SCALA MILLETTIEARUM

A survey of the genera of the Millettieae (Legum.-Pap.)
with methodological considerations

BY

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In commemoration of the centenary of
George Bentham (22. ix. 1800 — 10. ix. 1884)

CONTENTS

SUMMARY

In the present revision the tribe *Millettieae* comprises 43 genera, 4 of which are either new, or former subgenera or sections here raised to generic rank: *Austrosteenisia, Endosamara, Imbralyx,* and *Paraderris.* The genera *Brachypterum, Callerya, Deguelia, Philenoptera,* and *Sarcodum,* generally not accepted for 50 years or longer, have been reinstated. The genera *Derris, Lonchocarpus,* and *Millettia* received a more restricted circumscription than usual. *Ostryocarpus* includes also the commonly accepted genera *Aganope* and *Xeroderris.* The rather common and rather widespread genera *Muellera* and *Pongamia* have been reduced to *Lonchocarpus* and *Millettia* respectively.

New combinations on specific rank are limited to the type-species of new or hitherto untypified genera, viz. *Austrosteenisia blackii, Callerya nitida, Endosamara racemosa, Imbralyx albiflorus, Paraderris cuneifolia.* One more combination, *Afgekia filipes,* not a type-species, is made.

All genera as here conceived are defined by a monothetic set of characters, most genera have also unique characters. The genera *Apurimacia, Craspedolobium, Derris, Lonchocarpus, Margaritolobium, Millettia, Paraderris, Philenoptera, Platycyamus,* and *Requienia* lack unique characters.

A key is presented, also containing genera that are likely to be mistaken for members of the *Millettieae.* The genera are presented in alphabetical order as no unambiguous subdivision of the tribe could be made.

Two different (but complementary) numero-cladistic methods have been applied (chapters 5, 6, and 7). Zandee's three-taxon-statements-permutation method resulted in numerous possible cladograms with many parallels. With a more restricted selection of characters it did not result into a fully resolved cladogram. Meacham's compatibility analysis, slightly modified, resulted in three different meagre cliques of mutually compatible characters, therewith exactly indicating the cause of the complexity already intuitively recognized.

The tribe is paraphyletic and, in order to obtain a more satisfactory picture of its natural structure (if attainable at all in this tribe), similar treatments will have to be made of the "surrounding" tribes *Dalbergieae, Bossiaeeae, Brongniartieae, Robinieae, Phaseoleae* (at least its subtribe *Glycininae s.l.*), and *Abreae.* Also more (new) characters have to be found and considered, as the characters used in this study have insufficient mutual compatibilities.

ACKNOWLEDGEMENTS

1. WHY THIS REVISION?

Slightly more than ten years ago I started a revision of the S. E. Asiatic species of the genus *Millettia*. The distinction of the described species did not seem too difficult and after a few years I could recognize most of them on sight. More alarming was a growing "pile" of flowering material that could represent either unknown species of *Millettia* or species of other genera. The latter appeared to be the case, but the genera to which the material belonged were, in flowering stage, not or hardly distinguishable from *Millettia*. Moreover, these genera were (at that time) still placed in different tribes. I tried to rearrange the existing supraspecific taxa in order to obtain genera with differentiating characters. I submitted these proposed initial changes to Dr. R. M. Polhill, who reacted with little enthusiasm, to put it mildly; he warned me that I was touching a world-wide problem that could not be satisfactorily solved on the basis of a regional S. E. Asiatic revision only. He suggested either a wider scope, or maintenance of the (then) present generic circumscription. I plumped for the first suggestion, and presented on the first International Legume Conference (Kew, 1978) a key to the genera. It appeared that the generic relations in this tribe (then called *"Tephrosieae"*) were about as complex as those in the *Mimosoideae-Ingeae* and in the *Papilionoideae-Phaseoleae,* and Dr. B. Verdcourt assured me that, according to his experience, he doubted if a satisfactory solution was possible at all.

As this study (see chapters 6 & 7) demonstrates, he was correct. During the elaboration of the tribal treatment in the framework of the Proceedings of this Legume Conference, I found more and more unsolved (or unsolvable) problems. After the treatment was written I decided to continue the project for some time, were it alone for a more precise description of the complexity observed. A revision of the tribe based on species revisions would have been the best 'attack', but this would inhibit too much the planned contributions to the treatment of the *Papilionoideae* for the Flora Malesiana, the Flora of Thailand, and the "Flore du Cambodge, du Laos, et du Viet-Nam".

A compromise between moderately heavy leaning on existing literature randomly checked with herbarium material and what can be considered a "selective search for difficulties" appeared to be possible, resulting in the present revision. It was considered to be "completed" after smaller groupings with monothetic sets of characters (see chapter 5) were obtained and after two supplementary numero-cladistic approaches had failed to result into one, unambiguous grouping of these smaller groups. The next step necessary to obtain "better" genera and a classification thereof will be species revisions of the 'genera' here distinguished, and to start the whole comparison of "all with all" all over again. I hope that within the frameworks of the larger floras now in progress a new and better generic arrangement can be achieved after a few decades.

2. DEVELOPMENT OF THE CONCEPT OF THE TRIBE MILLETTIEAE

The history of the tribe *Millettieae* can be summarized as the history of three groups and of some "nomadic" genera. The history of the 'nomadic' genera (e. g. *Disynstemon, Sarcodum, Hesperothamnus, Craspedolobium*) cannot be generalized, and is presented in the nomenclatural and taxonomic notes under these genera in the taxonomic part. The three groups are:

1. The genera 'around *Tephrosia*'. These comprise subshrubs or herbs with woody base of the stem (*Mundulea, Chadsia, Requienia, Ptycholobium, Lupinophyllum,* and *Caulocarpus*).
2. The genera 'around *Millettia*'. These comprise woody plants with dehiscent pods (e. g. *Callerya, Wisteria, Afgekia, Fordia, Dewevrea, Craibia, Schefflerodendron, Platysepalum*).
3. The genera 'around *Derris*'. These comprise woody plants with indehiscent pods (e. g. *Ostryocarpus, Leptoderris, Kunstleria, Lonchocarpus, Piscidia*).

In the first natural subdivision covering all *Leguminosae*, De Candolle (1825) put the three groups almost completely together in his tribe *Loteae*, subtribe *Galeginae* (as "*Galegeae*"). This subtribe comprised also the presently separated tribes *Galegeae (s. s.), Robinieae,* and even some *Dalbergieae* (e. g. *Machaerium*). He distinguished a tribe *Dalbergieae*, consisting of the genera *Dalbergia, Pterocarpus,* with some allies, plus the genera *Derris, Pongamia,* and *Deguelia* of group 3. In 1837, Bentham added the first discovered genera of group 2 to the tribe *Loteae*, subtribe *Galeginae*, and transferred the genera *Lonchocarpus* and *Muellera* to the tribe *Dalbergieae*. Miquel (1855) described the tribe *Millettieae*, containing the East Asiatic genera of the groups 2 and 3, and *Mundulea* of group 1. The rest of group 1 was maintained in the tribe *Loteae*, subtribe *Galeginae*.

In his monograph of the tribe *Dalbergieae* Bentham (1860) noted the difficulties in distinguishing the groups 2 and 3. He considered the dehiscence of the pod the best expedient for the basis of the distinction of the tribes *Galegeae* and *Dalbergieae*. He raised the former subtribe *Galeginae* to tribal rank in 1865 and placed the groups 1 and 2 in it, maintaining group 3 in the *Dalbergieae*. This situation was maintained untill 1964, when Hutchinson raised most of Bentham's subtribes to tribal rank and described some more new tribes. Gillett (Flora of Tropical East Africa, 1971) combined groups 1 and 2 in the tribe *Tephrosieae*. The system adopted by Hutchinson is discussed by Polhill (1981), who contributed most tribal treatments in the Proceedings of the first International Legume Conference (Kew, 1978, see Polhill & Raven, 1981). In Polhill's system the tribe *Millettieae* (as "*Tephrosieae*") reached its present extension and, as explained in the next chapter, I expect that in the future the concept will become more extended.

3. DELIMITATION OF THE MILLETTIEAE AND RELATED TRIBES

The contents of this chapter will be disappointing for those who expect a final answer to the question suggested by the title. The answers given below are the ones at present possible, but the delimitation of the *Millettieae* from the related tribes needs to be revised completely after these 'surrounding' tribes are investigated in more detail than has been done up till now. I will restrict the delimitations to a discussion on the monothetic 'kernel' of characters surrounded by a more vague polythetic 'pericarp', that in combination provides the only possibility to distinguish the tribes.

The concepts "monothetic" and "polythetic" are explained in more detail in chapter 6. In short, a *monothetic* set of characters is the set present in all members of a taxon (i. e. at least in a particular stage of their life), characteristic for the taxon in that combination, but the characters (may) occur separately also in surrounding taxa, but not in that particular combination. A *polythetic* (set of) character(s) is not present in all members, but occurs in a majority of members, and occurs also in the surrounding taxa, but not in the observed combination. *Unique* characters do not belong to either category, but the *Millettieae* have no unique characters on tribal level.

In the relational scheme presented by Polhill (1981, p. 199) the tribe *Millettieae* (as "*Tephrosieae*") has a central position. There are sets of characters in common with many other tribes. An 'imprecise' rearrangement of this scheme, presented in Polhill's fig. 4 (below, same page) shows that the tribe is supposed to represent the recent members of a relatively old group, ancestral to all other tribes with 'more advanced' flower structure.

In order to give a complete survey on the delimitation of the recent tribe, I should give the relations to all other Papilionoid tribes. I consider this a useless undertaking in the present stage of my knowledge. This can better be done in the framework of a complete cladistic rearrangement on tribal level, which is beyond the scope of the present study. I will restrict the discussion to the seven tribes, tabulated in table 3.1. The tabulated characters form a monothetic set with a few polythetic ones (i. e. the characters listed with "most" or "usually") and they are abstracted from Polhill & Raven (1981). The unique characters, as far as present, are mentioned in the lowermost row.

Instead of discussing the characters in this table I prefer to do that from a speculative and incomplete cladogram (fig. 3.3) I derived from the characters mentioned in table 3.2. The cladogram is different from the usual shapes of cladograms in two aspects: 1. The exceptions have been indicated by white or black parts of the squares or rectangles indicating the characters. 2. The terminal taxa mentioned are those without apomorphic characters: one main line in the cladogram ends in the *Millettieae,* only definable by being "non-*Dalbergieae-Brongniartieae-Robinieae-Phaseoleae*". This position indicates that the tribe *Millettieae* is paraphyletic (see chapter 5 for discussion on this matter). In a more detailed cladogram the group would have consisted of several lines parallel to each other, placed below the groups forming the (here) holophyletic (Ashlock, 1971; Holmes, 1980) group of the *Phaseoleae*.

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Table 3.1. The main characters of the tribe *Millettieae* and the related, surrounding tribes.

	Dalbergieae	*Robinieae*	*Brongniartieae* *Bossiaeeae*	*Millettieae*	*Phaseoleae*	*Abreae*	*Galegeae*
Woodrays	generally uniseriate	pluri- & uniseriate	unknown	pluriseriate	pluriseriate	pluriseriate	—
Twigs	woody	woody	woody	woody	few woody, most herbaceous	woody	herbaceous
Inflorescence	panicles or derived corymbs	panicles or axillary racemes	panicles or axillary racemes or flowers solitary	panicles or pseudo-racemes or derived pseudopanicles	usually pseudo-racemes or derived pseudopanicles (few panicles)	pseudoracemes	racemes or flowers solitary
Hypanthium	usually distinct	usually distinct	indistinct	usually indistinct	indistinct	indistinct	indistinct
Wing petals	free from keel	adherent to keel	free from keel	mostly adherent to keel	adherent to keel	adherent to keel	adherent to keel
Keel petals	imbricate subfree	valvately connate	valvately connate	usually valvately connate	valvately connate	valvately connate	valvately connate
Pod	indehiscent	dehiscent	dehiscent	dehiscent or indehiscent	dehiscent, few indehiscent	dehiscent	dehiscent
Seed chamber	present	absent	absent	mostly absent	absent	absent	absent
Seeds	1 or few	usually several	1 or few	1 or few	1 to several	several	few or several
Radicle	straight or folded	folded	straight or folded	folded, few straight	folded	folded	folded
Non-protein amino-acids & amines	absent	only canavanine	absent or only canavanine	various	various	absent	canavanine
Unique character	primitive flower structure	none	distinct aril	none	most genera 3-foliolate; basiscopic side enlarged	alkaloids, pari-pinnate leaves	herbaceous

Table 3.2. Apomorphies used for the tribal scheme (table 3.3).

1. reduced hypanthium
2. connate keel petals
3. specialized seed chambers
4. numerous ovules (over 15)
5. stipulae spinose
6. scattered spines
7. dehiscent pods
8. style with pollen scrape hairs
9. bird flower syndrome
10. herbaceous climbers
11. trees
12. woody lianas
    (shrubs, considered primitive)
14. 2n = 42
15. 3-foliolate leaves, with basiscopic side lateral leaflets enlarged
16. stipellae gland-like
17. pseudoracemes/pseudopanicles
18. axillary racemes
19. hyaline multicellular glandular hairs
20. pod samaroid, 1-seeded
21. bracteoles absent
22. pluriseriate woodrays
23. uniseriate woodrays
    (primitive condition of 22 & 23 = both combined)
24. 2-lipped calyx
25. distinct aril

From both phylogenetic and taxonomic points of view I have no objections against paraphyletic groups, because these are as monophyletic (in the sense of Simpson, 1961, and Mayr, 1974) as holophyletic groups are. Löther (1972) links the "objective existence" (i. e. "the existence in nature, independent of man's ability to perceive them", Wiley, 1981, p. 72) of taxa to their supposed monophyly. Löther regards taxa (in his reasonings confined to species) as being substantial systems (*"materielle Systeme"*) with their own role, place, and evolutionary tendencies (as formulated by Simpson, 1961). As evolution is supposed to work actually on population level, an evolutionary event leading to a holophyletic higher group (here *Phaseoleae*) does not have effect on the other (unchanged or changed in another way) existing populations which form the remainder of the original group ("pre-*Millettieae*", now forming the present *Millettieae*). Even though the recent paraphyletic *Millettieae* and the recent holophyletic *Phaseoleae* share the same ancestral group ("pre-*Millettieae*") both are claimed (here) to "exist" in the sense of Simpson, Löther, and Wiley. I agree with the cladists (excluding the "transformed cladists"), that only apomorphic characters define groups, but I prefer to restrict this to the "side-branches" of the evolutionary tree.

In short, (syn-)apomorphies define side-branches, the paraphyletic rest-group forms the continuation of the main branch (either "the" main branch, or the continuation of

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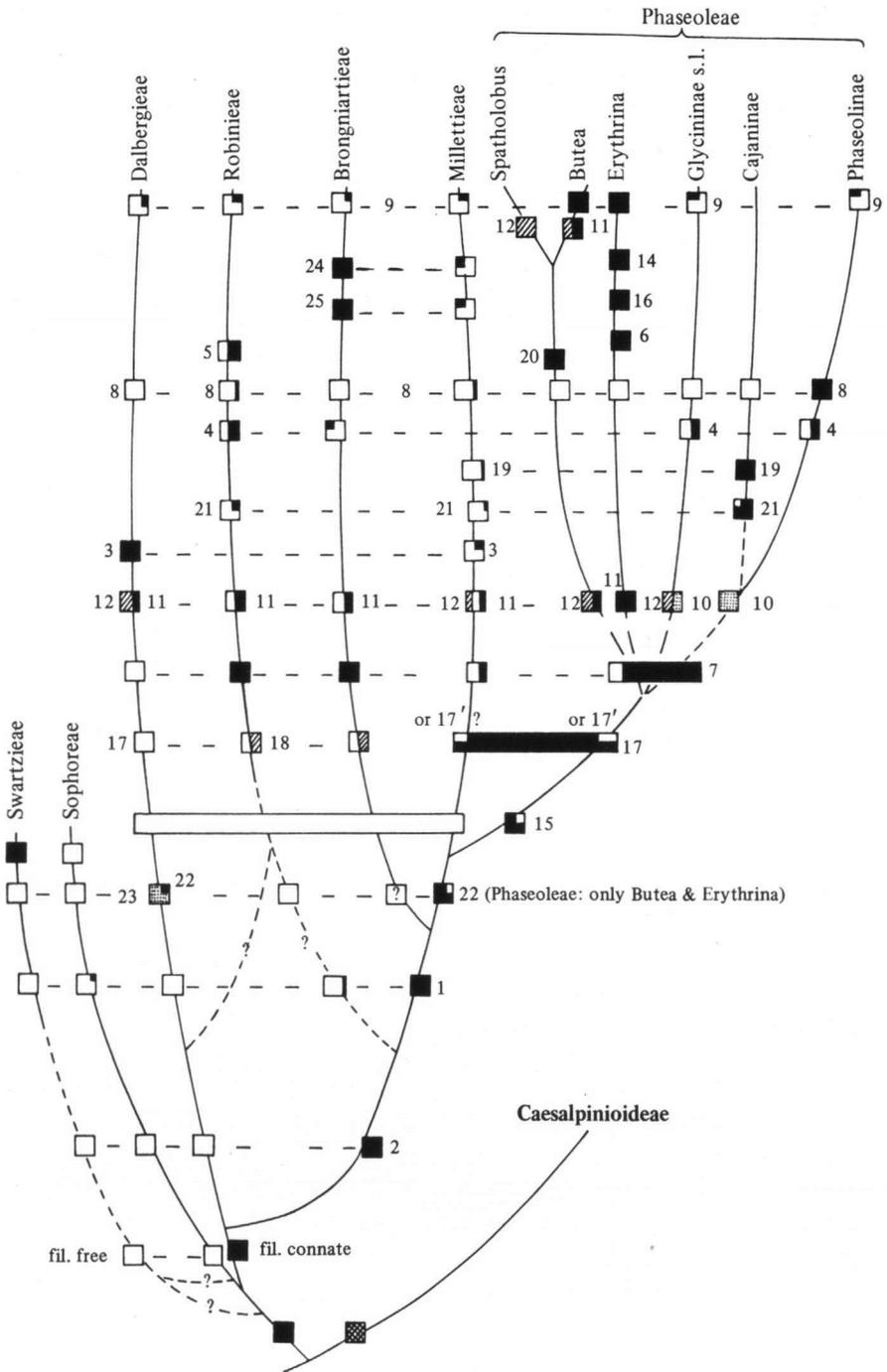
Table 3.3. Cladogram of the tribe *Millettieae* and surrounding, "related" tribes.

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any side-branch). This is the way I prefer to construct trees, and this is deviating from the usual procedures. See further the chapters 5, 6, and 7.

In the cladogram of table 3.3 the holophyletic group *Phaseoleae* is defined by the combination of characters 15 (constant 3-foliolate leaves) and 7 (dehiscent pods). Exceptions do occur (indicated by white sectors), the combination is thus polythetic. The *Phaseoleae* with *Millettieae* together form the next holophyletic group, defined by character 17 (pseudoracemes and pseudopanicles), correlated with the presence of complicated free amino-acids and amines (not in the scheme). The *Millettieae* show many plesiomorphic characters (not or rarely present in *Phaseoleae*), lack autapomorphies, and thus form a paraphyletic (terminal) group. Fossils from the period before segregation of the *Phaseoleae* will thus be recognized as "belonging" to the *Millettieae*, but the phylogenetic implications of this view will be elaborated later in a separate paper.

The tribe *Brongniartieae* is defined by the presence of a distinct aril and a two-lipped calyx, both either autapomorphic or plesiomorphic characters. In the first case the *Brongniartieae* are a side-branch, in the latter case, the continuous line should have been drawn towards the *Brongniartieae* (with or without *Bossiaeeae*, not taken up in the cladogram) and the holophyletic group *Millettieae* plus *Phaseoleae* would have been a side-branch. Disposition of the tribe *Robinieae* is not yet possible: The group needs a detailed reinvestigation of the generic characters and I expect that at least some genera (e. g. *Sesbania, Hebestigma*) can better be transferred to the *Millettieae*.

Robinieae have often a distinct hypanthium, a plesiomorphic inheritance of the *Dalbergieae*-grade of the pre-*Dalbergieae*. The *Robinieae* have free amino-acids (only canavanine), and a more advanced flower structure, similar to that of *Millettieae* and *Phaseoleae*, here marked as character 2 (connate keel petals), but correlated with wings adherent to the keel, and the tendency to monadelphous stamens with (or without) basal fenestrae.

The entire holophyletic group from *Dalbergieae* to *Phaseoleae* has fused filaments, contrary to the *Sophoreae* and *Swartzieae* and the subfamily *Caesalpinioideae*. Exceptionally, fusion of filaments does occur in these groups, but only at their base, and not forming such a distinct sheath or tube as in the *Dalbergieae* and *Phaseoleae*.

The tribe *Sophoreae* is at present under revision (also cladistically) by Dr. C. H. Stirton (Kew) and I am curious to see his interpretation of the relationships of the *Sophoreae* with *Swartzieae* and *Caesalpinioideae* on one hand, and with *Dalbergieae* and "higher" tribes on the other.

The tribe *Abreae* (only comprising the genus *Abrus*) is not depicted in the cladogram. Morphologically, *Abrus* resembles *Millettieae*, except in the paripinnate leaves, but the presence of alkaloids ("instead of" flavonoids, free amino-acids and amines) suggests closer relation with generally "more advanced" tribes, e. g. *Genisteae*.

Also the herbaceous tribe *Galegeae* is not depicted. A cladistic reinterpretation of the structural differences correlated with the herbaceous habit (epulvinate leaf rachis, nodal anatomy) is too much beyond the scope of this revision. The flower structure of the *Galegeae* is, disregarding the specialization, similar to that of the *Millettieae*.

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4. CHARACTERS FOR GENERIC DELIMITATION

Many characters used in the delimitation of the genera of the *Millettieae* can merely be scored as 'present or absent'. Designation (to put it provocatively) of primitive or derived character-states is, as will be explained in chapter 5, 6, and 7, a complicated matter. Some parts, or organs, used as generic characters need some explanation.

Inflorescence

In the next paragraph the flower structure in the *Millettieae* is generalized, and comparison of the structure with that in the tribe *Dalbergieae* reveals that the tribe *Dalbergieae* can be considered to be the outgroup of the *Millettieae*. If this outgroup designation is indeed correct, the uniform inflorescence structure of the *Dalbergieae*, viz. true panicles and variations of it, must be considered a primitive character-state. In the tribe *Millettieae* panicles occur in about half the number of the genera here distinguished. The other half is characterized by "pseudoracemes" or "pseudo-panicles", differing from true racemes and true panicles in bearing the flowers on brachyblasts instead of on elongated axes. The brachyblasts are usually wart-like or short cylindric, and because they are axillary to a bract I consider them homologous to an axis. The reduction of lateral flower-bearing axis to a brachyblast is then to be considered the direction of the evolutionary trend. In the scheme of table 4.1 the assumed reductional series are depicted. The scheme of table 4.1 is very hypothetical, and only vaguely supported by other characters, as demonstrated below and in chapter 7. In the following explanation the frequent use of "is" (and related verbs) should be read as "is supposed to (be)".

The designated outgroup *Dalbergieae* renders the terminal panicle as the most primitive condition. The following three different reductional series can be hypothesised:

Series I represents a reduction (I-a) of the vegetative basal part of the inflorescence bearing twig, followed by three different reductions. Specialization to rami- and caulinascent panicles occurs in some species of *Callerya*. Subseries I-b ends in an axillary raceme, and this subseries is represented by some genera of the *Robineae* and by *Apurimacia*, where both axillary panicles and axillary racemes occur in the same (single) species. Subseries I-e leads to the peculiar kind of pseudoraceme typical for *Paraderris* and predominant in *Lonchocarpus* (*s.s.*). The link between this kind of pseudoraceme and its plesiomorphic axillary panicle is probably contradicted by 4 species of *Lonchocarpus*, discussed under *Philenoptera*. In subseries I-c, the lateral branches of the axillary panicle are reduced to short and slender brachyblasts. Transitional situations occur in *Kunstleria*, *Spatholobus* (tribe *Phaseoleae*), *Ostryocarpus* (e. g. *Derris thyrsiflora*) and some species of *Derris* (*s.s.*). In *Derris* sect. *Dipteroderris* pseudopanicles (I-d) predominate. Further reduction of the brachyblasts to short cylindric or warty ones (as in some spp. in *Derris* sect. *Dipteroderris*) will cause its indistinctness from the (also secondary) pseudopanicles in subseries IV-a.

In reductional series II the terminal panicle is reduced to a terminal raceme (both

conditions present in *Wisteria* and in *Afgekia*), followed by a reduction to axillary racemes (in most genera of the tribe *Robinieae*). The genus *Peteria* (*Robinieae*) has terminal (i. e. leaf-opposed) racemes.

It is conceivable that axillary racemes can aggregate into secondary panicles indistinguishable from primitive ones. Whatever the explanation, some members of the *Robinieae* have terminal and/or axillary panicles.

Reductional series III is more or less parallel to series I. Reduction of lateral branches to short cylindric brachyblasts with scattered flowers is followed by reduction of the vegetative part of the inflorescence bearing twig. The conditions at both sides of the arrows III-b, III-c, and III-e occur in *Millettia*. Specialization to rami- and caulinascent pseudoracemes occurs in *Fordia,* a genus hardly distinguishable from *Millettia* on account of other characters. For convenience, I gave the secondary aggregations to pseudopanicles a different number IV. As pseudopanicles do not occur in genera with true panicles, I regard pseudopanicles as derived from branches with axillary pseudo-racemes. The combination of the latter two conditions occurs in *Millettia* (*s. s.*) (similar to the combined occurrence of the inflorescence type at both sides of the arrow I-d in *Derris s. s.*).

Pseudopanicles with few-flowered brachyblasts, either derived from axillary pseudo-racemes with few-flowered brachyblasts (III-e) or from secondary pseudopanicles (IV-b) are very rare. This condition is occasionally met with in *Millettia* sect. *Fragiliflorae*. As demonstrated in the following paragraph on the phytochemistry, the supposedly more derived chemical constituents (some flavonoid skeletons and free amino-acids and amines) are correlated with the more derived inflorescences in this scheme. The genera with panicles lack the free amino-acids and amines, but some do accumulate them, particularly some species here accommodated in *Callerya* and formerly in *Millettia* sect. *Eurybotryae*. This may indicate that the panicles in these species are secondary, viz. derived from conditions as III-e and IV-b. These putative secondary panicles are (at least in this stage of the study) indistinguishable from putative primitive panicles. Investigation on species level may clarify this conflicting situation.

Flower structure with notes on flower biology

An extensive general survey of the structure of the Papilionoid flower is given by Taubert (1894, pp. 82—94). Surveys emphasizing the functional aspects are given by Goebel (1924, pp. 38—62), Leppik (1966), and Polhill (1976, pp. 163—194). I will not repeat the well-known general features. Flowers with a bird-pollination syndrome are rare in the tribe *Millettieae*; they occur in the American genus *Dahlstedtia* and in the Madagascan genus (or *Tephrosia*-segregate) *Chadsia*. One species of *Millettia* (*M. theuszii*) has also bird-flowers. The majority of genera has rather similarly constructed bee-flowers, and a few scattered species with a very falcate keel have pollen-pump flowers.

The generalized construction of the majority of the *Millettieae* flowers is considered (Polhill, 1981, pp. 200—204) to be slightly more advanced than the flowers in the tribe

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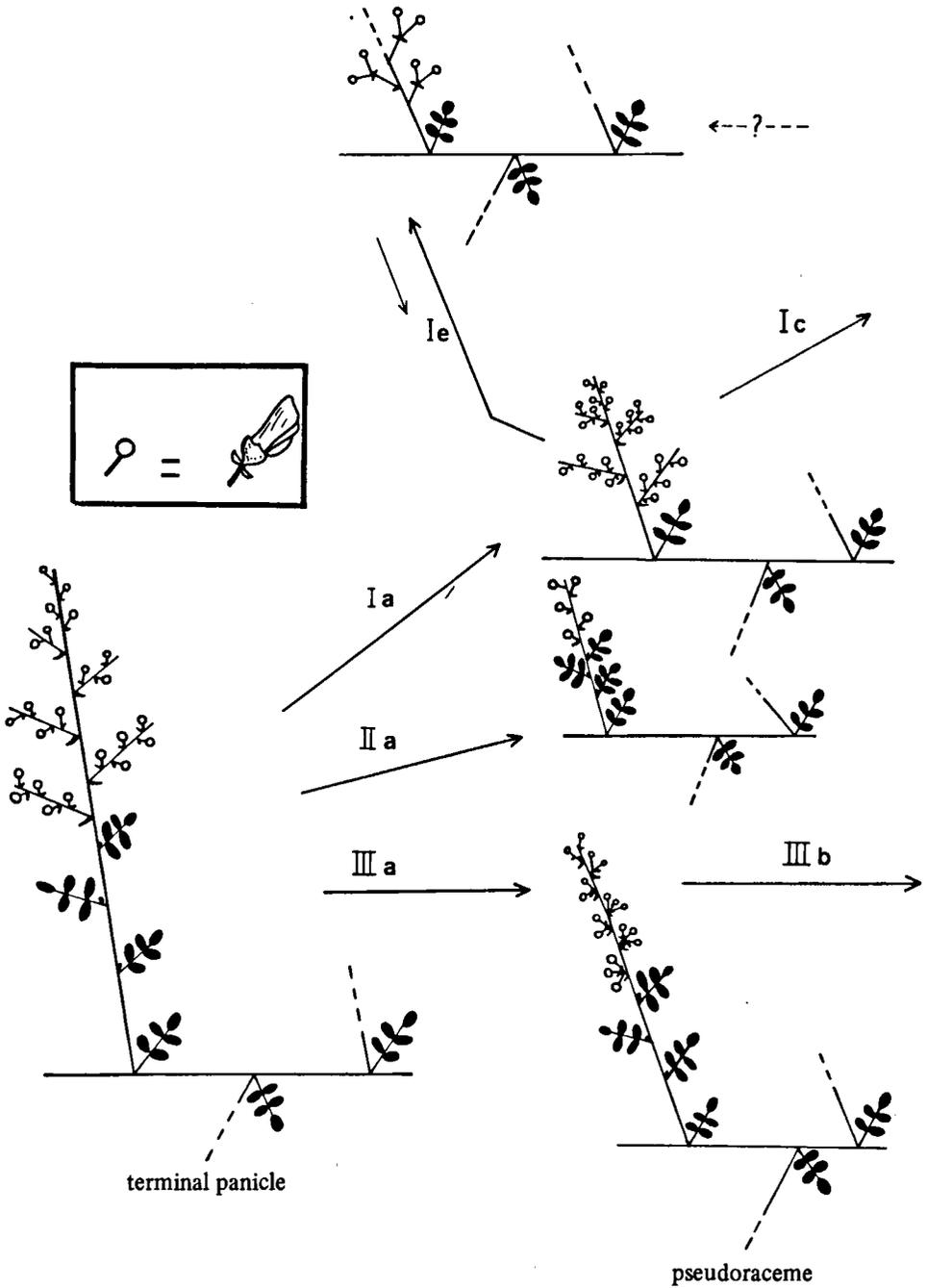
Fig. 4.1. Hypothesized transformation scheme of the inflorescences in the tribe *Millettieae*.

Id

IVa
secondary
pseudopanicle

Ib   axill. raceme

IIb

IIId

IIIc

?

IVa

pseudoraceme

?

IIIe

IVb ? →

secondary pseudopanicle

? IVc

secondary panicle
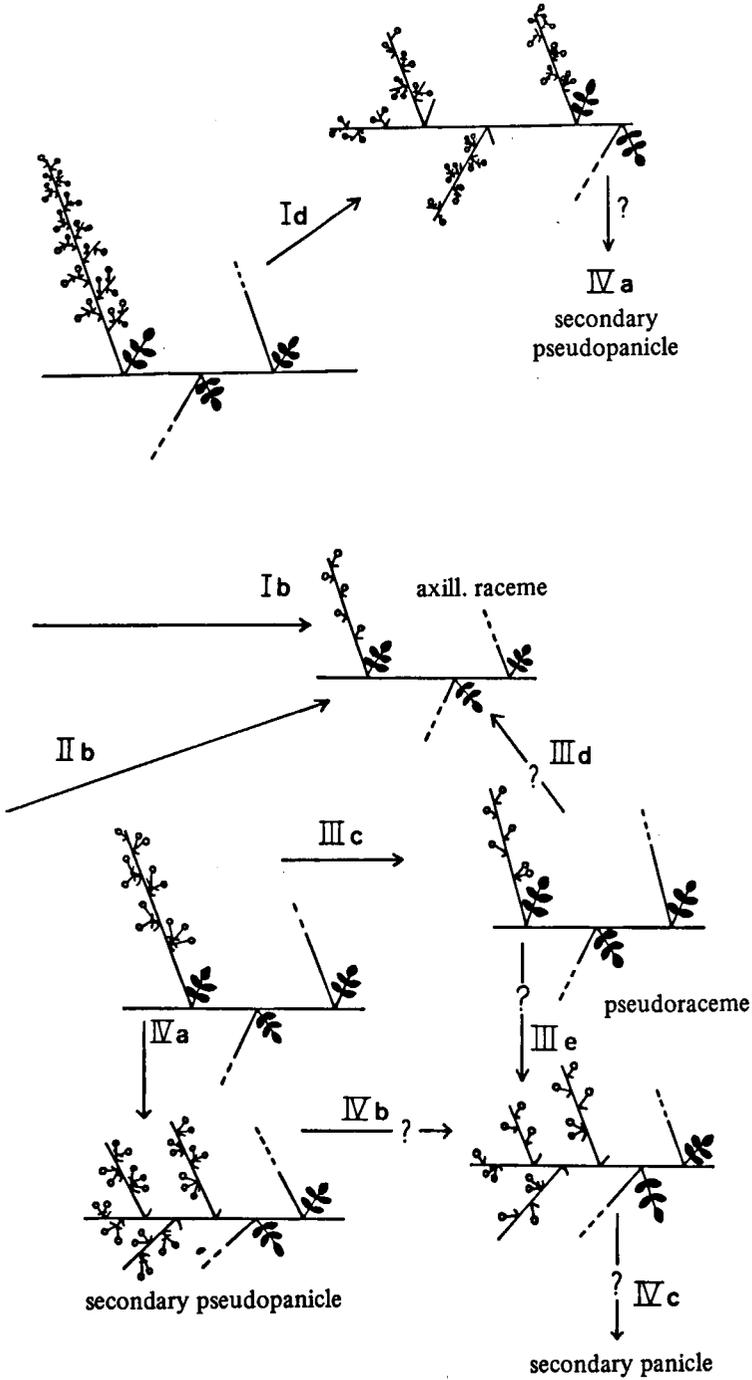
Dalbergieae (Polhill, 1981, pp. 233—235); the standard can have basal, protruding callosities, functioning as lids on the basal fenestrae of the staminal tube (possibly preventing desiccation of the disk). The wing-petals are generally (with a few exceptions) adhering to the keel. The sculptured part of the wing blade is, in *Millettieae*, confined to the basal part, as far as I have seen it (i. e. only the distinct cases visible under a binocular dissecting microscope). Its outside serves as a grip for the bee's feet, and, on its inside, glandular tissue excretes the adhesive between wings and keel. A survey of the different types of petal sculpturing in *Papilionoideae* is given by Stirton (1981). The upper filament is either adnate to the sheath formed by the other nine filaments, or free from it. If the upper filament is adnate, its basal part is usually free leaving at either side an opening called a basal fenestra. In the genus *Millettia* and in some possibly related genera basal fenestrae occur in combination with a free upper stamen (see note under *Millettia*). The functioning of such a generalized flower can best be illustrated by describing a landing of a bee on such a flower (fig. 4.2).

Bees or bumble-bees are attracted by the profuse inflorescence, the smell and a greenish (in fact ultraviolet) patch at the base of the reflexed standard. They hold their legs on transverse ridges near the base of the wing-blades. The mutually adhering unit of joined keel blades adhering to the wing-petals bends slightly downwards because of the elasticity of the four free wing- and keel-claws. The mouthpieces are forced below the basal callosities of the standard, which leads the way via two basal fenestrae of the staminal sheath to the disk surrounding the ovary stalk. After the landing the upper edge of the joined keel blades bursts open (1 a, b), and the stiffer unit of ovary/style and staminal brush touches the bee's abdomen (1). As the majority of the *Millettieae* species are (genetically) incompatible there are no special constructions to prevent self-pollination. The bee starts pumping the nectar, thereby moving its centre of gravity. The elastic wing- and keel-claws bend up- and downwards (2 a) and the staminal brush touches the abdomen repeatedly (2 b). After the visit the basal callosities of the standard close the basal fenestrae again and the procedure may be repeated a few more times, whereby cross-pollination takes place.

As far as is known the *Tephrosieae* are pollinated mainly by bees and bumble-bees and co-evolution may have occurred. On occasion of the International Legume Conference, Kalin Arroyo (1978) presented a paper, unfortunately unpublished, reporting on the pollination biology of four Amazonian woody species from the *Dalbergieae* and *Millettieae*. These species are completely dependent on a rather complicated pollination process. It appeared that all four are self-incompatible and that certain bee species had preferences for one of them, which they visited in the early morning. Later the bees were chased away by another species of bees, but before the first retired to the legume species of its second choice, it tried other specimens of the first species, and Kalin Arroyo argued that this short period was the actual period of (potential) cross-pollination. Herbarium taxonomists could recognize this breeding-mechanism by the relative small number of pods on an originally rich-flowered inflorescence. Data are of course scanty, but it is striking that most wild collections of tropical Asian species usually bear only a few pods per inflorescence, while in specimens gathered e. g. in Botanical Gardens, where "unnatural" pollination takes
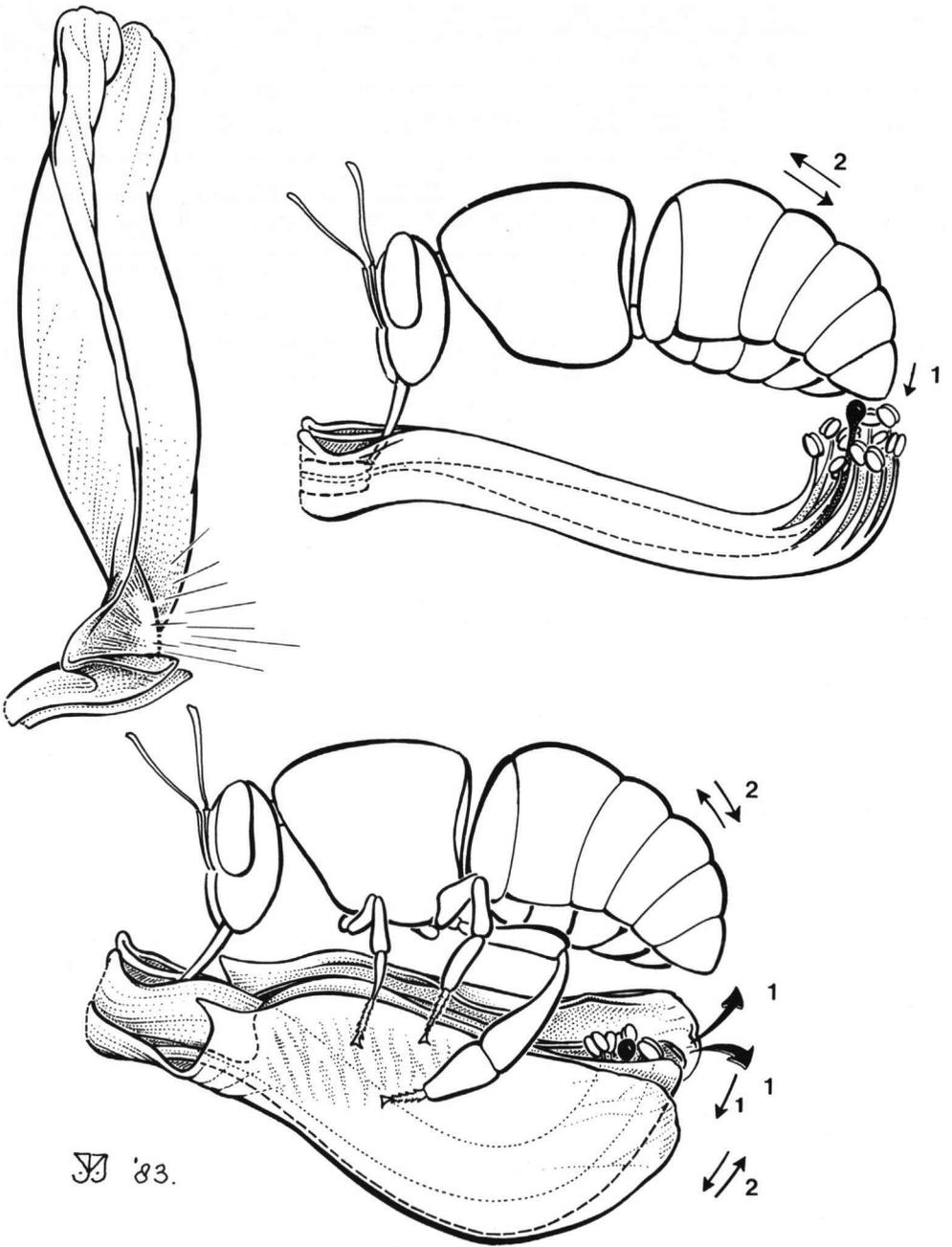
Fig. 4.2. The nectar-obtaining/pollination mechanism with an "idealized", moderately sized, papilionoid bee-flower.

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place, usually much more pods per specimen can be found. I observed this in e. g. *Derris* (*Paraderris*) *elliptica*, and I tend to generalize from this that the Asian species of the *Millettieae* (*Tephrosia* excepted) may also have a natural pollination biology similar to that of the four species studied by Kalin Arroyo.

Continuing to speculate, I think that, if selection pressure has worked on pollination biology, and assuming that the ancestral species of the *Millettieae* were also self-incompatible, it is probable that parallel development of the same features in the flower has occurred in different already existing lineages.

All morphological features mentioned above may or may not be present. The basal callosities may be present or absent; the wing petals are occasionally free from the keel; the transverse ridges on the wing blades may be distinct or indistinct; the upper filament may be free or adnate to the sheath formed by the other nine filaments; the basal fenestrae may be combined with a free upper filament or with an adnate one; the disk can be distinct or may consist only of some nectariferous tissue inside the distinct or indistinct hypanthium. Most imaginable combinations do occur; combinations have no "Naturnotwendigkeit" (Popper, 1982, p. 381).

Also the relative sizes of bees and flowers may vary. Large bees can pollinate small flowers, but the opposite is probably impossible.

The outgroup *Dalbergieae* has a slightly simpler flower construction: the wing petals do not adhere to the keel, the keel petals are free and overlap along the lower edge, in some species of *Dalbergia* the upper edges of the keel petals are adherent. *Dalbergieae* lack basal callosities and basal fenestrae and the upper filament is always free.

Pollen

A survey of the pollen morphology of selected genera of the *Millettieae, Dalbergieae,* and *Phaseoleae* has been given by Hazelhorst (in prep.). The outcome was not very impressive from a systematic point of view. A predominant "basic" type, without much variation, occurs in the genera that caused the central taxonomic problems (i. e. *Derris, Millettia,* and *Lonchocarpus*). A morphological series of different pollen types was found within the genus *Callerya* (as here conceived), and a few species of *Millettia* have pollen with pustules. This kind of pollen is believed (Muller, Pacqué, pers. comm.) to be correlated with bird-pollination. In one of these two species (*Millettia theuszii*) this is possible because of its larger flowers with free stamens and the red calyx, but the other species (*Millettia extensa*) has small bee-flowers and, as far as I found mentioned on field labels, no red colours in the flowers. Hazelhorst will present a detailed account on the species he investigated, and I refer further to his forthcoming paper.

Fruit

The tribe *Millettieae* has dry pods, either dehiscent or indehiscent. The indehiscent pods may dehisce in extreme dry environment (e. g. in herbaria) whereas they do not dehisce in their natural environment. Some apparently indehiscent pods do dehisce along the sutures during the swelling and germination of the seed, e. g. in *Pongamia pinnata.*

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The endocarp is usuallly entirely woody, but in e. g. *Brachypterum* the woody part surrounds only the seeds. This construction is called "seed-chamber" by Polhill (1981, sub *Dalbergieae*) and this situation (considered autapomorphic) predominates in the outgroup *Dalbergieae*. In the tribe *Millettieae* the sclereids ("fibres") of the endocarp are orientated at an angle of about 45° with the longitudinal axis of the pod (fig. 4.3). In the dehiscent pods the outer layers of the endocarp are supposed to desiccate earlier than the inner layers and the open valves obtain the spiral shape of fig. 4.3, middle picture.

According to some handbooks on plant anatomy this resulting spiral twisting can be demonstrated by a model from two different kinds of paper. The natural situation is best approached if the "endocarp" is made from ruled paper, and the "exocarp" from neutral (e. g. typing) paper (in various handbooks, different models of exocarps are demonstrated). In ruled paper the (fragmented) fibres are mainly parallel to the lines, and the model "endocarp" must be cut with the longitudinal axis 45° to the lines. Both pieces of paper are wetted and glued together with arabic gum, or any other water-soluble glue. If the model is placed on a table with the "exocarp" upwards, this will desiccate first. Later the endocarp desiccates and curls the "valve" into a spiral. The result, however, is a valve twisted exactly the other way round as found in genera like *Tephrosia, Millettia* (*p. p.*), *Wisteria, Indigofera, Cytisus, Vigna,* etc., viz. with the endocarp and seeds at the outside of the spiral! This means that the paper model is too simple. Fahn & Zohary (1955) demonstrated that the endocarp in Legumes with spiral valves consists of two or three different layers. Their study does not explain why these valves do spiral "inwards", despite the desiccation starting from the outside. A more detailed study seems necessary.

Forced drying of "woody" pods of *Wisteria* resulted in explosion of the pods. During the desiccation process tension increases till the sutures burst; the valves curl inwards, sometimes throwing the seeds some metres away. I don't know if this also happens in the natural habitat.

The shape of the pod is generally characteristic for the genera as here conceived, and in the plates I—V (chapter 9) most kinds of pods are depicted.

The seeds are usually flattened, in some species they are subglobose. The thicker seeds are described by Corner (1951) as "overgrown", and this peculiar feature is discussed in a note under *Callerya*. The seed shape is the one usual in *Papilionoideae*; there may be a small (rim-)aril; the hilum is generally small and elliptic (except in *Afgekia*); the lens is indistinct. The embryo has usually a curved radicle, pointing (as usual) to the former micropyle. A few genera have (occasionally) a straight radicle in their embryos. This may be a secondary, derived condition (reversed character state) as Polhill (1971) depicts (his fig. 2) immature embryos with a curved radicle (his fig. 2.14b) and mature embryos with a straight radicle (his fig. 2.15b). Whatever the explanation, the outgroup *Dalbergieae* has generally embryos with distinct straight radicles, and this may indicate its primitive character state.

The germination of the seeds is variable. There are indehiscent pods, where the cotyledons remain in the fruit, and the plumule penetrates the half-decayed pod wall

'endocarp (ruled paper)

arabic gum in between

'exocarp' (neutral paper, e.g. typing paper)

true pod valve with the fibres of the endo-
carp directed as in the model above

the paper 'pod valve' above, after desicca-
tion of the 'exocarp' prior to desiccation
of the 'endocarp', showing the 'seed' at
the outside of the spiral. This model is
thus oversimplified, see text
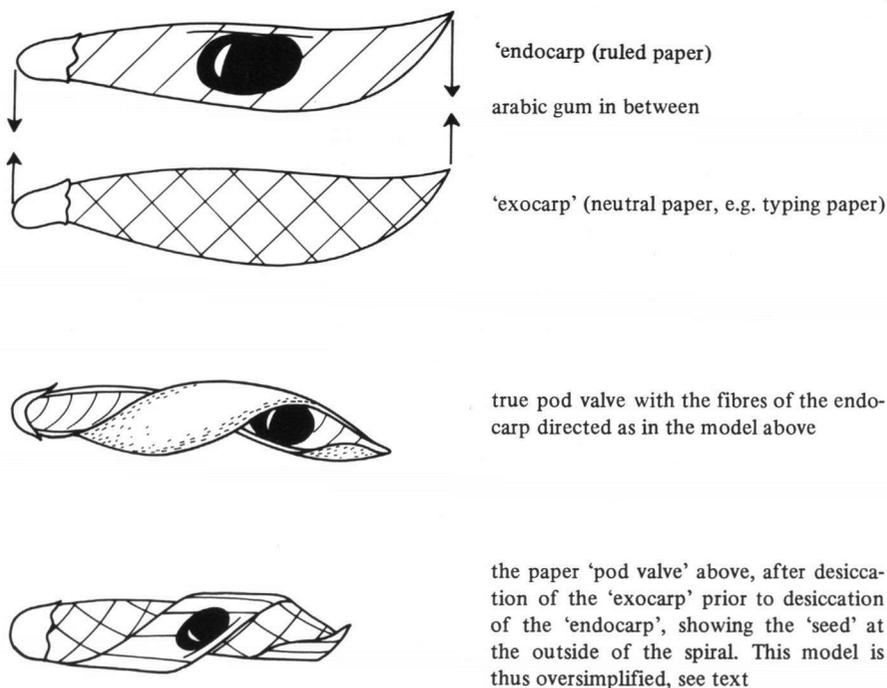
Fig. 4.3. Spiral dehiscence of pods in some *Millettieae*.

(*Heliciopsis*-type, De Vogel, 1979), as in *Derris* and *Ostryocarpus* (*p. p. majore*). The usual way of germination is with foodstoring cotyledons either resting on the soil, or uplifted by the hypocotyl (*Sloanea*-type, De Vogel, 1979).

The seeds are protected against herbivores by poisonous free amino-acids, amines, and flavonoids. The chemical characters are discussed below, but for general interest the toxicity of the amino-acids must be mentioned. Rosenthal (1982, 1983) described in detail the metabolic system of the beetles belonging to the family *Bruchidae,* which are specialized on toxic seeds of Papilionoids. 100 % of the seeds dropped below the mother-plant is destroyed by these beetles and only the seeds that have been dispersed far away have some chance to germinate. This explains why *Lonchocarpus* and *Millettia* species, though locally not uncommon, never grow gregariously (Janzen, in Polhill & Raven, 1981, presented a recent survey).

Chemistry

This paragraph has been written in close cooperation with Prof. Dr. R. Hegnauer and Dr. S. V. Evans.

Surveys of available chemical knowledge in *Leguminosae* have repeatedly been written even as early as 1816 (A. P. de Candolle), the major recent ones being Harborne c. s. (1971), and various contributions in Polhill & Raven (1981, part 2).

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Studies on free basic non-protein amino acids and amines that are stored in seeds of *Millettieae* (*"Tephrosieae"*) have been made by Bell c.s. (1978, canavinine), Fellows c.s. (1978, 2-amino-imidazole derivatives), and Evans c.s. (1984, basic non-protein amino acids and amines). A survey of the distribution and structures of flavonoid compounds including rotenoids found in the genera *Derris* (*s. l.*), *Lonchocarpus* (*s. l.*) and some supposedly related genera was presented by Gomes c.s. (1981).

Non-protein amino acids and rotenoids are assumed to have a function in plant defense against herbivores. Their biosynthesis and catabolism are still incompletely known (Rosenthal, 1982, Crombie, 1984). This incomplete knowledge impedes to a certain extent a promising taxonomic use of the chemical features mentioned. Nevertheless, accumulation of each individual compound or class of compounds represents a character of a given taxon.

For the application of characters as elaborated in chapters 6 and 7 I used two types of chemical characters, i.e. non-protein amino acids (and amines) and flavonoid compounds, because they are reported in literature as taxonomically rewarding.

Non-protein amino acids and amines. Evans c.s. (1984) showed that arginine is the only protein(-ogenic) amino acid present in free state in appreciable amounts in seeds of many taxa of *Millettieae*. This may indicate a biosynthetic relation with the non-protein amino acids that are accumulated by many members of this tribe in their seeds (Bell c.s., 1978, Fellows c.s., 1978, Evans c.s., 1984). I tentatively accepted as characters the accumulation of the following compounds: Canavanine, Homoarginine, gamma-Hydroxyhomoarginine (OH-Homoarginine), Enduracidine, Amino-imidazolinyl-acetic acid (PPN), 2-Amino-imidazole (2-AI), and 1,5-Dideoxy-1,5-imino-D-mannitol (LU 1) (abbreviations used in table 6.3).

Flavonoid compounds. In a study of flavonoids of *Derris s. l.* and *Lonchocarpus s. l.*, Gomes c.s. (1981) treated chalcones, flavanones, flavanonols, flavonols, aurones, auronoles, bêta-hydroxychalcones, flavones, isoflavones, 3-phenyl-coumarins, pterocarpans, isoflavans, and coumarochromenes. They stressed the advantage of taking into consideration biosynthetic sequences in the elaboration of the flavonoid skeletons as well as subsequent modifications of basic skeletons, such as introduction or removal of hydroxyl groups, methylation of hydroxyls and isoprenylations and their subsequent modifications. I decided to make use of the following basic skeletons on presence/absence scores based on the flavonoid data reported by Gomes c.s.: Flavanones, flavonols, flavones, isoflavones, pterocarpans + isoflavans (occurring in the same OTU's), and rotenoids.

I am aware that the use of the chemical characters mentioned in the treatment applied in chapters 6 & 7 has some drawbacks. The most serious one is a considerable lack of information, as several lower taxa (i.e. species of the studied genera) have not yet been investigated for the characters used. Moreover, it is far more easy to demonstrate presence of a given compound than to prove its absence. Different parts of the plants (flowers, leaves, bark, wood, roots, seeds) were investigated and the simple scoring from non-homologous organs provides another difficulty. This is especially true for flavonoids showing different patterns within one species. If e.g. for a species only seeds and for another species only leaves have been analyzed, the comparison of these

flavonoid patterns becomes rather meaningless; this was already accentuated, in more general terms, by De Candolle (1816). Another noteworthy point is that in Papilionoids many isoflavonoids, particularly isoflavans and pterocarpans, are phytoalexins; they may be lacking in healthy plants or parts of plants, but be present after infection or mechanical stress.

Gomes c. s. did not take into account the last two mentioned points in their statistical analysis and this weakens their conclusions. It is assumed that flavonoid patterns evolved parallel in many plant taxa from Bryophytes to Composites. Nevertheless, flavonoid types and oxidation/methylation patterns represent characters applicable in estimations of similarity of taxa. One should, however, use them carefully and preferably compare only patterns of the same of the plant parts when working at lower taxonomic levels (species and genera).

Vegetative anatomy

The wood anatomy of the tribe *Millettieae* (as *"Tephrosieae"*) was surveyed by Baretta-Kuipers (1981). The transfer of the *Dalbergieae* subtribe *Lonchocarpinae* to the *Millettieae* is supported by the arrangement of the pluriseriate rays in the secondary wood, but also the genera *Vatairia, Vataireopsis, Hymenolobium,* and *Andira,* maintained by Polhill (1981) in the tribe *Dalbergieae,* have these pluriseriate woodrays. As discussed in the previous chapter, the distinction of these tribes is (poorly) supported by several characters when used in combination.

A survey of the vegetative anatomy of leaves and twigs of herbarium material has been carried out by B. Keijner in the framework of his M. Sc. thesis (unpublished). He found differences in the mesophyll structure and distinguished three types. In many genera only one type was found, and in some others (e. g. the obvious candidates for heterogeneous amalgamation of species: *Callerya* and *Millettia*) more than one type was found. Keijner's report needs extension of the observations before it can be published.

Chromosome numbers

The chromosome numbers in the tribe *Millettieae* vary between 2n = 16 and 24 (Goldblatt, 1981, as *"Tephrosieae"*). Polyploid complexes are unknown in this tribe. In my previous survey (Geesink, 1981) the chromosome numbers were mentioned under the headings of the genera, and I have not repeated them here.

5. NATURAL CLASSIFICATION, A DESIRE FOR THE IMPOSSIBLE?

A review of Angiosperms as a whole shows that every morphological character that is used to distinguish families and orders can in other groups vary at the level of genera and species.

G.L. Stebbins (1974) 37

Natural taxa exist in nature independent of man's ability to perceive them.

(after) E. O. Wiley (1981) 72

Taxonomy . . . has no theory . . .

W. M. Wheeler (1939) 192

To an outsider, the classification of organisms may seem a complicated jigsaw puzzle, resulting in an abstract picture, especially when he discovers that taxonomist's views appear to vary from the inductivistic one above, bottom right, to the theory-loaded one above, top right, combined with the fact that most practising taxonomists are aware of the statement above, left, without bothering too much about its relevance. After Wallace's and Darwin's publication of the concept of what the latter called "natural selection" as an evolutionary mechanism, it has been generally held that the much older evolution hypothesis became a 'scientific' theory. This idea caused changes in thought in biology as well as in other fields of human activity. The philosophical question whether "natural selection" and Spencer's expression "survival of the fittest" is a tautology or an expression with subject and predicate, is still discussed (Hull, 1974, pp. 66—69; Ruse, 1981, p. 71; Brady, 1982).

Since the end of the last century, many taxonomists have tried to construct classifications that reflect assumed phylogenies, or, at least, considered that an ideal to be approached. In this chapter, I would like to discuss the more general aspects of the possibilities of attaining that goal, while in the next chapter the (un)attainability of this ideal will be demonstrated on a complex genus group in the tribe *Millettieae* together with a discussion on the related question about the "reality" of taxa.

The differences in approach can roughly be characterized as:
1. phenetic and *2. phyletic (phylogenetic)*.

It is wrong to assume that all pheneticists do not consider phylogeny (see Sneath & Sokal, 1973, chapters, 1, 2, and 6). Some of them apply very sophisticated ways of character weighting, which they consider to be applicable for the construction of phylogenetic trees (e. g. Joly, 1969, Sastre, 1971).

Recently, the phyletic approach has been divided into:
2a. classical (or *"evolutionary"*, as Mayr, 1974 and Wiley, 1981 call it), and *2b. cladistic.*

The main differences between these three approaches are tabulated in table 5.1. For a more detailed survey see e. g. Charig (1982).

The *classical* approach is characterized by a lack of strict rules. Any taxonomic case is considered separately and interpretation of character states and their relative weight is mainly assessed by intuition, thus it is openly subjective. Rosen, Nelson & Patterson (in Hennig, 1979, p. ix) consider it even "dependent mainly on consensus or authority".

The *cladists* claim to apply objective operational rules while constructing cladograms. These rules are clearly and critically surveyed by De Jong (1980). He distinguishes four groups of arguments: *a.* Arguments consistent with evolutionary theory and "giving

Table 5.1. Comparison of different approaches in systematics.

PHENETIC approach (generalized, only the points objected to by phylogeneticists are mentioned).	Wiley (1981). CLADISTIC approach	Beckner (1959). "EVOLUTIONARY" approach (synthesis of Simpson, 1945, and Mayr, 1942, 1953).
1. Taxa are recognized by a number of correlating characters. Criterion for (natural) affinity is "overall similarity".	1. Taxa exist in nature independent of man's ability to perceive them. Criterion for phylogenetic affinity is (supposed) common descent. Common descent is recognized by the detection of (syn)apomorphies.	1. Taxa are not definable according to his criteria, but are "specifically biological" concepts. (Beckner, p. 16, 17). Rules for recognition of "natural" affinities cannot be generalized.
2. The classification with the highest number of correlated characters is "the best" one (whether its taxa are mono- or polyphyletic belongs to the realm of speculation).	2. Natural taxa must be holophyletic, defined on (a set of) apomorphic characters.	2. Every taxon must be monophyletic (whether they are so, is often impossible to judge).
3. Both monothetic and polythetic definitions are applied.	3. No explicit preference for monothetic or polythetic definitions is given, but all "accepted" cladograms have a strict monothetic character.	3. Every taxon must (or "may"? R. G.) be polythetic ("polytypic") with respect to a set of morphological characters.
4. Phylogeny can be reconstructed as a speculative byproduct of the classification which is based on overall similarity.	4. Classification must reflect the (reconstructed) phylogeny *strictly*; gaps filled in by fossils are given artificial rank ("plesion").	4. No polythetic ("polytypic") group is to be assigned as a taxon of certain rank, if it can be assigned to a lower rank. (Arguments for higher ranks are interpreted from e. g. "Bauplan" concepts.)
5. The problem of paraphyletic groups is not considered.	5. Paraphyletic groups are not holophyletic, and its "members" need similar or higher rank as the holophyletic group(s) higher up the cladogram.	5. Paraphyletic groups not considered, but Simpson (1961) and Mayr (1969, 1974) consider them natural and thus monophyletic.

clue to" the direction of evolutionary change; *b*. Arguments consistent with evolutionary theory but "not giving clue"; *c*. False arguments; *d*. Arguments based on tendencies in established phylogenies; and a fifth argument, viz. *e*. Argument of correlation of applied arguments. He discusses no less than 21 rules applied by various cladists, and after critical evaluation he concludes that only one rule (viz. the outgroup comparison rule) is *generally* applicable, the remaining 20 suffer to various extent from one or more shortcomings. De Jong only accepts category *a*. as useful.

In my opinion, the category *d.,* as far as based on *homologous* tendencies in established phylogenies can be considered stronger (to be added to category *a*.) than De Jong does, but I agree that the arguments of category *d*. are certainly not generally applicable, but merely form a "polythetic set of arguments in special cases". I will not go further into this matter.

Some optimistic cladists consider their "hypothetico-deductive" method scientifically superior to the subjective approach of the classical taxonomists (see Panchen, 1982, versus Gaffney, 1979). For a survey of the arguments against the claimed superiority see Mayr (1974, specially pp. 96 & 97). The vehemency of the "debate" between supporters of the classical and cladistic approach is notable, and I can recommend Mayr's (1974, 1981), Ashlock's (1974, 1979), Van Valen's (1978), Hull's (1979), Wiley's (1981, chapter 7), Cartmill's (1981), Panchen's (1982), and Charig's (1982) more balanced contributions to the discussion. In connection with this, one may also compare Beckner (1959), Löther (1972), and De Hoog (1981), who survey the general methodology of taxonomy.

As Mayr (1974) states, the main difference between classical and cladistic approaches is not so much the analysis (he calls it even "superb" in 1982, p. 227), but in the "translation" of the cladogram into a "natural" classification: Cladists accept only strictly monophyletic groupings which would be better called "holophyletic", as Ashlock (1971) and Holmes (1980) propose, while classical taxonomists have no objections to paraphyletic groupings. Paraphyletic is used here (and in following chapters as well) in the sense of Hennig (1950, 1966) as the definitions of the concepts paraphyletic and polyphyletic have become confused since. Platnick (1977) gives a survey of this confusion, but I disagree with his conclusion; I prefer to maintain Hennig's original rather wide concept, as does Holmes (1980) in his attempt to eliminate ambiguity in cladistic terminology. The later, refined subconcepts should (have) receive(d) new names.

Another notable point of difference between cladistic and classical approaches is the cladists' strong emphasis on descent in those cases where genealogy and genetic similarity do not lead to congruent results. This is a consequence of their view on paraphyly and polyphyly. The problems set out above are not new, merely revived. For example, Engler (1926, pp. 146—167) surveyed and discussed several of them, viz. the discrepancy between genealogy and genetic similarity, parallel developments, and monophyly vs. polyphyly.

In order to demonstrate the practicability of the methods mentioned, I will start with an elaboration of a relatively simple case of three ultimate (fossil) taxa, the phylogeny of which is "known" with reasonable certainty. After this rather detailed elaboration I

will continue with a more complex case of four recent taxa, which show "reticulate" affinities.

It will sound very obvious, when one states that only complete series of fossils can lead to an objectively "true" phylogeny, but even then there are problems: the following example illustrates that the increase of data results into a more complex phylogeny, even though the first set of available data was already considered to be a rather luxurious one. The same example is also used to test whether the cladistic analysis of exclusively the three ultimate taxa ("end products") does reflect the "actual" phylogeny correctly.

In table 5.2 two slightly different phylogenies of a Miocene genus of mice (*Muridae*) from a group of islands (then isolated) in the present province Gargano (Italy) are presented. For details concerning the distribution and stratigraphy see Freudenthal (1971, 1976). On the horizontal axis the size of the first lower molar is given, which roughly correlates with its morphology. The vertical axis is the time, derived from a postulated (true or not) linear increase in size of that first molar in lineage II (the heavy line). The complete period is estimated a 10^5—10^6 years (Freudenthal, pers. comm.). The left hand phylogeny is redrawn from a preliminary one (a smooth sort of flat seaweed in a M. Sc. report, Geesink, 1971) and based on the fossils from 10 localities (fissure fillings) out of the 15 available in 1970. In the succeeding years more localities were found and Freudenthal, 1976, gives a more complete phylogeny based on 24 thanatocoenoses selected from a total of about 75.

To elucidate the apparent gaps discovered in it later, I have added the complete variation known in 1976 and projected it on the same (relative) time axis (Table 5.2, right hand figure). The main differences are the filled-in gaps and some more lineages assumed between the strata FD and C9 (these abbreviations refer to the localities). In the 1971 version this block seemed one variable species. Another difference is the interruption of lineage II between C9 and FH.

Related to the constant increase in length, the morphology shows a "reversal" (larger teeth showing a more primitive morphology). A plausible explanation for this observation is this interruption (C9/FH) in the lineage, which can be explained by the assumption that the populations were replaced by slightly different ones from neighbouring islands (Freudenthal, 1976). Furthermore, the possibility of the incorrectness of the assumed parameter may play a role. Whatever the explanation, FH is the "highest" level at which lineages I and II are hardly discernable and this level is also the highest level, where *Cricetidae* (hamsters) were still found (the hamsters showed similar evolutionary radiation, but occur only between R1 and FH). Probably all populations (mice, hamsters, and all other terrestrial groups) became extinct there (level FH) and were replaced by ones from neighbouring islands, but the extinction in the lineages I and III cannot be discovered.

One can only guess how the reconstructed phylogeny would look like if still more localities had been found. Extrapolating, one can expect more lineages, and there may be gaps in the present (1976) version. It must also be noted that only characters of the first lower molar (which correlated with those of the third upper molar) were taken into
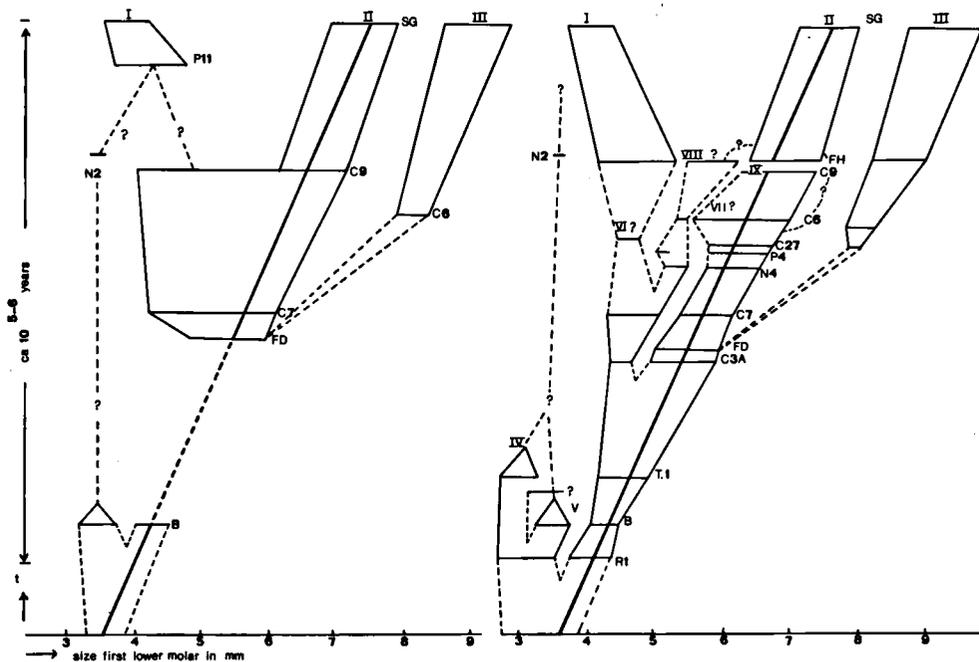
Table 5.2. The phylogeny of the Gargano-mice. Lefthand figure: reconstruction 1971. Righthand figure: reconstruction 1976.

account. Fossils are always fragmentary, and one can only speculate about interesting ecological and other important factors.

The reason for comparing these two phylogenies is to show what happens with an increase in information, in an example where even in 1971 the state of knowledge was already a relative luxurious one in vertebrate palaeozoology with 10 different strata in such a relatively short period estimated at 10^5—10^6 years.

I could not resist the temptation to try to "reconstruct" an assumed phylogeny, as if the data of only the highest stratigraphical level had been known (SG in the table). With three taxa involved (and assuming the reallocation of two branches from the same point meaningless) only three alternative cladograms are possible, depicted in table 5.3. The plausible corresponding synamorphies are filled in there, and 5.3.a is "true" (plausible) if the increase in size and number of crests is considered apomorphic; 5.3.b is "true" if the transformation series are reversed. The third alternative, 5.3.c. is not plausible, as "lineage I" cannot be supplied with reasonable apomorphies (but it can be transferred to a plausible tree).

If an outgroup is considered, e.g. lineage IV (though already extinct in SG) from 5.2.b, only 5.3.d (which corresponds with 5.3.a) is plausible and this illustrates the necessity of outgroup-comparison (De Jong, 1980; Wiley, 1981, p. 110). This cladistic analysis thus provides exactly the reconstructions we made in 1971 and 1976. The conclusion is that the cladistic approach is besides logically consistent also synthetic, at least in principle.

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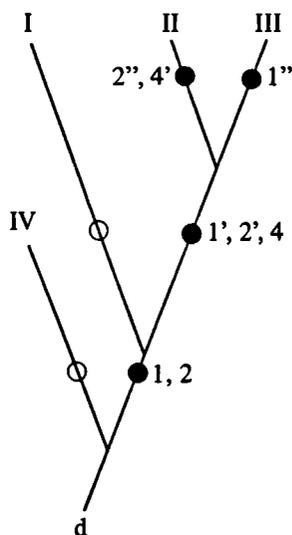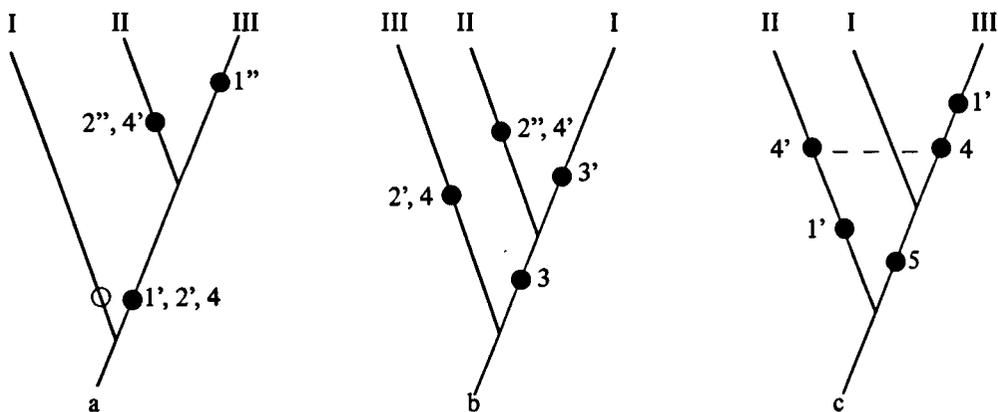
Table 5.3. Cladistic reconstruction of the Murideae from the SG level. See text for explanation. Symbols of the applied apomorphies: 1 M1 larger; 1' M1 still larger; 1" M1 largest; 2 M1 with up to 5 crests; 2' with up to 6 crests; 2" with up to 7 crests; 3 M1 smaller; 3' M1 smallest; 4 M1 more hypsodont; 4' M1 even more hypsodont; 5 M1 not hypsodont.

Another conclusion, I consider obvious from the "true" phylogeny of these giant rats, is contradictory to the usual cladistic claim that cladograms depict cladogenetic information and not anagenetic information. This claim is wrong and due to lack of "stratophenetic experience" (Gingerich, 1979). The opposite is true, cladograms depict anagenetic information mainly: The synapomorphy of the "middle rat" and the "giant rat" is the tendency to become larger correlated with multiplication of the molar crests. The characters themselves, from which this synapomorphy is generalized, are obtained during anagenesis of the lineages. A further consequence of this view is that lineages cannot be identical to taxa.

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Returning to taxa and the possibilities to group them: with 4 taxa involved the picture becomes more complicated, especially when characters are not correlated with others.

The following example (Table 5.4) is elaborated to show alternative dendrograms (cladograms), and how to select from them on different grounds (phenetically, or using two ways of cladistic approach, or classically).

This example is also expounded to demonstrate the operational principle of a computer program, conceived by Zandee (1985), although it was designed for more complicated cases, like the one in the next chapter.

In Zandee's concept the usual cladistic procedure is reversed; i.e. apomorphic character states are not established *a priori*, but follow from a search for the apomorphies according to the scheme and its permutations (BAC and CAB). The
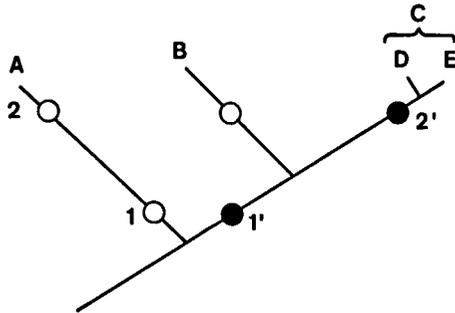
philosophy behind this basal clade (three taxon statement) is that two out of three given "taxa" (which together are supposed to form a holophyletic higher "taxon") are genealogically closer to each other than one of them to the third, in other words: two form a holophyletic "taxon" of lower rank recognizable on account of a shared (set of) apomorphic character(s), which the third "taxon" does not have. The apomorphic nature of a character state can be detected by means of outgroup comparison. Zandee (1985) interprets this rule to imply that the character state(s) present in the base-level "taxa" (D and E together = C) of the three taxon statement is considered to represent the apomorphic state if it is not present in the sistergroup (B) and in the outgroup (A).

The result is that C has the synapomorphy 2', the sistergroup B shows the plesiomorphic state 2, as does the first outgroup A. The next step is either a subdivision of the holophyletic "taxa" (A, B, and C) or their agglomeration with other available "taxa" resulting in sets at other levels which are submitted to the same procedure. Sets of "taxa" for which no synapomorphy can be found are rejected (e.g. the "empty" cladograms in table 5.5).

Only in this way additional levels of clades of holophyletic nature are provided. In practice, sets of "taxa" are derived initially from a data matrix (like table 5.4, which is a reduced part of table 6.4; an extended version of the latter was actually computed). This reduced matrix (5.4) shows that only part of the characters used are correlated, and that others are distributed differently.

A   B   C   D

Brachypterum   Paraderris   Lonchocarpus   Phacelanthus

1. Tree

2. Liana

3. Brachyblast with
   spirally arranged
   flowers

4. 2–3 Flowers on
   top of common
   pedicel

5. Standard with
   basal callosities

6. Standard without
   basal callosities

7. Keel obtuse

8. Keel falcate

9. Pod winged

10. Pod not winged

11. Aminoacids C & D
    present

12. Aminoacid G
    present
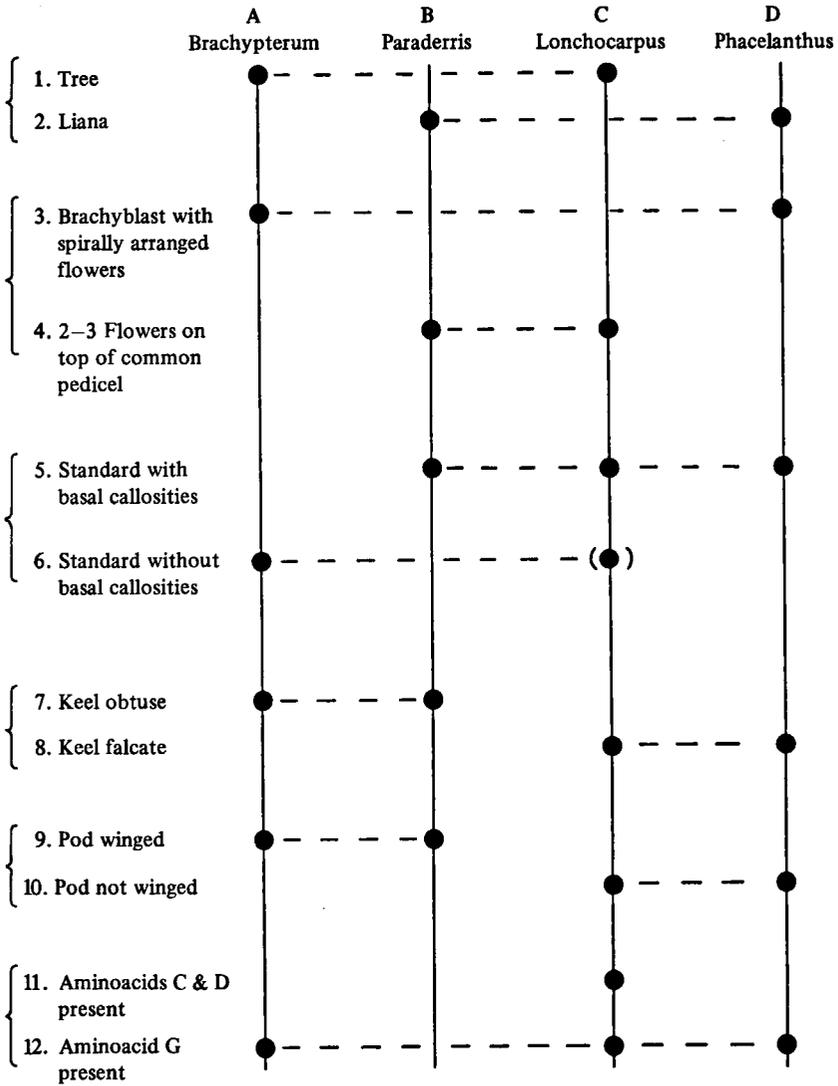
Table 5.4. Character matrix, derived from table 6.4.

With only 4 taxa 15 different schemes (primary cladograms according to Nelson & Platnick, 1981, pp. 174—199) are possible, provided (again) that the reallocation (turning) of the uppermost clades (B and C, D and E in the basal clade above) is considered without symbolic meaning. All 15 schemes are depicted in table 5.5 and the characters are filled in on the branches. For example, in scheme 5.5.1 the characters 7 and 9 are shared by taxa A and B, and characters 12, 3, 1 and (6) are considered parallel developments in lineages CD, D and C respectively.

This is elaborated (in this example by hand) for all 15 alternatives cladograms. In fact I should call these alternative schemes dendrograms (or phenograms), as apo/plesio-morphies are not (yet) denoted. Of the 15 cladograms nine could be filled in with characters in all branches, the remaining six had "empty" branches in the basal clades.

From these schemes it can be shown, that the differences in approach of pheneticists, cladists, and classical taxonomists can be regarded as a matter of selection from the alternative schemes on account of different philosophies. (In fact the comparison of all possibilities is hardly ever done: usually taxonomists consider at most *some* alter-natives. In this example all are considered, in order to be able to compare the selection procedures, which are in practice performed *a priori*.)

I will present the different approaches in a generalized, simplified way, as the variation within each kind of approach is too wide to allow a clear survey.

1. For the ("generalized, simplified") pheneticists, desiring to find groupings with the greatest "overall similarity", alternative 5.5.1 will probably be the most acceptable, as both groups AB and CD have 2 correlated characters, and CD even has two more, which it, however, shares with A resp. B. Four other characters have to be considered as parallel structures (or developments). All the other schemes (phenograms or dendrograms for the pheneticists) have a lower number of correlated characters and may therefore be "rejected". In this case the "overall similarity" consists of the set of absolutely correlating and partly correlating characters (for a comparison of correlating and compatible characters see chapter 7). Many modern pheneticists refine their character analysis by some way of character weighting.

2a. For the ("generalized, simplified") cladist two approaches are possible, when all possibilities have been written out. The first approach (most generally used) is to consider only the putative synapomorphies which are *a priori* denoted on various grounds (see Hennig, 1979, pp. 93—128). If the characters 1, 2, 4, 5, 8, 9, 11, and 12 are considered apomorphic and 3, 6, 7, and 10 plesiomorphic, which is in my opinion the most plausible morphologically, eight alternative schemes have to be considered, depicted in table 5.6 with the same numbering as in 5.5.

The eight schemes are all possible cladograms, as the filled in characters are considered (syn-)apomorphies. Choosing between the first three is difficult, as they lack an outgroup. The (in neo-cladistic circles) popular parsimony principle can be applied, on which I will comment at the end of this chapter. The principle states that the hypothesis with the lowest number of premises is the most probable one (if not the "true" one) and it may be translated for cladistic purposes into the greatest probability of the cladogram with the "fewest *ad hoc* statements that explain the full array of available data" (Wiley, 1981, pp. 20, 110—113). *Ad hoc* statements are interpreted (by him) as (sym-)plesiomorphies and these are consequently left out in table 5.6. The opposite is the highest number of (syn-)apomorphies, whether or not combined with the lowest number of parallel developments (which also have an *ad hoc* character). This interpretation is heavily criticized by Panchen (1982), Cartmill (1981), and Johnson (1982). I will reflect on this matter at the end of this chapter.

This leaves **1, 2** (both with four synapomorphies and five parallels), **4,** and **5** (both with three synapomorphies and five parallels) to be considered, the first two schemes with the disavantage of no outgroup, and the last two schemes with the disavantage of one synapomorphy less than the others. Further discrimination between these four seems impossible to me, except on other, auxiliary evidence (from other disciplines, e. g. ontogeny, geography, genetics, etc.).

One could add more characters, and find them fitting better in one of the four (or in another, initially rejected, scheme), but with the characters provided in matrix 5.4 the cladist is left with at least four equally plausible cladograms. And because of the cladistic prolegomenon, that cladograms have to be translated directly into a tree, and then into a classification, he is also left with at least four possible classifications.

2b. The other cladistic approach is followed by Zandee (1985), who has objections against *a priori* designation of apomorphic character states. His reasoning is that one has to consider all alternative dendrograms of table 5.5, and that one should judge from the character distribution patterns (by means of three-taxon statements permutation
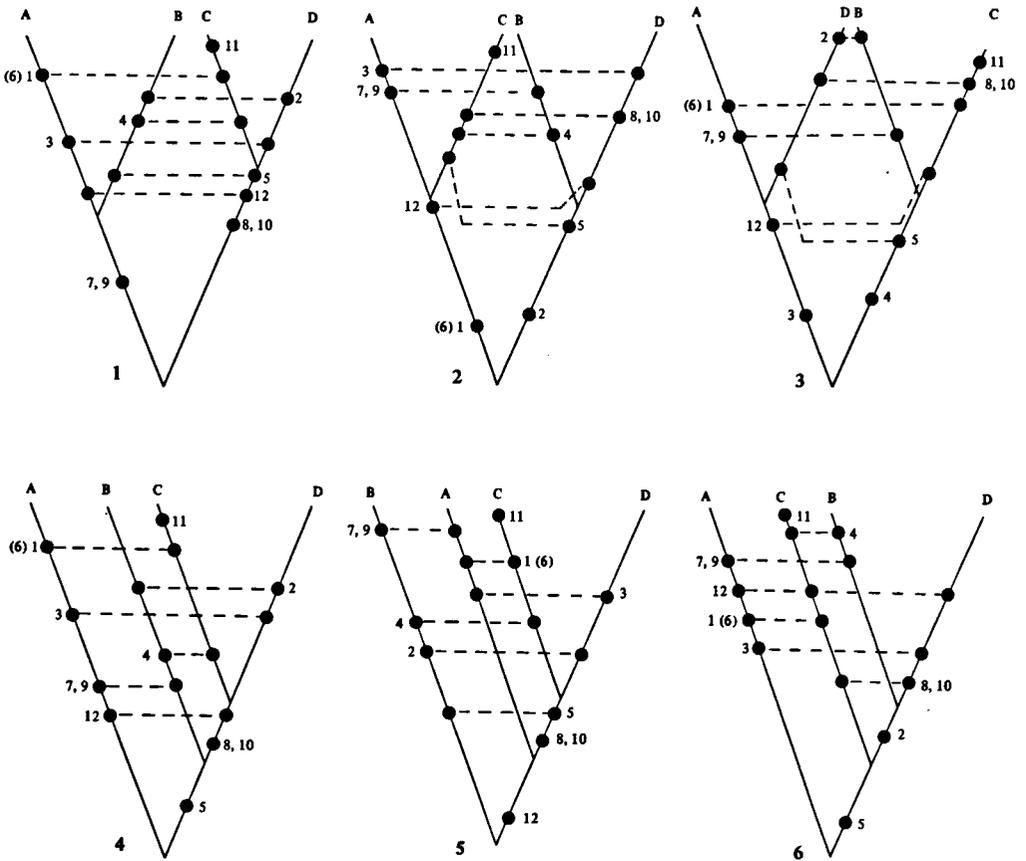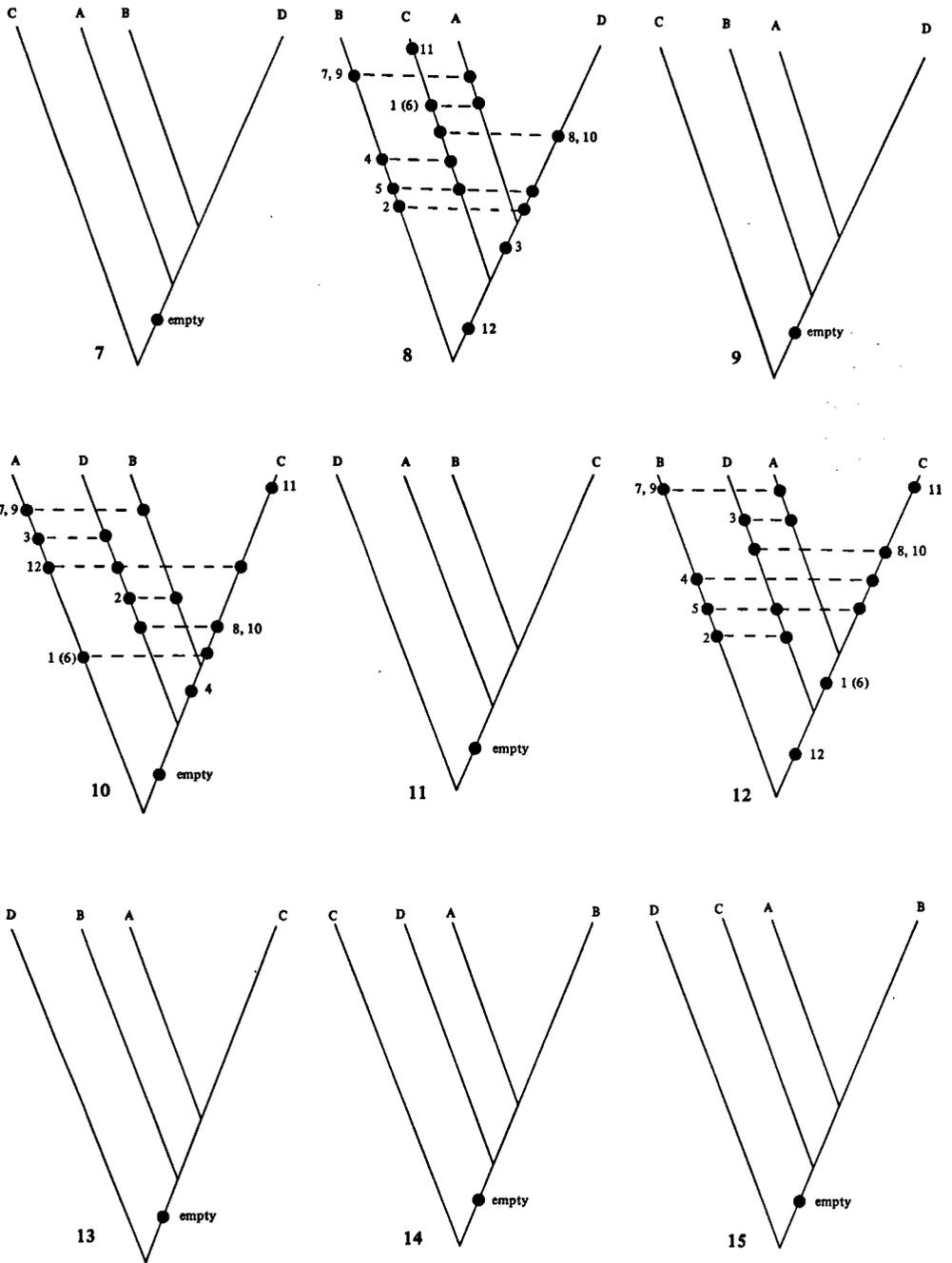
Table 5.5. The fifteen possible cladograms with the corresponding characters of table 5.4.

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and application of the out-group rule) which characters show the pattern of the apo/plesiomorphies of the basal clade shown a few pages before. To the schemes that show such a pattern (the latter six do, the first three, that lack an outgroup do not), other, auxiliary evidence should provide the criteria for chosing between them. It will be clear that this procedure will leave the investigator with more possible schemes than he had after *a priori* designation of the apomorphic states. The approach is more "objective" and the result is a higher number of possible schemes.

3. For the ("generalized, simplified") classical taxonomist the case may be impossible to solve. The "solution" may be to group the four OTU's (operational taxonomic units) together, which can be defended with supposed "reticulate" evolution as an *ad hoc* "clincher". Unless he has some prejudice (e. g.: "The shape of the pods is of greatest importance to distinguish the genera of *Leguminosae*") he will find the choice between the schemes impossible. With the prejudice expressed above for example, he will look for supporting characters correlating with the differences in the shape of the pods, and he will probably plump for scheme **1**. If the classical taxonomist has no objection against the designation of supposed apomorphic characters as "typical" characters for the group (like Mayr, 1974, stated on p. 95) and if he used the apomorphic characters as designated *a priori* above, he will end up with the same schemes as the 'a prioristic' cladist. The difference, however, will be that the classical
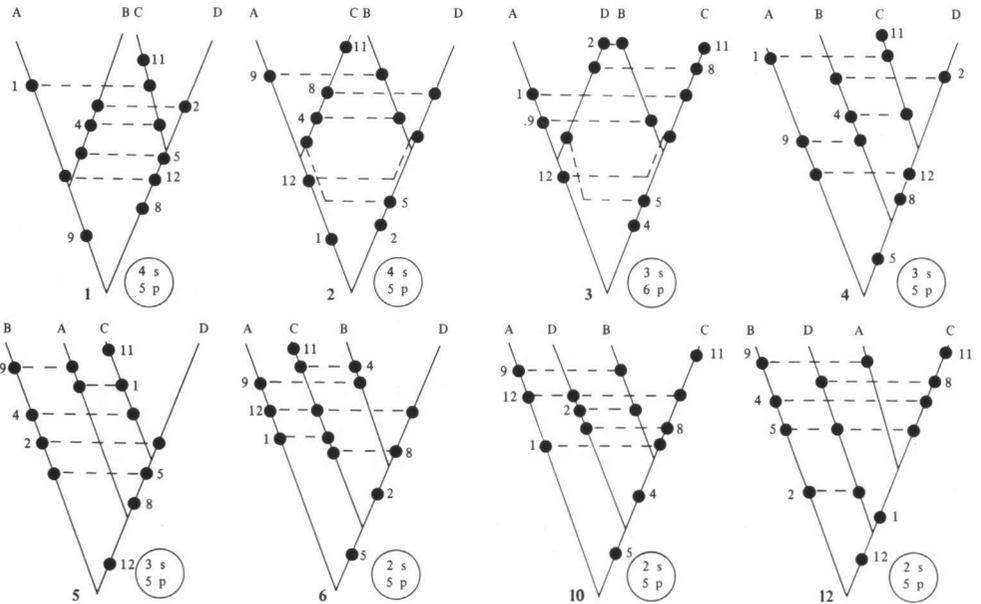
Table 5.6. The eight fully resolved cladograms (of table 5.5). The numbers of synapomorphies and parallels are encircled.

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taxonomist will regard three out of the four (**1, 4** and **5**) possibilities as three different evolutionary ways leading towards the same classification. Classical taxonomists consider paraphyletic groups as natural groups, and despite the possible paraphyletic origin, A and B will (generally) be grouped together. The grouping of C and D is without problems of course. Scheme **2** will be a different alternative.

There are many more aspects to the differences between phenetic, cladistic and classical approaches, as the views sketched above are greatly simplified, and restricted to what I regard as the major differences. From the example with the four taxa it was demonstrated that by means of three (or four) different approaches slightly different sets of possibilities are selected as the most plausible ones.

In the following chapter I will demonstrate what happened with 22 OTU's with 61 characters, and with 8 selected OTU's with 43 characters, and I will show that it is impossible to choose on objective grounds a supposed "true" cladogram from the overwhelming number of possible ones.

I will continue this general chapter with some reflections on axiomatic reasoning and the parsimony principle as far as applied to dendrograms (cladograms) and close with a tentative conclusion.

All three approaches set out above have some kind of axiomatic (or hypothetico-deductive) reasoning. The pheneticist is reasoning: *IF* (in fact *SINCE*) the highest number of correlated characters leads to the best classification, then *THIS* dendrogram is the one to be selected. The cladist's reasoning is: *IF* these are the apomorphic characters, and some particular ones are more likely to have developed in parallel, then *THIS* cladogram is (or: *THESE* cladograms are) the one(s) to be selected. And the classical taxonomist's reasoning is: *IF* these characters are the most important ones in the supposed evolution of the given group, then *THIS* dendrogram (cladogram) reflects the supposed evolution best.

I omitted in the last two statements the translation from the dendrograms or cladograms into a classification, as I consider this an independent action to be performed after selection of the supposed correct dendro- or cladogram(s).

In order to find which of the three reasonings will in general be the most correct one, i.e. will lead to a scheme which has the greatest chance of reflecting the phylogeny (assuming that the pheneticist has also phylogenetic ulterior motives), we must compare the premises and the reasoning: a test based on actual data (i.e. complete series of fossils) is generally impossible because fossils are lacking or too fragmentary. This view is also expressed by Cartmill (1981).

Thus a selected scheme can (generally) *never be* tested, except for its structure of reasoning (the "polythetic" set of criteria: logical structure, explanatory power, testability, predictive power with regard to yet unknown characters, etc.). This is probably an important point, as in biology, and certainly in evolutionary taxonomy, a logically soundly presented theory need not be *true*.

Popper (1982, pp. 381—382) discusses the intrinsic uncertainty of biological statements, due to unknown "contingent factors", and consequently considers

biological statements (laws) different from physical laws, which, according to Popper at least, seem to suffer less from these contingent factors.

This makes me think that at least certain biological laws do not have a status comparable to physical laws with sufficient "Naturnotwendigkeit" (Popper called it so; it is difficult to translate: "Necessarily, inevitably true" comes closest and, following Van Valen, 1976-a, I propose to add "within its domain"; see also the epilogue at the end of this chapter).

I have understood from various philosophical discussions, that the boundary between hypothesis and theory is not so sharp and some biological theories may have the character of "eternal hypotheses" which are in a constant need of confirmation. Evolutionary theory, as far as applied to (series of) fossils, will be (at least close to) a "true" theory. Classification of living organisms which is supposed to reflect phylogeny has a strong hypothetical background and character.

Panchen (1982) even considers the cladists' claim of hypothetico-deductive methodology wrongly interpreted; he argues that the cladists' reasoning structure is a kind of the logicians "*modus tollens*" and demonstrates this with the way sister- and outgroups are chosen. This objection will, in my opinion, not hold for Zandee's (1985) method. By first presenting all possibilities (still based on monothetically defined "taxa"; in the future polythetically defined "taxa" may also become treatable) the denotion of a possible apomorphic character state is deduced *per hypothesis* (= possible cladogram). The final choice is performed, not by artificial (*ad hoc*) application of any sort of parsimony (s. l.) principle (see Johnson, 1982 for a critical survey), but on account of auxiliary, biological evidence, and this is then dependent on biological knowledge of the group concerned. The heuristic character of this approach is evident.

The parsimony principle is generally applied in physical sciences, apparently with little need for critical reflection. In the (moderate amount of) philosophical literature I have searched, I only found Van Orman Quine (1964) to express philosophical doubts in general on the principle without presenting an operational alternative, as he admits.

Gaffney (1979, p. 96—101) gives a general discussion, in the framework of reflections on phylogeny, concluding that it is "more than a convention": it is a necessary principle to be applied in the hypothetico-deductive method. Panchen (1982) disagrees strongly with this conclusion, as already stated above; he finds the usual cladistic procedure not hypothetico-deductive at all and the cladists' use of the parsimony not "homologous" (my interpretation) with its general (in physics) use. He considers its application (in more complicated cases with non-correlating apomorphies) a way to reach a cladogram with the *fewest* homoplasies, and "bizarre", because the selected hypothesis (cladogram) is then falsified only *the fewest number of times!* Cartmill (1981), even more rigorously, reduces this kind of reasoning to a "rule of thumb", and emphasizes the use of fossil evidence as a test procedure. Furthermore Panchen (1982) argues that there are more and different ways of applying the principle. He cites Sneath & Sokal (1973: 321): (1) a minimum number of evolutionary steps, (2) a minimum of mutational steps, and (3) a minimum tree length. In all three cases *the evolution* is supposed to have

proceeded parsimoniously, which he considers refuted by what is known about molecular evolution.

The way Wiley (1981, p. 113) translates parsimony has in Panchen's (1982) opinion nothing to do with parsimony, but is just an artificial way to be able to choose between possible cladograms. If we take the use of the word "parsimony" that wide to include all these variants (just for convenience), the risk is that the cladist will end up (and be happy) with *just a parsimonious* cladogram. This is what the "transformed cladists" claim, and this is heavily criticized by e. g. Charig (1982) and Ball (1983, and 1984, in prep.).

I cannot believe that any sort of parsimony is applicable in fields of science dealing with unique processes, e. g. history in general, or in evolution. Moreover, Van Steenis (1957, 1969, 1976) argues that chance has played an important role in evolution. These arguments have, however, the structure of an *ad hoc* "sledgehammer", as they give no direction to solve the problem of "how to detect natural (i. e. phylogenetic) affinities".

The example of the (relatively simple) reconstruction of the possible phylogeny of the three taxa of fossil mice showed that modern cladism with application of the outgroup rule led to the (probably) correct answer, but so did the phenetic and the classic approaches as well. In the more complicated case of the four taxa with partly correlating characters, the phenetic approach led to the selection of one scheme on account of greatest overall similarity. The cladistic approach led to four possible schemes, being equally parsimonious (which is a dubious criterion). The classical taxonomist could not choose either, and would have murmured "reticulate evolution" as an *ad hoc,* pseudo-explanation. Zandee's (1985) approach is methodologically the most sound one in my opinion (but see also chapter 7). It may lead in more complex groups towards an incredible number of possible cladograms, between which it is difficult or impossible to choose, dependent on the state of biological, auxiliary knowledge of the group concerned.

An obvious conclusion could be that museum- and herbarium taxonomists are best off (for complex groups) with the phenetic approach, giving clear results in terms of differences and similarities, but it will remain irritating that the results (classifications) need not to reflect the phylogeny of the group concerned. The classical approach is mainly phenetic in its analysis, though more recently at least some classical taxonomists (Mayr, 1974) have adopted Hennig's apomorphy rule, and do not have objections against cladistic *analysis,* for the purpose of reconstructing the assumed phylogeny.

The structure of a classical taxonomical reasoning is neither illogical (see Beckner, 1959, Buck & Hull, 1966, and De Hoog, 1981), nor metaphysical (Wanntorp, 1980, argues this); only the choices are subjective to some extent, and thus as doubtful as *a priori* denotion of apomorphies!

In a more complicated example (to be elaborated in the next chapter) the number of possibilities has increased enormously. I think that in such more complicated cases, only by means of a classico-phenetic approach a practical classification can be proposed, but without the illusion that it reflects phylogeny.

This conclusion, I admit, is disappointing, because illusions are often more attractive than the blunt reality .....

With this open end I want to argue that there is, in my opinion, not (yet?) a generally applicable, "best" method to detect natural affinities, but I consider the ideal worth the struggles.

> If the goal of biological classification is *not* to represent one or more aspects of phylogenetic development, what *is* the goal of biological classification?
>
> (D. L. Hull, 1979, p. 438)

Epilogue on the concept "domain"

Van Valen's article (1976-a) made me realize that the concept "domain" is important in reflections on theories. He argues that, by analogy of this mathematical concept (e. g. in functions: $f(x,y) = x^2 + 2xy + y^2$, x and y form the domain; the function *only* tells something about x and y).

Theories also have a domain. The concept can best be understood by means of a well-known example from physical science: The question whether the newer theories on quantum-mechanics and relativity (of place and time) have *replaced* classical (Newton-) mechanics, can, at least partly, be answered in the negative by realizing that the compared theories have different domains: The trajectory of a thrown stone can be better described and understood in the (methaphorical) terms of Newton's theory than in those of quantum-mechanics or relativity-theory, but the physics of its components (atoms, electrons, bosons, etc.) belong to the domains of the other theories.

Van Valen (1976-a) qualifies the concept "domain" as follows (p. 232): "the domain of a theory is of utmost importance, but is frequently overlooked", and he continues (p. 233):" . . . it has never been possible to fix the boundaries of the domain deductively. The domain, after nearly two centuries, is still indefinite and epistemologically depends on the imagination of discoverers of new solids whose boundaries do or do not conform to the theorem (can be read as "theory" in general, R. G.). Knowledge of the truth or domain of a hypothesis in natural science depends in the same way on the imagination of those who test it".

6. DERRIS, MILLETTIA, AND LONCHOCARPUS: THE PROBLEM OF THE COMPLEX GENUS

More has been written about the concept of the genus than about any other rank above the species.
P. H. Davis & V. H. Heywood (1963) 103

It is not surprising to find how few authors have dared to define the genus.
E. Mayr (1942, 1982-ed.) 283

Both mottoes illustrate that there has been some discussion about the genus concept. Surveys on the genus concept in botany are given in two symposium proceedings, published in Bull. Torr. Bot. Club 67, 5 (1940) 349—389 and in Chron. Bot. 14, 3 (1953) 92—160. Since then, general attention has shifted back to both the species concept and (more recently) to taxa in general. The genus level, however, is a name-providing taxonomic level, and taxonomists have to consider all, partly conflicting, aspects of it in order to present an optimal classification.

The genera *Derris, Millettia,* and *Lonchocarpus* form the large "central" group of the tribe *Millettieae.* The first survey which led to a relative stability of the generic concepts was Bentham's (1860, 1865). He was not very convinced of the natural delimitation he proposed, which was clearly expressed in the following sentence:

> "From *Tephrosia, Coursetia,* and *Robinia* on the one side, to *Pongamia* and *Müllera* on the other, the genera *Gliricidia, Mundulea, Millettia, Derris* and *Lonchocarpus* (with some smaller allied ones) form a gradual passage, the three first, with a more or less dehiscent pod, being perhaps best placed in the *Galegeae;* the two last, in which it scarcely ever shows any tendency to split into two valves, remaining in the *Dalbergieae".*
> G. Bentham, 1860 (Synopsis Dalbergieae, p. 4).

It is evident that Bentham did not consider his classification very satisfactory, and with accumulating material the original distinctions became weaker indeed. The condensed historical survey presented in Table 6.1. may illustrate this.

In 1886 Hemsley described the genus *Fordia,* cauliflorous understorey treelets from Continental S. E. Asia with "technical" characters of *Millettia.* Dunn (1911-a) added more species from Sumatra, Malaya, and Borneo.

Taubert (1894) largely copied Bentham's system, and referred to *Lonchocarpus* in a note under *Millettia.*

During the preparation of his monograph of *Millettia,* Dunn (1911-b) reinstated *Padbruggea* and described *Adinobotrys* (which is congeneric with *Whitfordiodendron* independently described a few months earlier) on account of the combination of paniculate inflorescences, few ovules and indehiscent pods. Dunn (1912) left other species (of *Millettia*) with paniculate inflorescences in *Millettia* sections *Eurybotryae, Austromillettia,* and *Bracteatae.* The first two sections are transferred to *Callerya* in this paper, while the last is raised to generic level.

In 1910, Dunn segregated the African species of *Derris* as a separate genus, *Leptoderris,* on account of their narrow calyx and petals (in fact only the standard) and the constant presence of stipellae. In 1911 (Dunn, 1911-c) he erected a new section

Table 6.1 Characters used between 1860 and 1971 to distinguish the genera of the "central" group

Galegeae subtribus Tephrosiinae or Millettieae Pod dehiscent		Dalbergieae subtribus Lonchocarpinae or Lonchocarpeae Pod indehiscent			
Fordia	*Millettia*	*Pongamia*	*Lonchocarpus*	*Derris*	*Leptoderris*
Treelets	Trees, or shrubs, or lianas	Trees	Trees, or shrubs, or lianas	Lianas, few trees	Lianas, few shrubs
Stipellae + or 0	Stipellae + or 0	Stipellae 0	Stipellae generally 0	Stipellae generally 0	Stipellae + (0 in 1 sp.)
Keel falcate Pod (tardily) dehiscent	Keel falcate Pod (tardily) dehiscent	Keel falcate Pod indehiscent (dehiscent during germination)	Keel falcate Pod indehiscent (except a few spp.)	Keel obtuse Pod indehiscent	Keel obtuse Pod indehiscent
Wings absent on sutures	Wings absent on sutures, some spp. 2 crests on upper or both sutures	Wings absent	Wings absent (except one sp.) but crest on upper suture sometimes more or less distinct	Wing on upper, some spp. on both sutures (except one inland sp. with pod similar to Pongamia)	Wing on upper suture
Excl. character: Cauliflorous under-storey treelets Ovules 2—4. Seeds 2	*Excl. character:* Pod thick	*Excl. character:* Pod thick, adapted to sea-dispersal			*Excl. character:* Narrow standard Slightly narrow calyx
W. Malesia	Tropical Africa and tropical Asia	Tropical Asia	Tropical America and tropical Africa	Tropical Asia, 1 mangrove sp. also E. Africa, 5 spp. tropical America	Tropical Africa

Caudaria for some deviating African species of *Lonchocarpus*. This section is here (and earlier) considered synonymous with *Millettia*.

Harms (1921) described a new genus *Craspedolobium,* which can roughly be characterized as either a *Derris* with dehiscent pods or as a *Millettia* with the upper suture winged.

Corner (1940) noted the striking resemblance in flowering stage between the only species of *Pongamia* (in Malaya) and a species of *Millettia*.

Ducke (1942) transferred the American species of *Derris* to *Lonchocarpus* subg. *Phacelanthus,* which is nomenclaturally wrong. Macbride (1943) corrected this and extended it, even considering *Lonchocarpus* entirely synonymous with *Derris* (but new combinations were made only for Peruvian species).

Ducke (1953) described a species of *Phacelanthus* with dehiscent pods as the first American *Millettia*.

Haumann (1954) described the difficulties distinguishing *Millettia* from *Lonchocarpus,* but he did not propose any change in concepts.

The species of *Derris* with panicles were transferred to the reinstated genus *Aganope* by Polhill (1971), who also sank *Ostryoderris* into it. His transfer of the Australian species of *Lonchocarpus* to *Kunstleria* will be discussed under the latter genus. The "traditional" characters of the central core of the above mentioned genera are tabulated in table 6.2.

Alarmed by my initial plans to merge the tribes *Dalbergieae* and *Millettieae* entirely, Polhill (1977) proposed to transfer the subtribe *Lonchocarpinae* (including *Lonchocarpus*, *Derris*, *Aganope* and *Pongamia*) from the tribe *Dalbergieae* together with Hutchinson's *Millettieae* to the tribe *Tephrosieae* (but *Millettieae* is the correct name).

The confusing genera were then finally together in one tribe. Polhill's suggestion was followed by me (Geesink, 1981) in a preliminary rearrangement of the *Millettieae* (as *"Tephrosieae"*). Many problems had to be left unsolved in that paper due to the publication deadline of the symposium proceedings.

Even after the above mentioned emendations by earlier authors, the basic genera *Derris, Millettia,* and *Lonchocarpus* did not consistently differ in even one character.

The easiest solution would be to lump *Derris, Lonchocarpus* and *Millettia* all together into a moderately large genus *Derris* (approx. 500 species), which would still be much smaller than e. g. *Ficus (Moraceae,* c. 800 spp.), *Dendrobium (Orchidaceae,* c. 1500 spp.), *Indigofera (Leguminosae,* c.700 spp.), or *Astragalus (Leguminosae,* with approx. 2000 multispecies). This solution would have at least four serious disadvantages:

1. The predictability of other properties (different from the ones used for the definition of the concept) would decrease, and with it the content of potential information.
2. It would transfer the problem of the relationship between the included species to infrageneric level.
3. The delimitation from the surrounding genera would become even more problematical because of the enlarged concept. Metaphorically: the lumping snowball would start rolling.

Table 6.2. Subdivisions of *Millettia, Lonchocarpus,* and *Derris* (situation up to c. 1970) with the characters traditionally used.

Millettia Pod not winged, dehiscent			*Lonchocarpus* Pod not winged, dehiscent				*Derris* Pod not winged, dehiscent			
Callerya (as "Padbruggea" and "Whitfordiodendron")	*Millettia*	*Otosema*	*Philenoptera* (*Paniculati*)	*Lonchocarpus*	*Phacelanthus* (*Fasciculati*)	*Caudaria*	*Derris*	*Paraderris*	*Brachypterum*	*Ostryocarpus* (as 'Aganope')
Tree, liana	Tree, liana, shrub	Tree, liana, shrub	Tree, shrub	Tree, shrub	Liana	Tree, shrub	Liana	Liana	Tree, liana	Liana
Panicle	Pseudoraceme Pseudopanicle	Pseudoraceme Pseudopanicle	Panicle	Pseudoraceme with 2 flowers on brachyblast	Pseudoraceme Pseudopanicle	Pseudoraceme	Pseudoraceme Pseudopanicle	Pseudoraceme with 2 flowers on brachyblast	Pseudoraceme	Panicle
Standard with or without basal callosities	Standard without basal callosities	Standard with basal callosities	Standard with indistinct basal callosities	Standard with basal callosities	Standard with basal callosities	Standard with basal callosities	Standard without basal callosities	Standard with basal callosities	Standard without basal callosities	Standard without basal callosities (except *Xeroderris*)
Tropical Asia	Tropical Africa Tropical Asia	Tropical Asia	Tropical Africa	Tropical America (1 sp. also in W. Africa)	Tropical America	Tropical W. Africa	Tropical Asia (5 spp. in Tropical America)	Tropical Asia	Tropical Asia	Tropical Africa Tropical Asia Tropical America

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4. It would undoubtedly lead to increased nomenclatural instability, as the chance that such a concept would be followed regionally or even in smaller areas is probably slight. Locally the differences between the (sub-) groups are more distinct than over their complete ranges.

The latter disadvantages may need further explanation: Van Valen (1964) has given a clear survey of the conflicting character of four aims in the classification of organisms:

    I. To reflect phylogeny as closely as practicable;

   II. To reflect diversification and similarity;

 III. To separate taxa only where "gaps" occur;

 IV. To be usable or convenient.

For the taxonomy of recent organisms, II and III overlap largely, but Van Valen explicitly listed III separately for the taxonomy of fossils within phyletic lines, in those cases where transitional forms are known. In my opinion, the relative weight of the aims differs with the taxonomic levels. For the name providing taxa (family-genus-species-ranks) II, III and IV prevail over I, but I may prevail over the others for the intermediate and higher ranks. As a consequence I have a preference for sliding the ranks (slightly) so that the level of greatest diversification corresponds with a name providing (in this case the genus) level, even when it seems to conflict with "proper" classification.

This pragmatic procedure may sound alarming, but I am convinced it is followed in e. g. *Phaseoleae* bij Verdcourt (1970, 1971), which has led to a relative stability since (Baudet, 1977, 1978, Lackey 1977, 1981, and some floristic treatments).

A characteristic of the three genera *Derris, Millettia,* and *Lonchocarpus* is a similar subdivision on account of their inflorescences.

I have tried to find rearrangements of the subgroups of these genera in order to obtain definable genera, which is impossible with the traditional characters given in table 6.2.

In 1981 I suggested (p. 246, halfway) that cladistic interpretation ("phylogenetic weighting") of characters might be of some use for clarifying affinities of groups within the tribe *Sophoreae* with other papilionoid tribes, but such an approach could help in this case as well, especially in view of the strong and persisting claim of scientific superiority of this method by e. g. Wanntorp (1980), already discussed in the previous chapter.

For this purpose I have treated the units of the subdivision (see table 6.2) and some surrounding genera as OTU's. These OTU's are characterized by a set of characters and are to be considered monothetic groups (Wiley, 1981, p. 79), but not necessarily holophyletic. The most objective way to find the most probable phylogenetic relationships between these OTU's is to elaborate all possibilities and to select as late as possible in the procedure. This is possible by means of the formalization of concepts and the computer program by Zandee (1985), which is explained in the previous chapter.

The 53 OTU's and 59 characters used are tabulated in table 6.3. The data on flavonoids in this matrix became available later, and the data on free amino-acids and amines were less complete than here presented. Also some morphological characters were not yet completely known (e. g. presence of disk, radicle straight or folded), so

that for the first computer run only the numbered OTU's and the numbered characters were used. The unique characters (only indicated by a cross mark at the bottom of table 6.3) were only listed as "present" (and for technical reasons also the OTU's lacking unique characters were listed as such).

The first run was made with 22 OTU's and 60 characters, 36 of which are enumerated in table 6.4. According to a precursory run it appeared that the number of realized strictly monothetic sets was so high (2348) that it made further elaboration financially unaffordable. It was decided that the program was to be run first with 8 selected OTU's with the same 43 characters (only 35 of which were then discriminating or partially discriminating). With 8 OTU's the theoretical maximal number of the three taxon statements is 46895 (Zandee, pers. comm.). The total number of realized three taxon statements containing (syn)apomorphies (= putative ones!) was 1539, thus distinctly less than the theoretical maximum number. This may show that there is at least *some* structure in the group.

Any formalized procedure has intrinsic uncertainties and loss of information, due to the necessary simplification of the basic data. In this case some characters are not as positively "present" (1) or "absent"(0) as stated in table 6.3: *Paraderris* has one species with unwinged pods, although in some specimens the upper suture has an indistinct crest. *Lonchocarpus* (*s. s.*) has four species with paniculate inflorescences, which is considered here as "double apomorphic" character (reversal), and is discussed later in this chapter. *Phacelanthus* has at least one species with the number of leaflets up to 17, but is not scored for this character. *Millettia* has two species with 2 crests on the upper suture and one species with a crest also on the lower suture. These crests are not considered homologous with the wings of *Derris* (*s. l.*), and are thus scored as "0".

The capital types in the lower part of table 6.4 are free amino-acids and amines, analyzed by Evans (1984) who has generously put his results at my disposal.

Before any computer program was run, I made some "rough" cladograms for the same 8 OTU's by hand, which are depicted in table 6.5. The central one (b) is an "underbuilt" traditional system (Bentham, 1865; Taubert, 1894; Geesink, 1981) and the left and right hand ones represent other schemes with different putative synapomorphies in the primary branches. All three possibilities suffer from exceptions and parallelisms considered unparsimonious (in a wide sense) by Wiley (1981) and other cladists.

The output of the computer analysis was rather impressive, several hundred partial cladograms could be drawn, consisting of all sorts of combinations of sistergroups with outgroup. This number was unmanageable, and the whole procedure was repeated with the added restriction, that no parallels were "allowed" in the outgroup. A third run prohibited parallels to occur at all, and from this last run it was evident that no complete cladogram could be drawn without parallels. These second and third runs were made in order to find acceptable "skeleton" cladograms consisting of primary branchings. Later, the higher branches could be filled in by means of the output of the first and of the second run. During this trial-and-error phase of trying out the possible skeleton cladograms it appeared that certain cladograms had to be rejected because the primary branches ("lower clades") would have become "empty" when other OTU's (outside

Characters	No. in Table 6.4	Disyn.	Spath.	Kunst.	Behai.	Cyclo.	Dahls.	Dewev.	Pla. cy.	Phil.	Scheff.	Calle.	Aus. M.	Ostr.	Agan.	Xero.	Derr.	Parad.	Brach.	Lepto.	L. muh. + L. m.	Lonch.	Muell.	Apur.	Berg.	Phace.	Am. D.	Pisc.	Sarc.	Endos.	Wist.	Afg.	P. ops.	Neod.	Marg.	Fordia	Hesp.	Pong.	Caud.	Mill.	Craib.	Crasp.	Pla. sep.	Mund.	Chads.	Caul.	Lup.	Req.	Ptych.	Teph.	Burk.	Imbr.	Anth.	Aus. teen.
Tree	21	0	0	0	1	(1)	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0
Liana	22	1	1	1	0	0	0	1	0	(1)	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Shrub	23	0	0	0	0	1	1	0	0	0	1	0	0	(1)	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	0	0	(1)	1	0	0	1	1	1	1	1	1	0	0
N lfl. ≥ 15	24	0	0	0	0	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	1	0	0	0	0	(1)	0	(1)	0	0	1	1	0	0	1	1	0	0	0	0	(1)	1	0	0	(1)	0	0	0	0	0	0	0	0	0	(1)
N lfl. ≤ 13	25	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	(1)	1	(1)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Stipel. +	26	1	1	(1)	1	1	0	0	1	1	1	1	1	1	0	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	0	0
Stipel. 0	27	0	0	1	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1
Term. rac.	28	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Axill. pan.	29	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Term. pan.	30	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	(1)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1
Term. ps. rac.	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Axill. ps. rac.	32	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	0	(1)	0	1	0	1	0	0	0	0	0	0
Term. ps. pan.	33	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Br. bl. call.	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0
Br. bl. thin	35	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Br. bl. ap. 2f	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Flowers > 15 mm		1	0	0	0	0	1	0	1	0	(1)	(1)	(1)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	(1)	(1)	0	1	1	0	0	0	0	1	0	0	(1)	(1)	0	1	1	1	1	0	0	0	(1)	0	(1)	0	0
Cal. teeth +	37	1	1	1	1	1	1	1	1	1	0	1	(1)	0	(1)	0	0	0	0	1	(1)	0	1	0	1	0	0	0	1	0	1	1	1	1	1	1	0	1	0	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calyx trunc.	38	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	0	0	0	1	0	1	(1)	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Br. oles +	39	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	(1)	1	1	1
Br. oles 0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0
St. b. cal. +	41	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	(1)	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	0	1	1	0	1	1	0
St. b. cal. 0	42	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	1
U. fil. free	43	0	1	1	1	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	(1)	0	0	0	0	1	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
U. fil. adnate	44	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	(1)	1	1	1	1	(1)	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1
Keel obt.	45	(1)	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	(1)	1	(1)	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Keel falc.	46	(1)	0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	0	0	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Disk distinct		0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	0	(1)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Sut. long. wing.	47	0	0	0	0	1	1	0	1	(1)	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pod 4-winged	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pod unwinged	49	1	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	(1)	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Pod dehiscent	50	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	(1)	0	0	0	(1)	0	0	1	1	1	0	1	0	1	1	0	0	1	1	1	1	1	0	1	1	1	(1)	1	0	1	1	0		
Pod indehisc.	51	0	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	?	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0		
Valves "thick"	52	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	(1)	1	0	1	0	0	0	1	1	1	0	1	0	1	1	0	1	0	1	1	0	1	0	(1)	0	0	0	0	0	1	1	0		
Valves "thin"	53	0	1	1	1	1	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	0	1	1	1	0	0	0	1	(1)	?	1	1	0	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0	1		
Radicle straight		0	0	0	0	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
LU 1	54	0	0			0	0		0	0			(1)	0	(1)	1	0	1	0	1	1	1		1	0	0	0	0		0	0	1		0	0	0	0	0							0								0	0
Canavanine	55	1	0			1	1		1	1			0	0	0	0	0	0	0	0	0	0		1	0	1	1	1		0	0	0		1	0	1	1	0							0								1	0
Enduracidine	56	0	0			0	0		0	0			0	0	0	0	0	0	0	0	1	0		0	0	0	0	0		0	0	0		0	0	0	0	0							0								0	0
PPN	57	0	0			0	0		0	0			0	0	0	0	0	0	0	0	0	0		0	0	0	0	0		0	0	0		0	0	0	0	0							0								0	0
2 AI	58	0	0			0	0		0	0			0	0	1	0	1	0	1	0	0	0		(1)	0	1	0	0		0	0	0		0	1	0	0	0		0	0	1	1			(1)							0	0
Homoarginine	59	0	0			0	0		1	0			(1)	0	0	0	0	1	0	1	1	0		0	0	0	0	0		1	0	1		1	1	0	0	(1)		1							1		0	1	0
OH-Homoarginine	60	0	0			0	0		1	0			0	0	0	0	1	0	1	1	0		1	0	(1)	0	0	0		1	0	1		1	1	0	0	(1)	0								1		0	0	0
Flavanones		0							0						0	0	0			1			1	0	0					1		1			1				1															
Flavonols		0							0						0	0	0			1			0	0	0					0					1				1				1											
Flavones		0							0						0	0	0			1			0	0	0					1					1				0				1											
Isoflavones		0							0						0	1	1			0			0	1	1					0					1				1				0											
Pterocarpans & Isoflavans		1							1						0	0	0			0			1	1	0					0					0				0				0											
Rotenoids		0							0						1	1	0			(1)			1	1	1					0					0				1				1										1	
Unique characters		×	×	×	×	×	×	×		×						×			×	×	×			×			×	×	×	×	×	×	×	×	×	×			×			×		×			×	×	×	×	×		×	×		×

Table 6.3. The character matrix of the considered OTU's. Only the numbered characters and the OTU's of table 6.4 have entered the computer runs.

"Beckner-reduktion": red. — red. — reduced — red. — reduced — eventual reduction discussed

Table 6.4. The character matrix, a slightly extended version of which was run in Zandee's computer program.

		Derris	Parad.	Brachypt.	Leptod.	Lonch.	Phac.	Mill.	Tephr.
21	Tree	0	0	1	0	1	0	1	0
22	Liana	1	1	1	1	0	1	1	0
23	Shrub	0	0	0	1	1	0	1	1
24	n leafl. ⩾ 15	0	0	1	0	0	1	1	1
25	n leafl. ⩽ 13	1	1	0	1	1	1	1	1
26	Stipellae +	(1)	0	1	1	(1)	0	1	0
27	Stipellae 0	1	1	0	0	1	1	1	1
28	(Term. raceme	0	0	0	0	0	0	0	0)
29	(Axill. pan.	0	0	0	0	0	0	0	0)
30	(Term. pan.	0	0	0	0	0	0	0	0)
31	Term. ps. rac.	0	0	0	0	0	1	1	1
32	(Axill. ps. rac.	1	1	1	1	1	1	1	1)
33	Term. ps. pan.	1	1	1	1	1	1	1	0
34	Brachybl. call.	0	0	1	1	0	1	1	1
35	Brachybl. ± thin	1	0	0	0	0	0	0	0
36	2 fl. on brachybl.	0	1	0	0	1	0	0	0
37	Calyx teeth +	0	0	0	0	1	0	1	1
38	(Calyx truncate	1	1	1	1	1	1	1	1)
39	(Br. oles present	1	1	1	1	1	1	1	1)
40	Br. oles absent	0	0	0	0	0	0	0	1
41	Stand. bas. call. +	0	1	0	0	1	0	1	1
42	Stand. bas. call. 0	1	0	1	1	(1)	1	1	1
43	Upper fil. free	0	0	0	0	0	0	1	1
44	(Upper fil. adnate	1	1	1	1	1	1	1	1)
45	Keel obtuse	1	1	1	1	1	0	0	0
46	Keel falcate	0	0	0	0	1	1	1	1
47	Pod 1 or 2 winged	1	1	1	1	0	0	0	0
48	(Pod 4 winged	0	0	0	0	0	0	0	0)
49	Pod not winged	0	0	0	0	1	1	1	1
50	Pod dehiscent	0	0	0	0	0	(1)	1	1
51	Pod indehiscent	1	1	1	1	1	1	0	0
52	Pod valves thick	0	0	0	0	(1)	0	1	0
53	Pod valves thin	1	1	1	1	1	1	(1)	1
54	A	(1)	1	(1)	0	1	1	0	0
59	F	0	0	0	0	0	0	1	1
60	G	0	0	(1)	0	(1)	(1)	1	1

the 8 treated ones) were added. Other skeleton cladograms could not be provided with putative (plausible or not, that was a later difficulty) apomorphies in accordance with the three taxon statements. The choice was either to construct cladograms with synapomorphies in the lower branches but with "empty" higher ones, or vice versa. Only one

41
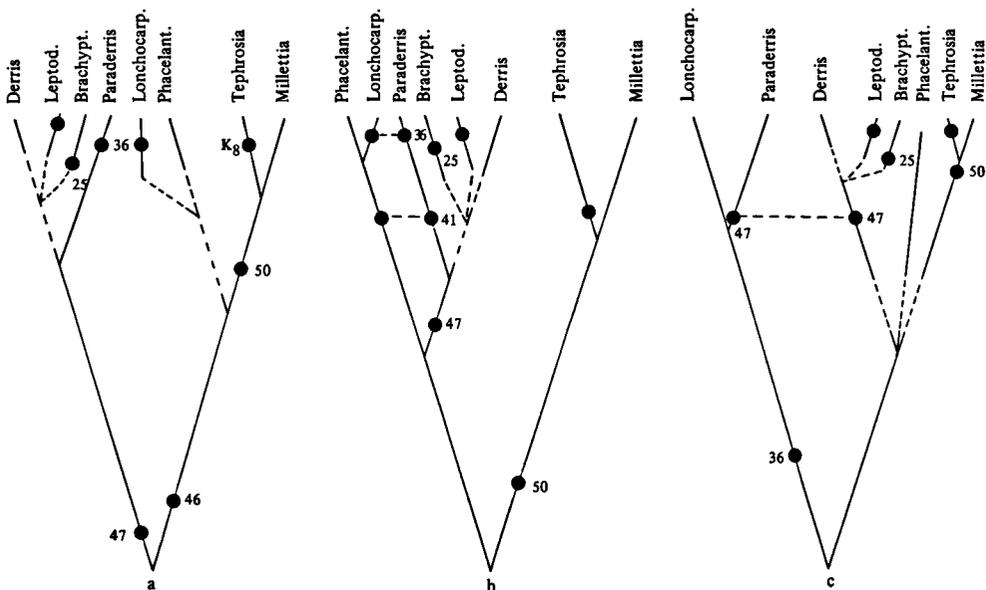
Fig. 6.5. The three "rough" cladograms made by hand.

skeleton cladogram survived this selection procedure more or less, and this is depicted in table 6.6.

Except for the basal dichotomy (just above the heavy horizontal bar) the cladogram of table 6.6 is very poor indeed. The uppermost branches show autapomorphies only in *Tephrosia* and in *Leptoderris*; the other OTU's show a reticulate pattern of parallel structures.

The synapomorphies of the intermediate branchings are weak, as many of them are only partially "true", which is indicated by black and white sectors. In a discussion with R. M. Polhill on the difficulties concerning the definitions of the "lower" tribes of the *Papilionoideae* (i. e. *Swartzieae, Sophoreae, Dalbergieae, Tephrosieae,* and *Robinieae*) Polhill noted the significant instability of certain characters in these groups, while in the "higher" tribes characters are generally more fixed. Translated into cladistic terms, this could mean that the instable, varied expression of character states is the plesiomorphic state, and not always one particular character state. This seems a challenging idea to me, and in this cladogram (6.6) the predominantly plesiomorphic character symbols can then be read as completely plesiomorphic. The apomorphic character symbols with a small white sector can be read as either also plesiomorphic or as apomorphic with a small number of members which show a reversal in that particular character state.

But, besides this evasion, I can think of seven other kinds of difficulties, which can explain the unsatisfactory patterns of table 6.6 (and of other, already "rejected" alternative schemes as well), viz.:

42
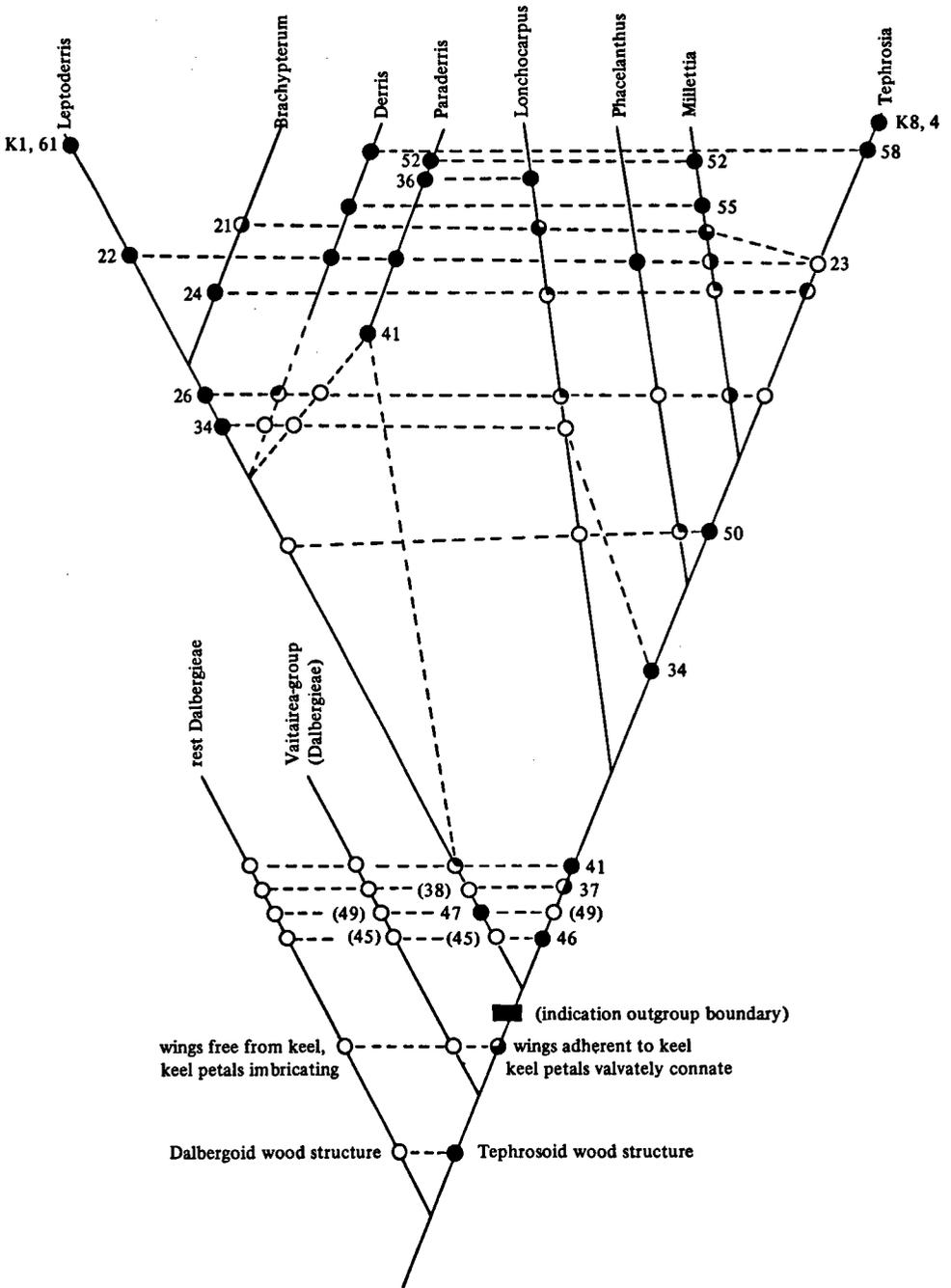
Fig. 6.6. The "final" cladogram, resulting from a combination of the second and third computer run.

1. Accepting the evolutionary mechanism to consist of divergence and extinction, I understand that divergence actually occurs (and has occurred) at individual to population level, and that extinction occurs at the same level (the "loosers" after "natural selection") as well as at higher, taxonomic levels. In the latter case the actual extinction takes place also on individual to population level, but if this has occurred worldwide in a relatively short period, it can be generalized in terms of "extinction of taxa".

Much has been written about the "reality" and related qualities of taxa (see Van Steenis, 1957, Löther, 1972, and Hull, 1976, 1979 for a recent revival). An earlier survey of this problem is given by Simpson (1961, pp. 114—119), and my (present) opinion on this matter is that *all* taxa *should* be holophyletic entities (existing in nature, with an own role, place and evolutionary tendencies, after Simpson, 1961) or substantial systems (*"materielle Systeme"* sensu Löther, 1972), but only part of the distinguished taxa may be so, and the rest consists of artificial classes. The main difficulty is that the pile of plant specimens, labelled in the herbarium as a taxon with a particular rank, does not "tell" to which category it belongs. In the words of Bentham (1861, p. 133): "The *Species*, in the ordinary traditional acceptation of the word, designates the whole of the individuals supposed to be descended from one original plant, or pair of plants. But this definition is practically useless — for we have no means of ascertaining the hereditary history of individual plants (or better: ancestral populations or species, R. G.) ....". So, there are *kinds of* taxa, and in the last pages of chapter 7, I propose to distinguish three different ones. For colleagues with paleontological experience, it will be clear that taxa can only be distinguished in one particular time-cross-section (e. g. the Recent). Diachronic successive taxa become more indistinguishable, when the fossil record becomes more complete. The diachronic series consists of gradually connected taxa (either slowly or saltatory evolved) with ancestral taxa of lower rank and with putative future taxa of higher rank which may (or may not) radiate from them. Thus, within a lineage, not only the boundary between the taxa is gradual, but also their rank changes gradually. Also Mabberley (1984) refers to this very fundamental problem.

In connection with this view, the lack of generic pattern in the *Millettieae* can be understood if a relatively low rate of extinction is assumed at that point of time, where the ancestral species of the present "complex genus group" formed a "complex species group". Something is known about the supposed mechanisms causing "complex species" (see e. g. Leenhouts, 1966, and Van Valen, 1976-b), and these are briefly discussed below, under 3, 4, and 5.

2. Beckner (1959) introduced the distinction between polytypic and monotypic definitions of taxa. These concepts were renamed *"polythetic"* and *"monothetic"* by Sneath (1962) in order to avoid confusion with similarly named concepts. These renamings, and the usefulness of the concepts, were later (but not yet generally) accepted. Wiley (1981, pp. 79, 80) discusses these concepts without, however, expressing a distinct preference for one of them. His cladograms, at least the ones which are discussed in an atmosphere of acceptability, all show a clear monothetic character. A consequence of monothetic definition is the assumption that once an apomorphy has

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developed, it is either supposed not to change any more, or to develop into a further apomorphy (a → a′ → a″). Reversals cannot be recognized *a priori*. Allowing a polythetic taxon concept has the advantage to be probably more natural (see e. g. Mayr, 1982, pp. 189, 190) and the disadvantage to have the possibility of groups without discriminating characters (see e.g. Baas c.s., 1982, pp. 198—199, for an example of polythetic group definitions).

· **3.** Another difficulty is the suspicion of parallel developments of functional characters in existing lineages. This aspect is discussed by Stebbins (1974, pp. 39—49) in connection with life forms, adapted to certain circumstances, with analogies in pollination and seed biology. Selection pressure can roughly be defined as that (polythetic) set of influences which causes evolutionary deviation of the development which the group would have undergone without these influences.

A nice example of a known *lack* of such a pressure (compared to the evolution on the mainland) is demonstrated by the evolutionary divergence of the fossil mice from Gargano (chapter 5). In that case the (lacking) factor is the absence of hunting carnivores (assumed, from the absence of remains in the rich fossil beds).

In the *Millettieae,* functional characters (which may have developed in co-evolution with certain groups of bees and bumble-bees) are e. g. the presence of a differently coloured patch on the standard, whether or not combined with basal callosities and fenestrae at the base of the upper filament. In case we would have designated the functional character 5 (from table 5.5) as suspect of parallel developments, we could have rejected the cladograms **4, 6,** and **10** of table 5.6.

I discussed a few functional aspects in the paragraph on flower structure and flower biology in chapter 4. Many tribes of the *Papilionoideae* are defined on fruit characters, (polythetically) combined with vegetative and flower characters. Of course one can rearrange the tribes completely, but I will not pursue this notion, as a more optimistic colleague is attempting to do (even cladistically!).

4. The best known disturbing factor is hybridization. If this can be demonstrated in recent taxa, it is a valid argument. But if it is merely assumed in (early) history of the group concerned, it is an untestable *ad hoc* hypothesis, even though it does have explanatory power. Lotsy (1914, 1931) considered it the most important cause of evolutionary change. There is no distinct evidence in the *Millettieae* that hybridization between species or genera does occur (except possibly in *Tephrosia*, which has a "suspect" species pattern). The chromosome number varies from 16 to 24 and no polyploid complexes are (yet) known in this group.

5. Phylogenetic reversals are difficult to recognize, except in a few cases. Two examples are given: All (American) species of *Lonchocarpus* (*s. s.*) have within their inflorescences the flowers paired on top of a common brachyblast, except *L. mühlbergianus,* which has panicles (also three more species, see note under *Philenoptera*). The branches of the panicle in *L. mühlbergianus*, however, differ in one respect from the supposed "truly primitive" panicles (as e. g. in *Philenoptera* and *Callerya*): the most proximal two flowers are opposite instead of spirally arranged, and this may indicate that the racemose arrangement is secondary, viz. derived from a biflorous condition. Not all branches of the panicle show this opposite arrangement of

the proximal flowers, and if this opposite condition had not occurred at all, the inflorescence would have been indistinguishable from the "truly primitive" paniculate ones.

Another example is the 10—30-flowered brachyblast of *Tephrosia elliptica* (Bosman & De Haas, 1983, p. 449). The species is confined to the Lesser Sunda Islands and Queensland, and its closest relative (sister species) is probably the widespread *T. purpurea,* which has brachyblasts with up to 8 flowers. In the inflorescence schemes considered evolutionary plausible (see chapter 4), a reduction series from many-flowered racemes to a reduced number of flowers on brachyblasts is assumed. Has the opposite direction been followed here? And who knows how often this has occurred with other characters? (I am well aware that this is a rhetorical question.)

6. Cladistically experienced colleagues may have already guessed another probable cause of the "failure": many of the OTU's used may not be holophyletic but para- or polyphyletic "restgroups". Most suspect are the OTU's *Callerya, Millettia* (even *s. s.*), *Ostryocarpus* (*s. l.*) and *Derris* (even *s. s.*).

Assuming that the cladistic approach is methodologically sound (which, exclusively for the purpose of reconstructing assumed cladogenetic evolution, I believe to be true), the "failure" is thus an indirect proof of the probable para- or polyphyly of at least some OTU's. This result has, in my opinion, consequences for the possibility of translating classical systems into cladistic ones. The demand for (most probably) holophyletic OTU's is apparently a necessity to obtain any informative cladistic result.

7. Overlap of the morphological "range" due to divergence. The fossil mice (chapter 5) demonstrate the *closing* of an originally existing gap due to divergence. The gaps in the lineages ancestral to the later lineages I and II show slightly wider gaps on level C3A and C7 (table 5.2) than on level C9. The gaps may even be absent on level C9 (they were unnoticed in 1971) and it may be concluded that the higher gaps are merely arbitrarily depicted in order to obtain a plausible tree.

Above the species level the morphological ranges may become overlapping due to parallel developments without any exchange of genes: they just "invented" the same characters independent from each other. If the relic characters of the ancestral taxa become outnumbered by the newly developed homoplasies, they will be difficult or impossible to detect. The result is then a complex group, which is only arbitrarily subdividable. The advantage of these assumptions is that hybridization needs not to be assumed. I doubt whether dedicated cladists will feel at ease when they construct a tree with one or two synapomorphies and numerous homoplasies.
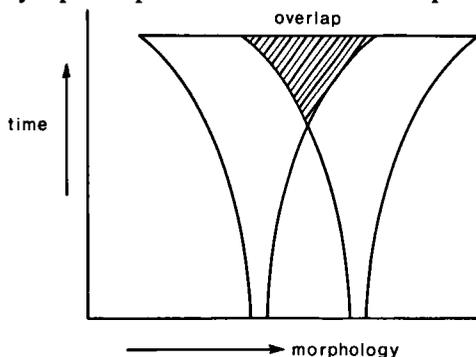
Zandee (1985) has also tried his method on other plant groups, and it appeared in those cases that the method provided some more alternatives (as was expected), which could already be deduced after the first run (without the homoplasy-restrictions of the second and third run).

Taking into account (i) the uncertainties discussed in the previous chapter, (ii) the impossibility of constructing a proper cladogram from the overwhelming number of possible partial ones, (iii—x) the difficulties discussed above, plus (xi) the fact that Zandee (1985) obtained much better results in other, less complex groups, I feel obliged to give up the desire to detect the phylogeny of this group. The lack of results is due to the combination of the difficulties (roughly summarized: lack of biological knowledge) discussed above. In order to obtain better results, I think the procedure should be repeated taking taxa of lower rank (species, sections) as OTU's, but this can only be performed after revisions (and rearrangements) are available of all groups involved. Elaboration of this ideal is considered too far removed from the program I have in mind for treatment of the Malesian *Papilionoideae*.

Summarized conclusion: The present state of knowledge of this group does not allow cladistic analysis. In his introductory chapter on the *Papilionoideae*, Polhill (1981, p. 202) makes the following significant remark on the genera of the *Millettieae* (as *"Tephrosieae"*): "Early misjudgements of generic criteria and the combination of relatively unspecialized flowers, inflorescences and vegetative structure with labile fruits have produced a sadly confused taxonomic situation, for which miraculous cures are repeatedly sought". I can only add, that I have tried yet another remedy, but for the time being, again, ... in vain!

Table 7.1. The character matrix for the compatibility analysis. The number of the character states refer to the numbers of the character states in table 6.4.

7. CHARACTER COMPATIBILITY AND THE DECISIONS ON GENERIC DELIMITATION

"Character non facit genus" it is true; but a genus without a character is of no assistance to the mind of the naturalist.

(G. Bentham, 1861, p. 151)

There could be a relation between results obtained with Zandee's method (1985) as outlined in chapter 6, and with Meacham's (1981) compatibility analysis. The latter method can also be (slightly) modified so that in first instance phenetically based schemes are obtained, from which cladograms can be derived.

I shall outline this slightly modified way, demonstrated by the (again slightly) modified character matrix of the previous chapter (table 6.4). The modifications in the matrix (table 7.1) are: *1*. The OTU "American *Derris*" was added, because this OTU is very similar (in number of shared character states) to *"Phacelanthus"*, but differs from it in the winged pod (as in *Derris s. s.*). *2*. I excluded those characters that occurred more than twice with both character states scored, because these characters have appeared to be incompatible in any case. *3*. Meacham's manual method requires characters with only two character states. Multistate characters can either be "combined" to a binary state, or be "dissected" into its binary components (see Meacham, 1981, p. 595). In this character matrix the exceptions are also included; if a character state occurred only in a minority of the members of the OTU, this state is scored between brackets, and the corresponding majority is scored as "fully occurring".

Compatibility means (in profane language) that characters (each having two states) have such a distribution (if taken pairwise over OTU's) that only one basic relational scheme results. A few examples may be necessary. The most obvious case of compatibility is present, when characters are either completely (positively or negatively) correlated or completely exclusive, i. e. all OTU's share either A's or B's, or A/B over both characters:

```
        OTU's  a  b  c  d  e  .  .  .  .  .  .  .  .  .  .  .  z

Characters
          1  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A
          2  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A
                                                             completely correlated
          1  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B
          2  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B


          1  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A  A
          2  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B  B
                                                             completely exclusive
          1  A  A  A  A  A  A  A  A  B  B  B  B  B  B  B  B  B  B
          2  B  B  B  B  B  B  B  B  A  A  A  A  A  A  A  A  A  A
```

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But besides these conditions of correlation, character distributions can also partly exclude or include each other in such a way that certain character states do not contradict ("bite") each other:

```
1 A A A A A A B B B B B B B B B B B B
                                         the A's partly inclusive
2 A A A B B B B B B B B B B B B B B B

1 B B B B B B B B B B B B A A A A A A
                                         the A's partly exclusive,
2 A A A A A A B B B B B B B B B B B B     the B's overlapping
```

The effect of the overlapping character states (B, above) is discussed later in this chapter. Compatibility is only the case when not all four combinations of the two states are scored in the matrix. The following example shows two incompatible characters:

```
1 A A A A A A A A B B B B B B B B B B
                                         incompatible
2 A A A B B B B B A A A A A B B B B B
```

The first step is thus to compare all the combinations of all (binary) character states, for which the triangular scheme (copied from Meacham's table 15) was filled in. It will be clear that this manual method is limited by the number of characters used. I think that about 8 characters are the limit for manual treatment; a larger number requires electronic processing.

The encircled groups of four combinations of character states represent the pairs of fully compatible characters, underlined in the enumeration, top right in table 7.2. The groups between brackets represent the characters that would have been compatible, if the above mentioned exceptional character states would have been ignored.

From these "fully compatible" and "bracketed compatible" character sets the scheme in table 7.2, bottom, can be drawn; the drawn lines correspond to the "fully compatible" sets, and the broken lines to the "bracketed compatible" sets. The next step is to find the largest "clique" (as Meacham calls it) of fully compatible characters, i. e. the largest group of characters *all* mutually connected by drawn lines. This resulted in three cliques of three mutually compatible characters, viz. 6/9/10, 3/8/9, and 5/6/9.

And these cliques are very meagre, as is demonstrated in the next step, called by Meacham "popping the tree(s)". The crux of this method is that one clique of fully compatible characters leads to one basic tree only, because, as it were, the conflicting evidence has been excluded. This basic tree is a simple, undirected, connected graph without "cycles", i.e. each node has three or less lines attached. The graph is comparable in shape with a "Wagner-network" (see Farris, 1970, and Wagner, 1980), but then without hypothetical ancestor and also without directed (to apomorphy) character states. The nodes represent agglomerations of (one or more) OTU's. In the case of more OTU's at the end of branches the "tree" will not be fully resolved. For convenience I will refer to these basic trees as "unrooted phenograms". The actual

2

(2/3) (2/7) (3/4) <u>3/8</u> <u>3/9</u> (3/10) <u>5/6</u> (5/7) <u>5/9</u> (5/10) (6/7) (6/8) <u>6/9</u> <u>6/10</u>
(7/8) <u>7/9</u> (7/10) <u>8/9</u> (8/10) <u>9/10</u> (4/11) (5/11) (6/11) (7/11) <u>9/11</u> (10/11)

3

4

5

6

7

8

9

10

11

   1   2   3   4   5   6   7   8   9   10

Table 7.2. The detection of the compatible sets and cliques. The upper figure is the matrix in which the occurring combinations of character states are scored. The encircled groups of four combinations correspond with the fully compatible sets, depicted in the lower figure as solid lines. The bracketed groups of four combinations correspond with the broken lines in the lower figure.
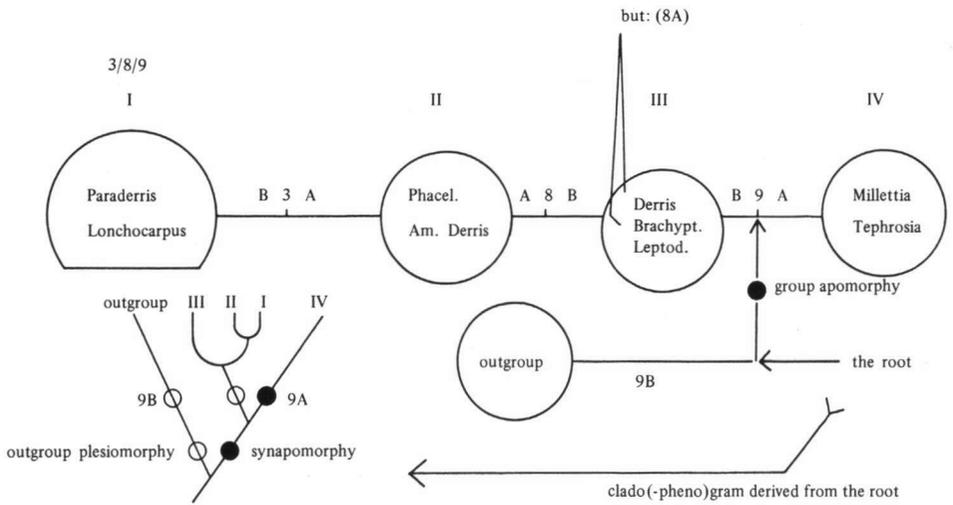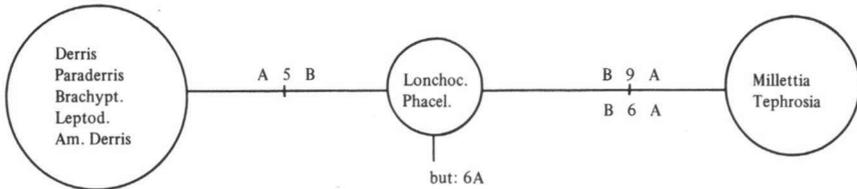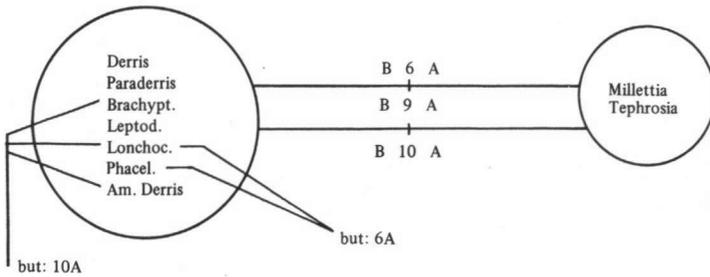
Fig. 7.3. The unrooted phenograms derived from the three cliques of mutually compatible characters.

"popping the trees" is a straightforward action. Any arbitrarily chosen first character of the clique divides the group into two subgroups; e. g. the two states of character 9 divide *Millettia* plus *Tephrosia* from the other group of OTU's. The next chosen character divides the rest-group into two subgroups, etc. etc.

The three "unrooted phenograms" derived from the three cliques are depicted in table 7.3. In this table, however, two disturbing character states (besides 8 A, being a case of "bracketed" compatibility) are noted, viz. 6 A, occurring in *Lonchocarpus* and in *Phacelanthus,* and 10 A, occurring in *Brachypterum,* in American *Derris,* and in *Lonchocarpus.* Initially I ignored these disturbances, but Zandee (pers. comm.) pointed out their noteworthy cause: in Meacham's concept, compatibility means "at least one combination of character states not occurring", and this leads always and unambiguously to one unrooted phenogram. There is, however, one type of character distribution, that is compatible in Meacham's sense, but it does not lead to an unambiguous basic tree, and that is the case of the overlapping character states in the last case of compatibility depicted above:

1   A   A   A   A   A   A   A   A   B   B   B   B   B   compatible,
                                                                but A's overlapping
2   B   B   B   B   B   B   A   A   A   A   A   A   A

The combination BB does not occur, and therefore the characters are compatible. But no subdivision can be made, due to overlap. This kind of undesired compatibility can be called "group-incompatibility despite character compatibility". It means for the possible unrooted phenograms, that branches derived from this kind of compatibility must be specially considered. In later instances, if the B-state appears to be (possibly) apomorphic, it can be used in the cladogram. If the overlapping (A) state must be considered apomorphic, the corresponding unrooted phenogram must either be rejected, or is provided with a parallel apomorphy.

The unrooted phenograms can be made into rooted ("normal") phenograms by choosing one of the internodes, mark its midpoint, call it "the root" and connect a new edge to it with an "outgroup" attached. In fact, a cladistic procedure has crept in here, but there is hardly such an explicit analogon to "outgroup" in the phenetic procedures, so that this example may be more clear. This outgroup (e. g. *Ostryocarpus,* or *Callerya*) has e. g. character 9 in the state B, and this determines the root halfway the internode with character 9. The original group then needs a synapomorphy (e. g. flowers clustered within the inflorescence, while the outgroup has true panicles considered as plesiomorphic). This "rooting action" is demonstrated by the clado-phenogram figured below the unrooted phenogram corresponding with the clique 3/8/9. The further procedure is identical to the last operations in Zandee's method, as this method also leads to rooted phenograms from which cladograms can be derived by interpreting the character states as "apo-" vs. "plesiomorphic" with the outgroup rule.

Elaboration of the procedure in this example does not serve any useful purpose. A clique of just three characters is too meagre to build fully resolved phenograms or cladograms: starting with t = 9 OTU's in the character matrix (table 7.1) a fully resolved

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binary tree will count t = 9 terminal vertices ("leaves") and t − 1 = 8 internal vertices, connected by a total of 2t − 2 = 16 edges. Each edge results from a "popping the trees"-action. This implies that there must be at least 16 characters in the largest clique in order to "pop" a fully resolved binary tree with no parallel in it. The consequence for the given example will be that in the higher branches (of the fully resolved "unrooted phenograms" of table 7.3) numerous parallels will appear. This was already demonstrated after application of Zandee's method (in the previous chapter).

Furthermore, these fully resolved "unrooted phenograms" will become even more meagre when the fully compatible cliques obtained from the modified character matrix (table 7.1) are checked for their compatibility in the large matrix (corresponding with table 6.3). By adding OTU's to the character matrix the number of compatibilities will either remain constant or decrease, but never increase because incompatible character sets will remain incompatible forever.

Checking the compatibilities with the "large" matrix "destroyed" the following compatibilities: 8/9 became incompatible by the OTU *Pongamia*, 5/6 by *Craspedolobium*, 6/9 by *Callerya* and *Pongamia* (again), 6/10 by *Hesperothamnus*, *Sarcodum*, and *Endosamara*, and 9/10 by *Antheroporum*. This leaves (from the selected characters) 3/8, 3/9, and 5/9 as compatible sets. These sets do not form one clique, but again three (further impoverished) cliques. Of these characters, 8 and 9 are chemical characters that must be considered with caution, as they are not checked for all members of the OTU's and thus may prove to become exceptional scores if more analyses are made. The phenetically based unrooted phenogram contains only one morphological character, viz. 3 that can be generalized to "Inflorescence structure".

Meacham's method has thus provided the actual cause of this complexity: the extremely low number of compatible character sets, which will, obviously, not come as a surprise. Meacham's method provides the possibility to analyse exactly which characters are compatible and how many sets of compatible characters are present.

Where Zandee's method leads to an unmanagable number of possible phenograms, Meacham's method leads quickly to the actual cause. In the reversed case, if many compatible characters are found, it may be difficult to find the largest clique, as Meacham explains on pp. 596—598. Zandee's method will then lead rather quickly to the tree or the few trees corresponding with this largest clique. In the finishing stages of this revision, Zandee had developed a way to combine both methods into one algorithm, but after the first runs new difficulties have arisen that must be overcome before publication.

In *conclusion*, the combined uses of Zandee's three taxon statement permutations and Meacham's character compatibility analysis form a powerful "tool-kit" to handle both relatively simple character matrices (visually only recognizable by the relatively high number of correlated characters) and more complex character matrices.

This leaves us with the final decision on generic delimitations: the aim of this study. The only conclusion, supported by the lack of results in the form of *the* tree, or *the* cladogram, or even *the* phenogram, is to construct none of these. This means that the

OTU's used all deserve the same taxonomic rank (genus in this case) and that the next higher taxonomic rank is the tribal one (and this is a paraphyletic taxon, as has been explained in chapter 3).

There is, however, one generally applicable possibility to reduce the number of the terminal genera somewhat, and that is *Beckner's principle 3* (1959, 1968-edition, p. 73): "No polytypic (read "polythetic", R. G.) group is to be assigned status as a taxon of rank j if it can reasonably be assigned to rank j minus one". This rule prevents "inflation of taxonomic rank", which is often observed in those specialized revisions where the "surrounding" allied groups ("outgroups" in cladistic jargon) are excluded from comparison. Beckner's rule can, however, not be strictly applied, since it would exclude the formation of monotypic (in the meaning of containing only one taxon of lower rank, e. g. species) higher taxa (e. g. genera).

This is often contradictory to the "feeling of ranks" acquired by experienced taxonomists in the case of species so much different from their supposed closest relative (either in cladistic or in genetic sense), that they do deserve such a high rank.

There are in the *Millettieae* some mono- or "oligotypic" OTU's which can easily be reduced to a subgroup of another OTU. Other cases are doubtful; one could either reduce them, maintain them in generic rank for convenience sake (stability of names) when they have already been entered in some floras in generic rank. In the first mentioned cases I have reduced them, in the second case usually not (except *Xeroderris*, see the note under *Ostryocarpus*). The "victims" of Beckner's anti-inflation rule are e. g. *Pongamia* and *Muellera,* which are discussed under *Millettia* and *Lonchocarpus* (*s. s.*) resp. Several monotypic genera are proposed to be maintained, and a few (strong enough) deviating original subgroups have been raised to generic level, e. g. *Endosamara, Brachypterum, Paraderris,* and *Deguelia* (consists of *Phacelanthus* combined with American *Derris.*

In order to keep this chapter limited in size, I hope I may suffice with reference to the taxonomic notes under nearly all generic descriptions, where characters and "relatives" (in terms of characters shared, not cladistically defined) are discussed. As most accepted genera have numerous connections in terms of "at least some characters shared", I have restricted the comparison with "related" (again only in terms of characters shared) genera to those which have a similar "Gestalt-perception", the "overall-impression" of the dried specimens.

The *criterion* applied to consider genera different from each other is the presence in both compared genera of a monothetic set (preferably supported by unique characters, but these were onlyu found in a few genera) consisting of at least two morphological characters. I think that the arguments for the opinion that a single character is insufficient for delimitation on specific and generic level have been put forward often enough, so that I may refer here to Van Steenis' (1957, Introduction, and statement 14 on p. ccxxv) strong opinion in this matter which I (largely) endorse.

Application of this principle made apparent that the wide concepts of the larger genera *Lonchocarpus* (*s. l.*), *Derris* (*s. l.*), and *Millettia* (*s. l.*) cannot be maintained, simply because they do not differ in even one constant character, and such concepts,

though convenient from the point of view of stability of names, do not serve any practical purpose. This is demonstrated for the *Millettia/Derris/Lonchocarpus*-case in the beginning of the previous chapter. The only way to obtain definable groups is to raise the next available lower rank (subgenera and sections) to the generic one, but fortunately not all sections of e. g. *Millettia* need to be raised. I tried to keep the group under the generic name *Millettia* as large as possible.

The question remains, what *kind of* taxa are then obtained? In most theoretical reflections on taxa synthetic inclinations can be observed. Kalkman (1982); and earlier Bentham (1861) formulated what I call the "synthetic taxon concept exclusively based upon hope". This concept consists, in my view, of three qualities with regard to their additional information content:

1. The *minimal quality* without any additional information content. This concept is applicable for those taxa which are based upon either one unique character combined with a polythetic set, or upon a monothetic set of at least two characters. When newly discovered features are compared, these either suggest previously unknown and different, "minimal", or, in the worst case, nonsensical relationships. This is generally the case in groups where classical taxonomists apply terms as "reticulate evolution", "complex groups" and the like. Experience has shown that e. g. pollen features, or vegetative features do then not correlate with any macromorphological feature.

The "minimal quality" concept is evident for most members of the group here under study. Newly discovered taxa of lower rank (members of the group) are likely to possess combinations of characteristics that spoil the original distinctness of the "minimal taxon". If they have not (yet) spoiled the distinctness, "minimal taxa" have a certain degree of predictability with regard to newly collected specimens only. In case of "spoiled distinction" the taxon cannot be maintained and will usually have to be merged with another, usually also "minimal" taxon, and in some cases a "snowball-effect" may provide the necessity to merge more taxa as well. This is not so disturbing, as the minimal taxon has only one quality, and that is its single name that indicates the group of individuals (or species) possessing that particular set of characters and nothing more. These taxa are recognizable and accessible by means of a key.

2. The *genetic quality*. Morphologically not distinguishable from the previous concept, but newly found features appear to correlate with the original set of defining characters. These taxa have a certain degree of predictability with regard to still undiscovered additional characters. These taxa correspond with the first part of Kalkman's (1982) "hopeful, synthetic taxon concept", translated: "These individuals share a large number of characteristics, so their genomes will be largely similar". On species level these taxa with genetic information content may correspond (but not: do inevitably correspond) with Simpson's (1961) genetic species in its turn synonymous to Mayr's partly misleading term "biological" species. For higher taxa one can replace "individuals" by "species" (though not without problems) or any taxon lower than the higher one herewith defined.

3. The *phylogenetic quality*. I have very low expectations of original "minimal taxa" having this quality, but, at least theoretically, it is not completely excluded. It is

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conceivable, that the few characters "defining" the taxon correspond with the apomorphic character state that made the taxon to be recognizably different from its ancestral population. More often, if not always, only "genetic taxa" will possess this (or those) "true apomorphic" character(s), but it remains doubtful, as explained in chapter 5, that this apomorphy can always be detected.

If this is the case (and I doubt if this aim is attainable in many groups of Angiosperms), also the last part of Bentham's and Kalkman's synthetic taxon concept is fulfilled: "These individuals share a large number of characteristics, so their genomes may be largely similar, and they may have originated from a more recent common ancestral population" (compared with another group of individuals with a lower degree of similarity).

It is generally agreed upon that this synthetic circumscription is applicable to species, but higher taxa are sometimes differently conceived (if at all); the ad-hoc clincher is "classes" (in the logical sense, not as the taxonomic rank). This is a very fundamental problem, discussed by e. g. Löther (1972, p. 238), Hull (1976, p. 183), and the recent follow-up does not allow a concise summary here.

In *conclusion*, category 3 may include category 2, but, at least theoretically it may include category 1 only. Category 2 always includes category 1. This means, that category 1 is basal, and this is generally differently worded in the conceptual sphere as: "Taxa can only be distinguished, when they are different in at least a few features then called characters". This may sound all to obvious, but the famous sibling species spoil the picture.

The presentation (in chapter 9) of genera (i. e. groups of species overestimated to this rank by necessity) is an enumeration, with some notes on the differences with the "most similar" genera. Most of these genera will have "minimal qualities", but a few may have other qualities. I cannot see the difference, due to lack of support of characters. This may become more clear after more (new) characters have been checked, some of which may provide compatible sets with one of the characters used in this study.

8. GEOGRAPHICAL DISTRIBUTIONS

Generalizations on geographical distribution patterns are hardly possible with the distressingly labile extension of the largest genera. The tribe is pantropical with a few genera extending northwards (see notes under *Wisteria* and *Callerya* on *Millettia japonica*). The formerly conceived disjunct distributions of *Lonchocarpus* and *Derris* are no longer disjunct, as long as the distinction of *Austrosteenisia* (a new genus comprising the Australian "*Lonchocarpus*"-species) and *Deguelia* (part of which was the disjunct "American *Derris*") is followed. On a smaller scale, disjunction occurs in *Sarcodum,* with one species from Thailand, Indo-China, and Philippines to the Moluccas, and another, undescribed species in the Solomon Islands. In the American genus *Lonchocarpus* (*s.s.*), one species occurs at both sides of the Atlantic. I have insufficient knowledge do dare to speculate whether this is a relic-distribution or a case of introduction by man. The latter possibility seems not very probable, as the species grows in undisturbed primary vegetations.

Most genera here distinguished have either a restricted, "endemic" distribution, or (and these are mostly the candidates for heterogeneous amalgamates of species *Callerya* and *Millettia*) are widespread but not disjunct.

9. TAXONOMIC PART

In a rather late stage of the preparation of the manuscript I found that the oldest legitimate name on tribal rank is *Millettieae* and not *Tephrosieae*, as was generally accepted since Hutchinson (1964). This complicated the preceding text slightly, as I had to use the phrase (as *"Tephrosieae"*) in most references to post-Hutchinson literature, also to my own preliminary treatment (1981).

In order to save some space and time I have abbreviated the often cited books and papers as much as possible. These abbreviations follow more or less the abbreviation procedure of the Flora of East Tropical Africa and other British floras of African areas. The list of these abbreviated references is given below. It is followed by a glossary of terms used in a way slightly different than usual. This glossary differs in a few minor points (e. g. dorsal/ventral is changed to upper/lower) from that given in my previous preliminary treatment of 1981.

In the key some genera of other tribes likely to be confused with genera of *Millettieae* have been added. If a specific epithet is added, the genus is either monotypic or the species mentioned is deviating from the rest of the genus in a previously passed key character. Binomials between brackets indicate species without a legitimate combination in the accepted genus.

GLOSSARY

Axillary. If mentioned in combination with a flower or an inflorescence, it means originating from the axil of a leaf, not of a bract.

Brachyblast. A shortened branch with flowers, in the axil of a bract, unless indicated otherwise. The shortened branch can also be reduced to a wart or may consist of a peduncle with 2 (—5) flowers on its apex, or it can be a node with a few flowers. In the latter case 2 or 3 flowers originate from the axils of 3 or 4 closely placed bracts respectively, one of which represents the bract subtending the reduced brachyblast.

Bract. A subulate to triangular scale below or within an inflorescence. The bract can be herbaceous to dry and hard, and is not differentiated into a petiole and a blade.

Bracteoles. Two small bract-shaped scales usually on the pedicel, sometimes on the calyx-cup. Their axillary buds, if present, never develop (but see note under Lonchocarpus).

Caulinascent. (Inflorescences) Emerging from the main stem (trunk).

Lower (or carinal). The side of a papilionoid flower corresponding with the keel and within the ovary and pod with the side opposite to the placenta. In non-resupinate flowers it is the abaxial side. In some literature this side is called "ventral". This term is considered ambiguous and confusing, as "ventral" refers to the adaxial side.

Panicle. Within the panicle the flowers are never on brachyblasts. The flowers are arranged in racemes and the racemes into panicles.

Pseudopanicle. A panicle composed of pseudoracemes.

Pseudoraceme. Flowers inserted on brachyblasts, and the brachyblasts arranged into a raceme.

Raceme. Within a raceme the flowers are never inserted on brachyblasts; the flowers are solitary in the axil of a bract.

Raminascent. (Inflorescences) Emerging from the branches.

Upper (or vexillary). The side of a papilionoid flower corresponding with the standard and within the ovary and pod with the placenta. In non-resupinate flowers this is the adaxial side. In some literature this side is called "dorsal". This term is considered ambiguous and confusing, as "dorsal" refers to the abaxial side.

ABBREVIATIONS OF THE REFERENCES

A.L.S. — R. M. Polhill & P. H. Raven (ed.). 1981. Advances in Legume Systematics. Part 1 & 2.

Benth., Syn. D. — G. Bentham, 1860. Synopsis of Dalbergieae, a tribe of Leguminosae. J. Proc. Linn. Soc., Suppl. to Vol. 4: 1—134.

B.H. 1 — G. Bentham & J. D. Hooker. 1862—1867. Genera Plantarum 1. (Leguminosae: 1865).

E. P. 3 — P. Taubert. 1891—1894. Leguminosae. In: A. Engler & K. Prantl, Die Natürlichen Pflanzen-familien 3,3: 70—388.

E.P. Nachtr. 1 — H. Harms. 1897. Nachträge 1 zum 2—4 Teil. Die Natürlichen Pflanzenfamilien.

E.P. Nachtr. 2 — H. Harms. 1900. Nachträge 2, id.

E.P. Nachtr. 3 — H. Harms. 1908. Nachträge 3, id.

E.P. Nachtr. 4 — H. Harms. 1915. Nachträge 4, id.

F. Austr. 2 — G.Bentham. 1864. Leguminosae, Flora Australiensis 2.

F. Bras. 15,1 — G.Bentham. 1859 (Galegeae), 1862 (Dalbergieae). In: C.F.P. von Martius, Flora Brasiliensis 15,1.

F.B.I. 2 — J. G. Baker. 1876, 1878. Leguminosae. In: J. D. Hooker, Flora of British India 2.

F. Cong. 5 — L. Hauman & A. Cronquist. 1954. Galegeae. In: Flore du Congo Belge et du Ruanda-Urundi 5.

F. Cong. 6 — L. Hauman. 1954. Dalbergieae. Id. 6.

F.G.I.-C. 2 — F. Gagnepain. 1913—1920. Leguminosae-Papilionoideae. In: H. Lecomte, Flore Génerale de l'Indo-Chine 2.

F. Jav. 1 — C. A. Backer & R. C. Bakhuizen van den Brink. 1964 ("1963"). Flora of Java 1.

F.M.P. 1 — H. N. Ridley. 1922. The Flora of the Malay Peninsula 1.

F. Pan. — J. D. Dwyer, c. s. 1965, 1980. Flora of Panama 5, fam. 83. Leguminosae. Ann. Miss. Bot. G. 52,1 & 67,3.

F. Peru — J. F. Macbride. 1943. Flora of Peru. Publ. Field Mus. Nat. Hist., Bot. 13,3.

F. Sur. — G. J. H. Amshoff. 1939. Flora of Suriname 2,2: 1—257.

F.T.E.A. — R. M. Polhill. 1971. Dalbergieae. In: Flora of Tropical East Africa. Leguminosae 3, Papilionoideae 1. — J. B. Gillett. 1971. Tephrosieae. Id.

F.W.T.A. — J. Hutchinson & J. M. Dalziel. 1958. Flora of West Tropical Africa (2nd ed.) Vol. 1, pt. 2.

Hutch., Gen. 1 — J. Hutchinson. 1964.The Genera of Flowering Plants 1.

L.T.A. — J. G. Baker. 1926—1929. The Leguminosae of Tropical Africa 1—3.

L. Nod. — O. N. Allen & E. K. Allen. 1981. The Leguminosae. A Source Book of Characteristics, Uses and Nodulation.

N. Am. F. — P. A. Rydberg. 1923, 1924. Galegeae. In: North American Flora 24, 3 & 4.

T.S. Mex. — P. C. Standley. 1922. Trees and Shrubs of Mexico. Contr. U. S. Nat. Herb. 23: 465—484, 506—515.

MILLETTIEAE

Millettieae Miq., Fl. Ind. Bat. 1 (1855) 137; Hutch., Gen. 1: 380 (*p. p. maj.*). — Type: *Millettia* W. & A.
Tephrosieae (Benth.) Hutch., Gen. 1: 394 (*p.p.*); A.L.S.: 245. — *Galegeae* subtribe *Tephrosiinae* (*"Tephrosieae"*) Benth., Gen. Pl. 1: 444; E. P. 3: 267. — Type: *Tephrosia* Pers.
Lonchocarpeae (Benth.) Hutch., Gen. 1: 380 (*p. p. maj.*). — *Dalbergieae* subtribe *Lonchocarpinae* (*"Lonchocarpeae"*) Benth., Gen. Pl. 1: 454; E. P. 3: 341. — Type: *Lonchocarpus* Kunth.

Trees, lianas or shrubs. Leaves pulvinate, generally imparipinnately compound, in a few genera 1-foliolate or pinnately 3-foliolate, or digitately 3—7-foliolate. Stipellae present or absent. Leaflets (1—) 5—17 (—> 40), usually (sub)opposite, alternate in *Craibia* and in *Schefflerodendron*; undersurface with simple hairs or glabrous, with hyaline pearl-glands in *Schefflerodendron*; some species (in *Ostryocarpus* and in *Lonchocarpus*) with pellucid dots. Inflorescences various, panicles (rarely racemes), pseudoracemes or pseudopanicles (i.e. within the raceme-like or panicle-like inflorescences the flowers fascicled on 2—10-flowered brachyblasts), sometimes on leafless branches or (combined with) rami- or caulinascent inflorescences (in *Callerya* and in *Fordia*). Bracteoles generally present, absent in *Afgekia, Chadsia, Endosamara,* and *Tephrosia,* in some species (of *Callerya*) inserted halfway the calyx-cup. Calyx various, with 4 or 5 more or less distinct lobes. Corolla papilionoid. Standard with or without basal callosities. Wings generally adherent to the keel (free in some spp. of *Lonchocarpus* and in *Wisteria*). Keel petals valvately connate. Filaments connate, the upper one free or not, usually with two basal fenestrae along the lower margins. Anthers versatile, in *Afgekia* with a tuft of hairs at either end. Disk indistinct or distinct, then ± tubular and surrounding the stipe of the ovary (different in *Deguelia*). Ovary with 1—17 ovules. Style usually terete and more glabrous towards the stigma, in some spp. of *Tephrosia* the style flattened and variously bearded. Stigma capitate. Pod various, dehiscent or indehiscent, winged or not; valves woody, or coriaceous or membranous, in the latter case the seeds sometimes (in *Brachypterum*) covered by an indurated part of the endocarp, forming a seed-chamber. Seeds flat or round in cross-section, with a small or large rim-aril or hilar tongue; seed-coat hard or coriaceous; embryo with a folded or straight (in *Ostryocarpus p. p.* and *Cyclolobium*) radicle. Seedlings of the "Heliciopsis-type" or the "Sloanea-type", the first leaves 1-foliolate or compound, alternate or (sub)opposite. 2n = 16, 20, 22 or 24. Notable diversity of flavonoid compounds and free animo-acids and amines.

Distribution. 43 genera. Tropical; few genera extending to subtropical areas, one (*Wisteria*) temperate.
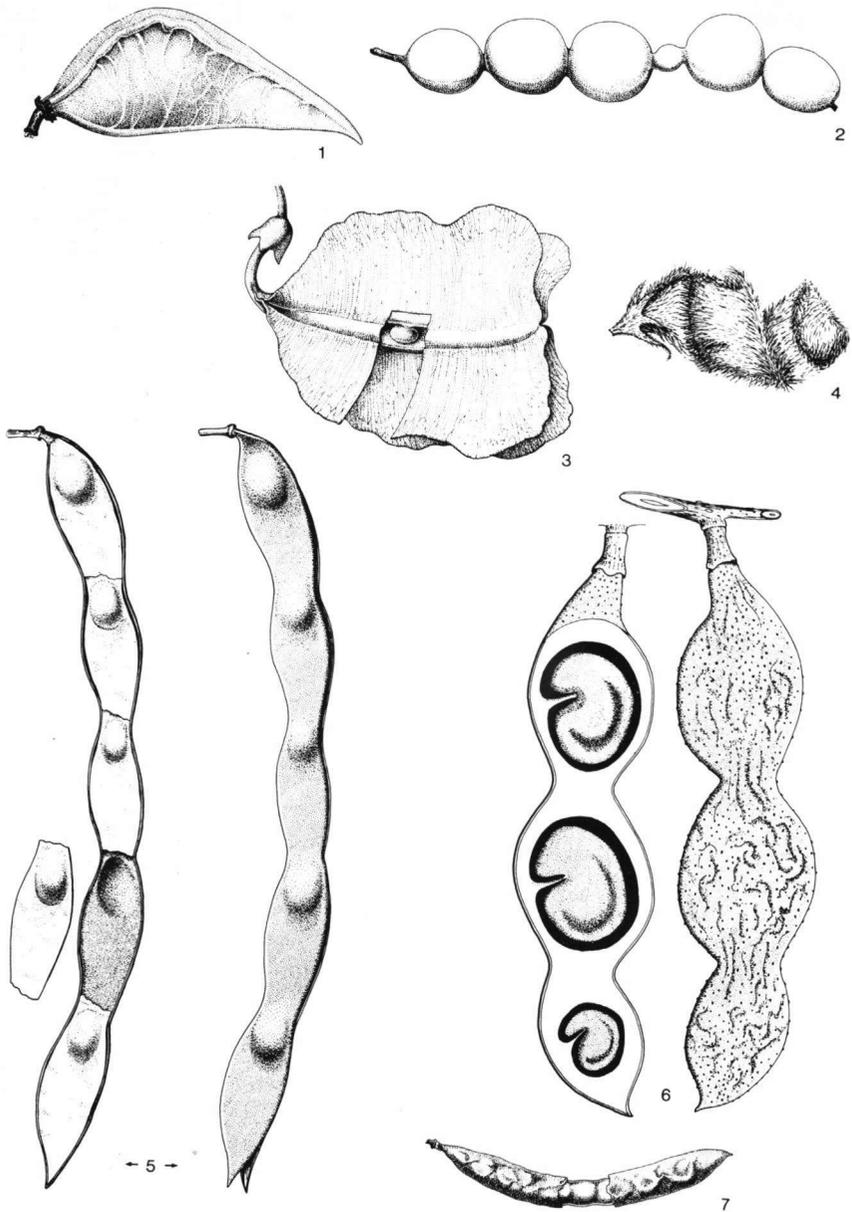
Plate I, 1—7. *Millettieae*. The erratic pods. — 1.*Pongamiopsis amygdalina* (Baill.) R. Vig., × 1 (SF Madagascar 12733); 2. *Lonchocarpus* (*Muellera moniliformis* L.ƒ.), × ½ (Grewal & Persaud 38); 3. *Piscidia piscipula* (L.) Sargent, × 1 (Ørstedt s.n.); 4. *Ptycholobium contortum* (N. E. Br.) Brummitt, × 2 (Acocks 16796, after drawing by H. Wood, Kew Bull. 35, p. 463); 5. *Endosamara racemosa* (Roxb.) Geesink, × ½ (Maxwell 74—735); 6. *Millettia pachycarpa* Drake, × ½ (Garrett 714); 7. *Sarcodum scandens* Lour., × ½ (Poilane 1457).

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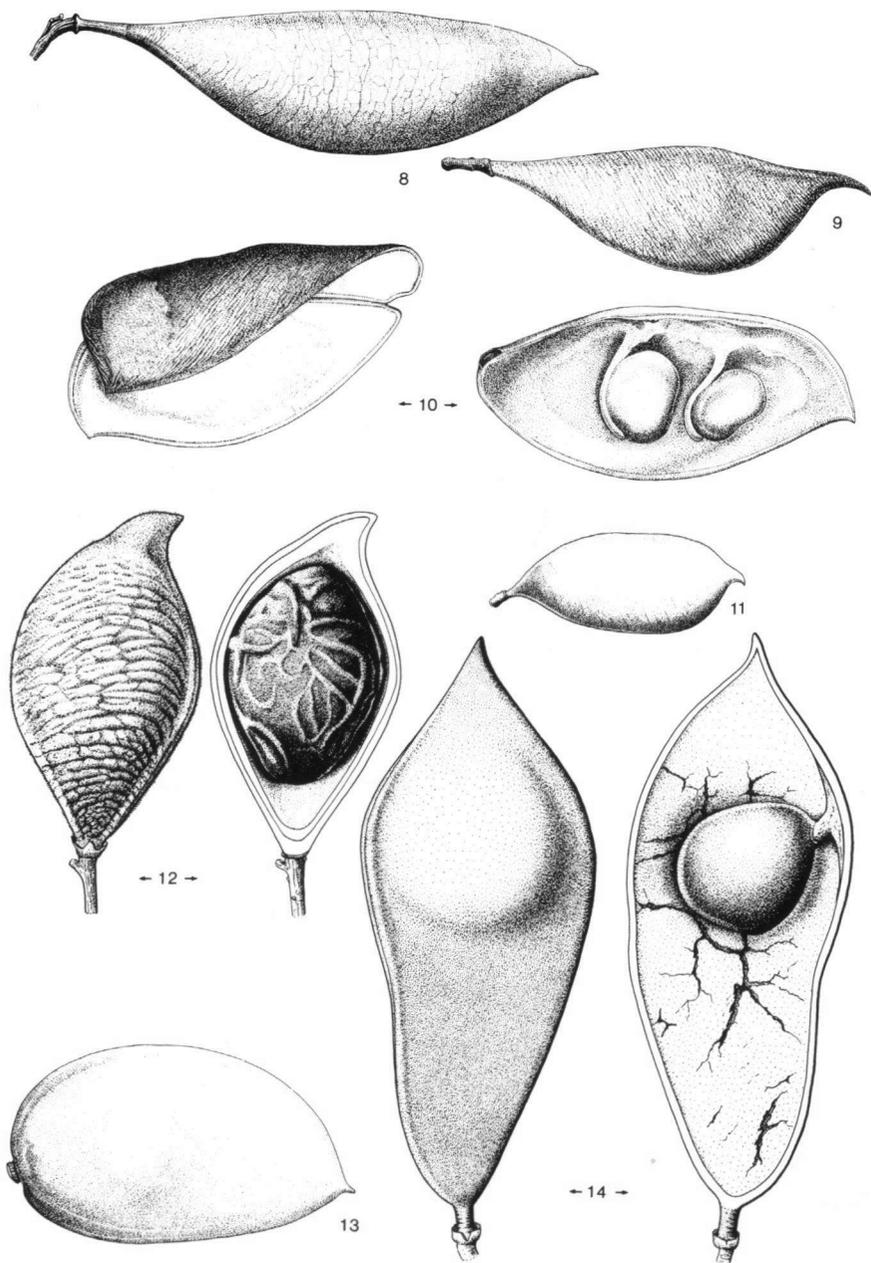
Plate II, 8—14. *Millettieae*. The biconvex thick-walled pods. — 8. *Schefflerodendron adenopetalum* (Taub.) Harms, × ½ (De Wilde & De Wilde-Duyfjes 2738); 9. *Craibia grandiflora* (Mich.) Bak. ƒ., × ¾ (Bjørnstad AB 2427); 10. *Afgekia sericea* Craib, × ¾ (Kerr 8057); 11. *Antheroporum pierrei* Gagnep., × ½ (Van Beusekom c. s. 2704); 12. *Callerya* (*Whitfordiodendron erianthum* (Benth.) Merr.), × ½ (S. 32165); 13. *Paraderris* (*Derris malaccensis* Prain), × 1 (S. 14074); 14. *Callerya* (*Whitfordiodendron atropurpureum* (Wall.) Merr.), × ½ (SF 40782).
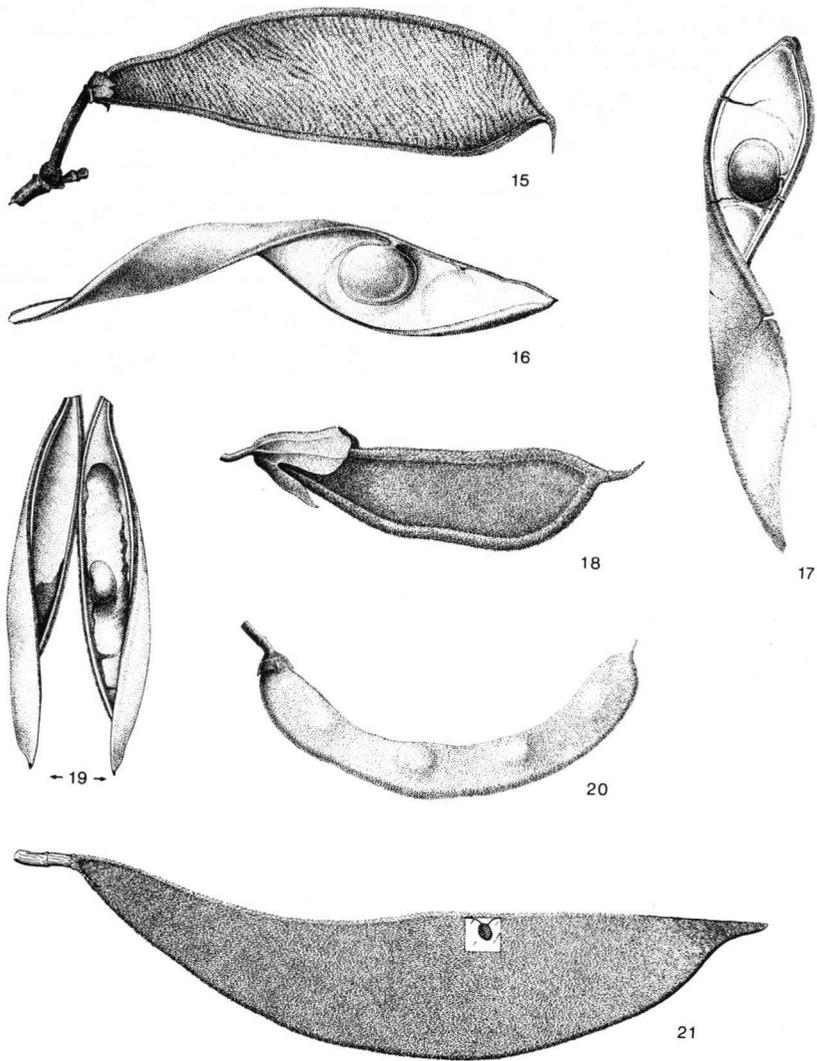
Plate III, 15—21. *Milletieat*. The flat thick-walled pods. — 15. *Neodunnia hysterantha* Peltier, ined., × 1 (Keraudren-Aymonin c. s. 25640); 16. *Wisteria chinensis* DC., × ½ (Von Siebold s. n.); 17. *Platysepalum chevalieri* Harms, × ¾ (C. Donis 2023); 18. *Platysepalum pulchrum* Louis ex Harms (young pod), × ¾ (J. Louis 16508); 19. *Disynstemon paullinioides* (Bak.) Peltier, × 1 (Keraudren 381); 20. *Bergeronia sericea* M. Mich., × 1 (Balansa 1380); 21. *Imbralyx album* (Ridl.) Geesink, × ½ (Soepadmo & Mahmud 9053).
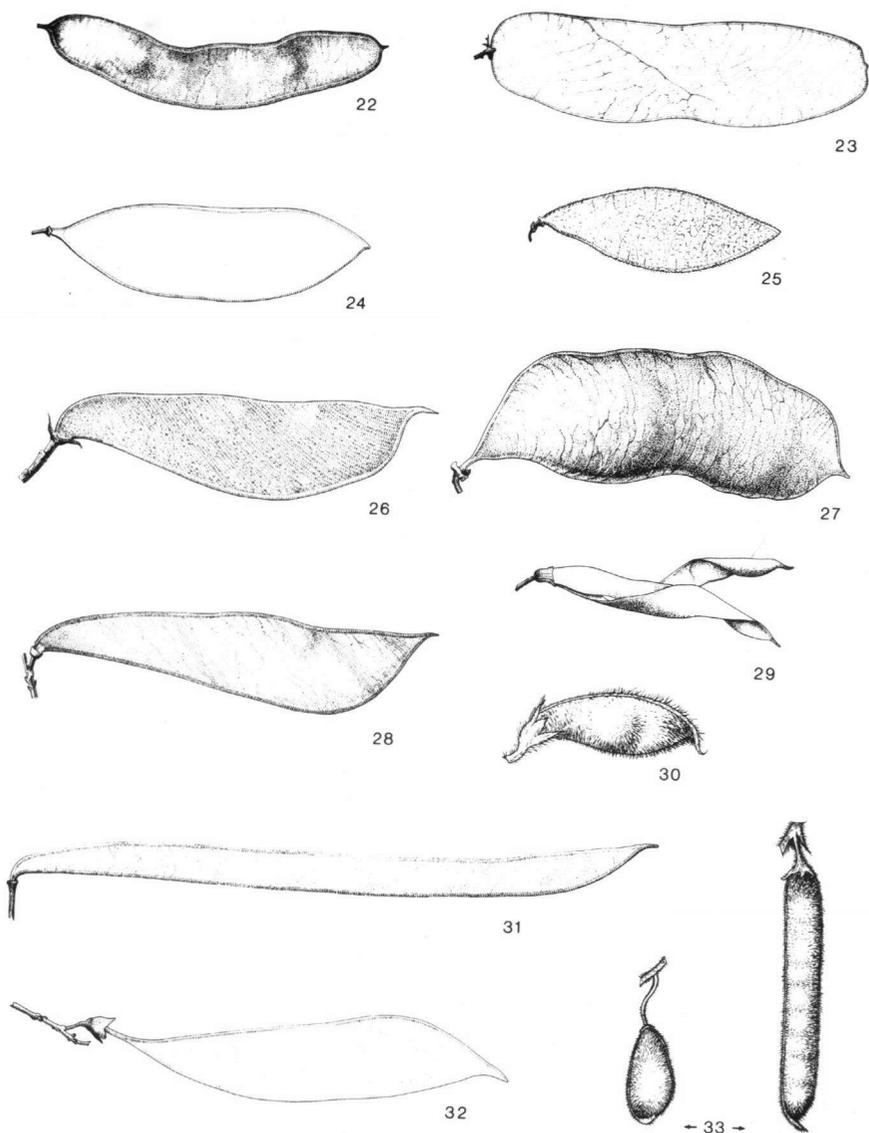
Plate IV, 22—33. *Millettieae*. The unwinged thin-walled pods. — 22. *Austrosteenisia blackii* (F. Muell.) Geesink, × 1 (L. S. Smith 9828); 23. *Kunstleria calamitata* Kornet, ined., × 1 (SAN 39751); 24. *Lonchocarpus latifolius* Kunth, × ½ (Hb. d'Alleizette 1843); 25. *Behaimia cubensis* Griseb., × 1 (C. Wright 2355); 26. *Burkilliodendron album* (Ridl.) Sastry, × 1 (Burkill & Haniff 12493); 27. *Dahlstedtia pentaphylla* (Taub.) Burkart, × ½ (Klein 1391); 28. *Fordia* cf. *coriacea* Dunn, × ½ (S 24583); 29. *Mundulea pungens* R. Vig., × 1 (Hb. d'Alleizette s. n.); 30. *Requienia sphaerocarpa* DC., × 2 (Dinter 315, after drawing by H. Wood, Kew Bull. 35, p. 471); 31. *Chadsia antungyensis* Leandri, × ½ (Leandri 958); 32. *Philenoptera* (*Lonchocarpus laxiflorus* Guill. & Perry), × ¾ (Schimper 1778); 33. *Lupinophyllum lupinifolium* (DC.) Hutch., × 2 (Buchanan s. n., after drawing by H. Wood, Kew Bull. 35, p. 463).
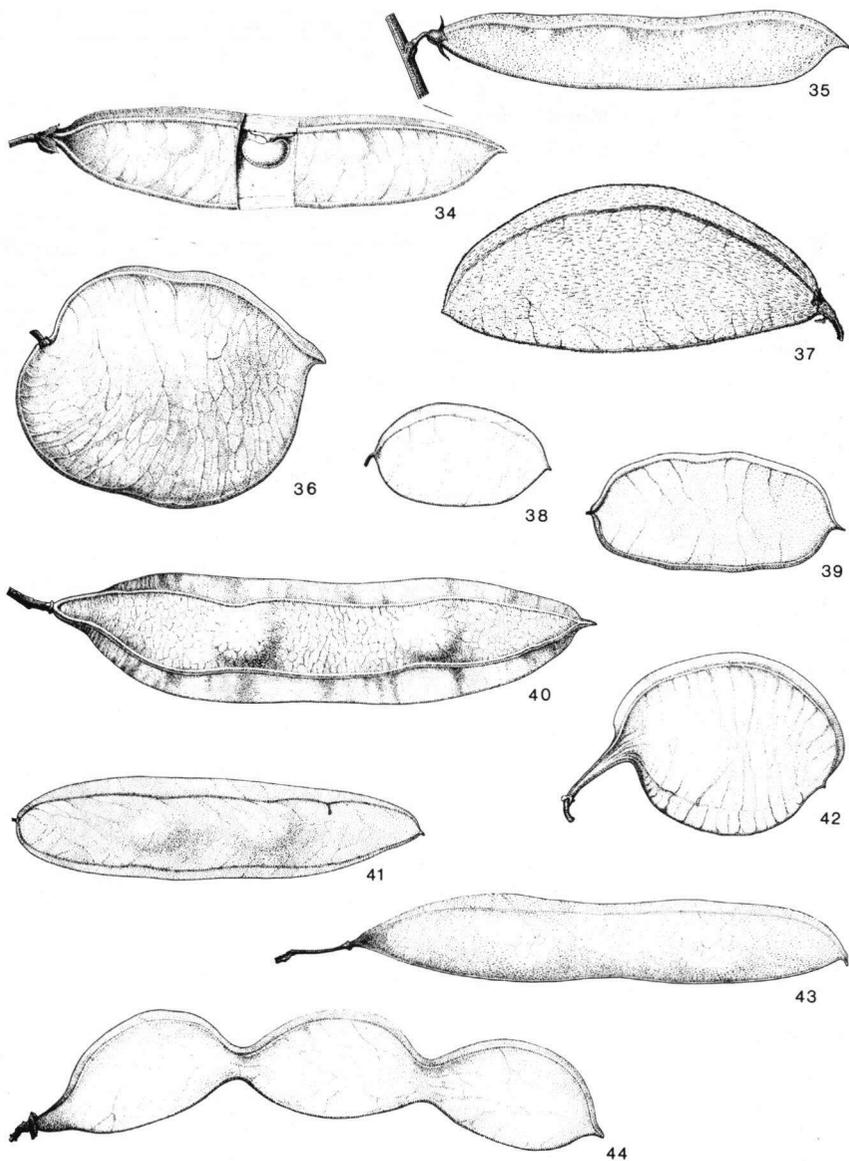
Plate V, 34—44. *Millettieae*. The winged thin-walled pods. — 34. *Platycyamus regnellii* Benth., × ½ (Regnell 8-bis); 35. *Craspedolobium schochii* Harms, × 1 (Henry 9241 A); 36. *Derris trifoliata* Lour., × 1 (Carp. coll. 96, Leiden); 37. *Leptoderris* cf. *ledermannii* Harms, × 1 (Leeuwenberg 2115); 38. *Deguelia* (*Derris negrensis* Benth.), × ½ (Ule s. n.); 39. *Paraderris* (*Derris elliptica* (Roxb.) Benth.), × ½ (Van Heurn s. n.); 40. *Ostryocarpus* (*Xeroderris stuhlmannii* (Taub.) Mendonça & Sousa), × ½ (Morogoro forest officer s. n., Kew); 41. *Ostryocarpus* (*Aganope thyrsiflora* (Benth.) Polhill), × ½ (Maxwell 81—233); 42. *Cyclolobium blanchetianum* Tul., × 1 (Balansa 4425); 43. *Brachypterum scandens* (Roxb.) Miq., × 1 (Put 2333); 44. *Ostryocarpus* (*Aganope heptaphylla* (L.) Polhill), × ½ (SF 33277).

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KEY TO THE GENERA

1. All leaves simple or unifoliolate 2
— Leaves compound, at least those below the inflorescences 9
2. Shrubs, trees, or lianas; branches of herbarium specimens distinctly woody ... 3
— (Small) shrubs with herbaceous branches 13
3. Lianas. — Panicles terminal. Calyx distinctly lobed. Upper filament free. Pod thin leathery, flat, not falcate. *Malay Peninsula* .... **Kunstleria curtisii** Prain
— Trees of shrubs. — Panicles terminal or axillary, or (pseudo)racemes axillary . 4
4. Upper filament free. — Pod stipitate, orbicular, membranous, upper or both sutures narrowly winged. *South America* .... **Cyclolobium**
— Upper filament distinctly adnate to the other 9 5
5. Shrubs. Calyx with 5 subulate teeth. — Racemes slender, 2—5 together in a leaf axil. Pod falcate, 2-seeded. *Malay Peninsula* ....
.... **Burkilliodendron album** (Ridl.) Sastry
— Trees. Calyx with broader lobes 6
6. Calyx lobes distinctly imbricate. Pod densely dark brown hairy. *Malay Peninsula* .
.... **Millettia unifoliolata** Prain
— Calyx lobes usually apert or valvate, rarely slightly overlapping. Pod (sub)glabrous 7
7. Within the axillary pseudoracemes the flowers 2 together on top of a slender common peduncle. *Mexico* .... **Lonchocarpus unifoliatus** Benth.
— True panicles or true racemes 8
8. Axillary panicles or racemes. Hypanthium distinct. Pod thickly woody (c. 10 mm), reticulately nerved with several seeds, each in a compartment. *S. America* ....
.... *Poecilanthe (Robinieae)*
— Terminal panicles. Hypanthium indistinct. Pod thinner woody (2—3 mm), with 1(—3) seeds, not in compartments. *West Africa* .... **Craibia simplex** Dunn
9. Vegetative leaves (far) below the inflorescences with 3 leaflets 10
— Vegetative leaves with 5 or more leaflets (though sometimes mixed with 3-foliolate leaves) 22
10. Upper filament adnate to the other 9, the tube with basal fenestrae or not 11
— Upper filament distinctly free, the tube without distinct basal fenestrae 18
11. Flowers in distincly demarcated terminal or axillary (pseudo)racemes. Trees or lianas. Leaflets with looping nerves 12
— Flowers either in axillary clusters, or in terminal or leaf-opposed pseudoracemes, or aggregated with progressively reduced subtending leaves. Herbs with woody stem or small shrubs. Leaflets usually with either indistinct or conspicuously closely parallel nerves extending to the margins 13
12. Leaflets digitately 3-foliolate. Flowers in terminal short racemes. Stamens dimorphic, the upper 5 filaments with a narrowly triangular free part, and about half as long as the linear free parts of the lower 5 filaments. *Madagascar* ....
.... **Disynstemon paullinioides** (Bak.) Peltier
— Leaves pinnately 3-foliolate. Flowers in seemingly true racemes. Stamens not dimorphic. *Burma* .... **Millettia trifoliata** Dunn

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13. Ovule 1. Pod 1-seeded 14
— Ovules several. Pod with 2 or more seeds 15
14. Leaves pinnately 3-foliolate. Flowers in axillary fascicles, tending to aggregate terminally. *W. Australia* .... (*Paratephrosia lanata* Domin) **Tephrosia**
— Leaves all 1-foliolate. Flowers in axillary fascicles. *West Tropical and South Africa* .... **Requienia**
15. Pods zig-zag folded or curved upwards, thin-walled, indehiscent. — Leaves digitately 3-foliolate or 1-foliolate. *Tropical and South Africa, Arabia (Oman)* ... . **Ptycholobium**
— Pod straight 16
16. Leaflets pinnately arranged or all leaves unifoliolate. *Pantropical* ..... **Tephrosia**
— Most leaflets digitately arranged, mixed with some unifoliolate leaves. *Tropical and S. Africa* 17
17. Leaves with a distinct pedicel. Pods from prostrate infructescences geocarpic, all pods (sub)sessile .... **Lupinophyllum**
— Leaflets sessile, without a distinct common rachis. Pods never geocarpic, distinctly stipitate .... **Caulocarpus**
18. Plants erect. Calyx (always?) glabrous inside. *Tropical America* 19
— Lianas. Calyx distinctly hairy inside. *S. E. Asia* 20
19. Shrubs. Lateral nerves indistinct. Flowers solitary or 2 together in the axils of unifoliolate or simple leaves. Pod coriaceous, not winged. *Mexico* .... *Genistidium dumosum* I. M. Johnst. (*Robinieae*)
— Trees. Lateral nerves distinct. Flowers in terminal panicles. Pod thin-woody or leathery; upper suture winged. *Brazil* .... **Platycyamus regnellii** Benth.
20. Pseudoracemes. Ovules 5—8. Pod dehiscent, with the upper suture winged. *China* .... **Craspedolobium schochii** Harms
— Panicles or pseudopanicles. Ovules 2(—4). Pod indehiscent, either samaroid or flat, strap-shaped and not winged. *India to West Malesia* 21
21. Stipellae absent. Ovules ± halfway the ovary. Calyx lobes about straight. Pod strap-shaped, not samaroid .... **Kunstleria**
— Stipellae present or absent. Ovules halfway to subapical in the ovary. Calyx lobes usually squarrose. Pod samaroid with 1 apical seed .... *Spatholobus* (*Phaseoleae*)
22. Leaves (sub)opposite. — Trees. Panicles. Pod thin-woody, dehiscent, usually 2-seeded. *Cuba* .... *Hebestigma cubense* Urb. (*Robinieae*)
— Leaves alternate 23
23. Leaflets digitately arranged 15
— Leaflets pinnately arranged 24
24. Lateral leaflets distinctly alternate 25
— Lateral leaflets (sub)opposite 27
25. Undersurface of leaflets with coloured, hyaline pearl-glands. — Racemes often 2—4 together, axillary. Pod thick-woody. *Tropical Africa* .... **Schefflerodendron**
— Undersurface of leaflets without such glands 26
26. Panicles terminal, sometimes combined with axillary pseudoracemes. Leaflets up to 11 per leaf. Pod flat. *Tropical Africa* .... **Craibia**

69

— Racemes or pseudoracemes from the axils of dropped leaves. Leaflets 11—13 per leaf. Pod inflated. *Tropical America* .... *Diphysa (Robinieae)*

27. Lateral nerves 4—31 pairs, straight and usually very close to each other. Bracteoles generally absent. Flowers fascicled 28

— Lateral nerves either less than 15 pairs, or, if more than 15 pairs, the leaflets "large" and the lateral nerves always curved and distant. Bracteoles present, if absent then flowers not in fascicles 30

28. Filaments dilated at apex. Style $^1/_4$—$^1/_5$ the length of the ovary. *Mainly Madagascar* .... **Mundulea**

— Filaments terete, narrower towards the apex. Style longer, about $^1/_2$ as long as to about as long as the ovary 29

29. Flowers 3—6 cm long, with bird-pollination syndrome. Flowers in fascicles on leafless nodes. *Madagascar* .... **Chadsia**

— Flowers 8—26 mm long, with bee-pollination syndrome. Pseudoracemes terminal or leaf-opposed, in a few species the flowers in fascicles on leafless nodes. *Pantropical, also in Madagascar* .... **Tephrosia**

30. Flowers in an elongated raceme, with the flowers neither paired nor clustered . 31

— Flowers in panicles, in pseudoracemes, in pseudopanicles, in axillary fascicles, or in short axillary racemes 35

31. Racemes axillary 32

— Racemes terminal. — Lianas. Bracteoles generally absent 34

32. Stipellae present. Style glabrous 33

— Stipellae generally absent. Style often bearded along upper edge . tribe *Robinieae*

33. Bracts shorter than the corresponding flowerbuds. Disk absent. Pod dry, dehiscent, without walls between the seeds. *Tropical S. America* .... **Apurimacia**

— Bracts longer than the corresponding flowerbuds. Disk distinct. Pod with a fleshy exocarp and a dry endocarp with walls between the seeds. *S. E. Asia* .. **Sarcodum**

34. Upper filament free. Bracts larger than the corresponding flowerbuds. Petals yellow with red. Racemes erect. Pod inflated. Seeds with a long, strap-shaped hilum and a correspondingly long and fleshy funicle. *Burma, Thailand, S. China.* .... **Afgekia**

— Upper filament adnate to the other 9. Bracts smaller than the corresponding flowerbuds. Petals blue or white. Racemes pendulous. Pod flattened. Seeds with an elliptic hilum and a short funicle. *China, Japan, N. America* .... **Wisteria**

35. Flowers in axillary fascicles or in short axillary racemes 36

— Flowers in panicles or in pseudoracemes or in pseudopanicles 37

36. Calyx with subequal short lobes. Upper filament adnate to the other 9, with 2 basal fenestrae. Pod woody, falcate; exocarp not separating from the endocarp. *Madagascar* .... **Neodunnia**

— Calyx with the lower lobe longer and more acute than the other lobes. Upper filament free. Pod with exocarp separating from the endocarp; exocarp inflated into a reticulate bladder. *Tropical America* .... *Diphysa (Robinieae)*

70

37. Flowers usually*) in wide panicles (with the flowers singly in the axil of a bract), sometimes in terminal racemes, but then combined with axillary racemes ("leafy panicle") 38
— Flowers in pseudoracemes or in pseudopanicles**) 63
38. Upper filament adnate to the other 9 39
— Upper filament free from the other 9, or adnate at base only 49
39. Standard with 2 distinct basal callosities. — Flowers 12—17 mm long. Pod flat, woody, tardily dehiscent. *Malay Peninsula, China, Indo-China* .... **Imbralyx**
— Standard without basal callosities, though sometimes with the basal margin thickened 40
40. Wing petals free from the keel. Keel petals free from each other and their lower margins overlapping in bud. — Hypanthium usually distinct 41
— Wing petals adnate to the keel. Keel petals valvately connate. — Hypanthium usually indistinct 43
41. Ovule 1, basal. Stigma minute, not penicillate. Hypanthium about ⅓—½ as long as the calyx tube. Pod with a basal seed-chamber and a distal wing, or turgid and spongy-fibrous. — Leaflets alternate or (sub)opposite. *Brazil and Guianas* .....
.... *Vatairea* (incl. *Vataireopsis*)(*Dalbergieae*)
— Ovule(s) ± halfway the ovary. Stigma more or less distinctly penicillate. Hypanthium shorter. Pod flat and winged along the suture(s) or drupe-like. — Leaflets (sub)opposite 42
42. Panicles terminal. Pod drupe-like. Ovary elliptic, thick-walled, without prominent submarginal nerves. *Tropical America, one species also in Africa* ....
.... *Andira* (*Dalbergieae*)
— Panicles mainly axillary. Pod strap-shaped, flat, with 2 subparallel nerves with the centrally placed seed-chamber in between. *Tropical America* ....
.... *Hymenolobium* (*Dalbergieae*)
43. Panicles axillary or on leafless branches (originating from axils of fallen leaves) 44
— Panicles mainly terminal, but often combined with axillary ones 45
44. Wing-blades falcate. Upper filament with 2 fenestrae next to its base. Pod stipitate, woody, indehiscent, with 4 broad wings. *Tropical America* .... **Piscidia**
— Wing-blades suborbicular. Upper filament without fenestrae. Pod woody, dehiscent, without wings. Seed in compartments. *Tropical America* ....
.... *Poecilanthe* (*Robinieae*)
45. Shrubs. Calyx tubular. Flowers 20—30 mm long, with bird-pollination syndrome, i. e. flowers elongate with red petals. *Brazil*. **Dahlstedtia pinnata** (Benth.) Malme
— Trees or lianas, or shrubs. Calyx cupular. Flowers 6—25 mm long, with bee-pollination syndrome, i. e. not elongated and petals not predominantly red ... 46
46. Trees or shrubs. Leaves translucent-punctate or not. *America* (4 spp. only; see note under *Philenoptera*) .... **Lonchocarpus** (*p. p.*)

*) *Aganope thyrsiflora* (Benth.) Polhill (sub **Ostryocarpus**) and **Kunstleria** have the lateral branches of the panicle often rather short and few-flowered, but always with more than 10 scars of bracts or flowers.

) Some species in **Derris and **Piscidia** have intermediate stages between short lateral branches of the panicle and more distinct brachyblasts, with up to 10 spirally arranged flowers.

— Trees, or shrubs, or lianas. Leaves not translucent-punctate. *Old World* 47
47. Flowers 8—15 mm long. Calyx with distinct lobes. *Africa, Australia, New Guinea*
. . . . 48
— Flowers 6—8 mm long. Calyx with short teeth. *China, Indo-China, and Thailand* . . . . **Antheroporum**
48. Trees, rarely shrubs or lianas. Staminal tube curved upwards. Ovules 4—8. *Africa* . . . . **Philenoptera**
— Lianas. Staminal tube straight. Ovules 14—17. *Australia and New Guinea* . . . . **Austrosteenisia**
49. Standard with 2 distinct basal callosities, or with a distinct transverse ridge at the distal part of its claw. 50
— Standard without basal callosities, or only the margin thickened at base 54
50. Stipellae present. *S. E. Asia* 51
— Stipellae absent. *Africa or America* 52
51. Bracts longer and broader than corresponding flowerbuds. Panicles axillary, usually with leaves on the lower nodes, always with leaf-scars. Pod inflated. Seed with a long, strap-shaped hilum and a correspondingly long and fleshy funicle. *Burma, Thailand, S. China* . . . . **Afgekia**
— Bracts usually longer than the corresponding flowerbuds, rarely also broader. Panicles usually discrete, terminal or axillary. Pods not inflated, though often swollen around the thick seeds. Hilum and funicle ellipsoid, not elongated. *S. E. Asia* . . . . (*Padbruggea*) **Callerya**
52. Axillary panicles below the apex of branches which continues vegetatively after a flowering period. — Pod thin with a wing on both sutures. *Tropical Africa.* . . . . .
. . . . [*Xeroderris stuhlmannii* (Taub.) Mendonça] **Ostryocarpus**
— Panicles axillary, or terminal, sometimes combined with axillary racemes in the upper leaves or on leafless branches 53
53. Stipules herbaceous. Calyx with 2 subequal lips. Standard with a transverse ridge in the distal part of its claw. Pod thick woody. *W. Africa* . . . .
. . . . **Dewevrea bilabiata** M. Micheli
— Stipules spinose. Calyx with 4 rounded lobes, the upper one 2-lobed. Distal ridge of standard claw absent. Pod coriaceous, moniliform of 1-seeded. *Mexico and southern U.S.A.* . . . . *Olneya tesota* A. Gray (*Robinieae*)
54. Bracts longer than the corresponding (young) flowerbuds. — Lianas. Stipellae present 55
— Bracts shorter than the corresponding flowerbuds 57
55. Leaflets more than 17 pairs. Pod with a fleshy exocarp and a thin, dry endocarp. — Bracteoles present. *Indo-China, Philippines, Moluccas, and Solomon Islands* . . . .
. . . . **Sarcodum**
— Leaflets less than 10 pairs. Pod dry, thin and dehiscent 56
56. Pod valves separating into an entire exocarp and a lomented endocarp; the "loments" samaroid. Bracteoles absent.*Burma, Thailand* . . . . **Endosamara**
— Pod valves not separating into exocarp and complicated endocarp. Bracteoles

present. *Japan* (see under **Callerya, Sarcodum,** and **Wisteria**) . . . .

. . . . **Millettia japonica** (Sieb. & Zucc.) A. Gray

57. Flowers small, 7 mm or less. — Calyx distincly toothed. Pod thin, leathery, strap-shaped (not falcate), 1—3-seeded. *W. Malesia* . . . . **Kunstleria**
— Flowers of moderate size, 10 mm or longer 58
58. Trees or erect shrubs 59
— Lianas 62
59. Lower calyx lobe more acute and longer than the other lobes. Panicle corymboid. Pod with a flat endocarp and an inflated reticulately nerved bladder-like exocarp. *Tropical America* . . . . *Diphysa* (*Robinieae*)
— Calyx truncate or with subequal lobes. Pod without such a peculiar exocarp . . . 60
60. Stipellae distinct. Pod thin-woody with a wing along the upper suture. *Peru*
. . . . **Platycyamus ulei** Harms
— Stipellae absent or minute. Pod without wings 61
61. Calyx lobes distinct, about as long as the cup. Stipellae minute. Pod membranous, flat, indehiscent, transversely reticulate. Seed 1. *Cuba* . . . .
. . . . **Behaimia cubensis** Griseb.
— · Calyx lobes indistinct or much shorter than the cup. Stipellae absent. Pod thick, woody, indehiscent. Seeds 1—4. *S. E. Asia* . . . .
. . . . (*Whitfordiodendron*) **Callerya**
62. Bracteoles either halfway on the calyx, or at its base. Pod thickly woody without wings; seeds ± round in cross-section. *S. E. Asia and Australia* . . . . **Callerya**
— Bracteoles always at the base of the calyx. Pod flat, woody or coriaceous, with (rarely without) wings; seeds laterally flattened. *Africa and S. E. Asia* . . . .
. . . . **Ostryocarpus**
63. Pseudoracemes terminal or arranged in a (terminal) pseudopanicle or 2 or 3 (rarely more) pseudoracemes together in a leaf-axil 64
— Pseudoracemes single, axillary, sometimes (on leafless branches) below the leaves 74
64. Upper filament free. — Pseudoracemes exclusively terminal 65
— Upper filament adnate to the other 9 67
65. Shrubs. Upper calyx lobes not enlarged. Standard without a basal ridge. *America* 66
— Trees, shrubs, or lianas. Upper calyx lobes enlarged, covering the standard completely. Standard with a ridge across the distal part of the claw. *Tropical Africa* . . . . **Platysepalum**
66. Stipellae absent. Root thick, tuberous. Stipules spinose. Style glabrous. *N. America* . . . . *Peteria* (*Robinieae*)
— Stipellae present. Root not swollen. Stipules herbaceous. Style bearded along upper edge. *Tropical America* . . . . *Barbieria* (*Phaseoleae*)
67. Standard with 2 distinct basal callosities 68
— Standard without basal callosities, though sometimes with the basal margin thickened 69

68. Filaments dilated to the apex. Style conspicuously short. — Shrubs (probably here only **M. sericea**) . . . . **Mundulea**
—   Filaments terete, narrower towards the apex. Style of usual length. — Trees, shrubs, or lianas . . . . **Millettia**
69. Flowers 2 (rarely combined with 1- or 3-flowered brachyblasts) on top of a common peduncle. — Pod generally indehiscent, flat, without wings. *America and W. Africa* . . . . **Lonchocarpus**
—   Flowers scattered (or condensed) along the brachyblasts 70
70. Brachyblasts thin, with (1 or) 2—8 scattered flowers. Disk and hypanthium indistinct. — Pod with a longitudinal wing along upper or both sutures . . . . . **Derris**
—   Brachyblasts callose, with the flowers condensed. Either disk conspicuous or hypanthium distinct 71
71. Standard rather narrow (l/w = 1.4—3). Hypanthium distinct. Upper filament adnate to the base of the standard. — Stipellae present. Pod with the upper suture usually winged. *Tropical Africa* . . . . **Leptoderris**
—   Standard broader (l/w = 0.8—1.2). Hypanthium not distinct. Upper filament usually free from the base of the standard 72
72. Pods numerous per infructescence, thin, with the upper suture broadly winged and the seed-compartments darker coloured than the rest of the pod. Either trees with 17—41 leaflets per leaf, or lianas with 7—17 leaflets per leaf. — Disk conspicuously 10-lobed. *S. E. Asia and N. Australia* . . . . **Brachypterum**
—   Pods usually few per infructescence; upper suture winged or not. Either trees with less than 17 leaflets per leaf, or lianas with usually 5—21 (—35) leaflets per leaf. — Disk distinct or not. *Asia or America* 73
73. Lianas. Disk conspicuous, also with a gland between upper filament and the base of the standard. Pod thin, indehiscent or rarely dehiscent, upper suture winged or not. *Northern part of South America* . . . . **Deguelia**
—   Trees, shrubs, or lianas. Disk distinct or not. Gland between upper filament and base of standard absent. Pod thick-woody, dehiscent; upper suture not winged. *Old World, or (Hesperothamnus) N. America* . . . . **Millettia**
74. Standard with 2 distinct basal callosities. — Upper filament connate with the other 9, at base with 2 fenestrellae. *Tropical Africa, S. E. Asia, Australia* . . . . `75
—   Standard without distinct basal appendages, sometimes the basal margin thickened. *Pantropical, i. e. also in America* 77
75. Flowers 2 or 3(—5) together on the top of a slender peduncle. Pod more or less woody with one or two wings (in *Derris malaccensis* also without wings). *S. E. Asia* . . . . **Paraderris**
—   Flowers 2—5 scattered on warty or cylindric brachyblasts, often mixed with single-flowered nodes in the same inflorescence. Pod without wings, only in *Millettia xylocarpa* (some varieties in Thailand and Indo-China) with 2 wing-like ridges along the upper or both sutures 76
76. Pod inflated, 1- (rarely 2-)seeded. Seeds elliptic in cross-section. — *Sandy coasts of S. E. Asia (in New Guinea and Queensland also inland)* . . . .
. . . . [*Pongamia pinnata* (L.) Pierre] **Millettia**

— Pod flat, (1—) 2—5-seeded. Seeds lens-shaped, ± flat in cross-section. *Tropical Africa, S. E. Asia* .... **Millettia**

77. Upper filament free (loosely adhering in *Margaritolobium* and *Millettia p.p.*) . 78
— Upper filament adnate to the other 9, usually with 2 fenestrae at base 82

78. Herbaceous twiners or subshrubs with herbaceous twigs. (*Phaseoleae*) 79
— Trees, lianas, or shrubs with woody twigs 80

79. Flowers 2—5 per brachyblast. Hairs on wings and keel absent. Stigma with a basal tuft of hairs. *Burma, Thailand*...................... *Cruddasia insignis* Prain
— Flowers 2 per brachyblast. Hairs on wings and keel usually present. Stigma without a basal tuft of hairs. *Thailand, Indo-China, Tropical Africa* .... *Ophrestia*

80. Upper calyx lobes acute. Pod indehiscent, submoniliform, falcate, thickly woody; valves confluent between the seeds. — Trees. *Tropical S. America* ....
.... **Bergeronia sericea** M. Micheli
— Upper 2 calyx lobes rounded or indistinct. Pod thin-woody 81

81. Trees or lianas. Leaflets more than 11 per leaf. Pod strap-shaped, not falcate, with numerous plumose appendages along the upper suture. *Tropical Africa* ....
.... *Dalbergiella* (*Dalbergieae*)
— Shrubs. Leaflets 5 per leaf. Young pods flat, without such plumose appendages; ripe pods unknown. *Venezuela* .... **Margaritolobium luteum** (Johnst.) Harms

82. Ovules 2. Pseudoracemes rami- or caulinascent, or axillary or supra-axillary to leaves (i. e. within a flowering specimen some pseudoracemes are inserted slightly above the leaf-axil). Pod falcate, (thinly) woody. *S. E. Asia*............. **Fordia**
— Ovules 2 or more, but not with the above mentioned characters combined 83

83. Brachyblasts 3- or more-flowered 84
— Brachyblasts 2-flowered, often mixed with single flowers in the same pseudo-raceme 86

84. Pod with a wing along the upper suture 70
— Pod without wings 85

85. Lianas. Stipellae absent. Pods usually indehiscent. *Tropical S. America* ....
.... (*Lonchocarpus* subg. *Phacelanthus*) **Deguelia**
— Shrubs. Stipellae present. Pods dehiscent. *Tropical Africa, Tropical Asia, or* (*Hesperothamnus*) *N. America* .... **Millettia**

86. Pod moniliform, i. e. seeds round in cross-section and the pod constricted between the seeds. *Tropical America* .... (*Muellera*) **Lonchocarpus**
— Pod flattened. Seeds lens-shaped 87

87. Pod with a wing along the upper suture. Lianas. *Tropical Asia, Northern Australia* .... **Derris**
— Pod without wings. Shrubs, lianas, or trees............................ 88

88. Shrubs. Stipellae present. Calyx lobes acute. — Pod dehiscent. *Tropical S. America*.. **Apurimacia**
— Trees or rarely lianas. Stipellae generally absent. Calyx lobes acute or, usually, indistinct 89

89. Deciduous treelets. Ovules 8—10. Seed generally 1. *Madagascar.* — Lowermost flowers in the inflorescence from bud-scales................... **Pongamiopsis**

— Evergreen or deciduous trees, rarely evergreen lianas. Ovules 2—12. Seeds 2 or more, rarely 1 90
90. Trees, rarely lianas. Flowers mostly 2 together on the top of a common peduncle. *Tropical America, L. sericeus also in W. Africa* .... **Lonchocarpus**
— Trees. Most flowers single, some 2 together on a small warty brachyblast. *India, Burma, Indo-China, and China* .... **Millettia** sect. **Podocarpae**

GENERA
(IN ALPHABETIC ORDER)

Afgekia

Afgekia Craib, Bull. Misc. Inf. Kew (1927) 195; Fl. Siam. Enum. 1 (1928) 395; Hutch., Gen. 1: 368; Burtt & Chermsirivathana, Not. Roy. Bot. Gard. Edinb. 51 (1971) 131—133; A.L.S.: 254; L. Nod.: 26. — Type: *A. sericea* Craib.

Lianas. Leaflets 9—19, (sub)opposite. Stipellae present. Flowers in terminal racemes or in pseudo-axillary panicles, but then with some (scars of) vegetative leaves at the base of the rachis of the panicle. Bracts longer than the corresponding flower-buds, in one species also broader. Bracteoles absent or minute. Flowers 20—25 mm long. Hypanthium indistinct. Calyx lobes 5, rather long and acute in *A. sericea* and *A. mahidolae,* the lateral 2 and the lower one triangular in *A.filipes,* the upper two shorter than the other three in the first two species, indistinct to obscurely rounded in *A. filipes.* Standard blade ovate to elliptic, reflexed at base; basal callosities distinct *with closely above them 2 curved laminal callosities (lacking in A. filipes).* Wings about as long as the keel, obtuse at apex. Keel broadly falcate. Upper filament adnate (in *A. filipes* slightly adherent) to the other 9. Basal fenestrae distinct. *Anthers with a basal tuft of hairs, the vexillary anther with basal and apical tufts of hairs (except A. filipes with glabrous anthers).* Disk annular to cylindric. Ovary hairy; ovules 2 or 3. Pod tardily dehiscent, inflated, woody; sutures without wings. Seeds 1 or 2, ellipsoid to somewhat lenticular; *funicle swollen, elongated; corresponding hilum* $^1/_8$—$^1/_2$ *the circumference of the seed, strap-shaped;* radicle folded.

Distribution. Three species in South China, Burma, and Thailand.

Taxonomy. The genus consists of two closely allied species, *A. sericea   A. mahidolae,* and a third, in many characters more primitive species, *A. filipes,* which is formally proposed below. The first two species occur in rather open, deciduous vegetation types, while the last species inhabits evergreen forests as a canopy liana. This species was originally described in *Adinobotrys,* which was considered a synonym of *Padbruggea* by Craib (1928). The general habit, the shape of the calyx, and the glabrous anthers are indeed similar to certain species of *Padbruggea,* which is here considered a synonym of *Callerya.* It differs in the absence of bracteoles and in the long pedicels. The

pods were unknown until 1975, but then it appeared that the seeds showed an elongated fleshy funicle with a corresponding elongated hilum, though less distinct than in both known species of *Afgekia*. The characters in which *A. filipes* differs from *Callerya* are all characteristic for *Afgekia*, so I propose to transfer *Adinobotrys filipes* to *Afgekia*:

Afgekia filipes (Dunn) Geesink, *comb. nov.*

Adinobotrys filipes Dunn, Bull. Misc. Inf. Kew (1911) 195—196. — *Padbruggea filipes* (Dunn) Craib, Fl. Siam. Enum. 1 (1928) 397. — Lectotype (proposed here): China, Yunnan. *Henry 11.610* (K).

Antheroporum   Pl. II—11

Antheroporum Gagnepain, in: Lecomte, Not. Syst. 3 (1915) 180; F.G.I.-C. 2: 467; Hutch., Gen. 1: 379; Wei, Act. Phytotax. Sin. 19 (1981) 351; A.L.S.: 254; L. Nod.: 51. — Lectotype (Hutch.): *A. pierrei* Gagnep.

Trees. Leaflets 5—9, (sub)opposite. Stipellae absent. Flowers in terminal panicles. Bracts longer than the corresponding flowerbuds, soon caducous. Bracteoles absent. Flowers 8—10 mm long. Hypanthium indistinct. Calyx with 5 short teeth. Standard blade elongated obovate, *length-width ratio c. 2—2.5,* reflexed in the upper few mm; basal callosities absent. Wings and keel about equally long: wings generally obtuse; keel about falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk inconspicuous. Ovary hairy; ovules 2. Pod dehiscent, inflated, thick woody, without wings. Seed 1 (rarely 2), ellipsoid; radicle folded.

Distribution. One species in South China (there recently discovered, see Wei, l. c.), Indo-China, and Thailand.

Taxonomy. Gagnepain originally considered the apical pores of the anthers a distinctive character, but a closer look showed that the anthers are longitudinally dehiscent with broad slits, giving in some specimens the appearance of terminal pores in younger stages. This was already noted by Hutchinson (l. c.).

The genus stands rather isolated. Small flowers with elongated standard occur only in *Leptoderris,* the pod reminds slightly of *Pongamia* (here reduced to *Millettia*). Greatest similarity is with *Callerya,* from which it differs in the small flowers with elongated standard, the adnate upper filament, and the pod with valves inflated already in early stages. It differs from *Imbralyx* in the subtruncate calyx, smaller flowers with elongated standard, and again in the pod with convex valves.

Gagnepain originally described two species. Abundant material, mainly collected by Poilane in Indo-China, showed different combinations of the originally differentiating characters, so that distinction of two species is unnecessary. This has been elaborated by two students, Anja van der Niet and Els Bakker, during a course in 1979 (unpublished report).

Apurimacia   Pod not depicted, as Pl. IV—29 and 31

Apurimacia Harms, Fedde Rep. 19 (1923) 10; F. Peru: 385; Burkart, Legum. Argent. (1952) 257; Hutch.,
    Gen. 1: 370; A.L.S.: 256, 279; L.Nod.: 59. — T y p e : *A. michelii* (Rusby) Harms.

Shrubs. Leaflets 5—19. Stipellae present. Flowers in axillary pseudoracemes, some-
times in axillary racemes. Brachyblasts, if present, slender with 2 apical flowers. Bracts
shorter than the corresponding flowerbuds. Bracteoles present.Flowers 10—13 mm
long. Hypanthium indistinct. Calyx with 5 acute lobes, the upper 2 higher connate.
Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and
keel petals about equally long, both subfalcate. Upper filament adnate to the other 9.
Basal fenestrae distinct. Disk indistinct. Ovary nearly glabrous; ovules 2—6. Pod
dehiscent, rather thin woody, as in *Tephrosia*. Seeds reniform, flat; radicle folded.

D i s t r i b u t i o n . Two or four species in drier parts of tropical S. America (Bolivia,
Peru, Argentina).

T a x o n o m y . The habit has features that remind me of *Tephrosia*: leaflets are hairy,
rather thick and relatively small and the pod looks similar. The genus differs in the
presence of stipellae and bracteoles, the open basal fenestrae and the absence of a disk.
The inflorescence is similar (in all but one species) to that of *Lonchocarpus* (*s. s.*) but
Apurimacia differs in the constant presence of stipellae, the absence of basal callosities,
in the dehiscent fruit (although some *Lonchocarpus spp.* have dehiscent pods as well)
and in the more xeric habit.

Austrosteenisia   Pl. IV—22

Austrosteenisia Geesink, *gen. nov.*
    Generi *Callerya* similis, sed alis brevioribus legumineque membranaceo differt. — T y p u s : *A. blackii*
    (F. Muell.) Geesink, *comb. nov.*; basionym: *Millettia blackii* F. Muell., Fragm. Phytogr. Austr. 2 (1861)
    123. The genus is named after Prof. Dr. C. G. G. J. van Steenis, already generically commemorated in
    Steenisia Bakh. f. (*Rubiac.*), who "caught" me for Malesian botany, and expressed earlier doubt about
    the inclusion of these species in *Lonchocarpus*.

Lianas. Leaflets 7—17. Stipellae present in the type species, lacking in the second
species. Flowers in terminal panicles. Bracts shorter than the corresponding flower-
buds. Bracteoles present. Flowers about 10 mm long. Hypanthium indistinct. Calyx
with 5 subequal lobes. Standard blade about orbicular, reflexed at base; basal callosities
absent. Wings with a "normal" claw *and a strongly reduced blade.* Keel petals falcate.
Staminal tube straight. Upper filament adnate to the other 9. Basal fenestrae distinct.
Disk distinct. Ovary hairy; ovules 14—17. Pod indehiscent, flat, membranous, without
wings. Seeds 4—7, reniform, laterally flattened; radicle folded.

D i s t r i b u t i o n . Two species in Northern Australia, one also in New Guinea.

T a x o n o m y . Originally described as *Millettia blackii* by Ferdinand von Mueller in
1861, the type species was soon transferred to *Lonchocarpus* by Bentham in 1864 on

account of the indehiscent pod. Bentham's concept of *Lonchocarpus* was so wide, that it included paniculate (mainly African) species, here distinguished as the genus *Philenoptera*, as well as pseudoracemose species, here distinguished as the genera *Deguelia* and *Lonchocarpus* (*s. s.*). Bentham probably interpreted the reduced wings and the high number of ovules in these Australian species as specific characters, and expected ("but as yet unknown in Asia", Fl. Austr. 2: 271) that species of *Lonchocarpus* (in his concept) would sooner or later turn up in East Asia to fill in the large geographical gap. A second species with similar flower structure was described in 1933 as *Lonchocarpus stipularis* by C. T. White. Both Australian species were reduced by Polhill (1971) to *Kunstleria* on account of the thin pod with both sutures concave and the relatively small flowers. There are, however, some differences with the other species of *Kunstleria*. In the Australian species the number of leaflets and ovules is much higher, the staminal tube is not bent (a unique character), the wings are much reduced, the standard reflexes near the base of its blade, the upper filament is adnate to the others, and the flowers are somewhat larger (c. 10 vs. 6—8 mm in *Kunstleria*). I have tried to find similarities with other Australian tribes, also in the tribes with free filaments, but in vain. Therefore, I regard these Australian species as a distinct genus with structural similarities to the more "primitive" genera *Callerya* and *Ostryocarpus*, differing from both in the above mentioned characters except the flower size.

Behaimia

Behaimia Grisebach, Cat. Pl. Cub. (1866) 77; E.P. 3: 342; B.H. 1: 1002; León & Alain, Fl. Cuba 2 (1951) 332; Hutch., Gen. 1: 382; A.L.S.: 235, 256; L. Nod.: 97. — Type: *B. cubensis* Griseb.

Trees. Leaflets 9—13, (sub)opposite. Stipellae minute, soon caducous. Flowers in axillary panicles. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers about 12 mm long. Hypanthium indistinct. *Calyx 2-lipped* with a *2-topped upper lip and a 3-lobed lower lip. Standard blade orbicular, reflexed at base*; basal callosities absent. Wings and keel petals about equally long, all obtuse. Upper filament free. Basal fenestrae absent. Disk indistinct. Ovary hairy; ovules 5 or 6. Pod indehiscent, membranous, without wings, flat, *transversely reticulately nerved*. Seed usually 1, rarely 2, flat, reniform; radicle folded.

Distribution. One species in Cuba.

Taxonomy. The bilabiate calyx and the flat, distinctly reticulately nerved pods places *Behaimia* rather apart. *Dewevrea*, an African genus with alternate leaflets, also has a bilabiate calyx, but with an entire lower lip. The original publication mentions 2 free upper filaments and 7 connate ones, which is copied in some publications. This must have been observed in old flowers where the upper filament had already dropped. I only observed one free upper filament, but the other 9 filaments have a longer free part than in most other genera; especially the upper 4 filaments in the sheath are connate only up to halfway.

Bergeronia M. Micheli, Mém. Soc. Phys. Genève 28, 7 (1883) 38; E.P. 3: 343; Burkart, Legum. Arg. (1952) 235; A.L.S.: 256, 279; L. Nod.: 99. — Type: B. sericea M. Micheli.

Trees. Leaflets 9—13, (sub)opposite. Stipellae absent. Flowers in axillary pseudoracemes. Bracts slightly longer than the corresponding flowerbuds, soon caducous. Brachyblasts reduced to a node bearing 2 (or 1) flowers. Bracteoles present. Flowers about 15 mm long. Hypanthium indistinct. Calyx campanulate with 4 acute lobes, the upper one 2-topped. Standard blade about orbicular, apparently not reflexed at base; basal callosities absent. Wings and keel petals about equally long, all obtuse. Upper filament free. Basal fenestrae absent or indistinct. Disk inconspicuous. Ovary hairy; ovules 1—6 (or more?). Pod indehiscent, rather thick without wings, *curved upwards in up to half a circle*; *valves continuous between the seeds*. Seeds reniform, ellipsoid in cross section; radicle folded.

Distribution. One species in N. Argentina and Paraguay.

Taxonomy. The relationships must be with *Lonchocarpus,* the differences being the free upper filament and the upcurved thick pod. In *Bergeronia* the brachyblast is reduced to a mere node with two flowers, mixed in the same inflorescence with 1-flowered nodes. Allen & Allen (L. Nod.: 99) describe the fruit as falling apart into indehiscent loments, but this is a wrong translation of Burkart's description.

Brachypterum   Pl. V—43

Brachypterum (W. & A.) Benth., Comm. Legum. Gener. (1837) 37, *nom. cons. prop.* (Taxon 33, 1984, in press); Benth. in Miq., Pl. Jungh. (1852) 253; Miq., Fl. Ind. Bat. 1 (1855) 138. — *Dalbergia* subg. *Brachypterum* W. & A., Prodr. 1 (1834) 264. — *Derris* sect. *Brachypterum* (W. & A.) Benth., Syn. Dalb.: 101; B.H. 1: 549; F.B.I. 2: 240; Thothathri, Bull. Bot. Surv. India 3,2 (1961) 175; A.L.S.: 256; Thothathri, Fasc. Fl. India 8 (1982) 1. — *Derris* subg. *Brachypterum* (W. & A.) Kurz, J. As. Soc. Beng. 45, 2 (1876) 276 (p. p., see note below). — *Deguelia* sect. *Brachypterum* (W. & A.) Taubert, in E.P. 3,3: 345. — Type: B. scandens (Roxb.) Miq., based on Roxb., Pl. Corom. 2, 1805, pl. 192: *Dalbergia scandens* Roxb., *Derris scandens* (Roxb.) Benth.; for combination in *Deguelia,* see note below.
Solori Adans., Fam. 2 (1763) 327, *nom. rejic. prop.* — Type: "H. M. 6, T. 22" (= B. scandens (Roxb.) Miq., but heterotypic under the present Art. 10, ICBN).

Lianas or trees. Leaflets (7—) 13—41 (or more?), opposite or subopposite. Stipellae present, though small. Flowers in axillary pseudoracemes, in some species in terminal pseudopanicles. Brachyblasts callose, warty or cylindric, with 2—5 flowers. Bracts shorter than corresponding flowerbuds. Bracteoles present. Flowers 6—10 mm long. Calyx with 5 short lobes. Standard blade elliptic to orbicular, reflexed at base; basal callosities absent, though corresponding margin sometimes curved in younger stages. Wings and keel petals about equally long; wings obtuse to subfalcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk distinct, cylindric or 10-lobed. Ovary hairy; ovules 2—10. Pod indehiscent, thin papery, strap-shaped, with distinct, chartaceous, *darker coloured* (*when dried*) *"chambers" surrounding the seeds*; upper suture with a *broad* longitudinal wing. Seeds 1—4(—7), reniform; radicle folded.

Distribution. Six species from India to Malesia, *B. scandens* extending to N. Australia. *Derris koolgibberah* (Australia and New Guinea) also belongs here.

Nomenclature. 1. (The genus) *Brachypterum* is generally known as the section *Brachypterum* of *Derris* in a wider sense. *Derris* (in this wider taxonomic sense) is conserved against *Deguelia* Aublet (which represents American *Derris*, see also following note), against *Salken* Adanson (which represents *Derris trifoliata*, the type species of *Derris s.s.*, though heterotypic under the present Art. 10, I.C.B.N.) and against *Solori* Adanson. The last name is based on plate 22 from Rheede's Hortus Malabaricus Vol. 6, which shows clearly a plant belonging to *Derris* section *Brachypterum*. From the vernacular name, the description, and the region of origin, the plate is always identified with the species generally known as *Derris scandens* (Roxb.) Benth., the type species of this section, and I see no reason to doubt this identification. This means that the oldest available name in generic rank is *Solori* and not *Brachypterum* (which dates from 1837). *Brachypterum* has only been treated on generic level by Miquel (1855), and since 1860 authors have followed Bentham's reduction to sectional rank. Although both *Solori* and *Brachypterum* are about equally obscure names, I have proposed *Brachypterum* as a *nomen conservandum* (Taxon 1984, in press), as it repeats the generally used sectional name.

2. Kurz raised Bentham's *Derris* section *Brachypterum* to subgeneric rank in 1876. He mentioned Bentham's section (*"Eu-"*)*Derris* between brackets and included its type species *Derris trifoliata* (as the synonym *D. uliginosa*) as well. This action suggests that the subgeneric name *Brachypterum* is superfluous in the circumscription "when published" as it contains "the type of a name which ought to have been adopted under the rules" (art. 63, ICBN). The rewording in the Sydney Code emphasises that a name is "permanently attached" to its type, in this case *Derris scandens,* which is included by Kurz as well. Kurz's combination *Derris* subg. *Brachypterum* is thus validly published and legitimate with *D. scandens* as its type species, but at the same time incorrect in the circumscription when published. I have added Kurz's combination in the synonymy of both *Brachypterum* and *Derris* with a "p.p." mark.

3. Pittier (1917) created some confusion by considering the Asiatic species *Derris scandens* (Roxb.) Bentham a later homonym of the American species *Derris scandens* (Aublet) Pittier, and he proposed to rename the first species *Derris timorensis* (DC.) Pittier. This is not in accordance with the present rules and when the American species is treated under *Derris* it has to be renamed *D. pterocarpus* (DC.) Killip, as was accepted so by Amshoff (1939). See further the note on American *Derris* under *Deguelia*.

Taxonomy. During the last hundred years this genus was considered to be a section of *Derris* in a wider sense. *Brachypterum* differs from *Derris* (*s.s.*) in the higher (though slightly overlapping) number of smaller leaflets, in the callose consistency of the brachyblasts, in the presence of a distinct cylindric or lobed disk, in the more papery strap-shaped pods with acute base and apex and with discrete, darker coloured, chartaceous "chambers" around the seeds, and in the accumulation of 3-phenyl-

coumarine. Furthermore, the general "facies" is different, mainly caused by the more numerous and smaller leaflets, the longer inflorescences, and the more numerous pods per infructescence. See further the notes under *Derris s. s.*

Burkilliodendron
<div style="text-align: right">Pl. IV—26</div>

Burkilliodendron Sastry, Bull. Bot. Surv. India 10 (3–i–1969) 243; Whitmore, Treefl. Mal. (1972) 289; A.L.S.: 256. — *Burkillia* Ridley, F.M.P. 5 (1925) 304, *nom. illeg., non Burkillia* West & West (1907) = *Algae—Chlorophyta.* — *Alloburkillia* Whitmore, Gard. Bull. Sing. 24 (9–viii–1969) 4. — T y p e : *B. album* (Ridl.) Sastry.

Shrubs. Leaves unifoliolate, petiole bipulvinate. Stipellae present. Flowers in axillary racemes, these *2 per axil, seemingly collaterally inserted.* Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 6—8 mm long. Hypanthium indistinct. Calyx campanulate with 5 short teeth, the lower ones longer. Standard blade about orbicular, about halfway reflexed; basal callosities absent. Wings and keel petals about equally long. Wings obtuse. Keel more falcate and acute. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk inconspicuous. Ovary hairy; ovules 2. Pod dehiscent, thin-woody, flat, falcate, without wings. Seeds 2, lens-shaped; radicle folded.

D i s t r i b u t i o n . One species in Malaya (Perak). Apparently very rare.

N o m e n c l a t u r e . The illegitimate name *Burkillia* was replaced by two different names by two authors in 1969, independent from each other.

T a x o n o m y . This monotypic genus, possibly only known from the type collection, was formally described by Ridley in 1925, based on an unpublished detailed description by S. T. Dunn, who actually discovered that this was an unknown genus. Dunn considered it to be related to *Millettia* (especially its sect. *Albiflorae,* distinguished here as the genus *Imbralyx*) and to *Fordia.* In my opinion the differences with these two groups are more striking than the similarities, and I think *Burkilliodendron* does probably not belong to the tribe *Millettieae.*

The short inflorescence, consisting of two seemingly collateral axillary racemes with rather small and feeble flowers remind me of the *Phaseoleae* subtribe *Glycininae,* and more specifically of the genus *Glycine. Glycine* consists of a few herbaceous species with generally more ovules. The pod in *Glycine* is narrower and with walls between the seeds. As explained in chapter 3, the subtribe *Glycininae* is transitional between the rest of the tribe *Phaseoleae* and the tribe *Millettieae,* so that the position of *Burkilliodendron* in either of these tribes does not make much difference, and I doubt if any unambiguous criterion to separate these tribes will ever been found.

Callerya
<div style="text-align: right">Pl. II—12, 14; also as in Pl. III—16</div>

Callerya Endlicher, Gen., Suppl. 3 (1843) 104. — *Marquartia* Vogel, Nov. Act. Acad. Caes. Leop.- Carol. Nat. Cur. 19, Suppl. 1 (1843) 35, *nom. illeg. (non Marquartia* Hasskarl, 1842 = *Pandanus*). — T y p e :

Marquartia tomentosa Vogel (=) *Callerya nitida* (Benth.) Geesink, *comb. nov.*; basionym: *Millettia nitida* Bentham, Lond. J. Bot. 1 (1842) 484.

Padbruggea Miquel, Fl. Ind. Bat. 1 (1855) 150; Craib, Fl. Siam. Enum. 1 (1928) 396; F.M.P. 1: 587; F. Java 1: 615; A.L.S.: 259; L. Nod.: 487. — Type: *P. dasyphylla* Miq.

Millettia subg. *Nothomillettia* (*"Notho-Millettia"*) Miq. ex Kurz, J. As. Soc. Beng. 45,2 (1876) 173. — Type: *M. atropurpurea* (Wall.) Benth.

Adinobotrys Dunn, Bull. Misc. Inf. Kew (1911) 194; E.P. Nachtr. 4: 137; F.M.P. 1: 586. — Lectotype (proposed here): *A. atropurpureus* (Wall.) Dunn (*Millettia atropurpurea* (Wall.) Benth.; *Pongamia atropurpurea* Wall., Pl. As. Rar. 1 (1829) 70. t. 78).

Whitfordiodendron Elmer, Leafl. Philipp. Bot. 2 (1910) 743; Merrill, Pap. Mich. Acad. Sc. Arts Lett. 19 (1934) 159; A.L.S. 260; L. Nod.: 694. — *Whitfordia* Elmer, Leafl. Philipp. Bot. 2 (1910) 689, *nom. illeg.* (*non* Murrill. 1908 = *Fungi*). — Type: *W. scandens* Elmer (in case Elmer's rectification is not considered a valid publication, the author should be cited as "Elmer ex Merrill", 1934, l.c.).

Millettia sect. *Eurybotryae* Dunn, J. Linn. Soc., Bot. 41 (1912) 135. — Lectotype (proposed here): *M. reticulata* Benth.

Millettia sect. *Austromillettia* (*"Austro-Millettia"*) Dunn, J. Linn. Soc., Bot. 41 (1912) 135. — Lectotype (proposed here): *M. australis* (Endl.) Benth.

Lianas or trees (few species). Leaflets 5—11, (sub)opposite. Stipellae present or absent. Flowers in terminal and/or axillary panicles, in a few species the panicles cauli- and raminascent. Bracts generally longer than the corresponding flowerbuds, in a few species also broader, covering the buds completely. Bracteoles present, in two species inserted on the calyx. Flowers 10—18 mm long. Hypanthium indistinct to distinctly cup-shaped. Calyx usually truncate, in some species with 4 or 5 low lobes or short teeth, in a few species with relatively large lobes. Standard blade ovate to orbicular, reflexed at base; basal callosities present or absent. Wings and keel petals about equally long, both obtuse or subfalcate. Wings free from the keel in *Millettia japonica*. Upper filament free from the other 9. Basal fenestrae absent. Disk generally present. Ovary glabrous or hairy; ovules 1—10 (or more?). Pod indehiscent or tardily dehiscent, thin to thick woody, flat, inflated around the generally ellipsoid seeds, without wings. Seeds 1—10, ellipsoid (ripe seeds not yet known for all species); radicle folded (as far as known).

Distribution. About 16 species, 13 in S. E. Asia, two confined to N. Australia, and one (*"Millettia japonica"*) in Japan.

Nomenclature. Taxonomically *Callerya* consists, as here conceived, of the agglomeration of *Whitfordiodendron, Padbruggea,* and two sections originally in *Millettia.* The oldest available name in generic rank is *Callerya* Endlicher, a nearly forgotten synonym of *Millettia.* In *Whitfordiodendron* and *Padbruggea* five combinations have already been made, two of which even in combination with both generic names. In case one would consider nomenclatural conservation of either *Padbruggea* or *Whitfordiodendron* instead of the reintroduction of an entirely obscure name (hitherto even without any combination in it), one would save three resp. five combinations which are already made. Because the number of more or less established names is low, and the concept of *Callerya* as here proposed is wider than that of the obvious candidates for nomenclatural conservation, I don't feel too guilty about having

refrained from proposing any of these two names for conservation, and I propose to reintroduce the practically forgotten name *Callerya* for this group of *Millettia*-allies with paniculate inflorescences.

Taxonomy. Dunn (1911-b, 1912) distinguished the genera *Adinobotrys* and *Padbruggea* from *Millettia* on account of a combination of the presence of true panicles, stipitate ovaries with few ovules, and one-seeded indehiscent or very tardily dehiscent pods with large ellipsoid seeds. In the original descriptions *Adinobotrys* differed from *Padbruggea* in the absence of stipellae, absence of basal callosities on the standard, and in the presence of recurved auricles on upper and lower margin of the wings. These distinctions are rather weak, and study of new material has reduced the number of differences to zero or, arbitrarily, to only one.

In comparison with *Millettia* the low number of ovules is an arbitrary character; it appeared to be variable even at species level as well as overlapping with the numbers in many species from different sections in *Millettia*. The stipitate ovary in meaningless as differentiating character: practically all *Leguminosae* have more or less stipitate ovaries. A possibility to keep *Padbruggea* and *Adinobotrys* (which is taxonomically identical to the earlier described genus *Whitfordiodendron*) separate from the bulk of *Millettia* is to redefine the group on account of the truly paniculate inflorescences, which correlates with a polythetic set of characters. In that case, three sections of *Millettia* (in the circumscription of Dunn, 1912) need to be transferred, viz. *Eurybotryae*, *Austromillettia*, and *Bracteatae*. On account of the very peculiar pod and the absence of bracteoles I propose here to raise sect. *Bracteatae* to generic level (as *Endosamara*). *Eurybotryae* and *Austromillettia* do not differ from *Padbruggea* and *Adinobotrys* (*Whitfordiodendron*) even in one constant character, so that merging of these four groups seems the only possibility. The "facies" of these groups is similar. With this merging the original weak distinction between *Padbruggea* and *Adinobotrys* (*Whitfordiodendron*) is lost*). *Millettia speciosa*, *M. fordii*, and *M. reticulata* lack stipellae and have basal callosities, thus leaving subdivision on account of only one of these (or any other) characters, which is considered arbitrary. When combined in the proposed way, the resulting genus *Callerya* (the oldest available name in generic rank) differs from *Millettia s. s.* in the paniculate inflorescence and the free upper filament, combined with a polythetic set of characters, viz. relatively thick inflorescental rhaches, very tardily dehiscent to indehiscent, flat pods with big ellipsoid seeds.

Callerya differs from *Philenoptera* in the free upper filament and in distribution from *Ostryocarpus* in the unwinged pod and the thick seeds. In my opinion, these genera are closer related to *Callerya* than to *Millettia s. s.*

Anatomy. Corner (1951) described the seed of *Millettia* (*Adinobotrys*, *Whitfordiodendron*, *Padbruggea*) *atropurpurea* as "overgrown", i. e. the seed is relatively large compared to its pod and the seed coat does not differentiate into

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*) Based on a study carried out by G. Thijsse during a student course in 1980.

palissade and hour-glass layer but remains "embryonic". The drawing (Corner's fig. 26) shows a sclerenchymatic more-layered epidermis, with a different but rather undefinable layer under it. In order to confirm the sclerenchymatic character of the epidermis and to define the underlying layer, I made a few hand-cut sections through the seed coat of the same species and found in the first sample, to my astonishment, a distinct palissade layer. This material originated from Indo-China, an area with a relatively long dry period.

Material from Malaya showed the pattern depicted by Corner, but only in a particular sectional direction. It appeared that Corner's drawing is a cross-section of horizontally elongated, palissade-like cells, which are orientated parallel to the antiraphe, at least in the part of the seed coat where I made the section. This particular type of cells in the seed coat deserves further investigation. The surface view, given by Corner, may have originated from another part of the seed coat where the cells in the palissade layer are arranged vertically. The hour-glass layer is indeed absent. The characterization of the epidermis as "remaining embryonic" is somewhat exaggerated. Gunn (1981) does not mention the characteristics of "overgrown seeds", and probably the concept needs redefinition.

Caulocarpus
<div style="text-align: right">Pod not depicted; as in Pl. IV—29, but stipitate</div>

Caulocarpus E. G. Baker, L.T.A. (1926) 169; Hutch., Gen. 1 (1964) 398; L. Nod. 151; Brummitt, Kew Bull. 35 (1980) 464 (not accepted, but commented upon). — T y p e : *C. gossweileri* Baker.

Shrubs. Leaflets 1—5, digitately arranged, without rachis. Stipellae absent. Flowers single, axillary, sometimes from the axils of leaf-scars. Bracts thus absent. Bracteoles absent. Flowers c. 15 mm long. Hypanthium indistinct. Calyx with 5 distinct teeth. Standard blade broadly obovate, apparently not reflexed; basal callosities absent. Wings and keel petals about equally long; wings obtuse; keel falcate. Upper filament free. Basal fenestrae marked but not distinct. Disk indistinct. Ovary hairy; style bearded along upper edge; ovules 5—8 (or more?). Pod stipitate, further as in *Tephrosia*. Seeds 4—7, subglobose, laterally slightly flattened; radicle folded.

Distribution. One species in Tropical Africa (Zambia and Angola).

Taxonomy. The genus differs from *Tephrosia* in the sessile, digitately arranged leaflets, the free upper filament, and in the stipitate pod. It may represent a section or subgenus of *Tephrosia,* but this can only be established after a monographic subdivision of the latter genus.

Chadsia
<div style="text-align: right">Pl.IV—31</div>

Chadsia Bojer, in L. Bouton, Rapp. Ann. Trav. Soc. Hist. Nat. Ile Maurice 12 – 13 (1842) 52; Ann. Sci. Nat., sér. 2, 20 (1843) 104; B.H. 1: 497; E.P. 3: 272; Hutch., Gen. 1: 377; A.L.S.: 256; L. Nod.: 160. — T y p e : *C. flammea* Bojer.

Shrubs. Leaflets (1—) 3—9 (or more?), digitately or pinnately arranged, opposite or alternate. Stipellae absent. Flowers in axillary sessile fascicles, these often from the

axils of dropped leaves, giving the appearance of ebracteate pseudoracemes. Brachyblasts thick warty, with up to 5 (or more?) flowerbuds, 1—3 of which develop. Bracts shorter than the corresponding flowerbuds. Bracteoles absent. Flowers 2—10 cm long, showy, with bird-pollination syndrome. Hypanthium indistinct. Calyx with 4 long, acuminate lobes, the upper one 2-topped. Standard long, obovate to spathulate, reflexed at base; basal callosities absent. Wings shorter than the keel, obtuse; keel long-falcate to acuminate, curved upwards. Upper filament adnate to the other 9. Basal fenestrae present, but not very distinct. Disk indistinct. Ovary hairy; ovules 6—8 (or more?). Pod dehiscent, thin woody (thicker than in *Tephrosia*), flat, convex around the seeds, without wings. Seeds 6—8 (or more?), ellipsoid; radicle folded.

Distribution. 18 species in Madagascar.

Taxonomy. The rather stiff leaflets with straight nerves suggest close relationship with *Tephrosia*. It is remarkable that the insertion of the leaflets varies from digitately to pinnately arranged and even strictly alternate in the only 5 species that I have investigated. *Chadsia* corollas are recorded to be red, scarlet, or orange, and many species have probably a green (or ultraviolet) patch on the standard.

Craibia   Pl. II—9

Craibia Dunn, J. Bot. 49 (1911) 106; E.P. Nachtr. 4: 136; L.T.A.: 244; F. Cong. 5: 52; F.W.T.A.: 527; Hutch., Gen. 1: 378; F.T.E.A.: 146; A.L.S.: 256; L. Nod.: 189. — Type: *C. brevicaudata* (Vatke) Dunn.

Treelets. Leaflets 1—11, alternate. Stipellae present or absent. Flowers in terminal panicles, sometimes combined with axillary racemes, occasionally only in terminal racemes. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 12—30 mm long. Hypanthium indistinct. Calyx with 5 short teeth or with 5 distinct lobes. Standard blade about orbicular, reflexed at base, basal callosities absent. Wings and keel petals about equally long, both obtuse or subfalcate. Upper filament free, in some species adherent in the middle. Basal fenestrae generally distinct. Disk indistinct. Ovary hairy; ovules 2—6. Pod dehiscent, thin woody, flat, without wings. Seeds lens-shaped, *with a cupular aril one sided elongated and clasping the funicle;* radicle folded.

Distribution. 10 species in Tropical Africa.

Taxonomy. The dehiscent pod and the variable adherence of the upper filament to the other 9 suggests a relationship with *Millettia*. The alternate insertion of the leaflets is shared with *Schefflerodendron* (also African), which differs in a number of other characters. The peculiar aril is unique.

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Craspedolobium

Pl. V—35

Craspedolobium Harms, Fedde Rep. 17 (1921) 135; Hutch., Gen. 1: 372; A.L.S.: 256; L. Nod.: 191. —
    Type: *C. schochii* Harms.

Lianas. Leaflets 3, lateral ones opposite. Stipellae present. Flowers in axillary
pseudoracemes. Brachyblasts warty, with 3—5 flowers. Bracts shorter than the
corresponding flowerbuds. Bracteoles present. Flowers about 10 mm long.
Hypanthium indistinct. Calyx *also hairy inside,* with 4 lobes, the upper one two-topped.
Standard about orbicular, reflexed at base; basal callosities distinct. Wings and keel
about equally long, both obtuse. Upper filament free from the other 9. Basal fenestrae
indistinct. Disk distinct. Ovary hairy; ovules 5—8. Pod dehiscent, thin woody, flat, with
a short wing on the upper suture. Seeds 2 (or more?), flat, lens-shaped; radicle folded.

Distribution. One species in Yunnan (S. W. China). Only few collections extant.

Taxonomy. This genus is intermediate between *Phaseoleae-Glycininae (s. l.)* and
Millettieae. The calyx is also hairy inside, as in *Kunstleria* and some species of
Spatholobus. The fruit is *Derris*-like, but dehiscent. The apparently constantly
3-foliolate leaves (at least near the inflorescences) with symmetrical lateral leaflets
suggest relationship with *Spatholobus,* from which it differs in the woody dehiscent
pods with a *Derris*-wing, the higher number of ovules, and the central insertion of the
seeds. Leaves from the vegetative sphere of the plant are not (yet) collected, so that the
constancy of the 3-foliolate leaves is unknown. More completely collected specimens
are needed.

Cyclolobium

Pl. V—42

Cyclolobium Bentham, Comm. Legum. Gener. (1837) 28; F. Bras.: 229; Benth., Syn. Dalb.: 51; B.H. 1: 545;
    E. P. 3: 336; Hutch., Gen. 1: 389; A.L.S.: 256; L. Nod.: 204. — Type: *C. brasiliense* Bentham.

Shrubs or treelets. Leaves 1-foliolate. Stipellae present. Flowers in axillary panicles
or in axillary racemes, or 2—4 racemes seemingly collateral from a leaf-axil. Flowers
10—15 mm long. Bracts shorter than the corresponding flowerbuds. Bracteoles
present. Hypanthium indistinct. Calyx with 5 lobes. Standard blade about orbicular,
reflexed at base; basal callosities absent. Wings and keel petals obtuse, equally long or
the wings shorter. Upper filament free from the other 9. Basal fenestrae distinct. Disk
distinct. Ovary hairy; ovules 2—4 (or more?). Pod indehiscent, *stipitate, orbicular,* thin
woody; upper suture with a narrow wing, in at least one species also the lower suture
with a wing or crest. Seeds 2 or 3, more or less transversely elongated; radicle straight.

Distribution. About 5 species in tropical South America.

Taxonomy. The genus resembles *Ostryocarpus* in most characters, differing in the
1-foliolate leaves and in the shorter, suborbicular pod which is long stipitate. The lobed
calyx reminds me of African *Philenoptera,* from which it differs in the free upper
filament, in the 1-foliolate leaves, and in the pod.

Dahlstedtia Malme, Ark. Bot. 4, 9 (1905) 4; E.P. Nachtr. 3: 171; Hutch., Gen. 1: 384; A.L.S.: 256, 279; L
    Nod.: 213. — T y p e : *D. pinnata* (Benth.) Malme.

Shrubs. Leaflets (3—)5—7, (sub)opposite or occasionally alternate. Stipellae absent.
Flowers in panicles, usually from the axils of fallen leaves, *with bird-pollination
syndrome.* Bracts shorter than the corresponding flowerbuds. Bracteoles present, soon
caducous. Flowers 20—30 mm long. Hypanthium distinct. Calyx long tubular with
4 lobes, the upper one 2-topped. Standard blade elliptic, not reflexed; basal callosities
absent. Wings and keel petals about equally long, both obtuse *and with very short
auricles.* Upper filament adnate to the other 9. Basal fenestrae distinct. Disk indistinct.
Ovary nearly glabrous; ovules 2—4 (or more?). Pod indehiscent, slightly inflated, thin
woody, with a wing-like edge along both sutures. Seeds 1—4, reniform, elliptic in
cross-section; radicle folded.

D i s t r i b u t i o n . Possibly only one species in southern Brazil.

T a x o n o m y .The bird-pollination syndrome is easily recognized (see also chapter 4)
on account of a set of characters in different parts of the flowers. The syndrome is so
conspicuous, that it masks the relation to other taxa as far as flower characters are
concerned. The shape of the pod, the inflorescence, and (in combination) the rather
atypical vegetative features remind me of *Philenoptera/Lonchocarpus.* Especially the
position of the lowermost pair of flowers on their axis seems similar to the position in
Lonchocarpus muehlbergianus: in the lowermost pair the flowers are opposite, some-
times in the next pair as well, while the more apically inserted flowers are spirally
arranged. This may indicate that the panicle is secondary, viz. derived from a pseudo-
raceme with biflorous brachyblasts, as in the majority of species of *Lonchocarpus* (*s. s.*).

Deguelia Aublet, Hist. Pl. Guiane 2 (1775) 750, t. 300 (*nom. rejic.* vs. *Derris* in a wider sense). — T y p e : *D.
    scandens* Aublet.
Clompanus Aublet, Hist. Pl. Guiane 2 (1775) 773 (*nom. rejic.* vs. *Lonchocarpus* in a wider sense, see note
    below); Steudel, Nom. ed. 2 (1840) 386 ("*Clomopanus*"). — T y p e : *C. paniculata* Aublet.
Phyllocarpus Riedel ex Endl., Gen., Suppl. 2 (1842) 97, *non* Riedel ex Tulasne. — T y p e : *P. pterocarpus*
    (DC.) Endl. ex B.D. Jackson.
Lonchocarpus sect. *Fasciculati* Benth., Syn. Dalb.: 98; F. Bras.: 275; B.H. 1: 548. — *Lonchocarpus* subg.
    Phacelanthus Pittier, Contr. U.S. Nat. Herb. 20, 2 (1917) 45; Ducke, Trop. Woods 69 (1942) 2; Bol.
    Tecn. Inst. Agron. Norte 28 (1953) 35; Polhill, Kew Bull. 25 (1971) 270; Biochem. Syst. Ecol. 9 (1981)
    141; A.L.S.: 257, 279. — T y p e : not designated.
Derris p.p. (only the American species): Benth., Syn. Dalb.: 106; F. Bras.: 287; F. Sur.: 272; F. Peru 13,3:
    256; Polhill, Kew Bull. 25 (1971) 270; A.L.S.: 246, 257. — T y p e : not appropriate.

Lianas. Leaflets 5—9(—17), (sub)opposite. Stipellae (always?) absent. Flowers
usually in rather elongated, axillary pseudoracemes, these sometimes combined into
pseudopanicles; brachyblasts short, cylindric, with 3—6 scattered flowers. Bracts
shorter that the corresponding flowerbuds. Bracteoles present. Flowers 6—15 mm

long. Hypanthium indistinct. Calyx usually truncate with 4 or 5 short teeth, often oblique because of the slightly longer lower tooth. Standard blade elliptic to orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long; both usually obtuse, in some species the keel falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk present, *forming two glands, one adaxial, one abaxial to the base of the upper filament* (not checked for all species!). Ovary hairy; ovules (1 or) 2—4. Pod indehiscent (dehiscent in one species, described as *Millettia occidentalis*), rather thin and stiff, with or without a longitudinal wing along the upper suture. Seeds 1 or 2 (or 3), usually reniform; radicle folded.

Distribution. About 16 species in the northern part of S. America.

Nomenclature. *Lonchocarpus* Kunth (in a wider sense) is conserved against *Clompanus* Aublet (ICBN), after the formal proposal was made by Rickett & Stafleu in 1959 (Taxon 8: 294). The proposal was not accompanied by an interpretation of the type species *Clompanus paniculata* Aubl. The generic synonymy was taken (Stafleu, pers. comm.) from the listing by Dalla Torre & Harms (Gen. Siph. 3834), which in its turn was probably taken from Von Post & Kuntze (Lex.: 336). This is the oldest generic identification I found. I did not find the name interpreted in the literature cited under Aublet, Hist. in Stafleu & Cowan (TL-2). In two older. dictionaries, viz. Steudel (Nomenclator 2nd ed.) and Kuntze (Rev. Gen. 1), *Clompanus* Aubl. was supposed to represent a Legume without generic identification. Amazingly, the name is neither mentioned in Taubert (E.P. 3: 343), nor in the four supplements, nor in Amshoff's (1939), nor in Lemée's (1952) treatments of the *Leguminosae* of Surinam and French Guyana respectively.

As I propose here (see chapter 7) to transfer *Lonchocarpus* subgenus *Phacelanthus* (= sect. *Fasciculati*) to *Deguelia*, it is of nomenclatural significance to what part of the former larger genus concept *Clompanus* actually belongs.

Aublet's description (unfortunately not accompanied by a plate) reads:

> 1. CLOMPANUS (*paniculata*) floribus purpureis, paniculatis; ramulis scandentibus; foliis alternis; foliolis oppositis, ovatis, glabris, integerrimis.
> Clompanus funicularis. Tali bocompol mera. RUMPH. *Herb. Amboïn. tom.* v. *pag.* 70. *cap.* 37. *tab.* 37. *fig.* 2. [This part of the protologue is later interpreted as *Entada* (Legum.-Mim.); another, heterotypic *Clompanus* Rafin. is interpreted as *Sterculia,* R. G.]
> Cette Liane croît au bord de la crique S. Régis, en sortant des paletuviers (= mangrove, R. G.), d'où l'on aperçoit les bâtiments de la sucrerie.

Aublet placed the genus in the Class *Diadelphia Decandria,* which mainly consists of Papilionoids. Therefore it is reasonable to assume that the genus *is* a Papilionoid. It is apparently a liane with panicle-like inflorescences with purple flowers. The leaflets are opposite (wich excludes the identification with the larger part of *Dalbergia* and with *Machaerium*). The number of leaflets is unfortunately not mentioned, nor the consistency of the liane (woody or herbaceous). This means that, besides the possibility of identification with *Lonchocarpus* (in that case the climbing habit with panicle-like

inflorescences indicates subg. *Phacelanthus!*), also the possibility of identification with climbing *Phaseoleae* should not be excluded. Furthermore, there are also a few species of *Dalbergia* with (at least occasionally) opposite leaflets. Identification with "American *Derris*" is also possible, especially because pods were apparently lacking in the material Aublet had in hand. Identification with other Legumes seems less probable.

I have tried to locate the actual type specimen(s), and did not find it in Herbarium Banks (BM). The lack of a plate and the very short description (compared to other ones in the Hist. Pl. Guiane) suggest that there is no extant specimen (P.J.M. Maas, pers. comm.). In Ducke's (1942) and Macbride's (1943) generic concepts *Lonchocarpus* subg. *Phacelanthus* belongs to *Derris*, and followers of this generic concept should be warned that conservation of *Derris* against *Clompanus* is necessary, if the concept (of *Derris*) includes *Lonchocarpus* subg. *Phacelanthus* only (thus excluding the type of *Lonchocarpus s.s.*). Ducke (1942) conceived the genus in this way, though with incorrect acceptance of the generic name *Lonchocarpus*. If the concept (of *Derris*) comprises *Lonchocarpus s.s.* as well (Macbride, 1943), conservation is not necessary, as *Clompanus* is rejected in favour of *Lonchocarpus*.

Taxonomy. The genus *Deguelia,* as here conceived, combines the notorious "American *Derris*" with *Lonchocarpus* subg. *Phacelanthus* (= sect. *Fasciculati*) in the same circumscription as given by Ducke (1942), though illegitimately treated there under *Lonchocarpus* (see nomenclatural note above). I have accepted this concept after long hesitation and discussions with R. M. Polhill (K) and M. Sousa S. (MEX). Until quite recently I stuck to the opinion that, as American *Derris* did not differ in any macromorphological character from Asiatic *Derris*, the former should be considered to consist of "members of" *Derris*. But, after I recognized the Asiatic *Derris* to contain generically different components, I had to reconsider "American *Derris*" as well, and now I agree with Ducke's, Polhill's, and Sousa's opinion. With the generic distinction of *Derris* (*s.s.*) and *Brachypterum* in Asia, "American *Derris*" acquired a small set of characters in which it differs from both.

From *Derris* (*s.s.*) it differs in the more elongated inflorescences, in the shorter, thicker brachyblasts, and in the disk. From *Brachypterum* it differs in the disk, in the shape of the pods, and in a set of polythetically distributed characters. Comparison of the flower structure of "American *Derris*" and *Lonchocarpus* subg. *Phacelanthus* (which I initially planned to transfer to *Millettia*) revealed another, small but significant character, viz. an unusual shape and place of the disk shared by both groups. It consists of two glands, one between the bases of the upper filament and the ovary, and one on the abaxial side of the base of the upper filament. I could not check this character in all species, but I found it in all specimens from both groups that I saw. Other characters mentioned in previous literature, viz. sculptured part of the base of the wing blades and a falcate keel, appeared not to be constant in the species observed, but both characters were observed in both groups. These characters are neither present in *Lonchocarpus* (*s.s.*), nor in *Derris*, nor in *Brachypterum,* but are frequently found in *Millettia*. The probable "function" of the sculptured part of the wing blade is discussed in chapter 4.

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One species, described as *Millettia occidentalis* (from Brazil), has even dehiscent pods, and from all these characters it may be concluded that *Deguelia*, as here conceived has significant similarities with both *Derris* and *Millettia*. As discussed in chapters 6 and 7 I do not consider this sufficient reason to lump *Derris* with *Millettia* (*Lonchocarpus* and many surrounding genera would then sink into it as well).

The groups, as separated here, can be keyed out, possess a small monothetic set of characters though within an irritatingly wide and polythetical range of other characters. In fact, *Deguelia* differs from *Millettia* only in the peculiar disk, but it is not yet known whether this character is constant indeed. Lumping with *Millettia* would expand the diagnosis of *Millettia* with *Lonchocarpus*-like and with *Derris*-like pods. In *Millettia*, the similarity with sect. *Caudaria* (originally described in *Lonchocarpus*, but transferred to *Millettia* by Polhill, 1971) is most striking; the differences are again in the habit and in the disk. These groups may well represent two closely allied (maybe even "sister"-) groups.

Derris

Derris Lour., Fl. Cochinch. (1790) 432, *nom. cons.*; Benth., Syn. Dalb.: 101; B.H. 1: 549; F.B.I. 2: 240; F. Austr. 2: 272; E.P. 3,3: 345 (sub *"Deguelia"*); F.G.I.-C. 2: 447; F.M.P. 1: 593; L.T.A.: 552; F. Cong. 6: 31; Thothathri, Bull. Bot. Surv. India 3,2 (1961) 175; F. Java 1: 616; Hutch., Gen. 1: 384; A.L.S.: 256; L. Nod.: 224; Thothathri, Fasc. Fl. Ind. 8 (1982) 1. (Citations restricted to Asiatic sect. or subg. *Derris* (*"Euderris"*), for American spp. see under *Deguelia*.). — *Pterocarpus* [L., Fl. Zeyl. (1747) 196] O. Kuntze, Rev. Gen. 1 (1891) 202, *non* L. (1754, *nom. rejic.*), *nec* N. J. Jacquin (1763, *nom. cons.*). — *Derris* subg. *Brachypterum* (W. & A.) Kurz, J. As. Soc. Beng. 45, 2 (1876) 276, p. p. (see nomenclatural note under *Brachypterum*). — Type: *Derris trifoliata* Lour. (*typus conservandus*).
Salken Adanson, Fam. 2 (1763) 322, *nom. rejic.* — Type: "H.M. 8, t. 46" (= *D. trifoliata* Lour.).

Lianas. Leaflets (3 or) 5—9 (—13), opposite or rarely subopposite. Stipellae present or absent. Flowers in axillary pseudoracemes, these often combined into terminal or axillary pseudopanicles; inflorescences often from the axils of fallen leaves; brachyblasts rather thin with (1 or) 2—8 scattered flowers. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 6—10 (—15) mm long. Hypanthium indistinct. Calyx usually truncate with 4 or 5 short lobes or teeth, usually oblique because of longer lower lobe. Standard blade elliptic to orbicular, reflexed at base; basal callosities absent, but base of blade slightly incurved in some species. Wings and keel petals about equally long; both usually obtuse; keel subfalcate in some species. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk absent. Ovary hairy; ovules 2—5 (—8). Pod indehiscent, rather thin and stiff, with either a longitudinal wing on both sutures or only on the upper suture. Seeds 1 or 2 (or 3), usually reniform; radicle folded.

Distribution. About 40 species in S.E. Asia, one of which extending from E. Africa to Australia and the West Pacific (*D. trifoliata,* a mangrove species), and one endemic species in N. Australia. The 4 or 5 species in tropical South America are transferred to *Deguelia* (see there).

Nomenclature. *Derris* (in a wider sense than above) is conserved over *Deguelia* Aubl., *Salken* Adans., and *Solori* Adans. The first one is here accepted in generic rank, and the last element belongs to the section (or subgenus) *Brachypterum,* which is raised here to generic rank; see under *Brachypterum.*

Taxonomy. The reasons to divide the formerly larger conceived genus *Derris* into three genera (i.e. *Derris s.s., Brachypterum,* and *Paraderris*) are given in chapter 7. The only character that can be used for the unification of these three groups is the presence of a longitudinal wing either on the upper suture or on both sutures. As this seems not to be correlated with other characters, this is not a sufficient base to consider *Derris* (*s.l.*) an unarbitrarily defined genus. *Derris* (*s.s.*) differs from *Ostryocarpus* in the adnate vexillary filament with basal fenestrae, in the absence of a disk, in the flower-bearing axes condensed into shorter, up to 8-flowered (thin) brachyblasts, and in the folded radicle of the embryo. *Derris* (*s.s.*) differs from *Brachypterum* in the generally lower number of leaflets, the non-callose consistence of the brachyblasts, the absence of a disk, and in the more rounded pods without distinct seed chambers. It differs from *Paraderris* in the inflorescence and in the absence of distinct basal callosities of the standard blade. All these genera have also a characteristic "facies", while *Derris* (*s.s.*) lacks a characteristic "facies", possibly because it may represent a rest-group, remaining after the more characteristic groups are separated from it.

Dewevrea   Pod not depicted; as Pl. II—14, and III—16

Dewevrea M. Micheli, Bull. Soc. Bot. Belg. 37 (1898) 47; E.P. Nachtr. 2: 131; L.T.A.: 255, 256; F. Cong. 5: 61; Hutch., Gen. 1: 377; A.L.S.: 257; L. Nod.: 233. — Type: *D. bilabiata* M. Micheli.

Lianas. Leaflets 5—7, (sub)opposite. Stipellae absent. Flowers in terminal and axillary panicles with the flower-bearing branchlets in the lower part of the panicles tending to resemble cylindric brachyblasts, but these with 5 or more flowers. Bracts shorter than the corresponding flowerbuds. Bracteoles minute, soon caducous. Flowers about 15 mm long. Hypanthium distinct. *Calyx 2-lipped,* the upper one 2-topped, *the lower one entire.* Standard blade elliptic, reflexed at base; basal callosities not distinct, *the claw more or less callose with a thicker ridge at the distal part.* Wings and keel petals not adhering, even the keel petals very loosely adherent, about equally long, both falcate. Upper filament free from the other 9. Basal fenestrae indistinct. Disk distinct, 10-lobed. Ovary hairy; ovules 3—5. Pod tardily dehiscent, thick woody, flat, convex around the seeds, without wings. Seeds reniform to quadrate, elliptic in cross-section; radicle folded.

Distribution. Two or probably only one species in Equatorial West Africa.

Taxonomy. This genus is characterized by the bilabiate calyx, the free wing petals, the scarcely adherent keel petals, and the distinct hypanthium which surrounds a 10-lobed disk. It is generally considered to be related to *Millettia* on account of the dehiscent pod and of the tendency to shortened flower-bearing branchlets. The distinct

hypanthium is rather rare in this tribe; it occurs only in the E. Asiatic section *Podocarpae* of *Millettia*. A quite similar ridge at the distal part of the claw of the standard occurs also in *Wisteria*.

Disynstemon

Disynstemon R. Viguier, Notul. Syst. 14 (1951) 175; Peltier, Adansonia sér. 2, 17 (1977) 201; A.L.S.: 257. — Type: *D. madagascariense* R. Viguier (= *D. paullinioides* (Bak.) Peltier).

Lianas. Leaflets 3, digitately arranged. Stipellae *2*, just below the lateral leaflets. Flowers in terminal (short) racemes. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers c. 17 mm long. Hypanthium indistinct. Calyx 5-lobed, the upper 2 lobes rounded, the lower 3 ± acute. Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long, both subfalcate. Upper filament adnate to the other 9. Basal fenestrae absent. *Free parts of the upper 5 filaments broader and much shorter than the free parts of the lower 5 filaments* (but anthers equal). Disk indistinct. Ovary hairy; ovules 7 or 8. Pod dehiscent, thick woody; valves convex with a papery, partly separating inner layer; without wings. Seeds 3—5, reniform, elliptic in cross-section; radicle folded.

Distribution. One species in Madagascar.

Taxonomy. At first glance this genus seems misplaced in this tribe. The shape of the androecium is unique for this genus, but the constant digitately 3-foliolate leaves and the absence of basal fenestrae suggest relations elsewhere, e. g. in or near *Genisteae* (*s. l.*), although stipellae ought to be absent in these tribes. An analysis of the chemical constituents has been carried out by Dr. Evans (pers. comm.) and revealed absence of alkaloids (characteristic for *Genisteae*) and presence of canavanine, present in many genera of the *Millettieae*.

Endosamara

Endosamara Geesink, *gen. nov.* — *Millettia* sect. *Bracteatae* Dunn, J. Linn. Soc., Bot. 41 (1912) 135. Generi *Callerya* similis, sed bracteolis nullis endocarpioque lomentis separabilibus differt. — Typus: *E. racemosa* (Roxb.) Geesink, *comb. nov.*; basionym: *Robinia racemosa* Roxb., Fl. Ind. 3 (1832) 329. — *Millettia racemosa* (Roxb.) Benth. in Miq., Pl. Jungh. (1852) 249, footnote.

Lianas. Leaflets 9—13, (sub)opposite. Stipellae present. Flowers in terminal and axillary panicles. Bracts longer than the corresponding flowerbuds. Bracteoles absent. Hypanthium indistinct. Calyx subtruncate with 4 or 5 indistinct lobes. Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long; keel falcate. Upper filament free from the other 9. Basal fenestrae absent. Disk present, cylindric. Ovary glabrous; ovules 4 or 5. Pod dehiscent, separating into two valves consisting of the exocarp only; *endocarp lomented, forming an envelope around each seed with a flat, wing-like part, dropping like an Acer-mericarp*. Seeds 4 or 5, obliquely ellipsoid; radicle folded.

Distribution. One (possibly two) species from South India eastwards through Burma and Indo-China to the Philippines.

Taxonomy. The type species, *Endosamara racemosa,* was placed by Dunn (1912) in the monotypic section *Bracteatae* of *Millettia*. He noted the separating endocarp, but from the scanty fruiting material at his disposal he may have considered the lomentation of the endocarp as an artefact. This lomentation of the endocarp is, as far as I know, unique in the *Leguminosae. Diphysa* and *Glottidium* (both genera of the tribe *Robinieae*), *Schizolobium* (*Caesalpinioideae-Caesalpinieae*), and *Wallaceodendron* (*Mimosoideae-Ingeae*) also have separating endocarps, in the first three genera entirely separating from the exocarp, and in *Wallaceodendron* apparently also rupturing into one-seeded envelopes, which, however, are not samaroid. In *Butea, Spatholobus, Erythrina subumbrans* (all *Phaseoleae-Glycininae s. l.*) and in *Pterolobium* (*Caesalpinioideae-Caesalpinieae*) the entire pod is samaroid and drops slown down by the rotating wing. All genera mentioned are quite unrelated, and *Endosamara* shows the greatest similarity with *Millettia* sect. *Eurybotryae* (here under *Callerya*),and with *Sarcodum*. It differs from both in the lack of bracteoles and in characters of the pod.

Fordia Pl. IV—28

Fordia Hemsley, in Forbes & Hemsley, J. Linn. Soc. 23 (1886) 160; E.P. 3: 271; E.P. Nachtr. 4: 137; Dunn, Bull. Misc. Inf. Kew (1911) 63; F.M.P. 1: 586; Hutch., Gen. 1: 378; Whitmore, Treefl. Mal. 1 (1972) 293; A.L.S.: 257; L. Nod.: 289. — Type: *F. cauliflora* Hemsl.

Treelets. Leaflets 3—25, (sub)opposite. Stipellae present in *F. cauliflora,* absent or occasionally present in other species. Flowers in *rami- and/or caulinascent* pseudo-racemes, in some species combined with axillary *or supra-axillary* ones. Brachyblasts thick cylindric with up to 8 scattered flowers. Bracts shorter than the corresponding flowerbuds. Flowers 10—15 mm long. Hypanthium indistinct. Bracteoles present. Calyx truncate with 5 short lobes or teeth. Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long, both (sub)-falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk inconspicuous. Ovary hairy; ovules 2 (rarely 3). Pod tardily dehiscent, subfalcate, rather thin woody, flat, without wings. Seeds 1 or 2, flat lens-shaped; radicle folded.

Distribution. About 10 species, in continental S. E. Asia, Malaya, Sumatra, Borneo, and the Philippines. Most species occur in Malaya; 1 species is recently discovered in Flores. The species from Malaya and eastwards inhabit the dark understorey of evergreen lowland forests, which is unique among Asiatic Papilionoids. Other Papilionoids prefer more exposed habitats, and are in evergreen areas either confined to riversides, or to the canopy as lianas, among which are a few cauliflorous ones, e. g. *Strongylodon* (*Phaseoleae*) and *Callerya*.

Taxonomy. The genus *Fordia* is characterized by the rami- and/or caulinascent inflorescences and the capacity to flower and germinate in the dark understorey of

evergreen forests, combined with a monothetic set of characters: acuminate to caudate leaflets, subtruncate calyx, inconspicuous disk, 2 ovules, and flat, thin woody, tardily dehiscent pods. The similarity in "facies" and in characters is most strikingly with some groups of *Millettia*. Herbarium specimens resemble "at glance" those of the African section *Caudaria* (formerly in *Lonchocarpus*, since 1971 transferred to *Millettia*), but the closest resemblance is probably with the continental S. E. Asiatic group around *Millettia pulchra*, which differs in the axillary inflorescences and a higher number of ovules. If the relations of *Millettia* would not have been so various and complex, I would not have hesitated to regard *Fordia* as a subgeneric or sectional taxon in *Millettia*, but the extension of the circumscription of *Millettia* with the mentioned characters of *Fordia* convinced me that generic distinction contributes to more clearness, as explained in chapter 7. This has earlier already been expressed by Dunn (1911-c, p.63): "It is true that in spite of these characters (i.e. the ones mentioned above, R. G.) it might well have found a place within the heterogeneous collection of groups which, even at that time, constituted the genus *Millettia*, but its author judged, no doubt, that it was more for the convenience of botanists to found upon it a new genus than to add a fresh type to that already perplexing collection".

Imbralyx   Pl. III—21

Imbralyx Geesink, *gen. nov.* — *Millettia* sect. *Albiflorae* Dunn, J. Linn. Soc., Bot. 41 (1912) 136. Named after
   the *imbricate calyx*. Generi *Callerya* similis, sed calycis lobis imbricatis filamentisque monadelphis
   differt. — T y p u s : *I. albiflorus* (Prain) Geesink, *comb. nov.*; basionym: *Millettia albiflora* Prain, J. As.
   Soc. Beng. 66, 2 (1897) 92, 364.

Trees. Leaflets 1 or (3 or) 5 or 7, (sub)opposite. Stipellae absent. Flowers either in terminal and axillary panicles, or in axillary pseudoracemes with the lower placed brachyblasts rather elongated and with 5—7 scattered flowers; the higher brachyblasts wart-like. Bracts shorter than the corresponding flowerbuds, *the latter spindle-shaped*. Bracteoles present. Flowers 12—17 mm long. Hypanthium distinct. Calyx with 4 imbricate, *acute* lobes, the upper one 2-topped. *Petals white*. Standard blade about orbicular, reflexed at base; basal callosities distinct. Wings and keel petals about equally long, both slightly falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk absent. Ovary hairy; ovules 2—8. Pod dehiscent, without wings, short velvety. Seeds (no ripe ones seen) flat (also when ripe?); radicle folded.

Distribution. Four species in S. China, Peninsular Thailand, Malaya, and Sumatra.

Taxonomy. This genus was formerly considered to be a section of a wider conceived genus *Millettia*. The characteristic combination of: 1. panicles (in *I. albiflorus*), 2. transitional inflorescences to pseudoracemes (in *M. unifoliolata*, in *M. nivea*, and in *M. leptobotrya*), 3. distinctly imbricate calyx lobes, 4. characteristic spindle-shaped flowerbuds, 5. white petals, 6. distinct hypanthium, 7. adnate upper filament, 8. velvety falcate pods, and 9. glabrous leaflets with a raised nerv-

ation/venation strikingly similar on both surfaces, makes this group probably homogeneous and recognizable. Inclusion in *Callerya* would extend the description (of *Callerya*) with the characters 2, 3, 4, 6, and 7. Inclusion in *Millettia* would violate the (weak) distinction of it with *Callerya* and extend its description with the characters 1, 3, and 9. Ripe seeds are still unknown in these rare species, but the flat, unripe seeds give the impression that they may become thick (possibly "overgrown", see under *Callerya*) at full maturity.

The best expedient seems to be to consider this group on the same (generic) level as both *Callerya* and *Millettia*, but I am fully aware that "slightly broader minded" colleagues would consider this situation a kind of "proof" that *Callerya* and *Millettia* should not be maintained as different genera. For reasons, discussed in chapter 7, I prefer to distinguish the groups mentioned as genera.

Kunstleria   Pl. IV—23

Kunstleria ("Kuenstlera" auct.) Prain in King, J. As. Soc. Beng., Nat. Hist. 66, 2 (1897) 109, 464; King et al., Ann. R. Bot. Gard., Calc. 9,1 (1901) 27; F.M.P. 1: 599; Hutch., Gen. 1: 382; Polhill, Kew Bull. 25 (1971) 263; A.L.S.: 257; L. Nod.: 368. — Type: *K. curtisii* Prain.

Lianas. Leaflets 1—11, (sub)opposite. Stipellae absent. Flowers in terminal and axillary panicles. Bracts usually slightly longer than the corresponding flowerbuds, soon caducous. Bracteoles present. Flowers (4—)5—7 mm long. Hypanthium indistinct. Calyx *also hairy inside,* with 2 rather broad upper lobes and 3 narrower acute lower lobes. Standard blade broadly ovate to obovate, slightly reflexed halfway the lamina, basal callosities absent. Wings and keel petals about equally long, both obtuse; wings loosely adherent to the keel; keel petals overlapping below, *coherent.* Upper filament free from the other 9, *but adnate for up to ³/₄ the length of the standard claw.* Basal fenestrae indistinct. Disk distinct, consisting of 10 processes. Ovary hairy; ovules (1 or) 2(—4). Pod indehiscent, flat, strap-shaped, thin leathery, without wings or crests, rusty brown pubescent with usually distinct reticulate nerves outside. Seeds 1 (—3), flat, broadly reniform; radicle short, folded.

Distribution. Eight species in West Malesia and the Philippines, not in Java. The 2 species from Australia and New Guinea are transferred to *Austrosteenisia.*

Taxonomy. *Kunstleria* is characterized by paniculate inflorescences with small flowers similar to those of *Spatholobus,* from which it differs in the centrally placed seed(s), in the wider range in the number of leaflets (1—11 vs. 3 in *Spatholobus*), and in the constantly symmetric lateral leaflets (the lateral leaflets in *Spatholobus* are either symmetric or asymmetric with the basiscopic side enlarged). In *Kunstleria* the keel petals are overlapping and the overlapping parts are coherent. This character is more variable in *Spatholobus,* where the keel petals can be either free, or valvately connate along the lower edge, or overlapping and confluent. Much (especially flowering) material was found under the unidentified material of *Spatholobus,* illustrating the close resemblance.

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The overlapping keel petals are characteristic for the tribe *Dalbergieae,* and this character, combined with the lack of free amino-acids and amines in the seeds (also in *Callerya* and *Ostryocarpus*) indicates close affinity (both genetic and phylogenetic) with *Dalbergieae.*

For a discussion of the affinities of the Australian species, referred to *Kunstleria* by Polhill (1971), see under *Austrosteenisia.*

The genus *Kunstleria* is under revision by Mrs. Diedel Kornet (L).

Leptoderris   Pl. V—37

Leptoderris Dunn, Bull. Misc. Inf. Kew (1910) 386; E.P. Nachtr. 4: 144; L.T.A.: 554; F. Cong. 6: 32;
    F.W.T.A.: 519; Polhill, Kew Bull. 25 (1971) 265; F.T.E.A.: 76; A.L.S.: 257, 277; L. Nod.: 383. —
    Lectotype: *L. goetzei* (Harms) Dunn, proposed here, see note below.

Lianas, occasionally erect shrubs with straggling branches. Leaflets 3—9, (sub)opposite. Stipellae present. Flowers in pseudoracemes or in pseudopanicles; pseudoracemes axillary; pseudopanicles either terminal with several lateral branches, or axillary with 1 or 2 lateral branches, or terminal pseudopanicles combined with axillary pseudoracemes in the upper leaves. Brachyblasts callose, warty or short cylindrical. Bracts shorter than corresponding flowerbuds. Bracteoles present. Flowers 5—10 mm long. Hypanthium distinct (in most species?). Calyx lobes 4, distinct to obscure, the upper one 2-topped. Standard blade elliptic, reflexed at base, *length-width ratio (1.4—) 2—3*; basal callosities absent or indistinct. Wings shorter than the keel, both obtuse at apex and the base of their claws adnate to the staminal tube. Basal fenestrae distinct. *Upper filament adnate to the claw of the standard* to various degree and adnate to the other 9 halfway. *The staminal sheath adnate to the base of the claws of the wings and the keel.* Disk absent. Ovary hairy; ovules 1—3. Pod indehiscent, flat, thin leathery, distinctly reticulately nerved outside; upper suture with one longitudinal wing. Seed 1 or 2 (occasionally 3), laterally flattened, about symmetrically reniform, radicle folded.

Distribution. About 20 species in tropical Africa.

Nomenclature. Dunn (1910) originally comforted 14 (thus syntype-) species in his newly described genus. Allen & Allen (1981) were the first authors who designated a type species, viz. *L. trifoliolata* Hepper (1956). As this species does not belong to the original set of species, their choice was contrary to Art. 7.4 (ICBN), which requires lectotypes to be selected from the original syntypes. In accordance with this rule, I propose here to designate *L. goetzei* (Harms) Dunn as a proper lectotype.

Taxonomy. Fruiting material of this genus resembles *Derris* so much, that Hutchinson (1964) reduced *Leptoderris* to *Derris*. *Leptoderris* differs from *Derris* sect. *Derris* (to which it is most similar) in its narrower standard, in the callose consistency of the brachyblasts, in the presence of a more or less distinctly developed hypanthium, in the filaments adnate to the petal claws, and in the still unknown, but different structure

of the free guanidino compounds in the seeds. The narrow, medium-sized standard and the guanidino compounds are unique characters. The distinct hypanthium is possibly a primitive character, shared by many *Sophoreae, Dalbergieae, Robinieae,* and a few more genera of the *Millettieae.* Similarly callose brachyblasts are found in some groups of *Millettia,* in *Deguelia, Brachypterum,* as well as in some more isolated genera. The pollen structure is in part similar to that in *Ostryocarpus, Craibia,* and *Endosamara,* but also the "basic" (i.e. the most common pollen type in the *Millettieae,* Hazelhorst, in prep.) and intermediate pollen types occur.

Lonchocarpus Pl.I—2, IV—24; also as Pl. IV—32

Lonchocarpus Kunth, in H.B.K., Nov. Gen. Sp. 6, ed. fol. (1824) 300, ed. qu. (1824) 383, *nom. cons.*; Benth., Syn. Dalb.: 85; F. Bras.: 275; B.H. 1: 548; E.P. 3: 343; Pittier, Contr. U.S. Nat. Herb. 20 (1917) 37—93; T.S. Mex.: 512; F. Sur.: 141; F. Peru 13,3: 256 (sub *Derris*); Léon & Alain, Fl. Cuba 2 (1951) 330; Burkart, Legum. Argent. (1952) 231; F.W.T.A.: 522; Hutch., Gen. 1: 383; F. Pan.: 39; A.L.S.: 257, 279; L. Nod.: 395. — Type (*typus conservandus,* but see Polhill, 1971, p. 262, footnote, and Cowan, Taxon 8, 1959, p. 259): *L. sericeus* (Poir.) DC.
Muellera ("*Müllera*" *auct.*) Linnaeus *f.*, Suppl. Pl. (1782) 53, 329, *nom. cons.* vs. *Coublandia, nom. rejic. prop.* vs. *Lonchocarpus* (see nomenclatural note below); Poiret in: Lamarck, Enc. Méth. 4,1 (1797) 372 (sub "*Muller*" = "*Mullera*"); Benth., Syn. Dalb.: 117; F. Bras.: 290:B.H. 1: 550; E.P. 3: 344; E.P. Nachtr.1: 202; T.S. Mex.: 515; F. Sur.: 147; Burkart, Legum. Argent. (1952) 234; Hutch., Gen. 1 (1964) 395; F. Pan.: 36; A.L.S.: 258, 279; L. Nod. 449. — Type: *M. moniliformis* Linn. *f.*, *nom. illeg.* (see nomenclatural note below).
Coublandia Aublet, Hist. Pl. Guiane (1775) 937, t. 356 (& 300, pod only), *nom. rejic.* vs. *Muellera, nom. rejic. prop.* vs. *Lonchocarpus* (see note below on *Muellera*); Lamarck, Enc. Méth. 2,1 (1786) 142. — *Coublana* Cothenius, Disp. (1790) 25, *nom. illeg.* or *orth. var. illeg.* — Type: *C. frutescens* Aubl.
Sphinctolobium Vogel, Linnaea 11 (1837) 417. — Type: *S. virgilioides* Vogel.
Neuroscapha Tulasne, Ann. Sci. Nat. Bot. 20, sér. 2 (1843) 137. — Type: not designated.
Cyanobotrys Zuccarini, Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4, 2 (1845) 28. — Type: *C. mexicana* Zucc.
Willardia J. N. Rose, Contr. U. S. Nat. Herb. 1 (1891) 97; E.P. 3: 275; T.S. Mex.: 483; N. Am. F.: 234; Hermann, J. Wash. Acad. Sci. 37 (1947) 427; F. Pan.: 802: Hutch., Gen. 1: 378: A.L.S.: 260, 279; L. Nod.: 695. — Type: *W. mexicana* (S. Watson) J. N. Rose.
Terua Standley & Hermann, J. Wash. Acad. Sci. 39 (1949) 306; Hutch., Gen. 1: 380; L. Nod.: 650 — Type: *T. vallicola* Standley & Hermann.

Trees, less often shrubs. Leaflets (1 or 3 or) 5—15 (—23), (sub)opposite. Stipellae generally absent, but in some species constantly present. Flowers usually in axillary pseudoracemes, in several species in axillary or terminal pseudopanicles. Brachyblasts rather thin with (1 or) 2 (rarely 3) flowers on its apex, with as many bracts at their base. In some species the brachyblasts reduced, then (within the pseudoraceme/panicle) the 2 (or 3) flowers clustered with 3 (or 4) bracts (respectively). Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 6—25 mm long. Hypanthium indistinct. Calyx usually truncate with 4 or 5 minute teeth, in a few species 4-lobed with the upper one 2-topped. Standard blade broadly ovate to obovate, reflexed at base; basal callosities generally distinct. Wings and keel petals about equally long; wings obtuse; keel distinctly falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk (always?) absent. Ovary hairy; ovules 2—9(—12). Pod indehiscent, papery to thin woody, in a few species (belonging to *Terua* and *Willardia,* reduced here

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to synonymy) tardily dehiscent and thin woody; sutures without wings, thickened or not. Seeds 1—7 (or more?), lens-shaped or reniform; radicle folded.

Distribution. About 150 species in Central and tropical South America, of which one, *L. sericeus,* also occurring in West Africa.

Nomenclature. The genus *Icthyoctonum* Boiv. ex Baillon is generally cited as a synonym of *Lonchocarpus.* As this name was invalidly published, I have refrained from formal treatment.

Muellera. As explained under the taxonomical notes, I regard *Muellera* as a group of (3 or 4) species belonging to *Lonchocarpus* sect. *Punctati.* Nomenclaturally this has complex consequences that are best illustrated by the nomenclatural history of the type-species, *Muellera moniliformis* L.f. This species was earlier described by Linnaeus (senior) in a dissertation by Jacob Alm, published in 1775 (23 - vi), as *Coronilla monilis,* based on a collection made by Dalberg in Surinam. Linnaeus listed the species as nr. 157.

Independently, Aublet published a new genus and species, *Coublandia frutescens,* based on his own collections, also in 1775. The exact date of publication is unknown, but TL-2 mentions "between June and September 1775". Linnaeus' and Aublet's species are always considered conspecific since De Candolle (1825) discovered this.

In 1782, Linnaeus *f.* described a new genus *Muellera* (as *Müllera*) on p. 33 of his Supplement on Systema Vegetabilium, and on p. 329 the species belonging to it; he named it *M. moniliformis,* citing a (probably *the*) Dalberg collection and an illustration, made by Maria Sybilla Merian (her plate 35), without citation of his father's earlier name.

Schreber, the editor of the 8th volume of Amoenitates (1885), mentioned in a footnote under *Coronilla monilis* the identity with *Muellera moniliformis.* This identification was later followed by Richter (Codex, 1835—1839) and Savage (Catalogue, 1945).

The herbarium of Linnaeus (LINN) contains two branches (one flowering and one fruiting), numbered 157 (but without further notes or names, microfiche at L) and I consider this material to be the type of both names. As the generic name *Coublandia* is older than *Muelllera,* the latter has been conserved, as it was more generally accepted. The name of the type species *Muellera moniliformis* L.f., however, is illegitimate (superfluous, as it is based on the type of *Coronilla monilis* L.). The name should be recombined with either the epithet *"monilis"* or *"frutescens"* depending on the unknown priority. The chance that Linnaeus' name is older may be greater, but this is not certain, and I will not recombine the name, as I consider *Muellera* (taxonomically) synonymous with *Lonchocarpus.* As the date of publication of *Muellera* is earlier than that of *Lonchocarpus,* and *Lonchocarpus,* even in the strict sense adopted here, contains far more species (about 150 vs. 3 or 4 in *Muellera*) I have proposed (Taxon 33, 1984, in press) to conserve *Lonchocarpus* over *Muellera.* As *Muellera* was already conserved over *Coublandia,* this conservation should be left intact, analogous to the similar conservation of *Millettia* over *Pongamia* besides the maintained conservation of *Pongamia* over *Pongam* (Geesink, Taxon 31, 1982, p. 327).

Furthermore, I will not establish here the combination in *Lonchocarpus*; I prefer to leave this to future monographic treatments, the authors of which may (or may not) agree with my view.

Taxonomy. In the concept here proposed, the genus is restricted to the former type subgenus combined with the two former satellite genera *Terua* and *Willardia*. In the present concept the genus is characterized by the rather thin brachyblasts with (1 or) 2 (or 3) flowers on top within axillary pseudoracemes or pseudopanicles, combined with flat, reniform or lens-shaped seeds, and the polythetic set of generally exstipellate leaves and generally indehiscent, thin-walled, wingless pods.

Terua. The genus *Terua,* already considered a synonym of *Lonchocarpus* by Sousa (1981) differed exclusively in the tardily dehiscent pods. As this character was formerly the distinction between the tribes *Dalbergieae* and *"Tephrosieae"* (or *Galegeae s.l.*), *Terua* was placed in the latter tribe. This character is arbitrary, as explained in chapter 4, and I agree with Sousa's amalgamation with *Lonchocarpus s.s.*

Willardia. The 6 species, treated by Hermann (1947) under *Willardia,* are supposed to differ from *Lonchocarpus s.s.* by the combination of dehiscent pods and free, spreading wings, and a higher (but overlapping) number of leaflets and ovules. If the character of the free and spreading wings would have been constant, I would have considered *Willardia* at least a coherent, distinct group which, awaiting comparison with *Lonchocarpus* at species level, could have been maintained at generic rank, but I found in *Willardia eriophylla* the wings firmly adnate to the keel by means of distinct lateral folds both in wings and keel petals. According to the drawings by Sousa (1981) the wings are free indeed in *W. schiedeana* and in the type species, *W. mexicana,* they are explicitly described as being free. It will depend, in my opinion, on the specific relationship of those and other species described under *Willardia,* whether the genus can either be restricted to a smaller number of species, or may represent an infrageneric taxon within *Lonchocarpus.* As *Willardia,* as conceived by Hermann (1947), Standley (T. S. Mex.) and Rydberg (N. Am. F.) does not differ in even one constant character from *Lonchocarpus s.s.* (but including *Terua*) I prefer to consider it a synonym. This opinion was also suggested by Sousa (1981, and pers. comm.).

Philenoptera. The distinction between *Lonchocarpus s.s.* and the paniculate *Philenoptera* is discussed under the latter genus.

Phacelanthus. The former subgenus *Phacelanthus* (= section *Fasciculati*) is transferred to *Deguelia* and discussed there.

Muellera. The group of three (or four) species, generally combined in the genus *Muellera,* is characterized by pods with strong constrictions between the seeds (if more than one seed is present). In the type species, *M. moniliformis,* the seeds are thick and the pod tends to rupture into one-seeded "loments" (without discrete articulations) dispersed by water (either rivers or possibly even sea-water), as this species occurs mainly in the back-mangrove and on sandy coasts (A. Gentry, J. Lindeman, pers. comm.). In the two (or three) other species the seeds are slightly flatter, but the pods are more constricted than those of *Lonchocarpus (s.s.).*

The floral characters are similar to those of *Lonchocarpus (s.s.)* and the leaves are

pellucid-punctate (at least in the type species and in *M. mexicana*). I regard the deviating pod-character (compared to *Lonchocarpus*) as an adaptation to aquatic dispersal and I prefer to regard it as delimiting on species-level. The pellucid-punctate leaflets are unique to section *Punctati,* and I consider the species of *Muellera* as belonging to this section. I would not have considered *Muellera* and *Lonchocarpus* (*s. s.*) congeneric if *Muellera* would have formed merely an extra section or subgenus, but because it has its closest relatives within a discrete section, I cannot but reduce it. This case is analogous to that of *Pongamia* (see under *Millettia*).

Lupinophyllum   Pl. IV—33

Lupinophyllum Hutch., Gen. Fl. Pl. 2 (1967) 626. — *Lupiniphyllum* Gillett ex Hutch., Gen. 1 (1964) 398,
   nom. inval.; L. Nod.: 406 — Type: *L. lupinifolium* (DC.) Hutch.

Shrublets with erect (and?) or creeping branches. Leaflets 1—7, digitately arranged. Stipellae present. Flowers in axillary and terminal pseudopanicles, combined with axillary pseudoracemes. Brachyblasts small, 2-flowered. Bracts shorter than the corresponding flowerbuds. Bracteoles absent. Flowers 5—7 mm long. Hypanthium indistinct. Calyx with 5 distinct lobes. Standard blade orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long; wings obtuse, keel subfalcate. Upper filament adnate to the other 9. Basal fenestrae slightly open, slit-like. Disk indistinct. Ovary hairy; ovules 6—8. Pods from aerial inflorescences dehiscent, as in *Tephrosia* 4—8 seeded; *pods from prostrate inflorescences geocarpic, short, indehiscent, 1- (or more?) seeded.* Seeds ellipsoid, *marmorated*; radicle folded.

Distribution. One species in tropical Africa, from Senegal southwards.

Taxonomy. Brummitt (1980) reduced Hutchinson's genus *Lupinophyllum* again to *Tephrosia* on account of its similarity to certain species of *Tephrosia,* some of which occasionally have stipellae, and another one (here under *Caulocarpus*) having digitately arranged leaflets. Awaiting a subdivision of *Tephrosia,* the genus seems tentatively distinct enough on account of the digitate leaflets, trailing habit, geocarpic fruit, and presence of stipellae combined. See also note under *Tephrosia.*

Margaritolobium   Pod not depicted, unknown

Margaritolobium Harms, Fedde Rep. 19 (1923) 67; Hutch., Gen. 1: 369; A.L.S.: 257, 279; L. Nod.: 420. —
   Type: *M. luteum* (F. M. Johnston) Harms.

Deciduous shrubs with scaly buds. Leaflets 5, (sub)opposite. Stipellae absent. Flowers in pseudoracemes from the axils of fallen leaves. Brachyblasts reduced to a node bearing 2 flowers from the axils of 3 bracts, together with nodes with single flowers from the axil of 1 bract in the inflorescence. Bracts shorter than the corresponding flowerbuds. Bracteoles absent. Flowers about 7 mm long. Hypanthium more or less distinct. Calyx with 4 short lobes, the upper one retuse. Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long; wings obtuse; keel subfalcate. Upper filament loosely adhering to the other 9. Basal

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fenestrae distinct. Disk indistinct. Ovary hairy; ovules 5. Pod supposed to be dehiscent (Harms, 1923), apparently still unknown. Young pods flat, without wings. Ripe seeds unknown.

D i s t r i b u t i o n. One species on Margarita Island, Venezuela.

T a x o n o m y. Because of its distribution, this genus is usually compared with *Lonchocarpus*, from which it differs in the absence of bracteoles, the loosely adherent upper filament, the absence of basal callosities, and the supposedly dehiscent pod. The genus reminds me more of *Millettia*, where scaly buds occur in deciduous species; a discrete hypanthium is sometimes developed (both features in sect. *Podocarpae*), and the upper filament varies from adnate to free.

Margaritolobium differs from *Millettia* in the absence of bracteoles. Most critical characters are also shared by *Bergeronia* from Paraguay and N. Argentina, from which it differs in the shorter bracts, the more distinct hypanthium, the more falcate keel, the more adherent upper filament, and the more distinct basal fenestrae.

Millettia Pl. I—6; also as in II—13, III—16, 17 and IV—28

Millettia Wight & Arnott ("Milletia" auct.), Prodr. Fl. Pen. Ind. Or. 1 (1834) 263, *nom. cons. prop.* (Taxon 30, 1982, p. 327); B.H. 1: 498; F.B.I. 2: 104; E.P. 3: 270; Merr., Philipp. J. Sc. 5 (1910) 70; Dunn, J. Linn. Soc., Bot. 41 (1912) 123; F.G.I.-C.: 361; L.T.A.: 216; F. Cong. 5: 5; F.W.T.A.: 524; Gillett, Kew Bull. 15 (1961) 19; F. Java 1: 595; Hutch., Gen. 1: 377; F.T.E.A.: 122; A.L.S.: 257; L. Nod.: 435. — T y p e : *M. rubiginosa* W. & A.

Pongam Adanson, Fam. 2 (1763) 322, 593, *nom. rejic.* vs. *Pongamia* Vent., *nom. rejic. prop.* vs. *Millettia*. — *Galedupa* Lamarck, Enc. 2 (1788) 594, *nom. illeg.*; E.P. 3: 344; — *Pungamia* Lamarck, Tabl. Enc. (1796) t. 603, *nom. illeg.* — *Derris* sect. *Pongam* (Adans.) Bennett, J. Bomb. Nat. Hist. Soc. 68 (1972) 302. — T y p e : Rheede, Hort. Mal. 6 (1686) t. 3.

Pongamia Vent., Jard. Malm. (1803) t. 28, *nom. cons., nom. rejic. prop.* vs. *Millettia*; Benth., Syn. Dalb.: 115; B.H. 1: 549; F.B.I. 2: 239; F. Austr. 2: 273; Prain, J. As. Soc. Beng. 66 (1897) 94; F.G.I.-C 2: 441; F.M.P. 1: 593; Thothathri, Bull. Bot. Surv. India 3 (1961) 417; F. Java 1: 616; A.L.S.: 259; L. Nod.: 543. — T y p e : *P. glabra* Vent., *nom. illeg.* (=) *P. pinnata* (L.) Pierre.

Berrebera Hochstetter ("*Berebera*" auct.), Flora 27 (1844) 597 (valid publ.); Flora 29 (1846) 597 (descr.). — T y p e : *B. ferruginea* (Hochst.) Hochst.

Fornasinia Bertol., Nov. Comm. Acad. Sc. Inst. Bon. 9 (1849) 591, t. 1 (=Misc. Bot. 8, 1849, p. 18, t. 1). See note below. — T y p e : *F. ebenifera* Bertol.

Otosema Benth. in Miq., Pl. Jungh. (1852) 248, footnote. — T y p e : not designated.

Malaparius Rumph. ex Miq., Fl. Ind. Bat. 1 (1858) 1082. — T y p e : *M. flavus* Miq. (=) *Pongamia pinnata* (L.) Pierre.

Cajum O. Kuntze, Rev. Gen. 1 (1891) 167. — T y p e : *Cajum pinnatum* (L.) O. Kuntze (misinterpretation of *Caju* Rumph. = *Sindora*, see De Wit, Bull. Bot. Gard.Buitenz., Ser. III, vol 18, 1949, p. 8).

Lonchocarpus sect. *Caudaria* Dunn, Lond. J. Bot. 49 (1911) 15, see Polhill, Kew Bull. 25 (1971) 260. — T y p e : not designated.

Hesperothamnus T.S. Brandegee, Univ. Calif. Publ., Bot. 6 (1919) 499; T.S. Mex.: 484; N. Am. F.: 235; Hutch., Gen. 1: 430; A.L.S.: 257, 279; L. Nod.: 327. — T y p e : *H. littoralis* (T. S. Brandegee) T. S. Brandegee.

Selerothamnus Harms, Fedde Rep. 17 (1921) 325. — T y p e : not designated.

Shrubs, lianas, or trees. Leaflets 1—35 (or more?), (sub)opposite. Stipellae generally present. Flowers in axillary pseudoracemes, or these combined into terminal and/or

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axillary pseudopanicles. Brachyblasts usually rather thick cylindric with up to 8 (—10) flowers scattered mainly on the apical part, or wart-like, or, in some species, reduced to indistinct nodes with 2 flowers from the axils of 3 bracts, and then mixed with nodes with single flowers in a raceme-like inflorescence. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 10—26 mm long. Hypanthium generally indistinct or, in a few species, hollow (sect. *Podocarpae*). Calyx either truncate with 4 or 5 short lobes or teeth, or with 4 or 5 distinct, valvate, or very shortly imbricate lobes. Standard blade broadly ovate to obovate, reflexed at base; basal callosities present or absent. Wings and keel petals about equally long, both (sub)falcate, in a few species obtuse. Upper filament free or adnate to the other 9. Basal fenestrae generally distinct. Disk generally distinct, always indistinct in the species with a hollow hypanthium (sect. *Podocarpae*). Ovary hairy; ovules 1—7 (or more?). Pod tardily dehiscent, thin or thick woody, flat, or inflated only around the ellipsoid seeds, without wings or, in a few species, with 2 wing-like crests either at the upper suture, or at both sutures. Seeds generally flat, lens-shaped or quadrate, in a few species ellipsoid; radicle folded.

Distribution. About 90 species from Africa to Malesia, one species (the coastal species *Pongamia pinnata*) from India to N. Australia and the W. Pacific, in New Guinea and N. Australia also growing inland. About 5 species in California and in Mexico (see note on *Hesperothamnus*, below).

Nomenclature. **Pongamia.** As explained below, *Pongamia* is considered to belong taxonomically to *Millettia* sect. *Fragiliflorae*. The (complex) nomenclatural consequences are explained in the proposal to conserve *Millettia* over *Pongamia* (Geesink, Taxon 31, 1982, p. 327). The proposal has passed the Committee, but, with the closing of this manuscript, the homotypy of *Galedupa* Lamarck and *Pungamia* Lamarck was still doubted upon by one member of the Committee.

Fornasinia. Dunn (1912) listed *Fornasinia ebenifera* Bertoloni (described from "Aethiopia") in the "doubtful species", noting that the drawing left no doubt about the generic identity (i. e. *Millettia*), but that he could not place the drawing and description in any species known to him. The descriptions of both the genus *Fornasinia* and its single species are extensive and provided with a clear plate showing floral details and a pod with distinctly transversely elongated seeds with a rim-aril.

The description and the depicted pod and seeds are *Millettia*-like, but the panicle with the flowers laxly distributed reminded me of *Philenoptera*, particularly of the species generally known as *Lonchocarpus laxiflorus*. The standard, however, is described as adpressed-hairy, and the colour slides of the type specimens (BOLO), which were kindly sent by Prof. Cristofolini, showed that the standard is densely white sericeous. The slides also showed that the original plate was very accurate, and the species could be identified as *Millettia grandis* (E. Mey.) Skeels (synon. *M. caffra* Meisn.) from South Africa! According to Stearn (Botanical Latin, p. 215) "Aethiopia" was a general indication of Africa, particularly the part South of the Sahara desert, and this explained Bertoloni's indication "Habitat in Aethiopia calidiore in regione Caffrorum" (p. 589). Other details, e. g. the conspicuous scaly buds, and the depicted piece of durable wood

(an exceptional condition in *Millettia s.s.*) agree with this S. African species. Fortunately the epithet *grandis* is older than *ebenifera*, so that this common S. African species needs not to be renamed.

Taxonomy. **Pongamia.** Because of the overestimation of the character dehiscence/ indehiscence of the pods, *Pongamia* and *Millettia* have always been placed in different tribes, *Dalbergieae* and *Galegeae* (*Millettieae, Tephrosieae*) respectively, the distinction between which was exclusively based on this character since Bentham (1860). After the redefinition of the tribe *Dalbergieae* and the transfer of its subtribe *Lonchocarpinae* to the *Millettieae* (as *"Tephrosieae"*) by Polhill (1977) the genera came finally together (again). The resemblance between *Pongamia* and certain species of *Millettia* was already noticed earlier (Bentham, 1852; Miquel, 1855).

Corner (1940, pp. 372 & 375) noted that (in flowering stage) *Pongamia pinnata* is easily confused with *Millettia hemsleyana* (a synonym of the continental Asiatic and W.-Malesian species *M. xylocarpa*). Unaware of Corner's note I reached the same conclusion in 1976 and proposed (in litt. to B. Krukoff & R. M. Polhill) to transfer a part of *Millettia* (corresponding with Bentham's genus *Otosema*) to *Pongamia*. This proposal was received without much enthusiasm, to put it mildly, but later investigation on the delimitation and content of the *Millettia xylocarpa*-complex carried out by G. Thijsse and Ingrid de Kort (two students following a course in 1980) confirmed this idea, which finally led to my decision to unite them and to the proposal to conserve *Millettia* over *Pongamia*.

Taxonomically, *Pongamia pinnata* belongs to *Millettia* sect. *Fragiliflorae*, characterized by lax, pulvinate, axillary pseudoracemes with the upper flowers singly and scattered but the lower ones on reduced brachyblasts, consisting of a small node with two (rarely three) flowers from the axils of three (resp. four) bracts. The flowerbuds are "closed" with a small opening which later develops into a subentire calyx with 4 or 5 short lobes. The buds are curved, forming a sharp angle with the pedicel. The most striking character of this section is the pulvinate base of the pseudoraceme, similar to the pulvinus of the leaf rachis. In *Pongamia pinnata* the indehiscence of the fruit is probably a specific adaptation to the coastal habitat. The pods can be transported by sea water, but the germination of the seed (during which the pod dehisces along its sutures!) takes place in fresh water, viz. in the *Barringtonia*-zone slightly higher up the beach (Schimper, 1891, pp. 71—77; Van Steenis, 1965, p. (9), and pers. obs.).

Locally, *Pongamia pinnata* occurs in inland localities as well (e. g. in New Guinea and in N. Australia) and is sometimes also planted. Some collections from Borneo were impossible to identify, and may belong to either *Pongamia pinnata* or *M. xylocarpa* (the number of ovules is discriminating but overlapping, like other characters as flower size and hairiness of the leaves) which illustrates the close resemblance. Also pollen characters (Hazelhorst, in prep.) and chemical characters (see chapter 4) confirmed the mutual similarity.

Bennet (1972) noted the similarity of the pod of *Pongamia pinnata* with certain species of *Derris* (especially *D. cuneifolia,* but it is even more distinct in *D. malaccensis* var. *aptera*) and he transferred *Pongamia* to *Derris*. He did not include it in sect.

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Paraderris, which would have been logical from his reasoning but he established a new monotypic section *Pongam* under *Derris*. On account of the more distinct similarity with *Millettia* sect. *Fragiliflorae* and the adaptive morphology of the pod (which is suspect for parallel origin) I disagree with Bennet's transfer to *Derris*.

Otosema. Bentham (1852, p. 248, footnote) divided the then known species of *Millettia* over two genera, thereby proposing *Otosema* as a new one. *Otosema* was characterized, according to Bentham, by the presence of basal callosities on the standard blade, combined with the upper filament which he thought to be adnate to the other nine, but the reality appeared later to be more complex. In 1865, he noted that the upper filament is "plus minus" adnate, and suggested to reduce *Otosema* to sectional rank. Baker (1876, p. 108) followed this suggestion more or less and reduced it to subgeneric rank. Dunn (1912) did not distinguish subgenera and mentioned *Otosema* merely in historical perspective, probably aware that its distinction could only be made on account of the presence of basal callosities. As explained in chapter 4, this is a "functional" character and therefore very likely to be of para- if not even of polyphyletic origin. It is not correlated with other characters, and therefore, though after hesitation, I decided not to follow Bentham's distinction of *Otosema* in his circumscription.

The complexity of the free/adnate upper filament is extensively reflected upon by Gillett (1961, pp. 37—39). He discovered that this character is variable within a species and develops in several species in an unexpected way. Normally the free upper filament is free from the other nine from the initial stages onwards and remains so. But in several species listed by him it becomes adherent or adnate after the staminal tube is already several millimeters long. In various Asiatic species I found the striking combination of a free upper filament with the presence of basal fenestrae, combined or not with the presence of basal callosities on the standard. This variable attachment of the upper filament may be a unique feature in *Millettia*, but renders its use as a discriminating generic character impossible.

Millettia sect. Podocarpae. The Indo-Chinese section *Podocarpae* consists of a few deciduous species with conspicuously large, subglobose scaly buds, seemingly true racemes (with occasionally two flowers placed close together) from the axils of scars of the leaves of the previous year (or wet season). The pedicel bears no bracteoles and the receptacle is hollow, thus forming a small but distinct hypanthium. The above mentioned characters of inflorescence and flowers are characteristic for the mainly American tribe *Robinieae,* and initially I was inclined to raise the sect. *Podocarpae* to generic rank and transfer it to the *Robinieae.* But in the excellent and rich collections made by Poilane in Indo-China (mainly at P), a few specimens were found with inflorescences young enough to show that between the occasional paired flowers a dormant, soon-caducous bud is present, indicating that the node bears a strongly reduced brachyblast and that the structure is similar to the pseudoraceme in sect. *Fragiliflorae.* Scars of bracteoles were also found on young pedicels. The conspicuous buds covered with scales are also present in *Millettia* sections *Compresso-gemmatae* and *Fragiliflorae,* and this leaves the presence of a small but distinct hypanthium as the only distinguishing character. This character is a bit doubtful to apply as several species of

Millettia, Callerya, Lonchocarpus, and *Paraderris* also have an enlarged receptacle, sometimes provided with a distinct disk. In conclusion, there is no reason to separate the section from *Millettia*, but the combination of the above mentioned characters renders it a distinct group with similarity to certain *Robinieae* (especially the genus *Gliricidia*).

Lonchocarpus sect. **Caudaria**. This section was originally described by Dunn (1911-c), characterized by long, "tail-like" inflorescences with distinct brachyblasts. Dunn referred the section to *Lonchocarpus* on account of the indehiscent pods. The group is, however, rather unique in *Lonchocarpus*. The other African group generally referred to *Lonchocarpus* is *Philenoptera* with paniculate inflorescences, and the group referred to *Lonchocarpus* with distinct and similar brachyblasts is subg. *Phacelanthus* (sect. *Fasciculati*), here merged with American *Derris* in the genus *Deguelia*. Polhill (1971, p. 260) has transferred section *Caudaria* to *Millettia* on account of the occasionally dehiscent pods with "quadrate" seeds (a character which seems to hold for African *Millettia*, but only for some Asiatic ones), and because the group does not fit in the combination of other characters in any group he reckoned to *Lonchocarpus*. In conclusion I agree with this transfer.

The reasons to keep the paniculate species of **Millettia** apart as a genus, are discussed under *Callerya*.

Hesperothamnus. This genus, occurring in California and in Mexico with about 5 species, and later described independently as *Selerothamnus* by Harms, is in no single morphological character different from *Millettia*, not even from sect. *Millettia*. In my 1981 paper, I wrongly noted the presence of basal callosities on the standard blade (as "inflexed auricles"). The question whether *Hesperothamnus* really may have originated from Afro-Asiatic *Millettia* allies cannot be answered. The impossibility to find any character or combination of characters in which it differs from *Millettia* shows at least the close genetic similarity.

In the seeds of one species, Evans (pers. comm.) traced 2-amino-imidazole, while he found gamma-hydroxy-homoarginine in *Millettia*. Also according to Evans the foundation of a genus solely on account of this character combined with its geography is too speculative.

Therefore, I cannot but regard *Hesperothamnus* as the American representatives of *Millettia*, sect. *Millettia*. The group differs from *Lonchocarpus* in the thick brachyblasts with more than 3 (scattered) flowers, together with stipellate leaflets and dehiscent pods; from *Deguelia* in the erect habit, the stipellate leaflets, and dehiscent pods.

Mundulea   Pl. III—29; also as Pl. III—31

Mundulea (DC.) Benth. in Miq., Pl. Jungh. (1852) 248; B.H. 1: 497; F.B.I. 2: 110; E.P. 3: 270; L.T.A.: 216; F.W.T.A.: 527; Hutch., Gen. 1: 395; F.T.E.A.:155; A.L.S.: 258; L. Nod.: 450. — *Tephrosia* sect. *Mundulea* DC., Prodr. 2 (1825) 249. — Type: *M. sericea* (Willd.) A. Chev.

Shrubs or treelets. Leaflets 5—31 (or more?), (sub)opposite. Stipellae absent. Nerves as in *Tephrosia,* except in *M. sericea* with herbaceous leaves and S-shaped nerves. Flowers in terminal pseudoracemes, in some species combined with axillary

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ones. Brachyblasts warty with up to 4 flowers. Bracts shorter than the corresponding flowerbuds. Bracteoles absent. Flowers 12—26 mm long. Hypanthium indistinct. Calyx usually truncate with 4 short lobes, the upper one 2-topped, in some species the lobes acuminate. Standard blade elliptic to orbicular, reflexed at base; basal callosities present. Wings and keel petals about equally long; wings straight, usually obtuse; keel falcate. Filaments dilated at apex. Upper filament adnate to the other 9; basal fenestrae distinct. Disk indistinct. Ovary hairy; ovules 6—10 (or more?). Style short, strongly recurved. Pod dehiscent, thin woody, flat, convex around the seeds, without wings, sutures thickened. Seeds 4—8, ellipsoid; radicle folded.

Distribution. About 15 species in Madagascar, one of which (*M. sericea*) extends to Africa, India, and Sri Lanka (elsewhere cultivated), and one species in South Africa.

Taxonomy. *Mundulea* is strikingly similar to *Tephrosia*, differing only in the apically dilated filaments, the short, recurved style, and the tendency to have more elongated flowers and in some chemical tendencies (see Basu, 1976). The most commonly known species, *M. sericea* (syn.: *M. suberosa*) has herbaceous, *Millettia*-like leaflets, which is the most probable explanation for the often made conclusion that *Mundulea* is "intermediate between *Tephrosia* and *Millettia*". All other species, how-ever, have more xeromorphic, *Tephrosia*-like leaflets. Two species, posthumously published from manuscripts of R. Viguier (1950) should be removed from *Mundulea*, viz. *M. phylloxylon*, which is a true *Phylloxylon* (tribe *Indigofereae*) with biramous hairs, and *M. pungens*, a shrub with spinose stipules, terete filaments and an elongated style, which is probably a true *Tephrosia*. As repeated in a note under *Tephrosia*, a judgement whether *Mundulea* deserves generic rank or a lower one (then as subgenus or section under *Tephrosia*) depends on the relation with eventual subdivisions still to be made within *Tephrosia*, and with the other satellite genera mentioned under *Tephrosia*.

Uses. According to Greenway (1936) the powdered bark of *Mundulea sericea* contains very active (and even dangerous) fish poisons, recorded to be more toxic than the isoflavonoids of *Paraderris* (*Derris elliptica*, *D. cuneifolia*) and *Lonchocarpus nicou*. Recent chemical investigations (Basu, 1976, Gomes et al., 1981) have elucidated the chemical structure of the various components.

Neodunnia   Pl. III—15

Neodunnia R. Viguier, Notul. Syst. 14 (1950) 72; A.L.S.: 258; L. Nod.: 456. — T y p e : *N. atrocyanea* R. Vig.
    (Lectotype by Allen & Allen, L. Nod.)

Deciduous treelets or shrubs with globose scaly buds. Leaflets 11—21, (sub)oppo-site. Stipellae absent. *Flowers seemingly 2—8 together, but in fact single from the axils of bud scales and from the lowermost leaves of a just sprouted axillary bud* (which develops further as a vegetative branch). Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flower 11—15 mm long. Hypanthium indistinct. Calyx 4-toothed,

the upper tooth 2-topped. Standard blade about orbicular, reflexed at base; basal callosities distinct. Wings and keel petals about equally long; wings obtuse; keel falcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk indistinct. Ovary hairy; ovules 6—9 (or more?). Pod dehiscent, thin or thick woody, flat, without wings. Seeds flat, lens-shaped; radicle folded (only young seeds observed).

Distribution. Five species in Madagascar.

Taxonomy. In habit, both in flower and in fruit the plants resemble *Millettia*, and Peltier (pers. comm.) felt inclined to regard this genus as a section of *Millettia*. The inflorescence, however, is different from any inflorescence known in *Millettia*, and therefore I prefer to keep *Neodunnia* separate.

Ostryocarpus   Pl. V—40, 41, 44; also as Pl. II—13

Ostryocarpus Hook., *f.* in Hook. Niger Fl. (1849) 316; Benth., Syn. Dalb.: 85; B.H. 1: 548; E.P. 3: 343; Nachtr. 4: 144; L.T.A.: 546; F. Cong. 6: 13; Hutch., Gen. 1: 382; A.L.S.: 259; L. Nod.: 476. — Type: *O. riparius* Hook. *f.*

Aganope Miquel, Fl. Ind. Bat. 1 (1855) 151; Polhill, Kew Bull. 25, 2 (1971) 266; A.L.S.: 254. — *Derris* sect. *Aganope* (Miq.) Benth., Syn. Dalb.: 103; B.H. 1: 549; Thothathri, Bull. Bot. Surv. India 3,2 (1961) 175. — *Derris* subg. *Aganope* (Miq.) Kurz, J. As. Soc. Beng. 45, 2 (1876) 277. — *Deguelia* sect. *Aganope* (Miq.) Taubert, in E.P. 3,3: 345. — Lectotype: *A. floribunda* Miq. (= *A. thyrsiflora* (Benth.) Polhill).

Ostryoderris Dunn, Bull. Misc. Inf. Kew (1911) 363; E.P. Nachtr. 4: 144; L.T.A.: 561; F.W.T.A.: 521; F Cong. 6: 48—52; L. Nod.: 477.— Lectotype: *O. impressa* Dunn.

Xeroderris Roberty, Bull. Inst. Fr.-Afr. Noire, Sér. A, 16 (1954) 353; Mendonça & Sousa, Bol. Soc. Brot., Sér. 2, 42 (1969) 831; F.T.E.A.: 91; L. Nod.: 699. — Type: *X. chevalieri* (Dunn) Roberty.

Lianas. Leaflets 7—11, (sub)opposite. Stipellae present or absent. Flowers in terminal and/or axillary panicles. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 10—15 mm long. Hypanthium indistinct. Calyx with 5 short lobes or teeth, usually truncate. Standard blade broadly ovate to orbicular, reflexed at base; basal callosities absent, present in *Xeroderris stuhlmannii*. Wings hardly adnate to the keel, about as long as the keel, both usually obtuse; keel slightly falcate in *Aganope heptaphylla* and *A. leucobotrya*. Upper filament free or only adnate at base to the other 9. Basal fenestrae absent. Disk present. Ovary hairy; ovules 4—10. Pod indehiscent, flat, thin leathery, distinctly reticulately nerved outside; upper or both sutures with a longitudinal wing (but absent in species referred to *Ostryocarpus s. s.*). Seeds generally 1—6, laterally flattened, longitudinally or transversely elongate; radicle straight in mature seeds, but in some species (at least in *Aganope leucobotrya*) folded in young seeds.

Distribution. Six species from tropical Africa to S. E. Asia, throughout Malesia.

Taxonomy. The genus, as here conceived, consists of *Derris* sect. *Aganope* from tropical Asia, and of the African genera *Ostryoderris, Ostryocarpus*, and *Xeroderris*. The group is characterized by truly paniculate inflorescences, usually free wing-petals,

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and generally *Derris*-like pods, i. e. indehiscent, rather thin and with longitudinal wings along both sutures. Some species have less distinct wings (i. e. *Aganope heptaphylla,* generally known as *Derris sinuata,* and *Ostryocarpus s. s.*). Because of the more free wing-petals the genus is transitional between *Dalbergieae* and *Millettieae*, but the group has pluriseriate woodrays (Baretta-Kuipers, 1981) (also in *Ostryocarpus s. s.,* Ter Welle, pers. comm.) and the fruit is so similar to that of *Derris* sect. *Dipteroderris*, that I consider *Ostryocarpus* more similar to *Derris* than to any group of *Dalbergieae*.

The distinction from *Callerya* is very weak. *Callerya* has the wing-petals more firmly adherent to the keel, and lacks longitudinal wings along the suture(s) of the pod. When flowering, the similarity in general habit is more striking than the differences. *Ostryocarpus* and *Callerya* share primitive characters, viz. truly paniculate inflorescences and the lack of canavanine and other free amino-acids or amines (Evans, 1984). *Kunstleria* and *Spatholobus* (*Phaseoleae*) also lack these compounds; their relation is discussed under *Kunstleria*.

Xeroderris, here considered congeneric with *Ostryocarpus*, represents a single species occurring in semi-arid areas (savannahs in tropical Africa). It has seasonal leaf-shedding as well as two basal callosities on the standard. On account of this combination of characters one may regard *Xeroderris* generically different (but then as a "minimal" taxon), but I prefer to regard it as a species adapted to a habitat drier than that of the remaining species. This treatment is consistent with my decision not to keep *Padbruggea* and *Whitfordiodendron* separate only on account of the presence of basal callosities.

Paraderris   Pl. II—13, V—39

Paraderris (Miq.) Geesink, *gen. nov., stat. nov.*; *Derris* sect. *Paraderris* Miq., Fl. Ind. Bat. 1 (1855) 145;
   Benth., Syn. Dalb.: 111; B.H. 1: 549; Thothathri, Bull. Bot. Surv. India 3,2 (1961) 190; A.L.S.: 256;
   Thothathri, Fasc. Fl. India 8 (1982) 3. — *Deguelia* sect. *Paradeguelia* Taubert, in E. P. 3: 345, *nom. illeg.*
   — Lectotype (proposed here): *Paraderris cuneifolia* (Benth.) Geesink, *comb. nov.* (basionym:
   Derris cuneifolia Benth. in Miq., Pl. Jungh., 1852, p. 253, see note on nomenclature below).

Lianas. Leaflets 5—19, opposite, often obovate. Stipellae absent, occasionally present but then much reduced. Flowers in axillary pseudoracemes, less often aggregated into pseudopanicles. Brachyblasts rather thin with (1 or) 2 or 3 (—5) flowers on their apex, with as many bracts at their bases. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 10—25 mm long. Hypanthium distinct, *flat.* Calyx with 5 short lobes. Standard blade elliptic to orbicular, reflexed at base; basal callosities distinct and large (but absent in *Derris luhaiensis*). Wings and keel petals about equally long; obtuse to subfalcate. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk distinct, *flat to slightly hollow, saucer-shaped.* Ovary hairy; ovules 1—7. Pod indehiscent, leathery to thick woody; either both sutures with a longitudinal wing or only the upper suture winged, or (in some specimens of *D. malaccensis*) without wings. Seeds 1—3, lens-shaped; radicle folded.

Distribution. About six species (or less, depending on the taxonomy of the *P. cuneifolia*-group) from India to New Guinea, not in Australia, not in the Pacific. *Derris*

elliptica is widely cultivated in various tropical countries for the insecticidal isoflavonoid rotenone, mainly obtained from ground roots.

Nomenclature. In Miquel's original publication of the section *Paraderris* he mentioned two species, *D. cuneifolia* and *D. montana*, both earlier described by Bentham. As far as I am aware, lectotypification has not been proposed earlier. A preliminary investigation, carried out by four students, revealed that both original species probably belong to a complex with more names involved. Therefore I choose the best known of the two names as the lectotype. It will, most probably, after future confirmation of the students' investigation, also turn out to be the oldest epithet in the complex. In its original publication, however, it seems as if *D. cuneifolia* was super-fluous when published, as it contained the validly published *Galedupa marginata* [Wall., Cat. 5896] Roxb. (Fl. Ind. III, 1832, p. 241) in the synonymy. On the previous page, however, Bentham proposed another, heterotypic, new combination *Derris marginata* (Roxb.) Bentham, based upon *Dalbergia marginata* Roxb. (also Fl. Ind. III, 1832, p. 241). Unfortunately, this page reference is an error; on p. 241 the heterotypic *Galedupa marginata* is described, and the correct page number is *230*. This error is repeated in Bentham's Synopsis Dalbergieae (1860) and may cause some confusion.

Taxonomy. *Paraderris* is generally considered to be a distinct section of *Derris* in a wider sense. The reasons to regard it separate on generic rank are given in chapter 7. Resemblances are most obvious with *Derris* (*s.s.*) in fruiting stage, and with *Lonchocarpus* (*s.s.*) when flowering. It differs from *Derris* (*s.s.*) by the inflorescences with the flowers on top of a common pedicel, the larger flowers (though with over-lapping size ranges), the large basal callosities of the standard (but absent in one species) and in the relatively large, saucer-shaped disk. It differs from *Lonchocarpus* in the climbing habit, winged pods (absent in some specimens of *D. malaccensis*) and in the saucer-shaped disk, combined with the geographical distribution. *Paraderris* has a distinct characteristic "overall impression", mainly determined by the regular distance between the jugae, the usually obovate leaflets, and the rather long inflorescences with relatively large flowers (in most species). This is probably the reason why flowering specimens are often pre-identified as *Millettia*, from which genus it differs in the inflorescence structure and in the pods (but see the notes under *Millettia*).

Philenoptera   Pl. IV—32, also as in Pl. IV—24

Philenoptera [Fenzl, Flora 27 (1844) 312, *nom. nud.*; Roberty, Bull. Inst. Fr. Afr. Noire sér. A, 16,2 (1954) 354.] A. Richard, Tent. Fl. Abyss. 1 (1847) 232. — Type: *P. schimperi* A. Rich.
Lonchocarpus sect. *Paniculati* Bentham, J. Proc. Linn. Soc. 4, Suppl. (1860) 87, 96; F. Bras.: 283; E.P. 3: 347; L.T.A.: 547—552; F. Cong. 6: 5—13; F.W.T.A.: 522—524; Polhill, Kew Bull. 25 (1971) 259—263; F.T.E.A.: 65—73; A.L.S.: 257. — Lectotype (proposed here, see note below): *Lonchocarpus philenoptera* Benth.
Capassa Klotzsch in Peters, Naturw. Reise Mossamb., Bot. 1 (1861) 27, t. 5; Mendonça & Sousa, Webbia 19 (1965) 831—836: Sousa, Consp. Fl. Ang. 3 (1966) 367. — Type: *C. violacea* Klotzsch.

Shrubs, small trees, or lianas (few species). Leaflets (1 or 3—) 5—15, (sub)opposite.

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Stipellae usually present. Flowers in terminal and/or axillary panicles. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 8—15 mm long. Hypanthium indistinct. Calyx with 4 lobes, the upper one 2-topped, in some species with 4 or 5 subulate, teeth. Standard blade broadly ovate to orbicular, reflexed at base; basal callosities indistinct or absent. Wings and keel petals about equally long, both usually obtuse; keel slightly falcate in some species. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk present. Ovary hairy, ovules 4—8. Pod indehiscent, flat, papery to coriaceous; sutures slightly thickened, in one species the upper suture with a distinct longitudinal wing. Seeds 1—4 (—8), laterally flattened, often transversely elongate; radicle folded.

Distribution. About 15 species in tropical Africa, and possibly 4 species in S. America, see note below.

Nomenclature. 1. Lectotypification of *Lonchocarpus* sect. *Paniculati*. Apparently this section was not typified on an earlier occasion. Bentham most probably intended to reduce Richard's and Fenzl's genus *Philenoptera* to sectional rank, and therefore typification with Bentham's species *L. philenoptera* seems most appropriate. The name itself, however, is superfluous, as it contains *Philenoptera schimperi* (*"schimperiana"*) in the synonymy and thus it is illegitimate. The species description is apparently based on (see F.T.E.A.: 67, 68, and preceding discussions by Mendonça & Sousa, l.c. and Polhill, l.c.) the flowers of a species, one year later validly described as *Capassa violacea* Klotzsch, combined with the fruits of *Lonchocarpus laxiflorus* Guill. & Perr. As both elements are involved in another taxonomic controversy discussed below, viz. the separation of the genus *Capassa* Klotzsch, I initially preferred to lectotypify Bentham's section with an apparently unproblematical name and species (e.g. *L. cyanescens* Benth.), but this would only allow some nomenclatural freedom on sectional (eventually subgeneric, see below) level, because on generic level *Philenoptera* Rich. is typified by *P. schimperi* Rich., which is a synonym of *Lonchocarpus laxiflorus* Guill. & Perr.! I think lectotypification should be done in accordance with Bentham's intention, and therefore I herewith designate *L. philenoptera* Benth. (*nom. illeg.*), and more precisely, the element *Philenoptera schimperi* Rich. (cited by Bentham as *"Philenoptera schimperiana* Hochst., Pl. Schimp. exs., et A. Rich. Fl. Abyssin. i. p. 232") as the lectotype. This element (species) is sometimes cited as *P. schimperi* (or *"schimperiana"*) Hochst. in (or "ex") Rich. Hochstetter distributed exsiccatae, with a provisional name, but without a description.

2. Pittier (1917, p. 45) proposed to raise Bentham's sections *Paniculati* and *Fasciculati* to subgeneric rank. He did so in accordance with the nomenclatural rules (as far as applicable to 1917) for the latter section, proposing an actual name (combination) for it, but for section *Paniculati* he made a suggestion. This cannot be considered a valid publication of the same name in subgeneric rank, and I left it out of the formal synonymy.

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3. Unfortunately, Pittier (1917) named a section of the American genus *Lonchocarpus s. s.* (his subgenus "Eulonchocarpus") *Philenopteri*. This section consists of American species with the flowers paired on top of a common pedicel, and it should not be confused with the paniculately flowered genus *Philenoptera*.

Taxonomy. 1. The question whether the species, generally known as *Lonchocarpus capassa* Rolfe, belongs either to this group (genus *Philenoptera* or section *Paniculati*), or to *Derris s. l.* (Harms, 1902, 1915), or represents a separate monotypic genus *Capassa* is extensively discussed by Mendonça & Sousa (1965) and Polhill (1971). I agree with Polhill's conclusion that the similarities with *L. laxiflorus* are too conspicuous to justify separation *only* on account of the winged upper suture of the pod.

2. *Philenoptera* is the "most primitive" group in a wider conceived genus *Lonchocarpus* (inclusion on account of similar pods). *Philenoptera* is here considered rather "central" in the *Millettia (s. l.) -Derris (s. l.) -Lonchocarpus (s. l.)*-complex, as it shows connections to all groups distinguished in this complex (see chapters 6 and 7). It differs in but a few characters from the groups generally believed to represent the "most primitive" subgroups of *Derris s. l.* and *Millettia s. l.*, viz. the genera (as here conceived) *Ostryocarpus* and *Callerya* resp. It differs from *Ostryocarpus* in the habit (shrubs or small trees vs. lianas), the distinct calyx lobes, the adnate vexillary filament, and in the generally wingless pod. It differs from the Àsiatic genus *Callerya* partly in the habit, the distinct calyx lobes, the adnate upper filament, in the indehiscent pod, and in a few characters with a polythetic distribution. *Philenoptera* species are often confused with *Millettia (s. s.)* species, but they differ in the paniculate inflorescences with the flowers single (vs. variously fascicled) in the axil of a bract, and in the indehiscent pods. The reasons to keep the group separate on genus level are complicated, as discussed in chapter 7, and in the following note.

3. Bentham (1860, also in F. Bras.) listed *Lonchocarpus praecox* under his section *Paniculati*. Furthermore, he described the other American species *Lonchocarpus araripensis* and *L. subglaucescens* (both in a series belonging to *Lonchocarpus s. s.* (his sect. *"Eulonchocarpus"*) also with true panicles. Mrs. Azavedo-Tozzi (pers. comm.) brought to my attention that *L. muehlbergianus* also has true panicles.

As already discussed in chapter 6, the opposite insertion of the basal two flowers in the partial inflorescences of the last mentioned species can be considered an indication that the raceme-like partial inflorescence is derived from an originally biflorous condition, but in the other three species all flowers are alternate (the lowermost two sometimes subopposite). *L. araripensis* and *L. subglaucescens* have punctate leaves, indicating membership of the section *Punctati* of *Lonchocarpus s. s.*

Lonchocarpus praecox does not show obvious characters which link it distinctly to species belonging to *Lonchocarpus s. s.*, and therefore Bentham (1860) considered it to be the only American representative of his sect. *Paniculati*. All mentioned American species, however, lack stipellae and possess reduced calyx lobes, both uncommon

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features in the African *Philenoptera* (and there not in combination). This transitional morphological situation is either due to close relationship or to convergence. *Philenoptera* species accumulate canavinine (see chapter 4) in the seeds, which is not recorded in *Lonchocarpus s. s.*, but the four species mentioned above are not (yet) tested for it.

The only (weak) reasons for which I keep *Philenoptera* separate at generic level are: *a.* that it can be keyed out; *b.* that it forms a geographically isolated group (when the disturbing four species mentioned above are kept in *Lonchocarpus s. s.*), and *c.* that merging will cause the necessary further merging of several related groups in order to maintain some kind of consistency of the proposed system, as is explained in chapter 7. In the scope of the present study this unsatisfactory situation cannot be solved. Revision and comparison at species level is necessary and fortunately in progress, being carried out by Mrs. Azavedo-Tozzi in the framework of her revision of the Brazilian species of *Lonchocarpus* and related groups.

Piscidia   Pl. I—3

Piscidia L., Syst. Nat., ed. 10 (1759) 1151, 1155, 1376, *nom. cons.*; Benth., Syn. Dalb.: 116; B.H. 1: 550; E.P.
    3: 345; Léon & Alain, Fl. Cuba 2 (1951) 333; F. Pan.: 35; Hutch., Gen. 1: 384; Rudd, Phytologia 18
    (1969) 473; A.L.S.: 259, 279; L. Nod.: 525. — *Ichthyomethia* P. Browne, Civ. Nat. Hist. Jam. (1756)
    296, *nom. rejic.*; T.S. Mex.: 510. — *Piscipula* Loefl., Iter Hisp. (1758) 275. — Type: *P. erythrina* L.,
    nom. illeg. (= *P. piscipula* (L.) Sargent, *Erythrina piscipula* L. 1753).
Canizaresia Britton, Mem. Torr. Bot. Cl. 16 (1920) 69. — Type: *C. cubensis* (Urban) Britton (=*Piscidia
    cubensis* Urban).

Trees. Leaflets 5—27, (sub)opposite. Stipellae absent. Flowers in axillary panicles or in pseudoracemes. Brachyblasts (when present) rather thin, with up to 10 closely placed flower(bud)s. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 12—18 mm long. Hypanthium distinct (in all species?). Calyx with 4 distinct lobes; the upper lobe with 2 more rounded apices. Standard blade about orbicular, reflexed about halfway the blade. Basal callosities indistinct. Wings and keel petals subfalcate, about equally long, with relatively long claws. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk absent. Ovary hairy, *with 2 longitudinal ridges at either side*; ovules 8—10 (or more?). Pod indehiscent; body rather woody, laterally slightly flattened; *wings 4, broad, pairwise inserted nearby but distant from both "sutures"*. Seeds laterally flattened, reniform or lens-shaped; radicle folded.

Distribution. Seven species with a few varieties, in Central America, extending to the West Indies and one species also in Florida.

Nomenclature. The nomenclatural history of the genus name and of all species is extensively discussed by Rudd (l. c.).

Taxonomy. Bentham (1860) considered *Piscidia* distinct from *Lonchocarpus* exclusively on account of the broadly 4-winged pod, and he maintained the genus on the same arguments of "convenience" as he also maintained e. g. *Muellera*. These cases are,

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however, different: *Muellera* can be assigned to a subgroup of *Lonchocarpus* (see under *Lonchocarpus s.s.*), but *Piscidia* would (in case of reduction) form a subgroup on its own. *Piscidia* has axillary panicles, the lateral branches of which are in some species contracted into more-flowered brachyblasts, while in *Lonchocarpus* the brachyblasts have either two apical flowers or are (secondarily?) replaced by branches with distant flowers (in four species only). The hypanthium in *Piscidia* was distinct in the (3) species I studied and I never observed a hypanthium in *Lonchocarpus s.s.* In *Piscidia* the standard reflexes halfway the blade, but in *Lonchocarpus* it does so at the base. This means that *Piscidia* is distinguishable in both flowering and in fruiting stages and on account of more than one character.

Platycyamus   Pl. V—34

Platycyamus Bentham, in Martius, Fl. Bras. 15,1 (1862) 323; B.H. 1: 531; E.P. 3: 363; Hutch., Gen. 1: 446; A.L.S.: 259; L. Nod.: 533. — Type: *P. regnellii* Benth.

Trees. Leaflets 3—11, (sub)opposite. Stipellae present. Flowers in terminal panicles. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Hypanthium indistinct. Calyx with 4 distinct lobes, the upper one 2-topped. Flowers 15—25 mm long. Standard about orbicular, reflexed at base; basal callosities absent. Wings and keel petals subfalcate, the keel more falcate, and in dried flowers (after boiling) the wings free from the keel. Upper filament free from the other 9. Basal fenestrae indistinct. Disk distinct, consisting of 10 nearly free nectaries. Ovary hairy, ovules 4. Pod indehiscent (always?), flat, thin woody, with the upper suture distinctly longitudinally winged, the lower suture indistinctly winged. Seeds 2 or 3, reniform, laterally flattened; radicle folded.

Distribution. Two species: *P. regnellii* in Brazil, and *P. ulei* in Peru.

Taxonomy. The genus is sometimes placed in the tribe *Phaseoleae*, because of the trifoliolate leaves in *P. regnellii*. In this species the basiscopic side of the lateral leaflets is often enlarged as in many *Phaseoleae*. The other species has 4 or 5 pairs of lateral leaflets which are almost symmetric. The pods are similar to those of *Derris* and *Craspedolobium*.

Platysepalum   Pl. III—17, 18

Platysepalum Welw. ex J. G. Baker in Oliver, Fl. Trop. Afr. 2 (1871) 131; E.P. 3: 272; Nachtr. 4: 137; L.T.A.: 251; F. Cong. 5: 63; F.W.T.A.: 524; Hutch., Gen. 1: 376; F.T.E.A.: 120; A.L.S.: 259; L. Nod.: 536. — Type: *P. violaceum* Welw. ex J. G. Baker.

Trees, or shrubs, or lianas. Leaflets 5—17, (sub)opposite. Stipellae present. Flowers in terminal pseudoracemes or in terminal pseudopanicles. Brachyblasts warty with up to 5 (or more?) flowerbuds. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers 13—30 mm long. Hypanthium indistinct. *Calyx with 2 broadly expanded, rounded upper lobes* and 3 elongated, acute lower lobes. Standard

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broadly cordate, reflexed at base; *basal callosities forming a continuous ridge along the distal part of the claw.* Wings and keel petals strongly falcate with obtuse apex. Upper filament free from the other 9. Basal fenestrae distinct. Disk distinct, 10-lobed. Ovary hairy; ovules 5 or 6. Pod tardily dehiscent, rather thick woody, flat, without wings; sutures distinctly thickened. Seeds 3—5, lens-shaped; radicle folded.

Distribution. About 12 species in tropical Africa, most species in West tropical Africa.

Taxonomy. This genus could easily be considered to be a section of *Millettia*, of which it differs in the enlarged upper calyx lobes, and in the peculiar shape of the basal callosities of the standard, similar as in *Wisteria*. It seems more convenient to continue generic separation.

Pongamiopsis   pl. I—1

Pongamiopsis R. Viguier, Notul. Syst. 14 (1950) 74; A.L.S.: 259. — Type: *P. amygdalina* (Baill.) R. Viguier (lectotype, proposed here).

Deciduous treelets with globose scaly buds. Leaflets 9—11, (sub)opposite. Stipellae absent. Flowers in rather short, axillary pseudoracemes with most flowers single from 1 bract, some nodes with 2 flowers from 3 bracts; the lowermost flowers from bud scales. Bracts shorter than the corresponding flowerbuds. Flowers 12—15 mm long. Bracteoles present. Hypanthium indistinct. Calyx 4-lobed, the upper lobe 2-topped. Standard blade about orbicular, reflexed at base; basal callosities absent. Wings and keel petals about equally long, obtuse. Upper filament adnate to the other 9. Basal fenestrae distinct. Disk indistinct. Ovary hairy; ovules 8—10. Pod indehiscent, woody (in *P. amygdalina*) or coriaceous (in *P. pervilleana*), inflated around the seed(s), without wings. Seeds 1 (rarely 2), subglobose; radicle folded.

Distribution. Two species in Madagascar.

Taxonomy. *P. amygdalina* was originally described in *Millettia*, from which it differs in the shorter pseudoracemes with even some flowers from the axils of bud scales, and in the discrepancy in the numbers of ovules and seeds. *P. pervilleana* was originally described in *Diphaca* (*Aeschynomeneae*, synonym of *Ormocarpum*), from which it differs in the indistinct hypanthium, and the 1- (or 2-) seeded pods with a different texture. It must be noted, however, that the general impression is indeed similar to *Ormocarpum*, mainly because of the small and dull leaflets. Hutchinson (1964) placed the genus in the synonymy of *Aeschynomene*, probably on account of an incidental observation of 2 phalanges of 5 stamens (in fact a ruptured sheath) and of a slight similarity of the pod of *P. pervilleana* with a loment of some *Aeschynomene* species.

Ptycholobium Harms, in Engl., Pflanzenw. O.-Afr. 3,1 (1915) 591; Brummitt, Kew Bull. 35 (1980) 460; L.
    Nod.: 569. — T y p e : *P. plicatum*(Oliv.) Harms.
Sylitra E. Meyer, Comm. Pl. Afr. Austr. 1 (1836) 114; L.T.A.: 167, 168; Hutch., Gen. 1 (1964) 397; L. Nod.
    638; *nom. illeg.* (*non Sulitra* Medik. = *Lessertia, nom. cons.*) — T y p e : *S. biflora* E. Meyer.

Shrubs. Leaflets 1—3, digitately arranged, with a short rachis. Stipellae absent.
Flowers single or in fascicles in the axils of vegetative leaves. Brachyblasts, when
present, short, up to 3- (or more?) flowered. Bracts absent. Bracteoles absent. Flowers
6—10 mm long. Hypanthium indistinct. Calyx with 5 distinct lobes. Standard blade
obovate, reflexed halfway; basal callosities absent. Wings and keel petals about equally
long; wings obtuse; keel subfalcate. Upper filament adnate to the other 9. Basal
fenestrae distinct. Disk indistinct. Ovary hairy; ovules 3—7 (or more?). Pod
indehiscent, or dehiscent along the lower suture (probably only in dried herbarium
material), thin coriaceous, either zig-zag folded, or coiled upwards in up to a full circle,
or slightly upcurved. Seeds 3—6, reniform, elliptic in cross-section; radicle folded.

D i s t r i b u t i o n . Three species in tropical and South Africa, and in Arabia (Oman),
most diversity in West and South Africa.

N o m e n c l a t u r e . Brummitt (1980) considers *Sulitra* Medikus and *Sylitra* E. Meyer
homonymous. Art. 64.2 (ICBN) defines heterotypic variants homonymous when the
names "are so similar that they are likely to be confused". In the list of examples,
however, there is no example of y-u variants and, personally, I do not find it very likely
that they will be confused. Preamble 9 tells us, on the other hand, that in case of doubt
"established custom is followed" and then the balance points to homonymy in this case,
if recent publications are considered of more importance than older ones. Personally, I
would not object to re-establishment of *Sylitra*.

T a x o n o m y . *Ptycholobium* differs from *Tephrosia* in the 1—3 digitately arranged
leaflets, the axillary fascicles and the shape of the pods. The digitate arrangement of the
leaflets does not occur in *Tephrosia,* if *Caulocarpus* and *Lupinophyllum* are also
considered to represent separate genera. The shape of the pod is unique in this group.
The indehiscence is a bit dubious, as I found a few pods with the lower suture open (*in
sicco*), but this may be an artefact caused by quick drying.

Requienia DC., Ann. Sci. Nat. 4 (1825); E.P. Nachtr. 4: 135; Hutch., Gen. 1: 396; A.L.S.: 259; Brummitt,
    Kew Bull. 35 (1980) 469; L. Nod. 577. — T y p e : *R. obcordata* (Lamarck ex Poir.) DC.

Shrubs, apparently with creeping branches. Leaves unifoliolate. Stipellae absent.
Flowers single, axillary. Bracts absent. Bracteoles absent. Flowers 6—10 mm long.
Hypanthium indistinct. Calyx with 5 distinct lobes. Standard blade obovate, apparently
not reflexed; basal callosities absent. Wings and keel petals about equally long; wings
obtuse; keel subfalcate. Upper filament adnate to the other 9. Basal fenestrae distinct.

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Disk indistinct. Ovary hairy; ovule 1. Pod as in *Tephrosia,* but 1-seeded. Seed sub-globose, laterally slightly flattened; radicle folded.

Distribution. Three species in South Africa and West tropical Africa, South of the Congo River.

Taxonomy. The genus is usually considered a close ally of *Tephrosia,* from which it differs in the combination of unifoliolate rounded leaves, single axillary flowers, and the single ovule. As Brummitt (1980) argues, this is a monothetic set, none of the characters being unique. Re-evaluation of its status depends on a monographic sub-division of *Tephrosia.*

Sarcodum   Pl. I—7

Sarcodum Lour., *nom. rejic.* vs. *Clianthus* (*Galegeae*), Fl. Cochinch. (1790) 425, 461; B.H. 1: 498; E.P. 3: 272; Hutch., Gen. 1: 405 (in synon. of *Clianthus*); F. Java 1: 596 (in synon. of *Clianthus*); A.L.S.: 259. — Type: *S. scandens* Lour.

Lianas. Leaflets 19—27, (sub)opposite. Stipellae present. Flowers in axillary racemes, from the axils of apical leaves, *the vegetative apical bud dormant during anthesis and fruit-setting.* Flowers 12—17 mm long. Bracts longer than the corresponding flowerbuds. Bracteoles present. Hypanthium indistinct. Calyx with 5 short teeth, the upper 2 rather distant from the lower 3. Standard blade elliptic, reflexed at base; basal callosities absent. Wings and keel petals about equally long; wings free from the keel; the keel petals more falcate. Upper filament free from the other 9. Basal fenestrae indistinct. Disk distinct. Ovary glabrous; ovules 4—7. *Pod sausage-shaped; exocarp fleshy; endocarp thin woody, dehiscent apparently after desiccation of the exocarp,* forming walls between the seeds. Seeds ellipsoid, with a rather elongated hilum; radicle folded.

Distribution. Two species, one extending from Indo-China and the Philippines to the Moluccas, the other species once found in the Solomon Islands.

Nomenclature. The genus was placed in the synonymy of *Clianthus* (*Galegeae*) by Merrill (J. Bot. 66, 1928: 265).

Taxonomy. The genus is distinct on account of its pod with fleshy exocarp and the endocarp forming compartments. The endocarp seems to open only along the upper margin, probably after desiccation of the exocarp. The inflorescence can be described as a "leafy panicle"with an arrested vegetative apical bud. Merrill proposed in 1928 to transfer this genus to the Australian genus *Clianthus,* which is, however, a genus of herbaceous climbers with more specialized flowers and a "normal" dry pod. *Clianthus* belongs to the (closely allied) tribe *Galegeae.*

Sarcodum resembles *Millettia japonica* (which I consider to belong to *Callerya*) in its habit, flower characters, and in the fleshy exocarp, but in *M. japonica* the pod is flat and not so convex around the seeds and this species has a "true" terminal panicle.

Schefflerodendron Harms, Engl. Bot. J. 30 (1901) 87; E. P. Nachtr. 3: 163; L.T.A.: 250; Léonard & Letour,
    Bull. Soc. Bot. Belg. 82 (1950) 295; F. Cong. 5: 58; Hutch., Gen. 1: 379; F.T.E.A.: 153; A.L.S.: 260;
    L. Nod.: 595. — T y p e *S. usambarense* Harms.

Trees. *Vegetative parts and calyx covered by macroscopic glands.*Leaflets (4 or)
5—10, alternate. Stipellae present. Flowers in axillary racemes,these often 2—4 to-
gether. Bracts shorter than the corresponding flowerbuds. Bracteoles present. Flowers
12—16 mm long. Hypanthium indistinct. Calyx with 4 short lobes, the upper one
2-topped. Standard blade about orbicular, reflexed at base; basal callosities absent.
Wings and keel petals about equally long, both subfalcate. Upper filament free from the
other 9. Basal fenestrae absent. Disk indistinct. Ovary hairy; ovules 3 or 4. Pod
dehiscent, thick woody, convex around the seed(s), without wings. Seeds 1 or 2, thick
lens-shaped, slightly laterally flattened; radicle folded.

D i s t r i b u t i o n . Three or four species in tropical Africa.

T a x o n o m y . The genus stands apart because of the glands on the vegetative parts
and on the calyx. These glands seem to be similar to those of the subtribe *Cajaninae*
(*Phaseoleae*). The African genus *Craibia* also has distinctly alternate leaflets, but lacks
the glands and has pseudopanicles. The general appearance is *Millettia*-like.

Tephrosia   Pod not depicted; as in Pl. IV—29, 30, 31, and 33

Tephrosia Pers., Syn. 2 (1807) 328, nom. cons.; Miq., Fl. Ind. Bat. 1 (1855) 292; F. Bras.: 45; F. Austr. 2
    (1864) 202; F.B.I. 2: 110; E.P. 3: 269; Nachtr. 4: 135; F.G.I.-C.: 269; F.M.P.: 581; L.T.A.: 170; F. Sur.:
    163; Forbes, Bothalia 4 (1948) 951; Wood, Rhodora 51 (1949) 233; León & Alain, Fl. Cuba 2 (1951) 303;
    Burkart, Legum. Argent. (1952) 253: F.W.T.A.: 527; F. Cong. 5: 85; F. Java: 593; Ali, Biologia 10
    (1964) 23; Hutch., Gen. 1: 396; F.T.E.A.: 157; A.L.S.: 260; L. Nod.: 645; Bosman & De Haas, Blumea
    28 (1983) 421. — *Cracca* L., Sp. Pl. (1753) 752, nom. rejic. (vs. *Cracca* Benth.); Amoen. Acad. 3 (1756)
    18; N. Am. F.: 157. — *Colinil* Adans., Fam. 2. (1763) 327, nom. inval. — T y p e : *T. villosa* (L.) Pers.
Erebinthus Mitchell, Diss. Brev. Princip. Bot. Zool. (1769) 32, nom. rejic. prop. (Taxon 33, 1984, in prep.) —
    T y p e : no combination made (BM, hb. Banks = *Tephrosia spicata* (Walt.) T. & G.).
Needhamia Scopoli, Introd. (1777) 310, nom. rejic. — T y p e : *Vicia littoralis* Jacq.
Reineria Moench, Suppl. Meth. (1802) 44, nom. rejic. — T y p e : *R. reflexa* Moench.
Brissonia Necker ex Desv., J. Bot. 3 (1814) 78, nom. illeg., see De Kort & Thijsse, Blumea 30 (1984) 90.
Crafordia Rafin., Specchio 1 (1814) 156 (*fide* Merr., Ind. Raf., 1949). — T y p e : *C. bracteata* Rafin.
Kiesera Reinw., Syll. Pl. Nov. 2 (1828) 11 (*"Kieseria" auct.*); Miq., Fl. Ind. Bat. 1 (1855) 290. — T y p e : *K.
    sericea* Reinw.
Xiphocarpus Presl, Symb. Bot. 1 (1830) 13, t. 7. — T y p e : *X. martinicensis* Presl.
Apodynomene E. Meyer, Comm. Pl. Afr. Austr. 1 (1836) 111. — T y p e : not designated.
Pogonostigma Boiss., Diagn. Pl. Orient. 1, 2 (1843) 39. — T y p e : not designated.
Catacline Edgew., nom. illeg. (provisional name), J. As. Soc. Beng. 16, 2 (1847) 1214. — T y p e : *C. sericea*
    Edgew., nom. illeg.
Macronyx Dalz., Hook. J. Bot. Kew Misc. 2 (1850) 35. — *Seemanantha* Alef., Bonplandia 10 (1862) 264. —
    T y p e : *M. strigosus* Dalz.
Balboa Liebman ex Didrichsen, Vid. Medd. Nat. For. Kjøb. (1853) 106, nom. rejic. vs.*Balboa* Planchon &
    Triana. — T y p e : *B. diversifolia* Liebman ex Didrichsen.
Paratephrosia Domin, Fedde Rep. 11 (1912) 261; E.P. Nachtr. 4: 135; A.L.S.: 259; L. Nod.: 492. — T y p e :
    P. lanata (Benth.) Domin.

Shrubs or herbs with woody base. Leaves generally pinnately compound, in some species unifoliolate. Leaflets 3—37, (sub)opposite. Stipellae absent, in very few species constantly present, in a few species sometimes present. Nerves 4—31 pairs, usually ending in a marginal nerve, usually closely parallel, usually straight, never S-shaped, usually forming a sharp angle with the midrib. Flowers usually in terminal or axillary pseudoracemes, these leaf-opposed in some species, in some other species reduced to an axillary fascicle. Brachyblasts usually warty with 2—8 (—30) flowers. Bracts shorter than the corresponding flowerbuds. Bracteoles absent, in some species sometimes present only in some flowers. Flowers 6—15 (—26) mm long. Hypanthium indistinct. Calyx usually with 4 distinct lobes, the upper one 2-topped. Standard blade narrowly obovate to (in most species) suborbicular, either not reflexed, or reflexed at the middle, rarely reflexed at the base; basal callosities present or (less often) absent. Wings and keel petals about equally long, obtuse to falcate, the wings sometimes free from the keel. Upper filament free or adnate to the other 9, in latter case with a sub-basal callosity, next to similar callosities on the adjacent filaments and the basal fenestrae "closed" (i. e. upper filament free at the base, but pressed against the neighbouring filaments); in some species these callosities absent and the basal fenestrae slightly open. Disk generally distinct. Style terete or, in most (?) species, dorso-ventrally flattened and twisted 90° at its base, either with a row of hairs on the vexillary edge (when not twisted), or on both edges, or glabrous; stigma penicillate at base or not; ovules 1—20. Pod dehiscent, thin woody, flat, convex around the seeds, usually straight. Seeds 1—20, reniform, globular, or transversely ellipsoid; radicle folded.

Distribution. Over 400 species in tropical areas with a distinct dry season, pan-tropical, most species in Africa.

Nomenclature. Most synonyms mentioned above were quickly checked for nomenclatural complications and the description was compared with the description given above. They were copied on authority of the regional monographers Forbes (1948), Wood (1949), Ali (1964), and Bosman & De Haas (1983). The following synonym, however, needs further explanation.

Erebinthus Mitchell. This genus was described in Act. Acad. Nat. Cur. 8 (1748) App. 210 without species names connected to it. The work was reprinted in Diss. Brev. Princip. Bot. Zool. (1769) 32, which I saw at Kew. Wood (1949) mentioned *Erebinthus* in the synonymy of *Tephrosia spicata,* but did not propose the name for rejection in favour of *Tephrosia,* as he was probably only aware of the pre-Linnean edition. The type specimen (BM) consists of two species, identified by Wood as *T. spicata* and *T. hispidula.* He mentioned it, however, only under *T. spicata,* and thereby the specimen is lectotypified by the branch identified so. Recently (Taxon, 1984, in press) I have proposed to reject *Erebinthus.*

Taxonomy. *Tephrosia* is generally easily recognizable. The leaflets are rather stiff, often (narrowly) obovate, and the nerves are straight, forming a sharp angle (usually 10°—30°) with the midrib. The genus has over 400 species, thus belonging to the largest Legume genera: *Astragalus* (over 2000 spp.), *Acacia* (about 1200 spp.), *Indigofera*

(about 800 spp.) and *Crotalaria* (about 600 spp.). As far as I know, the cause (in terms of evolutionary biology/population genetics) of the high numbers of distinguishable species is unknown. Polyploidy is either not recorded or plays a minor role (Polhill, 1982, p. 5). In *Crotalaria* gene flow in population does occur (Polhill, 1982, p. 5), but the fruit setting of isolated plants and the relative high number of pods per inflorescence suggests self-pollination or some kind of apomixis in *Crotalaria* and in *Indigofera*. In *Astragalus*, in *Acacia*, and in *Tephrosia* the relative number of pods per inflorescence is lower (with exceptions of course), and these genera may be suspect for either hybrid complexes or some kind of apomixis (e. g. pseudogamy, see Stace, 1980, p. 162).

In *Tephrosia* four groups were often regarded as distinct genera on account of unique characters and/or a monothetic set:

1. *Requienia* consists of three species with broadly elliptic to orbicular or broadly obovate, unifoliolate leaves and single, axillary flowers with 1 ovule per ovary. This is a strictly monothetic set, none of the characters being unique.
2. *Ptycholobium* also has three species; these have unifoliolate or digitately, sometimes stipellate 3-foliolate leaves, axillary clusters of few flowers, and a zig-zag folded or strongly curved pod. The pod shape is unique, the other characters form a monothetic set.
3. The monotypic genus *Caulocarpus* was distinguished on account of the combination of a stipitate pod and unifoliolate or digitately 3—5-foliolate leaves without distinct rachis.
4. *Lupinophyllum*, monotypic as well, is characterized by unifoliolate or digitately 3—7-foliolate leaves and small, geocarpic pods.

All the above mentioned characters are copied from Brummitt's notes (1980) on these segregate genera. He regarded *Requienia* and *Ptycholobium* as distinct genera, but considered *Caulocarpus* and *Lupinophyllum* as synonyms of *Tephrosia* on account of aprioristic weighting of characters. He gave subgeneric rank to the collection of *Tephrosia* species with hair-fringed styles as subg. *Barbistyla,* characterized by longitudinal rows of hairs along one or both style margins, and by the absence of a tuft of hairs just below the stigma. The remainder of *Tephrosia* was considered by him to form the other subgenus *Tephrosia* that is characterized by a glabrous, often flattened and/or twisted style recorded to have a penicillate apex (just below the stigma). According to Bosman & De Haas (1983), however, the penicillate apex is absent in several species.

This subdivison (and I think Brummitt will agree with this notion) is artificial. Subgenus *Barbistyla* has the style fringed in different ways: either one-sided or two-sided, the hairs directed either upwards or downwards, the style can be twisted 90° at base or not, and a generalization of these character states in the expression "style somehow fringed with hairs" has a great chance to be "pluriphyletic" at least. The remainder, subg. *Tephrosia,* is paraphyletic at least, a situation to which I do not have serious objections, but I feel preference for a more detailed subdivision based on more characters (mono- and polythetic sets, eventually with unique characters), e. g. on sectional level; this can only be done in the framework of an entire, monographic revision. Wood (1949) avoided the problem by not giving a taxonomic rank to the "barbistyled species" he revised for North America.

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As long as such a revision has not been made, I find it impossible to have an opinion on the generic distinction of the four genera characterized above. It is true that all four are characterized by a monothetic set, and two of them even by unique characters (though these two are not considered to be separate genera by Brummitt). I also agree that these four groups may represent "natural taxa", but distinction on generic level should depend on the relationships with the surrounding genera (*Millettia, Mundulea,* and *Chadsia*) and on a finer subdivision to be made in *Tephrosia.* After comparison with the three genera mentioned, I got the impression that the position of *Mundulea* is crucial for the decision to be made. If *Mundulea* is kept separate from *Tephrosia* on generic level on account of its dilated filaments, the absence of a disk, its short, recurved style, and its tendency to have more elongated flowers, then all mentioned genera deserve generic rank as well. So with some hesitation (based on incomplete knowledge of *Tephrosia*), I have raised these groups to generic level. There are chemical differences between *Tephrosia* and *Mundulea* as well, but these are based on investigation of the most *Millettia*-like species of *Mundulea* only (see note under *Mundulea*).

Paratephrosia was described on account of the combination of axillary fascicles, long calyx teeth, and 1-ovuled ovary. These characters are not rare in *Tephrosia,* but, as far as I know, not in this combination. *Paratephrosia* can thus be defined on account of this monothetic set, but I do not think its rank should be the generic one. A detailed study of e. g. the Australian species can reveal the most closely related species and, awaiting such a treatment, I tentatively reduce this monotypic genus to the synonymy of *Tephrosia.*

Wisteria   Pl. III—16

Wisteria Nutt., Gen. 2 (May/June 1818) 115, *nom. cons.* ("*Wistaria*" *auct.*); B.H. 1: 499; E.P. Nachtr. 1: 201;
    Hutch., Gen. 1: 378; A.L.S.: 260; L. Nod.: 696. — *Phaseoloides* Duhamel, Traité Arb. Arbust. 2 (1755)
    115, *nom. rejic.* ("*Phaseolodes*" O. K.). — *Kraunhia* Rafin., Med. Repos. 2,5 (1808) 353, *nom. nud.*
    ("*Kraunshia*" *auct.*, "*Krauhnia*" *auct.*); E.P. 3: 271 (as "*Kraunhia* Steudel"); N. Am. Fl.: 184. —
    Thyrsanthus Elliott, J. Acad. Nat. Philad. 1 (after 23 June 1818) 371, *non* Schrank (1814) =
    Primulaceae. — *Bradleya* Britton, Man. (1901) 548 (*non Bradlea* Adans., *nec Bradleya* Vellozo =
    Violaceae). — Type: *W. speciosa* Nutt., *nom. illeg.* = *W. frutescens* (L.) Poiret.
Diplonyx Rafin., Fl. Ludov. (1817) 101, *nom. rejic.* — Type: *D. elegans* Rafin.
Bradburya Rafin., Fl. Ludov. (1817) 104, *nom. rejic.* vs. *Bradburia* Torr. & Gray (= *Compos.*). — Type: *B.*
    scandens Rafin.

Lianas, sometimes erect shrubs. Leaflets 7—21, (sub)opposite. Stipellae present. Flowers in terminal racemes, in some species also combined with a few axillary racemes, these often from the axils of leaf scars. Bracts usually longer than the corresponding flowerbuds, but generally very soon caducous. Bracteoles generally absent, generally present in *W. brachybotrys,* and occasionally also present in some flowers only. Flowers 15—30 mm long. Hypanthium indistinct. Calyx 4-lobed, the upper lobe 2-topped and its apices more obtuse. Standard blade suborbicular, reflexed at base; basal callosities distinct, *forming a ridge at the distal part of the claw, often also with 2 processes.* Wings free from the keel and about equally long. Upper filament free from the other 9. Basal fenestrae indistinct. Disk distinct. Ovary hairy; ovules 4—8 (or

more?). Pod tardily dehiscent, thin or thick woody, usually compartmented, without wings. Seeds reniform to lens-shaped; radicle folded.

Distribution. Probably 6 species in China, Japan, and temperate North America. Two species (*W. sinensis* and *W. floribundus*) cultivated as ornamentals in temperate regions.

Nomenclature. Despite the complexity of the here presented protologue, all questions seemed (to my astonishment) well-settled.

Taxonomy. This genus is the only entirely temperate representative of the tribe. Because of the occurrence in Japan, and the similarity in "habit", also *Millettia japonica* is sometimes considered to belong to *Wisteria,* but it differs in the not compartmented pod, in the constant presence of bracteoles, in the absence of basal callosities, and in the glabrous ovary. The wings, however, are also free from the keel in this species. Because of the generally paniculate inflorescence, often combined with axillary racemes and the dehiscent pods, it is better referred to *Callerya*, at least for the time being.

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INDEX TO CLADISTIC JARGON AND ASSOCIATED TERMS

Terms are only indexed if they are explained or if there is a reference to explaining literature. The terminology adopted is that of Holmes (1980) and deviates only in details from that of Wiley (1981). In the text, some uncommon terms were applied, adopted from "The species concept in Palaeontology" (Syst. Ass. Publ. 2, 1956: 139).

INDEX TO NAMES OF TAXA (Taxonomic part, chapter 9, only)

Accepted generic names in roman type; new combinations and new generic names in **bold** type; generic, subgeneric, and sectional synonyms in *italics*; combinations in roman type.

The page number referring to the formal taxonomic treatment in **bold** type; reference to the couplet number of the key between parentheses. The plates are not indexed (referred to in the formal treatments).

The generic names **Callerya, Derris, Lonchocarpus,** and **Millettia** are mentioned on many pages. I have limited their entries to their places in the key and their formal treatments.