SYSTEMATICS AND EVOLUTION OF XANTHOPHYLLUM

(*Polygalaceae*)

BY

R. VAN DER MEIJDEN

E. J. BRILL / LEIDEN UNIVERSITY PRESS
LEIDEN 1982

This book can be cited as:

MEIJDEN, R. VAN DER. 1982. Systematics and evolution of Xanthophyllum (Polygalaceae). E. J. Brill/Leiden University Press (Leiden Botanical Series, vol. 7). 159 pp., 22 figs.

In the Leiden Botanical Series will be published papers of a monographic nature from the entire field of botany (including its history, bibliography, and biography) which by their length (100 printed pages or more) are unsuitable for publication in journals. Information can be obtained from the editors, Rijksherbarium, Schelpenkade 6, Leiden, The Netherlands.

World distributor for publications of the Universitaire Pers, Leiden: E. J. Brill, Postbus 9000, 2300 PA Leiden, The Netherlands.

ISBN 90 04 06594 6

PRINTED IN THE NETHERLANDS

CONTENTS

Summary vi
Introduction vii
Acknowledgements vii

GENERAL PART

1. Notes on morphology and discussion on evolution of characters 1
1.1. Growth of twigs 1
1.2. Phyllotaxis 2
1.3. Stipules or pseudostipules; nodal and foliar glands 2
1.4. Axillary buds 4
1.5. Venation 5
1.6. Idioblasts 7
1.7. Inflorescence 7
1.8. Ontogeny of the flower 8
1.8.1. Initial development 8
1.8.2. Retardation of median abaxial petal 12
1.9. Full-grown flowers 12
1.9.1. Petals 12
1.9.2. Stamens 14
1.9.3. Anthers 14
1.10. Remarks on flower biology 15
1.11. Ovary 16
1.12. Stigma 20
1.13. Fruit 20
1.14. Seed 21
1.14.1. Testa 21
1.14.2. Development of embryo 23
1.14.3. Morphology of embryo 26
1.15. Seedlings 28
1.16. Literature 29
2. Phylogeny of *Xanthophyllum* 30
2.1. Affinities of the *Polygalaceae* with other families 30
2.2. Position of *Xanthophyllum* in the *Polygalaceae* 32
2.3. Phylogenetic relation of *Xanthophyllum* groups 32
2.3.1. The problem of *Xanthophyllum fragrans*: an old allopolyploid species? 35
2.3.2. The position of *Xanthophyllum ramiflorum*: another allopolyploid species? 36
2.4. Evolution at species level 37
2.5. Reflections 37
2.6. Literature 37
3. Classification 38
4. Habitat, distribution, dispersal, plant-geography 41
4.1. Habitat 41
4.2. Distribution 41
4.3. Dispersal 44
4.4. Discussion: migration from the East 44
4.5. Literature 46

SPECIAL PART

Notes on the key and the descriptions 47
Key to the species 51
Xanthophyllum 60
Index to taxonomic names 157

SUMMARY

The present work comprises the first revision of all species of *Xanthophyllum*; 93 species (22 new) have been distinguished with 5 subspecies (1 new) and 2 varieties (both new). Seven subgenera are proposed (4 new) of which one has been divided into 2 sections and 2 subsections. Keys to all taxa have been included. In the General Part the (sub)generic and (sub)sectional characters are discussed separately in order to find arguments regarding the direction of the evolution of those characters in the 'Hennigian' way of reasoning. From this it has been concluded that the Polygalaceae are derived from the *Malpighiaceae-Vochysiaceae-Trigoniaceae*-complex, and secondly that *Xanthophyllum* belongs to a *derived* tribe of the *Polygalaceae* (and not to a separate family *Xanthophyllaceae*). The lack of information on the genomes of the species appeared to be a serious problem in the reconstruction of the evolution within *Xanthophyllum:* one subgenus with 'gigas'-characters may represent an old allopolyploid hybrid; it is suggested that hybridization may have been important in the evolution of the genus. Although only two species, endemic to N. Queensland, do not occur in Malesia-Southeast Asia, it is shown that Australia must have been the centre of origin of the genus. The fact that Wallace's Line is still respected by all species is regarded as an indication that West Malesia is a secondary centre of speciation.

INTRODUCTION

The genus *Xanthophyllum* was the last one to be done for the revision of the *Polygalaceae* for *Flora Malesiana*. Because it had never been revised before, covered only a restricted area, and would probably comprise a number of undescribed species, the non-Malesian species were included. The number of undescribed species appeared to be greater than expected: I described 37 new species (of which 22 in the present paper), being 40 % of the total number of accepted species. The major reason for the high number of new species is the fact that many (17) have been discovered only after (1957–)1961. Also the superficial similarity of the collections must have played a role, as well as the fact that the species are economically of no known use.

After succeeding in combining the flowering with the fruiting collections, it became apparent that the genus comprised a number of rather well-defined infrageneric groups. The renewed interest in methods for the reconstruction of evolution induced me to try the 'Hennigian' method (hitherto mainly used in systematics of animal groups) on a group of flowering plants, also in the hope of helping to bring back the discussion to the practical work.

Characters of the wood will be described in a separate paper (Peletier-Bridgwater & Baas, 1982). Pollen morphologically *Xanthophyllum* differs hardly from other *Polygalaceae*. A survey of the pollen morphology will be published separately.

ACKNOWLEDGEMENTS

This study could not have been made without the generosity of the following herbaria, which kindly put their collections (c. 14,000 sheets) at my disposal: Ann Arbor (AFS), Berkeley (UC), Bogor (BO), Brisbane (BRI), Bruxelles (BR), Cambridge, Mass. (A), Copenhagen (C), Edinburgh (E), Firenze (FI), Genève (G), Kepong (KEP), Kew (K), Kuching (SAR), Kyoto (KYO), Leiden (L), London (BM), Melbourne (MEL), München (M), New York (NY), Paris (P), Sandakan (SAN), Singapore (SING), Utrecht (U), Wageningen (WAG), Wien (W), Wroclaw (WRSL), Zürich (Z). I am much indebted to Dr. R.C. Bakhuizen van den Brink for rendering the diagnoses in Latin. I want to express my thanks to Dr. F.S.P. Ng (Forest Research Institute, Kepong, Malaya) for the stimulating correspondence.

GENERAL PART

1. Notes on morphology and discussion on evolution of characters

In *Xanthophyllum* I distinguish eight groups of species which I think to be monophyletic. These groups are:

group 1 (subgenus 5. *Brunophyllum*, 5 species)
group 2 (subgenus 7. *Macintyria*, 1 species)
group 3 (subgenus 6. *Grandiflorum*, 1 species)
group 4 (subgenus 3. *Triadelphum*, 5 species)
group 5 (subgenus 2. *Coriaceum*, 1 species)
group 6 (subgenus 4. *Exsertum*, 3 species)
group 7 (subgenus 1. *Xanthophyllum*, section 1. *Xanthophyllum*, 16 species)
group 8 (subgenus 1. *Xanthophyllum*, section 2. *Eystathes*, 61 species)

Sometimes I will refer to the subsections: *group 8a* (subsection *Jakkia*; 47 species), *group 8b* (subsection *Eystathes*; 14 species), or to groups of species within subsection *Jakkia*.

In this chapter I will try to compare the subgenera and sections in their separate characters, and often also to compare these characters with those of other genera of the family. For brevity I will avoid the terms 'subgenus' and '(sub)section' in this chapter, as well as the names of those taxa; they will be referred to by the word 'group' and their group-number as indicated above. (The group-numbers have no (hidden) meaning at all. Not wanting to give more weight to the chosen linear sequence of the subgenera, I gave each group a number which differs from that in the linear sequence.) The aim of the discussions is to find for each character arguments to make hypotheses on the transformation-series of that character for the eight groups, i.e., to find arguments for the phylogenetic relations between these groups. I will use for practical reasons some of the terminology of Hennig (1966); this is based on a Darwinistic view on evolution. In that terminology the change of a character in a monophyletic group of organisms is called a *transformation*. The character-state from which a transformation *starts* is called **plesiomorphous**, the derived character-state of such a transformation is called **apomorphous**. These concepts are more or less synonymous to the words 'primitive', resp. 'derived', but those words are ambiguous at least in (botanical) literature. It will appear that quite often these concepts cannot be applied because of lack of evidence or of knowledge of the specific character.

1.1. Growth of twigs

The twigs of all species elongate in flushes. In each twig of a growing period the terminal bud becomes aborted and one of the axillary buds of the nearest leaf will produce the new shoot after a resting period. The internode with the aborted terminal bud at its end usually grows further for a short period; later, when the next shoot has developed, the aborted terminal bud of the former season is visible at the end of a short, slender part of last season's twig pressed against the basal part of the new twig. Very rarely the terminal bud produces a new shoot in addition to the one developed in the axil of the upper leaf (seen once), or forms an inflorescence (seen a few times in different species).

Discussion – Sympodial growth has not been reported for any other genus of the *Polygalaceae*, nor is it known to me from related families. Also considering the way in which the sympodial structure arises, I am convinced that it is a synapomorphous character of all groups of *Xanthophyllum*.

1.2. Phyllotaxis

One of the difficulties met with when examining the phyllotaxis in *Xanthophyllum* is the fact that the shoots so often produce only a few leaves, a fact already noted by Raciborski (1900, p. 53); he mentions for *36. X. vitellinum* (3 or) 4 or 5 as the normal number of leaves of a shoot. In *25 X. tardicrescens* I noted that each shoot bears only 1 or 2 (or 3) leaves! At first sight such shoots look much longer, because the successive (sympodial) shoots usually form a continuous line and the older shoots still bear their leaves, possibly at least for four growing periods. Not having been able to examine living branches of *Xanthophyllum* species I cannot give a complete picture of the phyllotaxis in the genus.

Especially in species of the *vitellinum*-group (group 8a) I found that there is a certain regularity in the length of the internodes of a shoot: a long internode is followed by a shorter internode, alternate with a longer one; at the end of a shoot the last two leaves are often placed opposite or nearly so. I came to the conclusion that the leaves are placed in four rows, and can be regarded to be decussate, with the leaves of each pair shifted; the same can be observed in the lower parts of the inflorescences. The shifted-decussate phyllotaxis seems to be confined to part of the species of group 8a; further I only observed it in a seedling of *88. X. obscurum* (group 1); in that seedling the scale leaves are also decussate at base, the opposite pairs soon becoming shifted.

Discussion – No other author seems to have noted that peculiar arrangement of the leaves in certain species of *Xanthophyllum*. In literature, *Xanthophyllum* species are reported to have alternate leaves. Only Ng (1975, p. 89) describes a seedling (also of *88. X. obscurum*, but another specimen than the one I mentioned above) as having spiral leaves. I have no arguments to doubt records of alternate or spiral leaves. Indeed, the phyllotaxis of most collections of herbarium material seems to be 'normally' alternate. In view of my own observations that shifted-decussate leaves occur in some species, and of the difficulties caused by the shortness of the sympodial shoots, the phyllotaxis of *Xanthophyllum* species still remains incompletely known.

The shifted-decussate phyllotaxis is not confined to (a part of) the genus *Xanthophyllum*; I also observed it in collections of *Bredemeyera floribunda* (tribe *Polygaleae*). Due to the incompleteness of the data on phyllotaxis in the family the character cannot be used for phylogenetic reasoning.

1.3. Stipules or pseudostipules; nodal and foliar glands

In *Xanthophyllum* 'glands' are found: a) on the lower side of the leaf blade (all species), b) on the petiole (minority of species), c) on the sepals (many species), d) on the bracts (some species), e) on the nodes of the twigs (groups 1, 3, 4, 5, part of species of group 8b, uncertain in group 6), and f) on the nodes of the inflorescence axis (same groups as under e), and part of group 7). In *Xanthophyllum* the glands are circular, usually with a slightly

Table 1. Glands in the *Polygalaceae*.

glands / taxa	nodal		laminar	type
	on twigs	on inflorescence		
Xanthophyllum				A
group 1	×	×	× 4)	
2	–	–	×	
3	(×) 2)	–	× 4)	
4	×	×	× 4)	
5	×	×	× 4)	
6	uncertain	uncertain	× 4)	
7	–	×,– 3)	×	
8	– 1)	– 1)	×	
Moutabeae	×,–	×	×	B
Polygaleae	×,–	×,–	–	B

Interpretation: × plesiomorphous; – apomorphous

Notes:
1) In group 8b about half of the species have a pair of minute (0.1–0.2 mm long), bluntly conical nodal appendages; their structure is unlike type A or B, and different from the laminar glands of those species.
2) In group 3 nodal glands are scarce, usually only a single one is present on each twig.
3) In group 7 constantly present in species 1–5, absent in the other species; in the latter, glands are usually present on the bracts.
4) Glands on petioles have not been observed.

elevated margin. An exception is formed by the nodal glands of group 8b (see Table 1, note 1).

Nodal and foliar glands of a different type occur also in the tribe *Moutabeae*; nodal glands are absent only in *Barnhardtia*, foliar glands are present in all genera, including *Eriandra* (the latter contrary to Van Royen & Van Steenis, 1952). In the *Moutabeae* the glands are shortly conical, with a small pit at the top.

In the tribe *Polygaleae* foliar glands have not been reported; nodal glands have been found in *Securidaca, Polygala* (minority of species), *Atroxima, Carpolobia*, and *Monnina*. In those genera their form varies from crateriform to conical-truncate, sometimes thorn-like in some *Polygala* species.

Structure, function, and development of the glands are unknown. Recent anatomical studies (Dickison, 1973; Styer, 1977) did not reveal much on this subject.

Discussion – a) Homology of nodal and foliar glands

The question whether nodal glands are homologous to stipules, or homologous to laminar or petiolar glands, is very complex, as can be deduced from the situation in the *Vochysiaceae* (compare Stafleu, 1953, p. 146–148, and his fig. 2). In that family stipules are usually present, like in the related families *Trigoniaceae* and *Malpighiaceae*. Absence or

reduction of the stipules is considered to be 'a further specialization' (Stafleu, 1952, p. 225) in *Callisthene*. In *Qualea* 'diametrically opposed specializations' occur: stipules may be normal, or be 'transformed', or be 'represented by glands'; or 'axillary glands' are present on the nodes next to normal stipules; the axillary glands may grow out to form 'true extrafloral nectaries'. In *Qualea cordata* the specimens I studied had 'stipular glands' as well as differently formed 'axillary glands', which sometimes had grown out to form 'extrafloral nectaries'. From a comparison of the form of the nodal glands in the *Polygalaceae* with those of *Qualea*, it seems probable to me that the nodal glands as observed in *Securidaca, Polygala, Carpolobia,* and *Atroxima* are homologous to the axillary glands and extrafloral nectaries of *Qualea* (not homologous to stipules). In the *Moutabeae* similarly formed glands are also found at the apical part of the petioles, and at the basal part of the leaf blades along the margins; probably those glands, too, are not homologous to stipules. In *Xanthophyllum* group 8b the 'nodal appendages' may be homologous to 'true' or 'transformed' stipules; the nodal glands of some other groups of *Xanthophyllum* are probably homologous to laminar glands. As far as the nodal structures are concerned, Weberling (1974) arrived to the same conclusions (the nodal appendages of *Xanthophyllum* group 8b escaped his attention).

An additional argument that nodal glands in the *Polygalaceae* are homologous to laminar glands follows from observations in *Xanthophyllum* group 7. In some species of that group nodal glands occur on the inflorescence axes (not on the vegetative nodes!); in other species such glands are absent, but there similar glands occur on the (sub)persistent bracts. (Only in *3. X. sulphureum* the nodal glands differ markedly from the laminar glands.) The fact that obviously closely related species may have either nodal or bract glands may also indicate that those structures are homologous.

b) Phylogenetic interpretation

Stipules (or homologous structures) are present in the related families *Trigoniaceae, Vochysiaceae,* and *Malpighiaceae*. The absence of stipules is thus clearly a synapomorphous character of the three tribes of the *Polygalaceae*. The presence of 'nodal appendages' in *Xanthophyllum* group 8b is then probably caused by regression, to be interpreted, however, as an autapomorphous condition of group 8b.

Laminar glands are present in all the representatives of the *Malpighiaceae* I examined, as well as in *Trigoniastrum (Trigoniaceae)*; I found no laminar glands in *Trigonia (Trigoniaceae)*, nor in representatives of the *Vochysiaceae*. Because in the latter family homologous structures ('axillary glands', etc.) are found, which also occur in the *Polygalaceae*, I assume that the presence of laminar, and of nodal glands are both plesiomorphous character-states in the *Polygalaceae*. The apomorphous character-states ('absence') must then have been developed parallel in the three tribes.

Without a better knowledge of the development of the glands, I cannot interprete the difference in the form of the glands between *Xanthophyllum* and *Polygaleae-Moutabeae*.

1.4. Axillary buds

In *Xanthophyllum* there are at least two axillary buds per leaf axil, the upper one generative, the lower one, which is often very indistinct, vegetative. Both buds are usually close together in the leaf axil. The buds consist of two equal scales which cover the vegetation

point; the scales are usually c. 0.5 mm long, often slightly hairy; the scales of the generative bud are often deciduous during development of the inflorescence, those of the vegetative bud may remain attached to the base of the developing twig. Such is the situation in the groups 1–6 and in the great majority of the species of group 7; in the latter group the upper bud is occasionally supra-axillary. In group 8 an unusually large variation is found in the axillary buds. In group 8b most leaf axils have three or more axillary buds; in some species these buds are close together, but in other species they are well-separated. In *75. X. virens* the leaf axils may have up to seven buds in row, the upper one up to 20 mm above some look longer because the buds are placed on stalk-like outgrowths of the twig, like in *74. X. lateriflorum* (where the scales occasionally reach the length of 2.5 mm). Also in other subgroups of group 8 species have sometimes more than two axillary buds in the leaf axils, usually not more than three (or four). In one third of the number of species of group 8 the scales of the upper axillary buds are constantly, or at least mostly, longer than 3 mm. The form and size of the scales, and their direction in space, are often very specific. One of the extremes found in the development of the axillary bud is represented by *45 X. bracteatum* (Fig. 15), with its usually elliptic, up to 30 mm long scales. Peculiar, too, is the clove-like form of the buds of *42. X. clovis*, or the distinctly supra-axillary ovate bud of *47. X. korthalsianum*, or the erect bud of *43. X. reflexum*, which is closely pressed to the twig. The latter four species are probably closely allied, but large axillary buds are also constant for the *beccarianum*-group.

Discussion – Serial axillary buds occur in all tribes of the *Polygalaceae* and also in the *Trigoniaceae*; usually they are inconspicuous. Only in group 8 of *Xanthophyllum* they are present in various apomorphous conditions.

1.5. Venation

In *Xanthophyllum* three types of venation can be distinguished. The coarsely reticulate venation type (Fig. 10B) is characteristic for all species of groups 1–6. The scalariform venation type is confined to the species of group 7 (Fig. 10C). The finely reticulate venation type is found in group 8 (Fig. 10A). Not a single species showed intermediate venation types, nor a type of venation characteristic for another group. The difference is so clear that I decided to use it as the primary character for the identification key to the species.

I made the following observations on the venation in other genera of the family and in related families. The venation of the leaves of *Carpolobia (Polygaleae), Diclidanthera (Moutabeae), Trigonia* and *Trigoniastrum (Trigoniaceae)*, and of the *Malpighiaceae* genera *Mascagnia, Microsteira, Peixotoa,* and *Tetrapteris* seemed to be comparable with the 'coarsely reticulate' venation type of *Xanthophyllum*. The venation of the leaves of *Qualea* (depicted wrongly in Stafleu, 1953) and of *Vochysia* resembled the 'finely reticulate' venation type of *Xanthophyllum* group 8. The scalariform venation type was not observed. As the coarsely reticulate type is found in two of the three related families, and occurs in representatives of the other tribes in the *Polygalaceae*, it seems probable to me that it represents the plesiomorphous character-state in the *Polygalaceae* (and in *Xanthophyllum*).

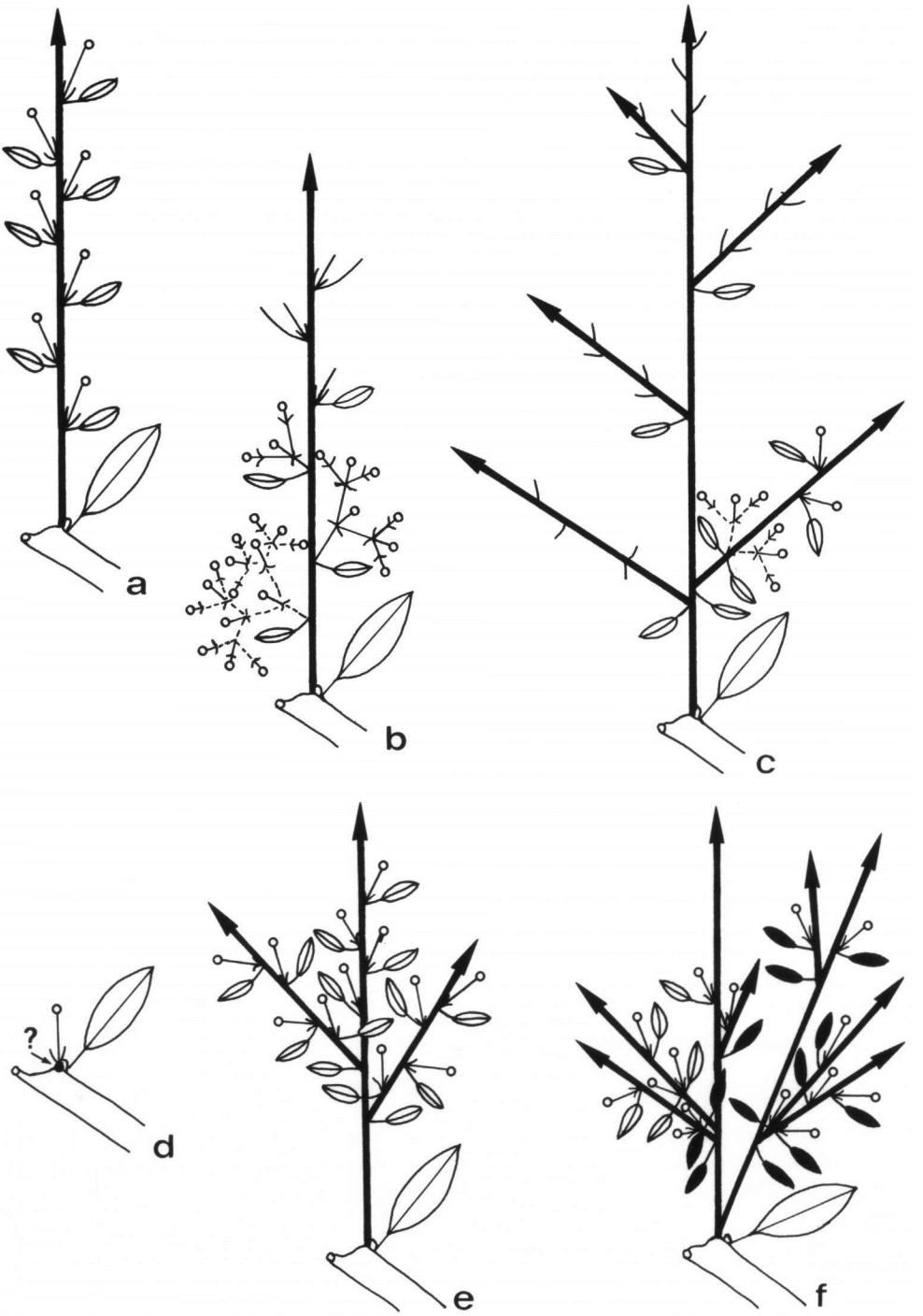


Fig. 1. Inflorescence types; for explanation see the text.

1.6. Idioblasts

The finest vein branches in *Xanthophyllum* leaves end in remarkable, large cells with spiral thickenings (Dickison, 1973). These cells, in Dickison's terminology 'tracheoidal idioblasts', are characteristic for all *Xanthophyllum* species (also present in *60b. X. eurhynchum* subsp. *maingayi*, in which Dickison, *l.c.*, p. 111, could not find them). In *Moutabea, Diclidanthera*, and *Barnhardtia* such cells or at least cells that are probably homologous to the *Xanthophyllum*-idioblasts are reported by Styer (1977); he did not mention them for *Eriandra*. Unfortunately Styer neglected Dickison's publication.

In the tribe *Polygaleae* possibly homologous structures occur in *Badiera* and *Polygala* (Solereder, 1899, p. 110). Rao & Mody (1961) report 'prominent tracheoid idioblasts' in two species of *Vochysia (Vochysiaceae)*. Possibly homologous cells are reported by Solereder (1899, p. 115) for *Trigoniastrum (Trigoniaceae)*.

Discussion – The present state of knowledge on the 'idioblasts' is incomplete, especially because no author performed a study in which those, and similar structures, have been compared beyond the boundaries of tribes and families. It is not unlikely that the presence of the idioblasts mentioned can be regarded as a plesiomorphous character-state in the *Polygalaceae*.

1.7. Inflorescence

In *Xanthophyllum* the inflorescences are situated axillary and subapically, very rarely terminally too; sometimes they are also present on, or confined to the older, leafless nodes. The inflorescence can be thought as to exist out of two separate branching systems. One is the (racemose) system of main and side axes (in Fig. 1 the bold lines), the second is the (cymose) system, present in the axils of the (primary) bracts of main and side axis. The racemose system gives a repetition of the branching system of the vegetative parts (with alternate or shifted-decussate branches and bracts; sometimes with serially arranged side axes). The sequence of flowering is from base to apex; the length of the axis is indeterminate.

The cymose nature of the second branching system is not directly visible. In most *Xanthophyllum* species and in the great majority of *Polygalaceae* genera the flowers seem to be arranged like in a normal raceme, e.g. solitary in the axil of a bract; remarkable is only the presence of two 'bracteoles' at the base of the pedicel of each flower. In a number of *Xanthophyllum* species, as well as in *Barnhardtia (Moutabeae)* and in the American species of *Bredemeyera (Polygaleae)* the primary bracts may contain more than one flower (each flower with two 'bracteoles'). A closer analysis of these partial inflorescences demonstrates that they represent dichasial inflorescences in which, however, *all axes have been reduced completely*; only the pedicels of the flowers and the 'bracteoles' (which are thus bracts of second or higher order) are present. The number of flowers per partial inflorescence is the highest in the basal part of the main inflorescence axes, in the apical part the partial inflorescences are generally 1-flowered. In *Barnhardtia, Bredemeyera*, and in most species of *Xanthophyllum* the partial inflorescences are up to 3-flowered. In some *Xanthophyllum* species (from group 7 and 8) the partial inflorescences are up to 11-flowered, in *Xanthophyllum* group 2 they may consist of c. 30 flowers. Because also in the latter situation each flower seems to have two small bracts at the base of its pedicel, the absence of dichasial

axes makes the analysis of these multi-flowered condensed partial inflorescence difficult.

Combinations of various states of the racemose and the cymose branching systems in *Xanthophyllum* have been depicted in Fig. 1. Fig. 1a gives the situation as present in the groups 1, 3, 4, 5, 6, part of group 7, and part of group 8. Fig. 1b gives the scheme of the inflorescence in group 2. Fig. 1c, 1e, and 1f give inflorescence types as present in several species of groups 7 and 8. Fig. 1d gives the reduced inflorescence of *26. X. parvifolium*, in which the inflorescence produces only a single flower, and the twigs only a single inflorescence. That situation may be seen as an extreme reduction; inflorescences of the type of Fig. 1a, but with a very limited number of flowers occur in species 23–25.

Except for *Barnhardtia* and *Bredemeyera*, the genera of other *Polygalaceae* are of the type depicted in Fig. 1a; sometimes the main axis of the inflorescence may be seemingly branched because of concaulescence of serial axillary inflorescences. In related families (*Trigoniaceae, Vochysiaceae, Malpighiaceae*) the (racemose) inflorescence axes are mostly branched, the partial (cymose) inflorescences are always stalked, more-flowered.

Discussion – The question whether the branched or the unbranched inflorescence type can be regarded as the plesiomorphous character-state in *Xanthophyllum* must remain unanswered. Within the *Polygalaceae* it seems probable that the unbranched inflorescence represents the plesiomorphous character-state. The inflorescence in the related families, however, is usually branched, pointing to the reverse direction. Anyway, which one of the possibilities is plesiomorphous, it must be assumed that the apomorphous conditions have independently developed in the different tribes; reversions in the evolution can then hardly be detected.

However, the complete reduction of the axes of the partial inflorescences, characteristic for all *Polygalaceae*, is a peculiar, but clearly autapomorphous character of the family.

1.8. Ontogeny of the flower

1.8.1. Initial development

The orientation of the sepals is constant for all species and quincuncial. The orientation of the petals, however, seemed irregular at first; also the situation that *Xanthophyllum* flowers, 5-merous in sepals and petals, have (usually) only eight stamens is abnormal. I want to acknowledge here the great help of two of my colleagues. Dr. W. van Heel skillfully made the preparations and the photographs of the very young flower buds. Dr. W. Vink provided me with a kind of reasoning by which it became possible to understand a little more of this complex matter.

Fig. 2a shows the very young floral apex of *8. X. affine* (group 7) with the sepals removed. The slightly asymmetric pentagonal floral apex is nearly flat. The primordium of petal 1 (carina) has separated completely from the floral apex, petal 2 is beginning to separate; petals 3, 4, and 5 are not yet separated. Thus petal 1 has been initiated earlier than petal 2, and petal 2 earlier than petals 3–5. It also means that petal 1 must be situated at the greatest distance from the activity centre of the floral apex (which in this kind of a flat floral apex nearly coincides with the topographical centre of it) (Vink, 1970, pp. 267 *seq.*, especially p. 268). Assuming that, also in the case of *Xanthophyllum*, a primordium of a flower part is initiated at the point farthest from the activity centre of the floral apex, it is

possible to make a theoretical construction drawing of the flower, starting from an arrangement of the flower parts as shown in Fig. 2a. The construction drawing has been made on the basis of the following conditions: 1) floral apex flat, 2) sepals arranged exactly in a 2/5 spiral, 3) first sepal half as thick as the radius of the floral apex. With those conditions, which all fit the situation found in *X. affine* flowers, it was possible to make Fig. 2e. In the pentagonal figure enclosed by the sepals, the greatest distance from the centre of the floral apex is at position p1: at that place the first petal will be formed. The next position is p2, and so on. With the petals formed, the outer stamens will be initiated: first the stamens at the greatest distance from the centre: at positions 1 and 2, then at 3 and 4. For an unknown reason not one but two stamens are formed adaxially* before petal 3 and 4 at positions 5 and 6 (see below). Stamens 7 and 8 follow later. Now only a limited space in the very centre of the floral apex is available for the two median carpels a and b.

It should be noted that the staminal position at the abaxial* side cannot be filled in the construction drawing simply because there is no room for a stamen. In Fig. 2c it is clearly visible, moreover, that petal 1 has a retarded development in comparison to the neighbouring petals 2 and 5. Stamens 3 and 4 are thus forced towards the median plane through the unequal enlargement of the adjoining petals, further limiting the space for the expected abaxial* median stamen.

The arrangement nicely explains the differences in insertion of the stamens in relation to the sepals and the petals. There is one important deviation from the hypothesis of initiation at the most distant location available: the stamen position alternating with petals 3 and 4 is not used (see Fig. 2b) and instead two positions slightly higher are used. Remarkably enough, the initial development of the floral apex of *Polygala speciosa* (Payer, 1857, pp. 139–144, t. 31 fig. 1–9) is exactly like the one in *Xanthophyllum affine*: in *Polygala speciosa*, too, the median adaxial* staminal position is not filled (see also chapter 1.8.2). In *Polygalaceae* this unused position is never filled and stamens are never connate over this position. This means a structural change, basal to the family as a whole.

In *Xanthophyllum* the number of stamens is 8 for *all* species; in only three species the number varies: in *75. X. virens* some collections have 7 stamens (1 instead of 2 before the carina); in *89. X. papuanum* some collections have 9 stamens (3 instead of 2 before the carina), and in *90. X. ecarinatum*, in which the number varies between 7 and 10 (according to literature and labels; I only saw flowers with 8 or occasionally with 9 stamens).

Discussion – I have not seen comparable studies of a floral apex from a representative of the tribe *Moutabeae*. *Xanthophyllum* and *Polygala* flowers are very different in full-grown state. However, because even *Xanthophyllum* and *Polygala* flowers are very similar in early stages, it is probable that the initial development of the flowers of *all* members of the *Polygalaceae* is similar. The absence of the median adaxial stamen is then to be regarded as an *aut*apomorphous character of the family!

This also means that the presence of 8 stamens is a plesiomorphous character *within* the family; deviating numbers are thus apomorphous, which in this case holds for an increasing number (of 9 or 10, in *Eriandra*, *Diclidanthera*, and some specimens of *Xanthophyllum* species), and also for a reduced number (5 or 4, in *Salomonia*, *Carpolobia*, and *Atroxima*); see further the discussion in chapter 1.9.1.

* Adaxial and abaxial in reference to the inflorescence axis, not to the flower axis.

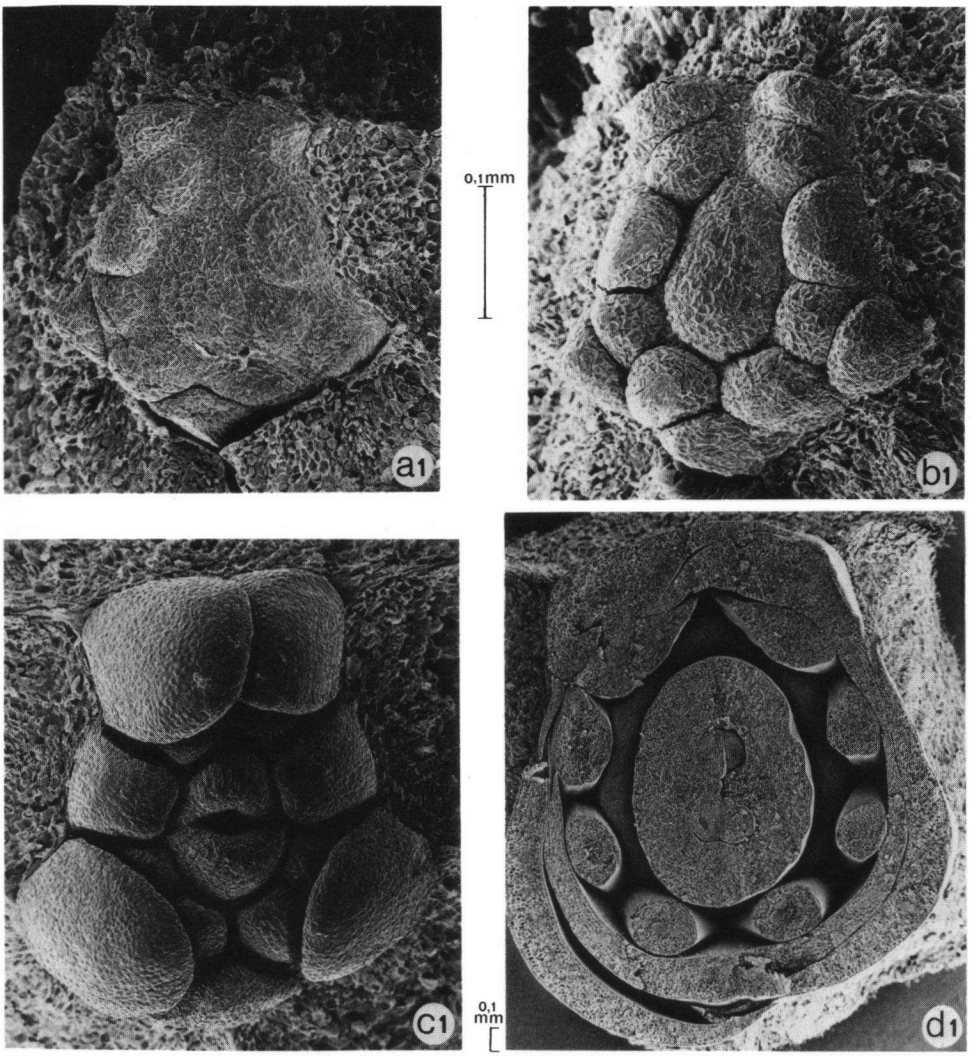
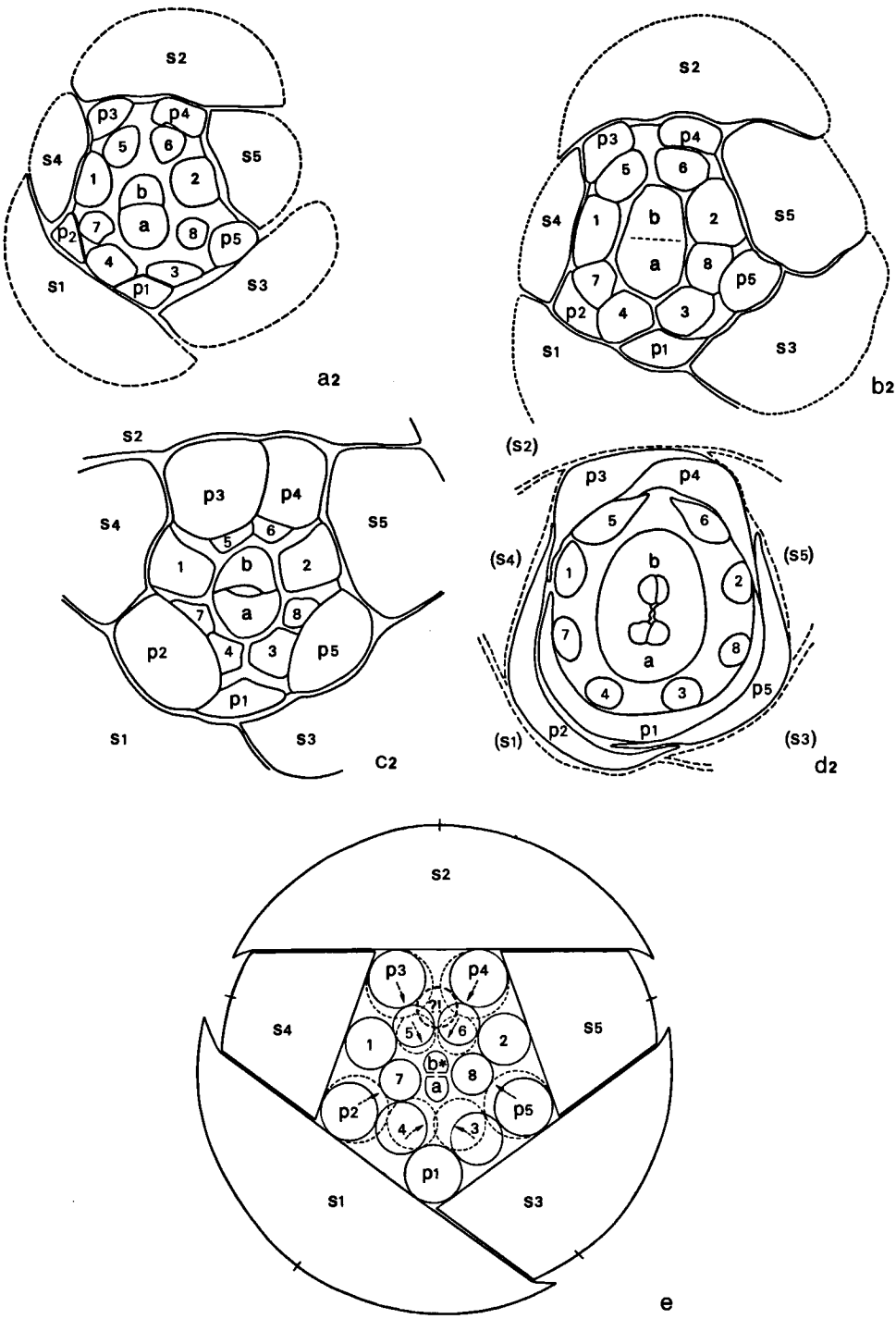


Fig. 2. Floral apex. — a1–d1. S.E.M. photographs of successive stages; a2–d2 interpretation of the photographs; e. construction drawing of floral apex. — Successive sepal numbers indicated as s1–5, petals as p1–5, stamens as 1–8, carpels as a and b. For further explanation see the text (a1–d1: *S. X. affine*).


s2
p3
p4
5
6
s4
s5
1
b
2
a
p2
7
8
p5
4
3
s1
p1
s3
a2
s2
p3
p4
5
6
s4
s5
1
b
2
a
7
8
p5
p2
4
3
s1
p1
s3
b2
s2
s4
p3
p4
5
6
s5
1
b
2
a
7
8
p2
4
3
p5
p1
s1
s3
c2
(s2)
p3
p4
5
6
(s4)
(s5)
1
b
2
7
a
8
4
3
p5
(s1)
p2
p1
(s3)
d2
s2
p3
p4
s4
s5
1
5
6
2
b*
a
7
8
p2
4
3
p5
p1
s1
s3
e

For the relations within the genus *Xanthophyllum* the number of stamens gives no information as deviating numbers are not constant within the species or species groups in question.

1.8.2. Retardation of median abaxial petal

The normal type of flower in *Xanthophyllum* is one with unequal petals; *X. affine* is a representative with this flower type.

As shown above, the median abaxial petal (carina) is the one to be initiated first. Very soon, however, this petal is retarded in its enlargement in comparison with the neighbouring petals. Fig. 2c shows that petals 2 and 5 are already considerably larger than petal 1. Because of this difference in size increment, petal 2 already covers the margin of petal 1. Although the limited material available did not contain a stage in which the other margin of petal 1 is in the same way covered by petal 5, such an event can easily be envisaged and must be inferred from Fig. 2d, where the carina has enlarged considerably to enclose four stamens and is covered completely by its neighbouring petals. Thus the aestivation of the petals in larger buds (carina inside) does not reflect the sequence of initiation of the petals (carina initiated first).

Payer (1857, p. 140) describes the expansion of the carina in *Polygala* as rapid, but this observation is in relation to the expansion of the other petals. From careful study of his figures (t. 31 fig. 9 & 10) it appears that the carina is for some time of the same size as the stamen primordia and thus is also retarded in its early development (compare carina and stamen size in Fig. 2c of *X. affine*).

In both *Polygala* and *Xanthophyllum affine* the carina shows the same ontogeny: initiated first, retardation, followed by a huge expansion.

In the less usual type of flower in *Xanthophyllum* the petals are (almost) equal and the carina is covered by only one of its neighbouring petals (number 2). No early stages of this flower type are available and the interpretation of this *apotact* arrangement must be highly speculative. Further ontogenetic studies of *Xanthophyllum* flowers are needed.

Discussion – See under the following chapter 1.9.1.

1.9. Full-grown flowers

1.9.1. Petals

In group 1 there are two species with equal petals, two with unequal petals (and one of which the flowers are not known). In those with unequal petals, the middle petal (carina) is the shortest one; the lateral and upper petals are very narrow, the lateral petals are longer than the upper ones. In group 2 the petals are unequal, and very similar to the petals of group 7 and 8: the carina is short, and usually strongly hairy outside, the lateral petals are somewhat wider and usually shorter than the upper petals. In group 3 the petals are equal; they are twice as long as the longest petals of any other *Xanthophyllum* species. In group 4 and 5 the lateral petals are similar to the carina in size and form, all three are spoon-shaped and convex in the upper part; the upper petals are narrow and rather flat. In group 6 the petals are equal and shorter than the stamens and the gynoecium. In group 7 and 8 the petals are unequal, like those in group 2.

In the tribe *Moutabeae* the five (in *Eriandra* also four) petals are equal. In the tribe *Polygaleae* they are unequal. In *Atroxima* and *Carpolobia* the petals are like those of groups 2, 7, and 8 of *Xanthophyllum*. In the majority of *Polygaleae* genera, however, the number of petals is reduced to 3, or the upper petals are markedly reduced in form and size. The carina is then always the largest petal, and is convex in transverse and in longitudinal view.

Discussion – At first sight Chodat's (1896) opinion that the flower of *X. ecarinatum*, with equal petals and (sometimes) 10 stamens, is the most 'primitive' flower in the genus seems plausible (although the occurrence of 10 stamens is an exception even in *90. X. ecarinatum*).

However, if my conclusion that the absence of the median adaxial stamen is an *aut*apomorphous character of the family is true (see chapter 1.8.1), the reverse opinion (that the flowers of *X. ecarinatum* show many apomorphous conditions) is not so improbable as it may seem to be. Moreover, the fact (see chapter 1.8.2) that both in *Xanthophyllum affine* and in *Polygala speciosa* the carina has a retarded development is an additional argument for the assumption that the flower type of *X. affine* represents the plesiomorphous condition in *Xanthophyllum*; flowers with equal petals (or with a number of stamens deviating from 8) then represent apomorphous conditions.

These assumptions are also supported by a comparison of the two flower types in each group (equal petals *versus* unequal petals) separately with the comparable types of other groups. It is then obvious that the differences between the flowers of the different groups with *unequal* petals are small. However, the differences between the flowers of the different groups with *equal* petals are considerable. From these observations it may be concluded that the character-state 'petals equal' must have arisen independently in groups 3 and 6, and in part of group 1, and that the flowers with markedly unequal petals represent the plesiomorphous character-state.

Finally another argument can be mentioned to support the conclusion that the flowers with unequal petals represent the plesiomorphous condition in *Xanthophyllum*. In most flowers with unequal petals the upper two petals have a (usually yellow) coloured spot at the inner side which, because those petals are usually strongly reflexed in anthesis, may be seen as insect-attracting marks. According to the field labels of collections of *89. X. papuanum* and *90. X. ecarinatum* the (equal) petals of these species also have yellow marks at the inner side. In the flowers of these species, however, the upper petals are *not* reflexed, and the yellow marks are thus not exposed. Assuming that the marks did loose their insect-attracting function long ago (see chapter 1.10) one may explain the presence of the not-exposed yellow marks by the reasoning that these marks (in terms of selection pressure) have become a neutral feature, so that they could persist even in flowers with (equal) petals which (no longer) expose the marks.

Summarizing, it is very likely that *Xanthophyllum* flowers with equal petals have developed independently in the groups 1, 3, and 6, and that flowers with unequal petals represent the plesiomorphous character-state. This means that the resemblance of the flowers of group 2 with those of groups 7 and 8 does not indicate a common ancestry of these three groups.

1.9.2. Stamens

In full-grown flowers the eight stamens take the same positions as in the very young flowers, e.g. four stamens are epipetalous, two are alternipetalous, and two are situated before the carina. The epipetalous stamens are adnate at base to the petals. The carinal stamens are adnate to the carina or free; usually they are also connate basally.

Possibly because they did examine too few species, nearly all authors dealing with *Xanthophyllum* describe the stamens as being free from each other; in quite a number of species they form, however, a clear 'staminal tube'. When carefully dissecting, rather often a thin tissue can be observed connecting the stamens at their base.

In group 4 (as well as in *70. X. cucullatum*, and occasionally in *61. X. wrayi*) the stamens are triadelphous: the 'carinal' stamens are connate, and the six remaining stamens are connate in two groups: each of the lateral alternipetalous stamens is connate to its neighbours; as the latter are connate to their petals, the corolla easily falls apart into three parts.

In group 6 the stamens are free from each other, except in *86b. X. stipitatum* var. *glabrum*, where the filaments form a 'tube' by their closely intertwined hairs. Only in that group the stamens are distinctly longer than the petals.

In the tribe *Polygaleae*, the filaments are connate in all genera to form a 'tube' which is split at the upper median side. In all genera the epipetalous stamens are adnate to their petals. In the tribe *Moutabeae* the petals are connate in their lower half (except in *Barnhardtia*), and the filaments are inserted halfway or higher on the petals; together the filaments are connate into a tube. In *Barnhardtia* the stamens are triadelphous, as in group 4 of *Xanthophyllum*, but as in the other *Moutabeae* the filaments seem to be inserted on the upper half of the petals.

Discussion – The character-state 'epipetalous stamens adnate to their petals' obviously is the plesiomorph character-state for the family. The character-state 'stamens connate' is probably plesiomorph, too. 'Stamens not connate', as well as 'stamens triadelphous' are then apomorphous states, but probably not of the same but of parallel transformation series. The triadelphous stamens in *Xanthophyllum* group 4 and in *Barnhardtia* are to be regarded as parallel developments, not showing an argument for common ancestry. Within *Xanthophyllum* the plesiomorphous state is present in part of the species of group 1, in group 5 and in part of group 8; in group 7 connate stamens are only as a rare exception found in *1. X. flavescens*. Because the apomorphous condition varies within group 8, the character-state 'stamens free' cannot be a synapomorphy of the groups 2, 3, 6, 7, and (part of) 8, but must have evolved independently in at least some of these groups.

Finally, it seems reasonable to assume that the character-state of the stamens of group 6 ('stamens longer than petals') is an autapomorphy.

1.9.3. Anthers

In *Xanthophyllum* the anthers develop in the usual way: four microsporangia form two thecae, each splitting lengthwise introrsely from apex downwards when ripe.

According to Chodat (1896b), who is, however, not very precise in his annotations, the thecae in the tribe *Polygaleae* have a falciform slit at the inner apical side; at the end of the usually rather short slits some tissue of the thecae vanishes to form a pore-like structure.

In the tribe *Moutabeae* the thecae develop like in the tribe *Polygaleae*, but pores are not formed.

The difference between the anthers of *Xanthophyllum* and those of other *Polygalaceae* can be brought back to a difference in the transverse connections of the loculi at the apex of the anthers.

Discussion – The published information on the structure and the development of the anthers in the family is not very precise. That is unfortunate, because I think that the anthers provide a character which is important for phylogenetic reasoning. As far as I can see, the anthers of *Polygaleae* and *Moutabeae* have basically the same character state. The anther type of *Xanthophyllum* is rather common in dicotyledons, whereas that of the other *Polygalaceae* is rather special. Hence it is probable that the anther type of *Xanthophyllum* represents the plesiomorphous state of the character in the family.

1.10. Remarks on flower biology

In most *Xanthophyllum* species (except those of group 1, 3, and 6) the stigma is situated at exactly the same height as the anthers. As the anthers open introrsely, one should expect that there is a mechanism in the flower to prevent self-pollination. Apparently that is not the case. I conclude this from the frequent observations of germinated pollen grains on the stigma of unopened flowers. Together with the observation that the pollen tubes may grow from inside the theca into the stigma, and the fact that the anthers very often form a narrow ring around the stigma, the conclusion must be that bud-pollination is the rule in most species of *Xanthophyllum*. The fact that fruitsetting is abundant in most *Xanthophyllum* species and that seedsetting seems to be normal, may serve as an indication that this bud-pollination is effective; the only species in which the fruits often appeared to be infertile belongs to group 6 (in which bud-pollination is almost impossible because of the relative positions of stigma and anthers).

This casts a strange light on the specializations of the *Xanthophyllum* flowers, which look so well adapted for cross-pollination by flying insects! Only the flowers with *equal* petals (group 1, 3, and 6) cannot be self-pollinated, whereas in probably all species with strongly zygomorphous, 'papilionoid' flowers bud-pollination seems to be frequent, if not the exclusive form of pollination. Not only by their papilionoid structure the bud-pollinating flowers seem to be designed to attract the attention of insects, also the production of nectar and large quantities of pollen makes the flowers attractive to insects.

According to many field labels many species, moreover, have bright yellow spots at the inner side of the (usually white) upper petals, exactly at the place where these petals bend upwards: those yellow spots, too, nicely fit the picture of insect-attracting flowers. Indeed, as can be detected from collector's notes, insects are abundantly visiting flowers of that kind. Yet those yellow spots must date from long ago, when cross-pollination was still a common feature of *Xanthophyllum* flowers (see also chapter 1.9.1).

In other genera of the *Polygalaceae* it is also observed that pollen grains germinate already in bud, growing into the stigma of the same flower: Rao (1964; see pl. 17) reports that phenomenon for *Polygala erioptera* and for *Salomonia*.

Discussion – In view of my deductions and of the observations of Rao (*l.c.*) and Venkatesh (1956), the conclusions of Brantjes & Van der Pijl (1980) and of Breteler & Smissaert-

Houwing (1977) are not convincing. Brantjes & Van der Pijl found strange pollen grains on the stigmas of (several) *Polygala* and *Muraltia* species. They prematurely concluded a connection of pollinating insects with different structures of the stigma. Apparently they have not checked whether bud-pollination can be excluded, which is surprising as many authors mention the frequent occurrence of autogamy in *Polygala* (see Miller, 1971). Breteler & Smissaert-Houwing take as the sole indication for cross-pollination by insects in *Carpolobia lutea* the observation that a specimen cultivated in a Wageningen greenhouse did not produce fruits. This is far too weak an argument to assume obligatory cross-pollination.

The probability that bud-pollination may be the exclusive form of pollination for most *Xanthophyllum* species is interesting with regard to the evolution of these plants. It is generally thought that obligate self-pollination will lead eventually to extinction of populations and, at last, of species. In that connection the observation (admittedly only once) of specimens with functionally female flowers in *1. X. flavescens* may be an indication of the escape route.

1.11. Ovary

According to previous authors *Xanthophyllum* differs from other *Polygalaceae* by its 1-locular ovaries with 4–16 ovules situated in two double rows. Other *Polygalaceae* have as many locules as carpels (2–8), and always one ovule per carpel. However, for *Xanthophyllum* this picture is somewhat misleading.

The ovary of all *Xanthophyllum* species is syncarpous and consists of two carpels which are situated in the median plane of the flower. The margins of each carpel are slightly folded inwards in most species; however, in group 7 (and 3?) the margins are folded inwards till the middle of the ovary. In the first case the ovary is 1-locular, or 2-locular only at the very base. When the margins of the carpels are folded inwards till the middle of the ovary, the resulting septs are usually completely fused in the lower third of the ovary, and touching but free in the remaining part; in *1. X. flavescens* the slit between the margins of the carpels disappears after fertilization of (one of) the ovule(s), thus forming a complete sept.

With respect to number and orientation, the ovules of *Xanthophyllum* species differ from all other *Polygalaceae*. The ovules are inserted on the carpel margins. If each carpel has two ovules, the four ovules in the ovary may be inserted all at the same height (apparently in pairs), or all at different heights. However, in most groups each carpel has 4–8 ovules. An exception is *92. X. fragrans* with c. 20 ovules per carpel; in *16. X. arnottianum* also carpels with three ovules occur.

In all other *Polygalaceae* each carpel bears only a single ovule, which is placed at the apex of the locule, exactly in central position. Because each ovule is thus placed precisely at the same distance of each of the fused strands of the synlateral/synmarginal veins it becomes innervated from both sides, leading to a peculiar double innervation (Leinfellner, 1972).

From a morphological point of view (Leinfellner, 1971, 1972) there is no principal difference between the structure of the ovary of *Xanthophyllum* and that of other *Polygalaceae*. Leinfellner distinguished two parts in the ovary of *Polygalaceae*: a lower part in which the margins of each carpel are congenitally fused and the carpels are connate ('syn-

ascidiate part'), and an upper part in which the margins of each carpel are not fused but are connate to the margins of another carpel ('synplicate part'). In *8. Xanthophyllum affine* (group 7) he demonstrated that the ovary is synascidiate in the lower third, and synplicate in the upper part. In other *Xanthophyllum* species the synascidiate part is less well developed. In other *Polygalaceae* Leinfellner concluded that the ovary is synascidiate for its largest part, the synplicate zone being confined to the basal region of the style. He also concluded that the innervation of both types of ovaries is quite homologous.

Leinfellner's observations were made from fully developed ovaries, and were interpreted from an idealistical-morphological point of view ('Das Gynözeum von *Xanthophyllum* besitzt .... die grundsätzlich gleiche Bauweise wie das der übrigen zweikarpelligen *Polygalaceen*, und die bestehenden Unterschiede sind nur quantitativer Art'; 1972, p. 52). His opinions on the interpretation of differences in the structure of the ovaries are, however, in good agreement with the ontogenetical theory of Rohweder (1967, p. 416). In Rohweder's opinion the ontogenetical early stage of the carpel of *Ranunculaceae* is an obliquely ascidiate structure, annular in lower transverse view (ascidiate part), half-open in upper transverse view (plicate part). Recent S.E.M.-studies in *Ranunculaceae* (Van Heel, 1981) seem to be in strong agreement with Rohweder's view.

It is thus possible to assume one common ontogenetically identical stage of the ovaries of all *Polygalaceae*, analogous to the one described by Rohweder in *Ranunculaceae*. That, however, has not been studied yet.

From the possible common initial stage the ovaries in *Xanthophyllum* and in other *Polygalaceae* develop quite differently. In *Xanthophyllum* the ovules develop only in the expanding synplicate part, i.e., along the two margins of each carpel; in other *Polygalaceae* a single, median ovule develops in the transitional zone of the synascidiate and synplicate part during the expansion of the ovary.

Discussion – The kind of difference in the structure of the ovary between that of *Xanthophyllum* and that of other *Polygalaceae* has a resemblance to the differences found in the family *Ranunculaceae*. In that family (with free carpels!) both ascidiately developed 1-ovuled ovaries and plicately developed more-ovuled ovaries occur, sometimes even in the same genus, like in *Delphinium* (Van Heel, pers. comm.). Important in this connection is the development of the ovaries in the other *Ranunculaceae* genera *Clematis* and *Anemone*. In these genera in an early stage of ontogeny ovules are formed in the plicate part of the carpel as well as in the ascidiate part. The two pairs of ovules in the plicate part have a retarded development until they finally stop growing completely; only the median ascidiate ovule develops further into the single, fertile ovule. That situation might be used as an example in which the ontogeny shows a recapitulation of the phylogeny of the *Ranunculaceae*. Even if it could be demonstrated that the ascidiate more-ovuled condition is the plesiomorphous character-state in the *Ranunculaceae*, the synascidiate more-ovuled condition in *Xanthophyllum* might be apomorphous in the *Polygalaceae*, depending on the character-state in the out-group of the *Polygalaceae*; unfortunately the variation in the number of ovules in the related families is similar to that in the *Polygalaceae*, and I have not been able to make assumptions as to the character-states in related families. It seems unacceptable to me to make any choice in this particular question.

As to the character of the reduced (or incomplete) septs, comparison with the out-group

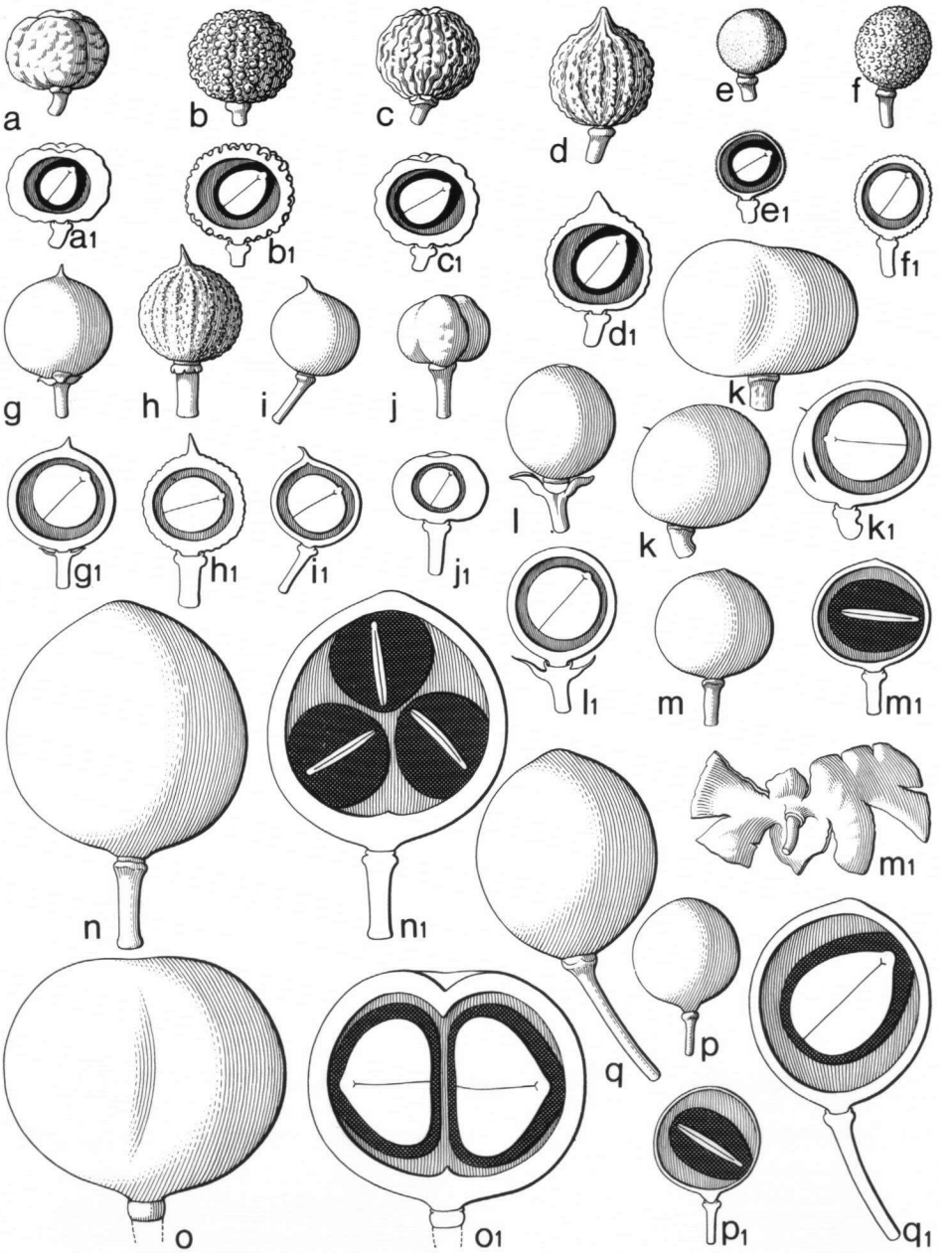
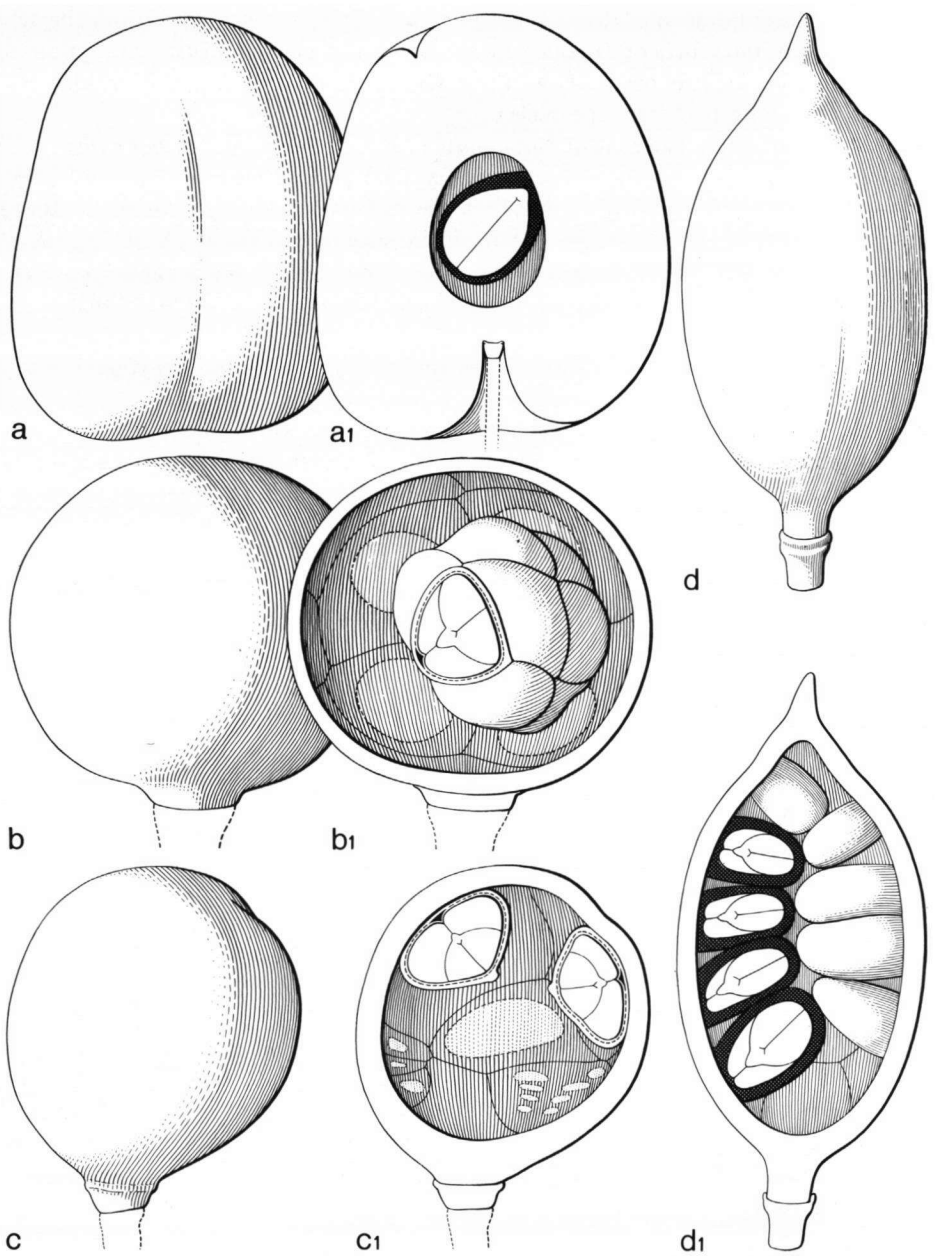


Fig. 3A. Fruits with (simplified) longitudinal sections, all x 0.43; black: albumen. — a. *60b. X. eurhynchum* subsp. *maingayi*; b. *60a. X. eurhynchum* subsp. *eurhynchum*; c. *61. X. wrayi*; d. *62. X. venosum*; e. *37. X. incertum*; f. *16. X. arnottianum*; g–i. *8. X. affine*; j. *11. X. schizocarpon*; k. *1. X. flavescens*; l. *14. X. rufum*; m. *93. X. octandrum*; n. *aff. 85. X. amoenum*, see note 2; o. *66. X. sylvestre*; p. *79. X. ellipticum*; q. *48b. X. discolor* subsp. *macranthum* (a: *KEP 40454*; b: *De Wilde 12908*; c: *FRI 5509*;



d: *KEP 99297*; e: *Rahmat si Boeea 11260*; f: *Subramanian 1186*; g: *Goudenough 1455*; h: *SAN 26071*; i: *Endert 4371*; j: *Elmer 21519*; k: *Achmad 207*; l: *S 17002*; m: *Webb & Tracey 5963*; n: *FRI 2324*; o: *Kostermans 742*; p: *Achmad 837*; q: *Wenzel 3437*). — Fig. 3B. Fruits with (simplified) longitudinal sections. all x 0.37; black: albumen. — a. *65. X. ngii*; b. *88. X. obscurum*; c. *89. X. papuanum*; d. *90. X. ecarinatum* (a: *KEP 78252*; b: *Kostermans 12518*; c: *BW 4871*; d: *SAN 25312*).

leads to the assumption that the condition in *Xanthophyllum* is an apomorph character-state: in none of the genera of *Trigoniaceae, Vochysiaceae*, and *Malpighiaceae* a syncarpous 1-celled ovary occurs (the ovary of the *Vochysiaceae* genera *Erisma* and *Erismadelphus* is monocarpellate with two, resp. one ovule).

Anyway, statements like that of Hutchinson (1967, p. 337) that *Xanthophyllum* is 'the most primitive genus .... with a 1-locular ovary with parietal placentas' are misleadingly dogmatic, and have no scientific value. Yet that opinion obviously has been the starting point for the explanation by Milby (1976) of the structure of the ovary of *Polygala*. Although I cannot give an answer to the question of the plesiomorph number of ovules of the family, I am sure that Milby's 'hypothesized derivation' (*l.c.* p. 1324) of that ovary is wrong.

The difference in the number of ovules of the groups *within Xanthophyllum* can be interpreted independently of the question which number of ovules per carpel is the plesiomorphous or the apomorphous character-state in the *family*. The high number of ovules (c. 20) for group 3 is probably an autapomorphous character-state. As the character-state 'ovules 2 per carpel' is found only in group 2 and in part of group 8, it seems reasonable to consider that, too, as apomorphous.

1.12. Stigma

In *Xanthophyllum* the stigma has two forms: slightly bilobed (groups 2, 6, 7, and 8), or peltate (groups 1, 3, 4, and 5). The slightly bilobed stigma of *72. X. bibracteatum* and *73. X. burkillii* (group 8) differs from all other species with that type of stigma in being larger than the apex of the style.

Discussion – From a taxonomical point of view the stigma is a useful character below the genus level; that is also the case in other genera of the *Polygalaceae*. It is difficult, however, to use the character for phylogenetical discussions at or above the genus level because I cannot find arguments to make the decision which of the types would be the plesiomorphous or the apomorphous character-state.

1.13. Fruit

In Fig. 3 the variation in form, size, and number of seeds, and in the seed-type has been depicted. With the exception of group 2 (Fig. 3A-m; Fig. 22 i & j), the fruits are indehiscent in all groups. In group 2 the fruit must (in a strict sense) be regarded as a loculicidally dehiscent capsule, although the irregular way in which it is dehiscent is an indication that this condition is probably derived from an indehiscent fruit type.

A strong correlation exists between the size of the fruit and the number of seeds per fruit:

a) Fruits 1–2 cm diam., seed(s) 1 (or 2): groups 2, 4, 5, 7, and 8 (exception in group 8: *66. X. sylvestre*, fruit up to 7 cm, seeds 1–4; *65. X. ngii*, fruit up to 8 cm, seed 1).
b) Fruits 5–15 cm diam., seeds 4 to c. 20: groups 1, 3, and 6.

Small fruits are globular or sometimes apically pointed, large fruits are globular, pear-shaped or ellipsoid.

In all but one species the fruits are unilocular. In *1. X. flavescens* (group 7) the fruit (usually) becomes bilocular directly after the beginning of seedsetting; the congenitally fused margins of the carpels, forming a complete sept in the lower third part of the ovary but only touching each other higher up, become connate till the apex after fertilization of the ovule(s). Usually, only one ovule develops into a seed in that species, so that the second locule becomes aborted and is difficult to trace in the fruitwall (Fig. 3A-k1); the sept is more easily visible if in each of the cells a seed is produced (Fig. 3A-k2), as is not exceptional in that species.

In the *Moutabeae* the fruit is indehiscent too (not known from *Barnhardtia*): nut-like in *Eriandra* and *Diclidanthera*, a berry in *Moutabea*. In the *Polygaleae* the fruit is a loculicidal capsule in about half of the genera, an indehiscent nut or berry in the other half; only in *Monnina* dehiscent as well as indehiscent fruits occur.

In the related families *Trigoniaceae, Vochysiaceae*, and *Malpighiaceae* the fruit is very often a capsule.

Discussion – Large, many-seeded fruits with large (up to 5 cm wide) seeds (as characteristic of *89. X. papuanum*) are usually regarded to be 'primitive', compared to small, one-seeded fruits. I see no reason, however, to translate the term 'primitive' into plesiomorphous. Indeed, the reverse seems to be more probable in this case. The problem is that the properties of fruit and seed are so intricately linked to reproductive 'strategies'. Fruits and seeds can be used in a phylogenetical reasoning only when much is known of these ecological facets, which obviously is not the case in *Xanthophyllum* (and other tropical tree genera). The opinion that the large, many-seeded fruits of *Xanthophyllum* are 'primitive' has no scientific value at all, and it is impossible to use the terms plesiomorphous and apomorphous at the present stage of knowledge.

1.14. Seed

1.14.1. Testa

My knowledge on the structure of the different types of testas is incomplete as it is almost exclusively based on study of mature, dry seeds. In group 1 the testa consists of two layers; the outer layer seems to be surrounded by an epiderm-like outer part. In *88. X. obscurum*, Ng (1975), describing fresh material, observed the outer layer to be 'thick' (probably 2–3 mm), 'sweet, pulpy-fibrous .... (i.e., the seed coat is a sarcotesta)'; when dry, the many seeds of that species seem to be glued together into a ball, and to be enveloped in a tough, fibrous tissue. The second, inner layer of the testa is hard, 0.1–0.2 mm thick, and consists of hard, prismatic cells. Probably the testa of seeds of other species of group 1 is built in the same way, with the difference that the outer layer seems to be not 'fibrous'; in *91. X. chartaceum* the inner prismatic layer is distinctly less than 0.1 mm thick and the outer layer, too, seems to be thinner. In groups 2 and 3 the testa consists of three layers: a c. 0.1 (group 2) or 0.05 (group 3) mm thick, leathery, dark outer layer, a soft, rather thick (thickness not measurable) middle layer (possibly a sarcotesta), and a hard inner layer of nearly 0.2 mm thick, consisting of long, dark, prismatic cells. In groups 4 and 5 the outer layer of the testa is soft and less than 0.1 mm thick, in group 5 the inner layer of prismatic cells is distinctly less than 0.1 mm, in group 4 that layer is somewhat more than

Table 2. Summary of testa types, embryo types, and quantity of albumen in *Xanthophyllum*

number of testa layers	thickness	embryo	albumen	group
3	middle layer thick	flat	copious	2; 3
2	outer layer thick	flat	copious	6
2	outer layer thick	thick	scarce	1
2	outer layer thin	flat	copious	4
2	outer layer thin	thick	scarce	8a
2	both layers thin	thick	scarce	5; 8b; *91. X. chartaceum* (group 1)
1	thin	thick	absent	7

0.1 mm thick. In group 6 herbarium labels report the seeds to be 'edible' and 'sweet'. The outer layer is often absent in dried collections, probably because of activities of gluttonous insects. In a rare case I found an undamaged seed, of which the outer layer was about 4 mm thick, and consisted of very long, thin-walled cells, giving it the image of a long, velvety indumentum; the inner layer, again, consisted of prismatic cells and was 0.1–0.2 mm thick.

In group 8a the testa is like that of group 4. In group 8b the inner layer of prismatic cells is very thin (hardly visible); the outer layer is soft and rather thin, except in *65. X. ngii* in which it is about 3 mm thick. The testa of group 8b resembles that of group 7, but differs in sticking to the seed when dry.

In group 7 the testa is very thin, and seemingly absent in dry material because it sticks to the inner side of the pericarp and not to the embryo which thus looks as if naked. The inner layer of prismatic cells is probably lacking completely. In two characters the testa of group 7 differs from all other types of testa: in the raphe and in the chalazal area. In all other testa types the raphe is narrow and runs straight to the chalazal area into the hypostase (see below), where it gives off many short radially arranged branches. In group 7 the raphe is wider, it branches already before reaching the chalazal area, and branches widely and diffusely at the chalazal side; the hypostase is not developed.

In all testa types but that of group 7 a corky tissue ('hypostase') develops soon after fertilization of the ovule near the base of the nucellus (as the ovule is anatropous, the hypostase is formed at the upper side of the ovule, called the 'chalazal area'). The hypostase forms a usually well-defined circular or elliptical area except in species with a thick sarcotesta. (The hypostase is not to be mistaken for the indistinct scar ('hilum') at the base of the seed; that is somewhat elongate and (nearly) reaches at one side the slightly protruding micropylar pore.) In ripe seeds the hypostase forms a strong connection between the testa and the albumen; if the latter tissue copiously envelops the embryo the albumen is firmly attached to the testa.

It remained unclear to me whether the testa is formed only by the relatively thick outer integument of the ovule, or also partly by the inner integument; in the few slides of young

seeds I examined the inner integument disappeared soon. Chodat (1896b) mentions that only the outer integument forms the testa; his remark (based on Rodrigue, 1893) that the inner layer of long prismatic cells is not present in *Xanthophyllum* is probably based only on material of the common *1. X. flavescens*, which has the reduced testa type of group 7.

I did not examine the testa of other members of the family; according to Chodat (*l.c.*) many different types can be distinguished, which are characteristic for groups of species.

Discussion – Table 2 presents a summary of the testa types occurring in *Xanthophyllum*, combined with a rough indication of the embryo type (see chapter 1.14.3.) and the quantity of albumen.

It is very apparent that the characters of the testa show no correlation with the form of the embryo, which is strongly correlated with the quantity of the albumen surrounding it (for more information on the embryo types, see chapter 1.14.3). Yet the combination of these characters strongly coincides with the groups I have distinguished (with the exception of the reduced 2-layered testa, which through parallel development occurs in three groups).

Whatever type of testa and embryo may have been the plesiomorphous one in *Xanthophyllum* (possibly the 2-layered type with a thin outer layer), one must conclude that the apomorphous conditions cannot be placed in one transformation series. The apomorphous conditions must have been developed along different and independent lines, or be the result of reticulate relationships, or they have been changed in the course of evolution through (unknown) adaptive processes by which earlier character-states have been eliminated.

Anyhow, I am unable to see a pattern in this confusing array of seemingly independent variation, apart from the assumptions that the seed type of group 7 and that of group 8b have been derived independently from the seed type of group 8a (see chapter 1.14.3).

1.14.2. Development of embryo

The following is based on slides of different stages of developing fruits of *62. X. venosum (FRI 1877)* (group 8) from the FAA collection at Kepong, Malaysia, and on old liquid preserved material of *1. X. flavescens* (group 7).

In *X. venosum*, just after fertilization, it can be noted that the inner integument, which is 2 or 3 layers thick, does not fully enclose the nucellus at the micropylar area; the micropyle is formed by the thick outer integument only. Soon the nucellus develops into a bulky tissue (transient perisperm), which becomes centrally absorbed by nuclear endosperm. At the chalazal side the hypostase tissue is differentiating. When the seed has reached about half its mature size, the embryo-sack is still filled with much nuclear endosperm, which at the outer side is becoming cellular; perisperm is hardly traceable except at the chalazal side. In that stage the young embryo is beginning to grow rapidly, absorbing the nuclear endosperm. In the mature seed the embryo has thick, half-globular cotyledons and is enveloped by a rather thin layer of cellular endosperm, at the chalazal side with a thin remnant of perisperm.

In *1. X. flavescens* the development is different from the half-mature stage onwards: the embryo still does not seem to grow until the seed is almost at maximum size and almost completely filled with nucelar endosperm (when dried in that stage, the seed strongly collapses as if it is void; dried half-mature seeds of group 8 already possess a recognizable cel-

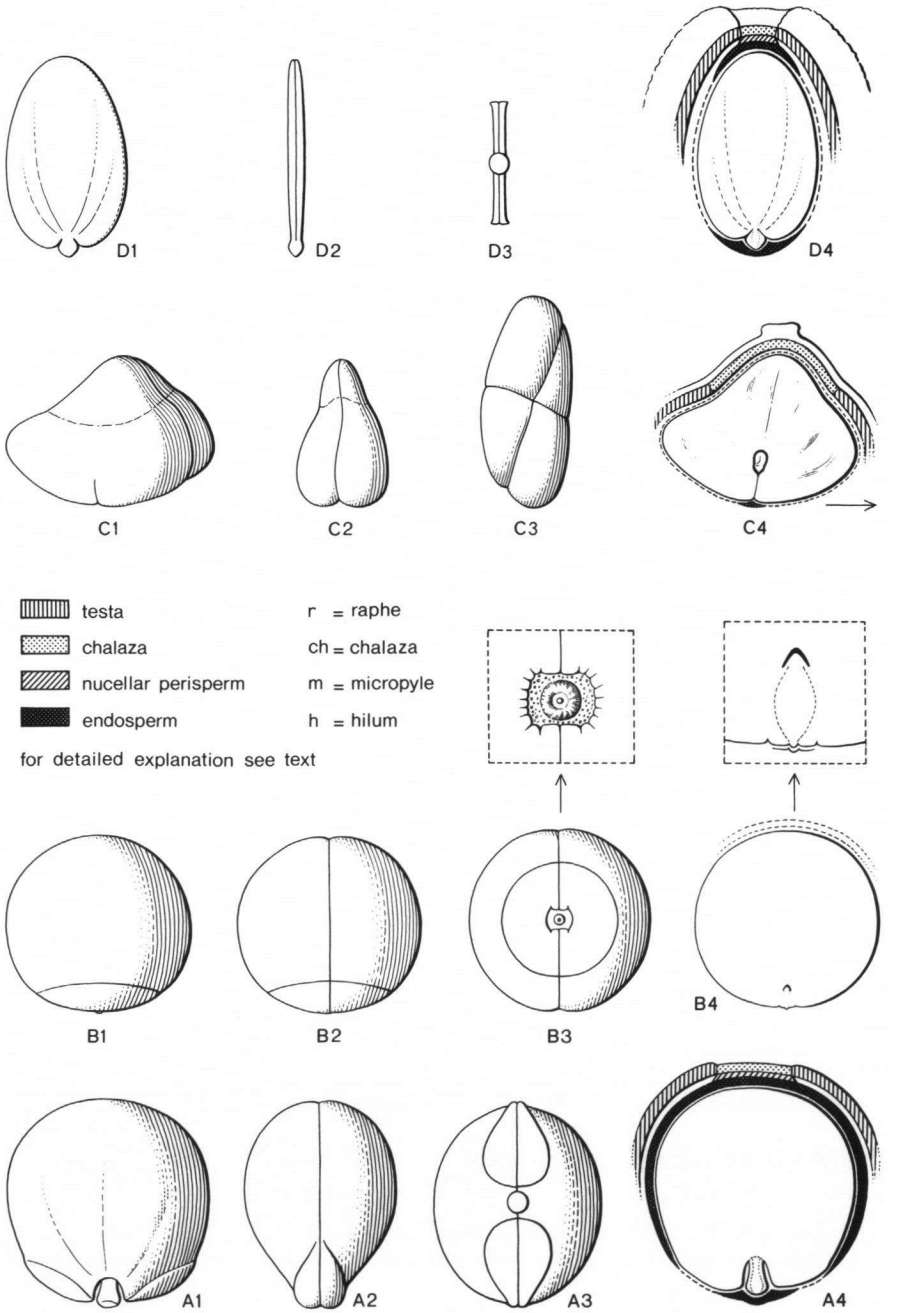
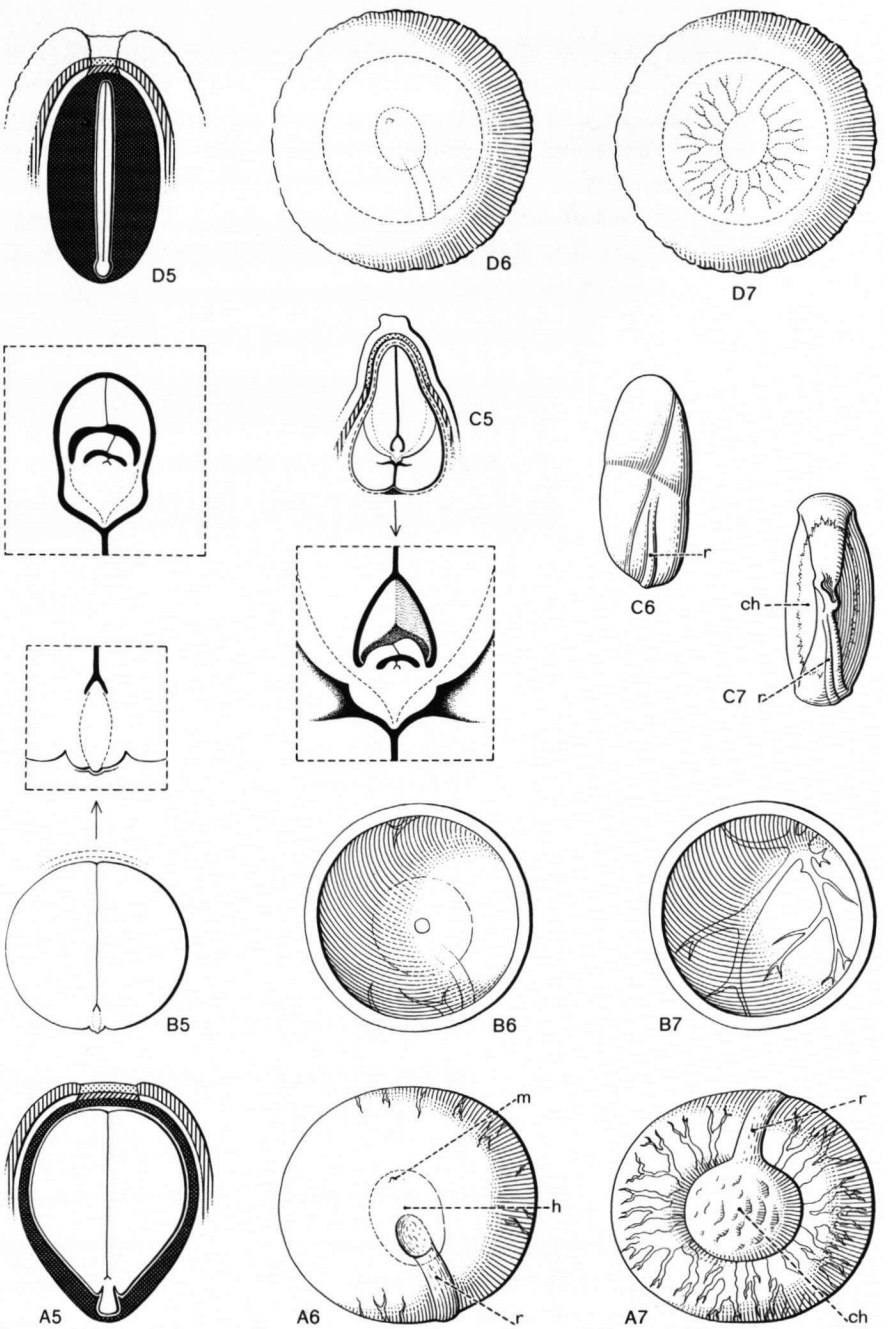


Fig. 4. Seed and embryo types. – A. subg. *Xanthophyllum* sect. *Eystathes*; B. subg. *Xanthophyllum* sect. *Xanthophyllum*; C. subg. *Brunophyllum*; D. subg. *Exsertum*. – 1. embryo, backside; 2. embryo, lateral side; 3. embryo, seen from below; 4 & 5. embryo, longitudinal sections; 6. testa seen from below



(except B, in which the testa has been depicted as glued to the inner side of the pericarp); 7. as 6, but seen from above (A: *Achmad 1568*; B: *Achmad 207*; C: *BW 4871*; D: *FRI 2324*).

lular embryo). Probably a very short time before the seed is ripe the young embryo ends its resting time; when full grown, the embryo completely fills the testa, having absorbed practically all of the endosperm and perisperm. Thus the *ripe* seed of *X. flavescens* is 'without endosperm'! The difference of the *flavescens*-seed 'without endosperm' and the *venosum*-embryo 'enveloped by endosperm' can be brought back to a difference in time of development of the young embryo only.

As far as I can judge from observations on dry material, only in species of group 7 the embryo development is very late; in species of other groups it seems to be more gradual like in *62. X. venosum*.

1.14.3. Morphology of embryo

In group 1 the embryos are larger than in other groups, especially so in *89. X. papuanum* and *88. X. obscurum*. In these species the ripe embryo is broadly triangular in lateral view, up to 2.5 cm high (Fig. 4 c), at base up to 4–6 cm wide (when dry). In both species the cotyledons are attached to each other in the very centre of the embryo, thus covering the plumule which is differentiated into a series of decussate scale-like leaflets. From the short radicle to the base the cotyledons are each cut longitudinally by the 'lateral cleavages'. (It must be noted that the description of Ng (1975) of the ripe seeds of *X. obscurum* is different from what I have seen: in his drawing the radicle is situated at the base of the embryo, just peeping out; such might be the situation just before germination when the petioles of the cotyledons are forcing the radicle and plumule downwards through the narrow space between the lateral cleavages and the cleavage between the cotyledons.)

Peculiar is the fact that the cotyledons of *X. obscurum* have a distinct, finely reticulate nervation system just below their epiderm with strands radiating from the petiole; these nerves contain very tough spiral fibres that successfully resist the sharpness of a lancet. In no other species with thick cotyledons I observed more than three 'primary' nerves, and never such a finely reticulate venation.

In ripe seeds of *X. papuanum* and *X. obscurum* very little albumen is present; remnants are only visible centrally at the base of the cotyledons and near the hypostase. Possibly, because of differences in the testa of these species (see above), the seeds behave differently in drying, remaining attached to the inner side of the pericarp in *X. papuanum*, and seemingly glued together into a ball in *X. obscurum*.

In the other species of group 1 the embryos are smaller, with shorter lateral cleavages and less thickened cotyledons. They are enveloped by more albumen; the albumen is distinctly visible at the back parts of the cotyledons, at their base and apex, and it is thin along their margins. In *87. X. brevipes* the lateral cleavages are absent, the radicle is just exserted at the base; in the seed of that species the halves of the albumen are approximately as thick as each of the cotyledons.

In other groups the seeds vary little. In all the plumule is not differentiated into more than two leaflets (or seems to be not differentiated at all) and the radicle is always situated at the base. There are two broad categories: one with thin foliaceous cotyledons enveloped by copious albumen (groups 2, 3, 4, 6), and one with thick cotyledons covered by little or seemingly no albumen (groups 5, 7, 8). In addition to the list of Dahlgren (1980) it can be noted that chlorophyll-containing embryos occur in both of these categories.

Seeds with flat cotyledons are globular in groups 2 and 4, somewhat angular because of pressure in the many-seeded fruits of group 3, and bean-shaped in the species of group 6 (Fig. 4 d).

Seeds with globular embryos can be divided into two types, and a heterogeneous rest-type. In group 7 (Fig. 4 b) the radicle is not protruding; in dried state minute particles of albumen are visible on the radicle, probably all that is left of the albumen in the ripe seed. In group 8 the radicle is protruding a little and the cotyledons are slightly cordate at their base (Fig. 4 a). At their lateral-basal sides the cotyledons form two flat areas, each of which is corresponding to that of the other cotyledon. In these flat regions probably the absorption of the albumen during the development of the seed has been stronger than elsewhere, because in the ripe seed the flat areas are covered only by a very thin layer of albumen; the rest of the embryo is more or less uniformly covered by a rather thin but distinct layer of albumen.

The seed of group 5 has a protruding radicle as have the seeds of group 8a, but there are no flat areas; the albumen is very thin along the lateral sides of the embryo, and elsewhere it is rather thin but distinct.

The embryo of group 8b looks like that of group 7, differing in its complete but very thin layer of albumen enclosing the embryo.

Discussion – a) Binary character-states

As a rule there is a very strong correlation between the quantity of albumen in the seeds and the form of the embryo. Probably this can be generalized for most dicotyledons, but it suffices to note that this is the case in the *Polygalaceae*. Embryos are either flat and enveloped by much albumen, or thick and enveloped by little or no albumen. 'Intermediate' stages are very scarce: only in *87. X. brevipes* the embryo is as thick as both halves of the albumen. I am convinced, moreover, that the *X. brevipes* seed is not representing a true intermediate condition, but represents a special (autapomorphous) character-state in that species.

The binary nature of the embryo-albumen character-states causes difficulties for the argumentation on character-states in *Xanthophyllum* because I am unable to find transformation series (except in group 1; see below). In such a situation it is (almost) impossible, moreover, to detect regressive, apomorphous character-states, as well as to recognize parallel developments.

b) Phylogenetic interpretation

Apart from the considerations mentioned above, the nature of the character-state 'embryo flat', occurring in groups 2, 3, 4, and 6, is difficult to interpret, if De Vogel's (1980) theories on the morphology and function of dicotyledonous seedlings are taken into consideration: De Vogel distinguishes flat cotyledons in two categories, one which is homologous to thick cotyledons (with a haustorial or foodstoring function), and one which is homologous to the first pair of leaves ('paracotyledons', with an assimilatory function after germination of the seed). In the seed, these types of cotyledons cannot be recognized with certainty, the difference becoming apparent during and after germination only. It should be noted, moreover, that the difference between thick, foodstoring cotyledons and flat haustorial ones is hardly of importance in the opinion of De Vogel. Returning to the flat cotyledons of *Xanthophyllum* groups 2, 3, 4, and 6: it may well be that the flat em-

bryos belong to different types. This, however, cannot be examined in the seed, but only in seedlings; unfortunately no seedlings are known from any representative of the four groups concerned.

Thick embryos occur in groups 1, 5, 7, and 8. In group 1 each species known thus far has a different form of embryo, covered by various quantities of albumen, in *91. X. chartaceum* even with a different testa. Yet the seeds in those species can rather easily be put into a morphological series, with the seeds of *88. X. obscurum* at one side, those of *87. X. brevipes* at the other end. Although I cannot find arguments which of those embryo types represents the plesiomorphous condition *of group 1*, it seems probable to me that the morphological series actually represents a transformation series.

With the aid of characters of the testa another morphological series can be made, with the seed type of group 8a at one side, that of group 8b in an intermediate position, and the seed type of group 7 at the other end. The type of group 8b is probably derived from the type of group 8a, considering the reduced testa of 8b. The type of group 7 may be derived from that of group 8b, as a further reduction of the type of group 8a. Because I cannot find other characters which can be considered as synapomorphous for groups 8b and 7, the seed types of these groups will probably represent different autapomorphous conditions.

The seed type of group 5 is very similar to that of group 8b, differing only in the (exserted) radicle. I think that the similarity of the seeds of groups 5 and 8b is due to parallel development (see further chapter 2.3.2).

Concluding, the question which of the seed types represents the plesiomorphous character-state in *Xanthophyllum* cannot be answered yet.

1.15. Seedlings

I have seen only three seedlings. Ng (1975) described seedlings of two other species, and gave me permission to cite here the text of a letter on seedlings addressed to me. No seedlings are known from groups 2, 3, 4, and 5.

From group 8a Ng (*l.c.*) described a seedling of *32b. X. griffithii* (subsp. *erectum*), photographed in his fig. VIII.2. It has a distinct hypocotyl, and thick, sessile, spreading cotyledons which are free from the testa, followed by one pair of opposite normal leaves, and then followed by two alternate leaves. As such, the seedling belongs to De Vogel's (1980) '*Sloanea* (sub)type'. Ng (pers. comm.) mentions the same seedling type for *60b. X. eurhynchum* subsp. *maingayi* ('*X. palembanicum*').

Both seedlings from group 8b have been seen by me, one of *65. X. ngii* liquid preserved (BO), one dried specimen of *67. X. lanceatum* (BM). Both have a very short hypocotyl, the testa is still present around the cotyledons after germination, the cotyledons are pushed apart but are not spreading. The epicotyl of *X. ngii* bears one pair of opposite scars (of scale leaves?), followed by normal alternate leaves. The epicotyl of *X. lanceatum* has three rows of 3–12 serially arranged buds, higher up followed by two opposite scars (first normal leaves opposite?), then followed by two flushes of normal leaves. Probably both seedlings belong to De Vogel's '*Chisocheton* subtype'.

Seedlings of group 7 are (Ng, pers. comm.) like those of group 8a; in *14. X. rufum* the pair of opposite leaves is sometimes reduced to scales; *8. X. affine* bears alternate leaves right from the start.

Ng (pers. comm.) gives the following description of seedlings of *85. X. amoenum* and *86. X. stipitatum* (both group 6): they 'bear two pairs of opposite, or subopposite leaves, followed by alternate leaves. In both cases there are no scale leaves'. Supposing that the first pair is formed by the (foliaceous) cotyledons, these seedlings belong to De Vogel's '*Macaranga* type'.

From group 1 seedlings are only known from *88. X. obscurum*, one (*FRI 1376*) seen by me from liquid preserved material, the other one (*FRI 21007*; not seen) described and photographed (fig. VIII.3) by Ng (*l.c.*). The plants seen by me and by Ng differ markedly in th the following characters. The plant described by Ng has spreading cotyledons, of which the sarcotesta (not the endotesta?) comes off easily; the epicotyl bears one pair of scale leaves, followed by one pair of opposite leaves. In *FRI 1376* the cotyledons had been pushed apart, the testa still adhering, the epicotyl with 11 or 12 scale leaves in shifted-decussate pairs, followed by alternate leaves. The plant described by Ng as well as *FRI 1376* belongs to the '*Chisocheton* subtype' (if indeed the endotesta is not shed in *FRI 21007*). Ng's fig. VIII.1.F-J gives drawings of the fruit and seed; these show a number of differences with characters I observed in *X. obscurum*, notably the much thicker pericarp, the much lower number of seeds, and the (exserted) radicle of the embryo. These characters as well as those of the depicted seedling (*FRI 21007*) are suggestive of *65. X. ngii*.

Discussion – The limited number of observations on seedlings of *Xanthophyllum* does not permit conclusions for phylogenetic discussions. It is interesting, however, to note that seedlings belonging to the '*Chisocheton* subtype' have been found both in group 8b and in group 1. That type rather closely resembles the seedling type which De Vogel (*l.c.*, p. 112) considers to be the most primitive.

1.16. Literature

Brantjes, N.B.M. & L. van der Pijl. 1980. Pollination mechanisms in Polygalaceae. Acta Bot. Neerl. 29: 56–57.

Breteler, F.J. & A.A.S. Smissaert-Houwing. 1977. Revision of Atroxima Stapf and Carpolobia G. Don (Polygalaceae). Meded. Landbouwhogeschool Wageningen 77-18: 1–45.

Chodat, R. 1893. Monographia Polygalacearum. II. Mém. Soc. Phys. Hist. Nat. Genève 31(2): 1–492.

—— 1896. Polygalaceae. In: Engler, A. & K. Prantl, Die natürlichen Pflanzenfamilien III, 4: 323–345.

Dahlgren, R. 1980. The taxonomic significance of chlorophyllous embryos in angiosperm seeds. Bot. Notis. 133: 337–341.

Dickison, W.C. 1973. Nodal and leaf anatomy of Xanthophyllum (Polygalaceae). Bot. J. Linn. Soc. 67: 103–115.

Heel, W. van. 1981. A S.E.M. investigation on the development of free carpels. Blumea 27: 499–522.

Hennig, W. 1966. Phylogenetic systematics. (transl. D.D. Davis & R. Zangerl). Univ. Illinois Press, Chicago.

Hutchinson, J. 1967. The genera of flowering plants. Vol. 2. Clarendon Press, Oxford.

Leinfellner, W. 1971. Das Gynözeum von Krameria und sein Vergleich mit jenem der Leguminosae und der Polygalaceae. Oesterr. Bot. Z. 119: 102–117.

—— 1972. Zur Morphologie des Gynözeums der Polygalaceen. Oesterr. Bot. Z. 120: 51–76.

Milby, T.H. 1976. Studies on the floral anatomy of Polygala (Polygalaceae). Amer. J. Bot. 63: 1319–1326.

Miller, N.G. 1971. The Polygalaceae in the southeastern United States. J. Arn. Arbor. 52: 267–284.

Ng, F.S.P. 1975. The fruits, seeds and seedlings of Malayan trees. VIII. Polygalaceae. Malayan For. 38: 85–89.

Payer, J.-B. 1857. Traité d'organogénie comparée de la fleur. Victor Masson, Paris.
Raciborski, M. 1900. Ueber die Verzweigung. Ann. Jard. Bot. Btzg 17: 1–67.
Rao, A.N. 1964. An embryological study of Salomonia cantoniensis. New Phytologist 63: 281–288.
Rao, T.A. & K.J. Mody. 1961. On terminal sclereids and tracheoid idioblasts. Proc. Indian Acad. Sci. 53: 257–262.
Rodrigue, A. 1893. Structure du tégument seminal des Polygalacées. Bull. Herb. Boiss. 1: 450–463; 513–541; 571–583.
Rohweder, O. 1967. Karpellbau und Syncarpie bei Ranunculaceen. Ber. Schweiz. Bot. Ges. 77: 375–432.
Royen, P. van, & C.G.G.J. van Steenis. 1952. Eriandra, a new genus of Polygalaceae from New Guinea. J. Arn. Arbor. 33: 91–95.
Solereder, H. 1899. Systematische Anatomie der Dicotyledonen. Ferdinand Enke, Stuttgart.
Stafleu, F.A. 1952. A monograph of the Vochysiaceae. II. Callisthene. Acta Bot. Neerl. 1: 222–242.
—— 1953. A monograph of the Vochysiaceae. III. Qualea. Acta Bot. Neerl. 2: 144–217.
Styer, C.H. 1977. Comparative anatomy and systematics of Moutabeae (Polygalaceae). J. Arn. Arbor. 58: 109–145.
Venkatesh, C.S. 1956. The special mode of dehiscence of anthers of Polygala and its significance in autogamy. Bull. Torrey Bot. Club 83: 19–26.
Vink, W. 1970. The Winteraceae of the Old World. I. Pseudowintera and Drimys – Morphology and taxonomy. Blumea 18: 225–354.
Vogel, E.F. de. 1980. Seedlings of dicotyledons. Structure, development, types. Pudoc, Wageningen.
Weberling, F. 1974. Weitere Untersuchungen zur Morphologie des Unterblattes bei den Dikotylen. VII. Polygalales; VIII. Koeberlina Zucc. Beitr. Biol. Pfl. 50: 277–289.

2. Phylogeny of Xanthophyllum

2.1. Affinities of the Polygalaceae with other families

Polygalaceae are considered to be a 'natural' family of which affinities with other families are unclear. With the discovery of *Barnhardtia* (1926) and the inclusion subsequently of *Diclidanthera* (conform the opinion of Hallier, 1912, p. 172–174) into the *Polygalaceae* the limits of the family are reached at present. Inclusion of *Krameria* (Hutchinson, 1957) must be rejected, as well as the supposed line of affinities between *Caesalpiniaceae, Krameriaceae, Polygalaceae via Xanthophyllum* (Airy Shaw, 1979). The connection of *Krameria* with the *Leguminosae* is generally rejected; Leinfellner (1972) showed differences of enough importance. His study of the ovary of *Krameria* and ovaries of *Polygalaceae* reveals similarities, but his conclusion that *Krameria* 'den *Polygalaceen* viel näher (steht) als den *Leguminosen*' is a little premature because its flowers are very unlike those of *Polygalaceae* in the orientation of the petals, the structure of the inflorescence, sepals, and anthers, etc. In fact, examining material of some *Krameria*-species gave me no hints at all of similarities with members of *Polygalaceae*. So the idea of Hutchinson (a connection between *Polygalaceae, Krameriaceae, Violales, Capparidales*) can be rejected. *Krameria* is still a genus of which the affinities are totally unclear. In my opinion it might be worthwhile to investigate affinities of *Krameriaceae* with *Tremandraceae*, which show similarities in the structure of the anthers. The latter family is the closest relative of *Polygalaceae* according to Melchior (1964) who places *Tremandraceae* and *Polygalaceae* as the only two families in the same

'Unterreihe'. But again, I see no similarities between *Tremandraceae* and *Polygalaceae* when examining material of these families.

In the most recent classification Cronquist (1981) includes both the *Krameriaceae* and the *Tremandraceae* into the order *Polygalales*, to which further belong the *Malpighiaceae, Trigoniaceae, Vochysiaceae*, and *Polygalaceae*. The inclusion of the first two families seems incorrect to me. The relationship between the second group of families will be discussed below.

Similarities of different kinds come into the picture when considering another line of possible relationships: that between *Polygalaceae, Trigoniaceae, Vochysiaceae, Malpighiaceae* (and from the latter family either to *Sapindales*, or to *Rutales*, or to *Geraniales* – those possibilities will not be discussed here). Especially a close affinity between *Polygalaceae* and *Vochysiaceae* is mentioned by the majority of authors dealing with major classifications. No detailed studies have been performed, however, to verify such an assumption. Considering the possibility of a certain kinship between these families, I came upon a number of similarities (apart from many differences, of course).

In all these families extrafloral nectaries occur on sepals, bracts, nodes, and/or leaves. Samaroid fruits are present in members of all families. The corolla is strongly zygomorphous, and often less than five petals have been developed. Apart from *Malpighiaceae*, there is a similarity in the stamens which are reduced in number (less than 10) and are often connate in adaxially split tubes; triadelphous stamens are found in *Trigoniaceae* (three species of one genus) and *Polygalaceae* (four species of two tribes). The number of carpels is often 3 (but sometimes 2, 4, or 5 in the *Malpighiaceae*; 1 in two aberrant genera of the *Vochysiaceae*), but in the *Polygalaceae* 3 carpels occur only in *Atroxima* and *Carpolobia*. Also the number of ovules per carpel is a (weak) point of similarity. Usually this is 1 or 2, sometimes 4–8 (part of *Xanthophyllum; Callisthene; Qualea*); rarely more numerous (*Xanthophyllum fragrans; Euphronia*). The flowers of the *Malpighiaceae, Trigoniaceae*, and *Vochysiaceae* differ, however, from those of the *Polygalaceae* in having their plane of symmetry at a sharp angle to the median plane.

Further it can be mentioned that lianas or scandent plants occur in all families, that the venation pattern of the leaves seems to be fairly similar, that special cells (chapter 1.6) occur in the *Polygalaceae, Vochysiaceae* (and possibly in the *Trigoniaceae*), and that the families (including the *Malpighiaceae*) show similarity in wood anatomical respects (Heimsch, 1942).

What are the consequences of a possible relationship between *Polygalaceae, Trigoniaceae, Vochysiaceae*, and *Malpighiaceae*? Under the assumption that the *Polygalaceae* are monophyletic indeed, the family shows a number of *autapomorphous characters*:

1) the unique pollen type
2) the sessile partial inflorescences
3) absence of stipules
4) absence of the median adaxial stamen

Perhaps also the difference in the plane of symmetry of the flower can be considered as an autapomorphous character of the *Polygalaceae*, being possibly a reversion in the evolution of that condition.

2.2. Position of Xanthophyllum in the Polygalaceae

In the previous chapter a number of character-states has been discussed. Of those which showed differences on the infra-familiar level, this led to assumptions on the state of three characters, *viz.:*

1) the sympodial growth of the twigs (chapter 1.1)

2) the way of dehiscence of the anthers (chapter 1.9.3)

3) the presence of septs in the ovary (chapter 1.11)

In the characters 1 and 3 *Xanthophyllum* shows an apomorphous condition, in character 2 probably the plesiomorphous condition. The character-state 'fruits indehiscent' (chap-1.13) is apomorphous, too, but parallel apomorphous states occur in the tribe *Moutabeae* and *Polygaleae*. One character (the number of ovules per carpel; chapter 1.11) could not be used because I could not decide whether the apomorphous state of that character is one ovule per carpel, or two (or more). This point is not any more that important as it may seem to be, because the differences between *Xanthophyllum* and the other *Polygalaceae* are smaller than generally has been assumed. Separation of *Xanthophyllum* as a (monotypic) family can hardly be defended because the *Polygalaceae s.s.* would become a paraphyletic group. For the same reason elevation of the tribe *Helleboreae* to family level would lead to a paraphyletic family *Ranunculaceae s.s.* (compare chapter 1.11).

The *Moutabeae* have some characters in common with *Xanthophyllum*, and some with the *Polygaleae*. I do not have enough arguments to assume that they are closer related to the *Polygaleae* than to *Xanthophyllum*. Thus one should not change Chodat's (1896) solution to split the family into three tribes, *Polygaleae, Moutabeae*, and *Xanthophylleae*.

It is a pity that Cronquist (1981) still maintains the *Xanthophyllaceae* next to the *Polygalaceae*. Apart from the errors in his key to the families of the order *Polygalales*, the given differences between his *Xanthophyllaceae* and the *Polygalaceae s.s.* are suspect, even on paper.

2.3. Phylogenetic relations of Xanthophyllum groups

In Table 3 a survey is presented of all characters which I have used for the circumscription of the infrageneric groups, indicating the different character-states, their distribution over the groups, and the supposed plesiomorphous condition. It should be noted that the choice of the number of a character-state has no meaning whatsoever for the presumed position of that condition in a certain transformation series; in fact, character-states with the same number may have been developed parallel.

For the characters E, F, H, K, and M, I was unable to formulate an idea on the presumed plesiomorphous condition. For each of them I made a choice, which thus is based on a 'feeling' rather than on facts. Three of the alternatives of the phylogenetic relations are depicted in Fig. 5.

In none of the models the occurrence of parallel developments could be excluded. (Model I: M4 in groups 2, 4, and 6; F2 in group 2 & 7 & 8 and group 6. Model II: M4 and F2 as above, A2 in group 2 and group 7 & 8.) In model III, in which M4 is regarded as a synapomorphous character for group 2 & 4 & 6, a great number of parallel character-states occur (A2, C1, F2, H2, K2, L3); that model is thus less acceptable than models I or II. As it is the only model in which the flat embryo (M4) is a *syn*apomorphous character-state

Table 3. Survey of characters.

character (with reference to ch. 1) \ group	1	2	3	4	5	6	7	8	presumed plesiomorphous condition a)	b)
A Nodal glands (ch. 1.3) 1. present 2. absent	1	2	1	1	1	1(?)	2	2	1	
B Venation (ch. 1.5) 1. coarsely reticulate 2. finely reticulate 3. scalariform	1	1	1	1	1	1	2	3	1	
C Petals (ch. 1.9.1) 1. equal 2. carina different 3. upper petals different	1,2	2	1	3	3	1	2	2	2	
D Stamens (ch. 1.9.2) 1. triadelphous – c) 2. longer than petals 3. otherwise ('normal')	3	3	3	1	3	2	3	3	3	
E Number of ovules per carpel (ch. 1.11) 1. 2 2. 4–c. 8 – d) 3. c. 20	2	1	3	2	2	2	2	1,2	?	(2)
F Stigma (ch. 1.12) 1. peltate 2. bilobed	1	2	1	1	1	2	2	2	?	(1)
G Fruit, dehiscence (ch. 1.13) 1. dehiscent 2. indehiscent	2	1	2	2	2	2	2	2	2	
H Fruit, size (ch. 1.13) 1. 1–2 cm diam. 2. 5–15 cm diam.	2	1	2	1	1	2	1	1(2)	?	(1)
K Number of seeds (ch. 1.13) 1. 1 (or 2) 2. 4 or more	2	1	2	1	1	2	1	1	?	(1)
L Testa (ch. 1.14.1) 1. 1 layer 2. 2 layers, outer thin 3. 2 layers, outer thick 4. 2 layers, reduced 5. 3 layers	3(4)	5	5	2	4	3	1	2,4	2?	
M Embryo and albumen (ch. 1.14.3) 1. thick with 'lateral cleavages', albumen scarce 2. thick with flat sides, albumen scarce 3. thick, globular, albumen 0 or scarce 4. flat, albumen copious	1	4	4	4	3	4	3	2,3	?	(2)

a) according to chapter 1 – b) choice (for Fig. 5) – c) also in *70. X. cucullatum* – d) in *16. X. arnottianum* also 2 or 3 – e) in *66. X. sylvestre* 1–4.

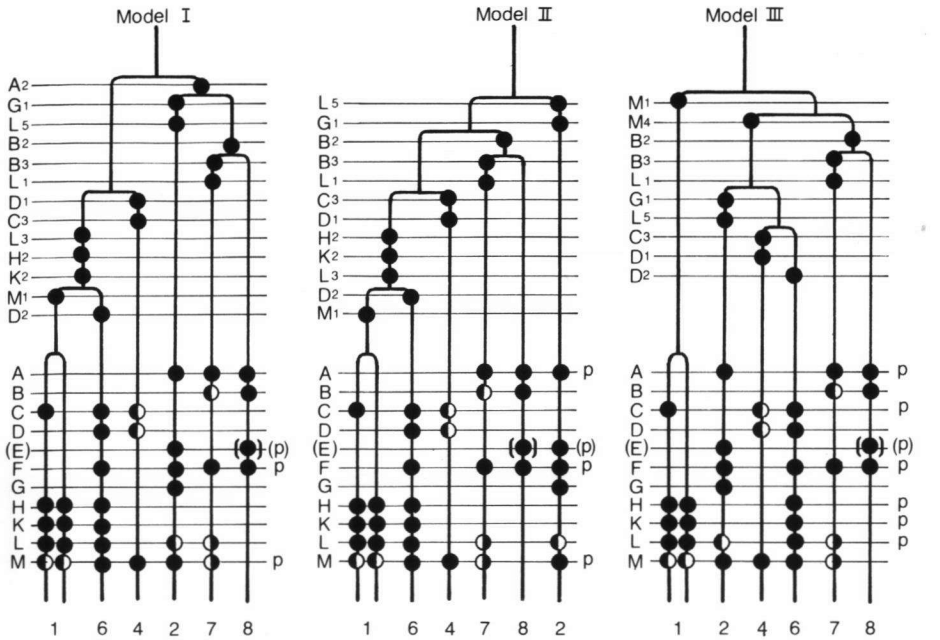


Fig. 5. Alternative models of phylogenetic relations in *Xanthophyllum*. — ● ◐ ◑: different apomorphous character-states. — p: apomorphous condition developed parallel. — A2, G1, etc.: character-states according to Table 3. — A, B, etc.: characters, survey. — 1, 6. etc.: groups in *Xanthophyllum*.

(for group 2 & 4 & 6), I must conclude that that character has developed parallel indeed (as I already assumed in chapter 1.14).

The difference between the remaining alternatives is not great. In model I three monophyletic groups can be distinguished (group 1 & 6; group 4; group 2 & 7 & 8), in model II four (group 1 & 6; group 4; group 7 & 8; group 2). In both models there is no synapomorphous character for group 1 & 4 & 6.

Discussion – The close relation between groups 1 and 6 is surprising when considering the numerous differences between the species of those groups, especially in the form of the embryo: it is hard to imagine that the character-states M1 (embryo thick with lateral cleavages, albumen scarce) and M4 (embryo flat, albumen copious) would represent two stages in the same transformation series. Here again the problem arises that the embryo-albumen character seems to be binary (without intermediate stages; see chapter 1.14). Such supposedly binary characters may be treacherous in phylogenetic reasoning, especially so because the germination stage is a very critical one in the life-cycle of plants. It is well imaginable that embryo and seedling are more liable to adaptive processes than other semaphoronts. One must expect then, that parallel adaptations have occurred in different phylogenetical lines. Some indirect evidence follows from De Vogel's observations (1980, p. 60). In (Malesian) woody dicots about half of the genera examined had seedlings with flat assimilating cotyledons. In herbaceous dicots the percentage of such seedlings is much higher

(c. 99%). From these data it may be deduced that flat assimilating cotyledons have an adaptive preference over foodstoring or haustorial cotyledons outside the woodlands. Returning to *Xanthophyllum* it may mean that the difference between character-state M1 and M4 may be of less importance than it seems to be at first sight. If so, group 1 and/or group 6 may represent paraphyletic groups!

At the present stage of knowledge those possibilities are too ill-founded to be of use for the practical work. In *Xanthophyllum* the direction of the evolution of different characters is uncertain in too many cases to justify the assumption that group 1 and 6 belong to the same monophyletic line. For such an assumption additional evidence is necessary.

Another complicating factor in the reconstruction of the evolution in *Xanthophyllum* is that 'reticulate' evolution (because of hybridization in ancient times) cannot be excluded. This will be discussed below.

2.3.1. The problem of Xanthophyllum fragrans: an old allopolyploid species?

The following account is a speculation on the effects of allopolyploidy for the practical work of taxonomists who try to include phylogenetic reasoning in their results. It must be very clear to the reader that the most important facts, *viz.*, chromosome numbers of *Xanthophyllum* species concerned, are unknown. Of course I will try to check in following studies the validity of my assumptions; at this moment, however, I must continue without the knowledge of chromosome characters.

Xanthophyllum fragrans grows very locally in N. Queensland (see under the species, no. 92). The species has some singularities: 1) petals twice as long as the second-largest in the genus (3–5 times as long as the petals of most species); 2) about twice the number of ovules as in other species with many ovules; 3) the longest anthers of all species; 4) by far the largest laminar glands; 5) the largest pollen grains. Those singularities, present in different parts of the plant, are similar in one respect: quantitatively they differ from character-states in other species in being larger or more. Especially in cultivated plants such phenomena are known as *'gigas' growth.* Quite often (but not in all cases observed) gigas forms are polyploids (see Schwanitz, 1967, p. 66 *seq.*).

When more collections of the extremely rare species became available by the kind help of the botanical staff in Atherton, Queensland, also the wood could be examined (Peletier-Bridgwater & Baas, 1982). In two different characters the wood of *X. fragrans* shows clear gigas characters; in wood anatomy this might be associated with polyploidy too.

Hence it seems acceptable, although chromosome numbers of *Xanthophyllum* species are totally unknown, to assume that *X. fragrans* is indeed a polyploid species and to examine theoretically the implications of that assumption for the phylogeny of the genus.

The next question must be whether *X. fragrans* is an autopolyploid or an allopolyploid species. Also when neglecting the gigas characters I can find no living species with enough characters in common with *X. fragrans* to permit the assumption that *X. fragrans* is an autopolyploid from such a species. (It should be noted, however, that Gottschalk (1976, p. 24, 101 *seq.*) refers to gigas characters as typical for *auto*tetraploids.)

It seems most probable that the original interspecific cross took place between a species of group 1 and a species of group 2. Reasons behind this assumption are:

– The only other (endemic) Australian species (*93. X. octandrum*, group 2) has a number

of similarities with *X. fragrans:* the seed type (testa, embryo), and the habit of the dry leaves. In nearly all other characters they are quite different.

– *90. X. ecarinatum* (group 1) from Borneo is similar (the gigas characters excepted) in the petals, the inflorescence, the nodal glands, and in the fruits (form, size, number of seeds, indehiscence). It differs, however, in the seeds (as well as in the gigas characters).

This is not to say that I suppose a relatively recent hybridization between the two species mentioned, but that the supposed parents were from the phylogenetical lines (groups 1 and 2) to which nowadays these two species belong.

For the practical taxonomic work hybrids are always embarrassing, usually showing a number of more or less intermediate character-states. It becomes very embarrassing indeed when a hybrid may have some characters in common with one parent, other characters in common with the other parent, together with some features of its own. If the parental lines have diverged in such a way that they can be separated at present into different subgenera, a hybrid dating back from ancient times cannot be placed in one of both subgenera, and the formation of a new subgenus is unnatural since such a subgenus is bi-phyletic.

Also the fact that the method which I adopted in trying to trace the phylogenetic affinities permits only monophyly as the evolutionary model (Hennig, 1966) leads unavoidable to serious problems (or errors), because allopolyploidy is, of course, essentially non-monophyletic!

Discussion – See under chapter 2.3.2.

2.3.2. The position of Xanthophyllum ramiflorum: another allopolyploid species?

Xanthophyllum ramiflorum, the only species (no. 81) of group 5, differs from the species of group 4 in the stamens (not being triadelphous), and in the structure of the seed (see Table 3). In group 4 the embryo is flat and enveloped by copious albumen, whereas in group 5 the embryo is globular, the albumen (almost) lacking, and the testa strongly reduced.

When assuming a monophyletic relationship between groups 5 and 4, the stamens of group 5 may be supposed to represent the plesiomorphous character-state in that group, in which case C3 is the only synapomorphous character of the combined group. The structure of the seed of group 5 might be 'explained' by the assumption that it represents an autapomorphous reversion of the evolution of the embryo character M4, combined with a reduction of the testa. If the stamens of group 5 would have been triadelphous too, and if the testa would have been similar to that of group 4, I would not have hesitated to assume that the difference in the seed of group 5 had been caused by reversion of the evolution of that character. Considering these differences I think that this assumption is improbable.

Assuming, however, that group 5 has originated by hybridization, it is less difficult to 'explain' its characters. Most of its characters would then be of a 'parent species' belonging to group 4. The characters of the seed (and the stamens) would be those of a 'parent species' belonging to group 7 or 8b.

Discussion – Allopolyploidy is a common phenomenon in angiosperms. Apart from mutation, it is supposed to be one of the major mechanisms for speciation in angiosperms (Stebbins, 1950, 1974; Gottschalk, 1976). In *Xanthophyllum* allopolyploidy might have

been the cause of the existence of *92. X. fragrans* (group 3) and *78. X. ramiflorum* (group 5). Both groups have only a single species. How would have been the situation if both groups each had developed a dozen species since their supposedly hybridogeneous origin? In the absence of genetical data, I think that the idea of such a possible hybridogeneous origin would not have occurred to me. Then, phylogenetic reasoning according to the Hennigian model would have led to false suggestions. It is also far from certain that no other groups than 3 and 5 are of hybridogeneous origin; I simply have no arguments for such an assumption, but it cannot be excluded either!

2.4. Evolution at species level

Because it appeared to be impossible to find the directions in the evolution of *Xanthophyllum* at group level (more or less subgeneric), much of what would be written on the supposed evolution at species level will be even more speculative. Therefore I have severely restricted my notes on the phylogenetic relations of the species in the Special Part. One may note, too, that the number of species which are incompletely known is rather high; also for that reason the assumptions on the recent history of the species would be very speculative.

2.5. Reflections

Disappointing as the results are of my fervent (and time-consuming) attempts to get a glance on the picture of evolution in the *species* I studied, and despite the fact that the method of reasoning I used cannot detect polyphylesis of species groups (allopolyploidy), I am convinced that I have not merely wasted my time in trying to use the Hennigian approach of work on the species I studied. The (unexpected) results on the *genus* and *family* level are of enough importance, I think; with another approach I would almost surely have been unable to make a verifiable contribution on the effects of the evolution in the genus and family.

2.6. Literature

Airy Shaw, H.K. 1973. J.C. Willis' A dictionary of the flowering plants and ferns. Ed. 8. Univ. Press, Cambridge, U.K.

Chodat, R. 1896. Polygalaceae. In: Engler, A. & K. Prantl, Die natürlichen Pflanzenfamilien III, 4: 323–345.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.

Gottschalk, W. 1976. Die Bedeutung der Polyploidie für die Evolution der Pflanzen. Fortschritte der Evolutionsforschung. Band VII. Fischer Verlag, Stuttgart.

Hallier, H. 1912. L'origine et le système phylétique des angiospermes exposés à l'aide de leur arbre généalogique. Arch. Néerl. Sci. Exact. Nat., sér. 3b, 1: 146–234.

Heimsch, C. 1942. Comparative anatomy of secondary xylem of the 'Gruinales' and 'Terebinthales' of Wettstein with reference to taxonomic groupings. Lilloa 8: 83–198.

Hennig, W. 1966. Phylogenetic systematics. (transl. D.D. Davis & R. Zangerl). Univ. Illin. Press, Chicago.

Hutchinson, J. 1957. The families of flowering plants. Clarendon Press, Oxford.

Leinfellner, W. 1972. Zur Morphologie des Gynözeums der Polygalaceen. Oesterr. Bot. Z. 120: 51–76.

Melchior, H. 1964. A. Engler's Syllabus der Pflanzenfamilien. II. Angiospermen. Gebr. Borntraeger, Berlin-Nikolassee.

Peletier-Bridgwater, S. & P. Baas. 1982. Wood anatomy of Xanthophyllum Roxb. IAWA Bull. n.s., 3: in the press.
Schwanitz, F. 1967. Die Evolution der Kulturpflanzen. Bayer. Landwirtschaftsverlag, München.
Stebbins, G.L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.
—— 1974. Flowering plants. Evolution above the species level. Belknap Press/Harvard Univ. Press, Cambridge, Mass.
Vogel, E.F. de. 1980. Seedlings of dicotyledons. Structure, development, types. Pudoc, Wageningen.

3. Classification

From chapter 2 it could be concluded that groups 1 and 6 may be closely related; in many respects the evidence for that assumption is not yet convincing. At present I will treat these groups as separate units, at the same rank as group 4. The evidence pointing to a close relation between groups 7 and 8 is sufficient for me to take them together in a grouping equal in rank to group 4. Because the position of group 2 may be interpreted differently (compare Fig. 5, models I and II), I also keep that group apart, in rank equal to group 4. The possibly bi-phyletic groups 3 and 5 are difficult to place, as long as it has not been proven that they originated from hybridization indeed. Both groups must be kept separate, too.

In view of the important differences between the groups it seems appropriate to give them the rank of subgenus, and to distinguish groups 7 and 8 on the sectional level.

Thus *Xanthophyllum* will be divided as follows:

subgenus	1. *Xanthophyllum*	
section	1. *Xanthophyllum*	(= group 7)
section	2. *Eystathes*	(= group 8)
subgenus	2. *Coriaceum*	(= group 5)
subgenus	3. *Triadelphum*	(= group 4)
subgenus	4. *Exsertum*	(= group 6)
subgenus	5. *Brunophyllum*	(= group 1)
subgenus	6. *Grandiflorum*	(= group 3)
subgenus	7. *Macintyria*	(= group 2)

Section *Eystathes* can be subdivided further:

subsection	*Jakkia*	(= group 8a)
subsection	*Eystathes*	(= group 8b)

Within subsection *Jakkia* the following groups of species may be distinguished: a) the *vitellinum*-group (species 30–47), b) the *beccarianum*-group (48–58), c) the *eurhynchum*-group (59–63), and d) a 'rest-group' (17–29). Because the rest-group is heterogeneous, a formal subdivision of subsection *Jakkia* is impossible at the present state of knowledge.

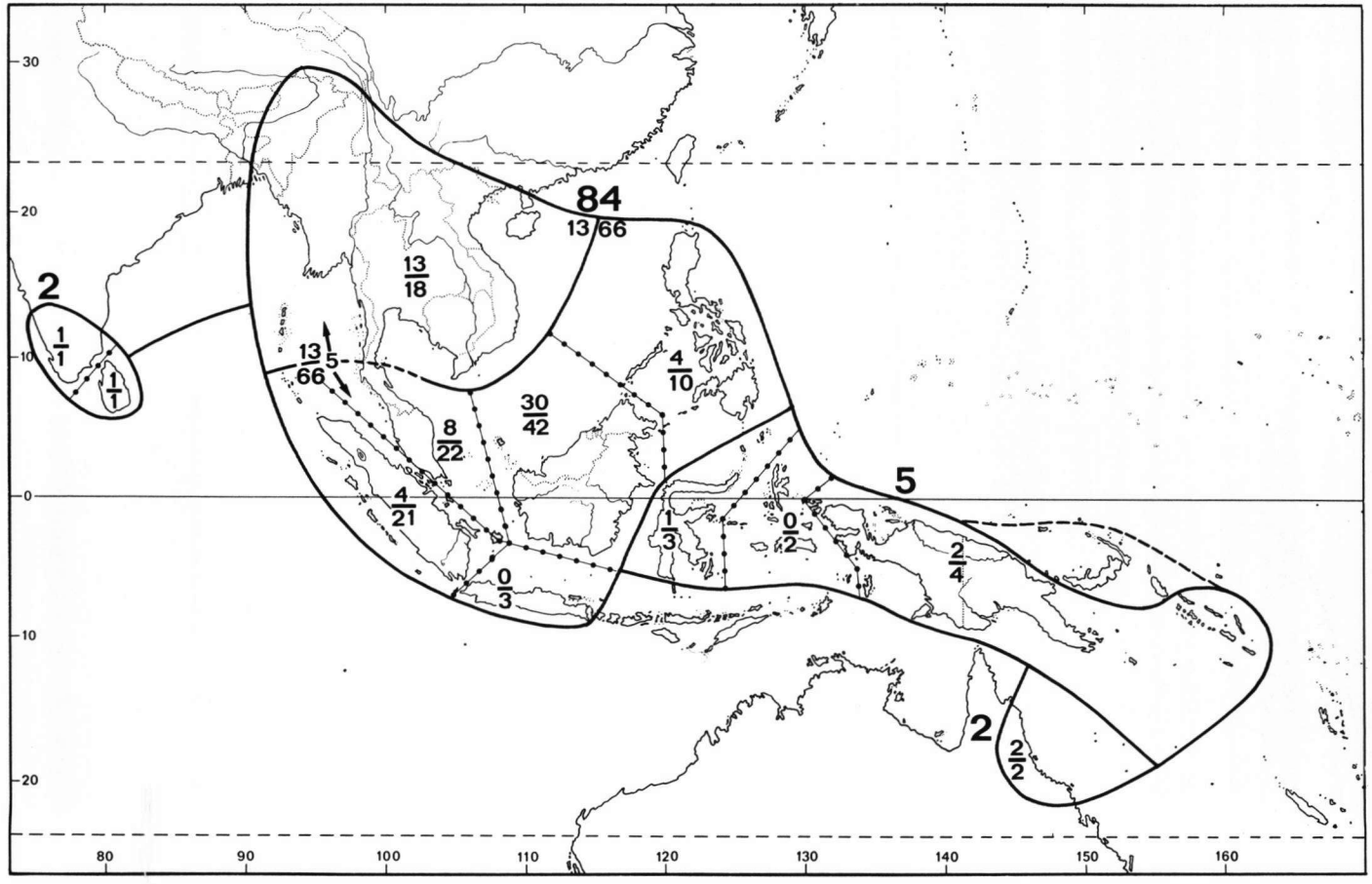


Fig. 6. Generalized area of *Xanthophyllum* with phytogeographical demarcation lines and species density; above the hyphen the number of endemic species, below the hyphen the total number of species.

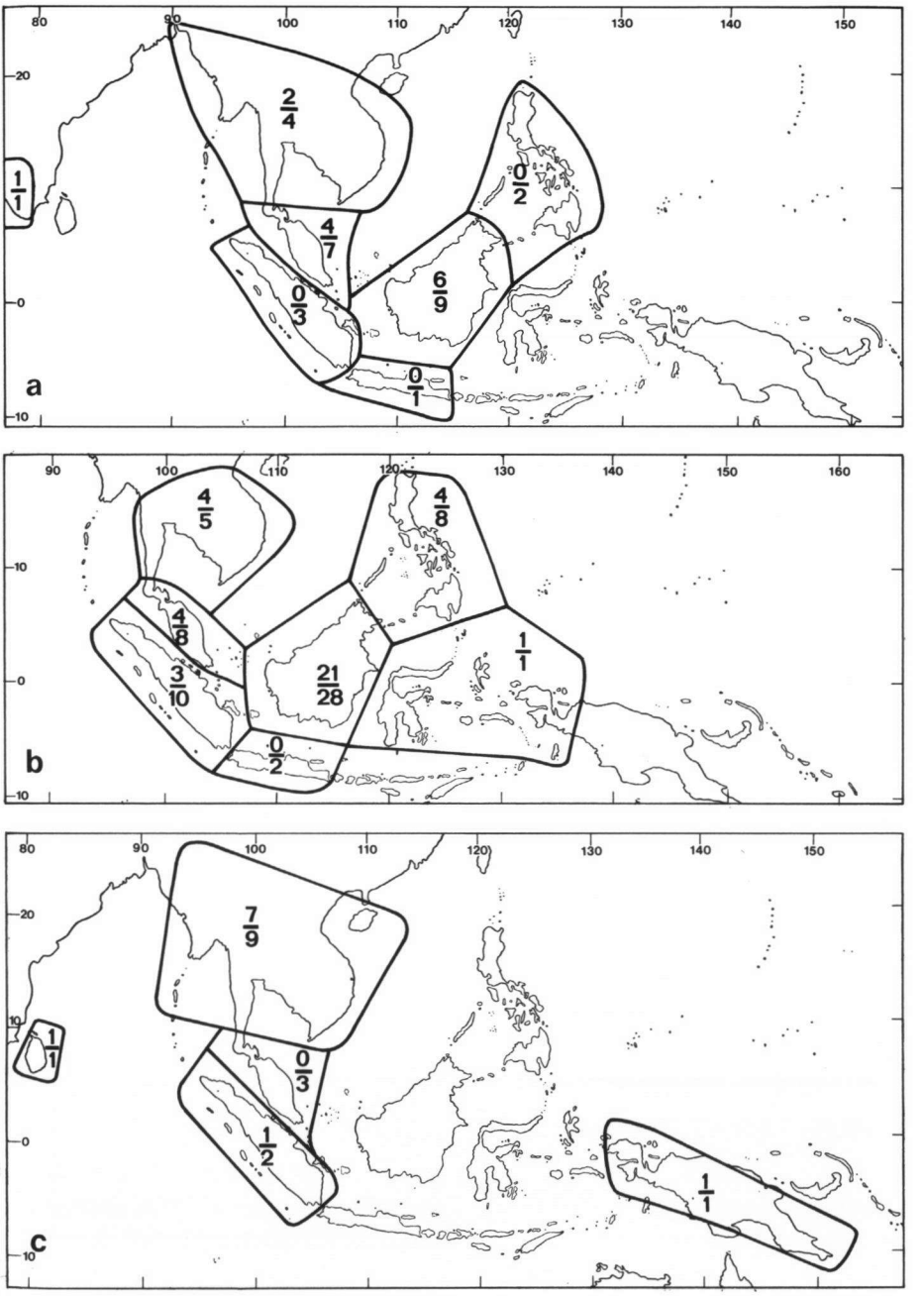


Fig. 7. Species densities of subg. *Xanthophyllum*; above the hyphen the number of endemic species, below the hyphen the total number of species. — a. sect. *Xanthophyllum*; b. subsect. *Jakkia*; c. subsect. *Eystathes*.

4. Habitat, distribution, dispersal, plant-geography

4.1. Habitat

Eighty species of *Xanthophyllum* occur in the lowland tropical rain forest, usually in very low frequencies; most specimens of those species have been collected below 500 m altitude, but occasionally specimens have been collected up to 1200(–1500) m altitude. Five species (nos. 13, 28, 35, 37, 54) are usually found between 500–1200(–1500) m altitude, but also lower. Another five species occur nearly exclusively in the submontane rain forest (nos. 33, 49, 69, 84, 86). About a dozen species are sometimes found in freshwater swamp forests (Anderson, 1963; Corner, 1978), but they are not confined to that habitat, except *78. X. ramiflorum* (see below). The habitat of the species occurring north of the Isthmus of Kra is often not indicated on the labels; with the exception of *67. X. lanceatum* and *75. X. virens* these species seem also to be confined to rain forests. *X. lanceatum* is confined to stream banks and marshes. Only *X. virens* occurs in the monsoon forests, tolerating rather long dry periods.

The habitat of *78. X. ramiflorum* differs from all other species, being confined to the 'padang' peat swamp forest on a very poor, sandy, wet soil. Its sclerophyllous habit (with coarse leaves, a feature which is exclusive for this *Xanthophyllum* species) supports the growing evidence that sclerophylly is an adaptation to nutrient-deficiency rather than to drought (Beadle, 1966; see also Van Steenis, 1979, p. 168–169).

4.2. Distribution

Fig. 6 gives the generalized area of *Xanthophyllum*, showing its distribution in SE. Asia and Malesia, extending to S. India and Ceylon in the west, and to N. Queensland and the Solomon Islands in the east. Its northern boundary runs from the foothills of the Himalayas through S. Yunnan to Hainan. In Malesia the genus is not found on Nusa Tenggara (Lesser Sunda Islands), and (probably because it is overlooked there) not in the Bismarck Archipelago.

At species level the accepted plant-geographical demarcation lines are remarkably well respected: not one species crosses Wallace's Line between Borneo and Sulawesi (Celebes), and only five species are found both north and south of the Isthmus of Kra in Peninsular Thailand against 79 species occurring either north or south of that line. Also Strait Torres (between Australia and New Guinea) functions as a demarcation line for the *Xanthophyllum* species.

Borneo has the highest number of species as well as the highest number of endemic species. This pattern does not deviate from the general trends in the distribution of rain forest species (Van Steenis, 1981, p. 75).

The absence from Nusa Tenggara (Lesser Sunda Islands) may be due to the too dry environment; the presence of a considerable number of species in continental Southeast Asia, however, indicates that at least some species may tolerate dryer periods. Strictly numerically one would be inclined to consider West Malesia as the primary centre of speciation of the genus.

At the subgeneric level the picture differs considerably (Fig. 7 & 8) (for practical rea-

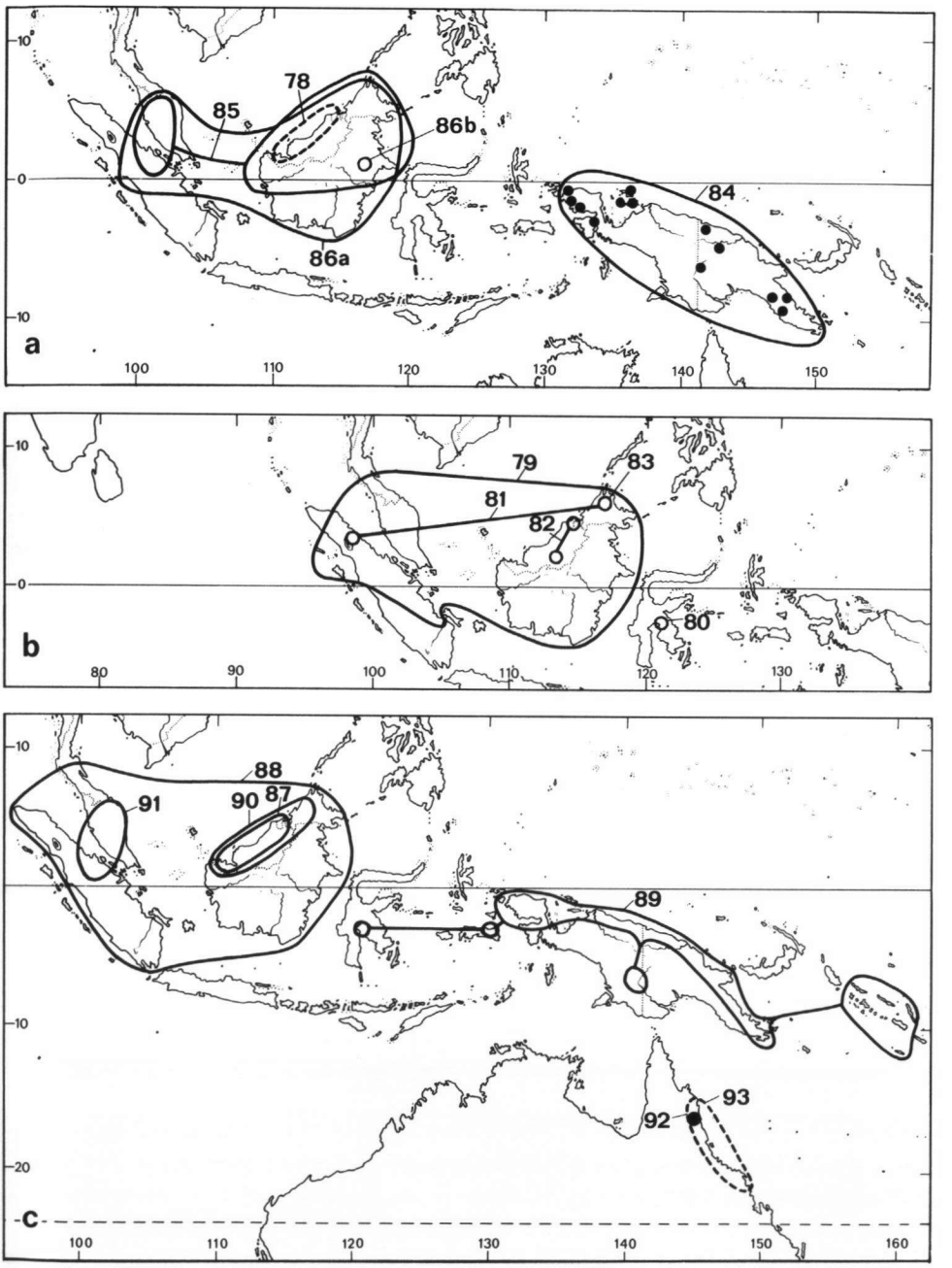


Fig. 8a. Generalized area of *78. X. ramiflorum* (subg. *Coriaceum*), and of subg. *Exsertum* (species 84–86). — Fig. 8b. Generalized area of subg. *Triadelphum* (species 79–83). — Fig. 8c. Generalized area of the species (87–91) of subg. *Brunophyllum*, of subg. *Grandiflorum (92. X. fragrans)*, and of subg. *Macintyria (93. X. octandrum)*.

Table 4. Summarized distribution of subgenera.

	SE. Asia	W. Malesia	E. Malesia (incl. New Guinea)	Australia	Figure
Subg. 1. *Xanthophyllum*	+	+	+	–	7
Subg. 2. *Coriaceum*	–	+	–	–	8a
Subg. 3. *Triadelphum*	–	+	+	–	8b
Subg. 4. *Exsertum*	–	+	+	–	8a
Subg. 5. *Brunophyllum*	–	+	+	–	8c
Subg. 6. *Grandiflorum*	–	–	–	+	8c
Subg. 7. *Macintyria*	–	–	–	+	8c

Table 5. Summarized distribution of subgenera

	SE. Asia	W. Malesia	E. Malesia (excl. New Guinea)	New Guinea-Australia
Subg. 1. *Xanthophyllum*	+	+	+	+
Subg. 2. *Coriaceum*	–	+	–	–
Subg. 3. *Triadelphum*	–	+	+	–
Subg. 4. *Exsertum*	–	+	+	–
Subg. 5. *Brunophyllum*	–	+	+	+
Subg. 6. *Grandiflorum*	–	–	–	+
Subg. 7. *Macintyria*	–	–	–	+

Table 6. Survey of subgenera occurring east and/or west of Wallace's Line.

	west	east
Subg. 1. *Xanthophyllum*	+	+
Subg. 2. *Coriaceum*	+	–
Subg. 3. *Triadelphum*	+	+
Subg. 4. *Exsertum*	+	+
Subg. 5. *Brunophyllum*	+	+
Subg. 6. *Grandiflorum*	–	+
Subg. 7. *Macintyria*	–	+

sons the species density of subg. *Xanthophyllum* has been depicted in three maps: Fig. 7 a–c, for the sections and subsections).

From Table 4 follows that the highest number of subgenera is found in West Malesia (5), followed by East Malesia (4), Australia (2), and Southeast Asia (1).

That picture changes considerably when New Guinea and Australia are taken together, as representing a geologically coherent area which only very recently has been divided into two by the submersion of the shallow Strait Torres. See Table 5.

The highest number of subgenera is found in West Malesia (5), followed by New Guinea–Australia (4) and East Malesia (4) and Southeast Asia (1).

A further simplification leads to the survey of Table 6. It is then apparent that the number of subgenera east of Wallace's Line is higher than that west of it. At this point the conclusions on the phylogeny of the subgenera should be taken into consideration. Subgenus 3 ('group 5'; see chapter 1) and subgenus 6 ('group 3') must be left out because both are possibly of hybrid origin. The only difference in representation east and west of Wallace's Line is then caused by subgenus 7 ('group 2') which is only found in the east.

4.3. Dispersal

Some species have a rather wide or very disjunct area. *1. X. flavescens* covers the whole area of section *Xanthophyllum* except S. India (Fig. 7a); *89. X. papuanum* occurs from Sulawesi to the Solomon Islands (Fig. 8c); *81. X. montanum* (Fig. 8b) is only known from Mt Kinabalu in N. Borneo, and near Lake Toba in Sumatera. It is rather improbable that those areas are the result of special adaptations: seeds of all species are thick and heavy, fruits are smooth and have a compact pericarp. Very likely the diaspores (probably the fruits; in subgenus 7 probably the seeds) will sink in water. The fruits are indehiscent except those of subgenus 7, which are irregularly 2-valved, exposing 1 (or 2) rather large seed(s). That condition may be one of the reasons of the rather small area of the subgenus: the exposed seeds may dry out earlier than those covered by the fruit wall.

Endozoochory can be excluded because the seeds are too large (at least c. 1 cm diam.), although fruits have been reported to be eaten (Ng, 1972, p. 352); this is also confirmed on a label: 'Birds are very fond of the fruit' (*68. X. hainanense: Tsang & Fung 621*). The sarcotesta of *85. X. amoenum*, *86. X. stipitatum*, and *88. X. obscurum* are edible, too. The embryo itself may be inedible in some species because of its content of saponine (*67. X. lanceatum*).

Long-distance dispersal may be ruled out because the fabulous agents responsible for that can hardly be expected to respect plant-geographical demarcation lines. Thus with the very few facts in hand I can only conclude that the areas have been formed gradually over land, gravitation being the main agent of (short-distance) dispersal (barochory). It must be concluded then that some areas have required long periods of time to reach their present size.

4.4. Discussion: migration from the East

On the subgeneric level it seems to be somewhat more likely that *Xanthophyllum* has originated east of Wallace's Line than west of it, because subgenus 7 is found only in the East. Under the assumption that the genus originated in West Malesia, the only species of

subgenus 7 (*93. X. octandrum*) should have passed Wallace's Line without leaving a trace in West Malesia. (Because Strait Torres is formed only in geologically recent times it can probably not have acted as a barrier for the dispersal of the species.) Another objection to that assumption is that I cannot find a subgenus in West Malesia from which subgenus 7 could have been derived.

The reverse assumption, e.g. that the genus originated east of Wallace's Line seems to be more likely. It may be added here, that species of subgenus 5 must have crossed Strait Torres in an earlier period, if my assumption (see chapter 2.3.1) that *92. X. fragrans* is a hybrid between species of subgenera 5 and 7 is correct. As Strait Torres is at present an ecological rather than a historic-geographical boundary (compare Van Steenis, 1979, p. 169), the possible withdrawal of subgenus 5 from Australia may be caused by the desiccation of the Australian mainland.

Another argument supporting the assumption that subgenus 7 and thus the whole genus has originated in New Guinea-Australia can be derived from the combination of the facts on the distribution of other genera of the *Polygalaceae* with the evidence of 'continental drift' (assuming that the species in S. India and Ceylon reached their present area from Indochina). The present-day distribution of the family may be called 'pan-tropical'; its greatest diversity on the generic level is clearly found in South America and Africa. There is not any indication (recent, nor fossil) that the *Polygalaceae* originated in Laurasia: all evidence leads to the conclusion that the *Polygalaceae* is a Gondwanaland family. *Xanthophyllum* being the single representative of its tribe, and West Malesia never having been a part of Gondwanaland, it can be excluded that *Xanthophyllum* has originated in West Malesia.

The tribe *Moutabeae*, too, did not originate in Malesia. Its only genus outside South America, *Eriandra* (which is endemic to New Guinea and the Solomon Islands), has derived characters (ovary 7- or 8-locular); also the wood of *Eriandra* has derived characters (Styer, 1977).

In the tribe *Polygaleae* there is at least one strong argument to assume a connection between New Guinea-Australia and South America: the genus *Bredemeyera* (incl. *Comesperma*; see Van Steenis, 1968) is distributed in both regions.

Returning to *Xanthophyllum*, I think that it was formerly present only in New Guinea-Australia; all present-day subgenera must have been represented at that time, as each of them still has a species east of Wallace's Line. In the middle Tertiary (Miocene; 25 million years ago) Australia must have reached Malesia (Hamilton, 1979), in which period *Xanthophyllum* actually spread to the areas which are now called West Malesia. Subsequent to that event a secondary centre of speciation has originated in subgenus 1, and less distinctly so in the subgenera 2, 4, and 5. Desiccation of the Australian area may have prevented a similar explosion of species in that area, or may have caused the extinction of many species there.

Admittedly, the postulated migration of *Xanthophyllum* from Australia-New Guinea into West Malesia and Southeast Asia seems to be unlikely when looking at Fig. 6 because of the low number of species east of Borneo. Similar examples of other eastern angiosperm genera with a secondary centre of speciation in West Malesia are very scarce in literature.

I wish to point to an exactly matching type of distribution, *viz.* of the species of the genus *Helicia* of the *Proteaceae*, revised and mapped by H. Sleumer (1955, p. 165, fig. 13). This genus also possesses a rather low number of species in the rain forest of Queensland

but a high number of species in Malesia and also in continental Southeast Asia, with one disjunct species in South Peninsular India and Ceylon. Ecologically *Helicia* possesses also the same features as *Xanthophyllum*: rain forest trees of the lowland and hills provided with large, heavy, one-seeded fruits. Its range and ratio of the density of species in the secondary centre of speciation in Malesia and Southeast Asia, its habitat and its means of dispersal being equal, this points to the homology of the ranges of *Helicia* and *Xanthophyllum*, and hence to similar origin. As there are no doubts that *Proteaceae* (including *Helicia*) stem from the Australian part of Gondwanaland, the range of the latter is a weighty argument to accept a similar origin for the present range of *Xanthophyllum*.

Unlike the *Proteaceae*, fossil evidence will probably not provide important new evidence on the history of the *Polygalaceae*, because the pollen grains probably cannot be identified on the genus level; only macrofossils of the wood or fruits of *Xanthophyllum* may be identifiable, but none are known thus far.

4.5. Literature

Anderson, J.A.R. 1963. The flora of the peat swamp forests of Sarawak and Brunei, including a catalogue of all recorded species of flowering plants, ferns and fern allies. Gard. Bull. Str. Settl. III, 20: 131–228.

Beadle, N.C.W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47: 992–1007.

Corner, E.J.H. 1978. The freshwater swamp-forest of South Johore and Singapore. Gard. Bull. Sing., Suppl. 1: 1–266.

Hamilton, W. 1979. Tectonics of the Indonesion region. Geol. Surv. Prof. Paper no. 1078. Washington.

Ng, F.S.P. 1972. In: Whitmore, T.C. (ed.), Tree flora of Malaya. Vol. 1. Longman, London.

Sleumer, H. 1955. Proteaceae. In: Flora Malesiana I, 5: 147–206.

Steenis, C.G.G.J. van. 1968. Notes on Bredemeyera (Comesperma) with a new Papuan species and the Australian species listed (Polygalaceae). Acta Bot. Neerl. 17: 377–384.

—— 1979. Plant-geography of East Malesia. Bot. J. Linn. Soc. 79: 97–178.

—— 1981. Rheophytes of the world. Sijthoff & Noordhoff, Alphen a/d Rijn.

Styer, C.H. 1977. Comparative anatomy and systematics of Moutabeae (Polygalaceae). J. Arn. Arbor. 58: 109–145.

SPECIAL PART

NOTES ON THE KEY AND THE DESCRIPTIONS

In the descriptions characters in colour, indumentum, and nervation have been mentioned only if they *differ* from the situation as present in the majority of the species of the (sub)section or subgenus. The form of the leaves has only been mentioned in exceptional cases; mostly it varies from ovate to lanceolate.

All *measurements* of parts of the flowers are taken from boiled flowers from dried material. Other measurements have been taken from dry material.

If the *fine venation* is little protruding (or obscure) one can make the venation visible by scratching off a small part (about 1 × 1 cm^2) of the upper or lower side of the leaf blade between the secondary nerves.

Presence or absence of *papillae* at the lower side of the leaf blade should be examined with a rather high magnification (c. ×25). Compare Fig. 9 a, b.

Number of *secondary nerves*. The first pair of rather weak nerves *at the very base* of the leaf blade, as well as the nerves in the acuminate part, have been disregarded when counting the number of secondary nerves.

Literature under the species has been abbreviated according to M.J. van Steenis-Kruseman, Citation of serials and some books. In: Flora Malesiana, ser. I, 5 (1956) cxlv–clxv.

Geographical names have been spelled according to the latest edition (1980) of 'The Times' atlas of the world; names not in that atlas have been spelled according to the original labels.

Unless stated otherwise, *lectotypes* have been assigned by the present author.

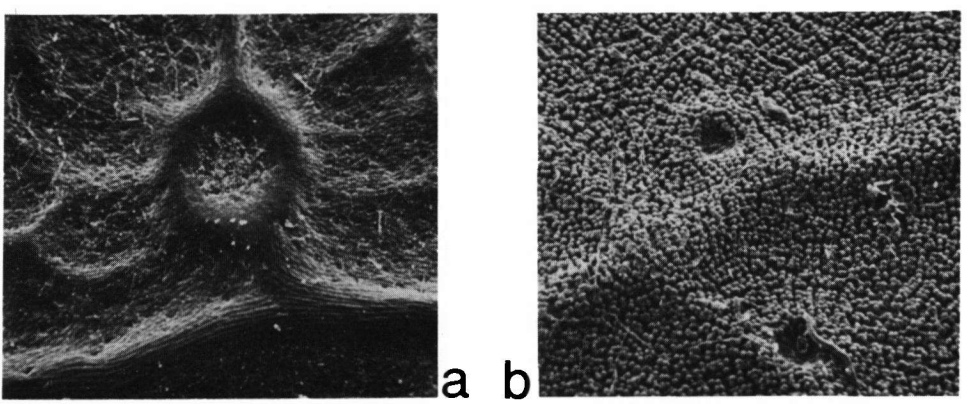


Fig. 9. Surface of lower side of leaf blade with laminar glands. – a. surface smooth; crateriform gland; b. surface glaucous-papillose; 2-pitted glands; both x 53 (a: *29. X. tenuipetalum*; b: *49. X. penibukanense*).

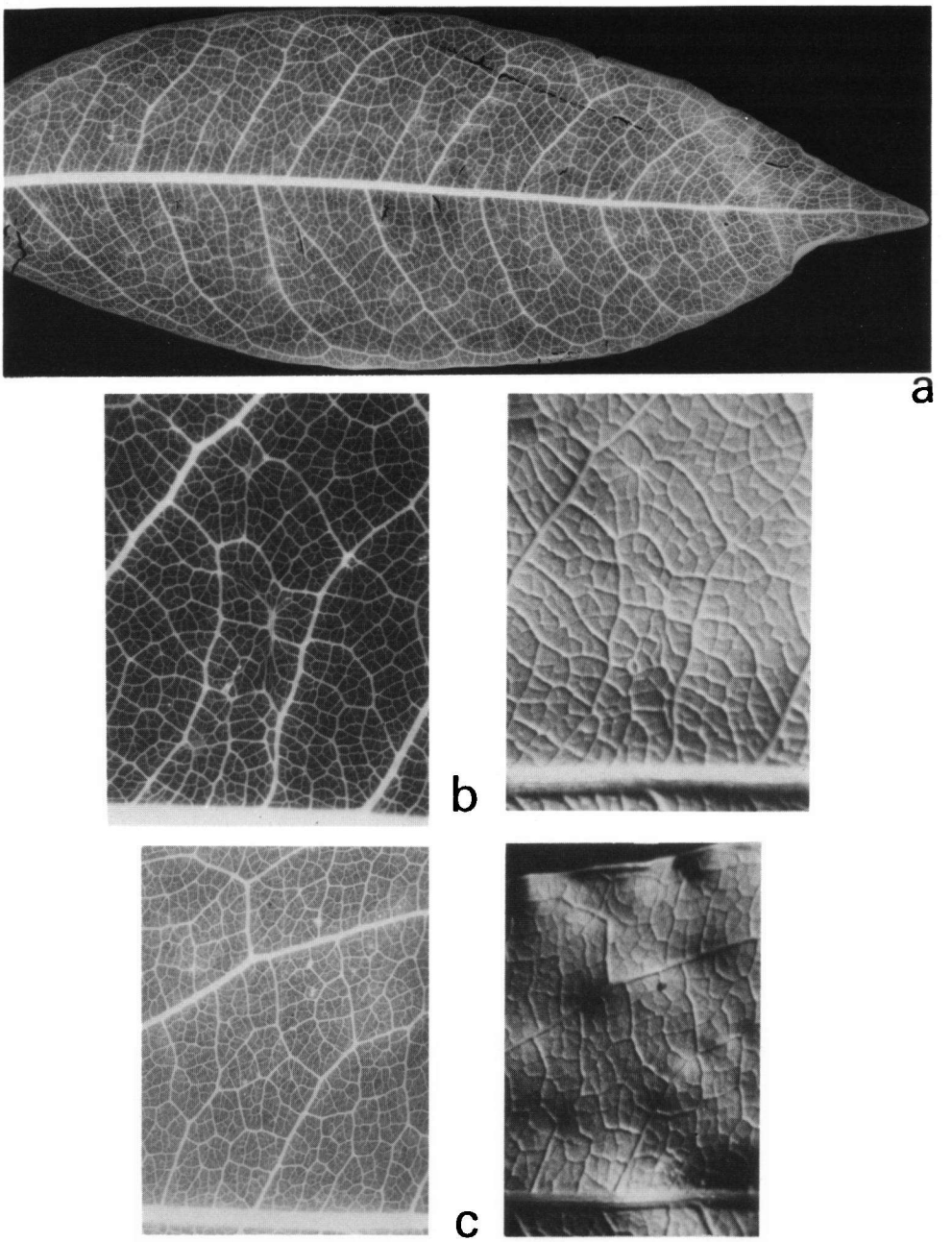


Fig. 10A. Finely reticulate venation (see Key to the species). — a. cleared leaf, x 1.5, b, c. part of leaf, at right before clearing, at left after clearing, both x 4.5 (a. *67. X. lanceatum, Falconer 598*; b. *75. X. virens, Fl. Thailand 1709*; c. *27. X. philippinense, Elmer 15335*).

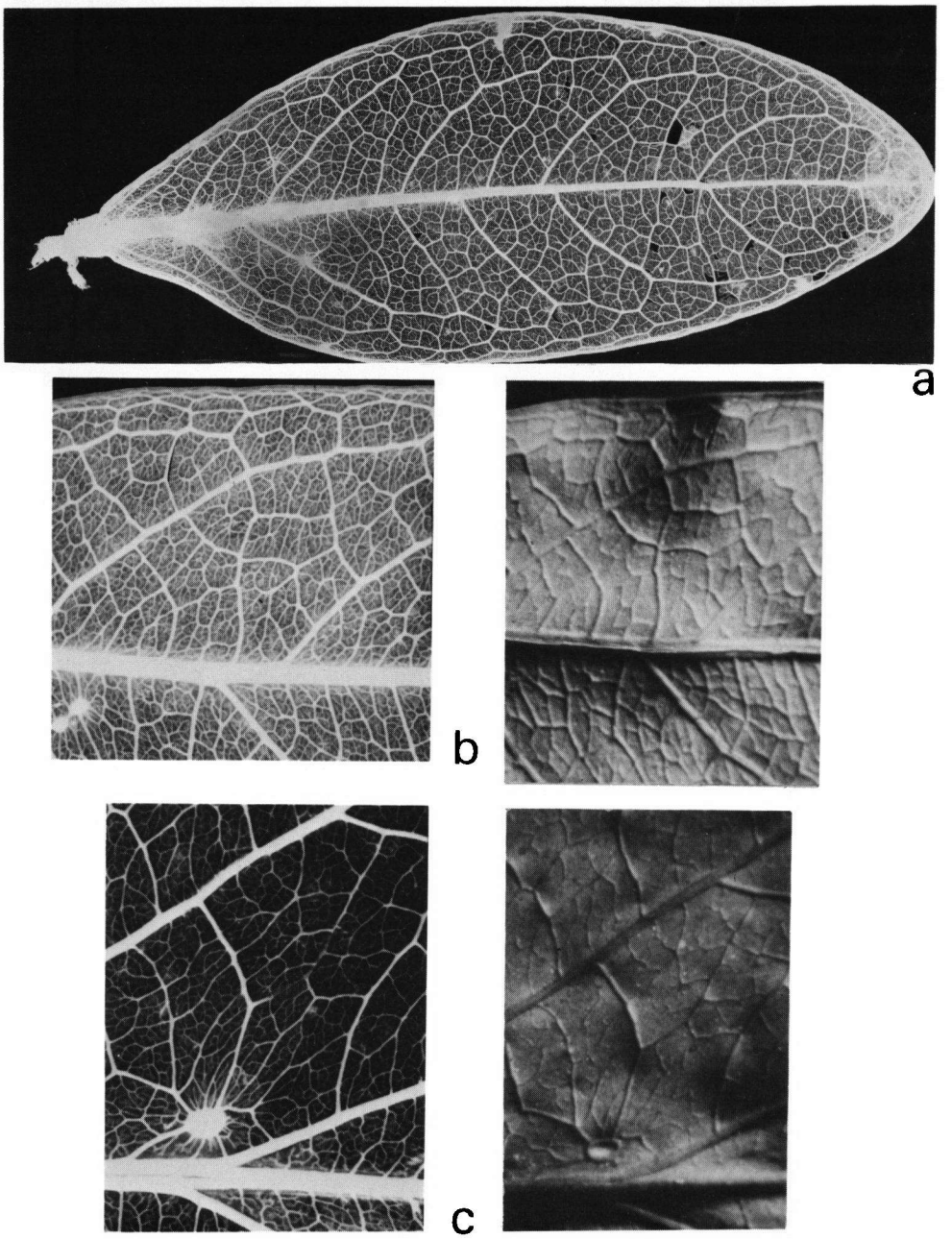


Fig. 10B. Coarsely reticulate venation (see Key to the species). — a. cleared leaf, x 1.5; b, c. part of leaf, at right before clearing, at left after clearing, both x 4.5 (a. *88. X. obscurum, Kostermans 107*; b. *81. X. montanum, SAN 46726*; c. *83. X. hildebrandii, Clemens 26048*).

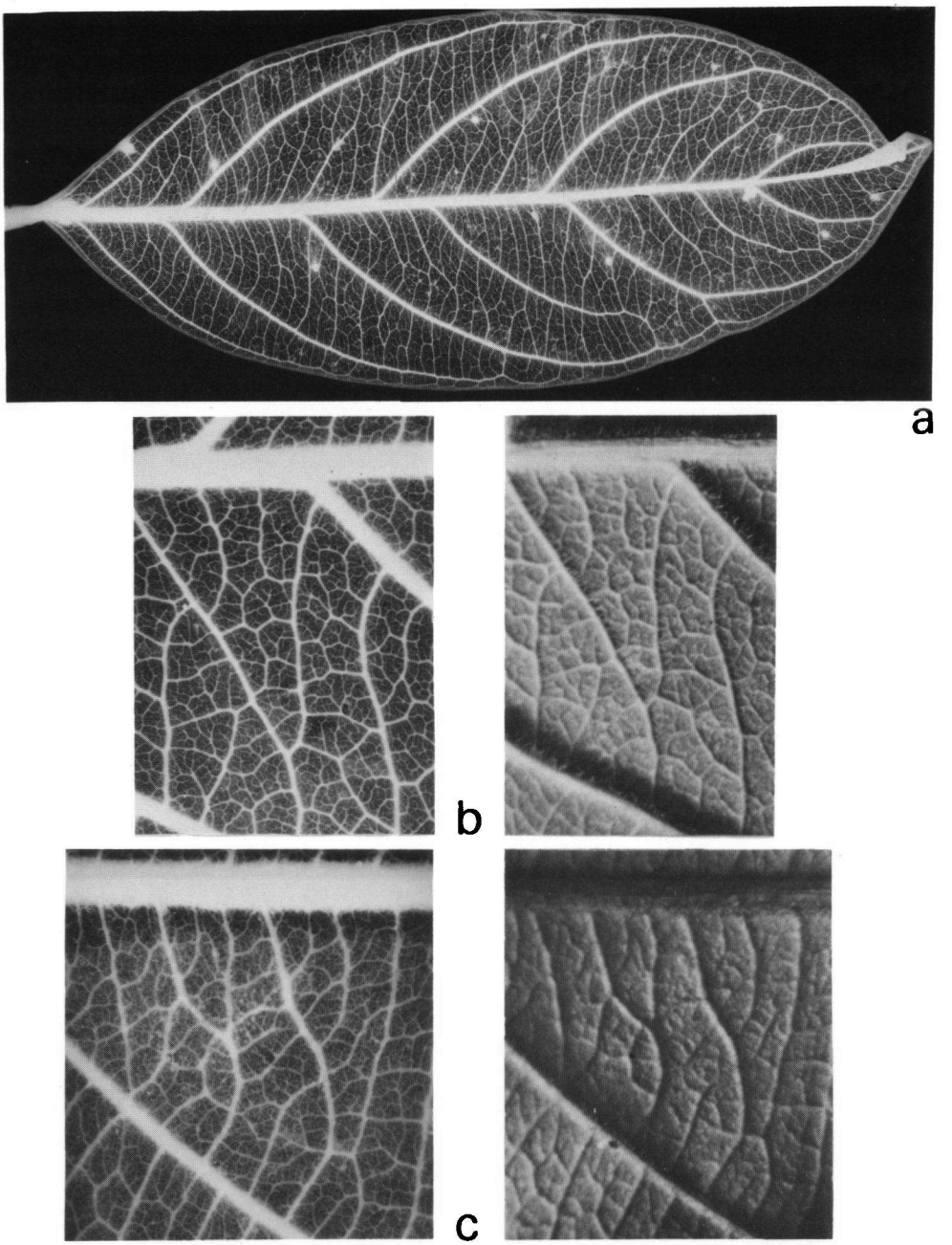


Fig. 10C. Scalariform venation (see Key to the species). — a. cleared leaf, x 1.5; b, c. part of leaf, at right before clearing, at left after clearing, both x 4.5 (a. *8. X. affine, SAN 21455*; b. *3. X. sulphureum, FRI 4178*; c. *5. X. eberhardtii, Poilane 7710*).

KEY TO THE SPECIES

1 a. Venation of 3rd order reticulate, see Fig. 10A, B (only intersecondary nerves reaching the nearestby secondary nerve, the true tertiary nerves running in angular lines between primary (midrib) and secondary nerve and there not seemingly crossing it towards the margin) 2

b. Venation of 3rd order scalariform, see Fig. 10C (tertiary nerves predominantly parallel and perpendicular to primary nerve (midrib), usually running straight from primary to secondary nerve, and there usually seemingly crossing it towards the margin; finer nervature reticulate) 3

2 a. Venation coarsely reticulate, see Fig. 10B (nerves of 3rd and 4th order forming usually irregular, polygonal areolae of 2 × 2 mm^2 or larger, venation within these areolae tree-like branched or dividing it into very unequal, not predominantly quadrangular parts) 18

b. Venation finely reticulate, see Fig. 10A (veins of 3rd and 4th order rather regularly subdivided into predominantly square areolae of about 1 × 1 mm^2) 40

3 a. Inflorescence axis at the nodes with 2 crateriform or cap-like glands 4

b. No glands present at the nodes of inflorescence axis 8

4 a. Leaves smooth at lower side 5

b. Leaves finely glaucous-papillose at lower side . . . . . **3. X. sulphureum**

5 a. Leaves glabrous to minutely appressedly hairy at lower side 6

b. Leaves distinctly patently hairy at lower side 7

6 a. Leaf base cuneate to rounded. Blade 5–25 × 2–12 cm. Nerves 4–10 pairs. **1. X. flavescens**

b. Leaf base cordate. Blade 20–50 × 6.5–25 cm. Nerves 14–20 pairs . **2. X. bullatum**

7 a. Leaf base cordate. Petiole 6–8 mm long. Nerves 7–10 pairs . . . . . **5. X. eberhardtii**

b. Leaf base obtuse to rounded. Petiole 8–12 mm long. Nerves 12 or 13 pairs. **4. X. cockburnii**

8 (3) a. Leaves distinctly patently hairy at lower side 9

b. Leaves glabrous to minutely appressedly hairy at lower side 12

9 a. Leaves smooth at lower side. Ovary and fruit glabrous or sometimes hairy in 2 rows in upper half 10

b. Leaves glaucous-papillose at lower side. Ovary and fruit hairy all round or in 4 rows in upper half . . . . . **14. X. rufum**

10 a. Inflorescence brownish hairy. Fruit apically pointed, dark when dry 11

b. Inflorescence axis greyish white hairy. Fruit apically rounded, creamish when dry. **9. X. pubescens**

11 a. Petiole 3–6.5 mm long. Sepals caducous in fruit, brownish hairy. Fruit smooth. Carina patently hairy outside . . . . . **13. X. annamense**

b. Petiole (4–)8–14(–16) mm long. Sepals persistent in fruit, greyish hairy. Fruit with 8 or more ribs. Carina appressedly hairy outside . . . . . **12. X. velutinum**

12 (8) a. Ovary and fruit glabrous or hairy in 2 or 4 rows in upper half, or sometimes sparsely minutely appressedly hairy all round 13
b. Ovary and fruit densely half-patently brownish hairy all round . **16. X. arnottianum**
13 a. Ovary and fruit glabrous or hairy in 2 rows, hairs greyish or ovary sometimes minutely sparsely appressedly hairy all round 14
b. Ovary and fruit hairy on 4 ribs in apical half, hairs brown . . . . **15. X. macrophyllum**
14 a. Leaves smooth at lower side 15
b. Leaves glaucous-papillose at lower side . . . . . **11. X. schizocarpon**
15 a. Midrib protruding at lower side (protruding to sunken at upper side) 16
b. Midrib flat at lower side (protruding at upper side) . . . . . **10. X. resupinatum**
16 a. Inflorescence axis branched, except in upper part not densely set with flowers or scars of pedicels 17
b. Inflorescence axis branched or unbranched, very densely set with flowers and scars of pedicels . . . . . **6. X. hosei**
17 a. Pedicel 1–1.5(–4) mm long. Sepals thickened basally, not fleshy, when dry middle brown with light coloured margin; outer sepals very sparsely minutely hairy. **7. X. ferrugineum**
b. Pedicel (2–)4–10 mm long. Sepals, if thickened, somewhat fleshy, without a lighter coloured margin; outer sepals more densely hairy . . . . . **8. X. affine**
18 (2) a. Flowers solitary in the axil of each bract or in the lower bracts with 3(–9) together. Ovary either glabrous inside, or petals equal and shorter than the stamens. Fruit indehiscent, 1–many-seeded 19
b. Flowers in lower part of inflorescence in separate clusters of up to 30 flowers. Ovary hairy inside and petals unequal, longer than the stamens. Fruit 1(or 2)-seeded, separating to near base with 2 valves, which, upon drying, rupture laterally. **93. X. octandrum**
19 a. Leaf blade at lower side with glands smaller than 0.9 mm diam., or glands (rather) numerous and then either situated near midrib or near or on the margin. Petals up to 2 cm long. Pedicel up to 15 mm long 20
b. Leaf blade at lower side in basal part with (1 or) 2 large glands, these 0.9–3.3 mm diam. Petals 5.5–6.5 cm long. Pedicel 15–25 mm long . . . . . **92. X. fragrans**
20 a. Leaf blade glaucous-papillose at lower side 21
b. Leaf blade smooth at lower side 22
21 a. Petiole (5–)8–12 mm long. Leaf blade 7–20 × 3–8 cm. Petals 7.5–8.5 mm long. Fruit 1-seeded . . . . . **78. X. ramiflorum**
b. Petiole 1.5–3 mm long. Leaf blade 2.6–7.5 × 0.7–2.6 cm. Petals 15–16 mm long. Fruit with 10 or more seeds . . . . . **87. X. brevipes**
22 a. Laminar glands either indistinct or in majority situated on or near margin 23
b. Laminar glands rather numerous and distinct, 0.5–1.1 mm diam., nearly all situated at base of secondary veins near midrib . . . . . **83. X. hildebrandii**
23 a. Flowering (flowers unknown in *91. X. chartaceum, 82. X. contractum*) 24
b. Fruiting 32
24 a. Stamens triadelphous, i.e. 6 stamens connate in 2 groups, and the remaining 2 stamens connate 25
b. Stamens either free or all connate except between upper petals 27

25 a. Leaf blade in upper half with at least 6 glands situated on the margin. Anthers shortly hairy along slits and at base 26
b. Laminar glands sometimes situated near margin of leaf blade but never present on the margin itself. Anthers completely glabrous . . . . . **81. X. montanum**
26 a. Filaments and style densely and rather shortly patently hairy . . . . **80. X. celebicum**
b. Filaments and style glabrous . . . . . **79. X. ellipticum**
27 (24) a. Petals nearly equal in size and form 28
b. Petals unequal, the lower middle one (carina) very distinct from upper ones. **88. X. obscurum**
28 a. Pedicel 1.5–4 mm long. Stamens shorter than petals 29
b. Pedicel at least 8 mm long. Stamens longer than petals 30
29 a. Filaments (nearly) free. Petals 7–8.5 mm long. Outer sepals 2.5–3.5 mm long, inner sepals 3–4.5 mm long . . . . . **89. X. papuanum**
b. Filaments connate to nearly halfway. Petals 9.5–12 mm long. Outer sepals 4–5.5 mm long, inner sepals 6–7 mm long . . . . . **90. X. ecarinatum**
30 a. Petals 7–12 mm long. Stamens 11–13(–16) mm long. Anthers glabrous or with a few hairs at base, 0.7–0.9 mm long 31
b. Petals 14–16 mm long. Stamens 17–22 mm long. Anthers hairy from base to apex, 1.0–1.3 mm long . . . . . **84. X. suberosum**
31 a. Petals (8–)9–11(–12) mm long. Style hairy to apex. Laminar glands 6–10(–20). **85. X. amoenum**
b. Petals 7–7.5(–8) mm long. Style glabrous in upper half. Laminar glands 0–2(–4). **86. X. stipitatum**
32 (23) a. Fruit small, less than 2 cm diam. (mature fruit not known in *82. X. contractum*), 1(or 2)-seeded 33
b. Fruit large, many-seeded 36
33 a. At least 6 glands situated on the leaf margin itself in upper part of leaf blade . . . 34
b. Laminar glands absent from margin of leaf blade 35
34 a. Pedicel 3–6(–8) mm long . . . . . **79. X. ellipticum**
b. Pedicel 7–9.5 mm long . . . . . **80. X. celebicum**
35 a. Petiole 3.5–5 mm long. Fruit up to 0.9 cm diam., basally shortly stipitate. **81. X. montanum**
b. Petiole 9–10 mm long. Fruit (immature?) c. 2 cm diam., c. 3 mm stipitate. **82. X. contractum**
36 (32) a. Pericarp strongly wrinkled outside when dry 37
b. Pericarp remaining smooth when dry 38
37 a. Fruit globular to pear-shaped, black . . . . . **91. X. chartaceum**
b. Fruit ellipsoid, attenuate at apex and at base when dry, orange to brown. **90. X. ecarinatum**
38 a. Fruit not black. Seeds (nearly) without albumen, with very thick cotyledons . . . 39
b. Fruit black. Seeds with copious albumen, with thin cotyledons. **84–86. X. suberosum, X. amoenum, X. stipitatum**
39 a. Seeds sticking to the pericarp when dry . . . . . **89. X. papuanum**
b. Seeds sticking together in drying, leaving shining reddish marks on inner side of the pericarp . . . . . **88. X. obscurum**

40 (2) a. Ovules 8–16* (also visible in fruit, if the pericarp has been longitudinally split into two halves) 41
b. Ovules 4*, very rarely 3 or 5 or 6 (except in *66. X. sylvestre* and in *65. X. ngii* also visible in fruit) 54
41 a. Hairs on petiole 1–1.5 mm long (exceptionally c. 0.4 mm long) 42
b. Petioles glabrous or with hairs not longer than 0.1 mm 46
42 a. Sepals and inflorescence axis with hairs 0.1–0.2 mm long (exceptionally 0.4 mm long) 43
b. Sepals and inflorescence axis with hairs about 1 mm long . . . . . **56. X. trichocladum**
43 a. Leaf blade flat or only midrib raised in a shallow depression 44
b. Leaf blade bullate between the tertiary nerves . . . . . **55. X. reticulatum**
44 a. Pedicel 7.5–14 mm long. Anthers 1.5–2.2 mm long. Flowers 12.5–16.5 mm long . 45
b. Pedicel 2.5–4.5(–5) mm long. Anthers 0.9–1.4 mm long. Flowers 11–12 mm long. **54. X. purpureum**
45 a. Petiole 5–6 mm long. Flowers 16–16.5 mm long. Anthers c. 2.2 mm long. **52. X. beccarianum**
b. Petiole 1.5–2.5(–3) mm long. Flowers c. 12.5 mm long. Anthers 1.5–1.6 mm long. **53. X. pedicellatum**
Note: If petiole 10–12 mm long, see note under *55. X. reticulatum.*
46 (41) a. Leaf blade smooth at lower side 47
b. Leaf blade glaucous-papillose at lower side 49
47 a. Axillary buds shorter than 2 mm. Midrib protruding above 48
b. Axillary buds 2.5–6 mm long. Midrib usually slightly sunken in basal half of the blade . . . . . **48. X. discolor**
48 a. Leaf base attenuate. Pedicel 8–15 mm long. Ovary (nearly) glabrous. Style very sparsely hairy . . . . . **58. X. laeve**
b. Leaf base cordate to cordate-truncate. Pedicel 4–4.5 mm long. Ovary and style densely hairy . . . . . **57. X. erythrostachyum**
Note: Compare also *16. X. arnottianum.*
49 (46) a. Carina densely appressedly hairy outside. Testa thin, wrinkled when dry. Albumen nearly absent. Radicle not protruding. (Fruit unknown in *73. X. burkillii*) . 50
b. Carina glabrous or nearly so outside. Testa brittle and not wrinkled when dry. Albumen thin only near the lower sides of the cotyledons. Radicle shortly protruding . 51
50 a. Outer sepals 4.6 × 3.9–4.3 mm, inner sepals 6.3–6.5 × 4.9–5.1 mm. Petals ciliate only just above base. Anthers 0.8–0.9 mm long . . . . . **73. X. burkillii**
b. Outer sepals 2.7–3.4 × 2.1–2.6 mm, inner sepals 4.0–4.5 × 3.1–4.4 mm. Petals all ciliate to apex. Anthers 1.1–1.2 mm long . . . . . **72. X. bibracteatum**
51 a. Petioles not transversely wrinkled, wrinkled only longitudinally 52
b. Petioles distinctly transversely wrinkled 53

* Directions for the *dissection of the ovary*. I could not avoid to use the number of ovules as important character in the key. Because the ovules are thick, and completely fill the space within the ovary, one should dissect the ovary carefully *at the upper side only*; afterwards style and gynophore can be cleft longitudinally, and after bending the parts apart, the two halves of the ovary come free easily. Cutting *through* the ovary, especially when performed from the lateral side, will lead to erroneous information.

52 a. Ovary and style (glabrous? to) minutely appressedly hairy. Petiole (8–)10–14 mm long. Nerves 11–14 pairs ..... **50. X. pseudoadenotus**

b. Ovary and style densely patently hairy. Petiole 4–9 mm long. Nerves 6–13 pairs. **51. X. pulchrum**

53 a. Petiole 8–15 mm long, gradually widened into the attenuate leaf base. Lower pair of nerves reaching beyond the middle of the leaf blade ..... **49. X. penibukanense**

b. Petiole 3–6(–7) mm long, abruptly ending into the cuneate to cordate leaf base. Nerves in lower part of leaf blade not reaching to the middle of the blade. **48. X. discolor**

54 (40) a. Inflorescence with more than 1 flower. Leaf blades, at least averagely, more than 5 cm long 55

b. Flower (and fruit) solitary, subapical, only one per twig. Leaf blade 1.6–5(–6) × 0.5–1.6(–1.9) cm ..... **26. X. parvifolium**

55 a. Ovary (and fruit) glabrous outside or very sparsely hairy and then soon glabrescent, or fruit hairy only around the style scar 56

b. Ovary and fruit densely hairy (or rather sparsely hairy and not glabrescent in *59. X. retinerve*) 63

56 a. Axillary buds 3–5, the upper one situated 5–15 mm above the leaf axil. Inflorescence branched 57

b. Axillary buds 2 or 3 (or 4), all close together in the leaf axil. Inflorescence unbranched 58

57 a. Petiole 5–6 mm long. Petals c. 7 mm long, the upper ones hairy inside to apex. Style rather densely hairy. Fruit (unknown) probably rather densely hairy around the style scar ..... **71. X. geminatum**

b. Petiole 7–10 mm long. Petals c. 12 mm long, the upper ones hairy inside only above base. Style nearly glabrous or sparsely hairy to halfway. Fruit (mature fruit unknown) nearly glabrous around style scar ..... **76. X. andamanicum**

58 a. Petiole distinctly transversely wrinkled. Upper petals hairy inside only just above base 59

b. Petiole not transversely wrinkled, irregularly longitudinally wrinkled. Upper petals hairy inside to near apex ..... **21. X. tenue**

59 a. Pedicel 5–8 mm long (fruits not known) 60

b. Pedicel 1.5–3.5 mm long (in fruit up to 5 mm, rarely longer) 61

60 a. Laminar glands 0.3–0.4 mm diam., situated in upper part of blade, mostly near the margin. Carina hairy outside in apical region. Anthers 0.5–0.6 mm long, hairy. **19. X. poilanei**

b. Laminar glands 0.4–0.5 mm diam., also present in basal half of leaf blade. Carina glabrous outside, only ciliate at apex and base. Anthers 0.3–0.4 mm long, glabrous. **20. X. ovatifolium**

61 a. Leaf blade at lower side glaucous-papillose, fine venation distinctly protruding . 62

b. Leaf blade smooth at lower side, fine venation indistinct .... **22. X. subcoriaceum**

62 a. Petiole (6–)7–11(–14) mm long. Axillary buds very densely shortly hairy, not soon glabrescent. Inner sepals c. 2.5 mm long. Anthers hairy at base .... **17. X. nigricans**

b. Petiole 5–6.5 mm long. Axillary buds soon glabrescent. Inner sepals c. 4 mm long. Anthers glabrous or with very few hairs at base ..... **18. X. borneense**

63 (55) a. Leaf blade glaucous-papillose at lower side 64
b. Leaf blade smooth at lower side 83
64 a. Most axillary buds, at least those in upper half of a shoot, 3 mm long or longer . 65
b. Most axillary buds up to c. 2 mm long 73
65 a. Axillary bud situated in the leaf axil, sessile 66
b. (Upper) axillary bud situated (1.5–)3–15 mm above the leaf axil and placed on a 0.5–1.5 mm long stalk ..... **47. X. korthalsianum**
Note: Compare also *74. X. lateriflorum*.
66 a. Scales of axillary bud not thickened at apex 67
b. Scales of axillary bud at apex with 2 distinct thickenings ..... **42. X. clovis**
67 a. Petiole (excl. attenuate leaf base) up to 17 mm long 68
b. Petiole 26–31 mm long ..... **41. X. petiolatum**
68 a. Axillary buds erect, usually with their flat side pressed against the twig 69
b. Axillary buds half-patent to patent, with their flat side perpendicular to the twig . 70
69 a. Petals 6–8 mm long. Outer sepals 1.6–2.5 mm long, inner sepals 2.6–3.3 mm long. Anthers 0.4–0.5 mm long ..... **32. X. griffithii**
b. Petals c. 13 mm long. Outer sepals 3.2–3.7 mm long, inner sepals 3.7–5.4 mm long. Anthers c. 0.7 mm long ..... **44. X. angustigemma**
70 a. Axillary buds up to 8 mm long. Petals 6.5–10 mm long. Anthers 0.5–0.7 mm long 71
b. Axillary buds 7–20 mm long. Petals 14–17 mm long. Anthers 1.0–1.2 mm long. **45. X. bracteatum**
71 a. Petiole 10–17 mm long. Leaf blade (10–)18–28 cm long. Petals 8–10 mm long. Anthers 0.6–0.7 mm long. Fruit irregularly wrinkled when dry 72
b. Petiole 4–12 mm long. Leaf blade 4–12(–15) cm long. Petals 6.5–8 mm long. Anthers c. 0.4 mm long. Fruit nearly smooth when dry ..... **32. X. griffithii**
72 a. Flowers in basal part of inflorescence in clusters of 7–9. Petiole c. 1.5–2 mm diam. Longest petals c. 8 mm long ..... **34. X. geesinkii**
b. Flowers in basal part of inflorescence solitary or rarely with 2 together. Petiole 3–4 mm diam. Longest petals 8.5–10 mm long ..... **35. X. cochinchinense**
73 (64) a. Axillary buds (2 or) 3–5, the upper one situated (2–)2.5 mm or more above the leaf axil, or buds more than 3 and close together 74
b. Buds seemingly single or 2 or 3, close together in the leaf axil 77
74 a. Upper axillary bud sessile on the twig 75
b. Upper axillary bud placed on a 1–2.5 mm long stalk. (Flowers unknown). **74. X. lateriflorum**
75 a. Leaf base attenuate to cuneate 76
b. Leaf base cordate ..... **70. X. cucullatum**
76 a. Upper petals 8.5–11 mm long, hairy inside only just above base. Carina auriculate. **75. X. virens**
b. Upper petals 11–15.5 mm long, hairy inside to near apex. Carina gradually widened from base to apex ..... **69. X. punctatum**
77 (73) a. Inflorescence at least basally branched, with more than 6 flowers (sometimes seemingly unbranched if lower bracts resemble leaves). Fruit apically rounded .. 78
b. Inflorescence unbranched, bearing only 3–6 flowers. Fruit (immature) apically pointed ..... **24. X. pauciflorum**

78 a. Filaments of upper stamens slightly S-curved, above base with a blunt appendage directed inwards. Fruit globular, 1.1–1.7 cm diam. 79
b. Filaments more or less straight, without appendages above base. Fruit (unknown in *64. X. novoguinense*) broadly ellipsoid or apple-shaped, 3.5–8 cm diam. 81
Note: See also *69. X. punctatum*.

79 a. Axillary buds projecting outwards, at least 2 times as long as wide 80
b. Axillary buds more or less enclosed between the base of the petiole and a low ridge of the twig, not projecting outwards, wider than high . . . . . **30. X. impressum**

80 a. Petiole 4–8(–9) mm long. Leaf blade 4–8(–10) × 1–4(–5) cm (in juvenile shoots up to 10 × 2.5 cm). Inner sepals 2.6–3.0 mm long. Anthers 0.4 mm long. **32. X. griffithii**
b. Petiole 9–14 mm long. Leaf blade 8–16 × 2–5(–7.5) cm. Inner sepals 4.4–5.5 mm long. Anthers 0.5–0.7 mm long . . . . . **33. X. monticolum**

81 (78) a. Petiole 6–10 mm long. Axillary buds 1 or 2. Nerves 5–8 pairs. Fruit (unknown in *64. X. novoguinense*) large, up to 8 cm diam., apple-shaped, pericarp up to 3 cm thick 82
b. Petiole 3–5 mm long. Axillary buds 2 or 3. Nerves c. 8–14 pairs. Fruit broadly ellipsoid to nearly globular, up to 3.5 cm diam., pericarp up to 3 mm thick. **67. X. lanceatum**

82 a. Petals c. 7 mm long. Pedicel 1.5–2.5 mm long . . . . . **64. X. novoguinense**
b. Petals 10–12 mm long. Pedicel 3–4.5 mm long . . . . . **65. X. ngii**

83 (63) a. Most axillary buds, at least in upper half of a shoot, 3 mm long or longer . . 84
b. Most axillary buds up to c. 2 mm long 92

84 a. Axillary buds up to 11 mm long and basally strongly thickened, or more than 3 times as long as wide and ± acute, or smaller than 8 mm 85
b. Axillary buds (8–)11–20(–30) × 6–12(–14) mm, c. 1–3 times as long as wide, flat, at base attenuate and not thickened, at apex rounded to obtuse. (Flowers unknown) . . . . . **46. X. heterophyllum**

85 a. Axillary buds half-patent to patent, glabrous or sparsely shortly hairy 86
b. Axillary buds erect, flattened against the twig, very densely shortly hairy. **43. X. reflexum**

86 a. Axillary buds at base narrow, not thickened 87
b. Axillary buds at base wide and strongly thickened 88

87 a. Petals 6.5–8 mm long. Inner sepals 2.6–3.0 mm long. Anthers c. 0.4 mm long. Fruit up to 1.1 cm diam., appressedly hairy . . . . . **32. X. griffithii**
b. Petals 10.5–11.5 mm long. Inner sepals 4.3–5.6 mm long. Anthers 0.6–0.9 mm long. Fruit up to 1.5 cm diam., patently hairy . . . . . **37. X. incertum**

88 a. Inflorescence branched. Petiole 8–14 mm long or much longer. Leaf blade with 7 or more pairs of nerves 89
b. Inflorescence unbranched. Petiole 4–6.5 mm long. Leaf blade with 3–5 pairs of nerves . . . . . **23. X. neglectum**

89 a. Petiole 8–18 mm long, exceptionally longer. Nervation at lower side of leaf blade distinctly protruding, or leaf blade much shorter than 20 cm 90
b. Petiole (18–)25–30 mm long. Leaf blade 22–42 cm long, finer nervation at lower side indistinct . . . . . **40. X. ceraceifolium**

90 a. Leaf blade c. 4–6 times as long as wide. Petiole (8–)15–18(–24) mm long, if shorter than 15 mm, then leaf base cordate. Nerves (9–)13–20 pairs. Anthers (0.6–)0.7–1.2 mm long 91

b. Leaf blade up to c. 3 times as long as wide. Petiole 8–14(–16) mm long. Nerves (6 or) 7–9(–11) pairs. Leaf base never cordate. Anthers 0.4–0.6(–0.7) mm long. **36. X. vitellinum**

91 a. Leaf base cuneate to rounded, or cordate with the margins curved upwards and connate above the apex of the petiole. Petals (8.5–)9.5–12.5(–14.5) mm long. Anthers (0.6–)0.7–0.9(–1.0) mm long ..... **38. X. adenotus**

b. Leaf base cordate, flat, or with only little upturned margins. Petals 15–18.5 mm long. Anthers 1.1–1.2 mm long ..... **39. X. palawanense**

92 (83) a. Midrib sunken above over most of its length 93

b. Midrib flat above or protruding, then sometimes with a groove in basal half ... 101

93 a. Leaf blade and petiole glabrous to minutely densely appressedly hairy 94

b. Leaf blade patently hairy at lower side. Petiole densely hairy with a mixture of short and long hairs ..... **63. X. malayanum**

94 a. Flowering 95

b. Fruiting 98

95 a. Upper petals hairy inside only at base 96

b. Upper petals densely patently hairy inside to near apex ..... **61. X. wrayi**

96 a. Nerves 3–7 pairs. Filaments free at base 97

b. Nerves 12–20 pairs. Filaments 1–3 mm connate ..... **62. X. venosum**

97 a. Petioles glabrous or hairy only in the upper groove. Finer venation at lower side not very distinct ..... **60. X. eurhynchum**

b. Petioles densely hairy all round. Finer venation at lower side very distinctly protruding ..... **59. X. retinerve**

98 (94) a. Fruit not densely set with thick warts, nor ribbed 99

b. Fruit densely set with thick warts or verrucate and ribbed 100

99 a. Petiole glabrous or minutely hairy in the upper groove. Fruit densely hairy, smooth to slightly wrinkled or 2–4-sulcate, sometimes finely rugose, up to 1.5 cm diam. **60. X. eurhynchum**

b. Petiole densely hairy all round. Fruit rather sparsely hairy, smooth, up to 2.2 cm diam. ..... **59. X. retinerve**

100 a. Fruit apically shortly but distinctly beaked, strongly verrucately ribbed. **62. X. venosum**

b. Fruit apically rounded, densely set with thick warts. **60, 61. X. eurhynchum, X. wrayi**

101 (92) a. Region of the twig above the leaf axil and the 2–4 very small and inconspicuous axillary buds densely shortly hairy 102

b. Twig glabrous above the leaf axil. Axillary buds glabrous or sparsely hairy and soon glabrescent 103

102 a. Petiole glabrous or minutely hairy in the upper groove. Finer nervation at lower side of leaf blade not very distinct. Fruit either densely set with thick warts, or densely hairy and smooth to slightly wrinkled or 2–4-sulcate or finely rugose. **60. X. eurhynchum**

b. Petiole minutely densely appressedly hairy all round. Finer nervation at lower side of leaf blade very distinctly protruding. Fruit rather sparsely hairy, smooth. **59. X. retinerve**

103 a. Axillary buds (2 or) 3–7, the upper one situated at least 1–2 mm above the leaf axil 104

b. Axillary bud(s) seemingly 1, or 2, rarely 3, close together in the leaf axil 105

104 a. Inflorescence branched, in basal half flowers 1–7 together, lowermost bracts opposite, lowermost bracts of side axis opposite. Petals 6.5–9 mm long. **75. X. virens**

b. Inflorescence unbranched or branched only at base, all bracts alternate, flowers all solitary. Petals (8.5–)9–11.5 mm long . . . . . **77. X. zeylanicum**

105 a. Inflorescence branched 106

b. Inflorescence unbranched 110

106 a. Filaments of upper stamens slightly S-curved, above base with a blunt appendage directed inwards. Fruit up to 2 cm diam., 1- or 2-seeded 107

b. Filaments nearly straight, without appendages. Fruit up to 7 cm diam., 1–4-seeded. **66. X. sylvestre**

Note: Compare also *16. X. arnottianum.*

107 a. Axillary buds projecting outwards, at least 1.5 mm long. Fruit smooth, style scar at apex 108

b. Axillary buds rounded, 0.3–1.1 mm long, often sunken in the tissue of the twig or enclosed by a ridge. Fruit with a shallow groove from base to the strongly excentrical style scar . . . . . **31. X. colubrinum**

108 a. Petiole 8–18(–24) mm long. Leaf blade 8–47 cm long, with 7–20 pairs of nerves. 109

b. Petiole 4–8(–9) mm long. Leaf blade 4–8(–10) cm long, with 4 or 5 (or 6) pairs of nerves . . . . . **32. X. griffithii**

109 a. Leaf blade c. 4–6 times as long as wide. Petiole (8–)15–18(–24) mm long. Nerves (9–)13–20 pairs. Anthers (0.6–)0.7–0.9(–1.0) mm long . . . . . **38. X. adenotus**

b. Leaf blade up to c. 3 times as long as wide. Petiole 8–14(–16) mm long. Nerves (6 or) 7–9(–11) pairs. Anthers 0.4–0.6(–0.7) mm long . . . . . **36. X. vitellinum**

110 (105) a. Ovary (half-)patently, fruit patently hairy 111

b. Ovary and fruit appressedly hairy 112

111 a. Nerves c. 8–10 pairs. Pedicel of flowers 4.5–6, of fruits 8–11 mm long. Petals 13–19 mm long. Anthers 0.8–1.2 mm long . . . . . **28. X. ancolanum**

b. Nerves 3–5 pairs. Pedicel of flowers c. 2 mm long, of fruits c. 4.5 mm long. Petals 7–10 mm long. Anthers 0.3–0.4 mm long . . . . . **23. X. neglectum**

Note: Compare also *16. X. arnottianum.*

112 a. Inner sepals 2.0–2.5 mm long 113

b. Inner sepals 2.8–3.5 mm long 115

Note: With fruiting material, try both ways.

113 a. Inflorescence axis sparsely shortly hairy. Carina (nearly) glabrous outside. Anthers 0.5–0.7 mm long 114

b. Inflorescence axis densely shortly hairy. Carina densely hairy outside in upper part. Anthers 0.3–0.4 mm long . . . . . **31. X. colubrinum**

114 a. Leaf base truncate to cordate. Carina auriculate. Filaments 0.7–1.0 mm connate. **25. X. tardicrescens**

b. Leaf base cuneate to rounded. Carina gradually enlarged, not auriculate. Filaments free . . . . . **22. X. subcoriaceum**

115 a. Anthers 0.4–0.7 mm long. Gynoecium somewhat shorter than the carina 116

b. Anthers c. 1.2 mm long. Gynoecium c. 2 mm longer than the carina. Secondary nerves c. 5–7 pairs (difficult to count). Laminar glands 1–6. Petiole usually with a pair of glands about halfway . . . . . **27. X. philippinense**

116 a. Petiole with 2 distinct glands usually situated in basal half or near base. Nerves at least 6–8 pairs (in upper part difficult to count because of the very distinct finer nervation). Laminar glands numerous. Upper petals rather sparsely ciliate at apex. **29. X. tenuipetalum**

b. Petiole without glands. Nerves 4 or 5 pairs. Laminar glands 2–4(–10). Upper petals with a dense tuft of hairs at apex . . . . . **68. X. hainanense**

XANTHOPHYLLUM

Xanthophyllum Roxb., Pl. Corom. 3 (1820) ('1819') 81, *nom. cons.* – Type cons.: *X. flavescens* Roxb.

Pelae [Hermannus, Fl. Zeyl. (1717) 24 ('*Paelae*')] Adanson, Fam. 2 (1763) 448, *nom. rejic.*; *Banisterodes* [L., Fl. Zeyl. (1747) 192 ('*Bannisterioides*')] O. Kuntze, Rev. Gen. Pl. 1 (1891) 45, *nom. illeg.* – Type (see note): *Xanthophyllum zeylanicum* Meijden.

Eystathes Lour., Fl. Coch. 1 (1790) 235, *nom. rejic.* – Type: *E. sylvestris* Lour. (= *X. sylvestre*).

Kaulfussia Dennst., Schlüssel Hort. Malab. (1818) 30, *nom. invalid.* – Type: *K. geminiflora* Dennst., *nom. illeg.* (= *X. arnottianum*).

non Kaulfussia Nees, Horae Phys. Berol. 53 (1820) 16. – Type: *K. amelloides* Nees (*Compositae*).

non Kaulfussia Bl., Enum. Pl. Jav. (1828) 260, *nom. illeg.* – Type: *Aspidium aesculifolia* Bl., *op. cit.* 143 = *Christensenia aesculifolia* (Bl.) Maxon (*Pteridophyta – Marattiaceae*).

Jakkia Bl., Cat. (1823) 17; Bijdr. (1825) 60 ('*Jackia*'). – Type: *J. vitellina* Bl. (= *X. vitellinum*).

non Jackia Wall. in Roxb., Fl. Ind. 2 (1824) 321, *nom. illeg.* – Type: *J. ornata* Wall. = *Jackiopsis ornata* (Wall.) Ridsd., Blumea 25 (1979) 295 (*Rubiaceae*).

non Jackia Sprengel, Syst. Veg. (1826) 10, 85, *nom. illeg.* – Type: *J. spectabilis* Sprengel = *Eriolaena spectabilis* (Sprengel) Hook. *f.* (*Sterculiaceae*).

Guatteria Bl., Fl. Java (1830) 100. – Type: *G. incerta* Bl. (= *X. incertum*).

Skaphium Miq., Fl. Ind. Bat., Suppl. (1861) 357. – Type: *S. lanceatum* Miq. (= *X. lanceatum*).

Macintyria F. Muell., Fragm. Phyt. Austr. 5 (1865) 8. – Type: *M. octandra* F. Muell. (= *X. octandrum*).

Shrubs or trees, (1.5–)3–50 m high. Twigs terete, rather short, sometimes only a few internodes long, usually glabrous or soon glabrescent, to hairy; terminal bud of a shoot reduced, usually shortly stalked and appressed against the new shoot; nodes usually little thickened, smooth, sometimes bearing crateriform or cap-like glands or a low ridge rarely bearing minute (stipular?) appendages. *Axillary buds* seemingly single or usually 2, usually patent to half-patent, less often up to 8 in a single longitudinal row, the upper bud always larger than the lower one(s), all axillary or 1 or more supra-axillary; bud scales 2, opposite, equal, usually less than 1.5(–3) mm long, persistent or usually caducous, usually soon glabrescent, sometimes in their axils bearing secondary buds; adventitious buds sometimes

numerous in each node of older twigs, then usually giving rise to inflorescences. *Leaves* alternate (or spiral), in subsection *Jakkia* sometimes shifted-decussate (alternately having shorter and longer internodes between successive leaves); *petiole* up to 3 cm long but rarely longer than 1.5 cm, shallowly grooved above, rounded below, mostly very closely set with transverse, rounded ridges, sometimes faintly longitudinally wrinkled, rarely smooth, mostly glabrous, usually black, sometimes with 1 or 2 indistinct (rarely with 2–4 distinct) protruding or crateriform glands; *leaf blade* ovate to lanceolate, very rarely ± linear-lanceolate, (1.5–)4–18(–50) × (0.5–)1–8(–25) cm, base cuneate to rounded-attenuate or sometimes cordate, margin entire or very rarely slightly crenate, apex usually shortly acuminate or cuspidate; yellow, green, red brown or black when dry, usually more or less coriaceous, (sub)glabrous above, glabrous to hairy below and usually smooth, nearly always with few to numerous glands, these mostly flat and crateriform, sometimes protruding, mostly varying between 0.1–0.4 mm diam. but occasionally larger; nervature: lower side usually more distinctly nerved than upper side, midrib mostly protruding above, protruding or very rarely flat below, secondary nerves few to numerous, arched, never reaching the margin, usually forming a more or less distinct intramarginal nerve in apical half of the leaf blade, basal nerves sometimes reaching to more than halfway the leaf blade, tertiary nerves scalariform or reticulate, nerves of higher order forming irregular or regular areolae, each with a free, branched veinlet bearing 1 or more tracheoidal idioblasts. *Inflorescence* usually in apical and middle leaf axils, sometimes on the bare twigs, rarely terminal, branched or mostly unbranched, few- to many-flowered (or very rarely 1-flowered), flowers in basal half solitary or with 2 or 3 together (rarely in clusters of up to 30), in apical half nearly always solitary; nodal glands sometimes present, then usually crateriform; bracts usually alternate, as well as the bracteoles small, soon caducous, bracts sometimes with crateriform glands. *Flowers* bilaterally symmetrical or sometimes nearly regular, pedicelled. *Sepals* 5, quincuncial, sometimes all equal but usually inner (lateral) sepals up to twice as long and wide as the outer sepals, ciliate, sometimes partly set with few, small, pitted glands. *Petals* 5, usually dissimilar, 5–25 (or very rarely 55–65) mm long, usually white or the upper petals with a yellow spot, less often yellow, pink, or purple when fresh, when dry creamish, orange, reddish or black, nearly always ciliate at base; carina (lower petal) usually unguiculate, often auriculate, more or less boat-shaped, usually covering stamens and style, rarely shorter than those, usually more hairy than other petals (sometimes glabrous) and (in flowers with unequal petals) somewhat smaller; lateral and upper petals usually a little constricted just above the insertion, usually narrower than the carina, upper petals often reflexed. *Stamens* nearly always 8, rarely 7, 9, or 8–10; 4 epipetalous, 2 placed at the base of the carina and adnate with it or not, 2 alternipetalous and opposite the lateral sepals; *filaments* basally often up to 0.2 mm connate except between the upper stamens, rarely connate up to halfway, very rarely triadelphous (alternipetalous filaments connate to adjoining filaments), usually hairy above the base; *anthers* basifix or less often versatile, apically opening with slits, (0.2–)0.3–1.2(–3.2) mm long, nearly always hairy at the base, sometimes hairy along the slits. *Disc* annular, on the outside slightly ribbed, nearly always glabrous. *Gynoecium* usually as long as androecium; *ovary* usually 0.5– 1 mm stipitate, syncarpous, composed of 2 median carpels, 1-locular or sometimes semi-2-locular, glabrous to very densely hairy outside, nearly always glabrous inside; *style* gradually narrowed towards apex, slightly curved or less often straight, glabrous to very densely hairy, nearly

always caducous at the beginning of seed setting; *stigma* usually small and slightly bilobed, sometimes peltate; *ovules* 2-seriate, 4 or (6–)8–c. 20, very rarely c. 40, rarely 5, only exceptionally less than 4, descendingly apotropous, anatropous, sessile (raphe extremely short), bitegmic, crassinucellate, after fertilization soon forming a hypostase at chalazal side. *Fruit* indehiscent or very rarely irregularly 2-valved, often globular, c. 1–15 cm diam. diam., pericarp thick or thin, usually hard. *Seed* 1 in the majority of species, or seeds up to 20; testa usually well-developed, of various structure, sometimes forming a sarcotesta, sometimes very reduced and sticking to the pericarp in drying; albumen copious to nearly absent in ripe seeds; embryo (rather) large, usually ± globular, sometimes triangular-broadly ovoid or flat, cotyledons creamish or sometimes green, plumule usually indifferentiated, radicle usually small. Germination hypo- or epigeal, testa shedded or not.

Note. The Code (Appendix III, no. 4281) indicates '*Banisterioïdes. Lin.*' as the type of *Pelae* Adanson. According to art. 10.1, the type of a genus is a species. *Bannisterioides* L. is not a species but a generic name; apparently the editors of Appendix III have noticed that no specific name was available in *Pelae*. As the name *Xanthophyllum zeylanicum* Meijden (this paper, species 77) is based on the same material as *Bannisterioides* L. and *Pelae* Adanson, *Xanthophyllum zeylanicum* should be designated as the type of *Pelae* Adanson to be in accordance with the provisions of art. 10.1.

KEY TO THE SUBGENERA

1a. Tertiary nerves coarsely reticulate, areolae usually not smaller than 2 × 2 mm² ... 2
b. Tertiary nerves scalariform, or finely reticulate, areolae 1 × 1 mm² or smaller. – Fruit mostly 1-seeded, indehiscent. Embryo globular. Albumen 0 or forming a rather thin layer. Stigma ± bilobed. Testa (1- or) 2-layered. (Species 1–77).
1. subg. **Xanthophyllum**

2a. Ovules 8 or more. Fruit indehiscent ... 3
b. Ovules 4. Fruit irregularly 2-valved. – Fruit 1-seeded. Testa 3-layered. Embryo flat. Albumen copious. Stigma ± bilobed. (Species 93) ... 7. subg. **Macintyria**

3a. Fruit 1-seeded ... 4
b. Fruit 4–more-seeded ... 5

4a. Stamens monadelphous. Embryo globular. Albumen very scarce. – Testa 2-layered, thin. Stigma peltate. (Species 78) ... 2. subg. **Coriaceum**
b. Stamens triadelphous. Embryo flat. Albumen copious. – Testa 2-layered, rather thin. Stigma peltate. (Species 79–83) ... 3. subg. **Triadelphum**

5a. Cotyledons flat, much thinner than the enveloping albumen ... 6
b. Cotyledons thick and with little albumen, if flattened laterally, albumen about as thick as cotyledon. – Testa 2-layered. Stigma peltate. (Species 87–91).
5. subg. **Brunophyllum**

6a. Stamens shorter than petals. Stigma peltate. Testa 3-layered. (Species 92).
6. subg. **Grandiflorum**
b. Stamens longer than petals. Stigma ± bilobed. Testa 2-layered. (Species 84–86).
4. subg. **Exsertum**

1. Subgenus Xanthophyllum

Nodal glands absent, nodal appendages sometimes present in subsection *Eystathes*. Axillary buds sometimes very long, usually thickened basally, subacute, sometimes hairy. *Petiole* sometimes with glands, sometimes hairy. *Leaf blade* sometimes hairy, base rarely cordate; tertiary nerves finely reticulate, or scalariform. *Inflorescences* usually branched. *Sepals* usually densely minutely greyish hairy out- and inside, sometimes with longer or differently coloured hairs, the inner ones often subglabrous in marginal area and often slightly keeled. *Petals* unequal, ciliate above base; carina unguiculate, boat-shaped, auriculate or not, usually densely hairy outside; lateral and upper petals narrow, usually oblanceolate to ± linear, more or less flat, slightly constricted basally, usually glabrous outside, usually slightly hairy inside above insertion of filaments, upper petals often reflexed. *Ovary* sometimes semi-2-locular, glabrous to hairy; style usually hairy; stigma small, slightly 2-lobed, very rarely wider than apex of style; ovules 4 to c. 20. *Fruit* indehiscent, usually globular, usually c. 1.5–2 cm diam. *Seed(s)* 1 (or 2), rarely up to 4; testa 1- or 2-layered; albumen present or not; embryo globular, plumule not differentiated.

Species: 77 (1–77).

DIAGNOSTIC KEY TO THE SECTIONS

1a. Tertiary nerves scalariform. Testa sticking to the inner side of the fruitwall in drying. Albumen absent . . . . . a. sect. **Xanthophyllum**

b. Tertiary nerves finely reticulate. Testa sticking to the rest of the seed in drying. Albumen present, though sometimes scarce . . . . . b. sect. **Eystathes**

1a. Section Xanthophyllum

Twigs usually densely patently hairy, sometimes glabrous. *Petiole* usually more or less smooth, sometimes with glands. *Leaf blade:* tertiary nerves scalariform, protruding. *Petals:* carina usually shortly unguiculate. *Ovary* sometimes semi-2-locular (the margins of the carpels touching the other ones along their length), glabrous, sometimes hairy in 2–8 rows, rarely hairy all round: ovules 6–16, or in *16. X. arnottianum* 4–10, in *8. X. affine* very rarely 5. *Fruit* globular or sometimes pointed or 4-sulcate, smooth or sometimes tuberculate. *Seed(s)* 1 or occasionally 2 (in *1. X. flavescens* often 2); testa reduced, without hard inner layer, sticking to the pericarp in drying, the raphe widely branched, hypostase not developed; albumen absent in ripe seed; radicle not exserted.

Species: 16 (1–16).

Notes. 1. The character-state 'ovary hairy in rows' is unique for section *Xanthophyllum*.

2. *8. X. affine* is probably heterogeneous, but I did not succeed in splitting it; the taxonomic level of the related species 6–11 is thus unbalanced. The position of *16. X. arnottianum* is somewhat uncertain (see there).

1. Xanthophyllum flavescens

Fig. 3 A-k

X. flavescens Roxb., Pl. Corom. 3 (1820) 82, t. 284, fig. 2; Wallich, Cat. (1831) 4198 B; Roxb., Fl. India, ed. Carey, 2 (1832) 221; Walp., Rep. 1 (1842) 248; Drury, Handb. Ind. Fl. 1 (1864) 56; Kurz, J. As. Soc. Beng. II, 42 (1873) 79, 80; Prelim. Rep. For. Pegu (1875) 26; For. Fl. Br. Burma 1 (1877) 81; Brandis, Indian Trees (1906) 44, excl. syn.; Prain, Bengal Pl. (1963) 158. – Lectotype: *Roxburgh s.n.* (BM) ('May, 1811; Sp N. 363–p.3034, *Xanthophylla flavescens*, this is a large tree, found on Thothoree hill, flowers all yellow').

non X. flavescens auct.: Wight & Arn. (*et auct. al.*), Prod. (1834) 39 (= *16. X. arnottianum*) – Thwaites, Enum. (1858) 23; Trimen, Handb. Fl. Ceylon 1 (1893) 84 (= *77. X. zeylanicum*) – A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209 (see below, note 1) – Fern.-Vill., Nov. App. (1880) 14; S. Vidal, Sinopsis (1883) 13 (= *36. X. vitellinum*).

X. excelsum (Bl.) Miq., Fl. Ind. Bat. 1, 2 (1858) 129; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274; Binnend., Ann. Jard. Bot. Btzg 1 (1876) 172; King, Mat. Fl. Mal. Pen. (1890) 142, *p.p. (sub X. affine)*; Koord. & Valeton, Icon. Bog. 1, 1 (1897) 11–13, *p.p. (sub X. affine β excelsa)*; Boerl., Cat. Hort. Bog. (1899) 58; Koord. & Valeton, Bijdr. Booms. Java 5 (1900) 298; Racib., Ann. Jard. Bot. Btzg 17 (1900) 53; Boorsma, Bull. Dép. Agr. Ind. Néerl. 16 (1908) 3; Gagnepain, Desv. J. Bot. 21 (1908) 253; Fl. Gén. I.-C. 1 (1909) 246; Backer, Schoolfl. Java (1911) 80; Koord., Exk. Fl. Java 2 (1912) 453; Koord.-Schum., Syst. Verz. 1 (1912) Fam. 145, p. 2–4; Bold., Cat. Herb. Pl. Hort. Bog. Cult. (1914) 84; Merr., En. Born. (1921) 326, *p.p.*; Ridley, Fl. Mal. Pen. 1 (1922) 143, *p.p. (sub X. affine)*; Merr., En. Philip. (1923) 386, *p.p.*; Burkill, Gard. Bull. S. S. 3 (1923) 35, *p.p.*; Endert, Tectona 18 (1925) 97; Doct. v. Leeuwen, Zoocecidia (1926) 273; Heyne, Nutt. Pl. (1927) 901; Craib, Fl. Enum. Siam. (1931) 105; Burkill, Dict. (1935) 2268; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 222; Masam., Enum. Phan. Born. (1942) 380; Wyatt-Smith, Mal. For. Rec. 17 (1952) 80, 363, *p.p.; op. cit.* 23-2 (1963) fig. 10, *p.p. (sub X. affine)*; Backer & Bakh. *f.*, Fl. Java 1 (1963) 201; Ng, Fed. Mus. J. n.s. 13 (1971) 137; in Whitmore, Tree Fl. Mal. 1 (1972) 354, fig. 1, *p.p.* – *Jakkia excelsa* Bl., Bijdr. (1825) 62 (*'Jackia'*); G. Don, Gen. Hist. Dichl. Pl. 1 (1831) 368. – *Monnina excelsa* (Bl.) Sprengel, Syst. Veg. 3 (1827) 265; Steudel, Nom. ed. 2, 2 (1841) 157. – *Banisterodes excelsum* (Bl.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *HB 1324, p.p.* (L, sheet 908.172-17; iso L, U).

? *X. eglandulosum* Griffith, Notul. 4 (1854) 537, t. 598, fig. 4; see: doubtful species, D2.

X. adenopodum Miq., Fl. Ind. Bat., Suppl. (1861) 393; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277. – *X. affine* var. *adenopodum* (Miq.) Koord. & Valeton, Icon. Bog. 1, 1 (1897) 11. – Type: *Diepenhorst HB 2334* (BO; iso BO, K, U).

X. glandulosum Merr., Philip. Gov. Lab. Bur. Bull. 35 (1905) 34; Gagnepain, Desv. J. Bot. 21 (1908) 252; Merr., En. Philip. (1923) 485. – Lectotype: *Merrill 2335* (A; iso SING).

X. floriferum Elmer, Leafl. Philip. Bot. 5 (1913) 1674. – Lectotype: *Elmer 12871* (L; iso A, BM, BO, C, E, FI, G, K, P, U, W, Z).

X. multiramosum Elmer, Leafl. Philip. Bot. 5 (1913) 1676; Merr., Philip. J. Sc. 27 (1925) 29. – Lectotype: *Elmer 8701* (L; iso A, BO, E, G, FI, K, W, Z).

X. obliquum Craib, Kew Bull. (1922) 235; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 223. – Type: *Kerr 5766* (K; iso BM).

X. obliquum var. *viride* Craib, Kew Bull. (1922) 236. – Type: *Kerr 5766A* (K; iso BM).

X. siamense Craib, Kew Bull. (1922) 236; Fl. Siam. Enum. (1931) 107: Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 222; Wang, Acta Phytotax. Sin. 6 (1957) 225. – Type: *Kerr 3583* (K; iso BM).

X. loheri Merr., Philip. J. Sc. 27 (1925) 29. – Type: *Loher 14978* (A; iso K, M).

X. pallidum Ridley, Kew Bull. (1938) 113; Masam., Enum. Phan. Born. (1942) 380. – Type: *Beccari 729* (K).

Tree 8–36 m high, up to 1 m d.b.h. Twigs glabrous. *Petiole* (5–)7–15 mm long, often seemingly longer when leaf base is attenuate, mostly in apical half with two rather distinct glands. *Leaf blade* (5.2–)7–18(–25) × (2.3–)3–7(–12) cm, base often long attenuate with the margins of the leaf blade curved upwards and gradually grading into the ridges of

the petiole; upper side yellowish green to yellowish brown; lower side: secondary nerves (4–)6–8(–10) pairs, usually forming a rather distinct intramarginal nerve, venation sometimes indistinct; glands 1–10, scattered, 0.3–0.6(–0.9) mm diam., basal glands usually absent if petiole bears glands. *Inflorescences* often several together on one thickened node, rarely unbranched, as long as or longer than the leaves; axes slender, somewhat flattened, slightly grooved, thickened on the nodes and there with usually distinct, protruding glands, brownish, densely minutely patently hairy; flowers usually with 3 together. *Pedicel* (2.5–) 3–4.5 mm long, rarely longer, densely minutely half-patently greyish hairy. *Sepals:* outer sepals 2.3–3.0(–3.6) × 1.4–2.7 mm; inner sepals 3.0–4.1 × 2.3–3.7 mm. *Petals* bright yellow, or white and the upper petals with a yellow spot, or fully white, when dry yellowish, the longest one (6–)7–8(–8.5) mm long; carina basally more or less densely hairy, in upper part outside densely patently hairy to glabrous, inside rather densely hairy to glabrous; lateral petals usually glabrous outside, mostly glabrous inside, upper petals reflexed, ciliate basally or up to 2/3rd their length, usually glabrous outside, inside patently hairy or at base only. *Stamens:* filaments very rarely c. 1 mm connate; anthers (0.4–)0.5–0.6 (–0.65) mm long. *Ovary* glabrous to hairy in apical region on 4 ribs, very rarely (in one coll.) loosely hairy all over, often semi-2-locular; style sometimes glabrous in basal part; ovules 8–12, rarely 6. *Fruit* 1- to often 2-locular, the second chamber often reduced and seemingly enveloped by the pericarp; usually globular, up to c. 2 cm diam., smooth to irregularly low-tuberculate, rarely densely tuberculate, rather dull to somewhat shiny, yellowish to brownish; pericarp usually hard; pedicel up to 6(–7) mm long. *Seed(s)* 1 or 2.

Distribution. E. India. – Bangla Desh. – N. Vietnam. – Laos. – S. Burma. – Thailand. – S. Cambodia. – S. Vietnam. – Malaya: Kedah (7 coll.), Kelantan (5), Pankor I. (7), Trengganu (3), Perak (9), Pahang (10), Selangor (2), Negri Sembilan (2), Malacca (1), Johore (9). – Sumatera: mainland (8 and 7 uncertain), Simaluë I. (10), ? Bangka (1 uncertain). – Jawa (numerous coll. in West, 6 localities in Central, 3 in East). – Borneo: Sarawak (4th Div.: 2), Sabah (19 and 11 uncertain), Kalimantan (9 and 7 uncertain). – Philippines: Luzon (20), Mindoro (2), Palawan (6), Masbate (1), Guimaras (1), Negros (2), Mindanao (5).

Notes. 1. The name of this widely distributed species has been hardly used since the misconception of A.W. Bennett (1872) in the leading Flora of British India of the species with that name; *X. flavescens sensu* Bennett ('ovary and style strigose') includes in fact four other species (*16. X. arnottianum, 36. X. vitellinum, 75. X. virens, 77. X. zeylanicum*). Due to the fact that Roxburgh (1820) gave a good description of *X. virens*, adding only a short diagnosis for *X. flavescens* in which he did not mention that its ovary was glabrous, Bennett will have thought that Roxburgh's plant (ovules 8–10 according to Bennett) belonged to the Deccan Peninsula species *16. X. arnottianum* (with its hairy ovary and style) in which Bennett counted 4–9 ovules; as the Ceylonese, Sumatran and Javanese specimens have a hairy ovary with 4 ovules, one can understand Bennett's opinion. Apparently the resulting confusion led to the disappearance of the name *flavescens*.

2. Despite the large number of synonyms and its large area *X. flavescens* is not very variable. On Sumatra a high percentage of fruiting collections has 2-locular fruits (see chapter 1.13), often producing 2-seeded fruits. *Thorenaar 416* differs in having leaf blade and petiole minutely hairy, and in the brownish indumentum of the inflorescence axis; it possibly may represent a new taxon.

3. Closely resembling *8. X. affine*, and nearly always combined with that species in one taxon. The only reliable character distinguishing it from the latter species is the presence of nodal glands in the inflorescence. Due to the variability of *X. affine* it is difficult to identify sterile collections of both species. Differences are found in the petiole; in *X. flavescens* the petiole is glabrous and often bears a pair of glands, in *X. affine* the petiole is minutely hairy, and eglandular.

2. Xanthophyllum bullatum

X. bullatum King, J. As. Soc. Beng. II, 59 (1890) 142; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Ridley, Fl. Mal. Pen. 1 (1922) 144; Henderson, Gard. Bull. S.S. 4 (1928) 222; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 356, fig. 1; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 146. – Lectotype: *King's Coll. 3258* (K; iso FI, L).

Shrub or small tree 3–4.5 m high, 6 cm d.b.h. Twigs appressedly hairy. *Petiole* c. 12–22 mm long, rather densely minutely appressedly hairy. *Leaf blade* 20–50 × 6.5–25 cm; base cordate; upper side yellowish green, bullate between midrib and secondary nerves, midrib strongly protruding to flat, secondary nerves rather strongly protruding, venation finely protruding; lower side creamish brown to light brownish green, minutely hairy on the nerves, secondary nerves 14–20 pairs, protruding, mostly forming a nearly complete, rather distinct intramarginal nerve, venation sometimes rather obscure; glands rather few and situated mainly along the margin, or numerous and scattered, 0.3–0.6 mm diam., basal glands (1 or sometimes 2 pairs) at very base on midrib. *Inflorescences* shorter than the leaves, mostly elongate and often very densely set with flowers; axes appressedly to patently minutely hairy, light to very dark brownish, with large, protruding nodal glands. *Pedicel* 5–7 mm long, very densely minutely appressedly reddish brown hairy. *Sepals* minutely appressedly reddish brown hairy; outer sepals c. 4.5 × 3 mm, with or without protruding glands; inner sepals c. 6.5 × 3.7 mm, keeled. *Petals* white, when dry yellowish, the longest one 12 mm long; carina in apical part rather shortly appressedly hairy outside, minutely so inside, further glabrous; other petals glabrous outside, glabrous or ciliate at base, shortly hairy or not inside in basal part, the lateral petals strongly bent, the upper petals strongly S-curved. *Stamens:* filaments glabrous or sparsely shortly hairy at base; anthers 0.8–1.2 mm long, ciliate along slits. *Ovary* slightly ribbed; style glabrous in basal part, apically shortly appressedly hairy; ovules 8–10. *Fruit* globular, up to 2 cm diam., dull, rather smooth, light brown; pericarp rather thin, not very hard.

Distribution. Malaya: Perak (6 coll.), Trengganu (1), Selangor (3).

Note. Characterized by its large, cordate leaf blades, the densely flowered inflorescences (in the latter resembling *6. X. hosei*), and the colour of the indumentum of the sepals. Two collections of the *8. X. affine*-complex (*Shah 1360, 1579*) resemble *X. bullatum* vegetatively but differ in the absence of nodal glands, the colour of the indumentum of the sepals, the less densely flowered inflorescences, and in the more hairy filaments.

3. Xanthophyllum sulphureum

Fig. 10C

X. sulphureum King, J. As. Soc. Beng. II, 59 (1890) 143; Gagnepain, Desv. J. Bot. 21 (1908) 252 ('*sulfureum*'); Ridley, Fl. Mal. Pen. 1 (1922) 145; Wyatt-Smith, Mal. For. Rec. 17 (1952) 81, 363; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 363, fig. 4 (excl. *FRI 8041*). – Lectotype: *King's Coll. 8097* (L; iso BM, FI, G, K, P, SING, Z).

Small to large tree (according to King 30–50 m high). Twigs finely reticulately wrinkled, brownish hairy, glabrescent. Axillary buds up to 2.8 mm long but often much smaller, rounded, densely hairy. *Petiole* 9–13 mm long, very densely patently hairy. *Leaf blade* 9–20 × 2.8–7.5 cm; upper side yellowish green, dull, midrib basally slightly protruding to slightly sunken and rather densely hairy, upwards sunken and glabrous, nerves and venation rather obscure; lower side, glaucous-papillose, rather densely hairy especially on the nerves, secondary nerves 6–8 pairs, forming a rather distinct intramarginal nerve; basal glands perhaps always present but mostly hidden by the very protruding midrib and then scarcely visible, rarely not so and then distinct, c. 0.5 mm diam., other glands apparently few or possibly absent. *Inflorescences* shorter than the leaves; axes rather smooth, very densely brownish hairy, with distinct, large, protruding 'cap-like' nodal glands. *Pedicel* c. 4 mm long, rather stout, very densely patently brownish pubescent. *Sepals* densely brownish patently shortly hairy at both sides; outer sepals 4.0 × 3.7 mm long; inner sepals 5.0 × 4.2 mm long, some with glandular spots, distinctly keeled. *Petals* yellow, when dry yellowish, the longest one 11 mm long; carina very densely (nearly velvety) patently pubescent outside, densely pubescent inside in apical part; other petals woolly-tufted outside. *Stamens:* filaments nearly glabrous; anthers 0.5–0.55 mm long, cohering around the style. *Ovary* containing 16 ovules. *Fruit* globular, c. 2 cm diam., light brownish, dull, finely tuberculate; pericarp hard.

Distribution. Malaya: Perak (1 coll.; 3 uncertain), Kelantan (1; 2 uncertain), Pahang (1).

Note. Insufficiently known. Vegetatively resembling *12. X. velutinum*, differing in the finely papillose leaf blades, the less strongly protruding intramarginal nerve and the lower number of laminar glands. See also under *14. X. rufum* and *4. X. cockburnii*.

4. Xanthophyllum cockburnii Meijden, *spec. nov.*

Gemmae axillares 2, ad 1.5 mm longae, dense pilosae. Lamina subtus laevis, dense pilis patentibus induta, nervis e paribus 12 vel 13; glandulae 15–20, valde conspicuae. Inflorescentia valde ramosa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo 11 mm longo; carina extus velutinoso-pilosa. Antherae c. 0.8 mm longae. Ovarium glabrum; stylus pilosus; ovula 8. Fructus ignotus.

Typus: *FRI 8041* (L; iso K, KEP).

Tree 20 m high, 30 cm d.b.h. Axillary buds densely patently hairy. *Petiole* 8–12 mm long, densely hairy. *Leaf blade* 11–17 × 3.5–7 cm, base rounded to obtuse; upper side slightly bullate between midrib and secondary nerves, greenish or brownish yellow, midrib rather obscure, finely protruding to flat, secondary nerves obscure; lower side creamish to greenish yellow, rather densely patently hairy on the nerves, secondary nerves 12 or 13 pairs, forming a complete intramarginal nerve, fine venation obscure; glands c. 15–20 0.2–0.4 mm diam., those at very base distinct, situated on midrib. *Inflorescences* shorter

than to as long as the leaves; axes very densely reddish brown pubescent, with rather large nodal glands. *Pedicel* 4.5 mm long. *Sepals* densely patently reddish brown hairy; outer sepals 3.8–4.0 × 2.9–3.1 mm; inner sepals 3.8–4.0 × 3.0–3.3 mm, keeled. *Petals* white, when dry yellowish, the longest one 11 mm long; carina light yellowish velutinous outside, rather densely hairy inside in apical part; other petals glabrous or slightly hairy apically, not ciliate at base. *Stamens:* anthers 0.8–0.85 mm long, minutely hairy. *Ovary* containing 8 ovules. *Fruit* unknown.

Distribution. Malaya: Pahang (Rompin Dist., upper Anak Endau R., near Johore border: *FRI 8041*).

Note. Insufficiently known. The single collection was identified as *X. sulphureum*, the flowers of which species show indeed a strong resemblance; the flowers of *X. sulphureum* differ, however, by their smaller anthers and nearly glabrous filaments. Vegetatively both species are easily separated: *3. X. sulphureum* has less secondary nerves which leave the midrib under a sharper angle, and do not form an intramarginal nerve, and its finer venation is very prominent.

5. Xanthophyllum eberhardtii

Fig. 10C

X. eberhardtii Gagnepain [in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 223, *nom. inval.*] Not. Syst. 9 (1941) 141; Weberl., Beitr. Biol. Pfl. 50 (1974) 278, 280, fig. 1, I. – Type: *Eberhardt 3051* (P).

Small tree, 10–14 m high. Twigs brownish. Axillary buds densely hairy. *Petiole* 6–8 mm long, transversely wrinkled, densely patently hairy. *Leaf blade* 10–17 × 4–6.5 cm, base cordate; upper side bright yellowish, greenish or brownish; lower side lighter than upper side, rather densely patently hairy, secondary nerves 7–10 pairs, forming an irregular intramarginal nerve; glands about 8–10, situated near the base and some above the middle, 0.4–0.5 mm diam. *Inflorescences* shorter than the leaves; axes very densely reddish brown pubescent, with distinct, protruding, hollow nodal glands. *Pedicel* c. 3–4 mm long, rather densely patently pubescent. *Sepals* densely brownish more or less patently hairy outside; outer sepals 4.1 × 3.7 mm; inner sepals 5.2 × 4.0 mm, keeled. *Petals* yellowish when dry, the longest one 11 mm long; carina rather sparsely shortly appressedly pubescent outside, glabrous inside; upper petals up to halfway hairy inside. *Stamens:* anthers 0.8–0.9 mm long, hairy. *Ovary* semi-2-locular; ovules 8. *Fruit* globular, light brownish, finely pustulate; pericarp rather thin.

Distribution. Vietnam: Thua Thien (Valley of Thuy Cam: *Eberhardt 3051*; locality unknown: *Poilane 7710*).

Note. The cordate leaf base may not be a constant character, like in other species. *X. eberhardtii* differs from *3. X. sulphureum* in the longer anthers, the indumentum of the carina, and in the smooth leaf blade; from *4. X. cockburnii* in the key characters. From *13. X. annamense* it differs in the nodal inflorescence glands and in the longer, differently hairy flowers.

6. Xanthophyllum hosei

X. hosei Ridley, Kew Bull. (1938) 113; Masam., Enum. Phan. Born. (1942) 380. – Lectotype: *Hose 311* (K; iso BM, L).

Small tree, up to 3.5 m high, d.b.h. 3 cm. Twigs minutely appressedly hairy, soon glabrescent, or glabrous. *Petiole* 7–10 mm long, minutely appressedly hairy. *Leaf blade* 12–21 × 4.5–10 cm, base rounded to more or less obtuse, apex rather suddenly cuspidate to acuminate; upper side slightly bullate between midrib, secondary nerves, and intramarginal nerve, dark greyish green, midrib sunken, rather wide, other nervation finely protruding; lower side lighter coloured, sparsely minutely appressedly hairy in basal part especially on the nerves, secondary nerves 7–11 pairs, forming a distinct, (nearly) complete intramarginal nerve; glands 8 to very numerous, scattered, (0.2–)0.3–0.4 mm diam., basal glands larger. *Inflorescences* branched or unbranched, up to 12 cm long; axes slightly thickened, curved, smooth, dull, minutely very densely appressedly hairy, internodes (except at very base) very short, c. 0.5–1 mm long, thus giving the inflorescence a very dense-flowered appearance. *Pedicel* 2.5–4 mm long, grooved, densely minutely appressedly hairy. *Sepals* glabrous to sparsely minutely appressedly hairy inside; outer sepals 2.1–2.5 × 2.5–2.8 mm, with 2–4 glandular spots, minutely densely appressedly hairy outside; inner sepals 3.5–3.8 × 2.2–2.6 mm, rather distinctly keeled and there densely minutely appressedly hairy, further more or less glabrous outside. *Petals* yellowish when dry, the longest one c. 8.5 mm long; carina sparsely appressedly hairy outside in middle part, glabrous inside; other petals ciliate to halfway, further glabrous. *Stamens:* filaments wide at base, sparsely appressedly hairy ad- and abaxially to about halfway, further glabrous; anthers 0.85–1.05 mm long, ciliate along slits. *Ovary* nearly sessile, ribbed; style glabrous in basal 1/3rd part, upwards rather densely appressedly hairy till the apex; ovules 7–10. *Fruit* (very young) not ribbed, finely pustulate; style persistent, recurved; sepals persistent.

Distribution. Borneo: Sarawak (4th Div.: 4 coll.; uncertain: 1st Div., 1 coll.).

Note. Due to the wide circumscription of the *8. X. affine*-complex this species is not as sharply defined as would be desirable. Its densely flowered inflorescence seems to be characteristic enough to distinguish it from the *X. affine*-complex though its rank as a separate species may be too high. One collection (*S 34534*) closely resembles it in most characters but differs in the habit of the inflorescence.

7. Xanthophyllum ferrugineum

X. ferrugineum Meijden, Bot. J. Linn. Soc. 67 (1973) 118. – Type: *S 23906* (L; iso K, KEP, L, SING).

Tree up to 25 m high, up to 40(–60) cm d.b.h. Twigs glabrous. *Petiole* 9–14 mm long. *Leaf blade* 8–20 × 3–7 cm; upper side bright yellow to yellowish green, nerves finely protruding to rather obscure but mostly more distinct above than on lower side; lower side: midrib not very protruding, secondary nerves c. 5–7 pairs, finely protruding to rather obscure, intramarginal nerve indistinct, tertiary nerves finely protruding to obscure, fine venation mostly obscure; glands rather few, mainly situated near margin, 0.4–0.6 mm diam., basal glands similar. *Inflorescences* shorter than the leaves; axes more or less flattened, yellowish brown, densely to rather sparsely shortly patently hairy. *Pedicel* 1–1.5(–4) mm

long, densely minutely appressedly greyish hairy. *Sepals* possibly persistent in fruit, middle-brown with light brown margin when dry; outer sepals 3.7–4.8 × 3.5–4 mm, (sub)glabrous outside, often with (sometimes minute) glandular spots; inner sepals 4–5 × 4–4.2 mm, thickened in middle basal part, minutely appressedly hairy especially on the midrib, glabrous along the margin. *Petals* yellow, or white and the upper petals with a yellow spot, when dry yellowish, the longest one 8.5–10 mm long; carina very densely patently pubescent outside, densely pubescent in apical part inside; other petals glabrous or with few hairs in apical part outside. *Stamens:* anthers 0.5–0.7 mm long, minutely hairy. *Ovary* smooth or ribbed, glabrous, rarely sparsely appressedly hairy all round, apically often greyish hairy in 4 short rows; ovules 8–14. *Fruit* (immature) partly enclosed by the persistent sepals, ovoid, finely tuberculate, dull, yellowish brown.

Distribution. Borneo: Sarawak (1st Div.: 4 coll.: 3rd Div.: 6; 5th Div.: 1), Brunei (1), Sabah (Gaya I.: 2; Tawau: 2).

Notes. 1. *FRI 022014* (Malaya, Trengganu, Ulu Setiu) may belong to this species.

2. Undoubtedly related to the *8. X. affine*-complex; characterized by the key characters (sepals, pedicel) and the coriaceous, rather obscurely nerved, bright yellow leaf blades. No collections are known to me which are intermediate to *X. affine. S 14975* possibly belongs to this species, but differs in having the ovary sparsely hairy all round and in the less coriaceous leaf blades.

8. Xanthophyllum affine

Fig. 2, 3 A g–i, 10C, 11

X. affine Korth. *ex* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 271; Kurz, J. As. Soc. Beng. II, 42 (1873) 80; A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209; Kurz, For. Fl. Br. Burma 1 (1877) 82; Fern.-Vill., Nov. App. (1880) 14; King, Mat. Fl. Mal. Pen. (1890) 142, *p.p.*; Chodat in E. & P., Nat. Pfl. Fam. III, 4 (1896) 345; Koord. & Valeton, Icon. Bog. 1, 1 (1897) 11–13, p.p. (*a genuina*), t. 11, *p.p.*, excl. fig. 12–14; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 45; Brandis, Indian Trees (1906) 44; Gagnepain, Desv. J. Bot. 21 (1908) 253; Ridley, J. Fed. Mal. St. Mus. 4 (1909) 5; J. Str. Br. R. As. Soc. 59 (1911) 73; J. Fed. Mal. St. Mus. 10 (1920) 82 (*sub X. kingii*); Merr., En. Born. (1921) 326, *p.p. (sub X. excelsum)*; Ridley, Fl. Mal. Pen. 1 (1922) 143, *p.p.*; Burkill, Gard. Bull. S. S. 3 (1923) 35, *p.p. (sub X. excelsum)*; Merr., En. Philip. (1923) 386, *p.p. (sub X. excelsum)*; Baker, Hook. J. Bot. 62 (1924) Suppl. 7; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 345; Henderson, *op. cit.* 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Chodat in Merr., Pl. Elm. Born. (1929) 133; Craib, Fl. Siam. Enum. (1931) 105; Burkill, Dict. (1935) 2268, *p.p.*; Keith, N. Born. For. Rec. 2 (1938) 225; Doct. v. Leeuwen, Ned. Kruidk. Arch. 51 (1941) 166, 167; Masam., Enum. Phan. Born. (1942) 379; Wyatt-Smith, Mal. For. Rec. 17 (1952) 80, 363, *p.p. (sub X. excelsum)*; Balan Menon, *op. cit.* 19 (1956) 34; Wyatt-Smith, *op. cit.* 23-2 (1963) fig. 10, *p.p.*?; Meijer, Bot. News Bull. Sandakan 7 (1967) 88; Ng, Fed. Mus. J. n.s. 13 (1971) 137; in Whitmore, Tree Fl. Mal. 1 (1972) 354, fig. 1, *p.p.*; Corner, Gard. Bull. Sing. Suppl. 1 (1978) 146, 211 (excl. *no. 29341*). – *Banisterodes affine* (Miq.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – *X. excelsum* var. *affine* (Miq.) Boerl., Cat. Hort. Bog. (1899) 59; Heyne, Nutt. Pl. (1927) 901. – Lectotype: *Korthals s.n.* (L, 908.171-1714; iso A).

non X. affine auct.: K. Sch. & Hollr., Fl. Kais. Wilh. Land (1889) 68; K. Sch. & Laut., Fl. Schutzgeb. (1901) 388 (= *89. X. papuanum*) – Koord., Minah. (1898) 344 (= *29. X. tenuipetalum*) – Ridl., J. Fed. Mal. St. Mus. 10 (1920) 82 (= *75. X. virens*).

? *X. eglandulosum* Griffith, Notul. 4 (1854) 537, t. 598, fig. 4; see: doubtful species D2.

X. sarawakense Chodat, Bull. Herb. Boiss. 4 (1896) 262 ('*sarawakensis*'); Gagnepain, Desv. J. Bot. 21 (1908) 252; Masam., Enum. Phan. Born. (1942) 381. – Type: *Beccari 3459* (K; iso FI, K, P).

X. affine var. *puberulum* Craib, Fl. Siam. Enum. 1 (1931) 105. – Lectotype: *Kerr 7642* (K; iso E).

Tree, rarely a shrub, up to 15(–20) m high, sometimes up to c. 30 m high, up to 40(–95) cm d.b.h. Twigs mostly very densely, sometimes rather sparsely, patently to appressedly minutely greyish hairy, glabrescent. Axillary buds 2 (or 3), often seemingly single, the upper bud often stalked, rarely supra-axillary for more than 0.5 mm. *Petiole* (5–)6–11(–17) mm long, more or less densely minutely greyish hairy all round or at the upper side only, eglandular. *Leaf blade* rarely linear-lanceolate, 6.5–18(–35) × (2–)3–8(–13) cm, base cuneate to rounded-attenuate, sometimes attenuate with the margins of the leaf blade curved upwards and gradually grading into the ridges on the petiole, apex sometimes cuspidate; upper side sometimes slightly bullate between secondary nerves, yellowish to rather dark greyish green, often with a lighter strip along midrib and base of secondary nerves, midrib protruding to flat, rarely slightly sunken, in basal part often with a groove and often minutely hairy; lower side concolorous or more brownish, sometimes more or less densely minutely hairy in basal part, secondary nerves 5–16 pairs, usually forming a more or less distinct intramarginal nerve in the apical half, intramarginal nerve rarely (nearly) complete to the base; glands very variable in number and size, usually distinct (see note 3). *Inflorescences* shorter than the leaves; axes smooth, minutely greyish hairy; bracts sometimes with distinct glands. *Pedicel* (2–)4–11 mm long, rarely longer, densely minutely greyish hairy. *Sepals* persistent or not in fruit, sometimes with small glands; outer sepals 1.7–5.5 × 1.8–4.7 mm; inner sepals 2.1–7.8 × 2.1–5.2 mm. *Petals* white (or rarely pink), the upper ones with an orange-yellow spot, when dry yellowish, the longest one 6–17 mm long; carina appressedly to half-patently, sometimes patently hairy outside, inside appressedly hairy or sometimes glabrous; other petals sometimes quite glabrous, usually hairy outside at base, upper petals hairy inside or only at base. *Stamens:* filaments glabrous to sparsely appressedly hairy in basal part; anthers 0.5–1.3(–1.6) mm long. *Ovary* often semi-2-locular, smooth to distinctly ribbed, sometimes tuberculate, glabrous or sometimes greyish hairy in 2(–4) rows in apical part; ovules usually 8–12, very rarely 6 or 5, rarely up to 16. *Fruit* globular or somewhat longer than wide, rounded or slightly but sometimes rather sharply beaked apically, up to 1.5 cm diam., smooth to pustulate or tuberculate, sometimes ribbed, creamish to brown; pericarp not very thick; sepals (sub)persistent in fruit or not.

Distribution. E. India ('Khasya': *Lehmann 408* in herb. Griffith, K, BM). – Laos (Chieng Kwang: *Kerr 21149*; alt. 1500 m). – S. Thailand (16 coll.). – Malaya (numerous coll.; in Cameron Highlands up to 1500 m). – Sumatera (21); Bangka (1). – Borneo: Sarawak (numerous coll.), Brunei (3), Sabah (numerous coll.). – Philippines: Culion (*Herre 1028, FB 28895*), Busuanga (*Weber 1555*).

Notes. 1. Most authors have included *1. X. flavescens* in this species; see note 3 under that species.

2. Because of the wide circumscription of *X. affine* the related species *6. X. hosei, 7. X. ferrugineum*, and *9. X. pubescens* differ only in few characters from that (complex) species. Not wanting to broaden the concept of *X. affine* further, I preferred to distinguish the taxa on the species level.

3. In this circumscription, *X. affine* is far more variable than any other *Xanthophyllum* species. This is very apparent in the dimensions of petals, sepals, and anthers. Variability in the length of the sepals is ± 20–25% in other species, ± 50–55% in *X. affine*; in that of

the petals ± 15–20% in other species, in *X. affine* ± 4(–70)%; the length of the anthers varies in other *Xanthophyllum* species ± 0.10–0.15 mm in anthers up to 1.0 mm long, and ± 15–20% in longer anthers; in *X. affine* the anthers vary ± 44(–77)%. Vegetatively too, *X. affine* is more variable than other species. In most species the difference between the highest and the lowest number of nerves is about 3; the highest variability is found in *48. X. discolor* subsp. *discolor* (nerves 5–13) and in *51. X. pulchrum* (nerves 6–13); in *X. affine* the range is from 5 to 16 pairs. Variability in number and size of the leaf glands is also very large in *X. affine*.

The most obvious conclusion is that *X. affine* is not homogeneous and should be subdivided further. I have spent much time trying to split it up. First it was necessary to bring flowering and fruiting collections together into groups by means of resemblance in vegetative characters. Doing this separately for Malaya and Borneo, from where many collections were available, it became apparent that collections with rather few and rather large leaf glands usually had relatively small sepals, petals and anthers, whereas collections with numerous and rather small leaf glands have larger sepals, petals and anthers. In Fig. 11 the average diameter of the leaf glands is plotted against the length of the inner sepals; for this purpose only the collections of Malaya and Borneo were used. From this diagram it is not clear whether two groups of points can be segregated by the oblique line. If, however, it could be established that there is also a correlation with another character (hypothetical dotted lines), this complex of differences would be sufficient to divide *X. affine* into two taxa. That other character might be found in the fruits.

Examining fruiting collections on number and size of leaf glands, it appeared that collections with a certain type of fruits had leaf glands rather few and large instead of many and small leaf glands. The fruits were characterized by: sepals (sub)persistent and pericarp with wax in a minute reticulate pattern (strong handlens!). Unfortunately both characters are not constant in herbarium collections because of different ways of preparing collections in the field. The remainder of the fruiting collections, those with caducous sepals and smoothly waxy fruits, were rather heterogeneous with respect to number and size of the leaf glands: the majority having numerous and small leaf glands, but collections with few and rather large glands were also present.

Very few collections are available with flowering as well as fruiting twigs from the same tree. It is therefore not certain that *X. affine* can be subdivided indeed into two groups, one with rather small flowers, (sub)persistent sepals, pericarp with a minute reticulum of wax, and leaves with rather few and large glands, and the other group with rather large flowers, caducous sepals, fruits without reticulate wax, and leaves with many and rather small glands.

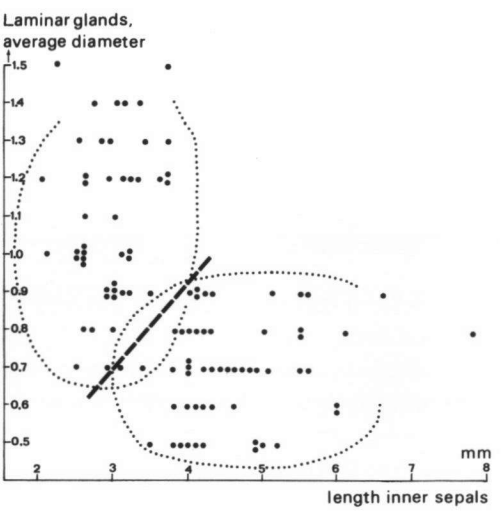


Fig. 11. Scatter diagram of *8. X. affine*; for explanation see text.

Thus, for the time being I have no good grounds to make a formal subdivision of *X. affine*. Yet I will present some figures of the two hypothetical groups, which might help future investigations on this subject.

Group a: Glands on lower side of the leaf blade 3–20(–28), (0.4–)0.5–0.9(–1.0) mm diam. Sepals: outer sepals (2.0–)2.5–4.5(–5.5) × (2.0)2.6–3.5(–4.7) mm; inner sepals (3.5–)3.8–6.0(–7.8) × (2.7–)3.2–4.5(–5.2) mm. Petals: longest petal (7.5–)9–12(–17) mm long. Stamens: anther (0.7–)0.75–1.1(–1.3) mm long, rarely up to 1.6 mm long. Fruit, if waxy, smooth; sepals caducous.

Group b: Glands on lower side of leaf blade (0–)2–9(–13), (0.5–)0.7–1.3(–1.5) mm diam. Sepals: outer sepals (1.7–)1.9–2.5(–2.7), rarely up to 3.1 mm long, (1.7–)1.8–2.7(–3.2) mm wide; inner sepals (2.1–)2.5–3.2(–3.7) x (1.9–)2.3–3.4(–3.8) mm. Petals: longest petal (6–)6.5–8(–9) mm long. Stamens: anther (0.45–)0.5–0.8(–0.85) mm long. Fruit waxy, usually at base with a minute reticulum of wax; sepals (sub)persistent.

The areas of these groups are nearly completely equal. Surprisingly enough members of different groups seem to grow only very rarely in the vicinity of each other, suggesting some ecological differences.

9. Xanthophyllum pubescens Meijden, *spec. nov.*

Xanthophyllum spec. B Ng in Whitmore, Tree Fl. Mal. 1 (1972) 365, fig. 5.

Gemmae axillares, ut videtur singulae, usque ad 1.5 mm longae, dense pilis longiusculis indutae. Lamina subtus laevis, densiuscule pilis patentibus induta, nervis e paribus 8–9, glandulae (2–)7–14(–18), magnae. Inflorescentia ramosa, bracteis basalibus alternatus. Petala inaequalia, petalo longissimo 12–13 mm longo; carina extus densissime pilis brevibus semi-patentibus induta. Antherae 1.1–1.5 mm longae. Ovarium glabrum; stylus pilosus; ovula 8–13. Fructus immaturus obovoideus, tristis, tenuiter pustulatus. Semina ignota.

Typus: *KEP 110387* (KEP; iso K, L).

Shrub or small tree up to 12 m high, 5 cm d.b.h. Twigs more or less brownish hairy. Axillary buds densely patently rather shortly hairy. *Petiole* 10–12 mm long, hairy like twig. *Leaf blade* 15–28 × 5.5–9.5 cm; upper side greenish, more or less densely hairy on the nerves, glabrescent, midrib flat to slightly protruding; lower side lighter coloured, rather densely patently hairy, secondary nerves 8 or 9 pairs, forming a more or less distinct intramarginal nerve; glands (2–)7–14(–18), scattered, (0.5–)0.6–0.8(–1) mm diam. *Inflorescences* up to 10 cm long; axes densely patently greyish hairy; in basal part flowers with 3 together; bracts with 2 large glands. *Pedicel* 5–8 mm long, very densely minutely greyish patently hairy. *Sepals* densely to very densely patently greyish hairy outside; outer sepals 3.8–4.0 × 2.7–4.0 mm; inner sepals 5.2–6.1 × 3.8–4.5 mm, slightly keeled. *Petals* white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–13 mm long; carina very densely shortly half-patently whitish hairy outside, in apical part rather densely hairy inside; other petals glabrous or basally ciliate, or the upper petals minutely hairy inside above the base. *Stamens:* anthers 1.1–1.5 mm long, sometimes cohering around the stigma, ciliate along slits. *Ovary* containing 8–13 ovules. *Fruit* (immature) obovoid, dull, finely pustulate.

Distribution. Malaya: Pahang (2 coll.), Johore (4).

Note. Closely related to the *8. X. affine*-complex, differing in the indumentum of the vegetative parts. Considering that in other species hairs of vegetative parts are either long, or short to absent, I decided to separate it from the heterogeneous *X. affine*-complex.

10. Xanthophyllum resupinatum

X. resupinatum Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – Type: *SAN 29838* (L; iso K, SING).

Tree up to 25 m high, 40 cm d.b.h. Twigs glabrous. Axillary buds very inconspicuous, more or less enclosed between basal part of the petiole and the twig. *Petiole* 4.5–7 mm long, often appearing longer because of the narrow leaf base, transversely wrinkled. *Leaf blade* 6–12.5 × 2.7–5 cm, attenuate into a narrow petiole-like part; upper side (very) shiny, greenish to dark olive-greenish, midrib distinctly protruding; lower side yellowish brown to greenish brown, very shiny, midrib flat to faintly sunken, rarely faintly protruding or protruding as a narrow crest, secondary nerves 4–7 pairs, forming an incomplete, indistinct intramarginal nerve, tertiary nerves rather indistinct to obscure; glands very few, mostly situated above the middle, 0.3–0.7 mm diam. *Inflorescences* shorter than the leaves; axes grooved, densely minutely appressedly greyish hairy. *Pedicel* slightly grooved, 4–5 mm long, very densely minutely appressedly greyish hairy. *Sepals* dark brown to blackish; outer sepals c. 3 × 2.4–3 mm, with scattered, indistinct, small glandular spots, sometimes with 2 protruding glands halfway; inner sepals c. 4–4.8 × 2.8–3.5 mm, slightly keeled, with few glandular spots. *Petals* white, when dry dark brownish, the longest one 7–9 mm long; carina very densely half-patently greyish pubescent outside, slightly hairy inside in apical part; other petals glabrous. *Stamens:* anthers 0.5–0.7 mm long, faintly hairy. *Ovary* dark brownish, ribbed, slightly appressedly hairy on the ribs in apical part, or glabrous; ovules 9–14. *Fruit* 1.2 cm diam., blackish, slightly shiny, finely pustulate; pericarp rather thin, hard.

Distribution. Borneo: Sarawak (3rd Div.: 3 coll.), E. Sabah (11), N. Kalimantan (Nunukan I.: 1).

Note. The name has been chosen because the leaves look, at first sight, upside-down, the midrib being prominent above and flat beneath, a unique character in *Xanthophyllum.*

11. Xanthophyllum schizocarpon

Fig. 3 A-j

X. schizocarpon Chodat in Merr., Pl. Elm. Born. (1929) 136; Masam., Enum. Phan. Born. (1942) 381. – Lectotype: *Elmer 21519* (L; iso BM, BO, BR, C, G, K, M, P, SING, U, Z).

Tree 10–25 m high, 35 cm d.b.h. Twigs minutely appressedly hairy in younger parts to glabrous. Axillary buds 2 or 3, the upper one 0–3 mm above the axil. *Petiole* 5–7 mm long, minutely appressedly hairy to glabrous. *Leaf blade* 4.5–12 × 1.5–4.5 cm; upper side greyish green, midrib sunken; lower side glaucous-papillose, minutely appressedly hairy on nerves, secondary nerves 6 or 7 pairs, not forming an intramarginal nerve, finer venation indistinct; glands numerous, scattered, c. 0.2 mm diam., basal glands (if present) c. 0.5 mm diam. *Inflorescences* often shortly supra-axillary, often 2 per leaf axil, unbranched, shorter

than the leaves; axes faintly grooved, brownish, minutely appressedly hairy; lower bracts opposite. *Pedicel* 6–8 mm long, slightly grooved, minutely densely more or less appressedly greyish hairy. *Sepals:* outer sepals c. 3.8 × 2.3 mm long; inner sepals c. 4.3 × 3.2 mm long, slightly keeled. *Petals* yellow, when dry yellowish, the longest one 6–7 mm long; carina rather densely appressedly hairy outside, shortly hairy inside in apical part; lateral petals glabrous inside, further like the upper ones, upper petals glabrous to shortly hairy outside, shortly patently hairy inside up to 2/3rd. *Stamens* 8 (or 9); anthers c. 0.3 mm long. *Ovary* slightly ribbed, brownish, appressedly hairy on median ribs; ovules 6–8. *Fruit* irregularly globular, c. 1.5 cm diam., mostly wider than high, irregularly 4-sulcate, dull, light greenish to yellowish brown; pericarp hard and irregular in thickness.

Distribution. Borneo: Sarawak (3rd Div., Anap R., Mersing hill: *S 21915, 21964*), Sabah (near Tawau: *Elmer 21519*). Identity uncertain: *SAN 25303, 36305.*

Notes. 1. Characterized by the papillose leaf blade, the supra-axillary buds, and the irregularly formed fruit. *SAN 36305* probably belongs to this species, differing in the smooth, minutely hairy lower side of the leaf blade, and in the glabrous ovary. *SAN 25303* may belong to this species, differing in the shortly densely patently hairy leaf blade.

2. *S 23201* (allied to *55. X. reticulatum*) has a similarly shaped fruit, in that collection probably induced by gall-forming insects.

12. Xanthophyllum velutinum

X. velutinum Chodat, Bull. Herb. Boiss. 4 (1896) 259. – Type: *Beccari 1629* (K; iso FI, G, P, W).

Tree 5–25 m high, d.b.h. 60 cm. Twigs densely set with short and long hairs, longer hairs 0.3–0.8 mm long. Axillary buds 1–3 mm long, hairy like the twig. *Petiole* (4–)8–14 (–16) mm long, hairy like the twig. *Leaf blade* (6–)9–22 × 3–9 cm, apex cuspidate or sometimes acuminate; upper side greyish green, in basal part sometimes sparsely hairy especially on the nerves and midrib, midrib distinctly sunken, nerves and intramarginal nerve slightly sunken to flat and rather obscure, venation obscure; lower side brownish, hairy like the twig, rarely rather sparsely hairy, secondary nerves 8–11 (or 12) pairs, strongly protruding, forming a strongly protruding intramarginal nerve; glands (7–)10 or more, scattered, (0.2–)0.3–0.4(–0.6) mm diam., basal glands 0.9–1.2 mm long. *Inflorescences* about as long as the leaves; axes ribbed, very densely patently brownish hairy in the basal part; flowers with 3 together. *Pedicel* 1.5–6.5 mm long, ribbed, very densely patently brown pubescent, rarely shortly hairy. *Sepals* persistent in fruit, greyish hairy; outer sepals 2.1–3.2 × 1.7–3.0 mm, with 2–4 glandular spots; inner sepals 3.5–5.3 × 2.4–3.4 mm, distinctly keeled. *Petals* white or yellow, when dry brownish orange, the longest one 9.5–10.5 mm long; carina more or less densely appressedly hairy outside, sparsely appressedly hairy inside in middle part; other petals ciliate in basal half, glabrous outside, upper petals reflexed. *Stamens:* filaments rather sparsely appressedly hairy till apex; anthers (0.75–)0.8–1.2 mm long, usually cohering around the stigma, ciliate along slits. *Ovary* sessile, distinctly ribbed, glabrous or sometimes hairy on 2 ribs down to halfway; style reflexed at end of anthesis; ovules (6–)8–12. *Fruit* (immature) ovoid, very sharply beaked, with 8 or more distinct ribs, finely pustulate to tuberculate, dull, greyish brown; pericarp thick, hard; pedicel crowned by persistent sepals.

Distribution. Borneo: Sarawak (1st Div.: 7 coll.; 4th Div.: 1), Brunei (4), Sabah (11).

Note. Vegetatively resembling *3. X. sulphureum* and *14. X. rufum*; see there.

13. Xanthophyllum annamense

X. annamense Gagnepain [in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 220, *nom. inval.*] Not. Syst. 9 (1941) 141. – Lectotype: *Poilane 21897* (P; iso K, SING).

Shrub or tree up to 18 m high, up to 15 cm d.b.h. Twigs yellowish brown hairy. Axillary buds densely hairy. *Petiole* 3–6.5 mm long, densely patently hairy. *Leaf blade* 3–15 × 1–4.5 cm; upper side greyish (sometimes yellowish) green, midrib sometimes hairy till the apex, glabrescent; lower side yellowish green, yellowish brown pubescent, secondary nerves 5–8 pairs, forming an indistinct intramarginal nerve, tertiary nerves scalariform, but in small-leaved specimens reticulate-scalariform; glands 2–6, 0.3–0.4 mm diam. *Inflorescences* shorter than the leaves; axes smooth, densely yellowish brown patently hairy; lower bracts often leaf-like and rather large. *Pedicel* 5–7 mm long, finely grooved, very densely rather shortly brownish patently hairy. *Sepals* densely half-patently brownish hairy outside; outer sepals 2.8–3.0 × 2.3–2.6 mm; inner sepals 3.5–4.0 × 2.8–3.2 mm. *Petals* yellowish when dry, the longest one c. 9 mm long; carina very densely brownish pubescent on either side of the apical part; other petals hairy outside at apex. *Stamens:* anthers 0.7–0.8 mm long, hairy. *Ovary* semi-2-locular, slightly 2-sulcate, dark brown when dry; style very densely half-appressedly reddish brown pubescent; ovules 8. *Fruit* globular, c. 1.8 cm diam., dull, with small, pointed style-scar, brownish; pericarp rather thick, hard.

Distribution. Vietnam: Hué (4 coll.), Quang Nam (1), Dong Nai (2); alt. 700–1500 m.

Notes. 1. For differences with *5. X. eberhardtii*, see there.

2. Gagnepain (*l.c.*) described the species as having only 4 ovules. In the Paris specimen (*Poilane 21897*) bearing his drawing of a dissected young flower I counted, however, 8 ovules, like in all other collections of *X. annamense*.

14. Xanthophyllum rufum

Fig. 3 A-l, 12

X. rufum A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 210; King, Mat. Fl. Mal. Pen. (1890) 144; Maingay, Kew Bull. (1890) 113; Gagnepain, Desv. J. Bot. 21 (1908) 252; Ridley, Fl. Mal. Pen. 1 (1922) 145; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2269; Wyatt-Smith, Mal. For. Rec. 17 (1952) 81, 362; Balan Menon, *op. cit.* 19 (1956) 34; Wyatt-Smith, *op. cit.* 23-2 (1963) fig. 5, 9; Meijer, Bot. News Bull. Sandakan 7 (1967) 87; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 361, fig. 4. – *Banisterodes rufum* (A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Type: *Maingay 139 = 1616* (K; iso K).

X. flavum Ridley, Kew Bull. (1925) 77. – Type: *Brooks 7368* (K; iso K).

X. heteropleurum Chodat in Merr., Pl. Elm. Born. (1929) 134; Masam., Enum. Phan. Born. (1942) 380; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 363. – Lectotype: *Elmer 21502* (L, sheet 926.195-183; iso BM, BO, BR, BRI, C, G, K, L, M, P, SING, Z).

Tree up to 32 m high, 40 cm d.b.h. Twigs rufous-hairy. Axillary buds up to 1.8 mm long, but often much smaller, densely pubescent. *Petiole* 7–21 mm long, densely patently pubes-

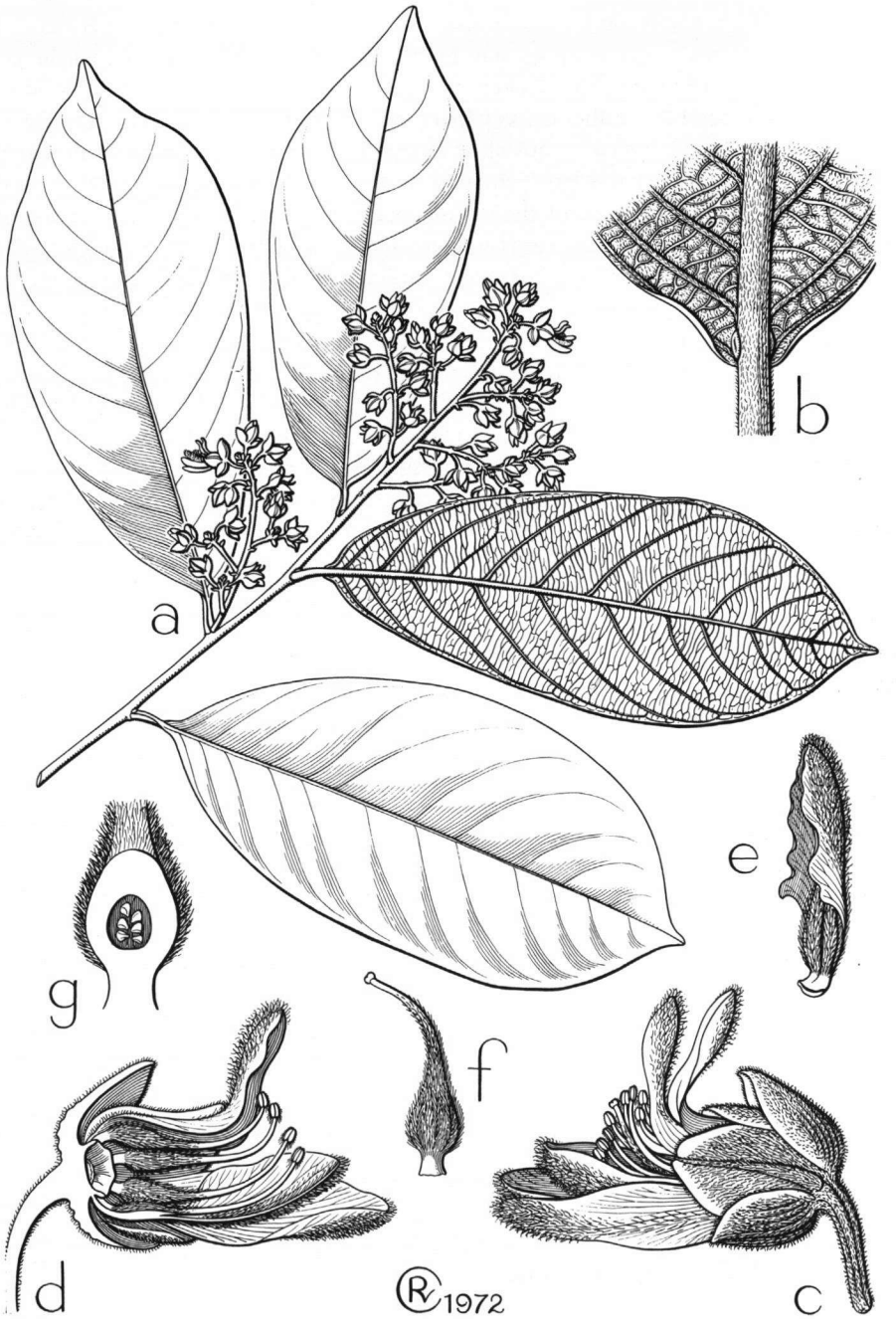


Fig. 12. *14. X. rufum.* — a. habit, x 0.5; b. base of leaf, x 2; c. flower, x 3; d. flower, longitudinal section, gynoecium removed, x 3; e. carina with two stamens enclosed, x 3; f. gynoecium, x 3; g. ovary, longitudinal section, x 6 (a–g: *SAN 36554*).

cent, more or less glabrescent, apically often with large glands. *Leaf blade* 8–25 × 4–13 cm, base sometimes cordate; upper side bright (neon-like) yellow-green to light greyish green, midrib and nerves slightly sunken, venation indistinct; lower side light brownish to brownish green, papillose, rather densely hairy, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve in apical or rarely also in basal part; glands very numerous, c. 0.1 mm diam., basal glands large, situated on the midrib at the very base of the leaf and then obscure, or at very apex of the petiole and then conspicuous. *Inflorescences* sometimes unbranched, shorter than to as long as the leaves; axes finely ribbed, very densely rufous-hairy; bracts conspicuous, persistent, often with distinct glands, bracteoles small, subpersistent. *Pedicel* 4.5–7(–10) mm long, ribbed, very densely rufous-hairy. *Sepals* persistent or not, sometimes present under fully ripe fruits (then up to c. 12 mm long), very densely rufous-hairy outside, glands present or not, inconspicuous; outer sepals c. 4–6 × 4–6 mm, mostly slightly ribbed; inner sepals c. 5–7 × 4–6 mm, keeled. *Petals* white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–15 mm long; carina very densely yellowish brown pubescent outside, inside hairy in apical part; other petals pubescent outside on apical part or only apically tufted. *Stamens:* filaments glabrous; anthers 0.4–0.6 mm long, shortly hairy at base or glabrous. *Ovary* very densely rufous-pubescent all round or pubescent in 4(–8) rows, the median rows mostly longer than the lateral ones; style very densely rufous-pubescent, glabrous in apical part; ovules 12–14. *Fruit* globular, up to 1.8 cm diam., often with 2–4, sometimes hairy ridges running down from the style-scar, yellowish green, dull, finely tuberculate; pericarp rather thick, hard; not rarely some sepals present.

Distribution. Malaya: Kedah (4 coll.), Perak (15), Kelantan (2), Trengganu (1), Selangor (6), Pahang (6), Negri Sembilan (4), Malacca (9), Johore (4). – Sumatera (6, widely scattered). – Borneo: Sarawak (1st Div.: 5. 3rd Div.: 3. 4th Div.: 2; 5th Div.: 1), Brunei (2), Sabah (Tenom: 1; E. part: 10), Kalimantan (13).

Notes. 1. In most Bornean collections the ovary is hairy all round (or sometimes hairy in 8 rows), and the sepals are more or less persistent in fruit ('*X. heterophyllum*' Chodat). In Malaya ('*X. rufum*') and Sumatera ('*X. flavum*' Ridley) the ovary is usually hairy in 4 rows, and the sepals are soon dropping off. These differences are not consistent in Malaya, however, as sometimes the ovary is hairy all round (*KEP 110368*), or the sepals are persistent (*Scortechini 1943*). Apart from those I did not find other differences; therefore it is not necessary to distinguish varieties based on these conspicuous but minor and grading differences.

2. Vegetatively resembling *3. X. sulphureum* (in which the intramarginal nerve is rather indistinct, and the laminar glands are scarce), and *12. X. velutinum* (in which the leaf blade is not papillose, and the indumentum of the vegetative parts is brownish, not rufous).

15. Xanthophyllum macrophyllum

X. macrophyllum Baker, Kew Bull. (1896) 21; Airy Shaw, Kew Bull. (1940) 252; Masam., Enum. Phan. Born. (1942) 380; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Type: *Gov. Creagh s.n.* (K; iso BM).

Shrub or tree up to 25 m high, up to 30 cm d.b.h. Twigs glabrous. *Petiole* 10–18 mm long, with (0–)2(–4) very distinct glands. *Leaf blade* (10–)14–28 × (3.8–)4.5–10 cm, base often curved upwards and decurrent-attenuate; upper side sometimes slightly bullate between the secondary nerves, greenish, midrib slightly to distinctly protruding, rarely slightly sunken, nerves finely protruding; lower side mostly brownish green, secondary nerves 7–10 pairs, forming a nearly complete rather protruding intramarginal nerve; glands mostly rather few, scattered, 0.4–0.5 mm diam. *Inflorescences* sometimes unbranched, shorter than the leaves; axes grooved, appressedly brown-velvety; bracts often opposite, with 2 small indistinct glands. *Pedicel* 2–12 mm long, appressedly brown-velvety. *Sepals* shortly appressedly brownish hairy outside, ribbed inside; outer sepals 5–6.5 × 3.8–6.2 mm; inner sepals 6–7.2 × 3.7–6.2 mm. *Petals* yellow, or white and the upper ones with a yellow spot, when dry yellowish to dark-brown, the longest one 13–16 mm long; carina appressedly velvety outside, more or less densely hairy inside in apical part; other petals glabrous or hairy outside on apical part. *Stamens:* anthers 0.55–0.75(–0.8) mm long, shortly hairy. *Ovary* sessile or shortly stipitate, creamish brown, often c. 8-ribbed when dry, the median ribs most prominent and hairy over 1/3–2/3rd their length, the other ribs hairy on apical part only; ovules 6–14. *Fruit* c. 2 cm diam., brownish to blackish, ribbed in apical part, thick-walled.

Distribution. Borneo: Sarawak (1st Div.: 3 coll.; 3rd Div.: 3. 4th Div.: 3; 5th Div.: 1), Sabah (12).

Note. Recognizable by the characteristic indumentum of the flowering parts. Vegetatively resembling collections of the *8. X. affine*-complex, in which, however, large petiolar glands are always absent.

16. Xanthophyllum arnottianum

Fig. 3 A–f, 13

X. arnottianum Wight, Ill. Ind. Bot. 1 (1840) 50, t. 23, fig. 9; Beddome, Fl. Sylv. Anal. Gen. 3 (1869) 19, pl. III, fig. 2, 2. – Lectotype: *Herb. Wight propr. 60, pencil number 53* (E, label: 'Courtallum, March 1835, ovules about 4 to each placenta in pairs'; iso E, G, K, L).

X. angustifolium Wight, Ill. Ind. Bot. 1 (1840) 50, t. 23, fig. 1–8; Beddome, Fl. Sylv. Anal. Gen. 3 (1869) 19, pl. III, fig. 1, ('2'); Drury, Handb. Ind. Fl. 1 (1864) 56. – *X. flavescens* var. *angustifolium* (Wight) A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209. – Lectotype: *Herb. Wight propr. 55* (E).

X. roxburghianum Wight, Ill. Ind. Bot. 1 (1840) 50; Drury, Handb. Ind. Fl. 1 (1864) 57. – Lectotype: *Herb. Wight propr. 51* (E).

X. undulatum Wight, Ill. Ind. Bot. 1 (1840) 50; Drury Handb. Ind. Fl. 1 (1864) 57. – Lectotype: *Herb. Wight propr. 54* (E).

X. geminiflorum [Dennst.] Alston in Trimen, Handb. Fl. Ceyl. 6 (1931) Suppl. 16, *nom. illeg.*, excl. syn. – *Kaulfussia geminiflora* Dennst., Schlüssel Hort. Malab. (1818) 30, *nom. illeg.* – [*Karin-kara* Rheede, Hort. Malab. 4 (1673) 49, t. 23.] – Lectotype: Tab. 23 in Rheede, *l.c.*

X. flavescens auct., non Roxb.: Wight & Arn., Prod. (1834) 39; A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209 (var. *1. flavescens, p.p.*); Gagnepain, Desv. J. Bot. 21 (1908) 252; Bourdillon, For. Trees Trav. (1908) 21; Gamble, Fl. Pres. Madras 1 (1915) 59; C.E.C. Fischer, Rec. Bot. Surv. India 9 (1921) 27; Purkayastha in Chowdhury & Ghosh, Indian Woods 1 (1958) 59, *p.p.*

Small tree up to 7 m high, 20 cm d.b.h. Twigs minutely patently hairy, glabrescent. *Petiole* 4–7(–11) mm long, transversely wrinkled, brownish, usually minutely patently

hairy, glabrescent. *Leaf blade* 4–15 × (0.8–)1.5–7 cm, upper side greyish to yellowish green, midrib slightly protruding to flat, lower side concolorous, secondary nerves 4–8 pairs, forming a usually distinct intramarginal nerve, tertiary nerves scalariform, in small-leaved collections irregularly scalariform-reticulate; glands 2–7, one pair situated near base, the other ones, if present, situated in the middle and apical parts, 0.3–0.6 mm diam. *Inflorescences* branched or not, up to 6(–8) cm long; axes rather strongly thickened on the nodes, slightly grooved, rather densely yellowish brown patently hairy; in the basal part flowers with 3 together; bracts usually with 2 distinct glands. *Pedicel* 3.5–6 mm long, very densely minutely patently hairy. *Sepals* all or some with 2–4 rather distinct, mostly somewhat protruding glands; outer sepals 1.5–3.6 × 2.0–2.6 mm; inner sepals 3.9–4.5 × 3.5–4.5 mm. *Petals* white to light yellow, when dry yellowish, the longest one 7–10 mm long; carina more or less densely appressedly hairy outside, inside densely hairy at least in middle part; other petals glabrous. *Stamens:* anthers 0.7–1.0 mm long, ciliolate along slits. *Ovary* often semi-2-locular, half-patently brownish pubescent; ovules 4–10, either mostly 4 or 5, or mostly 7 or 8. *Fruit* irregularly globular, up to 2 cm diam., often apically with an excentric blunt beak, often with 2 distinct and a few indistinct ridges running down from the apex, often tuberculate in between, dark green to brownish; pericarp hard.

Distribution. S. India (29 coll.; Coorg, Kerala, Tirunevelli).

Notes. 1. Most specimens from S. India had 4 (or 5) ovules per ovary; in other specimens I counted 7 or 8 ovules. No other characters appeared to be correlated with this difference. My colleague Dr. C.E. Ridsdale kindly provided me with two richly flowering collections. Dissecting 120 flowers of each, the variation in the number of ovules per ovary appeared to be as shown in Fig. 13: one collection (*Ridsdale AA*, unbroken line) had 4–6 (–8) ovules, the other one (*Ridsdale 455*, broken line) (4–)6–8(–10) ovules. This proves that the variation in the number of ovules in *X. arnottianum* is not binary, like I thought before. The variation must be gradual, with a different optimum for individual specimens. I am convinced that this difference has no taxonomic value in this species, strongly contrasting to the situation in section *Eystathes*, in which 48 species have (exclusively) 4 ovules, and 13 species have 8 or more ovules. Thus I share Bennett's (1872) opinion that there is only one species in S. India.

2. *X. arnottianum* takes a special position in section *Xanthophyllum*: a) It is the only species in which the ovary may contain 4 ovules (see under note 1). b) The ovary is always hairy all round, never in rows. Also in *14. X. rufum*, in which the ovary may be hairy all round, the hairs are concentrated in rows, a feature which is exclusive for species of section *Xanthophyllum* (7, 8, 10, 11, 12, 15). c) Another character (shared however with *13 X. annamense*) may be mentioned too: in small-leaved collections the tertiary nerves are reticulate rather than scalariform. In the three characters *X. arnottia-*

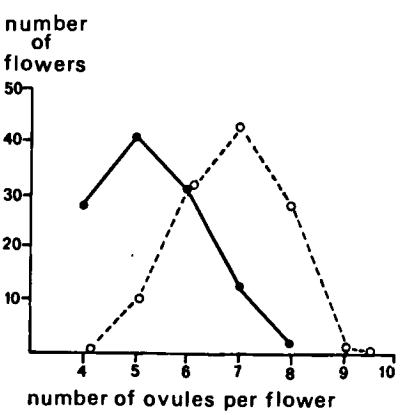


Fig. 13. Variation in number of ovules in *16. X. arnottianum*; for explanation see text.

num resembles species of section *Eystathes*. Although highly hypothetically, one might assume that this species is of hybridogeneous origin (compare chapter 2.3.3). In that case *X. arnottianum* cannot, however, remain in section *Xanthophyllum* but should be placed in a separate section. Further investigations seem to be required.

3. *Xanthophyllum geminiflorum* [Dennst.] Alston is superfluous under art. 63.1 of the Code because Alston refers to both *X. flavescens* Roxb. and *X. virens* Roxb.

1b. Section Eystathes

Section *Eystathes* (Lour.) Meijden, Bot. J. Linn. Soc. 67 (1973) 117. – *Eystathes* Lour., Fl. Coch. 1 (1790) 235. – Type: *X. sylvestre* (Lour.) S. Moore.

Twigs sometimes hairy. Axillary buds sometimes 3(–7), sometimes erect. *Leaves* sometimes shifted-decussate. *Leaf blade:* tertiary nerves finely reticulate, mostly distinctly protruding. *Inflorescences:* bracts sometimes opposite in basal part. *Petals:* carina usually distinctly unguiculate. *Stamens:* filaments sometimes connate over up to 3 mm, rarely occasionally triadelphous, sometimes with a knob-like appendage at inner side. *Ovary* mostly densely hairy all round, rarely glabrous; stigma very rarely wider than the apex of the style; ovules 4 or 8–16 (rarely more, exceptionally 5 or 6). *Fruit* mostly globular, smooth or rarely tuberculate. *Seed(s)* 1 or occasionally 2, very rarely up to 4; testa with or without a hard inner layer; albumen thin but distinct; radicle exserted or not.

Species: 61 (17–77).

KEY TO THE SUBSECTIONS

1a. Testa with a hard inner layer. Albumen forming a distinct layer. Embryo laterally near the base with 2 flattened areas. Radicle exserted . . . . . 1. subsect. **Jakkia**

b. Testa without a hard inner layer. Albumen very thin. Embryo without flattened areas near the base. Radicle not exserted . . . . . 2. subsect. **Eystathes**

1b-1. Subsection **Jakkia** Meijden, *stat. nov.*

Jakkia Bl., Cat. (1823) 17. – Type: *J. vitellina* Bl.

Twigs and inflorescence axes without nodal appendages. Axillary buds mostly 2 (seemingly single) and close together, rarely up to 4 or the upper one supra-axillary. *Seed* 1 or seeds occasionally 2; testa with a hard inner layer; albumen forming a rather thin, distinct layer, which is very thin at the lateral sides of the cotyledons near the base of the embryo; embryo laterally near the base with 2 flattened areas, radicle exserted.

Species: 47 (17–63).

Note. The subsection can be divided into three groups and a heterogeneous rest-group (see chapter 3). Notes on the systematics of the *beccarianum*- and the *eurhynchum*-group can be found under *48. X. discolor* and *60. X. eurhynchum*, respectively.

17. Xanthophyllum nigricans

X. nigricans Meijden, Bot. J. Linn. Soc. 67 (1973) 119. – Type: *SAN 48764* (KEP; iso K).

Small tree up to 15 m high, 20 cm d.b.h. Twigs finely longitudinally wrinkled. Axillary buds 2 or 3 (or 4), 1.5–2.2 mm long, very densely shortly patently light-brown hairy. *Petiole* (6–)7–11(–14) mm long. *Leaf blade* 3.5–12 × 1.2–5.5 cm; upper side greyish olive-green (to brownish); lower side concolorous, or bluish because of thin waxy layer, (glaucous-)papillose, secondary nerves 5 or 6 (or 7) pairs, forming a more or less distinct intramarginal nerve; glands rather scarce or sometimes apparently absent, situated on or near the midrib, 0.1–0.2 mm diam., basal ones often slightly larger. *Inflorescences* unbranched, shorter than the leaves; axes flattened, angular, black, very sparsely appressedly hairy; flowers with 1–3 together. *Pedicel* 2.0–2.5 mm long, black, nearly glabrous. *Sepals* glabrous outside, densely very shortly more or less patently hairy inside at base, further glabrous inside; outer sepals 1.8 × 1.7 mm; inner sepals 2.5 × 2.1 mm. *Petals* white, when dry dark reddish, very sparsely appressedly hairy outside, faintly ciliolate apically, the longest one 8 mm long. *Stamens:* anthers c. 0.3 mm long. *Ovary* black, glabrous; style glabrous or basally very sparsely appressedly hairy; ovules 4. *Fruit* globular, up to 1.3 cm diam., dull, slightly wrinkled, brownish; pedicel up to 3 mm long.

Distribution. N. Borneo: Brunei (Labuan I.: 1 coll.), Sabah (14).

18. Xanthophyllum borneense

X. borneense Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277; Masam., Enum. Phan. Born. (1942) 379. – Lectotype: *Korthals s.n.* (L; iso G, K, L, U, W).

X. glabrescens Ridley, Kew Bull. (1938) 113; Masam., Enum. Phan. Born. (1942) 380. – Type: *Hose 38* (K; iso BM, E, L, SING).

Small tree up to 5(–8?) m high. Twigs more or less reticulately wrinkled. Axillary buds 2 (or 3), 1.2–1.8(–3.0) mm long. *Petiole* c. 5–6.5 mm long. *Leaf blade* 4–16 × 1.5–7 cm, margin undulate, apex acutish; upper side slightly bullate to flat between secondary nerves, greenish to brownish; lower side glaucous-papillose, secondary nerves 4–6 pairs, forming a rather distinct intramarginal nerve; glands numerous, scattered, 0.1– 0.2 mm diam. *Inflorescences* unbranched, about as long as the leaves; axes flattened basally, angular, dull, light brownish, glabrous. *Pedicel* 1.5–2.5 mm long, dull, brownish, glabrous. *Sepals* glabrous outside; outer sepals 3.0 × 2.1 mm; inner sepals 3.8 × 2.8 mm. *Petals* light brownish or orange when dry, minutely ciliate apically, the longest one 10–11 mm long; carina sparsely appressedly minutely hairy outside. *Stamens:* anthers c. 0.3 mm long, glabrous or with very few short hairs at base. *Ovary* completely glabrous; style very sparsely more or less appressedly hairy; ovules 4. *Fruit* globular to broadly ovoid, c. 1.8 cm diam., smooth, brown; pedicel c. 5 mm long.

Distribution. Borneo: Sarawak (1st Div., Kuching, Selang For. Res.: *S 8451*; 4th Div., Baram R.: *Hose 38*); identity uncertain: Sabah (*SAN 53303, 51297*); Kalimantan (locality uncertain: *Korthals s.n.*).

19. Xanthophyllum poilanei

Fig. 14

X. poilanei Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – Type: *Poilane 29505* (L; iso P).

Shrub or tree up to 18 m, 50 cm d.b.h. Axillary buds 2, 0.5–1.2 mm long. *Petiole* 5–10 mm long. *Leaf blade* 3.8–7 × (1–)1.3–3.5 cm; upper side greenish brown, lower side concolorous, secondary nerves c. 4 or 5 pairs, forming an indistinct intramarginal nerve; glands 2–6, situated in upper 2/3rd, mostly near margin, 0.3–0.4 mm diam., basal glands absent. *Inflorescences* unbranched, shorter than the leaves; axes a little flattened, dark reddish, very sparsely appressedly hairy; bracts and bracteoles relatively long-persistent. *Pedicel* 5–7 mm long, reddish, glabrous. *Sepals* glabrous outside; outer sepals 2.5 × 2.5 mm; inner sepals 4.0 × 2.8 mm. *Petals* white, in bud pink, when dry orange, shortly hairy apically and basally outside, ciliate apically, the longest one 9–10 mm long. *Stamens:* anthers 0.5–0.6 mm long, ciliate along slits. *Ovary* glabrous, brown; style rather sparsely appressedly hairy; ovules 4. *Fruit* unknown.

Distribution. Vietnam (Mui Bach Ma: *Poilane 29932*; Quang Nam, 'Poste C': *Poilane 29505*; 'Haute course de la rivière de Cu-bi': *Poilane 12254*).

20. Xanthophyllum ovatifolium

X. ovatifolium Chodat, Bull. Herb. Boiss. 4 (1896) 258. – Type: *Haviland 2090* (K; iso BM, L, SAR, SING).

Axillary buds 2 (or 3), 1.0–1.8 mm long. *Petiole* 3.5–4.5(–6.5) mm long; glands present or not. *Leaf blade* 3.5–9.5 × 1.4–6.0 cm, apex sometimes cuspidate; upper side rather dull, brownish to greenish, midrib little protruding at base; lower side dull, secondary nerves c. 3 or 4 pairs, not forming an intramarginal nerve; glands 8–20, usually situated halfway between margin and midrib, 0.4–0.5 mm diam., basal glands usually present, 0.5–0.6 mm diam. *Inflorescences* shorter than the leaves, unbranched; axes slightly flattened, brownish, glabrous to very sparsely appressedly hairy. *Pedicel* 7–8 mm long, glabrous. *Sepals* glabrous outside; outer sepals c. 2.8 × 1.7 mm; inner sepals 3.0–3.5 × 1.8–2.0 mm. *Petals* white, when dry light brownish, ciliate at apex and base, further glabrous, the longest one 9–10 mm long. *Stamens:* anthers 0.3–0.4 mm long, glabrous. *Ovary* glabrous; style sparsely appressedly hairy basally; ovules 4. *Fruit* unknown.

Distribution. Borneo: Sarawak (1st Div., Kuching: 5 coll.).

21. Xanthophyllum tenue

X. tenue Chodat in Merr., Pl. Elm. Born. (1929) 135; Masam., Enum. Phan. Born. (1942) 382; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Type: *Elmer 21355* (G; iso BM, BO, BR, C, G, K, L, M, P, SING, U, Z).

Tree up to 25 m high, 40 cm d.b.h. Twigs glabrous to rather densely very shortly patently hairy. Axillary buds 2 (or 3), 1.5–2.5 mm long, shortly hairy, sometimes irregular and

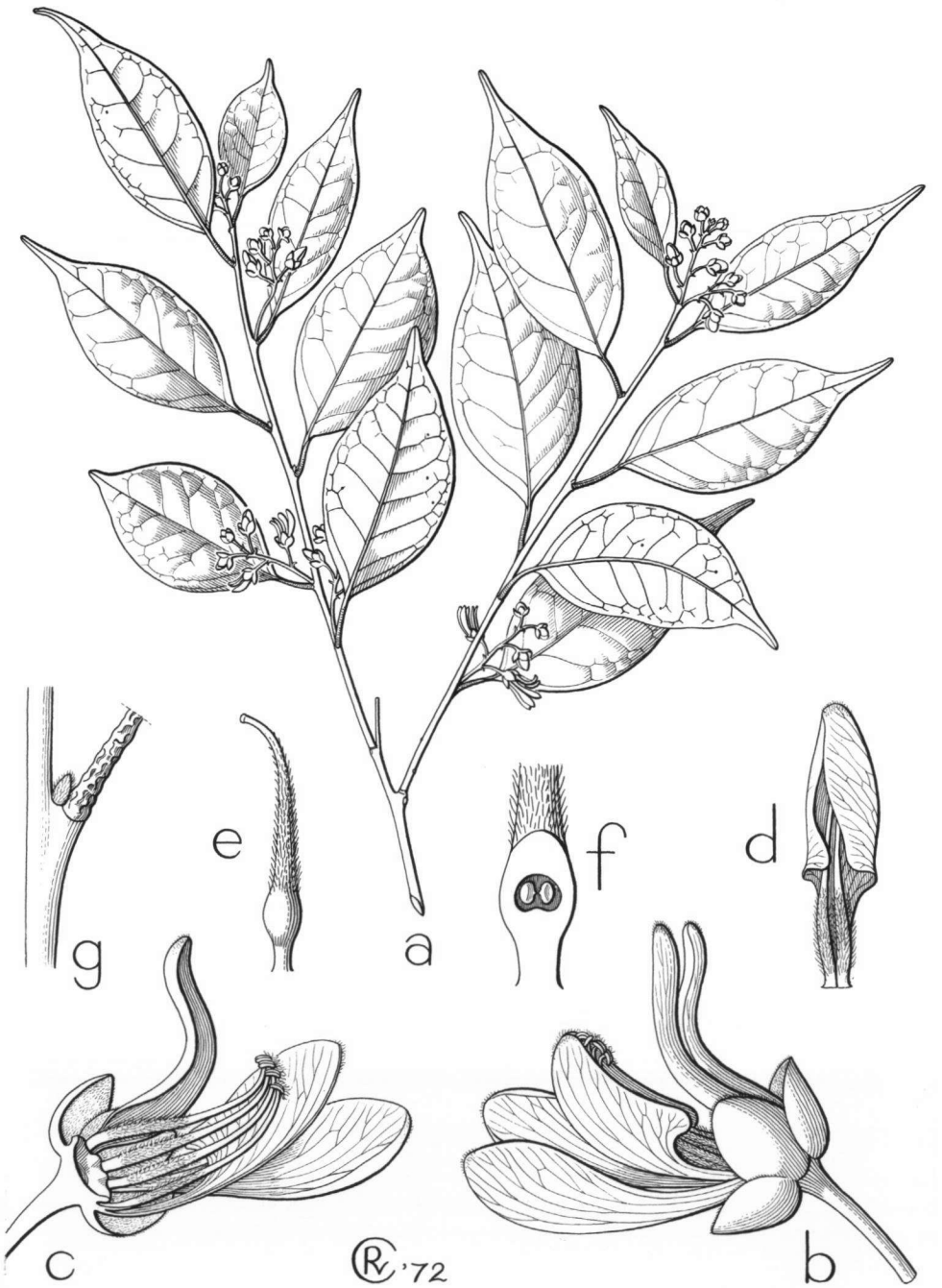


Fig. 14. *19. X. poilanei.* — a. habit, x 2/3; b. flower, x 4; c. flower, longitudinal section, gynoecium removed, x 4; d. carina with two stamens enclosed, x 4, e. gynoecium, x 4; f. ovary, longitudinal section, x 8, g. leaf axil, x 4 (a–g: *Poilane 29505*).

larger because of cork-forming in apical region. *Petiole* 6–11 mm long, not transversely wrinkled, shortly patently hairy to glabrous; glands absent or small. *Leaf blade* (5–)7–16 × (2.0–)2.5–6.5 cm; upper side slightly bullate to flat between secondary nerves, dull, greyish green to light reddish brown, midrib glabrous to patently minutely hairy in basal half; lower side mostly rather dull, yellowish green, glabrous to minutely patently hairy, midrib slightly protruding to flat, secondary nerves 4–6 pairs, mostly forming a rather indistinct intramarginal nerve, venation mostly not very protruding, sometimes rather indistinct; glands (0–)4–25, often situated near midrib, 0.3–0.5(–0.7) mm diam.; basal glands often present, relatively large. *Inflorescences* much shorter than the leaves, unbranched; axes slightly angular, sparsely to rather densely patently shortly hairy. *Pedicel* (2.5–)4–6 (–10) mm long, rather sparsely to densely minutely hairy. *Sepals* nearly glabrous outside; outer sepals 2.1–2.8 × 1.3–2.5 mm, inner sepals 2.5–4.0(–4.5) x 1.5–3.2 mm. *Petals* yellowish or white, when dry orange, the longest one 8–9(–11.5) mm long; carina sparsely to rather densely appressedly hairy outside, inside hairy to halfway or up to the apex; other petals glabrous to sparsely hairy outside, lateral petals hairy inside to halfway, upper petals hairy inside to apex. *Stamens:* filaments nearly free or connate over up to 1.5 mm; anthers c. 0.4 mm long. *Ovary* glabrous or less often rather sparsely appressedly hairy and probably soon glabrescent; style glabrous or less often sparsely appressedly hairy in basal part; ovules 4. *Fruit* globular, up to 1.8 cm diam., dull, wrinkled, light greenish brown; pericarp soft, thin; pedicel mostly up to 7 mm long, reddish.

Distribution. Borneo: Sarawak (3rd Div.: 1 coll.; 4th Div.: 2), Sabah (Mt Tras Madi: 2; Mt Kinabalu: 12; Tawau: 6), N. Kalimantan (near Mt Kongkemul: 2).

Note. Closely related to *22. X. subcoriaceum*, differing in the smooth petiole, the longer sepals, and in the indumentum of the petals. Vegetatively resembling *23. X. neglectum*, differing in the smooth petiole. See also under the latter species.

22. Xanthophyllum subcoriaceum

X. subcoriaceum (Chodat) Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – *X. ellipticum* var. *subcoriaceum* Chodat in Merr., Pl. Elm. Born. (1929) 134; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Lectotype: *Elmer 21710* (K; iso BM, BO, BR, C, G, L, M, P, SING, U, Z).

Shrub or small tree up to 15 m high, 20 cm d.b.h. Axillary buds 2 (or 3), (0.5–)1.0–2.7 mm long. *Petiole* 5–8.5 mm long. *Leaf blade* 5–12 × 1.5–5.5 cm, base sometimes more or less rounded, margin mostly strongly curved upwards when dry, apex cuspidate to acuminate; upper side sometimes slightly bullate between secondary nerves, dull, light greyish green to olive-green, secondary nerves mostly indistinct, venation mostly indistinct, sometimes scarcely visible, less often finely protruding; lower side yellowish green, secondary nerves (3 or) 4–6 pairs, forming a distinct intramarginal nerve, venation usually obscure; glands (0–)2–12, situated at some distance off the midrib, 0.2–0.4 mm diam. *Inflorescences* unbranched, about as long as the leaves; axes angular, light brown, sparsely appressedly shortly hairy; lowermost bracts sometimes leaf-like. *Pedicel* 2.5–3.5 mm long, mostly light brown, glabrous to sparsely minutely appressedly hairy. *Sepals* (nearly) glabrous outside; outer sepals 1.6–1.8 × 1.4–1.8 mm; inner sepals 2.0–2.5 × 2.0–2.5 mm. *Petals* white, when dry orange, faintly ciliate apically, outside glabrous except at base, the longest one

8–10 mm long. *Stamens:* anthers 0.5–0.7 mm long, sparsely hairy at base. *Ovary* 0.5–1.5 mm stipitate, subglabrous to rather densely appressedly hairy, rather soon partly glabrescent; style sparsely appressedly hairy; ovules 4. *Fruit* at first more or less ellipsoid with a sharp beak because of subpersistent style, when mature globular, c. 1.7 cm diam., smooth, light green to brown, rather dull to shiny; pericarp thin; pedicel up to 5(–7) mm long, mostly light brown.

Distribution. Borneo: Sarawak (1st/2nd Div.: 1 coll.; 3rd Div.: 3), Brunei (1), Sabah (Mt Kinabalu: 4; Tawau: 8).

Note. Closely related to *21. X. tenue* (see there). Resembling and probably related to *23. X. neglectum*, differing in the appressedly hairy ovary and the less hairy style, the smaller sepals, and in the indistinctly nerved leaf blades. Differing from *25. X. tardicrescens* in the key characters.

23. Xanthophyllum neglectum

X. neglectum Meijden, Bot. J. Linn. Soc. 67 (1973) 119. – Type: *SAN 24222* (L; iso K, KEP, L, SING).

X. palembanicum auct., non Miq.: Keith, N. Born. For. Rec. 2 (1938) 225.

Tree up to 20 m high, 20 cm d.b.h. Axillary buds 2, elliptic to ovate-oblong, 1.5–4(–6) mm long, acute, light yellowish brown. *Petiole* 4–6.5 mm long, glabrous to sparsely very shortly hairy especially in the upper groove. *Leaf blade* 5–12 × 1.8–5.5 cm, margin undulate; upper side dull, greyish green; lower side rather dull, sometimes slightly waxy, secondary nerves 3–5 pairs, forming a rather indistinct intramarginal nerve; glands 2–8, not in basal part, 0.2–0.3(–0.4) mm diam. *Inflorescences* unbranched, 1.5–5(–8) cm long, shorter than the leaves, bearing 3 or 4(–7) flowers; axes c. 0.5 mm diam., slightly flattened basally, light brown, rather sparsely patently shortly hairy. *Pedicel* c. 2 mm long, slightly grooved, rather densely patently shortly hairy. *Sepals:* outer sepals 2.2–2.5 × 2.0–2.3 mm; inner sepals 2.8–3.5 × 2.2–3.0 mm. *Petals* white or yellowish, when dry light brownish, the longest one 7–10 mm long; carina nearly glabrous to rather densely hairy outside, shortly hairy at both sides basally; other petals nearly glabrous except for some hairs at the base and apex. *Stamens:* filaments of abaxial 4 stamens basally widened and slightly thickened; anthers 0.3–0.4 mm long. *Ovary* patently hairy; ovules 4. *Fruit* (immature) ovoid, dull greyish green, hairy, slightly wrinkled when dry; pericarp rather soft; pedicel up to 4.5 mm long, light brown.

Distribution. E. Borneo: E. Sabah (21 coll.), E. Kalimantan (5).

Notes. 1. Specially selected branches of only 2 cm diam. are used by local Dayak people in Southeast Borneo to make light-weighted, flexible axe-handles with very good properties for cutting even the biggest trees.

2. Vegetatively resembling *21. X. tenue* (see there) as well as forms of *32c. X. griffithii* subsp. *angustifolium*. Differing from *24. X. pauciflorum* in the longer axillary buds, the smooth lower surface of the leaf blades, and in the patently hairy ovary; *FB 23372* from Mindanao seems to take an intermediate position between both species.

24. Xanthophyllum pauciflorum

X. pauciflorum Meijden, Bot. J. Linn. Soc. 67 (1973) 119. – Type: *S 21934* (L; iso K, KEP, P, SING).

Tree up to 21 m high, 25 cm d.b.h. Twigs about as thick as the petioles, only a few internodes long. Axillary buds 2, 0.5–1.3 mm long. *Petiole* 3.5–4.5 mm long. *Leaf blade* 4.8–8(–9) × 1.2–2.2(–3.5) cm, apex cuspidate to acuminate; upper side olive- to dark green, rather dull; lower side glaucous-papillose, secondary nerves 4–6 pairs, not forming an intramarginal nerve; glands 2–7, 0.1(–0.2) mm diam. *Inflorescences* unbranched, much shorter than the leaves, bearing only 3–6 flowers; axes slender, slightly flattened, glabrous to sparsely very shortly patently hairy. *Pedicel* 1.5–2.5(–3) mm long, very shortly patently hairy. *Sepals* with a small apical tuft; outer sepals 2.0–2.2 × 1.5–1.8 mm, very sparsely very shortly hairy outside; inner sepals c. 2.7 × 3.0 mm, glabrous outside. *Petals* yellowish, when dry yellowish orange, very sparsely hairy to glabrous outside, apically slightly tufted and distinctly ciliate, basally rather densely hairy at both sides, the longest one 7.5–8.5 mm long. *Stamens:* anthers c. 0.4 mm long, with few hairs at base. *Ovary* appressedly hairy; ovules 4. *Fruit* (immature) ovoid-globular, olive-brown, smooth, with a distinct remainder of the style, roughly pubescent, glabrescent.

Distribution. Borneo: Sarawak (3rd Div., Mersing hill: 4 coll.).

Note. See under *23. X. neglectum* and *25. X. tardicrescens.*

25. Xanthophyllum tardicrescens

X. tardicrescens Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – Type: *S 24331* (L; iso K, KEP).

Small tree up to 6 m high, 6 cm d.b.h. Twigs dull, bearing 1 or 2 (or 3) leaves per shoot. Axillary buds 2 (or 3?), smaller than 1 mm. *Petiole* 3.5–5 mm long. *Leaf blade* 7–16 × 2–5 cm, base rounded-truncate to -cordate; upper side dark greyish green, very dull, secondary nerves slightly sunken, venation obscure; lower side olive-greenish, dull, secondary nerves 3 or 4 pairs, the basal nerves long, reaching often beyond the middle of the leaf, or forming an intramarginal nerve, venation not distinct; glands 6–12, scattered, 0.2–0.3 mm diam. *Inflorescences* unbranched, about as long as the leaves; axes grooved, not flattened, nearly glabrous, light brown; flowers often with 2 or 3 together; bracts relatively long-persistent. *Pedicel* 3.5–4.5 mm long, sparsely very shortly appressedly hairy. *Sepals* sometimes apically with tiny glandular spots; outer sepals 2.0 × 2.1 mm; inner sepals 2.3 × 2.3 mm. *Petals* white, the upper ones with a yellow spot, when dry yellowish orange, the longest one 7–8 mm long; carina nearly glabrous outside; other petals glabrous. *Stamens:* filaments connate over 0.7–1.0 mm, very shortly hairy above base, further glabrous; anthers probably c. 0.7 mm long. *Ovary* very shortly stipitate, more or less appressedly hairy; ovules 4. *Fruit* (immature) smooth, slightly shiny, yellowish green, sparsely appressedly hairy, glabrescent; pericarp very thin.

Distribution. Borneo: Sarawak (1st Div., Arboretum Semengoh: 3 coll.).

Note. Closelv related to *24. X. pauciflorum*, differing in characters of the leaf blade, the longer pedicels, connate filaments, and the longer anthers. Differing from *22 X. subcoriaceum* in the characters used in the key.

26. Xanthophyllum parvifolium

X. parvifolium Meijden, Bot. J. Linn. Soc. 67 (1973) 119. – Type: *S 5396* (L; iso K, KEP, SING).

Small tree up to 9 m high, 12 cm d.b.h. Twigs forming very short shoots bearing 2 or 3 leaves, the young ones very slender, c. 0.5 mm diam. Axillary buds 2, 0.7–1.2 mm long. *Petiole* 2–2.5 mm long. *Leaf blade* 1.6–5(–6) × 0.5–1.6(–1.9) cm, base rounded to cuneate; upper side shiny, yellowish or greenish brown, midrib flat or slightly protruding, nervation finely protruding to obscure; lower side glaucous-papillose, yellowish to reddish brown, secondary nerves 1–3 pairs, rather indistinct, forming an indistinct intramarginal nerve, venation rather indistinct; glands rather numerous, scattered, very small though relatively distinct, up to 0.1 mm diam. *Flowers* unknown. *Infructescences* subapical, no more than one per twig, consisting only of the pedicel of the fruit, infructescence axis 0. *Fruit* very shortly stipitate, globular, up to 1.1 cm diam., dull, light brown, very sparsely shortly appressedly hairy; pericarp rather thin; pedicel slender, 6.5–10 mm long, completely glabrous. *Seed* 1; abortive ovules 3.

Distribution. Borneo: Sarawak (1st Div., Sabal For. Res.: 1 coll.; 4th Div., Lambir hills: 2 coll.).

Note. After its publication as a new species two additional collections became available, confirming its characters: the 1-flowered inflorescences and the very small leaves. Unfortunately, however, flowers are still unknown. Without those, the relationship with other species can not be established.

27. Xanthophyllum philippinense

Fig. 10A

X. philippinense Chodat, Bull. Herb. Boiss. 4 (1896) 261; Merr., En. Philip. (1923) 387. – Type: *Vidal 2092* (K).

Twigs often with numerous adventitious buds on older nodes. *Petiole* 6–10 mm long, often grading into the narrow leaf base, mostly in middle part with glands. *Leaf blade* 7–14 × 2.5–6 cm, apex acutish; upper side shiny to rather dull; lower side more or less concolorous, rather dull, secondary nerves c. 5–7 pairs, apically hardly distinguishable; glands 1–6, 0.4–0.6 mm diam. *Inflorescences* unbranched or with one side branch, up to 5 cm long, often several together in the leaf axils; axes rather dark, sparsely minutely hairy; lower bracts (sub)opposite. *Pedicel* c. 3.5 mm long, reddish brown, densely minutely hairy. *Sepals:* outer sepals c. 2.5 × 2 mm; inner sepals c. 3.5 × 3 mm. *Petals* orange when dry, the longest one c. 12 mm long; carina faintly appressedly hairy outside near apex; other petals nearly glabrous. *Stamens:* filaments widened but hardly thickened above their base and there densely more or less woolly hairy, further glabrous; anthers c. 1.2 mm long. *Ovary* c. 2 mm stipitate, appressedly hairy; style very long (c. 10 mm), exserting over about 2 mm from the carina, faintly appressedly hairy; ovules 4. *Fruit* c. 2 cm diam., smooth, light brown, faintly hairy; pedicel 2.5–6(–8) mm long, minutely hairy. *Seed(s)* 1 or 2.

Distribution. Philippines: Luzon (9 coll.), Mindoro (1), Mindanao (2).

Notes. 1. Insufficiently known; the only flowering collection (the type) consists of the end of a single twig.

2. In open flowers the stigma is exserted from the carina; this may mean that cross-pollination is obligatory; see chapter 1.10.

28. Xanthophyllum ancolanum

X. ancolanum Miq., Fl. Ind. Bat., Suppl. (1861) 394; Chodat, Bull. Herb. Boiss. 4 (1896) 261. – Lectotype: *Junghuhn s.n.* (L; iso U).

X. ancolanum β *angustifolia* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 275. – Lectotype: ? *Korthals s.n.* (L, sheet 908.171-1738; iso G, K, U, W).

X. palembanicum Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277. – Lectotype: *Teysmann HB 3533* (L; iso BO, U).

non X. palembanicum auct.: King (*et auct. al.*), Mat. Fl. Mal. Pen. (1890) 137 (= *60. X. eurhynchum*) – Keith, N. Born. For. Rec. 2 (1938) 225 (= *23. X. neglectum*).

X. sumatranum Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 275; Baker, Hook. J. Bot. 62 (1924) Suppl. 7. – Lectotype: *Korthals s.n.* (L; iso G, L, U).

Shrub or small tree up to 4 m high, 4 cm d.b.h. Twigs glabrous to densely shortly hairy. Axillary buds c. 1–2.5 mm long, hairy; older nodes often with numerous adventitious buds. *Petiole* (5–)7–15 mm long, not transversely wrinkled, glabrous to densely shortly hairy, apically sometimes with glands. *Leaf blade* 10–26 × (2.5–)3.5–10.5 cm, apex shortly acuminate to cuspidate; upper side greyish green, rather dull; lower side green, secondary nerves 8–10 pairs, at least in apical part forming an intramarginal nerve; glands mostly rather numerous, scattered, 0.2–0.5 mm diam., basal glands often present. *Inflorescences* situated at end of young twigs, but also axillary and on old nodes (plant partly ramiflorous), 1 (or 2) in each axil, erect to strongly reflexed, unbranched, or sometimes with a side branch; axes 1–11 cm long, dark, rather sparsely shortly hairy; lower bracts (sub)opposite. *Pedicel* 4.5–6 mm long, dark, rather sparsely minutely patently hairy. *Sepals* dark purple; outer sepals 2.5–3.8 × 2.1–3.1 mm; inner sepals 4.2–5.2 x 3.0–3.9 mm. *Petals* when dry light to dark orange, the longest one 13–19 mm long; carina long unguiculate, sparsely very shortly appressedly hairy outside; other petals very sparsely hairy outside to glabrous. *Stamens:* filaments connate over (0.7–)2.0–2.5 mm, slightly widened and hardly thickened above base; anthers 0.8–1.2 mm long, very shortly hairy at base. *Ovary* c. 2 mm stipitate, half-patently hairy; style exserted from the carina for less than 0.5 mm, sparsely hairy in 2 rows; ovules 4. *Fruit* (immature) shortly stalked, more or less globular, slightly beaked, brownish, hairy; pedicels 8–11 mm long.

Distribution. Sumatera (Mt Bandahara: 1 coll.; mountains north of Padang: 9; Muaradua: 1).

Note. Resembling *37. X. incertum*, differing in the shorter axillary buds, the higher number of secondary nerves, the longer pedicels, and in the not-thickened filaments.

29. Xanthophyllum tenuipetalum

Fig. 9 a

X. tenuipetalum Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – Type: *BW 3990* (L; iso FI, K, KEP, SING, W).

X. affine auct., non Miq.: Koord., Minah. (1898) 344.

Tree up to 26 m high, d.b.h. 40 cm. Axillary buds 2 (or 3), 0.5–2.5 mm long, basally

wrinkled, in apical part smooth or slightly keeled. *Petiole* 6–9 mm long, often appearing somewhat longer because of the attenuate leaf base, always with 2 rather distinct glands usually situated in the middle part or at the (very) base. *Leaf blade* 9–20 × 3.5–11 cm; upper side slightly bullate between the secondary nerves, shiny, dark to brownish green, nervation often very distinct; lower side slightly shiny, secondary nerves c. 6–8 pairs, apically difficult to count, forming an irregular and fine intramarginal nerve or ending in the venation; glands mostly very numerous, scattered, c. 0.3–0.5 mm diam. *Inflorescences* also in lower leaf axils, unbranched or rarely with one short branch, up to 7 cm long; axes rather slender, smooth, very densely shortly more or less appressedly hairy; flowers with 3 together or in the apical part solitary; lower bracts (sub)opposite. *Pedicel* 2–4 mm long, very densely nearly appressedly shortly hairy. *Sepals:* outer sepals 1.8–2.9 x 1.9–3.0 mm; inner sepals 2.9–3.5 × 2.6–3.2 mm. *Petals* rather thin, white (or yellow?) when fresh, when dry light brown or orange, not covering the stamens in anthesis, the longest one 10.5–12.5 mm long; carina long unguiculate, apically ciliate, rather sparsely to rather densely more or less appressedly woolly hairy outside in apical region and slightly so near the base, inside glabrous; other petals ciliate at very apex, near base sparsely to rather densely hairy on either side. *Stamens* 8 or rarely occasionally 9; filaments connate over 0.1–0.5 mm, rather densely more or less appressedly woolly hairy in basal half, glabrous upwards; anthers (0.5–) 0.6–0.7 mm long, sparsely ciliolate along slits, sparsely and shortly hairy at base. *Ovary* appressedly hairy; style rather sparsely hairy; ovules 4. *Fruit* globular, 1.8–2.0 cm diam., slightly shiny, light brown, faintly appressedly hairy; pericarp rather thin; pedicel up to 6 mm long.

Distribution. Sulawesi (Minahassa: 1 coll.; Malili: 3; Kendari: 3; Muna I.: 1). – Maluku Is.: Taliabu (Sumaja: 1), Kai I. (1). – New Guinea: W. Irian Jaya (Vogelkop peninsula: 5).

30. Xanthophyllum impressum Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, plus minusque inclusae inter petioli basin atque cristam demissam eiusdem ramuli, 1.5–2 mm latae, pro circa 1 mm eius longitudimis nudae. Lamina subtus papillosae; glandulae probabiliter numerosae, minutae. Inflorescentia ramosa, bracteis basalibus oppositis. Petala inaequalia, petalo longissimo 8.5–10.5 mm longo; carina extus dense appresse pilosa. Antherae 0.6–0.7 mm longae. Ovarium densissime pilis semipatentibus indutum; stylus pilosus; ovula 4. Fructus globosus, 1.7 cm diam.; pericarpium tenue. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *SAN 31500* (L; iso KEP, SING).

Tree up to 23 m high, 20 cm d.b.h. Axillary buds, when resting, mostly more or less enclosed between the base of the petiole and a low ridge of the twig, 1–1.8 × 1.5–2 mm, for about 1 mm of its length uncovered; scales strongly thickened, especially at base, but leaving a narrow scar. *Petiole* 10–14 mm long, sometimes with glands. *Leaf blade* 10–20 × 3.5–9 cm, apex acutish to shortly acuminate; upper side rather dull, greyish green; lower side light yellowish green, papillose, secondary nerves c. 8 or 9 pairs, not forming an intramarginal nerve; glands scattered, probably rather numerous but often seemingly absent, 0.05–0.2 mm diam., exceptionally larger. *Inflorescences* up to 20 cm long; axes reddish brown, densely minutely appressedly hairy; lower bracts (sub)opposite. *Pedicel* 1.5–4 mm

long, grooved, appressedly shortly hairy. *Sepals:* outer sepals 2.0–2.5 × 2.6–3.3 mm; inner sepals 3.2–3.7 × 3.2–3.3 mm. *Petals* white, the upper ones with a yellow spot, when dry orange to dark red, sometimes with incrustations, the longest one 8.5–10.5 mm long; carina densely more or less appressedly hairy outside; other petals glabrous outside. *Stamens:* filaments widened and thickened above base, there appressedly hairy, further glabrous; anthers 0.6–0.7 mm long, hairy to (sub)glabrous at base. *Ovary* nearly sessile, half-patently hairy; ovules 4. *Fruit* globular, c. 1.7 cm diam., dull, smooth, light brownish, appressedly hairy.

Distribution. E. Borneo: E. Sabah (Lahad Datu: 5 coll.; Madai: 1; Mostyn: 2), E. Kalimantan (Sangkulirang: 1). – Philippines: Catanduanes (*BS 75447*).

Notes. 1. Related to the *vitellinum*-group, characterized by its axillary buds. In that character *X. impressum* resembles *31. X. colubrinum* from which it differs in many other characters.

2. The only specimen known from outside Borneo (*BS 75447*, SING) is found on Catanduanes I., an island in the eastern part of the Philippines. I assume that at present distribution data from the Philippines are insufficient.

31. Xanthophyllum colubrinum

X. colubrinum Gagnepain, Desv. J. Bot. 21 (1908) 249; Bull. Soc. Bot. France 56 (1909) 35; Fl. Gén. I.-C. 1 (1909) 244, t. 18; in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 219. – Lectotype: *Thorel 1168* (P; iso E, P).

Tree up to 20 m, 50 cm d.b.h. Axillary buds 0.3–1.1 mm long, often a little sunken into the tissue of the branch or enclosed by a ridge. *Petiole* 6–9(–14) mm long, often with small glands. *Leaf blade* (4.5–)6–12 × 1.8–7 cm, apex acutish; upper side yellowish green to light reddish brown, midrib mostly protruding, sometimes nearly flat, venation rather distinctly protruding; lower side: secondary nerves c. 5–7 pairs, not forming an intramarginal nerve, fine venation very distinct; glands 2–12, situated near the margin, (0.2–)0.3–0.5(–0.8) mm long. *Inflorescences* unbranched or branched; axes rather densely yellowish shortly patently hairy; in lower part flowers with 5(–7) together, often solitary in upper part; lower bracts (sub)opposite. *Pedicel* 2.5–3.5 mm long, dark reddish, densely shortly patently hairy. *Sepals:* outer sepals 1.7–2.3 × c. 2 mm, inner sepals 2.0–2.5 × 2.0–2.5 mm. *Petals* pink, when dry dark reddish, the longest one 5.5–7(–7.5) mm long; carina densely shortly patently hairy outside; other petals with very few hairs at apex. *Stamens:* filaments widened and thickened above base and there rather sharply bent and rather densely hairy, further glabrous; anthers 0.3–0.4 mm long. *Ovary* shortly appressedly hairy; ovules 4. *Fruit* globular, up to 2 cm diam. (or, according to Gagnepain, *l.c.*, 1909, p. 244, the size of a small apple), dull, wrinkled when dry, with a shallow groove from the strongly excentrical style scar to the pedicel (or, according to Gagnepain, *l.c.*, 4-sulcate); pericarp rather thick, hard. *Seed(s)* 1 or 2.

Distribution. Laos (Kampong Soai: 1 coll.). – Vietnam: Quang Nam (1), Kontum (1), Binh Dinh (1), Thu Dau Mot (5), Bien Hoa (4), locality uncertain: *Thorel 1168, Poilane 31816*. – Cambodia: Phnom Penh (1). – SE. Thailand: Bampe (1).

Notes. 1. Closely related to *32. X. griffithii*, from which it differs in its reduced axillary buds (see also under *30. X. impressum*), in the distinctly protruding finely reticulate venation, the larger laminar glands, the pink petals, and (possibly) in its fruits.

2. The great majority of the collections had been infected by gall insects; galls were induced in the ovaries, and often in the nodes of the twigs.

32. Xanthophyllum griffithii

X. griffithii Hook. *f. ex* A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 210; King, Mat. Fl. Mal. Pen. (1890) 136; Maingay, Kew Bull. (1890) 114; Brandis, Indian Trees (1906) 45; Gagnepain, Desv. J. Bot. 21 (1908) 251; Ridley, Fl. Mal. Pen. 1 (1922) 149; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Henderson, *op. cit.* 4 (1928) 222; Burkill, Dict. (1935) 2269; Wyatt-Smith, Mal. For. Rec. 17 (1952) 80, 362; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 357, fig. 2 (excl. var. *curtisii* and var. *montanum*); Mal. For. 38 (1975) 85, fig. 8.1 A–E, 8.2. – *Banisterodes griffithii* (Hook. *f. ex* A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *Griffith s.n.* (K).

non X. griffithii auct.: Rolfe, Hook. J. Bot. 23 (1885) 210; Vidal, Rev. Pl. Vasc. Filip. (1886) 51; Ceron, Cat. Pl. Herb. Manilla (1892) 19 (= *36. X. vitellinum*).

X. parvum Chodat, Bull. Herb. Boiss. 4 (1896) 264. – Type: *Beccari 2953* (M; iso FI, G, L).

X. gracile Chodat, Bull. Herb. Boiss. 4 (1896) 256; Koord. & Valeton, Bijdr. Booms. Java 5 (1900) 302; Backer, Schoolfl. Java (1911) 80; Koord., Exk. Fl. Java 2 (1912) 454. – Type: unannotated sheet in K, with label '*X. pseudopulchrum* Chodat, type' and 'Java?'.

X. pseudostipulaceum Merr., Philip. J. Sc. 10 (1915) Bot. 316; En. Philip. (1923) 387. – Lectotype: *BS 21135* (L; iso A, BM, BO, BRI, K, P, SING).

non X. pseudostipulaceum auct.: Meijer. Bot. News Bull. Sandakan 7 (1967) 87; Weberl., Beitr. Biol. Pfl. 50 (1974) 279, fig. 1, II (= *46. X. heterophyllum*).

X. griffithii var. *angustifolium* Ng, Fed. Mus. J. n.s. 13 (1971) 137; in Whitmore, Tree Fl. Mal. 1 (1972) 358, fig. 2. – Type: *Osman CF 23692* (SING; iso KEP).

Tree up to 27 m high, 40 cm d.b.h. Twigs glabrous to minutely patently hairy. Axillary buds erect to half-patent, (1.5–)3–8 mm long, not thickened at base, glabrous to densely minutely hairy; enclosing a pair of nearly similar buds of second order (those at base of a new twig often half-patent). *Petiole* 4–12 mm long, sometimes with 1 or 2 glands in apical part. *Leaf blade* 4–12(–15) × 1–4.5(–9) cm, apex sometimes cuspidate; upper side dark green to brownish; lower side lighter coloured, smooth to glaucous-papillose, secondary nerves 4–6 pairs, usually forming an indistinct intramarginal nerve in apical half; glands 4–20, scattered but often near midrib, 0.2–0.3 mm diam. *Inflorescences* up to 10 cm long, at very base with 2 side-axes or with a pair of buds of second order; axes often reddish brown, densely minutely patently hairy; lower bracts opposite. *Pedicel* 1–4.5 mm long, grooved, densely minutely appressedly hairy. *Sepals* sometimes with 2 glands in apical part; outer sepals 1.6–2.5 × 2.1–2.7 mm; inner sepals 2.6–3.3 × 2.1–3.0 mm. *Petals* white, the upper ones with a yellow spot, when dry dark red to orange-red, the longest one (5–)7–8 mm long; carina densely more or less appressedly hairy outside; other petals glabrous to appressedly hairy outside in apical part. *Stamens:* filaments widened above base and with a knob-like, densely hairy appendage at inner side, further glabrous; anthers (0.3–)0.4(–0.5) mm long. *Ovary* 0.5–2 mm stalked, more or less appressedly hairy; ovules 4. *Fruit* globular, up to 1.5 cm diam., more or less smooth, brown, appressedly hairy; pedicel up to 4 mm long.

Note. The plants with erect axillary buds are confined to a restricted area in Central

Malaya, where they are locally common and inhabit a nearly uninterrupted area. Because they do not differ in characters of the flowers, I think that these specimens cannot be split off as a separate species. However, they differ in the axillary buds and probably in their ecology as well. Therefore I think that the subspecific rank is waranted (subsp. *erectum*).

The remaining collections cover a much wider but disrupted area. The plants seem to be confined to hill tops at rather low altitudes. Vegetatively they strongly vary in the length of the axillary buds and in the structure of the lower surface of the leaf blade.

The collections from Mergui (Burma) differ from all other collections of the species in their smaller petals and shorter anthers; in general appearance resembling subsp. *erectum* they lack, however, the (derived) character of the axillary buds of that subspecies. In view of the considerable gap in the area between Mergui and the nearest localities of the species in Malaya (Kedah), the Mergui collections may belong to a relict population. The taxonomic position of the Mergui collections is important as the type collection of *X. griffithii* is from that area. Under the present Code this implies that it will belong to the 'typical' subspecies. However, *'var. griffithii' sensu* Ng (1972) is identical to my subsp. *erectum*, except in comprising the type collection of *X. griffithii*. Under the presumption that a) subsp. *erectum* is a 'younger' taxon than *X. griffithii* as a whole, and b) that the type of *X. griffithii* is a representative of a relict population, Ng's decision cannot be maintained. However, if the Mergui collections would be included in the other subspecies, that taxon should be called 'subsp. *griffithii*'. In order to avoid confusion between *'var. griffithii' sensu* Ng and 'subsp. *griffithii*' I have chosen for the practical solution to distinguish the Mergui collections as a separate subspecies (subsp. *griffithii*). The third subspecies may then retain its recent epitheton *'angustifolium'*. (I must admit that it took me a long time to decide in this particular question; in 1978 I still maintained subsp. *angustifolium* as a separate species, thus returning the loans under the name '*X. parvum* Chodat'.)

KEY TO THE SUBSPECIES

1a. Axillary buds half-patent 2
b. Axillary buds erect and flattened against the twig . . . . . c. subsp. **erectum**
2a. Longest petals 5–6 mm long. Anthers 0.3 mm long . . . . . a. subsp. **griffithii**
b. Longest petals 6.5–7.8 mm long. Anthers 0.4 mm long . . . . . b. subsp. **angustifolium**

a. subsp. griffithii

X. griffithii Hook. *f. ex* A.W. Bennett, excl. Malayan coll.

Axillary buds half-patent, lanceolate, 5–6 mm long, glabrous. *Petiole* c. 8–11 mm long. *Leaf blade* up to 10 × 4 cm; lower side glaucous-papillose, secondary nerves 4–6 pairs; glands c. 0.2 mm diam. *Pedicel* 3.5 mm long. *Sepals:* outer sepals 2.0 × 1.8 mm; inner sepals 2.5 × 2.1 mm. *Petals:* longest one 5–6 mm long. *Stamens:* anthers 0.3 mm long. *Fruit* unknown.

Distribution. Burma (Mergui, 3 coll.).

b. subsp. **angustifolium** (Ng) Meijden, *stat. nov.*

X. griffithii var. *angustifolium* Ng, Fed. Mus. J. n.s. 13 (1971) 137. – *X. parvum* Chodat. – *X. gracile* Chodat. – *X. pseudostipulaceum* Merr.

Axillary buds half-patent, elliptic to lanceolate, 1.5–8 mm long, at base often stalk-like constricted, more or less flat, wrinkled, glabrous or soon glabrescent. *Petiole* 4–8(–9) mm long. *Leaf blade* 4–8(–10) × 1–4(–5) cm, in juvenile shoots up to 10 × 2.5 cm; lower side glaucous-papillose to (nearly) smooth and not glaucous, secondary nerves 4 or 5 (or 6) pairs; glands 0.2–0.3 mm diam. *Pedicel* 1.5–4.5 mm long. *Petals:* longest ones 6.5–7.8 mm long. *Stamens:* anthers 0.4 mm long. *Fruit* c. 1.1 cm diam.

Distribution. Malaya: Perak (3 coll.), Selangor (14), Negri Sembilan (2), Malacca (3). – Sumatera: Inderagiri (Tjerenti: 1). – Borneo: Sarawak (1st Div.: 11; 2nd Div.: 1; 3rd Div.: 3; 5th Div.: 2), Sabah (Mt Kinabalu: 2; Tawau: 1), E. Kalimantan (Berau R.: 1). – Philippines: Luzon (5).

Notes. 1. Especially in Malaya narrow-leaved forms have been collected. The plants are sterile, and probably represent youth forms only, without taxonomic value.

2. The collections from Malaya and from the Philippines are strikingly similar, whereas most of the material from Borneo is different in some minor points: leaf blades are wider, and less papillose at lower surface, and the axillary buds are shorter.

3. The type of *X. gracile* Chodat is a sheet without collector's name or number, with the annotation '? Java'. Almost certainly the material has been collected in Borneo, however. Later references of *X. gracile* from Java refer to small-leaved collections of *36. X. vitellinum*.

4. A collection from Laos (*Kerr 20798*) is related to this subspecies, differing in the longer leaf blades with more numerous and smaller glands. It possibly represents a new taxon which, however, is insufficiently known.

c. subsp. **erectum** Meijden, *subsp. nov.*

X. griffithii Hook. *f. ex* A.W. Bennett, excl. Mergui coll.

Gemmae axillares erectae atque ad ramulum eundem compressae. Petalum longissimum 6.5–8 mm longum.

Typus: *KEP 98851* (L; iso K, KEP, SING).

Axillary buds erect or nearly so and flattened in their upper part against the twig, ovate to ovate-lanceolate, rarely elliptic, (3–)4–8 mm long, basally convex, slightly wrinkled, glabrous to densely minutely hairy. *Petiole* 6–12 mm long. *Leaf blade* 5–12(–15) × 2–(–9) cm; lower side glaucous-papillose, secondary nerves c. 5 or 6 pairs; glands c. 0.2 mm diam. *Pedicel* 1–2(–3) mm long. *Petals:* longest one (6.5–)7–8 mm long. *Stamens:* anthers 0.4(–0.5) mm long. *Fruit* up to 1.5 cm diam.

Distribution. Malaya: Kedah (3 coll.), W. Trengganu (4), Perak (12), Selangor (24), W. Pahang (2), Negri Sembilan (2), Malacca (10).

33. Xanthophyllum monticolum Meijden, *spec. nov.*

X. griffithii var. *montanum* Ng, Fed. Mus. J. n.s. 13 (1971) 137; in Whitmore, Tree Fl. Mal. 1 (1972) 359, fig. 2. – Type: *Dolman CF 27610* (SING; iso KEP).

Gemmae axillares ut videtur singulae, patentes, (1.0–)1.8–2.9 mm longae. Petiolus 9–14 mm longus. Lamina subtus papillosa; glandulae 4–16, saepe adsunt in parte dimidia propre costam. Inflorescentia ramosa, bracteis basalibus opposites. Sepala interiora 4.4–5.5 mm longa. Petala inaequalia, petalo longissimo 10.5 mm longo; carina extus dense appresse pilosa. Antherae 0.5–0.7 mm longae. Ovarium dense semi-patenter pilosum; stylus dense pilosus; ovula 4. Fructus globosus, c. 1.7 cm diam., pericarpio molli. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.
Typus: *Chew Wee-Lek 765* (L; iso KEP).

Tree up to 10 m high, 20 cm d.b.h. Axillary buds often appressed against the petiole, (1.0–)1.8–2.9 mm long, base wrinkled, apex acute. *Petiole* 9–14 mm long. *Leaf blade* 8–16 × 2–5(–7.5) cm, upper side usually dark green, sometimes brownish; lower side glaucous-papillose, secondary nerves 6–8 (or 9) pairs, in apical part forming a weak intramarginal nerve; glands 4–16, mostly in basal half near midrib, 0.2–0.3 mm diam., basal glands sometimes present, slit-like, c. 0.8 mm long. *Inflorescences* up to 12 cm long; axes angular, basally flattened, grooved, very densely minutely patently yellowish brown hairy; flowers solitary or in basal part with 2 together; lower bracts (sub)opposite. *Pedicel* 3.5–5 mm long, slightly grooved, very densely appressedly hairy. *Sepals:* outer sepals 2.6–3.0 × 2.5–3.0 mm; inner sepals 4.4–5.5 × 3.0–4.5 mm. *Petals* whitish, when dry dark orange red, the longest one 10.5 mm long; carina rather densely appressedly hairy outside, subglabrous inside; other petals outside in basal part shortly appressedly hairy, further glabrous. *Stamens:* filaments widened above base and with a knob-like, rather densely hairy appendage at inner side, further glabrous; anthers 0.5–0.7 mm long. *Ovary* half-patently hairy, up to 1.5 mm stipitate, inserted on a rather wide, minutely hairy receptacle; ovules 4. *Fruit* globular, c. 1.7 cm diam., dark, shortly patently hairy; pericarp rather soft.

Distribution. Malaya: Cameron Highlands (11 coll.), Fraser's Hill (1), Mt Benom (2).

Notes. 1. *X. monticolum* seems to take an intermediate position between *32. X. griffithii* and *36. X. vitellinum*. It might be hybridogeneous. Ecologically it is rather well separated from both.

2. The present species differs from *34. X. geesinkii* in the shorter axillary buds and in the inflorescence, and from *35. X. cochinchinense* also in the characters of the leaf blades.

34. Xanthophyllum geesinkii Meijden, *spec. nov.*

Gemmae axillares 2, gemma superiore semi-patente, (2.7–)4–5 mm longa. Lamina nervis e paribus 8–9, subtus papillosa; glandulae 3–10. Inflorescentia ramosa, bracteis basalibus oppositis, floribus 7–9 fasciculatis. Sepala interiora 3.2 mm longa. Petala inaequalia, petalo longissimo 8 mm longo; carina extus sat dense breviter appresse pilosa. Antherae c. 0.7 mm longae. Ovarium dense appresse pilosum; stylus pilosus; ovula 4. Fructus globosus, c. 1.5 cm diam., pericarpio sat molli. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateralibus subcompressa.
Typus: *Winit 1922* (K).

Tree up to 15 m high. Axillary buds (2.7–)4–5 mm long. *Petiole* 10–15 mm long, c. 1.5–2 mm diam., at apex sometimes with large glands. *Leaf blade* 10–28 × (2.5–)3.2–5.5

cm; upper side yellowish brownish green; lower side glaucous-papillose, secondary nerves c. 8 or 9 pairs, not forming an intramarginal nerve; glands 3–10, situated about halfway between midrib and margin, 0.2–0.3 mm diam., basal glands c. 0.6–0.7 mm diam., sometimes shifted to apex of petiole. *Inflorescences* about as long as the leaves, branches (sub)opposite, with 2 (or 3) together; axes basally flattened and ribbed, densely minutely patently hairy; flowers in clusters of c. 7–9 together; lower bracts opposite. *Pedicel* 3 mm long, densely minutely half-patently hairy. *Sepals:* outer sepals 2.3 × 1.6 mm; inner sepals 3.2 × 2.1 mm. *Petals* white, the upper ones with a yellow spot, when dry dark reddish, the longest one 8 mm long; carina rather densely shortly appressedly hairy outside in middle and apical part; other petals glabrous outside. *Stamens:* anthers c. 0.7 mm long. *Ovary* appressedly hairy; ovules 4. *Fruit* globular, c. 1.5 cm diam., brown, wrinkled; pericarp rather thin; pedicel 4–6 mm long.

Distribution. Thailand: North (Lampang, Mê Chawk: *Winit 1922*), Southeast (Koh Mai See I., 5 km south of Koh Chang I.: *Geesink & Phengklai 6658*).

Note. See under *33. X. monticolum*. Differing from *35. X. cochinchinense* in the characters used in the key.

35. Xanthophyllum cochinchinense Meijden, *spec. nov.*

Gemmae axillares 2 (vel 3), gemma superiore semi-patenti ad patenti, (2.5–)4–5.5(–7) mm longa. Lamina nervis e paribus (8 vel) 9–11, subtus papillosa; glandulae numerosae. Inflorescentia ramosa, bracteis basalibus oppositis. Flores solitarii vel raro bini. Sepala interiora 3.2–4.3 mm longa. Petala inaequalia, petalo longissimo 8.5–10 mm longo; carina extus densiuscule pilis brevibus appressis induta. Antherae 0.6–0.7 mm longae. Ovarium densissime pilis brevibus appressis indutum; stylus pilosus; ovula 4. Fructus globosus, c. 1.5 cm diam., pericarpio molli. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *Chevalier 39928* (P; iso L).

Small tree up to 5 m high, 7 cm d.b.h. Axillary buds 2 (or 3), upper bud often appressed against the petiole, (2.5–)4–5.5(–7) mm long, acute; buds of second order often present. *Petiole* 11–17 mm long, 3–4 mm diam. *Leaf blade* (11–)18–23 × 5–12 cm, base rounded to attenuate, apex rounded to subacute, rarely shortly acuminate; upper side slightly bullate between secondary nerves, yellowish green; lower side greenish, glaucous-papillose, secondary nerves (8 or) 9–11 pairs, forming an intramarginal nerve in apical half; glands numerous, scattered but mainly near midrib, 0.2–0.3 mm diam., basal glands rather indistinct. *Inflorescences* shorter than the leaves; axes basally flattened, grooved, very densely minutely half-appressedly yellowish hairy; flowers solitary or rarely in basal part of inflorescence with 2 together; lower bracts (sub)opposite. *Pedicel* 1.5–3.5 mm long, hairy like inflorescence axis. *Sepals* often with more or less protruding incrustations; outer sepals 2.1–2.9 x 2.5–3.5 mm; inner sepals 3.2–4.3 × 2.6–3.1 mm. *Petals* white or yellowish, the carina pinkish to lilac; when dry orange, the longest one 8.5–10 mm long; carina shortly appressedly hairy outside especially in middle and apical part; other petals glabrous outside. *Stamens:* filaments distinctly widened above base, hardly thickened; anthers 0.6–0.7 mm long. *Ovary* shortly appressedly hairy inserted excentrically on a wide, flat, sometimes hairy receptacle; ovules 4. *Fruit* globular, c. 1.5 cm diam., brown, dull, shortly appressedly hairy; pericarp rather soft, rather thin, faintly wrinkled when dry.

Distribution. Vietnam: Bien Hoa (1 coll.), Dong Nai (Blao: 3).

Note. Resembling, and closely allied to *36. X. vitellinum*; differing in the papillose leaf blades, the higher number of secondary nerves, the somewhat longer anthers, and in the appressedly hairy ovary. I prefer to distinguish this taxon as a separate species rather than as a subspecies of *X. vitellinum*. See also under *33. X. monticolum* and *34. X. geesinkii*.

36. Xanthophyllum vitellinum

X. vitellinum (Bl.) Dietr., Syn. Pl. 2 (1840) 1277; Walp., Rep. 1 (1842) 248; Hassk., Cat. Hort. Bog. (1844) 227; Pl. Jav. Rar. (1848) 296; Miq., Fl. Ind. Bat. I, 2 (1858) 129: Hassk., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 193; Miq., *op. cit.* 1 (1864) 272; Teysm. & Binnend., Cat. Hort. Bog. (1866) 218; Chodat, Monogr. Polygal. (1891) t. 9, fig. 1, 2; t. 12, fig. 4 c–e; Burck, Wand. Bot. Tuin Btzg (1892) 31; Wiesner, Ann. J. Bot. Btzg, Suppl. 2 (1898) 97, t. 3; Boerl., Cat. Hort. Bog. (1899) 58; Koord. & Valeton, Bijdr. Booms. Java 5 (1900) 294; Valeton, Icon. Bog. 1, 4 (1901) 9–12, t. 79; Gagnepain, Desv. J. Bot. 21 (1908) 251; Fl. Gén. I.-C. 1 (1909) 243; Backer, Schoolfl. Java (1911) 80; Koord.-Schum., Syst. Verz. 1 (1912) Fam. 145, p. 4–5; Koord., Exk. Fl. Java 2 (1912) 453; Merr., En. Born. (1921) 326; Baker, Hook. J. Bot. 62 (1924) Suppl. 7; Doct. v. Leeuwen, Zoocecidia (1926) 273, 274; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 218; Backer & Bakh. *f.*, Fl. Java 1 (1963) 200. – *Jakkia vitellina* Bl., Cat. (1823) 17, 64; Nees, Fl. Bot. Zeit. 8 (1825) 120 ('*Jackia*'); Bl., Bijdr. (1825) 61 ('*Jackia*'); G. Don, Gen. Hist. Dichl. Pl. 1 (1831) 368. – *Monnina vitellina* (Bl.) Sprengel, Syst. Veg. 3 (1827) 265; Steudel, Nom. ed. 2, 2 (1841) 157. – *Banisterodes vitellinum* (Bl.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *Anonymus s.n.* (L, sheet 908.172-56; iso BO, L, MEL, U).

Jakkia longifolia Bl., Bijdr. (1825) 61 ('*Jackia*'); G. Don, Gen. Hist. Dichl. Pl. 1 (1831) 368 ('*Jackia*'). – *Monnina longifolia* (Bl.) Sprengel, Syst. Veg. 3 (1827) 265. – *X. longifolium* (Bl.) Dietr., Syn. Pl. 2 (1840) 1277; Hassk., Cat. Hort. Bog. (1844) 228; Miq., Fl. Ind. Bat. I, 2 (1858) 129; Hassk., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 194. – *Monnina macrophylla* Steudel, Nom. ed. 2, 2 (1841) 157, *nom. illeg.* – *Banisterodes longifolia* (Bl.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *HB 1324 p.p.* (L, sheet 908.172-79; iso L, MEL, U).

X. paniculatum Miq., Fl. Ind. Bat., Suppl. (1861) 393; Baker, Hook. J. Bot. 62 (1924) Suppl. 7. – Type: *Teysmann HB 4304* (U; iso K, MEL).

X. hookerianum King, J. As. Soc. Beng. II, 59 (1890) 139; Ridley, Fl. Mal. Pen. 1 (1922) 144; Burkill, Dict. (1935) 2268; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 359. – Lectotype: *King's Coll. 5997* (K; iso BM, FI, G, L, SING).

X. kunstleri King, J. As. Soc. Beng. II, 59 (1890) 139; Ann. R. Bot. Gard. Calc. 5 (1896) 137, pl. 162; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 45; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2268; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 359. – Lectotype: *King's Coll. 3512* (SING; iso BM).

X. curtisii King, J. As. Soc. Beng. II, 59 (1890) 138; Ridley, Fl. Mal. Pen. 1 (1922) 146; Burkill, Dict. (1935) 2269; Koriba, Gard. Bull. Sing. 17 (1958) 19, 51, fig. 1; F. Hallé *c.s.*, Trop. Trees & Forests (1978) 56; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 146, 211. – *X. griffithii* var. *curtisii* (King) Ng in Whitmore, Tree Fl. Mal. 1 (1972) 359, fig. 2. – Lectotype: *Curtis 1591* (SING; iso K, SING, Z).

X. robustum Chodat, Bull. Herb. Boiss. 4 (1896) 262; Merr., En. Born. (1921) 326; En. Philip. 2 (1923) 387; Masam., Enum. Phan. Born. (1942) 381; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Lectotype: *Vidal 40* (L, not K, as Chodat cites; iso A, K, L).

X. robustum var. *elmeri* Chodat in Merr., Pl. Elm. Born. (1929) 136; Masam., Enum. Phan. Born. (1942) 381. – Lectotype: *Elmer 21225* (L; iso BO, BM, BR, C, G, K, M, P, SING, U, Z).

X. griffithii auct., non A.W. Bennett: Rolfe, Hook. J. Bot. 23 (1885) 210; Vidal, Rev. Pl. Vasc. Filip (1886) 51; Ceron, Cat. Pl. Herb. Manilla (1892) 19.

X. flavescens auct., non Roxb.: Fern.-Vill., Nov. App. (1880) 14; Vidal, Sinopsis (1883) 13.

Shrub or tree up to 30 m high, 36 cm d.b.h. Axillary buds (see also note 1) varying from narrowly triangular with strongly thickened base and then often 1.5–3 mm long, to rhomboid-ovate or ovate-oblong and then often 6–11 mm long. *Petiole* 8–14(–16) mm long, very often with a pair of glands in apical half. *Leaf blade* 8–20(–30) × 3.5–10(–11) cm, sometimes a few leaves of a twig smaller; upper side greyish green to yellowish brown, midrib protruding to nearly flat in basal half; lower side: secondary nerves (6 or) 7–9(–11) pairs, in apical half forming an indistinct intramarginal nerve; glands mostly more than 10, situated near midrib or scattered, 0.2–0.4 mm diam., basal glands mostly present. *Inflorescences* branched, 8–30 cm long, branches often in pairs in lower part; axes basally mostly strongly flattened, grooved, glabrous to densely shortly patently or less often appressedly hairy; in basal part flowers with up to 3 together, solitary in apical part; lower bracts nearly opposite. *Pedicel* 1.5–5.5 mm long, very rarely longer, grooved, densely shortly patently (sometimes appressedly) hairy. *Sepals* basally often more or less thickened and wrinkled; outer sepals (1.7–)2.0–3.3(–3.9) × 1.9–4.0 mm; inner sepals (2.6–)3.0–5.3(–5.7) × (2.5–)3.0–4.0(–5.0) mm. *Petals* dark yellow to white, when dry orange to dark reddish and often with white incrustations, the longest one (7–)8–12, exceptionally up to 15.5 mm long; carina densely appressedly hairy outside; other petals glabrous outside or with a few hairs at apex. *Stamens* 8, very rarely 9; filaments free or connate over up to 0.7 mm, widened above base and with a knob-like, rather densely hairy appendage at inner side, further glabrous; anthers 0.4–0.6(–0.7) mm long. *Ovary* subsessile or up to 1 mm stipitate, half-patently hairy; style hairy in basal half, little hairy upwards; ovules 4. *Fruit* globular, up to 1.8 cm diam., often wrinkled when dry, rather dull or rarely shiny, usually light brown, sometimes dark reddish brown, hairy; pericarp rather thin.

Distribution. Malaya: Pinang I. (5 coll.), S. Kelantan (3), Trengganu (3), Perak (15), Pankor I. (2), Pahang (8), Selangor (7), Negri Sembilan (4), Malacca (2), Johore (7), Singapore (10), Sembilan Is. (Rembia I.: 1). – Sumatera: mainland (widely scattered: 9), Simaluë I. (7), Siberut I. (1). – Jawa (36 coll., and c. 40 by Koorders; not uncommon in West Jawa, 7 localities in Central Jawa, 5 localities in East Jawa). – Borneo: Sarawak (1st Div.: 2; 3rd Div.: 3), Sabah (3 coll. in western half, 16 in E. Sabah), Kalimantan (7). – Philippines: Babuyan (Camiguin: 1), Luzon (20), Mindanao (4). – Identity doubtful (see note 2): Anambas Is. (Jemaja I.: 1).

Notes. 1. In this circumscription *X. vitellinum* is very variable in its axillary buds and in its flowers. I have tried to divide the collections into two groups, differing in form and size of the axillary buds. Generally, collections with rather large and flat axillary buds ('*curtisii*-type') seemed to have smaller flowers than those with basally thickened, smaller buds ('*vitellinum*-type'). In Sumatera, Malaya, and Borneo both types occur. The Philippine collections often had the axillary buds of the '*curtisii*-type' and flowers of the '*vitellinum*-type'. In Jawa no collections of the '*curtisii*-type' could be found and the flowers are generally somewhat larger than elsewhere. I think that it is better not to divide the species in infraspecific taxa.

2. Three collections from Sumatera, Riouw District (*bb 24833, 27509, 30108*) and an (otherwise different) collection from Borneo (*S 23996*) have an unusual type of axillary buds. The buds are globular to ovoid, 1.5–2.5 mm long, rather strongly thickened in the

middle and apical part. Such buds also occur in the sterile collection *SF 20520* from Anambas Is., in which, however, most axillary buds are very large and flat, c. 10–12 × 5–6 mm, resembling those of *46. X. heterophyllum*.

3. A collection with a label of *De Vriese & Teysmann* (L, sheet 908.18-259 & 260) from Seram (Maluku Is.) probably belongs to *X. vitellinum*; this species has never been found east of Wallace's Line. In habit, the collection strongly reminds of material of *X. vitellinum* from Jawa. Probably the label does not belong to the mounted specimen.

37. Xanthophyllum incertum (Bl.) Meijden, *comb. nov.* Fig. 3A–e

Guatteria incerta Bl., Fl. Jav. (1830) 100, t. 49 B. – *Monoon incertum* (Bl.) Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 19. – Lectotype: *Van Hasselt s.n.* (L, sheet 908.171-1694).

? *X. acuminatissimum* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 276. – Lectotype: *Korthals s.n.* (L, sheet 908.171-1691; iso L, U); see note 3.

Small tree to 10 m high. Axillary buds narrowly triangular to lanceolate, (2–)4.5–10(–11) mm long, more or less wrinkled; buds of second order rarely present. *Petiole* (6–)8–10(–12) mm long. *Leaf blade* 6–16(–22) × 2.3–5.5(–8) cm, apex cuspidate; upper side dark green, shiny; lower side green, secondary nerves 5 or 6 (or 7) pairs, in apical part forming an intramarginal nerve; glands few, 0.2 mm diam., basal glands sometimes present. *Inflorescences* branched or unbranched, up to 7 cm long; axes densely shortly hairy; in basal part flowers with 3 together; lower bracts (sub)opposite. *Pedicel* 1.5–2 mm long, densely shortly more or less appressedly hairy. *Sepals* sometimes with tiny glandular spots; outer sepals 2.8–3.5 × 3.1–4.1 mm; inner sepals 4.3–5.6 × 3.1–4.2 mm. *Petals* pinkish or reddish white, when dry orange, the longest one 10.5–11.5 mm long; carina shortly and rather sparsely appressedly hairy outside; other petals more or less glabrous or sometimes sparsely shortly hairy outside in apical part. *Stamens:* filaments free or connate over 0.5(–1) mm, widened above base and with a knob-like, shortly (half-)appressedly hairy appendage at inner side, further glabrous; filaments of lateral alternipetalous stamens hairy to base in two rows; anthers 0.6–0.9 mm long. *Ovary* patently hairy; style nearly glabrous to rather densely appressedly hairy; ovules 4. *Fruit* globular, c. 1.5 cm diam., more or less shiny, brown, densely patently hairy; pedicel up to 3.5(–6) mm long.

Distribution. Sumatera (around Lake Toba: 13 coll.; Mt Sago, Pajakumbuh: 1). – West Jawa (Mt Karang: 2; Mt Sawal, Lake Pendalu: 2).

Notes. 1. For differences with *28. X. ancolanum*, see there. Closely allied to *36. X. vitellinum*, differing in the axillary buds and the stamens. In Sumatera the species is rather easily separated from the latter, whereas the few collections from W. Jawa seem to have a stronger affinity to *X. vitellinum*.

2. The type collection differs from all other fruiting collections in having long (6 mm) pedicels.

3. The (sterile) type of *X. acuminatissimum* Miq. may be allied to *X. incertum*, but differs in the shorter axillary buds and the papillose leaf blades. The description of *X. incertum* does not include this material.

38. Xanthophyllum adenotus

X. adenotus Miq., Fl. Ind. Bat., Suppl. (1861) 393; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 275. – Lectotype: *Teysmann HB 509* (BO; iso U).

X. cordatum Korth. *ex* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274; Merr., En. Born. (1921) 325; Ridley, Kew Bull. (1925) 77; Chodat in Merr., Pl. Elm. Born. (1929) 133; Keith, N. Born. For. Rec. 2 (1938) 225; Masam., Enum. Phan. Born. (1942) 379; Meijer, Bot. News Bull. Sandakan 7 (1967) 87. – Lectotype: *Korthals s.n.* (L, sheet 908.171-1925).

non X. cordatum auct.: Merr., En. Philip. (1923) 386 (= *39. X. palawanense*).

X. cordatum f. *aequale* Chodat in Merr., Pl. Elm. Born. (1929) 313. – Lectotype: *Elmer 20215* (L; iso BM, BO, BR, C, G, K, M, P, SING, U, Z).

X. arsatii C.E.C. Fischer, Kew Bull. (1932) 176; Masam., Enum. Phan. Born. (1942) 379. – Type: *Arsat 1213* (K).

Shrub or small tree up to 10 m high, 25 cm d.b.h. Twigs glabrous or rarely minutely patently hairy. Axillary buds oblong or sometimes ovate-lanceolate, (1.3–)3–6(–10.5) mm long, the longer ones strongly thickened at base and usually suddenly widened and flattened upwards, usually glabrous, the smaller ones less distinctly flattened and usually rather densely shortly hairy; buds of second order often present. *Petiole* (8–)15–18(–21) mm long, glabrous to rather densely minutely hairy, usually with 2 small, protruding glands. *Leaf blade* (linear-)lanceolate, (9–)22–47 × (1.3–)5–10(–15.5) cm; base usually cordate with the margins curved upwards and connate above the apex of the petiole, or flat and rounded to broadly cuneate, apex acutish; upper side usually slightly bullate between secondary nerves and intramarginal nerve, greyish green to brown; lower side usually brownish, glabrous to minutely patently hairy all over, secondary nerves (9–)13–20 pairs, mostly forming a distinct, nearly complete intramarginal nerve; glands 2–6(–20), usually near the midrib (if few, only present in basal part), 0.3–0.4 mm diam. *Inflorescences* sometimes also axillary on the older nodes; axes slightly angular, slightly grooved, main axis basally usually sparsely minutely appressedly hairy, side axes and main axis in upper part more densely hairy; flowers solitary or very rarely with 2 together; lower bracts opposite. *Pedicel* (1–)1.5–2(–3.5) mm long, more or less distinctly grooved, densely minutely appressedly to patently hairy. *Sepals* often with minute, rather distinct glands; outer sepals (2.1–)2.8–3.8(–4.1) × (2.4–)3.0–4.9 mm; inner sepals 3.0–5.5 × (2.8–)3.4–4.6 mm. *Petals* pinkish to pale violet, the upper petals with a yellow spot, when dry dark red, the longest one (8.5–)9.5–12.5(–14.5) mm long; carina rather densely appressedly hairy outside, inside sparsely minutely hairy in apical part only, further glabrous; other petals very sparsely minutely hairy above base outside, sparsely patently hairy outside near apex, inside glabrous to hairy up to about halfway. *Stamens:* filaments free or connate over 1(–2) mm, widened above base and especially those of abaxial stamens with a more or less distinct (half-)patently hairy knob-like thickening at inner side, further glabrous; anthers (0.6–)0.7–0.9(–1.0) mm long, ciliate along slits. *Ovary* (half-)patently hairy; style (rather) sparsely half-patently hairy in basal half, very sparsely hairy in apical half, glabrous near apex; ovules 4. *Fruit* globular, 1.5–1.8 cm diam., rather dull, light to reddish brown, distinctly hairy; pericarp thin, brittle.

Distribution. Sumatera. – Borneo.

Notes. 1. In Borneo *X. adenotus* is vegetatively a variable species, especially in the form of the base of the leaf blade and in the indumentum of the petiole. In spite of the

great differences in the type collections of *X. arsatii* and *X. cordatum*, it was impossible to separate the material into two clearly defined groups. Var. *lineare* may represent a local variant with smaller and narrower leaf blades, short axillary buds, and small petals. *39. X. palawanense* is probably an off-shoot of this species.

2. Surprisingly, no collections are thus far known from Malaya.

KEY TO THE VARIETIES

1a. Leaf blade (4.5–)5–10(–15.5) cm wide. Secondary nerves 13–20 pairs, forming a nearly complete intramarginal nerve . . . . . a. var. **adenotus**

b. Leaf blade 2–5.2 cm wide. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve . . . . . b. var. **lineare**

a. var. **adenotus**

Axillary buds (1.8–)3–6(–10.5) mm long. *Petiole* (10–)15–21 mm long, glabrous or hairy. *Leaf blade* (15–)22–47 × (4.5–)5–15.5 cm, base cordate to cuneate. Secondary nerves 13–20 pairs, forming a distinct, nearly complete intramarginal nerve. *Flowers:* upper petals glabrous or hairy inside to about halfway.

Distribution. Sumatera (5 coll.). – Borneo: Sarawak (24), Brunei (1), Sabah (60), Kalimantan (10).

b. var. **lineare** Meijden, *var. nov.*

Gemmae axillares 1.3–2.2 mm longae, in parte superiore anguste triangulares. Petiolus (8–)10–12(–18) mm longus. Lamina lineari-lanceolata, (9–)13–30 cm longa, (1.3–)2–5.2 cm lata, nervis e paribus 9–14. Petala superiora intus pilosa usque ad circa dimidiam.

Typus: *SAN 57294* (K).

Axillary buds at upper side partly enclosed by a distinct ridge formed by the twig, 1.3–2.2 mm long. *Petiole* (8–)10–12(–18) mm long, glabrous. *Leaf blade* linear-lanceolate with more or less parallel sides over most its length, (9–)13–30 × (1.3–)2–5.2 cm, base rounded to obtuse. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve. *Flowers* rather small in all parts; upper petals shortly patently hairy inside to about halfway. *Fruit* unknown.

Distribution. Borneo: Sabah (Lahad Datu, Mt Silam: 3 coll.).

39. Xanthophyllum palawanense

X. palawanense Elmer, Leafl. Philip. Bot. 5 (1913) 1673 ('*palawanensis*'). – Lectotype: *Elmer 12931* (L; iso A, BO, FI, P, U, W).

X. cordatum auct., non Miq.: Merr., En. Philip. (1923) 386.

Small tree up to 8 m high, 5 cm d.b.h. Twigs sparsely minutely hairy, glabrescent, older nodes often strongly thickened and with numerous adventitious buds. Axillary buds

oblong, 6–9 mm long, basally narrowed and strongly thickened, sparsely shortly hairy, glabrescent. *Petiole* 15–18 mm long, more or less densely shortly hairy, with 2(–4) more or less distinctly protruding small glands. *Leaf blade* ovate-oblong to ovate-lanceolate, rarely elliptic, c. 20–40 × (6–)8–12(–15) cm, base cordate, the margins at base flat or only little upturned, apex gradually narrowed to shortly acuminate; upper side often slightly bullate between secondary nerves and intramarginal nerve, dark green to greenish brown; lower side sparsely minutely hairy on the nerves in basal part, secondary nerves 9–12 pairs, often irregular, forming a nearly complete, somewhat irregular, intramarginal nerve; glands few, situated in middle and basal part, 0.2(–0.4) mm diam. *Inflorescences* sometimes also on older shoots from adventitious buds, up to 22 cm long; axes angular, slightly grooved, densely shortly patently hairy; lower bracts opposite. *Pedicel* 2–3.5 mm long, grooved, densely shortly half-patently hairy. *Sepals:* outer sepals 3.5–4.3 × 4.3–5.0 mm; inner sepals 5.0–5.9 × 4.3–4.5 mm. *Petals* dark red when dry, the longest one 15–18.5 mm long; carina rather densely shortly appressedly hairy outside, glabrous inside except at base; other petals minutely sparsely appressedly hairy in basal part out- and inside, further glabrous. *Stamens:* filaments widened and slightly thickened above base and only there rather densely half-patently hairy; anthers 1.1–1.2 mm long, ciliate along slits. *Ovary* stipitate over 1–1.5 mm, half-patently hairy; style densely hairy in basal part, upwards sparsely hairy to near apex; ovules 4. *Fruit* globular, c. 1.7 cm diam., dull, brown, rather distinctly half-patently hairy; pericarp rather thin, brittle; pedicel up to 5–6 mm long.

Distribution. Philippines: Palawan (5 coll.), Jolo (2), Tawitawi (1).

Note. Closely allied to *38. X. adenotus*, differing in the key characters. The distribution is peculiar, because the distance between Palawan and Jolo I. and Tawitawi I. is much greater than between Palawan and Borneo, where *X. adenotus* is found.

40. Xanthophyllum ceraceifolium

X. ceraceifolium Meijden, Bot. J. Linn. Soc. 67 (1973) 117. – Type: *S 14822* (L; iso K, SING).

Small tree up to 15 m high, 16 cm d.b.h. Axillary buds elliptic to oblong, 5–7 mm long. *Petiole* (18–)25–30 mm long. *Leaf blade* 22–42 × 7–15.5 cm; upper side rather dull, greenish, lower side dull, concolorous, secondary nerves c. 8–10 pairs, little protruding, in apical part forming an indistinct intramarginal nerve, venation obscure; glands 2–8, 2 situated at the very base and 0.6–1.0 mm diam., the other ones (if present) scattered, sometimes close to midrib, 0.5 mm diam. *Inflorescences* much shorter than the leaf; axes strongly flattened basally, grooved, brown, minutely hairy; lower bracts (sub)opposite. *Pedicel* 2.5–3.5 mm long, grooved, densely shortly patently hairy. *Sepals:* outer sepals 2.8–3.5 × 3.6–4.4 mm; inner sepals 4.5–4.9 × 3.6–4.7 mm. *Petals* yellowish, when dry dark red with large incrustations, glabrous inside, the longest one 9–10.5 mm long; carina appressedly hairy outside. *Stamens:* filaments widened above base and with a distinct, rather shortly (half-)appressedly hairy knob-like thickening at inner side, further glabrous; anthers 0.6 mm long. *Ovary* nearly sessile, appressedly hairy; ovules 4. *Fruit* unknown.

Distribution. Borneo: Sarawak (1st Div., Semengoh Arboretum: 4 coll.); identity uncertain: Sabah (*SAN 37933*).

Note. Allied to *36. X. vitellinum*, differing in the leaves. In the indistinctness of the nervation resembling *43. X. reflexum*.

41. Xanthophyllum petiolatum Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, erectae, c. 11–12 mm longae. Petiolus 26–31 mm longus. Lamina subtus papillosa; glandulae 1–3. Inflorescentia valde ramosa, bracteis basalibus oppositis. Petala inaequalia, petalo longissimo 11.5 mm longo; carina extus dense appresse pilosa. Antherae 0.7 mm longae. Ovarium dense appresse pilosum; stylus pilosus; ovula 4. Fructus ignotus.

Typus: *SAN 17480* (L; iso BRI, K, KEP, SING).

Tree 14 m high. Twigs minutely patently hairy. Axillary buds erect, oblong, c. 11–12 × 4 mm, base broad, rounded, apex rounded. *Petiole* 26–31 mm long. *Leaf blade* 6–13.5 × 4–7 cm, base rounded, apex rounded to slightly obtuse; upper side: midrib sunken in apical half, slightly protruding in basal half, secondary nerves slightly sunken; lower side glaucous-papillose, secondary nerves 6–8 pairs, forming an indistinct intramarginal nerve in apical part, venation hardly protruding; glands 1–3, situated in middle and apical part, mostly c. 0.4 mm diam., basal glands sometimes present, rather large. *Inflorescences* up to 15 cm long; axes dark, patently, extremely shortly hairy; lower bracts opposite. *Pedicel* 4 mm long, grooved, densely very shortly half-patently hairy. *Sepals:* outer sepals 2.9 × 3.3 mm, slightly pustulate; inner sepals 4.0 × 3.3 mm. *Petals* dark red when dry, the longest one 11.5 mm long; carina densely appressedly hairy outside; other petals glabrous to sparsely shortly hairy outside. *Stamens:* filaments connate over 0.5–0.8 mm between upper and lateral petals, connate over c. 1.5 mm between lateral petals and carina, the free parts constricted at very base and then widened and with a distinct densely hairy knob-like thickening at inner side, further glabrous; anthers 0.7 mm long. *Ovary* c. 1.5 mm stipitate, appressedly hairy; ovules 4. *Fruit* unknown.

Distribution. Borneo: Brunei (Andalau For. Res.: *SAN 17480*).

Note. Allied to *36. X. vitellinum*, differing vegetatively.

42. Xanthophyllum clovis (Steenis *ex* Meijden) Meijden, *stat. nov.*

X. vitellinum var. *clovis* Steenis *ex* Meijden, Bot. J. Linn. Soc. 67 (1973) 120. – Type: *SAN 15156* (L; iso BRI, K, SING).

Tree up to 14 m high. Axillary buds with the form of a clove; scales 6.5–12 mm long, at base slightly enlarged and convex, distinctly enlarged at the rounded to slightly emarginate apex, and there with 2 more or less distinctly protruding knob-like appendages; buds of second order c. 5–6 mm long, hardly thickened at apex. *Petiole* 9–17 mm long. *Leaf blade* 8.5–18 × 3.5–6.5 cm; upper side greenish to brownish; lower side glaucous-papillose, secondary nerves c. 7 or 8 pairs, forming an indistinct intramarginal nerve in apical half; glands few to rather numerous, mostly near the midrib, c. 0.2–0.3 mm, basal ones up to 0.5 mm diam. *Inflorescences* up to 20 cm long; axes dark, minutely patently hairy; in basal part flowers in clusters of up to 7 together; lower bracts opposite. *Pedicel* 4.5 mm long, slightly grooved, densely very shortly more or less appressedly hairy. *Sepals:* outer sepals 3.0 × 3.2 mm; inner sepals 4.1 × 4.1 mm, with tiny glandular spots at apex. *Petals* dark red when

dry, the longest one 8.5 mm long; carina appressedly hairy outside; other petals glabrous outside, the upper ones sparsely ciliate to halfway. *Stamens:* filaments widened above base and with a distinct densely appressedly hairy knob-like appendage at inner side, further glabrous; anthers 0.5 mm long. *Ovary* subsessile, half-patently hairy; style hairy in two rows to near apex; ovules 4. *Fruit* unknown.

Distribution. Borneo: Brunei (1 coll.), Labuan I. (1), Sabah (Sipitang, Mengalong For. Res.: 1).

Note. Allied to and closely resembling *36. X. vitellinum*, differing in the axillary buds and the papillose leaf blades.

43. Xanthophyllum reflexum Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, erectae, 3–4.5 mm longae. Lamina subtus laevis; glandulae 2 (vel 3). Inflorescentia ramosa, bracteis basalibus oppositis. Petala inaequalia, petalo longissimo 13–14 mm longo; carina extus dense appresse pilosa, petalis ceteris reflexis, glabris. Antherae 0.7–0.8 mm longae. Ovarium dense pilis semi-patentibus indutum; stylus pilosus; ovula 4. Fructus ignotus.
Typus: *S 32576* (L).

Small tree up to 10 m high, 12 cm d.b.h. Twigs minutely patently hairy. Axillary buds erect, appressed against twig, scales laterally flattened, triangular, 3–4.5 mm long, minutely densely patently hairy. *Petiole* 9–10 mm long, densely minutely hairy. *Leaf blade* 11–18 × 3.5–5.5 cm; upper side rather dull, dark greenish to yellowish brown, midrib a little sunken, nervation rather obscure; lower side nearly concolorous, secondary nerves c. 6–9 pairs, not very distinct, in apical part forming an indistinct intramarginal nerve, venation rather obscure; glands 2 (or 3), situated near base, 0.4–0.7 mm diam. *Inflorescences* shorter than the leaves; axes dark, very densely more or less patently hairy; lower bracts opposite. *Pedicel* 2.5–3 mm long, slightly grooved, very densely shortly patently hairy. *Sepals:* outer sepals 2.2–2.5 × 3.4–3.6 mm; inner sepals 3.8–3.9 × 3.6–4.9 mm. *Petals* yellowish white, when dry dark red, the longest one 13–14 mm long; carina densely more or less appressedly hairy outside; other petals glabrous. *Stamens:* filaments widened above base and with a knob-like shortly (half-)appressedly hairy appendage at inner side, further glabrous; anthers 0.7–0.8 mm long, hairy or nearly glabrous at base. *Ovary* subsessile, half-patently hairy; ovules 4. *Fruit* unknown.

Distribution. Borneo: Sarawak (1st Div., Semengoh Arboretum: *S 15198, S 32576*).

Note. Allied to *36. X. vitellinum*, differing in the axillary buds; in that character it resembles *32b. X. griffithii* subsp. *angustifolium* and *44. X. angustigemma*, but otherwise those taxa are very different. In the leaf blade slightly resembling *40. X. ceraceifolium.*

44. Xanthophyllum angustigemma Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, erectae ad patenter erectae, 3.5–5 mm longae. Lamina subtus papillosa; glandulae numerosae. Inflorescentia ramosa, bracteis basalibus oppositis. Petala inaequalia, petalo longissimo c. 13 mm longo; carina extus dense pilis semi-patentibus induta. Antherae 0.7 mm longae. Ovarium densissime pilis semi-patentibus indutum; stylus pilosus; ovula 4. Fructus ignotus.
Typus: *FB 21201* (P).

Axillary buds erect or nearly so, mostly flattened against twig; scales ovate-lanceolate, 6–9 mm long, not thickened at base; buds of second order distinct, 3.5–5 mm long. *Petiole* 10–14 mm long. *Leaf blade* c. 6–12 × 2.5–5.8 cm; upper side greyish green to brownish green; lower side glaucous-papillose, secondary nerves c. 5–7 pairs, usually forming an indistinct intramarginal nerve in apical part; glands rather numerous, scattered, 0.1–0.2 mm diam. *Inflorescences* about as long as the leaves; axes dark, minutely patently hairy; in basal part flowers with 3 together; lower bracts opposite. *Pedicel* 3.5–4 mm long, very densely whitish shortly patently hairy. *Sepals:* outer sepals 3.2–3.7 × 2.9–3.3 mm; inner sepals 3.7–5.4 × 2.3–3.2 mm. *Petals* dark red when dry, the longest one c. 13 mm long; carina densely half-patently hairy outside; other petals faintly hairy along midrib outside. *Stamens:* filaments c. 2 mm connate, the free parts constricted at very base and then widened and slightly thickened, only there densely half-patently hairy; anthers 0.7 mm long. *Ovary* half-patently hairy; ovules 4. *Fruit* unknown.

Distribution. Philippines: Luzon (prov. Camarines: *FB 21201*, P), Samar (Tagaslian, Borongan: *PNH 5802*, A, L, SING).

Note. Allied to *36. X. vitellinum*, differing in the axillary buds; see also under *43. X. reflexum*.

45. Xanthophyllum bracteatum

Fig. 15

X. bracteatum Chodat, Bull. Herb. Boiss. 4 (1896) 258; Merr., En. Philip. 2 (1923) 386. – Type: *Vidal 968* (K).

Axillary buds (ob)ovate-oblong to linear-lanceolate, 7–20 × 1.5–6 mm, basally slightly wrinkled, acute, more or less flat. *Petiole* 5–11(–14) mm long, sometimes with glands. *Leaf blade* 9.5–25 × 3–8 cm, rounded-attenuate to cordate; upper side (yellowish) green, midrib nearly flat to distinctly protruding; lower side glaucous-papillose, secondary nerves 10–12 pairs, forming a rather distinct intramarginal nerve; glands scattered, numerous, 0.1–0.2 mm diam. *Inflorescences* up to 10 cm long; axes (rather) densely minutely patently hairy, smooth to pustulate, angular, reddish; flowers solitary or in basal part with up to 3 together, sometimes turned upside-down; lower bracts opposite. *Pedicel* 5–7 mm long, slender, very densely patently shortly whitish hairy. *Sepals:* outer sepals c. 3 × 2.1 mm; inner sepals c. 5–5.5 × 4–4.5 mm. *Petals* dark red when dry, the longest one c. 14–17 mm long; carina rather densely more or less appressedly hairy outside in middle and apical part; other petals nearly glabrous outside. *Stamens:* filaments connate over 1–3 mm, widened and hardly thickened above base, basally rather densely whitish hairy in 2 rows; anthers c. 1.0–1.2 mm. *Ovary* more or less patently whitish hairy; ovules 4. *Fruit* (immature) globular, yellowish brown; pericarp thin.

Distribution. Philippines: Luzon (7 coll.).

Note. Allied to *36. X. vitellinum*, differing in the axillary buds and in the flowers. In the large axillary buds resembling *46. X. heterophyllum*, which, however, has rounded or obtuse bud scales.

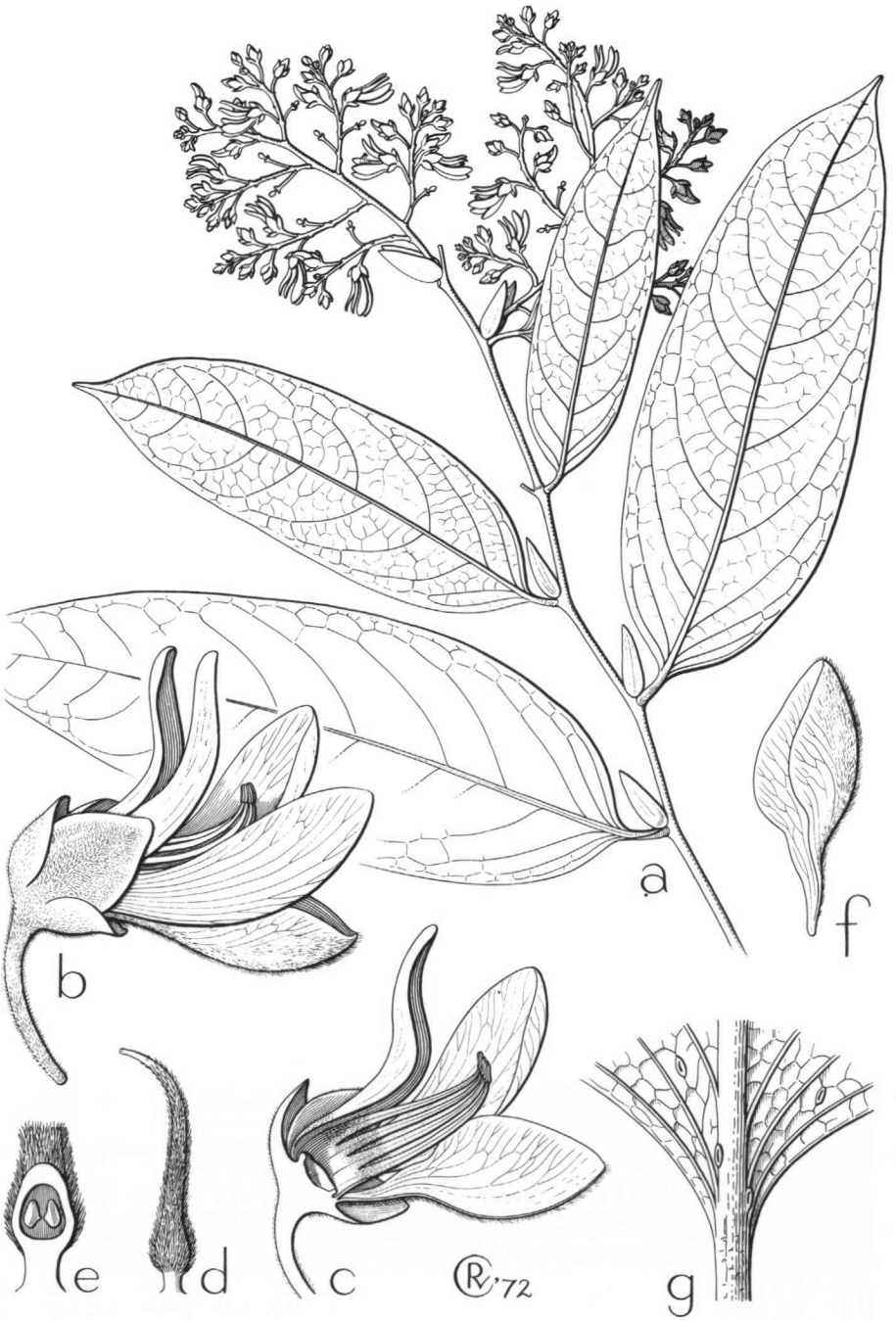


Fig. 15. *45. X. bracteatum.* — a. habit, x 0.5; b. flower, x 3; c. flower, longitudinal section, gynoecium removed, x 3; d. gynoecium, x 3; e. ovary, longitudinal section, x 6; f. carina without stamens, x 3; g. leaf base with laminar glands, x 2.5 (a–g: *BS 28512*).

46. Xanthophyllum heterophyllum Meijden, *spec. nov.*

X. pseudostipulaceum auct., non Merr.: Meijer, Bot. News Bull. Sandakan 7 (1967) 87; Weberl., Beitr. Biol. Pfl. 50 (1974) 279, fig. 1, II.

Gemmae axillares ut videtur singulae, semi-patentes, ellipticae ad oblongae, (8–)11–20(–30) mm longae, 6–12(–14) mm latae; squamae planae. Lamina subtus laevis; glandulae paucae vel numerosae. Inflorescentia ramosa, bracteis basalibus oppositis. Flores proprii ignoti. Ovarium pilosum; ovula 4. Fructus globosus, c. 1.7 cm diam.; pericarpium molle. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosus, basi lateraliter subcompressa.

Typus: *SAN 15371* (L; iso BRI, KEP).

Tree up to 33 m high, 70 cm d.b.h. Axillary buds elliptic to oblong, (8–)11–20(–30) × 6–12(–14) mm; scales flat, wrinkled, indistinctly nerved, more or less shiny, sometimes in middle part with 1–4 rather indistinct glands, base shortly attenuate, apex rounded to obtuse. *Petiole* 7–15 mm long. *Leaf blade* (3–)4.5–12(–19) × (1.8–)2.5–5(–7.5) cm, apex shortly acuminate to cuspidate; upper side more or less shiny, brownish green; lower side yellowish brown, secondary nerves 7–10(–12) pairs, not forming an intramarginal nerve; glands few to many, mostly situated in middle and apical part, 0.2–0.4 mm diam. *Inflorescences* branched; axes densely patently shortly hairy; lower bracts opposite. *Flowers* unknown. *Fruit* globular, up to 1.7 cm diam., shiny, brown, slightly hairy; pericarp rather soft; pedicel 1.5–2.5 mm long, densely shortly patently hairy. *Seed* 1; 3 ovules abortive.

Distribution. Borneo: Sarawak (1st Div., Arboretum Semengoh: 1 coll.), Brunei (Andalau For. Res.: 1), Sabah (Beaufort: 2; Gaya I.: 2; Beluran: 1; near Sandakan: 10).

Notes. 1. Although quite a number of collections are known, these are either vegetative or in fruit. Yet it seems fairly certain that it is allied to *36. X. vitellinum*, differing in the axillary buds. See also under *45. X. bracteatum*.

2. The sterile collection *SF 20520* from Anambas Is. resembles *X. heterophyllum*; see *36. X. vitellinum*, note 2.

47. Xanthophyllum korthalsianum

X. korthalsianum Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277. – Lectotype: *Korthals s.n.* (L, sheet 908.171-1711; iso K, L, U).

Tree up to 21 m high, 23 cm d.b.h. Axillary buds inserted (1.5–)3–15 mm above the axils on 1–2 mm long stalks; scales elliptic to linear-lanceolate, 6–18 × 1.5–8 mm long, faintly nerved. *Petiole* 7–10 mm long, glands present or not. *Leaf blade* 8–14 × 2.5–5 cm; upper side often slightly bullate between the secondary nerves, mostly dark green, secondary nerves finely protruding to obscure, venation obscure to finely protruding; lower side glaucous-papillose, secondary nerves 6–8 pairs, forming a more or less distinct intramarginal nerve; glands either not numerous, mostly situated near midrib, and c. 0.3 mm diam., or numerous, scattered, and 0.1–0.2 mm diam. *Inflorescences* shorter to much longer than the leaves, the lower branches distinctly supra-axillary, (sub)opposite; axes densely minutely hairy, more or less grooved, angular. *Pedicel* 1.5–2 mm long, grooved, densely patently minutely hairy. *Sepals* glabrous inside except for a few hairs at the very base; outer sepals c. 2 × 2 mm; inner sepals c. 3.5 × 3 mm. *Petals* incompletely known, carina and lateral

petals unknown; upper petal probably c. 8.5 mm long, sparsely hairy at apex. *Stamens:* unknown. *Ovary* patently whitish hairy (short and long fine hairs mixed); style and stigma unknown; ovules 4. *Fruit* unknown.

Distribution. Central Sumatera (Berapit: 1 coll.). – Borneo: Sarawak (3rd Div., Kapit: 1), Kalimantan (Sintang: 1; Puruktjahu: 1).

Note. Incompletely known, especially in the flowers. Allied to *36. X. vitellinum*, differing in the axillary buds.

48. Xanthophyllum discolor

Fig. 3A–q

X. discolor Chodat, Bull. Herb. Boiss. 4 (1896) 257; Ridley, Fl. Mal. Pen. 1 (1922) 147; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2268; Wyatt-Smith, Mal. For. Rec. 23-2 (1963) fig. 8; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 356, fig. 1. – Type: *Ridley 6199* (K; iso BM, K).

X. hypoleucum Merr., Pl. Elm. Born. (1929) 135 (excl. *BS 44034*); Keith, N. Born. For. Rec. 2 (1938) 225; Masam., Enum. Phan. Born. (1942) 380; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Lectotype: *Elmer 21752* (L; iso BO, BR, C, G, M, SING, U, Z). (*X. multiglandulosum* Merr., *in sched.*)

X. discolor subsp. *macranthum* Meijden, Bot. J. Linn. Soc. 67 (1973) 118. – Type: *BS 24454* (L; iso A, BM, BRI, K, L, P, SING).

X. macranthum Chodat *ex* Elmer, Leafl. Philip. Bot. 5 (1913) 1674, *nomen* (probably based on *Clemens 969*).

X. flavo-virens Elmer, Leafl. Philip. Bot. 10 (1939) 3776, *nom. inval. (anglice)*; based on *Elmer 16902* (BO, C, L, P, U, W).

Very low shrub or small tree, 1–10 m high, up to 10 cm d.b.h. Axillary buds narrowly triangular, c. 2.5–6 mm long, basally and centrally thickened, acute, shiny. *Petiole* 3–6(–7) mm long, often rather shiny. *Leaf blade* 3.8–25 × 1.6–10 cm, base obtuse to cordate or cuneate, apex acutish; upper side rarely faintly bullate between the secondary nerves, light to dark greyish green, midrib mostly slightly sunken, sometimes a little protruding, venation rather indistinct; lower side glaucous-papillose to nearly smooth, secondary nerves (5 or) 6–13 pairs, forming a mostly rather indistinct intramarginal nerve; glands numerous, scattered, c. 0.1 mm diam., the basal ones often somewhat larger. *Inflorescences* unbranched or rarely with one branch, much shorter than to three times as long as the leaves; axes mostly very slender, mostly less than 1 mm thick, (rather) sparsely minutely hairy; in basal part flowers usually with 3 together; bracts small, either with 2 large glands (in Bornean material) and then rather long-persistent, or eglandular (in Malayan and Philippine collections) and then soon caducous; lower bracts (sub)opposite. *Pedicel* 2–25 mm long, slightly grooved, appressedly to patently, sparsely to rather densely hairy, rarely glabrous. *Sepals* rarely glabrous outside; outer sepals (1.5–)2–4 × (1.3–)2–3.5 mm, without or with (in most Bornean material) very distinct glands; inner sepals 3–6 × 4–6 mm. *Petals* white or pinkish, when dry brownish to dark reddish, nearly glabrous, apically with few hairs, basally inside slightly hairy, the longest one 11–23 mm long. *Stamens:* filaments free or connate over up to 2 mm; anthers 2.0–2.5 mm long, minutely hairy all over. *Ovary* sessile to distinctly stipitate, appressedly whitish hairy; ovules 8–15. *Fruit* globular, up to 1.8–3 cm diam., dull, light brownish; pericarp thin, rather brittle.

Distribution. Malaya. – Borneo. – Philippines.

Notes. 1. The delimitation of the species of the *beccarianum*-group (species 48–58) was difficult until I noted that the relative length of the pedicel provided a useful character vegetative parts. It then became apparent that most species show a kind of congruent variation in the form of the base of the leaf blade. Consequently, the identification of sterile collections is almost impossible without the use of additional floral data.

2. The Philippine collections differ in a number of quantitative characters, reminding of the 'gigas'-characters (see chapter 2.3.1) mentioned for *92. X. fragrans*.

3. The collections from Malaya differ in some respects from those from Borneo: shorter petioles, shorter leaf blades, a longer gynophore, and absence of distinct glands on the bracts. I think that these differences are insufficient, however, to distinguish these groups on a formal taxonomic level.

KEY TO THE SUBSPECIES

1a. Inflorescence less than half as long as the leaves. Inner sepals 3–3.8 mm long. Longest petals 11–15 mm ..... a. subsp. **discolor**

b. Inflorescence 0.5–3 times as long as the leaves. Inner sepals 5–6 mm long. Longest petals 15–23 mm long ..... b. subsp. **macranthum**

a. subsp. **discolor**

X. discolor Chodat. – *X. hypoleucum* Merr.

Very low shrub or small tree up to 10 m high. Secondary nerves (5 or) 6 or 7(–9) pairs. *Inflorescences* mostly much less than (rarely up to) half as long as the leaves, often few-flowered. *Pedicel* 2–8.5 mm long. *Sepals:* outer sepals (1.5–)2–2.5 × (1.3–)2–2.5 mm; inner sepals 3–3.8 × 4–4.5 mm. Longest *petals* 11–15 mm long. *Fruit* up to 1.8 cm diam.

Distribution. Malaya: border of Pahang-Johore (2 coll.), Johore (2), Singapore (4). – Borneo: Sarawak (2), Brunei (1), Sabah (13), Kalimantan (3).

b. subsp. **macranthum** Fig. 3A-q

X. discolor subsp. *macranthum* Meijden. – *X. macranthum* Chodat *ex* Elmer. – *X. flavo-virens* Elmer.

Low shrub or small tree up to 8 m high. Secondary nerves 6–13 pairs. *Inflorescences* half as long to three times as long as the leaves, many-flowered. *Pedicel* 10–25 mm long. *Sepals:* outer sepals 2.8–4 × 2.2–3.5 mm; inner sepals 5–6 × 4.2–6 mm. Longest *petals* 15–23 mm long. *Fruit* up to 3 cm diam.

Distribution. Philippines: Luzon (2 coll.), Samar (3), Mindoro (2), Panay (2), Mindanao (4), Basilan (4), Tawitawi (1).

49. Xanthophyllum penibukanense

Fig. 9 b

X. penibukanense Heine, Mitt. Bot. Staatssamml. München 6 (1953) 215; Pfl. Clemens Kinab. (1953) 50; Meijer, Bot. News Bull. Sandakan 7 (1967) 88. – Lectotype: *Clemens 40794* (M; iso B, BM, G, K, L).

Small shrub or tree up to 12 m high, 30 cm d.b.h. Axillary buds ovate-oblong, 3.2–7 mm long, acute, flat, but basally strongly thickened, there often with exuberant cork-forming which may hide the scale completely, greyish to cream-coloured, more or less shiny. *Petiole* 8–15 mm long but often seemingly much longer because of the long-attenuate leaf base. *Leaf blade* (5–)7–28 × 2.3–10 cm, base long-attenuate, upper side dark green, shiny, midrib slightly sunken to slightly protruding basally, further slightly protruding, secondary nerves and venation very distinct, sometimes even more distinct than at lower side; lower side glaucous-papillose, secondary nerves c. 4–6 pairs, first nerves reaching to halfway or further, intramarginal nerve in apical part rather distinct; glands very numerous, scattered, 0.1–0.2 mm diam. *Inflorescences* unbranched, shorter than the leaves; axes minutely rather sparsely appressedly hairy to nearly glabrous; in basal part flowers with up to 3 together. *Pedicel* 2.5–6 mm long, more or less smooth, minutely sparsely to densely, appressedly hairy. *Sepals* sparsely hairy along the midrib to (nearly) glabrous outside, often some with rather distinct glandular spots; outer sepals 2.7–2.9 × 2.1–2.4 mm; inner sepals 3.1–3.3 × 3.0–3.2 mm. *Petals* creamish white to light purplish, the upper ones with a yellow spot, when dry orange, glabrous outside, apically and basally sparsely ciliate, the longest one 11–13 mm long. *Stamens:* filaments connate over up to 2.5 mm; anthers c. 1.2–1.8 mm long, often minutely hairy all over. *Ovary* 1–2 mm stipitate, glabrous to densely appressedly whitish hairy; style thinly appressedly hairy in basal part, further glabrous; ovules 8–12. *Fruit* sometimes distinctly stipitate, globular, c. 1.5 cm diam., more or less shiny, brownish, glabrous or nearly so; pericarp thin; pedicel up to 10 mm long.

Distribution. Borneo: Sarawak (3rd Div.: 3 coll.; 4th Div.: 1; 5th Div.: 1), Sabah (Penampang: 1; Tenom: 1; Kinabalu region: 8), E. Kalimantan (Tarakan I.: 1; near Mt Kongkemul: 1).

Note. Very variable in the indumentum of the ovary. See also under *48. X. discolor.*

50. Xanthophyllum pseudoadenotus Meijden, *spec. nov.*

X. stapfii Chodat, Bull. Herb. Boiss. 4 (1896) 260, *p.p., pro specim. Haviland 1620.*

Gemmae axillares ut videtur singulae, semipatentes, 3–6 mm longae. Lamina nervis e paribus 11–14, subtus papillosa; glandulae numerosae. Inflorescentia indivisa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo c. 15 mm longo (immaturo); carina subglabra. Antherae 2.0 mm longae. Ovarium minute appresse pilosum; stylus minute appresse pilosus; ovula 9–11. Fructus globosus, c. 1.5 cm diam.; pericarpium tenue. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *Haviland 2113* (K).

Small tree up to 9 m high, 12 cm d.b.h. Axillary buds oblong, 3–6 mm long, basally strongly thickened, obtuse, probably glabrous; secondary and adventitious buds often present, numerous. *Petiole* (8–)10.5–14 mm long, smooth. *Leaf blade* 13–32 × 5–10.5

cm, base attenuate to cordate, apex acutish; upper side dark green, often slightly bullate between the secondary nerves, midrib protruding, often with a groove from halfway down; lower side glaucous-papillose, secondary nerves 11–14 pairs, forming a rather distinct complete intramarginal nerve; glands numerous, smaller than 0.1 mm diam. *Inflorescences* 1.5–6 cm long, also arising from adventitious buds on older nodes, unbranched; axes minutely appressedly hairy (hairs 0.1 mm long). *Pedicel* 5–6 mm long, minutely appressedly hairy (hairs 0.1 mm long). *Sepals:* outer sepals 2.0 × 2.0 mm; inner sepals 3.2 × 2.7 mm. *Petals* subglabrous, brownish orange when dry, the longest one about 15 mm long. *Stamens:* filaments c. 1.5 mm connate; anthers 2.0 mm long, ciliate along slits. *Ovary* minutely appressedly hairy (hairs 0.1–0.2 mm long); style glabrous in apical part; ovules 9–11. *Fruit* globular, c. 1.5 cm diam., minutely appressedly hairy; pericarp thin, brittle; pedicel up to 7 mm long.

Distribution. Borneo: Sarawak (1st Div.: 3 coll.; 3rd Div.: 2; 4th Div.: 2; 5th Div.: 1), Sabah (Beaufort hill: 1).

Note. Resembling *51. X. pulchrum* subsp. *stapfii*, differing in the shorter, appressed hairs of inflorescence and flowering parts, in the greater number of secondary nerves which form a distinct intramarginal nerve, in the longer pedicel, and in the smaller sepals.

51. Xanthophyllum pulchrum

X. pulchrum King, J. As. Soc. Beng. II, 59 (1890) 141; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 164; Gagnepain, Desv. J. Bot. 21 (1908) 252; Ridley, Fl. Mal. Pen. 1 (1922) 146; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 361, fig. 3; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 27, 147, 211. – Lectotype: *King's Coll. 2859* (L; iso Fl, G, K, L, P, Z).

X. stapfii Chodat, Bull. Herb. Boiss. 4 (1896) 260 (excl. *Haviland 1620*); in E. & P., Nat. Pfl. Fam. III, 4 (1896) 345 (*'stapferi'*); Merr., En. Born. (1921) 326; Masam., Enum. Phan. Born. (1942) 381. – Lectotype: *Haviland 532* (K).

X. densiflorum Chodat, Bull. Herb. Boiss. 4 (1896) 256; Merr., En. Born. (1921) 325; Masam., Enum. Phan. Born. (1942) 379. – Type: *Beccari 2442* (K).

Small shrub to small tree, up to 8 m high. Twigs glabrous to minutely patently hairy. Axillary buds ovate, 1.8–3.5(–5?) mm long, very thick (mostly not especially basally), obtuse, light brown and often more or less reddish, often irregular because of cork-forming. *Petiole* 4–9 mm long, the young ones nearly smooth, not transversely wrinkled, glabrous to minutely densely patently hairy all round, the older ones soon becoming transversely cracked, more or less corky; glands often present, mostly rather distinct. *Leaf blade* (5.5–)7.5–30 × 2.4–11.5 cm; base rounded-cordate, rarely rounded, obtuse, or cuneate-rounded, apex acutish, rarely rounded; upper side rarely bullate between midrib and secondary nerves, greyish green, midrib slightly sunken to flat, rarely indistinctly protruding; lower side glaucous-papillose, secondary nerves (6 or) 7–12 (or 13) pairs, forming mostly an indistinct intramarginal nerve in apical half; glands numerous, scattered, c. 0.1–0.2 mm diam. *Inflorescences* situated at end of young twigs but also axillary, not rarely on old nodes, unbranched, shorter than the leaves, many-flowered; axes stiff, minutely patently hairy; in basal part flowers with up to 3 together. *Pedicel* 2.5–3.5(–4.5) mm long, finely grooved, very densely minutely patently hairy. *Sepals* often with rather distinct glands;

outer sepals 2.1–5.0 × 2.7–4.2 mm; inner sepals 3.2–6 × 3.2–4.9 mm. *Petals* pink or whitish, when dry red or brownish orange, slightly hairy apically and basally inside, further glabrous, the longest one 13–18 mm long. *Stamens:* anthers (1.3–)1.7–2.5(–3.6) mm long, faintly hairy at base, sparsely ciliate along slits. *Ovary* up to 2 mm stipitate, patently light brownish pubescent; style glabrous in apical part; ovules 12–16. *Fruit* globular, up to 2.0 cm diam.; pericarp thin.

Distribution. Malaya. – Sumatera. – Borneo.

Note. See under *48. X. discolor.*

KEY TO THE SUBSPECIES

1a. Secondary nerves 6 or 7 pairs. Longest petals 12–16 mm long. Anthers 1.3–1.8 mm long ..... a. subsp. **pulchrum**

b. Secondary nerves 7–13 pairs. Longest petals 15–18 mm long. Anthers (1.7–)2.1–3.6 mm long ..... b. subsp. **stapfii**

a. subsp. **pulchrum**

X. pulchrum King.

Petiole 4–6.5 mm long. Secondary nerves (6 or) 7 pairs. Outer *sepals* 2.1–4.0 × 2.7–3.9 mm, inner sepals 3.2–4.7 × 3.4–4.3 mm. Longest *petals* 12–16 mm long. *Anthers* 1.3–1.8 mm long.

Distribution Malaya: Kedah (Bintang For. Res.: 1 coll.), Pinang I. (1), Perak (15), W. Trengganu (3), E. Pahang (Panching For. Res.: 1), Johore (2). – Sumatera: North (Asahan region: 2).

b. subsp. **stapfii** (Chodat) Meijden, *stat. nov.*

X. stapfii Chodat, Bull. Herb. Boiss. 4 (1896) 260 (excl. *Haviland 1620*). – *X. densiflorum* Chodat.

Petiole (4–)5–9 mm long. Secondary nerves 7–12 (or 13) pairs. Outer *sepals* 3.4–5.0 × 3.1–4.2 mm, inner sepals 3.6–6.0 × 3.2–4.9 mm. Longest *petals* 15–18 mm long. *Anthers* (1.7–)2.1–2.5(–3.6) mm long.

Distribution. Borneo: Sarawak (1st Div.: 10 coll.; 3rd Div.: 3; 4th Div.: 1), Kalimantan (2).

Note. Resembles *50. X. pseudoadenotus*; see there.

52. Xanthophyllum beccarianum

X. beccarianum Chodat, Bull. Herb. Boiss. 4 (1896) 257; Monogr. Polygal. (1891) t. 9, fig. 3; Merr., En. Born. (1921) 325; Masam., Enum. Phan. Born. (1942) 379; Meijer, Bot. News Bull. Sandakan 7 (1967) 87. – Lectotype: *Beccari 2230* (G; iso K, M, W).

Tree up to 12 m high, 17 cm d.b.h. Twigs very densely patently hairy (hairs up to 10 mm long). Axillary buds triangular-ovate, 0.5–4.5 mm long, basally strongly thickened, acutish. *Petiole* 5–6 mm long, very densely hairy. *Leaf blade* 9.5–19 × 4–8 cm, base cordate, apex acutish; upper side dark green; lower side glaucous-papillose, rather sparsely hairy, midrib rather densely hairy, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve in apical part; glands numerous, scattered, c. 0.1 mm diam. *Inflorescences* unbranched, shorter than the leaves; axes densely minutely hairy (hairs up to 0.4 mm long); in basal part flowers with up to 3 together, sometimes turned upside-down. *Pedicel* 7.5–9.5 mm long, densely patently minutely hairy (hairs up to 0.25(–0.4) mm long). *Sepals* nearly glabrous (very shortly hairy); outer sepals 2.5–2.7 × 3.0–3.6 mm, with rather distinct glandular spots; inner sepals 3.2–4.0 × 2.8–3.4 mm. *Petals* orange-red when dry, glabrous except for the ciliate base, the longest one c. 16–16.5 mm long, minutely hairy at base along margin, further glabrous. *Stamens:* anthers 2.2 mm long. *Ovary* patently hairy; style glabrous in apical half; ovules 13. *Fruit* (immature) apically pointed; pedicel c. 10–12 mm long.

Distribution. Borneo: Sarawak (1st Div., vicinity of Kuching: 8 coll.).

Note. *S 13559* resembles this species, differing in the shorter hairs of the vegetative parts (up to 0.3–0.4 mm long) and the shorter pedicel (6 mm).

53. Xanthophyllum pedicellatum Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, semipatentes, pilosae, 1.5–3.5 mm longae. Lamina subtus papillosa atque pilosa; glandulae numerosae. Inflorescentia indivisa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo 12.5 mm longo; carina subglabra. Antherae 1.5–1.6 mm longae. Ovarium dense semipatenter pubescens; ovula 9–11. Fructus globosus, c. 2.2 cm diam.; pericarpium tenue. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *SAN 15009* (L; BRI, KEP, SING).

Shrub to tree 3.5–23 m high, 60 cm d.b.h. Twigs densely patently brownish hairy, glabrescent. Axillary buds narrowly triangular, 1.5–3.5 mm long, hairy. *Petiole* 1.5–2.5(–3) cm long, very densely patently hairy. *Leaf blade* (5–)9–11 × (1–)1.5–3(–4) cm, base cuneate to rounded or slightly cordate, apex usually acutish; upper side dark green, shiny, lower side glaucous-papillose, hairy mainly on midrib, secondary nerves c. 7 or 8 pairs, forming an indistinct intramarginal nerve or not; glands very numerous, scattered, c. 0.1 mm diam. *Inflorescences* unbranched, as long as the leaves; axes densely minutely patently hairy, some hairs up to 0.5 mm long. *Pedicel* (9–)10–15 mm long, minutely patently hairy. *Sepals* very sparsely minutely hairy outside, glabrous inside except at very base; outer sepals c. 2–2.5 × 2 mm; inner sepals c. 3–3.5 × 2–2.4 mm. *Petals* pinkish, when dry orange-red, glabrous except for ciliate base, the longest one 12.5 mm long. *Stamens:* anthers 1.5–1.6 mm long, sparsely minutely hairy at base. *Ovary* nearly sessile, half-patently brownish pubescent; style glabrous in apical part; ovules 9–11. *Fruit* globular, c. 2.2 cm diam., light brownish, hairy; pericarp thin.

Distribution. Borneo: E. Sabah (near Sandakan: 10 coll.; Lahad Datu: 3; Tawau: 1); identity doubtful: Sarawak (1st Div., Bako National Park: *S 34392*).

54. Xanthophyllum purpureum

X. purpureum Ridley, Kew Bull. (1938) 114. – Type: *Moulton 174* (K; iso SING).
X. molle Ridley, Kew Bull. (1938) 114. – Type: *Haviland & Hose 3158* (K; iso SAR).

Shrub or small tree up to 5 m high, 10 cm d.b.h. Twigs very densely patently hairy. Axillary buds narrowly triangular, (1.5–)3–5 mm long, basally thickened. *Petiole* c. 5 mm long, densely hairy. *Leaf blade* (6–)10–20 x (1.5–)2.5–9 cm, base cordate to rounded-attenuate, rarely cuneate, apex acutish; upper side green, midrib slightly sunken to flat; lower side glaucous-papillose, more or less densely hairy all over or only on nerves, secondary nerves (5 or) 6 or 7 pairs, not or only in apical part forming an intramarginal nerve; glands numerous, scattered, c. 0.1 mm diam. *Inflorescences* unbranched, shorter than the leaves, often curved downwards; axes sparsely minutely hairy (hairs up to 0.2 mm long); in basal part flowers with 3 together. *Pedicel* 2.5–5 mm long, minutely densely hairy (hairs up to 0.2–0.3 mm long). *Sepals* rather densely minutely hairy outside (hairs 0.1 mm long), subglabrous inside, often with tiny, rather indistinct glandular spots; outer sepals 1.8–3.0 × 2.1–2.6 mm; inner sepals 2.7–4.3 × 2.7–3.5 mm. *Petals* (light) purple to rosa-violet, when dry orange-red, ciliate at base and apex, further glabrous, the longest one 11–12(–14?) mm long. *Stamens:* filaments free or 0.4 mm connate; anthers 0.9–1.4 mm long, glabrous to shortly hairy at base. *Ovary* subsessile or c. 1.5 mm stipitate, patently hairy; style glabrous in apical half; ovules 8–14. *Fruit* globular, 1.2–1.5 cm diam., usually with remnant of style, hairy; pericarp thin; pedicel curved.

Distribution. Borneo: Sarawak (1st Div.: 1 coll.; 4th Div.: 9; 5th Div.: 4), Sabah (western part: 8; eastern part: 2), NE. Kalimantan (near Mt Kongkemul: 2).

55. Xanthophyllum reticulatum

X. reticulatum Chodat in Merr., Pl. Elm. Born. (1929) 136. – Lectotype: *Elmer 21119* (L; iso BM, BO, BR, BRI, C, G, K, M, P, SING).

Small tree 2.5–15 m high. Twigs very densely patently hairy (hairs up to 1 mm long). Axillary buds narrowly triangular, 4–6(–7.5) mm long, hairy. *Petiole* c. 5 mm long, densely pubescent. *Leaf blade* 7–19 × 3–5.5 cm, base obtuse to rounded, apex acutish; upper side dark green, midrib, secondary nerves and part of finer nervation sunken, midrib hairy at very base; lower side green, smooth or indistinctly papillose, hairy on midrib and on basal part of nerves, secondary nerves c. 8 pairs (difficult to count), tertiary nerves strongly protruding, leaf blade bullate in-between; finer nerves not strongly protruding; glands numerous, scattered, c. 0.1 mm diam. *Flowers* unknown. *Infructescences* 0.8–4.5 cm long, unbranched; axes shortly sparsely hairy (hairs up to 0.25 mm long). *Fruit* globular, c. 1.5 cm diam., sessile, with remnant of style, hairy; pedicel 5–10.5 mm long, minutely patently hairy (hairs up to 0.2 mm long). *Seed* 1; abortive ovules 11–13.

Distribution. Borneo: SE. Sabah (4 coll.).

Note. Insufficiently known. *S 23201* resembles this species, but differs in the following characters: ovules 4?; fruit thickened in apical part and there 4-sulcate (possibly infected by gall wasps; fruit resembling that of *11. X. schizocarpon*); its pedicel 11–12 mm long,

densely hairy (hairs 0.5 mm long); petiole 10–12 mm long; secondary nerves c. 5 or 6 pairs; leaf blade less distinctly bullate between the tertiary nerves.

56. Xanthophyllum trichocladum

X. trichocladum Chodat in Merr., Pl. Elm. Born. (1929) 137; Masam., Enum. Phan. Born. (1942) 382; Meijer, Bot. News Bull. Sandakan 7 (1967) 87. – Lectotype: *Elmer 21549* (L; iso BM, BO, BR, C, G, K, M, P, SING, U, Z).

Shrub or small tree up to 12 m high, 13 cm d.b.h. Twigs very densely patently hairy. Axillary buds ovate-oblong, (1.5–)2.5–5(–6) mm long, densely hairy. *Petiole* c. 4–7 mm long, very densely hairy. *Leaf blade* 11–31 × 3–9 cm, base cordate, covering upper side of petiole, apex acutish; upper side green, dull, hairy on the midrib, midrib distinctly sunken, rarely flat, secondary nerves and intramarginal nerve faintly sunken, rarely slightly protruding, venation little protruding; lower side glaucous-papillose, pubescent all over, secondary nerves c. 9(–12) pairs, forming a distinct intramarginal nerve; glands very numerous, scattered, c. 0.1 mm diam. *Inflorescences* unbranched, shorter than to as long as the leaves or sometimes with one side branch at very base; axes very densely brownish patently pubescent (most hairs 0.5–0.8 mm long); flowers often turned upside-down. *Pedicel* 5–7 mm long, very densely brownish hairy (hairs up to 1.0 mm long); pedicels of flower buds at first curved downwards, of open flowers turned upwards and often half-twisted, rarely straight, pedicels of fruits curved downwards again. *Sepals* very densely brownish pubescent outside (hairs up to 1.0 mm long); outer sepals 3.2–3.8(–4.0) × 2.7–3.2 mm; inner sepals 3.2–4.2(–5.6) × 3.2–4.2 mm. *Petals* pink, the upper ones with a yellow spot, when dry dark reddish, the longest one 13(–16) mm long; carina glabrous to sparsely appressedly hairy outside along central veins; other petals glabrous except for a few hairs at base, sometimes sparsely ciliate in basal part. *Stamens:* filaments free or 0.1–0.5(–1.5) mm connate; anthers 2.2–3.0 mm long, faintly hairy at base, ciliolate along slits. *Ovary* patently hairy; ovules 11–16. *Fruit* globular, about 1.5 cm diam., densely hairy; pericarp rather thin; sepals subpersistent in fruit.

Distribution. Borneo: Sarawak (1st Div., Arboretum Semengoh: 2 coll.; 3rd Div.: 1), E. Sabah (13), E. Kalimantan (Samarinda: 1).

57. Xanthophyllum erythrostachyum

X. erythrostachyum Gagnepain, Desv. J. Bot. 21 (1908) 250; Bull. Soc. Bot. France 56 (1909) 36. – Type: *Forbes 1671* (P; iso FI, L).

X. forbesii Baker, Hook. J. Bot. 62 (1924) Suppl. 7, *nom. superfl.* – Type: *Forbes 1671* (BM; iso SING).

Axillary buds 0.8–1.9 mm long, minutely hairy, glabrescent. *Petiole* 4–10 mm long, partly covered by the cordate leaf base or not. *Leaf blade* 10–20.5 x 4–5.5 cm, base cordate and flat or with the margins curved upwards, to cordate-truncate, apex distinctly acuminate; upper side dull, greyish green, midrib distinctly protruding, nervation rather obscure; lower side greenish, secondary nerves 8–10 pairs, rather indistinct, forming an indistinct intramarginal nerve in upper part, venation rather obscure; glands few to numerous,

0.2–0.3 mm diam. *Inflorescences* unbranched or with one side branch, up to 8 cm long; axes angular, orange, rather sparsely appressedly minutely hairy. *Pedicel* 4–4.5 mm long, rather densely appressedly minutely hairy. *Sepals:* outer sepals 2.7–3.0 × 1.8–2.2 mm, with rather distinct glands; inner sepals 3.9–4.0 × 2.7–3.2 mm. *Petals* whitish tinged with rosa, when dry reddish orange, the longest one 13 mm long; carina outside glabrous to rather sparsely patently minutely hairy near base, near apex very sparsely appressedly hairy, further glabrous; other petals glabrous. *Stamens:* filaments free or 0.3 mm connate; anthers 1.0–1.2 mm long, glabrous at base, ciliate along slits. *Ovary* appressedly to half-patently rather shortly brownish hairy; ovules 11 (or perhaps also 4?). *Fruit* unknown.

Distribution. Sumatera: North (Aceh, Gajo Lands, Aer Panas-Roema Boender: *Van Steenis 10075*), South (Lampung, Penang-goengan: *Forbes 1671*).

Notes. 1. *Van Steenis 10075* differs from the type collection in its longer petioles (c. 10 mm long, in the type c. 4 mm long). My annotations say that its ovary contained 4 ovules. As it is a very fragmentary collection, with only one flower and no flower buds, I could not check this again. In other respects the collection strongly resembles the type collection of which all ovaries contained exactly 11 ovules. Only in *16. X. arnottianum* both 4 as well as 8 or more ovules have been found. I think that I made a mistake in attributing 4 ovules to Van Steenis' collection.

2. Probably allied to *48. X. discolor*, but differing in many characters.

58. Xanthophyllum laeve

X. laeve Meijden, Bot. J. Linn. Soc. 67 (1973) 118 (*'laevis'*). – Type: *Lörzing 5537* (L; iso BO).

Shrub or small tree, 3–6 m high. Axillary buds c. 1 mm long. *Petiole* 5–7 mm long. *Leaf blade* 4.5–13.5 × 1.9–5.3 cm, apex cuspidate; upper side greenish to reddish brown, dull, midrib sunken, hardly visible, nerves obscure to slightly protruding; lower side light greenish to reddish brown, secondary nerves c. 5 pairs, rather indistinct to slightly protruding, forming an indistinct intramarginal nerve, venation indistinct; glands rather few, situated near the midrib, 0.3–0.4 mm diam. *Inflorescences* branched or unbranched, shorter than the leaves; axes glabrous, more or less smooth. *Pedicel* 8–15 mm long, grooved, dark, glabrous. *Sepals:* outer sepals 1.8–2.1 × 2.4 mm; inner sepals 2.8–3.0 × 2.8 mm. *Petals* white with red spots, when dry reddish orange, the longest one 11–13 mm long; carina shortly sparsely appressedly hairy outside, shortly hairy inside; other petals sparsely hairy outside near apex. *Stamens:* anthers c. 0.5 mm long. *Ovary* glabrous or with a few hairs, black; style very sparsely more or less appressedly hairy; ovules 8. *Fruit* unknown.

Distribution. Sumatera: North (southwest of Medan, Sibolangit: *Lörzing 5537, 12637*).

Note. Insufficiently known. Characterized by its subglabrous gynoecium and the rather obscure nervation of the leaves. Possibly belonging to the *beccarianum*-group, although its axillary buds are smaller, and the petals are slightly more hairy.

59. Xanthophyllum retinerve Meijden, *spec. nov.*

Gemmae axillares plerumque 3, inconspiquae, breviter dense pilosae. Lamina subtus laevis; glandulae 0–2. Inflorescentia sparse ramosa, bracteis basalibus oppositis. Petala inaequalia, petalo longissimo c. 6.5 mm longo; carina extus appresse pilosa. Antherae 0.3–0.4 mm longae. Ovarium dense appresse pilosum; stylus appresse pilosus; ovula 4. Fructus globosus, c. 2.2 cm diam.; pericarpium sat durum, c. 4 mm crassum. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *FRI 14860* (L).

Tree up to 12 m high, 20 cm d.b.h. Twigs sparsely shortly appressedly hairy, glabrescent; axillary region shortly densely appressedly hairy. Axillary buds mostly 3, inconspicuous, shortly densely appressedly hairy, the upper one 1–2 mm supra-axillary, sometimes more distinct and up to 0.8 mm long. *Petiole* 6–16 mm long, appressedly shortly hairy. *Leaf blade* 7–14 × 2.5–5 cm, apex shortly acuminate to cuspidate; upper side (greenish) brown, midrib sunken to slightly protruding; lower side reddish brown, sometimes glaucous, sparsely shortly hairy, secondary nerves 5–7 pairs, sometimes forming an indistinct intramarginal nerve; glands 0–2, mostly close to midrib, 0.2(–0.4) mm diam. *Inflorescences* up to 10 cm long, with 2 opposite branches directly above base; axes densely appressedly shortly hairy; lower bracts of side axes opposite. *Pedicel* 2–2.5 mm long, densely appressedly shortly hairy. *Sepals* sometimes with tiny glands; outer sepals 1.4–1.5 × 1.3–1.4 mm; inner sepals 2.1–2.2 × 2.2–2.3 mm. *Petals* white, when dry orange-red, glabrous inside, the longest one c. 6.5 mm long; carina appressedly hairy outside; other petals sparsely hairy apically. *Stamens:* anthers 0.3–0.4 mm long. *Ovary* (sub)sessile, faintly ribbed, densely shortly appressedly hairy; ovules 4. *Fruit* globular, up to 2.2 cm diam., smooth, rather dull, brown, sparsely appressedly hairy; pericarp c. 4 mm thick, rather hard; pedicel up to 4 mm long.

Distribution. Malaya: Perak (2 coll.), Trengganu (3), Pahang (Fraser's Hill: 1).

60. Xanthophyllum eurhynchum

Fig. 3A-a, b

X. eurhynchum Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277; King, Mat. Fl. Mal. Pen. (1890) 137; Gagnepain, Desv. J. Bot. 21 (1908) 252; Baker, Hook. J. Bot. 62 (1924) Suppl. 7. – Type: *Korthals s.n.* (L, sheet 908.171-2186; iso K, L, U).

X. maingayi Hook. *f. ex* A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 210: King, Mat. Fl. Mal. Pen. (1890) 136; Gagnepain, Desv. J. Bot. 21 (1908) 252; Burkill, Gard. Bull. S. S. 3 (1923) 35; Wyatt-Smith, Mal. For. Rec. 17 (1952) 362; Balan Menon, *op. cit.* 19 (1956) 34; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 360, fig. 3; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 146, 147, 211. – *Banisterodes maingayi* (A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *Maingay 137 (= 2201)* (K; iso G, L).

X. verrucosum Chodat, Bull. Herb. Boiss. 4 (1896) 263; Ridley, Fl. Mal. Pen. 1 (1922) 147; Henderson, Gard. Bull. S. S. 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Wyatt-Smith, *op. cit.* 17 (1952) 364. – Lectotype: *King's Coll. 8164* (L; iso BM, FI, K). See note 5.

X. palembanicum auct., non Miq.: King, Mat. Fl. Mal. Pen. (1890) 137; Gagnepain, Desv. J. Bot. 21 (1908) 251; Ridley, Fl. Mal. Pen. 1 (1922) 149; Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Watson, Mal. For. Rec. 5 (1928) 249; Craib, Fl. Siam. Enum. (1931) 105; Burkill, Dict. (1935) 2269.

Shrub or tree, 3–20 m high, up to 20 cm d.b.h. Twigs glabrous to minutely patently

hairy, mostly soon glabrescent; axillary region shortly densely patently hairy. Axillary buds 2–4, usually less than 0.5 mm long, mostly very densely patently hairy, the upper one sometimes slightly supra-axillary. *Petiole* 3–9(–11), exceptionally up to 14 mm long, glabrous to shortly rather densely hairy in the upper groove, rarely (in some Sumatran collections) shortly hairy all round; glands mostly indistinct. *Leaf blade* rarely linear-lanceolate, (2.5–)3.5–15(–18) × (1–)2–5(–7) cm, apex acuminate to cuspidate; upper side sometimes slightly bullate between the secondary nerves, greyish green, midrib slightly sunken or sometimes flat to slightly protruding; lower side rather dull, mostly glabrous, yellowish green, secondary nerves 3–5 (or 6) pairs, forming a rather distinct intramarginal nerve; glands (0–)2–7(–11), 0.1–0.3(–0.4) mm diam. *Inflorescences* solitary or with 2 together, mostly unbranched or sometimes with a few short side axes at base; axes angular to terete, minutely hairy; flowers solitary or in basal part with 3 together; bracts and bracteoles relatively long-persistent. *Pedicel* (1–)2–4(–7.5) mm long, densely minutely hairy. *Sepals:* outer sepals 1.6–2.3 × 1.4–2.3 mm; inner sepals 2.6–3.6 × 2.0–3.3 mm. *Petals:* white, when dry yellowish, the longest one 7–8.5(–9) mm long; carina mostly bent outwards in open flowers, thus exposing the stamens, rather densely appressedly hairy outside, inside minutely hairy in apical part, ciliate in basal half; other petals glabrous to sparsely hairy outside at apex. *Stamens:* anthers (0.4–)0.5 mm long. *Ovary* (sub)sessile, more or less ribbed, more or less appressedly hairy with hairs of different length; ovules 4. *Fruit* globular to broadly ellipsoid, sometimes irregularly 2–4-sulcate, 1.2–1.8 cm diam., more or less smooth to strongly warty, light brown, velvety to densely appressedly hairy.

Distribution. S. Thailand. – Malaya. – Sumatera. – Collections not identified to the subspecies: Malaya: Kedah (1 coll.), Pinang I. (1), Perak (19), Pankor Is. (3), Kelantan (5), Pahang (13), Selangor (21), Negri Sembilan (7), Malacca (5), Johore (6). Singapore (1).

Notes. 1. In this circumscription *X. eurhynchum* is very variable in the sculpture of the fruit, varying from more or less smooth (subsp. *maingayi*) to strongly tuberculate (subsp. *eurhynchum*). The subspecies are sympatric only in Pinang I. and in the Pankor Is.; in the southern part of S. Thailand both taxa occur in different localities. Apart from the fruit the subspecies differ little; subsp. *maingayi* usually has smaller flowers and leaves. Within subsp. *eurhynchum* the collections from Sumatera differ a little from the other ones in their longer leaves.

2. In my opinion the character-state 'fruits tuberculate' is a *syn*apomorphous character of species 59–63. (The plesiomorphous condition is then 'fruit smooth', like in *59. X. retinerve*.) The character-state 'fruit more or less smooth' is then an *aut*apomorphous character of *X. eurhynchum* subsp. *maingayi*, and *not* the plesiomorphous condition in the *eurhynchum*-group. I may defend this assumption by pointing to the fact that the fruits of subsp. *maingayi* are never 'normally' smooth, but have a unique, irregular form when dry.

3. Differing from *61. X. wrayi* in the number of secondary nerves, the (sub)glabrous upper petals, and in the free stamens. For differences with *59. X. retinerve*, see there.

4. King (1890) recognized three species, Chodat (1896) mentioned four species, Ridley (1922) distinguished two species, and lately Ng (1972) reduced all these to one. As it is not always clear what other authors had in mind when using a certain name, I have given only the nomenclaturally necessary references under the subspecies.

5. The lectotype of *X. verrucosum* is not *Curtis 1617*, as chosen by Ng (1972), because

it is not certain that that collection has been seen by Chodat. The Leiden duplicate of *King's Coll. 8164* unmistakably bears Chodat's label.

KEY TO THE SUBSPECIES

1a. Fruit with distinct warts arranged in longitudinal rows (Fig. 3A-b). a. subsp. **eurhynchum**

b. Fruit more or less smooth, transversely wrinkled or finely rugose or irregularly grooved (Fig. 3A-a) ..... b. subsp. **maingayi**

a. subsp. **eurhynchum** Fig. 3A-b

X. eurhynchum Miq. – *X. verrucosum* Chodat.

Fruit globular, 1.5–1.8 cm diam., strongly warty, densely appressedly hairy between the warts.

Distribution. S. Thailand (2 coll.). – Malaya: Kedah (4), Pinang I. (5), Perak (13), S. Pankor I. (2). – Sumatera (7).

b. subsp. **maingayi** (Hook. *f. ex* A.W. Bennett) Meijden, *stat. nov.* Fig. 3A-a

X. maingayi Hook. *f. ex* A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 210. – Lectotype: *Maingay 137 (= 2201)* (K; iso G, L). – *X. palembanicum auct., non* Miq.

Fruit broadly ellipsoid, often irregularly formed, 1.2–1.5 cm diam., sometimes 2–4-sulcate, surface at lateral sides usually with depressions of irregular size or transversely wrinkled, sometimes finely rugose, very densely shortly velvety.

Distribution. S. Thailand (4 coll.). – Malaya: Pinang I. (1), Kelantan (4), Trengganu (13), N. Pankor I. (1), Pahang (18), Selangor (20), Negri Sembilan (4), Malacca (9), Johore (11). Singapore (10).

61. Xanthophyllum wrayi Fig. 3A-c

X. wrayi King, J. As. Soc. Beng. II, 59 (1890) 138; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 164; Gagnepain, Desv. J. Bot. 21 (1908) 251; Ridley, Fl. Mal. Pen. 1 (1922) 148: Burkill & Henderson, Gard. Bull. S. S. 3 (1925) 346; Henderson, *op. cit.* 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2268; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 363, fig. 5: Corner, Gard. Bull. Sing., Suppl. 1 (1978) 147, 211. – Lectotype: *Curtis 677* (SING; iso P, W).

X. puberulum Ridley, J. Str. Br. R. As. Soc. 73 (1916) 139; Henderson, Gard. Bull. S. S. 4 (1928) 222. – Lectotype (Ng in Whitmore, Tree Fl. Mal. 1, 1972, 363): *Ridley 13390* (*'13396'*) (SING).

Shrub to small tree, up to 10 m high. Twigs shortly densely patently to appressedly hairy, rarely glabrous except for the densely hairy area above the leaf axil. Axillary buds 2 or 3, densely hairy, up to c. 0.5 mm long. *Petiole* (5–)7–11(–14) mm long, usually not transversely wrinkled, densely minutely hairy all round, rarely hairy only in the upper groove, often with rather distinct protruding glands. *Leaf blade* 10–30 × 3.5–13 cm, base

rarely cordate; upper side often slightly bullate between the secondary nerves, mostly greyish green, midrib deeply sunken and mostly hairy in basal part; lower side yellowish green, rather dull, minutely hairy or rarely glabrous, secondary nerves 8–15 pairs, forming a distinct intramarginal nerve; glands (2–)4–14, often (very) close to the midrib, sometimes present only in upper part, (0.3–)0.5–0.7 mm diam. *Inflorescences* shorter than to about as long as the leaves; axes strongly ribbed, flattened at base, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. *Pedicel* 2.5–7 mm long, densely minutely patently hairy. *Sepals:* outer sepals 2.1–3.0 × 1.5–2.1 mm, sometimes with small glands; inner sepals 2.8–4.0 × 2.0–2.5 mm. *Petals* white to lilac, the upper ones with a yellow spot, when dry yellowish, the longest one 5.8–7.5(–8.0) mm long; carina densely minutely hairy in apical part outside and inside; other petals sparsely hairy outside in apical part, lateral petals minutely hairy inside above insertion of filaments, upper petals rather densely patently hairy inside up to apex. *Stamens:* filaments connate over 0.5–2 mm or sometimes triadelphous, sparsely minutely hairy in basal part to densely more or less patently hairy in middle part; anthers 0.4–0.5 mm long. *Ovary* patently to appressedly hairy; style patently hairy in basal part, in apical half sparsely hairy to glabrous; ovules 4. *Fruit* more or less globular, up to c. 1.5 cm diam., verrucately ribbed to strongly tuberculate-warty, apically rounded or with the style-scar sunken; pedicel 2–6 mm long.

Distribution. Malaya: Pinang I. (4 coll.), Kelantan (4), Perak (22), Pahang (5), Selangor (11), N. Johore (1).

Note. Closely resembling *60. X. eurhynchum* (see there) and *62. X. venosum*; from the latter differing in the shorter, hairy petioles, the shorter petals, and the hairy upper petals.

62. Xanthophyllum venosum

Fig. 3A–d

X. venosum King, J. As. Soc. Beng. II, 59 (1890) 139; Ridley, Fl. Mal. Pen. 1 (1922) 222. – Lectotype: *King's Coll. 10804* (SING; iso BM, K).

Shrub to small tree up to 10 m high. Twigs rather densely hairy in axillary area, further glabrous to sparsely minutely hairy. Axillary buds 2–4, up to 0.5 mm long, hairy. *Petiole* (12–)15–21(–27) mm long, glabrous to sparsely minutely hairy, not transversely wrinkled, often with glands. *Leaf blade* 12.5–40 × 4.5–12(–13) cm, base cuneate to rounded or cordate; upper side often slightly bullate between the secondary nerves, greenish to yellowish brown, midrib deeply sunken; lower side yellowish green, mostly glabrous, secondary nerves 12–20 pairs, forming a distinct intramarginal nerve; glands mostly numerous, scattered, 0.1–0.2 mm diam. *Inflorescences* sometimes also on older nodes, shorter than the leaves; axes strongly flattened basally, ribbed, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. *Pedicel* 2–4 mm long, minutely hairy. *Sepals:* outer sepals 2.3–3.3 × 2.1–3.3 mm, often with glands; inner sepals 2.8–4.0 × 2.5–4.0 mm. *Petals* light purple, when dry pale yellow, the longest one 8.5–11.5 mm long; carina sparsely minutely appressedly hairy outside, glabrous inside; other petals slightly hairy basally, further glabrous. *Stamens:* filaments connate over (0.5–)1–3 mm, rarely some filaments free; anthers 0.5–0.9 mm long. *Ovary* (sub)sessile, ribbed,

appressedly hairy; ovules 4. *Fruit* ovoid, c. 2 × 1.5 cm, apically shortly but distinctly beaked, strongly verrucately ribbed; pedicel 3–5 mm long, minutely hairy.

Distribution. Malaya: Perak (2 coll.), Trengganu (2), Pahang (10), Selangor (26), Negri Sembilan (2), Johore (2).

Note. Resembling *61. X. wrayi* and *60. X. eurhynchum*; see under both species.

63. Xanthophyllum malayanum

X. malayanum Meijden, Bot. J. Linn. Soc. 67 (1973) 118: Ng in Whitmore, Tree Fl. Mal. 1 (1972) 365, fig. 5 ('*spec. A*'); Corner, Gard. Bull. Sing., Suppl. 1 (1978) 146. – Type: *FRI 7732* (KEP; iso K, L).

Tree up to 10 m high, 10 cm d.b.h. Twigs very densely brownish patently hairy with a mixture of very small and long hairs. Axillary buds nearly completely covered by indumentum, narrowly triangular, possibly up to 2.5 mm long. *Petiole* 4–10 mm long, very densely patently pubescent. *Leaf blade* 5–24 × 1.5–8.5 cm, base obtuse to slightly cordate, apex obtuse to cuspidate; upper side greyish green to light brownish, midrib and nerves sunken, venation obscure; lower side concolorous, rather densely patently pubescent, secondary nerves 5–8 pairs, forming a distinct intramarginal nerve; glands 2–8, up to 0.1 mm diam. *Inflorescences* unbranched or basally with a pair of side axes, shorter than to as long as the leaves; axes strongly flattened and ribbed at base, densely rather shortly hairy, mixed with longer patent hairs; bracts and bracteoles small, relatively long-persistent. *Pedicel* 2.5–5.5 mm long, ribbed, minutely densely patently hairy. *Sepals:* outer sepals 2.4–3.0 x 2.1–3.1 mm; inner sepals 3.4–3.8 × 2.9–3.5 mm. *Petals* purplish, when dry brownish orange, the longest one 7.5–10 mm long; carina minutely hairy outside, inside minutely appressedly hairy in apical and basal part; other petals minutely patently hairy in apical part outside, upper petals inside glabrous to rather densely patently hairy. *Stamens:* filaments free or 1 mm connate, exserted from the carina in open flowers; anthers c. 0.5–0.7 mm long. *Ovary* more or less patently pubescent; ovules 4. *Fruit* (immature) shortly beaked or apically rounded, verrucately ribbed.

Distribution. Malaya: Pahang (4 coll.), Johore (3).

Note. Differing from the other species of the *eurhynchum*-group in the indumentum of the vegetative parts, and in the axillary buds.

1b-2. Subsection Eystathes

Twigs and inflorescence axes sometimes with minute nodal appendages. Axillary buds (2 or) 3–5(–7), often all distant and supra-axillary. *Seed(s)* 1(–4); testa without a hard inner layer; albumen very thin; embryo without flattened areas near the base, radicle not exserted.

Species: 14 (64–77).

64. Xanthophyllum novoguinense Meijden, *spec. nov.*

Gemmae axillares ut videtur singulae, patentes, usque ad 1.6 mm longae. Lamina subtus papillosa; glandulae sat numerosae. Inflorescentia in parte basali ramosa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo c. 7 mm longo; carina extus lanata. Antherae 0.35–0.4 mm longae. Ovarium appresse pilosum; stylus pilosus; ovula 4. Fructus ignotus.

Typus: *Ledermann 9629* (L).

Tree up to 30 m high, 40 cm d.b.h. Axillary buds 0.8–1.6 mm long, faintly keeled. *Petiole* 6–10 mm long. *Leaf blade* 4–13.5 × 1.3–6.5 cm; upper side green; lower side light green, papillose, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve or not; glands rather numerous, scattered, c. 0.2–0.4 mm diam., basal glands c. 0.6–1.5 mm diam. *Inflorescences* up to c. 8 cm long; axes light brownish, slender, rather thinly minutely hairy; in basal part flowers with 3 together. *Pedicel* 2.5 mm long, grooved, rather densely minutely more or less patently hairy. *Sepals:* outer sepals 2.4 × 2.1 mm; inner sepals 2.9 × 2.5 mm. *Petals* yellowish orange when dry, the longest one c. 7 mm long; carina woolly hairy outside in apical half; other petals outside with a few hairs at apex and at base. *Stamens:* anthers 0.35–0.4 mm long. *Ovary* appressedly hairy; ovules 4. *Fruit* unknown.

Distribution. New Guinea: W. Irian Jaya (Sorong, Warsamson: *BW 5702, 11619, 12454*), Papua New Guinea (Sepik: *Ledermann 9629*).

Notes. 1. Insufficiently known: only a single flowering collection is known. It remains to be confirmed that the characters of the seed fit those of subsect. *Eystathes* indeed. The flowering collection resembles *65. X. ngii*, differing only in the length of the petals.

2. Part of the flowers of the type collection have abnormally developed ovules; these vary in number from 1–3 and they are placed basally in the ovary and have a distinct funiculus. The majority of the ovaries, however, contained 4 laterally inserted, sessile ovules.

65. Xanthophyllum ngii

Fig. 3B-a

X. ngii Meijden, Bot. J. Linn. Soc. 67 (1973) 119; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 365, fig. 5 ('*spec. C*'). – Type: *Dorst 65E.2P.655*, 10-xii-1920 (L, sheet 922.258-213; iso BO, L, W).

Tree up to 35 m high, diam. at 5 m 65 cm. Nodal appendages extremely small, present on very short straight ridges adjoining the insertion of the petiole. Axillary buds 0.5–1(–1.5) mm long, blackish, rather densely hairy. *Petiole* 7.5–10 mm long. *Leaf blade* 6–17 × 1.7–6.5 cm, base rounded to narrowly cuneate, margin slightly undulate, apex acutish to shortly acuminate; upper side yellowish green or brownish, midrib nearly flat to slightly protruding, sometimes at very base a little sunken; lower side glaucous-papillose, secondary nerves 5–8 pairs; glands 6–12, situated halfway between midrib and margin or near midrib, 0.3–0.5 mm diam., the basal ones mostly larger. *Inflorescences* about as long as the leaves; axes flattened at base, blackish, rather densely shortly hairy; lower bracts (sub)opposite. *Pedicel* 3–4.5 mm long, very densely more or less appressedly shortly hairy. *Sepals* shortly rather sparsely appressedly hairy outside, (sub)glabrous inside; outer sepals 2.2–2.9 × 2.0–2.8 mm; inner sepals 3.1–3.6 × 2.5–3.2 mm. *Petals* brownish orange when dry, the longest one 10–12.5 mm long; carina shortly appressedly hairy outside along median veins, further glabrous outside; other petals sparsely hairy at apex, further glabrous

outside. *Stamens:* anthers 0.3–0.4 mm long, sparsely hairy at base. *Ovary* subsessile, shortly appressedly hairy; style sparsely appressedly hairy at very base only, further glabrous; ovules 4. *Fruit* more or less apple-shaped, up to 8 cm diam., the very short pedicel enveloped by the pericarp; pericarp very hard, in mature fruit up to 3 cm thick when dry. *Seed* 1 (or '1–more' according to Ng, *l.c.*), up to 2 cm diam.

Distribution. Malaya: E. Trengganu (2 coll.), Central Pahang (2), Negri Sembilan (1). – Sumatera (Jambi, Inderagiri, Palembang: 7).

Notes. 1. Ng (1972) described it ('*spec. C*') as having '1–more' seeds; I only saw one-seeded fruits.

2. In flower resembling *64. X. novoguinense* (see there), and *67. X. lanceatum*, but differing from the latter in the large fruits, the petiole, the number of secondary nerves, and in the length of the petals.

66. Xanthophyllum sylvestre

Fig. 3A–o

X. sylvestre (Lour.) S. Moore, Hook. J. Bot. 63 (1925) 255; Merr., Comm. Lour. (1935) 229. – *Eystathes sylvestris* Lour., Fl. Coch. 1 (1790) 235; Fl. Coch. 1, ed. Willd. (1793) 289; J.E. Smith in Rees, Cycl. 14 (1819) eyn–eys; Steudel, Nom. Bot. ed. 1 (1821) 331; DC. Prod. 1 (1824) 618; Sprengel, Syst. Veg. 2 (1825) 219 ('*Eustathes*'); Gen. Pl. 1 (1830) 311 (*sub Melicocca* L.); G. Don, Gen. Hist. Dichl. Pl. 1 (1831) 675; Meijden, Taxon 20 (1971) 647. – *Valentinia sylvestris* (Lour.) Raeuschel, Nom. Bot. ed. 3 (1797) 109. – Lectotype: *Loureiro s.n.* (BM).

X. pomiferum Boerl. & Valeton *ex* Boerl., Cat. Hort. Bog. (1899) 59; Boerl. & Valeton, Icon. Bog. I, 4 (1901) 7, t. 78: Bold., Cat. Hort. Bog. Cult. (1914) 84; Heyne, Nutt. Pl. 2 (1950) 1505. – Lectotype: *Anonymus, cult. in Hort. Bog. I.K.37* (BO, sheet B 83174; iso BO, K, L).

X. laoticum Gagnepain [in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 220, fig. 13–19, *nom. inval.*] Not. Syst. 9 (1941) 141. – Lectotype: *Poilane 20745* (P).

Tree up to 30 m high, 50 cm d.b.h. Nodal appendages relatively distinct, up to 0.2(–0.3) mm long. Axillary buds 2 or 3, up to 1.5(–3) mm long, keeled, sometimes wrinkled at base, glabrous or apically hairy. *Petiole* 4–7 mm long, not or indistinctly transversely wrinkled. *Leaf blade* 5–15 × 2.3–5.5 cm, base truncate to narrowly cuneate, margin slightly undulate, apex acutish to acuminate; upper side yellowish to brownish green, midrib in basal half with a central groove; lower side concolorous, secondary nerves 6–9 (or 10) pairs, not forming an intramarginal nerve; glands few to numerous, 0.2–0.4 mm diam., the basal ones often elongate, up to 0.8 mm long. *Inflorescences* as long as to mostly much longer than the leaves; axes mostly flattened at base, more or less densely patently shortly hairy. *Pedicel* 2–5 mm long, very densely patently shortly hairy. *Sepals:* outer sepals c. 2 × 1.8–2.4 mm; inner sepals c. 2.4 × 2.4 mm. *Petals* white, the upper ones with a yellow spot, when dry yellowish, the longest one 5–7.5 mm long, appressedly to patently hairy outside, densely hairy inside apically; other petals sparsely hairy at apex, (sub)glabrous outside or rather densely hairy on median veins. *Stamens:* filaments sparsely hairy to nearly glabrous; anthers 0.2–0.3(–0.4) mm long, glabrous to hairy at base. *Ovary* appressedly hairy; style sparsely hairy; ovules 4. *Fruit* globular or (said to be) apple-shaped, up to 7 cm diam., brownish, rather shiny, wrinkled when dry; pericarp up to 5 mm thick, soft. *Seed(s)* 1(–4), up to 2.5 cm long.

Distribution. Laos: Luang Prabang (3 coll.). – Vietnam: Nghe An (1), Quang Tri (4);

locality uncertain: *Poilane 30068*. – Thailand: Kanchanaburi (1), Pattani (1). – Cambodia: Sre Umbell (1).

Notes. 1. Resembling *67. X. lanceatum*, differing in the leaves, anthers, and fruits.

2. The reduction of *X. pomiferum* Boerl. to this species might be wrong. That species has been described (as having 6 stamens, which is a mistake for 8) from a tree in the Hortus Bogoriensis, said to have been collected originally by Lobb in 'Borneo'. In the richly flowering type material I counted exclusively (5 or) 6 ovules per ovary, never 4. That is a unique character in sect. *Eystathes*; all other specimens I examined had either 4, or 8–more ovules per ovary. Combined with the circumstance that it may have originated from Borneo (although Lobb's labels are often uncertain; see Fl. Males. I, 1, 1950, 325), *X. pomiferum* may represent a species different from *X. sylvestre*. Unfortunately, the tree in the Hortus Bogoriensis is lost now. I have not included the characteristics of the collections of *X. pomiferum* in the description of *X. sylvestre*.

67. Xanthophyllum lanceatum

Fig. 10A

X. lanceatum (Miq.) J.J. Smith, Ic. Bogor. 4 (1912) 109, t. 334; Gorter, Indische Mercuur 34 (1911) 410 (*'lanceolatum'*); Tropenpfl. 16 (1912) 50; Hegi, Fl. Mitteleur. 5-1 (1925) 87 (*'lanceolatum'*); Heyne, Nutt. Pl. (1927) 901; Burkill, Dict. (1935) 2268. – *Skaphium lanceatum* Miq., Fl. Ind. Bat., Suppl. (1861) 357; Kurz, J. As. Soc. Beng. II, 40 (1871) 46; Scheffer, Nat. Tijd. Ned. Ind. 34 (1874) 105. – Type: *Teysmann HB 3752* (BO; iso U).

X. glaucum Wallich *ex* Hassk., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 193; Wallich, Cat. (1831) 4199; Kurz, J. As. Soc. Beng. II, 42 (1873) 80; A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209; Kurz, For. Fl. Br. Burma 1 (1877) 81; King, Mat. Fl. Mal. Pen. (1890) 136; Gage, Rec. Bot. Surv. India 3 (1904) 24; Williams, Bull. Herb. Boiss. sér. 2, 5 (1905) 219; Brandis, Indian Trees (1906) 44; Gagnepain, Desv. J. Bot. 21 (1908) 251; Fl. Gén. I.-C. 1 (1909) 245; Ridley, J. Str. Br. R. As. Soc. 59 (1911) 73; *op. cit.* 73 (1916) 140; Fl. Mal. Pen. 1 (1922) 147; Watson, Mal. For. Rec. 5 (1928) 249; Crevost & Pételot, Bull. Econ. Indochine (1929) 138; Craib, Fl. Siam. Enum. (1931) 105; Burkill, Dict. (1935) 2268; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 219; Henderson, J. Mal. Br. R. As. Soc. 17 (1939) 36; Stadelman, For. Southeast Asia (1966) 186; Ng in Whitmore, Tree Fl. Mal. 1 (1973) 357, fig. 1. – *Banisterodes glaucum* (Wallich *ex* Hassk.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Type: *Wallich 4199* (K; iso E, G, P, W).

X. microcarpum Chodat, Bull. Herb. Boiss. 4 (1896) 263. – Type: unknown (see note 2).

Low shrub or small tree 3–12 m high, 18–20 cm d.b.h. Twigs often sparsely appressedly hairy when young, soon glabrescent. Nodal appendages bluntly conical to triangular, up to 0.2 mm long but often smaller. Axillary buds 2–3, up to 2 mm long, sessile or the upper very shortly stipitate, acutish, often distinctly keeled, more or less densely shortly hairy. *Petiole* 3–5 mm long, more or less indistinctly transversely wrinkled, brownish, often sparsely thinly hairy when young, glabrescent. *Leaf blade* 5–14 × 1.4–4.0(–5.5) cm long, margin more or less distinctly undulate, often a little incurved, apex acutish, rarely shortly acuminate; upper side yellowish green to brown, midrib flat to slightly protruding in apical half, in basal half with a central groove; lower side light yellowish or brownish, papillose, midrib glabrous or sometimes sparsely appressedly hairy, secondary nerves mostly hardly distinct from finer veins, c. 8–14 pairs, not forming an intramarginal nerve; glands mostly numerous, 0.2–0.3 mm diam., but sometimes larger (up to 0.8 mm) and then of irregular form. *Inflorescences* mostly longer to much longer than the leaves, basally branched but

sometimes seemingly unbranched if lower bracts resemble normal leaves; axes mostly distinctly flattened basally, rust-brown, more or less densely patently shortly hairy; in basal part flowers with 3–5 together, solitary in apical part. *Pedicel* 2.0–3.5 mm long, more or less densely patently shortly hairy. *Sepals:* outer sepals 1.7–2.2 × 1.5–2.0 mm; inner sepals 2.2–2.7 × 2.0–2.9 mm. *Petals* pinkish or white, the upper ones often with a yellow spot, when dry yellowish, the longest one 6–9 mm long; carina rather densely (woolly-) hairy outside; other petals hairy at very apex. *Stamens* 8, rarely in some flowers 9; anthers 0.3–0.5 mm long. *Ovary* appressedly hairy; ovules 4. *Fruit* broadly ellipsoid to globular, 1.2–3.5 cm diam., mostly greyish brown; pericarp often wrinkled when dry, rather thick, soft. *Seed(s)* 1 or 2.

Distribution. ?Banghla Desh ('Jhar': *Griffith 258*). – Burma (widely scattered: 17 coll.). – Thailand (widely scattered: 27). – Laos (10). – S. Vietnam (9). – Cambodia (11). – Malaya: Perlis (1), Langkawi Is. (1), Kedah (Port Wellesley: 1), N. Kelantan (2), Central and E. Pahang (4), Johore (1). – Sumatera (vicinity of Palembang: 4).

Notes. 1. A common species from stream-banks, with the largest distributional area within this subsection, and little variation in its characters except in the size of the ripe fruit.

2. Chodat cited material of *X. microcarpum* to be in Kew and Genève; I have not seen collections which were suitable to be selected as a lectotype. The typification of *X. microcarpum* is unimportant because it is absolutely certain that it is conspecific with '*X. glaucum*'.

68. Xanthophyllum hainanense

X. hainanense Hu, J. Arn. Arb. 6 (1925) 142; Chun, Sunyatsenia 1 (1934) 258, fig. 3; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 218; Masam., Fl. Hain. (1943) 152 ('*Zanthophyllum*'); Chun *c.s.*, Fl. Hain. 1 (1964) 369; Anonymus, Icon. Corm. Sinic. 2 (1972) 575, 1151, fig. 2880. – Lectotype: *McClure 9421* (E; iso BM, C, G, K, P).

X. racemosum Groff, Lignaam, Agric. Rev. 2-1 (1924) 26 (*n.v.*), *nomen*; Merr., J. Arn. Arb. 6 (1925) 133, 134, according to Merrill based on *McClure 9440* (syntype of *X. hainanense* Hu).

Shrub to tree, up to 18 m high, up to 21 cm d.b.h. Twigs reticulately wrinkled or smooth. Axillary buds 2 (or 3), 0.5–1(–1.5) mm long. *Petiole* 7–10 mm long. *Leaf blade* (3–)5–10(–13) × 2.2–4(–5.5) cm, margin undulate, apex shortly acuminate to cuspidate; upper side green to reddish brown, midrib protruding or rarely flat; lower side usually thinly glaucous (but not papillose), secondary nerves 4 or 5 pairs, not forming an intramarginal nerve; glands 2–4(–10), often present only near the base, 0.4–0.6(–0.8) mm diam. *Inflorescences* unbranched, shorter than to as long as the leaves; axes terete, shortly more or less patently hairy. *Pedicel* 3–4.5 mm long, rather densely more or less appressedly hairy. *Sepals* sometimes with small, scattered glandular spots; outer sepals 1.8–2.1 × 1.3–1.6 mm; inner sepals 2.8–3.3 × 1.8–2.3 mm. *Petals* white, when dry yellowish, the longest one 10–12 mm long; carina half-patently hairy outside, slightly hairy inside at apex; other petals densely hairy at apex. *Stamens:* filaments half-patently hairy to near the apex; anthers 0.4–0.6 mm long. *Ovary* very densely whitish appressedly hairy; ovules 4. *Fruit* globular, 0.8–c. 1.5 cm diam., shiny, brown; pericarp thin; pedicel up to 6(–11) mm long.

Distribution. SE. China: Guangxi (southeast of Shangsi, 'Shang-sze': *Tsang 22134, 22652*); Hainan (8 coll.).

Note. I clearly made a mistake (1973) in attributing 'var. *occidentale*' (= *69. X. punctatum*) to this species; the differences are found in the axillary buds, the leaves, the petals, and in the anthers.

69. Xanthophyllum punctatum Meijden, *spec. nov.*

X. hainanense var. *occidentale* Meijden, Bot. J. Linn. Soc. 67 (1973) 118. – Type: *Dickason 9142* (L; E).

Gemmae axillares 2–4, gemma superiore supra-axillari per 3–6(–9) mm. Lamina basi cuneata usque ad attenuata, subtus papillosa; glandulae numerosae. Inflorescentia plerumque ramosa, bracteis basalibus oppositis vel alternatis. Petala inaequalia, petalo longissimo (11–)13–16 mm longo; carina extus dense lanata, petalis ceteris intus patenter pilosis. Antherae (0.6–)0.7–0.8(–1.0) mm longae. Ovarium dense pilis patentibus vel raro appressis indutum; stylus pilosus; ovula 4. Fructus globosus, c. 1.6 cm diam.; pericarpium sat tenue. Semen 1. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *Parkinson 5016* (K; iso BM).

Shrub or small tree up to 10 m high. Twigs glabrous to shortly patently hairy. Axillary buds 2–4, mostly distant, 0.8–1.5(–2.5) mm long, rounded or acutish, mostly minutely hairy, the upper one 3–6(–9) mm supra-axillary but sometimes all buds close together. *Petiole* 5–11(–15) mm long, sometimes with glands. *Leaf blade* (4.5–)6–19 × (2–)3–6 cm; upper side green to greyish green, midrib sunken to slightly protruding; lower side glaucous-papillose, secondary nerves 6–11 pairs, usually forming an indistinct intramarginal nerve; glands either numerous, scattered and 0.1–0.2 mm diam., or rather few and mostly close to midrib and then c. 0.4 mm diam. *Inflorescences* mostly branched, usually shorter than the leaves; axes densely patently shortly hairy; in basal part flowers usually in clusters; lower bracts opposite or alternate; upper axillary buds forming a new inflorescence during a number of growth periods. *Pedicel* (3.5–)5–9(–11) mm long, densely patently (rarely appressedly) shortly hairy. *Sepals* often with tiny glandular spots, which in dry material sometimes contain a white excretion; outer sepals (2.0–)2.6–3.8(–4.2) × 2.0–2.7(–3.6) mm; inner sepals 3.7–5.2(–6.2) × (2.5–)3.0–4.2 mm. *Petals* white to pale pink, when dry yellowish orange, the longest one (11–)13–16 mm long; carina rather densely woolly or rarely (*Pételot 3271*) sparsely appressedly hairy outside, inside hairy at base and apex; other petals hairy at base and apex outside, the upper ones patently hairy inside to near apex or rarely (*Pételot 3271*) hairy only at very base; upper petals sometimes laterally auriculate on one side. *Stamens:* filaments free or up to 0.5 mm connate; anthers (0.6–)0.7–0.8(–1.0) mm long, sometimes ciliate along slits. *Ovary* patently to appressedly hairy; ovules 4. *Fruit* globular, c. 1.6 cm diam., dull greyish brown; pericarp rather thin.

Distribution. Burma (widely scattered: 8 coll.). – Thailand: North (2), South (2). – Vietnam: North (Ha Coi: 2), Central (Hué: 2).

Notes. 1. The delimitation of the species as presented here does not satisfy me, especially regarding the inclusion of *Pételot 3271*, which has different axillary buds and small differences in the flowers. This specimen has not been used for the Latin diagnosis.

2. The epitheton refers to the minute white spots which are visible on the sepals in dried state (a character shared with *70. X. cucullatum*), caused by excretions from the glands on the sepals. The gritty substance is not soluble in water, ethanol, nor in hydrochloric acid. In no other *Xanthophyllum* species I found any indication that the so-called glands indeed produce a secretion.

70. Xanthophyllum cucullatum Meijden, *spec. nov.*

Gemmae axillares (4 vel) 5, gemma superiore supra-axillari per 2.5–3.5 mm. Lamina basi cordata, subtus papillosa; glandulae numerosae. Inflorescentia basi ramosa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo 11.5–12 mm longo; carina extus dense patenter pilosa, petalis ceteris intus dense pilosis. Stamina triadelphia. Antherae 0.75–0.8 mm longae. Ovarium dense semi-patenter pilosum; stylus pilosus; ovula 4, raro 3. Fructus ignotus.

Typus: *Kermode 16774* (K).

Shrub, 1.8 m high. Twigs shortly patently hairy. Axillary buds (4 or) 5, c. 1 mm long, rounded, densely patently brownish hairy, the upper one 2.5–3.5 mm supra-axillary. *Petiole* 9–11.5 mm long, indistinctly transversely wrinkled, shortly patently hairy. *Leaf blade* 9.5–13 × 3.5–4.5 cm, base cordate, apex obtuse; upper side yellowish green, midrib sunken in basal part; lower side glaucous-papillose, shortly hairy, secondary nerves c. 7–10 pairs, forming an incomplete intramarginal nerve; glands numerous, scattered, but mainly near midrib, 0.1–0.2 mm diam., the basal ones larger. *Inflorescences* branched at base, shorter than the leaves; axes slightly flattened, finely grooved, densely shortly patently rufously hairy; in basal part flowers with 3 together. *Pedicel* 5.5 mm long, grooved, shortly densely patently rufously hairy. *Sepals* with brownish hairs, with tiny glands; outer sepals 2.1–2.6 × 2.4 mm, the glands often containing whitish excretions; inner sepals 4.2–4.3 × 3.0–3.3 mm. *Petals* cucullate at apex, white, tinged with purple, when dry orange, the longest one 11.5–12 mm long; carina densely patently hairy outside especially in apical half, patently hairy inside in apical part and at base; other petals slightly hairy apically, at base shortly hairy out- and inside, the upper ones patently hairy inside to near apex. *Stamens* triadelphous: only filaments of lateral and upper stamens connate for c. 0.5 mm; anthers 0.75–0.8 mm. *Ovary* half-patently brownish hairy; ovules (3 or) 4. *Fruit* unknown.

Distribution. Burma: Kyaikkami ('Amherst') (Misty Hollow, Dawnas: *Kermode 16774*).

Note. Resembling *69. X. punctatum*, sharing the white-spotted sepals (see under *X. punctatum*) and the hairy inside of the petals. The differences are in the axillary buds, the base of the leaf blade, the cucullate petals, and the triadelphous stamens.

71. Xanthophyllum geminatum Meijden, *spec. nov.*

Gemmae axillares 4 vel 5, gemma superiore supra-axillari per 10–15 mm. Lamina subtus papillosa; glandulae numerosae. Inflorescentia valde ramosa, ramulis plerumque 2 in eadem axilla. Petala inaequalia, petalo longissimo c. 7 mm longo; carina ambae in parte apiculati breviter patenter pilosa; petala superiora intus ad apicem pilosa. Antherae 0.6 mm longae. Ovarium glabrum vel in parte dimidia superiore sparse pilosum; stylus dense pilosum; ovula 4. Fructus ignotus.

Typus: *Dussaud 104* (P; iso L).

Tree up to 20 m high. Nodal appendages minute, indistinct. Axillary buds 4 or 5, distant, 1.5–2 mm long, the upper one 10–15 mm supra-axillary. *Petiole* 5–6 mm long. *Leaf blade* 8–14 × 2.5–4.5 cm; upper side brownish green; lower side glaucous-papillose, secondary nerves at least 7 pairs (hardly distinguishable in apical region), forming an irregular intramarginal nerve in apical part; glands numerous, scattered, c. 0.1 mm diam. *Inflorescences* also in lower leaf axils, often with 2 together, c. 6–11 cm long, much branched, the branches usually 2 in the axil of the bracts; axes basally usually flattened, rather sparsely minutely hairy, at the nodes with 0.1–0.2 mm long appendages; lower bracts (sub)opposite. *Pedicel* c. 6 mm long, minutely hairy. *Sepals* sparsely minutely hairy outside, (sub)glabrous inside; outer sepals 1.9 × 1.6 mm; inner sepals 3.0 × 2.3 mm. *Petals* white, when dry yellowish orange, the longest one c. 7 mm long; carina shortly patently hairy in apical part out- and inside; lateral petals glabrous outside, inside glabrous in apical half; upper petals glabrous outside, patently hairy inside to apex. *Stamens:* anthers 0.6 mm long. *Ovary* subsessile, glabrous, or sparsely appressedly hairy in apical half; style rather densely appressedly hairy; ovules 4. *Fruit* unknown.

Distribution. Laos (between Vientiane and Luang Prabang: 1 coll.; Xieng Khouang: 2). – Identity doubtful: Thailand (Chieng Mai, Doi Sutep: *Fl. Thailand 6835*).

Note. Insufficiently known; characterized by the indumentum of the gynoecium, the ovary being glabrous at least in basal part, the style being hairy. In the hairy upper petals similar to *69. X. punctatum*, but differing in the much smaller size of all petals. See also under *76. X. andamanicum*.

72. Xanthophyllum bibracteatum

X. bibracteatum Gagnepain, Desv. J. Bot. 21 (1908) 252; Bull. Soc. Bot. France 56 (1909) 35; Fl. Gén. I.-C. 1 (1909) 256; Crevost & Pételot, Bull. Econ. Indochine (1929) 138; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 222. – Lectotype: *Bon 4295* (P; iso K).

Small tree up to 6 m high. Axillary buds 2 or 3, c. 1(–1.5) mm long, minutely appressedly hairy, glabrescent, the upper one sometimes slightly supra-axillary. *Petiole* 5–9 mm long, apically often with 2 rather distinct glands. *Leaf blade* 7–17 × 2–7.5 cm, base rarely rounded-cordate, apex acutish; upper side green to yellowish brown, midrib slightly sunken to slightly protruding; lower side glaucous-papillose, secondary nerves 6–8 pairs, forming an indistinct intramarginal nerve; glands very numerous, scattered, 0.1–0.2 mm diam., basal glands present at very base or at apex of petiole, c. 0.5 mm diam. *Inflorescences* also in lower leaf axils, short and dense, 1.5–4 cm long; axes densely appressedly shortly hairy; at least in basal half flowers with 3 together. *Pedicel* c. 4 mm long, rather densely appressedly shortly hairy. *Sepals* sometimes with tiny glandular spots; outer sepals 2.7–3.4 × 2.1–2.6 mm; inner sepals 4.0–4.5 × 3.1–4.4 mm. *Petals* pale yellow, when dry orange-brown, the longest one 12–15 mm long; carina shortly densely appressedly hairy outside, inside appressedly hairy only in basal half; other petals in basal part shortly hairy out- and inside, further glabrous. *Stamens:* filaments free or connate over up to 1.5 mm: anthers 1.1–1.2 mm long, ciliolate along the slits. *Ovary* appressedly whitish hairy; stigma bilobed, larger than the apex of the style; ovules 8 or 9. *Fruit* globular, up to c. 2.2 cm diam., brownish, slightly shiny; pericarp thin; pedicel up to 6 mm long.

Distribution. N. Vietnam: Ninh Thai (5 coll.), Bac Kan (1), Hoa Binh (1), Santong (1), Nghe An (1).

Notes. 1. *X. bibracteatum* and *73. X. burkillii* are very much alike, and probably closely related. Both have 8 or 9 ovules, and a thickened stigma. It is hardly imaginable that the thickened stigma would represent the plesiomorphous character-state in the subsection, or that it represents a parallel development as the species resemble each other so closely; thus it probably is a synapomorphous condition. If the relatively high number of ovules would be the plesiomorphous condition in the subsection, the character-state 'ovules 4' must be a synapomorphous condition. However, the differences between the species with 4 ovules are considerable whereas *X. bibracteatum* and *X. burkillii* have many characters in common. It is thus more likely to assume that the relatively high number of ovules also represents a synapomorphous condition in both species.

2. Differing from *73. X. burkillii* in the flowers.

73. Xanthophyllum burkillii

X. burkillii J.R. Drumm. & Dunn, Kew Bull. (1920) 245; Burkill, Rec. Bot. Surv. India 10 (1925) 239; Calder *c.s., op. cit.* 11 (1926) 156. – Lectotype: *Burkill 36767* (K).

Tree. Axillary buds 3, seemingly 2, c. 1 mm long, keeled, the upper one 1(–2.5) mm supra-axillary, adventitious buds sometimes present on older nodes. *Petiole* 5–7 mm long. *Leaf blade* (4–)5–11 × 2.5–4 cm, apex acutish; upper side dull, dark green, midrib slightly protruding to nearly flat at base; lower side glaucous-papillose, secondary nerves 5 or 6 pairs, in upper part forming an indistinct intramarginal nerve; glands rather numerous, scattered, c. 0.2 mm diam., basal glands sometimes present. *Inflorescences* sometimes also present on older nodes, unbranched, 3–5.5 cm long; axes rather sparsely minutely appressedly hairy; bracts and bracteoles relatively long-persistent. *Pedicel* 6–7 mm long, rather sparsely minutely appressedly hairy. *Sepals:* outer sepals c. 4.6 × 3.9–4.3 mm; inner sepals 6.3–6.5 × 4.9–5.1 mm. *Petals* orange-brown when dry, the longest one 15–16 mm long; carina shortly appressedly hairy outside and inside; other petals minutely appressedly hairy outside especially at base and apex, inside minutely hairy at apex, shortly hairy in basal part. *Stamens:* anthers 0.8–0.9 mm long, ciliolate along the slits. *Ovary* whitish appressedly hairy; style very densely appressedly hairy, sparsely so in apical half; stigma bilobed, somewhat larger than the apex of the style; ovules 9. *Fruit* unknown.

Distribution. E. India: Outer Abor hills (Pasighat: *Burkill 36767, 36864*).

Note. Insufficiently known. See further under *72. X. bibracteatum.*

74. Xanthophyllum lateriflorum

X. lateriflorum Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 318. – Type: *Teysmann HB 3899* (U; iso BO, L).

Shrub or small tree, 5–6 m high. Axillary buds (2 or) 3(–5), distant, the upper one 3–5 (–15) mm supra-axillary, usually shortly stipitate (stalk up to 3 mm long), more or less oblong, c. 1–2 mm long (excl. stalk), more or less acute. *Petiole* 3.5–4.5(–6) mm long. *Leaf blade* 4–8 × 1.5–3.5 cm, apex acuminate to cuspidate; upper side dark green; lower side glaucous-papillose, secondary nerves c. (5–)7 or 8 pairs, not forming an intramarginal nerve; glands c. 6–8(–10), usually near midrib, 0.1–0.3 mm diam., basal ones somewhat larger. *Flowers* unknown. *Infructescences* shorter than the leaves, unbranched; axes minutely hairy. *Fruit* (immature) globular, sessile, rather sparsely minutely appressedly hairy; pedicel 3–3.5 mm long, minutely appressedly hairy. *Seed* (immature) 1; abortive ovules 3.

Distribution. Sumatera (vicinity of Palembang: 4 coll.; Lampong: 1).

Note. Insufficiently known. Probably related to *75. X. virens*, differing in the axillary buds, the shorter petiole, and the smaller leaf blade.

75. Xanthophyllum virens

Fig. 10A, and front cover

X. virens Roxb., Pl. Corom. 3 (1820) 81, t. 284, fig. 1; Sprengel, Syst. Veg. 2 (1825) 219 ('*virescens*'); Wallich, Cat. (1831) 4197; Roxb., Fl. Ind. ed. Carey 2 (1832) 221; Dietr., Syn. Pl. 2 (1840) 1277 ('*virescens*'); Wight, Ill. Ind. Bot. 1 (1840) 49, 50, t. 23, fig. 10 (*sub X. flavescens, sphalm.*); Drury, Handb. Indian Fl. 1 (1864) 56; Beddome, Fl. Sylv. Anal. Gen. 3 (1869) xix, pl. III, fig. 2, 1–3; Kurz, J. As. Soc. Beng. II, 42 (1873) 79, 80; Prelim. Rep. For. Pegu (1875) 26; For. Fl. Br. Burma 1 (1877) 81; Gagnepain, Desv. J. Bot. 21 (1908) 251; Craib, Fl. Siam. Enum. (1931) 107; Gagnepain in Humbert, Suppl. Fl. Gén. I.-C. 1 (1939) 219; Purkayastha in Chowdhury & Ghosh, Indian Woods 1 (1958) 60. – *X. flavescens* var. *virens* (Roxb.) A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 209; Craib, Bull. Misc. Inf. Kew (1911) 14. – Lectotype: *Roxburgh s.n.*, 1812 (BM).

X. affine auct., non Miq.: Ridley, J. Fed. Mal. St. Mus. 10 (1920) 82.

Tree up to 30 m high, 1 m d.b.h. Nodal appendages c. 0.1 mm long. Axillary buds 3–7, 0.5–1.6 mm long, the upper one (2–)3–10(–20) mm supra-axillary. *Petiole* (5–)6–12 mm long, often in apical part with small, usually not protruding glands. *Leaf blade* (6.5–) 10–23 × 2.5–7.5 cm, margin slightly undulate, often somewhat irregular, apex acutish; upper side dark or greyish green, midrib protruding to flat, in basal part with a central groove; lower side usually brownish to yellowish green, smooth to papillose, secondary nerves 7–10 pairs, forming an indistinct intramarginal nerve; glands either 0–3 (or 4) and often of an irregular form, or numerous and 0.1–0.2 mm diam., the basal glands larger. *Inflorescences* usually 2 per leaf axil, 5–20 mm supra-axillary, as long as or longer than the leaves, much branched, the basal branches with 1–3 together; axes flattened basally, sparsely minutely hairy at the nodes with minute appendages; flowers with 1–7 together; lower bracts opposite. *Pedicel* 2.5–5.5 mm long, minutely patently to appressedly hairy, sometimes subglabrous. *Sepals:* outer sepals 1.4–2.2 × 1.0–1.9 mm: inner sepals (1.9–)2.3–3.3 × 1.6–3.5 mm. *Petals* white or pinkish, the upper ones with a yellow spot, when dry yellowish orange, the longest one 6.5–11 mm long; carina sparsely to densely appressedly hairy outside, inside sparsely hairy in apical part; other petals glabrous or sparsely hairy at apex. *Stamens:* anthers 0.3–0.5 mm long. *Ovary* appressedly hairy (except *Poilane 20720* which is patently hairy); style rarely (*Watson 264*) only basally hairy; ovules 4. *Fruit* unknown.

Distribution. Banghla Desh (Sylhet: 2 coll.; Chittagong hill tracts, c. 70 mile north of Rangamati: 1). – Burma (Taung-gyi: 1; Pyinmana: 1; Pegu: 1). – Thailand: North (10), Central (near M. Uthai Thani: 1), South (around Isthmus of Kra: 5). – Identity doubtful: Malaya: Kelantan (1), Perak (7).

Notes. 1. In this circumscription *X. virens* is one of the few species in which the lower surface of the leaf blade varies from smooth to papillose.

2. The collections from Malaya are all sterile; they may not belong to this species.

3. Similar to *69. X. punctatum*, differing in the key characters, as well as ecologically: *X. punctatum* is a montane species, whereas *X. virens* grows at low altitudes in the monsoon-forests.

4. See also under *68. X. hainanense*.

5. In some collections all flowers examined had only 7 stamens; instead of two carinal stamens, only a single one is present in those plants.

76. Xanthophyllum andamanicum

X. andamanicum King, J. As. Soc. Beng. II, 59 (1890) 135; Ann. R. Bot. Gard. Calc. 5 (1896) 136, pl. 160; Chodat in E. & P., Nat. Pfl. Fam. III, 4 (1896) 345; Brandis, Indian Trees (1906) 44; Hundley & Ko, List Trees Burma ed. 3 (1961) 18. – Lectotype: *King's Coll. s.n.* (L; iso FI, G).

Tree 30–35 m high, c. 1 m d.b.h. Nodal appendages up to 0.1 mm long, usually very indistinct. Axillary buds 4 (or 5), c. 1 mm long, distant, the upper one 5–10(–12) mm supra-axillary. *Petiole* 7–10 mm long. *Leaf blade* (5–)6–13 × 2.5–5 cm, margin more or less undulate, apex acutish; upper side brownish to greenish, midrib sometimes grooved; lower side glaucous-papillose, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve; glands usually numerous, scattered, c. 0.1 mm diam. *Inflorescences* sometimes also in lower leaf axils, c. 4–6 cm long; axes flattened, sparsely minutely hairy, at the nodes with minute appendages; lower bracts (sub)opposite. *Pedicel* c. 5 mm long, minutely appressedly hairy. *Sepals* (sub)glabrous outside, inside only basally hairy; outer sepals 2.3–2.6 × 1.6–1.8 mm; inner sepals 3.0–3.3 × 2.2–2.7 mm. *Petals* white, the upper ones with a yellow spot, when dry yellowish, the longest one 12 mm long; carina outside densely hairy only near apex, glabrous inside; other petals outside with a few hairs at apex and base. *Stamens:* anthers 0.6–0.8 mm long, with very few hairs at base. *Ovary* subsessile, glabrous; style nearly glabrous or sparsely hairy to halfway; ovules 4. *Fruit* (immature) globular, smooth; pericarp rather thin.

Distribution. Andaman Is.: S. Andaman (4 coll.).

Note. The species is known only from S. Andaman I.; recently a new flowering collection became available, confirming its characters. Vegetatively similar to *75. X. virens* and *71. X. geminatum*, differing in characters of the flowers.

77. Xanthophyllum zeylanicum Meijden, *spec. nov.*

X. flavescens auct., non Roxb.: Thwaites, Enum. (1858) 23; Trimen, Handb. Fl. Ceylon 1 (1893) 84.
X. geminiflorum auct., non Alston: Alston in Trimen, Handb. Fl. Ceylon 6, Suppl. (1931) 16, excl. type; Ooststr., Blumea, Suppl. 1 (1937) 206 (see note, as well as note 3 under *16. X. arnottianum*).

Gemmae axillares (2 vel) 3 vel 4(–6), gemma superiore supra-axillari per 1–4(–6) mm; squamae minus quam 1 mm longae. Lamina subtus laevis; glandulae sparsae. Inflorescentia indivisa vel sparse ramosa, bracteis basalibus alternatis. Petala inaequalia, petalo longissimo (8–)8.5–11.5 mm longo; carina extus appresse pilosa. Antherae 0.5–0.6 mm longae. Ovarium dense semi-patenter usque ad appresse pilosum; stylus appresse pilosus; ovula 4. Fructus globosus, c. 1.5 cm diam.; pericarpium tenue atque subcoriaceum, vel crassius atque durum. Semen 1 vel semina 2. Testa e stratis 2 formata. Albumen tenue. Embryo globosa, basi lateraliter subcompressa.

Typus: *Herb. Hermann*, vol. 2, folio 51, left hand plant, '*Bannisterioides*' (BM; iso *139 'Boromus'*, L).

Tree 15–20 m high. Axillary buds in basal part of a shoot 2, close together, in middle and apical part (2 or) 3 or 4(–6), 0.5–1 mm long, the upper bud 1–4(–6) mm supra-axillary, base slightly thickened and sometimes stalk-like constricted. *Petiole* (4.5–)5.5–8 mm long, rather often with 2 tiny glands halfway. *Leaf blade* (5–)6–16 × (2–)2.5–7 cm; upper side yellowish brown; lower side sometimes faintly waxy, green to yellowish green, secondary nerves c. 5 or 6 pairs (hardly distinguishable in apical region), not forming an intramarginal nerve; glands 7–25, scattered but mostly near midrib, 0.2–0.3 mm diam., the basal ones, if present, up to 0.7 mm diam. *Inflorescences* unbranched or sometimes with a side branch, shorter than the leaves; axes angular, sparsely minutely hairy; lower bracts alternate. *Pedicel* 3–6 mm long, subglabrous to very shortly appressedly hairy. *Sepals* sometimes with tiny glandular spots; outer sepals (1.2–)1.7–2.5 × 1.3–2.2 mm; inner sepals 2.3–3.0 x (1.6–)2.0–3.2 mm. *Petals* yellowish when dry, the longest one (8–)8.5–11.5 mm long; carina appressedly hairy outside (sometimes only apically); other petals glabrous to sparsely hairy at apex outside. *Stamens:* anthers 0.5–0.6 mm long. *Ovary* half-patently to appressedly hairy; ovules 4. *Fruit* globular, c. 1.5 cm diam., smooth, dull, dark green, brownish, or greyish, appressedly hairy apically; pericarp thin and more or less leathery, or thicker and hard; pedicel 4–7 mm long.

Distribution. Sri Lanka: SW. part (between Colombo and Galle: 18 coll.).

Note. Already during more than two centuries the Ceylonese plants are known in botanical literature (dating back to *Paelae* Hermannus, Fl. Zeyl., 1717, 24). That it is still necessary to describe a *new* species is the result of a series of small errors. First, Linnaeus forgot to make a specific epithet for his generic name *Bannisterioides* (Fl. Zeyl., 1747, 192). Also Adanson described only the genus (*Pelae*; Fam. 2, 1763, 448), based on the Ceylonese plants. Secondly, Wight (1840) erroneously attributed Roxburgh's name *X. flavescens* to the Ceylonese plants; he must have meant that the Ceylonese plants belonged to Roxburgh's other species *X. virens*. Thwaites (1858), A.W. Bennett (1874; see under *1. X. flavescens*), and Trimen (1893) followed Wight's mistake. Thirdly, Alston (1931) made another error in attributing the name *Kaulfussia geminiflora* Dennst. (1818) to the Ceylonese plants. Apart from the difficult nomenclatural problems around the new names in Dennstedt's publication (resulting in the fact that Alston's name *Xanthophyllum geminiflorum* must be regarded as a *new name*, and not as a new combination), *Kaulfussia geminiflora* is based on *Karin-kara* Rheede (1763), which is the type of the South Indian species *16. X. arnottianum* (see under that species).

My studies revealed that the Ceylonese plants do not belong to *75. X. virens* Roxb., but represent a (related) endemic species, to be called *X. zeylanicum*, which differs from *X. virens* in the characters of the key.

2. Subgenus Coriaceum Meijden, *subg. nov.*

Glandulae nodulares distinctae. Carina petalis lateralibus subaequalis. Stigma peltatum. Fructus subglobosus, parvus, rufo-brunneus in sicco, semine 1. Testa tenuis, e stratis 2 formata. Albumen paucum. Embryo globosa, radicula brevi distincta.

Typus: *X. ramiflorum* Meijden.

Nodal glands distinct, c. 0.3 mm diam. Axillary buds indistinct when resting. *Leaf blade:* tertiary nerves coarsely reticulate, sometimes partly scalariform. *Inflorescences* inserted on older nodes, unbranched, few-flowered, axes up to 1.5 cm long, with minute nodal glands. *Sepals* glabrous except for ciliate margin. *Petals* glabrous in apical half out- and inside, lateral petals and carina spoon-shaped, upper petals narrower. *Stamens* monadelphous. *Ovary* glabrous; style glabrous; stigma peltate; ovules 8–12. *Fruit* indehiscent, stipitate, more or less globular, apically pointed, 1.2 cm diam. *Seed* 1; testa 2-layered, less than 0.1 mm thick, inner layer hard; albumen forming a rather distinct, thin layer which is very thin at lateral sides of cotyledons; embryo more or less globular, green, plumule undifferentiated, radicle exserted.

Species: 1 (78).

78. Xanthophyllum ramiflorum

Fig. 16

X. ramiflorum Meijden, Blumea 18 (1970) 392. – *Xanthophyllum spec.:* Anderson, Gard. Bull. Sing. 20 (1963) 152; Whitmore, Trop. Rain For. Far East (1975) 147. – Type: *Anderson S 16051* (L; iso SING).

Tree up to 30 m high, 27 cm d.b.h. Axillary buds 2, very indistinct when resting, apparently sunken into the tissue of the twig, the upper one when bursting with 2 broadly ovate c. 1–1.5 mm long persistent scales. *Petiole* (5–)8–12 mm long. *Leaf blade* coriaceous, 7–20 × 3–8 cm, apex obtuse to subacute; upper side brownish, midrib slightly sunken to flat; lower side pale, glaucous-papillose, secondary nerves c. 8 pairs, not forming an intramarginal nerve; glands numerous, c. 0.3 mm diam. *Inflorescences* solitary or with up to 9 together in the axils of the lower leaves and those of the already fallen ones, 1–10-flowered; axes up to 1.5 cm long, thin, glabrous; nodal glands very indistinct; bracts small, scale-like. *Pedicel* 8–10 mm long, glabrous. *Sepals* dark reddish when dry; outer sepals c. 4.0–4.2 x 2.6 mm; inner sepals 4.5–4.8 x 3.0–3.3 mm. *Petals* white, the upper ones with a purple mark, when dry yellowish, minutely patently hairy in basal half outside and inside, further glabrous; carina like the lateral petals but a little shorter; lateral petals 7.5–8.5 × 7 mm; upper petals up to 7 × 2 mm. *Stamens* 8, exceptionally 7, up to c. 5 mm long; filaments connate over c. 1.5–2 mm, densely shortly patently hairy up to about halfway, glabrous in apical part; anthers c. 0.7–0.8 mm long, minutely ciliate, very shortly hairy at base. *Ovary* light brownish, glabrous; style c. 5 mm long, glabrous; stigma peltate, oblique, rather large; ovules 8–12. *Fruit* stipitate, more or less globular, up to 1.2 cm diam., pustulate, dull, reddish brown, the style-scar more or less protruding and excentric.

Distribution. Borneo: Sarawak (1st Div., Bako National Park: 4 coll.; 2nd Div.: 2; 3rd Div.: 4; locality uncertain: 'Sinatang': 1), Brunei (Badas: 2).

Note. Different from all species of *Xanthophyllum* in its coarse leaves, and in its habitat (heath forest; see chapter 4.1).

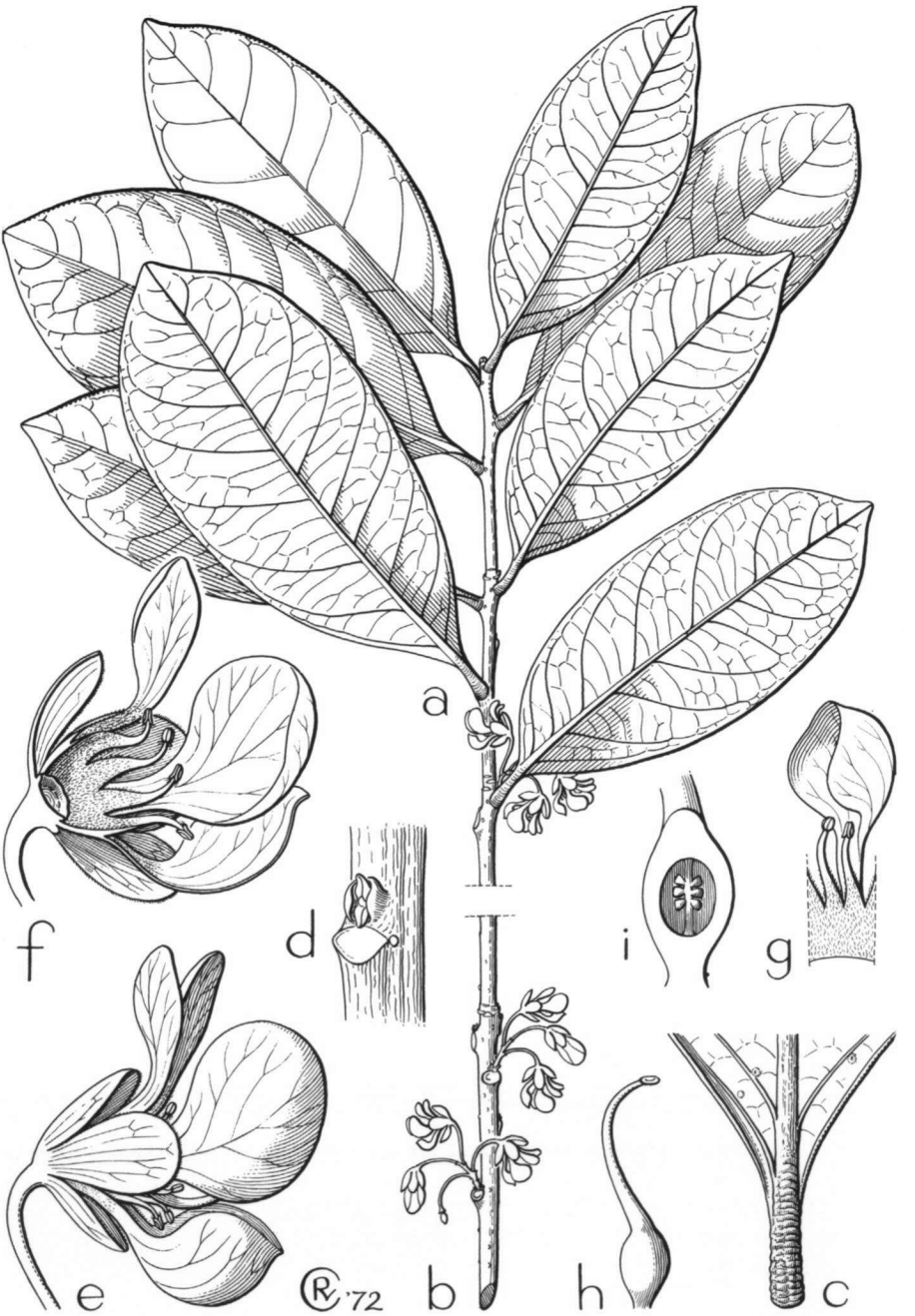


Fig. 16. *78. X. ramiflorum.* — a, b. habit, x 2/3; c. base of leaf blade with glands, x 2; d. part of twig with axillary bud, x 4; e. flower, x 4; f. flower, longitudinal section, gynoecium removed, x 4; g. lower petal, x 4; h. gynoecium, x 4; i. ovary, longitudinal section, x 8 (a–i: *S 16051*).

3. Subgenus Triadelphum Meijden, *subg. nov.*

Glandulae nodulares conspicuae. Carina petalis lateralibus subaequalis, cremea ad atro-aurantiaca in sicco. Ovarium 8–14-ovulatum; stigma peltatum. Fructus globosus, parvus ad mediocris, semine unico. Testa tenuiscula, e stratis 2 formata. Albumen copiosum. Embryo applanata.

Typus. *X. ellipticum* Miq.

Nodal glands usually distinct, 0.3–0.7 mm diam. Axillary buds seemingly single, small, the scales usually not fully covering the bracts of young inflorescences, 0.4–1(–1.5) mm long. *Leaf blade:* tertiary nerves coarsely reticulate. *Inflorescences* unbranched, axes slightly angular, dark, glabrous to sparsely hairy, with usually distinct nodal glands. *Sepals* glabrous outside, usually minutely hairy inside. *Petals* (sub)glabrous outside, lateral petals and the somewhat short carina spoon-shaped, upper petals narrower. *Stamens* triadelphous, connate parts c. 3–4 mm high. *Ovary* usually black, glabrous; style glabrous or hairy; stigma peltate; ovules 8–14. *Fruit* indehiscent, usually stipitate, 1–2 cm diam. *Seed* 1; testa 2-layered, c. 0.2 mm thick, inner layer c. 0.1 mm thick, hard; albumen copious, (nearly) separated into 2 halves; embryo flat, nerved, green, plumule undifferentiated, radicle exserted.

Species: 5 (79–83).

79. Xanthophyllum ellipticum

Fig. 3A-p, 17

X. ellipticum Korth. *ex* Miq., Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 276; A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 211; King, Mat. Fl. Mal. Pen. (1890) 140; Chodat in E. & P., Nat. Pfl. Fam. III, 4 (1896) 344; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 45; Gagnepain, Desv. J. Bot. 21 (1908) 253; Merr., En. Born. (1921) 326; Chodat in Merr., Pl. Elm. Born. (1929) 133, excl. var.; Fischer, Kew Bull. (1933) 487; Keith, N. Born. For. Rec. 2 (1938) 225; Masam., Enum. Phan. Born. (1942) 379; Meijer, Bot. News Bull. Sandakan 7 (1967) 88; Fox, Sabah For. Rec. 7 (1970) 65; Ng, Fed. Mus. J. n.s. 13 (1971) 137; in Whitmore, Tree Fl. Mal. 1 (1972) 357, fig. 3; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 146, 211. – *Banisterodes ellipticum* (Korth. *ex* Miq.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *Korthals s.n.* (L, sheet 908.171-1971; iso G, L, U).

X. citrifolium Chodat, Bull. Herb. Boiss. 4 (1896) 255; in E. & P., Nat. Pfl. Fam. III, 4 (1896) 345; Masam., Enum. Phan. Born. (1942) 379; Anderson, Gard. Bull. Sing. 20 (1963) 152. – Type: *Haviland 2110* (K; iso SING).

X. kingii Chodat, Bull. Herb. Boiss. 4 (1896) 255; Ridley, Fl. Mal. Pen. 1 (1922) 143; Watson, Mal. For. Rec. 5 (1928) 249; Craib, Fl. Siam. Enum. (1931) 106; Burkill, Dict. (1935) 2268; Wyatt-Smith, Mal. For. Rec. 17 (1952) 80, 361; *op. cit.* 23-2 (1963) iii, 12, 57. – Lectotype: *King's Coll. 8564* (K; iso MEL; see note).

Shrub or tree up to 30 m high, 40 cm d.b.h. Twigs glabrous to minutely hairy. *Petiole* (4–)5–7 mm long, glabrous to minutely hairy. *Leaf blade* 5–20 × 2–7 cm, margin often irregular, sometimes shallowly crenate because of glands; upper side usually brownish, midrib narrowly sunken; lower side more or less concolorous, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve; glands rather numerous, c. 0.4–0.8 mm diam., scattered but at least 8 present on the leaf margin itself, other glands (4–)6–10. *Inflorescences* often several together on the secondarily thickened nodes, shorter than the leaves. *Pedicel* c. 3–4 mm long, rather sparsely to rather densely minutely (woolly-)hairy. *Sepals* mostly nigrescent, glabrous to minutely hairy inside; outer sepals 3.0–3.8 x 1.8–2.2(–2.7) mm; inner sepals 3.8–4.8(–6.0) × 2.3–3.2(–4.5) mm. *Petals* white to light yellow, when

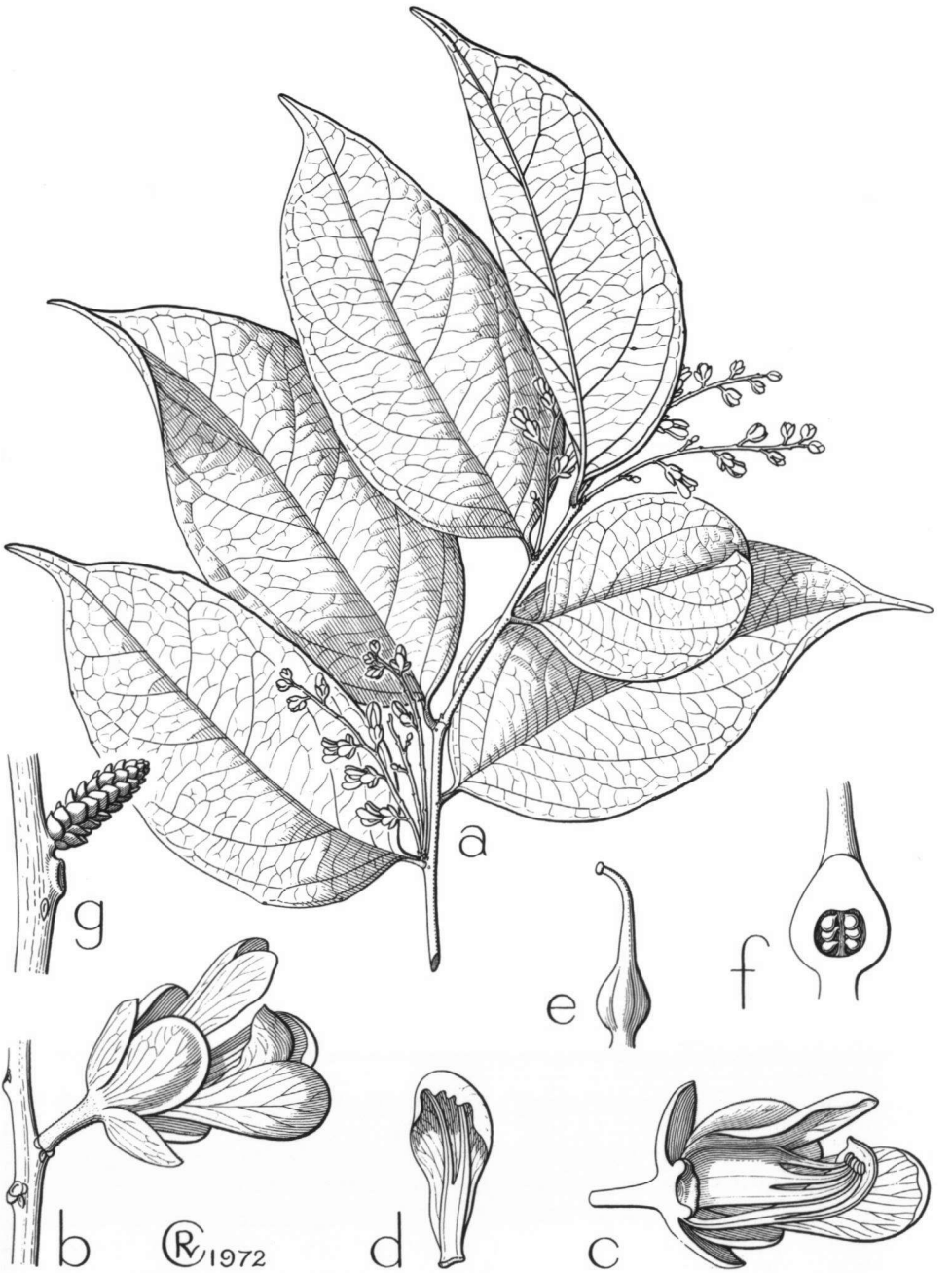


Fig. 17. *79. X. ellipticum.* — a. habit, x 0.5; b. flower and inflorescence axis, x 3; c. flower, longitudinal section, gynoecium removed, x 3; d. carina with two stamens enclosed, x 3; e. gynoecium, x 3; f. ovary, longitudinal section, x 6; g. part of twig with young inflorescence, x 4.5 (a–g: *S 25564*).

dry light brown to dark orange, inside minutely hairy only above base; carina 6–7(–8) mm long; other petals 8–9 mm long, lateral petals 3–4 mm wide, upper petals 1.5–2 mm wide. *Stamens:* filaments glabrous; anthers 0.4–0.6 mm long, shortly hairy at base, ciliolate along slits, often cohering around the stigma. *Ovary* subsessile; style glabrous; ovules 8–14. *Fruit* sessile, globular, 1.5–2.2 cm diam., smooth, dark reddish, somewhat shiny; pericarp thin, brittle; pedicel 3–6(–8) mm long. *Seed* often (sub)apical.

Distribution. S. Thailand (Kantang: 1 coll.). – Malaya: Pinang I. (1), Perak (6), Pahang (9), Johore (5). Singapore (6). – Sumatera: East (1), Southeast (1), Simaluë I. (7), Nias I. (1), Bengkalis I. (2), Riouw Arch. (Karimamum I.: 1). – Borneo: Sarawak (21), Brunei (8), Sabah (16), Kalimantan (7).

Note. Ng, *op. cit.* (1972) gives as a lectotype of *X. kingii 'Griffith s.n.'* (K), which, however, is not cited in the original publication by Chodat.

80. Xanthophyllum celebicum Meijden, *spec. nov.*

Glandulae nodulares sat distinctae. Gemmae axillares fasciculatae ad nodos vetustiores, squamulis concomitatae. Lamina subtus laevis; glandulae vulgo adsunt in parte dimidia superiore solum, interdum aliquot ad folii marginem positae, 8–12, dissitae. Inflorescentia indivisa, bracteis basalibus alternatis. Petala subaequalia, intus pilosa, petalis superioribus petalis ceteris angustioribus, petalo longissimo 7.5 mm longo. Stamina triadelphia. Antherae 0.6 mm longae. Ovarium glabrum; stylus sat dense pilosus; stigma capitatum; ovula 13. Fructus globosus, c. 1.5 cm diam., atrorufus, pericarpio tenui. Semen 1. Testa e stratis 2 formata. Albumen copiosum. Embryo applanata.

Typus: *bb Cel./II-393* (BO; iso BO, L).

Tree 25 m high. Older nodes usually with a cluster of adventitious buds. *Petiole* 5–7 mm long, not transversely wrinkled, more or less smooth. *Leaf blade* 8–15 × 3–6 cm; upper side green, midrib sunken; lower side concolorous, secondary nerves 5 or 6 pairs, not forming an intramarginal nerve; glands present only in apical half of the leaf blade, c. 0.2 mm diam., scattered but up to 6 present on the leaf margin itself, other glands c. 8–12. *Inflorescences* up to 4 cm long; nodal glands rather distinct. *Pedicel* 5–7 mm long, rather sparsely minutely woolly hairy. *Sepals* sparsely minutely hairy inside; outer sepals 4.0 × 2.5 mm; inner sepals 4.9 × 2.4 mm. *Petals* brownish orange when dry, the longest one 7.5 mm long; carina inside in middle part shortly appressedly sparsely hairy; other petals inside densely appressedly shortly hairy. *Stamens* triadelphous; filaments densely rather shortly hairy; anthers 0.6 mm long, sparsely hairy at base, ciliolate along slits. *Ovary* shortly stipitate, slightly pustulate; style rather densely shortly more or less patently (more or less woolly-) hairy; ovules 13. *Fruit* globular, c. 1.5 cm diam., smooth, dark reddish; pericarp thin; pedicel 7–9.5 mm long.

Distribution. Sulawesi: near Malili, Oesoe (*bb Cel./II-393*).

81. Xanthophyllum montanum Meijden, *spec. nov.* Fig. 10B

Glandulae nodulares sat distinctae. Gemmae axillares 2, squamulis concomitatae. Petiolus 3.5–5 mm longus. Lamina subtus laevis; glandulae (2–)4–8(–15), in parte mediana vel in parte superiore positae. Inflorescentia indivisa, bracteis basalibus alternatis. Petala paulum inaequalia, petalis superioribus petalis

ceteris angustioribus, omnia subglabra, petalo longissimo 6–6.5 mm longo. Antherae 0.6 mm longae. Ovarium glabrum; stylus glaber vel basi valde sparse minute pilosus; stigma capitatum; ovula 8–12. Fructus globosus, usque ad 0.9 cm diam., flavidus ad brunneo-virens, laevis, pericarpio tenui. Semen unicum. Testa tenuiscula, e stratis 2 formata. Albumen copiosum. Embryo applanata.

Typus: *SAN 46765* (L; iso K).

Tree up to 30 m high, 60 cm d.b.h. Nodal glands elliptic, 0.3–0.6 mm long. *Petiole* 3.5–5 mm long, indistinctly transversely wrinkled. *Leaf blade* (4–)6–9 × 1–2.5(–3.5) cm, apex gradually acuminate; upper side brownish green, midrib sunken; lower side concolorous, secondary nerves c. 6–8 pairs, forming an intramarginal nerve; glands (2–)4–8 (–15), present in middle and apical part, absent from margin itself but (in Sumatran coll.) rather close to the margin, or (in Bornean coll.) rather closely together and not near the margin, 0.3–0.6 mm diam. *Inflorescences* up to 3 cm long; nodal glands elongate, usually very distinct. *Pedicel* c. 5 mm long, sparsely minutely woolly hairy. *Sepals* minutely hairy inside; outer sepals c. 3.1 × 2.3 mm; inner sepals 3.5–4.3 × 2.3–2.8 mm. *Petals* yellowish brown when dry, the longest one 6–6.5 mm long; carina inside minutely hairy above base, upper petals minutely hairy inside. *Stamens:* filaments minutely hairy in basal part; anthers 0.6 mm long, glabrous. *Ovary* 0.5–0.7 mm stipitate, glabrous; style glabrous or only at base very sparsely minutely hairy; ovules 8–12. *Fruit* globular, up to 0.9 cm diam., yellowish to greenish brown, smooth, dull; pericarp thin; pedicel 4–5.5 mm long.

Distribution. Sumatera (near Lake Toba: *bb 5699; Frey-Wyssling 38*). – Borneo: Sabah (Mt Kinabalu: 9 coll.).

82. Xanthophyllum contractum Meijden, *spec. nov.*

Glandulae nodulares sat indistinctae. Gemmae axillares 2–3 mm longae, squamulis c. 0.5 mm longis. Petiolus 9–10 mm longus. Lamina subtus laevis; glandulae c. 12–18, plerumque positae 2–5 mm ab margine, parvae. Inflorescentia indivisa, bracteis basalibus alternatis. Flores ignoti. Fructus (immaturus) distincte stipitatus per c. 3 mm, ovoideus, glaber. Semen 1, evolutum ex 12 ovulis oppositis positis in parte dimidia superiore fructus immaturi. Testa e stratis 2 formata. Embryo applanata.

Typus: *Clemens 21664* (A; iso K, NY, SAR, Z).

Tree, flowering on older twigs from adventitious axillary buds. Nodal glands indistinct, elongated. *Petiole* 9–10 mm long. *Leaf blade* 14–20 × 6.5–8 cm, apex obtuse to very shortly acuminate; upper side yellowish green, midrib protruding; lower side: secondary nerves 8 or 9 pairs, not forming an intramarginal nerve; glands c. 12–18, mostly situated at 2–5 mm from the margin of the leaf blade, some scattered, 0.2–0.3 mm diam. *Inflorescences* up to 4 cm long; nodal glands present but very indistinct. *Flowers* unknown. *Fruit* (immature) c. 3 mm stipitate, ovoid, c. 2 × 1.2 cm, more or less fleshy, finely pustulate, light reddish, glabrous; pericarp hard; pedicel 5–6 mm long, glabrous. *Seed* 1, (sub)apical, developing from one of the 12 opposite ovules which are situated only in the apical half of the young fruit.

Distribution. Borneo: Sarawak (3rd Div., Batang Rajang, Gaat R.: *Clemens 21664*), Brunei (Biang hill: *Hotta 13348*).

83. Xanthophyllum hildebrandii Meijden, *spec. nov.* Fig. 10B

Glandulae nodulares distinctae. Gemmae axillares parvae, squamulis parvis. Petiolus laevis. Lamina laevis in utroque pagina; glandulae numerosae, magnae, plerumque positae valde propre costam. Inflorescentia indivisa; bracteis basalibus alternatis. Flores ignoti. Fructus (valde immaturus) stipitatus per 2.5 mm, ovoideus, ad partem apicalem munitus pustulam glandula similis, niger, glaber. Semen unicum, evolutum ex c. 12 ovulis positis in parte 2/3 superiore fructus immaturi.

Typus: *Clemens 26048* (L).

Petiole c. 6 mm long, not transversely wrinkled. *Leaf blade* c. 15 × 5–7 cm, papery thin; upper side dull, midrib sunken; lower side reddish brown, secondary nerves c. 7 pairs, in apical half forming a rather indistinct intramarginal nerve; glands numerous, mostly situated very close to midrib and a few scattered, 0.5–1.1 mm diam. *Inflorescences* 1 or 2 together; nodal glands distinct; axes up to 10 cm long, sparsely shortly woolly hairy. *Flowers* unknown. *Fruit* (very young) c. 2.5 mm stipitate, ovoid, apically with gland-like pustules, black, glabrous; pedicel 7–10 mm long, dark, minutely woolly hairy. *Seed* (immature) 1, (sub)apical, developing from one of c. 12 ovules situated in apical 2/3 part of the fruit.

Distribution. Borneo: Sabah (Mt Kinabalu, Dallas: *Clemens 26048*).

Notes. 1. The late F.H. Hildebrand, scientific assistant at the Rijksherbarium at Leiden (see Van Steenis, Fl. Males. Bull. no 28, 1975, 2517) recognized the *Clemens*-sheet, distributed without name and, in Leiden, pre-identified as a *Rosacea* (because of its superficial resemblance to *Prunus* and to *Parastemon*) as a member of *Xanthophyllum*. He recognized this collection, as well as numerous other sterile *Xanthophyllum* collections, using macroscopical characters of the wood of the twigs. I like to commemorate his work in the name of this species.

2. Incompletely known, yet undoubtedly allied to *81. X. contractum* and *79. X. ellipticum*, differing vegetatively and in the form of the young fruits.

4. Subgenus Exsertum Meijden, *subg. nov.*

Glandulae nodulares obscurae. Petala subaequalia, atro-rubra in sicco, quam stamina breviores. Ovarium nigrum in sicco, 8–16-ovulatum; stigma parvum, bilobum. Fructus globosus, majusculus, niger in sicco, seminibus 4 vel pluribus. Testa e sarcotesta crassa, fibrosa, atque striato interno duro formata. Albumen copiosum. Embryo applanata.

Typus: *X. amoenum* Chodat.

Presence of nodal glands uncertain. Axillary buds 2(–4), usually seemingly single, black when dry. *Leaf blade:* tertiary nerves coarsely reticulate. *Inflorescences* unbranched, up to 6–8 cm long, axes slightly angular, black when dry, rather sparsely woolly hairy, sometimes with indistinct nodal glands. *Sepals* nigrescent. *Petals* (sub)equal, spathulate-lanceolate, apex flat, (sub)glabrous outside, densely lanately ciliate. *Stamens:* filaments free, longer than petals, rather densely woolly hairy. *Ovary* black when dry, hairy inside, outside glabrous or hairy; stigma small, bilobed; ovules 8–16. *Fruit* indehiscent, globular, 2–6 cm diam., black when dry. *Seeds* c. 4–12, more or less bean-shaped, testa with rather thick and soft, fibrous outer layer and a hard inner layer; albumen copious, (nearly) separated into 2 halves; embryo flat, elliptic, nerved, plumule undifferentiated, radicle exserted.

Species: 3 (84–86).

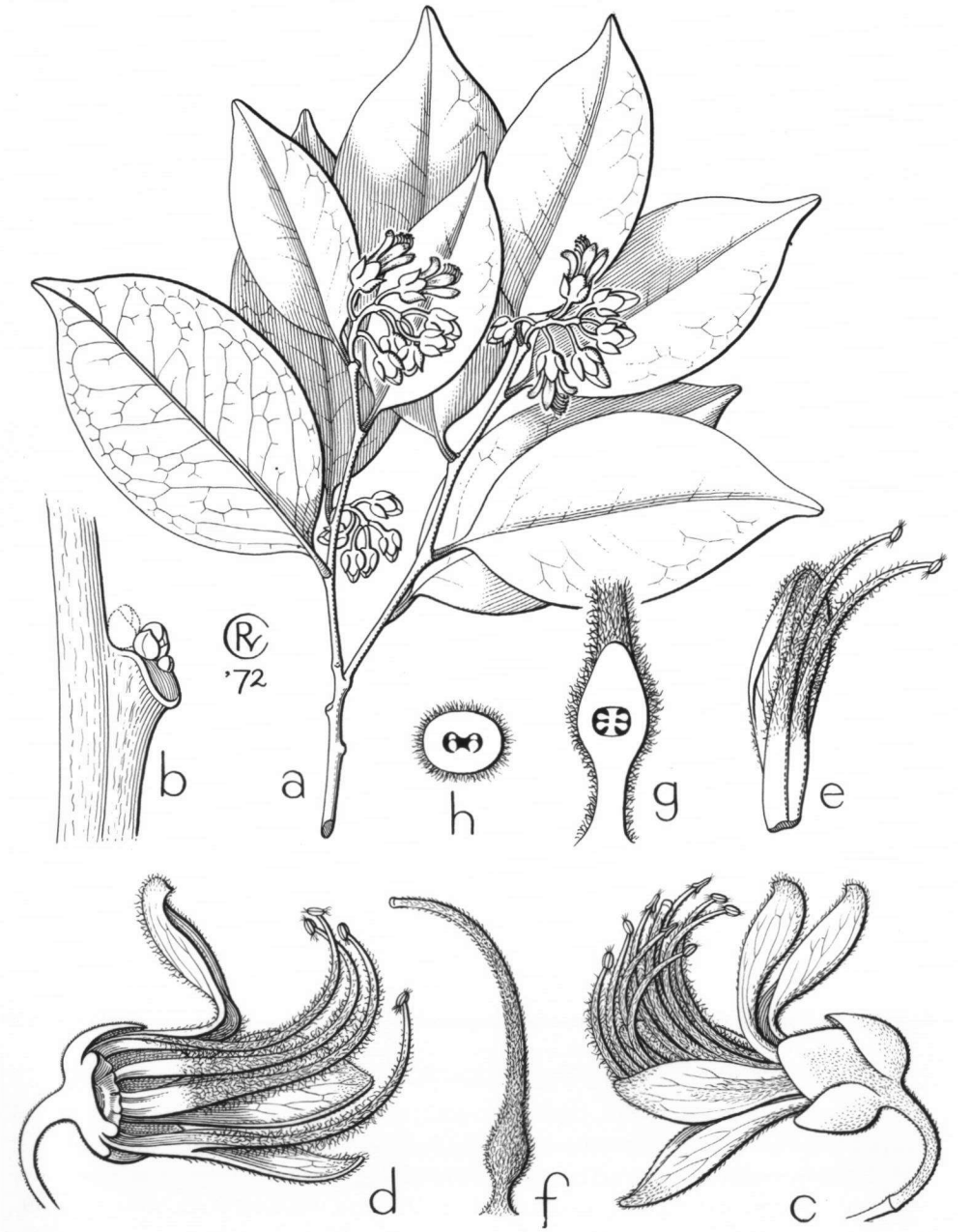


Fig. 18. *84. X. suberosum.* — a. habit, x 2/3; b. part of twig with axillary buds, x 2; c. flower, x 2; d. flower, longitudinal section, gynoecium removed, x 2; e. lower petal, x 2; f. gynoecium, x 2; g, h. ovary, longitudinal and cross section, x 4 (a–h: *Van Royen 3201*).

84. Xanthophyllum suberosum

Fig. 18

X. suberosum C.T. White, J. Arn. Arb. 10 (1929) 229. – Lectotype: *Brass 682* (K; iso BRI, L, P).

Tree up to 25 m high, up to 70 cm d.b.h. *Petiole* 6–7 mm long, black, sometimes glaucous. *Leaf blade* 4.5–11 × 2–5.5 cm; upper side olive-green, midrib narrowly sunken, nervation mostly rather indistinct; lower side reddish olive-green, secondary nerves c. 7–9 pairs, forming an indistinct intramarginal nerve, glands 10–14, sometimes more, mostly situated about halfway between midrib and margin, or near the margin, 0.1–0.3 mm diam., basal ones c. 0.3–0.4 mm diam. *Pedicel* 8–11 mm long, rather sparsely shortly lanate. *Sepals* sparsely minutely hairy outside, rather densely shortly hairy inside; outer sepals 3.5–5.5 × 3.5–4 mm; inner sepals 5–7.5 × 4–5 mm. *Petals* 14–16 mm long, white, when dry dark reddish, rather sparsely hairy outside, subglabrous inside. *Stamens:* filaments 17–22 mm long, glabrous at very base, further densely woolly hairy; anthers 1.0–1.3 mm long, hairy from base to apex. *Disc* densely hairy, with a small number of patent hairs on upper and lower lobes. *Ovary* very densely (velvety) hairy; style rather sparsely woolly hairy; ovules 10–16. *Fruit* (immature) c. 2 cm diam., shortly stipitate, finely pustulate, dark, distinctly bluish-waxy, hairy; pericarp c. 1–4 mm thick; pedicel slender, c. 15–18 mm long.

Distribution. New Guinea: Irian Jaya (mainland: 5 coll. – Geelvink Bay: Meos Num: 1; Biak: 2; Yapen: 9), Papua New Guinea (8).

Note. Closelv resembling *85. X. amoenum*, but known from too few collections. The kind of differences between both taxa may be comparable to those between the two *subspecies* of *48. X. discolor*. If collections of *X. suberosum* with ripe fruits and seeds can be examined, and if more flowering collections become available, the better solution may prove to be to rank *X. suberosum* as a subspecies of *X. amoenum*.

85. Xanthophyllum amoenum

Fig. 3A-n

X. amoenum Chodat, Bull. Herb. Boiss. 4 (1896) 259; in E. & P., Nat. Pfl. Fam. III, 4 (1896) 344; Gagnepain, Desv. J. Bot. 21 (1908) 252; Masam., Enum. Phan. Born. (1942) 379; Wyatt-Smith, Mal. For. Rec. 17 (1952) 80, 363; *op. cit.* 23-2 (1963) fig. 8; Anderson, Gard. Bull. Sing. 20 (1963) 152; Meijer, Bot. News Bull. Sandakan 7 (1967) 87; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 356, fig. 1. – Lectotype: *Haviland 2112* dated Jan. 16, 1893 (K).

non X. amoenum auct.: Keith, N. Borneo For. Rec. 2 (1938) 225 (= *86. X. stipitatum*).

X. stipitatum var. *nitidum* Chodat in Merr., Pl. Elm. Born. (1929) 137; Masam., Enum. Phan. Born. (1942) 381. – Lectotype: *Elmer 21668* (L; iso BM, BO, BR, BRI, C, G, K, P, SING, Z).

X. stipitatum var. *pachyphyllum* Chodat in Merr., Pl. Elm. Born. (1929) 137; Masam., Enum. Phan. Born. (1942) 381. – Lectotype: *Elmer 21493* (L; iso BM, BO, BR, BRI, C, G, K, L, M, P, SING).

Tree up to 35 m high, d.b.h. up to 80 cm. Axillary buds 2 or 3, the upper one up to 2 mm long. *Petiole* 4.5–10.5 mm long. *Leaf blade* 4–14 × (1–)2–7 cm; upper side deep brown to reddish brown, midrib narrowly sunken, nervation rather obscure to rather distinct; lower side sometimes waxy, secondary nerves 5–7, not forming an intramarginal nerve; glands 6–10(–20), scattered, 0.1–0.4(–0.5) mm diam. *Pedicel* 8–15 mm long, rather densely minutely lanate. *Sepals:* outer sepals 2.5–3 × 1.8–2.2 mm, minutely rather densely hairy at both sides; inner sepals 4–4.5 × 1.8–2.4 mm, hairy outside along midrib, inside densely hairy at base, further more or less glabrous. *Petals* (8–)9–11(–12) mm

long, white ('3 lower with yellow centre'; *Haviland 2112*), when dry dark reddish, glabrous outside, inside lanate especially in basal and apical part. *Stamens:* filaments 11–13(–16) mm long; anthers 0.7–0.9 mm long, glabrous or with a few hairs at base. *Disc* glabrous. *Ovary* stipitate, (glabrous? or) densely lanate; style lanate; ovules 8–16. *Fruit* globular or less often ovoid, up to c. 5 cm diam., sometimes bluish waxy, hairy or apparently glabrous; pericarp 1–10 mm thick. *Seeds* 6 or more.

Distribution. Malaya: Kedah (1 coll.), Kelantan (2), Trengganu (3), Perak (4), Pahang (4), Selangor (6), Negri Sembilan (2), Malacca (2). – Sumatera: Inderagiri (2). – Borneo: Sarawak (17), Brunei (3), Sabah (19), Kalimantan (7).

Notes. 1. The number of flowering collections of *X. amoenum* and of *86. X. stipitatum* is very small. Collections with ripe seeds are also very scarce. This means that the identification of the collections is mainly based on vegetative characters. In Malaya *X. stipitatum* and *X. amoenum* can be readily distinguished by the size of the leaf blades; they also differ in the number of laminar glands. The Bornean material is vegetatively more variable than the Malayan material. If the difference in the number of laminar glands holds true for Borneo as well, *X. stipitatum* is little more variable in Borneo than in Malaya. In that case the conclusion must be that *X. amoenum* is much more variable in Borneo than in Malaya. This conclusion must be verified by comparison of new flowering collections.

2. Some fruiting and sterile collections (identified by me as *Xanthophyllum spec.*) resemble *X. amoenum* vegetatively. They are distinguished by the protruding midrib of the leaves; the material may be divided into three groups:

1) Pedicel and infructescence axis rather sparsely to densely shortly woolly hairy. Laminar glands 6–20. – Distribution: Borneo: Sarawak (5th Div., Limbang: *S 32289*), Brunei (*Hotta 12639*), Labuan I. (*KEP 35438*), Sabah (Gaya I.: *SAN 64061*; Beaufort: *SAN 15077, 15233 50356*; Sandakan, Leila For. Res.: *SAN 26367*).
2) Pedicel and infructescence axis glabrous. Laminar glands few, with very small centre and wide margin. – Distribution: Borneo: Kalimantan (W. Kutai: *Endert 4984*).
3) Pedicel and infructescence axis glabrous, laminar glands absent. – Distribution: Malaya: Kelantan (Jeli For. Res.: *FRI 2324*, fruiting; Lebir For. Res.: *KEP 115956*; Upper Aring R.: *FRI 4459*), Pahang (Putat For. Res.: *KEP 31514*; Bilut For. Res.: *KEP 23498*; Krau Game For. Res.: *FRI 3547*).

Ng (*l.c.* 1972, p. 361) mentioned these collections in a note under *X. obscurum* (= species 88).

86. Xanthophyllum stipitatum

X. stipitatum A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 210; King, Mat. Fl. Mal. Pen. (1890) 140; Chodat in E. & P., Nat. Pfl. Fam. III, 4 (1896) 345; Ridley, Fl. Mal. Pen. 1 (1922) 145; Henderson, Gard. Bull. S. S. 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2268; Wyatt-Smith, Mal. For. Rec. 17 (1952) 81, 361; Balan Menon, *op. cit.* 19 (1956) 34; Meijer, Bot. News Bull. Sandakan 7 (1967) 87; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 363, fig. 5; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 147. – *Banisterodes stipitatum* (A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Type: *Maingay 140 (= 3292)* (K; iso K).

X. stipitatum var. *borneense* Chodat in Merr., Pl. Elm. Born. (1929) 137. – Lectotype: *Elmer 21298* (L; iso BM, BO, C, G, K, M, SING, U, Z).

X. amoenum auct., non Chodat: Keith, N. Borneo For. Rec. 2 (1938) 225.

Tree up to 50 m high, 1.20 m d.b.h. Axillary buds 2(–4), c. 2 mm long. *Petiole* 3–8 mm long. *Leaf blade* (2.5–)4–13 × (1–)2–7 cm; upper side mostly greyish brown to dark brown, sometimes reddish brown, midrib slightly sunken, nerves mostly obscure; lower side concolorous, sometimes more or less waxy, secondary nerves 5 or 6 pairs, not forming an intramarginal nerve, finely protruding to rather obscure; glands few, 0–2(–4) per leaf, situated near the base and in the middle, 0.1–0.2 mm diam. *Pedicel* c. 8–12 mm long, dark, minutely lanate. *Sepals* densely minutely hairy inside at base, further almost glabrous; outer sepals 1.8–3 × 1.8–2 mm; inner sepals 3–3.5 × 2–2.5 mm. *Petals* 7–7.5(–8) mm long, dark reddish when dry, glabrous outside, hairy inside at base and sometimes also in apical part. *Stamens:* filaments 11–13 mm long, shortly rather densely lanate, glabrous in apical part, free or (in var. *glabrum*) forming a 'tube' by their intertwined hairs; anthers c. 0.8 mm long, glabrous. *Disc* glabrous. *Ovary* densely lanate or rarely (sub)glabrous; style glabrous in upper half; ovules 8–12. *Fruit* c. 2–6 cm diam., often apparently sterile, shortly to long-stipitate, black, often waxy, glabrous or hairy; pericarp 0.5–1.5 cm thick; pedicel up to c. 15 mm long. *Seeds* c. 4–12.

Distribution. Malaya. – Sumatera. – Borneo.

Notes. 1. See under *85. X. amoenum.*

2. In Malaya the few collections with flowers all have a hairy ovary; all available fruits are also hairy. In Borneo the single flowering collection has a glabrous ovary; some fruiting collections have glabrous fruits, other collections have hairy fruits. The Bornean flowering collection differs from the Malayan ones also in the hairiness of the filaments (forming a 'tube' by their intertwined hairs; in Malayan collections the filaments are hairy but free). It seems plausible that the collections with glabrous fruits belong to the same taxon as the collection with the glabrous ovary and tube-like stamens, and that the collections with hairy fruits belong to the same taxon as the collections with a hairy ovary. It is uncertain, however, whether the character of the indumentum of the ovary is correlated with the character of the filaments. For that reason I have included only the Bornean flowering collection (together with a very similar sterile collection) in var. *glabrum*; the glabrous fruiting collections have been included in var. *stipitatum*.

3. Fruiting material in which the midrib of the leaves is protruding above has not been included; see under *85. X. amoenum*, note 2; especially 'group 3' shows resemblance with *X. stipitatum*.

KEY TO THE VARIETIES

1 a. Filaments forming a 'tube' by their intertwined hairs. Ovary (sub)glabrous. **b. var. glabrum**

b. Filaments free, hairy. Ovary densely lanate ..... **a. var. stipitatum**

a. var. stipitatum

X. stipitatum A.W. Bennett, incl. var. *borneense* Chodat.

Stamens: filaments free, hairy. *Ovary* densely lanate; style densely hairy basally.

Distribution. Malaya: Kedah (2 coll.), Perak (15), Trengganu (9), Pahang (11), Selangor (7), Negri Sembilan (2), Malacca (3), Johore (19). Singapore (2). – Sumatera: Central (3). – Borneo: Sarawak (1st Div.: 4; 5th Div.: 1), Brunei (1), Sabah (11), Kalimantan (31).

b. var. **glabrum** Meijden, *var. nov.*

Filamenta 'tubum' formantia per eorum pilis sese amplectentibus. Ovarium glabrum vel pilis paucis appressis; stylus ad basin tenuiter pilosus.
Typus: *Endert 3493* (L; iso BO, K, SING).

Stamens: filaments forming a 'tube' by their intertwined hairs. *Ovary* glabrous or with a few appressed hairs; style thinly hairy basally.

Distribution. Borneo: Kalimantan (Long Petah: *Endert 3493*; identity uncertain: *Endert 3318*).

5. Subgenus Brunophyllum

Subg. *Brunophyllum* Meijden, Bot. J. Linn. Soc. 67 (1973) 117. – Type: *X. scortechinii* King (= *X. obscurum*).

Nodal glands usually distinct, c. 0.3–0.5 mm diam. *Leaf blade:* tertiary nerves coarsely reticulate. *Inflorescences* unbranched. *Sepals* glabrous to minutely hairy outside, usually woolly-ciliate, usually minutely hairy inside. *Petals* unequal with the carina boat-shaped, or equal, (sub)glabrous outside. *Stamens* 8(–10), filaments free or up to 6 mm connate, densely woolly hairy. *Ovary* glabrous to hairy; style glabrous or hairy at base; stigma peltate; ovules 8–18(–23). *Fruit* indehiscent, pear-shaped to ovoid, large. *Seeds* 8–more, large: testa 2-layered, outer layer usually thick (thin in *91. X. chartaceum*), soft, inner layer hard; embryo broadly triangular-ovoid and with little albumen, to flattened-ovoid and covered by much albumen; cotyledons cordate, usually seemingly peltate (except in *87. X. brevipes*), plumule usually differentiated into a number of small scales, radicle fully enveloped by the cotyledons or just exserted at base.
Species: 5 (87–91).

87. Xanthophyllum brevipes

X. brevipes Meijden, Bot. J. Linn. Soc. 67 (1973) 117. – Type: *S 26838* (L; iso L).

Tree up to 35 m high, 40 cm d.b.h. Twigs (sometimes?) all curved downwards, pendent. Nodal glands often indistinct. *Petiole* 1.5–3 mm long. *Leaf blade* 2.6–7.5 × 0.7–2.6 cm, apex acuminate to cuspidate; upper side brown to olive-green, midrib sunken; lower side olive-greenish brown, papillose, secondary nerves c. 10 pairs, little more distinct than finer nerves, forming an indistinct intramarginal nerve; glands more than 10, in a row between margin and midrib, c. 0.1 mm diam. *Inflorescences* 2–5-flowered; axes hardly thicker than pedicel, glabrous. *Pedicel* c. 7 mm long, glabrous. *Sepals* minutely ciliate, further glabrous; outer sepals c. 3.5 × 3.5 mm; inner sepals c. 4 × 4.5 mm. *Petals* unequal, white, when dry

orange-brown, faintly ciliate, the longest one 15–16 mm long; carina unguiculate, boat-shaped, ciliate only at base; lateral petals narrowly boat-shaped; upper petals more or less straight, with cup-shaped apex. *Stamens:* filaments c. 0.5 mm connate, rather densely shortly hairy in basal part; anthers c. 1.0 mm long, glabrous. *Ovary* shortly stipitate, orange-brown, glabrous; style glabrous; ovules 18. *Fruit* pear-shaped (to broadly ovoid?), up to 4 cm diam., strongly wrinkled when dry, shiny, brown; pericarp probably very fleshy; pedicel 12–15 mm long, blackish, shiny. *Seeds* more than 10, flattened-ovoid, c. 1 cm long; albumen nearly absent from lateral sides of cotyledons, at the broad side of these forming a layer equal in thickness to each cotyledon; embryo elliptic in side view, flattened transversely, cordate at base; cotyledons thickened; plumule not differentiated; radicle slightly exserted.

Distribution. Borneo: Sarawak (1st Div.: 6 coll.; 4th Div.: 2), Brunei (2).

Note. P.S. Ashton (on *BRUN 631*) mentions that the habit of the tree is very reminiscent of old specimens of *Salix (alba) babylonica* because of its pendent twigs.

88. Xanthophyllum obscurum

Fig. 3B-b, 10B

X. obscurum A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 211; King, Mat. Fl. Mal. Pen. (1890) 141; Ridley, J. Str. Br. R. As. Soc. 33 (1900) 45; Fl. Mal. Pen. 1 (1922) 144; Heyne, Nutt. Pl. (1927) 902; Henderson, Gard. Bull. S. S. 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Wyatt-Smith, *op. cit.* 17 (1952) 81, 363; Balan Menon, *op. cit.* 19 (1956) 34; Wyatt-Smith, *op. cit.* 23-2 (1963) fig. 8; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 361, fig. 3; Mal. For. 38 (1975) 89, fig. 8.1 F–J, 8.3, 8.4; Corner, Gard. Bull. Sing., Suppl. 1 (1978) 147, 211. – *Banisterodes obscurum* (A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Type: *Maingay 144 (= 3115)* (K).

X. insigne A.W. Bennett in Hook. *f.*, Fl. Br. Ind. 1 (1874) 211; King, Mat. Fl. Mal. Pen. (1890) 144. – *Banisterodes insigne* (A.W. Bennett) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype: *Maingay 143 (= 3343)* (K; iso K).

X. scortechinii King, J. As. Soc. Beng. II, 59 (1890) 140; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 163; Gagnepain, Desv. J. Bot. 21 (1908) 253; Ridley, Fl. Mal. Pen. 1 (1922) 143; Henderson, Gard. Bull. S. S. 4 (1928) 222; Watson, Mal. For. Rec. 5 (1928) 249; Burkill, Dict. (1935) 2268; Wyatt-Smith, Mal. For. Rec. 17 (1952) 81, 361; Balan Menon, *op. cit.* 19 (1956) 34; Wyatt-Smith, *op. cit.* 23-2 (1963) t. 5; Ng in Whitmore, Tree Fl. Mal. 1 (1972) 363, fig. 3. – Type: *Scortechini 2079* (SING; iso BM, FI, G, L, SING).

Tree up to 47 m high, d.b.h. 70 cm. Twigs often strongly thickened on the nodes and with adventitious buds. Nodal glands usually distinct, sometimes elongate, c. 0.5 mm diam. *Petiole* 5–11(–15) mm long. *Leaf blade* (4–)7.5–17 × (1.5–)3.5–9 cm, apex rounded to obtuse or sometimes very shortly acuminate; upper side dark or greyish red-brown, rarely green, midrib flat to protruding; lower side concolorous or darker than upper side, midrib protruding or flat, secondary nerves c. (3–)6–9 pairs, sometimes in upper part forming an intramarginal nerve; glands 2–16, usually situated near the margin of the leaf blade, sometimes on the margin itself, (0.2–)0.5–0.7(–1.2) mm diam. *Inflorescences* sometimes also on the older nodes, shorter than the leaves; axes angular, black, glabrous to sparsely shortly lanate. *Pedicel* 3–11 mm long, glabrous to sparsely hairy. *Sepals* black; outer sepals 2.8–5.5 × 2.8–6 mm; inner sepals 4–7.5 × 3.5–7 mm. *Petals* unequal, white or purple, the upper ones with a yellow or green spot, when dry black, inside glabrous or rather densely woolly hairy above insertion of filaments and at apex, the longest one

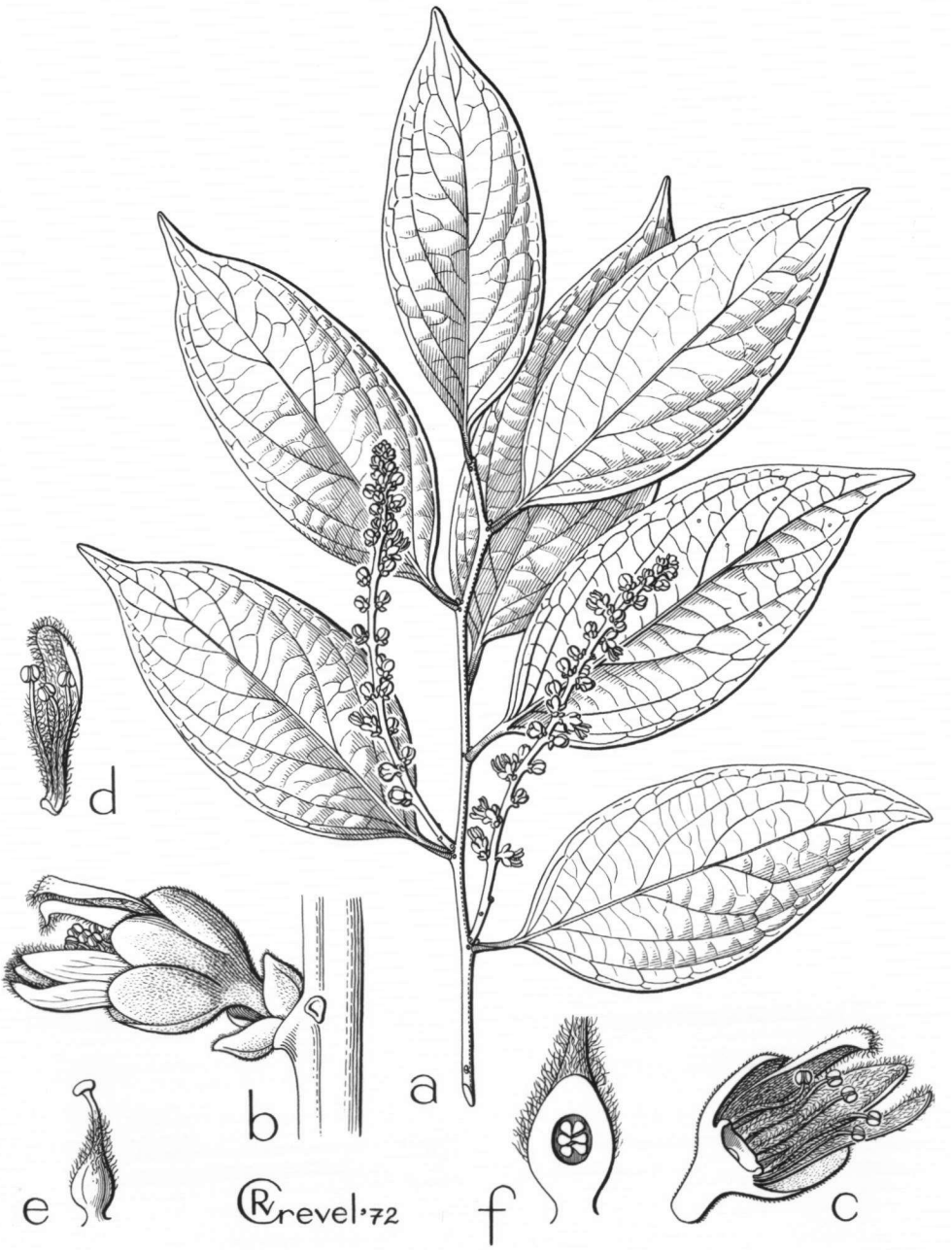


Fig. 19. *89. X. papuanum.* — a. habit, x 2/3; b. flower and part of inflorescence axis, x 4; c. flower, longitudinal section, gynoecium removed, x 4; d. lower petal with three stamens, x 4; e. gynoecium, x 4; f. ovary, longitudinal section, x 8 (a–f: *Hoogland 5072*).

14–19 mm long; carina boat-shaped, 9.5–16 mm long; lateral petals more or less spathulate, distinctly longer than upper petals and carina; upper petals more or less linear, flat to slightly channelled, curved upwards. *Stamens* 7.5–12 mm long; filaments connate over (0.1–)1–3 mm, glabrous in basal part, free parts of filaments lanate in basal part, hairs often intertwined, thus forming a filamental 'tube', glabrous upwards; anthers 0.7–1.7 mm long, glabrous to minutely hairy, free or attached to each other around the stigma. *Ovary* black, glabrous; style black, glabrous; ovules 8–18. *Fruit* globular, very large, the largest up to 14 cm diam., dull pinkish brown, with numerous small dark spots; pericarp 0.5–2 cm thick. *Seeds* 8–16, sticking together in drying like a ball, each c. 2–6 cm wide; testa 2-layered, outer layer thick, soft, fibrous, inner layer c. 0.1 mm thick; albumen nearly absent, usually visible only at base; embryo thick, triangular in side-view, plumule and radicle situated in the very centre of the embryo, the plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically with numerous vessel-like elements forming a regularly reticulate pattern.

Distribution. S. Thailand (Nakhon Si Tammarat: 1 coll.). – Malaya: Kedah (4), Pinang I. (2), Kelantan (2), Trengganu (2), Perak (7), Pahang (7), Selangor (5), Negri Sembilan (1), Malacca (7), Johore (4). Singapore (3). – Sumatera (widely scattered: 12). – Borneo: Sarawak (12), Sabah (Southwest: 4; Southeast: 1), Kalimantan (24).

Notes. 1. In the present circumscription *X. obscurum* is very variable; until recently I distinguished two species: *X. obscurum s.s.* and *X. scortechinii*, corresponding with Ng's revision. In recent years some new flowering material became available which appeared to be 'intermediate' in several characters. A reconsideration of this material led me to widen my concept of *X. obscurum*; now I think that *X. scortechinii* does not even merit infraspecific status.

2. Peculiar is the presence of a dense network of vessel-like elements in the cotyledons. The vessels consist of double rays of 'tracheoidal idioblasts' of the kind Dickison (1973) described from mature leaves. The ontogenetically early occurrence of these cells and the fact that in the closely related species *89. X. papuanum* the spiral thickenings in these cells have not been formed, may be promising for comparative anatomical research.

3. Ng (*l.c.*) combined the names *X. obscurum* and *X. insigne* under the first one. The lectotypes which I have chosen must belong to the original sheets but they differ in some respects from Bennett's descriptions: *Maingay 143 (= X. insigne)* has petals 14–19 mm long (Bennett: 12–16 mm); its petioles are c. 15 mm long (Bennett: 2–2.5 cm). *Maingay 144 (= X. obscurum)* has petals of 14 mm long (Bennett: 6–8! mm); its petioles are 7–8 mm long (Bennett: 6 mm); I counted 5–7 pairs of secondary nerves (Bennett: 8–10 pairs).

89. Xanthophyllum papuanum

Fig. 3B-c, 19

X. papuanum Whitmore *ex* Meijden, Bot. J. Linn. Soc. 67 (1973) 119; Whitmore, Guide For. Br. Sol. Is. (1966) 92, 151; Paijmans, Land Research Ser. 29 (1971) 107; Versteegh, Med. Landb. Hogesch. Wageningen 71-19 (1971) 63; Eddowes, Commerc. Timbers P.N.G. (1977) 46 ('Boxwood'). – Type: *Hoogland 5072* (L; iso K).

X. affine auct., non Miq.: K. Sch. & Hollr., Fl. Kais. Wilh. Land (1889) 68; K. Sch. & Laut., Fl. Schutzgeb. (1901) 388.

Tree up to 43 m high, up to 1.1 m d.b.h. *Petiole* 5–9 mm long. *Leaf blade* 5–14 × 2.8–9.3 cm; upper side greyish mid-green, rarely yellowish brown, midrib mostly sunken, sometimes flat, rarely protruding; lower side concolorous, secondary nerves c. 5 or 6 pairs; glands 6–10(–14), in middle part close to the midrib, in upper part often along margin and midrib, 0.4–0.5 mm diam. *Inflorescences* about as long as to longer than the leaves; axes angular, brown, rather densely shortly lanate; in basal part flowers with 3(–7) together. *Pedicel* 3–4 mm long, ribbed, densely shortly lanate. *Sepals* brownish, shortly lanate outside; outer sepals 2.5–3.5 × c. 2 mm; inner sepals 3–4.5 × c. 2.5 mm. *Petals* (sub)equal, obovate-lanceolate, 7–8.5 mm long, with slightly cupped apex, white, when dry orange-brown, outside with a few woolly hairs along midrib, woolly-ciliate especially at apex, inside woolly hairy. *Stamens* 8 or 9, the middle carinal stamen rather often developed; filaments free or 0.1 mm connate, densely lanate to apex; anthers 0.7–0.8 mm long, sparsely woolly hairy. *Ovary* 0.5–0.7 mm stipitate, inside glabrous to sparsely hairy, outside densely shortly lanate on median rib, further glabrous; style basally densely shortly lanate, upwards nearly glabrous; ovules 14–16. *Fruit* pear-shaped, c. 5–15 cm long, 3–12 cm diam., reddish brown to greyish greenish brown, often with darker spots; pericarp c. 0.5 cm thick, hard; pedicel up to 5 mm long. *Seeds* mostly more than 8, rarely less, sticking to the pericarp in drying, broadly triangular-ovoid, up to 5 cm wide when dry; testa 2-layered, outer layer thick, soft, not fibrous, inner layer less than 0.1 mm thick, hard; albumen nearly absent, usually visible only at the base; embryo thick, triangular in side-view, plumule and radicle situated below the centre of the embryo, plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically without vessel-like elements; top of radicle hardly exserted at base.

Distribution. Sulawesi (Palopo, Boea: 1 coll.). – Maluku Is. (Moluccas): Seram (Kiandarat: 1). – New Guinea: Irian Jaya (Salawati I.: 1 – Geelvink Bay: Numfoor I.: 1; Yapen I.: 1; Mios Waar I.: 1 – mainland: 36), Papua New Guinea (mainland: 32; Fergusson I.: 1). – Solomon Is.: Choiseul (2), Ghanongga (3), Gizo (1), Kolombangara (4), Baga (2), Rendora (1), New Georgia (1), Santa Isabel (3), Malaita (1), Guadalcanal (4), Rennell (2).

Notes. 1. In a number of collections all flowers examined have 9 stamens: 3 instead of 2 stamens are placed before the adaxial petal.

2. *X. papuanum* has the widest area east of Wallace's Line. In the western part of its area only a few collections are known; possibly it is undercollected there. In the islands of the Bismarck Archipelago the species is probably overlooked.

90. Xanthophyllum ecarinatum

Fig. 3B–d

X. ecarinatum Chodat, Bull. Herb. Boiss. 4 (1896) 254; in E. & P., Nat. Pfl. Fam. III, 4 (1896) 344; Merr., En. Born. (1921) 325; Masam., Enum. Phan. Born. (1942) 379; Meijer, Bot. News Bull. Sandakan 7 (1967) 87. – Type: *Haviland 1768* (K; iso SAR).

X. kalimantanum Meijden, Bot. J. Linn. Soc. 67 (1973) 118. – Type: *Hub. Winkler 2464* (L; iso BM, BO, K, L, P, WRSL).

Tree up to 25 m high, 16 cm d.b.h. *Petiole* (1.5–)4–6.5 mm. *Leaf blade* (ovate-)oblong, (3–)7–17 × (1–)2.8–7 cm, apex acuminate to cuspidate; upper side dark reddish brown to dark olive-green, midrib slightly protruding to flat, or sunken in basal part; lower side

concolorous, secondary nerves 5–7 pairs, forming a rather indistinct intramarginal nerve; glands 0–8, situated in middle and apical part, (0.1–)0.2–0.4 mm diam. *Inflorescences* (much) shorter than the leaves; axes lanate; flowers solitary or in basal part with up to 3 together. *Pedicel* (1.5–)3–4 mm long, dark, sparsely lanate. *Sepals* black when dry; outer sepals (3–)4–5.5 × (1.5–)2.5–3.5 mm; inner sepals (3.5–)6–7 × (1.5–) 2.5–4 mm. *Petals* subequal, 9.5–12 mm long, white, the upper ones with a yellow spot, when dry nearly black, ciliate to apex, inside hairy above insertion of filaments. *Stamens* 8(–10); filaments connate over c. 5–6 mm, glabrous at base, upwards densely (woolly) hairy; anthers 0.5–0.65 mm long, glabrous to sparsely woolly hairy at base. *Ovary* stipitate over 2.5–3 mm, dark, glabrous or with a few rather long hairs; style glabrous to rather sparsely lanate; ovules 12–18(–23). *Fruit* ellipsoid, up to 11 × 6 cm, attenuate at base and apex, often more or less smooth, orange to dark brown; pericarp rather soft, c. 0.5 mm thick. *Seeds* 8 or more, like those of *89. X. papuanum*, but albumen forming a thin layer along outer side of the cotyledons.

Distribution. Borneo: Sarawak (1st Div.: 5 coll.: 3rd Div.: 3; 4th Div.: 4; locality unknown: Mt Soekan: *Hose 7*), Sabah (Crocker Range For. Res.: 1; Kinabalu region: 7), Kalimantan (2).

Notes. 1. Like *88. X. obscurum* this species is rather variable, and I originally distinguished two taxa in it which could not be maintained with the increasing number of collections.

2. In all flowers which I dissected I only found 8 stamens. As Chodat (*l.c.*) mentions to have found 8–10 stamens, and B.C. Stone (on label *Stone 13580*) mentions to have counted 7–10 stamens, I must conclude that my observations are incomplete.

91. Xanthophyllum chartaceum

X. chartaceum Meijden, Bot. J. Linn. Soc. 67 (1973) 118. – Type: *FRI 10705* (L; iso K, KEP).
Xanthophyllum spec. E Ng in Whitmore, Tree Fl. Mal. 1 (1972) 366.

Tree up to 30 m high, 1 m d.b.h. *Petiole* 3–4 mm long. *Leaf blade* 4.5–11.5 × 2–4.2 cm, papery thin, base nearly cordate to cuneate, apex acuminate to cuspidate; upper side very dark green, midrib flat to slightly protruding; lower side somewhat glaucous, concolorous, secondary nerves c. 5–7 pairs; glands very few, up to 3, about 0.1 mm diam., very indistinct. *Flowers* unknown. *Infructescences* short; axes black, glabrous. *Fruit* globular to more or less pear-shaped, up to 8.5 cm long, strongly wrinkled, when dry black, probably glabrous; pericarp rather thick, hard. *Pedicel* c. 5 mm long, black, glabrous. *Seeds* 8 or more, like those of *89. X. papuanum*, but both layers of the testa much thinner, and albumen forming a thin layer along the outer side of the cotyledons.

Distribution. Malaya: Kelantan (1 coll.), Perak (1), Trengganu (3), Pahang (1), Malacca (2). – Sumatera: Inderagiri (2).

Note. Because of its thin nigrescent leaves with few laminar glands, its habit is atypical in *Xanthophyllum*. As its flowers may be atypical too (i.e. in being possibly 'regular'), flowering material may have been collected already but identified wrongly.

Fig. 20. *92. X. fragrans.* — a. habit, x 0.5; b. flower, longitudinal section, gynoecium removed, x 1; c. lower petal, x 1; d. gynoecium, x 1; e. ovary, longitudinal section, x 2 (a–e: *Brass & White 264*).

6. Subgenus **Grandiflorum** Meijden, *subg. nov.*

Glandulae nodulares paucae. Petala subaequalia, maxima, in sicco aurantiaca. Ovarium c. 40-ovulatum; stigma peltatum. Fructus ellipsoideus, magnus, brunneolus, seminibus 8 vel pluribus. Testa crassiuscula, e stratis 3 formata, strato mediano spongioso. Albumen copiosum. Embryo applanata.

Typus: *X. fragrans* C.T. White.

Nodal glands usually absent but often present on at least one node per shoot. *Leaf blade:*

tertiary nerves coarsely reticulate. *Inflorescences* unbranched or with one side axis, nodal glands absent. *Petals* equal, large, glabrous outside. *Stamens:* filaments free. *Ovary* 6–10 mm stipitate, semi-2-locular, glabrous; style glabrous; stigma peltate; ovules numerous (39 or 40). *Fruit* indehiscent, ellipsoid, large. *Seeds* 8–more, more or less globular, c. 1.5 mm diam.; testa 3-layered, outer layer very thin, leathery, middle layer spongy, 0.2–2 mm thick, inner layer hard, c. 0.1–0.15 mm thick; albumen copious, (nearly) separated into 2 halves; embryo circular, flat, nerved, plumule undifferentiated, radicle exserted.

Species: 1 (92).

92. Xanthophyllum fragrans

Fig. 20, 21

X. fragrans C.T. White, Proc. R. Soc. Queensl. 50 (1938) 67. – Type: *Brass & White 264* (BRI; iso A, BM, BRI, G, K, P).

Tree 8–20 m high, 25–45 cm d.b.h. Twigs minutely hairy, glabrescent. *Petiole* 7–12 mm long, faintly wrinkled, minutely hairy, sometimes at very apex with 2 large glands. *Leaf blade* 8.5–21 × 4.5–8 cm; upper side greenish to reddish brown, midrib sunken in basal half; lower side concolorous, secondary nerves c. 7–9 pairs, not forming an intramarginal nerve; glands (1 or) 2, situated near the base, sometimes shifted to the apex of the petiole, 0.9–3.3 mm diam. *Inflorescences* shorter than the leaves; axes ribbed, densely shortly hairy; bracts usually with 2 circular glands. *Pedicel* 15–25 mm long, densely shortly lanate. *Sepals* minutely hairy outside, shortly hairy inside, sometimes with small, circular glands; outer sepals 6–8 × 3–6 mm; inner sepals 9–12 × 5–8 mm. *Petals* more or less spoon-shaped, 55–65 mm long, white, at inner side tinged violet, when dry orange-brown, ciliolate apically, shortly hairy inside basally. *Stamens* 8, rarely the abaxial median stamen present but then reduced and abortive; filaments 40–45 mm long, lanate in basal half, glabrous to hairy in apical part; anthers 2.2–3.2 mm long, glabrous or basally with very short, stiff hairs. *Gynoecium* somewhat longer than stamens. *Ovary* orange-brown when dry. *Fruit* up to 9 × 6 cm, when dry attenuate at base and apex, reddish brown, wrinkled.

Distribution. Australia, N. Queensland, north of Cairns (scattered localities between 16°04'–35'S, 145°15'–22'E; 9 coll.).

Notes. 1. Possibly a hybrid between species of subg. *Brunophyllum* and subg. *Macintyria*. See chapter 2.3.1.

2. Thanks are due to Mr. B.P.M. Hyland and his staff (C.S.I.R.O., Forest Research Institute, Atherton, Australia) for making the fine collections of this rare species which was known from the two syntype collections only.

3. Vegetatively strongly resembling the other Australian species, *93. X. octandrum*, but differing in the very large laminar glands.

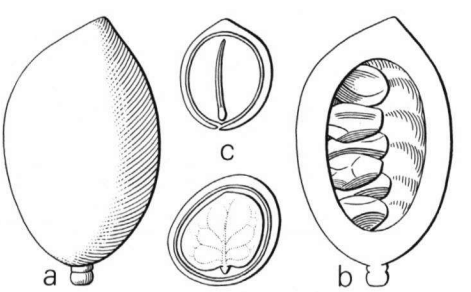


Fig. 21. *92. X. fragrans.* – a. fruit, x 0.5, b. fruit, longitudinal section, x 0.5, c. seed, two longitudinal sections, x 0.5 (a–c: *Hyland 7747*).

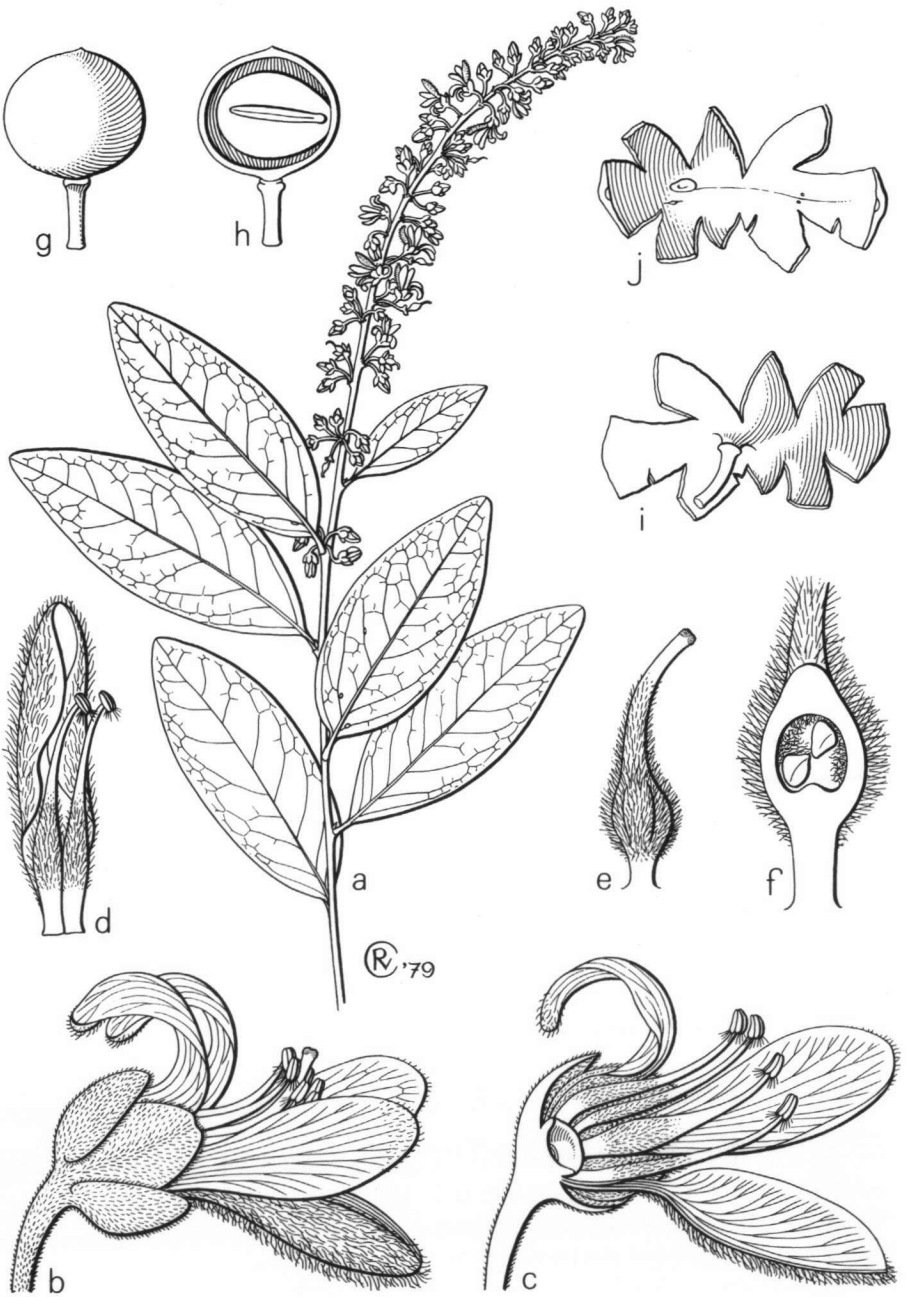


Fig. 22. *93. X. octandrum.* — a. habit, x 0.5; b. flower, x 3; c. flower, longitudinal section, gynoecium removed, x 3; d. carina, x 3; e. gynoecium, x 3, f. ovary, longitudinal section, x 6; g. fruit, x 1; h. schematic section of fruit and seed, x 1; i. opened fruit, from below, x 1; j. opened fruit, the seed removed, x 1 (a–f: *Hyland 9161*; g–j: *Webb & Tracey 5963*).

7. Subgenus Macintyria

Subg. *Macintyria* (F. Muell.) Meijden, Bot. J. Linn. Soc. 67 (1973) 117. – *Macintyria* F. Muell., Fragm. Phyt. Aust. 5 (1865) 8. – Type: *Macintyria octandra* F. Muell. (= *93. X. octandrum*).

Nodal glands absent. *Leaf blade:* tertiary nerves coarsely reticulate. *Inflorescences* unbranched or very rarely with a side axis, in basal part with clusters of up to 30 flowers. *Petals* unequal, carina unguiculate, not auriculate, lateral and upper petals oblanceolate to linear, almost flat, subglabrous outside. *Stamens:* filaments free, hairy above base. *Ovary* hairy; style hairy; stigma small, more or less bilobed; ovules 4. *Fruit* dehiscent, irregularly 2-valved, c. 1.8 cm diam. *Seed(s)* 1 (or 2), globular, c. 1.5 cm diam.; testa 3-layered, outer layer thin, leathery, middle layer spongy, c. 0.3 mm thick when dry (and often torn completely), inner layer hard, 0.15–0.2 mm thick; albumen copious, (nearly) separated into two halves; embryo broadly ovate, flat, nerved, green, plumule undifferentiated, radicle exserted.

Species: 1 (93).

93. Xanthophyllum octandrum

Fig. 3A-m, 22

X. octandrum (F. Muell.) Domin, Bibl. Bot. (1927) 306; C.T. White, Contr. Arn. Arb. 4 (1933) 54; Francis, Aust. Rain-forest Trees (1951) 379, 434, 435; J. Ogden, J. Biogeogr. 8 (1981) 405. – *Macintyria octandra* F. Muell., Fragm. Phyt. Aust. 5 (1865) 8. – *X. macintyrii* F. Muell., Fragm. Phyt. Aust. 5 (1865) 57, *nom. illeg.*; Bailey, Compr. Cat. Queensl. Pl. (1913) 44, fig. 27, 781, fig. 918. – *Banisterodes macintyrii* (F. Muell.) O. Kuntze, Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* – Lectotype (selected by Dr. J.H. Ross, South Yarra): *F. von Mueller s.n.* (MEL, no. 1004098, 'Salt Water Creek and mountain range, 8 Jan. 1865').

Shrub or tree up to 30 m high, up to 80 cm d.b.h. *Petiole* 6–9 mm long, not or faintly wrinkled transversely. *Leaf blade* 6–21 × 2–8 cm, apex rounded to shortly acuminate; upper side reddish brown to green, midrib sunken; lower side greenish brown to light green, secondary nerves c. 5–10 pairs, sometimes forming an indistinct intramarginal nerve; glands 2–4(–6), rarely more, mostly present in basal half of the leaf blade, 0.6–1.0 mm diam. *Inflorescences* about as long as the leaves or longer, in their basal part with irregularly spirally arranged clusters of up to c. 30 flowers, apically usually with solitary flowers; axes ribbed, densely minutely hairy; lowermost bracts often like small leaves with short petioles. *Pedicel* 4–5 mm long, densely shortly lanate. *Sepals* shortly lanate outside, appressedly hairy inside, sometimes with glandular spots; outer sepals 2.5–3.0 × 2.4–3.0 mm; inner sepals 2.8–3.5 × 2.7–3.1 mm. *Petals* unequal, white, when dry yellowish, the longest one 7.5–8.5 mm long; carina very densely lanate outside, inside hairy at apex and base; other petals sparsely lanate outside at apex, inside hairy above insertion of filaments. *Stamens:* filaments c. 5 mm long, appressedly hairy above base, further glabrous; anthers 0.5–0.7 mm long, with stiff hairs at base. *Gynoecium* somewhat longer than stamens. *Ovary* 0.8–1.0 mm stipitate, densely patently whitish hairy outside, inside lanate around the ovules; style patently hairy. *Fruit* more or less globular, but basally attenuate and strongly flattened, apically slightly beaked, dull, orange-brown to dark brown; dehiscent in a peculiar way: separating to near the base into two valves which, upon drying, rupture laterally.

Distribution. Australia, N. Queensland, coastal region between Cooktown and Mackay, 15°45'–21°S; 50 collections.

Notes. 1. In many collections the flowers seemed to be turned upside-down (pedicel twisted a half turn). I do not know whether they indeed turn the carina upwards or are situated on pendent twigs.

2. According to Ogden (*l.c.*) trees of this species can become very old: a ^{14}C-measurement gave 650 ± 100 years. In the same publication it is mentioned that some individual trees are *at least* 2594 years old; this should be confirmed by ^{14}C-measurements, too.

INCOMPLETELY KNOWN SPECIES

94. Xanthophyllum oliganthum

X. oliganthum C.Y. Wu, Acta Bot. Yunnanica 2 (1980) 75.

"Species X. excelso Bl. affinis, sed plantis arborescentibus, foliis ellipticis longe caudato-acuminatis, floribus luteo-albis, majoribus atque paucioribus, 1–1.2 cm. longis differt."

"Frutex ad arborescentem 2–4 m. altus; ramulis luteolo-fulvis. Folia chartacea elliptica 11–14 cm. longa, 2.5–5 cm. lata, apice caudato-acuminata, acumine 3 cm. longo, basi cuneata, margine undulata, glabra, costa utrinque prominenta, nervis lateralibus 6–7-jugis, nervis tertiariis parallelis; petiolo 5 mm. longo. Inflorescentia racemosa vel paniculata, terminalis, circ. 4 cm. longa, oligantha, pedicellis 6–7 mm. longis, dense puberulis; sepalis 5, inaequalibus, puberulis; petalis 5, fere aequalibus, luteo-albis 1–1.2 cm. longis, carina albo-puberula; staminibus 8, quarum 5 in basi petalorum adnatis, filamentis basi tumentibus, pubescentibus; ovario ovato, glabro, stipitato et disco praedito, stylo 9 mm. longo, dense fulto-albeque puberuli, stigmatibus bilobatis. Fructus globosus, 2–3 cm. diam.; seminibus sphaeroideis indigoticis, 1.6 cm. diam."

"Yunnan: He-kou, alt. 320 m., Apr. 28, 1961, S.J. Hsuan 61–0080 (typus, KUN); eod. loco. K.H. Tsai 367, Kiangxin 4."

Note. Description and picture leave no doubt that *X. oliganthum* belongs to sect. *Xanthophyllum*, as it has scalariform tertiary nerves. According to the description it differs from *1. X. flavescens* in a number of characters. As far as can be judged from this incomplete description, it comes near to *13. X. annamense* from Vietnam, differing however in the colour of the hairs on the carina (white; in *X. annamense* brown).

95. Xanthophyllum yunnanense

X. yunnanense C.Y. Wu, Acta Bot. Yunnanica 2 (1980) 77.

"Species nova affinis X. siamensi Craib, sed gemmis axillaribus 2; foliis lineari-lanceolatis, 8–15 cm. longis, 1.8–3.5 cm. latis; racemo axillari, dense puberuli; infructescentiis 2.5–3.4 cm. longis, fructibus juvenilibus basi pubescentibus, demum glabrescentibus valde insignis."

"Arbor 10–15 m. altus, 38 cm. diam.; ramulis glabris; gemmis 2 axillaribus, supra 1 majoribus. Folia coriacea lineari-lanceolata, 8–15 cm. longa, 1.8–3.5 cm. lata, apice acumina-

ta, basi cuneata, margine in sicco minute undulata, utrinque glabra, nervis lateralibus 7–8-jugis, nervis tertiariis reticulatis; petiolo fulvo, 0.6–1 cm. longo. Racemi axillares dense puberuli; flores non visi. Infructescentia 2.5–3.4 cm. longa, pedicellis crassis, circ. 5 mm. longis, dense testaceo-tomentosis. Fructus globosus 2 cm. diam., juvenilis basi pubescens, demum glabrescens; seminibus globosis, nigris, cotyledonibus crassis."

"Yunnan: Meng-hai, alt. 1800 m., July 1936, C.W. Wang 77281 (typus, KUN); Jinghong, da-meng-long, C.W. Wang 78313, 78369, 78457, alt. 1800–1950 m. in mix forest."

Note. This species, described only with immature fruits, is very difficult to place. Almost certainly it is not allied to *X. siamense (= 1. X. flavescens)* with which it is compared (because the latter species does not have a basally hairy ovary). It may be allied to *69. X. punctatum*, or to *72. X. bibracteatum.*

DOUBTFUL SPECIES

D1. Xanthophyllum bombayanum

X. bombayanum Chodat, Bull. Herb. Boiss. 4 (1896) 263; Blatter, J. Bomb. Nat. Hist. Soc. 34 (1930) 303. – Type: unknown.

Note. No *Xanthophyllum* species is known from Bombay. The type collection should be in K; the name of its collector was unknown to Chodat.

D2. Xanthophyllum eglandulosum

X. eglandulosum Griffith, Notul. 4 (1854) 537, t. 598, fig. 4; Kurz, J. As. Soc. Beng. II, 42 (1873) 80; For. Fl. Br. Burma 1 (1877) 81. – Type: unknown, 'In sylvis Mergue: March, 1835'.

Note. Kurz considered *X. griffithii* Hook. *f. ex* A.W. Bennett as a synonym of *X. eglandulosum* Griffith. Griffith's figures give a transverse and a longitudinal section of the ovary from which can be deducted that the ovary contained 8 ovules. This is never so in *X. griffithii.* In the transverse section the placentas are indicated as protruding, which leads to *X. flavescens* Roxb. or to *X. affine* Miq.; only from *X. flavescens* I have seen Griffith collections from Mergui, but none dating from March, 1835. Indirectly, the fact that Griffith mentions that the style is hairy but writes nothing about the hairiness of the ovary may mean that it is glabrous indeed, as in *X. flavescens.* Also the colour of the petals 'alba dedum luteo-fuscentia' can be used for petals of the last species. Without the type collection it is impossible to decide the true identity of *X. eglandulosum.*

EXCLUDED SPECIES

E1. Xanthophyllum glaucescens Miq., Fl. Ind. Bat. Suppl. (1860) 394; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274. – Type: *Teysmann HB 512* (U; iso BO, U). Identified by Kostermans as Litsea insignis (Bl.) Boerl. (*Lauraceae*).

E2. Xanthophyllum hebecarpum Chodat, Bull. Herb. Boiss. 4 (1896) 263; Ridley, J. Str. Br. R. As. Soc. 73 (1916) 139; Fl. Mal. Pen. 1 (1922) 149. – Type: *Curtis 1639* (K, *n.v.*). Identified by Symington, Kew Bull. (1937) 318 as **Ryparosa kunstleri** King (*Flacourtiaceae*); Sleumer, Fl. Males. I, 5 (1954) 48.

E3. Xanthophyllum subglobosum Elmer, Leafl. Philip. Bot. 5 (1913) 1676. – Lectotype: *Elmer 9470* (L; iso BM, E, G, W, Z). Identified by Merrill, En. Philip. (1923) 485 as **Siphonodon celastrineus** Griffith (*Celastraceae*); Ding Hou, Fl. Males. I, 6 (1964) 395.

E4. Xanthophyllum subglobosum var. *longifolium* Elmer, Leafl. Philip. Bot. 5 (1913) 1677. – Lectotype: *Elmer 13937* (L; iso A, BM, C, E, FI, G, K, P, W, Z). See under *E3*.

INDEX TO TAXONOMIC NAMES

Accepted names in roman type; new taxa and combinations in **bold type**; synonyms in *italics*. The numbers refer to the number of the accepted taxon. D: doubtful species; E: excluded species.

Banisterodes
affine 8
ellipticum 79
excelsum 1
glaucum 67
griffithii 32
insigne 88
longifolium 36
macintyrii 93
maingayi 60b
obscurum 88
rufum 14
stipitatum 86a
vitellinum 36
Bannisterioides 77

Eystathes sylvestris 66

Guatteria incerta 37

Jakkia ('*Jackia*')
excelsa 1
longifolia 36
vitellina 36

Kaulfussia geminiflora 16 (77)

Litsea insignis E1

Macintyria octandra 93
Monnina
excelsa 1
longifolia 36
macrophylla 36
vitellina 36
Monoon incertum 37

Paelae 77
Pelae 77

Ryparosa kunstleri E2

Siphonodon celastrineus E3, E4
Skaphium lanceatum 67

Valentinia sylvestris 66

Xanthophyllum
subg. Brunophyllum p. 144
subg. **Coriaceum** p. 133
subg. **Exsertum** p. 139
subg. **Grandiflorum** p. 150
subg. Macintyria p. 153
subg. **Triadelphum** p. 135
subg. Xanthophyllum p. 63
sect. Eystathes p. 81
subsect. Eystathes p. 121
subsect. **Jakkia** p. 81
sect. Xanthophyllum p. 63
acuminatissimum ?37
adenopodum 1
adenotus 38
var. adenotus 38a
var. **lineare** 38b
affine 8 (29, 75, 89)
f. *excelsa* 1
var. *adenopodum* 1
var. *puberulum* 8
amoenum 85 (86)
ancolanum 28
f. *angustifolia* 28
andamanicum 76
angustifolium 16
angustigemma 44
annamense 13
arnottianum 16
arsatii 38
beccarianum 52
bibracteatum 72

(Xanthophyllum)
bombayanum D1
borneense 18
bracteatum 45
brevipes 87
bullatum 2
burkillii 73
celebicum 80
ceraceifolium 40
chartaceum 91
citrifolium 79
clovis 42
cochinchinense 35
cockburnii 4
colubrinum 31
contractum 82
cordatum 38 (39)
f. *aequale* 38
cucullatum 70
curtisii 36
densiflorum 51b
discolor 48
subsp. discolor 48a
subsp. macranthum 48b
eberhardtii 5
ecarinatum 90
eglandulosum D2
ellipticum 79
var. *subcoriaceum* 22
erythrostachyum 57
eurhynchum 60
subsp. eurhynchum 60a
subsp. **maingayi** 60b
excelsum 1
var. *affine* 1
ferrugineum 7
flavescens 1 (16, 36, 77)
var. *angustifolium* 16
var. *virens* 75
flavo-virens 48b
flavum 14
floriferum 1
forbesii 57
fragrans 92
geesinkii 34

(Xanthophyllum)
geminatum 71
geminiflorum 16 (77)
glabrescens 18
glandulosum 1
glaucescens E1
glaucum 67
gracile 32b
griffithii 32 (36)
subsp. **angustifolium** 32b
subsp. **erectum** 32c
subsp. griffithii 32a
var. *angustifolium* 32b
var. *curtisii* 36
var. *montanum* 33
hainanense 68
var. *occidentale* 69
havilandii 8
hebecarpum E2
heterophyllum 46
heteropleurum 14
hildebrandii 83
hookerianum 36
hosei 6
hypoleucum 48a
impressum 30
incertum 37
insigne 88
kalimantanum 90
kingii 79
korthalsianum 47
kunstleri 36
laeve 58
lanceatum 67
laoticum 66
lateriflorum 74
loheri 1
longifolium 36
macintyrii 93
macrophyllum 15
maingayi 60b
malayanum 63
microcarpum 67
molle 54
montanum 81

(Xanthophyllum)
monticolum 33
multiramosum 1
neglectum 23
ngii 65
nigricans 17
novoguinense 64
obliquum 1
var. *viride* 1
obscurum 88
octandrum 93
oliganthum D1
ovatifolium 20
palawanense 39
palembanicum 28 (23, 60)
pallidum 1
paniculatum 36
papuanum 89
parvifolium 26
parvum 32b
pauciflorum 24
pedicellatum 53
penibukanense 49
petiolatum 41
philippinense 27
poilanei 19
pomiferum 66
pseudoadenotus 50
pseudostipulaceum 32b (46)
puberulum 61
pubescens 9
pulchrum 51
subsp. pulchrum 51a
subsp. **stapfii** 51b
punctatum 69
purpureum 54
racemosum 68
ramiflorum 78
reflexum 43
resupinatum 10
(Xanthophyllum)
reticulatum 55
retinerve 59
robustum 36
var. *elmeri* 36
roxburghianum 16
rufum 14
sarawakense 8
schizocarpon 11
scortechinii 88
siamense 1
stapfii 51b
stipitatum 86
var. *borneense* 86a
var. **glabrum** 86b
var. *nitidum* 85
var. *pachyphyllum* 85
var. stipitatum 86a
subcoriaceum 22
suberosum 84
subglobosum E3
var. *longifolium* E4
sulphureum 3
sumatranum 28
sylvestre 66
tardicrescens 25
tenue 21
tenuipetalum 29
trichocladum 56
undulatum 16
velutinum 12
venosum 62
verrucosum 60a
virens 75
vitellinum 36
var. *clovis* 42
wrayi 61
yunnanense D2
zeylanicum 77