiformity of the areas of subg. *Kingsboroughia* and sect. *Meliosma,* already observed in the beginning of this paragraph, is still more striking if one compares the centres of origin of the latter (minus the centre of ser. *Curvinervia;* see p. 417) with the area of the former (compare fig. 7a and b). This remarkable equiformity might be accidental, but I think there is more reason to assume a parallel development of distribution patterns. This would mean, therefore, that the present areas of the species of subg. *Kingsboroughia* represent not only their centres of survival, but to some extent also their centres of origin. Since, as we have seen, no arguments supporting this could be found in the distribution patterns and the morphology of the species of this subgenus, they will have to be sought elsewhere. Comparison with other groups and the application of generally accepted views on the origin and dispersal of Angiosperm taxa yields the following additional evidence in support of the possible homology between the bicentric area of sect. *Meliosma* and that of subg. *Kingsboroughia.*

In the first place I should like to point to the Asian areas of several other unrelated genera which show a bicentric distribution pattern similar to that of *Meliosma.* Unfortunately, due to lack of detailed evidence, the centres of such groups can only be conceived as centres of species frequency, though a more detailed analysis would probably reveal these centres of frequency to be centres of origin as well. One of the most striking examples is *Magnolia*, in the sense of Dandy (1950). This genus has been subdivided into subgenera and sections in about the same way as I have done with *Meliosma*. The centres of these infrageneric groups occupy essentially the same geographical positions as those of *Meliosma*, at least in Asia, but probably also in America. There are differences, of course, such as the better recent representation of *Magnolia* in America, but these do not affect the fundamental resemblance. Other well examined genera which have a similar bicentric distribution pattern in the northern hemisphere are for example *Alangium*, *Engelhardia*, and *Prunus* subg. *Laurocerasus sensu* Kalkman (1965). Certainly there are many more genera of this kind, but unfortunately adequate taxonomic revisions are very scarse. They must be selected from the lists given by Van Steenis (1962: 244—253).

Secondly, the location of the centres of the two areas under discussion, SW. China, Upper Burma, and Tonkin on the one hand, and West Central Malesia on the other, is not just fortuitous. They are part and, especially the former, main points of the region between Assam and Fiji which Takhtajan (1969) and A. C. Smith (1970) convincingly postulated to be the general area from which the Angiosperms initially dispersed. A similar conclusion is reached by van Steenis (1971) in his analysis of the distribution, past and present, of the Fagaceous matrix area. It is in the above area that significantly more, and more important, primitive forms are found than anywhere else, and from where pathways of evolution and dispersal can be shown to radiate to all other parts of the world. Moreover, within this large area is exactly the region comprising the eastern Himalayas, Assam, Yunnan, Upper Burma, North Vietnam, and eastern Asia, in which Takhtajan finds arguments to assume it to represent the primary centre of origin of the temperate flora of the northern hemisphere, and not solely a refugium of relicts or a secondary centre of development. It is, therefore, one of the most likely regions in which the centre of origin of a group could be situated, especially if this group has such a marked relict character as has sect. *Kingsboroughia*. However, West Malesia also must be considered as representing an important part of the area of early Angiosperm development and distribution, as may appear from the following.

Van Steenis (1964) in his essay on the plant geography of the mountain flora of Mt. Kinabalu, mentioned several ancient elements, part of which show a disjunct distribution similar to that of sect. *Hendersonia* (*M. rufo-pilosa*). After analysing the patterns in different groups of such polytopic taxa he made the assumption that there was an ancient mountain nucleus in Malaya and Sumatra, separated from the continent of Asia but connected with Borneo. He writes that this is also supported by the distribution of *Trigonobalanus*, a Fagaceous genus comprising two species, with remarkably primitive characters. Now it is the distribution of exactly this famous genus *Trigonobalanus* which shows a striking parallel to that of *Meliosma* subg. *Kingsboroughia*. Not only are the distribution patterns of the Malesian *Trigonobalanus verticillata* (Kinabalu, 1200—1500 m, Malay Peninsula, 1200 m, Celebes, 1100 m) and *M. rufo-pilosa* (see fig. 30) highly similar, but also the northern couple *M. alba* and *M. veitchiorum* have a counterpart, namely in *Trigonobalanus doichangensis* which was recently recognized and occurs in the mountains of N. Thailand (Forman, 1964). Thus it appears that the genus *Trigonobalanus* has a similar bicentric disjunct area as has *Meliosma* subg. *Kingsboroughia*, namely with one or two endemic species in continental SE. Asia on one hand, and one endemic species in Malesia on the other.

Concluding, I think that both the significant geographic position of the bicentric area of subg. *Kingsboroughia*, as well as the occurrence of several, if not many other groups, related and unrelated, and whether or not of a clear relict character, which show similar distribution patterns, plead very much in favour of the assumption that the centres of survival of the sections of subg. *Kingsboroughia* more or less coincide with their centres of origin. In this connection it will be clear that the Mexican refugium of *M. alba* (sect. *Kingsboroughia*) should be considered to be of secondary origin, which would agree with the probable history of its distribution (see part II, chapter C sub 1).

Consequently, on the base of the facts and assumptions given above, I advance the hypothesis that the bicentric areas, not only of *Meliosma* subg. *Kingsboroughia* and subg. *Meliosma* sect. *Meliosma*, but also that of *Trigonobalanus* and probably many other unrelated genera, are homologous, hence must have originated in the same period and under the same physiographical and climatological conditions. Minor dissimilarities in range need not be in contradiction with this, for instance the fact that the assumed centre of origin of sect. *Kingsboroughia* only coincides with that of the series *Rectinervia* of sect. *Meliosma* subsect. *Simplices* (compare fig. 7a and b) can be easily explained, as will be discussed in part II chapter D where a global reconstruction is given of the history of the distribution and the phylogeny of the entire genus *Meliosma*.

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PART II. FOSSIL EVIDENCE

A. INTRODUCTION AND GENERAL CONSIDERATIONS

In paleobotanical literature rather abundant records of fossil *Sabiaceae* occur, most of them of *Meliosma*. These records almost all refer to fossils from the Tertiary period, viz. from the Lower Eocene up to far into the Pliocene, only few being of Quaternary age. All collecting localities of fossil *Meliosma* are situated on the northern hemisphere, outside the tropics, and often up to rather high latitudes. From a preliminary survey of the relevant literature I came to the conclusion that a study of fossil *Meliosma* might add a valuable paleobotanical dimension to the taxonomic and distributional picture of this genus; therefore I have revised critically all data I could find. Before turning to the subject-matter, some general remarks will be made.

The fossil remnants of *Meliosma* are mainly of two kinds: fossilized endocarps and leaf-imprints. No fossil flowers are known, nor reliable pollen data, and only one or two times fossilized wood ascribed to *Meliosma* has been reported, which will not be included in this study.

As a general rule it can be observed that the identification of well-preserved, fossil, hard-walled seeds and fruits is mostly very well possible; they usually possess characters on the base of which they can be identified to still living families or genera with absolute certainty. In this respect the endocarps of *Meliosma* are almost ideal: they are characterized by an exclusive character combination (see part I chapter C sub d) and it appears that they are usually very well fossilized.

The identification of leaf-imprints, on the other hand, may provide difficulties, even if they are very well preserved. The reasons for this are obvious: on the one hand unrelated taxa may often show a high degree of convergence, whereas on the other hand the genotypic or phenotypic variation within one and the same species may be considerable.

Apart from certain very distinctive leaf-forms characteristic for particular genera or families, there are very many less characteristic forms which cannot so easily be classified, and sometimes this may prove impossible. The fact that not all paleobotanists seem to have an allround form knowledge of the occurrence of the various leaf-forms throughout Angiosperm families and genera, especially the tropical ones, may make their identifications even more questionable.

In *Meliosma* the leaf-types are generally not very characteristic. This holds particularly for the pinnate leaves which are, moreover, nearly always decomposed when shed, but also the simple leaves, especially when they have an entire margin, may easily be confused with leaves of other taxa. In fact, it is only the obovate-oblanceolate leaf with dentate margin, such as is found in several subspecies of *M. simplicifolia* which, with the help of its rather characteristic nervation pattern, may be referred with reasonable certainty to *Meliosma*. Indeed it is this type of leaf which predominantly figures in paleobotanical literature under the name of *Meliosma*. On the other hand, there are doubtless many paleobotanical records of various genera in families such as *Lauraceae*, *Rhamnaceae*, and *Combretaceae*, based on oblong to obovate or oblanceolate, entire leaves with looped nerves (often so-called 'laurophyllous' leaves), which may in reality be referable to *Meliosma*. Many of these will certainly remain *incognito* forever, as it is simply impossible to identify them.

It is remarkable that *Meliosma* appears very late in publications on fossil leaf assemblages;

Chaney and Sanborn (1933: 40), who first recognized fossil *Meliosma* for North America, remark that this 'may be due to the failure of paleobotanists to recognize this genus, which is not now distributed in temperate regions with which they are familiar. Leaves possibly referable to *Meliosma* are figured under other generic names in various Cretaceous and Eocene floras of the United States, and it may be supposed that the absence from them of so important a family as the *Sabiaceae* is more apparent than real.' This is probably correct, but it must be said that the fact that *Meliosma* until recently was an obscure genus in paleobotany goes along with the advantage that it has never been used as a dump for hard-identifiable forms, like several other genera such as *Rhamnus* and *Quercus*. On the contrary, I have come to the conclusion that the major part of the leaf-imprints referred to *Meliosma* do very probably belong to this genus indeed.

Though fossil leaves may certainly often give reliable evidence of the former occurrence of *Meliosma*, it is nevertheless clear that endocarps are more valuable in this respect. This is still more so since the subgenera and sections of *Meliosma* are each characterized by a particular type of endocarp which is also recognizable when fossilized. The leaves of *Meliosma*, however, do not have such a high diagnostic value on subgeneric and sectional level; moreover, fossils of pinnate leaves and simple leaves with entire margin are hardly or not at all recognizable as *Meliosma*, so that only the Asian sect. *Meliosma* subsect. *Simplices* and the American sect. *Lorenzanea* remain as the taxa of which the leaves are often well identifiable. However, the vegetative morphology of these two groups shows a good deal of parallel development which makes discrimination between them on the base of their leaves difficult.

An extra handicap is caused by the circumstance that in Eurasia and in America different schools of paleobotany have developed; European and Russian paleobotanists have specialized on carpology, more or less neglecting leaf-imprints, whereas in North America the reverse is the case. This has caused the queer situation that in *Meliosma* almost all fossil endocarps known have been found in Eurasia, but almost all leaf-imprints in America!

For the determination of the floristic composition of a paleoflora fossil fruits and seeds are generally much more satisfactory than leaf-imprints.There is, however, one respect in which fossil leaf assemblages are more useful than fossil fruits and seeds, viz. for the determination of the vegetation types to which fossil floras belonged and the environmental conditions indicated by them.

With regard to this, there are two ways of analyzing a fossil leaf assemblage. The first is, as we have seen, the analysis of the floristic composition, from which certain conclusions can be drawn as to the probable climatic conditions under which a flora lived. This method, however, is less safe because of the often considerable degree of unreliabilty of identifications of fossil leaves, and because the climatic implications of especially those assemblages which are of a more heterogeneous floristic composition, are often vague; many genera cover several climatic zones, for instance such 'tropical' genera as *Cinnamomum*, *Meliosma*, and *Diospyros*, or such 'temperate' genera as *Ulmus*, *Prunus*, and *Acer*.

The second method, analysis of the physiognomy of the leaves, may be considered a more direct method of analyzing the climatic and vegetational indications of a fossil leaf flora. It is probable that various physiognomic features of foliage can be related to climatic conditions, as has been demonstrated first by Bailey and Sinnott (1915, 1916) and later by Bews (1927) and Raunkiaer (1934). Many paleobotanists, such as Berry (1916), Chaney and Sanborn (1933), Sanborn (1935), Potbury (1937), MacGinitie (1937, 1941), Dorf (1936), and Koch (1963), consequently have based some of their analyzing methods on such correlations between leaf physiognomy and environment. In his comprehensive work on the tropical rain forest Richards (1952: 154) says: '.... conclusions as to the climates of Tertiary floras are perhaps more firmly based when they are drawn from a statistical study of leaf sizes and similar features .... than when .... they .... rest on the *taxonomic affinities* of the fossil flora rather than its physiognomy, which appears, at least as far as modern vegetation is concerned, to be a very sensitive index of environmental conditions.'

Perhaps the most striking correlation between climate and leaf physiognomy is found in the leaf margin, although this is admittedly eco-physiologically little understood. As originally pointed out by Bailey and Sinnott (1916) 'there is a very clearly marked correlation between leaf margin and environment in the distribution of Dicotyledons in the various regions of the earth'; leaves that have entire margins are overwhelmingly prevalent in lowland-tropical regions, and leaves that have non-entire margins are characteristic of mesophytic cold-temperate regions. These correlations are more strikingly shown among trees and large shrubs than among herbs. Normally, it is just the trees and shrubs which by means of their detached parts come into the geological record. The above correlations are not only significant in vegetations, but also on family-level; citing Bailey and Sinnott (1916): '.... such typical entire leaved woody families as the *Annonaceae*, *Lauraceae*, *Ebenaceae*, *Guttiferae*, *Rhizophoraceae*, *Myristicaceae*, *Sapotaceae*, *Apocynaceae* etc. are practically absent from mesophytic cold-temperate regions, as are such characteristically non-entire leaved families as the *Betulaceae*, *Aceraceae*, *Platanaceae* etc. from lowland tropical areas. Particularly significant, however, is the distribution of those families, *Malvaceae*, *Rosaceae*, *Ulmaceae*, *Fagaceae*, *Tiliaceae*, *Leguminosae*, which possess both types of leaf-margins. The non-entire types usually reach their optimum development in mesophytic temperate, cool upland, or equable environments, the entire types in lowland tropical or physiologically dry habitats, and the transitional forms in intermediate environments. To endeavor to explain all these correlations between leaf form and environment as mere coincidences would be very difficult. When it is taken into consideration, accordingly, that correlations between leaf form and environment occur in numerous families, genera, and even species, and in all parts of the tropical, temperate, and frigid zones, the effects of environment are clearly demonstrated.'

Bailey and Sinnott based their conclusions upon analyses of leaf margins of all Dicotyledonous species occurring in several tens of floras dealing with regions all over the world, and presented several instructive tables. Their observation, however, that correlations between leaf form (margin) and environment occur in numerous genera and even species is not documented and requires further confirmation.

Wolfe (1969)[1]) gave a few examples in support of the statement that within a given vegetational type in a limited region, the leaf margin percentage does not appear to vary greatly, even at different altitudes. There is a more significant correlation between leaf margin percentages and habitat, that is, whether species are typically slope or stream- or lake-side species. In support of these contentions Wolfe mentions data derived from Li (1963) and Hitchcock et al. (1959, 1961, 1964). MacGinitie (1953: 46) has noted that '.... fossil floras represent, almost without exception, the specialized streamside or lakeside floras of the time and place ....'. Fossil assemblages may, therefore, yield lower

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1) When this article was going in print I received another paper by Wolfe, in which methods of analysis of Tertiary floras are further discussed, viz.

Wolfe, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. Palaeogeography, Palaeoclimatology, Palaeoecology 9: 27—57.

Table 1

Recent floras (selected from Bailey & Sinnott, 1916, and a few from Wolfe, 1969)	species % with entire leaves		latitude
	trees	shrubs	
Malay States	90	82	1-6°
Brazil	87	76	0-30°
Nicaragua	86	71	11-15°
Central West Africa	85	80	0-10°
Hongkong	73	71	22°
Upper Gangetic Plain	73	71	26-28°
Taiwan (0-500 m)	61		22-25°
South New Zealand	53	68	40-47°
Simla Mts	53	60	31°
Taiwan (500-2000 m)	45		22-25°
East Central China	38	52	27-32°
SE. United States	36	54	30-36°
Italy	18	56	37-47°
East Central North America	10	37	36-42°
South Russia	8	52	40-50°
France	4	53	43-51°
North Russia	0	35	60-70°
Rocky Mts	0	40	40-60°
Average north temperate areas	2	41	
Average south temperate and subtropical areas	34	58	
Average tropics	81	77	

Tertiary floras (selected from literature)	species % with entire leaves	latitude
	trees, shrubs and (few) herbs	
Wilcox (SE. United States) - Lower Eocene (Berry, 1916) - 328 spp.	83	40°
Susanville (California) - .... Eocene (unpubl., Wolfe, in litt.) - 22 spp.	82	40°
Comstock (Oregon) - Upper Eocene (Sanborn, 1935) - 25 spp.	76	44°
La Porte (California) - Upper Eocene/Lower Oligocene (Potbury, 1935) - 41 spp.	70	40°
Gulf of Alaska region - Low Upper Eocene (Wolfe, 1969) - 62 spp.	65	60°
Goshen (Oregon) - Upper Eocene (Chaney & Sanborn, 1933) - 49 spp.	61	44°
Chalk Bluffs (California) - Middle Eocene (MacGinity, 1941) - 76 spp.	46	39°
Agatdalen (Greenland) - Lower Paleocene (Koch, 1963) - ± 35 spp.	37	70°
Collawash (Oregon) - Lower Miocene (cf. Wolfe, 1969) - 119 spp.	25	46°
Bridge Creek (Oregon) - Upper Oligocene (Chaney, 1925) - 20 spp.	15	44°

percentages of entire-margined species than the percentage based on the unknown flora of the entire region. According to Wolfe's argumentation this effect would be the better compensated the larger the flora is and the more localities are taken into consideration. Moreover, he argues, the probable over-representation of lacustrine and fluviatile plants also indicates that consideration of leaf margin percentages should be based on species rather than on specimens. Bailey and Sinnott (1916) note that in tropical forests the individual plants that have non-entire margins are relatively rare, and that a consideration of the percentage of leaves that have entire margins would probably produce an even stronger percentage gradient between the tropical and temperate vegetation than a consideration of the percentage of species; as observed above, in fossil assemblages the percentage should, however, be based solely on groups of specimens that form the fossil 'species'.

In table 1 leaf margin percentages are given of recent and fossil floras (only for Dicotyledonous species) in various regions of the earth.

From the examples in table 1, to which many more could be added, it can be seen that there is a marked gradient in the leaf margin percentage of recent floras, more or less according to the climatical zonation cq. geographical latitude at which they occur. If such leaf margin percentages may be considered a valid index for a rough characteristic of the macro-climatic zone in which a given flora occurs, this probably also holds for Tertiary floras, provided that the assemblages are large enough and are floristically more or less comparable. In the second column of table 1 it can be seen that there is as much variation in this respect in fossil as in recent floras.

In order to use leaf margin percentages as indicators of climates, climatological terms such as 'tropical', 'subtropical', etc. should be strictly defined and related to leaf margin percentages. There is, however, no full unanimity among climatological and vegetational specialists with regard to the boundaries between the major climatic and vegetational zones of the earth; especially the term 'subtropical' is used in different senses. The following definitions of some of the major vegetation types, given by Wolfe (1969) and somewhat condensed by me, are based on climatological criteria on the one hand and on vegetational criteria, amongst others by way of leaf margin percentages, on the other.

Tropical forest. The most commonly accepted definition of tropical climates used by climatologists is that the mean temperature of the coldest month is not below 18° C. The vegetation under this climate is often roughly considered tropical (rain) forest. However, several vegetations generally still regarded as tropical rain forest do occur under somewhat less mild climatic conditions. On the other hand, some vegetation types occurring in tropical climates under the above definition are more or less deviating in being floristically and physiognomically less complex, though in most respects similar to typical tropical rain forest. Such deviating tropical rain forest types, similar to the 'subtropical rain forest' in the sense of Richards (1952) and to the 'extratropical rain forest' in the sense of Wang (1961), have been proposed by Wolfe (1969) as a separate vegetation type, under the name 'paratropical rain forest'.

Paratropical rain forest is limited at higher latitudes by the presence of frost, under a mean annual temperature range from about 22° C to about 25° C, with a mean cold month temperature of about 15° C to 25° C. Extended dry periods are lacking¹). Leaf

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1) This seems to be an exaggerated statement as wide zones on both sides of the tropics are distinctly seasonal for macroclimatical reasons.

margin percentages for the paratropical rain forest vary from 57 up to 75, and its vegetation is predominantly broad-leaved evergreen, whether or not with some deciduous elements. The tropical rain forest *sensu stricto* would then occur under higher mean temperatures, and be mainly characterized by leaf margin percentages above 75, and by a more complex structure.

Subtropical forest occurs under a climate in which frosts may occur, though never severe or of long duration, and in which the mean annual temperature ranges from about 15° C to 19° C and the mean of the coldest months from about 6° C to 10° C. Leaf margin percentages vary from about 39 up to 55, and the vegetation is broad-leaved evergreen, sometimes with conifers and broad-leaved deciduous elements as important constituents.

Warm temperate forest occurs under a seasonal climate in which frosts can be expected during several months of the year. The mean annual temperature ranges from about 11° C to 16° C and the mean of the coldest month ranges from about —3° C to 5° C. Leaf margin percentages vary from about 20 up to 35, and the vegetation is broad-leaved deciduous and may have a significant amount of conifers intermixed. Broad-leaved evergreens are present but not dominant.

According to the above definitions, of the fossil floras listed in table 1 the Wilcox, Susanville, and Comstock assemblages might be considered to represent tropical vegetation *sensu stricto*, and the La Porte, Gulf of Alaska, and Goshen assemblages paratropical vegetation. This classification is supported by the floristic composition of the assemblages in question and additional physiognomic characters such as leaf texture and size, presence of drip-tips, etc.

It should be emphasized that the degree of reliability of the leaf margin index method is not yet quite clear; this method should preferably be applied in combination with as many other criteria as possible, to reach the most reliable approximations of the climates under which fossil floras existed.

I have discussed these paleobotanical analyzing methods at some lenght, since partly on the basis of these assumptions will be made concerning the possible history of the distribution of *Meliosma*.

B. ANNOTATED ENUMERATION OF FOSSILS (PUBLISHED AND UNPUBLISHED) RELATED TO MELIOSMA

In this chapter all references and collections of fossil *Meliosma* (endocarps and leaf-imprints) which I could trace are dealt with; they are arranged in alphabetical order according to the names under which they have been published. As far as possible I have tried to evaluate them; under each item I have given a brief commentary. As a rule the fossils themselves could not be examined; this was only possible in English and Dutch and in one German collection. In all other cases I have based my conclusions only on the descriptions and figures from the literature available. The figures published by various authors are mostly rather satisfactory; exact copies of many of them are given by me in a convenient arrangement, together with pictures of some reference specimens of recent species, to enable the reader to get an impression of similarities and dissimilarities.

The use of the terms length, breadth, height, ventral, dorsal, etc. of endocarps is in accordance with the criteria given in part I chapter C sub d. The term ‘plug’, often met

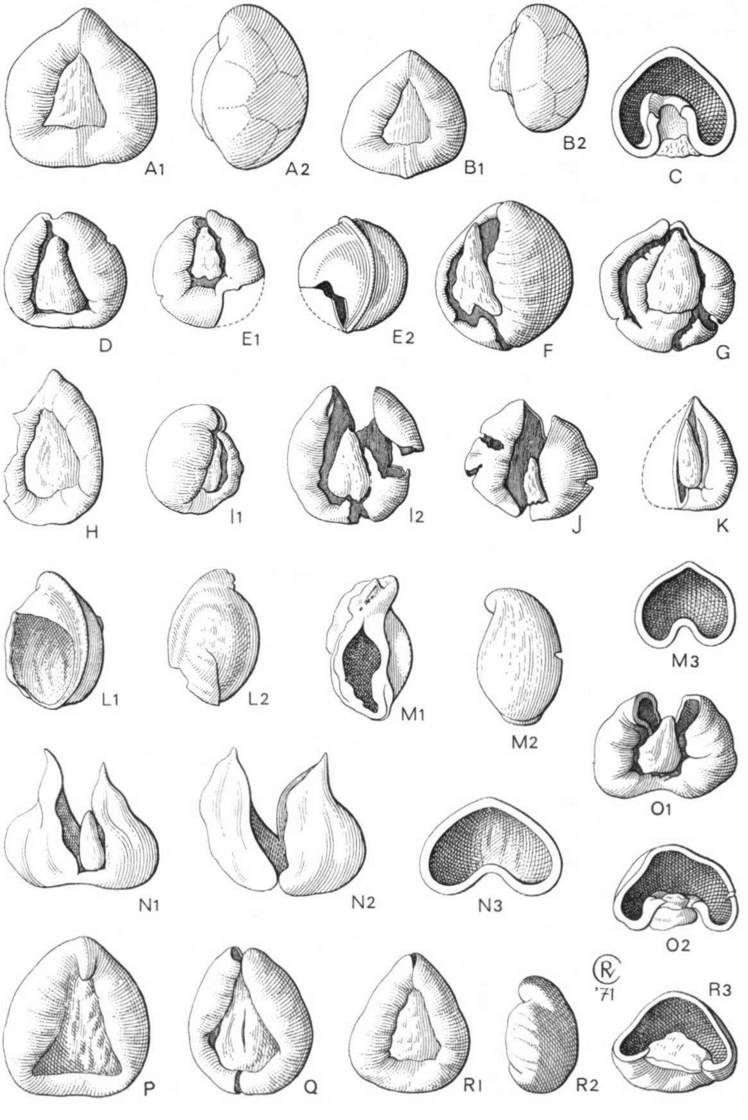

Fig. 8. *M. veitchiorum*, endocarps, all × 3.
Recent specimens: A1, 2 (*H. C. Chow 915*, W. Hupeh). — B1, 2 (*H. T. Tsai 57833*, Yunnan). — C (*Forrest 12766*, Yunnan).
Fossil specimens, all, except O, P, and R, copied from pictures in literature: D (Dorofeev, 1963, t. 35 f. 13). — E1, 2 (Dorofeev, 1957, t. 6 f. 3, 4). — F (Dorofeev, 1963, t. 35 f. 18). — G (Nikitin, 1965, t. 12 f. 6). — H (Nikitin, 1948, f. 11). — I1, 2 (Dorofeev, 1963, t. 35 f. 15, 16). — J (Kirchheimer, 1957, t. 43 f. 166 d). — K (C. & E.M. Reid, 1923, t. 11 f. 2). — L1, 2 (Szafer, 1954, t. 9 f. 9, 12). — M1—3 (Engelhardt & Kinkelin, 1908, t. 33 f. 10). — N1—3 (Ludwig, 1857, f. 27). — O1, 2 (C. & E.M. Reid, 1915, t. 11 f. 19, 20; coll. Rijks Geol. Dienst, Haarlem, The Netherlands). — P (coll. Zagwijn s.n., from Brunssum, Prov. of Limburg, The Netherlands; coll. Rijks Geol. Dienst, Haarlem, The Netherlands). — Q (van der Vlerk & Florschütz, 1950, f. 26). — R1—3 (coll. Zagwijn, nr. M1; Rijks Geol. Dienst, Haarlem, The Netherlands).

with in the literature, refers to the piece of hard vascular tissue which is often present in the ventral groove or pore of fossil endocarps.

This enumeration is not meant as a revision. It only intends to be a critical evaluation of fossil data to serve a phylogenetic and paleo-geographic interpretation of distribution patterns found in recent *Meliosma*.

1. **Bognoria venablesi** Chandler, Low. Tert. Floras South. Engl. 1 (1961) 243, t. 24 f. 11—13, f. 36.

Lower Eocene. Bognor, Sussex, England.

Remarks: Endocarp. One specimen, tentatively placed in *Sabiaceae* on the base of some resemblance to *Meliosma* endocarps. As noted by the author, it may or may not have anything to do with *Meliosma*; I cannot add any new suggestion to this.

2. **Cicer pliocaenicum** Szafer, Plioc. Flora Okol. Czorsztyna, Warszawa (1954) 40, t. 9 f. 7—12, t. 10 f. 2; Dorof. in Kolakowski, Akad. Nauk Gruzinsk. S.S.R., Suchumi, Vyp. 11 (1958) 358, *in synon.*; Szafer, Mioc. Flora Star. Gliwic, Inst. Geol, Prace, Warszawa 33 (1961) 45. — *Zelkova serrata sensu* Szafer, Polska Akad. Umiej., Rozpr. B, 72 (1947) 240, t. 7 f. 5—7, *non* Makino; Szafer (1961) l.c. — **Fig. 8-L 1,2.**

Upper Pliocene. Mizerna near Czorsztyn on the river Dunajec, Poland.

Remarks: Endocarps. Under the name *Cicer pliocaenicum* figures a mixture of material from Krosćienko (f. 7, 8?) and from Mizerna (f. 9—12). Dorofeev (1958) includes all this material in *Meliosma europaea* and this transfer has afterwards been accepted by Szafer (1961). The Krosćienko specimens, originally described as *Zelkova serrata*, possess typical characters of *M. alba* (see nr. 43). The endocarps from Mizerna, on the other hand, are like those of *M. veitchiorum*. They are rather depressed and have a median keel running out in a rather pronounced beak. According to the text the measurements of two specimens are: 7 by 5 mm and 7 by 4.5 mm, indicating length by height. Moreover, t. 9 f. 9, 12, shows a specimen of 7.4 mm length, *c.* 6 mm breadth and 5 mm height. These measurements, and the length/height ratio thus being 0.64—0.71, are well in agreement with those of *M. veitchiorum* endocarps (compare with fig. 9b).

3. **Meliosma aesculifolia** Chaney & Sanborn, Publ. Carn. Inst. Wash. 439 (1933) 84, t. 27 f. 1. — **Fig. 14-B.**

Upper Eocene. Goshen, Lane County, Oregon, U.S.A.

Remarks: Leaf-imprints. Few specimens, of which a well intact one has been depicted. The habit of this characteristic leaf strongly suggests *Meliosma*. The authors relate it to *M. dentata* from Mexico, but this is not very convincing, since there are some important discrepancies in the nervation which is much ascending and spaced in *M. dentata*. I do not know a recent American species of *Meliosma* (sect. *Lorenzanea*) of which the leaves come very close to the fossil depicted; on the other hand, leaves of the SE. Asian *M. dilleniifolia* ssp. *cuneifolia* and *M. parviflora* resemble the fossil to a great extent (compare fig. 14-B an b). There remain some slight differences, however, and for that reason I refrain from relating this fossil to any species group, nor to sect. *Meliosma* or sect. *Lorenzanea* in particular.

4. **Meliosma californica** Berry, J. Wash. Acad. Sc. 19 (1929) 99, f. 1, 2.

Lower Miocene. San Juan, California, U.S.A.

Remarks: Endocarp. One specimen, possibly *Meliosma*, but in the description and the rather poor picture I cannot find a basis to affirm Berry's identification.

5. **Meliosma cantiensis** Reid & Chandler, London Clay Flora (1933) 376, t. 18 f. 24—30, f. 13. — **Fig. 12-A 1, 2.**

Lower Eocene. Sheppey, Minster, and Herne Bay, Kent, England.

Remarks: Endocarps; about 40 specimens, most of which are locule-casts in which the endocarp wall has been reduced to a mere film, while in some it is completely worn away. They vary considerably in size and shape in accordance with the degree of abrasion. According to the text four endocarps show the following measurements: length 5, 8, 6.5, 6 mm, breadth 4.5, 8, 6, 5 mm, height 3.5, 5.5, 4.5, 4.5 mm, the height/length ratios thus being 0.70, 0.69, 0.69, 0.75, respectively. Six other endocarps of this colletion, measured by me in the British Museum (Nat. Hist.), show: length 7, 5.7, 5.7, 7, 7, 4.8 mm, height 5.5, 4.3, 4.5, 6.3, 5.3, 3.6 mm, the height/length ratios being 0.79, 0.75, 0.81, 0.90, 0.76, 0.75. There is no doubt that these endocarps are *Meliosma*, not only because of their external characters, but also of the presence of elongate, digitate (centipede-shaped) cells, lining the endocarp wall, which are, according to the authors, highly characteristic for the genus (l.c., f. 13). As the authors note, these *Meliosma* endocarps show the closest resemblance to those of *M. veitchiorum*, of which shape and measurements — taking into account the degree of abrasion of many of the fossils — rather well match those of the fossils; compare fig. 12-A and 8-A, B, and the measurements in fig. 9b. On the other hand, they say that there is a difference in the position of the ventral canal, which would be direct in endocarps of *M. veitchiorum*, and oblique in the fossils. Indeed it can be established from t. 18 f. 30 (fig. 4-B 2 in this paper), which shows the length section of an endocarp, that the ventral incurving of the endocarp wall, which forms the canal for the vascular bundle, leads obliquely into the locule. However, this is exactly the normal situation such as is found in *M. veitchiorum*, as illustrated by me in fig. 4-B 1. Reid and Chandler's conclusion, therefore, is not correct, and must be due to some error, possibly by confusing endocarps of *M. veitchiorum* and *M. alba*, the latter of which has indeed a rather direct ventral canal (compare fig. 4-B 3). Consequently, it can be concluded that the difference between the endocarps of *M. cantiensis* and of recent *M. veitchiorum* consists only in their proportional measurements, the height/length ratios being on the average distinctly more in *M. cantiensis* endocarps than in endocarps of recent *M. veitchiorum*, being *c.* 0.76 and *c.* 0.63 respectively.

6. **Meliosma cantiensis** Reid & Chandler: Chandler, Low. Tert. Floras South. Engl. 1 (1961) 112, 242, t. 12 f. 4 & 5, t. 24 f. 8 & 9. — **Fig. 12-B.**

Lower Eocene. Harefield (Middlesex), Bognor (Sussex), and Herne Bay (Kent), England.

Remarks: Endocarps; 16 specimens, all referable to *M. cantiensis* (nr. 5) on the base of their shape and measurements, except coll. nr. V. 29715 (l.c. t. 12 f. 4, 5), which is in my opinion of somewhat dubious nature, though definitely belonging to *Meliosma*.

7. **Meliosma caucasica** Dorofeev in Kolakowski, Akad. Nauk Gruzinsk, S.S.R., Suchumi, Vyp. 11 (1958) 357, t. 20 f. 1—8. — **Fig. 11-C 1, 2.**

Pliocene. Duab Kimmery, Caucasus, U.S.S.R.

Remarks: Endocarps. Several specimens, 3.1—4.4 mm long, 2.9—4.4 mm broad. Judging from the pictures the smaller of these measurements derive from somewhat deformed abnormally small specimens which are possibly atypical. The others, though being small as well, fall for the greater part within the variation range of *M. alba* endocarps (compare with fig. 9a), which they also resemble much in shape (compare fig. 11-A, B, and C); thus no difference can be established between these fossils and the smaller

M. alba endocarps. Dorofeev, l.c., was the first to realize that endocarps resembling the *M. europaea* type (fig. 8), mainly differing, however, by being much smaller, must represent a separate species.

8. **Meliosma cuneata** (Newb.) Berry, J. Wash. Acad. Sc. 29 (1939) 377, *pro parte*; Brown, U.S. Geol. Surv. Prof. Pap. 375 (1962) 61, *in synon.* — *Viburnum cuneatum* Newb., Proc. U.S. Nat. Mus. 5 (1883) 511; U.S. Geol. Surv. Mon. 35 (1898) 130, t. 57 f. 2. — *Parrotia cuneata* Berry, U.S. Geol. Surv. Prof. Pap. 91 (1916) 219; ibid. 156 (1930) 71, *pro parte.* — *Ficus artocarpoides sensu* Brown, U.S. Geol. Surv. Prof. Pap. 375 (1962) 61, t. 28 f. 7, *non* Lesquereux *pro min. parte.* — **Fig. 14-D.**

Lower Eocene. Tongue River, Montana, U.S.A.

Remarks: Leaf-imprint. One specimen, which bears some superficial resemblance with leaves of *M. simplicifolia* ssp. *rigida* and *yunnanensis*, or *M. lepidota* ssp. *dumicola*, but its combination of close-running and very steeply ascending nerves does not occur in *Meliosma*, as far as I know. Identification of this imprint is, moreover, handicapped by its lack of the finer venation. It is almost certain that this dubious fossil does not belong to *Meliosma*.

9. **Meliosma cuneata** *sensu* Berry, J. Wash. Acad. Sc. 29 (1939) 377, *non* (Newb.) Berry *pro parte*, f. 1. — *Parrotia cuneata sensu* Berry, U.S. Geol. Surv. Prof. Pap. 156 (1930) 71, *non* (Newb.) Berry *pro parte*, t. 12 f. 10. — **Fig. 10-E.**

Lower Eocene. Wilcox, Nevada County, Arkansas, U.S.A.

Remarks: Leaf-imprint. The fossil depicted in Berry (1930) t. 12 f. 10, was, together with some similar leaf-imprints, included under *Meliosma* (*Parrotia*) *cuneata* (see nr. 8), because the author considered the differences between the first and the latter to be unimportant. Judging from his picture (fig. 10-E in this paper) and the picture of the type of *M. cuneata* (fig. 14-D in this paper), I am certain that Berry's conclusion is wrong; the type of *M. cuneata*, probably being not at all *Meliosma* (see nr. 8), is quite different from Berry's Wilcox fossil, which indeed has much of a *Meliosma* leaf. The Wilcox fossil was compared by Berry with *M. dentata* from Mexico and with *M. glabrata* from Central America. It can, however, as well be matched against leaves of the SE. Asian *M. simplicifolia* ssp. *thomsonii* or ssp. *yunnanensis*, to which it is very similar in shape and dentation (compare fig. 10-E and e 1, 2). It appears, therefore, to be very difficult to make out whether the depicted Wilcox fossil might belong to the Old World sect. *Meliosma* or to the New World sect. *Lorenzanea*. I would even not ascribe it with full certainty to *Meliosma*, since it appears from the rather poor picture that the fossil leaf shows a definite tendency towards cancellate venation, and this is a character not found so distinctly in the taxa referred to above. I have not found a leaf of recent *Meliosma* which fully combines all characters of the fossil, though I must admit that I did not see sufficient recent American material. Concluding, it can only be said that the Wilcox fossil may belong to *Meliosma*, but, if so, it does not provide much evidence as to its infrageneric affinity.

10. **Meliosma europaea** C. & E. M. Reid, Meded. Rijksopsp. Delfst. (The Hague) 6 (1915) 113, t. 11, f. 19, 20, 21, 24, 35. — **Fig. 8-O 1, 2, P, R 1-3.**

Upper Middle Pliocene. Reuver, Swalmen, Prov. of Limburg, The Netherlands.

Remarks: Endocarps. Several specimens; measurements of the type specimen¹) (fig.

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¹) Coll. Rijks Geol. Dienst, Haarlem, The Netherlands.

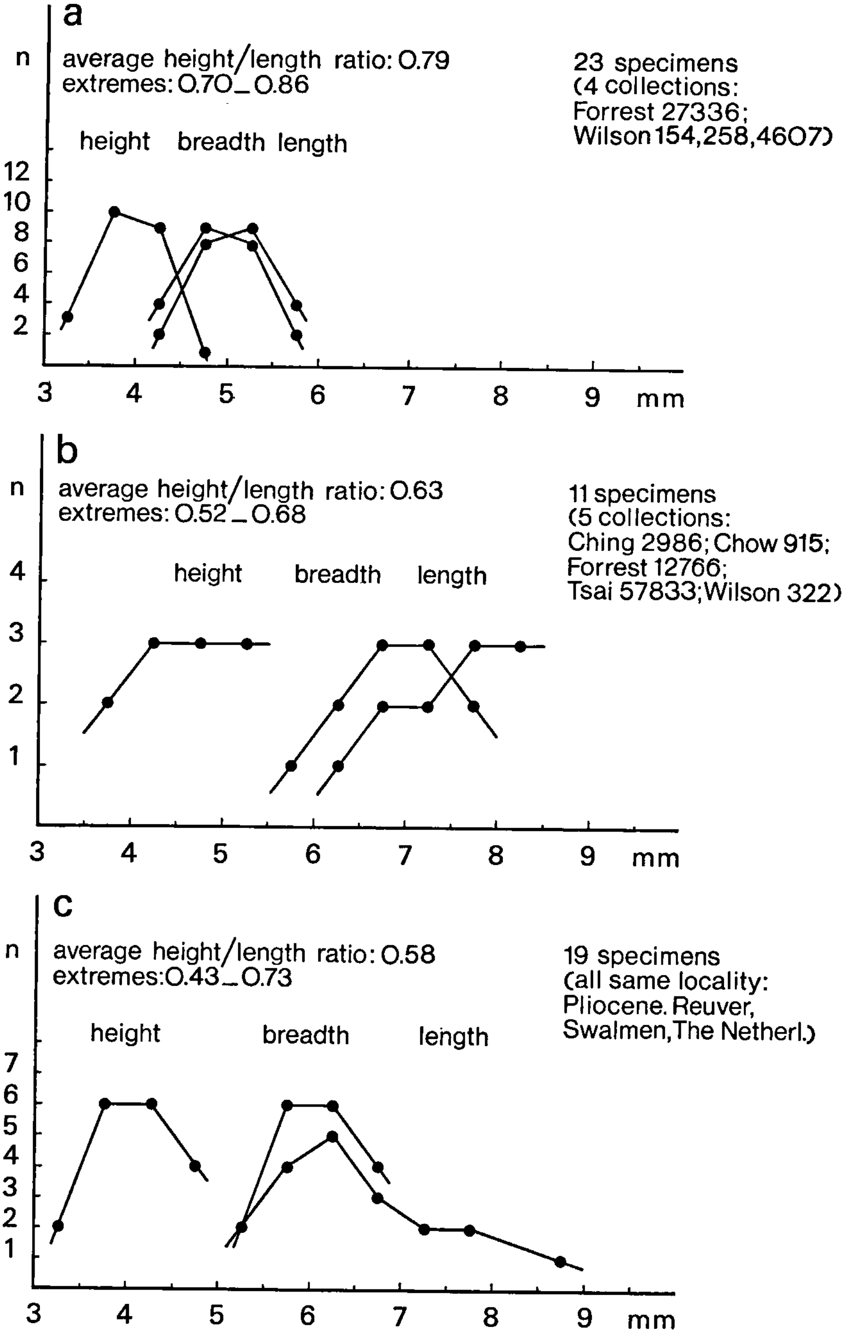

Fig. 9. Frequency curves of measurements of endocarps of a. *M. alba* (recent), b. *M. veitchiorum* (recent) and c. *M. veitchiorum* (fossil).

8-O 1, 2): length 6 mm, breadth 8 mm, height 4.5 mm, height/length ratio thus being 0.75. Unfortunately, the length and breadth measurements are not very characteristic for the species, since the type specimen is unusually short and widely cleft, the length therefore being less, the breadth much more than usual.

Apart from this first small collection from Reuver, several hundreds of specimens have been collected recently by Zagwijn[1]) at the type locality, all belonging to the same species as Reid's endocarps (fig. 8-R 1-3). Some 20 of the most intact, but otherwise randomly chosen specimens of this collection have been measured by me; these measurements have been worked up in a frequency curve (fig. 9c). It appears that length varies from 5—9 mm, with a peak at 6—6.5 mm, breadth varies from 5—7 mm, with a peak at *c.* 6 mm, and height varies from 3—5 mm, with a peak at *c.* 4 mm. Compared with the measurements of some endocarps of *M. veitchiorum* (fig. 9b), the measurements of these fossils fall almost entirely within the variation range of this species, though most of them are on the small side. The average height/length ratios are *c.* 0.6 and nearly 0.7 respectively (the fossils are somewhat crushed now and then and therefore flatter than usual). In all external characters, furthermore, the Reuver fossils are strikingly identical to the endocarps of *M. veitchiorum* (fig. 8-A, B, C). Also C. & E. M. Reid point to the resemblance between their fossils and endocarps of *M. veitchiorum*, and even confess that they at first thought that the former could be referred to that species. They state, however, that their endocarps are somewhat larger (!) than those of *M. veitchiorum*, being nearly as large as those of *M. beaniana* (= *M. alba*). This is puzzling, since this comment does obviously not fit in with the real measurements of endocarps of these Chinese species. Possibly, the authors did not have enough material at their disposition for comparison. Personally I do not hesitate at all to relate all these *M. europaea* fossils from Reuver to *M. veitchiorum*.

11. **Meliosma europaea** C. & E. M. Reid, Bull. Soc. Géol. Fr. sér. IV, 23 (1923) 337, t. 11 f. 2. — **Fig. 8-K.**

Lower Pliocene. Pont de Gail, Cantal, France.

Remarks: Endocarps. Measurements given, cited from the text: '9 big fragments .... the biggest corresponds with the medium size of *M. europaea* (= the Reuver fossils, see under nr. 10) and the smallest does not exceed the variation spectre of this species.' From this comment and from the description and the figure, it can be concluded that these endocarps belong to the same species as the Reuver fossils, and do not differ from the recent *M. veitchiorum*.

12. **Meliosma europaea** C. & E. M. Reid: Mädler, Abh. Senckenb. Naturf. Ges. 446 (1939) 119; Engelhardt & Kinkelin, ibid. 29 (1908) 274, t. 33 f. 10. — **Fig. 8-M 1-3.**

Lower Pliocene. Klärbecken bei Niederrad, Frankfurt am Main, W. Germany.

Remarks: Endocarp. One specimen, poorly depicted, 8 mm long, 6 mm broad, 4.8 mm high, height/length ratio thus being 0.6 (cf. measurements *M. veitchiorum* endocarps in fig. 9b). From measurements, picture, and Mädler's comment it can be concluded that this fossil is of the same character as those under nr. 10, and hence ought to be referred to *M. veitchiorum*.

13. **Meliosma europaea** C. & E. M. Reid: Szafer, Polska Akad. Umiej., Rozpr. B, 72 (1947) 135, t. 11 f. 11 & 12. — **Fig. 11-F.**

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[1]) Coll. Rijks Geologische Dienst, Haarlem, The Netherlands.

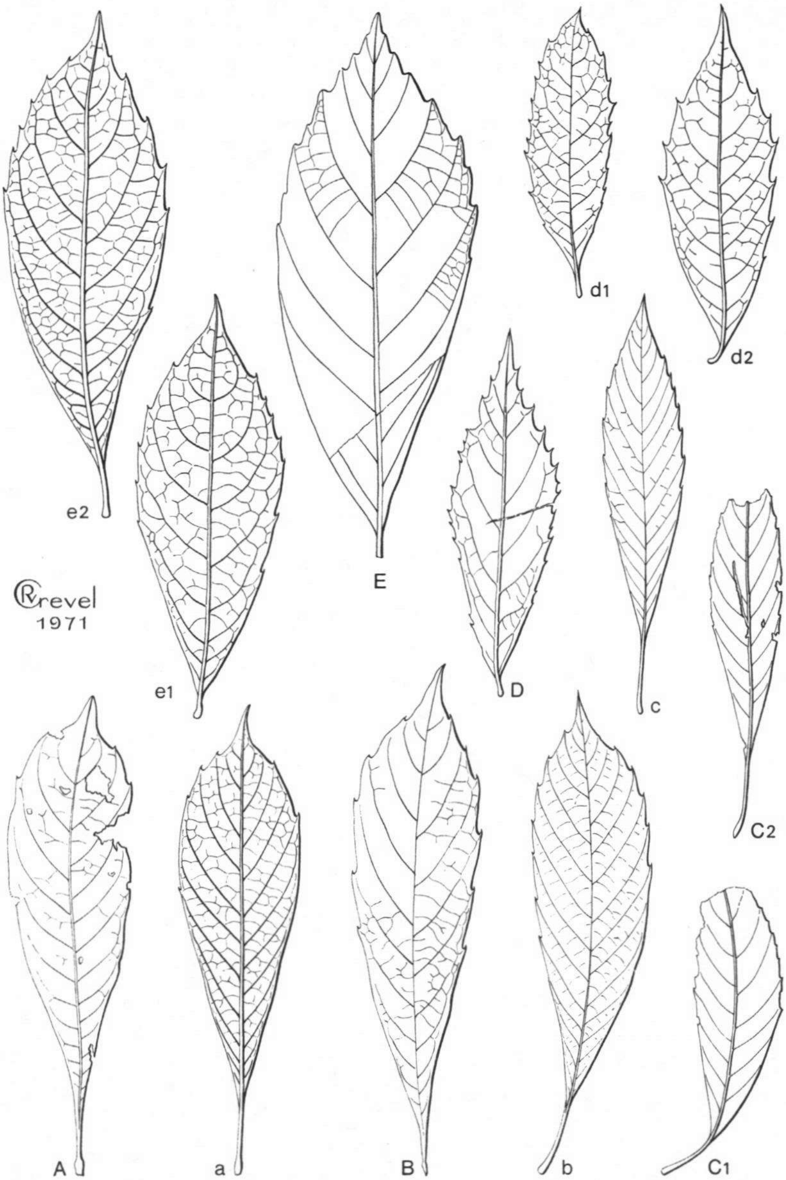

Fig. 10. Fossil leaf-imprints related to *Meliosma*, all, except C1, 2, copied from pictures in literature; reference specimens drawn after recent material. All × ½.

A. *M. goshenensis* (Chaney & Sanborn, 1933, t. 28 f. 3); a. *M. simplicifolia* ssp. *rigida* (*Kichiu, VII-1882*, Japan). — B. *M. goshenensis* (Potbury, 1935, t. 11 f. 7); b. *M. simplicifolia* ssp. *rigida* (*Bodinier 1437*, Hongkong). — C1, 2. *Meliosma sp.* (cf. Wolfe, 1969, t. 2 f. 2, copied from photographs); c. *M. simplicifolia* ssp. *rigida* (*Sasaki 293*, Japan). — D. *M. predentata* (MacGinitie, 1962, t. 7 f. 5); d1, 2. *M. dentata* (*Pringle 6381, 4371*, Mexico). — E. *M. cuneata sensu* Berry (Berry, 1930, t. 12 f. 10); e1. *M. dentata* (*Pringle 4371*, Mexico); e2. *M. simplicifolia* ssp. *yunnanensis* (*Forrest 15540*, Yunnan).

Lower Pliocene. Krościenko near Neumarkt, Poland.

Remarks: Endocarp. One crushed specimen, the measurements, length 6.3 mm, breadth 6.2 mm, being not therefore very reliable. It belongs certainly to *Meliosma* subg. *Kingsboroughia* and because of the presence of a rather big (3.4 by 1.9 mm) plug can possibly best be referred to *M. veitchiorum*.

14. **Meliosma europaea** C. & E. M. Reid: Nikitin, Dokl. Akad. Nauk S.S.S.R. 61 (1948) 1104, f. 11. — **Fig. 8-H.**

Miocene[1]. Voronovo on the River Ob, about 45 km above Kireevsk, W. Siberia, U.S.S.R.

Remarks: Endocarp. One specimen, somewhat damaged, nearly 9 mm long, *c.* 6 mm broad, hence in size matching the endocarps of *M. veitchiorum* (see fig. 9b). Also the shape is like in the endocarps of that species. The specimen is, however, rather long and narrow, but such endocarps do sometimes occur in *M. veitchiorum*. It is, moreover, somewhat damaged at one side, which may also cause its unusually narrow shape.

15. **Meliosma europaea** C. & E. M. Reid: Vlerk & Florsch., Nederl. i. h. IJstijdvak, Utrecht (1950) f. 26. — **Fig. 8-Q.**

Lower Pliocene. Icksberg near Kaldenkirchen, W. Germany.

Remarks: Endocarp. According to the figure this specimen is in shape as well as in measurements (8 mm long, 7 mm broad) not distinct from endocarps of *M. veitchiorum* (see fig. 9b, compare with fig. 8-A, B, C). The Icksberg fossils belong to the 'Reuverian flora', first described by C. & E. M. Reid (see under nr. 10).

16. **Meliosma europaea** C. & E. M. Reid: Dorofeev, Sbornik A. N. Kryshtofovitch, Akad. Nauk S.S.S.R. (1957) 303, t. 6 f. 3 & 4. — **Fig. 8-E 1, 2.**

Oligocene. Ekaterininskoye near Tara, Omsk region, W. Siberia, U.S.S.R.

Remarks: Endocarp. One specimen, length 6.5 mm, breadth 6.5 mm, height 3.0 mm. These measurements and the shape of the fossil are like in smaller endocarps of *M. veitchiorum* (see fig. 9b, compare with fig. 8-A, B, C) apart from that the fossil is somewhat flatter than usual, possibly as a result of compression.

17. **Meliosma europaea** C. & E. M. Reid: Kirchh., Laubgew. d. Braunkohlenzeit, Halle (Saale) (1957) 228, 561, t. 43 f. 166 d, e. — **Fig. 8-J.**

Upper Miocene. Salzhausen near Nidda, W. Germany.

Remarks: Endocarps. Several specimens, up to 9 mm long and 7 mm broad. Shape and measurements are in full accordance with those of *M. veitchiorum* endocarps (see fig. 9b, compare with fig. 8-A, B, C).

18. **Meliosma europaea** C. & E. M. Reid: Szafer, Mioc. Flora Star. Gliwic, Inst. Geol. Prace Warszawa 33 (1961) 70, t. 18 f. 16 & 17. — **Fig. 11-D.**

Upper Tortonian, Miocene. Stare Gliwice, Silesia, Poland.

Remarks: Endocarps. Several specimens; measurements of two depicted ones: length *c.* 4 mm, breadth *c.* 3.75 mm. This size and the outward appearance (subglobose, smooth, small plug) are similar as in small endocarps of *M. alba* (see fig. 9a, and compare fig. 11-A, B).

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[1] Originally designated as Pliocene, but later by Gorbunov, Dokl. Akad. Nauk S.S.S.R. 77 (1951) 101, found to be of Miocene age.

19. Meliosma europaea C. & E. M. Reid: Dorofeev, Tert. Floras West. Siberia (1963) 16, 20, 23, 28, 29, 34, 35, 208, t. 35 f. 13—18. — **Fig. 8-D, F, I 1, 2.**

a—d) Oligocene, e) Miocene. a) Rezhenka on the River Bolshaya Kirgizka, Tomsk region; b) Kompassky Bor on the Tym River, Tomsk region; c) Ekaterininskoye on the Abrosimovka River, Omsk region; d) Krasny Yar on the Irtysh River, Omsk region; e) Kireevskoye on the Ob River, Tomsk region; all western Siberia, U.S.S.R.

Remarks: a) Endocarp. One specimen (l.c., p. 16). No descriptions nor pictures are included, so that this reference cannot be further evaluated.

b) Endocarps. Two specimens (l.c., p. 20, 23). As under a).

c) Endocarp. One specimen (l.c., p. 28, t. 35 f. 13, 14). Measurements, taken from the pictures, are: length well over 6 mm, breadth 6,3 mm, height cannot be measured, but it is clear from the pictures that the endocarp must be somewhat depressed. The size of this endocarp is in nice agreement with those of *M. veitchiorum* (see fig. 9b), and also the shape, with the characteristic big triangular plug, is most similar to that of endocarps of this species (compare figs. 8-D and 8-A, B, C).

d) Endocarp. One specimen (l.c., p. 29, t. 35 f. 18). Measurements, taken from the picture: length 8,3 mm, breadth cannot be measured, but is approximately about the same, height *c.* 5 mm, height/length ratio thus being *c.* 0.6. This size, and the shape of the specimen, with big, triangular plug, are in nice agreement with typical *M. veitchiorum* endocarps (see fig. 9b and compare figs. 8-F and 8-A, B, C).

e) Endocarps. Seven specimens (l.c., p. 34, 35, t. 35 f. 15—17[1])). Measurements, taken from the pictures: length 6.5 mm and 7.5 mm, breadth ? mm and 6.5 mm, height *c.* 4 mm and ? mm respectively, the height/length ratio of the former specimen thus being somewhat over 0.6. These specimens again are in all visible characters identical to endocarps of *M. veitchiorum* (see fig. 9b and compare figs. 8-I 1, 2 and 8-A, B, C).

20. Meliosma europaea C. & E. M. Reid: Mai, Majewski & Unger, Geologie 12 (1963) 785, t. 3 f. 19.

Upper Pliocene or Lower Pleistocene. Rippersroda, Thüringen, E. Germany.

Remarks: Endocarp. One specimen, very damaged, probably originally 5.5 mm long and 4.5 mm broad. On the basis of the description and taking into consideration that fossil endocarps of sect. *Kingsboroughia* are usually easily recognizable, I assume this fossil to belong to that group, but refrain from relating it to any of the two recent species in particular.

21. Meliosma europaea C. & E. M. Reid: Nikitin, Akwitanskaja Semennaja Flora Lagernogo Sada (Tomsk) (1965) 77, t. 12 f. 6. — **Fig. 8-G.**

? Miocene. Lagernogo Sada, Tomsk, W. Siberia, U.S.S.R.

Remarks: Endocarps. Two specimens, 7 and 7.8 mm long, and 7 and 8 mm broad respectively; height not given. From these measurements and from the picture of one of the endocarps it can be concluded that these specimens must be very similar to endocarps of *M. veitchiorum* (see fig. 9b and compare with fig. 8-A, B, C).

22. Meliosma europaea C. & E. M. Reid: coll. Zagwijn, unpubl.[2]) — **Fig. 8-P.**

Pliocene. Brunssum, Prov. of Limburg, The Netherlands.

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[1]) Another picture (drawing) of the specimen in f. 15 is published in Takhtajan, Bachrameev & Padjenko, Osnowsi Paleontologii (1963) 566, f. 255.

[2]) Coll. Rijks Geologische Dienst, Haarlem, The Netherlands.

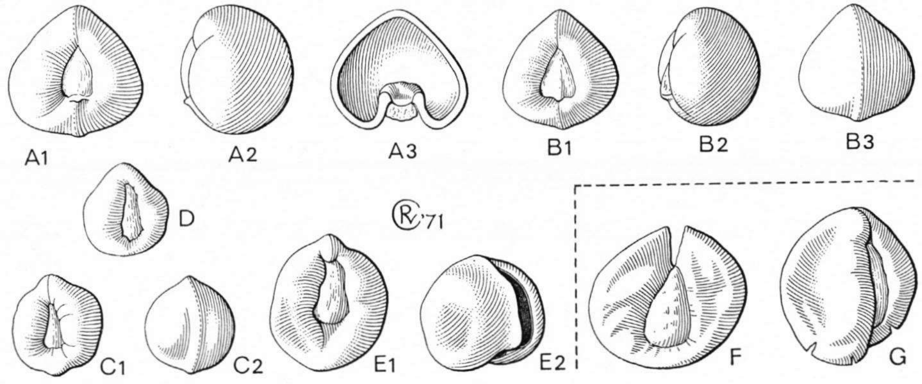

Fig. 11. *M. alba*, endocarps (F and G dubious, possibly small *M. veitchiorum* specimens), all × 3. Recent specimens: A1—3 (*Wilson 258*, W. Hupeh). — B1—3 (*Wilson 154*, W. Hupeh).
Fossil specimens: C1, 2 (Dorofeev in Kolakowski, 1958, t. 20 f. 2, 1). — D (Szafer, 1961, t. 18 f. 17). — E1, 2 (Szafer, 1947, t. 7 f. 7, 5). — F (Szafer, 1947, t. 11 f. 11). — G (coll. Mai s.n., from Meuro, Niederlausitz, E. Germany; coll. Rijksherbarium, Leiden, The Netherlands).

Remarks: Endocarp. One specimen, nearly 9 mm long, 8 mm broad, crushed, and without plug. Notwithstanding its deformation it is clear that this fossil is of the same type as most other *M. europaea* endocarps, having all characters in common with endocarps of *M. veitchiorum* (see fig. 9b and compare with fig. 8-A, B, C).

23. Meliosma goshenensis Chaney & Sanborn, Publ. Carn. Inst. Wash. 439 (1933) 84, t. 28 f. 2 & 3, t. 29 f. 1—3. — **Fig. 10-A.**

Upper Eocene. Goshen, Lane County, Oregon, U.S.A.

Remarks: Leaf-imprints. Five well-preserved specimens, of each of which a photograph was published, which hardly show any difference, even in detail, with leaves of certain recent species of *Meliosma*. The authors compare them with leaves of *M. panamensis* Standl. of Panama, which they are said to resemble very closely. Having no material of this species at my disposition, I could not check this, but the reference specimen depicted by the authors, is not very convincing. On the other hand, the resemblance to leaves of the Asian *M. simplicifolia* ssp. *rigida* and ssp. *fordii* is very striking (compare fig. 10-A and a) as was also noted by Chaney and Sanborn. Hence it appears to be difficult to specify the relationship of *M. goshenensis* either to the New World sect. *Lorenzanea* or to the Old World sect. *Meliosma* in particular, though I would rather relate it to the latter than to the former section.

24. Meliosma goshenensis Chaney & Sanborn: Potbury, Publ. Carn. Inst. Wash. 465, II (1935) 74, t. 11 f. 7. — **Fig. 10-B.**

Upper Eocene. La Porte, Plumas County, California, U.S.A.

Remarks: Leaf-imprint. One well-preserved specimen, almost identical to those mentioned under nr. 23, apart from its dentation in the lower half of the leaf (compare fig. 10-B and b). This is not an important difference, however, since in nearly all recent species of *Meliosma* dentation varies to a high degree. Hence for the La Porte leaf the same comment holds, as was given for the Goshen leaves under nr. 23.

25. Meliosma jenkinsii Reid & Chandler, London Clay Flora (1933) 375, t. 18 f. 16—23, text-f. 13 (*'jenkinsi'*). — **Fig. 12-D.**

Lower Eocene. London Clay, Sheppey and Herne Bay, Kent, England.

Remarks: Endocarps; 6 specimens, most of which locule-casts with remains of the endocarp wall still adhering. Measurements of three specimens are: length 10, 13, 9 mm, breath 9.5, 10, 7.5 mm, height 10.5, 10, 8.5 mm respectively, their height/length ratios hence being *c.* 1.1, 0.77, and 0.94. In shape as well as in anatomy and microscopical structure (elongate digitate cells lining the endocarp wall; see under nr. 5) these endocarps possess typical *Meliosma* characters. They should undoubtedly be placed in subg. *Kingsboroughia* sect. *Kingsboroughia* by the fact that the vascular bundle running through the ventral pore of the endocarp wall is situated in a ventral groove in the latter, and is still present in the shape of a spathulate ventral 'plug' at the ventral side of the endocarp. The morphology of these fossils is very similar to that of the endocarps of the recent *M. alba*; the short ventral canal through which the vascular bundle enters the endocarp is direct and circular (l.c., f. 19 and 20), not oblique as in *M. veitchiorum* and † *M. cantiensis* (compare fig. 4, B 1 and 3). Also the subglobose shape of the fossils is much like that in *M. alba*, but the size is very much bigger (compare figs. 11-A 1, B 1 and 12-D). It is, therefore, not possible to relate them to any of the two recent species of sect. *Kingsboroughia.*

26. Meliosma jenkinsii Reid & Chandler: Chandler, Low. Tert. Floras South. Engl. 1 (1961) 112, 242, t. 12 f. 6 & 7, t. 24 f. 3—7 (*'jenkinsi'*). — **Fig. 12-C, E, F.**

Lower Eocene. Harefield (Middlesex), East Cliff Shore, Sheppey, and Herne Bay (Kent), Bognor (Sussex), and Frinton (Essex), England.

Remarks: Endocarps; 7 specimens, all correctly included in *M. jenkinsii* and hence referable to subg. *Kingsboroughia* sect. *Kingsboroughia* on the base of characters mentioned under nr. 25. Measurements of three well-preserved specimens are: length 9.5, 10, 8 mm, breadth 8.5, 8.5, 7.75 mm, height 8, 8, 7 mm respectively, their height/length ratios thus being 0.84, 0.80, 0.87. All specimens are more or less abraded, except for one (l.c., t. 24 f. 3) which is unusually well-preserved and which gives a good impression of outward shape and structure of the endocarp wall; see fig. 12-C, and compare with the very similar but much smaller endocarps of *M. alba* in fig. 11-A, B. In some of the abraded specimens, on the other hand (l.c., t. 24 f. 6, 7), the shape of the locule-cast is rather well visible, especially in one which is depicted in fig. 12-F. In the latter specimen the lateral and ventral parts of the wall are wanting, which gives a good impression of the ventral shape of the seed (the seed in *Meliosma* is always more or less conformable to the shape of the locule!). The shape as well as the size of the seed of *M. jenkinsii* appears to be strikingly similar to the shape and size of the endocarp of the recent *M. rufo-pilosa* (subg. *Kingsboroughia* sect. *Hendersonia*). Both share the more or less beak-like processus at one end and the concave ventral side, which is flattened in the centre and surrounded by a strongly curved circumvallation; compare fig. 12-F and G 1, 2. This remarkable similarity also holds for the seeds of the fossil *M. cantiensis* (nrs. 5 and 6), as far as can be seen from casts of the ventral part of the locule (compare for example fig. 12-B). It has led me to some assumptions with regard to the phylogenetical development of the endocarp types in *Meliosma* (see part I chapter C sub d).

27. Meliosma miessleri Mai, Paläont. Abh., Abt. B, 2, 1 (1964) 109, t. 14 f. 19—24. — **Fig. 13-D 1, 2.**

Miocene. Hartau near Zittau, Oberlausitz, E. Germany.

Remarks: Endocarps. Several specimens, 3.5—5 mm long, 3—4.8 mm broad. The

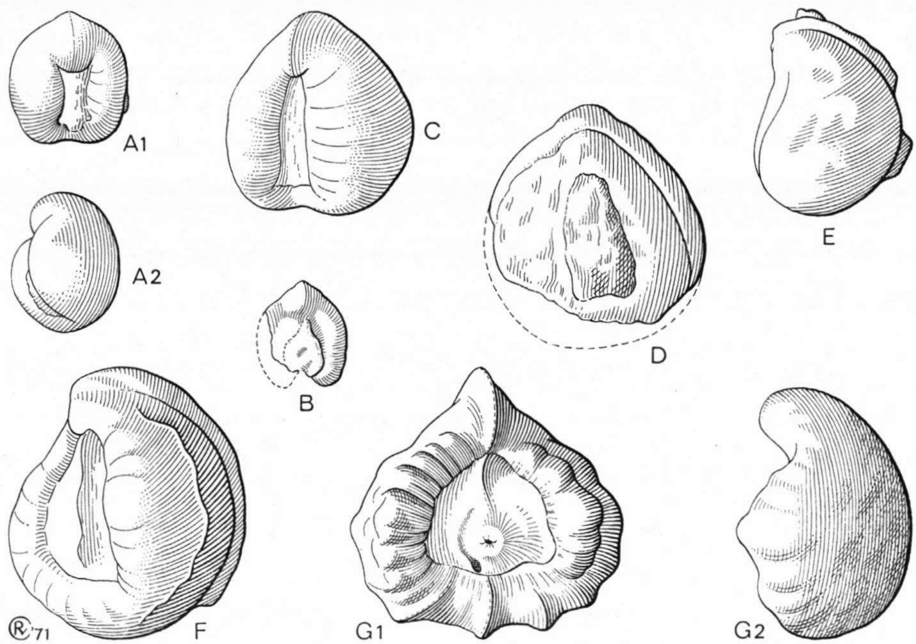

Fig. 12. Endocarps of *Meliosma* subg. *Kingsboroughia*, fossil (A—F) and recent (G), all × 3. A1, 2. *M. cantiensis*, perfect, somewhat worn endocarp, lateral and ventral view (Reid & Chandler, 1933, t. 18 f. 24, 25). — B. *M. cantiensis*, locule-cast, ventral view (Chandler, 1961, t. 24 f. 8). — C. *M. jenkinsii*, perfect endocarp, ventral view (ibid., t. 24 f. 3). — D. *M. jenkinsii*, much worn endocarp, ventral view (Reid & Chandler, 1933, t. 18 f. 17). — E. *M. jenkinsii*, locule-cast with dorsal wall remnants, lateral view (Chandler, 1961, t. 12 f. 6). — F. *M. jenkinsii*, locule-cast with dorsal wall remnants, ventro-lateral view (ibid., t. 24 f. 7). — G1, 2. *M. rufo-pilosa* (recent), perfect endocarp, ventral and lateral view (*Pennington 7942*, North Borneo).

(sub)globose shape, the distinct reticulum on the surface, the marginal canal inside, and the small, circular plug and ventral opening are characteristic for endocarps of sect. *Meliosma* (compare with figs. 22 and 29). It is, however, senseless to suggest a relationship of *M. miessleri* with any recent species or species-group of sect. *Meliosma*, since the type of endocarp involved is the most common one in this section and may be found in several of its species.

28. Meliosma myriantha Sieb. & Zucc. *fossilis* Nathorst, Kongl. Svensk. Vetensk. Akad. Handl. 20, 2 (1882) 59, t. 3 f. 17.

Upper Pliocene, possibly Pleistocene. Mogi, near Nagasaki, Japan.

Remarks: Leaf-imprint. Only one fragment which might well represent *M. myriantha*. However, the picture is not ideal, and the specimen, with tip and base wanting, seems too incomplete for a safe identification. Its belonging to quite another family might, therefore, be possible as well.

29. Meliosma myriantha Sieb. & Zucc.: Miki & Kokawa, Journ. Biol. Osaka City Univ. 13 (1962) 79, f. 10 Q.

Pleistocene. Kakinokoba, Goto Isl., Kyushu, Japan.

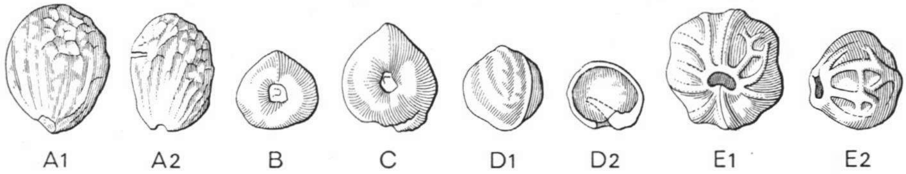

Fig. 13. Fossil endocarps of *Meliosma* subg. *Meliosma* sect. *Meliosma*, all perfect specimens, all × 3. A1, 2. *M. reticulata*, lateral view (Chandler, 1957, t. 15 f. 116, 113). — B. *M. sheppeyensis*, ventral view (Reid & Chandler, 1933, t. 18 f. 32). — C. *M. sheppeyensis*, ventral view (Chandler, 1961, t. 24 f. 10). — D1. *M. miessleri*, dorsal view (Szafer, 1964, t. 14 f. 20); D2. *M. miessleri*, length section (ibid., t. 14 f. 24). — E1, 2. *M. rigida foss.*, ventral and lateral view (Miki, 1941, f. 17 H).

Remarks: Endocarps. Several specimens, depressed-globose, with a keel and, judging from the picture, rather smooth, about 3 mm long and 2½ mm high. In my opinion Miki's identification is rather dubious, since *M. myriantha* endocarps are usually more globose, bigger, and distinctly reticulate on the surface (fig. 22-B). *M. dilleniifolia* ssp. *tenuis* (cf. fig. 22-D) might be a better alternative.

30. Meliosma predentata MacGinitie, Univ. Calif. Publ. Geol. Sci. 35 (1962) 115, t. 5 f. 3, t. 7 f. 2—5. — **Fig. 10-D.**

Upper Miocene. Kilgore, SW. of Valentine, Nebraska, U.S.A.

Remarks: Leaf-imprints. Abundant specimens which the author probably correctly relates to *M. dentata* (sect. *Lorenzanea*) from Mexico, the leaves of which are exactly matched by these imprints, even in minor details (compare fig. 10-D and d 1, 2). The temperate climatic conditions under which *M. dentata* lives are similar to those under which the Kilgore flora is assumed to have existed.

31. Meliosma reticulata (C. & E. M. Reid) Chandler, Bull. Brit. Mus. (Nat. Hist.) Geol. 3 (1957) 102, t. 15 f. 113—118. — *Calvarinus reticulatus* C. & E. M. Reid, Philos. Trans. Lond. 201 (B) (1910) 169, t. 15 f. 18—20. — **Fig. 13-A 1, 2.**

? Oligocene. Bovey Tracey and Heathfield, Devonshire, England.

Remarks: Endocarps. Six specimens, 3.75—4.25 mm long, 2.6—3 mm broad, 5—5.25 mm high. The general form, surface ornamentation, small size, and marginal canal inside relate these fossils doubtless to sect. *Meliosma*. They are obovoid, a character not so often occurring in *Meliosma*, for instance in *M. lepidota*, but in this species the endocarps are mostly bigger (compare with fig. 22-H 2, 3). On the other hand, also in view of the variability of the endocarps in most species of sect. *Meliosma*, there is no reason to relate *M. reticulata* to any recent species in particular.

32. Meliosma *cf.* **rigida** Sieb. & Zucc.: Miki, Jap. Journ. Bot. 11 (1941) 283, f. 17 H. — **Fig. 13-E 1, 2.**

Lower Pliocene. Hatagoya (pref. Gihu), Itirizuka (pref. Aiti), Simoiguta (pref. Gihu); all Central Honshu, Japan. Also found (*fide* Miki) in Huke (pref. Osaka) and Sidatani (pref. Mie), SW. Honshu.

Remarks: Endocarps. Three specimens from Hatagoya depicted. These are about globose, and 4—5 mm ø. These measurements, the reticulum, and the ventral pore which is not sunken in the endocarp wall, correspond very well with the characters found in endocarps of *M. simplicifolia* ssp. *rigida* (see fig. 22-P). From the other localities mentioned above no specimens are described or depicted.

33. **Meliosma rostrata** Chaney & Sanborn, Publ. Carn. Inst. Wash. 439 (1933) 85, t. 30. f. 2 & 4. — **Fig. 14-C 1, 2.**

Upper Eocene. Goshen, Lane County, Oregon, U.S.A.

Remarks: Leaf-imprints. Two specimens, belonging to a type which is not exclusively characteristic for *Meliosma*. The authors compare them with *M. herbertii* from Central America, with which they have every detail in common. The imprints might indeed originate from a *Meliosma* species, but in my opinion it will not be very difficult to find similar leaves in genera belonging to other families. If they have been correctly placed in *Meliosma*, they can only be related to sect. *Lorenzanea*, as no similar leaves are found in any SE. Asian *Meliosma* species (compare fig. 14-C 1, 2 and c).

34. **Meliosma rigida** Sieb. & Zucc.: Miki & Kokawa, Journ. Biol. Osaka City Univ. 13 (1962) 79, f. 8 R.

a) Pliocene. Iki Isl. (pref. Nagasaki), Kyushu, Japan.
b) Pleistocene. Shishimuta (pref. Oita), Kyushu, Japan.
c) Recent. Takenta (pref. Kagoshima), Kyushu, Japan.

Remarks: Endocarps. A few specimens from c) Takenta are depicted, which, on the base of the same characters as mentioned under nr. 32, have been probably correctly identified as *M. rigida* (= *M. simplicifolia* ssp. *rigida*). From localities a) and b) no specimens are described or depicted.

35. **Meliosma (?) shanwangensis** Hu & Chaney, Publ. Carn. Inst. Wash. 507 (1940) 76, t. 50 f. 8 & 9.

Miocene. Shanwang, Shantung, China.

Remarks: Leaf-imprints. Two specimens, indicated by the authors as of dubious relationships. They might indeed belong to *Meliosma*, but having very neutral characters, they could as well be related to some entirely other group.

36. **Meliosma sheppeyensis** Reid & Chandler, London Clay Flora (1933) 378, t. 18 f. 31—33. — **Fig. 13-B.**

Lower Eocene. Minster (Sheppey), Kent, England.

Remarks: Endocarps. Three rather well preserved specimens. Their measurements show: length 4, 3, and 4 mm, breadth 3.5, 3, and 3.3 mm, height 4, 3.5, and 4 mm, height/length ratio thus being 1.0, 1.17, and 1.0 respectively. The dorsal surface of these subglobose endocarps is highly convex, the ventral surface somewhat flattened, and roundly incurved at its centre to form the small, deep, circular canal which runs marginally into the locule (fig. 4-C6). The locule is lined with the centipede-shaped cells characteristic for *Meliosma* (see under nr. 5). Obviously, these endocarps are in all characters typical representants of sect. *Meliosma*. The surface of the endocarps is either smooth (possibly as a result of abrasion), or somewhat ribbed or lumpy. Since endocarps answering the above description are very common in sect. *Meliosma*, the *M. sheppeyensis* fossils cannot be related to any species group in particular, though they are of quite modern appearance (compare with fig. 22).

37. **Meliosma sheppeyensis** Reid & Chandler: Chandler, Low. Tert. Floras South. Engl. 1 (1961) 243, t. 24 f. 10. — **Fig. 13-C.**

Lower Eocene. Bognor, Sussex; Warden Point, Sheppey; both England.

Remarks: Endocarps; 4 specimens from Bognor and 3 from Sheppey, most of them perfect or somewhat abraded endocarps, a few being locule-casts. Only one of these,

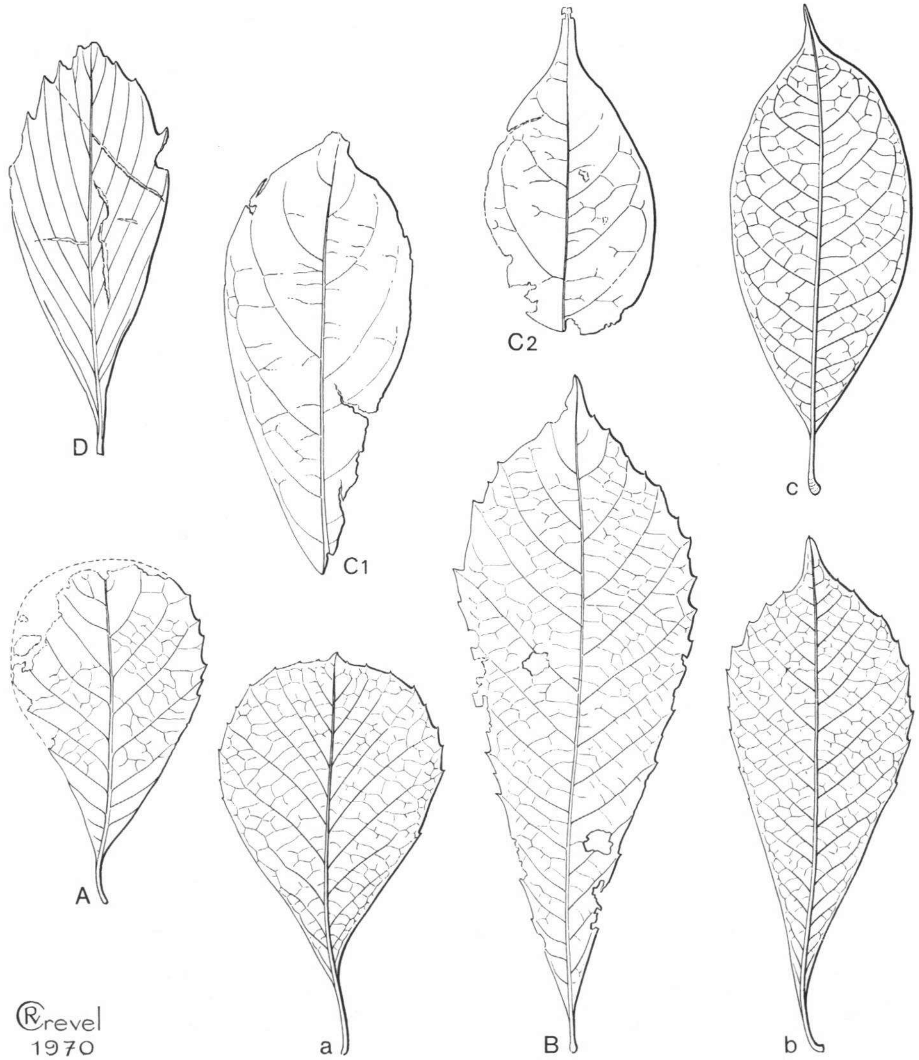

Fig. 14. Fossil leaf-imprints related to *Meliosma*, all copied from pictures in literature; reference specimens drawn after recent material. All × ½.

A. *M. truncata* (MacGinitie, 1941, t. 38 f. 1); a. *M. parviflora* (*Meyer 1509*, Chekiang). — B. *M. aesculifolia* (Chaney & Sanborn, 1933, t. 27 f. 1); b. *M. parviflora* (*F. T. Wang 23522*, Szechuan). — C1, 2. *M. rostrata* (Chaney & Sanborn, 1933, t. 30 f. 2, 4); c. *M. herbertii* (*Sintenis 4006*, Porto Rico). — D. *Viburnum cuneatum*, erroneously related to *Meliosma* ('*M. cuneata*') (Newberry, 1898, t. 57 f. 2; Brown, 1962, t. 28 f. 7).

from Bognor, has been depicted. Its measurements are: length 4 mm, breadth 4 mm, height 3.75 mm, height/length ratio thus being 0.94; the measurements of the other specimens are more or less similar. The fossils much resemble those described under nr. 36, but in view of the fact that they are of a rather common type, it is well possible that a mixture is involved of specimens belonging to more than one fossil species.

38. **Meliosma truncata** MacGinitie, Publ. Carn. Inst. Wash. 534 (1941) 146, t. 38 f. 1. — **Fig. 14-A.**

Middle Eocene. Chalk Bluffs, Sierra Nevada, California, U.S.A.

Remarks: Leaf-imprint. One specimen, which is compared by the author with leaves of several SE. Asian species of *Meliosma*, such as *M. dilleniifolia* ssp. *cuneifolia*, which it indeed resembles to some extent. However, it even more resembles leaves of *M. parviflora*, of some of which the fossil is an almost exact copy (compare fig. 14-A and a)! Moreover, within *Meliosma* this characteristic truncate leaf-type exclusively occurs in *M. parviflora*. In the American sect. *Lorenzanea*, on the contrary, no match to this fossil does exist as far as I know. See also under nr. 3 (*M. aesculifolia*).

39. **Meliosma wetteraviensis** (Ludw.) Mai, Paläont. Abh., Abt. B, 2, 1 (1964) 110. — *Hamamelis wetteraviensis* Ludwig, Palaeontographica 5 (1857) 105, t. 20 f. 27 a, b; Mädler, Abh. Senckenb. Naturf. Ges. 446 (1939) 119, *in synon.*; Kirchh., Laubgew. d. Braunkohlenzeit, Halle (Saale) (1957) 561. — **Fig. 8-N1—3.**

Lower Pliocene. Wetterau, Dorheim, W. Germany.

Remarks: Endocarp. One specimen, of which Ludwig published a rather unsatisfactory picture and which was lost afterwards for a long period. Though it seems to me that the fossil depicted by Ludwig can hardly belong to something else than *Meliosma* sect. *Kingsboroughia*, there was some controversy until the type was recovered and Mai (1964) finally related it to *M. europaea*. According to the rules of nomenclature the older epithet *wetteraviensis* has priority over *europaea*, and, consequently, *M. europaea* was correctly placed by Mai in the synonymy of *M. wetteraviensis*. Measurements of Ludwig's fossil (based on the picture): length *c.* 7 mm, breadth *c.* 8 mm, height *c.* 5 mm, height/length ratio thus being 0.7. These measurements, together with the other characters as far as visible from the picture, match those of endocarps of *M. veitchiorum* (see fig. 9b, compare with fig. 8-A, B, C).

40. **Meliosma wetteraviensis** (Ludw.) Mai: coll. Mai, unpubl.[1]) — **Fig. 11-G.**

Middle Miocene. Meuro, W. Senftenberg, Niederlausitz, E. Germany.

Remarks: 3 specimens, much crushed but well recognizable as belonging to *Meliosma* sect. *Kingsboroughia*. The length of the most intact specimen is *c.* 6.5 mm, height *c.* 4.5 mm, height/length ratio thus being *c.* 0.7. These measurements, however, are not quite reliable, as a result of the deformation of the endocarps. They resemble big *M. alba* endocarps, on the one hand, and small *M. veitchiorum* endocarps on the other. Though the rather big plug is more like that in *M. veitchiorum*, there is too much lack of good characters to relate these specimens to that species in particular (see fig. 9a, b, compare with figs. 8-A, B, C and 11-A, B).

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[1]) A few specimens in coll. Rijksherbarium, Leiden, The Netherlands.

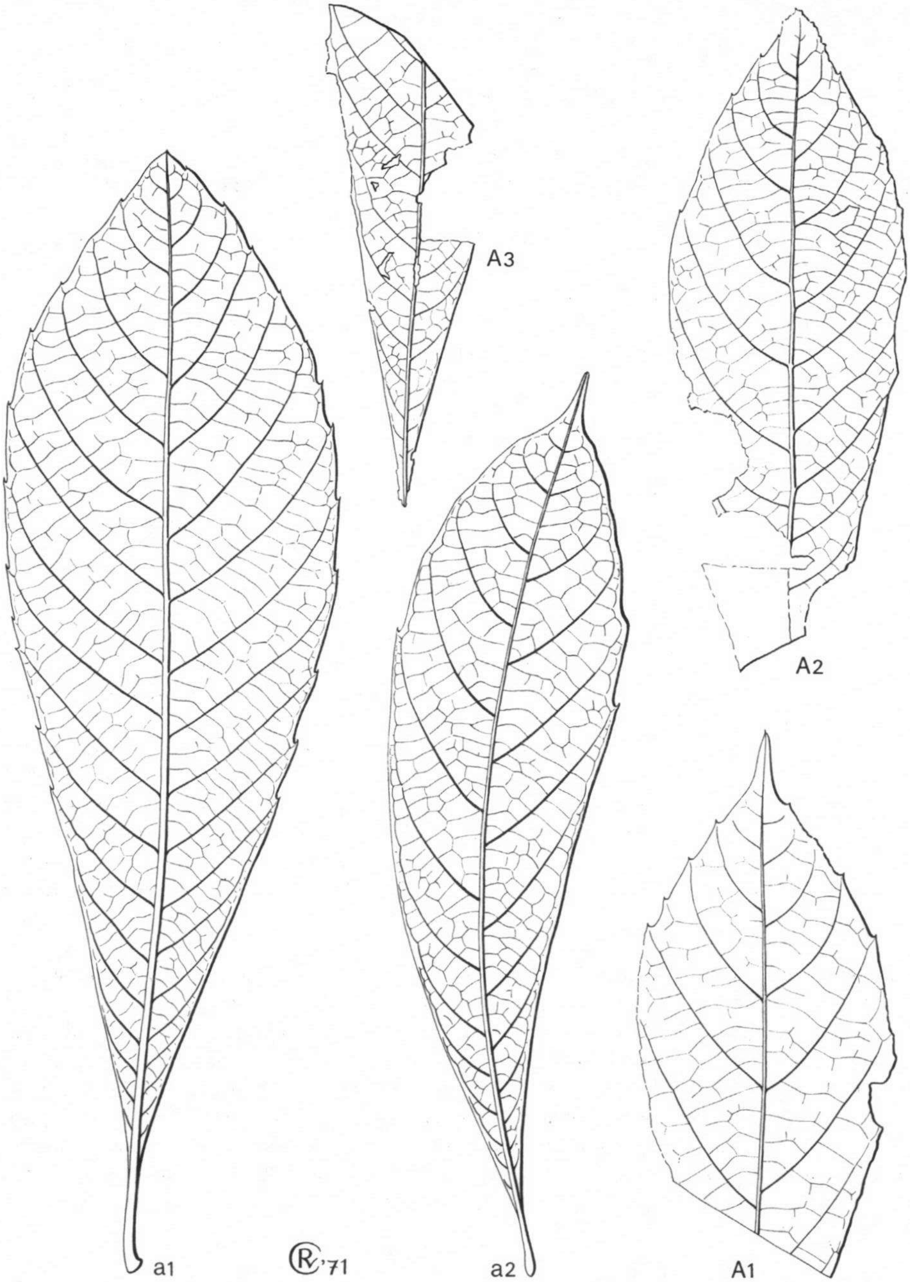

Fig. 15. Fossil leaf-imprints related to *Meliosma*, copied from unpublished photographs of fossils from Susanville, California, U.S.A. (see nr. 42, p. 91); reference specimens drawn after recent material. All × ½. A1—3. *Meliosma sp.*, fossil specimens; a1. *M. simplicifolia* ssp. *fruticosa* (*Kiah SF 35206*, Malay Peninsula), a2. *M. sellowii* (*Hatschbach 17910*, Brazil).

41. **Meliosma spec.:** Wolfe, U.S. Geol. Surv. Open-file Report (1969) t. 2 f. 2, t. 6 f. 2 A. — **Fig. 10-C 1, 2.**

Low Upper Eocene. Gulf of Alaska region, U.S.A.

Remarks: Leaf-imprints. Several well-preserved specimens, some of which Wolfe related to *M. pungens* (= *M. simplicifolia* cf. ssp. *thomsonii*). On request, Mr. Wolfe kindly sent me photographs of his fossils, from which I get the strong impression that they have been correctly related to *Meliosma*, with which they have every visible detail in common. Moreover, Mr. Wolfe informs me that his identifications are also based on characters of the veinlets which puts identification of fossil leaves on a much firmer basis. The Alaskan leaves are falling apart into two groups, one of which shows indeed a close similarity to leaves of *M. simplicifolia* ssp. *thomsonii*, the other specimens being very similar to leaves of *M. simplicifolia* ssp. *rigida* (compare fig. 10-C 1, 2 and b, c). I believe it is very probable that some, if not all of these leaf-imprints belong indeed to *Meliosma*; they show a close morphological relationship to the polymorphous, widespread SE. Asian species *M. simplicifolia.*

42. **Meliosma spec.:** unpublished. Photographs kindly placed at my disposal by Mr. J. A. Wolfe, Menlo Park, U.S.A. — **Fig. 15-A 1—3.**

Middle Eocene. Susanville, California, U.S.A.

Remarks: Leaf-imprints. Several specimens, well-preserved, and all of the same type. They are very similar to leaves of the SE. Asian *M. simplicifolia* ssp. *simplicifolia* and ssp. *fruticosa*, but even more so to leaves of *M. sellowii* from the Brazilian tropical rain forest, with which they are completely identical (compare fig. 15-A 1—3 and a 1, 2). There is no doubt that these characteristic leaf-imprints belong to *Meliosma*, within which they show the most close morphological relationship to the American sect. *Lorenzanea*. The Susanville flora is the most tropical assemblage yet known in western North America (Wolfe, in litt.).

43. **Zelkova serrata** Szafer *foss.*, Polska Akad. Umiej., Rozpr. B, 72 (1947) 240, t. 7 f. 5—7, *non* Makino; Kirchh., Die Laubgew. d. Braunkohlenzeit, Halle (Saale) (1957) 606, 656, t. 53 f. 198 b; Szafer, Plioc. flora okol. Czorsztyna, Warszawa (1954) 40, t. 9 f. 7, 8, *in synon.*; Dorof. in Kolakowski, Akad. Nauk Gruzinsk. S.S.R., Suchumi, Vyp. 11 (1958) 358, *in synon.*; Szafer, Mioc. Flora Starych Gliwic, Inst. Geol. Prace, Warszawa 33 (1961) 45. — **Fig. 11-E 1, 2.**

Lower Pliocene. Krościenko near Neumarkt, Poland.

Remarks: Endocarps. Eleven specimens, 4.5—6 mm long, 3.6—5 mm high (?)[1]), which were initially erroneously identified as *Zelkova serrata*, later as *Cicer pliocaenicum* (see nr. 2), and finally placed into the synonymy of *M. europaea* by Dorofeev, l.c By their measurements as well as by their rather globose shape (length/height ratio *c.* 0.8) and other characters these endocarps in every respect match those of *M. alba* (see fig. 9a and compare with fig. 11-A, B).

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[1]) As is often a problem in paleobotanical literature, it is not clearly stated which measurements refer to length, breadth, and height of the endocarps.

C. SYNTHESIS OF PALEOBOTANICAL AND TAXONOMIC DATA

1. SUBGENUS KINGSBOROUGHIA

a. Combination of fossil and recent taxa

Most of the fossil endocarps discussed in the foregoing chapter doubtless belong to subg. *Kingsboroughia* sect. *Kingsboroughia*, whereas none could be related to sect. *Hendersonia*. The fossils of this group have been described under relatively few names, viz. as *M. cantiensis* and *jenkinsii* from the Eocene of southern England and as *M. caucasica* and *wetteraviensis* (syn. *europaea*) from the Oligocene, Miocene, and Pliocene of Eurasia. The latter species have been found particularly abundantly and in quite a number of localities.

Looking at the first group, *M. cantiensis* and *jenkinsii* from the Eocene, discussed under the numbers 5, 6, and 25, 26, it is obvious that none of these fossils is quite identical to endocarps of the recent species of sect. *Kingsboroughia*, though there is sometimes much resemblance. It is true that the *M. cantiensis* endocarps are to a large extent similar to those of the recent *M. veitchiorum*, but they are distinctly more globose and mostly smaller. Furthermore, the fossils described under *M. jenkinsii* show a character combination which is even quite unknown in recent sect. *Kingsboroughia*, viz. a subglobose/ovoid shape and big size.

Looking now at younger fossils related to subg. *Kingsboroughia* sect. *Kingsboroughia*, mainly described under the names *M. europaea* or *wetteraviensis*, a strikingly different situation arises. Here nearly all can be related either to *M. alba* (nrs. 7, 18, 43) or mostly to *M. veitchiorum* (nrs. 2, 10—17, 19, 21, 22, 39), remaining only those under nrs. 20 and 40, which are too damaged for a satisfactory diagnosis. In all verifiable characters these fossil endocarps do not show any difference whatever with endocarps of one of the two recent species just mentioned. This morphologic relationship has been noticed before; most of the authors involved point to it, but nobody goes so far as to suggest the specific identity of fossil and recent species. The reasons for it, whether theoretical or resulting from a lack of material for comparison, will not be discussed here. It will be considered, on the contrary, what arguments can be brought forward, apart from that of the mere morphologic relationships, to support such a combination of fossil and recent species.

1. The fossils classed under the species *M. europaea* or *wetteraviensis* all are of comparatively young age, most of them dating from Pliocene or Miocene, and a few from Oligocene. It is logic that, the younger the fossils are, the more chance there is that they can be related to recent taxa. There is, however, a tendency among paleobotanists to adhere to the opinion that species of plants which lived in the Tertiary cannot be the same as recent species, even when their fossil remains do not show any difference. Szafer (1946), however, has argued conclusively that this extreme opinion cannot be upheld, especially not for Upper Tertiary fossils. In quite a number of cases it can be considered certain that a species which lived in the Tertiary still forms part of a present flora. In his 'Pliocene flora of Krościenko in Poland' Szafer (1946) reckons many of his fossils to recent species; his Eastasian elements comprise amongst others the following still existing species: *Chamaecyparis pisifera, Thuja orientalis, Picea polita, Carpinus laxiflora, Actinidia polygama, Phellodendron amurense, P. japonicum, Acer palmatum, A. japonicum, Cornus controversa.*

Many more examples from other authors could be mentioned, but all nearly exclusively concern geologically young fossils, mostly of Pliocene age. Only rarely examples are found of species figuring from the earlier Tertiary up to recent times, such as *Ceratophyllum submersum, Glyptostrobus europaeus, Ginkgo biloba, Juglans cinerea, Taxodium* *dubium*, *Metasequoia glyptostroboides*, *Najas marina*, *Dulichium vespiforme/spathaceum* (see Kirchheimer, 1957).

It may be that indeed such cases are as scarce as they seem to be, but an additional cause for their scarcity may be sought in the reluctance of paleobotanists to correlate older Tertiary fossils with recent material on the specific level, for reasons just referred to and discussed more amply by Szafer. In this connection it is the more remarkable to find that paleobotanical literature offers many cases of fossil species considered to have existed unchanged throughout several epochs of the Tertiary (e.g. Dorofeev, 1963). *Meliosma europaea* is such a case, having been recorded repeatedly from the Middle Oligocene up to in the Upper Pliocene. Why then would some of these long-lived fossil species not have been able to bridge the comparatively short time from the Pliocene up to the present day, escape destruction by the glaciations as so many others have, and still be found as 'living fossils'?

2. All fossil floras in which endocarps referable to *M. alba* or *veitchiorum* have been found, are of similar vegetational and floristic structure. They are commonly referred to as Arcto-Tertiary (Geo)flora(s), a concept originally introduced by Engler (1882: 327), as the '*arcto-tertiäre Element*', and since substantiated in large part by further paleobotanical research. Citing Wolfe (1969), p. 69: 'The concept[1]) fundamentally envisions that a broad-leaved deciduous forest of a particular floristic composition evolved in the Arctic during the Cretaceous[2]), persisted there during the early Tertiary, and, in response to the gradually cooling climate, migrated southward during the middle Tertiary into middle latitudes where the forest persists to-day in east-central Asia and southeastern North America. During its migration this flora supposedly underwent little change in floristic composition. The fundamental significance of this concept to plant geography is clear; the concept is accepted as fact in standard textbooks on plant geography such as Cain (1944) and Good (1953).'

Recently, however, serious objections have been advanced against the Arcto-Tertiary concept, firstly, on a theoretical basis, by Mason (1947), who argues that 'such concepts of floristic organization and development demand unity and stability of communities in time and space beyond what is possible in the light of the nature of floristic dynamics such as are bound up with the genetics of a population, the physiology of the individual, and the diversity and fluctuation of the environment.' Subsequent factual evidence against the validity of the Arcto-Tertiary concept was advanced by several other authors, lastly and most elaborately by Wolfe (1969). Wolfe clearly shows that 1 the Arcto-Tertiary concept never had a satisfactory stratigraphic foundation, 2 it is strongly contradicted by evidence from the Alaskan and Siberian assemblages of fossil plants. His conclusion is that the Arcto-Tertiary concept as currently used stands in the way of a proper understanding of floristic and vegetational history, and consequently should be discarded.

Following Wolfe (1969), I prefer, therefore, not to use such a vexed concept as that of the Arcto-Tertiary flora, but to indicate the fossil floras in question in a different way, namely as floras belonging to the mixed mesophytic forest type. The characteristics of its recent Chinese representation are fully described by Wang (1961). It exists under warm temperate conditions and is floristically diverse, notably in families such as *Salicaceae*, *Juglandaceae*, *Betulaceae*, *Fagaceae* (including the 'lobed' oaks), *Ulmaceae*, *Hamamelidaceae*, *Rosaceae*, *Aceraceae*, *Rhamnaceae*, and *Ericaceae*. Notable also is the presence of numerous

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[1]) In the narrowed sense that was gradually given to it by paleobotanists.

[2]) But according to some European authors during the Paleocene—Eocene (e.g. Mai, 1965).

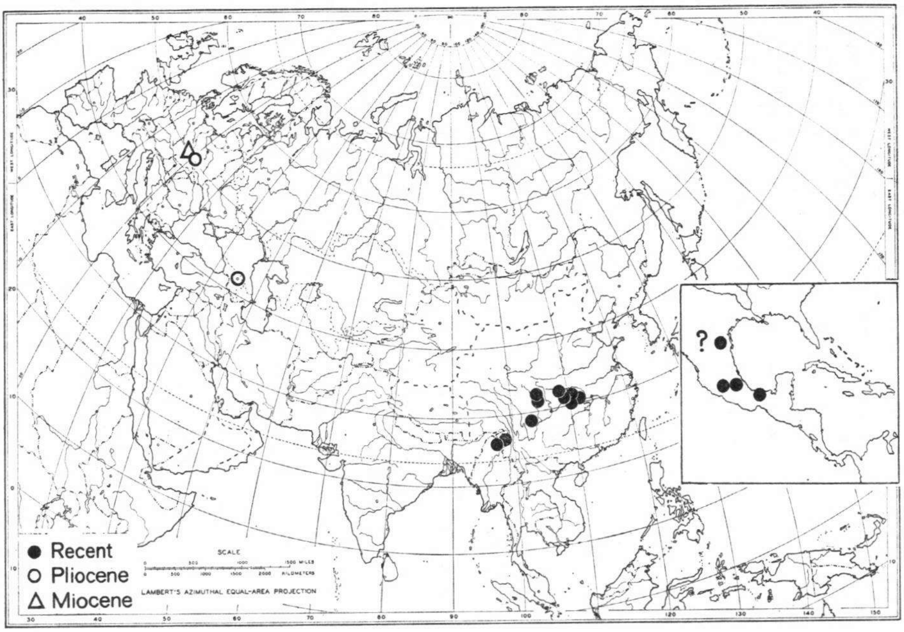

Fig. 16. Distribution of *M. alba*, recent and fossil (plotted on Goode's copyrighted map No. 5).

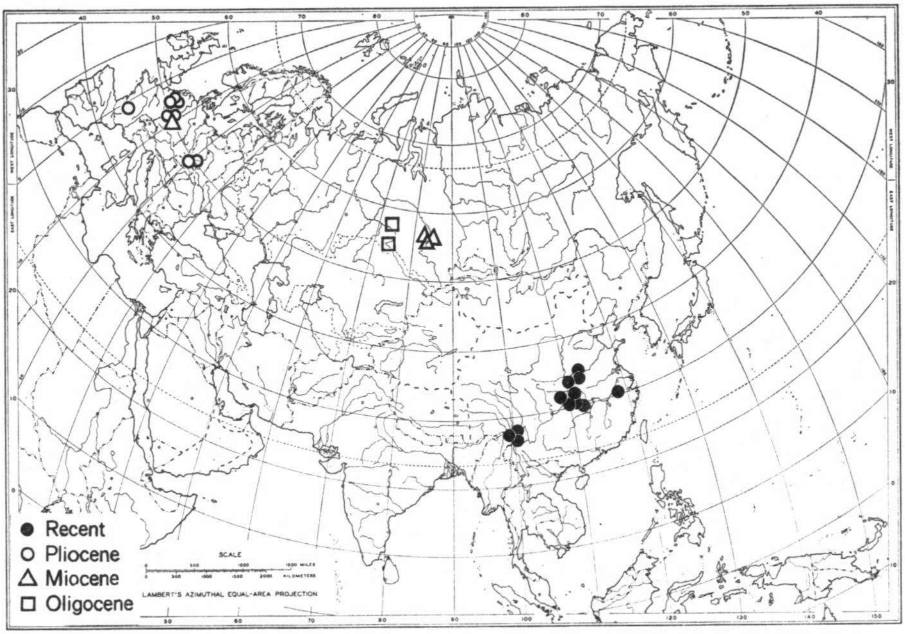

Fig. 17. Distribution of *M. veitchiorum*, recent and fossil (plotted on Goode's copyrighted map No. 5).

monotypic and oligotypic genera. No single genus or family dominates the canopy of the forest; next to most tropical forest types, the mixed mesophytic forest is the most complex and most diverse vegetational type extant.

On the basis of an analysis of the floristic composition of many North American Tertiary floras Wolfe (1969) concludes that as a recognizable vegetational and floristic unit the mixed mesophytic forest in North America developed in the Early and Middle Miocene. Though it is true that also from the American Oligocene already several floras are known which contain some mixed mesophytic genera, though certainly representing warm temperate vegetation these cannot be considered to belong to the mixed mesophytic forest.

However, in continental Asia, notably western Siberia, the mixed mesophytic forest in its typical floristic composition shows up earlier than in America, viz. in the Middle and Upper Oligocene, as can be established from the species lists in the summarizing work by Dorofeev (1963).

In fossil floras belonging to the mixed mesophytic forest type not only many the same genera but also numerous the same species turn up again and again, and hence must doubtless have existed during a great part of the Tertiary. Quite a number persist even up to the present day, whether or not conspecific to Tertiary species. Some of these are well-known relics, such as *Liriodendron*, *Sassafras*, and the ancient conifers *Gingko* and *Metasequoia*, still exclusive constituents of the mixed mesophytic forest, as are *Meliosma alba* and *veitchiorum*. Hence it would be nothing particular to find that these species already were part of the mixed mesophytic forest in Middle and Upper Tertiary, and — as relics — still hold the same position to-day.

3. The three recent species of subg. *Kingsboroughia* are 'senescent' in the sense of Cain (1944). From a historical point of view such species are considered to be relics of ancient floras which once had a wider distribution. They share the following characteristics:

a. Not only do two of the three species have discontinuous areas, but the areas of all three are also conspicuously small, which is quite exceptional in *Meliosma*. It is the more striking if one notices that *Meliosma alba* and *veitchiorum* occur in the same habitats and at the same altitudes, partly also in the same localities as *M. dilleniifolia* and *myriantha* (sect. *Meliosma* subsect. *Simplices* ser. *Rectinervia*), whereas the latter species appear to be much more widespread and common than the former (compare figs. 16 & 17 and 20 & 21). As far as can be judged from the available data, no particular ecological factor can be indicated to be responsible for the difference in distribution between these two groups of species. Even destruction of the natural habitat by human influence can hardly be considered a major cause for the limited occurrence of *M. alba* and *veitchiorum*, since this would have affected the other species too; there are, however, many localities where only *M. dilleniifolia* and *myriantha* have been collected, though these localities seem to be no less suited and accessible for *M. alba* and *veitchiorum*. On the contrary, it is even the very *M. alba* and *veitchiorum* of which the distribution may rather have been influenced positively by man, as these species are in esteem among the Chinese and are spared and even cultivated as ornamental trees. Nevertheless, *M. alba* and *veitchiorum* are usually reported in collectors' notes to be 'nowhere common', 'rare', 'local', or 'scattered' and even 'said to be always sterile in this part of China' (*M. veitchiorum* in N. Honan).

More or less the same can be said with respect to *M. rufo-pilosa*. It is subendemic as the other two species, and not at all common, having been collected at only two localities in N. Borneo and two in the Malay Peninsula. It is restricted to a narrow zone (1000—1500 m) in the lower montane rain forest, a habitat which it shares with the far more common *M. sumatrana* (sect. *Meliosma* subsect. *Pinnatae*), but that species has a wider ecological amplitude, occurring also in the lowland forest. Why is *M. rufo-pilosa* so rare and scattered, whereas there seems to be such ample opportunity for it to spread over adjacent low mountainous areas? Has it lost its former ground and retreated in some isolated sites?

Apparently, *M. rufo-pilosa* as well as *alba* and *veitchiorum* lack the potentialities to expand over adjacent areas, though these offer, as far as can be established with the present knowledge, equally favourable habitats.

b. Ecologically, the species of subg. *Kingsboroughia* are of narrow amplitude, being mountain species strictly bound to definite altitudes.

c. Their morphological characters are remarkably constant in comparison to those of most species of the other sections of *Meliosma*, as can be easily established by comparing their descriptions.

Species that are called 'senescent' on the basis of the properties mentioned, are often supposed to have lost much of their genetic plasticity and adaptation capacity, causing a reduced competitive ability which makes them unsuccessful in the struggle for life and certainly doomed in the long run. Though this unquestionably is an attractive hypothesis, I do not intend here to subscribe such an implicit meaning of the term 'senescent', as no proof has ever been furnished of any plant species having such a reduced genetic system. It is only meant here to produce evidence for the supposition that the species of subg. *Kingsboroughia* are relics of ancient floras, as indeed many of such relics in other groups share the characteristics mentioned above.

d. There is good evidence that subg. *Kingsboroughia*, particularly its sect. *Kingsboroughia* has been richer in species in former geologic periods. The fossil records nrs. 5, 6 and 25, 26 (*M. cantiensis* and *jenkinsii* from the Eocene) belong to this section but not to any of its recent species. This again may be interpreted as an indication that subg. *Kingsboroughia* is an ancient group which has left the peak of its development far behind.

In view of the arguments set forth above it can be hardly maintained that there is any ground to consider the fossils which have been related to *M. alba* and *veitchiorum* to represent independent, now extinct species. In my opinion the evidence is conclusive, and consequently the relevant fossil records will be treated accordingly.

Unfortunately, no fossils are known which could be related to subg. *Kingsboroughia* sect. *Hendersonia*, but this says little, since for various reasons on the whole few fossils have been found in tropical regions. The only known species of this section is, as we have seen, a rare endemic tree, characterized by a remarkable, probably very primitive type of fruit. Therefore it is probable that, just as *M. alba* and *veitchiorum*, also this species is a now isolated survivor of an old group which not only had a much wider distribution in the past but may also have been richer in species. Nothing can be deduced with regard to the former area of this section. The relict status of its *M. rufo-pilosa*, however, is evident enough; in this respect also the locations of its present occurrence are significant (see part I chapter E).

b. The distribution of Meliosma alba and veitchiorum and their relation to the mixed mesophytic forest

In fig. 16 and 17 the localities of *M. alba* and *veitchiorum* are mapped, those of the reliable fossil records included. It is clear that the present distribution of these two species is only a slight remnant of the situation in the past; they are relics in the true sense of the word. During the Upper Tertiary *M. alba* as well as *M. veitchiorum* must have occurred over an immense area, probably covering a wide zone over Eurasia, though, of course, it is not certain that they lived at the same time all over their fossil area. It is notable that they ranged much more northward than they do to-day, at least up to about lat. 50° and 57° respectively. This is in full accordance with paleoclimatological evidence, which indicates that during the Tertiary a much milder climate existed in the temperate zone of the northern hemisphere than is found there at present. The general picture of the climatic history of the Tertiary may be summarized as one of increasing temperatures during the early period, causing the spread of tropical and subtropical vegetation far to the north of their present limits. This climatic maximum was followed, albeit with many oscillations, by a long, slow deterioration of climate which culminated in the extensive glaciation of the Pleistocene period, the onset of which closed the Tertiary era. This general outline is commonly accepted among paleobotanists, and is still regularly corroborated and refined by additional evidence. As for the Late Tertiary in Central Europe, for instance, the many fossil floras which up to now have been analyzed, indicate more than ten rather regular fluctuations, varying from subtropical to temperate conditions, but with an ever increasing accent upon a moist-temperate climate (Szafer, 1946; Mai, 1967).

Judging from the numerous Middle and Upper Tertiary floras which have been found all over northern and middle Eurasia and North America, most of them indubitably of mixed mesophytic character, the mixed mesophytic forest must have covered a wide zone in that part of the world. The fact that it has such a limited occurrence at present is easily explained by the gradual deterioration of climate during the Late Tertiary, causing its southward regression. When the Pleistocene glaciation set in, it could only persist, in more or less depauperated composition, in a few restricted areas where remnants of it are still found to-day.

In this connection another peculiar phenomenon should be pointed out now. It is remarkable that, though the mixed mesophytic forest prevailed in northern and middle North America during the Upper Tertiary, no fossil *Meliosma* has there ever been recorded from that period. Of course it is possible that *Meliosma* did not occur in North America during the Upper Tertiary, but this is not very probable as appears from the following.

One may have noticed that nearly all Eurasian fossil records of *Meliosma* are based upon carpoliths. This kind of fossils, however, has only rarely been collected in North America. Almost all Angiosperm fossils recorded from America are leaf-imprints, and though specimens referable to sect. *Kingsboroughia* may very well occur among these, it is not surprising that they have never been identified, because of their lack of distinctive leaf characters, discussed in chapter A. But, even if there is as yet no fossil evidence of sect. *Kingsboroughia* occurring in America, the fact remains that *M. alba* still grows in a limited area in eastern Mexico (see fig. 16), where it lives in a habitat principally of the same character as the Chinese mixed mesophytic forest, namely the montane rain forest with Oaks and Pines (Knapp, 1965). Of course, *M. alba* did not originate two times and at different places; originally there must have been one single region from which it spread into other areas. Obviously this region can have been nowhere else than somewhere in southeastern Asia where the distributional centre of subg. *Kingsboroughia* is situated (see part I chapter E). Starting from this assumption, how then did *M. alba* reach Mexico? There is not much difficulty in finding an explanation for this question, if one bears in mind the history of the mixed mesophytic forest just referred to. During Middle—Upper Oligocene and Early—Middle Miocene (i.e. the time at which *M. alba* and *veitchiorum* occurred at lat. 50° and 57° respectively; see fig. 16 and 17), forests of mixed mesophytic character reached at times as far north as Alaska and Greenland (there is no disagreement as to this among paleobotanists). Furthermore, according to Hopkins (1967), Beringia lay above sea level throughout most of the Early and Middle Tertiary. Under such conditions, *M. alba* must have had the chance to extend its area up to high latitudes and to migrate via the Beringia land-bridge into the American continent. When, during the Upper Miocene and onwards, the climatic deterioration continued, the Asian and the American part of the population were segregated, and *M. alba* was gradually forced in southward direction, eventually to withdraw into its present Chinese and Mexican refugia under the influence of the Pleistocene glaciations. This part of the history of the distribution of *M. alba* finds its parallel in that of many other mesophytic temperate elements which show a transpacific disjunct distribution causing a close floristic relationship between East Asia and North America. This relationship is especially conspicuous on the generic level (Irmscher, 1922; Hu, 1935; Li, 1952), but there are also several species which have this Asiatic-American discontinuous distribution. Asa Gray (1859), who was the first to point to the affinities between the flora of Japan and (eastern) North America, listed more than fifty of such species. A number of these, however, have afterwards been claimed to represent two or three, often vicarious species (Li, 1952). On the other hand, one may expect new cases to show up as a result of closer taxonomic studies on a wider geographic basis, such as *M. alba* in this paper[1]). In general, however, the floristic relationship mentioned is best illustrated on the generic level. Though in North America most of the temperate, mesophytic, transpacific, disjunct genera are found only in the eastern part, several range much more southward. Some of these, such as *Carya*, *Liquidambar*, *Magnolia*, and *Nyssa*, are even associated with *M. alba* in its present Chinese and Mexican habitat (Knapp, 1965; Wang, 1961). It is striking, however, that *M. alba* does not occur in southeastern North America, where the mixed mesophytic forest is especially well developed, for on the basis of the distribution hypothesis just set forth, one might have expected this species also to occur in that part of the continent, the more so as so many other relic elements of Southeast Asiatic affinities are found there. It does not, however, but it might have been part of this vegetation in former times, and became extinct for some reason or other. In this connection also *M. veitchiorum* should be mentioned, the occurrence of which in America during the Late Tertiary may be considered equally well possible. This species, as well as *M. alba*, may very well turn up sooner or later among American carpolithic fossils, thus providing conclusive evidence for the above hypothesis.

It must be admitted that other migration tracks than that via Beringia could also account for the present disjunct distribution of *M. alba*. If, for instance, at some time in the Middle Tertiary a land connection existed between West Europe and the American continent, *M. alba* and also *M. veitchiorum* must have had the opportunity to migrate along this way into North America. Such a connection is indeed assumed in recent paleogeographical work (Termier & Termier, 1960) for the Paleocene—Eocene, and a narrow strait between the continents during the Oligocene—Miocene. Certainly, many existing European-American disjunct areas of mesophytic elements have come into being along this line, and this possibility must, therefore, be considered for the present case as well. It seems, though, that a former North Atlantic land connection between eastern North America and western Europe is less obvious from zoogeographical and zoopaleontological data (Van Steenis, 1962). However, whether this bridge or the other, or even

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[1]) For instance the East Asian *Menispermum dahuricum* and the eastern North American *M. canadense* may be suspected to be conspecific, considering the futile differences which separate them.

possibly both of them, made possible the migration of *M. alba* and/or *M. veitchiorum*, is not of fundamental importance, as it is obvious from the fossil record that both species may have occurred — though possibly not simultaneously — at both extremities of the Eurasian continent, thus in principle enabling them to enter into America from both sides. Still other migration routes could be fancied, viz. a transatlantic or a transpacific bridge, in some older geologic period, whether or not with the help of continental drifting. It is obvious, however, that for the present case the assumption of such migration routes is highly improbable. Geology does not provide any evidence of transpacific or transatlantic contacts between both continents during younger geologic times, at least not during the Tertiary. To date back the segregation of the Asiatic and the American components of *M. alba* before the Tertiary would demand an unimaginable genetic stability of this species. There is no indication of its existence before the Oligocene, whereas, moreover, the mere specific identity of its Chinese and Mexican populations pleads for their relatively recent segregation.

c. Synthesis

It has been shown so far, that the history of *M. alba* and *veitchiorum* is closely connected with that of the mixed mesophytic forest and can be traced back as far as the Middle Oligocene. Before that period neither these species nor the mixed mesophytic forest are found. In this connection it is important to take cognizance of a most interesting theory on the origin of the mixed mesophytic forest recently advanced by Wolfe (1969) on the basis of a thorough analysis of Tertiary fossil plant assemblages. He noted that not until the Eocene did significant numbers of mixed mesophytic genera become recognizable. These early mixed mesophytic genera of Eocene and Early Oligocene age, however, are mostly not constituents of floras of warm-temperate signature, but quite clearly most of the fossil assemblages in which they occur represent tropical or subtropical vegetation, on physiognomic criteria and overall floristic composition! 'Significant', he says, 'also is the fact that some of these genera (*Platycarya, Tetracentron, Trochodendron, Euptelea, Calycocarpum, Fortunearia*), although apparently widespread in the Paleogene tropical forests, have not been recorded from the mixed mesophytic forest as represented in the Neogene of western North America. The evidence thus indicates that some of the most characteristic genera now endemic to the mixed mesophytic forest attained their widest distribution in the Paleogene tropical forests and not in the Neogene mixed mesophytic forests. The modern distribution of many mixed mesophytic genera and alliances in fact indicates that many are fundamentally tropical or subtropical to-day, the mixed mesophytic representatives being only warm temperate outliers; the following genera exemplify this distribution: *Quercus, Akebia, Cocculus, Calycocarpum, Euodia, Vitis, Liriodendron, Magnolia, Liquidambar, Celastrus, Sageretia, Zizyphus, Alangium, Clethra.* It is, therefore, not surprising that paleobotanical evidence also indicates that many mixed mesophytic genera adapted themselves to warm temperate conditions after attaining a wide distribution in tropical forests during the Paleogene.'

Step by step the development of the North American warm-temperate vegetation can be followed during subsequent geologic periods, until it has acquired the typical floristic characteristics of the mixed mesophytic forests (Wang, 1961). From Wolfe's analysis it clearly appears that most floristic components of the mixed mesophytic forest of the Miocene of North America can be derived from Paleogene tropical and subtropical origin, albeit often in different phases.

A critical analysis like that by Wolfe for the Tertiary fossil floras of North America has never been made for Eurasia. Prominent authors like Kryshtofovitch (1929), Dorofeev

(1963), and Mai (1965) have all started *a priori* from the Arcto-Tertiary concept, which has much obscured objective reasoning. The acceptance of a primary centre of development in the Arctic and Temperate zones during the Upper Cretaceous and Paleo- and Eocene (Dorofeev, 1963; Mai, 1965) did not allow the possibility of close genetical relationships between Arcto-Tertiary floras and Paleo- or Neotropical floras. An unprejudiced analysis of the Eurasian Lower Tertiary floras, however, may prove the Arcto-Tertiary concept to be as invalid for Eurasia as it appears to be for America. Anyhow it is clear that in Siberia much the same overall vegetational development occurred as in Alaska (Wolfe, 1969). Consequently, it will be assumed here that the Eurasian mixed mesophytic forest, instead of being of Arcto-Tertiary origin, has similar complex genetical affinities with Paleogene tropical forests as has been shown by Wolfe for its American counterpart. In its typical floristic composition it shows up earlier in Eurasia than in America; it can already be recognized in Middle Oligocene floras of W. Siberia (Dorofeev, 1963) and somewhat later also in the Upper Oligocene of central Europe (Mai, 1967). According to Mai (1965), based on Kryshtofovitch (1955), these floras of mixed mesophytic character — by this author indicated as Arcto-Tertiary flora — migrated from northeastern Asia to western Eurasia (in this connection it may be significant that *Meliosma europaea* is found in western Siberia in older assemblages than in central Europe!).

Returning now to *Meliosma* sect. *Kingsboroughia*, it has been shown that within this section two groups of fossils can be distinguished. First, there is the group of Paleogene (Lower Eocene) endocarps of southern England which, though quite modern in shape and structure, in general do not show a close similarity to endocarps of recent species. Second, there is the group of mainly Neogene (Middle and Upper Oligocene, Miocene, Pliocene) endocarps of continental Eurasia which could nearly all be referred to either *M. alba* or *M. veitchiorum.*

The first group of Eocene fossils belongs to floras of a definitely tropical character and with very distinct Indo-Malayan relationships (Reid & Chandler, 1933; Chandler, 1964).

It is an established fact that, as in the Eocene of America (e.g. the Wilcox flora, Arkansas, U.S.A.), also in Eurasia tropical vegetation ranged far to the north. There has been much dispute, of course, how far it extended, and for instance Van Steenis (1962) has tried to invalidate Reid & Chandler's conclusions that the fossil material of the Eocene of southern England was autochthonous. It appears, nevertheless, that the best arguments are on the side of Reid & Chandler (Chandler, 1964). The Indo-Malayan character of these floras, however, is undisputed, and could be easily explained by Reid & Chandler on the basis of the widely accepted hypothesis of the existence of the Eocene Tethys Sea which covered the area where are now the Mediterranean, the Alps, the Carpathians, the Balkans, the Atlas, the Sahara, Egypt, Arabia, Palestine, Persia, and the Himalayas to the farthest confines of India (see Termier & Termier, 1960). The northern shores of this warm sea furnished the pathway from Indo-Malaya to western Europe. This hypothesis provides a fine explanation for the problem how tropical (?) montane members of the Southeast Asian-centered subg. *Kingsboroughia* could reach western Europe.

In this connection it is striking that the Eocene fossils do not belong to the presently tropical sect. *Hendersonia*, but to sect. *Kingsboroughia*, of which the two recent species do not occur under tropical, but under warm-temperate conditions. Of course it would be too simplistic to consider this an indication that hence the climate in southern England during the Eocene was warm-temperate rather than tropical. On the contrary: a much better explanation is available, in the form of one of two following alternatives.

First, one can imagine that sect. *Kingsboroughia*, of which the recent species occur under a warm-temperate climate, was a group of (sub)tropical ecology in the Eocene, which subsequently gradually adapted to warm-temperate conditions and became part of the mixed mesophytic forest during the climatic deterioration process in the Oligocene-Miocene.

The second explanation is a variant on the first one. It may be that sect. *Kingsboroughia* partly adapted itself to a warm-temperate climate, and partly remained a group of (sub)-tropical ecology. Such a cleavage would be analogous to the probable evolution process in sect. *Meliosma* subsect. *Simplices* which became subdivided into a 'warm-temperate' ser. *Rectinervia* and a '(sub)tropical' ser. *Curvinervia*. It must then, of course, be assumed that the '(sub)tropical' stock of sect. *Kingsboroughia* got extinct since, which would then explain the absence of a recent parallel of ser. *Curvinervia* in subg. *Kingsboroughia* (compare the maps of the supposed centres of origin of sect. *Meliosma* and subg. *Kingsboroughia* in fig. 7a and b).

Of course both explanations are purely hypothetical, but there is good reason to suppose that one of them is close to the truth, since they do not only well account for the available facts, but are also acceptable from a wider paleobotanical point of view, as may appear from the following.

Returning to Wolfe's hypothesis on the origin of the mixed mesophytic forest, it is repeated again that paleobotanical evidence indicates that many mixed mesophytic taxa adapted to warm-temperate conditions after attaining a wide distribution in tropical forests during the Paleogene. I think that for the understanding of the structure of sect. *Kingsboroughia* in time and space, this conception is highly significant, as the origin of its mixed mesophytic species *M. alba* and *veitchiorum* can be exemplary explained along this line. When in the later Eocene and Oligocene climatic and geographic conditions changed and tropical vegetations could not persist any longer at higher latitudes, some of its constituents became extinct, others withdrew, and still others became adapted to less favourable climatic conditions, the latter being the first constituents of the mixed mesophytic forest such as it becomes gradually better recognizable during the transition from Paleogene to Neogene. It is probable that, similarly, one or two Eocene tropical species of sect. *Kingsboroughia* were the ancestral stock from which *M. alba* and *veitchiorum* developed and became part of the mixed mesophytic forest.

Thus the seemingly incoherent situation of a sect. *Kingsboroughia* occurring under more or less tropical conditions in the Eocene, but being at present a group of exclusively warm-temperate ecology, finds a satisfactory explanation which is in full conformity with the above hypothesis on the origin of the mixed mesophytic forest.

2. SUBGENUS MELIOSMA

a. Combination of fossil and recent taxa

Unlike in subg. *Kingsboroughia*, of subg. *Meliosma* not only fossil endocarps have been found, but also fossil leaves. The fossil endocarps belonging to subg. *Meliosma* (chapter B, nrs. 27, 29, 31, 32, 34, 36, 37) are all definitely referable to sect. *Meliosma*; as far as I know none of sect. *Lorenzanea* have as yet been found. The fossil leaves, on the other hand, are referable to both sect. *Meliosma* and sect. *Lorenzanea*, but not to sect. *Meliosma* subsect. *Pinnatae*. This absence from paleobotanical records of fossil endocarps of sect. *Lorenzanea* and of fossil leaves of sect. *Meliosma* subsect. *Pinnatae* is not a serious inadequacy, for reasons given in chapter A.

Of the fossil endocarps known to belong to sect. *Meliosma* the numbers 27, 31, 36, 37 could not be differentiated to belong to any subsection, series, or species group in particular; they are found in Europe and date from the Lower and Middle Tertiary.

On the other hand, the numbers 29, 32, 34, including only Upper Tertiary and Quaternary endocarps, all found in Japan (Kyushu, Honshu), are referable to the recent species *M. myriantha* and *M. simplicifolia* ssp. *rigida* of subsect. *Simplices*. It is worthy of note that these taxa which grow at the present time in Japan already occurred there during the Pliocene and Pleistocene.

The first group of older European endocarps, however, described as *M. miessleri* (Miocene), *M. reticulata* (? Oligocene), and *M. sheppeyensis* (Lower Eocene), provide evidence of a more important level. They prove that sect. *Meliosma* already existed in the Lower Eocene, in which period its area must have extended as far north and west as southern England, and that it must have occurred in W. Europe up to in the Miocene. Furthermore, it appears that shape and structure of these fossils do not differ from those of still living species.

The identification of fossil leaves as belonging to *Meliosma* is not so reliable as that of endocarps, but in several cases the correctness of such identifications can hardly be doubted, since fossil and recent specimens are often almost identical and good alternative possibilities could not be found. This only holds, however, for the oblanceolate dentate leaf-type, with characteristic '*Meliosma* nervation and venation', since this has a fairly high diagnostic value. Just as in the fossil endocarps, it is striking that the leaf-imprints involved are so well in agreement with those of living species, even those from the Lower Eocene.

As we have seen in the previous chapter, the leaf-imprints under the numbers 3, 23, 24, 30, 38, 41, and 42, could be related with reasonable certainty to *Meliosma*, those under the numbers 9, 28, 33, and 35 being more dubious. Unlike in the fossil endocarps, these leaf-imprints have almost all been found in North America, hence it is interesting to know whether they belong to the American sect. *Lorenzanea* or possibly also to the SE. Asian sect. *Meliosma*; as will be pointed out later, there is good evidence to assume that these sections already existed in the Lower Tertiary. Unfortunately, it is generally very difficult to establish to which section the leaf-imprints belong, because of the very low degree of differentiation between the leaf-types of these two sections. There are, however, enough leaf features to assume that representatives of both sections are involved in the American material; the match is for most fossil leaves even better with recent forms from SE. Asia than with those from America. This particularly holds for the imprints described as *M. truncata* (nr. 38) and undescribed material from Alaska (nr. 41), and to a less degree also for the *M. aesculifolia* (nr. 3) and *M. goshenensis* (nr. 23, 24) fossils. On the other hand, *M. predentata* (nr. 30), the dubious *M. rostrata* (nr. 33), and undescribed material from Susanville, California (nr. 42) can be matched best against leaves of species of the American sect. *Lorenzanea*. From this I get the strong impression that in the Lower and Middle Tertiary of North America representatives occurred not only of the purely American sect. *Lorenzanea*, but also of the SE. Asian sect. *Meliosma* subsect. *Simplices*. Since fossil leaves are not quite conclusive in this respect, a final proof can only be provided by fossil endocarps from America. It is regrettable that up till the present so few carpolithic collections have been made in this continent; moreover, the only published fossil endocarp related to *Meliosma* (*M. californica*, discussed under nr. 4) is of dubious character. However, Mr. J. A. Wolfe, Menlo Park, Cal., informed me that *Meliosma* endocarps in a still unpublished collection from the early Oligocene Clarno nut-bed flora of Oregon (coll. Scott, Denver), all have characters diagnostic of the paleotropical species! Unfortunately, I did not receive further information upon a request in order to find out whether these endocarps belong to subg. *Kingsboroughia* or to subg. *Meliosma*.

If ever the SE. Asian sect. *Meliosma* subsect. *Simplices* occurred in North America, just as the SE. Asian sect. *Kingsboroughia* (see chapter B sub 1), the question arises along

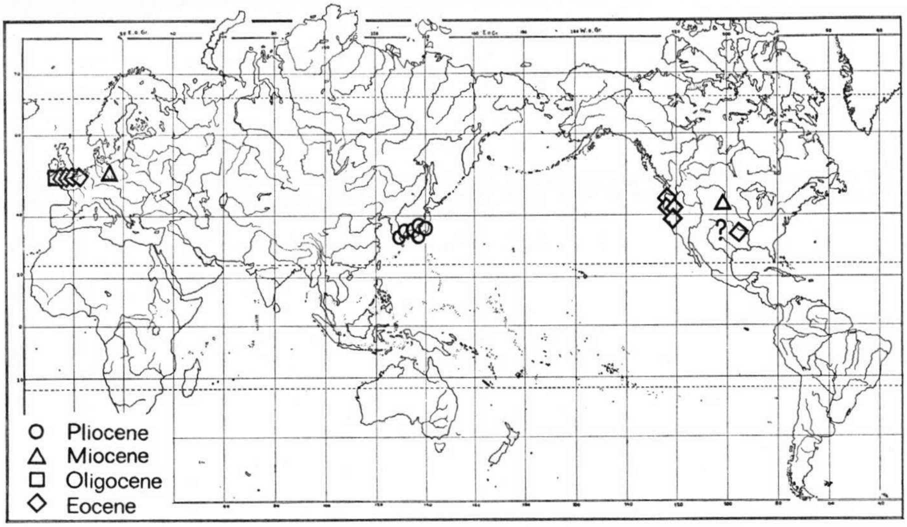

Fig. 18. Distribution of fossils related to *Meliosma* subg. *Meliosma*. Amercan localities all refer to finds of fossil leaves, Eurasian localities almost all to fossil endocarps.

which pathway and under what climatical conditions it may have migrated into this continent. In this connection the fossil assemblage from Alaska in which leaves occur which have been related to *Meliosma* (chapter B, nr. 41) is of primary importance (see fig. 18). If these leaves really belong to sect. *Meliosma* subsect. *Simplices*, which is very probable, this would mean that, at some time in the Eocene, members of a group now living under tropical to subtropical conditions (in Central China north to *c.* 30° N and in Japan to *c.* 36° N) passed Beringia (*c.* 60° N) and entered the American continent. The question may be posed then what climatical conditions may have existed at that high latitude at the time of this migration.

b. Arcto-Tertiary climate and possible migration via Beringia

As has been discussed in chapter A, one of the most valuable sources of information concerning paleoclimates are fossil leaf assemblages. The fossil leaf assemblage from the Early Ravenian of the Gulf of Alaska region, in which the probable occurrence of *Meliosma* sect. *Meliosma* has been established (see chapter B, nr. 41), has an entire leaf margin percentage of 65; this figure was based on 62 dicot. species (Wolfe, 1969). In terms of the percentages discussed previously (chapter A), the Lower Ravenian assemblage represents neither tropical rain forest nor subtropical forest, but the percentage is intermediate between that for the paratropical rain forest of Hongkong and that for the paratropical rain forest of Taiwan. Other assemblages from the Gulf of Alaska region, from Middle and Upper Ravenian (latest Eocene) and Kummerian (early Oligocene), have entire leaf margin percentages of respectively 54 (37 dicot. species), 20 (20 dicot. species), and 55 (± 18 dicot. species), thus indicating cooler climates. Also the floristic composition of the Lower Ravenian and the other assemblages is well corresponding with the supposed climates (Wolfe, 1969). If we accept Wolfe's criteria of floristic and physiognomic analysis of leaf assemblages, the conclusion cannot be escaped that during the Lower Ravenian (Low Upper Eocene) a broad-leaved evergreen forest flora existed in the Gulf of Alaska region, according to Wolfe suggesting paratropical climatic conditions. This discovery is of great importance for plant-geographic theories, since the existence at such a high latitude of a sub- or paratropical climate has always by many been considered an impossibility. One may also wonder why such a flora would never have been discovered before at such high latitudes, the more so as extensive previous work has been done on fossil Tertiary plants from Alaska, notably by Knowlton (1894) and Hollick (1936). In a very interesting historical survey Wolfe (1969) demonstrated how these and other authors dealing with high latitude Tertiary floras *a priori* started from certain historically grown theoretical ideas about Tertiary vegetation and floras which were largely based on misinterpretations of age and sequence of florules. These views gradually led towards a current Arcto-Tertiary concept, nowadays accepted as an undisputed fact by many paleo- and neobotanists (see p. 409). Prejudices resulting from this concept have often influenced ecological interpretation and dating of Tertiary leaf assemblages, which caused a serious loss of objectivity. Hence such floras from high latitudes were taken for granted to have grown under temperate to warm-temperate climatic conditions. This assumption was indeed corroborated by the ecological picture one could get from a superficial study of mixtures of fossil assemblages which grew under cold to warm climates. Nevertheless it appears that most authors were more or less aware of the complexity of the Tertiary Arctic floras, but this feature was not ascribed to great climatic fluctuations, but mainly to differences in latitude and altitude, e.g. by Chaney (1936, 1938, 1940), who most thoroughly discussed Arcto-Tertiary theories. Stratigraphic differentiation between the numerous Tertiary plant assemblages from high latitudes mostly was either erroneous, or was seriously neglected. An example of this view appears for instance from a passage as '.... all of the Tertiary Arctic floras are essentially similar in age, although it is clear that in Spitzbergen, Alaska, and probably elsewhere, more than a single horizon is represented' (Berry, 1930b: 10).

It is clear that many authors did not have an unprejudiced mind while drawing their conclusions. As in other sciences, in paleobotany objectivity is of eminent importance; floral history can only be unravelled by keeping individual fossil assemblages apart when comparing their floristic compositions and foliar physiognomics, before making a more generalized synthesis on the basis of accurate stratigraphic correlation.

The pioneer work by Wolfe (1969) along the last-indicated line of research has consequently shed a new light upon the Tertiary floras of North America. The evidence from his work on the Alaskan Tertiary floras, in addition to a considerable amount of data from other sources, strongly suggests that Tertiary climates were subject to several periodical, often rather rapid fluctuations, in response to which vegetations considerably changed in floristic and vegetational aspect. The effect of these fluctuations was of course more pronounced at high than at middle latitudes and more at middle than at low altitudes. In Alaska this agrees with differences between leaf margin percentages for the warm late Eocene and cool latest Eocene of about 45, and of the cool latest Eocene and warm early Oligocene of about 35, suggesting climatic fluctuations from paratropical to temperate to subtropical within a relatively short period. This picture, now revealed, makes full allowance for the possibility that SE. Asian plant taxa of subtropical to paratropical ecology migrated into the American continent via Beringia. In this connection it should be noted that the Alaskan Lower Ravenian leaf assemblage shows overwhelmingly paleotropical affinities (Wolfe, 1969). Thus the facts observed in the previous paragraph come to fit in a coherent framework. The occurrence of *Meliosma* leaves in the Eocene leaf assemblages from North America, which show closer morphological relationships with the Asian sect. *Meliosma* than with the American sect. *Lorenzanea*, now finds a plausible explanation. Since also sect. *Lorenzanea* must have had a much more northern distribution, especially during very warm intervals in the Lower Tertiary, it is well possible that at times representatives of both sections were part of the same floras. The possibility cannot even be excluded that species of sect. *Lorenzanea* migrated into Asia, though this is less probable because of its definitely more tropical ecology.

Though, as has been said before, fossil leaves are the only testimony as yet of the occurrence of sect. *Meliosma* in the Tertiary of America, there are good indications in support of that assumption. This would mean that after its Early Tertiary expansion to North America it became extinct during the subsequent regression.

Its distributional history would then resemble that of sect. *Kingsboroughia* which I also assume to have had its origin in Asia and expanded its range via Beringia to North America, with two differences, viz. (i) that its migration took place at a later period of the Tertiary, and (ii) that it maintained a foothold in Mexico (*M. alba*) as relict of this migration.

D. FINAL CONCLUSIONS AND CONSIDERATIONS

One of the most important conclusions which can be drawn from the fossil evidence is that subg. *Kingsboroughia* sect. *Kingsboroughia* and subg. *Meliosma* sect. *Meliosma* subsect. *Simplices* already existed in fully recognizable form in the Eocene. There is, moreover, some evidence from fossil leaf-imprints that also subg. *Meliosma* sect. *Lorenzanea* may already have been present at that time. Whether subg. *Kingsboroughia* sect. *Hendersonia* already occurred in the Eocene is not known but this is very probable, because its fruit characters are assumed to be more primitive than those of sect. *Kingsboroughia*, which was indeed already present in the Eocene. An additional argument in support of this is found in the assumed homology of the bicentric areas of subg. *Kingsboroughia* and subg. *Meliosma* sect. *Meliosma* (see part I chapter E); if in the Eocene sect. *Meliosma* was already subdivided into the subsections *Simplices* and *Pinnatae*, which is almost certain (see above), a similar subdivision would then probably as well have been the case in subg. *Kingsboroughia* because of the said assumed homology between the areas of the two subsections of sect. *Meliosma* and of the two sections of subg. *Kingsboroughia*. Consequently I assume that in the Eocene not only those sections and subsections existed of which fossils bear testimony, but also those of which fossil evidence is still wanting.

The question might be posed how subg. *Meliosma* sect. *Lorenzanea* may have reached America. It should be stated first that it is very improbable that this section split off from subg. *Meliosma* in the early Tertiary and then migrated into America via Beringia, as may have been performed by some species of sect. *Meliosma*. The following arguments plead against this: Though SE. Asia is obviously the most important centre of *Meliosma*, harbouring three of the four sections (and also the probably related genus *Sabia*), also Central America is probably an old centre of development of admittedly fewer, but not less significant taxa of *Sabiaceae*, viz. not only of sect. *Lorenzanea* but also of the interesting endemic genus *Ophiocaryon*, which is certainly closely related to *Meliosma*, showing a remarkable parallel development with that genus on the one hand, and more primitive characters on the other. The presence in tropical America of such a closely related, but well characterized genus with a set of important characters — in several respects intermediate between *Meliosma* and *Sabia* — cannot be plausibly explained by a migration via Beringia, which would have taken place proportionally so recently as in the early Tertiary; it much more pleads for the presence of an ancient Sabiaceous foothold in America of more primary nature. Furthermore, as said before, sect. *Lorenzanea* is morphologically equivalent to sect. *Meliosma*; since it appears to be probable from the fossil evidence that the latter section had already differentiated to a considerable extent in the early Tertiary, there is no reason to assume this to be different for sect. *Lorenzanea.* Moreover, as noted above, there are some indications that also sect. *Lorenzanea* was already present in the Eocene of America. A migration from SE. Asia into America in the early Tertiary would therefore not be well in agreement with its probable rather advanced degree of differentiation at that same period. Furthermore, from a preliminary investigation of material of sect. *Lorenzanea* I get the strong impression that the centre of differentiation and dispersal of its species is situated in Central America.

On the basis of these arguments I assume that sect. *Lorenzanea,* as well as the genus *Ophiocaryon,* are autochthonous American taxa, which were already present there before the Eocene, probably already long before the Tertiary.

It is another problem how the transpacific disjunction between subg. *Kingsboroughia* and subg. *Meliosma* sect. *Meliosma* on the one hand, and subg. *Meliosma* sect. *Lorenzanea* and the allied genus *Ophiocaryon* on the other, should be explained. From the relatively wide morphological gap between *Meliosma* and *Ophiocaryon* and the relatively narrow one between sect. *Meliosma* and sect. *Lorenzanea,* it might be logically concluded that the origin of *Meliosma* and *Ophiocaryon* dates from a rather more remote past than that of sect. *Meliosma* and *Lorenzanea.* This could suggest that the ancient connection between SE. Asia and Central America may have been of rather long duration. This is well corresponding with the conclusions of Van Steenis (1962: 345) who considers that 'the tropical transpacific bridge must, it seems, have been very ancient and effective — by size and duration — . . . .'. However, as in several other transpacific disjunct genera, there is no indication of a linkage between sect. *Meliosma* and sect. *Lorenzanea* via the Pacific. The most eastern localities of sect. *Meliosma* are found in New Guinea and New Britain; however, the East Malesian part of sect. *Meliosma* is represented by only one species, *M. pinnata,* the eastward expansion of which is probably of relatively young age. Moreover, this species belongs to subsect. *Pinnatae,* whereas it is much more the continental SE. Asian subsect. *Simplices* which shows the closest morphological relationship to sect. *Lorenzanea.* These facts hence rather suggest *a former, direct contact between SE. Asia and Central America, which became later broken,* than a linkage by way of migration via East Malesia and the Pacific.

The historic differentiation process of *Meliosma* into its recent morphological and distributional state of development has now been traced back as far as possible. A schematic reconstruction of the main phases of this differentiation has been attempted in fig. 19.

Phases I—IV of fig. 19 are purely hypothetical. They represent the main steps by which the genus *Meliosma* may have developed before the Tertiary period. Starting from a basic proto-*Meliosma* (phase I) the first differentiation that probably took place resulted in the origin of two taxa, A and B (phase II), respectively representing the predecessors of subg. *Kingsboroughia* and subg. *Meliosma,* which still are the most fundamentally different groups.

In phase III the subdivision of subg. *Meliosma* into sect. *Meliosma* and sect. *Lorenzanea* has come about, which may have been induced by, anyhow coincided with, the definite isolation between the SE. Asian and the central American parts of the genus. It is assumed that from then on the SE. Asian and central American centres of development became independent. From the probable homology between the present SE. Asian areas of subg. *Kingsboroughia* and sect. *Meliosma* (see part I chapter E), a simultaneous differentia-

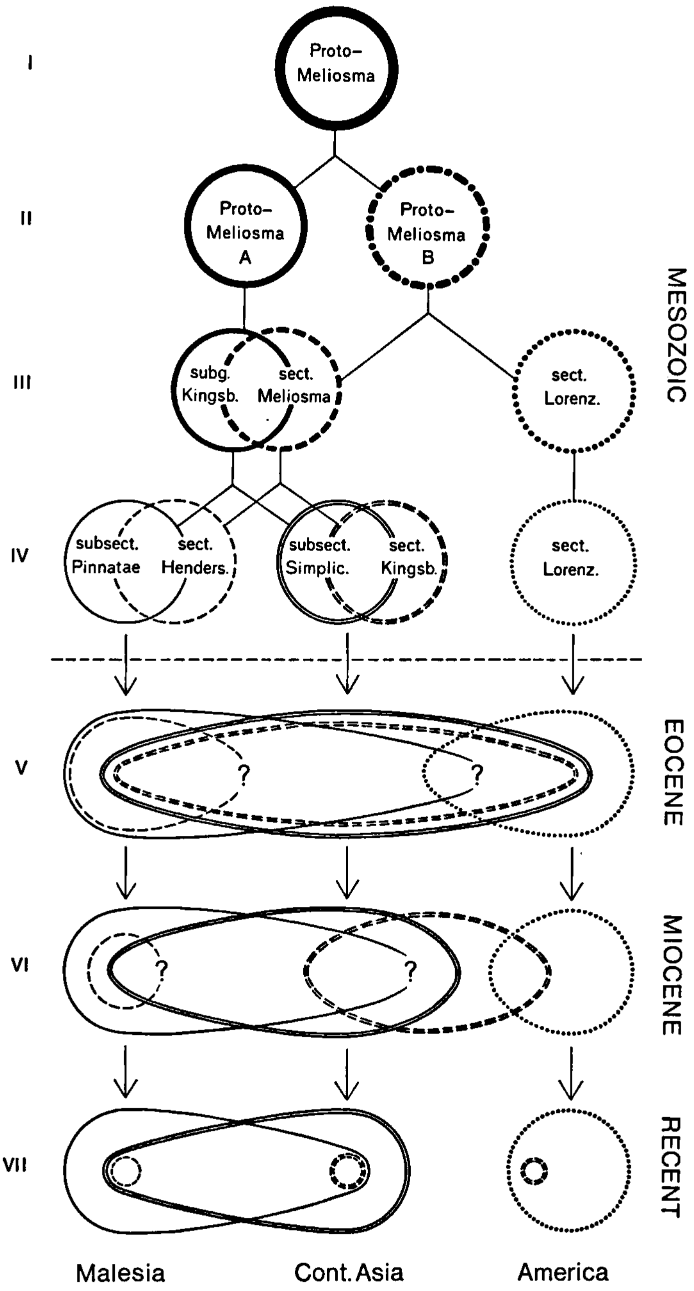

Fig. 19. Schematic reconstruction of the main phases of differentiation and distribution in *Meliosma*. Phases I—IV hypothetical, phases V—VII partly hypothetical, partly based on fossil evidence. See the text.

tion of these groups is assumed to have taken place into sect. *Kingsboroughia* and sect. *Hendersonia*, and subsect. *Simplices* and subsect. *Pinnatae* respectively (phase IV). Sect. *Lorenzanea* did not differentiate any further on subsectional level, probably because it possessed only a small part of the gene-pool of the genus.

The next three phases give the outlines of the history of *Meliosma* from the early Tertiary up to the present. This part of the scheme is partly hypothetical, partly based upon fossil evidence. The starting point is that in the early Eocene sections and subsections already existed, for which arguments have been given earlier in this chapter. In phase V is shown how in the Eocene the continental SE. Asian sect. *Kingsboroughia* and sect. *Meliosma* subsect. *Simplices* are supposed to have attained a wide distribution, both covering a wide zone of Eurasia, and the former possibly, the latter very probably entering North America via Beringia. Nothing is known about the Eocene distribution of the Malesian sect. *Hendersonia* and sect. *Meliosma* subsect. *Pinnatae*, but it may be assumed that also these taxa expanded far northward as a result of the favourable climatic conditions, just as probably did the American sect. *Lorenzanea*, of which the fossil evidence indicates that it extended far into North America, probably partly overlapping there the area of sect. *Meliosma* subsect. *Simplices*.

After this peak in the distributional history of *Meliosma* the gradual climatic deterioration during the middle Tertiary caused a shrinking of the various areas, although it is certain that fluctuations occurred. During a cool interval in the Miocene, for example, the distribution of *Meliosma* may have had the schematical pattern as shown in phase VI. All sections have then withdrawn considerably, though still occupying larger areas than they do at present. Only sect. *Kingsboroughia* still covers a wide circumpolar zone on the northern hemisphere, because this section — partly or entirely — adapted to the warm-temperate conditions that favoured the enormous spreading of the mixed mesophytic forest type in the later Tertiary (see chapter C sub 1). It is possible that also sect. *Meliosma* subsect. *Simplices* ser. *Rectinervia* had a similar wide distribution as had sect. *Kingsboroughia* in the later Tertiary. This series has at present similar warm-temperate climatic requirements as has sect. *Kingsboroughia*, and, as we have seen in part I chapter E, its probable centre of origin is located in the same region as that of sect. *Kingsboroughia*. Hence it might be supposed that the later Tertiary expansion of these groups followed homologous patterns; however, no fossil evidence of ser. *Rectinervia* is present to support this.

Then, at the onset of the Quaternary period with its Pleistocene glaciations, the above distributional pattern was definitively destroyed, and the various areas shrunk to their present size and location (phase VII). Sect. *Kingsboroughia*, still widely distributed as late as the Pliocene (see chapter C sub 1), retreated to its present Chinese and Mexican relict stations, while also its tropical counterpart sect. *Hendersonia* retained a typical relict position in W. Malesia. Sect. *Meliosma* and sect. *Lorenzanea*, on the other hand, have until the present remained widespread groups, though also their areas have shrunken to a considerable extent when compared to the early Tertiary situation. For this, however, climatical causes may be held solely responsible, which, however, cannot so easily account for the excessive retreat of subg. *Kingsboroughia* into a few isolated localities. It is not quite clear why this group has been so much less successful as compared with subg. *Meliosma*; this remarkable phenomenon has been discussed in chapter C sub 1.

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PART III. SPECIAL PART

PRESENTATION OF DATA

The arrangement of the taxa is more or less in an order that reflects their supposed relationships.

A full synonymy is given of each taxon recognized, including all relevant published names I could find, which are arranged firstly according to synonymous basionyms in chronological order, then to homotypical synonyms, also chronologically.

Literature references under each name are given as complete as possible. Only literature of which I considered the information value neglectably low has been omitted.

All types are mentioned, as well as the herbaria from where I have seen them. The abbreviations of these herbaria are in accordance with Index Herbariorum, 5th ed. (1964). Lectotypes have only been designated for taxa accepted in this revision, not for synonyms.

In species subdivided into subspecies, full references and typification are given under the latter; under such species only the synonyms are mentioned. I have deviated here from the usual practice, because the subspecies represent the units which will be mostly dealt with in local floristic practice, instead of the species.

Lists of specimens examined are not given, because the available space and time did not allow to do so. They will be published soon after this revision in a separate list and as Nr. 42 of the Flora Malesiana 'Identification Lists of Malesian Specimens', so that verification of my identification of specimens will be possible. This omitting of specimens lists does not mean much loss of essential information, since I have conscientiously summarized and evaluated geographical, ecological, and other data on the labels.

The distribution of each taxon is briefly indicated, into increasing detail according as the taxa involved are of lower systematical rank. Only reliable data have been included, rarely also from literature. Distribution maps are given of all taxa above variety rank; when ample data were available, a generalized outline of the area has been drafted, when not, every known locality has been indicated by a mark.

Under the heading 'Ecology' a summary is given of all reliable data I could find. Moreover, the ecological evidence is often discussed in the remarks to the taxa, mostly in combination with the distribution.

Field notes have been compiled from collectors' labels and from literature, and are summarized under the relative heading. Of course this information is mostly far from complete, and may not always be correct in every detail. The same holds for data mentioned under 'Uses'.

Vernacular names have not been selected on reliability, and are taken from every source I could find. Only now and then a reference is mentioned to literature comprising fairly long lists of names. Generally I cannot vouch for the correct spelling and application of these names.

The remarks to the taxa are often rather elaborate; they contain all taxonomic, distributional, and ecological topics which I considered relevant for a proper insight into the structure of the taxon involved. The remarks are thus an essential part of this revision.

GUIDE TO THE USE OF TECHNICAL TERMS IN KEYS AND DESCRIPTIONS

1. Leaves

a. In the length of leaflets and leaves the narrow apical parts of acuminate, cuspidate, or caudate leaf apices or long-attenuate leaf bases are *not* included.
b. By the term 'index' is meant the ratio of length and width of the blade (see a.) of leaf or leaflet.
c. In many taxa said to have entire leaves or leaflets, teeth may occasionally to regularly occur in leaves lower on the branches, very often in leaves of watershoots (in important cases this is especially mentioned in the text).
d. In taxa said to have glabrous leaves, some pubescence may occur on very young leaves; conversely, in taxa with pubescent leaves, leaves may often be more or less glabrescent when older (in important cases this is especially mentioned in the text).
e. In taxa with impressed midrib this character may sometimes be somewhat obscured when the midrib is pubescent. Very young leaves of taxa said to have the midrib impressed may sometimes show a flat to somewhat prominent midrib; as a general rule the impression of the midrib becomes more distinct as the leaves are older.

2. Inflorescences

a. In most taxa with terminal panicles, lateral panicles may rarely occur as an anomaly.
b. In some taxa to the term 'primary side-axes' is added between brackets: 'essentially secondary'; this refers to cases in which by a reduction process the main axis is no longer recognizable as such, and one or more primary side-axes have adopted the habit of a main axis (see fig. 1).
c. Bracts; see 3 c.

3. Flowers

a. For a reliable diagnosis of flower characters it is usually advisable to analyze not one, but a few flowers of a plant (usually there are plenty of them).
b. Mature buds can be recognized as such by the stage of full development of the anthers; the pollen is then ripe, and the anther-cells often have already dehisced.
c. Sessile flowers are situated in the axil of a bract which often joins the sepals and may be extremely similar to these; they should not be confused. For instance, in taxa said to have glabrous sepals, the bracts are often pubescent.
d. In the number of sepals is also included the outermost sepal when this occurs lower on the pedicel, adopting bracteole habit.
e. In most taxa the sepals are always more or less ciliolate-fimbriate on the margin (this character has no diagnostic value!); if this is the only form of pubescence, the sepals are called glabrous. They are considered pubescent only when hairs occur on their surface.
f. Whether the ovary is glabrous or pubescent can usually also be checked on specimens in fruit. If these had flowers with pubescent ovary, there is usually still visible a minute hairy patch, often attended with a style remnant, on the base of the fruit, close to the insertion of the pedicel (cf. fig. 28d).

4. Fruits

a. Measurements of fruits and endocarps, marked with the symbol 'ø', are always taken across, perpendicular to the plane of the median keel (see the notes on the topography of the endocarp on p. 365).

MELIOSMA

Bl., Cat. (1823) 32; Nees, Flora 8 (1825) 105; Endl., Gen. Pl. (1840) 1074; Bl., Rumphia 3 (1849) 196; Lindl., Veg. Kingd. ed. 3 (1853) 385; Planch., Ann. Sc. Nat. Bot. sér. 4, 3 (1855) 295, *in obs.*; Miq., Fl. Ind. Bat. 1, 2 (1859) 612; Benth. & Hook. *f.*, Gen. Pl. 1 (1862) 414; Baillon, Hist. Pl. 5 (1874) 346, 393, *pro parte, excl. Phoxanthus et Ophiocaryon*; Hook. *f.*, Fl. Br. Ind. 2 (1876) 3; Boerl., Handl. 1, 1 (1890) 290; Urban, Ber. Deut. Bot. Ges. 13 (1895) 211, t. 19; Warb. in E. & P., Nat. Pfl. Fam. 3, 5 (1895) 371; King, J. As. Soc. Beng. 65, ii (1896) 455; Urban, Symb. Ant. 1 (1900) 503; K. & V., Bijdr. 9 (1903) 115; Lecomte in Fl. Gén. I.-C. 2 (1908) 3; Ridl., Fl. Mal. Pen. 1 (1922) 513; Cufod., Oest. Bot. Z. 88 (1939) 246; How, Acta Phytotax. Sin. 3 (1955) 421; Cuatr. & Idrobo, Caldasia 7 (1955) 187; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 18; Back. & Bakh. *f.*, Fl. Java 2 (1965) 144. — Lectotype species: *M. lanceolata* Bl.

Millingtonia Roxb. [Hort. Beng. (1814) 3, *nomen*] Pl. Corom. 3 (1820) 50, t. 254, *non* Linn. *f.* (1781), *nec* Donn (1807); Fl. Ind. 1 (1820) 102; Schult. & Schult., Syst. Veg. Mant. 1 (1822) 68; ibid. 3, add. 2 (1827) 217; W. & A., Edinb. New Phil. J. 15 (1833) 178; Prod. 1 (1834) 115; Jack, Hook. J. Bot. 1 (1834) 377; Wight, Ic. 1 (1840) 142; Endl., Gen. Pl. (1840) 1074; Planch., Ann. Sc. Nat. Bot. sér. 4, 3 (1855) 295 ('*Mellingtonia*'). — Type species: *Millingtonia simplicifolia* Roxb.

Wellingtonia Meisn., Pl. Vasc. Gen. (Comm.) 2 (1840) 207, *in nota*; ibid., add. (1843) 346, *in synon.* — Type species: *Millingtonia simplicifolia* Roxb.

Kingsboroughia Liebm., Vid. Medd. Nat. For. Kjøbenhavn 2 (1850) 67; Walp., Ann. 3 (1852) 834; Lindl., Veg. Kingd. ed. 3 (1853) 385; Planch., Ann. Sc. Nat. Bot. sér. 4, 3 (1855) 295. — [*Llavea* Planch., Fl. Serres 5 (1849) 533c, *nomen, non* Lagasca (1816); Ann. Sc. Nat. Bot. sér. 4, 3 (1855) 295, *pro synon.*] — Type species: *Kingsboroughia alba* (Schlechtend). Liebm. = *M. alba* (Schlechtend.) Walp.

Lorenzanea Liebm., Vid. Medd. Nat. For. Kjøbenhavn 2 (1850) 69; Walp., Ann. 3 (1852) 835; Planch., Ann. Sc. Nat. Bot. sér. 4, 3 (1855) 295 ('*Lorenzeana*'); Hemsl., Biol. Centr. Am. 1 (1880) 216; Urban, Ber. Deut. Bot. Ges. 13 (1895) 211, *in nota.* — Lectotype species: *Lorenzanea glabrata* Liebm. = *M. glabrata* (Liebm.) Urb.

Oligostemon Turcz., Bull. Soc. (Imp.) Nat. Mosc. 31 (1858) 447, *non* Benth. (1865); Fedtsch., Svensk Bot. Tidskr. 19 (1924) 494. — Type species: *Oligostemon schlimii* Turcz.

Heterapithmos Turcz., Bull. Soc. (Imp.) Nat. Mosc. 32 (1859) 265; Fedtsch., Svensk Bot. Tidskr. 19 (1924) 493 ('*Heteropithmos*'). — Type species: *Heterapithmos floribunda* Turcz.

Atelandra Bello, An. Soc. Esp. Hist. Nat. 10 (1881) 289, t. 5, *non* Lindl. (1839). — Type species: *Atelandra laurina* Bello.

Evergreen or sometimes deciduous trees or shrubs, rufous-pubescent to glabrous. *Twigs* more or less lenticellate, often with conspicuous leaf-scars. *Buds* densely pubescent. *Leaves* simple or imparipinnate with subopposite leaflets; leaves or leaflets entire or dentate, with or without hairy domatia beneath; rachis and petioles, usually also petiolules, with a usually shallow and narrow, more or less conspicuous longitudinal groove above, usually with swollen base, articulately attached. *Inflorescence* terminal, sometimes axillary, a pyramidal panicle, poor to usually profuse, up to 4 times ramified, with alternate, articulately attached, often lenticellate axes. *Bracts* small, those of lower order usually soon caducous; cataphylls often present. *Bracteoles* absent, but sometimes one (or two) bracteole-like sepals present, lowered on the pedicel. *Flowers* numerous, sessile or short-pedicelled, small to minute, hermaphrodite, zygomorphic. *Sepals* 5, by reduction sometimes 4, rarely 3, sometimes by addition of empty bracts seemingly more, up to *c.* 13, and together forming a kind of involucre, equal or usually unequal and then mostly 3 about equal. *Petals* 5; 3 outer ones more or less unequal, mostly suborbicular and convex, rarely the largest one much wider than long and more or less reniform, the smaller ones irregularly shaped; 2 inner ones equal, much smaller, reduced, opposite the fertile stamens and more or less adherent to the base of the filaments, entire to bifid. *Disk* generally present, sometimes very reduced or absent, often irregularly shaped, as a rule with 5 more or less developed teeth, 4 of which paired, 1 unpaired, each pair opposite a fertile stamen. *Stamens* 5; 2 fertile, filament short, strap-shaped, flat, glabrous, incurved at the top, abruptly terminating in a wide varyingly shaped cup which bears two globose to elliptic transversely dehiscent anther-cells which are ripe in bud, springing back elastically when the flower opens; 3 staminodial, opposite the larger petals and more or less adherent to the base of these, deformed, broad, irregularly shaped, with 1 or 2 holes near the top in which fit the anther-cells of the fertile stamens, often coherent and forming a cup over the pistil. *Ovary* globose to ovoid or conical, 2-, very rarely 3-locular, apically contracted in a rather short, simple or 2-partible, cylindric or subulate to conical, rarely minute style, with simple or somewhat bifid, minute stigma; ovules 2 (1) in each locule, more or less superimposed, attached to the partition, hemi-anatrope. *Fruit* a drupe, subglobose to pyriform, small, glabrous, with one stone[1]); mesocarp pulpy, mostly thin; endocarp globose, pyriform, or semiglobose, 1-celled, stony to crustaceous, splitting in two valves, inside with a basilar rounded projection over which the seed is curved. *Vascular bundle* connecting pedicel and seed either running outside the endocarp wall (free in the pulpy mesocarp or in a groove on the ventral endocarp wall), or through a canal inside the endocarp wall. *Seed* sub- to semiglobose, more or less concave at the ventral side, with membranous testa, without endosperm. *Embryo* with rather long, two to three times folded radicle and more or less folded cotyledons.

Distribution: About 20—25 species, 15 of which in SE. Asia, and not more than *c.* 10 species in Central and South America. — Fig. 5.

The New World species belong to *Meliosma* subg. *Meliosma* sect. *Lorenzanea* which section is restricted to the New World; besides, there is one species of subg. *Kingsboroughia* which is widely spread in Asia but occurs also in Mexico (*M. alba*).

Correctly named fossils from the Tertiary are found widely distributed on the northern hemisphere, in Europe, Asia, and North America.

Ecology: In primary and secondary forests, especially in hills and mountains up to *c.* 3300 m, but also in lowlands. All or almost all species prefer everwet to moist, tropical to subtropical conditions. Some are hardy in mild temperate climates; these are deciduous and grow flush-wise.

Remarks. *Meliosma* can be subdivided into two subgenera which are well distinct and take very characteristic different positions, systematically and geographically; these subgenera, *Meliosma* (see below) and *Kingsboroughia* (see p. 516), can be identified with the key to the species. Only the Old World species of the genus are treated here.

I. Subg. MELIOSMA

Meliosma Bl. — *Millingtonia* Roxb. — *Wellingtonia* Meisn. — *Lorenzanea* Planch. — *Oligostemon* Turcz. — *Heterapithmos* Turcz. — *Atelandra* Bello — For full references see under the genus. — Type species: *M. lanceolata* Bl.

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[1]) Rarely two ovules instead of one per ovary develop, resulting in a didymous fruit.

Leaves simple or pinnate; when pinnate, rachis terminating in 3 leaflets¹). Sepals mostly 5 (or seemingly more; see note on p. 466). Outer petals narrowly imbricate, subrotund to broad-elliptic, all of them regular-shaped and hardly or not wider than long (fig. 33c). Vascular bundle (connecting pedicel and seed) situated in a long or short marginal canal inside the endocarp (fig. 4 C, D).

Distribution: In SE. Asia 12 species; see under the genus. — Fig. 5.

Ecology: See under the genus.

Remark. Subg. *Meliosma* can be subdivided into two sections, mainly on characters of the fruit. Sect. *Meliosma* is entirely SE. Asian; sect. *Lorenzanea* is entirely American. For descriptions, see below.

A. Sect. **Lorenzanea** (Liebm.) Beus., *stat. nov.*

Lorenzanea Liebm. — *Oligostemon* Turcz. — *Heterapithmos* Turcz. — *Atelandra* Bello — For full references see under the genus. — Lectotype species: *M. glabrata* (Liebm.) Urb.

Leaves simple. Ovary always glabrous. Endocarp wall relatively thick, more or less drawn out around the ventral perforation which often gives the mostly (sub)globose endocarp a somewhat pyriform shape (fig. 4 D 1).

Distribution: In tropical to subtropical Central and South America; exact number of species unknown, but not more than *c.* 10 (see remarks).

Remarks. Sect. *Lorenzanea* was originally described as a genus, but later included in *Meliosma* by Planchon (1855) and following authors (see references), because they could find no essential difference between these genera. The differences between the endocarps of both groups (see above, and the explanation on the morphology of the fruit in part I chapter C sub d) are in my opinion fundamental enough to justify a subdivision into two sections. For the rest sect. *Lorenzanea* and sect. *Meliosma* (as far as subsect. *Simplices* is concerned) are indeed extremely similar.

Within sect. *Lorenzanea* more than 50 species have been described, but a preliminary investigation of the material has convinced me that the great majority of these are artificial, and that the number of 'good' species must be many times lower, probably not more than 10. Sect. *Lorenzanea* badly needs a thorough revision to obtain a reliable picture of number and variability as well as of the distributional pattern of its natural taxa. It is not further dealt with in this paper.

B. Sect. **Meliosma**²)

Meliosma Bl. — *Millingtonia* Roxb. — *Wellingtonia* Meisn. — For full references see under the genus. — Lectotype species: *M. lanceolata* Bl.

Leaves simple or pinnate. Ovary glabrous or pubescent. Endocarp wall relatively thin, not drawn out around the ventral perforation; endocarp mostly (sub)globose, sometimes semiglobose or ellipsoid to obovoid (fig. 4 C).

Distribution & *Ecology*: In SE. Asia 12 species, not in America; see further under the genus.

Remark. In contrast with the more homogeneous sect. *Lorenzanea*, sect. *Meliosma* can

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¹) Anomalously 2 (1) leaflets.

²) Species 1—12 in this paper.

be subdivided into two subsections, subsect. *Simplices* and subsect. *Pinnatae*, which are obviously natural groups, each with its own distribution pattern. They are included in the key to the species; references and descriptions are found on p. 434 and p. 484 respectively.

KEY TO THE SPECIES

1. Leaves simple (Subg. *Meliosma* subsect. *Simplices* — p. 434).

2. All or most of the nerves straight or nearly so (but sometimes ± refracted) (Series *Rectinervia* — p. 435).

3. Ovary partly or entirely, but always distinctly pubescent.

4. Leaves obovate, often nearly spathulate, 3—11 by 2—8 cm, index 1¼—2, abruptly acuminate, often (sub)truncate at the apex; nerves 8—17 pairs, always several bifurcate or divided, straight, but often more or less refracted . . . . **1. M. parviflora**

4. Leaves obovate or elliptic to obovate-oblong or oblong, 3—24 by 1½—12 cm, index 1½—3(—3½), acute to cuspidate at the apex; nerves (6—)8—30 pairs, sometimes one or two bifurcate, most of them straight, never refracted . . . . **3. M. dilleniifolia**

3. Ovary glabrous.

5. Inner petals lanceolate, entire, 1¾—2¼ mm long. Leaf-base rounded or obtuse to acute, rarely nearly cuneate, sometimes emarginate, often oblique. Endocarps with more or less lumpy surface . . . . **2. M. myriantha**

5. Inner petals about halfway bifid, ⅔—1⅓ mm long. Leaf-base cuneate or attenuate, sometimes acute. Endocarps with smooth or lumpy surface. . . . . **3. M. dilleniifolia**

2. All or most of the nerves more or less but distinctly ascending (Series *Curvinervia* — p. 447), or dubious.

6. Plant with flowers.

7. Ovary pubescent.

8. Inner petals more or less deeply but distinctly bifid.

9. Panicles distinctly axillary . . . . **5. M. lepidota** ssp. **c**

9. Panicles terminal

10. Nerves distinctly ascending. . . . . **6. M. simplicifolia** ssp. **b**

10. All or most of the nerves straight or nearly so, but sometimes ± refracted . 4

8. Inner petals oblong to lanceolate, entire. . . . . **4. M. henryi** ssp. **a**

7. Ovary glabrous.

11. Inner petals oblong to lanceolate, entire.

12. Nerves 13—33 pairs. Leaves usually closely dentate. Leaf-base rounded or obtuse to acute, rarely nearly cuneate, sometimes emarginate, often oblique. **2. M. myriantha**

12. Nerves 4—17 pairs. Leaves usually toothless, sometimes remotely dentate. Leaf-base acute to attenuate or cuneate, not oblique.

13. Petioles $^1/_{16}$—$^1/_4$ x length of lamina. Upper surface of leaf with more or less prominent midrib. Leaves (sub)glabrous . . . . **4. M. henryi** ssp. **b** and **c**

13. Petioles $^1/_5$—$^1/_2$(—$^3/_4$) x length of lamina. Uppers urface of leaf with more or less impressed midrib. Leaves glabrous or pubescent.
5. M. lepidota ssp. **e**, **f**, and **g**

11. Inner petals more or less deeply but distinctly bifid.

14. Mature buds 1—1¼ mm ø. Leaves 3—15 by 1—3(—3½) cm, (sub)glabrous, without domatia, with more or less impressed midrib above; nerves 7—15 pairs; petioles ½—1½ cm.

15. Inner petals very faintly bifid, ½—⅔ mm, with blunt lobes . **7. M. paupera**

15. Inner petals somewhat more to somewhat less than halfway bifid, ½—1½ mm, with acute to more or less blunt lobes. . . . . **6. M. simplicifolia** ssp. **h**

14. Mature buds 1½—3 mm ø. Leaves 2—50 by ¾—18 cm, glabrous or pubescent, with or without domatia, with impressed or prominent midrib above; nerves 4—30 pairs; petioles ½—6(—10) cm.

16. Petioles $^1/_{20}$—$^1/_5$ x length of lamina.

17. Panicles distinctly axillary or ramiflorous. . **5. M. lepidota** ssp. **c** and **d**

17. Panicles distinctly terminal, or, when dubious, at least close-set together near or at the end of a flowering branch.

18. Leaves without teeth . . . . **6. M. simplicifolia**

18. Leaves closely to remotely spinously toothed, sometimes repand to sinuate.

19. Most of the nerves straight or nearly so. Deciduous trees or shrubs
3. M. dilleniifolia

19. Most of the nerves more or less but distinctly ascending. Evergreen trees or shrubs. . . . . **6. M. simplicifolia**

16. Petioles ¼—1(—1¼) x length of lamina.

20. Leaves elliptic or oblong, rarely obovate, obovate-oblong, or lanceolate, up to *c.* 15 cm long, glabrous or nearly so; petioles up to 1(—1¼) x length of lamina . . . . **5. M. lepidota** ssp. **a, b, c,** and **d**

20. Leaves obovate to obovate-lanceolate, or oblong to lanceolate, up to *c.* 25(—32) cm long, glabrous to densely pubescent, sometimes tomentose; petioles up to ⅓ x length of lamina . . . . **6. M. simplicifolia**

6. Plant with fruits.

21. Endocarps with smooth or nearly smooth surface.

22. Endocarps (5½—)6—8 mm ø . . . . **5. M. lepidota**

22. Endocarps subglobose, not oblique, 4—5½ mm ø (fig. 22 F 1, 2) **4. M. henryi** ssp. **b** and **c**

22. Endocarps depressed to semiglobose, very oblique, 3—4 mm ø (fig. 22 D 1, 2) **3. M. dilleniifolia**

21. Endocarps with more or less prominent but always distinct coarse to fine reticulum on the surface.

23. Endocarps up to 5 mm ø1)).

24. Leaves with 4—8 pairs of nerves; petiole (¼—)⅓—1(—1¼) x length of lamina **5. M. lepidota** ssp. **a**

24. Leaves with 7—33 pairs of nerves; petiole 1/20—1/3 x length of lamina.

25. Endocarps 2¼—4 mm ø. All or most of the nerves straight or nearly so, but sometimes ± refracted. Deciduous shrubs or trees 3

25. Endocarps (3—)3½—5 mm ø. All or most of the nerves more or less but distinctly ascending. Evergreen shrubs or trees.

26. Leaves 3—15 by 1—3(—3½) cm, without domatia, above with impressed midrib; nerves 7—15 pairs. Panicles poor, 7—14 cm, with very thin and slender, nearly filiform axes. Endocarps globose, hardly or not depressed or oblique, *c.* 4 mm ø (fig. 22 G 1, 2) . . . . **7. M. paupera**

26. Leaves 3—50 by 1—18 cm, with or without domatia, above with impressed to prominent midrib; nerves 7—25 pairs. Panicles (4—)10—50(—60) cm, with coarse to slender but not very thin and nearly filiform axes. Endocarps globose to subglobose, often depressed or oblique, 3—9 mm ø.

27. Fruits with a small pubescent patch near the base (remnant of pubescent ovary; fig. 28d) (Leaves above with glabrous midrib.). **4. M. henryi** ssp. **a**

27. Fruits only extremely rarely with such a hairy patch (and then leaves above with pubescent midrib) . . . . **6. M. simplicifolia**

23. Endocarps more than 5 mm ø.

28. Endocarps more or less but distinctly ellipsoid to obovoid (fig. 22 H 1—3). **5. M. lepidota** ssp. **b, d,** and **e**

28. Endocarps (sub)globose, not ellipsoid to obovoid.

29. Panicles distinctly axillary or ramiflorous. . . **5. M. lepidota** ssp. **c** and **f**

29. Panicles terminal.

30. Leaves (sub)glabrous, with 8—11 pairs of nerves. Endocarps with a few faint ribs, not distinctly reticulate. . . . . **5. M. lepidota** ssp. **f**

30. Leaves more or less but nearly always distinctly pubescent; if not, then more than 11 pairs of nerves. Endocarps more or less but distinctly, often very prominently, reticulate. . **6. M. simplicifolia** ssp. **a, b, d, (f),** and **(g)**

1. Leaves pinnate.

31. Leaf-rachis terminating in 3 (sometimes 2, very rarely 1) leaflets (fig. 33a). Outer petals widely ovate to orbicular, not or not much wider than long, with entire margin (fig. 33b, c). Endocarps inside with a marginal canal in which runs the vascular bundle connecting pedicel and seed (fig. 4C) (Sect. *Meliosma* subsect. *Pinnatae*, see p. 484).

32. Leaves 2—5(—6)-jugate; leaflets usually glabrous2)), sometimes (in specimens from Borneo) pubescent beneath, above always with more or less prominent midrib. Inner petals (1¼—)1½—2 (—3) mm, entire to retuse or slightly bifid at the top. Ovary glabrous. Endocarps ¾—2 cm ø **8. M. sumatrana**

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1) Intermediate cases are represented in both forks of the key.

2) Sometimes rachis and nerves of very young leaves somewhat pubescent.

32. Leaves 2—23-jugate; leaflets glabrous or pubescent, above with flat to impressed, rarely prominent midrib. Inner petals (⅓—)½—1(—1½) mm, always distinctly and rather deeply bifid. Ovary glabrous or pubescent. Endocarps ¼—1 cm ø.

33. Leaves (3—)6—18(—23)-jugate, with (10—)20—100 cm long rachis; leaflets only very rarely with a slight pubescence on midrib and nerves above. Panicles very big and lax, 50—150 cm long, pendulous, usually suddenly bent down at the base, with up to *c.* 90 cm long primary side-axes which are never subtended by (small) leaves.

34. Leaflets in middle and upper part of the leaf elliptic to lanceolate, very rarely a few linear-lanceolate, index (1½—)2—5(—7); petiolules 2—30 mm . **9. M. lanceolata**

34. Leaflets in middle and upper part of the leaf linear-lanceolate, index 5—10; petiolules (except that of top leaflet) absent or very short, up to *c.* 1 mm. **10. M. hirsuta**

33. Leaves 2—7(—9)-jugate (sometimes up to 12-jugate in specimens from Himalaya and China), with up to *c.* 40(—60) cm long rachis; leaflets usually more or less pubescent on midrib and nerves above, sometimes glabrous. Panicles not very big, lax to dense, 10—50(—70) cm long, usually erect, sometimes ± pendulous but almost never suddenly bent down at the base, with up to *c.* 35(—60) cm long primary side-axes which may be subtended by decrescent leaves.

35. Plants from Sumatra and Java.

36. Leaflets (sub)glabrous, usually (obscurely) toothed1). Panicles without decrescent leaves . . . . **9. M. lanceolata f. nervosa**

36. Leaflets sparsely to densely but always distinctly pubescent, at least on midrib and nerves, without teeth2). Panicles often with decrescent leaves. **11. M. pinnata**

35. Plants from other parts of Malesia.

37. Leaves (2—)3—10(—12)-jugate, pubescent or glabrous; index of leaflets (1—)1½—5. Sepals glabrous, rarely with a few hairs, outer petals glabrous. Ovary pubescent or glabrous . . . . **11. M. pinnata**

37. Leaves 2—6(—7)-jugate, more or less pubescent; index of leaflets (1—)1½—3. Sepals, sometimes also outer petals, densely pubescent on the outside. Ovary pubescent.

38. Leaves 2—6(—7)-jugate; leaflets without teeth2), usually firmly coriaceous. Outer petals usually pubescent on the outside. Endocarps 3½—5½(—8) mm ø. Medium-sized to big trees. . . . . **11. M. pinnata** ssp. **e**

38. Leaves 2—3(—4)-jugate; leaflets with or without teeth, chartaceous. Outer petals glabrous. Endocarps *c.* 7—8 mm ø. Small trees. **12. M. sarawakensis**

31. Leaf-rachis terminating in 1 (rarely 2) leaflet(s) of which the short petiolule is nearly always well marked against the rachis by an articulation (fig. 34a). Outer petals of irregular shape or mostly widely reniform, mostly much wider than long, with ± irregular margin and often emarginate at the top (fig. 34b). Endocarps inside without a marginal canal in which runs the vascular bundle (fig. 4 A, B) (Subg. *Kingsboroughia*, p. 516).

39. Leaves (6—)7—9-jugate. Inner petals hardly or not incised at the top. Ovary glabrous. Endocarps big, amply longer than 1 cm (Sect. *Hendersonia*, p. 517) . . . **13. M. rufo-pilosa**

39. Leaves (2—)3—6-jugate. Inner petals distinctly bifid. Ovary glabrous or pubescent. Endocarps smaller, much shorter than 1 cm (Sect. *Kingsboroughia*, p. 518).

40. Panicles 5—20 cm long. Ovary glabrous. Endocarps subglobose, applanate at the ventral side, (4—)4½—5½(—6) mm long . . . . **14. M. alba**

40. Panicles 25—*c.* 60 cm long. Ovary densely puberulous-pubescent. Endocarps about semiglobose, (6—)6½—8(—8½) mm long. . . . . **15. M. veitchiorum**

1. Subsect. *Simplices* (Warb.) Beus., *stat. nov.*3)

Sect. *Simplices* Warb. in E. & P., Nat. Pfl. Fam. 3, 5 (1895) 373, *pro parte, excl. sp. Americanae*; Cufod., Oest. Bot. Z. 88 (1939) 256; How, Acta Phytotax. Sin. 3 (1955) 426; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 20, 24; Vidal, Not. Syst. 16 (1960) 303.

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1) It may be impossible to identify specimens from NW. Sumatra; see remarks under *M. lanceolata.*

2) Leaflets of saplings and watershoots may be toothed, however.

3) Species 1—7 in this paper.

Leaves simple.

Lectotype species: *M. simplicifolia* (Roxb.) Walp.

Distribution: 7 species, mainly in continental SE. Asia, only 2 entering into Malesia. — Fig. 6.

Ecology: Predominantly subtropical.

Remarks. The arguments upon which the degradation of Warburg's sections *Simplices* and *Pinnatae* to subsections, and the introduction of the new sections *Lorenzanea* and *Meliosma* (see before) have been based, are explained in part I chapter B.

Subsect. *Simplices* is broken up into two groups, series *Rectinervia* (see below) and series *Curvinervia* (see p. 447), which are morphologically and geographically well-marked. They can be identified with the key to the species.

a. Series *Rectinervia* Beus., *ser. nov.*[1])

Frutices vel arbores parvae, deciduae. Folia nervis omnibus vel prope omnibus rectis vel subrectis.

Deciduous shrubs or small trees. Leaves with nerves that are all or almost all straight or almost straight.

Type species: *M. dilleniifolia* (Wall. *ex* W. & A.) Walp.

Distribution: Foot of the Himalaya, Central China, Japan. — Fig. 20 and 21.

Ecology: In mixed evergreen-deciduous broad-leaved forests, at low to high altitudes.

Remark. The distribution pattern of this series has been discussed in part I chapter E.

1. **Meliosma parviflora** Lecomte, Bull. Soc. Bot. Fr. 54 (1907) 676; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 201; Pei, Contr. Biol. Lab. Sc. Soc. China 9 (1934) 175; Cufod., Oest. Bot. Z. 88 (1939) 260; How, Acta Phytotax. Sin. 3 (1955) 436; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235; Krüssm., Handb. Laubgeh. 2 (1962) 128, t. 57 f ('*parvifolia*'). — Type: *Wilson 3314* (Szechuan), seen from A, K, P (holo).

M. dilatata Diels, Notizbl. Berl.-Dahl. 11 (1931) 212. — Type: *Meijer 1509* (Chekiang), seen from A, K, P. Paratypes: *Y. L. Keng 733*, *Ching & Tsao 610*, both seen from A.

Deciduous shrub or small tree up to *c.* 10 m. *Flowering twigs* terete, 1½—6 mm ø, often slightly zigzag, moderately to densely puberulous, glabrescent. *Leaves* (fig. 14a) obovate, often nearly spathulate, 3—11 by 2—8 cm, index 1¼—2, towards the base attenuate or cuneate, at the apex abruptly acuminate, often (sub)truncate, more or less remotely repand to usually spinously dentate towards the apex, chartaceous, dull or shining above, dull and paler beneath, glabrous above (sometimes slightly papillose on the midrib), beneath glabrous or very sparsely pubescent especially on midrib and nerves, usually with small hairy domatia in the axils of primary and secondary nerves; midrib above somewhat impressed to flat, beneath prominent; nerves 8—17 pairs, straight, but often more or less refracted, always several bifurcate or divided, those near the apex usually slightly ascending, never looped and joined but usually running out into teeth, above slightly elevated to slightly impressed, beneath distinctly prominent; venation distinct, reticulate to somewhat cancellate, above flat or slightly impressed, beneath slightly to distinctly prominent; petiole up to *c.* 2 cm, glabrous to somewhat puberulous. *Panicles* terminal, erect, lax to dense, widely to narrowly pyramidal, 10—35 cm, usually profusely branched up to the 4th order, branches usually spreading, stiff to rather flaccid, rather slender, terete to somewhat angular, densely puberulous to pubescent, bearing

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1) Species 1—3 in this paper.

numerous crowded flowers which are more or less spicately arranged; main axis terete, usually somewhat zigzag, densely puberulous to pubescent; primary side-axes few to many, up to c. 25 cm, the lower ones often subtended by small or reduced leaves; bracts ovate to ovate-lanceolate, up to *c.* 4 mm, densely pubescent. *Pedicels* absent or up to *c.* 2 mm. *Mature buds* 1⅓—2 mm ø. *Sepals* 5, broad-ovate, more or less equal, ½—⅔ mm, glabrous, with entire ciliolate margin, nearly always subtended by 1—10 empty bracts which are smaller, often minute, often pubescent at the outside. *Outer petals* glabrous. *Inner petals* ± halfway bifid, ½—1 mm, with acute, more or less divergent lobes which are mostly irregularly frayed-fimbriate, sometimes with a minute central lobule. *Stamens*: anther-cells ¼—⅓ mm ø; filaments ¾—1¼ mm. *Ovary* ½—⅔ mm, more or less but always distinctly pubescent. *Style* ½—1¼ mm, glabrous. *Fruit* globose, when ripe 5—6 mm ø; endocarp depressed-globose, oblique, 2½—4 mm ø, with distinct, moderately fine, rather prominent reticulum; median keel distinct, rather prominent and sharp, not ending in a ventral processus, at one end rather far curving outwards; ventral pore somewhat sunken (fig. 22A 1, 2).

Distribution: China (Northern Yangtze Provinces): W. Szechuan (Kiating; Omei Shan; Tachien lu; Chengtu plain; Sungpan Hsien), W. Hupeh (Ichang), S. Kiangsu (Ishing), N. Chekiang (Chun-an Hsien; Yu-hang). Rather common in W. Szechuan, in Kiangsu twice reported to be rare. — Fig. 20.

Ecology: In the northern mixed mesophytic forest zone, at low to medium altitudes, reported from about 90 up to 900 m. Found in open woods or thickets, often by roadsides, also on river-banks or along streams, and once collected in a garden.

Field notes: Said to be a somewhat spreading tree; this I also observed in specimens grown in the open in the Kew Botanic Gardens, which have conspicuously spreading twigs. The bark of the trunk is several times reported to be smooth, grey, and peeling off in large, thick to thin scales or strips which leave brownish scars on the trunk. The leaves are glossy green at both sides.

Vernacular names: *Meng tzu teng* ('thorn-covered vine'), name mentioned by Steward, l.c.

Uses: The wood is said to be very hard and heavy, for instance used for the axles of cart-wheels.

Remark. M. parviflora is a characteristic, well recognizable, and not very variable species, in habit showing the closest resemblance to *M. dilleniifolia* ssp. *cuneifolia.*

2. Meliosma myriantha Sieb. & Zucc. — *Quercus ijam ahoso* Sieb. *ex* Miq. — *M. pilosa* Lecomte — *M. myriantha* var. *discolor* Dunn — *M. stewardii* Merr. — For full references, see under the subspecies.

Deciduous shrub or small tree, up to *c.* 15 m. *Flowering twigs* terete to angular, 1½—4 mm ø, more or less pubescent, glabrescent. *Leaves* oblong or obovate-oblong, 5—25(—35) by 2—10(—13) cm, index (1½—)2—3(—3½), at the base rounded or obtuse to acute, rarely nearly cuneate, sometimes emarginate, often oblique, at the apex acute to cuspidate, usually along the whole margin closely to remotely spinously dentate, rarely (nearly) entire, membranaceous to chartaceous, dull or somewhat shining above, dull and paler beneath, above subglabrous to sparsely pubescent, beneath very sparsely to densely pubescent especially on midrib and nerves, and whether or not with small, usually inconspicuous hairy domatia in the nerve axils; midrib above flat to more or less impressed, beneath prominent; nerves 13—33 pairs, often close together, straight or nearly so, sometimes a few bifurcate, sometimes slightly ascending especially near the margin or towards the apex, running out into teeth, rarely a few looped and joined, above flat

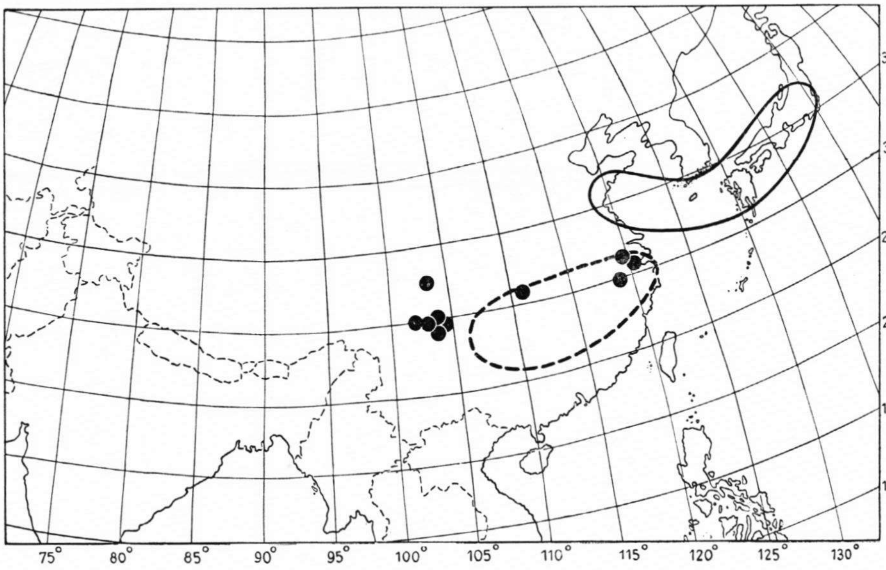

Fig. 20. Distribution of localities of *M. parviflora* (●), and generalized areas of *M. myriantha* ssp. *myriantha* (———) and ssp. *pilosa* (— — —).

or nearly so, beneath prominent; venation distinct or not, usually cancellate, above flat or nearly so, beneath flat to somewhat prominent; petiole (½—)1—4 cm, moderately to densely pubescent. *Panicles* terminal, erect, lax to dense, widely pyramidal, 6—25 cm, profusely to poorly branched up to the (3rd) 4th order, branches spreading, stiff to somewhat flaccid, rather slender, angular to flattened, moderately to densely puberulous or pubescent, bearing numerous solitary to crowded flowers; main axis angular to somewhat canaliculate, sparsely to densely puberulous or pubescent; primary side-axes few to many, up to *c.* 20 cm, the lower ones often subtended by small or reduced leaves; bracts ovate to ovate-lanceolate, up to *c.* 4 mm, sparsely to densely pubescent. *Pedicels* usually present, up to *c.* 4 mm. *Mature buds* 1½—2¼ mm ø. *Sepals* 5 or 4, broad-ovate, more or less unequal, the inner 3 or 4¾—1⅓ mm, the outer 2 or 1 usually smaller, often very minute, often lowered on the pedicel, all glabrous, with entire, ciliolate margin. *Outer petals* glabrous. *Inner petals* lanceolate, 1¾—2¼ mm, blunt to acute at the tip, entire, glabrous. *Stamens*: anther-cells ¼—⅓ mm ø; filaments *c.* 1 mm. *Ovary* ½—⅔ mm, glabrous. *Style* (½—)⅔—1 mm, glabrous. *Fruit* globose, when ripe 4½—5½ mm ø; endocarp (sub)-globose, hardly or not depressed or oblique, 3—4 mm ø, with usually distinct, fine, more or less prominent reticulum; median keel distinct, slightly prominent, rather blunt, not ending in a ventral processus; ventral pore neither sunken, nor spouted (fig. 22 B 1, 2).

Distribution: Central and West China, extreme South Corea, West and Central Japan. For details, see under the subspecies. — Fig. 20.

Ecology: In mixed mesophytic and deciduous broad-leaved forests at low to medium, rarely high altitudes, from nearly sea-level up to *c.* 2000 m. For details, see under the subspecies.

Remarks. *M. myriantha* is vegetatively generally well distinct from *M. dilleniifolia* by the shape of the leaf-base, whereas the shape of the inner petals serves as a fully reliable generative character. Moreover, a useful character is found in the shape of the endocarps. Otherwise, both species look very much alike, being probably closely allied.

M. myriantha is broken up into two usually well recognizable subspecies which cover replacing areas and occur in different forest formations.

KEY TO THE SUBSPECIES

1. Normal leaves toothed up to the base or nearly so; nerves (22—)24—33 pairs **a.** ssp. **myriantha**
1. Normal leaves in the lower half almost always (sub)entire; nerves 13—22(—25) pairs **b.** ssp. **pilosa**

a. ssp. **myriantha.** — *M. myriantha* Sieb. & Zucc., Abh. K. (Bayer.) Ak. Wiss. M.-Ph. Kl. (Münch.) 4, 2 [Fl. Jap. Fam. Nat. 1] (1845) 153; Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 93; Cat. Mus. Bot. 1 (Fl. Jap.) (1870) 23, 146; Franch. & Savat., En. Pl. Jap. 1 (1873) 91; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 145; Anon., Gard. Chron. ser. 3, 31 (1902) 30, f. 9; Nakai, Fl. Korea 1 (1909) 138; Matsum., Ind. Pl. Jap. 2 (1912) 335; Schneid., Ill. Handb. Laubholzk. 2 (1912) 254; Cufod., Oest. Bot. Z. 88 (1939) 259, *pro parte*; Rehd., Man. Cult. Trees & Shrubs (1940) 594; Hara, En. Sperm. Japon. 3 (1954) 120, *pro parte*; Makino, Ill. Fl. Jap. (1954) 348, f. 1042; How, Acta Phytotax. Sin. 3 (1955) 439, t. 58 f. 1—5, *pro parte*; Krüssm., Handb. Laubgeh. 2 (1962) 128; Ohwi, Fl. Japan (1965) 613. — Lectotype: *Von Siebold s.n. ex Herb. Zuccarinii* (Japan), seen from GH, W (holo).

[*Quercus ijam ahoso* Sieb. *in sched. ex* Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 93, *nom. invalid. in synon.*; Kew Index 2 : 674.]

Normal leaves dentate up to the base or nearly so, (very) sparsely pubescent beneath, usually membranaceous, sometimes chartaceous; nerves (22—)24—33 pairs.

Distribution: Japan: Honshu (western and central districts), Shikoku, Kyushu, Tsushima; S. Corea (Herschel Island, Quelpart Island); E. China: Shantung (Tsingtao; Tai-ching-kung), N. Kiangsu (Liu Lin Shan near Haichow). Common. — Fig. 20.

Ecology: In deciduous broad-leaved forests, at low to medium altitudes; in Shantung reported from *c.* 50 m elevation, in S. Corea collected at *c.* 600 m, in Japan usually between 600 m and 1000 m altitude.

Field notes: Fruit red when ripe.

Vernacular names: Japan: *Awabuki* or *Awafuki* (standard Japanese name), *Nukagawa* (several times mentioned in old collections); China: *Fa shu* (once reported from N. Kiangsu).

Uses: Ssp. *myriantha* is moderately hardy, and has been introduced in W. Europe and N. America, where it is grown successfully in several botanic gardens in the open, and is valued as an ornamental shrub or treelet.

b. ssp. **pilosa** (Lecomte) Beus., *stat. nov.* — *M. pilosa* Lecomte, Bull. Soc. Bot. Fr. 54 (1907) 676; Rehd. in Rehd. & Wils., J. Arn. Arb. 8 (1927) 164; Cufod., Oest. Bot. Z. 88 (1939) 260; How, Acta Phytotax. Sin. 3 (1955) 440; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235. — Type: *Wilson 1226* (Hupeh), seen from A, K, P (holo), W.

M. myriantha ('*myriacanthum*') var. *discolor* Dunn, J. Linn. Soc. Bot. 38 (1908) 358; Rehd. in Rehd. & Wils., J. Arn. Arb. 8 (1927) 164; Merr. & Chun, Sunyatsenia 1 (1930) 68; Pei, Contr. Biol. Lab. Sc. Soc. China 9 (1934) 175; Cufod., Oest. Bot. Z. 88 (1939) 259; How, Acta Phytotax. Sin. 3 (1955) 440. — Syntypes: *Dunn 2531*¹) (Fokien), seen from A, K; *2536*, not seen.

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¹) Erroneously cited by Dunn, l.c., as *2537*!

M. stewardii Merr., Philip. J. Sc. 27 (1925) 164; Hand.-Mazz., Symb. Sin. 7 (1933) 644; Cufod., Oest. Bot. Z. 88 (1939) 259, *in obs.* — Type: *Steward 2443* (Kiangsi), seen from A, E, K.

M. myriantha Sieb. & Zucc., *sensu* Cufod., Oest. Bot. Z. 88 (1939) 259, *pro parte*; *sensu* How, Acta Phytotax. Sin. 3 (1955) 439, *pro parte*; *sensu* Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235.

Normal leaves in the lower half almost always partly or entirely without teeth, sparsely to densely pubescent beneath, usually chartaceous, sometimes more membranaceous; nerves 13—22(—25) pairs.

Distribution: East and Central China: E. Szechuan, N. Kweichow, W. Hupeh, Hunan, Kiangsi, N. Fokien, Chekiang, S. Anhwei. Locally common. — Fig. 20.

Ecology: In usually dense woods and thickets of the mixed mesophytic type, at altitudes varying from 120 m up to *c.* 2000 m. Twice reported to occur on loamy soil.

Field notes: The bark is several times said to be grey and smooth. The leaves are shining dark green above and lighter beneath. The fruit is said to be scarlet or deep red when ripe.

Vernacular names: *Pao hua shu*, reported from Chekiang and Lushan in Kiangsi (see Steward, l.c.), the name is used for both varieties (see below).

Remark. Within ssp. *pilosa* two varieties can be distinguished which differ in the leaf-pubescence. They are not sharply separated and intermediate specimens do sometimes occur (For instance *Dunn 2531* from Fokien, described as var. *discolor*, has an intermediate type of leaf-pubescence; though the leaves are indeed somewhat discoloured beneath, I would not attach so much value to this character as to base a variety on it). There are no indications that these varieties prefer different habitats or altitudes, and both are found about equally frequent throughout the whole area.

b 1. var. **pilosa.**

Undersurface of the leaves covered with a dense layer of soft sericeous hairs.

b 2. var. **stewardii** (Merr.) Beus., *stat. nov.* — *M. stewardii* Merr. — For full references and typification, see under the subspecies.

Undersurface of the leaves only with more or less scattered hairs (somewhat closer set on midrib and nerves) or nearly glabrous.

3. Meliosma dilleniifolia (Wall. *ex* W. & A.) Walp. — *Millingtonia dilleniifolia* Wall. *ex* W. & A. — *M. tenuis* Maxim. — *M. tenuiflora* Miq. — *M. cuneifolia* Franch. — *M. flexuosa* Pamp. — *M. pendens* Rehd. & Wils. — *M. platypoda* Rehd. & Wils. — *Premna mairei* Lévl. — *M. mairei* Cufod. — *M. cuneifolia* var. *glabriuscula* Cufod. — *M. meliantha* Krüssm. — For full references and typification, see under the subspecies.

Deciduous shrub to small tree, up to *c.* 10(—15) m. *Flowering twigs* terete to angular, (1—)1½—5 mm ø, straight to somewhat zigzag, more or less pubescent, glabrescent. *Leaves* obovate or elliptic to obovate-oblong or oblong, 3—24 by 1½—12 cm, index 1½—3(—3½), at the base cuneate or attenuate, sometimes acute, at the apex acute to cuspidate, closely to remotely spinously dentate along the whole margin or only towards the apex, sometimes repand, herbaceous to chartaceous, dull or somewhat shining above, dull and paler beneath, subglabrous to rather densely pubescent especially beneath and on midrib and nerves, mostly with hairy domatia in the axils of primary nerves beneath, rarely also in some axils of secondary nerves; midrib above hardly to deeply impressed, beneath prominent; nerves (6—)8—30 pairs, straight or nearly so, sometimes one or two bifurcate, those near the apex usually somewhat ascending, never looped and joined but running out into teeth, above slightly prominent to impressed, beneath prominent; venation distinct or not, usually cancellate, above flat or nearly so, beneath flat to somewhat prominent; petiole up to *c.* 3½ cm, subglabrous to densely pubescent, rarely slightly winged. *Panicles* terminal, erect, sometimes deflexed, lax to dense, widely to narrowly pyramidal, (5—)10—35(—50) cm, profusely to poorly branched up to the 3rd or 4th order, branches spreading, sometimes more or less reflexed, stiff to somewhat flaccid, rather slender, angular to flattened, sparsely to densely puberulous or pubescent, bearing numerous solitary to crowded flowers; main axis angular to somewhat canaliculate, sometimes somewhat zigzag, sparsely to densely puberulous or pubescent; primary side-axes few to many, up to *c.* 15(—30) cm, the lower ones often subtended by small or reduced leaves; bracts ovate to lanceolate, up to *c.* 6(—15) mm, subglabrous to sparsely pubescent especially along the margin. *Pedicels* usually present, up to *c.* 4(—5) mm. *Mature buds* (1½—)1¾—3 mm ø. *Sepals* (6) 5 or 4, broad-ovate, more or less unequal, the inner 3 or 4¾—1¼(—1¾) mm, the outer 2 or 1 usually smaller, often very minute, often lowered on the pedicel, all glabrous, with entire, ciliolate margin. *Outer petals* glabrous. *Inner petals* ± halfway bifid, ⅔—1⅓ mm, with acute, rarely obtuse, more or less divergent lobes which are mostly fimbriate at the outer margin and/or tip, rarely with a minute central lobule. *Stamens*: anther-cells ¼—½ mm ø; filaments 1—1½ mm. *Ovary* ½—⅔ mm, usually glabrous, rarely more or less puberulous to pubescent. *Style* ½—1(—1¾) mm, glabrous. *Fruit* globose, when ripe 4—5(—6) mm ø; endocarp depressed to semiglobose, very oblique, 3—4 mm ø, with smooth surface or with fine, prominulous to impressed reticulum; median keel distinct, rather prominent and sharp, at one end often running out into a minute ventral processus, at the other end rather far curving outwards; ventral pore somewhat sunken (fig. 22 C 1, 2, D 1, 2).

Distribution: Southern Himalaya, West, Central, and East China, Japan. For details, see under the subspecies. — Fig. 21.

Ecology: In evergreen, deciduous, and coniferous mountain forest, at altitudes from *c.* 600 (rarely lower) up to at least 3300 m. For details, see under the subspecies.

Uses: All four subspecies (see below) are handsome ornamental shrubs or treelets; they are moderately hardy, especially ssp. *cuneifolia* which in nature occurs under the most extreme conditions. All are cultivated in several European and American botanic gardens.

Remarks. M. dilleniifolia is a variable species, showing a remarkable shifting of characters from the western towards the eastern end of its distributional area, especially in leaf-dentation, number of nerves, and shape of the panicle. Moreover, there are differences in the presence of domatia and in shape, pubescence etc. of the inner petals. This shifting of characters, however, is not a cline, since there are definite demarcations between four groups which are geographically separate and have different ecological requirements. In view of this geographic separation and of the fact that the characters mentioned are minor and not quite constant, I consider these groups subspecies, treating them similarly as in the other widespread complex species of *Meliosma.*

The subspecies *cuneifolia*, *flexuosa*, and *tenuis*, in sequence of their distribution from west to east, can be morphologically easily derived from each other, in the same sequence; ssp. *flexuosa* may be considered a specialized ssp. *cuneifolia*, and ssp. *tenuis* a specialized ssp. *flexuosa*, with an increasing accent on the same characters (e.g. fewer nerves, more remotely dentate to repand leaf margin, profuse to poor panicles, with increasingly twisted axes). At the western end of the area ssp. *cuneifolia* can similarly be derived from ssp. *dilleniifolia*, but here the situation is somewhat more complex, since a var. *multinervia* shifts in between; see the remarks under that variety.

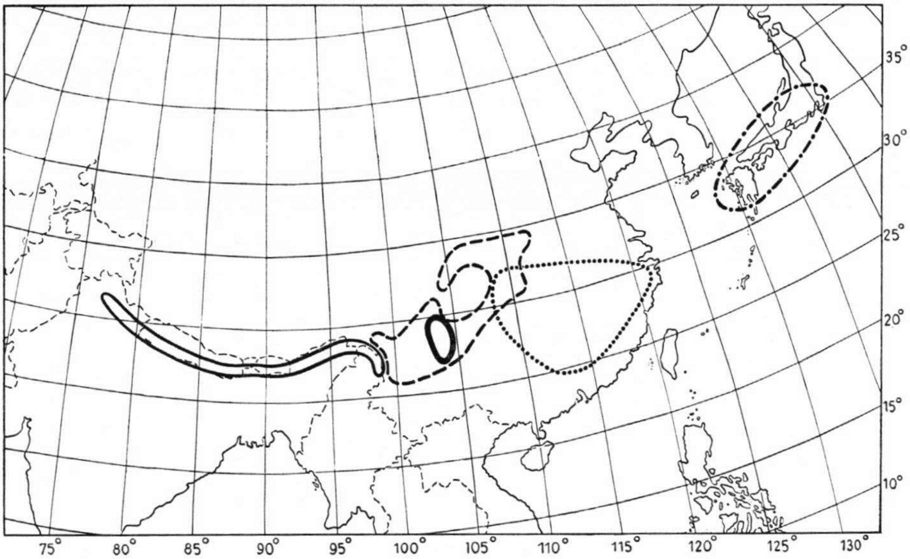

Fig. 21. Generalized areas of *M. dilleniifolia* ssp. *dilleniifolia* (———), ssp. *cuneifolia* (— — —), ssp. *flexuosa* (.....), and ssp. *tenuis* (—.—.—). The thick solid line indicates the area of ssp. *cuneifolia* var. *multinervia*.

KEY TO THE SUBSPECIES

1. Panicles erect, with usually straight to sometimes slightly zigzag-twisted main axis and ± straight, spreading but rarely reflexed secondary axes 2
1. Panicles erect to deflexed, with more or less zigzag-twisted main and mostly also secondary axes, the latter often reflexed 3
2. Domatia absent or very inconspicuous. Mature buds 1¾—2 mm ø. Lobes of inner petals glabrous. Endocarps with distinct reticulum (fig. 22 C 1, 2) . . . . a. ssp. **dilleniifolia**
2. Domatia present, rarely inconspicuous. Mature buds (1½—)2—2½(—3) mm ø. Lobes of inner petals distinctly fimbriate at least at the outer margin. Endocarps with smooth to faintly lumpy surface (fig. 22 D 1, 2) . . . . b. ssp. **cuneifolia**
3. Leaves with (10—)12—21 pairs of nerves; domatia mostly absent. Lobes of inner petals blunt, ciliolate to fimbriate only at the tip, sometimes with a minute central lobule. Endocarps with distinct reticulum (cf. fig. 22 C 1, 2) . . . . c. ssp. **flexuosa**
3. Leaves with (6—)8—14(—15) pairs of nerves; domatia always present, more or less conspicuous. Lobes of inner petals acute, fimbriate at the outer margin, never with a central lobule. Endocarps with smooth or nearly smooth surface (cf. fig. 22 D 1, 2) . . . . d. ssp. **tenuis**

a. ssp. **dilleniifolia.** — *Millingtonia dilleniifolia* Wall. *ex* W. & A., Edinb. New Phil. J. 15 (1833) 179; Wight, Ill. Ind. Bot. 1 (1840) 144. — *M. dilleniifolia* (Wall. *ex* W. & A.) Walp., Rep. 1 (1842) 423 (*'dilleniaefolia'*); Brandis, For. Fl. (1874) 115; Hook. *f.*, Fl. Br. Ind. 2 (1876) 4; Collett, Fl. Siml. (1902) 102, f. 33; Brandis, Ind. Trees (1906) 195; Bamb., Pl. Punjab (1916) 30; Osmaston, For. Fl. Kumaon (1927) 133; Rehd., Man. Cult. Trees & Shrubs (1940) 594; Kitamura in Kihara, Fauna Flora Nepal (1955) 176; Krüssm., Handb. Laubgeh. 2 (1962) 127, t. 57a (*'dillenifolia'*); Hara, Fl. East. Himal. (1966) 194. — Type: *Wallich 8116 in Herb. Hook.* (Nepal), seen from K, dupl. seen from E. K. W.

Leaves 7—30 by 4—15 cm, index 1½—2½, cuneate, acute, or attenuate at the base, closely and finely dentate, never repand, with teeth ending into mucros which may be the extension of a nerve, but as well of an intercalary vein, chartaceous to membranaceous, sparsely to densely pubescent, beneath without or with very inconspicuous domatia; nerves 13—27 pairs. *Panicles* erect, 14—28 cm, usually rather profuse, with straight main and side-axes, the latter rarely reflexed. *Mature buds* 1¾—2 mm ø. Lobes of *inner petals* acute, glabrous. *Ovary* glabrous. *Endocarps* with distinct, impressed reticulum (fig. 22 C 1, 2).

Distribution: Southern Himalaya: N. India (NE. Punjab; Kumaon; Nepal; Sikkim; Assam), extreme N. Burma (Maikha-Salween divide; Upper Adung Valley). Fairly common in most parts of the area. — Fig. 21.

Ecology: In evergreen oak forest at 2000—3300 m altitude. Reported to be found in thickets by streams and in shady forested ravine.

Field notes: Once said to be a solitary wide-spreading bush or small tree.

Vernacular names: N. India (mostly copied from local Floras; see references): *Gwep* or *Gweb* (NW. Provinces unspecified, N. Garhwal, Ranikhet), *Gulpha* or *Goguna* (N. Garhwal), *Goi* (NW. Himalaya unspecified), *Kann*, *Kanna*, or *Karkon* (Punjab), *Maigoza* (Tibet language, Nepal), *Shapra* and *Bakarshang* (Bashahr).

b. ssp. **cuneifolia** (Franch.) Beus., *stat. nov.* — *M. cuneifolia* Franch., Nouv. Arch. Mus. Hist. Nat. Paris sér. 2, 8 (1886) 211; Pl. David. 2 (1888) 29; Diels, Bot. Jahrb. 29 (1900) 452; Pamp., Nuov. Giorn. Bot. Ital. n.s. 18 (1911) 127; Hutch., Bot. Mag. 137 (1911) t. 8357; Schneid., Ill. Handb. Laubholzk. 2 (1912) 1029, f. 608; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 199, *pro maj. parte*; Hand.-Mazz., Symb. Sin. 7 (1933) 644; Chun, Sunyatsenia 1 (1934) 266; Cufod., Oest. Bot. Z. 88 (1939) 256; Rehd., Man. Cult. Trees & Shrubs (1940) 594; How, Acta Phytotax. Sin. 3 (1955) 437; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235, *pro parte*; Krüssm., Handb. Laubgeh. 2 (1962) 127, t. 57 e. — Type: *David s.n.* (Thibet, Moupine, VI-1869), seen from P (holo).

M. myriantha (*non* Sieb. & Zucc.) Diels, Bot. Jahrb. 29 (1900) 451 ('*myrianthum*'), *pro majore parte.*

M. platypoda Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 201; Cufod., Oest. Bot. Z. 88 (1939) 258; How, Acta Phytotax. Sin. 3 (1955) 436. — Type: *Wilson 1126* (Hupeh), seen from A, E, K, P. W.

Premna mairei Lévl., Sert. Yunnan (1916) 3; Cat. Pl. Yun-Nan (1917) 298; cf. Lauener, Not. R. Bot. Gard. Edinb. 27 (1967) 290. — Type: *E. E. Maire s.n.* (Yunnan, Long-Ky, VI-1912), seen from E (holo).

M. mairei Cufod., Oest. Bot. Z. 88 (1939) 257; How, Acta Phytotax. Sin. 3 (1955) 437. — Type: *E. E. Maire s.n.* (Yunnan, Chen-fong-shan, VII-1912), seen from W (holo).

M. cuneifolia var. *glabriuscula* Cufod., Oest. Bot. Z. 88 (1939) 257; How, Acta Phytotax. Sin. 3 (1955) 438. — Syntypes: *Cavalerie 4443*; *Chien 6144*; *Ching 4756*; *Faber 139*; *Fang 12769*; *Fenzel 1849*; *Forrest 6086, 21346*; *Handel-Mazzetti 2809, 2903, 3343, 4226, 5394*; *Hers H587, 2348*; *Liu 1199*; *E. E. Maire 99*; *Rock 14667, 16140*; *Schneider 1289, 1684, 1711*; *Smith 2352*; *Ten 166, 276, 303, 403, 522*; *Tsai 54081, 57820, 59528A, 59577, 59862*; *Tsiang 8918*; *Wang 67710, 71230, 71444, 71487*; *Wilson 959, 1458, 1458a, 3033, 3034, 3315*; nearly all seen from several herbaria.

Leaves 3—24 by 1½—10 cm, index (1½—)2—3(—3½), at the base cuneate or attenuate, rarely acute, closely to rather remotely dentate, sometimes slightly repand, with teeth usually ending into mucros which may be mostly the extension of a nerve but sometimes as well of an intercalary vein, chartaceous, subglabrous to moderately pubescent, beneath always with more or less conspicuous domatia; nerves 10—30 pairs. *Panicles* erect, 6—50 cm, usually not lax but rather profuse, usually with straight main and side-axes, the latter not reflexed. *Mature buds* (1½—)2—2½(—3) mm ø. Lobes of *inner petals* acute, fimbriate at the outer, sometimes also at the inner margin. *Ovary* glabrous, rarely somewhat pubescent. *Endocarps* with smooth to faintly lumpy surface (fig. 22 D 1, 2).

Distribution: China: extreme SE. Thibet, N. Yunnan. Szechuan, NW. Kweichow, S. Kansu, S. Shensi, NW. Honan, W. Hupeh. Exceedingly common in most parts of the area. — Fig. 21.

Ecology: In deciduous broad-leaved forests and montane coniferous forests, at altitudes from *c.* 1000 m (*c.* 650 m) up to at least 3300 m, on various soils such as loam, sand, and limestone. Found in open thickets as well as in dense shady forest, along streams, along roadsides, etc.

Field notes: Bark grey to greyish green. Leaves dark green above, pale green to glaucous beneath. Fruits black when ripe.

Vernacular names: *Lung sü mu* ('dragon's beard'), mentioned from Honan and Shensi; *P'ao hua shu* (also used for *M. myriantha*!), mentioned from E. Szechuan (*fide* Diels, l.c.).

Remarks. Ssp. *cuneifolia* is the most variable one of the four subspecies of *M. dilleniifolia*, and it covers the widest ecological range. To the east its area meets that of ssp. *flexuosa*, with an overlap in W. Hupeh; specimens with intermediate characters are not uncommon there. The western end of the area borders ssp. *dilleniifolia*; there is no evidence, however, that these subspecies actually come into contact.

Ssp. *cuneifolia* — treated as a species — was divided up by Cufodontis, l.c., into two varieties, viz. var. *typica* and var. *glabriuscula*, mainly on the base of the presence, respectively absence, of some pubescence on the lower side of the leaves. There are, however, many intermediate specimens, and since also the other characters mentioned by Cufodontis do not hold, it seems futile to recognize such varieties; hence I have not adopted them.

A somewhat deviating form, falling outside the normal variation pattern, is *Wilson 1126* from W. Hupeh, upon which *M. platypoda* Rehd. & Wils. has been based. It differs from the usual specimens by its larger sepals, its longer style, and by the long, appressed pubescence on midrib and nerves beneath, whereas domatia are lacking. In all other characters it is a normal representative of ssp. *cuneifolia.* It is certainly not a separate species; at most it might be considered a variety, but it might as well be a somewhat abnormal hybrid between ssp. *cuneifolia* and ssp. *flexuosa.* For the time being it is in my opinion premature to base a separate taxon on this single collection. On the other hand, there is good reason to maintain another taxon, earlier described as *M. mairei* Cufod., l.c., not as a species, but as a variety; see below.

b 1. var. **cuneifolia.**

Blades of well developed leaves 3—17 by 1½—7½(—9) cm, at or towards the base cuneate or attenuate, rarely acute, at the very base never obtuse and without winged petiole, more or less closely dentate usually only as extensions of the nerves but sometimes also of some intercalary veins, very sparsely puberulous to moderately pubescent; nerves 10—22(—26) pairs; petiole 4—30 mm, $\frac{1}{8}$—$\frac{1}{15}$ as long as the leaf-blade, more or less pubescent. *Panicles* (5—)10—30 cm.

For distribution and ecology, see under the subspecies. See the remarks under var. *multinervia.*

b 2. var. **multinervia** Beus., *var. nov.* — Type: *W. P. Fang 2688*, in L (holo), dupl. seen from A, E, P.

Premna mairei Lévl. — *M. mairei* Cufod. — *M. cuneifolia* var. *glabriuscula* Cufod., *pro parte, quoad syntypus Fang 12769.* — For full references and typification, see under the subspecies.

Laminae foliolorum bene evolutorum 10—24 × 4—10 cm, basin versus longe ad breviter attenuatae, ultima basi saepe obtusae et/vel alis angustis petiolo decurrentibus, dentibus tam continuationibus nervorum primorum quam saepe multarum intercalarium venarum, subglabrae ad parce puberulae, nervis 20—30 paribus, petiolo brevi 2—15 mm longo, 1/15—1/50 lamininae breviori, glabro vel parce puberulo. Paniculae 16—50 cm longae.

Blades of well developed leaves 10—24 by 4—10 cm, towards the base long- to short-attenuate, at the very base often obtuse, and /or with narrow wings decurrent on the petiole, more or less dentate not only as extensions of the nerves but often also of few to many intercalary veins, subglabrous to sparsely puberulous; nerves 20—30 pairs; petiole short, 2—15 mm, $^{1}/_{15}$—$^{1}/_{50}$ as long as the leaf-blade, glabrous to sparsely puberulous. *Panicles* 16—50 cm.

Distribution: Only found in extreme NE. Yunnan (Long Ky; Chen Fong Shan; Chenhsiung) and adjacent W. Szechuan (Mt. Omei). — Fig. 21.

Ecology: At altitudes from *c.* 650 m up to *c.* 1900 m, especially on Mt. Omei several times collected at *c.* 1800 m.

Field notes: Leaves glaucous beneath.

Remarks. Though I have seen a few intermediate specimens, it seems that var. *multinervia* keeps distinct from var. *cuneifolia*, since on Mt. Omei typical representatives of both varieties have been collected at the same altitudes. It is certainly neither a separate species, nor a hybrid population, and it is especially a remarkable taxon because of the peculiar fact that in several respects it is very similar to ssp. *dilleniifolia*, notably in its high number of nerve-pairs and its close dentation; it is a kind of prototype, from which one could imagine ssp. *dilleniifolia* as well as ssp. *cuneifolia* to be derived. In fact it takes a position in between; if it did not occur within the area of ssp. *cuneifolia* it could as well be considered a variety of ssp. *dilleniifolia*. Of course the evidence is insufficient, but it is an attractive point of view to consider var. *multinervia* a relict of the ancestral stock from which either both ssp. *dilleniifolia* and ssp. *cuneifolia*, or only ssp. *cuneifolia*, have developed. The situation of its well-defined area, moreover, might be considered logic for a hypothetical centre of development of the species group *M. parviflora—dilleniifolia—myriantha* (series *Rectinervia*); see p. 375.

c. ssp. **flexuosa** (Pamp.) Beus., *stat. nov.* — *M. flexuosa* Pamp., Nuov. Giorn. Bot. Ital. n.s. 17 (1910) 423; Chun, Sunyatsenia 2 (1934) 77; Cufod., Oest. Bot. Z. 88 (1939) 258; How, Acta Phytotax. Sin. 3 (1955) 438, t. 57 f. 14—16; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235; Krüssm., Handb. Laubgeh. 2 (1962) 128, t. 57 b. — Type: *Silvestri 1391* (Hupeh), not seen.

M. myriantha (*non* Sieb. & Zucc.) Diels, Bot. Jahrb. 29 (1900) 451 ('*myrianthum*'), *pro min. parte.*

M. pendens Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 200; Rehd. in Rehd. & Wils., J. Arn. Arb. 8 (1927) 165; Hand.-Mazz., Symb. Sin. 7 (1933) 644; Tsoong, Contr. Inst. Bot. Nat. Acad. Peiping 4 (1936) 81; Rhed., Man. Cult. Trees & Shrubs (1940) 594; Cufod., Oest. Bot. Z. 88 (1939) 258, *in obs.* — Type: *Wilson 326a, pro parte* (Hupeh), seen from A. Paratypes: *Henry 5849d*, seen from E, GH, W, *6000*, seen from K; *Wilson 326a, pro parte*, not seen, *1647*, seen from A.

M. cuneifolia Franch., *sensu* Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235, *pro parte.*

[? *M. meliantha* Krüssm., Handb. Laubgeh. 2 (1962) 128, t. 57 d, *nomen.*] See the remarks. — **Photogr. 2.**

Leaves 4—16 by 2—8 cm, index 2—2½, at the base attenuate or cuneate, sometimes acute, closely to rather remotely dentate to slightly repand, with teeth usually ending

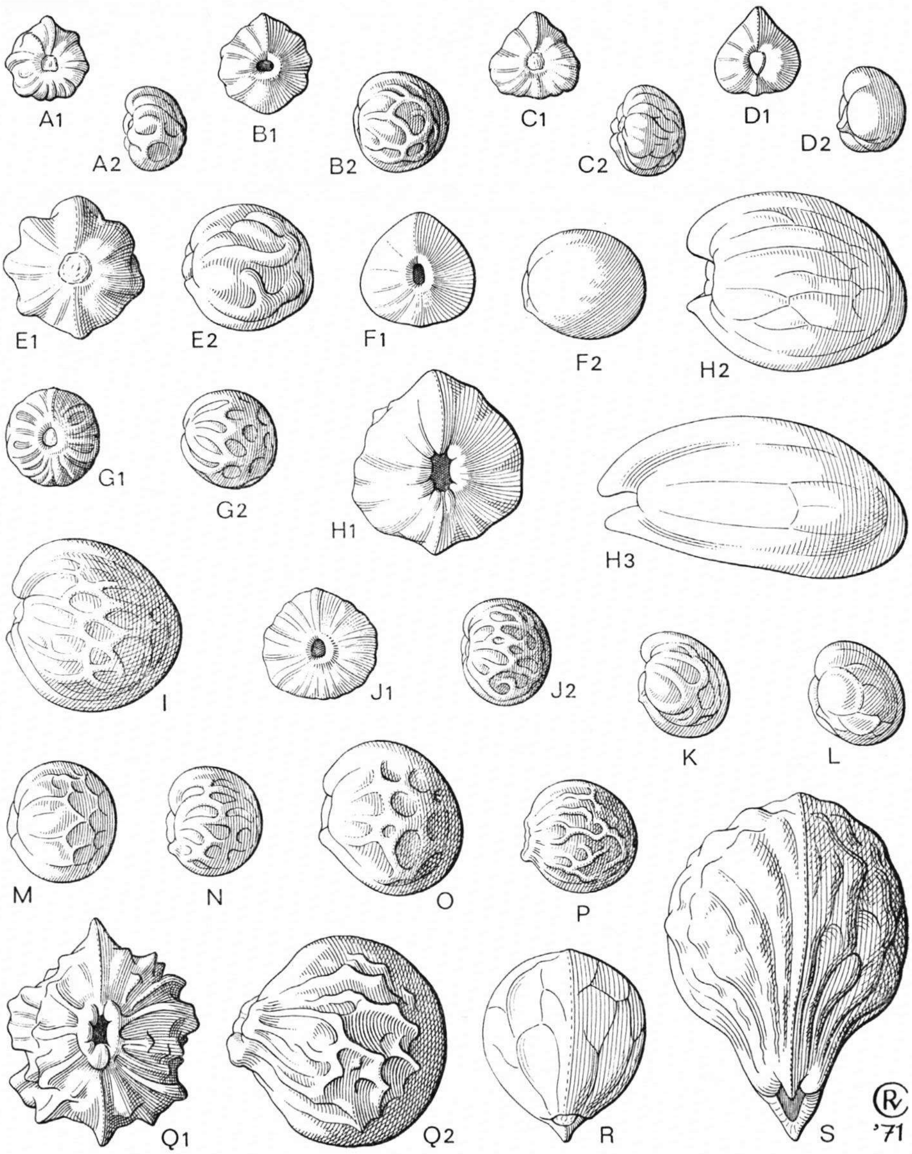

Fig. 22. Endocarps in subg. *Meliosma* (subsect. *Pinnatae* excluded). All × 3.
A1, 2. *M. parviflora* (*W. P. Fang 6044*). — B1, 2. *M. myriantha* ssp. *pilosa* (*Tang & Hsia 153*). — C1, 2. *M. dilleniifolia* ssp. *dilleniifolia* (*Watt 8397*). — D1, 2. *M. dilleniifolia* ssp. *cuneifolia* (*Wilson 1458*). — E1, 2. *M henryi* ssp. *thorelii* (*Henry 12647*). — F1, 2. *M. henryi* ssp. *henryi* (*Cavalerie 3312*). — G1, 2. *M. paupera* (*T. M. Tsui 795*). — H1—3. *M. lepidota* ssp. *lepidota* (*Korthals s.n.*). — I. *M. lepidota* ssp. *longipes* (*W. T. Tsang 27143*). — J1, 2. *M. lepidota* ssp. *squamulata* (*W. T. Tsang 25933*). — K. *M. simplicifolia* ssp. *simplicifolia* (*C. W. Wang 77878*). — L. *M. simplicifolia* ssp. *yunnanensis* (*Forrest 10381*). — M. *M. simplicifolia* ssp. *pungens* (*Wight 545*). — N. *M. simplicifolia* ssp.*fordii* (*C. W. Wang 78672*). — O. *M. simplicifolia* ssp. *thomsonii* (*Forrest 26651*). — P. *M. simplicifolia* ssp. *rigida* (*H. C. Chow 1891*). — Q1, 2. *M. simplicifolia* ssp. *laui* (*S. K. Lau 29*). — R. *M. dentata* (*Hinton 8431*). — S. *M. herbertii* (*Heller 729*). — R and S from Central America (subg. *Meliosma* sect. *Lorenzanea*).

in mucros which may be the extension of a nerve, but often as well of an intercalary vein, chartaceous, subglabrous to very sparsely pubescent beneath, with or usually without domatia; nerves (10—)12—21 pairs. *Panicles* erect to often deflexed, 7—22 cm, lax and sometimes poor, with more or less zigzag-twisted main and often also side-axes, the latter often reflexed. *Mature buds* 2—3 mm ø. Lobes of *inner petals* widely divergent, blunt, ciliolate to fimbriate only at the tip, sometimes with a minute central lobule. *Ovary* glabrous, sometimes sparsely puberulous to pubescent. *Endocarps* with distinct, fine, prominulous reticulation.

Distribution: East Central China: W. Hupeh, S. Shensi (Ta Pa Shan), S. Anhwei (Chiu Hwa Shan), Chekiang (near Siachu; Tien Tai Shan), N. Kiangsi (Lu Shan), Hunan (near Hsinhwa), N. Kwangtung (Yu Yuen). Locally common. — Fig. 21.

Ecology: In forests of the mixed mesophytic type, at altitudes from *c.* 600 m up to *c.* 1300 m. Reported to occur in dense shaded woods and in open thickets, sometimes at a stream or pond. Once said to grow on sandy soil.

Field notes: Bark grey, smooth, lenticellate. Leaves ornamental, dark green above, greyish or pale green beneath. Fruit reported to be red, with viscid 'seeds', but Steward, l.c., says it is black (?).

Vernacular names: *Chui Chih Pao Hua Shu* (*fide* Steward, l.c.).

Remarks. In W. Hupeh the area of this subspecies overlaps that of ssp. *cuneifolia*; see there.

The invalidly published name *M. meliantha* Krüssm., l.c., has been based upon a specimen which, judging from the picture of a leaf, may belong to ssp. *flexuosa*, or possibly to ssp. *cuneifolia*.

d. ssp. **tenuis** (Maxim.) Beus., *stat. nov.* — *M. tenuis* Maxim., Diagn. Pl. Nov. Jap. Mandsh. 4 & 5 (26-VI-1867) 262; Franch. & Savat., En. Pl. Jap. 1 (1873) 92; Matsum., Ind. Pl. Jap. 2 (1912) 336; Rehd., Man. Cult. Trees & Shrubs (1940) 594; Hara, En. Sperm. Japon. 3 (1954) 121; Makino, Ill. Fl. Jap. (1954) 348, f. 1043; Krüssm., Handb. Laubgeh. 2 (1962) 128; Ohwi, Fl. Japan (1965) 613. — Type: *Tschonoski s.n.* (Japan), seen from BO, GH, K, L, P, W.

M. tenuiflora Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (2-VII-1867) 93; Cat. Mus. Bot. 1 (Fl. Jap.) (1870) 23. — Type: *Keiske s.n.* (Japan), seen from L (holo).

Leaves 3—16 by 1½—7 cm, index (1½—)2—3, at the base attenuate to cuneate, sometimes acute, coarsely and rather remotely dentate to rather deeply repand with teeth usually ending into mucros which may be the extension of a nerve, but often as well of an intercalary vein, chartaceous to herbaceous, subglabrous to very sparsely pubescent, beneath always with more or less conspicuous domatia; nerves (6—)8—14(—15) pairs. *Panicles* erect to deflexed, 5—15 cm, lax and often poor, with more or less zigzag-twisted main and often also side-axes, the latter often reflexed. *Mature buds* 2—3 mm ø. Lobes of *inner petals* acute, fimbriate at the outer margin. *Ovary* glabrous. *Endocarps* with smooth surface or nearly so (cf. fig. 22 D 1, 2).

Distribution: Japan: Honshu (western and central districts, and just entering northern district), Shikoku, Kyushu. Common. — Fig. 21.

Ecology: In deciduous broad-leaved forests, at medium altitudes, usually collected between 600 m and 1200 m, sometimes lower. In woods and thickets.

Field notes: Bark dark greyish brown, smooth. Fruits glossy black when ripe.

Vernacular names: *Miyama-hahaso* (standard Japanese name), also *Miyamahoso* or *Mijama hoasa*.

b. Series *Curvinervia* Beus., *ser. nov.*1)

Frutices vel arbores parvae ad mediocres, sempervirentes. Folia nervis omnibus vel prope omnibus manifeste ascendentibus.

Evergreen shrubs or small to medium-sized trees. Leaves with nerves that are all or almost all distinctly ascending.

Type species: *M. simplicifolia* (Roxb.) Walp.

Distribution: Continental SE. Asia up to *c.* 30° N including E. and S. India and Ceylon, also in W. Malesia and Japan. — Fig. 27.

Ecology: In subtropical to tropical evergreen forests, at low to high altitudes.

Remarks. The distribution pattern of this series has been discussed in part I chapter E.

4. **Meliosma henryi** Diels — *M. thorelii* Lecomte — *M. mannii* Lace — *M. buchananifolia* Merr. — *M. affinis* Merr. — For full references, see under the subspecies.

Evergreen tree, small to medium-sized, up to *c.* 18 m. *Flowering twigs* terete to more or less angular, 1½—7 mm ø, sparsely puberulous to glabrous. *Leaves* obovate-oblong to obovate-lanceolate, sometimes oblong to lanceolate, 3—25 by 1—9 cm, index 2—4, at the base acute, cuneate, or attenuate, at the apex subacute to acuminate, sometimes short-cuspidate, entire or remotely spinously dentate especially towards the apex, chartaceous to usually firmly coriaceous, shining above, usually dull and slightly paler beneath, above (sub)glabrous, beneath subglabrous to faintly puberulous, and sometimes with minute hairy domatia in the axils of the nerves; midrib above somewhat prominent, beneath distinctly so; nerves 6—25 pairs, above slightly prominent to somewhat impressed, beneath slightly to distinctly prominent, ascending, usually looped and joined near the margin; venation distinct, sometimes inconspicuous, reticulate, prominulous beneath and above; petiole ½—3 cm, glabrous to puberulous. *Panicles* terminal, rarely axillary, erect, lax to rather dense, mostly widely pyramidal, (5—)10—35 cm, usually profusely branched up to the (2nd) 3rd or 4th order, branches spreading, terete to angular, usually rather stiff and coarse, to rather slender, sparsely to densely puberulous, bearing numerous solitary to crowded flowers; main axis terete to angular, sometimes shallowly canaliculate; primary side-axes usually many, up to *c.* 15 cm, the lower ones often subtended by small to reduced leaves; bracts ovate to linear-lanceolate, up to *c.* 5 mm, puberulous. *Pedicels* absent or present, up to *c.* 4 mm. *Mature buds c.* 2 mm ø. *Sepals* (3) 4 or 5, triangular to ovate, more or less unequal, the inner 3 or 4 *c.* 1 mm, the outer 1 or 2 smaller, often minute, often lowered on the pedicel, all glabrous, with entire ciliolate margin. *Outer petals* glabrous. *Inner petals* oblong to lanceolate, 1½—2⅓ mm, entire, glabrous. *Stamens*: anther-cells (⅕—)¼—⅓(—½) mm ø; filaments ¾—1⅓ mm. *Ovary* ½—¾ mm, glabrous to pubescent. *Style* ⅔—1⅓ mm, glabrous. *Fruit* globose to somewhat obovoid, when ripe 5—8 mm ø; endocarp globose to somewhat obovoid, hardly or not oblique, 4—6 mm ø, with or without reticulum; median keel distinct or not, blunt, only very rarely running out into a ventral processus or tubercle; ventral pore not sunken (fig. 22 E, F).

Distribution: NE. India (Assam), N. Burma, South and Central China, N. Laos, N. Vietnam. For details, see under the subspecies. — Fig. 23.

Ecology: In subtropical to tropical forests, at medium altitudes. For details, see under the subspecies.

Remarks. M. henryi is in general habit very similar to certain forms of *M. simplicifolia*, especially to ssp. *fordii* and ssp. *simplicifolia*, from which it is usually impossibly to be

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1) Species 4—7 in this paper.

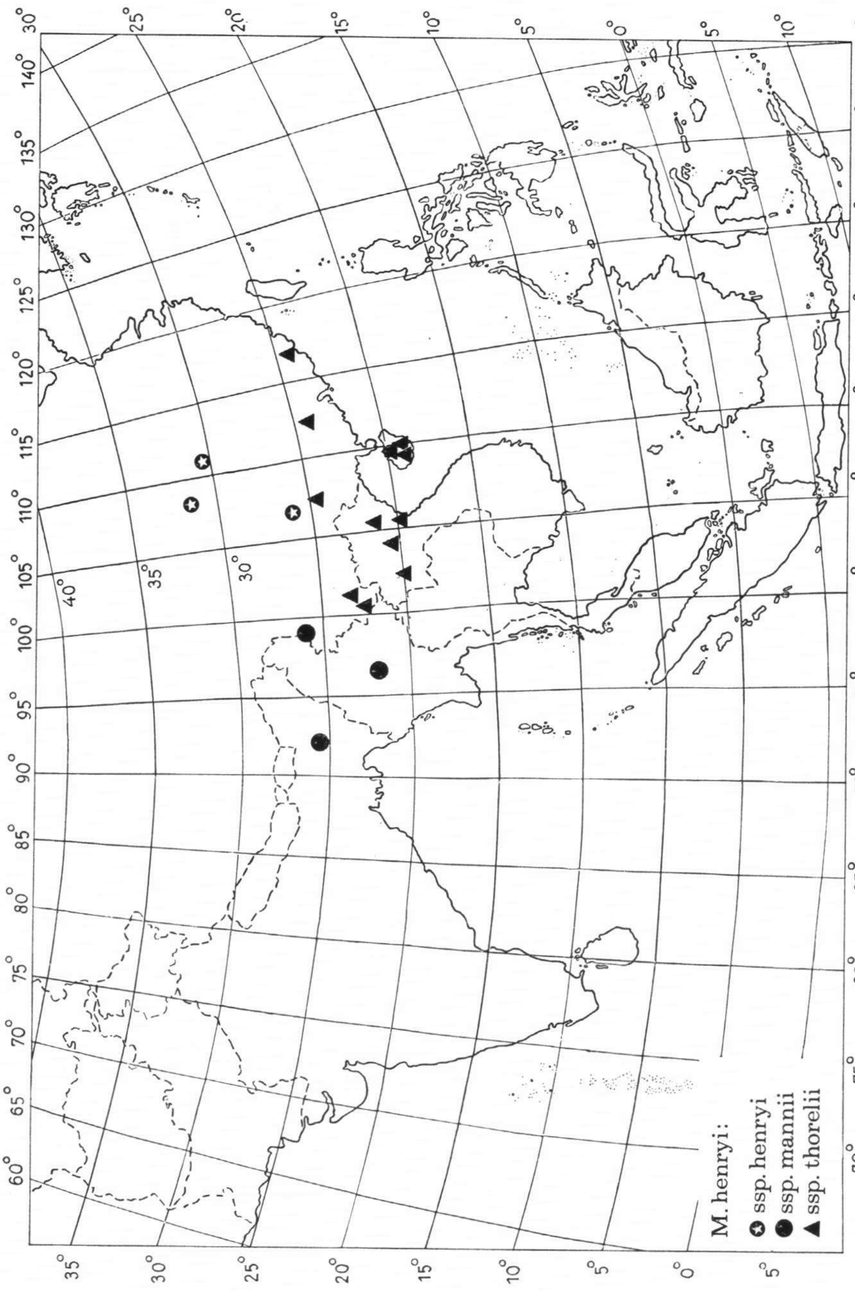

Fig. 23. Distribution of the subspecies of *M. henryi*.

distinguished in vegetative stage. It is, however, probably not so closely allied to *M. simplicifolia* as might be suspected at first sight, since there are good and constant generative characters separating them, notably in the inner petals and the endocarps (see the key). In addition to this, the area of *M. henryi* is entirely overlapped by that of *M. simplicifolia*, both species often occurring together at the same localities, and no indication of hybridization having ever been found.

It can be divided up in three well-marked subspecies, which — as do most subspecies of *M. simplicifolia* — diverge in different directions from a common centre in SW. China: ssp. *thorelii* to the south and east, ssp. *henryi* to the northwest, and ssp. *mannii* to the east and southeast. Since especially the latter two subspecies have not often been collected, the delimitation of the areas is not as clear as would be desirable, but the general picture seems quite obvious.

The three subspecies in question were considered good species by all former authors, but I have reduced them to subspecific rank for the following arguments. Though they are generally well-marked, there is some fading of the discriminative characters towards the area where the three subspecies meet. For instance, *Tsai 54553* from Lushuei (Yunnan) is more or less transitional towards ssp. *thorelii* in leaf- and fruit-characters, and hence has more or less arbitrarily been included in ssp. *mannii*. Furthermore, in *Thorel 3483* from Luang Prabang (Laos), and *Wang 75840* from Che-li (Yunnan), though definitely belonging to ssp. *thorelii*, the pubescence on the ovary is very reduced, resp. wanting. Then, the differences between ssp. *mannii* and ssp. *henryi* are essentially intergrading, and there is good reason to assume that transitional specimens would have been present, if more material — especially from Yunnan — would have been available. There is some lack of evidence, due to the scarcity of collections from critical localities; however, the general pattern, albeit somewhat fragmentary, is essentially the same as in the subspecies of *M. simplicifolia*: geographical (possibly also ecological (?); see the ecological remarks under the subspecies) isolation, a diverging of the areas from SW. China, and often the presence of transitional forms in contact zones between subspecies.

KEY TO THE SUBSPECIES

1. Ovary more or less, but distinctly and usually densely pubescent. Endocarp with distinct reticulum. Nerves (10—)15—25 pairs . . . . **a. ssp. thorelii**
1. Ovary glabrous or nearly so. Endocarp with smooth surface. Nerves 5—18 pairs.
    2. Leaves up to *c.* 12 by 3½ cm; nerves 5—10 pairs . . . . **b. ssp. henryi**
    2. Leaves up to *c.* 20 by 7½ cm; nerves 10—18 pairs. . . . . **c. ssp. mannii**

a. ssp. **thorelii** (Lecomte) Beus., *stat. nov.* — *M. thorelii* Lecomte, Bull. Soc. Bot. Fr. 54 (1907) 677; Fl. Gén. I.-C. 2 (1908) 4, f. 2 a, d, e, f; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 44. — Type: *Thorel 3483* (Laos), seen from L, P (holo).

M. buchananifolia Merr., Philip. J. Sc. 23 (1923) 250; Lingn. Sc. J. 5 (1927) 119; Cufod., Oest. Bot. Z. 88 (1939) 262; How, Acta Phytotax. Sin. 3 (1955) 429, t. 56 f. 1—4; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 40, t. 3 f. 5, 6. — Type: *MacClure 9732* (Hainan), seen from A, BM, E. K, P. W.

M. simplicifolia (*non* Walp.) Merr. & Chun, Sunyatsenia 1 (1930) 68.

M. affinis Merr., J. Arn, Arb. 21 (1940) 375; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 44; Vidal, Not. Syst. 16 (1960) 303. — Type: *Pételot 2125* (N. Vietnam), seen from A (holo), L, P.

Flowering twigs 3—7 mm ø. *Leaves* obovate-lanceolate or obovate-oblong, rarely oblong, up to *c.* 25 by 9 cm, index 2½—4, at the base acute to cuneate or somewhat attenuate, at the apex acuminate to subacute, with or without teeth; nerves (10—)15—25 pairs; petiole usually short and rather thick, sometimes longer and more slender. *Panicles* terminal, (10—)15—35 cm, branched up to the 4th order, with usually (very) coarse and rigid axes; primary side-axes up to *c.* 17 cm. *Flowers* rather crowded, sessile or short-pedicelled; pedicels up to *c.* 2 mm. *Inner petals* 2—2½ mm. *Ovary* usually densely, sometimes partly, pubescent. *Fruits* ± globose; endocarps (sub)globose, rarely somewhat ovoid, depressed or oblique, 5—6 mm ø, rather thick-walled (fig. 4 C 4), with more or less prominent, rather blunt reticulum; median keel mostly not very distinct and prominent, blunt; ventral pore not very wide and spouted (fig. 22 E 1, 2).

Distribution: S. China up to *c.* 25° N (cf. *M. simplicifolia* ssp. *fordii*): S. Yunnan (Szemao; Che-li Hsien), Kweichow (by side of Hung-shui-kiang, at Kwangsi border), Kwangtung (Peh-kiang; Heung Shan; several localities on Hainan), Fokien (Changchow); Laos (Luang Prabang; Na Hem, Prov. Sam Neua); N. Vietnam (Provinces Thanh Hoa and Hoa Binh). Apparently common on Hainan and in N. Vietnam and N. Laos (*fide* Poilane), probably much less so in the mainland of China. — Fig. 23.

Ecology: Probably in tropical rain forests, as follows from field notes and distribution range. Found at altitudes of about 500 m to 800—900 m, in Yunnan at higher elevation, viz. at 1100 m (Che-li) and 1500 m (Szemao). Several times reported to occur at streams, also in wooded ravines and in light mixed woods. In N. Vietnam said to occur on good, loamy, rocky soil.

Vernacular names: China: *Fa muk heung* (Hainan, once mentioned; see also *M. simplicifolia* ssp. *fordii* and ssp. *rigida*). Laos: *Co lêng* (Sam Neua). N. Vietnam: *Co phiên* (Thanh Hoa).

Remarks. See under the species.

b. ssp. **henryi.** — *M. henryi* Diels, Bot. Jahrb. 29 (1900) 452; Hemsl. in Hook., Ic. Pl. 9 (1907) t. 2832; Hand.-Mazz., Symb. Sin. 7 (1933) 644; Cufod., Oest. Bot. Z. 88 (1939) 262; How, Acta Phytotax. Sin. 3 (1955) 430, t. 56 f. 5—11. — Type: *Henry 5865* (Hupeh), seen from A, BM, K, P.

Flowering twigs 1½—3(—5) mm ø. *Leaves* oblong to lanceolate, up to *c.* 12 by 3½ cm, index 2—3½(—4), at the base acute or somewhat attenuate, at the apex acuminate to subacute, often somewhat falcate, usually entire, rarely finely dentate; nerves 5—10 pairs; petiole rather slender and comparatively long. *Panicles* usually terminal, sometimes axillary (type B; see fig. 1), (5—)10—20 cm, branched up to the 2nd or 3rd order, with coarse and rigid to usually slender axes; primary side-axes up to *c.* 6 cm. *Flowers* crowded or not, pedicelled; pedicels up to *c.* 4 mm. *Inner petals* 1½—2 mm. *Ovary* glabrous. *Fruits*[1]) ± obovoid; endocarps globose, *c.* 5 mm ø, not thick-walled, without or with very vague reticulum; median keel not or only vaguely visible; ventral pore not wide, not spouted (fig. 22 F 1, 2).

Distribution: China: Kwangsi (Nee Bai, border of Kweichow), Kweichow (Chuen Ning Shan, near Kweiyang; Majo), W. Hupeh (*sine loco*), E. Szechuan (Chen Keou Tin). Probably rare, as was also observed on a field-note from Kwangsi. — Fig. 23.

Ecology: Probably in subtropical evergreen broad-leaved forests, collected at 700 m and 1100—1250 m altitude. Reported to occur on sandy soil, in open woods, and in a temple-ground.

Field notes: Habit more or less like a privet (*Ligustrum* sp.). Bark brown, peeling off in thick elongated plates.

Remarks. See under the species.

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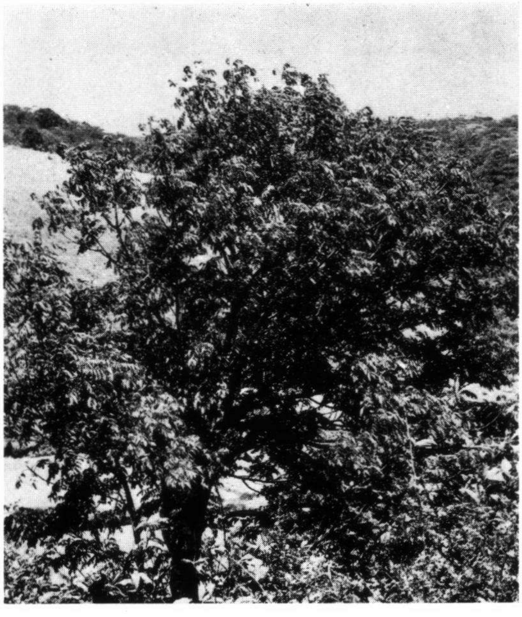
[1]) Only one specimen in fruit available.

Photogr. 1. The author's wife (1.75 m tall) holding an inflorescence of normal length of *M. lanceolata*. — Kebun Raja, Bogor, Indonesia. January 1970.

Photogr. 2. *M. dilleniifolia* ssp. *flexuosa*. — Twigs with remnants of inflorescences of the preceding year. A few fruits are still visible. Note the characteristic, zigzag-twisted, somewhat deflexed rachis of the panicles. — Kew Botanic Gardens. March 1971.

Photogr. 3. *M. veitchiorum*. — About 70 years old tree. Note the coarse branches and the rough, fissured bark. — Kew Botanic Gardens. March 1971.

Photogr. 4. *M. pinnata* ssp. *arnottiana* var. *oldhamii*. — About 4 m high treelet. Note the ascending branches. — Kew Botanic Gardens. March 1971.



Photogr. 5. *M. pinnata* ssp. *arnottiana* var. *arnottiana*. — Medium-sized tree. Though somewhat hidden by the leaves, it can still be seen that the way of branching is similar as in the tree of photogr. 4. — Hakgala, Ceylon. September 1969.

c. ssp. **mannii** (Lace) Beus., *Stat. nov.* — *M. mannii* Lace, Kew Bull. (1915) 113; Cald. et al., Rec. Bot. Surv. India 11 (1926) 89. — Lectotype: *Lace 5282* (Burma), seen from E (holo), K, L. Syntypes: *Lace 5371*, seen from E, K, L; *Mann 260*, seen from K.

Flowering twigs 2½—5(—7) mm ø. *Leaves* obovate-oblong, sometimes oblong, up to *c.* 20 by 7½ cm, index 2—3, at the base acute or somewhat attenuate, at the apex acuminate to subacute, without or rarely with some teeth, (sub)glabrous, sometimes with feeble domatia in the axils of the nerves beneath; nerves 10—18 pairs; petiole usually rather slender, short to rather long. *Panicles* terminal, 15—25 cm, branched up to the 3rd order, with rather coarse and rigid axes; primary side-axes up to *c.* 17 cm. *Flowers* rather crowded, sessile or short-pedicelled; pedicels up to *c.* 1 mm. *Inner petals* 1⅔—2 mm. *Ovary* glabrous or nearly so. *Fruits* ± obovoid; endocarps globose or somewhat obovoid, 4—6 mm ø, not thick-walled, without or with very vague reticulum; median keel not or only vaguely visible; ventral pore mostly wide and somewhat spouted.

Distribution: NE. India: Assam (Khasi Hills); N. Burma: Mandalay (Maymyo Plateau); China: W. Yunnan (Lushuei). Probably rare; only collected several times on Maymyo Plateau, and there reported to be frequent. — Fig. 23.

Ecology: Probably in tropical hill-forests. Found at 600—900 m (Khasi Hills), 900—1000 m (Maymyo), and 1400 m (Lushuei). In Maymyo reported to be found by streams.

Vernacular names: Burma (Maymyo): *Ye thit nee* (three times reported!).

Remarks. See under the species.

5. **Meliosma lepidota** Bl. — *M. squamulata* Hance — *M. pedicellata* K. & V. — *Machilus nervosa* Merr. — *M. monophylla* Ridl. — *M. lutchuensis* Koidz. — *M. vulcanica* Merr. — *M. dumicola* W. W. Smith — *M. bontocensis* Merr. — *M. tsangtakii* Merr. — *M. sterrophylla* Merr. — *M. caudata* Merr. — *M. coriacea* Merr. — *M. longipes* Merr. — *M. longepaniculata* Gagn. — *M. pakhaensis* Gagn. — *M. elliptica* Gagn. — *M. depauperata* Chun *ex* How — *M. spathulata* Vidal — *M. cinerea* Vidal — *M. tonkinensis* Vidal — *M. dumicola* var. *serrata* Vidal — *M. nana* Vidal — *M. dolichomischa* Vidal — For full references, see under the subspecies.

Evergreen shrub or tree, usually small, sometimes medium-sized, rarely large, up to *c.* 15(—22) m. *Flowering twigs* terete or somewhat angular upwards, 1½—7 mm ø, pubescent when young, soon glabrescent. *Leaves* elliptic or obovate to lanceolate or obovate-lanceolate, 2—32 by ¾—12(—18) cm, index (1¼—)1½—3(—4), at the base acute to attenuate or cuneate, sometimes rounded, at the apex acute to caudate, rarely obtuse, usually entire, sometimes remotely spinously dentate especially towards the apex, chartaceous to coriaceous, dull or shining above, dull and usually paler beneath, usually (sub)glabrous, beneath sometimes sparsely to moderately pubescent especially on midrib and nerves, without domatia; midrib and nerves above usually more or less impressed, sometimes flat to slightly elevated, beneath more or less promunent; nerves 4—15 pairs, usually strongly ascending, looped and joined near the margin or not; venation distinct, often more or less cancellate, above flat to prominilous, beneath more or less prominent; petioles usually rather long, 1—10 cm, (⅛—)⅕—¾(—1¼) as long as the leaf-blade, usually glabrous, rarely sparsely puberulous or pubescent. *Panicles* terminal or axillary, usually erect, sometimes more or less pendulous, lax to dense, widely to usually narrowly pyramidal, 3—30(—200) cm, poorly to profusely branched up to the 2nd or 3rd (4th) order, branches more or less spreading, stiff to flaccid, very slender to coarse, more or less angular, subglabrous to usually densely pubescent, bearing usually numerous solitary to crowded flowers which are sometimes spicately arranged; main axis present or absent and then one or more (up to 10) close-set primary side-axes taking over its function, terete to more

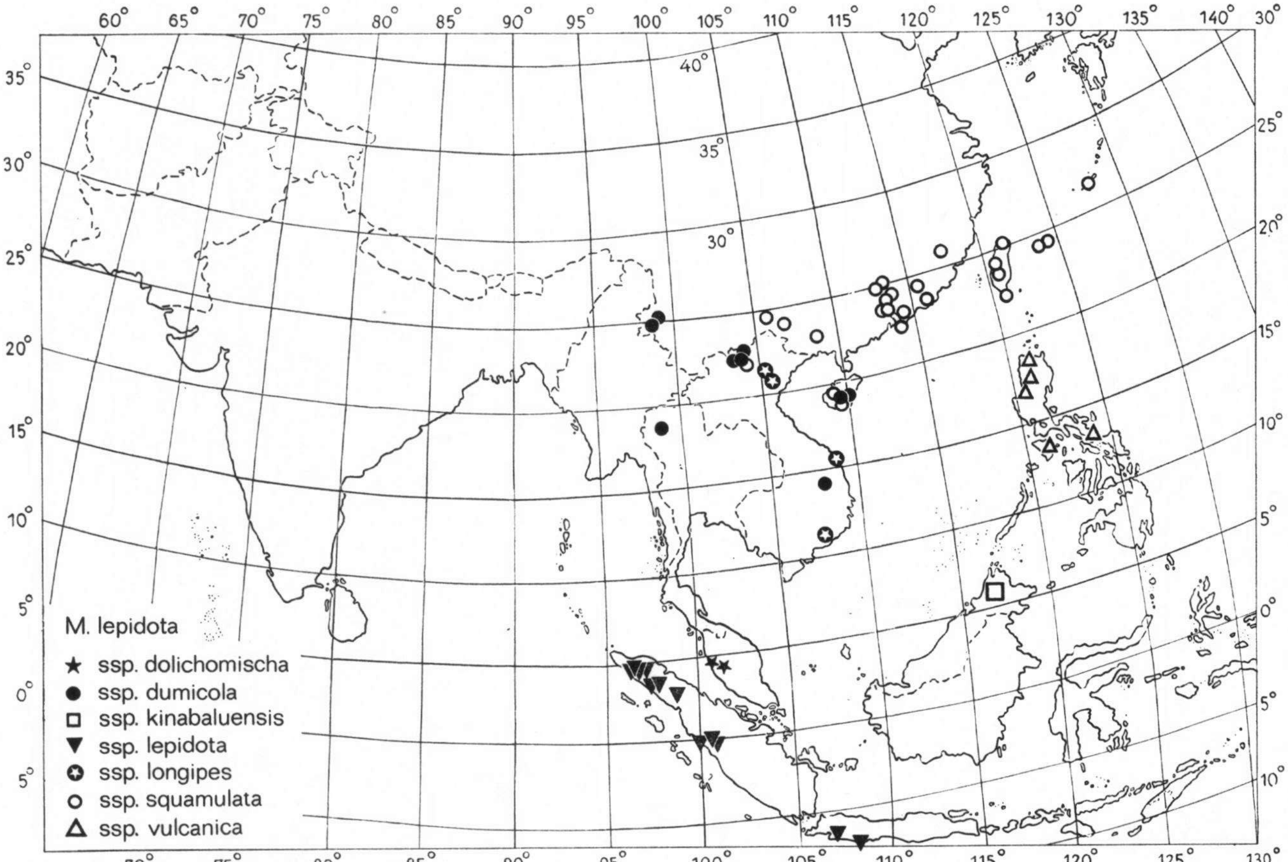


Fig. 24. Distribution of the subspecies of *M. lepidota*.

or less angular, flattened or shallowly canaliculate towards the top; primary side-axes[1] few to usually many, usually short, up to *c.* 15(—40) cm, sometimes subtended by normal to small leaves; bracts ovate to linear-lanceolate, up to *c.* 2(—6) mm, subglabrous to usually densely pubescent. *Pedicels* absent or present, up to *c.* 3(—5) mm. *Mature buds* 1½—3 mm ø. *Sepals* (4) 5[2], (round-)ovate, subequal, 1—2 mm, or the outer 1 or 2 smaller, often one lowered on the pedicel, glabrous or the outer ones somewhat pubescent, all with entire ciliolate margin. *Outer petals* glabrous. *Inner petals* ± lanceolate and entire, or bifid, (⅔—)¾—2½ mm, glabrous or somewhat ciliolate at margin or tip, when bifid never with a central lobule. *Stamens*: anther-cells ⅕—⅓(—½) mm ø; filaments ¾—1½ mm. *Ovary* ½—1 mm, glabrous, very exceptionally pubescent. *Style* (¼—½)—1(—1¼) mm, glabrous. *Fruit* (sub)globose, sometimes elliptic, when ripe 5—10 mm ø; endocarp globose to ellipsoid, oblique or not, hardly or not depressed, 4—8(—9) mm ø, without or with usually only slightly elevated rather fine reticulum; median keel distinct, more or less prominent; ventral pore whether or not sunken but never spouted (fig. 22 H, I, J).

Distribution: S. China, Taiwan, Riu Kui Islands, Philippine Islands, Vietnam, N. Thailand, Malay Peninsula, Sumatra, N. Borneo (Sabah), W. Java. For details, see under the subspecies. — Fig. 24.

Ecology: In evergreen forests under tropical or subtropical conditions, at medium to high altitudes; for details, see under the subspecies.

Remarks. M. lepidota displays a rather wide variation, especially in the ramification of its panicles which covers almost the whole range of possibilities found throughout *Meliosma.* Also the leaves vary much, though not so excessively as in *M. simplicifolia.* The variation in these two species is such that certain forms of one species may extremely resemble forms of the other, for instance *M. lepidota* ssp. *dumicola* and *M. simplicifolia* ssp. *fordii* from N. Vietnam. It must be admitted that there is not one single character by which *M. lepidota* and *M. simplicifolia* can be separated satisfactorily. Hence the criterium on which they are considered good species is found in combinations of characters which contrast them against each other as homogeneous groups. These combinations are for each species mainly composed as follows:

M. lepidota	*M. simplicifolia*
leaves rarely pubescent	leaves glabrous or pubescent
nerves always rather few	nerves mostly rather many
petioles mostly (rather) long	petioles not often rather long
panicles usually axillary	panicles usually terminal
inner petals entire or bifid	inner petals bifid
endocarps often elliptic	endocarps never elliptic

As an additional support to the concept that *M. lepidota* and *M. simplicifolia* are good, separate, species, it may be advanced that hybrids or transitional forms between them have not been found, though both have often been collected in the same localities. There is, however, sometimes (e.g. in N. Vietnam; see under *M. simplicifolia* ssp. *fordii*) some convergence in general habit between local populations of the two species, but this does, of course, not mean that interspecific genetical contact occurs.

Another fact which should be noted is, that the area of *M. lepidota* and that of *M. simplicifolia* ssp. *fordii* and ssp. *fruticosa* (taken as a unit; see the remark under *M. simplici-*

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[1] Often essentially secondary! See part I chapter C sub a.

[2] Only in *Ramos Bur. Sci. 40998* from the Philippines 6 or 7 sepals; see note on p. 466.

folia) coincide to a great extent; for further comment on this see part I chapter E sub a 1.

Within *M. lepidota* I have recognized seven subspecies, most of which were formerly considered species. The differences between them are on the same level as in other subspecies in *Meliosma*. Transitional forms between these subspecies, however, occur in only a few cases, which is logic, since there is perfect geographical isolation between most of them. See further the remarks under the subspecies.

KEY TO THE SUBSPECIES

1. Leaves with 4—8 pairs of nerves. Inner petals distinctly bifid, very rarely ± entire and truncate. Endocarps globose, 4—4½ mm ø . . . . **a.** ssp. **squamulata**
1. Leaves with 7—15 pairs of nerves. Inner petals bifid or entire. Endocarps globose or ellipsoid to obovoid, 6—8(—9) mm ø.
    2. Inner petals distinctly bifid.
        3. Leaves 1½—2(—2½) times as long as wide; petiole ¼—⅜ x length of blade. Panicles 5—15 cm. Mature buds 2—2½ mm ø. Endocarps ellipsoid to obovoid. . . . . **b.** ssp. **kinabaluensis**
        3. Leaves (1⅔—)2—3(—3½) times as long as wide; petiole (1/8—)1/6—⅓(—2/5) x length of blade. Panicles 3—30(—200) cm. Mature buds 1½—2(—2¼) mm ø. Endocarps globose or ellipsoid to obovoid.
            4. Endocarps (sub)globose, not higher than wide. . . . . **c.** ssp. **longipes**
            4. Endocarps long- to short-ellipsoid (always distinctly higher than wide; fig. 22 H 1—3). **d.** ssp. **lepidota**
    2. Inner petals entire, usually lanceolate.
        5. Inner petals 2½ mm. Panicles distinctly axillary or ramiflorous. Mature buds 2½—3 mm ø. **e.** ssp. **dolichomischa**
        5. Inner petals 1—1½ mm. Panicles terminal or crowded at the end of the twigs, rarely distinctly axillary. Mature buds 1⅔—2½ mm ø.
            6. Style less than ½ mm. Leaves (sub)glabrous. . . . . **f.** ssp. **vulcanica**
            6. Style ½—1 mm. Leaves sparsely to densely pubescent beneath, rarely subglabrous. **g.** ssp. **dumicola**

a. ssp. **squamulata** (Hance) Beus., *stat. nov.* — *M. squamulata* Hance, J. Bot. 14 (1876) 364; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 146; Oliv. in Hook., Ic. Pl. 16 (1887) t. 1598; Henry, Trans. As. Soc. Japan 24, Suppl. (1896) 29; Hayata, Ic. Pl. Formos. 1 (1911) 161; Dunn & Tutch., Kew Bull. add. ser. 10 (1912) 68; Matsum., Ind. Pl. Jap. 2 (1912) 336; Groff, Lingn. Sc. Bull. 2 (1930) 67; Kaneh., Formos. Trees ed. 2 (1936) 418, f. 373; Hatus., J. Jap. Bot. 14 (1938) 240; Cufod., Oest. Bot. Z. 88 (1939) 261; Merr. & Chun, Sunyatsenia 5 (1940) 115; Hara, En. Sperm. Japon. 3 (1954) 121; Walker, Imp. Trees Ryukyu Isl. (1954) 201, f. 122; How, Acta Phytotax. Sin. 3 (1955) 426; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 31, *in obs.*, t. 4 f. 5; Liu, Ill. Lign. Pl. Taiwan 2 (1962) 926, f. 763; Li, Woody Fl. Taiwan (1963) 503, f. 194. — Type: *Lamont s. n. in Herb. Hance nr. 19316* (Hongkong), not seen.

M. lutchuensis Koidz., Bot. Mag. Tokyo 27 (1913) 563; Hatus., J. Jap. Bot. 14 (1938) 240, *in synon.* — Type: ?? (written in Japanese), not seen.

Leaves oblong, rarely elliptic or lanceolate, 2—12 by ¾—7 cm, index (1½—)2—3(—3½), entire, the base acute to attenuate, the apex cuspidate to caudate, with blunt tip, glabrous, usually with a white waxy layer beneath, which gives them a glaucous appearance; midrib and nerves above more or less elevated, rarely flat to somewhat impressed; nerves 4—8 pairs; petiole 1—10 cm (¼—)⅓—1(—1¼) as long as the blade. *Panicles* terminal, sometimes axillary (type D, E, F, sometimes G or H; see fig. 1), 4—15(—20) cm, usually rather poor, lax to dense, consisting of 1 to 8 main (essentially primary side-) axes each ramified up to the 2nd order; primary (essentially secondary) side-axes short, up to *c.* 5(—10) cm. *Mature buds* 2½—3 mm ø. *Inner petals* up to about halfway bifid, sometimes only truncate, (¾—)1—1½ mm; lobes widely diverging, rather wide, glabrous, sometimes ciliolate. *Ovary* subglobose to ovate, (½—)¾—1 mm, glabrous. *Style* (½—)⅔—1(—1¼) mm. *Endocarp* subglobose, sometimes somewhat oblique or depressed, 4—5 mm ø, with more or less distinct, slightly prominulous, fine, irregular reticulum; median keel rather feeble, slightly elevated, blunt, running out into a very minute ventral tubercle or processus, or not; ventral pore small, not sunken (fig. 22 J 1, 2).

Distribution: S. China (up to *c.* 25°—26° N: S. Kweichow, Kwangsi, Kwangtung, S. Fokien), Taiwan, Ryu Kyu Islands. Often reported to be rather common to abundant. — Fig. 24.

Ecology: In evergreen broad-leaved forests in the tropical forest zone of S. China, at lower medium altitudes, usually at 600—1000 m, sometimes higher, up to *c.* 1200 m. Reported from dry hill-tops, moist valleys, on stony slopes, in thickets, on dry clay, and along stream.

Field notes: The leaves are often said to be pale glaucous beneath; indeed a whitish waxy layer can be observed there in most herbarium specimens, which is responsible for this pale colour.[1])

Vernacular names: China: *Ch'ing sin shu* ('Balance first tree') and *Te min muk* ('Wild cotton wood'), both once mentioned from Lung T'au Shan, Kwangtung; *Ban kai shue*, once mentioned from Lin Fa Shan, Kwangtung. Ryu Kyu Islands: *Nanban-awabuki* (Japanese), *Surumichi* (Okinawa name), both mentioned in Walker, l.c.

Uses: Wood mostly for fuel, sometimes for implements. Said to be often grown as an ornamental in western countries (see Walker, l.c.).

Remarks: This very characteristic, uniform subspecies is replaced west and southwest of its area by ssp. *dumicola* and ssp. *longipes*.

Ssp. *dumicola* occurs in about the same vegetation type, but at distinctly higher altitudes; in Hainan, for instance, where both subspecies have been found, ssp. *squamulata* reaches *c.* 1100 m, but ssp. *dumicola* seems to be confined to higher elevations, having been collected at *c.* 1800 m. For the rest the areas of ssp. *squamulata* and ssp. *dumicola* are rather well separated, but contact may occur in boundary regions. Such contact probably occurs in N. Vietnam (Cha Pa), where an intermediate specimen has been collected at 1400 m (see under ssp. *dumicola*). Ssp. *longipes* replaces ssp. *squamulata* in southern direction (Vietnam) occurring in about the same altitudinal zone; I have not seen transitional specimens.

b. ssp. **kinabaluensis** Beus., *ssp. nov.* — *M. pedicellata* (*non* K. & V.) Merr. & Perry, J. Arn. Arb. 20 (1939) 356. — Type: *Clemens 33631* (Borneo, Mt. Kinabalu), seen from L (holo).

Folia elliptica, raro oblonga, 3—15 × 1½—9 cm, plerumque edentata, interdum remote dentata, basi acuta ad rotunda et quodammodo attenuata, apice cuspidata cuspe acuta, glabra vel subtus parce pubescentia, nervis 8—14 paribus, petiolo 1—7½ cm laminae ¼—⅜ breviori. *Paniculae* terminales vel axillares, 5—15 cm, sat pauperae et tenues. *Petala interiora* bifida, 1—1¼ mm, lobis ± ciliolatis. *Ovarium* subglobosum, c. ½ mm, glabrum, stylo ½—1 mm longo. *Endocarpium* ± pyriforme, c. 8 mm longum, reticulo carinaeque elevatulae, processo ventrali minuto, poro ventrali lato.

Leaves elliptic, rarely oblong, 3—15 by 1½—9 cm, index 1½—2(—2½), usually entire, sometimes remotely dentate, the base acute to rounded and somewhat attenuate, the apex cuspidate with acute tip, above glabrous or sometimes somewhat pubescent on the midrib, subglabrous to sparsely pubescent beneath, usually with a white waxy layer beneath, which gives a glaucous appearance; midrib and nerves more or less impressed

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[1]) For wood characters, see Kanehira, Formosan Woods (1921) 82, t. 17 f. 97.

above; nerves 8—14 pairs; petiole 1—7½ cm, ¼—⅔ as long as the blade. *Panicles* terminal or axillary, solitary or a few together (type D, E, F, G, H; see fig. 1), 5—15 cm, rather poor and lax, ramified up to the 2nd (3rd) order; primary (essentially secondary!) side-axes up to *c.* 8 cm. *Mature* buds 2—2½ mm ø. *Inner petals* halfway or somewhat less bifid, 1—1¼ mm; lobes rather narrow, more or less ciliolate. *Ovary* subglobose, *c.* ½ mm, glabrous. *Style* ½—1 mm. *Endocarp*[1]) ± obovoid, *c.* 8 mm long, *c.* 6 mm ø, with rather wide and feeble reticulum; median keel only slightly elevated, blunt, at one end running out into a minute ventral processus; ventral pore wide, not sunken.

Distribution: Borneo; only known from Mt. Kinabalu, where several times collected. — Fig. 24.

Ecology: In primary montane tropical forest, found at elevations between 1700 and 2700 m.

Field notes: The lower surface of the leaves is often said to be white to light grey; in herbarium specimens indeed a whitish waxy layer can be often observed. The general colour of the leaves is reported to be glaucous.

Remarks. Ssp. *kinabaluensis* has a very low degree of variability, a characteristic which is also found in the other subspecies of *M. lepidota*, with the exception of ssp. *dumicola* and ssp. *longipes*. It is most similar to ssp. *dolichomischa* (Malay Peninsula) and to ssp. *lepidota* (Sumatra), with which it shares, amongst others, the more or less ellipsoid endocarp; all other subspecies have (sub)globose endocarps (but of ssp. *dumicola* the fruit is unknown). This may mean that the three Malesian subspecies are somewhat closer related mutually than to the other subspecies. On the other hand, there are many morphological links connecting the Malesian subspecies with forms of ssp. *dumicola* and ssp. *longipes* from Yunnan-Tonkin. One might, moreover, also expect that at least ssp. *kinabaluensis* would be morphologically also closely related to the adjacent ssp. *vulcanica* from the Philippines. This is not the case, however; it much better joins certain forms of ssp. *dumicola* (see there), and in this respect resembles ssp. *squamulata* from S. China. Hence, on the base of this fact, one might suppose a direct genetical relationship between ssp. *kinabaluensis* — and, consequently, also ssp. *dolichomischa* and ssp. *lepidota* — with the Yunnan-Tonkin subspecies, rather than a relationship, via ssp. *vulcanica* from the Philippines, with ssp. *squamulata* from S. China. The plant-geographical implications of these suppositions have been discussed in part I chapter E sub a1.

c. ssp. **longipes** (Merr.) Beus., *stat. nov.* — *M. longipes* Merr., J. Arn. Arb. 23 (1942) 178; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 27, t. 4 f. 1, 2. — Type: *Pételot 2588* (N. Vietnam), seen from A (holo).

M. coriacea Merr., J. Arn. Arb. 23 (1942) 178; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 43. — Type: *Pételot 2585* (N. Vietnam), seen from A (holo).

M. longepaniculata Gagn., Bull. Soc. Bot. Fr. 99 (1952) 11; Not. Syst. 14 (1952) 272; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 37, t. 6 f. 1—3. — Type: *Eberhardt 4023* (N. Vietnam), seen from L, P (holo).

M. depauperata Chun *ex* How, Acta Phytotax. Sin. 3 (1955) 427, t. 55; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 39. — Type: *H. Y. Liang 69818* (Kwangsi), seen from A. Paratypes: *W. T. Tsang 27143*, seen from E, P, *29109*, seen from BO, E, L, P, *30710*, seen from E, P, SING.

M. spathulata Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 29, t. 3 f. 1, 2; Not. Syst. 16 (1960) 307. — Type: *Chevalier 38572* (S. Vietnam), seen from P (holo).

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[1]) Only few specimens available!

M. nana Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 37, t. 6 f. 7—10; Not. Syst. 16 (1960) 306. — Type: *Poilane 22128* (S. Vietnam), seen from P (holo). Paratype: *Poilane 23721*, seen from P.

Leaves usually obovate-oblong or oblong, sometimes elliptic, obovate-lanceolate or lanceolate, (5—)8—32 by (2—)3—12(—18) cm, index (1⅔—)2—3(—3½), usually entire, sometimes with some remote teeth, the base acute to cuneate, often somewhat attenuate, the apex acute or acuminate to long cuspidate, with acute or blunt tip, (sub)glabrous, without waxy layer beneath; midrib impressed above; nerves 9—15 pairs, flat to somewhat impressed above; petiole 1⅓—7½(—10) cm, (⅛—)⅙—⅓(—⅖) as long as the blade. *Panicles* axillary or ramiflorous, solitary or a few together (type H, I, sometimes E or G; see fig. 1), 11—200 cm, often poor, lax, and with very slender axes, ramified up to the 2nd or 3rd order; primary (essentially secondary!) side-axes short to long, up to *c.* 40 cm. *Mature buds* 1½—2(—2¼) mm ø. *Inner petals* halfway or somewhat less bifid, ⅔—1(—1¼) mm; lobes narrow to wide, ciliolate or not. *Ovary* subglobose, ½—⅔ mm, glabrous, rarely pubescent. *Style* ½—⅔ mm. *Endocarp* subglobose, sometimes somewhat oblique, *c.* 7—8 mm ø, with distinct, slightly elevated, rather fine reticulum; median keel distinct, blunt to rather sharp, at one end running out into a minute or inconspicuous ventral processus; ventral pore not or not much sunken (fig. 22 I).

Distribution: S. China (Kwangsi: Shih Wan Ta Shan, near border N. Vietnam), N. Vietnam (Ha Coi and Tien Yen, near border Kwangsi; Mt. Bavi, pr. Sontay; Tuyên Quang), S. Vietnam (Tourane; Blao, Pr. Haut Donnaï). Locally fairly common. — Fig. 24.

Ecology: In primary (also secondary?) tropical forest, at low to medium altitudes, up to *c.* 1200 m. Reported from old and dense forests on good loamy soil, also from marshy thickets on clayish soil.

Field notes: Once reported to be a climbing shrub 7—8 m tall with a stem hardly as thick as a wrist. Usually, however, said to be a small shrub or treelet (often very small: 1—2 m high).

Vernacular names: S. Vietnam: *So'n vôi* (Vietnamese, once reported from Tourane), *Nga ôs* (Proto-Indochinese, once reported from Blao).

Remarks. This subspecies displays an unusual polymorphy in its general habit. It can vary from a small tree with normal appearance to a minute erect shrublet or a long, slender, sarmentose shrub (see under field notes). Its axillary panicles may be rather short and grouped at or near the end of the twigs, or long to extremely long and flaccid (up to 2 m; '*M. longepaniculata*'), and then mostly solitary and often ramiflorous. Its leaves may be short- to long-petioled ('*M. longipes*'), acute to cuspidate, and (when dry) have a pale greyish to dark brownred colour. In spite of this high degree of variability I believe ssp. *longipes* to be a natural unit, since it is homogeneous in flower and — as far as present — also in fruit characters. This opinion is also based on the evaluation of similar polymorphic tendencies in ssp. *dumicola*. Both subspecies have, in contrast to the other subspecies, apparently maintained a high degree of morphologic flexibility, which may partly be connected with differences in environmental conditions. Population studies in the field, especially in N. Vietnam, where extremely different froms have been found in the same region (Mt. Bavi; Tuyên Quang), might provide conclusive evidence in this respect.

See also the remarks under the other subspecies.

d. ssp. **lepidota.** — *M. lepidota* Bl., Rumphia 3 (1849) 199; Walp., Ann. 2 (1852) 224; Miq., Fl. Ind. Bat. 1, 2 (1859) 614; Sum. (1860) 203; Illustr. (1871) 73; Hance, J. Bot. 14 (1876) 364, *in obs.*; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 39, *in obs.* — Type: *Korthals s.n.* (Sumatra), seen from BO, K, L (holo), U, W.

M. pedicellata K. & V., Bijdr. 9 (1903) 134; Koord., Exk. Fl. Java 2 (1912) 545; K. & V. in Koord., Atlas 2 (1914) t. 379; Back. & Bakh. *f.*, Fl. Java 2 (1965) 144. — Type: *Koorders 26243* (Java), seen from BO, L.

Leaves oblong, sometimes somewhat ovate-oblong, rarely elliptic, 5—26 by (1½—)2—12 cm, index (1⅔—)2—3, entire, the base acute to attenuate, the apex acute to caudate with acute or blunt tip, glabrous (when young sometimes sparsely pubescent beneath), without waxy layer beneath; midrib and nerves above distinctly to hardly impressed; nerves 8—12(—14) pairs; petiole 1½—6 cm (⅙—)⅕—⅓(—½) as long as the blade. *Panicles* axillary, rarely terminal or ramiflorous, often several together near the end of a branch (type E, F, G, H, I; see fig. 1), 3—30 cm, rather poor and lax, ramified up to the 2nd order; primary (essentially secondary!) side-axes short, up to *c.* 6(—10) cm. *Mature buds* 1½—2 mm ø. *Inner petals* about halfway bifid, ¾—1 mm; lobes rather narrow, glabrous or more or less ciliolate. *Ovary* subglobose, *c.* ½ mm, glabrous. *Style* ½—1 mm. *Endocarp* obovoid to ellipsoid, (8—)9—14 mm long, 5½—8 mm ø, with or without rather wide and feeble reticulum; median keel distinct, more or less prominent, blunt to rather sharp, at one or both ends running out into a ventral, often somewhat beak-like processus; ventral pore rather wide, somewhat sunken (fig. 22 H1—3).

Distribution: Sumatra (not uncommon in Atjeh, Tapanuli, and West Coast), Java (only collected at Tjigenteng and near Nanggerang, Preanger). — Fig. 24.

Ecology: In primary montane tropical rain forests, at altitudes from 900 m up to 2600 m (Sumatra), in Java at 1050 m and 1600 m.

Field notes: Outer bark dark brown, finely corky, ½ mm, inner turning redbrown, ½ cm; wood ochre with reddish stripes.

Remark. Ssp. *lepidota* is very similar and probably most closely related to the adjacent ssp. *dolichomischa* and *kinabaluensis*; see the remarks under the latter subspecies. On the other hand, it shows a very close resemblance to certain forms of ssp. *longipes* from Vietnam from which it can sometimes only be distinguished by the shape of the endocarp.

e. ssp. **dolichomischa** (Vidal) Beus., *stat. nov.* — *M. dolichomischa* Vidal, Not. Syst. 16 (1960) 304. — *M. monophylla* Ridl., J. Str. Br. R. As. Soc. 54 (1910) 40, *nomen illeg.*, *non* Merr. (1909); Fl. Mal. Pen. 1 (1922) 514; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 27, *in obs.*; Vidal, Not. Syst. 16 (1960) 306. — Type: *Ridley s.n.* (Malay Peninsula), seen from K (holo). — **Fig. 25.**

Leaves elliptic to oblong, 4—22 by 2—10 cm, index 1½—2½, entire, the base acute to rounded or mostly attenuate, the apex acuminate to usually cuspidate with acute or blunt tip, glabrous or only very sparsely pubescent on midrib beneath, without waxy layer beneath; midrib impressed above, nerves 7—13 pairs, flat to somewhat impressed above; petiole (1—)3—10 cm, (¼—)⅓—½(—⅔) as long as the blade. *Panicles* axillary or ramiflorous, solitary or a few together (type E, G, H, I; see fig. 1), 6—25 cm, rather poor and lax, ramified up to the 2nd or 3rd order; primary (essentially secondary!) side-axes up to *c.* 10 cm. *Mature buds* 2½—3 mm ø. *Inner petals* lanceolate, *c.* 2½ mm, entire, hooding over the stamens, glabrous. *Ovary* subglobose to ovate, *c.* ⅔ mm, glabrous. *Style* ⅔—¾ mm. *Endocarp* as in ssp. *lepidota.*

Distribution: Malay Peninsula (Pahang: Cameron Highlands, several times collected; Perak: Hermitage Hill, once collected). — Fig. 24.

Ecology: In primary montane tropical rain forests, found at *c.* 1200 m and *c.* 1500 m altitude. Twice reported to occur along stream, once in dense forest on steep hill-side.

Field notes: Bark thick, red. Wood first white when cut, darkening to orange-brown. Leaves glaucous below.

Remark. See the remarks under *b.* ssp. *kinabaluensis.*

Fig. 25. *M. lepidota* ssp. *dolichomischa*. — a. flowering twig, × ½. — b. half-opened flower, × 4½. — c. outer petal with adhering staminode, × 9. — d. stamen with adhering inner petal, adaxial view, × 9. — e. stamen, abaxial view, × 9. — f. pistil with surrounding disk, × 9. — g. ovary, length section, × 9. — h. fruit, × 1½. — a—g from *Henderson SF 23488* and h from *Henderson SF 23492*.

f. ssp. **vulcanica** (Merr.) Beus., *stat. nov.* — *M. vulcanica* Merr., Philip. J. Sc. 11 (1916) Bot. 15; En. Philip. 2 (1923) 518. — Type: *Ramos BS 23657* (Philippine Islands), seen from K, L.

Machilus nervosa Merr., Philip. J. Sc. 4 (1909) Bot. 262; En. Philip. 2 (1923) 189; Salvore & Lagrimas, Philip. J. For. 4 (1941) 309; *cf.* Kosterm., Reinwardtia 5 (1960) 377; Bibl. Laur. 1 (1964) 919. — Lectotype (by Kostermans): *Curran FB 10846* (Philippine Islands), seen from K. Syntype: *Merritt FB 18009*, not seen.

M. bontocensis Merr., Philip. J. Sc. 20 (1922) 403; En. Philip. 2 (1923) 517; Kosterm., Reinwardtia 5 (1960) 377. — Type: *Ramos & Edaño BS 37756* (Philippine Islands), seen from A, K.

Leaves obovate-oblong or oblong, 5—16 by 2—6 cm, index 2—3, without or with very few teeth, the base acute or cuneate, sometimes slightly attenuate, the apex acute to acuminate or sometimes rounded, with acute to blunt tip, glabrous or only very sparsely pubescent on the midrib beneath, without waxy layer beneath; midrib above more or less impressed; nerves 8—11 pairs, above flat to somewhat impressed; petiole 2—4 cm, ⅕—⅓ as long as the blade. *Panicles* terminal, sometimes axillary (type A, H[1]); see fig. 1), 3—20 cm, rather profuse to poor, ramified up to the 3rd or 4th order; primary side-axes (mostly essentially primary!) up to *c.* 15 cm, usually subtended by normal to reduced leaves. *Mature buds* 2—2½ mm ø. *Inner petals* lanceolate, 1—1½ mm, entire, sometimes frayed at the tip, glabrous or slightly ciliolate at the margin. *Ovary* elliptic, ¾—1 mm, glabrous. *Style* very short, *c.* ¼ mm or less. *Endocarp*[2]) subglobose, rather oblique, 6—7 mm ø, with smooth surface apart from a few ribs; median keel distinct, rather prominent, at one end running out into a minute ventral processus; ventral pore somewhat sunken.

Distribution: Philippine Islands: Luzon (Apayao Subprov.: Mt. Magnas; Bontoc Subprov.: Mt. Pukis; Benguet Subprov.: Mt. Ugo; Sorsogon Prov.: Bulusan volcano), Mindoro (Pinamalayan). — Fig. 24.

Ecology: In primary tropical rain forests, from low altitudes up to *c.* 2000 m.

Remarks. This subspecies is unique in *M. lepidota* in the wide altitudinal range it covers. Originally, two species were recognized, one from low and one from high altitudes. There is, however, no essential difference between these, just only the leaves of the mountain specimens being more coriaceous and stronger-nerved than in plants from lower altitudes; the other differences mentioned by Merrill (Philip. J. Sc. 20, 1922, 403) do not hold.

Specimens from Benguet were described as a Lauraceous species, *Machilus nervosa*, and recognized as belonging to *Meliosma bontocensis* by Kostermans, l.c.

Ssp. *vulcanica* is the only subspecies of *M. lepidota* in which normal terminal panicles (type A; see fig. 1) have been found, though at least one other type is present, and still others may occur. In general habit it is more similar to certain forms of ssp. *longipes* from Vietnam than to ssp. *squamulata* from Taiwan or to ssp. *kinabaluensis* from Borneo, to which it is obviously less closely related (see there).

g. ssp. **dumicola** (W. W. Smith) Beus., *stat. nov.* — *M. dumicola* W. W. Smith, Not. R. Bot. Gard. Edinb. 13 (1921) 170; Merr., J. Arn. Arb. 19 (1938) 49; Cufod., Oest. Bot. Z. 88 (1939) 263; Merr. & Chun, Sunyatsenia 5 (1940) 114; How, Acta Phytotax. Sin. 3 (1955) 431; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 35, t. 5 f. 1—3; Vidal,

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[1]) Possibly also other types; little material available.

[2]) Only one specimen available!

Not. Syst. 16 (1960) 304. — Type: *Forrest 11879* (Yunnan), seen from A, E (holo), K.

M. tsangtakii Merr., Philip. J. Sc. 23 (1923) 251; Lingn. Sc. J. 5 (1927) 119; Cufod., Oest. Bot. Z. 88 (1939) 261; How, Acta Phytotax. Sin. 3 (1955) 432; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 36, *in obs.* — Type: *MacClure 9438* (Hainan), seen from A, E, K, P, W (fragm.). Paratype: *MacClure 9498*, seen from A.

M. sterrophylla Merr., J. Arn. Arb. 19 (1938) 48; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 44. — Type: *Pételot 4532* (N. Vietnam), seen from A (holo), P.

M. caudata Merr., J. Arn. Arb. 20 (1939) 346; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 29, t. 4 f. 3, 4. — Type: *Pételot 6342* (N. Vietnam), seen from A (holo), L, P.

M. pakhaensis Gagn., Not. Syst. 14 (1952) 273; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 27, t. 2 f. 1—7. — *M. elliptica* Gagn., Bull. Soc. Bot. Fr. 99 (1952) 11, *nomen illeg.*, *non* Hook. *f.* (1876); Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 27, *in synon.* — Type: *Poilane 25053* (N. Vietnam), seen from L, P (holo).

M. cinerea Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 31, t. 3 f. 3, 4; Not. Syst. 16 (1960) 304. — Type: *Poilane 35941* (S. Vietnam), seen from P (holo).

M. tonkinensis Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 34, t. 5 f. 4, 5; Not. Syst. 16 (1960) 307. — *M. fordii* (*non* Hemsl. *ex* Forb. & Hemsl.) Merr., J. Arn. Arb. 19 (1938) 49; Vidal, Not. Syst. 16 (1960) 305. — Type: *Pételot 5453* (N. Vietnam), seen from L, P (holo).

M. dumicola var. *serrata* Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 36; Not. Syst. 16 (1960) 304. — Type: *Forrest 26662* (Yunnan), seen from A (holo), E, K, W. Paratype: *Pételot 8594*, seen from P.

Leaves obovate-oblong to obovate-lanceolate, or oblong to lanceolate, rarely elliptic, 4—16 by 1½—8(—9½) cm, index (1¼—)2—3½(—4), usually entire, sometimes with some remote teeth, the base acute to cuneate, sometimes attenuate, the apex acuminate to long cuspidate, usually with blunt tip, above glabrous or sometimes somewhat pubescent on the midrib, beneath sparsely to moderately pubescent, rarely subglabrous, sometimes with whitish waxy layer beneath; midrib and nerves above more or less impressed; nerves (7—)8—14 pairs; petiole 1—6(—10) cm, ⅕—½(—¾) as long as the blade. *Panicles* terminal, rarely axillary (type D, E, sometimes G; see fig. 1), 5—20 cm, poor to profuse and usually dense, consisting of 1 to 10 main (essentially primary side-)axes each ramified up to the 2nd or 3rd order; primary (essentially secondary) side-axes short, up to *c.* 7 cm. *Mature buds* 1⅔—2¼ mm ø. *Inner petals* lanceolate to ligulate, 1—1½(—1⅔) mm, acute, blunt, or emarginate at the tip, glabrous or rarely a bit ciliolate at the margin. *Ovary* subglobose, ½—⅔ mm, glabrous. *Style* ½—1 mm. *Endocarp* not known.

Distribution: SW. China (W. Yunnan), N. Vietnam (several localities in Lao Khay Prov.), S. Vietnam (Ngok Pan, Kontum Prov., once collected), Hainan (Ngi Chi Leng; Fan Yah), Thailand (Doi Inthanon, once collected). Probably not common; only at Cha Pa collected several times. — Fig. 24.

Ecology: In (mostly?) primary tropical hill forest or evergreen broad-leaved forest, at altitudes from *c.* 1200 m up to *c.* 2400 m (Yunnan), most frequently found between 1400 and 1900 m. Reported from dense forest or densely forested ravines to open thickets. Once said to grow on good loamy soil.

Remarks. Ssp. *dumicola* is one of the more variable subspecies of *M. lepidota*, which has resulted in a relatively large number of synonyms. It is nevertheless a natural group, well marked against the other subspecies. In its characters it may show tendencies towards other subspecies; the most remarkable representant in this respect is *Poilane 25053* from N. Vietnam, described as *M. pakhaensis.* This plant has short-elliptic leaves with a white waxy layer beneath strongly recalling the leaves of ssp. *kinabaluensis*, whereas its unusual long petioles make one think of ssp. *squamulata*. It is, however, doubtless a true member of ssp. *dumicola*.

The white waxy layer on the lower surface of the leaves also occurs in *Forrest 11879* and *26662* from Yunnan and *Kerr 5290* from Thailand; this character, which usually is wanting in ssp. *dumicola*, is a link with ssp. *kinabaluensis* and ssp. *squamulata* in which it is a rather constant character.

Another collection, *Pételot 6342*, also from N. Vietnam, described as *M. caudata*, shows characters typical for ssp. *squamulata*, and is not impossibly a transitional form or hybrid between that subspecies and ssp. *dumicola*; it has the caudate leaf-apex, long petioles, and bifid inner petals of the former, but the nerves are too many and the leaf-margin shows a few teeth. It has more or less arbitrarily been included by me in ssp. *dumicola*, but it might almost as well be reckoned under ssp. *squamulata*. Another collection which is difficult to class, is *Pételot 6342* from N. Vietnam, described as *M. sterrophylla*, which may be considered a transition to ssp. *longipes* because of its tendency to develop ramiflory. The inner petals which might be decisive, are wanting, however, since the flowers are passed.

As to the localities of the above-mentioned deviating specimens it must be added that these are all situated in Lao Khay Province in N. Vietnam, especially near Cha Pa, hence close to the areas of ssp. *squamulata* and ssp. *longipes*; this critical area might be rewarding for population studies.

Ssp. *dumicola* and ssp. *longipes* (see there) are variable to a much higher degree than the other five subspecies of *M. lepidota*. Moreover, it can be established that almost all characters, found in the latter subspecies, are also present in ssp. *dumicola* or ssp. *longipes* or in both of them. They comprise about the whole variation pattern found throughout the other subspecies, and hence there is reason to assume that their genomes are much richer than those of the other subspecies. This would support the hypothesis that the Tonkin area is the distributional centre of *M. lepidota* (see p. 376).

6. Meliosma simplicifolia (Roxb.) Walp. — *Millingtonia simplicifolia* Roxb. — *Millingtonia integrifolia* Nees — *Millingtonia laxa* W. & A. — *Millingtonia congesta* W. & A. — *Millingtonia pungens* Wall. *ex* W. & A. — *Millingtonia acuminata* Royle — *Millingtonia integrifolia* Wall. *ex* Royle — *M. pungens* (Wall. *ex* W. & A.) Walp. — *M. rigida* Sieb. & Zucc. — *M. angulata* Bl. — *M. fruticosa* Bl. — *M. simplicifolia* Bl. — *Sabia densiflora* Miq. — *Sabia ? floribunda* Miq. — *M. rigida* var. *angustifolia* Miq. — *Quercus jamabuwa* Sieb. *ex* Miq. — *M. wightii* Planch. *ex* Brandis — *M. elliptica* Hook. *f.* — *M. ferruginea* Sieb. & Zucc. *ex* Hook. *f.* — *M. lancifolia* Hook. *f.* — *M. fordii* Hemsl. *ex* Forb. & Hemsl. — *M. patens* Hemsl. *ex* Forb. & Hemsl. — *M. yunnanensis* Franch. — *M. ferruginea* Kurz — *M. cambodiana* Pierre — *M. harmandiana* Pierre — *M. thomsonii* King *ex* Brandis — *M. monophylla* Merr. — *M. simplicifolia* var. *sootepensis* Craib — *M. callicarpaefolia* Hayata — *M. fischeriana* Rehd. & Wils. — *M. glomerulata* Rehd. & Wils. — *M. subverticillaris* Rehd. & Wils. — *M. velutina* Rehd. & Wils. — *M. loheri* Merr. — *M. forrestii* W. W. Smith — *M. pannosa* Hand.-Mazz. — *M. sinii* Diels — *M. trichocarpa* Hand.-Mazz. — *M. laui* Merr. — *M. petelotii* Merr. — *M. dolichobotrys* Merr. — *M. costata* Cufod. — *M. pseudopaupera* Cufod. — *M. rigida* var. *patens* Cufod. — *M. obtusa* Merr. & Chun — M. *donnaiensis* Gagn., *pro parte* — *M. evrardii* Gagn. — *M. hainanensis* How — *M. pseudopaupera* var. *pubisepala* How — *M. kontumensis* Vidal *ex* Gagn. & Vidal — *M. ochracea* Vidal *ex* Gagn. & Vidal — For complete references, see under the subspecies.

Evergreen shrub or tree, small to medium-sized, up to *c.* 20 m. *Flowering twigs* terete to angular, 2—8 mm ø, glabrous to densely puberulous to tomentose. *Leaves* elliptic or obovate to lanceolate or obovate-lanceolate, 3—50 by 1—18 cm, index 2—5(—6), at the base acute or attenuate to cuneate, at the apex acute to acuminate, sometimes cuspidate, rarely caudate or rounded, entire to spinously dentate usually especially towards the apex, chartaceous to coriaceous, dull or shining above, dull and paler beneath, glabrous to densely pubescent or tomentose, especially beneath and on midrib and nerves, sometimes with hairy domatia in the axils of the nerves beneath; midrib and nerves above prominent to impressed, beneath prominent; nerves 7—25 pairs, more or less ascending, sometimes looped and joined near the margin; venation distinct, reticulate or usually more or less cancellate, above prominulous to slightly impressed, beneath flat to prominent; petiole, ½—6(—7) cm, $\frac{1}{20}$—⅓ as long as the leaf-blade, glabrous to pubescent. *Panicles* terminal, very rarely axillary, erect, lax to rather dense, widely to narrowly pyramidal, (4—)10—50(—60) cm, usually profusely branched up to the 2nd, 3rd, or 4th order, branches more or less spreading, stiff to somewhat flaccid, slender to coarse, terete to angular, sparsely pubescent to densely tomentose, bearing numerous solitary to crowded or glomerulate flowers which are usually spicately arranged; main axis terete to angular, sometimes shallowly canaliculate; primary side-axes usually many, up to *c.* 25 cm, especially the lower ones often subtended by normal to small leaves; bracts ovate to linear-lanceolate, up to *c.* 8 mm, more or less pubescent. *Pedicels* usually absent, sometimes present, minute, up to *c.* 3 mm. *Mature buds* (1—)1½—3 mm ø. *Sepals* (4) 5, sometimes by addition of empty bracts seemingly more, up to 11(—13), (round-) ovate, equal or usually more or less unequal, the inner ones ¾—2 mm, the outer one(s) usually smaller, often minute, glabrous to pubescent, all with entire, usually ciliolate margin. *Outer petals* glabrous. *Inner petals* more or less deeply bifid, ½—1½ mm, with glabrous, sometimes fimbriate or ciliolate lobes, never with a central lobule. *Stamens*: anther-cells *c.* ⅛—½ mm ø; filaments ½—1½ mm. *Ovary* ½—¾(—1) mm, glabrous, very exceptionally pubescent. *Style* up to *c.* 1 mm, glabrous. *Fruit* (sub)globose, when ripe 4—10 mm ø; endocarp globose to subglobose, often depressed or oblique, 3—9 mm ø, with very vague to very strong and prominent reticulum; median keel more or less prominent, distinct or not; ventral pore somewhat sunken to somewhat spouted (fig. 22 K—Q).

Distribution: Ceylon, North, East, and Peninsular India, East Pakistan, Burma, South and Central China, Japan, Taiwan, Philippine Islands, Laos, Cambodia, Vietnam, Thailand, Malay Peninsula, Sumatra, Borneo, Java, Lesser Sunda Islands. For details see under the subspecies. — Fig. 27.

Ecology: Subtropical to tropical forests, under various conditions, usually in mountains up to *c.* 3000 m, but also at sea-level. For details see under the subspecies.

Remarks. M. simplicifolia is a very variable species, covering an enormous area in which it is adapted to many different habitats. It can be divided up into eight well-marked subspecies, five of which, ssp. *fordii*, ssp. *rigida*, ssp. *simplicifolia*, ssp. *thomsonii*, and ssp. *yunnanensis*, centre in SW. Yunnan, and diverge over different parts of the area; three subspecies, viz. ssp. *fruticosa*, ssp. *laui*, and ssp. *pungens*, do not centre in Yunnan, and are considered to have split off from ssp. *fordii*, ssp. *rigida*, and ssp. *thomsonii* respectively.

The latter three 'secondary' subspecies differ from the other five in that their characters link up almost exclusively with those of their counterpart 'primary' subspecies. Especially in ssp. *laui* and ssp. *pungens*, somewhat less so in ssp. *fruticosa*, it is clear that their discriminative characters are also present — but less pronounced and less universal — in the 'primary' subspecies to which they are connected. Moreover, the differences between the 'secondary' subspecies and their 'primary' counterparts are more or less quantitative, whereas the differences between the 'primary' subspecies are distinctly of a more qualitative kind.

All eight subspecies are mutually isolated, either geographically, or ecologically (occurring in different altitudinal zones or in different forest-types). In the contact zone between two adjacent subspecies transitional forms or hybrids are usually found. In fig. 26a scheme is given from which can be seen which subspecies come into contact and which

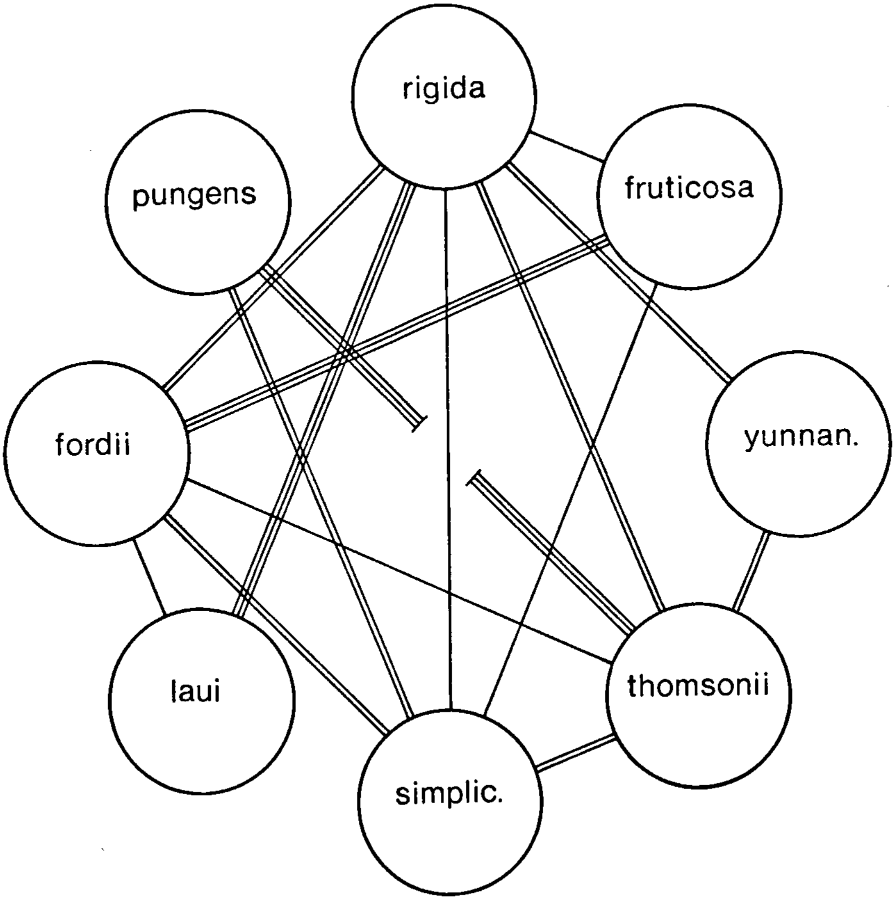

Fig. 26. Schema of geographical and morphological relationships between the subspecies of *M. simplicifolia*, indicated by:

a. *No connecting line:* Areas wide apart. No intermediate specimens known. Morphological relationship rather remote.
b. *Single line:* Areas adjacent or overlapping. No intermediate specimens observed, but possibly present. Morphological relationship moderate.
c. *Double line:* Areas adjacent or overlapping. Intermediate specimens present. Morphological relationship moderate to rather close.
d. *Triple line:* Areas adjacent (contact between *thomsonii* and *pungens* secondarily broken). Intermediate specimens present. Morphological relationship very close; species pairs consisting of one primary and one secondary subspecies, the latter assumed to be derived from the former.

do not; this has been based on the present knowledge of their distribution patterns and their ecology, and the occurrence of transitional or hybrid forms. The degree of morphological affinity between the subspecies is different; as a rule it can be observed that adjacent subspecies, for instance ssp. *rigida* and ssp. *fordii*, have more characters in common than have subspecies without contact zones, for instance ssp. *simplicifolia* and ssp. *laui*. Such wide-apart subspecies, when compared, give the impression of different species, and I should certainly have treated them accordingly, if not more evidence had been available.

KEY TO THE SUBSPECIES

1. Sepals[1] 6—11(—13).
   2. Leaves of flowering twigs usually entire, sometimes with some teeth, oblong, sometimes lanceolate. Sepals[1] (8—)9—11(—13). . . . . **a.** ssp. **pungens**
   2. Leaves of flowering twigs usually with many teeth, rarely entire of nearly so, and then usually oblong to oblong-lanceolate. Sepals[1] 6—8(—12).
      3. Leaves 7—32 cm, with distinctly pubescent midrib above; nerves 7—22 pairs. Panicles (8—)15—50 cm, branched up to the (2nd) 3rd (4th) order, belonging to type A (see fig. 1). Mature buds 1½—2 (—2½) mm ø. Sepals[1] 6—8(—12). Endocarps (4½—)5½—7 mm ø (fig. 22 O) **b.** ssp. **thomsonii**
      3. Leaves 3—15 cm, with usually glabrous, sometimes sparsely puberulous or pubescent midrib above; nerves 7—14 pairs. Panicles 4—20(—25) cm, branched up to the 2nd (3rd) order, belonging to types D (usually), E, F. G. or H (see fig. 1). Mature buds *c.* 2½(—3) mm ø. Sepals[1] 5(—7). Endocarps 3½—4½ mm ø (fig. 22 L). . . . . **c.** ssp. **yunnanensis**
1. Sepals (4—)5.
   4. Leaves up to *c.* 15 cm, (sub)glabrous; nerves 7—14 pairs. Mature buds *c.* 2½(—3) mm ø. Inner petals 1—1½ mm, with divergent, broad lobes (cf. fig. 3a) . . . . **c.** ssp. **yunnanensis**
   4. Leaves up to *c.* 45 cm, glabrous to densely pubescent; nerves 7—25 pairs. Mature buds 1—2 (—2¼) mm ø. Inner petals (½—)⅔—¾(—1) mm, lobes divergent or not, usually rather narrow (fig. 3 b—d).
      5. Panicles branched up to the 2nd (3rd) order, belonging to type C (rarely A, E. G, or H) (see fig. 1), nearly always (very) densely tomentose; primary side-axes rarely subtended by leaves. Leaves sparsely to densely but always distinctly pubescent to tomentose, at least on midrib and nerves; without domatia. Style *c.* 1½—2 times as long as the ovary.
         6. Endocarps (6—)7—9 mm ø. Leaves oblong to lanceolate, sometimes somewhat ovate-oblong, usually entire or with one or two teeth, densely tomentose beneath **d.** ssp. **laui**
         6. Endocarps (3½—)4—5 mm ø. Leaves usually obovate-oblong to obovate-lanceolate, sometimes oblong to lanceolate, usually distinctly dentate, sometimes with very few or without teeth, beneath sparsely to rather densely pubescent, sometimes tomentose **e.** ssp. **rigida**
      5. Panicles branched up to the (2nd) 3rd or 4th order, belonging to type A (rarely C) (see fig. 1), sparsely pubescent to moderately tomentose; lower primary side-axes often subtended by normal to small or reduced leaves. Leaves glabrous to densely pubescent, rarely tomentose, with or without domatia. Style about as long as the ovary or shorter.
         7. Leaves with or without domatia; midrib on the upper side of the full-grown leaf glabrous or nearly so, more or less prominent, rarely flat; petiole $^{1}/_{20}$—$^{1}/_{8}$ x length of blade. Mature buds 1½—2 mm ø. Inner petals with entire lobes, which are sometimes slightly fimbriate or ciliolate at the very tips (fig. 3d). Endocarps 3½—4½(—5) mm ø, usually more or less oblique and with prominent keel (fig. 22 K). **f.** ssp. **simplicifolia**
         7. Leaves with or without domatia; midrib on the upper side of the full-grown leaf more or less but distinctly pubescent, more or less impressed to flat; petiole $^{1}/_{20}$—$^{1}/_{6}$(—¼) x length of blade. Mature buds 1½—2 mm ø. Inner petals usually with fimbriate, rarely entire lobes which are rarely minutely ciliolate at the very tips (fig. 3c). Endocarps (4½—)5½—8 mm ø, often more or less oblique and with prominent keel (fig. 28c) **g.** ssp. **fruticosa**
         7. Leaves without domatia; midrib on the upper side of the full-grown leaf glabrous to pubescent, prominent to impressed; petiole ($^{1}/_{20}$—)$^{1}/_{10}$—⅓ x length of blade. Mature buds 1—1⅓(—1½) mm ø. Inner petals with entire lobes, which are sometimes minutely ciliolate at the very tips (cf. fig. 3d). Endocarps 3—5 mm ø, not oblique and with hardly or not prominent keel (fig. 22 N) . . . . **h.** ssp. **fordii**

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[1] See note on p. 466.

a. ssp. **pungens** (Walp.) Beus., *stat. nov.* — *Millingtonia pungens* Wall. *ex.* W. & A., Edinb. New Phil. J. 15 (1833) 178; Prod. 1 (1834) 115; Wight, Ic. 3 (1845) t. 964/3. — *M. pungens* (Wall. *ex* W. & A.) Walp., Rep. 1 (1842) 423; Ann. 1 (1848) 135; Thw., En. Pl. Zeyl. (1858) 59; Beddome, Fl. Sylv. 1 (1869) t. 160; ibid. 3 (1869) 77; Merr., Contr. Arn. Arb. 8 (1934) 94; Cufod., Oest. Bot. Z. 88 (1939) 263, *in obs.*; Vidal, Not. Syst. 16 (1960) 306. — *Millingtonia congesta* W. & A., Edinb. New Phil. J. 15 (1833) 178, *nom. invalid. in synon. sub Millingtonia pungens.* — Lectotype: *Wight 945* (Peninsular India), seen from E (holo), P. Syntype: '*Millingtonia pungens* Wall.' in Herb. Hook., not seen (see Remarks).

M. wightii Planch. *ex* Brandis, For. Fl. (1874) 116; Hook. *f.*, Fl. Br. Ind. 2 (1876) 4; Trim., Fl. Ceyl. 1 (1893) 314; Cooke, Fl. Pres. Bombay 1 (1902) 271; Brandis, Ind. Trees (1906) 194; Fyson, Fl. Nilg. Puln. Hill-tops 1 (1915) 92, t. 70; Gamble, Fl. Pres. Madras 1 (1918) 256. — Type: '*M. wightii* Planch.', *sine coll. et loco*, seen from K (holo).

Millingtonia simplicifolia (*non* Roxb.) Wall. *ex* Hook. *f.*, Fl. Br. Ind. 2 (1876) 4, *nom. invalid. in synon. sub M. wightii*; Cufod., Oest. Bot. Z. 88 (1939) 263, *in obs.* — Type: *Wallich 8114 A* (Sylhet), seen from K.

Leaves elliptic to oblong, sometimes lanceolate, 5—20(—30) by 2—8(—10) cm, index 2—3(—4), without or with some distant teeth1), acute to rounded at the base, acute to acuminate at the apex, usually distinctly pubescent on midrib and sometimes on nerves above, sparsely to moderately pubescent beneath especially on midrib and nerves, usually with *domatia* in the axils of the latter; midrib and nerves usually impressed above, sometimes flat or slightly prominent; nerves 7—18 pairs; petiole $^{1}/_{18}$—$\frac{1}{5}$ as long as the blade. *Panicles* lax to dense, (5—)10—55 cm, branched up to the 2nd (3rd) order; axes rather coarse, terete to slightly angular, densely short-tomentose, the lower primary ones almost always subtended by small leaves. *Flowers* crowded in dense glomerules, sessile; mature buds 2—2½ mm ø. *Sepals*2) (8—)9—11(—13). *Inner petals c.* 1 mm, slightly bifid; lobes divergent, wide, glabrous. *Style* about as long as the ovary. *Endocarps* (sub)globose, often rather irregular, 3½—5½ mm ø, with usually lax reticulum; median keel distinct but not very prominent, not running out into a ventral processus; ventral pore hardly or not sunken, not spouted (fig. 22 M).

Distribution: Ceylon (Central Province, common), SW. Peninsular India (rather common in the Nilghiri, Anamalai, Pulney, and Travancore hills; also collected in the Concan: *Dalzell s.n.*, *Stocks s.n.*), one collection in North Sumatra. — Fig. 27.

Ecology: In tropical hill-forests, from about 1500 m up to 2100 m altitude.

Vernacular names: SW. Peninsular India: *Tode* or *Toudet* (several times mentioned; name said to be used by the Burghers on the Nilghiris).

Remarks. There has been much confusion about the name of this subspecies; see Cufodontis, l.c., and Vidal, l.c. It was first described by Wight & Arnott under the name *Millingtonia pungens*, which was up till then a name only occurring on herbarium sheets of Wallich collections. Wight & Arnott explicitly refer to *M. pungens* Wall. *in Herb. Hook.*; however, during my recent visit at Kew Herbarium I could not trace this sheet. (Anyhow it is certainly not *Wallich Cat. 8114 G, pro parte*, as stated by Vidal, l.c.; sheets with this number bear the name *Millingtonia integrifolia* Wall,. which name is also used in Wallich's Catalogue). There are, on the other hand, several specimens from Nepal

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1) Sometimes with more teeth, e.g. in *Bourne s.n.* (12-VI-1896) from Coonoor, Madras; see also Wight, Ic. 3 (1845) t. 964/3. Furthermore, leaves lower on the branches and leaves of watershoots are usually dentate.

2) Actually only 5 sepals and 3 or more sepal-like empty bracts. See part I chapter C sub. c.

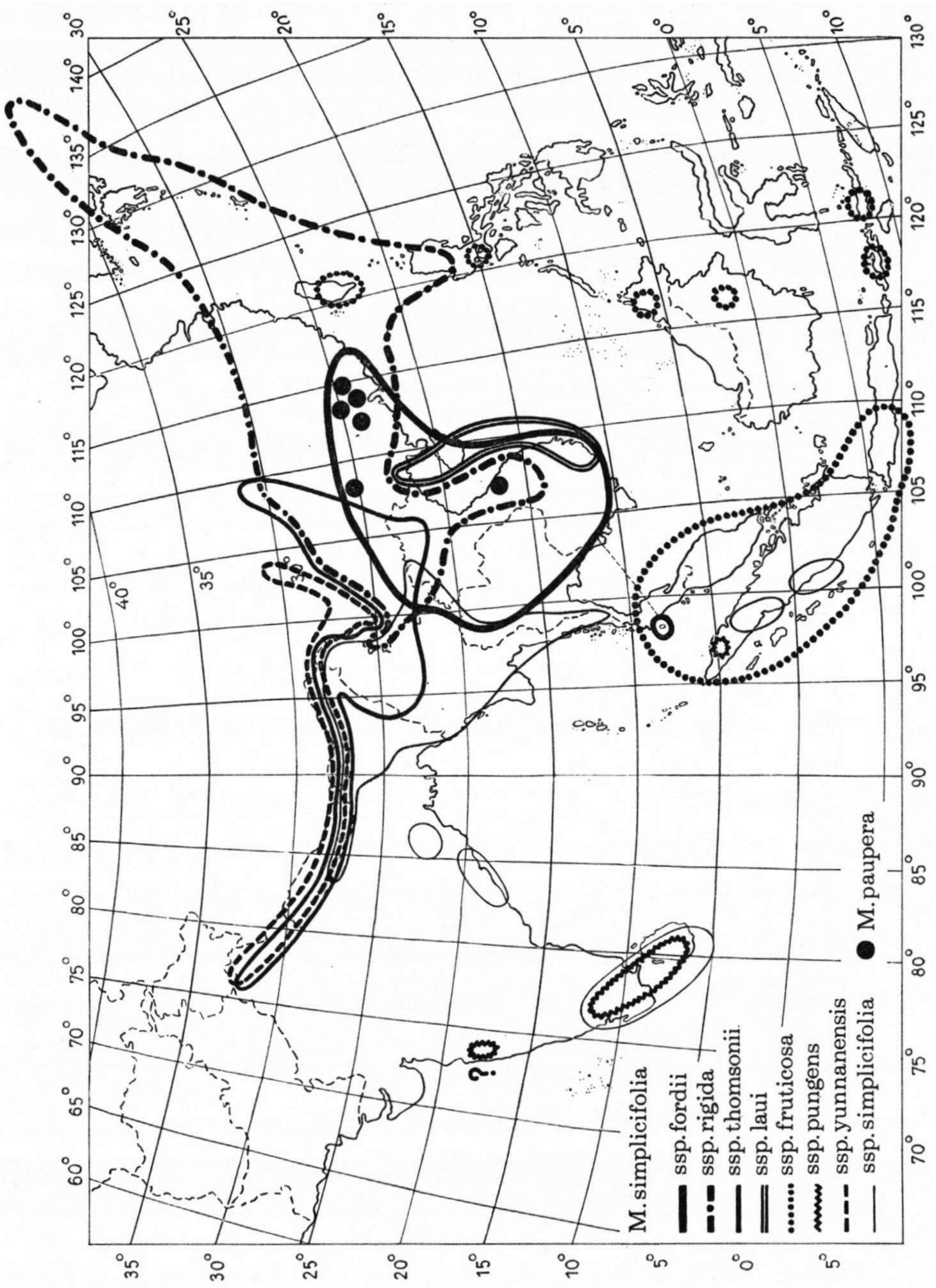

Fig. 27. Generalized areas of the subspecies of *M. simplicifolia*, and distribution of *M. paupera*.

and Kumaon numbered *Wallich 8114 E* and *F*¹) which are named *Millingtonia pungens* Wall. These are all specimens from the Himalaya, with more or less oblanceolate, distinctly dentate leaves. In the original diagnosis of *Millingtonia pungens*, however, the leaves are described as 'lanceolatis, integerrimis' and 'Neelgherries' is mentioned as locality; the authors, therefore, cannot have meant the above Wallich plants from the Himalaya.

Given these complications, it is not astonishing that Brandis, For. Fl. (1874) 116, in the original sense of Wallich, designated the epithet '*pungens*' to the Himalayan taxon, and illegitimately renamed *M. pungens* W. & A as *M. wightii* Planch. *ex* Brandis. Afterwards, Hooker *f.*, l.c., and all other authors followed Brandis, until Cufodontis, l.c., discovered the error; however, this author, and Vidal, l.c., wrongly attributed the changing of names to Hooker *f.*, instead of to Brandis.

In consequence of these facts it is clear that *M. pungens* should be restored in its original sense, and, to avoid further typification mistakes, I have chosen *Wight Cat. 945* as the lectotype of *Millingtonia pungens* Wall. *ex* W. & A.; this is the only collection number the authors mentioned with the description, and the specimens under this number fully conform to it.

The closest affinities of ssp. *pungens* are with ssp. *thomsonii* from the Himalayas, and less so with the more widespread ssp. *simplicifolia*. In various respects ssp. *thomsonii* much resembles ssp. *pungens*: both share the glomerate, comparatively big flowers with more than 5 sepals²), and the pubescence of the leaves is similar. The leaves of ssp. *thomsonii* are, however, usually obovate-oblong to lanceolate and rather closely dentate, and its panicles are usually more profusely branched. There is, moreover, usually a difference in number of 'sepals'²). The areas of ssp. *thomsonii* and *pungens* are now widely separated, but I think it probable that they have been in contact formerly and that ssp. *pungens* became split off from ssp. *thomsonii* (See the remarks under the species).

The differences between ssp. *pungens* and ssp. *simplicifolia* are much more conspicuous; there is no chance of confusing them. It stands to reason that they always have been considered separate good species, the more so since no other subspecies are found in the area where they occur. In this joint area they occupy different altitudinal zones, ssp.

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¹) The situation is even more complex because of the fact that *Wallich 8114 E* in the Wallich Herbarium at Kew ('*Mill. pungens*' Wall Napalia) is not mentioned in Wallich's Catalogue, whereas *Wallich Cat. 8114 D* (also '*Mill. pungens*' Wall Napalia) does not occur in the Wallich Herbarium, apart from a 'D' twig (indeed *M. pungens sensu* Wall.) on one of the 'E' sheets. However, several *Wallich 8114 D* sheets — all ssp. *simplicifolia*! — have been distributed to other Herbaria (BM, E, F, W), and these certainly cannot represent '*Mill. pungens*' of *Wallich Cat. 8114 D*. After some puzzling I have come to the following reconstruction of what mistake may have happened here. George Bentham, who did the compiling of the supplement of Wallich's Catalogue, may have meant to write:

C 'Mill. simplicifolia' Hort Calc
D 'Mill. simplicifolia' Napalia
E 'Mill. pungens' Napalia
F Kamaon

Erroneously he may have contracted D and E by writing down D, and then jumping to the name under E: *Mill. pungens*. Thus the text as it now is, reads:

C 'Mill. simplicifolia' Hort Calc
D 'Mill. pungens' Wall Napalia
F Kamaon

As a support to the possible correctness of the above reconstruction may be advanced that Hook. *f.*, Fl. Br. Ind. 2 (1876) 4, 5, cited *Wall. Cat. 8114 BCD* under *M. simplicifolia*, and *Wall. Cat. 8114 EF* under *M. pungens*, which is in full accordance with the labeling and the identity of the distributed Wallich specimens.

²) See note on p. 466.

simplicifolia reaching up to at least 1000 m, ssp. *pungens* occurring at higher altitudes, becoming abundant at *c.* 1500 m. Here and there they may come into contact, and, notwithstanding their fine morphological differences, it is very probable that they hybridize in such cases; I have seen one collection from the Nilghiris (*sine coll. et num.*) *ex* Herb. Hook. *f.* & Thoms., and one from Madras, *sine loco* (*Cole 59*), which are intermediates.

The single specimen collected near Takengon, in the Gajo Lands, North Sumatra (*Bangham 721*), which was correctly identified by Merrill (1934) as *M. pungens*, is geographically completely out of place and I cannot account for this distribution.

b. ssp. **thomsonii** (King *ex* Brandis) Beus., *stat. nov.* — *M. ferruginea* Kurz *ex* King, J. As. Soc. Beng. 65, ii (1896) 116, *nom. illeg.*, *non* Bl. (1823), *nec* Sieb. & Zucc. *ex* Hook. *f.* (1876). — *M. thomsonii* King *ex* Brandis, Ind. Trees (1906) 195. — Type (syntype of *M. ferruginea*): *Gamble 9704* (Darjeeling, Sikkim), seen from K (holo). Syntypes (only of *M. ferruginea*, all from Sikkim): *Thomson s.n.* (Lebong, 16-IV-1857), seen from K, L; *Gamble 320*, not seen.

M. pungens sensu Brandis, For. Fl. (1874) 116, *non* (Wall. *ex* W. & A.) Walp., *pro parte*; Hook. *f.*, Fl. Br. Ind. 5 (1876) 4, *pro parte, excl. spec. Japon.*, *Wall. Cat. 8114 F, G, et M. acuminata Royle* (*vide ssp. yunnanensis*); Collett, Fl. Siml. (1902) 102, *pro parte*; Brandis, Ind. Trees (1906) 194, *pro parte*; Bamb., Pl. Punjab (1916) 30, *pro parte*; Osmaston, For. Fl. Kumaon (1927) 133, *pro parte.*

M. subverticillaris Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 201; Cufod., Oest. Bot. Z. 88 (1939) 267; How, Acta Phytotax. Sin. 3 (1955) 445; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45, *in obs.* — Type: *Wilson 4600* (E. Szechuan), seen from A (holo), K.

M. forrestii W. W. Smith, Not. R. Bot. Gard. Edinb. 10 (1917) 52; Cufod., Oest. Bot. Z. 88 (1939) 265; Chatt. & Raiz., Ind. For. Nov. (1948) 386; How, Acta Phytotax. Sin. 3 (1955) 443; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 47; Vidal, Not. Syst. 16 (1960) 305. — Type: *Forrest 11744* (Yunnan), seen from A, E (holo), K.

M. trichocarpa Hand.-Mazz., Sinensia 5 (1934) 17, *non* Merr. (1938); Cufod., Oest. Bot. Z. 88 (1939) 265; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 49, *in obs.* — Type: *Y. Tsiang 4435* (Kweichow), seen from W (holo).

M. petelotii Merr., J. Arn. Arb. 29 (1938) 48; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45, t. 7 f. 7, 8. — Type: *Pételot 3556* (N. Vietnam), seen from P. Paratype: *Pételot 5862* (N. Vietnam), seen from P.

Leaves oblong or obovate-oblong to lanceolate or obovate-lanceolate, 7—40 by 2—16 cm, index 2—3½(—4), usually with many, often coarse teeth, rarely subentire, the base acute, the apex acute to short-cuspidate, more or less, but nearly always distinctly pubescent on midrib and often on nerves above, densely to very sparsely pubescent beneath, especially on midrib and nerves, very rarely with domatia in the axils of the latter; midrib and nerves flat or slightly prominent to impressed above; nerves 7—22 pairs; petiole ($^1/_{20}$—)$^1/_{15}$—⅕(—¼) as long as the blade. *Panicles* usually rather coarse and dense, (8—)15—50 cm, branched up to the (2nd) 3rd or 4th order; axes usually rather stiff, terete to slightly angular, densely short-pubescent to -tomentose, the lower primary ones whether or not subtended by small leaves. *Flowers* crowded, sessile; mature buds 1½—2(—2½) mm ø. *Sepals* 6—8(—12)1); the outer ones pubescent on the outside. *Inner petals c.* 1 mm, slightly bifid; lobes divergent, wide, glabrous or a bit ciliolate to fimbriate.

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1) See note on p. 466.

Style about as long as the ovary or somewhat shorter. *Ovary* usually glabrous, sometimes pubescent. *Endocarps* subglobose, usually oblique, (4½—)5½—7 mm ø, with rather wide, coarse reticulum; median keel usually prominent and rather sharp, sometimes running out into a very minute ventral processus; ventral pore not sunken, not spouted (fig. 22 O).

Distribution: Foot of the Himalaya: N. India (NE. Punjab; Kumaon; Nepal; Sikkim; Bhutan; Assam; Naga Hills), Upper Burma (only found at Mogok), China (S. and W. Yunnan; S. Kweichow; E. Szechuan), N. Vietnam (only found at Cha Pa and Phu Tho). Possibly rather rare in most parts of the area; only found more commonly in the NW. Provinces of India, and in extreme western Yunnan (Shweli-Salween Divide!). Since the localities are usually very scattered, the area can only be roughly delimitated. — Fig. 27.

Ecology: In evergreen forests, probably generally of the same type as those where ssp. *yunnanensis* occurs. In Yunnan at altitudes from about 2000 m up to at least 3100 m, in the Naga Hills found at 2400 m, but in the other parts of the area at lower altitudes, mainly from about 1200 m up to 1500 m, occasionally lower (*c.* 1000 m in E. Szechuan), or higher, at most 2000 m. See also the Remarks.

Vernacular names: N. India: *Sindare dabdabi* (Darjeeling, once mentioned), see also under ssp. *yunnanensis*; since this subspecies and ssp. *thomsonii* occur close together in N. India and probably are not discriminated by local people, most vernacular names will be in use for both of them. N. Vietnam: (*Cây*) *Phăng tiá* (Phu Tho, once mentioned).

Remarks. Ssp. *thomsonii* is closely related to ssp. *yunnanensis*, ssp. *rigida*, and ssp. *pungens*. As to the first pair of these, in the central and eastern part of its area ssp. *thomsonii* is quite different from ssp. *yunnanensis*, and no confusion will arise. Towards the western part, where the areas overlap, the differences fade, both showing intermediate characters: ssp. *yunnanensis* has larger leaves, larger inflorescences, and often more than 5 sepals; ssp. *thomsonii* has smaller, less pubescent leaves and smaller inflorescences. In a few essential characters, however, — ramification of the inflorescence and pubescence of the midrib — they maintain their identity; I have seen only one specimen which is exactly intermediate (*Duthie 19305* from NW. India). Judging from the ecological evidence (see above) it is probable that ssp. *thomsonii* and ssp. *yunnanensis* prefer different altitudinal zones in the western part of their areas, and thus avoid mixing up, though some hybridization probably occurs. In Yunnan, on the other hand, both occur in the same altitudinal zone, but it is evident that a sharp boundary between their areas exists here. Hence within one subspecies two ways of intersubspecific isolation, viz. altitudinal and geographical, can be observed.

From Taning Hsien, E. Szechuan, one remarkable collection is known (*Wilson 4600*, described as *M. subverticillaris*), which, though obviously belonging to ssp. *thomsonii*, displays several characters proper to ssp. *yunnanensis* (and, much less obviously, to ssp. *rigida*). Dentation, nervation, and pubescence of the leaves are typical for ssp. *thomsonii*, but their obovate-lanceolate shape reminds of ssp. *yunnanensis* or ssp. *rigida*. The number of sepals[1], which is an important character, is usually seven or eight[2], as is usual in ssp. *thomsonii*, but a number of five also occurs such as is found in most other subspecies. The outer sepals are densely pubescent, which is again a character of ssp. *thomsonii* (also of ssp. *rigida*). On the other hand, the ramification of the panicle, belonging to type D (see fig. 1), is much like in ssp. *yunnanensis*, not as in ssp. *thomsonii*. Summarizing, it can be stated that *Wilson 4600* joins ssp. *thomsonii* in principal characteristics, but shows some definite morphological affinities with ssp. *yunnanensis* (much less so with ssp. *rigida*). Though the areas of ssp. *thomsonii* and ssp. *yunnanensis*, as far as known to me, do not —

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[1] See note on p. 466.

[2] In the original description the number of sepals is said to be five, which is, however, not the rule!

respectively no longer — contact in E. Szechuan (the Red Basin lying in between), it may be possible that some ancient hybrid influence of ssp. *yunnanensis* still exists in E. Szechuan populations of ssp. *thomsonii* (See also below, sub ssp. *pungens* and ssp. *thomsonii*). The at first sight most striking character of '*M. subverticillaris*' is its subverticillate phyllotaxis. However, in ssp. *thomsonii*, and in other subspecies of *M. simplicifolia*, this phenomenon occasionally turns up, just as a variation on the alternate phyllotaxis. Hence not much value should be attached to this character.

Between the areas of ssp. *thomsonii* and ssp. *rigida* there is also some overlap. There are good indications that here too altitudinal isolation plays a part, ssp. *rigida* occupying a lower zone than does ssp. *thomsonii*; compare the notes on ecology of both subspecies. Only one rather obvious case of hybridization between them has been found (see under ssp. *rigida*).

There has been much confusion in the nomenclature of ssp. *thomsonii*, ssp. *yunnanensis*, and ssp. *pungens*; see the remarks under both the latter subspecies.

For the affinities between ssp. *thomsonii* and its derivative ssp. *pungens*, see under the latter subspecies.

Locally ssp. *thomsonii* comes into contact with ssp. *simplicifolia*; I have seen one specimen clearly intermediate between both, viz. *Stainton 4963*, from Nepal (collected at *c.* 1500 m).

c. ssp. **yunnanensis** (Franch.) Beus., *stat. nov.* — *M. yunnanensis* Franch., Bull. Soc. Bot. Fr. 33 (1886) 465; Pl. Delav. (1889) 147; Cufod., Oest. Bot. Z. 88 (1939) 262; How, Acta Phytotax. Sin. 3 (1955) 430; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45, *in obs.*; Vidal, Not. Syst. 16 (1960) 307. — Type: *Delavay 877* (Yunnan), seen from A, K, P (holo).

[*Millingtonia acuminata* Royle, Ill. Bot. Himal. (1835) 139, *nomen.*]

[*Millingtonia integrifolia* Wall. *ex* Royle, Ill. Bot. Himal. (1835) 139, *pro parte, nomen.* Type: *Wallich 8114 G* (Nepal), seen from K.]

M. pungens sensu Brandis, For. Fl. (1874) 116, *non* (Wall. *ex* W. & A.) Walp., *pro parte*; Hook. *f.*, Fl. Br. Ind. 2 (1876) 4, *pro parte, excl. spec. Japon. et Wall. Cat. 8114 E* (*vide ssp. thomsonii*); Collett, Fl. Siml. (1902) 102, *pro parte*; Brandis, Ind. Trees (1906) 194, *pro parte*; Bamb., Pl. Punjab (1916) 30, *pro parte*; Osmaston, For. Fl. Kumaon (1927) 133, *pro parte*; Hand.-Mazz., Symb. Sin. 7 (1933) 644; Merr., Brittonia 4 (1941) 110; Kitamura in Kihara, Fauna & Flora Nepal (1955) 176; Hara, Fl. East. Himal. (1966) 194.

M. fischeriana Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 203; Cufod., Oest. Bot. Z. 88 (1939) 263; Chun, Sunyatsenia 4 (1940) 243; Merr., Brittonia 4 (1941) 111, *in obs.*; How, Acta Phytotax. Sin. 3 (1955) 431; Vidal, Not. Syst. 16 (1960) 305. — Type: *Wilson 4817* (Mt. Omei, Szechuan), seen from A (holo), K.

Leaves obovate-oblong to obovate-lanceolate, sometimes oblong to lanceolate, 3—15 by 1—6 cm, index 2—4, the base acute to long-cuneate or slightly attenuate, the apex cuspidate to subcaudate, usually remotely spinously dentate especially towards the apex, sometimes (sub)entire, glabrous or very sparsely puberulous or pubescent especially on the midrib, sometimes with minute domatia in the axils of the nerves; midrib and nerves slightly impressed to prominent above; nerves 7—14 pairs; petiole $\frac{1}{16}$—$\frac{1}{5}$(—$\frac{1}{4}$) as long as the blade. *Panicles* lax to dense, 4—20(—25) cm, often narrow, poorly to rather profusely branched up to the 2nd (3rd) order, often composed of a tuft of up to about five main axes (essentially primary side-axes; type D. & E, see fig. 1); axes slender to rather coarse, terete to slightly angular, often rather short, moderately to densely pubescent, the lower primary ones often crowded, very often upright, often subtended by normal to small leaves. *Flowers* solitary to very crowded, (sub)sessile; mature buds 2½—3 mm ø. *Sepals* 5(—7)[1], rarely with a few hairs on the outside of the outer ones. *Inner petals* 1—1½ mm, slightly bifid; lobes divergent, wide, glabrous or sometimes a bit ciliolate or fimbriate. *Style* as long as the ovary or somewhat longer. *Endocarps* subglobose, more or less oblique, often somewhat triangular at ventral view, 3½—4½ mm ø, with more or less elevated, fine reticulum; median keel distinct and somewhat prominent, blunt, not running out into a ventral processus; ventral pore not sunken, not spouted (fig. 22L).

Distribution: Foot of the Himalaya: N. India (NE. Punjab; Kumaon; Nepal; Sikkim; Bhutan; N. Assam), extreme SE. Tibet, extreme N. Upper Burma, China (N. and NW. Yunnan; Szechuan: only found in Kuan Hsien and Omei Hsien). Common in most parts of the area. — Fig. 27.

Ecology: In evergreen broad-leaved forests dominated by oaks, on different soils (reported from sand and schists). Most common in Yunnan, where it occurs from about 2000 m up to at least 3200 m altitude, especially between 2500 and 3000 m. In Szechuan (Mt. Omei) frequently found between 1350 and 2000 m. Also at lower altitudes from Bhutan westwards, mostly from 1500 m up to about 2100 m, occasionally up to 2400 m. Often said to be found at streams, in open thickets, roadsides, and ravines. See also the Remarks.

Vernacular names (most several times mentioned): N. India: *Gōgua* or *Gugua* (Ranikhet, N. Garhwal), *Gōgsha* or *Charcharyiá Ghōgsá* (NW. Provinces, unspecified), *Busha* (Jaunsar), *Bushkua, Bekesh, Kapper* (all NW. Himalaya, unspecified), *Koda khebade* (Nepal, near Kathmandu).

Remarks. Specimens belonging to ssp. *yunnanensis* and ssp. *thomsonii*, especially from the Himalaya, often figure under the name *M. pungens*. They have, however, nothing to do with the real *M. pungens* from Peninsular India. The cause of this confusing situation has been dealt with under ssp. *pungens*.

The relation between ssp. *yunnanensis* and its neighbouring ssp. *rigida* and ssp. *thomsonii* has been discussed under those subspecies.

d. ssp. **laui** (Merr.) Beus., *stat. nov.* — *M. laui* Merr., Lingn. Sc. J. 14 (1935) 32; Cufod., Oest. Bot. Z. 88 (1939) 265; How, Acta Phytotax. Sin. 3 (1955) 441; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 49, t. 8 f. 1—6; Vidal, Not. Syst. 16 (1960) 306. — Type: *S. K. Lau 29* (Hainan), seen from A, E, K, P, W.

M. pannosa Hand.-Mazz.: Cufod., Oest. Bot. Z. 88 (1939) 265, *pro parte.*

M. evrardii Gagn., Not. Syst. 14 (1952) 273; Vidal, Not. Syst. 16 (1960) 305; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 49; — Type: *Evrard 2186* (S. Vietnam), seen from P (holo). Paratype: *Poilane 24776*, seen from L, P. The other paratype, *Poilane 29983* (seen from L, P), does not belong to ssp. *laui*, but to ssp. *rigida.*

Leaves oblong to lanceolate, sometimes somewhat obovate-oblong, 4—18 by 1½—7 cm, index 2—4, usually without, sometimes with very few teeth towards the apex, the base, acute to cuneate, the apex acuminate to short-cuspidate, hardly to distinctly pubescent on the midrib above, densely tomentose beneath; midrib and nerves flat to impressed above; nerves 8—17 pairs; petiole $\frac{1}{7}$—$\frac{1}{3}$ as long as the blade. *Panicles* rather lax, 10—25 cm, branched up to the 2nd or 3rd order; axes terete, densely short-tomentose, the primary ones usually not subtended by small leaves. *Flowers* crowded, sessile; mature buds *c.* 2 mm ø. *Sepals* 5, all or at least the outer ones woolly pubescent on the outside. *Inner petals* ¾—1 mm, about halfway or somewhat less bifid; lobes more or less divergent, usually rather narrow, slightly fimbriate at the tips. *Style* about 1½—2 times as long as the

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[1] See note on p. 466.

ovary. *Endocarps* (sub)globose, more or less oblique, (6—)7—9 mm ø, with coarse, rather to extremely prominent reticulum which sometimes passes into sharp ridges and tubercles; median keel sharp and prominent, at one end running out into a small ventral tubercle or processus or not; ventral part with the pore usually somewhat elevated to spouted (fig. 22 Q 1, 2).

Distribution: China (Hainan; S. Kwangsi: near Kwangtung border). S. Vietnam (Dalat; Haut Donnaï). Reported to be abundant locally in Hainan. — Fig. 27.

Ecology: Probably about the same as ssp. *rigida* (possibly under drier conditions?), by which its place is taken in adjacent areas and which occurs in about the same altitudinal zones: reported from 600—700 m in Hainan, and from 1200—1400 m in S. Vietnam. Reported to occur on moist steep slope, but also on dry clay, silt.

Vernacular names: Hainan: *Dengsun* (Lois, once noted).

Remarks. In its characters ssp. *laui* directly joins ssp. *rigida*, to which it is obviously most closely related, and of which I consider it a direct derivative (see the Remarks under the species). Though it is quite characteristic by its oblong to lanceolate, densely tomentose leaves and big endocarps with strong prominent reticulum, it may nevertheless be difficult to delimitate it sharply against adjacent ssp. *rigida* populations from Vietnam and Kwangsi which may be rather similar to less typical ssp. *laui*; it is possible that they are connected by a transitional zone. Ssp. *laui* is, nevertheless, a definite unit, characterized by the same standards as the other subspecies of *M. simplicifolia.* It shares most of its area with ssp. *fordii* which has partly been collected at the same altitudes. It may be that they show preferences for different forest types, but I could not find any support for this in the few collectors' notes available. It is possible, therefore, that ssp. *fordii* and ssp. *laui* do not hybridize where they occur together, thus assuming the habit of good species. Since they are quite different, there would be no objection to consider them separate species, if not ssp. *rigida* were the link between them. Nevertheless, hydridizing of ssp. *laui* and ssp. *fordii* should not be excluded. I have seen a somewhat dubious specimen from Hainan (*C. Wang 33093*) which might represent a hybrid between these subspecies; its panicle is more like in ssp. *laui* and its leaves are more like in ssp. *fordii.* Unfortunately the flowers are over, and hence do not provide much evidence.

e. ssp. **rigida** (Sieb. & Zucc.) Beus., *stat. nov.* — *M. rigida* Sieb. & Zucc., Abh. K. (Bayer.) Ak. Wiss. M.-Ph. Kl. (Münch.) 4, 2 (1845) 153 (Fl. Jap. Fam. Nat. 1: 45); Miq., Ann. Mus. Bot. Lugd. Bat. 3 (1867) 93; Cat. Mus. Bot. 1 (1870) 23; Franch. & Savat., En. Pl. Jap. 1 (1873) 91; Maxim., Bot. Jahrb. 6 (1884) 60; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 145, *pro parte, excl. M. pungens*; Henry, Trans. As. Soc. Japan 24, Suppl. (1896) 29; Dunn, J. Linn. Soc. Bot. 38 (1908) 358; Hayata, Ic. Pl. Formos. 1 (1911) 161; Dunn & Tutch., Kew Bull. add. ser. 10 (1912) 68; Chun, Sunyatsenia 1 (1933) 180; Hand.-Mazz., Beih. Bot. Centralbl. 52 (1934) 166; Masam., Fl. Geo. Stud. Yakus. (1934) 285; Kaneh., Formos. Trees ed. 2 (1936) 416, f. 372; Cufod., Oest. Bot. Z. 88 (1939) 267; Hara, En. Sperm. Japon. 3 (1954) 121; Makino, Ill. Fl. Jap. (1954) 348, f. 1044; Walker, Imp. Trees Ryukyu Isl. (1954) 200, f. 121; How, Acta Phytotax. Sin. 3 (1955) 444; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 47, *in obs.*, t. 7 f. 6; Liu, Ill. Lign. Pl. Taiwan 2 (1962) 925, f. 762; Li, Woody Fl. Taiwan (1963) 503; Ohwi, Fl. Japan (1965) 613. — Lectotype: *Von Siebold s.n. in Herb. Zuccarinii* (Japan), seen from GH (holo).

[*Quercus jama-buwa* Sieb. *in sched. ex* Miq., Ann. Mus. Bot. Lugd. Bat. 3 (1867) 93, *nom. invalid. in synon.*; Ind. Kew. 2: 695.]

[*M. rigida* var. *angustifolia* Miq., Cat. Mus. Bot. 1 (1870) 23, *nomen.* — Lectotype: *Von Siebold s.n.* (Japan), seen from L.]

M. ferruginea Sieb. & Zucc. *in sched. ex* Hook. *f.*, Fl. Br. Ind. 2 (1876) 4, *nom. invalid. in synon. sub M. pungens, non* Bl. (1823), *nec* Kurz *ex* King (1897). — Type: *Von Siebold s.n. in Herb. Hook.* (Japan), seen from K.]

M. pungens sensu Hook. *f.*, Fl. Br. Ind. 2 (1876) 4, *non* (Wall. *ex* W. & A.) Walp., *pro parte, quoad pl. Japon.*; Ito & Matsum., Tent. Fl. Lutch. (1899) 391; Brandis, Ind. Trees (1906) 194, *pro parte, quoad pl. Japon.*; Matsum., Ind. Pl. Japon. 2, 2 (1912) 335.

M. patens Hemsl. *ex* Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 145; Dunn & Tutch., Kew Bull. add. ser. 10 (1912) 68; How, Acta Phytotax. Sin. 3 (1955) 445, *in obs.* — *M. rigida* var. *patens* Cufod., Oest. Bot. Z. 88 (1939) 267. — Type: *Ford 6* (Hongkong, Victoria Peak and Saywan), seen from GH, K (holo), W (as nr. *985*!).

M. harmandiana Pierre, Fl. For. Cochinch. 5 (1897) t. 360; Lecomte in Fl. Gén. I.—C. 2 (1908) 4, f. 2 C; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45, t. 7 f. 1—5, *pro parte, excl. Tsang 30188*; Vidal, Not. Syst. 16 (1960) 305. — Type: *Harmand 1244 in Herb. Pierre* (Laos), seen from P (holo).

M. glomerulata Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 203; Cufod., Oest. Bot. Z. 88 (1939) 265; How, Acta Phytotax. Sin. 3 (1955) 442; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 47, *in obs.* — Type: *Henry 11737* (Yunnan), seen from E, K. Paratypes: *Henry 11737 a* and *b* (same locality), both seen from A, K.

M. loheri Merr., Philip. J. Sc. 10 (1915) Bot. 38; En. Philip. 2 (1923) 517. — Type: *Vanoverbergh 1131* (Luzon, Philippine Islands), seen from A, L, U, W. Paratypes: *McGregor BS 19630*, not seen; *Loher 368* (erroneously cited as *268*!), seen from K.

M. pannosa Hand.-Mazz., Anz. Ak. Wiss. Wien M.-N. Kl. 58 (1921) 179; Symb. Sin. 7 (1933) 644; Merr., Sunyatsenia 1 (1934) 200; Cufod., Oest. Bot. Z. 88 (1939) 265, *pro parte, excl. pl. Hainan.*; How, Acta Phytotax. Sin. 3 (1955) 442; Steward, Vasc. Pl. Low. Yangtze (1958) 235; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 50, *in obs., pro parte.* — Type: *Handel-Mazzetti 10704* (Kweichow), seen from A, W (holo).

M. costata Cufod., Oest. Bot. Z. 88 (1939) 266; How, Acta Phytotax. Sin. 3 (1955) 444; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45; Vidal, Not. Syst. 16 (1960) 304. — Type: *Coll. Sun Yat Sen Univ. 8212* (Kwangsi), seen from W (iso). Paratypes: *C. Wang 39247*, seen from A; *R. C. Ching 7657*, seen from A, W; *C. W. Wang 80501*, seen from A.

M. evrardii Gagn., Not. Syst. 14 (1952) 273, *pro min. parte*; see under ssp. *laui*.

Leaves usually obovate-oblong to obovate-lanceolate, sometimes oblong to lanceolate, 4—25(—32) by 1½—8—(11) cm, index (2—)3—5(—6), coarsely dentate to (sub)entire, the base long-cuneate to acute, the apex acute to cuspidate, above hardly to distinctly pubescent on midrib and sometimes on nerves, beneath sparsely to densely pubescent to tomentose, especially on midrib and nerves, but without domatia; midrib and nerves above usually distinctly impressed, sometimes flat; nerves 7—19 pairs; petiole ⅒—¼(—⅓) as long as the blade. *Panicles* lax to rather dense, 10—30 cm, branched up to the 2nd (3rd) order; axes about terete, more or less densely tomentose, sometimes woolly-pubescent, the primary ones only exceptionally subtended by small leaves[1]. *Flowers* more or less crowded, usually in dense glomerules, sessile; mature buds 1¾—2¼ mm ø. *Sepals* 5 (4), at least the outer ones sparsely to densely pubescent on the outside. *Inner petals* ⅔—¾ mm, usually less than halfway bifid; lobes hardly or not divergent, rather narrow, fimbriate or ciliolate at the tips. *Style* about (1½—)2 times as long as the ovary. *Endocarps* (sub)globose, not or not much oblique, (3½—)4—5 mm ø, with fine reticulum; median keel

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[1] Only found in *Y. W. Taam 1544* (Kwangtung), *Handel-Mazzetti 10704* (Kweichow), *Poilane 24776* (S. Vietnam), *Harmand 1244* (Laos), *Esguerra FB 31402* (Luzon), and *Ramos & Edaño BS 40491* (Luzon).

blunt to rather sharp, hardly to distinctly prominent, often at one end running out into a minute ventral processus or tubercle; ventral pore not sunken, often somewhat spouted (fig. 22P).

Distribution: China (S. and SW. Yunnan; Kwangsi; Kwangtung; Fokien; S. and Central Chekiang; Kiangsi; Hunan; Kweichow; SW. Hupeh), Laos (only found at Attopeu), S. Vietnam (only found at Hué), Philippine Islands (Luzon: Mountain Province), Taiwan (incl. Pescadores), Ryu Kyu Islands, Japan (Kyushu; Shikoku; Pacific side of Honshu up to *c.* 36° N). Rather common in Japan and Taiwan, local in China. — Fig. 27.

Ecology: In evergreen broad-leaved or laurophyllous forests, on different soils (sand, loamy schists, clay, silt), usually (China, Japan) at altitudes from 100 m up to 800—900 m, but occasionally higher: in Luzon reported from 1200—1600 m, in Vietnam from 1000—1400 m, and in Yunnan from 850 m up to even 2700 m. Occurring in dry (open hill-side, dry slope) as well as in wet (along stream, along ditch, on submerged soil) places.

Field notes: Bark grey, smooth. Branches brown. Leaves lustrous green above, sometimes glaucous beneath. Fruit blue-purple to purplish black.¹)

Vernacular names: China: *Fa muk heung* (once reported from Kwangtung; see also ssp. *fordii* and *M. henryi* ssp. *thorelii*!). Japan: *Yama biwa* (official Japanese name). Ryu Kyu Islands: *Yuinu-go* (Okinawa, *fide* Walker, l.c.). S. Vietnam: *(Cây) Hong* or *Da Tông* (Vietnamese, both once reported). Philippine Islands: *Gahatan* (Ifugao dial., Luzon, twice reported), *Lasuit* (Bondoc dial., *fide* Merrill, En. Philip. 2, 1923, 517).

Uses: Wood for umbrella handles, frames for sieves for sifting rice, carrying poles, etc., not good for fuel (see Walker, l.c.). In Luzon said to be used for fences and for fuel.

Remarks. Ssp. *rigida*, though well delimitated and recognizable as a natural unit (see the key), is variable in quite some characters, which led several authors to describe local forms as separate species. It is, for instance, always more or less pubescent, but amongst others in Hupeh and Kweichow specimens are found which are covered with a particularly dense, woolly tomentum ('*M. pannosa*'). The leaves in ssp. *rigida* are usually obovate-oblong to-lanceolate and distinctly dentate, but in Kwangsi they may be about oblong to lanceolate and entire or nearly so ('*M. costata*'). Furthermore, '*M. glomerulata*' from Yunnan was made a separate species mainly on the base of its lanceolate leaves and its pubescence which is thinner and more pale-coloured than usual; it is most probable that the type (*Henry 11737*) represents a hybrid or transitional form between ssp. *rigida* and ssp. *yunnanensis*; see below.

The area of ssp. *rigida* borders on or overlaps the areas of five or six other subspecies of *M. simplicifolia*, which substantially adds to the chance of confusing them. Several specimens have been collected which may be considered transitions or hybrids between ssp. *rigida* and an adjacent subspecies. For instance, *Henry 11737* from Yunnan just mentioned has some characters in common with specimens of ssp. *yunnanensis* from the same locality, though in most respects it matches ssp. *rigida* and hence is included here. *Cavalerie 2998* from Kweichow, on the other hand, is certainly intermediate between ssp. *thomsonii* and ssp. *rigida*, but has most characters in common with ssp. *thomsonii* to which I reckon it. Ssp. *rigida* specimens from Kwangsi ('*M. costata*') and Vietnam ('*M. evrardii*' *pro parte*) may show characters tending towards the adjacent and closely related ssp. *laui* (see there). Between the areas of ssp. *rigida* and ssp. *fordii* there is considerable overlap; it is very probable, however, that these subspecies are ecologically isolated to a large extent (see notes on ecology) and thus contact between them is prevented. Nevertheless it is well possible that some mixing of populations locally occurs (see under ssp. *fordii*). Also between ssp.

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¹) For wood characters, see Kanehira, Formosan Woods (1921) 83, t. 16 f. 96.

rigida and ssp. *thomsonii* there is a partly overlapping of the areas; on the available evidence it is probable that they keep apart by preference for different altitudinal zones (compare the notes on ecology). The next case of overlapping of areas is in Taiwan, where both ssp. *rigida* and ssp. *fruticosa* ('*M. callicarpaefolia*') occur. I suppose that here too they are ecologically separated, but the evidence from collectors' notes is inadequate on this point.

Quercus gilva var. *procera* Bl., Mus. Bot. Lugd. Bat. 1 (1850) 306, was included in the synonymy of *M. rigida* by Hara l.c. However, having seen the type material of this variety at Leyden, I found it indeed to belong to *Quercus gilva* Bl., and not to *Meliosma*. Probably, Hara was led to this erroneous reduction by the fact that *Quercus gilva* var. *procera* in Blume's paper is accompanied by the name *Jama biwa* which is the Japanese name for *M. rigida*. Blume copied this name from a label attached to the type specimen on which it was written with a question-mark.

f. ssp. **simplicifolia.** — *Millingtonia simplicifolia* Roxb. [Hort. Beng. (1814) 3, *nomen*] Pl. Corom. 3 (1820) 50, t. 254; Fl. Ind. 1 (1820) 103; Schult. & Schult., Syst. Veg. Mant. 1 (1822) 217; Spreng., Syst. Veg. 1 (1824) 36; Nees, Flora 8 (1825) 106; Schult. & Schult., Syst. Veg. Mant. 3, add. 2 (1827) 250; W. & A., Edinb. New Phil. J. 15 (1833) 179; Prod. 1 (1834) 115; Dietr., Syn. Pl. 1 (1839) 103; Griff., Notul. Pl. As. (1854) 162; Ic. Pl. As. (1854) t. 442; Anon., Ic. Roxb. 4 (1970) 40, t. 20. — [*Millingtonia integrifolia* Nees, Flora 8 (1825) 105, *nomen.*] — *M. simplicifolia* Walp., Rep. 1 (1842) 103; Hassk., Cat. Hort. Bog. (1844) 226; Thw., En. Pl. Zeyl. (1858) 59; Miq., Fl. Ind. Bat. 1, 2 (1859) 613; Sum. (1860) 203; Illustr. (1871) 73; Beddome, Fl. Sylv. 3 (1869) 77; Brandis, For. Fl. (1874) 116; Hook. *f.*, Fl. Br. Ind. 2 (1876) 5; Kurz, J. As. Soc. Beng. 45, ii (1876) 204; For. Fl. Br. Burma 1 (1877) 301; Trim., Fl. Ceyl. 1 (1893) 315; Prain, Bengal Pl. 1 (1903) 246; Duthie, Fl. Upp. Gangetic Plain 1, 1 (1903) 184; Brandis, Ind. Trees (1906) 194; Craib, Kew Bull. (1911) 33; Gamble, Fl. Pres. Madras 1 (1918) 256; Haines, Bot. Bihar & Orissa 2 (1921) 218; Craib, Fl. Siam. En. 1 (1926) 341; Merr., Contr. Arn. Arb. 8 (1934) 95; Kanj., Das & Purk., Fl. Assam 1 (1936) 327; Cufod., Oest. Bot. Z. 88 (1939) 261; Merr., Brittonia 4 (1941) 110; How, Acta Phytotax. Sin. 3 (1955) 428; Worthington, Ceyl. Trees (1959) 151; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 41, *in obs.*; Vidal, Not. Syst. 16 (1960) 307; Dansk Bot. Ark. 23 (1963) 35; Hara, Fl. East. Himal. (1966) 194. — Lectotype: *Roxburgh Ic. nr. 2104*, in Kew Library; reproductions in Roxb., Pl. Corom. l.c. and in Anon., Ic. Roxb. l.c.

[*Millingtonia laxa* W. & A., Edinb. New Phil. J. 15 (1833) 179, *nom. invalid. in synon. sub Millingtonia simplicifolia.*]

M. angulata Bl., Rumphia 3 (1849) 197; Walp., Ann. 2 (1852) 224; K. & V., Bijdr. 9 (1903) 131; Koord., Exk. Fl. Java 2 (1912) 545; Atlas 2 (1914) t. 378; Baker *f.* in Rendle, J. Bot. 62 (1924) Suppl. 30; Vidal, Not. Syst. 16 (1960) 304. — [*M. simplicifolia* Bl., Rumphia 3 (1849) 197, *in synon., nom. invalid.*] — Syntype: *? Blume s.n.* (Java), several sheets in L, fragm. in U.

Sabia densiflora Miq., Sum. (1860) 520; Illustr. (1871) 73, *in synon. sub M. simplicifolia.* — Type: *Junghuhn s.n.* (Angkola, Sumatra), seen from L, U (holo).

Sabia ? floribunda Miq., Sum. (1860) 203, 521; Kurz, J. As. Soc. Beng. 39, ii (1870) 74; Miq., Illustr. (1871) 73, *in synon. sub M. simplicifolia.* — *M. elliptica* Hook. *f.*, Fl. Br. Ind. 2 (1876) 5, *pro parte, quoad Sabia ? floribunda inclusa.* — Type: *Diepenhorst s.n.* (Priaman, Sumatra), seen from L, U (holo).

[*Millingtonia integrifolia* Wall. *ex* Royle, Ill. Bot. Himal. (1835) 139, *pro parte, nomen.*] — Type: *Wallich 8114 G* (Nepal), seen from F, K.

M. aff. thorelii (*non* Lecomte) Vidal, Dansk Bot. Ark. 23 (1963) 35.

Leaves obovate-oblong to obovate-lanceolate, rarely oblong to lanceolate, up to *c.* 50 by 18 cm, index (2—)2½—3½(—4), usually entire, sometimes more or less dentate[1]), the base long cuneate to acute, the apex acute to short-cuspidate, usually glabrous, above very rarely sparsely puberulous or pubescent on the midrib, especially in young leaves, beneath sometimes sparsely pubescent, often with domatia in the axils of the nerves; midrib and lesser so the nerves above nearly always more or less prominent, rarely flat or slightly impressed; nerves 8—23 pairs; petiole $\frac{1}{20}$—$\frac{1}{8}$ as long as the blade. *Panicles* rather lax, 10—45 cm, branched up to the 3rd or 4th order; axes slender, angular, sparsely to densely pubescent but never tomentose, the lower primary ones nearly always subtended by small to normal leaves. *Flowers* more or less crowded to solitary, (sub)sessile; mature buds 1½—2 mm ø. *Sepals* 5 (4). *Inner petals* ⅔—¾ mm, usually over halfway bifid, lobes more or less divergent, narrow, glabrous, sometimes slightly fimbriate or ciliolate at the very tips. *Style* about as long as the ovary or shorter. *Endocarps* subglobose, usually rather oblique, nearly triangular at ventral view, 3½—5(—7) mm ø, with more or less prominent, rather coarse reticulum; median keel usually very prominent, at one end sometimes running out into a minute ventral processus; ventral pore somewhat or not sunken, not spouted (fig. 22 K).

Distribution: Ceylon, SW. Peninsular India (from Mysore southward), NE. India (E. Ghats: Vizapatagam, local in Bihar and Orissa; Nepal; Sikkim; Bhutan; Assam; Manipur), East Pakistan (E. Bengal; Chittagong hill tracts), throughout Burma (southward up to Mergui), Thailand (northern; western: Tenasserim range), China (SW. Yunnan), N. Vietnam (only found in Lao Kay), Sumatra (only northern and West Coast), W. Java? (according to Blume, l.c.; never found since). Common in most parts of the area. — Fig. 27.

Ecology: In primary and secondary evergreen tropical forests, from sea-level up to about 1200 m, exceptionally at higher altitudes, up to 1500 m, in one case (N. Upper Burma) even at *c.* 2000 m. It is often reported to occur along watercourses, especially in Thailand, also in deep ravines with perennial water-supply (Haines, l.c.), and in moist low country (Trimen, l.c.).

Vernacular names (most once noted): Ceylon: *Elbedda, Elbetta*, or *Albadda-gass* (Sinhalese, many times), *Rawaniddala-gass* (mentioned by Thwaites, l.c.). NE. India: *Churri* (Nepal), *Patpati, Dant-rangi* (both from E. Bengal), *Kosru, Hingman-vaung* (both from Darjeeling), *Barbetbipa* (Garo Hills, Assam; for many other Assam names see Kanj., Das & Purk., l.c.). Burma: *Kasi-shillap, Prankinsa* (both Kachin), *Pet-taunggyaing, Payama* (both Burmese), *Lale or Lalay* (Karèn). Thailand: *Chaw karea* (or *Tsjakeria*), *Chaw kha rue poh, Po koean* (all Karèn), *Dua hu kwang* (Chiengmai). Sumatra: *Sumpa-mana-belawah, Simulingga* (both Karo), *Kaju gadis* (West Coast); *Medang-sungu* (Malay, N. Sumatra).

Remark. Ssp. *simplicifolia* is a rather uniform, well recognizable subspecies all over its area, which borders on or overlaps the areas of ssp. *fruticosa*, ssp. *pungens*, ssp. *fordii*, ssp. *rigida*, and ssp. *thomsonii*; see the remarks under the first four of these. I have not seen specimens which suggest contact with ssp. *rigida*; since there is not much overlap in areas and the latter has other requirements as to habitat, the possibility for such contact will probably not often occur.

g. ssp. **fruticosa** (Bl.) Beus., *stat. nov.* — *M. fruticosa* Bl., Rumphia 3 (1849) 198; Walp., Ann. 2 (1852) 224; Miq., Fl. Ind. Bat. 1, 2 (1859) 614; Illustr. (1871) 73; K. & V., Bijdr.

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[1]) Often in leaves of water-shoots, exceptionally in leaves of flowering twigs!

9 (1903) 133; Koord., Exk. Fl. Java 2 (1912) 545. — Lectotype: *? van Hasselt s.n.* (G. Pulusari, Java), seen from L (holo). Syntype: *Blume s.n.*, seen from L, U.

M. elliptica Hook. *f.*, Fl. Br. Ind. 2 (1876) 5, *pro parte, excl. Sabia ? floribunda* Miq.; King, J. As. Soc. Beng. 65, ii (1896) 456; Ridl., J. Str. Br. R. As. Soc. 33 (1900) 67; Fl. Mal. Pen. 1 (1922) 514; Burk. & Hend., Gard. Bull. S. S. 3 (1925) 364. — Syntypes (all from Malay Peninsula): *Griffith 1025, Maingay 463 pro parte, Lobb s.n.*, all seen from K.

M. lancifolia Hook. *f.*, Fl. Br. Ind. 2 (1876) 5; King, J. As. Soc. Beng. 65, ii (1896) 456; Ridl., Fl. Mal. Pen. 1 (1922) 514. — Type: *Maingay 463 pro parte* (Malay Peninsula), seen from BM, K (holo).

M. monophylla Merr., Philip. J. Sc. 4 (1909) Bot. 286; En. Philip. 2 (1923) 517; Vidal, Not. Syst. 16 (1960) 306. — *M. cambodiana* (*non* Pierre) Vidal, l.c. 304. — Syntypes (all from Philippine Islands): *Merrill 2339*, not seen; *Ahern's collector FB 431*, not seen, *3406*, seen from K, L.

M. callicarpaefolia Hayata, Ic. Pl. Formos. 3 (1913) 68; ibid. 6 (1916) 15, t. 2; Kaneh., Formos. Trees ed. 2 (1936) 414, f. 370; How, Acta Phytotax. Sin. 3 (1955) 430; Liu, Ill. Lign. Pl. Taiwan 2 (1962) 923, f. 760; Li, Woody Fl. Taiwan (1963) 502. — Syntypes: *Mori s.n.* (Baantankei, Taiwan, VII-1912), not seen; *Uyematsu s.n.* (Mt. Arisan, Taiwan, I-1913), photogr. seen from P. — **Fig. 28a—c.**

Leaves usually oblong to lanceolate, sometimes obovate to obovate-lanceolate, 5—40 (—45) by 2—15 cm, index 2—4(—5), entire or sparsely dentate especially towards the apex, the base acute to cuneate, the apex acute to acuminate, sometimes obtuse, above1) densely pubescent on midrib and sometimes on nerves and lamina, beneath glabrous to tomentose, sometimes with domatia in the axils of the nerves; midrib and nerves above flat to impressed; nerves 7—25 pairs; petiole $\frac{1}{20}$—$\frac{1}{6}$(—$\frac{1}{4}$) as long as the blade. *Panicles* usually lax, sometimes more dense, 10—50 cm, branched up to the 3rd (4th) order; axes slender, more or less angular, moderately pubescent to short-tomentose, the lower primary ones subtended by small leaves or not. *Flowers* more or less crowded to solitary, (sub)sessile; mature buds 1½—2 mm ø. *Sepals* 5 (4), the outer ones often somewhat pubescent on the outside. *Inner petals c.* ¾ mm, about halfway or somewhat less bifid; lobes divergent or not, usually rather narrow, more or less fimbriate, sometimes entire. *Style* about as long as the ovary or shorter. *Endocarps* globose, sometimes somewhat ellipsoid, often somewhat oblique, (4½—)5½—8 mm ø, with rather wide, coarse reticulum; median keel prominent, at one end often running out into a minute ventral processus; ventral pore not or not much sunken, not spouted.

Distribution: Thailand (Peninsula: only found in Surat), Malay Peninsula (Kedah; Penang I.; Perak; Pahang; Selangor; Malacca; Singapore), throughout Sumatra, W. Java, Lesser Sunda Islands (only collected on Sumbawa and Flores), Borneo (only found in W. Kutai and Sabah: Mt. Kinabalu, Tambunan), Philippine Is. (only in Luzon: Rizal Prov.), Taiwan (Alishan; South Cape). Apparently common in Sumatra and the Malay Peninsula, probably much rarer and occurring locally in the other parts of the area. — Fig. 27.

Ecology: In primary tropical rain forests, on various soil types, reported to occur on limestone, sand, volcanic loam, and andesite. At altitudes from sea-level up to 2400 m.

Field notes: Bark smooth, grey to brown, lenticellate, paperthin. Inner bark pale brown to dark brownred. Wood2) reddish to redbrown. Fruit yellow to pale red when ripening, dark red to brown when ripe.

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1) In older leaves sometimes wearing off.

2) See Kanehira, Formosan Woods (1921) 82, t. 16 f. 92, 93.

Fig. 28. *M. simplicifolia* ssp. *fruticosa*. — a. fruiting twig, × ½. — b. detail of leaf undersurface, × 2½. — c. endocarp, in different positions, × 2½.
M. henryi ssp. *thorelii*. — d. ripe fruit with hairy patch near the base (remnant of ovary pubescence), × 3. a—c from *Kadim & Noor 395*, d from *W. Y. Chun 7301*.

Vernacular names (all once noted): Malay Peninsula: *Bua palu* (Selangor), *Mĕdang kĕrkulu*, *Mĕngading* (Malacca). Sumatra: *Lĕlagan* (Gajo language, Atjeh), *Kaju si raga*, *K. djarap*², *K. gasir* (all Asahan), *K. ardong*² (Toba), *Kabung*² (Tapanuli), *Masadih pajo* (Simalur), *Kĕndung* (Palembang), *Rĕdjang* (Djambi). Java: *Ki tiwu* (Preanger). Flores: *Kaju sar*. Philippine Islands: *Malaligas* (Tagalog dial., Luzon, *fide* Merrill, En. Philip. 2, 1923, 517).

Remarks. Ssp. *fruticosa* displays some local variation, though by far not so much as ssp. *fordii*. Especially its leaves may vary from nearly glabrous to densely villous-pubescent, and from rather small and elliptic (*'M. elliptica'*) to big and (oblong-)lanceolate (*'M. lancifolia'*). Its discriminative characters, however, are rather constant. Only towards the southeastern and northeastern end of the distributional area, viz. on Java, Sumbawa, and Flores, and on Taiwan, it looses a bit of its subspecific identity, the inner petals being (nearly) entire instead of fimbriate. It is most closely related to ssp. *fordii*, its distributional area nicely linking up with the area of that subspecies. Certainly ssp. *fruticosa* has split off from ssp. *fordii*, just as ssp. *pungens* from ssp. *thomsonii* and ssp. *laui* from ssp. *rigida* (see the remarks under the species). Specimens from Taiwan (*'M. callicarpaefolia'*) (of which I have seen no fruits) might almost as well be included in ssp. *fordii*, but I have chosen the other solution since these plants possess more *fruticosa* characters (size of the flowers, faint domatia) and link up much better with ssp. *fruticosa* specimens from Luzon and even more so with specimens from Mt. Kinabalu (Borneo) than they do with the much nearer Kwangtung populations of ssp. *fordii*.

The other, but somewhat less closely allied subspecies is ssp. *simplicifolia* the area of which joins, and even partly overlaps in Sumatra, that of ssp. *fruticosa* in the Northwest. Though these subspecies have often been confused, they can nearly always very well be identified by their midrib characters, by their inner petal lobes being fimbriate or not, and by the size and shape of their endocarps (see the key). A remarkable fact is that ssp. *fruticosa* and ssp. *simplicifolia* both occur in Sumatra and have often been collected there in the same regions, no transitional form having ever been found. It is possible that they occur together and behave as species, but there is good evidence that they are altitudinally isolated; in areas where both subspecies are found (West Coast, Tapanuli, Atjeh) ssp. *fruticosa* has only been collected at high altitudes, well over 1000 m, whereas ssp. *simplicifolia* does not seem to exceed 900—1000 m. In the remaining part of Sumatra, however, only ssp. *fruticosa* has been found sofar, and mostly at low altitudes.

h. ssp. **fordii** (Hemsl. *ex* Forb. & Hemsl.) Beus., *stat. nov.* — *M. fordii* Hemsl. *ex* Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 144; Dunn & Tutch., Kew Bull add. ser. 10 (1912) 68; Hand.-Mazz., Symb. Sin. 7 (1933) 645; Beih. Bot. Centralbl. 52 (1934) 166; Merr. & Chun, Sunyatsenia 2 (1935) 271; Cufod., Oest. Bot. Z. 88 (1939) 263; How, Acta Phytotax. Sin. 3 (1955) 432, t. 56 f. 12—18; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 34, *in obs.*, t. 5 f. 6—8. — Type: *Ford 23* (Kwangtung), seen from GH, K (holo).

M. cambodiana Pierre, Fl. For. Cochinch. 5 (1897) t. 360; Lecomte in Fl. Gén. I.-C. 2 (1908) 5; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 42. — Type: *Pierre 645* (Cambodia), seen from K, L, P (holo).

M. simplicifolia var. *sootepensis* Craib, Kew Bull. (1911) 33; Fl. Siam. En. 1 (1926) 341; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 42, *in obs.* — Type: *Kerr 535* (N. Thailand), seen from BM, K (holo), P.

M. velutina Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 202; Cufod., Oest. Bot. Z. 88 (1939) 267; How, Acta Phytotax. Sin. 3 (1955) 445; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 49; Vidal, Not. Syst, 16 (1960) 307. — Type: *Henry 12114* (Yunnan), seen from A (holo), K.

M. sinii Diels, Notizbl. Berl.-Dahl. 11 (1931) 213; Cufod. Oest. Bot. Z. 88 (1939) 265; How, Acta Phytotax. Sin. 3 (1955) 443; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 47, *in obs.* — Type: *S. S. Sin 8255* (Kwangsi), seen from A, W.

M. dolichobotrys Merr., J. Arn. Arb. 19 (1938) 47; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 36, t. 6 f. 4—6. — Type: *Pételot 4801* (N. Vietnam), seen from A (holo), L, P.

M. pseudopaupera Cufod., Oest. Bot. Z. 88 (1939) 264; How, Acta Phytotax. Sin. 3 (1955) 435, t. 57, f. 7, 8. — *M. paupera* (*non* Hand.-Mazz.) Merr., Lingn. Sc. J. 14 (1935) 32. — Type: *S. K. Lau 432* (Hainan), seen from A, E, K, W (holo). Paratypes: *S. K. Lau 27242, 27441*, both seen from A.

M. obtusa Merr. & Chun, Sunyatsenia 5 (1940) 115; How, Acta Phytotax. Sin. 3 (1955) 434. — Type: *F. C. How 73165* (Hainan), seen from A, GH.

M. donnaiensis Gagn., Bull. Soc. Bot. Fr. 99 (I-1952) 10; Not. Syst. 14 (XII-1152) 272, *pro maj. parte*; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 44, t. 2 f. 8-14; Vidal, Not. Syst. 16 (1960) 304. — Lectotype (Gagn. & Vidal, l.c.): *Poilane 22239* (S. Vietnam), seen from L, P (holo). Paratypes: *Poilane 21917, 22193*, both seen from L, P.

M. hainanensis How, Acta Phytotax. Sin. 3 (1955) 433, t. 57; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 34, *in obs.* — *M. rigida* (*non* Sieb. & Zucc.) Merr. & Chun, Sunyatsenia 5 (1940) 115. — Type: *F. C. How 72560* (Hainan), seen from A. Paratype: *F. C. How 72214*, seen from A, P.

M. pseudopaupera var. *pubisepala* How, Acta Phytotax. Sin. 3 (1955) 436, t. 57 f. 9—11. — *M. paupera* (*non* Hand.-Mazz.) Chun, Sunyatsenia 4 (1940) 243, *pro parte*. — Type: *C. Wang 32270* (Kwangtung), not seen.

M. ochracea Vidal *ex* Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 42; Vidal, Not. Syst. 16 (1960) 306. — *M. donnaiensis* (*non* Gagn. I-1952) Gagn., Not. Syst. 14 (XII-1952) 272, *pro min. parte*. — Type: *Poilane 23472* (S. Vietnam), seen from P (holo).

M. kontumensis Vidal *ex* Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 42; Vidal, Not. Syst. 16 (1960) 305. — Type: *Poilane 35521* (S. Vietnam), seen from P (holo).

M. harmandiana (*non* Pierre) Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 45, *pro parte, quoad Tsang 30188.*

Leaves obovate-oblong to obovate-lanceolate or oblong to lanceolate, 3—25(—34) by 1—8(—10) cm, index (2—)2½—4, usually entire, sometimes with a few remote teeth, rarely predominantly dentate, the base long-attenuate or -cuneate to acute, the apex acute to acuminate, sometimes obtuse to rounded, above usually (sub)glabrous, sometimes pubescent on midrib and less so on nerves and blade, beneath usually subglabrous to sparsely, sometimes rather densely short-pubescent especially on midrib and nerves, but always without domatia; midrib and nerves above usually somewhat prominent, sometimes more or less impressed; nerves 9—20 pairs; petiole ($\frac{1}{20}$—)$\frac{1}{10}$—$\frac{1}{3}$ as long as the blade. *Panicles* lax to rather dense, 10—40 cm, branched up to the 3rd or 4th order, sometimes composed of a tuft of up to about four main axes (essentially primary side-axes; type E, see fig. 1); axes thin and slender, angular, thinly to rather densely pubescent (but not densely rufous tomentose as in ssp. *rigida*), the lower primary ones almost always subtended by small leaves. *Flowers* solitary and short-pedicelled to rather crowded and sessile (but not very densely glomerate as in ssp. *rigida*); mature buds 1—1⅓(—1½) mm ø. *Sepals* 5 (4), the outer ones usually densely pubescent on the outside, rarely tomentose. *Inner petals* ½—¾ mm, usually about halfway bifid; lobes more or less divergent, usually narrow, sometimes slightly ciliolate at the very tips. *Style* about as long as the ovary. *Endocarps* globose to somewhat depressed-globose, 3—5 mm ø, with fine reticulum;

median keel hardly or not prominent, not running out into a ventral processus; ventral pore not or not much sunken, not spouted (fig. 22 N).

Distribution: China (up to *c.* 26° N: S. Yunnan; S. Kweichow; Kwangsi; S. Kiangsi; Kwangtung, incl. Hainan), Laos, Vietnam, Cambodia, Thailand (northern; eastern; one isolated locality in the Peninsula). — Fig. 27.

Ecology: In evergreen tropical (hill-)forests, in dense to open woods, on sandy or clayish soil, often on slopes, also in dry places. At altitudes from 300—1000 m, in Yunnan and N. Vietnam reported from 1000—1500 m.

Field notes: In China the leaves are usually reported to be glaucous beneath, lustrous green above.

Vernacular names: China: *Heung pei shue*, *Fa muk heung*, both twice mentioned from Kwangsi and Kwangtung (the latter name is also used for ssp. *rigida* and *M. henryi* ssp. *thorelii*). S. Vietnam: *Krôn*, *Par pam*, *Rönga us*, *Sron pinh* (all from Blao), *Pam pro* (Djiring), all Proto-Indochinese names once mentioned from the Prov. of Haut Donnai.

Remarks. Ssp. *fordii* is very variable and may deceivingly resemble other subspecies and even species. Nevertheless, its different forms share a number of characters by which they can be united into a natural, coherent taxon. These characters are found in the panicle, the flowers, and the endocarps; in vegetative state it is very difficult to recognize ssp. *fordii*.

Ssp. *fordii* is closely allied to ssp. *simplicifolia* to the West, to ssp. *rigida* to the North, and to ssp. *fruticosa* to the South and East, against which taxa it can be delimitated rather sharply. In N. Thailand and SW. Yunnan it borders on the area of ssp. *simplicifolia*, and here ssp. *fordii* resembles ssp. *simplicifolia* rather closely (described as var. *sootepensis* of *M. simplicifolia*!), but is generally well distinct by its elliptic to lanceolate leaves and globose, feebly keeled endocarps, whereas ssp. *simplicifolia* usually has obovate to obovate-lanceolate leaves and more or less oblique, much stronger keeled endocarps with a coarser reticulation on the surface. A few specimens with intermediate characters may be found in this boundary area between the two subspecies.

Though the leaves in ssp. *fordii* are usually entire and glabrous or nearly so, populations in Kwangsi, Hainan, and the Kwangtung-Tonkin border area often have more or less entire and pubescent leaves ('*M. hainanensis*', '*M. sinii*'), thus showing resemblance to ssp. *rigida*. This subspecies, however, can still be recognized by its panicles without decrescent leaves, with coarser, less branched axes covered with a usually dense layer of rufous tomentum, whereas its flowers are much more glomerately arranged. Moreover, it seems that where this pubescent-dentate-leaved form of ssp. *fordii* occurs, ssp. *rigida* is usually absent and replaced by the closely allied ssp. *laui* which is much more distinct from ssp. *fordii* than is ssp. *rigida*. Still, in certain parts of Yunnan and Kwangsi (Yao Shan) ssp. *fordii* and ssp. *rigida* may occur together, and hybridization may play a part there. Some of the pubescent-dentate-leaved specimens of ssp. *fordii* may be of hybrid origin. In general, however, ssp. *fordii* and *rigida* keep well separate, probably mainly as a result of their preference for different forest formations (see notes on Ecology).

Forms of ssp. *fordii* with more or less pubescent leaves but few or no teeth closely resemble specimens of the Malesian ssp. *fruticosa*, but the leaves of the latter are often provided with domatia, its inner petals are usually fimbriate, and its flowers are bigger, as are the endocarps which are also stronger keeled and have a coarser reticulation. Obviously, however, ssp. *fruticosa* is closely allied to ssp. *fordii* from which I consider it to be a direct derivative (see the remarks under the species). Specimens of the latter from Taiwan (of which I have seen no fruits) might almost as well be included in ssp. *fordii*; see the remarks under ssp. *fruticosa*. For the relation between ssp. *fordii* and ssp. *laui*, see under the latter.

Not only may confusion arise between ssp. *fordii* and its adjacent subspecies, but this may even occur on the specific level. In N. Vietnam (Cha Pa) ssp. *fordii* is found in the same locality as *M. lepidota* ssp. *dumicola*, and it is remarkable how close the superficial resemblance between them is in that place, even to such an extent that specimens belonging to *M. lepidota* ssp. *dumicola* were formely included in *M. fordii* (*Pételot 5453*, later described as *M. tonkinensis*). Apparently, however, they keep well separate in their essential characters.

The situation in ssp. *fordii* becomes even more complex because of the fact that locally several rather different forms may be found together in the same area. This is especially the case in Hainan, where, apart from the typical ssp. *fordii*, a pubescent-leaved form (‘*M. hainanensis*’) and a small-leaved form (‘*M obtusa*’, ‘*M. pseudopaupera*’) occur. Here population studies in the field might be rewarding to find out in how far these forms are mutually connected by transitions.

For the relationship of *M. simplicifolia* ssp. *fordii* with *M. paupera*, see the remarks under that species.

7. **Meliosma paupera** Hand.-Mazz., Anz. Ak. Wiss. Wien M.-N. Kl. 58 (1921) 150; Symb. Sin. 7 (1933) 645; Merr., Sunyatsenia 1 (1934) 199; Cufod., Oest. Bot. Z. 88 (1939) 264; Chun, Sunyatsenia 4 (1940) 243; How, Acta Phytotax. Sin. 3 (1955) 434, t. 57 f. 4—6; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 33, t. 4 f. 6, 7. — *M. donnaiensis* Gagn., Not. Syst. 14 (1952) 272, *pro min. parte*. — Type: *Handel-Mazzetti 10820* (Kweichow), seen from A, W (holo).

M. paupera var. *repanda-serrata* Merr., Sunyatsenia 1 (1934) 200; Cufod., Oest. Bot. Z. 88 (1939) 264 (‘*repando-serrata*’); How, Acta Phytotax. Sin. 3 (1955) 435. — Type: *Tso 20950* (Kwangtung), seen from A.

Evergreen shrub or small tree, up to *c.* 9 m. *Flowering twigs* terete to angular, 1½—3(—4) mm ø, glabrous or with few hairs. *Leaves* oblong to lanceolate, sometimes more or less obovate-oblong to obovate-lanceolate, 3—15 by 1—3(—3½) cm, index 2½—5, at the base acute or attenuate to cuneate, at the apex subacute to acuminate, sometimes cuspidate entire to remotely spinously (sinuate-)dentate especially towards the apex, chartaceous, dull or somewhat shining above, dull and usually paler beneath, glabrous or somewhat puberulous on the midrib above, subglabrous to sparsely puberulous beneath, without domatia; midrib above more or less impressed, beneath prominent; nerves 7—15 pairs, more or less ascending and usually looped and joined near the margin, above flat to slightly elevated, beneath more or less prominent; venation distinct, reticulate, above flat or nearly so, beneath more or less prominulous; petiole ½—1½ cm, somewhat pubescent to subglabrous. *Panicles* terminal, erect, lax and poor, pyramidal, 7—14 cm, branched up to the 3rd or 4th order, branches more or less spreading, flaccid, very thin and slender, sparsely to moderately appressed-pubescent, bearing numerous solitary to rather crowded flowers; main axis angular, usually shallowly canaliculate; primary side-axes about 8—15, up to *c.* 8 cm, the lower ones subtended by normal to small leaves; bracts ovate to linear-lanceolate, up to *c.* 2 mm, moderately to densely pubescent. *Pedicels* absent or present, minute, up to *c.* 1 mm. *Mature buds* 1—1¼ mm ø. *Sepals* (4)5, (round-)ovate, more or less unequal, the inner 3 or 4 ⅔—¾ mm, glabrous, the outer 2 or 1 smaller, often minute, glabrous or somewhat pubescent on the back, all with entire, ciliolate margin. *Outer petals* glabrous. *Inner petals* slightly bifid, ½—⅔ mm, with more or less spreading, blunt, more or less ciliolate or fimbriate lobes, never with a central lobule. *Stamens:*

anther-cells $\frac{1}{7}$—$\frac{1}{8}$ mm ø; filaments $\frac{1}{2}$—$\frac{2}{3}$ mm, glabrous. *Ovary* subglobose, *c.* $\frac{1}{2}$ mm, glabrous. *Style* $\frac{1}{4}$—$\frac{1}{3}$ mm, glabrous. *Fruit* globose, when ripe *c.* 5 mm ø; endocarp globose, hardly or not depressed or oblique, *c.* 4 mm ø, with distinct, fine, prominulous reticulum; median keel slightly elevated, blunt, not running out into a ventral processus; ventral pore neither sunken, nor spouted (fig. 22G 1, 2).

Distribution: SE. China (up to *c.* 26° N; cf. *M. simplicifolia* ssp. *fordii*): Kwangsi (Paishou Dist., along Shuang-chiang; N. of Luchen), S. Kweichow (Sandjio), Kwangtung (Yang Shan Dist.; Lochong; Wung Yuen Dist.), Kiangsi (Kiennan Dist.); S. Vietnam: Prov. Thua Thien (upper course of Bo Giang). Apparently not common, a few times reported to be rare. — Fig. 27.

Ecology: In light tropical woods, at low medium altitudes; reported from 350—450 m (S. China). Found in woods or thickets on steep to gentle, dry slopes, also along streams, on loam or clay soils and on schists (cf. *M. simplicifolia* ssp. *fordii*).

Field notes: The leaves are once said to be glaucescent beneath.

Remarks. M. paupera is very closely allied to *M. simplicifolia* ssp. *fordii*, from which I consider it to be derived. It partly covers the same area and has been found in the same localities. Probably it prefers also about the same habitat, as far as can be deduced from what is known about their ecology. Morphologically, *M. paupera* is very similar to the poorer, small-leaved forms of *M. simplicifolia* ssp. *fordii* such as occur especially on Hainan ('*M. pseudopaupera*'!). Transitions between them, however, have never been found. In general, several differences separate *M. paupera* from *M. simplicifolia* ssp. *fordii*; the size of leaves and panicles of the latter is usually much larger than in *M. paupera*, whereas this species has extremely tiny, almost thread-like inflorescence axes and very minute flowers such as do not occur in *M. simplicifolia* ssp. *fordii*. In cases of doubt the inner petals provide conclusive, always constant characters (see the key) to distinguish both taxa.

2. Subsect. *Pinnatae* (Warb.) Beus., *stat. nov.*[1])

Sect. *Pinnatae* Warb. in E. & P., Nat. Pfl. Fam. 3, 5 (1895) 372, *pro parte, excl. M. alba*; Cufod., Oest. Bot. Z. 88 (1939) 252, *excl. M. veitchiorum et beaniana*; How, Acta Phytotax. Sin. 3 (1955) 446, *idem*; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 23, 26; Vidal, Not. Syst. 16 (1960) 308, *excl. M. veitchiorum et beaniana*.

Leaves pinnate.

Lectotype species: *M. pinnata* (Roxb.) Walp.

Distribution: 5 species, mainly in Malesia, only 1 species entering continental SE. Asia. Predominantly tropical. — Fig. 7.

Remark. See under subsect. *Simplices* (p. 434).

8. Meliosma sumatrana (Jack) Walp., Ann. 1 (1848) 135; Miq., Fl. Ind. Bat. 1, 2 (1859) 617; Sum. (1860) 203; Illustr. (1871) 75; Hook. *f.*, Fl. Br. Ind. 2 (1876) 6; Koord., Minah. (1898) 408; Suppl. Cel. 2 (1922) 7, t. 56; ibid. 3 (1922) 28; Merr., En. Born. (1921) 363; En. Philip. 2 (1923) 518; Contr. Arn. Arb. 8 (1934) 95; Merr. & Perry, J. Arn. Arb. 20 (1939) 357. — *Millingtonia sumatrana* Jack, Mal. Misc. 2 (7) (1822) 30; Hook., J. Bot. 1 (1834) 378; Merr., J. Arn. Arb. 33 (1952) 236. — Type: *Jack s.n.* (Pulo Nias, Sumatra), not seen.

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1) Species 8—12 in this paper.

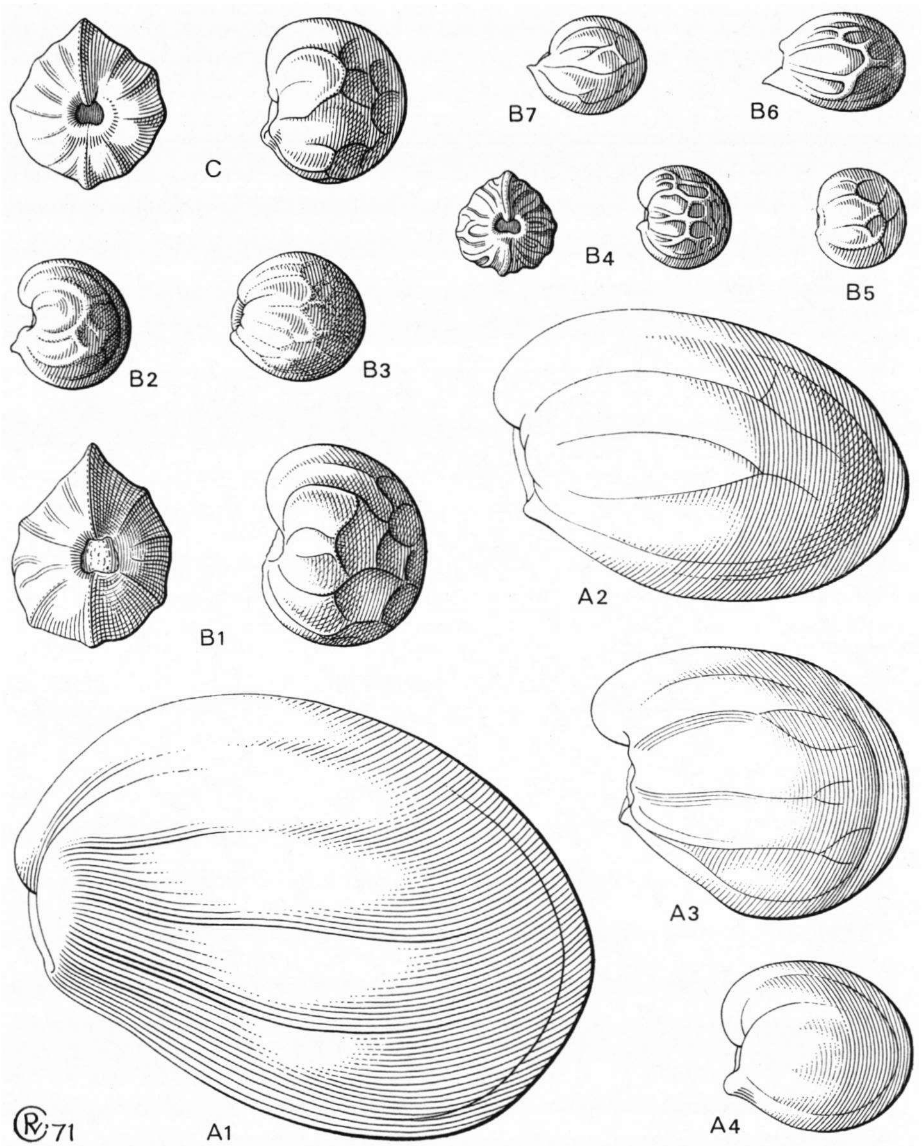

Fig. 29. Endocarps in subg. *Meliosma* sect. *Meliosma* subsect. *Pinnatae*. All × 3.

A1—4. *M. sumatrana* (respectively *Wood SAN A 3652, Endert 2917, Cockburn KEP/FRI 10920, Añonuevo PNH 13641*). — B1. *M. sarawakensis* (*Buwalda 6460*). — B2. *M. pinnata* ssp. *humilis* (*Pullen 6025*). — B3. *M. pinnata* ssp. *pendula* (*Edaño 40242*). — B4. *M. pinnata* ssp. *pinnata* (*King s.n.*, IX-1875). — B5. *M. pinnata* ssp. *arnottiana* (*Steward, Chiao & Cheo 814*). — B6. *M. pinnata* ssp. *macrophylla* (*Schram BW 5964*). — B7. *M. pinnata* ssp. *macrophylla* (*Henty NGF 27456*). — C. *M. lanceolata* (*cult. in Hort. Bogor. III-J-21*).

M. nitida Bl., Cat. (1823) 32; Nees, Flora 8 (1825) 106; Hassk., Tijdschr. Nat. Gesch. Phys. 10 (1843) 139; Cat. Hort. Bog. (1844) 226; Bl., Rumphia 3 (1849) 202, t. 169; Walp., Ann. 2 (1852) 225; Miq., Fl. Ind. Bat. 1, 2 (1859) 617; Sum. (1860) 203, 520; Illustr. (1871) 74; King, J. As. Soc. Beng. 65, ii (1896) 457; K. & V., Bijdr. 9 (1903) 117; Koord., Gedenkb. Jungh. (1910) 177; Exk. Fl. Java 2 (1912) 546, f. 81; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 4; Koord., Atlas 2 (1914) 377; Ridl., Fl. Mal. Pen. 1 (1922) 515; Baker *f.* in Rendle, J. Bot. 62 (1924) Suppl. 30; Burk. & Hend., Gard. Bull. S. S. 3 (1925) 364; Heyne, Nutt. Pl. (1927) 1002; Merr. & Perry, J. Arn. Arb. 20 (1939) 357, *in obs.*; Back. & Bakh. *f.*, Fl. Java 2 (1965) 145. — *Millingtonia nitida* Schult. & Schult., Syst. Veg. Mant. 3, add. 2 (1827) 250; Dietr., Syn. Pl. 1 (1839) 103. — Lectotype: *? Blume s.n.* (Java), and syntype, seen from L.

Irina integerrima Bl., Bijdr. 5 (1825) 231, *non* Hassk., Pl. Jav. Rar. (1848) 284 (*'Irine'*); Walp., Rep. 1 (1849) 416; Bl., Rumphia 3 (1849) 202, *in synon. sub M. nitida.* — Type: Unknown (G. Megamedung, Java).

M. nitida var. *tridentata* Bl., Rumphia 3 (1849) 203; Walp., Ann. 2 (1852) 225; K. & V., Bijdr. 9 (1903) 120; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 5. — Syntype: *? Blume s.n.* (Harriang, Patudja etc., Java), seen from L.

M. nitida var. *cerasiformis* Bl., l.c.; Walp., l.c.; K. & V., l.c.; Koord.-Schum., l.c. — Syntype: *? Blume s.n.* (G. Salak, Java), seen from L.

M. nitida var. *splendens* Bl., l.c.; Walp., l.c.; K. & V., l.c. 121; Koord.-Schum., l.c. — Syntype: *Korthals s.n.* (Sumatra), seen from L.

M. confusa Bl., Rumphia 3 (1849) 200; Walp., Ann. 2 (1852) 225; Miq., Fl. Ind. Bat. 1, 2 (1859) 616; Sum. (1860) 203, 520; Illustr. (1871) 74. — [*Millingtonia pinnata* (*non* Roxb.) Korth. *in sched. ex* Bl., l.c., *in synon.*] — Syntype: *Korthals s.n.* (Sumatra), seen from BO, K, L, U, W.

M. cuspidata Bl., Rumphia 3 (1849) 202; Miq., Fl. Ind. Bat. 1, 2 (1859) 617; Illustr. (1871) 74; Hall. *f.*, Med. Rijksherb. 1 (1910) 2; Merr., En. Born. (1921) 362. — *M. lanceolata* Bl.: Miq., Illustr. (1871) 74, *pro parte.* — Syntype: *Korthals s.n.* (G. Sakumbang, Borneo), seen from L, U.

M. pinnata (*non* Walp.) Koord., Minah. (1898) 408.

M. diepenhorstii Val., Ic. Bog. 2 (1904) 195, t. 150. — Type: *Diepenhorst s.n.* (Sumatra), not seen.

M. elmeri Merr., Pl. Elm. Born. (1929) 177. — Type: *Elmer 21578* (Borneo), seen from BM, BO, K, L, SING, U.

M. philippinensis Merr. & Perry, J. Arn. Arb. 20 (1939) 357. — Type: *Wenzel 2534* (Philippine Islands), seen from A (holo). Paratypes: *Wenzel 2945*, seen from A, BO, *3331*, seen from BO, GH; *Mallonga FB 27000*, seen from A; *Ramos & Edaño BS 37368*, seen from BO; *Alvarez FB 25173*, seen from A; *Edaño BS 39054*, *39101*, not seen; *Clemens BS 15599*, seen from A; *Elmer 10531*, seen from A, BM, BO, K, *11178*, seen from A, BM, BO, GH, K, L, U, W, *13297*, *13771*, both seen from A, BM, BO, E, GH, K, L, U, W.

Evergreen tree, small to medium-sized, sometimes big, up to 15—20(25) m. *Flowering twigs* terete, mostly stout, 2—15 mm ø, glabrous, rarely puberulous, sometimes with conspicuous leaf-scars. *Leaves* 2—5(—6)-jugate; rachis terete, 6—50 cm, including the up to *c.* 25(—30) cm long petiole which may be shorter or longer than the rest of the rachis, up to *c.* 10(—15) mm across, glabrous, rarely slightly pubescent, usually with distinctly swollen base, lenticellate or not; leaflets usually elliptic to lanceolate, sometimes ovate to ovate-lanceolate or obovate to obovate-lanceolate, (3—)5—35(—50) by (1½—)2½—15 (—20) cm, index (1—)1½—3(—4½), usually increasing in size towards the top of the leaf, the base cuneate to rounded, shortly narrowed into the petiolule, at the apex acuminate to caudate, with usually entire, sometimes remotely spinous-dentate margin, chartaceous to firmly coriaceous, usually more or less shining on both sides, sometimes dull beneath, paler beneath than above, above glabrous, beneath rarely more or less pubescent especially on midrib and nerves, without domatia; midrib slightly prominent above, very prominent beneath; nerves (5—)7—13(—19) pairs, ascending, nearly always looped and joined often into a marginal nerve, above flat to slightly prominent or impressed, beneath usually distinctly prominent; venation distinct, reticulate, sometimes more or less cancellate, above flat to slightly prominent or impressed, beneath more or less prominent; petiolules very short or up to *c.* 6 cm, terminal one usually longest, glabrous, rarely more or less pubescent, usually distinctly swollen at the base especially in older leaves. *Panicles* usually terminal, occasionally axillary1)), erect, usually narrowly, sometimes widely pyramidal, 7—50(—75) cm, usually profusely branched up to the 4th order, branches spreading or not, rather stiff and coarse, terete to more or less grooved and angular, sparsely to densely puberulous, bearing numerous crowded flowers; main axis terete to shallowly canaliculate; primary side-axes few to usually many, usually rather short, up to *c.* 30 cm, the lower ones exceptionally subtended by small to reduced leaves; bracts ovate to narrowly triangular, up to *c.* 6 mm, more or less puberulous. *Pedicels* absent or short, up to *c.* 2 mm. *Mature buds* (1½—)2—3(—3½) mm ø. *Sepals* 5 or 4, ovate, unequal, the inner 3 or 4 *c.* 1—2 mm, the outer 1 or 2 usually smaller, often minute, sometimes lowered on the pedicel, usually glabrous, sometimes puberulous on the outside, especially the outer ones, with entire or 2- or 3-lobed, often ciliolate margin. *Outer petals* glabrous. *Inner petals* elliptic to lanceolate or strap-shaped with wide-truncate tip, (1¼—)1½—2(—3) mm, acute to slightly bifid or retuse and frayed at the tip, glabrous. *Stamens:* anther-cells ¼—⅓ mm ø; filaments 1—2 mm. *Ovary* ½—1 mm, glabrous. *Style* ½—1 mm, glabrous. *Fruit* globose to short-ellipsoid, when ripe 1—3 cm ø, with rather thick spongy to pulpy mesocarp; endocarp ellipsoid, sometimes nearly globose, ¾—2 cm ø, with almost smooth to somewhat lumpy surface, often with a few faint to sharply prominent ribs; median keel distinct, slightly elevated to sharply prominent, at one end often running out into a more or less prominent curving, at the other end sometimes into a minute tubercle; ventral pore mostly rather wide, usually somewhat sunken (fig. 29A 1—4).

Distribution: West and Central Malesia: (not yet found in Peninsular Thailand), throughout Malay Peninsula (incl. Penang I., not found on Singapore I.), throughout Sumatra (incl. islands west of it: Nias, Batu Is., Sipora), Anambas Is., Banka, West and Central Java (residencies Banten, Djakarta, Preanger, Banjumas, and Semarang), throughout Borneo, Philippine Islands (Mindanao), Celebes. Common all over the area. — Fig. 30.

Ecology: In primary and secondary lowland and montane tropical rain forests, up to *c.* 2200 m altitude. Found on various soils, fertile as well as infertile, in dry to wet localities, in dense to open forests, by streams as well as on hill-tops and ridges.

Field notes: Often a crooked tree, irregularly branched. Trunk sometimes with small buttresses which are once said to be spreading as surface roots. Bark surface grey to brown, smooth, with lenticells, often with shallow fissures, sometimes said to be dimpled, patchy or scaly. Inner bark ½—1 cm thick, soft, fibrous, light yellow or dirty white, soon turning pink, brownish, reddish, or rusty after exposure. Sapwood said to be whitish, yellowish, creamy orange, or brownish. Sap without special smell or taste. Leaves bright green on both sides. Flower colour varying from white, cream, or greenish, to partly or entirely pinkish to red. Fruit first yellow, then yellow with red to red when ripe; pulp white, turning quickly blood-red on exposure, finally becoming black, sweetish to tasteless.

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1) Mostly as an aberration; not referable to one of the axillary types in fig. 1.

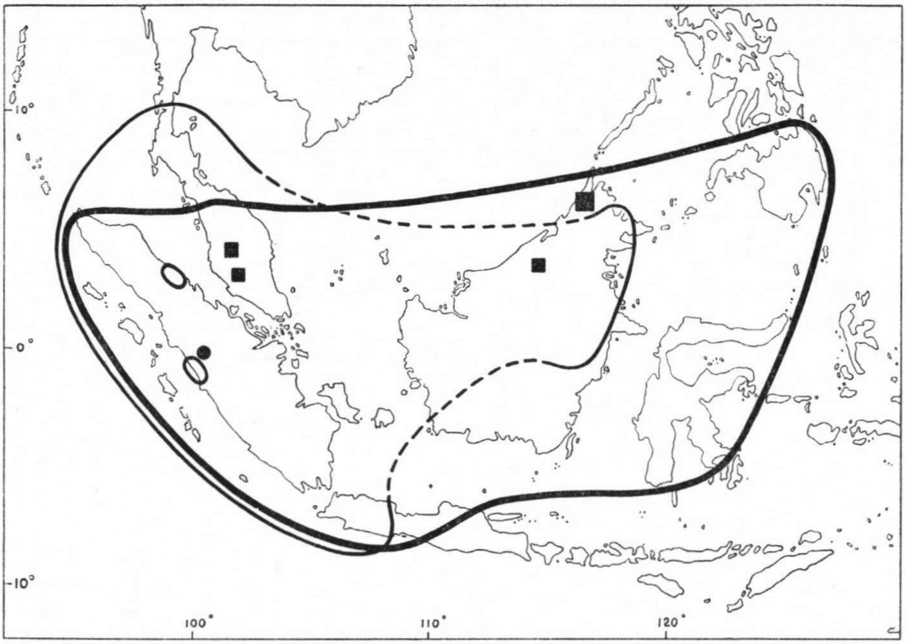

Fig. 30. Generalized areas of *M. sumatrana* (thick line) and *M. lanceolata* (thin line); the small oval areas indicate the localities of *M. lanceolata* var. *polyptera*.
The distribution of *M. hirsuta* is indicated by a solid circle, and that of *M. rufo-pilosa* by solid squares.

Vernacular names: Malay Peninsula (all once mentioned): *Pa-ang* (Sakai name), *Mĕngading besar*, both from Pahang; *Buah mata ikan* (Temuan, Selangor); *Pokoh haran* (Negri Sembilan); *Pokoh ravoa antoo, P. mata gajah, P. pai gigi, P. graô jantan, P. pinang plandog, Membuloh, Pudding utan, Kaju kahwa kantu*, all from Malacca; *Pelantu*. Sumatra (most once noted): *Laon, Sringkut, Si paturut*, all from Karo country; *Kaju ining*[2] (twice mentioned), *Kaju durung*[2], both from Tapianuli; *Tampa bussie* (Priaman); *Marazat* (Mt. Kerintji). Java: *Ki tiwu* (*landuk*) (*bodas*), Sundanese, many times mentioned; *Ki huut* (once from Udjong Kulon). Borneo (most once noted): *Bulitiap* (Kenyah dial.), *Malak* (Kayan dial.), *Bulu manuk* (Iban name, three times mentioned), *Bitonok* (land Dayak name), all from Sarawak; *Bung lai* (Sungai dial.) *Kĕriyan* (Dusun language), *Kapas*[2] or *Gapas*[2] (Dusun language, twice reported), *Tunjang* (Murut dial.), *Limpangot* (Murut dial.), all from Sabah; *Tandao* or *Tambalilin* (Dayak language, Tidung dial.), *Djangkanggunung* (Bandjar language, Riom Kanan dial.), both from SE. Borneo. Philippine Islands (Mindanao, most once mentioned; see also Merr., En. Philip. 2, 1923, 518): *Karabu-rabu, Kadabudabo, Carabo-rabo*, or *Daborabo* (Manobo dial., Bukidnon Prov., three times reported), *Mahagkol, Magobaylung, Yagabogan* (all Mabono dial.), *Bentinguasay* and *Gepulu* (?) (both from Zamboanga Prov.), *Waat* (Cebuano name, Mt. Apo), *Salalab* (Moro dial.), *Gimbingimbing* and *Garong* (both Subanon dial.), *Sumagasa* (Bagobo dial.). Celebes: see Koorders, Minah. (1898) 408, for many names; in addition the following names can be given, all once noted: *Enggolokia* (W. Toradja dial.), *Putu*[2] or *Situi* (Tobela language, Barreë dial., Malili), *Pobumengo* (Gorontalo), *Dama* (Torai dial., Menado).

Uses: The wood is said to be almost useless, sometimes used for firewood. The species was proposed by Koorders & Valeton, l.c., for reforestation purposes. On Mindanao the triturated bark and leaves are several times reported to be in use as a medicine applied for wounds, to soothe itchy skin or — charred and put in water — against tympanites. On Mindanao the species is also said to be used in agricultural ritual. The fruits are many times reported to be edible.

Remarks: M. sumatrana is very constant in its discriminative characters (especially the prominent midrib and entire inner petals), but there is nevertheless some geographical variation. Some of such regional forms have been described as separate species or varieties, but since there is much overlap between them, it is senseless to maintain such taxa. In broad outline the variation pattern can be characterized as follows.

In the northern part of Borneo (Sarawak, Sabah), which is the centre of the area, the species attains its widest variability; in Sumatra and the Malay Peninsula this is much less the case, whereas variation sinks to a minimum in Java, Celebes, and Mindanao. In the following generalized scheme this geographical variation pattern is illustrated by five important characters.

Range of variability of *M. sumatrana* in different parts of its range, illustrated by five important characters

	number of leaflet pairs	size of leaflets in cm	toothed leaf margin	size of the fruit	leaves pubescent
Java, Celebes	(2–)3–5	rather small, max. 20(–25) x 7½(–9)	very rarely	rather small	never
Mindanao	(2–)3–4(–5)	small to medium, max. 25(–33) x 10(–12)	rarely	small	never
Malay Peninsula	(2–)3–5(–6)	small to rather big, max. 30 x 10(–12)	occasionally	rather small to medium	never
Sumatra	2–4(–5)	small to rather big, max. 30 x 13	often	rather small to medium	never
Borneo	2–4(–5)	small to very big, max. 35(–50) x 15(–20)	sometimes	rather small to big	often

As general tendencies may be noticed that towards the centre of the area leaflets and fruits increase in size and dentate leaflets become more common. Moreover, the number of leaflet pairs decreases when the leaflets are larger.

In Docters van Leeuwen, Zoocecidia of the Neth. East Indies (1926) 339, f. 612, a leaf-gall has been described on a *M. sumatrana* specimen from Celebes. This type of galls (usually ball-shaped, *c.* 4 mm, ending in a short mucro, and surrounded by a calyx-like circumvallation) is rather commonly met with in this species, not only in specimens from Celebes, but also from Borneo, Sumatra, and the Malay Peninsula. The galls do not only occur on the lower surface of the leaflets, but also on the upper surface, and on rachis and petiolules, often very many crowded together.

9. **Meliosma lanceolata** Bl., Cat. (1823) 32; Nees. Flora 8 (1825) 106; Hassk., Cat. Hort. Bog. (1844) 226; Bl., Rumphia 3 (1849) 200, t. 168. *pro parte*; Walp., Ann. 2 (1852) 224; Miq., Fl. Ind. Bat. 1, 2 (1859) 614; Sum. (1860) 203, 520; Illustr. (1871) 74, *pro parte*; Hook. *f.*, Fl. Br. Ind. 2 (1876) 7; King, J. As. Soc. Beng. 65, ii (1896) 458; Ridl., J. Str.

Br. R. As. Soc. 33 (1900) 67; K. & V., Bijdr. 9 (1903) 125; Hall. *f.*, Med. Rijksherb. 1 (1910) 2, *in obs.*; Koord., Gedenkb. Jungh. (1910) 177; Exk. Fl. Java 2 (1912) 546; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 3; Merr., En. Born. (1921) 363; Ridl., Fl. Mal. Pen. 1 (1922) 516, f. 51; Baker *f.* in Rendle, J. Bot. 62 (1924) Suppl. 30; Craib, Fl. Siam. En. 1 (1926) 340; Ridl., Kew Bull. (1926) 63; Merr., Pl. Elm. Born. (1929) 176; Back. & Bakh. *f.*, Fl. Java 2 (1965) 145. — *Millingtonia lanceolata* Schult. & Schult., Syst. Veg. Mant. 3, add. 2 (1827) 250; Dietr., Syn. Pl. 1 (1839) 103. — Lectotype: *? Blume s.n.* (G. Salak, Java), and several syntypes, all seen from L.

M. lanceolata var. *pendula* Bl., Rumphia 3 (1849) 201; Walp., Ann. 2 (1852) 224; K. & V., Bijdr. 9 (1903) 127; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 3. — Syntypes: *? Blume s.n.* (Java), *Korthals s.n.* (Sumatra), seen from L.

M. lanceolata var. *membranacea* Bl., l.c.; Walp., l.c.; K. & V., l.c.; Koord.-Schum., l.c. — Syntype: ? *Blume s.n.* (Java), seen from L.

M. lanceolata var. *chartacea* Bl., l.c.; Walp., l.c.; K. & V., l.c.; Koord.-Schum., l.c. — Syntypes: *Korthals s.n.* (Sumatra, Borneo), seen from L.

M. lanceolata var. *obliqua* Bl., l.c.; Walp., l.c.; K. & V., l.c.; Koord.-Schum., l.c. — Syntype: *Korthals s.n.* (Sumatra), seen from L.

M. polyptera Miq., Sum. (1860) 203, 520; Illustr. (1871) 73; Filet, Plantk. Woordenb. (1888) 38. — Lectotype: *Diepenhorst s.n.* (Priaman, Sumatra), seen from BO, L (holo), U. Syntype: *Teysmann s.n.* (Lubu Alung, Sumatra), seen from BO, L, U.

M. levis King, J. As. Soc. Beng. 65 ,ii (1896) 457; Ridl., Fl. Mal. Pen. 1 (1922) 515. — Type: *King's Collector 7893* (Malay Peninsula), seen from BO, K, L, P, SING.

M. nervosa K. & V., Bijdr. 9 (1903) 129; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 3; Koord., Exk. Fl. Java 2 (1912) 546; Atlas 2 (1914) t. 376; Fl. Tjibodas 2 (1923) 158; Merr. & Perry, J. Arn. Arb. 20 (1939) 359, *in obs.*; Back. & Bakh. *f.*, Fl. Java 2 (1965) 145. — Lectotype: *Koorders 7132* (Tjibodas, Java), seen from L (holo). Syntypes: *Koorders 7135, 7136, 12633, 12638, 12648,* all seen from BO, L.

[*M. lanceolata* var. *microphylla* Binnendijk *ex* K. & V., Bijdr. 9 (1903) 130, *nomen, in obs.*] — Type: Cult. in Hort. Bog., not seen.

M. lanceolata var. *genuina* Hochr., Candollea 6 (1936) 467. — Type: *Hochreutiner 710* (Java), seen from L. — **Photogr. 1.**

Evergreen tree, small to medium-sized, sometimes big, up to *c.* 25(—30) m. *Flowering twigs* terete, usually stout, 4—12 mm ø, glabrous to slightly pubescent, glabrescent, often with conspicuous leaf-scars. *Leaves* (3—)7—18(—25)-jugate; rachis terete, (10—) 30—100 cm, including the 5—30 cm long petiole, up to *c.* 8 mm ø, glabrous to more or less pubescent and glabrescent when older, usually with distinctly swollen base, usually more or less lenticellate; leaflets usually oblong to lanceolate, sometimes elliptic, linear-lanceolate, or ovate, rarely the uppermost ones obovate-oblong, hardly or not asymmetrical, (3—)5—20(—25) by (1—)2—7(—11) cm, index (1—)2—5(—7), not or only slightly increasing in size towards the top of the leaf, often the lowermost pairs much smaller, the base usually acute to rounded, sometimes cuneate or attenuate, often oblique, the apex acuminate to cuspidate, sometimes caudate, with entire to remotely spinously dentate, often revolute margin, moderately to firmly coriaceous, more or less shining above, dull beneath, above glabrous or rarely slightly pubescent on midrib and nerves, beneath usually (sub)glabrous, sometimes sparsely to moderately pubescent especially on midrib and nerves, always without domatia; midrib usually deeply impressed above and very prominent beneath; nerves 5—16 pairs, ascending, looped and joined near the margin or not, above usually deeply impressed, sometimes flat, beneath distinctly prominent; venation distinct, reticulate, flat or impressed above, slightly to very prominent beneath; petiolules ⅕—3 cm, terminal one usually longest, glabrous to pubescent, in older leaflets usually distinctly swollen at the base. *Panicles* terminal, nearly always pendulous and lax, rarely erect (then also small), pyramidal, usually big, (15—)50—150 cm, usually profusely branched up to the 3rd order, branches more or less spreading, at base more or less thickened, usually very slender, rarely more coarse, terete to angular, rather stiff, more or less pubescent, bearing numerous glomerulate or crowded flowers which are usually spicately arranged, the glomerules often with regular interspaces; main axis terete, often bent down abruptly at the base; primary side-axes many, usually long, up to *c.* 90 cm, never subtended by small or reduced leaves; bracts ovate to narrowly triangular, up to *c.* 5 mm, more or less pubescent. *Pedicels* absent or very short, up to *c.* 1 mm. *Mature buds* 1½—2 mm ø. *Sepals* 5 (4), ovate, more or less unequal, the inner 3 or 4 *c.* 1 mm, the outer 2 or 1 usually much smaller, often minute and sometimes slightly keeled, sometimes somewhat lowered on the pedicel, all glabrous, with entire, usually ciliolate margin. *Outer petals* 1½—2 mm, glabrous. *Inner petals* about halfway bifid, *c.* ⅔ mm, with ciliolate, rarely glabrous lobes, usually with a minute central lobule. *Stamens:* anther-cells ⅕—⅓ mm ø; filaments *c.* 1 mm. *Ovary* (½—)⅔(—1) mm, usually densely, sometimes sparsely pubescent, very rarely glabrous or with a few hairs only. *Style c.* ½ mm, glabrous. *Fruit* (sub)globose, when ripe 7—10 mm ø; endocarp subglobose, often somewhat depressed to applanate at the ventral side, usually strongly oblique, (5—)6—9 mm ø, with usually distinct, rather coarse, mostly sharply prominent reticulum; median keel sharp and prominent, at one end often running out into a small to minute ventral processus or tubercle; ventral pore not or not much sunken (fig. 29C).

Distribution: W. Malesia: Peninsular Thailand south of the Isthmus of Kra, throughout the Malay Peninsula, throughout Sumatra (incl. Simalur and Batu Islands), Banka, W. Java (residencies Bantam, Batavia, and Preanger), Central and Northheast Borneo (Sabah: only collected in Labuk and Tawao; Indonesian Borneo: only collected on Bluu and Dengeg Rivers, and in W. Kutai on Belajan River). Not uncommon, except in Borneo and Flores. — Fig. 30.

Ecology: In primary and secondary tropical rain forests, usually at low and medium altitudes, but occasionally ascending above 1500 m, up to 2900 m (see below, under f. *nervosa*). Growing on various soils; found on volcanic loam, sandy loam, granitic sand, and at the foot of limestone rocks. It is found especially in young and open secondary forests, where it is soon reproductive, but also in old, dense forests, whether or not in open places or along streams.

Field notes: Trunk often rather crooked, sometimes more straight, usually without, sometimes with small buttresses. Outer bark grey to brown, rather smooth, later with longitudinal cracks, thin, often lenticellate. Inner bark ½—1 cm, several times said to be (light) red, orange brown, or red brown, also dirty white and then turning rusty after exposure. Wood soft, white or pale yellow to light yellow brown. Crown low, irregular and lax, with few usually crooked branches. The conspicuous big leaves are rather crowded at the end of the twigs. Leaflets normal green above, paler beneath, when young red-brownish. Flowers white or yellowish to pink or red (sometimes different colours in the same panicle). Fruits first dirty red, then bluish black when ripe.

Vernacular names: Malay Peninsula: *Medang siri* (Malacca, once mentioned), Sumatra: *Kabung*[2] (*blumut*) (Batak language, Simelungun dial., a few times mentioned), *Bulung manuk* (Batak language, Karo dial., once mentioned), *Sondang* or *Sontang* (Timor in N. Sum., once mentioned), *Kaju buluk hudjan* (Lampong, once mentioned), *Tutun surin* (or *seulang*) (*pajo*), *Tutun tungkè ali*, *Angkè foluh pajo*, *Surin sito bulung*, and *Silaora* (all mentioned from Simalur Island), W. Java: *Ki tiwu* (Sundanese, often used, as well as for *M.*

pinnata and *M. sumatrana*, also with the addition *lalaki, përsawon*, or *mindi bodas*), *Surèn leuweung* (Sundanese, once mentioned). See also under var. *polyptera* and f. *nervosa*.

Remarks. *M. lanceolata* is generally very well characterized by its big pendulous panicles and its long leaves with many usually lanceolate leaflets. Nevertheless it shows a wide variation especially in number but also in shape and size of the leaflets and in shape and size of the panicles. On the islands west of Sumatra (Simalur, Nias, Batu Islands) populations are found with normal inflorescences but only 3—5-pinnate leaves, and elliptic, sometimes subrotund, big leaflets. Transitions to this extreme are common, hence I do not consider it adequate to describe it as a separate taxon. There is another deviating form, however, which takes a separate position. It has many small, mostly lanceolate leaflets, which otherwise do not differ from those of *M. lanceolata*. The panicles are even identical to those of that species. In view of the wide variability in the leaves of *M. lanceolata*, I prefer to include it here. I have reduced it to a variety of *M. lanceolata*, and it can be distinguished as follows:

a. var. **polyptera** (Miq.) Beus., *stat. nov.* — *M. polyptera* Miq. — For references and typification, see under the species.

Leaves 12—25-jugate, with at most 50 cm long rachis (including the petiole); leaflets oblong to linear-lanceolate, small, (3—)4—11 by 1—2(—2½) cm, index 3—7, without teeth, glabrous.

Distribution: Sumatra: Asahan (Huta Padang; Kuala Masihi), W. Coast (Priaman; Lubuk alung). — Fig. 30.

Ecology: At low altitudes. Reported from primary forest on 'red soil'.

Field notes: Once said to be a tree of 27 m.

Vernacular names: *Badar badar* (Lubuk alung), *Tandikat batu* (Priaman), *Simarpapàhu* (Huta Padang).

Remarks. It may be that var. *lanceolata* and var. *polyptera* have replacing areas, but since collections of the latter are scarce, this is not clear.. Hence I prefer to consider them varieties rather than subspecies.

From SE. Borneo (M. Teweh) a sterile specimen is known (*Boschbouwproefstation bb. 10088*), which is somewhat dubious. It is much like var. *polyptera*, but the leaflets are densely pubescent. It also reminds of a multifoliolate form of *M. pinnata* ssp. *ridleyi*, but since no inflorescences are available, this specimen remains dubious.

b. var. **lanceolata.**

Leaves (3—)6—18-jugate, with up to *c.* 100 cm long rachis (including the petiole); leaflets elliptic to lanceolate, medium-sized to big, 5—20(—25) by (2—)2½—7(—10) cm, index (1½—)2—5(—6), without or with teeth, glabrous or pubescent.

Distribution, ecology, etc.: See under the species.

Remarks. In the lowland parts of its area var. *lanceolata* is nearly always very constant in the main characters. Mainly at higher elevations, however, forms occur which deviate considerably, often to such an extent that it is very difficult to separate them from less typical forms of the otherwise well distinct *M. pinnata* ssp. *ferruginea* and ssp. *ridleyi*; in a few cases, especially when the material is incomplete, this can only be done by a specialist who is thoroughly acquainted with habitus and variability of both species.

For instance, a form with erect, unusually short panicles (sometimes only 15 cm long) and other deviating characters may be met with. It occurs mainly in the montane zone; transitional forms are found lower, and these show a more or less gradual fading of typical *lanceolata* characters, according as they have been collected at higher altitudes. Specimens of this mountain form have been described from Java by Koorders & Valeton, l.c., as *M. nervosa*. In my opinion this species should be reduced to formal rank; see below.

1. forma **lanceolata.**

Leaves (3—)6—18-jugate, with elliptic to lanceolate, glabrous to pubescent leaflets. Panicles pendulous, usually much longer than 50 cm. Inner petals ciliolate. Ovary pubescent.

Distribution, ecology & vernacular names: See under the species.

2. forma **nervosa** (K. & V.) Beus., *stat. nov.* — *M. nervosa* K. & V. — For references and typification see under the species.

Leaves not more than 8(—10)-jugate, with usually elliptic glabrous leaflets. Panicles erect, shorter than *c.* 50 cm, minimum length *c.* 15 cm. Inner petals mostly glabrous. Ovary pubescent to glabrous.

Distribution & ecology: In mountains from *c.* 1300 m up to at least 2900 m. In Sumatra collected on Mt. Singalang and Mt. Kerintji between 2400 and 2900 m (in mossy *Vaccinium* forest), also lower, e.g. at *c.* 1300 m on Mt. Tanggamus (S. Sumatra) and at *c.* 1500 m in the Karo country (N. Sumatra). In Java often collected between 1600 m and 2100 m in montane forest on Mt. Gedeh (Tjibodas), but also at *c.* 2200 m on Mt. Papandajan, at *c.* 2000 m in the Bandung forest garden, and on Mt. Kendeng (between Mt. Patuha and Mt. Tilu). In Flores once collected on Mt. Mandosawu at 1400 m alt. (the lowland form has never been found in Flores!).

Field notes: Often a medium-sized, sometimes big tree (30 m tall and 1 m thick!).

Vernacular names: Java: *Ki tjermeh badak* (or *beureum*) (mentioned by K. & V., l.c., from Tjibodas).

Remark. See under the species.

10. **Meliosma hirsuta** Bl., Rumphia 3 (1849) 200; Walp., Ann. 2 (1852) 225; Miq., Fl. Ind. Bat. 1, 2 (1859) 616; Sum. (1860) 203; Illustr. (1871) 74; Merr., En. Born. (1921) 363. [— *Aglaia hirsuta* Korth. *in sched. ex* Bl., l.c., *nomen.*] — Lectotype: *Korthals 867* (Sumatra), seen from BO, L (holo). Syntype: *Korthals s.n.*, several sheets in L, U.

Evergreen small tree, *c.* 5 m. *Flowering twigs* terete, probably as in *M. lanceolata*. *Leaves* 15—20 (or probably more)-jugate; rachis 50—100 cm, including the 10—20 cm long petiole, up to *c.* 6 mm across, more or less hirsute, usually with distinctly swollen base, sometimes sparsely lenticellate; leaflets (sub)sessile, those in medium and upper part of the leaf linear-lanceolate, 10—20(—25) by (1½—)2—3 cm, index 5—10, the lower ones (ovate-)lanceolate to ovate, gradually decreasing in length towards the base of the leaf, up to only *c.* 3 cm, index up to 2, the base rounded to acute, sometimes slightly oblique, the apex acuminate to caudate, with entire to remotely spinously dentate margin, thin-chartaceous, dull above, dull and much paler beneath, above glabrous except for some pubescence on the midrib, beneath moderately to sparsely hirsute especially on midrib and nerves, without domatia; midrib above flat to slightly impressed, prominent beneath; nerves widely apart, (5—)8—12 pairs, flat above, prominent beneath, ascending and looped and joined into a distinct marginal nerve situated at 2—4 mm from the margin; venation district, wide, reticulate, flat above, prominulous beneath; petiolules absent or very short, up to *c.* 1 mm, terminal one often longer, up to *c.* 8 mm, densely hirsute, not swollen at the base. *Panicles* and *flowers* as in typical *M. lanceolata*, but *sepals* up to *c.* 1½ mm, and *petals*[1]) and *stamens* unknown. *Fruit* as in *M. lanceolata.*

Distribution: Sumatra: Westcoast (G. Malintang), only one collection, rare (*fide* Korthals *in sched.*).

Remarks: This was by Blume erroneously recorded to occur '*in inferiore insula Borneo*'.

M. hirsuta is doubtless very closely related to *M. lanceolata*, but very well distinct by its leaf-characters.

See also *Canarium angustifolium* under the dubious species (p. 348).

11. **Meliosma pinnata** (Roxb.) Walp. — *Millingtonia pinnata* Roxb. — *M. ferruginea* Bl. — *Millingtonia ferruginea* (Bl.) S.&S. — *Sapindus microcarpus* W. & A. — *Millingtonia arnottiana* Wight — *Wellingtonia arnottiana* (Wight) Meisn. — *Millingtonia sambucina* Jungh. — *M. arnottiana* (Wight) Walp. — *M. floribunda* Bl. — *M. glauca* Bl. — *M. oldhamii* Max. — *M. rhoifolia* Max. — *M. sambucina* (Jungh.) Miq. — *M. wallichii* Planch. *ex* Hook. *f.* — *M. colletiana* King — *M. ridleyi* King — *M. luzonensis* Merr. — *M. multiflora* Merr. — *M. pendula* Merr. — *M. kirkii* Hemsl. & Wils. — *M. sylvatica* Elm. — *Fraxinus fauriei* Lévl. — *M. elegans* Ridl. — *M. reticulata* Merr. — *M. macrophylla* Merr. — *M. acuminatissima* Merr. — *M. macgregorii* Merr. — *M. paucinervia* Merr. — *M. tongcalingii* Elm. — *M. megalobotrys* Merr. — *Rhus bofillii* Lévl. — *M. brachybotrys* Merr. — *M. angustifolia* Merr. — *M. hachijoensis* Nakai — *M. sorsogonensis* Elm. *ex* Merr. — *M. sinensis* Nakai — *M. microcarpa* (W. & A.) Craib — *M. crassifolia* Hand.-Mazz. — *M. clemensiorum* Merr. — *M. trichocarpa* Merr. — *M. glandulosa* Cufod. — *M. oldhamii* var. *glandulifera* Cufod. — *M. rhoifolia* ssp. *barbulata* Cufod. — *M. apoensis* Elm. — *M. cannarioides* Elm. — *M. macrocarpa* Elm. — *M. bartlettii* Merr. & Perry — *M. confertiflora* Merr. & Perry — *M. humilis* Merr. & Perry — *M. schlechteri* Merr. & Perry — *M. annamensis*Gagn. — *M. chapaensis* Gagn. — *M. poilanei* Gagn. — *M. quangnamensis* Gagn. — *M. simang* Gagn. — *M. microcarpa* var. *angustata* Vidal *ex* Gagn. & Vidal — *M. microcarpa* var. *chapaensis* (Gagn.) Vidal *ex* Gagn. & Vidal — *M. oldhamii* var. *rhoifolia* (Max.) Hatus.

Evergreen, sometimes deciduous tree, small to very big, up to *c.* 42 m. *Flowering twigs* terete to slightly canaliculate, 2—12(—14) mm ø, glabrous to densely pubescent, usually soon glabrescent, often with conspicuous leaf-scars. *Leaves* 2—11-jugate; rachis terete, (2—)5—40(—60) cm, including the up to *c.* 15(—25) cm long petiole, up to *c.* 8 mm across, glabrous to densely pubescent, lenticellate or not; leaflets usually ovate, elliptic, or obovate to ovate-oblong, oblong, or obovate-oblong, sometimes lanceolate, often asymmetric, 1½—25(—38) by 1—10(—18) cm, index (1—)1½—4(—5), usually increasing in size towards the top of the leaf, the base usually acute to rounded, sometimes truncate, attenuate, or cuneate, rarely slightly emarginate, often oblique, the apex acuminate to cuspidate, rarely caudate, with entire or remotely spinously dentate, often revolute margin, chartaceous to coriaceous, usually shining above, dull and paler beneath, usually slightly to densely pubescent, especially beneath and on midrib and nerves, sometimes quite glabrous, often with domatia in the axils of the nerves beneath; midrib flat to impressed above, more or less prominent beneath; nerves 3—15 pairs, ascending, looped and joined or not, flat or impressed above, more or less prominent beneath, sometimes inconspicuous; venation distinct to inconspicuous, reticulate to cancellate, slightly impressed to prominulous above, often more or less prominent beneath; petiolules up to 5 cm, terminal one usually longest, glabrous to densely pubescent, not or not much swollen at the base. *Panicles* terminal, erect, sometimes somewhat pendulous, dense to

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[1]) Fide Blume, l.c.: '*petalis staminiferis filamento brevioribus subbilobis*'; I could not find any petals left.

lax, widely to narrowly pyramidal, 10—55(—70) cm, usually profusely branched up to the 4th order, branches usually spreading, stiff to rather flaccid, slender to coarse, more or less grooved and angular, densely tomentose to puberulous, bearing numerous solitary to usually crowded flowers; main axis angular to shallowly canaliculate; primary side-axes usually many, up to 35(—60) cm, the lower ones sometimes subtended by small to reduced leaves; bracts ovate to narrowly triangular, up to *c.* 5(—10) mm, more or less pubescent. *Pedicels* absent or short, up to 3(—4) mm. *Mature buds* (1½—)2(—3) mm ø. *Sepals* 5 or 4, ovate, unequal, the inner 3 or 4 1—1½ mm, the outer 1 or 2 usually smaller, often minute, sometimes lowered on the pedicel, sometimes slightly keeled, glabrous or pubescent on the outside, all with entire, usually ciliolate margin. *Outer petals* usually glabrous, sometimes pubescent on the outside. *Inner petals* more or less deeply bifid, (⅓—)⅔(—1) mm, glabrous, ciliolate or fimbriate at the tips, often with a minute central lobule, often frayed at the tips. *Stamens*: anther-cells ⅕—⅓ mm ø; filaments *c.* 1 mm. *Ovary* (½—)⅔(—1) mm, glabrous to densely pubescent. *Style* ½—1½ mm, glabrous. *Fruit* (sub)globose to obovoid, when ripe (3—)4—10(—11) mm ø, with thin mesocarp; endocarp (sub)globose, sometimes almost semiglobose or short-ellipsoid, oblique or not, (2½—)3½—9(—10) mm ø, with more or less prominently reticulate surface; median keel usually distinct and more or less prominent, at one end sometimes running out into a small to minute processus or tubercle, and sometimes curving outwards at the other end; ventral pore usually rather narrow, whether or not sunken (fig. 29 B 2—7).

Distribution: Ceylon, SW. Peninsular and NE. India, Burma, South and Central China, extreme S. Corea, S. Japan, Taiwan, Philippine Islands, Laos, Vietnam, Thailand, Malay Peninsula, Sumatra, Borneo, Java, Lesser Sunda Islands, Celebes, Moluccas, New Guinea, New Britain. For details see under the subspecies. — Fig. 32.

Ecology: In forests under moist tropical to subtropical, sometimes warm-temperate conditions, on various soils, from sea-level up to *c.* 3000 m altitude. For details, see under the subspecies.

Remarks. *M. pinnata* covers a very large area in which it has developed a complex and wide variation pattern. It can be divided up into nine well-marked subspecies. Four of these are widely distributed, whereas five have a limited distribution. The first group, viz. ssp. *arnottiana*, ssp. *ridleyi*, ssp. *macrophylla*, and ssp. *ferruginea*, are considered primary subspecies; they centre in W. Malesia. The subspecies of the second group occur scattered at the periphery of the area of *M. pinnata*; I consider them secondary offsplits from the primary subspecies, viz. ssp. *pinnata* and ssp. *angustifolia* from ssp. *arnottiana*, and ssp. *pendula*, ssp. *sylvatica*, and ssp. *humilis* from ssp. *macrophylla*[1]). See fig. 31.

The areas of the secondary subspecies partly or entirely fall within the area of the primary subspecies from which they are derived, but they are ecologically isolated from these, usually by preference for different altitudinal zones; transitional or hybrid forms are sometimes found. The areas of the four primary subspecies, on the other hand, all touch or only slightly overlap mutually, but generally they are perfectly replacing, and usually there is also different ecological preference. Due to the scarcity of collections from critical regions, especially from Sumatra, Borneo, and Celebes, it is mostly not clear, however, how the relation is in contact zones. There is some evidence that one or two mutually may behave as good species, whereas one or two others may be connected by transitional forms, but in general the evidence required is still wanting. In this respect the picture is not so complete as it is in *M. simplicifolia*.

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[1]) *M. sarawakensis* (species nr. 12) is considered a derivative of *M. pinnata* ssp. *ridleyi*, having reached species level.

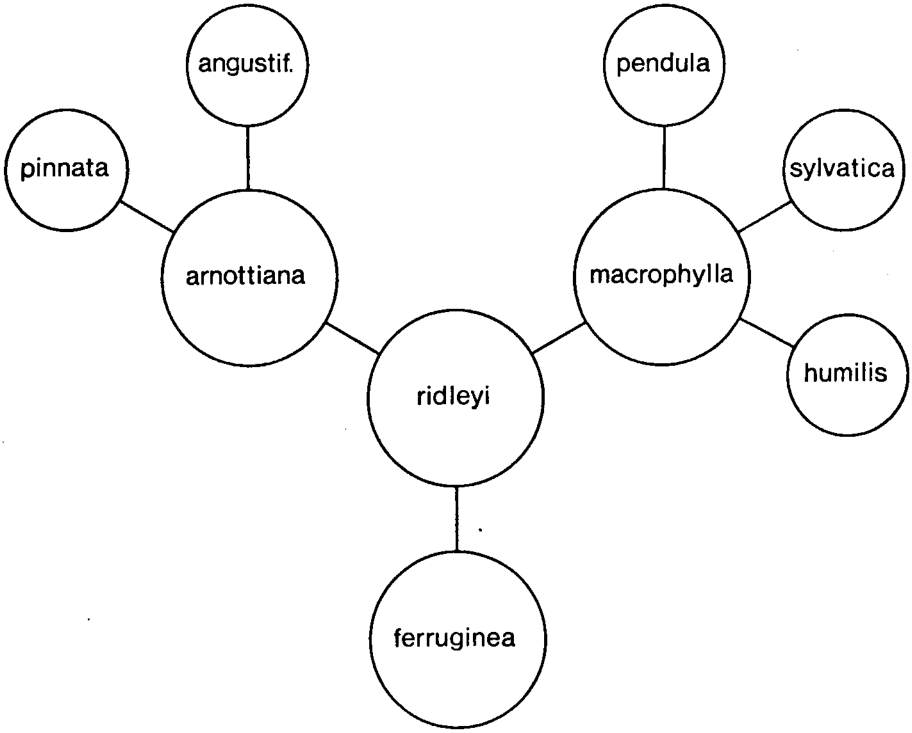

Fig. 31. Morphological relationships between the subspecies of *M. pinnata*. Big circles indicate the supposed primary subspecies, small circles the supposed secondary subspecies. See the text.

KEY TO THE SUBSPECIES

1. Ovary glabrous or only with a few hairs. Sepals and petals always glabrous.
   2. Leaves 3—5-jugate; leaflets dentate (sometimes only a few teeth!), with domatia in the axils of the nerves beneath which are sometimes obscured by very dense tomentum of the leaf-blade **i.** ssp. **humilis**
   2. Leaves (3—)4—10(—12)-jugate; leaflets dentate or not, without domatia, never with very dense tomentum.
      3. Leaflets entire, index (1—)1½—3, mostly rounded or obtuse to truncate or emarginate at the base. Medium-sized to big trees . . . . **f.** ssp. **macrophylla**
      3. Leaflets dentate (sometimes very sparsely!), index (1—)1½—5, acute or rounded, obtuse, truncate or emarginate at the base. Small to medium-sized trees, rarely shrubs.
         4. Leaves (5—)6—10(—12)-jugate; leaflets glabrous, with acute base. Panicles without cataphylls. **a.** ssp. **pinnata**
         4. Leaves (3—)4—6(—7)-jugate; leaflets more or less pubescent, rarely subglabrous, whether or not with acute base. Panicles with or without cataphylls.
            5. Leaflets moderately to rather densely villous-pubescent (often more or less glabrescent when older!), mostly (especially lower ones) rounded to truncate at the base, index 1½—3(—4). Endocarps 6—7 mm ø, without ventral processus (fig. 29 B 3). (Above *c.* 1800 m altitude.) **g.** ssp. **pendula**
            5. Leaflets sparsely to densely short-pubescent, rarely subglabrous, mostly with acute base, index 1½—4(—5). Endocarps 5—7½ mm ø, mostly with a small but distinct ventrol processus (see fig. 29 B 6, 7) (Below *c.* 1000 m latitude[1]).

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[1] See note on p. 513.

6. Leaves (3—)4—6(—7)-jugate; leaflets acute at the base . . . . . **h.** ssp. **sylvatica**

6. Leaves 3—5(—6)-jugate; lateral leaflets rounded to truncate at the base. **f.** ssp. **macrophylla** (Celebes form)

1. Ovary entirely, rarely partly, but always densely pubescent[1]). Sepals and petals glabrous or pubescent.

7. Sepals and usually also outer petals moderately to densely pubescent on the outside[2]). Leaves 2—6(—7)-jugate; leaflets entire[3]), index (1—)1½—3. . . . . **e.** ssp. **ferruginea**

7. Sepals and petals glabrous or rarely a few hairs on the outer sepals only. Leaves (2—)3—11-jugate; leaflets entire or dentate, index (1—)1½—5.

8. Leaves (4—)6—11-jugate; leaflets entire, glabrous, above with more or less prominent to sometimes flat midrib. . . . . **c.** ssp. **angustifolia**

8. Leaves (2—)3—7(—8)-jugate; leaflets entire or dentate, usually more or less pubescent, sometimes glabrous, often with domatia in the axils of the nerves beneath; above with more or less impressed, sometimes flat midrib.

9. Endocarps 4½—9(—10) mm ø, usually with more or less sunken ventral pore (cf. fig. 29 B 1). Inner petals with fimbriate or ciliolate, rarely glabrous lobes. Leaflets never with domatia **d.** ssp. **ridleyi**

9. Endocarps (2½—)3—4½ mm ø, not with sunken ventral pore (fig. 29 B 5). Inner petals with usually glabrous, sometimes at the tips ciliolate or frayed lobes. Leaflets with or without domatia **b.** ssp. **arnottiana**

a. ssp. **pinnata.** — *Millingtonia pinnata* Roxb. [Hort. Beng. (1814) 3, *nomen*] Fl. Ind. 1 (1820) 103; Schult. & Schult., Syst. Veg. Mant. 1 (1822) 218; Spreng., Syst. Veg. 1 (1824) 36; Nees, Flora 8 (1825) 106; W. & A., Edinb. New Phil. J. 15 (1833) 179; Dietr., Syn. Pl. 1 (1839) 103; Wight, Ill. Ind. Bot. 1 (1840) 144; Anon., Ic. Roxb. 4 (1970) 38, t. 19. — *M. pinnata* Max., Diagn. Pl. Nov. Jap. Mandsh. 4 & 5 (1867) 263, *in obs.*; Hook. *f.*, Fl. Br. Ind. 2 (1876) 6; Prain, Beng. Pl. 1 (1903) 246; Brandis, Ind. Trees (1906) 195; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 208, *in nota*; Gamble, Fl. Pres. Madras 1 (1918) 256; Kanj., Das & Purk., Fl. Assam 1 (1936) 329; Hundley & U Chit Ko Ko, List of Trees, etc. from Burma ed. 3 (1961) 59. — Lectotype: *Roxburgh Ic. nr. 2104*, in Kew Library; reproduction in Anon., Ic. Roxb., l.c.

Small to medium-sized tree, up to *c.* 15 m. *Leaves* (5—)6—10(—12)-jugate; leaflets lanceolate, sometimes (especially the lower ones) oblong, the upper ones often more or less obovate-lanceolate, usually medium-sized, up to *c.* 20 by 5 cm, index 2—5, acute at the base, more or less dentate, chartaceous to somewhat coriaceous, (sub)glabrous, without domatia. *Panicles* erect, not much spreading, not dense, with rather stiff, slender axes; lower primary axes not subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* glabrous. *Endocarps* (sub)globose, not or not much oblique or depressed, 3½—4½ mm ø, with distinct, fine, more or less prominent reticulum, with distinct, prominulous median keel which at one end usually runs out into a very minute ventral processus; ventral pore not or only slightly sunken (fig. 29 B 4).

Distribution: NE. India: E. Ghats (Madgol Hills of Vizagapatam), Sikkim, Bhutan, Assam (Plains Districts, Khasi Hills, Garo Hills, Naga Hills, W. Manipur); E. Pakistan (E. Bengal, Sylhet, Chittagong), W. Upper Burma? Common in most parts of the area. — Fig. 32.

Ecology: In tropical rain and hill forests, at rather low altitudes, usually up to *c.* 1000 m, occasionally higher, up to *c.* 1500 m.

Field notes: Bark grey or brownish outside, dark green underneath the cuticle, inside

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1) In ssp. *ferruginea* and ssp. *arnottiana* rarely specimens have been observed with (sub)glabrous ovary. See remarks under those subspecies.

2) Sometimes deviating specimens occur with glabrous sepals and petals. These cannot be properly identified with this key.

3) Leaflets of saplings and watershoots usually dentate.

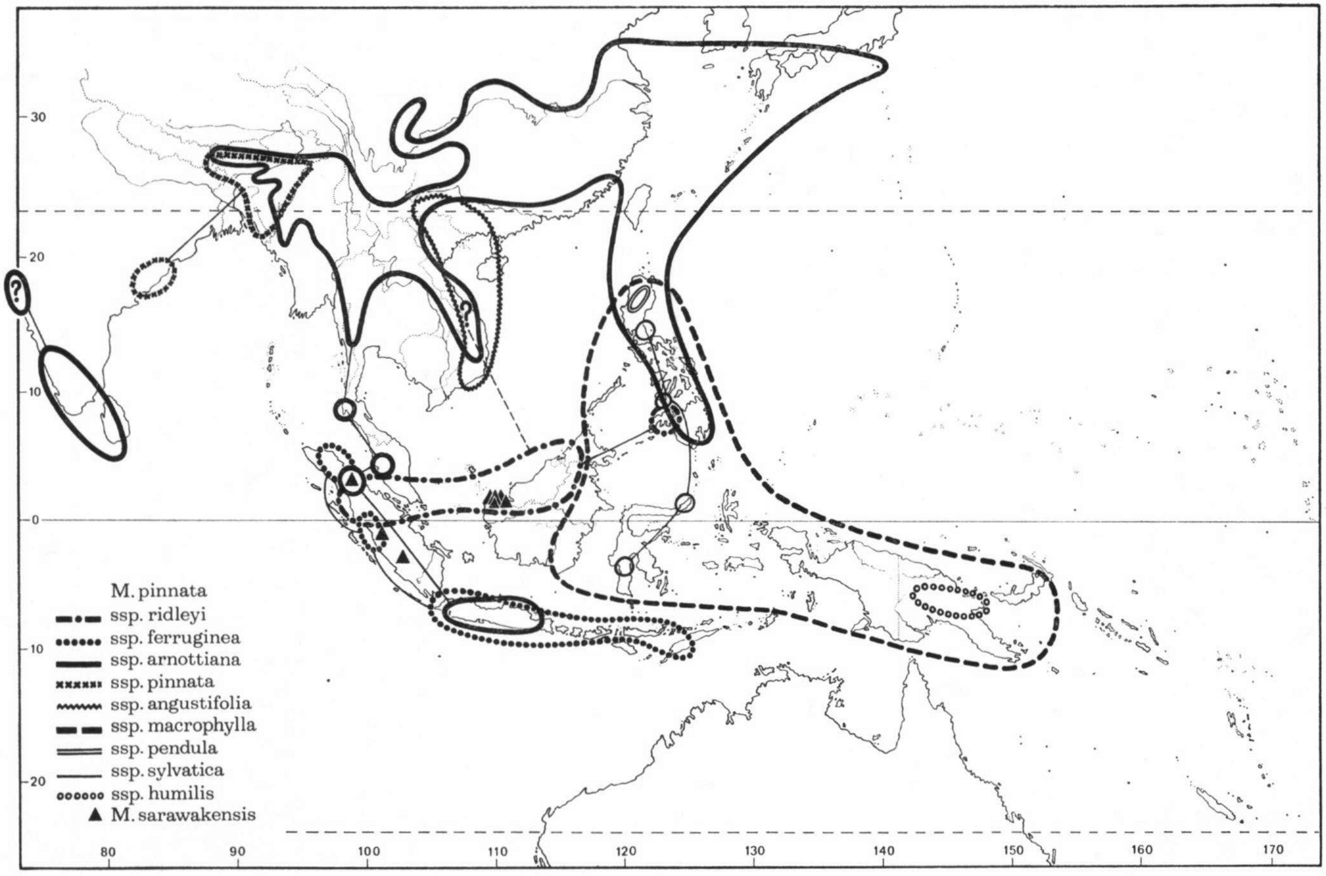

Fig. 32. Generalized areas of the subspecies of *M. pinnata*, and distribution of *M. sarawakensis*.

red, oxidising to brown after exposure. Wood light, porous and brittle, of no timber value (*fide* Kanj., Das & Purk., l.c.).

Vernacular names: Sikkim: *Dabdabe, Dhabdabi*, or *Dagdakti* (several times mentioned). Bengal: *Bativa* (*fide* Prain, l.c.). Assam: many names mentioned by Kanj., Das & Purk., l.c. Burma: *Petkanan* (*fide* Hundley & U Chit Ko Ko, l.c.).

Uses: In Assam the young leaves are eaten by the Miris, cooked with fish (*fide* Kanj., Das & Purk., l.c.).

Remarks. The area of ssp. *pinnata* partly replaces that of ssp. *arnottiana*. The latter subspecies, moreover, is typically montane, whereas ssp. *pinnata* is mainly restricted to altitudes below 1000 m. Though ssp. *arnottiana* is apparently rare in the hills of NE. India, it may locally (e.g. Darjeeling, Khasi Hills) come into contact with ssp. *pinnata*, judging from the intermediate specimens found there (see the remarks under ssp. *arnottiana*).

b. ssp. **arnottiana** (Walp.) Beus., *stat. nov.* — *Sapindus ? microcarpus* W. & A., Prod. 1 (1834) 112, *nom. illeg.*, *non* Ruiz & Pavon (1804); Wight, Ill. Ind. Bot. 1 (1840) 142; Walp., Rep. 1 (1842) 416, 423. — *Millingtonia arnottiana* Wight, Ill. Ind. Bot. 1 (1840) 144, t. 53. — *Wellingtonia arnottiana* Meisn., Pl. Vasc. Gen. (Comm.) 2 (1840) 207, *in nota*. — *M. arnottiana* Walp., Rep. 1 (1842) 423; Thw., En. Pl. Zeyl. (1858) 59; Beddome, Fl. Sylv. 1 (1869) t. 160; ibid. 3 (1869) 77; Hook. *f.*, Fl. Br. Ind. 2 (1876) 6; Trim., Fl. Ceyl. 1 (1893) 315; Brandis, Ind. Trees (1906) 195; Fyson, Fl. Nilg. Puln. Hill-tops 1 (1915) 92, t. 71; Gamble, Fl. Pres. Madras 1 (1918) 256; Kanj., Das & Purk., Fl. Assam 1 (1936) 329; Worthington, Ceylon Trees (1959) 150; Hundley & U Chit Ko Ko, List of Trees etc. from Burma ed. 3 (1961) 59. — *M. microcarpa* Craib, Fl. Siam. En. 1 (1926) 340, *nom. illeg.*; Cufod., Oest. Bot. Z. 88 (1939) 255, *in obs.*; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 51, t. 9 f. 2—4; Vidal, Not. Syst. 16 (1960) 309. — Type: *Wight 554* (India), seen from E, K (holo).

Millingtonia sambucina Jungh., Tijdschr. Nat. Gesch. Phys. 8 (1841) 365. — *M. sambucina* Miq., Illustr. (1871) 74; K. & V., Bijdr. 9 (1903) 137, *in obs.* — *M. glauca* Bl., Rumphia 3 (1849) 200, t. 168 B, *nom. illeg.*; Walp., Ann. 2 (1852) 225; Hassk., Hort. Bog. 1 (1858) 140; Miq., Fl. Ind. Bat. 1, 2 (1859) 615; Illustr. (1871) 74, *in synon.*; K. & V., Bijdr. 9 (1903) 135; Hall. *f.*, Med. Rijksherb. 1 (1910) 2; Koord., Exk. Fl. Java 2 (1912) 546; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 2; Koord., Fl. Tjibodas 2 (1923) 157; Baker *f.* in Rendle, J. Bot. 62 (1924) Suppl. 30. — Types: *Junghuhn s.n.* (Java, G. Malabar), type of *M. sambucina*, syntype of *M. glauca*; *? Blume s.n.* (Java, *sine loco*) and *Junghuhn s.n.* (Java, G. Lamongan), syntypes of *M. glauca*. All seen from L.

M. floribunda Bl., Rumphia 3 (1849) 200; Walp., Ann. 2 (1852) 225; Miq., Fl. Ind. Bat. 1, 2 (1859) 615; Illustr. (1871) 74; K. & V., Bijdr. 9 (1903) 137; Hall. *f.*, Med. Rijksherb. 1 (1910) 2; Koord., Exk. Fl. Java 2 (1912) 546. — *M. glauca* var. *floribunda* K. & V., Bijdr. 9 (1903) 137. — Type: *? Blume s.n.* (Java, Limbangan), seen from L.

M. oldhamii Maxim., Diagn. Pl. Nov. Jap. Mandsh. 4 & 5 (26-VI-1867) 263 ('*oldhami*'); Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (2-VII-1867) 94; Cat. Mus. Bot. 1 (Fl. Jap.) (1870) 23; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 145; Diels, Bot. Jahrb. 29 (1900) 452; Pamp., Nuov. Giorn. Bot. Ital. n.s. 18 (1911) 173; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 206; Rehd. & Wils., J. Arn. Arb. 8 (1927) 165; Hand.-Mazz., Symb. Sin. 7 (1933) 646; Pei, Contr. Biol. Lab. Sc. Soc. China 9 (1934) 175; Rehd., J. Arn. Arb. 15 (1934) 10; ibid. 18 (1937) 217; Cufod., Oest. Bot. Z. 88 (1939) 253; Rehd., Man. Cult. Trees & Shrubs (1940) 595; Koidz., Acta Phytotax. Geobot. 12 (1943) 117; Hara, En. Sperm. Japon. 3 (1954) 120; Walker, Imp. Trees Ryukyu Isl. (1954) 199, f. 120; How, Acta Phytotax. Sin. 3 (1955) 449; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235; Vidal, Not. Syst. 16

(1960) 309; Liu, Ill. Lign. Pl. Taiwan 2 (1962) 924, f. 761; Krüssm., Handb. Laubgeh. 2 (1962) 128, t. 57 c; Ohwi, Fl. Japan (1965) 613; Lauener, Not. R. Bot. Gard. Edinb. 27 (1967) 290. — Type: *Oldham 183* (Corea), seen from A, K, L.

M. rhoifolia Maxim., Diagn. Pl. Nov. Jap. Mandsh. 4 & 5 (1867) 262; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 146; Henry, Trans. As. Soc. Japan 24, Suppl. (1896) 29; Hayata, Ic. Pl. Formos. 1 (1911) 161; Matsum., Ind. Pl. Japon. 2 (1912) 336; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 208; Kaneh., Formos. Trees ed. 2 (1936) 416, f. 371; Cufod., Oest. Bot. Z. 88 (1939) 254; How, Acta Phytotax. Sin. 3 (1955) 447; Liu *et al.*, Quart. J. Taiwan Mus. 8 (1955) 503; Vidal, Not. Syst. 16 (1960) 309; Li, Woody Fl. Taiwan (1963) 503. — *M. oldhamii* var. *rhoifolia* Hatusima, Mem. Fac. Agr. Kagoshima Univ. 7 (1970) 315. — Syntypes: *Oldham 85* (Taiwan), seen from K, *86/1* (Taiwan), seen from A, BM, K, P, W.

M. wallichii Planch. *ex* Hook. *f.*, Fl. Br. Ind. 2 (1876) 6; Forb. & Hemsl., J. Linn. Soc. Bot. 23 (1886) 146; Brandis, Ind. Trees (1906) 195; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 207; Kanj., Das & Purk., Fl. Assam 1 (1936) 328; Cufod., Oest. Bot. Z. 88 (1939) 255; How, Acta Phytotax. Sin. 3 (1955) 450. — Type: '*M. wallichii Planch.*' *in Herb. Hook.* (Assam, Khasi Hills), seen from K (holo), L, P, U, W.

M. colletiana King, J. As. Soc. Beng. 65, ii (1896) 116; Brandis, Ind. Trees (1906) 195. — Type: *? Badal Khan 71* (Burma, Maymyo Hill), seen from BM, K.

M. luzonensis Merr., Publ. Gov. Lab. Philip. 29 (1905) 24; Elm., Leafl. Philip. Bot. 2 (1908) 492, *in obs.* ('*luzonica*'); Merr., En. Philip. 2 (1923) 517. — Type: *Elmer 6267* (Philippine Islands), seen from K[1]).

M. multiflora Merr., Publ. Gov. Lab. Philip. 29 (1905) 25; En. Philip. 2 (1923) 517. — Type: *Barnes FB 930* (Philippine Islands), seen from BM, K, L, SING.

M. kirkii Hemsl. & Wils., Kew Bull. (1906) 154; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 207; Hand.-Mazz., Symb. Sin. 7 (1933) 646; Cufod., Oest. Bot. Z. 88 (1939) 254; How, Acta Phytotax. Sin. 3 (1955) 448. — Type: *Wilson 2371* (Szechuan), seen from A, K.

M. ferruginea (*non* Bl.) Koord., Gedenkb. Jungh. (1910) 177.

Fraxinus fauriei Lévl. in Fedde, Rep. 8 (1910) 285; cf. Lauener, Not. R. Bot. Gard. Edinb. 27 (1967) 290. — Type: *Faurie 1867* (Corea), seen from A, E (holo), W.

Rhus bofillii Lévl., Mém. Acad. Ci. Barcelona 12 (1916) 562; cf. Lauener, Not. R. Bot. Gard. Edinb. 27 (1967) 290. — Type: *d'Argy s.n.* (Kiangsu, Suo Se, Tcha T'chan, 1846—66) seen from A (fragm.), E (holo).

M. hachijoensis Nakai, Bot. Mag. Tokyo 36 (1922) 124; Hara, En. Sperm. Japon. 3 (1954) 120; Ohwi, Fl. Japan (1965) 613. — Type: *Nakai s.n.* (Japan, Hachijo Is.), not seen.

M. sinensis Nakai, J. Arn. Arb. 5 (1924) 80; Merr., Lingn. Agr. Rev. 4, 2 (1927) 129; Rehd. & Wils., J. Arn. Arb. 8 (1927) 165. — *M. oldhamii* var. *sinensis* Cufod., Oest. Bot. Z. 88 (1939) 253; How, Acta Phytotax. Sin. 3 (1955) 449. — Type: *Wilson 3038, pro parte* (Hupeh, Patung Hsien), seen from A, K. Paratypes: *Wilson 463*, seen from A, E, K, W, *1650*, seen from A, *3038, pro parte* (Hupeh, Chang Yang Hsien), seen from A, E, W, *3038bis* (Hupeh, Chang Lo Hsien), not seen, *4602*, seen from A, K; *Silvestri 3355*, seen from A, K, P; *Henry 5863*, seen from A, E, K, P, W.

M. clemensiorum Merr.[2]), J. Arn. Arb. 19 (1938) 47; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 54. — Type: *Clemens 3775* (S. Vietnam), seen from K.

[*M. apoensis* Elm., Leafl. Philip. Bot. 10 (1939) 3784, *nom. inval.*, art. 36.] — Type: *Elmer 11960* (Philippine Islands), seen from A, BM, BO, E, K, L, W.

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[1]) The ovaries of this specimen are pubescent, not glabrous, as stated in the description.

[2]) See the remarks, p. 504.

[*M. cannarioides* Elm., Leafl. Philip. Bot. 10 (1939) 3785, *nom. inval.*, art. 36.] — Syntypes: *Elmer 16297* and *17086* (Philippine Islands), both seen from A, BO, K, L, U, W.

M. glandulosa Cufod., Oest. Bot. Z. 88 (1939) 252; How, Acta Phytotax. Sin. 3 (1955) 448. — Syntypes: *Steward, Chiao & Cheo 814* (Kweichow), seen from A, W; *Coll. Sun Yat Sen Univ. 21667* (Kwangsi), seen from W; *C. Wang 39531* (Kwangsi), seen from A; *T. S. Tsoong* (= *Z. S. Chung*) *83417* (*sine loco*), seen from A.

M. oldhamii var. *glandulifera* Cufod., Oest. Bot. Z. 88 (1939) 253; How, Acta Phytotax. Sin. 3 (1955) 450. — Type: *R. C. Ching 2783* (Anhwei), seen from A, W.

M. rhoifolia ssp. *barbulata* Cufod., Oest. Bot. Z. 88 (1939) 254; How, Acta Phytotax. Sin. 3 (1955) 447. — Syntypes: *Handel-Mazzetti 12235* (Hunan), seen from A, W; *Mell 668* (Kwangtung), seen from A; *C. L. Tso 20653, 21156* (Kwangtung), the latter seen from W; *Y. Tsiang 1357*[1] (Kwangtung), seen from BO, E, P; *Canton Christian Coll.* (= *To & Tsang*) *12256, 12572, 12673* (Kwangtung), seen from E, W; *W. T. Tsang 27673* (Kwangsi), seen from A; *T. S. Tsoong* (= *Z. S. Chung*) *83303, 83551* (*sine loco*), the latter seen from A.

M. veitchiorum (*non* Hemsl.) Chun, Sunyatsenia 4 (1940) 244.

M. angustifolia (*non* Merr.) Chun, Sunyatsenia 4 (1940) 243, *pro parte, quoad specim. Ko 53630, 54779.*

M. annamensis Gagn., Bull. Soc. Bot. Fr. 99 (1952) 9; Not. Syst. 14 (1952) 274; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 53, *in synon.* — Syntypes: *Poilane 13570* (S. Vietnam), seen from P; *Kerr 21127*[2] (Laos), seen from K, L, P.

M. chapaensis Gagn., Bull. Soc. Bot. Fr. 99 (1952) 10; Not. Syst. 14 (1952) 274; Vidal, Not. Syst. 16 (1960) 308. — *M. microcarpa* var. *chapaensis* Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 54, t. 9 f. 5, 6, *comb. illeg.*; Not. Syst. 16 (1960) 309. — Type: *Pételot 3801* (N. Vietnam), seen from P (holo).

M. quangnamensis Gagn.[3], Bull. Soc. Bot. Fr. 99 (1952) 12; Not. Syst. 14 (1952) 275; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 55, t. 9 f. 7—9. — Type: *Poilane 31436* (S. Vietnam), seen from L, P (holo).

M. simang Gagn., Bull. Soc. Bot. Fr. 99 (1952) 12; Not. Syst. 14 (1952) 274; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 55, t. 9 f. 10, 11. — Type: *Poilane 22249* (S. Vietnam), seen from P (holo).

M. microcarpa var. *angustata* Vidal in Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 53, *comb. illeg.*; Not. Syst. 16 (1960) 309. — Type: *Poilane 22346* (S. Vietnam), seen from P.

M. ferruginea (*non* Bl.) Back. & Bakh. *f.*, Fl. Java 2 (1965) 145, *pro parte, quoad M. glauca et floribunda.*

Small to medium-sized, rarely big tree, up to *c.* 20(—30) m. *Leaves* (2—)3—7(—8)-jugate; leaflets ovate to ovate-oblong, or elliptic to oblong or lanceolate, especially the upper ones sometimes more or less obovate to obovate-oblong, small to big, up to *c.* 25 by 10 cm, index (1—)1½—4(—5), acute to rounded or truncate at the base, entire or dentate, chartaceous to coriaceous, sometimes almost herbaceous, moderately pubescent to glabrous, often with domatia in the axils of the nerves beneath, above with impressed to flat midrib. *Panicles* erect, spreading, lax to dense, lower primary side-axes usually subtended by small or reduced leaves. *Sepals* glabrous or the outer ones rarely with a few

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[1] Abusively cited as *W. Y. Chun 1357*.

[2] Abusively cited as *21.227*.

[3] See the remarks, p. 504.

hairs. *Petals* glabrous, inner petals sometimes a bit ciliolate or frayed at the tips of the lobes. *Ovary* densely pubescent, very rarely only with a few hairs1). *Endocarps* (sub)globose, not or not much depressed, hardly or not oblique, (2½—)3—4½ mm ø, with distinct, more or less prominent, fine reticulum, with slightly to rather strongly prominent, blunt to rather sharp median keel which does not run out into a ventral processus or tubercle; ventral pore not sunken, sometimes a bit elevated (fig. 29 B 5).

Distribution: Ceylon, SW. Peninsular India (W. Ghats: from S. Canara southward; also in Bombay Prov.), NE. India (Assam: Khasi & Jaintia Hills; Darjeeling; Naga Hills; Manipur; Lushai Hills), Upper Burma (probably also southward in the Tenasserim range), Thailand (northern; western: Tenasserim range; Peninsular: only found at Pang-nga), Laos (only collected near Chieng Kwang), N. Vietnam (only collected at Cha Pa), S. Vietnam (Quang Nam Prov.; near Da Nang; Lang Bian massive), China (Yunnan; Szechuan; Kweichow; W. Hupeh; Hunan; N. Kwangsi; N. Kwangtung; Kiangsi; Chekiang; Fukien; S. Anhwei; S. Kiangsu), Taiwan (incl. Botel Tobago), extreme S. Corea (Quelpart I.; Herschel I.; Port Chusan), Japan (Ryu Kyu Is.; Tsushima; Honshu: Suwo Prov.; Hachijo I.), Philippine Islands (Luzon; Mindanao; Batan Is.), Malay Peninsula (only found in Perak: Cameron Highlands and Tapah Hill), N. Sumatra (only found in Karo Country), Java (G. Salak; G. Gedeh: Tjibodas; G. Malabar: Pengalengan; G. Lamongan; G. Ungarang: Limbangan). Common in most parts of the area; rare in W. Malesia. — Fig. 32.

Ecology: In tropical montane rain forests, tropical and subtropical hill evergreen forests, and in mixed mesophytic forests, from *c.* (600—)800 m up to *c.* 2500 m (in Yunnan up to *c.* 2700 m), in Central and East China, Formosa, Japan, and Corea generally lower, usually below *c.* 1200 m, sometimes almost at sea-level (see also the remarks). Found in primary as well as in secondary, dense to open forests and thickets, on good loamy or volcanic soils, but also on limestone if the climate is wet enough. Under warm-temperate climatical conditions the subspecies is deciduous; otherwise it is evergreen.

Field notes: In the tropical forests of Malesia the subspecies sometimes develops buttresses up to *c.* 1½ m high. In young trees branches ascending, spreading, forming a narrow crown, in older trees more wide-spreading, forming a round crown. Bark dark to light grey, smooth, in old trees sometimes distantly shallowly fissured. Inner bark soft, fibrous, with 'fingers' tapering outwards into granular tissue, pale pinkish brown to dull red or redbrown, also said to be white, and turning salmon red on exposure. Wood2) light and soft, fibrous, easily split, white, with large pores and beautiful grain, with prominent rays, heartwood in older trees striped reddish and white (like a tiger; see vern. names India). Leaflets beneath pale green, often glaucous. Fruits said to be reddish, green brown, or black when ripe.

Vernacular names: Ceylon (see Trimen, l.c., and Worthington, l.c.): *Wal-bilin* or *Nikadawulu* (Sinhalese), *Kusavi* (Tamil). SW. India (see Gamble, l.c.): *Kusavi* or *Thagari* (Tamil), *Huli Makay* (name by the Burghers, meaning 'tiger-like'; see field notes), *Koli* (Nilghiris, once mentioned). NE. India: see Kanj., Das & Purk., l.c., sub *M. wallichii*; also: *Theira* (Lakher Language, once mentioned). Burma: *Tun* (Chin language; *fide* Hundley & U Chit Ko Ko, l.c.). Thailand (all once mentioned): *Makawk bua* (Lampang), *Makawk doi* (Chiengmai), *Cha faew* (Chiengmai: Doi Sutep). S. Vietnam: *Si mang* (Proto-Indochinese, once mentioned). China (all once mentioned): *Shan ts'at* ('Mountain lacquer', Kwangtung), *Tu Kuo Shu* (Kiangsu), *Nanking K'o Nan Shu* (Kiangsu, *fide* Steward, l.c.).

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1) E.g. in *Ramos BS 80111* from the Philippine Islands and *Forrest 27091* from Upper Burma.

2) See Kanehira, Formosan Woods (1921) 83, t. 16 f. 94, 95.

Japan: *Ryukyu-awabuki* and *Fushi-no-ha-awabuki* (*fide* Ohwi, l.c.), *Sakunoki* or *Sakudamo* (Hachijo I., *fide* Nakai, l.c.), *Yanbaru-awabuki* or *Nurude-awabuki* (Ryukyu Is., Japanese, *fide* Walker, l.c.), *Tisan* or *Yuichin-ganashi* (Okinawa names, *fide* Walker, l.c.). Philippine Islands: *Adopo*, *Adupong*, *Aropong*, *Bantinan*, *Kamug* (all Igorot names from Luzon, *fide* Merr., En. Philip. 2, 1923, 518); also *Bae* (Ifugao, once mentioned). Sumatra: *Kabung sillang bulung* (Batak language, once mentioned). Java: *Ki tiwu (lalakkie)* and *Ki surèn* (from the Preanger, Sundanese, a few times mentioned, the first name also used for other *Meliosma* species), *Dangdur bulu* and *Kawayang* (both once mentioned from G. Gedeh).

Uses: The timber is worthless, used as firewood, and occasionally for rafters, clogs, boxes, and small objects. The young leaves may be eaten and are used as fodder for pigs (see Walker, l.c.). Trees from the Central China population (var. *oldhamii*) are moderately hardy and are grown as ornamentals in the open under mild temperate climatical conditions; the subspecies is cultivated in N. America and in Europe, amongst others in the Kew Botanic Gardens.

Remarks. Ssp. *arnottiana* displays a rather wide variability, though not as much as might be expected on the basis of its large area. This variability is especially found in the degree of pubescence, dentation, and texture of the leaflets, less so in the number of leaflets, furthermore also in the size of the flowers and the absence or presence of distinct pedicels. Also in habit it may vary from a small deciduous treelet up to a large evergreen tree. I found it impossible, however, to delimit well-distinguished groups within the subspecies; the variation is continuous and often follows irregular patterns. It is to be expected, of course, that a taxon covering such a wide area has been described under many local names; consequently, the number of synonyms is considerable. Most of these local names do not have significance; quite a number had already been reduced to synonymy by former authors, many have been added here. A few deserve some comment. '*M. oldhamii*', for instance, is the commonly used name for deciduous populations of ssp. *arnottiana*, occurring in the northern and northwestern part of the area. However, I can by no means delimit this group satisfactorily from the remaining evergreen part of ssp. *arnottiana*; the transition from evergreen to deciduous is certainly not a sharp one. Nevertheless, for practical purposes it may be advisable to distinguish both groups, each under its own name. I maintain them, therefore, as varieties.

b1. var. **arnottiana. — Photogr. 5.**

Evergreen small to large trees. Leaflets usually chartaceous to coriaceous. Flowers usually relatively small, mostly crowded and sessile or almost so.

Distribution: See under the subspecies; not in the northern and northwestern part of the area (see var. b2).

Ecology: In evergreen forests.

b2. var. **oldhamii** (Maxim.) Beus., *stat. nov.* — **Photogr. 4.**

Deciduous small to medium-sized trees, sometimes shrubs. Leaflets membranaceous. Flowers usually relatively big, mostly not very crowded and distinctly pedicelled. — For typification and references, see under the subspecies.

Distribution: Central East China (E. Kweichow, E. Szechuan, W. Hupeh, S. Kiangsi, S. Anhwei, Chekiang, S. Kiangsu), extreme S. Corea, S. Japan, Ryu Kyu Islands.

Ecology: Mainly restricted to mixed mesophytic forests.

Remark. Not sharply distinguishable and connected by many transitions to the typical variety.

Another name, now placed in the synonymy, which has been in common use for specimens from Assam, is *M. wallichii*; typical '*M. wallichii*' specimens represent transitional forms between ssp. *arnottiana* and ssp. *pinnata*. In leaf characters they take a position between these subspecies, whereas the ovary is glabrous or only somewhat pubescent. They have been found in the overlapping part of the areas of ssp. *pinnata* and ssp. *arnottiana* (Khasi Hills, Darjeeling), usually at medium altitudes, but also higher. It is not impossible that this intermediate form sometimes forms independent populations which may be locally more common than ssp. *arnottiana*. More or less arbitrarily, I have included '*M. wallichii*' in the synonymy of ssp. *arnottiana* because the type specimens have most characters in common with that subspecies.

In Vietnam the situation is particularly complex, due to the occurrence of somewhat aberrant forms and to the fact that the area here overlaps with that of ssp. *angustifolia*. With regard to the latter, I consider for instance the specimens *Poilane 11293* and *13570* from Quang Tri Prov. to be probably transitional forms between this subspecies and ssp. *arnottiana* (see also under ssp. *angustifolia*). A remarkable aberrant form is *Poilane 31436* from Quang Nam Prov. ('*M. quangnamensis*'), which is very densely ferrugineous-pubescent in most parts. It is certainly not a separate species but its position is somewhat obscure, since it has every character in common with the Malesian ssp. *ridleyi*. The endocarps might provide conclusive evidence, but unfortunately the specimen is in flowering state. In view of the distributional patterns of ssp. *arnottiana* and ssp. *ridleyi* a possible presence in S. Vietnam of the latter or of intermediates between both should not be excluded. In this respect also the somewhat deviating specimen *Clemens 3775* from Mt. Bani near Da Nang ('*M. clemensiorum*') should be mentioned. I am inclined to refer both to ssp. *ridleyi*, but the material is insufficient to draw definite conclusions; hence, for the time being, I hesitatingly include these deviating forms in ssp. *arnottiana* (see also the remarks under ssp. *ridleyi*).

Furthermore, mention should be made of the relation between ssp. *arnottiana* and ssp. *pendula* in the Philippine Islands (for the relation to ssp. *macrophylla*, see under that subspecies). In the mountains of Luzon both subspecies have been collected, viz. ssp. *pendula* above 1800 m altitude and ssp. *arnottiana* from *c.* 800—900 m up to *c.* 2400 m. Locally, e.g. on Mt. Santo Thomas, they have been found together, but I have not seen doubtless intermediate specimens. It is possible that in such localities these subspecies mutually behave as species; population studies in the field might yield more evidence with regard to this.

The same problem arises in West Malesia, where ssp. *arnottiana* has been collected rarely. In Sumatra and in Java its relation to ssp. *ferruginea* is interesting since there is an altitudinal zone of overlap between both, though ssp. *ferruginea* occurs generally lower than ssp. *arnottiana*. In Java, for instance, the situation is as follows: ssp. *ferruginea* is by far the most common of both, ssp. *arnottiana* having only been collected on a few mountains. Of these mountains it is only G. Salak and G. Gedeh where both subspecies have been found. Only of G. Gedeh more detailed ecological evidence is available: Koorders, Fl. Tjibodas 2 (1923) 157, states that ssp. *ferruginea* occurs at *c.* 1400 m altitude and that ssp. *arnottiana* ('*M. glauca*') occupies a zone between 1800 and 2400 m, being especially abundant at *c.* 2200 m. This does suggest the existence of ecological differentiation, but since ssp. *arnottiana* on other mountains also grows at lower altitudes, the situation remains unclear.

c. ssp. **angustifolia** (Merr.) Beus., *stat. nov.* — *M. angustifolia* Merr., Philip. J. Sc. 21 (1922) Bot. 348; Lingn. Sc. J. 5 (1927) 119; Chun, Sunyatsenia 1 (1934) 266; 4 (1940) 243, *pro parte*; Merr. & Chun, ibid. 2 (1934) 11; Cufod., Oest. Bot. Z. 88 (1939) 256; Merr., J. Arn. Arb. 23 (1942) 179; How, Acta Phytotax. Sin. 3 (1955) 450, t. 58, f. 10—14; Gagn. & Vidal in Fl. Camb. Laos & Vietn. 1 (1960) 50, t. 8 f. 7—14; Vidal, Not. Syst. 16 (1960) 308. — Type: *Mc Clure 8507* (Hainan), seen from A, P.

M. lanceolata (*non* Bl.) Lecomte, Bois Indoch. (1926) 142, t. 45; Vidal, Not. Syst. 16 (1960) 309.

M. crassifolia Hand.-Mazz., Sinensia 3 (1933) 191. — Type: *R. C. Ching 8290* (Kwangsi), seen from W (holo). Paratype: *R. C. Ching 8047*, seen from W.

M. poilanei Gagn., Bull. Soc. Bot. Fr. 99 (1952) 11; Not. Syst. 14 (1952) 275; Vidal, ibid. 16 (1960) 309. — Syntypes (all from S. Vietnam): *Poilane 19912, 21222, 21782, 22168, 30299, 30948*, all seen from L, P (holo); *Hayata 197*, seen from P (holo); *Evrard 2193*, seen from L, P (holo).

Small tree, up to *c.* 15(—18) m. *Leaves* (4—)6—11-jugate, leaflets oblong to lanceolate, usually small, up to *c.* 10(—13) by 3(—4) cm, index 2—5, acute at the base, entire, coriaceous, glabrous, without domatia, above with more or less prominent to flat midrib, often with inconspicuous nerves and venation. *Panicles* erect, spreading or not, lax to rather dense, with rather stiff axes, lower primary side-axes usually subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* densely pubescent. *Endocarps* (sub)-globose, rarely somewhat depressed, hardly or not oblique, 3—5 mm ø, with distinct, more or less prominent reticulum, with not very prominent, blunt to rather sharp median keel which sometimes runs out into a very minute ventral tubercle; ventral pore hardly or not sunken.

Distribution: Extreme southern China (extreme SE. Yunnan; SW. Kwangsi; Hainan), N. Vietnam (not in E. Tonkin), S. Vietnam. Common. — Fig. 32.

Ecology: Probably about the same as ssp. *arnottiana* (possibly under drier conditions?) by which its place is taken in adjacent areas and which occurs in about the same altitudinal zone; reported from 200—950 m in Hainan and from *c.* 500 m up to *c.* 1600 (—2000) m on the continent. Reported from primary and secondary, dense to open forests, forest margins, and thickets. In Hainan once said to occur in evergreen *Querco-Castanetum* above 700 m. Found on sandy as well as on clayish and loamy soils, usually in dry, but also in moist places, e.g. along streams.

Field notes: Bark grey, branches dark grey, stiff. Leaves pale green beneath. Fruits said to be orange-red or red (when ripe?).

Vernacular names: For several names used in Vietnam, see Gagn. & Vidal, l.c.

Remarks. Ssp. *angustifolia* is a characteristic, not very variable taxon, closely related to ssp. *arnottiana* from which it has very probably split off. The leathery texture of the leaflets suggests that it may have a somewhat other ecological preference than has ssp. *arnottiana*. Its relatively small area is partly overlapped by that of ssp. *arnottiana*; from this overlapping part in Vietnam a few specimens are known which are not impossibly transitions or hybrids between both (see the remarks under ssp. *arnottiana*).

With regard to the partly replacing areas of ssp. *angustifolia* and ssp. *arnottiana*, I point to the remarkable similarity between these and the areas of *M. simplicifolia* ssp. *rigida* and ssp. *laui* (see fig. 27).

d. ssp. **ridleyi** (King) Beus., *stat. nov.* — *M. ridleyi* King, J. As. Soc. Beng. 65, ii (1896) 458; Ridl., J. Str. Br. R. As. Soc. 33 (1900) 67; Fl. Mal. Pen. 1 (1922) 516; Gagn. & Vidal in Fl. Camb., Laos & Vietn. 1 (1960) 55, *in obs.* — Type: *Ridley 6342* (Singapore), seen from BM, K (holo), SING, W.

M. elegans Ridl., J. Str. Br. R. As. Soc. 54 (1910) 40; Fl. Mal. Pen. 1 (1922) 515. — Type: *Curtis 3754* (Malay Peninsula), seen from K (holo), SING.

M. paucinervia Merr., Philip. J. Sc. 10 (1915) Bot. 39; En. Philip. 2 (1923) 518. — Type: *Reillo BS 16436* (Philippine Islands), seen from BM, K, L.

M. trichocarpa Merr., Pap. Mich. Ac. Sc. 24, 1 (1938) 80, *nom. illeg.*, *non* Hand.-Mazz. (1934). — *M. bartlettii* Merr. & Perry, J. Arn. Arb. 20 (1939) 356. — Type: *Rahmat 9319* (Sumatra), seen from L, US. Paratypes (all from Sumatra): *Rahmat 6848*, seen from SING, *7505*, not seen, *7930*, seen from SING, *9210*, seen from L, US.

M. confertiflora Merr. & Perry, J. Arn. Arb. 20 (1939) 359. — Type: *Clemens 26961* (Borneo), seen from A, BO, K, L. Paratype: *Clemens 26961bis*, seen from A, BO, K, L.

Shrub or usually a small to medium-sized tree, up to *c.* 20 m. *Leaves* (2—)3—7(—8)-jugate; leaflets oblong to lanceolate, the upper ones sometimes obovate to obovate-lanceolate, small to usually medium-sized, up to *c.* 20(—25) by 6(—8) cm, index (1½—) 2—4(—4½), the base acute, rarely rounded, usually entire, sometimes with a few small teeth, rarely with many coarse teeth, chartaceous, sometimes coriaceous, densely villous-pubescent to glabrous, always without domatia. *Panicles* erect, spreading or not, usually rather lax and slender, with stiff to usually rather flaccid axes; lower primary side-axes mostly subtended by small or reduced leaves. *Sepals* and *outer petals* glabrous¹). *Inner petals* with fimbriate or ciliolate tips, rarely quite glabrous. *Ovary* densely pubescent. *Endocarps* subglobose to very depressed and oblique, sometimes almost semiglobose, 4½—9(—10) mm ø, with vague to distinct, more or less prominent, rather wide reticulum, with slightly to strongly prominent, blunt to very sharp median keel which often at one end runs out into a minute ventral processus, the curving at the other end sometimes far drawn out into a blunt beak; ventral pore hardly to rather deeply sunken.

Distribution: Central Sumatra: Asahan, Tapanuli (Mandailing), West Coast (G. Sago); S. Malay Peninsula: Selangor (G. Semangkok), Johore (Castlewood; 13½ mile Mawai-Jemaluang Road), Singapore (several localities); Borneo: Sarawak (Kuching, Semengoh For. Res.; Lundu, G. Gading; Bau; G. Pueh; Bario, Kalabit Highlands), Sandakan (Beaufort: Beaufort Hill; Ranau: Mt. Kinabalu and several other localities), W. Kutai (near Loma Petah; G. Amai Ambit); Philippine Islands: Mindanao (Zamboanga: Santa Maria); S. Vietnam? Scattered distribution, locally common, e.g. Singapore, Asahan, W. Sarawak, Mt. Kinabalu). — Fig. 32.

Ecology: In primary and secondary lowland or low-montane tropical rain forests, from sea-level up to *c.* 1400 m altitude. Reported from sandy and clayish, black and brown soils, from mixed lowland Dipterocarp as well as from Kerangas forest.

Field notes: Once said to be a woody climber (probably exceptional). Bole once said to be buttressed at the base. Bark mostly smooth, sometimes somewhat scaly or slightly fissured, grey to brown. Inner bark fibrous, pinkish to red or redbrown, turning brown after exposure. The young branches, inflorescence-axes, and leaf-rachises are sometimes (Singapore) covered with a dense layer of soft dark reddish brown hairs. Sepals sometimes said to be purple. Fruit often ± hairy ('*trichocarpa*'), once said to be bright purple.

Vernacular names: Sumatra: *Kaju si* (*mardjuhut*) (*ni*) *manuk* (four times mentioned), *K. rokkam*, *K. rube gala*, *K. si hasur* (all once mentioned), all from Asahan; *Modang halimponan* (twice mentioned, Mandailing language), from Tapanuli.

Remarks. Ssp. *ridleyi* is rather variable when compared to the other subspecies of *M. pinnata*, especially in number and dentation of leaflets, in the degree of pubescence, and in shape and size of the endocarps. In the Malay Peninsula, for instance, a form with few subglabrous and somewhat dentate leaflets has been found ('*M. elegans*'), as well as a beautiful, densely rufous-pubescent form with distinctly more and entire leaflets ('*M.*

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¹) Only in *Mikil 41927* from Mt. Kinabalu the sepals have been found to be pubescent.

ridleyi'). It is not astonishing that such different plants have been described as separate species; only by studying material from Borneo it becomes clear that these extremes are connected by a range of transitions. Another form from Dallas, Kinabalu, which has rather condensed panicles, has been described as *M. confertiflora*. This again is merely a local form without any systematical significance, as is *M. paucinervia*, with very lax panicles, from Mindanao. Yet, in spite of this variation, it is obvious that ssp. *ridleyi* is a natural unit, probably most closely related to the adjacent ssp. *arnottiana* from which it differs least of all subspecies, mainly in shape and size of the endocarps, but also in some less important characters; an especially close resemblance has been observed between ssp. *ridleyi* and some deviating specimens from S. Vietnam which have been tentatively included in ssp. *arnottiana* (see the remarks under the latter). Furthermore, the area of ssp. *ridleyi* borders on or somewhat overlaps the areas of ssp. *ferruginea* and ssp. *macrophylla*. The relation between ssp. *ridleyi* and these subspecies has been discussed under the latter.

Finally, it should be noted that the area of ssp. *ridleyi* fully overlaps that of *M. sarawakensis*; this is not accidental, since the latter is probably a derivative of ssp. *ridleyi* (see the remarks under *M. sarawakensis*).

From SE. Borneo, Muara Teweh, I have seen a dubious sterile specimen (*Boschbouwproefstation bb. 10088*) which may represent a multifoliolate form of ssp. *ridleyi*, but which also shows a good deal of resemblance to *M. lanceolata* var. *polyptera*; see there. Furthermore, from Mt. Kinabalu, Mesilau Cave and River (*c.* 1200—1500 m alt.), I have seen two collections (*Sadau 49721*, *Chew & Corner RSNB 4324*) which probably belong to ssp. *ridleyi*, but deviate in having glabrous ovaries and unusually coriaceous leaflets. They give the impression, however, to be somewhat abnormal, the panicles having rather stunted axes and swollen bracts and sepals, the flowers being probably sterile.

e. ssp. **ferruginea** (Bl.) Beus., *stat. nov.* — *M. ferruginea* Bl., Cat. (1823) 32, *non* Sieb. & Zucc. *ex* Hook. *f.* (1876), *nec* Kurz *ex* King (1896); Nees, Flora 8 (1825) 106; Hassk., Cat. Hort. Bog. (1844) 226; Bl., Rumphia 3 (1849) 200; Walp., Ann. 2 (1852) 225; Miq., Fl. Ind. Bat. 1, 2 (1859) 616; Illustr. (1871) 74; K. & V., Bijdr. 9 (1903) 121; Koord., Exk. Fl. Java 2 (1912) 546; Koord.-Schum., Syst. Verz. 1 (1912) fam. 166, 1; Koord., Atlas 2 (1914) t. 375; Fl. Tjibodas 2 (1923) 157; Back. & Bakh. *f.*, Fl. Java 2 (1965) 145, *pro parte, excl. M. glauca et floribunda*. — *Millingtonia ferruginea* Schult. & Schult., Syst. Veg. Mant. 3, add. 2 (1827) 250; Dietr., Syn. Pl. 1 (1839) 103. — Lectotype: *? Blume s.n.* (Java), seen from L.

Medium-sized to big tree, up to *c.* 42 m. *Leaves* 2—6(—7)-jugate; leaflets elliptic to oblong, the basal ones sometimes a bit ovate, the upper ones sometimes more or less obovate, usually rather big, up to 25(—38) by 10(—18) cm, index (1—)1½—3, the base rounded to truncate or emarginate, sometimes acute, entire[1]), firmly coriaceous, sparsely to rather densely pubescent, rarely subglabrous, rarely with domatia. *Panicles* erect, spreading, lax to rather dense, usually with rather coarse axes; lower primary side-axes usually subtended by small or reduced leaves. *Sepals* usually densely pubescent, rarely on the outside sparsely so to subglabrous. *Outer petals* moderately to densely pubescent on the outside, rarely glabrous. *Inner petals* with fimbriate or ciliolate tips. *Ovary* partly or entirely but almost always distinctly and densely pubescent, very rarely nearly glabrous. *Endocarps* subglobose, often somewhat depressed and oblique, 3½—5½(—8) mm ø, with rather vague to distinct, more or less prominent reticulum, with usually very prominent,

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1) Leaves of saplings and 'watershoots' always with dentate leaflets.

rather sharp median keel which does not run out into a ventral processus or tubercle; ventral pore not or not much sunken.

Distribution: Sumatra (Atjeh: Takengon; East Coast: Simalungun and Karo Lands, several localities; West Coast: G. Sago, G. Korintji), throughout Java, Lesser Sunda Islands (Bali; Flores; Sumbawa; Timor: only one collection by Teysmann). Locally common, especially in Java. — Fig. 32.

Ecology: In primary lowland and montane tropical rain forests, from 200—300 m up to *c.* 1600 m altitude, preferably in dense forests on fertile, often volcanic soils. In Java and the Lesser Sunda Islands only in places where the climate is everwet.

Field notes: Bole cylindrical, straight, sometimes crooked, at the base up to *c.* 2½ m ø, without or with up to *c.* 2 m high buttresses. Crown variable in shape and size. Bark on the surface grey to brown, smooth, sometimes a bit peeling or shallowly fissured to (deeply) cracked, about ¾—1½ cm thick, easily detachable. Inner bark pale brown to brownred or orange, with streaks, also said to be dirty white and turning orange brown when exposed to the air as a result of the discolouring of the initially colourless watery exudation. Wood soft, yellowish to pinkish white. Leaflets pale greyish to glaucous green beneath. Fruits brownred to black when ripe.

Vernacular names: Sumatra (all once mentioned): *Sĕkapong* (Atjeh: Takingeun), *Sontang* (East Coast, Simelungun dial.), *Sihubung* (West Coast: G. Korintji). Java: see K. & V., l.c., for several names; especially often mentioned are the Javanese names *Gijubuk* (Banjumas; Semarang), *Cĕmpong* or *Gompong* (Madiun; Kediri, also on Bali!), whereas the Sundanese names *Kitiwu* (Preanger) and *Ki tjĕrmé badak* (Tjibodas) are also used for other species of *Meliosma*. Lesser Sunda Islands (most once mentioned): *Sambuk* (Bali), *Gĕmpong* (Bali, twice mentioned; see Java), *Tanggo*, *Tawu*, *Mladja* (all reported as Endeh language, Flores), *Lohot*, *Raok* (both Flores), *Kaju mangkok* (W. Sumbawa).

Uses: The subspecies was proposed by Koorders & Valeton, l.c., for reforestation purposes.

Remarks. Ssp. *ferruginea* is usually well recognizable from all other subspecies of *M. pinnata* by its on the outside pubescent sepals and petals. Especially towards the ends of its area, viz. in N. Sumatra (e.g. *Lörzing 4137, 11718*, from Sibolangit) and on the Lesser Sunda Islands (e.g. *Kostermans & Wirawan 558, 740*, from Flores, and *Kostermans 18217, 19186*, from Sumbawa), however, apart from normal ones, also forms occur in which these characters are imperfectly or not at all developed. Such specimens may also lack the pubescence on the ovary and may have almost glabrous leaflets. These extreme forms are not easily identifiable, and may be confused either with. *M. lanceolata* f. *nervosa* (see there), or with the closely related ssp. *macrophylla* and ssp. *ridleyi*. As to ssp. *macrophylla* there is good reason to consider deviating specimens of ssp. *ferruginea* from Flores and Sumbawa transitional forms towards it; if more material were available, not only from the eastern Lesser Sunda Islands, but perhaps also from S. Celebes and the Moluccas, a transitional zone between their areas might be evident. This would fit into the picture, since these subspecies have the same ecological requirements and occupy adjacent, replacing areas. In N. Sumatra, however, where the areas of ssp. *ferruginea* and ssp. *ridleyi* come into contact, the situation is more complicated. There is some evidence that

Fig. 33. *M. pinnata* ssp. *macrophylla*. — a. flowering twig, × ⅓. — b. half-opened flower, × 5. — c. outer petal with adhering staminode, × 10. — d. flower with outer petals removed and stamens snapped backward, × 10. — e—g. stamen with adhering inner petal, in different positions, × 10. — h. pistil with surrounding disk, × 10. — i. ovary, length section, × 10. — j. ripe fruit, × 3. — k and l. endocarp in different positions, × 3. — a—i from *Sulit PNH 32941* and j—l from *Kostermans 6911*.


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b
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their areas might be replacing, the area of ssp. *ferruginea* being disrupted, that of ssp. *ridleyi* shifting in between (see fig. 32), but this is not certain, due to the scarcity of Sumatran collections of both subspecies. The only evidence for overlapping of areas are two specimens from G. Sago, one being ssp. *ridleyi*, the other (*Maradjo 441*), which is sterile, being a sapling or watershoot of ssp. *ferruginea*. For the relation between ssp. *ferruginea* and ssp. *arnottiana*, see under the latter.

Between the areas of the Javanese and of the Sumatran populations of ssp. *ferruginea* a wide gap was found; it is, however, not certain whether ssp. *ferruginea* indeed does not occur in S. Sumatra.

f. ssp. **macrophylla** (Merr.) Beus., *stat. nov.* — *M. macrophylla* Merr., Philip. J. Sc. 7 (1912) Bot. 294; En. Philip. 2 (1923) 517. — Type: *Fénix Phil. Pl. 483* (Philippine Islands), seen from U.

M. lanceolata var. *obliqua* (*non* Bl.) Koord., Minah. (1898) 408; Suppl. 2 (1922) 7, t. 55; ibid. 3 (1922) 28.

M. wallichii (*non* Planch. *ex* Hook. *f.*) Koord., Minah. (1898) 408.

M. tongcalingii Elm., Leafl. Philip. Bot. 8 (1915) 2815. — Type: *Elmer 11929* (Philippine Islands), seen from A, BM, E, K, L, W.

M. megalobotrys Merr., Philip. J. Sc. 11 (1916) Bot. 16; En. Philip. 2 (1923) 517. — Type: *Ramos BS 23516* (Philippine Islands), seen from A, K.

[*M. sorsogonensis* Elm. *in sched. ex* Merr., En. Philip. 2 (1923) 517, *nomen, pro synon.*] — Type: *Elmer 16014* (Philippine Islands), seen from A, BO, G, K, L, U, W.

[*M. macrocarpa* Elm., Leafl. Philip. Bot. 10 (1939) 3786, *nom. inval.*, art. 36.] — Type: *Elmer 12855* (Philippine Islands: Palawan), seen from A, K, L, U, W.

M. ferruginea (*non* Bl.) Merr. & Perry, J. Arn Arb. 20 (1939) 356. — **Fig. 33.**

Medium-sized to large tree, up to *c.* 42 m. *Leaves* (3—)5—9-jugate; leaflets elliptic to oblong or ovate to ovate-oblong, the upper ones sometimes obovate to obovate-oblong, medium-sized to rather big, up to *c.* 20 by 9 cm, index (1—)1½—3, the base rounded or obtuse to truncate or emarginate, sometimes more acute, entire, rarely with a few teeth (population Celebes; see remarks), chartaceous to firmly coriaceous, very sparsely to densely pubescent, always without domatia. *Panicles* erect and spreading, lax and slender to rather dense; lower primary side-axes usually subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* glabrous, rarely with a few scattered hairs. *Endocarps* subglobose, sometimes more obovoid or depressed, more or less oblique, 3½—5 mm ø, exceptionally 5—7½ mm ø (population Celebes; see remarks), with vague to distinct and prominent reticulum, with rather sharp and prominent median keel which at one end mostly runs out into a small but distinct ventral processus or tubercle; ventral pore somewhat sunken (fig. 29 B 6, 7).

Distribution: E. Malesia: E. Borneo (E. Sandakan; Berao; W. & E. Kutai; Tandjung), Philippine Islands (Luzon; Leyte; Mindanao; Palawan), Celebes (Minahasa; Malili), Moluccas (Halmahera; Ceram), throughout New Guinea, New Britain. Fairly common in most parts of the area. — Fig. 32.

Ecology: Usually in primary, rarely in secondary tropical rain forests, at low to medium altitudes; in Borneo only collected below 100 m, in the other parts of the area also higher, up to *c.* 1100—1200 m, in W. New Guinea once at 1800 m. In Borneo usually found in lowland Dipterocarp forests. Generally reported to occur on clayish, loamy, or sandy clayish soils, also on red earth, on volcanic soil, and on loamsoil on limestone. It is rarely found in occasionally submerged areas. Once (New Guinea) said to occur on peaty soil, and there developing stiltroots.

Field notes: Bole mostly straight, cylindrical, up to at least 1 m ø at the base, usually developing 1½—2½ m high buttresses, sometimes without buttresses, once said to be stiltrooted (see under ecology). Bark grey to brown, or patchy brown-white-grey, smooth, sometimes with shallow vertical cracks, not or little peeling, with vertical rows of lenticels. Inner bark *c.* 1 cm thick, soft, light brown or pink to brown-red, inside paler, sometimes said to be streaked with cream, with some colourless sticky exudate (which is also said to be red brown!); it is said to be rapidly darkening upon exposure or 'a bright orange-brown stain quickly appears between bark and sapwood'. Wood very light and soft; sapwood white to pale pink or brown, when fresh with bright brown sap streaks, heartwood absent or present, darker than the sapwood. The fruit is said to be brown to black.

Vernacular names: Borneo: *Surian* (E. Kutai, few times mentioned). Philippine Islands (generally once mentioned): Luzon: *Arocong* (Igorot language), *Balilang-uak* (Tagalog, a corruption of *Barilan ng uak*), further mentioned by Merrill, En. Philip. 2 (1923) 517: *Agosos* (Tag.), *Morau* (S. L. Bis.), *Muñgapong* (Bik.); Mindanao: *Magasorod* (Bagobo dial.). Celebes (all from Minahasa, mentioned by Koorders, Minah., 1898, 408): *Kaju-saut-rintek* (Tooelooe language), *Papako* (Tontemboan language), *Mumping* (Tonsea language), *Liasan* (Ratahan language). Moluccas: *Bais* (Ceram, Alfur language?, once mentioned). W. New Guinea (most once noted): *Tubuk* or *Sebotebuk* (Mooi language, Sorong, twice reported), *Serajema* (Manikiong language, Manokwari), *Marwaskeipi* (Roberbai, Japen dial.), *Bagare* (Kapauku language, Wissel Lakes), *Biedewon* or *Iediewat* (Muju language, Div. of S. New Guinea). E. New Guinea (all once noted): *Morrotuno* and *Waito* (both Wapi language, Miwaute, Sepik Dist.), *Frikipa* (Orne language, Kaiye, Sepik Dist.), *Tapuha* (N. Managalase, N. Div.), *Kufi* (Kutubu language, S. Highl.), *Uliga* (Amele language, Madang Dist.).

Remarks. Ssp. *macrophylla* is the most common and widespread of the East Malesian subspecies group, characterized by a glabrous ovary by which it is readily distinguished from the West Malesian subspecies. Within its large area a few other subspecies occur, viz. ssp. *pendula*, *sylvatica*, and *humilis*, which have much more limited areas and probably represent offsplits from it. These three subspecies are ecologically well isolated from ssp. *macrophylla* (for details, see the remarks under them); apart from one or two cases (see under ssp. *humilis*) I have not seen intermediate forms, but more may show up when more material from critical altitudinal zones is collected.

In Borneo the area of ssp. *macrophylla* is, as far as can be judged from the available evidence, sharply delimited against that of the West Malesian ssp. *ridleyi*, which, moreover, appears to prefer a higher altitudinal zone (only in Borneo ssp. *macrophylla* seems to be restricted to lowland forests below *c.* 100 m altitude!). To the Southwest the area of ssp. *macrophylla* borders on that of ssp. *ferruginea* which inhabits the Lesser Sunda Islands. The latter two subspecies are huge trees, very similar in general habit, and they have been confused sometimes. Nevertheless, they are usually well distinct, mainly by flower characters, though in both subspecies there is a tendency to loose some of these characters; it is possible that populations with intermediate characters occur in the islands around the Flores and Banda Seas. (See the remarks under ssp. *ferruginea*.)

In the Philippine Islands ssp. *macrophylla* is sympatric with ssp. *arnottiana*, but they prefer different altitudinal zones, the first being a lowland subspecies not exceeding *c.* 900 m, the latter being a montane subspecies occurring from *c.* 800 up to *c.* 2400 m (once recorded from *c.* 600 m). Intermediate specimens have not been seen by me.

In general, ssp. *macrophylla* has quite constant characters; there is some geographical variation between on the one hand the specimens from Borneo and the Philippines, which have always at least 6-jugate leaves, and on the other hand those from Celebes, the Moluccas and New Guinea in which also 4- or 5-jugate leaves occur. In Celebes, however, the situation is particularly complex, since, next to normal specimens, several plants have been found there, even in the same areas, which deviate considerably in having leaflets with a few teeth and much larger endocarps than usual (*Boschbouwproefstation bb. 14135, 19556, Forman 266, Kjellberg 2480, Koorders 18789*, all from Minahasa or Malili). According to the notes on the labels some of these specimens have been taken from rather small trees (8—12 m), not from medium-sized to large trees as is usual in ssp. *macrophylla*. Also the leaf texture suggests that they come from lower-storey trees. The other characters, however, indicate a very close relationship with normal ssp. *macrophylla*. It is possible that they represent a specialized form of that subspecies, but I prefer not to describe it because of lack of more evidence.

g.ssp. **pendula** (Merr.) Beus., *stat. nov.* — *M. pendula* Merr., Publ. Gov. Lab. Philip. 29 (1905) 25; En. Philip. 2 (1923) 518. — Type: *Elmer 6245* (Philippine Islands), seen from K.

M. reticulata Merr., Philip. J. Sc. 5 (1910) Bot. 195; En. Philip. 2 (1923) 518. — Type: *Ramos BS 5594* (Philippine Islands), seen from K. Paratype: *Curran FB 15803*, not seen.

M. macgregorii Merr., Philip. J. Sc. 10 (1915) Bot. 37; En. Philip. 2 (1923) 517. — Type: *McGregor BS 19749* (Philippine Islands), seen from K, L. Paratype: *Merrill 4600*, seen from K.

Small to medium-sized tree, up to *c.* 20 m. *Leaves* (3—)4—6-jugate; leaflets elliptic to oblong, rarely lanceolate, the upper ones usually more or less obovate to obovate-oblong, rather small to medium-sized, up to 18(—20) by 7(—11) cm, index 1½—3(—4), the lower ones at the base nearly always rounded or (sub)truncate to obtuse, the upper ones more or less acute, sparsely to rather closely but nearly always distinctly dentate[1]), chartaceous to firmly coriaceous, moderately to rather densely villous-pubescent, more or less glabrescent, without domatia. *Panicles* erect and spreading to somewhat pendulous and rather flaccid, slender and rather lax; lower primary side-axes mostly subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* glabrous. *Endocarps* subglobose, slightly oblique, 6—7 mm ø, with rather vague, slightly elevated reticulum, with hardly to moderately prominent, blunt median keel, the latter not running out into a distinct ventral processus or at most into a very minute tubercle; ventral pore hardly or not sunken (fig. 29 B 3).

Distribution: Philippine Islands: Luzon (Mountain Province: Mt. Data, Mt. Pukis, Mt. Pulog, Mt. Santo Thomas, Mt. Tabayoc, Mt. Polis, Mt. Natoo, Mt. Nañgaoto). Not uncommon in the mountains.

Ecology: In primary montane tropical rain forests at altitudes from *c.* 1800 m up to *c.* 2500 m. Reported to be found in mossy forest, in ravines as well as on exposed ridges.

Field notes: Bark thick, checked. Wood soft, said to be soon assuming an orange-brown colour.

Vernacular name: *Anitap* (Igorot language); *fide* Merr., En. Philip. 2 (1923) 518.

Uses: The leaves are once said to be used for smoking by the Igorots.

Remarks. Ssp. *pendula* replaces the lowland and lower hill ssp. *macrophylla* at high elevations (in this respect being comparable to ssp. *humilis* from New Guinea). Though contact between both may occur, it is as well possible that an altitudinal gap exists between

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[1]) Sometimes almost all leaflets entire, only one or two having a few teeth, rarely with no teeth at all (e.g. *Loher 383*).

them; the former is only reported from above 1800 m, the latter from below *c.* 900 m. I have not seen specimens intermediate between both.

Compare also the remarks under ssp. *arnottiana.*

h. ssp. **sylvatica** (Elm.) Beus., *stat. nov.* — *M. sylvatica* Elm., Leafl. Philip. Bot. 2 (1908) 492; Merr., En. Philip. 2 (1923) 518. — Type: *Elmer 9132* (Philippine Islands), seen from A, BO, E, K, L, W.

M. acuminatissima Merr., Philip. J. Sc. 10 (1915) Bot. 36; En. Philip. 2 (1923) 517. — Type: *Escritor BS 19417* (Philippine Islands), not seen (see remarks).

M. brachybotrys Merr., Philip. J. Sc. 12 (1917) Bot. 275; En. Philip. 2 (1923) 517. — Type: *Ramos & Edaño BS 26567* (Philippine Islands), seen from K.

Slender shrub or treelet, up to *c.* 5 m. *Leaves* (3—)4—6(—7)-jugate; leaflets elliptic to usually oblong or lanceolate, the upper ones usually more or less obovate-oblong to -lanceolate, usually medium-sized, up to *c.* 18 by 6 cm, index 1½—4(—5), acute at the base, sparsely to rather closely, always distinctly dentate[1]), chartaceous, very sparsely to moderately pubescent, without domatia. *Panicles* erect, spreading, usually slender and rather lax; primary side-axes (mostly?) not subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* glabrous. *Endocarps* subglobose, often somewhat ellipsoid, more or less oblique, 5—6 mm ø, with distinct, more or less prominent reticulum, with rather sharp and prominent median keel which at one end runs out into a small but distinct ventral processus; ventral pore somewhat sunken.

Distribution: Philippine Islands: Luzon (Tayabas Prov.: Mt. Pular, Mt. Banahao, Mt. Dingalan, Lucban; Rizal Prov.: Bosoboso), Negros (Dumaguete: Cuernos Mts.); Celebes (Minahasa: Bojong; Central Celebes: Latimodjong Mts.). Perhaps locally (Tayabas!) common. — Fig. 32.

Ecology: In primary lowland tropical rain forests, usually not above 750 m altitude[2]), growing in the shrub layer.

Field notes: Slender, suberect or bent shrub or treelet of a sparsely branched habit. Bark smooth, grey and brown mottled. Wood white, soft, easily breakable. Leaves once said to be light bluish green beneath.

Remarks. Ssp. *sylvatica* is closely related to ssp. *macrophylla.* The most striking difference between them is found in their physiognomy, the former being a small undergrowth treelet, the latter a large forest tree. The main systematical differences are found in the dentation and the shape of the base of the leaflets. These fit nicely in the spectre of character combinations present in the subspecies of *M. pinnata,* and I feel justified, therefore, in considering ssp. *sylvatica* a subspecies of that species, instead of a separate species. The great difference in habit between ssp. *macrophylla* and ssp. *sylvatica* may be explained in terms of its function to keep both genetically apart in the actual situation of their having overlapping areas (see fig. 32), and occurring in the same altitudinal zone (see notes on ecology). It is to be expected that in the complex stratification of a lowland tropical rain forest ecological isolation exists between two potentially interbreeding taxa if one forms part of the shrub layer, the other of the canopy or emergent layer (see also part I chapter D). I have not seen intermediate specimens; however, in this respect the following may be of importance.

Of the species *M. acuminatissima* Merr., which I have tentatively placed in the synonymy of ssp. *sylvatica,* I have not seen the type, but, judging from the description, it comes

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[1]) Possibly rarely entire; see remarks.

[2]) *Sands 383* from Latimodjong Mts. (Celebes), however, was collected as high as 2000 m!

very close to that subspecies. It has, however, entire glabrous leaflets, thus taking a position between ssp. *sylvatica* and ssp. *macrophylla*. Hence, it might represent an intermediate form, which is also possible in view of the collecting locality (Luzon: Tayabas); no more evidence being available, however, I confine myself to this remark.

i. ssp. **humilis** (Merr. & Perry) Beus., *stat. nov.* — *M. humilis* Merr. & Perry, J. Arn. Arb. 20 (1939) 358; ibid. 22 (1941) 263, *in obs.* — Type: *Brass 5050* (New Guinea), seen from BO. Paratypes: *Clemens 4465, 4828, 5288, 6262*, all seen from A.

M. schlechteri Merr. & Perry, J. Arn. Arb. 22 (1941) 262. — Type: *Schlechter 18272* (erroneously cited as *18292*) (New Guinea), seen from L.

Small to medium-sized tree, up to *c.* 20 m. *Leaves* 3—5-jugate; leaflets elliptic to oblong, rarely short-lanceolate, the upper leaflets usually more or less obovate to obovate-oblong, usually rather small, up to *c.* 15(—24) by 6(—9) cm, index (1—)1½—3(—3½), the base acute, often somewhat attenuate, the lower leaflets sometimes rounded at the base, sparsely to rather closely dentate[1]), chartaceous to firmly coriaceous, beneath subglabrous to rather densely pubescent, sometimes densely villous-tomentose, always with more or less distinct domatia in the axils of the nerves beneath (obscure in densely tomentose leaflets!). *Panicles* erect, spreading, mostly rather lax and with slender axes; lower primary side-axes often subtended by small or reduced leaves. *Sepals* and *petals* glabrous. *Ovary* glabrous. *Endocarps* subglobose, somewhat depressed and rather oblique, 5½—7½ mm ø[2]), with more or less vague, slightly elevated reticulum, with very prominent, rather sharp median keel which at one end runs out into a small but distinct ventral processus; ventral pore somewhat sunken (fig. 29 B 2).

Distribution: E. New Guinea (Highlands Districts; Madang Dist.; Morobe Dist.). Common. — Fig. 32.

Ecology: In primary and secondary, montane, tropical rain forests, between *c.* 1000 and 3000 m altitude. Observed as an understorey tree in dense forests such as *Castanopsis-Nothofagus* forest, on ridges as well as on stream banks, but also often reported from several kinds of disturbed forest, such as bamboo regrowth, old garden land, transition between coniferous forest and treefern grassland, and even from open grassland. Once reported from limestone ridge.

Field notes: Once said to be a scandent sprawling small tree (probably exceptional). Buttresses not observed. Bark grey to brown, smooth, with big lenticels. Inner bark straw-coloured to pink, red, or reddish brown (due to discolouring, as in other subspecies?), exuding 'resin'. Wood white to light brown, with conspicuous rays and clear growth rings, said to be of moderate weight and hardness. Petioles, peduncle, and pedicels purplish to redbrown; buds reddish. Fruits dark red to black when ripe.

Vernacular names (all, except one, once reported): *Mansalong* (Finschhafen), *Kokopong* (Nako language, E. Madang Dist.), *Kass* (Maring language), *Mappam* (Enga language, twice mentioned from W. Highl. Dist.).

Uses: Once said to be used as housing timber, free from borers.

Remarks. Ssp. *humilis* is closely allied to ssp. *macrophylla*, mainly differing by its dentate leaflets with domatia. Its area is restricted to the mountains of E. New Guinea, where it replaces ssp. *macrophylla* which is mainly found below 1000 m altitude (cf. ssp. *pendula* from Luzon). It is remarkable that ssp. *humilis* has as yet been collected, even rather abundantly, only in E. New Guinea, whereas one might expect it as well in W.

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[1]) Sometimes only a few leaflets dentate, rarely none (*Brass 30720*).

[2]) Sometimes smaller but then infected by insects.

New Guinea; this may be due, however, to the much less intensive collecting in W. New Guinea. In this connection it is remarkable that the only two collections which might be considered transitions between ssp. *humilis* and ssp. *macrophylla* have been found in W. New Guinea, viz. *Brass & Versteegh 13140* (leaflets with domatia, but without teeth), collected at 800 m, and *Vink & Schram BW 8785* (leaflets without domatia, but with some teeth), collected at 1800 m.

12. Meliosma sarawakensis Ridl., Kew Bull. (1933) 193; Merr. & Perry, J. Arn. Arb. 20 (1939) 359. — *M. grandifolia* Lecomte, Bull. Soc. Bot. Fr. 54 (1909) 676, *nom. illeg.*, *non* Urban (1895); Merr., En. Born. (1921) 362. — Lectotype: *Beccari 3572* (Sarawak), seen from F, K. Syntype (*M. grandifolia*): *Beccari 3621*, seen from F, K. Paratypes (*M. sarawakensis*): *Haviland 742*, seen from BM, K, L, SING, *763*, seen from K.

M. confusa var. *laxior* Baker *f.* in Rendle, J. Bot. 62 (1924) Suppl. 30. — Type: *Forbes 2794* (Sumatra), seen from BM.

M. latifolia Ridl., Kew Bull. (1933) 193; Merr. & Perry, J. Arn. Arb. 20 (1939) 359, *in obs.* — Type: *Haviland & Hose 3627* (Sarawak), seen from K (holo).

Evergreen, small tree, up to *c.* 10 m. *Flowering twigs* terete, 2½—5(—7) mm ø, densely pubescent, later more or less glabrescent, sometimes with a few big leaf-scars. *Leaves* 2—3(—4)-jugate; rachis terete, 12—30 cm, including the 6—15 cm long petiole, up to *c.* 5 mm across, densely short-tomentose, later more or less glabrescent, usually with more or less swollen base, hardly or not lenticellate; leaflets usually elliptic to oblong, the lower ones often more or less ovate to ovate-oblong, the upper ones often more or less obovate to obovate-oblong, sometimes somewhat asymmetrical, (2—)5—22 by (1½—)3—12 cm, index (1—)1½—3, mostly distinctly increasing in size towards the top of the leaf, the base usually acute to rounded, sometimes cuneate (upper leaflets) or truncate (base leaflets), often somewhat attenuate, often oblique, the apex more or less acuminate, sometimes subacute or cuspidate, with entire to remotely spinously dentate margin, chartaceous, shining to dull above and beneath, moderately to rather densely pubescent especially beneath and on midrib and nerves, often partly glabrescent when older, never with domatia; midrib more or less impressed above, distinctly prominent beneath; nerves 6—12 pairs, ascending, usually looped and joined, prominulous to slightly impressed above, more or less prominent beneath; venation distinct, reticulate and somewhat cancellate, prominulous or sometimes slightly impressed above, prominulous beneath; petiolules up to *c.* 1½(—3) cm, terminal one usually longest, tomentose, often somewhat swollen at the base. *Panicles* terminal, usually more or less pendulous, flaccid, lax, narrowly pyramidal, (20—)25—55 cm, not profusely branched up to the 2nd or 3rd order, the branches spreading, more or less flaccid, usually slender, terete to more or less angular, densely tomentose, bearing numerous flowers crowded to dense spikes; main axis terete to somewhat angular; primary side-axes few to rather many, up to *c.* 25(—35) cm, the lower ones usually subtended by reduced leaves; bracts ovate to usually narrowly triangular or linear-lanceolate, up to *c.* 4 mm, densely pubescent. *Pedicels* (almost) absent. *Mature buds c.* 2 mm ø. *Sepals* 5 (4), ovate to ovate-lanceolate, the inner 3 or 4 1—1½ mm, the outer 1 or 2 usually much smaller, often minute, densely pubescent on the outside, with entire margin. *Outer petals* glabrous. *Inner petals* about halfway or somewhat less bifid, ½—⅔ mm, glabrous, sometimes with a minute central lobule. *Stamens*: anther-cells ¼—⅓ mm ø; filaments *c.* 1 mm. *Ovary* ½—⅔ mm, densely pubescent. *Style* ½—⅔(—1) mm, glabrous. *Fruit* (sub)globose, when ripe ¾—1 cm ø; endocarp depressed- to almost semiglobose, applanate at the ventral side, strongly oblique, 6—7(—8) mm ø, with usually distinct, more or less sharply prominent reticulum; median keel sharp and very prominent, not at one end running out into a ventral processus or tubercle, at the other end rather far curving outwards; ventral pore rather sunken (fig. 29 B 1).

Distribution: Sumatra: Asahan, Riouw (Indragiri: Muara Padjenki), Palembang (Tandjung Ring on Beliti River); N. Borneo: Sarawak (G. Santubong, G. Serapi, G. Wa, G. Mattang, Sampadi For. Res., all near Kuching). Fairly common near Kuching. — Fig. 32.

Ecology: Primary lowland tropical rain forests, up to *c.* 800 m altitude.

Field notes: Once said to be a climber; probably a straggling treelet is meant. The sepals are redbrown to purple.

Vernacular names (both once mentioned): Borneo: *Bulu manok* (Iban name, Kuching); see also *M. sumatrana.* Sumatra: *Kaju rube boras* (Asahan).

Remarks. The closest affinity of *M. sarawakensis* is doubtless with *M. pinnata* ssp. *ridleyi* to which it is very similar in all characters (they even share the red sepals; see field notes) except two; see further. This is also in conformity with the distributional areas of both, which overlap and show similar patterns. Only after some hesitation I have maintained *M. sarawakensis* as a separate species and not made it a subspecies of *M. pinnata.* It would fit rather well into that species, if it not were distinguished from it by a wider range of characters than are the subspecies of *M. pinnata* mutually. The most important of its characters are the 2- or 3-jugate leaves and the densely pubescent sepals. These characters are indeed also found in *M. pinnata* ssp. *ferruginea*[1]), but this subspecies is quite different from *M. sarawakensis* in various other aspects. An additional argument to the specific status of *M. sarawakensis* is found in the fact that it is found together with *M. pinnata* ssp. *ridleyi* in the same area and at the same altitudes in Sarawak (near Kuching) and in Sumatra (Asahan), without any sign of hybridization. On morphological and geographical grounds I consider it a derivative of *M. pinnata* ssp. *ridleyi*; in this respect it can be compared with *M. paupera* and *M. simplicifolia* ssp. *fordii.*

II. Subg. KINGSBOROUGHIA (Liebm.) Beus., *stat. nov.*[2])

Kingsboroughia Liebm. — *Llavea* Planch. — For full references see under the genus (p. 429). — Type species: *Kingsboroughia alba* (Schlechtend). Liebm. = *Meliosma alba* (Schlechtend.) Walp.

Leaves pinnate; rachis terminating in 1 leaflet (anomalously 2 leaflets) of which the petiolule is marked against the rachis by an articulation (fig. 34a). Sepals mostly 4. Outer petals widely imbricate, the biggest one ± widely reniform, much wider than long, the smaller ones ± irregular-shaped, not (much) wider than long (fig. 34b). Vascular bundle (connecting pedicel and seed) situated outside the endocarp, either running in a groove at the ventral side of it, or freely in the pulpy mesocarp (fig. 4A, B).

Distribution: Three species, one in West Malesia, one in West to East Central China, and one in NE. Upper Burma, Central China, and South Mexico, a remarkable disjunction. — Fig. 5.

Ecology: In tropical or subtropical to warm-temperate, montane forests, at altitudes from *c.* 1000 m up to *c.* 2000 m, occasionally up to *c.* 3000 m.

Remarks. The position of this interesting subgenus has been amply discussed in part II

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[1]) Within subsect. *Pinnatae* pubescent sepals only occur in *M. sarawakensis* and *M. pinnata* ssp. *ferruginea.* They have also once been found in a deviating specimen (*Mikil 41927* from Mt. Kinabalu) belonging to *M. pinnata* ssp. *ridleyi.*

[2]) Species 13—15 in this paper.

chapter C sub 1. Several good arguments and a wealth of fossil evidence plead in favour of the hypothesis that subg. *Kingsboroughia* is an ancient relict group.

The two most important characters, that of the position of the vascular bundle in the fruit and that of the terminal leaflet (see description), have never been noticed before; they are discussed in part I chapter C sub f.

A. Sect. **Hendersonia**[1]

Arbores sempervirentes. Fasciculus vasculorum pedicellum cum semine connectens mesocarpium libere percurrens.

Evergreen trees. Vascular bundle connecting pedicel and seed running freely in the mesocarp. — **Fig. 4A.**

Type species: *M. rufo-pilosa* Hend.

Distribution: Only one species occurring rarely and scattered in the Malay Peninsula and North Borneo.

13. **Meliosma rufo-pilosa** Hend., Gard. Bull. S. S. 7 (1933) 96, t. 18; Merr. & Perry, J. Arn. Arb. 20 (1939) 360. — Type: *Henderson SF 23657* (Malay Peninsula), seen from BM, K, L, SING (holo).

Evergreen tree, medium-sized to big, up to *c.* 30 m. *Flowering twigs* terete, 5—10 mm ø, stout, abruptly terminating in a tuft of leaves and inflorescences, glabrous, often with many big conspicuous leaf-scars. *Leaves* (6—)7—9-jugate; rachis terete, more or less flattened towards the base, (13—)25—50(—65) cm, including the (3½—)6—16 cm long petiole, up to *c.* 5 mm ø, moderately to densely pubescent, not swollen at the base, hardly or not lenticellate; leaflets elliptic to oblong, sometimes ovate(-oblong), sometimes a bit asymmetrical, (2—)3—15 by (1½—)2—6 cm, index 1½—3, somewhat increasing in size and length towards the top of the leaf, the base obtuse to truncate, sometimes emarginate, sometimes oblique, often slightly attenuate at the very base, the apex acuminate, with entire margin, chartaceous, usually somewhat shining above, dull and paler beneath, glabrous or minutely puberulous on midrib and basal part of nerves above, (sub)glabrous beneath except for the sparse to dense pubescence on midrib and lesser so on nerves, always without domatia; midrib impressed above, prominent beneath; nerves 7—18 pairs, ascending, looped and joined, nearly flat to somewhat impressed above, prominent beneath; venation fine, very distinct, reticulate, slightly elevated above, distinctly prominent beneath; petiolules 1—6 mm, densely pubescent. *Panicles* terminal, one or a few crowded together at the end of a twig, erect, rather dense to lax, pyramidal, 30—50 cm, including the 0—20 cm long peduncle, profusely branched up to the 4th order, branches spreading, somewhat flaccid, more or less canaliculate and angular to flattened, densely pubescent, bearing numerous solitary flowers; main axis somewhat lenticellate towards the base; primary side-axes well-spaced, about 8—15, up to *c.* 30 cm, not lenticellate, the lower ones never subtended by small or reduced leaves; bracts narrowly triangular to lanceolate, up to *c.* 4 mm, densely pubescent. *Pedicels* 1—3 mm, densely pubescent. *Sepals* (3) 4, ovate, (sub)equal, *c.* 1½—2 mm, the outer one often much smaller, rarely minute, usually lowered on the pedicel, glabrous or somewhat pubescent at the outside; margin flimsy, more or less ciliolate, entire or sometimes with some coarse irregular teeth. *Outer petals c.* 1½ mm long, 1½—2½ mm wide. *Inner* petals ligular, usually somewhat widened towards the top, ¾—1 mm; top entire or with an undeep incision,

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[1] Species 13 in this paper.

blunt, minutely ciliolate. *Stamens:* anther-cells $\frac{1}{5}$—$\frac{1}{4}$ mm ø; filaments $\frac{3}{4}$—1 mm. *Ovary* $\frac{1}{2}$—$\frac{3}{4}$ mm, glabrous. *Style* ($\frac{1}{2}$—)$\frac{2}{3}$—1 mm, glabrous. *Fruit* globose, when ripe 1$\frac{1}{2}$—2 cm ø, with moderately thick, fleshy mesocarp; endocarp semiglobose, broad-ovate to subcordate at ventral view, 11—13 mm long and wide, 7—8 mm high, with relatively thin wall, with slightly lumpy surface, especially lumpy and somewhat furrowed at the ventral curving of the wall; median keel faint, hardly elevated but at one end drawn out into a conspicuous, laterally flattened, downwards-curved, blunt beak; ventral side rather deeply concave with a smooth, wide-ovate to suborbicular central part from the centre of which protrudes the ± conical hilus of the seed (fig. 12 G 1, 2).

Distribution: W. Malesia: Malay Peninsula (Pahang: Cameron Highlands; Pahang Selangor: Genting Highlands), Borneo (Sarawak: Baram, Gunong Mulu; Sabah: Mt. Kinabalu complex: Tenompok; Kambarango; Kundasang; Sosopodon For. Res.). Rare, perhaps locally more common (reported to be fairly frequent at Tenompok). — Fig. 30.

Ecology: In primary montane tropical rain forest, found between 1350 m and 1700 m. Found on steep hillsides, along stream, and on stony soil.

Field notes: Big tree with deep rounded crown, bole once said to have *c.* 2 m high buttresses. Bark smooth, grey to brown, with lenticells in vertical rows ('scarred', 'dippled'). Inner bark soft, fibrous, orange to reddish outside, pale fawn to white towards the cambium. Sapwood pale brown. Twigs pale brown, rough, lenticellate, with darker leaf-scars. Leaves pale green. Fruit yellow to orange when ripe.

Vernacular names: Sengkuang, once reported from Genting Highlands, Malay Peninsula.

Remarks. The very remarkable morphology of the endocarp of *M. rufo-pilosa* is discussed in part I chapter C sub d. A discussion on the supposed ancient-relict character of this species is given in part II chapter C sub 1.

B. Sect. **Kingsboroughia**[1]

Deciduous trees. Vascular bundle connecting pedicel and seed running in a ventral groove in the endocarp wall. — **Fig. 4 B.**

Distribution: Two species, one in West to East Central China, and one in NE. Upper Burma, Central China, and South Mexico.

14. **Meliosma alba** (Schlechtend.) Walp., Rep. 2 (1843) 816; Planch., Fl. Serres 5 (1849) 533 c; Hemsl., Biol. Centr. Am. Bot. 1 (1880) 216; Urb., Symb. Ant. 1 (1900) 504; Standl., Contr. U.S. Nat. Herb. 23 (1923) 709. — *Millingtonia alba* Schlechtend., Linnaea 16 (1842) 395; Planch., Ann. Sc. Nat. Bot. 4 (3) (1855) 295 ('*Mellingtonia*'). — *Kingsboroughia alba* Liebm., Vid. Medd. Nat. For. Kjøbenhavn (1850) 67; Walp., Ann. 3 (1853) 835. — Type: *Schiede s.n.* (Jalapa, Mexico, IV-1829), seen from K.

M. beaniania Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 205; Cufod., Oest. Bot. Z. 88 (1939) 252; Rehd., Man. Cult. Trees & Shrubs (1940) 595; Merr., Brittonia 4 (1941) 111; How, Acta Phytotax. Sin. 3 (1955) 447, t. 58 f. 6—9; Vidal, Not. Syst. 16 (1960) 308; Krüssm., Handb. Laubgeh. 2 (1962) 127. — Type: *Wilson 258, pro parte* (Ichang, Hupeh), seen from A (holo), K. Paratypes: *Wilson 258, pro parte* (Hsing-shan Hsien, Hupeh), seen from A, E (an holotyp. dupl.?), W (an holotyp. dupl. ?), *154*, seen from BM, E, K, *627*, seen from A, E, K, W, *4606*, seen from A, *4607*, seen from A, BM, K; paratype *Wilson 258a*, seen from K, does not belong here, but to *M. pinnata* ssp. *arnottiana.*

Deciduous tree, small to big, up to *c.* 25(—30) m. *Flowering twigs* terete, 3—8 mm ø,

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[1] Species 14 and 15 in this paper.

not stout and not abruptly terminating in a tuft-like leafy inflorescence, glabrous, when young somewhat pubescent and soon glabrescent, with less conspicuous and big leaf-scars. *Leaves* (2—)3—6-jugate; rachis terete, 4—20(—25) cm, including the 2—10 cm long petiole, up to *c.* 2 mm ø, glabrous to slightly pubescent, usually slightly swollen at the base, often somewhat lenticellate; leaflets ovate to ovate-oblong or elliptic to oblong, often asymmetrical, 2½—15 by 1½—6 cm, index 1½—3(—3½), usually much increasing in size towards the top of the leaf, the base acute or attenuate to rounded, often oblique, the apex acuminate, with entire to closely spinously denticulate margin, chartaceous, usually somewhat shining above, dull and paler beneath, glabrous above, beneath only with small hairy domatia in the axils of the nerves, usually also in the axils of secondary nerves; midrib impressed above, prominent beneath; nerves 5—10 pairs, ascending and looped and joined, flat or slightly impressed above, more or less prominent beneath; venation distinct, reticulate, flat above, prominulous beneath; petiolules 1—5 mm, glabrous. *Panicles* usually precocious, axillary, usually a few crowded together at the end of a twig, also often on short lateral twigs, usually pendulous, dense to rather lax, pyramidal, 5—20 cm, including the ½—5 cm long peduncle, usually profusely branched up to the 3rd or 4th order, branches spreading, somewhat flaccid, more or less canaliculate and angular to flattened, densely pubescent, bearing numerous solitary flowers; main axis more or less lenticellate; primary side-axes few to about 12, up to *c.* 15 cm, not or not very much lenticellate, never subtended by small or reduced leaves; bracts narrowly triangular to lanceolate, up to a few mm, glabrous to puberulous. *Pedicels* (1—)2—4 mm, subglabrous to sparsely puberulous. *Sepals* (3)4, ovate, (sub)equal, 1½—2⅓ mm, the outer one often much smaller, sometimes lowered on the pedicel, sometimes minute or absent; margin flimsy, usually somewhat ciliolate, entire or with some coarse irregular teeth. *Outer petals c.* 1⅔ mm long, 2—3½ mm wide. *Inner petals* ligular, nearly halfway bifid, 1—1½ mm, with acute to rounded, entire, ciliolate lobes. *Stamens:* anther-cells ⅓—⅖ mm ø; filaments 1—1½ mm. *Ovary* ¾—1 mm, glabrous. *Style* 1—1⅔ mm, glabrous. *Fruit* globose, when ripe *c.* 6 mm ø, with thin fleshy mesocarp; endocarp depressed subglobose, broad-ovoid to nearly round at ventral view, 4—6 mm long and wide, 3—4½ mm high, with smooth surface; median keel faint to rather distinct, slightly elevated, blunt, sometimes somewhat sharper, at one end usually forming a rounded prominence; ventral side applanate, with a narrow shallow depression which is filled with a triangular to wedge-shaped plug (fig. II A, B).

Distribution: NE. Upper Burma (Myitkyina, Hpimaw Hill; Ku-lu, 25°15′ N, 98°35′ E); Central China: Szechuan (Shih Chuan Hsien, near Pien Kou; Lungan Fu; Ma-pien Hsien; Cheng Kou Tin; S. Wushan), W. Hupeh (Patung Hsien; Ichang; Hsing-shan Hsien). Probably rare in N. Burma, in China nowhere common, but occurring scattered throughout western Hupeh and Szechuan. America: S. Mexico: Prov. Vera Cruz (Jalapa; San Andres), Prov. Mexico (*sine loco*); possibly also in E. Mexico, reported from Prov. Nuevo Léon (Villa Santiago) by Record & Hess (1943). — Fig. 16.

Ecology: In N. Burma occurring in evergreen broad-leaf oak-forests, at altitudes of about 2100—2400 m. (In Mexico found in the same vegetation type: montane rain-forests with oaks; cf. Knapp, Veget. Nord- u. Mittelamerika (1965) 291, 292.) In Central China restricted to mixed mesophytic forests and forest remnants, generally between 1000 m and 1500 m, but also higher, at *c.* 2000 m. Found in dense to open forests or thickets, along streams or not, often in open country and along roadsides (spared and even planted by local people).

Field notes: The species is said to be one of the handsomest and most striking of Chinese trees; when flowering (mostly before the leaves appear!) the tree is covered with a mass of creamy-white flowers, and forms a striking object in the landscape. The fruit is black.

Vernacular names: China *Ku-ku-lan-shu* (colloquial in Hupeh; *fide* Rehd. & Wils., l.c.), Mexico: *Palo blanco* (Jalapa; see Schlechtend., l.c.), Ayón (*fide* Record & Hess, 1943).

Uses: In China, *M. alba* is commonly associated with temples and wayside shrines. The species has been introduced in W. Europe an N. America by Wilson, in 1907, and is now successfully cultivated in several public and private botanic gardens. It is somewhat less hardy than its relative *M. veitchiorum*. According to Record & Hess (1943) the timber has the consistency and appearance of Soft maple (*Acer rubrum* L.) and is highly esteemed locally for making furniture.

Remarks: The Chinese representatives of this species were described as *M. beaniana*. When studying American species of *Meliosma*, I found to my surprise that the type of *M. alba* from Mexico, described early in the nineteenth century, equals *M. beaniana* even in minute characters. The Mexican and the SE. Asian plants do belong without any doubt to one and the same species; even differences of varietal rank could not be observed. Hence, instead of the epithet *beaniana*, the elder name *alba* should be adopted for the SE. Asian representatives of this species.

Fossil endocarps belonging to *M. alba* have been found in several localities outside SE. Asia; they are discussed in part II chapter C sub 1, followed by a hypothesis concerning the origin of the present disjunct area.

15. **Meliosma veitchiorum** Hemsl., Kew Bull. (1906) 155; Bean, Kew Bull. (1910) 173, photogr. facing p. 175; Schneid., Ill. Handb. Laubholzk. 2 (1912) 1030; Rehd. & Wils. in Sarg., Pl. Wils. 2 (1914) 204; Rehd., J. Arn. Arb. 8 (1927) 165; Man. Cult. Trees & Shrubs (1940) 594; Cufod., Oest. Bot. Z. 88 (1939) 252; How, Acta Phytotax. Sin. 3 (1955) 446; Steward, Man. Vasc. Pl. Low. Yangtze (1958) 235; Vidal, Not. Syst. 16 (1960) 309; Krüssm., Handb. Laubgeh. 2 (1962) 128, t. 57 f. — Type: *Wilson 1046, pro parte* (Szechuan), seen from K.

M. longicalix Lecomte, Bull. Soc. Bot. Fr. 54 (1907) 675. — Syntypes: *Farges 1223* (Szechuan), seen from L, P; *Wilson 1046, pro parte* (Hupeh), seen from A, E, K, W. — **Fig. 34, Photogr. 3.**

Deciduous tree, small to medium-sized, up to *c.* 20 m. *Flowering twigs* terete, 7—15 mm ø, (very) stout, often with extremely short (a few cm) internodes, abruptly terminating in a tuft-like leafy inflorenscence, glabrous, usually with many big conspicuous leaf-scars. *Leaves* (3—)4—5(—6)-jugate; rachis terete, often flattened above, (10—)15—55 cm, including the (3—)5—17 cm long petiole[1]), up to *c.* 5 mm ø, subglabrous to densely pubescent, not swollen at the base, usually somewhat lenticellate towards the base; leaflets elliptic to oblong, sometimes ovate(-oblong), sometimes a bit asymmetrical, 2½—15(—20) by 1½—8(—10) cm, index 1½—3, somewhat increasing in size towards the top of the leaf, the base acute to truncate, sometimes oblique, often slightly attenuate at the very base, the apex acute to acuminate, with entire or sometimes slightly crenulate to coarsely (mucronulate-) serrate (in vegetative parts only!) margin, herbaceous to chartaceous, hardly or not shining, paler beneath than above, glabrous or minutely puberulous on midrib above, beneath (sub)glabrous or with a sparse pubescence mainly on midrib and nerves, always without domatia; midrib nearly flat to impressed above, distinctly prominent beneath; nerves 5—15 pairs, ascending, not or not distinctly looped and joined, flat to somewhat impressed above, flat to somewhat prominent beneath; venation fine, more or less distinct, reticulate, flat above, flat to prominulous beneath; petiolules 1—20

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[1]) According to Hemsley, Kew Bull. (1906) 155, the largest leaves are nearly 1 m long.

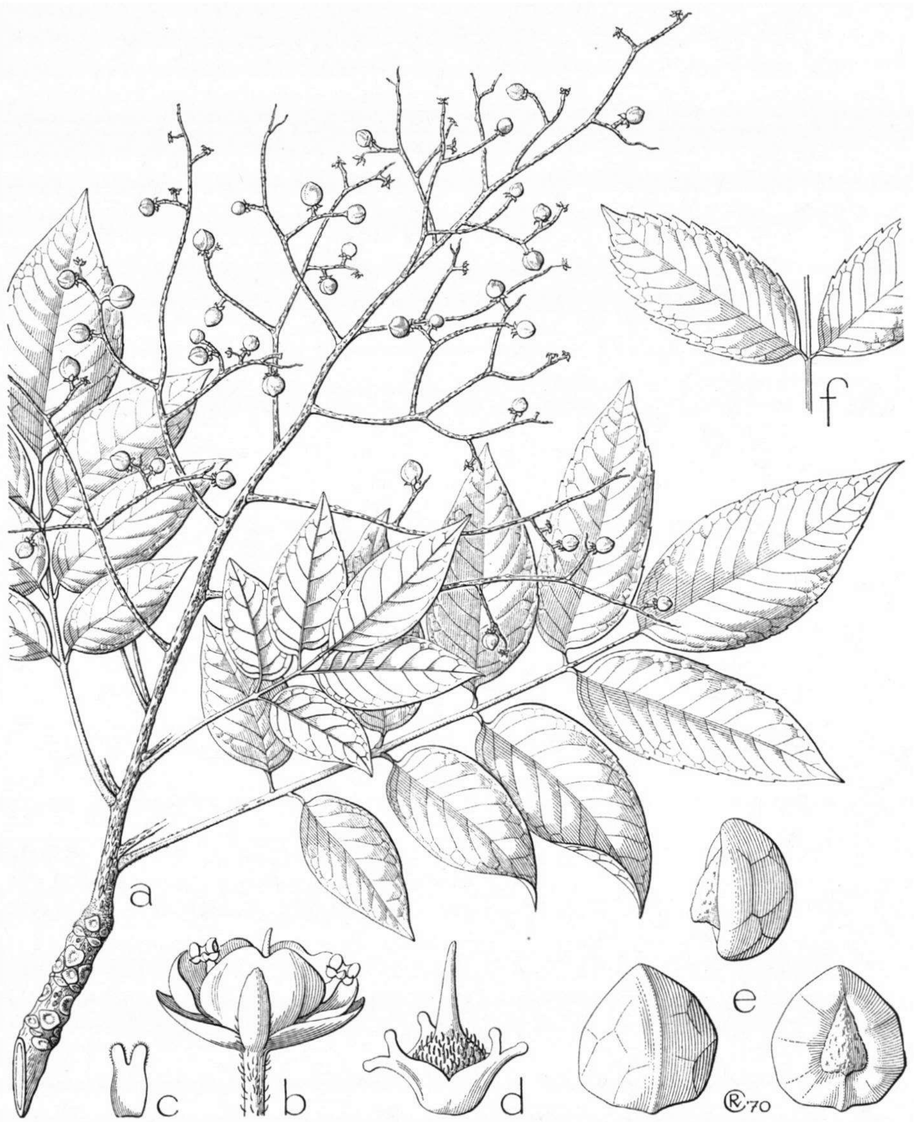

Fig. 34. *M. veitchiorum*. — a. fruiting twig, × ⅓. — b. open flower, × 5. — c. inner petal, × 10. — a. pistil with surrounding disk, × 10. — e. endocarp in different positions, × 3. — f. pair of leaflets from vegetative twig, × ⅓. — a—d from *Wilson 322*, e from *Tsai 57833*, and f from *Hers H 1806*.

mm, glabrous to moderately pubescent. *Panicles* terminal, only one at the end of a twig, erect to more or less pendulous, rather dense to lax, pyramidal, 25—*c.* 60 cm, including the up to a few cm long peduncle, profusely branched up to the 4th (5th) order, branches spreading, often somewhat flaccid, more or less angular or canaliculate to flattened, sparsely to moderately puberulous or somewhat pubescent, bearing numerous solitary flowers; main axis (very) densely lenticellate; primary side-axes standing rather wide apart, about 12—20, up to *c.* 45 cm, sparsely to very densely lenticellate as are often the axes of 2nd and 3rd order, the lower ones always subtended by normal to small or reduced leaves; bracts lanceolate, up to *c.* 2 mm, glabrous, ciliolate at the margin. *Pedicels* ½—6 mm, moderately puberulous/pubescent. *Sepals* (3)4(5), (widely) ovate, the inner ones (sub)equal, 1½—2½ mm, the outer one often much smaller and narrower, rarely minute, rarely lowered on the pedicel, glabrous or somewhat pubescent at the outside; margin flimsy, ciliolate or not, entire or sometimes with some coarse irregular teeth. *Outer petals* 1½—2 mm long, 1½—3½ mm wide. *Inner petals* ligular, up to halfway bifid, *c.* 1 mm, with rounded, entire, ciliolate lobes. *Stamens*: anther-cells ⅓—⅖ mm ø; filaments 1¼—2 mm. *Ovary* (⅔—)1 mm, densely pubescent to puberulous. *Style* ¾—1½ mm, glabrous or with a few hairs near the base. *Fruit* globose, when ripe well over 1 cm ø, with moderately thick, fleshy mesocarp; endocarp semiglobose, cordate to broad-ovoid at ventral view, 6—8½ mm long, 5½—8 mm wide, 3½—5½ mm high, with smooth surface or with a few faint lumps and ribs; median keel distinct, slightly elevated, blunt to rather sharp, at one end more prominent and often forming a blunt beak; ventral side with a more or less wide and distinct depression which is filled with a triangular to wedge-shaped plug.

Distribution: West to East Central China: Yunnan (Wei Se Hsien; Chienchuan; S. Chungtien; Lin Ti Ping Mt.), E. Szechuan (Cheng Kou Ting; S. Wushan), W. Hupeh (Patung Hsien; Fang Hsien; Changyang Hsien; Hsing-shan Hsien), N. Honan (Lushih; Sung Hsien; Tsi Yüan Hsien), S. Anhwei (Hwang Shan). Locally abundant, but in general rare and local. — Fig. 17.

Ecology: In mixed mesophytic forests and forest remnants, generally at 1000—2000 m, in Yunnan collected at 2700 m and 2900 m altitude. Found in dense to open forests and woodlands, along streams or not, also along roadsides, sometimes as a solitary tree evidently spared (or planted ?) by the local people. In N. Honan the tree is said to be always sterile.

Field notes: Tree about of the habit of a walnut-tree (see photogr. 3) with relatively thick trunk and with ascending, very slightly spreading, coarse branches forming a loose pyramidal crown. Bark grey, roughly fissured and with age exfoliating in small irregularly shaped flakes. The stout twigs, covered with very conspicuous leaf-scars and terminating into big, globose, brown buds look in winter like drumsticks. The leaflets are dull to rich shining green above and pale green beneath with red midrib; the rachis is purplish red. The fleshy fruit is black when ripe. In spring, leaves and panicles appear about simultaneously.

Vernacular names: *Ta kao cha shu* (E. Szechuan, once mentioned), *Nan mu* or *Nuan mu* (N. Honan, several times reported), *Hung king yeh* ? (N. Honan, once mentioned).

Uses: This interesting beautiful tree has been introduced in W. Europa and N. America in 1900, where it is successfully cultivated in the open (amongst others in Kew Botanic Gardens). It is quite hardy, but it grows very slowly.

Remarks. Finds of fossil endocarps of this species, and a discussion on its former distribution, are found in part II, chapter B and C.

EXCLUDED AND DUBIOUS SPECIES

[*Meliosma anacardioides* Blenk, Flora 67 (1884) 370, *nomen.*] — This name is cited in an enumeration of *Meliosma* species having leaves with pellucid dots; it is probably copied from a label on a sheet. The specimen could not be traced.

Meliosma ? cavaleriei Lévl. in Fedde, Rep. 9 (1911) 457; cf. Lauener, Not. R. Bot. Gard. Edinb. 27 (1967) 283, 290. — Type: *Cavalerie 1027* (Kweichow), not seen. — Lauener, l.c., has identified this specimen as *Ampelopsis chaffanjonii* (Lévl.) Rehd. (*Vitaceae*).

[*Meliosma celebica* Warb. *ex* Dihm, Beih. Bot. Centralbl. 21, 1 (1907) 125, *nomen.*] — Type: *Warburg 15416* (Celebes: Bojong) — I have not seen the type specimen which probably got lost during the war.

Meliosma laurina Bl., Rumphia 3 (1849) 198; Walp., Ann. 2 (1852) 224; Miq., Fl. Ind. Bat. 1, 2 (1859) 614; Illustr. (1871) 73; Merr., En. Born. (1921) 363; Hallier *f.*, Beih. Bot. Centralbl. 39, 2 (1921) 161; Kosterm., Bibl. Laur. 1 (1964) 951. — Type: *S. Müller s.n.* (Borneo: G. Sakumbang), seen from L (holo), U. — As was noted by Hallier *f.*, l.c., the type specimens consist of a mixture, viz. inflorescences of *M. sumatrana* and leaves of *Cryptocarya reticulata* Bl. (*Lauraceae*).

[*Meliosma maculata* Lecomte *ex* Le Renard, Morot J. Bot. 2, 1 (1908) 308, *nomen.*] — This name, probably copied from a label, was used for a specimen from China (Szechuan) of which the anatomy of the petiole was described; I could not identify it on these data.

Meliosma petiolaris Miq., Sum. (1860) 519, 203; Illustr. (1871) 73, *in obs.* — Type: *Junghuhn s.n.* (Sumatra: Angkola), seen from L. — This species was later referred by Miquel himself to *Xylosma leprosipes* Clos which is now known as *Bennettiodendron leprosipes* (Clos) Merr. (*Flacourtiaceae*).

[*Meliosma timorensis* Bl. *ex* Blenk, Flora 67 (1884) 370, *nomen.*] — See above, under *M. anacardioides.*

Pimela angustifolia Bl., Mus. Bot. 1 (1850) 226. — *Canariopsis angustifolia* Bl. *ex* Miq., Fl. Ind. Bat. 1, 2 (1859) 653. — *Canarium angustifolium* Miq., Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 117; H. J. Lam, Bull. Jard. Bot. Btzg III, 12 (1932) 179, t. 11 f. 71d, sub *C. rigidum* Zipp.; Leenh., Fl. Mal. I, 5 (1956) 296. — Type: *? Zippel s.n.* (? New Guinea), seen from L. — The material under this name was excluded from the *Burseraceae* by Leenhouts, l.c., and tentatively assigned to *Meliosma.* This may be correct, and it should then be placed close to *M. lanceolata* and *M. hirsuta.* At first sight, it is very similar to the latter species, but there are important differences in nervation and pubescence. If it belongs to *Meliosma* it would certainly be a new species, but I refrain from including it because I am not sure about its identity; unfortunately, the specimens consist of young leaves only, with many characteristic narrow leaflets, but in absence of woody parts it cannot be identified with certainty. Moreover, on the original labels as the place of origin is mentioned 'Nov. Guinea', in Blume's handwriting. However, this would not fit in the distribution pattern of *Meliosma,* since species of this kind only occur in western Malesia; if New Guinea indeed is the correct locality, '*Canarium angustifolium*' can hardly belong to *Meliosma.* Its identity will probably remain uncertain until more satisfactory material has been found.

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